TABLE 22.1   Classification of the Fungi

Group	Common name	Features
Microsporidia	Microsporidia	Intracellular parasites of animals; greatly reduced, among smallest eukaryotes known; polar tube used to infect hosts

Chytrids (paraphyletic)[a]
  Chytridiomycota
  Neocallimastigomycota
  Blastocladiomycota
	Chytrids	Mostly aquatic and microscopic; flagellated gametes and zoospores

Zygomycota (paraphyletic)[a]
  Entomophthoromycotina
  Kickxellomycotina
  Mucoromycotina
  Zoopagomycotina
	Zygospore fungi	Reproductive structure is a unicellular zygospore with many diploid nuclei in a zygosporangium; hyphae coenocytic; usually no fleshy fruiting body

Glomeromycota	Arbuscular mycorrhizal fungi	Form arbuscular mycorrhizae on plant roots; only asexual reproduction is known
Ascomycota	Sac fungi	Sexual reproductive saclike structure known as an ascus, which contains haploid ascospores; hyphae septate; dikaryon
Basidiomycota	Club fungi	Sexual reproductive structure is a basidium, a swollen cell at the tip of a specialized hypha that supports haploid basidiospores; hyphae septate; dikaryon

[a]The formally named groups within the chytrids and Zygomycota are each thought to be monophyletic, but their relationships to one another (and to microsporidia) are not yet well resolved.

occur in some species, or it may occur so rarely that biologists have never observed it. Species in which no sexual stage has been observed were once placed in a separate taxonomic group because knowledge of the sexual life cycle was considered necessary for classifying fungi. Now, however, these species can be related to other species of fungi through analysis of their DNA sequences.

Sexual reproduction in most fungi features an interesting twist: There is no morphological distinction between female and male structures, or between female and male individuals, in most groups of fungi. Rather, there is a genetically determined distinction between two *or more* **mating types**. Individuals of the same mating type cannot mate with each other, but they can mate with individuals of another mating type within the same species, thus avoiding self-fertilization. Individuals of different mating types differ genetically but are often visually and physiologically indistinguishable.

Microsporidia are highly reduced, parasitic fungi

Microsporidia are unicellular parasitic fungi. They are among the smallest eukaryotes known, with infective spores that are only 1–40 μm in diameter. About 1,500 species have been described, but many more species are thought to exist. Their relationships among the eukaryotes have puzzled biologists for many decades.

Microsporidia lack true mitochondria, although they have reduced structures, known as **mitosomes**, that are derived from mitochondria. Unlike mitochondria, however, mitosomes contain no DNA—the mitochondrial genome has been completely transferred to the nucleus. Because microsporidia lack mitochondria, biologists initially suspected that

they represented an early lineage of eukaryotes that diverged before the endosymbiotic event from which mitochondria evolved. The presence of mitosomes, however, indicates that
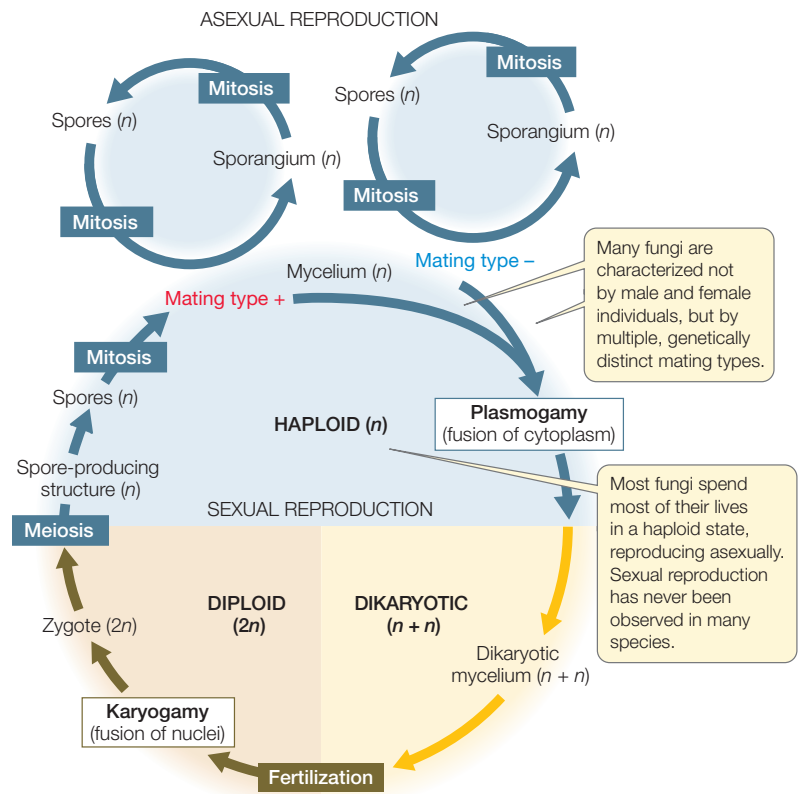

FIGURE 22.12 A Generalized Fungal Life Cycle   Environmental conditions may determine which mode of reproduction—sexual or asexual—takes place at a given time.

The polar tube injects the contents of the spore into its host.

Here the polar tube is still coiled within the spore.
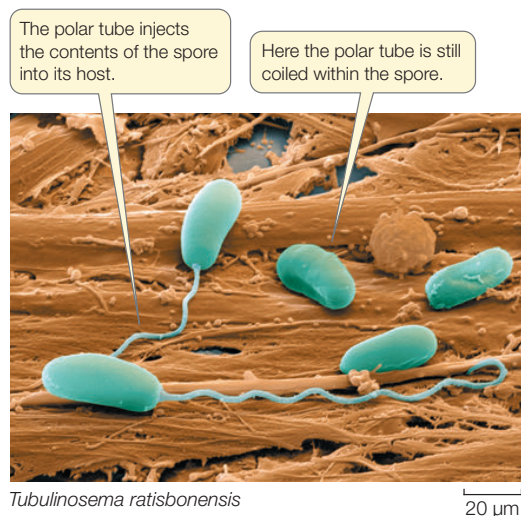
Tubulinosema ratisbonensis

20 μm

FIGURE 22.13 Invasion of the Microsporidia The spores of microsporidia grow polar tubes that transfer the contents of the spores into the host's cells. The species shown here infects many animals, including humans.

this hypothesis is incorrect. DNA sequence analysis, along with the fact that their cell walls contain chitin, has confirmed that the microsporidia are in fact highly reduced, parasitic fungi, although their exact placement among the fungal lineages is still being investigated.

Microsporidia are obligate intracellular parasites of animals, especially of insects, crustaceans, and fishes. Some species are known to infect mammals, including humans. Most infections by microsporidia cause chronic disease in the host, with effects that include weight loss, reduced fertility, and a shortened life span. The host cell is penetrated by a polar tube that grows from the microsporidian spore. The function of the polar tube is to inject the contents of the spore, the sporoplasm, into the host (**FIGURE 22.13**). The sporoplasm then replicates within the host cell and produces new infective spores. The life cycle of some species is complex and involves multiple hosts, whereas other species infect a single host. In some insects, parasitic microsporidia are transmitted vertically (i.e., from parent to offspring). Reproduction is thought to be strictly asexual in some microsporidians, but includes poorly understood asexual and sexual cycles in other species.

Most chytrids are aquatic

The **chytrids** include several distinct lineages of mostly aquatic microorganisms once classified with the protists. However, morphological evidence (cell walls that consist primarily of chitin) and molecular evidence support their classification as early-diverging fungi. In this book we use the term "chytrid" to refer to all three of the formally named clades listed as chytrids in Table 22.1, but some mycologists use this term to refer to only one of those clades, the Chytridiomycota. There are fewer than 1,000 described species among the three groups of chytrids.

Chytrids reproduce both sexually and asexually. Like the animals, most chytrids that reproduce sexually possess flagellated gametes. The spores (called zoospores) are also flagellated (**FIGURE 22.14A**). The retention of flagella in the spores and gametes reflects the aquatic environment in which fungi first evolved. Chytrids are the only fungi that include species with flagella at any life cycle stage.
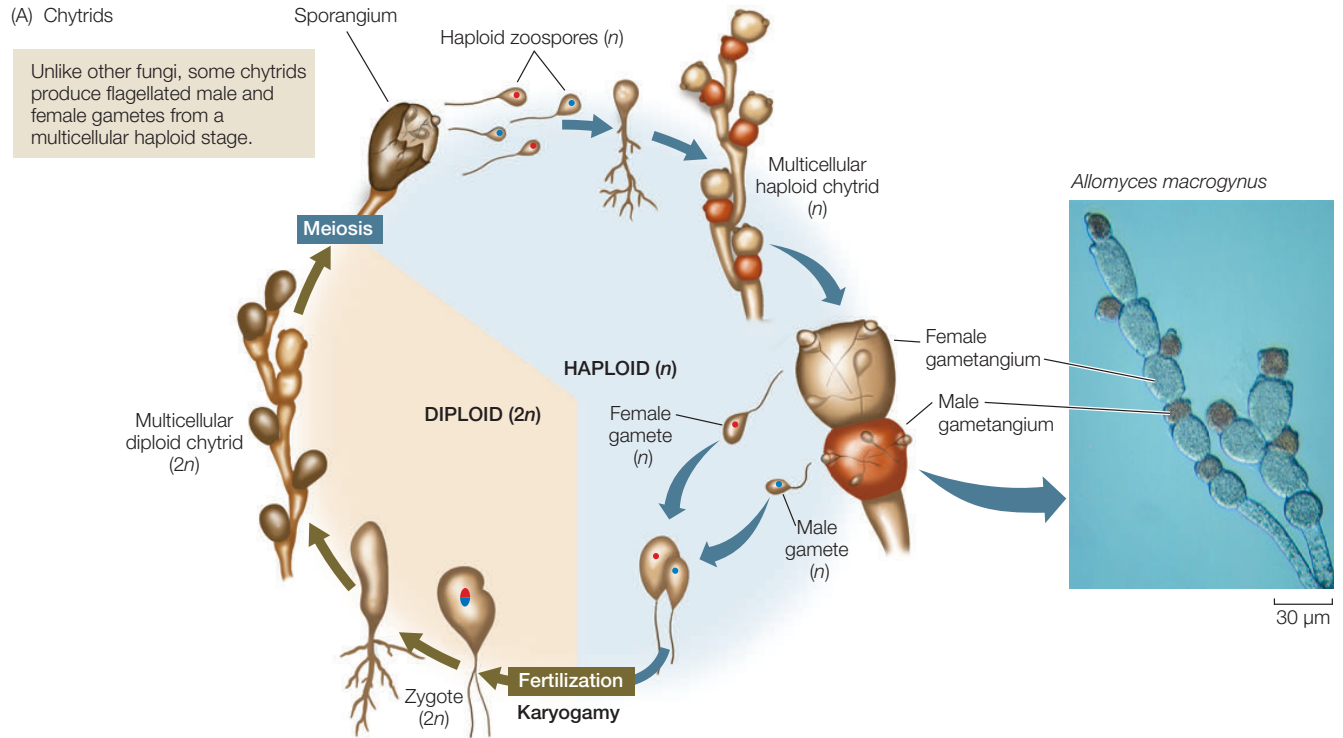
The chytrids are diverse in form. Some are unicellular, others have rhizoids, and still others have coenocytic hyphae. They may be parasitic (on organisms such as algae, mosquito larvae, nematodes, and amphibians) or saprobic. Some have complex mutualistic relationships with foregut-fermenting animals such as cattle and deer. Many chytrids live in freshwater habitats or in moist soil, but some are marine.

Some fungal life cycles feature separate fusion of cytoplasms and nuclei

Most members of the remaining four groups of fungi are terrestrial. Although the terrestrial fungi grow in moist places, they do not have motile gametes, and they do not release gametes into the environment, so liquid water is not required for fertilization. Instead, the cytoplasms of two individuals of different mating types fuse (a process called **plasmogamy**) before their nuclei fuse (a process called **karyogamy**). Sexual species of terrestrial fungi include some zygospore fungi, sac fungi, and club fungi.

Zygospore fungi reproduce sexually when adjacent hyphae of two different mating types release chemical signals that cause them to grow toward each other. These hyphae produce gametangia, which are specialized cells for reproduction that are retained as part of the hyphae. In the gametangia, nuclei replicate without cell division, resulting in multiple haploid nuclei in both gametangia. The two gametangia then fuse to form a zygosporangium that contains many haploid nuclei of each mating type (**FIGURE 22.14B**). Haploid nuclei of different mating types then pair up to form multiple diploid nuclei within the zygosporangium. A thick, multilayered cell wall develops around the zygosporangium to form a well-protected resting stage that can remain dormant for months. In harsh environmental conditions, this resting stage may be the only cell that survives as the surrounding cells of the hyphae die. At this stage the single surviving cell is known as a **zygospore**, which is the basis of the name of the zygospore fungi. When environmental conditions improve, the nuclei within the zygospore undergo meiosis and one or more stalked **sporangiophores** sprout, each bearing a sporangium. Each sporangium contains the products of meiosis: haploid nuclei that are incorporated into spores. These spores disperse and germinate to form a new generation of haploid hyphae.

The zygospore fungi include four major lineages of terrestrial fungi that live on soil as saprobes, as parasites of insects and spiders, or as mutualists of other fungi and invertebrate animals. They produce no cells with flagella, and only one diploid cell—the zygospore—appears in the entire life cycle. Their hyphae are coenocytic. Most species do not form a fleshy

(A) Chytrids

Unlike other fungi, some chytrids produce flagellated male and female gametes from a multicellular haploid stage.

Sporangium

Haploid zoospores (n)

Multicellular haploid chytrid (n)

Allomyces macrogynus

Female gametangium

Male gametangium

Meiosis

HAPLOID (n)

DIPLOID (2n)

Multicellular diploid chytrid (2n)

Female gamete (n)

Male gamete (n)

30 µm

Zygote (2n)

Fertilization

Karyogamy

(B) Zygospore fungi (Zygomycota)

The single-celled zygospore is the only diploid cell in the life cycle of zygospore fungi.

Hypha of – mating type

Hypha of + mating type

Spores

Gametangia (n)

Sporangium

Sporangiophore

HAPLOID (n)

DIPLOID (2n)

Plasmogamy

Rhizopus stolonifer

25 µm

Sporangiophore

Meiosis

Zygospore

Zygosporangium

After the surrounding cells of the hyphae die, this dormant unicellular stage, with multiple diploid nuclei, is called the zygospore.

Multiple diploid nuclei form within the zygosporangium.

Fertilization

Karyogamy

FIGURE 22.14 Sexual Life Cycles of Chytrids and Zygospore Fungi (A) Chytrids are the only fungi that possess flagella at any stage of the life cycle. Their flagellated gametes and zoospores link them to the animals. (B) The unicellular zygospore, which contains multiple diploid nuclei, is a resting structure unique to the zygospore fungi.

fruiting structure. Instead, the hyphae spread in a radial pattern from the spore, with occasional stalked sporangiophores reaching up into the air (**FIGURE 22.15**).

More than 1,000 species of zygospore fungi have been described. One species you may have seen is *Rhizopus stolonifer*, the black bread mold. *Rhizopus* produces many stalked sporangiophores, each bearing a single sporangium containing hundreds of minute spores (see Figure 22.14B).

Go to ANIMATED TUTORIAL 22.1
Life Cycle of a Zygospore Fungus
PoL2e.com/at22.1

Arbuscular mycorrhizal fungi form symbioses with plants

Arbuscular mycorrhizal fungi (Glomeromycota) are terrestrial fungi that associate with plant roots in a symbiotic, mutualistic relationship (see Figure 22.10B). Fewer than 200 species have been described, but 80–90 percent of all plants have associations with them. Molecular systematic studies have suggested that arbuscular mycorrhizal fungi are the sister group to the Dikarya (sac fungi and club fungi; see Figure 22.11).

The hyphae of arbuscular mycorrhizal fungi are coenocytic. These fungi use glucose from their plant partners as their primary energy source, converting it into other, fungus-specific sugars that cannot return to the plant. Arbuscular mycorrhizal fungi are only known to reproduce asexually.

The dikaryotic condition is a synapomorphy of sac fungi and club fungi

In the two remaining groups of fungi—the sac fungi and the club fungi—some stages have a nuclear configuration other than the familiar haploid or diploid states (**FIGURE 22.16**). In these fungi, karyogamy (fusion of nuclei) occurs long after plasmogamy (fusion of cytoplasm), so that *two genetically different haploid nuclei coexist and divide within each cell of the mycelium*. This stage of the fungal life cycle is called a **dikaryon** ("two nuclei") and its ploidy is indicated as $n + n$. The dikaryon is a synapomorphy of these two groups, which are placed together in a clade called **Dikarya**.

Eventually, specialized fruiting structures form, within which pairs of genetically dissimilar nuclei—one from each parent—fuse, giving rise to zygotes long after the original "mating." The diploid zygote nucleus undergoes meiosis, producing four haploid nuclei. The mitotic descendants of those nuclei become spores, which germinate to give rise to the next haploid generation.

A life cycle with a dikaryon stage has several unusual features. First, there are no gamete *cells*, only gamete *nuclei*. Second, the only true diploid structure is the zygote, although for a long period the genes of both parents are present in the dikaryon and can be expressed. In effect, the dikaryon is neither diploid ($2n$) nor haploid (n). Rather, it is dikaryotic ($n + n$). Therefore a harmful recessive mutation in one nucleus may be compensated for by a normal allele on the same chromosome in the other nucleus, and dikaryotic hyphae often have characteristics that are different from their n or $2n$ products.
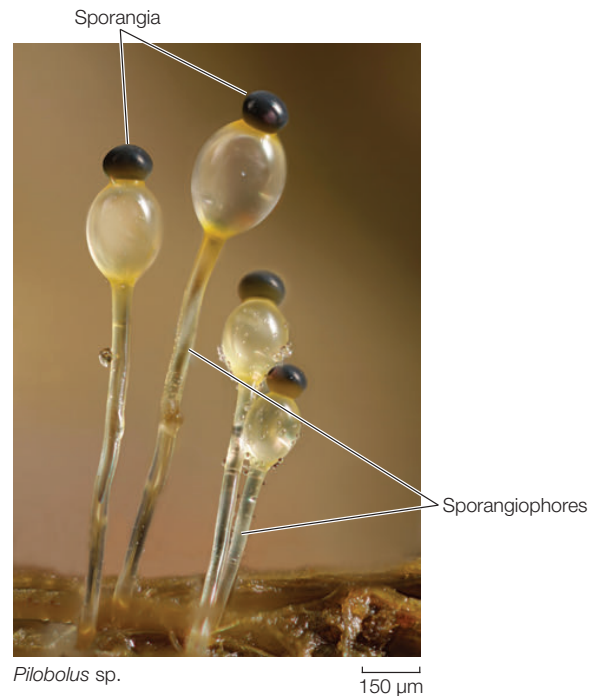

Sporangia

Sporangiophores

Pilobolus sp.

150 μm

FIGURE 22.15 Zygospore Fungi Produce Sporangiophores These transparent structures are sporangiophores produced by a zygospore fungus growing on decomposing animal dung. The sporangiophores grow toward the light and end in tiny sporangia, which the stalked sporangiophores can eject as far as 2 meters. Animals ingest sporangia that land on grass and then disseminate the spores in their feces.

The dikaryotic condition is perhaps the most distinctive of the genetic peculiarities of the fungi.

Go to ACTIVITY 22.2 Life Cycle of a Dikaryotic Fungus
PoL2e.com/ac22.2

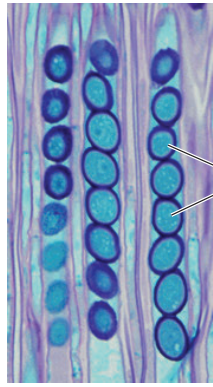### The sexual reproductive structure of sac fungi is the ascus

The **sac fungi** (Ascomycota) are a large and diverse group of fungi found in marine, freshwater, and terrestrial habitats. There are approximately 64,000 known species, almost a third of which are the fungal partners in lichens. The hyphae of sac fungi are segmented by more or less regularly spaced septa. A pore in each septum permits extensive movement of cytoplasm and organelles (including nuclei) from one segment to the next.

Sac fungi are distinguished by the production of sacs called **asci** (singular *ascus*), which after meiosis and spore cleavage contain sexually produced haploid **ascospores** (see Figure 22.16A). The ascus is the characteristic sexual reproductive structure of the sac fungi. In the past, the sac fungi were classified on the basis of whether or not the asci are contained within a specialized fruiting structure known as an **ascoma** (plural *ascomata*) and on differences in the morphology of that fruiting structure. DNA sequence analyses have resulted in a revision of these traditional groupings, however.

SAC FUNGUS YEASTS Some species of sac fungi are unicellular yeasts. The 1,000 or so species in this group are among the most important domesticated fungi. Perhaps the best known is baker's, or brewer's, yeast (*Saccharomyces cerevisiae*; see Figure 22.2), which metabolizes glucose obtained from its environment into

(A) Sac fungi (Ascomycota)

In sac fungi, the products of meiosis are borne in a microscopic sac called an ascus. The fleshy fruiting bodies consist of both dikaryotic and haploid hyphae.
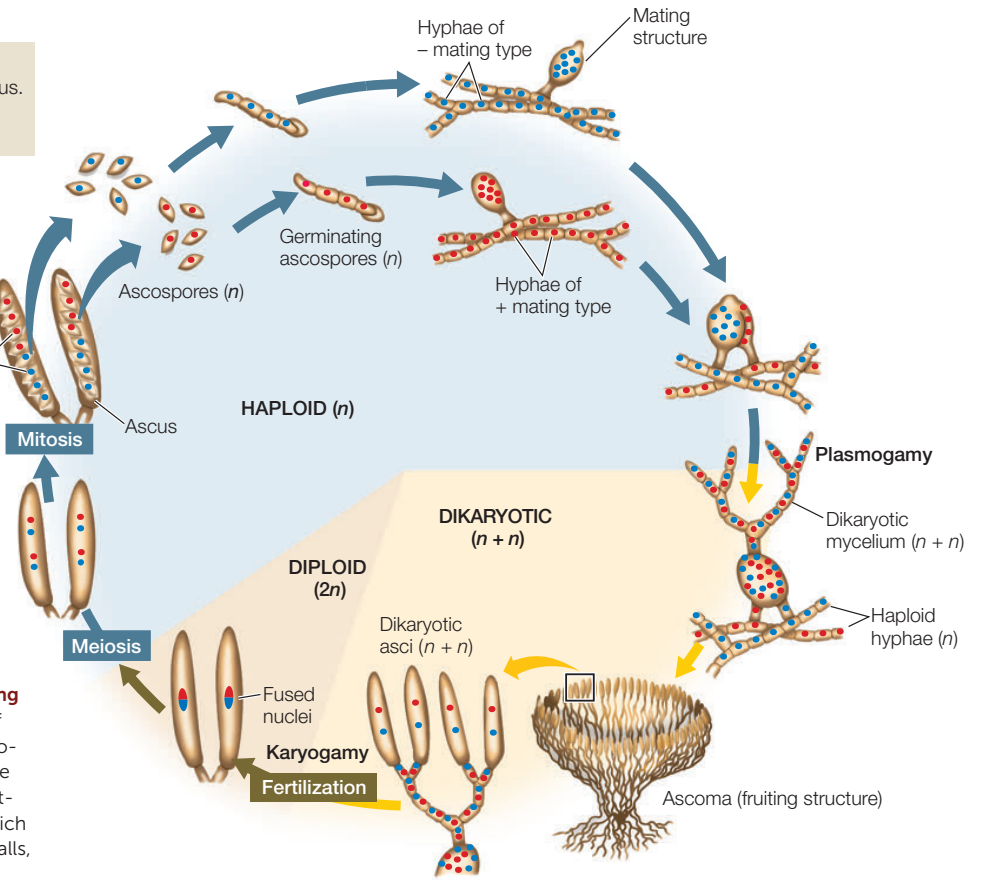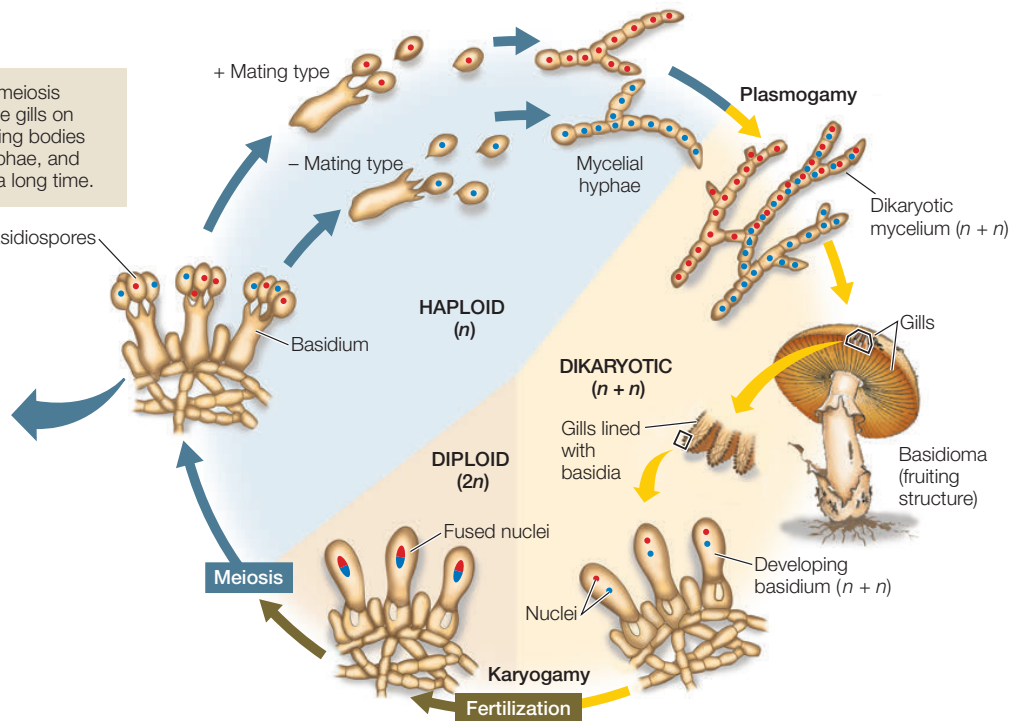

40 µm   Ascus

Ascospores

Ascus

Mitosis

Ascospores (n)

Germinating ascospores (n)

Hyphae of – mating type

Mating structure

Hyphae of + mating type

HAPLOID (n)

Plasmogamy

Dikaryotic mycelium (n + n)

DIKARYOTIC (n + n)

Haploid hyphae (n)

DIPLOID (2n)

Dikaryotic asci (n + n)

Fused nuclei

Meiosis

Karyogamy

Fertilization

Ascoma (fruiting structure)

FIGURE 22.16 Sexual Life Cycles among the Dikarya   (A) The fruiting structure of sexually reproducing sac fungi is the ascoma, often a cup-shaped structure. (B) The sexual species of club fungi produce fruiting structures known as basidiomata, which include many familiar mushrooms, puffballs, and bracket fungi.

(B) Club fungi (Basidiomycota)

In club fungi, the products of meiosis are borne on the surface of the gills on pedestals called basidia. Fruiting bodies consist solely of dikaryotic hyphae, and the dikaryotic phase can last a long time.

Basidiospores

50 µm   Basidium

+ Mating type

– Mating type

Mycelial hyphae

Basidium

Plasmogamy

Dikaryotic mycelium (n + n)

HAPLOID (n)

Gills

DIKARYOTIC (n + n)

Gills lined with basidia

Basidioma (fruiting structure)

DIPLOID (2n)

Developing basidium (n + n)

Fused nuclei

Nuclei

Meiosis

Karyogamy

Fertilization

ethanol and carbon dioxide by fermentation. It forms carbon dioxide bubbles in bread dough and gives baked bread its light texture. Although they are baked away in bread making (which produces the pleasant aroma of baking bread), the ethanol and carbon dioxide are both retained when the yeast ferments grain into beer. Other sac fungus yeasts live on fruits such as figs and grapes and play an important role in the making of wine. Many others are associated with insects. In the guts of some insects, they provide enzymes that break down materials that are otherwise difficult for the insects to digest, especially cellulose.

Sac fungus yeasts reproduce asexually by budding. Sexual reproduction takes place when two adjacent haploid cells of opposite mating types fuse. In some species, the resulting zygote buds to form a diploid cell population. In others, the zygote nucleus undergoes meiosis immediately to form an ascus. Depending on whether the products of meiosis then undergo mitosis, a yeast ascus usually contains either eight or four ascospores, which germinate to become haploid cells. The sac fungus yeasts have lost the dikaryon stage.

FILAMENTOUS SAC FUNGI Most sac fungi are filamentous species, such as the cup fungi (**FIGURE 22.17A**), in which the ascomata are cup-shaped and can be as large as several centimeters across (although most are much smaller). The inner surfaces of the ascomata, which are covered with a mixture of specialized hyphae and asci, produce huge numbers of spores. The edible ascomata of some species, including morels and truffles (**FIGURE 22.17B**), are regarded by humans as gourmet delicacies (and can sell at prices higher than gold). The underground ascomata of truffles have a strong odor that attracts mammals such as pigs, which then eat and disperse the fungus. Humans sometimes take advantage of pigs' attraction to truffles and use pigs to locate truffles for human consumption.

The sexual reproductive cycle of filamentous sac fungi includes the formation of a dikaryon, although this stage is relatively brief compared with that in club fungi. Many filamentous sac fungi form multinucleate mating structures (see Figure 22.16A). Mating structures of two different mating types fuse and produce a dikaryotic mycelium, containing nuclei from both mating types. The dikaryotic mycelium typically forms a cup-shaped ascoma, which bears the asci. Only after the formation of asci do the nuclei from the two mating types finally fuse. Both nuclear fusion and the subsequent meiosis that produces haploid ascospores take place within individual asci. The ascospores are ultimately released (sometimes shot off forcefully) by the ascus to begin the new haploid generation.

The sac fungi also include many of the filamentous fungi known as molds. **Molds** consist of filamentous hyphae that do not form large ascomata, although they can still produce asci and ascospores. Many molds are parasites of flowering plants.

(A) *Cookeina tricholoma*

(B) *Morchella esculenta*

FIGURE 22.17 Sac Fungi   (A) These brilliant red cups are the ascomata of a cup fungus. (B) Morels, which have a spongelike ascoma and a subtle flavor, are considered a culinary delicacy by humans.

Chestnut blight and Dutch elm disease are both caused by molds. The chestnut blight fungus, which was introduced to the United States in the 1890s, had destroyed the American chestnut as a commercial species by 1940. Before the blight, this species accounted for more than half the trees in the eastern North American forests. Another familiar story is that of the American elm. Sometime before 1930, the Dutch elm disease fungus (first discovered in the Netherlands, but native to Asia) was introduced into the United States on infected elm logs from Europe. Spreading rapidly—sometimes by way of connected root systems—the fungus destroyed great numbers of American elm trees.

Other plant pathogens among the sac fungi include the powdery mildews that infect cereal crops, lilacs, and roses, among many other plants. Mildews can be a serious problem to farmers and gardeners, and a great deal of research has focused on ways to control these agricultural pests.

Brown molds of the genus *Aspergillus* are important in some human diets. *A. tamarii* acts on soybeans in the production of soy sauce, and *A. oryzae* is used in brewing the Japanese alcoholic beverage sake. Some species of *Aspergillus* that grow on grains and on nuts such as peanuts and pecans produce extremely carcinogenic (cancer-inducing) compounds called aflatoxins.

Penicillium is a genus of green molds, of which some species produce the antibiotic penicillin, presumably for defense against competing bacteria. Two species, *P. camembertii* and *P. roqueforti*, are the organisms responsible for the characteristic strong flavors of Camembert and Roquefort cheeses, respectively.

The filamentous sac fungi can also reproduce asexually by means of conidia that form at the tips of specialized hyphae (**FIGURE 22.18**). Small chains of conidia are produced by the millions and can survive for weeks in nature. The conidia are what give molds their characteristic colors.

The sexual reproductive structure of club fungi is the basidium

Club fungi (Basidiomycota) produce some of the most spectacular fruiting structures found among the fungi. These fruiting structures, called **basidiomata** (singular *basidioma*), include
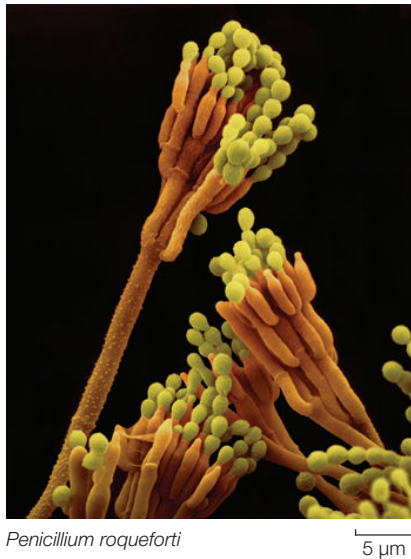
Penicillium roqueforti

5 μm

FIGURE 22.18 Conidia Chains of conidia (yellow) are developing at the tips of specialized hyphae arising from a *Penicillium* mold; compare the conidia of this species (which is used to produce "bleu" cheese) with the species shown on p. 450.

mushrooms of all kinds, puffballs (see Figure 22.4), and the bracket fungi often encountered on trees and fallen logs in a damp forest. About 30,000 species of club fungi have been described. They include about 4,000 species of mushrooms, including both poisonous and edible species (**FIGURE 22.19A**). Bracket fungi (**FIGURE 22.19B**) play an important role in the carbon cycle by breaking down wood. They also do great damage to both cut lumber and timber stands. Some of the most economically damaging plant pathogens are club fungi, including the rust fungi and smut fungi that parasitize cereal grains. In contrast, other club fungi contribute to the survival of plants as fungal partners in ectomycorrhizae.

The hyphae of club fungi characteristically have septa with small, distinctive pores. As these hyphae grow, haploid nuclei of different mating types meet and fuse, forming dikaryotic hyphae. The dikaryotic mycelium grows and eventually, when triggered by rain or another environmental cue, produces a basidioma. The dikaryon stage may persist for years, or even centuries. This pattern contrasts with the life cycle of the sac fungi, in which the dikaryon is found only in the stages leading up to formation of the asci.

The **basidium** (plural *basidia*), a swollen cell at the tip of a specialized hypha, is the characteristic sexual reproductive structure of the club fungi (see Figure 22.16B). In mushroom-forming club fungi, the basidia typically form on specialized structures known as gills. The basidium is the site of nuclear fusion and meiosis and thus plays the same role in the club fungi as the ascus does in the sac fungi and the zygosporangium does in the zygospore fungi.

After nuclei fuse in the basidium, the resulting diploid nucleus undergoes meiosis, and the four resulting haploid nuclei are incorporated into haploid **basidiospores**, which form on tiny stalks on the outside of the basidium. A single basidioma of the common bracket fungus *Ganoderma applanatum* can produce as many as 4.5 *trillion* basidiospores in one growing season. Basidiospores typically are forcibly discharged from their basidia and then germinate, giving rise to hyphae with haploid nuclei.

CHECKpoint CONCEPT 22.3

✓ Explain the concept of mating types. How are they different from male and female sexes?

✓ Explain how the microsporidia infect the cells of their animal hosts.

✓ What feature of the chytrids suggests that the fungi had an aquatic ancestor?

✓ What is the role of the zygospore in the life cycle of zygospore fungi?

✓ What distinguishes the fruiting structures of sac fungi from those of club fungi?

(A) *Amanita muscaria*

(B) *Trametes versicolor*

FIGURE 22.19 Club Fungus Basidiomata (A) Fly agaric is poisonous to humans, as are many species in the genus *Amanita*. Various species of *Amanita* account for about 95% of the human fatalities from mushroom poisoning. (B) Saprophytic bracket fungi are agents of decay on dead wood.

Fungi are of interest to biologists because of the roles they play in interactions with other organisms. But fungi can also be useful as tools for studying environmental problems and for finding solutions to those problems.

> ### CONCEPT 22.4   Fungi Can Be Sensitive Indicators of Environmental Change

We've already noted the important roles that fungi play in ecosystems, from decomposers to pathogens to plant mutualists. These diverse ecological roles have led to the use of fungi in studies of environmental change and in environmental remediation.

Lichen diversity and abundance indicate air quality

Lichens can live in many harsh environments where few other species can survive, as we saw in Concept 22.2. In spite of their hardiness, however, lichens are highly sensitive to air pollution because they are unable to excrete any toxic substances they absorb. This sensitivity means that lichens are good biological indicators of air pollution levels. It also explains why they are not commonly found in heavily industrialized regions or in large cities.

Monitoring the diversity and abundance of lichens growing on trees is a practical and inexpensive system for gauging air quality around cities (**FIGURE 22.20**). Maps of lichen diversity provide environmental biologists with a tool for tracking the distribution of air pollutants and their effects. Sensitive biological indicators of pollution, such as lichen growth, allow biologists to monitor air quality without the use of specialized equipment. Lichens are naturally distributed across the environment, and they can also provide a long-term measure of the effects of air pollution across many seasons and years.

Fungi record and help remediate environmental pollution

Each year, biologists deposit samples of many groups of organisms in the collections of natural history museums. These museum collections serve many purposes. Biologists borrow specimens from these museums to study many aspects of evolution and ecology, and the collections document changes in the biota of our planet over time.

Collections of fungi made over many decades or centuries provide a record of the environmental pollutants that were present when the fungi were growing. Biologists can analyze these historical samples to see how different sources of pollutants were affecting our environment before anyone thought to take direct measurements. These long-term records are also useful for analyzing the effectiveness of cleanup efforts and regulatory programs for controlling environmental pollutants.

We have already seen that fungi are critical to the planetary carbon cycle because of their role in breaking down dead organic matter. Fungi are also used in remediation efforts to help clean up sites that have been polluted by oil spills or contaminated with toxic petroleum-derived hydrocarbons. Many

FIGURE 22.20 More Lichens, Better Air   Lichen abundance and diversity are excellent indicators of air quality. (A) Many lichen species show luxuriant growth on trees in suitable environments with few pollutants in the air. (B) As air quality declines, so do the number and diversity of lichens.

herbicides, pesticides, and other synthetic hydrocarbons are broken down primarily through the action of fungi.

Reforestation may depend on mycorrhizal fungi

When a forest is cut down, it is not just the trees that are lost. A forest is an ecosystem that depends on the interaction of many species. As we have discussed, many plants depend on close relationships with mycorrhizal fungal partners. When trees are removed from a site, the populations of mycorrhizal fungi there decline rapidly. If we wish to restore the forest on the site, we cannot simply replant it with trees and other plants and expect them to survive. The mycorrhizal fungal community must be reestablished as well. For large forest restoration projects, a planned succession of plant growth and soil improvement is often necessary before forest trees can be replanted. As the community of soil fungi gradually recovers, trees that have been inoculated with appropriate mycorrhizal fungi in tree nurseries can be planted to reintroduce greater diversity to the soil fungal community.

Fungi can be sensitive indicators of environmental change

Biologists analyzed museum samples of lace lichens (*Ramalina menziesii*) collected near San Francisco, California, from 1892 to 2006 for evidence of lead contamination. They measured concentrations of lead (Pb) as well as the ratios of its isotopes ^{206}Pb and ^{207}Pb. The latter measurement was used to determine the source of lead contamination. Possible sources included a lead smelter that operated in the area from 1885 to 1971 (which produced emissions with a ^{206}Pb/^{207}Pb ratio of about 1.15–1.17); leaded gasoline in use from the 1930s to the early 1980s, peaking in 1970 (with a ^{206}Pb/^{207}Pb ratio of 1.18–1.23); and resuspension of historic lead contamination as atmospheric aerosols in recent decades (with an intermediate ^{206}Pb/^{207}Pb ratio of about 1.16–1.19).[a]

Before analyzing the data, use the information provided above to formulate hypotheses about these questions: What trends in atmospheric lead concentrations would you expect to see? What ^{206}Pb/^{207}Pb ratios would you expect to find at different times from the late 1800s to the early 2000s?

1. Plot lead concentration in the lichen samples against year of sample collection. Make a second plot of ^{206}Pb/^{207}Pb ratio against year of sample collection.

2. Do your analyses support the hypotheses you formulated? Are your hypotheses consistent with your analyses of both lead concentrations and ^{206}Pb/^{207}Pb ratios through time? If not, how would you modify your hypotheses, and what additional tests can you design to test your ideas?

SAMPLE	YEAR COLLECTED	LEAD CONCENTRATION (µg OF Pb/g OF LICHEN)	^{206}Pb/^{207}Pb RATIO
1	1892	11.9	1.165
2	1894	4.0	1.155
3	1906	13.7	1.154
4	1907	22.9	1.157
5	1945	49.9	1.187
6	1957	34.2	1.185
7	1978	50.9	1.221
8	1982	10.0	1.215
9	1983	4.6	1.224
10	1987	1.0	1.198
11	1988	1.3	1.199
12	1995	1.9	1.202
13	2000	0.4	1.184
14	2006	1.8	1.184

[a]A. R. Flegal et al. 2010. *Environmental Science and Technology* 44: 5613–5618.

CHECKpoint CONCEPT 22.4

✓ What are some advantages of using surveys of lichen diversity and museum collections of lichens to measure long-term changes in air quality, compared with direct measurements of atmospheric pollutants?

✓ Can you develop a strategy for tree harvest that would ease the difficulty and expense of reforestation projects by retaining viable communities of mycorrhizal fungi?

Whether living on their own or in symbiotic associations, fungi have spread successfully over much of Earth since their origin from a protist ancestor. An earlier ancestor of fungi also gave rise to the choanoflagellates and the animals, as we will describe in Chapter 23.

Q Have antibiotics derived from fungi eliminated the danger of bacterial diseases in human populations?

ANSWER Beginning in the 1940s, antibiotics derived from fungi ushered in a "golden age" of freedom from bacterial infections. Today, however, that golden age may be coming to an end. Many antibiotics are losing their effectiveness as pathogenic bacteria evolve resistance to these drugs (**FIGURE 22.21**). Some bacterial diseases, such as tuberculosis, are increasingly serious health problems because of the evolution of new strains that are resistant to most classes of antibiotics.

Why do bacteria evolve resistance to antibiotics? Mutations that allow bacteria to survive in the presence of an antibiotic are favored by selection in a bacterial population whenever an antibiotic is used. Such mutations often carry a cost to the bacteria, so they may be selected against in the absence of regular antibiotic use. To reduce the rate of evolution of antibiotic resistance, antibiotics should be used only for the

Penicillium notatum

The top three bacterial strains fail to grow in the "zone of inhibition" surrounding the mold.

This bacterial strain is resistant to the antibiotic produced by *P. notatum*.

FIGURE 22.21 Penicillin Resistance In a petri dish similar to those in Alexander Fleming's lab, four strains of a pathogenic bacterium have been cultured along with *Penicillium* mold. One strain is resistant to the mold's antibiotic substance, as is evidenced by its growth up to the mold.

treatment of appropriate bacterial diseases, and then used to completely clear the bacterial infection.

Most medical antibiotics are chemically modified forms of the substances that are found naturally in fungi and other organisms. Fungi naturally produce antibiotic compounds to defend themselves against bacterial growth and to reduce competition from bacteria for nutritional resources. These naturally occurring compounds are usually chemically modified to increase their stability, improve their effectiveness, and facilitate synthetic production.

From the late 1950s to the late 1990s, no new major classes of antibiotics were discovered. In recent years, however, three new classes of antibiotics have been synthesized based on the information learned from naturally occurring antibiotics, leading to improved treatment of some formerly resistant strains of bacteria.

Fungi have also been used to combat non-bacterial diseases. One of the more unusual applications of fungi is in the war against malaria, one of the biggest killers of humans in sub-Saharan Africa. Biologists have discovered that two species of fungi, *Beauveria bassiana* and *Metarhizium anisopliae*, can kill malaria-causing mosquitoes when applied to mosquito netting. Mosquitoes have not yet shown evidence of developing resistance to these biological pathogens, as they have to most chemical pesticides.

SUMMARY

CONCEPT 22.1 Fungi Live by Absorptive Heterotrophy

■ Fungi are **opisthokonts** with **absorptive heterotrophy** and with **chitin** in their cell walls. Fungi have various nutritional modes: some are **saprobes**, others are parasites, and some are mutualists. **Yeasts** are unicellular, free-living fungi. **Review Figure 22.1**

■ The body of a multicellular fungus is a **mycelium**—a meshwork of filaments called **hyphae**. Hyphae may be **septate** (having **septa**) or **coenocytic** (multinucleate). **Review Figure 22.3**

■ Fungi are often tolerant of hypertonic environments, and many are tolerant of extreme temperatures.

CONCEPT 22.2 Fungi Can Be Saprobic, Parasitic, Predatory, or Mutualistic

■ Saprobic fungi, as decomposers, make crucial contributions to the recycling of elements, especially carbon.

■ Many fungi are parasites of plants, harvesting nutrients from plant cells by means of **haustoria**. **Review Figure 22.5**

■ Certain fungi have relationships with other organisms that are both **symbiotic** and **mutualistic**.

■ Some fungi associate with unicellular green algae, cyanobacteria, or both to form **lichens**, which live on exposed surfaces of rocks, trees, and soil. **Review Figure 22.9**

■ **Mycorrhizae** are mutualistic associations of fungi with plant roots. They improve a plant's ability to take up nutrients and water. **Review Figure 22.10**

■ **Endophytic fungi** live within plants and may protect their hosts from herbivores and pathogens.

CONCEPT 22.3 Major Groups of Fungi Differ in Their Life Cycles

■ The microsporidia, chytrids, and zygospore fungi diversified early in fungal evolution. The mycorrhizal fungi, sac fungi, and club fungi form a monophyletic group, and the latter two groups form the clade **Dikarya**. **Review Figure 22.11, Table 22.1, and ACTIVITY 22.1**

■ Many species of fungi reproduce both sexually and asexually, although most fungi spend most of their lives in a haploid, asexual state. When sexual reproduction does occur, it usually occurs between individuals of different **mating types**. **Review Figure 22.12**

■ The **microsporidia** are highly reduced unicellular fungi. They are obligate intracellular parasites that infect several animal groups.

■ The three distinct lineages of **chytrids** all have flagellated gametes. **Review Figure 22.14A**

■ In the sexual reproduction of terrestrial fungi, hyphae fuse, allowing "gamete" nuclei to be transferred. **Plasmogamy** (fusion of cytoplasm) precedes **karyogamy** (fusion of nuclei).

■ **Zygospore fungi** have a resting stage with many diploid nuclei, known as a **zygospore**. Their fruiting structures are simple stalked **sporangiophores**. **Review Figure 22.14B and ANIMATED TUTORIAL 22.1**

■ **Arbuscular mycorrhizal fungi** form symbiotic associations with plant roots. They are only known to reproduce asexually. Their hyphae are coenocytic.

■ In sac fungi and club fungi, a mycelium containing two genetically different haploid nuclei, called a **dikaryon**, is formed. The dikaryotic ($n + n$) condition is unique to the fungi. **Review Figure 22.16 and ACTIVITY 22.2**

■ **Sac fungi** have septate hyphae; their sexual reproductive structures are **asci**. Many sac fungi are partners in lichens. Filamentous sac fungi produce fleshy fruiting structures called **ascomata**. The dikaryon stage in the sac fungus life cycle is relatively brief. **Review Figure 22.16A**

■ **Club fungi** have septate hyphae. Many club fungi are plant pathogens, although mushroom-forming species are more familiar to most people. Their fruiting structures are called **basidiomata**, and their sexual reproductive structures are **basidia**. The dikaryon stage may last for years. **Review Figure 22.16B**

CONCEPT 22.4 Fungi Can Be Sensitive Indicators of Environmental Change

■ The diversity and abundance of lichen growth on trees provide sensitive indications of air quality. **Review Figure 22.20**

■ Museum collections of fungi provide a historical record of atmospheric pollutants that were present when the fungi were growing. Fungi are often useful in environmental remediation.

■ Reforestation projects require restoration of the mycorrhizal fungal community.

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is22

Go to LaunchPad at **macmillanhighered.com/launchpad** for additional resources, including LearningCurve Quizzes, Flashcards, and many other study and review resources.

Animal Origins and Diversity

Entomologists collecting insects from a tree canopy in the Yungas rainforest of Argentina. Such research illuminates the vast number of insect species that remain undescribed by science.

About 1.3 million species of animals have been discovered and named by biologists. One group of animals, the insects, accounts for more than 1 million of these species, or more than half of all known species of living organisms. Although these numbers may seem incredibly large, they represent a relatively small fraction of the total animal diversity that is thought to exist on Earth.

As recently as the 1980s, many biologists thought that about half of existing insect species had been described, but today they think that the number of described insect species may be a much smaller fraction of the total number of living species. Why did they change their minds?

A simple but important field study suggested that the number of existing insect species had been significantly underestimated. Knowing that the insects of tropical forests—the most species-rich habitat on Earth—were poorly known, entomologist Terry Erwin made a comprehensive sample of one group of insects, the beetles, in the canopies of a single species of tropical forest tree, *Luehea seemannii*, in Panama. Erwin fogged the canopies of 19 large *L. seemannii* trees with a pesticide and collected the insects that fell from the trees in collection nets. His sample contained about 1,200 species of beetles—many of them undescribed—from this one species of tree.

Erwin then used a set of assumptions to estimate the total number of insect species in tropical evergreen forests. His assumptions included estimates of the number of species of host trees in these forests, the proportion of beetles that specialized on a specific species of host tree, the relative proportion of beetles to other insect groups, and the proportion of beetles that live in trees versus leaf litter. From this and similar studies, Erwin estimated that there may be 30 million or more species of insects on Earth. Although recent tests of Erwin's assumptions suggest 30 million was an overestimate, it is clear that the vast majority of insect species remain to be discovered.

Erwin's pioneering study highlighted the fact that we live on a poorly known planet, most of whose species have yet to be named and described. Much of the undiscovered diversity occurs among several groups of physically small yet biologically diverse animal groups, although even many larger species of animals continue to be discovered.

Q Besides beetles, which other groups of animals are thought to contain many more species than are known at present?

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CONCEPT 23.1 Distinct Body Plans Evolved among the Animals

How do we recognize an animal? The answer may seem obvious for familiar animals, but consider the sponges, which were once thought to be plants, or the rotifers, which are smaller than some protists.

The general characteristics often used to recognize animals include multicellularity, heterotrophy (using nutrients produced by other organisms), internal digestion, and motility (independent movement). Although these features are useful, none is diagnostic for all animals. Some animals do not move independently (at least during certain life stages), and some plants and fungi do have limited movement. Many parasitic animals lack a gut for internal digestion, and many other organisms (notably the fungi) are multicellular and heterotrophic. So what evidence leads us to group the animals in a single clade?

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Animal monophyly is supported by gene sequences and cellular morphology

The most convincing evidence that all the organisms considered to be animals share a common ancestor comes from phylogenetic analyses of their gene sequences. Relatively few complete animal genomes are available, but more are being sequenced each year. Analyses of these genomes and of many individual gene sequences have shown that all animals are indeed monophyletic. A currently well supported phylogenetic tree of the animals is shown in **FIGURE 23.1**.

Surprisingly few morphological features are shared across all animal species. The morphological synapomorphies (shared, derived traits) that are present are evident primarily at the cellular level. They include several unique features of the junctions between animal cells and a common set of extracellular matrix molecules, including collagen and proteoglycans. Although some animals in a few groups lack one or another of these cellular characteristics, it is believed that these traits were possessed by the ancestor of all animals and were subsequently lost in those groups.

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FIGURE 23.1 Animal Phylogeny This tree presents the best-supported current hypotheses of the evolutionary relationships among major groups of animals. The traits highlighted by red circles will be explained as you read this chapter. (See Analyze the Data 23.1 at LaunchPad.)

Similarities in the organization and function of Hox and other developmental genes provide additional evidence of developmental mechanisms shared by a common animal ancestor. The Hox genes specify body pattern and axis formation, leading to developmental similarities across animals (see Chapter 14).

The common ancestor of animals was probably a colonial flagellated protist similar to existing colonial choanoflagellates (**FIGURE 23.2A**), which have similarities to the multicellular sponges (**FIGURE 23.2B**). Why did these early animal ancestors begin to form multicellular colonies? One hypothesis is that multicellular colonies are more efficient than are single cells at capturing their prey. Experiments with living species of choanoflagellate show that they spontaneously form multicellular colonies in response to signaling compounds that are found on certain species of planktonic bacteria they eat (**FIGURE 23.3**).

Once multicellular colonies were formed in the ancestral animal lineage, it is likely that certain cells in the colony began to be specialized—some for movement, others for nutrition, others for reproduction, and so on. Once this functional specialization had begun, cells could continue to differentiate. Coordination among groups of cells could have improved by means of specific regulatory and signaling molecules that guided differentiation and migration of cells in developing embryos. Such coordinated groups of cells eventually evolved into the larger and more complex organisms that we call animals.

Nearly 80 percent of the 1.8 million named species of living organisms are animals, and millions of additional animal species await discovery. Evidence about the evolutionary relationships among animal groups can be found in fossils, in patterns of embryonic development, in the morphology and physiology of living animals, in the structure of animal proteins, and in gene sequences. Increasingly, studies of higher-level relationships have come to depend on genomic sequence comparisons, as genomes are ultimately the source of all inherited trait information.

Basic developmental patterns and body plans differentiate major animal groups

Distinct layers of cells form during the early development of most animals. These cell layers differentiate into specific organs and organ systems as development continues. The embryos of **diploblastic** animals have two cell layers: an outer **ectoderm** and
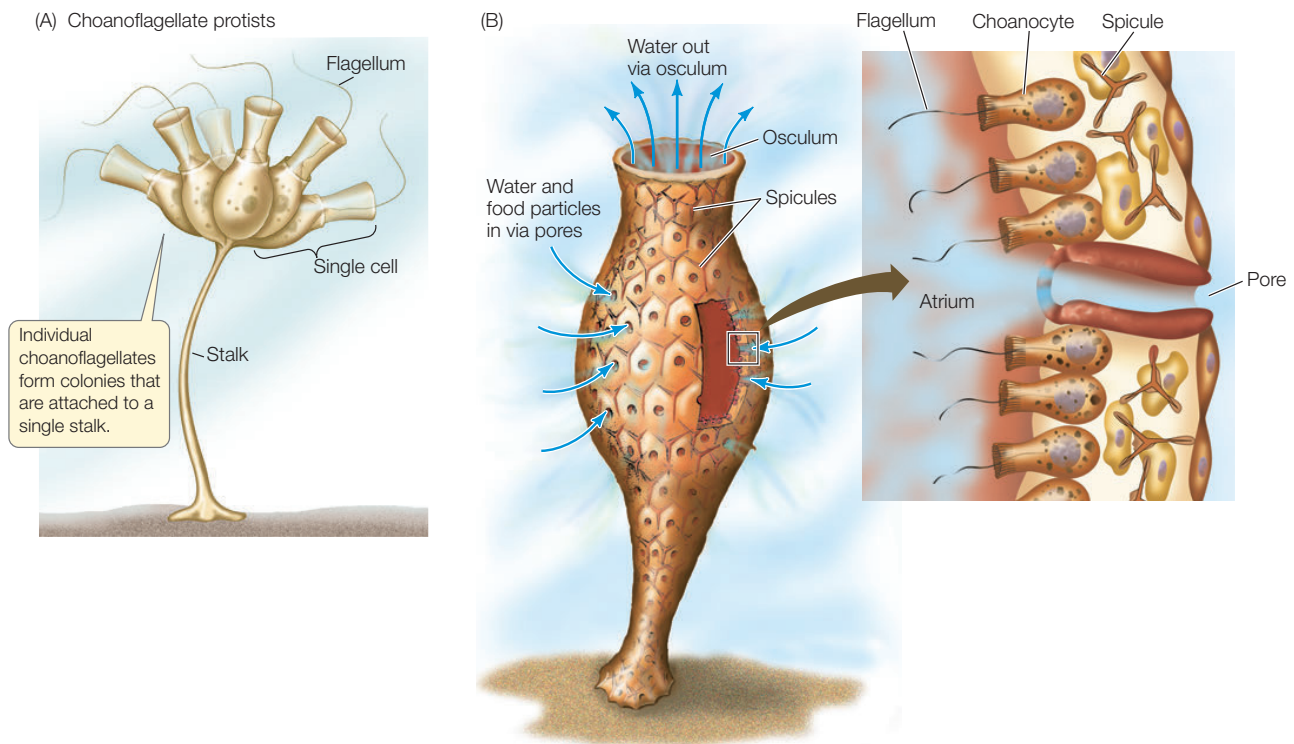
FIGURE 23.2 Choanocytes in Sponges Resemble Choanoflagellate Protists   (A) The similarity of choanoflagellate protist colonies to sponge choanocytes supports an evolutionary link between this protist lineage and the animals. (B) A sponge moves food-containing water through its body by beating the flagella of its choanocytes—specialized feeding cells. Water enters through small pores and passes into water canals or an open atrium, where the choanocytes capture food particles from the water. The spicules are supportive, skeletal structures.

FIGURE 23.3 What induces choanoflagellates to form multicellular colonies?
The choanoflagellate *Salpingoeca rosetta* forms multicellular, rose-shaped colonies (rosettes) at low frequencies in natural conditions. The rosette colonies are more efficient than are single cells at capturing some prey species of planktonic bacteria. Rosanna Alegado and her collaborators investigated the chemical signals that induce the choanoflagellates to form multicellular colonies when environmental conditions favor the rosette formations.[a]

HYPOTHESIS

Multicellular colonies of *S. rosetta* are induced by chemical compounds found on specific species of planktonic bacteria.

METHOD

1. Isolate individual species of bacteria from an environmental sample of *S. rosetta* and its associated bacterial community.
2. Use a combination of antibiotics to produce a bacteria-reduced culture line of *S. rosetta* that does not spontaneously form rosette colonies (the RCA line, for "rosette colonies absent").
3. Feed the RCA line with each of the isolated species of bacteria from step 1. Record any rosette colony formation.
4. Isolate compounds that induce multicellular colony formation from rosette-producing bacteria identified in step 3.

RESULTS

Alegado and colleagues tested various compounds from *Algoriphagus* and found that RIF-1, a sulfonolipid produced by the bacteria, is the signal that induces formation of multicellular colonies in *S. rosetta*.

In an environmental sample with many diverse bacteria, *S. rosetta* forms occasional multicellular colonies.

After treatment with antibiotics, no multicellular colonies were produced.

The addition of high concentrations of planktonic bacteria in the genus *Algoriphagus* induces the *S. rosetta* to form multicellular colonies.
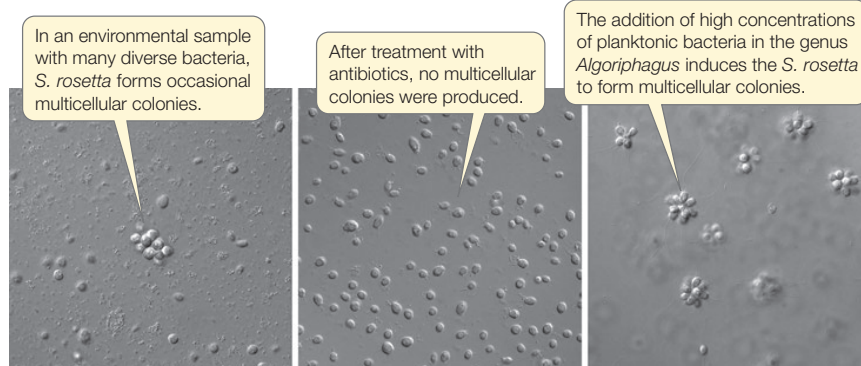
CONCLUSION

A chemical signal (RIF-1) from a particular species of prey bacteria can induce the formation of multicellular colonies in some species of choanoflagellates.

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]R. A. Alegado et al. 2012. *eLife* 1:e00013.

During early development in many animals, in a process known as gastrulation, a hollow ball one cell thick indents to form a cup-shaped structure. The opening of the cavity formed by this indentation is called the blastopore:

Blastopore

Gastrulation will be covered in detail in Chapter 38. The point to remember here is that the overall pattern of gastrulation immediately after the blastopore stage divides the triploblastic animals into two major groups:

- In the **protostomes** (Greek, "mouth first"), the mouth arises from the blastopore, and the anus forms later.
- In the **deuterostomes** ("mouth second"), the blastopore becomes the anus, and the mouth forms later.

Although the developmental patterns of animals are more varied than suggested by this simple dichotomy, phylogenies based on DNA sequences indicate that the protostomes and deuterostomes are distinct clades. These groups are known as the **bilaterians** (named for their usual bilateral symmetry), and they account for the vast majority of animal species.

The general structure of an animal, the arrangement of its organ systems, and the integrated functioning of its parts are referred to as its **body plan**. As Chapter 14 described, the regulatory and signaling genes that govern the development of body symmetry, body cavities, segmentation, and appendages are widely shared among the different animal groups. Although the myriad animal body plans cover a wide range of morphologies, they can be seen as variations on four key features:

- The symmetry of the body
- The structure of the body cavity
- The segmentation of the body

an inner **endoderm**. Embryos of **triploblastic** animals have, in addition to ectoderm and endoderm, a third distinct cell layer, **mesoderm**, between the ectoderm and the endoderm. The existence of three cell layers in embryos is a synapomorphy of triploblastic animals, whereas the diploblastic animals (ctenophores, placozoans, and cnidarians) retain the ancestral condition. Some biologists consider sponges to be diploblastic, but since they do not have clearly differentiated tissue types or embryonic cell layers, the term is not usually applied to them.

• The existence and location of external appendages that are used for sensing, feeding, locomotion, mating, and other functions

Each of these features affects how an animal interacts with its environment.

Most animals are symmetrical

The overall shape of an animal can be described by its **symmetry**. An animal is said to be symmetrical if it can be divided along at least one plane into similar halves. Animals that have no plane of symmetry are asymmetrical. Placozoans and many sponges are asymmetrical, but most other animals have some kind of symmetry, which is governed by the expression of regulatory genes during development.

In organisms with **radial symmetry**, body parts are arranged around a single axis at the body's center:

Radial symmetry

Any plane through the main body axis of this sea anemone divides the animal into similar halves.

Main axis
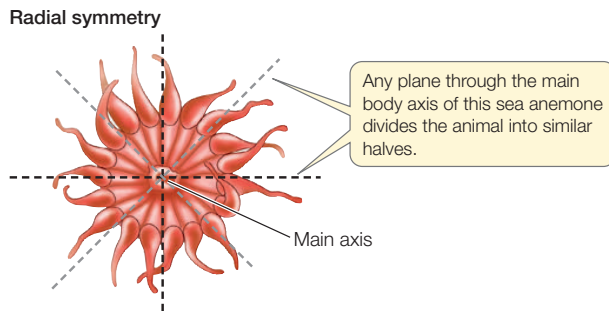
A perfectly radially symmetrical animal can be divided into similar halves by any plane that contains the central axis. However, most radially symmetrical animals are slightly modified, so fewer planes can divide them into identical halves. Some radially symmetrical animals are sessile (they remain fixed in one place) or drift with water currents. Others move slowly but can move equally well in any direction.

Bilateral symmetry is characteristic of animals that have a distinct front end, which typically precedes the rest of the body as the animal moves. A bilaterally symmetrical animal can be divided into mirror-image (left and right) halves by a single plane that passes through the midline of its body. This plane runs from the front, or **anterior**, end of the body, to the rear, or **posterior**, end:

Bilateral symmetry

Dorsal (back)

A single plane through the anterior–posterior midline divides the animal into mirror-image halves.

Anterior (head)

Posterior (tail)

Ventral (belly)
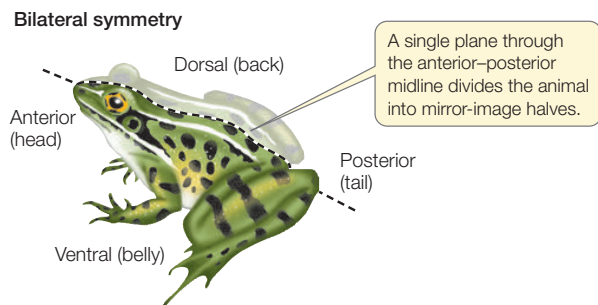
A plane at right angles to the midline divides the body into two dissimilar sides, its **dorsal** (top) and **ventral** (bottom) halves.

Bilateral symmetry is strongly correlated with **cephalization** (Greek *kephalos*, "head"), which is the concentration of sensory organs and nervous tissues at the anterior end of the animal. Cephalization has been evolutionarily favored because the anterior end of a bilaterally symmetrical animal typically encounters the environment first.

The structure of the body cavity influences movement

Animals with three embryonic cell layers (see Figure 23.1) can be divided into three types based on the presence and structure of an internal, fluid-filled **body cavity**.

• **Acoelomate** animals such as flatworms lack an enclosed, fluid-filled body cavity. Instead, the space between the gut (derived from endoderm) and the muscular body wall (derived from mesoderm) is filled with masses of cells called mesenchyme (**FIGURE 23.4A**). These animals typically move by beating cilia.

• **Pseudocoelomate** animals have a body cavity called a pseudocoel, a fluid-filled space in which many of the internal organs are suspended. A pseudocoel is enclosed by muscles (mesoderm) only on its outside; there is no inner layer of mesoderm surrounding the internal organs (**FIGURE 23.4B**).

• **Coelomate** animals have a body cavity, the coelom, that develops within the mesoderm. It is lined with a layer of muscular tissue called the peritoneum, which also surrounds the internal organs. The coelom is thus enclosed on both the inside and the outside by mesoderm (**FIGURE 23.4C**).

The structure of an animal's body cavity strongly influences the ways in which it can move. The body cavities of many animals function as **hydrostatic skeletons**. Fluids are relatively incompressible, so when the muscles surrounding a fluid-filled body cavity contract, fluids shift to another part of the cavity. If the body tissues around the cavity are flexible, fluids squeezed out of one region can cause another region to expand. The moving fluids can thus move specific body parts. (You can see how a hydrostatic skeleton works by watching a snail emerge from its shell.) A coelomate animal has better control over the movement of the fluids in its body cavity than a pseudocoelomate animal does. An animal that has longitudinal muscles (running along the length of the body) as well as circular muscles (encircling the body cavity) has even greater control over its movement.

In terrestrial environments, the hydrostatic function of fluid-filled body cavities applies mostly to relatively small, soft-bodied organisms. Most larger animals (as well as many smaller ones) have hard skeletons that provide protection and facilitate movement. Muscles are attached to those firm structures, which may be inside the animal or on its outer surface (in the form of a shell or cuticle).

Segmentation improves control of movement

Segmentation—the division of the body into segments—is seen in many animal groups. Segmentation facilitates specialization of different body regions. It also allows an animal to

(A) Acoelomate (flatworm)

Gut (endoderm)

Muscle layer (mesoderm)

Ectoderm

Mesenchyme

Acoelomates do not have enclosed body cavities.

(B) Pseudocoelomate (roundworm)

Gut (endoderm)

Pseudocoel (cavity)

Muscle (mesoderm)

Internal organs

Ectoderm

The pseudocoel is lined with mesoderm, but no mesoderm surrounds the internal organs.

(C) Coelomate (earthworm)

Gut (endoderm)

Internal organ

Peritoneum (mesoderm)

Coelom (cavity)

Muscle (mesoderm)

Ectoderm

The coelom and the internal organs are surrounded by mesoderm.

FIGURE 23.4 Animal Body Cavities (A) Acoelomates, like this marine flatworm, do not have enclosed body cavities. (B) Pseudocoelomates have a body cavity bounded by endoderm and mesoderm. (C) Coelomates have a peritoneum surrounding the internal organs in a region bounded by mesoderm.

Go to ACTIVITY 23.1 Animal Body Cavities
PoL2e.com/ac23.1

alter the shape of its body in complex ways and to control its movements precisely. If an animal's body is segmented, muscles in each individual segment can change the shape of that segment independently of the others. In only a few segmented animals is the body cavity separated into discrete compartments, but even partly separated compartments allow better control of movement. Segmentation occurs in several groups of protostomes and deuterostomes.

In some animals, such as annelids (earthworms and their relatives), similar body segments are repeated many times (**FIGURE 23.5A**). In other animals, including most arthropods, segments differ strikingly from one another (**FIGURE 23.5B**). The dramatic evolutionary radiation of the arthropods (including the insects, spiders, centipedes, and crustaceans) was based on changes in a segmented body plan that features muscles attached to the inner surface of an external skeleton, including a variety of external appendages that move these animals. In some animals, distinct body segments are not apparent externally—for example, the segmented vertebrae of vertebrates, including humans. Nonetheless, muscular segmentation is clearly visible in humans with well-defined, muscular bodies (**FIGURE 23.5C**).

Appendages have many uses

Getting around under their own power allows animals to obtain food, to avoid predators, and to find mates. Even some sedentary species, such as sea anemones, have larval stages that use cilia to swim, thus increasing the animal's chances of finding a suitable habitat.

Appendages that project externally from the body greatly enhance an animal's ability to move around. Many echinoderms, including sea urchins and seas stars, have large numbers of tube feet that allow them to move slowly across the substrate. Animals whose appendages have become modified into limbs are capable of highly controlled, more rapid movement. The presence of jointed limbs has been a prominent factor in the evolutionary success of the arthropods and the vertebrates. In four independent instances—among the arthropod insects and among the vertebrate pterosaurs, birds, and bats—body plans emerged in which limbs were modified into wings, allowing these animals to use powered flight.

Appendages also include many structures that are not used for locomotion. Many animals have antennae, which are specialized appendages used for sensing the environment. Other appendages (such as claws and the mouthparts of many arthropods) are adaptations for capturing prey or chewing food. In some species, appendages are used for reproductive purposes, such as sperm transfer or egg incubation.

Nervous systems coordinate movement and allow sensory processing

The bilaterian animals have a well-coordinated central nervous system. More diffuse nervous systems, called **nerve nets**, are present in some other animals, such as jellyfishes and their relatives. Nervous systems appear to be completely absent in a few sessile animal groups, such as sponges.

The central nervous system of bilaterians coordinates the actions of muscles, which allows coordinated movement of appendages and body parts. This coordination of muscles permits highly effective and efficient movement on land, in water, or through the air. The central nervous system is also essential for the processing of sensory information gathered from a wide variety of sensory systems. Many animals have sensory systems for detecting light, for forming images of their environment (sight), for mechanical touch, for detecting

(A) *Nereis succinea*

All of the segments of this marine annelid are similar.

Setae

Tail segments are modified for hunting and defense.

Abdominal segments are modified for digestion and reproduction.

The muscles of the human abdomen are segmented.

Anterior segments have fused and bear appendages for locomotion and feeding.

(B) *Hadrurus arizonensis*

(C) *Homo sapiens*
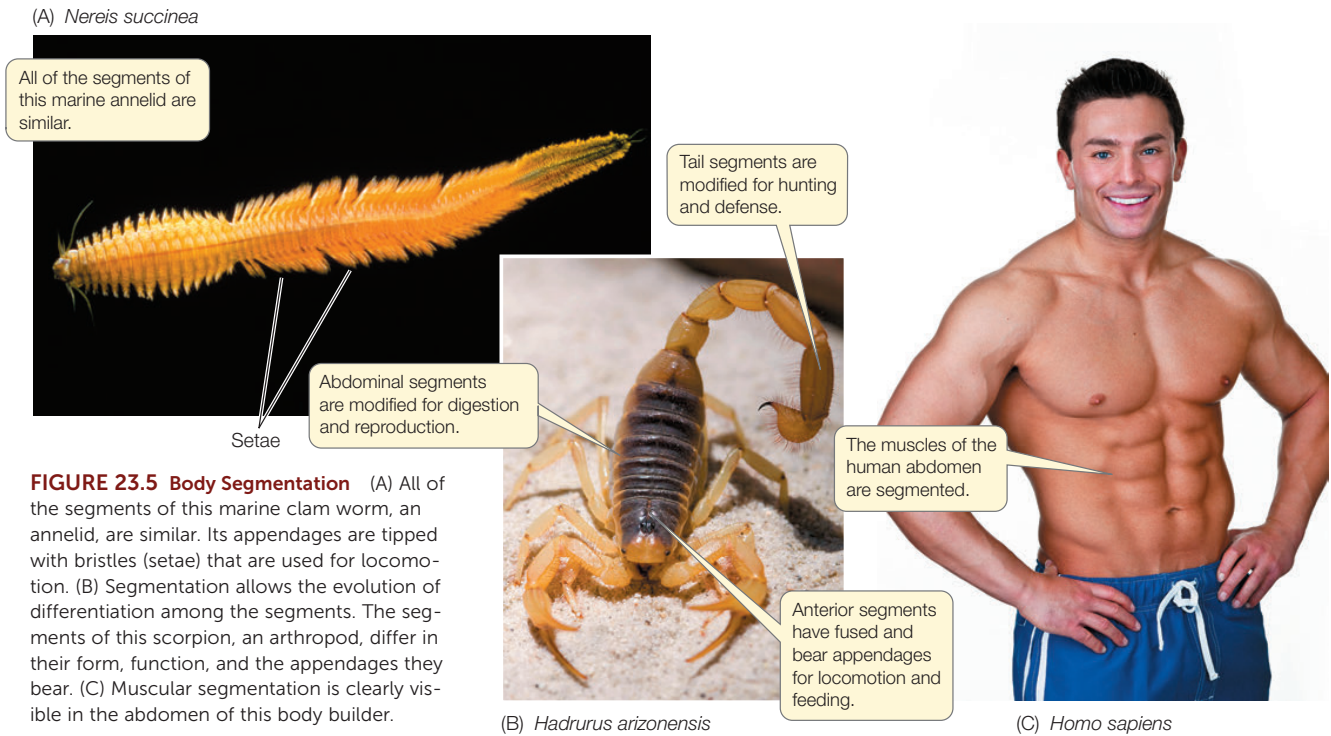
FIGURE 23.5 Body Segmentation (A) All of the segments of this marine clam worm, an annelid, are similar. Its appendages are tipped with bristles (setae) that are used for locomotion. (B) Segmentation allows the evolution of differentiation among the segments. The segments of this scorpion, an arthropod, differ in their form, function, and the appendages they bear. (C) Muscular segmentation is clearly visible in the abdomen of this body builder.

movement, for detecting sounds (hearing), for detecting electrical fields, and for chemical detection (e.g., taste and smell). These sensory systems allow animals to find food, and the ability of animals to move allows them to capture or collect food from their environment. These same abilities also allow most animals to move to avoid potential predators or to search for suitable mates. Most animals can also assess the suitability of different environments and move appropriately in response to that information.

Go to **MEDIA CLIP 23.1**
Nervous Systems Lead to Efficient Predators
PoL2e.com/mc23.1

CHECKpoint CONCEPT 23.1

✓ Describe the difference between diploblastic and triploblastic embryos, and between protostomes and deuterostomes.

✓ Describe the main types of symmetry found in animals. How can an animal's symmetry influence the way it moves?

✓ Explain several ways in which body cavities and segmentation improve control over movement.

Variations in body symmetry, body cavity structure, life cycles, patterns of development, and survival strategies differentiate the many animal species. **TABLE 23.1** summarizes the living members of the major animal groups we will describe in the rest of this chapter.

CONCEPT 23.2 Some Animal Groups Fall outside the Bilateria

Looking at Figure 23.1, you can see that the protostome and deuterostome animals together comprise a monophyletic group known as the **Bilateria**. Some major traits that support the monophyly of bilaterians (in addition to genomic analyses) are strong bilateral symmetry, the presence of three distinct cell layers in embryos (triploblasty), and the presence of at least seven Hox genes (see Chapter 14). There are, however, four animal groups—the sponges, ctenophores, placozoans, and cnidarians—that are not bilaterians.

The simplest animals, the sponges, have no distinct tissue types. All other animals groups are usually known as **eumetazoans**. Two groups treated here as eumetazoans, the ctenophores and placozoans, have weakly differentiated tissue layers (placozoans also lack a nervous system), so some biologists exclude these two groups from Eumetazoa as well. Most eumetazoans have some form of body symmetry, a gut, a nervous system, and tissues organized into distinct organs (although there have been secondary losses of some of these structures in some eumetazoans).

Go to **ACTIVITY 23.2 Sponge and Diploblast Classification**
PoL2e.com/ac23.2

Sponges are loosely organized animals

Although they have some specialized cells, **sponges** have no distinct embryonic cell layers and no true organs. Early naturalists classified sponges as plants because they were sessile and lacked body symmetry.

TABLE 23.1	Summary of Living Members of the Major Animal Groups					
	Approximate number of living species described	Major subgroups, other names, and notes			Approximate number of living species described	Major subgroups, other names, and notes
Sponges	8,500	Demosponges, glass sponges, calcareous sponges		**Ecdysozoans**		
Ctenophores	250	Comb jellies		Kinorhynchs	180	Mud dragons
Placozoans	2	Additional species have been discovered but not yet formally named		Loriciferans	30	Brush heads
				Priapulids	20	Penis worms
				Nematodes	25,000	Roundworms
Cnidarians	12,500	Anthozoans: Corals, sea anemones Hydrozoans: Hydras and hydroids Scyphozoans: Jellyfishes		Horsehair worms	350	Gordian worms
				Tardigrades	1,200	Water bears
				Onychophorans	180	Velvet worms
				Arthropods		
PROTOSTOMES				Chelicerates	114,000	Horseshoe crabs, sea spiders, and arachnids (scorpions, harvestmen, spiders, mites, ticks)
Arrow worms	180	Glass worms				
Lophotrochozoans						
Bryozoans	5,500	Moss animals		Myriapods	12,000	Millipedes, centipedes
Flatworms	30,000	Free-living flatworms; flukes and tapeworms (all parasitic); monogeneans (ectoparasites of fishes)		Crustaceans	67,000	Crabs, shrimps, lobsters and crayfishes, barnacles, copepods
Rotifers and relatives	3,800	Rotifers, hairy-backs, spiny-headed worms, and jaw worms		Hexapods	1,020,000	Insects and their wingless relatives
				DEUTEROSTOMES		
Ribbon worms	1,200	Proboscis worms		Echinoderms	7,500	Crinoids (sea lilies and feather stars); brittle stars; sea stars; sea urchins; sea cucumbers
Brachiopods	450	Lampshells				
Phoronids	10	Sessile marine filter feeders		Hemichordates	120	Acorn worms and pterobranchs
Annelids	19,000	Polychaetes (generally marine; may not be monophyletic) Clitellates: Earthworms, freshwater worms, leeches		Chordates		
				Tunicates	2,800	Sea squirts (ascidians), salps, and larvaceans
				Lancelets	35	Cephalochordates
Mollusks	117,000	Monoplacophorans Chitons Bivalves: Clams, oysters, mussels Gastropods: Snails, slugs, limpets Cephalopods: Squids, octopuses, nautiloids		Vertebrates	65,000	Hagfishes, lampreys, chondrichthyans, ray-finned fishes, coelacanths, lungfishes, amphibians, reptiles (including birds), and mammals

Sponges have hard skeletal elements called **spicules**, which may be small and simple or large and complex. Three major groups of sponges, which separated soon after the split between sponges and the rest of the animals, are distinguished by their spicules. Members of two groups (demosponges and glass sponges) have skeletons composed of silicaceous spicules made of hydrated silicon dioxide (**FIGURE 23.6A,B**). These spicules have greater flexibility and toughness than synthetic glass rods of similar length. Members of the third group, the calcareous sponges, take their name from their calcium carbonate spicules (**FIGURE 23.6C**).

The body plan of all sponges—even large ones, which may reach a meter or more in length—is an aggregation of cells built around a water canal system. Sponges bring water into their bodies by beating the flagella of their specialized feeding cells, the **choanocytes** (see Figure 23.2B). Water, along with any food particles it contains, enters the sponge by way of small pores and passes into the water canals or a central atrium, where choanocytes capture food particles.

A skeleton of simple or branching spicules, often combined with a complex network of elastic fibers, supports the body of most sponges. Sponges also have an extracellular matrix, composed of collagen, adhesive glycoproteins, and other molecules, that holds the cells together. Most sponges are filter feeders. A few species are carnivores that trap prey on hook-shaped spicules that protrude from the body surface.

(B) *Euplectella aspergillum*

(A) *Xestospongia* sp.

FIGURE 23.6 Sponge Diversity (A) The great majority of sponge species are demosponges, such as this barrel sponge. (B) As in the demosponges, the supporting structures of glass sponges are silicaceous spicules. The pores and water canals "typical" of the sponge body plan are apparent in both (A) and (B). (C) The spicules of calcareous sponges are made of calcium carbonate.

(C) *Sycon* sp.

Spicules

Most of the 8,500 species of sponges are marine animals. Only about 50 species of sponges live in fresh water. Sponges come in a wide variety of sizes and shapes that are adapted to different movement patterns of water. Sponges living in intertidal or shallow subtidal environments are subject to strong wave action and attach firmly to the substrate. Most sponges that live in slowly flowing water are flattened and are oriented at right angles to the direction of current flow, allowing them to intercept water and the food it contains as it flows past them.

Sponges reproduce both sexually and asexually. In most species, a single individual produces both eggs and sperm, but individuals do not self-fertilize. Water currents carry sperm from one individual to another. Sponges also reproduce asexually by budding and fragmentation.

Ctenophores are radially symmetrical and diploblastic

Ctenophores, also known as comb jellies, were until recently thought to be most closely related to the cnidarians (jellyfishes, corals, and their relatives). But ctenophores lack most of the Hox genes found in all other eumetazoans, and recent studies of their genomes have indicated that ctenophores were among the earliest lineages to split from the remaining animals.

Ctenophores have a radially symmetrical, diploblastic body plan. The two cell layers are separated by an inert, gelatinous extracellular matrix called **mesoglea**. Ctenophores, unlike sponges, have different openings for food entry and waste elimination: food enters through a mouth, and wastes are eliminated through two anal pores.

Ctenophores move by beating cilia rather than by muscular contractions. Most of the 250 known species have eight comblike rows of cilia-bearing plates, called **ctenes** (**FIGURE 23.7**).

(B) *Mnemiopsis leidyi*

(A)

Gut

Tentacle sheath

Ctenes

Pharynx

Mouth

Tentacle

Prey adhere to the sticky cells that cover the tentacles.

Mouth
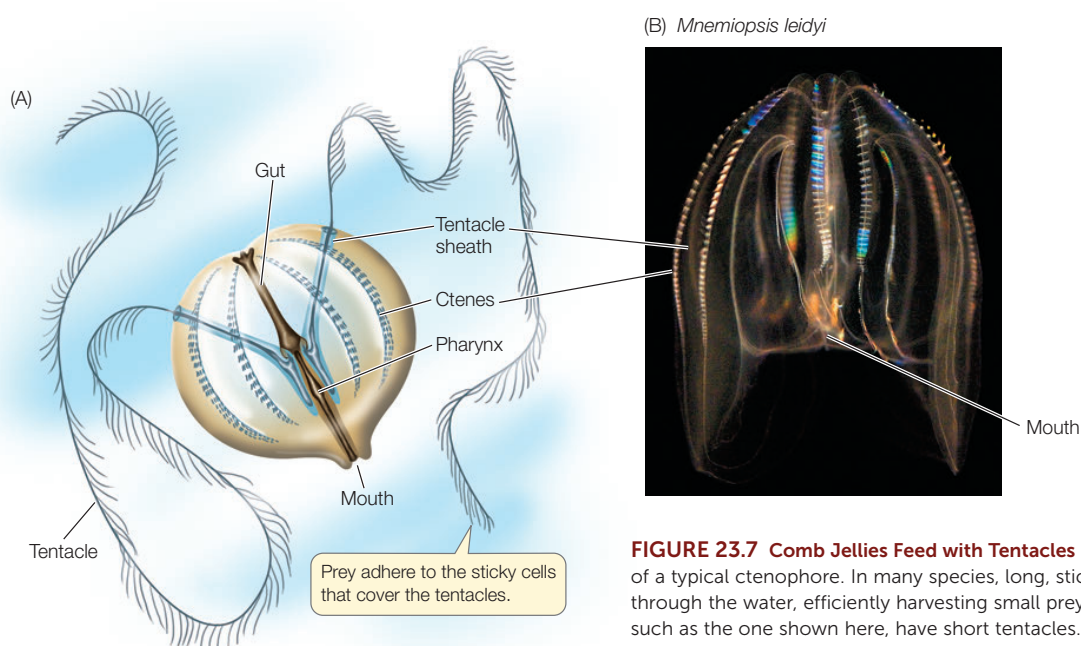
FIGURE 23.7 Comb Jellies Feed with Tentacles (A) The body plan of a typical ctenophore. In many species, long, sticky tentacles sweep through the water, efficiently harvesting small prey. (B) Other species, such as the one shown here, have short tentacles.

The feeding tentacles of ctenophores are covered with cells that discharge adhesive material when they contact prey. After capturing its prey, a ctenophore retracts its tentacles to bring the food to its mouth. In some species, the entire surface of the body is coated with sticky mucus that captures prey. Most ctenophores eat small planktonic organisms, although some eat other ctenophores. Ctenophores are common in open seas and can become abundant in protected bodies of water, where large populations may inhibit the growth of other organisms.

Ctenophore life cycles are uncomplicated. Gametes are released into the body cavity and then discharged through the mouth or the anal pores. Fertilization takes place in open seawater. In nearly all species, the fertilized egg develops directly into a miniature ctenophore, which gradually grows into an adult.

Go to MEDIA CLIP 23.2
Ctenophores
PoL2e.com/mc23.2

Placozoans are abundant but rarely observed

Placozoans are structurally very simple animals with only four distinct cell types (**FIGURE 23.8A**). Individuals in the mature life stage are usually observed adhering to surfaces (such as the glass of aquariums, where they were first discovered, or to rocks and other hard substrates in nature). Their structural simplicity—they have no mouth, gut, or nervous system—initially led biologists to suspect they might be the sister group of all other animals. Most phylogenetic analyses have not supported this hypothesis, however, and some aspects of the placozoans' structural simplicity may be secondarily derived. They are generally considered to have a diploblastic body plan, with upper and lower epithelial (surface) layers that sandwich a layer of contractile fiber cells.

Recent studies have found that placozoans have a pelagic (open-ocean) stage that is capable of swimming (**FIGURE 23.8B**), but the life history of placozoans is incompletely known. Most studies have focused on the larger adherent stages that can be found in aquariums, where they appear after being inadvertently collected with other marine organisms. The transparent nature and small size of placozoans make them very difficult to observe in nature. Nonetheless, it is known that placozoans can reproduce both asexually as well as sexually, although

the details of their sexual reproduction are poorly understood. They are found in warm coastal seas around the world.

Cnidarians are specialized carnivores

The **cnidarians** (jellyfishes, sea anemones, corals, and hydrozoans) make up the largest and most diverse group of nonbilaterian animals. The mouth of a cnidarian is connected to a blind sac called the **gastrovascular cavity**. The gastrovascular cavity functions in digestion, circulation, and gas exchange, and it also acts as a hydrostatic skeleton. The single opening serves as both mouth and anus.

The life cycle of many cnidarians has two distinct stages, one sessile and the other motile (**FIGURE 23.9**), although one or the other of these stages is absent in some groups. In the sessile **polyp** stage, a cylindrical stalk is attached to the substrate. The motile **medusa** (plural *medusae*) is a free-swimming stage shaped like a bell or an umbrella. It typically floats with its mouth and feeding tentacles facing downward.

Mature polyps produce medusae by asexual budding. Medusae then reproduce sexually, producing eggs or sperm by meiosis and releasing the gametes into the water. A fertilized egg develops into a free-swimming, ciliated larva called a **planula**, which eventually settles to the bottom and develops into a polyp.

Cnidarians have epithelial cells with muscle fibers that contract and enable the animals to move, as well as simple nerve nets that integrate their body activities. They are specialized carnivores, using the toxin in harpoonlike structures called **nematocysts** to capture relatively large and complex prey. Some cnidarians, including many corals and anemones, gain additional nutrition from photosynthetic endosymbionts that live in their tissues.

> **LINK**
>
> The importance of protist endosymbionts in coral colonies is discussed in **Concept 20.4**

Of the roughly 12,500 living cnidarian species, all but a few live in the oceans. The smallest cnidarians can hardly be seen without a microscope. The largest known jellyfish is 2.5 meters in diameter, and some colonial species can reach lengths in excess of 30 meters. Three clades of cnidarians have many species, some of which are shown in **FIGURE 23.10**. The anthozoans

(A)

(B)
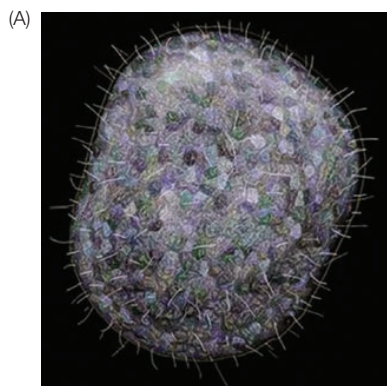
FIGURE 23.8 Placozoan Simplicity (A) As seen in this artist's rendition, adult placozoans are tiny (1–2 mm across), flattened, asymmetrical animals. (B) Recent studies have found a weakly swimming pelagic stage of placozoan to be abundant in many warm tropical and subtropical seas.
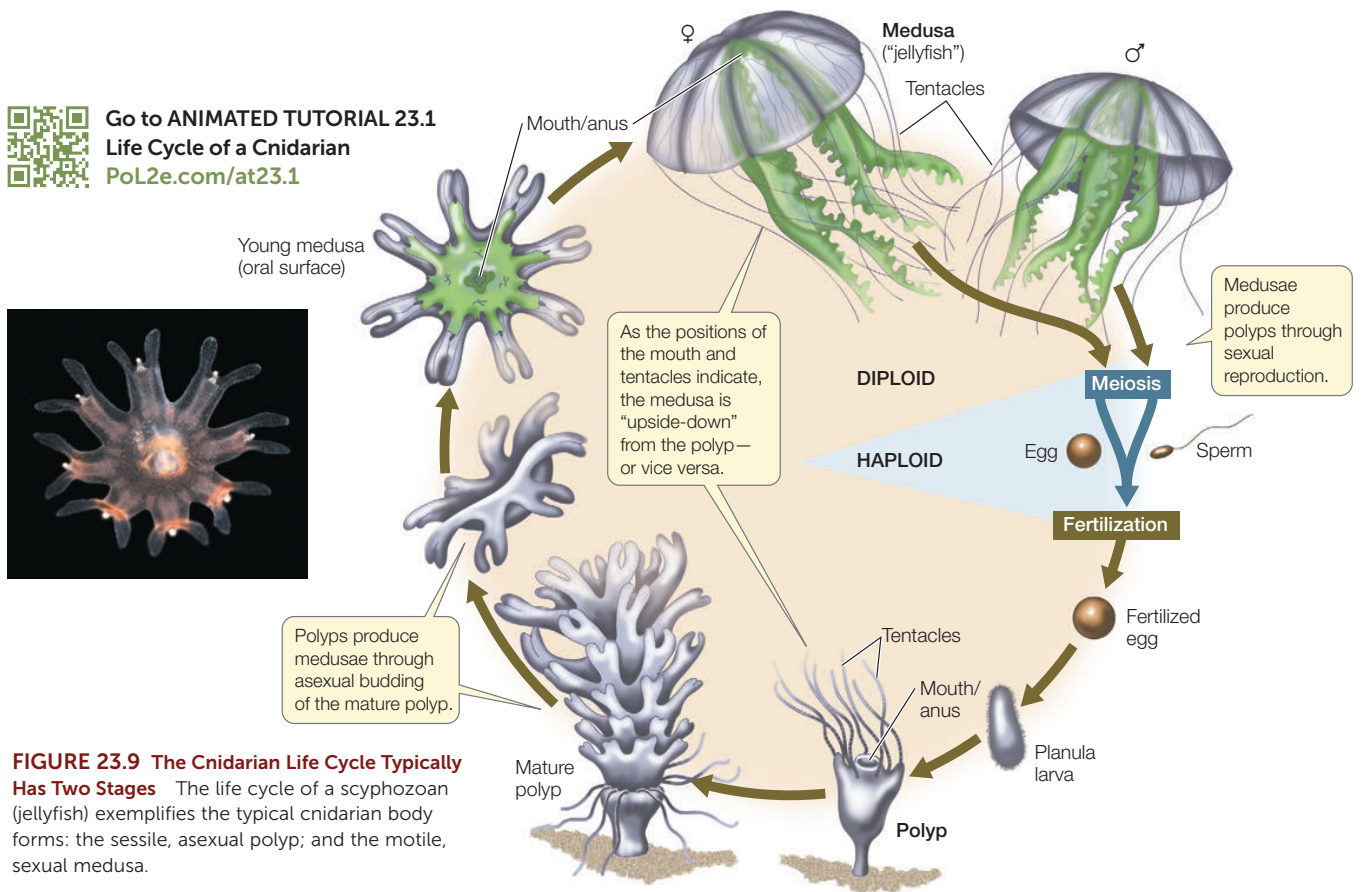
FIGURE 23.9 The Cnidarian Life Cycle Typically Has Two Stages The life cycle of a scyphozoan (jellyfish) exemplifies the typical cnidarian body forms: the sessile, asexual polyp; and the motile, sexual medusa.

(A) *Diadumene leucilena*

(B) *Netrostoma setouchina*

(C)

FIGURE 23.10 Diversity among Cnidarians (A) Sea anemones are sessile, living attached to a marine substrate. Water currents carry prey into the nematocyst-studded tentacles. (B) A jellyfish illustrates the complexity of a scyphozoan medusa. (C) Numerous corals species on a reef in Indonesia.

include sea anemones, sea pens, and corals. The scyphozoans are commonly known as jellyfishes or sea jellies. The less familiar hydrozoans include both freshwater and marine species.

CHECKpoint CONCEPT **23.2**

✓ Why are sponges and placozoans considered to be animals, even though they lack the complex body structures found among most other animal groups?

✓ How does feeding differ between ctenophores and cnidarians?

✓ Can you think of any advantages to the biphasic life cycle (sessile polyp and motile medusa) of many cnidarians?

In Concept 23.1 we noted that the name protostome means "mouth first," a developmental synapomorphy that links these animals. The vast majority of animals are protostomes.

CONCEPT 23.3 Protostomes Have an Anterior Brain and a Ventral Nervous System

The protostomes are a highly diverse group of animals. Although their body plans are extremely varied, they are all bilaterally symmetrical animals whose bodies exhibit two major derived traits:

- An anterior brain that surrounds the entrance to the digestive tract
- A ventral nervous system consisting of paired or fused longitudinal nerve cords

Other aspects of protostome body organization differ widely from group to group. Although the common ancestor of the protostomes likely had a coelom, subsequent modifications of the coelom distinguish many protostome lineages. In at least one protostome lineage (the flatworms), the coelom has been lost (that is, the flatworms reverted to an acoelomate state). Some lineages are characterized by a pseudocoel (see Figure 23.4B). In two of the most prominent protostome groups, the coelom has been highly modified:

- The arthropods lost the ancestral condition of the coelom over the course of evolution. Their internal body cavity has become a hemocoel, or "blood chamber," in which fluid from an open circulatory system bathes the internal organs before returning to blood vessels.
- Most mollusks have an open circulatory system with some of the attributes of the hemocoel, but they retain vestiges of an enclosed coelom around their major organs.

The evolutionary relationships of one small group of protostomes, the **arrow worms** (see Figure 23.1), have been debated for many years. Although recent gene sequence studies clearly identify arrow worms as protostomes, there remains some question as to their exact placement within the protostomes.

The 180 living species of arrow worms are small (3 mm–12 cm) marine predators of planktonic protists and small fish.

The protostomes can be divided into two major clades—the lophotrochozoans and the ecdysozoans—largely on the basis of DNA sequence analysis. However, there are also some morphological characteristics that unite most members of these two groups.

Go to ANIMATED TUTORIAL 23.2
An Overview of the Protosomes
PoL2e.com/at23.2

Cilia-bearing lophophores and trochophore larvae evolved among the lophotrochozoans

Lophotrochozoans derive their name from two different features that involve cilia: a feeding structure known as a lophophore and a free-living larva known as a trochophore. Neither feature is universal for all lophotrochozoans, however.

Several distantly related groups of lophotrochozoans (including bryozoans, brachiopods, and phoronids) have a **lophophore**, a circular or U-shaped ring of ciliated, hollow tentacles around the mouth (**FIGURE 23.11A**). This complex structure is

(A) *Plumatella repens*   Lophophore composed of tentacles

(B) *Reteporella couchii*
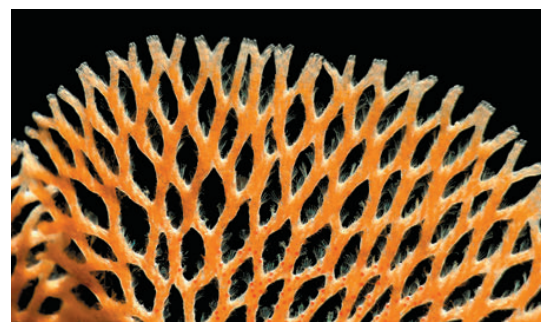
FIGURE 23.11 Bryozoans Form Colonies (A) The extended lophophores of its individual members dominate the anatomy of this colonial bryozoan. (B) The rigid orange tissue of this marine bryozoan colony connects and supplies nutrients to thousands of individual animals.

an organ for both food collection and gas exchange. The lophophore appears to have evolved independently several times, although it may be an ancestral feature that has been lost in many groups. Nearly all animals with a lophophore are sessile as adults, using the lophophore's tentacles and cilia to capture small floating organisms from the water.

Go to MEDIA CLIP 23.3
Feeding with a Lophophore
PoL2e.com/mc23.3

Some lophotrochozoans, especially in their larval form, use cilia for locomotion. The larval form known as a **trochophore** moves by beating a band of cilia:

Stomach

Band of cilia

Mouth

Intestine

Anus
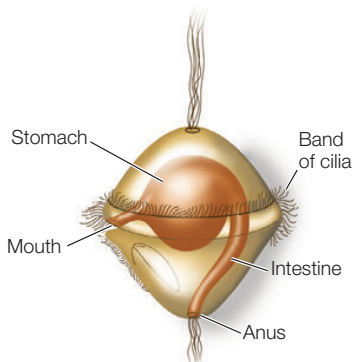
This movement of cilia also brings plankton closer to the larva, where the plankton can be captured and ingested (similar in function to the cilia of the lophophore). Trochophore larvae are found among many of the major groups of lophotrochozoans, including the mollusks, annelids, ribbon worms, and bryozoans. This larval form was probably present in the common ancestor of lophotrochozoans, although it has been subsequently lost in several lineages.

Lophotrochozoans range from relatively simple animals with a blind gut (that is, a gut with a single opening that both takes in food and expels wastes) and no internal transport system to animals with a complete gut (having separate entrance and exit openings) and a complex internal transport system. A number of these groups exhibit wormlike bodies, but the lophotrochozoans encompass a wide diversity of morphologies, including a few groups with external shells. Included among the lophotrochozoans are species-rich groups such as flatworms, annelids, and mollusks, along with many less well known groups, some of which have only recently been discovered.

BRYOZOANS   Most of the 5,500 species of **bryozoans** ("moss animals") are colonial animals that live in a "house" made of material secreted by the external body wall. Almost all bryozoans are marine, although a few species occur in fresh or brackish water. A bryozoan colony consists of many small (1–2 mm) individuals connected by strands of tissue along which nutrients can be moved (**FIGURE 23.11B**). The colony is created by the asexual reproduction of its founding member, and a single colony may contain as many as 2 million individuals. Rocks in coastal regions in many parts of the world are covered with luxuriant growths of bryozoans. Some bryozoans create miniature reefs in shallow waters. In some species, the individual colony members are differentially specialized for feeding, reproduction, defense, or support.

Bryozoans can also reproduce sexually. Sperm are released into the water, which carries the sperm to other individuals. Eggs are fertilized internally; developing embryos are brooded before they exit as larvae to seek suitable sites for attachment to the substrate.

FLATWORMS   Most of the 30,000 species of **flatworms** are tapeworms and flukes; members of these two groups are internal parasites, particularly of vertebrates (**FIGURE 23.12A**).

FIGURE 23.12 Flatworms (A) The fluke diagrammed here is representative of many parasitic flatworms. Absorbing nutrition from the host animal's gut, these internal parasites do not require elaborate feeding or digestive organs and can devote most of their bodies to reproduction. (B) The bright coloration of this terrestrial flatworm from Borneo resembles some species of venomous snakes, and may provide it protection from predation.

(A) Diagram of a typical parasitic flatworm

Anterior

Pharyngeal opening

Gut

The gut has a single opening to the exterior, which serves as both "mouth" and "anus."

Egg capsule

Testis

Yolk gland

This parasitic flatworm's body is filled primarily with sex organs.

Seminal receptacle

Ovary

Vagina

Posterior
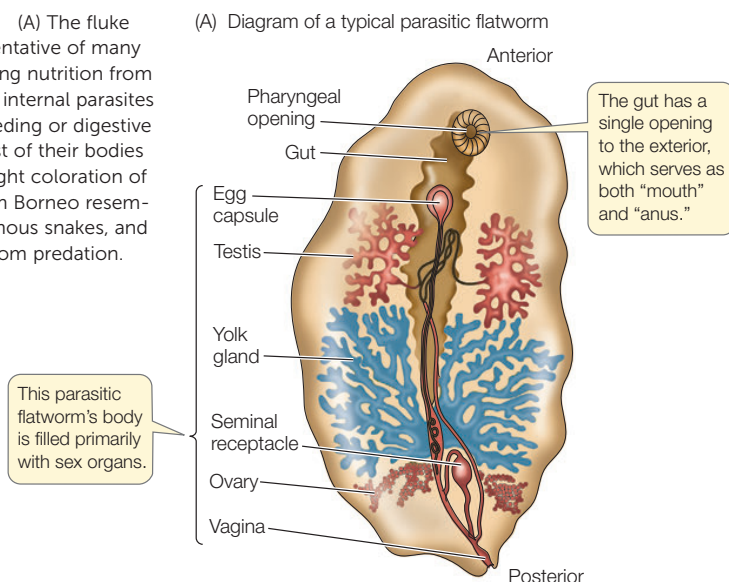
(B) *Bipallium everetti*

Because they absorb digested food from the guts of their hosts, many parasitic flatworms lack digestive tracts of their own. Some cause serious human diseases, such as schistosomiasis, which is common in parts of Asia, Africa, and South America. The species that causes this devastating disease has a complex life cycle involving both freshwater snails and mammals as hosts. Other flatworms are external parasites of fishes and other aquatic vertebrates. The turbellarians include most of the free-living species (**FIGURE 23.12B**).

Flatworms lack specialized organs for transporting oxygen to their internal tissues. Lacking a gas transport system, each cell must be near a body surface, a requirement met by the dorsoventrally flattened body form. In flatworms that have a digestive tract, this consists of a mouth opening into a blind sac. The sac is often highly branched, forming intricate patterns that increase the surface area available for the absorption of nutrients. Most free-living flatworms are cephalized, with a head bearing chemoreceptor organs, two simple eyes, and a small brain composed of anterior thickenings of the longitudinal nerve cords. Free-living flatworms glide over surfaces, powered by broad bands of cilia.

ROTIFERS   Most species of **rotifers** are tiny—50–500 μm long, smaller than some ciliate protists—but they have specialized internal organs (**FIGURE 23.13**). A complete gut passes from an anterior mouth to a posterior anus. The body cavity is a pseudocoel that functions as a hydrostatic skeleton. Rotifers typically propel themselves through the water by means of rapidly beating cilia rather than by muscular contraction.

The most distinctive organ of rotifers is a conspicuous ciliated organ called the corona, which surmounts the head of many species. Coordinated beating of the cilia sweeps particles of organic matter from the water into the animal's mouth and down to a complicated structure called the mastax, in which food is ground into small pieces. By contracting muscles around the pseudocoel, a few rotifer species that prey on protists and small animals can protrude the mastax through their mouth and seize small objects with it.

Most species of rotifers live in fresh water. Some species rest on the surfaces of mosses or lichens in a desiccated, inactive state until it rains. When rain falls, they absorb water and become mobile, feeding in the films of water that temporarily cover the plants. Most rotifers live no longer than a few weeks.

Both males and females are found in some species of rotifers, but only females are known among the bdelloid rotifers (the b in "bdelloid" is silent). Biologists have concluded that the bdelloid rotifers may have existed for tens of millions of years without regular sexual reproduction. In general, lack of genetic recombination leads to the buildup of deleterious mutations, so long-term asexual reproduction typically leads to extinction (see Concept 15.6). However, recent studies indicate that bdelloid rotifers may avoid this problem by taking up fragments of genes directly from the environment during the desiccation–rehydration cycle.

Such a mechanism allows genetic recombination among individuals in the absence of direct sexual exchange.

Go to MEDIA CLIP 23.4
Rotifer Feeding
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RIBBON WORMS   **Ribbon worms** (nemerteans) have simple nervous and excretory systems similar to those of flatworms. Unlike flatworms, however, they have a complete digestive tract with a mouth at one end and an anus at the other. Small ribbon worms move slowly by beating their cilia. Larger ones employ waves of muscle contraction to move over the surface of sediments or to burrow into them.

Within the body of nearly all of the 1,200 species of ribbon worms is a fluid-filled cavity called the rhynchocoel, within which lies a hollow, muscular **proboscis**. The proboscis, which is the worm's feeding organ, may extend much of the length of the body. Contraction of the muscles surrounding the rhynchocoel causes the proboscis to evert (turn inside out) explosively through an anterior pore (**FIGURE 23.14A**). The proboscis may be armed with sharp stylets that pierce prey and discharge paralytic toxins into the wound.

Ribbon worms are largely marine, although there are some freshwater and terrestrial species. Most ribbon worms are less than 20 centimeters long, but individuals of some species reach 20 meters or more. Some genera include species that are conspicuous and brightly colored (**FIGURE 23.14B**).

(A) *Philodina roseola*

Anterior

Cilia
Corona
Mouth
Mastax
Digestive gland
Pseudocoel
Gonad
Stomach

A complete gut passes from an anterior mouth to a posterior anus.

Intestine

"Foot" with "toes"

Anus

Posterior
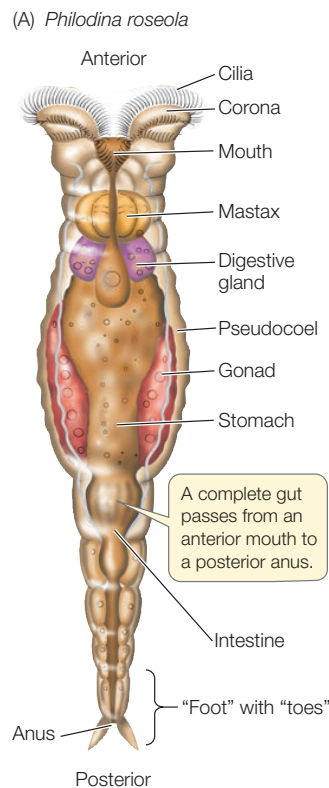
(B) *Philodina* sp.

FIGURE 23.13 Rotifers   (A) The individual diagrammed here reflects the general structure of many rotifers. (B) A light micrograph reveals the internal complexity of these tiny animals.

(A)

Rhynchocoel

Floating in a cavity called the rhynchocoel, the proboscis can be everted rapidly.

Proboscis

Proboscis retractor muscle

Proboscis pore

Mouth

Intestine

Anus

The tip of the everted proboscis bears a sharp, nail-shaped stylet.

(B) *Baseodiscus cingulatus*
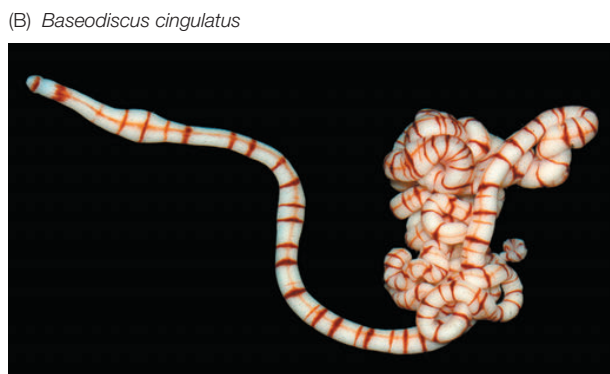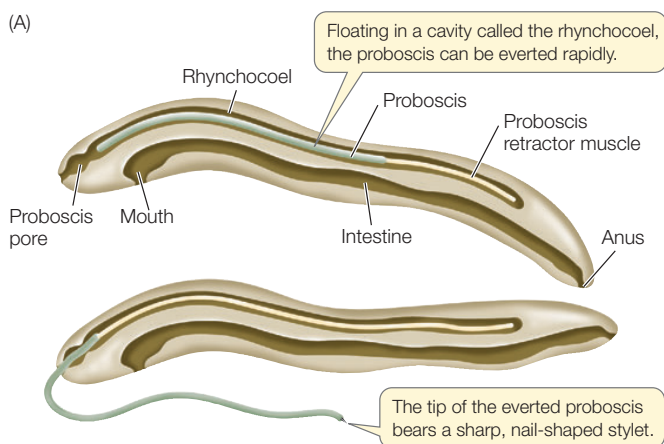
FIGURE 23.14 Ribbon Worms (A) The proboscis is the ribbon worm's feeding organ. (B) Although most nemerteans are small, some marine species such as this one can reach several meters in length.

Go to MEDIA CLIP 23.5
Explosive Extrusion of Ribbon Worm Proboscis
PoL2e.com/mc23.5

BRACHIOPODS AND PHORONIDS Like bryozoans (see Figure 23.11A), brachiopods and phoronids also feed using a lophophore, but this structure may have evolved independently in these groups. Although neither the brachiopods nor the phoronids are represented by many living species, the brachiopods—which have shells and thus leave an excellent fossil record—are known to have been much more abundant during the Paleozoic and Mesozoic eras.

Brachiopods (lampshells) are solitary marine animals with a rigid shell that is divided into two parts connected by a ligament (**FIGURE 23.15**). Although brachiopods superficially resemble bivalve mollusks, shells evolved independently in the two groups. The two halves of the brachiopod shell are dorsal and ventral, rather than lateral as in bivalves. The lophophore is located within the shell. Most brachiopods are 4–6 centimeters

long. More than 26,000 fossil brachiopod species have been described, but only about 450 species survive.

The 10 known species of **phoronids** are small (5–25 cm long), sessile worms that live in muddy or sandy sediments or attached to rocky substrates. Phoronids are found in marine waters, from the intertidal zone to about 400 meters deep. They secrete tubes made of chitin, within which they live (**FIGURE 23.16**). Their cilia drive water into the top of the lophophore, and the water exits through the narrow spaces between the tentacles. Suspended food particles are caught and transported to the mouth by ciliary action. Eggs are fertilized internally, and the embryos are either released into the water or, in species

Laqueus sp.

Lophophore ring

Tentacles

FIGURE 23.15 Brachiopods The lophophore of this North Pacific brachiopod can be seen between the valves of its shell. Although its shell resembles those of the bivalve mollusks (see Figure 23.19D), it evolved independently.

(B)

Anterior

Lophophore tentacles

Mouth

The anus is outside the ring of tentacles.

Anus

Outer covering (chitinous tube)

Gut

Posterior

(A) *Phoronis mulleri*

Tentacles

FIGURE 23.16 Phoronids (A) This phoronid has two lophophores, each composed of rings of tentacles. (B) The phoronid gut is U-shaped, as seen in this generalized diagram.

FIGURE 23.17 Annelids Have Many Body Segments The segmented structure of the annelids is apparent both externally and internally. Many organs of this earthworm, a common annelid, are repeated serially.

with large embryos, retained in the parent's body, where they are brooded until they hatch.

ANNELIDS As discussed in Concept 23.1, segmentation allows an animal to move different parts of its body independently of one another, giving it much better control of its movement. A clear and obvious example of segmentation is seen in the body plan of the **annelids** (**FIGURE 23.17**; see also Figure 23.5A).

In most large annelids, the coelom in each segment is isolated from those in other segments. A separate nerve center called a ganglion (plural ganglia) controls each segment. Nerve cords that connect the ganglia coordinate their functioning. Most annelids lack a rigid external protective covering. Instead, they have a thin, permeable body wall that serves as a general surface for gas exchange. These animals are thus restricted to moist environments because they lose body water rapidly in dry air. The approximately 19,000 described annelid species live in marine, freshwater, and moist terrestrial environments.

Many annelids have one or more pairs of eyes and one or more pairs of tentacles (with which they capture prey or filter food from the surrounding water) at the anterior end of the body (**FIGURE 23.18A**). In some species, the body wall of most segments extends laterally as a series of thin outgrowths called parapodia. The parapodia function in gas exchange, and some species use them to move. Stiff bristles called setae protrude
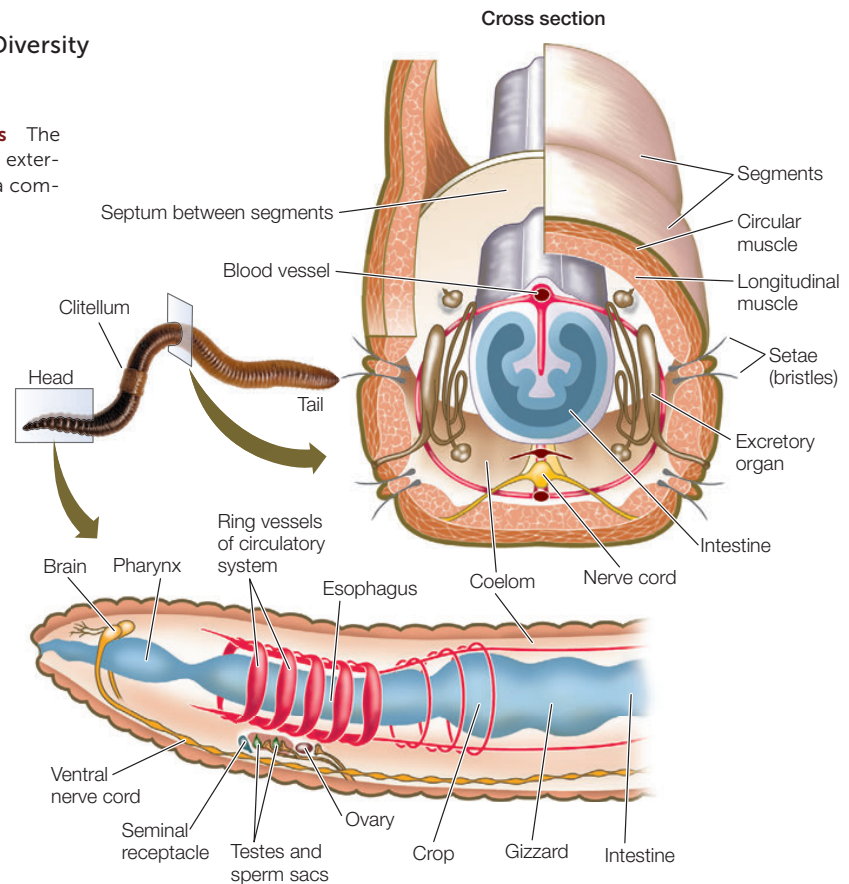
FIGURE 23.18 Diversity among the Annelids (A) "Fan worms," or "feather duster worms," are sessile marine annelids that grow in chitinous tubes, from which their tentacles extend and filter food from the water. (B) Pogonophorans live around hydrothermal vents deep in the ocean. As in fan worms, their tentacles protrude from chitinous tubes. They do not possess a digestive tract, however, and obtain most of their nutrition from endosymbiotic bacteria. (C) This hermaphroditic freshwater leech is brooding a clutch of fertilized eggs.

from each parapodium, forming temporary contact with the substrate and preventing the animal from slipping backward when its muscles contract.

Some annelids, such as the pogonophorans, secrete tubes made of chitin and other substances, in which they live (**FIG-URE 23.18B**). Pogonophorans have lost their digestive tract (they have no mouth or gut). So how do they obtain nutrition? Part of the answer is that pogonophorans can take up dissolved organic matter directly from the sediments in which they live or from the surrounding water. Much of their nutrition, however, is provided by endosymbiotic bacteria that live in a specialized organ known as the trophosome. These bacteria oxidize hydrogen sulfide and other sulfur-containing compounds, fixing carbon from methane in the process. The uptake of the hydrogen sulfide, methane, and oxygen used by the bacteria is facilitated by hemoglobin in the pogonophorans' tentacles. It is this hemoglobin that gives the tentacles their red color (see Figure 23.18B).

Oligochaetes have no parapodia or anterior tentacles, and they have only four pairs of setae bundles per segment. Earthworms—the most familiar oligochaetes—burrow in and ingest soil, from which they extract food particles. All oligochaetes are hermaphroditic; that is, each individual is both male and female. Sperm are exchanged simultaneously between two copulating individuals. Eggs and sperm are deposited outside the adult's body, in a cocoon secreted by the clitellum (see Figure 23.17). Fertilization occurs within the cocoon after it is shed, and when development is complete, miniature worms emerge and immediately begin independent life.

Leeches, like oligochaetes, lack parapodia and tentacles (**FIGURE 23.18C**). They live in freshwater, marine, and terrestrial habitats. The leech coelom is not divided into compartments, and consists of a large, fluid-filled cavity. Groups of segments at each end of the body are modified to form suckers, which serve as temporary anchors that help the leech move. With its posterior sucker attached to a substrate, the leech extends its body by contracting its circular muscles. The anterior sucker is then attached, the posterior one detached, and the leech shortens itself by contracting its longitudinal muscles.

Many leeches feed on vertebrate hosts by making an incision from which blood flows. A feeding leech secretes an anticoagulant into the wound to keep the blood flowing. For centuries, medical practitioners used leeches to treat diseases they believed were caused by an excess of blood or by "bad blood." Although most leeching practices (such as inserting a leech in a person's throat to alleviate swollen tonsils) have been abandoned, *Hirudo medicinalis* (the medicinal leech) is used medically even today to reduce fluid pressure and prevent blood clotting in damaged tissues, to eliminate pools of coagulated blood, and to prevent scarring. The anticoagulants of certain other leech species contain anesthetics and blood vessel dilators and are being studied for possible medical uses.

Go to MEDIA CLIP 23.6
Leeches Feeding on Blood
PoL2e.com/mc23.6

MOLLUSKS   The most diverse group of lophotrochozoans are the **mollusks**, with about 117,000 species that inhabit a wide array of aquatic and terrestrial environments. There are four major clades of mollusks: chitons, gastropods, bivalves, and cephalopods. Although these groups differ dramatically in morphology, they all share the same three major body components: a foot, a visceral mass, and a mantle (**FIGURE 23.19A**).

- The molluscan **foot** is a muscular structure that originally was both an organ of locomotion and a support for internal organs. In cephalopods such as squids and octopuses, the foot has been modified to form arms and tentacles borne on a head with complex sensory organs. In other groups, such as clams, the foot is a burrowing organ. In some groups the foot is greatly reduced.

- The heart and the digestive, excretory, and reproductive organs are concentrated in a centralized, internal **visceral mass**.

- The **mantle** is a fold of tissue that covers the organs of the visceral mass. The mantle secretes the hard, calcareous shell that is typical of many mollusks.

In most mollusks, the mantle extends beyond the visceral mass to form a mantle cavity. Within this cavity lie gills that are used for gas exchange. When cilia on the gills beat, they create a current of water. The gill tissue, which is highly vascularized (contains many blood vessels), takes up oxygen from the water and releases carbon dioxide. Many mollusks use their gills as filter-feeding devices. Other mollusks feed using a rasping structure known as the radula to scrape algae from rocks. In some mollusks, such as the marine cone snails, the radula has been modified into a drill or poison dart.

Except in cephalopods, molluscan blood vessels do not form a closed circulatory system. Blood and other fluids empty into a large, fluid-filled hemocoel, through which fluids move around the animal and deliver oxygen to the internal organs. Eventually the fluids reenter the blood vessels and are moved by a heart.

The approximately 1,000 living species of **chitons** (**FIGURE 23.19B**) are characterized by eight overlapping calcareous plates, surrounded by a structure known as the girdle. These plates and girdle protect the chiton's internal organs and muscular foot. The chiton body is bilaterally symmetrical, and the internal organs, particularly the digestive and nervous systems, are relatively simple. Most chitons are marine omnivores that scrape algae, bryozoans, and other organisms from rocks with their sharp radula. An adult chiton spends most of its life clinging to rock surfaces with its large, muscular, mucus-covered foot. It moves slowly by means of rippling waves of muscular contraction in the foot. Fertilization in most chitons takes place in the water, but in a few species fertilization is internal and embryos are brooded within the body.

Gastropods are the most species-rich and widely distributed mollusks, with about 85,000 living species. Snails, whelks, limpets, slugs, nudibranchs (sea slugs), and abalones are all gastropods. Most species move by gliding on their muscular foot, but in a few species—the sea butterflies and heteropods—the foot is a swimming organ with which the animal moves through open ocean waters. The only mollusks that live in terrestrial

(A) Generalized molluscan body plan

In all mollusk lineages, a **mantle** covers the internal organs of the visceral mass.

Mantle
Shell
Intestine
Stomach
Radula
Anus
Mouth
Mantle cavity
Digestive gland
Heart
Foot
Gills

(B) Chitons

Intestine
Stomach
Shell plates
Head
Radula
Anus
Mouth
Foot
Digestive gland
Gills in mantle cavity

Tonicella lineata

(C) Gastropods

Intestine
Mantle
Mantle cavity
Gill
Shell
Anus
Heart
Siphon
Salivary gland
Cephalic tentacles
Head
Stomach
Mouth
Foot

The **radula** is a unique molluscan feeding structure modified for scraping.

Achatina fulica

(D) Bivalves

Digestive gland
Shell
Stomach
Heart
Mouth
Intestine
Mantle (covers inside of shell)
Anus
Siphons
Foot
Gill
Mantle of lower shelf

Chlamys varia

(E) Cephalopods

Intestine
Shell
Beak
Head
Stomach
Arms
Mantle
Tentacle
Radula
Digestive gland
Siphon
Mantle cavity
Gill
Heart

In cephalod mollusks, the foot is modified into arms and tentacles.

Sepioteuthis lessoniana

FIGURE 23.19 Organization and Diversity of Molluscan Bodies (A) The major molluscan groups display different variations on a general body plan that includes three major components: a foot, a visceral mass of internal organs, and a mantle. In many species, the mantle secretes a calcareous shell. (B) Chitons have eight overlapping calcareous plates surrounded by a girdle. (C) Most gastropods have a single dorsal shell, into which they can retreat for protection. (D) Bivalves get their name from their two hinged shells, which can be tightly closed. (E) Cephalopods are active predators; they use their arms and tentacles to capture prey.

environments—land snails and slugs—are gastropods (**FIGURE 23.19C**). In these terrestrial species, the mantle tissue is modified into a highly vascularized lung.

Clams, oysters, scallops, and mussels are all familiar **bivalves**. The 30,000 living species are found in both marine and freshwater environments. Bivalves have a very small head and a hinged, two-part shell that extends over the sides of the body as well as the top (**FIGURE 23.19D**). Many clams use their foot to burrow into mud and sand. Bivalves feed by taking in water through an opening called an incurrent siphon and filtering food from the water with their large gills, which are also the main sites of gas exchange. Water and gametes exit through the excurrent siphon. Fertilization takes place in open water in most species.

There are about 800 living species of **cephalopods**—squids, octopuses, and nautiluses. Their excurrent siphon is modified to allow the animal to control the water content of the mantle cavity. The modification of the mantle into a device for forcibly ejecting water from the cavity through the siphon enables these animals to move rapidly by "jet propulsion" through the water. With their greatly enhanced mobility, cephalopods (which first appeared early in the Cambrian) became the major predators in the open waters of the Devonian oceans. They remain important marine predators today.

Cephalopods capture and subdue prey with their tentacles (see Figure 23.20B). As is typical of active, rapidly moving predators, cephalopods have a head with complex sensory organs, most notably eyes that are comparable to those of vertebrates in their ability to resolve images. The head is closely associated with a large, branched foot that bears the tentacles and a siphon (**FIGURE 23.19E**). The large, muscular mantle provides an external supporting structure. The gills hang in the mantle cavity. Many cephalopods have elaborate courtship behavior, which can involve striking color changes.

Many early cephalopods had a chambered external shell divided by partitions penetrated by tubes through which gases and liquids could be moved to control the animal's buoyancy. Nautiluses are the only surviving cephalopods that have such external chambered shells, although squids and cuttlefishes retain internal shells.

Shells have been lost several times among the mollusks, as in several groups of gastropods, including the slugs and nudibranchs (**FIGURE 23.20A**). These shell-less gastropods gain some protection from predation by being distasteful or toxic to many species. The often brilliant coloration of nudibranchs is aposematic, meaning it serves to warn potential predators of toxicity. Among the cephalopods, the octopuses have lost both external and internal shells (**FIGURE 23.20B**). Their lack of shells allows octopuses to escape predators by squeezing into small crevices.

Go to MEDIA CLIP 23.7
Octopuses Can Pass through Small Openings
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Ecdysozoans must shed their cuticles

The distinguishing characteristic of **ecdysozoans** is their external covering, or **cuticle**, which is secreted by the underlying epidermis (the outermost cell layer). The cuticle provides these animals with both protection and support. Once formed, however, the cuticle cannot grow. How, then, can ecdysozoans increase in size? They do so by shedding, or **molting**, the cuticle and replacing it with a new, larger one. This molting process gives the clade its name (Greek *ecdysis*, "to get out of").

Go to MEDIA CLIP 23.8
Molting a Cuticle
PoL2e.com/mc23.8

A soft-bodied arthropod from the Cambrian, fossilized in the process of molting, shows that molting evolved more than 500 million years ago (**FIGURE 23.21A**). An increasingly rich array of molecular and genetic evidence, including a set of Hox genes shared by all ecdysozoans, suggests they have a single common ancestor. Thus molting of a cuticle is a trait that may have evolved only once during animal evolution.

Before an ecdysozoan molts, a new cuticle is already forming underneath the old one. Once the old cuticle is shed, the new one expands and hardens. Until it has hardened, though,

(A) *Chromodoris kuniei*

(B) *Octopus bimaculoides*

FIGURE 23.20 Mollusks in Some Groups Have Lost Their Shells (A) Nudibranchs ("naked gills"), also called sea slugs, are shell-less gastropods. This species is brightly colored, alerting potential predators of its toxicity. (B) Octopuses have lost both the external and internal shell, which allows these cephalopods to squeeze through tight spaces.

(A)

Molted exoskeleton

Emerging animal

FIGURE 23.21 Molting, Past and Present   (A) A 500-million-year-old fossil from the Cambrian captured an individual of a long-extinct arthropod species in the process of molting, demonstrating that molting is an evolutionarily ancient trait. (B) This tailless whip scorpion has just emerged from its discarded exoskeleton and will be highly vulnerable until its new cuticle has hardened.

(B) *Heterophrynus batesi*   Molted exoskeleton

The newly emerged whip scorpion's body is still soft and vulnerable.

the animal is vulnerable to its enemies, both because its outer surface is easy to penetrate and because an animal with a soft cuticle moves slowly or not at all (**FIGURE 23.21B**).

In many ecdysozoans that have wormlike bodies, the cuticle is relatively thin and flexible. Such a cuticle offers the animal some protection but provides only modest body support. A thin cuticle allows the exchange of gases, minerals, and water across the body surface, but it restricts the animal to moist habitats. Many species of ecdysozoans with thin cuticles live in marine sediments from which they obtain prey. Some freshwater species absorb nutrients directly through their thin cuticles, as do parasitic species that live within their hosts.

The cuticles of other ecdysozoans, notably the arthropods, function as external skeletons, or **exoskeletons**. These exoskeletons are thickened by layers of protein and a strong, waterproof polysaccharide called **chitin**. An animal with a rigid, chitin-reinforced exoskeleton can neither move in a wormlike manner nor use cilia for locomotion. A hard exoskeleton also impedes the passage of oxygen and nutrients into the animal, presenting new challenges in other areas besides growth. New mechanisms of locomotion and gas exchange evolved in those ecdysozoans with hard exoskeletons.

To move rapidly, an animal with a rigid exoskeleton must have body extensions that can be manipulated by muscles. Such appendages evolved in the late Precambrian and led to the **arthropod** (Greek, "jointed foot") clade. Arthropod appendages exist in an amazing variety of forms. They serve many functions, including walking and swimming, gas exchange, food capture and manipulation, copulation, and sensory perception. Arthropods grasp food with their mouths and associated appendages and usually digest it internally. Their muscles are attached to the inside of the exoskeleton.

The arthropod exoskeleton has had a profound influence on the evolution of these animals. Encasement within a rigid body covering provides support for walking on dry land, and the waterproofing provided by the cuticle keeps the animal from dehydrating in dry air. These features have allowed arthropods to invade terrestrial environments several times.

The evolution of the diverse arthropods and their relatives will be described in greater detail in Concept 23.4. Here we describe the other major groups of ecdysozoans.

NEMATODES   **Nematodes** (roundworms) have a thick, multilayered cuticle that gives their unsegmented body its shape. As a nematode grows, it sheds its cuticle four times. Nematodes exchange oxygen and nutrients with their environment through both the cuticle and the gut, which is only one cell layer thick. Materials are moved through the gut by rhythmic contraction of a highly muscular organ, the pharynx, at the worm's anterior end. Nematodes move by contracting their longitudinal muscles.

Nematodes are probably the most abundant and universally distributed of all major animal groups. About 25,000 species have been described, but the actual number of living species may be in the millions. Many are microscopic, but the largest known nematode reaches a length of 9 meters (it is a parasite in the placentas of sperm whales). Countless nematodes live as scavengers in the upper layers of the soil, on the bottoms of lakes and streams, and in marine sediments. The topsoil of rich farmland may contain 3–9 billion nematodes per acre. A single rotting apple may contain as many as 90,000 individuals.

One soil-inhabiting nematode, *Caenorhabditis elegans*, serves as a model organism in the laboratories of many geneticists and developmental biologists. It is ideal for such research because it is easy to cultivate, matures in 3 days, and has a fixed number of body cells.

(A)

Brain

Pharynx

Ventral nerve

Excretory tube

Testis

Anus

Nematodes shed their cuticle four times.

Cuticle

Dorsal nerve

The large gut (blue) and testis (red) fill most of the body of a male *Trichinella spiralis*.

(B)
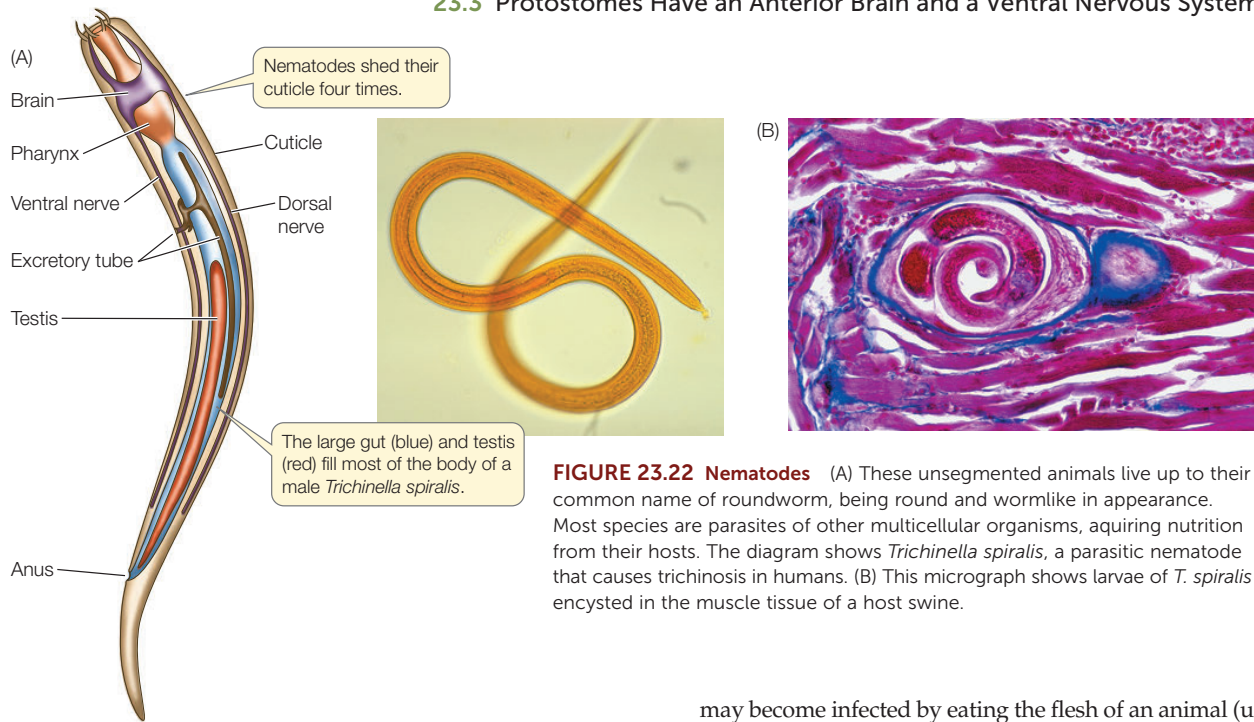
FIGURE 23.22 Nematodes (A) These unsegmented animals live up to their common name of roundworm, being round and wormlike in appearance. Most species are parasites of other multicellular organisms, aquiring nutrition from their hosts. The diagram shows *Trichinella spiralis*, a parasitic nematode that causes trichinosis in humans. (B) This micrograph shows larvae of *T. spiralis* encysted in the muscle tissue of a host swine.

Many nematodes are predators, feeding on protists and small animals (including other roundworms). Most significant to humans, however, are the many species that parasitize plants and animals (**FIGURE 23.22A**). The nematodes that parasitize humans (causing serious diseases such as trichinosis, filariasis, and elephantiasis), domesticated animals, and economically important plants have been studied intensively in an effort to find ways of controlling them.

The structure of parasitic nematodes is similar to that of free-living species, but the life cycles of many parasitic species have special stages that facilitate the transfer of individuals among hosts. *Trichinella spiralis*, the species that causes the human disease trichinosis, has a relatively simple life cycle. A person

may become infected by eating the flesh of an animal (usually a pig) that has *Trichinella* larvae encysted in its muscles (**FIGURE 23.22B**). The larvae are activated in the person's digestive tract, emerge from their cysts, and attach to the intestinal wall, where they feed. Later they bore through the intestinal wall and are carried in the bloodstream to muscles, where they form new cysts. If present in great numbers, these cysts can cause severe pain or death.

HORSEHAIR WORMS   About 350 species of the unsegmented **horsehair worms** have been described. As their name implies, these animals are extremely thin in diameter; they range from a few millimeters up to a meter in length. Most adult horsehair worms live in fresh water among the leaf litter and algal mats that accumulate near the shores of streams and ponds. A few species live in damp soil.

APPLY THE CONCEPT

There are two major groups of protostomes

The table shows a small sample of amino acid residues that have been used to reconstruct the relationships of some major animal groups. (The full dataset includes data on 11,234 amino acid positions across 77 species of animals.)

1. Construct a phylogenetic tree of these seven animals using the parsimony method (see Chapter 16). Use the sponge as your outgroup to root the tree. Assume that all changes among amino acids are equally likely.

2. How many changes (from one amino acid residue to another) occur along each branch on your tree?

3. Which branch on your tree represents the eumetazoans?

4. The protostomes? The lophotrochozoans? The ecdysozoans? The deuterostomes?

Animal	AMINO ACID POSITION											
	1	2	3	4	5	6	7	8	9	10	11	12
Sponge	P	P	M	S	V	R	Q	N	L	V	I	L
Clam	E	A	M	R	I	K	L	S	I	V	I	L
Earthworm	E	P	M	R	I	K	L	S	I	V	M	L
Tardigrade	E	K	M	R	I	R	L	N	L	V	L	L
Fruit fly	E	K	M	R	I	S	L	D	L	V	L	L
Sea urchin	E	P	M	R	V	R	Q	N	L	T	V	K
Human	E	P	I	R	V	R	Q	N	L	T	V	K

An adult horsehair worm exits the wood cricket it parasitized during its larval development.

FIGURE 23.23 Horsehair Worm Larvae Are Parasitic The larvae of this horsehair worm (*Paragordius tricuspidatus*) can manipulate its host's behavior. The hatching worm causes the cricket to jump into water, where the worm will continue its life cycle as a free-living adult. The insect, having delivered its parasitic burden, drowns.

Horsehair larvae are internal parasites of freshwater crayfishes and of terrestrial and aquatic insects (**FIGURE 23.23**). An adult horsehair worm has no mouth, and its gut is greatly reduced and probably nonfunctional. Some species feed only as larvae, absorbing nutrients from their hosts across the body wall. But other species continue to grow and shed their cuticles even after they have left their hosts, suggesting that some adult worms may be able to absorb nutrients from their environment.

SMALL MARINE CLADES There are several small, relatively poorly known groups of benthic marine ecdysozoans. The 20 species of **priapulids** are cylindrical, unsegmented, wormlike animals with a three-part body plan consisting of a proboscis, trunk, and caudal appendage ("tail"). It should be clear from their appearance why they were named after the Greek fertility god Priapus (**FIGURE 23.24A**). The 180 species of **kinorhynchs** live in marine sands and muds and are virtually microscopic; no kinorhynchs are longer than 1 millimeter. Their bodies are divided into 13 segments, each with a separate cuticular plate (**FIGURE 23.24B**). The minute (less than 1 mm long) **loriciferans** were not discovered until 1983. About 100 living species are known to exist, although only about 30 species have been described. The body is divided into a head, neck, thorax, and abdomen and is covered by six plates, from which the loriciferans get their name (Latin *lorica*, "corset"; **FIGURE 23.24C**).

CHECKpoint CONCEPT **23.3**

✓ How does an animal's body covering influence the way it breathes, feeds, and moves?

✓ Why are most annelids restricted to moist environments?

✓ Briefly describe how the basic body organization of mollusks has been modified to yield a wide diversity of animals.

✓ What are three ways in which nematodes have a significant impact on humans?

We will turn now to the arthropods. Members of the four arthropod subgroups not only dominate the ecdysozoan clade but are also among the most diverse animals on Earth.

FIGURE 23.24 Benthic Marine Ecdysozoans Members of these groups are marine bottom-dwellers. (A) Most priapulid species live in burrows on the ocean floor, extending the proboscis for feeding. (B) Kinorhynchs are virtually microscopic. The cuticular plates that cover their bodies are molted periodically. (C) Six cuticular plates form a "corset" around the minute loriciferan body.

(A) *Priapulus caudatus* — Proboscis, Trunk, Caudal appendage ("tail")

(B) *Pycnophyes* sp. — Cuticular plates

(C) *Nanaloricus mysticus* — Proboscis, Spines, Cuticular plates

Arthropods Are Diverse and Abundant Animals

Arthropods and their relatives are ecdysozoans with paired appendages. Arthropods are an extremely diverse group of animals in numbers of species. Furthermore, the number of individual arthropods alive at any one time is estimated to be about 10^{18}, or a billion billion. Among the animals, only the nematodes are thought to exist in greater numbers.

Several key features have contributed to the success of the arthropods. Their bodies are segmented, and their muscles are attached to the inside of their rigid exoskeletons. Each segment has muscles that operate that segment and the jointed appendages attached to it. Jointed appendages permit complex movements, and different appendages are specialized for different functions. Encasement of the body within a rigid exoskeleton provides the animal with support for walking in the water or on dry land and provides some protection against predators. The waterproofing provided by chitin keeps the animal from dehydrating in dry air.

Representatives of the four major arthropod groups living today are all species-rich: the chelicerates (including the arachnids—spiders, scorpions, mites, and their relatives), myriapods (millipedes and centipedes), crustaceans (including shrimps, crabs, and barnacles), and hexapods (insects and their relatives). Phylogenetic relationships among arthropod groups are currently being reexamined in light of a wealth of new information, much of it based on gene sequences. These studies suggest that the chelicerates are the sister group to the remaining arthropods, and that the crustaceans may be paraphyletic (some crustaceans are more closely related to hexapods than to other crustaceans). There is strong support for the monophyly of arthropods as a whole.

The jointed appendages of arthropods gave the clade its name, from the Greek words *arthron*, "joint," and *podos*, "foot" or "limb." Arthropods evolved from ancestors with simple, unjointed appendages. The exact forms of those ancestors are unknown, but some arthropod relatives with segmented bodies and unjointed appendages survive today. Before we describe the modern arthropods, we will discuss those arthropod relatives.

Arthropod relatives have fleshy, unjointed appendages

Until fairly recently, biologists debated whether the **velvet worms** (onychophorans) were more closely related to annelids or arthropods, but molecular evidence clearly links them to the arthropods. Indeed, with their soft, fleshy, unjointed, claw-bearing legs, velvet worms may be similar in appearance to the arthropod ancestor (**FIGURE 23.25A**). The 180 species of velvet worms live in leaf litter in humid tropical environments. Their soft, segmented bodies are covered by a thin, flexible cuticle that contains chitin. They use their fluid-filled body cavities as hydrostatic skeletons. Fertilization is internal, and large, yolky eggs are brooded within the female's body.

Tardigrades (water bears) also have fleshy, unjointed legs and use their fluid-filled body cavities as hydrostatic skeletons (**FIGURE 23.25B**). Tardigrades are tiny (0.5–1.5 mm long) and

(A) *Macroperipatus torquatus*

(B) *Macrobiotus sapiens*

FIGURE 23.25 Arthropod Relatives with Unjointed Appendages (A) Velvet worms have unjointed legs and use the body cavity as a hydrostatic skeleton. (B) Tardigrades can be abundant on the wet surfaces of mosses and plants and in temporary pools of water.

lack both a circulatory system and gas exchange organs. The 1,200 known species live in marine sands and on temporary water films on plants, as well as in ephemeral pools. When these films and shallow pools dry out, the animals also lose water and shrink to small, barrel-shaped objects that can survive for at least a decade in a dormant state. Tardigrades have been found in densities as high as 2 million per square meter of moss.

Chelicerates are characterized by pointed, nonchewing mouthparts

In the **chelicerates**, the head bears two pairs of pointed appendages modified to form mouthparts, called chelicerae, which are used to grasp (rather than chew) prey. In addition, many chelicerates have four pairs of walking legs. The 114,000 described species are placed in three major clades: sea spiders, horseshoe crabs, and arachnids.

The sea spiders (pycnogonids) are a poorly known group of about 1,000 marine species (**FIGURE 23.26A**). Most are small, with leg spans less than 1 cm, but some deep-sea species have leg spans up to 60 cm. A few sea spiders eat algae, but most are carnivorous, eating a variety of small invertebrates.

There are four living species of horseshoe crabs, but many close relatives are known from fossils. Horseshoe crabs, which have changed very little morphologically during their long

(A) *Pseudopallene* sp.

(B) *Limulus polyphemus*

FIGURE 23.26 Two Small Chelicerate Groups (A) Although they are not spiders, it is easy to see why sea spiders were given their common name. (B) Horseshoe crabs are an ancient group that has changed very little in morphology over time.

fossil history, have a large horseshoe-shaped covering over most of the body. They are common in shallow waters along the eastern coast of North America and the southern and eastern coasts of Asia, where they scavenge and prey on bottom-dwelling animals. Periodically they crawl into the intertidal zone in large numbers to mate and lay eggs (**FIGURE 23.26B**).

Arachnids are abundant in terrestrial environments. Most arachnids have a simple life cycle in which miniature adults hatch from internally fertilized eggs and begin independent lives almost immediately. Some arachnids retain their eggs during development and give birth to live young.

The most species-rich and abundant arachnids are the spiders, scorpions, harvestmen, mites, and ticks (**FIGURE 23.27**). More than 60,000 described species of mites and ticks live in soil, leaf litter, mosses, and lichens, under bark, and as parasites of plants and animals. Mites are vectors for wheat and rye mosaic viruses and cause mange in domestic animals as well as skin irritation in humans.

Spiders, of which about 50,000 species have been described, are important terrestrial predators with hollow chelicerae, which they use to inject venom into their prey. Some species have excellent

vision that facilitates elaborate courtship displays and allows the spiders to hunt their prey. Others spin elaborate webs made of protein threads in which they snare prey. The threads are produced by modified abdominal appendages connected to internal glands that secrete the proteins, which solidify on contact with air. The webs of different groups of spiders are strikingly varied, and this variation enables the spiders to position their snares in many different environments for many different types of prey.

Mandibles and antennae characterize the remaining arthropod groups

The remaining three arthropod groups—the myriapods, crustaceans, and hexapods—have mouthparts composed of mandibles rather than chelicerae, so they are together called **mandibulates**.

FIGURE 23.27 Arachnid Diversity
(A) Known for their web-spinning abilities, spiders are expert predators. (B) A desert scorpion assumes the animal's aggressive attack position. These arachnids are fearsome predators, and their sting can be dangerous to humans. (C) Harvestmen, also called daddy longlegs, are scavengers. (D) Mites include many free-living species as well as blood-sucking, external parasites.

Go to MEDIA CLIP 23.9
Elaboration of Courtship
Displays: Even Spiders Twerk
PoL2e.com/mc23.9

(A) *Lycosa* sp.

(B) *Androctonus* sp.

(C) *Leiobunum rotundum*

(D) *Brevipalpus phoenicis*

(A) *Scolopendra hardwicki*

FIGURE 23.28 Myriapods   (A) Centipedes have modified appendages that function as poisonous fangs for capturing active prey. They have one pair of legs per segment. (B) Millipedes, which are scavengers and plant eaters, have smaller jaws and legs than centipedes do. They have two pairs of legs per segment.

(B) *Polydesmus* sp.

Mandibles are often used for chewing as well as for biting and holding food. Another distinctive characteristic of the mandibulates is the presence of sensory antennae on the head.

The **myriapods** comprise the centipedes, millipedes, and their close relatives. Centipedes and millipedes have a well-formed head with the mandibles and antennae characteristic of mandibulates. Their distinguishing feature is a long, flexible, segmented trunk that bears many pairs of legs (**FIGURE 23.28**). Centipedes, which have one pair of legs per segment, prey on insects and other small animals. In millipedes, two adjacent segments are fused so that each fused segment has two pairs of legs. Millipedes are detritivores. More than 3,000 species of centipedes and 9,000 species of millipedes have been described, and many more species probably remain unknown. Although most myriapods are less than a few centimeters long, some tropical and subtropical species are ten times that size.

Crustaceans are the dominant marine arthropods today, and they are also common in freshwater and some terrestrial environments. The most familiar crustaceans are the shrimps, lobsters, crayfishes, and crabs (all decapods; **FIGURE 23.29A**) and the pillbugs (isopods; **FIGURE 23.29B**). Additional species-rich groups include the amphipods, ostracods, copepods

(A) *Graspus graspus*

(B) *Armadillidium vulgare*

(E) *Lepas anatifera*

(C) *Cyclops strenuus*

(D) *Triops longicaudatus*
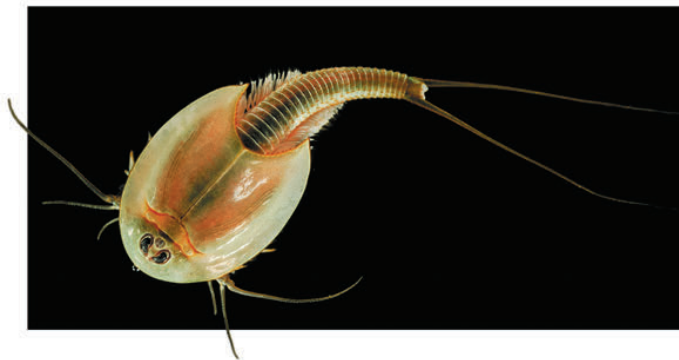
FIGURE 23.29 Crustacean Diversity   (A) This decapod crustacean is a "Sally Lightfoot" crab from the Galápagos. (B) This pillbug, a terrestrial isopod, can roll into a tight ball when threatened. (C) Minute copepods such as this one are an important link in aquatic food chains. (D) Tadpole shrimp are branchiopods, not to be confused with the decapod crustaceans commonly called shrimp, or with the brachiopods seen in Figure 23.15. (E) Barnacles are sessile, attaching to a substrate by their muscular stalks and feeding with retractable feeding appendages (the delicate, tentacle-like structures seen here).

(**FIGURE 23.29C**), and branchiopods (**FIGURE 23.29D**), all of which are found in freshwater and marine environments.

Barnacles are unusual crustaceans that are sessile as adults (**FIGURE 23.29E**). Adult barnacles look more like mollusks than like other crustaceans, but as the zoologist Louis Agassiz remarked more than a century ago, a barnacle is "nothing more than a little shrimp-like animal, standing on its head in a limestone house and kicking food into its mouth."

Go to MEDIA CLIP 23.10
Barnacles Feeding
PoL2e.com/mc23.10

Most of the 67,000 described species of crustaceans have a body that is divided into three regions: head, thorax, and abdomen (**FIGURE 23.30A**). The segments of the head are fused together, and the head bears five pairs of appendages. Each of the multiple thoracic and abdominal segments usually bears one pair of appendages. The appendages on different parts of the body are specialized for different functions, such as gas exchange, chewing, capturing food, sensing, walking, and swimming. In many species, a fold of the exoskeleton, the carapace, extends dorsally and laterally back from the head to cover and protect some of the other segments.

The fertilized eggs of most crustacean species are attached to the outside of the female's body, where they remain during their early development. At hatching, the young of some species are released as larvae; those of other species are released as juveniles that are similar in form to the adults. Still other species release eggs into the water or attach them to an object in the environment.

More than half of all described species are insects

During the Devonian period, more than 400 million years ago, some mandibulates colonized terrestrial environments. Of the several groups (including some crustacean isopods and decapods) that successfully colonized the land, none is more prominent today than the six-legged **hexapods**: the insects and their relatives. Insects are abundant and diverse in terrestrial and freshwater environments. Only a few insects live in salt water.

The wingless relatives of the insects—the springtails, two-pronged bristletails, and proturans—are probably the most similar of living forms to insect ancestors. These insect relatives have a simple life cycle; they hatch from eggs as miniature adults. They differ from insects in having internal mouthparts. Springtails can be extremely abundant (up to 200,000 per square meter) in soil, leaf litter, and on vegetation and are the most abundant hexapods in the world in terms of number of individuals (rather than number of species).

More than 1 million of the 1.8 million described species of living organisms are insects. As we discussed at the beginning of this chapter, biologists have estimated that many millions of insect species remain to be discovered. Like crustaceans, insects have a body with three regions—head, thorax, and abdomen. They have a single pair of antennae on the head and three pairs of legs attached to the thorax. In most groups of insects, the thorax also bears two pairs of wings. Unlike other arthropods, insects have no appendages associated with their abdominal segments (**FIGURE 23.30B**).

Insects can be distinguished from springtails and other hexapods by their external mouthparts and by antennae that contain a motion-sensitive receptor called Johnston's organ. In addition, insects have a derived mechanism for gas exchange in air: a system of air sacs and tubular channels called tracheae (singular *trachea*) that extend from external openings called spiracles inward to tissues throughout the body (see Figure 31.10). Insects use nearly all species of plants and many species of animals as food.

TABLE 23.2 lists the major insect groups. Two groups—the jumping bristletails and silverfish—are wingless and have
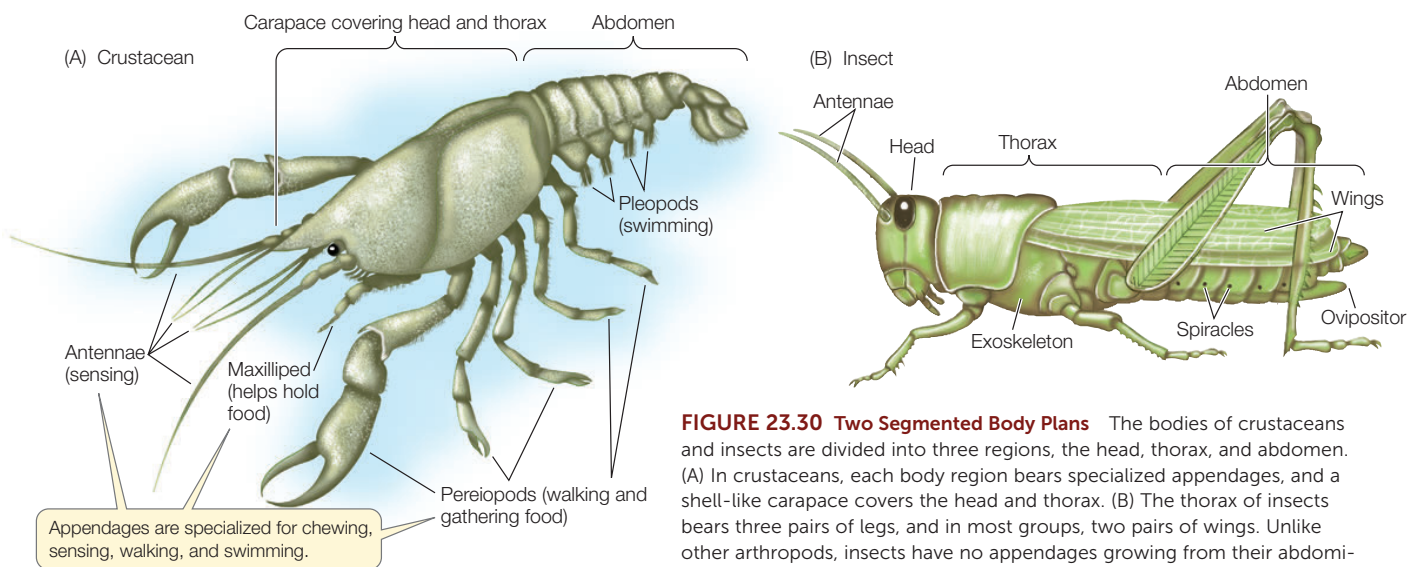
FIGURE 23.30 Two Segmented Body Plans The bodies of crustaceans and insects are divided into three regions, the head, thorax, and abdomen. (A) In crustaceans, each body region bears specialized appendages, and a shell-like carapace covers the head and thorax. (B) The thorax of insects bears three pairs of legs, and in most groups, two pairs of wings. Unlike other arthropods, insects have no appendages growing from their abdominal segments.

TABLE 23.2   The Major Insect Groups[a]

Group	Approximate number of described living species
Jumping bristletails (Archaeognatha)	515
Silverfish (Thysanura)	560
PTERYGOTE (WINGED) INSECTS (PTERYGOTA)	
Mayflies (Ephemeroptera)	3,250
Dragonflies and damselflies (Odonata)	5,900
Neopterans (Neoptera)[b]	
Ice-crawlers (Grylloblattodea)	35
Gladiators (Mantophasmatodea)	15
Stoneflies (Plecoptera)	3,750
Webspinners (Embioptera)	465
Angel insects (Zoraptera)	40
Earwigs (Dermaptera)	2,000
Grasshoppers and crickets (Orthoptera)	24,000
Stick insects (Phasmida)	3,000
Cockroaches (Blattodea)	4,650
Termites (Isoptera)	2,700
Mantids (Mantodea)	2,400
Booklice and barklice (Psocoptera)	5,750
Thrips (Thysanoptera)	6,000
Lice (Phthiraptera)	5,100
True bugs, cicadas, aphids, leafhoppers (Hemiptera)	104,000
Holometabolous neopterans (Holometabola)[c]	
Ants, bees, wasps (Hymenoptera)	117,000
Beetles (Coleoptera)	388,000
Twisted-wing parasites (Strepsiptera)	610
Lacewings, ant lions, mantidflies (Neuropterida)	5,900
Dobsonflies, alderflies, fishflies (Megaloptera)	350
Snakeflies (Raphidoptera)	250
Scorpionflies (Mecoptera)	760
Fleas (Siphonaptera)	2,100
True flies (Diptera)	155,000
Caddisflies (Trichoptera)	14,300
Butterflies and moths (Lepidoptera)	158,000

[a]The hexapod relatives of insects include the springtails (Collembola; 3,000 spp.), two-pronged bristletails (Diplura; 600 spp.), and proturans (Protura; 10 spp.). All are wingless and have internal mouthparts.
[b]Neopteran insects can tuck their wings close to their bodies.
[c]Holometabolous insects are neopterans that undergo complete metamorphosis.

simple life cycles, like the springtails and other close insect relatives. The remaining groups are all pterygote insects. **Pterygotes** have two pairs of wings, except in some groups where one or both pairs of wings have been secondarily lost. Secondarily wingless groups include the parasitic lice and fleas, some beetles, and the worker individuals in many ants.

Hatchling pterygotes do not look like adults, and they undergo substantial changes at each molt. The immature stages of insects between molts are called **instars**. A substantial change that occurs between one developmental stage and another is called **metamorphosis**. If the changes between its instars are gradual, an insect is said to have **incomplete metamorphosis**. If the change between at least some instars is dramatic, an insect is said to have **complete metamorphosis**. In many insects with complete metamorphosis, the different life stages are specialized for different environments and use different food sources. In many species, the larvae are adapted for feeding and growing, whereas the adults are specialized for reproduction and dispersal.

Go to MEDIA CLIP 23.11
Complete Metamorphosis
PoL2e.com/mc23.11

LINK
Insect metamorphosis is under the control of hormones, as described in **Concept 35.5**

Pterygote insects were the first animals in evolutionary history to achieve the ability to fly. Flight opened up many new lifestyles and feeding opportunities that only the insects could exploit, and it is almost certainly one of the reasons for the remarkable numbers of insect species and individuals, and for their unparalleled evolutionary success.

Molecular data suggest that insects began to diversify about 450 million years ago, about the time of the appearance of the first land plants (although earliest known fossil insects are only about 400 million years old). The earliest hexapods evolved in a terrestrial environment that lacked any similar organisms, which in part accounts for their remarkable success. But the success of the insects is also due to their wings. Homologous genes control the development of insect wings and crustacean appendages, suggesting that the insect wing evolved from a dorsal branch of a crustacean-like limb:
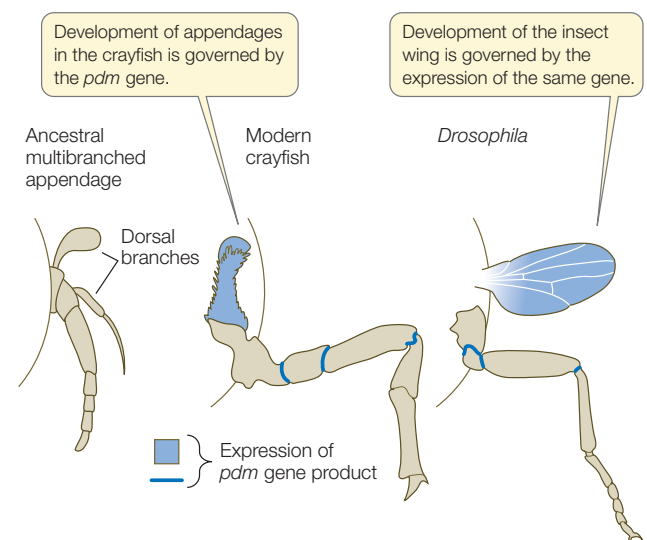
APPLY THE CONCEPT

More than half of all described species are insects

The following data were used by entomologist Terry Erwin to estimate the undescribed diversity of insects. Review the design of Erwin's experiment in the opening story of this chapter. Then use Erwin's data to answer the questions and consider how changes in the assumptions may affect the estimates.[a]

Approximate number of beetle species collected from *Luehea seemannii* trees:	1,200
Estimated number of host-specific beetles in this sample:	163
Number of species of canopy trees per hectare of forest:	70
Percentage of beetle species living in canopy (as opposed to ground-dwelling species):	75%
Percentage of beetles among all insect species:	40%

[a]T. L. Erwin. 1982. *Coleopterists Bulletin* 36(l): 74–75; T. L. Erwin and J. C. Scott. 1980. *Coleopterists Bulletin* 34(3): 305–322.

1. From the data above, estimate the number of insect species in an average hectare of Panamanian forest. Assume that the data for beetles on *L. seemannii* are representative of the other tree species, and that all the species of beetles that are *not* host-specific were collected in the original sample. Remember to sum your estimates of the number of (a) host-specific beetle species in the forest canopy; (b) non-host-specific beetle species in the forest canopy; (c) beetle species on the forest floor; and (d) species of all insects other than beetles.

2. Use the following information to estimate the number of insect species on Earth. There are about 50,000 species of tropical forest trees. Assume that the data for beetles on *L. seemannii* are representative for other species of tropical trees, and calculate the number of host-specific beetles found on these trees. Add an estimated 1 million species of beetles that are expected across different species of trees (including temperate regions). Estimate the number of ground-dwelling beetle species based on the percentage used in question 1. Now estimate the number of species of insects found worldwide, based on the percentage of beetles among all insect species.

3. The estimates in questions 1 and 2 are based on many assumptions. Do you think these assumptions are reasonable? Why or why not? Would you argue for a different set of assumptions? How do you think these changes in assumptions would affect your calculations? Can you think of ways to test your assumptions?

The dorsal limb branch of crustaceans is used for gas exchange. Thus the insect wing probably evolved from a gill-like structure that had a gas exchange function.

The adults of most flying insects have two pairs of stiff, membranous wings attached to the thorax. True flies, however, have one pair of wings and a pair of stabilizers called haltares. In winged beetles, one pair of wings—the forewings—forms heavy, hardened wing covers. Flying insects are important pollinators of flowering plants.

Two groups of pterygotes, the mayflies and dragonflies (**FIGURE 23.31A**), cannot fold their wings against their bodies. This is the ancestral condition for pterygote insects, and the mayflies and dragonflies are not closely related to one another. Members of these groups have predatory or herbivorous aquatic larvae that transform into flying adults after they crawl out of the water. Dragonflies (and their relatives the damselflies) are active predators as adults. In contrast, adult mayflies lack functional digestive tracts. Mayflies live only about a day, just long enough to mate and lay eggs.

All other pterygote insects—the **neopterans**—can tuck their wings out of the way upon landing and crawl into crevices and other tight places. Some neopteran groups undergo incomplete metamorphosis, so hatchlings of these insects are sufficiently similar in form to adults to be recognizable. Examples include the grasshoppers (**FIGURE 23.31B**), roaches, mantids, stick insects, termites, stoneflies, earwigs, thrips, true bugs (**FIGURE 23.31C**), aphids, cicadas, and leafhoppers. They acquire adult organ systems, such as wings and compound eyes, gradually through several juvenile instars.

More than 80 percent of all insects belong to a subgroup of the neopterans called the **holometabolous** insects (see Table 23.2), which undergo complete metamorphosis (**FIGURE 23.31D**). The many species of beetles account for almost half of this group (**FIGURE 23.31E**). Also included are lacewings and their relatives; caddisflies; butterflies and moths (**FIGURE 23.31F**); sawflies; true flies (**FIGURE 23.31G**); and bees, wasps, and ants, some species of which display unique and highly specialized social behaviors (**FIGURE 23.31H**).

CHECKpoint   CONCEPT 23.4

✓ What features have contributed to making arthropods among the most abundant animals on Earth, both in number of species and number of individuals?

✓ Describe the difference between incomplete and complete metamorphosis.

✓ Can you think of some possible reasons why there are so many species of insects?

The majority of Earth's animal species are protostomes, so it is not surprising that the protostome groups display a huge variety of different body plans and other characteristics. We will now consider the diversity of the deuterostomes, a group that contains far fewer species than the protostomes but which is even more intensively studied and, not incidentally, is the group to which humans belong.

(A) *Libellula depressa*, Odonata

(B) *Brachystola magna*, Orthoptera

(C) *Graphosoma lineatum*, Hemiptera

(D) *Gumaga* sp., Trichoptera

(E) *Cetonia aurata*, Coleoptera

(F) *Papilio machaon*, Lepidoptera

(G) *Poecilanthrax willistoni*, Diptera

(H) *Mischocyttarus flavitarsis*, Hymenoptera

FIGURE 23.31 Diverse Winged Insects   (A) Unlike most flying insects, a dragonfly cannot fold its wings over its back. (B) Orthopteran insects such as grasshoppers undergo several larval molts (instars), but the juveniles resemble small adults (incomplete metamorphosis). (C) Hemipterans are "true" bugs. (D–H) Holometabolous insects undergo complete metamorphosis. (D) A larval caddisfly (right) emerges from its case constructed from silk and sand. (E) Coleoptera is the largest insect group; beetles such as this rose chafer account for more than half of all holometabolous species. (F) The swallowtail butterfly is found in most parts of North America. (G) This bee fly is a true fly. Although bee flies cannot sting, most potential predators avoid them because of their resemblance to bees. (H) This western paper wasp is a hymenopteran, a group in which most members display social behaviors.

CONCEPT
23.5

Deuterostomes Include Echinoderms, Hemichordates, and Chordates

It may surprise you to learn that you and a sea urchin are both deuterostomes. Adult sea stars, sea urchins, and sea cucumbers—the most familiar echinoderms—look so different from adult vertebrates (fishes, frogs, lizards, birds, and mammals) that it is difficult to believe all these animals are closely related. Two major pieces of evidence indicate that the deuterostomes share a common ancestor not shared with the protostomes:

- Deuterostomes share a pattern of early development in which the mouth forms at the opposite end of the embryo from the blastopore, and the blastopore develops into the anus (this is opposed to the protostomes, in which the blastopore becomes the mouth).

- Recent phylogenetic analyses of the DNA sequences of many different genes offer strong support for the shared evolutionary relationships of deuterostomes.

Note that neither of the above factors is apparent in the morphology of the adult animals.

Although there are far fewer species of deuterostomes than of protostomes (see Table 23.1), the deuterostomes are of special interest because they include many large animals—including humans—that strongly influence the characteristics of ecosystems. Many deuterostome species have been intensively studied in all fields of biology. Complex behaviors are especially well developed among some deuterostomes and are a vast and fascinating field of study in themselves (see Chapter 40).

There are three major clades of living deuterostomes:

• **Echinoderms**: sea stars, sea urchins, and their relatives
• **Hemichordates**: acorn worms and pterobranchs
• **Chordates**: sea squirts, lancelets, and vertebrates

All deuterostomes are triploblastic and coelomate (see Figure 23.4C). Skeletal support features, where present, are internal rather than external. Some species have segmented bodies, but the segments are less obvious than those of annelids and arthropods.

Go to ANIMATED TUTORIAL 23.3
An Overview of the Deuterostomes
PoL2e.com/at23.3

The earliest deuterostomes were bilaterally symmetrical, segmented animals with a pharynx that had slits through which water flowed. Echinoderms evolved their adult forms with unique symmetry (in which the body parts are arranged along five radial axes) much later, whereas other deuterostomes retained the ancestral bilateral symmetry.

The echinoderms and hemichordates (together known as **ambulacrarians**) have a bilaterally symmetrical, ciliated larva (**FIGURE 23.32A**). Adult hemichordates also are bilaterally symmetrical. Echinoderms, however, undergo a radical change in form as they develop into adults (**FIGURE 23.32B**), changing from a bilaterally symmetrical larva to an adult with **pentaradial symmetry** (symmetry in five or multiples of five). As is typical of animals with radial symmetry, echinoderms have no head, and they move equally well (but usually slowly) in many directions. Rather than having an anterior–posterior (head–tail) and dorsal–ventral (back–belly) body organization, echinoderms have an oral side (containing the mouth) and an opposite aboral side (containing the anus).

Echinoderms have unique structural features

About 13,000 species of echinoderms in 23 major groups have been described from fossil remains. They are probably only a small fraction of those that actually lived. Only 6 of the 23 major groups known from fossils are represented by species that survive today. Many clades of echinoderms became extinct during the periodic mass extinctions that have occurred throughout Earth's history (see Table 18.1). Nearly all of the 7,500 extant species of echinoderms live only in marine environments.

In addition to having pentaradial symmetry, adult echinoderms have two unique structural features. One is a system of calcified internal plates covered by thin layers of skin and some muscles. The calcified plates of most echinoderms are thick, and they fuse inside the entire body, forming an internal skeleton. The other unique feature is a **water vascular system**, a network of water-filled canals leading to extensions called **tube feet**. This system functions in gas exchange, locomotion, and feeding (see Figure 23.32B).

FIGURE 23.32 Bilaterally Symmetrical Echinoderm Larvae become Radially Symmetrical Adults (A) The ciliated larva of a sea star has bilateral symmetry. Hemichordates have a similar larval form. (B) The radially symmetrical adult sea star displays the canals and tube feet of the echinoderm water vascular system, as well as the calcified internal skeleton. The body's orientation is oral–aboral rather than anterior–posterior.

(A) Sea star larva (bilateral symmetry)

Ciliated arms

The sea star larva moves through the water by beating its cilia.

Each arm has a full complement of organs. This arm has been drawn with the digestive glands removed to show the organs lying below.

(B) Adult sea star (pentaradial symmetry)

The anus is on the **aboral** (top-facing) surface.

Madreporite

Gonad

Tube feet

Radial canal

Ring canal

Stomach

Digestive glands

The mouth is on the **oral** surface, facing the seafloor.

Skin gill

Coelom

Digestive gland

Gonad

Ampulla

Suction cup

Calcareous plate

Water canal

(A) *Comanthina schlegeli*

(B) *Strongylocentrotus purpuratus*

(C) *Pseudocolochirus* sp.

(D) *Asterias rubens*

(E) *Ophiothrix spiculata*

FIGURE 23.33 Echinoderm Diversity (A) The flexible arms of this feather star are clearly visible. (B) Sea urchins are important grazers on algae in the intertidal zones of the world's oceans. (C) Sea cucumbers are unique among echinderms in having an anterior–posterior rather than an oral–aboral orientation of the mouth and anus. (D) Sea stars are important predators on bivalve mollusks such as mussels and clams. Suction tips on its tube feet allow a sea star to grasp both shells of the bivalve and pull them open. (E) The arms of the brittle star are composed of hard but jointed plates.

Members of one major extant clade, the crinoids (sea lilies and feather stars), were more abundant and species-rich 300–500 million years ago than they are today. There are some 80 described living sea lily species, most of which are sessile organisms attached to a substrate by a stalk. Feather stars (**FIGURE 23.33A**) grasp the substrate with flexible appendages that allow for limited movement. About 600 living species of feather stars have been described.

Unlike the crinoids, most of the other surviving echinoderms are motile. The two main groups of motile echinoderms are the echinozoans (sea urchins and sea cucumbers; **FIGURE 23.33B,C**) and asterozoans (sea stars and brittle stars; **FIGURE 23.33D,E**).

The tube feet of the different echinoderm groups have been modified in a great variety of ways to capture prey. Sea lilies, for example, feed by orienting their arms in passing water currents. Food particles strike and stick to their tube feet, which are covered with mucus-secreting glands. The tube feet transfer food particles to grooves in the arms, where ciliary action carries the particles to the mouth. Sea cucumbers capture food with their anterior tube feet, which are modified into large,

feathery, sticky tentacles that can be protruded from the mouth. Periodically, a sea cucumber withdraws the tentacles, wipes off the material that has adhered to them, and digests it.

Many sea stars use their tube feet to capture large prey such as annelids, gastropod and bivalve mollusks, small crustaceans such as crabs, and fishes. With hundreds of tube feet acting simultaneously, a sea star can grasp a bivalve in its arms, anchor the arms with its tube feet, and by steady contraction of the muscles in its arms, gradually exhaust the muscles the bivalve uses to keep its shell closed (see Figure 23.33D). To feed on a bivalve, a sea star can push its stomach out through its mouth and then through the narrow space between the two halves of the bivalve's shell. The sea star's stomach then secretes enzymes that digest the prey.

Go to MEDIA CLIP 23.12
Sea Star Feeding on a Bivalve
PoL2e.com/mc23.12

Most sea urchins eat algae, which they catch with their tube feet from the plankton or scrape from rocks with a complex rasping structure. Most of the 2,000 species of brittle stars ingest particles from the upper layers of sediments and assimilate the organic material from them, although some species filter suspended food particles from the water, and others capture small animals.

Hemichordates are wormlike marine deuterostomes

The roughly 120 species of hemichordates—acorn worms and pterobranchs—have a body organized in three major parts, consisting of a proboscis, a collar (which bears the mouth), and

(A)

Saccoglossus kowalevskii

(B)
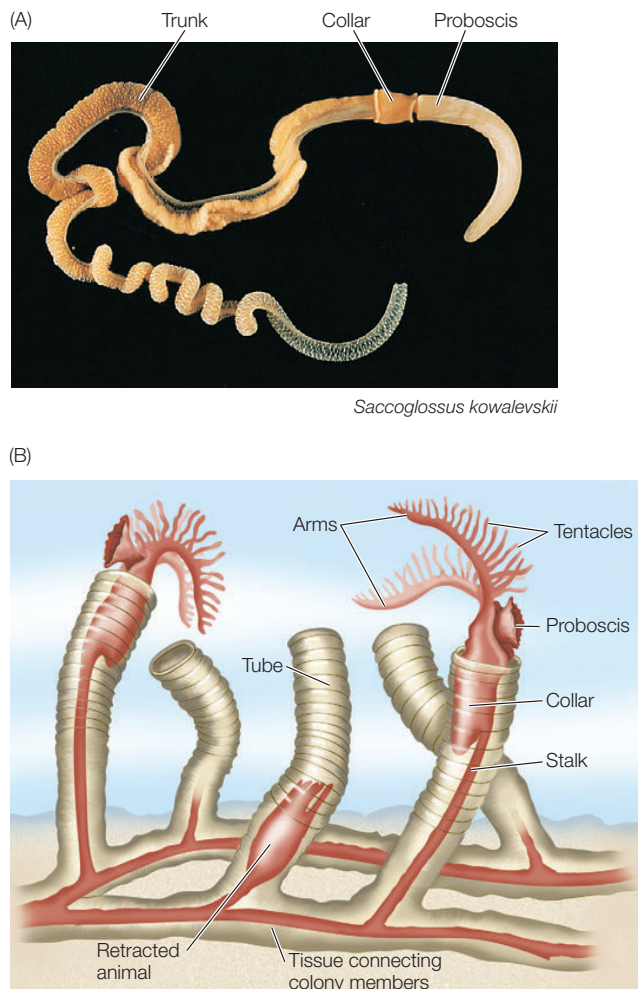
FIGURE 23.34 Hemichordates (A) The proboscis of an acorn worm is modified for burrowing. (B) The structure of a colonial pterobranch.

a trunk (which contains the other body parts). The 90 known species of acorn worms range up to 2 meters in length (**FIGURE 23.34A**). They live in burrows in muddy and sandy marine sediments. The digestive tract of an acorn worm consists of a mouth behind which are a muscular pharynx and an intestine. The pharynx opens to the outside through a number of pharyngeal slits through which water can exit. Highly vascularized tissue surrounding the pharyngeal slits serves as a gas exchange apparatus. Acorn worms breathe by pumping water into the mouth and out through the pharyngeal slits. They capture prey with the large proboscis, which is coated with sticky mucus to which small organisms in the sediment stick. The mucus and its attached prey are conveyed by cilia to the mouth. In the esophagus, the food-laden mucus is compacted into a ropelike mass that is moved through the digestive tract by ciliary action.

The 30 living species of pterobranchs are sedentary marine animals up to 12 millimeters long that live in a tube secreted

by the proboscis. Some species are solitary; others form colonies of individuals joined together (**FIGURE 23.34B**). Behind the proboscis is a collar with anywhere from one to nine pairs of arms. The arms bear long tentacles that capture prey and function in gas exchange.

Chordate characteristics are most evident in larvae

As mentioned earlier, it is not obvious from examining the morphology of adult animals that echinoderms and chordates share a common ancestor. The evolutionary relationships among some chordate groups are not immediately apparent either. The features that reveal these evolutionary relationships are seen primarily in the larvae—in other words, it is during the early developmental stages that their evolutionary relationships are evident.

There are three principal chordate clades: the **lancelets** (also called cephalochordates), **tunicates** (also called urochordates), and **vertebrates**. Adult chordates vary greatly in form, but all chordates display the following derived structures at some stage in their development (**FIGURE 23.35**):

- A dorsal hollow nerve cord
- A tail that extends beyond the anus
- A dorsal supporting rod called the notochord

The **notochord** is the most distinctive derived chordate trait. It is composed of a core of large cells with turgid fluid-filled vacuoles, which make it rigid but flexible. In most tunicates the notochord is lost during metamorphosis to the adult stage. In most vertebrate species, it is replaced during development by vertebrae that provide support for the body.

The ancestral pharyngeal slits (not a derived feature of this group) are present at some developmental stage of chordates but are often lost in adults. The pharynx, which develops around the pharyngeal slits, functioned in chordate ancestors as the site for oxygen uptake and the elimination of carbon dioxide and water (as in acorn worms). The pharynx is much enlarged in some chordate species (as in the pharyngeal basket of the lancelet in Figure 23.35B).

Adults of most lancelets and tunicates are sessile

The 35 species of lancelets are small animals that rarely exceed 5 centimeters in length. The notochord, which provides body support, extends the entire length of the body throughout their lives (see Figure 23.35B). Lancelets are found in shallow marine and brackish waters worldwide. Most of the time they lie covered in sand with their head protruding above the sediment, but they can swim. They filter prey from the water with their pharyngeal basket.

All members of the three major tunicate groups—the sea squirts, salps, and larvaceans—live in marine environments. More than 90 percent of the 2,800 known species of tunicates are sea squirts (also called ascidians). Individual sea squirts range in length from less than 1 millimeter to 60 centimeters. Some sea squirts form colonies by asexual budding from a single founder. Colonies may measure several meters across. The baglike body of an adult sea squirt is enclosed in a tough tunic,

(A)

A sea squirt larva has all the chordate features, some of which are lost in the adult.

Ciona sp.

Tail

Dorsal hollow nerve cord

Notochord

Pharyngeal slits

Gut

(B)

Pharyngeal slits

Notochord

Dorsal hollow nerve cord

Gut

Branchiostoma lanceolatum

An adult lancelet retains all the chordate features and also has a much enlarged pharyngeal basket.

Anus

Tail
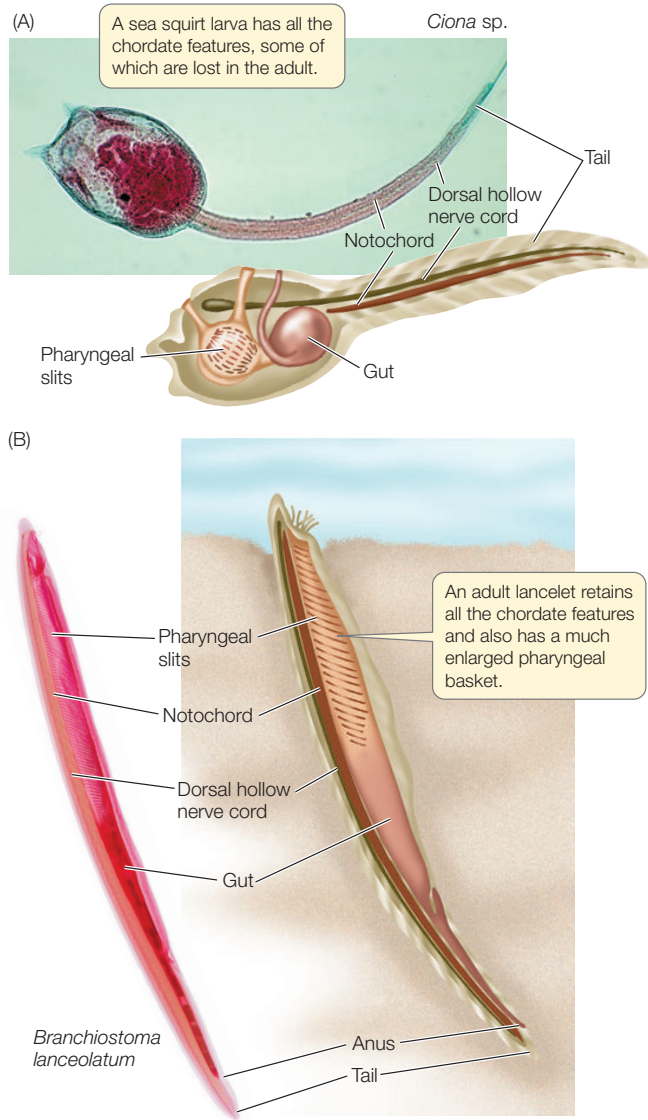
FIGURE 23.35 The Key Features of Chordates Are Most Apparent in Early Developmental Stages   The pharyngeal slits of both the tunicate and the lancelet develop into a pharyngeal basket. (A) The sea squirt larva (but not the adult) has all three chordate features: a dorsal hollow nerve cord, postanal tail, and notochord. (B) All three chordate synapomorphies are retained in the adult lancelet.

Clavelina dellavallei

FIGURE 23.36 An Adult Tunicate   The transparent tunic and the pharyngeal basket are clearly visible in this sea squirt.

tadpolelike larvae suggest a close evolutionary relationship between sea squirts and vertebrates (see Figure 16.4).

As we have discussed, the hemichordates, echinoderms, lancelets, and tunicates are marine animals. The lineage that led to the vertebrates is also thought to have evolved in the oceans, although probably in an estuarine environment (where fresh water meets salt water). Vertebrates have since radiated into marine, freshwater, terrestrial, and aerial environments worldwide.

The vertebrate body plan can support large, active animals

The vertebrates take their name from the unique, jointed, dorsal **vertebral column** that replaces the notochord during early development as their primary supporting structure. The individual elements in the vertebral column are called vertebrae. Four other key features characterize the vertebrates as well (**FIGURE 23.37**):

- An anterior skull with a large brain
- A rigid internal skeleton supported by the vertebral column, which also encloses the spinal cord
- Internal organs suspended in a coelom
- A well-developed circulatory system, driven by contractions of a ventral heart

The internal skeleton provides support for an extensive muscular system, which receives oxygen from the circulatory system and is controlled by the central nervous system. The evolution of these features allowed many vertebrates to become large, active predators, which in turn allowed the vertebrates to diversify widely (**FIGURE 23.38**).

There are two groups of living jawless fishes

The **hagfishes** are thought by many biologists to be the sister group to the remaining vertebrates (see Figure 23.38). Hagfishes (**FIGURE 23.39A**) have a weak circulatory system, with three small accessory hearts (rather than a single, large heart), a partial cranium or skull (containing no cerebrum or cerebellum,

which is the basis for the name "tunicate" (**FIGURE 23.36**). The tunic is composed of proteins and a complex polysaccharide secreted by epidermal cells. The sea squirt pharynx is enlarged into a pharyngeal basket that filters prey from the water passing through it.

In addition to its pharyngeal slits, a sea squirt larva has a dorsal hollow nerve cord and a notochord that is restricted mostly to the tail region (see Figure 23.35A). Bands of muscle that surround the notochord provide support for the body. After a short time swimming in the plankton, the larvae of most species settle on the seafloor and transform into sessile adults. The swimming,

The anterior skull of vertebrates contains the brain and many sensory organs.

Spines (modified rays)

Dorsal fins

Vertebral column

Rays (structures supporting fins)

Caudal fin

Heart

Liver

Pelvic fin (paired appendage)

Gut   Gonad

Anal fin

Cross section

Muscles

Spinal cord

Vertebra

Kidney

Gonad

Gut

Coelom

Peritoneum

Vertebrates have an internal skeleton, supported by a vertebral column that encloses the dorsal spinal cord…

…a well-developed circulatory system…

…and internal organs suspended in a large coelom.

FIGURE 23.37 The Vertebrate Body Plan   A ray-finned fish illustrates the structural elements common to all vertebrates. In addition to the paired pelvic fins, these fishes have paired pectoral fins on the sides of their bodies (not seen in this cutaway view).

two main regions of the brain of other vertebrates), and no jaws or stomach. They also lack separate, jointed vertebrae and have a skeleton composed of cartilage. Thus some biologists do not consider hagfishes vertebrates, and use instead the term "craniates" to refer collectively to the hagfishes and the vertebrates. Some analyses of gene sequences suggest, however, that hagfishes may be more closely related to the vertebrate lampreys (**FIGURE 23.39B**); in this phylogenetic arrangement, the two groups are collectively called the cyclostomes ("circle mouths"). If in fact the hagfishes and lampreys do form a monophyletic group, then hagfishes must have secondarily lost many of the major vertebrate morphological features during their evolution.

FIGURE 23.38 Phylogeny of the Living Vertebrates   This phylogenetic tree shows the evolution of some of the key innovations among the major groups of vertebrates.

The 80 known species of hagfishes are unusual marine animals that produce copious quantities of slime as a defense. They are virtually blind and rely largely on the four pairs of sensory tentacles around their mouth to detect food. Although they have no jaws, hagfishes have a tonguelike structure equipped with toothlike rasps that they can use to tear apart dead organisms and to capture their principal prey, annelid worms. Hagfishes have direct development (no larvae), and individuals may actually change sex from year to year (from male to female and vice versa).

Go to MEDIA CLIP 23.13
Hagfish Slime
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Vertebrae

Jaws, teeth, paired fins

Bony skeleton, swim bladder/lung

Lobe fins

Internal nares (nasal openings into the mouth)

Terrestrial limbs and digits

Amniote egg

Hagfishes

Lampreys

Chondrichthyans

Ray-finned fishes

Coelacanths

Lungfishes

Amphibians

Amniotes

Jawless fishes

Lobe-limbed vertebrates

Bony vertebrates

Gnathostomes ("jaw mouths")

(A)

Eptatretus stoutii

(B)

Petromyzon marinus

FIGURE 23.39 Modern Jawless Fishes (A) Hagfishes burrow in the ocean mud, from which they extract small prey. They also scavenge on dead or dying fish. Their degenerate eyes led to their being miscalled "blind eels." (B) Sea lampreys are ectoparasites that attach to the bodies of living fish and use their large, jawless mouths to suck blood and flesh. They can survive in both fresh and salt water, as this individual attached to a salmon returning to its spawning ground will do.

Although the lampreys and hagfishes may look superficially similar (with elongate eel-like bodies and no paired fins), they differ greatly in their biology. Lampreys have a complete skull and distinct and separate (although rudimentary) vertebrae, all cartilaginous rather than bony. Lampreys undergo a complete metamorphosis from filter-feeding larvae known as ammocoetes, which are morphologically quite similar in general structure to adult lancelets. The adults of many species of lampreys are parasitic, although several lineages of lampreys evolved to become nonfeeding as adults. These nonfeeding adult lampreys survive only a few weeks after metamorphosis—just long enough to breed. In the species that are parasitic as adults, the round mouth is a rasping and sucking organ that is used to attach to their prey and rasp at the flesh (see Figure 23.39B).

The nearly 50 species of lampreys either live in fresh water or live in coastal salt water and move into fresh water to breed. Some species of lampreys are critically endangered because of recent habitat changes and losses.

Jaws and teeth improved feeding efficiency

Many kinds of jawless fishes were found in the seas, estuaries, and fresh waters of the Devonian period, but hagfishes and

Jawless fishes

Early jawed fishes
(placoderms, now extinct)

Modern jawed fishes
(cartilaginous and ray-finned fishes)
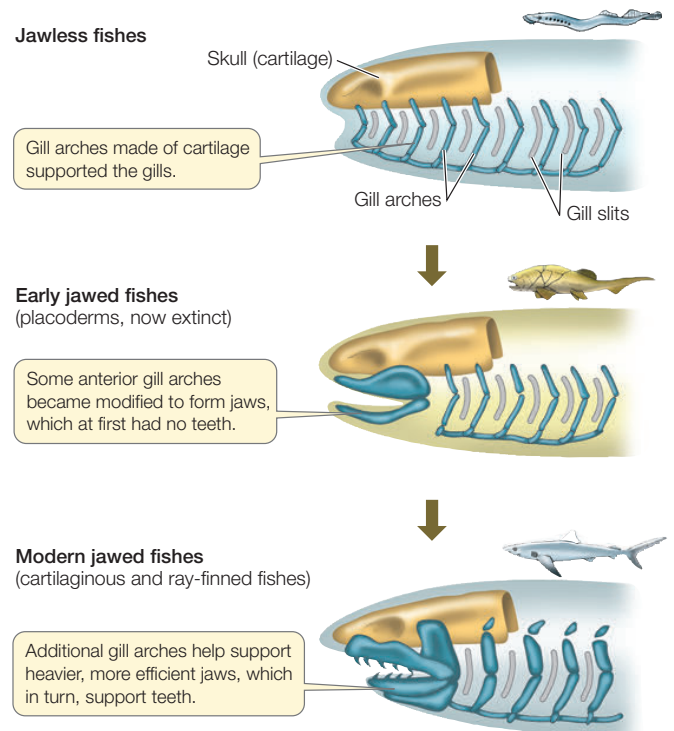
FIGURE 23.40 Verterbrate Jaw Evolution Jaws of vertebrates are derived from modifications of the anterior gill arches of jawless fishes.

lampreys are the only jawless fishes that survived beyond the Devonian. Late in the Ordovician, some fishes evolved jaws via modifications of the skeletal arches that supported the gills (**FIGURE 23.40**). Those fishes and their descendants are referred to as **gnathostomes** (Greek, "jaw mouths"). Jaws greatly improved feeding efficiency, as an animal with jaws can grasp, subdue, and swallow large prey. Jawed fishes rapidly diversified during the Devonian period, eventually replacing the jawless fishes in dominance of the seas.

The earliest jaws were simple, but the evolution of teeth made feeding even more efficient. In predators, teeth function crucially both in grasping and in breaking up prey. In both predators and herbivores, teeth enable an animal to chew both soft and hard body parts of their food. Chewing also aids chemical digestion and improves an animal's ability to extract nutrients from its food.

Fins and swim bladders improved stability and control over locomotion

Most jawed fishes have a pair of pectoral fins just behind the gill slits and a pair of pectoral fins anterior to the anus. Paired fins stabilize the position of jawed fishes in water (and in some cases, help propel them). Median dorsal and anal fins also stabilize the fish, or may be used for propulsion in some species. In many fishes, the caudal (tail) fin helps propel the animal and enables it to turn rapidly.

Several groups of gnathostomes became abundant during the Devonian. Among them were the **chondrichthyans**—sharks,

(A) *Charcharodon carcharias*

Dorsal fin

Caudal fin   Pelvic fin   Pectoral fin

(B) *Taeniura lymma*

The pectoral fins of stingrays are modified for propulsion; their other fins are greatly reduced.
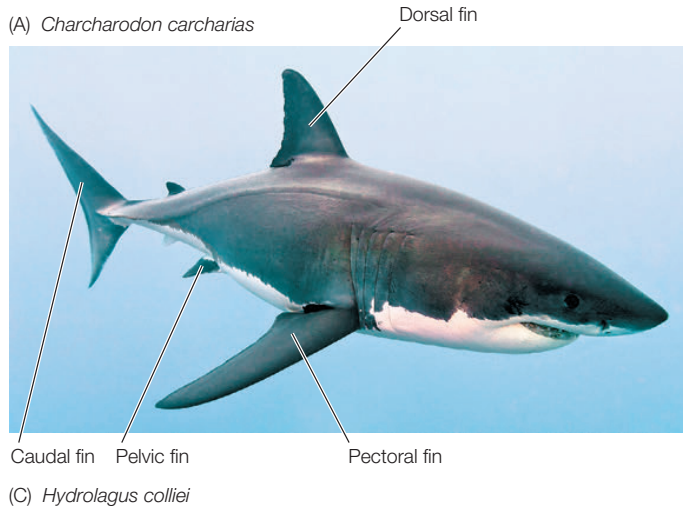
(C) *Hydrolagus colliei*

FIGURE 23.41 Chondrichthyans   The fins of chondrichthyans lack supportive rays. (A) Most sharks, such as this great white shark, are active marine predators. (B) The fins of skates and rays, represented here by a ribbontail stingray, are modified for feeding on the ocean bottom. (C) A chimaera, or ratfish.

skates, and rays (about 1,000 living species) and chimaeras (40 living species). Like hagfishes and lampreys, these fishes have a skeleton composed entirely of firm but pliable cartilage. Their skin is flexible and leathery, sometimes bearing scales that give it the consistency of sandpaper. Sharks move forward by means of lateral undulations of their body and caudal fin (**FIGURE 23.41A**). Skates and rays propel themselves by means of vertical undulating movements of their greatly enlarged pectoral fins (**FIGURE 23.41B**).

Most sharks are predators, but some feed by straining plankton from the water. Most skates and rays live on the ocean floor, where they feed on mollusks and other animals buried in the sediments. Nearly all cartilaginous fishes live in the oceans, but a few are estuarine or migrate into lakes and rivers. One group of stingrays is found in river systems of South America. The less familiar chimaeras (**FIGURE 23.41C**) live in deep-sea or cold waters.

One lineage of aquatic gnathostomes gave rise to the bony vertebrates, which soon split into two main lineages—the **ray-finned fishes** and the **lobe-limbed vertebrates**. Bony vertebrates have internal skeletons of calcified, rigid bone rather than flexible cartilage. In early bony vertebrates, gas-filled sacs that extended from the digestive tract supplemented the gas exchange function of the gills by giving the animals access to atmospheric
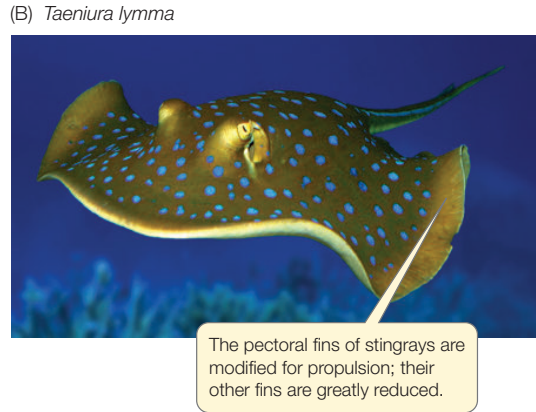
oxygen. These features enabled those fishes to live where oxygen was periodically in short supply, as it often is in freshwater environments. These lunglike sacs evolved into **swim bladders** (organs of buoyancy), as well as into the lungs of tetrapods. By adjusting the amount of gas in its swim bladder, a fish can control the depth at which it remains suspended in the water while expending very little energy to maintain its position.

The outer body surface of most species of ray-finned fishes is covered with flat, thin, lightweight scales that provide some protection or enhance movement through the water. The gills of ray-finned fishes open into a single chamber covered by a hard flap, called an operculum. Movement of the operculum improves the flow of water over the gills, where gas exchange takes place.

Ray-finned fishes began to radiate during the Mesozoic era and continued to radiate extensively throughout the Tertiary period. Today there are about 32,000 known living species, encompassing a remarkable variety of sizes, shapes, and lifestyles (**FIGURE 23.42**). The smallest are less than 1 centimeter long as adults; the largest weigh as much as 900 kilograms. Ray-finned fishes exploit nearly all types of aquatic food sources. In the oceans they filter plankton from the water, rasp algae from rocks, eat corals and other soft-bodied colonial animals, dig animals from soft sediments, and prey on virtually all kinds of other fishes. In fresh water they eat plankton, devour insects, eat fruits that fall into the water in flooded forests, and prey on other aquatic vertebrates and, occasionally, terrestrial vertebrates.

CHECKpoint   CONCEPT 23.5

✓ What are three developmental patterns the earliest deuterostomes had in common?

✓ What are some of the ways that echinoderms use their tube feet to obtain food?

✓ What synapomorphies respectively characterize the chordates and the vertebrates?

✓ How do the hagfishes differ from the lampreys in morphology and life history? Why do some biologists not consider the hagfishes to be vertebrates?

(A)

A cleaner wrasse (*Labroides phthirophagus*) feeds on parasites off the body of a much larger brown surgeonfish (*Acanthurus nigrofuscus*).
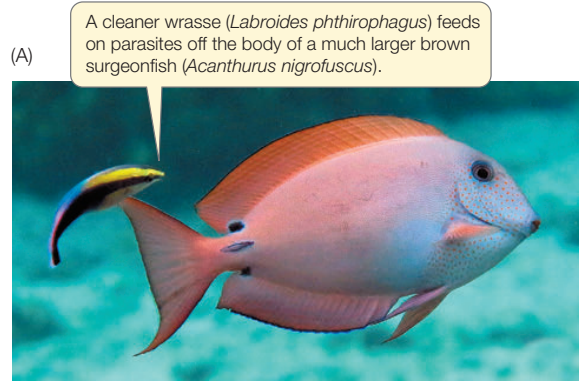
(B) *Phyllopteryx taeniolatus*

FIGURE 23.42 Ray-Finned Fishes (A) The two ray-finned species shown here are mutualists in their coral reef ecosystem. The larger surgeonfish illustrates the body plan most commonly associated with this highly diverse clade. (B) This slow-moving weedy seadragon relies on its unusual morphology to provide camouflage in swaying seaweed.

In some fishes, the lunglike sacs that gave rise to swim bladders became specialized for another purpose: breathing air. That adaptation set the stage for the vertebrates to move onto the land.

CONCEPT 23.6 Life on Land Contributed to Vertebrate Diversification

The evolution of lunglike sacs in fishes set the stage for the invasion of the land. Some early ray-finned fishes probably used those sacs to supplement their gills when oxygen levels in the water were low, as lungfishes and many groups of ray-finned fishes do today. But with their unjointed fins, those fishes could only flop around on land. Changes in the structure of the fins first allowed some fishes to support themselves better in shallow water and, later, to move better on land.

Jointed fins enhanced support for fishes

In the lobe-limbed vertebrates, the paired pelvic and pectoral fins developed into more muscular fins that were joined to the body by a single enlarged bone. The modern representatives of these lobe-limbed vertebrates include the coelacanths, lungfishes, and tetrapods.

(A) *Latimeria chalumnae*

(B) *Protopterus annectens*

FIGURE 23.43 The Closest Relatives of Tetrapods (A) The African coelacanth, discovered in deep waters of the Indian Ocean, represents one of two surviving species of a group that was once thought to be extinct. (B) All surviving lungfish species, such as this African lungfish, live in the Southern Hemisphere.

The coelacanths flourished from the Devonian until about 65 million years ago, when they were thought to have become extinct. However, in 1938 a commercial fisherman caught a living coelacanth off South Africa. Since that time, hundreds of individuals of this extraordinary fish, *Latimeria chalumnae*, have been collected. A second species, *L. menadoensis*, was discovered in 1998 off the Indonesian island of Sulawesi. *Latimeria*, a predator of other fishes, reaches a length of about 1.8 meters and weighs up to 82 kilograms (**FIGURE 23.43A**). Its skeleton is composed mostly of cartilage, not bone. The cartilaginous skeleton is a derived feature in this clade because it had bony ancestors.

 Go to MEDIA CLIP 23.14
Coelacanths in the Deep Sea
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Lungfishes were important predators in shallow-water habitats in the Devonian, but most lineages died out. The six surviving species live in stagnant swamps and muddy waters in South America, Africa, and Australia (**FIGURE 23.43B**).

Eusthenopteron
380 mya
Fully aquatic; lobed fins

Tiktaalik
375 mya
Aquatic; lobed limbs
intermediate between
fins and legs

Acanthostega
365 mya
Semiterrestrial
tetrapod

■ Humerus
■ Radius
■ Ulna
■ Distal elements of
fin/wrist/hand
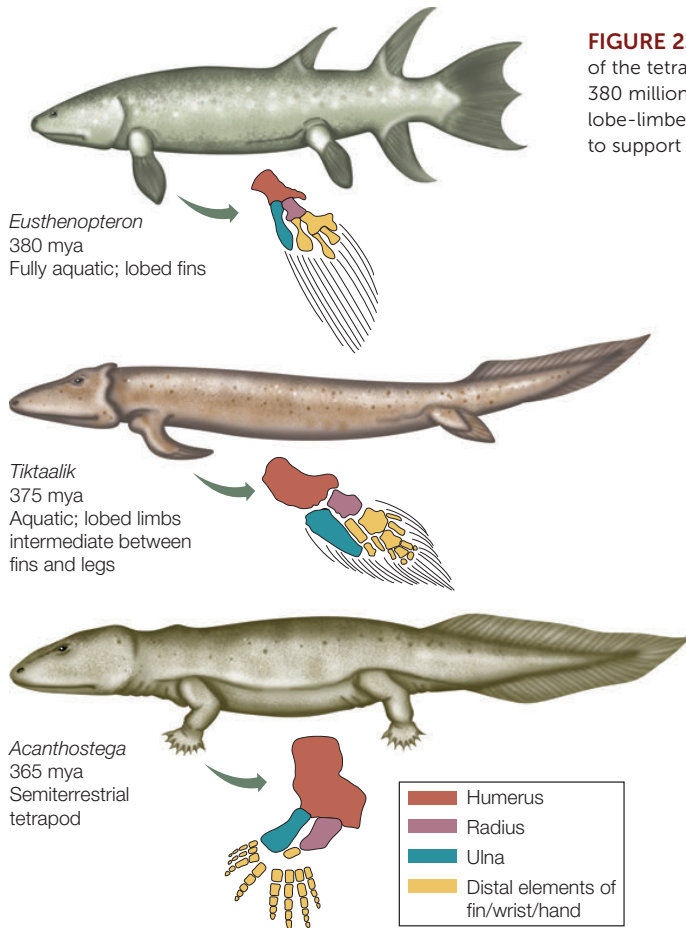
FIGURE 23.44 Tetrapod Limbs are Modified Fins The major skeletal elements of the tetrapod limb were already present in aquatic lobe-limbed vertebrates some 380 million years ago. The relative sizes and positions of these elements changed as lobe-limbed vertebrates moved to a terrestrial environment, where limbs were used to support and move the animal's body on land.

Amphibians adapted to life on land

Most modern amphibians are confined to moist environments because they lose water rapidly through the skin when exposed to dry air. In addition, their eggs are enclosed within delicate membranous envelopes that cannot prevent water loss in dry conditions. In some amphibian species, adults live mostly on land but return to fresh water to lay and fertilize their eggs (**FIGURE 23.45**). The fertilized eggs give rise to larvae that live in water until they undergo metamorphosis to become terrestrial adults. However, many amphibians (especially those in tropical and subtropical areas) have evolved a wide diversity of additional reproductive modes and types of parental care. Internal fertilization, for example, evolved many times among the amphibians. Many species develop directly into adultlike forms from fertilized eggs laid on land or carried by the parents. Other species of amphibians are entirely aquatic, never leaving the water at any stage of their lives, and many of these species retain a larval-like morphology.

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Life Cycle of a Frog
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The more than 7,000 known species of amphibians living on Earth today belong to three major groups: the wormlike, limbless, tropical, burrowing or aquatic caecilians (**FIGURE 23.46A**), the tail-less frogs and toads (collectively called anurans; **FIGURE 23.46B**), and the tailed salamanders (**FIGURE 23.46C,D**).

Anurans are most diverse in wet tropical and warm temperate regions, although a few are found at very high latitudes. There are far more anurans than any other amphibians, with well over 6,000 described species and more being discovered every year. Some anurans have tough skins and other adaptations that enable them to live for long periods in very dry deserts, whereas others live in moist terrestrial and arboreal environments. Some species are completely aquatic as adults. All anurans have a very short vertebral column, with a strongly modified pelvic region that is adapted for leaping, hopping, or propelling the body through water by kicking the hind legs.

The more than 600 described species of salamanders are most diverse in temperate regions of the Northern Hemisphere, but many species are also found in cool, moist environments in the mountains of Central America, and a few species penetrate into tropical regions. Many salamanders live in rotting logs or moist soil. One major group has lost lungs, and these species exchange gases entirely through the skin and mouth lining—body parts that all amphibians use in addition to their lungs. A completely aquatic lifestyle has evolved several times among the salamanders (see Figure 23.46D). These aquatic species have arisen through a developmental process known as **neoteny**, or the retention of juvenile traits (such as gills) by delayed somatic development. Most species of salamanders

Lungfishes have lungs derived from the lunglike sacs of their ancestors as well as gills. When ponds dry up, individuals of most species can burrow deep into the mud and survive for many months in an inactive state while breathing air.

Evidence suggests that some early aquatic lobe-limbed vertebrates began to use terrestrial food sources, became more fully adapted to life on land, and eventually evolved to become ancestral **tetrapods** ("four legs"). How was this transition from an animal that swam in water to one that walked on land accomplished? Fossil evidence suggests that limbs able to prop up a large fish and make the front-to-rear movements necessary for walking evolved while these animals still lived in water. These limbs appear to have functioned in holding the animals upright in shallow water, perhaps even allowing them to hold the head above the water's surface. These same structures were then co-opted for movement on land, at first probably for foraging on brief trips out of water (**FIGURE 23.44**). The basic skeletal elements of those limbs can be traced through major changes in limb form and function among the terrestrial vertebrates.

An early split in the tetrapod tree led to two main groups of terrestrial vertebrates: the **amphibians**, most of which remained tied to moist environments, and the **amniotes**, many of which adapted to much drier conditions.
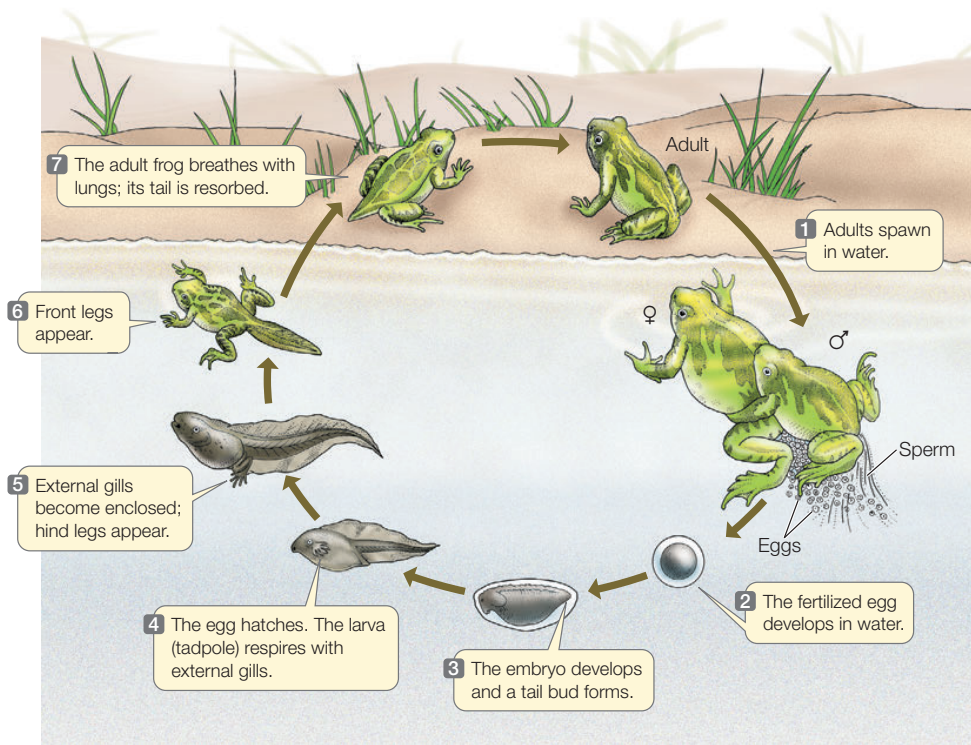
FIGURE 23.45 In and Out of the Water Most early stages in the life cycle of many amphibians take place in water. The aquatic tadpole transforms into a terrestrial adult through metamorphosis. Some species of amphibians, however, have direct development (with no aquatic larval stage), and others are aquatic throughout life.

7 The adult frog breathes with lungs; its tail is resorbed.

Adult

1 Adults spawn in water.

6 Front legs appear.

♀

♂

Sperm

5 External gills become enclosed; hind legs appear.

Eggs

4 The egg hatches. The larva (tadpole) respires with external gills.

2 The fertilized egg develops in water.

3 The embryo develops and a tail bud forms.

have internal fertilization, which is usually achieved through the transfer of a small jellylike, sperm-embedded capsule called a spermatophore.

Many amphibians have complex social behaviors. Most male anurans utter loud, species-specific calls to attract females of their own species (and sometimes to defend breeding territories), and they compete for access to females that arrive at the breeding sites. Many amphibians lay large numbers of eggs, which they abandon once they are deposited and fertilized. Some amphibians lay only a few eggs, which are fertilized

(A) *Siphonops annulatus*

(B) *Bufo periglenes*

(C) *Salamandra salamandra*

(D) *Eurycea waterlooensis*

FIGURE 23.46 Diversity among the Amphibians (A) Burrowing caecilians superficially look more like worms than amphibians. (B) A golden toad pair in Costa Rica. This species has recently become extinct, one of many amphibian species to do so in the past few decades. (C) A European fire salamander. (D) This Austin blind salamander's life cycle remains aquatic; it has no adult terrestrial stage. The eyes of this cave dweller have become greatly reduced.

(A)

(B)
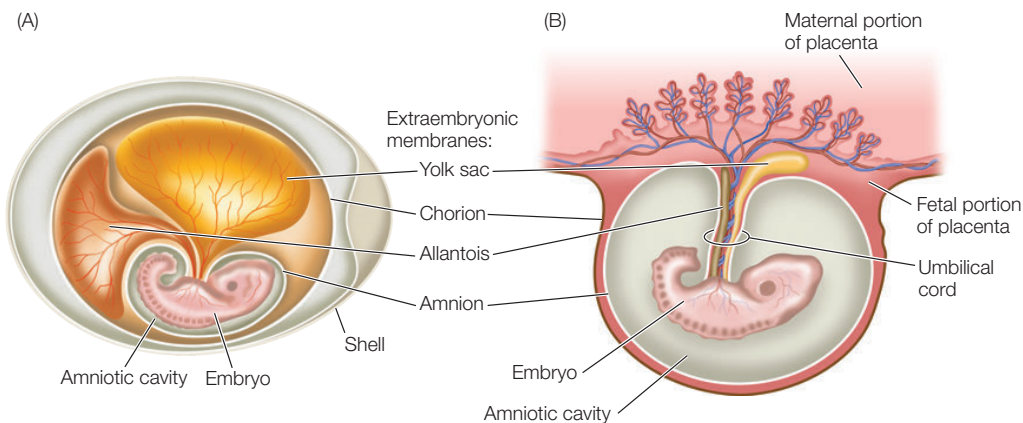
FIGURE 23.47 **The Amniote Egg** (A) The evolution of the amniote egg, with its water-retaining shell, four extraembryonic membranes, and embryo-nourishing yolk, was a major step in adaptation to the terrestrial environment. A chick egg is shown here. (B) In mammals, the developing embryo is retained inside the mother's body, with which it exchanges nutrients and wastes via the placenta. Note the correspondence between the various membranes in (A) and (B).

Go to ACTIVITY 23.3 The Amniote Egg
PoL2e.com/ac23.3

and then guarded in a nest or carried on the backs, in the vocal pouches, or even in the stomachs of one of the parents. A few species of frogs, salamanders, and caecilians are viviparous, meaning they give birth to well-developed young that have received nutrition from the female during gestation.

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Answering a Mating Call
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Amphibians are the focus of much attention today because populations of many species are declining rapidly, especially in mountainous regions of western North America, Central and South America, and northeastern Australia. Worldwide, about one-third of amphibian species are now threatened with extinction or have disappeared completely in the last few decades. Scientists are investigating several hypotheses to account for these population declines, as described in Chapters 1 and 22.

Amniotes colonized dry environments

Several key innovations contributed to the ability of amniotes to exploit a wide range of terrestrial habitats. The **amniote egg** (which gives the group its name) is relatively impermeable to water and allows the embryo to develop in a contained aqueous environment (**FIGURE 23.47A**). The leathery or brittle, calcium-impregnated shell of the amniote egg retards evaporation of the fluids inside but permits passage of oxygen and carbon dioxide. The egg also stores large quantities of food in the form of yolk, allowing the embryo to attain a relatively advanced state of development before it hatches. Within the shell are extraembryonic membranes that protect the embryo from desiccation and assist its gas exchange and excretion of waste nitrogen.

LINK

The roles of the extraembryonic membranes of the amniote egg are discussed in **Concept 38.5**

In several different groups of amniotes, the amniote egg became modified, allowing the embryo to grow inside (and receive nutrition from) the mother. For instance, the mammalian egg lost its shell whereas the functions of the extraembryonic membranes were retained and expanded (**FIGURE 23.47B**).

Other innovations evolved in the organs of terrestrial adults. A tough, impermeable skin, covered with scales or modifications of scales such as hair and feathers, greatly reduced water loss. Adaptations of the vertebrate excretory organs, the kidneys, allowed amniotes to excrete concentrated urine, ridding the body of waste nitrogen without losing a large amount of water in the process.

During the Carboniferous, amniotes split into two major groups: the **reptiles** and the lineage that eventually led to the **mammals** (**FIGURE 23.48**).

Reptiles adapted to life in many habitats

The lineage leading to modern reptiles began to diverge from other amniotes more than 300 million years ago. More than 19,000 species of reptiles exist today, more than half of which are birds. Birds are the only living members of the otherwise extinct dinosaurs, the dominant terrestrial predators of the Mesozoic.

The **lepidosaurs** constitute the second-most species-rich clade of living reptiles. This group is composed of the **squamates** (lizards, snakes, and amphisbaenians—the last a group of mostly legless, wormlike, burrowing reptiles with greatly reduced eyes) and the **tuataras**, which superficially resemble lizards but differ from them in tooth attachment and several internal anatomical features. Many species related to the tuataras lived during the Mesozoic era, but today only two species, restricted to a few islands off New Zealand, survive (**FIGURE 23.49A**).

The skin of a lepidosaur is covered with horny scales that greatly reduce loss of water from the body surface. These scales, however, make the skin unavailable as an organ of gas
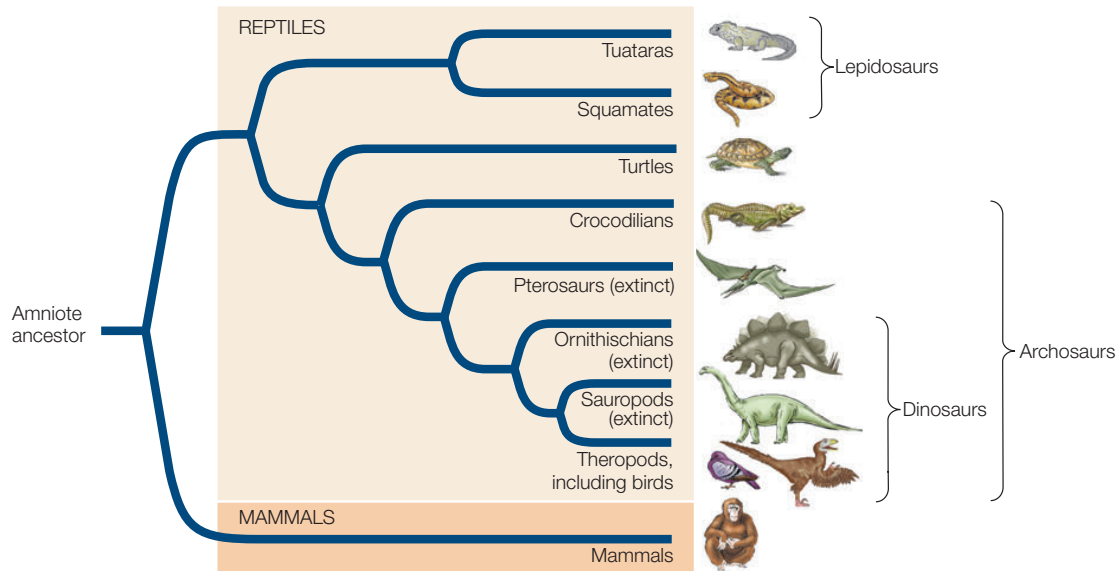
FIGURE 23.48 Phylogeny of Amniotes   This tree of amniote relationships shows the primary split between mammals and reptiles. The reptile portion of the tree shows a lineage that led to the lepido-saurs (snakes, lizards, and tuataras), another to the turtles, and a third to the archosaurs (crocodiles, several extinct groups, and the birds).

(A) *Sphenodon punctatus*

(B) *Triceros jacksonii*

(C) *Diadophis punctatus*

(D) *Chelonoidis nigra abingdonii*

FIGURE 23.49 Reptilian Diversity   (A) The tuatara represents one of only two surviving species in a lineage that diverged long ago. (B) The Jackson's chameleon is native to east Africa but was introduced to Hawaii in 1972. (C) The ringneck snake of North America is harmless to humans. It coils its tail to reveal a bright orange underbelly, which dis-tracts potential predators from the vital head region. (D) Galápagos tor-toises are the largest turtles and among the largest reptiles. They have been documented to live for more than 100 years in the wild.

exchange. Gases are exchanged almost entirely via the lungs, which are proportionally much larger in surface area than those of amphibians. A lepidosaur forces air into and out of its lungs by bellowslike movements of its ribs. The three-chambered lepidosaur heart partially separates oxygenated blood from the lungs from deoxygenated blood returning from the body. With this type of heart, lepidosaurs can generate high blood pressure and can sustain a relatively high metabolism.

Most lizards are insectivores, but some are herbivores; a few prey on other vertebrates. Many lizards walk on four limbs (**FIGURE 23.49B**), although limblessness has evolved repeatedly in the group, especially in burrowing and grassland species. The largest lizard, which grows as long as 3 meters and can weigh more than 150 kilograms, is the predaceous Komodo dragon of the East Indies.

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Komodo Dragons Bring Down Prey
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One major group of limbless squamates is the snakes (**FIGURE 23.49C**). All snakes are carnivores, and many can swallow objects much larger than themselves. Several snake groups evolved venom glands and the ability to inject venom rapidly into their prey.

The **turtles** comprise a reptilian group that has changed relatively little since the early Mesozoic. In these reptiles, dorsal and ventral bony plates form a shell into which the head and limbs can be withdrawn in many species (**FIGURE 23.49D**). The dorsal shell is a modification of the ribs. It is a mystery how the pectoral girdles evolved to be inside the ribs of turtles, making them unlike any other vertebrates. Most turtles live in aquatic environments, but several groups, such as tortoises and box turtles, are terrestrial. Sea turtles spend their entire lives at sea except when they come ashore to lay eggs. Human exploitation of sea turtles and their eggs has resulted in worldwide declines of these species, all of which are now endangered. A few species of turtles are strict herbivores or carnivores, but most species are omnivores that eat a variety of aquatic and terrestrial plants and animals.

Crocodilians and birds share their ancestry with the dinosaurs

Another reptilian clade, the **archosaurs**, includes the crocodilians, pterosaurs, dinosaurs, and birds. Only the crocodilians and birds are represented by living species today. Modern **crocodilians**—crocodiles, caimans, gharials, and alligators—are confined to tropical and warm temperate environments (**FIGURE 23.50A**). All crocodilians are carnivorous; they eat vertebrates of all kinds, including large

mammals. Crocodilians spend much of their time in water, but they lay their eggs in nests they build on land or on floating piles of vegetation. The eggs are warmed by heat generated by decaying organic matter that the female places in the nest. The female provides other forms of parental care as well: typically, she guards the eggs until they hatch, and in some species, she continues to guard and communicate with her offspring after they hatch.

Dinosaurs rose to prominence about 215 million years ago and dominated terrestrial environments for about 150 million years. However, only one group of dinosaurs, the **birds**, survived the mass extinction at the end of the Cretaceous. During the Mesozoic, most terrestrial animals more than a meter long were dinosaurs. Many were agile and could run rapidly; they had special muscles that enabled the lungs to be filled and emptied while the limbs moved. We can infer the existence of such muscles in dinosaurs from the structure of the vertebral column in fossils. Some of the largest dinosaurs weighed as much as 70,000 kilograms.

Biologists have long accepted the phylogenetic position of birds among the reptiles, although birds clearly have many unique, derived morphological features. In addition to the strong morphological evidence for this placement, fossil and molecular data emerging over the last few decades have provided definitive supporting evidence. Birds are a specialized group of **theropods**, a clade of predatory dinosaurs that shared such traits as a bipedal stance, hollow bones, a furcula ("wishbone"), elongated metatarsals with three-fingered feet, elongated forelimbs with three fingers, and a pelvis that points backward. Modern birds are homeothermic, meaning they regulate their body temperatures at a relatively constant temperature through physiological control. Although we cannot directly assess this physiological trait in extinct species, many fossil theropods share morphological traits that suggest they may have been homeothermic as well.

(A) *Caiman crocodilus*

(B) *Struthio camelus*

FIGURE 23.50 Archosaurs (A) Caimans, alligators, and their relatives live in tropical and warm temperate climates. The spectacled caiman is the most common crocodilian throughout much of tropical Central and South America. (B) Birds are the other living archosaur group. This common ostrich is a palaeognath, a group that includes several flightless and weakly flying birds of the Southern Hemisphere. Flightless members of this early-diverging group lack the sternum keel structure that anchors the flight muscles of other bird groups.

(A)

Impressions of feathers can be seen around the fossilized skeletons.

(B)

FIGURE 23.51 Mesozoic Bird Relatives The fossil record supports the evolution of birds from other dinosaurs. (A) *Microraptor gui* was a feathered dinosaur from the early Cretaceous (about 140 mya). (B) Dating from roughly the same time frame, *Archaeopteryx* is the oldest known birdlike fossil.

> **LINK**
> Homeothermy and its physiological control are described in **Concept 29.3**

The living bird species fall into two major groups that diverged about 80–90 million years ago from a flying ancestor. The few modern descendants of one lineage include a group of secondarily flightless and weakly flying birds, some of which are very large. This group, called the palaeognaths, includes the South and Central American tinamous and several large flightless birds of the southern continents—the rheas, emu, kiwis, cassowaries, and the world's largest bird, the ostrich (**FIGURE 23.50B**). The second lineage, the neognaths, has left a much larger number of descendants, most of which have retained the ability to fly.

The evolution of feathers allowed birds to fly

During the Mesozoic era, about 175 million years ago, a lineage of theropods gave rise to the birds. Recent fossil discoveries show that the scales of some theropod dinosaurs were modified to form feathers. The feathers of many of these dinosaurs were structurally similar to those of modern birds (**FIGURE 23.51**).

The evolution of feathers was a major force for diversification. Feathers are lightweight but are strong and structurally

complex. The large quills of the flight feathers on the wings arise from the skin of the forelimbs to create the flying surfaces. Other strong feathers sprout like a fan from the shortened tail and serve as stabilizers during flight. The feathers that cover the body, along with an underlying layer of down feathers, provide birds with insulation that helps them survive in virtually all of Earth's climates.

> **Go to MEDIA CLIP 23.17**
> **Falcons in Flight**
> **PoL2e.com/mc23.17**

The bones of theropod dinosaurs, including birds, are hollow with internal struts that increase their strength. Hollow bones would have made early theropods lighter and more mobile. Later, the hollow bones of theropods facilitated the evolution of flight. The sternum (breastbone) of flying birds forms a large, vertical keel to which the flight muscles are attached.

Flight is metabolically expensive. A flying bird consumes energy at a rate 15–20 times faster than a running lizard of the same weight. Because birds have such high metabolic rates, they generate large amounts of heat. They control the rate of heat loss using their feathers, which may be held close to the body or elevated to alter the amount of insulation they provide. The lungs of birds allow air to flow through unidirectionally rather than by pumping air in and out. This flow-through structure of the lungs increases the efficiency of gas exchange and thereby supports an increased metabolic rate.

> **LINK**
> You can read more about the effects of flying on metabolic rate in **Concept 29.2**. See **Concept 31.2**, pp. 652–653, for a description of the breathing system of birds

There are about 10,000 species of living birds, which range in size from the 150-kilogram ostrich to a hummingbird weighing only 2 grams (**FIGURE 23.52**). The teeth so prominent among other dinosaurs were secondarily lost in the ancestral birds, but birds nonetheless eat almost all types of animal and plant material. Insects and fruits are the most important dietary items for terrestrial species. Birds also eat seeds, nectar and pollen, leaves and buds, carrion, and fish and other vertebrates. By eating the fruits and seeds of plants, birds serve as major agents of seed dispersal.

Mammals radiated as non-avian dinosaurs declined in diversity

Small and medium-sized mammals coexisted with the large dinosaurs throughout most of the Mesozoic era, and most of the major groups that are alive today arose in the Cretaceous. After the non-avian dinosaurs disappeared during the mass extinction at the end of the Cretaceous, mammals increased dramatically in numbers, diversity, and size. Today mammals range in size from tiny shrews and bats weighing only about 2 grams to the blue whale, the largest animal on Earth, which measures up to 33 meters long and can weigh as much as 160,000 kilograms. Mammals have far fewer, but more highly differentiated, teeth than do fishes, amphibians, or reptiles. Differences among

(A) *Grus canadensis*

(B) *Aegolius acadicus*

(C) *Piranga olivacea*

FIGURE 23.52 Some Diverse Birds (A) Sandhill cranes feed on plants, insects, small reptiles, and even small mammals. As in other crane species, their mating and courtship behavior includes an elaborate dance display. (B) Owls such as this northern saw-whet owl are nighttime predators that can locate prey using their sensitive auditory systems. (C) Perching, or passeriform, birds such as this scarlet tanager comprise the most species-rich group of birds.

mammals in the number, type, and arrangement of teeth reflect their varied diets.

Four key features distinguish the mammals:

- Sweat glands, which secrete sweat that evaporates and thereby cools an animal
- Mammary glands, which in females secrete a nutritive fluid (milk) on which newborn individuals feed
- Hair, which provides a protective and insulating covering
- A four-chambered heart that completely separates the oxygenated blood coming from the lungs from the deoxygenated blood returning from the body (this last characteristic evolved independently in the archosaurs, including modern birds and crocodiles)

Mammalian eggs are fertilized within the female's body, and the embryos undergo a period of development in the female's body in an organ called the uterus. In the uterus, the embryo is contained in an amniotic sac that is homologous to one of four membranes found in the amniotic egg (see Figure 23.47). The embryo is connected to the wall of the uterus by an organ called a placenta. The placenta allows for nutrient and gas exchange, as well as waste elimination from the developing embryo, via the female's circulatory system. Most mammals have a covering of hair (fur), which is luxuriant in some species but has been greatly reduced in others, including the cetaceans (whales and dolphins) and humans. Thick layers of insulating fat (blubber) replace hair as a heat-retention mechanism in the cetaceans. Humans learned to use clothing for heat retention when they dispersed from warm tropical areas.

The approximately 5,700 species of living mammals are divided into two primary groups: the **prototherians** and the

therians. Only five species of prototherians are known, and they are found only in Australia and New Guinea. These mammals, the duck-billed platypus and four species of echidnas, differ from other mammals in lacking a placenta, laying eggs, and having sprawling legs (**FIGURE 23.53A**). Prototherians supply milk for their young, but they have no nipples on their mammary glands. The milk simply oozes out and is lapped off the fur by the offspring.

Most mammals are viviparous

Members of the viviparous therian clade are further divided into the **marsupials** and the **eutherians**. Females of most marsupial species have a ventral pouch in which they carry and feed their offspring (**FIGURE 23.53B**). Gestation (pregnancy) in marsupials is brief; the young are born tiny but with well-developed forelimbs, with which they climb to the pouch. They attach to a nipple but cannot suck. The mother ejects milk into the tiny offspring until they grow large enough to suckle. Once her offspring have left the uterus, a female marsupial may become sexually receptive again. She can then carry fertilized eggs that are capable of initiating development and can replace the offspring in her pouch should something happen to them.

Eutherians include the majority of mammals. Eutherians are sometimes called placental mammals, but this name is inappropriate because some marsupials also have placentas. Eutherians are more developed at birth than are marsupials, and no external pouch houses them after they are born.

The more than 5,300 living species of morphologically diverse eutherians are divided into 20 major groups (**TABLE 23.3**). The relationships of the major groups of eutherians to one another have been difficult to determine because most of the major groups diverged in a short period of time during an explosive adaptive radiation. The two most diverse groups are the rodents (**FIGURE 23.53C**) and bats (**FIGURE 23.53D**), which together comprise about two-thirds of the species. Rodents are traditionally defined by the unique morphology of their teeth,

(A) *Ornithorhynchus anatinus*

(B) *Didelphis virginiana*

(C) *Erethizon dorsatum*
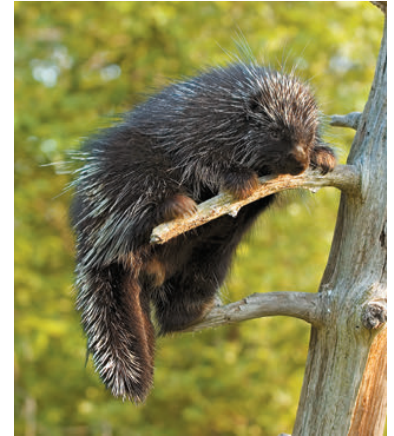
(D) *Leptonycteris curasoae*

(E)

(F) *Tursiops truncatus*

FIGURE 23.53 Mammalian Diversity (A) The duck-billed platypus is one of the five surviving species of prototherians—mammals that lay eggs. (B) Female marsupial mammals have a ventral pouch in which they nurture their offspring, which are extremely small at birth. The young of this opossum have grown large enough to leave her pouch. (C–F) Eutherian mammals. (C) Almost half of all eutherians are rodents, such as this North American porcupine. (D) Flight evolved in the common ancestor of bats. Virtually all bat species are nocturnal. (E) Many large mammals are important herbivores in terrestrial environments. Nowhere are these assemblages more spectacular than on the grass and brushlands of the African continent. (F) Bottlenose dolphins are cetaceans, a cetartiodactyl group that returned to the marine environment.

which are adapted for gnawing through substances such as wood. The bats probably owe much of their success to the evolution of flight, which allows them to exploit a variety of food sources and colonize remote locations with relative ease.

Go to MEDIA CLIP 23.18
Bats Feeding in Flight
PoL2e.com/mc23.18

Grazing and browsing by members of several eutherian groups helped transform the terrestrial landscape. Herds of grazing herbivores feed on open grasslands, whereas browsers feed on shrubs and trees. The effects of herbivores on plant life favored the evolution of the spines, tough leaves, and difficult-to-eat growth forms found in many plants. In turn, adaptations to the teeth and digestive systems of many herbivore lineages allowed these species to consume many plants despite such defenses—a striking example of coevolution. A large animal can survive on food of lower quality than a small animal can, and large size evolved in several groups of grazing and browsing mammals (**FIGURE 23.53E**). The evolution of large herbivores, in turn, favored the evolution of large carnivores able to attack and overpower them.

TABLE 23.3	Major Groups of Living Eutherian Mammals	
Group	**Number of described living species**	**Examples**
Rodents (Rodentia)	2,337	Rats, mice, squirrels, woodchucks, ground squirrels, beaver, capybara
Bats (Chiroptera)	1,171	Fruit bats, echo-locating bats
Even-toed hoofed mammals and cetaceans (Cetartiodactyla)	469	Deer, sheep, goats, cattle, antelopes, giraffes, camels, swine, hippopotamus, whales, dolphins
Shrews, moles, and relatives (Soricomorpha)	428	Shrews, moles, solenodons
Primates (Primates)	396	Lemurs, monkeys, apes, humans
Carnivores (Carnivora)	284	Wolves, dogs, bears, cats, weasels, pinnipeds (seals, sea lions, walruses)
Rabbits and relatives (Lagomorpha)	92	Rabbits, hares, pikas
African insectivores (Afrosoricida)	50	Tenrecs, golden moles
Spiny insectivores (Erinaceomorpha)	24	Hedgehogs
Armadillos (Cingulata)	21	Armadillos
Tree shrews (Scandentia)	20	Tree shrews
Odd-toed hoofed mammals (Perissodactyla)	16	Horses, zebras, tapirs, rhinoceroses
Long-nosed insectivores (Macroscelidea)	15	Elephant shrews
Anteaters and sloths (Pilosa)	10	Anteaters, tamanduas, sloths
Pangolins (Pholidota)	8	Asian and African pangolins
Hyraxes and relatives (Hyracoidea)	5	Hyraxes, dassies
Sirenians (Sirenia)	4	Manatees, dugongs
Elephants (Proboscidea)	3	African and Indian elephants
Colugos (Dermoptera)	2	Flying lemurs
Aardvark (Tubulidentata)	1	Aardvark

Several lineages of terrestrial eutherians subsequently returned to the aquatic environments their ancestors had left behind (**FIGURE 23.53F**). The completely aquatic cetaceans—whales and dolphins—evolved from artiodactyl ancestors (whales are closely related to the hippopotamuses). The seals, sea lions, and walruses also returned to the marine environment, and their limbs became modified into flippers. Weasel-like otters retain their limbs but have also returned to aquatic environments, colonizing both fresh and salt water. The manatees and dugongs colonized estuaries and shallow seas.

CHECKpoint CONCEPT 23.6

✓ Many amphibians have a biphasic life cycle that includes an aquatic larva and a terrestrial adult. What are some exceptions to this common pattern?

✓ In the not-too-distant past, the idea that birds were reptiles met with skepticism. Explain how fossils, morphology, and molecular evidence now support the position of birds among the reptiles.

✓ Contrast the reproductive modes of prototherians, marsupials, and eutherians.

The biology of one eutherian group—the primates—has been the subject of extensive research. The behavior, ecology, physiology, and molecular biology of the primates are of special interest to us because this lineage includes humans.

CONCEPT 23.7 Humans Evolved among the Primates

The **primates** evolved from a lineage of relatively small, arboreal, insectivorous eutherians. Grasping limbs with opposable digits are one of the major adaptations to arboreal life that distinguish primates from other mammals. Primates underwent extensive evolutionary radiation throughout the Tertiary (**FIGURE 23.54**).

Two major lineages of primates split late in the Cretaceous

About 90 million years ago, late in the Cretaceous period, the primates split into two main clades: the prosimians and the anthropoids. **Prosimians**—lemurs, lorises, and galagos—once lived on all continents, but today they are restricted to Africa, Madagascar, and tropical Asia. Most prosimians are arboreal and noctural. There has been a remarkable radiation of lemurs on Madagasgar, where there are also diurnal and terrestrial species. Tarsiers were once considered prosimians as well, although today we know that they are more closely related to monkeys and apes than to lemurs, lorises, and galagos.

FIGURE 23.54 Phylogeny of the Primates
The phylogeny of primates is among the best studied of any major group of mammals. This tree is based on evidence from many genes, morphology, and fossils.

Bipedal locomotion evolved in human ancestors

About 6 million years ago in Africa, a lineage split occurred that would lead to the chimpanzees on the one hand and to the **hominid** clade, which includes modern humans and their extinct close relatives, on the other.

The earliest protohominids, known as ardipithecines, had distinct morphological adaptations for **bipedal locomotion** (walking on two legs). Bipedal locomotion frees the forelimbs to manipulate objects and to carry them while walking. It also elevates the eyes, enabling the animal to see over tall vegetation to spot predators and prey. Bipedal locomotion is also energetically more economical than quadrupedal locomotion (walking on four legs). All three advantages were probably important for the ardipithecines and their descendants, the australopithecines (**FIGURE 23.55**).

The first australopithecine skull was found in South Africa in 1924. Since then australopithecine fossils have been found at many sites in Africa. The most complete fossil skeleton yet found was discovered in Ethiopia in 1974. The skeleton, approximately 3.5 million years old, was that of a young female who has since become known to the world as "Lucy." Lucy was assigned to the species *Australopithecus afarensis*. Fossil remains of more than 100 *A. afarensis* individuals have since been discovered, and there have been recent discoveries of fossils of other australopithecine species that lived in Africa 4–5 million years ago.

Experts disagree over how many species are represented by australopithecine fossils, but it is clear that multiple species of hominids lived together over much of eastern Africa several million years ago. A lineage of larger species (weighing about 40 kilograms) is represented by *Paranthropus robustus* and *P. boisei*, both of which died out between 1 and 1.5 million years ago. A lineage of smaller australopithecines gave rise to the genus *Homo*.

Early members of the genus *Homo* lived contemporaneously with *Paranthropus* in Africa for about a million years. Some 2-million-year-old fossils of an extinct species called *H. habilis* were discovered in the Olduvai Gorge, Tanzania. Other fossils of *H. habilis* have been found in Kenya and Ethiopia. Associated with these fossils were tools that these early hominids used to obtain food.

Another extinct hominid species, *Homo erectus*, arose in Africa about 1.6 million years ago. Soon thereafter it had spread as far as eastern Asia, becoming the first hominid to leave Africa. Members of *H. erectus* were nearly as large as modern people, but their brains were smaller and they had comparatively thick

The second primate lineage, the **anthropoids**—tarsiers, New World monkeys, Old World monkeys, and apes—began to diversify shortly after the mass extinction event at the end of the Cretaceous, in Africa and Asia. New World monkeys diverged from Old World monkeys and apes slightly later, but early enough that they might have reached South America from Africa when those two continents were still close to each other. All New World monkeys now live only in South and Central America, and all of them are arboreal. Many of them have long, prehensile tails with which they can grasp branches. Many Old World monkeys are arboreal as well, but a number of species are terrestrial. No Old World primate has a prehensile (grasping) tail.

About 35 million years ago, a lineage that led to the apes separated from the Old World monkeys. Between 22 and 5.5 million years ago, dozens of species of apes lived in Europe, Asia, and Africa. The Asian apes (gibbons and orangutans), African apes (gorillas and chimpanzees), and humans are their modern descendants.

Australopithecus africanus

Paranthropus aethiopicus

Paranthropus robustus

Paranthropus boisei

Australopithecus afarensis (Lucy)

Ardipithecine ancestors

The Paranthropus lineages coexisted with species of Homo and Australopithecus in Africa.

No fossils are known of this lineage until 95,000 years ago.

Homo floresiensis (extinct 17,000 years ago)

Homo erectus (extinct 250,000 years ago)

Homo neanderthalensis (extinct 28,000 years ago)

Homo ergaster

Homo sapiens (now worldwide)

Several species of Homo co-existed in Africa, Asia, and Europe until recently.

Homo habilis

Expansion from Africa 60,000–70,000 years ago.

Expansion into the New World 12,000–20,000 years ago.

- ▬ Africa only
- ▬ Expansion out of Africa

4.0   3.0   2.0   1.0   Present

Millions of years ago

FIGURE 23.55 A Phylogenetic Tree of Hominids At times in the past, more than one species of hominid lived on Earth at the same time. Originating in Africa, hominids spread to Europe and Asia multiple times. All but one of these closely related species are now extinct; modern *Homo sapiens* have colonized nearly every corner of the planet.

skulls. The cranium, which had thick, bony walls, may have been an adaptation to protect the brain, ears, and eyes from impacts caused by a fall or a blow from a blunt object. What would have been the source of such blows? Fighting with other *H. erectus* individuals is a possible answer.

Homo erectus used fire for cooking and for hunting large animals, and made characteristic stone tools that have been found in many parts of Africa and Asia. Populations of *H. erectus* survived until at least 250,000 years ago, although more recent fossils may also be attributable to this species. In 2004 some 18,000-year-old fossil remains of a small *Homo* were found on the island of Flores in Indonesia. Since then, numerous additional fossils of this diminutive hominid have been found on Flores, dating from 95,000 to 17,000 years ago. Many anthropologists think that this small species, named *H. floresiensis*, was most closely related to *H. erectus*.

Human brains became larger as jaws became smaller

In another hominid lineage that diverged from *H. erectus* and *H. floresiensis*, the brain increased rapidly in size, and the jaw muscles, which were large and powerful in earlier hominids, dramatically decreased in size. These two changes were simultaneous, which suggests that they might have been developmentally linked. These changes are another example of

evolution by neoteny (which, you may recall from our discussion of amphibians, is the retention of juvenile traits through delayed somatic development). Human and chimpanzee skulls are similar in shape at birth, but chimpanzee skulls undergo a dramatic change in shape as the animals mature (**FIGURE 23.56**). In particular, the jaw grows considerably in relation to the brain case. As human skulls grow, relative proportions much closer to those of the juvenile skull are retained, which results in a large brain case and small jaw compared with those of chimpanzees. A mutation in a regulatory gene that is expressed only in the head may have removed a barrier that had previously prevented this remodeling of the human cranium.

The striking enlargement of the brain relative to body size in the hominid lineage was probably favored by an increasingly complex social life. Any features that allowed group members to communicate more effectively with one another would have been valuable in cooperative hunting and gathering as well as for improving one's status in the complex social interactions that must have characterized early human societies, just as they do ours today.

The chimp skull undergoes much more dramatic change in development than does the human skull.

The skulls of juvenile chimpanzees and humans are quite similar to each other.

Pan

Homo
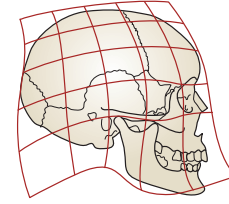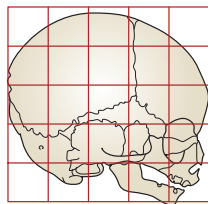
FIGURE 23.56 Neoteny in the Evolution of Humans   The skulls and heads of juvenile chimpanzees and humans start out relatively similar in shape. The grid over the skulls shows how the various bony elements change in their relative proportions through maturation. The adult human skull retains a shape closer to its juvenile shape, resulting in a brain that is much larger relative to other parts of the skull (notably the jaw).

of the cold steppes and grasslands that occupied much of Europe during periods of glacial expansion. Early modern humans also spread across Asia, reaching North America perhaps as early as 20,000 years ago, although the date of their arrival in the Americas is still uncertain. Within a few thousand years, they had spread southward through North America to the southern tip of South America.

Several *Homo* species coexisted during the mid-Pleistocene, from about 1.5 million to about 250,000 years ago. All were skilled hunters of large mammals, but plants were important components of their diets as well. During this period another distinctly human trait emerged: rituals and a concept of life after death. Deceased individuals were buried with tools and clothing, supplies for their presumed existence in the next world.

One species, *Homo neanderthalensis*, was widespread in Europe and Asia between about 500,000 and 28,000 years ago. Neanderthals were short, stocky, and powerfully built. Their massive skull housed a brain somewhat larger than our own. They manufactured a variety of tools and hunted large mammals, which they probably ambushed and subdued in close combat. Early modern humans (*H. sapiens*) expanded out of Africa between 70,000 and 60,000 years ago. Then, about 35,000 years ago, *H. sapiens* moved into the range of *H. neanderthalensis* in Europe and western Asia, so the two species must have interacted with each other. Neanderthals abruptly disappeared about 28,000 years ago. Many anthropologists believe that Neanderthals were exterminated by those early modern humans. Scientists have been able to isolate large parts of the genome of *H. neanderthalensis* from recent fossils and to compare it with our own. These studies suggest that there was some limited interbreeding between the two species while they occupied the same range. As a result, in humans with Eurasian ancestry, 1–4 percent of the genes in their genomes may be derived from Neanderthal ancestors.

Early modern humans made and used a variety of sophisticated tools. They created the remarkable paintings of large mammals, many of them showing scenes of hunting, found in European caves. The animals they depicted were characteristic

CHECKpoint   CONCEPT 23.7

✓ Describe the differences between Old World and New World monkeys.

✓ What leads biologists to conclude that the evolution of brain size and jaw size may be functionally linked?

✓ What evidence leads biologists to think that limited interbreeding between *Homo sapiens* and *H. neanderthalensis* took place after *H. sapiens* expanded out of Africa?

Q   Besides beetles, which other groups of animals are thought to contain many more species than are known at present?

ANSWER   It is perhaps easier to list the groups of animals for which a nearly complete inventory of living species has been completed than to list all the groups for which many new species remain to be described. Among the insects, the best-studied group in terms of species is the butterflies, which are widely collected and studied. There are still many species of other lepidopterans (such as moths), however, remaining to be discovered. Most other major insect groups contain many undescribed species. Among the vertebrates, most species of birds and mammals have been described, although several new species of mammals are still discovered and named each year. Species discovery and description remains high for almost all other major groups of animals.

After insects, and perhaps even rivaling the insects in undiscovered diversity, are the nematodes. Although known nematode diversity is only about 1/40th of the known insect diversity (in terms of number of described species), the taxonomy of nematodes is much more poorly studied than that of insects. Some biologists think there are likely to be species-specific parasitic nematodes of most other species of multicellular organisms. If so, then there may be as many species of nematodes as there are of plants, fungi, and other animals combined.

Most of the other diverse groups of animals contain many as yet undetected species, judging from the rate of new species descriptions. In particular, flatworms (especially the parasitic flukes and tapeworms), marine annelids, mollusks, crustaceans, myriapods, and chelicerates all contain large numbers of undescribed species. Among the vertebrates, the rate of discovery of new species remains particularly high for the fishes and amphibians.

SUMMARY

CONCEPT 23.1 Distinct Body Plans Evolved among the Animals

- Animals share a set of derived traits not found in other groups of organisms, including similarities in the sequences of many of their genes, the structure of their cell junctions, and the components of their extracellular matrix. **Review Figure 23.1**

- Patterns of embryonic development provide clues to the evolutionary relationships among animals. **Diploblastic** animals develop two embryonic cell layers; **triploblastic** animals develop three cell layers.

- Differences in their patterns of early development characterize two major clades of triploblastic animals, the **protostomes** and the **deuterostomes**.

- Animal **body plans** can be described in terms of **symmetry**, **body cavity** structure, **segmentation**, and type of appendages.

- Most animals have either **radial symmetry** or **bilateral symmetry**. Many bilaterally symmetrical animals exhibit **cephalization**, with sensory and nervous tissues in an anterior head.

- On the basis of their body cavity structure, animals can be described as **acoelomates**, **pseudocoelomates**, or **coelomates**. **Review Figure 23.4 and ACTIVITY 23.1**

- Segmentation takes many forms and improves control of movement, especially if the animal also has appendages.

CONCEPT 23.2 Some Animal Groups Fall outside the Bilateria

- All animals other than **sponges**, **ctenophores**, **placozoans**, and **cnidarians** belong to a large, monophyletic group called the **Bilateria**. **Eumetazoans**, which have tissues organized into distinct organs, include all animals other than sponges. **Review ACTIVITY 23.2**

- Sponges are simple, asymmetrical animals that lack differentiated cell layers and true organs. Sponges have skeletons made up of silicaceous or calcareous **spicules**. They create water currents and capture food with flagellated feeding cells called **choanocytes**. Choanocytes are an evolutionary link between the animals and the choanoflagellate protists.

- The two cell layers of the radially symmetrical ctenophores are separated by an inert extracellular matrix called **mesoglea**. Ctenophores move by beating comblike plates of cilia called **ctenes**. **Review Figure 23.7**

- The life cycle of most cnidarians has two distinct stages: a sessile **polyp** stage and a motile **medusa**. A fertilized egg develops into a free-swimming larval **planula**, which settles to the bottom and develops into a polyp. **Review Figure 23.9 and ANIMATED TUTORIAL 23.1**

CONCEPT 23.3 Protostomes Have an Anterior Brain and a Ventral Nervous System

- Protostomes ("mouth first") are bilaterally symmetrical animals that have an anterior brain surrounding the entrance to the digestive tract and a ventral nervous system. Protostomes comprise two major clades, the lophotrochozoans and the ecdysozoans. **Review ANIMATED TUTORIAL 23.2**

- **Lophotrochozoans** include a wide diversity of animals. Within this group evolved **lophophores** (a complex organ for food collection and gas exchange) and free-living **trochophore** larvae. These features were subsequently lost in some lineages. The exact placement of **arrow worms** within the protostomes remains uncertain.

- Lophophores, wormlike body forms, and external shells are each found in many distantly related groups of lophotrochozoans. The most species-rich groups of lophotrochozoans are the **flatworms**, **annelids**, and **mollusks**.

- Annelids are a diverse group of segmented worms that live in moist terrestrial and aquatic environments. **Review Figures 23.17 and 23.18**

- Mollusks underwent a dramatic evolutionary radiation based on a body plan consisting of three major components: a **foot**, a **mantle**, and a **visceral mass**. The four major living molluscan clades—**chitons**, **bivalves**, **gastropods**, and **cephalopods**—demonstrate the diversity that evolved from this three-part body plan. **Review Figure 23.19**

- **Ecdysozoans** have a **cuticle** covering their body, which they must **molt** in order to grow. Some ecdysozoans, notably the **arthropods**, have a rigid cuticle reinforced with **chitin** that functions as an **exoskeleton**. New mechanisms of locomotion and gas exchange evolved among the arthropods.

- **Nematodes**, or roundworms, have a thick, multilayered cuticle. Nematodes are among the most abundant and universally distributed of all animal groups. **Review Figure 23.22**

- **Horsehair worms** are extremely thin; their larvae are internal parasites.

- Many ecdysozoan groups are wormlike in form. Members of several species-poor groups of marine ecdysozoans—**priapulids**, **kinorhynchs**, and **loriciferans**—have thin cuticles.

- One major ecdysozoan clade, the arthropods, has evolved jointed, paired appendages that have a wide diversity of functions.

CONCEPT 23.4 Arthropods Are Diverse and Abundant Animals

- Arthropods are the dominant animals on Earth in number of described species, and among the most abundant in number of individuals.

SUMMARY   (*continued*)

- Encasement within a rigid exoskeleton provides arthropods with support for walking as well as some protection from predators. The waterproofing provided by chitin keeps arthropods from dehydrating in dry air.

- Jointed appendages permit complex movements. Each arthropod segment has muscles attached to the inside of the exoskeleton that operate that segment and the appendages attached to it.

- Two groups of arthropod relatives, the **velvet worms** and the **tardigrades**, have simple, unjointed appendages.

- **Chelicerates** have a two-part body and pointed mouthparts that grasp prey; most chelicerates have four pairs of walking legs.

- Mandibles and antennae are synapomorphies of the **mandibulates**, which include **myriapods**, crustaceans, and hexapods.

- **Crustaceans** are the dominant marine arthropods and are also found in many freshwater and some terrestrial environments. Their segmented bodies are divided into three regions (head, thorax, and abdomen) with different, specialized appendages in each region.

- **Hexapods**—insects and their relatives—are the dominant terrestrial arthropods. They have the same three body regions as crustaceans, but no appendages form in their abdominal segments. Wings and the ability to fly first evolved among the insects, allowing them to exploit new lifestyles. **Review Figure 23.30**

CONCEPT 23.5   Deuterostomes Include Echinoderms, Hemichordates, and Chordates

- Deuterostomes vary greatly in adult form, but based on the distinctive patterns of early development they share and on phylogenetic analyses of gene sequences, they represent a monophyletic group. There are far fewer species of deuterostomes than of protostomes, but many deuterostomes are large and ecologically important. **Review ANIMATED TUTORIAL 23.3**

- **Echinoderms** and **hemichordates** both have bilaterally symmetrical, ciliated larvae.

- Most adult echinoderms have **pentaradial symmetry**. Echinoderms have an internal skeleton of calcified plates and a unique **water vascular system** connected to extensions called **tube feet**. **Review Figure 23.32**

- Hemichordate adults are bilaterally symmetrical and have a three-part body that is divided into a proboscis, collar, and trunk. They include the acorn worms and the pterobranchs. **Review Figure 23.34**

- Chordates fall into three principal subgroups: **lancelets**, **tunicates**, and **vertebrates**.

- At some stage in their development, all chordates have a dorsal hollow nerve cord, a postanal tail, and a **notochord**. **Review Figure 23.35**

- Tunicates include the sea squirts, which are sessile filter feeders as adults. Lancelets live buried in the sand of shallow marine and brackish waters.

- The vertebrate body is characterized by a rigid internal skeleton, which is supported by a **vertebral column** that replaces the notochord, internal organs suspended in a coelom, a ventral heart, and an anterior skull with a large brain. **Review Figure 23.37**

- The evolution of jaws from gill arches enabled individuals to grasp large prey and, together with teeth, cut them into small pieces. **Review Figure 23.40**

- **Chondrichthyans** have skeletons of cartilage; almost all species are marine. The skeletons of bony vertebrates are made of bone. Among the bony vertebrates, **ray-finned fishes** have colonized most aquatic environments.

CONCEPT 23.6   Life on Land Contributed to Vertebrate Diversification

- Lungs and jointed appendages enabled one lineage of **lobe-limbed vertebrates** to colonize the land. This lineage gave rise to the **tetrapods**. **Review Figure 23.44**

- The earliest split in the tetrapod tree is between the **amphibians** and the **amniotes** (**reptiles** and **mammals**).

- Most modern amphibians are confined to moist environments because they and their eggs lose water rapidly. **Review Figure 23.45 and ANIMATED TUTORIAL 23.4**

- An impermeable skin, efficient kidneys, and an egg that could resist desiccation evolved in the amniotes. **Review Figure 23.47 and ACTIVITY 23.3**

- The major living reptile groups are the **lepidosaurs** (**tuataras**, lizards, snakes, and amphisbaenas), **turtles**, and **archosaurs** (**crocodilians** and **birds**). **Review Figure 23.48**

- **Mammals** are unique among animals in supplying their young with a nutritive fluid (milk) secreted by mammary glands. There are two primary mammalian clades: the **prototherians** (of which there are only five species) and the species-rich **therians**. The therian clade is subdivided into the **marsupials** and the **eutherians**. **Review Table 23.3**

CONCEPT 23.7   Humans Evolved among the Primates

- Grasping limbs with opposable digits distinguish **primates** from other mammals. The **prosimian** clade includes the lemurs, lorises, and galagos; the **anthropoid** clade includes tarsiers, monkeys, apes, and humans. **Review Figure 23.54**

- **Hominid** ancestors developed efficient **bipedal locomotion**. Several species of *Homo* coexisted in parts of the world until recently. **Review Figure 23.55**

- In the lineage leading to *Homo*, brains became larger as jaws became smaller. The two events appear to be developmentally linked and are an example of evolution via **neoteny**. **Review Figure 23.56**

See **ACTIVITY 23.4** for a concept review of the major groups of organisms.

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is23

Go to LaunchPad at **macmillanhighered.com/launchpad** for additional resources, including LearningCurve Quizzes, Flashcards, and many other study and review resources.

PART 5
Plant Form and Function

24

The Plant Body

Kenaf is being grown as an alternative source of pulp for paper production.

People use plants and substances made from them not only for food but also for fiber, fuel, shelter, and medicines. The clothes you are wearing probably contain cotton, and the paper this book is printed on comes from wood pulp. About 5,000 years ago, Egyptians found that when stems of the papyrus plant (*Cyperus papyrus*) were peeled and dried, they could be formed into sheets that were easier to write on and store than parchment made from animal skins. About 3,000 years later, the Chinese invented a new method of papermaking that persists today: they mixed fibrous plant materials with water, mashed the mixture into a pulp, and pressed it into sheets, which they then dried.

With the advent of computers, economists predicted a lower demand for paper and therefore for the trees that provide the wood pulp used in papermaking. But this has not happened. Every year, U.S. residents use about 500 kilograms of paper per person, and paper constitutes about one-third of all solid waste. In both Europe and the United States, 90 percent of the forest cover that existed when papermaking was invented has disappeared because of the demand for fiber for paper as well as wood for energy production, heating, and construction. To regenerate these forests and to provide a sustainable resource for papermaking, there is considerable interest in growing fibrous crops that can substitute for trees.

Kenaf (*Hibiscus cannabinus*) is an angiosperm that grows readily and rapidly in Asia and parts of Africa. Although it does not produce wood, kenaf has stems rich in fiber. It has been cultivated for three millennia in Asia, where its fiber is used to make bags, rope, dry bedding for animals, and even sails. There is now interest in using kenaf fiber for papermaking. Compared with southern pine trees, the current main source of pulp for paper, kenaf grows more rapidly (it matures in months rather than years), produces more fiber per hectare of land, and requires less water and fewer chemicals when used in paper production. Newspapers and greeting cards made from kenaf paper are stronger, yet thinner, than products made from typical wood pulp. The future of this plant as a resource for papermaking looks bright.

Q What are the properties of the kenaf plant that make it suitable for papermaking?

The Plant Body Is Organized and Constructed in a Distinctive Way

Plants must harvest energy from sunlight and mineral nutrients from the soil. Because they are stationary (sessile), they cannot move to find a more favorable environment or to avoid predators. Their body plan and physiology allow plants to respond to these challenges:

- Stems, leaves, and roots have structural adaptations that enable plants anchored to one spot to capture scarce resources effectively, both above and below the ground.

- Their ability to grow throughout their lifetimes enables plants to respond to environmental cues by redirecting their growth to exploit environmental opportunities, as when roots grow toward a water supply. We will return to plant–environment relationships in Chapter 28.

In Chapter 21 we saw how modern plants arose from aquatic ancestors, giving rise to simple land plants and then vascular plants. Despite their obvious differences in size and form, all vascular plants have essentially the same simple structural organization. This chapter describes the basic architecture of the largest group of vascular plants, the angiosperms (flowering plants), and shows how so much diversity (there are more than 250,000 species of angiosperms) can literally grow out of such a simple basic form. In this chapter we focus on the angiosperms' three kinds of vegetative (nonsexual) organs: roots, stems, and leaves. We will cover reproductive organs in Chapter 27.
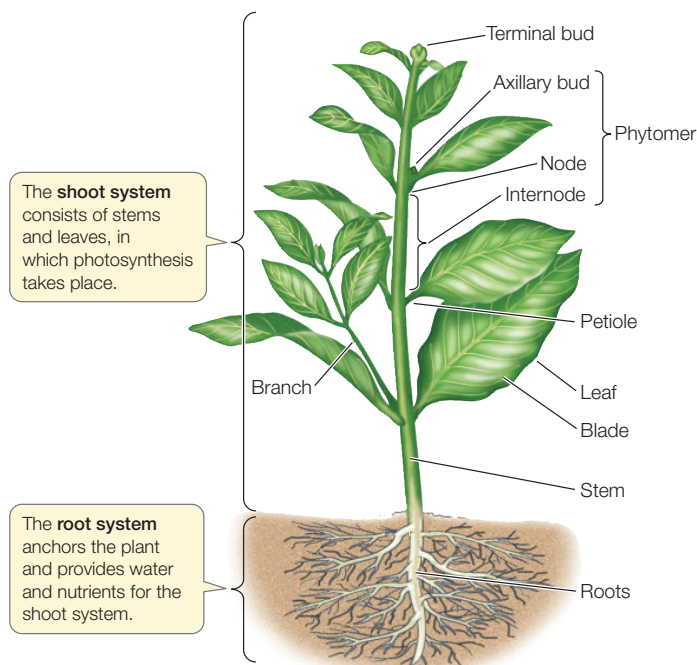
Plant organs are organized into two systems (**FIGURE 24.1**):

- The **root system** anchors the plant in place. **Roots** absorb water and dissolved minerals and store the products of photosynthesis. The extreme branching of roots and their high surface area-to-volume ratios allow them to absorb water and mineral nutrients from the soil efficiently.

- The **shoot system** consists of the stems, leaves, and flowers. The **leaves** are the chief organs of photosynthesis. The **stems** hold and orient the leaves to the sun and provide connections for the transport of materials between roots and leaves. The flowers are shoots modified for reproduction.

Shoots are composed of repeating modules called **phytomers**. Each phytomer consists of a node carrying one or more leaves; an internode, which is the interval of stem between two nodes; and one or more axillary buds, each of which forms in the angle where the leaf meets the stem. A **bud** is an undeveloped shoot that can produce another leaf, a phytomer, or a flower.

As noted in Chapter 21, most angiosperms belong to one of two major clades (see Figure 21.27). **Monocots** are generally narrow-leaved plants such as grasses, lilies, orchids, and palms. **Eudicots** are generally broad-leaved plants such as soybeans, roses, sunflowers, and maples. These two clades, which account for 97 percent of angiosperm species, differ in several important structural characteristics (**FIGURE 24.2**).

Plants develop differently than animals

The four processes that govern the development of all organisms, whether plant or animal, are determination (the commitment of an embryonic cell to its ultimate fate in the organism); differentiation (the specialization of a cell); morphogenesis (the organization and spatial distribution of cells into tissues and organs); and growth (increase in body size). In plants, these processes are influenced by three properties unique to plants: meristems, cell walls, and the totipotency of most cells.

> **LINK**
> The processes of development are described in **Concept 14.1**

MERISTEMS Plants grow throughout their lifetimes. Although adult humans, for example, have stem cells to replace tissues lost through damage or apoptosis, these cells do not contribute to further growth. In contrast, plants have **meristems** that are capable of producing new roots, stems, leaves, and flowers throughout the plant's life, enabling the plant to continue growing.

CELL WALLS Plant cells are surrounded by a **cell wall**. This rigid extracellular matrix makes it impossible for cells to move from place to place as they do in animal development. Instead, plant morphogenesis occurs through alterations in the plane of cell division at cytokinesis, which in turn change the direction of cell expansion and thereby the direction in which a piece of tissue grows (**FIGURE 24.3**). Plant cytokinesis occurs along a cell plate laid down by Golgi vesicles (see Figure 7.7B). Unlike animal cells, in which the location of cytokinesis depends on

The **shoot system** consists of stems and leaves, in which photosynthesis takes place.

The **root system** anchors the plant and provides water and nutrients for the shoot system.

Terminal bud
Axillary bud
Phytomer
Node
Internode
Petiole
Branch
Leaf
Blade
Stem
Roots

FIGURE 24.1 Vegetative Plant Organs and Systems The basic plant body plan, with root and shoot systems, and the principal vegetative organs.

the location of the middle of the mitotic spindle, the location of the plant cell plate is determined earlier—during interphase.

TOTIPOTENCY   In animals, only early embryonic cells are totipotent, although some stem cell populations, such as those in bone marrow, are multipotent (capable of differentiating into a few different cell types). In contrast, in plants even

These planes of cell division lead to an increase in thickness (radial expansion). In some cases, cell division in this plane leads to a branch.

Apical–basal axis

These planes of cell division lead to an increase in length (apical–basal expansion).

FIGURE 24.3 Cytokinesis and Morphogenesis   The plane of cell division can determine the growth pattern of a plant organ, as in this section of a shoot.

differentiated cells are pluripotent, and most are totipotent (see Figure 14.3). This means a plant can readily repair damage wrought by the environment or herbivores.

LINK

See **Concept 13.4** for the use of totipotency in plant biotechnology

The plant body has an apical–basal axis and a radial axis

Two basic patterns are established early in plant embryogenesis (embryo formation) (**FIGURE 24.4**):

- The **apical–basal** axis: the arrangement of cells and tissues along the main axis from root to shoot

- The **radial** axis: the concentric (circular) arrangement of the tissue systems (which we will discuss in the next section)

Both axes are best understood in developmental terms. We focus here on embryogenesis in the model eudicot *Arabidopsis thaliana*, in which the process has been intensively studied.

FIGURE 24.2 Comparing the Two Major Angiosperm Clades
The figure shows the major structural differences between monocots and eudicots.

	Monocots	Eudicots
Embryos	One cotyledon	Two cotyledons
Stems	Vascular tissue scattered	Vascular tissue arranged in concentric circles
Leaf venation	Veins usually parallel	Veins form a network
Root system	Fibrous (no main root)	Taproot (main root) usually present
Flowers	Floral organs usually in multiples of three	Floral organs usually in multiples of four or five
Pollen	Pollen grain with single furrow or pore	Pollen grain with three furrows or pores

Shoot

Root

Radial axis

Apical–basal axis

Apical–basal pattern

Epidermis (dermal)

Ground

Vascular

Radial pattern

FIGURE 24.4 Two Patterns for Plant Morphogenesis   (A) The apical–basal pattern is the arrangement of cells and tissues along the main axis from root to shoot. (B) The radial pattern determines the concentric arrangement of tissues.
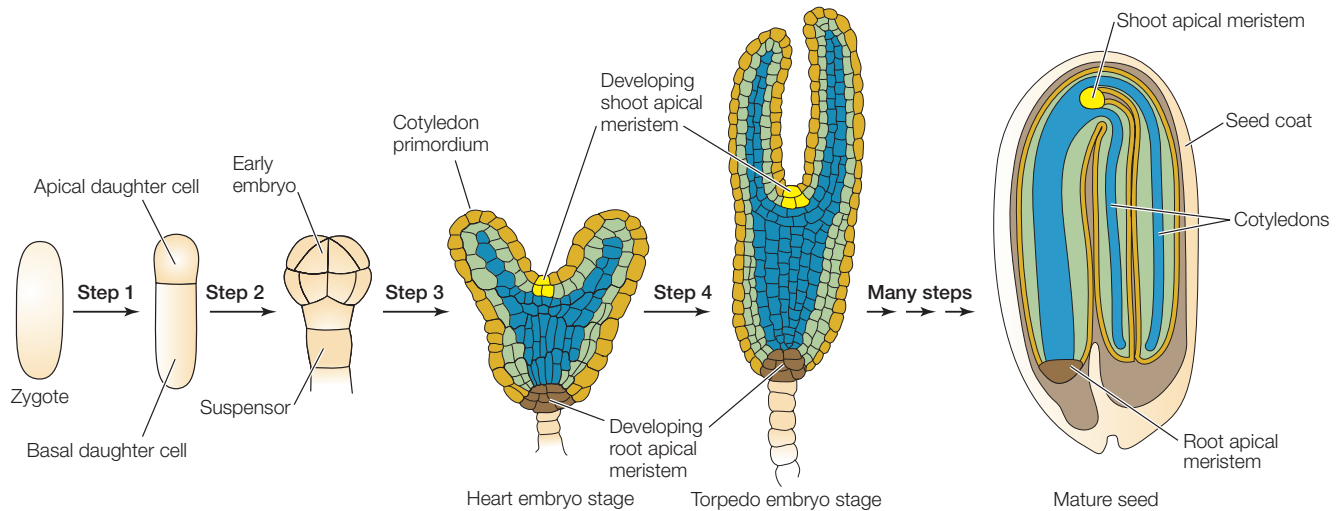
FIGURE 24.5 **Plant Embryogenesis** The basic body plan of the model eudicot *Arabidopsis thaliana* is established in several steps. By the heart embryo stage, the three tissue systems are established: the dermal (gold), ground (light green), and vascular (blue) tissue systems. These tissues are shown in the mature seed, which develops after many more stages.

The first step in the formation of a plant embryo is a mitotic division of the zygote that gives rise to two daughter cells (**FIGURE 24.5, STEP 1**). An asymmetrical plane of cell division results in an uneven distribution of cytoplasm between these two cells, which face different fates. Signals in the smaller, apical (upper) daughter cell induce it to produce the embryo proper, while the other, larger daughter cell produces a supporting structure, the **suspensor** (**FIGURE 24.5, STEP 2**). This division not only establishes the apical–basal axis of the new plant but also determines its polarity (which end is the tip, or apex, and which is the base). A longer, thinner suspensor and a more spherical or globular embryo are distinguishable after just four mitotic divisions (see Figure 14.1).

In eudicots, the initially globular embryo develops into the characteristic heart stage as the **cotyledons** ("seed leaves") start to grow (**FIGURE 24.5, STEP 3**). Further elongation of the cotyledons and of the apical–basal axis of the embryo gives rise to the torpedo stage, during which some of the internal tissues begin to differentiate (**FIGURE 24.5, STEP 4**). Between the cotyledons is the **shoot apical meristem**; at the other end of the axis is the **root apical meristem**. These meristems contain undifferentiated cells that will divide to give rise to the shoot and root systems.

As shown in Figure 24.5, step 2, the plant embryo is first a sphere and later a cylinder. The root and stem retain a generally cylindrical shape throughout the plant's life. You can see this most easily in the trunk of a tree. By the end of embryogenesis, the radial axis of the plant has been established. The embryonic plant contains three tissue systems, arranged concentrically, that will give rise to the tissues of the adult plant body.

The plant body is constructed from three tissue systems

A **tissue** is an organized group of cells that have features in common and that work together as a structural and functional
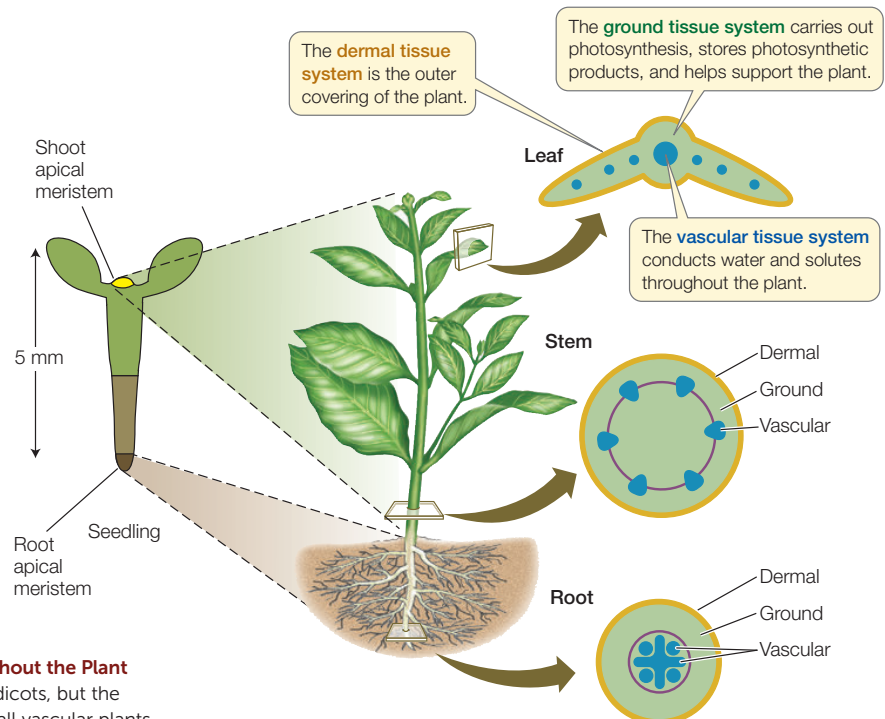
FIGURE 24.6 **Three Tissue Systems Extend throughout the Plant Body** The arrangement shown here is typical of eudicots, but the three tissue systems are continuous in the bodies of all vascular plants.

unit. In plants, tissues, in turn, are grouped into **tissue systems**. Despite their structural diversity, all vascular plants are constructed from three tissue systems: dermal, vascular, and ground. These three tissue systems are established during embryogenesis and ultimately extend throughout the plant body in a concentric arrangement (**FIGURE 24.6**). Each tissue system has distinct functions and is composed of different mixtures of cell types.

DERMAL TISSUE SYSTEM   The **dermal tissue system** forms the **epidermis**, or outer covering, of a plant, which usually consists of a single cell layer. Epidermal cells are typically small. Some of them differentiate to form one of three specialized structures:

- *Stomata*, which are pores for gas exchange in leaves (see Figure 25.13)
- *Trichomes*, or leaf hairs, which provide protection against insects and damaging solar radiation (see Figure 28.7)
- *Root hairs*, which greatly increase root surface area, thus providing more surface for the uptake of water and mineral nutrients (see Figure 24.8)

Aboveground epidermal cells secrete a protective extracellular **cuticle** made of cutin (a polymer composed of long chains of fatty acids), a complex mixture of waxes, and cell wall polysaccharides. The cuticle limits water loss, reflects potentially damaging solar radiation, and serves as a barrier against pathogens.

As the stems and roots of woody plants expand, the epidermis is shed and is replaced by a dermal tissue called periderm. As we will see in Concept 24.3, this tissue includes an outer layer of cork that is impermeable to water and gases.

GROUND TISSUE SYSTEM   Virtually all the tissue lying between dermal tissue and vascular tissue in both shoots and roots is part of the **ground tissue system**, which therefore makes up most of the plant body. Ground tissue contains three cell types.

Parenchyma cells are the most abundant ground tissue cells. They have large vacuoles and relatively thin cell walls. They perform photosynthesis (in the shoot) and store protein (in seeds) and starch (in roots).
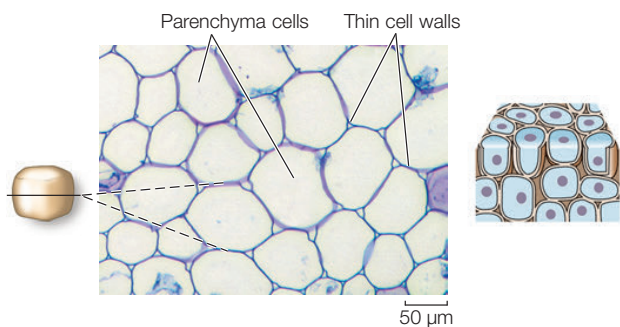
Collenchyma cells are elongated and have unevenly thickened primary cell walls. They provide support for growing tissues such as stems. The familiar "strings" in celery consist primarily of collenchyma cells.

Collenchyma cells   Unevenly thickened cell walls

50 μm
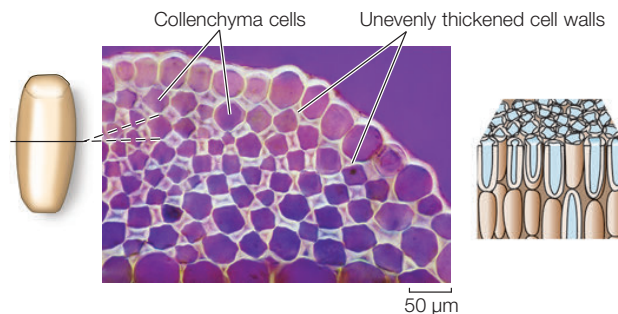
Sclerenchyma cells have very thick secondary walls reinforced with the polyphenol polymer **lignin**. Most sclerenchyma cells undergo programmed cell death (apoptosis; see Concept 7.5), but their strong cell walls remain to provide support for the plant. There are two types of sclerenchyma cells: fibers and sclereids. Elongated **fibers** provide relatively rigid support to wood and other parts of the plant, within which they are often organized into bundles. When wood is used to make high-quality paper, the wood pulp must be treated extensively to break down and remove the lignin in the fibers.

Fibers   Thick cell walls

50 μm
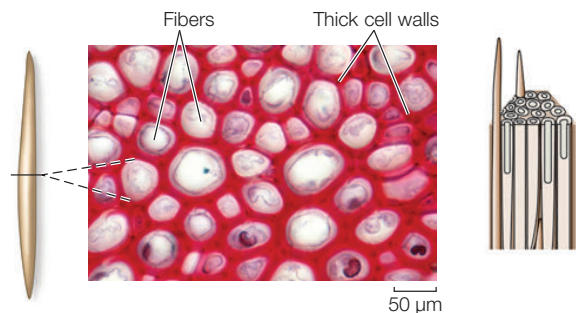
The bark of trees owes much of its mechanical strength to long fibers. **Sclereids** occur in various shapes and may pack together densely, as in a nut's shell or in some seed coats.

Parenchyma cells   Thin cell walls

50 μm

Sclereids   Thick cell walls

50 μm
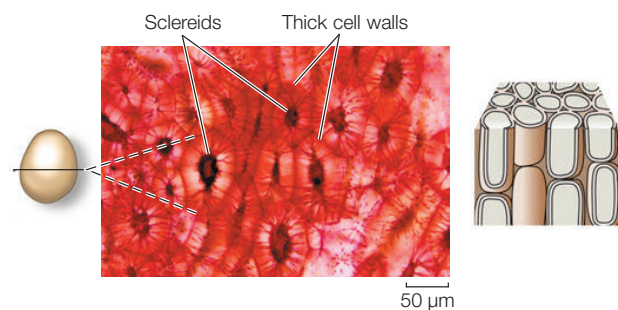
Isolated clumps of sclereids, called stone cells, in pears and some other fruits give them their characteristic gritty texture.

VASCULAR TISSUE SYSTEM   The **vascular tissue system** is the plant's plumbing or transport system—the distinguishing feature of vascular plants. Its two constituent tissues, the xylem and phloem, distribute materials throughout the plant.

> **LINK**
>
> The functions of xylem and phloem are described in
> **Concepts 25.3 and 25.4**

Xylem distributes water and mineral ions taken up by the roots to all the cells of the roots and shoots. It contains two types of conducting cells—tracheids and vessel elements—which, like most sclerenchyma cells, are dead when mature. **Tracheids** are spindle-shaped cells, with thinner regions in the cell wall called pits through which water can move with little resistance from one tracheid to its neighbors. **Vessel elements** are larger in diameter than tracheids. They meet end-to-end and partially break down their end walls, forming an open pipeline for water conduction. The xylem also contains living parenchyma cells that regulate the movement of ions into the conducting cells.
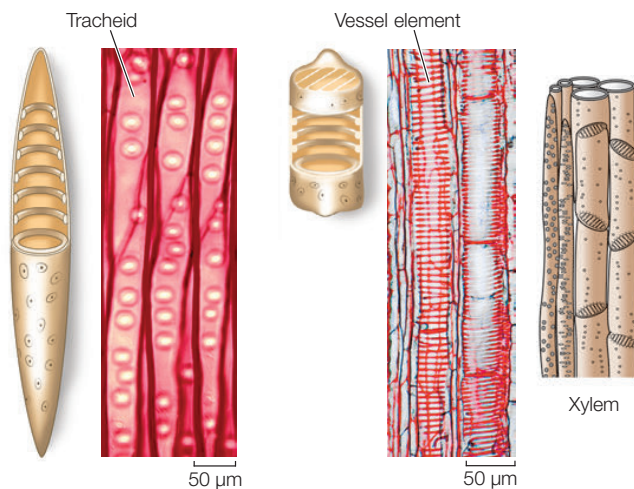
Phloem **Phloem** generally consists of living cells. It transports carbohydrates (primarily sugars) from sites where they are produced (called sources) to sites where they are used or stored (called sinks). Sources are often photosynthetic organs (such as leaves) but also include nonphotosynthetic storage organs (such as tubers and seeds) when they are drawn on to supply sugars to other parts of a plant. Sinks include growing tissues, roots, and developing flowers and fruit. The characteristic cells of the phloem are **sieve tube elements**, which, like vessel elements, meet end-to-end, forming sieve tubes. Instead of the ends of the cells breaking down, however, the sieve tube elements are connected by plasmodesmata (see Figure 4.7), which form a set of pores called a sieve plate. Although still alive, mature

sieve tube elements have lost much of their cellular contents; adjacent, fully functional **companion cells** are connected to the sieve tube elements by plasmodesmata and perform many of the phloem's metabolic functions.
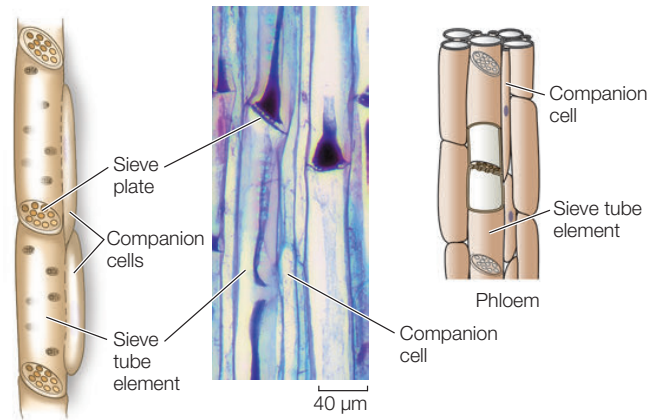
Xylem and phloem tissues may also contain fibers, which provide structural support.

> **CHECKpoint   CONCEPT 24.1**
>
> ✓ Make a table listing the three tissue systems of plants and their functions.
> ✓ What are the similarities and differences between plant and animal development?
> ✓ What are the similarities and differences between a root and a shoot?
> ✓ A mutant strain of *Arabidopsis thaliana* lacks apical–basal polarity in the embryo. What would you expect the phenotype of the plant to be?

We've discussed the basic body plan and tissue systems of plants, and how the apical–basal axis and radial axis arise during embryo development. Now let's see how the cells and tissues we have just described allow the embryo to build an adult plant body.

> **CONCEPT 24.2   Apical Meristems Build the Primary Plant Body**

As noted above, plants and animals differ in how they develop and function. Whereas animals use their mobility to forage for food, plants stay in place and grow toward resources, both above and below the ground. So plant shoots grow toward sunlight, and roots grow toward water and minerals in the soil. In most animals, growth is **determinate**: it ceases when the adult state is reached. Some plant organs, such as most leaves and flowers, show this characteristic. By contrast, the growth of roots and shoots is **indeterminate**, an open-ended process which can be lifelong.

Terminal bud

Axillary bud

Leaf primordia

The **terminal bud** contains a shoot apical meristem.

Shoot apical meristem

Axillary bud primordium

In woody plants the **vascular cambium** and **cork cambium** thicken the stem and root.

Lateral meristems:
Cork cambium
Vascular cambium

100 μm

Root apical meristem

Root cap
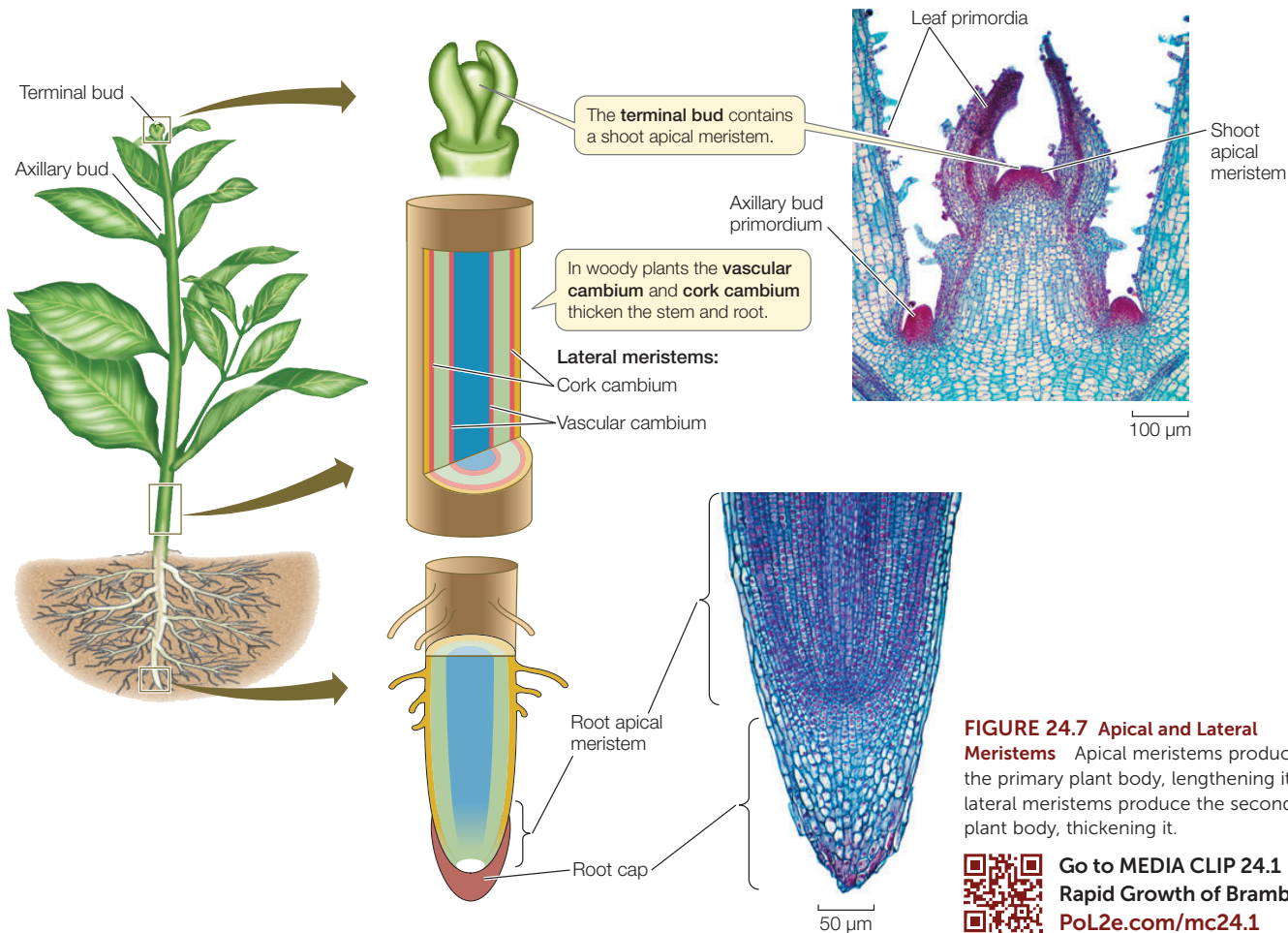
FIGURE 24.7 Apical and Lateral Meristems Apical meristems produce the primary plant body, lengthening it; lateral meristems produce the secondary plant body, thickening it.

Go to MEDIA CLIP 24.1
Rapid Growth of Brambles
PoL2e.com/mc24.1

50 μm

Plants grow in two ways (**FIGURE 24.7**):

- **Primary growth** results in the formation and lengthening of shoots and roots. **Apical meristems** produce primary growth, giving rise to the primary plant body. All seed plants have a primary plant body.

- **Secondary growth** increases plant thickness. **Lateral meristems** produce secondary growth, resulting in the secondary plant body. Secondary growth occurs in woody eudicots, such as trees and shrubs. Monocots typically do not undergo secondary growth.

The remainder of this section will focus on primary growth. We will return to secondary growth in Concept 24.3.

A hierarchy of meristems generates the plant body

Even before a seed germinates, the plant embryo inside the seed has two meristems: a shoot apical meristem at the end of the embryonic shoot and a root apical meristem near the end of the embryonic root (see Figure 24.5). The dividing cells of the meristems are comparable to animal stem cells: after their division, one daughter cell is capable of differentiating, and the other retains its undifferentiated phenotype.

The apical meristems form the root and shoot organs of the adult plant. They do so by producing three **primary meristems**.

From the outside to the inside of the root or shoot, which are both cylindrical, the primary meristems are the **protoderm**, the **ground meristem**, and the **procambium**. These meristems, in turn, give rise to the three tissue systems:

Apical meristems	→ Primary meristems	→ Tissue systems
Root or shoot apical meristem	Protoderm ——————→	Dermal tissue system
	Ground meristem ——→	Ground tissue system
	Procambium ————→	Vascular tissue system
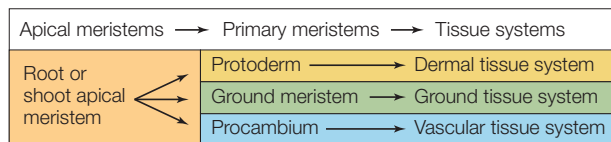
In plants that have secondary growth, the lateral meristems represent an additional level in the meristem hierarchy; for this reason, lateral meristems are also referred to as secondary meristems.

Not all meristems fit within this framework. The totipotency of many plant cells means that even differentiated, non-meristematic cells can give rise to new meristems under certain circumstances. Examples include some forms of asexual reproduction and the propagation of plants from stem cuttings. The ability of non-meristematic cells to further divide is important in wound repair.

The root apical meristem gives rise to the root cap and the root primary meristems

The root apical meristem produces all the cells that contribute to growth in the length of a root (**FIGURE 24.8A**). Some of the daughter cells from the apical (tip) end of the root apical meristem contribute to a **root cap**, which protects the delicate growing region of the root as it pushes through the soil. The root cap secretes a mucopolysaccharide (slime) that acts as a lubricant. Even so, the cells of the root cap are often damaged or scraped away and must therefore be replaced constantly. The root cap is also the structure that detects the pull of gravity and thus controls the downward growth of roots.

Above the root cap, the cells in the root tip are arranged in several zones. The apical and primary meristems constitute the **zone of cell division**, the source of all the cells of the root's primary tissues. Daughter cells of the divisions of the apical meristem become the three cylindrical primary meristems: the protoderm, the ground meristem, and the procambium. These meristems in turn produce all the cells of the three tissues systems in the root. Just above this zone is the **zone of cell elongation**, where the newly formed cells are elongating and thus pushing the root farther into the soil. Above that zone is the **zone of cell maturation**, where the cells are completing their differentiation. These three zones grade imperceptibly into one another; there is no abrupt line of demarcation.

In the middle of the root apical meristem is a quiescent center, where cell divisions are rare. The rare divisions produce cells that ultimately become the root apical meristem.

The products of the root's primary meristems become root tissues

The products of the three primary meristems (the protoderm, ground meristem, and procambium) are the tissue systems of the mature root: the epidermis (dermal tissue), cortex (ground tissue), and stele (vascular tissue) (**FIGURE 24.8B**).

The protoderm gives rise to the epidermis, an outer layer of cells that protect the root and absorb mineral ions and water. Many of the epidermal cells produce long, delicate root hairs (**FIGURE 24.8C**).

Internal to the protoderm, the ground meristem gives rise to a region of ground tissue that is many cells thick, called the **cortex**. The parenchyma cells of the cortex are relatively unspecialized and often serve as storage depots. The innermost layer of the cortex is the **endodermis** (see Figure 24.8B). Unlike the cell walls of other cortical cells, those of the endodermal cells contain suberin, a waterproof substance. Strategic placement of suberin in only certain parts of the cell wall enables the cylindrical ring of endodermal cells to control the movement of water and dissolved mineral ions into the vascular tissue system.

> **LINK**
>
> The role of the endodermis is described in more detail in **Concept 25.3**

Interior to the endodermis is the vascular cylinder, or **stele**, produced by the procambium. The stele consists of three types of cells: pericycle, xylem, and phloem. The **pericycle** consists of one or more layers of parenchyma cells. It has three important functions:

- It is the tissue from which lateral roots arise.
- It can contribute to secondary growth by giving rise to lateral meristems that thicken the root.
- Its cells contain membrane transport proteins that export nutrient ions into cells of the xylem.

(A)

Lateral root meristem

Epidermis

Zone of cell maturation

Zone of cell elongation

Zone of cell division

Primary meristems:

Protoderm

Ground meristem

Procambium

New daughter cells are produced in the **root apical meristem**. Most daughter cells differentiate into the primary tissues of the root.

Quiescent center

Some daughter cells become part of the **root cap**, which is constantly being eroded away.

(B) Epidermis — Developing lateral root

Cortex — Endodermis — Stele

(C)

Root hairs

1 mm

FIGURE 24.8 Tissues and Regions of the Root (A) Diagram of a longitudinal section of a root, showing how cell division creates the complex structure of the root. (B) A cross-section through a region of a willow root. Note the emerging lateral root, which arises from tissues deep within the root. (C) Root hairs, seen with a scanning electron microscope.

APPLY THE CONCEPT

Meristems build roots

A research team investigated how long root cells continued to divide after being produced by the root apical meristem. They incubated germinating bean seeds for 2 hours with their roots suspended in water containing radioactive thymidine, which is taken up by dividing cells and incorporated into their DNA as it replicates (making the DNA radioactive).

After this incubation period, the researchers removed some of the seeds (time 0 in the table) and took longitudinal slices from the roots (see Figure 24.8A). They transferred the rest of the seeds to water containing nonradioactive thymidine and left them there for various times (12, 36, and 72 hours) before taking root slices. They tallied the number of radioactive cells found in each of the four regions of each root and compared those numbers with the total number of cells in each region. The table shows the results.

TIME AFTER TRANSFER (hr)	RADIOACTIVE CELLS/TOTAL CELLS			
	ROOT CAP	ROOT APICAL MERISTEM	ZONE OF CELL ELONGATION	ZONE OF CELL MATURATION
0	0/63	90/115	0/32	0/22
12	2/58	95/110	16/29	0/27
36	36/60	45/119	14/30	12/31
72	12/24	0/116	2/31	30/32

1. At 0 hours, why did only root apical meristem cells contain radioactive thymidine?

2. For each region, calculate the percentage of radioactive cells and plot that percentage over time.

3. Explain the rise and fall in the percentage of radioactive cells in each region.

At the very center of the root of a eudicot lies the xylem. Seen in cross section, it typically has the shape of a star with a variable number of points (**FIGURE 24.9A**). Between the points are bundles of phloem. In monocots, a region of parenchyma cells called the **pith** typically lies in the center of the root, surrounded by xylem and phloem (**FIGURE 24.9B**). Pith, which often stores carbohydrate reserves, is also found in the stems of eudicots.

The root system anchors the plant and takes up water and dissolved minerals

Water and mineral nutrients enter most plants through the root system, which is located in the soil. Although hidden from view, the root system is often larger than the visible shoot system. For example, the root system of a 4-month-old winter rye plant (*Secale cereale*) was found to be 130 times larger than the shoot system, with almost 13 million branches that had a cumulative length of over 500 kilometers! The large size of root systems gives them an enormous surface area for absorbing water and nutrients from the soil.

The root system of angiosperms originates in an embryonic root called the radicle. In most eudicots the radicle develops as a primary root (called the **taproot**) that extends downward by tip growth and outward by initiating **lateral roots** (**FIGURE 24.10A**).

In monocots, the radicle-derived initial root is short-lived. Monocots form a **fibrous root system** composed of numerous thin roots that are all roughly equal in diameter (**FIGURE 24.10B**). These roots are **adventitious**: they arise from stem tissues above the initial root. Fibrous root systems often form dense networks of roots near the soil surface, binding the soil together. The fibrous root systems of grasses, for example, may protect steep hillsides where runoff from rain would otherwise cause erosion.

(A) Eudicot stele — Endodermis, Pericycle, Cortex, Phloem, Xylem, 150 μm
(B) Monocot stele — Endodermis, Phloem, Xylem, Cortex, Pith, 1 mm
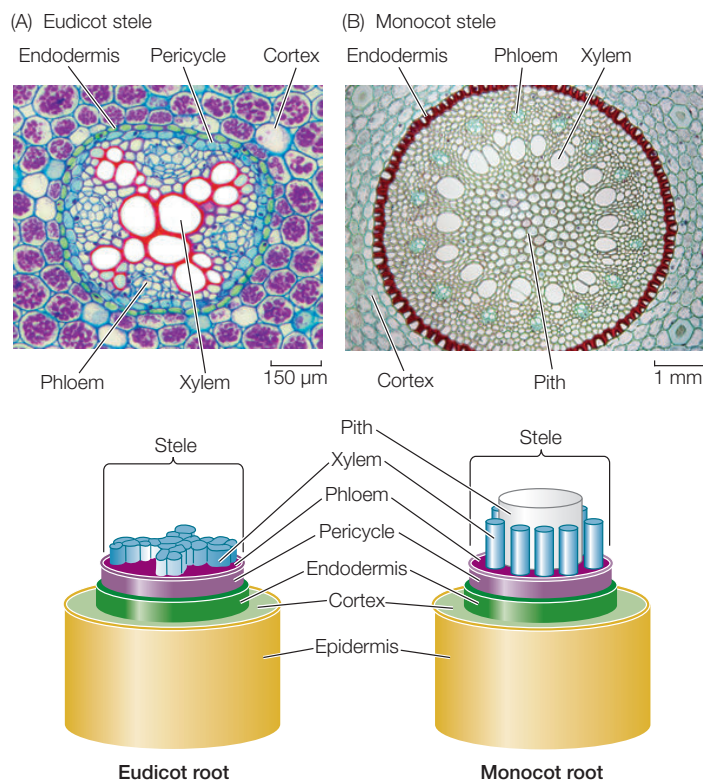
FIGURE 24.9 Products of the Root's Primary Meristems The protoderm gives rise to the epidermis, the outermost layer of cells. The ground meristem produces the cortex, the innermost layer of which is the endodermis. The vascular tissues of the root are found in the stele, which is the product of the procambium. The arrangement of tissues in the stele differs in the roots of (A) eudicots and (B) monocots.

Go to ACTIVITY 24.1 Eudicot Root
PoL2e.com/ac24.1

Go to ACTIVITY 24.2 Monocot Root
PoL2e.com/ac24.2

Eudicot root — Stele, Pith, Xylem, Phloem, Pericycle, Endodermis, Cortex, Epidermis

Monocot root — Stele

(A) Taproot system

Lateral root

Taproot

(B) Fibrous root system

Leaves (bulb)

Adventitious roots
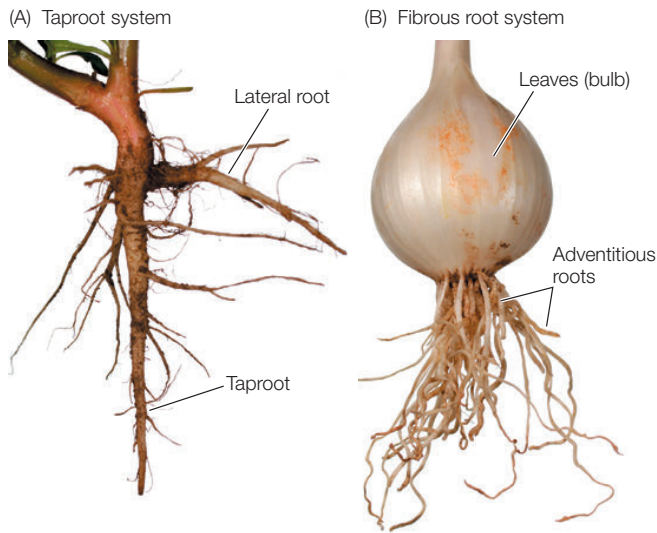
FIGURE 24.10 Root Systems of Eudicots and Monocots
(A) Eudicots typically have taproot systems, as in the seedling of the herb epazote. (B) This garlic bulb shows the fibrous root system typical of monocots.

The products of the shoot's primary meristems become shoot tissues

The shoot apical meristem, like the root apical meristem, forms three primary meristems: protoderm, ground meristem, and procambium. These primary meristems, in turn, give rise to the three shoot tissue systems. The shoot apical meristem repetitively lays down the beginnings of leaves and axillary buds (corresponding to the phytomers in Figure 24.1). Leaves arise from bulges called leaf primordia, which form as cells divide on the sides of the shoot apical meristem (see Figure 24.7). Bud primordia form above the bases of the leaf primordia, where they may initiate new shoots. The growing stem has no protective structure analogous to the root cap, but the leaf primordia can act as a protective covering for the shoot apical meristem.

As in roots, the shoot protoderm, ground meristem, and procambium give rise, respectively, to the shoot epidermis, the shoot cortex, and the shoot vascular system. The vascular tissue of young stems is divided into discrete **vascular bundles** (**FIGURE 24.11**). Each vascular bundle contains both xylem and

(A) Eudicot

500 μm

The vascular tissues in stems are organized into bundles.

Xylem

Phloem

Fibers

Eudicot vascular bundle

100 μm

(B) Monocot

500 μm

Xylem

Phloem

Monocot vascular bundle

50 μm
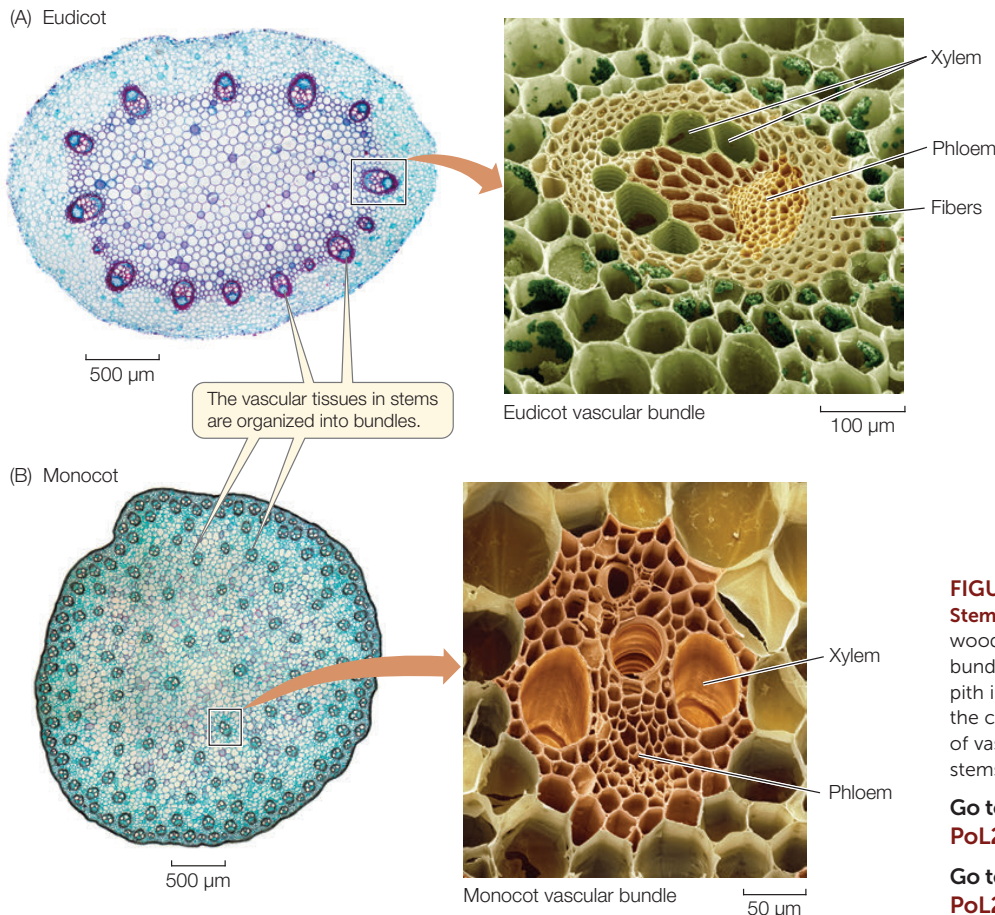
FIGURE 24.11 Vascular Bundles in Stems (A) In herbaceous and young woody eudicot stems, the vascular bundles are arranged in a cylinder, with pith in the center and the cortex outside the cylinder. (B) A scattered arrangement of vascular bundles is typical of monocot stems.

Go to ACTIVITY 24.3 Eudicot Stem
PoL2e.com/ac24.3

Go to ACTIVITY 24.4 Monocot Stem
PoL2e.com/ac24.4

phloem. In eudicots, the vascular bundles are arranged along the periphery and appear in a circle in cross section, but in monocots they are scattered throughout the stem.

Leaves are photosynthetic organs produced by shoot apical meristems

For most of its life, a plant produces leaves from shoot apical meristems. As shown in Figure 24.7, leaves originate from leaf primordia at the sides of the shoot apical meristem. Unlike the growth of roots and stems, the growth of leaves is finite, or determinate: leaves generally stop growing once they reach a predetermined mature size and shape.

Typically, the **blade** of a leaf is a thin, flat structure. In many eudicots, the blade is attached to the stem by a stalk called a **petiole** (see Figure 24.1). Often the petiole can adjust the orientation of the leaf blade relative to the rays of the sun, ranging from perpendicular to the light rays (to maximize photosynthesis) to parallel (to prevent overheating). Some leaves track the sun over the course of the day, moving so that they constantly face it. Monocots typically do not have petioles, and the base of the leaf may form a sheath that wraps around the stem.

Leaf anatomy is beautifully adapted to carry out photosynthesis and to support that process by exchanging the gases O_2 and CO_2 with the environment, limiting evaporative water loss, and exporting the products of photosynthesis to the rest of the plant. **FIGURE 24.12** shows a section of a typical eudicot leaf in three dimensions.

Most eudicot leaves have two zones of photosynthetic parenchyma tissue called **mesophyll** (which means "middle of the leaf"). The upper layer or layers of mesophyll, which consist of elongated cells, constitute a zone called palisade mesophyll. The lower layer or layers, which consist of irregularly shaped cells, constitute a zone called spongy mesophyll. Within the
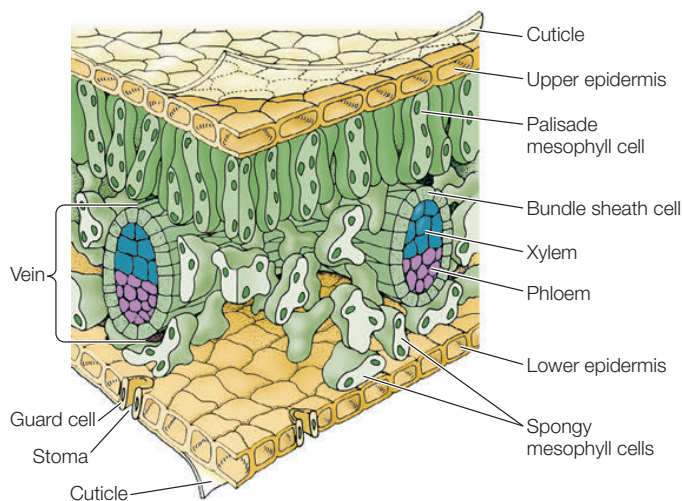
mesophyll is a network of air spaces through which CO_2 can diffuse to photosynthesizing cells. Vascular tissue branches extensively throughout the leaf, forming a network of veins that extend to within a few cell diameters of all its cells, ensuring that the mesophyll cells are well supplied with water and mineral nutrients by the xylem. The products of photosynthesis are loaded into the phloem of the veins for export to the rest of the plant.

> **LINK**
>
> Photosynthesis is described in **Concepts 6.5 and 6.6**

Covering virtually the entire leaf on both its upper and lower surfaces is a layer of nonphotosynthetic epidermal cells. These cells secrete a cuticle that is impermeable to water. Although the epidermis keeps water in the leaf, it also keeps out CO_2—which is needed for photosynthesis. Therefore water and gases are exchanged through pores in the leaf called stomata (see Concept 25.3).

Plant organs can have alternative forms and functions

Flowering plants are incredibly diverse in form. Leaves, stems, and roots of many shapes can perform the basic functions of plant life: photosynthesis, the acquisition of water and nutrients, sensing the environment, and reproduction. These plant organs may also be modified to serve more specialized functions.

Taproots, for example, often function as nutrient storage organs, as in carrots, sugar beets, and sweet potato (**FIGURE 24.13A**). In some monocots—corn and some palms, for example—adventitious roots function as props to help support the shoot (**FIGURE 24.13B**). **Prop roots** are critical to these plants, which, unlike most eudicot tree species, are unable to support aboveground growth through the thickening of their stems.

Various modifications of stems are also seen in nature. The tuber of a potato, for example—the part of the plant eaten by humans—is not a root but rather an underground stem. The "eyes" of a potato are depressions containing axillary buds—in other words, a sprouting potato is just a branching stem (**FIGURE 24.13C**). Many desert plants have enlarged, water-retaining stems (**FIGURE 24.13D**). The runners of strawberry plants are horizontal stems from which roots grow at frequent intervals (**FIGURE 24.13E**). If the links between the rooted portions are broken, independent plants can develop on each side of the break—a form of vegetative (asexual) reproduction (see Concept 7.1).

Leaves are sometimes highly modified for special functions. For example, some leaves serve as storage depots for energy-rich molecules, as in the bulbs of onions. In succulents, the leaves store water. The protective spines of cacti are modified leaves (see Figure 24.13D). Other plants have modified portions of leaves called tendrils that support the plant by wrapping around other structures or plants (**FIGURE 24.13F**).

These are all examples of vegetative plant organs whose functions deviate from the norm. The evolution of these novel roles for established organs is an example of natural selection working with what is already present, as well as an example

Labels: Cuticle, Upper epidermis, Palisade mesophyll cell, Bundle sheath cell, Xylem, Phloem, Lower epidermis, Spongy mesophyll cells, Vein, Guard cell, Stoma, Cuticle

FIGURE 24.12 Eudicot Leaf Anatomy This three-dimensional diagram shows a section of a eudicot leaf.

Go to ACTIVITY 24.5 Eudicot Leaf
PoL2e.com/ac24.5

(A)

(B)

Taproots modified for storage

Prop roots

(C) Branches

(D)

(E)

Tuber (modified stem)

(F)

Barrel (enlarged stem)   Spines (modified leaves)

Shoots

Runner (horizontal stem)

FIGURE 24.13 Modified Roots, Stems, and Leaves (A) The taproots of some eudicots, such as carrots (*Daucus carota*) and sugar beets (*Beta vulgaris*), are nutrient storage organs. (B) The stems of this hala tree (*Pandanus tectorius*), a monocot, are supported by prop roots. (C) A potato (*Solanum tuberosum*) is a modified stem called a tuber; the sprouts that grow from its eyes are shoots, not roots. (D) The stem of this barrel cactus (*Echinocactus grusonii*) is enlarged to store water. Its highly modified leaves serve as thorny spines. Most of this plant's photosynthesis occurs in the stem. (E) The runners of strawberries (*Fragaria* sp.) are horizontal stems that produce roots and shoots at intervals. Rooted portions of the plant can live independently if the runner is cut. (F) The tips of some leaves, as in this red bryony vine (*Bryonia dioica*), are modified into tendrils.

Tendril (modified leaf)

of the interaction between evolution and development—the topic of evolutionary developmental biology (evo-devo).

LINK

See **Concepts 14.4 and 14.5** for a discussion of evolutionary developmental biology

In Concept 24.4 we will return to the modification of plant organs—in this case, the ways they have been manipulated by artificial selection to meet the needs of humans.

CHECKpoint CONCEPT **24.2**

✓ What is the difference between determinate and indeterminate growth? What plant organs undergo each type of growth?

✓ What are the selective advantages of indeterminate growth?

Primary growth forms the plant organs and lengthens them. We now turn to secondary growth, in which some organs can grow in thickness.

Terminal bud

This year's growth

Bud scale

Epidermis

Cortex

Primary phloem

Vascular cambium

Pith

Primary xylem
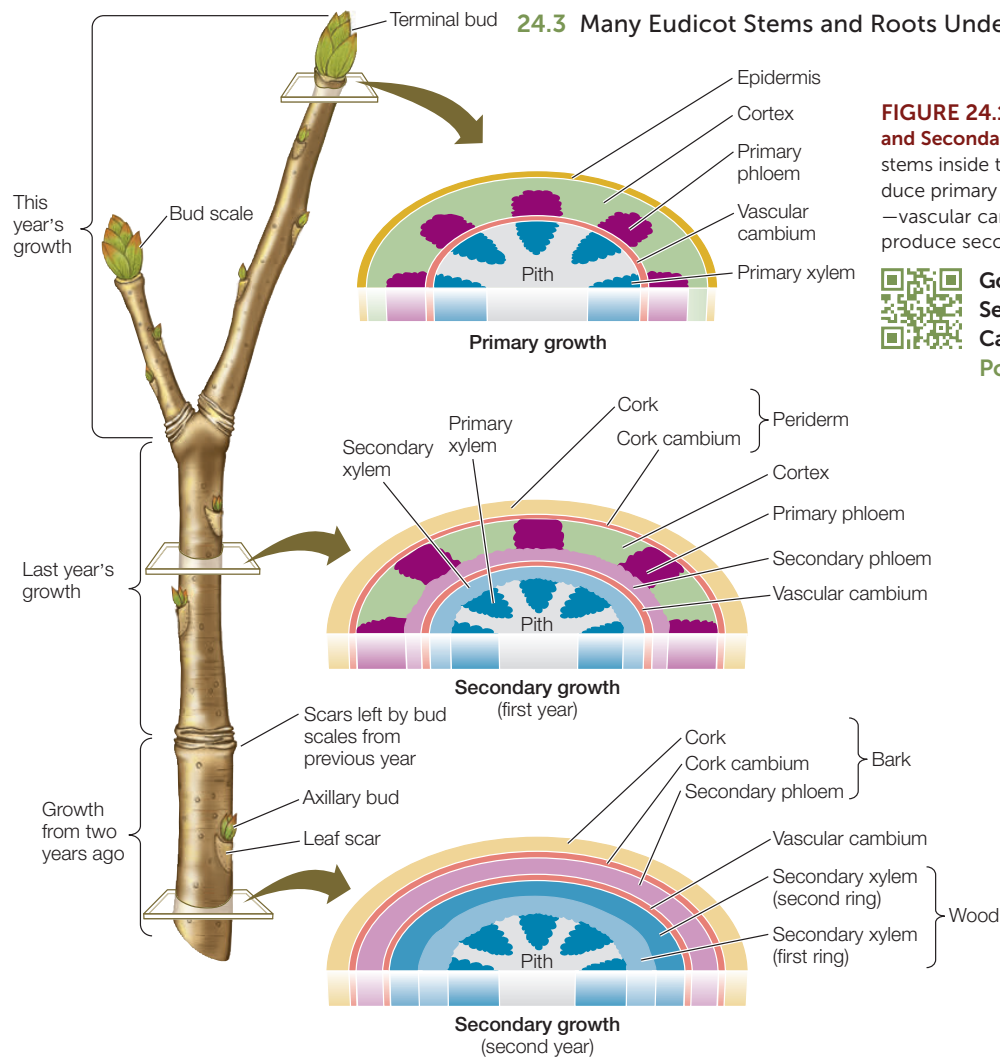
Primary growth

FIGURE 24.14 A Woody Twig Has Both Primary and Secondary Tissues The shoot apical meristems inside the buds of this dormant twig will produce primary growth in spring. Lateral meristems —vascular cambium and cork cambium—will produce secondary growth.

Go to ANIMATED TUTORIAL 24.1 Secondary Growth: The Vascular Cambium
PoL2e.com/at24.1

Last year's growth

Secondary xylem

Primary xylem

Cork

Cork cambium

Periderm

Cortex

Primary phloem

Secondary phloem

Vascular cambium

Pith

Secondary growth
(first year)

Scars left by bud scales from previous year

Axillary bud

Leaf scar

Growth from two years ago

Cork

Cork cambium

Secondary phloem

Bark

Vascular cambium

Secondary xylem (second ring)

Secondary xylem (first ring)

Wood

Pith

Secondary growth
(second year)

CONCEPT 24.3 Many Eudicot Stems and Roots Undergo Secondary Growth

As we mentioned earlier, the roots and stems of some eudicots develop a secondary plant body, the tissues of which we commonly refer to as wood and bark. These tissues are derived by secondary growth from the two lateral meristems:

- The **vascular cambium** produces cells that make up secondary xylem (wood) and secondary phloem (inner bark).

- The **cork cambium** produces mainly waxy-walled protective cells. It supplies some of the cells that become outer bark.

Although secondary growth occurs in broadly similar ways in both roots and stems, the details differ. We focus on stems in our discussion here.

Each year, deciduous trees lose their leaves, leaving bare branches and twigs in winter. These twigs illustrate both primary and secondary growth (**FIGURE 24.14**). The apical meristems of the twigs are enclosed in buds protected by bud scales. When the buds begin to grow in spring, the scales fall away,

leaving scars, which show us where the bud was and allow us to identify each year's growth. The woody portions of the twig are the product of primary and secondary growth. Only the buds and the newest growth from the apical meristem consist entirely of primary tissues.

In the stem, the vascular cambium is initially a single layer of cells lying between the primary xylem and the primary phloem within the vascular bundles. A stem increases in diameter when the cells of the vascular cambium divide, producing secondary xylem cells toward the inside of the stem and secondary phloem cells toward the outside (see Figure 24.14). Each year the vascular cambium produces a new layer of secondary xylem and a new layer of secondary phloem, further increasing the diameter of the stem.

The successive layers of secondary xylem, which constitute the **wood**, all continue to conduct water and minerals for many years. A given year's secondary phloem, however, is active in transport of sugars for only that year; the sieve tube elements and companion cells are crushed as the next year's layer of secondary phloem is formed and pushes outward.

The cork cambium initially forms just inside the epidermis (see Figure 24.14). This meristematic tissue produces layers

Secondary xylem (one year's growth) · Vascular cambium · Bark · Cork cambium · Cork

Pith · Spring wood · Summer wood · Secondary phloem
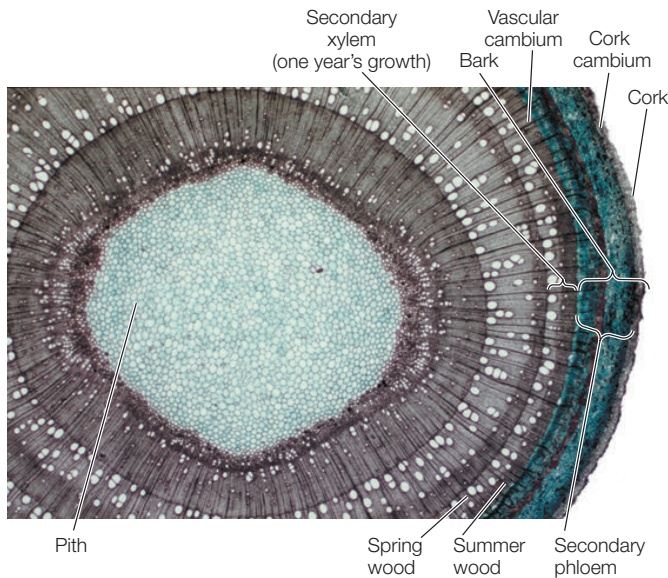
FIGURE 24.15 Annual Rings Rings of secondary xylem are a noticeable feature of this cross section from a tree trunk.

of **cork**, a protective tissue composed of cells with thick walls waterproofed with suberin. The cork cambium and the cork constitute a secondary dermal tissue called **periderm**. Once the periderm forms, the epidermis flakes off, leaving the cork as the outmost layer. The cork prevents excessive water loss and protects the plant from herbivores and pathogens.

As secondary growth of a stem continues, the expanding vascular tissue stretches and breaks the outer layers of the cortex and the initial periderm, which ultimately flake away. A new cork cambium arises from the underlying secondary phloem and produces a new periderm. The periderm and the secondary phloem—that is, all the tissues external to the vascular cambium—constitute the **bark**.

Cross sections of most tree trunks (which are mature stems) in temperate-zone forests reveal annual rings in the wood (**FIGURE 24.15**), which result from seasonal changes in environmental conditions. In spring, when water is relatively plentiful, the tracheids or vessel elements produced by the vascular cambium tend to be large in diameter and thin-walled. Such wood is well adapted for transporting large quantities of water and mineral nutrients. As water becomes less available in summer, narrower cells with thicker walls are produced, which make this summer wood darker and sometimes more dense than the wood formed in spring. Thus each growing season is recorded by a clearly visible annual ring. Trees in the moist tropics do not experience these seasonal changes, so they do not lay down such obvious regular rings. In temperate-zone trees, variations in temperature or water supply during the growing season can sometimes lead to the formation of more than one "annual" ring in a single year.

Only eudicots and other non-monocot angiosperms, along with many gymnosperms, have a vascular cambium and a cork cambium and thus undergo secondary growth. The few

monocots that form thickened stems—palms, for example—do so without secondary growth. Palms have a very wide apical meristem that produces a wide stem, and dead leaf bases add to the diameter of the stem. Almost all monocots grow in essentially this way, as do other angiosperms that lack secondary growth.

CHECKpoint CONCEPT 24.3

✓ Compare primary and secondary growth, creating a table with the following headings: the plant groups that undergo them; the organs that are involved during the plant life cycle; the meristems that are involved; and the products of the meristems.

✓ Why are annual rings used to determine the age of a tree trunk?

Natural selection has acted on the plant body plan to produce a remarkable diversity of plant forms. In the next section we will see how artificial selection by humans on the plants that provide us with food and fiber has greatly altered plant form as well.

CONCEPT 24.4 Domestication Has Altered Plant Form

We have seen in this chapter that a very simple plant body plan—with roots, stems, leaves, meristems, and relatively few tissue and cell types—underlies the diversity of the flowering plants that cover our planet. Although differences in form among species are expected, members of the same plant species can be remarkably diverse in form as well. From a genetic perspective, this observation suggests that minor differences in genomes or gene regulation can underlie dramatic differences in plant form. (Nevertheless, some plant species do differ greatly in genome size, content, and organization.)

The form of the plant body is subject to natural selection. Phenotypes that can outcompete their peers for scarce resources have the highest fitness. Some plants have developed a viny, climbing phenotype that gives them access to light in crowded conditions. Others have a branched phenotype that puts neighboring plants in the shade. Still others have a deep and extensive root system that gives them access to water. Clearly, the vegetative body plan is as important in terms of evolution as are phenotypes relating directly to reproduction, such as flower morphology.

When humans domesticated crops and chose from nature those phenotypes most suitable for cultivation, they set in motion a long experiment in artificial selection of the plant body. For example, in the case of corn (maize), farmers selected plants with tall, compact growth and few branches, minimizing competition among individual plants. Corn was domesticated from the wild grass teosinte, which still grows in the hills of Mexico (**FIGURE 24.16**). One of the most conspicuous

FIGURE 24.16 Corn Was Domesticated from the Wild Grass Teosinte Beginning more than 8,000 years ago in Mexico, farmers favored plants with minimal branching. Reducing the number of branches results in fewer ears per plant but allows each ear to grow larger and produce more seeds.

differences between teosinte and domesticated corn is that teosinte, like other wild grasses, is highly branched, with many shoots, whereas domesticated corn has a single shoot. This morphological difference is due in large part to the activity of a single gene called *TEOSINTE BRANCHED 1* (*TB1*). The protein product of *TB1* regulates the growth of axillary buds. The allele of *TB1* in domesticated corn represses branching, whereas the allele in teosinte permits branching. Similarly, in the domestication of rice, farmers selected for a vertical orientation of the upper leaves so that sunlight could reach all the leaves and photosynthesis was maximized.

It may be hard to believe that a single species, *Brassica oleracea* (wild mustard), is the ancestor of so many familiar and morphologically diverse crops, including kale, broccoli, brussels sprouts, and cabbage (see Figure 15.5). An understanding of how the basic body plan of plants arises makes it possible to appreciate how each of these crops was domesticated. Starting with morphologically diverse populations of wild mustard, humans selected and planted the seeds from variants with the trait they found desirable. Many generations of such artificial selection produced the crops that fill the produce section of the supermarket and the stands of the farmers' market.

Q What are the properties of the kenaf plant that make it suitable for papermaking?

ANSWER Kenaf is a biennial, herbaceous plant that grows rapidly from very active shoot apical meristems (Concept 24.1), reaching a height of 4–5 meters in 5 months. There are more than 500 known genetic strains of kenaf. Over the centuries since its domestication, kenaf has been selected to grow taller and to branch less (Concept 24.4). In addition, the plant's adventitious roots have become longer, at about 2 meters (Concept 24.2), and more numerous, better adapting the plant to soils that are waterlogged.

Kenaf stems are harvested for fiber (**FIGURE 24.17**). The phloem fibers are 3 millimeters long, somewhat longer than the fibers in wood; longer fibers are desirable for stronger products. In addition, the cell walls in kenaf stems are rich in cellulose but relatively poor in lignin. This makes kenaf easier to pulp than wood, which requires strong chemical treatments to hydrolyze the lignin in its cell walls. Furthermore, 1 hectare of kenaf produces 11–17 tons of fiber suitable for pulp and paper production; this is at least three times more than a hectare of southern pine trees produces. And bear in mind that it takes 5 months to grow the kenaf and 20 years to grow the pines!

The main uses of kenaf today are for the manufacture of rope, fiber-based bags, particleboard, and most recently, paper. The last use looks increasingly viable economically.

FIGURE 24.17 Kenaf Stems The stem of kenaf plants is rich in long phloem fibers. Their low lignin content makes the fibers attractive for making paper as well as other products. Paper derived from kenaf fibers has been used for printing newspapers.

SUMMARY

CONCEPT 24.1 The Plant Body Is Organized and Constructed in a Distinctive Way

■ The vegetative organs of flowering plants are **roots**, which form a **root system**, and **stems** and **leaves**, which (together with flowers, which are sexual organs) form a **shoot system**. **Review Figure 24.1**

■ Plant development is influenced by three unique properties of plants (compared with animals): **meristems**, the presence of **cell walls**, and the totipotency of most plant cells.

■ During embryogenesis, the **apical–basal** axis and the **radial** axis of the plant body are established, as are the **shoot apical meristem** and the **root apical meristem**. **Review Figures 24.4 and 24.5**

■ Three **tissue systems**, arranged concentrically, extend throughout the plant body: the **dermal tissue system**, **ground tissue system**, and **vascular tissue system**. **Review Figure 24.6**

■ The vascular tissue system includes **xylem**, which conducts water and mineral ions absorbed by the roots to the shoot, and **phloem**, which conducts the products of photosynthesis throughout the plant body.

CONCEPT 24.2 Apical Meristems Build the Primary Plant Body

■ **Primary growth** is characterized by the lengthening of roots and shoots and by the proliferation of new roots and shoots through branching. Some plants also undergo **secondary growth**, by which they increase in thickness.

■ **Apical meristems** generate primary growth, and **lateral meristems** generate secondary growth. **Review Figure 24.7**

■ Apical meristems at the tips of shoots and roots give rise to three **primary meristems** (**protoderm**, **ground meristem**, and **procambium**), which in turn produce the three tissue systems of the plant body.

■ The root apical meristem gives rise to the **root cap** and the three primary meristems. The cells in the root tip are arranged in three zones that grade into one another: the **zone of cell division**, **zone of cell elongation**, and **zone of cell maturation**. **Review Figure 24.8**

■ The vascular tissue of roots is contained within the **stele**. It is arranged differently in eudicot and monocot roots. **Review Figure 24.9 and ACTIVITIES 24.1 and 24.2**

■ The root system of eudicots typically consists of a **taproot** and **lateral roots**. Monocots typically have a **fibrous root system** made up of **adventitious** roots. **Review Figure 24.10**

■ In stems, the vascular tissue is divided into **vascular bundles**, each containing both xylem and phloem. **Review Figure 24.11 and ACTIVITIES 24.3 and 24.4**

■ Eudicot leaves have two zones of photosynthetic **mesophyll** cells that are supplied by veins with water and minerals. **Review Figure 24.12 and ACTIVITY 24.5**

■ The organs of the primary plant body may be modified to perform specialized functions. **Review Figure 24.13**

CONCEPT 24.3 Many Eudicot Stems and Roots Undergo Secondary Growth

■ Two lateral meristems, the **vascular cambium** and **cork cambium**, are responsible for secondary growth. The vascular cambium produces secondary xylem (**wood**) and secondary phloem (inner **bark**). The cork cambium produces a protective tissue called **cork**. **Review Figures 24.14 and 24.15 and ANIMATED TUTORIAL 24.1**

CONCEPT 24.4 Domestication Has Altered Plant Form

■ Although the plant body plan is simple, it can be changed dramatically by minor genetic differences, as evidenced by the natural diversity of wild plants.

■ Crop domestication involves artificial selection of certain desirable traits found in wild populations. As a result of artificial selection over many generations, the body forms of crop plants are very different from those of their wild relatives. **Review Figure 24.16**

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is24

Go to LaunchPad at **macmillanhighered.com/launchpad** for additional resources, including LearningCurve Quizzes, Flashcards, and many other study and review resources.

25

Plant Nutrition and Transport

KEY CONCEPTS

25.1 Plants Acquire Mineral Nutrients from the Soil

25.2 Soil Organisms Contribute to Plant Nutrition

25.3 Water and Solutes Are Transported in the Xylem by Transpiration–Cohesion–Tension

25.4 Solutes Are Transported in the Phloem by Pressure Flow

An aerial view of the border between Haiti (left) and the Dominican Republic (right) provides a dramatic illustration of the extent of soil degradation in Haiti.

The 2010 earthquake was a catastrophe for Haiti, the poorest country in the Western Hemisphere. More than 200,000 people died, and more than a million people were left homeless. The urban infrastructure in the capital city was destroyed. Amid the outpouring of help from the rest of the world came a realization that another disaster has been occurring in Haiti for decades: the destruction of its forests and farms. Plants need fertile soil to grow, and in Haiti that has been in increasingly short supply.

Haiti shares the island of Hispaniola with the Dominican Republic. The two countries have had dramatically different policies with regard to land conservation, with equally dramatic results. While the Dominicans have carefully managed their land, the story of Haiti is one of overexploitation. First, Spanish colonists planted sugarcane, a crop that depleted the soil. Then the French colonists that followed them cut down forests to plant coffee and tobacco for export to Europe. After the former slaves revolted and expelled the Europeans in the early 1800s, land speculators chased out indigenous farmers from fertile valleys and planted export crops such as corn and beans. Today only 4 percent of the forests that existed when the Europeans arrived in 1492 remain. As Haitians have said, "Te a fatige (The earth is tired)." Because there are few plant roots to stabilize the soil, especially in Haiti's many mountainous regions, rain washes the soil into the sea. From an airplane window it is easy to see the 120-mile-long border between the two countries. The Dominican side is verdant and forested, while the Haitian side is devoid of plant life and has lost most of its soil.

As human land use intensifies, ecological disasters like Haiti's are becoming all too common. Today, parts of sub-Saharan Africa's farmland are losing their topsoil as a result of poor land management, swelling populations, and a challenging climate. Crop failures, starvation, and large-scale human displacements are inevitable consequences. The need for a better understanding of how plants interact with the soil is a pressing human concern.

Q How can soil be managed for optimal plant growth?

CONCEPT 25.1 Plants Acquire Mineral Nutrients from the Soil

Like all organisms, plants are made up primarily of water and molecules that contain the major elements of life. Nearly all plants are **autotrophs** that obtain carbon from atmospheric carbon dioxide through the carbon-fixation reactions of photosynthesis. They obtain carbon, hydrogen, and oxygen from air and water, so these elements are plentiful as long as plants have an adequate water supply.

The plant body contains other elements as well. Nitrogen, for example, is essential for the synthesis of proteins and nucleic acids. Plants obtain nitrogen, directly or indirectly, through the activities of bacteria and fungi, as we will see later in this chapter. In addition, proteins contain sulfur (S), nucleic acids contain phosphorus (P), and chlorophyll contains magnesium (Mg). Metal ions also play important biochemical roles in plants. For example, Fe^{2+} is used as a cofactor in electron transport in mitochondria and chloroplasts. Plants obtain these and other mineral nutrients mainly from the soil. Mineral nutrients dissolve in water in the soil as ions, forming a solution—called the **soil solution**—that surrounds the roots of plants.

LINK

The major elements of life are described in **Chapter 2**, and the chemical reactions of photosynthesis in **Concepts 6.5 and 6.6**

Nutrients can be defined by their deficiency

A plant nutrient is called an **essential element** if its absence causes severe disruption of normal plant growth and reproduction. An essential element cannot be replaced by any other element. There are two categories of essential elements:

- **Macronutrients** have concentrations of at least 1 gram per kilogram of the plant's dry matter. There are six macronutrients:

    Nitrogen (taken up as NO_3^- or NH_4^+)
    Phosphorus (taken up as PO_4^{3-})
    Potassium (taken up as K^+)
    Sulfur (taken up as SO_4^{2-})
    Calcium (taken up as Ca^{2+})
    Magnesium (taken up as Mg^{2+})

- **Micronutrients** have concentrations of less than 0.1g/kg of the plant's dry matter. They include iron (Fe^{2+}), chlorine (Cl^-), manganese (Mn^{2+}), zinc (Zn^{2+}), copper (Cu^{2+}), nickel (Ni^{2+}), boron (BO_3^{-3}), and molybdenum [$Mo(O_4)^{2-}$].

Plants show characteristic symptoms, most noticeable in leaves, that can be used to diagnose deficiencies of essential elements (**FIGURE 25.1**). With proper diagnosis, the missing nutrient(s) can be provided in the form of a supplement, or **fertilizer**.

Experiments using hydroponics have identified essential elements

The essential elements for plants were largely identified by growing plants **hydroponically**—that is, with their roots suspended in nutrient solutions instead of soil:
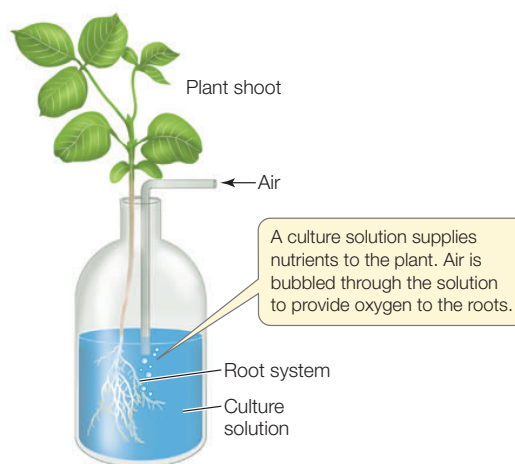
Growing plants in this manner allows for greater control of nutrient availability than is possible in a complex medium like soil.

In the first successful experiments of this type, performed a century and a half ago, plants grew seemingly normally in solutions containing only calcium nitrate [$Ca(NO_3)_2$], magnesium sulfate ($MgSO_4$), and potassium phosphate (KH_2PO_4).

FIGURE 25.1 Mineral Nutrient Deficiency Symptoms The plants on the left were grown with a full complement of essential nutrients. The yellow leaves of the center plants are typical of iron deficiency, while the stunted growth of the plants on the right indicate nitrogen deficiency.

Go to ANIMATED TUTORIAL 25.1 Nitrogen and Iron Deficiencies PoL2e.com/at25.1

Healthy   Iron-deficient   Nitrogen-deficient

FIGURE 25.2 Nickel Is an Essential Element for Plants Using highly purified minerals in a hydroponic solution, Patrick Brown and his colleagues tested whether barley can complete its life cycle in the absence of nickel.[a] Other investigators showed that no other element could substitute for nickel.

HYPOTHESIS

Nickel is an essential element for plants.

METHOD

1. Grow barley plants for three generations in hydroponic solutions containing 0, 0.6, and 1.0 μM nickel sulfate ($NiSO_4$).
2. Harvest seeds from 5 or 6 third-generation plants in each of the groups.
3. Determine the nickel concentration in some of the seeds from each plant.
4. Germinate the other seeds from the same plants in a nickel-free hydroponic solution and plot the success of germination against nickel concentration.

Concentration in nutrient solution
- 0 μM $NiSO_4$
- 0.6 μM $NiSO_4$
- 1.0 μM $NiSO_4$

Each point shows results for seeds from a single third-generation plant.
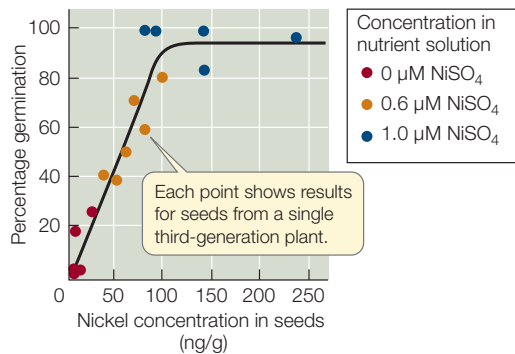
RESULTS

There was a positive correlation between seed germination and nickel concentration. There was significantly less germination at the lowest nickel concentrations.

CONCLUSION

Barley seeds require nickel in order to germinate and complete their life cycle.

ANALYZE THE DATA

A. What do the blue points have in common? Why are there five blue points instead of just one?
B. What is the biological meaning of the zero/zero point?
C. Why didn't the investigators examine only the plants grown without nickel in their hydroponic solution?
D. Plant biologists define the critical value for a mineral nutrient as that concentration in plant tissue that results in a 15 percent reduction in the optimal yield of the plant. Using maximum germination percentage in this experiment as the optimal yield, estimate the critical value for nickel.

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]P. H. Brown et al. 1987. *Plant Physiology* 85: 801–803.

A solution missing any of these compounds could not support normal plant growth. Tests with other compounds that included various combinations of these same elements soon established the six macronutrients listed above.

Identifying micronutrients by this experimental approach proved to be more difficult because of the small amounts involved. Sufficient amounts of a micronutrient can be present as contaminants in the environment used to grow plants. Therefore nutrition experiments must be performed in tightly controlled laboratories with special air filters that exclude microscopic mineral particles, and they must use only the purest available chemicals. Furthermore, a seed may contain enough of a micronutrient to supply the embryo and the resultant second-generation plant throughout its lifetime. There might even be enough left over to pass on to the next generation of plants. Thus even if a plant is completely deprived of a micronutrient, it may take a long time for deficiency symptoms to appear. The most recent micronutrient to be listed as essential was nickel, in 1983 (**FIGURE 25.2**).

Soil provides nutrients for plants

Most terrestrial plants grow in soil, which provides plants with a number of benefits:

- Anchorage for mechanical support of the shoot
- Mineral nutrients and water from the soil solution
- O_2 for root respiration in root tissues from air spaces between soil particles
- The services of other soil organisms

Soils have both living and nonliving components. The living components include plant roots as well as populations of bacteria, fungi, protists, and animals such as earthworms and insects. The nonliving portions of the soil include rock fragments ranging in size from large stones to clay particles 2 μm or less in diameter. Soil also contains water and dissolved mineral nutrients, air spaces, and dead organic matter:
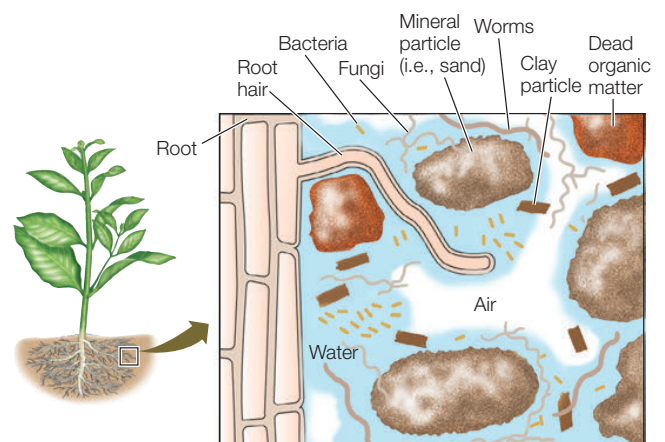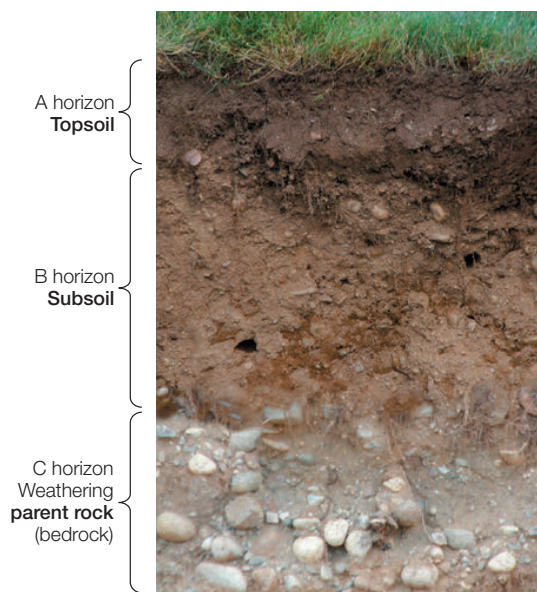
FIGURE 25.3 **A Soil Profile** The A, B, and C horizons of a soil can sometimes be seen at construction sites such as this one in Massachusetts. The darker upper layer (the A horizon) is home to most of the living organisms in the soil.

Although soils vary greatly, almost all of them have a soil profile consisting of several horizontal layers, called **horizons**. Soil scientists recognize three major horizons—termed A, B, and C—in a typical soil (**FIGURE 25.3**):

- The A horizon is the **topsoil** that supports the plant's mineral nutrient needs. It contains most of the soil's living and dead organic matter.

- The B horizon is the **subsoil**, which accumulates materials from the topsoil above it and the parent rock below.

- The C horizon is the **parent rock** from which the soil arises.

Parent rock is broken down into soil particles (weathered) in two ways:

- Mechanical weathering is the physical breakdown of materials by wetting, drying, and freezing.

- Chemical weathering is the alteration of the chemistry of the materials in the rocks by oxidation, water, and acids.

The soil's fertility (its ability to support plant growth) is determined by several factors. The size of the soil particles in the A horizon, for example, is important in determining nutrient retention and other soil characteristics. Mineral nutrients in the soil solution can be **leached** (washed away) from the A horizon downward by rain (or irrigation) and thereby become unavailable to plants. Tiny clay particles bind a lot of water,

and mineral nutrients are not readily leached from them, but clay particles pack tightly and leave little room for air. Large sand particles have opposite properties; they provide plenty of air spaces but do not retain water or nutrients. A **loam** is a soil that is an optimal mixture of sand, clay, and silt (mineral particles intermediate in size between sand and clay) and thus has sufficient supplies of air, water, and nutrients for plants.

In addition to mineral particles, soils contain dead organic matter, largely from plants. Soil organisms break down dead leaves and other organic materials that fall to the ground into a substance called **humus**. This material is used as a food source by microbes that break down complex organic molecules and release simpler molecules into the soil solution. Humus also improves the texture of soil and provides air spaces that increase oxygen availability to plant roots.

Ion exchange makes nutrients available to plants

Chemical weathering results in clay particles covered with negatively charged chemical groups (**FIGURE 25.4**). These negatively charged clay particles bind the positively charged ions (cations) of minerals that are important for plant nutrition, such as potassium (K^+), magnesium (Mg^{2+}), and calcium (Ca^{2+}). This binding prevents the cations from being leached out of the soil, but to become available to plants, they must be released from the clay particles into the soil solution.

Recall that the root surface is covered with epidermal cells bearing root hairs (see Figure 24.8C). Proteins in the cell membrane of these cells actively pump protons (H^+) out of the cells, as we'll describe in Concept 25.3. In addition, cellular respiration in the roots releases CO_2, which dissolves in the soil water and reacts with it to form carbonic acid. This acid ionizes to form bicarbonate and free protons:

$$CO_2 + H_2O \rightleftharpoons H_2CO_3 \rightleftharpoons H^+ + HCO_3^-$$

Proton pumping by the root cells and ionization of carbonic acid both act to increase the proton concentration in the soil
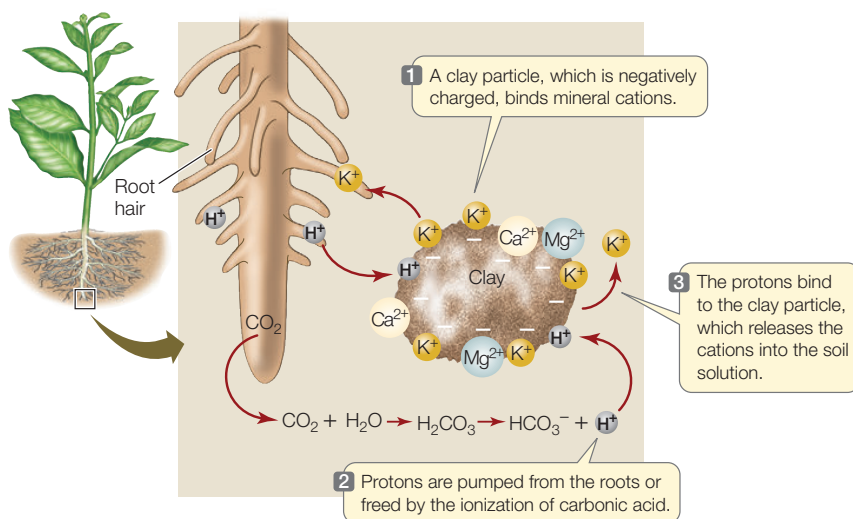
FIGURE 25.4 **Ion Exchange** Plants obtain some mineral nutrients from the soil in the form of positive ions bound to clay particles in the soil.

surrounding the root. The protons bind more strongly to clay particles than do mineral cations; in essence, the protons trade places with the cations in a process called **ion exchange** (see Figure 25.4). Ion exchange releases mineral nutrient cations into the soil solution, where they are available to be taken up by roots. Soil fertility is determined in part by the soil's ability to provide nutrients in this manner.

There is no comparable mechanism for binding and releasing negatively charged ions. As a result, important anions such as nitrate (NO_3^-) and sulfate (SO_4^{2-}) may be leached from the A horizon.

Fertilizers can be used to add nutrients to soil

Leaching and the harvesting of crops may deplete a soil of its nutrients, in which case the growth of subsequent crops on that soil will be reduced. Three ways to restore the nutrient content of soils are shifting agriculture, organic fertilizers, and inorganic (chemical) fertilizers.

SHIFTING AGRICULTURE   In the past, when the soil could no longer support a level of plant growth sufficient for agricultural purposes, people simply moved to another location. This nomadic existence allowed the soil to replenish its nutrients naturally, by weathering of the parent rock and gradual accumulation and breakdown of organic matter. These processes take a long time, but that was not a problem as long as a lot of land was available. After many years in other locations, the people could return to their original land, which was again able to support farming. Today the food needs of a large human population are too great to allow land to be left unfarmed for a long time; in addition, most people live more settled lives now and do not want to move.

ORGANIC FERTILIZERS   Humus is used as a food source by soil organisms, which in turn release simpler molecules to the soil solution. For example:

$$\text{Leaf proteins} \xrightarrow{\text{Bacteria}} NH_4^+ \xrightarrow{\text{Bacteria}} NO_3^-$$
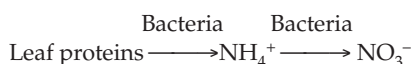
These simpler molecules can dissolve in soil water and be taken up by plant roots.

Farmers can increase the nutrient content of soil by adding organic materials such as compost (partially decomposed plant material) or manure (the waste from farm animals), which is a particularly good source of nitrogen. In either case, these **organic fertilizers** add nutrients to the soil much more rapidly than natural processes, but still allow for a slow release of ions, with little leaching, as the materials decompose.

INORGANIC FERTILIZERS   Because organic fertilizers may still act too slowly to restore fertility if a soil is to be farmed every year, **inorganic fertilizers** are used to supply mineral nutrients directly in forms that can be immediately taken up by plants. Inorganic fertilizers are characterized by their "N-P-K" percentages. A 5-10-10 fertilizer, for example, contains 5 percent nitrogen (as NH_4^+), 10 percent phosphate (P_2O_5), and 10 percent potash (K_2O) by weight (of the nutrient-containing

compound, not as weights of the elements N, P, and K). Sulfur, in the form of ammonium sulfate [$(NH_4)_2SO_4$], is also occasionally added to soils.

To return to our example of nitrogen, inorganic fertilizers reach plants by this process:

$$\text{Chemical manufacture} \rightarrow NH_4^+ \xrightarrow{\text{Bacteria}} NO_3^-$$
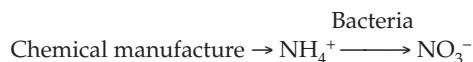
The manufacture of nitrogen fertilizer begins with an energy-intensive industrial process in which N_2 is combined with H_2 at high temperatures and pressures in the presence of a catalyst to form ammonia (NH_3). This process accounts for about 2 percent of the world's energy use, mostly in the form of natural gas. Although organic and inorganic fertilizers have the same effects on crop nutrition, their costs are very different: manure and compost are free, whereas NH_4^+ made in a factory can be very expensive.

> **LINK**
>
> The cycling of nitrogen through biological systems is described in **Chapter 45**, and some of the prokaryotes that participate in that cycling are described in **Concept 19.3**

> **CHECKpoint**   CONCEPT **25.1**
>
> ✓ What are the differences between:
>   a. macronutrients and micronutrients?
>   b. organic and inorganic fertilizers?
>   c. the availability to plant roots of a cation and an anion?
> ✓ Outline an experimental method for determining whether an element is essential to a plant.
> ✓ A label on a bin in a market states "Organic apples, grown without chemical fertilizers." Are these apples different in terms of plant molecules than they would be if they were grown with chemical fertilizers?

We have just described some of the physical and chemical aspects of soils that are vital to plant nutrition. But many other organisms besides plants inhabit soils. We will turn now to the effects of those organisms on plants.

CONCEPT 25.2   Soil Organisms Contribute to Plant Nutrition

One gram of soil contains from 6,000 to 50,000 bacterial species and up to 200 meters of fungal hyphae, although both are largely invisible to the naked eye. Many of these soil organisms consume living and dead plant materials. Plants have an array of defenses they can use against potentially harmful soil organisms (which we will describe in Chapter 28). In many cases, however, plants *actively encourage* fungi and bacteria to infect their roots. Here we describe the resulting "intercellular trading posts," where products are exchanged to the mutual benefit of plants and a few very special soil microbes. In

these interactions—called symbioses (singular *symbiosis*)—the plants usually "trade" the products of photosynthesis, which the microbes use as an energy source, for other essential elements, such as phosphorus and nitrogen, which the microbes can supply.

> **LINK**
>
> These plant–microbe interactions are examples of mutualism, one of five major types of interspecies interactions discussed in **Concept 43.1**

We will focus on two important plant–microbe interactions:

- Arbuscular mycorrhizae, a plant–fungus symbiosis (see Figure 22.10)
- Symbiotic nitrogen fixation, an association of nitrogen-fixing bacteria (see Concept 19.3) with plant roots

We'll begin by describing how these associations form. Then we'll see how they benefit the plants and their microbial partners.

Plants send signals for colonization

In the case of both arbuscular mycorrhizae and symbiotic nitrogen fixation, the roots of the potential host plant secrete signaling molecules that attract the soil organisms. These signals contribute to the specificity of the interactions, because only one or a few microbe species will respond to a particular signal molecule.

FORMATION OF MYCORRHIZAL ASSOCIATIONS   In the case of arbuscular mycorrhizae, plant roots produce chemical signal molecules called **strigolactones** that stimulate rapid growth of fungal hyphae toward the root (**FIGURE 25.5A**). In response, the fungi signal the plant to form a prepenetration apparatus (PPA), which guides the growth of the fungal hyphae into the root cortex. The sites of nutrient exchange between fungus and plant are the arbuscules, which form inside root cortical cells. Despite the intimacy of this association, the plant and fungal cytoplasms never mix—they are separated by two membranes, the fungal cell membrane and the periarbuscular membrane (PAM), which is continuous with the plant cell membrane.

FORMATION OF NITROGEN-FIXING NODULES   A group of plants called legumes (family Fabaceae) can form symbioses with several species of soil bacteria collectively known as rhizobia, which live in nodules that form on the legumes' roots. The roots of legumes release flavonoids and other chemical signals that attract the rhizobia (**FIGURE 25.5B**). The flavonoids also stimulate the bacteria to secrete Nod (nodulation) factors, which cause cells in the root cortex to divide and form the plant tissue that constitutes the root nodule. Bacteria enter the root via an infection thread, analogous to the PPA in mycorrhizal associations, and eventually reach cells inside the root nodule. There the bacteria are released into the cytoplasm of the nodule cells, enclosed in plant membrane–derived vesicles that are functionally equivalent to the PAM. The bacteria differentiate into **bacteroids**—the form of the bacteria that can fix nitrogen.

A COMMON MECHANISM   There is increasing evidence that nodule formation depends on some of the same genes and mechanisms that allow mycorrhizal associations to develop. For example, both processes involve folding in of the cell membrane to allow entry of the fungal hyphae or rhizobia. The similarities in the structures formed (see Figure 25.5) are striking, considering that the symbioses involve members of two different groups of organisms (fungi and bacteria).

> **LINK**
>
> The fact that similar genes and developmental processes are used in two different types of symbiosis provides a striking demonstration of the principles of evolutionary developmental biology; see **Concept 14.4**

Mycorrhizae expand the root system

In most vascular plants, the roots alone cannot support an optimal growth rate—they simply cannot reach all the nutrients available in the soil. Mycorrhizae, which occur in more than 90 percent of terrestrial plants, expand the root surface area

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APPLY THE CONCEPT

Soil organisms contribute to plant nutrition

Researchers grew lemon seedlings in soils that contained phosphate fertilizer, arbuscular mycorrhizal fungi, or both. The table shows the mean dry weight of the seedlings after 6 months.

1. What do these results tell us about the role of phosphate fertilizer in the growth of lemon plants?

2. Why didn't the mean weight of the seedlings increase when the amount of phosphate fertilizer, in the absence of mycorrhizae, was doubled?

PHOSPHATE FERTILIZER ADDED (g)	MYCORRHIZAE PRESENT	SEEDLING DRY WEIGHT (g)
0	No	1
0	Yes	10
12	No	28
12	Yes	166
24	No	20
24	Yes	210

FIGURE 25.5 Roots Send Signals for Colonization Plant roots send chemical signals to arbuscular mycorrhizal fungi (A) and nitrogen-fixing bacteria (B) to stimulate colonization. Both processes do not occur in all plants.

(A)

Cortical cells
Epidermis
Strigolactones
Spore

1 Plant roots produce strigolactones that stimulate rapid growth of fungal hyphae toward the root.

Hypha

Fungal signal

2 Fungal signal stimulates plant to produce a pre-penetration apparatus (PPA).

PPA

3 Fungal hyphae enter the PPA and are guided to the root cortex.

4 Fungus grows along the root length.

5 Hyphae induce formation of new PPA structures inside cortical cells.

PAM

6 Hyphae enter PPAs and branch to form arbuscules, where nutrients are exchanged.

Root tip

(B)

Cortical cells
Root hair
Rhizobia

1 Root hairs release chemical signals such as flavonoids that attract rhizobia.

2 Rhizobia proliferate and cause a root hair to curl and an infection thread to form.

Infection thread

3 Stimulated by Nod factors secreted by bacteria, root cells begin to divide.

4 The infection thread grows into the cortex of the root.

5 The infection thread releases bacterial cells, which become bacteroids in the root cells.

6 The nodule forms as plant cells continue to divide and become infected with bacteria.

Bacteroids

10-fold to 1,000-fold (see Figure 22.10A). Fungal hyphae are also much finer than root hairs; they can get into pores in the soil that are inaccessible to roots. Mycorrhizae thus probe a vast expanse of soil for nutrients and deliver them into root cortical cells.

The primary nutrient that the plant obtains from a mycorrhizal interaction is phosphorus. In exchange, the fungus obtains an energy source: the products of photosynthesis. In fact, up to 20 percent of the photosynthate (carbohydrates produced by photosynthesis) of terrestrial plants is directed to and consumed by arbuscular mycorrhizal fungi.

Rhizobia capture nitrogen from the air and make it available to plant cells

Although nitrogen is essential for the survival of plants, they cannot use atmospheric N_2 because they lack the biochemical machinery to break the very stable triple bond that links the two N atoms in N_2. Some bacteria, however, have an enzyme called **nitrogenase** that enables them to convert N_2 into a more reactive and biologically useful form, ammonia (NH_3), by a process called **nitrogen fixation**:

$$N_2 + 6\,H \rightarrow 2\,NH_3$$

1 The enzyme nitrogenase binds a molecule of nitrogen gas.

2 A reducing agent (e.g., ferrodoxin) transfers three successive pairs of hydrogen atoms to N_2.

3 The final products—two molecules of ammonia—are released, freeing the nitrogenase to bind another N_2 molecule.

Substrate: Nitrogen gas (N_2)

Enzyme: Nitrogenase

Enzyme binds substrate

Reduction

Reduction

Reduction

Product: Ammonia (NH_3)

Nitrogenase

FIGURE 25.6 Nitrogenase Fixes Nitrogen Throughout the chemical reactions of nitrogen fixation, the reactants are bound to the enzyme nitrogenase. A reducing agent transfers hydrogen atoms to a molecule of nitrogen gas (N_2), and eventually the final product—ammonia (NH_3)—is released. This reaction requires a large input of energy: about 16 ATPs.

This process is by far the most important route by which nitrogen enters biological systems. Two types of organisms can fix nitrogen:

• Free-living (nonsymbiotic) organisms in soil and water (e.g., *Azotobacter* bacteria and *Nostoc* cyanobacteria)

• Symbiotic organisms living in other organisms (e.g., rhizobia in the roots of legumes)

Biological nitrogen fixation is the reduction of nitrogen gas, and it requires a great deal of energy. It proceeds by the stepwise addition of three pairs of hydrogen atoms to N_2 (**FIGURE 25.6**).

> **LINK**
> You can review reduction–oxidation reactions in **Concept 6.1**

Nitrogenase is strongly inhibited by oxygen. Many free-living nitrogen-fixing bacteria are anaerobes that live in environments that naturally contain little or no O_2. The environment in the plant root tissues is typically aerobic, but the nodules provide the rhizobia with the conditions necessary for nitrogen fixation (see Figure 25.5B). Within a nodule, O_2 is maintained at a low level that is sufficient to support aerobic respiration by the bacteria (which is necessary to supply energy for the fixation reaction) but not so high as to inactivate nitrogenase. The O_2 level is regulated by a plant-produced protein called **leghemoglobin**, which is an O_2 carrier. Leghemoglobin is a close relative of hemoglobin, the red, oxygen-carrying pigment of animals, and is thus an evolutionarily ancient molecule.

As with mycorrhizae, maintaining nitrogen-fixing bacteria is costly to the plant, consuming as much as 20 percent of all of the energy stored in photosynthate. Relatively few plant species are legumes, but those species are important to humans because they can be grown in nitrogen-poor soil. They include peas, soybeans, clover, alfalfa, and some tropical shrubs and trees. Most other plants depend on nitrogen fixed by free-living bacteria in the soil or released by the breakdown of proteins present in dead organic matter.

Some plants obtain nutrients directly from other organisms

Although the majority of plants obtain most of their mineral nutrients from the soil solution (with the help of fungi), some, such as carnivorous and parasitic plants, use other sources.

CARNIVOROUS PLANTS There are about 500 carnivorous plant species that obtain some of their nutrients by digesting arthropods. These plants typically grow in boggy soils where little nitrogen or phosphorus is available. Digestion (hydrolysis) of arthropod prey helps provide those missing nutrients. A well-known example of a carnivorous plant is the Venus flytrap (genus *Dionaea*; **FIGURE 25.7A**), which has a modified leaf with two halves that fold together. When an insect touches trigger hairs on the leaf, its two halves quickly come together, and their spiny margins interlock and trap the insect before it can escape. The leaf then secretes enzymes that digest the prey.

PARASITIC PLANTS Approximately 1 percent of flowering plant species derive some or all of their water, nutrients, and even photosynthate from other plants. **Hemiparasites** can photosynthesize but derive water and mineral nutrients from the living bodies of other plants. Mistletoes, for example, carry out some photosynthesis, but they parasitize other plants for water and mineral nutrients and may derive some photosynthetic products from them as well. Dwarf mistletoe (*Arceuthobium americanum*) is a serious parasite in forests of the western United States, destroying more than 3 billion board feet of lumber per year. **Holoparasites** are completely parasitic and do not perform photosynthesis. Witchweed (*Striga*) is a serious parasite of crops, causing more than $1 billion a year in corn losses in Africa (**FIGURE 25.7B**).

A COMMON ASSOCIATION Interestingly, strigolactone, the molecule made by plant roots that attracts arbuscular mycorrhizal fungi, is closely related to the molecule that *Striga* is attracted to as it seeks potential hosts. The mycorrhizal

(A)

(B)

FIGURE 25.7 Nutrients from Other Organisms (A) The Venus flytrap (*Dionaea muscipula*) obtains nitrogen from the bodies of arthropods trapped inside the plant when its specialized leaves snap shut. (B) Purple witchweed (*Striga hermonthica*) parasitizes sorghum plants.

association is ancient (more than 400 million years old) and predates the evolution of parasitic plants. Scientists hypothesize that the ancestors of modern *Striga* evolved to take advantage of a compound that was already produced by plants to attract beneficial soil microbes. This is an example of "opportunistic evolution," the repurposing of preexisting processes rather than the development of new processes.

CHECKpoint CONCEPT 25.2

✓ Compare the events that occur when arbuscular mycorrhizal fungi and rhizobia infect a plant root. What is the nutritional advantage to the plant in each case?

✓ How might you turn wheat, a plant that does not have symbiotic relationships with nitrogen-fixing bacteria, into a nitrogen-fixing plant? What biochemical challenges would you face?

✓ How do the nutritional needs of holoparasitic plants differ from those of carnivorous plants?

✓ What characteristics are shared among nonparasitic plant–parasitic plant, plant–mycorrhizal fungus, and plant–rhizobia associations?

Now that we have learned about plant nutrients in the soil, let's consider how soil water, with its dissolved nutrients, enters the plant root, and how it moves from the root to the rest of the plant body.

Water and Solutes Are Transported in the Xylem by Transpiration–Cohesion–Tension

Plants require water to carry out photosynthesis, to transport solutes between plant organs, to cool their leaves by evaporation, and to maintain the internal pressure that supports their bodies. Here we focus on how water moves into and out of plant cells and between different parts of the plant.

Differences in water potential govern the direction of water movement

Water moves into and out of plant cells by osmosis. In plant cells, the direction of water movement is determined by **water potential** (**psi**, Ψ), defined as the tendency of a solution (water plus solutes) to take up water from pure water across a membrane. Whenever water moves across a selectively permeable membrane by osmosis, it moves toward the region of lower (more negative) water potential (**FIGURE 25.8A, LEFT**). Water potential is expressed in megapascals (MPa), a unit of pressure. Atmospheric pressure—"one atmosphere"—is about 0.1 MPa, or 14.7 pounds per square inch (a typical pressure in an automobile tire is about 0.2 MPa).

> **LINK**
>
> You can review the structure and function of the cell membrane in **Chapter 5**; **Concept 5.2** describes osmosis

Water potential has two components:

- **Solute potential** (Ψ_s): As solutes are added to pure water, the concentration of free water is reduced, the tendency to take up water increases, and water potential decreases. (In terms of cells, as solutes are added to the environment, it becomes hypertonic relative to the cells.)

- **Pressure potential** (Ψ_p): When any closed compartment takes up water, it tends to swell. The walls of the compartment, however, resist that swelling (think of blowing up a balloon). The result is an increase in internal pressure in the compartment, which decreases the tendency to take up more water (increases the water potential; **FIGURE 25.8A, RIGHT**).

We can express the effects of solute potential and pressure potential on water potential in the form of an equation:

$$\Psi = \Psi_s + \Psi_p$$

By definition the solute potential of pure water is zero; because added solutes decrease water potential, solute potential is usually negative. Pressure potential is defined as zero when it equals atmospheric pressure. Pressure potentials less than atmospheric pressure are negative, and those greater than atmospheric pressure are positive.

In a plant cell (**FIGURE 25.8B**), the cell wall resists the swelling that would otherwise occur as the cell takes up water (see

(A)

In this tube, the solute potentials on the two sides of the membrane differ, but the pressure potentials are the same.

The right side of the tube has a lower water potential, so there is net movement of water to the right and the volume on this side will increase.

Pure water
$\psi = 0$ MPa   Membrane

Solution
$\psi_p = 0$ MPa
$\psi_s = -1.0$ MPa
$\psi = -1.0$ MPa

In this tube, a piston is used to increase the pressure potential of the right side.

The water potentials of the two sides are equal, so there is no net movement of water.

Pure water
$\psi = 0$ MPa

Solution
$\psi_p = +1.0$ MPa
$\psi_s = -1.0$ MPa
$\psi = 0$ MPa

(B)

The inside of the cell has a lower solute potential than the surrounding water. The cell has a pressure potential of zero.

The cell has a lower water potential than the water outside, so there is net movement of water into the cell.

Pure water
$\psi = 0$ MPa

Flaccid cell
$\psi_p = 0$ MPa
$\psi_s = -1.0$ MPa
$\psi = -1.0$ MPa

The cell has a negative solute potential, but has a positive pressure potential.

The pressure potential of the cell balances its solute potential, so the cell's water potential is zero. There is no net movement of water.

Pure water
$\psi = 0$ MPa

Turgid cell
$\psi_p = +1.0$ MPa
$\psi_s = -1.0$ MPa
$\psi = 0$ MPa

FIGURE 25.8 Water Potential, Solute Potential, and Pressure Potential   (A) A theoretical illustration of water potential. (B) The effect of differences in water potential on a plant cell.

Go to ANIMATED TUTORIAL 25.2
Water Uptake in Plants
PoL2e.com/at25.2

also Figure 5.3C). The resulting **turgor pressure** is equivalent to the pressure potential exerted by the piston in Figure 25.8A. Water will enter plant cells by osmosis until the pressure potential exactly balances the solute potential. At this point the cell is said to be "turgid"—that is, it has a significant positive pressure potential. The physical structure of many plants is maintained by the (positive) pressure potential of their cells; if the pressure potential drops (for example, if the plant does not have enough water), the plant wilts (**FIGURE 25.9**).

Water and ions move across the root cell's cell membrane

The movement of a soil solution containing mineral ions across a root cell's cell membrane faces two major challenges:

- The membrane is hydrophobic, whereas water and mineral ions are polar.
- Some mineral ions must be moved against their concentration gradients.

These two challenges are met by the activities of membrane proteins.

AQUAPORINS   Aquaporins are membrane channels through which water can diffuse (see Figure 5.5). Although aquaporins were first discovered in animal cells, they are also abundant in plant cell membranes. The abundance and activity of aquaporins are both regulated so that the rate of osmosis can be controlled. But the direction of osmosis is always the same: water moves to the region of more negative water potential.

ION CHANNELS AND PROTON PUMPS   When the concentration of an ion in the soil solution is greater than that inside the

The cells in this plant have low turgor pressure and the plant is wilted.

The water potential of cells of this plant is zero because the negative solute potential is balanced by an equally positive pressure potential. The plant is upright because its cells are turgid.
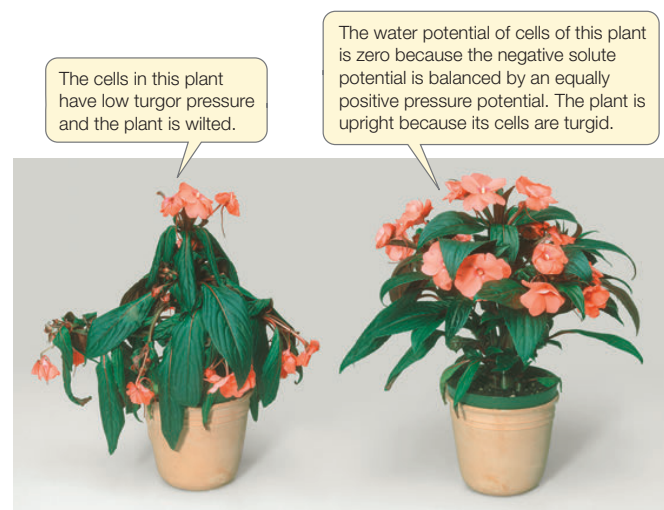
FIGURE 25.9 A Wilted Plant   A plant wilts when the pressure potential of its cells drops (its cells have low turgor pressure).

1 A proton pump generates differences in H⁺ concentration and electric charge across the membrane.

2 The difference in electric charge causes cations such as K⁺ to enter the cell.

3 A transport protein couples the diffusion of H⁺ to the transport (against an electrochemical gradient) of anions such as Cl⁻ into the cell.
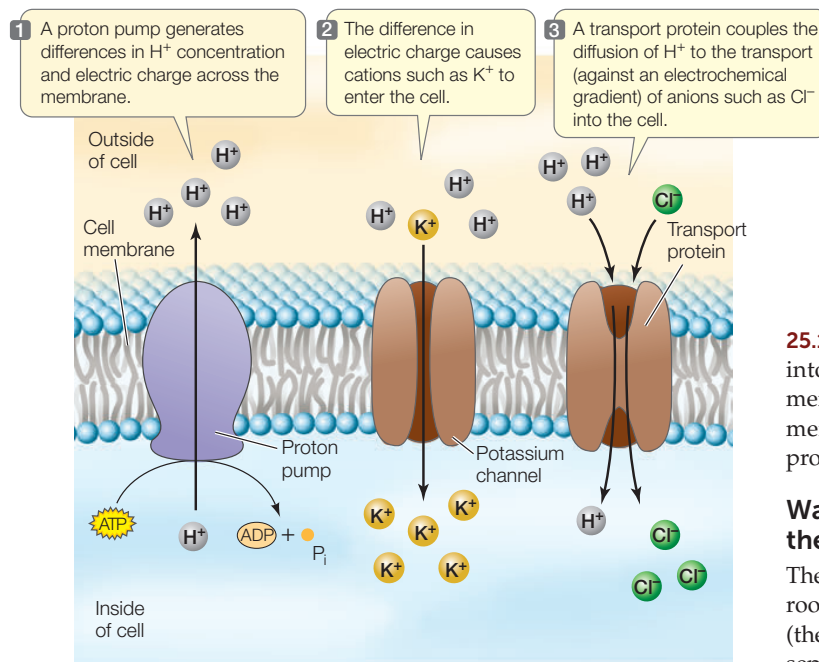
FIGURE 25.10 Ion Transport into Plant Cells
The active transport of protons (H^+) out of the cell by a proton pump (step 1) drives the movement of both cations (step 2) and anions (step 3) into the cell.

25.10, STEP 2). Anions such as chloride (Cl^-) are moved into the cell against an electrochemical gradient by a membrane transport protein that couples their movement with that of H^+ (**FIGURE 25.10, STEP 3**). These processes are examples of secondary active transport.

Water and ions pass to the xylem by way of the apoplast and symplast

The journey of water and ions from the soil through the roots to the xylem follows two pathways—a fast lane (the apoplast) and a slower lane (the symplast)—either separately or in tandem:

root cells, transport proteins can move the ion into the root cells by facilitated diffusion. The concentrations of many mineral ions in the soil solution, however, are lower than those inside the plant. In addition, electric charge differences play a role in the uptake of mineral ions. For example, a negatively charged ion that moves into a negatively charged cellular compartment is moving against an electrical gradient, and this movement requires energy. Concentration and electrical gradients combine to form an electrochemical gradient. Uptake against an electrochemical gradient requires active transport.

> **LINK**
>
> Electrochemical gradients are discussed in more detail in **Concept 34.2**

Animals use a Na^+–K^+ pump to generate a Na^+ gradient that can be used to drive the uptake of other solutes (see Figure 5.7). Instead of a Na^+–K^+ pump, plants have a **proton pump**, which uses energy from ATP to move protons out of the cell against a proton concentration gradient (**FIGURE 25.10, STEP 1**). Because protons (H^+) are positively charged, their accumulation outside the cell has two results:

- An electrical gradient is created such that the region just outside the cell becomes more positively charged than the inside of the cell.

- A proton concentration gradient develops, with more protons just outside the cell than inside the cell.

With the inside of the cell more negative than the outside, cations such as potassium (K^+) move into the cell down the electrical gradient through specific membrane channels (**FIGURE**

Water and solutes can move in the **symplast** by crossing a cell membrane and passing through plasmodesmata.

Water and solutes can move through the **apoplast** without passing through a cell membrane.
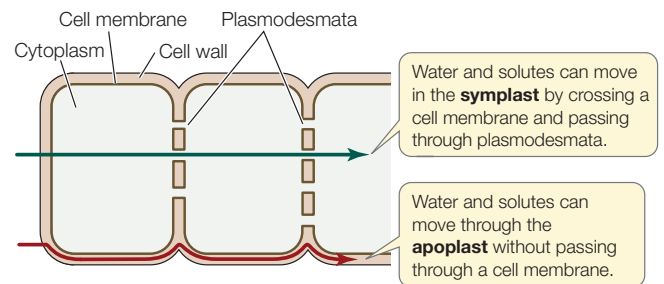
- The **apoplast** (Greek *apo*, "away from"; *plast*, "living material") consists of the cell walls, which lie outside the cell membranes, and intercellular spaces (spaces between cells), which are common in many plant tissues. The apoplast is a continuous meshwork through which water and solutes can flow without ever having to cross a membrane.

- The **symplast** (Greek *sym*, "together with") passes through the continuous cytoplasm of the living cells connected by plasmodesmata. The selectively permeable cell membranes of the root cells control access to the symplast, so movement of water and solutes into the symplast is tightly regulated.

Water and minerals that pass from the soil solution through the apoplast can travel freely as far as the endodermis, the innermost layer of the root cortex (**FIGURE 25.11**).

The endodermis is distinguished by the presence of the **Casparian strip**. This waxy, suberin-impregnated region of the endodermal cell wall forms a hydrophobic belt around each endodermal cell where it is in contact with other endodermal cells. The Casparian strip acts as a seal that prevents water and ions from moving through spaces between the endodermal

The **Casparian strip** prevents water and solutes in the apoplast from passing between the endodermal cells into the stele.

At the Casparian strip, water and solutes in the apoplast must enter the symplast to cross the endodermis.

Inside the stele, solutes are actively transported into the apoplast and water follows passively, forming the xylem sap.

Water and solutes travel through the symplast or apoplast until they reach the endodermis.

FIGURE 25.11 Pathways to the Root Xylem Water and solutes can move into the root through the symplast and apoplast until they reach the endodermis (dark green). There the water and solutes must enter the symplast to bypass the Casparian strip (red). Once inside the stele, the water and solutes enter the xylem (blue).

Go to ACTIVITY 25.1 Apoplast and Symplast of the Root
PoL2e.com/ac25.1

cells; instead, water and ions enter the cytoplasm of the endodermal cells. Water and ions already in the symplast can enter the endodermal cells through plasmodesmata.

> **LINK**
>
> The Casparian strip is functionally equivalent to the tight junctions found in some animal tissues; see **Figure 4.18**

Once they have passed the endodermal barrier, water and minerals remain in the symplast until they reach parenchyma cells in the pericycle or xylem. These cells then actively transport mineral ions into the apoplast of the stele. As ions are transported into the solution in the cell walls of the stele, water potential in the apoplast becomes more negative; consequently, water moves out of the cells and into the apoplast by osmosis. In other words, ions are transported actively, and water follows passively. The end result is that water and minerals end up in the xylem, where they constitute the xylem sap.

Water moves through the xylem by the transpiration–cohesion–tension mechanism

Once water has arrived in the xylem, it is all uphill from there! Consider the magnitude of what xylem accomplishes. A single maple tree 15 meters tall has been estimated to have some

177,000 leaves, with a total leaf surface area of 675 square meters—1.5 times the area of a basketball court. During a summer day, that tree loses 220 liters of water *per hour* to the atmosphere by evaporation from its leaves. To prevent wilting, the xylem must transport 220 liters of water 15 meters from the roots up to the leaves every hour.

How is the xylem able to move so much water to such great heights? Part of the answer lies in the structure of the xylem, which we described in Chapter 24. Recall that xylem vessels consist of a long "straw" of cell walls, which provide both structural support and the rigidity needed to maintain a pressure gradient within the xylem sap. Early experiments ruled out two possible ways that had been hypothesized for moving water up through these vessels from roots to leaves: upward pressure and capillary action.

Upward pressure would move water by "pushing the bottom." A simple experiment in 1893 ruled out this mechanism: A tree was cut at its base, and the sawed-off upper stem was placed in a vat of poison that killed living cells. (Recall that mature xylem is made up of dead cells.) The poison continued to rise through the trunk, even though cells were killed along the way. This observation showed that a living "pump" is not required to push the xylem sap up a tree. Furthermore, the roots were absent, yet upward flow in the trunk continued, demonstrating that the roots do not provide upward pressure. When the poison reached the leaves and killed them, however, all further movement up the trunk stopped, demonstrating that leaves must be alive for water to move in the xylem.

Capillary action was also ruled out as the mechanism that makes water rise in the xylem. Water molecules have strong cohesion, so a column of water can indeed rise a short distance

3 Tension pulls water from the veins into the apoplast surrounding the mesophyll cells...

4 ...which in turn pulls water in the veins of the leaves upward and outward...

2 Water evaporates from mesophyll cell walls.

1 During **transpiration** water vapor diffuses out of the leaf through pores called stomata.

Leaf

Vein

Mesophyll cell

H_2O

5 ...which in turn pulls the water column in the xylem of the shoot and root upward.

Stem

Xylem

6 Cohesion between water molecules forms a continuous water column from the roots to the leaves.

Root

H_2O

7 Water moves into the xylem by osmosis.

Xylem

8 Water enters the root from the soil by osmosis.

H_2O

H_2O

FIGURE 25.12 The Transpiration–Cohesion–Tension Mechanism Transpiration causes evaporation from mesophyll cell walls, generating tension on the water in the xylem. Cohesion among water molecules in the xylem transmits the tension from the leaf to the root, causing water to flow through the xylem from the roots to the atmosphere.

Go to ANIMATED TUTORIAL 25.3
Xylem Transport
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Go to MEDIA CLIP 25.1
Inside the Xylem
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in a thin tube (e.g., a straw or a xylem vessel) by capillary action, but calculations have shown that xylem vessels, at 100 μm in diameter, are simply too wide to get water to the top of a 15-meter tree in this fashion. In fact, the maximum height for a water column raised by capillary action alone in a 100-μm-diameter vessel is only 0.15 meters.

LINK

You can review the properties of water in **Concept 2.2**

Almost a century ago, the **transpiration–cohesion–tension** theory was proposed to explain water transport in the xylem (**FIGURE 25.12**). According to this theory, the key elements of xylem transport are:

• *Transpiration*: evaporation of water from cells within the leaves

• *Cohesion* of water molecules in the xylem sap as a result of hydrogen bonding

• *Tension* on the xylem sap resulting from transpiration

The concentration of water vapor in the atmosphere is lower than that in the air spaces between the cells of a leaf. Because of this difference, water vapor diffuses out of the leaf in a process called **transpiration**. Within the leaf, water evaporates from the moist walls of the mesophyll cells and enters the intercellular air spaces. As water evaporates from the aqueous film coating each cell, the film shrinks back into tiny spaces in the cell walls, increasing the curvature of the water surface and thus increasing its surface tension. Because of hydrogen bonding, water molecules have cohesion, and therefore the increased tension (negative pressure potential) in the surface film draws more water into the cell walls, replacing that which was lost by evaporation. The resulting tension in the mesophyll draws water from the xylem of the nearest vein into the apoplast surrounding the mesophyll cells. The removal of water from the veins, in turn, establishes tension on the entire column of water

(A)

Guard cells

Stoma

10 µm
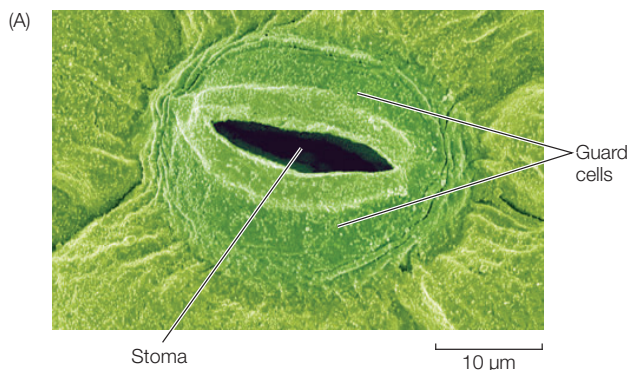
FIGURE 25.13 Stomata Regulate Gas Exchange and Transpiration
(A) Scanning electron micrograph of an open stoma formed by two sausage-shaped guard cells. (B) Potassium ion (K^+) concentrations affect the water potential of the guard cells, controlling the opening and closing of stomata. Negatively charged ions (e.g., Cl^-) that accompany K^+ maintain electrical balance and contribute to the changes in water potential that open and close the stomata.

(B)

Cl^- K^+

Guard cells

Stoma

H_2O

Cellulose microfibrils

H_2O K^+

Cl^-

1 In the light, guard cells actively pump protons out, thus facilitating the entry of K^+ and Cl^-.

2 Higher internal K^+ and Cl^- concentrations give guard cells a more negative water potential, causing them to take up water. The resulting increase in turgor pressure stretches the cells and opens the stoma.

3 In the absence of light, K^+ and Cl^- diffuse passively out of the guard cells, and water follows by osmosis. The guard cells shrink and the stoma closes.

contained in the xylem, so that the column is drawn upward all the way from the roots.

Each part of this model is supported by evidence:

- The difference in water potential between the soil solution and air is huge, on the order of –100 MPa. This difference generates more than enough tension to pull a water column up the tallest tree.

- There is a continuous column of water in the xylem, which is caused by cohesion.

- Measurements of xylem pressures in cut stems show a negative pressure potential, which indicates considerable tension.

In addition to its role in xylem transport, transpiration has the added benefit of cooling a plant's leaves (much as humans sweat to cool off). The evaporation of water from mesophyll cells consumes heat, thereby decreasing the leaf temperature. A farmer can hold a leaf between thumb and forefinger to estimate its temperature; if the leaf doesn't feel cool, that means transpiration is not occurring and it must be time to water.

Although transpiration provides the driving force for the transport of water and minerals in the xylem, it also results in the loss of tremendous quantities of water from the plant. How do plants control this loss?

Stomata control water loss and gas exchange

In Chapter 6 we described photosynthesis, which has the general equation

$$CO_2 + H_2O \rightarrow carbohydrate + O_2$$

Leaves are the chief organs of photosynthesis, so they must have a large surface area across which to exchange the gases O_2 and CO_2. This surface area is provided by the mesophyll cells being surrounded by abundant air spaces inside the leaf (see Figure 25.12), which are also the location of the evaporation

that drives water movement in the xylem. The epidermis of leaves and stems minimizes transpirational water loss by secreting a waxy cuticle, which is impermeable to water. However, the cuticle is also impermeable to CO_2 and O_2. How can the plant balance its need to retain water with its need to obtain CO_2 for photosynthesis?

Plants have met this challenge with the evolution of **stomata** (singular *stoma*): pores in the leaf epidermis, typically on the underside of the leaf (**FIGURE 25.13A**). There are up to 1,000 stomata per square millimeter in some leaves, constituting up to 3 percent of the total surface area of the shoot. Such an abundance of stomata could lead to excessive water loss. But stomata are not static structures. A pair of specialized epidermal cells, called **guard cells**, controls the opening and closing of each stoma.

When the stomata are open, CO_2 can enter the leaf by diffusion, but water vapor diffuses out of the leaf at the same time. Closed stomata prevent water loss but also exclude CO_2 from the leaf. Most plants open their stomata when the light intensity is sufficient to maintain a moderate rate of photosynthesis. At night, when darkness precludes photosynthesis, their stomata are closed; no CO_2 is needed at this time, and water is conserved. Even during the day, the stomata close if water is being lost at too great a rate.

APPLY THE CONCEPT

Water and solutes are transported in the xylem by transpiration–cohesion–tension

Suppose you measure water potential (Ψ) in a 100-m-tall tree and its surroundings and obtain the results in the table. Note that gravity exerts a force of –0.01 MPa per meter of height above ground.

1. Is the water potential in the leaf sufficiently low to draw water to the top of the tree?

2. Would transpiration continue if soil water potential decreased to –1.0 MPa?

3. What would you expect to happen to the xylem water potential if all of the stomata closed?

REGION	Ψ (MPa)
Soil water	–0.3
Xylem of root	–0.6
Xylem of trunk	–1.2
Inside of leaf	–2.0
Outside air	–58.5

Stomata can respond rapidly to changes in light, CO_2 concentration, and water loss. Plants can also change their total number of stomata in response to longer-term changes in environmental conditions.

LIGHT AND CO_2 CONCENTRATION   Guard cells can respond to changes in light and CO_2 concentration in a matter of minutes by changing their solute potential. The absorption of light by a pigment in the guard cell's cell membrane activates a proton pump (see Figure 25.10), which actively transports H^+ out of the guard cells and into the apoplast of the surrounding epidermis. The resulting electrochemical gradient drives K^+ into the guard cells, where it accumulates (**FIGURE 25.13B**). Negatively charged chloride (Cl^-) ions and organic ions also move into and out of the guard cells along with the K^+ ions, maintaining electrical balance. The increased concentration of K^+ and other solutes inside the guard cells makes the solute potential of the guard cells more negative. Water then enters by osmosis, increasing the turgor pressure of the guard cells. The guard cells change their shape, becoming more turgid in response to the increase in pressure potential, so that a space—the stoma—appears between them. The stoma closes in the absence of light: the proton pump becomes less active, K^+ ions diffuse passively out of the guard cells, water follows by osmosis, the pressure potential decreases, and the guard cells sag together and seal off the stoma. Guard cell membranes are particularly rich in aquaporins, making guard cells well adapted for the rapid water movements involved in stomatal responses.

WATER   Stomata also respond to water availability. Water stress is a common problem for plants, especially on a hot, windy day, when plants might close their stomata even when the sun is shining. The water potential of the leaf's mesophyll cells is the cue for this response. If the mesophyll becomes dehydrated, its cells release the hormone abscisic acid, which causes the stomata to close.

REGULATION BY STOMATA NUMBER   A plant can regulate water loss not just by the opening or closing of stomata, but by changing the number of stomata. This occurs much more slowly, over a period of days to weeks. Trees can reduce stomata numbers by shedding leaves, or by making new leaves that have few stomata.

CHECKpoint   CONCEPT 25.3

✓ What distinguishes water potential, solute potential, and pressure potential?

✓ What are the roles of transpiration, cohesion, and tension in xylem transport?

✓ If *Arabidopsis* is exposed to high CO_2 concentrations, the new leaves that form on the plant have fewer stomata than they would have had under normal conditions. Why do you think this might be advantageous?

Now that we understand how leaves obtain the water and CO_2 required for photosynthesis, let's examine how the products of photosynthesis are transported to other parts of the plant where they are needed.

CONCEPT 25.4   Solutes Are Transported in the Phloem by Pressure Flow

As photosynthesis occurs in the leaf, the carbohydrate products of photosynthesis (photosynthate; mainly sucrose) diffuse to the nearest small vein, where they are actively transported into sieve tube elements. The movement of carbohydrates and other solutes through the plant in the phloem is called **translocation**. These solutes are translocated from sources to sinks:

- A **source** is an organ (such as a mature leaf or a storage root) that *produces* (by photosynthesis or by digestion of stored reserves) more carbohydrates than it requires.

- A **sink** is an organ (such as a root, flower, developing fruit or tuber, or immature leaf) that *consumes* carbohydrates for its own growth and storage needs.

Sources and sinks can change roles. For example, storage roots (such as sweet potatoes) are sinks when they accumulate carbohydrates, but they are sources when their stored reserves are mobilized to nourish other organs in the plant.

LINK

The anatomy of sieve tube elements is described in **Concept 24.1**

Sucrose and other solutes are carried in the phloem

Evidence that the phloem carries sucrose and other solutes initially came in the 1600s, when Marcello Malpighi removed a ring of bark (containing the phloem) from the trunk of a tree, while leaving the xylem intact—that is, he "girdled" the tree. Over time, the bark in the region above the girdle swelled:

A ring of bark is removed to girdle the tree.

Solutes accumulate in the phloem above the girdle, causing swelling.

Time

Bark

Wood
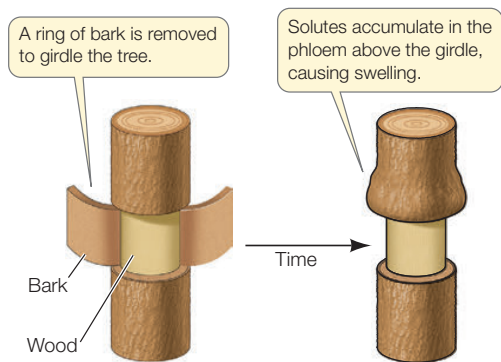
Malpighi correctly concluded that the solution coming from the leaves above the girdle was trapped in the bark. Later, the bark below the girdle died because it was no longer receiving sugars from the leaves. Eventually the roots, and then the entire tree, died.

More recently plant biologists have analyzed the contents of phloem with the help of aphids. These insects feed on plants by drilling into sieve tube elements with a specialized organ, the stylet. The pressure potential in the sieve tube is higher than that outside the plant, so the phloem sap is forced through the stylet and into the aphid's digestive tract. So great is the pressure that sugary liquid is forced through the insect's body and out its anus:

The aphid's stylet has successfully penetrated the sieve tube.

Sieve tube element

Longistigma caryae   Sap droplet
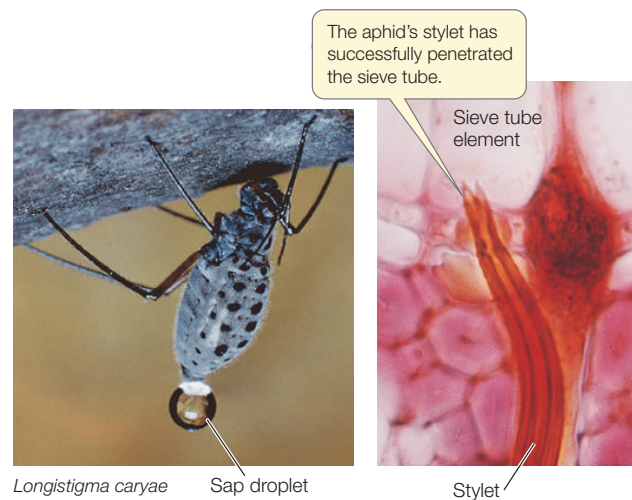
Stylet

If an aphid is frozen in the act of feeding, its body can be broken off the plant stem, leaving the stylet intact. Phloem sap continues to flow out of the stylet for hours.

Several observations have come from analyzing phloem sap in this way, as well as from other experiments:

- Ninety percent of the phloem solutes consist of sucrose, with the rest hormones, other small molecules such as mineral nutrients and amino acids, and viruses.
- The flow rate can be very high, as much as 100 centimeters per hour.

1 Transpiration pulls water up xylem vessels.

Xylem

Sieve tube

Source cell

Companion cell

2 Source cells load sucrose into companion cells. The sucrose enters phloem sieve tubes, reducing water potential…

H_2O

Sucrose

3 …so water is taken up from the xylem by osmosis, raising the pressure potential in the sieve tube.

Sieve tube element

Sieve plate

Sink cell

4 Internal pressure differences drive the phloem sap along the sieve tube to sink cells.

Sucrose

6 …and water moves back into the xylem by osmosis.

5 Sucrose is unloaded into sink cells, increasing the water potential in the sieve tube…

FIGURE 25.14 The Pressure Flow Model
Differences in water potential produce a pressure gradient that moves phloem sap from sources to sinks.

Go to ANIMATED TUTORIAL 25.4
The Pressure Flow Model
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- Different sieve tube elements conduct their contents in different directions (up or down the stem, for example). Movement in the phloem as a whole is bidirectional, but it is unidirectional within an individual sieve tube.
- Movement of sap in the phloem requires living cells, in contrast to movement in the xylem.

The pressure flow model describes the movement of fluid in the phloem

The observations described above led to the **pressure flow model** as an explanation for translocation in the phloem (**FIGURE 25.14**). According to this model, sucrose is actively transported at a source into companion cells, from which it flows through plasmodesmata into the sieve tube elements. This gives those cells a higher sucrose concentration than the surrounding cells (a more negative solute potential), and water therefore enters the sieve tube elements from the xylem by osmosis. The entry of this water increases turgor pressure (causes a more positive pressure potential) at the source end of the sieve tube, so that the entire fluid content of the sieve tube is pushed toward the sink end of the tube—in other words, the sap moves in response to a pressure gradient. In the sink, the sucrose is unloaded both passively and by active transport, and water moves back into the xylem. In this way, the gradient of solute potential and pressure potential needed for the movement of phloem sap (translocation) is maintained.

Two steps in phloem translocation require metabolic energy:

- Transport of sucrose and other solutes from sources into companion cells and then into the sieve tubes; called "loading"
- Transport of solutes from the sieve tubes into sinks; called "unloading"

The need for metabolic energy is the reason why phloem transport, unlike xylem transport, requires living cells.

Two general routes can be taken by sucrose and other solutes as they move from the mesophyll cells into the phloem. In many plants, sucrose and other solutes follow an apoplastic pathway: they leave the mesophyll cells and enter the apoplast before they reach the sieve tube elements. Specific sugars and amino acids are then actively transported into cells of the phloem. Because the solutes cross at least one selectively permeable membrane in the apoplastic pathway, selective transport can be used to regulate which specific substances enter the phloem. In other plants, solutes follow a symplastic pathway: the solutes remain within the symplast all the way from the mesophyll cells to the sieve tube elements. Because no membranes are crossed in the symplastic pathway, a mechanism that does not involve membrane transport is used to load sucrose into the phloem.

In sink regions, the solutes are actively transported *out* of the sieve tube elements and into the surrounding tissues. This unloading serves several purposes: it helps maintain the gradient of solute potential, and hence of pressure potential, in the sieve tubes; it helps build up high concentrations of carbohydrates in storage organs, such as developing fruits and seeds;

and it moves nutrients to parts of the plant that are growing rapidly, such as shoots that form after the winter.

CHECKpoint   CONCEPT 25.4

✓ Deer sometimes graze on evergreen trees by eating bark during the winter when other food is scarce. In the spring, those trees may die. How does this happen?

✓ What would happen if the ends of sieve tubes were blocked and did not allow phloem sap to flow through them?

✓ Make a table that compares the flow of fluids in xylem and in phloem with respect to the driving force for movement; where flow occurs; whether the cells are alive; and whether the driving pressure is positive or negative.

Q How can soil be managed for optimal plant growth?

ANSWER   Every year, 25 billion tons of topsoil (A horizon) are lost worldwide from potentially arable land. This loss reduces the nutrient content (Concept 25.1) and water-holding capacity (Concept 25.3) of the remaining soil. It therefore creates added demand for fertilizers and irrigation to restore the soils, but these inputs are too expensive in most areas of the world, and they can have adverse effects on the rest of the environment. For example, adding fertilizer to soils can pollute nearby waters or result in excess salts in the soil, and huge irrigation projects destroy natural habitats and can lead to flooding.

Faced with these challenges, scientists and farmers (often the same people!) have invented methods of sustainable farming. In the United States, for example, a branch of the federal government called the Natural Resource Conservation Service (formerly the Soil Conservation Service) was established in response to the country's experiences with soil degradation during the Dust Bowl of the 1930s.

There are several strategies to sustain the structure, nutrient content, and water-holding capacity of soil. One of these strategies is crop rotation. Different plants have different nutritional requirements and so remove different nutrients from the soil as they grow and are harvested. For example, corn requires large amounts of nitrogen, whereas soybeans harbor nitrogen-fixing bacteroids in their roots (Concept 25.2). In the midwestern United States, corn and soybeans are planted in alternate growing seasons.

Another strategy is conservation tillage. This refers to methods such as plowing that are used to prepare soil for planting. Conservation tillage can help maintain soil and reduce soil losses. If you fly over any heavily farmed area of the United States, look out the window and you will see contour plowing patterns; these patterns are used to control runoff of

the topsoil during heavy rains. More recently, it has become increasingly common for farmers to leave behind on the field up to half of the stems and leaves of plants that are harvested for grain (**FIGURE 25.15**). The farmers plow these crop residues back into the soil, where they help maintain soil structure, bind water, and provide nutrients because they are organic matter that builds up humus. More than one-third of the farmland in the United States is now being farmed in this way.

Our increasing understanding of plants and their relationship to soils will doubtless lead to more sustainable practices in the future.

Seedlings of current crop

Residue from previous crop

FIGURE 25.15 Conservation Tillage   These soybean plants are growing amidst the residue of corn plants that were harvested for their grain. The crop residues help conserve the soil.

SUMMARY

CONCEPT 25.1 Plants Acquire Mineral Nutrients from the Soil

- Plants are photosynthetic **autotrophs** that require water and certain mineral nutrients to survive. They obtain most of these mineral nutrients as ions from the **soil solution**.

- The **essential elements** for plants include six **macronutrients** and several **micronutrients**. Plants that lack a particular nutrient show characteristic deficiency symptoms. **Review Figure 25.1 and ANIMATED TUTORIAL 25.1**

- The essential elements were discovered by growing plants **hydroponically** in solutions that lacked individual elements. **Review Figure 25.2**

- Soils supply plants with mechanical support, water and dissolved ions, air, and the services of other organisms. **Review Figure 25.3**

- Protons take the place of mineral nutrient cations bound to clay particles in soil in a process called **ion exchange**. **Review Figure 25.4**

- Farmers may use shifting agriculture or **fertilizer** to make up for nutrient deficiencies in soil.

CONCEPT 25.2 Soil Organisms Contribute to Plant Nutrition

- Signaling molecules called **strigolactones** induce the hyphae of arbuscular mycorrhizal fungi to invade root cortical cells and form arbuscules, which serve as sites of nutrient exchange between fungus and plant. **Review Figure 25.5A**

- Legumes signal nitrogen-fixing bacteria (rhizobia) to form **bacteroids** within nodules that form on their roots. **Review Figure 25.5B**

- In **nitrogen fixation**, nitrogen gas (N_2) is reduced to ammonia in a reaction catalyzed by **nitrogenase**. **Review Figure 25.6**

- Carnivorous plants supplement their nutrient supplies by trapping and digesting arthropods. Parasitic plants obtain minerals, water, or products of photosynthesis from other plants.

CONCEPT 25.3 Water and Solutes Are Transported in the Xylem by Transpiration–Cohesion–Tension

- Water moves through biological membranes by osmosis, always moving toward regions with a more negative water potential. The

water potential (Ψ) of a cell or solution is the sum of its **solute potential** (Ψ_s) and its **pressure potential** (Ψ_p). **Review Figure 25.8 and ANIMATED TUTORIAL 25.2**

- The physical structure of many plants is maintained by the positive pressure potential of their cells (**turgor pressure**); if the pressure potential drops, the plant wilts.

- Water moves into root cells by osmosis through aquaporins. Mineral ions move into root cells through ion channels, by facilitated diffusion, and by secondary active transport. **Review Figure 25.10**

- Water and ions may pass from the soil into the root by way of the **apoplast** or the **symplast**, but they must pass through the symplast to cross the endodermis and enter the xylem. The **Casparian strip** in the endodermis blocks further movement of water and ions through the apoplast. **Review Figure 25.11 and ACTIVITY 25.1**

- Water is transported in the xylem by the **transpiration–cohesion–tension** mechanism. Evaporation from the leaf produces tension in the mesophyll, which pulls a column of water—held together by cohesion—up through the xylem from the root. **Review Figure 25.12 and ANIMATED TUTORIAL 25.3**

- **Stomata** allow a balance between water retention and CO_2 uptake. Their opening and closing is regulated by **guard cells**. **Review Figure 25.13**

CONCEPT 25.4 Solutes Are Transported in the Phloem by Pressure Flow

- **Translocation** is the movement of the products of photosynthesis, as well as some other small molecules, through sieve tubes in the phloem. The solutes move from **sources** to **sinks**.

- Translocation is explained by the **pressure flow model**: the difference in solute potential between sources and sinks creates a difference in pressure potential that pushes phloem sap along the sieve tubes. **Review Figure 25.14 and ANIMATED TUTORIAL 25.4**

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is25

26 Plant Growth and Development

Plant geneticist Norman Borlaug, seen here in a field of semi-dwarf wheat, carried out a program of genetic crosses that led to high-yielding varieties of wheat and saved millions of people from starvation.

In their constant search for ways to help farmers produce more food for a growing population, biologists have developed cereal crops whose physiology allows them to produce more grain per plant (a higher yield). When a plant produces a lot of seeds, however, the sheer weight of the seeds may cause the stem to bend over or even break. This makes harvesting the seeds impossible: think of how hard it would be to get enough food for your family if you had to pick up seeds on the ground, some of which had already sprouted.

In 1945 the U.S. Army temporarily occupied Japan, which it had defeated in the Second World War. During the war, Japan, an island nation with a limited amount of land suitable for farming, was blockaded and could not import food. How had Japan been able to grow enough grain to feed its people? The answer lay in the fields: the Japanese had bred genetic strains of rice and wheat with short, strong stems that could bear a high yield of grain without bending or breaking. This innovation made an impression on an agricultural advisor who happened to be among the first wave of U.S. occupiers, and seeds of the Japanese strains were sent back to the United States.

A decade later, Norman Borlaug, a plant geneticist who was working in Mexico at the time, began genetic crosses of what were known as semi-dwarf wheat plants from Japan with wheat varieties that had genes conferring rapid growth, adaptability to varying climates, and resistance to fungal diseases. The results were new genetic strains of wheat that produced record yields, first in Mexico and then in India and Pakistan in the 1960s. At about the same time, and using a similar strategy, scientists in the Philippines developed new semi-dwarf strains of rice with equally spectacular results. People who had lived on the edge of starvation now produced enough food. Countries that had been relying on food aid from other countries were now growing so much grain that they could export the surplus. The development of these new semi-dwarf strains began what was called the "Green Revolution." Borlaug was awarded the Nobel Peace Prize for his research on wheat, which is estimated to have saved a billion lives.

Q What changes in their growth patterns made the new strains of cereal crops produced by the Green Revolution so successful?

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CONCEPT 26.1 **Plants Develop in Response to the Environment**

</div>

Plants are sessile (nonmobile) organisms that must seek out resources above and below the ground. Plants have several characteristics that distinguish them from animals and allow them to obtain the resources that they need to grow and reproduce:

- *Meristems*. Plants have permanent collections of stem cells (undifferentiated, constantly dividing cells) that allow them to continue growing throughout their lifetimes (see Concept 24.2).
- *Post-embryonic organ formation*. Unlike many animals, plants can initiate development of new organs such as leaves and flowers throughout their lifetimes.
- *Differential growth*. Plants can allocate their resources so that they grow more of the organs that will benefit them most—for example, more leaves to harvest sunlight or more roots to obtain water and nutrients.

The development of a plant—the series of progressive changes that take place throughout its life—is regulated in many ways. Several key factors are involved in regulating plant growth and development:

- *Environmental cues*, such as day length
- *Receptors* that allow a plant to sense environmental cues, such as photoreceptors that absorb light
- *Hormones*—chemical signals that mediate the plant's adaptations and effects of environmental cues, including those sensed by receptors
- The plant's *genome*, which encodes regulatory proteins and enzymes that catalyze the biochemical reactions of development

We will explore these factors in more detail later in this chapter. But first let's look at the initial steps of plant development—from seed to seedling—and the environmental cues and internal responses that guide those steps.

The seed germinates and forms a growing seedling

Concepts 24.1 and 27.1 describe the events of plant development and reproduction that lead to the formation of seeds. Here we begin with the seed, the structure that contains the plant embryo. Unlike most animal embryos, plant embryos may be held in "suspended animation" inside the seed, with development halted, for long periods. If development stops, even when external conditions (such as water supply) are adequate for growth, the seed is said to be **dormant**. Development restarts when the seed **germinates** (sprouts).

DORMANCY   Seed dormancy may last for weeks, months, years, or even centuries: in 2005, a botanist was able to germinate a date palm seed recovered from a 2,000-year-old storage bin at Masada in Israel. Plants use several mechanisms to maintain dormancy:

- *Exclusion of water or oxygen* from the embryo by an impermeable seed coat
- *Mechanical restraint* of the embryo by a tough seed coat
- *Chemical inhibition* of germination
- *Photodormancy*: some seeds require a period of light or dark to germinate
- *Thermodormancy*: some seeds require a period of high or low temperature to germinate

Dormancy can be broken by factors that overcome these mechanisms. For example, passage through an animal's digestive system may damage the seed coat, or burial beneath soil (in darkness) might trigger germination.

Seed dormancy is a common phenomenon, so it must have selective advantages for plants. Dormancy ensures survival during unfavorable conditions and results in germination when environmental conditions are most favorable for growth and development of the young plant. For example, to avoid germination in the dry days of late summer, some seeds require exposure to a long cold period (winter) before they will germinate; this ensures that the plant has the entire growing season to mature. Dormancy also helps seeds survive long-distance dispersal, allowing plants to colonize new territory.

GERMINATION   Seeds begin to germinate when dormancy is broken. For example, a seed may germinate after a germination inhibitor is washed away in heavy rain, which means the soils will have plenty of water and germination will be possible.

The first step in germination is the uptake of water, called **imbibition** (from *imbibe*, "to drink in"). A dormant seed contains very little water: only 5–15 percent of its weight is water, compared with 80–95 percent for most other plant parts. Seeds also contain polar macromolecules, such as cellulose and starch, that attract and bind polar water molecules. Consequently a seed has a very negative water potential (see Concept 25.3) and will take up water if the seed coat is permeable. The force exerted by imbibing seeds, which expand severalfold in volume, demonstrates the magnitude of their water potential. Imbibing cocklebur seeds can exert a pressure of up to 1,000 atmospheres (approximately 100 kilopascals, or 15,000 pounds per square inch).

As a seed takes up water, it undergoes metabolic changes: enzymes are activated, RNA and then proteins are synthesized, the rate of cellular respiration increases, and other metabolic pathways are activated. In many seeds, cell division is not initiated during the early stages of germination. Instead, growth results solely from the expansion of small, preformed cells.

As the seed begins to germinate, the growing embryo obtains chemical building blocks for its development—carbohydrates, amino acids, and lipid monomers—by hydrolyzing (see Figure 2.8) starch, proteins, and lipids stored in the seed. These reserves are stored in the **cotyledons**—embryonic leaves—or in the **endosperm**—a seed tissue specialized for storage. Germination is completed when the **radicle** (embryonic root) emerges from the seed coat. The plant is then called a **seedling**.

(A) Monocot (corn)

1 A coleoptile (a cylindrical sheath of cells) protects the early shoot as it grows to the soil surface.

First foliage leaf

Coleoptile

Primary root (covered by a sheath)

2 After the shoot emerges from the soil, it continues to elongate, and the leaves emerge.

(B) Eudicot (bean)

1 The shoot apex of most eudicots is protected by the cotyledons as the upper part of the plant is pulled above the soil surface.

2 When the shoot elongates, the first foliage leaves emerge.

Foliage leaf

Apical hook

Seed coat

Cotyledons

Primary root

Secondary roots

FIGURE 26.1 Patterns of Early Shoot Development (A) In grasses and some other monocots, growing shoots are protected by a coleoptile until they reach the soil surface. (B) In most eudicots, the growing point of the shoot is protected within the cotyledons.

Go to ACTIVITY 26.1
Monocot Shoot Development
PoL2e.com/ac26.1

Go to ACTIVITY 26.2
Eudicot Shoot Development
PoL2e.com/ac26.2

If the seed germinates underground, the new seedling must elongate rapidly (in the right direction!) and cope with a period of life in darkness or dim light. A series of photoreceptors direct this stage of development.

The pattern of early shoot development varies among the flowering plants. **FIGURE 26.1** shows the shoot development patterns of monocots and eudicots. In monocots, the growing shoot is protected by a cylindrical sheath of cells called the **coleoptile** as it pushes its way through the soil. In eudicots, the shoot is usually protected by the cotyledons.

Several hormones and photoreceptors help regulate plant growth

This survey of the early stages of plant development illustrates the many environmental cues that influence plant growth. A plant's responses to these cues are prompted and maintained by two types of regulators: hormones and photoreceptors. Both types of regulators act through signal transduction pathways (series of biochemical steps within a cell that occur between a stimulus and a response).

LINK

The general characteristics of signal transduction pathways are discussed in **Concepts 5.5 and 5.6**

Hormones are chemical signals that act at very low concentrations at sites often distant from where they are produced. Plant hormones are different from animal hormones (**TABLE 26.1**; see also Chapter 35). Each plant hormone plays multiple regulatory roles, and

interactions among them can be complex. Several hormones regulate the growth and development of plants from seedling to adult (**TABLE 26.2**). Other hormones are involved in the plant's defenses against herbivores and microorganisms (which we will discuss in Chapter 28).

Photoreceptors are proteins with pigments associated with them. Light acts directly on photoreceptors, which in turn regulate developmental processes that need to be responsive to light, such as the many changes that occur as a seed germinates and a seedling emerges from the soil. Note that this effect of light as an information source is different from the effect of light as an energy source in photosynthesis.

Genetic screens have increased our understanding of plant signal transduction

In Chapter 14 we described how genetic studies can be used to identify the steps along a developmental pathway. You will recall the reasoning behind these experiments: if a mutation in a gene involved in a certain biochemical process disrupts a

TABLE 26.1	Comparison of Plant and Animal Hormones	
Characteristic	**Plant hormones**	**Animal hormones**
Size, chemistry	Proteins, small organic molecules	Peptides, proteins, small molecules
Site of synthesis	Usually at many locations	Specialized glands or cells
Site of action	Local or distant	Usually distant, transported
Effects	Often diverse	Often specific
Regulation	By biochemical feedback	By central nervous system, ions, or feedback

developmental event, then that biochemical process must be essential for that developmental event. Similarly, genetic studies can be used to analyze pathways of receptor activation and signal transduction in plants: if proper signaling does not occur in a mutant strain, then the mutated gene must be involved in the signal transduction process. Mapping the mutated gene and identifying its function are starting points for understanding the signaling pathway. *Arabidopsis thaliana*, a member of the mustard family, has been a major model organism for plant biologists investigating signal transduction.

One technique for identifying the genes involved in a plant signal transduction pathway is illustrated in **FIGURE 26.2**. This technique, called a **genetic screen**, involves creating a large collection of randomly mutated plants and identifying those individuals that are likely to have a defect in the pathway of interest. Plant genes can be randomly mutated in two ways:

- By insertion of transposons (see Concepts 12.2 and 12.3) or T DNA (see Concept 13.2)
- By treatment of seeds with chemical mutagens, most commonly ethyl methane sulfonate or radiation

In both cases, the treated plants are grown and then examined for a specific phenotype, usually a characteristic that is known to be influenced by the pathway of interest. Once mutant plants have been selected, their genotypes are compared with those of wild-type plants. Mutant *Arabidopsis* plants with altered developmental patterns have provided a wealth of new information about the hormones present in plants and the mechanisms of hormone and photoreceptor action.

CHECKpoint CONCEPT 26.1

✓ Describe how monocots and eudicots differ in their early development.

✓ Seeds of the Australian shrub *Acacia myrtifolia* require extreme heat (fire) to germinate. How do you think fire might work as an environmental cue to break dormancy? What would be the selective advantage of this mechanism for breaking dormancy?

✓ Seedlings grown in the dark grow thin and tall, a phenomenon called etiolation. How would you set up a genetic screen using *Arabidopsis* to investigate the signaling pathway that controls etiolation?

With this overview of plant development, we will begin our examination of the specific regulatory mechanisms that underlie these events. Two hormones—gibberellins and auxin—have prominent roles in plant development.

RESEARCH TOOLS

FIGURE 26.2 A Genetic Screen Genetics of the model plant *Arabidopsis thaliana* can be used to identify the steps of a signal transduction pathway. If a mutant strain does not respond to a hormone (in this case, ethylene), the corresponding wild-type gene must be essential for the pathway (in this case, ethylene response). This method has been instrumental to scientists in understanding plant growth regulation.

1 A phenotype of interest is chosen, in this case response to ethylene. Elongation of wild-type seedlings in the dark is inhibited by ethylene (right).

No ethylene added   Ethylene added

2 Seeds are treated with a mutagen and then planted.

Many seeds suspended in a mutagen solution in a test tube

3 The treated plants are grown in the dark in the presence of ethylene and then screened. One mutant individual shows insensitivity to the hormone (uninhibited growth).

Ethylene-insensitive mutant

Ethylene-sensitive (wild-type) plants

4 The gene involved in ethylene signaling is mapped, cloned, and studied.

Gene required for ethylene response

CONCEPT 26.2 Gibberellins and Auxin Have Diverse Effects but a Similar Mechanism of Action

The discovery of two key plant hormones exemplifies the experimental approaches that plant biologists have used to investigate the mechanisms of plant development. **Gibberellins** (of which there are several active forms) and **auxin** were the first plant hormones to be identified, early in the twentieth century. In both cases, the discoveries came from observations of natural phenomena:

- *Gibberellins*: In rice plants, a disease caused by the fungus *Gibberella fujikuroi* resulted in plants that grew overly tall and spindly.

TABLE 26.2 Plant Growth Hormones

Hormone	Common structure	Typical activities
Abscisic acid		Maintains seed dormancy; closes stomata
Auxin (indole-3-acetic acid)		Promotes stem elongation, adventitious root initiation, and fruit development; inhibits axillary bud outgrowth, leaf abscission, and root elongation
Brassinosteroids		Promote stem and pollen tube elongation; promote vascular tissue differentiation
Cytokinins		Inhibit leaf senescence; promote cell division and axillary bud outgrowth; affect root growth
Ethylene		Promotes fruit ripening and leaf abscission; inhibits stem elongation and gravitropism
Gibberellins		Promote seed germination, stem growth, and ovule and fruit development; break winter dormancy; mobilize nutrient reserves in grass seeds

- *Auxin*: Charles Darwin and his son Francis noted that canary grass seedlings would bend toward the light when placed near a light source.

In both cases, a chemical substance was isolated that could cause the phenomenon:

- Gibberellic acid (see Table 26.2) made by the fungus caused rice plants to overgrow. Later it was found that plants also make gibberellic acid, and that applying it to plants caused growth.
- Auxin (indole-3-acetic acid) applied asymmetrically to the growing tips of seedlings caused cell expansion on the side away from the light, and this resulted in bending toward the light.

In each case, mutant plants that do not make the hormone exhibit a phenotype expected in the absence of the hormone, and adding the hormone reverses that phenotype (**FIGURE 26.3**):

- Tomato plants that do not make gibberellic acid are very short; supplying them with the hormone results in normal growth.
- *Arabidopsis thaliana* individuals that do not make auxin are also short; supplying them with that hormone reverses that phenotype.

Note that the phenotype involved—short stature, or dwarfism—is similar in both cases. This

FIGURE 26.3 Hormones Reverse a Mutant Phenotype (A) The two mutant dwarf tomato plants in this photograph were the same size when the one on the right was treated with gibberellins. (B) The short phenotype of this mutant *Arabidopsis* was reversed in the plant on the right by supplying auxin.

1 The embryo imbibes H$_2$O and swells.	2 The embryo secretes gibberellins that diffuse into the aleurone layer, where they trigger the synthesis of hydrolytic enzymes.	3 The hydrolytic enzymes move into the endosperm.	4 The enzymes digest the proteins and starch in the endosperm, releasing monomers (amino acids and sugars) from which the embryo synthesizes new cells.

FIGURE 26.4 Gibberellins and Seed Germination During seed germination in cereal crops, gibberellins trigger a cascade of events that result in the conversion of starch and protein stores in the endosperm into monomers that can be used by the developing embryo.

Go to ACTIVITY 26.3 Events of Seed Germination
PoL2e.com/ac26.3

observation exemplifies a concept that is important to keep in mind when studying plant hormones: their actions are not unique and specific, as is the case with animal hormones (see Table 26.1).

The three-part approach outlined above for gibberellins and auxin—observation, hormone isolation, and analysis of mutant plants—has been used to identify other plant hormones.

Gibberellins have many effects on plant growth and development

The functions of gibberellins can be inferred from the effects of experimentally decreasing concentrations of gibberellins or blocking their action at various times in plant development. Such experiments reveal that gibberellins have multiple roles in regulating plant growth.

STEM ELONGATION The effects of gibberellins on wild-type plants are not as dramatic as their effects on dwarf plants. We know, however, that gibberellins are indeed active in wild-type plants because inhibitors of gibberellin synthesis cause a reduction in stem elongation. Such inhibitors can be put to practical uses. For example, plants such as chrysanthemums that are grown in greenhouses tend to get tall and spindly. Because such plants do not appeal to consumers, flower growers spray them with gibberellin synthesis inhibitors to control their height.

FRUIT GROWTH Gibberellins can regulate the growth of fruit. Grapevines that produce seedless grapes develop smaller fruit than varieties that produce seed-bearing grapes. Biologists wanting to explain this phenomenon removed seeds from immature seeded grapes and found that this prevented normal fruit growth. This suggested that the seeds are sources of a growth regulator. Biochemical studies showed that developing seeds produce gibberellins, which diffuse out into the immature fruit tissue. Spraying young seedless grapes with

a gibberellin solution, which causes them to grow as large as seeded ones, is now a standard commercial practice.
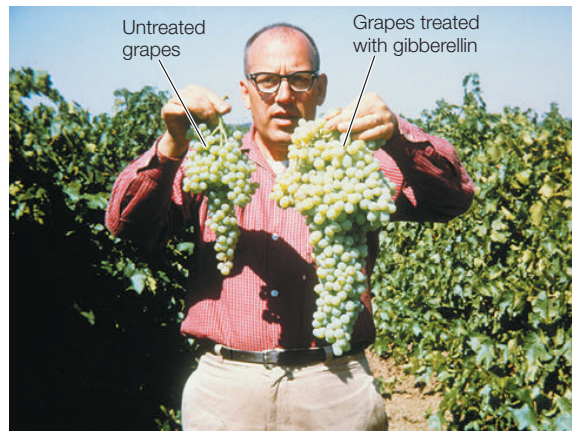
MOBILIZATION OF SEED RESERVES As noted in Concept 26.1, an important event early in seed germination is the hydrolysis of stored starch, proteins, and lipids. In germinating seeds of barley and other cereal crops, the embryo secretes gibberellins just after imbibition. The hormones diffuse through the endosperm to a surrounding tissue called the **aleurone layer**, which lies underneath the seed coat. The gibberellins trigger a cascade of events in the aleurone layer, causing it to synthesize and secrete enzymes that digest proteins and starch stored in the endosperm (**FIGURE 26.4**). These observations have practical importance: in the beer-brewing industry, gibberellins are used to enhance the "malting" (germination) of barley and the

breakdown of its endosperm, producing sugars that are fermented into alcohol by yeast.

The transport of auxin mediates some of its effects

As we noted above, auxin was discovered in the context of **phototropism**: a response to light in which plant stems bend toward a light source. Auxin is made in the shoot apex (tip) and diffuses down the shoot in a polar (unidirectional) fashion, stimulating cell expansion. Note that this use of "polar" differs from its use in chemistry, where it means hydrophilic (see Concept 2.2). Unidirectional longitudinal movement of auxin occurs in other plant organs as well. For example, in a leaf petiole, which connects the leaf blade to the stem, auxin moves from the leaf blade end toward the stem. In roots, auxin moves unidirectionally toward the root tip.

Polar transport of auxin depends on four biochemical processes that may be familiar from earlier chapters (**FIGURE 26.5**):

• *Diffusion across a cell membrane.* Polar (hydrophilic) molecules diffuse across cell membranes less readily than non-polar (hydrophobic) molecules (see Concept 5.2).

• *Membrane protein asymmetry.* Active transport, or efflux, carriers (see Concept 5.3) for auxin are located only in the portion of the cell membrane at the basal (bottom) end of the cell.

• *Proton pumping/chemiosmosis.* Proton pumps (see Concept 25.3) remove H^+ from the cell, thereby increasing the pH inside the cell and decreasing the pH in the cell wall. Proton pumping also sets up an electrochemical gradient, which provides potential energy to drive the transport of auxin by the carriers mentioned above.

• *Ionization of a weak acid.* Indole-3-acetic acid (the chemical name for auxin; see Table 26.2) is a weak acid; in solution it forms ions (H^+ and A^-, where A^- stands for indole acetate) that are in equilibrium with the non-ionized acid (HA):

$$A^- + H^+ \rightleftharpoons HA$$
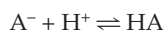
When the pH is low, the increased H^+ concentration drives this reaction to the right, and HA (non-ionized auxin) is the predominant form. When the pH is higher, there is more A^- (ionized auxin).
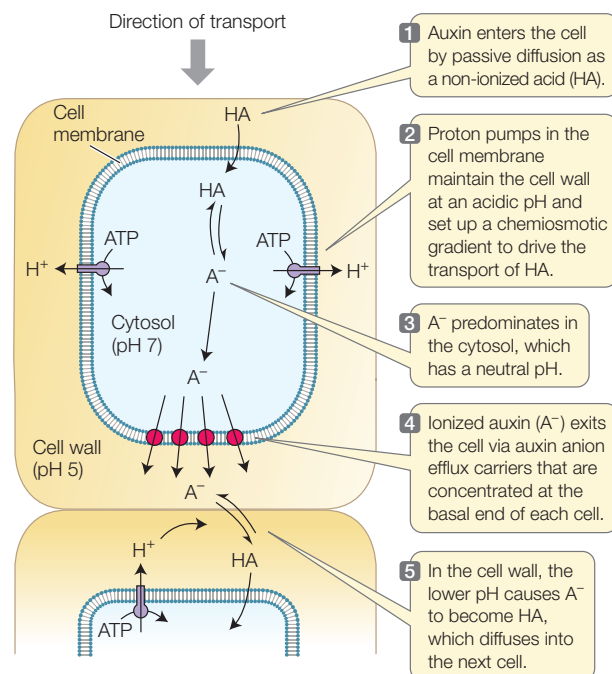
FIGURE 26.5 Polar Transport of Auxin Proton pumps set up a chemiosmotic gradient that drives the uptake of non-ionized auxin (HA) and the efflux of ionized auxin (auxin anion; A^-) through the basally placed auxin anion efflux carriers, leading to a net movement of auxin in a basal direction.

Whereas polar auxin transport distributes the hormone along the longitudinal axis of the plant, lateral (side-to-side) redistribution of auxin is responsible for directional plant growth. This redistribution is carried out by auxin efflux carriers that move from the base of the cell to one side; because of this, auxin exits the cell only on that side of the cell, rather than at the base, and moves sideways within the tissue.

This lateral movement of auxin explains the bending of canary grass seedlings toward light. When light strikes a canary grass coleoptile on one side, auxin at the tip moves laterally toward the shaded side. The asymmetry thus established is

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APPLY THE CONCEPT

Gibberellins and auxin have diverse effects but a similar mechanism of action

Oat seedlings with coleoptiles 20 mm long were exposed to light from one side and checked for bending after 6 hours (see photo on p. 562). Various regions of the seedlings were covered with foil to block the light. The results varied depending on which region of the coleoptile was covered (see table).

1. Which part of the coleoptile senses the light?

2. For each treatment, what would happen if supplementary auxin were applied to the coleoptiles on the same side as the light? On the side away from the light?

REGION COVERED	BENDING
1. None	Yes
2. All	No
3. Apical 5 mm	No
4. Apical 10 mm	No
5. Apical 5–10 mm	Yes
6. Apical 10–15 mm	Yes

(A) Phototropism

1 Auxin moves to the shaded side within the tip.

2 The redistributed auxin moves down the coleoptile.

3 A higher auxin concentration causes more rapid growth by cell expansion on the shaded side. The tip curves toward the light.

Light

Coleoptile

Auxin

The cells on the shaded side expand more than those on the other side.

(B) Negative gravitropism of shoot

1 Auxin moves downward in response to gravity.

2 A higher auxin concentration causes more rapid growth on the lower side. The tip curves upward.

FIGURE 26.6 Plants Respond to Light and Gravity Phototropism (A) and gravitropism (B) occur in shoot apices in response to a redistribution of auxin.

Go to ANIMATED TUTORIAL 26.1
Tropisms
PoL2e.com/at26.1

negative gravitropism; that of roots, which bend downward, is positive gravitropism.

Auxin plays many roles in plant growth and development

Like the gibberellins, auxin has multiple roles in plant growth and development.

ROOT INITIATION   Cuttings from the shoots of some plants can produce roots and develop into entire new plants. For this to occur, cells in the interior of the shoot, originally destined to function only in food storage, must change their fate and become organized into the apical meristem of a new root (this is an example of the remarkable totipotency of plant cells; see Concept 14.1). Shoot cuttings of many species can be made to develop roots by dipping the cut surfaces into an auxin solution. These observations suggest that in an intact plant, the plant's own auxin plays a role in the initiation of lateral roots.

LEAF ABSCISSION   In contrast to its stimulatory effect on root initiation, in leaves auxin inhibits the detachment of old leaves from stems. This detachment process, called **abscission**, is the cause of autumn leaf fall. Recall that the blade of a leaf produces auxin that moves toward the petiole. If the blade is cut off, the petiole falls from the plant more rapidly than if the leaf had remained intact. If the cut surface is treated with an auxin solution, however, the petiole remains attached to the plant, often longer than an intact leaf would have. The timing of leaf abscission in nature appears to be determined in part by a decrease in the movement of auxin through the petiole.

APICAL DOMINANCE   Auxin helps maintain **apical dominance**, a phenomenon in which the apical bud (the very top/first bud that will form leaves) inhibits the growth of axillary buds (side buds; see Figure 24.1), resulting in the growth of a single main stem with minimal branching. A diffusion gradient of auxin from the apex of the shoot down the stem results in lower branches receiving less auxin and therefore branching more, while higher branches receive more auxin and branch less.

FRUIT DEVELOPMENT   Fruit development normally depends on prior fertilization of the ovule (egg), but in many species, treatment of an unfertilized ovary with auxin or gibberellins causes **parthenocarpy**: fruit formation without fertilization. Parthenocarpic fruits form spontaneously in some cultivated varieties of plants, including seedless grapes, bananas, and some cucumbers.

maintained as polar transport moves auxin down the coleoptile, so that in the growing region below, the auxin concentration is highest on the shaded side. Cell expansion is thus increased on that side, causing the coleoptile to bend toward the light (**FIGURE 26.6A**). The same type of bending also occurs in eudicots:

Light

Light is not the only signal that can cause redistribution of auxin. Auxin moves to the lower side of a shoot that has been tipped sideways, causing more rapid growth in the lower side and hence an upward bending of the shoot. Such growth in a direction determined by gravity is called **gravitropism** (**FIGURE 26.6B**). The upward gravitropic response of shoots is defined as

CELL EXPANSION   The expansion of plant cells is a key process in plant growth. Because the plant cell wall normally resists expansion of the cell, it plays a key role in controlling the rate and direction of plant cell growth. Auxin acts on the cell wall to regulate this process.

The expansion of a plant cell is driven primarily by the uptake of water, which enters the cell by osmosis. As it expands, the cell contents press against the cell wall, which resists this force (producing turgor pressure; see Figure 25.8). The cell wall is an extensively cross-linked network of polysaccharides and proteins, dominated by cellulose fibrils (see Figures 2.10 and 4.15). If the cell is to expand, some adjustments must be made in the wall structure to allow the wall to "give" under turgor pressure. Think of a balloon (the cell surrounded by a membrane) inside a box (the cell wall).

> **LINK**
>
> Water movement and turgor pressure in plant cells are discussed in **Concept 25.3**

The **acid growth hypothesis** explains auxin-induced cell expansion (**FIGURE 26.7**). This hypothesis proposes that protons (H^+) are pumped from the cytoplasm into the cell wall, lowering the pH of the wall and activating enzymes called expansins, which catalyze changes in the cell wall structure such that the polysaccharides adhere to each other less strongly. This change loosens the cell wall, allowing it to stretch as the cell expands. Auxin is believed to have two roles in this process: to increase the synthesis of proton pumps, and to guide their insertion into the cell membrane. Several lines of evidence support the acid growth hypothesis. For example, adding acid to the cell wall to lower the pH stimulates cell expansion even in the absence of auxin. Conversely, when a buffer is used to prevent the wall from becoming more acidic, auxin-induced cell expansion is blocked.

At the molecular level, auxin and gibberellins act similarly

The molecular mechanisms underlying both auxin and gibberellin action have been worked out with the help of genetic screens (see Figure 26.2). Biologists started by identifying mutant plants whose growth and development are insensitive to the hormones; that is, plants that are *not* affected by added hormone. Such mutant plants fall into two general categories:

- *Excessively tall plants*. These plants resemble wild-type plants given an excess of hormone, and they grow no taller when given extra hormone. They grow tall even when treated with inhibitors of hormone synthesis. Their hormone response is always "on," even in the absence of the hormone. It is presumed that the normal allele for the mutated gene codes for an inhibitor of the hormone signal transduction pathway. In wild-type plants, the signal transduction pathway is "off" unless stimulated by the hormone—therefore the plants are sensitive to added hormone. In the mutant plants the pathway is always "on"; the plant grows tall and is insensitive to added hormone.

- *Dwarf plants*. These plants resemble dwarf plants that are deficient in hormone synthesis (see Figure 26.3), but they do not respond to added hormone. In these mutant plants the hormone response is always "off," regardless of the presence of the hormone.
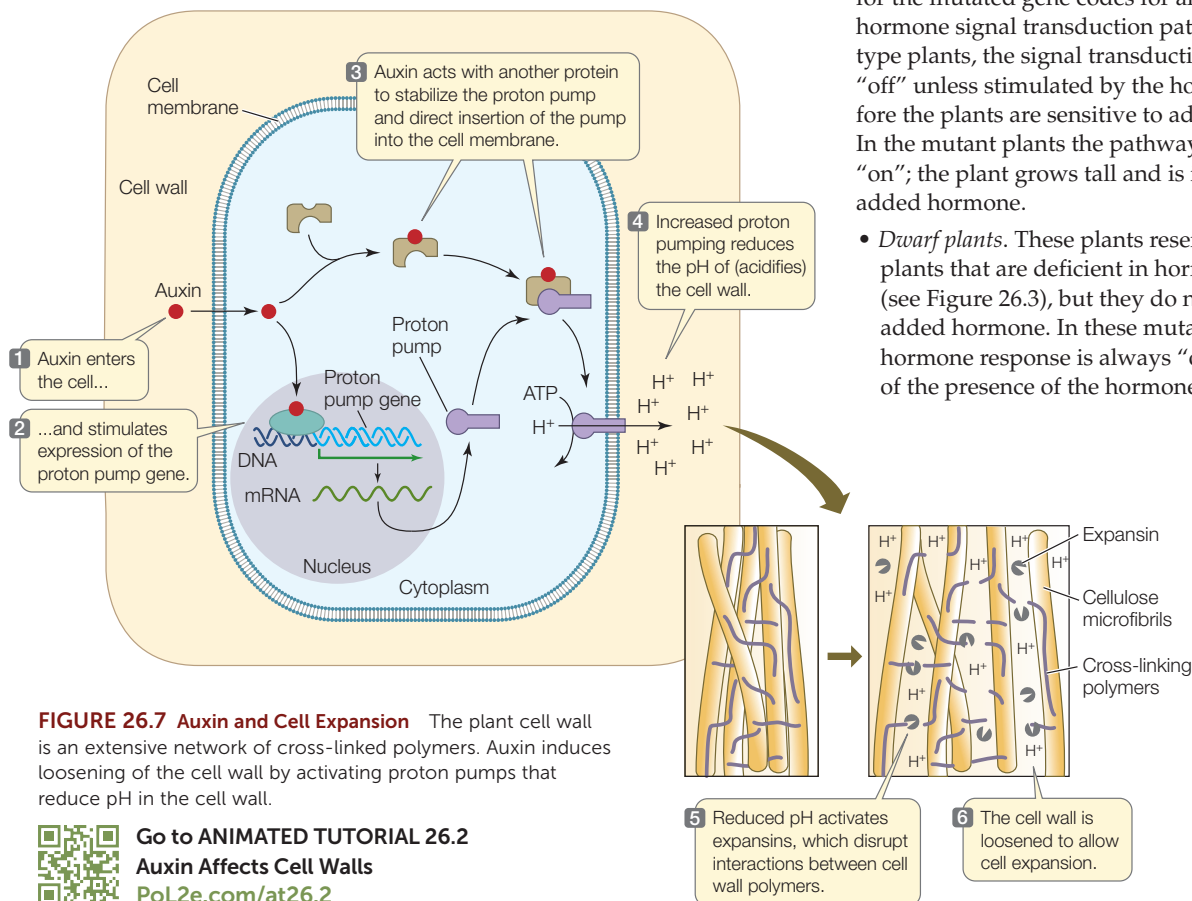
FIGURE 26.7 Auxin and Cell Expansion   The plant cell wall is an extensive network of cross-linked polymers. Auxin induces loosening of the cell wall by activating proton pumps that reduce pH in the cell wall.

1 Auxin enters the cell...

2 ...and stimulates expression of the proton pump gene.

3 Auxin acts with another protein to stabilize the proton pump and direct insertion of the pump into the cell membrane.

4 Increased proton pumping reduces the pH of (acidifies) the cell wall.

5 Reduced pH activates expansins, which disrupt interactions between cell wall polymers.

6 The cell wall is loosened to allow cell expansion.

Go to ANIMATED TUTORIAL 26.2
Auxin Affects Cell Walls
PoL2e.com/at26.2

APPLY THE CONCEPT

Gibberellins and auxin have diverse effects but a similar mechanism of action

The aleurone layer of germinating barley can be isolated and studied for the induction of α-amylase, the enzyme that catalyzes starch hydrolysis. Predict the amount of α-amylase activity in aleurone layers subjected to the following treatments:

1. Incubation with gibberellic acid

2. Incubation with auxin

3. Incubation with gibberellic acid in the presence of an inhibitor of DNA transcription to mRNA

4. Incubation without gibberellic acid

5. Incubation without gibberellic acid in the presence of an inhibitor of transcription

6. Incubation with gibberellic acid in the presence of an inhibitor of the proteasome

7. Incubation without gibberellic acid in the presence of an inhibitor of the proteasome

Nucleus

1 In the absence of hormone, a repressor inhibits transcription of growth-stimulating genes.

Repressor

Transcription factor

DNA

Gibberellin or auxin

Cytoplasm

Receptor

Nuclear envelope

2 Hormone binds to a receptor protein, and the complex enters the nucleus.

Nucleus

3 The hormone–receptor complex binds to the repressor.

Ubiquitin

4 Binding stimulates the addition of ubiquitin to the repressor.

Transcription factor

Repressor

DNA

5 The repressor is broken down in the proteasome. Growth-stimulating genes are now transcribed.

Proteasome

DNA

Transcription

mRNA

Remarkably, some mutations of both types turned out to affect the same gene. How could this be? The mystery was solved once biologists figured out how auxin and gibberellins work in wild-type plants. Of course, the actual proteins involved with the two hormones are different, but the actions of both hormones are similar: they act by removing a repressor from a transcription factor that stimulates the expression of growth-promoting genes (**FIGURE 26.8**). The hormones bind to a receptor protein, which in turn binds to the repressor. Binding of the hormone–receptor complex stimulates polyubiquitination of the repressor, targeting it for breakdown in the proteasome (see Figure 11.19).

LINK

Review the process of transcription initiation in **Concept 11.1**

The features of this pathway explain how different mutations in the same gene can have seemingly opposite phenotypes. The mutations described above turned out to be in the gene that encodes the repressor protein. One region of the repressor protein binds to the transcription factor. This is the mutated region in the excessively tall plants: the growth-promoting genes are always "on" because the repressor does not bind to the transcription factor to inhibit transcription. Another region of the repressor protein causes it to be removed from the transcription factor. This is the mutated region in the dwarf plants: the growth-promoting genes are always "off" because the repressor is always bound to the transcription factor.

The receptors for both auxin and gibberellins contain a region called an **F-box** that facilitates protein–protein interactions necessary for protein breakdown. Whereas animal genomes have few F-box–containing proteins, plant genomes have hundreds, an indication that this type of gene regulation is common in plants.

FIGURE 26.8 Gibberellins and Auxin Have Similar Signal Transduction Pathways Both hormones act to stimulate gene transcription by inactivating a repressor protein.

Go to MEDIA CLIP 26.1
Gibberellin Binding to Its Receptor
PoL2e.com/mc26.1

The same approaches that led to the discovery of auxin and gibberellins have revealed several other classes of plant hormones. These hormones are diverse in their actions and affect many of the same developmental processes as auxin and gibberellins.

CONCEPT 26.3   Other Plant Hormones Have Diverse Effects on Plant Development

The discoveries of gibberellins and auxin have led to the isolation of additional classes of plant hormones (see Table 26.2). These hormones have multiple effects, and they interact with one another in many cases.

Ethylene is a gaseous hormone that promotes senescence

Whereas the cytokinins (see below) delay senescence (aging), another plant hormone promotes it: the gas **ethylene** (see Table 26.2), which is sometimes called the senescence hormone. When streets were lit by gas rather than by electricity, leaves on trees near street lamps dropped earlier in the fall than those on trees farther from the lamps. We now know why: ethylene, a combustion product of the illuminating gas, caused the early abscission. Whereas auxin inhibits leaf abscission, ethylene strongly promotes it; thus the ratio of auxin and ethylene controls abscission.

FRUIT RIPENING   By promoting senescence, ethylene speeds the ripening of fruit. As a fruit ripens, it loses chlorophyll and its cell walls break down, making the fruit softer; ethylene promotes both of these processes. Ethylene also causes an increase in its own production. Thus once ripening begins, more and more ethylene forms, and because it is a gas, it diffuses readily throughout the fruit and even to neighboring fruits on the same or other plants. The old saying that "one rotten apple spoils the barrel" is true. That rotten apple is a rich source of ethylene, which speeds the ripening and subsequent rotting of the other fruit in a barrel or other confined space.

LINK

The action of ethylene in fruit ripening is an example of positive feedback; see **Figure 1.8**

Farmers in ancient times poked holes in developing figs to make them ripen faster. Wounding causes an increase in ethylene production by the fruit, and that increase promotes ripening. Today commercial shippers and storers of fruit hasten ripening by adding ethylene to storage chambers. This use of ethylene is the single most important use of a natural plant hormone in agriculture and commerce. Conversely, ripening can be delayed by the use of "scrubbers" and adsorbents (binding substances) that remove ethylene from the atmosphere in fruit storage chambers.

These stored tomatoes were treated with ethylene to promote ripening.

As flowers senesce, their petals may abscise (fall off). Flower growers and florists often immerse the cut stems of ethylene-sensitive flowers in dilute solutions of silver thiosulfate before selling them. Silver salts inhibit ethylene action by interacting directly with the ethylene receptor—thus they delay senescence, keeping flowers "fresh" for a longer time.

STEM GROWTH   The stems of many eudicot seedlings (which lack protective coleoptiles) form an **apical hook** that protects the delicate shoot apex while the stem grows through the soil.

Apical hook

The apical hook is maintained through an asymmetrical production of ethylene, which inhibits the expansion of cells on the inner surface of the hook. Once the seedling breaks through the soil surface and is exposed to light, ethylene synthesis stops, and the cells of the inner surface are no longer inhibited. Those cells now expand, and the hook unfolds, raising the shoot apex and the expanding leaves into the sun. Ethylene also inhibits stem elongation in general, promotes lateral swelling of stems (as do the cytokinins), and decreases the sensitivity of stems to gravitropic stimulation. The short, thick, and exaggerated

apical hook constitutes the "triple response," a well-characterized stunted growth habit observed when plants are treated with ethylene.

Cytokinins are active from seed to senescence

Like bacteria and yeasts, some plant cells, such as parenchyma cells, can be grown in a liquid or solidified medium containing sugars and salts. For continuous cell division, cultured plant cells also require a type of hormone called a **cytokinin**, first isolated from corn. More than 150 different cytokinins have been isolated, and most are derivatives of adenine.

Cytokinins have a number of different effects (see Table 26.2), in many cases by interacting with auxin:

- Adding an appropriate combination of auxin and cytokinins to a growth medium induces rapid proliferation of cultured plant cells.
- In cell cultures, a high cytokinin-to-auxin ratio (i.e., a medium containing more cytokinin than auxin) promotes the formation of shoots; a low ratio promotes the formation of roots.
- Cytokinins can cause certain light-requiring seeds to germinate even when they are kept in constant darkness.
- Cytokinins usually inhibit the elongation of stems, but they cause lateral swelling of stems and roots (the fleshy roots of radishes are an extreme example).
- Cytokinins stimulate axillary buds to grow into branches. The auxin-to-cytokinin ratio controls the extent of branching (bushiness) of a plant; a high ratio inhibits branching, a low ratio stimulates it.
- Cytokinins delay the senescence of leaves. If leaf blades are detached from a plant and floated on water or a nutrient solution, they gradually turn yellow and show other signs of senescence. If instead they are floated on a solution containing a cytokinin, they remain green and senesce much more slowly. Roots contain abundant cytokinins, and cytokinin transport to the leaves delays senescence:

This leaf was treated with cytokinin, which delays senescence.

This detached leaf was not treated.

Cytokinin appears to act through a pathway that includes proteins similar to those in two-component systems, a type of signal transduction pathway commonly found in bacteria. Indeed, this pathway was one of the first of its kind discovered in eukaryotes. The two components in such a system are:

- a *receptor* that can act as a protein kinase, phosphorylating itself as well as a target protein

- a *target protein*, generally a transcription factor, that regulates the response

Genetic screens in *Arabidopsis* for abnormalities in the response to cytokinin have identified the receptor (AHK; *Arabidopsis histidine kinase*) and the target protein (ARR; *Arabidopsis response regulator*). The target protein acts as a transcription factor when phosphorylated. The cytokinin signal transduction pathway also includes a third protein (AHP; *Arabidopsis histidine phosphotransfer protein*), which transfers phosphates from the receptor to the target protein (**FIGURE 26.9**). The plant genome has more than 20 genes that are expressed in response to this signaling pathway.

Brassinosteroids are plant steroid hormones

In animals, steroid hormones such as cortisol and estrogen, which are formed from cholesterol, have been well studied for decades (see Chapter 35). In the 1970s, biologists isolated a steroid from the pollen of rape (*Brassica napus*; sometimes called canola), a member of the mustard family. When applied to various plant tissues, this hormone stimulated cell expansion, pollen tube elongation, and vascular tissue differentiation, but it inhibited root expansion. Mutant plants with defects in brassinosteroid responses are stunted:

Mutant

A defect in the brassinosteroid signaling pathway results in stunted growth of this mutant *Arabidopsis*.

Wild-type
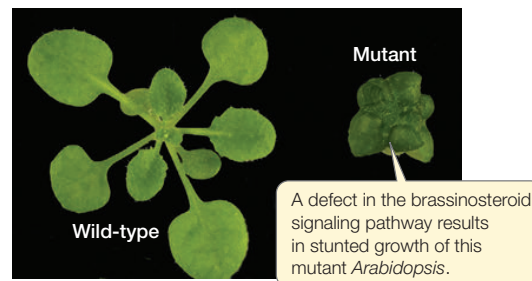
Dozens of chemically related, growth-affecting **brassinosteroids** have been found in plants. Like other plant hormones, brassinosteroids have diverse effects (see Table 26.2):

- They enhance cell expansion and cell division in shoots.
- They promote xylem differentiation.
- They promote growth of pollen tubes during reproduction.
- They promote seed germination.
- They promote apical dominance and leaf senescence.

The signaling pathway for these plant steroids differs sharply from those for steroid hormones in animals. In animals, steroids diffuse through the cell membrane and bind to receptors in the cytoplasm. In contrast, the receptor for brassinosteroids is an integral protein in the cell membrane.

Abscisic acid acts by inhibiting development

The hormone **abscisic acid** is found in most plant tissues. Many of its actions involve inhibition of other hormones' actions in the plant (see Table 26.2):

- *Prevention of seed germination*. Abscisic acid prevents seeds from germinating on the parent plant before the seeds are

Outside of cell

Cytokinin

1 As long as cytokinin is not bound to its receptor (AHK)...

Receptor (AHK)

Cell membrane

Cytoplasm

Nuclear envelope

Nucleus

Genes that respond to cytokinin

DNA

Promoter

2 ...cytokinin response genes are not expressed.

Outside of cell

3 Binding of cytokinin to its receptor causes a change in shape that exposes the active site for the protein kinase domain of the receptor.

Cytokinin

Receptor

P

4 An intermediate protein (AHP) is phosphorylated...

Cytoplasm

AHP

P

Nuclear envelope

Nucleus

P

Transcription factor (ARR)

P

5 ...enters the nucleus, and phosphorylates a transcription factor (ARR).

P

DNA

Promoter

Transcription

mRNA

6 The phosphorylated transcription factor binds to promoters of more than 20 cytokinin response genes, initiating their transcription.

FIGURE 26.9 The Cytokinin Signal Transduction Pathway Plant cells respond to cytokinins through a two-component signal transduction pathway involving a receptor and a target protein.

dry. Premature germination, termed vivipary, is undesirable in cereal crops because the grain is ruined for human consumption if it has started to sprout. Viviparous seedlings are unlikely to survive if they remain attached to the parent plant and are unable to establish themselves in the soil.

- *Promotion of seed dormancy*. Abscisic acid promotes seed dormancy and inhibits the initiation of germination events, such as the hydrolysis of stored macromolecules, by gibberellins.

- *Reaction to stress*. Abscisic acid is a "stress hormone" that mediates a number of plant responses to pathogens and environmental stresses. We will describe some of these effects in Chapter 28. For now, consider that when the air is dry, abscisic acid stimulates the closure of stomata to prevent water loss by transpiration (see Concept 25.3).

Abscisic acid provides examples of the complex interactions between plant hormones. Whereas abscisic acid promotes seed dormancy, gibberellic acid inhibits it; whereas abscisic acid inhibits seed germination, both gibberellic acid and ethylene promote it. How the signaling pathways used by these hormones interact is under intense study by plant molecular biologists.

> **CHECKpoint**   **CONCEPT 26.3**
>
> ✓ Which plant hormones affect cell expansion, and what is the effect in each case?
>
> ✓ At the grocery store, you can buy plastic bags that keep fruit fresh for a much longer period than other containers. How do you think they work?
>
> ✓ A mutant strain of corn shows vivipary. Why is this a disadvantage for the plant and the crop, and what gene might be involved?

As we have seen, plant development is strongly influenced by the environment. For example, in Concept 26.1 we alluded to the role of photoreceptors whose responses to light guide the early growth of seedlings. We will now turn to the molecular nature of these and other plant photoreceptors.

CONCEPT 26.4 Photoreceptors Initiate Developmental Responses to Light

Plants are completely dependent on sunlight for energy, so it is not surprising that they have multiple ways to sense light and respond appropriately. A number of physiological and developmental events in plants are controlled by light, a process called **photomorphogenesis**. Plants respond to two aspects of light: its *quality*—that is, the wavelengths of light to which the

plant is exposed; and its *quantity*—that is, the intensity and duration of light exposure.

Chapter 6 described how chlorophyll and other photosynthetic pigments absorb light of certain wavelengths (see Figure 6.17) and how plants use light energy to synthesize carbohydrates. Here we consider how light affects plant development. Light influences seed germination, phototropism, shoot elongation, initiation of flowering, and many other important aspects of plant development. Several photoreceptors take part in these processes.

Phototropin, cryptochromes, and zeaxanthin are blue-light receptors

An action spectrum for the phototropic response of a coleoptile (**FIGURE 26.10**) shows that blue light at a wavelength of 436 nm is the most effective in stimulating that response. To identify the blue-light-absorbing molecule involved, biologists have taken a genetic approach using the model plant *Arabidopsis*.

> **LINK**
>
> Action spectra are discussed in **Concept 6.5**

By obtaining blue-light-insensitive *Arabidopsis* mutant plants from a genetic screen, researchers were able to identify the gene for a blue-light receptor protein located in the cell membrane, called **phototropin**. This protein has a flavin mononucleotide associated with it that absorbs blue light at 436 nm. Light absorption leads to a change in the shape of the protein that exposes an active site for a protein kinase, which
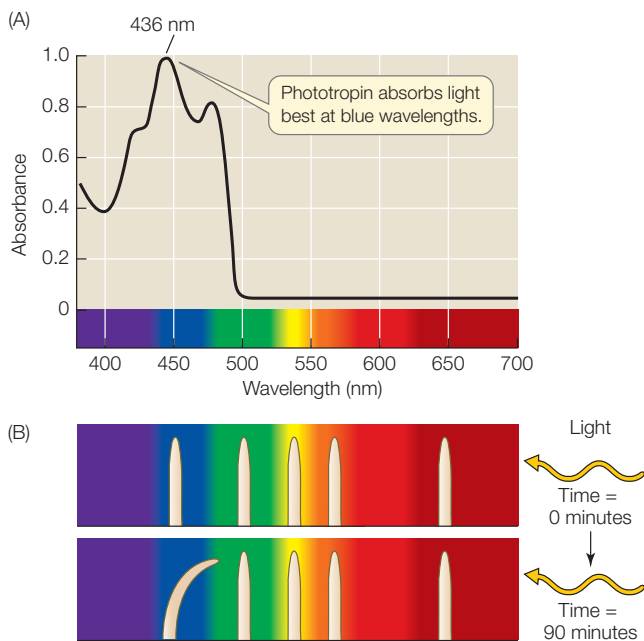
in turn initiates a signal transduction cascade that ultimately results in stimulation of cell expansion by auxin. Phototropin also participates with another type of blue-light receptor, the plastid pigment **zeaxanthin**, in the light-induced opening of stomata (see Figure 25.13).

A third class of blue-light receptors is the **cryptochromes**, proteins with yellow pigments that absorb blue and ultraviolet light. These pigments are located primarily in the plant cell nucleus and affect seedling development and flowering. The exact mechanism of cryptochrome action is not yet known. Strong blue light inhibits cell expansion through the action of cryptochromes, although the most rapid responses are mediated by phototropin.

Phytochrome senses red and far-red light

Plants also have responses that are specific to light in the red region of the spectrum. Here are two examples:

- Lettuce seeds spread on soil will germinate only in response to light. Even a brief flash of dim light will suffice. This response prevents the seeds from germinating when they are so deep in the soil that the seedlings would not be able to reach the light before their seed reserves ran out.

- Adult cocklebur plants flower when they are exposed to long nights. If there is even a brief flash of light in the middle of the night, they do not flower. This response enables plants to flower in the appropriate season.

The action spectra of these processes show that they are induced by red light (650–680 nm). This indicates that plants must have a photoreceptor that absorbs red light.

What is especially remarkable about these red light responses is that *they are reversible by far-red light* (710–740 nm). For example, if lettuce seeds are exposed to brief, alternating periods of red and far-red light in close succession, they respond only to the final exposure. If it is red, they germinate; if it is far-red, they remain dormant (**FIGURE 26.11**). This reversibility of the effects of red and far-red light regulates many other aspects of plant development, including flowering and shoot development.

The basis for the effects of red and far-red light is a bluish photoreceptor in the cytosol of plants called **phytochrome**. Phytochrome exists in two interconvertible isoforms, or states. The molecule undergoes a change in shape when it absorbs light at particular wavelengths. The default or "ground" state, which absorbs principally red light, is called P_r. When P_r absorbs a photon of red light, it is converted into the other isoform, P_{fr}. The P_{fr} isoform preferentially absorbs far-red light; when it does so, it is converted back into P_r:

FIGURE 26.10 Action Spectrum for Phototropism The absorption spectrum for phototropin (A) is similar to the action spectrum for the bending of a coleoptile toward light (B). After 90 minutes, only the coleoptiles exposed to blue light bend.
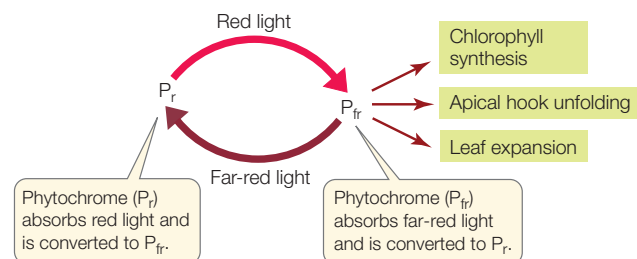
INVESTIGATION

FIGURE 26.11 Photomorphogenesis and Red Light   Lettuce seeds will germinate if exposed to a brief period of light. The action spectrum for germination indicated that red light was most effective in promoting it, but far-red light would reverse the effect if presented right after the red light. Harry Borthwick and his colleagues asked what the effect of repeated alternating flashes of red and far-red light would be. In each case, the final exposure determined the germination response. This observation led to the conclusion that a single, photo-reversible molecule was involved. That molecule turned out to be phytochrome.[a]

HYPOTHESIS

The effects of red and far-red light on lettuce seed germination are mutually reversible.

METHOD

Expose lettuce seeds to alternating periods of red light R for 1 minute and far-red light FR for 4 minutes.

R   R FR …   R FR R FR R FR R   R FR R FR R FR R FR

Seeds germinate if the final exposure is to red R …

…and remain dormant if the final exposure is to far-red FR .

RESULTS

Germinated seed   Ungerminated seed

Most germinate   Few germinate … Most germinate   Few germinate
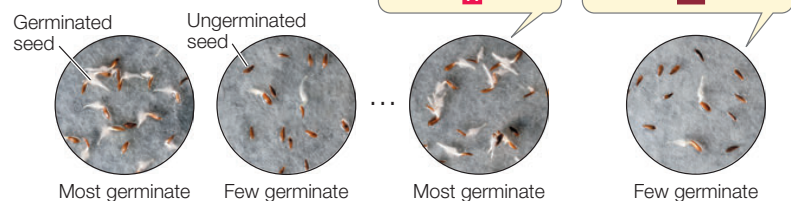
CONCLUSION

Red light and far-red light reverse each other's effects.

ANALYZE THE DATA

Seven groups of 200 lettuce seeds each were incubated in water for 16 hours in the dark. One group was then exposed to white light for 1 minute. A second group (controls) remained in the dark. Five other groups were exposed to red (R) and/or far-red (FR) light. All the seeds were then returned to darkness for 2 more days. The table shows the number of seeds that germinated in each group.

Condition	Seeds germinated
1. White light	199
2. Dark	17
3. R	196
4. R then FR	108
5. R then FR then R	200
6. R then FR then R then FR	86
7. R then FR then R then FR then R	198

A. Calculate the percentage of seeds that germinated in each case.
B. What can you conclude about the photoreceptors involved?

Go to **LaunchPad** for discussion and relevant links
for all **INVESTIGATION** figures.

[a]H. Borthwick et al. 1952. *Proceedings of the National Academy of Sciences USA* 38: 662–666.

P_{fr}, not P_r, is the active isoform of phytochrome—the form that triggers important biological processes in various plants. These processes include chlorophyll synthesis, apical hook unfolding, and leaf expansion.

The ratio of red to far-red light determines whether a phytochrome-mediated response will occur. For example, in full daylight the ratio is about 1.2:1; because there is more red than far-red light, the P_{fr} isoform predominates. But for a plant growing in the shade of other plants, the ratio may be as low as 0.13:1, and most phytochrome is in the P_r isoform. The low ratio of red to far-red light in the shade results from absorption of red light by chlorophyll in the leaves overhead, so less of the red light gets through to the plants below. Shade-intolerant species respond by stimulating cell expansion in the stem and thus growing taller to escape the shade (similar to the behavior of etiolated seedlings grown in the dark). Similarly, shade cast by other plants prevents germination of seeds that require red light to germinate (see Figure 26.11).

Phytochrome stimulates gene transcription

How does phytochrome—or more specifically, P_{fr}—work? Phytochrome is a cytoplasmic protein composed of two subunits (**FIGURE 26.12**). Each subunit contains a protein chain and a nonprotein pigment called a chromophore. In *Arabidopsis*, there is a gene family that encodes five slightly different phytochromes, each functioning in different photomorphogenic responses.

The transcription of genes involved in phytochrome responses is changed when P_r is converted into the P_{fr} isoform. When P_r absorbs red light, the chromophore changes shape, which leads to a change in the conformation of the phytochrome protein from the P_r isoform to the P_{fr} isoform. Conversion to the P_{fr} isoform exposes two important regions of the protein (see Figure 26.12), both of which affect transcriptional activity:

- Exposure of a *nuclear localization signal sequence* (see Figure 10.20) results in movement of P_{fr} from the cytosol to the nucleus. Once in the nucleus, P_{fr} binds to transcription factors and thereby stimulates expression of genes involved in photomorphogenesis.

- Exposure of a *protein kinase* domain causes the P_{fr} protein to phosphorylate itself and other proteins involved in red-light signal transduction. Those proteins change the activity of other transcription factors.

The effect of this activation of transcription factors is quite large: in *Arabidopsis*, phytochrome affects an amazing 2,500 genes (10 percent of the entire genome) by either increasing or

1 The phytochrome chromophore absorbs red light.

2 Changes in the conformation of the chromophore induce changes in the shape of the phytochrome protein, exposing a nuclear localization signal sequence and a protein kinase domain.

Chromophore

Red light

Far-red light

Two subunits of phytochrome

P_r

Nuclear localization signal sequence (NLS)

Protein kinase domain

P_{fr}

3 P_{fr} moves to the nucleus.

Cytoplasm

Nucleus

Other proteins

P

Transcription factor

4 Some P_{fr} interacts directly with transcription factors to change transcription.

Changes in transcription

5 Some P_{fr} acts as a protein kinase, phosphorylating other proteins that in turn affect transcription.

DNA

Changes in transcription

FIGURE 26.12 Phytochrome Stimulates Gene Transcription Phytochrome is composed of two subunits, each containing a protein chain and a chromophore. When the chromophore absorbs red light, phytochrome is converted into the P_{fr} isoform, which activates transcription of phytochrome-responsive genes.

decreasing their expression. Some of these genes are related to other hormones. For example, when P_{fr} is formed at the time of seed germination, genes for gibberellin synthesis are activated and genes for gibberellin breakdown are repressed. As a result, gibberellins accumulate and seed reserves are mobilized (see Figure 26.4).

Circadian rhythms are entrained by photoreceptors

The timing and duration of biological activities in living organisms are governed in all eukaryotes and some prokaryotes by what is commonly called a biological clock: an oscillator within cells that alternates back and forth between two states at roughly 12-hour intervals. The major outward manifestations of this clock are known as **circadian rhythms** (Latin *circa*, "about"; *dies*, "day"). In plants, circadian rhythms influence, for example, the opening (during the day) and closing (at night) of stomata in *Arabidopsis* and the elevation toward the sun (during the day) and lowering (at night) of leaves in bean plants.

LINK

For a description of the role of circadian rhythms in animal behavior, see **Concept 40.4**

The circadian rhythms of plants can be reset, or entrained, within limits, by light–dark cycles that change. Consider what happens when plants adapt to day length as the seasons change during the year. The action spectrum for plant entrainment indicates that phytochrome (and to a lesser extent,

blue-light receptors) is very likely involved. At sundown, phytochrome is mostly in the active P_{fr} isoform. But as the night progresses, P_{fr} is gradually converted back into the inactive P_r isoform. By dawn, most phytochrome is in the P_r state, but as daylight begins, it is rapidly converted into P_{fr}. The switch to the P_{fr} isoform resets the plant's biological clock. However long the night, the clock is still reset at dawn every day. Thus while the total period measured by the clock does not change, the clock adjusts to changes in day length over the course of the year.

CHECKpoint   CONCEPT 26.4

✓ Trace the events that occur in the phytochrome-mediated germination response of lettuce seeds, from the reception of light to alteration in gene expression.

✓ Compare the wavelengths of light absorbed by chlorophyll (see Figure 6.17) and by phototropin (see Figure 26.10). How does the difference influence a plant's responses to light when a plant grows beneath a forest canopy?

✓ How would you show that a physiological process in a plant is brought about by phytochrome?

Q What changes in their growth patterns made the new strains of cereal crops produced by the Green Revolution so successful?

ANSWER It is only recently that plant biologists have discovered why semi-dwarf wheat and rice have short stems (**FIGURE 26.13**). This knowledge has come from an understanding of the effects of various hormones on plant growth and development (Concept 26.1), the signal transduction pathways for response to these hormones (Concepts 26.2 and 26.3), and the biochemical pathways for the synthesis of these hormones. It turns out that the genes involved in wheat and in rice are different.

In semi-dwarf wheat, the mutant allele that produces short plants is involved in signal transduction in response to gibberellin. The gene involved is called *Rht* ("reduced height"). The mutant allele was first seen in Japanese semi-dwarf varieties. It is dominant, so its phenotypes are readily seen. Norman Borlaug used conventional plant breeding to transfer the *Rht* mutant allele into wheat strains in Mexico. In addition to having short stature and not falling over when bearing a high grain yield, *Rht* mutant plants put a greater proportion of their photosynthate into making seeds than wild-type plants do. This higher "harvest index" is also a major reason why most wheat varieties today carry an *Rht* mutation.

A hint that *Rht* might be involved in hormone regulation came when semi-dwarf plants harboring *Rht* mutations were found to be insensitive to added gibberellin and did not grow to normal height when the hormone was applied. *Rht* encodes the transcriptional repressor in the gibberellin signal transduction pathway (see Figure 26.8). Mutations in semi-dwarf plants are in the region that binds the gibberellin receptor and that signals polyubiquitination and degradation in the proteasome. Thus in the mutant plants, the repressor is always bound to the transcription factor, inhibiting its activity and keeping the gibberellin response "off." This mutation therefore results in shorter stature.

In semi-dwarf rice, the mutant allele that produces short plants is involved with gibberellin *synthesis*. The gene involved is called *sd-1* ("semi-dwarf"). In contrast to semi-dwarf wheat, rice plants with mutations in *sd-1* are sensitive to gibberellin—that is, the semi-dwarf phenotype can be corrected by supplying gibberellin. This observation indicates that the signal transduction machinery is intact in the mutant

FIGURE 26.13 Semi-Dwarf Rice   A short variety of rice (left) produces higher yields of grain than its taller counterpart (right). The semi-dwarf rice produces less than normal amounts of gibberellins.

plants but that they lack the hormone. Indeed, *sd-1* encodes an enzyme that catalyzes one of the last steps in gibberellin synthesis.

SUMMARY

CONCEPT 26.1 Plants Develop in Response to the Environment

- Plant development is regulated by environmental cues, receptors, hormones, and the plant's genome.

- Seed **dormancy**, which has adaptive advantages, is maintained by a variety of mechanisms. When dormancy ends, the seed **germinates** and develops into a **seedling**. Review Figure 26.1 and ACTIVITIES 26.1 and 26.2

- **Hormones** and **photoreceptors** act through signal transduction pathways to regulate plant growth and development.

- **Genetic screens** using the model organism *Arabidopsis thaliana* have contributed greatly to our understanding of signal transduction pathways in plants. Review Figure 26.2

CONCEPT 26.2 Gibberellins and Auxin Have Diverse Effects but a Similar Mechanism of Action

- **Gibberellins** stimulate growth of stems and fruits as well as mobilization of seed reserves in cereal crops. Review Figure 26.4 and ACTIVITY 26.3

- **Auxin** is made in cells at the shoot apex and moves down to the growing region in a polar manner. Review Figure 26.5

- Lateral movement of auxin, mediated by auxin efflux carriers, is responsible for **phototropism** and **gravitropism**. Review Figure 26.6 and ANIMATED TUTORIAL 26.1

- Auxin plays roles in lateral root formation, leaf **abscission**, and **apical dominance**.

- The **acid growth hypothesis** explains how auxin promotes cell expansion by increasing proton pumps in the cell membrane, which loosens the cell wall. Review Figure 26.7 and ANIMATED TUTORIAL 26.2

- Both auxin and gibberellins act by binding to their respective receptors, which then bind to a transcriptional repressor, leading to the repressor's breakdown in the proteasome. Review Figure 26.8

CONCEPT 26.3 Other Plant Hormones Have Diverse Effects on Plant Development

- **Cytokinins**, most of which are adenine derivatives, often interact with auxin. They promote plant cell division, promote seed germination in some species, and inhibit stem elongation, among other activities.

- Cytokinins act on plant cells through a two-component signal transduction pathway. Review Figure 26.9

SUMMARY *(continued)*

■ The ratio of auxin to **ethylene** controls leaf abscission. Ethylene promotes senescence and fruit ripening. It causes the stems of eudicot seedlings to form a protective **apical hook**. In stems, it inhibits elongation, promotes lateral swelling, and decreases sensitivity to gravitropic stimulation.

■ **Brassinosteroids** promote cell expansion, pollen tube elongation, and vascular tissue differentiation but inhibit root elongation. Unlike animal steroids, these hormones act at a cell membrane receptor.

■ **Abscisic acid** inhibits seed germination, promotes dormancy, and stimulates stomatal closing in response to dry conditions in the environment.

CONCEPT **Photoreceptors Initiate Developmental**
26.4 **Responses to Light**

■ **Phototropin** is a blue-light receptor protein involved in phototropism. **Zeaxanthin** acts in conjunction with phototropin to mediate the light-induced opening of stomata. **Cryptochromes** are blue-light receptors that affect seedling development and flowering and inhibit cell expansion. **Review Figure 26.10**

■ **Phytochrome** is a photoreceptor that exists in the cytosol in two interconvertible isoforms, P_r and P_{fr}. The relative amounts of these two isoforms are a function of the ratio of red to far-red light. Phytochrome plays a number of roles in **photomorphogenesis**. **Review Figure 26.11**

■ The phytochrome signal transduction pathway affects transcription in two ways: the P_{fr} isoform interacts directly with some transcription factors and influences transcription indirectly by phosphorylating other proteins. **Review Figure 26.12**

■ **Circadian rhythms** are changes that occur on a daily cycle. Light can entrain circadian rhythms through photoreceptors such as phytochrome.

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is26

Go to LaunchPad at **macmillanhighered.com/launchpad** for additional resources, including LearningCurve Quizzes, Flashcards, and many other study and review resources.

27

Reproduction of Flowering Plants

The poinsettia is a popular Christmas flower. But the red "flowers" are not flowers at all; instead, they are leaves (bracts). The flowers are yellow structures in the center of a group of red leaves and are not visible in this photograph.

Dairy farmer Albert Ecke was fascinated by the red and green shrubs that grew all over southern California and were used by Mexican-Americans for red dye. The shrub, *Euphorbia pulcherrima*, got the name "poinsettia" from the man who first brought it to the United States: the first U.S. ambassador to Mexico, Joel Roberts Poinsett. In the early 1900s, Ecke started selling the plants at his farm in Hollywood. But two challenges stood in the way of his making this plant a commercial success.

First, although poinsettias generally bloomed in the fall and early winter in the mild climate of southern California, when Ecke grew them in fields in Hollywood, the formation of flowers was unreliable. Biologists later found that the flowering of poinsettias required at least a 14-hour night for several weeks. Any interruption in the long night—by passing cars or street lamps, for example—inhibited flowering. So Ecke's son Paul moved the growing operation south, to isolated fields far from Los Angeles. A second challenge was that the plants were tall and gangly. Although pretty, they were hard to transport and not attractive indoors. Paul Ecke found a variety of poinsettia that was much more compact. He propagated this variety and eventually developed it into the short potted plant that is so popular today. The Eckes decided that the time of flowering was just right for making the poinsettia a "Christmas flower," so they promoted this now portable plant as a holiday decoration, blanketing live television shows with free plants between Thanksgiving and Christmas. The campaign was successful: more than 100 million poinsettias are now sold in the United States during the winter holidays every year, making it the nation's best-selling potted plant.

Breeding more attractive flowering plants that are easier to grow is an ongoing part of floriculture, the industry involved with the production of floral crops. You may be surprised to learn that the brightly colored "flowers" of poinsettias are not flowers at all. The red parts of the plant that we most notice and appreciate are actually specialized leaves called bracts. The poinsettia has a single tiny yellow female flower, without petals, surrounded by male flowers.

Q How did an understanding of angiosperm reproduction allow floriculturists to develop a commercially successful poinsettia?

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CONCEPT **Most Angiosperms Reproduce**
27.1 **Sexually**

</div>

Most angiosperms (flowering plants) have evolved to reproduce sexually because this strategy results in the genetic diversity that is the raw material for evolution. Sexual reproduction in angiosperms involves mitosis, meiosis, and the alternation of haploid and diploid generations (see Figure 7.3). There are several important differences between sexual reproduction in angiosperms and in vertebrate animals (see Chapter 37):

• Meiosis in plants produces spores, which undergo mitosis to produce gametes; in animals, meiosis usually produces gametes directly.

• In most plants, there are multicellular diploid (sporophyte) and haploid (gametophyte) life stages (alternation of generations); in animals, there is no multicellular haploid stage.

• In plants, the cells that will form gametes (germline cells) develop in the adult organism, usually in response to environmental conditions; in animals, the germline cells are set aside before birth.

LINK

The life cycles of plants have many unique characteristics, which are detailed in **Chapter 21**

The flower is the reproductive organ of angiosperms

In angiosperms, flowers contain male or female gametophytes or often both. As we saw in Concept 21.5, a generalized flower consists of four concentric groups (whorls) of organs arising from modified leaves: the carpels, stamens, petals, and sepals.
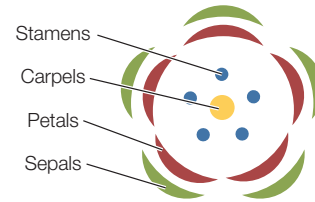
The parts of the flower are all derived from a modified shoot apical meristem.

• Carpels are the female sex organs that contain the developing female gametophytes (inside ovules).

• Stamens are the male sex organs that produce microspores, the first cells of the developing male gametophytes.

The differentiation of these organs is controlled by specific transcription factors (see Figure 14.12).

As you know, flowers come in many shapes, sizes, and forms. Some have both stamens (male sex organs) and carpels (female sex organs); such flowers are termed perfect (**FIGURE 27.1A**). Imperfect flowers, by contrast, are those with only male or only female sex organs. Male flowers have stamens but not

(A) Perfect: lily (*Lilium* sp.)
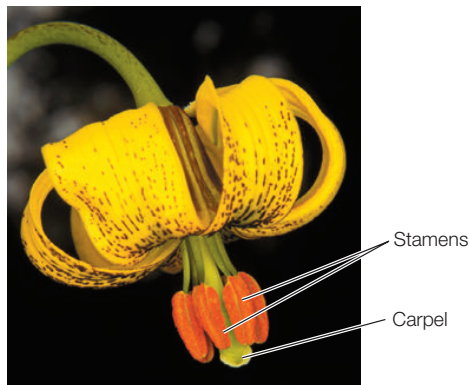
Stamens
Carpel

(B) Imperfect monoecious: corn (*Zea mays*)

Male flower with stamens

Female flowers with carpels

(C) Imperfect dioecious: Red campion (*Silene dioica*)

Female flowers with carpels

Male flower with stamens

FIGURE 27.1 Perfect and Imperfect Flowers (A) A lily is an example of a perfect flower, meaning one that has both male and female sex organs. (B) Imperfect flowers are either male or female. Corn is a monoecious species: both types of imperfect flowers are borne on the same plant. (C) Red campion is a dioecious species; some red campion plants bear male imperfect flowers, and others bear female imperfect flowers.

carpels, and female flowers have carpels but not functioning stamens. Some plants, such as corn, bear both male and female flowers on the same individual plant; such species are called **monoecious** ("one housed"; **FIGURE 27.1B**). In **dioecious** ("two-housed") species, individual plants bear either male-only or female-only flowers; an example is red campion (**FIGURE 27.1C**).

Angiosperms have microscopic gametophytes

FIGURE 27.2 shows the development of angiosperm gametophytes. These haploid, microscopic gamete-producing structures develop from haploid spores in the flower:

- Each female gametophyte (megagametophyte) is called an **embryo sac**, and it develops inside an ovule. One or more ovules are contained inside an ovary, which is the lower part of a carpel.
- Male gametophytes (microgametophytes), which are also called **pollen grains**, develop in the anther, which is part of the stamen.

FEMALE GAMETOPHYTE   Of the four haploid megaspores resulting from meiosis, three undergo apoptosis (programmed cell death). Typically, the remaining megaspore undergoes

three mitotic divisions without cytokinesis, producing eight haploid nuclei, all initially contained within a single cell—three nuclei at one end, three at the other end, and two in the middle. Subsequent cell wall formation leads to an elliptical, seven-celled megagametophyte with a total of eight nuclei:

- At one end of the megagametophyte are three small cells: the egg cell and two cells called synergids. The egg cell is the female gamete, and the synergids participate in fertilization by attracting the pollen tube. The tube enters one of the synergids before the sperm cells are released for fertilization.
- At the opposite end of the megagametophyte are three antipodal cells, which eventually degenerate by apoptosis.
- In the large central cell are two **polar nuclei**.

The megagametophyte, or embryo sac, is the entire seven-cell, eight-nucleus structure.

MALE GAMETOPHYTE   The four haploid products of meiosis in the stamen each develop a cell wall and undergo a single mitotic division, producing four two-celled pollen grains (male gametophytes) that are released into the environment. The two cells in a pollen grain have different roles:

- The generative cell divides by mitosis to form two sperm cells that participate in double fertilization. (In some plants

FIGURE 27.2 Sexual Reproduction in Angiosperms   The embryo sac is the female gametophyte; the pollen grain is the male gametophyte. The male and female cells meet and fuse in the embryo sac. Angiosperms have double fertilization, in which a zygote and an endosperm nucleus form from separate fusion events—the zygote from one sperm and the egg, and the endosperm from the other sperm and the two polar nuclei.
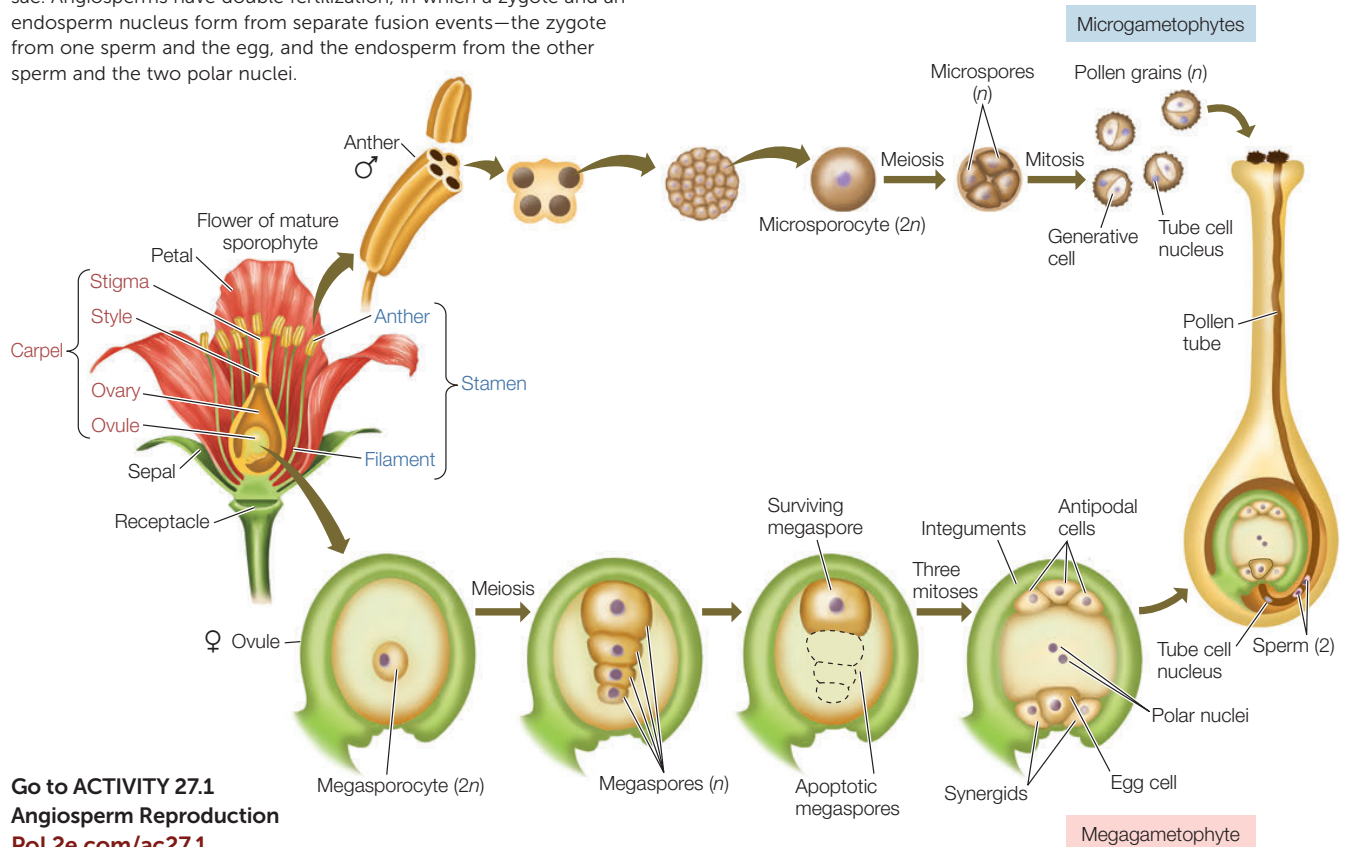
**Go to ACTIVITY 27.1
Angiosperm Reproduction
PoL2e.com/ac27.1**

this division takes place before pollen is released from the anther, resulting in three-celled pollen grains.)

- The tube cell forms the elongating pollen tube that delivers the sperm to the embryo sac after the pollen grain is transferred to a stigma (part of the female reproductive organ)—a process called **pollination**.

Go to MEDIA CLIP 27.1
Pollen Germination in Real Time
PoL2e.com/mc27.1

Angiosperms have mechanisms to prevent inbreeding

As we discussed in Concept 21.4, the evolution of pollen in the seed plants made it possible for male gametes to reach the female gametophyte in the absence of liquid water. The transfer of pollen from plant to plant presents its own challenges, however. In the first seed plants to evolve, tiny pollen grains were carried to stigmas by wind. Wind-pollinated flowers have sticky or featherlike stigmas, and they produce a great number of pollen grains because of the low probability of an individual grain encountering a suitable stigma. More recently in evolutionary time, most angiosperms have come to rely on animals such as insects and birds for pollination. Pollen transport by animals greatly increases the probability that pollen will get to a female gametophyte of the same species.

> **LINK**
>
> The evolution of plant–pollinator interactions and their effects on plant speciation are described in **Concepts 17.4 and 21.5**

Some plants self-pollinate: that is, they are fertilized by pollen that lands on the stigma of a flower on the same plant, or even the same flower. Mendel's garden peas, for example, reproduce in this way, so he had to remove stamens to control the parentage of his genetic crosses (see Figure 8.1). Self-pollination mitigates the difficulties of wind or animal pollination of a distant flower. However, "selfing" leads to homozygosity, which can reduce the reproductive fitness of offspring (known as inbreeding depression). Most plants have evolved mechanisms that prevent self-pollination and thus self-fertilization.

SEPARATION OF MALE AND FEMALE GAMETOPHYTES Self-fertilization is not possible in dioecious species, which bear only male or female flowers on an individual plant. Pollination in dioecious species is accomplished only when one plant pollinates another. In monoecious plants, which bear both male and female flowers on the same plant, the physical separation of male and female flowers is often sufficient to prevent self-fertilization. Some monoecious species prevent self-fertilization by staggering the development of male and female flowers so they do not bloom at the same time, making these species functionally dioecious.
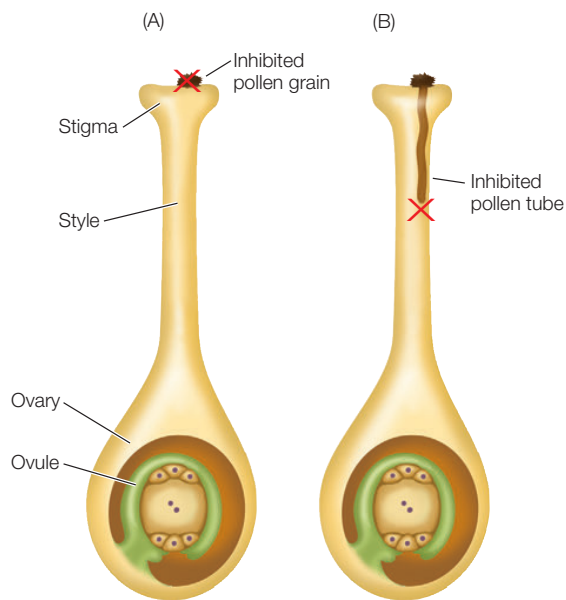
FIGURE 27.3 Self-incompatibility In a self-incompatible plant, pollen is rejected if it expresses an *S* allele that matches one of the *S* alleles of the recipient carpel. There are two mechanisms of rejection: (A) the pollen may fail to germinate, or (B) the pollen tube may die before reaching an ovule. Both mechanisms prevent the egg from being fertilized by a sperm from the same plant.

GENETIC SELF-INCOMPATIBILITY A pollen grain that lands on a stigma of the same plant will germinate and fertilize the female gamete only if the plant is self-compatible (capable of self-pollination). To prevent self-fertilization, many plants are genetically **self-incompatible**. This mechanism depends on the ability of a plant to determine whether pollen is genetically similar or genetically different from "self." Rejection of "same-as-self" pollen prevents self-fertilization.

Self-incompatibility in plants is controlled by a cluster of tightly linked genes called the *S* locus (for self-incompatibility). The *S* locus encodes proteins in the pollen and style that interact during the recognition process. A self-incompatible species typically has many alleles of the *S* locus. The pollen phenotype may be determined by its own haploid genotype or by the diploid genotype of its parent plant. In either case, if the pollen expresses an allele that matches one of the alleles of the recipient carpel, the pollen is rejected. Depending on the type of self-incompatibility, the rejected pollen either fails to germinate or the pollen tube is prevented from growing through the style (**FIGURE 27.3**); either way, self-fertilization is prevented.

A pollen tube delivers sperm cells to the embryo sac

When a genetically appropriate pollen grain lands on the stigma of a compatible carpel, it germinates. As with seed germination, a key event is water uptake by pollen, in this case from the stigma. Germination involves the development of a pollen tube. The pollen tube either traverses the spongy tissue of the style or, if the style is hollow, grows on the inner surface of the style until it reaches an ovule. The pollen tube typically

grows at the rate of 1.5–3 millimeters per hour, taking just 1–2 hours to reach its destination, the female gametophyte.

The growth of the pollen tube may be guided in part by a chemical signal produced by the synergids in the female gametophyte. If one synergid is destroyed, the ovule still attracts pollen tubes, but destruction of both synergids renders the ovule unable to attract pollen tubes, and fertilization does not occur. The attractant appears to be species-specific: in some cases, isolated female gametophytes attract only pollen tubes of the same species.

Angiosperms perform double fertilization

The pollen tube grows down the style, under the direction of the haploid tube cell. Meanwhile the generative cell divides once (if it hasn't already done so) to form two haploid sperm cells. Once the pollen tube reaches the embryo sac, one of the two synergids degenerates, and the two sperm cells are released into its remains. *Two fertilization events occur* (**FIGURE 27.4**):

- One sperm cell fertilizes the egg cell, producing the diploid zygote, which forms the new sporophyte embryo.

- The other sperm cell fertilizes the central cell of the embryo sac, when the sperm fuses with the two polar nuclei. This fusion forms a triploid nucleus that undergoes rapid mitosis to form a specialized nutritive tissue, the **endosperm**. The endosperm's primary function is nourishment of the developing embryo. In some plants, notably cereals, the endosperm persists in the mature seed and contains reserves that provide chemical building blocks for the germinating seedling while it is underground and cannot perform photosynthesis.

This process of double fertilization is a characteristic feature of angiosperm reproduction. The remaining cells of the female gametophyte—the antipodal cells and the remaining synergid—eventually degenerate, as does the pollen tube nucleus.

Embryos develop within seeds contained in fruits

Fertilization initiates the highly coordinated growth and development of the embryo, endosperm, integuments, and carpel. The integuments—tissue layers immediately surrounding the ovule—develop into the seed coat, and the ovary becomes the fruit that encloses the seed (see Figure 27.2).

In Chapter 26 we described the events in plant embryonic development and its hormonal control. As seeds develop, they prepare for dispersal and dormancy by losing up to 95 percent of their water content. You can see this desiccation by comparing corn grains (e.g., popcorn) with ripe corn from the cob or a can. The embryo inside a dry seed contains very little water but is still alive; it has protective proteins that keep its cells in a viscous state.

In angiosperms, the ovary—together with the seeds it contains—develops into a fruit after fertilization has occurred. Fruits have two main functions:

- They protect the seed(s) from damage by animals and infection by microbial pathogens.

- They aid in seed dispersal.

A **fruit** may consist of only the mature ovary and seeds, or it may include other parts of the flower. Some species produce fleshy, edible fruits, such as peaches and tomatoes, whereas the fruits of other species are dry or inedible (**FIGURE 27.5**; see also Figure 21.26).

The diverse forms of fruits reflect the varied strategies plants use to disperse their progeny. Because plants cannot move, their progeny need some mechanism for separating

FIGURE 27.4 Double Fertilization Two sperm are involved in two nuclear fusion events, hence the term "double fertilization." One sperm is involved in the formation of the diploid zygote and the other in the formation of the triploid endosperm. The events shown here are for two-celled pollen grains; for three-celled pollen grains, the generative cell divides before the pollen is released from the anther.

Go to ANIMATED TUTORIAL 27.1
Double Fertilization
PoL2e.com/at27.1

Three antipodal cells

Tube cell

Polar nuclei

Generative cell

Tube cell nucleus

Egg

Synergids

1 Initially the pollen tube consists of two haploid cells: the generative cell and the tube cell.

2 The generative cell divides mitotically, producing two haploid sperm cells. One synergid degenerates when the pollen tube arrives.

3 The sperm cells are released from the pollen tube.

4 One sperm cell fertilizes the egg cell forming the zygote, the first cell of the 2n sporophyte generation.

5 The other sperm cell fertilizes the central cell of the embryo sac when the sperm nucleus fuses with the two polar nuclei.

(A)

The fruit is derived from the ovary wall and aids in seed dispersal.

Seed

Fruit

Endosperm nucleus (3n)

Endosperm

Zygote (2n)

Embryo

FIGURE 27.5 Angiosperm Fruits (A) There are a variety of fruits, but most have seed containing the embryo, surrounded by a fruit that derives from the wall of the ovary. Some examples include (B) garden pea, (C) tomato, and (D) corn.

(B) Seed with embryo Fruit (ovary wall)

(D)

Endosperm

(C)

Embryo

Seed with embryo   Fruit (ovary wall)   Fruit (ovary wall)

germination and growth to sexual maturity. Some, like those of the thistle, are carried to new locations by wind:

Others attach themselves to animals (or to your clothes and shoes):
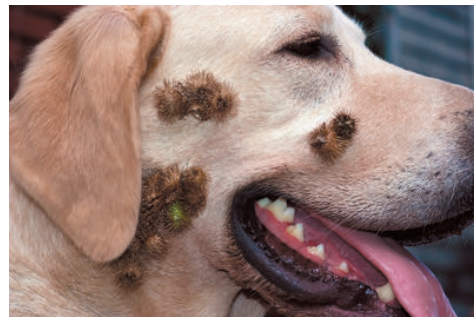
Water disperses some fruits; coconuts have been known to float thousands of miles between islands. Seeds swallowed whole by an animal along with fruits such as berries travel through the animal's digestive tract and are deposited some distance from the parent plant (see Apply the Concept in Chapter 21, p. 444).

themselves from their parent. Fruits are clearly an important way to move seeds away from the parent plant. Wide dispersal of progeny may not always be advantageous, however. If a plant has successfully grown and reproduced, its location is likely to be favorable for the next generation too. Some offspring do indeed stay near the parent, as is the case in many tree species, whose seeds simply fall to the ground. This strategy, however, has several potential disadvantages. If the species is a perennial (see Concept 27.2), offspring that germinate near their parent will be competing with their parent for resources, which may be too limited to support a dense population. Furthermore, even though local conditions were good enough for the parent to produce at least some seeds, there is no guarantee that conditions will still be good the next year, or that they won't be better elsewhere. Thus in many cases, seed dispersal is vital to a species' survival.

Some fruits help disperse seeds over substantial distances, increasing the probability that at least a few of the many seeds produced by a plant will find suitable conditions for

CHECKpoint CONCEPT **27.1**

✓ Make a table that compares the haploid and diploid life stages of a human and a corn plant with regard to (1) the relative sizes of the haploid and diploid stages, (2) how many cells are in the haploid stage, (3) the names of the haploid cells, (4) the time in the life cycle that the haploid stage occurs, (5) the location of the haploid cells, and (6) how the haploid stages develop in males and females. (Refer to Chapter 37 for information on human reproduction.)

✓ Describe the processes that angiosperms use to ensure a genetically diverse population.

✓ The two sperm that participate in plant double fertilization are genetically identical. Are the two products of fertilization genetically identical?

Now that we have described the cellular aspects of angiosperm reproduction, let's turn to the events that signal a transition from vegetative growth of the shoot to the formation of flowers.

> **CONCEPT 27.2** Hormones and Signaling Determine the Transition from the Vegetative to the Reproductive State

Flowering represents a reallocation of energy and materials away from making more roots, stems, and leaves (vegetative growth) to making flowers and gametes (reproductive growth). Flowering can happen at maturity as part of a predetermined developmental program (as in a dandelion plant in summer) or in response to environmental cues such as light or temperature (as with the poinsettias we described at the opening of this chapter). In either case, flowering is initiated through a cascade of changes in gene expression.

Herbaceous plants fall into three categories based on when they mature and initiate flowering and what happens after they flower:

- **Annuals** complete their lives within a year. Annuals include many crops important to humans, such as corn, wheat, rice, and soybeans. When the environment is suitable, annuals grow rapidly. After flowering, they channel most of their energy into the development of seeds and fruits. Then the rest of the plant withers and dies.

- **Biennials** take two years to complete their life cycle. They are much less common than annuals and include carrots, cabbage, and onions. Typically, biennials produce only vegetative growth during their first year and store carbohydrates in underground roots (carrots) or stems (onions). In their second year, they use most of the stored carbohydrates to produce flowers and seeds rather than vegetative growth, and the plant dies after seeds form.

- **Perennials** live three or more—sometimes many more—years. Maple trees, for example, can live up to 400 years. Perennials include many wildflowers as well as trees and shrubs. Typically these plants flower each year but stay alive and keep growing the next season.

Shoot apical meristems can become inflorescence meristems

The transition from purely vegetative growth to the flowering state requires a change in one or more apical meristems in the shoot system. As we described in Chapter 24, shoot apical meristems continually produce leaves, axillary buds, and stem tissues (**FIGURE 27.6A**) in a kind of unrestricted growth called indeterminate growth.

A shoot apical meristem becomes an **inflorescence meristem** (recall that an inflorescence is a cluster of flowers; see Figure 21.19) when it ceases production of leaves and stems and produces other structures: smaller leafy structures called bracts (such as the red leaves in poinsettias), as well as new meristems in the angles between the bracts and the stem (**FIGURE 27.6B**). These new meristems may also be inflorescence meristems, or they may be **floral meristems**, each of which gives rise to a single flower.
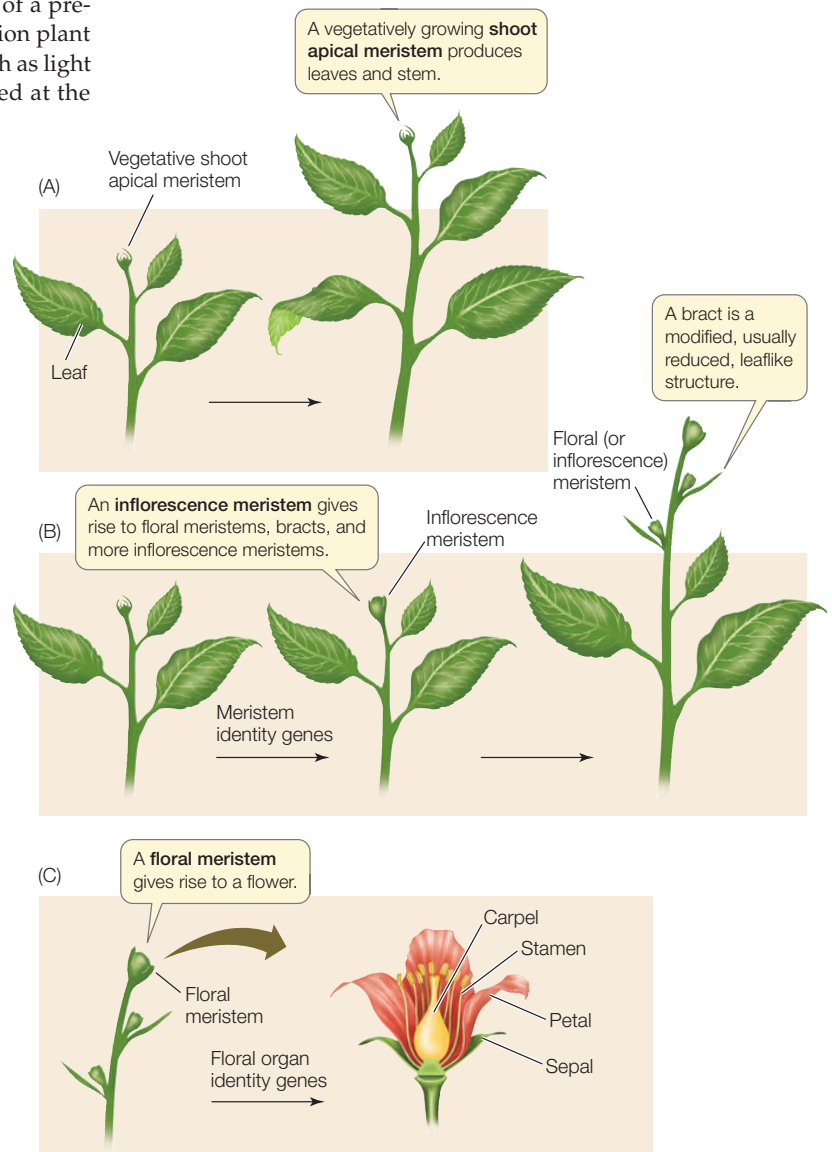
FIGURE 27.6 The Transition to Flowering (A) A shoot apical meristem produces vegetative organs without producing flowers. (B) A shoot apical meristem becomes an inflorescence meristem when it ceases production of leaves and stems and produces other structures. (C) A floral meristem becomes a single flower.

Each floral meristem typically produces four consecutive whorls, or spirals, of organs—the sepals, petals, stamens, and carpels—separated by very short internodes, which keep the flower compact (**FIGURE 27.6C**). In contrast to shoot apical meristems and some inflorescence meristems, floral meristems are responsible for determinate growth—growth of limited extent, like that of leaves.

A cascade of gene expression leads to flowering

The genes that determine the transition from shoot apical meristems to inflorescence meristems and from inflorescence meristems to floral meristems have been studied in model organisms such as *Arabidopsis thaliana*.

MERISTEM IDENTITY GENES Expression of two **meristem identity genes** initiates a cascade of further gene expression that leads to flower formation. Expression of the genes *LEAFY* and *APETALA1* is both necessary and sufficient for flowering. Evidence for the role of these genes is both genetic and molecular. For example, a mutant allele of *APETALA1* leads to continued vegetative growth, even if conditions are suitable for flowering. However, if plants are genetically modified so that the wild-type *APETALA1* gene is strongly expressed in the shoot apical meristem, the plant will flower regardless of environmental conditions. This is powerful evidence that *APETALA1* plays a role in switching shoot apical meristem cells from a vegetative to a reproductive fate (see Figure 27.6B).

FLORAL ORGAN IDENTITY GENES The products of the meristem identity genes trigger the expression of **floral organ identity genes**, which work in concert to specify the successive whorls of the flower (see Figure 27.6C). Floral organ identity genes are homeotic genes that cause the development of specific structures. In plants, the products of homeotic genes are transcription factors that determine whether cells in the floral meristem will be sepals, petals, stamens, or carpels. An example is the gene *AGAMOUS*, a class C gene that causes florally determined cells to form stamens and carpels in the "ABC" system described in Chapter 14 (see Figure 14.12).

Depending on the species, plants initiate these gene expression changes, and the events that follow, in response to either internal or external cues. Among external cues, the most studied are photoperiod (day length) and temperature. We will begin with photoperiod.

Photoperiodic cues can initiate flowering

The study of how light affects the transition to flowering began with two observations in the early twentieth century:

- A mutant tobacco strain appropriately called Maryland Mammoth grew 5 meters tall (normal tobacco is about 1.5 m tall). Instead of flowering in summer, it continued to grow until the late fall frost killed it. Farmers in Virginia were frustrated because they could not get seed of this luxuriant plant for the next year's crop.

Mammoth tobacco

Wild-type tobacco

- Because of improvements in agricultural techniques, soybean yields became so great that it was hard for farmers to harvest all the plants at once. So they tried planting the seeds in groups, several weeks apart. Unfortunately, the resulting plants all formed flowers and seeds at the same time.

The explanation for both of these observations was the same: the signal that set the plants' shoot apical meristems on the path to flowering was the length of daylight, or **photoperiod**. When soybeans experienced days of a certain length, they flowered, regardless of how "old" they were. Maryland Mammoth tobacco *could* flower, but it did not do so in Virginia because it died when the weather got cold. When the plant was grown in a greenhouse to prevent freezing, however, it flowered in December, when the days were short. Maryland Mammoth is now grown commercially in Florida.

Greenhouse experiments measured the day length required for different plant species to flower. Maryland Mammoth tobacco did not flower if exposed to more than 14 hours of light per day; flowering was only initiated once day length became shorter than 14 hours, as it does in December. Other plants (such as soybeans and henbane) flowered only when the days were long (**FIGURE 27.7**).

Plants vary in their responses to photoperiodic cues

Plants that flower in response to photoperiodic stimuli fall into two main classes, although there are variations on these patterns:

- **Short-day plants** (**SDPs**) flower only when the day is *shorter* than a critical maximum. They include poinsettias and chrysanthemums as well as Maryland Mammoth tobacco. Thus, for example, we see chrysanthemums in nurseries
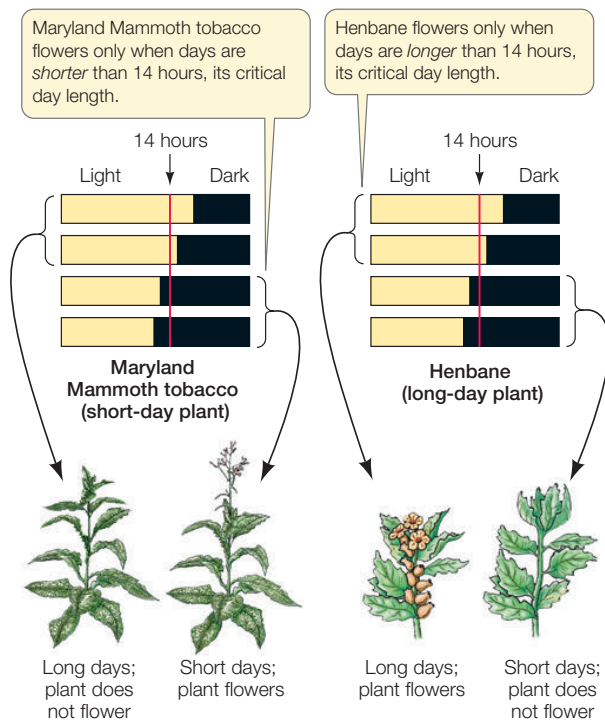
FIGURE 27.7 Photoperiod and Flowering By artificially varying the length of daylight in a 24-hour period, biologists showed that the flowering of Maryland Mammoth tobacco is initiated when the days become shorter than a critical length. Maryland Mammoth tobacco is thus called a short-day plant. Henbane, a long-day plant, shows an inverse pattern of flowering.

in fall and poinsettias in winter (as noted at the opening of this chapter).

- **Long-day plants** (**LDPs**) flower only when the day is *longer* than a critical minimum. Spinach and clover are examples of LDPs. Spinach tends to flower and become bitter in the summer and is therefore normally planted in early spring.

Photoperiodic control of flowering serves an important role: it synchronizes the flowering of plants of the same species in a local population. This synchronization promotes cross-pollination and successful reproduction. It also means that floriculturists can vary light exposures in greenhouses to produce flowers at any time of year.

Night length is the key photoperiodic cue that determines flowering

The terms "short-day plant" and "long-day plant" assume that the key events that induce flowering occur in the daytime. What about the night? After all, short-day plants could just as easily be called "long-night plants," and long-day plants could be called "short-night plants." As it turns out, *night length is indeed the critical factor that induces flowering*, as a series of greenhouse experiments confirmed (**FIGURE 27.8**). In a greenhouse, the overall length of a day or night can be varied irrespective of the 24-hour natural cycle. For example, if cocklebur, an SDP, is
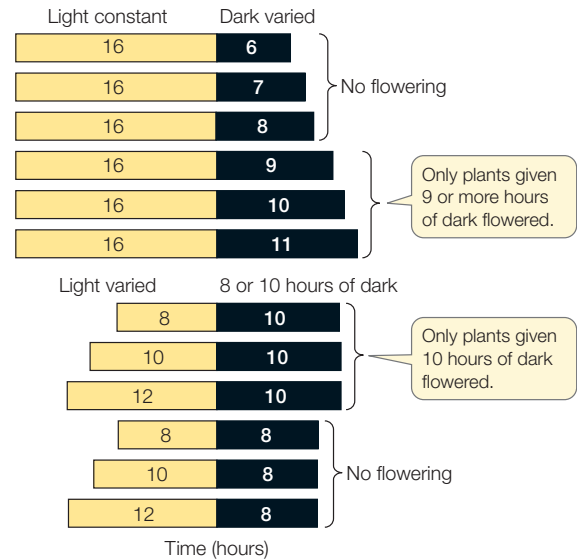
FIGURE 27.8 Night Length and Flowering Greenhouse experiments using cocklebur, an SDP, demonstrated that night length, not day length, is the environmental cue that initiates flowering.

exposed to several long periods of light (16 hours each), it will still flower as long as the dark period between them is 9 hours or longer. This 9-hour inductive dark period also induces flowering even if the light period varies from 8 hours to 12 hours.

Biologists noticed that when the inductive dark period was interrupted by a brief period of light, the flowering signal generated by the long night disappeared. It took several days of long nights for the plant to recover and initiate flowering. Interrupting the day with a dark period had no effect on flowering. A clue as to what occurred in the plant when the flash of light was given came when biologists determined the action spectrum for the wavelengths of light that were effective. As with lettuce seed germination (see Figure 26.11), red light was most effective at breaking the "night" stimulus, and its effect was reversible by far-red light. This indicated that the photoreceptor involved in regulating flowering is phytochrome.

LINK

The properties of phytochrome as a photoreversible photoreceptor of red and far-red light are described in **Concept 26.4**

Go to ANIMATED TUTORIAL 27.2
The Effect of Interrupted Days and Nights
PoL2e.com/at27.2

Plants sense night length by measuring the ratio of the P_{fr} and P_r isoforms of phytochrome. During the day there is more light in the red than in the far-red range. By the end of the day, much of the P_r has absorbed red light and been converted to P_{fr}. At night there is a gradual, spontaneous conversion of this P_{fr} back to P_r. The longer the night, the more P_r there is at the beginning of the next day. An SDP flowers when the ratio of P_{fr} to P_r is low at the end of the night, whereas an LDP flowers

APPLY THE CONCEPT

Hormones and signaling determine the transition from the vegetative to the flowering state

The experiments reported on in Figure 27.8 were repeated using a long-day plant (LDP) that normally flowers when days are 16 hours (or longer) and nights are 8 hours (or shorter). The plant was subjected to the light regimes listed in the table.

1. List the light regimes that should have resulted in flowering.

2. Predict the effect of adding a brief period of far-red light in the middle of the dark period of each light regime.

3. Predict the effect of adding a brief period of red light in the middle of the dark period of each light regime.

A. 14 hours light + 6 hours dark	G. 8 hours light + 8 hours dark
B. 14 hours light + 7 hours dark	H. 10 hours light + 8 hours dark
C. 14 hours light + 8 hours dark	I. 12 hours light + 8 hours dark
D. 14 hours light + 10 hours dark	J. 8 hours light + 10 hours dark
E. 14 hours light + 12 hours dark	K. 10 hours light + 10 hours dark
F. 14 hours light + 14 hours dark	L. 12 hours light + 10 hours dark

when this ratio is high. You can compare this mechanism to an hourglass egg timer. The sand in the top chamber is analogous to P_{fr} and gradually runs down (is converted to P_r) over the course of the night; the shorter the night, the more sand remains at the top at dawn. To "reset" an hourglass timer, you simply turn it over; this would be analogous to dawn of the next day, when P_r begins being converted back to P_{fr}.

The flowering stimulus originates in the leaf

The photoperiodic receptor for flowering, phytochrome, is located in the leaf, not in the shoot apical meristem. "Masking" experiments can show this: if a single leaf of an SDP growing under short-night conditions is covered to simulate a long-night exposure, the shoot apical meristems will transition to flowering as if the entire plant were exposed to long nights (**FIGURE 27.9**). Masking the buds (leaving the leaves exposed) does not induce flowering.

Because the receptor of the photoperiodic stimulus (phytochrome in the leaf) is physically separated from the tissue on which the stimulus acts (the shoot apical meristem), the inference can be drawn that a signal travels from the leaf through the plant's tissues to the shoot apical meristem. Unlike animals, plants do not have a nervous system, so the signal must be a diffusible chemical. Biologists have found additional evidence that a diffusible signal travels from the leaf to the shoot apical meristem:

- If a photoperiodically induced leaf is immediately removed from a plant after the inductive dark period, the plant does not flower. If the induced leaf remains attached to the plant for several hours, however, the plant flowers. This result suggests that something is synthesized in the leaf in response to the inductive dark period, and then moves out of the leaf to induce flowering.

- If two or more cocklebur plants are grafted together, and if one plant is exposed to inductive long nights and its graft partners are exposed to noninductive short nights, all of the plants flower.

- In several species, if an induced leaf from one species is grafted onto another, noninduced plant of a different spe-

cies, the recipient plant flowers. This indicates that the same diffusible chemical signal is used by both species.

Although the diffusible signal was given a name, **florigen** (**FT**), meaning "flower inducing," decades ago, the nature of the signal was only recently explained.

Florigen is a small protein

The characterization of florigen was made possible by genetic and molecular studies of the model organism *Arabidopsis*, an LDP. Three genes are involved (**FIGURE 27.10**):

- *FT* (*FLOWERING LOCUS T*) codes for florigen. FT is a small protein (20 kDa molecular weight) that can travel through plasmodesmata. It is synthesized in phloem companion cells in the leaf and diffuses into the adjacent sieve tube elements, where it moves with the phloem to the shoot apical meristem.

- *CO* (*CONSTANS*) codes for a transcription factor that activates the synthesis of FT. Like *FT*, *CO* is expressed in phloem companion cells in the leaf. CO protein is expressed all the time but is unstable; an appropriate photoperiodic stimulus stabilizes CO so that there is enough to turn on FT synthesis.

- *FD* (*FLOWERING LOCUS D*) codes for a protein that binds to FT protein when it arrives in the shoot apical meristem. The FD protein is a transcription factor that forms a complex with FT protein; the complex activates promoters for meristem identity genes, such as *APETALA1* (*AP1*).

Genetic studies have shown that the *FT* gene is involved in photoperiod signaling in many species:

- Transgenic plants (e.g., tobacco and tomato) that express the *Arabidopsis FT* gene at high levels flower regardless of day length.

- Transgenic *Arabidopsis* plants that express high levels of *FT* genes from other plants (e.g., rice and tomato) flower regardless of day length.

Whereas photoperiod induces flowering via the FT–FD pathway in some plants, in many other species flowering is induced by other stimuli through other pathways.

INVESTIGATION

FIGURE 27.9 The Flowering Signal Moves from Leaf to Bud

Phytochrome, the receptor for photoperiod, is in the leaf, but flowering occurs in the shoot apical meristem. To investigate whether there is a diffusible substance that travels from leaf to bud, James Knott exposed a single leaf of cocklebur plants to the inductive dark period.[a]

HYPOTHESIS

The leaves measure the photoperiod.

CONCLUSION

The leaves measure the photoperiod. Therefore, some signal must move from the induced leaf to the flowering parts of the plant.

METHOD

Grow cocklebur plants under long days and short nights. Mask a leaf on some plants and see if flowering occurs.

Masked leaf

Control

Plant with masked leaf
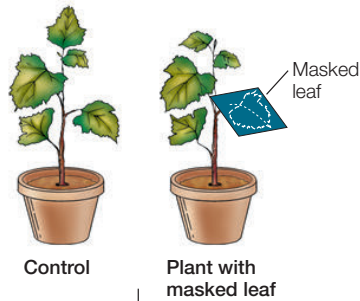
RESULTS

If even one leaf is masked for part of the day—thus shifting that leaf to short days and long nights—the plant will flower.

Burrs (fruit)

Masked leaf
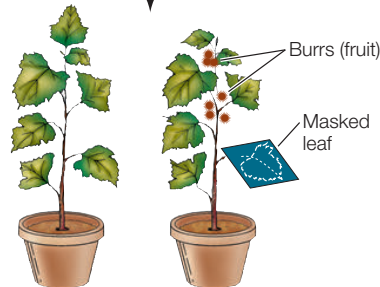
ANALYZE THE DATA

In related experiments, leaves were removed from plants before the plants were exposed to the inductive dark period. There were six plants in each condition.[b]

Condition	Number of plants that flowered
No inductive dark period, intact plant	0
Inductive dark period, intact plant	6
Inductive dark period, all leaves removed	0
Inductive dark period, all but one leaf removed	6

A. Do the data support the conclusion of the experiment by Knott described above? Explain your answer.

B. How would you modify the experiments shown in the table to find out how many days of the inductive dark period are required before the signal is produced? Would you expect the results to be different for the intact plants and plants with only one leaf? Why or why not?

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]J. E. Knott. 1934. *Proceedings of the Society of Horticultural Science* 31: 152–154.
[b]K. C. Hamner and J. Bonner. 1938. *Botanical Gazette* 100: 388–431.

1 Photoperiodic stimulus at leaf companion cell stabilizes CO, which acts as a transcription factor.

Photoperiodic stimulus

CO

DNA

Transcription

Translation

FT

Companion cell

Sieve tube element

FT

FT

2 FT is made and enters sieve tube element through plasmodesmata.

Flowering

5 AP1 is made and acts to initiate flowering.

Shoot apical meristem

AP1

Translation

Translation

Transcription

DNA FT FD

AP1

4 FT combines with FD and the complex acts as a transcription factor for *AP1*.

3 FT is transported through the phloem up to the terminal bud.

FT

CO	CONSTANS protein
FT	FLOWERING LOCUS T protein (florigen)
FD	FLOWERING LOCUS D protein
AP1	APETALA1 protein

FIGURE 27.10 Molecular Biology of Flowering

The protein florigen (FT) is made in the phloem companion cells of a leaf and travels in the sieve tube elements from the leaf to the shoot apical meristem. There FT combines with another protein to stimulate transcription of genes that initiate flowering.

Flowering can be induced by temperature or gibberellins

TEMPERATURE   In some plant species, notably certain cereal crops, the environmental signal for flowering is exposure to cold temperatures, or **vernalization** (Latin *vernus*, "spring"). In both wheat and rye, we can distinguish two categories of flowering behavior. Spring wheat, for example, is a typical annual plant: it is sown in the spring and flowers in the same year. Winter wheat is sown in the fall, grows into a seedling, overwinters (often covered by snow), and flowers the following summer. If winter wheat is not exposed to cold, it will not flower normally in the next growing season. Vernalization evolved in plants adapted to grow in climates with harsh winters and a short growing season. It is a remarkable phenomenon:

- Plants seem to "remember" that they have been exposed to winter. When the weather gets warmer, exposed plants flower sooner than genetically identical plants that were not exposed to cold.

- Plants seem to "know" how long winter lasted, flowering sooner if the winter was long.

Some strains of *Arabidopsis* require vernalization, and those strains have been useful in figuring out the molecular pathway involved (**FIGURE 27.11**). The gene *FLC* (*FLOWERING LOCUS C*) encodes a transcription factor that blocks the FT–FD pathway by inhibiting expression of FT and FD. Cold temperatures inhibit the synthesis of FLC protein epigenetically: the chromatin is modified so that the *FLC* gene is not expressed (it is silenced). The longer the cold, the more cells there are that have the *FLC* gene silenced. This allows the FT and FD proteins to be expressed and flowering to proceed. Similar proteins control some steps in vernalization in cereals.

> **LINK**
>
> Chromatin modification is a common way to regulate gene expression; see **Concept 11.3**

In addition to the well-known effects of cold temperature, there is also an effect of elevated temperature on flowering. Recently, biologists identified a transcription factor that increases the expression of the florigen gene *FT* and is more active at elevated temperatures (27°C as opposed to 22°C). The plants exposed to warm temperatures flower earlier, typically with smaller flowers and fewer seeds. This has important implications for the effects of climate change on crops. As Earth's climate gets warmer, food production may be reduced because of premature activation of the flowering pathway.

GIBBERELLINS   *Arabidopsis* plants do not flower if they are genetically deficient in gibberellin synthesis or if they are treated with an inhibitor of gibberellin synthesis. These observations implicate gibberellins in flowering. Direct application of gibberellins to buds in *Arabidopsis* results in activation of the meristem identity gene *LEAFY*, which in turn promotes the transition to flowering (see Concept 14.3).

Winter-annual *Arabidopsis* without vernalization

Winter-annual *Arabidopsis* with vernalization

FIGURE 27.11   Vernalization   A genetic strain of *Arabidopsis* (winter-annual *Arabidopsis*) requires vernalization for flowering. Without it, the plant is large and vegetative (left), but when exposed to a cold period, it is smaller and flowers (right).

Some plants do not require an environmental cue to flower

Some plants flower in response to cues from an "internal clock." For example, flowering in some strains of tobacco is initiated in the terminal bud when the stem has grown four phytomers in length (recall that stems are composed of repeating units called phytomers; see Figure 24.1). If a terminal bud and a single adjacent phytomer are removed from a plant this size and planted, the cutting will flower because the bud has already received the cue for flowering. But the rest of the shoot below the bud that has been removed will not flower because it is only three phytomers long. After it grows an additional phytomer, it will flower. These results suggest that there is something about the *position* of the bud (atop four phytomers of stem) that determines its transition to flowering.

> **LINK**
>
> The role of positional information in morphogenesis in both plants and animals is described in **Concept 14.3**

The bud might "know" its position by the concentration of some substance that forms a positional gradient along the apical–basal axis of the plant. Such a gradient could be formed, for example, if the root makes a diffusible inhibitor of flowering whose concentration diminishes with plant height. When the plant reached a certain height, the concentration of the inhibitor would become sufficiently low at the tip of the shoot to allow flowering. The relationship between environmental factors and flowering are summarized below:
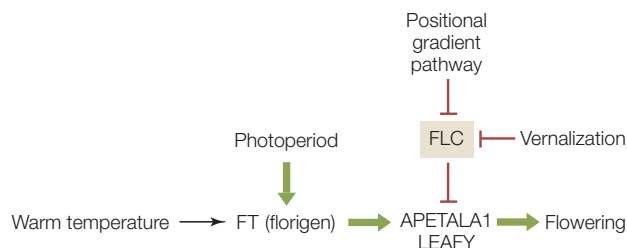
APPLY THE CONCEPT

Hormones and signaling determine the transition from the vegetative to the flowering state

Describe the genes and mutations that could be involved in each of the following observations:

1. A mutant plant flowers without its normal inductive dark period. When a leaf from the mutant plant is grafted onto an unexposed wild-type plant, the recipient plant flowers.

2. A mutant plant does not flower when exposed to the normal inductive dark period. When a leaf from a mutant plant that has been exposed to the inductive dark period is grafted onto an unexposed wild-type plant, the recipient plant flowers.

3. A plant that does not usually require vernalization flowers only after exposure to cold.

4. If a gene is coupled to an active promoter and expressed at high levels in the shoot apical meristem, flowering is induced even in the absence of an appropriate photoperiodic stimulus.

5. If a gene is experimentally overexpressed in the leaf, flowering is induced. Overexpression of the gene in the shoot apical meristem does not, however, induce flowering.

CHECKpoint   CONCEPT 27.2

✓ How do shoot apical meristems, inflorescence meristems, and floral meristems differ, and what are the genes that control the transitions between them?

✓ Explain why "short-day plant" is a misleading term.

✓ If an LDP is exposed to its inductive dark period and one of its leaves is removed and grafted onto an SDP that has not been exposed to its inductive dark period, what will happen?

✓ How would you show that vernalization acts through the *FLC* gene?

Sexual reproduction is not the only way in which angiosperms give rise to more plants. We will now turn to some ways in which plants can reproduce asexually.

CONCEPT 27.3   Angiosperms Can Reproduce Asexually

A plant that reproduces asexually produces progeny genetically identical to itself (clones). This mode of reproduction has the disadvantage of not generating the diversity of offspring that sexual reproduction can produce. But if a plant is well adapted to its environment, the parent plant can pass on to all its progeny a combination of alleles that function well in that environment, and which might otherwise be separated by sexual recombination. Furthermore, the plant avoids the costs of producing flowers and the potentially unreliable processes of cross-pollination and seed germination. Many plants are capable of both sexual and asexual reproduction and can switch between the two depending on environmental conditions or the stage in their life cycle.

Angiosperms use many forms of asexual reproduction

Asexual reproduction is often accomplished through the modification of vegetative organs such as roots, stems, or leaves, which is why the term **vegetative reproduction** is sometimes used to describe asexual reproduction in plants. Another type of asexual reproduction, **apomixis**, involves flowers but no fertilization.

VEGETATIVE REPRODUCTION   The totipotency of plant cells is dramatically shown when a cell from a fully differentiated organ gives rise to an entire new plant. Strawberries, for example, produce horizontal stems, called stolons or runners, that grow along the soil surface, form roots at intervals, and establish potentially independent plants (see Figure 24.13E). Another example is bamboo, which has underground stems called rhizomes that can form an entire forest (**FIGURE 27.12A**). Fleshy underground stems, such as potato tubers, produce multiple plants from "eyes" (see Figure 24.13C). Garlic can produce multiple plants from bulbs, which are also modified stems (**FIGURE 27.12B**). Even leaves can be the source of new plants, as in the succulent *Kalanchoe* (**FIGURE 27.12C**).

Plants that reproduce vegetatively often grow in environments such as eroding hillsides, or places where conditions for seed germination are unreliable. Plants with stolons or rhizomes, such as beach grasses, rushes, and sand verbena, are common on coastal sand dunes. Rapid vegetative reproduction enables these plants, once introduced, not only to multiply but also to stay ahead of the shifting sand; in addition, the dunes are stabilized by the extensive network of rhizomes or stolons that develops. Vegetative reproduction is also common in some deserts, where for much of the time the environment is unsuitable for seed germination and the establishment of seedlings.

Vegetative reproduction is efficient in an environment that is stable over the long term. A change in the environment, however, can leave an asexually reproducing species at a disadvantage. For example, the English elm tree (*Ulmus procera*) reproduces by suckers and is incapable of sexual reproduction. In 1967 a fungal pathogen called Dutch elm disease first struck English elms. The population lacked genetic diversity, and no individuals had genes that would confer resistance to the pathogen. Today the English elm is all but gone from England.

APOMIXIS   Some plants produce flowers but use them to reproduce asexually rather than sexually. Dandelions, blackberries, some citrus trees, and some other plants reproduce by the asexual production of seeds, called apomixis. In sexual reproduction,

(A)

These bamboo shoots all arise from the same underground stem.

(B)

Each clove of garlic is a branch of a bulb and can give rise to a new plant.

(C)

The plantlets forming on the margin of this *Kalanchoe* leaf will fall to the ground and become independent plants.
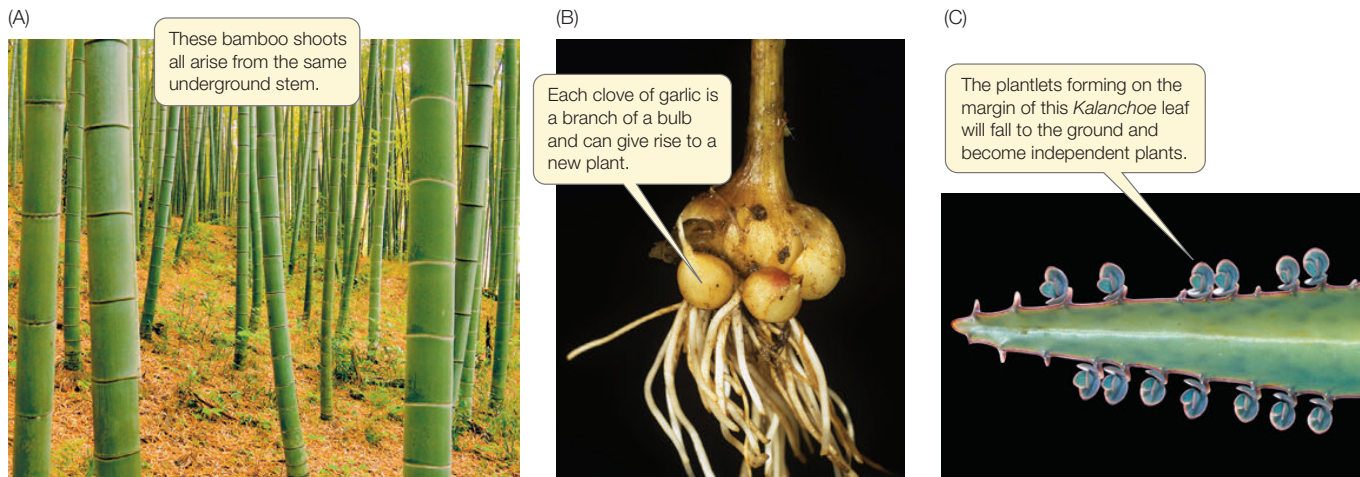
FIGURE 27.12 Vegetative Reproduction (A) The rhizomes of bamboo are underground stems that produce plants at intervals. (B) Bulbs are short stems with large leaves that store nutrients and can give rise to new plants. (C) In *Kalanchoe*, new plantlets can form on leaves.

seeds form from the union of haploid gametes in the embryo sac. But in apomixis, one of two other things happens:

- The cell in the ovule that is supposed to undergo meiosis fails to do so, resulting in a diploid egg cell, which then goes on to form an embryo and seed.
- Diploid cells from the integument surrounding the embryo sac form a diploid embryo sac, and the sac goes on to form an embryo and seed.

In both cases, seed and fruit development proceeds normally. But the genetic consequences are profound: *apomixis produces clones*.

Some agriculturally important plants are hybrids that are derived from the crossing of two genetically different species. Because these hybrids have two sets of chromosomes that are not homologous to one another, they cannot undergo meiosis and are sterile. This means they cannot form the seeds and fruits that are desired by people by ordinary means. In citrus, apomixis occurs naturally, which gets around this problem. Kentucky bluegrass, a mainstay of lawns, reproduces in this manner as well.

Many important crops, such as corn, are grown as hybrids because the offspring of a cross between two inbred, homozygous genetic strains are often superior to either of their parents, a phenomenon called hybrid vigor (see Concept 8.2). Unfortunately, once farmers have obtained a hybrid with desirable characteristics, they cannot use those plants for further crosses with themselves (selfing) to get more seeds for the next generation. You can imagine the genetic chaos when a hybrid, which is heterozygous at many of its loci (e.g., *AaBbCcDdEe*, etc.), is crossed with itself: there will be many new combinations of alleles (e.g., *AabbCCDdee*, etc.), resulting in highly variable progeny. The only efficient and reliable way to reproduce the hybrid is to maintain populations of the original parents to cross again each year. That is exactly what seed companies do. For farmers, it means buying new seeds every year—an expensive proposition.

If a hybrid carried a gene for apomixis, however, it could reproduce asexually, and its offspring would be genetically identical to itself (**FIGURE 27.13**). New hybrids could be developed that would be adapted to specific environments and could be propagated by the farmers on the spot. Investigators are searching for genes that promote apomixis; these could be introduced into desirable crops and allow them to be propagated indefinitely. Such a gene has been identified in corn, but the yield of the variety that contains it is low.

Vegetative reproduction is important in agriculture

One of the oldest methods of vegetative reproduction used in agriculture consists of simply making cuttings of stems, inserting them in soil, and waiting for them to form roots and become autonomous plants. The cuttings are usually encouraged to root by treatment with auxin, as described in Concept 26.2.

Woody plants can be propagated asexually by **grafting**: attaching a bud or a piece of stem from one plant to a root or root-bearing stem of another plant. The part of the resulting plant that comes from the root-bearing "host" is called the **stock**; the part grafted on is the **scion** (**FIGURE 27.14**). The vascular cambium of the scion associates with that of the stock, forming a continuous cambium that produces xylem and phloem. The cambium allows the transport of water and minerals to the scion and of photosynthate to the stock. Much of the fruit grown for market in the United States is produced on grafted trees, as are wine grapes. One advantage of this method is that a desirable scion (one that produces good fruit, for example) can be grafted onto a genetically different stock that has other desirable qualities, such as disease-resistant roots.

Another method widely used for asexual plant propagation is **meristem culture**, in which pieces of shoot apical meristem are cultured on growth media to generate plantlets, which can then be planted in the field. This strategy is vital when uniformity is desired, as in forestry, or when virus-free plants are the goal, as with strawberries and potatoes.

Two strains of corn are crossed.

×

The F₁ offspring are heterozygous and show hybrid vigor.

Sexual reproduction

Apomixis

F₂

F₂, F₃, F₄, …

Sexual reproduction by crossing of F₁ plants results in many genotypes and phenotypes, and overall hybrid vigor is lost.

Apomixis of F₁ plants produces offspring genetically identical to the F₁ plants, and hybrid vigor is retained.
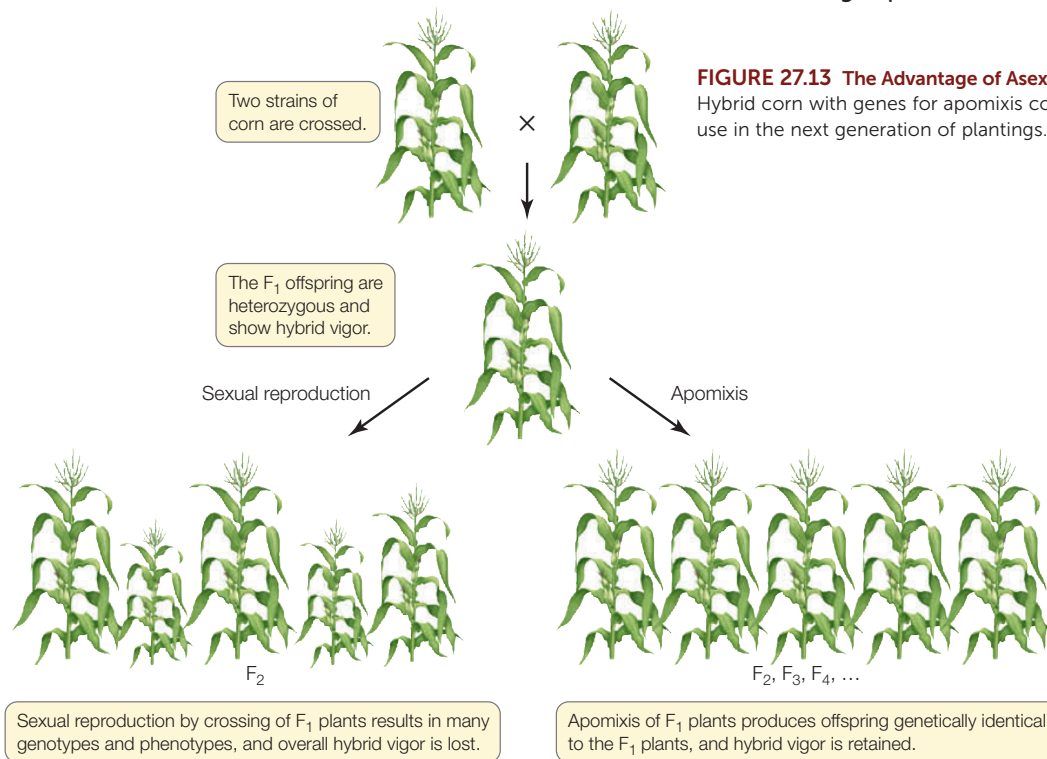
FIGURE 27.13 The Advantage of Asexual Reproduction by Apomixis Hybrid corn with genes for apomixis could be planted by farmers for use in the next generation of plantings.

CHECKpoint   CONCEPT 27.3

✓ What are the advantages and disadvantages of asexual as compared with sexual reproduction in plants?

✓ What kinds of gene mutations would you search for that might promote apomixis?

✓ Most of the navel orange trees that once grew all over southern California are derived by grafting and apomixis from a single tree that still exists in Riverside, CA. How would you prove this?

Q How did an understanding of angiosperm reproduction allow floriculturists to develop a commercially successful poinsettia?

ANSWER   The poinsettia illustrates well how the concepts of plant physiology and reproduction are used in floriculture. As Albert Ecke found, poinsettias are short-day plants, using the long nights of winter as a signal for flowering (Concept 27.2). In fact, the poinsettia's inductive dark period of 14 hours was among the first described in a flowering plant. The Eckes' plants did not flower consistently until they moved their growing operations from urban Los Angeles to an isolated rural region with less light pollution. Today the plants are grown in greenhouses, where the photoperiod is carefully regulated.

A second important factor in the poinsettia's commercial success was the plant's growth habit. In Mexico, the wild relatives of cultivated varieties grow up to 3 meters tall, with few branches (**FIGURE 27.15**; compare these plants with the 0.5 m tall plants in the photograph at the opening of this chapter). Paul Ecke found a variety that was much shorter and formed an attractive, branching plant with axillary shoots. These compact poinsettias were initially propagated asexually by grafting to native plants (Concept 27.3).

The cause of the compact phenotype was assumed to be a dwarfing gene, but several observations cast doubt on this assumption. First, heat treatment of short, branching plants changed their phenotype to the tall, less branched growth habit. Second, heat-treated plants would regain their short, branch-

Scion

In grafting, the scion is aligned so that its vascular cambium is adjacent to the vascular cambium in the stock.
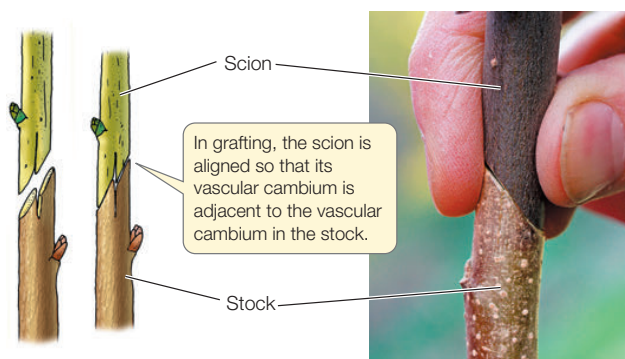
Stock

FIGURE 27.14 Grafting   Grafting—attaching a piece of a plant to the root or root-bearing stem of another plant—is a common horticultural technique. The "host" root or stem is the stock; the upper grafted piece is the scion. In the photo, a scion of one apple variety is being grafted onto a stock of another variety.

FIGURE 27.15 A Wild Relative of Poinsettia Poinsettias growing in the wild in Mexico have an entirely different growth habit from the commercially propagated plants sold for holiday decorations.

ing growth habit if they were grafted onto untreated short, branching plants. These and other results pointed to a transmissible infective agent as the cause of the short, branching phenotype.

Dr. Ing-Ming Lee at the U.S. Department of Agriculture isolated a bacterium called *Phytoplasma* from the short, branching plants and proved by experiments that it was the causative agent of the compact growth habit. When young plants with the tall growth habit were inoculated with the bacteria, they grew up short and branching. It is suspected that the bacteria change cytokinin levels in the plants, since this hormone regulates branching (see Concept 26.3).

Many new varieties of poinsettias have been generated by conventional sexual reproduction (Concept 27.1). You can look for the phenotypes of these varieties next holiday season. They include stiff stems, new colors (such as white), and longer lifetimes for the colorful bracts.

SUMMARY

CONCEPT 27.1 Most Angiosperms Reproduce Sexually

- Sexual reproduction promotes genetic diversity in a population. The flower is an angiosperm's structure for sexual reproduction.

- Flowering plants have microscopic gametophytes. The megagametophyte is the **embryo sac**, which typically contains eight nuclei in seven cells. The microgametophyte is the two- or three-celled **pollen grain**. **Review Figure 27.2 and ACTIVITY 27.1**

- Following pollination, the pollen grain delivers sperm cells to the embryo sac by means of a pollen tube.

- Angiosperms exhibit double fertilization, forming a diploid zygote that becomes the embryo and a triploid **endosperm** that stores reserves. **Review Figure 27.4 and ANIMATED TUTORIAL 27.1**

CONCEPT 27.2 Hormones and Signaling Determine the Transition from the Vegetative to the Reproductive State

- In **annuals** and **biennials**, flowering and seed formation are followed by the death of the rest of the plant. **Perennials** live longer and reproduce repeatedly.

- For a vegetatively growing plant to flower, a shoot apical meristem must become an **inflorescence meristem**, which in turn must give rise to one or more **floral meristems**. These events are determined by specific genes. **Review Figure 27.6**

- Some plants flower in response to **photoperiod**. **Short-day plants** (**SDPs**) flower when nights are longer than a critical length specific to each species; **long-day plants** (**LDPs**) flower when nights are shorter than a critical length. **Review Figures 27.7 and 27.8 and ANIMATED TUTORIAL 27.2**

- The mechanism of photoperiodic control of flowering involves phytochromes and a diffusible protein signal, **florigen** (**FT**), which is formed in the leaf and is translocated to the shoot apical meristem. **Review Figures 27.9 and 27.10**

- In some angiosperms, exposure to cold—called **vernalization**—is required for flowering. In others, internal signals (such as gibberellin) induce flowering. All of these stimuli converge on the **meristem identity genes**.

CONCEPT 27.3 Angiosperms Can Reproduce Asexually

- Asexual reproduction allows rapid multiplication of organisms that are well suited to their environment.

- **Vegetative reproduction** involves the modification of a vegetative organ for reproduction. **Review Figure 27.12**

- Some plant species produce seeds asexually by **apomixis**. **Review Figure 27.13**

- Woody plants can be propagated asexually by **grafting**. **Review Figure 27.14**

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is27

Go to LaunchPad at **macmillanhighered.com/launchpad** for additional resources, including LearningCurve Quizzes, Flashcards, and many other study and review resources.

Plants in the Environment

A field of wheat infected with the wheat rust fungus (right) has a much reduced growth rate and produces much less grain than an uninfected field of wheat that is resistant to the fungus (left).

In late 1998, William Wagoire, a plant geneticist in Uganda, was astounded when he noticed some red blotches on the stems of wheat plants he was breeding. Wheat rust (*Puccinia graminis*), the fungus that causes the blotches, had supposedly been rendered almost extinct 25 years previously by the "Green Revolution," when a gene from rye plants had been crossed into wheat, making it resistant to this fungal disease. This landmark achievement had protected the crop that provides one-third of the human diet from a mold that can devastate it.

Two generations of farmers worldwide had never seen an epidemic of wheat rust, but its presence in history is vivid. Even the ancient Romans feared this disease, worshipping a god, "Robigus," who was thought to help their crop ward off the mold. In the seventeenth century, the early colonists in Massachusetts almost starved because the wheat they planted got infected with wheat rust. In 1917, an epidemic of wheat rust in the United States reduced the crop by one-third, leading to widespread panic.

Wagoire used DNA markers to identify the strain of wheat rust he had found (called Ug99 for Uganda 1999). When he compared it with known strains, which are stored in a few laboratories, he found that his strain was new and unique. Clearly, Ug99 had evolved a way to get around the resistance genes in modern wheat.

When the blotches of wheat rust on a stem burst, they release thousands of spores, any one of which can be carried by the wind to a susceptible plant. When you consider that 1 hectare of an infected wheat field can release more than 10 billion spores, the possibility of epidemic spread becomes apparent. Ug99 has begun a relentless path of infection, carried by prevailing winds. By 2001 it had infected wheat in Kenya; in 2003 it was in Ethiopia; in 2006 it crossed the Red Sea to Yemen; in 2009 it was in Iran; at the same time, winds carried the spores south to Zimbabwe and South Africa. Biologists fear that Ug99 could reach central Asia and Australia by prevailing winds, and even North America by the "747 route," accidentally dusting a traveler's clothes somewhere in the now widespread infective region. The Borlaug Global Rust Initiative has been set up to try to use knowledge of plant and fungal biology to stop the spread of this disease before it is too late.

Q How can knowledge of plant and fungal biology be used to prevent the spread of wheat rust?

<div style="background: light gray box">

CONCEPT **Plants Have Constitutive and**
28.1 **Induced Responses to Pathogens**

</div>

Botanists know of dozens of diseases that can kill a wheat plant, each of them caused by a different pathogen, each of which in turn has many different genetic strains. Plant pathogens—which include fungi, bacteria, protists, and viruses—are part of nature, and for that reason alone they merit our study in biology. Because we humans depend on plants for our food, the stakes in our effort to understand plant pathology are especially high. That is why, just as medical schools have departments of pathology, universities in agricultural regions have departments of plant pathology.

Successful infection by a pathogen can have significant effects on a plant, reducing photosynthesis and causing massive cell and tissue death. Plants and pathogens have evolved together in a continuing "arms race": pathogens have evolved mechanisms with which to attack plants, and plants have evolved mechanisms for defending themselves against those attacks. Like the responses of the human immune system, the responses by which plants fight off infection can be either **constitutive**—always present in the plant—or **induced**—produced in reaction to the presence of a pathogen.

Physical barriers form constitutive defenses

As with humans and their skin, a plant's first line of defense is its outer surfaces, which can prevent the entry of pathogens. The parts of stems and leaves exposed to the outside environment are covered with cutin, suberin, and waxes. These substances not only prevent water loss by evaporation but can also prevent fungal spores and bacteria from entering the underlying tissues. The plant cell wall is also an important physical barrier to pathogens and can be strengthened further as an induced defense response (as we will see in the next section).

In addition to using physical barriers to prevent infection, plants use chemical warfare. Unlike animals, plants cannot flee from animals that eat them, so they make molecules that deter or destroy herbivores, as we will see in Concept 28.2. Some of these constitutively synthesized molecules also inhibit pathogens. For example, in plantains (*Plantago*), iridoid glycosides, which are glucose molecules covalently linked to short-chain fatty acids, inhibit the growth of fungal pathogens.

When constitutive defenses fail to deter a pathogen, plants initiate induced resistance mechanisms. As we discuss these mechanisms, refer to the overview in **FIGURE 28.1**.

Induced responses can be general or specific

Plant pathogens cause the host plant to activate various chemical defense responses. A wide range of molecules called **elicitors** have been identified that trigger these defenses. These molecules vary from peptides made by bacteria to cell wall fragments from fungi. Elicitors can also be derived from fragments of plant cell wall components broken down by pathogens. Plants have receptors that recognize elicitors and initiate the induced defense responses.

The responses of plants to elicitors can be described in terms of the "plant immune system." Two forms of immunity are recognized (see Figure 28.1):

1. Some elicitors (PAMPs) bind to cell surface receptors, resulting in general immunity.

2. When certain pathogenic enzymes attack the plant cell wall, the breakdown products are recognized as elicitors by a membrane receptor.

3. Some elicitors bind to cytoplasmic receptors (R), resulting in specific immunity.

4. Signaling molecules trigger cellular responses, including the production of defensive molecules.

5. Defensive molecules such as phytoalexins and PR proteins attack the pathogen directly.

6. Some PR proteins serve as "alarm signals" to cells that have not yet been attacked.

7. Polysaccharides and extensin strengthen the cell wall and block plasmodesmata.

FIGURE 28.1 Pathogens Induce Plant Resistance The presence of a pathogen stimulates the plant to produce defensive molecules that work in many different ways.

Go to ANIMATED TUTORIAL 28.1
Signaling between Plants and Pathogens
PoL2e.com/at28.1

- General immunity is triggered by general elicitors called pathogen associated molecular patterns (PAMPs). PAMPs are usually molecules that are produced by entire classes of pathogens, such as the protein flagellin (found in bacterial flagella) or the polysaccharide chitin (found in fungal cell walls). Thus general immunity is an overall response rather than a response that is triggered by a specific pathogen in a particular plant. PAMPs are recognized by transmembrane receptors called pattern recognition receptors, which activate signaling pathways that lead to general immunity.

- Specific immunity is triggered by specific elicitors called effectors. Effectors include a wide variety of specific pathogen-produced molecules that enter the plant cell. Once inside the cell, effectors bind to cytoplasmic receptors called R proteins that trigger the specific immunity response.

> **LINK**
>
> The human immune system, with its general (innate) and specific (adaptive) defenses, is described in **Chapter 39**

General and specific immunity both involve multiple responses

Many of the signaling pathways associated with general and specific immunity are the same, although the latter is specific for particular pathogens in particular plants, and is much stronger than general immunity. Both forms of immunity involve signaling pathways that are triggered by binding between the elicitors (PAMPs or effectors) and their receptors. These pathways lead to various responses:

- *Formation of NO and reactive oxygen species*: Receptor binding triggers the rapid production of nitric oxide (NO) and reactive oxygen species such as hydrogen peroxide (H_2O_2). These reactive molecules are toxic to some pathogens, and they are components of signal transduction pathways leading to local and systemic (plant-wide) defenses.

- *Polymer deposition*: Polymers such as lignin are deposited on the inside of the cell wall to strengthen the wall. These macromolecules may also block the plasmodesmata, limiting the ability of pathogens to spread from cell to cell through these channels (see Figure 28.1, step 7).

- *Hormone signaling*: Some pathways result in the production of plant hormones, including salicylic acid and jasmonic acid. We will describe the roles of these hormones in immunity later in the chapter.

- *Changes in gene expression*: Signal transduction cascades lead to changes in gene expression. The upregulated genes include pathogenesis-related (PR) genes and genes encoding the production of antimicrobial substances called phytoalexins.

PHYTOALEXINS **Phytoalexins** are small molecules produced within hours of an infection by plant cells near the infection site. They are antibiotic-like molecules, toxic to pathogens. An example is camalexin, a phytoalexin made by the model organism *Arabidopsis thaliana* from the amino acid tryptophan:

Tryptophan   Camalexin
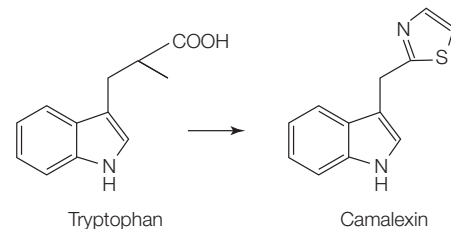
PATHOGENESIS-RELATED PROTEINS Plants produce several types of **pathogenesis-related**, or **PR**, **proteins**. Some are enzymes that break down the cell walls of pathogens. Chitinase, for example, is a PR protein that breaks down chitin, a distinctive component of fungal cell walls. In some cases the breakdown products of the pathogen's cell walls serve as elicitors that trigger further defensive responses. Other PR proteins may serve as alarm signals to plant cells that have not yet been attacked, so they can initiate defensive responses of their own (see Figure 28.1, step 6). PR proteins are not rapid-response weapons; rather, they act more slowly, perhaps after other mechanisms have blunted the pathogen's attack.

APPLY THE CONCEPT

Plants have constitutive and induced responses to pathogens

Because you are a biology student, your nonscientist neighbors are confident that you know all about plants. A neighbor brings you a potted plant he bought 3 weeks ago from a nursery. The leaves have brown spots. He bought another plant of the same species from a different nursery 3 weeks ago, and that plant has no spots.

1. You suspect that the spots are caused by either a disease or a nutritional deficiency. Given a large supply of the plants and soils involved, how would you distinguish between these possibilities?

2. Assuming that the spots are caused by a fungal disease, how would you investigate at the molecular level the mechanism for formation of the brown leaf spots?

3. You go to the nursery where the neighbor bought the infected plant and find several pots of plants with no brown spots on their leaves. What plant characteristics might account for the absence of spots?

Specific immunity is genetically determined

Pathogen genes that code for elicitors of specific immunity are called **avirulence (*Avr*) genes**; there are hundreds of such genes, and they vary among pathogen species and strains. When an elicitor enters a plant cell, it may encounter an R protein, a cytoplasmic receptor protein encoded by a **resistance (*R*) gene**. There are hundreds of *R* genes, each encoding a receptor that is specific for one or a few elicitors. If a plant receptor binds to an elicitor, a signal transduction pathway is set in motion that triggers the plant's specific immunity. This type of resistance is called **gene-for-gene resistance** because it involves a recognition event between two specific molecules: one determined by an *Avr* gene in the pathogen and the other determined by an *R* gene in the plant (**FIGURE 28.2**).

If the plant has no receptor to bind to the elicitor made by a particular species or strain of pathogen, the plant does not recognize the pathogen and does not turn on specific inducible defenses. The lack of a receptor makes the plant especially susceptible to that pathogen. There is an ongoing coevolutionary "arms race" between pathogens attempting to evade detection by plants and plants evolving ways to detect them. A major goal of plant breeders for the past 50 years has been to identify *R* and *Avr* genes and to breed new *R* genes into crops to make them more resistant to pathogens. This effort speeds up the arms race that occurs naturally.

Specific immunity usually leads to the hypersensitive response

As we described earlier, some induced defenses, such as polymer deposition, help prevent spread of the pathogen to the rest of the plant. Specific immunity often takes this a step further: cells around the site of infection undergo apoptosis (programmed cell death) in what is called the **hypersensitive response**. This prevents spread of the pathogen by depriving it of nutrients. Some of the cells also produce phytoalexins and other toxic chemicals before they die. Surrounding (still living) cells produce cell wall polysaccharides to seal off plasmodesmata and prevent the spread of the pathogen to healthy tissues. The dead tissue, called a necrotic lesion, contains and isolates what is left of the infection. The rest of the plant remains free of the infecting pathogen:

Necrotic lesion

> **LINK**
>
> Apoptosis, or programmed cell death, is involved in many normal biological processes; see, for example, **Concept 14.3**. The cellular events of apoptosis are described in **Concept 7.5**

General and specific immunity can lead to systemic acquired resistance

The hypersensitive response contrasts with **systemic acquired resistance**, a general increase in the resistance of the entire plant to a wide range of pathogens. It is not localized and not limited to the pathogen that originally triggered it, and its effect may last as long as an entire growing season. This defensive response is initiated by salicylic acid:

Salicylic acid

Salicylic acid production is triggered by receptor binding in both general and specific immunity; salicylic acid then acts as a signal to turn on various defense responses.

Systemic acquired resistance is accompanied by the synthesis of PR proteins. Infection in one part of a plant can lead to the export of salicylic acid to other parts, where it triggers the production of PR proteins ahead of the spread of infection. Infected plant parts also produce the closely related compound methyl salicylate (also known as oil of wintergreen). This volatile (readily forms a gas) substance travels to other plant parts through the air and may trigger the production of PR proteins in neighboring plants that have not yet been infected.

Another type of systemic acquired resistance is a more specific defense against viruses whose genomes are made of RNA. The plant uses its own enzymes to convert some of the

1 If the host and pathogen have matching *R* and *Avr* genes, the plant will resist the pathogen…

Receptor encoded by *R* gene

Pathogen effector encoded by *Avr* gene

RESISTANT · H_2O_2, NO · Local responses · Systemic responses · SUSCEPTIBLE · SUSCEPTIBLE · SUSCEPTIBLE

2 …but if either half of the *R*–*Avr* pair is missing, specific immunity is not elicited.

FIGURE 28.2 Genes and the Response to a Pathogen If an *Avr* gene in a pathogen that codes for an elicitor "matches" an *R* gene in a plant that codes for a receptor, the receptor binds the elicitor, and specific immunity results. In addition to the production of H_2O_2 and NO, responses may include gene activation and modifications of signaling proteins.

single-stranded RNA of the invading virus into double-stranded RNA (dsRNA) and to chop that dsRNA into small pieces called small interfering RNAs (siRNAs). The siRNAs interact with another cellular component to degrade viral mRNAs, blocking viral replication. This phenomenon is an example of RNA interference (RNAi) (see Figure 13.9). The siRNAs spread rapidly through the plant by way of plasmodesmata, providing systemic resistance.

CHECKpoint   CONCEPT 28.1

✓ Compare constitutive and induced responses to pathogens.

✓ Explain the inherited traits involved in both constitutive and induced responses to pathogens.

✓ If a group of plants is sprayed with oil of wintergreen, they all show resistance to a variety of pathogens. Explain how this occurs.

Pathogens are not the only foes of plants; plants must also defend themselves against herbivores, animals that eat plants. Because they are sessile, plants cannot run away from herbivores, but that does not mean they are defenseless against their would-be consumers, as we will see next.

CONCEPT 28.2   Plants Have Mechanical and Chemical Defenses against Herbivores

Herbivores depend on plants for energy and nutrients. Their foraging activities cause physical damage to plants, and they often spread pathogens among plants as well. While the majority of herbivores are insects (**FIGURE 28.3**), most other groups of animals also include some herbivores. Plants have both constitutive and induced mechanisms to protect themselves from herbivory.

Constitutive defenses are physical and chemical

Plants have a number of constitutive anatomical features, such as trichomes (leaf hairs), thorns, and spines that may be specialized for defense. Some plants have insoluble crystals of salts such as calcium oxalate that damage the tissues of insects that consume the plants. In addition, normal plant features, including thick cell walls and tree bark, may deter some herbivores.

Plants resort to "chemical warfare" to repel or inhibit other herbivores, using special chemicals called **secondary metabolites**. These substances are referred to as "secondary" because, unlike molecules such as sugars and amino acids, they are not used for basic cellular processes. The more than 10,000 known secondary metabolites range in molecular mass from about 70 to more than 390,000 daltons, but most are small (**TABLE 28.1**). Some are produced by only a single plant species, whereas others are characteristic of entire genera or even families. The effects of defensive secondary metabolites on animals are

diverse. Some act on the nervous systems of herbivorous insects, mollusks, or mammals. Others mimic the natural hormones of insects, causing some larvae to fail to develop into adults. Still others damage the digestive tracts of herbivores.

An example of a secondary metabolite is canavanine, an amino acid that is similar to the amino acid arginine:

Arginine   **Canavanine**

A seemingly slight chemical difference…   *…produces an inactive protein.*
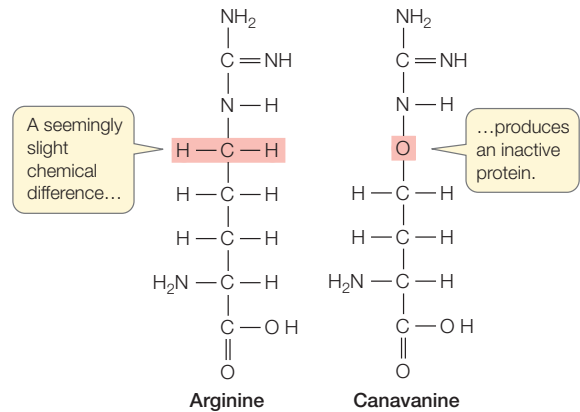
When an insect larva consumes canavanine-containing plant tissue, the canavanine is incorporated into the insect's proteins in some of the places where the insect's mRNA codes for arginine. The enzyme that charges the tRNA specific for arginine fails to discriminate accurately between the two amino acids. The structure of canavanine, however, is different enough from that of arginine that some of the resulting proteins end up with a modified tertiary structure and hence reduced biological activity. These defects in protein structure and function lead to developmental abnormalities that kill the insect.
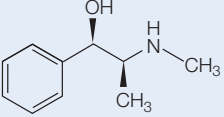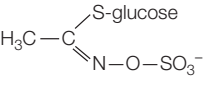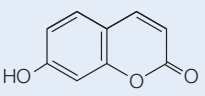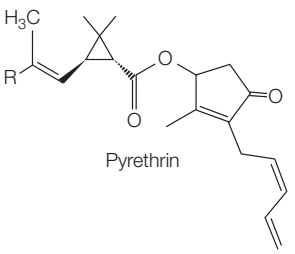
(A) *Locusta migratoria*

(B) *Manduca sexta*

FIGURE 28.3 Insect Herbivores   The great majority of herbivores are insects. (A) Some herbivores, such as this locust, are generalists that will attack nearly any plant. (B) Others are specialists, like this tobacco hornworm (the caterpillar of the Carolina sphinx moth), which feeds only on tobacco plants and a few closely related species.

TABLE 28.1 Secondary Metabolites Used in Plant Defense

Class	Type	Role	Example
Nitrogen-containing	Alkaloids	Neurotoxin	Nicotine in tobacco
	Glycosides	Inhibit electron transport	Dhurrin in sorghum
	Nonprotein amino acids	Disrupt protein structure	Canavanine in jack bean
Ephedrine (an alkaloid)			
Nitrogen- and sulfur-containing	Glucosinolates	Inhibit respiration	Methylglucosinolate in cabbage
Methylglucosinolate			
Phenolics	Coumarins	Block cell division	Umbelliferone in carrots
	Flavonoids	Phytoalexins	Capsaicin in peppers
	Tannins	Inhibit enzymes	Gallotannin in oak trees
Umbelliferone			
Terpenes	Monoterpenes	Neurotoxins	Pyrethrin in chrysanthemums
	Diterpenes	Disrupt reproduction and muscle function	Gossypol in cotton
	Triterpenes	Inhibit ion transport	Digitalis in foxglove
	Sterols	Block animal hormones	Spinasterol in spinach
	Polyterpenes	Deter feeding	Latex in *Euphorbia*
Pyrethrin			

While the mechanisms of action of secondary metabolites and their presence in plant tissues are circumstantial evidence of their role in defense, experiments can be done to provide cause-and-effect evidence. Nicotine, for example, kills insects by acting as an inhibitor of nervous system function, and its function in tobacco is presumed to be insecticidal. Yet commercial varieties of tobacco and related plants that produce nicotine are still attacked, with moderate damage, by pests such as the tobacco hornworm (see Figure 28.3B). Given that observation, does nicotine really deter herbivores? Biologists answered this question conclusively with a study that used tobacco plants in which an enzyme involved in nicotine biosynthesis had been inhibited, lowering the nicotine concentration in the plants by more than 95 percent. These low-nicotine plants suffered much more damage from insect herbivory than normal plants did (**FIGURE 28.4**).

Plants respond to herbivory with induced defenses

The first step in a plant's response to an attack by an herbivore is to sense the attack, either by means of changes in membrane potential or by means of chemical signals. The detection of an herbivore attack then triggers signal transduction pathways that induce plant defenses.

MEMBRANE SIGNALING The cell membrane is the part of the plant cell that is in contact with the environment. Within the first minute after an herbivore strikes, changes in the electric potential of the cell membrane occur in the damaged area. The continuity of the symplast (see Concept 25.3) ensures that the signal travels over much of the plant within 10 minutes.

CHEMICAL SIGNALING When some insects (such as caterpillars) chew on a plant, substances in the insect's saliva combine with fatty acids derived from the consumed plant tissue. The resulting compounds act as elicitors to trigger both local and systemic responses to the herbivore. In corn, the elicitor produced by one particular moth larva has been named volicitin for its ability to induce production of volatile signals that can travel to other plant parts—and to neighboring corn plants—and stimulate their defensive responses.

INVESTIGATION

FIGURE 28.4 Nicotine Is a Defense against Herbivores The secondary metabolite nicotine, made by tobacco plants, is an insecticide, yet most commercial varieties of tobacco are susceptible to insect attack. Ian Baldwin demonstrated that a tobacco strain with a reduced nicotine concentration was much more susceptible to insect damage than native tobacco was.[a]

HYPOTHESIS

Nicotine helps protect tobacco plants against insects.

METHOD

Create a strain of low-nicotine tobacco plants.

↓

Plant normal (control) and low-nicotine (mutant) plants together in a field where they are accessible to insects.

↓

Assess the extent of leaf damage at 2-day intervals.

In the experimental plants, a gene coding for a key enzyme in the biosynthetic pathway to nicotine was inhibited.

Nicotine concentrations were 95% lower in the modified plants.

Hornworm

Normal (control)   Low-nicotine plants
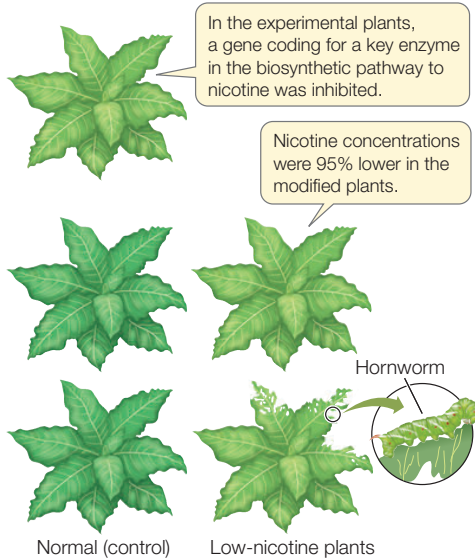
RESULTS

The low-nicotine plants suffered more than twice as much leaf damage as did the normal controls.
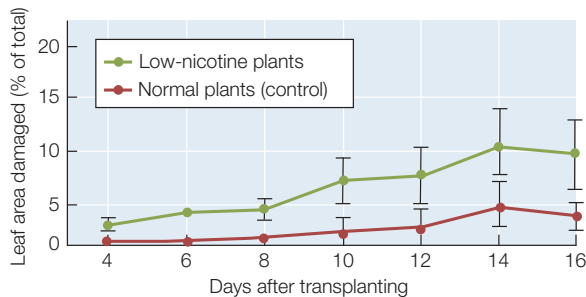
CONCLUSION

Nicotine provides tobacco plants with at least some protection against insects.

ANALYZE THE DATA

In a separate experiment, Baldwin and his colleagues showed that treatment with jasmonic acid (jasmonate) increased the concentration of nicotine in normal tobacco plants but not in the low-nicotine plants. The researchers planted a group of normal and low-nicotine plants and treated them with jasmonate 7 days after planting. The plants were assessed for herbivore damage every 2 days after being planted. The results are shown in the graph.
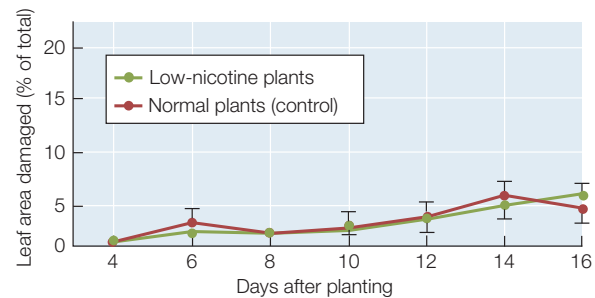
A. Compare these data to those at left for the untreated plants. What was the effect of jasmonate treatment on the resistance of normal plants to herbivore damage? What was the effect on low-nicotine plants?

B. What do these data reveal about the role of nicotine in preventing herbivore damage?

C. Explain how jasmonate could have had the effect it did on the low-nicotine plants, even though their nicotine levels were still low after jasmonate treatment.

D. The error bars at each data point are the standard error of the mean (SEM). What statistical test (see Appendix B) would you use to determine the possible significance of differences between the jasmonate-treated and untreated plants? At 10 days, the mean damage ± SEM for untreated low-nicotine plants was $6.0 ± 1.5$ % ($n = 36$), and for treated low-nicotine plants it was $2.2 ± 0.6$ % ($n = 28$). Run a statistical test comparing the two results, calculate the P-value, and comment on significance.

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]P. Steppuhn et al. 2004. *PLOS Biology* 2: e217.

SIGNAL TRANSDUCTION PATHWAY The perception of damage from herbivory can initiate a signal transduction pathway in the plant that involves the plant hormone **jasmonic acid (jasmonate)** (**FIGURE 28.5**; also see Figure 28.4, Analyze the Data):

Jasmonic acid
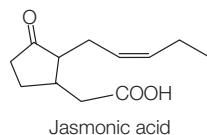
When the plant senses an herbivore-produced elicitor, it makes jasmonate, which triggers many plant defenses, including the synthesis of protease inhibitors. The inhibitors, once in an insect's gut, interfere with the protease-catalyzed digestion of proteins and thus stunt the insect's growth. Jasmonate also "calls for help" by triggering the formation of volatile compounds that attract insects that prey on the herbivores attacking the plant. Similarly, the volatile compounds induced by volicitin in corn attract wasps that parasitize

1 Perception of tissue damage by an herbivore causes formation and release of elicitor.

2 Elicitor binds to a receptor on phloem companion cells.

3 Receptor activation causes hydrolysis of a membrane lipid, forming jasmonate.

4 Jasmonate travels through plasmodesmata from companion cell to sieve tube element.

5 Jasmonate enters the damaged area and other areas of the plant.

6 Jasmonate binds to JAZ, an inhibitor, releasing a transcription factor.

7 The transcription factor enters the nucleus, increasing expression of a gene that codes for a protease inhibitor.

FIGURE 28.5 A Signaling Pathway for Induced Defenses against Herbivory The chain of events initiated by herbivory that leads to the production of a defensive chemical can consist of many steps. These steps may include the synthesis of one or two hormones, binding of receptors, gene activation, and finally, synthesis of the defensive chemical.

herbivorous caterpillars, so the "call for help" is a recurrent theme in plant–insect interactions.

Why don't plants poison themselves?

Why don't the constitutive defensive chemicals that are so toxic to herbivores and pathogens kill the plants that produce them? Plants that produce toxic defensive chemicals generally use one of several measures to protect themselves.

COMPARTMENTALIZATION Isolation of the toxic substance is the most common means of avoiding exposure. Plants store their toxins in vacuoles if the toxins are water-soluble. If they are not water-soluble, the toxins may be dissolved in latex (a complex mixture of dissolved molecules and suspended particles) and stored in a specialized compartment, or they may be dissolved in waxes on the epidermal surface. Such compartmentalized storage keeps the toxins away from mitochondria, chloroplasts, and other parts of the plant's metabolic machinery.

LINK

Both plants and animals use compartmentalization to isolate toxins and waste products that occur as by-products of some biochemical reactions; see **Concept 4.3**

STORAGE OF PRECURSORS Some plants store the precursors of toxic substances in one type of tissue, such as the epidermis, and store the enzymes that convert those precursors into the active toxin in another tissue, such as the mesophyll. When an herbivore chews part of the plant, cells are ruptured, the enzymes come into contact with the precursors, and the toxin is produced. The only part of the plant that is damaged by the toxin is that which was already damaged by the herbivore. Plants such as sorghum and some legumes, which respond to herbivory by having molecules that produce cyanide when ingested by animals, are among those that use this type of protective measure. Cyanide is a potent inhibitor of cellular respiration, and when people eat such plants, they first cook them or otherwise prepare them (e.g., soaking, fermenting, drying) to inactivate the cyanide-producing molecules.

MODIFIED PROTEINS Some plants have modified proteins that do not react with the toxin. As noted above, canavanine resembles arginine and therefore plays havoc with protein synthesis in insect larvae. In plants that make canavanine, the enzyme that catalyzes bond formation between arginine and its counterpart tRNA molecule discriminates correctly between arginine and canavanine, so canavanine is not incorporated into the plant's proteins.

Plants don't always mount a successful defense

Milkweeds such as *Asclepias syriaca* store their defensive chemicals in latex in specialized tubes called **laticifers**, which run alongside the veins in the leaves. When damaged, a milkweed releases copious amounts of toxic latex from its laticifers. Field

studies have shown that most insects that feed on neighboring plants of other species do not attack laticiferous plants, but there are exceptions. One population of beetles that feeds on *A. syriaca* exhibits a remarkable prefeeding behavior: these beetles cut a few veins in the leaves before settling down to dine. Cutting the veins causes massive latex leakage from the adjacent laticifers and interrupts the latex supply to a downstream portion of the leaf. The beetles then move to the relatively latex-free portion and eat their fill.

Latex from laticifer

This is just one of many ways that herbivores circumvent plant defenses. A successful plant defense exerts strong selection pressure on herbivores to get around it somehow; a successful herbivore, in turn, exerts strong selection pressure on plants to develop new defensive strategies. One can imagine, for example, that over time *A. syriaca* might evolve to have thicker walls around the base of its laticifers, such that the beetles can no longer cut them, or to produce a different toxin that does not depend on laticifers.

LINK

You can find more examples of the "evolutionary arms race" between plants and herbivores in **Concept 43.4**; see especially **Figures 43.10 and 43.11**

CHECKpoint   CONCEPT 28.2

✓ Using a plant growing near you as an example, describe anatomical features that help plants avoid herbivores.

✓ A mutant strain of a plant makes jasmonate constitutively. What would be the herbivory defense phenotype of this plant?

✓ You have isolated a secondary metabolite from apple tree leaves. What circumstantial and experimental evidence would you use to show that the metabolite prevents the herbivorous larva of the moth *Spilonota ocellana* from damaging apple orchards?

In addition to coping with their biological enemies, plants must survive in their physical environment. Plants have a number of responses that allow them to cope with stressful environmental conditions.

Plants Adapt to Environmental Stresses

In an ever-changing environment, plants face several potential stressors: drought, submersion, heat, cold, and high concentrations of salt and heavy metals in the soil. Here we will focus on the overall mechanisms by which plants deal with extremes of climate and soil conditions. You will see that in these cases, as with defenses against pathogens and herbivores, there are constitutive defenses as well as induced responses.

Go to MEDIA CLIP 28.1
Leaves for Every Environment
PoL2e.com/mc28.1

Some plants have special adaptations to live in very dry conditions

Many plants, especially those living in deserts, must cope with extremely limited water supplies. A variety of anatomical and life-cycle adaptations allow plants to survive under these conditions. Many of these adaptations are ways to avoid or reduce the inevitable water loss through transpiration that occurs during active photosynthesis (see Concept 25.3). Other adaptations help plants tolerate the high levels of light and heat that are often found in deserts.

DROUGHT AVOIDERS   Some desert plants have no special structural adaptations for water conservation. Instead, these desert annuals, called drought avoiders, simply evade periods of drought. Drought avoiders carry out their entire life cycle—from seed to seed—during a brief period in which rainfall has made the surrounding desert soil sufficiently moist for growth and reproduction (**FIGURE 28.6**). A different drought avoidance strategy is seen in deciduous perennial plants, particularly in

FIGURE 28.6 Desert Annuals Avoid Drought   The seeds of many desert annuals lie dormant for long periods, awaiting conditions appropriate for germination. When they do receive enough moisture to germinate, they grow and reproduce rapidly before the short wet season ends. During the long dry spells, only dormant seeds remain alive.

Africa and South America, that shed their leaves in response to drought as a way to conserve water. These plants remain dormant until conditions are again favorable for growth.

LEAF STRUCTURES Most desert plants are not drought avoiders, but rather grow in their dry environment year-round. Plants adapted to dry environments are called **xerophytes** (Greek *xeros*, "dry"). Three structural adaptations are found in the leaves of many xerophytes:

- Specialized leaf anatomy that reduces water loss
- A thick cuticle and a profusion of trichomes over the leaf epidermis, which retard water loss
- Trichomes that diffract and diffuse sunlight, thereby decreasing the intensity of light impinging on the leaves and the risk of damage to the photosynthetic apparatus by excess light

In some xerophytes, the stomata are strategically located in sunken cavities below the leaf surface (known as stomatal crypts), where they are sheltered from the drying effects of air currents (**FIGURE 28.7**). Trichomes surrounding the stomata slow air currents further. Cacti and similar plants have spines rather than typical leaves, and photosynthesis is confined to the fleshy stems (see Figure 24.13D). The spines may help the plants cope with desert conditions by reflecting solar radiation or by dissipating heat. The spines also deter herbivores.

WATER-STORING STRUCTURES Succulence—the possession of fleshy, water-storing leaves or stems—is another adaptation to dry environments (**FIGURE 28.8**). This adaptation allows plants to take up large amounts of water when it is available (such as after a brief thunderstorm) and then draw on the stored water during subsequent dry periods. Other adaptations of succulents include a reduced number of stomata and a variant form of photosynthesis, both of which reduce water loss.

FIGURE 28.8 Succulence *Aloe vera* stores water in its fleshy leaves.

ROOT SYSTEMS THAT MAXIMIZE WATER UPTAKE Roots may also be adapted to dry environments. Cacti have shallow but extensive fibrous root systems that effectively intercept water at the soil surface following even light rains. The tamarugo tree (**FIGURE 28.9**) obtains water through taproots that grow to great depths, reaching water supplies far underground, as well as from condensation on its leaves. The Atacama Desert in northern Chile often goes several years without measurable rainfall, but the landscape there has many surprisingly large shrubs.

SOLUTE ACCUMULATION Xerophytes and other plants that must cope with inadequate water supplies may accumulate high concentrations of the amino acid proline or of secondary metabolites in their vacuoles. This solute accumulation lowers the water potential in the plant's cells below that in the soil, which allows the plant to take up water via osmosis. Plants living in saline environments share this and several other adaptations with xerophytes, as we will see shortly.

> **LINK**
> Review the principles of water potential and water movement in **Concept 25.3**

FIGURE 28.7 Stomatal Crypts Stomata in the leaves of some xerophytes, in this case oleander (*Nerium oleander*), are located in sunken cavities called stomatal crypts. The trichomes (hairs) covering these crypts trap moist air.
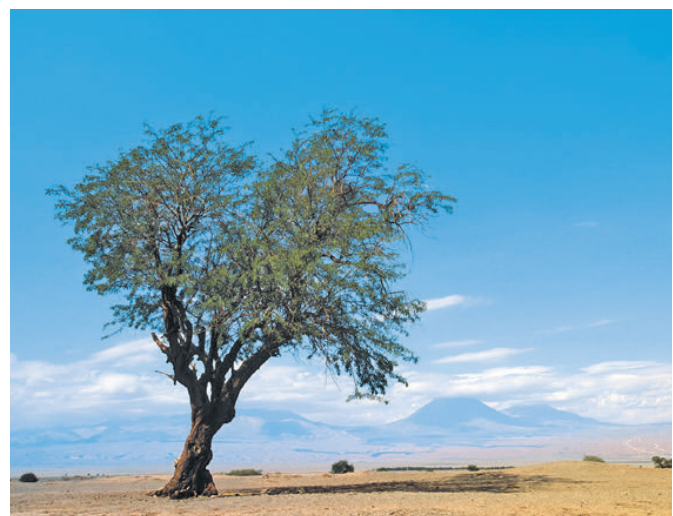
FIGURE 28.9 Mining Water with Deep Taproots In the Atacama Desert in Chile, the roots of this tamarugo tree (*Prosopis tamarugo*) must grow far beneath the soil surface to reach water.

Some plants grow in saturated soils

For some plants, the environmental challenge is the opposite of that faced by xerophytes: too much water. They live in environments so wet that the diffusion of oxygen to their roots is severely limited. These plants have shallow root systems that grow slowly; oxygen levels are likely to be highest near the surface of the soil, and slow growth decreases the roots' need for oxygen.

The root systems of some plants adapted to swampy environments, such as coastal mangrove habitats, have **pneumatophores**, which are extensions that grow out of the water and up into the air (**FIGURE 28.10A**). Pneumatophores contain lenticels (openings) that allow oxygen to diffuse through them, aerating the submerged parts of the root system.

Many submerged or partly submerged aquatic plants have large air spaces in the leaf and stem parenchyma and in the petioles. Tissue containing such air spaces is called **aerenchyma** (**FIGURE 28.10B**). Aerenchyma stores oxygen produced by photosynthesis and permits its ready diffusion to parts of the plant where it is needed for cellular respiration. Aerenchyma also imparts buoyancy. Furthermore, because aerenchyma contains far fewer cells than most other plant tissues, metabolism in aerenchyma proceeds at a lower rate, so the need for oxygen is much reduced.

Plants can respond to drought stress

The adaptations of xerophytes for coping with dry environments are generally constitutive—they are always present—and under normal conditions they prevent the plants from experiencing drought stress. When conditions become so dry that even xerophytes are stressed, the plants turn to inducible responses. The same responses are found in many other plants, including those that are not adapted to grow in dry climates.

When the weather is abnormally dry, the water content of the soil is reduced, and less water is available to plants. If a plant cannot take up water from the soil, it cannot grow. Indeed, inadequate water supply is the single most important factor that limits production of our most important food crops. Extreme water deficits in plant cells have two additional major biochemical effects: a reduction in membrane integrity as the polar–nonpolar forces that orient the lipid bilayer are reduced, and changes in the three-dimensional structures of proteins. A plant can suffer irreversible damage when the structure of its cells is compromised in these ways.

When plants sense a water deficit in their roots, a signaling pathway is set in motion that initiates several measures to conserve water and maintain cellular integrity. This pathway begins with the production of the hormone abscisic acid (see Concept 26.3) in the roots. This hormone travels from the roots to the shoot, where it causes stomatal closure and initiates gene transcription that leads to other physiological events that conserve water and cellular integrity (**FIGURE 28.11**).

Many plant genes whose expression is altered by drought stress have been identified, largely through research using DNA microarrays, proteomics, and other molecular approaches (see Chapters 12 and 13). One group of proteins in which production is upregulated during drought stress is the *l*ate *e*mbryogenesis *a*bundant (LEA; pronounced "lee-yuh") proteins. These hydrophobic proteins also accumulate in maturing seeds as they dry out (hence their name). The LEA proteins bind to membrane proteins and other cellular proteins to stabilize them, preventing them from clumping together as seeds dry out.

FIGURE 28.10 Plant Adaptations to Water-Saturated Habitats
(A) The submerged roots of mangrove trees obtain oxygen through pneumatophores. (B) This cross section of a petiole of the yellow water lily (*Nymphaea mexicana*) shows the air-filled channels of aerenchyma tissue.

(A)

Pneumatophores are root extensions that grow out of the water, under which the rest of the roots are submerged.

(B)

Cells obtain oxygen through projections into the open channels of air-filled aerenchyma tissue.

Open channel

Vascular bundle

75 µm

3 Abscisic acid causes the stomata to close, conserving water in leaves.

LEA proteins

Transcription factor

Transcription

DNA

Abscisic acid

4 Abscisic acid binds to a transcription factor to upregulate expression of genes coding for LEA proteins, which stabilize other proteins.

2 Abscisic acid travels through the xylem to the leaves.

1 Drought stress causes an increase in abscisic acid.

FIGURE 28.11 A Signaling Pathway in Response to Drought Stress Acclimation to drought stress begins in the root with the production of the hormone abscisic acid.

Plants can cope with temperature extremes

Temperatures that are too high or too low can stress plants and even kill them. Plant species differ in their sensitivity to heat and cold, but all plants have their limits. Any temperature extreme can damage cellular membranes:

- High temperatures destabilize membranes and denature many proteins, especially some of the enzymes of photosynthesis.
- Low temperatures cause membranes to lose their fluidity and alter their permeabilities to solutes.
- Freezing temperatures may cause ice crystals to form, damaging membranes.

Plants have both constitutive defenses and inducible responses for coping with temperature extremes.

ANATOMICAL ADAPTATIONS   Many plants living in hot environments have constitutive defenses similar to those of xerophytes. These adaptations include hairs and spines that dissipate heat and leaf forms that intercept less direct sunlight.

HEAT SHOCK RESPONSE   The plant inducible response to heat stress is similar to the response to drought stress in that new proteins are made, often under the direction of an abscisic acid–mediated signaling pathway. Within minutes of experimental exposure to raised temperatures (typically a 5°C–10°C increase), plants synthesize several kinds of **heat shock proteins**. Among these proteins are chaperonins, which help other proteins maintain their structures and avoid denaturation.

Threshold temperatures for the production of heat shock proteins vary, but 39°C is sufficient to induce them in most plants.

COLD-HARDENING   Low temperatures above the freezing point can cause chilling injury in many plants, including crops such as rice, corn, and cotton as well as tropical plants such as bananas. Many plant species can adjust to cooler temperatures through a process called **cold-hardening**, which requires repeated exposure to cool temperatures over many days. A key change during the hardening process is an increase in the proportion of unsaturated fatty acids in cell membranes, which allows them to retain their fluidity and function normally at cooler temperatures (see Figure 2.12). Plants have a greater ability to modify the degree of saturation of their membrane lipids than animals do. In addition, low temperatures induce the formation of proteins similar to the LEA proteins related to drought stress and heat shock, which protect against chilling injury (see Figure 28.11).

If ice crystals form within plant cells, they can kill the cells by puncturing organelles and cell membranes. Furthermore, the growth of ice crystals outside the cells can draw water from the cells and dehydrate them. Freeze-tolerant plants have a variety of adaptations to cope with these problems, including the production of antifreeze proteins that slow the growth of ice crystals.

Some plants can tolerate soils with high salt concentrations

Salty, or saline, environments (high in Na^+, K^+, Ca^{2+}, and Cl^-) are found in nature in diverse locales, from hot, dry deserts to moist, cool coastal marshes. Much of the land in Australia is naturally saline. In addition, agricultural land can become increasingly saline as a result of irrigation and the application of chemical fertilizers. This salinization, which can eventually make land unsuitable for farming, is an increasing problem worldwide (**FIGURE 28.12**).

FIGURE 28.12 Salty Soil   Accumulation of salt from irrigation water in an area with inadequate drainage has caused this soil in central California (San Joaquin Valley) to become unsuitable for most plant growth.

APPLY THE CONCEPT

Plants adapt to environmental stresses

The *Arabidopsis* gene *cor15a* is under the control of a promoter that responds to environmental conditions. *Arabidopsis* plants were genetically modified with a copy of the *cor15a* promoter fused to a reporter gene that is expressed as an enzyme that is readily detected in leaf extracts (see Concept 13.2, p. 260 for information about the use of reporter genes to study gene expression). The genetically modified plants were transferred to environments kept at two different temperatures (19°C and 2°C), and the reporter enzyme activity in their leaves was measured at different times after the transfer. The results are shown in the table.[a]

HOURS AFTER TRANSFER	ENZYME ACTIVITY (UNITS/g LEAF PROTEIN)	
	19°C	2°C
12	0.35	3.21
24	0.51	5.66
36	0.45	9.65
48	0.60	10.10
72	0.49	11.33

1. Plot these data with hours after transfer on the *x* axis and enzyme activity on the *y* axis. What can you conclude about the role of *cor15a*?

2. In a separate experiment, plants were kept at 19°C for 36 hours in the presence of abscisic acid, and the enzyme activity was 8.99. What can you conclude from this result?

3. How would you investigate the possible role of *cor15a* in the plant's response to drought? Why would you expect that there might be such a role?

[a]S. S. Baker et al. 1994. *Plant Molecular Biology* 24: 701–713.

Because of its high salt concentration, a saline environment has a very negative water potential. To obtain water from such an environment, a plant must have an even more negative water potential (see Concept 25.3); otherwise water will diffuse out of its cells, and the plant will wilt and die. Plants in saline environments are also challenged by the potential toxicity of sodium ions, which inhibit enzymes and protein synthesis.

Plants that are adapted for survival in saline soils are called **halophytes**. Most halophytes take up Na^+, and many take up Cl^-, into their roots and transport those ions to their leaves, where they accumulate in the central vacuoles of leaf cells, away from more sensitive parts of the cells. The accumulated salts in the tissues of halophytes make their water potential more negative than the soil solution and allow them to take up water from their saline environment.

Some halophytes have **salt glands** in their leaves. These glands excrete salt, which collects on the leaf surface until it is removed by rain or wind (**FIGURE 28.13**). This adaptation, which reduces the danger of poisoning by accumulated salt, is found in some desert plants and in some plants growing in mangrove habitats. The negative water potential in the salt-laden leaves also promotes water flow from the roots up through the xylem by transpiration–cohesion–tension (see Concept 25.3).

Some plants can tolerate heavy metals

High concentrations of heavy metal ions are toxic to most plants. Some soils are naturally rich in heavy metals as a result of normal geological processes or acid rain. The mining of metallic ores also leaves localized areas with high concentrations of heavy metals and low concentrations of nutrients. Such sites are hostile to most plants, and seeds falling on them generally do not produce adult plants.

Some plants can survive in these environments, however, by accumulating concentrations of heavy metals that would kill most plants. More than 200 plant species have been identified as **hyperaccumulators** that store large quantities of metals such as arsenic (As), cadmium (Cd), nickel (Ni), aluminum (Al), and zinc (Zn).

Perhaps the best-studied hyperaccumulator is alpine pennycress (*Thlaspi caerulescens*). Before the advent of chemical analysis, miners used the presence of this plant as an indicator of mineral-rich deposits. A *Thlaspi* plant may accumulate as much as 30 g/kg dry weight Zn (most plants contain 0.1 g/kg dry weight) and 1.5 g/kg dry weight Cd (most plants contain 0.001 g/kg dry weight). Studies of *Thlaspi* and other hyperaccumulators have revealed the presence of several common adaptations:

- Increased ion transport into the roots

- Increased rates of translocation of ions to the leaves

FIGURE 28.13 Excreting Salt This saltwater mangrove plant has specialized glands that excrete salt, which appears here as crystals on the leaves.

FIGURE 28.14 Phytoremediation   Plants that accumulate heavy metals can be used to clean up contaminated soils. Here, poplars are being used to remove contaminants from an air base.

• Accumulation of ions in vacuoles in the shoot

• Resistance to the ions' toxicity

Knowledge of these hyperaccumulation mechanisms and the genes underlying them has led to the emergence of **phytoremediation**, a form of bioremediation (see Chapter 13, p. 271) that uses plants to clean up environmental pollution in soils. Some phytoremediation projects use natural hyperaccumulators, whereas others use genes from hyperaccumulators to create transgenic plants that grow more rapidly in and are better adapted to a particular polluted environment. In either case, the plants are grown in the contaminated soil, where they act as natural "vacuum cleaners" by taking up the contaminants (**FIGURE 28.14**). The plants are then harvested and safely disposed of to remove the contaminants. Perhaps the most dramatic use of phytoremediation occurred after an accident at the nuclear power plant at Chernobyl, Ukraine (then part of the Soviet Union), in 1986, when sunflower plants were used to remove uranium from the nearby soil. Phytoremediation is now widely used to clean up land after strip mining.

CHECKpoint   CONCEPT 28.3

✓ Compare the constitutive and induced mechanisms that allow plants to cope with drought conditions.

✓ Describe a mechanism shared by plants that tolerate high concentrations of salts and those that tolerate heavy metals.

✓ If an inhibitor of abscisic acid synthesis were sprayed on a plant and the plant was exposed to drought conditions, what would happen?

Q   How can knowledge of plant and fungal biology be used to prevent the spread of wheat rust?

ANSWER   Today, *Puccinia graminis* strain Ug99 continues its spread and threatens wheat crops worldwide. In the Green Revolution of the 1960s to 1980s, wheat plants were bred to have the gene complexes *Sr24* and *Sr31*, *R* genes that conferred resistance to existing strains of wheat rust fungus (Concept 28.1). The first strain of Ug99 found in Uganda had *Avr* genes that form elicitor proteins that do not bind to *Sr31* and therefore overcome part of the plant's resistance. Then, in 2006 a new genetic variant of Ug99 was found in Kenya with additional *Avr* genes that allow the pathogen to overcome the *Sr24* gene resistance as well (**FIGURE 28.15**).

Because 90 percent of the wheat grown in the world has no resistance to this new strain of Ug99, an intensive search is under way for additional wheat resistance genes. In the regions where Ug99 infections are now present, some wheat plants grow that are resistant. Samples of both wheat plants and fungus are sent to laboratories, where, under high security and sterility, they are tested and examined for *Avr* and *R* genes. In addition, seeds from thousands of varieties of wheat, collected from all over the world, are being grown into seedlings and examined for *R* genes.

Wheat stem

This lesion was caused by a variant of Ug99 that overcomes the wheat plant's resistance.

These lesions were caused by a variant of Ug99 wheat rust fungus for which the wheat plant has resistance.
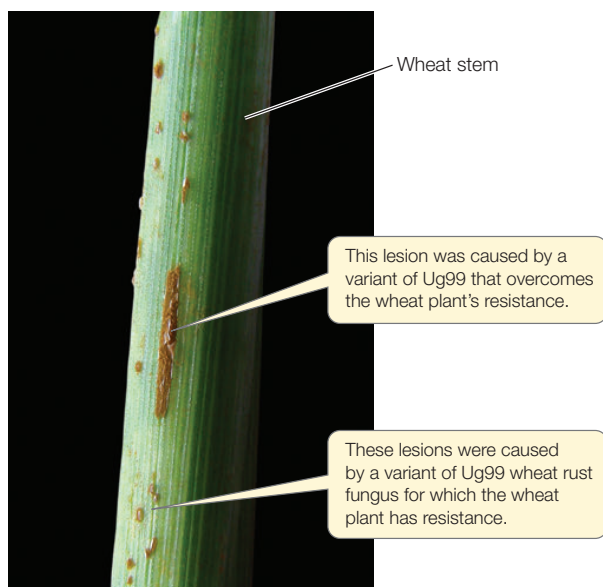
FIGURE 28.15 Overcoming Resistance to Pathogens Blotches caused by wheat rust are visible on the stem of a wheat plant. This plant has a gene called *Sr24* that confers resistance to the wheat rust pathogen, but it has also been infected by a variant of the pathogen, Ug99, that can overcome that resistance.

SUMMARY

CONCEPT 28.1 Plants Have Constitutive and Induced Responses to Pathogens

- Plants and pathogens have evolved together in a continuing "arms race": pathogens have evolved mechanisms for attacking plants, and plants have evolved mechanisms for defending themselves against those attacks.

- Some of the responses by which plants fight off pathogens are **constitutive**—always present in the plant—whereas others are **induced**—produced in reaction to the presence of a pathogen. **Review Figure 28.1 and ANIMATED TUTORIAL 28.1**

- Plants use physical barriers to block pathogen entry and seal off infected regions.

- **Gene-for-gene resistance** depends on a match between a plant's **resistance (R) genes** and a pathogen's **avirulence (Avr) genes**. **Review Figure 28.2**

- In the induced response to infection, cells produce **phytoalexins** and **pathogenesis-related (PR) proteins**, and the plant isolates the area of infection.

- The **hypersensitive response** (the formation of necrotic lesions) is rapid and localized.

- In **systemic acquired resistance**, salicylic acid activates defense responses throughout the plant.

CONCEPT 28.2 Plants Have Mechanical and Chemical Defenses against Herbivores

- Physical structures such as spines and thick cell walls deter some herbivores.

- Plants produce **secondary metabolites** as defenses against herbivores. **Review Table 28.1 and Figure 28.4**

- Hormones, including **jasmonic acid (jasmonate)**, participate in signaling pathways leading to the production of defensive compounds. **Review Figure 28.5**

- Plants protect themselves against their own toxic defensive chemicals by compartmentalizing those chemicals, by storing their precursors separately, or through modifications of their own proteins.

CONCEPT 28.3 Plants Adapt to Environmental Stresses

- **Xerophytes** are plants adapted to dry environments. Their structural adaptations include thickened cuticles, specialized trichomes, stomatal crypts, **succulence**, and long taproots. **Review Figure 28.7**

- Some plants accumulate solutes in their cells, which lowers their water potential so they can more easily take up water.

- Adaptations to water-saturated habitats include **pneumatophores**, extensions of roots that allow oxygen uptake from the air, and **aerenchyma**, tissue in which oxygen can be stored and can diffuse throughout the plant. **Review Figure 28.10**

- A signaling pathway involving abscisic acid initiates a plant's response to drought stress. **Review Figure 28.11**

- Plants respond to high temperatures by producing **heat shock proteins**. Low temperatures can result in **cold-hardening**.

- Plants that are adapted for survival in saline soils are called **halophytes**. Most halophytes accumulate salt. Some have **salt glands** that excrete salt to the leaf surface.

- Some plants living in soils that are rich in heavy metals are **hyperaccumulators** that take up and store large amounts of those metals in their tissues.

- **Phytoremediation** is the use of hyperaccumulating plants or their genes to clean up environmental pollution in soils.

See **ACTIVITY 28.1** for a concept review of this chapter.

[QR code] **Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is28**

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PART 6
Animal Form and Function

29

Fundamentals of Animal Function

A man exercises on a treadmill wearing a device that measures his rate of O_2 consumption. His speed can be controlled by adjusting the speed of the treadmill.

Animals have muscles and are able to move. This man on a treadmill provides a dramatic illustration as he uses his leg muscles to propel himself forward. His ancient ancestors did much the same thing to pursue prey and escape dangers. Today investigators are studying the man's exercise performance on a treadmill, where his speed of running can be controlled by adjusting the speed of the treadmill. As the surface of the treadmill moves backward, driven by an electric motor, the man has to run forward at the same speed if he is to avoid being carried backward and dumped on the floor.

Treadmills have been used to study many questions in animal biology. Chimpanzees, for example, can be trained to run on a treadmill on four legs or on only two legs. Then their abilities to run in both ways can be compared to learn about advantages and disadvantages of two-legged and four-legged running.

Studies of this kind help us better understand why humans became two-legged early in their evolution.

The man in the photo is breathing from a device that is measuring his rate of oxygen (O_2) consumption. From that information, investigators will be able to calculate the energy cost of his exercise.

One way to rate the efficiency of animal locomotion is to measure the energy cost to cover a certain distance. From measures of O_2 consumption on treadmills, for example, we know that a person expends about 300 kilojoules (70 kilocalories) per kilometer when jogging at a speed of 11 kilometers per hour.

The energy costs for birds to fly and for fish to swim can be measured in similar ways. Birds have been trained to fly in wind tunnels, and fish have been coaxed to swim in water tunnels. Then their O_2 consumption has been measured as they fly or swim.

Believe it or not, birds flying and fish swimming can cover distance much more cheaply—in terms of energy used—than mammals running. This may help explain why long-distance annual migrations have evolved principally in birds and fish rather than in mammals.

We humans have much higher costs to cover distance when swimming than fish do, in part because of the difference between swimming at the surface and swimming underwater. A person on a bicycle covers distance with roughly the same energy efficiency as a human-size fish swimming. So, to get a subjective sense of a fish's energy cost of covering distance, hop on a bicycle!

Q Why can we use a person's rate of O_2 consumption to measure the rate at which he or she consumes energy to run?

Animals Eat to Obtain Energy and Chemical Building Blocks

Animals are **heterotrophs**—organisms that require preformed organic molecules as food (see Concept 45.3). They obtain their energy by breaking the chemical bonds of organic compounds obtained from other organisms, and they build their tissues from preexisting organic compounds obtained from other organisms. Animals, in other words, eat organic matter, such as starch or fat, that other organisms synthesized, and they use that organic matter as their source of both energy and chemical building blocks.

In contrast, **autotrophs** obtain energy from inorganic sources and can synthesize organic compounds from inorganic precursors. Plants are examples of autotrophs. They obtain energy from sunlight and synthesize organic compounds, such as the sugar glucose, principally from H_2O and CO_2.

In most ecosystems, sunlight is the primary energy input. Plants and algae use some of the light energy in sunlight to carry out photosynthesis and build organic compounds from simple precursors. In the process, a small fraction of the light energy in sunlight is incorporated into the chemical bonds of the organic compounds that plants and algae make. Animals then ingest the organic compounds in the plant or algal material and use them as their sources of energy and chemical building blocks.

> **LINK**
> The flow of energy through ecological communities is discussed in **Concept 44.3**

Animals need chemical building blocks to grow and to replace chemical constituents throughout life

Why does an animal need the chemical building blocks it obtains by eating? One reason is growth. When an animal grows during its early development, it requires chemical building blocks—such as fatty acids and amino acids—to build each new cell it adds to its body.

Even after they are fully grown, animals need chemical building blocks throughout their lives. This important fact was discovered by using isotopic forms of carbon atoms and nitrogen atoms (see Concept 2.1 for a discussion of isotopes). Suppose you make some food in which the nitrogen atoms are nitrogen-15 instead of the usual isotope, nitrogen-14. Suppose, then, that you feed that food to a full-grown dog or other animal. After a few weeks you will find that many of the nitrogen-14 atoms in the dog's body have been replaced with nitrogen-15 atoms—even though the dog looks no different. If you then start to feed the dog regular food (with nitrogen-14 atoms) again, you will find that the nitrogen-15 atoms in the dog's body are gradually replaced with nitrogen-14 atoms.

Experiments such as this demonstrate that the atoms inside an adult animal's body are constantly exchanged with atoms in the animal's surrounding environment. For example, our red blood cells live for only about 4 months. When a red blood cell is at the end of its life span, it is broken down and replaced. As it breaks down, some of its constituents are excreted. For example, some of the iron from the cell is excreted. To replace the cell, our bodies need to get replacement constituents—such as replacement iron—from our environment.

Nearly all the cells in our body are engaged in the process of breakdown and replacement (although not necessarily on a 4-month schedule). As the process takes place, some atoms originally inside our body are lost, and some atoms are taken in from the environment. In humans, 2–3 percent of body protein is broken down and rebuilt every day! In the process, some of the amino acids in the initial proteins are lost and must be replaced. For this reason, we need to eat amino acid–containing foods all our lives, even after we are fully grown.

We have seen that individual atoms constantly come and go in an animal. Over time, therefore, an animal is not defined by its atomic building blocks. Instead it is defined by the organization of its body.

Animals need inputs of chemical-bond energy to maintain their organized state throughout life

Organization is the most essential attribute of life. Animals are organized at multiple levels. In individual cells, atoms are organized into molecules such as phospholipids and proteins. In turn, these individual molecules are organized into cellular structures such as the cell membrane and into cellular biochemical processes such as sequences of enzyme-catalyzed reactions.

Organization is also evident in animals at the level of the organism, in the ways cells relate to each other in tissues, organs, and multi-organ systems. Consider the structure of an individual tissue such as the retina of the vertebrate eye. In each part of the retina, individual nerve cells are highly organized in relation to each other (**FIGURE 29.1**), and this structural organization among cells is essential for vision. Another type of organization at the organismal level is the interaction of tissues and organs to form systems of organs that work together. A large set of organs—including the stomach, intestines, pancreas, and brain—must interact in an organized, coordinated way to carry out digestion, for instance (we will return to these topics in greater detail in Concept 29.4).

Recall the second law of thermodynamics, which tells us that, left to itself, any organized system tends to lose organization and become more random as time passes. Animals must combat this tendency because any loss of organization in an animal's body threatens the animal's well-being or even life itself.

> **LINK**
> You can review the laws of thermodynamics in **Concept 2.5**

For biologists, the best definition of **energy** is that it is the capacity to create or maintain organization. In essence, the reason animals need to obtain energy is so they can do work (of several types) to maintain their organization by combating the effects of the second law of thermodynamics.

To fully understand the need for energy, we need to recognize that energy exists in several forms, and that only some

Light

Retina

These cells sense light.

These cell layers process visual information.

These cells send visual information to the brain.
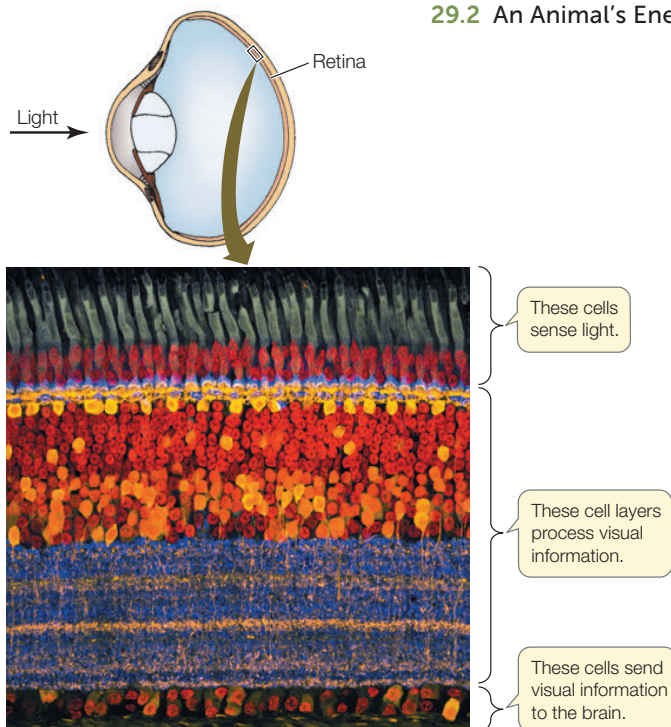
FIGURE 29.1 Highly Organized Cells in the Retina of a Chick's Eye In this highly magnified image of a chick's retina, the differently colored layers are different types of cells. The cells in the top layer are the rods and cones responsible for light sensing, and the layers of cells beneath are responsible for successive steps of image processing in the retina before visual information is sent to the brain.

forms can do work. In living organisms, heat is a form of energy that is unable to do work. To do work, animals need chemical-bond energy, also known as chemical energy. Moreover, when animals use chemical energy to do work, they convert that energy to heat, which they are unable to convert back to chemical energy. These principles explain why animals need to eat to obtain new chemical energy from their foods throughout their lives. As animals use chemical energy to do work, they convert it to heat. Thus they continually need more chemical energy, which they get by ingesting organic molecules that they can break down.

CHECKpoint   CONCEPT 29.1

✓ From what sources do autotrophs obtain chemical energy and chemical building blocks?

✓ Why is it necessary for animals to continue gathering chemical building blocks even after they've reached their full adult sizes?

✓ In what form does energy enter a heterotroph's body, and in what form does the majority of that energy inevitably leave?

Animals vary tremendously in how large their energy needs are. Among animals of any particular body size, some need 10 or even 50 times as much energy as others. Next we will discuss some of the reasons for this.

How much energy does an animal need? This is a complicated question because animals use energy for many different purposes. Every cell and tissue in an animal's body uses chemical energy every day to maintain its own internal organized state. Cells and tissues also use energy to do additional types of physiological work. When animals run, for example, their skeletal muscles use energy to generate mechanical forces for locomotion. An animal's heart muscle uses energy to pump blood. After a meal, the digestive tract uses energy to synthesize digestive enzymes and propel the ingested food through the gut. In this concept we look at how energy use is measured and at two major factors that determine an animal's total rate of energy use.

We quantify an animal's metabolic rate by measuring heat production or O_2 consumption

The word "consumed" is used in more than one way in studying animals. One of its most important uses is in discussing energy. When we say energy is "consumed" by an animal, we mean the energy is converted to heat. Energy cannot be destroyed. However, whereas chemical energy can do physiological work, heat cannot. For this reason, the conversion of chemical energy to heat has a huge consequence: the energy loses its ability to do work for the organism. This is why biologists say that energy converted to heat is "consumed" or used up.

An animal's **metabolic rate** is defined as its rate of energy consumption—in other words, the rate at which it consumes chemical energy and converts it to heat. Why are metabolic rates important? The main reason is that when energy is consumed, it needs to be replaced. An animal with a high metabolic rate needs to find and eat a lot of food per unit of time to replace the energy it is consuming. Animals with lower metabolic rates have lower food needs. All living animals have measurable metabolic rates and are found to produce heat when measurements are done with sensitive instruments. Even those animals that do not feel warm to the touch, such as frogs or earthworms, are producing heat. They do not warm up simply because they are losing heat as fast as they produce it.

How can we quantify an animal's metabolic rate? Because consumed energy becomes heat, one way is to measure an animal's rate of heat production. But measuring heat production directly is difficult, so biologists usually take advantage of a simple relationship. When organic matter is oxidized during aerobic metabolism, O_2 is used as heat is made (see Concept 6.2):

$$\text{Organic compound} + O_2 \rightarrow CO_2 + H_2O + \text{heat}$$
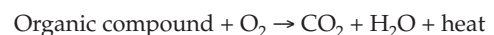
There is an approximately one-to-one relationship between the rate at which O_2 is used and the rate at which heat is produced. To quantify an animal's metabolic rate, therefore, we can measure its rate of O_2 use. Biologists nearly always use this method to quantify metabolic rates. The rate of O_2 use is usually called the rate of O_2 consumption. Note that in this case "consumption" refers to the combination of O_2 with other atoms. Thus

(A) Humans
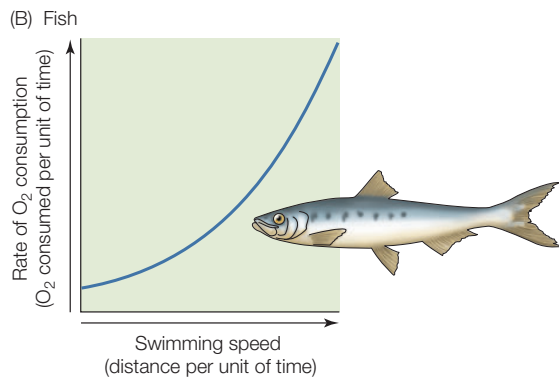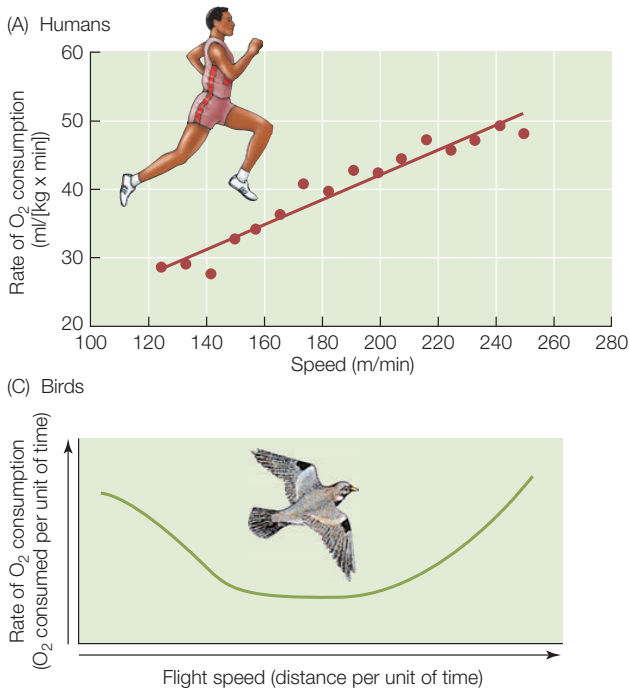
(B) Fish

(C) Birds

FIGURE 29.2 Cost of Exercise Rate of O_2 consumption as a function of forward speed for (A) people running, (B) fish swimming, and (C) birds flying.

"consumption" is being used in a different way than when we talk about energy consumption.

Physical activity increases an animal's metabolic rate

Physical activity often exerts a strong effect on an animal's metabolic rate. As a general rule, when people and other vertebrates engage in sustained exercise, their metabolic rate increases about tenfold between rest and all-out exertion. **FIGURE 29.2A** shows the results of a treadmill test—like the one we discussed at the chapter's start—on several people. When people run, their metabolic rate increases linearly with their speed. This is the usual relationship when animals cover distance by running or walking.

The relationship between speed and metabolic rate is different for animals that swim or fly. When fish swim, their metabolic rate increases exponentially with their speed because the resistance posed by the water increases exponentially with speed (**FIGURE 29.2B**). Birds show a U-shaped relationship between metabolic rate and speed (**FIGURE 29.2C**). At low speeds, a bird must maintain a high metabolic rate just to stay airborne. As it speeds up, its metabolic rate decreases because flight is

---

APPLY THE CONCEPT

An animal's energy needs depend on physical activity and body size

The graph shows the rate of energy consumption—energy cost per unit of time—of a flying parakeet as a function of its horizontal flight speed.[a] This graph can be used to quantify the energy cost per unit of distance. For assessing the efficiency of our cars, we often focus on miles per gallon. In other words, we focus on how far we can go per unit of energy used. In the graph for the bird, each dot shows the energy cost per unit of time (in kilojoules [kJ] per hour) at a particular speed (in kilometers per hour). Notice that if you divide speed in kilometers per hour by cost in kilojoules per hour, your result will be in kilometers per kilojoule:

$$\frac{km}{hr} \div \frac{kJ}{hr} = \frac{km}{hr} \times \frac{hr}{kJ} = \frac{km}{kJ}$$

In other words, your result will tell you how many kilometers a parakeet can travel for each kilojoule of energy it uses. This is a very similar concept to miles per gallon!

1. Calculate the value of kilometers per kilojoule for each of the eight dots on the graph.

2. Based on your answer to question 1, what is the best speed for the bird to fly at to cover as much distance as possible per unit of energy used?

[a]Tucker, V. A. 1968. *J. Exp. Biol.* 48: 67–87.
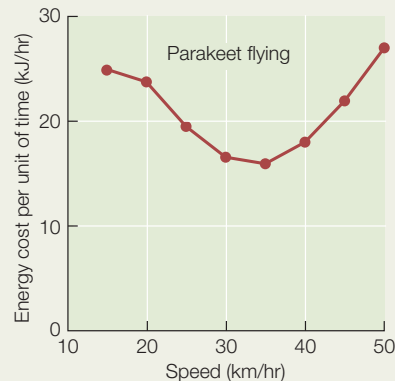
aided by the rapid flow of air over the wings. As the bird flies faster, however, its metabolic rate rises again, because flying at a high speed requires more effort than flying at a medium speed. Airplanes exhibit a similar type of relationship between their rate of energy consumption and speed.

Among related animals, metabolic rate usually varies in a regular way with body size

Species of terrestrial mammals vary in adult body size from about 20 grams in some mice (or even as small as 2 g in some shrews) to more than 5,000 kilograms (5,000,000 g) in elephants. When we look at related animals of widely different body sizes, do their metabolic rates vary in any particular way with their sizes?

To answer this question, we need to measure the metabolic rates of various species under standardized conditions. To standardize the conditions when studying mammals, investigators typically measure the metabolic rates of animals that are in a comfortable thermal environment and resting—and that have not eaten in the recent past. These measurements are called **basal metabolic rates** or **BMR**s.

The simplest way to compare the BMRs of mammals of different sizes is to express the rates per unit of body weight. To do this, we take the BMR for each animal and divide it by the animal's body weight to obtain BMR per gram, or BMR/g.

You might expect that BMR/g would simply be the same in all terrestrial mammals, from mice to elephants, but it isn't. If you start with mice and look at bigger and bigger species of mammals, BMR/g gets lower and lower. The "mouse-to-elephant" curve shows this (**FIGURE 29.3**). BMR/g is almost 20 times higher in a mouse than in an elephant. Relationships of this sort—in which animal characteristics are examined as functions of body size—are called **scaling relationships**.

What are the implications of the scaling relationship between BMR/g and body size in mammals? One thing we can deduce is that small mammals need much more food per gram of body weight than large mammals do—a fact that pet owners and zoo keepers need to keep in mind. Food requirements in relation to body size are also ecologically important. Suppose there are 100 mice and 1 rabbit living in a field or forest. If each mouse weighs 20 g and the rabbit weighs 2,000 g, the mice collectively weigh as much as the rabbit—2,000 g. You might therefore expect that both the mice and the rabbit would eat similar amounts of food each day. However, the mice will in fact eat about three times as much food as the rabbit, because the BMR/g is three times higher in a small mouse than in a medium-size rabbit.
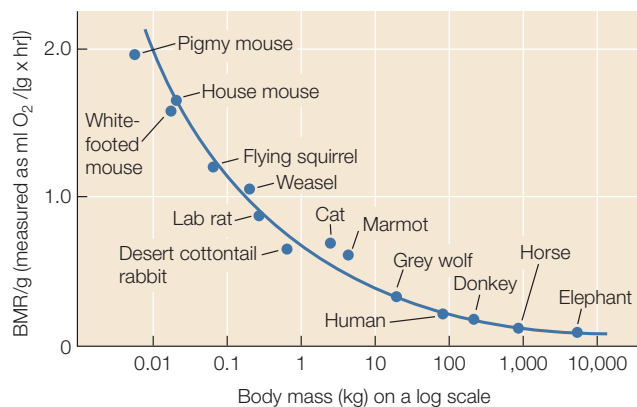
The same type of scaling relationship between metabolic rate per gram and body size (i.e., the same shape as seen in the mouse-to-elephant curve) is seen in almost all types of animals, including crabs, fish, lizards, and birds. Within each group of related species, metabolic rate per gram tends to decrease as body size increases.

> **CHECKpoint** **CONCEPT 29.2**
>
> ✓ Define "consumption" as it relates to energy in biological systems.
>
> ✓ Which is likely to require more food over a given time period, a group of 60 skates, each weighing 1 kg, or a pair of 30-kg sharks? Skates and sharks both belong to the same group of animals, the cartilaginous fish.
>
> ✓ Biologists sometimes quantify metabolic rates by measuring heat production despite the technical challenges of using this method. Why can an animal's metabolic rate be quantified by measuring its rate of heat production?

Physical activity and body size are only two of the factors that influence metabolic rates. Now we will look at some of the others.

> **CONCEPT 29.3** **Metabolic Rates Are Affected by Homeostasis and by Regulation and Conformity**

The cells inside an animal's body are bathed with body fluids called **tissue fluids** or, more formally, **interstitial fluids**. Suppose we ask, what is the environment of cells inside the body? The tissue fluids, which exist around and between cells, are that environment. For this reason, an animal's tissue fluids are sometimes called the animal's **internal environment**, whereas the outside world is the animal's **external environment**.

To see this distinction more clearly, suppose you are standing outside on a cold, dry day. Your external environment will have a low temperature and little moisture. However, inside your body, your body fluids will be warm and wet. The environment of your cells—your body's internal environment—will therefore be warm and wet.

Animals are classed as regulators and conformers

What happens inside an animal when its external environment changes? A discussion of temperature provides an excellent starting point for understanding the answer.

FIGURE 29.3 The Mouse-to-Elephant Curve in Basal Metabolic Rate Basal metabolic rate (measured as the rate of O_2 consumption) per gram of body weight in terrestrial mammals decreases dramatically as body size increases. The *x* axis is a logarithmic plot of body weight.

Some types of animals, such as mammals and birds, maintain a constant internal temperature, much in the way that a house with a furnace and an air conditioner maintains a steady inside temperature. Humans, for example, maintain a constant internal temperature of about 37°C (98.6°F). In these types of animals, if the temperature of the external environment changes, the internal temperature does not change. Such animals are called **regulators** and are said to exhibit regulation. By definition, **regulation** occurs when the internal environment stays constant even as the external environment changes (**FIGURE 29.4A**).

In other types of animals, such as fish and frogs, if the temperature of the external environment changes, the internal temperature changes to match the new external temperature. These animals are called **conformers** and are said to exhibit conformity. By definition, **conformity** occurs when the internal environment varies so that it always matches the external environment (**FIGURE 29.4B**).

The concepts of regulation and conformity can be applied to all characteristics of an animal's internal and external environments, not just temperature. Moreover, an animal that conforms in some characteristics may regulate in others. We've seen, for example, that fish are conformers in regard to temperature. They are regulators, however, in terms of the concentration of sodium (Na^+) ions, symbolized [Na^+], in their tissue fluids. If the sodium concentration of the external water changes, a fish keeps a constant [Na^+] in its tissue fluids, even though it lets its internal temperature change when the external temperature changes.

Regulation is more expensive than conformity

To think further about regulation and conformity, let's contrast a modern house with a simple log cabin without a stove or furnace. In terms of temperature, when we are inside the modern house, we are always comfortable. This happy state of affairs changes if we move to the cabin. In hot weather, we sometimes boil. In cold weather, we sometimes freeze. We also realize, however, that the cabin is not entirely bad. We have no fuel costs for the cabin, whereas we pay steep utility bills for the house. This contrast helps us understand the advantages and disadvantages of regulation and conformity in animals.

Regulation (such as we have in the modern house) provides stability but is energetically expensive. If an animal maintains a constant internal environment, its body cells enjoy constancy in their surroundings. This is the advantage of regulation. However, the animal must expend energy to maintain a constant internal environment when the outside environment varies. Regulation tends to increase an animal's metabolic rate. This is the disadvantage of regulation.

Conformity (such as we experience in the log cabin) does not provide stability but is energetically cheap. If an animal simply lets its internal environment change to match its external environment, the animal need invest no energy in the process. However, its cells must cope with considerable variation in their immediate surroundings.

Homeostasis is a key organizing concept

As the nineteenth century ended and the twentieth century began, physiologists were studying humans and "model"

(A) Temperature regulation

An animal's internal environment may be held constant when its external environment changes…

(B) Temperature conformity

…or the internal environment may be permitted to vary so that it matches the external environment.
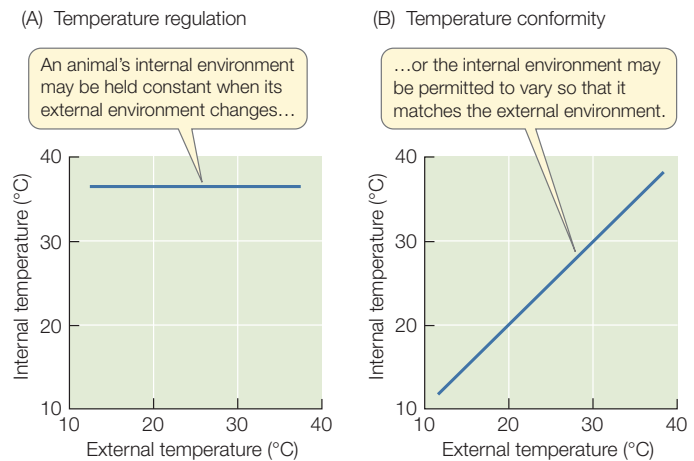
FIGURE 29.4 Regulation versus Conformity   These graphs from the study of temperature illustrate the general principles of (A) regulation and (B) conformity.

nonhuman animals such as dogs used in biomedical research. These investigators gradually realized for the first time that when people are healthy, their blood and tissue fluids are remarkably consistent in their characteristics from time to time. The investigators often focused their studies on the **blood plasma**, which is the blood solution in which the red blood cells and other blood cells are suspended. The investigators discovered that the concentration of glucose ("blood sugar") in a healthy person's blood plasma and tissue fluids is almost constant, whether a meal has just been eaten or not. They likewise discovered that temperature, pH, and the concentrations of major ions are approximately constant in the blood plasma and tissue fluids.

A famous early-twentieth-century physiologist, Walter Cannon, coined the term **homeostasis** to refer to this stability of the internal environment and the mechanisms that maintain the stability. To this day, homeostasis is an exceedingly important organizing concept in medicine, veterinary medicine, and many other fields of biology. The meaning of homeostasis has shifted a little over time; the term is sometimes used today to refer to any sort of stability or constancy in an animal.

Homeostasis, you will recognize, is a very similar concept to regulation. Homeostasis offers advantages, but as you can guess, it is energetically expensive. Accordingly, when we consider the entire animal kingdom, we find that homeostasis is not universal. Animals vary in their degrees of homeostasis.

Animals are classed as homeotherms or poikilotherms based on their thermal relationships with their external environment

Let's focus in greater detail on the temperature relationships of animals. These relationships have major effects on animal metabolic rates, as well as being important in many other ways.

Animals that maintain an approximately constant internal body temperature—such as mammals and birds—are said to exhibit **thermoregulation** and are called **homeotherms**. In most homeotherms, if a resting individual is exposed to a variety of external temperatures, its body temperature remains constant but its metabolic rate varies with external temperature as seen in **FIGURE 29.5**. Over a range of relatively mild external

temperatures, called the **thermoneutral zone** (**TNZ**), the animal's metabolic rate is constant.

At temperatures below the TNZ, a homeotherm's metabolic rate increases as the external temperature falls. This happens for the same reason that the furnace in a house burns fuel faster as the weather outdoors becomes colder. A homeotherm must progressively increase its rate of metabolic heat production as the external temperature becomes progressively colder, in order to offset its progressively increasing rate of heat loss.

At temperatures above the TNZ, a homeotherm's metabolic rate increases as the external temperature rises. This happens for the same reason that the air conditioner in a house works harder as the weather outdoors becomes hotter. As the animal's external temperature becomes progressively warmer, the animal must work progressively harder to keep its body temperature from rising. Its metabolic rate reflects this harder work by rising.

Most animals are not homeotherms, and their relationship between metabolic rate and temperature is different than that of homeotherms. Fish, frogs, sea stars, crayfish, and many other kinds of animals permit their body temperature to match their external temperature. Such animals are called **poikilotherms** or **ectotherms**. These two names reflect two complementary characteristics of these animals: The animals have body temperatures that are variable and that are determined by the external temperature. The prefix *poikilo* means "variable," and *ecto* means "external." The name poikilotherm emphasizes the variability of body temperature in these animals, and the name ectotherm emphasizes the fact that their external temperature determines their body temperature. In this book we favor the term poikilotherm.

An important question about poikilotherms is how high their body temperature can rise—and how low it can fall. Poikilotherms vary widely in their body temperature limits:

Dipsosaurus dorsalis

Some desert lizards and insects can tolerate body temperatures as high as 40–50°C.

Some Antarctic fish and crustaceans, such as krill, can remain fully active at body temperatures as low as –2°C.

Euphausia superba
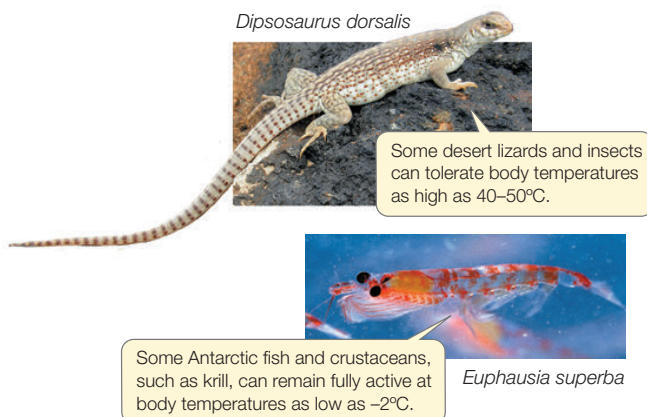
When the external temperature of a poikilotherm rises or falls, the animal's metabolic rate varies approximately exponentially (**FIGURE 29.6A**). The reason for this is that the animal's tissues become cooler or warmer as the external temperature varies. The tissues are cold in a cold environment and warm in a warm environment. Low tissue temperatures slow both biochemical processes (such as enzyme-catalyzed reactions; see Figure 3.22)

Metabolic rate rises as the external temperature falls below the TNZ because keeping the body warm requires increased energy use.

The thermoneutral zone (TNZ) is a range of external temperatures in which metabolic rate is minimal and does not change with external temperature.

Thermo-neutral zone

External temperature

Metabolic rate

Metabolic rate rises as external temperature rises above the TNZ because keeping the body cool requires increased energy use.

FIGURE 29.5 Homeothermy The metabolism–temperature relationship in mammals and birds.

Go to ACTIVITY 29.1 Thermoregulation in a Homeotherm
PoL2e.com/ac29.1

(A)

Metabolic rate

External temperature

(B)

This process's rate triples with each 10°C rise in temperature.

This process's rate doubles with each 10°C rise in temperature.

$(Q_{10} = 2)$

$(Q_{10} = 3)$

$$Q_{10} = \frac{R_T}{R_{T-10}}$$

$(Q_{10} = 1)$

This process is not temperature-sensitive.

Rate of process (arbitrary units)

Tissue temperature (°C)
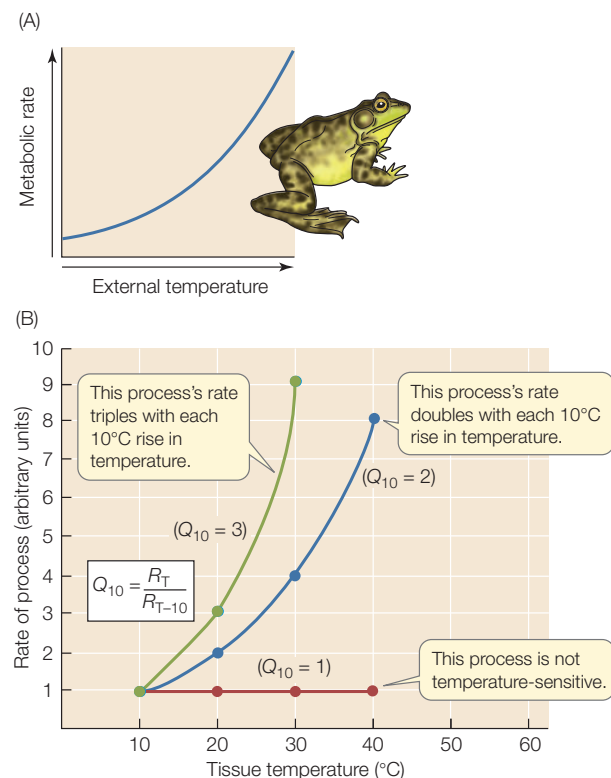
FIGURE 29.6 Poikilothermy and Q_{10} (A) The metabolism–temperature relationship in poikilothermic animals. Internal temperature increases as external temperature increases, and this speeds both biochemical and biophysical processes in the animal's body. (B) Q_{10} is a way to calculate the sensitivity of a rate, such as metabolic rate, to changes in tissue temperature.

and biophysical processes (such as diffusion), thereby slowing metabolism. High tissue temperatures do the opposite.

In a tissue, we can describe the temperature sensitivity of a reaction or process in numerical terms with Q_{10}, a factor that is easy to calculate. We simply divide the rate of the reaction or process at any particular tissue temperature, R_T, by the rate of that reaction or process at a tissue temperature 10°C lower, R_{T-10}:

$$Q_{10} = R_T/R_{T-10}$$

If a reaction or process is not sensitive to tissue temperature, it has a Q_{10} of 1. Most biological Q_{10} values are between 2 and 3 (**FIGURE 29.6B**). A Q_{10} of 2 means the rate of a reaction or process doubles as tissue temperature increases by 10°C; a Q_{10} of 3 means the rate triples. **FIGURE 29.7** uses the Q_{10} concept to help interpret how mud turtles respond to changes in temperature.

Poikilotherms often exert some control over their tissue temperatures by means of behavior. Because a poikilotherm's body temperature is determined by external temperature, the animal can adjust its body temperature by positioning itself in suitable environments (**FIGURE 29.8**). For example, if a poikilotherm's body temperature is too low, the animal can raise it by moving to a warmer place in its environment (if a warmer place is available).

Homeothermy is far more costly than poikilothermy

FIGURE 29.9 shows the metabolic-rate-versus-external-temperature relationship for a mammal or bird (homeotherm) on the same plot as that of a fish or lizard (poikilotherm) of the same body size. Notice that at each external temperature, the metabolic rate of the homeotherm is far higher than that of the poikilotherm. Notice especially, toward the left side of the graph, that in cold environments, as the external temperature falls, the metabolic rates of the animals become more different. With a falling external temperature, the homeotherm must make heat

INVESTIGATION

FIGURE 29.7 The Metabolic Rate of a Poikilotherm Slows Down as Temperature Decreases Jacqueline Litzgus and William Hopkins measured the standard metabolic rate of the mud turtle *Kinosternon subrubrum* at varying body temperatures.[a] They showed that temperature has a significant effect on standard metabolic rate in this species. The standard metabolic rate of a poikilotherm is its metabolic rate when resting and fasting. It can be measured at any body temperature of interest. (Poikilotherms do not have thermoneutral zones, explaining why the BMR concept does not apply to them.)

HYPOTHESIS

A mud turtle's standard rate of metabolism is influenced by its body temperature.

METHOD

1. Acclimate a group of wild-caught turtles to an external temperature of 30°C, by letting them live at that temperature for a long time. Deprive them of food so no food processing (which can increase metabolic rate) will occur during the experiment.

2. Place each turtle in a sealed chamber connected to a device that measures O_2 consumption for 24 hours. Periodically measure the rate of O_2 consumption inside the chamber.
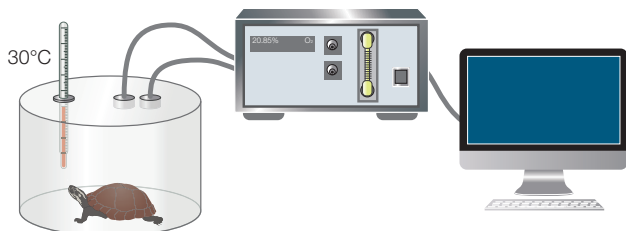
3. Repeat the acclimation and measurement processes at 20°C.
4. From the rates of O_2 consumption, calculate the average standard metabolic rate at each temperature.

RESULTS

The average standard metabolic rate at 20°C was 2.10 ml O_2 consumed/hour. The average standard metabolic rate at 30°C was 9.25 ml O_2 consumed/hour.

CONCLUSION

In turtles, which are poikilotherms, a lower external temperature results in a lower standard metabolic rate.

ANALYZE THE DATA

A. Calculate the value of Q_{10} for the mud turtle's standard metabolic rate. Based on the Q_{10} that you calculate, what would you expect the standard metabolic rate (expressed as rate of O_2 consumption) to be at 10°C?

B. The graph shows data for a single turtle recorded at 30°C. In calculating the turtle's standard metabolic rate, the researchers chose to use only the lowest 30% of O_2 consumption rates recorded. Why might the researchers have made this decision?
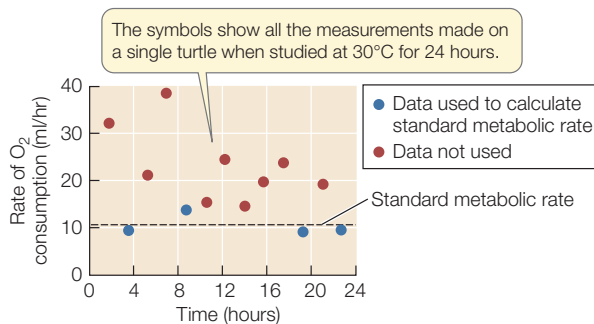
Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a] J. D. Litzgus and W. A. Hopkins. 2003. *Journal of Thermal Biology* 28: 595–600.

When the lizard's temperature gets low, it moves back into sun, and its temperature rises.

When the lizard's body temperature gets especially high, it moves to shade, and its temperature falls.

The lizard's temperature cycles up and down as it shuttles between sun and shade all day.

When the environment gets very hot in midday, the lizard may go briefly underground to lower its temperature.

The lizard leaves its underground burrow near sunrise and basks in the sun to warm to its preferred daytime body temperature.

The lizard returns to its cool underground burrow for the night.

Body temperature of lizard

Air temperature near ground surface

Temperature of burrow

FIGURE 29.8 Poikilotherms Often Use Behavior to Regulate Body Temperature Behavioral regulation of body temperature is particularly well developed in lizards. The body temperature of a lizard depends on the temperature of its external environment, but the lizard can regulate its body temperature by moving from place to place within its environment. The behavior of a desert species, the spiny lizard *Sceloporus serrifer*, is illustrated here.

faster and faster to keep its tissues warm, whereas the poikilotherm's tissues become colder, slowing its metabolism.

Over the course of an entire year, the average metabolic rates of mammals and birds living in their natural environments are typically 15–30 times higher than the average metabolic rates of fish and lizards in their natural environments (comparing animals of equal body size). This contrast dramatizes the advantages and disadvantages of homeothermy. The cells inside the body of a homeotherm function at approximately one temperature
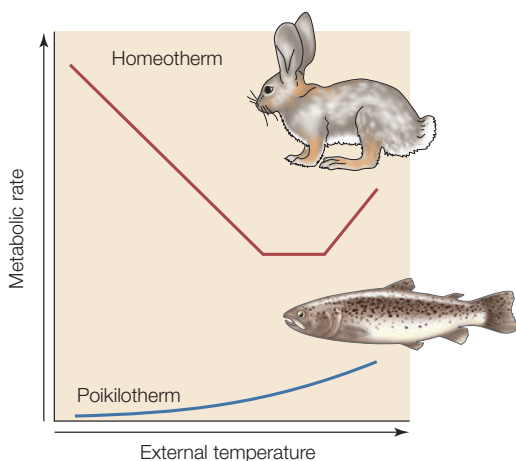
FIGURE 29.9 Metabolic Rate in a Vertebrate Homeotherm and a Vertebrate Poikilotherm of the Same Body Size This graph shows the typical relationships between metabolic rate and temperature for a homeotherm and a poikilotherm. Notice that at every temperature, the metabolic rate of the homeotherm is far higher than that of the poikilotherm.

whether the outside environment is cold or warm. The price of this regulation of body temperature is a 15- to 30-fold increase in the animal's food needs!

LINK

Maintenance of homeostasis can affect life-history tradeoffs—the amount of resources an animal can allocate to reproduction, growth, and defense; see **Concept 42.3**

Homeotherms have evolved thermoregulatory mechanisms

Mammals, birds, and insects are the major groups of homeothermic animals. Placental mammals have core body temperatures of about 37°C whether they live in cold or warm climates. Birds have higher body temperatures, about 39°C. Among insects, only some exhibit homeothermy. Moreover, the insects that display homeothermy do so just at certain times, such as during flight. Many moths, butterflies, bees, and dragonflies maintain relatively constant, high tissue temperatures in their thorax—the location of their flight muscles—when they are flying. Crickets and katydids are similar when singing. Honeybee hives also display homeothermy. Collectively, the workers in a hive keep the brood (their eggs and larvae) at about 32–36°C even when the outside air temperature is far lower than freezing or as hot as 50°C.

Go to MEDIA CLIP 29.1
Thermoregulation in Animals
PoL2e.com/mc29.1

All homeothermic animals have mechanisms for increasing their metabolic rate—therefore increasing their heat production—when their external environment is cold. In some of these mechanisms, ATP (see Concept 6.1) is the source of energy to make heat. ATP is an energy-shuttle compound in cells. It stores energy when food molecules are broken down. It then can itself be broken down, releasing that energy.

Both mammals and birds **shiver** to increase heat production. During shivering, skeletal muscles contract in such a way
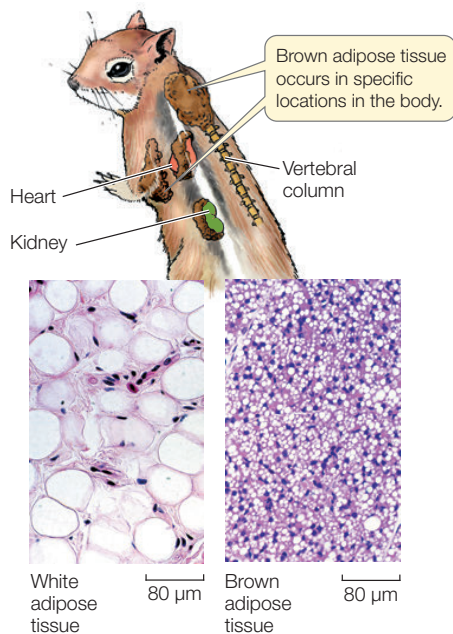
FIGURE 29.10 **Brown Adipose Tissue** In many mammals, specialized brown adipose tissue produces heat. Cells of white adipose tissue (left) contain large droplets of lipid but have a limited blood supply. Cells of brown adipose tissue (right) have many tiny lipid droplets, are packed with mitochondria, and are richly supplied with blood.

FIGURE 29.11 **Thermoregulation in a Honey Bee** This worker bee is foraging on a flower on a chilly day. During such behavior, the thorax is kept at a high, relatively stable temperature by heat produced by the flight muscles. The temperatures of the external surfaces of the bee, flower, and other plant parts are color-coded in this image, which was made by visualizing the surfaces at infrared wavelengths.

that they produce only subtle, quivering motions. The energy for these contractions comes from the chemical bonds of ATP. As molecules of ATP are used for contraction by the quivering muscles, chemical energy from ATP is converted to heat at a heightened rate.

Many mammals, but not birds, are also capable of **nonshivering thermogenesis**, in which thermogenesis (heat production) occurs without shivering. This process takes place in a specialized type of fatty tissue called **brown adipose tissue** (**BAT**) (**FIGURE 29.10**). The mechanism used by BAT to make heat is uncoupling of oxidative phosphorylation. In this process, no ATP is made. Instead, heat is made directly in the mitochondria because the proton gradient in the mitochondria is short-circuited.

> **LINK**
>
> Uncoupling during oxidative phosphorylation is discussed in **Concept 6.2**

When insects maintain a warm thorax during preparation for flight or during flight or singing, the flight muscles in their thorax provide the heat needed (**FIGURE 29.11**). In this case, the heat comes from ATP.

Besides heat production, body insulation is another important characteristic that allows homeotherms to maintain high tissue temperatures in cold environments. Fur and feathers provide high insulation. Heat is also often retained by specialized blood flow patterns (see Concept 32.5).

In hot environments, homeotherms often need to increase their rate of heat loss to keep from overheating. The most common way of doing this is to increase the rate of evaporation of water. When water turns from a liquid to a gas (water vapor), it absorbs a great deal of heat per gram (see Concept 2.2). This heat is removed from the animal when the vapor travels away in the atmosphere. Many large mammals—such as humans, horses, and camels—sweat to increase their rate of evaporation. Dogs pant. Honey bees in a hive spread water that they have collected on interior surfaces of the hive and then fan the moistened surfaces with their wings to speed evaporation.

Hibernation allows mammals to reap the benefits of both regulation and conformity

Mammalian hibernation is remarkable in many ways—one being that hibernators are able to reap the benefits of both regulation and conformity. Most hibernating species are relatively small. They include certain mice, hamsters, ground squirrels, groundhogs, marmots, bats, and small marsupials.

The usual pattern for a hibernator is that the animal functions as a homeotherm—regulating its body temperature near 37°C—during the warm months of the year. During the cold months, however, the animal suspends homeothermy and exhibits temperature conformity. It then allows its body temperature to match the external temperature over a wide range of temperatures, meaning in many cases that the body temperature falls as low as 0–10°C (**FIGURE 29.12**). **Hibernation** is the term for this winter period characterized by conformity.

When an animal functions as a temperature regulator, it experiences the advantages of a high, stable body temperature: its cells function in a consistent thermal environment. The animal faces high metabolic costs, however, like other homeotherms. When the animal functions as a temperature conformer, it experiences the advantages of conformity, namely that its metabolic costs are very low. Hibernators essentially switch between two metabolism–temperature curves resembling those in Figure 29.9.

By reducing energy needs, hibernation allows an animal to spend the winter continuously in a relatively protective and safe place, such as an underground burrow. The amount of
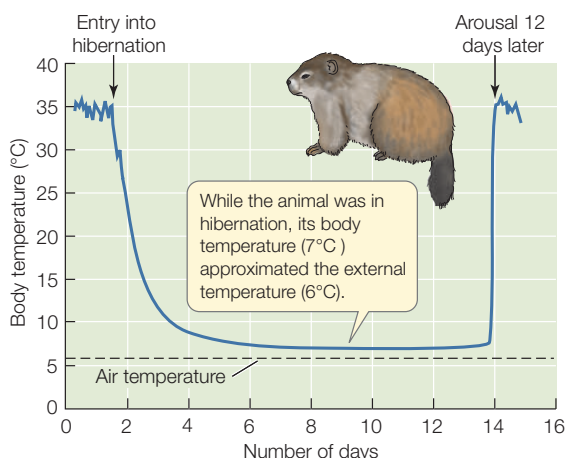
FIGURE 29.12 A Bout of Hibernation in a Groundhog This groundhog or woodchuck (*Marmota monax*) was living where the external temperature was 6°C. Its body temperature was over 35°C before and after the bout of hibernation, but during the 12 days of hibernation its body temperature was very close to the external temperature. Bouts of hibernation like the one shown here are interrupted by brief periods when the body temperature is high, but a hibernator stays continuously in its burrow throughout these events during the hibernating season.

metabolic fuel the animal requires is reduced to the point that the animal need not roam around its habitat in search of food. Instead, it can live entirely on body fat or on stored food it collected the previous summer.

CHECKpoint CONCEPT 29.3

✓ How would the pH of the interstitial fluids of a healthy, water-dwelling regulator be affected by a moderate increase in the pH of the external environment?

✓ Would a reaction that proceeds faster as temperature increases have a Q_{10} value higher or lower than 1?

✓ What is one advantage and one disadvantage of the conforming lifestyle?

✓ Does the metabolic rate of a homeotherm increase or decrease as external temperature decreases? Assume the temperature is below the homeotherm's thermoneutral zone. Would the answer differ for a poikilotherm?

Now that we've discussed how animals use energy, let's consider their body organization and the ways they make ATP.

CONCEPT 29.4 Animals Exhibit Division of Labor, but Each Cell Must Make Its Own ATP

Throughout the living world, structure and physiology—form and function—are intimately related. Often, form cannot be understood without understanding function, and vice versa.

Looking at the structure of animals, perhaps the first point worth noting is that animals typically consist mostly of water. Adult mammals (including us), for example, tend to be about 60 percent water. That water is said to be distributed in various body "compartments," which by definition are location categories rather than specific organs. Typically, most of the fluid in an animal's body is located within its cells. This fluid is called **intracellular fluid**, and the water in all the intracellular fluid throughout the body is said to be in the intracellular compartment. The rest of the fluid in the body is the **extracellular fluid**, said to be in the extracellular compartment. There are two subcategories of extracellular fluid, which we have already mentioned: the fluid portion of blood—termed the blood plasma—and the extracellular fluid found between cells in tissues throughout the body—termed the tissue fluid or, more formally, interstitial fluid.

Fluid compartments are separated from one another by physiologically active epithelia and cell membranes

How are the various fluid compartments kept separate in the body? There are two different scales of space we need to consider to answer this question, and they correspond to separation by epithelia and by cell membranes.

EPITHELIA Consider the following three examples in which fluids of two types lie close together:

- Blood plasma inside a blood capillary and tissue fluid surrounding the outside of the capillary
- Watery fluid inside the lumen (central cavity) of a vertebrate's intestines and tissue fluid in the intestinal wall
- Pond water on the outside of a submerged frog's skin and tissue fluid in the tissue of the frog's skin

In all three cases, the two fluids are separated by an **epithelium** (plural **epithelia**), which is a sheet of cells (epithelial cells) that covers a body surface or organ or lines a body cavity. The simplest and most common type of epithelium, called a **simple epithelium**, consists of just a single layer of cells that rests on a nonliving, highly permeable basement membrane (also called basal lamina; not to be confused with a cell membrane) that the cells help synthesize (**FIGURE 29.13**). Simple epithelia are exceedingly common. In our bodies, for example, a simple epithelium lines all our blood vessels and our intestines, as in the cases above. A simple epithelium also lines our kidney tubules, mammary glands, and sweat glands. In a frog, the skin consists entirely of living cells (unlike our skin, which has dead cells on the outside), and the outermost part of the skin is an epithelium.

Besides helping compartmentalize the body by separating fluids, an epithelium typically has numerous functional capabilities and plays major physiological roles. The cells of an epithelium, for example, commonly pump ions between the fluids on either side of the epithelium. Some epithelia secrete substances such as hormones, mucus, digestive enzymes, milk, or sweat. Some absorb nutrients from the gut. Other epithelia serve sensory functions, including smell and taste.
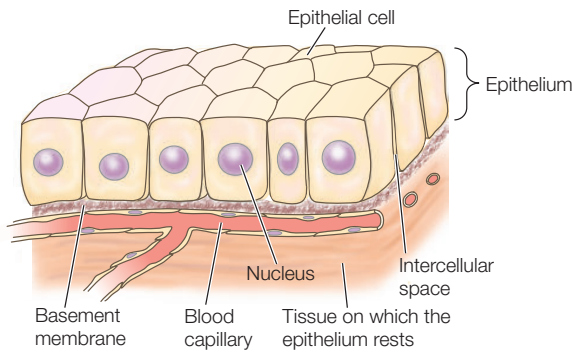
FIGURE 29.13 A Simple Epithelium A simple epithelium consists of a single layer of cells. The cells rest on a basement membrane that is nonliving but highly permeable to gases, water, and ions. Blood capillaries do not penetrate into the epithelium itself but instead are under the basement membrane.

CELL MEMBRANES At a much smaller scale, separation of fluid compartments is by cell membranes. Each cell has intracellular fluid inside separated from the extracellular fluid bathing the cell on the outside. The cell membrane separates the two. Cell membranes, like epithelia, have numerous functional capabilities and play major physiological roles. Cell membranes pump ions between the intracellular fluid and extracellular fluid. They often also play key roles in producing and receiving physiological signals.

> **LINK**
> You can review the properties of cell membranes and their transport and signaling functions in **Chapter 5**

Animals exhibit a high degree of division of labor

In multicellular organisms, individual cells need not perform for themselves all the functions required for life. Instead, cells can become specialized to perform just certain functions and depend on other cells in the body to perform others. Animals display a high degree of such division of labor.

For understanding the structure and function of an animal's body, we usually recognize cells, tissues, organs, and multi-organ systems as ever-more-complex levels in the hierarchy of organization of the animal body. A **tissue** is an assemblage of cells of similar type. An **organ** consists of two or more types of tissue with a defined structural relationship to each other. A **multi-organ system** consists of multiple organs working together.

As an example, **FIGURE 29.14** shows parts of the human digestive tract, including the detailed structure of the beginning of the small intestine. The small intestine itself is an organ. It consists of several tissue types: muscle layers, nervous tissue, connective tissue, an epithelium lining the lumen (central
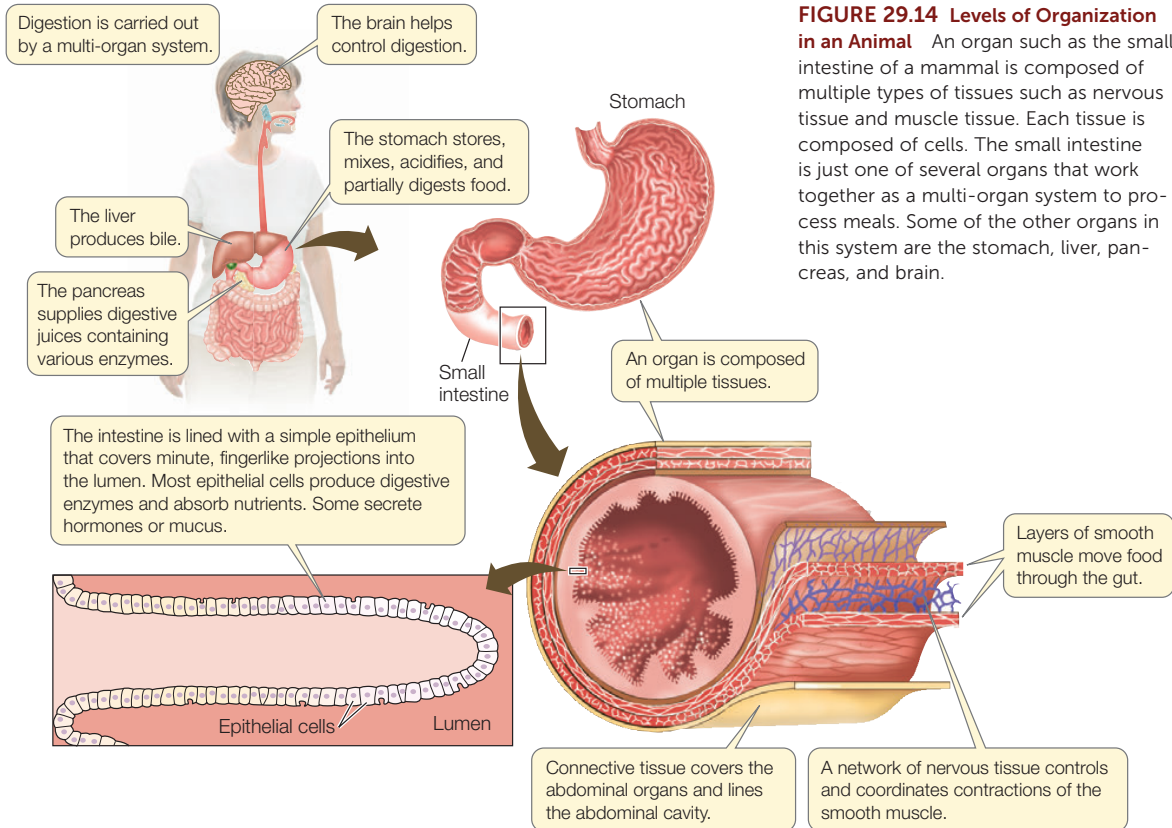
FIGURE 29.14 Levels of Organization in an Animal An organ such as the small intestine of a mammal is composed of multiple types of tissues such as nervous tissue and muscle tissue. Each tissue is composed of cells. The small intestine is just one of several organs that work together as a multi-organ system to process meals. Some of the other organs in this system are the stomach, liver, pancreas, and brain.

cavity), and so forth. Each of these tissue types consists principally of a single, specialized type of cell, such as smooth muscle cells in the muscle layers and nerve cells in the nervous tissue. During its normal function, the small intestine receives partially digested food from the stomach, digestive juices from the pancreas, and an emulsifying agent called bile from the liver, and it is controlled in part by the brain. The intestine, stomach, pancreas, liver, and brain are all organs, and they work together as a multi-organ system to process a meal.

Each organ in an animal's body is specialized to perform certain functions and is utterly dependent on other organs to perform other vital functions. The small intestine of a mammal, for example, requires O_2 for its survival and thus has a life-and-death dependency on the lungs, which take up O_2 from the atmosphere. The intestine also cannot carry out reproduction. Instead, an animal depends on its ovaries or testes to produce gametes. In turn, the lungs, ovaries, and testes depend on the intestine to supply them with nutrients.

Go to ACTIVITY 29.2 Tissues and Cell Types
PoL2e.com/ac29.2

Division of labor requires a rapid transport system

As a consequence of division of labor, organs often require inputs of materials from other organs, as exemplified by the small intestine needing O_2 from the lungs. Organs also need materials they make to be delivered to other organs. For example, wastes need to go to the kidneys and hormones need to be delivered to their targets.

Because of these needs, a rapid transport system is typically required for division of labor to be successful. Most types of animals have a circulatory system that serves this role. In many cases, the need for O_2 transport is the most pressing of all transport needs. For this reason, the sophistication of the circulatory system is usually correlated with metabolic rate (see Concept 32.1). Animals with high metabolic rates require high rates of O_2 transport and have evolved circulatory systems with exceptional abilities for rapid O_2 transport.

> **LINK**
> The diverse circulatory systems of animals are compared in
> **Concepts 32.1 and 32.2**

Each cell must make its own ATP

One of the most important principles in the study of animals is the fact that each cell must make its own ATP. ATP serves as the immediate energy source for most cellular functions, but it is not transported from cell to cell. Each cell must make its own ATP, and the rate of ATP supply in each cell depends on that particular cell's ability to synthesize ATP.

How, then, is energy transported in an animal's body? Energy is transported from organ to organ and from cell to cell in the form of food compounds, such as fatty acids or the sugar glucose, that can be broken down to release chemical energy. Each cell in the body takes up fatty acids or glucose from the blood and then breaks these compounds down internally to make ATP from the chemical energy released from chemical bonds.

Animal cells have aerobic and anaerobic processes for making ATP

Most animal cells make most of their ATP by processes that require O_2. Such processes are termed **aerobic**, or oxygen-requiring. In aerobic ATP production, there is, speaking roughly, a fixed relationship between ATP production and O_2 use. Thus the rate at which a cell can make ATP aerobically depends in part on the rate at which the cell is supplied with O_2 by the circulatory system or by other O_2-transport systems. Think back to the man running steadily on a treadmill in our opening photo. For a muscle cell in his legs to make ATP aerobically at a high rate—enabling the cell to have a high muscular power output—the cell must receive O_2 at a high rate.

Aerobic ATP production takes place mostly in the mitochondria of a cell, by the processes of electron transport and oxidative phosphorylation. During aerobic ATP production, all types of food molecules—sugars, lipids, and proteins—can be used as fuels, that is, as sources of chemical energy for ATP synthesis.

Some cells also have processes for making ATP without O_2. These mechanisms—termed **anaerobic**, meaning without oxygen—are not universally present. Brain cells in nearly all vertebrates, for example, have little ability to make ATP anaerobically. This explains why the vertebrate brain is quickly damaged by the absence of O_2 (as, for example, during a heart attack or stroke). However, many types of cells—including muscle, kidney, and gut cells—have well-developed mechanisms for making ATP anaerobically.

> **LINK**
> Aerobic and anaerobic metabolism are discussed in
> **Concepts 6.2 and 6.3**, respectively, and are compared in
> **Concept 33.3**

The most common process of anaerobic ATP production in animals is **anaerobic glycolysis**. In this mechanism, glycolysis (see Figure 6.7) is the only ATP-producing biochemical pathway that is operational (glycolysis is not itself either aerobic or anaerobic, but it is termed anaerobic glycolysis when it takes place where O_2 is lacking). The mitochondria, which require O_2, do not participate in anaerobic glycolysis. With only glycolysis operational, only sugars can be used as fuels. Anaerobic glycolysis produces just a small amount of ATP per sugar molecule, but it can process sugar molecules at exceedingly high rates and thus make ATP at extraordinary rates. However, ATP cannot be made for very long because anaerobic glycolysis produces lactic acid as its final product (see Figure 6.12A), and the lactic acid accumulates in the animal's body, eventually leading to imbalances that cause the process to stop. When people compete in mile or half-mile runs, much of the ATP used by their leg muscles is made anaerobically. This helps explain why the intensity of muscular work is high but the exercise cannot be continued for very long. Marathons must be run more slowly (mostly aerobically) to avoid this sort of fatigue.

CHECKpoint CONCEPT 29.4

✓ Could a single cell extracted from a multicellular organism survive on its own, similar to the way the lone cell of a unicellular organism does? Why or why not?

✓ In what form is energy transported from cell to cell?

✓ Why is permeability an essential attribute of compartmentalizing structures such as cell membranes and simple epithelia?

Before ending our introductory chapter on animals, we will now turn our spotlight on two additional topics of great importance: phenotypic plasticity and the ways animals control how they function.

CONCEPT 29.5 The Phenotypes of Individual Animals Can Change during Their Lifetimes

Although the genotype, or genetic constitution, of an individual animal is constant for the animal's entire life, countless examples are known of changes in an individual's phenotype, or observable characteristics. Change of this type is called **phenotypic plasticity**, which refers to an individual's ability to display two or more different phenotypes at different times during its life despite a constant genotype. When an individual's phenotype changes as a result of long-term exposure to a particular environment, the individual is said to **acclimate** or **acclimatize** to that environment.

Phenotypic plasticity is common at the biochemical level

Phenotypic plasticity occurs often at the biochemical level, and one of the most important ways it does so is by the action of **inducible enzymes**. Enzymes are called "inducible" if their concentrations in an animal's cells, rather than being constant, depend on the animal's environment or experiences. In other words, with inducible enzymes, the enzyme phenotype can change. Many fish and aquatic invertebrates, for example, have inducible enzymes that respond to long-term changes in body temperature. When winter comes and water temperature falls, these animals acclimatize over days or weeks by producing higher concentrations of enzymes that play key roles in energy metabolism. The fish and invertebrates thus have high concentrations of the enzymes in winter and low concentrations in summer. These enzyme changes make the metabolic functions of the animals less sensitive to long-term changes in temperature than they are to short-term changes.

Detoxification enzymes also provide outstanding examples of plasticity in enzyme phenotype. Human liver enzymes that detoxify ethanol (the alcohol in beer and wine) are usually almost absent in people who do not drink ethanol. However, if a person drinks ethanol regularly, higher concentrations of the enzymes are produced. This helps explain why people who regularly drink are more resistant to drunkenness than people who don't drink.

Enzymes known as P450 enzymes, found throughout the animal kingdom, play important roles in detoxifying a wide range of environmental toxins such as halogenated aromatic hydrocarbons (HAHs). Fish that live in polluted waters have higher levels of P450 enzymes than fish that live in pristine waters.

Phenotypic plasticity also occurs at the scales of tissues and organs

When individual small mammals—such as squirrels or mice—have been living in a warm environment, they have small amounts of brown adipose tissue (BAT; see Figure 29.10), the tissue responsible for nonshivering thermogenesis. Yet when the same individuals experience a cold environment over a period of days or weeks—and therefore become cold-acclimated—their BAT grows dramatically and becomes far more capable of producing heat at a high rate. Because of this plasticity, the animals need not invest in maintaining BAT when their environment is warm, but can have lots of BAT heat production when their environment is cold.

The tiny crustaceans known as water fleas (*Daphnia*), often abundant in freshwater ponds and lakes, display visibly dramatic phenotypic plasticity (**FIGURE 29.15**). They are pale-colored and contain almost no O_2-transporting hemoglobin when their environmental water has a high O_2 concentration. Their production of hemoglobin, being phenotypically plastic, changes in other circumstances, however. When individuals experience periods of low environmental O_2 concentration, they increase hemoglobin synthesis and turn bright red.

Phenotypic plasticity is under genetic control

How can alcohol detoxification enzymes be increased by the experience of drinking alcohol, and brown adipose tissue be increased by exposure to cold? More generally, how can mechanisms that help meet a stress be increased by that very stress?

The answer is that, over the course of evolution, natural selection can favor *patterns of response* to environmental
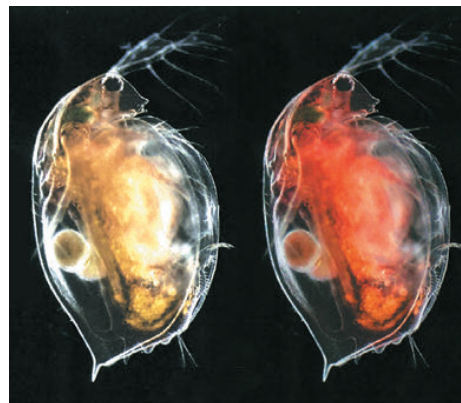
FIGURE 29.15 Phenotypic Plasticity During their lifetimes, individual water fleas (*Daphnia*) can be pale (left) or bright red (right), depending on whether they have been living in O_2-rich or O_2-poor water. The color change reflects how much hemoglobin the animals are synthesizing.

challenges. Phenotypic plasticity is a type of evolved genetic programming. During the evolution of phenotypic plasticity, natural selection—rather than favoring a fixed trait, such as sharp teeth in a carnivore—instead favors a genetic *program of responses* (such as programmed changes in gene expression) so that some environments lead to one set of responses and other environments lead to other sets of responses.

CHECKpoint CONCEPT **29.5**

✓ The metabolic rate of a poikilotherm increases immediately when the temperature of its environment increases. Is this an example of phenotypic plasticity? Explain your answer.

✓ How might a scientist justify determining the relative purity of a stream by measuring the concentrations of P450 enzymes in the fish that inhabit it?

Phenotypic plasticity is one way animals can control the ways they function. To close this chapter, we will now take a much broader look at animal control systems.

CONCEPT **Animal Function Requires Control**
29.6 **Mechanisms**

The nervous and endocrine systems are the principal systems that control or regulate the ways tissues and organs interact harmoniously throughout an animal's body. In addition, there are control systems in individual cells that control cellular processes such as biochemical reactions and cell division. The importance of controls is emphasized dramatically when controls fail. Cancer in part reflects a failure of control of cell division. Lethal fevers reflect failure of control of body temperature.

LINK

Cancer and regulation of the cell cycle are discussed in **Chapter 7**; see **Concept 7.3** and **pp. 148–149**

Homeothermy exemplifies negative-feedback control

In discussing animal control systems, the control of body temperature in humans and other mammals is a helpful example because it takes place in ways analogous to the familiar engineered systems we use to regulate temperature in our homes, as we mentioned earlier. Not all animal control systems operate in the same way as the control of body temperature, but many do.

The four essential elements of a control system are the controlled variable, sensors, effectors, and control mechanism. The **controlled variable** is the characteristic of an animal that is being controlled—body temperature in this example. **Sensors** detect the current level of the controlled variable. In body temperature regulation, the sensors are neural structures that detect the existing temperature in various parts of the body (e.g., skin, brain, and scrotum) and send the information to the control

mechanism in the brain. **Effectors** are tissues or organs that can change the level of the controlled variable. Shivering muscles, for example, are effectors because—by generating heat—they can change the body temperature. The **control mechanism** uses information from the sensors to determine which effectors to activate—and how intensely—to modify the controlled variable. The control mechanism for body temperature is composed of nerve cells located in and near the hypothalamus of the brain.

Go to ANIMATED TUTORIAL 29.1
The Hypothalamus
PoL2e.com/at29.1

In the regulation of mammalian body temperature, as shown in **FIGURE 29.16**, when the control mechanism receives information on the existing body temperature from the sensors, it compares the current body temperature with a set-point temperature—the temperature that is supposed to prevail, in this case 37°C. The control mechanism then activates effectors to reduce or remove the difference between actual body temperature and the set point. If the body temperature is lower than the set point, the control mechanism activates shivering or nonshivering thermogenesis, resulting in increased heat production, which tends to raise the body temperature until it equals 37°C. If the body temperature is higher than the set point, the control mechanism activates sweating or panting to reduce or remove the difference.

This control mechanism is an example of a **negative-feedback** system. The process is called "feedback" because after the control mechanism issues commands to effectors, it receives information on how its commands have altered the body temperature (the controlled variable). Information is "fed back" to
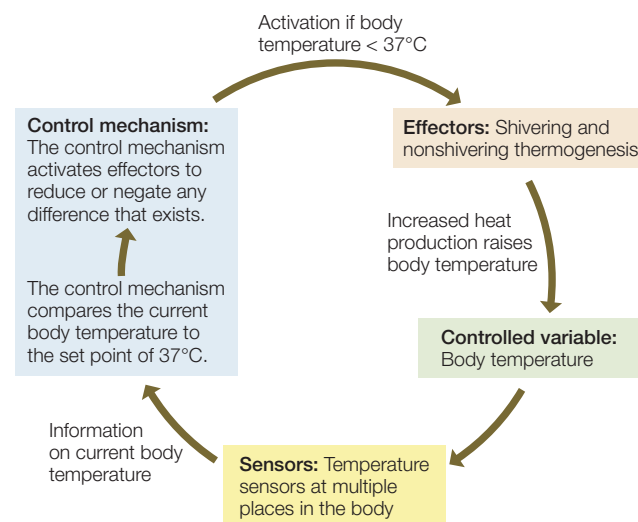
FIGURE 29.16 Negative Feedback: A Systems Diagram of the Temperature Control System of a Mammal The major components of this system are the controlled variable (body temperature), sensors, effectors, and the control mechanism. The system stabilizes body temperature by negative feedback.

the control mechanism. The process is described as "negative" because the control mechanism activates effectors in ways that reduce or negate any difference that exists between the body temperature and the set point. Negative feedback is a stabilizing influence and is often involved in maintaining homeostasis. In this case, it keeps the body temperature near 37°C.

Positive feedback occurs in some cases

Positive feedback occurs when deviations of a controlled variable from its existing level are increased or amplified by the action of the control mechanism. Positive feedback destabilizes a system. However, destabilization can sometimes be advantageous, provided it is ultimately brought under control. A nerve impulse is an example of positive feedback that lasts for a very brief time and then is terminated (see Figure 34.8).

The mammalian birth process depends on positive feedback. During the birth process, waves of contraction of a mother's uterine muscles are stimulated by the hormone oxytocin, which is secreted by neurons in the hypothalamus of the brain and released into the blood by the posterior pituitary gland. A control mechanism in the hypothalamus receives information from sensors in the uterus on the force of uterine contractions. When this control mechanism detects an increased force of contraction, it activates increased oxytocin secretion by the neurons in the hypothalamus, which are the effectors in this system. The heightened oxytocin secretion further increases the force of contraction in a self-reinforcing, positive-feedback loop (**FIGURE 29.17**). Ultimately the force becomes great enough to cause the fetus to

3. The control mechanism responds to increasing force by stimulating oxytocin secretion.

Control mechanism: Hypothalamic activation of oxytocin secretion

Stimulation

Effectors: Neurons that secrete oxytocin

2. Nerve impulses carry information to the brain.

Controlled variable: Force of uterine contraction

Uterus

4. Oxytocin, carried by the blood to the uterus, stimulates contraction.

1. Uterine contractions force the fetus against the cervix, stimulating sensors that detect mechanical forces.

Sensors: Mechanical sensors in cervix

Cervix

FIGURE 29.17 Positive Feedback: The Development of the Force Required for Birth to Occur in Mammals   This system produces an escalating force by positive feedback of uterine muscle contractions.

move from the uterus into the outside world, ending further stimulus for oxytocin production and uterine contractions.

Biological clocks make important contributions to control

Animals have self-contained, metabolic mechanisms of keeping track of time, known as **biological clocks**. These mechanisms do not require outside information to function. Instead, they have a self-contained ability to keep time. Biological clocks have several advantages. One of the most important is that they allow animals to anticipate future events, just as our watches let us anticipate when future events will occur.

The early experiments that convinced biologists of the existence of biological clocks focused on activities such as wheel-running in small mammals, such as mice and squirrels. Given a running wheel in a normal cage environment with day and night, nocturnal species of squirrrels tend to run on the wheel each night and to be inactive each day. They alternate between running and not running on a 24-hour cycle (**FIGURE 29.18A**). Investigators found that if they deprived these squirrels of an external day–night cycle, for example by keeping them in constant darkness, the squirrels still tended to alternate between periods of high and low running activity on an approximately 24-hour cycle (**FIGURE 29.18B**). This suggested that squirrels can keep time without external timing cues. To make sure that the squirrels were not receiving timing cues from their surroundings, investigators not only deprived the animals of an external day–night cycle but also isolated them from outside temperature variations, outside sounds, and any other outside cues imaginable. The squirrels still alternated between periods of high and low running activity. By now, based on revolutionary discoveries of the past 20 years, the mechanisms of biological clocks have been deciphered. Thus the existence of biological clocks has been confirmed by knowledge of the ways they work.

When an animal is prevented from receiving external timing cues, its biological clocks are said to free-run, and under these conditions they do not keep perfect time (see Figure 29.18B). They run fast or slow relative to actual time. Consider a biological clock that, in its free-running state, goes through an entire timing cycle in 23.8 hours. After 1 day of free-running, the clock will be 0.2 hour off, compared with the actual 24-hour solar-day rhythm. After 2 days it will be 0.4 hour off, and after 5 days it will be an entire hour off. In natural environments, this long-term drift is prevented because animals receive external timing cues and their biological clocks do not free-run. Each day, the clocks are reset to be synchronous with actual time—a process termed entrainment. Sunrise and sunset are the most commonly used cues for entrainment. In a natural environment, animals observe sunrise and sunset each day, and they use these indicators to synchronize their biological clocks with the actual 24-hour solar-day rhythm.

Biological clocks that have free-running timing cycles of about 24 hours are called **circadian clocks**. The word "circadian" means "about a day." It emphasizes that the self-contained, free-running periodicities of these clocks are not exactly 24 hours. By now we know of the existence of

(A)

Clock entrained to a light-dark cycle: On a cycle of 12 hour light/12 hour dark, the squirrel is mostly active in the dark and has a rest–activity cycle of 24 hours.

Clock free-running: In constant dark, the squirrel still expresses a daily cycle of rest and activity, but the period of the cycle (the time between successive activity bouts) is less than 24 hours. As a result, the squirrel starts its activity and ends its activity earlier each day.

FIGURE 29.18 Control of Activity by a Circadian Biological Clock The rest–activity cycle of flying squirrels (*Glaucomys volans*) responds to the light–dark cycle under which the squirrels are kept. The squirrels are nocturnal. All the data shown are for a single individual studied (A) with a light-dark cycle and (B) in continuous darkness. Each horizontal line corresponds to one 24-hour day. Where a horizontal line is shaded gray, the squirrel was running. In each set of data, ten successive days, numbered 1 to 10, are portrayed from top to bottom.

Go to ANIMATED TUTORIAL 29.2
Circadian Rhythms
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biological clocks that have free-running timing cycles of about 1 year, called circannual clocks. Many animals in the ocean, where there are lunar tides, have circatidal clocks. All require entrainment to keep exact time.

Circadian clocks are believed to be virtually universal among animals. In an individual animal, most or all cells have their own circadian clocks. A "master clock" is present in an individual, however, and sends out signals to other cells in the individual's body, keeping the body as a whole synchronized. In mammals, the master clock consists of nerve cells in parts of the brain called the suprachiasmatic nuclei.

APPLY THE CONCEPT

Animal function requires control mechanisms

To better understand the physiological mechanism of circadian clocks, Martin Ralph and colleagues used artificial selection to produce two strains of hamsters: one with a short circadian period and one with a long circadian period.[a] (The circadian period is the length of time between two successive days as timed by the clock.) When the suprachiasmatic nuclei (SCN; parts of the brain involved in controlling circadian rhythms) in some of these adult hamsters were destroyed, the animals became arrhythmic. After several weeks, the scientists transplanted SCN tissue from fetal hamsters into the brains of the adult hamsters with destroyed SCNs. Long-period adult hamsters received tissue from short-period fetuses, and short-period adults received tissue from long-period fetuses. The

effects of these treatments on the hamsters' circadian periods are shown in the table.

1. Why did destroying the SCN make the adult hamsters arrhythmic?

2. What result would you expect if SCN tissue from a long-period fetal hamster were transplanted into a long-period adult that had a destroyed SCN?

3. What do the results of the transplantation experiments tell you about where in the body the circadian rhythm phenotype (long versus short) is expressed?

[a]M. R. Ralph et al. 1990. *Science* 247: 975–978.

	TYPE OF RHYTHMICITY SHOWN AFTER VARIOUS TREATMENTS			
RECIPIENT	NO TREATMENT	SCN DESTROYED	SCN DESTROYED AND SHORT-PERIOD TRANSPLANT	SCN DESTROYED AND LONG-PERIOD TRANSPLANT
Short-period adult	Short period	Arrhythmic	Not done	Long period
Long-period adult	Long period	Arrhythmic	Short period	Not done

Biological clocks help control many animal functions. Circadian clocks can give animals an internal sense of when to wake up each day. They help control when animals are active and at rest. They also help control when the digestive system is most able to digest foods each day and when detoxification systems are most able to counteract toxic chemicals. Circannual clocks are known to control annual hibernation rhythms in some species of mammals, and they control annual reproductive rhythms in some animals, such as sheep.

LINK

Plants also have circadian clocks, which are entrained by light cues; see **Concept 26.4**

CHECKpoint **CONCEPT 29.6**

✓ Imagine a house with an air conditioner, furnace, and electric thermostat consisting of a thermometer and simple computer. For this control system, identify the controlled variable, sensor(s), effector(s), and control mechanism. Draw a negative-feedback loop for cooling a house using these components.

✓ What is the likely fate of a biological clock that is denied any chance for entrainment?

✓ Does negative feedback always have a diminishing effect on the controlled variable? That is, because it's "negative," does it always make the level of the controlled variable very low?

Q Why can we use a person's rate of O_2 consumption to measure the rate at which he or she consumes energy to run?

ANSWER To be able to do muscular work, muscle cells need ATP, which they must make themselves (Concept 29.4). As food molecules are broken down in muscle cells to provide energy to synthesize the ATP needed to power the work of muscles, O_2 is required in proportion to the energy released from the food molecules (Concept 29.2). Thus, logically, O_2 is required in proportion to the ATP that is made and broken down in metabolism. By measuring the rate at which O_2 is consumed, we can calculate the rate of breakdown of food molecules to release energy, the rate of ATP synthesis from that energy, and the rate of heat production as muscles liberate energy from ATP and use it to contract, converting it to heat.

The rate of oxygen consumption of a running horse can be determined remotely today with electronic devices that measure O_2 in inhaled and exhaled air by use of a mask. The data can then be stored in onboard digital memory or radioed.

SUMMARY

CONCEPT 29.1 Animals Eat to Obtain Energy and Chemical Building Blocks

■ Animals build new molecules and cells from ingested organic compounds. A growing animal adds new cells to its body, and all animals are constantly replacing worn-out molecules and cells.

■ An animal is characterized by the organization of its body's cells, tissues, and organs. **Energy** can be seen as the capacity to create or maintain this organization. **Review Figure 29.1**

CONCEPT 29.2 An Animal's Energy Needs Depend on Physical Activity and Body Size

■ An animal's **metabolic rate** is defined as its rate of energy consumption—the rate at which the animal uses chemical energy, turning it into heat. Metabolic rate can be quantified by measuring the rate of O_2 consumption or (far less commonly) by measuring the rate of heat production.

■ Physical activity increases an animal's metabolic rate, but the exact relationship between activity level and metabolic rate varies. **Review Figure 29.2**

■ **Basal metabolic rate** (**BMR**) is the metabolic rate of a resting, fasting individual in a comfortable thermal environment. When BMR is expressed per unit of body weight in grams, it is called BMR/g.

■ Smaller mammals consistently have higher BMR/g than larger mammals do. This is an example of a **scaling relationship**. An animal with a high BMR/g must consume more food relative to its body weight than an animal with a lower BMR/g. **Review Figure 29.3**

CONCEPT 29.3 Metabolic Rates Are Affected by Homeostasis and by Regulation and Conformity

■ Within the animal body, cells exist in an **internal environment** of **tissue fluids**. Conditions outside the body are the **external environment**.

■ Animals that maintain a consistent internal environment despite variation in the external environment are called **regulators**. **Conformers** are animals in which the internal environment varies to match the external environment. **Review Figure 29.4**

■ Regulation of the internal environment is more energetically expensive than conformity.

■ **Homeostasis** refers to the stability of an animal's internal environment and the mechanisms that maintain this stability.

■ **Homeotherms** exhibit thermoregulation, maintaining a constant internal temperature by varying metabolic rate and insulation with external temperature. Above or below a specific temperature range called the **thermoneutral zone** (**TNZ**), metabolic rate increases to compensate for increased heat input or to offset heat loss, respectively. **Review Figure 29.5 and ACTIVITY 29.1**

SUMMARY *(continued)*

■ Most animals are **poikilotherms** (**ectotherms**), with body temperatures that vary with, and match, external temperature. Metabolic rates decrease as temperature drops and increase as temperature rises. **Review Figures 29.6 and 29.7**

■ The sensitivity of a reaction or process to changes of internal (tissue) temperature can be expressed as the numerical factor Q_{10}, which usually has a value of 2 to 3. **Review Figures 29.6B and 29.7**

■ A poikilotherm can exert some control over its tissue temperature through behavior, by moving to a more favorable location. **Review Figure 29.8**

■ Homeothermy expends more energy than poikilothermy. **Review Figure 29.9**

■ Homeothermic heat-producing mechanisms used by mammals include **shivering**, the subtle contraction of the skeletal muscles to convert ATP to heat; and **nonshivering thermogenesis** (**NST**) in **brown adipose tissue**, which produces heat directly in the mitochondria by short-circuiting oxidative phosphorylation. Insects sometimes regulate their thoracic temperature using heat generated from ATP by the flight muscles in their thorax **Review Figures 29.10 and 29.11**

■ In hot environments, homeothermic animals increase their rate of heat loss by sweating or panting, processes that increase heat transfer to the environment by evaporation of water.

■ Mammalian **hibernation** refers to a strategy of reducing energy (and thus food) needs by entering a state of thermoconformity during extended cold periods. **Review Figure 29.12**

CONCEPT 29.4 Animals Exhibit Division of Labor, but Each Cell Must Make Its Own ATP

■ The fluids in an animal's body are distributed among various body compartments. **Intracellular fluid** is inside the body's cells and is said to be in the intracellular compartment. **Extracellular fluid**, which includes blood plasma and interstitial fluid, is outside the cells and is said to be in the extracellular compartment.

■ Different extracellular fluids are separated by **epithelia**, sheets of cells that cover a body surface or organ or line a body cavity. **Review Figure 29.13**

■ The boundary between intracellular fluids and extracellular fluids is formed by cell membranes.

■ Animals exhibit a high degree of division of labor. This division of labor typically necessitates a rapid transport system to distribute materials among parts of the body.

■ Cells, **tissues**, **organs**, and **multi-organ systems** represent ever-more-complex levels in the hierarchy of organization of the animal body. **Review Figure 29.14 and ACTIVITY 29.2**

■ Each cell must make its own ATP. Cells may use **aerobic** (with oxygen) or **anaerobic** (without oxygen) processes to produce ATP.

CONCEPT 29.5 The Phenotypes of Individual Animals Can Change during Their Lifetimes

■ **Phenotypic plasticity** refers to an individual's ability to display two or more different phenotypes at different times during its life. Phenotypic plasticity is a way for an animal to **acclimate** or **acclimatize** to changes in its environment. **Review Figure 29.15**

■ At a biochemical level, phenotypic plasticity often involves **inducible enzymes**, enzymes that change in abundance or type in response to an animal's environment.

■ Phenotypic plasticity also occurs at the level of tissues and organs.

■ The capacity for phenotypic plasticity is genetically based and is subject to natural selection.

CONCEPT 29.6 Animal Function Requires Control Mechanisms

■ The four essential elements of a control system are the **controlled variable**, **sensors**, **effectors**, and **control mechanism**. The controlled variable is the property or characteristic of an animal that is being controlled. Sensors detect the current level of the controlled variable. Effectors are tissues or organs that can change the level of the controlled variable. The control mechanism uses information from the sensors to determine which effectors to activate—and how intensely—to modify the controlled variable.

■ A control mechanism may involve **negative feedback**, in which the control mechanism activates effectors in ways that reduce or negate any difference that exists between the controlled variable's actual state and its set point. Negative feedback is stabilizing. **Review Figure 29.16 and ANIMATED TUTORIAL 29.1**

■ **Positive feedback** occurs when deviations of a controlled variable from its existing level are increased or amplified by the action of the control mechanism. Positive feedback is destabilizing but still can be advantageous. **Review Figure 29.17**

■ Animals have self-contained mechanisms of keeping track of time, known as **biological clocks**, that allow the animals to anticipate future events. Biological clocks that have free-running timing cycles of about 24 hours are called **circadian clocks**. Some animals also have circannual or circatidal clocks. **Review Figure 29.18 and ANIMATED TUTORIAL 29.2**

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is29

30

Nutrition, Feeding, and Digestion

Herds of wildebeest move across a savanna in Kenya during the Serengeti migration.

Let's imagine we are lucky enough to travel in a hot-air balloon over the savannas of East Africa. Most of the animals below us will ignore the steady rushing sound of our hot-air burner. Thus as we float in a gentle breeze less than 100 feet above them, we will be able to observe their ordinary daily lives.

Textbooks tell us that Earth is dynamic. Let's use the wonders of human imagination to look at the scene below us dynamically. Let's pretend that we can see energy and matter traveling from place to place.

Light that has traveled 93,000,000 miles through cosmic space from the sun steadily strikes the grasses and thinly scattered trees. Through photosynthesis, these plants convert a small percentage of the light energy into chemical energy in the bonds of organic molecules they manufacture. The remainder of the sunlight energy—more than 99 percent of it—turns to heat as it strikes the savanna.

As the plants synthesize the organic molecules of their bodies, they extract CO_2 from the air to provide the carbon atoms they need. Some plants—but not many—can even take nitrogen from the air to build their proteins.

The zebras, wildebeests, and other herbivores below us need the tissues of plants to sustain their lives because they depend on organic compounds for the energy and atoms they require. Dynamically, as the grasses and trees grow and make new organic matter, the animals eat a portion of the organic matter. Some of the organic compounds in the plants are particularly valuable because—while the animals require them—they can be difficult for the animals to obtain in adequate amounts. Proteins are often in this category.

We'll see many herbivores below us. The flux of energy from the sun into the plants is great enough for many herbivores to survive by exploiting it.

Only rarely, however, will we see a lion, cheetah, or hyena eat one of the herbivores. Organisms cannot live on heat. Yet the plants turn some of their chemical energy into heat, and the herbivores turn some to heat as well. Thus by the time the plants and herbivores have used the chemical energy from photosynthesis, only a small percentage of it is left. Only a few carnivores can get enough chemical energy to exist, so carnivore populations are smaller than herbivore populations.

In the midst of all these dynamic fluxes, each animal below us must somehow meet its needs for both energy and chemical substances. The study of how animals meet this challenge is the study of **nutrition**.

Q What are some of the specific types of organic molecules that animals must obtain in their foods, and why do they need them?

You will find the answer to this question on page 641.

Food Provides Energy and Chemical Building Blocks

Animals—being heterotrophs (see Concept 29.1)—obtain their energy and chemical building blocks from eating other organisms. For animals in the wild, this process is frequently dangerous. For example, Thomas Ruf, Claudia Bieber, and Christopher Turbill recently studied various species of mammals that hibernate, asking whether individuals have different death rates when they are hibernating and not hibernating. When an individual is hibernating, it remains continually in an underground burrow, out of sight. When the same individual is awake, its metabolic rate is far higher and it has to venture out of its burrow to collect food. Ruf and his colleagues found that, on average, the odds of dying each month are five times higher when an individual is awake rather than hibernating. They attributed this difference to the dangers of getting food. As modern humans in an industrialized society, we may have a hard time understanding this. When we need food, we go to a supermarket, and maybe have an ice-cream treat on our way. For animals in the wild, getting food is risky. Plant eaters can be seen by predators and possibly attacked while they munch on grass or leaves. Meat eaters face the very real risk that animals they attack may fight back and injure them, possibly leading to blood loss or infection.

Eating must be of great importance for animals to risk their lives to get food. What exactly do animals require from their food? We discussed these needs briefly in Chapter 29. First, because animals are heterotrophs, they require chemical-bond energy to live: they need organic molecules that they can break down to release energy that they can then use to move about, pump blood, synthesize body parts, and carry out the other energy-demanding requirements of life. Second, animals eat because they require chemical building blocks. They need materials that they can use to build the parts of their bodies—such as amino acids to build proteins, fatty acids to build cell membranes, and calcium to build a skeleton. This need for chemical building blocks is far more complicated than you might imagine, because animals often cannot synthesize for themselves certain molecules they require for life. They need to get those specific molecules from food.

Food provides energy

We quantify the energy content of a food by measuring the amount of heat the food produces when it is completely burned in the presence of oxygen, producing CO_2, H_2O, and other fully oxidized chemical products (**FIGURE 30.1**). We can determine the energy content of a food this way because both burning and aerobic animal respiration follow the same chemical rules. Burning takes place by different chemical steps than respiration, but the products of the two processes are almost identical. Heat is one product. Therefore the amount of heat released by burning a food is close to the same as that produced when an animal metabolically breaks down the same food (and we can correct for any differences by use of chemical rules).

Food energy values in the United States are typically expressed in calories and kilocalories. A **calorie** (**cal**) is the amount of heat required to raise the temperature of 1 gram of water by 1°C, and a **kilocalorie** (**kcal**) is 1,000 times greater. We can use these units for any type of energy, not just heat, because all forms of energy are proportional to one another.

Confusion arises because people often refer to kilocalories as "calories" in everyday life. When you see the word "calories," you should check whether calories or kilocalories are being used. In the Nutrition Facts on food packages in the United States, for example, the energy values reported as "calories" are actually kilocalories (**FIGURE 30.2**). The **joule** is an alternative, metric unit for measuring energy (1 calorie = 4.2 joule). Most countries in the world use the joule, and scientists almost always use it in their scientific work.

Let's consider a meal of macaroni and cheese for which the Nutrition Facts are presented in Figure 30.2. As

Thermometer

Electrical leads for igniting sample

4 The amount of heat released is calculated by measuring how much the water warms, using a high-accuracy thermometer.

Insulated container

Water

3 The surrounding water absorbs the heat from the combustion.

Motorized stirrer

2 An electric signal ignites the food sample, which burns explosively in the pure O_2. The amount of heat released is proportional to the amount of available chemical energy in the final sample.

Fine wire in contact with sample

"Bomb" (reaction chamber)

1 A weighed sample of food is sealed in a thick-walled reaction chamber called the "bomb" that is filled with pure oxygen (O_2), and the bomb is submerged in water in an insulated container.

Pure O_2

Food sample

FIGURE 30.1 Food Energy Values Are Measured by Explosive Combustion in a Bomb Calorimeter

Nutrition Facts

Serving Size 1 cup (228 g)
Servings Per Container 2

Amount Per Serving

Calories 250   Calories from Fat 110

% Daily Values*

Total Fat 12g	**18%**
Saturated Fat 3g	**15%**
Trans Fat 0g	
Cholesterol 30mg	**10%**
Sodium 470mg	**20%**
Total Carbohydrate 31g	**10%**
Dietary Fiber 0g	**0%**
Sugars 5g	
Protein 5g	**10%**

Vitamin A 4%	●	Vitamin C 2%
Calcium 20%	●	Iron 4%

*Percent Daily Values are based on a 2,000 calorie diet. Your Daily Values may be higher or lower depending on your calorie needs.

FIGURE 30.2 A Nutrition Label of the Sort Used in the United States This is the label for a particular brand of macaroni and cheese. Although this label refers to "calories," the values on it are in fact kilocalories.

you can see, each serving supplies 250 kcal. When the meal is sitting on your plate waiting to be eaten, this energy is in the form of chemical energy—in the chemical bonds of the starch, fats, and other molecules in the meal. After you've eaten the macaroni and cheese, if your body breaks down all the molecules in it to release their energy, your body will produce 250 kcal of heat as it uses the energy.

How much chemical energy does an animal consume each day, converting the chemical energy to heat? Metabolic rate provides the answer (see Concept 29.2). An animal's metabolic rate, expressed per day, is the amount of energy the animal converts to heat per day. What if we focus specifically on people? A rule of thumb is that adults in modern society use an average of 2,000–2,500 kcal per day in their daily mix of rest and activity. For general purposes, you can be sure you don't overeat and gain weight by adding up the energy values of all the foods you eat each day and making sure the total is no more than 2,000–2,500 kcal.

There are three major types of food molecules: lipids (fats and oils), carbohydrates, and proteins. Lipids are about twice as dense with energy as carbohydrates and proteins. Lipids yield about 9.4 kcal per gram when they are broken down, compared with 4.1 kcal/g for carbohydrates and 4.5 kcal/g for proteins. As you might expect, foods containing lots of lipids tend to provide lots of kilocalories per serving.

Chemical energy from food is sometimes stored for future use

When an animal eats foods containing more chemical energy than the animal needs, the animal often stores some or all of the extra chemical energy for future use. Animals store energy mostly in the form of lipids. This makes sense because lipids are particularly energy dense. Stored materials need to be carried around until they are used. For each gram of lipid that an animal stores and carries, it gets more than 9 kcal of energy—a large amount—when it finally uses the lipid. Animals do not need to eat lipids to store lipids. They can convert carbohydrates and proteins to lipids to store chemical energy.

Animals also store glycogen, a type of carbohydrate (specifically, polymerized glucose), but they do not store nearly as much energy as glycogen as they store as lipid. Glycogen is always stored with a lot of water bound to its molecules. When all this water is taken into account, the glycogen is heavy, and its energy density is only about 1 kcal/g.

Why do animals store glycogen at all if its energy value is only 1 kcal/g compared with more than 9 kcal/g for lipids? The answer is that some tissues require carbohydrates as their energy source. When glycogen is broken down, it yields the sugar glucose. The vertebrate brain gets its energy almost

APPLY THE CONCEPT

Food provides energy and chemical building blocks

MET, the *m*etabolic *e*quivalent of *t*ask, is an index of the intensity of physical activity. Exercise physiologists define the resting metabolic rate as 1 MET and increasingly energetic activities as multiples of 1 MET. Walking at 4 miles per hour has a value of about 3 METs (i.e., it uses 3 times as much energy per unit of time as resting quietly). Jogging (7 mph) requires about 8 METs, and vigorous running (10 mph) about 12 METs. Assuming that your resting metabolic rate is 80 kcal/hr, fill in the table with the time it would take you to burn off the calories from the listed foods while resting, jogging, or running.

FOOD	KILOCALORIES	TIME REQUIRED TO BURN OFF CALORIES		
		RESTING	JOGGING	RUNNING
Mixed carrots and peas, half-pound	136			
Beer, one 12-oz bottle	145			
Potato chips, kettle-cooked, 30 chips	225			
Sports energy bar (e.g., chocolate power bar)	250			
Double cheeseburger	440			
Chicago-style deep-dish pizza, half-pound	720			

entirely from glucose. Thus glycogen stores can directly meet the brain's energy needs. When skeletal muscles employ anaerobic glycolysis to make ATP for exercise (see Concept 29.4), they also need glucose as their energy source.

Proteins are not usually used as storage compounds. There are large masses of protein in an animal's body. Muscles are principally proteins, for example. However, these proteins are in use, rather than being stored for future use.

Food provides chemical building blocks

The molecules in an animal's body are made from the molecules in the animal's food. For carrying out this process, animals have enormous capacities to interconvert molecules. Lipid molecules can be converted to carbohydrate molecules, and certain amino acids can be converted to others, for example. These are just two of the many interconversion processes that occur in animals.

As an animal grows, its food must meet both its energy needs and its needs for chemical building blocks to form a larger and larger body. The need for chemical building blocks does not end with adulthood, however. As stressed in Concept 29.1, adult animals constantly rebuild their bodies. Mammals, for example, rebuild 2–3 percent of the protein molecules in their bodies every day. Much of this rebuilding is carried out by recycling building blocks within the body. Recycling is not perfect, however. For this reason, adults have a steady need throughout their lives for new building blocks that they obtain by eating.

> **LINK**
>
> For more on the reactions that interconvert macromolecules and their constituent monomers, see **Concepts 2.2–2.4, 3.1, and 3.2**

Some nutrients in foods are essential

The word "essential" has a particular meaning in the study of nutrition. An **essential nutrient** is one that an animal cannot synthesize for itself. We will start our discussion of essential nutrients by focusing on the **standard amino acids**: the 20 kinds of amino acids that animals use to build proteins (see Concept 3.2). These amino acids exemplify the distinction between essential and nonessential nutrients.

Biochemists have discovered that animals can synthesize some of the 20 standard amino acids but not others. Adult humans, for example, can synthesize 12 of the standard amino acids by rearranging the subparts (carbon skeletons and functional groups) of other molecules in their diet. Those 12 amino acids are *nonessential*. The remaining eight amino acids cannot be synthesized by adult humans. These **essential amino acids**—isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine—must be obtained fully formed in the diet. The list of essential amino acids tends to be similar from one type of animal to another, but there are important differences. Infant humans, for example, require histidine in their diet as well as the eight amino acids that are essential for adults.

You might wonder: Where do the essential amino acids come from? Plants and algae can synthesize all 20 standard

Eight essential amino acids for adult humans

Grains (corn in tortilla chips)

Tryptophan
Methionine
Valine
Threonine
Phenylalanine
Leucine
Isoleucine
Lysine

Legumes (beans in bean dip)
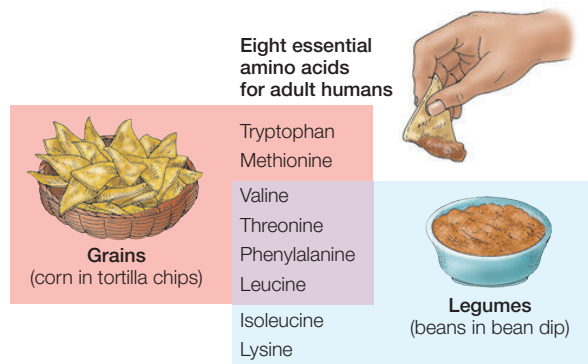
FIGURE 30.3 A Common Food Combination Provides All Eight Essential Amino Acids All around the world, cultures exist in which corn and beans are major parts of the daily diet. We mimic this diet when we snack on tortilla chips and bean dip. Eaten together, these two foods provide all the essential amino acids required by adult humans. (Corn by itself often does not provide enough lysine or isoleucine, and beans often do not provide enough methionine or tryptophan.) When two or more foods must be eaten to get all eight essential amino acids, it is important to eat the foods at about the same time.

amino acids. For this reason, animals can obtain their essential amino acids by eating plants or algae. Different plants and algae vary in their proportions of amino acids. For an animal to get all of its essential amino acids in adequate quantities, it may therefore need to eat more than one kind of plant or alga. For adult humans, combinations of grain foods and legume foods—such as corn and beans—are often effective in providing all the essential amino acids (**FIGURE 30.3**).

Foods of animal origin—such as milk, eggs, and meat—tend to be good sources of all eight essential amino acids. Cows, chickens, and other farm animals get their essential amino acids by eating plants. They build those amino acids into proteins in their bodies or in the products they make, such as milk and eggs. We then get the amino acids when we eat them.

Animals also need certain **essential fatty acids**. There are a great many kinds of fatty acids, but in humans and many other animals only two are commonly essential: alpha-linolenic (α-linolenic) acid and linoleic acid. If α-linolenic acid is essential for an animal, the animal must either eat it in its diet or eat very similar fatty acids that can be converted to it by simple reactions. Alpha-linolenic acid and these other fatty acids are called the omega-3 fatty acids. Linoleic acid and other fatty acids that are closely similar to it are the omega-6 fatty acids.

Vitamins are a third group of essential nutrients. Vitamins are difficult to define chemically. This is true because needs for various vitamins have evolved independently or relatively independently, meaning that different vitamins often have unrelated chemical structures. Vitamin A provides an excellent illustration of the evolutionary history of a vitamin:

Vitamin A (retinol)
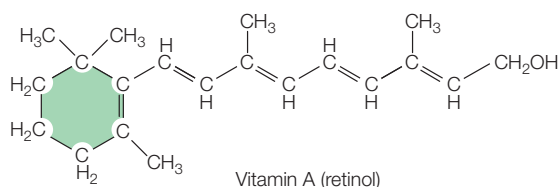
TABLE 30.1	A Full List of Vitamins Required by Humans		
Vitamin	**Some sources in human diet**	**Some functions**	**Deficiency symptoms**
WATER-SOLUBLE			
B_1 (thiamin)	Liver, legumes, whole grains	Coenzyme in cellular respiration	Beriberi, loss of appetite, fatigue
B_2 (riboflavin)	Dairy foods, meat, eggs, green leafy vegetables	Coenzyme in FAD	Lesions in corners of mouth, eye irritation, skin disorders
B_3 (niacin)	Meat, fowl, liver, yeast	Coenzyme in NAD and NADP	Pellagra, skin disorders, diarrhea, mental disorders
B_5 (pantothenic acid)	Liver, eggs, yeast	Found in acetyl CoA	Adrenal problems, reproductive problems
B_6 (pyridoxine)	Liver, whole grains, dairy foods	Coenzyme in amino acid metabolism	Anemia, slow growth, skin problems, convulsions
Biotin	Liver, yeast, bacteria in gut	Found in coenzymes	Skin problems, loss of hair
B_{12} (cobalamin)	Liver, meat, dairy foods, eggs	Formation of nucleic acids, proteins	Pernicious anemia, psychological disorders
Folic acid	Vegetables, eggs, liver, whole grains	Coenzyme in formation of heme and nucleotides	Anemia
C (ascorbic acid)	Citrus fruits, tomatoes, potatoes	Formation of connective tissues; antioxidant	Scurvy, slow healing, poor bone growth
LIPID-SOLUBLE			
A (retinol)	Fruits, vegetables, liver, dairy foods	Key part of visual pigments; regulation of nervous system development	Night blindness
D (cholecalciferol)	Fortified milk, fish oils; also made in the body in presence of sunshine	Absorption of calcium and phosphate	Rickets
E (tocopherol)	Meat, dairy foods, whole grains	Muscle maintenance, antioxidant	Anemia
K (menadione)	Liver; also made by gut microbes	Blood clotting	Blood-clotting problems

When animals evolved vision, they used a slightly modified version of this complex structure for light collection in their eyes. But they did not evolve an ability to make the structure! Instead, they depended on getting the structure, already made, from plants and algae that synthesize the structure and incorporate it into pigments (e.g., β-carotene, see p. 121) that help collect light for photosynthesis. To this day, humans and many other animals must obtain vitamin A as a fully formed ("prefabricated") chemical structure in their diets because they cannot synthesize it themselves, yet they require it for vision and certain other functions.

All the vitamins are carbon compounds, and they are needed in just tiny amounts. Thus we can quickly define a **vitamin** as an essential carbon compound required in tiny amounts. **TABLE 30.1** summarizes the 13 vitamins commonly recognized as required by humans. Note that vitamins fall into two groups: those that are soluble in water and those that are soluble in lipids. The list of vitamins varies a bit among animals. For example, most mammals can make their own ascorbic acid, so it is not a vitamin for them. However, primates—including humans—cannot synthesize ascorbic acid, and for them it is a vitamin (vitamin C). Vitamin D is a special case because humans can synthesize it if their skin is exposed to sunlight. Vitamin D is essential for people only if they have inadequate sun exposure, as is often true in winter when people stay indoors or wear heavy clothing.

Go to ACTIVITY 30.1 **Vitamins in the Human Diet**
PoL2e.com/ac30.1

The final category of essential nutrients is the **essential minerals**. These are chemical elements that animals require in addition to carbon, oxygen, hydrogen, and nitrogen (the most abundant elements in organic molecules). Familiar examples of essential minerals are calcium, iodine, and iron (**TABLE 30.2**).

We need some essential minerals in substantial quantities. Calcium, for example, is the fifth most abundant element in the human body. A 70-kg person contains about 1.2 kg of calcium. Calcium is a component of calcium phosphate, the principal structural material in bones and teeth, and is also necessary for nerve function and muscular contraction (see Concepts 33.1 and 34.3). We lose calcium from our bodies in urine, sweat, and feces, so it must be replaced regularly. Humans require about 1 g of calcium per day in their diet.

We require some of the other essential minerals in only small amounts. Iron is one of these. It is the oxygen-binding atom in hemoglobin and myoglobin (see Concept 32.5) and is also a component of enzymes in the electron transport chain. Yet the total amount of iron in the tissues of a 70-kg person is only about 4 g. Only tiny amounts (10–20 mg) are required in the diet each day to replace iron lost from the tissues.

Go to ACTIVITY 30.2 **Mineral Elements Required by Animals**
PoL2e.com/ac30.2

Nutrient deficiencies result in diseases

The lack of any essential nutrient in an animal's diet produces a state of deficiency called **malnutrition**. When malnutrition is

TABLE 30.2 A Partial List of Minerals Required by Animals

Element	Some sources in human diet	Major functions
NEEDED IN LARGE AMOUNTS		
Calcium (Ca)	Dairy foods, eggs, green leafy vegetables, whole grains, legumes, nuts, meat	Found in bones and teeth; blood clotting; nerve and muscle action; enzyme activation
Magnesium (Mg)	Green vegetables, meat, whole grains, nuts, milk	Required by many enzymes; found in bones and teeth
Phosphorus (P)	Dairy foods, eggs, meat, whole grains, legumes, nuts	Found in nucleic acids, ATP, and phospholipids; bone formation; found in buffers; metabolism of sugars
Sodium (Na)	Table salt, dairy foods, meat, eggs	Nerve and muscle action; water balance; principal positive ion in extracellular fluids
NEEDED IN SMALL AMOUNTS		
Chromium (Cr)	Meat, dairy foods, whole grains, legumes, yeast	Glucose metabolism
Cobalt (Co)	Meat, tap water	Found in vitamin B_{12}; formation of red blood cells
Copper (Cu)	Liver, meat, fish, shellfish, legumes, whole grains, nuts	Found in active site of many redox enzymes and electron carriers; production of hemoglobin; bone formation
Iodine (I)	Fish, shellfish, iodized salt	Found in thyroid hormones
Iron (Fe)	Liver, meat, green vegetables, eggs, whole grains, legumes, nuts	Found in active sites of many redox enzymes and electron carriers, hemoglobin, and myoglobin
Manganese (Mn)	Organ meats, whole grains, legumes, nuts, tea, coffee	Activates many enzymes
Zinc (Zn)	Liver, fish, shellfish, and many other foods	Found in some enzymes and some transcription factors; insulin physiology

chronic, it leads to a specific **deficiency disease** related to the missing nutrient. Scurvy, for example, is a deficiency disease caused by inadequate amounts of a vitamin (see Table 30.1). This complex illness has many debilitating symptoms, including bleeding gums, and is ultimately fatal if not cured. Scurvy was a major problem for sailors at sea, who often had no fresh foods during long trips, until physicians learned in the eighteenth century that it is caused by deficiency of a nutrient, later identified as vitamin C. The disease disappeared when sailors made a point of eating limes or other citrus fruits that provide ample vitamin C.

LINK

Deficiencies of essential minerals—for example, iodine—can also cause disease; see **Concept 35.4**

CHECKpoint CONCEPT 30.1

✓ Imagine that a slice of pizza contains 300 kcal of energy. Using only the energy stored in the pizza, what is the maximum amount of water you could heat by 1°C? (Hint: Start by converting kilocalories to calories and express your final answer in grams.)

✓ Which of these food molecules will produce the most heat per gram if burned in the presence of oxygen: lipids, carbohydrates, or proteins?

✓ Do all organisms require the same essential amino acids?

Now that we have discussed why animals require food, let's turn to the methods they use to get food.

CONCEPT 30.2 Animals Get Food in Three Major Ways

If we look at animals in the broadest way possible, we realize that they get their food in three major ways. Some target easily visible, individual food items. Some collect tiny—often invisibly tiny—food particles, which they must gather in great numbers to obtain a sufficient amount. Finally, some depend on symbioses with microbes to obtain critical food needs.

These three methods are not mutually exclusive. Many animals employ two methods. For example, as we note below, there is a growing realization that we humans are probably far more dependent on microbes than previously thought.

Some animals feed by targeting easily visible, individual food items

An osprey (fish hawk; *Pandion haliaetus*) catching a fish provides an iconic example of feeding by targeting easily visible, individual food items (**FIGURE 30.4**). The osprey spots an individual fish from the air while flying. Then it plunges to the water to seize the fish with its talons in a targeted way. This type of feeding also occurs when a lion kills a zebra with a bite to its neck, or when a crab grasps a clam with its claws and crushes the clam's shell to get to the meat inside.

Animals that eat leaves and grasses also exemplify this type of feeding. As a deer plucks leaves from a tree, it targets each leaf. Many grazing animals are remarkably selective, targeting some types of plants but avoiding others. Bees target individual flowers to collect their nectar and pollen. Squid catch fish one at a time.

FIGURE 30.4 An Osprey Eats by Targeting Individual Food Items

Suspension feeders collect tiny food particles in great numbers

The water in a lake or ocean often contains great numbers of suspended organic particles, many of them too tiny to be seen with the naked eye. For example, photosynthesis in bodies of water is typically carried out by single-celled algae suspended in the water's sunlit, upper layers. Each milliliter of this water can contain hundreds or thousands of individual algal cells, each microscopically small. Tiny animals that eat the algae are often also abundant. Dead algal cells, dead microscopic animals, and the feces of tiny animals are additional types of common, suspended organic particles. Here we use the term "particles" to refer to small organic objects that may be plant or animal, living or dead.

Clams, many fish, many aquatic insects, and numerous other aquatic animals have evolved ways of collecting tiny particulate foods. Such animals are called **suspension feeders** in recognition of the fact that they feed on suspended particles.

These animals were originally called filter feeders because people assumed they use sievelike or filterlike body parts to collect particles. However, we realize today that many of these animals do not sieve or filter the water, and specialists now prefer the more general term "suspension feeders."

Collecting tiny particles is not the only challenge suspension feeders face. To obtain sufficent amounts of food, these animals also must be able to collect the particles in huge numbers. A single clam eats millions of individual algal cells each day. Suspension feeders usually do not target individual food particles, but instead collect huge numbers indiscriminately.

A common definition of suspension feeding is that it is a process by which an animal collects individual food particles that are only 1/100th the size of the animal or smaller. By this definition, many whales are classed as suspension feeders. About half the living species of whales have no teeth. Instead, they have closely spaced plates (made of a material like our fingernails) that allow them to collect small organisms from the water (**FIGURE 30.5A**). Some of the biggest whales, measuring 20–30 meters long, feed principally on crustaceans that are each about the size of a rice grain. These whales are suspension feeders by the definition we are using. The two biggest fish alive today, the whale shark (*Rhincodon typus*) and basking shark (*Cetorhinus maximus*), are also suspension feeders, as are the huge devil (manta) rays (*Manta*).

Most suspension feeders, however, are less than 30 centimeters long and feed on particles that are microscopic or nearly microscopic in size. These small suspension feeders include sardines, anchovies, menhadens, and many other commercially important fish. They also include scallops, mussels, clams, and many other aquatic invertebrates (**FIGURE 30.5B**).

Many animals live symbiotically with microbes of nutritional importance

A **symbiosis** is an intimate, long-term association between two different types of organisms. Many animals have evolved

(A)
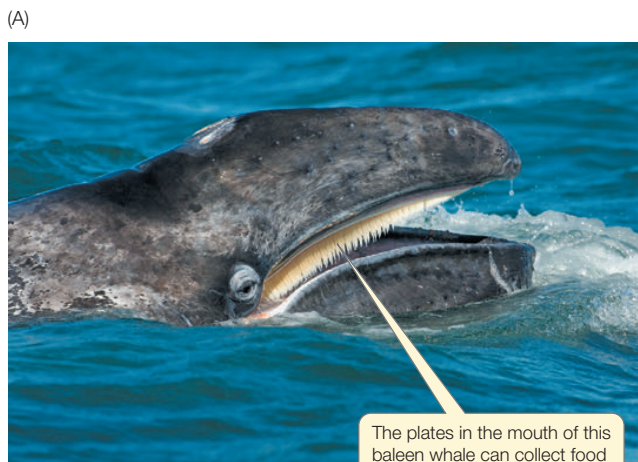
The plates in the mouth of this baleen whale can collect food objects the size of rice grains.

Eschrichtius robustus

FIGURE 30.5 Two Suspension Feeders   (A) A toothless grey whale showing the array of plates in its mouth. The plates, made of a fingernail-like material, are called baleen, and the toothless whales

(B)
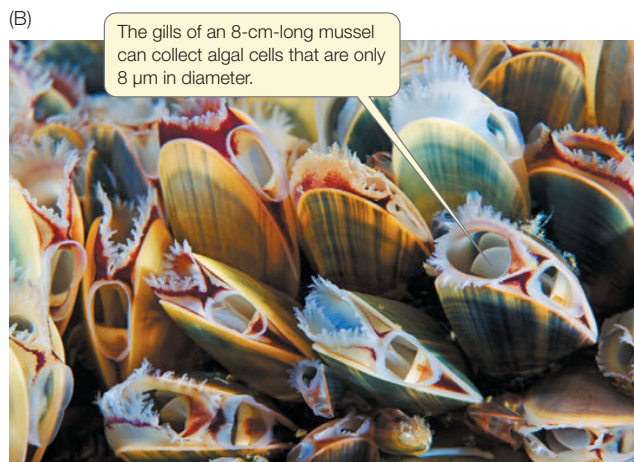
The gills of an 8-cm-long mussel can collect algal cells that are only 8 µm in diameter.

Mytilus edulis

are often called baleen whales. (B) Mussels (a type of mollusk) feed by pumping environmental water over and through their gills, which remove tiny food particles from the water.

(A) A tropical coral-reef ecosystem
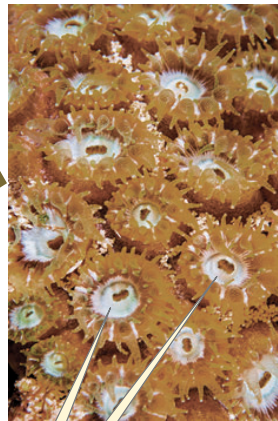
Each coral is made up of many individual polyps.

(B) A single coral polyp in section

Tentacle   Mouth

Epidermis

Gastrovascular cavity

Gastrodermis with algal cells
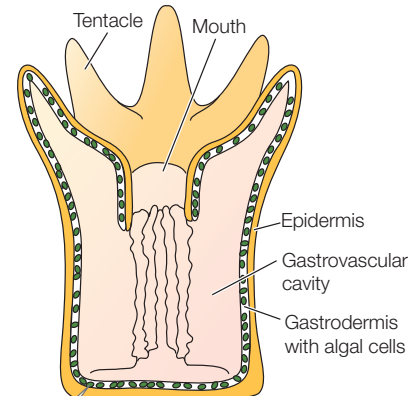
Populations of symbiotic algae live in the gastrodermis. Photosynthetic products from the algae pass directly to the animal cells in each polyp.

FIGURE 30.6 Reef-Building Corals Live Symbiotically with Algal Cells Corals, unlike most animals, are photosynthetic and require sunlight. (A) Coral reefs consist of a diverse array of corals. Each coral is a large colony of hydra-like polyps, which build the coral's skeleton. (B) Algal cells (often called zooxanthellae) live inside the cells of a polyp's gastrodermal cell layer. The algae carry out photosynthesis, synthesizing glucose and other nutritionally important molecules for the polyp. Polyps also feed heterotrophically by using stinging cells on their tentacles to capture tiny animals that swim by.

symbioses with microbes, such as bacteria or algae, in which the microbes synthesize nutritionally important molecules for the animals. Because the microbes live inside the animals, the animals do not eat them. However, molecules transported directly from the microbes to the animals serve the same functions as foods, and thus we will call such molecules foods.

All reef-building corals contain algae (**FIGURE 30.6**). The cells of these algae live inside the cells of the corals. A reef-building coral is an animal–algal symbiosis composed of a cnidarian animal (resembling a hydra or anemone) and a specific species of alga in the genus *Symbiodinium* (see Concept 20.4). The algal cells contain photosynthetic pigments that are responsible for some of a coral's coloration. By carrying out photosynthesis, the algal cells produce food molecules such as glucose. Some of these food molecules then diffuse out of the algal cells into the animal cells and become food for the heterotrophic animal cells. This symbiosis is of extreme importance nutritionally. Corals can lose their algal cells when stressed (a process called bleaching). If that happens, the corals deteriorate and will die unless they obtain new algal cells.

Animals have also evolved nutritionally important symbioses with many types of microbes that are heterotrophic rather than photosynthetic. The ruminant mammals—including cows, sheep, moose, antelopes, deer, and giraffes—are the most famous examples. All ruminants are herbivores and eat foods such as grasses and leaves. They have evolved a complex stomach that consists of four chambers through which food passes sequentially (**FIGURE 30.7**). The first of these chambers, the rumen, is huge, occupying more than 10 percent of the animal's body. It is filled with a microbial community consisting of a complex and changeable mix of bacteria, protozoa, yeasts, and fungi living in a nonacidic, saliva-like fluid.

When a ruminant eats, its food (after chewing) goes directly to the rumen, which acts like a fermentation vat. Here the resident microbes attack the food, breaking it down and

transforming it in ways the animals cannot. The processes carried out by the microbes are called **fermentations** because they take place without O_2 (the rumen is anoxic). Three functions of the rumen microbes are particularly important:

- They break down cellulose and hemicelluloses (cellulose-like compounds; see Figure 2.10). Vertebrate animals by themselves cannot break these compounds down and thus cannot obtain nutritional value from cellulose, one of the most abundant organic materials on land (see Concept 30.3). By breaking down cellulose, the microbes turn it into small molecules (short-chain fatty acids, such as acetic acid) that the ruminant can absorb into its blood and use for chemical energy.

- The microbes make several types of B vitamins and amino acids that are essential nutrients for the ruminants.

- The microbes enable ruminants to recycle nitrogen, one of the chemical elements that is often in short supply. The microbes take up waste nitrogen from the ruminant's metabolism and convert it to microbial protein. The animal then digests this protein, obtaining amino acids from which it can synthesize animal proteins. Animals without this recycling process simply excrete their waste nitrogen, and then need to replace it by finding nitrogen-rich foods.

One of the breaking stories in the study of animal nutrition is the recent realization that heterotrophic microbes probably play important nutritional roles in most animals, not just in animals such as ruminants that have evolved large fermentation

Esophagus

Rumen

Reticulum

1 The contents of the rumen are periodically regurgitated into the mouth for rechewing.

2 The rumen and reticulum serve as fermentation vats for the mixed microbial community. The microbes ferment cellulose, forming short-chain fatty acids that diffuse into the blood.

4 The abomasum functions similarly to our stomach. It secretes hydrochloric acid and protein-digesting enzymes. The microbes are killed and partly digested here, then passed on to the small intestine where digestion is completed and absorption occurs.

3 The mixture of fermented food and micro-organisms passes through the omasum, where it is concentrated by removal of water.

FIGURE 30.7 A Ruminant's Stomach Bison, like all ruminants, have a specialized stomach with four compartments that enables them to obtain energy and nutrients from coarse, otherwise indigestible plant material through fermentation. The fermentation is carried out by a mixed microbial community of bacteria, protists, yeasts, and fungi that is housed primary in the rumen, which is not acidified.

vats. The microbes of greatest interest are those that live in the lumen—the central cavity—of the intestines and other parts of the gut and collectively are called the **gut microbiome**.

Humans have a large gut microbiome, consisting mostly of bacteria, which we acquire during birth and after we are born. People differ in the composition of their gut microbiome, and increasing evidence indicates that the gut microbiome has important effects on individual digestion, nutrition, and metabolism.

LINK

For more on the diverse microbes in the gut microbiome and their possible effects on animal nutrition and human health, see **Concepts 19.3 and 41.1**

CHECKpoint CONCEPT 30.2

✓ A newly hatched, nearly microscopic octopus larva and a fist-sized oyster may both feed on the same type of microscopic animals suspended in the water column. Why is the oyster considered a suspension feeder whereas the octopus larva is not?

✓ Reef corals are animals. However, they can be severely damaged if the water in which they live becomes cloudy, blocking sunlight from reaching them. Why?

✓ Rabbits have large fermentation chambers like ruminants do. However, unlike ruminants, rabbits are *hind*gut fermenters. Ingested food does not pass through their fermentation chamber (their cecum; see Figure 30.8) until *after* it leaves their stomach and small intestine. With the functional significance of symbiotic fermentation in mind, how might you explain the common sight of a rabbit eating its own feces?

✓ Certain large worms, called hydrothermal-vent worms, living on the ocean floor have no mouth, gut, or anus. Does this imply that they are not receiving any nutrients from the surrounding environment? Which of the three major ways of getting food might these worms employ?

Now that we have surveyed the ways in which animals get foods, let's turn to the ways they process their foods after ingestion. Processing is as important as the chemical composition of food in determining the nutrients that animals obtain.

CONCEPT 30.3 The Digestive System Plays a Key Role in Determining the Nutritional Value of Foods

After animals ingest foods, the foods usually pass through a tubular digestive tract—a tubular gut—in most cases. The foods enter at the mouth, and later their indigestible components exit as feces at the other end of the tube, the anus. Exceptions to this pattern exist. For example, in animals with symbiotic microbes (see Concept 30.2), sugars or other nutritional compounds synthesized by the microbes enter the animal tissues directly without needing to pass through the digestive tract. For the rest of this chapter we will focus mainly on food processing by the digestive tract.

The inner walls of the digestive tract are lined, from mouth to anus, with an epithelium (usually a simple epithelium; see Figure 29.13):

Glucose and other nutrient molecules from digested food must be transported across the gut epithelium to enter the blood.

Gut lumen

Cross section of gut

Blood capillary

Glucose from meal

Gut epithelial cell

Basement membrane
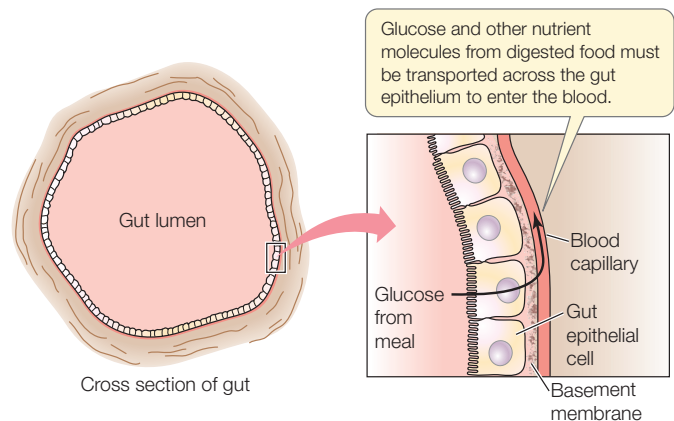
FIGURE 30.8 Digestive Systems Are Diverse, but They All Carry Out Digestion and Absorption In each group of animals, specific regions of the digestive tract vary from species to species, in part because different species are adapted to different diets.

After being ingested, food materials are in the gut lumen on the inside of this epithelium (i.e., enclosed by the epithelium). The blood vessels of the gut are located in the tissues in the walls of the gut, surrounding the epithelium. Thus for food materials to enter the blood for transport to cells throughout the body, they must cross the gut epithelium. Most materials in the foods animals ingest cannot do that. The molecules of carbohydrates, lipids, and proteins in foods are far too large and complex to cross the gut epithelium.

The digestive system's principal function is to perform two processes that together permit food materials to be taken into the blood and used: digestion and absorption. Here we define them in ways that apply to most animals. **Digestion** is the breakdown of food molecules in the gut lumen by enzyme action to produce smaller molecules that can cross the gut epithelium to enter the blood. **Absorption** is the process of transporting molecules from the gut lumen into the blood. The mechanisms of both digestion and absorption are specific for certain types of molecules. For the most part, the molecules that an animal can absorb are the very ones that the animal's digestion produces.

The digestive systems of all animals carry out digestion and absorption. This is true even though digestive systems are diverse in their detailed anatomy and physiology (**FIGURE 30.8**).

Digestive abilities determine which foods have nutritional value

To see a critically important aspect of animal nutrition, let's consider what happens if a person eats cellulose, the principal material in the cell walls of plants (see Concept 2.3). Cellulose molecules are very large, and they are unable to pass through the gut epithelium from the gut lumen into the blood. Moreover, humans have no way to digest cellulose: we have no cellulose-digesting enzymes, and unlike ruminants, we don't have a rumen stocked with symbiotic microbes that can break down cellulose molecules into smaller pieces. As a consequence, we get no nutritional benefit from cellulose. Even though cellulose molecules contain a lot of chemical energy that would be useful for us, we cannot access that energy. If we eat cellulose, it simply stays inside our gut lumen and is eliminated in our feces.
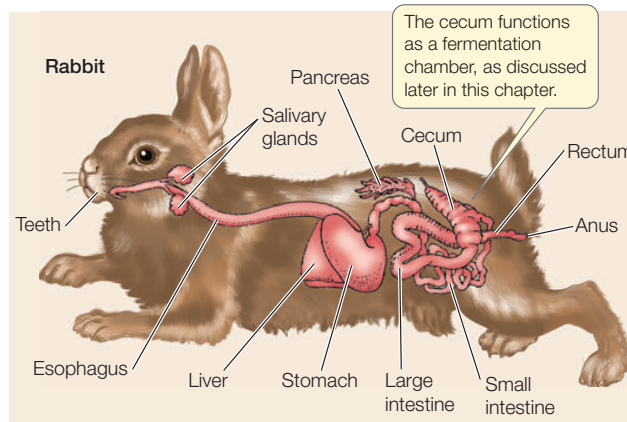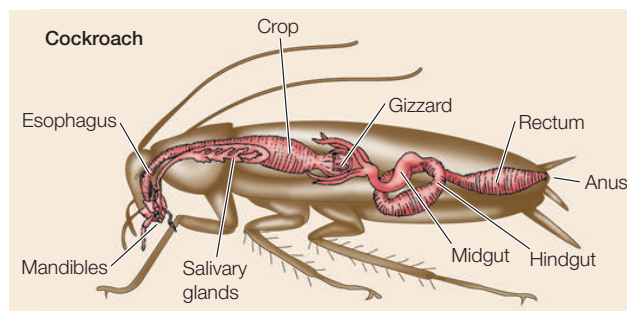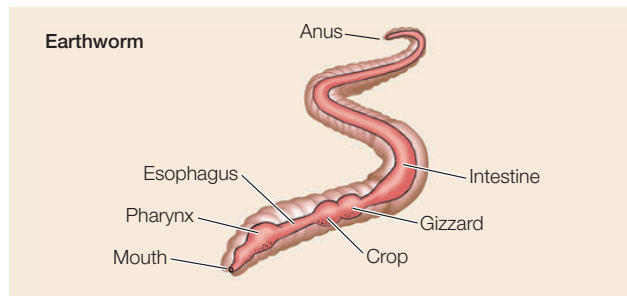
This example illustrates that the nutritional value of a food depends on more than its chemical composition. It also depends on an animal's ability to process the food so its components can be absorbed into the blood and delivered to the cells of the animal's body.

Animals are diverse in the foods they can digest

Each digestive enzyme is specific in the types of chemical bonds it can break (although some enzymes are more specific than others). **FIGURE 30.9** shows the digestion of a short

FIGURE 30.9 The Digestion of a Short Protein by Three Protein-Digesting Enzymes Each enzyme is specific for peptide bonds between particular types of amino acids. Arg = arginine; Gly = glycine; Leu = leucine; Pro = proline; Tyr = tyrosine.
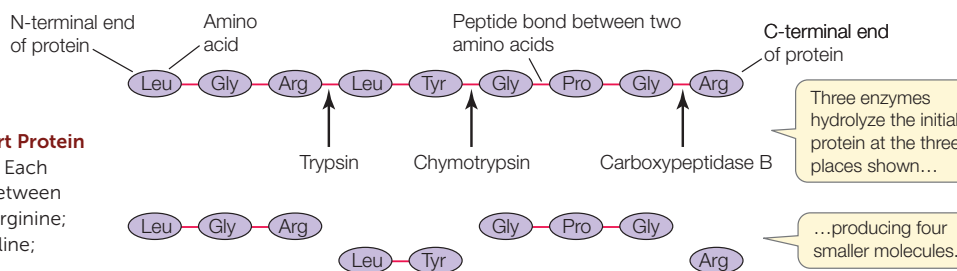
protein molecule by three protein-digesting enzymes (carboxypeptidase B, chymotrypsin, and trypsin). Each of these three enzymes acts specifically on peptide bonds between particular types of amino acids. Together, the enzymes break three of the peptide bonds in the protein, producing four small molecules from the single large molecule.

Because each digestive enzyme is specific in the types of bonds it can break, an animal's ability to digest foods is strictly determined by the particular digestive enzymes the animal synthesizes. An animal can break the types of chemical bonds in foods for which it has suitable digestive enzymes. It generally cannot break other types of bonds.

As a consequence of these principles, two related species can eat the same food but derive different nutritional value from it (because different sets of digestive enzymes may have evolved in the two species). For a vivid example, let's contrast species of mammals that eat lots of insects—such as insectivorous (insect-eating) bats—with other species of mammals that avoid insects or eat few of them. Insects are rich in a sugar named trehalose, which is not found in most other foods consumed by mammals. For trehalose in a mammal's gut lumen to be absorbed into the mammal's blood, each molecule of trehalose must be broken into two smaller molecules by a digestive enzyme called trehalase:

$$\text{Trehalose} \xrightarrow{\text{Trehalase}} \begin{array}{l}\text{Glucose} \\ \text{Glucose}\end{array}$$
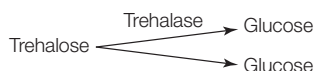
Insectivorous mammals have evolved the ability to produce lots of trehalase. Thus when they ingest insects, they are able to digest the trehalose in them, breaking each molecule into two molecules of glucose that they absorb into their blood and use. These mammals get a great deal of nutritional benefit from trehalose in their diet. In contrast, related species of mammals that do not eat insects typically have not evolved the ability to produce much trehalase. If they eat trehalose, they get almost no nutritional value from it. Thus two related mammals could eat identical meals of insects and obtain radically different nutritional benefits.

As we have seen, cellulose provides another example of these same points. Humans get no nutritional value from cellulose because we cannot digest it, but ruminants obtain a great deal of nutritional value from it because their symbiotic microbes break down cellulose. Among insects, some species are like people and get no nutritional value from cellulose. By contrast, certain wood-eating insects produce cellulose-digesting enzymes that allow them to digest cellulose and absorb it. And other wood-eating insects, such as some termites, maintain symbioses with microbes that break down cellulose for them.

Digestive abilities sometimes evolve rapidly

One of the most revealing discoveries in the study of human nutrition in the past decade concerns the digestion of milk sugar, lactose, by various human populations. When humans are first born, we produce the digestive enzyme lactase in our intestines. For this reason, babies can readily digest lactose in their mother's milk, breaking each lactose molecule into two

FIGURE 30.10 Rapid Evolution Occurring in Cattle-Raising Tribes Has Enabled People in the Tribes to Digest Milk Sugar throughout Life   Most African people have little or no ability to digest lactose (milk sugar) in adulthood. However, tribes that raise cattle, such as the Maasai, often exhibit high frequencies of distinctive genes that code for synthesis of lactase (an enzyme that digests lactose) throughout life.

parts (the monosaccharides galactose and glucose) that the infants can absorb and use. In most human populations, however, people stop making lactase as they grow older; by the time they are adults, they make little or no lactase and thus are unable to digest and use milk sugar. Most African tribes follow this pattern: the people in the tribes make lactase as infants but lose that ability in adulthood.

Researchers went to Africa to answer the question, What happens in African tribes that raise cattle? Certain tribes maintain herds of cattle that have enormous cultural significance. Tribal life is centered on caring for the herds. The cattle are used as special gifts, and the people use the blood and milk of the cattle as important foods (**FIGURE 30.10**).

The researchers discovered that in many cattle-raising tribes, the people have evolved the ability to synthesize lactase in adulthood. Thus, unlike most adult Africans, adults in the cattle-raising tribes can digest milk sugar all their lives. This ability to synthesize lactase in adulthood has evolved independently several times. We know this because the gene mutations responsible for lactase synthesis differ among tribes.

From this research came another important discovery—that nutritional processes can evolve rapidly in human populations. Some of the mutant genes responsible for adult lactase synthesis in African tribes first appeared, through the process of mutation, only about 5,000 years ago (a short time on an evolutionary time scale). Today these genes are widespread in the tribes where they occur.

Almost 100 percent of white-skinned people in northern Europe, such as white-skinned Dutch and Danish people, synthesize lactase as adults. How can this be? A large body of evidence indicates that the relevant mutant genes in northern European populations first appeared after their ancient ancestors migrated out of Africa and into Europe. Thus mutations that maintain lactase production in adulthood occurred in the European populations independently from the mutations in

the African tribes we just discussed. Possibly the mutant genes in northern Europe were favored by natural selection because people there eat large amounts of milk, cheese, and other dairy products.

When people from northern Europe immigrated to North America centuries ago, all of them probably had genes enabling them to synthesize lactase in adulthood. However, they intermarried with people who immigrated from other parts of the world. Today about 75 percent of white-skinned people in North America produce lactase in adulthood, but 25 percent do not and may have sufficient problems with digesting dairy products to be lactose intolerant.

Digestive abilities are phenotypically plastic

Individual animals—from fish to mammals—often modify their production of digestive enzymes during their lifetimes in response to the types of foods they are eating. In this way individuals can adaptively modify the nutritional values of foods.

If a lab rat has been eating a low-protein diet but is switched to a high-protein diet, its digestive tract starts to increase production of protein-digesting enzymes within 24 hours. A week later, when the response is fully developed, the rat will secrete protein-digesting enzymes at rates that are five times higher than before the switch in diet. By means of this digestive phenotypic plasticity, a rat that starts to eat a lot of protein soon develops a greatly enhanced ability to digest protein and thus tap dietary proteins for energy and amino acids. Conversely, when a rat that has been eating lots of protein is suddenly deprived of protein, it will greatly reduce production of protein-digesting enzymes.

Similarly, if a rat is given increased amounts of carbohydrates in its diet, it will increase production of carbohydrate-digesting enzymes. If it is given lots of lipids, it will increase lipid-digesting enzymes.

Parallel changes take place in absorption mechanisms. For example, researchers have observed that when people start to eat lots of sugar after a period of eating little sugar, their absorption mechanisms for taking up the products of sugar digestion become more effective.

CHECKpoint   CONCEPT **30.3**

✓ Are the terms "digestion" and "absorption" interchangeable? Compare the two.

✓ Humans derive no energy from the cellulose molecules in brussels sprouts. Does this imply that cellulose molecules, and brussels sprouts in general, are low in chemical energy?

✓ Why might the ability to produce lactase into adulthood be beneficial to people living in cultures heavily dependent on dairy products?

At this point we have discussed the fundamentals of nutrition, food gathering, and extraction of energy and nutrients from food. With this background, let's now take a closer look at the digestive systems of vertebrate animals.

CONCEPT **30.4** **The Vertebrate Digestive System Is a Tubular Gut with Accessory Glands**

The vertebrate digestive system consists of a tube, extending from mouth to anus and called the gut, that receives secretions from certain nearby glands, most notably the liver and pancreas (**FIGURE 30.11**; also see the bottom panel of Figure 30.8). The tissues of the gut wall are arranged in concentric layers (**FIGURE 30.12**). Surrounding the gut lumen is the gut epithelium, a functionally dynamic cell layer. Most cells in the epithelium are digestive–absorptive cells, which produce distinctive proteins, such as digestive enzymes, that function in digestion and absorption. In addition to the dominant digestive–absorptive cells, the gut epithelium also contains scattered mucus-secreting cells, plus scattered endocrine cells that secrete hormones involved in controlling the digestive tract (as you will see in Concept 30.5). Surrounding the epithelium and its underlying connective tissue (together called the mucosa) is a tissue layer called the submucosa, which contains blood and lymph vessels that carry absorbed nutrients to the rest of the body. The submucosa also contains a network of neurons that help control the secretory functions of the gut.

Two layers of smooth muscle surround the submucosa. The inner layer, composed of circular muscles, encircles the gut and constricts it when it contracts. The outer layer, composed of longitudinal muscles, shortens the gut when it contracts. Between the two muscle layers is a second network of neurons, which coordinates contractions of the muscle layers so that food materials in the gut are pushed along by waves of contraction called **peristalsis** or, at times, are pushed back and forth. The passage of materials through the gut is further controlled by sphincter muscles located at several places, such as the entrances to the stomach and small intestine. Sphincter muscles encircle the gut, and they contract so tightly that they seal off one part of the gut from another except when they are opened briefly in a controlled manner to let food materials pass through.

The neuron networks in the gut wall make up the enteric nervous system. This system is part of the autonomic nervous system, which controls many body functions without any need of conscious input and, in general, without voluntary control (see Concept 34.5).

An interesting aspect of the open central cavity of the gut tube, the gut lumen, is that it is anoxic, meaning it is devoid of O_2. Tapeworms and other gut parasites thus must have the ability to live without O_2, a very unusual ability for animals.

Several classes of digestive enzymes take part in digestion

Like most enzymes, the digestive enzymes are proteins. They break chemical bonds by hydrolysis, a reaction that splits a bond by adding a water molecule (see Figure 2.8). The digestive enzymes are classified in two ways. One is based on the type of food molecules the enzymes digest. Lipases hydrolyze bonds of lipids; proteases and peptidases hydrolyze the bonds between adjacent amino acids in proteins; and carbohydrases hydrolyze the bonds between adjacent sugar units of

(A)

(B)
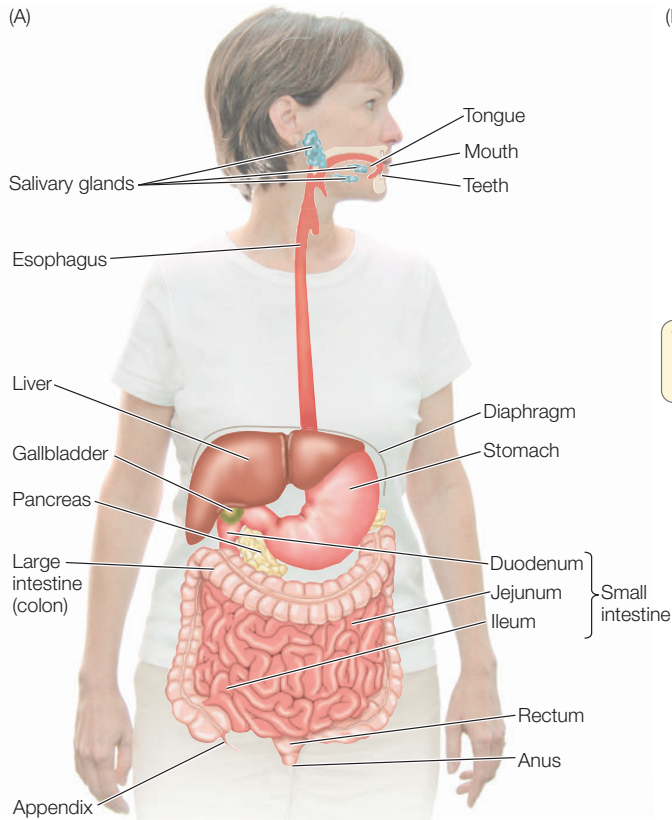
FIGURE 30.11 The Human Digestive System (A) The mouth, esophagus, and stomach are parts of the foregut. The small intestine corresponds to the midgut, and the large intestine corresponds to the hindgut. Three accessory glands shown are the salivary glands, liver, and pancreas. (B) The ducts via which secretions of the liver and pancreas enter the midgut lumen.

Go to ACTIVITY 30.3 The Human Digestive System
PoL2e.com/ac30.3
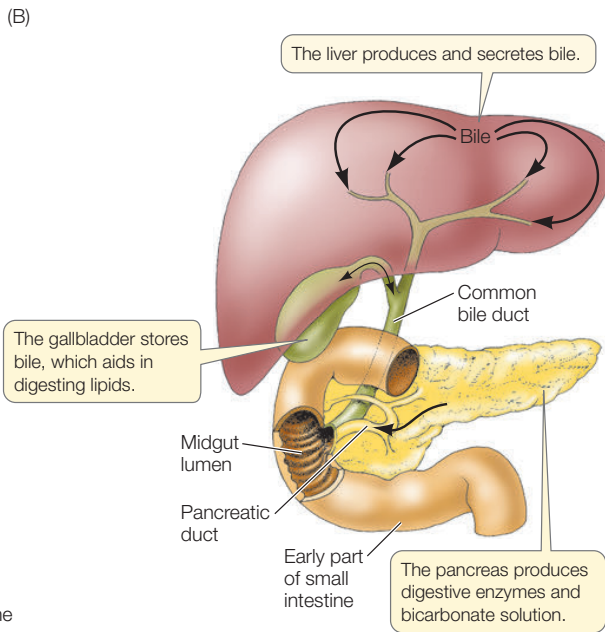
carbohydrates. Besides these general names, specific names are used for specific enzyme proteins.

Digestive enzymes are also classed by where they act:

• *Intraluminal enzymes* are secreted into the gut lumen and digest food molecules in the lumen.

• *Membrane-associated enzymes* are attached to the epithelial cells lining the gut lumen. They act when food molecules in the lumen come in contact with the gut epithelium.

• *Intracellular enzymes* are inside some of the gut epithelial cells and are involved in protein digestion.

Digestive enzymes typically act in sequences. Food proteins, for example, are first attacked by protein-digesting enzymes in the stomach that break the protein molecules into relatively large pieces. Other protein-digesting enzymes in the intestines then break these pieces into smaller pieces.

Processing of food starts in the foregut

The digestive tract begins with the **foregut**, which consists of the mouth, esophagus, and stomach—and in some animals, an expanded food-storage chamber (crop) or food-grinding chamber (gizzard) ahead of the stomach. When most vertebrates eat, they simply seize food with their mouth, then swallow it whole. Fish, amphibians, birds, and non-avian reptiles eat this way. Mammals, however, chew their food by using their teeth and jaw muscles, and as they chew, they start the process of carbohydrate digestion by secreting saliva from their salivary glands into their mouth cavity. Mammalian saliva contains a starch-digesting enzyme, amylase.

FIGURE 30.12 Tissue Layers of the Vertebrate Gut The organization of tissue layers is the same in all regions of the gut, but specialized adaptations of specific tissues characterize different regions.
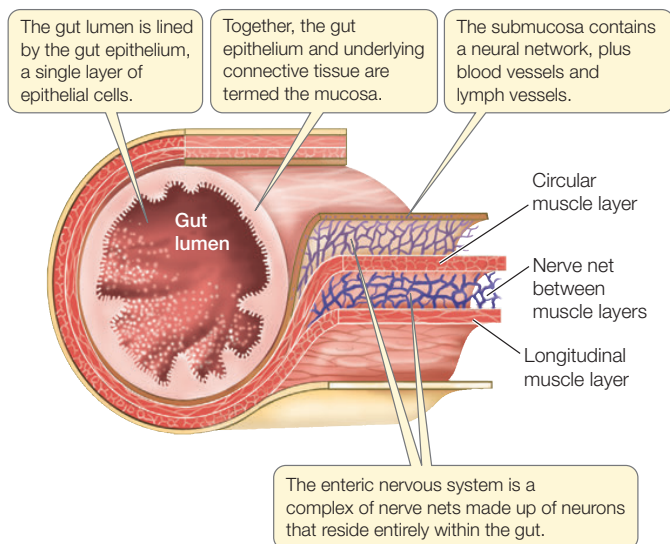
The esophagus typically serves simply as a passageway for food to reach the stomach from the mouth. Each time we swallow, a sphincter at the start of our esophagus opens briefly (under control of the enteric nervous system) to let food pass from our mouth into our esophagus. Then, after peristalsis has moved the food from the start of the esophagus to the end, the sphincter at the entrance to the stomach briefly opens to permit the food to enter the stomach.

The stomach is an expanded part of the foregut that, in most vertebrates, performs four major functions. First, the stomach serves as a storage chamber for newly ingested food. It can hold a large meal that is awaiting processing. Second, the stomach secretes hydrochloric acid (HCl), which mixes with food in the stomach lumen, helping cause food disintegration. When you think about the pHs that are sometimes achieved in the stomach, you will probably be amazed that living cells are capable of secreting the acid needed. In humans and dogs, the contents of the stomach lumen during meal processing can reach a pH of 0.8—the same as that of battery acid and ten times more acidic than lemon juice! Acid-secreting cells in the stomach epithelium secrete protons (H^+ ions) into the lumen, using energy from ATP, to achieve this astounding pH. The third major function of the stomach is to begin protein digestion. Certain cells in the stomach epithelium secrete protein-digesting enzymes called pepsins into the stomach lumen, where these enzymes start to break up proteins. Finally, the stomach mechanically squeezes food and mixes it with the acid and digestive enzymes. This is achieved by contractions of the smooth muscles in the stomach wall.

A fascinating challenge that had to be met during evolution arises from the fact that protein-digesting enzymes could potentially digest the very cells that synthesize them, killing the cells! The evolutionary solution to this challenge is that these enzymes are synthesized and secreted in inactive forms. Stomach cells synthesize and secrete pepsins as inactive pepsinogens, for example. Only after the pepsinogens arrive in the stomach lumen are they activated (by exposure to HCl) to form pepsins:

Low pH converts pepsinogens to pepsins. Newly formed pepsins activate other pepsinogen molecules.

Acid-secreting cell

Enzyme-secreting cell

Pepsinogen   Pepsin

HCl

Stomach lumen

Stomach epithelium
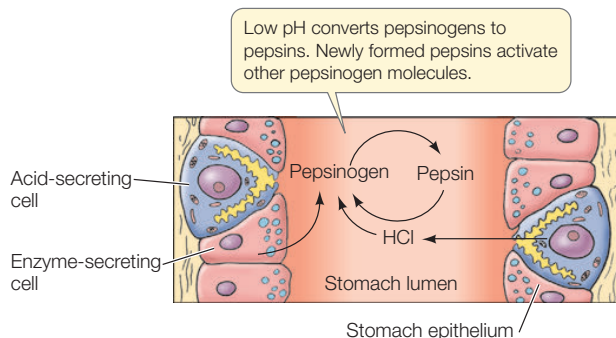
As we have noted, some vertebrates have evolved a fermentation vat for microbial symbionts in specialized, nonacidic parts of the foregut. All such animals are classified as **foregut** fermenters. The ruminants are one such group (see Figure 30.7). Kangaroos, hippos, sloths, colobus monkeys, and a few ground-dwelling, herbivorous birds are also foregut fermenters.

Food processing continues in the midgut and hindgut

After leaving the stomach, food travels through the **midgut** and **hindgut**, which are the first and second parts of the intestines. In humans and other mammals, the two parts differ in diameter: the midgut has a smaller diameter and is termed the small intestine; the hindgut has a larger diameter and is called the large intestine. The distinction between "small" and "large" does not apply in many vertebrates, however, because the two parts—although they differ in function—are the same in diameter. This is often the case in fish, for instance.

Fermentation vats for heterotrophic microbial symbionts have evolved as parts of the midgut or hindgut in some vertebrates. These animals, like the foregut fermenters, are all herbivores. Some fish, including catfish, carp, and tilapia, are **midgut fermenters**. Horses, zebras, rabbits (see Figure 30.8), rhinos, and apes are **hindgut fermenters**. So are geese, chickens, and ostriches. All profit from being able to ferment cellulose and hemicelluloses, greatly enhancing the energy value of plant foods.

The midgut is the principal site of digestion and absorption

The midgut is the principal site of digestion of all three major food categories: proteins, carbohydrates, and lipids. It is also typically the principal site of nutrient absorption. The products of digestion of all three categories of food are absorbed in the midgut, as are vitamins, minerals, and water.

In many vertebrates the inner midgut wall is highly folded, and the folds bear fingerlike projections called **villi** (singular *villus*) (**FIGURE 30.13**). In turn, each cell of the gut epithelium bears many microscopic projections called **microvilli**. Together, the midgut wall foldings, the villi, and the microvilli vastly enlarge the area of the luminal surface of the midgut epithelium (luminal surface = the surface facing toward the gut lumen). This huge surface area is of great functional importance for two reasons. First, many membrane-associated digestive enzymes are attached to the luminal surface of the gut epithelium. Second, absorption occurs across this surface.

Material from the stomach enters the midgut in a regulated manner. A sphincter muscle, the pyloric sphincter, seals off the stomach from the midgut when it is contracted. Under control of hormones and the enteric nervous system, this sphincter opens briefly to allow controlled, small squirts of digesting material to enter the midgut from the stomach. This measured introduction of material into the midgut ensures that the midgut digestive and absorptive processes are not overwhelmed and can keep up.

Both the pancreas and the liver are connected by ducts to the early part of the midgut (see Figure 30.11B). Digestive juices secreted by the pancreas and emulsifying agents secreted by the liver flow into the midgut lumen via these ducts. The pancreatic digestive juices contain a host of digestive enzymes, including ones that hydrolyze proteins, carbohydrates, and lipids. They also contain bicarbonate ions (HCO_3^-) that neutralize

In most vertebrates, an enormous absorptive surface is achieved by the sheer length of the tubular small intestine…

…and the folding of its lining.

Intestinal folds

Villi

Blood and lymph vessels

Blood capillaries

Villus

Fingerlike **villi** increase the surface area of these folds…

…and the epithelial cells covering the villi bear **microvilli**, increasing the absorptive surface area still more.

Microvilli

Epithelial cell

Lymph vessel

FIGURE 30.13 Folds, Villi, and Microvilli Make the Surface Area of the Midgut Epithelium Enormous   The large surface area increases the midgut's ability to absorb nutrients. It also increases the area of the surface to which membrane-associated digestive enzymes are attached.

the highly acidic pH of the material that enters the midgut from the stomach. The pancreas synthesizes and secretes protein-digesting enzymes as inactive molecules termed proenzymes. Only after they reach the midgut lumen are they enzymatically activated to hydrolyze food proteins.

Large food molecules are broken down into their smallest molecular subunits during digestion in the midgut. Proteins are broken down into amino acids; carbohydrates into simple monosaccharides (see Concept 2.3) such as glucose, galactose, and fructose; and lipids into fatty acids and glycerol (glycerin) (see Concept 2.4). These small molecules are then absorbed.

Let's now look briefly at the digestion and absorption of each of the major food categories. Recall that protein digestion starts in the stomach. It continues in the midgut lumen, where the products of stomach digestion are broken down further by protein-digesting enzymes made by the pancreas and gut epithelium (see Figure 30.9). These processes produce both single amino acids and short chains of two or three amino acids, which are absorbed into midgut epithelial cells. Inside these cells, the short chains are further hydrolyzed, so that the final product of protein digestion consists of just single amino acids. These are then transported into the blood vessels in the submuscosa, completing absorption.

In mammals, carbohydrate digestion starts in the mouth with the action of saliva enzymes that help break down starches. It is completed in the midgut. Often the final step in carbohydrate digestion in the midgut is the hydrolysis of a disaccharide—consisting of two linked simple sugar molecules—into two monosaccharide (simple sugar) molecules. The enzymes responsible are called disaccharidases. (Two of the midgut disaccharidases—lactase and trehalase—have been discussed earlier in this chapter.) The monosaccharides are then absorbed across the cells of the midgut epithelium to enter the submucosal blood vessels.

Lipid digestion starts and ends primarily in the midgut. Lipids present a special challenge for digestion because they are not water-soluble. The liver meets this challenge by secreting bile

into the midgut. Bile salts and other bile components act as detergents, emulsifying food lipids in the midgut lumen into great numbers of tiny droplets. The lipids then have a high surface area, allowing lipid-digesting enzymes to break the lipids into fatty acids and glycerol. The bile salts then continue to associate with the fatty acids, keeping them in solution until the fatty acids are absorbed into midgut epithelial cells. An interesting characteristic of bile salts is that they are not modified by this process, and in fact are reabsorbed and then reused in processing one meal after another. After fatty acids and glycerol are absorbed into midgut epithelial cells, they are reassembled into simple lipid molecules, which form aggregates with proteins synthesized by the cells. These lipoprotein aggregates—in which the lipids are emulsified by the proteins—then pass into lymph vessels in the submucosa, and later they enter the bloodstream.

The cellular mechanisms by which digestive products enter and leave the gut epithelial cells during absorption include diffusion, facilitated diffusion, and secondary active transport. Of these, the most important is secondary active transport (see Concept 5.3), which requires ATP that the midgut epithelial cells synthesize.

LINK

The various mechanisms for moving molecules across membranes are discussed in **Concepts 5.2 and 5.3**

The hindgut reabsorbs water and salts

The hindgut—called the large intestine or colon in mammals—has two main functions. First, it stores indigestible wastes, in the form of accumulated feces, between defecations. The feces are stored in the final portion of the hindgut, the rectum, until eliminated.

Second, the hindgut completes the reabsorption of needed water and salts from the gut contents prior to elimination of the feces. This may sound like a humble function, but it is vitally important. In humans, about 7 liters of a watery solution containing Na^+, Cl^-, and other ions are secreted from the blood into the gut per day to facilitate processing of food. This large volume needs to be returned to the blood. Diseases such as cholera and dysentery can block reabsorption of water and salts by the

hindgut, and in such cases a person can rapidly lose such massive quantities of water and salts through diarrhea that death quickly results.

We have seen how the vertebrate digestive system digests and absorbs a single meal. Finally we will look more closely at nutrition from meal to meal.

CONCEPT **30.5** **The Processing of Meals Is Regulated**

Most animals do not eat continuously. Instead, they alternate between an absorptive state (food in the gut) and a postabsorptive state (no food in the gut). This alternation poses two important challenges. First, for blood homeostasis to be maintained, the concentrations of glucose and other nutrient molecules in the blood plasma must be stabilized, so they do not skyrocket during meals and plummet between meals. Second, nutrients must be stored while they are abundant during the absorptive state and then released from those stores between meals.

Hormones help regulate appetite and the processing of a meal

Vertebrates have more than ten different types of scattered endocrine (hormone-producing) cells in the gut epithelium. The endocrine cells in one region secrete different hormones than the endocrine cells in other regions. This means that location-specific endocrine signals can be sent between gut regions to help coordinate the processing of a meal, complementing the coordination provided by the enteric nervous system.

When an animal eats and food arrives in its stomach, endocrine cells in the stomach epithelium secrete the hormone gastrin into the blood. Gastrin then travels in the blood to all the other stomach epithelial cells, some of which are specialized to synthesize acid (HCl) or pepsins. Gastrin stimulates these cells to secrete acid and pepsins, which help break down the food (**FIGURE 30.14**).

The entry of acidified, partly digested food material into the midgut initiates several important endocrine controls. Recall

that the material is released into the midgut in small bursts. Each burst stimulates two distinct sets of endocrine cells in the midgut epithelium (actually there are more than two sets, but we will discuss two here). One set releases secretin (the first hormone ever identified) into the blood, and the other releases cholecystokinin (CCK). When these two hormones reach the stomach, they tend to inhibit stomach acid secretion and muscle contraction (see Figure 30.14). This inhibition is maintained until the midgut has processed the current burst of material from the stomach. The two hormones also affect the pancreas and liver. Secretin stimulates the pancreas to secrete bicarbonate, which flows in the pancreatic juice to the midgut, where it neutralizes the acidity of the recently arrived stomach material. Secretin and CCK, acting synergistically, also stimulate the pancreas to secrete its digestive enzymes—and the liver to secrete bile—into the midgut.

Appetite is also controlled in part by hormones. For example, when the stomach is empty, it secretes ghrelin (pronounced gre-lin), a hormone that stimulates appetite. Another hormone, leptin (named after a Greek word for "thin"),
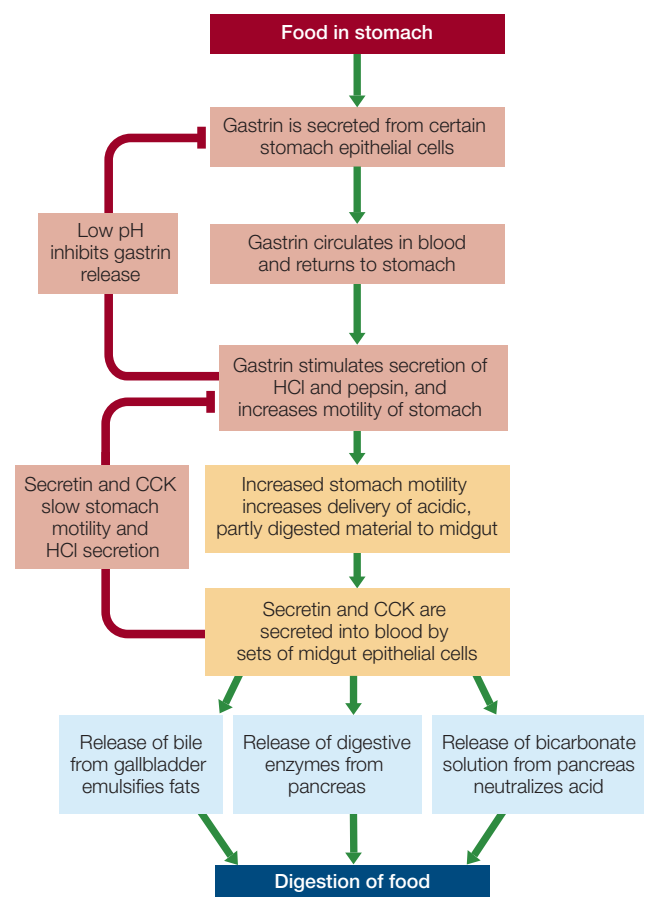
FIGURE 30.14 Hormones Control the Processing of a Meal
The hormones gastrin, cholecystokinin (CCK), and secretin are involved in feedback loops that control the processing of food in the digestive tract. Red lines indicate inhibitory actions; green lines indicate stimulatory actions.

provides information to the brain to suppress appetite. Leptin is secreted by fat cells. High leptin levels indicate that there are many fat cells, and thus there is not a great need to eat. Leptin was discovered, and its properties are still being explored, through studies of mutant mice (**FIGURE 30.15**).

Go to ANIMATED TUTORIAL 30.1
Parabiotic Mice Simulation
PoL2e.com/at30.1

Insulin and glucagon regulate processing of absorbed food materials from meal to meal

Insulin and glucagon are two of the most important hormones that regulate blood nutrient levels—and the storage and release of nutrients in the body—as animals switch back and forth between the absorptive and postabsorptive states. Both hormones originate in the pancreas. The pancreas is composed of two major parts. The cells in one part perform the exocrine functions we have already discussed—secreting digestive enzymes and bicarbonate into the pancreatic ducts to be carried to the midgut. The other part of the pancreas consists of structures termed the islets of Langerhans. The cells here are endocrine cells that secrete hormones into the blood. One subset of the endocrine cells, called beta (β) cells, secretes insulin. Another subset, the alpha (α) cells, secretes glucagon.

As a meal is processed, glucose, fatty acids, and other products of digestion enter the blood in abundance. Insulin is secreted at this time. It stimulates many types of cells in the body to take up glucose. In this way insulin plays two major roles. It stabilizes the blood glucose concentration, keeping it from rising too high (**FIGURE 30.16**). It also promotes the use and storage of glucose when glucose is available in abundance. Insulin stimulates both liver and muscle cells to synthesize glycogen from blood glucose, thereby storing the glucose for future use. Insulin also has roughly parallel effects on blood fatty acids and amino acids. It stimulates uptake of both from the blood, storage of fatty acids by formation of lipids in fat cells, and use of amino acids for protein synthesis.

During the postabsorptive state between meals, insulin secretion stops, and the pancreas secretes glucagon. In many ways, glucagon's effects are the opposite of insulin's. Glucagon promotes both breakdown of glycogen into glucose molecules and release of glucose into the blood. In this way it helps stabilize the blood glucose concentration by preventing the

INVESTIGATION

FIGURE 30.15 A Single-Gene Mutation Leads to Obesity in Mice   In mice the *Ob* gene codes for the protein leptin, a satiety (feeling of fullness) factor that signals the brain when enough food has been consumed. The recessive *ob* allele is a loss-of-function allele. Accordingly, *ob/ob* mice do not produce leptin; they do not experience satiety and thus become obese. The receptor protein in the brain that responds to leptin is coded by the *Db* gene. Mice homozygous for the recessive loss-of-function allele *db* cannot respond to leptin, even if they produce it, and they become obese.[a]

HYPOTHESIS

Mice that cannot produce the protein leptin will not become obese if they are able to obtain leptin from an outside source.

METHOD

1. Create two strains of genetically obese laboratory mice, one of which lacks functional leptin (genotype *ob/ob*) and one which lacks the receptor for leptin (genotype *db/db*).
2. Create parabiotic pairs by surgically joining the circulatory systems of a non-obese (wild-type) mouse with a partner from one of the obese strains.
3. Allow mice to feed at will.

Parabiotic pair

Wild-type mouse   Genetically obese mouse
(*Ob/–* and *Db/–*)   (either *ob/ob* or *db/db*)

RESULTS

Parabiotic *ob/ob* mice obtain leptin from the wild-type partner and lose fat. Parabiotic *db/db* mice remain obese because they lack the leptin receptor and thus the leptin they obtain from their partner has no effect.
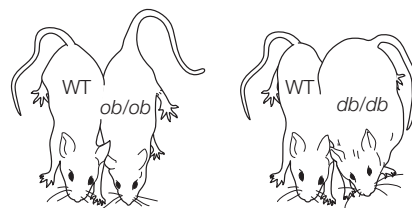
CONCLUSION

The protein leptin is a satiety signal that acts to prevent overeating and resultant obesity.

ANALYZE THE DATA

In a further experiment, leptin was purified and injected into *ob/ob* and *Ob/Ob* (wild-type) mice daily. The data in the table were collected before the injections began (baseline) and 10 days later.

Characteristic measured	Baseline		Day 10	
	ob/ob	*Ob/Ob*	*ob/ob*	*Ob/Ob*
Food intake (g/day)	12.0	5.5	5.0	6.0
Body mass (g)	64	35	50	38
Metabolic rate [ml O$_2$/(kg × hr)]	900	1,150	1,100	1,150
Body temperature (°C)	34.8	37.0	37.0	37.0

A. Do the data support the hypothesis that leptin is a satiety signal? Why or why not?

B. Discuss what factors might explain the loss of body mass in the *ob/ob* mice.

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]D. L. Coleman and K. P. Hummel. 1969. *American Journal of Physiology* 217: 1298–1304.
 D. L. Coleman. 1973. *Diabetologia* 9: 294–297.
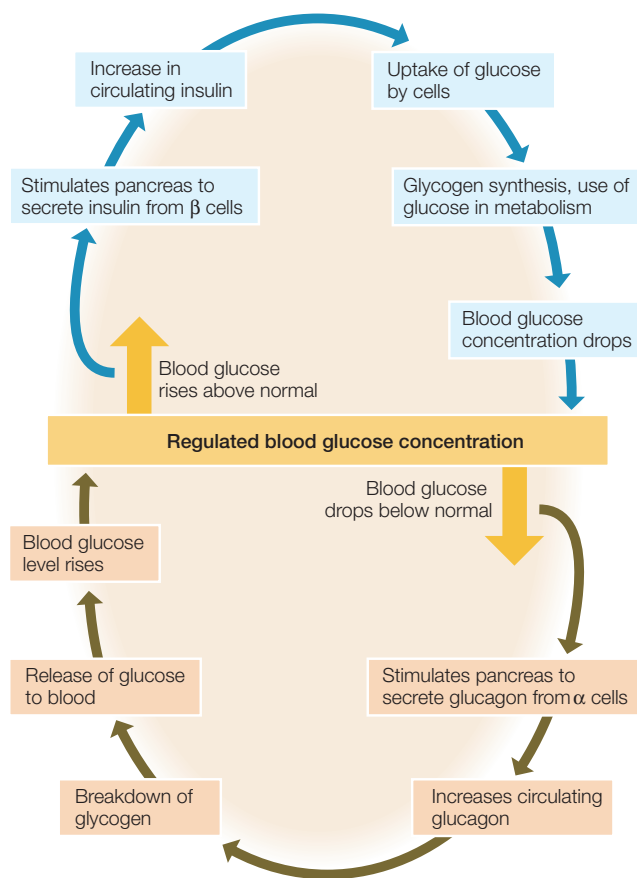
FIGURE 30.16 Regulating Glucose Concentration in the Blood
Insulin (blue) and glucagon (brown) together maintain homeostasis in blood glucose concentration by negative feedback. Stability of blood glucose concentration is important for several reasons. One is that glucose, obtained from the blood, is the brain's essential source of metabolic energy.

Go to ANIMATED TUTORIAL 30.2
Insulin and Glucose Regulation
PoL2e.com/at30.2

concentration from falling too low (see Figure 30.16). It also ensures that cells throughout the body have a glucose supply even when foods are not being digested. In addition, glucagon stimulates breakdown of stored lipids and release of fatty acids into the blood.

CHECKpoint CONCEPT 30.5

✓ Blood glucose concentration is often said to be subject to negative feedback control by insulin. Explain.

✓ Why is it important that the endocrine cells in the gut epithelium do not all secrete the same hormone?

✓ Glucose is not normally found in a person's urine. Particularly in earlier decades, glucose in the urine was used as a diagnostic indication of diabetes. In one form of diabetes, termed Type I, the β cells in the islets of Langerhans are defective. Why would this condition lead to glucose in the urine?

Q What are some of the specific types of organic molecules that animals must obtain in their foods, and why do they need them?

ANSWER Animals must obtain all their essential amino acids in their foods because they are not able to synthesize those amino acids and will develop deficiency diseases if they have inadequate amounts (Concept 30.1). Many types of mammals require eight amino acids, called the essential amino acids: isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine. Similarly, animals are unable to synthesize vitamins and essential fatty acids. To get adequate amounts, they must obtain these molecules in their foods. Two points should be stressed for fully understanding these concepts. First, the essential nutrients are not the same for all animals (Concept 30.1). Second, microbial symbionts sometimes provide essential nutrients, in which case animals do not literally need to eat the nutrients (Concept 30.2). Ruminants, for example, do not need to ingest certain required B vitamins—even though they are unable to synthesize them—because the microbial symbionts in their rumen synthesize the vitamins.

SUMMARY

CONCEPT 30.1 Food Provides Energy and Chemical Building Blocks

■ Animals are heterotrophs that derive their energy and chemical building blocks from eating other organisms.

■ A measure of the energy content of food is the **calorie** (**cal**), the amount of heat required to raise the temperature of 1 gram of water by 1°C. What we typically refer to as "calories" in our food are actually **kilocalories** (**kcal**). The metric unit for measuring energy is the **joule**. **Review Figures 30.1 and 30.2**

■ There are three major types of food molecules: lipids (fats and oils), carbohydrates, and proteins. Lipids contain about twice as many calories per unit of weight as carbohydrates and proteins. Animals store extra energy as lipids and glycogen.

■ Food provides carbon skeletons, termed **essential**, that animals cannot synthesize themselves.

■ Adult humans require eight **essential amino acids** and at least two **essential fatty acids**. **Review Figure 30.3**

■ **Vitamins** are essential carbon molecules needed in tiny amounts. They are either water-soluble or lipid-soluble. **Review Table 30.1 and ACTIVITY 30.1**

■ **Essential minerals** are chemical elements that are required in the diet in addition to carbon, hydrogen, oxygen, and nitrogen. **Review Table 30.2 and ACTIVITY 30.2**

■ **Malnutrition** results when any essential nutrient is lacking from the diet. Chronic malnutrition causes **deficiency diseases**.

(continued)

SUMMARY *(continued)*

CONCEPT 30.2 Animals Get Food in Three Major Ways

■ Animals can be characterized by how they acquire their food. Some animals feed on easily visible food items that they eat by targeting them individually. **Suspension feeders** (or filter feeders) are aquatic animals that feed indiscriminately on large numbers of tiny food particles that they collect from the surrounding water. **Review Figures 30.4 and 30.5**

■ Some animals rely on **symbiosis** with microbes to obtain at least some of their nutrients. Reef-building corals, for example, contain photosynthetic algae that supply carbon compounds to the coral. Microbes in the rumen of ruminants break down cellulose that the animals are unable to digest. **Review Figures 30.6 and 30.7**

CONCEPT 30.3 The Digestive System Plays a Key Role in Determining the Nutritional Value of Foods

■ In most animals, digestion takes place in a tubular gut that has two openings: the mouth and the anus. Food is processed within the gut lumen. **Review Figure 30.8**

■ **Digestion** is the enzymatic breakdown of food molecules into smaller molecules that can cross the gut epithelium. The process of transporting molecules from the gut lumen into the blood is called **absorption**.

■ Each digestive enzyme can break only specific types of chemical bonds in food molecules. For example, the sugars trehalose and lactose are broken down by trehalase and lactase, respectively. **Review Figure 30.9**

■ The nutritional value of a food depends on the ability of an animal's digestive tract to process the food in such a way that nutrients in the food can be absorbed.

■ Animal species vary in the digestive enzymes they produce and thus in their ability to gain nutritional value from specific food molecules.

■ An individual animal can adjust its digestive and absorptive capabilities in response to changes in its diet.

CONCEPT 30.4 The Vertebrate Digestive System Is a Tubular Gut with Accessory Glands

■ The vertebrate digestive system consists of a tubular gut and several secretory organs—notably the liver and pancreas—that aid in digestion. **Review Figure 30.11 and ACTIVITY 30.3**

■ The gut consists of an inner gut epithelium that secretes mucus, enzymes, and hormones and absorbs nutrients; a submucosa containing blood and lymph vessels; two layers of smooth muscle; and a nerve network called the enteric nervous system, which is part of the autonomic nervous system. **Review Figure 30.12**

■ **Peristalsis** moves food along the length of the gut. Sphincters block food passage at certain locations but relax at controlled moments to let food through.

■ Digestive enzymes are categorized on the basis of the types of food molecules they hydrolyze and by where they function (intraluminal, membrane-associated, or intracellular).

■ The vertebrate gut can be divided into several compartments with different functions. The **foregut** includes the mouth, esophagus, and stomach. The **midgut** is the principal site of digestion and absorption. The **hindgut** stores waste between defecations and reabsorbs water and salts from the feces.

■ Digestion begins in the mouth in mammals. Mammals chew their food, and their saliva contains the starch-digesting enzyme amylase.

■ The stomach breaks up food, begins the process of protein digestion, and controls the flow of food materials to the small intestine. Stomach cells secrete HCl, pepsinogen (the inactive form of pepsin), and mucus that protects the stomach wall.

■ In most vertebrates, absorptive areas of the gut are characterized by a large surface area produced by extensive folding, including **villi** and **microvilli**. **Review Figure 30.13**

■ Digestive juices secreted by the pancreas and emulsifying bile secreted by the liver flow into the lumen of the early part of the midgut. Bicarbonate ions from the pancreas neutralize the pH of the food entering from the stomach.

■ Some animals have fermentation chambers where symbiotic microbes help break down foods, synthesize B vitamins, and recycle nitrogen. The host animal is classified as a **foregut fermenter**, **midgut fermenter**, or **hindgut fermenter**, based on the location of the fermentation compartment within the digestive tract.

CONCEPT 30.5 The Processing of Meals Is Regulated

■ Animals alternate between an absorptive state (food in the gut) and a postabsorptive state (no food in the gut).

■ The actions of the stomach and small intestine are controlled by hormones such as gastrin, secretin, and cholecystokinin (CCK). **Review Figure 30.14**

■ Food intake is governed by sensations of hunger and satiety, which are determined by brain mechanisms responding to feedback signals provided in part by the hormones ghrelin and leptin. **Review Figure 30.15 and ANIMATED TUTORIAL 30.1**

■ Insulin and glucagon from the pancreas control the glucose concentration of the blood. Insulin stimulates the uptake and use of glucose by many cells of the body. If blood glucose concentration falls, glucagon secretion increases, stimulating the liver to break down glycogen and release glucose to the blood. **Review Figure 30.16 and ANIMATED TUTORIAL 30.2**

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is30

Go to LaunchPad at **macmillanhighered.com/launchpad** for additional resources, including LearningCurve Quizzes, Flashcards, and many other study and review resources.

31

Breathing

Reinhold Messner on the summit of Mount Everest after ascending without supplemental oxygen.

Who knows when someone first tried to reach the top of Mount Everest? People have been living in the Himalayan highlands for 10,000–20,000 years, and it seems inevitable that some would have been intrepid explorers who climbed the mountains. We can be sure those prehistoric explorers had no tanks of compressed O_2. Whatever they accomplished, they did while breathing the natural air.

In the modern era of mountaineering, E. F. Norton was one of the first to try to reach Everest's summit while breathing natural air. In 1924 he reached 8,500 meters (28,000 feet)—just 300 meters (1,000 feet) from the top. Biologists at the time knew little about the challenges of extreme elevations. The overwhelming difficulty of climbing at 8,500 meters was a surprise. Norton tried to take charge of his situation by counting steps. Attempting to take 20 consecutive uphill steps, he never could and had to turn back.

When Reinhold Messner and Peter Habeler finally made the first recorded climb to the summit of Everest while breathing natural air in 1978, the extreme demands of the final 1,000 meters were well known. Messner is one of the most gifted mountaineers in history. By now he has climbed all 14 peaks in the world that are higher than 8,000 meters—all while breathing natural air. Yet he and Habeler required an entire hour to climb Everest's final 100 meters.

The most fundamental problem at high elevations is that the atmospheric pressure is far lower than at sea level. Of the molecules in the air, 21 percent are O_2 at all elevations. But because of the low pressure at high elevation, the air is dilute: the number of molecules per liter is reduced. An unusual aspect of this stress is that it is inescapable. People or other animals can escape the cold temperatures of high elevation by crawling into tents or burrows. The air they breathe, however, remains dilute everywhere. The breathing organs—the lungs—face an unavoidable challenge to take in enough O_2 to meet the body's

needs. At the peak of Everest, the air has only a third as many molecules per unit of volume as at sea level.

The highest permanent human settlements are at 3,500–4,500 meters, where the air is about 60 percent as concentrated as at sea level. Prehistoric people established such settlements at three places on Earth: the Andes, the Tibetan plateau, and the Ethiopian highlands. Biologists have recently discovered that genetic adaptations to high elevation have started to evolve in these populations even though they have been living there for only a few hundred generations. Some species of birds and mammals, such as guanacos and vicuñas, are highly adapted because of their long evolutionary histories in the high mountains.

Q Why is climbing uphill at 1.7 meters per minute (100 meters/hour) the most intense work that is possible for a human near Everest's summit?

<div style="column">

CONCEPT 31.1 Respiratory Gas Exchange Depends on Diffusion and Bulk Flow

The **respiratory gases** that animals must exchange with their environment are oxygen (O_2) and carbon dioxide (CO_2). Cells require O_2 from the environment so they can produce ATP by cellular respiration (see Concept 6.2). Specifically, O_2 is needed in the mitochondria of each cell because electrons removed from food molecules must have a final resting place after they pass through the mitochondrial electron transport chain, releasing the energy that the mitochondria use to make ATP. Their final resting place is in combination with O_2 to make water (see Figure 6.9). This water simply mingles with the rest of the water in an animal's body.

Cellular respiration also produces CO_2 because CO_2 is one of the products of the citric acid cycle (see Figure 6.8). Unlike the H_2O produced by cellular respiration, CO_2 cannot be allowed simply to accumulate in an animal's body water. CO_2 is often called a "gaseous acid" because it tends to lower the pH of the body fluids if it accumulates in them. It can also have other disadvantageous effects. For these reasons, as an animal takes in O_2 from its environment and delivers it to cells for use in cellular respiration, the animal must rid itself of the CO_2 made by cellular respiration by releasing the CO_2 into its environment.

LINK

You can review aerobic cellular respiration and the production of ATP in **Concept 6.2**

Think about the path an O_2 molecule must travel from the atmosphere to a mitochondrion inside a muscle cell in your calf. First the O_2 molecule must travel deep into your lungs. Then it must cross two simple epithelia to enter the blood: first the epithelium forming your lung wall and then the epithelium forming the wall of one of your blood capillaries. The molecule must then travel in the blood from your thorax to your leg to reach a blood capillary next to the muscle cell. Then, to enter the cell, the molecule must cross the wall of the blood capillary (an epithelium) and pass through the cell membrane of the muscle cell. Finally, the molecule must travel through the cell cytoplasm to reach and enter a mitochondrion. CO_2 must make essentially the same journey in reverse.

Notice that some of the steps in an O_2 molecule's trip from atmosphere to mitochondrion are very short (**FIGURE 31.1**). The distance across each epithelium is about 1 micrometer (μm) or less. The distance across a cell membrane is roughly 0.01 μm. The distance from the cell membrane of a muscle cell to the deepest mitochondrion inside the cell is likely to be only 5–50 μm.

By contrast, some of the other steps in an O_2 molecule's trip are extraordinarily long. To pass deep into your lungs from your nostrils, an O_2 molecule needs to travel about 500,000 μm (0.5 meter). To travel in your blood from your lungs to a muscle cell in your calf, the molecule needs to travel about 1,000,000 μm!

Distance is therefore one of the factors we need to take into account as we consider the travels of O_2 and CO_2 molecules between the atmosphere and an animal's cells.

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<div style="column">
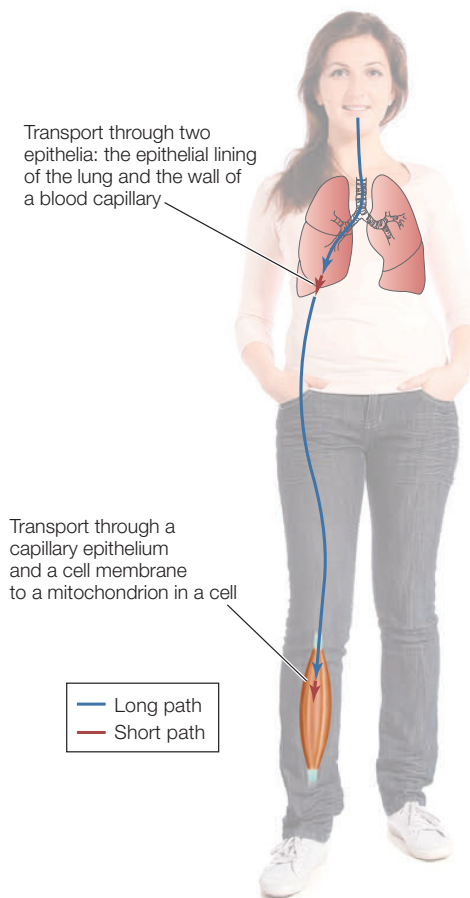
FIGURE 31.1 The Path of O_2 Molecules into an Animal's Body Consists of Long and Short Steps

Also note this important point: active transport mechanisms for O_2 do not exist (see Concept 5.3). This means that energy supplied by ATP cannot be used to drive O_2 through an epithelium or cell membrane. Instead, O_2 always crosses epithelia and cell membranes by diffusion. Much the same can be said for CO_2, although active transport of CO_2 is known in certain cases in the animal kingdom.

The diffusion of gases depends on their partial pressures

Atoms and molecules undergo ceaseless random motions at atomic–molecular scales of space. Diffusion results from these random motions (see Concept 5.2). If a certain type of molecule is more concentrated in one region of a solution than another, it is a simple statistical fact that random motions will carry more molecules away from the concentrated region than they will carry into it. In this way, the random motions cause a net transport of molecules from the concentrated region to neighboring dilute regions. This is the principle by which O_2 and CO_2 diffuse in a solution.

LINK

See **Concept 5.2** for further information about the diffusion of molecules in solution

</div>

Complexities arise where liquids and gases are in contact. When O_2 is present in a gas mixture, it is simply one of the types of gas molecules. For example, in air 21 percent of the molecules are O_2. When O_2 is present in a liquid, it is in solution. You have seen that when you dissolve sugar in water, the sugar molecules become invisible. O_2 does exactly the same thing. When it dissolves in water, the individual O_2 molecules fit in between water molecules and become invisible (bubbles, regardless of how tiny, are not in solution).

What happens when O_2 diffuses from a gas into an aqueous (watery) solution—so that the O_2 molecules switch from being in a gaseous to a dissolved state—or vice versa? How can we predict whether this diffusion will be from the gas to the liquid or in the opposite direction? Chemists have discovered that if you measure a property called **partial pressure**, you can solve this problem. O_2 always diffuses from where its partial pressure is high to where its partial pressure is low. Partial pressure is easily defined in a gas phase (not so easily in a liquid phase): it's simply the portion of the total pressure exerted by any particular gas, such as O_2, in a mixture of gases.

To clarify the relationship between concentration and partial pressure, suppose we have a gas phase in contact with a liquid phase, as in **FIGURE 31.2**. Within a gas phase, the concentration and partial pressure of O_2 are proportional to each other. O_2 always diffuses from where its concentration is high to where its concentration is low, for the reasons already discussed. Because concentration and partial pressure are proportional, O_2 also diffuses from where its partial pressure is high to where its partial pressure is low. Within a liquid phase, the same statements are true. Concentration and partial pressure are proportional, and O_2 always diffuses from places where both are high to places where both are low.

However, when O_2 diffuses *between* a gas phase and a liquid phase, its direction of diffusion cannot be predicted from its concentrations in the two phases. When diffusing from one phase to the other, O_2 moves from where its partial pressure is high to where it is low, even though this direction may be opposite to what concentrations would suggest (the partial pressures have the advantage that they take into account the effects of the solubility of O_2 in water, which the concentrations do not take properly into account). The same principles apply to all other gases, such as CO_2 and N_2.

The **law of diffusion for gases**—often called **Fick's law**—is expressed by the equation

$$\text{Rate of diffusion between two locations} = DA\frac{P_1 - P_2}{L}$$

where

- D, the diffusion coefficient, depends on the diffusion medium (air or water), the temperature, and the particular gas that's diffusing
- A is the cross-sectional area across which the gas is diffusing
- P_1 and P_2 are the partial pressures of the gas at the two locations
- L is the distance (diffusion path length) between the two locations

This equation applies to the diffusion of all gases, and it applies within a gas phase, within a liquid phase, and between gas and liquid phases. Partial pressures are expressed in units of pressure. Thus, the standard unit for partial pressure is the pascal (Pa). Alternative units in common use are atmospheres (atm) and millimeters of mercury (mm Hg), the latter referring to the height of a mercury column the pressure can support (1 atm = 760 mm Hg = 101.3 kilopascals).

Diffusion can be very effective but only over short distances

Let's ask the simple question, Can diffusion move lots of O_2 (or CO_2) from one place to another in a short period of time? The answer is both yes and no. This distinction is one of the most important concepts to understand about diffusion. As we'll see, the answer depends on the distance involved.

Notice that the distance between two locations, L, appears in the denominator of the diffusion equation. The rate of diffusion between two locations increases as the distance between the locations decreases.

Suppose O_2 on the outside of a cell is diffusing across the cell membrane into the cell. The distance, L, for this diffusion is very short—about 0.01 μm. Thus this diffusion will be very fast. In fact, if you were to arrange to have a high O_2 concentration outside a cell and a low concentration inside, diffusion would move enough O_2 into the cell in just *0.1 microsecond* to halve the concentration difference between outside and inside! This explains why all cells depend simply on diffusion for O_2 to pass into them through their cell membranes.

By contrast, suppose O_2 present in body fluids near your lungs is diffusing through your body fluids to a muscle cell in your calf. For this diffusion, L is much longer—about 1 meter. This diffusion therefore will be slow—far slower, in fact, than

A **gas phase** such as air

Where partial pressure is relatively high, concentration is also relatively high.

Across the interface, at a place where partial pressure is relatively high, concentration is not necessarily relatively high. The partial pressures dictate the direction of diffusion.

A **liquid phase** such as fresh water or tissue fluid

Where partial pressure is relatively high, concentration is also relatively high.

FIGURE 31.2 A Gas Always Diffuses from High Partial Pressure to Low Partial Pressure The concepts illustrated here apply to any gas. The gas is assumed to be in solution in the liquid phase. *Within* a gas phase or *within* a liquid phase, the partial pressure and concentration of a gas are proportional. Thus as the gas diffuses from high to low partial pressure, it also diffuses from high to low concentration. Concentration, however, is not a guide to diffusion across an interface *between* a gas and a liquid phase. Diffusion occurs from high to low partial pressure, but this does not necessarily mean the gas moves from where its concentration is high to where its concentration is low.

you might ever have imagined. If you had a high O_2 concentration near your lungs and a low concentration in your calf muscle, diffusion would require more than *30 years* to halve the concentration difference! Diffusion would obviously be totally useless for getting O_2 to your calf muscle.

We see, then, that diffusion can be very effective for moving O_2 over short distances but not over long distances. The founder of modern respiratory physiology, August Krogh, calculated an important rule of thumb for understanding diffusion. He analyzed a system in which O_2 had to diffuse through tissue to reach mitochondria that were carrying out cellular respiration at an average rate for animals, and he asked how thick the tissue could be. His answer was about 0.5 millimeter. Today, physiologists still use Krogh's rule of thumb and view 0.5 mm as the greatest distance over which O_2 can diffuse fast enough through tissue or tissue fluids to meet metabolic needs.

Gas transport in animals often occurs by alternating diffusion and bulk flow

Returning to Figure 31.1, we can see that diffusion is suitable for moving O_2 through the short steps in the path from the atmosphere to a muscle cell. It is not suitable, however, for the long steps.

This limitation explains why animals have often evolved processes of bulk flow to transport O_2 over long distances. **Bulk flow** refers to a flow of matter from one place to another. Winds and water currents are forms of bulk flow in the physical world. When you breathe, you create a bulk flow of air into and out of your lungs. The beating of your heart causes a bulk flow of blood through your blood vessels. Bulk flow can carry O_2 over long distances at high rates.

> **LINK**
>
> The systems that circulate blood throughout the bodies of animals are described in **Concepts 32.1 and 32.2**

Diffusion and bulk flow alternate in humans and other mammals (**FIGURE 31.3**). O_2 is carried by bulk flow over the long distance from the atmosphere to the depths of the lungs. Then it diffuses across the thin epithelia in the lungs to pass into the blood. O_2 is then again carried by bulk flow, in the circulating blood, to reach the legs. Finally, O_2 diffuses out of blood in the legs to cross a blood-capillary epithelium, cross a cell membrane, and finally reach a mitochondrion.

Breathing is the transport of O_2 and CO_2 between the outside environment and gas exchange membranes

The **gas exchange membranes** of an animal are thin layers of tissue—usually comprising only one or two simple epithelia—where the respiratory gases move between the animal's environmental medium—air or water—and its internal tissues. Our own gas exchange membranes, for example, are the membranes deep in our lungs where O_2 is removed from the air and enters our blood and where CO_2 leaves our blood and enters the air. All animals have gas exchange membranes of some type. O_2 moves into the internal tissues from the layer of environmental
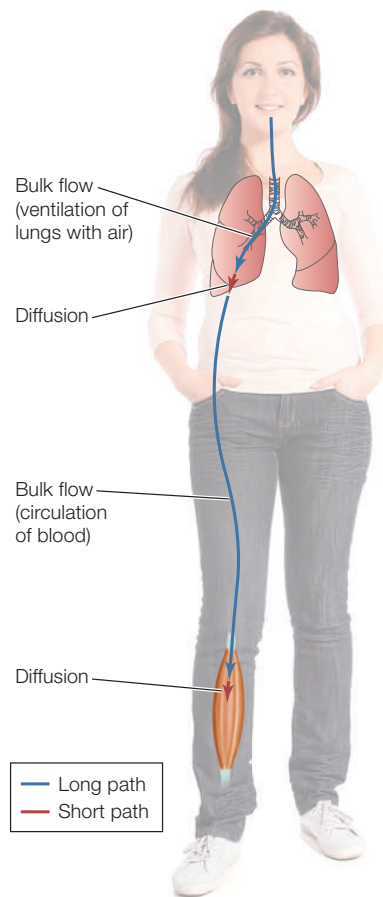
FIGURE 31.3 O_2 **Transport into an Animal Often Occurs by Alternating Bulk Flow and Diffusion** This alternation is clear if you read from top to bottom. Compare this figure with Figure 31.1.

medium immediately next to the gas exchange membranes, and CO_2 moves from the internal tissues into that layer.

How does O_2 from the outside world get to the layer of environmental medium next to the gas exchange membranes? And how does CO_2 move from that layer to the outside world? These questions are the subject of the study of breathing.

Breathing—also called **external expiration**—is the process by which O_2 and CO_2 are transported between the layer of environmental medium next to the gas exchange membranes and the outside world. **Ventilation** refers to bulk flow of air or water between the gas exchange membranes and the outside world. Breathing often occurs by ventilation. This is true in humans and most other vertebrates, for example. However, breathing can occur entirely by diffusion if the distances to be covered are short. Many tiny insects, such as gnats, are believed to breathe by diffusion.

Physiologists categorize breathing organs into two fundamental types: lungs and gills (**FIGURE 31.4**). **Lungs** are invaginated (folded inward) into the body, and their passages *contain* the environmental medium. **Gills** are evaginated (folded outward) from the body and are *surrounded* by the environmental medium. In general, air-breathing animals have lungs and water-breathing animals have gills, although exceptions occur.

When lungs are ventilated, air usually moves into them along lung passages during inhalation and then moves out

(A) Gills

External gills   Internal gills

(B) Lungs

Vertebrate lungs   Insect tracheal system
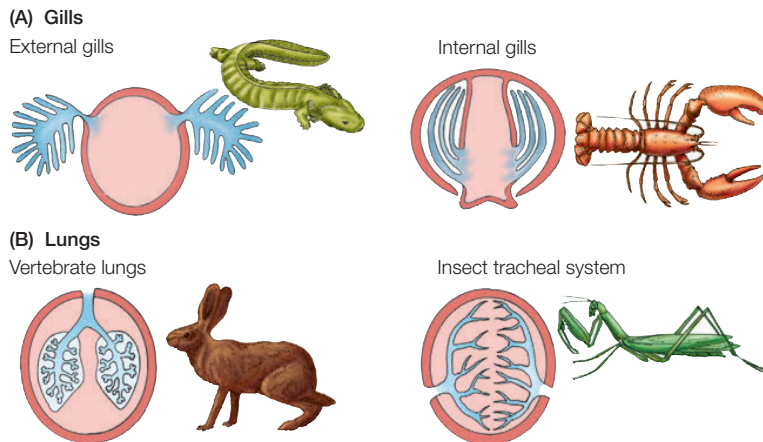
FIGURE 31.4 Gills and Lungs   Physiologists classify all specialized breathing organs (blue in these diagrams) as either gills or lungs, depending on whether they are (A) evaginated structures (folded outward from the body) that are surrounded by the environmental medium or (B) invaginated structures (folded inward into the body) that contain the environmental medium. The use of the word "lungs" does not always match everyday usage. For example, the tracheal breathing system of an insect (discussed later in this chapter) is a lung because it is invaginated and contains air, but it is rarely called a lung in everyday language. Gills are subdivided into external gills (which project directly into the animal's environment) and internal gills (which project into a protective gill chamber that is ventilated with water).

through the same passages during exhalation. This ventilation is described as **tidal** because air flow occurs first in one direction and then in the opposite direction in the same airways—in and out like the ocean tides. Humans exemplify tidal ventilation.

In animals with gills, breathing usually involves pumping water in a one-way stream over the gill surfaces. This water movement is the ventilation of the gills, and the ventilation is described as **unidirectional**.

Air and water are very different respiratory environments

Diffusion takes place much faster through air than water (a fact reflected by the value of D in the diffusion equation). If all factors that affect diffusion are kept constant except that diffusion may be through air or water, the rate of diffusion of O_2 will be about 200,000 times faster through air!

Sea turtle nests that become flooded provide a striking illustration of the difference in diffusion rates through air and water (**FIGURE 31.5**). Loggerhead sea turtles lay their eggs about 40 centimeters deep on ocean beaches and cover them with sand. Nathan Miller outfitted nests with tiny probes that continually monitored the partial pressure of O_2 in the nests. He found that the eggs received plenty of O_2 by diffusion through the sand from the atmosphere above, provided the spaces between sand grains were full of air (Krogh's rule does not apply in air). However, if the sand became flooded with water for a long period—so the spaces between sand grains were water-filled—the O_2 partial pressure in the nest could fall to zero, causing the death of many eggs.

In addition to its slow rate of diffusion through water, O_2 also is not very soluble in water. Suppose we have some fresh water in an aquarium and we bubble it continuously with air so that the water and air are at equilibrium with each other (in this state they have the same O_2 partial pressure). At 12°C the air will contain about 200 milliliters (ml) of O_2 in each liter. The water, however, will contain only about 7.7 ml of O_2 in each liter! The solubility of O_2 in water is so low that the amount present per liter is only about 4 percent as high as in air—even when the water is steadily bubbled with air.

The solubility of O_2 in water decreases as water temperature rises. Thus the concentration of O_2 in water tends to decrease as water warms. Fresh water at 24°C, for example, dissolves 6.2 ml of O_2 in each liter, substantially less than the 7.7 ml per liter dissolved at 12°C. Most aquatic animals are poikilothermic (see Concept 29.3). Thus as water warms, their body temperatures and rates of O_2 consumption increase (see Figure 29.6). At the same time, the amount of dissolved O_2 available from

> For the first 50 days, when the sand was mostly dry, the O_2 partial pressure in the nest was high…

> …but the O_2 partial pressure fell to zero for 2 days when the sand became temporarily saturated with water.

Hatching

> The O_2 partial pressure rose again after the sand dried out, but most eggs were dead when hatching occurred 10 days later.
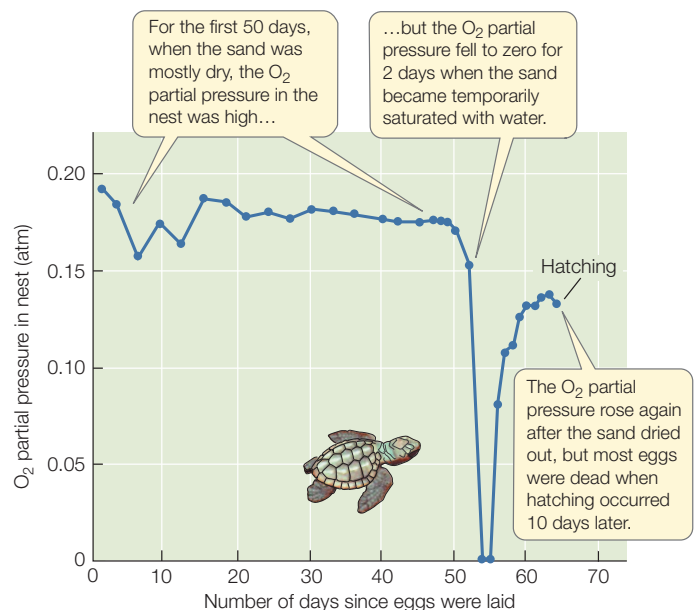
FIGURE 31.5 The O_2 Supply for Sea Turtle Eggs Depends on whether the Sand in which They Are Buried Is Dry or Wet   The O_2 partial pressure in a nest of sea turtle eggs depends on how fast the developing turtles use O_2 and how fast O_2 is resupplied by diffusion from the atmosphere. During the first 50 days of development in the nest studied here, the sand was dry and O_2 diffused into the nest as fast as the developing turtles used O_2—keeping the O_2 partial pressure in the nest high. When the sand became soaked with water for 2 days, as the developing turtles used O_2, the O_2 they used was not replaced, and their metabolism reduced the O_2 partial pressure to zero.

APPLY THE CONCEPT

Respiratory gas exchange depends on diffusion and bulk flow

The need for O_2 and the availability of O_2 can clash in fish as water temperatures rise. Water contains much less O_2 than an equal volume of air, and it requires more effort to be pumped over respiratory gas exchange surfaces. Another factor that affects respiration in water-breathing animals is temperature, which affects both their O_2 needs and the solubility of O_2 in water. Answer the following questions by constructing a graph from the data in the table. Use water temperature as your x axis.

1. How does water temperature influence the O_2 available to a water-breathing animal?

2. Why does water temperature affect the O_2 demands of a fish?

3. From the data, what is the evidence that O_2 availability is a limiting factor for metabolism in warm water?

WATER TEMPERATURE (°C)	O_2 CONCENTRATION OF WATER (ml/L)	AVERAGE METABOLIC RATE OF INACTIVE FISH [ml O_2/(kg × hr)]	AVERAGE METABOLIC RATE OF ACTIVE FISH [ml O_2/(kg × hr)]
5	9.0	8	30
15	7.0	50	110
25	5.8	140	255
35	5.0	225	285

4. From the data, what general argument would you make about the effect of environmental warming on the viability of aquatic species?

each liter of water decreases. Water-breathing animals can find themselves caught in a respiratory trap, in which their O_2 needs increase as O_2 availability decreases. This can weaken them—interfering with growth or reproduction—and even kill them if the mismatch between O_2 needs and O_2 availability becomes too great.

All the animals alive today with the highest metabolic rates are air-breathers. Water is a challenging place to live in terms of getting enough O_2, if an animal is a water-breather.

CHECKpoint CONCEPT 31.1

✓ Where in the human body do inhaled O_2 molecules first cross a cell membrane?

✓ Review the equation for Fick's law on p. 645. What happens to the rate of diffusion as A increases? As L increases?

✓ Many ocean fish depend on the phenomenon of upwelling, where cold, nutrient-rich water rises up from the depths to mix with warm, nutrient-poor water near the surface. Which has the greater potential to store O_2, warm water or cold water? And how might the concentration of O_2 influence a fish's ability to metabolize nutrients available in its environment?

Now that we have examined the basics of respiratory gas exchange, let's look at the diversity of structures and processes by which animals obtain O_2 and get rid of CO_2.

CONCEPT 31.2 Animals Have Evolved Diverse Types of Breathing Organs

Some types of animals do not have specialized breathing organs. Instead, they have body plans in which most of their cells

are close to a body surface. Planaria and other flatworms provide an example:

A flatworm (*Pseudobiceros* sp.)

Because of a flatworm's flat and thin body plan, O_2 can diffuse directly to each cell at a rate high enough to meet the cells' metabolic needs, simply by entering the body across an external surface. Likewise, CO_2 can exit the cells and the body by diffusion.

Sponges also lack specialized breathing organs:

Openings to internal passageways
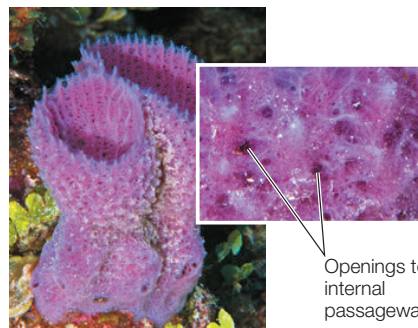
A sponge (*Niphates digitalis*)

The bodies of sponges are organized around an extensive system of internal passageways through which water flows continually, driven by beating flagella. All of a sponge's cells

are close enough to one of these passageways to receive O_2 by diffusion from the environmental water flowing through. CO_2 leaves the cells in the same way.

Most types of animals, however, have evolved specialized breathing organs. The reason is that in most animal body plans, the great majority of cells are far from an external body surface. If we look at a snail, a lobster, a fish, or a bird, we quickly see that most cells are much farther than 0.5 millimeters from a body surface. Even if the external body surface were freely permeable to O_2 and CO_2, Krogh's rule of thumb tells us that diffusion through body fluids, directly from the outside environment, could not possibly meet the needs of most cells for respiratory gas exchange.

Specialized breathing organs have large surface areas of thin membranes

In what ways are lungs and gills specialized for breathing? One of their most important features is they have large surface areas of thin gas exchange membranes. Both of these properties—large surface area and thinness—make perfect sense when we look at the diffusion equation. As you'll recall, O_2 and CO_2 cross the gas exchange membrane by diffusion. The equation tells us that a large area, A, helps ensure a high rate of diffusion. The equation also tells us that a short diffusion path, L, as exists with a thin membrane, aids rapid diffusion.

Whether the breathing organs are lungs or gills, a large surface area is achieved by complex patterns of tissue folding and branching. These foldings and branchings are invaginated into the animal's body in the case of lungs, and evaginated in the case of gills (see Figure 31.4).

Consider your own lungs. The area of the gas exchange membranes in them is about 130 square meters! That's the same as the floor area of a classroom for 80 students. All that surface area can fit into the small volume of your lungs because of branching and folding. The branching resembles that of a tree. Thus, to understand it better, you can think of your lungs as an upside-down tree, where your trachea, or windpipe, corresponds to the tree trunk. Your trachea branches to form two tubes, then each of those tubes branches, and those branches also branch—and so on until the final branches are 23 steps removed from the trunk—the trachea. Each final branch ends in a closed sac of gas exchange membrane that is itself highly folded to increase its surface area. The result is 130 square meters of thin membrane with air on one side and blood on the other side. By virtue of both its large area and thinness, this membrane is ideally suited for O_2 to diffuse rapidly into your blood and for CO_2 to diffuse rapidly out.

How else are lungs and gills specialized for breathing? Another way is the presence of a ventilation mechanism. Without ventilation, our lungs would not be useful. Muscles in our thorax and abdomen expand our lungs when we inhale and sometimes help to contract our lungs when we exhale, causing a bulk flow of air in and out. This bulk flow is as essential as the gas exchange membranes for our lungs to work.

Finally, most breathing organs need circulatory specializations because cells throughout the body depend on blood circulation to receive O_2 taken up in the lungs or gills. **Perfusion**

refers to blood flow through the capillaries or other small blood vessels of a tissue. Perfusion of the gas exchange membranes in a breathing organ must be rapid enough for the blood to pick up O_2 as fast as it is delivered by breathing. Then blood must circulate throughout the body at a high enough rate to deliver O_2 by bulk flow from the lungs or gills to meet the O_2 requirements of all the cells.

In short, most specialized breathing organs have three elements:

- A ventilation system that brings air or water rapidly to the gas exchange membrane
- A thin gas exchange membrane of large surface area, with air or water on one side and blood on the other side, for rapid diffusion
- A high rate of blood perfusion provided by the circulatory system, which also pumps blood rapidly between the lungs or gills and the rest of the body

The directions of ventilation and perfusion can greatly affect the efficiency of gas exchange

When ventilation is unidirectional, a key question is whether blood perfusion of the gas exchange membrane is in the same, or opposite, direction. Let's consider a water-breathing animal, although the principles we'll discuss apply whether the environmental medium is water or air. We can think of blood flow along the gas exchange membrane as being a fluid stream, and of water flow along the membrane as a second fluid stream. The entire system of blood and water flow is a **cocurrent system** (sometimes called a **concurrent system**) if the two fluid streams flow in the same direction. It is a **countercurrent system** if the two fluid streams flow in opposite directions. Gas exchange between blood and water is called **cocurrent gas exchange** in a cocurrent system and **countercurrent gas exchange** in a countercurrent system.

Keep in mind that as blood circulates in the body of a water-breathing animal, it flows back and forth between the gills and the systemic tissues. The **systemic tissues** in any animal are all the tissues other than those of the breathing organ. In the systemic tissues, the blood releases O_2 to the cells and picks up CO_2. Then the blood returns to the gills to unload CO_2 and pick up more O_2.

Also keep in mind how partial pressure affects the rate of gas diffusion. The diffusion equation shows this effect. For our present purposes, the partial pressures of interest are those in the water and blood at the gas exchange membrane. Thus we can think of P_1 and P_2 in the diffusion equation as being the O_2 partial pressures in the water and blood. The rate of diffusion is proportional to the difference between these two partial pressures.

Now let's follow the blood from the moment it arrives at the gas exchange membrane. At that moment, the blood has a low O_2 partial pressure because it has just returned from the systemic tissues. What is the O_2 partial pressure of the water the blood first encounters? In a cocurrent system (**FIGURE 31.6A**), this water is fresh and has a high O_2 partial pressure. Thus there is a large difference in O_2 partial pressure between the water and blood, and O_2 diffuses rapidly into the blood. However, as the blood and water flow in the same direction along the

(A) Cocurrent gas exchange

(B) Countercurrent gas exchange

Blood exits the exchange surface at a higher O_2 partial pressure when exchange is countercurrent.
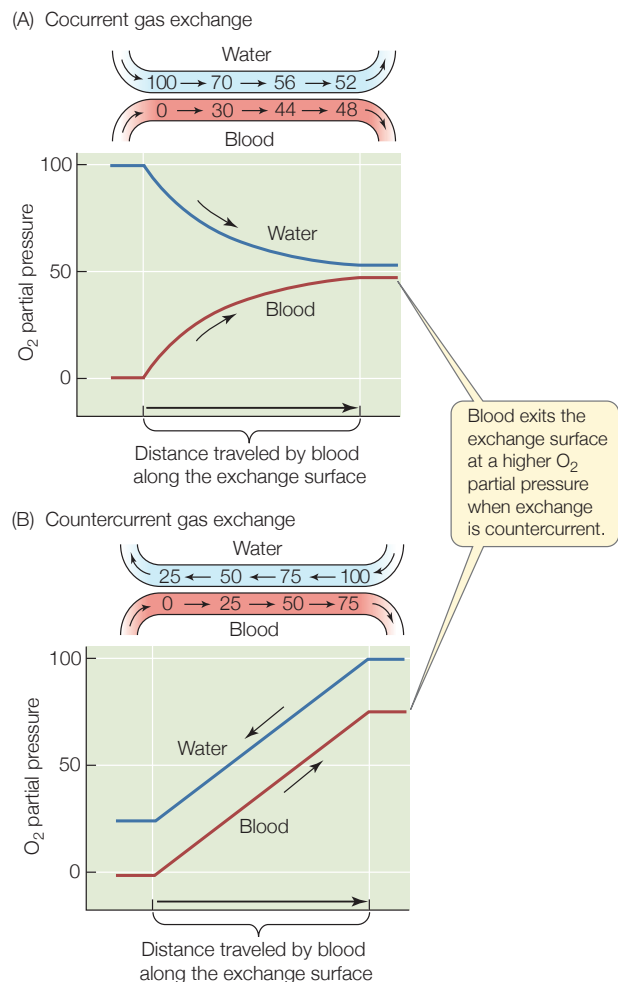
FIGURE 31.6 Countercurrent Gas Exchange Is More Efficient Than Cocurrent   (A) Cocurrent gas exchange. (B) Countercurrent gas exchange. The diagram above each graph depicts the flow of blood and environmental water along the gas exchange membrane. Numbers are O_2 partial pressures in arbitrary units. The blood reaches a higher O_2 partial pressure when gas exchange is countercurrent.

gas exchange membrane in a cocurrent system, the O_2 partial pressure of the blood rises whereas that of the water falls, so the difference in partial pressure becomes smaller and smaller. Accordingly, the rate of O_2 diffusion into the blood becomes lower and lower.

A key question to ask is, When the blood finally leaves the gas exchange membrane, what is the O_2 partial pressure of the water with which it last undergoes gas exchange? As Figure 31.6A shows, that O_2 partial pressure is far lower than that in fresh environmental water. The O_2 partial pressure of the blood cannot be any higher. Thus the blood O_2 partial pressure is doomed to being far lower than the O_2 partial pressure of fresh environmental water.

A countercurrent system works in a very different way (**FIGURE 31.6B**). In this system, What is the O_2 partial pressure of the water that the blood first encounters? This water is stale

and has a low O_2 partial pressure in comparison with fresh environmental water. Thus at the spot where blood first arrives at the gas exchange membrane, there is just a moderate difference in O_2 partial pressure between the water and blood in comparison to the difference in the cocurrent system, and O_2 diffuses into the blood at only a moderate rate by comparison. However, this moderate difference is maintained in the countercurrent system rather than becoming smaller as it does in the cocurrent system. As the blood flows along the gas exchange membrane and its O_2 partial pressure rises, the blood keeps encountering fresher and fresher water with a higher and higher O_2 partial pressure. For this reason, at every step of the way the O_2 partial pressure of the water is substantially higher than that of the blood. As a consequence, O_2 keeps diffusing into the blood at a substantial rate, even as the blood becomes richer and richer in O_2.

Now we come back to the same key question we asked earlier, When the blood finally leaves the gas exchange membrane, what is the O_2 partial pressure of the water with which it last undergoes gas exchange? In the countercurrent system, this water is entirely fresh environmental water and has a high O_2 partial pressure. The O_2 partial pressure of the blood can accordingly rise high enough to be relatively close to that of fresh environmental water.

In conclusion, blood leaves the gas exchange membrane with a higher O_2 partial pressure when exchange is countercurrent than when it is cocurrent. This difference occurs because, as blood flows through the gills, the blood takes up more O_2 from the water in a countercurrent system, where uptake continues at a substantial rate every step of the way along the whole length of the gas exchange membrane. A countercurrent system is more efficient in transferring O_2 from the environmental medium to the blood.

LINK

Countercurrent exchange is also important for thermoregulation in some animals; see **Figure 32.16**

Many aquatic animals with gills use countercurrent exchange

The gills of many aquatic invertebrates, such as clams and aquatic snails, employ countercurrent gas exchange. The gills of fish do also, and here we will look at those in detail.

The gills of a fish are supported by bone-reinforced gill arches positioned between the mouth cavity and the protective opercular flaps on the sides of the fish just behind its eyes (**FIGURE 31.7A**). The gill arches resemble vertical pillars with spaces—termed gill slits—in between. A fish pumps water unidirectionally into its mouth, through its mouth cavity, through its gill slits, over its gills, and out from under the opercular flaps.

Fish gills have an enormous surface area for gas exchange because they are extensively branched and folded. Each gill consists of two rows of long, flat filaments called gill filaments (**FIGURE 31.7B**). The upper and lower surfaces of each gill filament are folded into many flat folds—called secondary lamellae—that run perpendicular to the long axis of the filament

Opercular flap

(A)

Gill arches (under opercular flap)

Water enters through the mouth…

Mouth

…flows over the gills…

Gill arch

Gill filament

Gill slit

Opercular cavity

Opercular flap

…and exits via the opercular cavities under the opercular flaps.

Horizontal section through head

(B) Filament

Gill arch

Water flow

Deoxygenated blood enters (O₂ low)

(C)

Oxygenated blood leaves (O₂ high)

Water with high O₂ ventilates gills.

Water flow

O₂ diffuses from water into the blood over the entire length of a secondary lamella.

Secondary lamella

Deoxygenated blood

Oxygenated blood

Blood perfusion of the secondary lamellae is countercurrent to the flow of water over the secondary lamellae.

Afferent blood vessel

Efferent blood vessel

FIGURE 31.7 Fish Breathing (A) Water flows unidirectionally over the gills of a fish. (B) Gill filaments have a large surface area and thin tissues. (C) Blood flows through the secondary lamellae in the direction opposite (left to right) to the flow of water (right to left) over the lamellae. Blood flow is depicted by small blue and red arrows. Water flow is depicted by large blue arrows. "Afferent" here means flowing into the gills, and "efferent" means flowing out of them.

(**FIGURE 31.7C**). The secondary lamellae are the principal sites of respiratory gas exchange. Blood flows through small blood passages within each lamella, and these blood passages are separated from the water flowing over the gills by just a thin epithelium. This epithelium is the gas exchange membrane. Its total surface area is enormous because of the great numbers of filaments and secondary lamellae.

Blood flows unidirectionally through each secondary lamella, as Figure 31.7C shows, and the direction of water flow over the lamella is opposite to the direction of blood flow. Thus efficient, countercurrent gas exchange takes place. As blood enters a lamella, it is deoxygenated, or low in O_2 (see Concept 32.5). It gradually becomes oxygenated by taking up O_2 by diffusion from the water. If we focus on the spot where blood leaves a lamella, we see that the water on the outside of the lamella at that spot is water that has just started to flow across the gills. That water is accordingly high in O_2, ensuring that the blood is brought to the highest possible O_2 partial pressure before exiting the lamella and traveling to the systemic tissues.

Most fish ventilate their gills by means of a two-pump mechanism based on contractions of breathing muscles. One pump occurs in the mouth cavity. Muscles first expand the mouth cavity so it fills with water through the mouth. Muscles then contract the mouth cavity with the mouth closed, driving the water through the gill slits. The second pump occurs in the opercular cavities—the spaces under the opercular flaps. Muscles pull the opercular flaps away from the body wall, creating a sucking force that draws water through the gill slits into the opercular cavities. Muscles then pull the opercular flaps toward the body wall, discharging water.

Some highly active fish—such as tunas and some sharks—ventilate their gills by driving water across them as they swim. A swimming tuna holds its mouth open so that water is rammed into its mouth and across its gills by the fish's forward motion. Fish of this type can die if prevented from swimming.

Most terrestrial vertebrates have tidally ventilated lungs

The lungs of terrestrial vertebrates evolved as saclike outpocketings of the digestive tract. This ancient heritage is still reflected

today in the fact that, except in birds and some crocodilians, the finest branches of the tubular parts of the lungs end in closed, dead-end sacs of gas exchange membrane. Because of this structure, ventilation of the gas exchange membranes cannot be unidirectional but must be tidal: fresh air flows in and exhaled gas flows out by the same route. Without unidirectional ventilation, cocurrent and countercurrent gas exchange are not possible.

As we already noted, there are 23 levels of branching in the lungs of humans. Other mammals have similar levels of complexity. Amphibian lungs are much simpler and help us understand what vertebrate lungs probably were like early in their evolution. An amphibian lung has an open central cavity, which is surrounded by intricately folded, well-perfused membranes:

Amphibian lung   Lizard lung   Mammalian lung
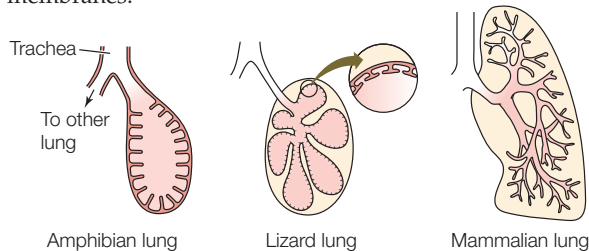
Compared with amphibians, some lizards exemplify increasing complexity in that each lung is subdivided into many separate parts served by separate airway tubes, instead of having a single, open central cavity (see above). The intricate branching of airways in the mammalian lung represents a further, more elaborate step in the same direction. The area of gas exchange membranes in the lungs of a mouse or rat is about ten times greater than the area in a mouse-size or rat-size lizard.

The inside surfaces of vertebrate lungs are coated with a thin layer of metabolically produced lipids and proteins called **lung surfactant**. By reducing surface tension at the surfaces of the lung epithelium, this material helps stabilize the complex three-dimensional structure of the gas exchange membranes. Infants born without adequate lung surfactant (a problem most often seen in premature infants) are in danger of dying unless they receive medical care because the interior surfaces of their lung membranes tend to stick together, requiring lots of effort to pull them apart with each inhalation.

In amphibians, the lungs are inflated by positive pressure. During each inhalation, the mouth cavity is first filled with air from the atmosphere. The mouth and nostrils are then sealed, and muscles contract the mouth cavity, raising the pressure high enough to drive air into the lungs. This mechanism is the same as

that used by air-breathing fish (such as lungfish) to fill their air-breathing organs, suggesting that amphibians carry over the mechanism from their fishlike ancestors.

With the evolution of reptiles, a major transition in ventilation took place. Air is drawn into the breathing system by suction. This is true in today's reptiles, including birds. It is also true in mammals. In most non-avian (non-bird) reptiles and in mammals, the lungs are expanded during inhalation, creating a lower air pressure inside the lungs than in the atmosphere, thereby sucking air into the lungs (see Concept 31.3 for greater detail in humans).

Birds have rigid lungs ventilated unidirectionally by air sacs

Birds and mammals both have high metabolic rates and thus require sophisticated lungs that can supply O_2 at high rates to the rest of the body. The lungs of birds and mammals, moreover, are both believed to have evolved from lungs similar to those seen in today's non-avian reptiles. The lungs of birds, however, are radically different from those of mammals.

The lungs of birds are often described as "rigid." This does not mean they are solid or hard, but rather that they do not change much in volume as a bird inhales and exhales.

The breathing system of a bird includes air sacs as well as lungs (**FIGURE 31.8A**); the air sacs are the parts that undergo

FIGURE 31.8 The Breathing System of a Bird (A) The lungs in the thorax are relatively rigid. The air sacs—of which there are usually nine— are located in the thorax and abdomen and serve as bellows to ventilate the lungs. (B) Arrays of numerous parabronchi in the lungs are the principal sites where gas exchange takes place. Air flows through the parabronchi unidirectionally. (C) Blind-ended air capillaries branch from the parabronchi. The interior surfaces of the air capillaries are the gas exchange membranes.

(A) Avian lungs and air sacs

Anterior air sacs

Lung Posterior air sacs

Trachea   Bronchus

(B) Arrangement of parabronchi and air sacs

Air flow

Anterior air sacs

Posterior air sacs

Trachea   Bronchus

Parabronchi

There are many parabronchi in each lung, each measuring 0.5–2.0 mm in diameter.

(C) Air capillaries

O_2 and CO_2 diffuse between the interior surface of each air capillary and the parabronchial lumen.

Air flow

Air capillaries Parabronchus

0.5 mm

(A) Inhalation

Anterior air sacs

Parabronchi

Posterior air sacs

The anterior air sacs expand and fill with gas that has passed through the lungs.

Air flows through the parabronchi from posterior to anterior.

Trachea

The posterior air sacs expand and fill with fresh air coming directly from the environment.

(B) Exhalation

The anterior air sacs are compressed, discharging stale gas stored in them.

As during inhalation, air flows through the parabronchi from posterior to anterior.

The posterior air sacs are compressed. The fresh air in them is directed primarily into the lungs.

- Fresh air
- Stale gas (i.e., depleted in O_2, enriched in CO_2)

FIGURE 31.9 Airflow in the Lungs and Air Sacs of Birds Airflow during (A) inhalation, when air sacs expand, and (B) exhalation, when air sacs contract. Air flows from posterior to anterior through the parabronchi during both inhalation and exhalation.

large changes in volume as a bird inhales and exhales. These thin-walled sacs connect to airways in the lungs and fill much of the internal space in a bird's body. The air sacs do not participate in exchange of O_2 and CO_2 between the air and blood. Instead, their function is ventilation. They expand and contract during inhalation and exhalation, acting like bellows and forcing air to flow past the gas exchange membranes in the rigid lungs.

Long, tiny tubes called parabronchi (singular parabronchus) are the most important airways for gas exchange in the lungs of a bird (**FIGURE 31.8B**). As astounding as it may sound, air flows through most of a bird's parabronchi *unidirectionally*, from posterior to anterior, during all phases of its breathing cycle, whether the bird is inhaling or exhaling! Air flows unidirectionally through the parabronchi because of coordinated actions of thoracic and abdominal muscles that expand and contract the anterior and posterior sets of air sacs (**FIGURE 31.9**). When a bird inhales, some of the incoming fresh air travels to the posterior of each lung and enters the parabronchi. That air then flows through the parabronchi from posterior to anterior and exits into anterior air sacs. Some of the incoming fresh air also inflates the posterior air sacs. Then, when the bird exhales, this fresh air in the posterior air sacs is driven into the parabronchi, again flowing from posterior to anterior. As this occurs, stale air exiting the parabronchi at the anterior end, plus stale air from the anterior air sacs, is exhaled into the atmosphere.

Go to ANIMATED TUTORIAL 31.1
Airflow in Birds
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Tiny air capillaries extend into the walls of each parabronchus from the parabronchial lumen (**FIGURE 31.8C**). These air capillaries are so minute that if the openings of 1,000 of them were lined up in a row, they would cover only 1 centimeter or less. The walls of the air capillaries are richly perfused with blood and serve as the gas exchange membranes. As air moves by bulk flow through the parabronchi, O_2 and CO_2 are thought to move in and out of the tiny air capillaries by diffusion. Gas

exchange with the blood is termed "cross-current"—a type of exchange intermediate in efficiency between cocurrent and countercurrent.

Insects have airways throughout their bodies

In insects (and spiders), a breathing system has evolved that is unlike that of any other animals (**FIGURE 31.10**). This breathing system is a type of lung because it consists of gas-filled tubules that are invaginated into the body from the body surface. The tubules branch everywhere in an insect's body. In fact they branch in such fantastically intricate ways that a gas-filled tubule comes close to every cell. In some cases tubules grow into cells, indenting the cell membrane inward. The tubules connect to the atmosphere at several openings, called spiracles, on the outside surface of an insect's body. O_2 makes its way directly from the atmosphere, through the gas-filled tubules, to each cell. CO_2 moves directly from all cells to the atmosphere. Because of this unique breathing system, blood flow is generally unimportant in delivering O_2 and getting rid of CO_2.

Most of the gas-filled tubules are called **tracheae**, and for this reason, insects are said to have a **tracheal breathing system**. The tracheae are lined with a thin, gas-permeable layer of chitin, which provides support and keeps them from collapsing shut. The finest tubules are called tracheoles. Air sacs are connected to the tracheae in many insects.

The air inside the tracheal breathing system is believed to be completely still in some insects. In these cases O_2 and CO_2 travel everywhere by diffusion. Keep in mind that Krogh's rule of thumb refers just to diffusion through water. Diffusion in air is much faster (200,000 times faster in the case of O_2) because random molecular movements are more vigorous in gases than in water. Because of the fast diffusion that can occur in air, insects can be moderately large (e.g., 0.5 cm long) and still have their gas exchange needs met by diffusion in the tracheal system, provided they are not very active.

In insects that are large or active, mechanisms have evolved to create bulk flow of air inside the tracheal system. Grasshoppers, for example, pump air through their tracheae

(A)

(B)

Eumorpha pandorus

(C)
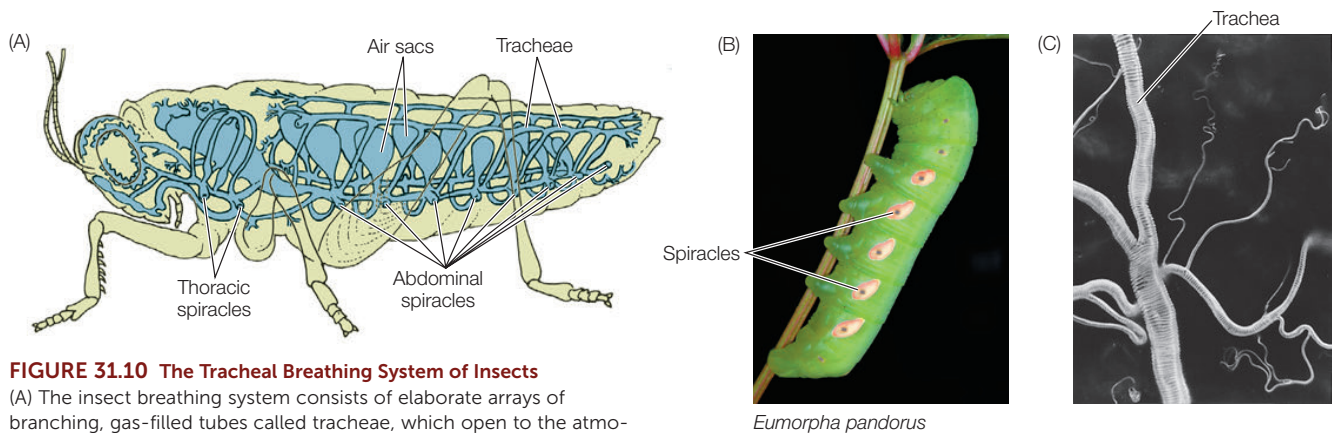
FIGURE 31.10 **The Tracheal Breathing System of Insects**
(A) The insect breathing system consists of elaborate arrays of branching, gas-filled tubes called tracheae, which open to the atmosphere through pores called spiracles. In many insects, air sacs connect to the tracheae and can act as bellows to cause tracheal ventilation. (B) The spiracles of a Pandorus sphinx moth larva are visible on the sides of its body. (C) This scanning electron micrograph shows an insect trachea dividing into smaller tracheae and tracheoles. All cells in an insect's body are close enough to one of these branches to receive O_2 directly from the tracheal system by diffusion.

by contracting and elongating their bodies. Bees use air sacs as bellows to drive air through their tracheae. The tracheae throughout an insect's body sometimes undergo steady, rhythmic contractions.

CHECKpoint   **CONCEPT 31.2**

✓ What process is responsible for the movement of O_2 into a flatworm's body?

✓ As blood flows along the gas exchange membrane, how does the difference in O_2 partial pressure between the environmental medium and blood vary in countercurrent and cocurrent systems?

✓ Why can't diffusion alone supply fresh O_2 molecules to the breathing systems of many organisms?

✓ Mammals, birds, and insects are the three groups of animals in which species with the highest known metabolic rates occur. Of these three groups, two—mammals and birds—have high-performance circulatory systems that can circulate blood rapidly throughout the body and perfuse tissues at high rates. Insects do not have high-performance circulatory systems. Explain.

Now let's take a closer look at the anatomy and function of mammalian lungs, focusing on the human breathing system.

CONCEPT 31.3   **The Mammalian Breathing System Is Anatomically and Functionally Elaborate**

In mammals, air enters the lungs through the oral cavity and the nasal passages, which join together in the pharynx, or throat (**FIGURE 31.11A**). Below the pharynx, the esophagus, or food

tube, directs food to the stomach, and the trachea, or windpipe, leads to the lungs. At the beginning of the trachea is the larynx, or voice box, which houses the vocal cords. The walls of the trachea and many further branches of the airways contain rings of cartilage, which help prevent airway collapse.

The trachea branches into two primary bronchi, one leading to each lung. Each primary bronchus then branches more than 20 times to generate the treelike structure of progressively smaller airways we discussed earlier (**FIGURE 31.11B**). At the farthest reaches of the branching airways, each tiny branch ends blindly in an **alveolar sac** of epithelial tissue (**FIGURE 31.11C**). The wall of each alveolar sac consists of numerous semispherical pocket-like structures called **alveoli** (singular *alveolus*). These alveoli number about 300 million in the two lungs of an adult person, creating an enormous surface area (**FIGURE 31.11D**) where gas exchange occurs (**FIGURE 31.11E**).

Most branches of the airway system in a mammal are not involved in the exchange of O_2 and CO_2 between the air and blood. These branches—including the trachea, primary bronchi, and most of the succeeding branches—are called the **conducting airways** because their principal function is to conduct flowing air in and out of the lungs during inhalation and exhalation.

Exchange of O_2 and CO_2 between the air and blood occurs in the **respiratory airways**. These are the parts of the lungs where the membranes between air and blood are thin and perfused with blood at high rates. The respiratory airways include the last few branches of the branching airway system—termed respiratory bronchioles—and the alveolar sacs, including the alveoli. In healthy human lungs, blood and air are separated by only about 0.5 μm in the alveoli. Bulk air flow—inflow and outflow—takes place in the respiratory bronchioles as a person inhales and exhales. But the air inside the alveoli is motionless. This means that as O_2 and CO_2 travel to and from the gas exchange membranes, they must diffuse across the central cavities of the alveoli. Moreover, as we already discussed, O_2 and CO_2 must diffuse across the two thin epithelia that line the alveoli and the surrounding blood capillaries. Diffusion occurs rapidly because the distances to be covered are minute.

(A)

The lungs lie within the thoracic cavity, which is bounded by the ribs and the diaphragm.

Trachea

Nasal passage

Oral cavity

Pharynx

Larynx

Pleural membranes line the thoracic cavity and also cover the lungs.

Intercostal muscles

Secondary bronchi

Primary bronchus

Heart

Bronchioles

Diaphragm

A primary bronchus enters each lung. There it branches into secondary bronchi, which branch still further, ultimately leading to fine tubes called bronchioles.

FIGURE 31.11 The Human Breathing System   The hierarchy of human breathing structures extends from the nose and mouth to the minuscule alveoli. Because lung capillaries are a bit larger in diameter than systemic capillaries, red blood cells pass through as shown in (E).

**Go to ACTIVITY 31.1 The Human Respiratory System
PoL2e.com/ac31.1**

(B) A plastic cast of the airways in the lungs
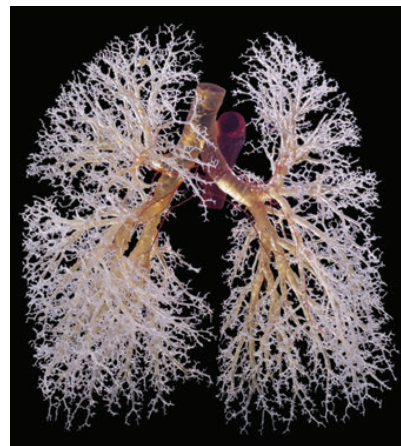
(D) An electron micrograph showing the fine structure of alveoli

Alveoli

Red blood cells

(C)

Fully oxygenated blood to heart

Oxygen-depleted blood from heart

Respiratory bronchiole

Alveoli

Alveolar sac

Alveoli

Smallest blood vessels (capillaries)

(E)

Oxygenated blood to heart

Epithelial cell of capillary wall

Red blood cell

O_2

In an alveolus, the air is very close to the blood flowing through the networks of capillaries surrounding the alveoli.

Epithelial cell of alveolus

CO_2

Alveolar walls and capillary walls are extremely thin, minimizing the distance that O_2 must diffuse.

Blood capillary

Interior of alveolus

Oxygen-depleted blood from heart

At rest, only a small portion of the lung volume is exchanged

The amount of air that moves in and out of the lungs per breath is called the **tidal volume** (**FIGURE 31.12**). When a person is at rest, it is called the resting tidal volume and amounts to about 0.5 liter. The maximal tidal volume—also called vital capacity—is the amount of air that moves in and out per breath when we inhale and exhale as vigorously as possible. It is about 5 liters. We use only about 10 percent of our maximal tidal volume when we breathe at rest.

A person's **respiratory minute volume** is the total volume of air that he or she inhales and exhales per minute. We calculate the minute volume by multiplying tidal volume (the volume exchanged per breath) by the number of breaths per minute. When people exercise and "breathe harder," they increase their tidal volume above the resting tidal volume, and they also take more breaths per minute than they do at rest. These two factors can produce a large increase in minute volume. At rest we breathe about 12 times per minute. With a resting tidal volume of about 0.5 liter, our resting minute volume is about 6 liters per minute. Well-conditioned athletes can breathe at least 30 times per minute at a tidal volume of over 3 liters, meaning they can increase their minute volume by a factor of more than 15!

Mammals and other animals with tidally ventilated lungs do not empty their lungs completely when they exhale. Some air is always left behind in the lungs. The amount left after a maximum exhalation is called the residual volume (see Figure 31.12). During normal breathing, whenever a mammal inhales, the fresh air mixes with stale air from the previous breath that was not exhaled. This mixing lowers the O_2 partial pressure at the alveolar gas exchange membranes but ordinarily presents no problems.

The lungs are ventilated by expansion and contraction of the thoracic cavity

Mammalian lungs are suspended in the thoracic, or chest, cavity, which is bounded on the top by the bones of the shoulders, on the sides by the rib cage, and on the bottom by a sheet of muscle, unique to mammals, called the **diaphragm**. Any increase in volume of the thoracic cavity pulls on the walls of the lungs, thereby expanding the lungs and causing inflation.

Two muscles or sets of muscles are critical for breathing: the diaphragm and the intercostal (from the Latin *costa*, "rib") muscles that run between adjacent ribs (see Figure 31.11A). The diaphragm is dome-shaped at rest, protruding upward from the abdomen into the thoracic cavity. It flattens when it contracts, so it protrudes less into the thoracic cavity, expanding it. There are two sets of intercostal muscles. One set enlarges the thoracic cavity when it contracts, and the other set makes it smaller when it contracts.
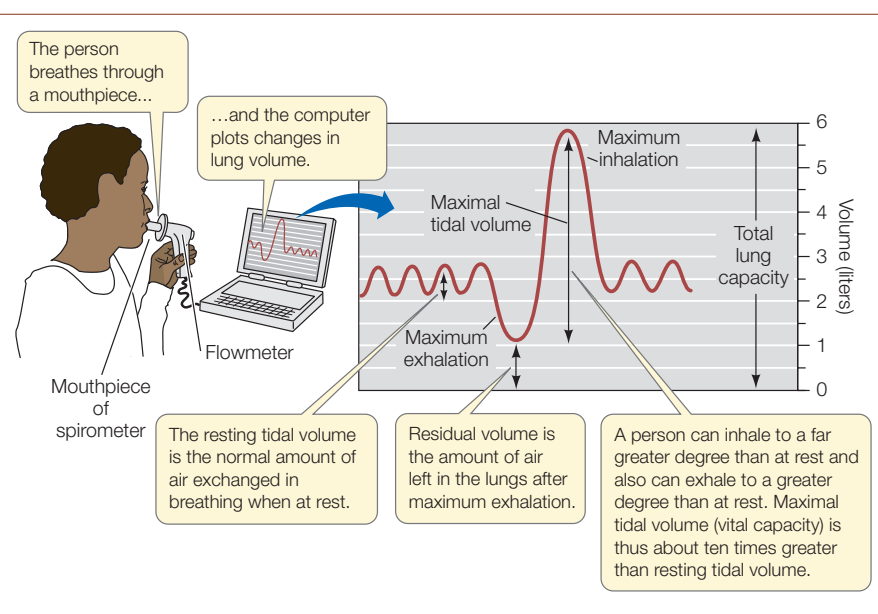
In humans at rest, inhalation is active but exhalation is passive (**FIGURE 31.13**). During inhalation, the diaphragm and certain intercostal muscles contract, expanding the thoracic cavity and lungs, which fill by suction (a lower pressure in the lungs than in the atmosphere). During exhalation at rest, these muscles simply relax, allowing the elastic recoil of the lungs and thoracic cavity to restore the relaxed lung volume. During exercise, additional breathing muscles come into play. Inhalation is more forceful, and muscle contractions are employed to make exhalation faster and more forceful than it is at rest.

The breathing rhythm depends on nervous stimulation of the breathing muscles

All the muscles involved in breathing require nervous stimulation to contract. The nerve impulses originate in the brain. These facts explain why a broken neck can kill a person rapidly. If the nerves carrying the breathing impulses from the brain to the breathing muscles are severed, the muscles stop contracting. Without artificial respiration, the person suffocates.

Physiologists have long sought the places in the brain where the breathing rhythm originates. Investigators recently identified these rhythm-generating (rhythmogenic) centers by studying thin slices of brain tissue taken from nestling rodents. Although these slices are cut off from all their normal connections with other parts of the nervous system, they remain functional for some time. Investigators have shown that two neural complexes in the medulla oblongata of the brain (a part of the brainstem) generate a breathing rhythm under these circumstances (**FIGURE 31.14**). These rhythm-generating centers, called the pre-Bötzinger complexes, are believed to be the beginning points for the nerve impulses that activate the muscles we use in breathing.

RESEARCH TOOLS

FIGURE 31.12 Measuring Lung Ventilation A spirometer is a device that measures tidal volume: the volume of air a person breathes in and out per breath.

The person breathes through a mouthpiece...

...and the computer plots changes in lung volume.

Flowmeter

Mouthpiece of spirometer

Maximum inhalation

Maximal tidal volume

Total lung capacity

Maximum exhalation

Volume (liters)

The resting tidal volume is the normal amount of air exchanged in breathing when at rest.

Residual volume is the amount of air left in the lungs after maximum exhalation.

A person can inhale to a far greater degree than at rest and also can exhale to a greater degree than at rest. Maximal tidal volume (vital capacity) is thus about ten times greater than resting tidal volume.

(A) Inhalation is active

Thoracic cavity expands during inhalation

Lung Lung

Heart

Pleural cavity

Diaphragm

During **inhalation**:
- Diaphragm contracts and flattens
- Some intercostal muscles contract
- Thoracic cavity expands because of these muscle actions
- Lungs expand
- Air is sucked in

(B) Exhalation is passive

Thoracic cavity contracts during exhalation

During **exhalation**:
- Diaphragm relaxes
- Intercostal muscles relax
- Thoracic cavity returns to its relaxed volume by elastic recoil
- Lungs return to their relaxed volume
- Gases in lungs are expelled

FIGURE 31.13 Resting Human Ventilation When a person is at rest, inhalation (A) is an active process driven by contraction of the diaphragm and some of the intercostal muscles. However, exhalation (B) is a passive process that occurs by elastic recoil; the thoracic cavity and lungs elastically return to their relaxed volume as soon as muscle contractions stop maintaining them in an expanded state.

During exertion, when tidal volume and breathing rate increase to meet a person's increased O_2 needs, muscle contractions aid both exhalation and inhalation.

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Airflow in Mammals
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(A) Slice of medulla oblongata

Hypoglossal nucleus

Pre-Bötzinger complex

(B) Simultaneous recordings from hypoglossal nucleus (top) and pre-Bötzinger complex (bottom)

2 The breathing rhythm is relayed to the hypoglossal nuclei from the pre-Bötzinger complexes.

2 s

Voltage

Time

1 The pre-Bötzinger complexes originate signals that control normal breathing.
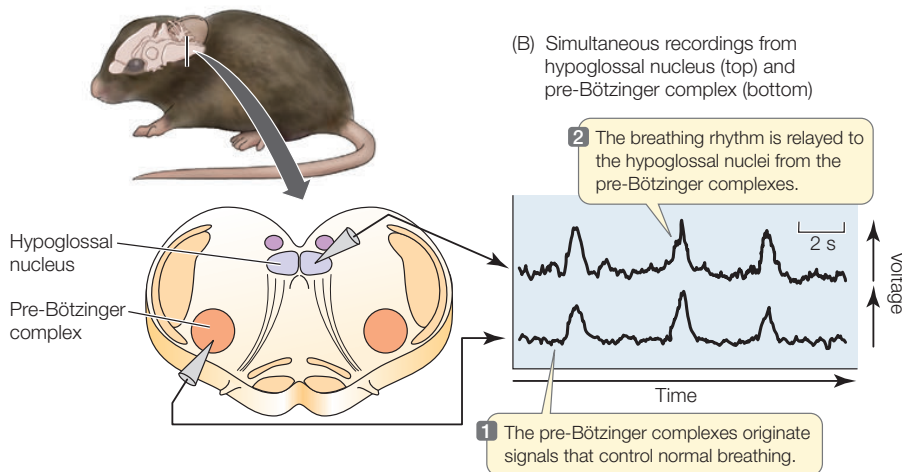
FIGURE 31.14 Where Does the Breathing Rhythm Originate? To find the neural tissue where the breathing rhythm starts, physiologists studied thin slices of living brain tissue from nestling mice. (A) This slice, cut from the medulla oblongata, has no connections to other parts of the nervous system. Its neural activity is therefore completely self-contained. (B) Electrical recordings were made from one of two clusters of nerve cells called the pre-Bötzinger complexes. The investigators found that these complexes generate electrical signals that control normal breathing. From simultaneous recordings from one of two other nerve cell clusters called the hypoglossal nuclei, the investigators found that the breathing rhythm that starts in the pre-Bötzinger complexes is relayed to the hypoglossal nuclei. In an intact mouse, the breathing rhythm would then be relayed to the breathing muscles via the hypoglossal nerves.

INVESTIGATION

FIGURE 31.15 The Respiratory Control System Detects Exercise
What is the metabolic feedback signal that controls ventilation during exercise? In experiments with dogs running on a treadmill at a constant speed but at varying upward slopes, the respiratory minute volume increased as the CO_2 partial pressure in the arterial blood increased.[a]

HYPOTHESIS

Arterial CO_2 partial pressure is a feedback stimulus controlling ventilation.

METHOD

1. Dogs are trained to run on a treadmill.
2. The dogs are equipped with instruments that measure respiratory minute volume and with arterial catheters that enable sampling of blood.
3. As a dog runs at a constant speed, the slope of the treadmill is changed to modify the metabolic workload.
4. Minute volume is plotted as a function of arterial CO_2 partial pressure.

Catheter for taking blood samples

To flowmeter and respiratory analyzer
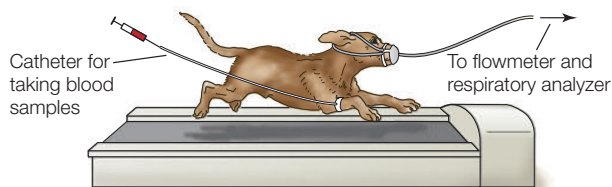
RESULTS

When the workload is altered by slowly changing the slope of the treadmill (no change in speed), the respiratory minute volume is a function of arterial CO_2 partial pressure.
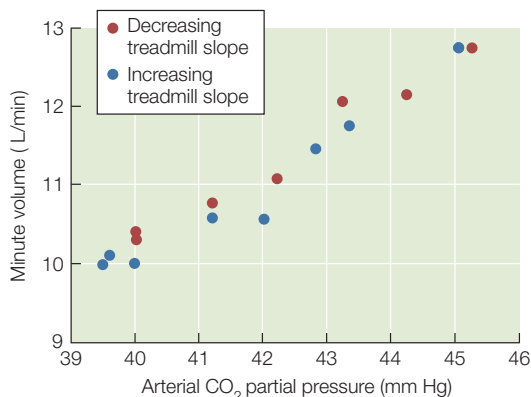
CONCLUSION

The data support the hypothesis that arterial CO_2 partial pressure is a metabolic feedback signal controlling ventilation in response to changes in workload.

ANALYZE THE DATA

Additional experiments were done in which the speed of the treadmill was changed instead of the slope to modify the metabolic workload. Again the respiratory minute volume (L/min) and arterial CO_2 partial pressure (P_{CO_2}, in units of mm Hg) were measured. The average values when the dogs were running at 3 mph were CO_2 partial pressure = 39.0 mm Hg and L/min = 9. The data for the first seven breaths after the treadmill speed was increased to 6 mph are shown in the table. After the dogs had run at 6 mph for several minutes, the values averaged CO_2 partial pressure = 41.0 mm Hg and L/min = 15.0. Plot these data and use the information to answer the questions.

Breath	P_{CO_2}	L/min
1	38.0	13.0
2	37.0	14.0
3	36.5	11.2
4	37.2	11.2

Breath	P_{CO_2}	L/min
5	37.2	12.0
6	36.8	13.0
7	37.2	13.0

A. Do these data support the hypothesis that CO_2 partial pressure is the feedback signal controlling ventilation? Why or why not?
B. How do you explain the average values after the dogs had been running at the higher speed for a few minutes?
C. Relate these results to those obtained in the experiment in which the slope of the treadmill was varied. Explain the differences between the results.

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]C. R. Bainton. 1972. *Journal of Applied Physiology* 33: 778–787.

Breathing is under negative-feedback control by CO_2

You might expect that a mammal's breathing would be regulated by the blood's O_2 content. In fish, blood O_2 is indeed the primary feedback stimulus for gill ventilation. However, mammals are relatively insensitive to falling levels of O_2 in arterial blood. Instead they are very sensitive to changes in blood CO_2.

To fully understand control of breathing by CO_2, it is important to recognize that CO_2 dissolved in the blood reacts with blood H_2O. This reaction forms carbonic acid (H_2CO_3), which

dissociates almost completely into H^+ ions and bicarbonate ions (HCO_3^-).

$$CO_2 + H_2O \rightleftharpoons H_2CO_3 \rightleftharpoons H^+ + HCO_3^-$$

What happens when the cells of your body increase their metabolism and therefore add CO_2 to the blood at an increased rate? There are two immediate consequences. First, the partial pressure of CO_2 in the blood rises. Second, the concentration of H^+ in the blood also rises, meaning the blood becomes more acidic and its pH falls. Chemosensitive (chemical-sensing) neural centers located on the ventral surface of the medulla oblongata in the brain (see Figure 31.14) independently monitor the blood CO_2 partial pressure and H^+ concentration. These centers detect the increases in CO_2 partial pressure and H^+ concentration. This information is then used to control breathing in a negative-feedback manner. Breathing is stimulated so that the respiratory minute volume increases. This increased ventilation increases exhalation of CO_2, helping the body get rid of CO_2 at an accelerated rate when the cells have increased their rate of CO_2 production. The increased ventilation also tends to return both the blood CO_2 partial pressure and H^+ concentration back toward their values that existed before CO_2 production increased.

What if, under different circumstances, your cells decrease the rate at which they add CO_2 to the blood? In this case, the blood CO_2 partial pressure and H^+ concentration initially tend to fall. The chemosensitive centers detect these changes, leading again to negative-feedback control of breathing. In this instance, breathing is inhibited, lowering the rate of CO_2 exhalation and causing the blood CO_2 partial pressure and H^+ concentration to rise.

These controls serve to adjust the respiratory minute volume so that the rate of CO_2 exhalation approximately matches the rate at which the cells of the body produce CO_2. The controls also stabilize the blood CO_2 partial pressure and H^+ concentration, by tending to bring them down if they start to rise and tending to bring them up if they start to fall.

In the experiment in **FIGURE 31.15**, dogs ran on a treadmill at a constant speed. The slope of the treadmill could be tilted up at various angles, allowing the researchers to vary the dogs' metabolic workload and thus their rates of CO_2 production. Negative-feedback systems rarely lead to complete stability. In this case, the CO_2 partial pressure in a dog's arterial blood tended to vary a little (it would have varied much more without negative feedback). The results demonstrate that a dog's respiratory minute volume is closely correlated with its blood CO_2 partial pressure. This evidence supports the idea that breathing is stimulated when the blood CO_2 partial pressure increases.

Go to MEDIA CLIP 31.1
Hunting on the Sea Bed with One Breath
PoL2e.com/mc31.1

Breathing is also under control of factors in addition to CO_2

You may have noticed that when you start running, your breathing rate increases almost immediately—far sooner than your blood CO_2 partial pressure would be expected to change. This everyday observation suggests that the simple act of moving muscles and joints may serve to accelerate ventilation during exercise. Investigators studied this possibility in the experiments on dogs we've been discussing (see Analyze the Data in Figure 31.15). For this purpose the dogs ran on a horizontal treadmill, and investigators altered the dogs' intensity of work by varying how fast they ran. When the dogs worked harder, respiratory minute volume sometimes increased to a greater extent than CO_2 partial pressure by itself would explain. According to the results of this study and other studies, information from receptors that detect motion in muscles and joints is used during exercise to help control the intensity of ventilation.

Blood O_2 partial pressure is also sometimes used in controlling the intensity of ventilation. O_2 partial pressure is not as influential as CO_2 partial pressure, and minor fluctuations in the O_2 partial pressure have little effect on ventilation. However, a large drop in blood O_2 partial pressure—such as might occur at high elevation—strongly stimulates ventilation.

In mammals, two sets of oxygen-sensing chemosensitive bodies detect the blood O_2 partial pressure. They are called peripheral chemoreceptors because they are not in the brain. They are positioned along the large arteries leaving the heart (see Figure 32.6). One set (by far the most important set in humans) is a pair of carotid bodies found along the carotid arteries in the neck. The second set consists of aortic bodies associated with the aorta. These bodies detect blood O_2 partial pressure and send information on it by way of nerves to the breathing control centers in the medulla oblongata.

CHECKpoint   CONCEPT 31.3

✓ The alveoli become filled with tissue fluid in several types of diseases, such as heart weakening that causes pulmonary edema. This condition is a health emergency. Why?

✓ In a healthy individual, how would the respiratory minute volume change in response to a decrease in blood pH?

✓ How could a neck injury that leaves the trachea and other air passageways intact result in an inability to breathe?

Q Why is climbing uphill at 1.7 meters per minute (100 meters/hour) the most intense work that is possible for a human near Everest's summit?

ANSWER Any particular type of sustained, physical work demands a certain amount of sustained metabolic effort and thus a certain, fixed rate of O_2 consumption (regardless of

elevation). Consequently a person's maximal rate of O_2 consumption determines the maximal sustained work intensity of which he or she is capable. A person's maximal rate of O_2 consumption decreases with elevation because O_2 becomes more dilute in the atmosphere as elevation increases (**FIGURE 31.16**). For this reason, maximal work intensity decreases with elevation. At the top of Mount Everest, hardly any work is possible. The maximal intensity of work is a slow walk.

FIGURE 31.16 A Person's Maximal Rate of O_2 Consumption Decreases as Elevation Increases   Each symbol represents one measurement on one person. Data from many studies were compiled to create this plot.
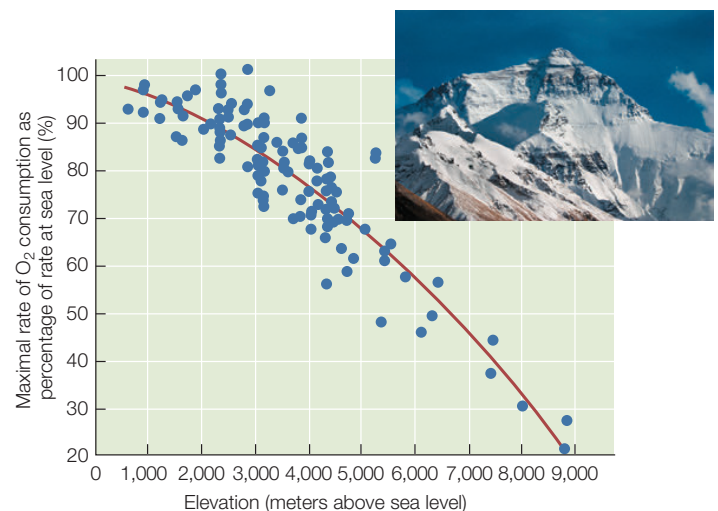
SUMMARY

CONCEPT 31.1 Respiratory Gas Exchange Depends on Diffusion and Bulk Flow

■ Most cells require a constant supply of O_2 and continuous removal of CO_2. These **respiratory gases** are exchanged between an animal's cells and the animal's environment by a combination of diffusion and **bulk flow**. **Review Figures 31.1 and 31.3**

■ A gas diffuses from where its **partial pressure** is high to where its partial pressure is low. The **law of diffusion for gases** (**Fick's law**) shows how various physical factors influence the diffusion rate of gases. Adaptations to maximize respiratory gas exchange influence one or more variables of Fick's law. **Review Figure 31.2**

■ As they move between an animal's internal tissues and the environment, respiratory gases diffuse across **gas exchange membranes**.

■ Breathing organs are classified based on their structure: **lungs** fold inward into the body; **gills** fold outward from the body. **Review Figure 31.4**

■ In water, gas exchange is limited by the low diffusion rate and low solubility of O_2 in water. O_2 becomes less soluble in water as water temperature increases. **Review Figure 31.5**

CONCEPT 31.2 Animals Have Evolved Diverse Types of Breathing Organs

■ Adaptations to maximize gas exchange include increasing the surface area for gas exchange and maximizing both **ventilation** with the respiratory medium and **perfusion** with blood. The gas exchange membranes are also very thin, which minimizes the distance gases must diffuse.

■ **Cocurrent gas exchange** occurs when perfusion flows in the same direction as ventilation; flows in opposite directions result in **countercurrent gas exchange**. The most efficient transfer of gases is achieved by countercurrent systems, such as those found in fish. **Review Figures 31.6 and 31.7**

■ Internal partitioning of the lungs is greater in mammals than in non-avian reptiles like lizards, and greater in these reptiles than in amphibians. Ventilation in all these groups is **tidal**.

■ The breathing system of birds includes air sacs that are filled and emptied tidally and act as bellows to ventilate the lungs. Air flows unidirectionally and continuously through the parabronchi (the

principal gas exchange parts) of bird lungs. **Review Figures 31.8 and 31.9, ANIMATED TUTORIAL 31.1**

■ Insects distribute air throughout their bodies in a system of **tracheae** and tracheoles. The circulatory system is not involved in gas exchange because all cells are supplied directly by the tracheal system. **Review Figure 31.10**

CONCEPT 31.3 The Mammalian Breathing System Is Anatomically and Functionally Elaborate

■ In mammalian lungs, the gas exchange surface area provided by the millions of **alveoli** is enormous, and the diffusion path length is short. **Review Figure 31.11 and ACTIVITY 31.1**

■ The **tidal volume** is the amount of air that moves in and out of the lungs per breath. The **respiratory minute volume** is the total volume of air that is inhaled and exhaled per minute. **Review Figure 31.12**

■ Inhalation occurs when contractions of the **diaphragm** and some of the intercostal muscles expand the thoracic cavity. In a resting person, when the diaphragm and intercostal muscles relax, the thoracic cavity contacts by elastic recoil, resulting in exhalation. During exercise, greater muscular forces are used, increasing the volume of air inhaled and exhaled per breath and the rate of breathing. **Review Figure 31.13 and ANIMATED TUTORIAL 31.2**

■ The breathing rhythm is generated by neurons in rhythm-generating centers in the medulla oblongata. **Review Figure 31.14**

■ The most important feedback stimulus for breathing is the level of CO_2 in the blood, which is detected by chemosensitive neural centers on the surface of the medulla oblongata. These centers detect both the blood CO_2 partial pressure and the blood pH, which indirectly reflects the level of CO_2. **Review Figure 31.15**

■ Breathing rate can also be affected by the onset of exercise (sensed by receptors that detect motion in muscles and joints) and by large changes in blood O_2 partial pressure (detected by chemosensitive carotid and aortic bodies on the large vessels leaving the heart). **See ACTIVITY 31.2 for a concept review of this chapter.**

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is31

Go to LaunchPad at **macmillanhighered.com/launchpad** for additional resources, including LearningCurve Quizzes, Flashcards, and many other study and review resources.

32 Circulation

Bluefin tuna are vigorous swimmers. They need more than strong swimming muscles to swim, because the muscles require ATP at high rates and thus need O_2 at high rates. The circulatory system bears responsibility for moving O_2 rapidly to the muscles from the gills.

If tuna, such as these bluefin tuna, lived on land, they would be as famous as wolves. Like wolves, bluefin tuna are carnivores that hunt in groups and depend on speed, strength, and awesome teeth to attack prey: in their case, other fish. Tuna are strong, mobile predators at the top of the food chain.

Judging by the length of time spent in motion, tuna are actually more mobile than wolves. Using their red swimming muscles, they swim continuously, day and night, at speeds of one to two body lengths per second. For bluefin, this means traveling continuously at speeds of 2–6 meters per second, interrupted at times by anaerobically fueled bursts of attack swimming at far higher speeds. Tuna rank with the elite endurance athletes of the sea.

To meet the oxygen (O_2) demands of their vigorous lifestyle, tuna have evolved some of the most elaborate gills known in fish: gills that can take up O_2 at high rates from seawater. However, the swimming muscles that must receive O_2 rapidly for endurance swimming are located in the abdomen, far from the gills.

Rapid circulation of blood is thus as important as elaborate gills for the steady, endurance swimming of tuna. As stressed in Concept 31.1, the flow of blood through an animal's circulatory system is a form of bulk flow. As such, it can move substances at high rates over long distances within the animal's body. Tuna researcher John Magnuson once commented that tuna are "astounding bundles of adaptations for efficient and rapid swimming." One of those adaptations is a high-performance circulatory system that can transport O_2 at high rates from the gills to the swimming muscles.

Tuna belong to the small set of fish that have warm bodies, and in this regard their circulatory system plays a second important role in swimming. In more than 99 percent of fish, body temperature equals water temperature. Only a tiny minority of fish are warm-bodied as tuna are. The entire body of a tuna is not warm, however. Just certain parts are. The red swimming muscles represent the largest mass of warm tissue. In bluefin tuna, those muscles remain at 25–35°C even when the ocean is as cold as 5°C. This warming of the red swimming muscles is believed to help the muscles maintain high power outputs. A specialized arrangement of blood vessels helps the swimming muscles retain heat and stay warm.

Q How can the arrangement of blood vessels help warm the swimming muscles in warm-bodied fish such as tuna?

You will find the answer to this question on page 678.

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CONCEPT   Circulatory Systems Can Be
32.1   Closed or Open

</div>

A **circulatory system** typically consists of a muscular pump (heart), a fluid (blood), and a series of conduits (blood vessels or channels) through which the blood is pumped. Because blood must flow close to all the cells of the body, the profusion of blood vessels is often spectacular when visualized (**FIGURE 32.1**).

For an animal to have a high degree of division of labor among its organs, a circulatory system is essential because it allows each organ to export its products promptly to other parts of the body and to receive promptly the products of other organs. With a circulatory system, O_2 taken up by gills or lungs can be delivered rapidly to all other organs (see Figure 31.3); hormones secreted by endocrine glands can be distributed quickly throughout the body; lipid molecules stored in body fat can be delivered rapidly to the cells of any organ where they are needed; and waste products of cell metabolism can be carried promptly to the kidneys for excretion.

The sophistication of the circulatory system in a species tends to be correlated with the species' need for circulatory O_2 transport. This is because O_2 transport is typically the most urgent circulatory function. Many minutes can go by without any transport of hormones, food molecules, or
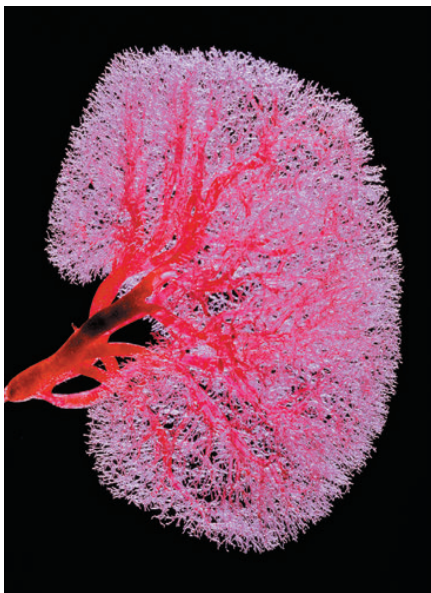
FIGURE 32.1 The Arteries of Visible Size That Carry Blood to the Human Kidney   To obtain this image, the arteries were injected with a liquid plastic that hardened after injection, and then the tissues were removed, leaving just this plastic cast. Keep in mind that, regardless of the complexity, the vessels visualized here are only the ones that can be seen with the naked eye. The microscopic vessels, which are even more profuse, are not visualized with this technique.

wastes—animals can tolerate such interruptions. However, animals typically cannot tolerate long interruptions in O_2 transport. For instance, if a person's blood circulation stops during a cardiac arrest, depriving brain cells of O_2, the person becomes unconscious within 20 seconds! When we consider how rapidly blood must flow in a circulatory system, the need for O_2 transport is typically the most important consideration because—of all the substances carried by blood flow—O_2 must be transported the fastest. This explains why animals that have evolved high metabolic rates (and therefore have high O_2 needs) also usually have evolved high-performance circulatory systems.

The vertebrate animals nicely illustrate the relationship between metabolic rate and circulatory function. Mammals and birds typically have far higher rates of blood flow and higher blood pressures than lizards, frogs, or fish of the same body size. This difference in circulatory performance correlates with differences in metabolic rates. Mammals and birds have far higher metabolic rates than lizards, frogs, or fish (see Concept 29.3) and therefore require circulatory systems that can deliver O_2 far faster. The same relationship is seen among types of fish. Fish species with high metabolic rates—such as the tuna in our opening story—have circulatory systems capable of higher performance than those of sluggish fish species. Similarly, among the mollusks, squid—which are fast-swimming predators—have high-performance circulatory systems compared with those of sedentary mollusks such as snails and clams.

Insects are the exception that proves the rule. Some insects, when flying, have very high O_2 needs per gram of body weight. Yet insects have modest, low-performance circulatory systems. The tracheal breathing system of insects accounts for this paradox. O_2 is brought to each cell of an insect by a branch of the animal's breathing system, not by blood circulation. The circulatory system, freed of responsibility to transport O_2, need not perform at a high level, despite the high metabolic rates of insects.

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LINK

The breathing system of insects is described in **Concept 31.2**; see especially **Figure 31.10**

</div>

Closed circulatory systems move blood through blood vessels

A circulatory system is **closed** if the blood is always contained within blood vessels as it circulates. The vertebrates again provide excellent examples and will be our focus here. The heart of a vertebrate pumps blood into large blood vessels called arteries (which we will discuss in more detail in Concept 32.2). The arteries branch like trees into smaller and smaller blood vessels as they carry the blood to tissues and organs throughout the body. The branches ultimately become so small in diameter that we cannot see them with the naked eye. Nonetheless, the blood always remains within vessels. As blood leaves tissues and organs, it flows through vessels that

merge into larger and larger vessels—the veins—that carry it back to the heart:
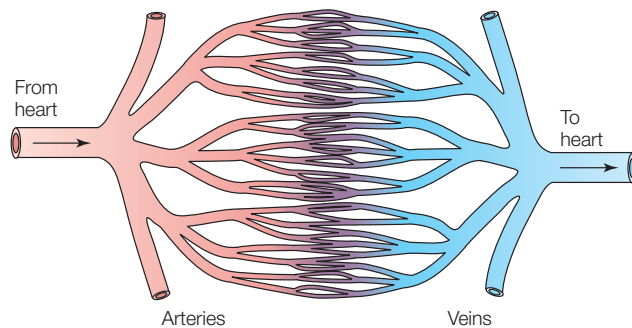
The blood vessels of smallest diameter—which we can see only with a microscope—are collectively called the vessels of the **microcirculation** and consist of arterioles, capillaries, and venules. The arterioles and capillaries are particularly critical for the functioning of a closed circulatory system. As we discuss them, an important point to recognize is that in the walls of all blood vessels, the layer of cells that immediately surrounds the blood is a simple epithelium (see Figure 29.13). For historical reasons, this layer of cells is called the **vascular endothelium**.

The walls of **capillaries** consist only of vascular endothelium. In other words, they consist only of a single layer of thin, flattened epithelial cells, less than 1 μm thick (**FIGURE 32.2A**). Moreover, capillaries are of tiny diameter. The open passage in a blood vessel is called the vessel lumen. In capillaries, the lumen is often just slightly larger in diameter than individual red blood cells. For this reason, the cells (~7–8 μm in diameter in humans) must pass through capillaries in single file (**FIGURE 32.2B**). In each tissue of the body, capillaries are found near every tissue cell. For instance, capillaries are positioned near every brain cell and every muscle cell. The number of capillaries is so great as to be almost unimaginable. Added together, for example, the capillaries in a single cubic centimeter of mammalian skeletal muscle or heart muscle are 10–30 meters long!

Capillaries are the principal sites in a closed circulatory system where blood releases O_2, nutrient molecules, hormones, and other substances to the tissues. They are also the principal sites where blood takes up CO_2 and other waste products from the tissues. Capillaries play these roles in part because they are so numerous. They are also suited to these roles because their walls are thin and often porous, allowing materials to move rapidly across their walls by diffusion and other means.

Arterioles are as important for the function of the microcirculation as capillaries are. The walls of an arteriole consist of an inner layer of vascular endothelium surrounded by an outer layer of smooth muscle cells that are under the control of the autonomic nervous system (described in Concept 34.5) and other control mechanisms. The muscle cells in the wall can adjust the diameter of an arteriole's lumen. Contraction of the muscle cells causes vasoconstriction, reducing the lumen diameter. Relaxation of the muscle cells allows the lumen diameter

to increase, a process called vasodilation. Control of the arteriole lumen diameter in these ways is called **vasomotor control**.

Why do changes in the lumen diameter matter? They are of enormous importance because they control where blood flows. The famous French physiologist Jean Poiseuille (pronounced *Pwa-sul*) demonstrated in the mid-19th century that the rate of fluid flow through a tube is extraordinarily sensitive to the diameter of the tube lumen because this rate depends directly on the 4th power of the diameter. In other words, if the diameter of the lumen of a tube is doubled, the flow rate through the tube increases by a factor of 16! Conversely, halving the diameter reduces flow to 1/16 of its previous rate. An arteriole precedes each capillary bed (set of interconnected capillaries) and controls the flow of blood into it (**FIGURE 32.3**). By controlling the diameters of the arterioles, the autonomic nervous system and other systems exert control over which capillary beds receive blood flow.

Several everyday examples illustrate arteriolar control of blood flow. The skin of people with fair complexions is often more pinkish in warm than in cold weather. This change reflects vasomotor control. Skin arterioles dilate in warm weather, permitting vigorous blood flow to the capillary beds near the skin
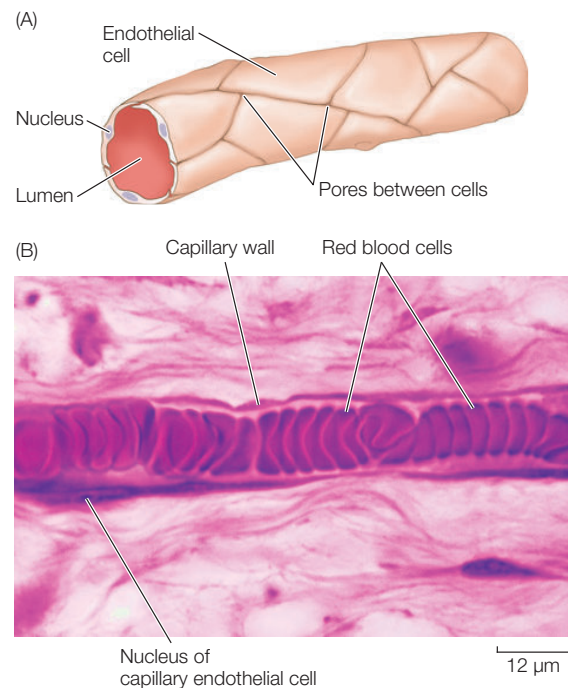
FIGURE 32.2 Blood Capillaries The capillaries may be small, but they are where blood flow accomplishes most of its missions. (A) The wall of a capillary consists of a single layer of highly flattened epithelial cells (called endothelial cells in this context). Pores (often termed fenestrations) are found between cells in the capillaries of some tissues but not others. (B) The diameter of the lumen of capillaries is small enough that red blood cells must move through in single file.

Go to MEDIA CLIP 32.1
Capillary Flow: A Tight Squeeze
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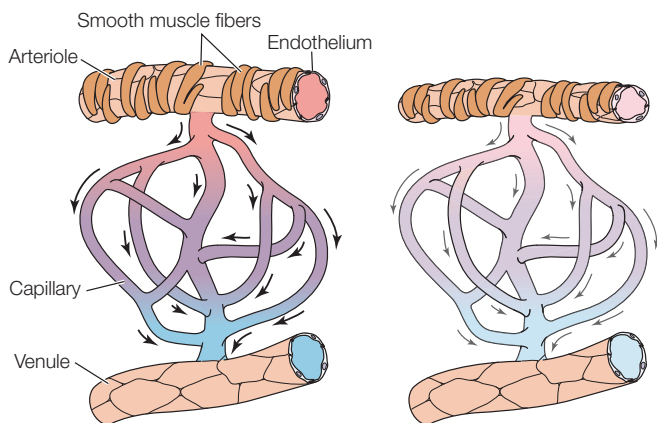
FIGURE 32.3 Arterioles Control the Flow of Blood into Capillary Beds (A) An arteriole with a large diameter allows for a high rate of blood flow. (B) The rate of blood flow drops dramatically when the arteriole diameter decreases.

surface—a response that makes the skin turn pink and helps metabolic heat leave the body. When people exercise, arterioles in their exercising skeletal muscles dilate, and arterioles in many other parts of their body constrict. These changes increase blood flow to the exercising muscles. Erection of the penis is one of the most familiar cases of arteriolar control. During sexual arousal, dilation occurs in arterioles that supply blood to the spongy tissue of the penis, permitting the spongy tissue to inflate with blood under high pressure (see Concept 37.2).

In general, closed circulatory systems can support higher levels of metabolic activity than the open systems we will discuss next, in part because they have a higher capacity to direct blood flow to the tissues that need it the most. In addition to vertebrates, other animals with closed circulatory systems are the annelid worms, such as earthworms, and the cephalopod mollusks, such as squid and octopuses.

In open circulatory systems, blood leaves blood vessels

A circulatory system is **open** if the blood exits blood vessels as it flows through the body. Arthropods—such as insects, spiders, crabs, and lobsters—have open circulatory systems, as do most mollusks. In an animal with an open circulatory system, the heart typically pumps blood into arteries that carry the blood for at least a short distance. Ultimately, however, the vessels end, and the blood pours out into spaces surrounded not by vascular endothelium but by ordinary tissue cells. After this, the blood makes its way back to the heart, not in veins but by flowing through channels called sinuses and lacunae. The sinuses and lacunae are (respectively) small and large spaces among ordinary tissue cells.

In an open circulatory system, no distinction exists between blood (the fluid pumped by the heart and flowing in the blood vessels) and interstitial fluid (the fluid found between cells in the ordinary tissues—also called tissue fluid; see Concept 29.4). Debate exists about the correct name to use for the fluid in open circulatory systems. Here we call it blood. Some biologists, however, prefer to call the fluid hemolymph, referring to the fact that it has attributes of both blood (*hemo*, "blood") and tissue fluid (lymph). Tissue cells are directly bathed by the blood or hemolymph. For this reason, the cells can readily take up O_2 and other materials from the blood, or release wastes into it.

Open circulatory systems are not very well understood, although we know they sometimes have very high rates of blood flow. They are thought to be limited in how well they can control where the blood goes. Circulation in a crayfish or lobster illustrates the pattern of flow in an open circulatory system (**FIGURE 32.4**). The heart pumps blood into arteries that carry the blood to most major parts of the body before ending. After the blood leaves the vessels, it makes its way through sinuses and lacunae to ventral blood spaces along the bases of the walking legs, where the gills arise. Sucking forces developed by the heart then pull the blood through the gills and back into the heart to be pumped again into the arteries.

APPLY THE CONCEPT

Circulatory systems can be closed or open

Atherosclerosis ("hardening of the arteries") is a potentially deadly chronic disease. The immediate problem is that fatty deposits—composed of lipids such as cholesterol and triacylglycerols—build up in blood vessels. Take out a ruler, and using the principles developed by Poiseuille (principles known today as Poiseuille's Law), estimate how much more slowly blood will pass through the atherosclerotic artery at the right, compared with the healthy artery to the left, assuming everything is the same except the fatty deposits. People start their lives with arteries like the one at the left.

Progression of atherosclerosis
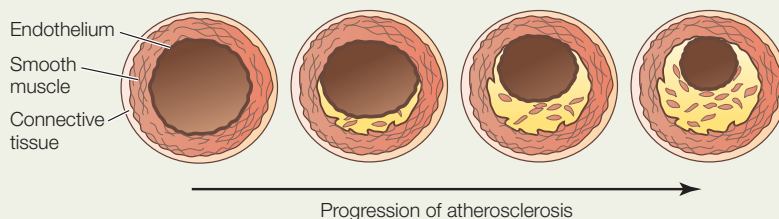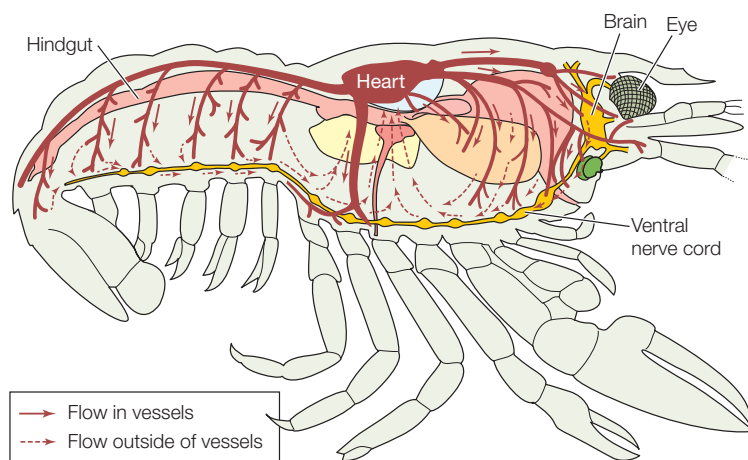
FIGURE 32.4 Blood Flow in the Open Circulatory System of a Crayfish or Lobster Crayfish and lobsters have many arteries, which extend forward and backward from the heart. The heart pumps blood into these arteries, which transport the blood to most parts of the body. The arteries end, however, and then the blood is released from vessels into sinuses and lacunae that are lined with ordinary systemic tissue cells rather than with vascular endothelium. After release from the arteries, blood from the anterior parts of the body flows posteriorly, and blood from the posterior parts of the body flows anteriorly. These flows converge on a ventral sinus (cavity) that runs along the bases of the principal legs. From there the blood returns to the heart. Although not shown here, the blood passes through the gills (which are attached at the bases of the principal legs) in this final step.

CHECKpoint CONCEPT 32.1

✓ What is the most fundamental distinction between open and closed circulatory systems?

✓ How do arterioles and capillaries differ structurally and functionally?

✓ A grasshopper and a clam both have open circulatory systems. What enables the grasshopper to be more active and sustain a higher metabolic rate?

For the rest of this chapter, we will focus mainly on the closed circulatory systems of vertebrates. One reason for this focus is that we ourselves have a closed circulatory system. We'll start by discussing the major patterns of blood flow throughout the vertebrate body.

CONCEPT 32.2 The Breathing Organs and Systemic Tissues Are Usually, but Not Always, in Series

For understanding circulation, we need to recognize two fundamentally different types of tissues or organs in the body of an animal: the systemic tissues and the breathing organs. The **systemic tissues** are all the tissues and organs of an animal's body other than the breathing organs (lungs or gills). They take up O_2 from the blood and add CO_2 to the blood. Conversely,

the **breathing organs** add O_2 to the blood and take up CO_2 from the blood. With these definitions in mind, we can also define the systemic circuit and the breathing-organ circuit.

The **systemic circuit** consists of the blood vessels (or blood channels in the case of an open circulatory system) that carry blood to and from the systemic tissues. The **breathing-organ circuit** consists of the blood vessels that carry blood to and from the breathing organs. This circuit can be called the pulmonary circuit or lung circuit in animals that breathe with lungs, or it can be called the gill circuit in those that breathe with gills.

A final set of important definitions applies to the visible blood vessels, the arteries and veins. These vessels are defined by direction of blood flow, not by the O_2 content of the blood they carry. **Arteries** are vessels that carry blood *away from* the heart. **Veins** carry blood *toward* the heart. Recall from Chapter 31 that **perfusion** refers to flow of blood through a tissue or organ.

Most fish have the systemic circuit and gill circuit connected in series

The most common circulatory plan in animals is for the systemic and breathing-organ circuits to be connected in series, meaning that blood flows through the two circuits sequentially: first through one circuit, then through the other, then back through the first.
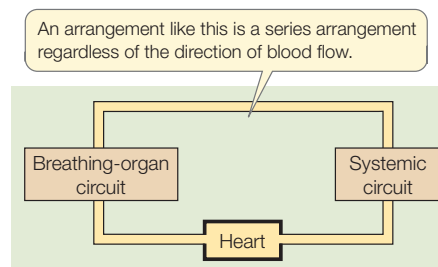
Fish display such a series arrangement (**FIGURE 32.5A**). The only exceptions are air-breathing species. In a typical fish, the heart pumps blood into arteries that lead directly to the gills. After the blood perfuses the gills and exits them, it is collected into additional arteries, which branch to supply blood to all the systemic tissues, from the brain in the head to the kidneys and swimming muscles in the abdomen. After perfusing the systemic tissues, the blood enters veins that take it back to the heart.

A series arrangement of this sort is considered to be the most efficient for delivering O_2. It is efficient because all the blood pumped to the systemic tissues is O_2-rich, having just passed through the gills. Moreover, all the blood pumped to the gills is O_2-depleted, having just exited the systemic tissues. Energy is not wasted in sending O_2-rich blood to the gills or O_2-depleted blood to the systemic tissues.

Natural selection has favored the evolution of a series arrangement in many types of animals. We have already seen,
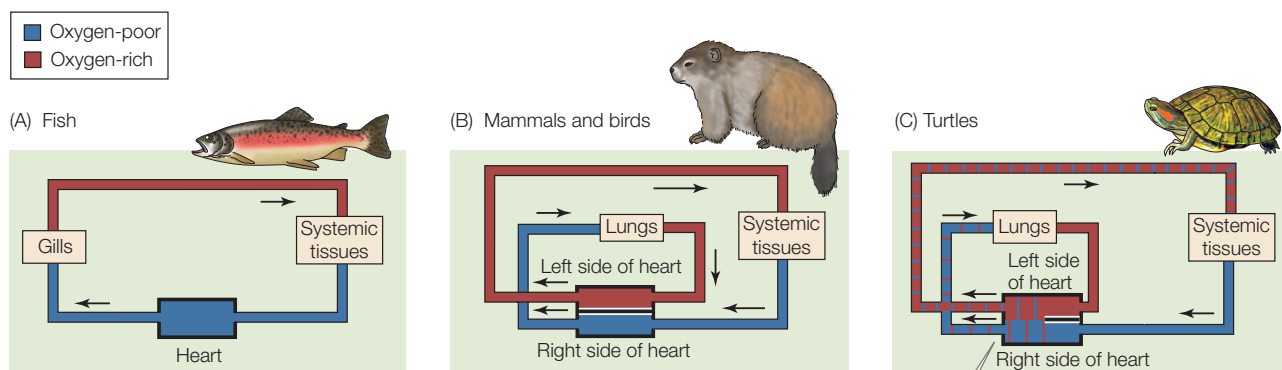
FIGURE 32.5 **Vertebrate Circulatory Plans** Shown here are typical circulatory plans for (A) fish, (B) mammals and birds, and (C) turtles and most other non-avian reptiles.

During prolonged diving, after blood from the systemic tissues enters the right side of the heart, it can be shunted into the left side of the heart and directly reenter the systemic circuit.

Go to ACTIVITY 32.1 Vertebrate Circulatory Systems
PoL2e.com/ac32.1

for example, that crustaceans have series circulation in their open circulatory systems (see Figure 32.4). After the blood of a crayfish or crab passes through the gills, the heart pumps it through the systemic circuit, and then the blood returns to the gills. Squid and octopuses, which have closed circulatory systems, also have the gill circuit and systemic circuit connected in series.

Mammals and birds have the systemic circuit and lung circuit connected in series

As we will see in more detail in Concept 32.3, mammals and birds have four-chambered hearts, adding complexities to understanding the circulatory plan. However, like fish, they have the systemic circuit and breathing-organ circuit connected in a high-efficiency series arrangement.

In a mammal or bird, blood passes through the heart twice to make a complete trip through the circulatory system. The heart is divided into right and left halves. Moreover, it is *completely divided*, meaning that sheets of tissue completely separate the right and left halves, so that blood flowing through the right and left sides of the heart cannot mix. As blood travels from the systemic circuit to the lung circuit, it passes through the right half of the heart. As it travels from the lung circuit to the systemic circuit, it passes through the left half of the heart. **FIGURE 32.5B** shows the circulatory plan. If you trace the flow of blood from any particular point back to the same point, you will see that blood passes from the systemic circuit to the lung circuit, then back to the systemic circuit, and so forth: a series circulation.

A limitation that fish face is that, after their heart pumps their blood, the blood must pass through both the gill and systemic circuits without receiving additional propulsive energy (an added push) from the heart. Mammals and birds have evolved circulatory plans without this limitation. In a mammal or bird, the heart pumps the blood just before it travels to the lungs, and it pumps it again just before it travels to the systemic circuit.

Amphibians and most non-avian reptiles have circulatory plans that do not anatomically guarantee series flow

What about circulation in the amphibians and non-avian reptiles such as turtles and lizards? Let's start with a few words about blood flow through the **ventricle**, the heart's largest and most muscular chamber. In fish, only O_2-depleted blood (from the systemic circuit) enters the ventricle. Thus when the ventricle contracts and ejects blood to flow to the gills, it ejects only O_2-depleted blood. In mammals and birds, the ventricle is divided into two anatomically separate chambers (as we will see in Figure 32.6). Only O_2-depleted blood enters the right chamber, which then ejects only O_2-depleted blood when it contracts. Only O_2-rich blood from the lungs enters the left chamber, which therefore pumps exclusively O_2-rich blood.

Adult amphibians and most non-avian reptiles have a single ventricle like fish, but blood flow in and out is far more complicated. The lumen of the single ventricle is not a wide-open space because it is occupied by crisscrossing strands of heart muscle and by sheets of connective tissue. Yet the lumen is not fully divided into subparts. O_2-rich blood from the lungs enters the ventricle at one point, while simultaneously, O_2-depleted blood from the systemic circuit enters it at another point. The ventricle pumps blood to both the lungs and the systemic circuit. In theory, therefore, O_2-rich and O_2-depleted blood can mix in the ventricle or be pumped to the wrong destination. Decades ago, when biologists knew only about anatomy, the hearts of these animals were often viewed erroneously as being defective intermediate stages in the evolution of vertebrates.

With data from functional studies, we now know that O_2-rich and O_2-depleted blood are often kept separate as they flow through the ventricle. Investigators have added fluids that can be seen with X-rays to blood of one oxygenation state or the other, for example, and often have observed that little mixing occurs between the O_2-rich and O_2-depleted blood. In these cases, a series circulation is maintained, with just a small amount of inefficiency as a result of mixing in the ventricle (**FIGURE 32.5C**). O_2-rich blood from the lungs is pumped by the

ventricle principally to the systemic circuit, and O_2-depleted blood from the systemic circuit is sent primarily to the lungs.

We also now realize from functional studies that sometimes an incompletely divided ventricle can have advantages for certain of these animals. When turtles dive underwater for long periods, for example, their lungs become useless. The turtles, however, have evolved control mechanisms whereby they can stop circulating blood to their lungs. Taking advantage of the fact that they have just a single, undivided ventricle, they direct blood that enters the ventricle from the systemic circuit so that the ventricle pumps it back into the systemic circuit, rather than sending it to the lungs. In this way, the turtles can pump blood round and round in the systemic circuit—permitting the circulatory system to perform all its functions other than gas transport from the lungs—during the time their lungs are useless.

CHECKpoint   CONCEPT 32.2

✓ What is the systemic circuit?

✓ Why is a series arrangement of the systemic and breathing-organ circuits efficient for O_2 transport?

✓ In a turtle that has been diving underwater for a long time, does blood pass through the systemic and lung circuits in series? Explain your answer.

By now you have learned a lot about hearts in a general way. But how do hearts work? What controls their regular beating? How do the cells of the heart muscle get the O_2 they need? We will address questions such as these in the next concept.

CONCEPT 32.3   A Beating Heart Propels the Blood

A **heart** is a discrete, localized pumping structure. Some animals with a circulatory system lack a heart. In earthworms and other annelid worms, for example, the blood is propelled entirely by peristaltic waves of contraction in muscular blood vessels. Some animals, by contrast, have more than one heart. Crayfish and lobsters, for instance, have a small accessory heart that helps perfuse their brain, in addition to their large, principal heart.

The muscle tissue of a heart is termed the **myocardium** (*myo*, "muscle"; *cardi*, "heart"). The cells of the myocardium often have distinctive properties, compared with skeletal muscle cells or smooth muscle cells. They are thus distinguished as cardiac muscle cells (see Concept 33.4).

The volume of blood pumped per beat by a heart is called the heart's stroke volume. A heart's cardiac output is the volume of blood the heart pumps per minute. We calculate cardiac output by multiplying stroke volume by the number of beats per minute, the heart rate. For example, when you are at rest, your heart has a stroke volume of about 70 milliliters per beat (volume pumped into the systemic circuit) and beats about 70 times per minute. Your resting cardiac output is thus about 5 liters per minute (70 ml/beat × 70 beats/min = 4,900 ml/min, or about 5 L/min).

During exercise, we increase both stroke volume and heart rate. An average young person can increase cardiac output about fourfold. Even at rest, however, the amazing performance of the heart is evident. At rest the heart pumps about 300 liters each hour, corresponding to 2.6 million liters per year and almost 200 million liters in an average lifetime.

Vertebrate hearts are myogenic and multi-chambered

Hearts are classified based on the answers to two questions: how is each beat initiated, and how many chambers are present?

Vertebrate hearts do not require nervous stimulation to beat. Instead, each beat is initiated within the myocardium in modified muscle cells, and the muscle of a vertebrate heart beats on its own, even when all connections to other tissues of the body are severed. Vertebrate hearts are classed as **myogenic**, meaning "beginning in muscle," to recognize that heartbeats originate in the muscle tissue. Mollusks, too, have myogenic hearts. Crustaceans do not, however, as we will see later.

Vertebrate hearts are also classed as multi-chambered because they consist of two or more distinct chambers. Fish hearts have two muscular chambers: an **atrium** (plural *atria*)—which is a thin-walled chamber through which blood passes on its way to the principal pumping chamber—and a thick-walled, highly muscular ventricle. Amphibian hearts have three chambers (two atria that empty into one partially divided ventricle), and the hearts of mammals and birds have four chambers. One-way valves are present where one heart chamber opens into another, ensuring than blood flows through the chambers in the correct order.

Let's take a closer look at the mammalian heart (**FIGURE 32.6**). It consists of four chambers: two highly muscular ventricular chambers, which contract together, and two less-muscular atria, which also contract together. O_2-depleted blood returning to the heart from the systemic tissues enters the right atrium and then flows through a one-way valve into the right ventricle. When the ventricles contract, the O_2-depleted blood is pumped into the pulmonary arteries leading to the lungs. O_2-rich blood delivered to the heart from the lungs enters the left atrium and then passes through a one-way valve into the left ventricle. When the ventricles contract, this O_2-rich blood is pumped into a massive artery, the **aorta**, from which it flows through branching arteries to the systemic tissues.

The cycle of contraction and relaxation of the heart is called the **cardiac cycle**. This cycle is divided into two phases: **systole** (pronounced sís-toll-ee), when the ventricles contract, and **diastole** (die-ás-toll-ee), when the ventricles relax (**FIGURE 32.7**).

Go to ANIMATED TUTORIAL 32.1
The Cardiac Cycle
PoL2e.com/at32.1

The ventricles pressurize the blood inside them when they contract, and this positive pressure—developed by contraction of the ventricular myocardium—is the principal force that drives blood through the blood vessels. The positive pressure developed by the right ventricle forces blood to flow to the
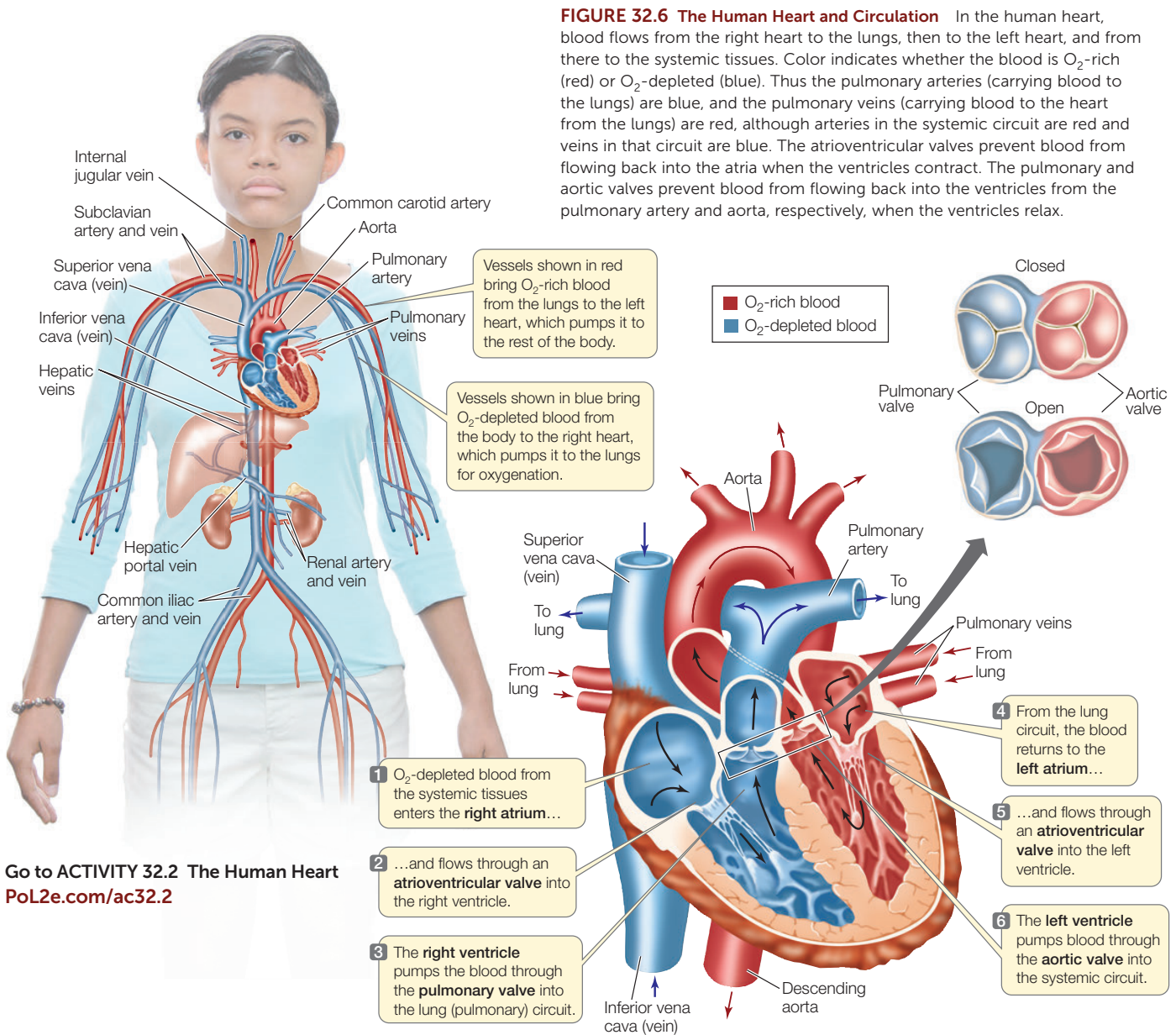
FIGURE 32.6 The Human Heart and Circulation In the human heart, blood flows from the right heart to the lungs, then to the left heart, and from there to the systemic tissues. Color indicates whether the blood is O_2-rich (red) or O_2-depleted (blue). Thus the pulmonary arteries (carrying blood to the lungs) are blue, and the pulmonary veins (carrying blood to the heart from the lungs) are red, although arteries in the systemic circuit are red and veins in that circuit are blue. The atrioventricular valves prevent blood from flowing back into the atria when the ventricles contract. The pulmonary and aortic valves prevent blood from flowing back into the ventricles from the pulmonary artery and aorta, respectively, when the ventricles relax.

Vessels shown in red bring O_2-rich blood from the lungs to the left heart, which pumps it to the rest of the body.

Vessels shown in blue bring O_2-depleted blood from the body to the right heart, which pumps it to the lungs for oxygenation.

■ O_2-rich blood
■ O_2-depleted blood

1 O_2-depleted blood from the systemic tissues enters the **right atrium**…

2 …and flows through an **atrioventricular valve** into the right ventricle.

3 The **right ventricle** pumps the blood through the **pulmonary valve** into the lung (pulmonary) circuit.

4 From the lung circuit, the blood returns to the **left atrium**…

5 …and flows through an **atrioventricular valve** into the left ventricle.

6 The **left ventricle** pumps blood through the **aortic valve** into the systemic circuit.

Go to ACTIVITY 32.2 The Human Heart
PoL2e.com/ac32.2

lungs and back to the heart. The positive pressure developed by the left ventricle forces blood to flow to all the systemic tissues and back. The left ventricle is more muscular than the right (see Figure 32.6) and develops higher pressures, which help ensure flow through the larger systemic circuit.

The **blood pressure** at any point in the circulatory system is the extent to which the pressure in the blood exceeds the pressure in the environment of the animal. As you might imagine, the blood pressure in the aorta rises and falls during the cardiac cycle, even though the aortic walls are elastic and therefore tend to dampen pressure changes. In healthy young people, the aortic pressure during systole is about 120 mm Hg (millimeters of mercury, referring to the height of a vertical column

of mercury that the pressure can support). The aortic pressure during diastole is about 80 mm Hg. These pressures undergo little change as blood flows through major arteries and can therefore be measured in the arm, as is usually done. They are typically quoted as a ratio: "120 over 80." **Hypertension** ("high blood pressure") is a disease in which the pressures are significantly higher than this norm.

Each heartbeat is initiated by pacemaker cells, which are modified muscle cells found in a localized part of the right atrial wall, the sinoatrial (S-A) node (**FIGURE 32.8A**). Cardiac muscle cells in the vertebrate myocardium are electrically coupled, meaning that when a particular cell undergoes electrical depolarization (a reversal of the electric charge difference across the

1 The ventricles fill with blood.

2 At the end of ventricular diastole, the atria contract, completing ventricular filling.

3 The ventricles contract, the atrioventricular valves close, and pressure in the ventricles builds up until the aortic and pulmonary valves open.

4 When the aortic and pulmonary valves open, blood is pumped out of the ventricles and into the aorta and pulmonary arteries.

5 The ventricles start to relax. Pressure in the ventricles falls, and since pressure is now greater in the aorta and pulmonary arteries, the aortic and pulmonary valves slam shut.

Aortic valve
Pulmonary valve
Left atrium
Right atrium
Atrioventricular valves
Left ventricle
Right ventricle

Ventricular diastole

Ventricular systole

FIGURE 32.7 The Cardiac Cycle The rhythmic relaxation (diastole) and contraction (systole) of the ventricles is called the cardiac cycle.

cell membrane) and consequently contracts, it initiates electrical depolarization and contraction in the cells next to it. Accordingly, when electrical depolarization and contraction are initiated at any one point in a mass of heart muscle, they spread rapidly throughout the muscle by moving from cell to cell. This process ensures that all the cells within a large mass of muscle depolarize and contract almost simultaneously. After the pacemaker cells in the S-A node initiate a wave of depolarization and contraction, the depolarization and contraction rapidly spread throughout the atria (**FIGURE 32.8B**, steps **1** and **2**). Depolarization cannot spread directly into the ventricles, however, because a sheet of fibrous connective tissue lies between the atrial and ventricular muscle masses.

(A) The conducting system and sinoatrial node

Sinoatrial (S-A) node
Right atrium
Atrioventricular (A-V) node
Right ventricle
Septum between ventricles
Left atrium
Fibrous connective tissue
Conducting system
Left ventricle

FIGURE 32.8 The Process of Activation of the Mammalian Heart during Each Heartbeat The muscle cells of the heart, like virtually all muscle cells, are activated to contract by electrical depolarization of their cell membrane. (A) Structures composed of modified muscle cells—the S-A node, A-V node, and conducting system—initiate and coordinate the spread of depolarization through the heart during each heartbeat. (B) Muscle cells in pink areas are depolarized during the successive stages shown. Cells in white areas are not depolarized; they are either awaiting depolarization or have repolarized following depolarization.

(B) The initiation and spread of depolarization during a heartbeat

Depolarized
Not depolarized
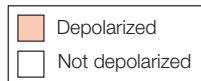
1 Depolarization begins in the S-A node and spreads outward through atrial muscle.

2 Although depolarization spreads rapidly throughout the atrial muscle, its spread into the A-V node is delayed. The depolarized atria start to contract.

3 Once the A-V node becomes depolarized, the depolarization spreads very rapidly into the ventricles along the conducting system. Atrial muscle starts to repolarize.

4 The nearly simultaneous depolarization of cells throughout the ventricular myocardium leads to forceful ventricular contraction.

S-A node
A-V node
Conducting system

APPLY THE CONCEPT

A beating heart propels the blood

A physician or nurse measures your blood pressure with (1) a stethoscope and (2) an inflatable pressure cuff and a pressure gauge, together called a sphygmomanometer. Typically the pressure cuff is placed around your upper arm, and the stethoscope is used to listen to the sounds of blood flowing through the artery at the crook of your elbow. When the cuff is inflated to a high enough pressure, only a background rumble is heard in the stethoscope. Then the physician or nurse slowly lowers the pressure in the cuff. Suppose the observations shown at the right are obtained.

1. Why is there no sound at the high cuff pressure, and why does the tapping start as the pressure is lowered?

2. Why does the tapping sound disappear after several steps of lowering the cuff pressure?

3. What pressure reading is closest to the systolic pressure? To the diastolic pressure?

CUFF PRESSURE (mm Hg)	SOUND
160	None
140	None
130	None
120	Tapping*
100	Tapping
80	Tapping
70	None
60	None
50	None

* Tapping occurs synchronously with heartbeats.

LINK

Electrical depolarization in muscle cells is described in **Concept 33.1**; **Concept 33.4** provides more details about the special characteristics of cardiac muscle

How, then, do electrical depolarization and contraction move from the atria to the ventricles? A set of modified muscle cells called the atrioventricular (A-V) node is situated near the junction of the atria and the ventricles (see Figure 32.8A). Electrical depolarization of the atria causes depolarization in this node after a slight delay. This delay is important because it ensures that the ventricles contract *after* the atria. Once depolarized, the cells of the A-V node relay the electrical depolarization into a system of modified muscle cells called the **conducting system** (see Figure 32.8A), in which the depolarization travels very rapidly from cell to cell, sweeping at high speed into the right and left ventricles (see Figure 32.8B, step ❸). As soon as muscle cells in the ventricles start to depolarize and contract, the wave of depolarization and contraction spreads rapidly from cell to cell within the ventricles (see Figure 32.8B, step ❹). The result is a strong, coordinated ventricular contraction.

Nerves to the heart and blood-borne hormones can strongly modify and control the beating of the heart. That is, even though the heart beats on its own, it is subject to controlling influences—termed extrinsic controls—exerted by the nervous and endocrine systems. We've all felt our heart pound after our adrenal glands secrete a rush of epinephrine and norepinephrine (adrenaline and noradrenaline) in response to fright or stress, and this is the most common way that we become aware of extrinsic controls. Both the pacemaker cells in the S-A node and the ordinary muscle cells of the myocardium are highly innervated by the autonomic nervous system. As experiments along the lines of the Investigation in **FIGURE 32.9**

show, the autonomic nervous system influences the S-A node to increase or decrease the heart rate. It also influences the ordinary myocardial cells to increase or decrease their force and speed of contraction.

LINK

The autonomic nervous system controls many involuntary processes, as discussed in **Concept 34.5**; **Concept 35.2** describes the numerous effects of epinephrine and norepinephrine

The myocardium must receive O_2

The cells of the heart muscle in all animals must have a way to obtain O_2. We know the most about this process in vertebrates.

In many types of fish, the myocardial cells get their O_2 directly from the blood flowing through the heart chambers. However, this way of getting O_2 can not meet cellular O_2 needs in hard-working, high-performance hearts, explaining the evolution of a coronary circulatory system.

A **coronary circulatory system** consists of arteries, capillaries, and veins inside (or closely associated with) the myocardium. In animals with a coronary circulation, the heart pumps O_2-rich blood into its own coronary arteries. This blood then flows through the coronary arteries to the coronary capillary beds in the myocardium, providing O_2 to all the cardiac muscle cells. Mammals and birds depend entirely on a coronary circulation for their cardiac muscle cells to receive O_2. Fish with high-performance hearts, such as tuna and salmon, depend in part on a coronary circulatory system.

Coronary artery disease is a common, life-threatening problem for people in today's world. Blockage of a coronary artery, by fatty deposits or clots, deprives some of the cardiac muscle cells of adequate O_2. When blockage becomes

INVESTIGATION

FIGURE 32.9 The Autonomic Nervous System (ANS) Helps Control Heart Rate by Affecting Pacemaker Cells   The voltage across the cell membrane of a cell is called the cell's membrane potential. Pacemaker cells have the unusual property that, after they complete a large cell-membrane depolarization (which causes a heart contraction), their membrane potential gradually creeps upward. This upward creep ultimately reaches a threshold at which it causes another large depolarization, leading to another heart contraction. The rate of upward creep determines heart rate, because it determines how much time passes from one depolarization to the next. The creep rate is determined by the properties of ion channels in the cell membrane. Investigators reasoned that signals from the ANS could affect the ion channels and thus affect the time required for threshold to be reached—a process that would in turn affect heart rate. They studied epinephrine, which is secreted by the sympathetic division of the ANS.[a]

HYPOTHESIS

The ANS neurotransmitter epinephrine influences the membrane potentials of pacemaker cells in ways that alter heart rate.

METHOD

1. Culture living S-A node tissue from an experimental animal in a dish. Insert an intracellular recording electrode into pacemaker cells.
2. Measure the membrane potential of pacemaker cells during resting heartbeats (the control) and after application of epinephrine.

RESULTS

1 The cell membrane depolarizes to cause a heart contraction.

2 After a depolarization, the cell membrane potential falls below the threshold.

A control cell takes about 150 msec to creep back up to threshold.

— Control cells
— Cells treated with epinephrine

3 The membrane potential gradually creeps upward…

4 …until the threshold is reached, triggering the next depolarization.

When epinephrine is applied, creep is speeded and heart rate increases.

CONCLUSION

The ANS neurotransmitter epinephrine influences heart rate by altering the membrane potentials of pacemaker cells.

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]H. Brown et al. 1979. *The Journal of Experimental Biology* 81: 175–204.

complete, a heart attack can occur, and the cells in the affected part of the myocardium can die.

An electrocardiogram records the electrical activity of the heart

Great numbers of muscle cells depolarize together each time a heart contracts (see Figure 32.8B). Because the cells undergo electrical depolarization simultaneously, their individual voltage signals add together to produce a large voltage signal. This voltage signal is so large, in fact, that it often can be readily detected on the surface of the body! An **electrocardiogram** (**ECG** or **EKG**) is simply a record of heart-related voltage differences on the surface of the body over time. EKGs can be recorded from all sorts of animals, even lizards or octopuses. They are an important tool for diagnosing heart problems in people and pets.

A simple EKG can be recorded using just two electrodes, such as one on the right arm and one on the left leg (**FIGURE 32.10**). For medical diagnoses, however, recordings are made from many pairs of electrodes, with each pair providing slightly different information.

Crustacean hearts are neurogenic and single-chambered

The hearts of crayfish, lobsters, crabs, and their relatives differ from those of vertebrates in several ways. Study of crustacean hearts thus helps us appreciate that evolution has produced diverse types of circulatory systems in animals.

The muscle cells of crustacean hearts require nervous stimulation to beat. Crustacean hearts are thus **neurogenic**, meaning that beating "begins in neural tissue." Some scorpions and spiders also have neurogenic hearts.

A ganglion—a cluster of multiple nerve cells—is associated with the dorsal wall of the single heart chamber in a crustacean heart (**FIGURE 32.11A**). One of the nerve cells in this cardiac ganglion acts as a pacemaker cell, rhythmically initiating nerve impulses. These impulses are then relayed by nerve cells to every muscle cell in the heart. The muscle cells in a crustacean heart contract simultaneously during a heartbeat because nerve cells stimulate all of them simultaneously—a very different mechanism than in vertebrate hearts. If the cardiac ganglion and the heart muscle are dissected apart, the ganglion continues to produce rhythmic nerve impulses, but the muscle cells stop contracting.

Both positive pressure and suction are crucial for heart function in crustaceans. The single-chambered heart is suspended by elastic ligaments in a blood-filled cavity (**FIGURE 32.11B**). All the vessels attached to the heart are arteries and carry blood away from the heart (see Figure 32.4). Three pairs of slits, called ostia (singular ostium), penetrate the heart wall
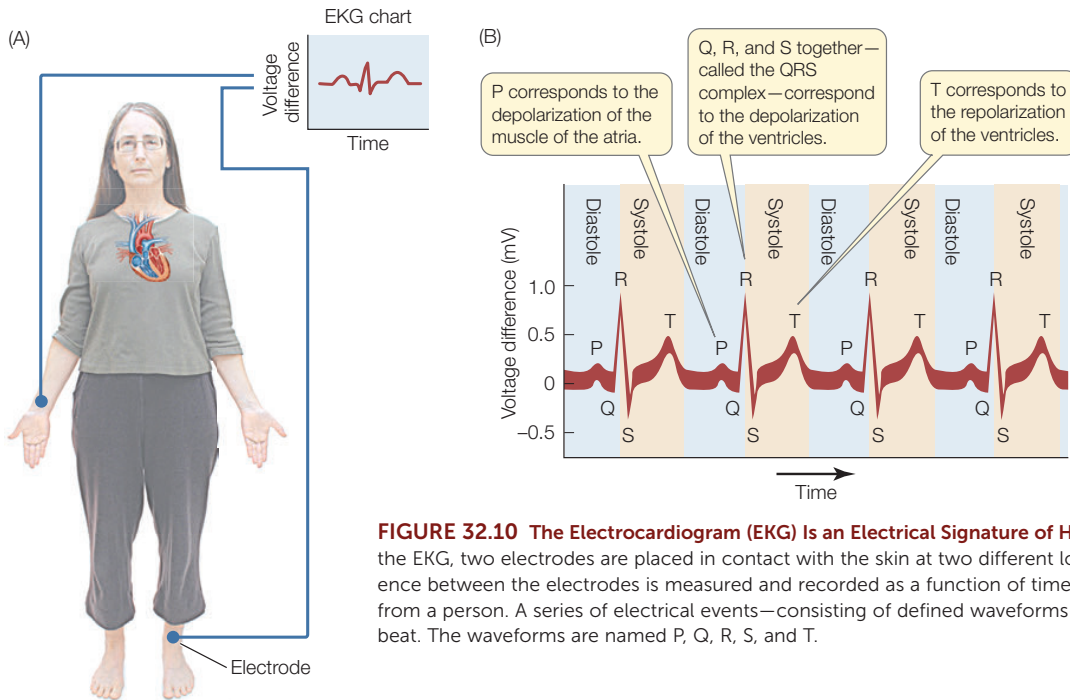
FIGURE 32.10 The Electrocardiogram (EKG) Is an Electrical Signature of Heart Action (A) To record the EKG, two electrodes are placed in contact with the skin at two different locations. The voltage difference between the electrodes is measured and recorded as a function of time. (B) A normal EKG record from a person. A series of electrical events—consisting of defined waveforms—occurs during each heartbeat. The waveforms are named P, Q, R, S, and T.

and act as one-way valves that allow blood to flow into but not out of the heart. When the heart contracts, the elastic ligaments are stretched like rubber bands, and the blood inside the heart is pressurized, forcing the blood to flow out into the arteries. Then, when the heart relaxes, the stretched elastic ligaments shorten, pulling the walls of the heart chamber outward and tending to cause suction inside the heart. This suction pulls blood into the heart chamber through the ostia, filling the heart in preparation for the next contraction.

CHECKpoint   CONCEPT 32.3

✓ What is a coronary artery?

✓ In the human heart, why do the ventricles contract after the atria, even though cardiac muscle cells directly activate neighboring cells?

✓ What results would you observe if you obtained a living crayfish heart and separated the cardiac ganglion from the heart muscle and then studied the two parts? What conclusions would you draw from the results?

Now that we have discussed circulatory plans and hearts, we will complete our examination of the circulatory system by focusing on the blood vessels.
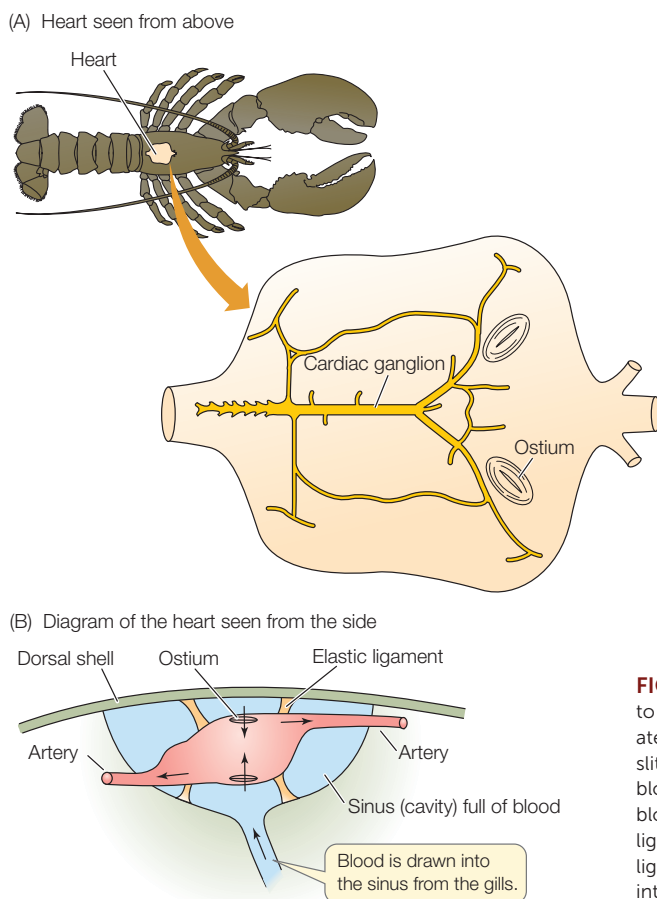
FIGURE 32.11 The Heart of a Lobster (A) The lobster heart is stimulated to beat by nerve impulses that originate in a cardiac ganglion (yellow) associated with the dorsal heart wall. (B) Blood enters the single heart chamber via slits in the heart wall called ostia. These slits act as one-way valves, allowing blood to enter the heart chamber but not exit. When the heart contracts, blood inside is forced into the arteries. Contraction also stretches the elastic ligaments. After contraction, when the heart muscle relaxes, the stretched ligaments pull the heart wall outward as they shorten, thereby sucking blood into the heart chamber through the ostia.

32.4 Many Key Processes Occur in the Vascular System

All the blood vessels, considered together, make up the **vascular system**. The circulatory system is sometimes called the **cardiovascular system** to emphasize that it consists of the heart plus the blood vessels.

The vascular system is an elaborate system in which the vessels in various parts are specialized to perform specific functions. Let's briefly review the vessels in the human circulatory system in the order that blood flows through them.

The arteries must withstand high pressures. To do this, they have thick walls composed of elastic fibers and layers of smooth muscle (**FIGURE 32.12**). The elasticity of the arteries allows them to play two critical, interrelated roles. Each time the heart beats, the arteries stretch a bit, dampening the pressure surge and storing in their stretched state some of the energy imparted to the blood by the heart. Then, during the next diastole, the stretched arteries return to their unstretched state, in the process squeezing the blood and helping maintain blood pressure while the heart is between beats. In this way the arteries play a pressure-dampening role and a pressure-storage role. Were it not for these processes, arterial blood pressure would vary much more than it does between systole and diastole, shooting sharply up and plummeting sharply down. The arteries branch and rebranch, carrying blood to all organs and tissues.

The blood then flows into microcirculatory beds where the arterioles and capillaries play the vital roles we discussed in Concept 32.1. Tiny arteries and the arterioles exercise vasomotor control over the flow of blood to the capillary beds. The capillaries are the principal sites of exchange of materials between the blood and the cells of the tissues.

Blood then enters tiny veins, which merge progressively with other veins, finally leading to the great veins that enter the heart. Blood pressure is far lower in the veins than in the arteries, and the walls of the veins are thinner and expand more easily (see Figure 32.12). A major role of the veins is to serve as a blood volume reservoir. Any blood that is not held elsewhere in the circulatory system is held in the veins.

Pressure and linear velocity vary greatly as blood flows through the vascular system

The principal driving force for blood to flow through the vascular system is the pressure imparted to the blood by the beating heart. The blood pressure represents potential energy. This potential energy is converted to energy of motion as the blood flows, and then it is lost as heat through a type of friction that occurs during blood flow. As a result, the blood pressure falls as the blood flows. Moreover, the pressure falls in direct proportion to the amount of work that must be done to make the blood flow.

Fluids flow easily through large-diameter tubes. For this reason, not much work needs to be done to cause blood to flow
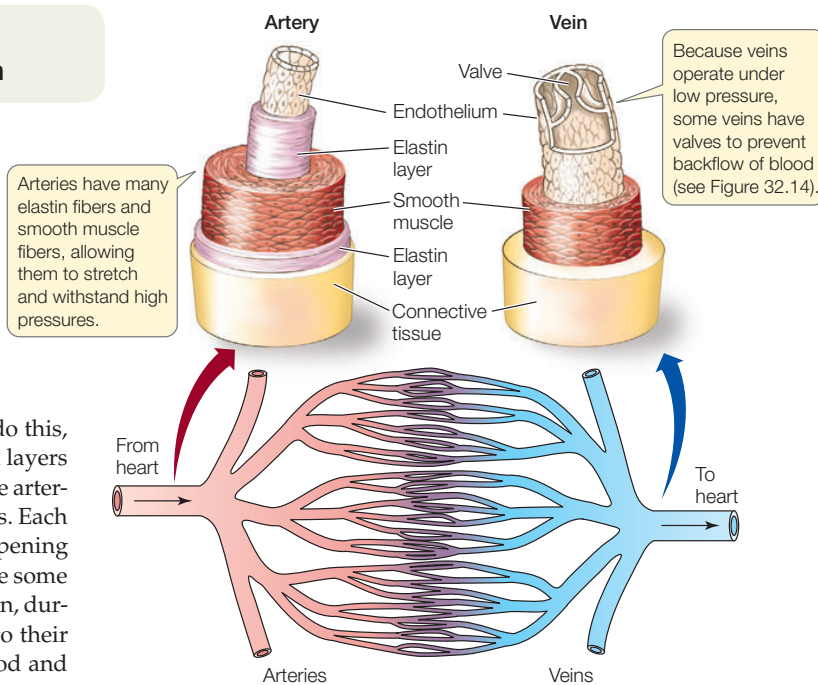
FIGURE 32.12 The Different Anatomical Characteristics of Arteries and Veins Match Their Functions

Go to ACTIVITY 32.3 Structure of a Blood Vessel
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through the large, or even medium-sized, arteries. With little work needing to be done, the blood pressure falls only moderately as blood flows through the beginning branches of the arterial vasculature (**FIGURE 32.13**).

In dramatic contrast, a great deal of work needs to be done to make blood flow through the microscopically tiny vessels of the microcirculation. This work results in a precipitous drop in blood pressure as blood flows through the arterioles,
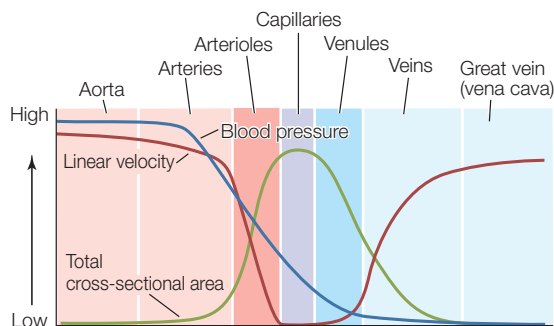
FIGURE 32.13 Blood Pressure and Rate of Flow Change Dramatically as Blood Flows through the Vascular System This graph shows how three critical characteristics of the circulatory system change from one end of the human vascular system to the other: the mean blood pressure (pressure averaged over the full cardiac cycle), the total cross-sectional area of the blood vessels, and the linear velocity of blood flow.

Contractions of skeletal muscles squeeze the veins.

Valve closed   Valve open

This squeezing moves the blood in the veins toward the heart because of one-way valves that prevent backflow.
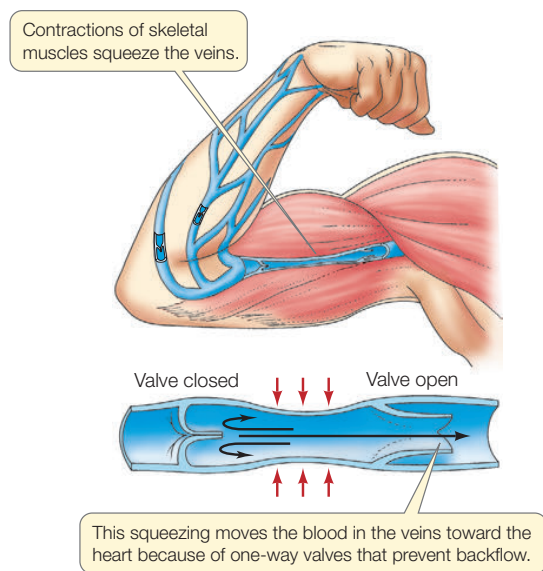
FIGURE 32.14 One-Way Flow   Veins have valves that prevent blood from flowing backward and allow contractions of skeletal muscles to help move blood toward the heart.

FIGURE 32.15 An Arctic Fox (*Vulpes lagopus*)

capillaries, and venules (see Figure 32.13). The loss of pressure is so great that, by the time the blood flows into the veins, its pressure is only a little higher than zero.

The low blood pressures in the veins help explain why one-way valves have evolved in the veins (valves do not occur in arteries). The pressure from the beating of the heart is reduced to such a low level in the veins that it may not always be sufficient to make blood flow back to the heart. With one-way valves, contractions of skeletal muscles can help propel blood to the heart (**FIGURE 32.14**).

Like blood pressure, the linear velocity of the blood—which is simply the linear distance the blood travels per second—also changes dramatically as blood travels through the vascular system (see Figure 32.13). Suppose that a river suddenly divides into 10,000 little streams that collectively have a cross-sectional area much greater than the cross-sectional area of the river. We all appreciate that water will flow more slowly after it enters the little streams. This same logic applies in the circulatory system. Individual capillaries have minute cross-sectional areas. The capillaries are so numerous, however, that their collective cross-sectional area is hundreds of times greater than the cross-sectional area of the aorta (see Figure 32.13). Accordingly, as blood flows from the aorta to the capillaries, it slows from an astounding linear velocity of more than 40 centimeters per second to almost zero.

Why does this slowing matter? Capillaries are less than 1 millimeter long. For the blood to exchange materials with the tissues, it must be moving very slowly as it passes through them.

Animals have evolved arrangements of blood vessels that help them conserve heat

When arctic foxes (**FIGURE 32.15**) walk over the snow and ice in winter—or when arctic gulls stand on winter ice—the tissues

in their foot pads and foot membranes are at temperatures near 0°C, even though the tissues in the core of their body (the thorax and abdomen) are at almost 40°C. By having near-freezing tissue temperatures in their feet, the animals conserve energy because they do not lose much heat across their feet. They also keep their feet dry because the tissues of their feet are too cold to melt the snow or ice. They do not risk getting frostbite because the temperature of their feet is highly controlled.

Heat is easily lost across body appendages of all kinds, including not only the legs and feet of mammals and birds, but also the tails and ear flaps (pinnae) of mammals. Many species have evolved ways to let the tissues in the outer ends of these appendages cool off as a way of conserving heat in their body core in cold environments.

How is the cooling of the tissues achieved? The cells in the appendages need O_2, so blood flow to the appendages can't simply be stopped to keep body heat from entering them.

Many types of mammals and birds have evolved arrangements of arteries and veins that allow them to conserve heat by **countercurrent heat exchange**. As we discuss this process, keep in mind that the blood vessels involved are arteries and veins—not capillaries. The walls of arteries and veins are far too thick for O_2 or other dissolved materials to pass through them. Heat, however, can pass through.

FIGURE 32.16A shows two arrangements of arteries and veins in an appendage. The diagrams show only one artery and one vein, but that's just for simplicity. In the arrangement at the left, the arteries and veins are far away from each other and do not interact. At the right, the arteries and veins are touching. The right-hand arrangement is termed countercurrent—a term that refers to two closely juxtaposed fluid streams flowing in opposite directions. In the countercurrent arrangement, heat can move from one fluid stream to the other. Countercurrent heat exchange can therefore occur.

What happens in an appendage with countercurrent heat exchange? As warm, arterial blood flows into the appendage, the warm blood comes close to venous blood that is leaving the appendage. This venous blood is cooler because it is returning from the far end of the appendage. Heat travels out of the warm

(A) Two possible arrangements of leg circulation

(B) Countercurrent heat exchange

→ Blood flow
⇒ Heat flow

34° | 37°

25° | 28°

Heat moves out of the warm arterial blood into the cooler venous blood and is carried back into the warm body core.

16° | 19°

10°

In this case, blood flow is in a countercurrent arrangement.

FIGURE 32.16 Countercurrent Heat Exchange   Here we look at blood flow and heat flow within a leg of a mammal standing in a cold environment. (A) Two different arrangements of arteries and veins are possible in the leg. In the countercurrent arrangement, the arteries and veins—carrying blood in opposite directions—are closely juxtaposed. (B) During countercurrent heat exchange, blood flows all the way to the outer end of an appendage and back, but heat does not. Heat takes a shortcut, enabling it to move back into the body core before it can be readily lost to the environment at the exposed outer end of the appendage.

arterial blood into the cooler venous blood (**FIGURE 32.16B**). This process continues as the arterial blood flows farther into the appendage—because even though the arterial blood gets cooler, the venous blood next to it also gets cooler. In this way, a lot of heat moves out of the arterial blood and into the venous blood in the upper parts of the appendage. Moreover—and this is very important—this heat is immediately transported back into the animal's body core as the venous blood flows back into the body. This heat is never carried by the blood to the outer end of the appendage, and therefore cannot be easily lost to the cold environment. The outer end of the appendage remains at a low temperature because the heat never gets to it.

The effectiveness of countercurrent heat exchange depends on how extensively the arteries and veins make contact with each other. With extensive, highly controlled interaction between the two sets of vessels, the tissues at the outer end of an appendage can be kept just above the freezing point, as in arctic foxes.

Tuna also use the countercurrent principle to keep their red swimming muscles warm (**FIGURE 32.17**). The red muscles are positioned in a very unusual place in tuna, deep in their body, nearer their backbone than their skin (see Figure 33.14). Tuna also have evolved a very unusual arrangement of arteries and veins. The longitudinal arteries and veins that carry blood along the length of their body are just under their skin. Branches from each longitudinal artery travel from the skin *inward* to the red swimming muscles. Veins from the red muscles travel *outward* to connect with a longitudinal vein. These arteries and veins—which are carrying blood to and from the red muscles—are closely juxtaposed and exceedingly numerous. Because the red swimming muscles work hard, they produce heat at a relatively high rate. The venous blood, flowing

outward from the muscles, tends to carry this heat away. However, the arteries carrying inward-flowing arterial blood are touching the veins. Heat from the venous blood thus moves into the arterial blood and is carried directly back to the swimming muscles. Because of this countercurrent heat exchange, the muscles retain the heat they make and are warmed by it.

Blood flow leaves behind fluid that the lymph system picks up

Most blood capillaries are so permeable that at their high-pressure arterial end, blood pressure squeezes fluid out of the blood in the capillaries and into the surrounding interstitial fluids. Before the blood leaves capillaries, it takes up some of this fluid again, but not all of it. These processes were first clarified by the physiologists E. H. Starling and E. M. Landis.

Starling and Landis realized that blood in the capillaries has a higher osmotic pressure (because it has more dissolved protein) than the interstitial fluids (see Concept 5.2). For this reason, water tends to be drawn *into* the blood in a capillary by osmosis

Red swimming muscle

White swimming muscle

Longitudinal vein

Longitudinal artery

Backbone

As venous blood flows outward, it loses heat to the closely juxtaposed arterial blood, which carries the heat inward again.
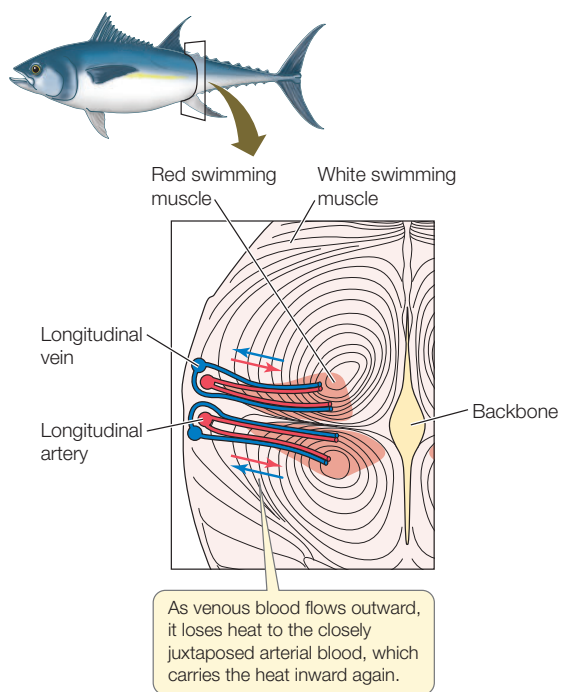
FIGURE 32.17 Countercurrent Heat Exchange Warms the Red Swimming Muscles of Tuna

FIGURE 32.18 Fluid Moves out of Capillaries into the Interstitial Fluids The widths of the thick red and black arrows symbolize relative magnitudes of the forces at work in the mammalian circulatory system. When blood pressure is greater than osmotic pressure, fluid leaves the blood in the capillaries, and when blood pressure falls below osmotic pressure, fluid returns to the blood in the capillaries. The balance of these two forces changes over the length of a capillary bed as blood pressure falls. The phenomena shown here occur in the systemic tissues. They do not normally occur in the lungs (where the alveoli could be flooded) because blood pressure is far lower in the lung circuit than in the systemic circuit.

Fluid is forced out of the blood in the capillary by blood pressure.

Fluid is pulled back into the blood in the capillary by osmotic pressure.

Systemic capillary

Blood pressure (40 mm Hg) Osmotic pressure (25 mm Hg) Blood pressure (16 mm Hg) Osmotic pressure (25 mm Hg)
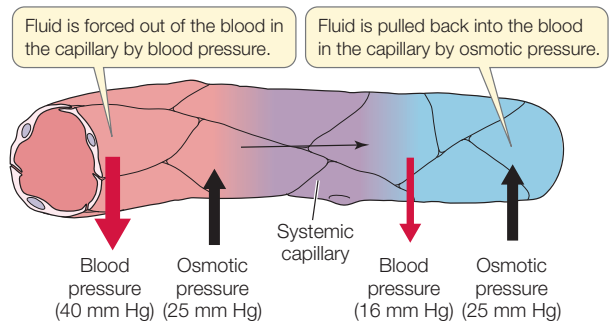
Arteriole end	mm Hg
Blood pressure	40
Osmotic pressure	−25
Net force, directed outward	15

Venule end	mm Hg
Blood pressure	16
Osmotic pressure	−25
Net force, directed inward	9

across the capillary walls. Water also tends to be driven *out* of the blood in a capillary by the high blood pressure inside the capillary. At the beginning of a capillary, where blood has just entered it, the effect of the blood pressure exceeds the effect of the osmotic pressure, and fluid moves out of the blood (**FIGURE 32.18**). Blood pressure falls, however, as blood flows through a capillary. At the end of the capillary, therefore, the effect of the osmotic pressure exceeds the effect of the blood pressure, and fluid moves from the interstitial fluids into the blood.

The net effect of these dynamic processes is a small loss of fluid from the blood. What is the fluid loss per day in adult humans, considering all the capillaries in the body and all the times that blood passes through them? Blood flow through the systemic capillaries leaves behind about 2–4 liters of fluid in a person's systemic interstitial fluids each day.

The **lymphatic system** collects this excess fluid (called lymph) and returns it to the blood. The lymphatic system is an elaborate system of vessels that is separate from the blood vascular system (**FIGURE 32.19**). Tiny lymphatic capillaries found in tissues throughout the body merge into progressively larger lymphatic vessels. Finally, certain of the lymphatic vessels connect with veins at the base of the neck, returning collected fluid to the blood.

FIGURE 32.19 The Lymphatic System A network of lymphatic vessels, equipped with one-way valves similar to those in veins, collects excess interstitial fluid from the systemic tissues. The vessels carry the fluid (called lymph) toward the base of the neck, where the fluid enters large lymphatic ducts that empty into veins (the subclavian veins) in the blood vascular system.

Lymph nodes act a bit like filters, removing objects from the lymph fluid. The nodes also contain large populations of lymphocytes and other cells of the immune system.

Thoracic duct

Thymus

Lymphatic vessels pick up fluid from tissues throughout the body and transport it as lymph, ultimately returning the lymph to the blood.

Spleen
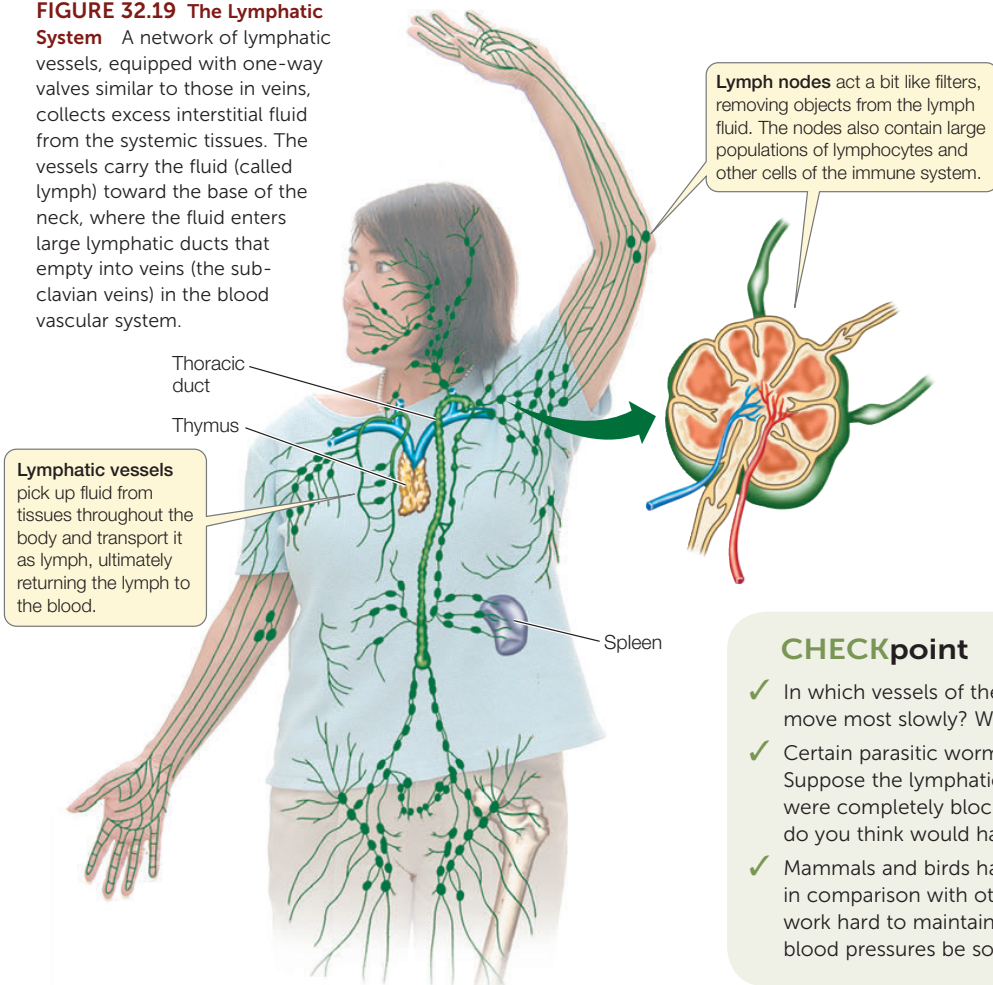
CHECKpoint CONCEPT 32.4

✓ In which vessels of the circulatory system does the blood move most slowly? Why, and why is this important?

✓ Certain parasitic worms can block lymphatic vessels. Suppose the lymphatic vessels draining a person's leg were completely blocked by a parasite infestation. What do you think would happen to the leg? Explain.

✓ Mammals and birds have very high aortic blood pressures in comparison with other animals, and the heart must work hard to maintain these pressures. Why must the blood pressures be so high?

Let's turn now to the fluid that the heart is pumping: the blood. What are the major components of blood, and what are their major functions?

CONCEPT
32.5 The Blood Transports O$_2$ and CO$_2$

Blood consists of cells suspended in a solution called **plasma**. The plasma typically contains many dissolved materials (solutes), such as glucose and other nutrient molecules, ions, waste products, hormones, and clotting proteins. In vertebrates, most of the cells suspended in the plasma are **red blood cells**, also called erythrocytes, which contain hemoglobin and carry O$_2$. The blood of vertebrates also contains a smaller number of **white blood cells** or leukocytes—cells of the immune system— as well as **platelets** (pinched-off fragments of cells), which are involved in blood clotting.

> **LINK**
>
> The functions of leukocytes in the immune system are discussed in **Chapter 39**

The most important function of the blood in most types of animals is to transport the respiratory gases, O$_2$ and CO$_2$. Blood proteins that combine with O$_2$, called **respiratory pigments**, have evolved to increase the amount of O$_2$ each milliliter of blood can carry. O$_2$ is not very soluble in aqueous (watery) solutions such as plasma. For this reason, a respiratory pigment is typically essential for the blood to carry a significant amount of O$_2$. Human blood in the lungs can dissolve only about 4 milliliters of O$_2$ in each liter of blood. Yet the blood actually carries about 200 milliliters of O$_2$ per liter as it leaves the lungs. The respiratory pigment in our blood (hemoglobin) is responsible for the difference.

When a respiratory pigment combines with O$_2$, the process is called **oxygenation**, and the pigment is said to be oxygenated. This choice of words is important. A respiratory pigment is not chemically oxidized when it combines with O$_2$, so the process is termed oxygenation, not oxidation. When a pigment releases O$_2$, the process is **deoxygenation**, and the pigment becomes deoxygenated.

In addition to transporting O$_2$, the blood also transports CO$_2$. When CO$_2$ is added to the blood, it reacts with water in the blood to form bicarbonate ions (HCO$_3^-$): $CO_2 + H_2O \rightleftharpoons H^+ + HCO_3^-$. Accordingly, most CO$_2$ is carried as bicarbonate. This bicarbonate can be lost across the gills into the environmental water in aquatic animals. In terrestrial animals, however, the bicarbonate is converted back to CO$_2$ in the lungs and CO$_2$ is exhaled.

Hemoglobin and hemocyanin are the two principal respiratory pigments

The respiratory pigment **hemoglobin** has evolved independently many times and is by far the most widespread respiratory pigment in animals. In occurs in almost all vertebrates. It also occurs in annelid worms, such as earthworms, and in some members of at least seven other phyla.

Hemoglobin is an iron-containing protein to which O$_2$ binds at the molecular sites (called heme sites) where iron atoms occur. In mammals and most other vertebrates, each hemoglobin molecule is an assembly of four protein subunits, each of which contains one iron atom (in heme; see Chapter 3, p. 47). In all vertebrates, hemoglobin is found inside red blood cells, where it is responsible for their red color.

Fully oxygenated hemoglobin is bright crimson red. Fully deoxygenated hemoglobin, however, is purple-red. The finger probes (pulse oximeters) that hospital patients wear to track blood oxygenation work by detecting how much hemoglobin is one color and how much is the other.

Red blood cells turn over rapidly, especially in mammals. In humans, each red cell circulates in the blood for only about 120 days before it is broken down and replaced by a new cell synthesized in the bone marrow. Under normal conditions, your blood contains about 5 billion red cells per milliliter, and your bone marrow produces about 2 million new cells every second.

Hemocyanin is the second most important respiratory pigment. It is found widely in mollusks, including squid, and in arthropods such as crabs, lobsters, horseshoe crabs, and spiders. The molluscan and arthropod forms evolved independently. Like hemoglobin, hemocyanin is a metal-containing protein to which O$_2$ binds at the molecular sites where metal atoms occur. The metal, however, is copper rather than iron. Hemocyanin is never found inside blood cells. Instead, it is always simply dissolved in the blood plasma.

Oxygenated hemocyanin is blue, and deoxygenated hemocyanin is colorless. Hemocyanin is usually not concentrated enough in the blood to give the blood a strong color, but in some animals that have lots of hemocyanin, the blood leaving the gills is a bright cobalt blue!

Respiratory pigments combine with O$_2$ reversibly

What gives respiratory pigments their ability to transport O$_2$? Their most important functional characteristic is that they combine *reversibly* with O$_2$. They take up O$_2$ when O$_2$ is abundant in their surroundings. They release O$_2$ when their surroundings are O$_2$-depleted. Both the uptake and release of O$_2$ occur automatically, and very quickly, as a simple consequence of the chemical properties of the pigments.

This chemical behavior is summarized with a graph like that shown in **FIGURE 32.20**. Such a graph is called an **oxygen equilibrium curve**, and the particular curve shown here is typical for adult humans. The *x* axis shows the partial pressure of O$_2$ in the blood (this is a measure of the concentration of O$_2$ dissolved in the blood plasma). The hemoglobin in the blood has a maximum amount of O$_2$ with which it can combine. The *y* axis shows the amount of O$_2$ bound to hemoglobin at each partial pressure as a percentage of this maximum.

> **Go to ANIMATED TUTORIAL 32.2**
> **Hemoglobin Loading and Unloading Simulation**
> PoL2e.com/at32.2

Let's focus on blood O$_2$ transport in a person. The O$_2$ partial pressure in the alveoli of a person's lungs is kept near 100 mm

Hg because of the control of breathing we discussed in Concept 31.3. This means that the O_2 partial pressure in blood oxygenated in the alveoli is also kept near 100 mm Hg. As shown by the "Loading" point on the graph in Figure 32.20, human hemoglobin combines with a maximum amount of O_2—about 100 percent of the O_2 it can possibly carry—when the O_2 partial pressure is near 100 mm Hg. In short, human hemoglobin becomes highly oxygenated in the lungs.

In the systemic tissues of a person at rest, the O_2 partial pressure, on average, is about 40 mm Hg. The "Unloading at rest" point on the graph shows the consequences. O_2 binding is only about 75 percent of maximum when human hemoglobin is at 40 mm Hg. When highly oxygenated blood from the lungs first flows into the capillaries of the systemic tissues, its oxygen binding is about 100 percent, but as soon as it is exposed to the partial pressure of 40 mm Hg that prevails in the systemic tissues, it releases some O_2 so that its oxygen binding falls to 75 percent. This is the process by which hemoglobin releases O_2 to the tissues. Later, when the blood flows back into the lungs, the hemoglobin is exposed once more to a partial pressure of about 100 mm Hg and therefore takes up O_2, so that its oxygen binding is once again about 100 percent.

During exercise, hemoglobin can greatly increase the amount of O_2 it releases in the exercising muscles. The O_2 partial pressure in exercising muscles often falls to about 20 mm Hg during moderately intense exercise because the muscle mitochondria are using O_2 rapidly. When hemoglobin is exposed to this partial pressure, its oxygen binding falls to only 35 percent (see "Unloading during exercise" in Figure 32.20). The hemoglobin thus releases much more of its O_2 than it does in resting tissues.

In summary, there are two major ways that the circulatory system increases O_2 delivery when we exercise. First, we circulate blood more rapidly than at rest (by increasing heart rate and stroke volume). Second, our hemoglobin releases more than twice as much O_2 each time it flows from the lungs to the exercising muscles.

During rest, hemoglobin O_2-binding drops from about 100% to 75% as the blood partial pressure falls from 100 mg Hg in arterial blood to 40 mm Hg in systemic capillaries.

During moderately intense exercise, hemoglobin O_2-binding drops more—from about 100% to about 35%—because the O_2 partial pressure falls to 20 mm Hg rather than 40 mm Hg.

FIGURE 32.20 Loading and Unloading of O_2 by Human Hemoglobin This curve—known as an oxygen equilibrium curve—shows the chemical behavior of human hemoglobin under conditions in arterial blood. Hemoglobin almost instantly adjusts its O_2 binding to match changes in the prevailing O_2 partial pressure, taking up or releasing O_2 as needed. The vertical green arrows show how much O_2 is unloaded by hemoglobin as it flows from the lungs through the systemic tissues during rest and exercise. The blood O_2 partial pressure is expressed in millimeters of mercury (mm Hg) of pressure.

Go to ACTIVITY 32.4 Oxygen-Binding Curves
PoL2e.com/ac32.4

Q How can the arrangement of blood vessels help warm the swimming muscles in warm-bodied fish such as tuna?

ANSWER The red swimming muscles produce considerable heat from their metabolism during steady, long-duration swimming in high-performance species of fish. In most species, however, this heat is lost to the environmental water as fast as it is produced, and the swimming muscles are not warmed by the heat they produce. This is true regardless of body size because heat moves readily through water, and in the gills it merely needs to move from one watery fluid, the blood, to another, the environmental water, to escape from the fish.

The key to keeping heat in the swimming muscles, so that they are warmed, is to prevent the heat they produce from leaving them. This is not possible in most fish because of the arrangement of the arteries and veins in the vasculature of the swimming muscles (**FIGURE 32.21**). Tuna (and certain sharks, such as great whites) have evolved a unique arrangement of arteries and veins to carry blood to and from their red swimming muscles, which are deep in the body (see Figures 32.17

CHECKpoint CONCEPT **32.5**

✓ By what factor does hemoglobin increase the capacity of human blood to carry O_2?

✓ What do we mean when we say that hemoglobin and hemocyanin combine reversibly with O_2?

✓ Myoglobin, the red pigment inside muscle cells that are specialized for endurance exercise (see Concept 33.3)—giving the cells a red color—is actually a type of hemoglobin. There's a property of respiratory pigments called oxygen affinity. It is a measure of how strongly a respiratory pigment and O_2 are chemically attracted. Red muscles need O_2 because they make ATP aerobically. Keeping this in mind, would you expect myoglobin to have a higher or lower oxygen affinity than the hemoglobin in the blood? Explain.

FIGURE 32.21 Tuna and other warm-bodied fish have a unique arrangement of arteries and veins

and 33.14). In this arrangement, as veins leave the swimming muscles—carrying heat with them—they come into close contact with the arteries carrying blood into the muscles. This arrangement allows countercurrent heat exchange to take place. Heat moves out of the venous blood into the arterial blood,

and the arterial blood carries the heat back into the swimming muscles. Heat made by the muscles thus has a hard time exiting them (very unlike the case in most fish), and the muscles are warmed to temperatures higher than that of the environmental water.

SUMMARY

CONCEPT 32.1 Circulatory Systems Can Be Open or Closed

- Animals with a high degree of division of labor need a **circulatory system** that transports respiratory gases, nutrients, hormones, and metabolic wastes throughout the body at high rates.

- O_2 transport is the most urgent function of the circulatory system in most types of animals. Because of this, animals with relatively high rates of O_2 consumption tend to have relatively high-performance circulatory systems. Insects are the exception that proves the rule. Although many insects have high rates of O_2 consumption, insects do not have high-performance circulatory systems because their tracheal breathing system, not their circulatory system, meets needs for O_2 transport.

- In **closed** circulatory systems—found in vertebrates, annelid worms, squid, and octopuses—the blood never leaves a system of vessels. In **open** circulatory systems—found in arthropods and most mollusks—the blood leaves vessels and bathes tissue cells directly. One advantage of closed circulatory systems is their ability to direct blood selectively to specific tissues.

- The blood in a closed circulatory system flows from the heart, through arteries, to the microscopic vessels of the **microcirculation**, which consists of arterioles, capillaries, and venules. Veins then carry blood back to the heart.

- **Capillaries** are the smallest vessels and are the principal sites of exchange of gases, nutrients, and other substances between the blood and the tissues. **Arterioles** control the rate of blood flow into the capillaries. **Review Figures 32.2 and 32.3**

- In open circulatory systems, the heart typically pumps blood into arteries that carry the blood for at least a short distance. These vessels then end and the blood flows out into the animal's tissues. The blood makes its way back to the heart through channels between the tissue cells called sinuses and lacunae. **Review Figure 32.4**

- In open circulatory systems there is no distinction between blood and interstitial fluid.

CONCEPT 32.2 The Breathing Organs and Systemic Tissues Are Usually, but Not Always, in Series

- The **systemic circuit** consists of the blood vessels (or blood channels in the case of an open circulatory system) that carry blood to and from the systemic tissues. The **breathing-organ circuit** consists of the blood vessels that carry blood to and from the breathing organs (lungs or gills).

- **Arteries** are vessels that carry blood away from the heart. **Veins** carry blood toward the heart.

- In most animals the systemic circuit and breathing-organ circuit are connected in series: the blood flows from one circuit to the other sequentially. Circulation in series is the most efficient way to deliver O_2 to the systemic tissues. **Review Figure 32.5A and B, ACTIVITY 32.1**

- Adult amphibians and non-avian reptiles have a partially divided ventricle that does not ensure series circulation. Some of these animals, such as turtles, can shunt blood away from the breathing-organ circuit at times when doing so may be advantageous, such as during prolonged diving. **Review Figure 32.5C**

CONCEPT 32.3 A Beating Heart Propels the Blood

- Vertebrate hearts are multi-chambered and **myogenic**; heartbeats are initiated by specialized muscle cells within the heart.

- The simplest vertebrate heart, found in fish, is two-chambered. It has an **atrium** that receives blood from the body and a **ventricle** that pumps blood out of the heart. Amphibians and non-avian reptiles have a three-chambered heart with two atria and one partially divided ventricle.

- The heart of mammals and birds has four chambers—two atria and two ventricles—with valves to prevent backflow. Blood flows from the right atrium and ventricle to the lungs, then to the left atrium and ventricle, and then to the rest of the body. **Review Figure 32.6 and ACTIVITY 32.2**

(continued)

SUMMARY (*continued*)

■ The **cardiac cycle** has two phases: **systole**, when the ventricles contract, and **diastole**, when the ventricles relax. **Review Figure 32.7 and ANIMATED TUTORIAL 32.1**

■ The heartbeat in mammals is initiated by pacemaker cells in the sinoatrial node that spontaneously depolarize, triggering a wave of depolarization that spreads through the atria and then spreads with a brief delay into the ventricles via the atrioventricular node and the **conducting system**. **Review Figure 32.8**

■ The autonomic nervous system controls heart rate by changing the rate of depolarization of the pacemaker cells. Norepinephrine from sympathetic nerves increases heart rate, and acetylcholine from parasympathetic nerves decreases it. **Review Figure 32.9**

■ In mammals and many other vertebrates, a **coronary circulatory system** supplies O_2 to the cells of the heart muscle (myocardium).

■ The depolarization of heart muscle cells can be detected on the surface of the body and recorded as an **electrocardiogram** (**ECG** or **EKG**). **Review Figure 32.10**

■ The hearts of crustaceans have one chamber and are **neurogenic**; the muscle cells of the heart require nervous stimulation to beat. **Review Figure 32.11**

CONCEPT 32.4 Many Key Processes Occur in the Vascular System

■ Arteries are composed of muscle fibers and elastic fibers that enable them to dampen the surge in pressure when the heart beats and store in their stretched state some of the energy imparted to the blood by the heart. Veins have thinner walls and have a high capacity for storing blood. **Review Figure 32.12 and ACTIVITY 32.3**

■ The pressure and linear velocity of blood vary greatly as it flows through the vascular system. Blood pressure is high in arteries and low in veins. Blood velocity is lowest in capillary beds. **Review Figure 32.13**

■ Veins have one-way valves that assist in returning blood to the heart under low pressure. **Review Figure 32.14**

■ Heat loss from certain regions of an animal's body—such as the extremities of the arctic fox and the red swimming muscles of tuna—can be reduced by countercurrent heat exchange. **Review Figures 32.15–32.17**

■ High blood pressure forces fluid out of the blood as it travels through the initial part of a capillary bed; osmotic pressure draws some of the fluid back into the blood as blood pressure falls. **Review Figure 32.18**

■ The excess fluid that does not reenter the blood as it travels through capillary beds is called lymph. The **lymphatic system** collects this fluid and returns it to the blood. **Review Figure 32.19**

CONCEPT 32.5 The Blood Transports O_2 and CO_2

■ In vertebrates, blood consists of a liquid **plasma** and cellular components (**red blood cells**, or erythrocytes; **white blood cells**, or leukocytes; and **platelets**). Red blood cells are produced in the bone marrow. **Hemoglobin**, the **respiratory pigment** in red blood cells, binds O_2 reversibly. Each hemoglobin molecule can carry a maximum of four O_2 molecules.

■ Hemoglobin binds O_2 when the partial pressure of O_2 is high and releases it when the partial pressure is low. Therefore hemoglobin picks up (loads) O_2 as it flows through a breathing organ and gives up (unloads) O_2 in the systemic tissues. This chemical behavior can be summarized in an **oxygen equilibrium curve**. **Review Figure 32.20, ACTIVITY 32.4, and ANIMATED TUTORIAL 32.2**

■ **Hemocyanin** is the respiratory pigment in mollusks and arthropods.

■ CO_2 reacts with blood water to form bicarbonate ions (HCO_3^-) and is transported mostly in the form of bicarbonate.

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities
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Muscle and Movement

A sphinx moth (*Hemaris thysbe*) uses its flight muscles to hover at a flower, collecting nectar with its long proboscis.

This moth, a type of sphinx or hawk moth, is sometimes mistaken for a hummingbird, accounting for its name, the hummingbird clearwing moth (*Hemaris thysbe*). Common in several parts of the United States and Canada, it feeds during daylight by hovering at flowers using rapid wingstrokes driven by the flight muscles in its thorax. It has a strikingly long proboscis that it can insert deeply into flowers to collect nectar. Other species of sphinx moth also have a striking proboscis, the most amazing being that of the famous Madagascar sphinx moth we mentioned at the start of Chapter 21. The hummingbird clearwing moth buzzes as it hovers because of the rapid movements of its flight apparatus.

Insects probably first took to the air about 350 million years ago. Over that long evolutionary time, diverse forms of flight have evolved, from the relatively slow and silent up-and-down wingstrokes of many butterflies, to the high-frequency buzzing wingstrokes of sphinx moths, to the very high frequency whining wingstrokes of mosquitoes. Today, engineers are studying insects to learn more about the aerodynamics of flight. Sphinx moths are of particular interest because they are powerful fliers that can quickly alternate between hovering and flying straight ahead at high speeds.

Muscle cells—one of the defining properties of animals—develop forces by means of interactions among fiber-like, contractile proteins within the cells. These forces typically set matter in motion. For example, the forces developed by the flight muscles of an insect set the wings in motion. For matter to be set in motion, an energy source is required. Insect flight-muscle proteins draw the necessary energy from adenosine triphosphate (ATP) made by the mitochondria in the muscle cells.

The great majority of muscle cells in the animal kingdom require a nerve impulse to activate each contraction: contractions and nerve impulses occur in a 1:1 ratio. Sphinx moths draw the interest of muscle physiologists because they are among the animals that have the highest frequencies of muscle contraction during flight while retaining this 1:1 ratio. Their wingstrokes can number more than 30 per second (30 Hz).

Per gram, insect flight muscle stands out as one of the tissues that attain the highest known rates of oxygen consumption. Physiologists reason that if high mechanical power generation is critical for ecological success—as it certainly is in powerfully flying insects—natural selection will have favored the evolution of muscle cells that have exceptional capacities to use O_2 to produce ATP to power muscle contraction. Electron micrographs of insect flight muscle show cells that are literally packed with contractile proteins and mitochondria.

Q Why is it likely that available space inside cells has limited the contents of contractile proteins and mitochondria in high-performance muscles?

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CONCEPT
33.1

Muscle Cells Develop Forces by Means of Cycles of Protein–Protein Interaction

</div>

Muscle tissue makes up a large portion of body mass in vertebrates and many other animals. In humans, for example, muscles account for almost half of body mass (**FIGURE 33.1**). Muscles are as important functionally as they are anatomically. They are the basis for virtually all behavior. They permit animals to run, fly, or swim to acquire food or escape dangers. In humans and some other mammals, muscles of the face account for changing facial expressions. Besides behavior, many other physiological actions also depend on muscle contraction, such as the circulation of blood by the beating of the heart.

There are several types of muscle tissue in the animal kingdom. The contractile mechanism is basically the same in most muscle types, however. We will begin our study of muscle function by focusing on the contractile mechanism in vertebrate **skeletal muscle**—the type of muscle that is attached to the bones of the skeleton and that provides the power for walking, flying, swimming, and other forms of locomotion.

Contraction occurs by a sliding-filament mechanism

Muscle tissue develops mechanical forces. This is its defining feature. In the scientific study of muscle, **contraction** refers to force development. A muscle does not necessarily *shorten* when it undergoes contraction. To see the distinction

FIGURE 33.1 Muscles Account for a Large Portion of Body Mass Andrea Vesalius produced this wood block print, the first accurate depiction of the skeletal muscles of the human body, in 1543. He was noted for posing his subjects as they might have stood in life.

between contraction and shortening, imagine grabbing a bar of steel attached to a concrete wall with your hand and pulling as hard as you can with your arm muscles. Your muscles will develop great forces, but they will not shorten because the bar of steel is immovable. For a muscle to shorten during contraction, the force it exerts must be greater than opposing forces. When you use your arm to pull on a drawer, your arm muscles shorten during contraction because the force they exert exceeds the opposing forces, and the drawer slides toward you.

The current theory of how muscle contracts is often known as the **sliding-filament theory**. This name describes what the process *looks* like and is useful in that way. When muscle cells contract in circumstances in which they shorten, tiny filaments in the cells look like they slide past each other during contraction. However, the name "sliding" can be misleading, because "slide" suggests effortless motion, like a sled sliding down a snow-covered hill. In fact, the motion of the filaments in muscle cells is not at all effortless. It is quite the opposite: during contraction, the filaments use energy from ATP to develop mechanical forces and pull on each other. The "sliding" of the filaments is merely a consequence of this energy-using, force-generating process.

Actin and myosin filaments slide in relation to each other during muscle contraction

The cells of skeletal muscle are sometimes called "cells" and sometimes "fibers." These two terms are synonyms: a **muscle fiber** is a muscle cell. The cells in vertebrate skeletal muscle are large and have many nuclei, making them multinucleate. During development they form through the fusion of many individual embryonic muscle cells called myoblasts. A muscle such as your biceps (the muscle that pulls your forearm up toward your upper arm) is composed of hundreds or thousands of muscle fibers that are organized in bundles surrounded by connective tissue (**FIGURE 33.2A**).

Muscle contraction results from the interaction of two contractile proteins that are abundant in each muscle fiber: **actin** and **myosin**. Molecules of actin are organized into **actin filaments**, also called thin filaments. Molecules of myosin are organized into **myosin filaments**, or thick filaments. These two kinds of filaments interdigitate in parallel arrays as seen in **FIGURE 33.2B**.

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LINK

Actin and myosin are also part of the cytoskeleton, which is responsible for other types of movement in cells; see **Concept 4.4**

</div>

Let's look now in more detail at the anatomical relationships among a muscle, its muscle fibers, and the actin and myosin filaments inside each fiber. Looking at Figure 33.2A and moving outward from the person's arm, you will see that a muscle is made up of bundles of long, parallel muscle fibers. Similarly, each muscle fiber is composed internally of long, parallel **myofibrils**, each of which is composed of arrays of actin

(A)

A **skeletal muscle** is made up of many bundles of **muscle fibers**.

Tendons

Muscle

Bundle of muscle fibers

Connective tissue

Single muscle fiber (cell)

Cell membrane

Nucleus

Myofibrils

Biceps muscle

Each muscle fiber is a multinucleate cell containing numerous **myofibrils**, which are highly ordered assemblages of thick myosin and thin actin filaments.

Mitochondria

Z line   M band   I band

Cross section of one myofibril near the middle of a sarcomere. This cross section shows how actin and myosin filaments are organized in three dimensions.

One **sarcomere**, bounded by a Z line at each end. Sarcomeres are the units of contraction.

H zone

A band

Single sarcomere

Actin filament

Myosin filament

(B)   Z line

Actin filament

Myosin filament

Titin

(C)   Z line   M band

FIGURE 33.2 The Structure of Skeletal Muscle   (A) Diagram of cellular structure. (B) Diagram of a single sarcomere. (C) Photograph of a single sarcomere under a light microscope.

Sarcomere

A band

H zone

I band

Where there are only actin filaments and titin molecules, the myofibril appears light; where there are both actin and myosin filaments, the myofibril appears dark.

1 μm

Go to ACTIVITY 33.1
The Structure of a Sarcomere
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and myosin filaments oriented parallel to the long axis of the myofibril.

Understanding the structure of a myofibril is critical. Figure 33.2A is drawn so you can view a myofibril from the side. From this view, you can see that a myofibril consists of repeating units called **sarcomeres**. Each sarcomere starts and ends with a Z line. Internally, as shown in Figure 33.2B, each sarcomere contains overlapping arrays of actin and myosin filaments, as we have already noted. At the far right of Figure 33.2A, the myofibril is shown in cross section so you can see the three-dimensional

arrangement of its actin and myosin filaments. In most regions of a myofibril, as the cross section shows, each thick myosin filament is surrounded by six thin actin filaments, and each actin filament sits within a triangle of three myosin filaments.

In side view, the structures we have been discussing give skeletal muscle a distinctly banded appearance when the muscle is examined under a simple light microscope. To see individual actin and myosin filaments, you would need to use an electron microscope because they are far too thin to be seen with a light microscope. When you look at muscle with a light

microscope, however, you see patterns that result from the organization of large sets of actin and myosin filaments—much as you can see black and white lines on a computer screen even though you cannot see the individual pixels that collectively give rise to the patterns. **FIGURE 33.2C** shows the banding pattern in a single muscle fiber as seen with a light microscope at fairly high magnification. By comparing Figures 33.2B and 33.2C, you can see how the bands seen with the light microscope line up with the actin and myosin filaments in a sarcomere. At lower magnification under a light microscope, the banding in a region of skeletal muscle looks like this:

15 µm
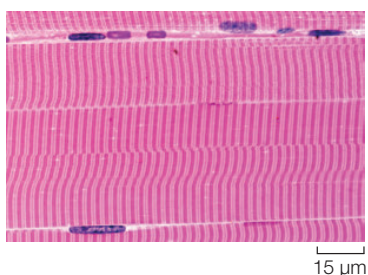
Because of this banding pattern, skeletal muscle is called striated muscle.

Before the molecular nature of the muscle banding pattern was known, the bands were given names that are still used today (see Figure 33.2B,C). Each sarcomere is bounded by Z lines, as already mentioned, which represent structures to which the actin filaments are attached. At the center of each sarcomere is a structure called the M band (for "middle"). It contains proteins that help hold the myosin filaments in position. Each myosin filament extends out symmetrically on either side of the M band. Collectively, the myosin filaments in each sarcomere give rise to a dark region—called the A band—centered on the M band.

Finally, in each sarcomere there are three relatively light bands: an H zone centered on the M band, and one half of an I band at each end of the sarcomere. These bands appear light because, unless a myofibril is fully contracted, the actin and myosin filaments do not overlap in them: only myosin filaments are found in the H zone, and only actin filaments are found in the I bands (see Figure 33.2B,C).

Within a sarcomere, the thick myosin filaments are held in their correct positions in three-dimensional space by molecules of a protein called **titin** (**FIGURE 33.3A**). This giant molecule is the largest known protein. A myosin filament consists of about 200–400 individual myosin molecules in a bundle. Each titin molecule in a sarcomere runs between the M band and a Z line, directly through a myosin filament along the filament's long axis. Between the end of the filament closest to the Z line and the Z line itself, the titin molecule is elastic, like a bungee cord. Collectively, the titin molecules do two things. They hold the myosin filaments in position, and if a sarcomere becomes stretched, their elasticity returns the sarcomere to its shorter length when the stretching forces relax.

A myofibril looks like Figure 33.3A when it is in its relaxed state. When a myofibril contracts in circumstances in which it can shorten, its sarcomeres shorten and the banding pattern changes to look like **FIGURE 33.3B**. The light-colored H zone and I bands become much narrower, and the dark Z lines move toward the A band. These changes are easy to see under a light microscope as Figure 33.3 shows. Why do they occur? At a molecular level, during contraction the actin and myosin filaments slide past each other, so that they overlap to an increased degree, shortening the muscle fiber. In each sarcomere the actin filaments slide into the H zone, the region occupied by only myosin filaments in the relaxed state. As they do so, the Z lines at opposite ends of the sarcomere are pulled closer to each other.

ATP-requiring actin–myosin interactions are responsible for contraction

To understand how a sarcomere develops mechanical forces during contraction, it is critical to understand the structures of myosin and actin molecules (**FIGURE 33.4**). A myosin molecule consists of two long polypeptide chains coiled together, each ending in a large globular head. A myosin filament is made up of many myosin molecules, the heads of which project sideways near the ends of the filament.
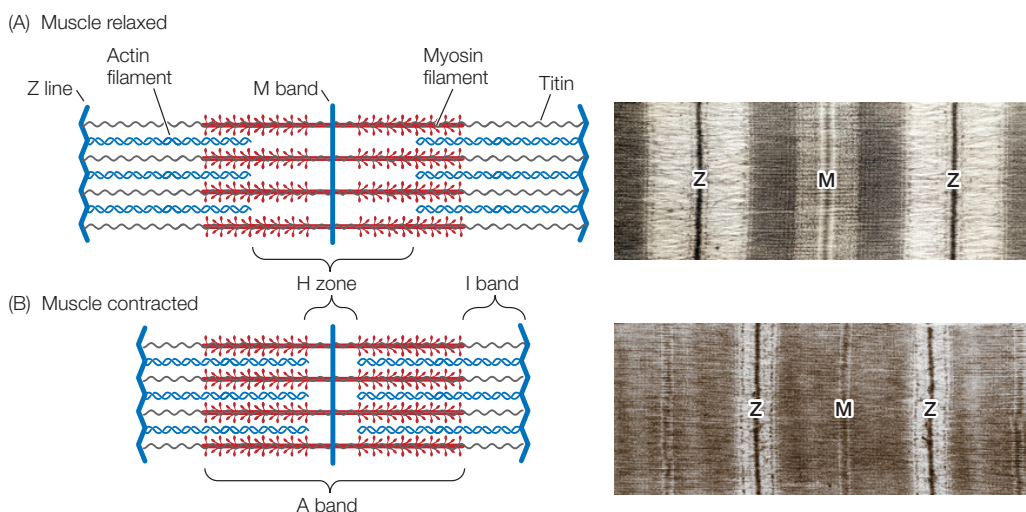
FIGURE 33.3 Sliding Filaments Diagrams and light-microscope images of (A) a relaxed sarcomere and (B) the same sarcomere shortened during contraction. The banding pattern of the sarcomere changes as it shortens. This shortening results from the sliding-filament contractile mechanism of muscle contraction.

(A) Muscle relaxed

Z line Actin filament M band Myosin filament Titin

H zone I band

(B) Muscle contracted

A band

FIGURE 33.4 The Structure of Actin and Myosin Filaments Myosin filaments are bundles of myosin molecules with globular heads and polypeptide tails. Actin filaments consist of two chains of actin monomers twisted together, along with two other proteins: tropomyosin and troponin.

Troponin has three subunits: one binds actin, one binds tropomyosin, and one binds Ca^{2+}.

Actin monomer   Tropomyosin   Troponin

Myosin molecule   Globular head

Linear polypeptide chain

Myosin heads have ATPase activity.

Single sarcomere

Myosin filament   Actin filament
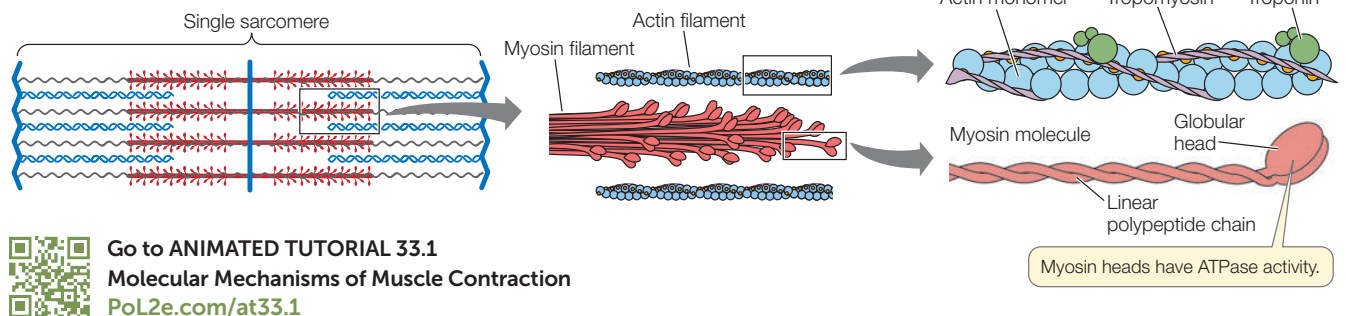
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Molecular Mechanisms of Muscle Contraction
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An actin filament consists of small actin monomers polymerized into two long chains that look like two strands of pearls twisted together. Twisting around each actin chain is another protein, **tropomyosin**, and attached to tropomyosin at intervals are molecules of still another protein, **troponin**. These molecules control contraction and relaxation, as we will see in the next section.

How do myosin and actin interact? The globular heads of myosin can bind to specific sites on actin, forming bridge-like links, called **cross-bridges**, between the myosin and actin filaments. Two functional properties of the myosin heads are exceedingly important. First, when a myosin head binds to an actin filament, the head's molecular shape (conformation) changes in such a way that the head bends and exerts a tiny force on the actin filament. This force causes the actin filament to be pulled a distance of 5–10 nanometers toward the M band along the myosin filament (see the transition from step 3 to step 4 in Figure 33.7). Second, when a myosin head is bound to actin, it has ATPase activity: that is, it binds to and hydrolyzes ATP, releasing energy. The energy released changes the molecular shape of the myosin head, causing it to disconnect from actin and unbend, returning to its extended position. At that point, the myosin head can again bind to actin and undergo another change of molecular shape that causes a tiny force to be exerted on the actin filament, moving the actin filament relative to the myosin filament.

Together, these details explain how the actin and myosin filaments in a sarcomere interact to develop mechanical forces and slide past each other during contraction. The details also help explain why the force a muscle fiber can exert during contraction depends on how many actin–myosin cross-bridges can form.

Rigor mortis—the stiffening of muscles soon after death—is still another muscle property that can be explained by the details of muscle contraction we are discussing. ATP is needed to break actin–myosin bonds. When ATP production ceases with death, actin–myosin bonds cannot be broken and muscles stiffen.

To fully understand contraction, remember that each myosin filament has many myosin heads near both ends and is surrounded by six actin filaments. As contraction takes place, numerous myosin heads go through cycles of interaction with the actin filaments. Their cycles of binding and release are not exactly synchronous, however. Accordingly, when a single myosin head breaks its contact with actin, other cross-bridges are still connected and flexing. As a result, the actin filaments do not slip backward.

Excitation leads to contraction, mediated by calcium ions

Muscle cells, as well as nerve cells (see Chapter 34), are excitable. A cell is **excitable** if its cell membrane can generate and conduct electrical impulses (action potentials). Cell membranes ordinarily have an electrical polarity in which the outside of the membrane is more positive than the inside. An **impulse**, or **action potential**, is a region of reversed polarity, also called depolarization (see Concept 34.2). In an excitable cell, after an impulse—a region of reversed polarity, or depolarization—is initiated at one point in a cell membrane, it travels along the full length of the cell membrane:

Region of depolarization as time passes
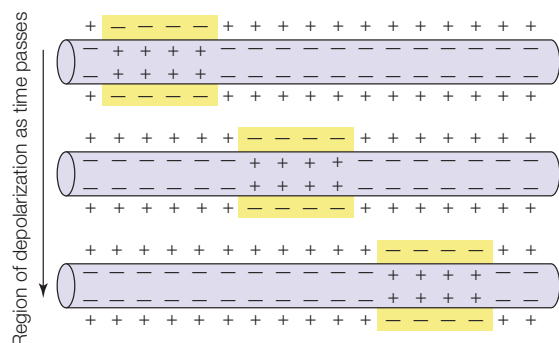
What triggers muscle cells to contract? In skeletal muscle, nerve impulses stimulate muscle fibers to contract. The nerve cells that are involved have long, threadlike cell processes (cell extensions) called axons (see Figure 34.2). Each muscle fiber is in physical contact with an axon of a nerve cell. The nerve cell is said to **innervate** the muscle fiber. The point of contact between the nerve cell and muscle fiber is known as a **neuromuscular junction** (**FIGURE 33.5**). When a nerve impulse arrives at the neuromuscular junction, it is said to excite the muscle fiber, and the event is called **excitation**. During excitation (see Concept 34.3), an impulse or action potential is initiated in the cell membrane of the muscle fiber and then travels the length of that cell membrane.
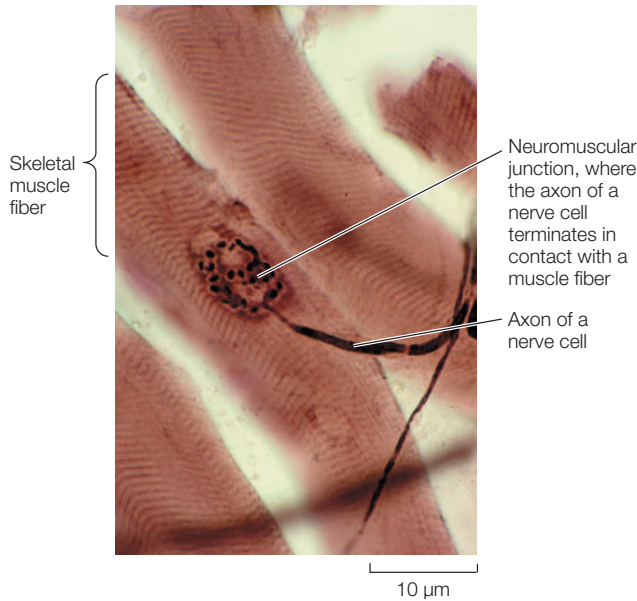
FIGURE 33.5 **Innervation of a Muscle Fiber** In this view of several muscle fibers, we see a nerve cell process (axon) from a far-away nerve cell that controls the contraction of one of the muscle fibers. The point of contact of the nerve cell process with the muscle fiber is called a neuromuscular junction. When the nerve cell is stimulated, an impulse travels along its axon to the neuromuscular junction and excites the muscle fiber. It is possible for one nerve cell to send a process to more than one muscle fiber. In such cases, all the muscle fibers that the nerve cell innervates are simultaneously excited, and contract together, when the nerve cell is stimulated.

Excitation–contraction coupling is the process by which the excitation of a muscle fiber leads to contraction of the muscle fiber. Several decades ago, when excitation–contraction coupling was first being investigated, researchers injected muscle fibers in a frog's leg with the bioluminescent protein aequorin, which is activated to emit light by calcium ions (Ca^{2+}). The researchers found that these injected fibers emitted a flash of light each time they were stimulated to contract. This elegant experiment announced to the world that Ca^{2+} plays a role in excitation–contraction coupling. After a muscle fiber is excited, Ca^{2+} is released into the general cytoplasm of the fiber from internal Ca^{2+}-storage locations. Ca^{2+} in the cytoplasm of an injected cell activates the aequorin, producing a flash of light.

Where is the Ca^{2+} stored in muscle fibers, and how is it released? A distinctive feature of muscle cells is that each cell has many spots where the cell membrane is indented inward into the cell cytoplasm to form a **transverse tubule**, or **T tubule** (**FIGURE 33.6**). The membrane that forms the walls of each T tubule is continuous with the outer cell membrane. Thus when an impulse or action potential travels along the outer cell membrane, it also travels inward along each T tubule, thereby spreading into the interior of the cell at multiple places via the system of multiple T tubules.

The T tubules of a muscle cell are physically very close to the endoplasmic reticulum of the cell. In a muscle cell, the cytoplasm is called the **sarcoplasm**, and the endoplasmic reticulum is called the **sarcoplasmic reticulum**. The sarcoplasmic reticulum is a closed compartment that surrounds every myofibril in a muscle cell (see Figure 33.6). Calcium pumps in the sarcoplasmic reticulum membrane take up Ca^{2+} from the sarcoplasm. Thus when a muscle cell is at rest there is a high

1 Black arrows symbolize an impulse or action potential. When an action potential in an axon arrives at the neuromuscular junction…

2 …it initiates an action potential in the muscle fiber cell membrane. That action potential spreads along the entire length of the cell membrane, and, as it does so, it spreads down the T tubules…

3 …which causes the sarcoplasmic reticulum to release Ca^{2+} from its internal stores of Ca^{2+}.

4 Released Ca^{2+} diffuses into sarcoplasm bathing the myofibrils, stimulating muscle contraction.

5 After stimulation by the nerve cell ends, Ca^{2+} is taken up from the sarcoplasm by the sarcoplasmic reticulum, terminating muscle contraction.

FIGURE 33.6 **T Tubules Spread Action Potentials into a Muscle Fiber** When an action potential is initiated in the cell membrane of a muscle fiber at a neuromuscular junction, the action potential spreads along the cell membrane. It also spreads via the T tubules to the deep interior of the muscle fiber, triggering the release of Ca^{2+} from the sarcoplasmic reticulum.

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The Neuromuscular Junction
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concentration of Ca^{2+} inside the sarcoplasmic reticulum and a low concentration in the sarcoplasm. Essentially, Ca^{2+} is stored inside the sarcoplasmic reticulum when a muscle cell is resting.

Spanning the space between the membranes of the T tubules and the membranes of the sarcoplasmic reticulum are two proteins that are physically connected. One of these, the dihydropyridine (DHP) receptor, is located in the T tubule membrane. It changes its conformation—its molecular shape—when an action potential reaches it. The other protein, the ryanodine receptor, is a Ca^{2+} channel located in the sarcoplasmic reticulum membrane.

The two receptor proteins act to release Ca^{2+} into the sarcoplasm when a muscle fiber is excited. When the DHP receptor is activated by an action potential traveling down a T tubule, both the DHP and ryanodine receptor proteins change conformation. As a consequence of this change, the ryanodine receptor (a Ca^{2+} channel) allows Ca^{2+} to leave the sarcoplasmic reticulum. Ca^{2+} then floods into the sarcoplasm surrounding the actin and myosin filaments (**FIGURE 33.7**, step 1).

The Ca^{2+} ions in the sarcoplasm then trigger actin and myosin to interact so that the muscle fiber contracts. How do the Ca^{2+} ions do this? Recall that strands of the protein tropomyosin are twisted around the chainlike actin polymers (see Figure 33.4), and molecules of the globular protein troponin occur at regular intervals. Each troponin molecule has three subunits: one binds actin, one binds tropomyosin, and one binds Ca^{2+}.

When a muscle fiber is at rest, the tropomyosin strands are positioned so they block the sites on actin filaments where myosin heads can bind. When Ca^{2+} is released into the sarcoplasm, it binds to troponin, changing troponin's conformation. Because troponin is bound to tropomyosin, this troponin change affects the conformation of tropomyosin, which twists enough to expose the actin–myosin binding sites (see Figure 33.7, step 2). Myosin heads can then form cross-bridges with actin (step 3). When a myosin head forms a cross-bridge, it is in a conformation that poises it to undergo its "power stroke,"

START

1 Ca^{2+} is released from the sarcoplasmic reticulum.

2 Ca^{2+} in the sarcoplasm binds troponin and exposes myosin-binding sites on the actin filaments.

3 Myosin heads bind to actin; release of P_i initiates power stroke.

4 In the power stroke, the myosin head changes conformation, bending so that the filaments are forced to slide past one another.

5 ADP is released; ATP binds to myosin, causing it to release actin.

6 ATP is hydrolyzed. The myosin head returns to its unbent, extended conformation.

7 As long as Ca^{2+} remains available, the cycle repeats and muscle contraction continues.

8 When excitation stops, Ca^{2+} is returned to the sarcoplasmic reticulum by Ca^{2+} pumps using ATP, and the muscle relaxes.

Tropomyosin Actin filament Troponin

Myosin-binding site Ca^{2+}

Myosin filament

FIGURE 33.7 Ca^{2+} Causes Muscle Contraction
When Ca^{2+} binds to troponin, it causes molecular conformation changes that expose the myosin-binding sites on actin. As long as the binding sites are exposed and ATP is available, actin and myosin go through cyclic interactions that use ATP bond energy to pull the actin and myosin filaments past each other, developing mechanical forces. P_i = inorganic phosphate.

APPLY THE CONCEPT

Muscle cells develop forces by means of cycles of protein–protein interaction

The force that a muscle fiber can generate depends on how many actin–myosin cross-bridges can form. This number in turn depends on the degree of overlap between the actin and myosin filaments in the sarcomeres. This overlap can vary considerably, as shown in Figure 33.3. When a muscle is stretched from its resting length, there is less overlap between the filaments. We can hypothesize that the force a muscle can produce during a given contraction will be a function of its length at the beginning of the contraction relative to its resting length. In an experiment, a bundle of muscle fibers can be attached at either end to an apparatus that can stretch the fibers and measure the force they generate when they are stimulated to contract. The results are shown in the table.

Plot these results with force generated on the *y* axis, and length of fibers at the beginning of contraction on the *x* axis. In answering the questions here, keep in mind that "length" refers to a percentage of resting length.

1. At what fiber length is a muscle's force-generating capacity greatest?

LENGTH OF FIBERS AT BEGINNING OF CONTRACTION AS PERCENTAGE OF RESTING LENGTH	FORCE GENERATED AS PERCENTAGE OF MAXIMUM FORCE
35%	10%
75%	50%
100%	100%
115%	100%
130%	80%
150%	50%
175%	10%

2. When a muscle is stretched to longer than its resting length, at what percentage of the resting length do you predict that the muscle fibers will not be able to generate any force?

3. Why does the force-generating capacity of a muscle decrease at exceptionally great muscle lengths? At exceptionally short lengths?

4. When you do a pull-up, which stages of the pull-up are most difficult, and why?

and it is bound to ADP and inorganic phosphate, P_i. Release of P_i activates the power stroke (step 4), during which the myosin head changes conformation, pulling the actin and myosin filaments past each other and releasing ADP. ATP then binds to the myosin head, causing myosin and actin to dissociate (step 5). Hydrolysis of the ATP then occurs, releasing energy (although the ADP and P_i stay bound to myosin) and leading to another conformational change in which myosin returns to its extended conformation (step 6). As long as Ca^{2+} remains available, the cycle then repeats (step 7).

When excitation ends, calcium pumps remove Ca^{2+} from the sarcoplasm (step 8). The conformations of troponin and tropomyosin then return to their original state, tropomyosin blocks the binding of myosin heads to actin, and contraction stops.

CHECKpoint CONCEPT 33.1

✓ Imagine planting your feet and trying to push through a concrete wall that's far too heavy to move. As you push, would you describe the associated muscles in your back, arms, and legs as contracting, shortening, lengthening, or a combination of these words? Explain.

✓ In a muscle fiber, how is force development aided by the overlapping arrangement of actin and myosin filaments?

✓ Describe how the concentration of Ca^{2+} in the sarcoplasmic reticulum of a muscle cell changes before, during, and after the cell is excited by a nerve impulse (action potential).

Now that we have seen how the contractile apparatus of a muscle generates forces, let's look at how these forces are put to use.

CONCEPT 33.2 Skeletal Muscles Pull on Skeletal Elements to Produce Useful Movements

Skeletal systems provide rigid structural elements against which the skeletal muscles pull to create directed movements. Two major types of skeletal systems exist in animals. In vertebrates, the skeleton is surrounded by the other tissues of the body (**FIGURE 33.8**) and is called an **endoskeleton** (*endo*, "inside") because it is deep inside the body. In arthropods, such as crabs and insects, the skeleton encases the rest of the body and is an **exoskeleton** (*exo*, "outside").

In vertebrates, muscles pull on the bones of the endoskeleton

The endoskeleton consists mainly of bone in most adult vertebrates. **Bone** is composed principally of an extracellular matrix of collagen protein fibers with insoluble calcium phosphate crystals deposited among them, giving the bone hardness and rigidity. Bone also contains several types of living cells throughout life. The activities of these cells make bone a dynamic tissue. It is not inert, as many people tend to assume. Bone is remodeled—that is, repaired or altered in shape—throughout life by the activities of its living cells. Because of this process, a bone can undergo modest changes in shape or structure to adjust to the forces placed on it. Bone also serves
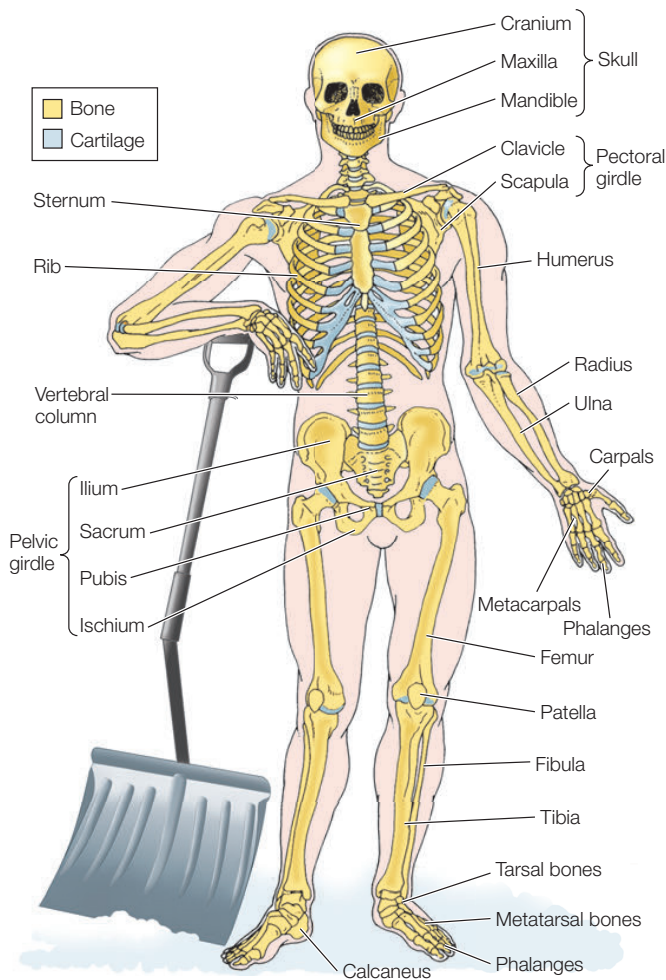
FIGURE 33.8 **The Human Endoskeleton** Bone and cartilage make up the internal skeleton of a human being. The human adult skeleton consists of more than 200 named bones, many of which are attached to other bones by moveable joints.

FIGURE 33.9 **Tuna Swimming** The blue line is a graph of swimming muscle mass. Where the line is highest, the muscle mass is greatest.

as a reservoir of calcium for the rest of the body, being in dynamic exchange with soluble calcium in the extracellular body fluids. This exchange is under the control of hormones, such as parathyroid hormone (see Figure 35.10), and vitamin D. The endoskeleton also includes cartilage in its structure. **Cartilage** is a flexible, rather than hard, form of skeletal tissue that plays several roles, such as imparting flexibility to skeletal elements (e.g., the rib cage).

To produce movements, muscles and bones work together around **joints**, the structures where two or more bones come together. Muscles attach to bones by bands of flexible connective tissue called **tendons**. Tendons often extend *across* joints. In such cases, muscles on one side of a joint exert forces on bones on the opposite side of the joint. Tunas, which are among the most powerful swimmers of all fish, provide dramatic examples. A tuna swims by beating its tail fin, but there are no muscles of any size in its tail. The massive swimming muscles of a tuna are in the middle of its body (**FIGURE 33.9**). Forces

developed by these muscles are transmitted to the tail by tendons that run from the swimming muscles to the tail fin across the joint at the base of the tail.

A muscle can exert force in only one direction. Thus for the bones at a joint to move in opposite directions, two muscles are required. These muscles work as an **antagonistic pair** in which the two have opposite actions: when one contracts, the other relaxes. You can see this action in the motions of your forearm (**FIGURE 33.10A**). When your biceps contracts, your triceps relaxes, and your forearm moves up because the tendons of the biceps cross the elbow joint to attach to the forearm. When your triceps contracts, your biceps relaxes, and your forearm moves down.

Different sets of muscles, coordinated by the nervous system, typically must work together to control complex sets of movements. For example, consider the large muscle on the back of your calf, the gastrocnemius muscle. When it contracts, the movement created depends on the state of contraction of the muscle on the front of your thigh, the quadriceps femoris (**FIGURE 33.10B**). If your quadriceps is not contracting strongly, contraction of your gastrocnemius bends your knee joint and lifts your calf as in walking. If your quadriceps is contracting strongly—an action that keeps your knee joint from bending—contraction of your gastrocnemius extends your foot as in jumping.

In arthropods, muscles pull on interior extensions of the exoskeleton

Crabs, lobsters, insects, and other arthropods have an exoskeleton that covers every part of their body. It is composed of the polymerized carbohydrate chitin, and in crabs and lobsters it is extensively hardened by deposition of calcium-containing minerals. An exoskeleton functions like armor, protecting the soft tissues of the body inside. However, the exoskeleton of an arthropod cannot grow after it is formed. As an arthropod grows, it must therefore replace its exoskeleton periodically with a new, larger version.
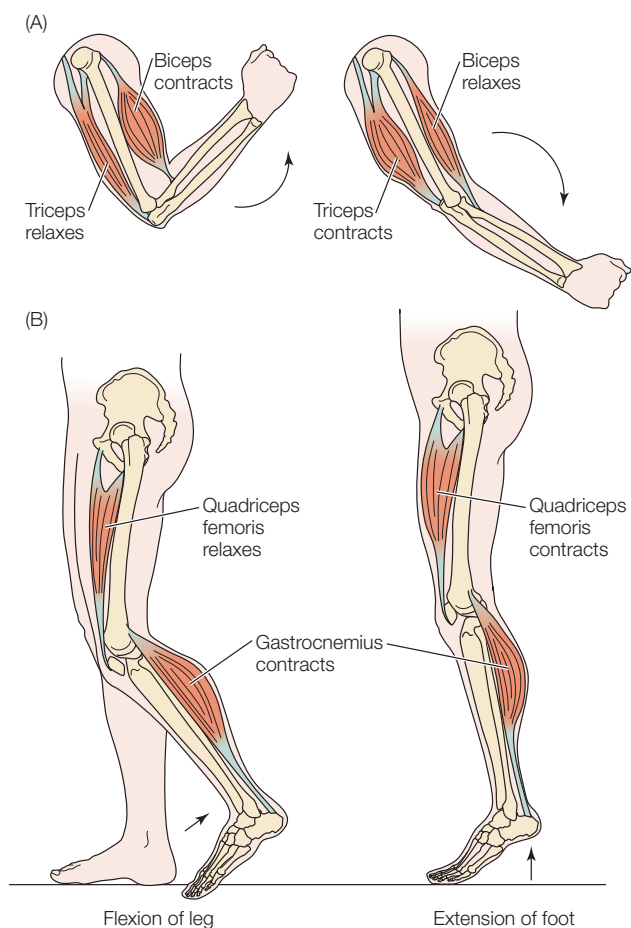
FIGURE 33.10 **Movements Result from Interactions of Muscles with the Skeletal System** (A) Antagonistic muscles are coordinated to allow the bones at a joint to move in opposite directions. (B) Different sets of muscles, coordinated by the nervous system, typically work together to control complex movements.

The skeletal muscles have a different relationship to the skeleton in arthropods than they do in animals with endoskeletons. Typically, where there is a joint between two parts of the exoskeleton, the exoskeleton projects inward, forming structures called apodemes to which the muscles inside the body attach. The large "pinching" claws at the end of a crab's front legs provide an excellent illustration. One side of each claw does not move, but the other side (the dactyl) connects to the leg by a joint and is moveable. At the joint, the moveable element of the claw has two apodemes to which two muscles attach (**FIGURE 33.11**). These muscles act as an antagonistic pair. When the larger of the two contracts, it pulls the claw closed with great force (leading to a pinching movement and a loud
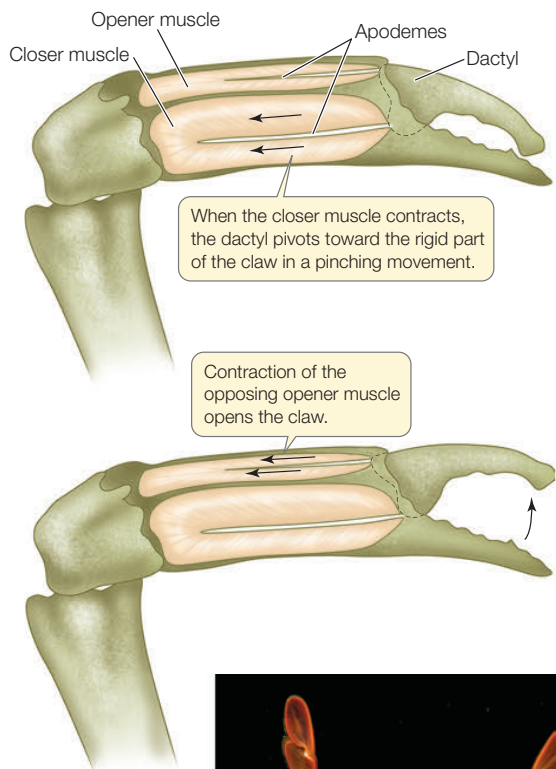
FIGURE 33.11 **In Animals with an Exoskeleton, Muscles Pull on Interior Projections of the Exoskeleton** This principle is illustrated here by the muscles that operate the claw of a crab. When the elements of the claw are pulled together, they exert high forces to gather food or pinch attackers. The arrows indicate the direction of movement of the apodemes and dactyl.

scream if your finger is caught!). The smaller of the two opens the claw with less force when it contracts.

Hydrostatic skeletons have important relationships with muscle

An animal is said to have a **hydrostatic skeleton** if its body or a part of its body becomes stiff and skeleton-like because of a high fluid pressure inside. The most familiar hydrostatic skeleton is the human erected penis; blood pressure, produced by
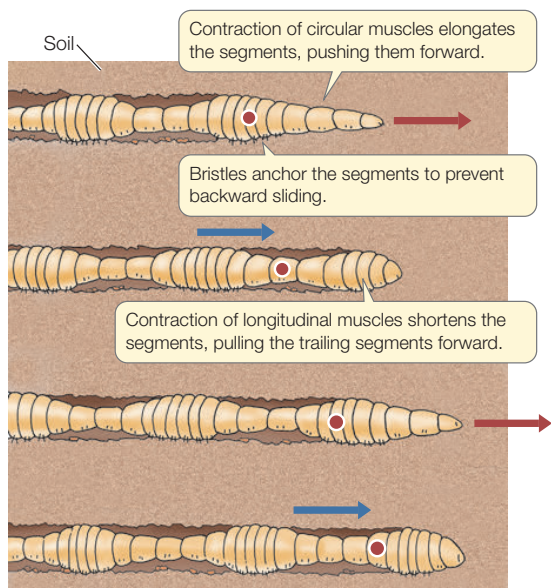
FIGURE 33.12 A Hydrostatic Skeleton Alternating waves of muscle contraction move the earthworm through the soil. The red dot enables you to follow changes in the position of one segment as the worm moves forward. Red arrows show forward extension of the body when contraction of circular muscles pressurizes the worm and the interior pressure forces the anterior end to extend forward. Blue arrows show trailing parts of the body being pulled forward while the anterior is anchored.

the beating of the heart muscle, gives it its rigid, skeleton-like character (see Concept 37.2).

An earthworm digs through soil by using muscles in its body wall to create a hydrostatic skeleton (**FIGURE 33.12**). Each time the worm moves forward (red arrows in the figure), contractions of certain muscles raise the pressure inside the worm to a high enough level that the front end of the worm's body expands forward through the soil, much as a ribbon-shaped balloon expands when inflated. The worm then anchors its front end and pulls its back end toward its front end (blue arrows in the figure) before repeating the process. Clams do much the same thing to dig into sand. Through muscular contractions, they cyclically inflate their foot under pressure, so that the foot shoves deeper into the sand, and then pull the rest of their body down toward the foot.

CHECKpoint CONCEPT 33.2

✓ What are some biological structures, apart from muscle, that allow animals with endoskeletons to perform complex movements?

✓ Can endoskeletal components continue to change shape and structure after an animal is done growing?

✓ Are all muscles that function in locomotion necessarily attached to hard skeletal elements?

Now that we have looked at how skeletal muscles work together with different skeletal systems, let's turn to the factors that affect the performance of the skeletal muscles.

CONCEPT 33.3 Skeletal Muscle Performance Depends on ATP Supply, Cell Type, and Training

Skeletal muscles vary in performance from one muscle to another and from time to time. Our postural and finger muscles illustrate differences among muscles. Our postural muscles sustain loads steadily over long periods of time, whereas our finger muscles typically contract quickly for brief periods.

Muscle power output depends on a muscle's current rate of ATP supply

Muscles perform work, by which we mean that they apply forces to bones or other structures—forces that often make the structures move. For understanding the performance of work by a muscle cell, the cell's fuel supply for work is often as important as the properties of its contractile apparatus. Muscle cells depend on ATP as their source of energy to do work. For this reason, their *rate* of doing work—their power output—at a given time can be only as high as the rate at which they supply their contractile apparatus with ATP.

Muscle cells have three systems for supplying the ATP they need for contraction. Here we term these the immediate, glycolytic, and oxidative systems:

- The *immediate system* uses preformed ATP. This ATP is already present in a cell when contraction begins. Some preformed ATP is present literally as ATP, but muscle cells can also store small amounts of preformed ATP in chemically combined form, such as in the compound creatine phosphate found in vertebrate skeletal muscles.

- The *glycolytic system* synthesizes ATP during the process of contraction by anaerobically breaking down carbohydrates (see Concepts 6.3 and 29.4). In vertebrates, crustaceans, and some other animals, this system produces lactic acid. It does not require O_2.

- The *oxidative system* also synthesizes ATP during the process of contraction, but unlike the glycolytic system, it employs aerobic breakdown of food molecules to synthesize ATP (see Concept 6.2). It requires O_2 because it depends on the citric acid cycle and electron transport, fully oxidizing carbohydrates and lipids to H_2O and CO_2.

These three systems vary greatly in how rapidly they can produce ATP and in how long they can continue to make ATP at a high rate. Accordingly, the power output and endurance of a working muscle cell vary with which system the cell is using to make ATP (**FIGURE 33.13**).

When a muscle cell starts to do work, the immediate system can supply ATP extremely rapidly, enabling the cell to achieve a very high power output. The immediate system can do this because it uses ATP made at an earlier time and already present in a cell when work starts. Only a small amount of preformed ATP can be present in a cell, however. Thus the immediate system can function for only a brief period of time.

The glycolytic system can synthesize ATP at a very high rate, although not as high a rate as that at which the immediate
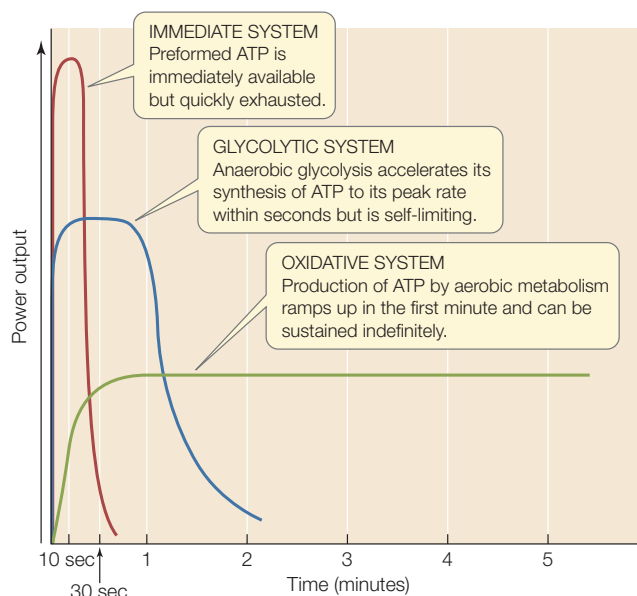
FIGURE 33.13 **Supplying Fuel for High Performance** Power output during all-out exertion is shown as a function of time when muscles are using the immediate, glycolytic, and oxidative systems for obtaining the ATP they need for contraction. This diagram refers to human performance.

system can supply ATP. However, the glycolytic system is self-limiting. For poorly understood reasons that may be related to the lactic acid it produces, the glycolytic system cannot keep making ATP indefinitely. As the glycolytic system makes ATP, it reaches a point at which it can no longer function, and then it must rest for a long time (tens of minutes or hours) before it can be used again to supply ATP.

The oxidative system makes ATP at a slower rate than the other two systems. However, its products—besides ATP—are simply H_2O and CO_2, which healthy animals can deal with effectively. Thus the oxidative system is not self-limiting and can continue making ATP for very long periods of time if a cell's supply of O_2 is sufficient for it to function.

A muscle cell that is capable of using all three systems of ATP supply varies in its performance, depending on which system it is using. To explore this important point, let's return to Figure 33.13. Keeping in mind that the power output of a contracting muscle cell depends directly on its rate of ATP supply, we see that *if we focus on power output*, the three systems of ATP supply rank as follows: the immediate system permits a muscle cell to reach highest power output, the glycolytic system ranks next, and the oxidative system permits the lowest power output. However, *if we focus on endurance*, the three systems rank in the opposite order: the immediate system permits the lowest endurance, the glycolytic system ranks next, and the oxidative system permits the greatest endurance.

These principles explain why, in human athletic competition, speed and endurance are inversely related. Sprints, such as the 100-yard dash, are run at a very high speed. They depend greatly on the immediate system for ATP, which permits

very high power output. The immediate system cannot supply ATP for very long, however, meaning sprints must be of short duration. Events like the half-mile run and mile run are performed at lower speeds and last longer than sprints. A key reason for these contrasts is that the half-mile and mile runs require too much ATP, in total, to be run with just the immediate system as their source of ATP. Thus they depend to a great extent on the glycolytic system, which permits muscle cells to have greater endurance than the immediate system but restricts performance to a lower power output and speed. A marathon requires far too much total ATP to be run with just the immediate and glycolytic systems as ATP sources. Only the oxidative system—based on O_2 use—can provide the amount of ATP a marathon requires. The speed of running in a marathon must therefore be lower than in races fueled by the immediate and glycolytic systems, although long endurance is possible.

Long-endurance casual sports such as jogging and swimming laps depend almost entirely on the oxidative system. This is true because the oxidative system can accelerate its ATP production quickly at the start, and then can meet all the ATP needs of these forms of exercise on a minute-by-minute basis, indefinitely. This is why these sports are described as aerobic.

Muscle cell types affect power output and endurance

All muscle cells are not equal in their capability to use the glycolytic and oxidative systems to synthesize ATP. Some cells principally use the glycolytic system, and others principally use the oxidative system. There are no cells, however, that depend principally on the immediate system, which can supply only small amounts of ATP.

Multiple muscle cell types typically occur within a single species of animal. Two major types are often recognized: **slow oxidative cells** (sometimes called slow-twitch cells) and **fast glycolytic cells** (fast-twitch cells). In vertebrates, these cell types are also called "red" and "white." Cells of the two types typically occur mixed together in the skeletal muscles of mammals. In some other animals, however, certain skeletal muscles are composed almost entirely of one muscle cell type or the other. For example, many fish have distinct masses of muscle that are visibly red or white (**FIGURE 33.14**). The red muscles are composed mostly of slow oxidative cells. The white muscles consist mostly of fast glycolytic cells.

Slow oxidative and fast glycolytic muscle cells differ in three main ways:

- Their principal mechanisms for making ATP
- Their mechanisms for taking up O_2 from the blood
- Their molecular forms of myosin; the two types of cells express different genes for myosin, and their molecular forms of myosin differ in ATPase (ATP-splitting) activity

Slow oxidative cells are poised to make most of their ATP aerobically using the oxidative system of ATP synthesis. These cells need lots of O_2. This explains why, in vertebrates, these cells have evolved high levels of the red, hemoglobin-like compound **myoglobin** in their sarcoplasm (making them red).
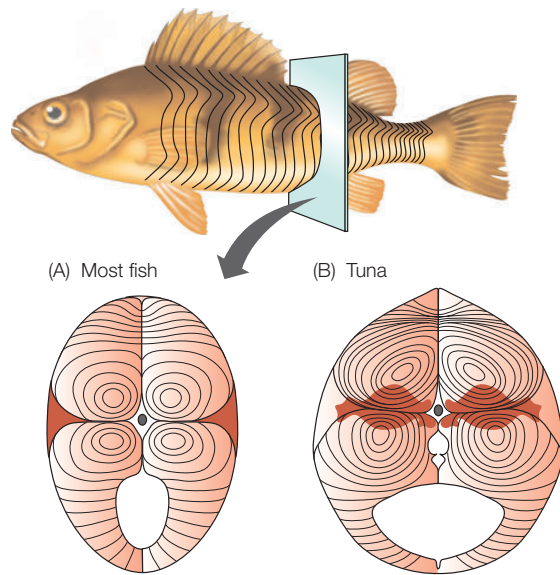
FIGURE 33.14 Red and White Swimming Muscles in Fish   The fish shown is a perch. The cross sections, made approximately where indicated on the fish, show the red (dark) and white (light) swimming muscles in (A) perch and most other fish and (B) tuna.

Myoglobin speeds entry of O_2 into cells from the cell surfaces. Slow oxidative cells also have large numbers of mitochondria and are rich in mitochondrial enzymes, notably the enzymes of the citric acid cycle and electron transport system (see Concept 6.2). They are not well endowed with the enzymes required for the glycolytic system to make ATP anerobically, however. Slow oxidative cells thus make most of their ATP aerobically. Accordingly, they can sustain ATP production for long, continuous periods of time, but their peak rates of ATP production are only moderately high (see Figure 33.13). Slow oxidative muscle cells also have molecular forms of myosin with relatively low ATPase activity, meaning they recycle actin–myosin cross-bridges at relatively low rates.

Because of their limited rates of ATP production and myosin properties, slow oxidative cells tend to contract and develop tension slowly (accounting for the word "slow" in their name). They are well suited for maintaining relatively low power output for sustained periods.

Fast glycolytic cells contrast with slow oxidative cells in all the ways we've mentioned. They have high levels of the enzymes needed for glycolytic, anaerobic ATP synthesis and thus can produce ATP very rapidly. They also have molecular forms of myosin with relatively high ATPase activity, meaning they can recycle actin–myosin cross-bridges rapidly. Because of their high rates of ATP production and myosin properties, fast glycolytic cells tend to contract and develop tension rapidly (thus they are "fast"). They also fatigue rapidly, however. They have relatively few mitochondria, and they lack myoglobin, so they are not red.

Fish use principally their red muscles, composed mainly of slow oxidative cells, during routine cruising, when they move slowly for long periods. They use principally their white muscles, composed mainly of fast glycolytic cells, during burst swimming, when they swim at high speeds to evade danger or catch prey. Their white muscles enable them to achieve very high power outputs for brief periods.

Individual people vary greatly in the proportions of red and white cells in their major muscles. These differences generally do not matter in sports done for fun. At the level of national or international competition, however, researchers know from many studies that champion long-distance runners, swimmers, and cyclists—who require endurance—tend to differ from champion weight-lifters, wrestlers, and sprinters—who require high power outputs for brief periods. The endurance athletes tend to have leg and arm muscles consisting mostly of slow oxidative muscle cells (**FIGURE 33.15**). The other athletes tend to have muscles with a high percent of fast glycolytic cells.

Training modifies muscle performance

Skeletal muscle has a remarkable ability to change its properties with use. In this way, muscle provides dramatic examples of phenotypic plasticity (see Concept 29.5). When a muscle

(A) Cross sections of leg muscles viewed under a light microscope

(B)
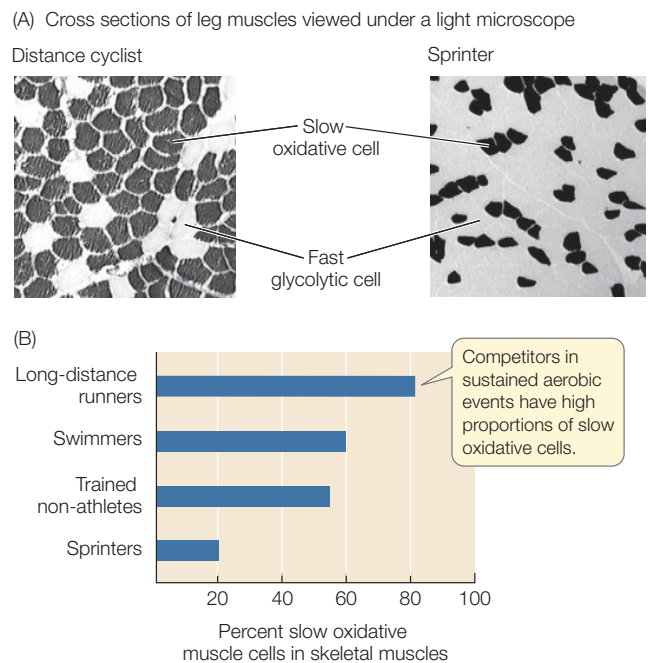
FIGURE 33.15 Competitive Athletes Tend to Have Muscle Fiber Types Corresponding to Their Sports   (A) People vary in the cellular composition of their skeletal muscles. In these microscopic images, cells were stained with a reagent that shows slow oxidative cells as dark and fast glycolytic cells as light. (B) At the level of international or national competition, athletes successful in sustained aerobic events tend to have a high percent of slow oxidative cells, whereas successful sprinters tend to have a high percent of fast glycolytic cells. These differences are caused by heredity, early development, and training. Differences among individuals in muscle cell composition do not matter in sports done for fun.

changes in response to use, the change is often termed a "training effect." We observe a familiar training effect when we lift weights or do other similar forms of exercise. Our muscles gradually become visibly larger. The number of muscle cells in a muscle does not change under these conditions. Instead, a muscle becomes larger because its already-existing cells increase in size (termed hypertrophy) by increasing their content of actin and myosin.

To fully understand training effects, two types of exercise need to be distinguished. **Endurance exercise** (endurance training) refers to steady, long-duration exercise such as cross-country running or long-distance cycling. **Resistance exercise** (resistance training) refers to exercise that generates particularly large forces, typically in relatively few repetitions spread over a short period of time. Weight-lifting and wrestling are forms of resistance exercise.

When people or research animals engage in training programs, endurance exercise causes their muscle cells to increase their numbers of mitochondria. It also causes some cells to transform from being fast glycolytic to being slow oxidative cells. It stimulates growth of additional blood capillaries in muscles—an effect that reduces the average distance between each muscle cell and O_2-carrying blood in its nearest capillary. All of these training effects enhance capabilities for steady, sustained forms of exercise. Recent studies have shown that the expression of more than 100 genes is dramatically increased in muscle cells during endurance training in people or laboratory animals. Conversely, more than 100 genes are silenced when a person's or animal's life is entirely sedentary. Changes in gene expression help control the changes in muscle properties that occur (hormonal and metabolic control mechanisms also play roles). Investigators have been searching for transcription factors that are upregulated by endurance exercise and that may help regulate expression of genes that control transformation of cells from fast glycolytic to slow oxidative (**FIGURE 33.16**).

When people or research animals engage in training with resistance exercise, as we have already seen, the training causes their muscle cells to build a bigger contractile apparatus, enabling the cells to better develop the forces required for weight-lifting or other resistance activities. Resistance exercise also causes some muscle cells to transform from slow oxidative to fast glycolytic.

INVESTIGATION

FIGURE 33.16 A Regulator of Muscle Fiber Type   In response to training with endurance exercise, skeletal muscles undergo changes that make the muscles more resistant to fatigue. How are these responses regulated? Some evidence indicated that a transcription factor called PPARδ ("PPAR delta"), which is present in skeletal muscle and is activated in response to endurance exercise, might stimulate the formation of slow oxidative cells, a key response to endurance training. Yong-Xu Wang and colleagues used transgenic mice to investigate whether artificially increasing the amount of active PPARδ would initiate exercise-associated responses in muscles even in the absence of endurance training.[a]

HYPOTHESIS

Activation of PPARδ is sufficient to drive formation of slow oxidative muscle fibers.

METHOD

1. Engineer a gene that encodes a permanently activated form of PPARδ.
2. Produce transgenic mice that synthesize the permanently activated form of PPARδ in skeletal muscle.
3. Test the transgenic mice for (a) muscle characteristics and (b) endurance. Error bars represent 1 standard error of the mean; the t-test was used to produce P-values (see Appendix B).

RESULTS

When trained to run on a treadmill, transgenic mice were able to run for a longer time before becoming exhausted than wild-type mice were.

Muscle tissue from the transgenic mice when examined by light microscopy had more slow oxidative muscle fibers (cells stained dark blue) than did muscle tissue from wild-type mice.

Wild-type mouse   Transgenic mouse

$P < 0.03$
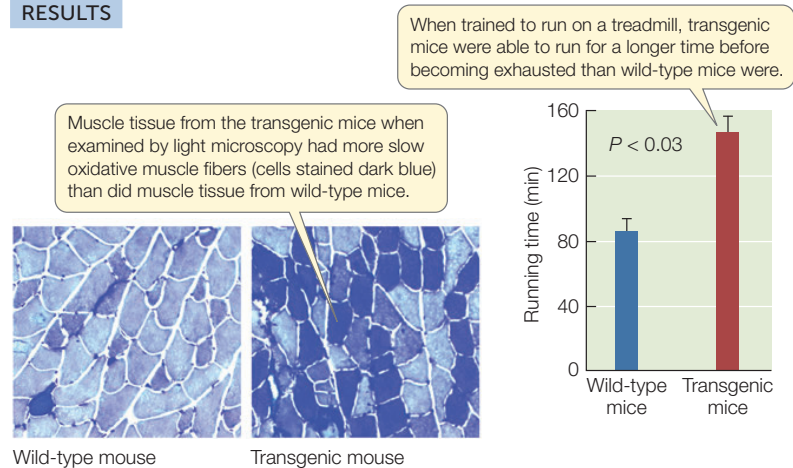
CONCLUSION

Activated PPARδ induces formation of slow oxidative muscle fibers and enhances endurance.

ANALYZE THE DATA

In a related experiment, using different sets of individual mice, the researchers tested the endurance of mutant mice that had no PPARδ transcription factor (see graph).

A. Based on these data, what can you conclude about the effect of PPARδ on fatigue resistance of muscle?

B. What would you expect to find if you examined cross sections of skeletal muscle tissue from the mutant mice?

$P < 0.0001$
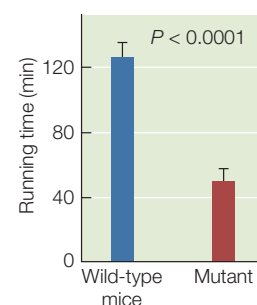
Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]Y.-X. Wang et al. 2004. *PLoS Biology* 2: e294.

CHECKpoint   CONCEPT **33.3**

✓ What factors prevent muscle cells from continuously using ATP provided by the immediate system to power contractions?

✓ Consider a muscle cell that contains myosin proteins specialized for rapid recycling of actin–myosin cross-bridges. Is the cell likely to make most of its ATP by using the glycolytic system or the oxidative system?

✓ Weekly measurements of an athlete's gastrocnemius (calf) muscle reveal that the density of capillaries in the muscle and the number of mitochondria per muscle cell are increasing. Would you predict that the athlete has been training for a lengthy marathon or lifting weights at the gym?

Skeletal muscles, as we have seen, are enormously important. We breathe using skeletal muscles, and the skeletal muscles are responsible for most behaviors, including athletic performance. Skeletal muscle is not the only type of muscle, however, and next we will look at the other types.

CONCEPT **33.4**   **Many Distinctive Types of Muscle Have Evolved**

Besides skeletal muscle, several other distinctive types of muscle have evolved. Vertebrate **cardiac muscle**—heart muscle—is one type. During each of our lives, our cardiac muscle beats regularly from our early embryonic development until we die.

Vertebrate cardiac muscle is both similar to and different from skeletal muscle

Like skeletal muscle, cardiac muscle appears striated when viewed under a light microscope. This is because the actin and myosin filaments in cardiac muscle are arranged in regular patterns in sarcomeres. In other ways, however, cardiac muscle differs morphologically from skeletal muscle. Cardiac muscle cells are much smaller than skeletal muscle cells, and unlike skeletal muscle cells, they have only one nucleus.

A key way that cardiac muscle differs from skeletal muscle is in the relationship of adjacent cells. In cardiac muscle, adjacent cells are electrically coupled by gap junctions that occur in structures called intercalated discs. At a gap junction, the sarcoplasms (cytoplasms) of two adjacent cardiac muscle cells are continuous with each other via tiny pores:

Two adjacent cells are shown here pulled apart. When together, the pores connect their sarcoplasms, and the overall structure joining them is called an intercalated disc.

Pore
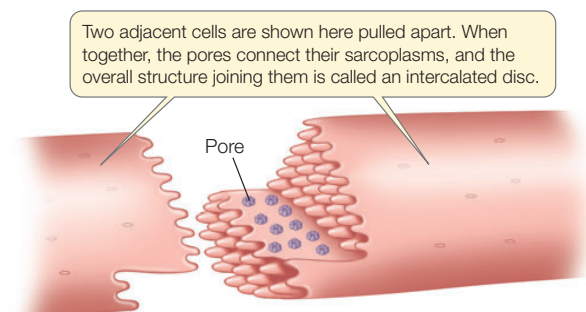
Because of this continuity, if one of the two cells is excited and an impulse spreads over its cell membrane, the impulse spreads directly to the second cell (see Figure 4.18 and Concept 4.5). Accordingly, when an impulse is initiated at any one point in a mass of heart muscle, it spreads rapidly throughout the muscle by moving directly from one cell to another. This process ensures that all the cells within a large mass of muscle are excited at approximately the same time. Thus all the cells contract almost simultaneously, raising the blood pressure in the heart to a high level and propelling the blood out of the heart and through the blood vessels.

In a vertebrate heart, certain of the cells in the heart muscle itself generate the heartbeat rhythm (see Concept 32.3 and Figure 32.8). The heart rhythm is thus very different from the breathing rhythm. The breathing muscles of vertebrates are skeletal muscles, and like all skeletal muscles, they contract only if stimulated by nerves. If a person suffers a neck fracture, he or she will stop breathing if the nerves that stimulate the breathing muscles are damaged. His or her heart will keep beating, however, because of the properties of certain of the cardiac muscle cells.

Go to MEDIA CLIP 33.1
Be Still My Beating Stem Cell Heart
PoL2e.com/mc33.1

Vertebrate smooth muscle powers slow contractions of many internal organs

In addition to skeletal and cardiac muscle, vertebrate animals have a third type of muscle known as **smooth muscle**. Structurally, smooth muscle cells are smaller than skeletal muscle cells. They are usually spindle-shaped, and each has a single nucleus. They are termed "smooth" because their actin and myosin filaments are not as regularly arranged as those in skeletal and cardiac muscle, and for this reason they do not have a striated appearance when viewed under a light microscope:

30 µm
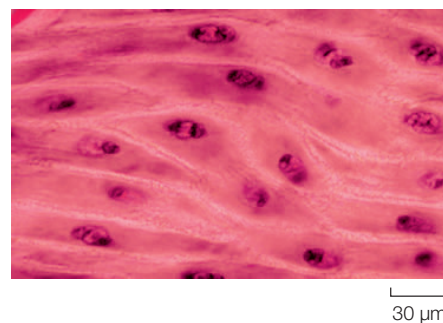
Smooth muscles provide the contractile forces for most of our internal organs, under the control of the nervous system. Smooth muscles in the walls of the digestive tract move food through the digestive tract. Smooth muscles in the walls of small arteries and arterioles adjust the diameters of these blood vessels, helping control blood flow through them. During sexual climax, smooth muscles in the ejaculatory passages of the male propel the ejaculation of semen, and in the female smooth muscles contribute to the rhythmic contractions of orgasm. Smooth muscles in the walls of the bladder produce forces for bladder emptying.

Some smooth muscle tissue, such as that in the walls of the digestive tract, consists of sheets of cells in which adjacent cells are in electrical contact through gap junctions. As a result, excitation of one cell can spread directly to adjacent cells, helping coordinate the contractions of the cells. This occurs during **peristalsis**, a pattern of contraction in which a wave of contraction moves along the gut tube from one end to the other.

> **LINK**
>
> The structure and function of the vertebrate gut are detailed in **Concept 30.4**

In both cardiac muscle and smooth muscle, excitation–contraction coupling depends on Ca^{2+} influx into the sarcoplasm, as it does in skeletal muscle. Details of excitation–contraction coupling differ among the three types of vertebrate muscle, however.

Go to ANIMATED TUTORIAL 33.2
Smooth Muscle Action
PoL2e.com/at33.2

Some insect flight muscle has evolved unique excitation–contraction coupling

Invertebrates have evolved a variety of specialized types of muscle. Here we discuss just three of them. Two of these, asynchronous flight muscle and catch muscle, are specialized to contract in unusual ways that are highly adaptive for the animals in which they occur. Another specialized type does not contract at all but instead has become modified to produce electricity!

The muscles that drive the wings during insect flight are of two types in terms of their excitation–contraction coupling. In about 25 percent of insect species, each contraction requires excitation. The sphinx moth in our opening photograph is one of these. Each excitation of a muscle cell brings about one contraction, meaning the ratio of excitations to contractions is 1:1. For muscle of this type to contract at a higher and higher frequency, all the processes of excitation–contraction coupling must take place faster and faster. At high frequencies, contraction becomes severely compromised in several ways as a result. Both muscular efficiency and power output diminish at high frequencies.

A different and unique form of muscle that has evolved only in insects solves these problems. It is termed **asynchronous muscle** because each excitation results in many contractions, meaning contractions are not synchronized in a 1:1 ratio with excitations. At high frequencies of contraction, asynchronous muscle maintains higher efficiency and greater power output than synchronous muscle. The reason asynchronous muscle has evolved in insects seems to be that it is well adapted in these ways to meeting the particular challenges of insect flight. Asynchronous muscle has evolved independently in insects about ten times and is found today in about 75 percent of insect species.

Catch muscle in clams and scallops stays contracted with little ATP use

A scallop or clam has a shell composed of two half-shells. One or two powerful adductor muscles connect these half-shells. Contraction of the adductor muscles pulls the two half-shells tightly together so that the animal becomes fully enclosed in its hard shell—a form of armor:

When we eat scallops, we in fact are eating just their adductor muscles.

Adductor muscle

A scallop or clam's adductor muscles sometimes need to remain contracted for long periods of time when predators are nearby.

The adductor muscles (and certain other muscles of mollusks) are able to enter a specialized state termed **catch** in which they maintain high contractile force for tens of minutes or even for hours with almost no use of ATP. The way catch works is not well understood. However, measurements show that catch muscles maintain contraction at a far lower ATP cost than most muscles. Catch is a highly controlled state that can be quickly ended by signals from the nervous system. Its energy-saving feature is adaptive for animals that have body armor that depends on muscular contraction to be effective.

Fish electric organs are composed of modified muscle

Electric eels (*Electrophorus*), which live in tropical rivers, can produce external voltage pulses as large as 700 volts. Electric rays (*Torpedo*) in the ocean also produce large external electric pulses, although they produce high electric currents (up to 20 amperes) rather than high voltages. Fish such as these use their electric pulses to stun prey. Many other fish produce small external electric pulses that they use to detect their surroundings for orientation.

The electric organs of nearly all electric fish have evolved from skeletal muscle and consist of modified muscle cells. These cells cannot contract because the contractile apparatus (e.g., actin and myosin) in each cell is poorly developed. However, the cell membranes of the muscle cells are unique in that the tiny voltage differences across the cell membranes of many cells all add together when the cells are excited during an electric pulse:

Central nervous system

Electric organ

Torpedo

During excitation, all the cell membranes in stacks of cells are polarized electrically in the same direction.
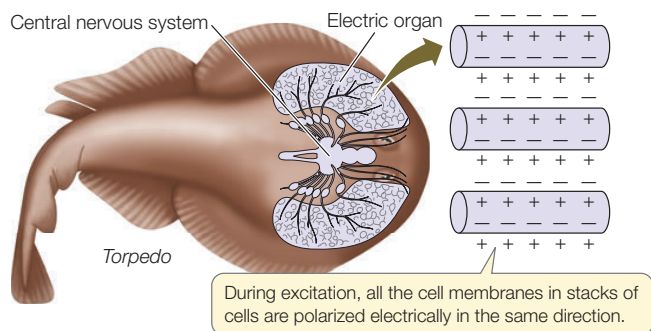
The voltage difference across each cell membrane is only about 0.1 V. In an electric organ, the voltage differences of many membranes add up, in the same way that the voltages of batteries add up when the batteries are connected in series. For this reason, an electric organ with 1,000 cell membranes can produce 100 V.

CHECKpoint   CONCEPT 33.4

✓ Why does the heart keep beating in victims of neck fractures, although the victims stop breathing?

✓ What type of muscle would be used in each of the following activities: the extension of a lizard's forelimbs during walking; the pumping of O_2-poor blood from a person's heart to his or her lungs; the expulsion of food during vomiting; the holding shut of a clam's shell?

✓ If needed, could the modified muscle cells of fish electric organs be used to generate forces for swimming? Why or why not?

Q Why is it likely that available space inside cells has limited the contents of contractile proteins and mitochondria in high-performance muscles?

ANSWER   FIGURE 33.17 is a highly magnified image of an insect flight muscle cell, obtained by electron microscopy. The inside of the cell is filled almost completely by mitochondria and contractile proteins. Open space is thus a scarce resource. Put simply, a high-performance muscle cell needs as large a
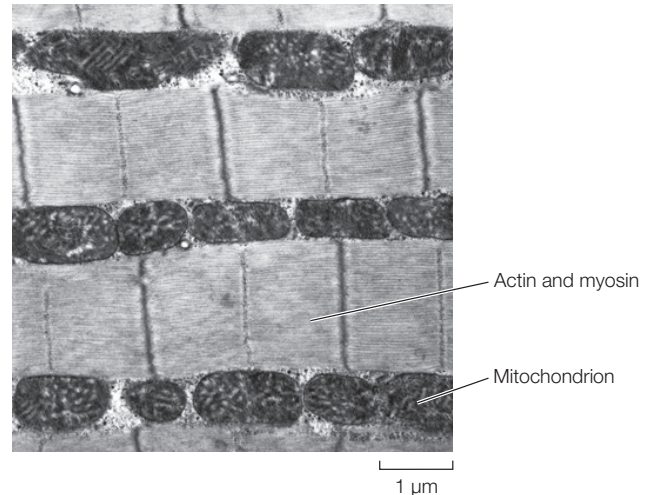
FIGURE 33.17 An Electron Micrograph Showing the Fine Structure of an Insect Flight Muscle Cell

set of contractile proteins as possible and as many mitochondria as possible—meaning there is a sort of "competition" for space in which the amounts of contractile proteins and mitochondria are each limited by space shortage. If, over evolutionary time, natural selection started to favor larger numbers of contractile protein molecules, the contractile proteins could edge out some of the mitochondria—jeopardizing the ability of the contractile proteins to get enough ATP. If natural selection started to favor more mitochondria, the mitochondria would edge out contractile proteins—jeopardizing the ability of the cell to use the ATP it could produce. The fact that space is limited has resulted in a sort of compromise in the use of space inside a high-performance muscle cell.

SUMMARY

CONCEPT 33.1 Muscle Cells Develop Forces by Means of Cycles of Protein–Protein Interaction

■ **Skeletal muscle** consists of bundles of **muscle fibers**. Each skeletal muscle fiber is a large, elongated cell containing multiple nuclei. **Review Figure 33.2 and ACTIVITY 33.1**

■ A skeletal muscle fiber contains numerous **myofibrils**, which contain bundles of **actin** and **myosin** filaments. The regular, overlapping arrangement of the actin and myosin filaments into **sarcomeres** gives skeletal muscle its striated appearance. **Review Figure 33.2**

■ **Contraction** is the development of force by a muscle. The molecular mechanism of contraction is described by the **sliding-filament theory** and involves the binding of the globular heads of myosin molecules to actin molecules to form **cross-bridges**. Upon binding to actin, a myosin head changes its conformation, causing the two filaments to move past each other. Release of the myosin heads from actin and their return to their original conformation requires ATP. **Review Figures 33.3 and 33.4 and ANIMATED TUTORIAL 33.1**

■ Nerve cells make contact with skeletal muscle fibers at **neuromuscular junctions**. In general, each muscle fiber in skeletal muscle is innervated by a single nerve cell. **Review Figure 33.5**

■ **Excitation** by a nerve impulse (action potential) stimulates a muscle fiber to contract by **excitation–contraction coupling**. An action potential spreads across the muscle fiber's cell membrane and through the **transverse (T) tubules**, causing Ca^{2+} to be released from the **sarcoplasmic reticulum**. **Review Figure 33.6 and ACTIVITY 33.2**

■ Ca^{2+} binds to **troponin** and changes its conformation, pulling the **tropomyosin** strands away from the myosin-binding sites on the actin filaments. The muscle fiber continues to contract until the Ca^{2+} is returned to the sarcoplasmic reticulum. **Review Figure 33.7**

CONCEPT 33.2 Skeletal Muscles Pull on Skeletal Elements to Produce Useful Movements

■ Skeletal systems provide structures against which skeletal muscles can pull to produce useful movements. **Endoskeletons** are internal systems of rigid supports, consisting of **bone** and **cartilage**, to which muscles are attached. **Review Figure 33.8**

■ **Tendons** connect muscles to bones. Muscles and bones work together around **joints** to produce movement. **Review Figures 33.9 and 33.10**

(continued)

SUMMARY *(continued)*

■ **Exoskeletons** are skeletons that enclose an animal, notably the hardened outer surfaces of arthropods. In arthropods muscles attach to apodemes, internal projections at the joints of the exoskeleton. **Review Figure 33.11**

■ **A hydrostatic skeleton** is said to exist if an animal's body or a part of its body becomes stiff and skeleton-like because of a high fluid pressure inside. **Review Figure 33.12**

CONCEPT 33.3 Skeletal Muscle Performance Depends on ATP Supply, Cell Type, and Training

■ Muscle contraction depends on a supply of ATP. Muscle cells have three systems for supplying ATP: the immediate system (preexisting ATP and creatine phosphate); the glycolytic system (anaerobic glycolysis); and the oxidative system (aerobic metabolism). The immediate system can fuel high muscle power output instantaneously but is exhausted within seconds. Glycolysis can regenerate ATP rapidly but is self-limiting. Oxidative metabolism delivers ATP more slowly but can continue to do so for a long time. **Review Figure 33.13**

■ **Slow oxidative muscle cells** have cellular properties (e.g., abundant mitochondria) that facilitate extended, aerobic work; **fast glycolytic muscle cells** generate great forces for short periods of time. In vertebrates, slow oxidative cells contain the hemoglobin-like compound **myoglobin**, making these cells red. **Review Figure 33.14**

■ Skeletal muscles contain varying proportions of slow oxidative cells and fast glycolytic cells, depending on genetic controls during muscle development and the demands placed on the muscles. The properties of muscles can be modified by training. **Review Figures 33.15 and 33.16**

CONCEPT 33.4 Many Distinctive Types of Muscle Have Evolved

■ **Cardiac muscle** cells are striated, uninucleate, and electrically connected by gap junctions, so that action potentials spread rapidly throughout masses of cardiac muscle and cause coordinated contractions. In vertebrates some modified cardiac muscle cells serve as the pacemaker cells for rhythmic beating of the heart.

■ **Smooth muscle** provides contractile force for internal organs such as the gut, blood vessels, and reproductive ducts. Some smooth muscle tissue (e.g., in the digestive tract) consists of sheets of cells that are electrically coupled through gap junctions, helping coordinate the contractions of adjacent cells. **Review ANIMATED TUTORIAL 33.2**

■ Some insects drive flapping of their wings with **asynchronous muscles**, which unlike most muscles undergo multiple contractions with each excitation.

■ **Catch** muscles, such as the adductor muscles of clams and scallops, can sustain strong contractions for long periods with little ATP.

■ The electric organs of nearly all electric fish evolved from skeletal muscle and consist of modified, noncontractile muscle cells.

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is33

Go to LaunchPad at **macmillanhighered.com/launchpad** for additional resources, including LearningCurve Quizzes, Flashcards, and many other study and review resources.

34 Neurons, Sense Organs, and Nervous Systems

The star-nosed mole has tiny eyes but large, specialized nose tentacles—correlated with the fact that it hunts in darkness for tiny prey that it locates by touch.

You might imagine that this strange-looking mammal exists only in some remote forest in one of Earth's most inaccessible places. Actually its home is in the eastern United States and Canada. If you live in that part of the world and like to walk in the wild outdoors, you have probably walked right by one. This mammal lives mostly underground, however, explaining why most people have never seen one. It's called the star-nosed mole (*Condylura cristata*) because its nose bears two symmetrical arrays of tentacles that surround the nostrils in a starlike pattern.

Star-nosed moles live in burrows in wet, marshy soils where tiny invertebrates are abundant. The moles are specialized to eat these minute animals. They eat lots of tiny worms and insects. Almost as amazing as their tentacled nose is the fact that the moles forage underwater to a great extent, as well as in their burrows. Most of what biologists know of them comes from studies of burrow foraging.

Why did their strange star-shaped nose evolve? Biologists have deduced that if star-nosed moles eat tiny animals, they must find and eat great numbers of them each day. The current hypothesis regarding the evolution of this strange nose is that it is an adaptation for rapid foraging on tiny prey in darkness.

The star-shaped nose is clearly a sensory organ. All you need to do to be convinced of that is to watch a mole for a few minutes. The moles constantly explore their environment with their tentacles. People at first hypothesized that the moles detect tastes or odors with their tentacles. Researchers have since learned that the sensory receptors in the tentacles are touch receptors.

The nose is no ordinary touch organ, however. The array of tentacles is about 1 centimeter in diameter—not very large. Yet there are about 25,000 tiny touch receptors (called mechanoreceptors) in the skin of the tentacles. And about 100,000 nerve processes (axons) travel from the tentacles to the mole's brain, carrying signals from the receptors. The star-nosed mole is believed to have the highest resolution touch perception found in a mammal. The brain uses this information to perceive potential food items.

The moles are active explorers. As they move from place to place in darkness, they investigate each potential food item in an intense flurry of moving tentacles, providing touch sensations to their brain. With this flow of information, they typically decide in less than a second whether to eat, allowing them to move on promptly in their ceaseless quest to find enough tiny animals to meet their daily food need.

Q How might the star-nosed mole's brain be specialized to process information from its nose?

Nervous Systems Are Composed of Neurons and Glial Cells

Animals need a way to transmit signals at high speeds from place to place within their bodies. Suppose, for example, that you are crowded with other people in the kitchen during a party and, being distracted, you put your hand behind you and lean on a hot stove. You respond immediately—pulling your hand away—because of nerve cells, also called neurons. Mammalian neurons routinely transmit signals at 20–100 meters per second! Thus a danger signal travels the length of your arm to reach your spinal column in less than 0.02 seconds, the first step in allowing you to respond. The speed of signal transmission by neurons is also evident in more ordinary actions. During banjo plucking, each pluck of a string takes place because of neuronal signals that originate by way of interactions among many neurons in the brain and travel to the player's fingers (**FIGURE 34.1**). These signals must move at enormous speeds for notes to burst from the instrument as fast as they do.

A neuron is a type of **excitable** cell, meaning its cell membrane can generate and conduct signals called impulses, or action potentials. The excitable nature of neurons is one of their key specializations. Most types of cells in an animal's body are not excitable. The two principal types that are excitable are neurons and muscle cells (see Concept 33.1). What do we mean by an impulse, or action potential? Cell membranes ordinarily have an electrical polarity in which the outside of the membrane is more positive than the inside. An impulse, or action potential, is a state of reversed polarity. In a region of the cell membrane where an impulse or action potential is present, the cell membrane is said to be depolarized because its electrical polarity is outside-negative instead of outside-positive. In an excitable cell, by definition, after an action potential is generated at one point in the cell membrane, it propagates over the whole membrane. During this process, the region of depolarization moves along the cell membrane, and the membrane is said to "conduct" the impulse:

FIGURE 34.1 **Banjo Plucking Dramatizes the Speed of Neuronal Signaling** For each finger pluck, nerve impulses are generated in the brain and travel down the spinal cord and out to the finger that plucks the string. The entire process occurs several times per second.

An impulse or action potential is a state in which the polarity across the cell membrane is reversed.

The impulse or action potential moves along the cell membrane, in a process called conduction, or propagation.

This conduction, or propagation, is what happens when a neuron carries a signal from the brain to the fingers, telling the fingers to pull away from danger or to pluck a banjo string. We will discuss action potentials in more detail in Concept 34.2.

Nervous systems are composed of two types of cells, neurons and glial cells. The neurons are excitable, as we have said, but the glial cells typically are not.

Neurons are specialized to produce electric signals

A **neuron**, or nerve cell, is a cell that is specially adapted to generate electric signals, typically in the form of action potentials. Neurons are very diverse in structure. Here we describe just their most common features. Neurons often are highly elongated. Because of this, they can act like telephone wires ("land lines"), carrying signals (action potentials) rapidly over long distances.

Another way in which neurons resemble telephone wires is that their signals travel to specific destinations—that is, to anatomically defined destinations. A neuron typically must make contact with a target cell for signals in the neuron to affect the target cell directly. Thus, in most cases, cells must be contacted by a neuron to receive the neuron's signals. The signals, in essence, are addressed: they are received only at defined locations. In short, signal transmission by neurons is *fast* and *addressed*.

Places where neurons make functionally relevant contact with other cells are called synapses. More specifically, a **synapse** is a cell-to-cell contact point that is specialized for signal transmission from one cell to another. One of the two cells at a synapse is a neuron. The other can be another neuron, or it can be some other type of cell such as a sensory cell or muscle cell. Signal transmission at a synapse is usually one-way. A signal arrives at the synapse by way of one cell, called the **presynaptic cell**, and leaves by way of another, the **postsynaptic cell**.

Most neurons have four anatomical regions:

- a set of dendrites
- a cell body
- an axon
- a set of presynaptic axon terminals

We can also think of a neuron as having four functional regions, which generally correspond to the anatomical regions (**FIGURE 34.2**).

The **dendrites** (from the Greek *dendron*, "tree") are relatively short cell processes (extensions) that tend to branch from the cell body like twigs on a shrub. They are typically the principal sites where incoming signals arrive from other cells. Hundreds or thousands of other cells—neurons or sensory cells—may bring signals to a single neuron. These cells typically make synaptic contact with the dendrites or cell body.
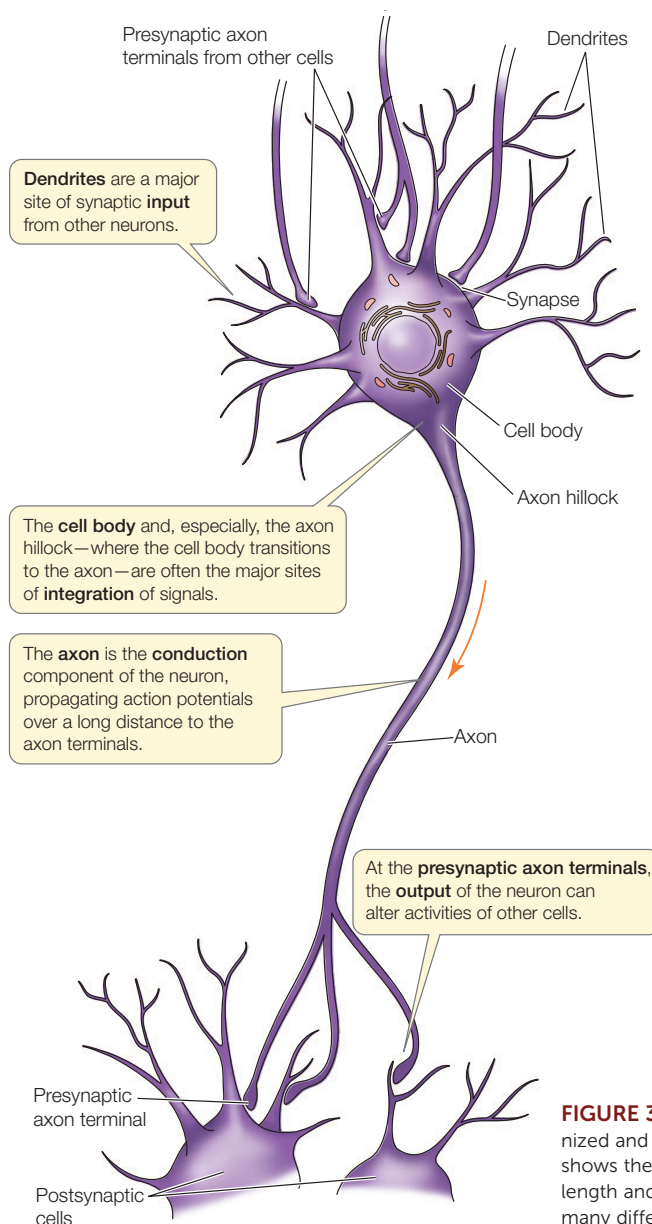
The **cell body** contains the nucleus and most of a neuron's other organelles. The most important function of the cell body is to combine and integrate incoming signals. Earlier we stressed that neurons achieve fast and addressed signal transmission. Of equal importance, neurons integrate signals. This means that a neuron can receive many inputs and combine them to produce a single output, and it can do this in ways that are adaptive and help promote harmonious function of the animal.

In most neurons, one cell process—the **axon**—is much longer than the others. The axon may extend a long distance. For instance, single axons extend from your spinal cord to your fingers. The axon is the part of a neuron that is anatomically specialized for long-distance signal conduction. Usually the signals (action potentials) conducted by the axon originate in or near the cell body and travel outward from the cell body.

Where the axon ends, it branches, and each of these branches terminates with a small swelling called a **presynaptic axon terminal**. These terminals make synaptic contact with other cells, enabling signals generated by the neuron to initiate signals in other neurons or in muscle cells. A neuron is said to **innervate** the cells with which its presynaptic axon terminals make synaptic contact.

A neuron, as we have stressed, is a single cell. Often the axons of many neurons travel together in a bundle from place to place, like a telephone cable composed of many wires. These bundles are called **nerves**. Individual neurons are far too small to be seen with the naked eye, but nerves consisting of many axons are often easily visible. Biologists use the term "nerve" only for axon bundles outside the brain and spinal cord. A bundle of axons in the brain or spinal cord is called a **tract** (or sometimes a commissure or connective).

Glial cells support, nourish, and insulate neurons

Glial cells, also called glia or neuroglia, are the second major type of cell in the nervous system. Unlike neurons, they typically are not excitable and do not conduct action potentials. Nonetheless, they are critically important. They are particularly numerous in mammals. Half the volume of the mammalian brain is glial cells, which are smaller than neurons and ten times more numerous than neurons.

Several distinct types of glial cells are present in the nervous system and play distinct roles. Certain glial cells help orient developing neurons toward their target cells during embryonic development. In adult vertebrates, glial cells in the brain and spinal cord provide metabolic support for neurons, help regulate the composition of the extracellular fluids bathing the neurons, and perform immune functions. Sometimes glial cells also assist signal transmission across synapses.

Presynaptic axon terminals from other cells

Dendrites

Dendrites are a major site of synaptic **input** from other neurons.

Synapse

Cell body

Axon hillock

The **cell body** and, especially, the axon hillock—where the cell body transitions to the axon—are often the major sites of **integration** of signals.

The **axon** is the **conduction** component of the neuron, propagating action potentials over a long distance to the axon terminals.

Axon

At the **presynaptic axon terminals**, the **output** of the neuron can alter activities of other cells.

Presynaptic axon terminal

Postsynaptic cells

FIGURE 34.2 A Generalized Neuron   Four *functional* regions of the cell are recognized and correspond approximately to the four major *anatomical* regions. The drawing shows the features typical of most neurons. The form of these features, including axon length and the density and branching pattern of dendrites, can vary greatly among the many different types of neurons.

(A)
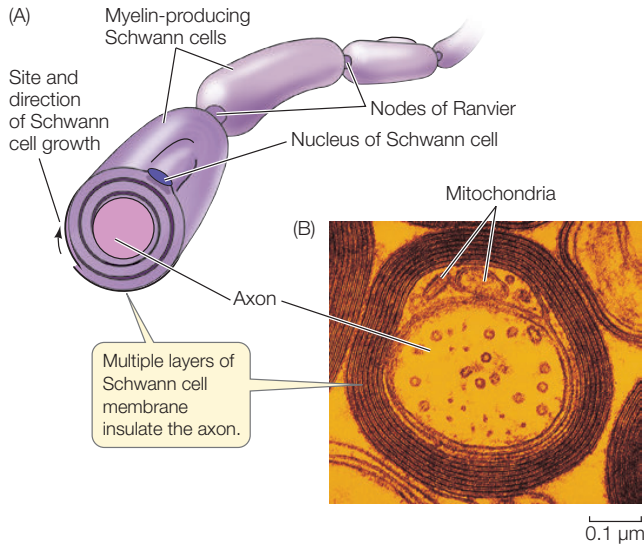
FIGURE 34.3 **Electrically Insulating an Axon** (A) Schwann cells wrap around the axon, enclosing the axon in many layers of lipid-rich Schwann cell membrane, called myelin, without intervening cytoplasm. Myelin provides electrical insulation to the axon. At the intervals between Schwann cells—the nodes of Ranvier—the axon is exposed. (B) A myelinated axon, seen in cross section at high magnification by use of an electron microscope.

In vertebrates, but generally not in invertebrates, certain glial cells insulate axons electrically by wrapping around them, covering them with concentric layers of lipid-rich cell membrane. In the brain and spinal cord, the cell membranes of glial cells called **oligodendrocytes** wrap around axons. In neurons outside the brain and spinal cord, glial cells of a different type, called **Schwann cells**, perform this function (**FIGURE 34.3**). This multilayered wrap of cell membranes on axons forms a lipid-rich, electrically nonconductive sheath called **myelin**. Parts of the nervous system that consist mostly of myelinated axons have a glistening white appearance and are sometimes called **white matter**. Not all vertebrate axons are myelinated, but those that are can conduct action potentials more rapidly than unmyelinated axons, as we will discuss in Concept 34.2.

CHECKpoint **CONCEPT 34.1**

✓ What is the most dramatic way in which typical neurons and typical glial cells differ functionally?

✓ Use a tape measure to measure the distance from your brain to the part of your spine at the same level as your shoulders, then measure the distance from that part of your spine to the tip of one of your index fingers. Estimate how fast action potentials would have to travel for you to pluck four strings on a guitar or banjo per second with your index finger. For simplification, assume that the action potentials merely need to travel the distance you've measured when your brain orders your finger to contract.

✓ What is meant when we say signals transmitted by a neuron are "addressed"?

We've now seen that nervous systems are composed of neurons and glial cells. In the next concept we will focus on how the neurons generate and transmit action potentials.

CONCEPT 34.2 **Neurons Generate Electric Signals by Controlling Ion Distributions**

The one feature common to all nervous systems is that they encode and transmit information in the form of action potentials. Some basic electrical principles help us understand how neurons produce action potentials and other electric signals. **Current** is a flow of electric charges from place to place. In a wire, electrons flow, and current is based on the flow of electrons. However, in the cells of organisms, current is based on the flow of ions in solution (see Concept 2.2), such as sodium ions (Na^+), potassium ions (K^+), or chloride ions (Cl^-). Each Na^+ ion, for example, bears a single positive charge. When Na^+ ions move from one place to another, positive charges flow, and this flow of charges is an electric current.

A **voltage**, also called an electric **potential difference**, exists if positive charges are concentrated in one place and negative charges are concentrated in a different place. Voltages *produce currents* because opposite charges attract and will move toward one another if given a chance. To illustrate, suppose positively charged ions are concentrated in one area and negatively charged ions are concentrated in another. Positive ions such as Na^+ will be attracted to and tend to flow toward the negative area, giving rise to a current.

Of all the background information that is helpful for understanding the electrical function of neurons, the locations where voltage differences can exist are most important.

- *No voltage differences exist from one place to another within open solutions such as the intracellular fluids of a cell.* In an open solution, positive and negative ions distribute themselves evenly so that there are no charge imbalances.

- *Voltage differences exist only across membranes such as the cell membrane.* A cell membrane is composed primarily of lipids (see Figure 5.1). Because ions have an electric charge, they tend to associate with water, not lipids, because water molecules are polar (see Concept 2.2). Moreover, the lipid molecules in a membrane, being hydrophobic, tend to associate with each other rather than with water or ions. Because of these principles, ions tend to remain in the aqueous solutions on either side of a membrane and do not readily cross the membrane. Consequently, positive ions may be concentrated on one side of a cell membrane while negative charges are concentrated on the opposite side.

Solutions that are not immediately in contact with a membrane are termed bulk solutions. We can summarize by saying that a bulk solution is electrically neutral and does not show charge differences from place to place, but a membrane may have a charge difference across it, caused by ion imbalances in the water immediately next to the membrane surfaces:

Within a few nanometers of the membrane on either side, net positive and negative charge concentrations may accumulate.

Farther away, in the bulk solution on either side, the net charge is zero.

Extracellular fluid

Bulk solution

Cell membrane (usually 6–8 nm thick)

Bulk solution

Cytoplasm
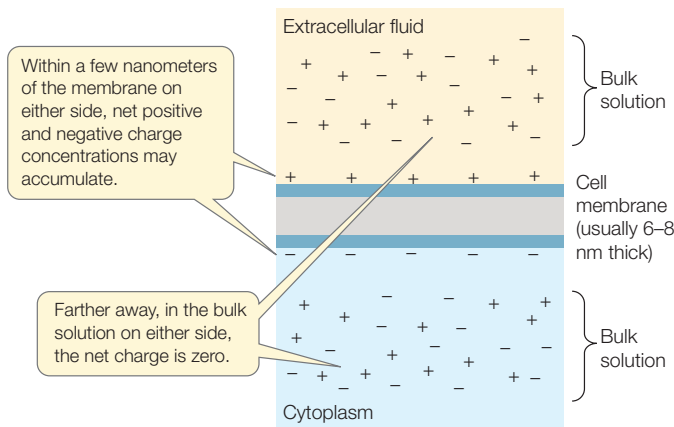
A voltage exists across a membrane that has a charge difference from one side to the other. This voltage (potential difference) is called the **membrane potential** and can be readily measured (**FIGURE 34.4**). A neuron is described as "resting" when it's not carrying a signal. In a resting neuron, the membrane potential is referred to as the **resting potential** and is typically between –60 and –70 millivolts (mV). The minus sign means that the inside of the cell is electrically negative relative to the outside. Membrane potentials are always written in this way: the sign (negative or positive) always refers to the charge inside relative to the charge outside.

Like other cell membranes, neuron cell membranes contain proteins that serve as ion transporters and channels (see Concept 5.2). Ions cannot pass through the membrane lipid bilayer, as we have just emphasized, and this permits charge differences to exist across a neuron cell membrane. However, ions can pass through the transporters and channels in the membrane. The transporter proteins and channel proteins determine the magnitudes and directions of the voltages and currents across the membrane.

Only small shifts of ions are required for rapid changes in membrane potential

As we talk in this chapter about the functions of neurons, we will often encounter cases in which rapid changes of the membrane potential are of critical importance. We need, therefore, to focus briefly on some key properties of these changes.

The membrane potential changes when ions are redistributed. During the rapid events of routine electrical signaling such as action potentials, ion redistribution occurs through membrane channel proteins. Channels are proteins that permit ions to cross the membrane by simple diffusion (see Concept 5.2).

Suppose that a membrane shifts from being negative on the inside to being positive on the inside. Suppose also that this change occurs because channels in the membrane allow a current of positive charges (ions) to flow inward across the membrane.

RESEARCH TOOLS

FIGURE 34.4 Measuring the Membrane Potential   An electrode can be made from a fine glass tube with a sharp tip filled with a solution that conducts electric charges. When such an electrode is inserted into an axon and another electrode is placed in the extracellular fluid just outside the axon, the difference in voltage across the axon cell membrane—called the membrane potential—can be measured.

Axon

3 The voltage difference between the electrode placed inside the axon and a reference electrode outside the axon is detected…

2 …and connected with a wire to an amplifier.

4 …and this small potential difference is displayed on a computer screen.

1 An electrode made from a glass tube (pulled to a sharp tip and open at the end) is filled with an electrically conducting solution…

Outside axon

Inside axon

Cell membrane

Outside axon

Inside axon

Outside axon

Amplifier

mV

0

–65

Time →

5 In an unstimulated neuron, a potential difference of about –65 mV is observed between outside and inside. This is the **resting potential**.

A critically important point is that only relatively small numbers of positive charges need to move through the membrane for this change of membrane potential to occur. This is true because only the charges within a few nanometers of the membrane surfaces are changing. Robert Schmidt and his colleagues once asked, Of all the ions within 1,000 nanometers of a membrane surface, what proportion are responsible for the membrane potential? Their answer was less than 100 out of every 1 million. Just a relatively few ions—positioned within a few nanometers of the membrane surfaces—are involved in rapid changes of membrane potential. The other ions, located in the bulk solutions on either side, are not directly involved.

Similarly, the current through the membrane moves only relatively small numbers of ions during rapid changes of membrane potential. The current is not changing the compositions of the bulk solutions: the compositions of the intracellular and extracellular fluids. A small current is sufficient to redistribute ions on the inner and outer membrane surfaces and lead to a large change in membrane potential—a phenomenon that is fundamental to how neurons generate signals.

Go to ANIMATED TUTORIAL 34.1
The Resting Membrane Potential
PoL2e.com/at34.1

The sodium–potassium pump sets up concentration gradients of Na$^+$ and K$^+$

One of the key membrane proteins is a transporter called Na$^+$-K$^+$-ATPase or the **sodium–potassium pump**. The protein goes through repeating cycles in which it actively transports ions. During each cycle, it uses the energy of an ATP molecule to expel three Na$^+$ ions from inside the neuron and to pump two K$^+$ ions into the neuron from the outside. Na$^+$ and K$^+$ are the principal positive ions in both the intracellular and extracellular fluids.

> **LINK**
>
> For more on the sodium–potassium pump see **Concept 5.3**

The sodium–potassium pump creates steady ion concentration differences between the intracellular and extracellular fluids. Because of it, the concentration of Na$^+$ is higher in the bulk fluids outside the neuron than inside, and the K$^+$ concentration is higher in the bulk fluids inside than outside.

The resting potential is mainly a consequence of K$^+$ leak channels

What is the cause of the resting potential? This voltage difference is principally the result of K$^+$ channels that are open all the time. As we have seen, K$^+$ is more concentrated inside a neuron than outside. Some (fewer than half) of the K$^+$ channels—channels that specifically permit K$^+$ to diffuse through the neuron cell membrane—are always open. They are like little holes in a bucket. Much as holes let water leak out of a bucket, these open channels let K$^+$ leak out of a neuron. K$^+$ diffuses out through these channels because of the K$^+$ concentration gradient (a higher K$^+$ concentration inside than outside).

This diffusion of K$^+$ (positive charges) out of a neuron leaves behind unbalanced negative charges inside the neuron. These negative charges tend to pull K$^+$ back into the cell because of the attraction of positive and negative charges. Remember that the charges we are discussing are positioned on the membrane surfaces. As K$^+$ leaks out, positive K$^+$ charges accumulate on the outer surface of the cell membrane. At the same time, unbalanced negative charges accumulate on the inner membrane surface. In this way, a voltage difference is created across the cell membrane.

In a resting neuron, K$^+$ is freer to cross the membrane than other ions because the channels for other ions are mostly closed. As a useful approximation, we can assume that only K$^+$ crosses. K$^+$ ions diffuse out through K$^+$ leak channels until the voltage difference—negative on the inside—pulls K$^+$ back inside with exactly the same force as the concentration gradient drives K$^+$ out. At this equilibrium point, K$^+$ stops moving through the membrane. There is no further net movement of K$^+$. The membrane potential in this equilibrium state is called the **equilibrium potential** of K$^+$. Simply put, if K$^+$ is the only ion that is free to diffuse across the cell membrane in a resting neuron, its diffusion drives the cell's membrane potential toward the K$^+$ equilibrium potential, which is the voltage difference that will draw K$^+$ into the cell to the same degree as the high inside K$^+$ concentration makes K$^+$ diffuse out.

The Nernst equation predicts an ion's equilibrium potential

Let's now look at the general principles that are exemplified by K$^+$ diffusion in a resting neuron. These are the principles of electrochemical equilibrium. The principles are easiest to understand when the channels for only one ion are open and, as a result, only one ion can diffuse across the membrane. When these conditions exist, we can say that the membrane is permeable to just the one ion.

Suppose the concentration of an ion is different on one side of a membrane than the other, and suppose also that one side is more positive than the other. In this case there will be two effects on ion diffusion. There will be a *concentration effect* on diffusion: the ion will tend to diffuse across the membrane from the side of high concentration to the side of low concentration. There will also be an *electrical effect* on diffusion: the ion will tend to diffuse across the membrane because of electrical attraction, moving toward the side where the charge on the cell membrane is opposite to the ion's charge. As the ion diffuses across the membrane, its diffusion will modify both effects by changing the electric charge difference and concentration difference across the membrane.

Ion diffusion across the membrane will continue until the concentration effect and electrical effect become equal and opposite. This is the state of **electrochemical equilibrium**: a state in which the electrical effect causes diffusion in one direction and the concentration (chemical) effect causes diffusion of equal magnitude in the opposite direction. When an ion has reached electrochemical equilibrium, there is no net diffusion of the ion across the membrane in either direction:
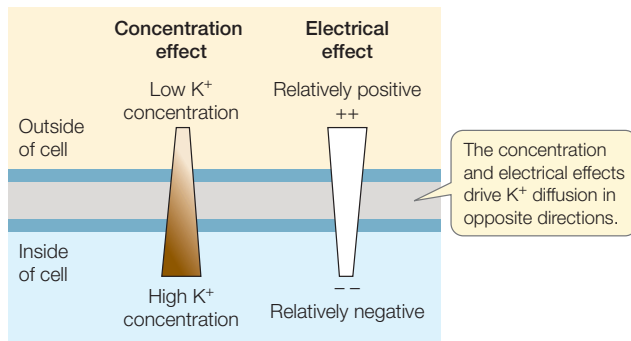
In studies of neurons, the electric potential difference at electrochemical equilibrium is usually called the equilibrium potential of the ion and is symbolized E_{ion}. This potential can be calculated from the ion concentrations inside and outside the cell membrane by use of a famous equation called the **Nernst equation**.

Expressions with brackets represent concentrations. Thus "[ion]" represents the concentration of the ion of interest.

$$\text{Potential difference at electrochemical equilibrium} = E_{ion} = 2.3\frac{RT}{zF}\log\frac{[ion]_{outside}}{[ion]_{inside}}$$

In this equation, z is the number of charges per ion, T is the absolute temperature, R is a constant (the universal gas constant), and F is another constant (the Faraday constant).

Go to ACTIVITY 34.1 The Nernst Equation
PoL2e.com/ac34.1

The Nernst equation can be used whenever we can assume that only a single ion is able to diffuse across a membrane. In such cases, the equation predicts the equilibrium membrane potential. For example, we have already said that in a resting neuron, just one ion, K^+, can readily cross the cell membrane because the open channels are mostly K^+ channels. Under these circumstances, K^+ is expected to diffuse to electrochemical equilibrium, and this diffusion is expected to determine the membrane potential. Taking account of the concentrations of K^+ inside and outside the cell, the K^+ equilibrium potential, E_K, calculated with the Nernst equation is about –85 mV, depending on temperature. The actual neuron resting potential, as we have said, is close to this, about –65 mV. The principal reason the equation's prediction is a little off is that resting neurons are slightly permeable to other ions besides K^+.

As we will see, the Nernst equation can be applied to any ion, not just K^+, and helps explain each of the major phases of an action potential. It can be used, in an approximate way, to calculate the equilibrium membrane potential whenever just one ion accounts for most diffusion across the membrane and other ions are diffusing to just a minor extent.

Ion distributions across nerve cell membranes are not always at equilibrium. In fact, they sometimes are far from equilibrium. In such cases, ions will move toward equilibrium. The principles of electrochemical equilibrium are then useful for predicting the direction of ion diffusion.

Gated ion channels can alter the membrane potential

Instead of being open all the time like the K^+ leak channels, most ion channels behave as if they contain gates: they are open under some conditions and closed under others. The channels for ions other than K^+ are gated channels for the most part. And even most K^+ channels are gated. Most gated channels are closed in a resting neuron, explaining why the K^+ leak channels determine the resting membrane potential.

We categorize gated channels on the basis of the agent that causes them to open or close (**FIGURE 34.5**):
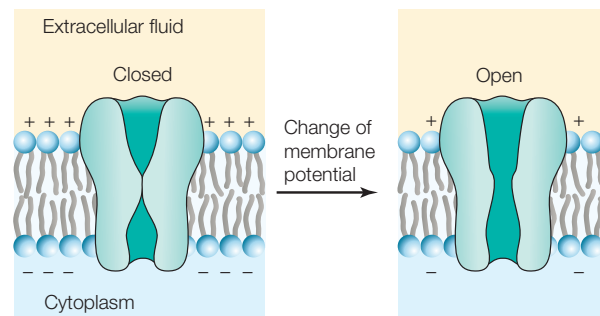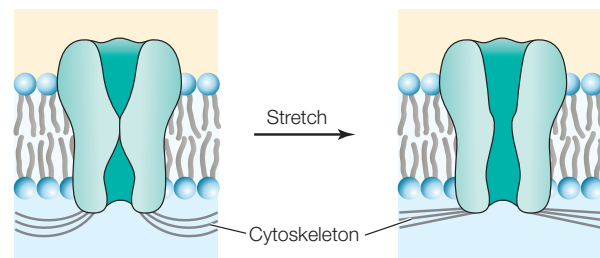
- **Voltage-gated channels** open or close in response to local changes in the membrane potential.
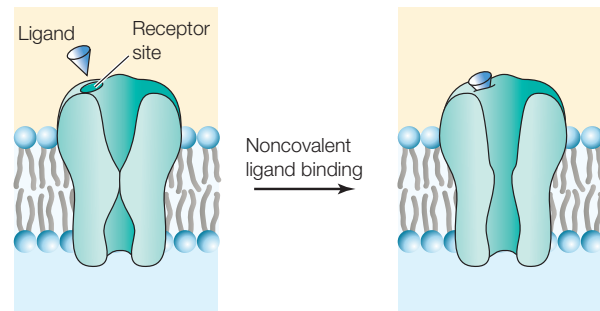
FIGURE 34.5 Three Types of Gated Ion Channels

- **Stretch-gated channels** open or close in response to stretch or tension applied to the cell membrane.
- **Ligand-gated channels** have binding sites where they bind noncovalently with specific chemical compounds that control them. A compound that controls a channel is termed a ligand of that channel. A ligand-gated channel opens and closes depending on whether it is bound to its ligand. Although Figure 34.5C shows a ligand-binding site on the outside of the cell membrane, binding sites (e.g., for second messengers) can also be on the inside.

Openings and closings of gated channels alter the membrane potential. For example, let's consider what happens in a resting neuron if some of the Na^+ channels in the cell membrane open (Na^+ channels are ordinarily closed in a resting neuron). If Na^+ channels open, Na^+ ions diffuse into the neuron from the outside. This is true because Na^+ is far from electrochemical equilibrium in a resting neuron. Na^+ is far more concentrated outside the cell than inside, and this concentration difference tends to drive diffusion into the cell. The electrical difference also tends to drive Na^+ diffusion into the cell because the cell membrane is negative on the inside in a resting neuron, attracting positive ions. The inward diffusion of Na^+—caused by both concentration and electrical effects—represents an inward flow of positive charges which makes the inside of the neuron cell membrane become less negative. In other words, the voltage difference across the membrane (the membrane potential)—which is ordinarily near –65 mV in a resting neuron—becomes smaller. Perhaps it becomes –60 mV instead of –65 mV.

Depolarization is said to occur whenever the charge on the inside of a neuron cell membrane becomes less negative—relative to the charge on the outside—than it is at rest. In Concept 34.1 we implied that depolarization is either present or absent. Actually, varying degrees of depolarization can occur.

Hyperpolarization can also take place. It occurs whenever the charge on the inside becomes *more* negative. Opening and closing of gated ion channels can cause either depolarization or hyperpolarization, depending on which ions are affected.

Changes in membrane potential can be graded or all-or-none, depending on whether a threshold is crossed

Two types of changes in membrane potential occur: graded and all-or-none. The type of change that occurs depends on whether a voltage threshold of about –50 mV is crossed. We will start by discussing graded changes.
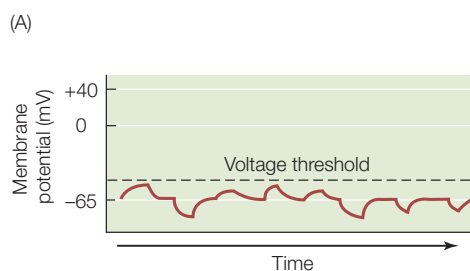
FIGURE 34.6A shows variations in membrane potential over time in a neuron in which the voltage threshold is not crossed. Note that the membrane potential can be high, low, or in between. These changes are described as **graded** because any value of the membrane potential is possible. The changes are caused by various gated ion channels opening or closing—some causing the membrane potential to shift in one direction, some causing it to shift in the other direction.

Graded changes of the membrane potential spread only a short distance from the locations of the ion channels that cause them. If a set of Na^+ channels opens, for example, the change in membrane potential will be greatest at the location along the cell membrane where the channels are found. The change will spread on either side. But it will become smaller and smaller at greater and greater distances from the channels:
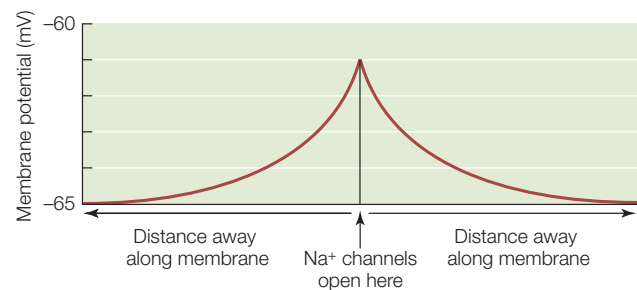
Let's now discuss all-or-none changes in the membrane potential. If a neuron depolarizes to the point that its inside charge is within about 50 mV of the outside charge, a massive, all-or-none event occurs: an impulse, or action potential, is triggered (**FIGURE 34.6B**). A membrane potential of about –50 mV is thus the voltage threshold for an action potential. An action potential is described as all-or-none because, when it occurs, it is always the same size. Action potentials are not graded. Moreover, as we'll soon discuss, an action potential does not become smaller and smaller as it moves away from the location on a cell membrane where it originates. It stays the same in size as it propagates along the cell membrane of the axon of the neuron.

FIGURE 34.6 Graded and All-or-None Changes in Membrane Potential (A) Graded changes in membrane potential may not reach the voltage threshold. (B) When graded changes in membrane potential reach the voltage threshold, the membrane generates a large all-or-none change in membrane potential—the action potential.

This graded potential is depolarized almost to threshold, but any depolarization less than threshold is inadequate.

This graded potential reaches the voltage threshold, triggering changes in ion channel gating that…

…produce an action potential.
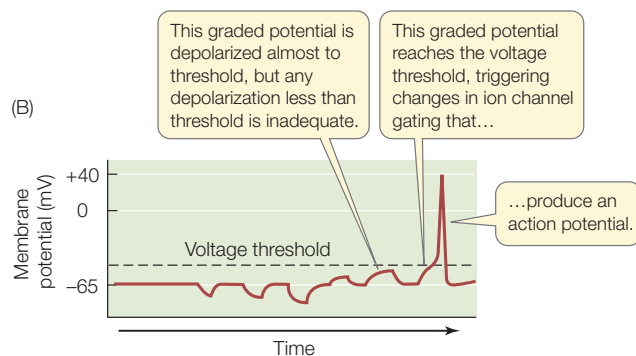
Graded changes give rise to all-or-none changes when the voltage threshold is crossed, and this interaction between the two types of changes provides one of the most important mechanisms by which a neuron carries out integration. Graded changes in membrane potential at a single location in the cell membrane add together. Suppose, for example, that a neuron simultaneously receives four signals—A, B, C, and D—that affect different types and numbers of gated ion channels in the neuron cell membrane, producing graded changes in the membrane potential. Suppose that at a particular spot on the cell membrane, signal A causes a 2.5-mV depolarization, B causes a 1.5-mV depolarization, C causes a 1-mV hyperpolarization, and D causes a 1-mV depolarization. All these graded changes in the membrane potential sum together. Thus at this particular spot, the membrane potential will be depolarized by 4 mV. It will be –61 mV instead of –65 mV as at rest.

The spot of greatest importance for this type of integration in a neuron is the axon hillock, where the axon arises from the cell body (see Figure 34.2). This is the spot where action potentials are most commonly initiated. A neuron may be receiving hundreds or thousands of signals at its dendrites and cell body. These signals bring about graded changes in membrane potential that spread to the axon hillock, where all the depolarizations and hyperpolarizations sum.

As this summation occurs, if the membrane potential at the axon hillock varies only in the range below about –50 mV, as in Figure 34.6A, no action potentials are produced. Moreover, no electric signals reach the axon terminals because the graded potentials disappear over the distance between the axon hillock and the axon terminals.

However, as the summation of graded potentials occurs, if the membrane potential at the axon hillock crosses the threshold as at the right in Figure 34.6B—that is, if it becomes –50 mV or even more depolarized—the axon hillock initiates an action potential. This action potential travels to the axon terminals, and the axon terminals then send signals to the other cells they innervate.

These processes are the major means by which a single neuron integrates its inputs to determine its outputs. In short, all the inputs create small, graded changes of membrane potential that sum together as they spread. If their integrated effect is a membrane potential that is not as depolarized as about –50 mV, the neuron produces no action potentials. But if their integrated effect is a membrane potential that is depolarized to at least –50 mV, the neuron generates one or more action potentials that propagate long distances down the axon.

An action potential is a large depolarization that propagates with no loss of size

An **action potential**, or **nerve impulse**, is a large, brief, localized change in the membrane potential—so large that the polarity reverses from inside-negative to inside-positive. During an action potential, the membrane depolarizes from –65 mV at rest to about +40 mV: a change of more than 100 mV. This event is extremely brief. It lasts only about 1 millisecond. It is also very localized: it is restricted to just a small region of the cell membrane.

An action potential propagates with no loss of size, however. Propagation occurs because an action potential at one location in the cell membrane of a neuron causes currents to flow that depolarize neighboring regions to the voltage threshold. When an action potential occurs in the axon hillock, currents flow into the neighboring region of the axon that is closer to the axon terminals, causing a graded depolarization there that is great enough that threshold is reached. That region then produces an action potential. Currents from that action potential then spread into the axon region still closer to the axon terminals. That region then produces an action potential. Each region of the axon stimulates the next region to produce an action potential until the action potential reaches the axon terminals. This process is what is meant by "propagation" in discussions of neuron function. Recall that action potentials are all-or-none and always the same size. Thus there is no loss of magnitude as an action potential propagates along the length of an axon.

Why does the cell membrane depolarize so profoundly during an action potential? And why does this depolarization end so quickly—within a millisecond? The properties of voltage-gated K^+ and Na^+ channels in the neuron cell membrane are chiefly responsible.

When the membrane potential in any local region of an axon reaches threshold, massive numbers of voltage-gated Na^+ channels in that region quickly open. Suddenly, therefore, the principal ion that can cross the membrane becomes Na^+, instead of K^+. This results in a sudden, rapid influx of Na^+ ions into that part of the axon because, as we discussed earlier, both the Na^+ concentration difference and the electrical difference across the cell membrane favor inward Na^+ diffusion. If Na^+ were the only ion that could cross the membrane at this stage and if enough time were available to reach electrochemical equilibrium, the membrane potential would become E_{Na}—the equilibrium potential for Na^+ (about +50 mV according to the Nernst equation). The membrane potential in fact almost reaches E_{Na}: it typically becomes about +40 mV (**FIGURE 34.7**, transition from A to B). Quickly, however, the Na^+ channels close, and voltage-gated K^+ channels, which respond in a delayed fashion to the local membrane potential, open in massive numbers. With the Na^+ channels closed and the voltage-gated K^+ channels open, the principal ion that can cross the membrane becomes K^+. K^+ diffuses out of the cell because K^+ is more concentrated inside than outside and also because, at this moment (with the membrane potential at +40 mV), the outside of the cell membrane is relatively negative, attracting K^+. The movement of K^+ out of the cell drives the membrane potential back toward –65 mV, which is close to E_K, the K^+ equilibrium potential (Figure 34.7C).

Positive feedback (see Concept 29.6) plays a major role in the depolarization phase of an action potential (**FIGURE 34.8**). Positive feedback occurs because the Na^+ channels are voltage-gated and the voltage across the neuron cell membrane is rapidly changing. When the cell membrane becomes partly depolarized, some voltage-gated Na^+ channels open. Na^+ ions then cross the cell membrane faster (diffusing from outside to inside) and depolarize the membrane even more. This greater depolarization causes more voltage-gated Na^+ channels to

(A) Resting membrane potential
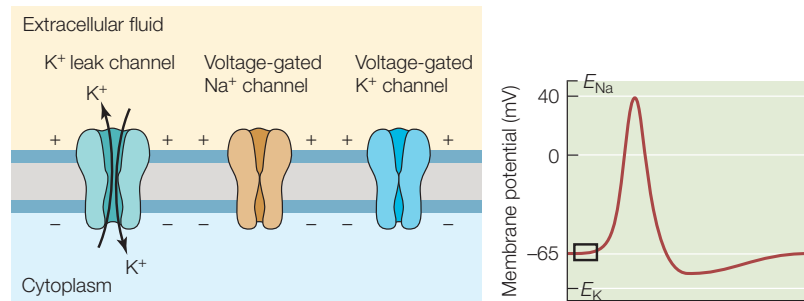
(B) Rising phase of action potential
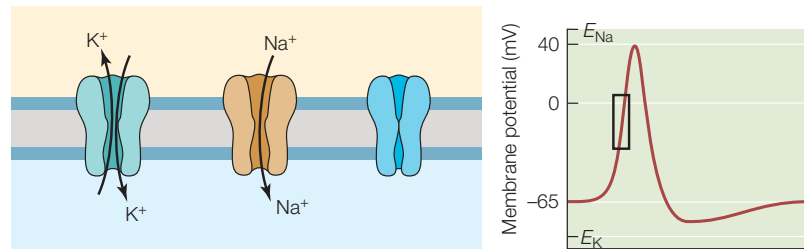
(C) Falling phase of action potential
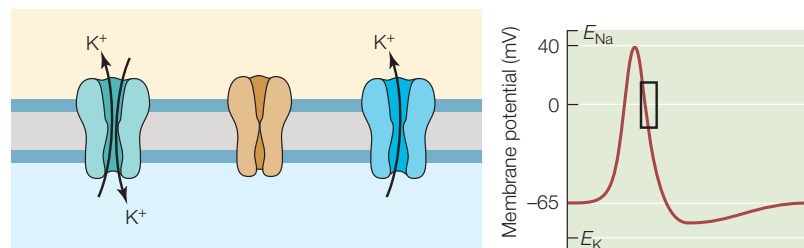
FIGURE 34.7 Production of an Action Potential
The diagrams to the left show changes in voltage-gated Na^+ and K^+ channels, and those on the right show changes in membrane potential during (A) rest, (B) the rising phase of an action potential, and (C) the falling phase. The black rectangles on the membrane potential curves indicate the part of the curve during which the events diagrammed at left occur. The closing of the Na^+ channels in (C) is of a specialized type (called inactivation) that cannot be reversed (i.e., the channels cannot reopen) for a brief period. K^+ leak channels are always open.

Go to ANIMATED TUTORIAL 34.2
The Action Potential
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open. This positive-feedback loop continues until all the voltage-gated Na^+ channels open and maximum depolarization (approaching E_{Na}) occurs.

Why does an action potential travel in just one direction along an axon? After any particular local part of the axon membrane has produced an action potential, it undergoes a brief refractory period during which it cannot produce another action potential. Thus as an action propagates along an axon, the region of the cell membrane just behind it is in its refractory period. Currents are able to induce an action potential only in the neighboring region in the direction of the axon terminals.

Action potentials travel particularly fast in large axons and in myelinated axons

Action potentials do not travel along all axons at the same speed. Because of physical laws, they tend to travel faster in large-diameter than in small-diameter axons. This principle has been particularly important in the evolution of invertebrate nervous systems. Many invertebrates have evolved axons of large diameter that increase the speed of conduction of action potentials to muscles on which the animals depend for
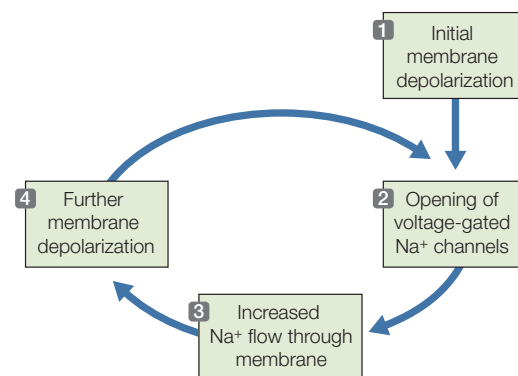
FIGURE 34.8 Positive Feedback Plays a Key Role in the Generation of an Action Potential During the rising phase of an action potential, positive feedback progressively drives all voltage-gated Na^+ channels to open.

rapid escape from danger. In squid, for example, the muscle cells used for escape swimming are innervated by giant axons that in some cases are 1 millimeter in diameter. These giant axons are relatively easy to manipulate and study. Many of the basic principles of neuron function were discovered by studying them.

Vertebrates have evolved an additional means of increasing the speed of conduction: myelination. When glial cells wrap around axons, covering them with myelin, they leave uncovered spaces, called **nodes of Ranvier**, in between (see Figure 34.3). In a myelinated axon, action potentials are generated only at the nodes of Ranvier, because voltage-gated ion channels are clustered at these nodes and also because the myelin-covered axon segments are too well insulated electrically to permit rapid ion fluxes (flows) across the cell membrane. As an action potential travels along a myelinated axon, it jumps from one node of Ranvier to the next, a process called saltatory ("jumping") conduction. For an axon of any particular diameter, an action potential travels far faster by saltatory conduction than it would by continuously traveling the entire length of the axon membrane:
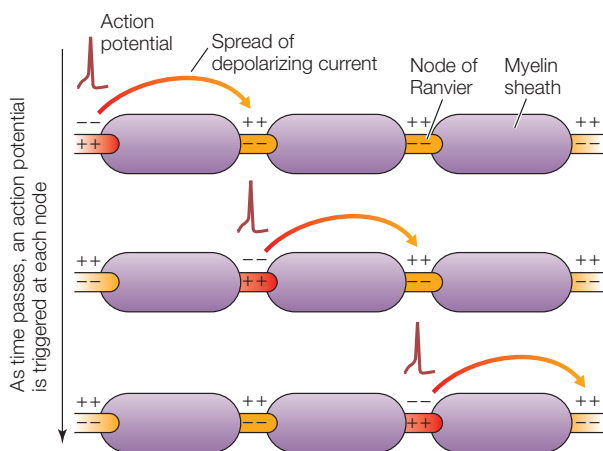
CHECKpoint CONCEPT 34.2

✓ What are the major differences in size and transmission between a graded potential and an action potential?

✓ What are two different evolutionary adaptations to speed the conduction of action potentials?

✓ Suppose the inner surface of a neuron cell membrane changes from being 60 mV more negative than the outer surface to being 50 mV more negative. Is the neuron closer to producing an action potential or farther from doing so? Explain.

Now that we have described how an action potential is generated and propagated along an axon, we will address the question of what happens when the action potential arrives at the axon terminal. How is the information communicated to the next cell?

CONCEPT 34.3 Neurons Communicate with Other Cells at Synapses

Recall that synapses are cell-to-cell contact points that are specialized for signal transmission from one cell to another. They play extremely important roles in information processing and integration. They also play central roles in learning and memory. A great deal of modern research on the function of the nervous system focuses on synapses.

Chemical synapses are most common, but electrical synapses also exist

The most common type of synapse is termed a **chemical synapse** because signals pass from cell to cell by means of molecules ("chemicals") released by the presynaptic cell. At a chemical synapse, the cell membranes of the pre- and postsynaptic cells are actually separated by an extremely narrow space, about 20–30 nm wide, termed the synaptic cleft. Action potentials cannot cross this space (although the space is bridged by occasional trans-synaptic protein molecules). When an action potential arrives at the end of the presynaptic cell, that cell releases a compound called a **neurotransmitter** into the synaptic cleft, and the neurotransmitter crosses the cleft. Acetylcholine is an example of a neurotransmitter:
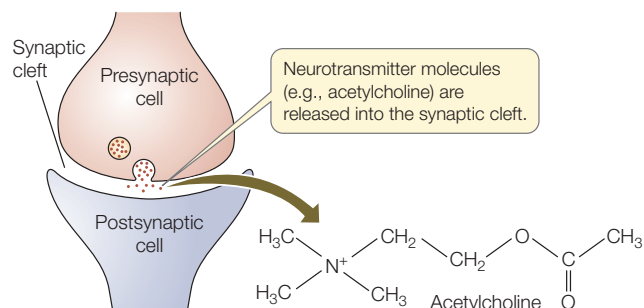
Neurotransmitter molecules diffuse across the synaptic cleft very rapidly because the distance is extremely short. The molecules then bind to receptor proteins in the cell membrane of the postsynaptic cell. These receptor molecules are specialized to generate an electrical change or some other sort of change when they bind to neurotransmitter molecules—completing signal transmission across the synapse. In many cases, the entire process of synaptic signal transmission takes just a few milliseconds.

Neurotransmitter molecules are rapidly removed from the synaptic cleft after they have been released into it by the presynaptic cell. Removal terminates the signal and is essential for the proper function of chemical synapses. Removal may occur by two principal mechanisms. The neurotransmitter molecules may be enzymatically broken down, or they may be taken up by nearby neurons or glial cells. In some well-known cases, neurotransmitter molecules are removed from the synapse by reuptake into the presynaptic cell.

In an **electrical synapse**, signal transmission is "all electrical" instead of employing a neurotransmitter. At such a synapse, the cell membranes of the pre- and postsynaptic cells are

joined by gap junctions at which the cytoplasms of the two cells are continuous (see Figure 4.18). Thus when an action potential arrives in the presynaptic cell, it can spread easily and directly to the postsynaptic cell. Signals cross electrical synapses with essentially no delay.

Electrical synapses have evolved principally where very fast, invariant signal transmission is advantageous. They are found in neurons that control escape swimming in some fish and crustaceans. They are also found in some tissues where great numbers of cells must be stimulated synchronously to act together, such as fish electric organs (see Concept 33.4).

The vertebrate neuromuscular junction is a model chemical synapse

Each muscle cell (muscle fiber) in a vertebrate skeletal muscle is typically innervated by one neuron, called a motor neuron. A muscle such as your biceps contains thousands of muscle cells, and many neurons are involved in innervating the whole muscle. However, each muscle cell is typically innervated by just one neuron, and the muscle cell will contract only if stimulated to do so by that neuron.

A **neuromuscular junction**—a type of chemical synapse—is a synapse between a motor neuron and a skeletal muscle cell (**FIGURE 34.9A**). This type of synapse, sometimes called a motor end-plate, has been studied intensively to understand how chemical synapses work. It is not entirely representative of all chemical synapses because it is specialized for a one-to-one relationship between nerve impulses and muscle contractions: each action potential in the presynaptic neuron depolarizes the postsynaptic (muscle) cell to threshold and produces an action potential in the postsynaptic cell. Chemical synapses in the brain do not operate this way, as we will discuss later in this chapter.

At a neuromuscular junction, the axon of the presynaptic neuron branches close to the muscle cell, creating several buttonlike axon terminals (called boutons) that are in synaptic contact with the muscle cell (**FIGURE 34.9B**). Each of these axon terminals contains spherical synaptic vesicles filled with molecules of acetylcholine (ACh), the neurotransmitter used by all vertebrate neuromuscular junctions (**FIGURE 34.9C**).

When an action potential arrives at an axon terminal, the terminal releases ACh into the synaptic cleft by a mechanism that depends on voltage-gated calcium channels. The action potential causes Ca^{2+} channels in the presynaptic membrane to open (see Figure 34.9C, step 1). Ca^{2+} diffuses into the axon terminal through the open channels because the concentration of Ca^{2+} is greater outside the cell than inside (step 2). Increased Ca^{2+} inside the terminal induces synaptic vesicles to fuse with the presynaptic membrane, releasing ACh into the synaptic cleft by exocytosis (step 3; see Figure 5.8B).
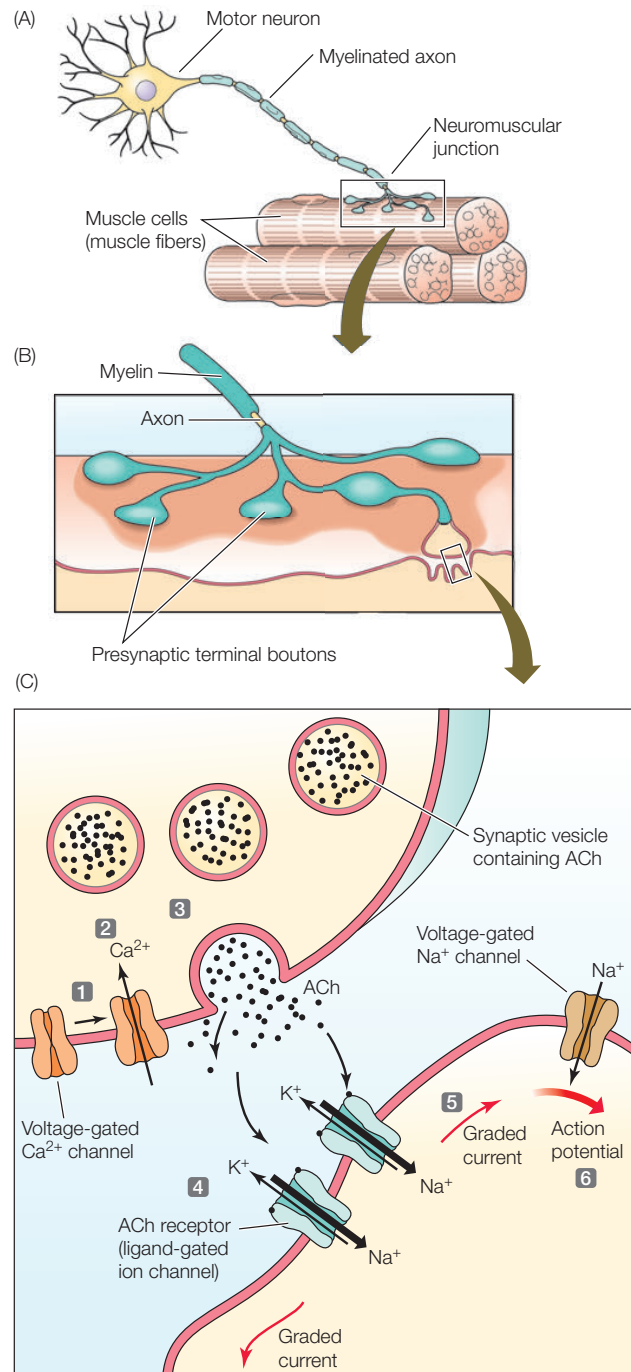
FIGURE 34.9 Synaptic Transmission at a Vertebrate Neuromuscular Junction   (A, B) A motor neuron communicates with a skeletal muscle cell at a neuromuscular junction. (C) The motor neuron releases acetylcholine (ACh) into the synaptic cleft, stimulating an action potential in the muscle cell.

Go to ANIMATED TUTORIAL 34.3
Synaptic Transmission
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Go to ANIMATED TUTORIAL 34.4
Neurons and Synapses
PoL2e.com/at34.4

Go to MEDIA CLIP 34.1
Put Some ACh Into It!
PoL2e.com/mc34.1

APPLY THE CONCEPT

Neurons communicate with other cells at synapses

How do we know that Ca^{2+} influx into the presynaptic neuron ending causes the release of neurotransmitter? The squid giant axon and its neuron endings are a convenient system for experiments because they are so large, making it possible to inject substances into the presynaptic cell at a synapse. Some of the substances that can be injected are Ca^{2+} ions and BAPTA, a substance that binds Ca^{2+} ions. Shown below are the results of a series of experiments using these substances.
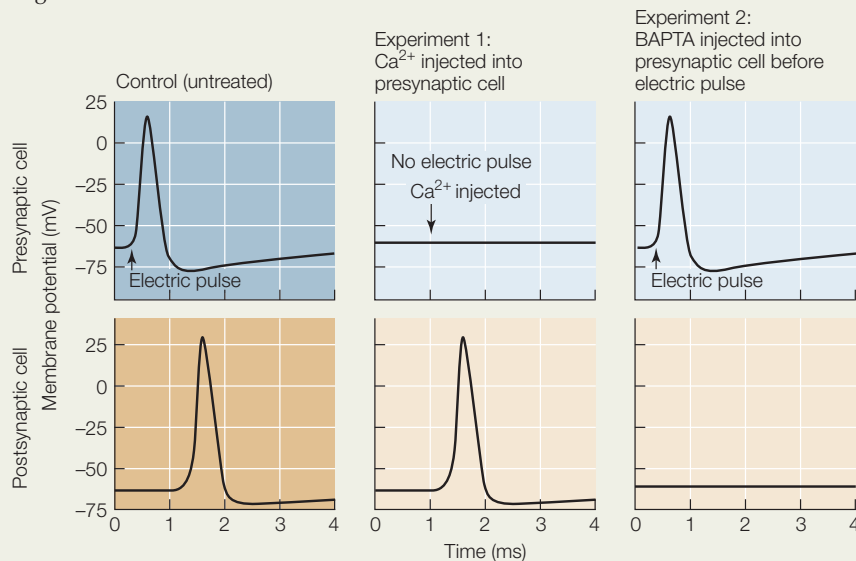
1. What is happening during the delay between the pre- and postsynaptic membrane events in the control condition?

2. Explain the postsynaptic response in the absence of a presynaptic electric signal in experiment 1.

3. Explain why there is a presynaptic but no postsynaptic response in experiment 2.

Many neurotransmitters are known

Several dozen neurotransmitters are now known, and more are being discovered all the time. They fall into three major chemical categories:

The response of the muscle cell depends on ligand-gated receptors in the postsynaptic cell membrane at the synapse (see Figure 34.5C). These receptors, which are gated by ACh, act as ion channels when they are open. When ACh is released into the synaptic cleft, it binds to the ACh-gated receptor proteins (step 4). These receptors open, allowing Na^+ and K^+ to diffuse through. Influx of Na^+ is dominant because of the locally prevailing ion and electrical gradients. The rapid influx of Na^+ causes a large, graded depolarization, which induces graded ionic currents that spread to neighboring regions of the postsynaptic membrane (step 5) where there are voltage-gated Na^+ and K^+ channels. The depolarization in these neighboring regions is great enough to exceed the threshold of the voltage-gated ion channels, setting off an action potential (step 6). This action potential is propagated throughout the cell membrane of the muscle cell, and it propagates into the cell's transverse tubules (T tubules), activating contraction.

- *Amino acids* that serve as neurotransmitters include glutamate, glycine, and γ-aminobutyric acid (GABA; γ = gamma).

- *Biogenic amines* include acetylcholine and also dopamine, norepinephrine, and serotonin.

- A variety of *peptides* (strings of amino acids) serve as neurotransmitters.

Each presynaptic neuron produces specific neurotransmitters. Some produce only one, and others produce two or more, but all presynaptic neurons are specific in the neurotransmitters they release. For simplicity, we'll assume as we go forward that each neuron releases one neurotransmitter.

Let's now consider a neuron that is functioning as the postsynaptic cell. In the brain, a postsynaptic neuron may have chemical synapses with hundreds or thousands of presynaptic neurons (**FIGURE 34.10**). Each of these neurons will use one neurotransmitter. However, different neurons may use different neurotransmitters. Collectively, the hundreds or thousands of presynaptic cells may use dozens of neurotransmitters.

LINK

The physical and molecular interactions of muscle contraction are described in **Concept 33.1**
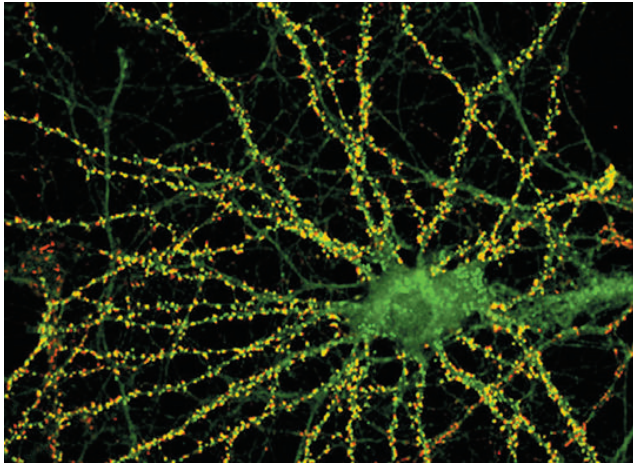
FIGURE 34.10 Synapses on a Single Postsynaptic Neuron in the Brain of a Mouse This image shows the cell body and many dendrites of a single neuron, labeled green. Synapses on the neuron are yellow. The synapses were labeled red, but the combination of green and red produces yellow at most synapses.

Moreover, the receptor proteins *for any particular neurotransmitter* in the cell membrane of the postsynaptic cell may be of two or more molecular types that have different actions. The action of a neurotransmitter at any particular synapse ultimately depends on the action of the specific receptor to which it binds there.

This complexity in synapse function helps us understand how brain function can be as complex as it is. The model chemical synapse we discussed, the neuromuscular junction, employs one neurotransmitter and one type of receptor. Modern brain scientists, however, seek to understand neurons that have great numbers of synapses that function with a variety of neurotransmitters, and often with a variety of receptor proteins for any given neurotransmitter.

Synapses can be fast or slow depending on the nature of receptors

Two broad classes of neurotransmitter receptors are recognized. These are fast, ionotropic receptors and slow, metabotropic receptors.

Ionotropic receptors are ligand-gated ion channels similar to the ACh receptor in the vertebrate neuromuscular junction. Neurotransmitter binding to an ionotropic receptor directly causes a fast, short-lived change in ion diffusion across the cell membrane of the postsynaptic cell. In this way it can directly cause an immediate change in the local membrane potential. This change may in turn initiate other changes in the postsynaptic cell.

Metabotropic receptors are not ion channels. Instead, they are commonly G protein–linked receptors (see Figure 5.14). Such receptors often exert their effects by controlling production of second messengers such as cyclic adenosine monophosphate (see Figure 5.17). Recall that second messengers carry messages to the interior of a cell, where they can exert controlling effects on a wide variety of cell mechanisms, and even on gene expression. Postsynaptic cell responses

mediated by metabotropic receptors are very diverse and are often slow and long-lived.

> **LINK**
>
> The structure and properties of G protein–linked receptors and the cellular responses they activate are described in **Concepts 5.5 and 5.6**

Fast synapses produce postsynaptic potentials that sum to determine action potential production

In Concept 34.2 we discussed the fact that graded depolarizations and hyperpolarizations of a cell membrane sum together to determine if the voltage threshold for action potential production is reached. This process is a key mechanism by which single neurons integrate their inputs. Let's now review the process with specific information on synaptic function.

At neuron-to-neuron synapses, when a postsynaptic ligand-gated ion channel opens, the change caused in the membrane potential of the postsynaptic cell is usually less than 1 mV! This is very different from what happens at a neuromuscular junction. The neuromuscular junction is specialized so that each presynaptic nerve impulse depolarizes the postsynaptic cell sufficiently for an action potential to be generated. Neuron-to-neuron synapses, by contrast, are specialized so that each presynaptic impulse produces just a fast, small, short-lived postsynaptic effect. The exact nature of the effect depends on the neurotransmitter employed and on the receptor protein, including which ion fluxes are altered.

- Synapses that depolarize the postsynaptic membrane are called **excitatory synapses**. They are so named because depolarization shifts the membrane potential toward the threshold for action potential production, increasing the likelihood that an action potential will be triggered. Excitatory synapses produce graded membrane depolarizations called **excitatory postsynaptic potentials** (**EPSPs**).

- Synapses that shift the membrane potential away from threshold are called **inhibitory synapses** because they lower the likelihood of action potential production. Inhibitory synapses produce graded membrane hyperpolarizations called **inhibitory postsynaptic potentials** (**IPSPs**).

Each individual EPSP or IPSP, produced at a single time by a single synapse, is usually less than 1 mV, as we have said, and disappears in 10–20 milliseconds. The EPSPs and IPSPs are typically produced at dendrites and at the cell body (the dendrites and cell body are the sites of the synapses).

EPSPs and IPSPs, being graded potentials, fade as they spread along the cell membrane of a postsynaptic neuron. When they spread, however, they affect the membrane potential in the part of the neuron near the axon hillock where action potentials are initiated. Membrane potentials must be present at a single time to sum together. They may originate from many spatially separate synapses (**FIGURE 34.11**). Summation is thus both temporal (dependent on time) and spatial. Keep in mind that each individual EPSP or IPSP lasts only 10–20 milliseconds. Thus the sum of the graded potentials changes from moment to moment.
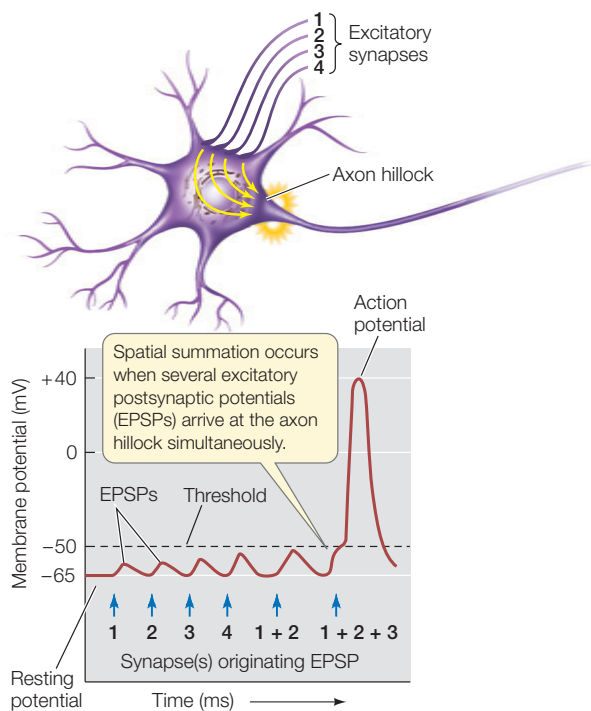
FIGURE 34.11 A Postsynaptic Neuron Carries Out Spatial Summation An individual neuron sums excitatory and inhibitory postsynaptic potentials received at spatially separate synapses. The graph shows changes in the membrane potential at the axon hillock. When the sum of the potentials present at one time depolarizes the axon hillock to threshold, the neuron generates an action potential.

Summation determines whether the postsynaptic cell produces action potentials. If the sum of EPSPs and IPSPs at the axon hillock is a depolarization great enough to reach threshold, the cell produces an action potential. If the depolarization is greater than threshold after the refractory period, the cell produces another action potential. In this way, a long period of depolarization above threshold results in a long sequence of closely spaced action potentials.

Synaptic plasticity is a mechanism of learning and memory

Synaptic plasticity is a phenomenon of extreme importance that is a principal focus of modern synapse research. **Synaptic plasticity** refers to the fact that synapses in the nervous system of an individual animal can undergo long-term changes in their functional properties and even their physical shape during the individual's lifetime. Such changes are currently hypothesized to be one of the major mechanisms of learning and memory.

Learning refers to the ability of an individual animal to modify its behavior as a consequence of individual experiences that took place at earlier times. For instance, if we have been accustomed to nibbling mushrooms while walking in the woods but one day we become deathly ill after doing so, we will change our behavior in the future: seeing mushrooms, we will no longer grab one for a snack. What is the mechanism by which such learning might occur? Synaptic plasticity is one hypothesis. According to this hypothesis, an individual's experiences at one time in its life can produce long-term changes in the individual's synapses, so that future experiences are then processed by the nervous system in altered ways.

> **LINK**
>
> Some of the many ways animal behavior is modified by learning and early experiences are described in **Concept 40.2**

Two model examples of synaptic plasticity illustrate its mechanisms and importance. Sea hares (marine mollusks in the genus *Aplysia*) pull their gills inside when certain parts of their body are touched:
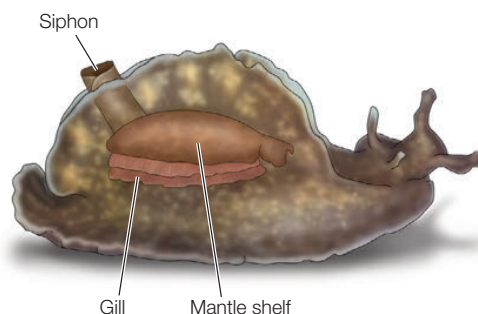
The sea hares learn from past experience how vigorously to do this. They withdraw their gills more vigorously if they have previously been exposed to a very noxious agent—a type of learning called sensitization. Sensitization occurs because of synaptic plasticity in synapses between the sensory neurons that detect touching and the motor neurons that stimulate the gill-withdrawal muscles. These synapses are said to be functionally strengthened when a sea hare is subjected to a noxious stimulus: the synapses become altered so that the amount of neurotransmitter released per presynaptic signal is increased, causing the postsynaptic cell to be excited to a greater degree by an identical presynaptic input. Long-term changes brought about by a second-messenger system are responsible.

Studies of the mammalian hippocampus provide a vivid example of synaptic plasticity in which synapses change not only in function but also in physical characteristics. The hippocampus lies deep within the brain:
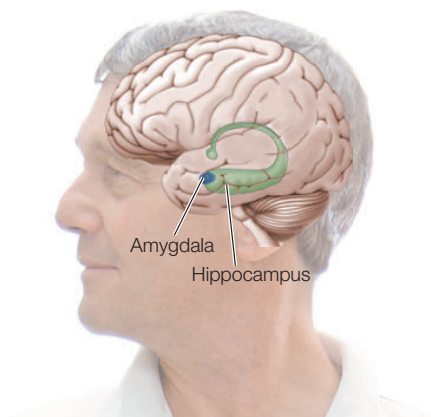
It is involved in spatial learning and memory formation. Studies have been carried out on living hippocampal tissue slices isolated from fully mature mice. Certain neuronal circuits can be stimulated in these preparations while neighboring circuits are not. Investigators have shown that when a circuit is repeatedly stimulated, certain of the postsynaptic structures in that particular circuit physically grow. Along with this physical response, the synapses also strengthen functionally. In this case, the number of active postsynaptic receptor molecules in each postsynaptic cell increases. Consequently, the cell responds more strongly to synaptic input from the presynaptic cell. Synaptic plasticity in this case has been shown to depend on second messengers, altered protein synthesis, and altered gene transcription in the postsynaptic cells. If you imagine some information being processed by circuits that are identical except that some have received a lot of prior stimulation and others have not, it is clear that the previously stimulated circuits will process the information differently, providing a basis for both learning and memory.

CHECKpoint   CONCEPT 34.3

✓ At a vertebrate neuromuscular junction, what would happen if a poison blocked the mechanism that removes acetylcholine from the synapse after it has had its usual effect?

✓ Consider the arrival of a single excitatory presynaptic signal at a single chemical synapse. What is the difference between the magnitude of the postsynaptic graded potential at a vertebrate neuromuscular junction and at a neuron-to-neuron synapse, and why does it matter?

✓ What is meant by synaptic plasticity, and speaking very generally, how could it be a mechanism of learning?

We have seen how neurons use ion pumps and ion channels to generate action potentials, and how action potentials trigger neurotransmitter release, allowing neurons to communicate with each other and with other cells. Next we'll look at how systems of neurons can receive sensory information.

CONCEPT 34.4   Sensory Processes Provide Information on an Animal's External Environment and Internal Status

Animals require information on their external environments to function successfully. They need to perceive where they are going, and they need information to locate food, find mates, and avoid danger. Animals have evolved an enormous variety of sensory processes that enable them to gather information on their external environments. Imagine, for example, a male moth, an insect-eating bat, and a migrating bird moving across the landscape on a moonless, pitch-black night in late summer. The moth might be able to detect a female of his species,

hundreds of yards away, by using sense organs that are extremely sensitive to odors that females release into the air. The bat might be able to zero in on him as he flies toward her by using echolocation. In this process, a bat emits bursts of vocal sound, at frequencies humans can't hear, and senses the echoes of these sounds that bounce off the moth. The moth, in turn, might use its own sense of hearing to detect the bat's vocalizations and take evasive action. Meanwhile the bird migrating overhead might use its eyes to locate a key star, which it can use as a navigational aid to fly south (see Concept 40.2).

Sensory processes are equally important for providing animals with information on their internal status. For instance, when we discussed breathing (see Chapter 31), we emphasized that the partial pressures of O_2 and CO_2 in an animal's blood are important indicators of whether it is breathing properly. Sensory processes have evolved that enable animals to measure their internal O_2 and CO_2 partial pressures so that they can adjust their rate of breathing. Other internal sensory processes provide animals with information on the amount of tension produced by their muscles during contraction. This information can be used to adjust stimulation of the muscles by the nervous system so that the tension is neither too high nor too low.

Sensory receptor cells transform stimuli into electric signals

Sensory processes depend on **sensory receptor cells**, which are cells, typically neurons, specialized to transform the energy of a stimulus—called stimulus energy—into an electric signal. Energy transduction is the process of changing one type of energy into another. A sensory receptor cell is said to carry out **sensory transduction** when it produces an electric signal from stimulus energy.

The electric signal that is produced then directly or indirectly causes action potentials to be generated in a neuron. The action potentials—which encode the initial stimulus—convey the sensory information to the brain or other integrative parts of the nervous system for processing and interpretation. In this way, the animal acquires a sensory perception of its external environment and its internal status.

Sensory receptor cells are highly specific in the stimuli to which they ordinarily respond. A receptor cell that responds to vibration does not respond to light, and vice versa. A cell that responds to sweet tastes responds to neither vibration nor light.

Some stimuli—such as light, heat, and mechanical motion—are clearly forms of energy. Thus when we speak of stimulus energy, our meaning is straightforward. But what do we mean when we speak of stimulus energy when the stimulus is a chemical compound such as a sweet-tasting molecule? In these cases we are not referring to the bond energy of the molecule (the energy that would be released by burning or respiration). Instead, in the case of chemical stimuli, when the stimulus molecule binds with a protein during sensory reception, a change takes place in the protein's conformation (molecular shape), and the energy involved in this process represents the stimulus energy.

(A) Ionotropic receptor cell

In this example, the stimulus opens a Na$^+$ channel.

Outside of cell

Stimulus-gated Na$^+$ channel

Na$^+$

Stimulus

Inside of cell

(B) Metabotropic receptor cell

In this example, the stimulus affects a receptor molecule that initiates a G protein–mediated cascade that controls an ion channel via a second messenger.

Stimulus

Na$^+$ (or K$^+$) channel

Receptor

G protein

Second messenger precursor

Second messenger

FIGURE 34.12 Sensory Receptor Cells Are Ionotropic or Metabotropic A metabotropic cell that affects an ion channel is illustrated here, but metabotropic cells do not always work in this way.

Sensory receptor cells depend on specific receptor proteins and are ionotropic or metabotropic

A **sensory receptor protein** is a membrane protein in a sensory receptor cell that initially detects a stimulus and directly or indirectly produces a graded change, called a receptor potential, in the cell's membrane potential. There are many types of sensory receptor proteins, and they respond to different kinds of stimuli. For example, some sensory receptor proteins respond to stretch. Others respond to particular chemicals. Still others respond to light. A receptor cell is specific in the sensory receptor protein it expresses, and this is one of the major reasons that receptor cells are highly specific in the stimuli to which they respond.

Receptor cells often have modified cell membranes with exceptionally large surface areas. The cell membrane, for example, may be greatly enlarged by the presence of microvilli, cilia, or membrane foldings. The enlarged cell membrane enables a receptor cell to have great numbers of receptor molecules, making the cell highly sensitive to stimuli:

Cone cells in vertebrate eyes have highly folded cell membranes in which great numbers of photoreceptor molecules are found.

Sensory receptor cells may be ionotropic or metabotropic. The meanings of these terms in this context are similar to their meanings in the study of synapses (see Concept 34.3).

An **ionotropic receptor cell** typically has a receptor protein that is a stimulus-gated Na$^+$ channel (**FIGURE 34.12A**). What happens during stimulus reception? First, the stimulus acts on the receptor protein. Second, the protein changes conformation so that it operates as an open Na$^+$ channel, and Na$^+$ diffuses in through the open channel, creating a receptor potential: a graded change in the cell membrane potential. Third, the graded change of membrane potential directly or indirectly results in action potentials.

A **metabotropic receptor cell** typically has a receptor protein that activates a G protein when exposed to the stimulus (**FIGURE 34.12B**; see also Figure 5.14). In most cases, the receptor *is* a G protein–linked receptor. Activation of the G protein typically leads to a change in the concentration of a second messenger in the receptor cell. This change can directly or indirectly alter ion fluxes across the cell membrane, producing a receptor potential. The receptor cell itself may then generate action potentials, or it may secrete a neurotransmitter that affects another cell that produces action potentials.

Sensation depends on which neurons in the brain receive action potentials from sensory cells

All sensory systems convey information to the brain or other integrative parts of the nervous system in the form of action potentials. Accordingly, the brain receives action potentials from all types of sensory systems. How, then, do we perceive some of these action potentials as representing light, others as representing smells, and still others as representing sounds? How do we decode the action-potential codes?

Much of the answer lies in physical separation in the brain, between areas that receive axons from various sensory systems. In vertebrates, axons from the eyes travel to a specific brain region called the visual cortex. In turn, action potentials arriving in the visual cortex are interpreted as representing light or other visual sensations. Axons from the inner ear travel to another brain region called the auditory cortex, where arriving action potentials are interpreted as representing sounds. The intensity of the sensations (e.g., the brightness of a light or loudness of a sound) is coded by the frequencies of the action potentials.

We can see the importance of these principles on occasions when action potentials are generated by the wrong stimulus. People sometimes see flashes of light when they are poked in the eye. A strong poke can produce action potentials in axons from the retina that go to the visual cortex. Because the action potentials arrive in the visual cortex, the brain interprets them as representing light.

The parts of the brain that receive particular types of sensory information are determined during development, at least in part by interaction with the axons conveying the information. In a person blind from birth, for example, the visual cortex does not simply occupy space in the brain, unused, for life. Instead, much of the brain region is taken over to serve other sensory functions.

Sensation of stretch and smell exemplify ionotropic and metabotropic reception

Animals commonly have stretch receptor cells associated with their muscles. These are types of **mechanoreceptors**: cells that

1 Stretching a muscle cell is the **stimulus**…

2 …that activates the opening of ion channels in stretch receptor dendrites, giving rise to a graded receptor potential…

3 …which spreads to the axon hillock, which generates action potentials when the receptor potential is great enough to trigger them.

4 The action potentials travel to the brain along the axon.

Muscle cell

Dendrites

Receptor cell body

Axon

Stretch

Voltage

Time

FIGURE 34.13 Stimulating a Crayfish Stretch Receptor Cell Produces Electric Signals Signal transduction in a stretch receptor cell of a crayfish can be investigated by measuring the membrane potential (voltage) at various places in the stretch receptor neuron (purple).

respond specifically to mechanical distortion of their cell membrane. When a muscle contracts, its stretching forces are applied to its stretch receptor cells, which provide the nervous system with information on the effectiveness of the contraction. Mechanoreceptors are typically ionotropic, as are thermoreceptors, which detect heat and cold.

A stretch receptor cell of a crayfish provides a model of how an ionotropic receptor cell generates action potentials. The receptor cell is a specialized neuron. When the cell membranes of its dendrites are stretched, stretch-gated Na^+ channels in the membranes open (see Figure 34.5B). Consequently, a graded, depolarizing receptor potential is produced and spreads to the axon hillock, and action potentials are generated there if the graded depolarization is above threshold (**FIGURE 34.13**). The rate at which action potentials are generated depends on the magnitude of the receptor potential, which depends on how much stretch the receptor cell detects.

Go to ANIMATED TUTORIAL 34.5
Mechanoreceptor Simulation
PoL2e.com/at34.5
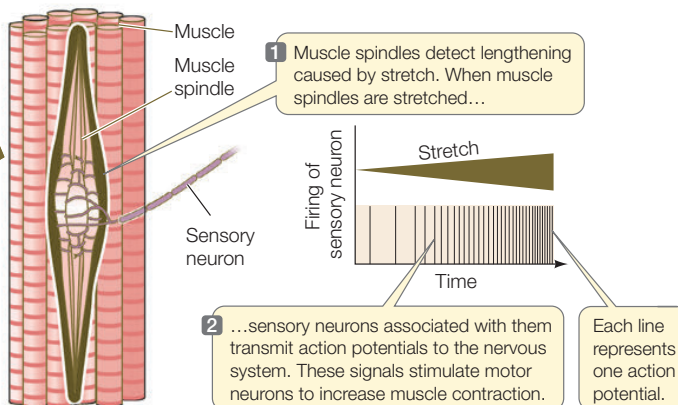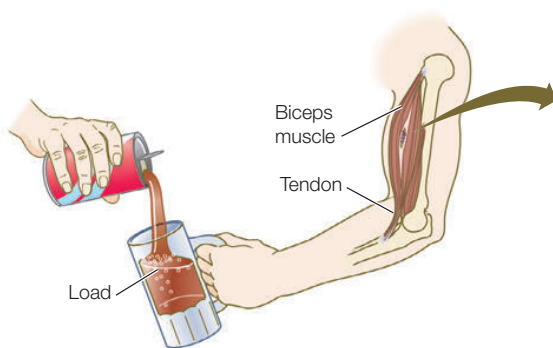
Stretch receptors associated with our biceps help us adjust the muscle's strength of contraction to match the load the muscle must sustain (**FIGURE 34.14**). For example, suppose someone pours a drink into a glass you're holding in your hand. Your biceps muscle tends to be stretched to a longer length as the weight of the glass increases. Receptors in the muscle detect this effect and encode it in the frequency of action potentials. Your nervous system then responds to the signals by stimulating stronger contraction as the glass fills, so that the glass does not pull your arm downward.

Now let's look at an example of metabotropic reception, our sense of smell. Chemicals detected by smell are called odorants, and the sense of smell is called olfaction. The sensory cells for odorants, called olfactory receptor cells, are specialized neurons. They exemplify **chemoreceptors**: cells that respond to the presence or absence of specific chemicals. Mammalian olfactory receptor cells illustrate the workings of metabotropic sensory cells (see Figure 34.12B). They also illustrate in a spectacular way the importance of receptor protein diversity and specificity.

The olfactory receptor cells of a mammal are found in the olfactory epithelium, a part of the lining of the internal nasal cavity. One end of each receptor cell projects into the mucus that covers the surface of this epithelium. The other end of the cell is an axon that extends into a part of the brain called the olfactory bulb (see Figure 34.25). Odorants must dissolve in the liquid of the mucus to be detected.

The receptor protein of a mammalian olfactory receptor cell is a G protein–linked receptor found in the part of the cell that projects into the mucus. When an odorant molecule binds to the receptor, the receptor activates a G protein. The G protein in turn activates an enzyme that causes an increase of a second messenger in the cytoplasm. The second messenger opens ion channels in the cell membrane, causing a graded

FIGURE 34.14 Negative Feedback: Sensory Signals from Stretch Receptors Enable the Nervous System to Control Muscle Contraction In vertebrates, tiny sensory organs called muscle spindles send information to the nervous system about how much a muscle is being lengthened by stretching. This information is used here to keep limb position stable by increasing the contractile force as the downward force increases.

Biceps muscle

Tendon

Load

Muscle

Muscle spindle

Sensory neuron

1 Muscle spindles detect lengthening caused by stretch. When muscle spindles are stretched…

Firing of sensory neuron

Stretch

Time

2 …sensory neurons associated with them transmit action potentials to the nervous system. These signals stimulate motor neurons to increase muscle contraction.

Each line represents one action potential.

depolarization, which in turn causes action potentials to be generated in the cell. These propagate into the brain by way of the cell axon.

One of the amazing aspects of these cells is the number of different G protein–linked receptor proteins (GPLRs) they can express. Each cell expresses just one type of GPLR and can detect only the odorant molecules that bind to that GPLR. However, the genome codes for many options. About 1,000 different GPLRs are found in mice, for example. Collectively, the tens of thousands of olfactory receptor cells—each with one type of GPLR—can detect a very wide range of odorants. Each specific type of GPLR typically can bind to a range of odorants. However, different types of GPLRs have different sets of odorants they bind. The combination of olfactory cells that are stimulated by any particular odorant is unique to that odorant. Consequently, the brain can interpret the pattern of signals from the olfactory cells as pointing to a particular smell.

Some animals have olfactory receptor cells of extraordinary specificity. Because these cells effectively respond to only one ordinary odorant, they can be extremely sensitive to it. The feathery antennae of some male moths have huge numbers of odorant receptor cells that respond in a highly specific way to pheromone molecules emitted by the females of their species (see Concept 40.4). These moths can detect a female when her pheromone molecules represent only 0.000000000000001 percent of the molecules in the air:

A male moth can detect the female pheromone at very low concentrations in the air passing over his antennae.

Auditory systems use mechanoreceptors to sense sound pressure waves

Sounds consist of waves of compression of the air. An easy way to understand the nature of sound is to envision a loudspeaker. A close look reveals that the membrane of a loudspeaker moves back and forth. When the membrane moves toward you, it compresses the air, creating a region of relatively high pressure that moves toward you like a wave (at the speed of sound). When the speaker membrane moves away from you, it creates a region of relatively low pressure that also moves toward you between the regions of high pressure. You thus experience a sound pressure wave of alternating high and low pressure. The frequency of these alternations accounts for tone or pitch. We perceive high frequencies as high-pitch, treble tones and low frequencies as low-pitch, bass tones.

The hearing organs of many different types of animals are based on a single principle. The hearing organ contains a thin membrane that is free to move when a sound pressure wave

strikes it—moving in when high pressure strikes and out when low pressure strikes. Specialized mechanoreceptors are linked to the membrane and detect the movements.

In an insect, the membrane is a simple structure in which a single area of membrane responds to all sound frequencies. A system of this sort is mainly useful for detecting sound presence or absence (and loudness), rather than discriminating one frequency from another.

The hearing system of mammals, by contrast, can separately detect many different frequencies. When we listen to someone playing the piano, our brain receives specific information on each frequency in the music, allowing us to perceive high notes as distinct from low notes.

In the ear of a mammal, the membrane that initially responds to sound pressure waves is the tympanic membrane (ear drum). On the inside of the tympanic membrane is an air-filled cavity called the middle ear (**FIGURE 34.15A**). Because the tympanic membrane has air on both sides, it is free to vibrate when a sound pressure wave strikes it. Three interconnected, delicate bones—called ossicles and named the malleus, incus, and stapes—are found in the middle ear (**FIGURE 34.15B**). They act as a lever system that turns vibrations of the tympanic membrane into more forceful vibrations of another flexible membrane called the oval window.

The oval window is part of the inner ear. Specifically, it is part of the **cochlea**, a coiled, fluid-filled tube where sound energy is transduced into electric signals. A cross section of the cochlea reveals that it is composed of three parallel canals separated by two membranes. Of these the **basilar membrane** is of particular importance (**FIGURE 34.15C**).

The basilar membrane gradually changes in width and stiffness from one end to the other. At the end nearest the oval window, it is only about 0.04 millimeters wide in the human ear and relatively stiff. It becomes progressively wider and more flexible until, at its far end, it is 0.5 millimeters wide and not as stiff.

When the sound pressure wave is transmitted into the cochlear fluid at the oval window, different frequencies in the sound pressure wave cause different, local regions of the basilar membrane to oscillate. Different regions move in response to different frequencies because of the gradations of membrane width and stiffness. Low-frequency vibrations (representing low pitches) have their greatest effect on the wide end of the membrane farthest from the oval window, setting that part into motion to a far greater degree than other parts (**FIGURE 34.16A**). Other frequencies affect other parts of the membrane (**FIGURE 34.16B**).

How is information on these oscillations sent to the brain? Sitting on the basilar membrane is a structure, the organ of Corti, that houses distinctive mechanoreceptor cells called hair cells (**FIGURE 34.15D**). Each hair cell bears extensions called stereocilia (the "hairs," which are actually microvilli, not cilia) that project into a semirigid membrane, the tectorial membrane. When a particular part of the basilar membrane oscillates, the stereocilia of the hair cells in that region are bent because they are effectively anchored at one end in the tectorial membrane but moving at the other end.

(A)

Pinna

Auditory canal

Sound pressure waves

1 Sound pressure waves travel through the auditory canal and vibrate the tympanic membrane.

Outer ear   Middle ear   Inner ear

(B)

2 The ossicles transmit vibrations of the tympanic membrane to the oval window of the cochlea.

3 Vibrations at oval window create pressure waves in fluid-filled cochlear canals.

Semicircular canal of the vestibular system

Auditory nerve

Ossicles { Stapes / Incus / Malleus

Tympanic membrane ("eardrum")

Cochlea

Oval window (under stapes)

Eustachian tube

Round window

FIGURE 34.15 The Human Ear The ear produces action potentials that are sent to the brain, permitting environmental sound pressure waves to be perceived.

Go to ACTIVITY 34.2 Structures of the Human Ear
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(C)

Vestibular canal

Reissner's membrane

Middle canal

Organ of Corti

Basilar membrane

Tympanic canal

4 Pressure waves in cochlear canals flex adjacent membranes.

Auditory nerve

Cross section of cochlea

(D)

Organ of Corti

Hair cell

Stereocilia

Tectorial membrane

Basilar membrane

Auditory nerve

5 When basilar membrane is flexed, it bends stereocilia on hair cells in the organ of Corti.

6 The movements of stereocilia are transduced into action potentials in the auditory nerve.

The hair cells transduce the bending motions of their stereocilia into electric signals. They do not produce action potentials. Instead, they synapse with neurons, and when they are stimulated by the bending of their stereocilia, they release a neurotransmitter that excites the neurons to produce action potentials, which travel to the brain. In this way, the frequency composition of a sound pressure wave is encoded by the particular hair cells that trigger action potentials as the wave exerts its effect in the inner ear (see Figure 34.16A).

The photoreceptors involved in vision detect light using rhodopsins

Both simple and complex animals have visual systems by which they sense and respond to light. The simplest visual systems give animals the ability to orient to the sun and sky. Complex visual systems provide animals with rapid and extremely detailed visual information about objects in their environments. Remarkably, the basic process of detecting light in visual systems has been conserved across the entire animal kingdom. **Photoreceptors** are sensory receptor cells that are sensitive to light. In all photoreceptors employed in vision, the sensory receptor protein is a member of a family of closely similar membrane pigments called **rhodopsins**. The rhodopsins act as G protein–linked receptors, and the photoreceptors are metabotropic receptor cells.

Detection of light depends on the ability of rhodopsins to absorb photons of light and undergo a change in molecular conformation (shape) as a consequence. A rhodopsin molecule consists of two parts: a protein, opsin (which alone is not photosensitive), and a nonprotein light-absorbing structure, 11-*cis*-retinal. The retinal part of each molecule is derived from vitamin A, explaining why sufficient vitamin A is essential for proper vision.

A rhodopsin molecule changes to a different isomer (arrangement of atoms in three-dimensional space) when it

(A) Oscillation of the basilar membrane in response to a low-frequency sound

Diagrammatic uncoiling of cochlea

Pressure waves travel down the vestibular canal and flex the basilar membrane at a frequency-specific region. Hair cells in that region are stimulated to send signals to the brain.

Vibrations from the tympanic membrane

Oval window (under stapes)

Pressure waves

Vestibular canal

Axons carrying action potentials to the brain

Wide (apical) end of basilar membrane

Narrow (basal) end of basilar membrane

Round window

Tympanic canal

Basilar membrane

(B) The human basilar membrane in its coiled form

Red numbers represent the sound frequencies, in Hertz, to which various parts of the membrane maximally respond.

Membrane width is diagrammed. It increases gradually from one end to the other.

7,000 5,000 1,000 800 4,000 200 20,000 Basal end 1,500 400 600 3,000 Apical end 2,000
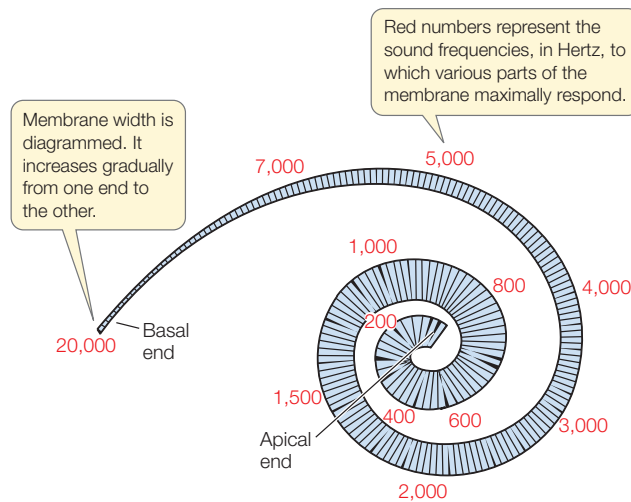
FIGURE 34.16 Frequencies in Sound Pressure Waves Are Transduced into Signals from Distinctive Sets of Hair Cells
(A) Each frequency causes oscillations at a particular region of the basilar membrane. Here low-frequency sound pressure waves are shown flexing a region of the basilar membrane far from the oval window. (B) Different regions of the basilar membrane move in response to different frequencies because of the gradations in the membrane's width and stiffness. Hair cells positioned along the basilar membrane produce signals that lead to generation of action potentials that encode the regions that are oscillating.

Go to ANIMATED TUTORIAL 34.6
Sound Transduction in the Human Ear
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absorbs light. When the 11-*cis*-retinal in a molecule of rhodopsin absorbs light, it undergoes a twist around one of its bonds, so its atoms become reoriented in space to the all-*trans*-retinal isomer:

Light
11-*cis*-retinal
All-*trans*-retinal
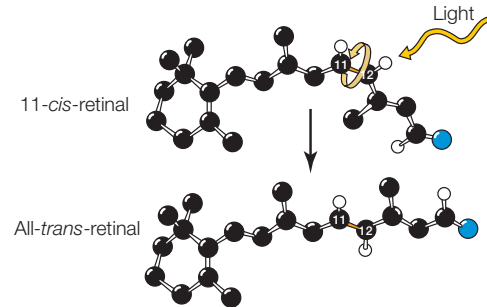
This change places strains on bonds in the opsin part of the molecule, changing the conformation of the opsin. The rhodopsin is thus activated. It in turn activates a G protein–mediated signal transduction cascade, in which a second messenger exerts effects on voltage-gated Na^+ channels in the photoreceptor cell membrane.

Go to ANIMATED TUTORIAL 34.7
Photosensitivity
PoL2e.com/at34.7

Metabotropic control has a huge potential advantage in that it can greatly amplify signals. With large numbers of rhodopsin molecules and strong amplification, some photoreceptor cells undergo a measurable change in membrane potential in response to just a single photon of light!

LINK
Signal amplification by metabotropic control is described in **Concept 5.6**

The vertebrate retina is a developmental outgrowth of the brain and consists of specialized neurons
Vertebrates have image-forming eyes. Like a camera, an image-forming eye has a lens that focuses images on an internal surface that is sensitive to light. The eye is a fluid-filled structure bounded by a tough connective tissue layer, as exemplified by the human eye:

Vascular and pigmented layer (choroid) Connective tissue (sclera) Ciliary muscle Cornea Retina Pupil Fovea Iris Optic nerve Fluid of anterior eye (aqueous humor) Lens Fluid of posterior eye (vitreous humor)
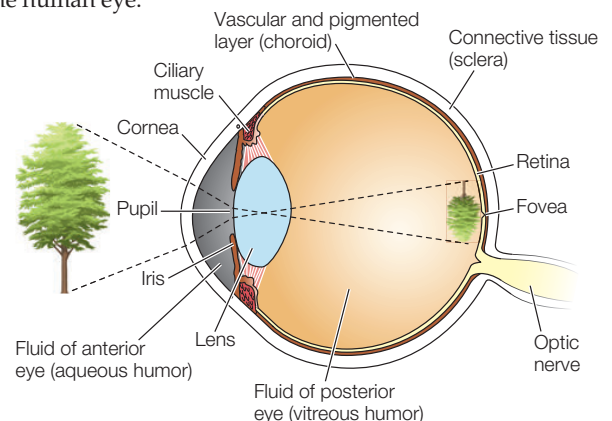
At the front of the eye, the connective tissue forms the transparent **cornea**. Just inside the cornea is the colored **iris**. Light enters the light-sensing part of the eye through the **pupil**, the central opening of the iris. The iris is equipped with small muscles that enlarge the diameter of the pupil in dim light and reduce it in bright light. Behind the iris is the **lens**, made of crystal-clear proteins called crystallins. In mammals, muscle cells pulling on the lens produce fine adjustments in its shape, focusing images on the photosensitive layer—the **retina**—at the back of the eye.

Go to ACTIVITY 34.3 Structure of the Human Eye
PoL2e.com/ac34.3

The retina is a developmental outgrowth of the brain and consists of several types of specialized neurons. Two types, the **rod** cells and **cone** cells, are the photoreceptor cells responsible for vision (**FIGURE 34.17A**). Both are specialized to have a large membrane area and large numbers of rhodopsin molecules. All rhodopsin molecules do not respond to the same wavelengths of light, even though their photoreceptive molecular subpart, the retinal, is the same. They differ in their opsins.

Rods outnumber cones in the human retina: 100 million rods versus 5 million cones. The rods are far more sensitive to light than the cones and are especially important for vision in dim light. Cones provide high-acuity color vision. Humans and some other primates have three types of cones, which are distinguished by having three different molecular forms of rhodopsin. These forms differ from one another in their sensitivities to various wavelengths of light, and all three differ from the single form of rhodopsin in rod cells (**FIGURE 34.17B**). As a group, the cone cells are able to detect and encode color because each wavelength of light has a unique collective effect on the three types.

Rod and cone cells do not produce action potentials. They only produce graded membrane potentials. Compared with other sensory receptor cells, they are unusual in that they hyperpolarize in response to their stimulus. How does this work? When in darkness, they have *open* Na^+ channels in their cell membranes. Na^+ ions entering by way of these channels depolarize the cells to some extent. When the cells are stimulated by light, the second messenger produced under G protein control *closes* Na^+ channels. This closing lowers the Na^+ current flowing into the cell, permitting the charge on the inside of the cell membrane to become more negative relative to the charge on the outside. This effect is graded, depending on the light intensity (**FIGURE 34.18**). The rod and cone cells synapse with other neurons in the retina and relay signals to them by way of graded neurotransmitter release.

A great deal of signal processing occurs in the retina before visual signals are relayed to the brain by way of axons in the optic nerve. Besides the visual photoreceptor cells (rods and cones), four types of visual integrating neurons—called bipolar cells, horizontal cells, amacrine cells, and ganglion cells—are found in the retina in a layered arrangement (**FIGURE 34.19**; see also Figure 29.1). A striking feature of the arrangement of these cells is that light must pass through the integrating cells (which are transparent) to stimulate the rods and cones! This unexpected arrangement is a by-product of the embryonic developmental path by which the eyes form from the brain. The photoreceptor cells
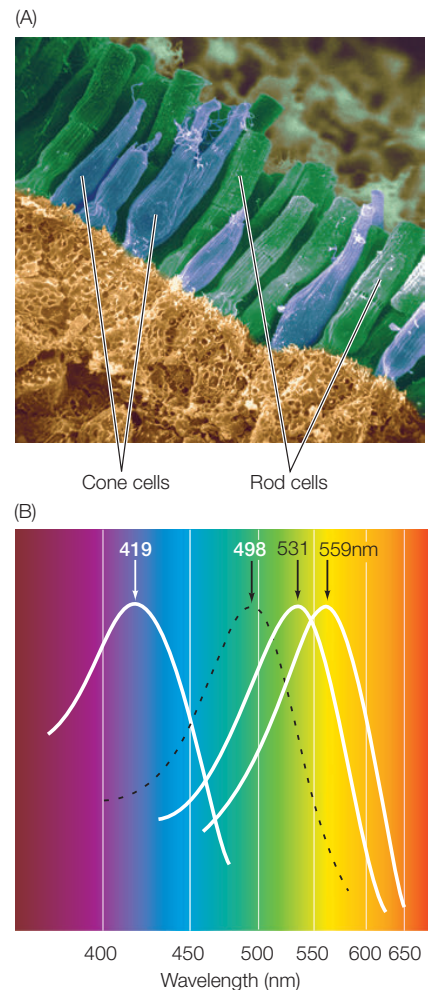
FIGURE 34.17 Rods and Cones (A) This scanning electron micrograph of photoreceptor cells in the retina of a mud puppy (an amphibian) shows cylindrical rods and tapered cones. The cells are artificially colored to distinguish them. (B) The three types of cone cells in the human retina differ in their absorption of the various wavelengths in the spectrum of light, and they therefore differ in their sensitivities to various wavelengths. The dashed line shows the spectral response of rod cells.

(rods and cones) synapse with bipolar cells, which in turn synapse with ganglion cells. In contrast to the cells in these straight-through connections from the back to the front of the retina, the horizontal cells and amacrine cells communicate laterally within the retina and in this way are able to extract information on the relative signal strengths in neighboring photoreceptor cells and neighboring bipolar cells. Horizontal cells help sharpen the perception of contrast between light and dark. Amacrine cells have several functions, including detecting motion. Ultimately, all of this information converges onto the ganglion cells, which are the only cells that produce action potentials. Axons of these cells converge to form the optic nerve and carry the action potentials to the visual cortex in the brain.

Each ganglion cell is said to have a defined, circular receptive field formed by the cells from which it receives signals. Some ganglion cells are excited by light falling on photoreceptor cells at the center of their receptive field and inhibited by

INVESTIGATION

FIGURE 34.18 A Rod Cell Responds to Light   The cell membrane of a rod cell hyperpolarizes—develops a more negative membrane potential—in response to a flash of light. Rod cells develop graded receptor potentials in response to the absorption of light energy.[a]

HYPOTHESIS

When a rod cell absorbs photons (light energy), its membrane potential changes in proportion to the strength of the light stimulus.

METHOD

1. Record membrane potentials from the inner segment of a rod cell.
2. Stimulate the rod cells with light flashes of varying intensity and record the results.

Outer segment (containing rhodopsin)

Light

Amplifier

Recording

Inner segment

Nucleus

The membrane potential controls the amount of neurotransmitter released.

Synaptic terminal (synapse with bipolar cell)

RESULTS

Light flash

A dim light stimulus results in a slight hyperpolarization.

Medium-intensity light

A bright light stimulus results in a strong hyperpolarization.

Membrane potential (mV)

−35

−45

−55

Time

CONCLUSION

The membrane potential of rod cells is depolarized in the dark and hyperpolarizes (becomes more negative) in response to light.

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]D. A. Baylor et al. 1979. *Journal of Physiology* 288: 589–634.

FIGURE 34.19 The Human Retina   The human retina consists of the visual photoreceptor cells (rods and cones) and four types of integrating neurons found, in a layered arrangement, at the back of the eye.

Integrating neurons—consisting of ganglion, amacrine, bipolar, and horizontal cells—are found in a layered arrangement in the retina.

1 Light travels through integrating neurons, which are transparent,…

2 …and is absorbed by the rods and cones (the visual photoreceptor cells) at the back of the retina.

Retina

To optic nerve

Photoreceptors

Amacrine cell

Bipolar cell

Cone Rod Pigmented epithelium

Light

Axons of ganglion cells

Ganglion cells

Horizontal cell

Sclera

4 …and finally converges on ganglion cells, which send action potentials via their axons to the brain.

3 Visual information from the rods and cones is processed by the integrating neurons…

Go to ACTIVITY 34.4
Structure of the Human Retina
PoL2e.com/ac34.4

Go to MEDIA CLIP 34.2
Into the Eye
PoL2e.com/mc34.2

the retina and brain. Each human retina sends a million axons to the brain. The visual cortex consists of hundreds of millions of neurons that receive and process the information from those million axons.

Some retinal ganglion cells are photoreceptive and interact with the circadian clock

One of the most revolutionary, recent discoveries about the mammalian eye is that 1–2 percent of the retinal ganglion cells are photoreceptive. Most ganglion cells (the other 98–99 percent) cannot directly detect light and function only to help integrate visual information that originates in the rods and cones.

The photoreceptive ganglion cells are not employed in vision. They have a relatively low sensitivity to light and do not produce images.

light falling on photoreceptor cells in the periphery. Other ganglion cells are inhibited by light falling in the center of their receptive field and stimulated by light falling on the periphery. The result is that the ganglion cells can communicate information to the brain about visual patterns such as spots, edges, and areas of contrast.

The huge numbers of cells involved in vision say a lot about the amount of processing of visual images that takes place in

Light

(A)

The compound eye of a fruit fly contains hundreds of ommatidia, each of which looks somewhat like a dot on the eye surface.

(B)

Corneal lens
Crystalline cone
Pigment cells
Rhodopsin
Photoreceptor (retinula) cell
One ommatidium
Axon that goes to brain
Basement membrane

FIGURE 34.20 Ommatidia: The Functional Units of Arthropod Eyes   (A) The micrograph shows the compound eye of a fruit fly. (B) The rhodopsin-containing retinula cells are the photoreceptors in ommatidia.

Rather than contributing to vision, these ganglion cells provide information simply on whether light is present and how bright it is. This information is used in two ways. It is relayed to the suprachiasmatic nuclei, where it is used to entrain the master circadian biological clock to the environmental rhythm of day and night (see Concept 29.6). The information is also employed in regulating the size of the pupils of the eyes, so the pupils are large in dim light and small in bright light.

The photoreceptive ganglion cells do not use rhodopsin. Instead, their sensory receptor protein is believed to be melanopsin.

Arthropods have compound eyes

Invertebrates have evolved a variety of types of eyes that differ from vertebrate eyes. Even the eyes of octopuses and squid, which look very similar to vertebrate eyes on the outside, have very different properties than vertebrate eyes.

The eyes of arthropods (insects, crayfish, crabs, and lobsters) are called **compound eyes** because each eye consists of many optical units, called **ommatidia** (singular *ommatidium*), each with its own lens. Light entering an ommatidium through its lens strikes photoreceptor (retinula) cells that contain rhodopsin and generate action potentials (**FIGURE 34.20**).

Each ommatidium of a compound eye is directed at a slightly different part of the visual world. The more ommatidia in the eye, the higher the resolution of the image compiled by the brain, rather like the pixel density in a computer monitor. The number of ommatidia in a compound eye varies from only a few in some ants to 800 in fruit flies and to 30,000 in some fast-flying predators such as dragonflies.

Animals have evolved a remarkable diversity of sensory abilities

Vision, hearing, olfaction, and touch are almost universal in animals. Animals use these sensory abilities to gather information about their external environment so they can move about

effectively, avoid dangers, and exploit opportunities. Some animals, in addition, have evolved unusual sensory abilities that let them make use of additional information sources, such as electric fields or Earth's magnetic field (see Figure 40.12). Moreover, some animals are able to use vision or hearing to gather information from parts of the electromagnetic spectrum or sound-frequency spectrum that are unfamiliar to us.

The philosopher Bertrand Russell titled one of his most famous books *Our Knowledge of the External World.* In this book he stressed that, as humans, we can only know about those aspects of our external environment that our human sensory systems detect. With this fact in mind, we realize that some animals that live around us perceive our external environment in very different ways than we do. They can see electromagnetic wavelengths to which we are blind or hear sound frequencies to which we are deaf.

The electromagnetic spectrum consists of electromagnetic energy at a broad range of wavelengths from 0 to over 100 micrometers (μm) (see Figure 6.16). Our eyes can see the wavelengths between 0.4 and 0.7 μm. We have names for the parts of the spectrum we cannot see: the wavelengths that are invisible to us even when our eyes are healthy. The wavelengths that are too long for our eyes to see (i.e., longer than 0.7 μm) are called **infrared wavelengths**. The wavelengths too short for our eyes to see (i.e., shorter than 0.4 μm) are called **ultraviolet wavelengths**.

Some snakes obtain vision-like images of their surroundings using infrared wavelengths. They are therefore able to see patterns of warmth and coolness in darkness—an ability that helps them find prey. The best-understood snakes with this ability are the pit vipers, such as rattlesnakes, which have specialized sense organs in pits near their eyes. The organ in each pit focuses infrared electromagnetic energy onto a membrane that can detect it, much like our eyes focus visible light onto our retina. Unlike the retina, the pit organ does not employ rhodopsins or similar molecules. Biologists still do not fully

understand the sensory mechanism by which infrared electromagnetic energy is detected.

This bamboo pit viper (*Trimeresurus gramineus*) has a sense organ that detects infrared wavelengths, located in a pit on each side of its head.

At the other end of the electromagnetic spectrum, many animals have eyes that can see ultraviolet wavelengths to which we are blind. Honey bees, for example, see flowers in different ways than we see them because they see in the ultraviolet. Many flowers that look uniform in color to our eyes have bold color patterns at the ultraviolet wavelengths bees see (see Figure 21.24). Many species of birds also see ultraviolet wavelengths. The eyes of these birds look much like ours. However, unlike the case in our eyes, their cornea and lens are transparent to ultraviolet wavelengths, permitting ultraviolet light to enter the eye, and the eye has specialized cone cells receptive to ultraviolet wavelengths.

The discovery of ultraviolet vision in birds led researchers to wonder, If the males and females of a species look identical to us, do they also look identical to the birds? Cedar waxwings (*Bombycilla cedrorum*), found almost everywhere in North America, are one species studied to answer this question. Male and female waxwings look the same to us. But we see only at 0.4–0.7 μm. When we use instruments to learn what the waxwings look like at shorter, ultraviolet wavelengths, we find that males and females look different. Thus the birds themselves can tell males and females apart by sight even though we cannot. This is equally true for many other species.

Some animals can sense electric fields—fields of voltage and current—enabling them to perceive their surroundings using information that's entirely foreign to us. The weakly electric fish provide examples. These fish produce weak electric fields in their surroundings by use of modified muscles (see Concept 33.4). Electric currents in these self-produced environmental fields pass through the outer skin layers of the fish, where sensory receptor cells detect the currents. The fish detect distortions in these fields caused by objects in their external environment; by analyzing these distortions, the fish can perceive the objects even in complete darkness. Fish in the genus *Gnathonemus* use this sensory ability to locate and capture stream insects at night.

African fish of the species *Gnathonemus petersii* are nocturnal. They find food using self-produced electric fields.

CHECKpoint   CONCEPT 34.4

✓ As a mosquito lands on your arm, a cell in the mosquito's leg responds to altered stretch within the leg. Another cell in its antennae detects the CO_2 exhaled by you and other animals. What types of sensory receptor proteins do these cells probably contain?

✓ Referring to the structure of the vertebrate retina, explain how it is possible for visual signals to be processed extensively in the retina itself.

✓ A range of sound frequencies is changed to a range of locations in the vertebrate cochlea. How does this happen?

Now that we have discussed cellular processes from action potentials to receptor function, let's examine how cells are organized to form the nervous systems of animals.

CONCEPT 34.5   Neurons Are Organized into Nervous Systems

A nervous system consists of many neurons, interacting with each other by way of synapses. When we say "many," we mean a huge number. The human brain is currently estimated to contain about 86 billion neurons!

The simplest nervous systems seen in animals alive today occur in anemones, corals, jellyfish, and other cnidarians. In these animals, the individual neurons are widely and relatively randomly dispersed throughout the body. Together they form a nerve net:
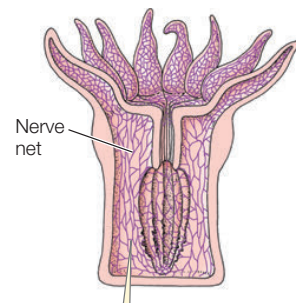
Nerve net

The sea anemone has a nerve net that serves simple behaviors such as contraction and relaxation.

Biologists generally assume that when nervous systems first evolved they were similar to nerve nets.

As nervous systems evolved further, they followed two major trends, centralization and cephalization. Some neurons became specialized to integrate the signals of other neurons. Most of these integrating neurons became clustered together in centralized integrating organs, rather than being distributed randomly throughout the body. **Centralization** refers to this evolutionary trend toward clustering. At the same time, the major integrating areas became concentrated toward the anterior end of the

animal's body, a trend called **cephalization** (from a Greek word for "head"). Mammals vividly exemplify the outcomes of these evolutionary trends. Most of the integrating neurons of a mammal are centralized in the brain and spinal cord, and the major integrating organ—the brain—is at the anterior end of the body in the head. Why has cephalization occurred? Most kinds of animals have particularly important sets of sense organs—such as eyes, ears, and sensory tentacles—at their anterior end. This is easy to understand because when an animal moves forward in its environment, its anterior end is the first to make contact with new dangers or opportunities. The concentration of integrating parts of the nervous system at the anterior end facilitates having a concentration of sense organs there.

Here we focus on the groups of animals with high degrees of centralization and cephalization. The nervous system in such animals consists of two major parts, the central and peripheral systems. The **central nervous system** (**CNS**) consists of relatively large structures that are composed principally of integrating neurons and their associated glial cells. The largest part of the CNS—containing the greatest number of neurons—is the **brain**.

The CNS functions as a control system, and like all control systems it needs to interact with sensors and effectors to function (see Concept 29.6). The sensors are the sensory cells and sense organs that we've just discussed. They provide the CNS with information on the animal's external environment and internal status. **Effectors** are cells or tissues that perform actions, that "carry out orders." Muscle cells are effectors because they can contract and produce motion under orders from the nervous system. Other types of effectors include glands, some of which secrete materials in response to signals from the nervous system, and specialized structures such as fish electric organs (which produce high currents or voltages when ordered to do so by the nervous system).

The **peripheral nervous system** (**PNS**) consists of neurons and parts of neurons that are located outside the CNS. These neurons are mostly engaged in two functions related to sensors and effectors. They bring sensory information from sense organs to the CNS. They also carry orders from the CNS to muscle cells or other effectors. For instance, if you touch a hot object with your fingers, neurons in the PNS carry sensory information from temperature sensors in your fingers to the CNS. Other neurons in the PNS carry signals from the CNS to muscles in your arm and fingers, ordering the muscles to contract and pull your fingers away. Nerves, as mentioned before, are bundles of axons grouped together in the PNS, analogous to telephone cables containing many wires.

Neurons are classed as interneurons, sensory neurons, or efferent (including motor) neurons.

- **Interneurons** are neurons that are confined to the CNS. Most neurons in the CNS are interneurons. For the most part, interneurons engage in integrative and information-storage functions.

- **Sensory neurons** function as sensory receptor cells or are neurons (also called afferent neurons) that carry signals to the CNS from sensory cells or organs.

(A)
Brain
Spinal cord

(B)
Brain
Subesophageal ganglion
Ganglia
Ventral nerve cord
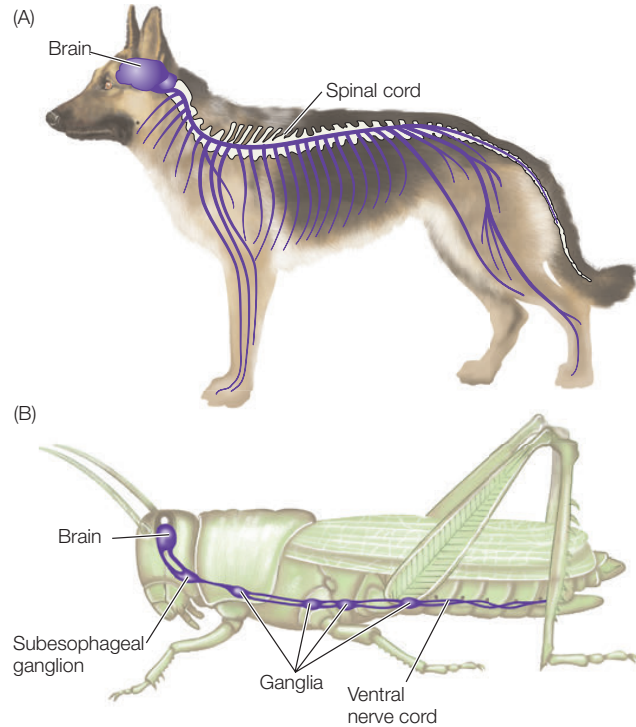
FIGURE 34.21 The Organization of Vertebrate and Arthropod Nervous Systems Only a few of the ganglia are shown in (B).

- **Efferent neurons** convey signals from the CNS to muscles or other effectors such as glands. Among these neurons, those that carry signals to skeletal muscles are called **motor neurons**.

The cellular components of nervous systems—the neurons, synapses, and sensory cells—are remarkably similar in the fundamental ways they function in all groups of animals. However, some animals differ substantially from others in the ways their neurons are organized to form their nervous systems. Let's briefly compare vertebrates and arthropods to see this point.

In vertebrates, the central nervous system is positioned in the dorsal part of the body (**FIGURE 34.21A**). It consists of two major parts: the brain in the head and the spinal cord that extends for most of the length of the body behind the brain. Both of these parts are to some degree hollow inside. In short, the vertebrate CNS is dorsal and hollow. The neurons and glial cells in the spinal cord form a continuous column of tissue, in the sense that the cord does not exhibit sharply differentiated subparts along its length.

In arthropods, such as insects and crayfish, the CNS is mostly positioned in the ventral part of the body (**FIGURE 34.21B**; see also Figure 32.4). It too consists of two major parts: the brain, and a ventral nerve cord that extends for most of the length of the body behind the brain. These structures are not hollow. In other words, the arthropod CNS is mostly ventral and solid. Moreover, instead of being a continuous column of tissue, the ventral nerve cord is composed of a series of alternating subparts. Arthropods are segmented (see Concept 23.1), and there is an enlarged structure called a ganglion (plural, ganglia) in each segment of the animal's body. Two strands of nervous tissue, called connectives, run from each ganglion to the next. (A word of warning: the

SYMPATHETIC DIVISION

Constricts pupils

Stimulates salivation

Constricts airways

Slows heartbeat

Stimulates digestion

Slight stimulation of glucose uptake and glycogen synthesis

Stimulates activity of intestines

Stimulates urinary bladder to contract

Stimulates penile erection or clitoral arousal

Dilates pupils

Inhibits salivation

Relaxes airways

Accelerates heartbeat

Inhibits digestion

Stimulates breakdown of glycogen and release of glucose

Inhibits activity of intestines

Relaxes urinary bladder

Stimulates orgasm, vaginal contraction

Cranial nerves

Cervical

Thoracic

Lumbar

Sacral

Celiac ganglion

Stimulates adrenal secretion of epinephrine and norepinephrine

Inferior mesenteric ganglion

Chain of sympathetic ganglia

→ Sympathetic postganglionic neurons (release norepinephrine)
→ Preganglionic neurons
→ Parasympathetic postganglionic neurons (release acetylcholine)

FIGURE 34.22 The Autonomic Nervous System The sympathetic and parasympathetic divisions work in opposition to each other in their effects on most organs. One stimulates an increase in activity, and the other causes a decrease in activity. The preganglionic neurons of both divisions mostly release acetylcholine.

word "ganglion" is also used in describing vertebrate nervous systems, but it has a very different meaning in discussing vertebrates and arthropods, as we'll soon see.)

The autonomic nervous system controls involuntary functions

The nervous system as a whole controls several types of effectors: skeletal muscles, smooth muscles, glands, and so forth. An important distinction is recognized between the part of the nervous system that controls skeletal muscles and the part that

controls all other effectors. This distinction is entirely different from the one between the CNS and PNS.

The **autonomic nervous system** (**ANS**) is the part of the nervous system (both CNS and PNS) that controls effectors other than the skeletal muscles. These effectors are called **autonomic** (or internal) **effectors**. We generally are unaware that they are being controlled, and we have little or no ability to influence them by conscious, voluntary effort. ("Autonomic" means involuntary or unconscious.) The ANS exists in all groups of vertebrates. Some invertebrates are also considered to have an ANS.

The ANS of a human or other mammal controls a wide variety of smooth muscles, such as those in the gut, blood vessels, bladder, eyes (e.g., iris muscles), airways of the lungs, and reproductive organs (e.g., during orgasm) (**FIGURE 34.22**). It controls a variety of exocrine glands (glands that secrete their

products elsewhere than into the blood) such as the tear and sweat glands. It also controls a few endocrine glands (glands that secrete hormones into the blood), most notably the adrenal medullary glands. And it controls color-change cells in fish, the acid-secreting cells of the stomach, and several other effectors.

The vertebrate ANS has three divisions. The **enteric division** is composed of the nerve cells internal to the gut wall (see Figure 29.14). Here we focus on the **sympathetic** and **parasympathetic divisions** (see Figure 34.22).

We can think of these two divisions as consisting mainly of efferent neurons that carry orders from the CNS to autonomic effectors. Each efferent pathway is composed of two neurons that synapse at a ganglion. (As we discuss this topic, remember that "ganglion" has different meanings in vertebrates and arthropods.) A vertebrate **ganglion** is a discrete, anatomically clustered set of neuron cell bodies in the PNS. The two neurons of each efferent pathway are described as preganglionic and postganglionic.

The preganglionic neurons of the parasympathetic division exit the CNS from two regions: a cranial region where the brain and spinal cord connect and a sacral region, the most posterior region of the spinal cord. The axons of these preganglionic neurons travel almost to their target cells before synapsing with the postganglionic neurons.

In contrast, the preganglionic neurons of the sympathetic division exit the CNS from the thoracic and lumbar regions of the spinal cord. Most of the ganglia of the sympathetic division lie next to the spinal cord, lined up in two chains on either side. Accordingly, the postganglionic neurons need to cover most of the distance to the target cells.

The most important neuronal difference between the sympathetic and parasympathetic divisions is that their postganglionic neurons employ different neurotransmitters where they synapse with target cells. The sympathetic neurons release norepinephrine as their neurotransmitter. The parasympathetic neurons release acetylcholine (ACh). In organs that receive both sympathetic and parasympathetic input, the target cells typically respond in opposite ways to norepinephrine and to ACh.

The sympathetic and parasympathetic divisions thus often work in opposition to each other, as emphasized in Figure 34.22. In this way, the two divisions—acting together—can control autonomic effectors in fine-tuned ways, adjusting their functions up or down as needed. For example, both divisions innervate the pacemaker of the heart. Sympathetic stimulation causes the heart rate to increase, and parasympathetic stimulation causes it to decrease.

The fight-or-flight response is the most famous effect of the sympathetic division. When the sympathetic division is strongly activated, it greatly increases the heart rate, force of heart contraction, and cardiac output. It dilates the passageways of the lungs and increases release of glucose into the blood from the liver. In all these ways, it prepares the body to meet an emergency. At the same time, it reduces less urgent activities such as digestion.
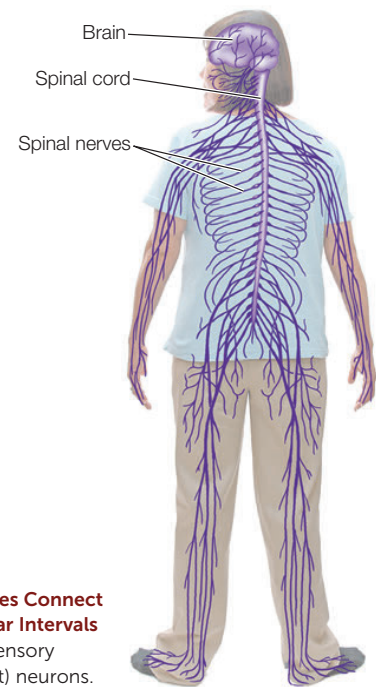
FIGURE 34.23 Spinal Nerves Connect to the Spinal Cord at Regular Intervals These nerves contain both sensory (afferent) and motor (efferent) neurons.

Spinal reflexes represent a simple type of skeletal muscle control

Now let's turn to control of the skeletal muscles. These effectors are controlled by the parts of the CNS and PNS other than the autonomic nervous system. Many of the neurons that control the skeletal muscles enter or leave the CNS in spinal nerves that connect with the spinal cord at regular intervals on each side (**FIGURE 34.23**). These nerves contain both motor neurons that carry orders from the CNS to the skeletal muscles and sensory neurons that bring information to the CNS, such as information from stretch receptors in the muscles.

As we all know, we can consciously or voluntarily control our skeletal muscles. This is possible because neurons in our brain can control signals in the motor neurons to the muscles. Also, however, some signals to the muscles originate by way of **spinal reflexes**. These are neuron-mediated responses that do not involve participation of the brain. Instead, all the neuron interactions occur in the spinal cord, requiring no conscious attention. Because spinal reflex systems are relatively simple, they are among the best-known vertebrate neural circuits.

We are all familiar with the spinal reflex known as the knee-jerk reflex (**FIGURE 34.24**). It occurs when a physician or nurse taps your knee with a little hammer and—if your nervous system is healthy—your lower leg jerks forward. The tap stretches the patellar tendon that connects your quadriceps muscle—the muscle on the forward-facing side of your thigh—to your tibia bone in your lower leg. The stretch caused by the tap stimulates stretch receptors in the muscle. These receptors initiate action potentials in sensory neurons, which propagate these action potentials along their axons to the spinal cord via a spinal nerve.

In the spinal cord, each sensory axon synapses with a motor neuron that serves the same muscle, the quadriceps. This synapse is excitatory and causes the motor neuron to generate action potentials. These signals travel in the axon of the motor

FIGURE 34.24 The Spinal Cord Coordinates the Knee-Jerk Reflex The spinal cord, shown in cross section, connects with spinal nerves by way of structures called the dorsal and ventral roots. Sensory neurons (red) enter the spinal cord through dorsal roots. Motor neurons (blue) leave via ventral roots. Some reflex pathways involve participation of an interneuron (green).

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Information Processing in the Spinal Cord
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3 The sensory neuron synapses with a motor neuron in the spinal cord.

Gray matter White matter

Dorsal root (sensory neurons)

Dorsal horn

Ventral horn

Ventral root (motor neurons)

Sensory neuron

Motor neurons

Spinal interneuron

Spinal nerve

4 The motor neuron conducts action potentials to the quadriceps, causing contraction.

Quadriceps muscle

2 Stretch receptors fire action potentials.

5 Simultaneously a spinal interneuron inhibits firing in the motor neuron for the antagonistic muscle.

1 A hammer tap stretches the tendon in the knee, stretching receptors in the quadriceps.

6 The leg jerks forward.

neuron via the spinal nerve to the quadriceps. There the action potentials excite the muscle at neuromuscular junctions. The muscle contracts, and your lower leg kicks forward.

There's more to the story. An additional important factor is that limb muscles are organized into opposing (antagonistic) pairs (see Concept 33.2). For contraction of the quadriceps to move your lower leg forward easily, the opposing muscle on the back of your thigh needs to relax. It does so because the sensory neurons coming from the stretch receptors also synapse onto interneurons in the spinal cord (see Figure 34.24, step 5). Those interneurons make inhibitory synapses onto the motor neurons that control the opposing muscle. The motor neurons are inhibited from stimulating that muscle to contract, allowing your lower leg to move forward when the quadriceps contracts.

These interactions among cells are unusually simple, but they nicely illustrate the interaction of sensory and motor neurons, interneurons, and the PNS and CNS in controlling contractions of skeletal muscles.

The most dramatic changes in vertebrate brain evolution have been in the forebrain

All vertebrate brains consist of three major regions: the forebrain (the most anterior part), midbrain, and hindbrain (the most posterior part). The most posterior part of the hindbrain is the medulla oblongata. All information traveling between the brain and spinal cord must pass through the medulla

oblongata. During the course of vertebrate brain evolution, the overall shape and relative size of the medulla oblongata have changed little (**FIGURE 34.25**).

In contrast, the cerebral hemispheres, which are a major component of the forebrain, have undergone dramatic changes during vertebrate evolution. Both mammals and birds have evolved especially large cerebral hemispheres (see Figure 34.25). This is noteworthy because the cerebral hemispheres are particularly important in carrying out high-order sensory, motor, and integrative functions. In humans, for example, the cerebral hemispheres are responsible for language and reasoning.

Mammals and birds also have brains that are about 10 times larger than the brains of lizards or other nonavian reptiles that are the same in body size. A mouse, for example, has a brain about 10 times larger than that of a mouse-sized lizard, and a parrot has a brain about 10 times larger than that of a parrot-sized lizard. The cerebral hemispheres account for much of this difference.

There are two take-home messages from these comparisons. First, mammals and birds have evolved strikingly large cerebral hemispheres, the neurons and glia of which are of enormous importance in high-order brain function. Second, brain size matters. The evolution of enhanced functionality in mammals and birds has gone hand in hand with large increases in the numbers of neurons. From this vantage, it is significant that primates and dolphins have the largest brains, for their body sizes, of all mammals.
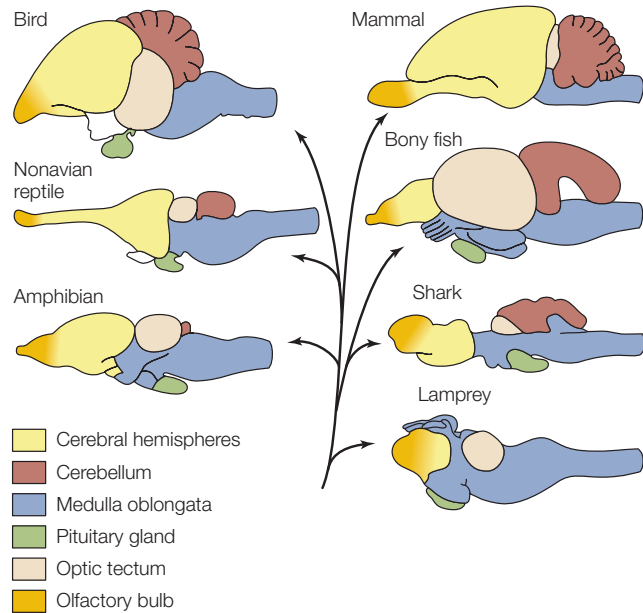
FIGURE 34.25 Evolution of the Vertebrate Brain A reasonably representative brain of a modern species in each group is shown. In the mammal, the large cerebral hemispheres keep us from seeing the pituitary, which is found in a position similar to other groups. The optic tectum is involved in processing visual information. Medulla oblongata, a term used with several variations in exact meaning, is here used in its most general sense.

We need to be careful not to overextrapolate the significance of these broad trends, however. Brain size matters in a general sense, but it does not matter when we look at all particulars. Some animals with small brains exhibit stunning behavioral capacities (see Figure 40. 8). Moreover, among human

beings—where the subject has been studied for well over a century—all the evidence available indicates that individual intelligence is not correlated with individual brain size. We know too little about brain function to explain how all these pieces of the puzzle fit together.

Location specificity is an important property of the mammalian cerebral hemispheres

In humans, the cerebral hemispheres (which together make up the cerebrum) are so enlarged that they cover most other parts of the brain. The outermost layer of the cerebral hemispheres is the **cerebral cortex**, a thin, important layer rich in cell bodies. The cerebral cortex is only about 4 millimeters thick, but it is folded into ridges (convolutions) that increase its size. The cerebral hemispheres play major roles in sensory perception, learning, memory, and conscious behavior. Indeed, they provide the neural resources for the great intellectual capacity of humans.

A curious feature of the mammalian nervous system is that the left side of the body is served (in both sensory and motor aspects) mostly by the right side of the brain, and the right side of the body is served by the left side of the brain. Thus sensory input from your right hand goes to your left cerebral hemisphere, and sensory input from your left hand goes to your right cerebral hemisphere.

Earlier we noted that all action potentials arriving in the brain are the same, even though some represent visual images, others represent sounds, and still others represent odors. Some action potentials from a person's touch receptors represent touches to the fingers, whereas others represent touches to the abdomen or feet. How does the brain process a simple, invariant electrical event—an action potential—and develop an accurate perception of the type of stimulus (sight, sound, or
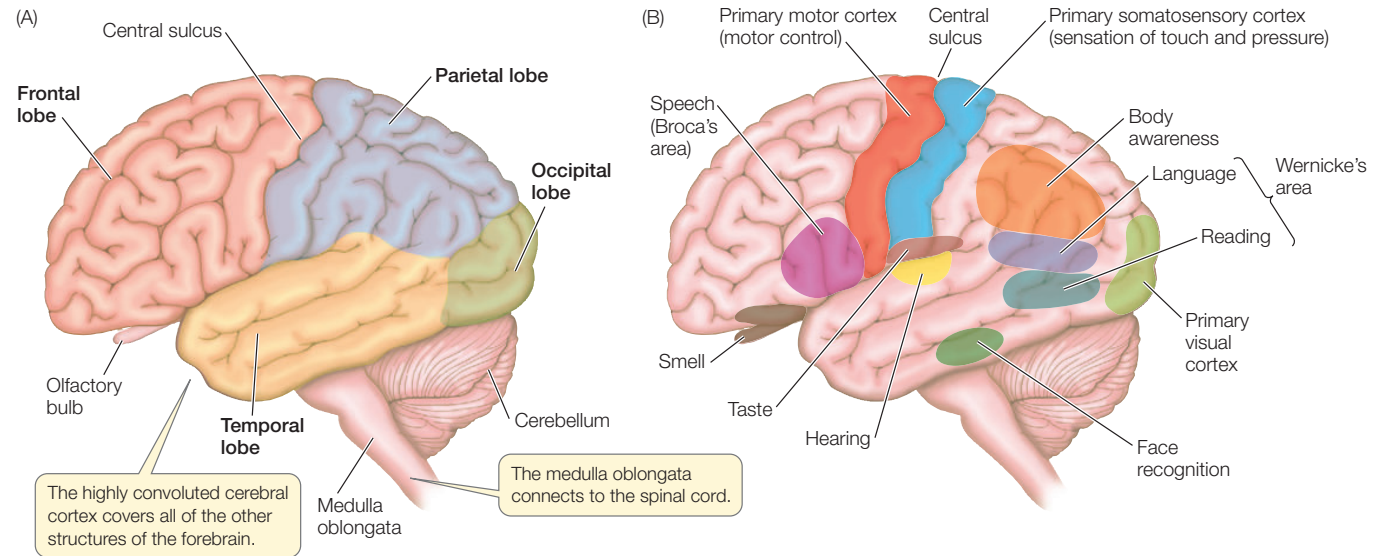
FIGURE 34.26 The Human Left Cerebral Hemisphere (A) The major anatomical regions of the cerebral cortex. (B) Different areas of the cerebral cortex have specific, localized functions.

Go to ACTIVITY 34.5 Structures of the Human Brain
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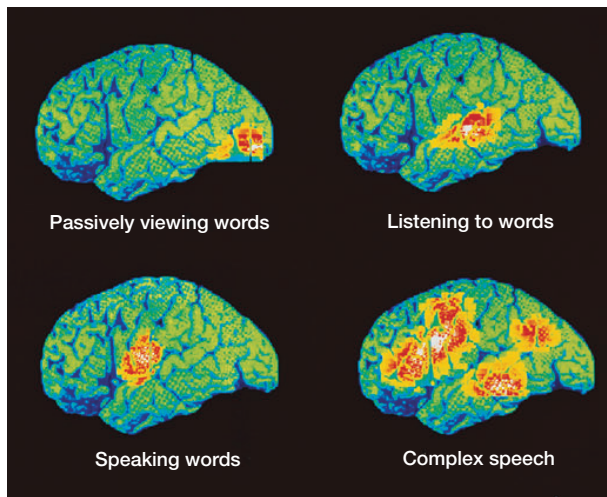
FIGURE 34.27 Imaging Techniques Reveal Active Parts of the Brain Positron emission tomography (PET) scanning reveals the brain regions activated by various aspects of language use. Radioactively labeled glucose is given to the subject. Brain areas take up radioactivity in proportion to their metabolic use of glucose. The PET scan visualizes levels of radioactivity in specific brain regions when a particular activity is performed. The red and yellow areas are the most active, green and blue the least active.

odor) that caused it, or an accurate perception of the place of origin of the stimulus?

Location specificity is one of the major mechanisms the brain uses to interpret the action potentials it receives. In each cerebral hemisphere, various specific regions are specialized in adults to carry out specific sensory and motor functions. Distinct regions are responsible for vision, hearing, and smell, for example (**FIGURE 34.26**). Axons from the retinas connect to the visual cortex, the region responsible for vision. Similarly, axons from the cochleas in the ears and axons from the odorant receptor cells in the nasal epithelium connect to the regions responsible for hearing and smell, respectively. Because of these physical connections, axons are effectively labeled in regards to the meaning of the action potentials they bring to the brain.

Motor functions are also localized. Moreover, combined sensory and motor functions often occur in certain, relatively localized brain areas. An explosive area of research at present is the exploration of sensory, motor, and combined sensory and motor localization by use of imaging methods that allow us to visualize where neurons exhibit evidence of increased electrical activity. For instance, the positron emission tomography (PET) images in **FIGURE 34.27** show brain regions where there is evidence of increased neuronal activity when several language functions are carried out. Functional magnetic resonance imaging (fMRI) is another technique used for similar research.

Localization of function is not limited to the cerebral hemispheres. **FIGURE 34.28**, for example, is a fMRI image of the brain of a person experiencing fear. The image indicates increased neuronal activity in the amygdala, a part of the forebrain (outside the cerebral hemispheres) that is well known to participate in fear responses. Abundant evidence points to the hippocampus, still another part of the forebrain, as being critical for spatial learning

and memory (we discussed synaptic plasticity in the hippocampus in Concept 34.3). Damage to the hippocampus renders mice and rats unable to solve maze problems that depend on learning the relationships of objects in space.

Brain regions have maps in some cases. In such regions, the parts of the brain that serve various anatomical regions of the body are physically related to each other in ways that mirror the physical relationships of the rest of the body. A well-known example is seen in the somatosensory ("body sensing") part of the cerebral cortex. Regions of the cerebral cortex that process sensory information from touch and pressure receptors on the body surface in the leg, hip, trunk, neck, and head are lined up (**FIGURE 34.29A**). Similarly, regions processing such information from the eyes, nose, lips, and jaw are lined up. In the illustration, the size of each body part in the drawing reflects the amount of cortical area devoted to the part. The large size of the lips, for example, reflects the fact that a large area is devoted to processing sensory signals from the lips.

Near the mapped somatosensory area of the cortex is a parallel, mapped motor area. You can see from the size of drawings of body parts in the motor area (**FIGURE 34.29B**) that large areas of motor cortex are devoted to sending motor signals to the hands and face.

Not all parts of the brain fit easily into the concepts of localized function and mapped brain regions. Thus we need to recognize that these concepts are both important and limited in their ability to clarify brain function.

A curious aspect of language processing in humans is that it resides principally in one cerebral hemisphere—which in about 85 percent of people is the left hemisphere. The two hemispheres share responsibilities for other functions. Individuals with damage to the left hemisphere frequently experience deficits in their ability to use or understand

A person who is afraid shows increased activity in the amygdala.
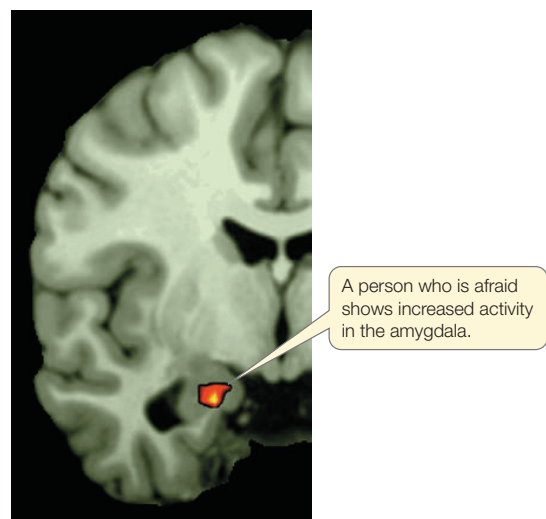
FIGURE 34.28 Source of the Fear Response Frightening situations—or even memories of such situations—activate the amygdala, as shown in this functional magnetic resonance image (fMRI) of the left side of the brain of a person experiencing fear.

FIGURE 34.29 The Body Is Represented in Maplike Ways in the Primary Somatosensory and Primary Motor Parts of the Cerebral Cortex The amount of cortical tissue devoted to various body parts is not even. More cortical tissue is devoted to some body parts than others, as reflected in the sizes of the parts in the drawings. (A) The primary somatosensory cortex. (B) The primary motor cortex.

The left side of the cerebral cortex communicates with the right side of the body, and vice versa.

(A) Primary somatosensory cortex

(B) Primary motor cortex
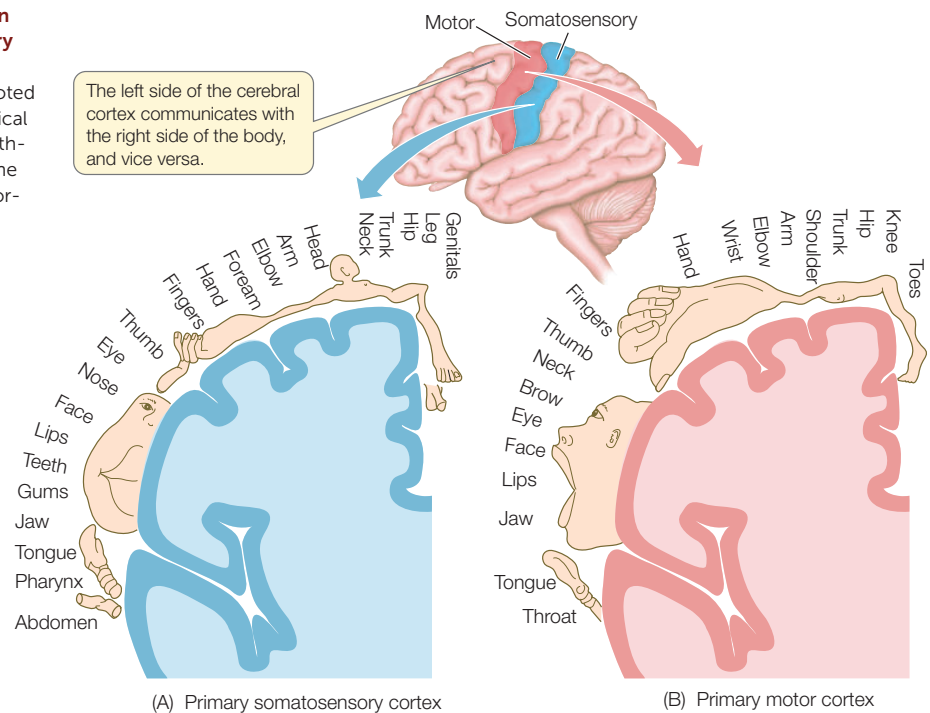
words. The deficit depends on the specific part of the left hemisphere that is damaged. Damage to Broca's area, for example, interferes with speech and writing, whereas damage to Wernicke's area interferes with understanding language (see Figure 34.26B).

The development of a full understanding of the brain is one of the great frontiers of twenty-first century biology. Many major unanswered questions remain. "What is consciousness?" is one of the most compelling.

CHECKpoint   CONCEPT 34.5

✓ Give two specific examples in which the sympathetic and parasympathetic divisions exert opposite effects on the function of an organ.

✓ Why is localization of function in the brain critical for sensory perception?

✓ What is cephalization of the nervous system, and why has it evolved in so many animals? Try to think this through using the knowledge you have gained about the relationships between the brain and sense organs.

Q How might the star-nosed mole's brain be specialized to process information from its nose?

ANSWER Just as large areas of cerebral cortex are devoted to processing sensory information from a person's lips and fingers (see Figure 34.29A), large areas of a star-nosed mole's cerebral cortex are devoted to processing sensory information from the tentacles of its nose. The drawings in **FIGURE 34.30A** show a mole in two ways: first, proportioned as it actually is and, second, proportioned in a way that reflects how much cortical tissue is devoted to processing sensory information from its specific body parts, such as its nose, eyes, whiskers, and anterior digging feet. Note that the amount of cortical tissue devoted to processing signals from the nose is larger than that devoted to the rest of the mole's body.

Additionally, a localized part of the cerebral cortex is devoted to receiving sensory information from the nose, and this part of the cortex is highly mapped. The tentacles surrounding each nostril are numbered from 1 to 11 in order from the most dorsal-pointing tentacle to the most ventral-pointing one. **FIGURE 34.30B** shows the relevant part of the cortex, including the places in the cortex that receive axons from the numbered tentacles. Note that the map of the cortical regions exactly mirrors the arrangement of the tentacles. By means of such localization in the cortex, the brain can readily determine the tentacle that originates any action potential that arrives by way of any particular axon from the nose.

The concepts of localized function and mapped brain regions apply to the star-nosed mole as much as they do to people, reflecting the fact that the mole's entire nervous system—including its sense organs—is highly integrated.

(A) Cortical magnification in star-nosed mole

Anatomical proportions

Proportion of cortex devoted to body regions

(B)

Dorsal

Mouth

Ventral
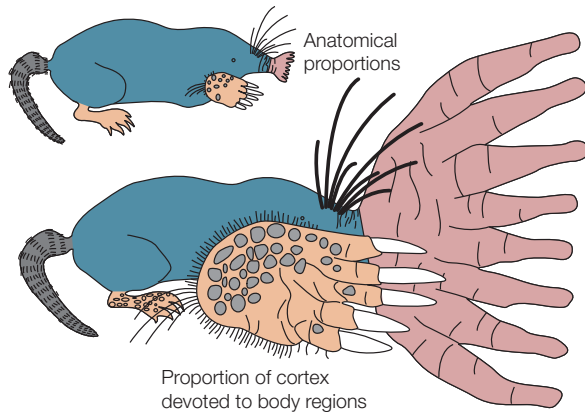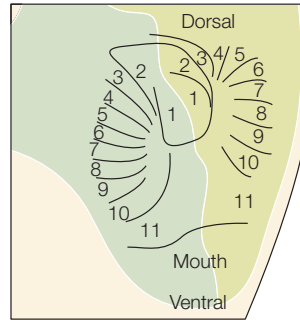
FIGURE 34.30 Representation of the Nose of the Star-nosed Mole in the Cerebral Cortex (A) Proportions of the body, and proportions of the cortex devoted to processing information from various parts of the body. (B) A part of the cerebral cortex, showing where sensory information arrives from the numbered tentacles of the nose.

SUMMARY

CONCEPT 34.1 Nervous Systems Are Composed of Neurons and Glial Cells

■ A **neuron** (nerve cell) is **excitable**; it is specially adapted to generate and propagate electric signals, typically in the form of action potentials. Neurons make functionally relevant contact with other cells at **synapses**.

■ Neurons usually have four anatomical regions: a set of **dendrites**, a **cell body**, an **axon**, and a set of **presynaptic axon terminals**. Dendrites receive signals from other neurons, and presynaptic axon terminals send signals to other cells. **Review Figure 34.2**

■ Unlike neurons, **glial cells** are usually not excitable. In vertebrates, they include **oligodendrocytes**, which form insulating **myelin** sheaths around axons in the brain and spinal cord, and **Schwann cells**, which perform the same function outside the brain and spinal cord. **Review Figure 34.3**

CONCEPT 34.2 Neurons Generate Electric Signals by Controlling Ion Distributions

■ Neurons have an electric charge difference across their cell membranes, called the **membrane potential**. The membrane potential is created by ion transporters and channels. The membrane potential is considered to be negative if the inside of the cell membrane is negative in relation to the outside. In inactive neurons, the membrane potential is called the **resting potential** and is negative. **Review Figure 34.4 and ANIMATED TUTORIAL 34.1**

■ The **sodium–potassium pump** concentrates K^+ on the inside of a neuron and Na^+ on the outside. In a resting neuron, K^+ leak channels allow K^+ to diffuse through the cell membrane. The resting potential is negative because a negative charge on the inside of the cell membrane is needed to balance the tendency for K^+ to diffuse outward because of its high internal concentration.

■ The **Nernst equation** can be used to predict a neuron's membrane potential. **Review ACTIVITY 34.1**

■ Most ion channels are gated: they open only under certain conditions. **Voltage-gated channels** open or close in response to local changes in the membrane potential. **Stretch-gated channels** open or close in response to stretch or tension applied to the cell membrane. **Ligand-gated channels** have binding sites where they bind noncovalently with specific chemical compounds that control them. **Review Figure 34.5**

■ When gated ion channels in the cell membrane of a neuron open or close, changes of the membrane potential called **depolarization** or

hyperpolarization can occur. Depolarization occurs when the inside of the cell membrane becomes less negative in relation to the outside.

■ When depolarization occurs, a key question is whether it is great enough for a voltage threshold to be reached. If the threshold is not reached, changes in the membrane potential are **graded**. **Review Figure 34.6A**

■ An **action potential**, or **nerve impulse**, is a rapid reversal in membrane potential across a portion of the cell membrane resulting from the opening and closing of voltage-gated Na^+ channels and K^+ channels. The voltage-gated Na^+ channels open when the cell membrane depolarizes to the voltage threshold. **Review Figures 34.6B, 34.7, and 34.8, and ANIMATED TUTORIAL 34.2**

■ An action potential is an all-or-none event that is conducted (propagated) along the entire length of a neuron's axon without any loss of magnitude. It is conducted along the axon because local current flow depolarizes adjacent regions of membrane so they reach voltage threshold. In myelinated axons, action potentials jump between **nodes of Ranvier**, patches of membrane that are not covered by myelin.

CONCEPT 34.3 Neurons Communicate with Other Cells at Synapses

■ A **synapse** is a cell-to-cell contact point specialized for signal transmission from one cell to another. Most synapses are **chemical synapses** (with **neurotransmitters**). Some are **electrical synapses**.

■ At a chemical synapse, when an action potential reaches the axon terminal of the presynaptic neuron, it causes the release of a neurotransmitter, which diffuses across the synaptic cleft and binds to receptors on the cell membrane of the postsynaptic cell. The postsynaptic cell is usually another neuron or a muscle cell. **Review ANIMATED TUTORIALS 34.3 and 34.4**

■ The vertebrate **neuromuscular junction** is a well-studied chemical synapse between a motor neuron and a skeletal muscle cell. Its neurotransmitter is acetylcholine (ACh). **Review Figure 34.9**

■ Synapses can be fast or slow, depending on the nature of their receptors. **Ionotropic receptors** are ion channels and generate fast, short-lived responses. **Metabotropic receptors** initiate second-messenger cascades that lead to slower, more sustained responses.

■ There are many different neurotransmitters and types of receptors. The action of a neurotransmitter depends on the receptor to which it binds.

SUMMARY   *(continued)*

■ Synapses between neurons can be either **excitatory** or **inhibitory**. A postsynaptic neuron integrates information by summation of graded postsynaptic potentials (which may be excitatory or inhibitory), in both space (spatial summation) and time (temporal summation). **Review Figure 34.11**

■ **Synaptic plasticity** is the process by which synapses in the nervous system of an individual animal can undergo long-term changes in their functional properties. Such changes are probably important in learning and memory.

CONCEPT 34.4 **Sensory Processes Provide Information on an Animal's External Environment and Internal Status**

■ **Sensory receptor cells** transduce information about an animal's external and internal environment into action potentials.

■ Sensory receptor cells have **sensory receptor proteins** that respond to sensory input, causing a graded change of membrane potential called a receptor potential.

■ An **ionotropic receptor cell** typically has a receptor protein that is a stimulus-gated Na^+ channel. A **metabotropic receptor cell** typically has a receptor protein that activates a G protein when exposed to the stimulus. **Review Figure 34.12**

■ The action potentials sent to the brain are interpreted as particular sensations based on which neurons in the brain receive them.

■ **Mechanoreceptors** are cells that respond specifically to mechanical distortion of their cell membrane and are typically ionotropic. Stretch receptors are mechanoreceptors. **Review Figures 34.13 and 34.14 and ANIMATED TUTORIAL 34.5**

■ **Chemoreceptors** are metabotropic receptor cells that respond to the presence or absence of specific chemicals. The sense of smell depends on chemoreceptors.

■ In the mammalian auditory system, sound pressure waves enter the auditory canal, where the tympanic membrane vibrates in response to them. The movements of the tympanic membrane are relayed to the oval window. Movements of the oval window create sound pressure waves in the fluid-filled **cochlea**. **Review Figure 34.15 and ACTIVITY 34.2**

■ The **basilar membrane** running down the center of the cochlea is distorted by sound pressure waves at specific locations that depend on the frequency of the waves. These distortions cause the localized bending of stereocilia of hair cells, mechanoreceptors in the organ of Corti. Pitch or tone is encoded by the specific locations along the basilar membrane where action potentials are generated. **Review Figure 34.16 and ANIMATED TUTORIAL 34.6**

■ **Photoreceptors** are sensory receptor cells that are sensitive to light. The photosensitivity of photoreceptor cells involved in vision depends on the absorption of photons of light by sensory receptor proteins called **rhodopsins**. Vertebrates have two types of visual photoreceptor cells, **rods** and **cones**. Color vision in humans arises from three types of cone cells with different spectral absorption properties. **Review Figure 34.17 and ANIMATED TUTORIAL 34.7**

■ When excited by light, vertebrate visual photoreceptor cells hyperpolarize. They do not produce action potentials. **Review Figure 34.18**

■ The vertebrate **retina** consists of four types of integrating neurons and the photoreceptor cells lining the back of the eye. Extensive processing of visual information occurs in the retina and also in the brain. **Review Figure 34.19 and ACTIVITIES 34.3 and 34.4**

■ Arthropods have **compound eyes** consisting of many optical units called **ommatidia**, each with its own lens. **Review Figure 34.20**

CONCEPT 34.5 **Neurons Are Organized into Nervous Systems**

■ Nerve nets are the simplest nervous systems. As nervous systems evolved further, they followed two major trends: **centralization**—the clustering of neurons into centralized integrating organs—and **cephalization**—the concentration of major integrating centers at the anterior end of the animal's body.

■ The **brain** and spinal cord make up the **central nervous system** (**CNS**). Neurons that extend or reside outside the brain and spinal cord make up the **peripheral nervous system** (**PNS**).

■ Neurons are classed as **interneurons**, **sensory neurons**, or **motor neurons**.

■ In vertebrates, the central nervous system is positioned in the dorsal part of the body. In arthropods, such as insects and crayfish, the CNS is primarily positioned in the ventral part of the body. **Review Figure 34.21**

■ The **autonomic nervous system** (**ANS**) is the part of the nervous system (both CNS and PNS) that controls involuntary functions. Its **enteric**, **sympathetic**, and **parasympathetic divisions** differ in anatomy, neurotransmitters, and effects on target tissues. The sympathetic and parasympathetic divisions usually exert opposite effects on an organ. **Review Figure 34.22 and ANIMATED TUTORIAL 34.8**

■ The vertebrate brain consists of a forebrain, midbrain, and hindbrain. During the course of vertebrate evolution, some parts of the brain (e.g., the medulla oblongata) have remained relatively unchanged, whereas other parts (e.g., the cerebral hemispheres) have changed dramatically. **Review Figure 34.25**

■ The cerebral hemispheres, including the **cerebral cortex** of each hemisphere, are the dominant structures of the human brain. **Review Figure 34.26**

■ In each cerebral hemisphere, specific regions are specialized to carry out specific sensory and motor functions, for example language functions and fear. **Review Figures 34.26–34.28 and ACTIVITY 34.5**

■ Some brain regions have maps: the parts of the brain that serve various anatomical regions of the body are physically related to each other in ways that mirror the physical relationships of the rest of the body. Examples are the somatosensory ("body sensing") and motor areas of the cerebral cortex. **Review Figures 34.29 and 34.30**

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is34

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Control by the Endocrine and Nervous Systems

This young man's muscles are being controlled simultaneously by the nervous and endocrine systems.

Two types of control of skeletal muscle are evident in this scene. First are the quick, moment-by-moment moves of the game. To return the ball with a backhand shot, this player runs to a good position to execute his return, plants his feet, pulls back the racket, focuses his eyes on the ball, and swings—all in a few seconds. His nervous system controls the muscle contractions responsible for these quick moves. In addition, this player's muscles are far different than they were before he entered puberty. His muscles have become more highly developed, larger, and stronger since puberty began—a process requiring years. His endocrine system has controlled these long-term muscle changes.

Castration revealed long ago that the testes—although they are just one part of the body—play a critical role throughout the body in male maturation. No one knows how the practice of castration began, because it started in prehistorical times, before written historical records

were kept. Presumably, farmers discovered that removal of the testes rendered male farm animals more docile, and then the practice was extended to people such as harem servants. Boys castrated prior to puberty do not undergo normal adolescent muscular and skeletal development, and their voices do not deepen because their vocal cords do not increase in length. By 1700, several thousand prepubescent boys were castrated each year in Italy to create adult male singers with high voices. Some of these castrati, as they were called, are legendary for being among the greatest opera singers the world has ever known.

The effects of castration pointed to the involvement of the testes in male maturation for thousands of years, but not until 1849 did someone carry out scientific experiments to understand why the testes matter. The German physiologist Arnold Berthold knew from farmers that when male chickens are castrated prior to sexual maturation,

they do not develop adult male characteristics. The fleshy crest (comb) on the top of a castrated male's head remains immature, for example. After Berthold castrated young male chickens, he transplanted surgically isolated testes into their bodies at abnormal locations. These chickens then matured normally, complete with adult combs.

These experiments started the modern study of endocrinology. Berthold concluded that the testes secrete a substance into the blood that circulates with the blood to all parts of the body and controls the development of other tissues. Substances of this type were named hormones about 50 years later, and in 1935, the key substance secreted by the testes was chemically identified and named testosterone.

Q Why are the skeletal muscles under control of both the nervous system and the endocrine system?

The Endocrine and Nervous Systems Play Distinct, Interacting Roles

All the cells in an animal's body need to act together harmoniously. During muscular exercise such as a game of tennis, for example, cells in the breathing muscles and heart need to work harder to ensure that the cells of the exercising skeletal muscles receive O_2 at an accelerated rate. Cells in the liver also need to contribute, by mobilizing stored glucose for use by the exercising muscles. When we survey all the tissues of the body, we quickly recognize that various cells are specialized to produce forces, store nutrients, make gametes, or secrete digestive juices. Some cells must also be specialized to carry out control and coordination throughout the body.

We saw in Chapter 34 that nerve cells are one type of cell specialized for control and coordination. Endocrine cells are the second principal type of cell specialized in this way. We will define endocrine cells and hormones in a formal way at the beginning of Concept 35.2. Here it's sufficient to say simply that endocrine cells secrete hormones into the blood. Nerve and endocrine cells work together to ensure that an animal functions in ways that are harmonious and coordinated, rather than clashing and disjointed.

Nerve and endocrine cells need to communicate with other cells to carry out their functions of control and coordination. Most such intercellular communication takes place by means of chemical signals that are released from a nerve cell (neuron) or an endocrine cell and travel to another cell, called the **target cell** (**FIGURE 35.1**). The signal molecules bind to receptors on the target cell, triggering a response in it. These responses can affect an animal's function, anatomy, and behavior.

The nervous and endocrine systems work in different ways

Most tissues and organs in an animal's body are affected by both the nervous and endocrine systems. The heart, for example, is subject to both nervous and endocrine controls. Why have two systems evolved rather than just one? The answer is undoubtedly complicated. One reason is that the nervous and endocrine systems work in different ways. The two systems are specialized to carry out different types of control and coordination.

As we saw in Chapter 34, neurons typically operate in ways similar to wires in a telephone system or computer network. A neuron is a cell specially adapted to generate brief signals—the nerve impulses, or action potentials—that travel at high speeds along its axon (see Figure 35.1A). The axon makes functional contacts—synapses—with only certain target cells, and only those cells are affected by the neuron. Each axon terminal releases a chemical signal—neurotransmitter—that affects the cell with which it has synaptic contact. This target cell responds quickly to the signal, and the signal ends rapidly because the neurotransmitter molecules released into a synapse are immediately either broken down or taken up into cells.

We see that nervous control has two essential features: it is *fast* and *addressed*. Neuronal signals are *fast* in that they travel
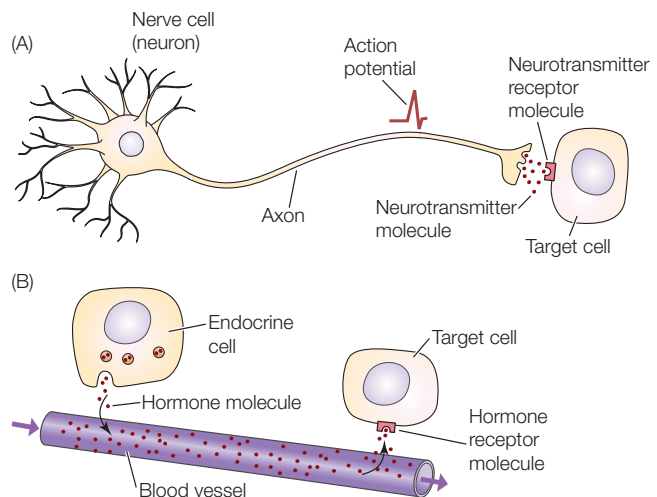
FIGURE 35.1 Chemical Signaling by Nerve and Endocrine Cells Both nerve cells (neurons) and endocrine cells release chemical signaling molecules (red dots) that affect target cells. (A) A nerve cell makes synaptic contact with a target cell at the end of its axon. Action potentials in the axon trigger release of neurotransmitter molecules at the synapse. These molecules then bind with neurotransmitter receptor molecules in the postsynaptic cell, initiating a response in the postsynaptic cell. (B) An endocrine cell releases hormone molecules into the blood. These molecules circulate throughout the body and bind with hormone receptor molecules on target cells, initiating responses.

rapidly and begin and end abruptly. Like a letter or an e-mail, they are *addressed* because they are delivered to highly defined target cells.

Unlike nerve cells, endocrine cells release their chemical signals—the hormones—into the blood. These chemical signals are then carried throughout the body by the circulation of the blood, potentially reaching all the cells present in most or all tissues and organs (see Figure 35.1B).

Endocrine control has two essential features, both of which distinguish it from nervous control: it is *slow* and *broadcast*. Individual hormonal signals are relatively *slow* because they operate on much longer time scales than individual neuronal signals. Initiation of hormonal effects requires at least several seconds or minutes because a hormone, once it is released into the blood, must circulate to target tissues and diffuse to effective concentrations within the tissues before it can elicit responses. After a hormone has entered the blood, it may act on target cells for a substantial amount of time—minutes, hours, or even days—before its blood concentration is reduced to ineffective levels by metabolic destruction or excretion. A final reason that endocrine signals can be slow is that they sometimes act on target cells by altering gene transcription and protein synthesis—processes that require at least many minutes to have effects on cell function.

Endocrine control is said to be *broadcast* because after a hormone is released into the blood, all cells in the body are potentially exposed to it. Those that respond are the ones that express a receptor protein for the hormone. That is, hormone action

has specificity, but its specificity depends not on addressed delivery of the chemical signal but on which cells have receptor molecules for the signal. In any one tissue, it is common for all cells to express receptor molecules for a particular hormone, meaning all cells in the tissue respond to a single release of the hormone. Moreover, cells in more than one tissue may respond, perhaps with different cell types responding in different ways. In principle, hormones may exert either limited or widespread effects, but in practice they commonly affect at least an entire tissue, and often multiple tissues.

Nervous systems and endocrine systems tend to control different processes

Lines of communication in the nervous system are capable of much finer control—in both time and space—than is possible for endocrine systems. Not surprisingly, the two systems tend to be used to control different functions in the body. The nervous system controls predominantly the fine, rapid movements of discrete skeletal muscles. The endocrine system typically controls more widespread, prolonged activities such as developmental or metabolic changes.

Consider, for example, the tennis player in our opening photo. Tennis requires rapid body movements that anticipate ball movements and an opponent's possible responses. It also requires specific control of multiple skeletal muscles in split-second time. These functions could only be coordinated by the nervous system. In contrast, the coordination of adolescent development requires adjusting the activities of many tissues over a prolonged period. In principle, the nervous system *could* carry out a coordination task of this sort. To do so, however, the nervous system would require tens of thousands of discrete axons between integrating centers (such as the brain) and target cells, and would need to send trains of impulses along all these axons for years. In contrast, endocrine glands can accomplish this task with greater economy, by secreting a relatively small number of long-lasting chemicals into the blood.

Most tissues in an animal's body are under dual control of the nervous and endocrine systems, as noted earlier. The tennis player's skeletal muscles illustrate this dual control. A single muscle, such as the biceps, typically contains thousands of muscle cells innervated by more than 100 motor neurons. The nervous system can selectively activate a few, many, or all of the motor neurons to control rapidly and precisely the amount of force the player's biceps generates. And it can separately control each of the other skeletal muscles in his body. Simultaneously—as days and months go by—testosterone and other hormones secreted steadily by endocrine glands during adolescence facilitate widespread muscle growth and development.

The nervous and endocrine systems work together

In spite of the differences between the nervous and endocrine systems, these two systems do not operate in mutually exclusive ways. On the contrary, they work together closely, and each system can affect the other.

The nervous system exerts control over the endocrine system in many well known ways. The brain initiates endocrine development of the gonads during puberty in mammals, for example. Moreover, throughout life the brain helps control the secretion of gonadal hormones, thyroid hormones, and other hormones. We will discuss these controls in Concepts 35.3 and 35.4.

Conversely, the endocrine system sometimes exerts control over the nervous system. Sex hormones from the testes and ovaries affect brain development during mammalian puberty, for example. Studies on rats, hamsters, and other research animals indicate that the sex hormones have an organizing effect on the development of certain neural circuits in the brain so that the circuits develop some different specific properties in females and males.

Chemical signaling operates over a broad range of distances

Animals use chemical signaling over a very broad range of spatial scales (**FIGURE 35.2**). In this concept we have discussed chemical signaling on two spatial scales—the two different scales of distance seen in nervous signaling and in endocrine signaling. However, chemical signaling also takes place on even shorter and even longer scales of distance.
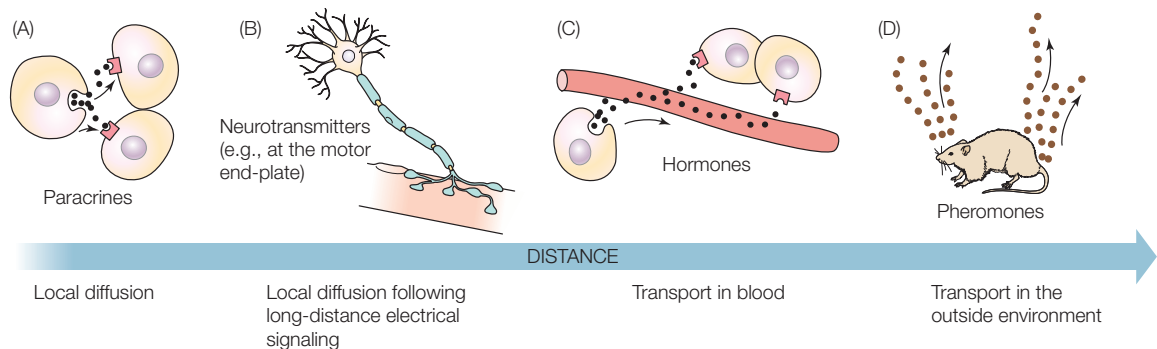
FIGURE 35.2 **Chemical Signaling Occurs over a Broad Range of Spatial Scales** (A) Cells communicate with neighboring cells in a tissue via molecules called paracrines. (B) Neurons have long processes (axons), at the ends of which they release molecules called neurotransmitters to communicate across synapses with target cells. (C) Endocrine cells secrete molecules called hormones that can travel long distances by circulating in the blood. (D) Animals give off molecules called pheromones that can communicate specific information (such as their sex) over very long distances to other members of their species.

Many chemical signals diffuse from cell to cell in a tissue without entering the blood. Two such types of signals are paracrines and autocrines. Paracrines are chemicals that are secreted by one cell and affect the functions of other, neighboring cells in a tissue by binding to receptors in or on the neighboring cells (see Figure 35.2A). Autocrines are chemicals that are secreted by a cell into the surrounding intercellular fluids and then diffuse to receptors on that very same cell and affect its functions (see Figure 5.10).

Neurotransmitters and hormones work at intermediate distances. Neurotransmitters resemble paracrines in that they move just short distances from cell to cell by diffusion, because only the width of a synaptic cleft separates a presynaptic neuron from its target cell. However, the secretion of neurotransmitters is controlled from farther away by electrical signals that travel the length of the presynaptic cell (see Figure 35.2B). Hormones are carried to the farthest reaches of an animal's body by the circulation of the blood (see Figure 35.2C).

Pheromones are chemical signals that an individual animal releases into its external environment and that exert specific effects (e.g., behavioral effects) on other individuals of the same species (see Figure 35.2D). Some pheromones travel hundreds of meters before reaching their targets.

CHECKpoint CONCEPT 35.1

✓ Why is endocrine control described as slow and broadcast?

✓ Why is it correct to say that both nervous and endocrine control depend on chemical signaling?

✓ If all cells in the body are bathed by a hormone, why are some affected while others are not?

Now that we've compared and contrasted the nervous and endocrine systems, let's turn our spotlight on the endocrine system.

CONCEPT 35.2 Hormones Are Chemical Messengers Distributed by the Blood

In Chapter 34 we discussed the nervous system in detail. Now we will turn to a detailed discussion of the endocrine system, starting by defining its fundamental properties.

Animals have two types of glands, which are termed exocrine and endocrine. All glands produce and secrete materials. The exocrine glands typically have outflow tubes, called ducts, that carry their secretions away. Examples include the mammary, salivary, and tear glands. In each case, the gland secretes a material (milk, saliva, or tears) that flows out by way of tubular ducts. The prostate gland, which contributes fluid to the semen, is another exocrine gland.

The **endocrine glands** do not have ducts (and therefore are sometimes called ductless glands). **Endocrine cells**, by definition, secrete their products into the blood flowing through nearby blood capillaries or other blood passages (keep in mind that in this book we use the term blood to refer to the fluid circulating in the circulatory system in all animals; see Concept 32.1). Because endocrine cells secrete into the blood, endocrine glands require only a blood supply, not ducts, for their secretions to be carried away.

In some cases, endocrine cells exist as single cells scattered within a tissue composed mostly of other cells, as we have observed in the gut epithelium (see Concept 30.5). In other cases, endocrine cells are aggregated (grouped) together to form discrete tissues or organs. These are the endocrine glands. Examples include the thyroid gland and adrenal glands.

The testes, ovaries, and pancreas illustrate a complexity that sometimes arises: these organs are composed of a mix of endocrine and non-endocrine tissues. A vertebrate testis, for example, consists mostly of tiny, non-endocrine tubules in which sperm are produced. In between these tubules are small aggregations of endocrine cells called the Leydig cells or interstitial cells. The testes are sometimes called endocrine glands. Technically, however, they are only partially endocrine glands.

A **hormone** is defined to be a chemical substance that is secreted into the blood by endocrine cells and that regulates the function of other cells that it reaches by blood circulation. An additional defining feature of hormones is that they act at very low blood concentrations: sometimes as low as 10^{-12} molar (moles per liter). Still another defining feature is that the effects of hormones on target cells are initiated by noncovalent binding of the hormone molecules to receptor protein molecules synthesized by the target cells. This feature gives hormones their specificity of action, as we stressed before. The specific action of a hormone on a target cell depends on the receptor proteins that the cell synthesizes and on the biochemical pathways the receptor proteins activate.

Growth, development, reproductive cycles, water balance, and long-term stress responses are some of the processes that typically are under primarily hormonal control in animals. This list reflects the fact that, as we discussed in Concept 35.1, hormones are well suited to control processes that involve many tissues and that occur on time scales of hours, days, months, or years.

Endocrine cells are neurosecretory or nonneural

Two broad classes of endocrine cells exist (**FIGURE 35.3**). Some, called **neurosecretory cells** or neuroendocrine cells, resemble neurons in that they are excitable cells that propagate action potentials. Others, called **nonneural endocrine cells** or epithelial endocrine cells, are not excitable.

The cell bodies of neurosecretory cells (see Figure 35.3A) are located in the central nervous system (CNS). These cells have axons, which typically extend outside the CNS. Neurosecretory cells release hormones into the blood at their axon terminals, instead of releasing neurotransmitters at synapses as neurons do. Often, groups of neurosecretory cells have their axon terminals positioned within a **neurohemal organ** (*neuro*, "related to neurons"; *hemal*, "related to blood"), a specialized part of the circulatory system in which the terminals are closely juxtaposed with the blood.

Neurosecretory cells provide a direct interface between the nervous and endocrine systems. Ordinary neurons make synaptic

(A) Neurosecretory cell

Action potential

Cell body in CNS

Capillary near axon terminal of secreting cell

Larger blood vessels

Target cells

Capillary near target cells

Receptor molecules

(B) Nonneural endocrine cell

Capillary near secreting cell

Larger blood vessels

Target cells

Receptor molecules

Capillary near target cells

Hormones (red dots), whether secreted by neurosecretory cells or nonneural cells, travel in the blood throughout the body to exert effects at distant sites on many target cells.

Only cells that possess receptor molecules that recognize and bind a specific hormone will respond to that hormone.

FIGURE 35.3 Two Types of Endocrine Cells The two principal types of endocrine cells are (A) neurosecretory cells and (B) nonneural endocrine cells.

contact with the dendrites and cell body of a neurosecretory cell in the CNS. The neurosecretory cell responds to neural activity in the CNS by secreting a hormone into the blood. The typical order of events in the function of a neurosecretory cell is that neurons in the CNS activate the cell by exciting it at synapses. The neurosecretory cell, in response, initiates and propagates action potentials. These action potentials activate hormone release into the blood at the cell's axon terminals. An example is provided by the cells that produce the hormone oxytocin in mammals. Oxytocin plays critical roles during the birth process and during nursing. It is secreted by neurosecretory cells in the hypothalamus of the brain.

The secretions of neurosecretory cells can quite properly be called hormones. Sometimes, however, scientists distinguish these secretions by calling them neurohormones or neurosecretions.

Nonneural endocrine cells (see Figure 35.3B) do not employ action potentials. They are typically stimulated to secrete their hormones by other hormones, for which they express receptor proteins. The typical order of events in the function of a nonneural endocrine cell is that the cell receives a hormonal signal from another gland. This hormone binds to receptor proteins, which initiate secretion by the nonneural endocrine cell. The cells of the anterior pituitary gland and thyroid gland provide examples.

Most hormones belong to one of three chemical groups

There is enormous diversity in the chemical structure of hormones, but we can classify most hormones into one of three groups:

• **Peptide and protein hormones** are molecules composed of chains of amino acids. They are water-soluble and therefore easily transported in the blood. Most hormones are in this group. Some are large molecules that may contain nearly 200 amino acid units (**FIGURE 35.4A**). Others are small molecules containing as few as three amino acid units. For simplicity, these hormones are often all referred to as peptide hormones (disregarding the fact that the larger ones are technically proteins), and we follow that practice here. During their synthesis, the peptide hormones are packaged in vesicles within the cells that make them. They are released by exocytosis (see Concept 5.4). Because water-soluble molecules cannot easily cross cell membranes, the receptors for peptide hormones are on the exterior of a target cell. There are dozens, perhaps hundreds, of peptide hormones, with diverse structures and effects.

• **Steroid hormones** are synthesized from cholesterol and share a similar structure of four interlinked rings (**FIGURE 35.4B**). Steroid hormones are lipid-soluble and readily pass through the membranes of the cells that synthesize them, but they do not dissolve well in blood plasma. Thus they are usually bound to carrier proteins for transport in the blood. Once they reach a target cell, they typically diffuse directly through its cell membrane. Most steroid receptors are found inside target cells, in the cytoplasm or nucleus.

• **Amine hormones** are small molecules that are modified amino acids. For example, both the thyroid hormone thyroxine and the fight-or-flight hormone epinephrine are made from the amino acid tyrosine (**FIGURE 35.4C**), and the hormone melatonin (which affects an animal's daily rhythms) is made from tryptophan. Depending on whether the modified amino acid is polar or nonpolar, an amine hormone may be water-soluble (can't readily cross membranes) or lipid-soluble (can readily cross membranes).

Receptor proteins can be on the cell surface or inside a cell

Some receptor proteins are positioned in the cell membrane of a target cell, as in the case of the receptors for peptide hormones and some amine hormones. The hormone binds to a part of the receptor protein that projects outside the cell membrane, and then the receptor molecule initiates processes that alter cell function. Many receptors of this type are G protein–linked receptors (see Concept 5.5) that, after binding to a hormone, initiate second messenger cascades inside the target cell. These

(A) Peterbide hormones

Insulin   Growth hormone
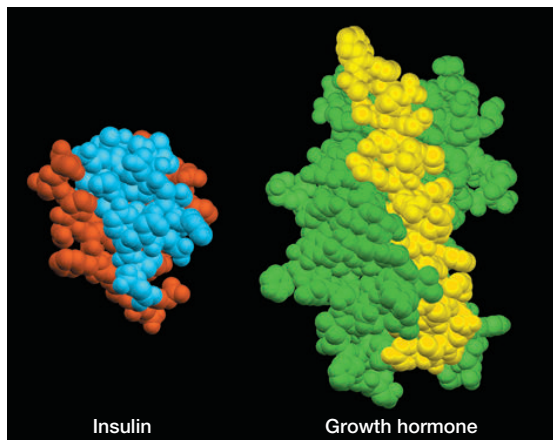
(B) Steroid hormones

Cholesterol
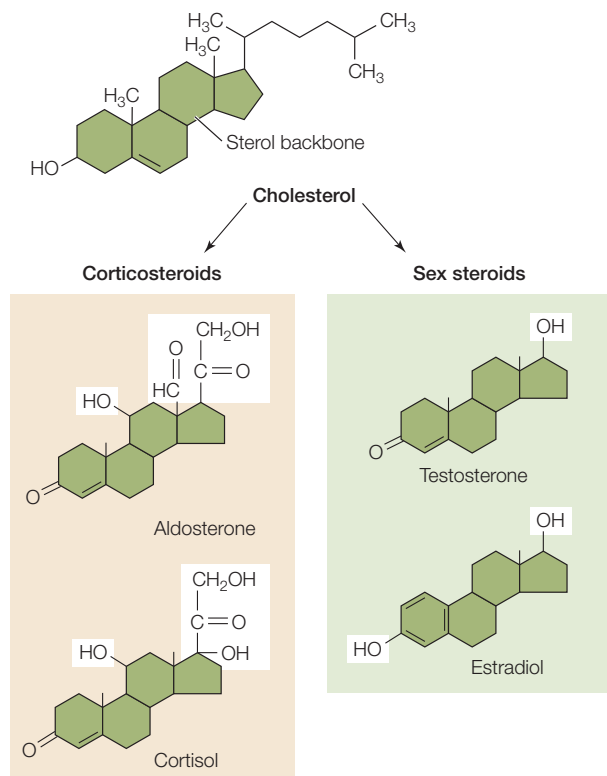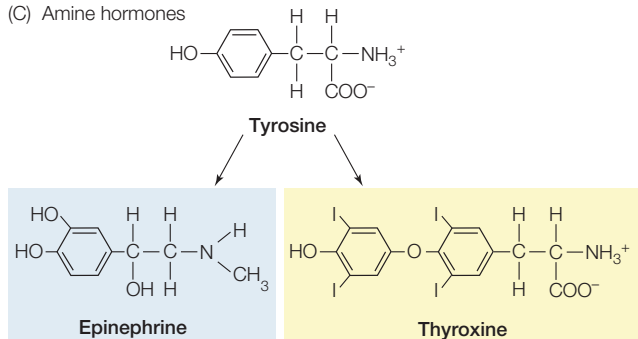
FIGURE 35.4 The Three Principal Chemical Classes of Hormones (A) Peptide hormones are composed of strings of amino acids. They include proteins and small polypeptide molecules. Shown here are two proteins, insulin and growth hormone. Each of these proteins consists of two subunits, which are shown in different colors. (B) Steroid hormones are modified from cholesterol molecules and all include a characteristic set of four ring structures, here called the sterol backbone and colored green. They include the corticosteroids produced by the adrenal cortex and the sex steroids produced primarily by the gonads. (C) Amine hormones are small molecules synthesized from single amino acid molecules. Thyroxine and epinephrine are both made from the amino acid tyrosine. The structures in B and C are in abbreviated form; not all carbon (C) atoms are shown.

cascades activate or inactivate enzymes in the cell cytoplasm, leading to the cell's response (see Figure 5.14).

Other receptor proteins are located inside the target cell, in the cytoplasm or nucleus. This is the case for the receptors for steroid hormones and some amine hormones. These hormones can diffuse through the cell membrane because they are lipid-soluble. When a steroid hormone binds to its receptor in the cytoplasm, the hormone–receptor complex usually moves to the cell nucleus. There it alters gene expression (transcription and translation), resulting in synthesis of new proteins. For example, when testosterone binds to receptors in the cytoplasm of skeletal muscle cells, testosterone–receptor complexes move into the nuclei of the cells and activate transcription of several genes. These genes include those that code for enhanced synthesis of the contractile proteins actin and myosin (see Concept 33.1). In this way, testosterone tends to bring about an increase in muscle mass.

LINK
You can learn more about the various types of receptor proteins in **Concept 5.5**

A target cell is not limited to expressing only a single kind of hormone receptor protein. Cells often express two or more receptor proteins, which make them target cells for two or more hormones.

The number of receptor molecules that a target cell has for a particular hormone can vary. In some cases, negative or positive feedback affects the number of receptor molecules that a target cell expresses. For example, continuous high concentrations of a hormone sometimes cause a target cell to decrease its number of receptors for the hormone. This decrease makes the cell less sensitive to the hormone, tending to offset the effect of the continuous high concentration. For example, in type II diabetes mellitus, chronically high levels of the hormone insulin (usually caused by excessive carbohydrate intake) lead to decreased production of insulin receptors throughout the body. As a result, cells become less sensitive to insulin.

LINK
The crucial role of insulin in regulating glucose metabolism is detailed in **Concept 30.5**

(C) Amine hormones

Tyrosine

Epinephrine   Thyroxine

Hormone action depends on the nature of the target cells and their receptors

The action of a hormone on a target cell depends on characteristics of the target cell—in particular, the receptor protein the cell expresses and the cellular processes activated by the receptor protein. For this reason, one hormone can have dramatically different effects on different cells.

In the course of evolution, many hormones have been conserved for long periods of evolutionary time, but their functions have changed as various types of animals have evolved. This pattern—in which a single hormone molecule evolves changing functions—arises because the actions of a hormone depend on the receptor systems, which can change. The peptide hormone prolactin provides a dramatic example.

Prolactin was first discovered in mammals, where it stimulates milk synthesis in the mammary glands (breasts). Prolactin has since been found in all other vertebrate phyla—from fish to birds—even though these other phyla have neither mammary glands nor milk. In salmon, prolactin is involved in stabilizing blood ion composition as the fish migrate between salt and fresh water. In birds, prolactin can stimulate nest building and parental care. The hormone—in one molecular form or another—has existed in vertebrates throughout their evolutionary history, but prolactin has taken on radically different functions in various vertebrate groups by evolution of the target cells it affects and their receptor systems.

Within one individual animal, some target cells for a hormone can have different receptor proteins and receptor systems than other target cells do. The hormone then elicits different responses from the different types of target cells. For example, in a sudden emergency, our fight-or-flight response is activated to help us confront the emergency. As part of this response, our adrenal medullary glands (**FIGURE 35.5**) secrete epinephrine and

FIGURE 35.5 The Adrenal Gland Consists of Two Glands within One Gland   An adrenal gland sits above each kidney. The gland consists of an outer cortex and an inner medulla, which produce different hormones.

The adrenal medulla produces epinephrine and norepinephrine.

The adrenal cortex produces steroid hormones: glucocorticoids, mineralocorticoids, and sex steroids.

Adrenal gland

Kidney

norepinephrine (sometimes known as adrenaline and noradrenaline), while at the same time our sympathetic nervous system (see Concept 34.5) exerts its effects. Within seconds, these hormones are circulating in our blood. We have at least five types of receptors for the hormones, all of them G protein–linked receptors. These receptors fall into two major categories—called α-adrenergic and β-adrenergic receptors—that bind epinephrine and norepinephrine with different degrees of ease. Cells of different tissues have different receptors. Moreover, even when different types of cells have the same receptor, they may respond very differently because the receptor activates different processes in different cell types. For these reasons, the hormones bring about a large range of responses in various tissues: faster and stronger beating of the heart, constriction of blood vessels in the skin, dilation of blood vessels in skeletal muscles, breakdown of glycogen to release glucose in the liver (see Figure 5.17), and a decrease in both blood flow and secretion of digestive enzymes in the gut.

LINK

Signal transduction pathways—the cellular processes activated by receptors—are discussed in **Concept 5.6**

A hormonal signal is initiated, has its effect, and is terminated

When endocrine cells are activated to secrete a hormone, they vary in how quickly they start hormone release. Peptide and amine hormones are usually synthesized prior to use. They can be secreted very rapidly because they are present in stored form in endocrine cells. In contrast, steroid hormones are typically synthesized on demand. Initiation of secretion of steroid hormones is relatively slow because of the need to synthesize the hormones before they can be released.

Just as there are processes for secreting a hormone into the blood, there are ways to remove it. Removal takes place in several ways. Target cells sometimes enzymatically degrade hormones. Certain organs, such as the liver and kidneys in vertebrates, also enzymatically degrade hormones. Hormones may also be excreted.

The removal processes ultimately terminate a hormone signal. The half-life of a hormone in the blood is the time required for half of a group of simultaneously secreted hormone molecules to be removed from the blood. Some hormones have half-lives measured in minutes, and in these cases an individual hormonal signal does not last long. Epinephrine, for example, has a half-life of 1–2 minutes, explaining why the jolt of a fight-or-flight response disappears quickly if we decide no emergency exists and we are safe. Other hormones have far longer half-lives. In the human bloodstream, for example, the hormones antidiuretic hormone (involved in water conservation), cortisol (involved in long-term responses to stress), and thyroxine (affects cellular metabolism) display average half-lives of about 15 minutes, 1 hour, and nearly 1 week, respectively. They may therefore have prolonged effects on target tissues.

When a hormone is secreted steadily over a period of time, the blood hormone concentration is determined by an interaction between the rate of secretion (adding hormone to the
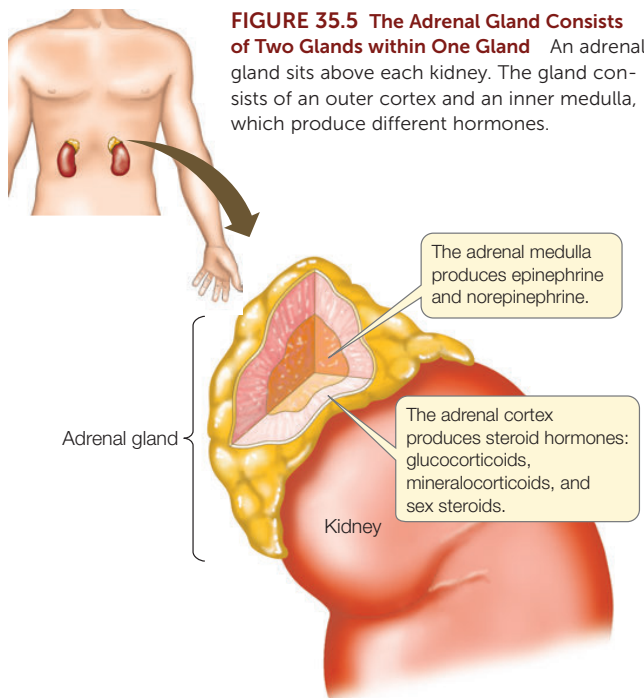
APPLY THE CONCEPT

Hormones are chemical messengers distributed by the blood

One way to characterize the time course of a hormone is to measure its half-life in the blood. A hormone's half-life can be measured in the laboratory by injecting some of the hormone and then determining the length of time required for the blood level of the hormone to fall from its maximum level halfway back to its baseline value. The table gives blood concentrations of the thyroid hormone thyroxine (T_4) following a 600-µg injection in a particular experiment. Plot these data.

1. Use the data in the table to estimate the half-life of 600 µg of T_4 in the bloodstream in this experiment. (The concentration at time 0 is the baseline.)

2. If you were trying to correct a hormone deficiency by administering hormone therapy and needed to keep the hormone level in the blood from falling too low, how would your dosing frequency differ for hormones with different half-lives?

TIME (hr) AFTER INJECTION	BLOOD CONCENTRATION (µg/100ml)
0 (just prior to injection)	7.5
6	13.7
12	12.3
24	11.1
36	10.7
48	10.3
60	9.9
72	9.5
84	9.3
96	9.1

blood) and the rate of removal. Removal of any particular hormone tends to take place at a fairly steady rate. Thus changes in the blood concentration of a hormone depend chiefly on changes in the rate at which the hormone is secreted.

The blood concentration is stabilized by negative feedback in many cases, making negative feedback a major theme in the study of endocrinology. During negative feedback, if the blood concentration rises above a set-point level, secretion of the hormone is inhibited.

LINK

Many physiological processes in animals have set points and are regulated by negative feedback; **Concept 29.6** describes the components of negative-feedback systems

When they are in the blood, some hormones are bound to carrier proteins. For example, steroid hormones must be bound with water-soluble proteins to be in solution in the blood. Carrier proteins often extend the half-lives of hormones.

Some hormones are converted to more active forms after they are secreted, a process called peripheral activation. A classic example is provided by the hormones of the thyroid gland. The thyroid secretes a molecule that contains four iodine atoms. This molecule is called thyroxine, T_4, or tetraiodothyronine (see Figure 35.4C). The hormone becomes more active when peripheral tissues enzymatically remove one of the iodine atoms, forming T_3, triiodothyronine.

CHECKpoint CONCEPT 35.2

✓ Growth hormone is a large, water-soluble peptide. Given these characteristics, how would you expect this hormone to interact with its target cells?

✓ Are sweat glands correctly described as endocrine glands?

✓ Name one major similarity and one major difference between an ordinary neuron and a neurosecretory cell.

For understanding the vertebrate endocrine system, one of the most important themes is that the brain often controls the secretion of hormones by the endocrine system. We will start with that theme as we now turn our attention to the vertebrate endocrine system.

CONCEPT 35.3 The Vertebrate Hypothalamus and Pituitary Gland Link the Nervous and Endocrine Systems

The **pituitary gland**, found at the base of the brain (**FIGURE 35.6A**; see also Figure 34.25), is sometimes called the "master gland" because it secretes hormones that control the functions of many other glands. It is attached by a stalk to a part of the brain called the **hypothalamus**. The pituitary has two parts—the **anterior pituitary** (adenohypophysis) and **posterior pituitary** (neurohypophysis). The two have different developmental origins, which helps account for marked differences in the way they function. Both parts of the pituitary have close functional links with the brain.

Hypothalamic neurosecretory cells produce the posterior pituitary hormones

The posterior pituitary is basically an extension of the brain (**FIGURE 35.6B**). Its hormones are synthesized and secreted by brain neurosecretory cells. The cell bodies of these cells are in the hypothalamus, where they receive synapses from other, ordinary brain cells (neurons). The axons of the neurosecretory cells extend into the posterior pituitary, where they terminate in a rich blood capillary network, forming a neurohemal organ where the hormones of the neurosecretory cells are secreted into the blood.

An important general principle is that different sets of neurosecretory cells secrete different hormones. We can apply this principle as we focus on the hypothalamus and posterior pituitary. In most mammals and also in many other vertebrates, there are two sets of neurosecretory cells, which secrete two

(A)

Hypothalamus

The human **pituitary gland** is the size of a blueberry, yet it secretes many hormones.

(B)

1 Two sets of hypothalamic neurosecretory cells produce antidiuretic hormone and oxytocin and transport them to the posterior pituitary.

Hypothalamus

Axons of hypothalamic neurosecretory cells

Stalk of pituitary

Capillaries

Anterior pituitary

Posterior pituitary

2 The hormones are released in the posterior pituitary and diffuse into blood capillaries...

Inflowing blood

3 ...then leave the posterior pituitary via the blood.

FIGURE 35.6 The Posterior Pituitary Gland (A) The human pituitary gland is located just below the hypothalamus of the brain. (B) The posterior pituitary is a neurohemal organ for neurosecretory cells in the brain. Two sets of neurosecretory cells in the hypothalamus produce two peptide hormones that are released in the posterior pituitary.

hormones, in the posterior pituitary system. Both hormones are short peptides containing nine amino acid units. In mammals these two hormones are **antidiuretic hormone** (**ADH**; also called vasopressin) and **oxytocin**. ADH helps control water excretion by the kidneys, as we will discuss in Chapter 36. Oxytocin controls milk ejection from the mammary glands and helps control contractions of the uterus during the birth process (see Figure 29.17).

Signals produced by the brain control secretion by these neurosecretory cells. In this way, the enormous computational and integrative powers of the brain can be marshaled to control secretion of the posterior pituitary hormones. When activated, the neurosecretory cells generate action potentials that travel to their axon terminals, leading to hormone release into the blood.

In short, in the posterior pituitary system, *brain neurons control the secretion of hormones into the general circulation by neurosecretory cells*. This is one type of interface between the nervous and endocrine systems—a type of interface that we commonly find in both vertebrates and invertebrates.

Hormones from hypothalamic neurosecretory cells control production of the anterior pituitary hormones

Unlike the posterior pituitary (which is a neurohemal organ), the anterior pituitary is an endocrine gland. The anterior pituitary hormones are synthesized in the anterior pituitary gland itself by nonneural endocrine cells (**FIGURE 35.7**). All the hormones are peptides or closely related to peptides.

Four of the hormones are known as **tropins**, or **tropic hormones**, meaning their principal functions are to control the activities of other endocrine glands. They are **adrenocorticotropic hormone** (**ACTH**), **follicle-stimulating hormone** (**FSH**), **luteinizing hormone** (**LH**), and **thyroid-stimulating hormone** (**TSH**). A different set of pituitary cells produces each tropic hormone. ACTH helps control the adrenal cortex (see Figure 35.5). Both FSH and LH, which together are called gonadotropins, control the gonads: the testes in males and the ovaries in females. TSH controls the thyroid gland.

The anterior pituitary gland also produces several other hormones. These hormones act on non-endocrine targets and therefore are not tropic hormones. They include **growth hormone** (**GH**; see Figure 35.4A), which acts on a wide variety of tissues to promote growth. They also include prolactin (which we've already mentioned), and melanocyte-stimulating hormone, which is named for its action on skin-color cells in amphibians.

How is secretion of the anterior pituitary hormones controlled? A critical role is played by a specialized vascular network, the **hypothalamo–hypophysial portal system** ("hypophysis" is an alternative name for pituitary). This vascular system consists of two capillary beds that are connected so that blood flows through them sequentially. Blood flows first through a capillary bed in the hypothalamus. Neurosecretory cells in the hypothalamus secrete hormones into the blood in this capillary bed. When the blood flows out of the hypothalamus, it travels a short distance to the second capillary bed, which is in the anterior pituitary. In this way, the hormones secreted by the hypothalamic neurosecretory cells are brought to the pituitary nonneural endocrine cells. These hormones control secretion by the endocrine cells in the pituitary. A typical sequence of action begins when ordinary brain neurons that synapse on the hypothalamic neurosecretory cells stimulate those cells to secrete hormones. Those hormones then travel to the anterior

Hypothalamus
Hypothalamic neurosecretory cells

→ Blood flow
→ Hormone secretion

Inflowing blood

These blood vessels constitute the **hypothalamo–hypophysial portal system.**

Anterior pituitary

1 Axon terminals of hypothalamic neurosecretory cells release hormones (RHs and IHs) into the hypothalamo–hypophysial portal system.

2 The RHs and IHs travel in the portal system to the anterior pituitary.

3 The RHs and IHs stimulate or inhibit the release of hormones (black dots) from anterior pituitary cells.

Posterior pituitary

4 Anterior pituitary hormones leave the gland via the blood.

FIGURE 35.7 The Anterior Pituitary Gland Cells of the anterior pituitary produce four tropic hormones that control other endocrine glands, as well as several other peptide hormones. These cells are controlled by releasing hormones (RHs) and inhibiting hormones (IHs) produced by neurosecretory cells in the hypothalamus. The RHs and IHs are delivered to cells in the anterior pituitary by blood flowing through portal blood vessels that run between the hypothalamus and the anterior pituitary through the pituitary stalk.

hormone by anterior pituitary cells, and for the tropic hormone then to control hormone secretion by the cells in a gland elsewhere in the body. A system of this type—in which endocrine cells act on each other in sequence—is called an **axis**.

One example is the hypothalamus–pituitary–adrenal cortex (HPA) axis. Some of the steroid hormones secreted by the adrenal cortex, including a class called glucocorticoids, are important in responding to long-term stress. When the brain, using its great computational capacity to integrate inputs, detects that an animal is under stress, some of the cells in the hypothalamus secrete corticotropin-releasing hormone. This releasing hormone

pituitary and control secretion by the anterior pituitary non-neural endocrine cells.

The hormones added to the blood by the neurosecretory cells in the hypothalamus are called **releasing hormones** (**RH**s) and **inhibiting hormones** (**IH**s; also called release-inhibiting hormones). Each RH or IH is specific in its actions. For example, there are separate RHs for growth hormone and thyroid-stimulating hormone. When the RH for growth hormone is secreted in the hypothalamus, it affects the specific cells in the anterior pituitary that secrete growth hormone, stimulating them to secrete (release) their hormone into the general circulation. The RH for thyroid-stimulating hormone, in contrast, stimulates the specific pituitary cells that secrete TSH.

In summary, in the anterior pituitary system, *neurosecretory cells in the brain control the secretion of hormones into the general circulation by other endocrine cells*. This is a second type of interface between the nervous and endocrine systems. It too is a type of interface that we commonly find in both vertebrates and invertebrates.

Endocrine cells are organized into control axes

A typical sequence in vertebrates is for a hormone secreted by brain neurosecretory cells to control the secretion of a tropic

External or internal condition detected and processed by the brain

→ = Stimulation
⊣ = Inhibition

or

Hypothalamus

Releasing hormone

Hormones secreted by peripheral glands may exert negative feedback on hypothalamic neurosecretory cells or anterior pituitary cells

Anterior pituitary

Pituitary tropic hormones may exert negative feedback on hypothalamic neurosecretory cells

Tropic hormone

Peripheral endocrine gland (e.g., adrenal cortex)

Hormone secreted by peripheral gland (e.g., cortisol)

FIGURE 35.8 Multiple Feedback Loops Control Hormone Secretion Multiple negative-feedback loops regulate the chain of command from hypothalamus to anterior pituitary to peripheral endocrine glands. For purposes of this diagram, the glands controlled by anterior pituitary tropic hormones are termed peripheral glands.

travels in the portal system to cells in the anterior pituitary gland that respond by increasing secretion of the tropic hormone adrenocorticotropic hormone (ACTH). ACTH then travels in the general circulation to the adrenal cortex, which responds by increasing secretion of glucocorticoids into the blood. In primates, the principal glucocorticoid is cortisol (see Figure 35.4B).

Negative feedback often takes place within an axis. How does it work? One way is that the hypothalamic neurosecretory cells and the endocrine cells of the anterior pituitary are often under negative-feedback control by the hormones of their target glands (**FIGURE 35.8**). For example, when the blood concentration of cortisol (or other glucocorticoids) increases following stimulation of the adrenal cortex by the HPA axis, blood cortisol tends to cause cells in the hypothalamus to reduce release of corticotropin-releasing hormone and cells in the anterior pituitary to reduce secretion of ACTH. This negative feedback helps stabilize the blood cortisol concentration at a relatively constant level.

Go to ANIMATED TUTORIAL 35.1
The Hypothalamus and Negative Feedback
PoL2e.com/at35.1

Hypothalamic and anterior pituitary hormones are often secreted in pulses

In many cases the brain stimulates the neurosecretory cells in the hypothalamus to secrete in pulses instead of continuously. Corticotropin-releasing hormone, for example, is typically secreted in mammals in two or three pulses per hour. Pulsed secretion of RHs or IHs often proves to be necessary for these hormones to act (**FIGURE 35.9**). Continuous secretion can lead target cells in the pituitary to reduce their numbers of RH or IH receptor molecules and thus reduce their sensitivity. Pulsed secretion is hypothesized to prevent this loss of sensitivity. At the next step in the axis, the anterior pituitary hormones are often also secreted in pulses.

INVESTIGATION

FIGURE 35.9 Effectiveness of Gonadotropin-Releasing Hormone (GnRH) Depends on a Pulsatile Pattern of Release   In adult monkeys, GnRH is released from the hypothalamus in short pulses, about once every 1–3 hours. When the supply of GnRH is stopped (for example, by removing or destroying the hypothalamus), the anterior pituitary no longer secretes FSH or LH, and levels of these gonad-regulating hormones decline. Early studies in rhesus monkeys showed that in such cases FSH and LH production could be restored by injections of GnRH, but only if GnRH was delivered in pulses rather than continuously. The two patterns of GnRH delivery, however, also resulted in very different *total* doses of GnRH, complicating the interpretation of these initial results. The researchers did further experiments to determine whether delivery of GnRH in pulses is critical to its function in stimulating the secretion of FSH and LH.[a]

HYPOTHESIS

The effectiveness of GnRH depends on the dose, not on the pattern of delivery.

METHOD

1. Administer GnRH to rhesus monkeys in which the hypothalamic cells responsible for GnRH secretion have been destroyed. Administer GnRH either continuously at 0.001, 0.01, 0.1, or 1.0 µg/min, or in pulses (one 6-min pulse per hr) at 1.0 µg/min.
2. Measure the concentrations of LH and FSH in the blood.

RESULTS
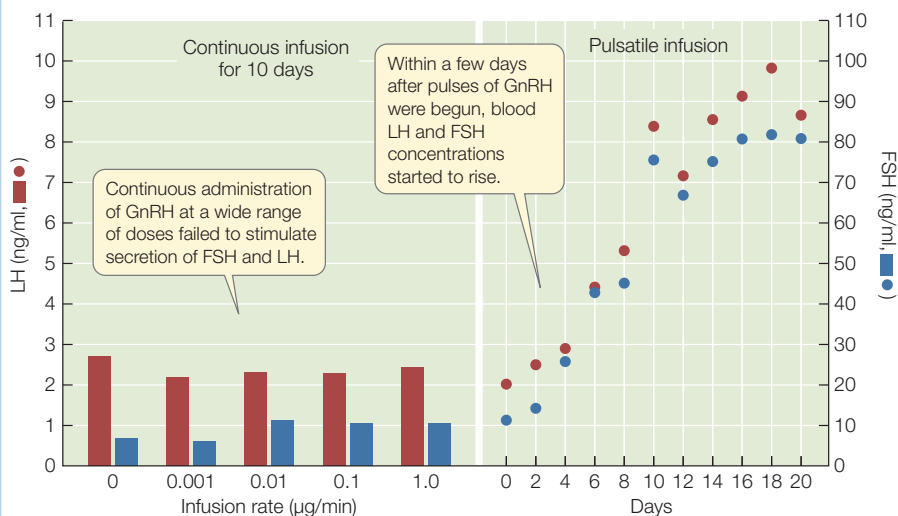
CONCLUSION

The hypothesis is not supported: the effectiveness of the GnRH depends on the pattern of delivery.

ANALYZE THE DATA

A. For delivery in pulses, GnRH was administered at 1 µg/min for 6 minutes once per hour. Which continuous rate delivered the same amount of GnRH per hour as the delivery in pulses? How much GnRH was delivered per hour at the lowest continuous rate? How much lower was this than the dose from pulses?

B. For interpreting this experiment, why is it important that one of the continuous delivery rates provides the same total dose per hour as the pulsatile delivery?

C. We now know that the anterior pituitary stops responding to GnRH if GnRH is always present. What does this tell you about how fast each pulse of GnRH disappeared from the bloodstream? Be as quantitative as possible, taking account of the GnRH dose that you calculated for the lowest continuous rate above.

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]P. E. Belchetz et al. 1978. *Science* 202: 631–633.

CHECKpoint   CONCEPT 35.3

✓ Considering the hierarchy of control, why might it be misleading to call the pituitary gland the "master gland"?

✓ Why are many anterior pituitary hormones called tropic hormones?

✓ Neurosecretory cells in the hypothalamus and cells in the anterior pituitary gland both have cortisol receptors. If they were to lose their cortisol receptors, these cells would immediately begin secreting unusually large amounts of corticotropin-releasing hormone and ACTH. Why?

The hypothalamus and anterior pituitary gland control the secretion of hormones from several other endocrine glands. We will now look at the hormones that some of these other glands release, and the functions of these hormones.

CONCEPT 35.4 Hormones Regulate Mammalian Physiological Systems

Hormones are involved in controlling and coordinating a wide range of mammalian physiological systems, and these regulatory processes in mammals often have parallels in other vertebrates. Here we take a brief look at the some of the major roles of hormones in the lives of mammals.

FIGURE 35.10 shows the locations of the principal mammalian endocrine glands and summarizes their major hormones and actions. In addition to the principal glands, many organs—such as the heart and stomach—are not named as glands but nonetheless contain endocrine cells. The box in the figure lists some of these. We discuss several endocrine control systems in other chapters, as **FIGURE 35.11** indicates.

Pineal gland
Melatonin: regulates circadian rhythms

Thyroid gland
Thyroid hormones, T_3 and T_4: increase cell metabolism; essential for growth and neural development
Calcitonin: lowers blood calcium levels, stimulates incorporation of calcium into bone

Parathyroid glands (on posterior surface of thyroid)
Parathyroid hormone (PTH): stimulates release of calcium from bone and absorption of calcium by gut and kidney

Adrenal cortex
Glucocorticoids (e.g., cortisol): mediate long-term metabolic responses to stress
Mineralocorticoids (e.g., aldosterone): involved in salt and water balance
Sex steroids

Adrenal medulla
Epinephrine (adrenaline) and *norepinephrine* (noradrenaline): stimulate immediate fight-or-flight reactions

Ovaries (female)
Estrogens: development and maintenance of female sexual characteristics
Progesterone: supports pregnancy

Testes (male)
Androgens (esp. testosterone): development and maintenance of male sexual characteristics

Hypothalamus
Releasing and inhibiting hormones: control the anterior pituitary
ADH and *oxytocin*: transported to and released from the posterior pituitary (below)

Anterior pituitary gland
Thyroid-stimulating hormone (TSH): stimulates the thyroid gland
Follicle-stimulating hormone (FSH): in females, stimulates maturation of ovarian follicles; in males, stimulates spermatogenesis
Luteinizing hormone (LH): in females, triggers ovulation and ovarian production of estrogens and progesterone; in males, stimulates production of testosterone
Adrenocorticotropic hormone (ACTH): stimulates secretory activity of the adrenal cortex
Growth hormone (GH): stimulates protein synthesis and growth
Prolactin: stimulates milk production
Melanocyte-stimulating hormone (MSH): controls skin pigmentation
Endorphins and *enkephalins*: pain control

Posterior pituitary gland (site of release of two hormones made by hypothalamic neurosecretory cells)
Oxytocin: stimulates contraction of uterus, flow of milk
Antidiuretic hormone (ADH): promotes water conservation by kidneys

Thymus (diminishes in adults)
Thymosins: play roles in the immune system

Pancreas (only certain parts, the islets of Langerhans, are endocrine)
Insulin: stimulates cells to take up and use glucose
Glucagon: stimulates liver to release glucose

Other organs include cells that produce and secrete hormones:

Organ	Hormone
White adipose tissue	Leptin
Heart	Atrial natriuretic peptide
Kidney	Erythropoietin
Stomach	Gastrin, ghrelin
Intestine	Secretin, cholecystokinin
Liver	Insulin-like growth factors

FIGURE 35.10 The Human Endocrine System

Go to ACTIVITY 35.1 The Human Endocrine Glands
PoL2e.com/ac35.1

Chapter 29
Fundamentals of Animal Function
Oxytocin (from the posterior pituitary) plays a critical role in controlling uterine muscle contractions essential for a baby to be born (see Figure 29.17).

Chapter 30
Nutrition, Feeding, and Digestion
Secretin and cholecystokinin (both from scattered endocrine cells in the midgut epithelium) help coordinate parts of the gut during meal processing (see Concept 30.5; Figure 30.14).

Ghrelin (from the stomach) and **leptin** (from white adipose tissue) help control appetite (see Concept 30.5; Figure 30.15).

Insulin and glucagon (both from the pancreas) regulate processing of absorbed food materials between meals (see Concept 30.5; Figure 30.16).

Chapter 36
Water and Salt Balance
Antidiuretic hormone (from the hypothalamus and the posterior pituitary) controls excretion of water by the kidneys (see Concept 36.5; Figure 36.9).

Chapter 37
Animal Reproduction
Follicle-stimulating hormone and luteinizing hormone (from the anterior pituitary) help control the menstrual and estrous cycles and are essential for male fertility (see Concept 37.2; Figure 37.11).

Estrogens (from the ovaries) help control the menstrual and estrous cycles (see Concept 37.2; Figure 37.11).

Progesterone and estrogens (from the ovaries and placenta) help control uterine development that is required for pregnancy (see Concept 37.2; Figure 37.11).

FIGURE 35.11 Several Endocrine Control Systems Are Discussed in Other Chapters Endocrine control is of such widespread importance that it features in many chapters in Part 6.

The thyroid gland is essential for normal development and provides an example of hormone deficiency disease

The thyroid gland is found in the neck, wrapped around the front of the trachea (windpipe) (see Figure 35.10). Two different cell types in the thyroid gland produce two different hormones. One hormone is thyroxine (T_4), described earlier, and the other is calcitonin (involved in calcium metabolism). Here we focus on T_4, an amine hormone that contains four iodine atoms (see Figure 35.4C). The presence of iodine in the T_4 structure is the reason for most of our dietary iodine requirement. The thyroid also releases a relatively small amount of T_3 (triiodothyronine)—a molecule formed by removal of an iodine from T_4—that has an iodine atom at only three of the four positions where T_4 does. T_3 is more active in affecting target cells, and after T_4 has been secreted into the blood, peripheral tissues convert it to T_3, as noted earlier. When biologists speak of "thyroid hormones," they mean T_4 and T_3 unless stated otherwise.

The thyroid hormones are vital during development and growth. They promote cellular amino acid uptake and protein

FIGURE 35.12 Goiter

synthesis. They enter cells and bind to an intracellular receptor that stimulates transcription of numerous genes. Insufficiencies of the thyroid hormones in a human fetus or growing child greatly retard mental and physical development. The thyroid hormones also are noted for elevating metabolic rate in mammals and birds.

Soils deficient in iodine occur in many parts of the world. Plants that grow in these soils tend to be low in iodine, and people who depend on local foods in these areas often suffer from iodine deficiency. Iodized table salt (salt containing traces of iodine) was invented to solve this problem. If people purchase iodized salt and use it in a customary way to salt their food, they get enough iodine regardless of whether or not they live in an iodine-deficient part of the world.

Impaired mental development caused by childhood deficiency of thyroid hormones—resulting from iodine deficiency—remains a massive worldwide problem because in many poverty-stricken regions, iodized salt is not readily available. Global human mental performance would be raised in a generation if iodine deficiency during pregnancy and childhood could be eliminated.

Goiter is another hormone deficiency disease that (in its most common form) results from inadequate dietary iodine. It illustrates that the proper operation of feedbacks in endocrine control systems can be critical for health. Goiter refers to an enlarged thyroid gland (**FIGURE 35.12**). It was common in many parts of the United States until use of iodized salt became the norm.

Adults develop goiter when they get too little iodine in their diet and, as a result, their thyroid produces inadequate amounts of thyroid hormones. When thyroid hormones are present in sufficient amounts in the blood, they exert negative feedback on the production of thyroid-stimulating hormone (TSH) by the anterior pituitary. This feedback does not take place in people producing only small amounts of thyroid hormones. Their blood levels of thyroid hormones are low, and

accordingly such people produce high levels of TSH due to a lack of negative feedback on TSH production. Their steady, high production of TSH stimulates their thyroid gland to grow to excessive size.

Sex steroids control reproductive development

Many hormones, including the thyroid hormones, play critical roles in mammalian development. In certain ways, however, the hormones of greatest importance for development are the sex steroids and the hypothalamic and pituitary hormones that control them.

The gonads—the testes of males and the ovaries of females—produce steroid hormones as well as gametes (sperm and ova). Many of these hormones are described as androgens or estrogens. Masculinizing steroid hormones are called **androgens** (Greek, "male-makers"). Testosterone is an androgen and is the principal hormone produced by the testes. It was named testosterone when it was discovered in 1935 for the two-fold reason that it was collected from testes and it belongs chemically to the family of cholesterol-like compounds (see Figure 35.4B).

Go to MEDIA CLIP 35.1
The Testosterone Factor
PoL2e.com/mc35.1

Feminizing steroid hormones are called **estrogens**. Two or more types of estrogen molecules are typically secreted, one often being estradiol (see Figure 35.4B). The ovaries produce estrogens and another female sex steroid, **progesterone**, that is involved principally in coordinating processes associated with pregnancy. During pregnancy, the placenta also secretes estrogens and progesterone. We will discuss these hormones—and the hormones that control their secretion—at length in Chapter 37.

Androgens are not exclusive to males, and estrogens are not exclusive to females. Both sexes make both androgens and estrogens. However, the relative blood concentrations differ in the two sexes. In some cases androgens are simply precursors in the synthesis of estrogens, to which androgens are converted by a process called aromatization.

During embryonic development, the sex steroids play a key role in controlling whether a human embryo develops phenotypically into a male or female. Androgens are required for male phenotypic development, and in their absence an embryo develops as a female. The sex of an individual mammal is determined genetically at the time of conception. Females inherit two X chromosomes, whereas males inherit an X and a Y chromosome (see Concept 37.1). At the start of embryonic development, the gonads and external genital structures are the same whether an individual is XX or XY. In males, early in development a gene on the Y chromosome, the *SRY* gene, causes the gonads to differentiate as testes (otherwise they become ovaries). As the differentiation into testes proceeds, the gonads of a male embryo begin to produce testosterone. In humans, starting 2–3 months after conception, testosterone increases from a low blood concentration to a high blood concentration, remains high for about 2 months, and then falls to a low concentration again because the gonads stop producing it rapidly. This period of high blood testosterone causes the external genital structures
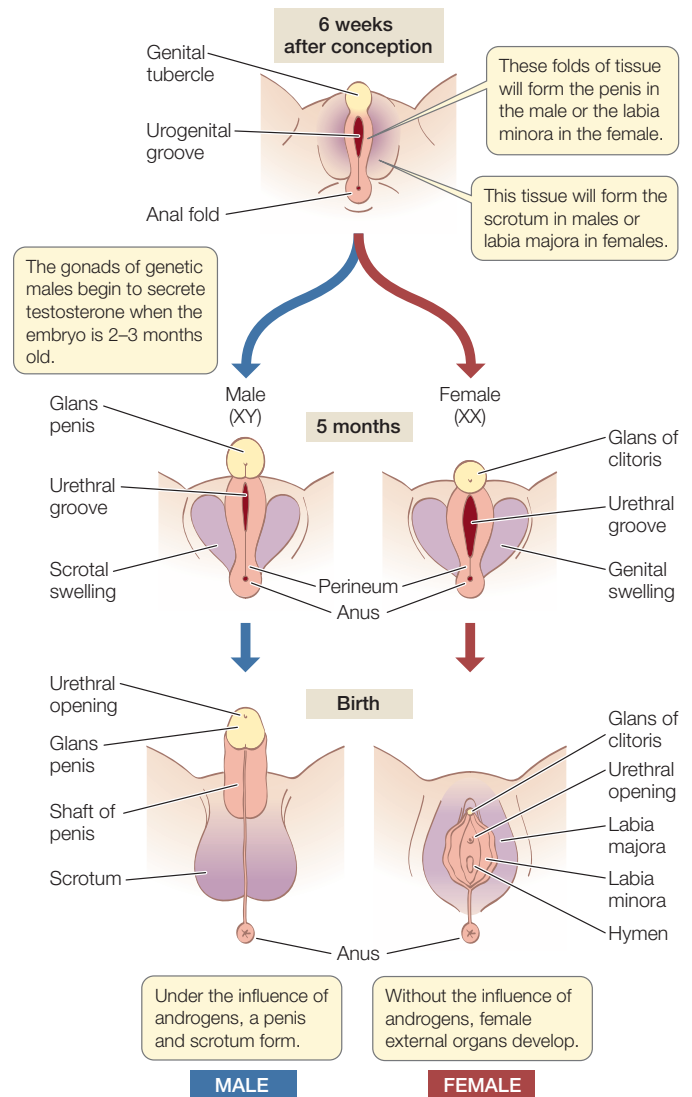
FIGURE 35.13 Sex Steroids Direct the Prenatal Development of Human Sex Organs   The external sex organs of early human embryos are undifferentiated. Testosterone promotes the development of male external sex organs. In its absence, female sex organs form.

to differentiate into the male form. Without testosterone, the structures differentiate into female form.

Particular external genital structures diverge into male or female form during this phenotypic sexual differentiation. The scrotum of males and certain labial folds of females develop from the same early structures (**FIGURE 35.13**). The head (glans) of the penis and the head of the clitoris also have the same embryonic origins. The gonads are initially located in the abdomen in both sexes. In males, the testes migrate out of the abdomen into the scrotum. The ovaries remain in the abdomen in females.

Just as hormones play a crucial role in embryonic development, they again play a crucial role at puberty. Recall that luteinizing hormone (LH) and follicle-stimulating hormone (FSH)—both anterior pituitary tropic hormones that act on the gonads—are together called the **gonadotropins**. Their secretion

by the anterior pituitary is under the control of hypothalamic neurosecretory cells that produce **gonadotropin-releasing hormone (GnRH)**. As we have been doing, let's focus on humans as we discuss the process of puberty.

When a person is between about 1 year of age and the start of puberty, the GnRH neurosecretory cells in the hypothalamus are quiet, producing a GnRH pulse only once every few hours. Puberty begins when these cells suddenly shift to producing GnRH pulses at a far higher rate, a change that results in a sustained increase in the average concentration of GnRH in blood flowing into the anterior pituitary. Despite many theories, researchers remain uncertain about the causes of the change in activity of the GnRH neurosecretory cells. The consequences, however, are well known and dramatic.

The anterior pituitary responds to the increase in the pulse rate of GnRH secretion with a large increase in FSH and LH secretion. In males, the elevated blood concentration of LH stimulates cells in the testes to produce testosterone vigorously. A large increase occurs in the blood concentration of testosterone, which (along with other androgens) brings about many changes. Testosterone enters cells, binds to intracellular receptors, and alters gene expression throughout the body. As a consequence, a boy's voice deepens, hair begins to grow on his face and body, his skeletal muscles increase in mass, and his testes and penis grow larger. The increased blood concentration of FSH stimulates the production of sperm.

In females, increased blood levels of LH stimulate the ovaries to increase production of estrogens. Concentrations of estrogens in the blood rise and initiate development of many traits: a girl's breasts, vagina, and uterus become larger; her hips broaden; she develops increased subcutaneous fat; and her menstrual cycles begin. Increased FSH stimulates the maturation of ovarian follicles, which are necessary for production of mature eggs (see Concept 37.1).

Sex steroids continue to play essential roles in reproductive cycles and sexual functioning throughout adulthood. We will discuss these roles in Chapter 37.

CHECKpoint CONCEPT 35.4

✓ Boys are occasionally born with a testicle missing from the scrotum. The missing testicle is nearly always in the abdomen, and its position can be corrected surgically. But why might a testicle be in the abdomen at birth?

✓ Explain why the thyroid gland can grow to great size when it secretes inadequate amounts of thyroid hormones because of iodine deficiency.

✓ What endocrine event in the hypothalamus initiates puberty?

Now that we've examined vertebrate endocrine systems, let's conclude with a look at endocrine systems in invertebrates. Of all the invertebrates, the insects are the best understood in this regard. A striking parallel is that endocrine controls are of enormous importance in insect development, just as they are in vertebrate development.

CONCEPT 35.5 The Insect Endocrine System Is Crucial for Development

Insects and other arthropods, such as crayfish and crabs, have elaborate endocrine systems. For example, many insects have antidiuretic and diuretic hormones that control excretion of water by the insect organs that serve kidney functions. Diuretic hormones promote excretion of a high volume of water. Some of the blood-sucking insects secrete diuretic hormones immediately after each blood meal. These hormones promote rapid excretion of much of the water in the blood, thereby concentrating the nutritious part of the meal (e.g., the blood proteins) in the gut.

The best-understood endocrine systems in insects control growth and development. A key feature of insects is that they have exoskeletons. For an insect to grow, it must periodically shed its exoskeleton and produce a larger one. This shedding process is called molting or ecdysis. The life of an insect consists of a series of discrete steps: growing followed by molting, then more growing followed by molting, and so on. Insects typically undergo changes in their external shape as they develop from young individuals to adults. However, the rigid exoskeleton cannot change shape between molts. This means that all the changes of external shape in the life of an insect must occur during molting. In this way, the molting process is intimately connected to both growth and morphological development (development of form).

Many hormones are involved in controlling the molting process, but three are of principal importance (**FIGURE 35.14**). We will start by discussing two of them and then address the

Neurosecretory cells that secrete PTTH have cell bodies in the brain…

…and axon terminals in the corpora allata.

The corpora allata also contain nonneural endocrine cells that secrete juvenile hormone.

Brain

Corpus cardiacum

Corpus allatum

PTTH

Prothoracic gland

Juvenile hormone

Ecdysone

Nonneural endocrine cells in the prothoracic glands secrete ecdysone.

FIGURE 35.14 Key Structures and Hormones in the Control of Insect Development Hormones are in red. PTTH = prothoracicotropic hormone

third. One is prothoracicotropic hormone (PTTH), a peptide tropic hormone secreted by brain neurosecretory cells. The second is ecdysone, a steroid secreted by nonneural endocrine cells in the prothoracic glands. PTTH controls secretion of ecdysone. In the regulation of molting, *neurosecretory cells in the brain control secretion of hormones into the general circulation by other endocrine cells*. This is one of the two types of interface between the nervous and endocrine systems that we identified in vertebrates. Invertebrates and vertebrates, we see, sometimes exhibit similar major organizational features.

The brain uses its integrative and computational powers to determine when each molt will occur. The neurosecretory cells that secrete PTTH receive synaptic inputs from other, ordinary brain neurons that control when the neurosecretory cells will secrete their hormone. PTTH is not released directly from the brain, however. In an arrangement reminiscent of that in the posterior pituitary gland in vertebrates, axons of the brain neurosecretory cells extend out of the insect brain and end in or near organs called the corpora allata (singular, corpus allatum). These are neurohemal organs, where PTTH is released into the blood from the axon terminals of the brain neurosecretory cells.

During each episode of PTTH secretion, the flow of blood carries the PTTH to the two prothoracic glands, where it stimulates an episode of ecdysone secretion. As the ecdysone circulates, it undergoes peripheral activation to form 20-hydroxyecdysone, a hormone that primarily affects the insect's epidermis, the layer of living tissue just inside the exoskeleton. The epidermis secretes the exoskeleton. The hormone, being a steroid, enters the epidermal cells. There it combines with intracellular receptors, which alter gene transcription patterns. As a result, the epidermal cells secrete enzymes that loosen their connection with the old exoskeleton, allowing the old exoskeleton to be shed. Then the epidermal cells synthesize a new, larger exoskeleton. In other words, a molt occurs.

Juvenile hormone (JH) is the third hormone of primary importance in the control of molting. It is secreted into the general circulation by nonneural endocrine cells in the corpora allata (see Figure 35.14). It is lipid-soluble and enters target cells (chemically it is a terpene and thus of a different sort than the other hormones we have discussed). Many types of cells in an insect's body have intracellular receptors for JH and respond to it by undergoing changes in gene transcription. JH controls an insect's body form as the insect molts. Some insects, such as moths and butterflies, undergo a complete metamorphosis during their development. Each individual starts life as a larva (caterpillar), retains its larval form for several molts, and then metamorphoses into an adult of radically different form (see Concept 23.4). Here we discuss the role of JH in such insects.

When a larva molts, it retains its larval form if JH is at high concentration in the blood during the molting process. During the early life of an individual, the blood concentration of JH is high. Molting thus results in a series of larger and larger larval forms (**FIGURE 35.15**). Later in life, however, JH secretion is reduced, and the JH concentration in the blood falls to a low level. At that point, when molting occurs, the juvenile form is not retained. Instead, the insect enters a resting stage of distinctive body form, called a pupa. During the inactive pupal stage, the insect's body
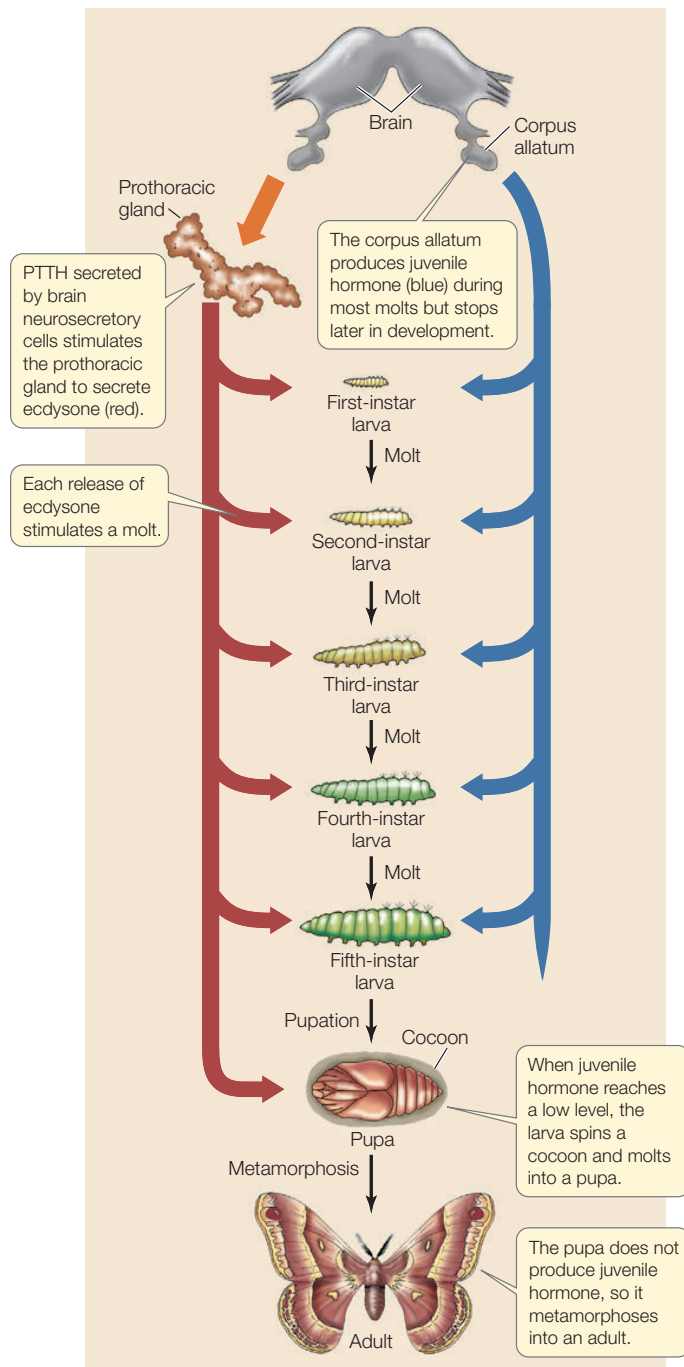
FIGURE 35.15 Hormonal Control of Molting and Metamorphosis in a Moth The silkworm moth *Hyalophora cecropia* is illustrated. An instar is a stage between molts. The ever-larger larval forms are thus referred to as successive larval instars.

Go to ANIMATED TUTORIAL 35.2
Complete Metamorphosis
PoL2e.com/at35.2

is extensively remodeled inside the pupal exoskeleton. Then, when the insect molts yet again without a high concentration of JH in the blood, the individual emerges as an adult.

CHECKpoint   CONCEPT 35.5

✓ Why is juvenile hormone called "juvenile" hormone?

✓ What two actions does ecdysone have on insect epithelial cells?

✓ In what way is there a fundamental similarity between (1) the control of ecdysone secretion by PTTH in insects and (2) the control of FSH secretion by GnRH in mammals?

Q Why are the skeletal muscles under control of both the nervous system and the endocrine system?

ANSWER   The muscles need to be controlled on two scales of spatial definition and two scales of time (Concept 35.1). The nervous and endocrine systems are suited to exerting control on these different scales—explaining why evolution has favored control by both systems. During a game of tennis, for example, the skeletal muscles of the arms, legs, and other parts of the body need to be controlled individually and on a moment-by-moment basis. Nervous control is suited to this task because it is addressed and fast. During adolescent development, muscles throughout the body need to be controlled together and on a sustained basis for many months as they grow and gain strength (Concept 35.4). Endocrine control is suited to this task because it is broadcast and slow.

SUMMARY

CONCEPT 35.1   The Endocrine and Nervous Systems Play Distinct, Interacting Roles

■ Nerve and endocrine cells control and coordinate the functions of the body by releasing chemical signals that travel to another cell, called the **target cell**. **Review Figure 35.1**

■ Neuronal signals are fast and addressed, whereas endocrine signals are slow and broadcast. The nervous system controls predominantly the fine, rapid movements of discrete skeletal muscles. The endocrine system typically controls more widespread, prolonged activities such as developmental or metabolic changes.

■ Animals use chemical signaling over a very broad range of spatial scales. Autocrines and paracrines act on, respectively, the cells producing the signals and on their immediate neighbors. Neurotransmitters and hormones work at intermediate distances. **Pheromones** are released into the environment and can affect targets hundreds of meters away. **Review Figure 35.2**

CONCEPT 35.2   Hormones Are Chemical Messengers Distributed by the Blood

■ Animals have two types of secretory glands: exocrine glands, which have ducts to carry away their secretions, and **endocrine glands**, which do not have ducts. **Endocrine cells** secrete chemical signals into the blood.

■ A **hormone** is a chemical substance that is secreted into the blood by endocrine cells and that regulates the function of other cells that it reaches by blood circulation.

■ Some endocrine cells are **neurosecretory cells**; they propagate action potentials and secrete hormones into the blood from their axon terminals. Other endocrine cells are **nonneural endocrine cells**; they are non-excitable cells that are typically stimulated to secrete their hormones by other hormones. **Review Figure 35.3**

■ Most hormones are **peptide hormones** (polypeptides or proteins), **steroid hormones**, or **amine hormones**. Peptide hormones and some amine hormones are water-soluble; steroids and some amine hormones are lipid-soluble. **Review Figure 35.4**

■ Receptors for water-soluble hormones are located on the cell surface of a target cell. Receptors for most lipid-soluble hormones are inside the cell.

■ Hormones cause different responses in different target cells, depending on each target cell's type of receptor and the processes activated inside the cell by binding of hormone to that receptor.

■ Each hormone has a characteristic half-life, the time required for half of a group of simultaneously secreted hormone molecules to be removed from the blood. Typical half-lives range from minutes to as long as a week.

CONCEPT 35.3   The Vertebrate Hypothalamus and Pituitary Gland Link the Nervous and Endocrine Systems

■ The **pituitary gland** has two parts—the **anterior pituitary** and **posterior pituitary**—which have different developmental origins and function in different ways. Both parts of the pituitary have close functional links with the brain.

■ The posterior pituitary is a neurohemal organ where hormones produced by hypothalamic neurosecretory cells are released into the blood. In mammals it secretes two peptide hormones: **antidiuretic hormone** (**ADH**) and **oxytocin**. **Review Figure 35.6**

■ The anterior pituitary is a nonneural endocrine gland that secretes four **tropic hormones** as well as **growth hormone** (**GH**), prolactin, and a few other hormones. It is controlled by **releasing hormones** (**RH**s) and **inhibiting hormones** (**IH**s; also called release-inhibiting hormones) produced by neurosecretory cells in the **hypothalamus**. **Review Figure 35.7**

■ Endocrine cells often act on each other in sequence, a system known as an **axis**. For example, the hypothalamus–pituitary–adrenal cortex (HPA) axis controls the adrenal secretion of glucocorticoids. **Review ANIMATED TUTORIAL 35.1**

■ Hormone release often is controlled by negative-feedback loops. **Review Figure 35.8**

■ Releasing hormones and inhibiting hormones are often released from the hypothalamus in pulses. Pulsed release is hypothesized to prevent loss of sensitivity in the target cells in the pituitary. **Review Figure 35.9**

(continued)

SUMMARY   *(continued)*

CONCEPT **Hormones Regulate Mammalian Physiological**
35.4 **Systems**

■ The thyroid gland is controlled by **thyroid-stimulating hormone** (**TSH**) and secretes the thyroid hormones thyroxine (T_4) and triiodo-thyronine (T_3), which control cellular metabolism. Iodine deficiency impairs thyroid hormone production and can lead to impaired mental development in children and to goiter in adults. **Review Figures 35.10–35.12 and ACTIVITY 35.1**

■ Sex steroids (**androgens** in males, **estrogens** and **progesterone** in females) are produced by the gonads under control of tropic hormones, called gonadotropins, secreted by the anterior pituitary gland. Sex steroids control prenatal sexual development, puberty, and adult reproductive functions. **Review Figure 35.13**

CONCEPT **The Insect Endocrine System Is Crucial for**
35.5 **Development**

■ Two hormones, prothoracicotropic hormone (PTTH) and ecdysone, control molting in insects. A third hormone, juvenile hormone (JH), prevents maturation. When an insect stops producing juvenile hormone, it molts into an adult. **Review Figures 35.14 and 34.15 and ANIMATED TUTORIAL 35.2**

See **ACTIVITY 35.2** for a concept review of this chapter.

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities
PoL2e.com/is35

Go to LaunchPad at **macmillanhighered.com/launchpad** for additional resources, including LearningCurve Quizzes, Flashcards, and many other study and review resources.

36

Water and Salt Balance

Salmon migrate between fresh water and the ocean. These Atlantic salmon spent the last few years in the ocean. To spawn, they now are swimming upstream to reach suitable spawning areas in the very river where they were conceived.

Salmon are amazing as they jump up waterfalls during their travels upstream. But even more amazing is something we don't see: the concentration of salts and water in their blood plasma stays almost constant as they migrate between the salty oceans and freshwater rivers. We humans can swim in the ocean or fresh water without upsetting our internal water and salt balance, because our skin does not allow water or salts to diffuse through it. However, fish are different. Some of their outer body surfaces—such as their gills and mouth membranes—are permeable to water and salts. To get oxygen, fish need gills that are highly permeable so that O_2 can diffuse easily into their blood from the water in which they swim. Gills that are highly permeable to O_2 are also highly permeable to water and salts. The blood plasma of fish can therefore gain water from or lose water to the surrounding environmental water by osmosis, and it can gain or lose ions by diffusion. For these reasons, fish do not resemble us

in the way they relate to the water and salts in their surroundings.

The blood plasma of salmon is about one-third as concentrated with salts as seawater. Each individual salmon starts life in fresh water, where its blood is far more concentrated than the environmental water in which it swims. During this stage of life, the salmon gains water by osmosis from its surroundings and loses salts by diffusion to its surroundings—processes that tend to dilute its blood. Later, the salmon migrates into the ocean, where its blood is far less concentrated with salts than its environment. During the years it lives in the ocean, it gains salts by diffusion from its surroundings and loses water by osmosis to its surroundings—processes that tend to make its blood become more concentrated.

Osmosis is relentless, whatever its direction. It carries water into or out of a salmon during every hour of the animal's life. Similarly, whatever the direction of salt diffusion, it too is relentless.

How, then, can the concentration of the blood plasma remain almost constant throughout a salmon's life? The salmon has mechanisms that allow it to control the concentration of its blood plasma. These cost energy, and they must be properly regulated by the nervous and endocrine systems.

Salmon dramatically illustrate homeostasis: stability of the internal environment (see Concept 29.3). For most cells in a salmon's body, the type of water in the fish's external environment—whether fresh water or seawater—is of almost no consequence. This is true because the cells are bathed by the tissue fluids, which are similar to blood plasma and therefore almost constant in composition. Because of this stable internal environment, the cells enjoy independence of the external environment.

Q How can a salmon keep the composition of its blood plasma stable regardless of whether it is swimming in seawater or fresh water?

CONCEPT 36.1 Kidneys Regulate the Composition of the Body Fluids

The body fluids of an animal are crucial for its survival because they provide the context in which all living functions take place. An animal's cells are bathed by its tissue fluids (intercellular fluids), which make up the environment of the cells: the animal's internal environment (see Concept 29.3). The organelles inside cells, such as the mitochondria and nucleus, are bathed by the intracellular fluids.

The body fluids have three properties: osmotic pressure, ionic composition, and volume. These properties are interrelated, but often it is helpful to think of them as three distinct characteristics.

• *Osmotic pressure*. The osmotic pressure is basically a measure of the total concentration of solutes (dissolved matter). Each individual dissolved entity makes an approximately equal contribution to the osmotic pressure. For example, if a body fluid has glucose, Na^+, and Cl^- dissolved in it, the individual dissolved entities are the individual glucose molecules, Na^+ ions, and Cl^- ions. Each—regardless of its type—makes a roughly equal contribution to the osmotic pressure. Osmotic pressures are important because they determine the direction of osmotic water movement. Water moves by osmosis from regions where the osmotic pressure (total solute concentration) is low to regions where the osmotic pressure (total solute concentration) is high.
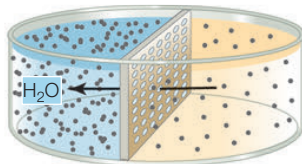
Water moves by osmosis from a region where the osmotic pressure is low to one where it is high. Dots symbolize individual dissolved entities.

A good way to remember this is to recognize that a solution low in solutes is high in water, and vice versa. Water moves by osmosis from where it is high to where it is low: from low osmotic pressure to high osmotic pressure.

• *Ionic composition*. The principal solutes in most biological solutions are Na^+, K^+, and Cl^-. Other ions, such as Ca^{2+}, also occur. Two solutions of the same osmotic pressure are often very different in ion concentrations. One solution, for example, might be rich in Na^+ and the other rich in K^+. Thus it is important to consider the concentrations of particular ions, not just the osmotic pressure. Ion concentrations are important for several reasons. One is that they help determine the direction of ion diffusion. Each particular type of ion (such as Na^+ or K^+) diffuses in response to its particular concentration differences from place to place.

• *Volume*. We experience the importance of body fluid volume every time we get a bruise that causes tissue swell-

FIGURE 36.1 Invisible Dynamism The water and salt exchanges between an animal and its environment often occur at high rates despite being invisible. A goldfish in its bowl may look almost inert. In fact, water is moving rapidly by osmosis into the fish's body from its environment, and the fish is producing urine equally rapidly to keep the volume of its internal body fluids constant.

ing. A body fluid may be correct in its osmotic pressure and ion concentrations but may still cause problems if its volume is wrong. Tissue swelling happens because of an accumulation of excess body fluids. Volume is always important even if we don't notice it. For example, consider a 100-gram goldfish in a goldfish bowl (**FIGURE 36.1**). The goldfish absorbs so much water from its surroundings by osmosis each day that if the water simply accumulated in its body, the fish would be one-third bigger each morning than it was the morning before. This swelling is prevented because the goldfish regulates its volume and voids the water as fast as it comes in. Large volumes of water are coming and going all the time, nonetheless.

"Water and salt balance" refers to homeostasis of the characteristics of the body fluids: their osmotic pressures, ionic compositions, and volumes. Such homeostasis is important because many of the functions of an animal depend on the characteristics of its body fluids.

LINK
You can review the processes of osmosis and diffusion in **Concept 5.2**

Kidneys make urine from the blood plasma

The kidneys—sometimes called the renal or excretory organs—of animals are exceptionally diverse, as we will see. In discussing the kidneys, a good starting point is to ask what similarities exist among the kidneys of various types of animals.

All kidneys consist of tubular structures that discharge a fluid directly or indirectly to the outside environment. The fluid that's excreted into the outside environment is the **urine**. Sometimes a single kidney consists of a single tubule. This is the case in crayfish and lobsters, for example. In contrast, a kidney may consist of great numbers of tubules. A vertebrate kidney, for example, consists of many microscopically tiny tubules called **nephrons**. There are about 1 million nephrons in a single human kidney.
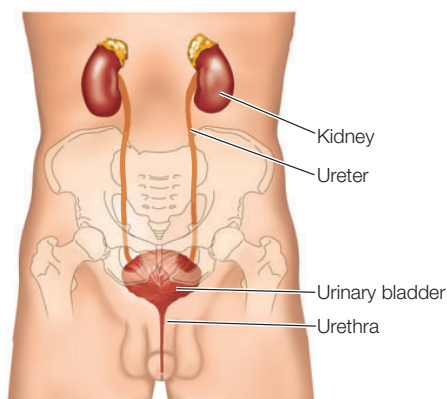
FIGURE 36.2 Major Parts of the Human Excretory System
The organs shown in yellow at the top of the kidneys are the adrenal glands, which are not part of the excretory system.

Go to ACTIVITY 36.1 The Human Excretory System
PoL2e.com/ac36.1

Each nephron (see Figure 36.11) produces urine. The nephrons discharge into a system of tubes that collects the urine from all of them and discharges it into a single tube, the ureter, that carries the fluid out of the kidney. In mammals, the two ureters carry the urine to the urinary bladder, and from there the fluid is expelled through the urethra during urination (**FIGURE 36.2**).

Go to MEDIA CLIP 36.1
Inside the Bladder
PoL2e.com/mc36.1

Kidneys typically make urine from the blood plasma. Recall that the blood plasma is the blood solution: the part of the blood other than the blood cells (see Concept 29.3).

In essence, a kidney tubule starts with one fluid—the blood plasma—and produces another fluid—the urine. We can analyze kidney function by thinking of the kidney as an input–output organ. How does its output (urine) differ from its input (plasma), and how and why does this transformation take place?

Kidneys regulate the composition and volume of the blood plasma

The most important characteristic of kidneys is that they regulate the composition and volume of the blood plasma. This is their primary function.

The kidneys regulate the composition of the blood plasma by selectively removing materials from the plasma. Think for a moment of a bottle containing a salty solution composed of water, Na^+, Cl^-, and other ions. Suppose there is a target osmotic pressure for the solution and that its current osmotic pressure is too low. We could raise the osmotic pressure to the target level by removing water from the solution. To be more realistic, however, suppose we can't remove only water. Suppose that when we remove water, we can't avoid also removing some ions. In this case, we could raise the osmotic pressure to the target level by unequally, or disproportionately, removing water and ions. If we remove lots of water but only small amounts of ions, the solution's osmotic pressure will go up. This exemplifies the way that kidneys usually work.

At this point we can define a **kidney** as an organ composed of tubular structures that produces an aqueous (watery)

solution—urine—for excretion. This solution is derived from the blood plasma. The kidney's primary function is to regulate the composition and volume of the blood plasma by means of controlled removal of solutes and water from the plasma.

Urine/plasma (U/P) ratios are essential tools for understanding kidney function

Suppose the osmotic pressure of an animal's blood plasma is 100 (we'll simply use numbers here and not worry about units of measure). Suppose that, at the same time, the animal's kidneys are excreting urine that has an osmotic pressure of 25. Notice that the urine (25) in this case is more watery (less concentrated with solutes) than the plasma (100).

One way to understand kidney function is to express the composition of the urine as a ratio of the composition of the plasma. Such a ratio is called a urine/plasma, or U/P, ratio. The U/P ratio is 0.25 in the case we're discussing (25/100 = 0.25). Specifically, this is an *osmotic* U/P ratio because it's the ratio of urine and plasma osmotic pressures.

Now recall that the function of making urine is to regulate the plasma. If the osmotic U/P ratio is 0.25, what is the effect on the composition of the plasma? *Both the water and the solutes in the urine come from the plasma.* We see then that when the kidneys make this watery urine, they take a lot of water out of the plasma but only a little solute. In this way the kidneys modify the composition of the plasma, causing it to become more concentrated. They are raising the osmotic pressure of the plasma.

Suppose, by contrast, that the osmotic U/P ratio is 2.0. In this case the urine is less watery than the plasma. When the kidneys make this urine, they take a lot of solute out of the plasma but only a little water. In this way they cause the plasma to become less concentrated.

These principles are of great importance. An animal's kidneys typically adjust the U/P ratio up and down to regulate the blood plasma. The principles allow us to interpret the effects of these adjustments:

- If the urine is less concentrated than the plasma (U/P ratio < 1), the kidneys are making the plasma become more concentrated.

- If the urine is more concentrated than the plasma (U/P ratio > 1), the kidneys are making the plasma become more dilute.

These principles can be applied to osmotic pressures (total solute concentrations), as we have done here. They can also be applied to individual ions. For example, if the urine is more concentrated in Na^+ than the plasma is, the effect will be to lower the plasma Na^+ concentration.

Our day-to-day urine concentrations illustrate these principles

Our urine osmotic pressure is constantly being adjusted up and down by our kidneys to regulate the osmotic pressure of our blood plasma. Human kidneys, at one extreme, can produce urine only one-tenth as concentrated as blood plasma: osmotic U/P = 0.1. At the other extreme, our urine can be four times more concentrated than our plasma: osmotic U/P = 4.0. Our kidneys use this range of variation to perform their regulatory functions.

Suppose you drink a great deal of water one day. Your blood plasma might then become too dilute. Sensory structures detect that the plasma osmotic pressure is tending to go down. In response, your kidneys start to make very dilute urine. The osmotic U/P, as we've said, could be as low as 0.1. To make this dilute urine, the kidneys unequally remove water and solutes from the plasma: lots of water, little solutes. This process keeps the plasma osmotic pressure from falling.

Suppose that at a different time you go out on a hike and run out of water, so you go 2 days without drinking. Your blood plasma might then become too concentrated. Your kidneys respond to sensory input in this case by making concentrated urine. The osmotic U/P could be as high as 4.0. To make this concentrated urine, the kidneys unequally remove water and solutes from the plasma: lots of solutes, little water. This process keeps the plasma osmotic pressure from rising.

Simultaneously, the kidneys adjust the volume of urine. They do this in ways that help keep plasma volume stable.

To summarize, our kidneys adjust both the composition and the volume of the urine to maintain homeostasis in the composition and volume of the blood plasma. We produce a high volume of dilute urine when we drink lots of water. We produce a low volume of concentrated urine when we are dehydrated. The kidneys, by regulating the composition and volume of the blood plasma in these ways, also regulate the composition and volume of the tissue fluids that bathe the cells of the body.

The range of action of the kidneys varies from one animal group to another

We have seen that the human kidney can adjust the osmotic U/P ratio to be between 0.1 and 4.0. Various types of animals differ in this regard. Why does the range of U/P ratios matter? It matters because the regulatory actions that the kidneys can perform depend on it.

The kidneys of most animals can produce urine that is more dilute than the blood plasma (osmotic U/P < 1). This means that the kidneys of most animals can help with problems of excess water in the body.

Animals vary a lot, however, in how concentrated their urine can be. In the great majority of animal groups, the osmotic U/P ratio cannot be higher than 1.0 because of the ways the kidneys function. Fish, amphibians, lizards, snakes, and turtles cannot produce urine that is more concentrated than their blood plasma. Nor can most aquatic invertebrates. *This means that if the blood plasma of these animals is becoming too concentrated, their kidneys cannot correct the problem* (only an osmotic U/P ratio higher than 1.0 will cause the plasma osmotic pressure to decrease).

Mammals, birds, and insects stand out because they are the only animals that can produce concentrated urine with an osmotic U/P ratio exceeding 1.0. Mammals have evolved the greatest abilities. Some desert mammals can achieve osmotic U/P ratios as high as 10 or even 20. Some insects can concentrate their urine to an osmotic U/P ratio of 8. Birds are more limited than mammals and insects but can have U/P ratios of 2–3. Notice that all three of these groups of animals live on land. The ability of their kidneys to make concentrated urine is a great asset as these animals try to keep their plasma osmotic pressure normal while facing risks of rapid dehydration in terrestrial environments.

Extrarenal salt excretion sometimes provides abilities the kidneys cannot provide

In some groups of animals, tissues or organs other than the kidneys have evolved the ability to excrete ions at high total concentrations—a process called **extrarenal salt excretion** (*extrarenal*, "outside the kidneys"). All the animals with extrarenal salt excretion exhibit two characteristics. First, they live in environments where they either face a high risk of dehydration or tend to gain excess salts during their routine daily lives. Second, they have kidneys that are too limited in their concentrating ability to meet these challenges fully.

Many birds and non-avian reptiles that live in close association with the ocean or in deserts have **salt glands**. These glands are located in the head and excrete highly concentrated salt solutions. Seabirds and sea turtles, for example, get overloaded with salts from eating marine (ocean) invertebrates, plants, and algae. They depend on their salt glands (**FIGURE 36.3**) to excrete excess

FIGURE 36.3 Salt Glands in Marine Birds and Sea Turtles (A) The position of the salt glands in a gull. In a bird, the fluid secreted by each gland enters a duct that empties into the nasal passages. The fluid then exits by way of the nostrils. (B) Fluid secreted by the salt glands exits the external tubular nostrils of a northern fulmar and then drips off the tip of the bird's bill. (C) Sea turtles, such as this leatherback sea turtle (*Dermochelys coriacea*), have salt glands, which secrete fluids that drip like tears from the area around the eyes.

(A)

Salt gland

(B)

A salty fluid drips from the bird's bill.

(C)

A salty fluid is expelled like tears.
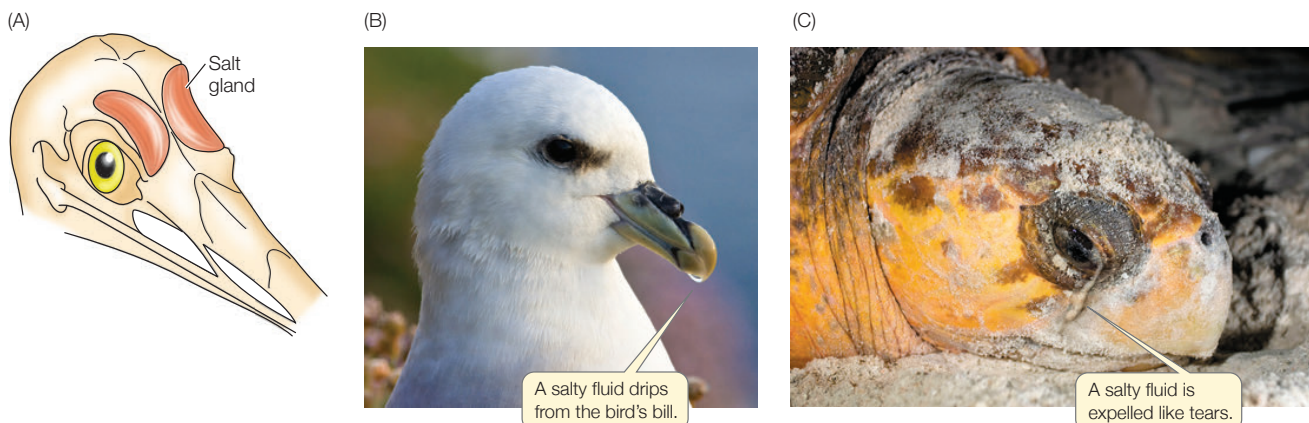
salts. Saltwater fish have specialized salt-excreting cells in their gills, as we will see in Concept 36.3. Mammals—including those living in the oceans—do not have extrarenal salt excretion. Biologists think this is because mammals can depend on their high-performance kidneys to meet all their needs for salt excretion.

CHECKpoint   CONCEPT 36.1

✓ Explain how production of urine with an osmotic U/P ratio of 0.3 helps raise the osmotic pressure of the blood plasma.

✓ Suppose a person eats lots of salty foods. What effect could this have on the composition of the person's blood plasma, and how do the kidneys combat it?

✓ The marine iguanas of the Galápagos Islands are unique among lizards because they principally eat ocean sea-weeds that are as salty as seawater. Periodically a marine iguana "sneezes" a salty solution out of its nostrils. The solution is made by salt glands in the iguana's head. Why do these animals have salt glands instead of relying entirely on their kidneys for excretion?

We have seen how kidneys regulate the composition and volume of the blood plasma by producing urine of varying osmotic pressure and volume. Next we will discuss the special challenges for excretion posed by proteins and other nitrogen-containing molecules when they are broken down.

CONCEPT 36.2   Nitrogenous Wastes Need to Be Excreted

When carbohydrates and fats are fully broken down during metabolism, the end products of the process are H_2O and CO_2 (see Concept 6.2), which are not difficult to eliminate. Proteins and nucleic acids, however, contain nitrogen atoms. Their breakdown therefore produces not only H_2O and CO_2 but also nitrogen-containing waste molecules termed **nitrogenous wastes**. These molecules can be toxic, creating special challenges.

Kidneys are occasionally defined as the organs of nitrogen excretion. This is a misleading definition because in fact the chief function of kidneys is regulation of the blood plasma. Moreover, whereas the kidneys are important in nitrogen excretion in some types of animals, they play little or no role in nitrogen excretion in many other types.

Most water-breathing aquatic animals excrete ammonia

During the breakdown of proteins and nucleic acids, nitrogen atoms are removed from the molecules in the form of amino groups ($—NH_2$), as shown near the top of **FIGURE 36.4**. The $—NH_2$ groups are easily converted to ammonia (NH_3) or ammonium ions (NH_4^+) without any investment of energy. Ammonia therefore

is the simplest and energetically cheapest nitrogenous waste to produce. The problem with ammonia is that it is highly toxic, and its concentration must be kept very low in the body fluids.

Crayfish, squid, most fish, and most other water-breathing animals excrete nitrogen principally as ammonia and for this reason are called **ammonotelic**. They are able to use ammonia as their principal waste because they can lose it rapidly and directly into their aquatic environment across their outer body surfaces. Ammonia is highly soluble in water and diffuses rapidly, so it can be lost readily across the gills and other permeable body surfaces as fast as it is produced, keeping internal concentrations low.

Most terrestrial animals excrete urea, uric acid, or compounds related to uric acid

Terrestrial animals typically must void nitrogenous wastes in their urine. Ammonia is so toxic that great volumes of urine would be required for it to be lost in the urine. The loss of water in urine would in fact be great enough to be dehydrating. Because of all these constraints, terrestrial animals almost never excrete nitrogenous wastes primarily as ammonia.

Instead, terrestrial animals incorporate waste —NH_2 groups into compounds that are far less toxic than ammonia. Producing these compounds requires ATP and thus has a metabolic cost. This is a disadvantage. However, the compounds have the advantage that they do not need to be excreted immediately. Their toxicity is low enough for them to be concentrated in the

FIGURE 36.4 Nitrogenous Wastes   The breakdown of proteins and nucleic acids produces nitrogenous wastes. Most water-breathing aquatic animals, including most fish, excrete nitrogenous wastes as ammonia. Most terrestrial animals and some aquatic animals excrete either urea or uric acid.
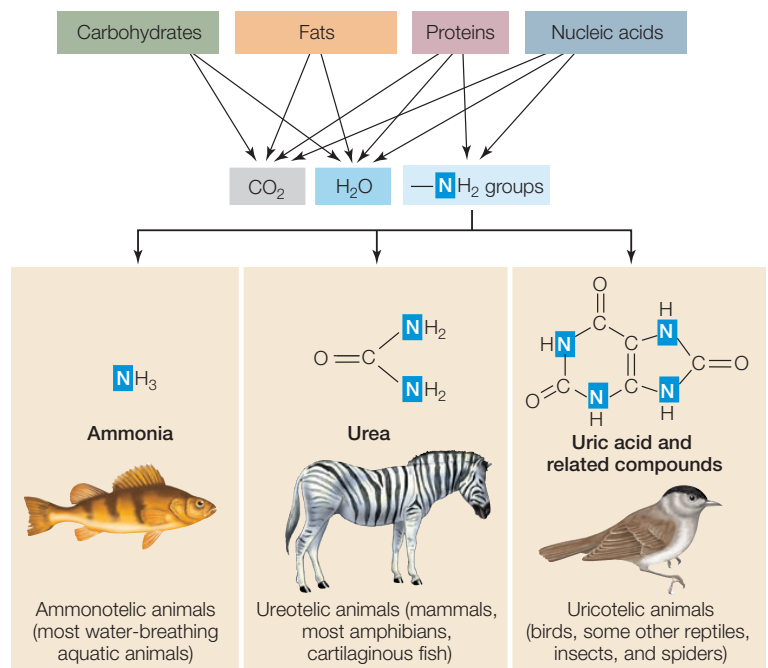
urine before they are excreted, reducing the amount of water required to excrete them:

- Mammals and most amphibians excrete waste nitrogen principally as urea and therefore are called **ureotelic** (see Figure 36.4). Urea is very soluble and relatively low in toxicity.

- Insects, spiders, and many reptiles (including birds) are **uricotelic**, meaning they excrete waste nitrogen mainly as uric acid or compounds related to uric acid. These nitrogenous wastes are poorly soluble in water and thus are often excreted in precipitated (solid or semisolid) form. Precipitation removes the compounds from solution, reducing their toxicity and the amount of water needed to excrete them. The whitish paste in bird droppings is uric acid.

Animals that live in different habitats at different developmental stages may change their primary nitrogenous waste when they change habitat. For example, the aquatic tadpoles of frogs and toads excrete ammonia across their gill membranes, whereas adult frogs and toads generally excrete urea.

CHECKpoint   CONCEPT 36.2

✓ Name the three major nitrogenous wastes. Which one is the most toxic?

✓ Desert-adapted species of mice and rats survive in deserts by minimizing their water losses. Most are herbivores: they eat mostly plant foods. Why might a desert mouse or rat tend to be dehydrated by eating a large meal of animal flesh?

✓ Some species of amphibians that live in arid or semiarid habitats excrete uric acid as adults, instead of urea as other adult amphibians do. What selective advantage would this adaptation have had for the early ancestors of these species?

Now that we have reviewed the three forms in which nitrogenous wastes can be excreted, let's focus on the challenges that animals face in Earth's major environments. We'll start with the aquatic environments: the ocean and bodies of fresh water such as lakes and rivers.

CONCEPT 36.3   Aquatic Animals Display a Wide Diversity of Relationships to Their Environment

A key question to ask regarding any water-breathing aquatic animal is, What is the animal's body fluid composition compared with the composition of the water in which it lives? The simplest way to address this question is to focus on the total solute concentration—the osmotic pressure:

- Some animals have body fluids that have the same osmotic pressure as the water in which they live. These animals are said to be **isosmotic** (*iso*, "equal") to their environment.

- Other animals have body fluids that have a higher osmotic pressure than the environmental water. These animals are termed **hyperosmotic**, (*hyper*, "higher") to their environment.

- Still other animals have body fluids that have a lower osmotic pressure than the environmental water. They are described as **hyposmotic** (*hypo*, "lower") to their environment.

We quantify osmotic pressure in terms of **osmolarity**. Recall that each separate dissolved entity in a solution—whether it is a glucose molecule, protein molecule, or Na^+ ion—contributes approximately equally to osmotic pressure. A solution is defined to be 1 osmolar—symbolized 1 *Osm*—if it has 6×10^{23} dissolved entities per liter (6×10^{23} is Avogadro's number). A solution that is 1 osmolar is 1,000 milliosmolar, symbolized m*Osm*.

Most invertebrates in the ocean are isosmotic with seawater

The simplest and energetically cheapest way for an animal to live in the ocean is for its body fluids to be the same in their total solute concentration as seawater. Animal life first appeared in the ocean, and we think the earliest animals were simply isosmotic with the seawater. Today nearly all invertebrates in the ocean—including lobsters, squid, corals, and sea stars—are isosmotic with seawater. Seawater has an osmotic pressure of almost exactly 1 *Osm*. The blood and other body fluids of most marine invertebrates thus have an osmotic pressure of about 1 *Osm*.

Ocean bony fish are strongly hyposmotic to seawater

There are more than 20,000 species of fish with bony skeletons in the ocean. Their body fluids are far more dilute, in terms of both osmotic pressure and the concentrations of major ions, than the seawater in which they swim. The osmotic pressure of their blood plasma and other body fluids is 0.3–0.5 *Osm* (300–500 m*Osm*), whereas that of seawater is 1 *Osm*. The fish maintain this difference by use of regulatory mechanisms and thus are classed as **hyposmotic regulators**.

Recall from our opening story about salmon that the gills, mouth membranes, and some of the other body surfaces of fish are permeable to water and salts. Because of this permeability and their dilute body fluids, ocean fish face two relentless, never-ending problems:

- *They tend to lose water* by osmosis from their dilute body fluids into the surrounding, more concentrated seawater (**FIGURE 36.5A**). Their steady loss of water tends to dehydrate them (living in the ocean is like living in a desert for these fish).

- *They also tend to gain ions*, such as Na^+ and Cl^-, by diffusion from the seawater into their more dilute body fluids. Their steady losses of water and gains of ions tend to make their blood and other body fluids become too concentrated.

Ocean bony fish expend about 8–17 percent of their metabolic energy each day to fix these problems. To replace the water they are losing, they drink the seawater and expend energy

(A) Ocean bony fish

Water loss by osmosis

Salt gain by diffusion

Gills

Fish drinks. Water is absorbed in the intestines by a mechanism employing ion absorption.

Hyposmotic to environmental water

Small amounts of urine, nearly isosmotic to plasma (osmotic U/P ≈ 1.0)

Active excretion of Na^+ and Cl^-

(B) Freshwater bony fish

Water uptake by osmosis

Salt loss by diffusion

Gills

Fish does not drink.

Hyperosmotic to environmental water

Large amounts of urine, very dilute compared with plasma (osmotic U/P < 1.0)

Active uptake of Na^+ and Cl^-

FIGURE 36.5 **Principal Water and Salt Exchanges in Bony Fish** The water and salt exchanges in ocean fish (A) are in many ways the opposite of those exchanges in freshwater fish (B).

in pumping ions across their intestinal wall so that water will enter their blood from their gut. They also use energy to excrete excess ions. The most concentrated urine their kidneys can produce (in terms of osmotic pressure) is U/P = 1.0. This is not sufficient to keep their body fluids more dilute than seawater. With inadequate kidneys, these fish have evolved vigorous extrarenal salt excretion. Specialized cells in their gills, known as mitochondria-rich cells or chloride cells, use ATP for active ion transport. These cells pump Na^+ and Cl^- out of the blood directly into the more concentrated seawater.

Why are the body fluids of these fish more dilute than seawater? Biologists do not know for certain. The preferred hypothesis today is that all the ocean bony fish evolved from freshwater ancestors, and that their dilute body fluids are a vestige of that earlier stage in their evolution.

All freshwater animals are hyperosmotic to fresh water

Animal life began in the oceans, as we've noted. During the long history of life, however, many phyla invaded rivers, streams, and lakes. Today's freshwater invertebrates include crayfish, shrimp, clams, snails, and cnidarians such as hydra.

In all these cases, the freshwater species are descended from ocean ancestors that had internal osmotic pressures near 1 *Osm*. The freshwater forms alive today, however, have internal osmotic pressures that are less than half that. Why?

An important general principle is that when the body fluids of an animal differ from the animal's environment in some way, the cost of maintaining this difference tends to be greater when the difference is large than when it is small. (We are familiar with an analogy in our apartments and homes. The cost of keeping them warm in winter depends on how warm we keep them. Maintaining a big difference between the temperature inside and outside requires more energy than keeping the inside just slightly warmer than the outside.) When invertebrates first invaded fresh water from the ocean, they had a very large difference between their internal osmotic pressure, 1 *Osm*, and the external osmotic pressure, which is about 0 *Osm* in fresh water. Maintaining this difference required a high rate of energy use. By reducing their internal osmotic pressure over the course of evolutionary time, the animals lowered their rate of energy use. All are hyperosmotic to freshwater and are **hyperosmotic regulators**. Their cost of regulation is lower, however, than it would be if they had retained their ancestral internal concentrations.

Vertebrates have undergone similar changes. Biologists generally believe that the ancestors of today's vertebrates were jawless fish, isosmotic with seawater, living in the ocean. They invaded fresh water, and over evolutionary time, their body fluids became more dilute. Probably they evolved an internal osmotic pressure of about 300–350 m*Osm*. At the same time, they evolved jaws. These early jawed fish with internal osmotic pressures near 300–350 m*Osm* diversified to give rise to today's freshwater fish. They also invaded two other major habitats. Some reinvaded the oceans, giving rise to nearly all the ocean fish alive today, as noted in the last section. Others invaded the land.

LINK

For more on the evolutionary origins of terrestrial animals, see **Concept 23.6**

Because their body fluids are more concentrated than fresh water, all of today's water-breathing freshwater animals—including fish, other water-breathing vertebrates, and invertebrates—face two relentless, never-ending problems that are the opposite of those faced by ocean fish (**FIGURE 36.5B**):

- *They tend to gain water* by osmosis from the dilute freshwater environment. Their steady gain of water tends to bloat them (recall that a goldfish gains water equal to about one-third of its body weight per day).

- *They also tend to lose ions*, such as Na^+ and Cl^-, by diffusion from their body fluids into their environment. Their steady gains of water and losses of ions tend to make their body fluids become too dilute.

Freshwater animals must invest energy to maintain their hyperosmotic state. To void the water they are gaining osmotically, their kidneys produce a large volume of urine per day. In most cases, the kidneys also produce urine that is far more

dilute than the blood plasma (osmotic U/P < 1.0). Producing a large volume of dilute urine costs energy, but it means the kidneys help keep the blood at its correct osmotic pressure. Lost salts have to be replaced. Freshwater animals have specialized active-transport cells that use ATP to pump Na^+ and Cl^- directly from their freshwater environment into their blood. These cells are in the gills of fish, crayfish, and clams. They are in the skin of adult frogs. The pumps are so effective that they take up a lot of Na^+ and Cl^- per day even though these ions are exceedingly dilute in fresh water.

> **LINK**
>
> You can review active transport processes in **Concept 5.3**

Some aquatic animals face varying environmental salinities

Some fish—notably salmon, sturgeon, and many eels—have life cycles in which they migrate between rivers and the ocean. Here we'll focus on salmon. They are conceived and undergo their early development in fresh water, complete much of their growth in the ocean, and finally return to fresh water to spawn. They switch between being typical hyperosmotic regulators when in fresh water to being typical hyposmotic regulators when in seawater (see Figure 36.5):

- A salmon in fresh water does not drink because it is already overloaded with water from osmosis. Upon entering the ocean, it starts to drink and activates intestinal ion transport mechanisms required to take water into its blood from the gut.

- When a salmon is in fresh water, its gills use ATP to pump ions into its blood from the surrounding water. In the ocean, its gills use ATP to pump ions out of its blood into the seawater.

- In fresh water, a salmon's kidneys produce abundant urine that is very dilute compared with the blood plasma (osmotic U/P < 1.0). In seawater, the kidneys produce just a small volume of urine that has about the same osmotic pressure as the blood plasma (osmotic U/P = 1.0).

These changes are controlled by hormones such as prolactin.

Many nonmigratory aquatic animals face a range of environmental options. For example, consider ocean invertebrates. They might move into coastal waters where seawater mixes with fresh water and salinities are intermediate. They might even move into freshwater streams.

Most marine invertebrates are **osmotic conformers** (osmoconformers), but a minority are **osmotic regulators** (osmoregulators). In osmotic conformers, the osmotic pressure of the body fluids is always the same as that of the environmental water. Thus when osmotic conformers enter more dilute water, their body fluids become more dilute to the same extent. We know this is stressful because most of these animals do not survive in water that is much more dilute than seawater. Marine mussels are an exception. They prosper at a wide range of salinities even though they are osmotic conformers (**FIGURE 36.6**).
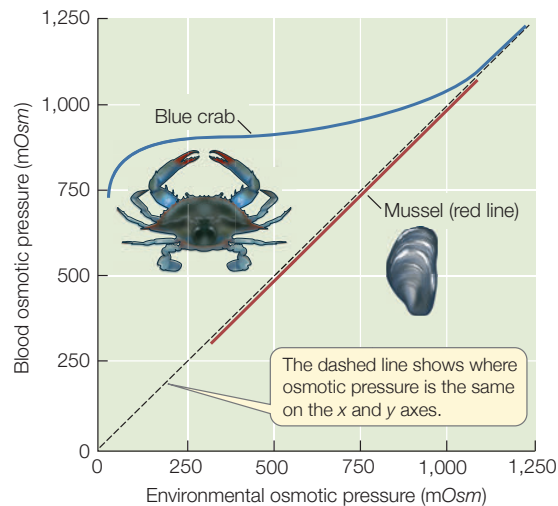
FIGURE 36.6 Osmotic Regulation and Conformity When ocean invertebrates enter waters where the salinities are lower than in the ocean, some (such as mussels) are osmotic conformers and allow their blood osmotic pressure to match the environmental osmotic pressure. Others (such as many crabs) are osmotic regulators. They keep the osmotic pressure of their blood from falling as low as the osmotic pressure in the environmental water, and their internal osmotic pressure is therefore more stable than the environmental osmotic pressure. The osmotic pressure of seawater is 1,000 m*Osm*.

Most marine invertebrates that prosper in dilute waters, including the blue crabs (*Callinectes sapidus*) that are abundant in the coastal waters of our east and Gulf coasts, are osmotic regulators. When living in the ocean, they are nearly isosmotic with seawater, but they are hyperosmotic regulators when in dilute waters, keeping their blood osmotic pressure higher than the environmental osmotic pressure (see Figure 36.6). They thus invest energy in osmotic regulation. In return, they have a more stable internal osmotic pressure than conformers, and this stability allows them to be successful over a broad range of external salinities.

> **LINK**
>
> The general principles of regulation versus conformity are discussed in **Concept 29.3**, along with specific coverage of thermal relationships of animals with their environment

CHECKpoint CONCEPT 36.3

✓ Some marine mussels are of exceptional commercial importance, being considered gourmet foods. From the viewpoint of water and salt balance, in what way are mussels exceptional?

✓ Do bony fish living in the ocean steadily gain or lose water by osmosis from the seawater, or do they neither gain nor lose in a steady manner? Explain.

✓ In what way do the bony fish living in the ocean exhibit extrarenal salt excretion?

Now that we've seen how various animals living in aquatic environments deal with fresh water and with seawater, let's turn to animals living on land.

> ## CONCEPT 36.4 Dehydration Is the Principal Challenge for Terrestrial Animals

Water balance and the risk of dehydration make up the single greatest challenge that terrestrial animals face. We all know that water spilled on a table will gradually disappear by evaporation as it forms gaseous water vapor in the air. Likewise, the internal body fluids of animals on land also tend to evaporate—a process that can concentrate the body fluids and reduce their volume.

The normal blood osmotic pressure of terrestrial vertebrates is typically 300–350 m*Osm*. The early ancestors of terrestrial vertebrates were freshwater fish with similar osmotic pressures, as noted in Concept 36.3. Amphibians, reptiles (including birds), and mammals—including us—retain osmotic pressures in this range.

Humidic terrestrial animals have rapid rates of water loss that limit their behavioral options

During the early stages of animal evolution, the body coverings of animals were relatively permeable to water. This is understandable, because animals spent their early evolution in aquatic environments. Because of their aquatic history, animals had body coverings that were highly water-permeable when they emerged onto land.

Today, some terrestrial animals—classed as **humidic**—continue to have outer body coverings that are highly permeable to water. Examples include millipedes, centipedes, land snails (except when they are withdrawn into their shells), and most amphibians. Water evaporates across the skin of a leopard frog at a rate similar to that of evaporation from an open water surface!

Although humidic animals live on land, they are not free to expose themselves continually to the open air. Their behavioral options are limited because they lose water so rapidly in the open air that if they are forced to remain there, they die within tens of minutes or a few hours. Humidic animals have two options. One is to stay in places where the humidity of the air is high, such as in thick grass or under logs. Their other option is to limit the time they spend in dehydrating situations and return often to places where they can rehydrate. A frog, for instance, might hop out into an open, sunlit area where there are lots of insects to eat, and it might stay there for a short while. A frog loses water rapidly in such a situation, however, and must soon return to a place, such as a pond edge, where it can replenish its body water.

Xeric terrestrial animals have low rates of water loss, giving them enhanced freedom of action

The terrestrial animals we're accustomed to seeing out in the open typically have body coverings that protect them from high rates of evaporative water loss. We see birds, snakes, lizards, mammals, insects, and spiders. All have evolved body coverings in which layers of lipids—waxy or greasy materials—prevent water in their body fluids from freely evaporating into the air. With this protection, these animals—termed **xeric**—can spend indefinite periods in the open air.

Mammals, birds, and other xeric vertebrates have lipids in the outermost cellular layers of their skin. Insects and spiders have a thin layer of lipids on the outside of their exoskeleton.

> **LINK**
>
> See **Concept 23.6** for more on the adaptations that allowed animals to colonize dry environments

Some xeric animals are adapted to live in deserts

A desert, by definition, is a terrestrial environment that receives so little rain that the availability of water exerts a dominant, controlling influence on the organisms living there. Animals adapted to live in deserts exploit multiple mechanisms for reducing their rates of water loss, so that they have very low water requirements.

Kangaroo rats (**FIGURE 36.7**) and a variety of other desert rodents have such low rates of water loss that when individuals finish nursing from their mother, most never drink again for the rest of their lives. How is this possible? These animals have multiple adaptations that reduce their rate of water loss:

- They live in deep, cool burrows during the heat of the day.
- They have exceptionally low rates of evaporation through their skin and produce dry feces.
- Their kidneys can produce urine 10–20 times more concentrated than their blood plasma (osmotic U/P = 10–20), the highest values known among all animals. By concentrating their urine to such a great extent, the animals can excrete their soluble wastes with very little water loss.

FIGURE 36.7 A Desert Kangaroo Rat   Distinctive rodents—many of which hop about on their hind legs like kangaroos—have evolved in all the world's deserts. Kangaroo rats—such as this Ord's kangaroo rat (*Dipodomys ordii*)—occur in the deserts of the American Southwest.

Desert rodents do need some water. Where does it come from? Kangaroo rats typically eat air-dried plant parts such as seeds. These provide a little water. The most important source of water for kangaroo rats, however, is the H_2O produced by the oxidation of organic molecules during metabolism (see Concept 6.2). This water is called **metabolic water** or oxidation water. All animals produce metabolic water, but it is important in the water budget only in animals that conserve water exceptionally well.

Many insects are also adapted outstandingly well to living in deserts. Some birds and mammals survive in deserts by eating the juicy bodies of desert insects or the leaves of juicy plants.

> **LINK**
>
> Plants that live in deserts also face numerous challenges; their adaptations to desert life are described in **Concept 28.3**

> **CHECKpoint**   **CONCEPT 36.4**
>
> ✓ What is metabolic water?
> ✓ Dromedary camels have kidneys that can produce urine eight times more concentrated than their blood plasma. The average concentrating ability of mammals of similar body size is about half as great. Why would camels benefit from having a higher concentrating ability than average?
> ✓ Humidic and xeric terrestrial animals differ in behavior because of their contrasting abilities to conserve body water. Speaking in broad terms, how do they differ in behavior, and why?

In the last two concepts we have considered ways in which aquatic and terrestrial animals meet the challenges they face in their environments. Earlier we stressed that the concentration and volume of an animal's urine are major considerations for understanding water and salt balance. To close the chapter, we will now examine how kidneys work and the characteristics of the urine they produce.

> **CONCEPT 36.5 Kidneys Adjust Water Excretion to Help Animals Maintain Homeostasis**

Kidney tubules—such as the nephrons of vertebrates—typically make urine in two steps. First, fluid derived from the blood plasma enters a kidney tubule at one end. This fluid is called the primary urine. Next, the volume and composition of the fluid are modified as it flows through the remainder of the tubular system in the kidney, forming the final product, called the definitive urine, which is excreted. During this modification step, materials may be *reabsorbed* from the urine. Materials may also be *secreted* into it. Here we focus on these processes in vertebrate kidneys.

Fluid enters a nephron by ultrafiltration driven by blood pressure

A vertebrate nephron is open at one end and closed at the other. Urine formation starts at the closed end, which consists

(A) The general form of a vertebrate nephron at the end where primary urine is formed
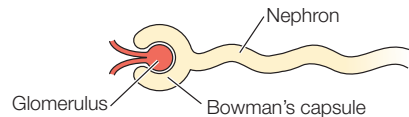
(B)
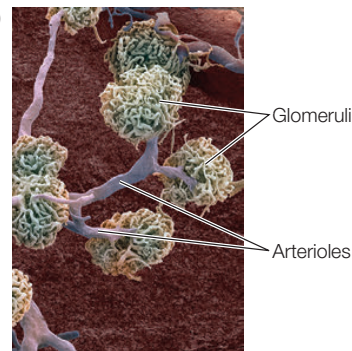
(C) A human glomerulus positioned in a Bowman's capsule
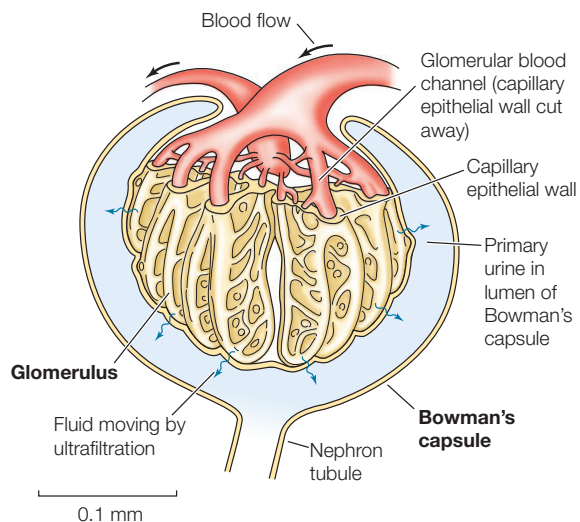
FIGURE 36.8 Primary Urine Is Produced in the Bowman's Capsules and Glomeruli   (A) At its closed end, each vertebrate nephron begins with a Bowman's capsule containing a glomerulus. (B) The glomeruli look like balls of capillaries served by arterioles in this electron micrograph; only blood vessels are seen here because other tissue has been digested away. (C) This drawing of a human Bowman's capsule with glomerulus shows the formation of primary urine by ultrafiltration.

**Go to ACTIVITY 36.2 The Vertebrate Nephron
PoL2e.com/ac36.2**

of a cup-shaped structure called a **Bowman's capsule** that encloses a dense cluster of blood capillaries called a **glomerulus** (plural *glomeruli*). The glomerulus sits within the Bowman's capsule much like a fist pushed into an inflated balloon (**FIGURE 36.8A,B**).

APPLY THE CONCEPT

Kidneys adjust water excretion to help animals maintain homeostasis

In analyzing kidney function, an important question is whether the nephrons reabsorb substances from the tubular fluid passing through them or secrete substances into the tubular fluid. A classic way to study this question starts with measuring the glomerular filtration rate (GFR). The GFR—the volume of fluid that passes into the Bowman's capsules of the kidneys per unit of time—can be calculated by using a marker substance (a substance artificially added to the blood) that is freely filtered out of the blood plasma (so that its concentration in the ultrafiltrate equals its plasma concentration) but *not* reabsorbed or secreted by the nephrons or other renal tubules. The amount of such a marker substance entering the Bowman's capsules equals the amount leaving the body in the definitive urine. Inulin, a polysaccharide, is the most commonly used marker substance. If a different substance *is* reabsorbed or secreted by the nephrons or other renal tubules, the amount of that substance leaving the body in the definitive urine will be either more than or less than the amount filtered. Consider the data

in the table. Assume that all three substances are freely filtered, and assume a urine flow rate of 1 milliliter (ml) per minute. As you address the questions asked, keep in mind that the amount of a substance in a solution is equal to its concentration in the solution times the volume of the solution. The concentrations of Na^+ are in milliequivalents (mEq) per liter (L).

1. What is the glomerular filtration rate (in ml/min)?
2. Is PAH secreted or reabsorbed? Justify your answer.
3. Is Na^+ secreted or reabsorbed? Justify your answer.

SUBSTANCE	CONCENTRATION IN BLOOD PLASMA	CONCENTRATION IN URINE
Inulin	1 mg/ml	125 mg/ml
Para-aminohippuric acid (PAH)	0.01 mg/ml	5.85 mg/ml
Na^+	140 mEq/L	70 mEq/L

Blood is delivered to each glomerulus at a relatively high pressure that's sufficient to force fluid from the blood plasma to pass through minute, porelike openings in the walls of the glomerular blood capillaries and then through the interior wall of the Bowman's capsule. This fluid enters the lumen (the open central cavity) of the Bowman's capsule and is the primary urine (**FIGURE 36.8C**).

The walls of the capillaries and of the Bowman's capsule do not allow all components of the blood to pass through. In this way, the blood is filtered as it moves through these structures. Blood cells and dissolved proteins in the plasma are filtered out and remain in the plasma. By contrast, water, salts, and small organic molecules such as glucose and amino acids pass through freely, entering the nephron. The process of forming primary urine is called **ultrafiltration**. The rate at which the primary urine is formed by all the nephrons functioning collectively is the **glomerular filtration rate** (**GFR**).

The primary urine is similar to the blood plasma in most ways except for lacking blood cells and proteins. The concentrations of ions (e.g., Na^+ and Cl^-) and of small molecules (e.g., glucose) in the primary urine are the same as those in the blood plasma. Moreover, the osmotic pressure of the primary urine is essentially equal to that of the plasma. In other words, the primary urine is isosmotic with the plasma.

As the primary urine flows through a nephron to form the definitive urine, more than half of the water and ions are typically reabsorbed into the blood plasma. More than 99 percent are reabsorbed in a person producing concentrated urine. This sounds inefficient at first. Why produce a large volume of primary urine and reabsorb most of it? The process gives the kidneys intimate access to the plasma. Humans, for example, have a GFR of about 120 milliliters per minute. At this rate the equivalent of all the plasma water in the body enters the

nephrons every 30 minutes! This rate enables the kidneys to remove wastes or toxins quickly and to make rapid adjustments in the plasma volume and composition.

Many types of animals are believed to employ ultrafiltration to produce primary urine. Besides vertebrates, these animals include squid and octopuses, and crustaceans such as crayfish.

The processing of the primary urine in amphibians reveals fundamental principles of nephron function

The amphibian nephron provides a model for understanding all vertebrate nephrons. The nephrons of freshwater fish and non-avian reptiles, and most of the nephrons of birds, are similar. The parts of a vertebrate nephron are termed "early" or "proximal" if they are relatively close to the Bowman's capsule. They are called "late" or "distal" if they are relatively far away. Along the entire length of a nephron, the nephron walls consist of a single layer of epithelial cells. However, these cells differ greatly in their structure and in the proteins they express from one part of a nephron to another.

An amphibian nephron consists of two highly convoluted segments, the proximal and distal convoluted tubules:

Distal convoluted tubule

Intermediate segment

Proximal convoluted tubule

Bowman's capsule

Fluid exits nephron and is excreted.
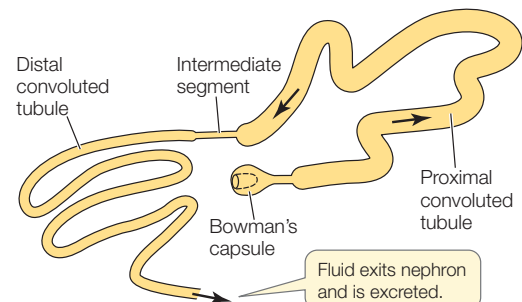
(A) Early tubule (proximal convoluted tubule) in amphibian or mammal

This degree of shading symbolizes an osmotic pressure equal to that of blood plasma

→ Active transport of NaCl

→ Osmosis of water

→ Flow of tubular fluid

The water permeability of the tubular wall (epithelium) is always high. Water osmoses out of tubular fluid so it stays isosmotic with plasma as NaCl is pumped out.

Tubular fluid

Tissue fluid surrounding tubule

Output is isosmotic with plasma but greatly reduced in volume compared to input.

FIGURE 36.9 Amphibian and Mammalian Kidney Tubules Operate in Fundamentally Similar Ways The lightness or darkness of the shading represents the osmotic pressure in the fluids inside and outside the tubules, with darker shading corresponding to higher osmotic pressures. In both amphibians and mammals, the tubules can switch between producing a high volume of relatively dilute urine (diuresis) and a low volume of relatively concentrated urine (antidiuresis), under control of antidiuretic hormone (ADH). (A) The functioning of the early tubule is similar in amphibians and mammals. (B, C) The greatest difference between amphibians and mammals is that in amphibians the tissue fluids surrounding the late tubules are isosmotic with blood plasma (B), whereas in mammals these tissue fluids reach a far higher concentration than blood plasma (C). This difference explains why amphibians and mammals differ in their maximum urine concentrations.

(B) Amphibian late tubule (distal convoluted tubule)

Diuresis (antidiuretic hormone low)

Antidiuresis (antidiuretic hormone high)

Low water permeability

High water permeability

High volume of dilute urine (osmotic U/P < 1.0)

Low volume of urine with osmotic U/P ≃ 1
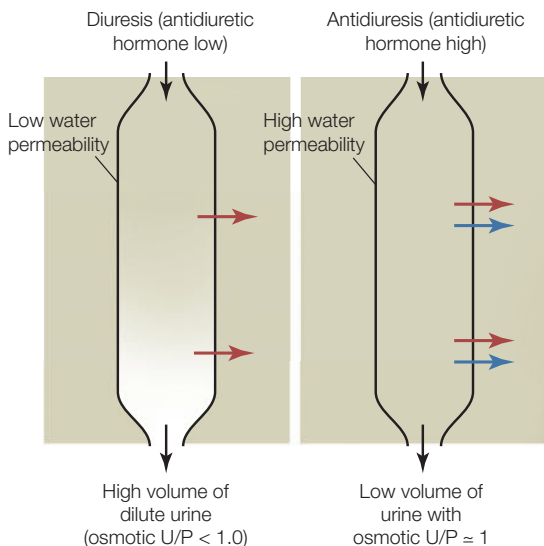
(C) Mammalian late tubule (collecting duct)

Diuresis (antidiuretic hormone low)

Antidiuresis (antidiuretic hormone high)

Low water permeability

High water permeability

High volume of dilute urine (osmotic U/P < 1.0)

Low volume of urine with osmotic U/P >> 1
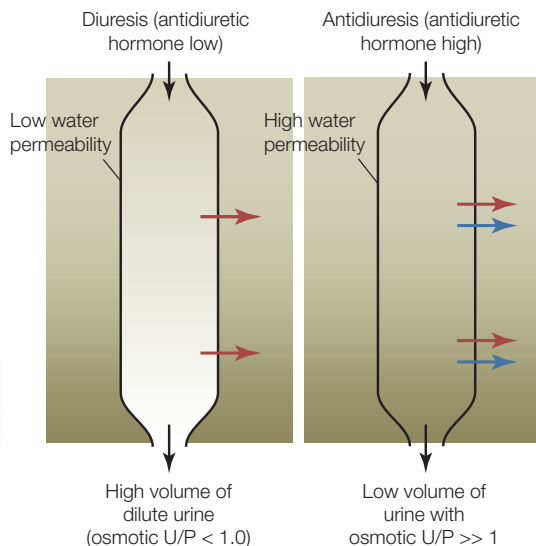
When primary urine flows out of the Bowman's capsule, it passes first through the proximal convoluted tubule (the early part of an amphibian nephron). The nephron wall in this segment is always highly permeable to water because **aquaporins** (water channel proteins; see Concept 5.2) are present at all times in the cell membranes of the epithelial cells composing the wall.

As the fluid in the tubular lumen—called **tubular fluid**—flows through the proximal tubule, Na^+ and Cl^- are removed by active transport and returned to the blood. This removal of Na^+ and Cl^- tends to make the tubular fluid more dilute than the blood plasma. However, as the tubular fluid tends to become dilute, water also moves out of it into the nearby, more concentrated blood plasma by osmosis. The end result is that the volume of the tubular fluid is greatly reduced as the fluid flows through the proximal tubule, but the osmotic pressure of the fluid remains unchanged and equal to that of the blood plasma (**FIGURE 36.9A**). The epithelial cells of the proximal tubule also actively transport glucose and amino acids out of the tubular fluid, returning these valuable molecules to the blood.

Farther along the nephron, the tubular fluid enters the distal convoluted tubule. The most important difference between the proximal and distal convoluted tubules is that the wall of the distal convoluted tubule has a variable permeability to water. This is believed to be controlled by insertion and retrieval of aquaporin proteins. Aquaporin molecules in the epithelial cells of the distal tubule can either be inserted in the cell membranes or not. If they are inserted, the cells are highly permeable to water. If they are not inserted, the cells are poorly permeable to water. Like the proximal tubule, the distal tubule pumps Na^+ and Cl^- out of the tubular fluid by active transport.

Insertion of aquaporins is controlled by **antidiuretic hormone (ADH)** secreted by the hypothalamus of the brain (see Concept 35.3). Variations in ADH secretion control whether the kidney produces abundant urine—a state called diuresis—or a small amount of urine—termed antidiuresis. ADH secretion also controls the concentration of the definitive urine (**FIGURE 36.9B**).

When the level of ADH is high, the wall of the distal convoluted tubule (the late part of the amphibian nephron) is highly permeable to water because aquaporin molecules are inserted

in the epithelial cell membranes. The distal tubule then acts much like the proximal tubule. Na$^+$ and Cl$^-$ are pumped out of the tubular fluid, and water follows by osmosis, so the osmotic pressure in the tubular fluid remains similar to that in the blood plasma. Accordingly, the kidney is in a state of antidiuresis. It produces a low volume of urine that is approximately isosmotic with the blood plasma (see Figure 36.9B, antidiuresis).

By contrast, when the level of ADH is low, aquaporin molecules are not inserted in the epithelial cell membranes, and the wall of the distal tubule is poorly permeable to water. Under these conditions, water in the tubular fluid cannot readily leave it, and most of the water that enters the distal tubule passes through and is excreted. Moreover, as Na$^+$ and Cl$^-$ are pumped out of the tubular fluid, the fluid becomes more and more dilute. The kidney is in a state of diuresis and produces a high volume of urine that is far more dilute that the blood plasma (see Figure 36.9B, diuresis).

ADH secretion is controlled in ways that help maintain homeostasis of the blood plasma. If the plasma is tending to become too dilute and full of water, sensors inform the brain, and ADH is not secreted—resulting in a high volume of dilute urine. In contrast, if the plasma is tending to become too concentrated and low in volume, ADH is secreted, and a low volume of concentrated urine is excreted.

Mammalian kidneys produce exceptionally high urine concentrations

The kidneys of amphibians regulate the urine so that the osmotic U/P ratio varies between values far less than 1.0 (urine more dilute than the blood plasma) and equal to 1.0 (urine isosmotic with the plasma). How do mammals produce exceptionally concentrated urine with a U/P ratio much higher than 1.0?

Mammalian nephrons function in ways that are fundamentally similar to those of amphibian nephrons. For example, the proximal convoluted tubule of a mammalian nephron (the early part of the nephron) is always highly permeable to water and reduces the volume of the primary urine without changing its osmotic pressure (see Figure 36.9A).

The most important difference between amphibian and mammalian kidneys is that the late tubules of the mammalian kidney—which are called **collecting ducts**—are surrounded with tissue fluids that in places are far more concentrated than the blood plasma. This difference explains how the mammalian kidney can produce urine that is more concentrated than the plasma. **FIGURE 36.9C** illustrates the mechanism. Tubular fluid travels through a collecting duct just prior to leaving the kidney as definitive urine. The tissue fluids surrounding the beginning of the collecting duct are similar to blood plasma in osmotic pressure. Along the length of the duct, however, the tissue fluids surrounding the duct have an ever-higher osmotic pressure, reaching an osmotic pressure far higher than that of the blood plasma, as Figure 36.9C shows. Na$^+$, Cl$^-$, and other salts cannot diffuse readily across the wall of a collecting duct, although they can cross by means of ion pumping when pumps are active.

When the ADH level is high, the wall of the collecting duct is highly permeable to water because aquaporins are inserted in the cell membranes of the epithelial cells composing the wall. As tubular fluid flows through the collecting duct, it loses water by osmosis into the concentrated tissue fluids surrounding the duct (and the blood then picks up this water). This process of water removal concentrates the salts in the tubular fluid (see Figure 36.9C, antidiuresis). Just before the tubular fluid leaves the collecting duct to enter the ureter and travel to the bladder, the tubular fluid comes to osmotic equilibrium with the tissue fluids of highest concentration. The osmotic pressure of the urine is thus far higher than that of the blood plasma. A low volume of highly concentrated urine is produced.

When the ADH level is low, the wall of the collecting duct has a low permeability to water because aquaporins are removed from the cell membranes of the epithelial cells composing the wall (see Figure 36.9C, diuresis). As tubular fluid flows through the collecting duct, it does not lose much water by osmosis into the surrounding tissue fluid. Moreover, Na$^+$ and Cl$^-$ are actively transported out of the tubular fluid, making the fluid more and more dilute as it moves through the collecting duct. A high volume of dilute urine is produced.

AQP-2 is the specific molecular form of aquaporin that is of greatest importance in controlling the water permeability of the collecting duct. Experiments have documented its important role (**FIGURE 36.10**).

How are the tissue fluids bathing the collecting ducts deep inside the kidney made highly concentrated? In a mammalian kidney, a portion of each nephron functions to increase the osmotic pressure of the tissue fluids surrounding it. This portion is a long, hairpin-shaped segment called the **loop of Henle** (pronounced Hen-lee), positioned immediately after the proximal convoluted tubule (**FIGURE 36.11**). All the nephrons in a mammalian kidney are organized so that their loops of Henle are parallel. This microscopic structure gives the entire kidney a visible structure. Each kidney has an outer layer, the renal cortex, where the Bowman's capsules and the convoluted tubules of the nephrons are found. Inside this cortical layer, the kidney has an inner layer called the renal medulla. This inner layer is composed of the loops of Henle and collecting ducts (see Figure 36.11). Parts of the medulla are said to be "deeper," the farther they are from the cortex.

The loops of Henle in a kidney work together to increase the osmotic pressure of the tissue fluids deep in the medulla. In this way, the loops create a gradient in the osmotic pressure of the medullary tissue fluids, so that the tissue fluids near the cortex are isosmotic with the blood plasma, but those deep in the medulla are far more concentrated. For example, in the human kidney, the osmotic pressure of the tissue fluids increases from about 300 m*Osm* near the cortex to about 1,200 m*Osm*—four times the blood osmotic pressure—in the deepest medullary tissue. To create this gradient, the loops of Henle use a mechanism called **countercurrent multiplication** (not to be confused with countercurrent exchange) in which the flow of tubular fluid in opposite directions in each loop (first into the medulla and then out) multiplies effects of active ion transport. The loops of Henle do not themselves concentrate the urine, but they set the stage for the urine to be concentrated in the collecting ducts.

INVESTIGATION

FIGURE 36.10 ADH Activates Insertion of Aquaporins into Cell Membranes Aquaporin proteins make some regions of renal tubules permeable to water. One type of aquaporin, AQP-2, is responsible for the permeability of the collecting duct cells in a mammal. How does antidiuretic hormone (ADH) act on molecules of AQP-2 to control the level of water permeability in renal cells?[a]

HYPOTHESIS

ADH controls water permeability by changing the cellular location of aquaporin molecules.

METHOD
1. Isolate collecting ducts from rat kidney.
2. Use immunochemical staining to localize AQP-2 molecules in collecting duct cells without ADH, then with ADH, and—finally—after the applied ADH is washed away.
3. Measure the water permeability of the collecting duct cells under the same three conditions.

RESULTS

Collecting duct cell   Inside collecting duct

Intracellular vesicle

Without ADH, AQP-2 molecules are mostly found in membranes of intracellular vesicles.

With ADH, AQP-2 molecules are mostly found in the cell membranes of the collecting duct cells.

AQP-2

After ADH washout, AQP-2 molecules are again sequestered in intracellular vesicles.

The change in AQP-2 location in the presence of ADH is accompanied by increased water permeability of duct cells.

CONCLUSION

In the absence of ADH, AQP-2 water channel molecules are sequestered intracellularly. When ADH is present, these water channels are inserted into the cell membranes, making the cells more permeable to water.

ANALYZE THE DATA

The results showed that ADH controls the location of AQP-2 molecules in collecting duct cells. Does ADH also affect the amount of AQP-2? The Brattleboro strain of rats does not produce ADH, and the DI strain of mice has a defect in the signaling pathway of the ADH receptor. The amount of AQP-2 produced in response to ADH and to an ADH receptor antagonist was studied in these animals. Values were normalized to baseline amounts in normal animals.

	Amount of AQP-2			
Treatment	Normal rat	Brattleboro rat	Normal mouse	DI mouse
Baseline	1.0	0.5	1.0	0.1
ADH	1.0	1.5	1.0	0.1
ADH receptor antagonist	0.5	0.5	0.5	0.1

A. How does ADH affect the amount of AQP-2 in normal and Brattleboro rats? Explain the difference in the responses of the two rat strains.

B. Why does ADH not have an effect on the amount of AQP-2 in DI mice?

C. Considering these data as a whole, construct a hypothesis to explain why Brattleboro rats can maintain AQP-2 levels at 50% of normal under baseline conditions. How would you test your hypothesis?

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]K. Fushimi et al. 1993. *Nature* 361: 549–552; S. Nielsen et al. 1995. *Proceedings of the National Academy of Sciences* 92: 1013–1017.

Each nephron empties into a collecting duct, and the fluid from the nephron then flows through the collecting duct from the cortex to deep in the medulla (see Figure 36.11). As the fluid flows through the collecting duct, it becomes definitive urine, which exits the collecting duct to flow to the bladder via the ureter draining the kidney (see Figure 36.2). Figure 36.9C, which we have already discussed, shows how the volume and concentration of the definitive urine are determined in the collecting duct, both when the ADH level is high and when it is low.

Birds differ from mammals in that only 10–30 percent of their nephrons have loops of Henle. This limits the concentrating ability of bird kidneys relative to mammalian kidneys.

The Malpighian tubules of insects employ a secretory mechanism of producing primary urine

The primary urine of insects is produced in blind-ended tubules, the **Malpighian tubules**, that open into the gut between the midgut and hindgut (**FIGURE 36.12**). Insects have a low-pressure, open circulatory system (see Concept 32.1) and do not use high blood pressure to cause ultrafiltration into the tubules. Instead, the epithelial cells in the tubule walls employ active transport to secrete KCl (or in some cases other salts) at a high rate into the tubular fluid, giving the tubular fluid a high osmotic pressure. The walls of the tubules are permeable to water. Water therefore enters the tubules by osmosis from the more dilute blood

Cortex
Medulla
Ureter

Connection of
a nephron to the
collecting duct

Nephron

Proximal convoluted
tubule

Bowman's
capsule

In the human kidney,
the osmotic pressure of
the tissue fluid here is
300 mOsm, but…

Artery

Cortex

Distal convoluted
tubule

Vein

Medulla

Loop of Henle

Tissue fluid osmotic pressure increases because
of the action of all the loops of Henle working together.

Medullary
blood vessels
(vasa recta)

Collecting duct

Collecting duct discharges
into the ureter

…the osmotic pressure
deep in the medulla is
1,200 mOsm.

FIGURE 36.11 The Mammalian Kidney
The Bowman's capsules and convoluted tubules
of the nephrons are in the kidney's outer region,
the cortex. Other tubules are in the internal region,
the medulla. The loops of Henle run parallel to one
another in the medulla, where they create a steep
gradient of osmotic pressure in the medullary tis-
sue fluid. After tubular fluid leaves each nephron,
it flows through a collecting duct to exit the kid-
ney. As the tubular fluid within the collecting duct
moves deeper and deeper into the medulla during
this process, it passes by tissue fluids that are more
and more concentrated.

Go to ANIMATED TUTORIAL 36.1
The Mammalian Kidney
PoL2e.com/at36.1

Go to ANIMATED TUTORIAL 36.2
Kidney Regulation Simulation
PoL2e.com/at36.2

3 As fluid flows through the hindgut, H$_2$O
and salts can be reabsorbed and returned
to the blood, or they can be added from
the blood. Most KCl used to make the
primary urine is reabsorbed.

Abdomen
of ant

2 Tubular fluid is
discharged
into the gut.

Hindgut

Midgut

Rectum

4 Some insects can concentrate
the urine in the rectum so
it is more concentrated than
blood plasma (up to U/P = 8).

1 In most insects, KCl from the blood plasma is secreted vigorously
into the lumen of the Malpighian tubules. Water from the plasma
enters by osmosis to keep the tubular fluid isosmotic with the
plasma. Other solutes enter by diffusion.

Hemocoel

5 Urine and feces
are eliminated
via the anus.

Malpighian
tubules

FIGURE 36.12 Urine Production in Insects
The Malpighian tubules project into the
hemocoel, the principal body cavity, which
is filled with blood because of the structure
of the open circulatory system. There the
tubules are bathed with blood. The tubules
form primary urine from the blood plasma by
a secretory mechanism. Insects use at least
three markedly different mechanisms to pro-
duce urine that is more concentrated than
blood plasma (osmotic U/P > 1.0), usually in
the rectum. They can also produce urine that
is more dilute than blood plasma (U/P < 1.0).

surrounding them, creating the primary urine. Other salts besides KCl enter by diffusion. The process is described as a "secretory mechanism" for producing primary urine.

The primary urine flows out of the Malpighian tubules into the hindgut and then flows through the hindgut, which greatly modifies the volume and composition of the fluid before it is excreted. Thus the excretory system consists of both the Malpighian tubules and the hindgut. One important function of the hindgut is to reabsorb the KCl used to produce primary urine, so the KCl can be used again in urine production.

CHECKpoint   CONCEPT 36.5

✓ Human patients suffering from heart failure often become unable to produce adequate amounts of urine, a condition known as kidney failure. How could heart failure lead to kidney failure?

✓ What is the difference between an ultrafiltration-based mechanism of producing primary urine and a secretion-based mechanism?

✓ Antidiuretic hormone (ADH) has the same effect on the late tubules of both amphibians and mammals: it increases the water permeability of epithelial cells that are otherwise poorly permeable to water. If the effect is the same, why do amphibian kidneys produce urine of the same osmotic pressure as the blood plasma when the ADH concentration is high, whereas mammals produce urine more concentrated than blood plasma?

Q How can a salmon keep the composition of its blood plasma stable regardless of whether it is swimming in seawater or fresh water?

ANSWER   When a salmon travels from seawater into fresh water, it reverses many of the processes it employs to maintain water and salt homeostasis. In seawater, cells in the gill epithelium actively transport Na^+ and Cl^- out of the blood plasma into the surrounding seawater (Concept 36.3). When a salmon enters fresh water, its gills reverse their direction of active ion transport, pumping Na^+ and Cl^- into the blood plasma from the surrounding river or pond water.

Drinking behavior also reverses. When in seawater, a salmon drinks to replace the water it steadily loses by osmosis across its external body surfaces. When the fish enters fresh water, it stops drinking.

Kidney function reverses as well. When a salmon is in seawater, its kidneys produce just a small amount of urine per day, and the urine has the same osmotic pressure as the blood plasma. This concentration, although maximal for a fish, is inadequate to keep the plasma concentration from rising. As a result, the gills must bear most of the responsibility for voiding excess ions in a way that will maintain the plasma hyposmotic to seawater. When a salmon enters fresh water, its kidneys switch to producing a large volume of dilute urine.

SUMMARY

CONCEPT 36.1 Kidneys Regulate the Composition of the Body Fluids

■ The body fluids of an animal have three characteristics: osmotic pressure, ionic composition, and volume.

■ **Kidneys** are organs composed of tubular structures that produce **urine**—an aqueous solution derived from the blood plasma—for excretion. The primary function of kidneys is to regulate the composition and volume of the blood plasma by means of controlled removal of solutes and water from the plasma. **Review Figure 36.2 and ACTIVITY 36.1**

■ Kidney function can be expressed in terms of the composition of the urine as a ratio of the composition of the blood plasma. Such a ratio is called a urine/plasma, or U/P, ratio. If the urine is less concentrated in total solutes than the plasma (osmotic U/P < 1), the kidneys are making the plasma become more concentrated. If the urine is more concentrated than the plasma (U/P > 1), the kidneys are making the plasma become more dilute.

■ Animals vary in the U/P ratios that can be achieved by their kidneys and thus in how concentrated their urine can be. Mammals, birds, and insects are the only animals that can produce concentrated urine with an osmotic U/P ratio exceeding 1.0.

■ Some groups of animals have tissues or organs other than the kidneys that excrete ions at high total concentrations—a process called **extrarenal salt excretion**. **Review Figure 36.3**

CONCEPT 36.2 Nitrogenous Wastes Need to Be Excreted

■ Metabolism of proteins and nucleic acids produces toxic **nitrogenous wastes**, which must be eliminated from the body. **Review Figure 36.4**

■ **Ammonotelic** animals produce ammonia as their primary nitrogenous waste. They are typically water-breathing aquatic animals that eliminate ammonia by diffusion across their gills or other permeable body surfaces.

■ Terrestrial animals nearly always excrete nitrogenous wastes that are far less toxic than ammonia. Synthesizing these alternative nitrogenous wastes requires investment of energy.

■ **Ureotelic** animals detoxify ammonia by converting it mostly to urea before excretion. These animals include mammals and most amphibians.

■ **Uricotelic** animals convert ammonia mostly to uric acid or other compounds closely related to uric acid. They include insects, spiders, and birds and some other reptiles. Uric acid and the compounds related to it can be excreted in precipitated form, resulting in little loss of water.

SUMMARY   *(continued)*

CONCEPT 36.3   **Aquatic Animals Display a Wide Diversity of Relationships to Their Environment**

■ **Osmolarity** is a measure of the overall solute concentration (osmotic pressure) of a fluid. An animal may have body fluids that have the same osmotic pressure as the animal's environment (**isosmotic**) or that have a higher (**hyperosmotic**) or lower (**hyposmotic**) osmotic pressure than the animal's environment.

■ Ocean bony fish are hyposmotic to their environment; they tend to lose water by osmosis and gain ions by diffusion. Freshwater fish are hyperosmotic to their environment; they tend to gain water by osmosis and lose ions by diffusion. To regulate the composition of their body fluids, both ocean and freshwater fish employ their kidneys, ion pumping mechanisms in their gills, and drinking behavior. **Review Figure 36.5**

■ Migratory bony fish such as salmon switch between being **hyperosmotic regulators** in fresh water and **hyposmotic regulators** in seawater.

■ Some marine invertebrates face varying environmental osmolarities. These animals can be **osmotic conformers** or **osmotic regulators**. Most marine invertebrates are osmotic conformers and do not survive well in dilute waters. **Review Figure 36.6**

CONCEPT 36.4   **Dehydration is the Principal Challenge for Terrestrial Animals**

■ Terrestrial animals can readily become dehydrated because of evaporative loss of water from their body fluids.

■ **Humidic** terrestrial animals have outer body coverings (i.e., skin, exoskeleton, or the like) that are highly permeable to water. Such animals lose water so rapidly by dehydration that they can tolerate only limited exposure to dehydrating conditions.

■ **Xeric** terrestrial animals have outer body coverings that highly limit evaporation of their body fluids. These animals can therefore spend indefinite periods in the open air. The low water permeability of their body coverings results from the presence of lipids.

■ **Metabolic water** is the water produced by the oxidation of food materials during metabolism. It sometimes serves as a major source of water for desert animals that have very low total water needs because they conserve water exceptionally well.

CONCEPT 36.5   **Kidneys Adjust Water Excretion to Help Animals Maintain Homeostasis**

■ Vertebrate kidneys consist of many tubules called **nephrons**.

■ The fluid first introduced into a nephron is the primary urine. This fluid is modified as it flows through the nephron by processes of reabsorption and secretion. The fluid that is excreted into the outside environment is the definitive urine.

■ Urine formation in a vertebrate nephron begins at the closed end of the nephron, which consists of a **Bowman's capsule** that surrounds a **glomerulus**. The primary urine is formed by **ultrafiltration**, during which fluid moves out of the blood plasma in the glomerulus and into the lumen of the Bowman's capsule, driven by the force of blood pressure. The primary urine is similar in composition to the blood plasma in most ways except for lacking blood cells and proteins. **Review Figure 36.8 and ACTIVITY 36.2**

■ The rate at which primary urine is introduced into all the Bowman's capsules collectively is the **glomerular filtration rate** (**GFR**).

■ The proximal convoluted tubule of a nephron reabsorbs water, Na^+, Cl^-, and certain other solutes, reducing the volume of the **tubular fluid** without changing its osmolarity.

■ **Antidiuretic hormone** (**ADH**) controls the function of the late kidney tubules: the distal convoluted tubules in amphibians and the **collecting ducts** in mammals. When the ADH concentration is high, **aquaporin** molecules are inserted in the cell membranes of the epithelial cells of the late tubules, making the cells water permeable. Consequently, the tubular fluid loses water by osmosis into the surrounding tissue fluids, reducing the volume of the tubular fluid and raising its concentration (an antidiuretic state). When the ADH concentration is low, the epithelial cells are poorly permeable to water. Thus, the volume of the tubular fluid is not reduced as much by osmosis, and the fluid is rendered dilute by removal of solutes (a diuretic state). **Review Figures 36.9 and 36.10**

■ When the concentration of ADH is high, an amphibian makes urine that is isosmotic with the blood plasma because the tissue fluids surrounding the distal convoluted tubules are isosmotic with plasma. A mammal, however, makes urine that has an osmotic pressure higher than the plasma because the tissue fluids surrounding the collecting ducts are hyperosmotic to the plasma.

■ In a mammal, the **loops of Henle** create a concentration gradient in the tissue fluids of the renal medulla by **countercurrent multiplication**. This is the mechanism by which the tissue fluids surrounding the collecting ducts are made hyperosmotic to the plasma. **Review Figure 36.11 and ANIMATED TUTORIALS 36.1 and 36.2**

■ The excretory system of an insect is composed of the **Malpighian tubules** (which join the gut at the junction of midgut and hindgut) and the hindgut. Primary urine is formed by a secretory mechanism, often driven by active transport of KCl into the Malpighian tubules. **Review Figure 36.12**

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities
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37

Animal Reproduction

The ability of rabbit populations to expand rapidly is based on distinctive features of their reproductive biology. European rabbits (*Oryctolagus cuniculus*) such as these are noted for their reproductive potential.

Rabbits are famed for their reproductive potential. Some of this fame is of a shocking kind. European rabbits (*Oryctolagus cuniculus*) were introduced into Australia around 1860 so they could be hunted for sport. Populations quickly grew into the millions, and today rabbits are blamed for dramatic habitat destruction in much of the country.

Reproductive biology is not the only factor that affects whether a species becomes a pest or an asset in the wild. The presence or absence of natural predators, for example, is also important.

Nonetheless, any analysis of rabbits must take into consideration that, for mammals of their body size, their reproductive biology endows them with an extraordinary capacity to multiply. One pair of European rabbits has the biological potential to produce 15 pairs in a year and (by the principles of exponential growth) more than 200 pairs in 2 years.

Two aspects of the reproductive biology of rabbits stand out in explaining this reproductive potential. First, rabbits exhibit postpartum estrus. Estrus, or "heat," is a behavioral state in which a female expresses readiness to mate. Females of most nonhuman mammals, including rabbits, avoid or repel males except when in estrus. Postpartum estrus is a specialized type of estrus in which a female enters heat immediately after she gives birth (*postpartum* means "following birth"). When a female rabbit gives birth, she of course has a litter of young to nurse. If a male is present, however, she also goes immediately into estrus and mates. Not uncommonly, she therefore supports two litters at once! As she nurses the just-born litter, she simultaneously nurtures a new litter in her uterus.

The second key reproductive characteristic of rabbits is induced ovulation. Ovulation is the release of eggs (ova) from the ovaries into the reproductive tract so they can potentially meet sperm. In most mammals, including humans, ovulation occurs independently of mating. Pregnancy thus has a large element of chance in whether it occurs. A female might mate and get lots of sperm, yet not become pregnant because her ovaries happen to release eggs at a different time. In a species with induced ovulation, by contrast, the act of mating directly causes ovulation to occur. When a female rabbit copulates, signals are immediately sent to her brain, which promptly sends signals to the ovaries, resulting in the release of eggs. The process guarantees that eggs will be present for fertilization in the female's reproductive tract at the same time that sperm are there to fertilize them.

Q What differences and similarities exist between mammals that exhibit induced ovulation and those that ovulate independently of mating?

In casual conversation, "having sex" refers to human sexual activity. Biologists, however, mean something far broader when speaking of sex. As applied to animals, the process of **sex** is a mechanism by which the genes of two individuals are combined to produce offspring. In the case of animal **sexual reproduction**, each parent produces specialized reproductive cells called **gametes** by meiosis. Because the gametes are products of meiosis, each gamete cell has only half as many chromosomes as the other cells in the body, and the gametes are diversified in their chromosomes and genes by independent assortment and crossing over (see Concept 7.4). The gametes of the female parent are relatively large, nonmotile cells called **eggs** or **ova** (singular, *ovum*). The gametes of the male, called **spermatozoa** or **sperm**, are small cells that swim, typically using flagella (**FIGURE 37.1A**). A sperm and egg fuse to produce a single-celled zygote that has a full set of chromosomes and develops into a sexually produced offspring (**FIGURE 37.1B**; see Chapter 38). In this way, chromosomes and genes from two parents are combined to produce each offspring, and the new individual is not genetically identical to either parent.

LINK

The genetic aspects of sexual reproduction and the diversity it generates are discussed in **Concepts 7.1 and 7.4**; the evolutionary consequences are discussed in **Concept 15.6**

During **asexual reproduction**, by contrast, the process of sex (combination of genetic material from two parents) does not occur. Instead, offspring are produced by just a single parent, usually by mitosis: parental cells with a full set of chromosomes divide to produce new offspring cells that each have the same full set of chromosomes. Offspring are thus genetically identical to their single parent. A variety of animals, mostly invertebrates, reproduce asexually. Usually they can also reproduce sexually. Budding and fission are the two most common types of asexual reproduction. In budding, new individuals form as outgrowths, or buds, from the bodies of other individuals. In fission, an individual splits into two or more pieces that grow into new individuals. Reef corals exemplify animals in which budding is a major mechanism of reproduction. Corals occasionally reproduce sexually with eggs and sperm. However, when a new colony is produced sexually, it starts with just one small polyp. The large reef structures with which we are familiar are produced by budding. The initial polyp produces other polyps by budding, resulting in a large colony of hundreds or thousands of genetically identical polyps (**FIGURE 37.2**).

Asexual reproduction has the advantage that it maintains favorable combinations of genes. An individual with a genotype that is highly suited to its environment can rapidly produce offspring with the same advantageous genotype by budding, fission, or other asexual means.

Most animals reproduce sexually

Most vertebrates reproduce only sexually, and the same can be said of many invertebrates. Almost all animals have the capacity to reproduce sexually even if, like corals, they also reproduce asexually. We will focus on sexual reproduction for the rest of this chapter.

Sexual reproduction can seem to us to be the obvious best option for producing offspring. Why would reproduction occur by any other means? However, sexual reproduction can have some disadvantages that asexual reproduction does not (see Concept 15.6). For example, potential mates have to find each other and succeed in mating despite the presence of competitors and predators. Possibly the greatest downside of sexual reproduction is that it breaks up favorable combinations of

(A)

10 μm

(B)
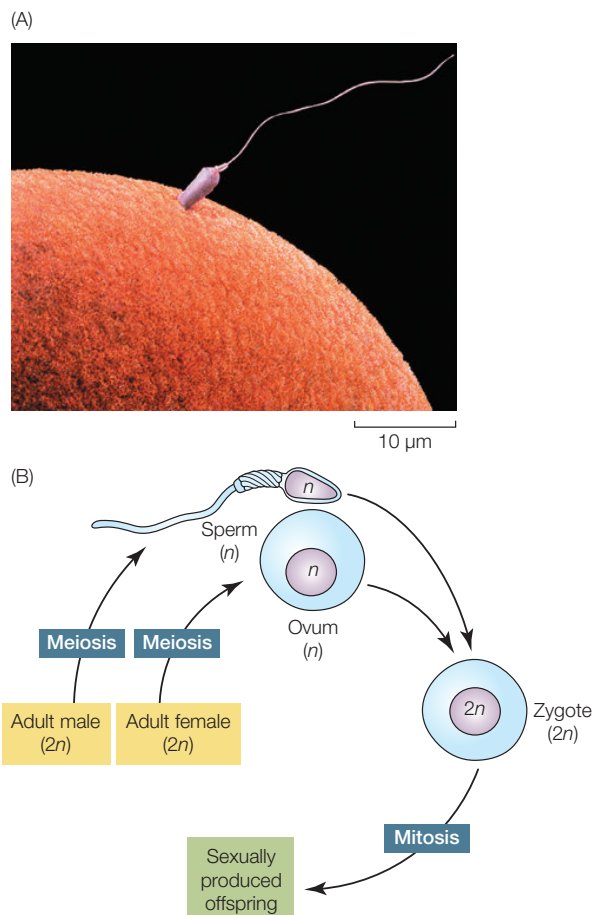
FIGURE 37.1 Sexual Reproduction in Animals   (A) The sperm and egg of a human. (B) The essence of animal sexual reproduction is the combination of genes from two individuals. Animals have diplontic life cycles (see Figure 7.3). The body cells that are not specialized for reproduction (called somatic cells) have two copies of each chromosome and thus are diploid ($2n$). The gametes, by contrast, have only a single copy of each chromosome and thus are haploid (n). When a sperm and egg combine, they form a single-celled zygote that is $2n$ (diploid), and the zygote subsequently multiplies by mitosis to develop into the adult.
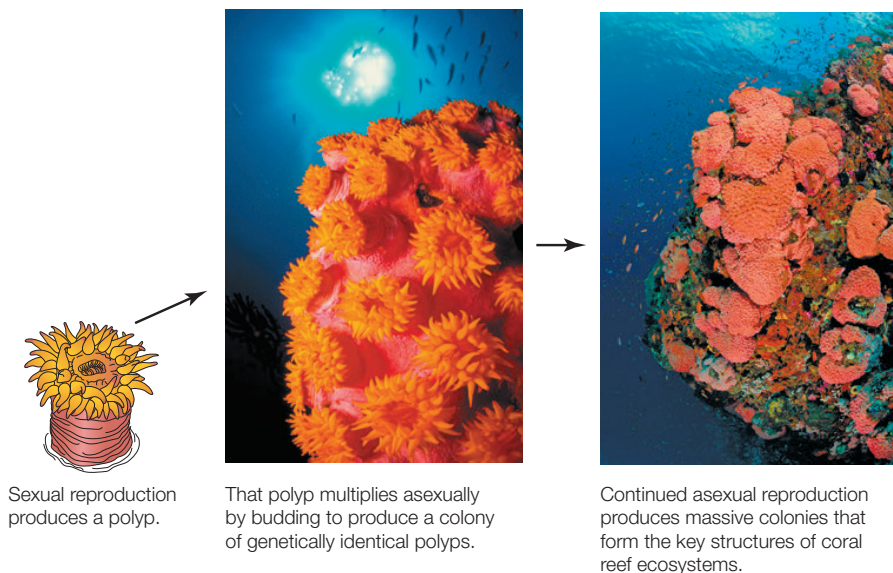
FIGURE 37.2 Asexual Reproduction in Animals Sexual reproduction in reef corals produces a single polyp, which then reproduces asexually by budding to produce a colony. Each polyp secretes skeletal material. The skeletal material of all the polyps in the colony fuses into a single structure, creating the massive skeletal structures that typify coral reefs.

Sexual reproduction produces a polyp.

That polyp multiplies asexually by budding to produce a colony of genetically identical polyps.

Continued asexual reproduction produces massive colonies that form the key structures of coral reef ecosystems.

genes. An individual with a genotype that is virtually perfect for its environment cannot simply pass that genotype along to its offspring. Biologists have theorized a great deal about why sex is so common despite this limitation (see Concept 15.6). According to one argument, the explanation lies in the changeable nature of environments. Environments, it is argued, change sufficiently—from time to time and from place to place—that no single genotype is likely to be highly successful for very long. Sexual reproduction has an enormous potential for producing genetic diversity in offspring, maximizing the odds that at least some offspring will succeed in a changing environment.

Among sexually reproducing animals, the two sexes, male and female, differ in three ways:

- Primary reproductive organs
- Accessory reproductive organs
- Secondary sexual characteristics

The **primary reproductive organs** (primary sex organs) are the **gonads**: the **ovaries** in females and **testes** (singular, *testis*)—sometimes called testicles—in males (**FIGURE 37.3**). These organs are "primary" because they produce the cells, the gametes, that will combine to produce a new individual.

The **accessory reproductive organs** (accessory sex organs) are the reproductive organs other than the gonads. In human males, for example, the ducts (e.g., the vas deferens) that carry sperm out of the testes to the urethra in the penis are accessory reproductive organs, as is the penis itself. Often, the accessory reproductive organs are more elaborate in females than males. The females of some animals, such as mammals and many sharks, nurture offspring internally for a long time before giving birth. In these cases, the uterus and other structures responsible for nurturing the young are among the accessory reproductive organs. In other animals, such as birds, the females lay eggs, and their accessory organs include the glands that add the shell or capsule to each egg. (Note that the term "egg" has two meanings in discussing reproduction. The female gamete

(ovum) is called an "egg," but a structure like a hen's egg is also called an "egg.")

The **secondary sexual characteristics** are properties of nonreproductive tissues and organs that are distinctive in each sex. These characteristics often result from the actions of sex hormones on nonreproductive structures. Facial hair, chest hair, and a deep voice are some of the secondary sexual

Secondary sexual characteristics

Vas deferens

Accessory reproductive organs

Penis

Epididymis

Scrotum

Testis

Primary reproductive organ
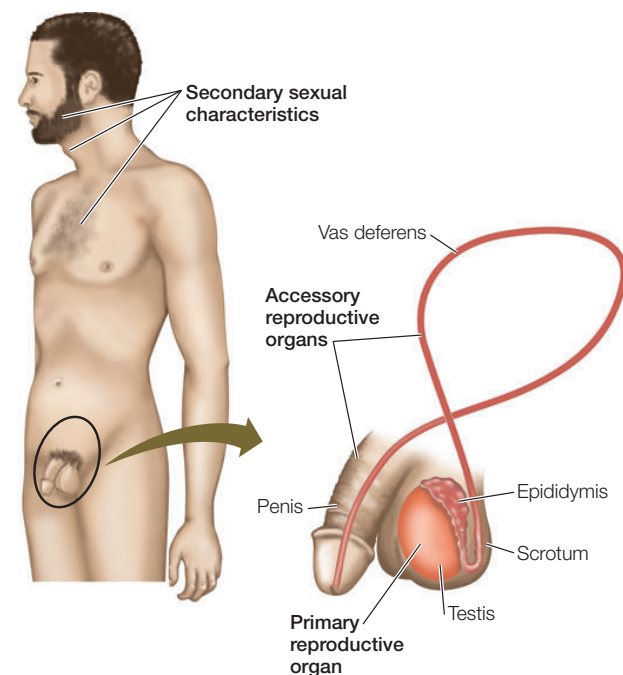
FIGURE 37.3 Sexually Reproducing Animals Have Three Types of Sex-Specific Characteristics Individuals of each sex have sex-specific primary reproductive organs (gonads) and accessory reproductive organs. They may also have sex-specific secondary sexual characteristics.

characteristics of human males (see Figure 37.3). The bright feather colors of many male birds and the enlarged horns of male caliper beetles (*Golofa porteri*) are also secondary sexual characteristics:

Female mallard ducks are mostly brown, and female caliper beetles do not have enlarged horns.
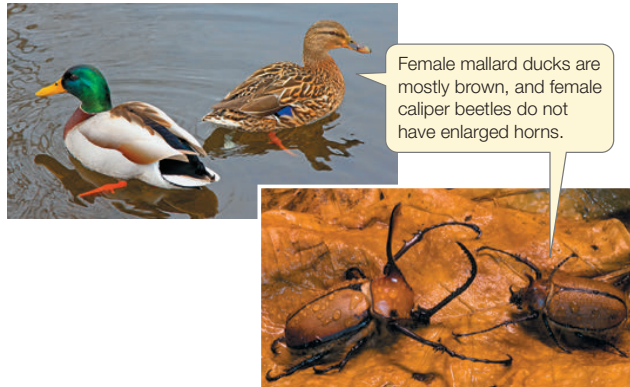
Secondary sexual characteristics are frequently subject to sexual selection.

Gametogenesis in the gonads produces the haploid gametes

Gametogenesis is the process by which gametes are produced. More specifically, it is called spermatogenesis in males and oogenesis in females. The process begins with diploid **germ cells** (diploid, denoted $2n$, means two copies of each chromosome per cell; see Figure 37.1). These are cells in the gonads that are capable of undergoing meiosis to produce gametes. The diploid germ cells divide by mitosis until they reach a stage at which they switch to meiosis. These mitotic divisions increase the numbers of cells that are available to undergo meiosis and thereby increase the number of haploid gametes produced (haploid, $1n$, means one copy of each chromosome per cell). Recall that meiosis consists of two cell divisions, meiosis I and meiosis II, during which the DNA is replicated only once (see Figure 7.11).

In adult males, sperm are typically produced continuously during the time of year when reproduction occurs (i.e., all year in human males). During this time, the populations of diploid germ cells in the testes multiply continuously, producing cells that go through the two meiotic divisions, resulting in four, equal-sized haploid cells from each diploid cell (**FIGURE 37.4A**). The haploid cells then mature into fully differentiated sperm.

Gametogenesis in females differs in two ways from that in males. First, meiosis typically produces only one gamete from each diploid germ cell because the cytoplasm of the diploid cell is divided in highly unequal ways during each of the two meiotic divisions (**FIGURE 37.4B**). One of the cells produced by meiosis is a large cell, the ovum. The others are tiny cells, called polar bodies, that degenerate.
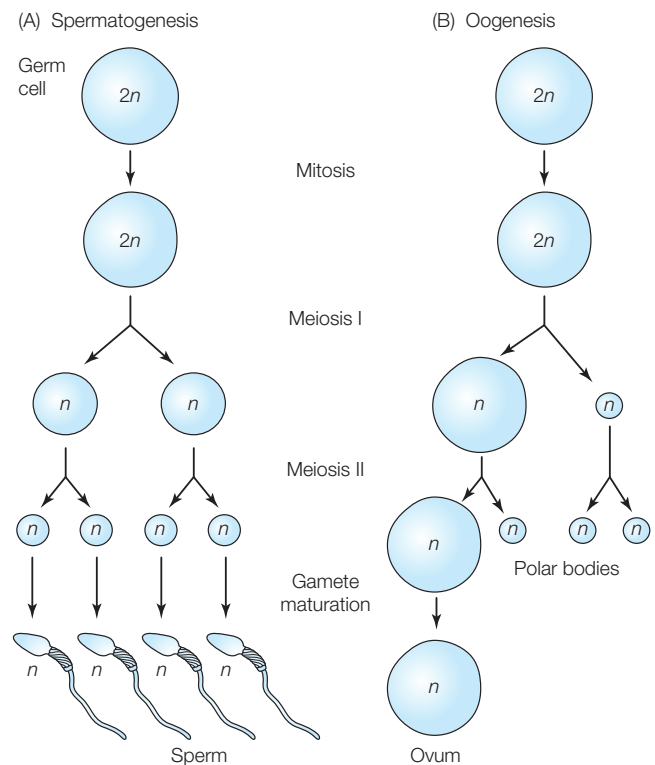
FIGURE 37.4 Gametogenesis Male and female germ cells proliferate by mitosis to produce an abundant supply of diploid cells that initiate and complete meiosis to produce sperm or ova. (A) Spermatogenesis. (B) Oogenesis. During oogenesis in many animals, the first polar body to be produced does not divide, so only two polar bodies are produced in total. $2n$ is the diploid number of chromosomes per cell; n is the haploid number. See Concept 7.4 for details of meiosis.

The second difference that often occurs is cellular developmental arrest during meiosis in females. When a cell destined to become an ovum is in arrest, it can continue to accumulate resources and grow, but its meiosis stops. Mammals exemplify developmental arrest during oogenesis. According to the prevailing view of most researchers, all the diploid germ cells in a young female placental mammal stop undergoing mitosis, begin meiosis (completing the very first step in meiosis I), and go into developmental arrest while the individual is a fetus in the uterus or shortly thereafter. The cells then remain in arrest for months or years until the individual matures to reproductive age. Then some of the arrested cells resume meiosis to become ova that are released from the ovaries. In humans, one of the arrested cells typically develops fully and is released from the ovaries during each month between the time a girl enters puberty (near age 10) and the time she goes through menopause (near age 50).

The gonads, in addition to having germ cells and producing gametes, typically contain somatic cells that contribute to reproduction. Somatic cells by definition do not produce gametes. If they divide, they do so strictly by mitosis. Certain somatic cells in the gonads provide metabolic support to the

(A)

Vas deferens

Epididymis

Sperm mature while being stored in the epididymis.

Testis

Seminiferous tubule

Sperm develop continuously over the great length of each seminiferous tubule.

(B) **Interstitial** (**Leydig**) **cells** in the tissue between seminiferous tubules secrete testosterone into blood flowing through the testis.

Lumen of seminiferous tubule (sperm project into it)

(C) Each **Sertoli cell** envelops, nourishes, and protects developing sperm.

Basement membrane of tubule

Male germ cell (2n)

Sertoli cell

Lumen of tubule

Sperm are shed into the lumen of the seminiferous tubule.

Head

Cell membrane

Acrosome

Nucleus

Centriole

Mitochondria within midpiece

Tail

Sperm (n)

FIGURE 37.5 The Mammalian Testis (A) Seminiferous tubules fill the testis and continuously produce millions of sperm during the reproductive season. (B) This cross section of a testis shows both a seminiferous tubule and groups of interstitial (Leydig) cells in the spaces between this tubule and adjacent tubules. (C) As germ cells undergo gametogenesis, the cells move from the outer region of the seminiferous tubule toward its center (shown by arrows; compare with Figure 37.4A), where sperm are shed into the lumen of the tubule.

Go to ACTIVITY 37.1 Spermatogenesis
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germ cells during gametogenesis. Somatic cells may also secrete hormones. The mammalian testis illustrates these points (**FIGURE 37.5**).

There are three principal cell types in a testis:

• Germ cells that produce the sperm

• Somatic **Sertoli cells** that assist sperm production

• Somatic **interstitial cells** (**Leydig cells**) that produce the steroid sex hormone **testosterone** (see Concept 35.4)

The testis is principally composed of long, coiling tubules, the **seminiferous tubules**. The lining of each tubule consists of germ cells in all the stages of gametogenesis and Sertoli cells. Sperm are shed into the lumen (open central cavity) of the tubule and make their way to the epididymis, a highly convoluted tubular structure attached to the outside of the testis, where the

sperm undergo maturation. The epididymis connects to the **vas deferens**, a tube that carries sperm out of the testis during ejaculation (see Figure 37.3). The endocrine interstitial cells are located in the spaces between adjacent seminiferous tubules.

Let's focus more closely on the somatic cells that support the germ cells during gametogenesis. In male vertebrates, spermatogenesis occurs in the midst of Sertoli cells (see Figure 37.5C). The Sertoli cells envelop the developing germ cells, provide nutrients, and help regulate sperm production. A striking fact is that the Sertoli cells constitute well over half the volume of each testis in a human or other mammal. This testifies to their importance.

Ova often have a more defined relationship with somatic support cells, in the sense that each ovum is associated with a specific set of support cells during its development. This is true in vertebrates and some invertebrates (e.g., insects). A developing ovum and its support cells are together called an **ovarian follicle**. In human females, as we've said, one cell that entered developmental arrest during fetal life typically develops to become an ovum released from the ovaries during each month of adult life. The developing ovum, termed an **oocyte**, is surrounded by somatic support cells—termed granulosa and theca cells—that multiply as development takes place (**FIGURE 37.6**). As the support cells multiply, they provide increased metabolic support, and the follicle grows enormously from a

The theca cells, granulosa cells, and corpus luteum secrete hormones, as discussed in Concept 37.2.

Theca cells
Granulosa cells
Antrum
Oocyte

Fully mature (Graafian) follicle

Stages of follicular maturation

Primordial follicle

Vein

Artery

Ovary

Degenerating corpus luteum

Corpus luteum

Ovulation of mature ovum by rupture

Ruptured follicle

Follicular cells left behind in the ovary after ovulation reorganize into a corpus luteum, as discussed in Concept 37.2.

A mature follicle seen in cross section in a light microscope

Mature follicle bulging on surface of ovary

FIGURE 37.6 The Mammalian Ovary Showing Stages of Follicle Development The stages of follicle development are shown in a clockwise series, starting at the upper left with a primordial follicle. In a human ovary, a primordial follicle progresses through all these stages in the course of approximately 28 days (one menstrual cycle). A new primordial follicle starts the next month. The clockwise arrangement is for learning purposes only. Follicles do not actually progress clockwise through an ovary.

Go to MEDIA CLIP 37.1
Human Ovulation
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primodial follicle to a mature (Graafian) follicle. Along the way, a fluid-filled cavity (antrum) opens up within it. Moreover, the follicle migrates to be at the very surface of the ovary, where at full maturity it bulges out like a large blister, 1.5–2 centimeters in diameter in a human. The release of an ovum from the ovary is called **ovulation**. In vertebrates, including humans, it occurs by rupture of the mature follicle.

Fertilization may be external or internal

Fertilization is the fusion of sperm and ovum. It can be external or internal. The product is a single diploid cell, the zygote, which develops into an embryo (see Chapter 38).

To achieve fertilization, most aquatic animals simply release their gametes into the water, a process termed **spawning**. Fertilization then occurs in the water outside the female's body and is described as **external fertilization**. In spawning species, the ducts and openings of the reproductive system can be similar in males and females because both sexes are simply releasing gametes into the environment. The zygotes typically do not receive parental care. They must develop into feeding larvae and find food before the yolk or other nutrients

provided in the ovum run out. Mass deaths of commercially important fish larvae sometimes occur when the larvae are only 2–3 weeks old because at that time the larvae exhaust the yolk provided in the eggs but fail to find food. With the larvae dead, adults are not produced.

Internal fertilization occurs when a male inserts sperm inside the reproductive tract of a female, permitting fertilization to occur inside the female's body. Most terrestrial animals employ internal fertilization—not surprising, because it ensures that the gametes and zygotes are kept moist. Some aquatic animals also employ internal fertilization.

Internal fertilization can have several advantages. It permits parental defense of the new zygotes. Some animals enclose each fertilized egg in a protective shell or capsule before laying the egg. This is true in birds (e.g., chicken eggs), insects, turtles, skates, and some sharks. Internal fertilization is essential for this process because sperm must reach the ovum before the shell is formed:

Skates enclose each egg in an egg case like this.

Some animals—notably mammals and certain sharks (e.g., requiem and hammerhead sharks)—keep fertilized zygotes in the female reproductive tract for an extended period of development during which nutrients are steadily provided, so the

Vitelline envelope

Cell membrane of ovum

Jelly coat

Ovum cytoplasm

1 Sperm contacts jelly coat. Species-recognition molecules in the jelly and sperm cell membrane must match.

Centriole   Actin

Acrosome

2 An acrosomal reaction occurs, with two consequences: an acrosomal process is extended, and protein-digesting enzymes are released.

Nucleus

Acrosomal process

3 Sperm digests its way through the jelly coat.

4 Sperm contacts the vitelline envelope. Once again, species-recognition molecules must match.

5 The cell membranes of sperm and ovum fuse. Within 1 second, the ovum undergoes changes to block polyspermy (the fast block). Within 15–60 seconds, the ovum undergoes additional changes to block polyspermy (the slow block). In 1–2 minutes the nucleus of the sperm enters the ovum.

Purple sea urchin
(*Strongylocentrotus purpuratus*)

FIGURE 37.7 Steps in the Fertilization of a Sea Urchin Ovum

Go to ANIMATED TUTORIAL 37.1
Fertilization in a Sea Urchin Egg
PoL2e.com/at37.1

young become large and developmentally advanced before birth. Another advantage of having the male insert sperm in the female reproductive tract is that the female can potentially store sperm for future use in fertilization (see Concept 37.3).

What are some of the ways that sperm are introduced into the female reproductive tract for internal fertilization? Mammals have a penis that is stiffened by an internal bone or by blood pressure (see Concept 37.2). Insects and some snails also have penises. Sharks have a specialized, penis-shaped fin element (clasper) with a groove. The clasper is inserted in the female genital opening, and sperm are washed down the groove into the female reproductive tract. Crabs assemble sperm into packets called spermatophores that they grasp with modified legs and insert. Squids and octopuses insert spermatophores by use of specialized tentacles. Birds achieve sperm transfer without a penis or similar organ, merely by the act of the male and female touching their cloacal openings together (a "cloacal kiss").

To achieve fertilization, a key challenge that must be met is for sperm and eggs of the same species to be brought together. This process involves both species recognition and synchronization.

Animal behavior often plays a major role in bringing sperm and eggs of the same species together. Males and females associate in species-specific ways (see Concept 40.6). They often also employ behaviors to signal reproductive readiness. For example, the females of many spontaneously ovulating species of mammals enter a sexually receptive behavioral condition called estrus, or "heat," only at times when there is a high likelihood that they are releasing ova from their ovaries (see Concept 37.2). Otherwise they ignore or repel males.

Important mechanisms also exist at the cellular level for bringing sperm of a species together with eggs of the same species. Ova often attract sperm with species-specific chemical attractants.

When sperm and ova meet, cellular mechanisms perform several functions. There are cellular mechanisms that prevent fertilization by sperm of the wrong species. Such recognition mechanisms are particularly important in aquatic species that practice external fertilization because the sperm and ova of different species mix in the aquatic environment. There are also cellular mechanisms that ensure that only a single sperm enters an ovum, regardless of how many sperm may be trying. These mechanisms are termed blocks to polyspermy.

Sea urchin ova, which have been studied to an exceptional extent, illustrate these mechanisms. To fertilize an ovum, an urchin sperm must first get through two protective layers that surround the ovum—a jelly coat and a proteinaceous vitelline envelope. **FIGURE 37.7** summarizes the successive mechanisms that ensure the sperm and ovum are of the same species, permit the sperm to reach the ovum, and block polyspermy. The cell membrane of the sperm ultimately fuses with that of the ovum, permitting the nucleus of the sperm to enter the ovum so a diploid zygote is formed.

The sex of an offspring is sometimes determined at fertilization

Sex determination is the process by which the sex of an individual becomes fixed. Sex determination is not understood in all animals, but among the animals in which it is understood, a wide variety of mechanisms are known.

Sex is determined at fertilization in humans and other placental mammals. This was first analyzed through studies of chromosomes. One pair of the chromosomes in a mammal is distinctive because the two chromosomes in the pair differ greatly in size in males. These are called the **sex chromosomes**. The larger and smaller are named X and Y, respectively. Human cells have 23 pairs of chromosomes. The two chromosomes in 22 of these pairs are always similar to each other in their appearance under a light microscope, regardless of whether an individual is male or female (see Chapter 7, p. 134). The 23rd pair consists of an X and a Y chromosome (in males) or two X chromosomes (in females).

Because adult females have two X chromosomes, during meiosis all ova receive an X chromosome. By contrast, the pair of sex chromosomes in a male consists of an X and a Y. Thus as sperm are produced, half receive an X chromosome and half receive a Y.

A human zygote's sex is determined at fertilization by the sex chromosomes it receives. It receives an X from its mother but may receive either an X or a Y from its father. A zygote that receives an X from both parents is XX and female. One that receives an X and a Y is XY and male.

Long after this chromosomal explanation of sex determination was known, researchers discovered a particularly critical gene that they named *SRY* (*s*ex-determining *r*egion of the *Y* chromosome). This one gene exerts exceptional influence on sexual development, although many other genes are involved. The gene is nearly always found on the Y chromosome. An XY zygote thus has the gene, which directs the primordial gonads (the gonads early in development) to become testes and secrete testosterone. An XX zygote lacks the *SRY* gene and develops into a female. Concept 35.4 and Figure 35.13 discuss how testosterone secretion in XY embryos leads to phenotypic sex differentiation.

Fruit flies (*Drosophila*) also have X and Y chromosomes (see Concept 8.3). Their mechanism of sex determination is very different, however, because the Y chromosome and its genes have no direct role.

Sex is not determined at fertilization in some animals. Of these, crocodilians and turtles are of particular interest because many species exhibit **environmental sex determination**. The sex of each individual is determined by the temperature it experiences during its embryonic development. American alligators, for example, become males if they develop at 32–33°C, have a 50:50 chance of becoming male or female at 34°C, and develop into females at 35°C. Great worry exists that these animals will be exceptionally vulnerable to global warming because temperatures that are higher than traditional norms may lead to maladaptive changes in their sex ratios.

Some animals undergo sex change

Some animals do not undergo sex determination. Instead, they can be males at one time and females at another during their lives. They are known as **sequential hermaphrodites**. Hermaphrodites are animals that can produce both sperm and ova. In sequential hermaphrodites, sperm and ova are not produced at the same time but instead are produced at different times in an individual's life. Sex change in these animals does not entail anything as dramatic as exchanging a penis for a vagina. The animals are aquatic and release their gametes into the water by spawning. Their accessory reproductive organs are suited to carrying either sperm or eggs to the outside. Sex change occurs in the type of gametes they produce. Great numbers of fish species, including many coral reef species, undergo sex change. The phenomenon also occurs in certain aquatic annelid worms, and in certain snails or other gastropod mollusks.

Biologists think that sex change has evolved in cases in which an individual's reproductive output—its production of offspring—is maximized by changing sex. What conditions affect reproductive output? A great many do, including a species' breeding system (the way in which males and females associate), social organization, and population density. Because of this complexity, many different types of sex change occur.

Anemonefish (*Amphiprion percula*), which live among the tentacles of a sea anemone, provide a well-studied example (**FIGURE 37.8**). Under many circumstances, the fish on a single sea anemone consist of one breeding male that spawns sperm, one breeding female that spawns ova, and several nonbreeding males that do not spawn. The breeding female is largest, and the breeding male is second largest. All the fish start life as males. When the female dies, the breeding male becomes the largest fish and turns into a female. One of the nonbreeding males becomes the new breeding male. According to the prevailing theory of sex change, the reason the breeding male changes to a breeding female is that he can have more offspring by being female. To see why, remember that there are only two breeding fish on an anemone. A fish of *any* size can produce huge numbers of sperm. If the biggest fish remained male, its reproductive output would be limited by the egg output of a smaller fish. By switching to producing eggs, the biggest fish increases the number of eggs that get fertilized and thus its reproductive output (because egg production increases with body size). Currently, investigators are starting to make progress in understanding the hormonal mechanisms of sex change (**FIGURE 37.9**).

FIGURE 37.8 Anemonefish (*Amphiprion percula*)   These reef fish, often called clownfish, gain protection from enemies by living among the tentacles of a sea anemone.

INVESTIGATION

FIGURE 37.9 Investigating the Mechanism of Sex Change In contrast to the anemonefish, females of the blackeye goby (*Coryphopterus nicholsii*) sometimes become males. Investigators have been studying the mechanism by which this occurs. By simply describing blood hormones, the investigators have found that the female-to-male transition is accompanied by a decline in the blood concentration of the female sex steroid 17β-estradiol and an increase in the concentration of the male sex steroid 11-ketotestosterone (11-KT). But do these changes in hormones *cause* the sex change? Are they *sufficient* to make a female change into a male? To find out, the investigators artificially manipulated the hormone levels.[a]

HYPOTHESIS

An increase in the concentration of 11-ketotestosterone (11-KT) is sufficient to cause female-to-male transition in blackeye gobies.

METHOD

1. Capture female blackeye gobies in the wild and hold in individual tanks.
2. Insert in each fish a hormone-releasing implant containing 11-KT or an implant with no hormone (control treatment). The implant is designed to release hormone gradually.
3. After 43 days of treatment, examine the gonads of the fish to determine the sex.

RESULTS

	Sex at end of treatment		
Treatment	Female	Transitional	Male
Control	13	0	0
11-KT or 11-ketoadrenosterone (converted to 11-KT in body)	0	1	13

Administration of 11-KT causes female blackeye gobies to become male.

CONCLUSION

The results support the hypothesis that an increase in the concentration of 11-KT is sufficient to cause female-to-male transition.

ANALYZE THE DATA

In a related experiment, 8 female fish were treated with fadrozole, a chemical that inhibits the synthesis of 17β-estradiol and thus should lower the concentration of this female sex hormone. At the end of treatment, 1 fish was still female, 5 fish were transitional, and 2 fish were male.

A. Was this treatment as effective as 11-KT (or 11-ketoadrenosterone) administration in causing females to become males? What data support your conclusion?

B. The researchers hypothesized that a decrease in 17β-estradiol causes sex change. Do the data support the hypothesis? Why or why not? What additional information would be helpful in deciding whether the hypothesis is supported?

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]F. J. Kroon and N. R. Liley. 2000. *General and Comparative Endocrinology* 118: 273–283.

Having surveyed the general aspects of animal gametogenesis and fertilization, we will next consider the male and female reproductive systems in mammals, using our own species as the primary example.

CONCEPT 37.2 The Mammalian Reproductive System Is Hormonally Controlled

Hormones play critical roles in almost every aspect of mammalian sexual reproduction. Follicle-stimulating hormone (FSH) and luteinizing hormone (LH), secreted by the anterior pituitary gland, are key players in both sexes (see Concepts 35.3 and 35.4). They are named for their roles in females, but the same hormones are secreted in males and exert major effects on tissues of the male reproductive system. Secretion of FSH and LH is controlled by neurosecretory cells in the hypothalamus of the brain. These cells secrete gonadotropin-releasing hormone (GnRH) into blood that travels to the anterior pituitary via the hypothalamo–hypophysial portal system (see Figure 35.7). In the pituitary, GnRH regulates the cells that secrete FSH and LH.

Somatic cells in the gonads produce steroid sex hormones. We often say that "the ovaries" or "the testes" secrete hormones, but it's important to recognize that only certain cells in the gonads are responsible. The principal sex steroid in males is testosterone, which we've already seen is secreted by the interstitial (Leydig) cells in the testes. In females, the somatic cells of the ovarian follicles secrete feminizing steroids called **estrogens**. Typically, two or more specific types of estrogen molecules are secreted, but here we refer to them simply as "estrogens." After follicles have ruptured during ovulation, the somatic cells remaining in the ovary reorganize and—in addition to estrogens—secrete another type of female sex steroid, **progesterone**,

(A) Front view

Ova mature in and are released by the **ovaries**.

Oviduct (fallopian tube)

Uterus

Ligament

Fimbria

Ovary

Endometrium

Myometrium

Cervix

Sperm are deposited in the vagina during copulation. The vagina is also the birth canal.

Ova released from the ovaries are taken into the **oviducts**, where they travel to the uterus. Fertilization occurs in the upper regions of the oviduct, where development of the zygote begins.

FIGURE 37.10 Reproductive Organs of the Human Female   The female reproductive organs are shown (A) from the front and (B) from the side.

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The Human Female Reproductive Tract
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The blastocyst implants in the **endometrium** of the uterus, where embryonic development continues.

The neck of the uterus is the cervix, which remains closed during pregnancy and dilates to allow childbirth.

(B) Side view

Ovary

Oviduct

Urinary bladder

Pubic bone

Urethra

Clitoris

Colon

Uterus

Cervix

Anus

Labia majora

Labia minora

Vagina

which is involved principally in coordinating processes associated with pregnancy. The placenta also secretes estrogens and progesterone during pregnancy.

LINK

For information on the roles of sex steroids during embryonic development, see **Concept 35.4**

Ova mature in the ovaries and move to the uterus

The ovaries are positioned in the lower abdomen, as seen in **FIGURE 37.10** (Figure 35.10 provides a larger perspective). Ova released from the ovaries make their way to the uterus by way of tubes called the **oviducts** or fallopian tubes. Each ovary is positioned near the funnel-shaped opening of an oviduct. When an ovum is discharged from a follicle at the surface of the ovary during ovulation, it is drawn into the oviduct, and then

it is propelled toward the uterus by beating cilia and contractions of smooth muscles.

Sperm are deposited in the vagina—a tubular structure that opens to the outside—during copulation (sexual intercourse). Fertilization of an ovum, if it occurs, takes place in the upper third of the oviduct. Sperm in the vagina enter the uterus at the cervix, travel through the uterus, and then travel up the oviduct to achieve fertilization. Sperm are often in the upper oviduct within 30 minutes, indicating that they are probably transported not only by their swimming powers but also by uterine contractions.

Passage of an ovum or zygote down the oviduct is relatively slow. It requires about 4 days in humans. If fertilization has occurred, the zygote undergoes its early development during this time and arrives in the uterus as an early embryo called a blastocyst (see Chapter 38). The uterus is a thick-walled organ consisting of two major parts: an outer layer of smooth muscle, the myometrium, and an inner, nurturing layer, the **endometrium**. The endometrium is highly vascular and composed of nutrient-providing cells, and it is where the zygote will develop further. After the blastocyst arrives in the uterus, it remains in the lumen for a few days and then buries itself in the endometrium by means of enzyme-catalyzed processes. The entry of the blastocyst into the tissue of the endometrium is termed **implantation**.

Ovulation is either induced or spontaneous

The immediate stimulus for ovulation is a surge in the blood concentration of LH. However, the cause of this surge differs between species that undergo induced and spontaneous ovulation.

Induced ovulation, described in our opening discussion, is ovulation triggered by copulation. Rabbits and certain cats, shrews, and camelids are induced ovulators. During copulation in an induced ovulator, the copulatory act stimulates key sensory neurons in the cervix. These neurons send action potentials to the brain, where the GnRH-secreting neurosecretory cells in the hypothalamus are stimulated. These cells release GnRH, resulting in a surge in LH secretion from the anterior pituitary into the general circulation. In rabbits that have been

APPLY THE CONCEPT

The mammalian reproductive system is hormonally controlled

In a famous and much-cited paper, M. C. Chang investigated the question: Are mammalian sperm altered by being in the female reproductive tract? He studied this question in rabbits. Because of the design of Chang's studies, the unusual properties of rabbits we've mentioned, such as induced ovulation, were not of any relevance. Chang collected freshly ejaculated semen from male rabbits. He diluted the semen, and then he injected it directly into the upper third of the oviduct of fertile females at various times relative to the time that ovulated ova arrived there. The results he obtained are shown in the table.[a]

1. What do these results indicate about the question Chang asked? Justify your answer.

TIMING OF SEMEN INJECTION	PERCENTAGE OF OVA FERTILIZED
Semen injected 6 hr prior to ovulation	78%
Semen injected 2 hr prior to ovulation	0%
Semen injected 2 hr after ovulation	0%
Semen held for 5 hr in the uterus of another rabbit and then injected 2 hr prior to ovulation	75%

2. In vitro fertilization is a procedure by which ova and sperm are collected and brought together in a dish. Are Chang's results relevant to in vitro fertilization?

[a]M. C. Chang. 1951. *Nature* 168: 697–698.

studied, the blood LH concentration increases in 1–2 hours to more than five times higher than usual. This LH surge causes the mature follicle to rupture.

Most mammals, including humans and other primates, are spontaneous ovulators. During **spontaneous ovulation**, follicle rupture and release of the mature ovum are again triggered by an LH surge. However, the timing of the surge is under control of endogenous hormonal cycles in the female. "Endogenous" refers to processes that originate within an animal. The hormonal cycles in a spontaneous ovulator occur on their own rhythm, more or less independently of whether copulation takes place. We will focus on spontaneous ovulation for the rest of our discussion of females.

In most species of mammals that display spontaneous ovulation, a female ovulates in cycles, as already implied. The duration of each cycle varies among species. For instance, cycles in rats and mice are typically 4–6 days, whereas the human cycle averages 28 days. The cycles repeat, over and over, during reproductive seasons (i.e., all year in humans) unless pregnancy occurs. If pregnancy occurs, the cycles stop.

Hormones have the remarkable feature that they can affect many tissues at once, as we stressed in Chapter 35. In female reproductive cycles, hormones coordinate the ovaries, uterus, and in some cases, behavior.

Primates menstruate in each cycle that does not result in pregnancy. **Menstruation** is a discharge of bloody material from the uterus via the vagina. During each cycle, the endometrium undergoes preparation for pregnancy. It develops glands and abundant vascularization, and it thickens (in humans, by a factor of three to five). If pregnancy fails to occur, much of the extra growth is sloughed off, creating the bloody discharge. The cycles of the reproductive system are called **menstrual cycles** because of this highly visible aspect.

Mammals other than primates do not menstruate or have menstrual cycles. Often, however, they undergo dramatic changes in behavior: they cyclically enter estrus. This is the most highly visible aspect of their cycles, which accordingly are called **estrous cycles**. (Note the cycles are "estrous" cycles, whereas the period of sexual receptivity is "estrus.") The

endometrium cyclically prepares for pregnancy and regresses during estrous cycles, but the regression occurs by reabsorption, not sloughing off, of tissue.

Hormones secreted by the brain, anterior pituitary gland, and ovaries are important for the cycles. These organs interact and affect each other to create the cycles. If pregnancy occurs, the embryo and uterus join in.

Hormone receptors are as important as hormones. Tissue responses to hormones are highly affected by the numbers of hormone receptors present, and hormones can cause cells to modify their receptor numbers.

To see how cycling occurs, let's look at the human menstrual cycle (**FIGURE 37.11**). By convention, each cycle is considered to start on the day menstruation begins, and that day is numbered day "0." Follicles start their development then, and ovulation (follicular rupture) occurs on day 14. Accordingly days 0–14 are called the follicular phase of the cycle. What happens over those 14 days? The answer is complex, but by mastering it you will be rewarded with an understanding of one of the most fascinating and important processes in the human body. Follow the steps listed here by referring to the circled numbers in Figure 37.11A–D:

① At the start, FSH and LH are secreted by the anterior pituitary at fairly high rates compared with the rates seen following ovulation during the previous cycle (compare with step 10). The FSH and LH stimulate development of follicles, including the one follicle that will mature and release its ovum. Specifically, they stimulate the somatic cells of that follicle—the granulosa and thecal cells—to secrete estrogen.

② Estrogen secretion gradually increases as the follicle develops.

③ The increasing estrogen secretion affects the endometrium, stimulating endometrial development that prepares the uterus to accept a blastocyst if fertilization occurs. Estrogen also simulates the endometrial cells to express progesterone receptors, preparing these cells to respond to progesterone later on.

(A) FSH and LH secreted by the anterior pituitary

(B) Events in the ovary

(C) Ovarian hormones

(D) Events in the endometrium of the uterus
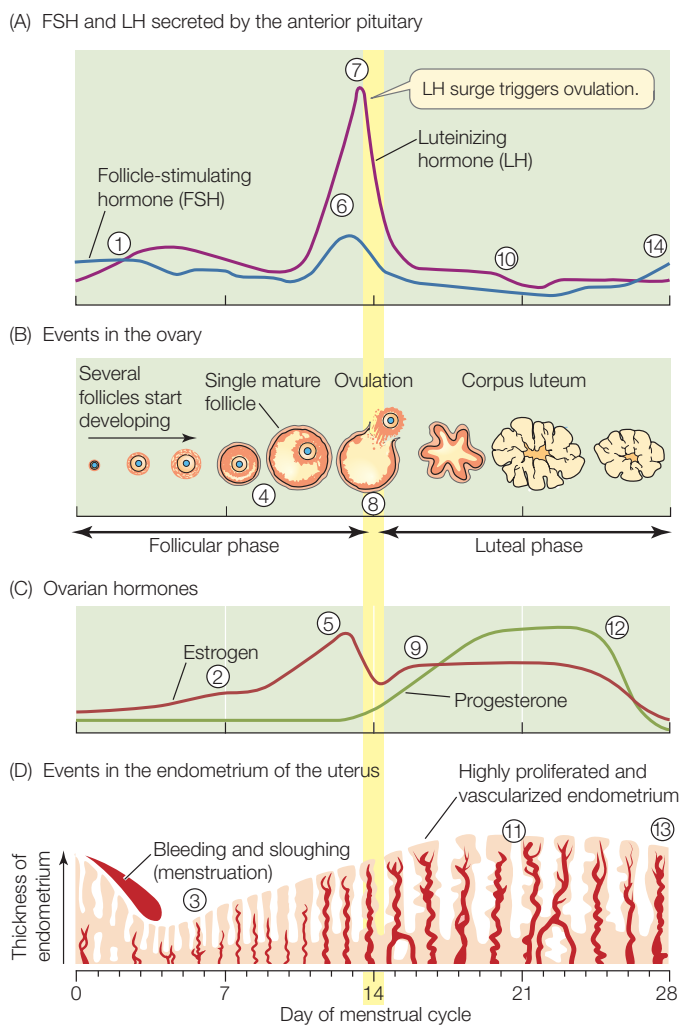
FIGURE 37.11 Events in the Human Female Reproductive Cycle   Circled numbers correlate with the sequence of events described in the text.

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The Menstrual Cycle
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④ In the second half of the follicular phase, the granulosa cells of the maturing follicle increase their numbers of LH receptors.

⑤ As day 14 approaches, the blood estrogen concentration is high.

⑥ At this stage, estrogen stimulates the anterior pituitary and possibly the brain to bring about increasing secretion of LH and FSH.

⑦ Finally, estrogen stimulation of the anterior pituitary causes the surge in LH secretion.

⑧ The LH surge has a strong effect on the follicle because of the abundance of LH receptors in the granulosa cells

(recall step 4). The follicle ruptures, and ovulation occurs. In mammals that (unlike humans) undergo estrus, the peak estrogen secretion at this time stimulates the behaviors of estrus. Estrus thus coincides with ovulation.

When the follicle ruptures, most of the somatic cells of the follicle are left behind in the ovary. LH (which, you'll recall, is *luteinizing* hormone) stimulates those cells to reorganize to form a new hormone-producing structure called the **corpus luteum** (see Figure 37.11B). If pregnancy has not occurred, the corpus luteum, at this stage known as a **corpus luteum of the cycle**, secretes for a finite length of time: about 10 days in humans. It then starts to undergo programmed degeneration, ceasing to function entirely on day 28 of the menstrual cycle. Days 14–28 are the luteal phase of the cycle. What happens during it? Again, follow the steps by referring to the circled numbers in Figure 37.11A–D:

⑨ The corpus luteum secretes progesterone (its principal secretion), estrogen, and a third hormone, inhibin.

⑩ These hormones, acting together, suppress FSH and LH secretion by the pituitary. In primates, this suppression is so strong that it prevents new follicles from starting to develop at this stage.

⑪ Progesterone secretion from the corpus luteum has a major effect on the endometrium. Exocrine glands in the endometrium are stimulated to secrete nutrient materials, and the endometrium becomes more vascularized. These changes fully prepare the endometrium to accept a blastocyst.

⑫ If fertilization has not occurred, the corpus luteum starts to undergo its programmed degeneration after about 10 days. This leads to a steep decline in progesterone and estrogen secretion.

⑬ Deprived of the luteal hormones (hormones secreted by the corpus luteum), the endometrium cannot maintain its highly developed state. It starts to regress, with menstruation beginning on day 0 of the next cycle.

⑭ The disappearance of luteal hormones also sets the stage for a new cycle to begin because the luteal hormones no longer act on the pituitary or brain to suppress FSH and LH secretion. FSH and LH increase, returning the cycle to step 1, in which development of a new follicle is stimulated.

Pregnancy is a specialized hormonal state

If fertilization takes place, the blastocyst burrows into the tissue of the endometrium within a few days after arriving in the uterus, and there is an urgent need to maintain the endometrium in its highly developed state. In humans and many other mammals, the endometrium is prevented from deteriorating by rescue of the corpus luteum. A signal of the existence of pregnancy is sent to the corpus luteum. In response, the corpus luteum does not undergo programmed degeneration and instead becomes a **corpus luteum of pregnancy**, which continues to grow and secrete hormones. The signal in primates

is a hormone, chorionic gonadotropin (CG), secreted by the blastocyst. In other words, the embryo emits a signal that tells the mother's tissues to maintain the uterus in a state suitable for pregnancy. The concentration of CG rises high enough in the mother's blood and urine to be easily detected, and many pregnancy tests work by detecting it.

The uterus requires progesterone to remain in a state suitable for pregnancy. In humans, after the corpus luteum is rescued, it provides adequate progesterone for 7–10 weeks. By then, the placenta—which also secretes progesterone—has become sufficiently well developed to take over.

The **placenta** is a structure in which maternal blood vessels and embryonic (or fetal) blood vessels are closely juxtaposed (see Figure 38.19). Thus in addition to its hormonal role, the placenta enables exchange of materials between mother and embryo. The blood of the mother and that of the embryo do not mix. However, nutrients and O_2 move across vessel walls from the maternal blood into the blood of the embryo, and CO_2 and other wastes move from the embryo into the maternal blood.

At the end of pregnancy, still another hormone, oxytocin (secreted by the hypothalamus and posterior pituitary gland; see Concept 35.3 and Figure 35.6) plays an essential role. As we have already discussed (see Figure 29.17), oxytocin stimulates the uterine muscle layer (the myometrium) to contract with ever-increasing force during the birth process so that the baby is expelled from the uterus. Following birth, oxytocin and the anterior pituitary hormone prolactin stimulate the mammary glands (breasts) to produce and eject milk.

Male sex organs produce and deliver semen

The testes of most mammals are located outside the body cavity in a sac of skin called the **scrotum** (see Figure 37.3). During early development they are inside the abdomen in the same positions as the ovaries, but they migrate into the scrotum as development proceeds (see Concept 35.4). In human males, the testes are normally in the scrotum all the time. In many other species, such as certain mice, the testes are in the scrotum only during the reproductive season, being withdrawn into the abdomen at other times. The testes of most mammals need to be about 2°C cooler than ordinary abdominal temperature (37°C) for normal production of viable sperm, and being in the scrotum permits this.

After sperm are produced in a testis, they are stored in the epididymis and vas deferens. The epididymis is a convoluted tubular structure located next to the testis in the scrotum (see Figure 37.5). The vas deferens is the tube that leads from the epididymis to the urethra, the passage in the penis through which urine and semen flow to the outside (see Figure 37.3). The vas deferens and urethra are endowed with smooth muscle, which contracts to propel semen during ejaculation.
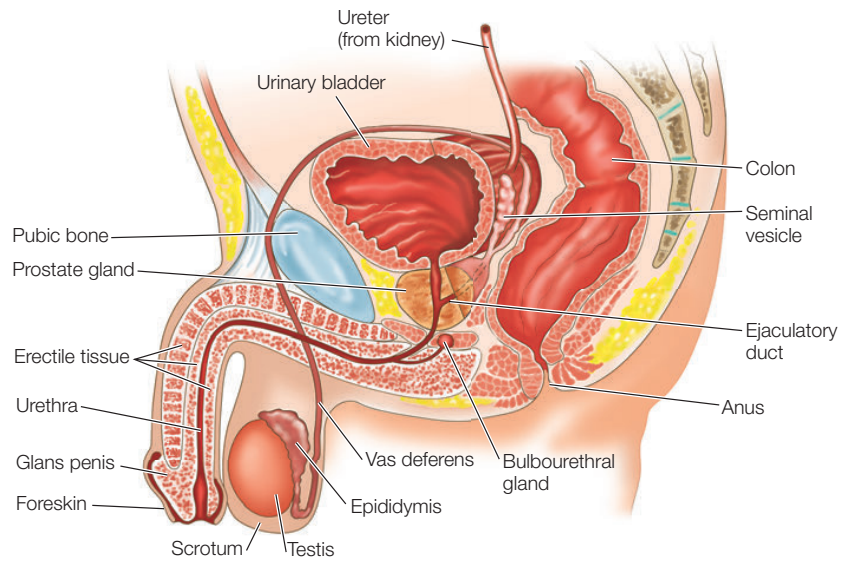
FIGURE 37.12 Reproductive Organs of the Human Male The two vas deferens, from the right and left testes, join at a point upstream from the single prostate gland. The foreskin, the skin covering the glans of the penis, is removed during circumcision.

Go to ACTIVITY 37.3 The Human Male Reproductive Tract
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Semen, the fluid expelled from the penis during ejaculation, consists of a mix of sperm and fluids secreted by male accessory reproductive glands. In humans, the glands that provide most of the fluids in semen are the paired seminal vesicles and the single prostate gland (**FIGURE 37.12**). Sperm are mixed with these fluids as ejaculation occurs. The fluids provide a supportive medium for the sperm, including fructose and other energy sources. The paired bulbourethral glands secrete a clear mucus prior to ejaculation. This fluid often emerges from the penis and may contain sperm even though it is not semen.

The shaft of the human penis is filled almost entirely by three compartments of spongy tissue that can be expanded with blood (see Figure 37.12). Erection occurs when these compartments are inflated with blood at high pressure until the penis is stiff. Nitric oxide (NO) is the agent that immediately controls erection. When NO is released from parasympathetic nerve endings in the penis, it leads to dilation of blood vessels that permit blood to fill the spongy tissues. NO is short-lived. It acts by increasing synthesis of cyclic GMP (cyclic guanosine monophosphate), which in turn acts as a second messenger (see Concept 5.6). Medications for erectile dysfunction (impotence) inhibit an enzyme that breaks down cyclic GMP. This permits the second messenger to act longer.

Many mammals have a bone in the penis that helps stiffen it for copulation. Included are dogs, seals, rodents, and some primates (but not humans).

Hormones play as crucial a role in male reproductive function as in female. Reproductive processes occur in far more steady ways in males than females, however, and the controlling hormones do not cycle in the dramatic ways seen in females.

Testosterone is required for spermatogenesis. In human males, the interstitial cells secrete an abundance of testosterone during a period of fetal life and again during the first year after birth. After that, testosterone levels remain low until puberty begins. At puberty, the blood testosterone level increases dramatically, and thereafter it stays high for the rest of life, although it declines gradually after middle age. Spermatogenesis begins at puberty when the testes mature and thereafter continues without interruption throughout life. Many nonhuman mammals exhibit strongly seasonal reproduction. In these animals, testosterone secretion and spermatogenesis often occur only in reproductive seasons. In those seasons, however, the animals exhibit the same steadiness as seen in humans in testosterone secretion and spermatogenesis.

The pituitary hormones FSH and LH play central roles in males. LH stimulates testosterone secretion by the interstitial cells. In this way it plays a mandatory role in spermatogenesis. FSH and testosterone, acting together, stimulate the Sertoli cells to support spermatogenesis.

Many contraceptive methods are available

Useful contraceptive methods are based on an accurate understanding of the biology of reproduction. They fall into a several categories (**TABLE 37.1**). The simplest to understand is abstinence.

TABLE 37.1	**Methods of Routine Contraception**			
Method	**How is the method used?**	**Annual failure rate[a] (pregnancies/100 women)**		**Helps prevent infection with STDs and HIV?[b]**
		Typical use	**Perfect use**	
Unprotected	No form of birth control	85	85	No
NON-TECHNOLOGICAL METHODS				
Abstinence	Not engaging in sexual intercourse	0	0	Yes
Fertility awareness methods (e.g., rhythm method)	Engaging in intercourse only on days of the ovarian cycle when fertility is judged to be low based on cervical mucus or standard cycle properties	24	3–5	No
Withdrawal (pulling out, coitus interruptus)	The man withdraws his penis prior to ejaculating.	22	4	No
Barrier methods				
Male condom	A sheath of impermeable material (usually latex) is fitted over the erect penis.	18	2	Yes, latex condoms
Female condom; diaphragm	A physical device is inserted in the vagina to block entry of sperm into the cervix and uterus.	12–21	5–6	Yes, condom; no, diaphragm
Spermicides	Chemical compounds that kill or immobilize sperm are inserted in the vagina.	28	18	No
Sponge	A sponge with spermicides is inserted in the vagina to absorb and kill sperm and block entry to cervix.	12–24	9–20	No
HORMONE-BASED CONTRACEPTIVES FOR WOMEN				
Oral hormones ("the pill")	A hormonal pill that prevents ovulation is taken daily; contains either a combination of estrogens and progestin (progesterone) or just progestin.	9	0.3	No
Hormones administered non-orally on long-term basis	Based on the same hormonal actions as the pill; hormones are delivered by long-acting injection, skin patch that releases them through the skin, vaginal ring, etc.	6–9	0.3	No
INTRAUTERINE DEVICES				
Intrauterine devices (IUD)	A small plastic or metal device is inserted semipermanently into the uterus. Some contain copper, others hormones. Device impairs sperm or prevents implantation.	0.2–0.8	0.2–0.6	No
STERILIZATION				
Vasectomy (male sterilization)	The vas deferens on each side is cut and tied so that sperm can no longer pass into the urethra and be ejaculated. Does not affect male hormone levels or sexual response.	0.15	0.10	No
Tubal ligation (female sterilization)	The oviducts are cut, tied, or clamped so that eggs cannot reach the uterus. Does not affect female hormone levels or sexual response.	0.5	0.5	No

[a]"Typical use" failure rates are based on real-world statistics for people who sometimes apply methods incorrectly or skip using them. "Perfect use" refers to using methods according to directions without fail, every time intercourse takes place. Methods of short-term contraception (e.g., "morning-after pill") are not included.
Source: J. Trussell. 2011. *Contraception* 83: 397–404.
[b]STD = sexually transmitted disease such as gonorrhea; HIV = human immunodeficiency virus.

Without sperm in the female reproductive tract, pregnancy cannot occur. Several methods are based on blocking sperm from entering the uterus during and after sexual intercourse. This is the rationale for condoms (male and female) and diaphragms. Some methods, such as birth control pills, manipulate a woman's hormone cycle so that ovulation does not occur.

Table 37.1 presents contraceptive failure rates in the United States according to a recent assessment. In many ways, the most informative aspect of the data is the comparison of failure rates for "typical" and "perfect" applications of the methods. Notice the large differences for some methods. For example, latex male condoms are estimated to have an annual failure rate of 2 pregnancies per 100 women (whose partners use condoms) when the condoms are used exactly according to directions. However, among people in the general population who say they use male condoms as their method of contraception, the failure rate is almost 10 times greater. This difference reflects deficiencies in how and when condoms are put on and removed, and it also reflects instances when avowed condom users skip using them. The message is clear: many methods are not very effective unless the users follow the directions in detail and without fail.

> ## CHECKpoint   CONCEPT 37.2
>
> ✓ What is the role of chorionic gonadotropin (CG) in human reproduction, and why is it a target for pregnancy tests?
>
> ✓ Where do the fluids come from that are expelled from a man's penis before and during ejaculation?
>
> ✓ Taking specific account of FSH, explain the relationship between the cycling of estrogen secretion and the cycling of follicle development during the human menstrual cycle.

In countless ways, reproduction must be integrated with the rest of an animal's life cycle. If reproduction requires nutrients, for example, it must be integrated with processes that provide nutrients. Thus a final aspect of reproduction is how it relates to other aspects of the life cycles of animals.

CONCEPT 37.3   Reproduction Is Integrated with the Life Cycle

Reproduction is an essential part of an animal's life cycle. Because of this, a full understanding of reproduction often involves asking questions about the life cycle. Does reproduction place limits on the rest of the life cycle? Does the life cycle compel reproduction to take place in certain ways? These are just some of the questions that arise.

Animals often gain flexibility by having mechanisms to decouple the steps in reproduction

In humans, the individual steps in the reproductive process are rigidly linked. Mating leads promptly to fertilization, fertilization leads promptly to embryonic development, and development adheres to a relatively rigid schedule, culminating in birth at a relatively fixed time after fertilization. Some other animals also show this sort of rigid sequencing. In cases like this, the individual steps in the reproductive process cannot be separately coordinated with conditions in the environment.

Many animal species, however, have evolved mechanisms of decoupling successive steps in the reproductive process, so that the time that elapses between one step and the next is flexible. Such mechanisms increase options for certain steps to be coordinated with environmental conditions independently of other steps.

Sperm storage in the female reproductive tract is a common mechanism that provides for flexible timing between copulation and fertilization. With sperm storage, fertilization can occur long after copulation.

Female blue crabs (*Callinectes sapidus*) illustrate the advantages of sperm storage. They typically copulate during only one short period in their lives. However, they store the sperm they acquire. Thus they can make and fertilize new masses of eggs for over a year. Queen honey bees store sperm for years. Sperm storage also occurs in certain other crustaceans and insects, and in certain bats, sharks, nonavian reptiles, and birds.

Embryonic diapause—a programmed state of arrested or profoundly slowed embryonic development—occurs in many animals. In cases of embryonic diapause, embryos start to develop but then stop for a while before continuing. This permits adjustment of the time between fertilization and completion of embryonic development.

Silkworm moths (*Bombyx*) use embryonic diapause to ensure that their offspring do not hatch out of their eggs in winter. The adult moths copulate, fertilization occurs, and the eggs are laid in the autumn of the year. These autumn-laid eggs are programmed to undergo a complete arrest of development (cessation of mitosis) early in embryonic development. After the eggs have entered this arrest, they must be exposed to a low temperature (5°C or lower) for about 2 months before they can emerge from the arrested state. These interacting processes—the programmed appearance of diapause and the need for extended cold exposure to terminate it—ensure that eggs laid in the autumn do not hatch into hungry caterpillars during winter. The eggs need winter cold to emerge from developmental arrest. They accordingly hatch in the spring.

> ### LINK
> Plants exhibit a similar strategy by using a variety of environmental cues to ensure that their seeds germinate when conditions are favorable for seedling growth; see **Concept 26.1**

Embryonic diapause in placental mammals is usually called **delayed implantation**. The reason for this name is that the developmental arrest involves postponing the implantation of the blastocyst into the endometrium.

One of the most astounding examples of embryonic diapause is in Antarctic fur seals (*Arctocephalus gazella*). This species uses
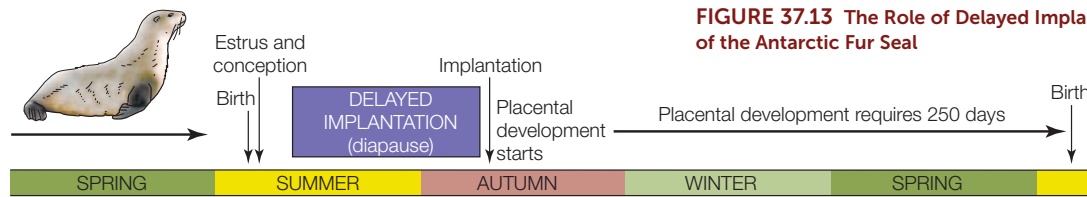
delayed implantation to achieve an exact match between the length of its reproductive cycle and the length of the calendar year. The challenge these seals face is that they have only a narrow window of time, early in the Antarctic summer, to give birth. If they give birth much earlier, their offspring can be killed by late winter storms. If they give birth much later, their offspring cannot grow as much as they need to before the next winter starts.

These fur seals have evolved a reproductive cycle in which the time between copulation and birth is almost exactly 365 days. Thus they give birth and copulate in the early summer one year, and they give birth to the offspring from that copulation 365 days later in the early summer of the next year.

However, the placental development of a young Antarctic fur seal (measured from implantation to birth) lasts only 250 days. If the seals were like people—with all the steps rigidly linked—a youngster conceived in the early summer would be born around March 1 in the cold of the Antarctic winter. The seals solve this problem with delayed implantation (**FIGURE 37.13**). After fertilization, the blastocyst enters the uterus, but it does not implant. Instead it goes into arrest for more than 3 months and then implants. At that point, 250 days remain before the proper birthing moment.

Some animals can reproduce only once, but most can reproduce more than once

One of the most important reproductive characteristics of a species is the number of times that individuals are physiologically capable of reproducing during their lives. In some animals, termed **semelparous**, each individual is physiologically programmed to reproduce only once. Octopuses, some fish, many insects, and many marine worms are semelparous.

Octopuses and Pacific salmon provide two dramatic examples. A species of octopus that is particularly well studied is *Octopus vulgaris*. Many other species are believed to resemble it. Males place spermatophores (packets of sperm) in the reproductive tracts of females during mating, and the females lay fertilized eggs soon after. At that point, a female stops eating and guards her eggs for 1–2 months (**FIGURE 37.14A**). Guarding her eggs is her final achievement, because she dies soon after her eggs hatch. Males also die at about the same time. Both the females and males reproduce only once in their lives.

The same is true of Pacific salmon such as sockeye salmon (*Oncorhynchus nerka*). After sockeye salmon grow to adulthood over a period of 1–4 years in the Pacific Ocean (see Concept 36.3), they migrate up rivers—sometimes hundreds of miles—before spawning. As soon as they enter the rivers from the sea, both sexes stop eating. Accordingly, they power their upriver migration entirely by breaking down their own body substance. After reaching a suitable spot to spawn, they release their gametes and die (**FIGURE 37.14B**).

When a species is semelparous, parents often sacrifice their own well-being to an extraordinary extent to provide the resources they need to produce their offspring. This is understandable because the parents have no future reproductive potential

(A)

(B)

FIGURE 37.14 Semelparity (A) In many species of octopuses, a female produces eggs just once in her life and guards them. She does not eat while guarding her eggs, and she dies after they hatch. (B) Sockeye salmon (*Oncorhynchus nerka*) expend enormous resources to reach freshwater spawning areas, then die after spawning.

after their single period of reproduction. By the time sockeye salmon spawn, they are often capable of little else but spawning because they have so thoroughly depleted their bodies.

Most animal species are **iteroparous**, meaning that individuals are physiologically capable of two or more separate periods of reproductive activity during their lives (i.e., multiple "iterations" of reproduction). In many species, for example, individuals reproduce at least once per year for as many years as they live.

The question of parental investment in offspring is far more complex in iteroparous animals than in semelparous ones. This is because when iteroparous parents produce offspring at any one time, they remain able to produce more offspring at future times. To gain the advantages of future reproduction, they must survive: as they reproduce, they must keep enough resources for themselves to preserve their own health. Their use of resources over their lives thus follows a different pattern than in semelparous species.

Seasonal reproductive cycles are common

In iteroparous animals that live in environments with regular seasonal cycles, the reproductive cycle is nearly always timed to coordinate with the environmental seasonal cycle. We humans are unusual in not showing such seasonality.

The most common pattern is for animals to reproduce in months when temperature, food supply, and other conditions are favorable—such as spring and summer—and suspend reproduction during unfavorable months such as those of winter. Some species of rabbits and mice, for example, shut down their gonads during winter. The testes of the males stop making sperm, become small, and sometimes are withdrawn from the scrotum into the abdomen. The testes then regrow, move into the scrotum, and resume sperm production in the spring. Females also suspend reproductive function and then restore it.

To describe life cycles like this, biologists often speak of animals as having a reproductive season and a nonreproductive season. In this context, "season" does not refer to the defined four seasons of the year. Instead, it refers to the months in which the animals are reproductive and those in which they are nonreproductive.

Some animals breed only once in each reproductive season. The red fox (*Vulpes vulpes*) of North America, for example, enters estrus for a single 1- to 6-day period—and ovulates once—each year during its reproductive season. Some other species of foxes and wolves are similar. If a female fails to mate at this time or loses her offspring, she does not enter estrus again until a full year later. Many birds also breed once per year.

Mammals more commonly superimpose an estrous cycle on their seasonal cycle. For example, during each month of her reproductive season each year, a female rat or mouse cycles in and out of estrus every 4–6 days unless she gets pregnant, as we've mentioned. Males produce sperm continuously during the months of the reproductive season.

Seasonal breeders require mechanisms to time their seasonal cycle. Often they employ environmental cues. Of these, the most important, in both invertebrates and vertebrates, is the amount of daylight per 24-hour day—termed the **photoperiod**.

For example, many mice enter reproductive readiness when the photoperiod is increasing or long (i.e., during "the long days" of late spring and early summer). In this case, photoperiod is being used as a signal that the time of year is spring or summer. Because photoperiod varies in a mathematically exacting way with the time of year, it provides unambiguous information.

> **LINK**
>
> Plants also use the photoperiod to time reproduction; see **Concept 27.2**

Circannual biological clocks are a second important mechanism for timing seasonal cycles. Sheep have internal timing mechanisms that time events for an entire year. Some other animals do as well. They use these circannual clocks to control their seasonal reproductive cycles.

> **CHECKpoint**   CONCEPT **37.3**
>
> ✓ If red foxes (*Vulpes vulpes*) enter estrus and ovulate only once a year, why are they not classed as semelparous?
>
> ✓ How does sperm storage provide flexibility in timing the parts of the reproductive cycle?
>
> ✓ Why, specifically, is embryonic diapause in mammals called delayed implantation?

Q What differences and similarities exist between mammals that exhibit induced ovulation and those that ovulate independently of mating?

ANSWER   There is one important similarity. Ovulation occurs in response to a surge in the blood concentration of luteinizing hormone (LH) in both groups of mammals. Mammals that display induced and spontaneous ovulation differ, however, in how the LH surge is produced. In a species with induced ovulation, the LH surge is a direct response to copulation. The physical act of copulation stimulates sensory neurons that send signals to the brain, and the brain responds by promptly initiating the LH surge. In this way there is a deterministic connection between the presence of sperm in the female reproductive tract and the presence of ova. When sperm are provided by copulation, ova are provided by ovulation almost simultaneously.

In species with spontaneous ovulation, the timing of the LH surge depends on endogenous hormonal cycles in the female. These cycles occur on their own rhythm, more or less independently of whether copulation takes place. Accordingly, chance plays a greater role in determining whether sperm and ova will be present in the female reproductive tract at the same time. The degree of chance is reduced by estrus in many species of mammals with spontaneous ovulation. Females enter estrus approximately when they ovulate. Nonetheless, in a species with spontaneous ovulation, the timing of copulation and that of ovulation may be sufficiently different (because the two are not directly causally linked) for sperm to be present in the appropriate parts of the oviducts when ova are not, or vice versa.

SUMMARY

CONCEPT 37.1 Sexual Reproduction Depends on Gamete Formation and Fertilization

■ In **sexual reproduction** the parents produce **gametes** that have only half as many chromosomes as the other cells in the body. The gametes of the female parent are relatively large, nonmotile cells called **eggs** or **ova**. Those of the male are small cells that swim, typically using flagella, and are called **spermatozoa** or **sperm**. The gametes fuse to produce a single-celled zygote that has a full set of chromosomes and develops into a sexually produced offspring. **Review Figure 37.1**

■ Gametes are produced by meiosis and therefore are diversified in their chromosomes and genes by independent assortment and crossing over. The new individual that is formed when gametes fuse is not genetically identical to either parent.

■ In **asexual reproduction** offspring are produced by mitosis and are genetically identical to their parent and to one another. Asexual reproduction produces no genetic diversity but has the advantage of maintaining favorable combinations of genes. **Review Figure 37.2**

■ In sexually reproducing animals, the male and female sexes differ in their **primary reproductive organs**, **accessory reproductive organs**, and **secondary sexual characteristics**. The primary reproductive organs are the **gonads**: the **ovaries** in females and **testes** in males. The accessory reproductive organs are the reproductive organs other than the gonads. The secondary sexual characteristics are sex-specific properties of nonreproductive tissues and organs, such as facial hair, chest hair, and a deep voice in human males. **Review Figure 37.3**

■ **Gametogenesis** occurs in testes and ovaries, where the **germ cells** proliferate mitotically, then undergo meiosis to produce gametes. **Review Figure 37.4**

■ The gonads, in addition to having germ cells and producing gametes, typically contain somatic cells that contribute to reproduction. In testes, for example, **Sertoli cells** assist sperm production and **interstitial cells** (**Leydig cells**) produce the sex hormone **testosterone**. **Review Figure 37.5 and ACTIVITY 37.1**

■ An **oocyte** (developing ovum) and its support cells are together called an **ovarian follicle**. The release of an ovum from the ovary is called **ovulation**. **Review Figure 37.6**

■ **Fertilization**—the fusion of sperm and ovum—can be external or internal. **External fertilization** is common among aquatic animals. To achieve fertilization, these animals simply release their gametes into the water, a process termed **spawning**. Fertilization then occurs in the water outside the female's body. **Internal fertilization** occurs when a male inserts sperm inside the reproductive tract of a female, permitting fertilization to occur inside the female's body.

■ For fertilization to occur, several steps must occur. In many animals these steps include species-specific binding of sperm to protective material surrounding the ovum, the acrosomal reaction, the sperm's passage through the protective layers covering the ovum, and the fusion of the sperm and ovum cell membranes. **Review Figure 37.7 and ANIMATED TUTORIAL 37.1**

■ The entry of a sperm into the ovum triggers blocks to polyspermy, which prevent additional sperm from entering the ovum.

■ **Sex determination** is the process by which the sex of an individual becomes fixed. In humans and other placental mammals, sex is determined at fertilization and depends on which **sex chromosomes** the zygote receives from its parents.

■ In some animals, sex is not determined at fertilization. Some of these species exhibit **environmental sex determination**, in which the sex of an individual is determined by the temperature it experiences during its embryonic development.

■ Some species are **sequential hermaphrodites**; they can be males at one time and females at another during their lives. **Review Figures 37.8, 37.9**

CONCEPT 37.2 The Mammalian Reproductive System Is Hormonally Controlled

■ Somatic cells in the gonads produce steroid sex hormones. The principal sex steroid in males is testosterone, which is secreted by the interstitial (Leydig) cells in the testes. In females, the somatic cells of the ovarian follicles secrete feminizing steroids called **estrogens**. After ovulation, the follicular somatic cells remaining in the ovary reorganize to form a **corpus luteum**, which secretes another type of female sex steroid, **progesterone**, which is involved principally in coordinating processes associated with pregnancy.

■ Ova mature in the female's ovaries, and after release (ovulation), they enter the **oviducts** (fallopian tubes). Sperm deposited in the vagina during copulation move through the cervix and uterus into the oviducts, where fertilization occurs. **Review Figure 37.10 and ACTIVITY 37.2**

■ If fertilization has occurred, the zygote undergoes its early development as it travels the length of the oviduct and arrives in the uterus as an early embryo called a blastocyst. The blastocyst buries itself in the **endometrium** of the uterus—a process called **implantation**.

■ Ovulation is either induced or spontaneous. **Induced ovulation** is ovulation triggered by copulation. In **spontaneous ovulation**, the timing of ovulation is under control of endogenous hormonal cycles in the female.

■ In most species of mammals that display spontaneous ovulation, a female ovulates in cycles. In primates these cycles are called **menstrual cycles**, in recognition of the fact that **menstruation**—the sloughing off of part of the endometrium—occurs in each cycle that does not result in pregnancy.

■ Mammals other than primates do not menstruate. Often, however, they undergo dramatic changes in behavior: they cyclically enter estrus (heat). Their cycles accordingly are called **estrous cycles**.

■ The human menstrual cycle is under the control of hormones secreted by the hypothalamus, anterior pituitary gland, somatic cells in the ovarian follicle, and the corpus luteum. **Review Figure 37.11 and ANIMATED TUTORIAL 37.2**

■ The uterus requires progesterone to support a pregnancy. In humans, chorionic gonadotropin, secreted by the blastocyst, signals the corpus luteum not to degenerate and instead to provide adequate progesterone for the first 7–10 weeks of pregnancy. By then, the **placenta**—which also secretes progesterone—is sufficiently well developed to take on this task.

■ The male reproductive organs produce and deliver **semen**. Semen consists of sperm suspended in a fluid that nourishes the sperm and facilitates fertilization. This fluid is produced by accessory reproductive glands, such as the prostate gland. **Review Figure 37.12 and ACTIVITY 37.3**

■ Spermatogenesis depends on testosterone secreted by the interstitial (Leydig) cells of the testes, which themselves are under the control of hormones produced in the anterior pituitary gland.

(continued)

SUMMARY *(continued)*

■ Methods of contraception (prevention of pregnancy) include abstention from intercourse and the use of technologies that decrease the probability of fertilization and implantation. **Review Table 37.1**

CONCEPT 37.3 **Reproduction Is Integrated with the Life Cycle**

■ Many animal species have evolved mechanisms of decoupling successive steps in the reproductive process. Such mechanisms increase options for certain steps to be coordinated with environmental conditions independently of other steps. These mechanisms include sperm storage and **embryonic diapause**, which in mammals is called **delayed implantation**. **Review Figure 37.13**

■ Some animals are **semelparous**: each individual is physiologically programmed to reproduce only once in its lifetime. Examples include octopuses and Pacific salmon. **Review Figure 37.14**

■ Most animal species are **iteroparous**, meaning that individuals are physiologically capable of two or more separate periods of reproductive activity during their lives. In iteroparous animals that live in environments with regular seasonal cycles, the reproductive cycle is nearly always timed to coordinate with the environmental seasonal cycle.

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Animal Development

Vertebrates have two lateral eyes, clearly seen as this hatchling Greek tortoise (*Testudo hermanni*) takes its first peek at its new environment.

In Homer's *Odyssey,* the mythic hero Odysseus visits the island of the Cyclopes, a race of one-eyed giants. He and his men come across an enormous cave inhabited by one of these beings. After feasting on the cyclops's stored food, they hide as the monster returns: "The cyclops … blotted out the light in the doorway. He was as tall and rugged as an alp. One huge eye glared out of the center of his forehead."

The one-eyed monster of Greek mythology has a basis in reality: a birth defect in humans that is known as holoprosencephaly (Greek, "one fore-brain"). The defect varies in severity. In its extreme form, as the name implies, the forebrain does not develop as two hemispheres but rather as one, and the face can develop with a single, centrally located eye. These extreme cases invariably lead to death of the fetus and a miscarriage. In less extreme cases, infants are born with cleft lips and cleft palates.

Several factors have been implicated in holoprosencephaly, most of them genetic. Mutations in several genes that are part of a family of signaling factors called the hedgehog family can cause this condition. The first *hedgehog* gene was discovered in fruit flies, where it plays a role in determining the differences in the body segments of the fly. The name arises from the fact that flies with a defect in this gene are hunched up and have a continuous covering of tiny projections, so they resemble a hedgehog. The homologous vertebrate gene, *Sonic hedgehog* (named for the video-game character), is critical in central nervous system development.

Environmental factors can also induce holoprosencephaly. A particularly powerful mutagen is a molecule (an alkaloid) found in certain plants, notably the corn lily (*Veratrum californicum*) and its relative in the eastern North America, false hellebore (*V. viride*). Cows and sheep grazing in fields where these plants grow have high incidences of stillbirths with extreme forms of holoprosencephaly. In fact, when the molecule was extracted and purified from corn lily, it was named cyclopamine. In humans, the ingestion early in pregnancy of certain drugs may also be associated with these birth defects. Research into how these environmental factors cause holoprosencephalic development is helping explain why Sonic hedgehog is critical in limb and nervous system development.

Q How does the Sonic hedgehog pathway control development of the vertebrate brain and eyes?

You will find the answer to this question on page 806

This chapter is contributed by Dr. Susan Douglas Hill, Michigan State University.

Fertilization Activates Development

The development of an animal, a plant, or a fungus is one of the most breathtaking processes you will encounter in your study of biology. In sexually reproducing animals, one cell, the fertilized egg, gives rise to an entire organism. Early investigators assumed that a tiny person was encapsulated in a human egg or sperm and that this "homunculus" required only the appropriate stimulus and nutrients for growth:
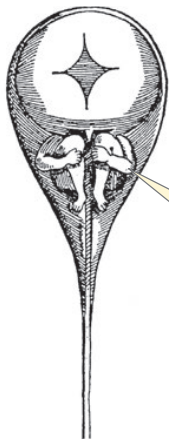
In 1695, Nicolas Hartsoeker depicted a homunculus as a tiny, fully formed infant inside the head of a sperm.

Improvement in microscopes allowed scientists to see that no tiny animal resides in either sperm or egg. That left the mystery—how does an organism achieve its final form?

You saw earlier that scientists obtain much information by studying "model" organisms (see Concept 1.1). Nowhere is this more true than in developmental biology. It is important to realize that certain animals are used as models, not because they represent the majority of the group under investigation, but because of particular characteristics that make them desirable for research, such as short developmental times and easy maintenance in a laboratory. Remember, too, that there are probably millions of animal species—many not yet discovered. Each has tweaked its development to adapt to its environment. The doors are open for further investigations in developmental biology.

Egg and sperm make different contributions to the zygote

Development usually begins with the union of egg and sperm to form a fertilized egg, or **zygote**. Egg cells are very large compared with other cells—and compared with sperm, they are gigantic. Even the non-yolky eggs of sea urchins and mammals are large compared with other cells, because they contain the materials and information needed to initiate and maintain early development. The cytoplasm of an egg contains most of the molecular machinery for cell division, energy production, and growth (yolk that provides nutrients for growth, mitochondria, ribosomes, etc.), as well as informational molecules such as transcription factors and messenger RNAs (mRNAs). These play important roles in setting up the signaling cascades that orchestrate the major processes of development discussed in Concept 14.1: determination, differentiation, morphogenesis, and growth.

The union of egg and sperm is complex. Many sperm are attracted to an egg. However, one sperm, and only one, must convey its nuclear material to the egg cytoplasm:
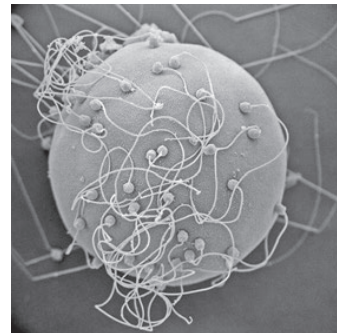
A sea urchin egg surrounded by sperm

All of the egg cell membrane may be available for sperm entry, as in sea urchins, or entry may be restricted to certain parts. In amphibians, for example, sperm can penetrate only half the egg surface. In *Drosophila*, sperm must enter through a tunnel whose position is fixed prior to fertilization.

Activation of an egg by a sperm brings about changes in the egg cell membrane and the release of ions from stores within the egg cytoplasm. These ion changes trigger a series of crucial events. Entry of additional sperm is blocked, metabolic rate rises, protein synthesis is initiated, and cytoplasm is reorganized.

Most of the sperm cytoplasm is discarded when the egg and sperm membranes fuse, but the nuclear material and usually the centrosome (the major microtubule organizing center of an animal cell) are transferred from the sperm to the egg. The centrosome then plays a major role in forming the zygote centrosome and organizing the zygote's microtubules. When egg and sperm nuclei join, the fertilized egg becomes a single-celled, diploid zygote that is ready for its first mitotic division.

> **LINK**
>
> **Concept 37.1** explains sperm–egg recognition and blocks to polyspermy (fertilization by more than one sperm)

Polarity is established early in development

Most animals have a defined head and tail, back and belly, and right and left sides. These differences are known as polarities and are usually established early in development. In most animals, polarities are established during early cell divisions as materials deposited in the egg cytoplasm by the mother are redistributed and segregated. In some animals, however, polarities are set in place before or at fertilization.

In the fruit fly *Drosophila melanogaster*, a favorite model organism, the position of the egg in the ovary determines both anterior–posterior (head–tail) and dorsal–ventral (back–belly) polarity. Cells that surround the egg, called follicle cells, pass mRNAs

from the mother to specific regions of the egg cytoplasm. After the egg is fertilized and development is underway, these mRNAs encode regulatory proteins that determine polarity.

In amphibians, another group of favorite model organisms, anterior–posterior and dorsal–ventral polarity are determined at fertilization by the position of the yolk and the point of sperm penetration. Cytoplasmic rearrangement following fertilization is easily observed in some frog species. In unfertilized eggs of these species, dense yolk granules are concentrated by gravity in the lower half of each egg, the **vegetal hemisphere**. This yolky vegetal hemisphere is unpigmented. In the top half of each egg, or **animal hemisphere**, the outermost (cortical) cytoplasm is heavily pigmented, while the pigment in the underlying cytoplasm is more diffuse. Sperm-binding sites occur only on the animal hemisphere. When a sperm enters the egg, the cortical cytoplasm rotates toward the site of sperm entry, producing a band of lightly pigmented cytoplasm called the **gray crescent** on the opposite side (**FIGURE 38.1**).

As we will soon see, the anus later forms within the gray crescent. Thus with the formation of the gray crescent, the zygote already has an anterior–posterior axis for a future head and tail, as well as a dorsal–ventral axis. The cytoplasmic rearrangement is initiated by the sperm centriole, which organizes microtubules in the egg cytoplasm in a parallel array that extends through the vegetal hemisphere. This cytoskeleton guides the shift of the cortical cytoplasm (see Concept 14.2), and the gray crescent appears.

Much of our understanding of developmental mechanisms builds on the insightful experiments of scientists in the late 1800s and early 1900s who used techniques that may seem primitive by today's standards but were very revealing. This point is beautifully illustrated by German biologist Hans Spemann's work, which also had a profound influence on future amphibian research. Similar experiments were carried out on many animals, and today's work is based on the results of these creative early investigators.

In the early 1900s, Spemann was studying the development of salamander eggs. With great patience and dexterity, he formed loops from single hairs taken from his baby daughter

FIGURE 38.2 **Importance of the Gray Crescent** Spemann's research revealed that normal development in salamanders depends on cytoplasmic determinants localized in the gray crescent.

(baby hair is finer than adult hair) and tied them around fertilized eggs, effectively dividing the eggs in half (**FIGURE 38.2**). When his loops bisected the gray crescent, both halves of the zygote developed into a complete embryo. When he tied the loops so the gray crescent was on only one side of the constriction, only the half with the gray crescent developed normally. The half lacking gray crescent material became an unorganized clump of cells, which, because of its characteristics, he referred to as the "belly piece." Spemann concluded that important cytoplasmic factors—now called **cytoplasmic determinants**—necessary for the establishment of polarity and development of a normal salamander are unequally distributed in the fertilized egg and reside in the gray crescent.

Experiments using amphibian eggs have contributed much to our understanding of development. Keep in mind, though, that although amphibians are useful models, many animals develop differently, and in many, polarities are not established until cell divisions are underway.

FIGURE 38.1 **The Gray Crescent** In frog eggs, rearrangement of the cytoplasm after fertilization creates the gray crescent and imposes anterior–posterior and dorsal–ventral axes on the egg.

CHECKpoint CONCEPT 38.1

✓ What normally initiates development?

✓ What does the sperm contribute to the zygote?

✓ What usually determines initial polarity in developing embryos?

✓ How are anterior–posterior and dorsal–ventral polarities established in fruit flies? In frogs?

We have now seen how the zygote forms and how polarities may be established. We will turn next to the early series of cell divisions that produce a multicellular embryo.

CONCEPT 38.2 Cleavage Creates Building Blocks and Produces a Blastula

Cleavage is the initial process that creates cellular building blocks to form the new organism by producing many smaller cells from one. Ultimately, as a result of cleavage, these smaller cells will differ in their cytoplasmic determinants. To understand cleavage, it is important to understand that no growth occurs at this stage. Cleavage divisions differ from other mitotic divisions in that there is no "gap" or growth phase between divisions, so no new cytoplasm is added. Thus as cells increase in number, they become smaller and smaller. The cells produced are called **blastomeres**. The cluster of cells produced is termed a **blastula**.

Early investigators thought that, through cleavage, genes were divided up so that each blastomere would later form its specific tissue or organ according to its restricted genetic makeup. We now know that this is not the case. Each blastomere receives the entire genome of the animal. Now we have the next mystery: How can cells that all have the same genetic information give rise to the diversity of cell types that we see in an adult? The answer depends on several mechanisms (see Concept 14.2).

During early stages of development, events are controlled by specific information passed on by the mother. Proteins and mRNAs, referred to as cytoplasmic determinants, are deposited in the cytoplasm of the egg as it matures. Early cleavages occur rapidly, and there is little or no transcription of mRNA in the zygote nucleus. Rather, mRNA already placed by the mother in the egg is used to direct protein synthesis. In most animals, it is not until the mid- to late blastula stage that the genome of the developing embryo takes over. Prior to that time, maternal factors control development. As we saw in the formation of the gray crescent, the cytoskeleton may redistribute such materials from one point to another. Also, at some point, as mitotic divisions continue, new cell membranes separate cytoplasmic determinants so they become distributed differentially among blastomeres (see Concept 14.2, especially Figure 14.7). These processes plus cell–cell communication play a role in the determination of blastomere fates. All of these processes are involved in the development of most animals, but as you will see, the stage at which each process comes into play differs from group to group. At some point, the fate of a blastomere becomes restricted or determined and it can no longer form an entire embryo.

Scientists have learned much about the developmental potential of blastomeres by separating them at different times of development. In such experiments, blastomeres are isolated to learn how they will develop on their own. It is also possible to leave all the cells together, label a specific cell (e.g., with a dye), and then identify the tissues and organs that form from that cell. A new technique called light sheet microscopy allows individual cells to be followed through many cleavages without the
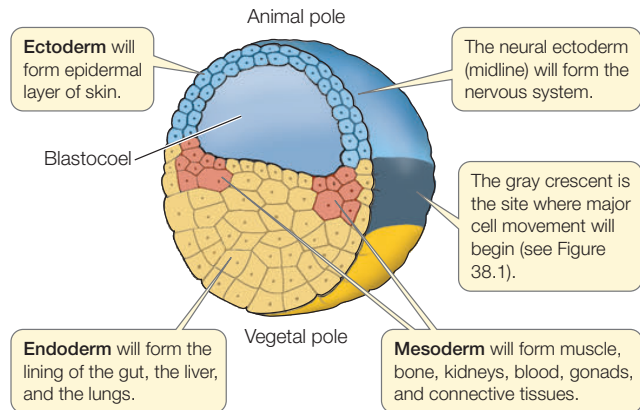
FIGURE 38.3 **Fate Map of a Frog Blastula** Colors indicate the portions of the early-stage frog embryo (blastula) that will form the three germ layers—ectoderm, mesoderm, and endoderm—and subsequently the frog's tissues and organs.

addition of a dye. Experiments of all types—isolation experiments and tracing experiments—have been used to generate **fate maps** for many species (**FIGURE 38.3**). To understand this, we need to explore different cleavage patterns.

Cleavage is easiest to understand in animals that produce eggs with little yolk, such as sea urchins. Blastomeres may be the same size or different. They will be the same size if the egg cytoplasm is divided equally among all the blastomeres. Unequal cytoplasmic divisions will result in large blastomeres and small blastomeres. As cleavage continues, the zygote becomes divided into progressively smaller blastomeres:
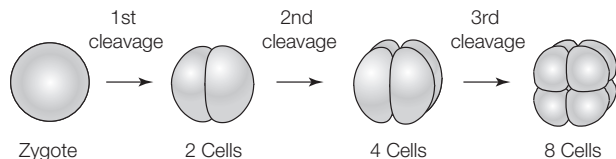
If the cytoplasm is completely divided by each cell division, cleavage is termed **complete cleavage**. If it is not, as you will see is the case in birds, insects, and some other animals, it is termed **incomplete cleavage**.

Two different patterns of cleavage that seem to have deep evolutionary roots are **radial cleavage** and **spiral cleavage**. These patterns are seen in eggs that have little yolk and undergo complete cleavage, such as those of snails and sea urchins. In all types of cleavage, the plane of cleavage (shown by the position of the new cell membrane that divides the cells) is determined by the orientation of the mitotic spindle. Differences in radial and spiral cleavage are readily seen after the third cleavage (the 8-cell stage).

At this time, in radial cleavage the four daughter cells lie directly above the four parent cells:
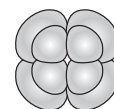
During spiral cleavage, mitotic spindles align so that, after the third and following cleavages, the four daughter cells lie in the grooves between the four parent cells, creating the appearance of a spiral:
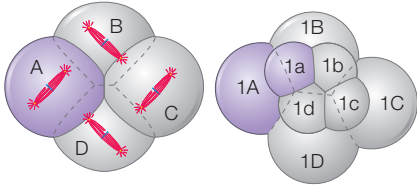
A spirally cleaving egg has the most thermodynamically stable shape possible. Appropriately sized soap bubbles assume the same configuration as a spirally cleaving egg.

You are probably most familiar with deuterostome animals, the large clade (group) that includes the vertebrates and all other chordates, echinoderms, and a few other groups. Echinoderms and several other deuterostomes display radial cleavage. Radial cleavage is considered to be the basic deuterostome pattern, although it is often highly modified in the presence of yolk.

The other large group of animals, the protostomes, includes most of the invertebrates. Protostomes do not have radial cleavage. Here we focus on the lophotrochozoans, a clade that includes about half of all animal phyla, including the annelids and mollusks. In the lophotrochozoans, spiral cleavage predominates.

> **LINK**
>
> **Concept 23.1** shows how early development determines body plans that reflect phylogenetic relationships among the animals; **Concept 23.3** discusses the protostomes, explaining that there are two major clades; **Concept 23.5** discusses the deuterostomes and some of their developmental characteristics

Specific blastomeres generate specific tissues and organs

Blastomeres become determined—irreversibly committed to specific fates—at different times in different species. In many protostomes with spirally cleaving eggs and in a few deuterostomes, blastomere fates are determined as early as the 2-cell stage. If one of these blastomeres is experimentally removed, a particular portion of the embryo will not form. This type of development has been called **mosaic development** because each blastomere appears to contribute a specific set of "tiles" to the final "mosaic" that is the adult animal (**FIGURE 38.4**).

A feature of many spirally cleaving eggs that is not seen in radially cleaving eggs is the production of a polar lobe, at the vegetal pole, during early cleavages. Cytoplasmic determinants as well as yolk are sequestered in this "out-pouching" during cell division and are then returned to a specific blastomere after cell

membranes have re-formed. If the polar lobe is removed experimentally, one abnormal larva develops that typically lacks specific structures (see Figure 38.4B). If the two blastomeres are experimentally separated, two abnormal larvae develop, each lacking very specific structures (see Figure 38.4C). These experiments clearly demonstrate one way in which information for further development is distributed to specific blastomeres.

In contrast to mosaic development, in **regulative development** the loss of some cells during cleavage does not affect the developing embryo. Instead, the remaining cells compensate for the loss. If blastomeres of a sea urchin egg are separated at the 2-cell stage, two half-sized, but complete, larvae form. Even at the 4-cell stage, separation produces four small larvae (**FIGURE 38.5**). We now know that cytoplasmic determinants are found in the cytoplasm of eggs showing both mosaic and regulative development. In animals that display regulative development, however, the distribution of these determinants happens later as cell divisions continue (see Concept 14.2; Figure 14.7). Regulative development is typical of vertebrate species, including humans.

As noted earlier, cleavage leads to the production of a ball of cells termed a blastula. Blastulas produced by radially cleaving eggs, and by those whose cleavage is derived from this basic pattern, have an inner fluid-filled cavity called a blastocoel (see Figure 38.3). The blastula of a sea urchin, for example, is
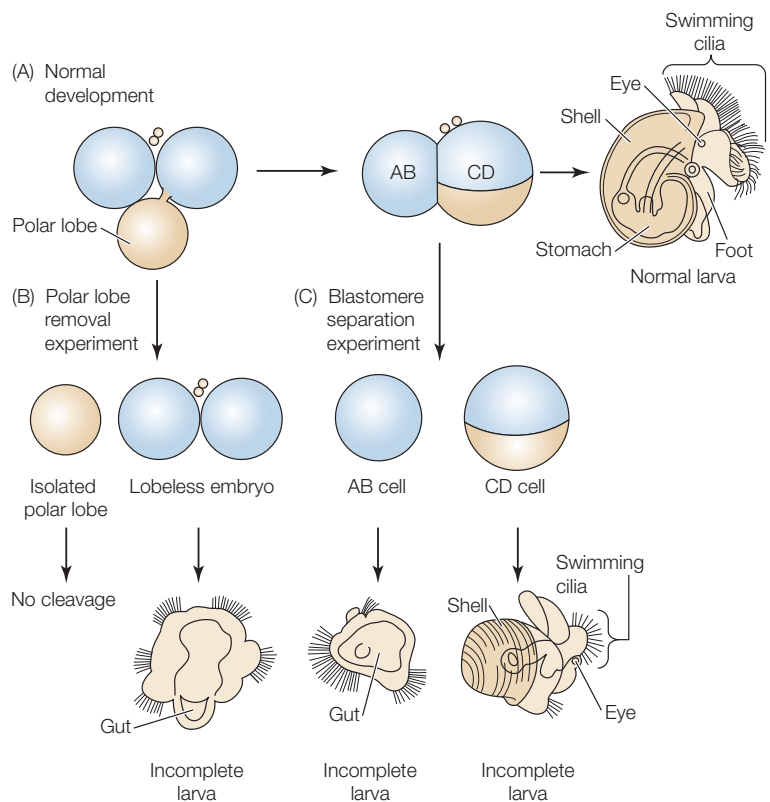
FIGURE 38.4 Mosaic Development of a Snail Egg (A) Normal development. (B) Removal of the polar lobe results in an abnormal, incomplete larva. (C) Separation of the two blastomeres results in two abnormal larvae, incomplete in different ways.
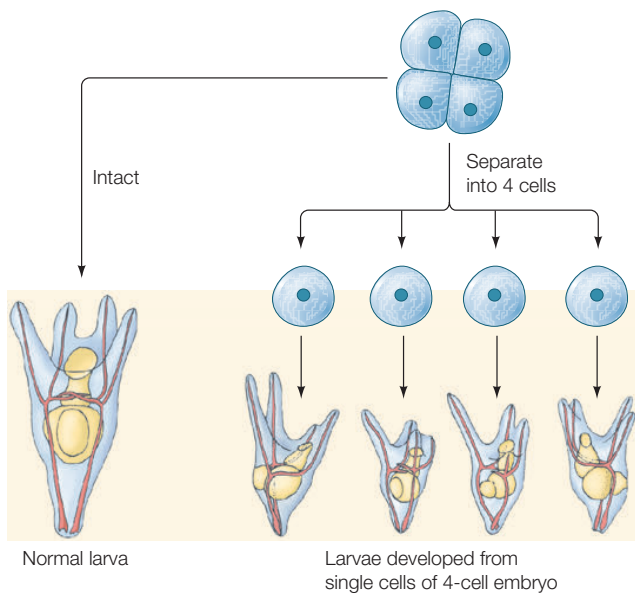
FIGURE 38.5 Regulative Development of a Sea Urchin Egg
Separation of four blastomeres results in four small but almost normal larvae.

a hollow sphere. Blastulas produced by spirally cleaving eggs may have a blastocoel, but often they are a solid ball of cells, without the fluid-filled space.

The amount of yolk affects cleavage

The amount of yolk has a profound effect on cleavage patterns and other developmental processes such as gastrulation, which we will discuss in Concept 38.3. Some eggs, such as those of sea urchins, snails, and placental mammals, have little yolk. Some, such as those of frogs and salamanders, have a moderate amount of yolk. Others, including those of birds and egg-laying mammals, are extremely yolky. As you will see, it is as if the presence of yolk slows down or impedes cell divisions. This means that the eggs of many animals do not follow the radial
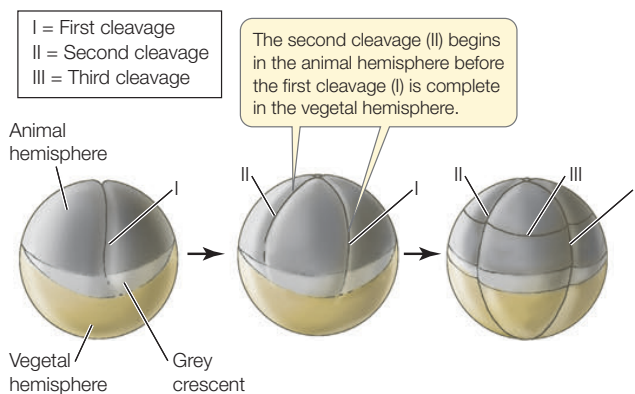
FIGURE 38.6 Complete Cleavage in a Frog Egg Cleavage proceeds more rapidly in the animal hemisphere that in the vegetal hemisphere.

or spiral cleavage patterns that we consider basic in deuterostomes and protostomes.

In eggs with little yolk, like those of sea urchins and snails, cleavage usually proceeds as described above and is complete.

In moderately yolky eggs like those of a frog, cleavage is complete and cell membranes form around every nucleus. However, cells divide more slowly in the yolk-filled vegetal hemisphere than in the animal hemisphere (**FIGURES 38.6** and **38.7A**). In the vegetal hemisphere, the yolk retards the process of division so that the second round of cleavage has begun in the animal hemisphere before the first round is completed in the vegetal hemisphere. In the example shown in Figure 38.6, the third cleavage is horizontal and occurs in the animal hemisphere. Because cells divide faster in the animal hemisphere, more cells are produced in the dorsal portion of the egg than in the ventral, resulting in an animal hemisphere consisting of small blastomeres and a vegetal hemisphere consisting of fewer, larger blastomeres. The blastocoel forms within the small blastomeres of the animal hemisphere.

In very yolky eggs such as those of a squid (a molluscan protostome), fish, bird, or egg-laying mammal (e.g., the platypus), the yolk remains undivided and the embryo forms as a small **blastodisc** of cleaving cells on the yolk surface (**FIGURE 38.7B**). The yolk never divides, and so the cleavage is incomplete. The disc of cells on top of the yolk enlarges and becomes several cells thick. For example, the blastula of a bird, or of the zebrafish shown in Figure 38.7B, is a flattened structure that sits atop the large undivided yolk and consists of an upper layer called epiblast, which will give rise to the embryo proper, and a lower hypoblast, with a fluid-filled space between the two. (Epiblast and hypoblast in the bird egg are shown in Figure 38.11.)

A different type of incomplete cleavage is seen in insects. In *Drosophila* eggs, for example, the original zygote nucleus undergoes a series of divisions unaccompanied by divisions of the cytoplasm. This early embryo, then, is a syncytium: a mass of cytoplasm in which several nuclei are surrounded by the same cell membrane. As development proceeds, nuclei migrate to the periphery of the egg, and cell membranes form (**FIGURE 38.7C**).

Cleavage in placental mammals is unique

Placental mammals have non-yolky eggs (which undergo development within the mother's body after fertilization), but their cleavage pattern differs from that of other non-yolky deuterostome eggs. You might expect that their eggs would show radial cleavage like sea urchin eggs. They do not. Remember that mammals evolved from a reptilian ancestor. As a result, several aspects of their development—such as the formation of epiblast and hypoblast, as well as of the yolk sac and allantois (which we will discuss in Concept 38.5)—were derived from processes in yolky eggs of reptiles, including birds. Other features, however, are unique. The two groups of placental mammals—the marsupials and the eutherians (see Concept 23.6) have evolved slightly different developmental steps. In this chapter, we will consider only eutherian development. Early cell divisions in eutherians do not follow the radial cleavage pattern. For example, at the second cleavage division, the two blastomeres divide in different

(A) Complete cleavage (frog)

Animal pole

Vegetal cells have incorporated yolk and are thus larger than the animal cells in the 16-cell embryo.

The planes of the second cleavage are displaced only slightly by yolk in the cytoplasm.

The embryo forms as a disc-shaped blastula that sits on top of the yolk mass.

(B) Incomplete cleavage (zebrafish)

In birds and fish, cleavage furrows do not penetrate the large yolk mass.

(C) Incomplete cleavage (*Drosophila*)

1 Mitosis (nuclear division) occurs without cell division.

3 The nuclei migrate to the inner edge of the cell membrane.

Nucleus

2 A syncytium—a single cell with many nuclei—is produced.

4 Cell membranes form between peripheral cells.

FIGURE 38.7 Some Patterns of Cleavage Differences in patterns of early embryonic development reflect differences in egg cytoplasm. (A) The frog is a model organism representing complete cleavage. (B) Zebrafish embryos illustrate incomplete cleavage, in which the large yolk mass limits the planes of cleavage. (C) Fruit flies have another type of incomplete cleavage. Nuclear staining reveals the syncytial nuclei characteristic of their early development. These nuclei migrate to the periphery of the egg. Cleavage furrows then move inward to separate the nuclei into individual cells.

planes, so that one blastomere cleaves vertically and the other horizontally, in a pattern called **rotational cleavage**:

Cleavage plane IIA

Cleavage plane I

Cleavage plane IIB
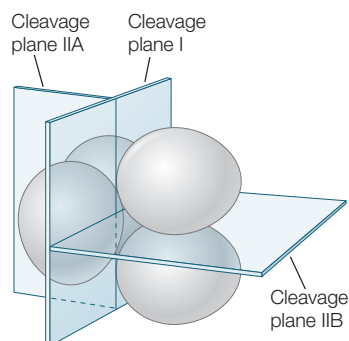
Blastomeres within the same egg divide at different times, so the eutherian egg may contain an odd number of cells. This is not usually the case during early cleavage in other groups. Finally, the mammalian genome is activated very early, so cleavage and development are governed by the new nuclei rather than by cytoplasmic determinants passed on from the mother. In most deuterostomes, this transition happens toward the end of the blastula stage.

Another unique feature of mammalian development occurs during the fourth cleavage, when the cells separate into two groups (**FIGURE 38.8A**). The **inner cell mass** will become the embryo, while the surrounding outer cells become an encompassing sac called the **trophoblast**. Trophoblast cells secrete fluid, creating a blastocoel with the inner cell mass at one end. At this stage, the mammalian embryo is called a **blastocyst**. Later, trophoblast cells will contribute to the formation of a unique mammalian organ, the placenta, which we will discuss in Concept 38.5.

In a mammal, fertilization occurs in the upper reaches of the mother's oviduct, and cleavage takes place as the zygote travels down the oviduct. When the blastocyst arrives in the uterus, it adheres to the lining of the uterus, which is called the endometrium. This starts the process of **implantation** in which the early embryo burrows into the uterine wall. In humans, implantation begins about 6 days after fertilization (**FIGURE 38.8B**).

(A)

The inner cell mass will form the embryo.

Trophoblast (outer cells)

Blastocoel

Blastocyst (cross section)

(B)

Oviduct

16–32 Cells (3–4 days postfertilization)

2–4 Cells (2 days postfertilization)

Implantation of blastocyst (6–7 days postfertilization)

Site of fertilization

Ovary

Uterus

Cervix

Vagina

Human embryo at 9 days

Wall of uterus

Developing placenta

Hypoblast

Inner cell mass

Epiblast

Trophoblast

Blastocoel

Endometrium

Developing amnion

Emerging chorionic villus

Lakes of maternal blood

Maternal blood vessel

FIGURE 38.8 A Human Blastocyst at Implantation   (A) The mammalian blastocyst consists of an inner cell mass adjacent to a fluid-filled blastocoel and surrounded by trophoblast cells. (B) Molecules and enzymes secreted by trophoblast cells allow the blastocyst to adhere to and burrow into the endometrium. Once the blastocyst is implanted in the uterine wall, the trophoblast cells send out chorionic villi—projections that increase the embryo's area of contact with the maternal bloodstream.

CHECKpoint CONCEPT 38.2

✓ What two major functions does cleavage perform?

✓ Compare radial and spiral cleavage. What determines the direction of the cleavage plane?

✓ What does experimental removal of the polar lobe of a snail egg demonstrate?

✓ Describe complete and incomplete cleavage and explain where mammals fit into this scheme.

✓ What type of development must a species have for identical twins to occur? What do you think leads to the development of such twins? How do you think fraternal twins are produced?

After formation of the blastula, the next stage of development is gastrulation. The developmental biologist Louis Wolpert once said, "It is not birth, marriage, or death, but gastrulation which is the most important time in your life."

CONCEPT 38.3 Gastrulation Produces a Second, then a Third Germ Layer

Gastrulation involves major movements of cells from the external surface to the interior of the embryo. These cell movements create a three-layered body plan and set the stage for development of the first organs. Triploblastic animals (see Concept 23.1) create all of their organs and tissues from three basic germ layers—ectoderm, endoderm, and mesoderm. These layers are formed by the process of gastrulation. The resulting embryo is known as a **gastrula**.

Just as the amount of yolk affects cleavage, it also affects how gastrulation occurs. The process is easiest to understand in radially cleaving eggs with little yolk, such as the much-studied eggs of sea urchins (**FIGURE 38.9**). One wall of the blastula (the vegetal pole) bulges inward, or invaginates, as if someone were poking a finger into a hollow ball. The new space that forms is the archenteron, or "first gut." The opening into the archenteron is the blastopore. Recall that in deuterostomes, the blastopore becomes the anus and the mouth (the second opening) forms opposite it. The outer layer of cells is now ectoderm, and the wall of the archenteron is endoderm and future mesoderm. The archenteron elongates, assisted by contractions of wandering cells called mesenchyme cells. The archenteron will eventually squeeze the blastocoel out of existence.

In eggs such as those of amphibians, which contain a moderate amount of yolk, cleavage continues to produce many ever-smaller cells in the animal hemisphere and larger cells in the vegetal hemisphere. To initiate gastrulation, some cells in the gray crescent invaginate to form a slitlike blastopore (**FIGURE 38.10**). Small blastomeres of the animal pole then begin to roll like a sheet over the dorsal lip of the blastopore and push into the blastocoel. At the same time, cell divisions continue to increase the number of cells. Because the small cells of the animal hemisphere continue to divide more rapidly than the larger cells of the vegetal hemisphere, these smaller cells grow over and surround the larger cells of the vegetal hemisphere. As these smaller cells reach the blastopore, they too

1 The vegetal pole of the blastula flattens.

2 Some cells change shape and move inward to form the archenteron.

3 Other cells break free, becoming mesenchyme.

4 Thin extensions of mesenchyme cells attach to the overlying ectoderm.

5 The archenteron elongates, assisted by the contraction of mesenchyme cells.

6 The mouth will form where the archenteron meets ectoderm.

Animal hemisphere

Mesenchyme

Ectoderm

Endoderm

Blastocoel

Archenteron

Mesenchyme

Blastocoel

Vegetal hemisphere

Blastopore

Archenteron

7 The blastopore will form the anus of the mature animal.

FIGURE 38.9 Gastrulation in a Sea Urchin Embryo During gastrulation, cells move to new positions. Invagination to form endoderm in this non-yolky egg is illustrated. The archenteron, or "first gut," remains connected to the exterior via the blastopore. Mesenchyme cells assist with gastrulation and will also form the temporary larval skeleton.

move inward so that the inward migration occurs all around the blastopore. These cells will form much of the endoderm and mesoderm of the developing embryo. The blastopore becomes the anus.

In very yolky eggs like those of birds, in which the blastodisc forms on top of the yolk, the blastopore forms as a groove in the primitive streak, a collection of cells marked at the anterior end by Hensen's node (**FIGURE 38.11**). Cells that will

become mesoderm and endoderm migrate inward through Hensen's node and all along the groove of the primitive streak.

Placental mammals retain the avian/reptilian gastrulation pattern, even though they lack yolk. Mammals and reptiles, including birds, are all amniotes (i.e., they produce eggs that develop extraembryonic membranes), so it is not surprising that they share certain patterns of early development. In Concept 38.2 we discussed the development of the mammalian inner cell mass and the outer trophoblast. As in avian development, the inner cell mass of placental mammals splits into an upper layer called the epiblast and a lower layer called the hypoblast

1 Gastrulation begins when cells in the region of the gray crescent move inward, forming the dorsal lip of the future blastopore.

2 Cells of the animal pole spread out, pushing surface cells below them toward and across the dorsal lip. These cells move into the interior of the embryo, where they form the endoderm and mesoderm.

3 The archenteron expands, destroying the blastocoel. The blastopore lip forms a circle, with cells moving to the interior all around the blastopore; the yolk plug is visible through the blastopore.

Animal pole

Blastocoel

Archenteron begins to form

Blastocoel displaced

Archenteron

Archenteron (future digestive tract)

Ectoderm

Mesoderm

Mesoderm (notochord)

Dorsal lip of blastopore

Vegetal pole

Dorsal lip of blastopore

Dorsal lip of blastopore

Endoderm

Ventral lip of blastopore

Yolk plug

FIGURE 38.10 Gastrulation in a Frog Embryo The colors in this diagram are matched to those in Figure 38.3, the frog fate map.

Go to ANIMATED TUTORIAL 38.1
Gastrulation
PoL2e.com/at38.1

Go to MEDIA CLIP 38.1
Frog Gastrulation Time-Lapse
PoL2e.com/mc38.1

Chick embryo viewed
from above

Flattened blastodisc
Yolk
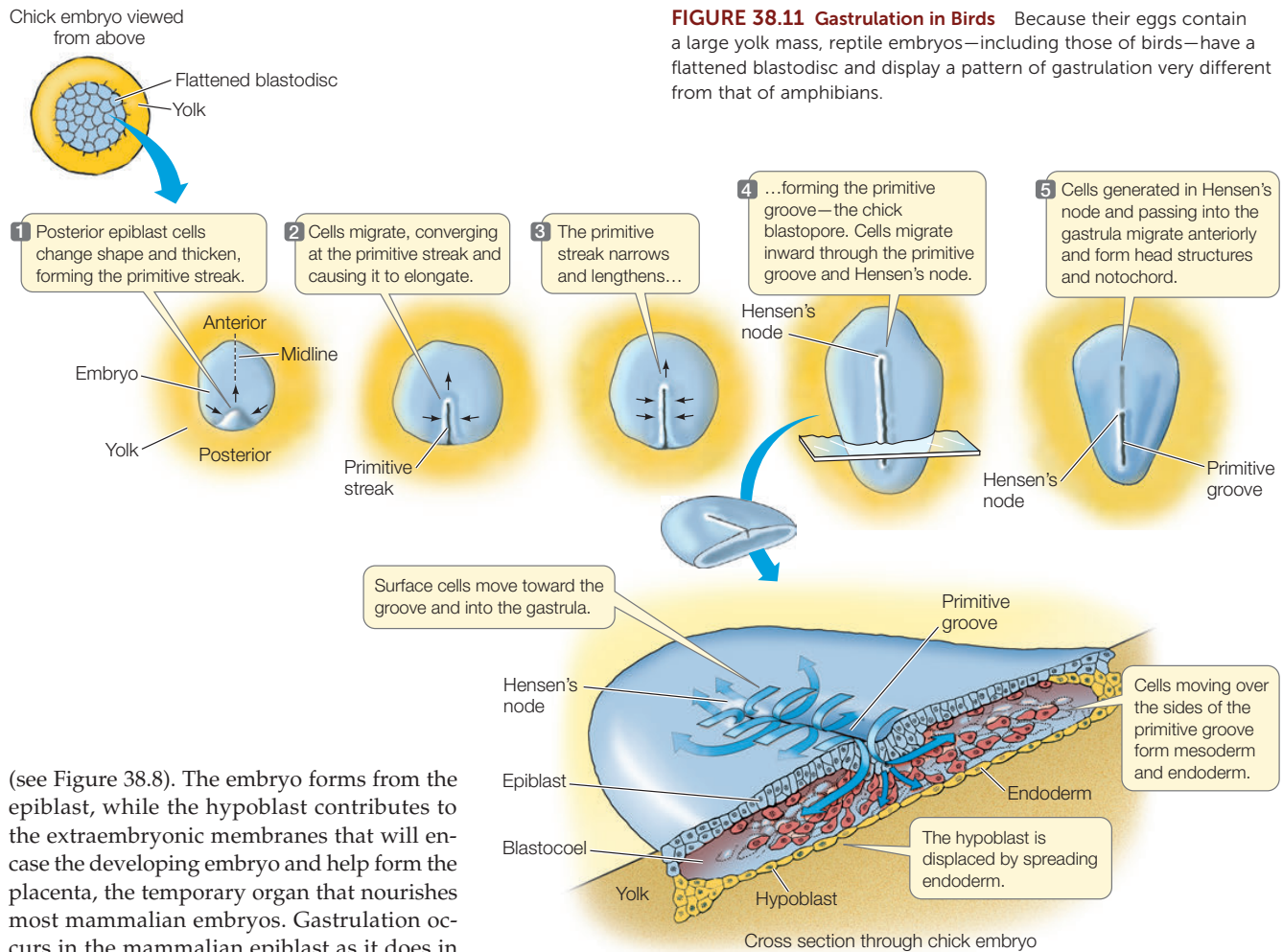
FIGURE 38.11 Gastrulation in Birds Because their eggs contain a large yolk mass, reptile embryos—including those of birds—have a flattened blastodisc and display a pattern of gastrulation very different from that of amphibians.

1 Posterior epiblast cells change shape and thicken, forming the primitive streak.

2 Cells migrate, converging at the primitive streak and causing it to elongate.

3 The primitive streak narrows and lengthens…

4 …forming the primitive groove—the chick blastopore. Cells migrate inward through the primitive groove and Hensen's node.

5 Cells generated in Hensen's node and passing into the gastrula migrate anteriorly and form head structures and notochord.

Anterior
Midline
Embryo
Yolk
Posterior

Primitive
streak

Hensen's
node

Hensen's
node

Primitive
groove

Surface cells move toward the groove and into the gastrula.

Primitive
groove

Hensen's
node

Cells moving over the sides of the primitive groove form mesoderm and endoderm.

Epiblast

Endoderm

Blastocoel

The hypoblast is displaced by spreading endoderm.

Yolk

Hypoblast

Cross section through chick embryo

(see Figure 38.8). The embryo forms from the epiblast, while the hypoblast contributes to the extraembryonic membranes that will encase the developing embryo and help form the placenta, the temporary organ that nourishes most mammalian embryos. Gastrulation occurs in the mammalian epiblast as it does in the avian epiblast. A primitive groove forms, and epiblast cells migrate through the groove to become layers of endoderm and mesoderm.

All three types of gastrulation described above can be found among the protostomes, but recall that there is a major difference in the fate of the blastopore. In protostomes, the blastopore (the first opening) becomes the mouth and the anus forms at some distance away; in deuterostomes, the blastopore becomes the anus, and the mouth breaks through secondarily. This is why animals are called protostomes ("mouth first") or deuterostomes ("mouth second").

LINK

For more on the differences between protostomes and deuterostomes, see **Concept 23.1**

Gastrulation results in the production of the three germ layers and sets the stage for the formation of the **coelom**, a space completely enclosed in mesoderm. Your body cavity—the space between the gut and body wall—is a coelom (see Concept 23.1). Because of the coelom, gut contractions and heartbeats are independent of an animal's outer body wall. To

understand the formation of the coelom, it is best to consider the mesoderm and coelom together.

In deuterostomes, the mesoderm often forms from the archenteron wall, and the coelom develops within in it, sometimes as a direct out-pouching of the archenteron (**FIGURE 38.12A**). This type of mesoderm and coelom formation is believed to be characteristic of deuterostomes, although it may be highly modified by yolk and other factors.

Protostomes show a different pattern that fits with the fact that specific blastomeres usually give rise to each tissue and organ (mosaic development). For example, in the snail *Ilyanassa*, one recognizable small blastomere, 4d, forms the bulk of the mesoderm. This single cell (4d) received information directing production of mesoderm from the polar lobe (see Figure 38.4), undergoes divisions and forms most of the mesoderm. The coelom forms as a split in the prospective mesoderm cells (**FIGURE 38.12B**).

Whatever the mechanism of gastrulation, the process produces an embryo with three germ layers—ectoderm, endoderm and mesoderm—that are positioned to influence one another through tissue interactions.

(A)

(B)
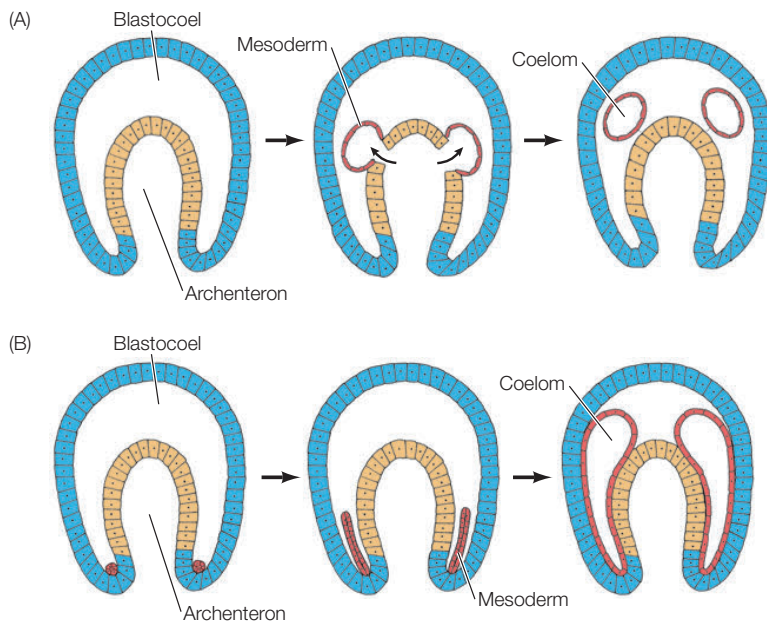
FIGURE 38.12 Formation of the Coelom Non-yolky eggs of deuterostomes and protostomes form their coeloms in different ways. (A) In deuterostomes, the coelom often forms as an out-pouching of the archenteron. (B) In protostomes, it forms as a split in the mesoderm.

CHECKpoint   CONCEPT 38.3

✓ What does the blastopore become in protostomes? What does it become in deuterostomes?

✓ What are the major similarities and differences between sea urchin gastrulation and frog gastrulation?

✓ Why is the primitive streak in the chick embryo the equivalent of the blastopore?

✓ Contrast mesoderm formation in the non-yolky eggs of a deuterostome such as a starfish with those of a protostome such as a snail. Compare coelom formation in these two groups.

Following gastrulation and the subsequent formation of three germ layers, an embryo is ready to start forming the organs of the new individual. Let's now look at that key process.

CONCEPT 38.4 Gastrulation Sets the Stage for Organogenesis and Neurulation in Chordates

Organogenesis refers to the phase in development in which all of the organs and organ systems form. We will discuss the organs sequentially, but keep in mind that in an actual embryo, the processes of organogenesis occur simultaneously. Here we focus on organogenesis principally in the chordates, the large clade that includes the vertebrates and all other animals that possess a notochord. These animals also possess a dorsal nerve

cord with a central cavity—a defining chordate characteristic (see Figure 16.4). The nerve cord and brain form by a process known as **neurulation**.

Each of the embryo's three germ layers gives rise to a defined set of tissues and organs:

• Ectoderm, the outer germ layer, forms the epidermis of the skin and structures such as hair, claws, and sweat glands, the brain and all of the nervous system, and pigment cells that provide color to skin, hair, feathers, and more.

• Endoderm, the innermost germ layer, produces the lining of the digestive tract and the organs that arise from it, among them the lungs, liver, pancreas, and gall bladder.

• Mesoderm, the middle layer that surrounds the coelom, gives rise to the notochord, heart, blood and blood vessels, urogenital system, muscles, bones, and the dermis (the inner layer of the skin). In vertebrates, the dermis interacts with the overlying ectoderm (the epidermis) to produce many structures, including scales, teeth, hair, feathers, horns, sweat glands, and mammary glands.

Taking a big-picture view, the basic body plan can be seen as a tube within a tube. The outer tube, arising from ectoderm and mesoderm, is the body wall. The inner tube, arising from endoderm and mesoderm, is the gut. In between is the coelom. The major organs and organ systems develop as elaborations of this basic plan.

As development proceeds, cells become recognizable as belonging to a particular type (neurons, blood cells, liver cells and so on). When a cell displays its final specialized characteristics, it is said to be **differentiated**. Differentiation takes place gradually throughout development and often into adult life. For example, mammalian red blood cells contain hemoglobin and lack nuclei. Old red blood cells are replaced continuously throughout the animal's life as new cells are produced and differentiate.

The notochord induces formation of the neural tube

In many chordates, some of the cells that move through the blastopore during gastrulation separate from the roof of the archenteron (**FIGURE 38.13**) and form the notochord (see Figure 23.35). In amphibians, for example, these are cells from the dorsal blastopore lip. In addition to providing structural support, the notochord plays a critical role during development because it induces the overlying ectoderm to form the dorsal nerve cord. **Induction** refers to the ability of one tissue to direct or lead another along a specific pathway of development. We now know that this is done by chemical signaling. Induction is one of the most important mechanisms in biology. It probably takes place in all animals and plays a role in the formation of most organ systems.

LINK

Some of the molecular mechanisms of induction are discussed in **Concept 14.2**; see especially **Figure 14.9**
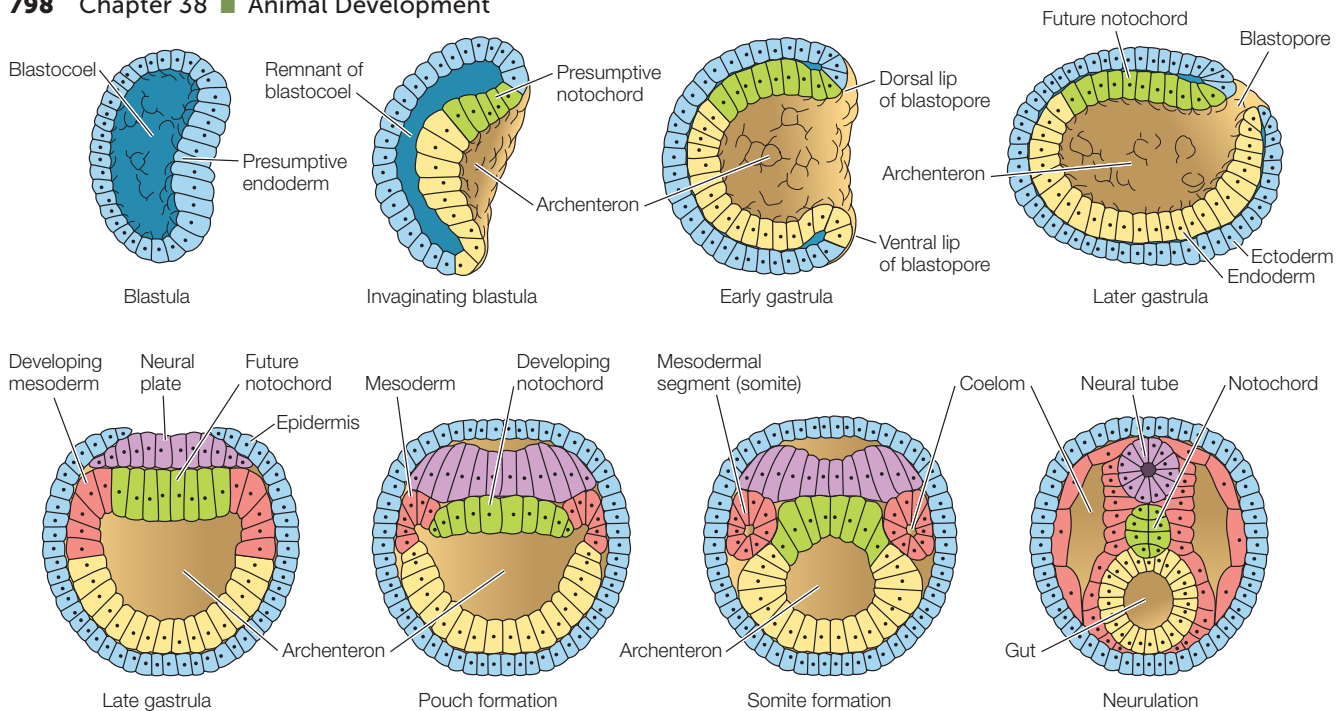
FIGURE 38.13 Gastrulation, Mesoderm Formation, and Neuru-lation in the Lancelet Amphioxus, a Non-vertebrate Chordate
In these classic descriptions (by Edwin Grant Conklin and Berthold Hatschek), the formation of tissue layers in a non-yolky chordate egg is clearly seen. Bottom row depicts sections of embryos cut at right angles to those in the top row.

Under the influence of the developing notochord, a portion of the dorsal ectoderm flattens and begins to roll up, forming first a neural plate and then a neural groove. When the edges of the groove grow together, they fuse to form the neural tube, and ectoderm closes over them. At its anterior end, the vertebrate neural tube forms three swellings, which will become the major divisions of the adult brain: the **hindbrain**, **midbrain**, and **forebrain**. The rest of the neural tube will become the spinal cord. If the neural tube does not close properly, serious problems result. Examples in humans include spina bifida (an opening in the spine that allows the spinal cord to protrude) and anencephaly (absence of a major portion of the brain).

APPLY THE CONCEPT

Gastrulation sets the stage for organogenesis and neurulation in chordates

What about the amphibian dorsal blastopore lip makes it so crucial to "organizing" the three germ layers? The distribution of β-catenin in the late blastula corresponds to the location of this organizer in the early gastrula. A series of experiments endeavored to ascertain whether β-catenin is "necessary and sufficient" for subsequent functions of the organizer. Review the results of these experiments in the table and answer the questions.

1. Which experiment shows that β-catenin is *necessary* for induction of the organizer? Explain.

2. Which experiment shows that β-catenin is *sufficient* (enough) for induction of the organizer? Explain.

3. What was the purpose of experiment B? Of experiment D?

4. This series of experiments demonstrates what is sometimes called the "find it, lose it, move it" approach to understanding a gene's function. Explain why this catchy phrase is appropriate.

EXPERIMENT	RESULT
A. "Knock out" β-catenin by injecting β-catenin antisense mRNA into frog egg (see Figure 13.9).	Dorsal lip of blastopore does not form.
B. Repeat experiment A, but follow injection of antisense mRNA with an injection of exogenous (i.e., from an external source) β-catenin protein into the egg.	Gastrulation is normal.
C. Inject exogenous β-catenin into ventral region of an early gastrula (where β-catenin does not normally occur).	A second site of gastrulation is stimulated, producing results similar to those of Spemann and Mangold (see Figure 38.14).
D. Repeat experiment C, but follow exogenous β-catenin with β-catenin antisense mRNA injected into same area.	Gastrulation is normal, occurring only at original site

Much of our understanding of induction comes from work that began on amphibian embryos in the early twentieth century and has continued since. When Hans Spemann and his student Hilde Mangold were studying the dorsal lip of the blastopore in frog eggs, they transplanted this region to another embryo at the same stage of development. The results were momentous. This small piece of tissue stimulated a second site of gastrulation, and a second complete embryo formed (**FIGURE 38.14**). Because the dorsal blastopore lip of amphibians was apparently capable of inducing host tissue to form an entire embryo, Spemann and Mangold dubbed it the **organizer**, and its action became known as primary embryonic induction. We now know that the dorsal blastopore lip is not responsible for the first inductive event in development, but because of its extreme importance, it is still referred to as the organizer. For more than 80 years, the organizer has been an active area of research. Hensen's node, which we discussed in Concept 38.3, acts as an organizer in birds, and a homologous region does so in mammals.

Molecular biologists are making great strides in working out the molecular mechanisms of the organizer. Thanks to a series of experiments in the 1980s and 1990s, we now know that the transcription factor β-catenin plays a key role in determining which cells become the organizer. It does this by triggering a complex series of interactions between various transcription factors and growth factors that control gene expression. Several of these transcription factors have been identified.

During the last century, clever experiments revealed the source and approximate molecular size of many inductive factors. Now, modern techniques are enabling scientists to determine the identity of many such molecules. One of the best-studied examples is the induction of the dorsal nerve cord in amphibians.

The development of the central nervous system depends on the activation of a specific genetic cascade within certain ectodermal cells that will become neuronal instead of epidermal. Work on amphibian embryos has shown that specific polypeptides released from the developing notochord act as inducers that control this activation. Two of these polypeptides that induce the formation of the neural tube are appropriately named Noggin and Chordin. They act, not by direct activation of genes, but rather by inhibiting the activity of another substance, the TGF-β bone morphogenetic protein BMP4 (**FIGURE 38.15**). Among its many actions, BMP4 induces the ectoderm to form epidermis. In the absence of BMP4, ectoderm forms neural tissue. By blocking the effect of BMP4, Chordin and Noggin allow the ectoderm to carry out its "default" differentiation of becoming neural.

INVESTIGATION

FIGURE 38.14 The Dorsal Lip Induces Embryonic Organization   In a classic experiment, Hans Spemann and Hilde Mangold transplanted the dorsal blastopore lip mesoderm of an early gastrula stage salamander embryo. The results showed that the cells of this embryonic region, which they dubbed "the organizer," could direct the formation of an entire embryo.[a]

HYPOTHESIS

Cytoplasmic factors in the early dorsal blastopore lip organize cell differentiation in amphibian embryos.

METHOD

1. Excise a patch of tissue from above the dorsal blastopore lip of an early gastrula stage salamander embryo (the donor).
2. Transplant the donor tissue onto a recipient embryo at the same stage. The donor tissue is transplanted onto a region of ectoderm that should become epidermis (skin).

RESULTS

2 …and a second set of dorsal neural structures forms in the recipient embryo.

1 The donor tissue induces a secondary invagination…

3 Eventually a complete secondary embryo forms, attached to the original embryo at the belly.
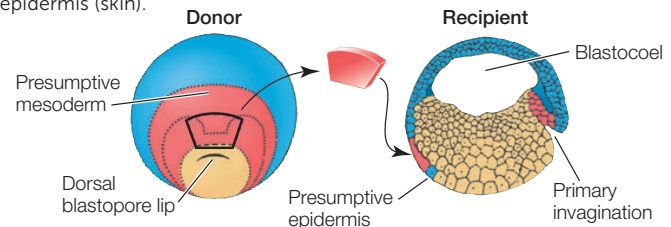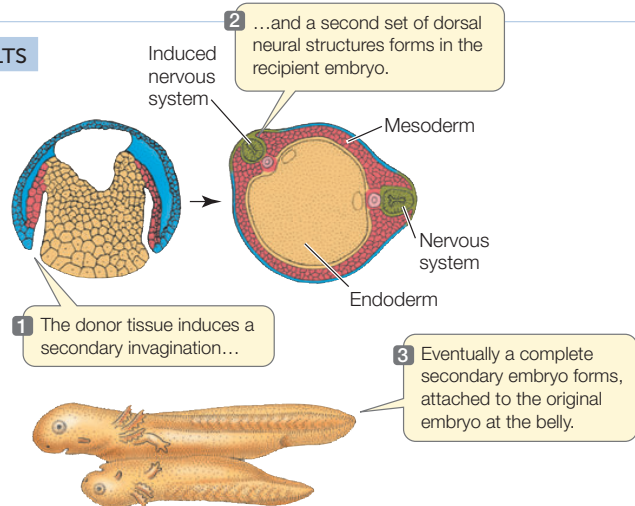
CONCLUSION

The cells of the dorsal blastopore lip can induce other cells to change their developmental fates.

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]H. Spemann and H. Mangold. 1924. *Roux' Arch. Entw. Mech.* 100: 599–638. Viktor Hamburger's translation appeared in *Foundations of Experimental Embryology*, 1964, (B.H. Willier and J.M. Oppenheimer, eds.), pp. 146–184.

Go to ANIMATED TUTORIAL 38.2
Tissue Transplants Reveal the Process of Determination
PoL2e.com/at38.2

INVESTIGATION

FIGURE 38.15 Differentiation Can Be Due to Inhibition of Transcription Factors When organizer cells involute to underlie dorsal ectoderm along the embryo midline, that overlying ectoderm becomes neural tissue rather than skin (epidermis). But do the organizer cells cause dorsal ectoderm to become neural tissue, or do they *prevent* this ectoderm from becoming skin?[a]

HYPOTHESIS

The default state of amphibian dorsal ectoderm is neural; it is induced by underlying mesoderm to become epidermis.

METHOD

1. Excise animal caps (presumptive ectoderm) from amphibian blastulas. Culture presumptive mesodermal cells from early gastrulas and extract BMP4. BMP4 is a growth factor released from the notochord that induces overlying ectoderm to become skin.
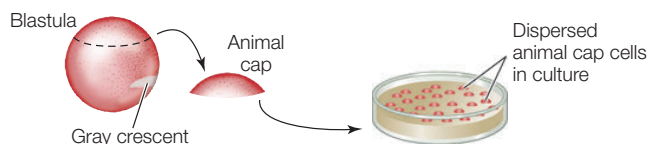
2. Prepare four separate cultures of embryonic ectodermal cells. Incubate with no additions (control); with BMP4 from step 1; with a BMP4 inhibitor; and with both molecules.
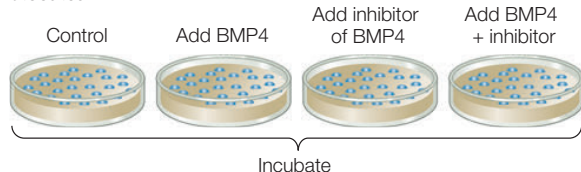
3. After incubation, extract mRNAs from the cultured ectodermal cells and run on gels to reveal expression of NCAM (a neural tissue marker) and keratin (an epidermal tissue marker).

RESULTS

Gels reveal that different treatments with BMP4 and its inhibitor alter patterns of gene expression in cultured ectodermal cells.
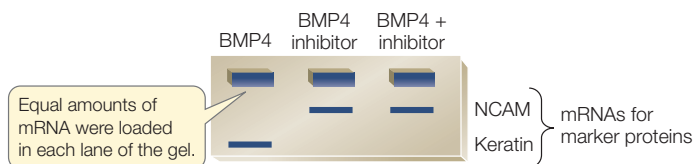
CONCLUSION

The organizer cells secrete an inhibitor of BMP4.

ANALYZE THE DATA

Use the gel results shown above to answer the questions.

A. Does BMP4 induce expression of neural-specific or epidermal-specific genes?

B. Does BMP4 block any gene expression in the ectodermal cells?

C. What is the evidence that BMP4 has an inductive and/or an inhibitory effect on gene expression in ectodermal cells?

D. Do these results support the hypothesis?

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]P. A. Wilson and A. Hemmati-Brivanlou. 1995. *Nature* 376: 331–333.

Another important factor controlling differentiation of the neural tube is Sonic hedgehog, symbolized Shh, the transcription factor mentioned at the start of this chapter. Shh is released by the notochord and diffuses into the ventral region of the neural tube, where it directs the development of this region into the ventral structures and circuits of the spinal cord. These circuits will carry the major output from the motor pathways of the nervous system.

LINK

Sonic hedgehog also plays an important role in the development of vertebrate limbs; see **Concept 14.3**

As the neural tube is closing, certain cells dissociate from it and come to lie between the neural tube and the overlying epidermis. These are known as **neural crest cells** (**FIGURE 38.16**). They are star-shaped cells that are termed "pluripotent" because they can differentiate in many different ways. Neural crest cells migrate extensively and have amazing developmental capacities. Not only do they form sensory neurons and major parts of the autonomic nervous system, but they are also responsible for most of the skull bones, the pigment cells, and many other structures. Without neural crest cells, vertebrates would not have heads, as we recognize them.

Mesoderm forms tissues of the middle layer

On either side of the forming notochord, three regions of mesoderm can be recognized—**somites**, **intermediate mesoderm**, and **lateral plate mesoderm** (see Figure 38.16). The vertebrate body plan, like that of annelids and arthropods, consists of repeating segments that are modified during development. These segments are first seen as the blocks of cells known as somites (**FIGURE 38.17**; also see Figure 38.16), then later as the repeating patterns of vertebrae, ribs, nerves, and muscles along the anterior–posterior axis as differentiation proceeds.

Somites form bones, cartilage, skeletal muscle, and the dermis of the skin.

Intermediate mesoderm forms much of our urinary and reproductive system.

Lateral plate mesoderm surrounds the coelom and lines the vertebrate body cavity (the peritoneal cavity). The peritoneal cavity makes up much of the coelom. The thin tissue layer that surrounds the peritoneal cavity is the peritoneum. (You may have heard of peritonitis, a severe inflammation of the covering of the internal organs. A major cause is the entry of bacteria into the peritoneal cavity, as occurs when an appendix ruptures.) The inner layer of

(A)

Neural crest cells
Somite
Neural tube
Intermediate mesoderm
Notochord
Archenteron
Surface ectoderm
Lateral plate outer layer
Coelom
Lateral plate inner layer
Yolky endoderm

(B)

Neural plate
Future neural crest cells
Neural tube
Neural crest cells

(C) Before closure

(D) After closure

Neural tube   Epidermis

Somite   Notochord   Coelom
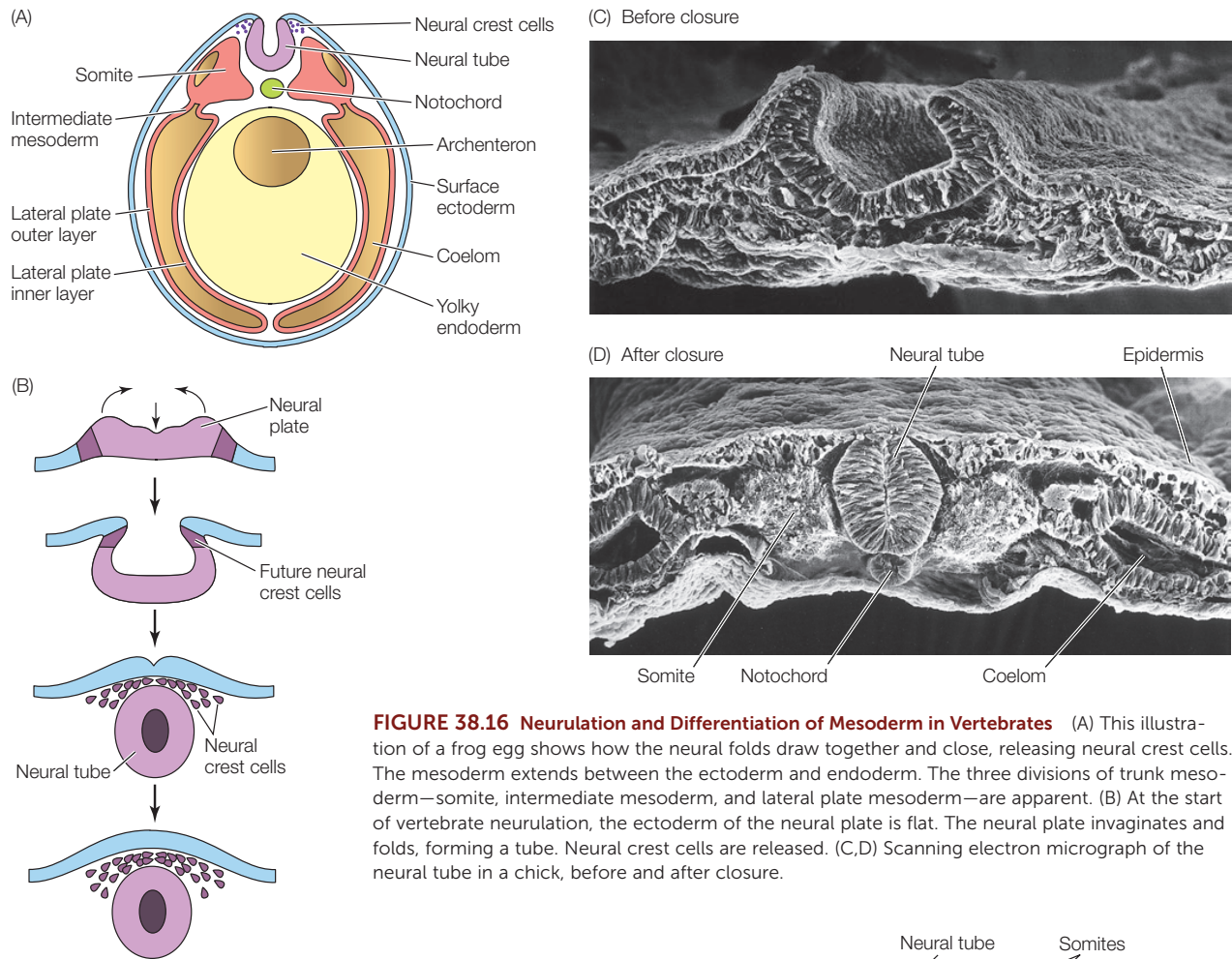
FIGURE 38.16 Neurulation and Differentiation of Mesoderm in Vertebrates (A) This illustration of a frog egg shows how the neural folds draw together and close, releasing neural crest cells. The mesoderm extends between the ectoderm and endoderm. The three divisions of trunk mesoderm—somite, intermediate mesoderm, and lateral plate mesoderm—are apparent. (B) At the start of vertebrate neurulation, the ectoderm of the neural plate is flat. The neural plate invaginates and folds, forming a tube. Neural crest cells are released. (C,D) Scanning electron micrograph of the neural tube in a chick, before and after closure.

lateral plate mesoderm lies close to the endoderm. It forms part of the peritoneum, the muscles of the digestive tract, and most of the circulatory system, including the heart. The outer layer of lateral plate mesoderm lies adjacent to the ectoderm and forms part of the peritoneum and some of the muscle of the body wall (see Figure 38.16).

CHECKpoint   CONCEPT 38.4

✓ What two major mechanisms are responsible for determining the differentiated state of a cell?

✓ What is the role of the notochord in neurulation?

✓ A chordate synapomorphy (a shared derived trait) is a hollow dorsal nerve chord (see Concept 23.5). How does the process of neurulation explain why the spinal cord has a central cavity?

✓ What major tissues does ectoderm form? What three major mesodermal regions form in chordates, and what does each form?

Neural tube   Somites

Mesodermal tissue (will become somites)
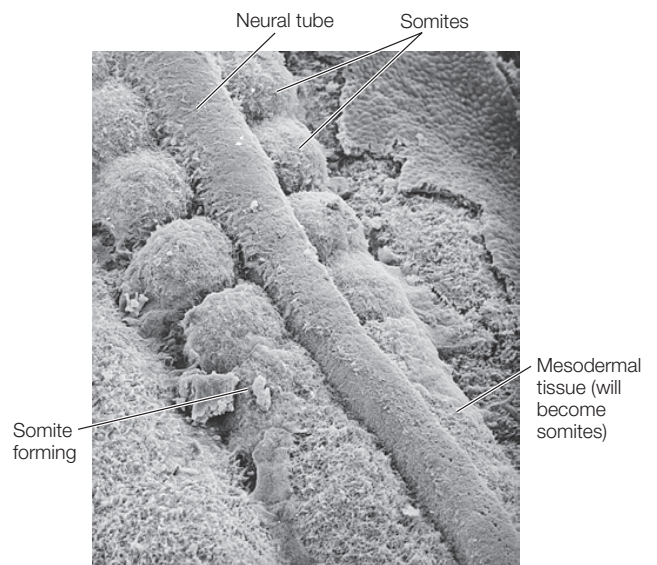
Somite forming

FIGURE 38.17 Body Segmentation In this scanning electron micrograph of somite formation in a chick embryo, the overlying ectoderm has been removed and the neural tube and somites are seen from above. Skeletal muscle, cartilage, bone, and the lower layer of the skin form from the somites.

We have seen how the three germ layers form the organs and tissues of the vertebrate embryo. Next we will focus on how they also protect and nourish the embryo in many of the animals with which you are most familiar.

CONCEPT 38.5 Extraembryonic Membranes Protect and Nourish the Embryo

A major step in the evolution of tetrapods (four-limbed vertebrates) was the formation of the amniotic egg, seen today in mammals and reptiles, including birds. We saw in Concept 23.6 the significance of this egg. It provides the embryo with a contained aqueous environment, freeing the processes of reproduction and development from dependence on an external water supply. The three germ layers that form the embryo also create the membranes that provide this protective environment.

Extraembryonic membranes form with contributions from all germ layers

Whether they develop inside or outside the mother's body, embryos of amniotes are surrounded by four **extraembryonic membranes** that function in protection, nutrition, gas exchange, and waste removal. The chicken embryo provides a good example, but the process is similar in other reptiles and in egg-laying mammals. (We will discuss placental mammals in the next section.) The four membranes are the yolk sac, allantois, amnion, and chorion (**FIGURE 38.18**).

- The **yolk sac** forms first, by extension of the endoderm and the inner layer of lateral plate mesoderm (see Figure 38.18A,B). These two layers grow around the yolk and enclose it. The inner layer of lateral plate mesoderm is special because it can form blood cells and blood vessels. The first blood cells of the embryo and the vessels that carry them— the vitelline artery and its branches—form in the mesoderm of the yolk sac. Stored yolk is not transferred directly to the gut of the embryo through the yolk stalk. Rather, it is

FIGURE 38.18 The Extraembryonic Membranes of Amniotes
In birds, other reptiles, and mammals, the embryo constructs four extraembryonic membranes. (A,B) Membrane outgrowth and fusion in 5- and 9-day embryos. (A) Developing amnion and chorion form from ectoderm and endoderm as seen in this 5-day chick embryo. The membranes will fuse when they meet dorsally (arrows), enclosing the embryo in 2 envelopes. The yolk sac and allantois form from endoderm and mesoderm. The yolk sac grows around the yolk (arrows) and the allantois forms a pouch. (B) Membranes surround the embryo in this 9-day embryo. Some will continue to expand as the embryo grows, but the yolk sac shrinks as yolk is used by the embryo. Fluids secreted by the amnion fill the amniotic cavity, providing an aqueous environment for the embryo. The allantois stores the embryo's waste products. The allantoic membrane will become pressed against the chorion and shell and functions in gas exchange between the embryo and its environment. (C) Developing chick in shell showing development of the circulatory system, which is well underway by day 7. Only the yolk sac and the allantois are capable of making blood vessels. As a result, they are involved in nutrient transport and gas exchange.

(A) 5-Day chick embryo (shell removed)

The first extraembryonic membrane is the **yolk sac**, which is forming in the 5-day embryo.

The mesoderm and ectoderm extend beyond the embryo to form the **chorion** and the **amnion**.

(B) 9-Day chick embryo (shell removed)

The mesodermal and ectodermal layers fuse below the yolk so that the chorion lines the shell.

Mesodermal and endodermal tissues form the **allantois**, a sac for metabolic wastes.

(C) 7-Day chick embryo

Go to ACTIVITY 38.1 Extraembryonic Membranes
PoL2e.com/ac38.1

digested by the endoderm of the yolk sac, and the products are transported to the embryo by the developing blood and blood vessels in the yolk sac wall (Figure 38.18C).

- The **allantois**, a sac for storage of metabolic wastes, is also an outgrowth of endoderm and the inner layer of lateral plate mesoderm (Figure 38.18A–C). Because the yolk sac and the allantois are the extraembryonic membranes that contain lateral plate mesoderm, they are the only two that develop blood vessels (Figure 38.18C).

- Ectoderm and the outer layer of the lateral plate mesoderm also grow out from the embryo and surround it (Figure 38.18A). Where they meet, they fuse, forming two membranes, an inner amnion and outer chorion (Figure 38.18B). The **amnion** surrounds the embryo and secretes fluid into the enclosed cavity, providing a protective, shock-absorbing environment.

- The **chorion**, located just beneath the egg's shell, forms a continuous membrane that limits water loss. The chorion cannot make blood vessels, but it fuses with the blood vessel–forming allantoic membrane, forming the chorioallantoic membrane that provides for exchange of O_2 and CO_2 between the embryo and the outside world (Figure 38.18C).

Extraembryonic membranes in mammals form the placenta

In placental mammals, the entire trophoblast becomes embedded in the endometrium of the uterus (see Figure 38.8). Hypoblast cells proliferate to form what in birds would be the yolk sac, even though there is little yolk in the eggs of placental mammals. In eutherian placental mammals, the allantois and chorion combine, forming the chorioallantoic placenta. These embryonic tissues, along with maternal tissue of the uterine wall (the endometrium), produce the placenta. Note that the placenta is a unique organ because it is composed of tissues from two organisms—the mother and her offspring. Interestingly, the yolk sac in mammals continues to be an early site of blood cell production as it is in birds, even though no or very little yolk is present. Meanwhile, the amnion grows around the embryo, enclosing it in a fluid-filled amniotic cavity (**FIGURE 38.19**). (A pregnant woman's "water breaks" when the amnion bursts during labor and releases the amniotic fluid.)

Human gestation is traditionally divided into three periods of roughly 12 weeks each, called trimesters. The first trimester is a time of rapid cell division and tissue differentiation, and the embryo is very sensitive during this time to damage from radiation, drugs, chemicals, and pathogens that can cause birth defects such as those referred to in the opening story of the chapter. By the end of the first trimester, most organs have started to form, and the embryo is about 8 centimeters long. At about this time, the human embryo is medically and legally referred to as a **fetus**.

Fish also make yolk sacs

Many fish also have a very yolky egg (see Figure 38.7B). They are not amniotes, however, so how do they obtain nutrients from this stored material? Embryonic fish produce a yolk sac, but it differs from that of amniotes. As the fish embryo forms, all three germ layers—ectoderm, mesoderm and endoderm—grow around the yolk. The yolk sac becomes vascularized as in amniotes, and materials are carried in the blood vessels to the embryo (**FIGURE 38.20**).
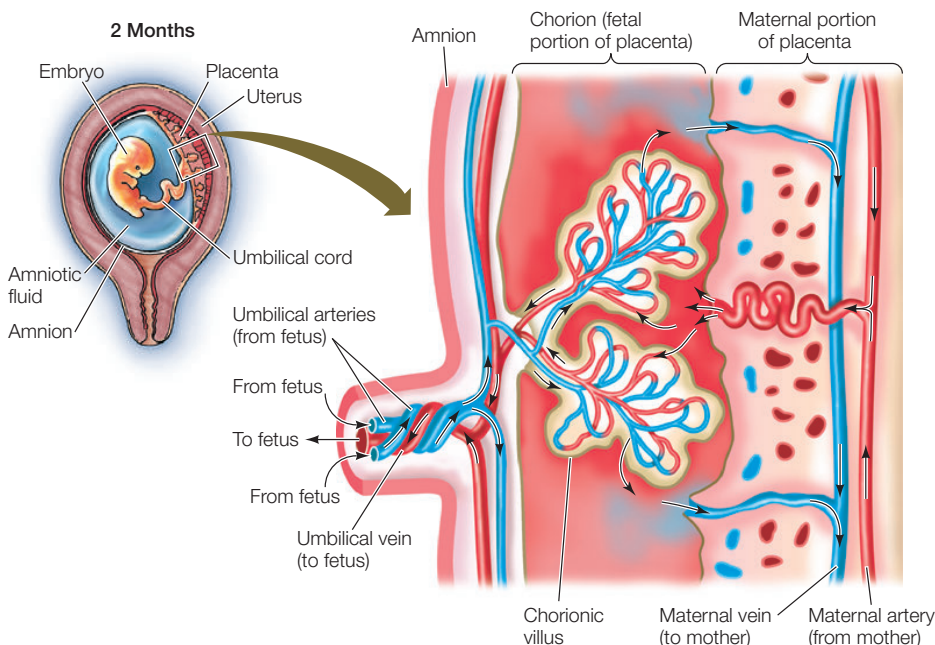
FIGURE 38.19 The Mammalian Placenta   In humans and other placental mammals, nutrients and wastes are exchanged between maternal and fetal blood in the placenta. This organ forms from both fetal tissue and tissues of the mother's uterine wall. The embryo is attached to the placenta by the umbilical cord. Embryonic blood vessels invade the placental tissue to form fingerlike chorionic villi. Maternal blood flows into the spaces surrounding the villi, allowing nutrients and respiratory gases to be exchanged between the maternal and fetal blood.
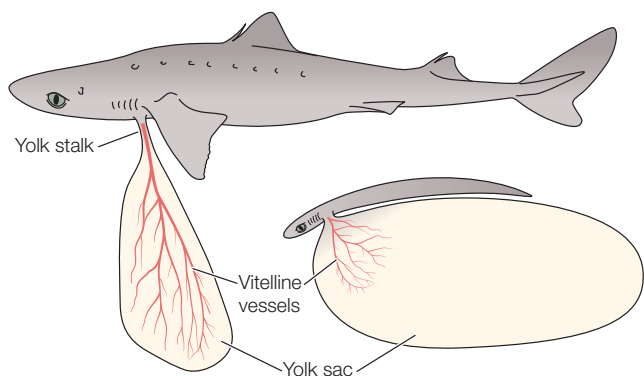
FIGURE 38.20 Fish Yolk Sac   The yolk sac in this developing shark is trilaminar because it is composed of all three tissue layers. Contrast this with the yolk sac of mammals, which forms from just two layers and thus is bilaminar.

CHECKpoint   CONCEPT 38.5

✓ What are the four extraembryonic membranes of a chick embryo? Describe their functions.

✓ Would you expect a frog embryo to have the same extra-embryonic membranes as a lizard? Why or why not?

✓ What function does the yolk sac have in both egg-laying and placental mammals?

✓ The yolk sac of fish is referred to as being trilaminar. Why is this term appropriate? How does a fish yolk sac differ from a chick yolk sac?

✓ What outstanding feature of the placenta makes it a unique organ?

We have now seen how a single-celled zygote becomes a complex organism, but development does not stop at birth or hatching. Animals must grow. For some, growth stops when they reach adulthood. Others grow throughout their lives. In either case, this growth is part of development. We will consider post-embryonic growth next.

CONCEPT 38.6   Development Continues throughout Life

No sexually produced animal is as large as its parent at birth or hatching. All must obtain nourishment and grow. Some animals immediately look like their parents and undergo **direct development** to reach full size. Others appear very different and spend part of their lives as one or more different forms, as they undergo **indirect development**.

A change in the proportions of various parts of an organism relative to one another as a consequence of unequal growth is known as **allometry**. Isometric growth is a 1:1 size increase; allometric growth is any change from this. Allometry is often seen in direct developers as parts of their body change in relative size and shape with growth. For example, at birth a human baby is not a miniature adult. Not only are many of its systems immature, but its overall morphology (form and shape) is also quite different than that of an adult. One difference is the ratio of head to trunk size. A baby's head is much larger in comparison with the rest of its body than an adult's head is, and the head stops growing much earlier in life than the rest of the body (**FIGURE 38.21**). It has been suggested that the large head of infant mammals, especially humans, corresponds to the large brain and development of the cerebral cortex. Many examples of allometry exist. Indeed, nearly all direct developers experience allometric growth of some sort.

Indirect development involves changes in morphology that can be dramatic. Many animals, both protostome and deuterostome, have a larval stage that may be quite unlike the adult.

FIGURE 38.21 Allometric Growth of a Human   Proportions of body parts change as an individual develops from fetus to adult.
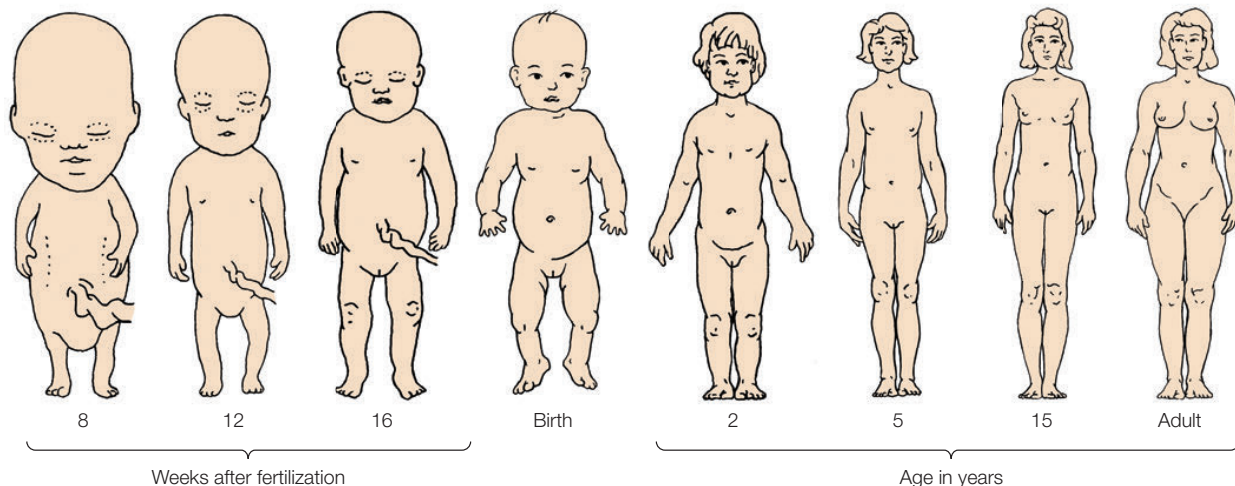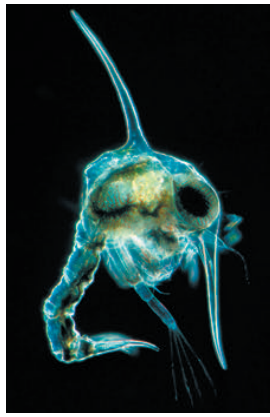
(A) Shore crab (*Carsinus maenas*)

(B) Sea star (*Asterias rubens*)

A familiar example is the monarch butterfly, which has a caterpillar that feeds on the milkweed plant on which its egg was placed, and a winged adult that can migrate from Canada to Mexico. **FIGURE 38.22** shows two larvae with which you might not be familiar.

A larval stage usually performs one of two important roles—or both. Like the caterpillar, it may be primarily a feeding stage. This is seen in animals that provision their eggs with little or moderate yolk resources. Insects, fish, and amphibians are prime examples of this lifestyle. Some adult insects do not feed at all. Ephemeridae—mayflies—last only 1 day as adults. (They are ephemeral, as their name tells us.) They molt from the pupal to adult stage, seek a mate, deposit eggs, and die, relying solely on energy stored by the larva.

Larvae may also play an important role in species distribution. This is especially true in animals in which the adult is sedentary or relatively so. Corals, for example, can reproduce by fragmentation, but new sites are colonized by swimming larvae. Some polychaete worms (capitellids) are rapid colonizers of freshly disturbed, organically rich areas (substrates of polluted harbors and beneath fish farms, oil spills, and whale falls—decaying whale carcasses on the ocean floor) that are widely distributed around the world. Larvae, swimming only with ciliary bands, are carried by currents and then settle in these areas.

When a larva transforms into an adult at metamorphosis, changes can be dramatic, as in the monarch and other butterflies and moths. Major portions of the body may be remodeled or even discarded (see Concept 23.4). Many amphibians lay their eggs in spring, and after quite rapid development, small tadpoles emerge. A tadpole feeds, and its size increases. At metamorphosis, the tadpole shows changes in virtually every system. Tail and gills are resorbed, and limbs grow. In many species, the tadpole stage is herbivorous whereas the adult is carnivorous. Accompanying this change is an alteration of gut length. The gut of a tadpole is actually several times longer than the gut of the small froglet it will become! A tunicate (sea squirt; see Figure 23.35A) tadpole settles and rapidly resorbs its tail, including the notochord and nerve cord. Since the three major chordate characteristics (notochord, hollow dorsal nerve chord, and post-anal tail) are no longer present, the adult tunicate does not resembles a chordate! The larva of the lamprey is so different from the adult that it was once considered a different species. It is still called by the earlier name of "ammocoetes."

CHECKpoint   CONCEPT 38.6

✓ Prior to the Renaissance, painters often depicted infants as miniature adults. Why do these babies not appear natural?

✓ In addition to head size, give another example of allometric growth in humans.

✓ What are two major functions of larvae?

As we have seen, the wonderful process that we recognize as development begins with the fusion of a single egg and a single sperm and continues throughout the entire life of the organism. Although not considered here, the processes of regeneration, wound healing, and aging are all developmental mechanisms. Medical interests in stem cell technology, in wound repair and regeneration, in the prevention of birth defects, and in many other areas, as well as a strong interest in the overlapping field of evolutionary biology, are adding impetus to our desire to understand developmental processes in many organisms. With all of the exciting techniques now available, the door for future studies is wide open.

Q How does the Sonic hedgehog pathway control development of the vertebrate brain and eyes?

ANSWER Sonic hedgehog (Shh) is a transcription factor secreted by the notochord (Concept 38.4). It diffuses to the overlying neural tube, where it induces differentiation of the ventral neural tube into motor neurons and other features of the ventral regions of the spinal cord. Shh also plays different inductive roles at other locations. At the anterior end of the neural tube where the forebrain will develop, the closed neural tube undergoes reciprocal inductive tissue interactions with the overlying ectoderm. Signaling molecules from the neural tissue induce the ectoderm to form the lens of the eye, and the developing lens produces signaling molecules that induce the underlying neural tissue to form an optic cup that will differentiate into the retina.

But why do these events happen bilaterally? Mesoderm that lies anterior to the notochord produces and releases Shh, as does the notochord. Shh induces the ventral region of the anterior neural tube to differentiate into the structures of the forebrain. One of the actions of Shh is to inhibit a transcription factor called Pax6 that is expressed by the neural tissue. Pax6 is essential for determination of the eye field (i.e., tissues that can form eyes; see Figure 14.22). The midline expression of Shh splits the eye field into two and also enables the forebrain to develop into left and right hemispheres.

When environmental factors affect the action of Shh, holoprosencephaly can result. When pregnant cows or sheep graze on *Veratrum californicum* at certain critical points in gestation,

FIGURE 38.23 Environmentally Induced Holoprosencephaly A stillborn lamb born of a ewe that grazed on corn lily leaves. Alkaloids in the plant interfered with the Sonic hedgehog signaling pathway in the embryo, resulting in fusion of the cerebral hemispheres and the formation of a single eye.

the embryo is exposed to cyclopamine and the Shh signaling pathway is blocked. Depending on when the exposure occurs, bilateral development of the forebrain may not take place, resulting in holoprosencephaly and cyclopia (**FIGURE 38.23**). Another area of great interest for humans is the observation that Shh requires cholesterol to be an effective signal. Abnormally low levels of cholesterol during pregnancy (such as might occur with the use of certain statin drugs) could cause some aspects of holoprosenecephaly.

SUMMARY

CONCEPT 38.1 Fertilization Activates Development

- One sperm and only one sperm must fertilize an egg. Fertilization activates the egg.
- Egg and sperm make different contributions to the **zygote**. The egg contributes a haploid nucleus, most of the molecular machinery for cell division, energy production, and growth (yolk, mitochondria, ribosomes, etc.), as well as informational molecules such as transcription factors and mRNAs. The sperm contributes its nuclear material and usually its centrosome, the major microtubule-organizing center.
- Cytoplasmic contents of the egg often are not distributed uniformly. Nutrient molecules, usually in yolk granules, are often found in the **vegetal hemisphere**. In amphibians, rearrangement of **cytoplasmic determinants** at fertilization establishes the major axes of the future embryo. **Review Figures 38.1 and 38.2**
- Fusion of egg and sperm nuclei produces a single-celled, diploid zygote.

CONCEPT 38.2 Cleavage Creates Building Blocks and Produces a Blastula

- **Cleavage** is a period of rapid cell division without cell growth. Usually, little if any gene expression occurs during cleavage. Cleavage can be complete or incomplete. It results in a ball or mass of cells called a **blastula**. **Review Figures 38.3 and 38.4**
- Cell membranes that form during cleavage segregate cytoplasmic determinants into different blastomeres.
- Some species undergo **mosaic development**, in which the fate of each cell is already determined at first division. Other species, including vertebrates, undergo **regulative development**, in which cell fates become determined later.
- **Radial cleavage** and **spiral cleavage** patterns are different. Both describe complete cleavage. Radial cleavage is the basal deuterostome pattern. Spiral cleavage occurs only in protostomes.
- The amount of yolk influences cleavage. Eggs with little yolk undergo complete cleavage. Very yolky eggs often undergo incomplete cleavage, so that part of the cytoplasm remains undivided.

SUMMARY   (*continued*)

■ Early cell divisions in eutherian mammals are unique. These cell divisions produce a **blastocyst** composed of an **inner cell mass** that will become the embryo and an outer layer of cells called the **trophoblast**. The trophoblast helps the embryo implant into the uterine wall. **Review Figure 38.8**

CONCEPT 38.3   Gastrulation Produces a Second, then a Third Germ Layer

■ **Gastrulation** involves massive cell movements during which cells move from the outside to the inside of the embryo. It produces three germ layers and places cells from various regions of the blastula into new associations with one another. **Review Figure 38.9**

■ The initial step of gastrulation is inward movement of certain blastomeres. The site of inward movement becomes the blastopore. Cells that move into the blastula become the endoderm and mesoderm; cells remaining on the outside become the ectoderm. **Review Figures 38.9 and 38.10 and ANIMATED TUTORIAL 38.1**

■ Gastrulation in reptiles, including birds, differs from that in sea urchins and frogs because the blastula forms as a flattened disc of cells atop the yolk. **Review Figure 38.11**

■ Although their eggs have very little yolk, placental mammals have a pattern of gastrulation similar to that of birds and other reptiles.

CONCEPT 38.4   Gastrulation Sets the Stage for Organogenesis and Neurulation in Chordates

■ **Organogenesis** is the process whereby tissues interact to form organs and organ systems.

■ The dorsal lip of the amphibian blastopore is a critical site for cell determination and has been called the **organizer**. **Review Figures 38.14 and 38.15 and ANIMATED TUTORIAL 38.2**

■ In the formation of the chordate nervous system, one group of cells that migrates through the blastopore becomes the notochord. The notochord induces the overlying ectoderm to form the neural tube. **Review Figure 38.16**

■ Preventing the differentiation of ectoderm into epidermis allows ectoderm to become neural tissue.

■ **Neural crest cells** are released from the closing neural tube. Neural crest cells migrate to different regions and form many parts of the vertebrate body—the sensory nervous system, bones of the head, pigment cells, and other structures. **Review Figure 38.16**

■ Mesoderm on either side of notochord forms **somites** that will give rise to muscle, bone, dermis and other tissues, **intermediate mesoderm** that will form urinary and reproductive tissues, and **lateral plate mesoderm** that encloses the coelom and gives rise to the heart, muscles of the digestive system, and other tissues. **Review Figures 38.16 and 38.17**

CONCEPT 38.5   Extraembryonic Membranes Protect and Nourish the Growing Embryo

■ Amniotic eggs contain four **extraembryonic membranes**. In reptiles, including birds, the **yolk sac** surrounds the yolk and provides nutrients to the embryo. The **chorion** lines the eggshell and participates with the allantois in gas exchange. The **amnion** surrounds the embryo and encloses it in an aqueous environment. The **allantois** is a storage sac for metabolic wastes and participates with the chorion in gas exchange (as part of the chorioallantoic membrane).

■ Only the yolk sac and the allantois can develop blood vessels.

■ The first blood cells and blood vessels appear in the yolk sac. **Review Figure 38.18 and ACTIVITY 38.1**

■ In eutherian mammals, the chorion and allantois interact with maternal uterine tissues to form a placenta, which provides the embryo with nutrients and gas exchange. The amnion encloses the embryo in an aqueous environment. **Review Figure 38.19**

■ The yolk sac of fish is trilaminar, meaning it is composed of all three germ layers.

CONCEPT 38.6   Development Continues throughout Life

■ Development continues throughout life. To attain adult size, organisms undergo **direct** or **indirect development**.

■ Not all parts of a body grow at the same rate. Unequal growth that results in differential growth of one body part relative to another is called **allometry**. Most direct developers display allometric growth.

■ Morphologies of adult and larval forms of the same species may be very different. Larval forms serve two major functions—feeding and/or species distribution. **Review Figure 38.22**

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities
PoL2e.com/is38

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39

Immunology: Animal Defense Systems

The siege of Athens by Sparta and its Peloponnesian allies made the city crowded and vulnerable to the spread of an infectious disease.

> As a rule, however, there was no ostensible cause; but people in good health were all of a sudden attacked by violent heats in the head, and redness and inflammation in the eyes, the inward parts, such as the throat or tongue, becoming bloody and emitting an unnatural and fetid breath.

The Athenian historian Thucydides wrote these words in 430 BCE. He was describing a rapidly spreading infectious disease, or plague, that was sweeping the city of Athens in ancient Greece, and would ultimately kill about one-third of its inhabitants.

One year earlier, in 431 BCE, the Spartans had surrounded Athens. Sparta was a rival state with a highly disciplined army, while Athens was near a port and had a powerful navy. The Athenian leader Pericles decided to take advantage of his naval supremacy. He instructed his soldiers to abandon the countryside to the Spartans, relying on the navy to keep the enemies out of the city and to keep the Athenians supplied with food. People living in the countryside poured into Athens.

As Athens became more crowded, deteriorating sanitation and close living conditions resulted in the city becoming an incubator for infectious diseases. In his famous *History of the Peloponnesian War*, Thucydides speculated that this disease came to Athens from Africa. His precise clinical description has provoked great debate among medical historians regarding its nature. In 1994 a burial ground was found near Athens that apparently contained the remains of several dozen people who died of the disease. Samples of dental pulp from the skeletons were examined using the polymerase chain reaction (PCR), and the results revealed the presence of DNA sequences from the bacterium that causes typhoid fever. Based on these results, it was proposed that the disease that killed so many Athenians was typhoid fever. Others disagree, using arguments based on a clinical description of typhoid fever today.

Whatever the cause, another passage from Thucydides (who was one of the few lucky survivors of the disease) is an interesting observation about immunity—the subject of this chapter:

> Yet it was with those who had recovered from the disease that the sick and the dying found most compassion. These knew what it was from experience and now had no fear for themselves; for the same man was never attacked twice, never at least fatally.

Q How can a person survive an infection and be resistant to further infection?

Animals Use Innate and Adaptive Mechanisms to Defend Themselves against Pathogens

Animals have a number of ways of defending themselves against **pathogens**—harmful organisms and viruses that can cause disease. These defense systems are based on the distinction between self—the animal's own molecules—and nonself, or foreign, molecules. Some defensive mechanisms are present all the time. For example, the skin is always present to protect a mammal from invaders. Other defenses are activated in response to invaders. These responses involve three phases:

- *Recognition phase*: The organism must be able to recognize pathogens and discriminate between self and nonself.
- *Activation phase*: The recognition event leads to a mobilization of cells and molecules to fight the invader.
- *Effector phase*: The mobilized cells and molecules destroy the invader.

There are two general types of defense mechanisms:

- **Innate defenses**, or nonspecific defenses, are inherited mechanisms that provide the first line of defense against pathogens. They include physical barriers such as the skin, molecules that are toxic to invaders, and phagocytic cells that ingest invaders. This system recognizes broad classes of organisms or molecules and gives a quick response, within minutes or hours. Some innate defenses are present all the time, whereas others are rapidly activated in response to an injury or invasion by a pathogen. All animals (and plants—see Chapter 28) have innate defenses.

> **LINK**
> Phagocytosis is a form of endocytosis in which a cell engulfs a large particle or another cell; see **Concept 5.4**

- **Adaptive defenses** are aimed at specific pathogens and are activated by the innate immune system. For example, cells in the adaptive defense system can make **antibodies**—proteins that will recognize, bind to, and aid in the destruction of specific pathogens, if the pathogens enter the body. Adaptive defenses are typically slow to develop and long-lasting. Adaptive defenses evolved in vertebrate animals.

Immunity occurs when an organism has sufficient defenses to successfully avoid biological invasion by a pathogen.

Innate defenses evolved before adaptive defenses

All animals have innate defenses against their enemies. For example, the crustacean *Tachypleus tridentatus*—the Japanese horseshoe crab—first appeared in the fossil record about 400 million years ago. It relies only on innate defenses. These defenses include barriers, defensive cells, and defensive molecules.

- Barriers include physical, chemical, and biological mechanisms for resisting infections (see Concept 39.2). The horse-

shoe crab has the hard exoskeleton that is characteristic of arthropods. This shell acts to protect the crab from invasion by pathogens.

Barrier: The first line of innate defense

- Cells involved in innate defenses include phagocytes that bind to microbial pathogens, ingest them by endocytosis, and destroy their large molecules by hydrolysis. Amebocytes in the blood of the horseshoe crab fulfill this defensive role.

Amebocytes

Phagocytes: The second line of innate defense
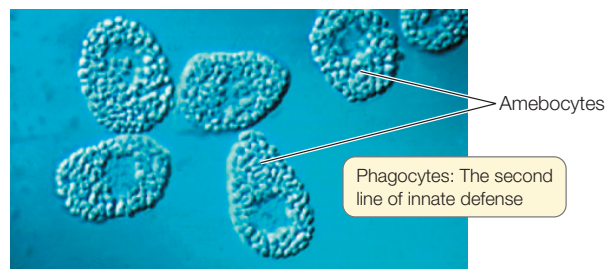
- Molecules that are toxic to invading pathogens are important in innate defense. The horseshoe crab has a wide array of such molecules that are released from cells in its blood. These molecules include peptides that disrupt the bacterial cell membrane, rendering it permeable; and peptides that bind to bacterial surfaces and cross-link them.

Granules contain defense molecules.

Blood cell
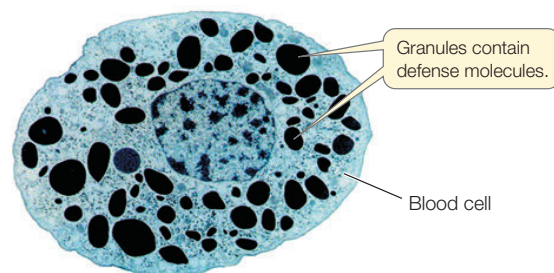
Studies of innate immunity, along with genome sequencing, have revealed that the recognition and activation phases of innate immunity evolved very early in animals. For example, animals as diverse as humans and fruit flies share a class of receptors, called Toll-like receptors, that participate in innate defense responses. In vertebrates, each Toll-like receptor recognizes and binds to a specific molecule that is found in a broad class of pathogens, such as a component of the bacterial cell wall. Binding sets off a signal transduction pathway that ends with the expression of genes for anti-pathogen molecules (**FIGURE 39.1**). This pathway exists in some form in many animal groups, including humans.
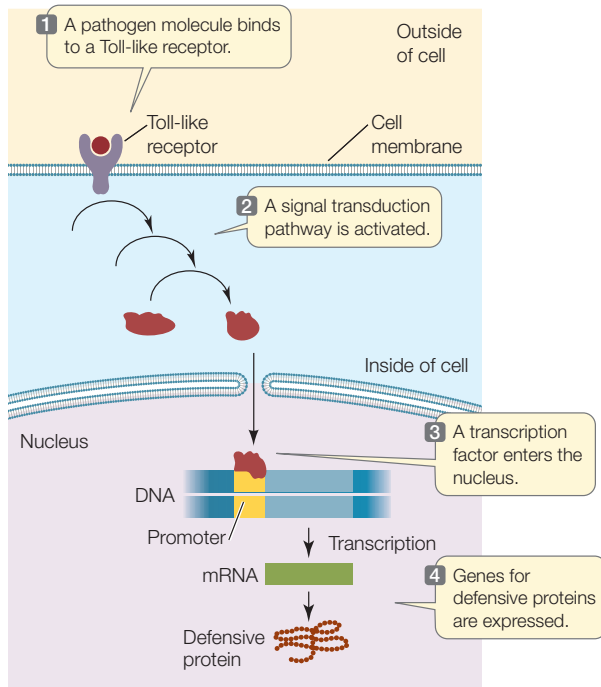
FIGURE 39.1 Cell Signaling and Innate Defense   Binding of a pathogen molecule to a Toll-like receptor initiates a signal transduction pathway that results in the expression of genes involved in innate defense.

Mammals have both innate and adaptive defenses

In mammals and other vertebrates, the innate and adaptive defenses operate together, usually in sequence, as a coordinated defense system. We will focus on these defenses for the rest of the chapter. **TABLE 39.1** gives an overview of innate and adaptive defenses during the course of an infection. Innate defenses are the body's first line of defense; adaptive defenses often require days or even weeks to become effective.

The major players in adaptive immunity are specific cells and proteins. These are produced in the blood and lymphoid tissues and are circulated throughout the body, where they interact with almost all the other tissues and organs.

One milliliter of human blood typically contains about *5 billion* red blood cells and *7 million* white blood cells. Whereas the main function of red blood cells is to carry oxygen throughout the body, **white blood cells** (also called leukocytes) are specialized for various functions in the immune system (**FIGURE 39.2**). There are two major groups of white blood cells: phagocytes and lymphocytes. **Phagocytes** are large cells that engulf pathogens and other substances by phagocytosis. Some phagocytes are involved in both innate and adaptive immunity. In particular, macrophages and dendritic cells play key roles in communicating between the innate and adaptive immune systems. **Lymphocytes** include B cells and T cells, which are involved in adaptive immunity; and natural killer cells, which are involved in both innate and adaptive immunity.

TABLE 39.1   Innate and Adaptive Immune Defenses

Response (time after infection by a pathogen)	System	Mechanisms
Early (0–4 hr)	Innate, nonspecific (first line)	Barrier (skin and lining of organs)
		Dryness, low pH
		Mucus
		Lysozyme, defensins
Middle (4–96 hr)	Innate, nonspecific (second line)	Inflammation
		Phagocytosis
		Natural killer cells
		Complement system
		Interferons
Late (>96 hr)	Adaptive, specific	Humoral immunity (B cells, antibodies)
		Cellular immunity (T cells)

TYPE OF CELL	FUNCTION
Basophils (I)	Release histamine and other molecules involved in inflammation
Eosinophils (A)	Kill antibody-coated parasites
Phagocytes:	
Neutrophils (I)	Stimulate inflammation
Mast cells (I)	Release histamine
Monocytes (I, A)	Develop into macrophages and dendritic cells
Macrophages (I, A)	Antigen presentation
Dendritic cells (I, A)	Present antigens to T cells
Lymphocytes:	
B lymphocytes (A)	Differentiate to form antibody-producing cells and memory cells
T lymphocytes (A)	Kill pathogen-infected cells; regulate activities of other white blood cells
Natural killer cells (I, A)	Attack and lyse virus-infected or cancerous body cells

FIGURE 39.2 White Blood Cells   White blood cells have key roles in both innate (I) and adaptive (A) immunity.

CHECKpoint   CONCEPT 39.1

✓ Make a table that compares innate and adaptive immunity.

✓ If you compared the genomes of an invertebrate (e.g., a crab) and a human with regard to the presence of genes for immunity, what might you find?

Now that we've seen a brief overview of innate and adaptive immunity, let's look at some of the innate defenses that mammals have against invading organisms.

CONCEPT 39.2   Innate Defenses Are Nonspecific

Innate, nonspecific defenses are general protection mechanisms that attempt to either stop pathogens from invading the body or quickly eliminate pathogens that do manage to invade. They are genetically programmed (innate) and "ready to go," in contrast to adaptive, specific defenses, which take time to develop after a pathogen or toxin has been recognized as nonself. In mammals, innate defenses include physical barriers as well as cellular and chemical defenses (**FIGURE 39.3**).

First line of innate defense:
Physical barriers
Skin, mucous membranes, chemicals

Pathogens

Penetration

White blood cell

Proteins

Second line of innate defense:
Cell-derived defenses
Phagocytosis, complement proteins, interferons, inflammation, fever
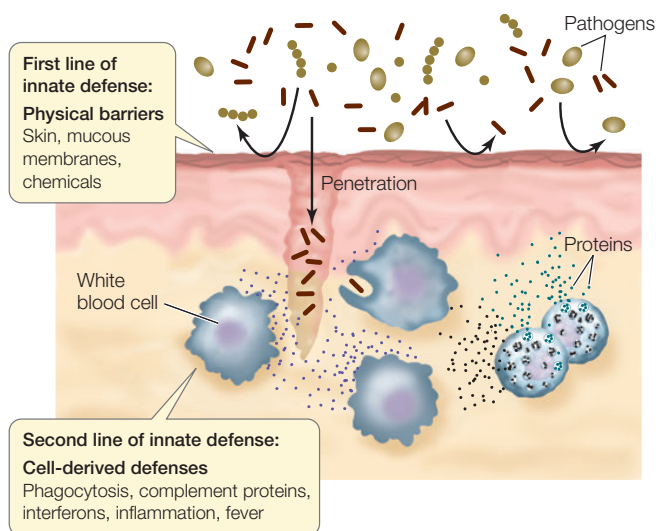
FIGURE 39.3 Innate Defenses   Physical barriers, cells, and proteins (complement and interferons) provide nonspecific defenses against invading pathogens.

Barriers and local agents defend the body against invaders

The first line of innate defense is encountered by a potential pathogen as soon as it lands on the surface of the animal. Consider a pathogenic bacterium that lands on human skin. The challenges (physical, chemical, and biological) faced by the bacterium just to invade the body are formidable:

- *The physical barrier of the skin*: Bacteria rarely penetrate intact skin (which explains why broken skin increases the risk of infection).

- *The saltiness of the skin*: This condition is usually not hospitable to the growth of the bacterium.

- *The presence of normal flora*: Bacteria and fungi that normally live in great numbers on body surfaces without causing disease will compete with potential pathogens for space and nutrients.

If a pathogen lands inside the nose or another internal organ, it faces other innate defenses:

- **Mucus** is a slippery secretion produced by mucous membranes, which line various body cavities that are exposed to the external environment. Mucus traps microorganisms so they can be removed by the beating of cilia (see Concept 4.4, pp. 74–75), which continuously move the mucus and its trapped debris toward the outside of the body.

- **Lysozyme**, an enzyme made by mucous membranes, cleaves bonds in the cell walls of many bacteria, causing them to lyse (burst open).

- **Defensins**, also made by mucous membranes, are peptides of 18–45 amino acids. They contain hydrophobic domains and are toxic to a wide range of pathogens, including bacteria, microbial eukaryotes, and enveloped (membrane-enclosed) viruses. Defensins insert themselves into the cell membranes of these organisms and make the membranes freely permeable to water and all solutes, thus killing the invaders:

Defensin

Cell membrane of pathogen
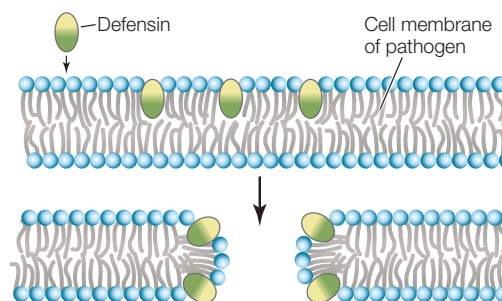
Defensins are also produced inside phagocytes, where they kill pathogens trapped by phagocytosis. Plants also produce molecules that kill pathogens (see Concept 28.1).

- Harsh conditions in the internal environment can kill pathogens. For example, the gastric juice in the stomach is a deadly environment for many bacteria because of the hydrochloric acid and proteases that are secreted into it.

Cell signaling pathways stimulate additional innate defenses

Pathogens that are able to penetrate the body's outer and inner surfaces encounter a second line of innate defenses. These include the activation of defensive cells. In some animals and plants, this activation involves recognition of nonself molecules by a class of receptors called **pattern recognition receptors** (**PRRs**). In mammals, these receptors are mainly present on phagocytes and natural killer cells. The Toll-like receptor shown in Figure 39.1 is an example. The molecules recognized by PRRs are called **pathogen associated molecular patterns** (**PAMPs**). These are molecules that are unique to large classes of microbes, such as bacterial flagellin and fungal chitin. Other well-known PAMPs include bacterial lipopolysaccharide, found in bacterial cell membranes, and nucleic acid variants that are unique to viruses, such as double-stranded RNA. Binding of PAMPs to PRRs stimulates signal transduction pathways that lead to a variety of responses. One response is the production of antimicrobial peptides such as defensins (see above). Other responses include phagocytosis of invading organisms, activation of natural killer cells, activation of the complement system, and production of cytokines.

PHAGOCYTOSIS   Pathogenic cells, viruses, and virus-infected cells can be recognized by phagocytes, which then ingest the invaders by phagocytosis:

Phagocyte

Yeast cell

5 μm
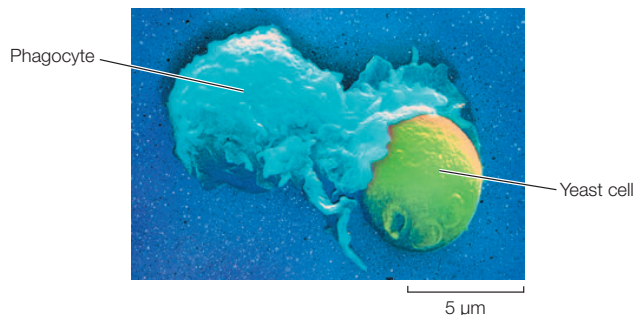
Once inside the phagocyte, the invader is killed either by hydrolysis within the lysosomes (see Figure 4.9) or by defensins.

NATURAL KILLER CELLS   One class of lymphocytes, known as **natural killer cells**, can distinguish between healthy body cells and those that are infected by viruses or have become cancerous. In the latter cases they initiate apoptosis (programmed cell death; see Concept 7.5) in the target cells. In addition to this nonspecific action, natural killer cells interact with the adaptive defense mechanisms by lysing target cells that have been tagged with antibodies.

COMPLEMENT PROTEINS   Vertebrate blood contains more than 20 different proteins that make up the antimicrobial complement system. Once this system has been activated, the proteins function in a characteristic sequence, or cascade, with each protein activating the next:

1. One complement protein binds to components on the surface of an invading cell. This binding helps phagocytes recognize and destroy the invading cell.

2. Another protein activates the inflammation response (see below) and attracts phagocytes to the site of infection.

3. Finally, other proteins lyse the invading cell.

The complement system can be activated by various mechanisms, including the innate and adaptive immune systems. In the latter case, the complement cascade is initiated by the binding of a complement protein to an antibody bound to the surface of the invading cell.

CYTOKINES   **Cytokines** are signaling proteins that are released by many cell types. Cytokines that are produced in response to PRR activation include inflammatory cytokines (some interleukins and tumor necrosis factor; see below) and **interferons**, which help increase the resistance of neighboring cells to infection. Interferons are found in many vertebrates, and their production is induced by a variety of molecules. One such inducer is double-stranded viral RNA; thus interferons are particularly important in defense against viruses. Interferons bind to receptors on the cell membranes of uninfected cells, stimulating a signaling pathway that inhibits viral reproduction if the cells are subsequently infected. In addition, interferons stimulate the cells to hydrolyze bacterial or viral proteins to peptides, an initial step in adaptive immunity.

Inflammation is a coordinated response to infection or injury

When a tissue is damaged because of infection or injury, the body responds with **inflammation**: redness, swelling, and heat near the damaged site, which can then become painful. This response can happen almost anywhere in the body, internally as well as on the outer surface. Inflammation is an important phenomenon: it isolates the area to stop the spread of the damage; it recruits cells and molecules to the damaged location to kill any pathogens that might be present; and it promotes healing.

Among the first responders to tissue damage are **mast cells**, which adhere to the skin and the linings of organs and release numerous chemical signals, including:

- **Tumor necrosis factor**, a cytokine protein that kills target cells and activates immune cells

- **Prostaglandins**, fatty acid derivatives that play roles in various responses, including the initiation of inflammation in nearby tissues

- **Histamine**, an amino acid derivative that increases the permeability of blood vessels to white blood cells and molecules so they can act in nearby tissues

The redness and heat of inflammation result from the dilation of blood vessels in the infected or injured area (**FIGURE 39.4**). Phagocytes enter the inflamed area, where they engulf pathogens and dead tissue cells. Phagocytes are responsible for most of the healing associated with inflammation. They produce several cytokines, which (among other functions) can signal the brain to produce a fever. This rise in body temperature accelerates lymphocyte production and phagocytosis, thereby speeding the immune response. In some cases pathogens are temperature-sensitive, and their growth is inhibited by the

FIGURE 39.4 Interactions of Cells and Chemical Signals Result in Inflammation Histamine and other signals are released from mast cells to initiate the inflammatory response. The chemical signals associated with inflammation attract phagocytes, which digest the pathogens and damaged cells.

4 Phagocytes engulf bacteria and dead cells.

6 Growth factors from white blood cells and platelets stimulate cell division in skin cells, healing the wound.

Splinter

Epithelium

Skin

Bacteria introduced by splinter

Mast cell

Phagocyte

Complement proteins

Dead phagocyte

Blood vessel

1 Damaged tissues attract mast cells which release histamine, which diffuses into the blood vessels.

2 Histamine causes the vessels to dilate and become leaky; complement proteins leave the vessels and attract phagocytes.

3 Blood plasma and phagocytes move into infected tissue from the vessels.

5 Histamine and complement signaling cease; phagocytes are no longer attracted.

Go to ACTIVITY 39.1 Inflammation Response
PoL2e.com/ac39.1

fever. The pain of inflammation results from increased pressure due to swelling, the action of leaked enzymes on nerve endings, and the action of prostaglandins, which increase the sensitivity of the nerve endings to pain. (Recall that in Chapter 3 we described aspirin and how it alleviates pain by blocking the synthesis of prostaglandins.)

Following inflammation, pus may accumulate. Pus is a mixture of leaked fluid and dead cells: bacteria, white blood cells, and damaged body cells. Pus is a normal result of inflammation, and is gradually consumed and further digested by macrophages. If there is a wound, platelets—small, irregularly shaped cell fragments that are present in the blood—aggregate at the wound site. The platelets produce growth factors that stimulate nearby skin cells to divide and heal the wound.

Inflammation can cause medical problems

Although inflammation is generally a good thing, sometimes the inflammatory response is inappropriately strong:

- In an **allergic** reaction, a nonself molecule that is normally harmless binds to mast cells, causing the release of histamine and subsequent inflammation (along with itchy, watery eyes, and rashes in some cases). The nonself molecule may come from food or from the environment—for example, from the surface of a plant pollen grain (as in hay fever) or a particle in dust.

- In **autoimmune diseases** such as rheumatoid arthritis, the immune system fails to distinguish between self and nonself, and attacks tissues in the organism's own body. In these cases the inflammation can be local, attacking an organ, or general, affecting tissues throughout the body.

- In **sepsis**, the inflammation that is due to a bacterial infection does not remain local. Instead it becomes widespread, with the dilation of blood vessels throughout the body. The resulting drop in blood pressure is a medical emergency and can be lethal.

CHECKpoint CONCEPT 39.2

✓ Outline the sequence of innate defenses encountered by a pathogenic bacterial cell if it is ingested in food.

✓ Antihistamines are used to treat the symptoms, such as sneezing, that are due to inflammation caused by irritants in the airways. How do you think antihistamines might work?

✓ A massive inflammation caused by a food allergy can be treated with an injection of epinephrine. Refer to the description of epinephrine's effects in Concept 35.2. How do you think this hormone relieves the inflammation symptoms?

In most instances innate immunity is sufficient to block a pathogen from affecting the body. But many pathogens are present in huge numbers (think of a viral infection), and some may escape the innate defenses and begin to proliferate in the body. In these cases, adaptive immunity takes over.

CONCEPT 39.3 The Adaptive Immune Response Is Specific

Long before the twentieth century, scientists suspected that blood was somehow involved in immunity against pathogens, but they did not have definitive experimental evidence for this. More than a century ago, Emil von Behring and Shibasaburo Kitasato at the University of Marburg in Germany performed a key experiment that suggested that blood contained important factors for adaptive immunity (**FIGURE 39.5**). They showed that guinea pigs injected with a sublethal dose of diphtheria toxin developed in their blood serum (the noncellular fluid that remains after blood is clotted) a factor that, when injected into other guinea pigs, was able to protect them from a lethal dose of the same toxin. In other words, the serum recipients had somehow acquired immunity. The response of the donor guinea pigs to the diphtheria toxin is an example of adaptive immunity: after exposure to the toxin, they made a protective factor that was not present before their exposure. Moreover, the immunity was specific: the factor made by the first guinea pig protected the others only against the specific toxin produced by the strain of bacteria with which the first guinea pig had been injected.

Based on the animal model, Behring realized that serum protection might work for human diseases as well. It did, and he won the Nobel Prize for his efforts in protecting children against diphtheria. Later, the agent of this immunity was identified as an antibody protein, and the process of acquiring immunity from antibodies received from another individual was called passive immunity.

LINK
Many bacteria produce toxins of various types; see **Concept 19.3**

The injection of antibodies to produce a passive immune response is an artificial system that allows an organism to mount a defense against a single pathogenic strain. Vertebrates have evolved systems of adaptive immunity that have the potential to recognize and eliminate

INVESTIGATION

FIGURE 39.5 The Discovery of Specific Immunity Until the twentieth century, most people did not survive an attack of diphtheria, but a few did. Emil von Behring and Shibasaburo Kitasato performed a key experiment using an animal model. They demonstrated that the factor(s) responsible for immunity against diphtheria was in the blood serum.[a]

HYPOTHESIS
Serum from guinea pigs injected with a sublethal dose of diphtheria toxin protects other guinea pigs that are exposed to a lethal dose of the same toxin.
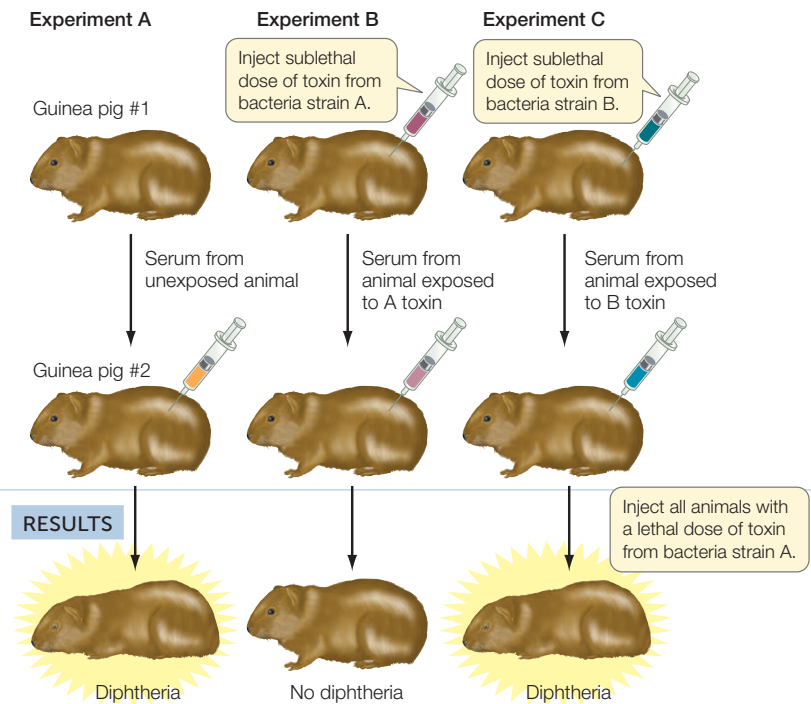
CONCLUSION
Serum of toxin-exposed guinea pigs is protective against later exposure to a lethal dose of toxin from the same genetic strain of bacteria, but not a different strain.

ANALYZE THE DATA
In their experiments, Behring and Kitasato used different doses of toxin to test the immunity of guinea pig #2 in each experiment. The results are shown in the table.

	Symptoms	
Experiment	0.5 ml dose	10 ml dose
A	Diphtheria	Diphtheria
B	No diphtheria	No diphtheria
C	Diphtheria	Diphtheria

A. Explain these data in terms of the level of protection afforded by the serum.

B. These experiments could be performed with either intact bacteria that cause diphtheria, or with a bacteria-free filtrate of a 10-day-old culture of the bacteria. Explain.

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]E. Behring and S. Kitasato. 1890. *Deutsche medizinisch Wochenschrift* 16: 1113–1114.

virtually any pathogen that may infect the body. We will now turn to some key features of adaptive immunity.

Adaptive immunity has four key features

Four important features of the adaptive immune system are: specificity; the ability to distinguish self from nonself; the ability to respond to an enormous diversity of nonself molecules; and immunological memory.

SPECIFICITY   B and T lymphocytes are crucial for the specificity of adaptive immune responses. T cell receptors and the antibodies produced by B cells recognize and bind to specific nonself substances called **antigens**, and this interaction initiates a specific immune response. Each T cell and each antibody-producing B cell is specific for a single antigen.

The sites on antigens that the immune system recognizes are called **antigenic determinants** or **epitopes**:

Antibodies **react with antigenic determinants.**

Antigenic determinants are small portions of antigens.
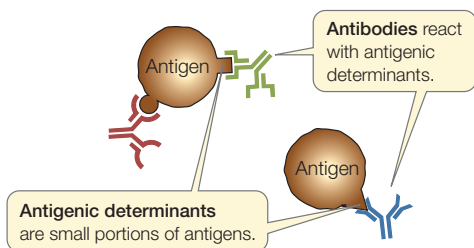
Antigen

Antigens are usually proteins or polysaccharides, and there can be multiple antigens on a single invading bacterium. An antigenic determinant is a specific portion of an antigen, such as a certain sequence of amino acids that may be present in a protein. A single antigenic molecule can have multiple different antigenic determinants. For the remainder of the chapter, we will often refer to antigenic determinants simply as "antigens."

DISTINGUISHING SELF FROM NONSELF   As we saw in Concept 39.2, the innate immune system can recognize certain nonself molecules (PAMPs), and mount defensive responses to the pathogens from which these nonself molecules were derived. The adaptive immune system recognizes both self and non-self molecules. The human body contains tens of thousands of different molecules, each with a specific three-dimensional structure capable of generating an immune response. Thus every cell in the body bears a tremendous number of antigens. A crucial requirement of an individual's immune system is that it recognize the body's own antigens and not attack them.

Normally, the body is tolerant of its own molecules—the same molecules that would generate an immune response in another individual. This occurs primarily during the early differentiation of T and B cells, when they first encounter self antigens. Any immature B or T cell that shows the potential to mount a strong immune response against self antigens undergoes apoptosis within a short time. This process is called **clonal deletion**.

A failure of clonal deletion can lead to an immune response within an individual to self antigens, or **autoimmunity**. Autoimmunity does not always result in disease, but a number of autoimmune diseases are common:

- People with systemic lupus erythematosis (SLE) have antibodies to many cellular components. These antibodies can cause serious damage when they bind to normal tissue antigens and form large circulating antigen–antibody complexes. These can become stuck in tissues and provoke inflammation.
- Hashimoto's thyroiditis is the most common autoimmune disease in women over age 50. Immune cells attack thyroid tissue, resulting in fatigue, depression, weight gain, and other symptoms associated with impaired thyroid function.

DIVERSITY   Pathogens take many forms: viruses, bacteria, protists, fungi, and multicellular parasites. Furthermore, each pathogenic species usually exists as many subtly different genetic strains, and each strain possesses multiple surface features. Estimates vary, but a reasonable guess is that humans can respond specifically to 10 million different antigens. Upon recognizing an antigen, the immune system responds by activating lymphocytes of the appropriate specificity.

To have the ability to respond to the large number of potential pathogens, the body needs to generate a vast diversity of lymphocytes that are specific for different antigens. These lymphocytes represent a pool from which specific cells are selected when needed.

- *Diversity is generated primarily by DNA changes*—chromosomal rearrangements and other mutations—that occur just after the B and T cells are formed in the bone marrow. Each B cell is able to produce only one kind of antibody; thus there are millions of different B cells. Similarly, there are millions of different T cells with specific T cell receptors. The adaptive immune system is "predeveloped"—*all of the machinery available to respond to an immense diversity of antigens is already there, even before the antigens are encountered.*
- *Antigen binding "selects" a particular B or T cell for proliferation*. For example, when an antigen fits the surface receptor on a B cell and binds to it, that B cell is activated. It divides to form a clone of cells (a genetically identical group derived from a single cell), all of which produce and/or secrete antibodies with the same specificity as the receptor (**FIGURE 39.6**). Binding, activation, and proliferation also apply to T lymphocytes. A particular lymphocyte is selected via binding and activation, and then it proliferates to generate a clone—hence the name **clonal selection** for this mechanism of producing an immune response.

IMMUNOLOGICAL MEMORY   After responding to a particular type of pathogen once, the immune system "remembers" that pathogen and can usually respond more rapidly and powerfully to the same threat in the future. This **immunological memory** usually saves us from repeats of childhood infectious diseases.

The first time a vertebrate animal is exposed to a particular antigen, it takes several days before the adaptive immune system produces antibodies and T cells specific for the antigen. This is the **primary immune response**. Immunological memory arises from the fact that activated lymphocytes divide and
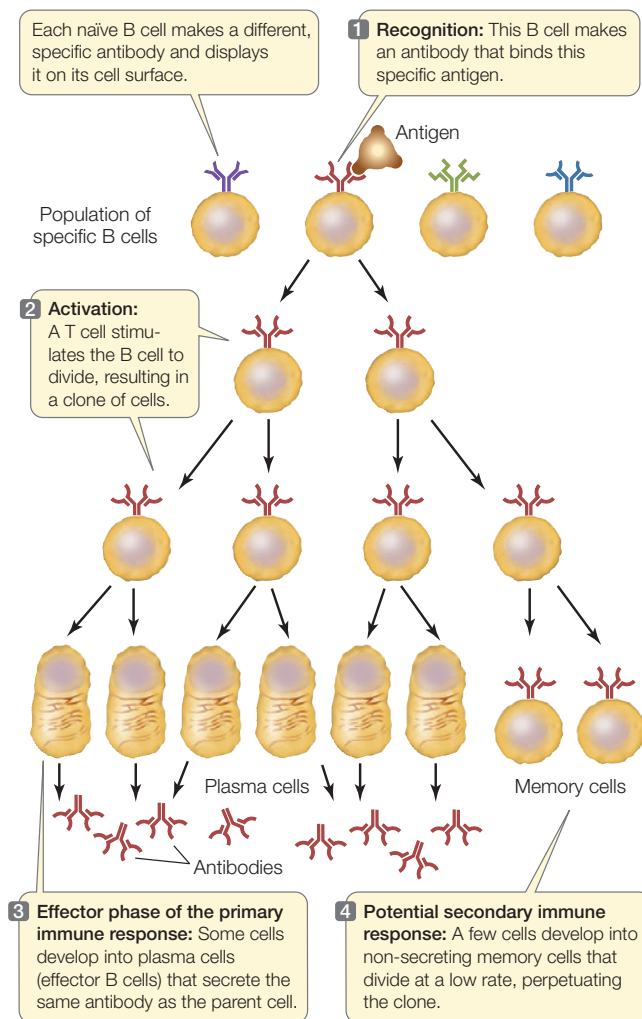
FIGURE 39.6 **Clonal Selection in B Cells** The binding of an antigen to a specific receptor on the surface of a B cell stimulates that cell to divide, producing a clone of genetically identical cells to fight that invader.

differentiate to produce *two types* of daughter cells: effector cells and memory cells (see Figure 39.6).

- **Effector cells** carry out the attack on the antigen. Effector B cells, called **plasma cells**, secrete antibodies. Effector T cells release cytokines and other molecules that initiate reactions that destroy nonself or altered cells. Effector cells live for only a few days.

- **Memory cells** are long-lived cells that retain the ability to start dividing on short notice to produce more effector and more memory cells. Memory B and T cells may survive in the body for decades, rarely dividing.

After a primary immune response to a particular antigen, subsequent encounters with the same antigen will trigger a much more rapid and powerful **secondary immune response**. The memory cells that bind with that antigen proliferate,

launching a huge army of plasma cells and effector T cells. The principle behind vaccination is to trigger a primary immune response that prepares the body to mount a stronger, quicker secondary response if it encounters the actual pathogen.

Macrophages and dendritic cells play a key role in activating the adaptive immune system

We have just seen how the adaptive immune system uses antigens to distinguish between self and nonself, and how it uses clonal selection to produce large numbers of specific B and T cells. In Concepts 39.4 and 39.5 we will focus on how these cells function to eliminate specific pathogens from the body. But how is the adaptive immune system activated in the first place?

One mechanism for eliminating pathogens in the innate immune system is phagocytosis. After ingestion of a pathogenic organism or infected host cell, phagocytic cells display fragments of the pathogen on their cell surfaces. These fragments function as antigens, and **antigen presentation** is one way that components of the innate immune system communicate with the adaptive immune system. Macrophages and dendritic cells play a key role in activating the adaptive immune system. After engulfing pathogens or infected host cells, these cells migrate to lymph nodes, where they present antigen to immature T cells. In addition, the antigen-presenting cells secrete cytokines and other signals that stimulate the activation and differentiation of the T cells.

Two types of adaptive immune responses interact

The adaptive immune system mounts two types of responses against invaders: the **humoral immune response** and the **cellular immune response**. These two responses work simultaneously and cooperatively, sharing many mechanisms. We will use the example of a viral infection in an overview of these two types of responses (**FIGURE 39.7**). These responses also occur when bacteria or other pathogens infect and grow inside host cells.

B cells that make antibodies are the workhorses of the humoral immune response, and **cytotoxic T (T_C) cells** are the workhorses of the cellular immune response. There are three phases in both types of immune response:

- *Recognition phase:* In both cellular and humoral immunity, recognition occurs when an antigen is inserted into the cell membrane of an antigen-presenting cell, with the unique antigen structure protruding from the cell membrane. In addition to dendritic cells and macrophages, developing B cells can also perform phagocytosis and function as antigen-presenting cells. Figure 39.7 shows a virus-infected host cell being engulfed by an antigen-presenting cell; in other cases, the free viral particles may be engulfed. The antigen on the surface of the antigen-presenting cell is recognized by a **T-helper (T_H) cell** bearing a T cell receptor protein that is specific for the antigen. In both humoral and cellular immunity, binding initiates the activation phase.

- *Activation phase:* When the T_H cell recognizes an antigen on an antigen-presenting cell, it propagates and releases cytokines that stimulate B cells and T_C cells bearing receptors

HUMORAL IMMUNITY

CELLULAR IMMUNITY

Virus-infected cell with surface antigen

Bind

Free viral particles

Bind

Antibodies

Bind and kill

B cells release antibodies that bind free viral particles and/or virus-infected cells.

T_C cells kill all cells with antigen exposed.

Phagocytosis

B cell

Antigen-presenting cell

Cytotoxic T cell (T_C)

Stimulate

Bind

Stimulate

T-helper cell (T_H)

The T_H cell regulates both the cellular and the humoral systems.

FIGURE 39.7 The Adaptive Immune System Humoral immunity involves the production of antibodies by B cells. Cellular immunity involves the activation of cytotoxic T cells that bind to and destroy self cells that are mutated or infected by pathogens. Details of these processes are described later in this chapter.

to the same antigen to divide. The results are a clone of B cells that function in humoral immunity and a clone of T_C cells that function in cellular immunity.

- *Effector phase:* In the humoral immune response, cells of the B clone produce antibodies that bind to viral particles and/or virus-infected cells. The bound antibodies attract phagocytes and complement proteins that engulf and destroy the virus and the virus-infected cells. In cellular immunity, cells of the T_C clone bind to virus-infected cells and destroy them.

CHECKpoint CONCEPT **39.3**

✓ List the four key features of the adaptive immune system.

✓ In 2009, the H1N1 strain of influenza was a worldwide epidemic. Notably, very old people, who had been alive during the 1918 flu outbreak, had low rates of H1N1 infection. Explain this in terms of immunological memory.

✓ Insulin-dependent (type 1) diabetes results from a destruction of the cells in the pancreas that make the hormone insulin (see Concept 30.5). One hypothesis for this disease is that it is caused by an autoimmune reaction. Explain how this might happen and how you would investigate your hypothesis.

APPLY THE CONCEPT

The adaptive immune response is specific

In humans, the dominant gene *D* codes for the RhD (Rhesus) protein on the surfaces of red blood cells. The recessive allele *d* does not encode a cell surface protein. If cells from an individual who is *DD* or *Dd* (Rh⁺) enter the bloodstream of an individual who is *dd* (Rh⁻), the Rh⁻ individual makes antibodies that react with the Rh⁺ cells. During development, the blood vessels of a mother and her fetus are near each other but do not mix. However, antibodies can pass through capillary walls between the two blood supplies.

1. Hemolytic disease of the newborn (sometimes resulting in stillbirth) can occur when antibodies from the mother pass into the fetal circulatory system. Fill in the table, which predicts RhD incompatibility.

2. During birth there is mixing of the blood supplies of mother and fetus. In a situation of RhD incompatibility,

MOTHER		FETUS		
GENOTYPE	Rh PHENOTYPE	GENOTYPE	Rh PHENOTYPE	RESULT
Dd		*Dd*		
dd		*Dd*		

the first birth does not result in a clinical problem. But a second RhD incompatible birth with this mother results in a hemolytic disease. Explain how this can happen (hint: immunological memory).

3. Today, RhD incompatibility does not result in stillbirths. The mother is treated with serum containing anti-RhD antibodies late in the first and subsequent pregnancies. How can this prevent the immunological reactions?

With this overview of the basic characteristics of adaptive immunity and the events of the immune response, we will now turn to some of the cellular and molecular details of how these events occur.

This binding of multiple antigens and multiple antibodies can result in large complexes that are easy targets for ingestion and breakdown by phagocytes.

There are five classes of immunoglobulins (Ig), and they differ in function and in the type of heavy chain constant region:

- IgG constitutes about 80 percent of circulating antibodies.
- IgD is a cell surface receptor on a B cell.
- IgM is the initial surface and circulating antibody released by a B cell.
- IgA protects mucous membranes exposed to the environment.
- IgE binds to mast cells and is involved with inflammation.

We will focus on IgG antibodies in this chapter.

Antibody diversity results from DNA rearrangements and other mutations

Each mature B cell makes antibodies targeted to only one single antigen. And there are millions of possible antigens to which a human can be exposed. How can the genome encode enough different antibodies to protect the body against all the possible pathogens? Although there are millions of possible amino acid sequences in immunoglobulins, there are not millions of different immunoglobulin genes. It turns out that instead of a single gene encoding each complete immunoglobulin, the genome of the differentiating B cell has multiple different coding regions for each domain of the protein, and diversity is generated by putting together different combinations of these regions. Shuffling of this genetic deck generates the enormous immunological diversity that characterizes each individual mammal.

Each gene encoding an immunoglobulin chain is in reality a "supergene" assembled by means of genetic recombination from several clusters of smaller genes scattered along part of a chromosome (**FIGURE 39.9**). Every cell in the body has hundreds of immunoglobulin genes located in separate clusters that are potentially capable of participating in the synthesis of both the variable and constant regions of immunoglobulin chains. In most body cells and tissues, these genes remain intact and separated from one another. But during B cell development, these genes are cut out, rearranged, and joined together in DNA recombination events. One gene from each cluster is chosen randomly for joining, and the others are deleted. In the case of one multigene set, the *J* genes, some of the extra sequences are removed by RNA splicing (**FIGURE 39.10**).

In this manner, a unique immunoglobulin supergene is assembled from randomly selected "parts." Each B cell precursor assembles two supergenes, one for a specific heavy chain and the other, assembled independently, for a specific light chain. This remarkable example of irreversible cell differentiation generates an enormous diversity of immunoglobulins from the same genome. It is a major exception to the generalization that all somatic cells derived from the fertilized egg have identical DNA.

Figure 39.9 illustrates the gene families that encode the constant and variable regions of the heavy chain in mice. There are multiple genes that encode each of the three parts of the variable region: 100 *V*, 30 *D*, and 6 *J* genes. Each B cell randomly selects one gene from each of these clusters to make the final coding sequence (*VDJ*) of the heavy-chain variable region. So the number of different heavy chains that can be made through this random recombination process is quite large:

100 *V* × 30 *D* × 6 *J* = 18,000 possible combinations

Now consider that the light chains are similarly constructed, with a similar amount of diversity made possible by random recombination. If we assume that the degree of potential light-chain diversity is the same as that for heavy-chain diversity, the number of possible combinations of light- and heavy-chain variable regions is:

18,000 different light chains × 18,000 different heavy chains = 324 million possibilities!

Other mechanisms generate even more diversity:

- When the DNA sequences that encode the *V*, *D*, and *J* regions are rearranged so that they are next to one another, the recombination event is not precise, and errors occur at the junctions. This imprecise recombination can create frameshift mutations, generating new codons at the junctions, with resulting amino acid changes.

- After the DNA sequences are cut and before they are rejoined, the enzyme terminal transferase often adds some nucleotides to the free ends of the DNA pieces. These additional bases create insertion mutations.

FIGURE 39.9 Super Genes Mouse immunoglobulin heavy chains have four domains, each of which is coded for by a gene selected from a cluster of similar genes. The immunoglobulin protein has one domain from each cluster.

The **variable region** for the heavy chain of a specific antibody is encoded by one *V* gene, one *D* gene, and one *J* gene. Each of these genes is taken from a pool of like genes.

The **constant region** is selected from another pool of genes.

Genes encoding variable region

$V_1, V_2...V_{\sim100}$ (variable) genes $D_1, D_2...D_{\sim30}$ (diversity) genes $J_1, J_2...J_6$ (joining) genes

Genes encoding constant region

DNA   1 2 3 4...100   1   2...30   1...6   μ δ   γ3   γ1   γ2β γ2α ε   α

FIGURE 39.10 Gene Recombination and RNA Splicing
Two types of rearrangement in the heavy-chain gene clusters are required for antibody formation. (A) Prior to transcription, DNA is rearranged to join one each of the *V*, *D*, and *J* genes into a variable region supergene. (B) After transcription, RNA splicing joins the *VDJ* region to the constant region.

Labels within figure:
(A) DNA rearrangement
Variable region · Constant region
V · *D* · *J* segments · *C* segments
Embryonic DNA
VDJ joining
B cell DNA · *V D J* · μ
After *V, D, J,* and *C* DNA segments have been joined, the resulting functional supergene is transcribed.
(B) Transcription and RNA splicing
Transcription
Primary RNA transcript · μ
Splicing of the primary RNA transcript removes the transcripts of any introns and of any extra *J* genes.
Splicing
mRNA · *V D J* μ
Translation
Assembly and display
B cell

• There is a relatively high spontaneous mutation rate in immunoglobulin genes. Once again, this process creates many new alleles and adds to antibody diversity.

LINK

The effects of DNA mutations on the amino acid sequences of proteins are described in **Concept 10.3**

When we include these possibilities with the millions of combinations that can be made by random DNA rearrangements, it is not surprising that the immune system can mount a response to almost any natural or artificial substance.

Once the DNA rearrangements are completed, each supergene is transcribed and then translated to produce an immunoglobulin light chain or heavy chain. These chains combine to form an active immunoglobulin protein.

Go to ANIMATED TUTORIAL 39.3
A B Cell Builds an Antibody
PoL2e.com/at39.3

Antibodies bind to antigens and activate defense mechanisms

Recall that antibodies have two roles in B cells after they undergo DNA rearrangements and RNA splicing. First, by being expressed on the cell surface, a unique antibody can act as a receptor for an antigen in the recognition phase of the humoral response (see Figures 39.6 and 39.7). Second, in the effector

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APPLY THE CONCEPT

The adaptive humoral immune response involves specific antibodies

Mammals have two kinds of light chains: the kappa (κ) and lambda (λ) chains, and each variable region consists of a V domain and a J domain. Imagine a strain of mouse that has a family of 350 genes encoding the κ V domain and 10 encoding the κ J domain, while the λ variable regions are encoded by 300 V and 5 J genes. The IgG heavy chain is encoded by 350 V, 8 J, and 5 D genes.

1. How many different types of antibodies can be made from these genes by recombination?

2. What are two other ways to generate antibody diversity from these genes?

phase of the humoral response, specific antibodies are produced in large amounts by a clone of B cells. These antibodies are secreted from the B cells and enter the bloodstream where they act in either of two ways:

- *Activation of the complement system*: When antibodies bind to antigens that are present on the surfaces of pathogens, they attract components of the complement system (see Concept 39.2). Some complement proteins attack and lyse the pathogenic cells. In addition, the binding of antibody and complement proteins stimulates phagocytes (monocytes, macrophages, or dendritic cells) to ingest the pathogens.

Receptor / *Antibody*

Cell membrane

Antigen

Binding of antibody to a receptor activates phagocytosis.

Macrophage
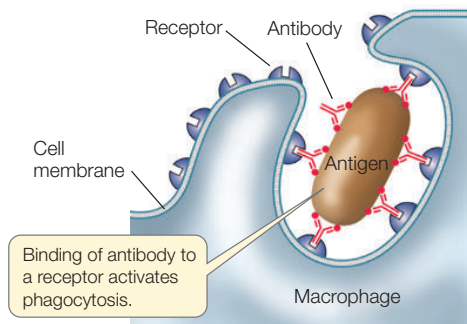
- *Activation of effector cells:* Because of its cross-linking function (see p. 819), antibody binding can result in large, insoluble antibody–pathogen or antibody–antigen complexes. These attract effector cells such as phagocytes and natural killer cells.

CHECKpoint   CONCEPT 39.4

✓ Sketch an IgG antibody, identifying the variable and constant regions, light and heavy chains, and antigen-binding sites.

✓ Assume that one IgG heavy chain is encoded by 1,500 base pairs of DNA, and that one IgG light chain is encoded by 600 base pairs of DNA. If each antibody were encoded by a different gene, how many base pairs of DNA would be needed for 10 million antibody genes? Is it possible for the human genome to contain all these genes? Explain your answer.

✓ The bacterium that causes diphtheria (see Figure 39.5) synthesizes a toxic protein. You have probably not been exposed to this bacterium or its toxin. At the present time, are you making B cells and antibodies that bind specifically to diphtheria toxin? Explain your answer.

✓ When an antigenic protein such as diphtheria toxin (see above) enters the bloodstream, clones of numerous B cells are produced. Explain.

The humoral immune response works in concert with the cellular immune response in adaptive immunity. Now let's turn to a closer examination of the cellular response.

CONCEPT 39.5 The Adaptive Cellular Immune Response Involves T Cells and Their Receptors

Two types of effector T cells (T-helper cells and cytotoxic T cells) are involved in the cellular immune response, along with proteins of the major histocompatibility complex (MHC proteins), which underlie the immune system's tolerance for the body's own cells.

Go to ANIMATED TUTORIAL 39.4
Cellular Immune Response
PoL2e.com/at39.4

T cell receptors specifically bind to antigens on cell surfaces

Like B cells, T cells possess specific membrane receptors. The T cell receptor is not an immunoglobulin, however, but a glycoprotein with a molecular weight of about half that of an IgG. It is made up of two polypeptide chains, each encoded by a separate gene (**FIGURE 39.11**). The two chains have distinct regions with constant and variable amino acid sequences. As in the immunoglobulins, the variable regions provide the site for specific binding to antigens. However, there is an important difference between immunoglobulin binding and T cell receptor binding: whereas an immunoglobulin can bind to an antigen whether it is present on the surface of a cell or not, a T cell receptor binds only to an antigen displayed by an MHC protein on the surface of an antigen-presenting cell.

MHC proteins present antigens to T cells and result in recognition

Recall that so far we have described two types of T cells: T_H and T_C cells. Both cell types express T cell receptors that bind to antigen on the cell surface. But the response of each cell type to binding is quite different. T_H binding results in activation of the adaptive immune response, whereas T_C binding results in death of the cell carrying the antigen. MHC proteins form complexes with antigens on cell surfaces and assist with recognition by the T cells, so that the appropriate type of T cell binds.

The MHC proteins are cell membrane glycoproteins. Two types of MHC proteins function to present antigens to the two different types of T lymphocytes:

- **Class I MHC** proteins are present on the surface of every nucleated cell in the mammalian body. They present antigens to T_C cells. These antigens can be fragments of virus proteins in virus-infected cells or abnormal proteins made by cancer cells as a result of somatic mutations.

- **Class II MHC** proteins are on the surfaces of macrophages, B cells, and dendritic cells. They present antigens to T_H cells. The three cell types ingest antigens and break them down; one of the fragments then binds to MHC II for presentation (**FIGURE 39.12**).

In humans, there are three genetic loci for class I MHC proteins and three for class II MHC proteins. Each of these six loci

The antigen and MHC molecules bind here.

α-chain

Variable regions

β-chain

Outside of T cell

Constant regions

A hydrophobic region anchors the chain in the cell membrane.

Inside of T cell
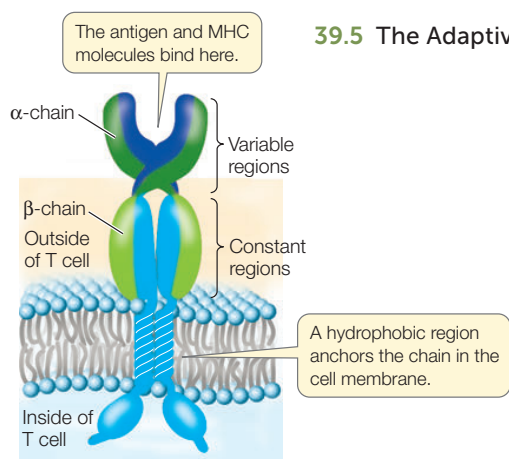
FIGURE 39.11 A T Cell Receptor The receptors on T lymphocytes are smaller than those on B lymphocytes, but their two polypeptides contain both variable and constant regions. As with the B cell receptors, the constant regions fix the receptor in the cell membrane, while the variable regions establish the specificity for binding to antigen.

has as many as 1,000 different alleles. With so many possible allele combinations, it is not surprising that different people are very likely to have different MHC genotypes. This is why it can be difficult to find a good "match" for organ donations. MHC proteins are "self" markers. To accomplish its role in antigen presentation, an MHC protein has an antigen-binding site that can hold a peptide of about 10–20 amino acids. The T cell receptor recognizes not just the antigenic fragment but also the class I or II MHC molecule to which the fragment is bound.
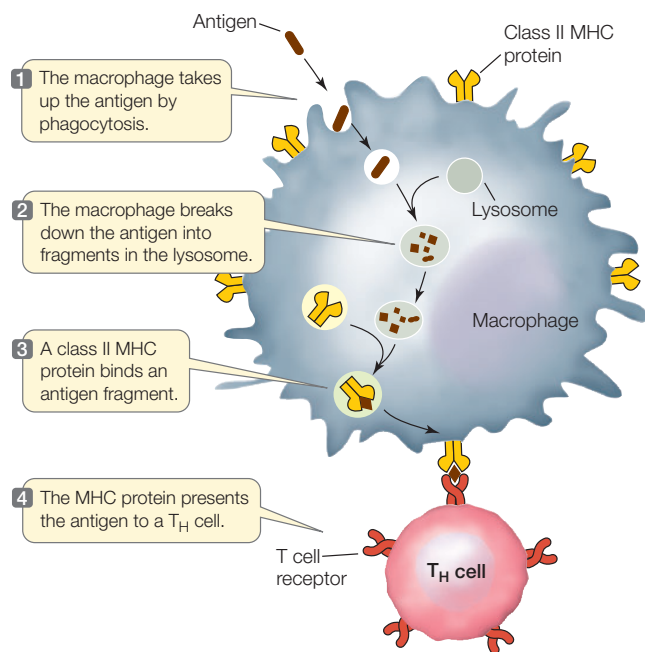
Information on MHC proteins, the cellular origins of antigens, and T lymphocytes is summarized in **TABLE 39.2**.

T_H cells contribute to the humoral and cellular immune responses

A T_H cell is activated when it has receptors that can bind a specific antigen on the surface of an antigen-presenting cell. This results in the rapid clonal propagation of the T_H cell. The T_H cells then release cytokines that stimulate other immune cells, including T_C cells, to propagate.

A T_H cell can also directly interact with a B cell that recognizes the same antigen. Like dendritic cells and macrophages, B cells are antigen-presenting cells. B cells take up antigens bound to their surface immunoglobulin receptors by endocytosis, break them down, and display antigenic fragments on class II MHC proteins. When a T_H cell binds to the displayed antigen–MHC II complex, it stimulates the B cell to propagate and to secrete antibodies.

Cytokines activate B cell proliferation.

B cell

T_H cell

The binding of antigen to a specific B cell receptor triggers endocytosis, degradation, and display of the processed antigen.

A T_H cell receptor recognizes an antigenic fragment bound to a class II MHC protein on a B cell.
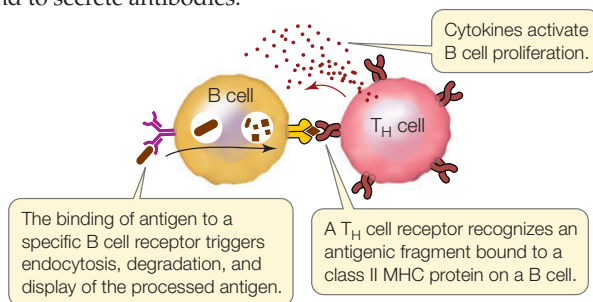
Activation of the cellular response results in death of the targeted cell

T_C cells are activated when they bind to cells carrying an antigen–MHC I protein complex, such as a virus-infected cell. This activation, along with signals from T_H cells, results in the production of a clone of T_C cells with the same specific receptor. When bound, the T_C cells do two things to eliminate the antigen-carrying cell:

- They produce perforin, which lyses the bound target cell.
- They stimulate apoptosis in the target cell.

Antigen

Class II MHC protein

1 The macrophage takes up the antigen by phagocytosis.

2 The macrophage breaks down the antigen into fragments in the lysosome.

Lysosome

Macrophage

3 A class II MHC protein binds an antigen fragment.

4 The MHC protein presents the antigen to a T_H cell.

T cell receptor

T_H cell

FIGURE 39.12 Macrophages Are Antigen-Presenting Cells A fragment of an antigen is displayed by MHC II protein on the surface of a macrophage. T cell receptors on a specific T-helper cell can then bind to and interact further with the antigen–MHC II protein complex.

Infected cell (one of many)

1 A T cell receptor recognizes an antigenic fragment bound to a class I MHC protein.

2 The T_C cell releases perforin…

3 …which lyses the infected cell before the viruses can multiply.

TABLE 39.2	The Interaction between T Cells and Antigen-Presenting Cells		
Presenting cell type	**Antigen presented**	**MHC class**	**T cell type**
Any cell	Intracellular protein fragment	Class I	Cytotoxic T cell (T$_C$)
Macrophages, dendritic cells, and B cells	Fragments from extracellular proteins	Class II	Helper T cell (T$_H$)

Regulatory T cells suppress the humoral and cellular immune responses

A third class of T cells called **regulatory T cells** (**Tregs**) ensures that the immune response does not spiral out of control. Like T$_H$ and T$_C$ cells, Tregs are made in the thymus gland, express the T cell receptor, and become activated if they bind to antigen–MHC protein complexes. But Tregs are different in one important way: the antigens that Tregs recognize are self antigens. The activation of Tregs causes them to secrete the cytokine interleukin-10, which blocks T cell activation and leads to apoptosis of the T$_C$ and T$_H$ cells that are bound to the same antigen-presenting cell (**FIGURE 39.13**).

The important role of Tregs is to mediate tolerance to self antigens. Thus they constitute one of the mechanisms for distinguishing self from nonself. There are two lines of experimental evidence for the role of Tregs:

- If Tregs are experimentally destroyed during development in the thymus of a mouse, the mouse grows up with an out-of-control immune system, mounting strong immune responses to self antigens—autoimmunity.

- In humans, a rare X-linked inherited disease occurs when a gene critical to Treg function is mutated. An infant with this disease, called IPEX (*i*mmune dysregulation, *p*olyendocrinopathy and *e*nteropathy, *X*-linked), mounts an immune response that attacks the pancreas, thyroid, and intestine. Most affected individuals die within the first few years of life.

AIDS is an immune deficiency disorder

There are a number of inherited and acquired immune deficiency disorders. In some individuals, T or B cells never form; in others, B cells lose the ability to give rise to plasma cells. In either case, the affected individual is unable to mount an immune response and thus lacks a major line of defense against pathogens. A more common disease that was first detected in the early 1980s is **acquired immune deficiency syndrome** (**AIDS**), which results from infection by **human immunodeficiency virus** (**HIV**).

The course of HIV infection provides a good review of adaptive immunity (see Figure 39.7). HIV is transmitted from person to person in blood, semen, vaginal fluid, or breast milk; the recipient tissue is either blood (by transfusion or injection) or a mucous membrane lining an organ. HIV initially infects macrophages, T$_H$ cells, and antigen-presenting dendritic cells
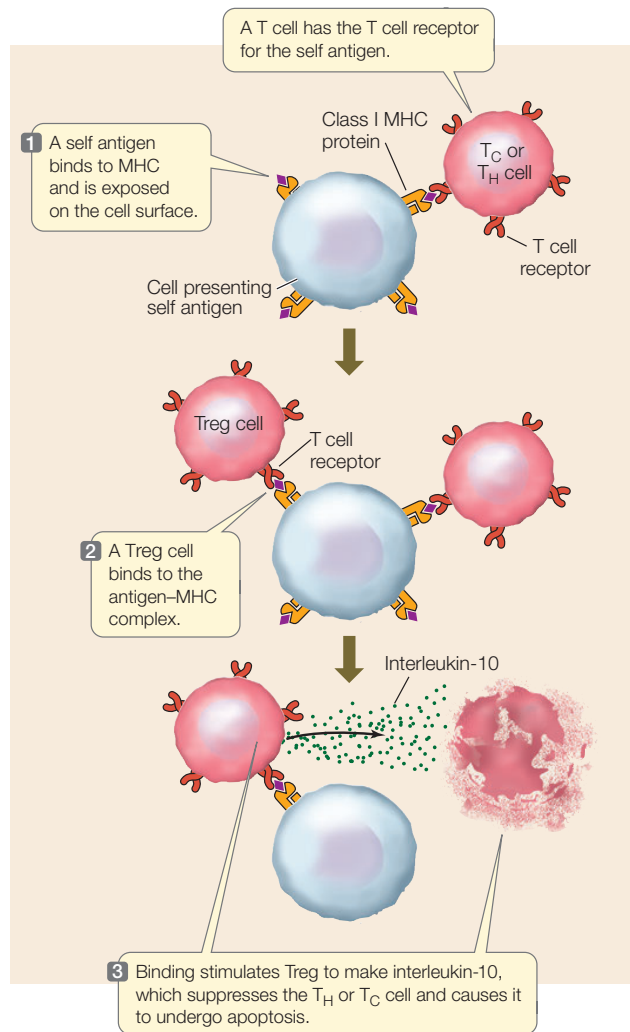
FIGURE 39.13 Tregs and Tolerance A special class of T cells called regulatory T cells (Tregs) inhibits the activation of the immune system in response to self antigens.

in the blood and tissues. At first there is an immune response to the viral infection, and some T$_H$ cells are activated. But because HIV infects the T$_H$ cells, they are killed both by HIV itself and by T$_C$ cells that lyse infected T$_H$ cells. Consequently, T$_H$ cell numbers decline after the first month or so of infection. Meanwhile, the extensive production of HIV by infected cells activates the humoral immune system. Antibodies bind to HIV and the complexes are removed by phagocytes. The HIV level in blood goes down. There is still a low level of infection, however, mostly because of the depletion of T$_H$ cells (**FIGURE 39.14**).

During this dormant period, people carrying HIV generally feel fine, and their T$_H$ cell levels are adequate for them to mount immune responses against other infections. Eventually, however, the virus destroys the T$_H$ cells, and their numbers fall to the point where the infected person is susceptible to infections that the T$_H$ cells would normally eliminate. These infections result in conditions such as Kaposi's sarcoma, a skin tumor caused by a herpes virus; pneumonia caused by the fungus *Pneumocystis jirovecii*; and lymphoma tumors caused by the Epstein–Barr virus. These conditions result from opportunistic

1 Soon after the initial HIV infection, the immune system destroys most of the virus.

2 The T_H cell concentration gradually falls and the HIV concentration rises.

3 As T_H cells are further reduced, immune function is impaired and opportunistic infections occur.

4 Almost all natural immunity is lost.

This is the set point of low-level HIV production.

T_H cell concentration

HIV concentration

FIGURE 39.14 The Course of an HIV Infection
An HIV infection may be carried, unsuspected, for many years before the onset of symptoms.

infections because the pathogens take advantage of the crippled immune system of the host. In addition, HIV infection somehow stimulates Treg cells, and these also downregulate the immune response. The combination of infections and a weakened immune response can lead to death within a year or two of development of full-blown AIDS.

The molecular biology of HIV and its life cycle have been intensively studied. Drug treatments are focused on inhibiting processes necessary for viral entry, assembly, and replication, such as the synthesis of cDNA from viral RNA by reverse transcriptase, and the cutting of the large precursor viral protein into mature, active proteins by viral protease. Combinations of such drugs result in long-term survival, a major achievement of molecular biology applied to medicine. Unfortunately, like many medical treatments, HIV drugs are not available to all who need them—particularly in poor regions of the world where AIDS is prevalent. As a result, there are about 1.7 million deaths per year worldwide from AIDS.

LINK

For more on the life cycle of HIV, see **Concept 11.2**

CHECKpoint CONCEPT 39.5

✓ Compare the T cell receptor and B cell receptor in terms of structure, diversity, and function.

✓ What are the similarities and differences in function between class I and II MHC proteins?

✓ What are the roles of T_H cells in cellular and humoral immunity?

✓ Since MHC proteins are highly variable and almost always differ among unrelated people, an organ transplant from one person to another will generally provoke a cellular immune response, and the organ will be rejected. Patients receiving organ transplants are treated with cyclosporin, a drug that inhibits T cell development. How do you think cyclosporin prevents rejection? What side effects might you expect in treated people?

Q How can a person survive an infection and be resistant to further infection?

ANSWER Almost 2,500 years after Thucydides's observations, we have some answers to this question. During the Athenian plague, innate immunity (Concept 39.2) kept most of the disease agent out of the body. Any agent that evaded the innate defenses was attacked by the adaptive immune system (Concepts 39.3–39.5). The agent was engulfed by macrophages or dendritic cells, which broke up the agent and presented fragments on its cell surface, in complexes with class II MHC proteins. The antigen-presenting cell migrated to a lymph node, where the MHC–antigen complex was recognized by T_H cells with the appropriate T cell receptors. Clones of these T cells developed, and some of these cells bound to B cells that displayed the same antigen on their surfaces. The B cells then formed clones of plasma cells, which made antibodies that bound to the agent. The antibody-bound agent was then destroyed by the complement system and phagocytes. Meanwhile, if cells were infected by the agent, a parallel series of events occurred in the cellular immune response, resulting in a clone of T_C cells that killed the infected cells (Concept 39.5). These two systems allowed Thucydides to survive the infection that killed so many of his fellow Athenians.

The T and B cells activated by the two adaptive immune responses also formed smaller clones of memory cells. When Thucydides took care of others in Athens who had the disease, the reentry of the pathogen into his body provoked a rapid, massive T and B cell response. This response prevented the pathogen from proliferating and making him sick again.

An important application of immunological memory is the use of **vaccines**. Exposure to an antigen in a form that does not cause disease can still initiate a primary immune response, generating memory cells without making the person ill. Later, if a pathogen carrying the same antigen attacks, specific memory cells already exist. They recognize the antigen and quickly overwhelm the invaders with a massive production of lymphocytes and antibodies (**FIGURE 39.15**).

Because the antigens used for immunization or vaccination are derived from pathogenic organisms, they must be altered so they cannot cause disease. This is achieved in a variety of ways, including inactivation of the pathogen by chemicals or heat, mutations that render the pathogen inactive, or recombinant DNA technology to make nonharmful peptides derived from the pathogen. The use of vaccines, especially in children,

FIGURE 39.15 Vaccination Immunological memory from exposure to an antigen that does not cause disease can result in a massive response to the disease agent when it appears later.

has been a great success in public health. In industrialized countries, widespread vaccination has completely or almost completely wiped out some deadly diseases, including small-pox, diphtheria, and polio.
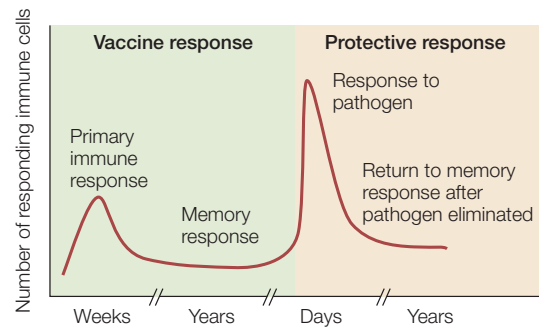
SUMMARY

CONCEPT 39.1 Animals Use Innate and Adaptive Mechanisms to Defend Themselves against Pathogens

■ Animal defenses against **pathogens** are based on the body's ability to distinguish between self and nonself.

■ **Innate defenses** are nonspecific, inherited mechanisms that protect the body from many kinds of pathogens. These defenses typically act rapidly.

■ **Adaptive defenses** are specific mechanisms that respond to specific pathogens. Adaptive defenses develop more slowly than innate defenses but are long-lasting.

■ Innate defenses evolved before adaptive defenses and include barriers, phagocytic cells, molecules that are toxic to pathogens, and a common recognition-signaling pathway. **Review Figure 39.1**

■ Many innate and adaptive defenses are implemented by cells carried in the circulatory and lymphatic systems. **Review Figure 39.2 and ANIMATED TUTORIAL 39.1**

CONCEPT 39.2 Innate Defenses Are Nonspecific

■ Innate defenses include physical barriers such as the skin, mucous membranes, and competing resident microorganisms. **Review Figure 39.3**

■ Circulating defensive cells, such as **phagocytes** and **natural killer cells**, work to eliminate invaders.

■ The vertebrate complement system consists of more than 20 different antimicrobial proteins that act to alter membrane permeability and kill targeted cells.

■ The **inflammation** response activates several types of cells and proteins that act against invading pathogens. **Mast cells** release **histamine**, which increases the permeability of blood vessels to aid in inflammation. **Review Figure 39.4 and ACTIVITY 39.1**

CONCEPT 39.3 The Adaptive Immune Response Is Specific

■ The adaptive immune system recognizes specific **antigens**, responds to an enormous diversity of **antigenic determinants** (also called **epitopes**), distinguishes self from nonself, and remembers the antigens it has encountered.

■ **Clonal selection** accounts for the specificity and diversity of the immune response and for **immunological memory**. **Review Figure 39.6**

■ Adaptive immunity includes the **humoral immune response**, which involves antibody production by B cells, and the **cellular immune response**, mediated by T cells. Both require specific receptors to bind to each antigen. **Review Figure 39.7**

CONCEPT 39.4 The Adaptive Humoral Immune Response Involves Specific Antibodies

See **ANIMATED TUTORIAL** 39.2

■ Naïve B cells are activated by binding of the antigen and by stimulation from T_H cells with the same specificity, and then form **plasma cells**. These cells synthesize and secrete specific antibodies.

■ The basic unit of an **immunoglobulin** is a tetramer of four polypeptides: two identical light chains and two identical heavy chains, each consisting of a **constant region** and a **variable region**. The variable regions determine the specificity of an immunoglobulin, and the constant regions of the heavy chain determine its class. **Review Figure 39.8 and ACTIVITY 39.2**

■ There are five classes of immunoglobulins, differing in function and in the constant region of the heavy chain.

■ B cell genomes undergo recombination events in which the genes that encode specific domains of the immunoglobulin variable regions are randomly selected from large clusters of genes. This DNA rearrangement yields millions of different immunoglobulin proteins. **Review Figures 39.9 and 39.10 and ANIMATED TUTORIAL 39.3**

CONCEPT 39.5 The Adaptive Cellular Immune Response Involves T Cells and Their Receptors

See **ANIMATED TUTORIAL** 39.4

■ T cell receptors are somewhat similar in structure to the immunoglobulins, having variable and constant regions. **Review Figure 39.11**

■ There are several types of T cells. **Cytotoxic T (T_C) cells** recognize and kill virus-infected cells or mutated cells. **T-helper (T_H) cells** direct both the cellular and humoral immune responses.

■ The genes of the major histocompatibility complex (MHC) encode membrane proteins that bind antigenic fragments and present them to T cells. **Review Figure 39.12**

■ **Regulatory T cells** (**Tregs**) inhibit the other T cells from mounting an immune response to self antigens. **Review Figure 39.13**

■ **Acquired immune deficiency syndrome** (**AIDS**) arises from depletion of the T_H cells as a result of infection with **human immunodeficiency virus** (**HIV**). **Review Figure 39.14**

See **ACTIVITY 39.3** for a review of the major human organ systems.

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities **PoL2e.com/is39**

Go to LaunchPad at **macmillanhighered.com/launchpad** for additional resources, including LearningCurve Quizzes, Flashcards, and many other study and review resources.

40

Animal Behavior

Within a coral reef ecosystem, individuals of some species of fish live in schools while individuals of other species move around in pairs. The behaviors shown by both types of fish help give structure to the fish community. Here we see a loose school of orange anthias fish at the left and a pair of golden butterflyfish (*Chaetodon semilarvatus*).

For scuba divers, the chance to see the diversity of fish in coral reef ecosystems is one of the greatest thrills of diving. Fish are by far the most diverse group of vertebrate animals. The number of described species of fish is only slightly lower than the number of all other types of vertebrates combined. Coral reefs are hotbeds of fish diversification. Fifteen percent of fish species—many of them dramatically colored—are found nowhere else and thus are endemic to coral reefs.

Without actually visiting reefs and looking hard at the fish living there, you might envision chaos. On any one reef, you might expect thousands of individuals, representing dozens of species, in endless random motion, mixing with each other in a riot of color.

In reality, however, the behaviors of the fish give a great deal of regularity and structure to these fish communities.

If you are able to visit a reef and watch closely, you will notice that individuals of some species occur almost entirely in single-species groups—schools—that often stay close to particular coral structures. Individuals of some other species—such as the butterflyfish seen here—swim about in pairs. Virtually every time you see them, they are in pairs. Individuals of still other species are always associated with sea anemones, often living among the anemones' tentacles. The ecological community is structured by the behaviors of the fish.

We can observe the same phenomenon in other types of communities, such as those of antelopes in the savannas of East Africa. Dozens of antelope species coexist in these grasslands—but not in chaos. Often when you see impala antelopes (*Aepyceros melampus*), for example, many of the individuals are in groups in which only one animal

has large antlers. This structuring of the ecological community results from behavior. In this case, a dominant male—the animal with antlers—defends an area in which he gathers females around him and repels other males that attempt to join the group.

"Social behavior" refers to the behavioral relationships of individuals with other individuals of their own species. On the coral reef in the photo, we see two types of social behavior: school formation and pair formation. Throughout the study of behavior, a central question is why the behaviors we observe have evolved. Regarding social behaviors, what advantages might they have for the animals that participate in them?

Q In what ways might schooling behavior and pairing behavior be advantageous for the individuals involved?

CONCEPT 40.1 Behavior Is Controlled by the Nervous System but Is Not Necessarily Deterministic

Animals are distinctive in that behaviors play central roles in their interactions with each other and with their environments. They can rapidly approach each other, flee from each other, vocalize, seek shelter, and migrate—all by using their muscles. Of all animal characteristics, adjustments of behavior are often the most visible responses to environmental change. Today, for example, many migratory animals are changing the timing of their migrations in response to climate change (**FIGURE 40.1**). Behavioral shifts of populations into new habitats closer to the poles may be the greatest hope of many to survive if conditions where they currently live become too warm.

> **LINK**
>
> The effects of climate change on ecosystems and communities are complex, and changes in the behavior of a species may not be sufficient to ensure its survival; see **Concept 45.5**

When an animal engages in behaviors, biologists today agree that the animal's nervous system activates and coordinates the behaviors. When lizards run, for instance, neurons stimulate their leg motions. Similarly, when people take part in animated conversations, their brains activate their hand movements and facial expressions. According to this viewpoint, although behaviors—such as leg motions and smiles—are fleeting and not in themselves material objects, they have a material basis: they arise from brain tissue, neurons, and the movements of ions that give rise to nerve impulses (see Concept 34.2).

Many types of evidence point to the neural basis of behavior

We know that particular types of human behavior depend on the function of particular brain regions. For example, if the part of a person's brain known as Broca's area (see Figure 34.26B) is badly damaged by accident or disease, the person may be perfectly fine in almost all ways but will have extreme difficulty with talking or writing. This sort of "negative" evidence (what goes wrong when a brain region is missing?) is complemented by positive evidence from brain-imaging studies in normal people. As seen in Figure 34.27, when a person speaks, specific brain regions show evidence of increased metabolism. These types of evidence point to a neural basis for complex behaviors involved in human communication.

Additional evidence for the neural basis of behavior comes from a very different source: the study of certain highly stereotyped animal behaviors, often called **fixed action patterns**, which are expressed by animals without prior learning and are often resistant to modification by learning. These behaviors point to control by the nervous system because they are sometimes elaborate and yet they depend solely on the simple presence of a healthy nervous system to be performed. A classic example is the
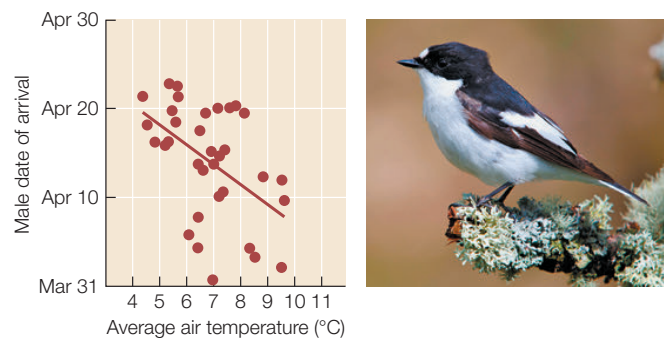
FIGURE 40.1 Migratory Birds Have Returned Earlier to the Netherlands in the Spring as Temperatures Have Risen Pied flycatchers (*Ficedula hypoleuca*) overwinter in Africa and migrate back to the Netherlands in the spring. Over a 34-year period, air temperature in the Netherlands has increased because of climate change, and males have arrived earlier. There has been a statistically significant correlation between average arrival date and average air temperature, as this graph shows. Each symbol corresponds to one year. Air temperatures were measured each year between March 16 and April 15, and all the measurements for each year were averaged to get the temperature plotted for the year.

begging behavior of gull chicks. In some species of gulls, adults have a red dot on their bills. The chicks, in a fixed action pattern, peck at the red dot when a parent returns to the nest from foraging, and this pecking stimulates the parent to regurgitate food. Pecking at a red dot is so stereotyped that newly hatched, naive gull chicks peck at models of gull heads with a red dot (although they respond only slightly to models without a dot) and even at red-dotted models of a beak without a head (**FIGURE 40.2**). Web spinning by some spiders is another example of a highly stereotyped, unlearned behavior. The spinning of a web involves hundreds or thousands of movements performed in sequence, and each time a spider builds a web, the sequence is largely the same. Yet in many species there is no opportunity for a spider to learn how to build a web from another spider because the adults die before their eggs hatch.
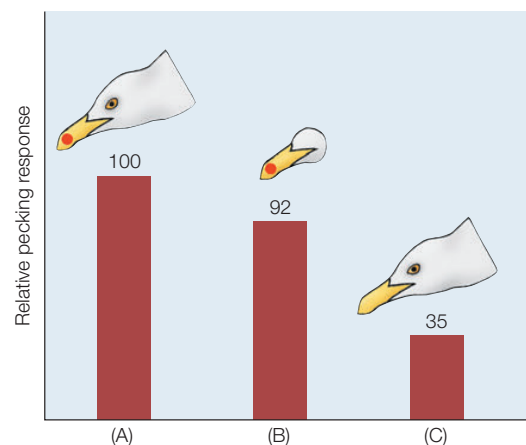
FIGURE 40.2 Expression of a Fixed Action Pattern (A) Herring gull (*Larus argentatus*) chicks instinctively peck at a cardboard model of an adult gull head with a red dot on the bill and (B) even at a model of just a bill with a red dot. (C) If presented with a model of a gull head without a red dot, the chicks respond to only a small extent.

Behaviors evolve

Recognizing that neural tissue gives rise to behaviors, we can expect behaviors to evolve. As is true of all tissues, the properties of neural tissue are in part encoded by genes, which are mutable and passed from generation to generation. If certain gene variants, or alleles, produce more adaptive behaviors than others, natural selection can favor those alleles. In this way the frequencies of alleles in a population can change so that the properties of the neural tissue—and the behaviors coded by the tissue—adaptively evolve.

Many studies establish that genes can exert important effects on behavior. Perhaps the most graphic evidence comes from studies of mutants in fruit flies (*Drosophila*). One of the most important examples involves mutations in a fruit fly gene named *per* (for *period*). (We now know that mammals have homologs of this same gene.) Around 1970, Seymour Benzer and his colleagues reported mutations in this gene that radically altered the flies' daily rhythm of activity under control of the circadian clock. To investigate these mutant flies, the investigators studied them in constant darkness, where their alternating periods of inactivity and activity were timed by their circadian clock, not by observations of day and night. In flies with ordinary, non-mutant *per* genes, each episode of activity started about 24 hours after the previous episode. One of the mutant alleles of *per* caused episodes of activity to be only about 19 hours apart. Another caused them to be about 29 hours apart. Studies of *per* thus demonstrated that single gene mutations sometimes alter behavior.

> **LINK**
>
> You can review the properties of circadian clocks in **Concept 29.6**

House mice (*Mus musculus*) in North America provide an elegant illustration of adaptive evolution of behavior in free-living wild populations. House mice did not live in North America prior to European colonization. They arrived as stowaways on European ships, presumably in random groups. Carol Lynch trapped wild house mice at five locations, from warm Florida to cold Maine. Within the mice from each location, she then paired males and females in her lab to obtain lab-born, lab-reared offspring, which she studied. All the mice studied had been born and grew up in exactly the same lab environment. When Lynch measured the nests they made, she found a trend: under identical conditions, the mice from progressively more northern populations tended to build bigger (and thus warmer) nests (**FIGURE 40.3**). This result points to the evolution by natural selection of a genetically controlled, behavioral propensity to build bigger nests in wild mouse populations that settled in locations where big nests are particularly advantageous.

Current studies with artificial selection indicate that behavior can evolve remarkably rapidly. In artificial selection (as opposed to natural selection), human researchers choose which combinations of animals have the most offspring, mimicking natural selection but in a highly controlled way. In one such experiment, researchers gave each mouse in a large population a running wheel and then monitored the number of revolutions
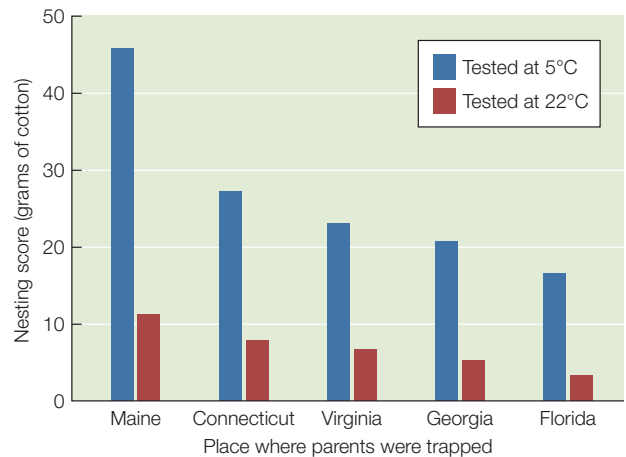
FIGURE 40.3 Nest Building by House Mice from Five Locations
All mice were born in the lab and tested under identical conditions. Their parents were trapped at the five locations shown. Mice were tested at two different temperatures. Nest building by each mouse was measured by summing the weight of cotton the mouse used to build four nests. The graph shows average nest building by the mice tested at each temperature.

each mouse voluntarily ran per day. Males that ran the highest numbers of revolutions were then mated with females that ran the highest numbers to produce a new generation of mice. When those mice grew to adulthood, they were put through the same process. This selection procedure was repeated generation after generation. After only 13 generations, the selected mice on average ran 12.1 kilometers per day, more than twice as far as control mice (5.5 kilometers per day). Primarily, the difference reflected faster running by the selected mice, rather than a longer time spent running. Studies revealed critical changes in the brains of the selected mice, indicating that a difference had evolved in the neural control of running behavior.

Despite its neural basis, behavior is not necessarily simplistically deterministic

Earlier we noted that behaviors are often fleeting and not in themselves material objects, but they have a material basis because they arise from neural tissue. Regarding human behavior, this dichotomy—nonmaterial behavior arising from material substance—attracts the attention of virtually all branches of scholarship. Biologists, psychologists, anthropologists, sociologists, theologians, and criminologists are all concerned with the dichotomy and ponder it.

Ever since the modern study of biology began, some scientists have argued for **biological determinism**. Determinism, as applied to behavior, means that the behaviors of animals are hardwired by genetics. In this view, an individual's genes orchestrate his or her neural properties in fixed ways that in turn affect his or her behavior in fixed ways, leading to predictable behaviors. Also, in this view populations of individuals, such as different racial groups, can differ genetically in ways that produce inflexible and predictable differences in behavior among the populations.

Almost all biologists are convinced that some simple animals exhibit determinism. Clams, for example, are inflexible in

many of their responses to their environment. Here, however, we focus on animals with advanced nervous systems. In particular, we focus on people.

Belief in human biological determinism flourished among some biologists in the nineteenth and early twentieth centuries. For example, at that time some prominent biologists believed (incorrectly) that a person's intelligence is determined by his or her inherited brain size. According to this discarded view, the mental capacities of racial groups could be predicted by measuring relative brain sizes. In the mid-twentieth century, the Second World War and the slaughter of people in gas chambers—based on a theory of genetic inferiority—greatly reduced enthusiasm for the biological determinist view of human behavior. Later, people who argue for the deterministic view became more vocal as the twentieth century drew to a close, a trend that has continued into the twenty-first century.

Students of biology need to be aware of the two sides in this debate. Arguments for and against determinism are too important to be lost in a fog. Many arguments for determinism found in books and magazine articles marketed to the general public are not well supported by objective, statistically supported, and relevant data of the sort required for ideas to be deemed scientific.

In what ways could the behavior of animals with advanced nervous systems not be simplistically deterministic despite its neural origins? Behavior is dramatically more flexible than any other biological trait. This is true in part because learning modifies behavior. In addition, recent discoveries (which we will shortly discuss) point to important epigenetic effects on behavior. These are non-genomic effects that can exert lifelong influences and may be transmissible from one generation to the next (see Concept 11.3). As animals develop and live their lives, each individual can interact in unique ways with its environment, and—because of learning and epigenetic effects—these interactions can result in dramatic behavioral differences among genetically similar individuals.

The greatest unresolved question in all of biology is probably the question of how the human mind emerges from the human brain. The unresolved nature of this question, despite its profound importance, emphasizes that scientists have much to learn about mental phenomena and the behaviors they unleash.

CHECKpoint   CONCEPT 40.1

✓ What physical objects provide the basis for animal behaviors?

✓ When a male robin is in reproductive condition, it has bright red breast feathers and will aggressively attack other male robins. It will also attack a simple tuft of red feathers on a stick. How does this seemingly maladaptive behavior relate to the concept of a fixed action pattern?

✓ Considering behaviors classified as fixed action patterns, in what way are they passed from one generation of a species to the next?

✓ How do experiments on artificial selection of wheel running in mice provide insight into the rate of evolution?

We have already noted that development and learning often affect an animal's behavior. Now we will focus on these important processes.

CONCEPT 40.2   Behavior Is Influenced by Development and Learning

The particulars of an individual animal's life—such as the exact place it lives and the exact appearances of its parents—are typically not predictable. Information about these particulars therefore cannot be inherited. Biologists think this is the fundamental reason why animals have evolved the ability to **learn**—by which we mean the ability of an individual animal to modify its behaviors as a consequence of individual experiences that took place earlier in its life. Suppose that a mouse living in a forest is less likely to be caught by a predator if it can rapidly return to its burrow. Prior to the mouse's birth, there would be no way to predict the location of that mouse's burrow or landmarks useful for finding the burrow. For this reason, natural selection could not provide inherited information on these particulars. However, natural selection has favored the evolution of learning abilities. A mouse inherits mechanisms by which it can learn locations. Then, during its life, it uses those mechanisms to incorporate specific information on its actual burrow location and useful landmarks into its escape behavior.

Lee Metzgar did experiments on white-footed mice (*Peromyscus leucopus*) to test the validity of the idea that animals learn about their surroundings in ways that aid their survival. An important background point for understanding Metzgar's experiments is that when these mice move around on the forest floor, they commonly run next to logs or sticks. An adult mouse was allowed to live for several days in a seminatural arena with a simulated forest floor, consisting of small logs, sticks, and dead leaves. There was no burrow in this room, but there were logs big enough to provide protection from aerial attack. Then the mouse was temporarily removed from the room and a hungry screech owl was introduced. Soon afterward, the mouse was returned to the room, along with a new mouse that lacked prior experience with the room. The arena was then observed until the screech owl caught one of the mice (**FIGURE 40.4**). To a strongly significant extent, the new mouse was the one more likely to be caught. However, if the logs, sticks, and leaves were replaced with new but similar items in different locations immediately before the test with the owl, the two mice in the room were equally likely to be caught. These results indicate that the experienced mouse learned the locations of logs and sticks during the days it lived in the room. It knew escape routes and places where it was safe, provided the logs and sticks were where the mouse had learned them to be.

Specific information of critical survival value is often learned during early postnatal development

Konrad Lorenz, one of the pioneers of the modern study of behavior, discovered that if he associated with young greylag geese (*Anser anser*) soon after they hatched, they thereafter treated him as if he were their parent. They associated with him instead of

FIGURE 40.4 **Screech Owls Prey on Mice**   Screech owls watch from perches above the forest floor. When an owl sees or hears a mouse, it drops from its perch and grasps the mouse with its talons unless the mouse behaviorally evades capture. The species shown here is an eastern screech owl (*Megascops asio*).

other geese and followed him everywhere. This attachment bordered on impossible to change. Lorenz named this phenomenon **behavioral imprinting** (not to be confused with genomic imprinting; see Concept 11.3). By now we know that imprinting occurs in many other species of birds and some other animals. Today behavioral imprinting is defined to be a type of learning that is distinctive because the learning takes place within a relatively narrow window of time early in postnatal life and, after that, is inflexible. Imprinting can have lifelong consequences. When male geese imprint on a person at the start of their lives, they later, in adulthood, prefer trying to mate with people. During normal development, geese imprint on—and establish a strong attraction to—their true parents and species.

Indigo buntings (*Passerina cyanea*) and some other bird species are noteworthy for navigating by the stars. As adults, the birds migrate at night, using the stars to determine the direction in which they fly. After this amazing phenomenon was first discovered, Stephen Emlen studied young buntings in a planetarium to learn more about the mechanism they use. Emlen established that the birds need to know the North Star to navigate correctly. But how do they know which star is the North Star? His experiments revealed that each young bird has to learn the correct star during its first few weeks after hatching. In the planetarium, Emlen could make the artificial sky rotate around any star he chose. Young birds learned to identify that star—the one the sky rotated around—and later, when they were under a natural sky, they treated that star as the North Star for the rest of their lives. When buntings develop outdoors in natural environments in the Northern Hemisphere, the sky appears to rotate around the true North Star (**FIGURE 40.5**). In this way, buntings in nature learn the true North Star.

Another type of early learning with enormous consequences—seen in many birds—is learning of species-specific songs. Darwin's finches in the Galápagos Islands provide just one of many examples (see Concept 17.3). In adulthood, the males of each finch species sing a species-specific song that attracts females (which do not sing) in a species-specific way. The songs are not inherited, however. Instead, each male learns the song he will sing for the rest of his life during a period of about 30 days, 10–40 days after he hatches. During that period a young male is in or near his nest, and his father sings nearby. The young male learns his song by an imprinting-like process by listening to (and later duplicating) his father's song. Particular brain regions, larger in males than in females, are required for this learning. If a young male's father dies and he learns the song of a different species by hearing an adult of a different species sing during his critical learning period, the young male will later sing an incorrect song and attract females of the incorrect species.

Early experience also has other, more global effects on behavior

A large body of knowledge points to early experience as having multiple, intricate lifelong effects. These effects are specific to each individual, depending on that individual's particular experiences. For example, an ongoing series of experiments on lab rats is bringing to light new revelations regarding behavior and early development. When they are carefully observed, rat mothers are found to exhibit different parenting behaviors. Two categories of mothers are recognized. Here we will call them "high-caring" and "low-caring." Mothers in both categories are statistically the same in how often they nurse their young and in the absolute amount of contact they have with their suckling offspring. They differ, however, in how much they lick and groom their young during nursing and in how much they adopt a favorable posture for easy suckling. Mothers in the high-caring category lick and groom a lot and adopt a favorable posture. Low-caring mothers lick and groom to a lesser extent and adopt a less favorable posture.

FIGURE 40.5 **The Stars in the Northern Hemisphere Seem to Make Circles around the North Star**   The stars seem to make circles around the northern end of Earth's axis—the position of the North Star—because of Earth's rotation. This apparent movement of the stars is evident in a long exposure of the northern sky, as in this photograph, in which the camera shutter was kept open for several hours.

Offspring of the two categories of mothers have been raised to adulthood and then studied in two potentially threatening environments that are new to them. In both environments, the adult offspring of low-caring mothers are far more likely to exhibit fear. For example, rats deprived of food for 24 hours were placed, one at a time, in a novel, brightly lit arena in which food was provided at only one place in the very center. This environment is intimidating because rats prefer low light and prefer not being out in the open. The behavioral differences between the two groups of rats were dramatic. Hungry adult offspring of low-caring mothers waited much longer than did hungry adult offspring of high-caring mothers to go to the food and start eating, and they spent far less time eating.

How can a young rat's early experiences change its behavior throughout its life? In the case we are discussing, epigenetic effects are in part responsible and play a pivotal role (see Concept 11.3). Key regulatory genes in stress-response biochemical and hormonal pathways are tagged with epigenetic marks in early life. The tagging of these genes is different in offspring of low- and high-caring mothers. Such differences in epigenetic marking (which by definition do not alter the DNA itself) are maintained throughout the life of an individual, permanently altering the individual's stress responses.

Malnutrition in early life is also known to affect epigenetic tagging in rats, as is abandonment. Marks from these early experiences persist into adulthood, altering gene expression and behavior throughout life.

In Africa, massive swarms of millions of migratory locusts (*Locusta*) sometimes form and fly across the landscape, causing devastation to crops wherever they land to eat. An amazing feature of this phenomenon is that each individual locust is capable of having two radically different behavioral phenotypes. One phenotype is that the individual avoids other individuals. A population of individuals expressing this phenotype is spread out and inconspicuous. Alternatively, each individual may be highly gregarious—meaning the population forms a swarm. Individual experience determines the phenotype. Individuals that are never forced to live closely together retain the solitary phenotype. The same individuals become a swarm if forced into close contact—for instance, if they are forced to feed next to each other, in the same places, because of food shortage.

CHECKpoint CONCEPT **40.2**

✓ In captive breeding programs for whooping cranes, an endangered species of bird, the young birds must be prevented from seeing people because otherwise they will not mate with cranes. How can this be?

✓ Do epigenetic marks alter the sequence of base pairs in an animal's genome?

✓ Penguins often breed in large groups in which nesting females are very close to each other, in contrast to some other species of birds in which nesting females are widely separated. Why might penguins have evolved particularly strong imprinting on their mothers?

Behavior is integrated with the other characteristics of animals. Next we will discuss a few ways in which behavior interacts with other aspects of animal function.

CONCEPT **40.3** **Behavior Is Integrated with the Rest of Function**

Escape running by pronghorn (*Antilocapra americana*) is one of the greatest spectacles of animal behavior on Earth (**FIGURE 40.6**). Although cheetahs (*Acinonyx jubatus*) achieve the highest speeds of all running animals (about 110 kilometers per hour), they can sustain those speeds for only a minute or two. Pronghorn can run at more than 50 kilometers per hour for tens of minutes—the highest *sustained* speeds known in running animals.

Pronghorn strikingly illustrate that an animal's behavior often depends on—and is integrated with—the animal's other characteristics. For pronghorn to *behave* as they do, their muscles must be able to produce enormous forces over long periods. For exercise to be sustained in this way, it has to be based on aerobic, oxygen-based ATP production (see Concept 33.3). Investigators have discovered that almost all aspects of pronghorn are specialized so that the animals can deliver O_2 at very high rates to their muscles, use the O_2 at very high rates to make ATP in the muscle cells, and use the ATP at very high rates to perform intense muscular work. For example, compared with other mammals of their size, pronghorn have exceptionally large lungs and skeletal muscles, and their muscle cells are exceptionally tightly packed with mitochondria.

Toads and frogs have evolved contrasting behavioral specializations that depend on their biochemistry of ATP synthesis

When toads such as the western toad (*Bufo boreas*) are chased, they hop away at modest speeds that they can maintain for many minutes. In contrast, when leopard frogs (*Rana pipiens*)

FIGURE 40.6 Pronghorn Run at the Fastest Sustained Speeds of Any Running Animals Their running behavior is possible only because they have also evolved systems of oxygen transport, ATP production, and muscular contraction that are up to the task. Pronghorn occur in grasslands from northern Mexico to southern Alberta and Saskatchewan.

APPLY THE CONCEPT

Behavior is integrated with the rest of function

When chased, both frogs and toads respond by hopping away until fatigue prevents them from going any farther—a behavior dependent on the synthesis and subsequent use of ATP during muscle contraction. Frogs hop away at high speeds using anaerobic glycolysis, a biochemical process that produces large amounts of ATP very rapidly but that can't be sustained for long periods of time. Toads use aerobic respiration, a process that produces less ATP per unit of time but that can operate for a much longer period. Suppose you make records of speed and duration for two cases of escape behavior as in the figure (these data, although modeled on actual data, are hypothetical).

1. Which animal fatigued more quickly?
2. Which strategy of ATP synthesis allowed for the achievement of a higher maximum speed?
3. Which animal traveled a greater distance? (Hint: Determining the number of squares under each graph of speed versus time will allow you to integrate the information and estimate distance traveled.)
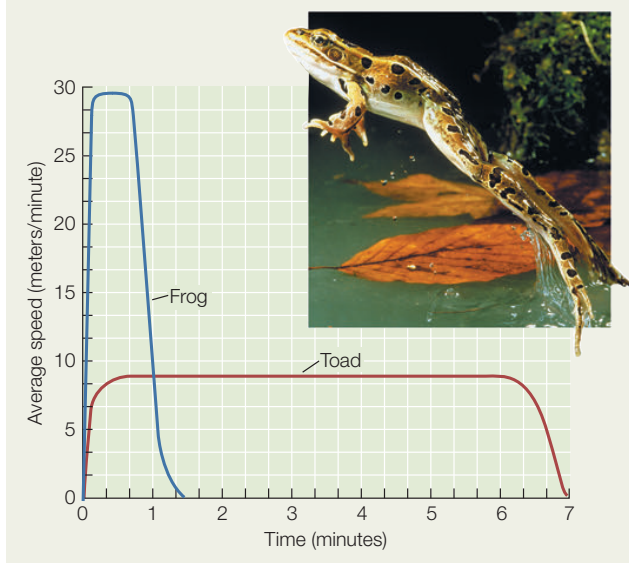
are chased, they leap away at lightning speeds—far faster than toads—but they become fatigued and stop leaping after a minute or two. These contrasting escape behaviors in toads and frogs reflect differences in the biochemical mechanisms that their leg muscles use to make ATP for escape running. Toads and frogs thus illustrate that there are often intimate links between escape behavior and the biochemistry of ATP synthesis.

The usual rule, when comparing related animals, is that aerobic ATP production is slow and resistant to fatigue, whereas anaerobic ATP production is fast and subject to rapid fatigue (see Concept 33.3). Enzyme studies show that toads have evolved high levels of enzymes required for *aerobic* ATP

production in their leg muscles. Frogs, by contrast, have an enzyme profile that emphasizes high rates of *anaerobic* ATP production. These evolved enzyme differences explain the differences in their hopping behavior.

Behaviors are often integrated with body size and growth

Many insects, such as crickets and katydids, sing to communicate with other members of their species. Among these insects there is a broad tendency for the tonal frequencies of their songs to vary regularly with body size. In a pipe organ, the large pipes produce the lowest frequencies of sound. For much the same reason, insect species of large body size tend to produce songs of lower frequency than species of small size. This same trend is observed in singing frogs. Body size helps determine how communication occurs in these animals.

In many species, individuals must grow to a large adult size before they can successfully consummate reproductive behaviors. Male elk (*Cervus elaphus*) in Scotland, for example, rarely father offspring before they are 5 years old, even though they are reproductively mature at 2 years of age. Being reproductively mature is not sufficient for successful reproductive behavior. A male must also be big enough and experienced enough to dominate other males.

When spotted hyenas (*Crocuta crocuta*) in a pack capture a zebra or antelope, they are famous for eating everything, including the skeleton, within minutes in a frenzy of feeding. For young hyenas to get food during this group feeding behavior, they need to be as effective as possible in grabbing bites to eat. Being able to bite through bone is a great advantage because it permits much faster feeding than trying to strip flesh off bone. A young hyena's feeding behavior is transformed—in ways that raise its odds of survival—as its jaws, jaw muscles, and teeth mature, permitting faster and faster bone consumption (**FIGURE 40.7**).

CHECKpoint CONCEPT 40.3

✓ Prior to mating, European eels swim for months at a time as they travel from their adult habitats in Europe to spawning grounds in the ocean near Bermuda, a distance of about 5,500 kilometers. This behavior depends on ATP production for the swimming muscles. Would you predict that European eels mostly use aerobic or anaerobic means of synthesizing ATP during this migration?

✓ Simply because of laws of physics, if an animal falls from a substantial height, its risk of injury from whole-body impact on the ground depends on its body size. For a mouse-size animal, the odds of being hurt by the whole-body impact of a fall are near zero. The risk, however, increases with body size to the point that for a horse, death is inevitable. How would this size-dependent trend affect the evolution of behaviors that involve leaping from branch to branch within trees?

✓ What aspects of pronghorn muscle cell physiology allow the animals to maintain high escape running speeds?
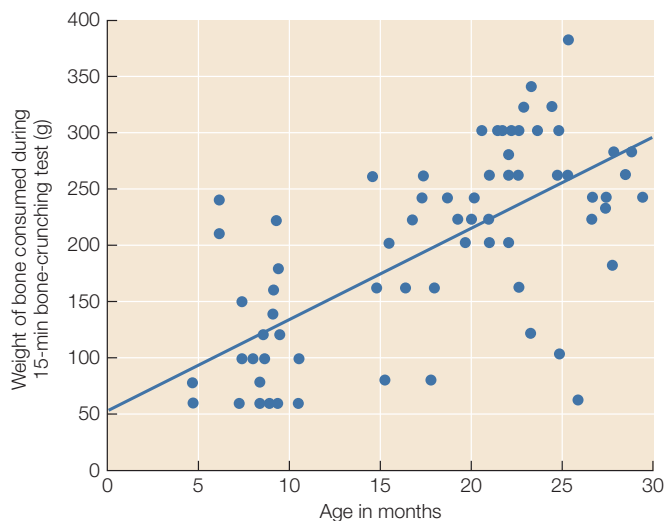
FIGURE 40.7 Young Hyenas Must Mature to Feed on Bone Rapidly
Spotted hyenas of various ages were given a standardized "bone-crunching test." The amount of bone they could consume in 15 minutes increased dramatically as they aged and their jaws and jaw muscles became stronger. Young animals are limited in their ability to compete with adults during group feeding behavior at a kill. The line was fitted by linear least-squares regression (see Appendix B).

Let's now turn our attention to travel behavior. Most animals move from place to place over the surface of Earth during their lives. Travel behavior of this sort can help animals find things they need, but also entails risks, including the risks of getting lost. Travel behavior is one of the important topics in the study of animal behavior.

| CONCEPT **Moving through Space Presents** |
| **40.4 Distinctive Challenges** |

For most animals, movement through space is critical for success. The distances covered may be short, as when animals search for food each day. Some animals, by contrast, travel almost halfway around the globe during seasonal migrations. Moving through space requires muscle function. It also requires that animals meet the challenges of navigation and orientation, ensuring that they can find their goals and return home. **Navigation** refers to the act of moving toward a particular destination or along a particular course. **Orientation** refers to adopting a position, or a path of locomotion, relative to an environmental cue such as the sun.

Trail following and path integration are two mechanisms of navigation

To navigate, animals sometimes simply follow trails. Foraging workers in many species of ants use this method. If certain workers find a food source, they use a pheromone to mark their path as they return to their colony's home. A **pheromone** is a chemical compound or mix of compounds that is emitted into the outside environment by individuals of a species and

that elicits specific behavioral responses from other members of the same species. One sex sometimes uses pheromones to attract the other sex. In the case of the ants, as worker ants return home from a profitable food source, they deposit minute quantities of their species-specific trail pheromone along the way. In this manner they leave behind a fully marked trail between the colony nest and the food source. Other workers then detect the pheromone and find the same food source by following the trail.
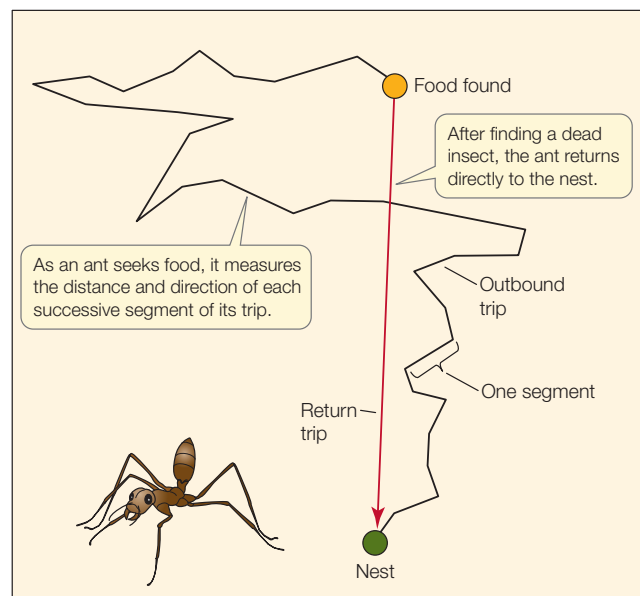
FIGURE 40.8 A Foraging Trip by a Worker Ant of a Desert Ant Species (*Cataglyphis*) The worker's outbound trip consists of a series of segments as the ant wanders the desert surface seeking dead bodies of heat-killed insects. At any point, however, the ant can return to its home nest quickly in a straight line. The ants accomplish this task with a brain that weighs 0.1 milligram!

Ants of the genus *Cataglyphis* are specialized to live in hot, dry deserts. Instead of using trail pheromones, they use path integration to navigate during foraging. Colonies of *Cataglyphis* live underground, where temperatures are mild. Worker ants emerge to collect food during the daytime, when the desert surface is fiercely hot. Their principal food is the dead bodies of other desert insects killed by overheating. Why do the workers forage during the heat of the day? The answer seems to be that this behavior enables them to find heat-killed insects promptly after death, before the bodies of the dead insects dry out. In this way the workers acquire water—which is extremely valuable in the desert—as well as food. Experiments have shown that a *Cataglyphis* worker that is searching far and wide for a dead body always knows how to run straight back to its underground nest. A worker does not retrace its path to get home. Instead, if it finds a dead body or starts to overheat, it returns home by the shortest possible, straight path. This behavior enables a worker to get underground quickly.

How does a foraging *Cataglyphis* worker know how to find its home nest without retracing its outbound travels? Let's think of the worker's outbound path as a series of segments (**FIGURE 40.8**). The worker monitors the length and the compass direction of each segment. Then, by a process called path integration, it integrates, or puts together, all this information on segment lengths and directions to know where it is relative to its nest. We know this sort of process can work because it closely resembles the process (called dead reckoning) that sailors often used 150 years ago to know where they were at sea on an hour-by-hour basis.

How does a *Cataglyphis* worker measure the length and direction of each segment of its foraging path? It measures the length of each segment by counting steps (**FIGURE 40.9**). It can determine the direction by several means, as we will soon discuss.

Animals have multiple ways of determining direction

Much of the earliest research on animal orientation focused on homing pigeons. These pigeons fly back to their home nests even after having been transported tens of

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INVESTIGATION

FIGURE 40.9 An Insect Odometer   Desert ants navigate by path integration, which requires information about both direction and distance. How do they measure distance? Matthias Wittlinger and his colleagues investigated the possibility that Saharan desert ants (*Cataglyphis fortis*) "count" steps to keep track of how far they've walked.[a] Because every stride is a certain length, the number of steps can theoretically measure the distance traveled.

HYPOTHESIS

Desert ants measure distance by keeping track of the number of steps they take.

METHOD

1. Train ants to walk from their nest to a feeder 10 meters away and then back to their nest.
2. Capture trained ants that have walked from the nest to the feeder and modify them before they start back to their nest. Separate them into three groups, with 25 ants in each group. Shorten the legs of one group ("Stumps") by removing their lower leg segments. Lengthen the legs of another group ("Stilts") by gluing pig bristle extensions to their legs. Leave the legs of the third group ("Normal") unchanged as a control.
3. Release the ants at the feeder, so that they can return to their nest. Measure how far they walk before they stop to search for the nest entrance (indicating that they've arrived where they expect the nest to be).
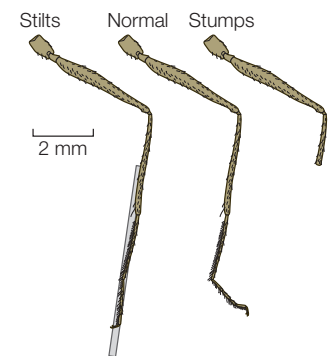
RESULTS

The ants with shortened legs did not walk far enough, because their stride was shorter than normal.[b]

The ants on stilts walked too far. They walked the number of steps that would have brought them to their nest with normal legs, but they overshot because their stride was longer than normal.
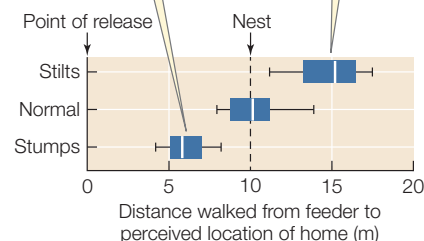
CONCLUSION

Desert ants behave as if they keep track of how far they travel by "counting" their steps.

ANALYZE THE DATA

In a second experiment, the same groups of ants (which had altered legs) were allowed to walk from their nest to the feeder on their altered legs and then return to their nest. The graph shows the distances the three groups of ants walked to get back to their nest.

1. How do these results differ from those obtained in the first experiment? Explain why they differ.

2. Why is this experiment an important control?

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]M. Wittlinger et al. 2006. *Science* 312: 1965–1967.
[b]The data are shown as a box plot. The vertical line inside the box is the median, the box indicates the middle 50% of the data, and the horizontal line that extends outside the box indicates the middle 90% of the data.

kilometers away. For instance, during both World Wars, homing pigeons were extensively used to carry messages. They were reared in home nests near command centers. They then were carried into battle and released with critical messages that they transported back to the command centers.

How can homing pigeons determine direction so they can fly home? One mechanism they use is a **sun compass**. They do not possess a physical compass. We say they have a sun compass because, in essence, they can determine where north, south, east, and west are by observing the sun. To understand the challenge of using the sun as a compass, suppose for a moment that you have no way to know the time of day and that you are suddenly dropped at an unfamiliar location. Suppose also that you see the sun just above the horizon. With the sun in that position, you would reason that when you face the sun, you are facing either east or west. Without knowing the time of day, however, you would not know which: east or west? From thought exercises like this, researchers hypothesized that when pigeons use the sun as a compass, the birds not only must observe the position of the sun but also must know the time of day so that they can calculate compass directions—north, south, east, and west—from the sun's position. The researchers hypothesized that pigeons use their circadian clock (see Concept 29.6) to provide the necessary information on time of day.

To test this hypothesis, the researchers (working in the Northern Hemisphere) released homing pigeons at a place from which the birds needed to fly south to return home. Think now about the compass position of the sun as it crosses the sky each day. (You can determine the sun's compass position by dropping an imaginary vertical line from the sun to the horizon and noting where the line intersects the horizon between east and west). The sun is in the east at sunrise, southeast at midmorning, south at noon, southwest at midafternoon, and west at sunset (**FIGURE 40.10**). Regardless of the time of day when pigeons were released, they tended to fly south. As shown in Figure 40.10A, in midmorning they flew at angle α to the right of the sun's position. Later in the day, in midafternoon, they flew at angle β to the left of the sun's position.

The pigeons were then placed in rooms where the lights were turned on 6 hours before sunrise and turned off 6 hours before sunset. After 2 weeks or so, their circadian clocks became entrained (see Concept 29.6) to the artificial light cycle. When the birds were then taken outdoors again and tested for their ability to return home, they did not fly south. For example, when released in midmorning, they flew east! This result provided strong evidence that the birds were using their circadian clocks to determine compass directions from the sun's position. In midmorning, the time-shifted birds thought the time was midafternoon because their internal clocks had been artificially reset. They flew at angle β to the left of the sun's position, traveling east (see Figure 40.10B).

By now, a wide variety of animals have been shown to have a sun compass. In most cases, their circadian clocks play an essential role.

Redundancy in mechanisms of orientation was one of the great discoveries to come from the early study of homing pigeons. Investigators found that instead of having a single orientation mechanism, the pigeons have multiple mechanisms. We now know that this sort of redundancy is observed often in the animal kingdom. Homing pigeons are able to find home on cloudy days when they cannot see the sun. A key orientation method they use on cloudy days is to detect Earth's magnetic field and orient to it. Homing pigeons also sometimes use landmarks such as hills to orient, and they may use odors, low-frequency environmental sounds, and learning from other pigeons.

Go to ANIMATED TUTORIAL 40.2
Homing Simulation
PoL2e.com/at40.2

Many insects and birds are able to determine compass directions by detecting patterns of polarized light in the sky. This

(A) Natural operation of sun compass

(B) Operation in a pigeon in which the circadian clock is entrained to be 6 hours off
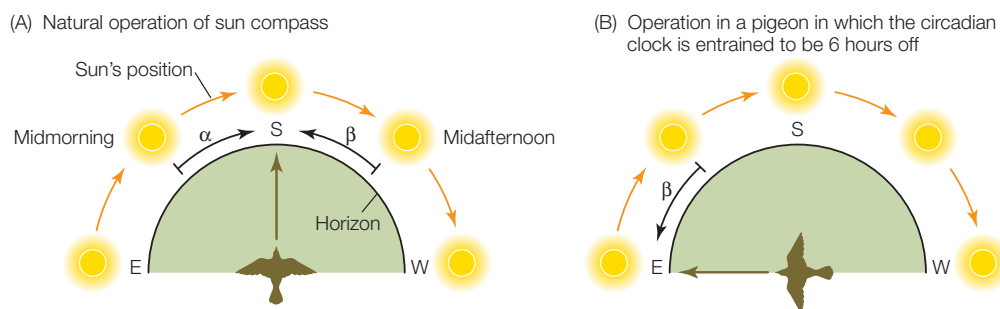
FIGURE 40.10 The Sun Compass of a Homing Pigeon Requires That the Pigeon Interpret the Sun's Position in the Sky Based on Knowledge of Time of Day A pigeon trained to fly south to find home was tested in the Northern Hemisphere. Here we see a bird's eye view of the southern horizon, from east to west, with the sun passing overhead between dawn and dusk. (A) The pigeon with its circadian clock functioning normally. Using time-of-day information from its circadian clock, the bird flies at angle α to the right of the sun in midmorning but at angle β to the left of the sun in midafternoon. (B) The pigeon with its circadian clock entrained so that the clock says the time is midafternoon when the actual time is midmorning. The pigeon flies at angle β to the left of the sun and thus flies east instead of south.

Go to ANIMATED TUTORIAL 40.1
Time-Compensated Solar Compass
PoL2e.com/at40.1

mechanism is particularly common in insects, where it depends on specialized photoreceptors. The atmosphere is filled with tiny particles, such as dust, water droplets, and ice crystals. When sunlight strikes such particles, the reflected light rays become polarized, or aligned parallel to one another, to some degree, giving rise to polarization patterns. These patterns are present even if there are only small patches of clear sky. For this reason, the "polarization compass" is often functional on cloudy days.

We discussed earlier how *Cataglyphis* ants in the desert employ path integration by measuring the distances and directions of all segments of a trip they make away from their nest. If a prominent landmark is present, the ants determine their direction of travel relative to the landmark. However, they function perfectly well without any landmarks. Under those circumstances the principal mechanism they use to determine direction is a compass based on polarized light detection. They also have a sun compass.

Birds that migrate at night can use the stars to determine their directions of travel (see Figure 40.5). A great many animals besides birds are now known to be able to orient by using Earth's magnetic field.

Honey bee workers communicate distance and direction by a waggle dance

Honey bees, like ants, live in colonies in which worker individuals perform services for the colony as a whole. When a worker bee goes on a foraging flight to gather food and finds flowers containing pollen and nectar, she returns to the hive and communicates her discovery to other workers by a specialized behavior called the waggle dance. During her foraging flight, she measures the distance and direction to the flowers. Her dance communicates both of those pieces of information to the other workers so that they also can fly to the flowers.

A bee that discovers a new patch of flowers measures the distance to the patch by monitoring the rate at which she flies past local landmarks (she measures this rate visually). To measure the direction to the flower patch, she monitors the angle of her flight relative to the compass position of the sun. Of course, as she measures these critical pieces of information, she is flying *horizontally* outdoors. After she returns to the hive, she performs her waggle dance on *vertical* honeycomb surfaces inside the hive, where it is dark and the sun cannot be seen. The marvel of the waggle dance is that it communicates the information on horizontal distance and angle to the sun while the bee is running ("dancing") on vertical surfaces in the dark.

During the dance, the bee moves in a repeating figure-eight pattern. She alternates half-circles to the left and right with a short, straight run between each half-circle (**FIGURE 40.11**). During each straight run, she waggles her abdomen. The duration of the straight, waggle run communicates the distance to the food source. The angle of the straight run relative to vertical communicates the direction to the food source. That angle matches the angle a bee needs to fly relative to the sun's compass position to find the food source. What happens if the sun is hidden by clouds? Honey bees can infer the position of the sun from atmospheric polarization patterns.
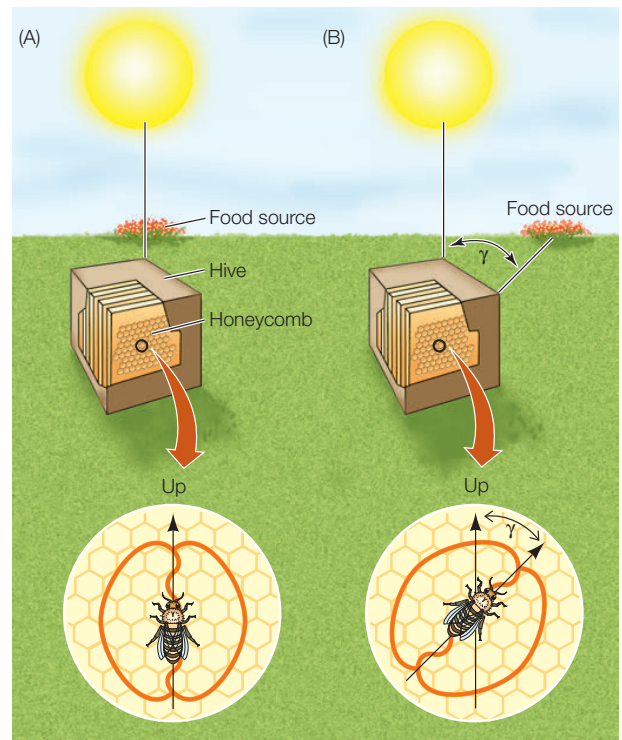
FIGURE 40.11 The Honey Bee Waggle Dance (A) A honey bee (*Apis mellifera*) worker runs straight up on the vertical surface of the honeycomb in a dark hive while wagging her abdomen to tell other workers in her hive that there is a food source in the direction of the sun. (B) When the waggle runs are at angle γ from the vertical, the other bees know that the same angle, γ, separates the direction of the food source from the direction of the sun.

Go to ACTIVITY 40.1 Honey Bee Dance Communication
PoL2e.com/ac40.1

Migration: Many animals have evolved periodic movements between locations

Today biologists are better able to track moving animals than ever before, because of technological innovations. Consequently, a revolution is underway in our understanding of migrations. For example, natural historians have long known that shorebirds called bar-tailed godwits (*Limosa lapponica*) spend their summers in Alaska and winters in New Zealand:

Bar-tailed godwit (*Limosa lapponica*)

Northern Florida
0°

Turtles exposed to magnetic fields mimicking those they would encounter at the northeastern edge of the gyre swam in a direction that would keep them within the gyre.

Northeastern edge
0°

Black arrows show the direction of current flow in the North Atlantic Subtropical Gyre.

Southern edge
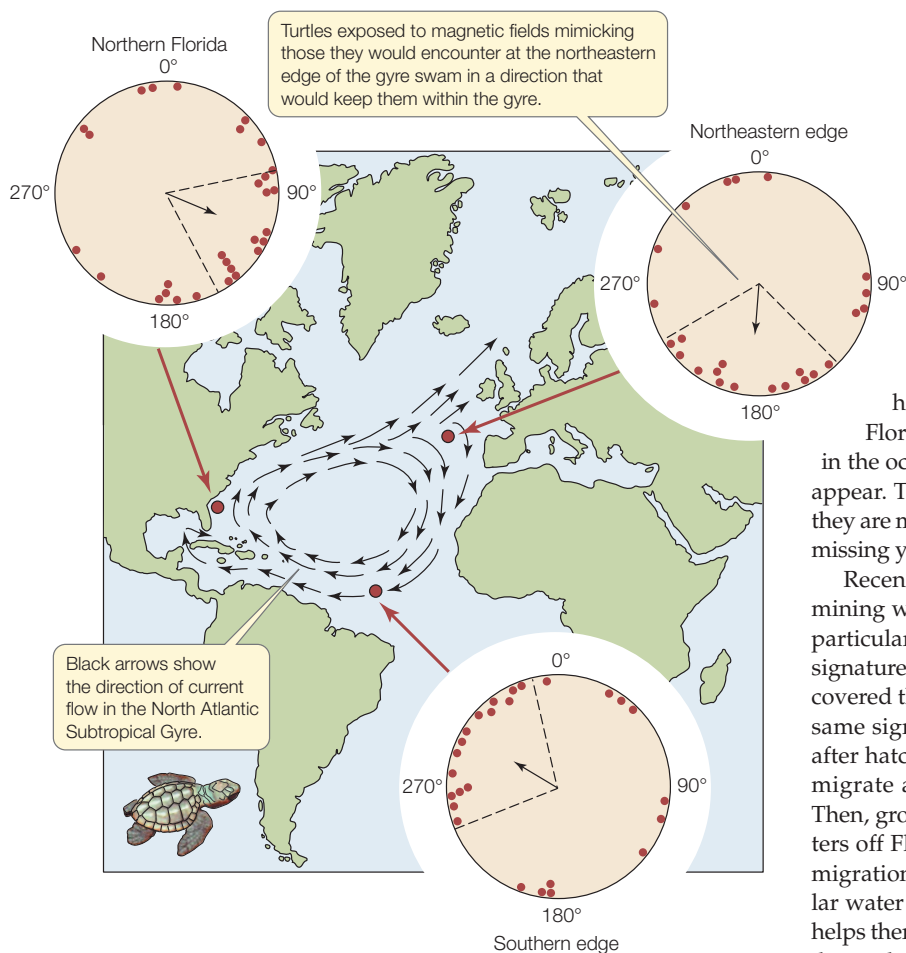
FIGURE 40.12 Young Loggerhead Sea Turtles Orient to Magnetic Fields as They Travel in a Giant Closed Circle across the Atlantic Ocean and Back Newly hatched loggerhead sea turtles, studied in a pool of water represented by the large tan circles, were exposed to magnetic fields that mimicked Earth's magnetic field at each of the three red-dotted locations in the ocean. Within each diagram of the pool (each large tan circle), each small dot shows the direction a turtle tried to swim, the solid arrow shows the average swimming direction, and the dashed lines show the 95% confidence limits for swimming direction. The data indicate that as sea turtles travel in the currents of the North Atlantic Subtropical Gyre, they orient relative to local magnetic fields to swim in directions that keep them within the closed circle of current flow.

Some of the mind-boggling details of their migrations could not be known, however, until individual birds could be outfitted with miniaturized electronics to track their flights. Researchers have just discovered that when the birds leave Alaska, they fly *nonstop* to New Zealand over the open water of the central Pacific Ocean—a trip of more than 10,000 kilometers. For the 6–9 days of the trip, the birds cannot eat or drink. They presumably do not sleep. Their flight muscles must engage in powering or controlling flight continuously day and night—not to mention the necessity of navigating accurately over endless expanses of water. As often happens in the practice of science, the tracking

studies of godits seem to raise more questions than they answer.

Specialists vary in the way they define migration. A useful general definition is that animals **migrate** when they periodically move from one location to a different location, remain for a substantial length of time, and later return.

One of the long-distance migrations that is currently best understood is that of young loggerhead sea turtles (*Caretta caretta*). Several decades ago, Archie Carr coined the term "the missing year" in describing these turtles, which hatch out of eggs on beaches in places such as Florida. For a while, the little turtles can be found in the ocean along the Florida coast, but then they disappear. The next time they are seen, about a year later, they are much bigger. Where have they been during their missing year, and how did they find their way back?

Recent genetic studies have been crucial for determining where the turtles go. The turtles that hatch in a particular region of Florida display a distinctive genetic signature in terms of allele frequencies. Researchers discovered that turtles in the ocean west of Africa have the same signature. This and other evidence indicate that after hatching in Florida, young loggerhead sea turtles migrate across the Atlantic Ocean to African waters. Then, growing as they go, they migrate back to the waters off Florida. The turtles do not need to power their migration entirely by swimming because a large circular water current (the North Atlantic Subtropical Gyre) helps them travel all along the way. As shown in **FIGURE 40.12**, the turtles use Earth's magnetic field to help them complete their journey and ensure that they do not get lost at sea. The tan circles in the figure show the results of experiments demonstrating that the turtles are able to orient their direction of swimming in relation to magnetic fields so that they stay in the circular water current.

CHECKpoint CONCEPT 40.4

✓ Why is an accurate circadian clock crucial to the sun compass method of orientation?

✓ In some species of ants, when workers employ a trail pheromone to mark a trail to a food source, each worker that goes to the food source adds more pheromone to the trail on its way home if it readily found food at the source. How could this process act as a positive feedback loop to draw large numbers of workers to a distinctively valuable food source?

✓ Why might natural selection favor the emergence of redundant methods of orientation?

Now we will turn to one of the themes with which we began this chapter, namely that animals often do not function alone. When animals interact with each other, behavior is the paramount way in which they do so.

A moment's reflection reveals that many animal species live in groups. Flocks of birds, schools of fish, and herds of antelopes are just a few examples. Many types of groups are considered societies. Specialists debate the exact meaning of a "society," but a broad, commonly used definition is that a **society** is a group of individuals of a single species, organized to some degree in a cooperative manner. The subject of **social behavior** includes both the behaviors of individuals that integrate the individuals into societies and the group behaviors of entire societies.

Living in a group has downsides. Grouping tends to make animals more visible. Diseases can spread more easily within a group, and a group may rapidly deplete food or other resources in the place where it is living.

Biologists presume that group living has evolved only if it provides advantages that exceed its disadvantages. Much of the research being done on societies today focuses on testing hypotheses regarding how individuals in a society benefit from living together in a group. Physiological advantages prevail in some cases. Penguins, for example, reduce their thermoregulatory costs in the cold of winter by huddling. Our focus here will be on potential behavioral advantages of group living.

Some societies consist of individuals of equal status

Sometimes the individuals in a flock, school, or herd seem to play similar, approximately equal roles in the function of the group. In a group of this sort, one advantage hypothesized for group living is that a group may enjoy enhanced sensory awareness of its environment because the members of the group can pool their individual sensory capabilities. A group of 50 vertebrate animals has 100 eyes instead of just 2. Groups may therefore have greater awareness of danger than individuals. One investigator found that a trained goshawk's success in capturing a pigeon in a flock decreased as the number of pigeons in the flock increased (**FIGURE 40.13A**). The larger the flock, the sooner one of the individuals in the

FIGURE 40.13 Group Living Provides Protection from Predators   Animals that live in groups can spread the cost of looking out for predators. (A) The larger the number of wood pigeons in a flock, the greater the chances that one of the pigeons will spot a goshawk before it attacks, and the lower the chances that the goshawk will capture one of the pigeons. (B) A young male Belding's ground squirrel gives an alarm call upon spotting a predator.
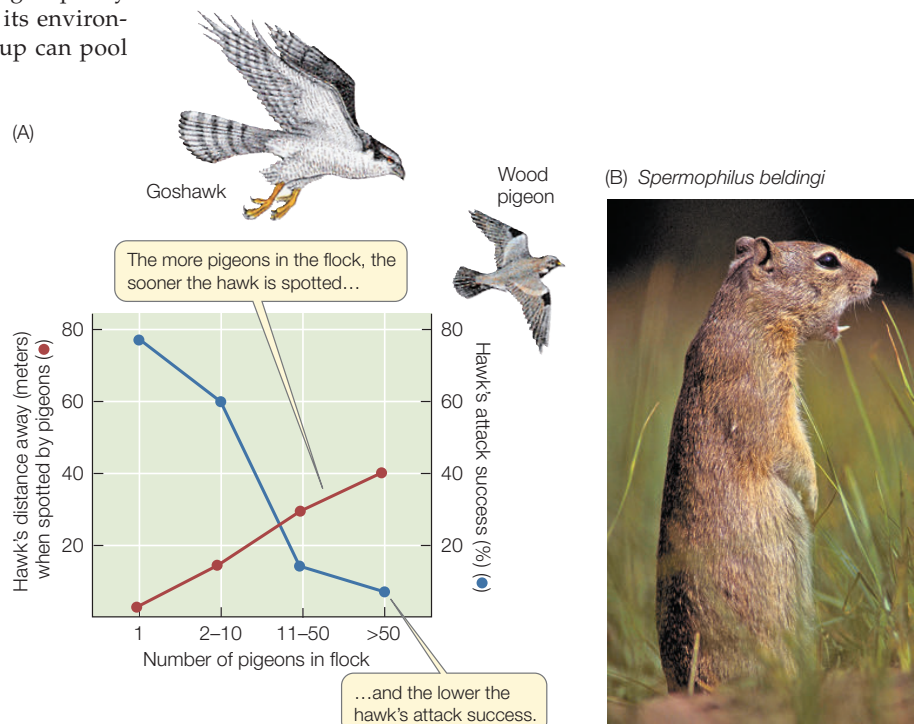
flock spotted the goshawk and started to fly away, stimulating the other individuals to take flight as well. Belding's ground squirrels, which live in large colonies in open meadows, use alarm calls to reduce predation risk. When an aerial predator such as a hawk arrives overhead, one of the squirrels that first spots the hawk gives a loud whistle (**FIGURE 40.13B**). Immediately, other individuals also whistle, and the animals run to their burrows or other shelter. Aerial predators almost never capture a ground squirrel after the alarm whistles have begun.

Animals in groups may also discover preferred environments more efficiently. In a recent experiment, investigators studied a species of fish that prefers to be in places where light levels are low. They studied schools of the fish of various sizes in a large aquarium that had both darkened and well-lit areas of water. The darkened areas moved from place to place, so the fish could not simply find a dark spot and stay there. The efficiency with which a school could find dark areas increased dramatically as the number of fish in the school increased (**FIGURE 40.14**). There is good reason to think that results would be similar if schools were seeking other desirable regions in the water, such as regions with abundant food.

Some societies are composed of individuals of differing status

A group of vervet monkeys (*Chlorocebus*) typically contains multiple subadult and adult males (**FIGURE 40.15**), along with females and youngsters. One of the adult males typically **dominates** all the other adult and subadult males in the group, meaning it "wins" during one-on-one behavioral contests with each of the others. This dominant male has by far the greatest chances of mating with the adult females in the group.

(A)

Goshawk

Wood pigeon

(B) *Spermophilus beldingi*

The more pigeons in the flock, the sooner the hawk is spotted…

…and the lower the hawk's attack success.

Hawk's distance away (meters) when spotted by pigeons (●)

Hawk's attack success (%) (●)

80

60

40

20

1   2–10   11–50   >50
Number of pigeons in flock

(A)

(B)

> The ability of a school to find dark areas improved as the number of fish in the school increased.

FIGURE 40.14 A School of Darkness-Preferring Fish Finds Dark Patches Faster as the Number of Fish in the School Increases Juvenile golden shiners (*Notemigonus*) prefer areas in the water where the light intensity is low. Schools were placed in an aquarium where dark areas were present but moved from place to place. (A) Three successive images of a school, taken 2 seconds apart, as the school finds and enters a dark patch. (B) An index of a school's effectiveness in finding dark patches. The index is plotted against the number of fish in the school. Vertical bars are 95% confidence intervals (see Appendix B).

Dominance by a particular male is even more evident in impala antelopes (*Aepyceros melampus*). If you ever go on safari in Africa and encounter a group of impala during the breeding season, you'll notice the existence of two subgroups. One subgroup consists entirely of males. By marking the animals in this type of subgroup, researchers established that these males do not get to mate with females. The second subgroup consists of a single male and a large number of females. This single male does essentially all of the mating! As you might guess, the dominant male—the single male in the group of females—must expend extraordinary effort to repel intruding males and intercept females that try to leave. This activity is exhausting, and dominant males tend to retain their dominance for only a few months.

LINK

Dominance behaviors may result in sexual selection, which would tend to favor increases in these behaviors in subsequent generations; see **Concept 15.2**

Within groups in which certain individuals have distinctive status—such as groups of vervet monkeys or antelopes with dominant males—individuals are able to benefit from group

FIGURE 40.15 An Adult Male Vervet Monkey Note his colorful genitalia, which signal his adult status.

living in the same ways we discussed in the last section. In addition, biologists hypothesize that the evolution of social systems based on distinctive status has taken place because such systems can provide additional benefits. In cases of dominant males, researchers currently hypothesize that the process of becoming dominant may often serve as a test of a male's strength, endurance, and other properties critical for success. Females that mate with the dominant male may thereby ensure that their offspring are genetically well endowed. In this way, both the individual males and the individual females that mate in such systems of social behavior realize advantages.

Eusociality represents an extreme type of differing status

In most animals, all the adult members of a social group are physiologically capable of reproducing, even though some may be behaviorally excluded from reproducing at certain times. An entirely different situation exists in many social insects, such as honey bees

In a honey bee colony, a single female—the queen—is reproductive and lays eggs. Occasionally she produces a few male offspring (drones) that are fertile, producing sperm. However, most of the thousands of other individuals in the colony—all of which are her offspring—are sterile female worker bees. Similar colony structures occur in many other types of bees, wasps, ants, and termites.

Eusociality refers to a social structure in which some members of a social group are nonreproductive and assist the reproduction of fertile members of the group, typically their mother. It represents an extreme form of differing status within a social group. Nearly all known cases of eusociality occur within the insects, although eusociality is also documented in naked mole rats (*Heterocephalus glaber*) and certain coral-reef shrimps.

All cases of structured, unequal reproductive status among adults in social groups raise the question of why evolution has produced systems in which the inequality exists. This question reaches its extreme manifestation in the eusocial animals. In discussing such questions, an important concept is altruism. As used in discussions of evolution, **altruism** refers to any characteristic of an individual that imposes a cost on that individual

while aiding another individual. Workers in eusocial colonies exemplify altruism because, whereas they themselves are unable to breed, they help another individual breed. Altruism also occurs if an individual—when seeing a predator—gives warning calls that draw the predator's attention to itself (endangering its life) while giving neighboring individuals a better chance to hide. The reasons why altruism exists have been hotly debated in evolutionary biology for a half century.

Go to MEDIA CLIP 40.1
Social Shrimps
PoL2e.com/mc40.1

CHECKpoint CONCEPT 40.5

✓ Name one advantage and one disadvantage of group living.

✓ Consider the phenomenon of mating exclusion, in which certain adult individuals in a group are excluded from mating. How does mating exclusion differ in groups with a dominant individual and in eusocial groups?

✓ What is altruism, and why might a biologist have difficulty reconciling it with the theory of evolution by natural selection?

Isolated individuals and entire ecological communities are at opposite ends of a spectrum of complexity in biological systems. Having started this chapter with a focus on individuals, we will now end by looking at some of the ways that behavior is important in communities.

CONCEPT 40.6 Behavior Helps Structure Ecological Communities and Processes

In ecological communities, the behaviors of animals often give critically important structure to the use of time and space and to interrelationships among species. One way that behavior has this effect is the structuring of the 24-hour day into activity periods. Some animals are active only during daylight hours. Others are active only at night. These behavioral differences can determine whether two species encounter each other. For example, because insect-eating bats are typically nocturnal, spending their days in secluded places such as caves and attics, diurnal insects are not threatened by the bats even though the two live in the same ecological community.

Behavior helps maintain species

In much of North America, the principal native mice are members of the genus *Peromyscus*, and it is common for two species in this genus to be found living in one general region. White-footed mice (*P. leucopus*) and cotton mice (*P. gossypinus*) are one example. When males and females of these two species are housed together in cages, they breed readily and produce fertile offspring. In nature, however, hybrids are rarely found. To a large degree, behavior explains this difference. In nature the two species prefer different types of woodlands. They thus live in different places and probably rarely meet. We can also hypothesize that if they were to meet, they would detect oddities in each other's interactive behavior and separate before mating. Many similar cases are known of species that can be demonstrated to be interfertile yet remain distinct in undisturbed natural habitats. Their behaviors keep them apart in such habitats. Behavior is thus a key factor in allowing species to maintain their species distinctions.

The species of Darwin's finches in the Galápagos Islands are of particular interest because intense study of the finches has provided unusually detailed insight into hybridization in the wild. Peter and Rosemary Grant have established by analyses of DNA that, among the several species of ground-living Darwin's finches, about 1 percent of birds that grow to adulthood in the wild are fertile hybrids of two distinct species. The hybridization that is observed demonstrates that the species of Darwin's finches are not genetically walled off from each other. Instead, behavior ordinarily keeps the species distinct. Males ordinarily learn their songs from their fathers (see Concept 40.2), and a female ordinarily will not mate with a male singing a song other than the correct one for her species. These behaviors prevent most cross-breeding.

LINK

Behaviors that prevent cross-breeding are an important mechanism of reproductive isolation and speciation; see **Concept 17.4**

Animals often behaviorally partition space into territories or home ranges

In many types of animals—including ones as diverse as fish, dragonflies, and birds—individuals within a single population restrict their movements to limited areas. For example, **FIGURE 40.16** shows use of space by six adult male white-footed mice within a 4-hectare forest. Each mouse roamed within a defined area on the forest floor, with almost no overlap among the areas occupied by the different mice.

In cases like this, behavior acts to structure the space available. Rather than interacting ecologically with the entire forest,
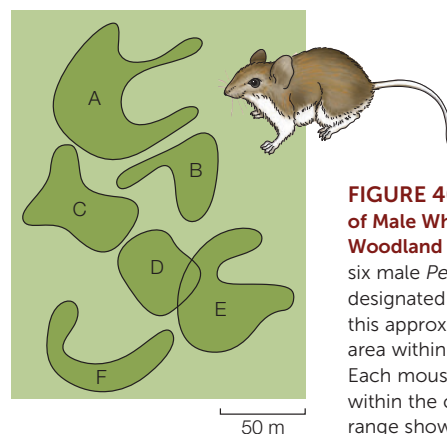
FIGURE 40.16 Home Ranges of Male White-footed Mice in a Woodland At the time of study, six male *Peromyscus leucopus*, designated A–F, were living in this approximately 4-hectare area within a large woodland. Each mouse moved around just within the circumscribed home range shown.

50 m

each individual interacts with the ecological community in just a small part, which is more or less distinct from the parts with which other, neighboring individuals are engaged.

The region occupied by an individual is known as its **territory** if the individual actively keeps out other individuals of the same species. A region is known as an individual's **home range** if other individuals are not excluded. Home ranges often overlap considerably. Both territories and home ranges provide familiarity. An individual occupying a territory or a home range learns all the locations within its living area where it can escape attacks or find resources or shelter. When an individual defends a territory, it enjoys the additional benefit of having sole use of any resources present.

Go to ANIMATED TUTORIAL 40.3
The Costs of Defending a Territory
PoL2e.com/at40.3

Behavior helps structure relationships among species

For understanding behavioral relationships among species in ecosystems, ecologists often use a **cost–benefit approach**. Such an approach assumes that an animal has only a limited amount of time and energy, and therefore—in its relationships with other species—cannot afford to engage in behaviors that cost more to perform than they bring in benefits. In cost–benefit analysis, ecologists quantify both costs and benefits. Then, by calculating relative costs and benefits, they make—and test—predictions about which behaviors to expect.

A specific case studied in detail by Bernd Heinrich is the choice of flowers in the foraging ecology of bumblebees (*Bombus*). As a bumblebee forages in a flower patch, it flies from flower to flower, landing on flowers to collect nectar (**FIGURE 40.17**). During this process, the bee must keep its flight muscles warm so it will be able to fly. Keeping them warm during flight is no problem because the working muscles produce heat at a high rate. Keeping them warm when the bee has landed on a flower requires extra heat production when the air is cold for the same reason a house furnace needs to make heat at an increased rate in cold weather. Adding all these considerations together, Heinrich calculated the energy cost per minute of foraging and determined that the cost is considerably greater in cold air than in warm air.

Heinrich also calculated the benefit of foraging. To do this, he measured how much nectar could be obtained from each flower and the sugar concentration of the nectar. Then he calculated the energy a bee could obtain from each flower by metabolically oxidizing the sugar in the flower's nectar.

One common flowering plant in Heinrich's study area was a rhododendron with large flowers. A bumblebee got 1.7 joules (J) of energy by taking the nectar from each rhododendron flower. In cold air at 0°C, a bee's cost of foraging was about 12.5 J per minute. Thus a bumblebee needed to harvest the nectar from only about 7 flowers each minute for its foraging benefit to equal its foraging cost. Actually, a bee could harvest 20 flowers per minute, receiving a benefit that far exceeded its cost—and enabling the bee to take energy back to its hive. Heinrich predicted

FIGURE 40.17 A Bumblebee Landing on a Flower to Collect Nectar

that bumblebees would forage on rhododendron flowers in both cold and warm weather, and this is what the bees do.

Another common plant was wild cherry. Heinrich noticed that bumblebees foraged on the cherry flowers only in warm weather. By applying his cost–benefit analysis, he discovered why. Cherry flowers are smaller than rhododendron flowers and provide only 0.2 J of energy each. Accordingly, at 0°C a bee would have to harvest more than 60 cherry flowers per minute just to get enough nectar to equal its cost of foraging. Bumblebees cannot harvest that many flowers per minute. Thus they would have to go into an energy deficit—spending more energy than they received—to forage on cherry flowers in 0°C air.

With this study, Heinrich showed that bumblebee foraging behavior is structured in ways that keep a bee in energy balance. This fact, in turn, structures the relationship between bumblebees and the plants that flower in their ecosystems.

Go to ANIMATED TUTORIAL 40.4
Foraging Behavior
PoL2e.com/at40.4

LINK
A cost–benefit approach can also be used to analyze life history trade-offs during evolution; see **Concept 42.3**

CHECKpoint CONCEPT 40.6

✓ How might Lee Metzgar's study (see Concept 40.2, Figure 40.4) on the survival of certain white-footed mice in the presence of screech owls help explain the existence of home range behavior?

✓ Imagine that on a cold day a bee requires 15 joules of energy per minute to forage continuously. If the bee can harvest 20 flowers of a certain species every minute, and gets 0.8 J of energy for each flower it visits, would it be to the bee's energetic benefit to forage on those flowers that day?

✓ Animals that actively defend a territory gain sole access to all the energy sources available in that territory, a major energetic benefit. What might some of the energetic costs of territory maintenance be?

Q In what ways might schooling behavior and pairing behavior be advantageous for the individuals involved?

than a single individual. For this reason, a school may detect predators sooner than an individual so that evasive action can be taken. Similarly, a school may be able to find valuable resources in the environment more rapidly or efficiently. Pairing behavior could have several advantages—one being that in male–female pairs, each individual is assured of a mate.

ANSWER   Schooling behavior can be advantageous in several ways. For example, a school has more sense organs

SUMMARY

CONCEPT 40.1   Behavior Is Controlled by the Nervous System but Is Not Necessarily Deterministic

- Changes in behavior are an important way for animals to respond to changes in their environment. **Review Figure 40.1**

- An animal's behaviors are activated and coordinated by the animal's nervous system.

- Some animal behaviors, called **fixed action patterns**, are highly stereotyped. They do not require learning and in fact are often resistant to modification by learning. **Review Figure 40.2**

- Animal behavior has a genetic basis and is subject to natural and artificial selection. Behavior therefore evolves. **Review Figure 40.3**

- Behavior is often flexible; it can be modified by an animal's experiences.

CONCEPT 40.2   Behavior Is Influenced by Development and Learning

- Many animals are able to **learn**—meaning that individuals can alter their behaviors on the basis of previous individual experiences.

- **Behavioral imprinting** is a process by which an animal learns to respond to a specific set of stimuli during a limited period early in postnatal life and thereafter the behavioral responses are fixed.

- Early experiences can affect the behavior of an animal for the remainder of its life. Some of these effects are consequences of epigenetic effects on gene expression.

CONCEPT 40.3   Behavior Is Integrated with the Rest of Function

- Behavior and other aspects of animal function are interdependent; the behavior of an animal is constrained by its physiological capacity to perform the required actions.

- Body structure, size, and growth rate can influence behavior, as can cellular biochemistry and metabolism. **Review Figure 40.7**

CONCEPT 40.4   Moving through Space Presents Distinctive Challenges

- Animals find their way in the environment by **navigation** (moving toward a particular destination or along a particular course) and **orientation** (adopting a position or trajectory relative to an environmental cue).

- Animals sometimes navigate by following trails, which in many cases are marked with **pheromones**. Navigation may also involve path integration. During this process, an animal integrates the distances and directions it travels to maintain an awareness of its position relative to a particular site. **Review Figures 40.8 and 40.9**

- Animals may sense direction by using information on the sun, magnetic fields, landmarks, and atmospheric polarization patterns. A sun compass involves not only observing the sun's position but

also knowing the time of day, information that can be provided by a circadian biological clock. Animals often have multiple, redundant mechanisms of orientation. **Review Figure 40.10 and ANIMATED TUTORIALS 40.1 and 40.2**

- Honey bees use a waggle dance to communicate the position of a food source relative to the hive. **Review Figure 40.11 and ACTIVITY 40.1**

- Some animals display remarkable feats of navigation when they **migrate**, traveling as far as thousands of kilometers between locations. **Review Figure 40.12**

CONCEPT 40.5   Social Behavior Is Widespread

- A **society** is a group of individuals of a single species that exhibits some degree of cooperative organization.

- Group living confers benefits such as greater foraging efficiency and protection from predators, but it also has costs, such as increased competition for food and ease of transmission of diseases. **Review Figures 40.13 and 40.14**

- Individuals in a society can be of equal status—as in a school of fish—or of unequal status—as in a group of impala antelopes. In some cases a single male **dominates** the other males in a group; this usually confers a reproductive advantage on the dominant male.

- An extreme form of unequal status is seen in cases of **eusociality**, in which some individuals in the group are infertile and assist the reproduction of fertile individuals, usually their mother and a few male siblings. Eusocial animals include the social insects (e.g., honey bees) and naked mole rats.

CONCEPT 40.6   Behavior Helps Structure Ecological Communities and Processes

- Behavioral differences help maintain species by decreasing the likelihood of interspecies breeding.

- An individual within a population often restricts its movements to a limited portion of the area occupied by the population as a whole. The smaller area is known as a **territory** if the individual actively keeps out other individuals of the same species, or as a **home range** if other individuals are not excluded. **Review Figure 40.16 and ANIMATED TUTORIAL 40.3**

- A **cost–benefit approach** can be used to investigate the adaptive value of specific behaviors. **Review ANIMATED TUTORIAL 40.4**

See **ACTIVITY 40.2** for a concept review of this chapter.

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is40

Go to LaunchPad at **macmillanhighered.com/launchpad** for additional resources, including LearningCurve Quizzes, Flashcards, and many other study and review resources.

PART 7
Ecology

A cow grazes in a mesquite-dominated former grassland in southeastern Arizona. Reducing grazing has failed to restore this region's grassland ecosystem.

The U.S.–Mexico Borderlands of southeastern Arizona have a colorful "Wild West" history peopled by Native Americans, Spanish explorers, cowboys, buffalo soldiers, outlaws and sheriffs, miners and ranchers, and railroad tycoons. This history has faded with time—except for one lasting legacy that dates from the cattle boom of the 1880s.

The first herds of cattle were brought to the Borderlands in 1687, when Spanish missions and settlements were established, but livestock numbers remained below 40,000 head until the 1880s. At that time, the end of the Apache Wars, the completion of transcontinental railroads (which opened huge markets for beef), and an influx of investment capital combined to bring 1.5 million animals to fatten on the free grass of Arizona's "open range." The sea of grass that had once grown "as high as the belly of a horse" was soon grazed to the ground.

The boom did not last long. A drought in 1892 and 1893 killed 75 percent of the cattle, leaving so many carcasses that one could walk across the San Simon Valley, it is said, without touching the ground. Prickly shrubs such as mesquite (*Prosopis* species) gained a toehold in the denuded landscape when torrential rains returned in the late 1890s, washing away soil and cutting deep gullies in the landscape. The once rich grasslands had been turned into shrublands that could support few cattle.

Soon thereafter, state and federal governments closed the "open range," substituting a lease system that would allow them to better manage public lands.

They tried to restore the grasses using a method that had worked for thousands of years in the grassy meadows of Europe: adjust the number of cattle up or down depending on meadow conditions. This method is based on the assumption that grazing depletes grasses that cattle prefer and thereby favors the growth of less desirable plants. If that is the case, then reducing the number of cattle should allow the desirable species to recover. Alas, "resting the range" has not worked in the arid Borderlands: shrubs have continued to spread, and grasses have not increased measurably.

Q Can basic ecological principles suggest why removing cattle has not restored grasses to the Borderlands?

You will find the answer to this question on page 862.

Ecological Systems Vary over Space and Time

During the Age of Exploration of the eighteenth and nineteenth centuries, the prospect of visiting unknown lands filled with unfamiliar plants and animals lured many European scientists—including Charles Darwin—to travel the world. They described and took careful measurements of a tremendous variety of environments and organisms on their journeys, thus initiating the study of two new topics: **physical geography**, the spatial distributions of Earth's climates and surface features; and **biogeography**, the spatial distributions of species. It soon became apparent that the distributions of species and environments are linked.

Organisms and their environments are ecological systems

The link between physical geography and biogeography is not surprising, because all organisms, humans included, are surrounded by and interact with an external environment that is made up of nonliving (**abiotic**) and living (**biotic**) components. These components—one or more organisms and the environment with which they exchange energy and materials—make up an **ecological system**.

The term "ecological" derives from **ecology**, a word that the German biologist Ernst Haeckel constructed in 1866 from the Greek roots *oikos*, "household," and *logia*, "study of." Haeckel meant this word to describe "the entire science of the relations of the organism to its external environment." Ecological knowledge is very old, for even the earliest humans understood a great deal about the plants and animals they depended on for food, the animals that competed with them for food, and the organisms and physical circumstances that presented natural hazards. Indeed, the earliest available religious texts and scholarly writings are full of ecological topics. By coining a formal term, however, Haeckel not only helped establish the study of "all those complicated interrelations described by Darwin as the conditions of the struggle for existence" as a formal science, but also underscored ecology's relevance to Darwin's theory of evolution by natural selection.

Ecological systems can be small or large

A system is defined by the interacting parts it contains. But scientists have a great deal of freedom to choose which set of interacting parts to study. In the case of ecological systems, we can draw a boundary around any part of the biological hierarchy from the individual organism on up (see Figure 1.5). Each successive level of this ecological hierarchy brings in new interacting parts at progressively larger scales of space and time.

At the smallest scale is the fundamental ecological unit: the individual organism and its immediate environment. Individuals remove materials and energy from the environment, convert those materials and energy into forms that can be used by other organisms, and by their presence and activities, modify the environment. In aggregate, these individual-level exchanges determine the nature and magnitude of interactions at higher levels of the hierarchy.

The individual organism is part of a **population**: a group of individuals of the same species that live, interact, and reproduce in a particular geographic area. The assemblage of interacting populations of different species within a particular geographic area forms a biological **community**. As we expand the geographic area included within the boundary of our ecological system, we include multiple communities in **landscapes** until, at the largest scale, we include all the organisms of Earth and the environments they occupy—the entire **biosphere**. Ecologists tend to replace the term "ecological system" with **ecosystem** when they are explicitly including the abiotic components of the environment, and in particular when they are considering communities and their environmental context.

Large ecological systems tend to be more complex than small ones, not only because they contain more interacting parts, but also because those parts interact over a greater span of space and time. The components of the biosphere, for example, are linked not only by the rapid and localized exchanges between individual organisms and their surroundings, but also by slower and more extensive migrations of organisms, great cycles of air and water movement, and even the much slower geological churning of Earth's crust.

Even when very small, however, ecological systems can be complex. Consider an ecosystem within each of us—the human intestine. It is one of the most densely populated ecosystems on Earth, hosting hundreds of species of bacteria, archaea, and yeasts, and on the order of 10^{12} individual microbes per gram of fecal material. The microbial cells in our bodies vastly outnumber our own trillion or so human cells, and their combined metabolism rivals that of an organ such as the human liver.

It's no surprise that microbes thrive in the mammalian gut. Mammals regulate the gut's physical environment within narrow limits of temperature and chemistry, and they supply it with a steady stream of ingested nutrients. Gut microbes metabolize food materials, including some that the host cannot digest, and excrete waste products that provide nutrition to the host or to other members of the microbial community. Microbial species interact with one another and with host cells by forming layers (biofilms) that coat the gut lining.

As with any system, these interactions determine the properties of the whole and its components: they affect host nutrition and immune function as well as the makeup of the microbial community itself. In fact, a number of human diseases—including infection by pathogenic gut microbes, irritable bowel syndrome, obesity, and wasting diseases such as kwashiorkor—have been linked to disruption of the gut's microbial community.

LINK

Human health is linked to the health of our microbial communities. Review the description of the communities of microbes that live on and in our bodies in **Concept 19.3**
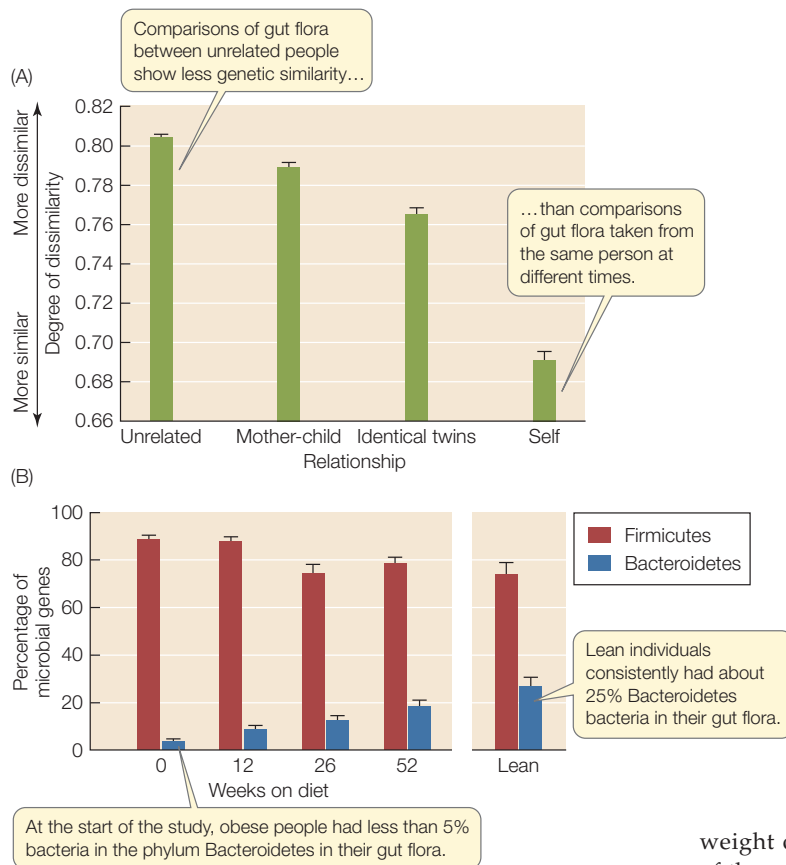
FIGURE 41.1 Genetics and Diet Affect the Composition of the Gut Microbial Community (A) The closer the genetic relationship between two people, the more similar their gut microbial communities are. (B) Obese people have proportionally more bacteria in the phylum Firmicutes, and proportionally fewer bacteria in the phylum Bacteroidetes, than do lean people. However, the microbial community of obese people approaches that of lean people as they lose weight on a calorie-restricted diet. Error bars indicate 1 standard error from the mean in both (A) and (B) (see Appendix B).

Ecological systems vary, but in ways that can be understood with scientific methods

The biotic and abiotic components of ecosystems are distributed unevenly in space, as European scientists discovered during the Age of Exploration. Individual ecosystems also change over time, as cattle ranchers in the Borderlands discovered to their dismay. Such variations may be bewildering at first, but further study often reveals repeated patterns that provide clues to their causes.

The ecosystem of the human gut illustrates this spatial and temporal variation, and scientists are using natural history observations, experiments, and modeling to understand it. With modern molecular methods (see Figure 12.6), we can now characterize the phylogenetic and functional properties of entire gut microbial communities, which is impossible with traditional culture techniques because many gut microbes won't grow outside the gut. The first surveys revealed bewildering variation: each person, it turns out, has a unique gut community. More recent work, however, has demonstrated that there is some order to this variation. The gut communities of genetic relatives, for instance, are more similar than are those of unrelated people (**FIGURE 41.1A**), suggesting that a host's genotype favors some microbes over others. In addition, the gut communities of obese and lean people differ in their ratios of two bacterial phyla. When obese people lose

weight on experimental calorie-restricted diets, the ratios of these two bacterial phyla become more like those of lean people (**FIGURE 41.1B**), suggesting that diet also affects the gut community. The relationship between gut community and obesity appears to be a two-way street, because systems models of nutrient processing by different microbial groups indicate that obesity might be related to how much energy the community can extract from food. This conclusion is supported by transplant experiments done with mice, whose gut ecology is similar to ours (**FIGURE 41.2**). Exciting results such as these open the door to new therapies that use ecological principles to restore human health by manipulating our "ecosystem within."

CHECKpoint **CONCEPT 41.1**

✓ What two components make up the external environment of organisms?

✓ Explain why ecological systems at large scales tend to be more complex than smaller-scale systems.

✓ Humans often experience digestive problems after taking a course of antibiotics to treat a bacterial infection. Why might this be so?

Variation over space and time can be seen in ecosystems at all scales, from the human gut to the entire biosphere. We will now turn to some of the physical factors that underlie this heterogeneity at the biosphere scale: Earth's climates and topography.

INVESTIGATION

FIGURE 41.2 The Microbial Communities of Genetically Obese Mice Contribute to Their Obesity Mice (*Mus musculus*) that are homozygous (*ob/ob*) for a particular gene, *Lep^ob*, are obese, but their *ob/+* and *+/+* littermates are lean. Like obese humans, *ob/ob* mice host a gut microbial community that is relatively rich in bacteria of the phylum Firmicutes and poor in Bacteroidetes. Does this gut community contribute to the obesity of *ob/ob* mice, or does it simply reflect their greater food consumption?[a]

HYPOTHESIS

The gut microbial community of obese mice contributes to their obesity.

METHOD

1. Rear +/+ mice to adulthood in a germ-free environment so that their guts contain no microbes.
2. Select 9 mice at random to have their guts inoculated with fecal material obtained from obese *ob/ob* donors, and select 10 mice at random to be inoculated with material from lean +/+ donors.
3. Verify that the recipient mice have developed microbial communities similar to those of the donors.
4. Feed both groups of recipient mice on mouse chow containing 3.7 kcal/g. Measure the food intake of the mice over the next 2 weeks.
5. Use a noninvasive body-scanning method to measure changes in the body fat content of the two groups of recipient mice over the same 2-week period.

RESULTS

Both groups of recipients gained body fat during the 2 weeks, but those inoculated with gut material from an *ob/ob* donor gained more body fat than mice that received +/+ gut material, even though they ate the same amount of food. Error bars indicate 1 standard error from the mean; bars with different letters are statistically different from one another.
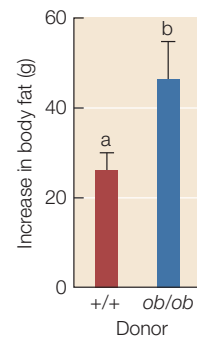
CONCLUSION

The Firmicutes-dominated gut community of obese mice contributes to their obesity.

ANALYZE THE DATA

Bacteria in the phylum Firmicutes are particularly adept at breaking indigestible dietary polysaccharides into monosaccharides and fatty acids that mammals can absorb. The researchers therefore hypothesized that the reason a Firmicutes-dominated gut community contributes to obesity is that it is more efficient at extracting energy from food. To evaluate this hypothesis, the researchers collected all feces produced in 24 hours by 13 *ob/ob* mice and 9 +/+ or *ob/+* littermates, then burned them in a closed chamber and used the temperature change to measure the energy content of each gram of feces. Error bars indicate 1 standard error from the mean; bars with different letters are statistically different from one another.

A. Do these results support the hypothesis that the gut communities of obese mice are more efficient at harvesting energy from ingested food? Explain.

B. Does it matter to your conclusion that *ob/ob* mice typically eat more chow than +/+ or *ob/+* mice?

C. Assume that mice store all the excess energy they obtain in the form of body fat, and that mouse fat contains 9.3 kcal/g. If the *ob/ob* recipient mice added 0.44 g more body fat than the +/+ recipients in 24 hours, how much more energy did they obtain from their food in this time period?

D. If both groups of recipients consumed 55 g of chow, what percentage of the energy consumed in chow does this extra energy gain represent? (Hint: Recall that the energy content of chow is 3.7 kcal/g.)
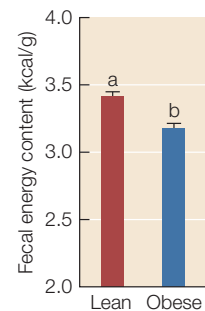
Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]P. J. Turnbaugh et al. 2006. *Nature* 444: 1027–1031.

Solar Energy Input and Topography Shape Earth's Physical Environments

Earth's physical environments vary enormously—from hot to cold, wet to dry, aquatic to terrestrial, salt water to fresh water. To this variation across space we must add variation over time, on scales from the very slow coming and going of oceans, mountains, or ice ages to the very fast shifts in temperature as clouds pass overhead. On the short time scales that we humans experience, physical conditions depend largely on solar energy input, which drives the circulation of the atmosphere and the oceans. Patterns of input and circulation determine whether a particular place at a particular time of year tends to be hot or cold, wet or dry—and as a consequence, the types of organisms found in that place.

> **LINK**
>
> Review the effects that changes in Earth's physical environments have had on the evolution of life in **Concept 18.2**

Variation in solar energy input drives patterns of weather and climate

All of us are familiar with **weather**, the atmospheric conditions—temperature, humidity, precipitation (rainfall or snowfall), and wind direction and speed—that we experience at a particular place and time. Averaged over long periods, the state of these atmospheric conditions and their pattern of variation over time constitute the **climate** of a place. In other words, climate is what you expect; weather is what you get. We and other organisms respond to both weather and climate. Responses to weather are usually short-term: animals may seek shelter from a sudden rainstorm (human animals open their umbrellas), and plants may close their stomata (small openings in the leaf epidermis) on a hot summer day to reduce water loss from their tissues. Responses to climate, by contrast, tend to involve adaptations that prepare organisms for expected conditions. Organisms in hot climates can tolerate heat; those that inhabit seasonal climates use cues such as day length to prepare for an impending hot, cold, or dry season.

Some global patterns of climate stem from variation in solar energy input over space. Because Earth is spherical, the sun's rays strike the planet at a shallower angle near the poles than near the equator (**FIGURE 41.3**). This difference results in less solar energy input at high latitudes (near the poles) than at low latitudes (near the equator), for two reasons. First, the energy of rays of sunlight is spread over a larger surface area at high latitudes. Second, more sunlight is reflected back into space by the atmosphere and Earth's surface when sunlight strikes at a shallow angle. A consequence is that air temperatures decrease from low latitudes to high latitudes. Averaged over the course of a year, air temperature drops by about 0.8°C with every degree of latitude (about 110 km) north or south of the equator.

At any given place, the sun's input also varies through the year, causing seasonal variation in climate. This **seasonality** is a consequence of the 23.5° tilt of Earth's axis of rotation relative to the plane of its yearly orbit around the sun. The tilt causes different latitudes to receive their greatest solar energy input at different times of the year (**FIGURE 41.4**). At the solstice in late June, the North Pole tilts toward the sun, and the sun is directly above the Tropic of Cancer (latitude 23.5° N): the Northern Hemisphere experiences summer, with its long days and warm temperatures. At the solstice in late December, the North Pole points away from the sun, the sun is directly above the Tropic of Capricorn (latitude 23.5° S), and the climate pattern is reversed: it is summer in the Southern Hemisphere and winter in the Northern Hemisphere. At the equinoxes in late March and late September, the sun is directly above the equator, and both hemispheres experience equal lengths of day and night. These seasonal variations in solar input are relatively small at the equator and become more pronounced toward the poles.

Toward the poles, sunlight strikes Earth at a shallow angle and is spread over a larger area, so that its energy is diffused.

At and near the Equator, sunlight strikes Earth at a steep angle, delivering more heat and light per unit area.

Toward the poles, more sunlight also is reflected by the atmosphere and Earth's surface when it strikes at a shallow angle.

North Pole (90° N)

Direction of Earth's rotation

Equator (0°)

South Pole (90° S)

FIGURE 41.3 Solar Energy Input Varies with Latitude The angle of incoming sunlight affects the amount of solar energy that reaches a given area of Earth's surface. On average, sunlight strikes Earth's surface at a steeper angle at low than at high latitudes. This results in greater input of energy at low (i.e., equatorial) latitudes because the energy is spread over a smaller area and because less sunlight is reflected back into space by the atmosphere and land surface.
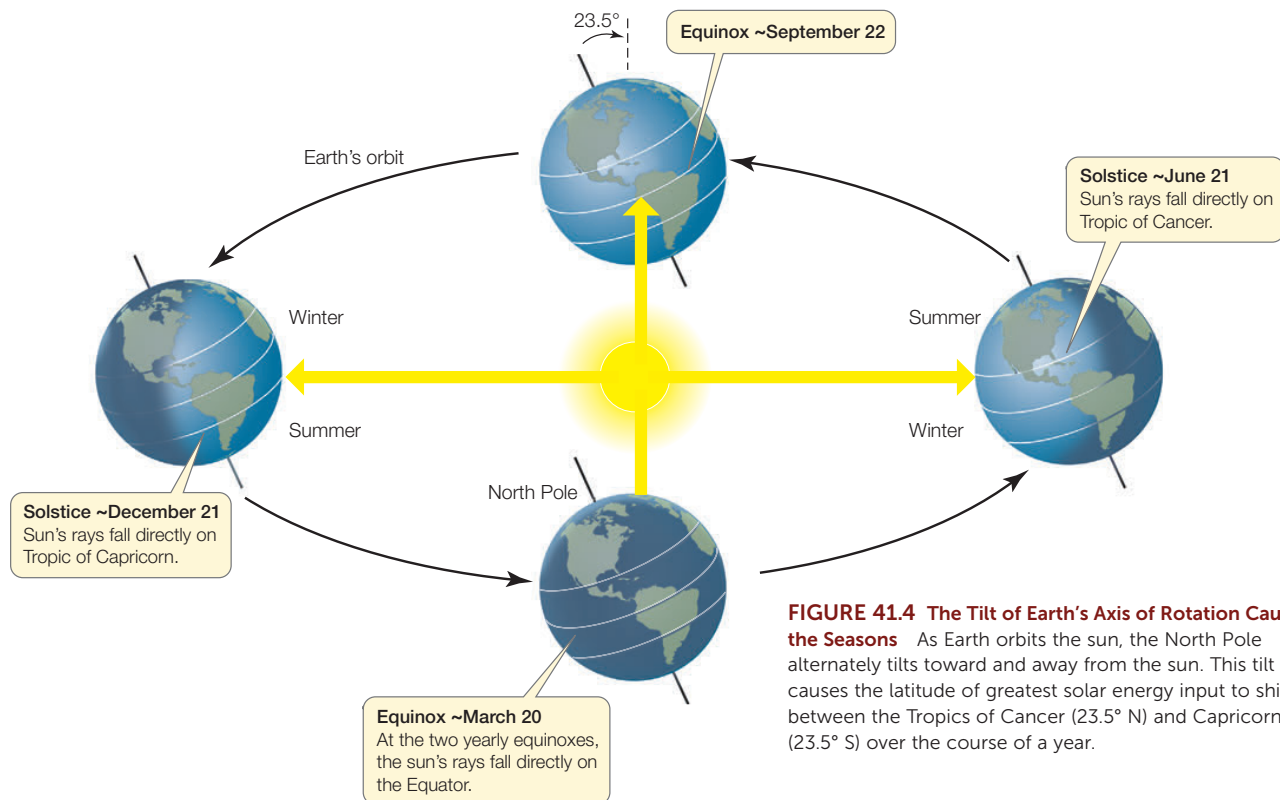
FIGURE 41.4 The Tilt of Earth's Axis of Rotation Causes the Seasons As Earth orbits the sun, the North Pole alternately tilts toward and away from the sun. This tilt causes the latitude of greatest solar energy input to shift between the Tropics of Cancer (23.5° N) and Capricorn (23.5° S) over the course of a year.

The circulation of Earth's atmosphere redistributes heat energy

The yearly input of solar energy is greatest in the **tropics** (the latitudes between the Tropics of Cancer and Capricorn) and decreases poleward. This latitudinal gradient in solar input drives the vast circulation patterns of Earth's gaseous atmosphere.

FIGURE 41.5 Tropical Solar Energy Input Sets the Atmosphere in Motion Intense sunlight in the tropics drives a vertical pattern of atmospheric circulation that reaches the subtropics and that results in high precipitation near the equator.
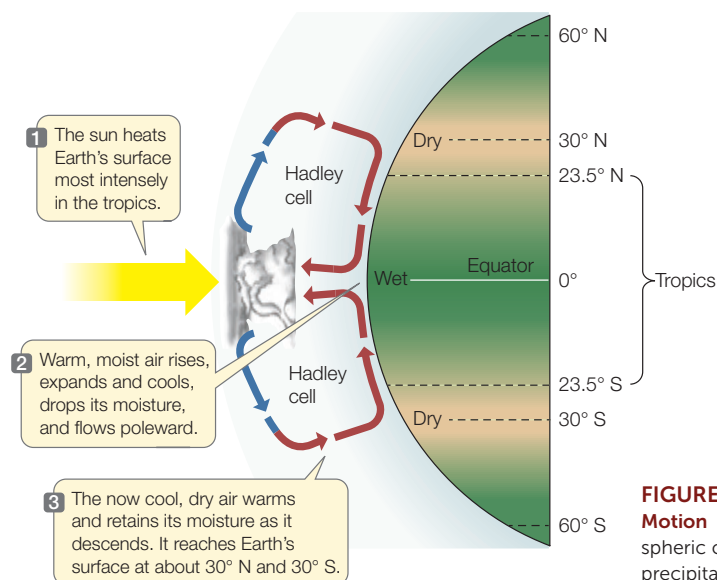
As the sun beats down on the tropics, the air there heats up—its molecules move faster (temperature is a measure of disordered molecular motion), colliding and pushing one another farther apart (see Concept 2.5). The heated air expands, becoming less dense and more buoyant, and rises. As it rises, it continues to expand and cool **adiabatically** (this is the principle on which an air conditioner works: when compressed gas is allowed to expand, it cools). The air rises to a level at which the surrounding air has its same temperature and density. Because tropical air gets so warm, it ascends to great altitudes before it stops rising.

Rising tropical air creates a vacuum that pulls in cooler, denser surface air from the north and south. As that air in turn heats, expands, and rises, it pushes the cool air above it to the side. As this air aloft moves away from the tropics, it radiates heat to outer space, becoming more dense and less buoyant. It sinks back toward Earth, is compressed by the overlying atmosphere, and warms adiabatically (the reverse of adiabatic cooling). It reaches Earth's surface at latitudes of roughly 30° N and 30° S, at which point some of it flows back toward the equator to replace air that is rising in the tropics. Thus it forms two cycles of vertical atmospheric circulation—one north and one south of the equator—called **Hadley cells** (**FIGURE 41.5**).

FIGURE 41.6 Global Atmospheric Circulation and Prevailing Winds
Because the speed of rotation of Earth's surface decreases with latitude, air flowing toward the equator lags behind the surface beneath it, whereas air flowing toward the poles moves faster than the surface beneath it. The resulting Coriolis effect explains patterns of prevailing surface winds.
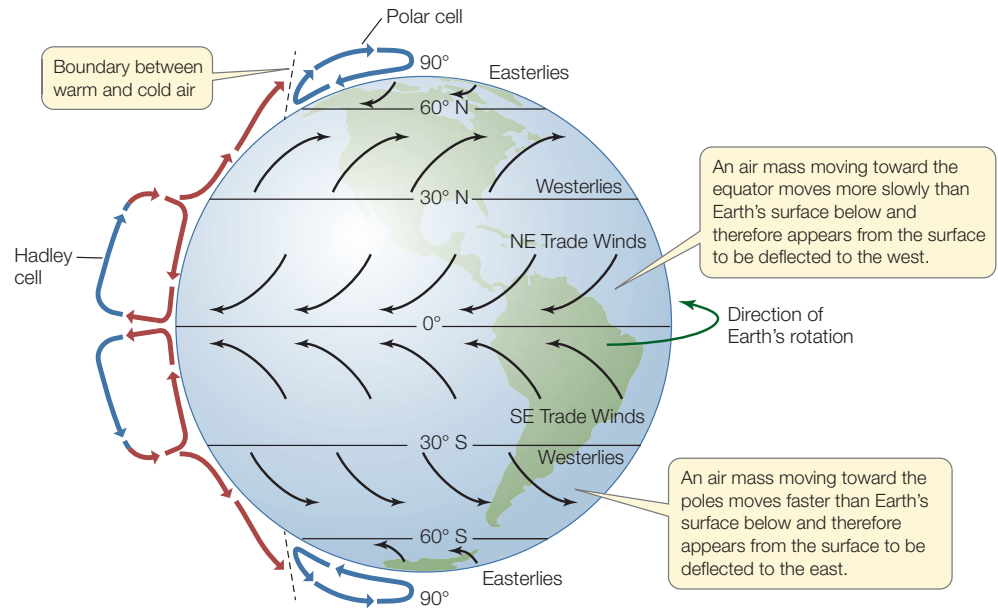
The Hadley cell circulation produces strong latitudinal patterns of precipitation. As water molecules in the tropics (most notably the oceans) absorb the intense sunlight there, they evaporate, so the air that rises in the tropics is rich in water vapor. As this warm, moist air expands and cools, fewer water molecules are moving fast enough to bounce apart after they collide. Instead, they form droplets of liquid water (or ice crystals), which grow and—when massive enough—fall to the ground as precipitation. Thus the warm, rising air of the Hadley cells drops most of its moisture near the equator as rain. The high-altitude air that eventually descends near 30° N and 30° S is largely depleted of water; moreover, because it warms as it descends and is compressed, the little water that remains stays in a gaseous state. Earth's great deserts are located around these latitudes.

Not all the descending air in the Hadley cells returns immediately to the tropics. Some of it continues to flow toward the poles, encountering and overriding frigid, dense polar air that is flowing equatorward as part of polar circulation cells that are smaller and weaker than the Hadley cells. The interaction of these warm and cold air masses generates the spinning winter storms that sweep from west to east through the middle latitudes between the tropics and the polar regions.

To better understand these storms and other patterns of horizontal air movement, we must consider one more thing—Earth's rotation on its axis from west to east (see Figure 41.3). We have already seen that the latitudinal gradient in solar input creates a latitudinal, or north–south, movement of air. The planet's rotation adds an east–west component to air movement. Because Earth is a sphere, the rotation of its surface is fastest at the equator, where its circumference is greatest, and slower toward the poles. Surface air that is not moving north or south is carried eastward at the same speed as the surface beneath it. But air that is moving toward the equator lags behind the faster-moving surface, and therefore appears from the surface to be deflected to the west. Conversely, air that is moving poleward races ahead of

the surface and appears to be deflected to the east. This **Coriolis effect** causes prevailing surface winds to blow from east to west in the tropics (the northeast or southeast trade winds, so called because of their importance during the era of trade by sailing ships), from west to east in the middle latitudes (the westerlies), and from east to west again above 60° N and 60° S latitude (the easterlies; **FIGURE 41.6**). The Coriolis effect also leads to the rotation of air characteristic of middle-latitude storms.

These aspects of atmospheric circulation combine to affect climate patterns by transferring an immense amount of heat energy from the hot tropics to the cold poles. Without this transfer, the poles would sink toward absolute zero in winter, and the equator would reach fantastically high temperatures throughout the year.

Ocean circulation also influences climate

The prevailing surface winds and Coriolis effect drive massive circulation patterns in the waters of the oceans, called currents, which carry materials, organisms, and heat with them. In the northern tropics, the trade winds drag surface water toward the west. When this water nears the western edge of an ocean basin, much of it flows northward, only to be turned to the east by the Coriolis effect and, at higher latitudes, by drag from the westerlies of the northern middle latitudes. This eastward flow turns south along the western edge of the continents and then westward again, completing a clockwise circuit, or **gyre**. The pattern in the Southern Hemisphere is essentially a mirror image of that just described, with surface circulation moving in counterclockwise rather than clockwise rotation (see Figure 41.7). The westward-flowing tropical water that is not caught up in these gyres flows back to the east in an equatorial countercurrent.

As they move poleward, tropical surface waters transfer heat from low to high latitudes, adding to the heat transfer that accompanies atmospheric circulation. The Gulf Stream and North Atlantic Drift, for example, bring warm water from the tropical
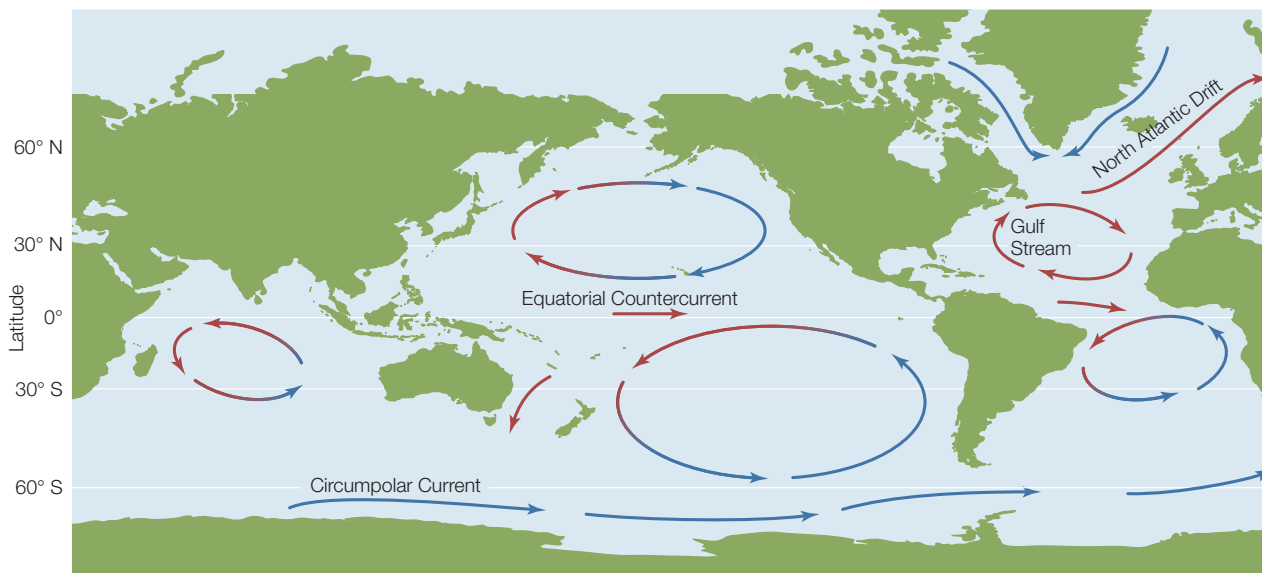
FIGURE 41.7 Ocean Surface Currents Ocean surface currents are characterized by giant patterns (gyres) of clockwise rotation in the Northern Hemisphere and counterclockwise rotation in the Southern Hemisphere, caused by frictional drag from prevailing winds (see Figure 41.6), the Coriolis effect, and deflection at the edges of continents.

Go to MEDIA CLIP 41.1
Perpetual Ocean Currents
PoL2e.com/mc41.1

Atlantic Ocean and the Gulf of Mexico north and east across the Atlantic (**FIGURE 41.7**), which warms the air above the North Atlantic. Westerlies then carry this air across northern Europe, moderating temperatures there. The effect on organisms is dramatic: polar bears roam the shores of Hudson Bay in Canada but are missing from comparable latitudes in Scotland or Sweden.

Surface currents are not the entire story, however. Gradients in water density caused by variation in temperature and salinity cause surface waters to sink in certain regions, forming deep currents. These deep currents return to the surface in areas of upwelling, completing a vertical ocean circulation. Thus oceanic circulation, like atmospheric circulation, is three-dimensional.

Oceans and large lakes moderate Earth's terrestrial climates because water has a high heat capacity, as we saw in Concept 2.2. This means that the temperature of water changes relatively slowly as it exchanges heat with the air it contacts and as it absorbs or emits radiant energy. As a result, water temperatures fluctuate less with the seasons and with the day–night cycle than do land temperatures, and the air over land close to oceans or lakes also shows less seasonal and daily temperature fluctuation.

Topography produces additional environmental heterogeneity

Earth's surface is not flat; it is crumpled into mountains, valleys, and ocean basins. This variation in the elevation of Earth's surface, known as **topography**, affects the physical environment.

Mountains, for example, are "weather formers." Because rising air expands and cools adiabatically, temperatures become cooler as elevation (distance above sea level) increases. If you climb a mountain, you will find that the temperature drops by about 1°C for each 220 meters of elevation gained. Where prevailing winds encounter a mountain range, air flows up the windward side of the range (the side facing into the wind). As the air cools, water vapor may condense or crystallize and fall as rain or snow. The leeward side of the mountain range (the side away from the wind) receives little precipitation because air descending on that side warms and retains any remaining

2 On the windward side of the mountain, air rises and cools, and water tends to change from a gaseous to a liquid or solid phase, falling as rain or snow. Wet conditions lead to relatively lush vegetation.

1 Prevailing winds pick up moisture over water bodies.

3 On the leeward side of the mountain, air descends and warms. Moisture remains in the atmosphere as water vapor, resulting in dry conditions.

FIGURE 41.8 A Rain Shadow Precipitation tends to be lower on the leeward side of a mountain range than on the windward side.

Go to ANIMATED TUTORIAL 41.1
Rain Shadow
PoL2e.com/at41.1

APPLY THE CONCEPT

Solar energy input and topography shape Earth's physical environments

Shown below are climate diagrams for three different localities. (Note the discontinuity in the precipitation axis in graph C.) Using the information in these diagrams and what you've learned about factors that determine climate, answer the following questions and explain the logic that led to your answer.

1. Which locality is near the equator?
2. Which locality has the greatest seasonality in temperature?
3. Which locality has the longest growing season?
4. Which locality is in the Northern Hemisphere?
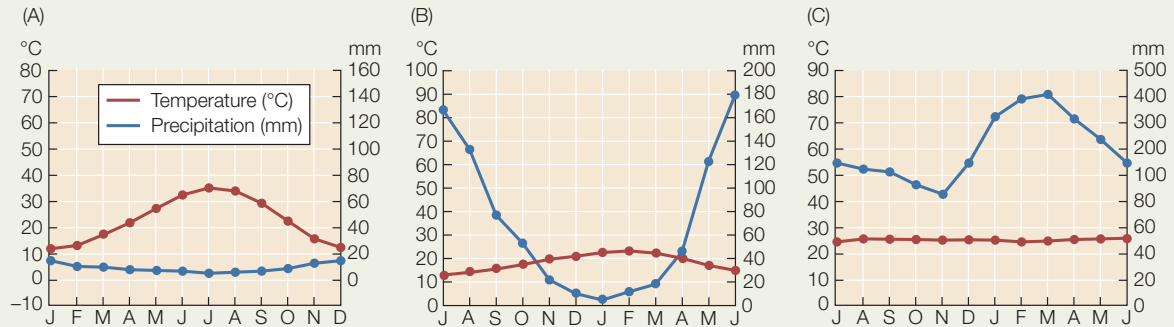
water in a gaseous state. Thus the mountain range is said to form a **rain shadow** (**FIGURE 41.8**). The difference in precipitation fosters more luxuriant growth of plants on the windward side than on the leeward side.

Topography also influences physical conditions in aquatic environments. The velocity of water flow, for example, is dictated by topography: water flows rapidly down steep slopes, more slowly down gradual slopes, and pools as lakes, ponds, or oceans in depressions. The depth of a water-filled depression determines the gradients of many abiotic factors, including temperature, pressure, light penetration, and water movement (see Figure 41.13).

Climate diagrams summarize climates in an ecologically relevant way

The climate at any location can be summarized in a **climate diagram**. Recognizing that ecological processes are strongly influenced by temperature and moisture, the German biogeographer Heinrich Walter superimposed graphs of average monthly temperature and average monthly precipitation through the year. He scaled the axes of the two graphs to incorporate the rule of thumb that plant growth requires at least 20 millimeters of precipitation per 10°C of temperature above freezing (0°C). This scaling makes it easy to see when conditions allow terrestrial plant growth—when temperature is greater than 0°C and the precipitation line is above the temperature line. This period is known as the growing season (**FIGURE 41.9**).
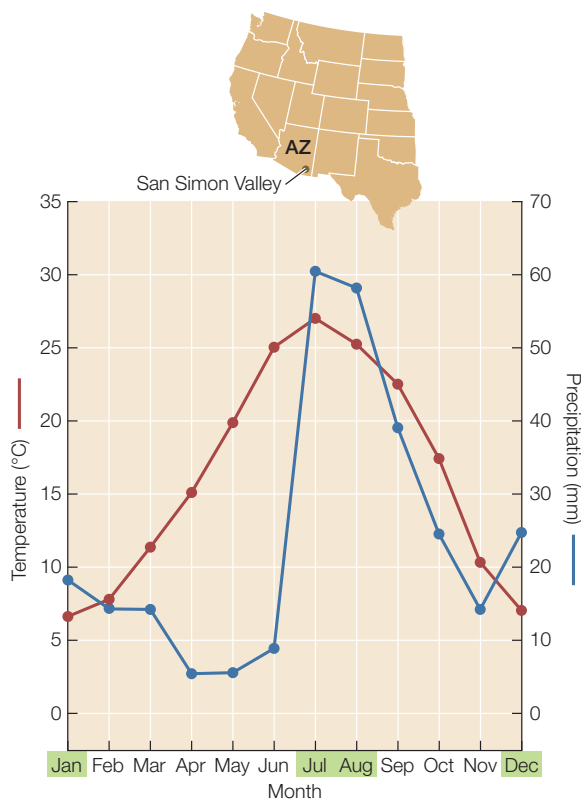
FIGURE 41.9 Climate Diagrams Summarize Climate in an Ecologically Relevant Way   Climate diagrams traditionally combine graphs of average temperature (left axis) and average precipitation (right axis) throughout the year, as shown here for San Simon Valley near the Arizona–New Mexico border. The summer solstice at the location in question (late June in the Northern Hemisphere, late December in the Southern hemisphere) is placed at the center of the diagram. The axes are scaled such that precipitation favors plant growth when the precipitation line is above the temperature line. The months highlighted in green are typically favorable for plant growth.

The patterns in the physical world that we have just discussed limit where organisms can live. For this reason, they strongly influence biogeography—the spatial distributions of species.

CONCEPT 41.3 Biogeography Reflects Physical Geography

An organism's physiology, morphology, and behavior—all aspects of its phenotype—affect how well it can tolerate a particular physical environment. For this reason, the physical environment of a place greatly influences what species can live there. Furthermore, we expect species that occur in similar environments to have evolved similar phenotypic adaptations to those conditions.

Similarities in terrestrial vegetation led to the biome concept

The European scientist–explorers who traveled the globe noticed that the vegetation found in climatically similar regions on different continents was strikingly convergent. This observation led to the concept of a **biome**: a distinct physical environment that is inhabited by ecologically similar organisms with similar adaptations. The species that occupy the same biome in geographically separate regions are often not closely related. Their similarities therefore reflect convergent evolution by natural selection (see Concept 16.1).

Terrestrial biomes are generally distinguished by the characteristics of their vegetation—whether the dominant plants are woody trees or shrubs, grasses, or broad-leaved herbaceous plants, and whether their leaves are big or small, deciduous (dropped seasonally) or evergreen. Characteristics of organisms other than plants also distinguish the biomes, since these characteristics represent adaptations to the vegetation as well as the climate. The distribution of terrestrial biomes is broadly determined by annual patterns of temperature and precipitation (**FIGURE 41.10**). Latitudinal gradients in average temperature and differences in its seasonal fluctuation separate tropical, subtropical, temperate, boreal, and polar biomes. Within those broad temperature zones, average annual precipitation and its pattern of seasonal fluctuation predict what biome will be found. In tropical biomes, for example, the length of the dry season determines
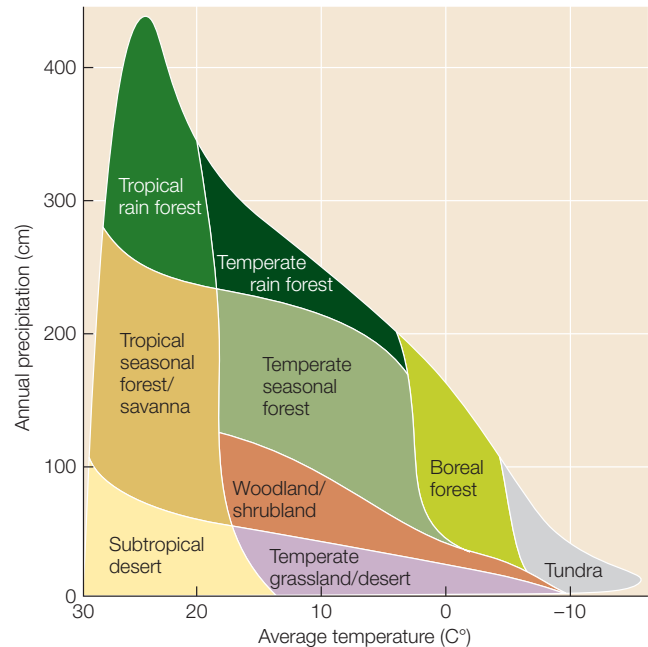
FIGURE 41.10 Terrestrial Biomes Reflect Average Annual Temperature and Precipitation Average annual temperature and precipitation strongly influence the structure of terrestrial vegetation.

whether tropical rainforest, tropical seasonal forest, or savanna develops. Elevation-associated gradients in temperature also determine the distribution of biomes; for example, tundra can be found on mountaintops, even in the tropics (**FIGURE 41.11**).

LINK

Some plant species can tolerate the cold temperatures of the tundra. You can find out more about plant adaptations to various environments in **Concept 28.3**

Climate is not the only factor that molds terrestrial biomes

Other features of the physical environment interact with climate to influence the character of terrestrial vegetation. Southwestern Australia, for example, has a "Mediterranean" climate with hot, dry summers and cool, moist winters. This climate generally supports woodland/shrubland vegetation. Succulent plants, which are well adapted to summer drought, are common in Mediterranean climates—but not in Australia, which has nutrient-poor soils. The lack of nitrogen in these soils makes it expensive for plants to construct the nitrogen-rich photosynthetic machinery of leaves. As a result, many plants produce long-lived leaves that are defended against herbivores in ways that do not require nitrogen (see Concept 28.2). These defenses include tough, indigestible cell walls, compounds that reduce the nutritional quality of leaves, and toxic oils and resins—features that also make the vegetation highly flammable. Plant material produced during the winter rains dries out during the summer and fuels intense fires that periodically sweep across the landscape. As a result, succulent plants, which are easily killed by fires, are rare in southwestern Australia.

Soil nutrients and fire bring us back to the desert grasslands of the U.S.–Mexico Borderlands. Grasslands—areas dominated by grasses and herbs rather than trees or shrubs—normally occur where precipitation is too scanty, or too sporadic, to support forests but is more plentiful than is typical of deserts. Fully one-fourth of Earth's land surface experiences such conditions, and much of this area supports grasslands. But grasslands are also found in some places where we do not expect them (**FIGURE 41.12**). Their presence in these places demonstrates that biome
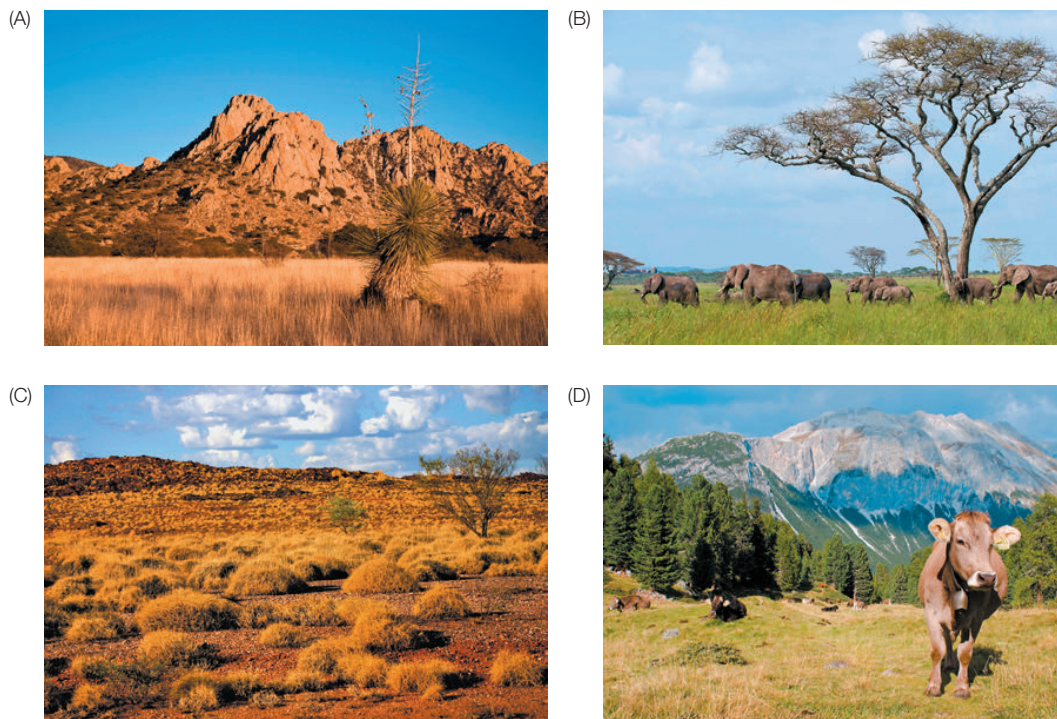
FIGURE 41.12 Similar Vegetation Types, Different Conditions Landscapes dominated by grasses, rather than trees or shrubs, are found throughout the world, sometimes under very different conditions. (A) The desert grassland of the U.S.–Mexico Borderlands, as it still appears in some places that have not been transformed into shrubland. (B) Grassland savanna of the Serengeti Plain, Tanzania, East Africa. (C) "Spinifex" grassland (genus *Triodia*) in Northern Territory, Australia. (D) Low-nutrient grassy meadows ("Magerwiesen") in the Swiss Alps.

boundaries are fuzzy and are not perfectly predicted by temperature and precipitation because other factors also affect the character of vegetation.

One such factor is fire, which rarely kills grasses but often kills shrubs and trees. Before humans arrived, the U.S.–Mexico Borderlands experienced periodic natural wildfires, ignited by lightning, that produced desert grassland rather than desert shrubland (see Figure 41.12A). Humans themselves have contributed to the establishment of grasslands in many areas. Fires lit by humans in the Serengeti Plain of northern Tanzania, Africa, may have helped convert the landscape from tropical seasonal forest to savanna, a biome in which grasses dominate and trees are widely scattered (see Figure 41.12B). Such human effects are not necessarily recent. Humans have inhabited Australia for at least 50,000 years, for instance, and their fires appear to have transformed some of the original woodlands in the arid "red center" of the continent into grasslands dominated by "spinifex" grasses (genus *Triodia*; see Figure 41.12C). Ecosystems in which grasses dominate are also found in other places where we might expect to find forests. When humans brought domesticated livestock into temperate regions such as the European Alps, they often converted forests into grassy meadows to feed their animals (see Figure 41.12D).

The properties of soils interact with climate, fire, or grazing to affect the character of vegetation. Trees and shrubs grow particularly slowly in nutrient-poor soils. Lack of sufficient nutrients might prevent a tree or shrub seedling from sending its roots deep enough in the soil to survive the next dry season, or from growing large enough to survive the next wildfire, or from being able to recover from being eaten. If so, then the availability of soil nutrients might tip the balance between woody vegetation and grassland in seasonally dry climates, fire-prone regions, or grazing lands. The examples of grasslands we have chosen (see Figure 41.12) do differ in their soils. Two of them—alpine meadows and the Australian spinifex—grow on relatively nutrient-poor soils, whereas the other two occupy richer volcanic soils.

The biome concept can be extended to aquatic environments

The biome concept can be applied to aquatic environments as well as terrestrial ones (**TABLE 41.1**), but there are some differences. In aquatic environments, there is no single group of organisms, like terrestrial plants, that is useful for distinguishing biomes. Furthermore, climate (atmospheric conditions of temperature, precipitation, and the like) is less important in determining what organisms grow in a region than are water depth and movement, temperature, pressure, salinity, and the characteristics of the substrate.

Go to ANIMATED TUTORIAL 41.3
Aquatic Biomes
PoL2e.com/at41.3

TABLE 41.1	Major Aquatic Biomes
Biome[a]	**Description**
FRESHWATER	
Rivers and streams	Flowing water. Many small, fast-flowing source streams form on high ground, feeding into networks of ever larger, slower-flowing streams and rivers. Biota adapted to constantly moving water.
Wetlands	Glades, swamps, and marshes. Biota adapted to water-saturated soil or standing fresh water.
Ponds and lakes	Significant bodies of standing fresh water. Ponds are smaller and shallower, subject to drying. Biotic zones determined by distance from shore and light penetration (see Figure 41.13A).
ESTUARINE	
Salt marshes	Cool-temperate stands of salt-tolerant grasses, herbaceous plants, and low-growing shrubs. Crucial to nutrient cycling and coastal protection. Habitat supports diverse aquatic and terrestrial life.
Mangrove forests	Tropical and warm subtropical coasts and river deltas. Dominated by mangrove trees with aerial roots (see Figure 28.11A). Rich in animal life; protect against coastal erosion.
MARINE	
Intertidal	Sandy or rocky coastlines subject to rising and falling tides; organisms adapted to withstand both submerged and dry conditions, as well as the force of waves and moving water.
Kelp forests	Found in shallow coastal waters of temperate and cold regions. Dominated by large, leaflike brown algae (kelp) that support a wide variety of marine life.
Seagrass beds	"Meadows" of grasses (see Figure 21.29C) found in shallow, light-filled temperate and tropical waters.
Coral reefs	Species-rich, highly endangered ecosystems of shallow tropical waters. Dependent on corals (see Figure 23.9C) and their photosynthetic endosymbionts (see Concept 20.4).
Open ocean	The pelagic zone (see Figure 41.13B) hosts photosynthetic planktonic (free-floating) organisms that support a rich array of marine animals. At the greatest depths, below the level of light penetration, the abyssal zone supports a fauna largely dependent on detritus that sinks down from pelagic regions.
Hydrothermal vents	Abyssal ecosystems warmed by volcanic emissions. Chemoautotrophic prokaryotes (see Concept 19.3) nourish large annelid worms (see Figure 23.17B) and other invertebrates.

[a]A benthic region—a bottom zone containing silt, sand, or some other substrate and the organisms that occur there—is part of all three biome types.

(A) Lake depth zones

The nearshore area supports rooted aquatic plants and diverse animal life.

Photosynthetic organisms are limited to the photic zone.

Littoral zone

Limnetic zone

Benthic zone (substrate)

Photic zone

Aphotic zone

(B) Oceanic zones

The intertidal zone is affected by wave action and exposure to air.

High tide   Low tide   Intertidal zone

Continental shelf

Pelagic zone (open ocean)

Photic zone (~200 m)

Benthic zone (seafloor)

Aphotic zone

Water temperature decreases and pressure increases with depth.

Abyssal zone (deepest ocean)

Hydrothermal vent

FIGURE 41.13 Water-Depth Zones   Freshwater (A) and marine (B) environments can be divided into water-depth zones.

Salinity distinguishes freshwater biomes (streams, ponds, and lakes), saltwater biomes (salt lakes and oceans), and estuarine biomes (at river mouths where fresh and salt water mix). Salt concentration strongly affects the ability of aquatic organisms to regulate the water content of their bodies (see Concept 36.1) and thus influences which species are found where.

Freshwater biomes can be distinguished by water movement. Streams form wherever precipitation exceeds the amount of water lost to the atmosphere or soil, and the excess water flows downhill. Streams start out small but grow as they join together, forming rivers that eventually reach a lake or ocean in most cases. Within streams, the velocity of the water's flow determines the strength of the current against which fish must swim and the amount of force that can dislodge bottom-dwelling insects and algae from the streambed. Water flow also determines the presence or absence of sediment. Rapid water flow scours away sediment, exposing rocky surfaces to which organisms can cling. As water slows, it deposits sediment, forming a soft bottom in which organisms can burrow.

Nonflowing biomes such as lakes and oceans can be divided into water-depth zones (**FIGURE 41.13**). The nearshore regions of lakes (**littoral zone**) and oceans (littoral or **intertidal zone**) are shallow, affected by wave action, and periodically exposed to air by fluctuations in water level. Here, different species live in different depth zones according to their tolerance of heat, desiccation, and wave energy.

Because only the surface water is in contact with air, dissolved oxygen concentrations are highest in surface waters. Light, too, penetrates only a short distance into water. Photosynthetic organisms are confined to this zone of light penetration, called the **photic zone**. Rooted aquatic vascular plants and their multicellular algal equivalents (as well as corals with their photosynthetic algal symbionts) grow where the photic zone extends to the bottom, sometimes forming communities with a complex vertical structure much like that of terrestrial plant communities. In the open-water **limnetic zone** of lakes and the **pelagic zone** of oceans beyond the continental shelf, the prominent photosynthesizers are **phytoplankton** (free-floating photosynthetic organisms).

No photosynthetic organisms inhabit the **aphotic zone**, below the reach of light, which as a consequence is sparsely populated. The lake bottom or ocean floor is called the **benthic zone**. Water is heavy, so pressure increases with water depth. Temperature generally decreases with depth because cold water is denser than warm water and sinks. Organisms that dwell in the deepest **abyssal zone** of the oceans experience very high pressures, low oxygen levels, and (except near hydrothermal vents) cold temperatures.

CHECKpoint   CONCEPT 41.3

✓ What is meant by a biome?

✓ What conditions limit the distribution of photosynthetic organisms in aquatic biomes? In terrestrial biomes?

✓ Is it legitimate to consider the human gut a biome? Explain your answer.

We have just seen why physical geography and biogeography are linked. But the distributions of species also are contingent on the movements of continents over Earth's history.

CONCEPT 41.4   Biogeography Also Reflects Geological History

During the Age of Exploration it became clear that spatial patterns in the physical environment were not sufficient by themselves to explain the distributions of organisms. The observations of one scientist in particular suggested an important role for geological history.

Barriers to dispersal affect biogeography

Alfred Russel Wallace—who, along with Charles Darwin, advanced the idea that natural selection could account for the evolution of life's diversity—first noticed an odd pattern of species distributions during a seven-year exploration of the

Malay Archipelago. He observed that dramatically different bird faunas inhabited two neighboring islands, Bali and Lombok. Wallace pointed out that these differences could not be explained by climate or by soil characteristics, because in those respects the two islands are similar. Instead, he suggested that the Malay Archipelago was divided into two distinct halves by a line (now known as Wallace's line; see Figure 41.14) that follows a deep-water channel separating Bali and Lombok. This channel is so deep that it would have remained full of water—and thus would have been a barrier to the movement of terrestrial animals—even during the glaciations of the Pleistocene era, when sea level dropped more than 100 meters and Bali and the islands to its west were connected to the Asian mainland. As a consequence, the terrestrial faunas on either side of Wallace's line evolved mostly in isolation over a long period.

> **LINK**
>
> The development of the theory of natural selection, and Darwin's and Wallace's contributions to it, are discussed in **Concept 15.1**

The movements of continents account for biogeographic regions

Wallace's observations of animal distributions worldwide led him to divide Earth's land masses into six continental-scale areas called **biogeographic regions**. Each biogeographic region encompasses multiple biomes and contains a distinct assemblage of species, many of which are phylogenetically related. Although Wallace based his regions' boundaries on animal distributions, schemes based on plants have similar boundaries, and the biogeographic regions as we define them today have changed little from those first proposed by Wallace, despite improvements in our understanding of phylogenetic relationships (**FIGURE 41.14**).

Many boundaries between biogeographic regions correspond to geographic barriers to movement. These barriers include bodies of water (for terrestrial organisms) and areas with extreme physical environments, such as deserts or high mountain ranges. At Wallace's line, for example, the Oriental biogeographic region is separated from the Australasian biogeographic region by a deep-water channel.

But not all biogeographic regions are bounded by obvious barriers, and some of them span several continents. It's not at all clear at first why there are major biogeographic boundaries in Mexico, northern Africa, and Asia; or why the Antarctic region includes the southern tips of South America and Africa as well as New Zealand.

These aspects of biogeographic patterns remained a mystery until the second half of the twentieth century, when the theory of continental drift became widely accepted. Until then, biogeographers could only propose unsatisfactory explanations for the distributions of many organisms, such as rare cross-ocean colonization events or transient appearances of land bridges. Take the distribution of southern beeches (genus *Nothofagus*), for example. These trees are found in South America, New Zealand, Australia, and on certain islands of the southern Pacific Ocean

FIGURE 41.14 Earth's Terrestrial Biogeographic Regions The terrestrial biogeographic regions we recognize today are essentially the six regions Wallace proposed based on their distinctive assemblages of animals; modern biogeographers add an Antarctic region. Today we know that the boundaries delineating these regions are largely the result of continental drift.

Go to ACTIVITY 41.1
Major Biogeographic Regions
PoL2e.com/ac41.1

Nothofagus sp.

FIGURE 41.15 Distribution of *Nothofagus* The modern distribution of southern beeches is best explained by their origin on Gondwana during the late Jurassic period. The breakup of Gondwana and subsequent continental drift resulted in the modern distribution of *Nothofagus* in South America, Australia, New Zealand, and some islands of the South Pacific.

(**FIGURE 41.15**). How could their distribution be explained, if not by several separate transoceanic colonization events?

Once the movements of the continents were understood, it became clear that they have shaped the distributions of organisms by creating and disrupting dispersal routes. The genus *Nothofagus* is now thought to have originated on the southern supercontinent Gondwana and to have been carried along when Gondwana broke apart and its fragments drifted to their present locations. Paleontologists have found fossilized *Nothofagus* pollen dated at over 80 mya in Australia, New Zealand, Antarctica, and South America. This fossil evidence pre-dates the breakup of these portions of Gondwana, suggesting that *Nothofagus* was once widely distributed across that supercontinent.

LINK

The movements of the continents over geological time are depicted in **Figure 18.12** and **Animated Tutorial 18.1**, and described in **Table 18.1**; see also **Apply the Concept** on p. 860

Our understanding of continental drift makes it clear that the major biogeographic regions occupy land masses that have been isolated from one another long enough to allow the organisms present at the time of isolation to undergo independent evolutionary radiations. The northern biogeographic regions (Nearctic and Palearctic) became isolated from the southern regions (Neotropical, Ethiopian, Oriental, Australasian, and Antarctic) during the Jurassic period, about 150 mya, when Pangaea broke into two great land masses, Laurasia to the north and Gondwana to the south (see Figure 41.15). Southern biogeographic regions subsequently became isolated from one another when

Gondwana began to break apart, about 130 mya. Neotropical, Ethiopian, Oriental, and Australasian regions were separated approximately 110 mya, and Antarctica became isolated from Australia around 60 mya. At about the same time, the Nearctic and Palearctic regions became isolated by the opening of the Atlantic Ocean, except for a periodic connection via the Bering land bridge between Asia and North America. Thus the biotas of the seven biogeographic regions developed largely in isolation throughout the Tertiary period (about 65 to 2.6 mya), when extensive evolutionary radiations of flowering plants and vertebrates took place.

More recently, continued movements of continents have eliminated some barriers to dispersal and have caused mixing of species that had previously been isolated, referred to as **biotic interchange**. The collision of India with Asia, for example, formed the Oriental biogeographic region and at the same time caused uplift of the Himalayas. These mountains separate the Oriental and Palearctic regions. Exchange of species between the Ethiopian and Palearctic regions became possible when Africa collided with Eurasia, but the Sahara and Arabian deserts present a climate-based barrier to such exchange. Similarly, mixing of species between the Neotropical and Nearctic regions began when a land bridge formed between South America and North America. During this Great American Interchange, many North American species displaced South American lineages and drove them to extinction. Currently the Mexican Plateau provides a climate-based barrier to the northward dispersal of tropical species that slows their mixing with the communities to the north.

Phylogenetic methods contribute to our understanding of biogeography

As we saw in Chapter 16, taxonomists have developed powerful methods of reconstructing phylogenetic relationships

APPLY THE CONCEPT

Biogeography also reflects geological history

Below is a phylogenetic tree of mammals based on molecular data, accompanied by the original and current distribution of each taxon.[a] The time course of major continental drift events over the last 150 million years is shown below the tree. Use these data to answer the following questions.

[a]J. W. Murphy et al. 2007. *Genome Research* 17: 413–421.

1. Which one node (split) in the tree most clearly corresponds to an event of continental separation?

2. Are there groups of mammals that appear to have dispersed to new areas following removal of a barrier to dispersal?

These dashed lines indicate that the earliest node in the tree may actually date to much earlier than 105 mya.

Group	Earliest fossils	Current native distribution
African insectivores	Africa	Madagascar, Africa
Long-nosed insectivores	Africa	Africa
Aardvarks	Africa	Africa
Elephants	Africa	Africa, Asia
Hyraxes	Africa	Africa, Middle East
Armadillos	South America	North, South America
Colugos ("flying lemurs")	SE Asia	SE Asia
Tree shrews	SE Asia	SE Asia
Primates	Europe	Tropics of Africa, Americas, Asia
Rabbits and pikas	Europe	North America, Eurasia
Rodents	Europe	Worldwide
Shrews, moles, hedgehogs	Laurasia	Worldwide except Australasia
Carnivora	Laurasia	Worldwide except Australasia
Pangolins	Laurasia	Africa, southern Asia
Odd-toed hoofed mammals	Laurasia	Worldwide except Australasia
Even-toed hoofed mammals	Laurasia	Worldwide except Australasia
Bats	Laurasia	Worldwide

Time (mya)

Pangaea splits into Laurasia (North America and Eurasia) and Gondwana (Antarctica, Africa, South America, and Australia)

Gondwana splits into India plus Madagascar, Africa, South America plus Australia plus Antarctica plus New Zealand

Madagascar separates from India

Laurasia splits into North America, Greenland, and Eurasia

Antarctica, South America, Australia, and New Zealand split

India collides with Asia

Africa collides with Eurasia

South America collides with North America

Time (mya)

among organisms. Biogeographers use phylogenetic information, in conjunction with the fossil record and geological history, to address questions about how the modern distributions of organisms came about. They begin by superimposing on a phylogenetic tree the geographic area that is or has been occupied by each group. By comparing the sequence and timing of splits (nodes) in the phylogenetic tree with the sequence of separation or connection of geographic areas, biogeographers

can determine where a lineage originated and reconstruct the history of its diversification and dispersal. For example, if a phylogenetic split coincides with the appearance of a barrier to dispersal, it is reasonable to conclude that the barrier caused the split by isolating portions of the original range of the ancestral species. If the phylogenetic split comes long before or after a barrier arises, then something else caused portions of the ancestral population to evolve in isolation from one another.

CHECKpoint **CONCEPT 41.4**

✓ What is Wallace's line?

✓ What kinds of barriers might limit the dispersal of terrestrial species? Of aquatic species?

✓ Biomes and biogeographic regions are two different concepts that relate to two different fundamental factors that mold the distributions of organisms. Explain.

As we have seen, the makeup of ecological systems on Earth is enormously variable over time and space. Recently, however, this variation has been greatly influenced by the activities of one species: *Homo sapiens*. How are our activities affecting ecological systems?

CONCEPT 41.5 **Human Activities Affect Ecological Systems on a Global Scale**

Some say that we are entering a new geological period, dubbed the "Anthropocene," or Age of Humans, because our activities are altering ecological systems on a global scale. Others say that the new age should be called the "Homogenocene," or Homogeneous Age, because the net effect of our activities is to make ecological systems less complex and more uniform. We affect ecological systems by using species for food or timber, by altering landscapes, by spreading organisms across the globe

FIGURE 41.16 Human Agricultural Practices Produce a Uniform Landscape The cultivation of crop plants for food and other uses diminishes the diversity of ecosystems. This monoculture is a field of soybean plants (*Glycine* sp.) in Mississippi.

without regard to natural barriers to dispersal, and as Concept 45.4 will describe, by changing Earth's climates.

We are altering natural ecosystems as we use them

When we use natural ecosystems—for example, through hunting, fishing, grazing, or logging—we remove individuals of particular species and thereby change their abundances. If we remove too many, we can even cause some species to disappear entirely—to go extinct. The resulting shifts in the relative abundances of components of natural ecosystems change the patterns of interaction among species, and thereby change how entire ecosystems function. The decreased abundance of grasses in relation to shrubs in the U.S.–Mexico Borderlands, for example, has reduced the ability of these lands to support grass-eating animals, whether domesticated or not.

We are replacing natural ecosystems with human-dominated ones

We have now converted almost half of Earth's land area into human-dominated ecosystems. Cities occupy only about 1 percent of the land area (about 1.5 million km^2), but an area roughly the size of South America (about 18 million km^2) is devoted to agriculture, and another roughly the size of Africa (about 35 million km^2) is managed as pasture or used as rangeland for cattle and other livestock.

Human-dominated ecosystems contain fewer interacting species than natural ecosystems and are therefore less complex. Pastures or heavily grazed rangelands, for example, often contain fewer species than do natural grasslands or forests. And when an area is converted to agriculture, monocultures (plantings of single crops) often replace species-rich natural plant communities (**FIGURE 41.16**). Furthermore, agricultural systems worldwide are dominated by a relatively few plant species. Some 19 species comprise 95 percent of total global crop production, and overall crop diversity is a tiny fraction of the approximately 350,000 named plant species on Earth.

Human activities are similarly reducing the complexity of natural landscapes. For example, when rivers are dammed to control flooding or tapped to irrigate crops, species-rich natural streamside ecosystems disappear. Similarly, conversion of land to human uses not only reduces the total area of natural vegetation that remains, but also breaks it into smaller fragments. Such changes, and others that we will discuss in the following chapters, simplify natural ecosystems and change the way they function.

We are blurring biogeographic boundaries

Humans are also moving organisms around on a global scale, sometimes deliberately—as when Spanish settlers brought domesticated cattle to the U.S.–Mexico Borderlands—and sometimes inadvertently. Only about 1 percent of inadvertent introductions result in self-sustaining populations in the new locality, but their cumulative effect on geographic distributions is huge. Of the insects found in both Europe and North America, for example, half are estimated to have been transported between the two continents by humans. Similarly, more than half of the plant species on many oceanic islands are not native, and in many continental

areas the figure is 20 percent or more. The pace of introductions is astonishing: for example, in California's San Francisco Bay, one new species on average became established every 12 weeks during the 1990s. Introducing new species to communities changes their species composition and adds novel interactions to the original system that may precipitate further changes in species abundances—even the complete loss of some species from the system.

This human-assisted biotic interchange is homogenizing the biota of the planet, blurring the differences among communities that evolved during long periods of continental isolation. One wonders how Alfred Wallace would draw the boundaries of biogeographic regions if he were using present-day data!

Science provides tools for conserving and restoring ecological systems

With the dawning of the Anthropocene, ecologists are called upon as never before to understand how humans are influencing Earth's ecological systems and how we can preserve their ability to sustain life on our planet. Accordingly, several new subdisciplines of ecology have emerged. The goal of **conservation ecology** is to understand the process of extinction and devise ways to prevent the extinction of vulnerable species. Often this requires that we protect the ecosystems of which these species are a part. The goal of **restoration ecology** is to restore the health of damaged ecosystems. These two fields are related because natural systems are sometimes altered so strongly that extinction will occur unless the systems are restored.

To achieve their goals, conservation and restoration ecologists deploy the same tools of scientific inquiry that all other biologists (and scientists) use: observation, questioning, logic, and experimentation (see Concept 1.5). They often begin with **natural history**—the observation of nature outside of a formal, hypothesis-testing investigation—because knowledge of nature is fundamental to all stages of ecological inquiry. Natural history observations are the source of new questions and hypotheses and are critical for the design of good experiments—ones that do not mislead us because they use unnatural conditions or leave out an important feature of the system. A lack of natural history knowledge often limits our ability to answer important questions. For example, we cannot fully answer the question "Has the introduction of honey bees caused declines in native bee species?" without knowing what bee species were present before honey bees were introduced and how abundant they were. It turns out that such information is available for only a handful of places on Earth.

As we saw in Chapter 1, scientists test hypotheses by seeing if their predictions are true. Sometimes we can use simple rules of logic to develop predictions. But with systems as complex as ecological systems, we often need to use a mathematical model, or perhaps even a computer simulation. What is critical is that we base the model on natural history knowledge about the system. In the case of the degraded rangeland system of the Borderlands, for example, predicting the conditions that would restore desirable grasses might require a complex model of the many factors that affect the growth of grasses relative to shrubs.

Conservation and restoration ecology are only two examples of the important practical applications of ecology in the

Anthropocene. The chapters that follow will highlight numerous additional examples.

> ### CHECKpoint   CONCEPT 41.5
> ✓ Identify two human activities that alter the distributions of species.
> ✓ In what ways do agricultural ecosystems differ from the natural ecosystems they replace?
> ✓ Suppose that your job is to design an experiment to see whether allowing natural wildfires, rather than suppressing them, can restore a certain shrubland in the U.S.–Mexico Borderlands to a grassland. What natural history knowledge would you want to have about fire in the Borderlands, and how would this knowledge influence the design of your experiment?

Now that we have explored some of the properties of ecological systems, we are ready to take a closer look at them, beginning with the smallest scales in the ecological hierarchy: individual organisms and populations.

> **Q** Can basic ecological principles suggest why removing cattle has not restored grasses to the Borderlands?

ANSWER   The physical environment of the Borderlands is strongly influenced by Earth's climate patterns: its position near 32° N latitude, where the warm, dry air of the Hadley cells descends, makes it an arid place (Concept 41.2). Aridity, combined with other features of the physical environment, determines the characteristics of organisms that live in the Borderlands (Concept 41.3). Ecological communities of the Borderlands are also affected by the region's history of geographic isolation from or connection with other regions (Concept 41.4). All of these principles prepare us to realize that grasslands in different locations may look similar but may respond very differently to human activities.

As we've seen, communities dominated by grasses do differ from one another (Concept 41.1, Figure 41.12). Some occupy moist and cool environments, whereas others, like the Borderlands, occupy dry and hot ones. Some, including many meadows and pastures in Europe and eastern North America, were once forests that were cleared to make way for grasses; managing the size of cattle herds in these places can conserve or restore the grassland ecosystem. Others, such as the tropical savannas of Africa, have long histories of evolution with grazing mammals, and so tolerate grazing well. Some grasslands in more arid regions, such as the Borderlands, originally experienced natural wildfires and may require periodic burning for their maintenance. Still others, such as the spinifex grasslands of Australia, grow on nutrient-poor soils that support sparse growth of grasses at best.

Armed with this understanding, you may see several possible reasons why the grasslands in the Borderlands were lost

and why "resting the range" by itself has not restored them. Perhaps periodic burning is needed. Perhaps the original landscape, without deep gullies that carry water away, must be re-created to return to the soil the water and nutrients that grasses require. Perhaps an interaction between fire and nutrients influences which vegetation type will be favored. And another thought may occur to you: perhaps it will be necessary to begin with dras-

tic restoration measures—for example, removal of the existing shrubs—before other measures will have a chance of success. Ecologists are now using natural history knowledge, experiments in natural grassland plots, and modeling as scientific tools (Concept 41.5) to explore all of these possibilities.

SUMMARY

CONCEPT 41.1 Ecological Systems Vary over Space and Time

- An **ecological system**, or **ecosystem**, consists of one or more organisms and the **biotic** and **abiotic** components of the environment with which they interact.

- Ecological interactions lead to evolution by natural selection.

- Ecological systems can be studied at scales in the biological hierarchy ranging from an individual organism and its immediate surroundings to **populations**, **communities**, **landscapes**, or the entire **biosphere**.

- Ecological systems are highly complex and variable but can be understood with scientific methods.

CONCEPT 41.2 Solar Energy Input and Topography Shape Earth's Physical Environments

- **Weather** is the state of atmospheric conditions in a particular place at a particular time, and **climate** is their average state and pattern of variation over longer periods.

- Latitudinal differences in solar energy input are caused by differences in the angle of the sun's incoming rays. **Seasonality** results from the tilt of Earth's axis of rotation relative to its orbit around the sun. **Review Figures 41.3 and 41.4**

- Latitudinal differences in solar energy input drive north–south patterns of atmospheric circulation. These patterns, in turn, influence latitudinal patterns of temperature and precipitation and distribute heat from low to high latitudes. **Review Figure 41.5**

- Prevailing winds result from the interaction of north–south atmospheric circulation with Earth's eastward rotation, which adds an east–west component to air movement because of the **Coriolis effect**. **Review Figure 41.6**

- Oceanic circulation patterns called **gyres** are caused by prevailing surface winds and by the Coriolis effect. These patterns redistribute heat from low to high latitudes and influence patterns of temperature and precipitation. **Review Figure 41.7**

- Variation in the elevation of Earth's surface, known as **topography**, affects the physical environment. **Review Figure 41.8 and ANIMATED TUTORIAL 41.1**

- **Climate diagrams** summarize climate at a particular location in an ecologically relevant way. **Review Figure 41.9**

CONCEPT 41.3 Biogeography Reflects Physical Geography

- A **biome** is a distinct physical environment that is inhabited by ecologically similar organisms with similar adaptations. The species that occupy the same biome in geographically separate regions may not be closely related phylogenetically but often show convergent adaptations.

- The distribution of terrestrial biomes is broadly determined by annual patterns of temperature and precipitation. **Review Figures 41.10 and 41.11 and ANIMATED TUTORIAL 41.2**

- Other features of the physical environment—particularly soil characteristics—interact with climate to influence the character of terrestrial vegetation. **Review Figure 41.12**

- Climate is less important in distinguishing aquatic biomes than are water depth and flow, temperature, pressure, salinity, and characteristics of the substrate. **Review Table 41.1, Figure 41.13, and ANIMATED TUTORIAL 41.3**

CONCEPT 41.4 Biogeography Also Reflects Geological History

- Alfred Russel Wallace first noticed a boundary between two distinct assemblages of terrestrial species, now known as Wallace's line, that reflected a barrier to dispersal, rather than a boundary between climates or soils.

- The world can be divided into **biogeographic regions**, each of which contains a distinct assemblage of species, many of which are phylogenetically related. **Review Figure 41.14 and ACTIVITY 41.1**

- The boundaries of biogeographic regions generally correspond to present or past barriers to dispersal and can be explained by continental drift. **Review Figure 41.15**

- Biogeographers use phylogenetic information, in conjunction with the fossil record and geological history, to determine how the modern distributions of organisms came about.

CONCEPT 41.5 Human Activities Affect Ecological Systems on a Global Scale

- Humans have converted almost half of Earth's land area into human-dominated ecosystems, which are much more homogenous and less complex than natural ecosystems. Remaining natural ecosystems occur in small, isolated fragments.

- Humans move species around the globe without regard to natural barriers to dispersal. These movements are homogenizing the biota of the planet.

- **Conservation ecology** and **restoration ecology** are new subdisciplines of ecology whose goals are to prevent extinction of species and to restore damaged ecosystems.

- Knowledge of **natural history** is essential to these subdisciplines, as it is to all ecological inquiry.

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities
PoL2e.com/is41

Go to LaunchPad at **macmillanhighered.com/launchpad** for additional resources, including LearningCurve Quizzes, Flashcards, and many other study and review resources.

42

Populations

A field worker sweeps for ticks in the forests near Millbrook, New York.

Ecologist Rick Ostfeld was studying white-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*) at the Cary Institute of Ecosystem Studies in Millbrook, New York, when an unexpected event took his work in a new direction. Ostfeld and his colleague Clive Jones were working on these rodents in order to understand what triggers the dramatic once-in-a-decade outbreaks of invasive gypsy moths (*Lymantria dispar*) that defoliate oak forests in North America. They suspected that the outbreaks start when the moths escape control by mice and chipmunks, which eat moth pupae.

In 1991, soon after the study began, one of the field assistants discovered that half his face was paralyzed and that he could not close one eyelid. (He devised a protective eye patch so that he could continue his fieldwork.) The eventual diagnosis was Lyme disease. Scientists at the time were only beginning to understand this disease, which

was not described until 1975 and whose cause—infection by bacteria of the genus *Borrelia*—was not identified until 1982. By 1991, epidemiologists had discovered that Lyme disease is transmitted by *Borrelia*-infected black-legged ticks (*Ixodes scapularis*) when they bite hosts, and that Lyme disease risk increases with the abundance of infected ticks. Tick hosts include white-tailed deer, birds, lizards, and small mammals as well as humans.

Millbrook turned out to be at the epicenter of the emerging Lyme disease epidemic, and Ostfeld turned his attention to black-legged ticks as the disease vectors (organisms that transmit pathogens). He had already been counting ticks on live-trapped mice and chipmunks. Now he began to study how the abundance of rodents and other vertebrate hosts affects tick abundance and infection rate. He discovered that small mammals are the primary reservoir for *Borrelia* (they harbor it without getting sick). Ticks are not infected when they hatch from eggs

as larvae; they become infected when they bite an infected host as a larva or nymph. It turns out that birds and lizards do not harbor *Borrelia*, and that most ticks are already infected by the time they are adults able to climb high enough into the vegetation to encounter large hosts such as deer.

From his previous work, Ostfeld already knew that rodent abundance soars when oaks produce a big acorn crop. Now he found that the number of tick larvae that survive to become nymphs, and of nymphs that survive to become adults, increases with rodent numbers. His next goal was to use this information about rodent, oak, and tick population sizes to determine how humans can slow the spread of Lyme disease.

Q How does understanding the population ecology of disease vectors help us combat infectious diseases?

Populations Are Patchy in Space and Dynamic over Time

In Chapter 41 we saw that individual organisms are the fundamental units of all larger ecological systems. Many important insights are gained by focusing on these fundamental units, but additional insights arise by studying **populations**—groups of individuals of the same species. Populations have properties that individuals do not have, and we cannot understand larger ecological systems, such as communities, without understanding their component populations. One important property of populations is abundance because, together with the average properties of individuals, abundance determines a species' ecological role in the larger community or ecosystem.

Humans have long had a practical interest in understanding what determines abundance because we want to manage our ecological interactions with other species. We want to know how to increase the abundance of organisms that provide us with resources such as food or fiber for clothing, how to conserve wild organisms that benefit us by acting as agents of pollination or pest control, and how to decrease the abundance of undesirable organisms such as crop pests, weeds, and pathogens. Understanding population ecology is a key to achieving these goals.

Population density and population size are two measures of abundance

"Abundance" has several meanings in ecology. We might consider a species abundant because there are many individuals in an area. If that same species occurs only in a small geographic region, however, we might consider it rare because the total number of individuals of that species is small. Depending on why they want to measure abundance, ecologists use one of two approaches. If they are interested in the causes or consequences of local abundance, they usually measure **population density**: the number of individuals per unit of area (for surface-dwelling organisms) or volume (for organisms that live in air, soil, or water). Alternatively, if ecologists are interested in the population as a whole, they usually measure **population size**: the number of individuals in the population.

Counting all the individuals in a population is practical only for very small populations in which individuals can be distinguished. For this reason, ecologists usually measure population density first. Then they multiply population density by the area or volume occupied by the entire population to estimate population size.

Abundance varies in space and over time

The abundance of organisms varies on several spatial scales. At the largest scale, as we saw in Chapter 41, many species are found only in a particular region, and their densities are zero elsewhere. Within that region, which is called the species' **geographic range**, the species may be restricted to particular kinds of environments, often called **habitats**, which may themselves be patchily distributed. For example, Edith's checkerspot butterfly (*Euphydryas editha*) is found from southern British Columbia and Alberta to Baja California, Nevada,

Utah, and Colorado (**FIGURE 42.1A**). Within this geographic range, it occurs in the open habitats (coastal chaparral, meadows, grasslands, or open woodlands) where the plants that its caterpillars eat are found. In the San Francisco Bay area, suitable food plants grow only in soils derived from a chemically unique rock called serpentine (**FIGURE 42.1B**). Outcrops of serpentine rocks constitute habitat "islands" for the butterflies—that is, patches of suitable habitat separated by areas of unsuitable habitat. Habitat patchiness has consequences for abundance that we will explore in Concept 42.5.

In any given locality, population densities are **dynamic**—they change over time. For example, abundances of rodents, black-legged ticks, and oak acorns vary greatly from year to year in the forests described in the opening story (**FIGURE 42.2**).

(A)

San Francisco Bay area

Geographic range of *E. editha*

(B)

Serpentine outcrops (potential butterfly habitat)

Colonization

The Morgan Hill population patch was probably the source of individuals for recolonization of other patches.

Euphydryas editha

10 km
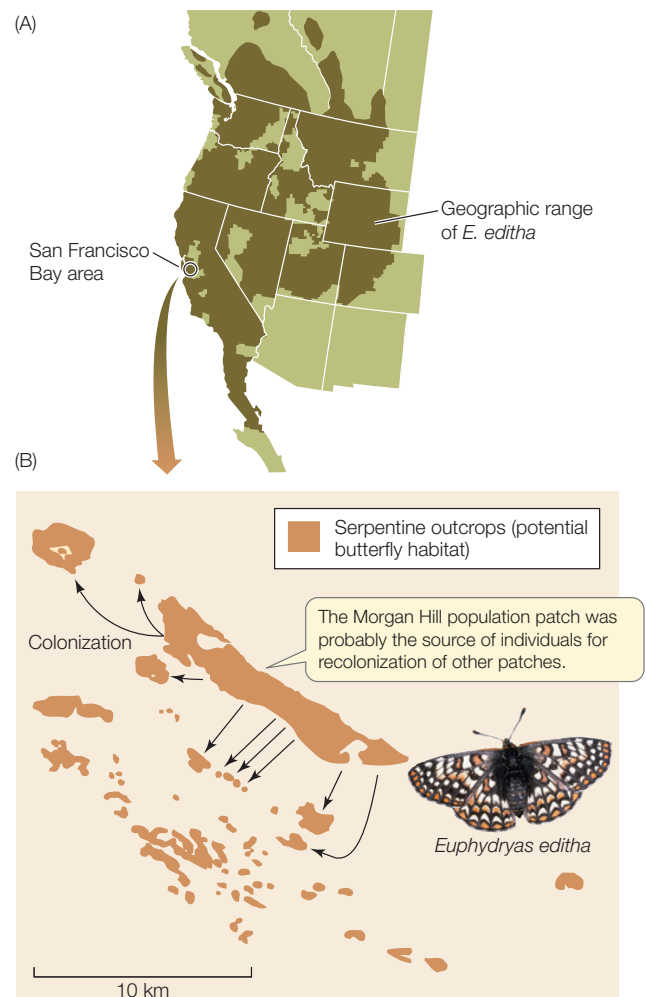
FIGURE 42.1 Species Are Patchily Distributed on Several Spatial Scales   (A) The geographic range of Edith's checkerspot butterfly (*Euphydryas editha*) extends from British Columbia and Alberta to Baja California. (B) Within the geographic range, the butterflies occur in patches of suitable habitat which, in the San Francisco Bay area, are on serpentine soils. Arrows indicate colonization events that are discussed in Concept 42.5.
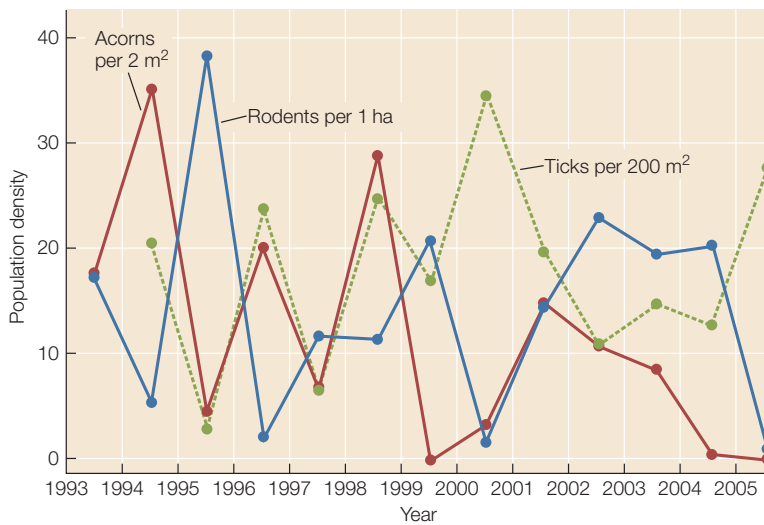
FIGURE 42.2 Population Densities Are Dynamic Densities of acorns, rodents, and nymphal black-legged ticks varied over time in an oak forest near Millbrook, New York. (Notice that the population density of each organism is measured on a spatial scale appropriate for that organism's average density; see Appendix C for definitions of units of area.)

CHECKpoint CONCEPT 42.1

✓ What aspects of abundance do population density and population size measure, respectively?

✓ Big-leaf mahogany (*Swietenia macrophylla*) is a valuable timber tree native to South American tropical rainforests. In Brazil, it is a species of conservation concern because natural populations are shrinking due to habitat destruction and illegal logging. In Sri Lanka and the Philippines, mahogany is grown in commercial plantations, but it has escaped cultivation and is now invading wild rainforest and harming native species. What goals would you set for managing wild mahogany populations in these different areas?

✓ The image in the opening story shows a field worker "sweeping" the forest floor with a cloth to which ticks will attach themselves, as if the cloth were a host animal. How would you use this method to estimate tick population size in a given area of forest?

Why do species abundances vary in time and space? To answer this question, we need to understand the processes that add individuals to or subtract them from populations.

CONCEPT 42.2 Births Increase and Deaths Decrease Population Size

The size of anything, whether a bank account or a population, changes over time through additions and subtractions. Consider the size of something in the future. The size of your bank account, for example, will be equal to the amount of money you have now, plus the amount that is added, minus the amount that is taken out. What differs between bank balances and population sizes are the processes that add or subtract. In the case of your bank account, deposits and interest add to your balance, while withdrawals and bank fees subtract from it. In the case of populations, births (or the production of new individuals via seeds in the case of seed plants) add individuals, while deaths remove individuals. To spell this out,

the number of individuals in a population at some time in the future =
the number now + the number that are born –
the number that die

If we turn this word equation into symbols, we have the most basic mathematical model of population size:

$$N_{t+1} = N_t + B - D \qquad \text{Equation 42.1}$$

where N is the population size, B is the number of births in the time interval from time t to time $t + 1$, and D is the number of deaths in that same interval. Ecologists call this equation the "birth–death" or **BD model** of population size.

We can use Equation 42.1 to understand population dynamics. Most often, the size of a population does not remain constant over time—the population grows or shrinks. Ecologists call the amount of change over a specific amount of time the growth rate of the population (a somewhat confusing term until we realize that when a population shrinks, its growth rate is negative). The population growth rate can be obtained from Equation 42.1 in two steps. First, we subtract N_t (the present population size) from both sides of the equation to obtain the change in population size:

$$N_{t+1} - N_t = \Delta N = (N_t - N_t) + B - D = B - D$$

The term ΔN is shorthand for the change in population size (using the convention that the Greek letter delta means "change in"). Next, we divide both sides by ΔT, the time interval from t to $t + 1$, to obtain the change per unit of time:

$$\frac{\Delta N}{\Delta T} = \frac{B - D}{\Delta T} = \frac{B - D}{(t+1)-t} = \frac{B - D}{1} = B - D \qquad \text{Equation 42.2}$$

This shows, logically enough, that the change in size over one time interval is the number of births minus the number of deaths during that interval.

Change in the size of a population can be measured directly only for very small, countable populations, such as a zoo population. Ecologists can get around this difficulty by keeping track of a sample of individuals over time. From this sample, they can estimate the number of offspring that the average individual produces, called the **per capita birth rate** (**b**), and the average individual's chance of dying, called the **per capita death rate** (**d**), in some interval of time. Per capita (literally, "per head") means "per individual." Total birth and death rates in the population can then be estimated by multiplying per capita birth and death rates by population size, so that $B = bN_t$ and $D = dN_t$. Substituting into Equation 42.1, we have

APPLY THE CONCEPT

Births increase and deaths decrease population size

Jane is a rancher who is considering shifting her operation from cattle to American bison (*Bison bison*), to take advantage of the demand for lean, healthy bison meat. To decide, she needs to know how well bison will do on her ranch. She buys 50 female bison that are already inseminated and places 10 of them, picked at random, into their own pasture. These 10 females serve as a sample from which Jane collects demographic data over one year. Use her data to answer the questions below.

1. How many total births and how many total deaths occurred in this sample population?

2. What were the estimated average per capita birth and death rates (*b* and *d*) for the entire bison herd, based on this sample?

3. What was the estimated per capita growth rate (*r*)?

4. Based on these estimates, what was the size of Jane's entire bison herd at the end of the year? (Hint: Use Equation 42.3.)

FEMALE #	ALIVE AT END OF YEAR?	NUMBER OF OFFSPRING
1	Yes	1
2	Yes	0
3	Yes	1
4	Yes	0
5	No	0
6	Yes	1
7	Yes	1
8	No	0
9	Yes	1
10	Yes	0

$$N_{t+1} = N_t + bN_t - dN_t$$

or equivalently,

$$N_{t+1} = N_t + (b - d)N_t$$

The value ($b - d$)—the difference between per capita birth rate and per capita death rate—represents the average individual's contribution to total population growth rate. This value is the **per capita growth rate**, which ecologists symbolize as *r*. Substituting *r* for ($b - d$), we have

$$N_{t+1} = N_t + rN_t \qquad \text{Equation 42.3}$$

By converting Equation 42.3 into an equation of growth rate analogous to Equation 42.2, we get

$$\frac{\Delta N}{\Delta T} = rN \qquad \text{Equation 42.4}$$

What happens if per capita birth rate is greater than per capita death rate, or if death rate is greater than birth rate, or if they are equal? If $b > d$, then $r > 0$, and the population grows. If $b < d$, then $r < 0$, and the population shrinks. If $b = d$, then $r = 0$, and the population size does not change.

We are now in a better position to understand why population sizes or densities change over time: they *have to* unless the number of births exactly equals the number of deaths. We are also in a better position to understand why population densities vary in space. We saw in Chapter 41 that barriers to dispersal can cause species to be absent from some places. Another possible reason for a species' absence from a place is a negative population growth rate. A species will not persist in a given location if its per capita growth rate, *r*, is negative there. Any population that decreases steadily in size over time eventually reaches a density of zero—that is, it goes extinct.

CHECKpoint   CONCEPT 42.2

✓ What is the relationship between per capita birth rate and the total number of births in a population during a time period?

✓ What do we need in addition to estimates of per capita birth and death rates in order to predict population size at some future time?

✓ What two strategies could Jane the rancher (see Apply the Concept on this page) use to expand her bison herd faster?

We can understand the dynamics of whole populations, and even some aspects of spatial variation in abundance, if we can estimate the average birth and death rates of the individuals that constitute those populations. What determines these variables?

CONCEPT 42.3   Life Histories Determine Population Growth Rates

The study of processes that influence birth, death, and population growth rates is known as **demography** (Greek *demos*, "population"; *graphia*, "description"). Ecologists who wish to understand such processes for a species usually begin by characterizing its **life history**: the sequence of key events, such as growth and development, reproduction, and death, that occur during an average individual's life. To describe the life history of the black-legged tick, for example, we begin with the first life stage—one of the thousands of eggs laid by an adult female in spring (**FIGURE 42.3**). If the egg survives, it hatches

FIGURE 42.3 Life History of the Black-Legged Tick The seasonality of the ticks' environment and the difficulty of obtaining the blood meal necessary to grow, molt, and reproduce have produced a 2-year life history that includes two long periods of winter dormancy.
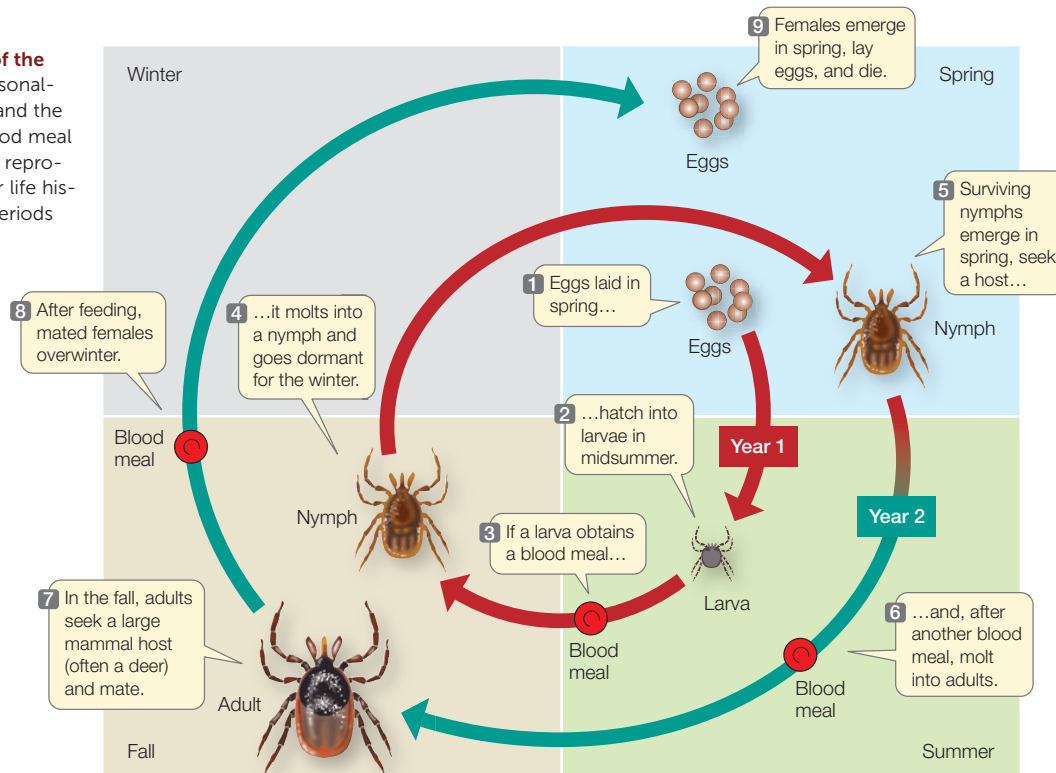
into a larva in midsummer. If the larva can obtain a blood meal from a mammal, bird, or lizard, it molts into a nymph and goes dormant for the winter. If it survives the winter, the nymph becomes active again the following summer and seeks another blood meal from a vertebrate host. If it is successful, it molts into an adult in the fall and seeks a large mammal host, such as a deer, raccoon, opossum—or human. If successful, it mates on this final host, and if it is a female, goes dormant for another winter, lays eggs in the spring, and dies.

Go to MEDIA CLIP 42.1
Dangerous Deer Ticks
PoL2e.com/mc42.1

Even this qualitative description of the tick's life history gives us important insights into its ecological interactions. But to estimate birth and death rates, we need more information about the timing of life events and the number of offspring produced. A quantitative tick life history would indicate at what ages individuals make transitions between life stages and how many do so successfully: the fraction of eggs that hatch successfully, of larvae that find a host and molt successfully into nymphs, and of nymphs that live through the winter, find a host, and molt into adults. In addition, a quantitative life history would indicate the number of eggs that the average adult female lays.

Obtaining such information is not easy, and ecologists still don't have all of it for black-legged ticks. We do have quantitative life histories, however, for other species, such as the common cactus finch (*Geospiza scandens*) in the Galápagos

archipelago. **TABLE 42.1** shows the life history, in table form, of a sample of 210 finches born on a single island in 1978. The table quantifies two important aspects of any life history: the fraction of individuals that survive from birth to different life stages (which are ages in the case of the finches), called **survivorship**; and the average number of offspring each surviving individual produces at those life stages, called **fecundity**. Survivorship can also be expressed as its opposite, **mortality**, which is the fraction of individuals that do not survive from birth to a given stage or age (mortality = 1 – survivorship).

Information on survivorship, fecundity, and the duration of life stages can be used to calculate per capita growth rates (r) for any life history. The calculations involved are complex, but it is not hard to see that survivorship and fecundity will affect r. All else being equal, the higher the fecundity and the higher the survivorship, the higher r will be. If reproduction shifts to earlier ages, r will increase as well.

Life histories are diverse

Species vary considerably in how many and what types of life stages they go through, how old they are when they begin to reproduce, how often they reproduce, how many offspring they produce, and how long they live. Most black-legged ticks spin out their lives over 2 years, whereas the life history of a periodical cicada spans nearly 2 decades. Other arthropods have life spans of days or weeks. Some species, like the tick, go through a discrete series of life stages of variable duration, each separated by a molt. Other species, such as common cactus finches and humans, develop continuously as they age. Some plants germinate, grow, flower, produce seeds, and die

TABLE 42.1	Quantitative Life History for 210 Common Cactus Finches Born in 1978 on Isla Daphne		
Calendar year	Age of bird (years)	Survivorship[a]	Fecundity[b]
1978	0	1.00	0.00
1979	1	0.43	0.05
1980	2	0.37	0.67
1981	3	0.33	1.50
1982	4	0.31	0.66
1983 Increased rain	5	0.30	5.50
1984	6	0.20	0.69
1985 Drought	7	0.11	0.00
1986	8	0.07	0.00
1987 Increased rain	9	0.07	2.20

[a]Survivorship = the proportion of the 210 birds that survived from birth to a given age.
[b]Fecundity = the average number of young born per female of a given age.

all in one growing season—they are annuals (see Concept 27.2). Other plants live for centuries. Some species spend long periods in a dormant state, whereas others are continuously active. Some organisms, including the tick, reproduce only once and then die; others, such as finches and humans, can reproduce multiple times.

Life histories vary not only among species but within species as well, including among human populations. For example, **life expectancy** (the age to which an average person survives) of the Aeta people of the Philippines, who hunt and gather wild food, is 16.5 years, and girls reach puberty at age 12. The Turkana, herders of East Africa, experience food shortages as frequently as the Aeta, but they have a life expectancy of 47.5 years, and Turkana women reach sexual maturity at age 15. In well-nourished United States populations, life expectancy is 78.2 years—much greater than for either the Aeta or the Turkana—yet girls in the U.S. reach puberty at age 12.5 years on average.

Resources and physical conditions shape life histories

Individual organisms must acquire materials and energy to maintain themselves and to fuel metabolism, growth, activity, defense, and reproduction. Materials and energy—and the time available to acquire them—constitute **resources** for organisms. Organisms also need physical conditions that they are able to tolerate. The primary distinction between resources and conditions is that resources can be used up (e.g., mineral nutrients, photons of light, time, space, or food items), whereas conditions are experienced but not consumed.

The rate at which an organism can acquire a resource increases with the availability of that resource in its environment, up to the point at which the organism's capacity to take in and process the resource is saturated. A plant's net photosynthetic rate, for example, increases with sunlight intensity (**FIGURE 42.4A**), and an animal's rate of food intake increases with the density of food (**FIGURE 42.4B**)—but in both cases we see a leveling off of intake rate at high resource availability.

Organisms use the resources they obtain for functions such as maintenance, growth (see Concept 29.1), defense (see Chapter 39), and

(A)
1 The rate of photosynthesis increases with increasing light intensity…

2 …until the light-harvesting apparatus of the plant becomes saturated and cannot make use of additional light.

Rate of photosynthesis

No light ⟶ Full sun
Light intensity

(B)

Seeds harvested per second

Seed density (no./cm²)
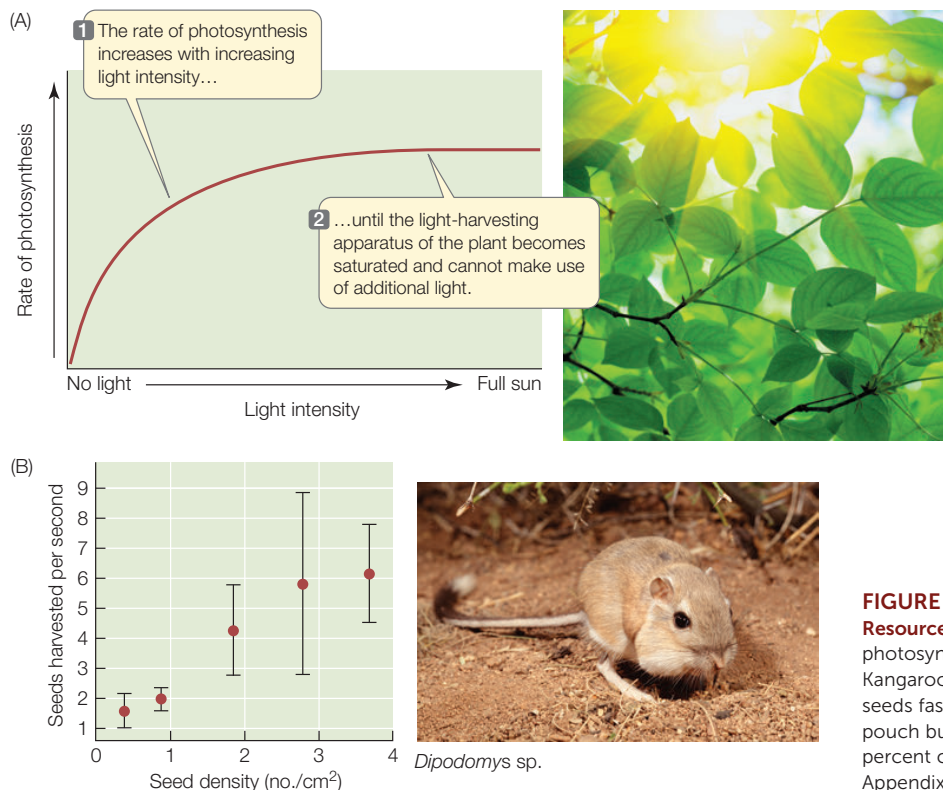
Dipodomys sp.

FIGURE 42.4 Resource Acquisition Increases with Resource Availability—Up to a Point (A) A plant's photosynthetic rate increases with light intensity. (B) Kangaroo rats (*Dipodomys* spp.) are able to harvest seeds faster as seed density increases. (Note the cheek pouch bulging with seeds.) Error bars indicate 95 percent confidence intervals around the mean. See Appendix B for discussion of statistical concepts.

FIGURE 42.5 **The Principle of Allocation** Organisms use resources (energy and time) to acquire more resources. The organism must then allocate acquired resources among competing life functions. In general, an organism's first priority is to maintain the integrity of its body. This figure assumes that the same amount of energy or time is allocated to resource acquisition in all three conditions.

(A) Typical conditions, normal resources

An allocation to acquiring resources…

…yields a certain amount of resource gain.

Resource acquisition

Reproduction

Growth

Defense

Maintenance

Maintenance needs must be met first. Remaining resources are divided among other activities.

(B) Typical conditions, abundant resources

Reproduction

Growth

Defense

Maintenance

When resources are abundant, more resources are gained and more are available after maintenance needs are met.

(C) Stressful conditions, normal resources

Reproduction

Growth

Defense

Maintenance

Stressful conditions mean more resources must be expended on maintenance and fewer are available for other purposes.

reproduction (see Chapter 37) (**FIGURE 42.5**). In addition, they must devote some resources to activities involved in obtaining more resources. The **principle of allocation** states that once an organism has acquired a unit of some resource (such as food), that bit of resource cannot be used for multiple functions at once.

In general, an organism's first priority is to maintain the integrity of its body. Investment in maintenance is greater in stressful than in unstressful environments because maintenance is more difficult under stressful physical conditions (as was illustrated for temperature in Concept 29.3). For example, the hotter their desert environment, the more time day-active lizards must spend in a cool retreat to keep body temperature below a lethal level, and thus the less time they have to look for food (see Figure 29.8). Once an organism obtains more resources than it needs for maintenance, it can allocate the excess to other functions, such as growing bigger or producing offspring. In general, as the average individual in a population acquires more resources, the average fecundity and survivorship increase.

Life-history variation among species and populations often reflects the principle of allocation. A species that invests heavily in growth early in life, for example, cannot simultaneously invest heavily in defense (e.g., protective structures or chemical defenses). As a consequence, it reaches adult size quickly, but at the cost of lower survivorship than a species that invests more in defense. A species that starts investing in reproduction early in life grows more slowly, and matures at a smaller adult size, than a species that waits to reproduce. Species that invest heavily in reproduction often do so at the expense of adult survivorship. They have high fecundity but short life spans. Such negative relationships among growth, reproduction, and survival are called **life-history trade-offs**.

The environment shapes much of this life-history variation because, together with a species' way of life, it determines the relative costs and benefits, in terms of survivorship and fecundity, of any particular allocation pattern. The Aeta people mentioned earlier, for example, live in an environment that imposes higher mortality than does that of the Turkana. High mortality

means that the benefit of early reproduction (more individuals survive to reproduce at least once) outweighs the fecundity benefit of growing to a larger adult size (in general, human females produce 0.24 more offspring per additional centimeter of height). Most Aeta women reach puberty and stop growing at about 12 years of age, at an adult height averaging 140 cm. For the Turkana, the lower mortality rate shifts the balance—the advantage of early reproduction is outweighed by the fecundity advantage of attaining a larger adult size. Turkana women mature at age 15 and at a height averaging 166 cm. In the United States, plentiful food and modern medicine reduce the cost of maturing early—girls grow fast and mature early, at an adult size equivalent to that of the Turkana.

In a similar way, the short summers in New York State make it advantageous for black-legged tick nymphs to invest in overwinter survival, even though it means that most individuals do not reproduce until their second year (see Figure 42.3), and a few take even longer. Ticks find their hosts by waiting: they climb up on vegetation, extend their forelegs, and climb aboard when a host bumps into them. Finding a host is such a rare event that a tick can expect at most one meal during the short growing season. As a result, nymphs do not allocate resources to further host-seeking behavior during their first season of life, but instead allocate resources to overwinter survival. The fact that ticks take 2 years to complete their life history is thus a consequence of the difficulty of encountering a host and the seasonality of the environment.

Species' distributions reflect the effects of environment on per capita growth rates

A population cannot persist in an environment where its per capita growth rate is negative, because its size would inevitably shrink to zero—it would go extinct. We can predict where populations are likely to be found if we know how resource availability and physical conditions affect survivorship and fecundity. Obtaining complete knowledge of life histories is often impossible for species in the wild, but even incomplete knowledge helps us understand species' distributions. **FIGURE 42.6** illustrates this

INVESTIGATION

FIGURE 42.6 Climate Warming Stresses Spiny Lizards Barry Sinervo and colleagues wanted to know whether climate warming will stress Mexican blue spiny lizards (*Sceloporus serrifer*) by reducing the number of hours they can remain outside their burrows without overheating. These lizards feed only during daytime and retreat to their cool burrows when their body temperature gets too high (see Figure 29.8). In 2008, the researchers conducted experiments in four locations in Mexico where these lizards had been found in 1975. Climate records indicated that the four locations did not warm at the same rate between 1975 and 2008, perhaps because they differ in such things as proximity to the ocean, elevation above sea level, and latitude.[a]

HYPOTHESIS

Spiny lizards have fewer hours to forage on hotter days.

METHOD

1. Construct model "lizards" that have the same thermal properties as real lizards.

A pair of grey model "lizards" is connected to a white data recorder.

2. At four sites in the Yucatán where lizards occurred in 1975, place replicate model lizards in various perches that real lizards use when they forage. Monitor body temperature T_b of the models each hour and record maximum daily air temperatures during the breeding season (March and April).

3. For each day, calculate the number of hours that the body temperature T_b of the model lizards exceeded 31°C—the temperature at which *S. serrifer* are known to stop foraging and retreat to their burrows—to arrive at a predicted number of inactive hours for real lizards.

4. Determine whether the predicted number of inactive hours increased with maximum daily air temperature.

RESULTS

The number of hours when $T_b > 31$°C increased by 0.74 hours for each °C of increase in maximum daily air temperature ($P < 0.001$).

Dashed lines represent the 95% confidence interval around the regression line.
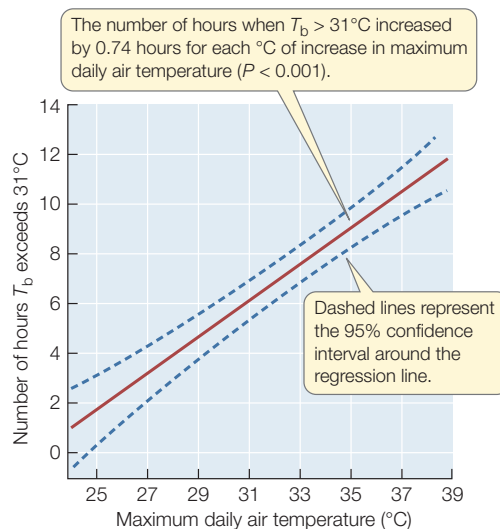
CONCLUSION

The hypothesis is supported by the data: *S. serrifer* can forage without overheating for fewer hours on days when maximum air temperature is higher.

ANALYZE THE DATA

Between 1975 and 2008, *S. serrifer* populations went extinct at two of the four sites monitored by Sinervo and colleagues. The graph at right shows March and April averages in 2008 for the number of hours (in some cases including hours after sundown!) when $T_b > 31$°C at the two "extinct" sites and at the two "persistent" sites. Error bars are 1 standard error of the mean (see Appendix B); sample size for each point is 240 observations (2 sites × 30 days × 4 lizard models). Use this graph to answer the questions below.

A. How did the hours available for foraging differ between the "extinct" sites (black symbols) and the "persistent" sites (green symbols)?

B. How might the availability of foraging time influence lizard fecundity, survivorship, and per capita growth rates?

C. Sinervo and colleagues knew that climate warming had taken place between 1975 and 2008 (for example, see Figure 45.13), the period during which some of the lizard populations had gone extinct. Is the extinction of some, but not all, lizard populations consistent with the conclusion that climate warming was one of the causes of extinction? Why or why not?
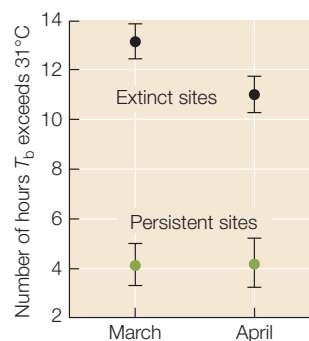
Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]B. Sinervo et al. 2010. *Science* 328: 895–899.

Sitophilus oryzae (rice weevil)   *Rhyzopertha dominica* (lesser grain borer)
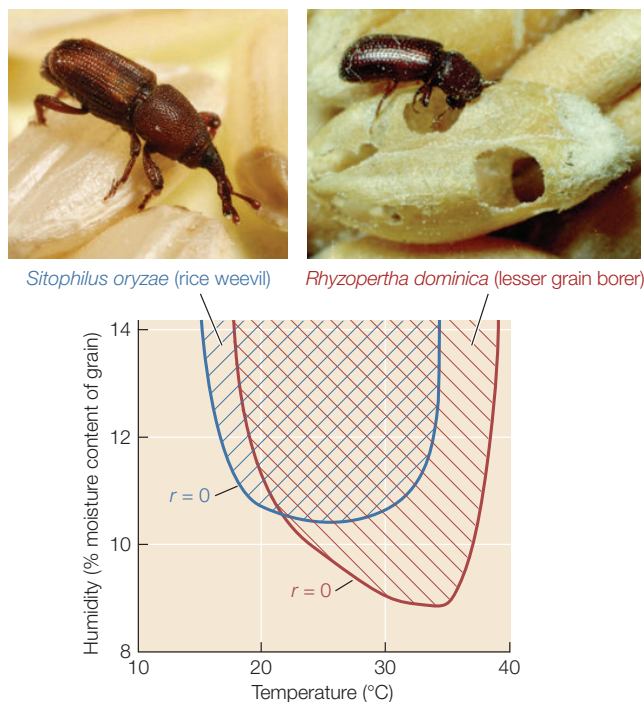
FIGURE 42.7 Environmental Conditions Affect Per Capita Growth Rates and Species Distributions Charles Birch's laboratory research revealed that *R. dominica* populations performed better under warmer conditions than did *S. oryzae* populations. The lines marked $r = 0$ indicate the limit of the conditions under which populations of each species can grow; within the hatched areas, per capita growth rates are positive for the species.

point for the lizard *Sceloporus serrifer*. By combining measurements of conditions in the lizard's natural environment with knowledge of its physiology and behavior, researchers were able to draw conclusions about how climate change is affecting the lizard's survivorship, fecundity, and distribution—with important implications for its conservation.

Sometimes it is possible to explore the links between environmental conditions, life histories, and species distributions with the help of experiments carried out in the laboratory. Charles Birch used this approach to understand why two species of beetles that infest stored grain are serious pests in some parts of Australia but not in others. In his laboratory, Birch reared populations of the rice weevil (Sitophilus oryzae, known in Birch's time as Calandra oryzae) and the lesser grain borer (Rhyzopertha dominica) under various conditions of temperature and humidity. He quantified beetle life histories for each set of conditions and used survivorship and fecundity data to calculate per capita growth rates for each species under those conditions. The results, summarized in **FIGURE 42.7**, explain the more tropical geographic range of R. dominica. In addition, both species had negative per capita growth rates in cool, dry environments. This finding suggested a strategy for managing stores of grain to minimize losses: keep the grain cool and dry.

CHECKpoint   CONCEPT **42.3**

✓ When kangaroo rats harvest seeds, they grab them with their front paws and put them into "grocery bags"—cheek pouches (see Figure 42.4B). Based on the graph in that figure, what do you think the harvest rate would be if seed density increased to 5 seeds/cm²? Explain.

✓ Female hummingbirds in the Rocky Mountains usually live long enough to reproduce for several summer seasons. If they still have young in the nest when the supply of food (nectar produced by flowers) declines toward zero at the end of the summer, they abandon the nest and the young. Can you explain this behavior in terms of the principle of allocation?

✓ In an experiment, ecologists added predatory fish to some streams, leaving other streams predator-free as controls. How would you expect size and age of first reproduction of prey fish to evolve in the presence of predators? (Hint: Consider the example of the Aeta and Turkana.)

✓ Explain how the results shown in Figure 42.7 are consistent with the grain borer *Rhyzopertha dominica* having a more tropical geographic range than the rice weevil *Sitophilus oryzae*. (Hint: See Concept 41.2.)

Knowing whether population growth rates are negative or positive in particular environments tells us why species are absent or present in those environments. But this knowledge does not help us understand why population densities vary among different locations where population growth rates are positive. To do so, we must take a closer look at the dynamics of population growth.

CONCEPT **42.4** **Populations Grow Multiplicatively, but the Multiplier Can Change**

We saw in Concept 42.2 that a population will grow as long as the per capita growth rate, r, is greater than zero. Recall also that r refers to a specific period of time (it might be a day, a week, or a year, depending on the species) over which we have estimated per capita birth and death rates. During this period the population will add a number of individuals that is precisely r times its initial size. In other words, growth is multiplicative. We saw this in Equation 42.3, which states that $N_{t+1} = N_t + rN_t$. What may not be obvious at first is that this pattern continues in the next time period: the population will again add a multiple r of its numbers, since $N_{t+2} = N_{t+1} + rN_{t+1}$. Because N_{t+1} was already larger than the initial population N_t, this means that an ever-larger number of individuals is added in each successive period, as long as the multiplier r remains constant.

Multiplicative growth with a constant r differs dramatically in its form from **additive growth**, in which a certain *number* (rather than a certain *multiple*) is added in each period:

Multiplicative growth adds a *multiple* of the population size (N) in each time period. In this example, the multiple remains constant at a value of 1, so a number equal to the population size at the beginning of each period is added by the end of that period.

Additive growth adds a certain *number* of individuals in each time period, rather than a multiple of the population size. In this example, the number remains constant at a value of 1.

Multiplicative growth with constant *r* can generate large numbers very quickly

We naturally tend to think in terms of additive growth, so multiplicative growth with an unchanging, positive multiplier astonishes us with the phenomenal numbers it can generate in a short time. For example, in 1911 L. O. Howard, then chief entomologist (insect scientist) of the U.S. Department of Agriculture, estimated that a pair of flies reproducing for the first time on April 15 would give rise to a population of 5,598,720,000,000 adults by September 10 if all the offspring survived and reproduced. Other entomologists disagreed with Howard's calculation—they pegged the number much *higher*!

Charles Darwin was well aware of the power of multiplicative growth:

> Every organic being naturally increases at so high a rate, that, if not destroyed, the earth would soon be covered by the progeny of a single pair. …As more individuals are produced than can possibly survive, there must in every case be a struggle for existence.

This ecological struggle for existence, fueled by multiplicative growth, is an essential part of natural selection and adaptation.

> **LINK**
>
> Darwin's theory of evolution by natural selection is described in **Concepts 15.1 and 15.2**

Populations growing multiplicatively with constant *r* have a constant doubling time

Multiplicative growth characterizes many phenomena that affect our everyday lives, such as interest-bearing bank accounts, fossil-fuel consumption, and radioactive decay (see Figure 18.1). Our tendency to think in additive terms impedes our ability to comprehend these phenomena and to understand their practical implications. For example, how much more money will we have in 5 years if we invest $1,000 in a bank account that earns

2 percent per year as opposed to 1 percent per year? How does the drop in the per capita growth rate from 2.20 percent per year in 1963 to the current 1.14 percent change our estimates of the future size of the global human population? Answering such questions requires an understanding of multiplicative growth.

Multiplicative growth with a constant *r* has a very striking property: a constant **doubling time**. A population growing in this way adds an ever-increasing number of individuals as time goes on. At some specific time, the number added exactly equals the initial population, and the population has doubled. As long as *r* does not change, the time the population takes to double will also remain constant. The doubling time depends on *r*—it gets shorter as *r* increases.

It is easy to see the implications of multiplicative growth with a constant, positive *r* if we think in terms of doubling times. For example, by doing so a municipality would see that even a seemingly small but constant growth rate of 3 percent per year would mean that its population would double every 23 years—and that its sewage treatment capacity and other such municipal services would need to do the same.

Go to ANIMATED TUTORIAL 42.1
Multiplicative Population Growth Simulation
PoL2e.com/at42.1

Density dependence prevents populations from growing indefinitely

If populations grow multiplicatively, why isn't Earth covered with flies, or any other organism? It turns out that populations do not grow multiplicatively with constant *r* for very long. Instead of continuing to increase (as in the red J-shaped curve in the graph below), population growth eventually slows, and population size usually reaches a more or less steady size (as in the blue S-shaped curve):

Growth slows and finally stops when the population reaches density *K*.

Initially, density-dependent growth is similar to multiplicative growth with constant *r*.
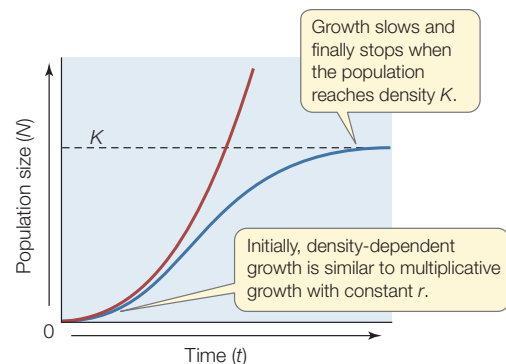
Go to ACTIVITY 42.1 **Population Growth**
PoL2e.com/ac42.1

Why do populations stop growing? Upon examination, we see that even though the population still adds a multiple of its previous size in each time period, the multiplier *r*, which determines what is added to the population, changes, rather than

APPLY THE CONCEPT

Populations growing multiplicatively with constant *r* have a constant doubling time

Yellow star-thistle (*Centaurea solstitialis*) is a spiny annual plant native to the Mediterranean region. The species has invaded several regions of the United States. It is a noxious weed that is unpalatable to livestock (including American bison). Jane, the rancher, discovers that 1 hectare of her 128-hectare pasture has been invaded by star-thistle. A year later, she finds that the weed population has grown to cover 2 hectares.

1. Based on the information above, how many hectares do you predict the star-thistle population will cover in 1, 2, and 3 more years if the population is growing additively by a constant number? How many hectares if the population is growing multiplicatively with constant *r*?

2. Imagine that Jane discovers the star-thistle population only after it has already covered 32 hectares of her pasture. How many years does she have until the weed completely covers the pasture if its population is growing additively by a constant number each year? How many years does she have if it is growing multiplicatively with constant *r*?

The invasive yellow star-thistle is noxious to grazing livestock.

remaining constant. As the population becomes more crowded, *r* decreases—in other words, *r* is **density dependent** (**FIGURE 42.8A**). At low population densities, per capita growth rates are at their highest. As the population grows and becomes more crowded, per capita birth rate tends to decrease and death rate to increase, and so *r* decreases toward zero. When *r* = 0, the population stops changing in size—in other words, it reaches an **equilibrium** size. That size is called the **carrying capacity**, or *K* (**FIGURE 42.8B**). *K* can be thought of as the number of individuals that a given environment can support indefinitely. If individuals are added to the population so that it exceeds the carrying capacity, the per capita growth rate becomes negative, and the population shrinks. If the population falls below *K*, the per capita growth rate becomes positive, and the population grows (see Figure 42.8B).

Go to ANIMATED TUTORIAL 42.2
Density-Dependent Population Growth Simulation
PoL2e.com/at42.2

Why does *r* decrease with crowding? When used by one organism, a resource becomes unavailable to other organisms. Therefore, as population density increases, each individual gets a smaller piece of the resource "pie" and has less to allocate to its life functions (see Figure 42.5). Per capita birth rate decreases, per capita death rate increases, and therefore *r* decreases with population density. Once again it is useful to spell this out:

Per capita growth rate =
the maximum possible value in uncrowded conditions –
an amount that is a function of density

When population density reaches *K*, the carrying capacity, the average individual has just the amount of resources it needs in order to produce enough offspring to have exactly replaced itself by the time it dies. When density is less than *K*, the average

individual can more than replace itself; when density is greater than *K*, the average individual has fewer resources than it needs to replace itself.

LINK

Density dependence results from intraspecific (within species) competition—mutually detrimental interactions among individuals of the same species—as we shall see in **Concept 43.2**

Now we are prepared to return to the question posed at the end of Concept 42.1: Why do species abundances vary in time and space?

Changing environmental conditions cause the carrying capacity to change

We have learned that resource availability in the environment affects an individual's success in acquiring resources (see Figure 42.4), and that physical conditions affect the costs of maintenance (see Figure 42.5). If these factors vary over space, then the carrying capacity will vary over space as well.

Similarly, if resource availability or environmental conditions are good in one year but bad in another, the population will find itself alternately above and below the current carrying capacity. As a result, populations will fluctuate around an average *K* over time. Figure 42.2 illustrates this dynamic for rodents and ticks in Millbrook, New York. Rodent densities tend to increase following years of high acorn production because the rodents have enough food to produce many offspring, and they tend to decrease following poor acorn years. Similarly, nymphal tick densities go up and down following high and low rodent years, respectively, because host abundance determines the success of larval ticks in obtaining a blood meal.

(A)

(B)

When the population is small, individuals have the maximum value of r.

At carrying capacity K, $r = 0$, and the population stops growing.

K

When the population density is below K, per capita growth rate is positive, and the population grows.

If the population exceeds K, per capita growth rate becomes negative, and the population shrinks.
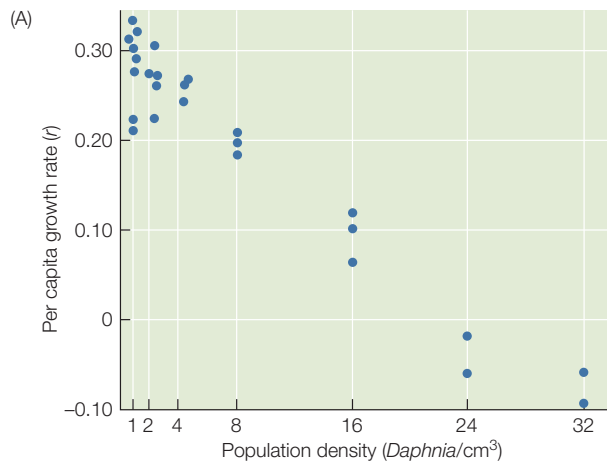
FIGURE 42.8 Per Capita Growth Rate Decreases with Population Density   (A) The decline in r as population density increases, as measured in a population of a small crustacean, *Daphnia pulex* (see Figure 42.10). (B) Schematic representation of density-dependent growth, in which r declines linearly with population density. This graph is an idealization—few species follow it exactly. For example, close inspection of (A) suggests that the decline in r for *Daphnia pulex* is not precisely linear.
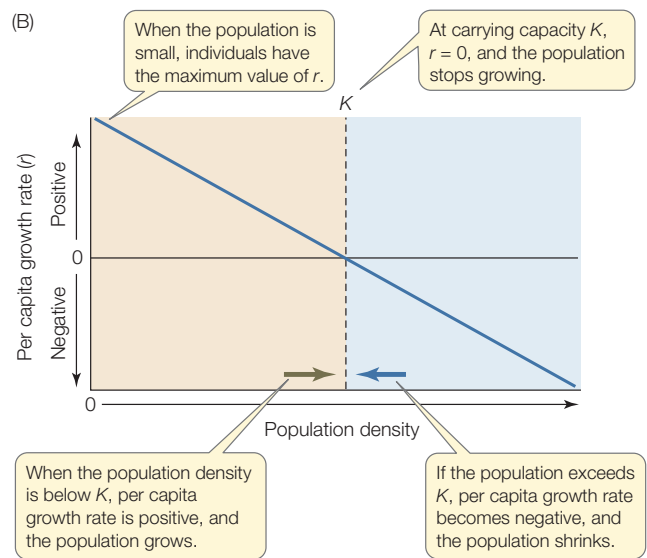
These increases and decreases are not immediate—there is a delay while acorns are converted into newborn rodents, and while newly fed larval ticks molt into nymphs.

A look back at Table 42.1 shows how temporal changes in the environment affected the fecundity of a group of 210 common cactus finches born on Isla Daphne in 1978. Notice that females produced no surviving young when they were 7 and 8 years old. These years followed a severe drought in 1985 that limited production of the seeds the finches eat. Conversely, fecundity was unusually high when the finches were 5 and 9 years old. These were the unusually wet years of 1983 and 1987, when food was plentiful.

Technology has increased Earth's carrying capacity for humans

The human population is unique among populations of large animals. Not only has it continued to grow, it has grown at an ever-faster per capita rate until very recently, as is indicated by its steadily decreasing doubling times (**FIGURE 42.9A**). The current population multiplier, or per capita growth rate (r), is somewhat above 1.1 percent per year, lower than the peak of 2.2 percent reached in 1963, because birth rates have declined faster than have death rates over the past 50 years. Even if this recent trend in r continues, however, the human population is projected to grow to 8 billion by 2025.

The human population growth rate has jumped with every technological advance that has raised carrying capacity by
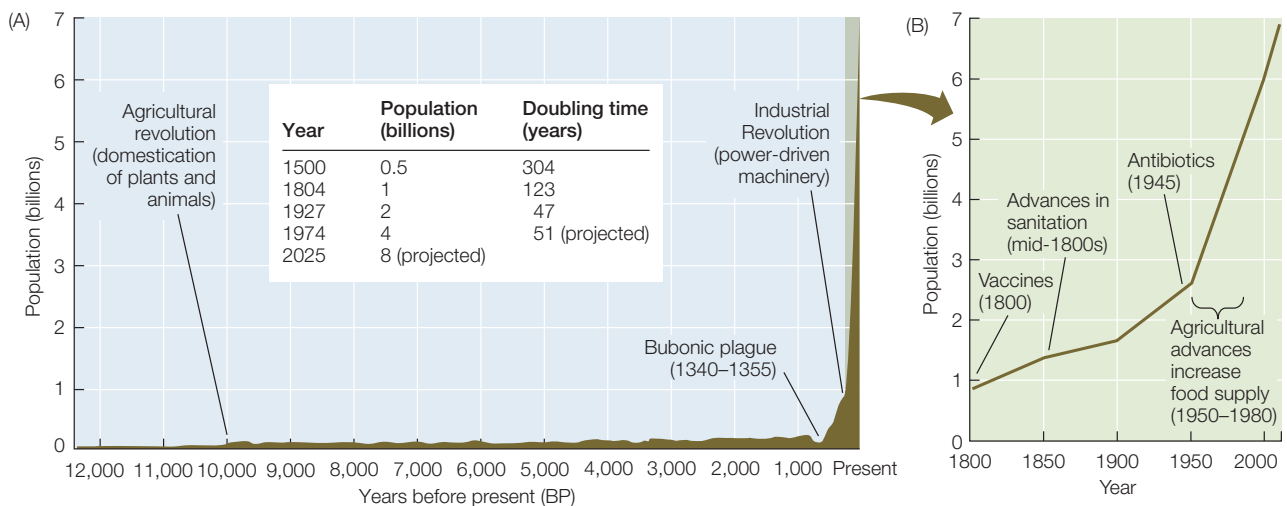
FIGURE 42.9 Human Population Growth   Advances in technology have allowed the human population to grow at an ever-faster per capita rate.

(A)

Year	Population (billions)	Doubling time (years)
1500	0.5	304
1804	1	123
1927	2	47
1974	4	51 (projected)
2025	8 (projected)	

(B)

increasing food production (thereby increasing per capita birth rate, b) or by improving health (thereby reducing per capita death rate, d). The first jump occurred with the rise of agriculture (about 10,000 years ago). In the nineteenth and twentieth centuries, advances in sanitation and the development of vaccines and antibiotics decreased death rates to an unprecedented low level (**FIGURE 42.9B**). Finally, the "Green Revolution" in agriculture more than doubled world grain production between 1950 and 1984. These increases in r correspond to shorter and shorter doubling times (see the table in Figure 42.9A) until very recently.

Human ingenuity has repeatedly stymied attempts to predict the future of the human population. The most famous attempt was that of Thomas Malthus, whose *Essay on the Principle of Population*, first published in 1798, provided Charles Darwin with a critical insight for his theory of natural selection. Malthus reasoned that the human population was growing multiplicatively, whereas its food supply was growing additively. He predicted that food shortages would limit human population growth, which he estimated would peak by the end of the nineteenth century. Malthus could not, of course, have anticipated the effects of medical discoveries and the Green Revolution.

Many believe that the human population has now overshot its long-term carrying capacity. They give two reasons. First, most twentieth-century technological advances relied on abundant fossil fuels instead of renewable biomass and muscle power, and fossil fuels are not renewable. Maintaining current levels of agricultural production depends heavily on fertilizers derived from natural gas, pesticides derived from oil, and petroleum-fueled engines that pump irrigation water, till the soil, and process and transport food. Similarly, the manufacture and distribution of medicines and diagnostic machinery depends on fossil fuels. World production of crude oil has continued to rise but cannot do so indefinitely because reserves are finite, and the same is true of coal, natural gas, and other fossil fuels. Eventually these fuels will be depleted.

A second reason many believe that our carrying capacity will decrease in the near future is the climate change and degradation of Earth's ecosystems that have been a consequence of our recent population expansion. We will consider these topics further in Chapters 44 and 45.

Population ecology tells us that any change in the size of the global human population must result from changes in birth and death rates. If the human population has indeed exceeded its long-term carrying capacity, it will ultimately have to shrink. We can bring this about voluntarily if we continue to reduce our per capita birth rate. The less pleasant alternative is to wait for the Four Horsemen of the Apocalypse—famine, pestilence, war, and death—to achieve a sustainable human population size.

LINK

Voluntary reduction of birth rates can be achieved by the use of the contraceptive methods described in **Table 37.1**

CHECKpoint   CONCEPT **42.4**

✓ Explain the fundamental difference between multiplicative and additive growth.

✓ Why don't populations grow indefinitely?

✓ Why do limits to population growth lead to natural selection? (Hint: Consider that individuals in a population vary in b and d as a result of inherited traits.)

So far we have considered the effects of two universal demographic processes—birth and death—on populations. But the dynamics of many populations are also influenced by the movement of individuals among populations. Such "open" populations grow when immigrants enter from the outside world and shrink when emigrants leave. Immigration and emigration affect populations in important ways.

CONCEPT **Immigration and Emigration Affect**
42.5 **Population Dynamics**

Many species occupy habitat patches that are separated from other patches by unsuitable environments (**FIGURE 42.10**; see also Figure 42.1). Each patch of suitable habitat occupied by the species can be thought of as a **subpopulation**, and the set of subpopulations in a region is known as a **metapopulation**. When subpopulations are not too isolated from one another, individuals occasionally move, or disperse, among them.

When dispersal is possible, each subpopulation changes as all populations do—through births and deaths—but with the added input of individuals that move *into* the subpopulation (immigrants) and loss of individuals that move *away* (emigrants). Adding the number of immigrants (I) and emigrants (E) to the BD growth model, we get the **BIDE model**:

$$\text{The number of individuals in a population}$$
$$\text{at some time in the future} =$$
$$\text{the number now + the number that are born +}$$
$$\text{the number that immigrate} -$$
$$\text{the number that die} -$$
$$\text{the number that emigrate}$$

In the BD model, populations are considered **closed systems** because there is no immigration or emigration—no individuals move into or out of them. In the BIDE model, subpopulations are considered **open systems** because individuals can move among them. This difference has a profound effect on population dynamics. In the BD model, a subpopulation that goes extinct stays extinct: once the subpopulation reaches zero, there are no individuals left to reproduce. With the BIDE model, however, immigration can bring an extinct subpopulation "back to life."

You may think that extinction is rare, but in fact it is fairly common in small habitat patches, even when the environment of the patch is favorable. When subpopulations are small, there is a reasonable possibility during any time period that by chance no female will give birth and that all adult individuals

FIGURE 42.10 A Metapopulation Has Many Subpopulations The coast of Scandinavia is characterized by natural freshwater rock pools, which constitute suitable habitat for small crustaceans of the genus *Daphnia* that feed by filtering algae from the water. Each rock pool that is occupied by *Daphnia* constitutes a subpopulation within a larger metapopulation.

Go to ANIMATED TUTORIAL 42.3
Metapopulation Simulation
PoL2e.com/at42.3

is, and the more subpopulations there are, but extinction will occur nonetheless. If subpopulations are connected by dispersal, however, the metapopulation as a whole will persist much longer, for two reasons. First, immigration can repopulate unoccupied patches, and "rescue" declining subpopulations from extinction. The repopulated patches, in turn, can colonize others, causing them to "wink on." Second, immigrants contribute to the genetic diversity within subpopulations by bringing new alleles with them. This gene flow combats the erosion of genetic diversity through genetic drift that can reduce *r* and compromise a species' evolutionary potential.

LINK

Gene flow and genetic drift are discussed in **Concept 15.2**

We can see the recolonization process at work in the metapopulation of Edith's checkerspot butterfly in the San Francisco Bay area (see Figure 42.1). Many subpopulations of this endangered butterfly went extinct during a severe drought that gripped California between 1975 and 1977. The only subpopulation that did not go extinct was the largest one, on Morgan Hill. The extinct subpopulations remained at zero density until 1986, when nine suitable habitat patches were recolonized from the Morgan Hill source population. Patches closest to Morgan Hill were most likely to be recolonized because adult butterflies do not fly very far.

will die—in which case the subpopulation will be extinct. Small populations are also more likely than large ones to go extinct following environmental disturbances.

Once a subpopulation goes extinct, it will remain at zero density—and its patch of habitat will remain unoccupied—unless individuals move into, and thus recolonize, the patch. Thus if there is no dispersal among patches, the subpopulations will "wink off" one by one. The time to extinction of the entire metapopulation is longer the larger each subpopulation

APPLY THE CONCEPT

Immigration and emigration affect population dynamics

In a study of subpopulations of *Daphnia* in Swedish rock pools (see Figure 42.10), ecologist Jan Bengtsson established a number of artificial rock pools that held either 12, 50, or 300 liters of water. He introduced the same number of *Daphnia* to each pool and then covered the pools with mesh, which prevented immigration or emigration. Over the next 4 years, Bengtsson returned repeatedly to count the *Daphnia*, thereby obtaining the average size of the subpopulation in each pool. If a subpopulation went extinct, he included only the nonzero values for the size of that subpopulation measured *before* extinction in calculating its average size. The table shows the grand average of these time-based averages for pools in which

the subpopulations went extinct, and for those in which they persisted. Use the table to explore how extinction risk changed with the volume of a pool and the number of *Daphnia* in it.[a]

1. Graph the relationship between pool size and percentage of subpopulations that went extinct, using size as the *x* axis. What does your graph show you?

2. Within each pool size, which subpopulations were at greatest risk of extinction?

3. How are these two results related to each other?

4. What might have happened if Bengtsson had not placed mesh over his experimental pools?

POOL SIZE (L)	NUMBER OF REPLICATE SUBPOPULATIONS	PERCENTAGE OF SUBPOPULATIONS GOING EXTINCT	GRAND AVERAGE SIZE OF PERSISTENT SUBPOPULATIONS	GRAND AVERAGE SIZE OF EXTINCT SUBPOPULATIONS
12	27	18.5	1,500	65
50	25	16	2,705	530
300	11	9.1	9,690	1,800

[a]J. Bengtsson. 1989. *Nature* 340: 713–715.

In Chapter 41 we saw that ecological knowledge has many important applications in our everyday lives—in medicine, agriculture, and other areas. Our understanding of the dynamics of populations and metapopulations provides tools that allow us to influence their fates, as several examples will illustrate.

CONCEPT 42.6   Ecology Provides Tools for Conserving and Managing Populations

For millennia, humans have tried to maintain or increase populations of desirable or useful species and reduce populations of species they consider undesirable. Such efforts are most successful if they are based on knowledge of how those populations grow and what determines their densities.

Knowledge of life histories helps us manage populations

Knowing the life history of a species helps us identify those life stages that are most important for the species' reproduction and survival, and hence for its population growth rate. Here are a few examples of how this knowledge can be applied.

CONSERVING ENDANGERED SPECIES   Populations of Edith's checkerspot butterfly in the San Francisco Bay area are threatened with extinction. Larval survival is critical to the population dynamics of these butterflies (see Figure 42.1). Temporal and spatial variation in butterfly density is tied to the availability of two larval food plants, California plantain (*Plantago erecta*) and purple owl's clover (*Orthocarpus densiflorus*), which are found only on serpentine soils. Maintaining healthy populations of these plants is critical for conservation of the butterflies, but the low-growing *Plantago* and *Orthocarpus* are suppressed by tall introduced grasses. Grazing by cattle can control the invasive grasses, and grazing is an important strategy for conserving *Euphydryas editha*. This example shows that achieving conservation goals is often compatible with human use of the environment.

MANAGING FISHERIES   The black rockfish (*Sebastes melanops*) is an important game fish that lives off the Pacific coast of North America. Rockfish grow continually throughout their lives. As is true of many animals, larger females produce more eggs than smaller females. Larger females also provision their eggs with larger oil droplets. Larger droplets provide more energy to the newly hatched larvae, allowing them to grow faster and survive better than larvae with smaller oil droplets.

These life-history characteristics have important implications for rockfish populations. Because fishermen prefer to catch big fish, intensive fishing off the Oregon coast between 1996 and 1999 reduced the average age of female rockfish from 9.5 to 6.5 years. Thus in 1999, females were, on average, smaller than in 1996. This change decreased the average number of eggs produced by females in the population and reduced the average growth rate of larvae by about 50 percent, causing a rapid decline in population density. Because a relatively small number of large females can produce enough eggs to maintain the population, one strategy for maintaining rockfish without shutting fishing down completely is to set aside a few no-fishing areas where some females are protected and can grow to large sizes.

REDUCING DISEASE RISK   Because adult black-legged ticks feed and mate primarily on large mammals—white-tailed deer for example—it seems logical that controlling deer densities would reduce the abundance of tick nymphs, which present the greatest risk of transmitting Lyme disease to humans. Surprisingly, experimental reductions in deer density have had little effect on subsequent nymph abundance. Studies of the tick's life history (see Figure 42.3) indicate that the success of larval ticks in obtaining a blood meal, not the number of them that hatch from eggs, has the greatest effect on the subsequent abundance of nymphs. As is true of rockfish, a few adult female ticks can produce enough eggs to maintain populations. Hence controlling the abundance of larval hosts (small mammals) is a more effective strategy for reducing tick populations than controlling the abundance of adult hosts (deer and other large mammals).

Knowledge of metapopulation dynamics helps us conserve species

Conservation biology strives to avoid the extinction of species. From studies of extinction rates, we know that the risk of extinction for a species with a metapopulation structure is affected by the number and average size of its subpopulations, and by rates of dispersal among them. Conservation planners therefore begin with an inventory of remaining areas of natural habitat and an evaluation of the risks to subpopulations in those areas. They then devise ways to protect as many habitat patches as possible, giving priority to those with the largest area because large patches potentially support the largest and most genetically diverse subpopulations. Planners also evaluate the quality of the patches, as measured by their carrying capacity for the species (often estimated from population densities), and develop ways to maintain their quality.

Finally, planners must consider opportunities for individuals to move among subpopulations (**FIGURE 42.11**). For some species (such as Edith's checkerspot butterfly, which can fly through

INVESTIGATION

FIGURE 42.11 Habitat Corridors Can "Rescue" Subpopulations from Extinction   Data from the experiments summarized here suggest that corridors between patches of habitat for small arthropod species increase the chances of dispersal, and thus of subpopulation persistence.[a]

HYPOTHESIS

Subpopulations of a metapopulation are more likely to persist if there are no barriers to dispersal.

METHOD

1. On seven replicate moss-covered boulders, scrape off the continuous cover of moss to create a cluster of 13 moss patches surrrounded by bare rock. A large central 50 × 50 cm moss "mainland" (M) is surrounded by 12 small patches of moss, each 10 cm^2 in area. In the "insular" treatment (I), the patches are surrounded by bare rock (which is inhospitable to small moss-dwelling arthropods and is thus a barrier to dispersal). In the "corridor" treatment (C), the patches are connected to the mainland by a 7- by 2-cm strip of live moss. In the "broken-corridor" treatment (B), the configuration is the same as in the "corridor" treatment, except that the moss strip is cut by a 2-cm strip of bare rock.
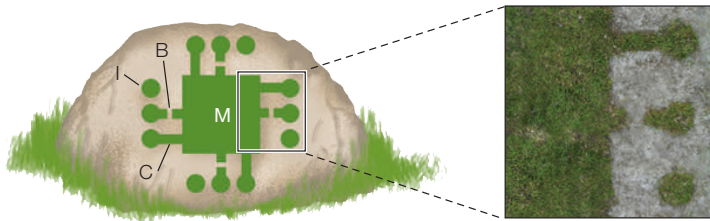
2. After 6 months, determine the number of small arthropod species present in each of the patches.

RESULTS

Patches connected to the mainland by corridors retained as many species as did the larger mainland patch to which they were connected. Significantly fewer species remained in the broken-corridor and insular treatments. Error bars indicate 1 standard error of the mean; bars with different letters are statistically different from one another.
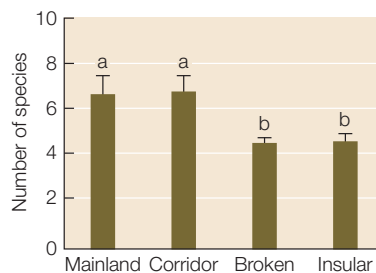
CONCLUSION

Barriers to dispersal reduce the number of subpopulations that persist in a metapopulation.

ANALYZE THE DATA

A. What percentage of the species present in the mainland patch was lost, on average, in the corridor patches?

B. What percentage of the species present in the mainland patch was lost, on average, in the insular and broken-corridor patches? What do these percentages tell you about the average risk of extinction for a subpopulation in a small patch?

C. The insular patches were two-thirds the size of the broken-corridor patches, because the latter contained 5 cm^2 of habitat in the corridor in addition to the 10 cm^2 in the patch itself. Did this difference in patch size affect subpopulation persistence?

D. What effect is patch size by itself expected to have on the persistence of a given species in a patch? Do you see evidence for this effect in the data?

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]A. Gonzalez and E. J. Chaneton. 2002. *Journal of Animal Ecology* 71: 594–602.

Go to ANIMATED TUTORIAL 42.4 Habitat Corridors
PoL2e.com/at42.4

FIGURE 42.12 A Corridor for Large Mammals
An overpass above the Trans-Canada Highway in Banff National Park, Alberta. Bears, elk, deer, and other large mammals use such overpasses as corridors to move between areas that would otherwise be effectively isolated from one another by the highway with its speeding traffic.

unsuitable habitat to reach a new serpentine outcrop), simple proximity of patches determines rates of dispersal and recolonization. For those species, patches that are distant from one another can be connected by a series of intervening patches that serve as "stepping stones." For other species, however, a continuous area of habitat through which individuals can move, called a **dispersal corridor**, is needed to connect subpopulations (see Figure 42.11). Dispersal corridors can sometimes be created by maintaining vegetation along roadsides, fence lines, or streams, or by creating bridges or underpasses that allow individuals to circumvent roads or other barriers to movement (**FIGURE 42.12**).

LINK

Strategies for conserving communities of interacting species are discussed in **Concept 44.5**

CHECKpoint   CONCEPT 42.6

✓ Describe three elements of a conservation plan for a species that has a metapopulation structure.

✓ What similarities do you see between the rockfish and black-legged tick examples summarized above, in terms of the factors that will determine whether a population grows or shrinks?

✓ Conservation plans for marine species such as rockfish often lack a corridor component. Why?

You may have noticed that this chapter has focused on single-species populations, but it has also mentioned interactions among species—rodents interacting with acorns and ticks, ticks with hosts and bacteria, butterflies with food plants and invasive plants. These ubiquitous interactions between species, which play important roles in their population dynamics, will be the subject of the next two chapters.

Q How does understanding the population ecology of disease vectors help us combat infectious diseases?

ANSWER   How frequently people come into contact with a dangerous pathogen depends on its abundance and distribution and on those of any disease vectors that transmit it to humans. Population ecology helps us understand what determines the abundance and distribution of pathogens and their vectors, and hence allows us to devise ways of controlling their abundance or avoiding contact with them.

By studying the survivorship and fecundity of the black-legged tick throughout its life history (Concept 42.3), Rick Ostfeld learned that it is the abundance of hosts for larvae and nymphs, rather than weather or the abundance of hosts for adult ticks, that determines tick abundance. Furthermore, Ostfeld ascertained that ticks become infected with *Borrelia* when they feed on infected hosts, and that small mammals are the most effective reservoirs for *Borrelia*. Long-term studies of rodent population dynamics had already shown that rodent abundance is positively correlated with acorn availability (Concept 42.4).

This knowledge suggests a simple and quick way to reduce the probability of contracting Lyme disease (Concept 42.6). Acorn production can be used to predict areas that are likely to become infested with disease-carrying ticks, and various measures can be taken to reduce the risk of human contact with those ticks. These measures include boosting public education efforts for several years after a big acorn crop, posting warning signs in high-risk areas, and alerting health-care specialists whose patients live or work in high-risk areas. A longer-term possibility that has yet to be assessed is to reduce the fraction of ticks that carry *Borrelia* by augmenting populations of hosts that do not harbor *Borrelia* (such as lizards and birds) in the host community. Ticks that bite these hosts will not become infected with *Borrelia*.

SUMMARY

CONCEPT 42.1 Populations Are Patchy in Space and Dynamic over Time

- **Population density** is the number of individuals of a species per unit of area (or volume). **Population size** is the total number of individuals in a population.

- The region within which a species lives is called the species' **geographic range**. Within that range, the species may be restricted to particular suitable **habitats**; these habitats may occur in patches separated by areas of unsuitable habitat. **Review Figure 42.1**

- Population densities vary over time as well as over space. **Review Figure 42.2**

CONCEPT 42.2 Births Increase and Deaths Decrease Population Size

- According to the **BD model**, the size of a population at some future time is the current size plus the number of births minus the number of deaths that occur until that time. Equations based on the BD model can be used to calculate a population's growth rate.

- Ecologists can estimate the **per capita growth rate** (*r*) by tracking births and deaths in a sample of individuals.

- Unless the per capita growth rate is zero, the size of a population must be changing. If *r* is positive, the population is growing. If *r* is negative, the population is shrinking.

CONCEPT 42.3 Life Histories Determine Population Growth Rates

- A species' **life history** describes the sequence of key events of growth and development, reproduction, and death that occur during an average individual's life. **Review Figure 42.3**

- The fraction of individuals that survive to particular life stages or ages is **survivorship**, and the average number of offspring they produce at those life stages or ages is **fecundity**. Survivorship and fecundity determine the per capita growth rate, *r*. **Review Table 42.1**

- Life histories are diverse; they vary both within and among species.

- To survive and reproduce, organisms need materials and energy and the time to acquire them—all of which constitute **resources**. Organisms also need physical conditions they are able to tolerate. Physical conditions differ from resources in that they are experienced, but not used up.

- The rate at which an organism can acquire resources increases with the availability of resources in its environment, up to a point. **Review Figure 42.4**

- The **principle of allocation** states that organisms must divide the resources they obtain among competing life functions. **Review Figure 42.5**

- The environment shapes life histories because it determines the relative costs and benefits of any particular pattern of allocation to different life functions.

- Species can persist only in environments in which their per capita growth rate is positive. **Review Figures 42.6 and 42.7**

CONCEPT 42.4 Populations Grow Multiplicatively, but the Multiplier Can Change

- Populations grow **multiplicatively**, increasing or decreasing by a multiple of their current size in each time period. As a result, populations that are increasing in size by a constant multiple have a constant **doubling time**. **Review ACTIVITY 42.1 and ANIMATED TUTORIAL 42.1**

- As a population becomes denser and the average individual's share of the resource "pie" shrinks, birth rates decline and death rates increase. Thus the per capita growth rate is said to be **density-dependent**. **Review ANIMATED TUTORIAL 42.2**

- When *r* = 0, the population reaches an **equilibrium** size. That size, called the **carrying capacity**, or *K*, is the number of individuals the environment can support indefinitely. **Review Figure 42.8**

- Changes in resource availability or physical conditions cause the carrying capacity to change.

- Technology has increased Earth's carrying capacity for humans, and the human population has responded by growing rapidly. **Review Figure 42.9**

CONCEPT 42.5 Immigration and Emigration Affect Population Dynamics

- The regional distribution of a species often takes the form of a **metapopulation**, a cluster of distinct **subpopulations** in separate habitat patches. **Review ANIMATED TUTORIAL 42.3**

- The **BIDE model** adds immigration and emigration to the BD model.

- Immigration can repopulate an area where a subpopulation has gone extinct. Immigration also corresponds to gene flow among subpopulations, which combats erosion of genetic diversity through genetic drift.

CONCEPT 42.6 Ecology Provides Tools for Conserving and Managing Populations

- Knowing the life history of a species makes it possible to identify those life stages that are most important for the species' population growth rate. That knowledge can be applied to reduce populations of species considered undesirable and to maintain or increase populations of desirable or useful species.

- Conservation efforts strive to protect as many large habitat patches as possible, because large patches host large populations with low risk of extinction, and a metapopulation with many subpopulations persists longer than one with few subpopulations.

- Providing continuous **dispersal corridors** of habitat through which individuals can move between patches helps maintain the larger metapopulation and so is important for many conservation efforts. **Review Figure 42.11 and ANIMATED TUTORIAL 42.4**

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is42

43

Ecological and Evolutionary Consequences of Interactions within and among Species

KEY CONCEPTS

43.1 Interactions between Species May Increase, Decrease, or Have No Effect on Fitness

43.2 Interactions within and among Species Affect Population Dynamics and Species Distributions

43.3 Species Are Embedded in Complex Interaction Webs

43.4 Interactions within and among Species Can Result in Evolution

Leaf-cutter ants of the tropical species *Atta cephalotes* carry coca leaves through the rainforest. The ants riding on the leaves act as "bodyguards," warding off parasitic flies that might otherwise lay their eggs on the larger worker ants.

On a morning walk in the Arizona desert, it's hard to resist the temptation to stop and watch the parades of colorful flower and leaf fragments that march across your path. The fragments aren't moving on their own, of course—they're being carried by *Acromyrmex versicolor*, one of the 47 described species of leaf-cutter ants. Leaf-cutter ants are tropical insects whose geographic range barely extends into North America. If you travel south through Mexico and into the Neotropics, however, you will see more and more ant highways and more and more different leaf-cutter species. Leaf-cutter ants originated in South America about 10 million years ago, crossing into North America only after the Panamanian land bridge connected the two continents.

Leaf-cutter ants are important herbivores of the Neotropics. A single underground nest can contain 8 million workers, occupy 20 cubic meters of soil, and consume more than 2 kilograms of plant material per day—enough to strip a large area of vegetation. Leaf-cutters aren't ordinary herbivores, however: they're fungus farmers! They cultivate a fungus in the nest that grows nowhere else on Earth, feeding it with the leaf fragments they harvest. Different leaf-cutter species cultivate different fungus species, all in the family Lepiotaceae.

The interaction between fungus and ant is an obligate one—neither species can live without the other—and it involves a remarkable array of specialized adaptations on the part of both partners. A new queen carries a pellet of fungus with her when she leaves her mother's nest and uses it to start her own small fungus garden, which she nourishes with her feces. She and the larvae that develop from her eggs feed on special nutrient-rich fungal structures. After the larvae pupate and metamorphose into worker ants, they collect leaf material to feed the growing fungus garden. As the colony expands, the workers dig new chambers, transport fragments of the fungus to those chambers, and take on other tasks as scouts, gardeners, nurses, garbage collectors, undertakers—and even bodyguards for the leaf harvesters.

Leaf-cutters associate with other species that influence their interaction with the fungus. A bacterium in the genus *Pseudonocardia*, carried on the ants' exoskeletons, manufactures antibiotics that suppress the crop-killing green mold *Escovopsis* but do not harm the cultivated fungus. And just recently, researchers discovered a nitrogen-fixing bacterium, *Klebsiella*, in the fungus gardens. Much remains to be learned about leaf-cutter interactions!

Q How could the intricate ecological relationship between leaf-cutter ants and fungus have evolved?

Interactions between Species May Increase, Decrease, or Have No Effect on Fitness

The interactions between leaf-cutter ants and their nest associates represent only a small fraction of the ants' interactions with other species. As they harvest leaves, the ants interact with many plant species. The ants themselves are consumed by parasitic flies, beetles, and pathogenic fungi, and the ant corpses that are hauled to the colony's refuse dump are consumed by many species of microbes. The leaf-cutter example illustrates one of life's certainties: at some point between birth and death, every organism will encounter and interact with individuals of other species. **Interspecific** (Latin, "between species") **interactions** affect each individual's life history, and thereby its success in surviving and reproducing, which in turn determines the individual's contribution to total population growth rate (see Concept 42.3; keep in mind that males contribute to the production of new individuals by inseminating females). This contribution to population growth rate is a measure of that individual's **fitness** (see Concept 15.4). By affecting survival and reproduction, interspecific interactions influence the dynamics and densities of populations, alter the distributions of species, and lead to evolutionary change in one or both of the interacting species.

Interspecific interactions are classified by their effects on fitness

The details of interspecific interactions are bewilderingly diverse, but we can cut through all those details by asking, "Does the interaction help or harm individuals of the participating species?" Or more specifically, "Does the interaction increase, decrease, or have no effect on survival and reproduction, and thus on fitness?" If we keep these questions in mind, we will see that there are only five broad categories of interspecific interactions (**FIGURE 43.1A**): competition (−/−), consumer–resource

(A)

Major Types of Species Interactions

Type of interaction	Effect on species 1	Effect on species 2
Competition	−	−
Consumer–resource: Predation, herbivory, parasitism	+	−
Mutualism	+	+
Commensalism	+	0
Amensalism	−	0

(B)

Competition
Green plants compete for light. Leaves of tall trees reduce the light available to plants growing on the forest floor.

(C)

Consumer–resource
The American bison feeds on the grasses of the Great Plains.

Amensalism, Commensalism
The large mammal unwittingly destroys insects and their nests. The cowbirds feed on insects disturbed by the bison's passage.

(D)
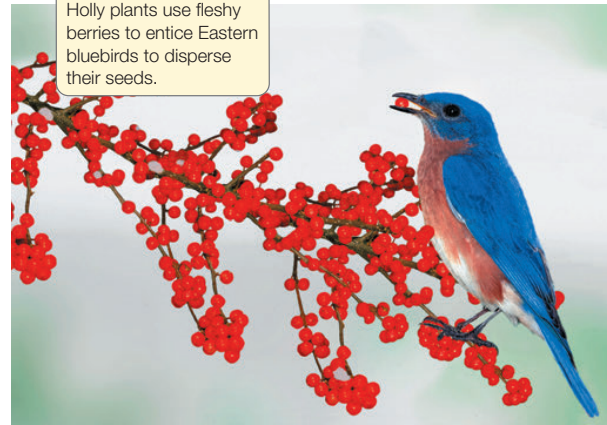
Mutualism
Holly plants use fleshy berries to entice Eastern bluebirds to disperse their seeds.

FIGURE 43.1 Types of Interspecific Interactions (A) Interactions between species can be grouped into categories based on whether their influence on fitness is positive (+), negative (−), or neutral (0). (B) The characteristics of canopy (treetop) and understory (low-growing) vegetation in a forest are largely a product of competition for light. (C) Commensalisms between large grazing ungulates (hoofed animals) and insect-eating birds are found in grassland environments around the world. (D) The interaction between berry-producing plants and berry-eating birds is a mutualism. Here an Eastern bluebird (*Sialia sialis*) gains nutrition by eating holly berries (*Ilex opaca*). The holly's seeds pass through the bird's gut unharmed, and are deposited in nutrient-rich feces away from the parent plant.

Go to ACTIVITY 43.1 Ecological Interactions
PoL2e.com/ac43.1

(+/−), mutualism (+/+), commensalism (+/0), and amensalism (−/0).

Interspecific competition refers to −/− interactions in which members of different species decrease one another's fitness because they require some of the same resources. Recall from Concept 42.4 that when an organism uses a resource, that resource becomes unavailable to other organisms, potentially reducing their survival and reproduction. We say "potentially" because not all resources are in short enough supply to limit these components of fitness. However, at any one time there is generally some **limiting resource** that is in the shortest supply relative to demand. Species that share limiting resources are likely to compete.

Competition may occur among organisms that consume the same food, whether they are African lions and spotted hyenas that attack wildebeest, or aphids and grasshoppers that eat the same plant. Even the interaction between the mold *Escovopsis* and leaf-cutter ants can be considered competitive, because both derive energy and nutrients from the fungus that the ants cultivate. But the limiting resource need not be food. Plants may be limited by availability of sunlight (**FIGURE 43.1B**) or inorganic nutrients in the soil. Some organisms are limited by water or space in which to grow (think of barnacles encrusting a rocky shore; see Figure 43.4) or in which to build a nest. Plants may even compete for the attention of animal partners that pollinate flowers or disperse seeds and thereby contribute to the plants' reproduction.

Consumer–resource interactions are those in which organisms gain their nutrition by consuming other living organisms or are themselves consumed. It's obvious why these are +/− interactions: the consumer benefits while the consumed organism—the resource—loses. Consumer–resource interactions include **predation**, in which an individual of one species (the predator) kills and consumes individuals of another species (the prey); **herbivory**, in which an herbivore consumes part or all of a plant (**FIGURE 43.1C**); and **parasitism**, in which a parasite consumes part of a host individual but usually does not kill it. These categories blur together to some degree. For example, herbivorous caterpillars that consume some of a plant's leaves (see Figures 28.4 and 28.5) are functionally similar to the parasitic black-legged ticks (see Figure 42.3) that consume some of a rodent's blood. And some parasites are functionally similar to predators because they consume so much of the host's body, or otherwise damage it so severely (e.g., some pathogenetic organisms; see pp. 393–394 and 454–455), that the host dies.

A **mutualism** is an interaction that benefits both species (+/+). The interaction between leaf-cutter ants and the fungus they cultivate is mutualistic: the ants feed, cultivate, and disperse the fungus; the fungus, in turn, converts inedible leaf fragments into special fungal structures that the ants can eat. The interactions between plants and pollinating or seed-dispersing animals (**FIGURE 43.1D**), or between humans and some of their gut bacteria (see Concept 41.1), are similarly beneficial to both partners. Mutualisms take many forms and involve many kinds of organisms. They also vary in how essential the interaction is to the partners.

Competition, consumer–resource interactions, and mutualism all affect the fitness of both participants. The other two defined types of interactions affect only one of the participants.

In **commensalism**, one participant benefits while the other is unaffected (+/0). Some examples involve species whose feeding behavior makes food more accessible for another. For example, the brown-headed cowbird (*Molothrus ater*) owes its common name to its habit of following herds of grazing cattle, foraging on insects flushed from the vegetation by their hooves and teeth. (*M. ater* has also been called the buffalo bird because it followed the bison herds that were once abundant across North America; see Figure 43.1C). The ungulate–cowbird interaction is commensal because the birds have no effect on ungulate fitness. In other cases, the feeding of one species benefits a second species by converting food into a form it can use. Cattle, for example, convert plants into dung, which dung beetles (see Figure 44.4) can use, but the dung beetles have no effect on the cattle. Dung beetles, in turn, are on the giving end of another commensalism: dung-dwelling organisms that cannot fly, such as mites, nematodes, and even fungi, attach themselves to the bodies of the beetles, which not only can fly but are very good at locating fresh dung. The hitchhikers have no apparent effect on dung beetle survival or reproduction.

Amensalism refers to interactions in which one participant is harmed while the other is unaffected (−/0). Elephants moving through a forest or bison grazing the plains crush insects and plants with each step (see Figure 43.1C), but the large mammals are unaffected by this carnage. Amensal interactions tend to be more accidental in nature than the other interactions, as these examples suggest.

The effects of many interactions are contingent on the environment

Ecologists find it useful to distinguish the five categories of interspecific interactions just described, but real interactions can be hard to categorize. Many interactions have both beneficial and harmful aspects, and the net effect of one species on another can be positive or negative depending on environmental conditions.

Sea anemones, for example, sting and consume small animals, including fish. But a select few fish species (mostly anemonefishes; genus *Amphiprion*) are protected by a special mucus coat and thus can live among the anemones' stinging tentacles (**FIGURE 43.2**). Although the benefit of this association to the anemonefishes is clear—they escape their own predators by hiding behind the anemones' nematocysts and can scavenge food caught by the anemones—more research is needed to clarify the consequences for the anemones. Are they nourished by

APPLY THE CONCEPT

Interactions between species may increase, decrease, or have no effect on fitness

Many animals that face uncertain food availability have evolved a tendency to collect and store more food than they can eat right away. Desert seed-eating rodents such as Merriam's kangaroo rat (*Dipodomys merriami*; see Figure 42.4B), for example, will harvest as many seeds as you put in front of them and bury the seeds in shallow deposits scattered around their territories. In some years, the plants in the desert environment produce few seeds, and the kangaroo rats eat all the seeds they have stored. In other years, the kangaroo rats store more seeds than they are able to eat, and the uneaten seeds germinate—they have been "planted." In those years, the plant species whose seeds kangaroo rats favor increase in abundance.

Researchers in southern Arizona monitored the effect of kangaroo rats on the large-seeded native bunchgrasses that the animals prefer. They fenced several plots of land with rodent-proof fences and removed kangaroo rats from half the plots. Over the next 15 years they compared the area covered by the grasses (a measure of their abundance) in plots with and without kangaroo rats.[a]

From 1931 to 1935, southern Arizona experienced a severe drought, and grass populations declined. Rains returned in 1935, and the year 1941 saw particularly high rainfall (for the desert). Examine the graph showing differences in grass abundance (relative to 1931 values) between the two types of plots and answer the following questions.

1. During the drought, did kangaroo rats have a positive, negative, or neutral effect on the grasses? Explain your reasoning.

2. Did the effect of kangaroo rats on grasses change after rains returned? Explain your reasoning.

3. What aspects of kangaroo rat behavior are detrimental to grasses? What aspects might help grasses?

4. Imagine a hypothetical kangaroo rat species that finds and eats 50% of the seeds in its environment without storing any. Redraw the blue line in the figure for this hypothetical animal.
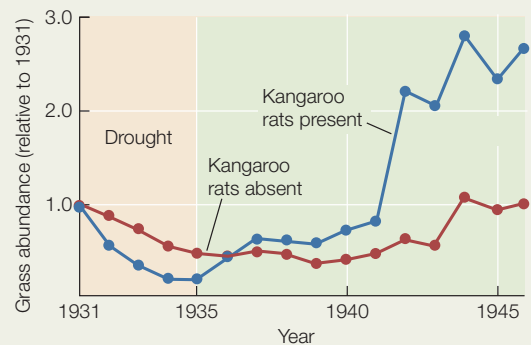
[a]H. G. Reynolds. 1950. *Ecology* 31: 456–463.

the fishes' nitrogen-rich feces? Do they suffer because the fish steal some of their prey? The net effect of the interaction for anemones may change from beneficial when food is scarce to detrimental when food is abundant.

Amphiprion ocellaris

FIGURE 43.2 Interactions between Species Are Not Always Clear-Cut   Ecologists long believed that the relationship between sea anemones and anemonefishes was a commensalism: that the fish, by living among the anemones' stinging tentacles, gained protection from predators. But could it also be considered a mutualism—if the fishes' feces provide nutrients that are important for the anemones—or competition—if the fish occasionally steal the anemones' prey?

CHECKpoint CONCEPT 43.1

✓ What is the criterion for classifying interspecific interactions?

✓ What type of interspecific interaction occurs between humans and their crop plants?

✓ Describe an experiment that would allow you to determine whether the effect of anemonefishes on sea anemones is positive, negative, or neutral.

Interspecific interactions affect population dynamics because they influence the contributions of individuals to population growth rate. How exactly are population dynamics affected?

CONCEPT 43.2 Interactions within and among Species Affect Population Dynamics and Species Distributions

Individual members of a population usually vary in their survival and reproduction, a point we will return to in Concept 43.4. Even so, we can sum up the contributions of all members to obtain the total population growth rate. The resulting value

is exactly equivalent to what we obtained by using averages in Concept 42.2. There we showed that the population growth rate equals the average individual's contribution (the per capita growth rate, r) multiplied by the number of individuals in the population (N). If r does not change, population size either grows at an ever-faster rate (if r is positive) or gradually shrinks to zero (if r is negative).

The value of r is not fixed, however, because of **intraspecific** (Latin, "within species") **competition**: mutually detrimental interactions among members of the same species that occur because they use the same limiting resources. As population density increases, per capita resource availability shrinks, the per capita growth rate decreases, and overall population growth slows (see Concept 42.4). This negative feedback (see Concept 1.2) dramatically alters the growth trajectory: instead of growing toward infinity, the population stops growing and fluctuates around a carrying capacity (K).

Interspecific interactions can modify per capita growth rates

Per capita growth rates are affected by interspecific as well as intraspecific interactions, and we can study how these interactions affect population dynamics by including both of them in an equation for population growth. The word equation on p. 874 describes the growth of a single population in which intraspecific competition causes r to decrease as population density increases. A competing species will decrease r by an additional amount that depends on its density:

per capita growth rate (r) of species A =

{maximum possible r for species A in uncrowded conditions –

an amount that is a function of A's own population density} –

{an amount that is a function of the population density of competing species B}

Notice that to describe this interaction, we need to write a pair of equations: one for species A and one for species B. Each equation consists of an expression that describes the growth of one species in the absence of the other, minus an expression that describes the effect of the other species.

Interspecific interactions other than competition can be described in a similar way. Depending on the type of interaction, we must either subtract or add the effect of the other species (see Figure 43.1A). In consumer–resource interactions, we subtract the effect of the consumer species (e.g., the predator) in the equation for the resource species (e.g., the prey), since the consumer increases the mortality of the resource species. Conversely, we add an effect of the resource species in the equation for the consumer, since the consumer benefits from the presence of the resource. In mutualistic interactions, we add an effect of each mutualist to the equation for the other. In commensal interactions, we add a term in the equation of the species that benefits, and in amensal interactions, we subtract a term in the equation of the species that is harmed. (In these two types of interactions, equations for the partner species contain no reciprocal terms, because, by definition, the partner is unaffected by the interaction.)

Go to ANIMATED TUTORIAL 43.1
Species Interactions and Population Dynamics
PoL2e.com/at43.1

Interspecific interactions affect population dynamics and can lead to extinction

Because interspecific interactions modify per capita growth rates, populations show different dynamics in the presence and absence of other species. The Russian ecologist Georgii F. Gause explored the effects of interspecific interactions on populations of several species of the protist *Paramecium* (see Figure 20.6). He grew these unicellular organisms in single-species

APPLY THE CONCEPT

Interactions within and among species affect population dynamics and species distributions

A leaf-cutter ant nest can be considered a community—an ecological system (see Concepts 1.2 and 41.1) in which the species are components that interact with one another. Major components of the system are shown as labeled boxes, and their interactions as arrows between those boxes.

Use the description of interactions within leaf-cutter ant nests in the opening story of this chapter to answer the following questions:

1. What is the sign of the following direct effects of each species on another?

Ants on fungus	Fungus on ants
Fungus on mold	Mold on fungus
Mold on bacteria	Bacteria on mold
Bacteria on ants	Ants on bacteria

2. Explain for each interaction the mechanism by which the fitness of interacting individuals is affected.

3. To which of the five categories of interspecific interactions does each pairwise interaction belong?

4. Explain how the spatial distribution of the green mold *Escovopsis* might affect the spatial distribution of leaf-cutter ant colonies.

(A)

(B)
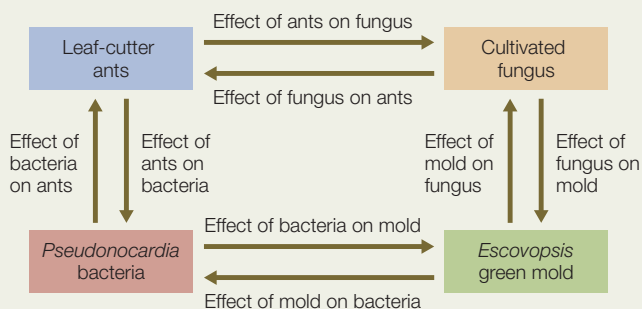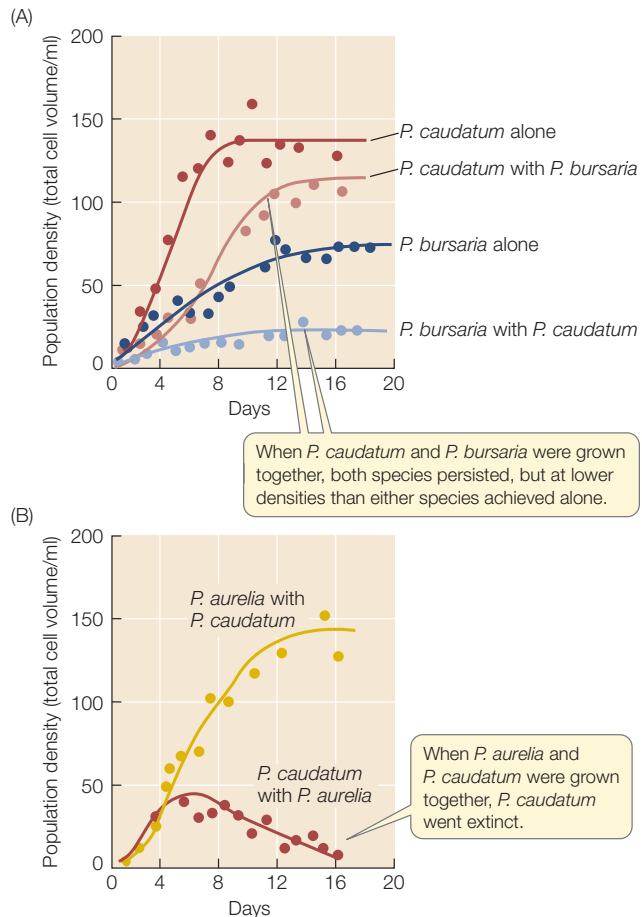
FIGURE 43.3 Interspecific Competition Affects Population Growth
(A) Some species of the unicellular protist *Paramecium* are able to coexist, but their populations grow more slowly, and reach lower equilibrium densities, when a competitor is present. (B) Competition between some *Paramecium* species results in local extinction of one species.

cultures and in cultures containing either a competing species of *Paramecium* or a protist predator, *Didinium*. To understand the results, Gause used both word equations, such as the one we gave earlier, and mathematical expressions of the same interactions. In the decades since Gause's work, mathematical models have proved to be important for understanding how interspecific interactions affect population dynamics. In the case of competition, all models lead to the following conclusions:

- The presence of a competitor always reduces population growth rate. In **FIGURE 43.3A**, notice that the slope of the curve of population density versus time is shallower in the presence of a competitor, because the competitor reduces the per capita growth rate from what it would be with intraspecific density dependence alone.

- When two competitors coexist, as in Figure 43.3A, they achieve lower equilibrium population densities than either would achieve alone.

- In some cases, as in **FIGURE 43.3B**, one competitor drives the other extinct.

Other types of interspecific interactions also affect population growth rates and average densities:

- In all interspecific interactions, the per capita growth rate of at least one species is modified by the presence of the other, sometimes positively and sometimes negatively.

- In all interspecific interactions, the average population density of at least one species differs in the presence and in the absence of the other species. Population densities are increased in species for which the interaction is positive and are decreased in species for which the interaction is negative.

- In interactions that have negative effects—that is, consumer–resource interactions, competition, and amensalism—local extinction of one or both of the interacting species is possible.

Interspecific interactions can affect species distributions

We have seen that a species may be absent from a particular location because barriers to dispersal have prevented the species from colonizing it (see Concept 41.4), or because the environment is unfavorable for the species' population growth (see Concept 42.3). We can now see that other species—not just physical conditions—may determine whether a population can persist. A site may be unfavorable because it lacks suitable prey or because it harbors a competitor or predator; conversely, an otherwise unfavorable site may become favorable if a mutualist is present.

FIGURE 43.4 shows an example of how competitive interactions can restrict the habitats in which species occur. The rock barnacle (*Semibalanus balanoides*) and Poll's stellate barnacle (*Chthamalus stellatus*) compete for space on rocky shorelines of the North Atlantic Ocean. Adult barnacles attach themselves permanently to rocks and filter food particles from the water that flows past them; therefore, occupying a space amounts to having the opportunity to feed. The planktonic (swimming) larvae of both *S. balanoides* and *C. stellatus* settle in the intertidal zone and metamorphose into immobile adults. There is little overlap between the areas occupied by adults; the smaller stellate barnacles generally live higher in the intertidal zone, where they face longer periods of exposure to air and desiccation than do rock barnacles.

In a famous experiment conducted more than 50 years ago, Joseph Connell removed each of the species from its characteristic zone and observed the response of the other species. Stellate barnacle larvae settled in large numbers throughout much of the intertidal zone, including the lower levels where rock barnacles are normally found, but they thrived at those levels only when rock barnacles were absent. The rock barnacles grew so fast when present that they smothered, crushed, or undercut the stellate barnacles. By outcompeting them for space, rock barnacles made the lower intertidal zone unsuitable for stellate barnacles. In contrast, removing stellate barnacles from higher in the intertidal zone did not lead to their replacement by rock barnacles; the rock barnacles were less tolerant of desiccation and so failed to thrive there even when stellate barnacles were absent.
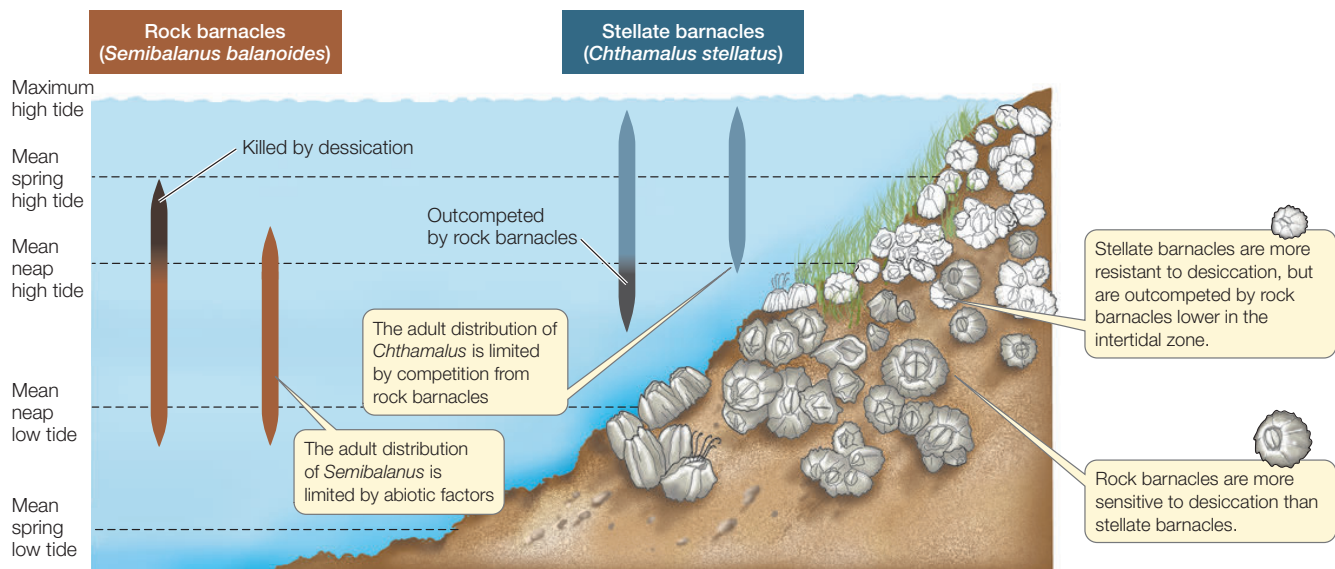
FIGURE 43.4 Interspecific Competition Can Restrict Distributions
The left-hand bar for each species shows the zone over which larvae settle, and thus the potential adult distribution. The right-hand bar shows the actual adult distribution. Competition with rock barnacles restricts stellate barnacles to a smaller portion of the intertidal zone than they could otherwise occupy.

Rarity advantage promotes species coexistence

Mathematical models of interspecific interactions have been useful not only in helping us understand how these interactions affect population dynamics and species distributions, but also by giving us insights into the conditions that allow interacting species to coexist.

Models of interspecific competition indicate that two competitors will coexist when individuals of each species suppress their own per capita growth rate more than they suppress the per capita growth rate of their competitor. In other words, intraspecific competition must be stronger than interspecific competition: *you harm yourself more than you harm your competitor*. When this is the case, a species gains a growth advantage when it is rare—that is, when it is at a low density and its competitor is at a high density—and this **rarity advantage** prevents the population from decreasing to zero. The result is coexistence.

One mechanism that can cause intraspecific competition to be stronger than interspecific competition is **resource partitioning**: differences between competing species in resource use. Individuals of the same species, which use very similar resources, will suppress their own per capita resource availability more than they suppress that of the competitor, unless the competitor uses identical resources. But this is unlikely, and if differences in resource use are sufficiently large, competing species can coexist (**FIGURE 43.5**).

Paramecium aurelia, for instance, outcompetes both *P. caudatum* and *P. bursaria*, but the latter two species can coexist (see Figure 43.3A) because *P. bursaria* can feed on bacteria in the low-oxygen sediment layer at the bottom of culture flasks, a

habitat that *P. caudatum* cannot tolerate. This partitioning of habitat is possible because *P. bursaria* harbors symbiotic algae that provide it with additional oxygen as a by-product of algal photosynthesis.

In the case of predators and prey, a number of processes can result in a rarity advantage that protects prey from being driven extinct by their predators. For example, prey may become harder to find as they become rarer because they can all hide in the best refuges; or they may be able to invest more in their defenses when they are at low densities and have more resources available per capita. Predators may also stop looking for rare prey and switch to a more abundant prey type.
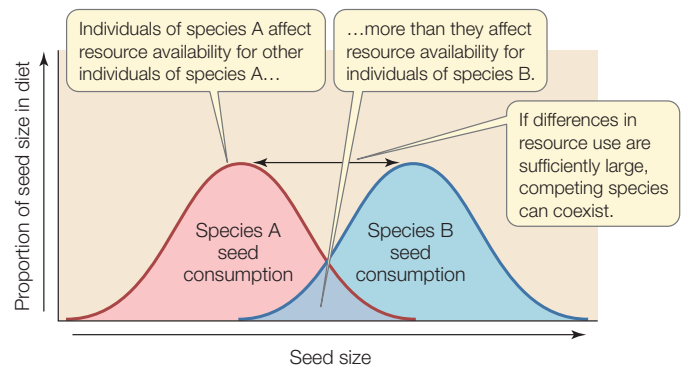
FIGURE 43.5 Resource Partitioning Can Cause Intraspecific Competition to Be Greater Than Interspecific Competition
When two species differ in their use of resources, individuals will have a greater effect on the availability of resources to individuals of their own species than to individuals of the other species. In this hypothetical scenario, birds of species A eat smaller seeds on average than birds of species B. Individuals of species A affect the food supply for their own species (smaller seeds) more than they affect the food supply for species B (larger seeds), and vice versa. In other words, the two species partition, or divide up, the seed resource.

Alternatively, some other limiting factor (such as availability of nest sites) may prevent the predators from becoming numerous enough to eat all the prey. The effect of such processes is that per capita growth rates may rebound when prey become rare, thus making their extinction less likely.

> ### CHECKpoint CONCEPT 43.2
>
> ✓ Describe the components of an equation for the per capita growth rate of a species that interacts with another species.
> ✓ Explain, in terms of resource availability, why the equilibrium population size of one species is reduced by the presence of a competing species.
> ✓ What are the possible outcomes of a predator–prey interaction in terms of the final population sizes of the two interacting species?

The examples of two-species interspecific interactions that we have discussed do not occur in isolation. As may already be apparent, they form parts of a larger web of interactions that connects any given species to many others living in the same area.

CONCEPT 43.3 Species Are Embedded in Complex Interaction Webs

Some species are specialized in their interspecific interactions, competing with, consuming, or being consumed by few other species. Examples include leaf-cutter ants, whose entire diet consists of fungal structures; yucca moths, which pollinate and oviposit only in flowers of specific *Yucca* species; and many parasitic insects that attack only a single host species. However, many species are involved in interactions of many types with diverse other species. For example, most animal-pollinated flowering plants are pollinated by more than one pollinator species, and few pollinators visit only one plant species. Furthermore, each species in a web of pollination interactions is connected to a much larger set of species that act as its competitors, hosts, consumers, and so forth. *Prosopis* shrubs (mesquite) are pollinated by many species of native bees and other insects, and their flowers and leaves are eaten, or harvested, by dozens of species of herbivorous insects, including leaf-cutter ants. Their seeds are eaten or dispersed by rodents, beetles, coyotes, foxes, and hoofed mammals, including cattle (see the opening story of Chapter 41). The roots of a *Prosopis* shrub interact with an entire community of soil fungi and bacteria as well as with roots of other plants. Each of the species that interacts with *Prosopis* in turn interacts with a constellation of other species.

Consumer–resource interactions form the core of interaction webs

These extensive webs of interspecific interactions may seem bewildering, but they make sense once we realize that they are organized around consumer–resource interactions—after all, everybody has to eat, or (to be more accurate) everybody needs energy and nutrients. Every species therefore participates in consumer–resource interactions as the consumer, the resource, or both. In addition, competition commonly occurs between consumers that use the same sources of energy and nutrients—for example, sunlight, chemical nutrients, or food—or (in the case of immobile organisms such as barnacles or plants) the space that gives them access to these resources. As we will see in Concept 43.4, even mutualisms usually involve consumers and resources. For example, leaf-cutter ants both feed and eat their fungus; algae that live inside the cells of sea anemones (see Figure 43.2) photosynthesize, producing carbohydrates that the animals consume, and in return, the anemones provide the algae with nitrogen. To be sure, energy and nutrients are not the only types of resources involved in interspecific interactions. Birds, for example, compete for nest sites that are safe for their offspring. Nevertheless, feeding, or **trophic** (Greek *trophes*, "nourishment"), interactions form the core of interaction webs.

Trophic interactions determine the flow of resources through communities. Nutrients and energy enter communities via organisms that obtain the *materials* that form their bodies from inorganic sources and that obtain the *energy* that fuels their metabolism from solar radiation or inorganic chemicals. These organisms are called **primary producers** because they convert energy and inorganic materials into organic compounds that can be used by the rest of the community. They are also called **autotrophs** (Greek, "self-feeders") because they create their own "food" from inorganic sources (see Concept 6.6).

Species that obtain energy by breaking apart organic compounds that have been assembled by other organisms are called **heterotrophs** (Greek, "other-feeders"). Heterotrophs that dine on primary producers are called **primary consumers**, or herbivores (Latin, "plant eaters"). Those that eat herbivores are called **secondary consumers**, or carnivores (Latin, "flesh eaters"); those that eat the flesh of secondary consumers are called **tertiary consumers**, and so on. These feeding positions—primary producers and primary, secondary, and tertiary consumers—are called **trophic levels**. Some organisms, called **omnivores**, feed from multiple trophic levels. **Decomposers** feed on waste products or dead bodies of organisms (**TABLE 43.1**).

Trophic interactions can be diagrammed as a **food web** that shows who eats whom. Arrows from resource to consumer species show how energy and materials flow, and species are arranged vertically according to trophic level (**FIGURE 43.6**). Food web diagrams do not show all the interactions within a community, but they do show the major ones, and many others can be inferred from them. Competition, for example, can be inferred whenever multiple consumers use the same resource: elk (*Cervus canadensis*) and American bison (*Bison bison*) compete for grass, and plants compete for sunlight and soil nutrients.

Losses or additions of species can cascade through communities

As the naturalist and conservationist John Muir noted in his 1911 book *My First Summer in the Sierra*, "When we try to

TABLE 43.1	The Major Trophic Levels		
Trophic level	**Source of energy**	**Examples**
Primary producers (photosynthesizers, chemoautotrophs; see Table 19.2)	Solar energy, inorganic chemicals	Green plants, protists, bacteria, archaea
Primary consumers (herbivores)	Tissues of primary producers	Elk, grasshoppers, gypsy moth larvae, pollinating bees, geese
Secondary consumers (carnivores)	Tissues of herbivores	Spiders, great tits, cheetahs, parasites
Tertiary consumers (carnivores)	Tissues of carnivores	Tuna, killer whales, parasites
Omnivores	Several trophic levels	Coyotes, opossums, crabs, robins, white-footed mice
Decomposers	Dead bodies and waste products of other organisms	Fungi, many bacteria, vultures, earthworms, dung beetles

Go to ACTIVITY 43.2 The Major Trophic Levels
PoL2e.com/ac43.2

pick out anything by itself, we find it hitched to everything else in the Universe." This poetic statement encapsulates an ecological fact: adding, removing, or changing the abundance of any species has effects that reverberate throughout an interaction web.

An example of what we might call the "Muir Effect" comes from Yellowstone National Park in Wyoming. Wolves (*Canis lupus*) in the park prey on large mammals, including elk (see Figure 43.6). Unrestricted hunting eliminated wolves from the park by 1926, and they were reintroduced in 1995. This shift in trophic interactions has had cascading effects on the entire ecosystem.

Park managers initiated annual censuses of elk in 1920. Concerned by the rapid increase in elk numbers after wolves

disappeared, they deliberately kept elk numbers in check for many years. But the removal of elk ceased in 1968, and elk densities increased rapidly after that (**FIGURE 43.7A**). The elk browsed aspen trees (*Populus tremuloides*) so heavily that no young trees were added to the population after 1960 (**FIGURE 43.7B**). The elk also browsed streamside willows (*Salix* spp.), with the result that beavers (*Castor canadensis*), which depend on willows for food, nearly went extinct locally.

After park managers reintroduced wolves in 1995, elk populations decreased, and as a consequence, young aspen now survive, willows regrow, and species associated with these trees (beavers as well as birds, insects, and many others) have increased. This history of removal and reintroduction illuminates a cascade of effects across trophic levels—a so-called **trophic cascade**. What happens to predators is felt not only by their prey, but also by the prey of their prey, and by many other species connected with all of them.
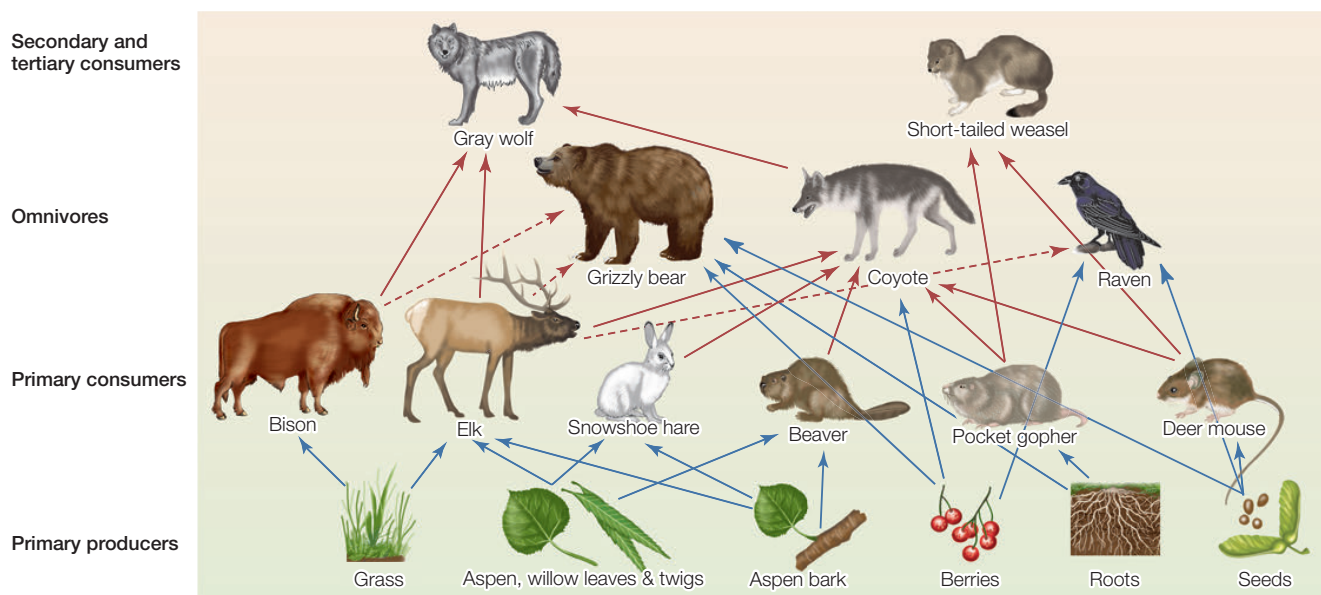
FIGURE 43.6 A Food Web in the Grasslands of Yellowstone National Park The arrows point from resource to consumer. Even this highly simplified food web is complex. Primary consumers eat plant material (blue arrows). Secondary and tertiary consumers are carnivores that kill and eat live animals (red arrows). Omnivores such as grizzly bears, coyotes, and ravens eat both plant and animal tissues; ravens and grizzlies also eat carrion (flesh of dead animals that they did not kill; dashed red arrows).

(A)

Elk populations grew rapidly when wolves were absent and park managers stopped removing elk.

Number of elk (thousand)

Wolves
eliminated
(1926)

Elk removal
suspended
(1968)

Wolves
reintroduced
(1995)

Year

(B)

Wolves
present

Wolves absent

In the absence of wolves, browsing by elk prevented the establishment of new aspens.

After wolves were reintroduced, aspen forests began to regenerate.

Percent of aspen population

1900–
1909
1910–
1919
1920–
1929
1930–
1939
1940–
1949
1950–
1959
1960–
1969
1970–
1979
1980–
1989
1990–
1999

Aspen origination decade

Wolves
eliminated
(1926)

Wolves
reintroduced
(1995)

(C) *Populus tremuloides* inside elk-exclusion fence

FIGURE 43.7 Removing Wolves Initiated a Trophic Cascade
(A) The elk population in Yellowstone National Park increased rapidly after wolves were eliminated and the park stopped removing elk. (B) Aspens did not become established when wolves were absent and abundant elk browsed the trees. (C) Researchers constructed an "elk exclusion" fence to demonstrate that aspen regenerated only inside the fence, where elk were absent.

Go to MEDIA CLIP 43.1
Wolf Cascade
PoL2e.com/mc43.1

The cascading effects of ecological interactions have implications for conservation

The Yellowstone study exemplifies the new scientific field of **conservation ecology** (one of many practical applications of ecology), and more specifically, the subfield of **restoration ecology**. Conservation ecology attempts to avoid the loss of elements or functions of an existing web of interactions, whereas restoration ecology provides scientific guidance for restoring lost elements or functions of a web. Reintroducing predators that humans once eliminated (naturally enough: a predator that eats our own prey or domestic animals is our competitor!) is a bold attempt to restore ancestral ecosystems. It also illustrates a bigger point: if we wish to restore or conserve ecological systems, we must consider the entire web of ecological interactions. And if we strive to conserve a particular species that is in danger of extinction, we must consider the web from the standpoint of that species, looking outward at all of its ecological interactions.

Nothing illustrates these points better than the problem of species introductions. As we saw in Concept 41.5, humans are

introducing many species to new places, both intentionally and unintentionally. These introductions not only blur biogeographic boundaries but also have the potential to alter interactions among native species. Species that are introduced into a region where their natural enemies are absent may reproduce rapidly and spread widely. Such **invasive species** are likely to have negative effects on native species that lack adaptations to compete with or defend themselves against the newcomers. Alternatively, introduced species may benefit some native species if they provide a resource that was not available previously. In all cases, they alter interaction webs, as we will see in Chapter 44.

Introduced invasive species can harm native species in several ways. Introduced yellow star-thistle (*Centaurea solstitialis*), for example, grows rapidly in grasslands and physically crowds out native species, covering entire areas with its spiny flowering heads (see p. 874). Other flowering plants alter relationships between native plants and their mutualists. Purple loosestrife (*Lythrum salicaria*), introduced into North America in the early 1800s, not only crowds out natives but also—adding insult to injury—competes with them for the attention of insect pollinators. The native species *Lythrum alatum*, for example, receives fewer visits from bumble bees, and produces fewer seeds as a result, when purple loosestrife is present.

Some invaders alter ecological interactions by causing extinctions of native species. Concept 22.3 described the case of an introduced sac fungus, a pathogen that drove the once-dominant American chestnut (*Castanea dentata*) to extinction. The chestnut has been replaced by oaks throughout the forests of the northeastern United States. Because acorn production varies greatly from year to year, whereas chestnuts produced consistent nut crops every year, the loss of chestnuts has precipitated dramatic year-to-year fluctuations in rodents, ticks, and Lyme disease (see Figure 42.2).

Organisms that are deliberately introduced to control pests can alter interactions among native species if they do not confine their attention to the pest species. *Rhinocyllus conicus*, for example, is a Eurasian weevil whose larvae eat developing seeds. It was introduced into North America in 1968 to control the invasive musk thistle (*Carduus nutans*). But when the abundance of musk thistle declined, the weevil moved on to the native Platte thistle (*Cirsium canescens*) and then to wavyleaf thistle (*C. undulatum*). The introduced weevil has become not only a consumer of native thistles but also a competitor of the native insects that eat thistles.

CHECKpoint   CONCEPT 43.3

✓ Why do some introduced species become invasive?

✓ At what trophic level would you place humans?

✓ What would a terrestrial landscape look like if its communities contained no decomposers?

The effects of interspecific and intraspecific interactions on individual members of a population depend on those individuals' characteristics. For instance, if individuals vary in heritable attributes that determine how much a competitor affects their access to resources, or that determine their risk of being eaten by a predator, then the interaction will result in evolution by natural selection.

CONCEPT 43.4   Interactions within and among Species Can Result in Evolution

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Both intraspecific and interspecific interactions can affect the success of an average individual in surviving and reproducing. But averages tell us only part of the story, because no individual is exactly average. Interactions will therefore affect individuals to different extents, causing them to vary in their contribution to population growth rate—that is, in their fitness. Heritable traits that cause greater benefit from positive interactions, or less harm from negative interactions, will become more common in the population. The dynamics of this evolutionary change (see Chapter 15) will depend on the mix of positive and negative effects that characterize an interaction. Let's consider some examples, starting with intraspecific competition.

Intraspecific competition can increase the carrying capacity

Equations for density-dependent population growth, such as the word equation in Concept 42.4, assume that all the individuals in a population are equally affected by its density. However, individuals often vary in phenotypic traits that affect how well they can use available resources. Consider the seed-eating finches of the Galápagos archipelago off the west coast of Ecuador (see Figure 17.7). The average beak size for any given finch species varies from island to island, and the beak size on any given island is close to the size that is best for processing one of the types of seeds available on the island (**FIGURE 43.8**).

Such patterns suggest that beak size has evolved in response to the available seeds. To visualize this process, consider the following scenario.

Imagine an island without finches that supports one abundant plant species producing seeds of a certain size and hardness. Suppose next that individuals of a finch species colonize the island. The new colonists will vary somewhat in beak size, which is related to body size—big birds have big, strong beaks. One beak (and body) size will be best: relative to this "optimal" size, smaller birds will have more difficulty cracking the seeds open, whereas larger birds will have to allocate more energy to maintenance of their larger bodies, thus leaving less for reproduction (see concept 42.3). Individuals with beaks closest to the optimal size will leave the most offspring. As a consequence, the average beak size will evolve toward the optimum by stabilizing natural selection (see Figure 15.13A). Furthermore, the carrying capacity (see Concept 42.4)—the number of birds that can be supported by the available seed crop—will increase as birds that convert seeds into offspring most efficiently come to predominate in the population.

LINK

Three patterns of natural selection—directional, stabilizing, and disruptive—are described in **Concept 15.4**

Interspecific competition can lead to resource partitioning and coexistence

Interspecific competition, like intraspecific competition, can lead to evolution, as is illustrated by another interaction in the Galápagos archipelago, between a finch and an insect. The small ground finch (*Geospiza fuliginosa*) consumes flower nectar as well as seeds. Small individuals are better at obtaining nectar from the islands' small flowers, but large individuals have larger beaks that are better at cracking seeds. Carpenter bees (*Xylocopa darwinii*) compete with *G. fuliginosa* for nectar on some islands but are absent from others. Small finches are affected more strongly by competition from bees than are larger individuals. As a consequence, the finches are larger in size, and drink less nectar, on islands where carpenter bees are present (**FIGURE 43.9**). This evolutionary shift means that resource use by *G. fuliginosa* has diverged from that of its bee competitors on islands where the two species coexist—an example of resource partitioning (see Concept 43.2) that resulted from natural selection.

Consumer–resource interactions can lead to an evolutionary arms race

Predators, parasites, and herbivores benefit if they can acquire lots of nutritious food quickly and inexpensively, whereas resource species benefit if they can evade or deter these natural enemies at little cost. The interests of consumer and resource species are obviously at odds. These opposing interests can lead to an "evolutionary arms race," in which prey continually evolve better defenses, predators continually evolve better offenses, and neither gains any lasting advantage over the other. The Red Queen summed up this situation in Lewis Carroll's

INVESTIGATION

FIGURE 43.8 Intra- and Interspecific Competition Influence the Morphology of Coexisting Species   In the Galápagos archipelago, seed-eating finches (*Geospiza* spp.) use their beaks to crack open seeds, which are often in short supply. Individuals with big beaks can crack large, hard seeds that individuals with small beaks cannot eat, whereas small-beaked birds gain more fitness than do large-beaked birds from eating small, soft seeds. Dolph Schluter and Peter Grant documented how the islands differed both in their seed resources and in the morphology of *Geospiza* species present.[a]

HYPOTHESIS

Differences in the morphology of finches among islands reflect interisland differences in the availability of seeds of different sizes.

METHOD

1. Determine which species of seeds can be eaten by *Geospiza* species with different beak sizes, and determine the species' food requirements.

2. On each island, measure the abundances of seeds of different plant species and calculate the availability of food for finches of different beak sizes.

3. From these measurements, calculate for each island how many finches of a given beak size could be supported if no other finch species were present (this is an estimate of carrying capacity). Do this for hypothetical finches with beak sizes that span the possible range for seed-eating *Geospiza* species.

4. Display the calculated results as a graph for each island, with beak size on the *x* axis and estimated carrying capacity on the *y* axis. A peak in the graph predicts a high carrying capacity for a finch species with that beak size. A low point means the opposite—a species with that beak size is predicted to achieve only a low equilibrium density.

5. On each graph, place a dot showing the mean beak size of each *Geospiza* species actually present on the island.

RESULTS

1. Each finch species present on an island had a beak size that matched a peak quite closely.
2. The species present differed in beak size, so that only one species "occupied" a peak.
3. The number of finch species present on an island increased with the number of distinct peaks in predicted carrying capacity.
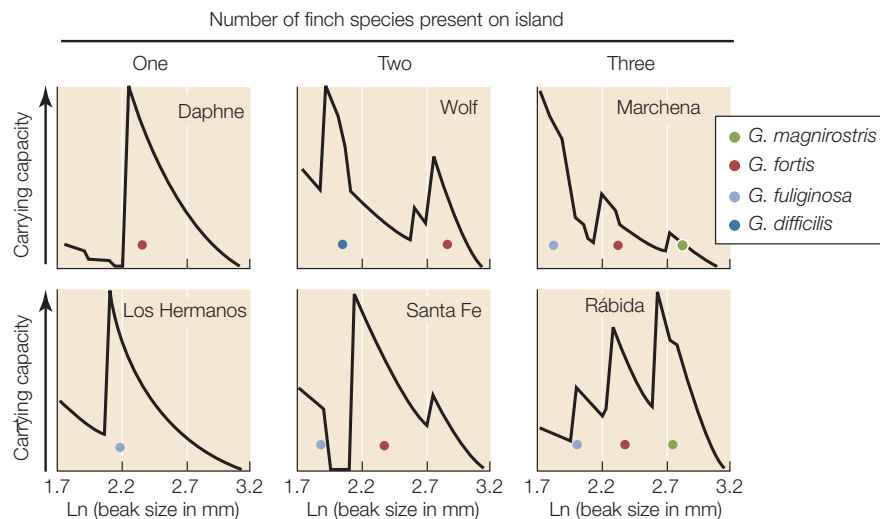
CONCLUSION

The availability of seeds of different sizes determines how many species of *Geospiza* occur on an island and what their beak sizes are.

ANALYZE THE DATA

A. Explain how intraspecific competition could cause the average beak size of a hypothetical finch species that colonizes an island to evolve to match a peak in carrying capacity.

B. Suppose the *G. fuliginosa* population on Marchena goes extinct, and the island is subsequently colonized by *G. fuliginosa* individuals from Rábida. Do you expect the average beak size of the colonizing population to increase or decrease through time? Explain your reasoning.

C. Explain how interspecific competition could cause peaks in seed availability to have no more than one associated finch species.

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]D. Schluter and P. R. Grant. 1984. *American Naturalist* 123: 175–196.

Geospiza fuliginosa

Xylocopa darwinii

Nectar Use and Size of *G. fuliginosa*

Island	Time spent feeding on flower nectar (%)	Mean size (wingspan, mm)
BEES ABSENT		
Pinta	10	59.8
Marchena	28	58.2
BEES PRESENT		
Fernandina	1	64.8
Santa Cruz	14	64.0
San Salvador	0	63.8
Española	0	64.7
Isabela	7	64.5

FIGURE 43.9 Finch Morphology Evolves in Response to Competition with Carpenter Bees   On those Galápagos islands where small ground finches are the sole pollinators of small flowers, the birds are small (as measured by their short wingspans). Small size lowers their energy requirements and may increase their ability to negotiate the flowers. On islands where carpenter bees compete with these finches for nectar, the birds are larger and have bigger, stronger beaks (which allows them to include seeds in their diet).

Through the Looking-Glass with the words "It takes all the running you can do, to keep in the same place."

Resource species have various defensive strategies available to them. Some mobile animals use speed, size, or weapons to thwart predators. Others hide or use camouflage to avoid being detected, or mimic unpalatable species (**FIGURE 43.10A**). Immobile organisms have other tricks up their sleeves; for example, they may have evolved thick armor, or they may be poisonous or not nutritious. In response to these strategies, natural selection in populations of consumers favors greater speed, size, or strength; keen senses; armor-piercing or crushing tools (**FIGURE 43.10B**); or means of detoxifying poisons.

Plants produce a great variety of defensive chemicals, as we saw in Chapter 28. Used in small quantities, many of these chemicals, including the caffeine of coffee and tea, the mustard oils of cabbages, the capsaicins of chilis, and the piperine of black pepper, spice up our own lives. But the production of such compounds evolved because they are toxic or repellant to some herbivores and pathogens. Defensive compounds explain in part why the leaf-cutter ant *Atta cephalotes* harvests leaves from only 17 of 332 plant species that grow in the Florencia Norte forest of Costa Rica: the terpene-like compounds (see Table 28.1) found in the leaves of many of the plants make them toxic either to the ants or to their fungus.

Many herbivores have evolved ways around plant chemical defenses. The caterpillars of *Heliconius* butterflies, for example, store or detoxify the cyanide-containing defensive compounds of the passionflower (*Passiflora*) vines they feed on, and even use these poisons as defenses against their own predators. Some *Passiflora* species, conversely, have evolved modified leaf structures that mimic butterfly eggs (**FIGURE 43.11**). Since female butterflies will not lay eggs on leaves that already carry eggs, these structures reduce the plant's probability of being eaten by *Heliconius* caterpillars.

Mutualisms involve conflict of interest

Mutualisms are often misunderstood. We sometimes hear that "bees visit flowers to pollinate them," or that "flowers provide food for their pollinators," but such statements imply an impossible evolutionary process

(A)
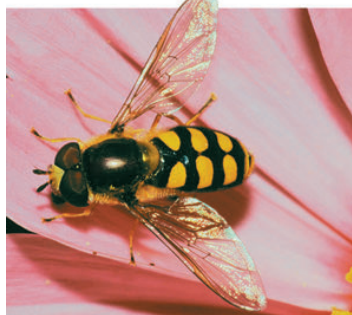
Episyrphus balteatus

Vespula vulgaris

(B) *Anodorhyncus hyacinthinus*

FIGURE 43.10 Defense Mechanisms and Evolutionary Arms Races   (A) The harmless hoverfly (above) gains protection by mimicking a dangerous stinging wasp (below) that predators have learned to avoid. (B) Brazil nuts (the seeds of *Bertholletia excelsa*) are protected by extremely hard shells that most birds cannot penetrate. The evolution of beak strength in the hyacinth macaw, however, has kept pace with the nut's hardness.

Bumps on the leaves of *Passiflora* mimic butterfly eggs.
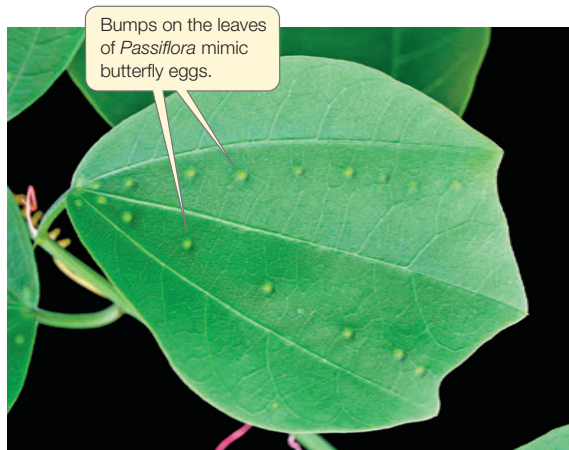
FIGURE 43.11 Using Mimicry to Avoid Being Eaten   The raised yellow bumps on these passionflower leaves resemble the eggs of the plant's principal herbivores, zebra butterflies (*Heliconius* spp.). Because female butterflies will not lay their eggs on leaves that already carry eggs, these "false eggs" protect the plant from being eaten by caterpillars.

in which species exhibit traits that evolved to benefit another species. As Charles Darwin said about his theory of natural selection (see Concept 15.1),

> If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection.

In truth, most pollinators visit flowers to get food and just happen to pollinate the flowers in the process; flowers provide food (usually as little as possible) to lure animals, not to fatten them up; birds and bees respond to any conspicuous color that signals the presence of food; and most flowers are visited by any animal that gains economically by doing so, whether it pollinates the plant or not. In the rough-and-tumble world of ecological interactions, species benefit other species not out of **altruism** but because acting in their own self-interest happens to benefit others.

LINK

The coevolution of plants and pollinators is discussed in **Concept 21.5**

APPLY THE CONCEPT

Interactions within and among species can result in evolution

Crabs feed on mussels, and individual young mussels can sometimes detect the presence of crabs and respond by developing a thicker protective shell as they grow to adult size. The abilities to detect and to respond to crabs are inherited traits.

On the Atlantic coast of North America, blue mussels (*Mytilus edulis*) face two non-native crab predators. The European green crab (*Carcinus maenas*) was introduced to the United States almost 200 years ago, and the Asian shore crab (*Hemigrapsus sanguineus*) arrived only 20 years ago. *C. maenas* has spread all along the Atlantic coast of North America, whereas *H. sanguineus* has not yet reached northern Maine. Have mussels evolved the ability to detect this new enemy and respond to it?

Researchers collected very young *M. edulis* from northern populations, which have experienced predation by *C. maenas* but not by *H. sanguineus*, and from southern populations, which have experienced both predator species. They grew mussels from each population on floating docks under three different conditions: no crab nearby (controls); a hungry *C. maenas* caged nearby; or a hungry *H. sanguineus* caged nearby. After 3 months, researchers measured mussel shell thickness.[a]

Use the graph to answer the following questions. Error bars indicate 95% confidence intervals of mean shell thickness; bars with different letters are statistically different from one another (*P* < 0.05). See Appendix B for discussion of statistical concepts.

1. Have mussel populations exposed to predation by non-native crabs evolved the ability to detect and respond to them by thickening their shells? Explain your answer.

2. Which comparison is critical to your conclusion?

3. Do mussels in southern populations have thinner shells than mussels in northern populations? Would a difference in average shell thickness between the two populations invalidate your conclusion? Why or why not?

4. What do these data suggest about how quickly evolution can take place?

In nature, northern *Mytilus edulis* populations have been exposed to *Carcinus* but not to *Hemigrapsus*…

…while southern populations have been exposed to both *Carcinus* and *Hemigrapsus*.

- Control (no crabs nearby)
- *Carcinus* nearby
- *Hemigrapsus* nearby
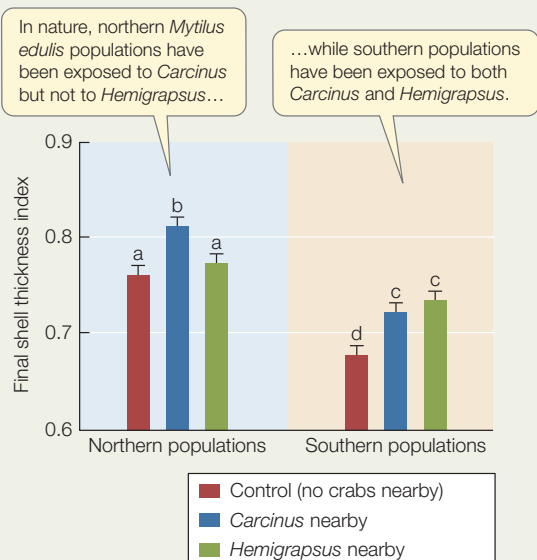
[a]A. S. Freeman and J. E. Byers. 2006. *Science* 313: 831–833.

All mutualisms involve "biological barter": the exchange of resources and services. Plants and pollinators exchange food (usually nectar or pollen) for pollen transport. Plants and frugivores exchange food (fruit) for seed dispersal. Some mutualists (such as ants and plants) exchange defense or parasite and pathogen control for food or shelter. Others (such as plants and mycorrhizae, or mammals and gut bacteria) exchange one kind of nutrient for another. In such "barter" systems, each species is selected to obtain the greatest benefit for the least cost. Therefore the net effect of the mutualism on fitness may vary depending on environmental conditions that influence the value and cost of the goods and services that are exchanged. Mycorrhizae, for example, benefit plants in nutrient-poor soils, but they can be a liability to plants in nutrient-rich soils, where the cost of feeding the mycorrhizae outweighs their value in nutrient uptake. Accordingly, plants in nutrient-rich soils excrete fewer carbohydrate-rich compounds from their roots, thus discouraging colonization by mycorrhizal fungi.

Go to ANIMATED TUTORIAL 43.2
An Ant–Plant Mutualism
PoL2e.com/at43.2

Because mutualisms are diverse and often complex, it is difficult to predict their consequences for the evolution of the species involved. Some mutualisms evolve into one-on-one relationships with ever-tighter reciprocal adaptation—leaf-cutter ants and fungus are a case in point. Others evolve into many-species relationships that rely on generalized adaptations; many mutualisms between plants and the animals that disperse their seeds fall into this category. Some mutualisms are unstable and dissolve into consumer–resource relationships. Understanding the conditions under which mutualisms follow different evolutionary trajectories is an active area of current research.

CHECKpoint CONCEPT 43.4

✓ What goods or services are exchanged in the "biological barter" between leaf-cutter ants and their fungus?

✓ Why might individual plants in populations within the geographic range of an insect herbivore contain high levels of defensive chemicals while individuals in populations outside the insect's range produce no defensive chemicals?

✓ We claimed that pollinators do not visit flowers "to pollinate them," but females of some yucca moth species carefully collect pollen, carry it to the next flower they visit, and place it on the stigma before depositing eggs in the flower's ovary. The eggs will hatch into larvae that eat some developing seeds. Does this behavior "annihilate" Darwin's theory of natural selection? Explain why or why not.

The ecological and evolutionary effects of interactions among species determine which species can coexist in an area and what their abundances are. The number of species present, their phenotypic attributes, and their relative abundances

determine the structure and function of communities—the topic of the next chapter.

Q How could the intricate ecological relationship between leaf-cutter ants and fungus have evolved?

ANSWER We have seen that interactions between species can be mutually beneficial, positive for one species and negative or neutral for the other, negative for one species and neutral for the other, or mutually detrimental (Concept 43.1). These interspecific interactions affect the fitness of the individuals involved (Concept 43.1), and any traits that increase the benefit of a positive interaction, or decrease the cost of a negative interaction, will therefore spread by natural selection (Concept 43.4).

Although more details remain to be discovered, we now can outline a scenario for the evolution of the remarkable ecological interaction between leaf-cutter ants and their cultivated fungus. Phylogenetic analysis (see Chapter 16) suggests that fungus cultivation originated when ancestors of the leaf-cutters began to feed on fungi growing on the refuse in their nests. Ant colonies that provided better growing conditions for these fungi—by providing more refuse and, eventually, by providing fresh leaf material (which the ants cannot themselves digest)—and that chose productive fungus varieties to propagate (by moving fungal masses into newly founded nests and into newly dug chambers in established nests)—had more food to eat, and thus higher fitness, than colonies that did not do these things (**FIGURE 43.12**). Thus fungus-tending behaviors evolved by natural selection. Conversely, fungi that provided better ant food ben-

The mound above ground is made up of soil excavated by the ants.

The fungus is cultured in garden chambers, each about the size of a football.

The dump chambers contain refuse.
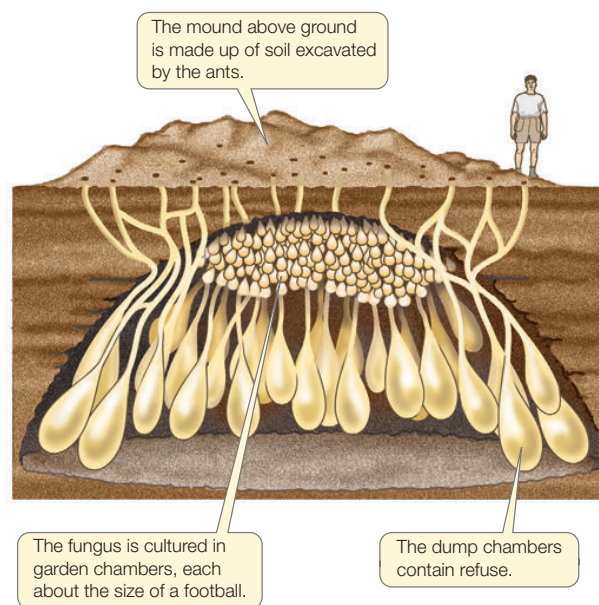
FIGURE 43.12 A Fungal Garden Diagram of the nest chamber of a large *Atta* leaf-cutter ant colony.

efited from faster ant colony growth and propagation, and these fungal adaptations also evolved by natural selection.

This history of reciprocal adaptation led to the great ecological success of leaf-cutter ants and their fungus. Leaf-cutter ants are not only the most important herbivores in the Neotropics, but also have expanded into dry environments, such as the Arizona desert, that are normally hostile to fungi.

SUMMARY

CONCEPT 43.1 Interactions between Species May Increase, Decrease, or Have No Effect on Fitness

- **Interspecific interactions** have consequences that affect the **fitness** of individuals and thus the dynamics and densities of populations and the distributions of species.

- Interspecific interactions can be divided into five broad categories depending on whether their effects on fitness are positive, negative, or neutral. **Review Figure 43.1 and ACTIVITY 43.1**

- **Interspecific competition** refers to mutually detrimental interactions in which members of two or more species use the same resource. Competition is generally strongest for the **limiting resource** that is in the shortest supply relative to demand.

- In **consumer–resource interactions**, the consumer gains nutrition and the resource species is killed or harmed. Consumer–resource interactions include **predation**, **herbivory**, and **parasitism**.

- A **mutualism** is a mutually beneficial interspecific interaction.

- **Commensalism**, in which one participant benefits while the other is unaffected, and **amensalism**, in which one participant is harmed while the other is unaffected, differ from other types of interspecific interactions in affecting only one of the participants.

- Many interspecific interactions have both beneficial and harmful aspects, and their effects may be contingent on environmental conditions. **Review Figure 43.2**

CONCEPT 43.2 Interactions within and among Species Affect Population Dynamics and Species Distributions

- The equation for density-dependent population growth, which describes **intraspecific competition**, can be extended to include the effects of interspecific competitors on per capita growth rates. Consumer–resource interactions and mutualisms can be described in a similar way by equations. **Review ANIMATED TUTORIAL 43.1**

- The per capita growth rate and the average population size of each interacting species are modified by the presence of the other in a way that depends on the type of interaction.

- In interactions with negative effects on one species (consumer–resource interactions, competition, and amensalism), local extinction of one or both of the populations of the interacting species is possible. **Review Figure 43.3**

- The presence or absence of other species can make an environment favorable or unfavorable for a species and so affect its distribution. **Review Figure 43.4**

- Coexistence of species competing for resources, and persistence of prey species and their predators, is possible if each species gains a growth advantage when it is rare. Differences between competing species in their use of resources, known as **resource partitioning**, are often great enough to generate such a **rarity advantage**. **Review Figure 43.5**

CONCEPT 43.3 Species Are Embedded in Complex Interaction Webs

- Most species are involved in webs of interaction with many other species.

- **Trophic** interactions, which determine the flow of energy and materials through communities, form the core of these interaction webs.

- Energy and materials enter communities through **primary producers**, which produce organic compounds from inorganic sources.

- Species that feed on primary producers are called **primary consumers**. Those that consume primary consumers are **secondary consumers**, and so on. These positions in the feeding hierarchy are called **trophic levels**. **Review Table 43.1 and ACTIVITY 43.2**

- Trophic interactions can be diagrammed as **food webs**. **Review Figure 43.6**

- Changes in species composition or abundance at higher trophic levels may cause a **trophic cascade** of changes at lower trophic levels. **Review Figure 43.7**

- Species introduced by humans to a new region where their natural enemies are absent may become **invasive species** that reproduce rapidly, spread widely, and alter interactions among the native species of the region.

CONCEPT 43.4 Interactions within and among Species Can Result in Evolution

- Intraspecific competition can increase the carrying capacity by causing selection for traits that allow individuals to use resources more efficiently.

- Interspecific competition can lead to resource partitioning and co-existence. It does so through selection for traits that allow individuals of one or both competing species to decrease use of resources that the competitor species uses. **Review Figures 43.8 and 43.9**

- The opposing interests of consumer species and resource species can lead to an "evolutionary arms race" in which resource species continually evolve better defenses and consumer species continually evolve better offenses.

- Mutualisms involve mutual exploitation and the exchange of goods and services. The fitness effects of mutualisms may vary with environmental conditions that affect the value and cost of the goods and services that are exchanged. **Review ANIMATED TUTORIAL 43.2**

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is43

Go to LaunchPad at **macmillanhighered.com/launchpad** for additional resources, including LearningCurve Quizzes, Flashcards, and many other study and review resources.

44 Ecological Communities

This coffee plantation uses high-intensity sun cultivation techniques that increase crop yield at the expense of species diversity.

As we sip our morning cup of coffee, we can send silent thanks to *Coffea arabica*, the plant that yields 70 percent of our coffee beans. This understory shrub or small tree of tropical forests originated in the Ethiopian highlands as a natural hybrid between *C. canephora* ("robusta" coffee, from which we get the other 30 percent) and *C. eugenioides*, both of which hail from western and central Africa.

Coffea arabica has probably been cultivated in Ethiopia for 1,500 years, although the earliest written description of the plant dates to a tenth-century set of physician's notes. Molecular genetic evidence indicates that its cultivation spread to Yemen about 575 CE. Coffee was widely traded within the Muslim world, in spite of controversy there about the use of stimulants (see the opening story of Chapter 5), and the first coffeehouses were in Arabia. Arabs tried to corner the coffee market by banning exports of plants and fertile seeds, but the Dutch managed to smuggle some live plants out of Yemen. The beverage reached Italy in the 1600s and later spread through Europe.

By the 1700s, coffee cultivation had reached Southeast Asia and the Americas. Coffee is now one of the most valuable export commodities of the developing world, second only to oil. As demand has grown, worldwide coffee production has risen from about 5 million metric tons per year in the 1970s to about 7 million metric tons today, and coffee production employs some 25 million people in developing countries.

Coffee is grown mainly in tropical regions, using a variety of cultivation methods. The least intensive, traditional method is to plant coffee in the shade of undisturbed forests. This practice embeds coffee in natural forest communities, conserving most of their original plant and animal species. Medium-intensity shade cultivation replaces the forest with a low-diversity plantation of trees, under which the coffee is grown. High-intensity sun cultivation uses no shade trees; modern genetic cultivars are planted at high densities, heavily pruned, and subsidized with fertilizer, herbicides, and pesticides. Thus the more intensive methods increasingly replace natural communities with human-constructed communities that contain far fewer species. High-intensity methods increase coffee yields, but they sacrifice the greater biological diversity that traditional methods maintain, cause greater pollution, and require costly labor and chemicals.

Q Can we use principles of community ecology to improve methods of coffee cultivation?

You will find the answer to this question on page 914.

Communities Contain Species That Colonize and Persist

We saw in Chapter 43 that the abundances, distributions, and even phenotypes of species are affected by their interactions with other species. These interactions occur in the context of an ecological **community**—the group of species that occur together in a geographic area. Ecologists have practical reasons for wanting to know why communities contain the species that they do—we depend on them for all manner of natural resources and services. And like other dynamic systems, a community's components (species) and their interactions determine how well it functions. Understanding how communities are put together and how they work is essential to conserving them, as we will see.

Despite the simple definition of community, ecologists must make some practical decisions about how to draw the boundaries of a community, or about which species to include in a study. Sometimes there are obvious changes in habitat that indicate a community boundary. A pond, for example, defines a group of aquatic species that interact much more with one another than with terrestrial species outside the pond. Often ecologists choose to study a representative portion of a single habitat, such as a 10- × 10-meter area of forest. But even a small area may contain so many species that ecologists decide to focus their attention on subsets of species. Those subsets may be defined taxonomically, by a habitat or location, by some character traits, or by the types of interactions the species engage in. Hence biologists may speak of the bird community of a certain island, the *Daphnia* community of rock pools (see Figure 42.10), the microbial community of the human gut, or the community of grazing herbivores in the marine rocky intertidal zone.

Regardless of how we delineate them, communities can be characterized in terms of which species they contain, or their **species composition**. Communities are also characterized by how many species they contain, and by how abundant each species is. These three attributes of communities— species composition, the number of species, and how abundant each species is—are components of **community structure**.

The mix of species in a community is determined by the same factors that explain the distributions of individual species; as we saw in Concept 42.1, a species can occur in a location only if it is able to colonize that location and persist there. Species may fail to colonize a community, or be lost from it, for any of several reasons. Individuals of a species may simply never reach the location—consider how few dispersers from a mainland are likely to reach a remote island before they perish! Once colonists have arrived, they may be unable to tolerate the environmental conditions, or a resource or an essential mutualistic partner may be missing. Species may be excluded by competitors, predators, or pathogens. Finally, some species may go locally extinct because their populations are so small that, by chance, all the individuals die at some point without reproducing (see Concept 42.5).

> **LINK**
>
> The abundances of the species that persist in a community are determined by the population-level processes discussed in **Chapters 42 and 43**

We can think of communities as being assembled through such gains and losses of individual species. The processes of community assembly are well illustrated by Krakatau, a small (17 km^2) volcanic island in the Sunda Strait of Indonesia (see Figure 44.10). The volcano exploded in 1883, sterilizing what was left of the island and covering it with a thick layer of ash. Scientists quickly mounted expeditions to observe the return of life to the island, and they have surveyed it periodically ever since. By 1886, seeds of 10 plant species that grow on nearby tropical beaches had floated to Krakatau (**FIGURE 44.1A**), and wind had brought seeds or spores of 14 additional species of grasses and ferns. Tree seeds had arrived on the wind by the 1920s. As the forest canopy closed in, some pioneering plant species that require high levels of light disappeared from Krakatau's now-shady interior. Once forests developed, fruit-eating birds and bats began to be attracted to the island, bringing new animal-dispersed seeds with them.

FIGURE 44.1 Vegetation Recolonized Krakatau (A) Beach-adapted plants such as *Ipomoea pes-caprae* (beach morning glory) were among the first organisms to take hold on the denuded island. (B) One century after a massive eruption left Krakatau an ash-covered shell, vegetation once again covers much of the island.

(A)

(B)

Now, more than a century after Krakatau exploded, the island appears from afar to be covered by stable plant communities (**FIGURE 44.1B**). But a closer look reveals that their species compositions continue to change as new species colonize and earlier colonists go extinct.

CHECKpoint   CONCEPT **44.1**

✓ Describe at least two ways in which ecologists decide which species to include in a community study.

✓ Describe the processes that are involved in community assembly.

✓ As new species have colonized Krakatau, the densities of some existing species have changed, even though these species have not gone extinct. Why? (Hint: see Concept 43.2.)

Krakatau provides a dramatic illustration of a general pattern: the species composition of communities changes over time. Species composition also changes over space. In spite of this turnover of species in space and time, are there general rules that govern which species we find where and when?

CONCEPT **44.2**   Communities Change over Space and Time

Ecologists have noted repeated patterns of spatial and temporal change, or **turnover**, in species composition. These patterns demonstrate that the species we find in one place and time are not a random subset of those that potentially could be there. Let's take a closer look at these patterns and what they mean.

Species composition varies along environmental gradients

We saw in Chapter 41 that physical conditions on Earth change over long distances—consider how temperature changes with latitude, or pressure with ocean depth. Physical conditions can also change on small spatial scales (see Concept 41.1). If we climb a steep tropical mountain, for example, we traverse gradients in temperature and moisture, and because different species have different tolerance limits, we encounter constantly changing plant communities. In coffee-growing regions, we would find coffee plantations between about 1,300 and 1,500 meters in elevation, where coffee grows best—reflecting its evolutionary origin in African highlands.

Ecologists have characterized how plant communities change along environmental gradients on Krakatau. Environments there range from shoreline habitat that is buffeted by wind and waves to inland habitat that varies in elevation from sea level to 800 meters at the highest point, and from gentle ash-covered slopes to steep rocky cliffs. The composition of Krakatau's plant communities is similar in locations with similar conditions and different in locations with different conditions. These spatial changes are easy to see from afar because the species in different habitats tend to look different (compare Figure 44.1A,B), just as

vegetation in the tropical rainforest biome differs from vegetation in tropical savanna (see Concept 41.3). Sandy beaches are dominated by low-growing herbs and vines, bordered inland by a fringe of short trees and shrubs; gentle inland slopes are dominated by taller trees with an understory of vines and ferns, and the summit, often in the clouds, supports a thick growth of short, moss-covered trees.

Spatial turnover in the species composition of communities often signals hard-to-see gradients. The rock outcrops that provide habitat for Edith's checkerspot butterfly near San Francisco (see Figure 42.1), for example, contain soils derived from serpentine rock, which is unusually high in heavy metals such as chromium and nickel. If we measure off a transect—a straight line used for ecological surveys—running from a non-serpentine to a serpentine area and identify the plants that occur in evenly spaced samples along it, we will find that several species drop out and new ones appear partway along the transect, where heavy-metal concentrations jump (**FIGURE 44.2**).

The early naturalist–explorers who documented associations of climate and vegetation—the biomes described in Concept 41.3—likewise documented associations of particular animal species with particular vegetation. Some animal species, such as Edith's checkerspot butterfly, are found in certain plant communities because the plants they eat grow there. In other cases, animals are associated with particular plant communities because plants modify physical conditions such as temperature and humidity and because plants contribute to **habitat structure**: the horizontal and vertical distribution of objects in the habitat. The vertical distribution of leaves and the density, size, and surface texture of plant stems influence which species are present by determining the effectiveness of their methods for obtaining food, avoiding predators, building nests, and so on. Morphological, physiological, and behavioral traits of animals adapt them for the structure of the habitats with which they are associated (**FIGURE 44.3**).

Several processes cause communities to change over time

Species composition changes not only over space, but also over time. Krakatau is not unique in this regard—all communities, not just those in the early stages of assembly, are dynamic. Over longer periods, of course, the species composition of communities reflects evolution. But species turnover also occurs over much shorter periods. Three major processes contribute to this dynamism: extinction and colonization, disturbance, and climate change.

EXTINCTION AND COLONIZATION   Ecological communities are likely to change even in a constant environment because species may go locally extinct and be replaced by new species that arrive from time to time. As we saw in Concept 44.1, there are several reasons why a species may go locally extinct. Dispersal is an ongoing process that delivers a constant influx of new individuals to all but the most isolated locations. When individuals arrive at a location that already contains a population of their species, they add to its size (and genetic diversity); when those individuals are members of a new species,
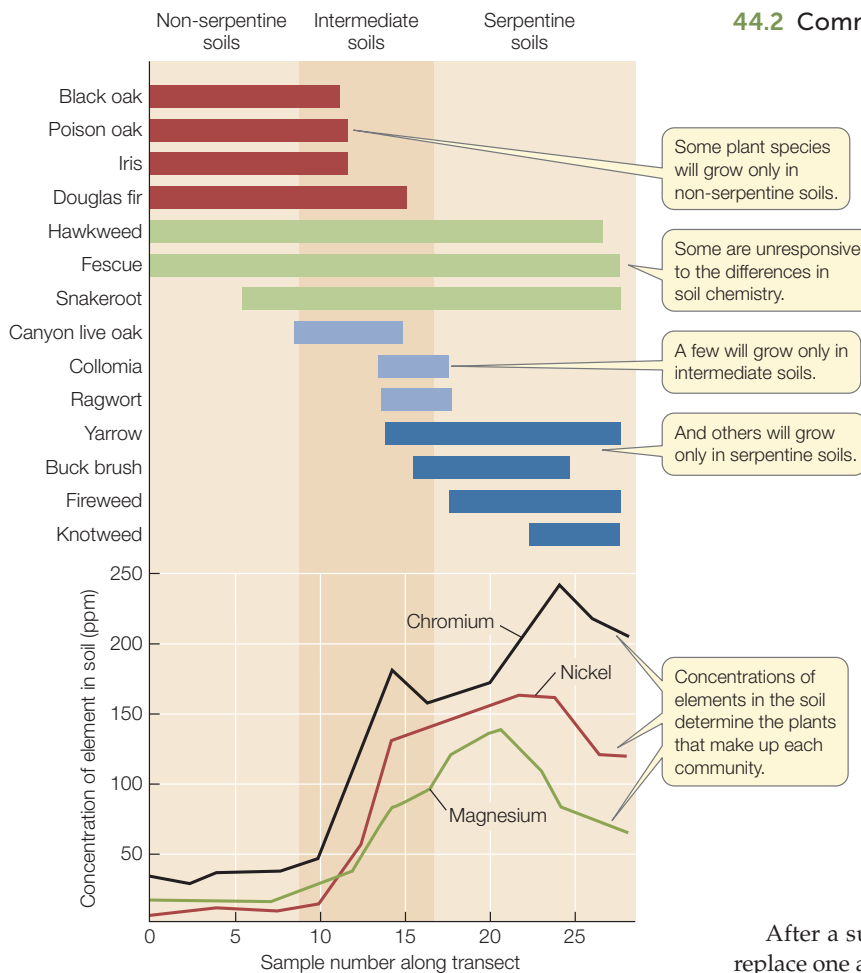
FIGURE 44.2 **Change in Species Composition along an Environmental Gradient** Ecologists sampled plant species along a transect running from non-serpentine to serpentine soils. They found that as concentrations of heavy metals in the soil changed, some species dropped out of the plant community and new ones appeared. Bars indicate samples in which a given species was present.

they can establish a new population and add another species to the community.

DISTURBANCE An event that causes sudden environmental changes—referred to as a **disturbance**—can change the species composition of a community. Examples of such events are volcanic eruptions, wildfires, hurricanes, landslides, and human activities. Such disturbances can wipe out some or all of the species in communities and alter the physical environment. Sudden change can also occur without the destruction of a resident community. New environments can appear, for example, when a glacier melts away, a depression fills with rainwater—or a large mammal deposits dung.

After a sudden change in the environment, species often replace one another in a relatively predictable sequence called **succession**. A fresh pile of elephant dung, for example, is colonized by a predictable sequence of dung beetle species (family Scarabidae). These animals feed on the dung and lay their eggs in it. Some species typically arrive early and are then replaced by later arrivals (**FIGURE 44.4**).

Go to MEDIA CLIP 44.1
Dung Beetles
PoL2e.com/mc44.1

Several factors are responsible for successional sequence. One key factor is variation in the colonizing ability of species. The first species to arrive in newly available habitat are good dispersers. The early-arriving dung beetles tend to be strong fliers with excellent senses of smell, or are "hitchhikers" that ride on dung-producing animals and colonize dung as it is produced. Similarly, the first plant species on Krakatau were those with seeds that are readily dispersed by water or wind. A second factor is that environmental conditions in the disturbed site change over time. Early-arriving dung beetles must cope
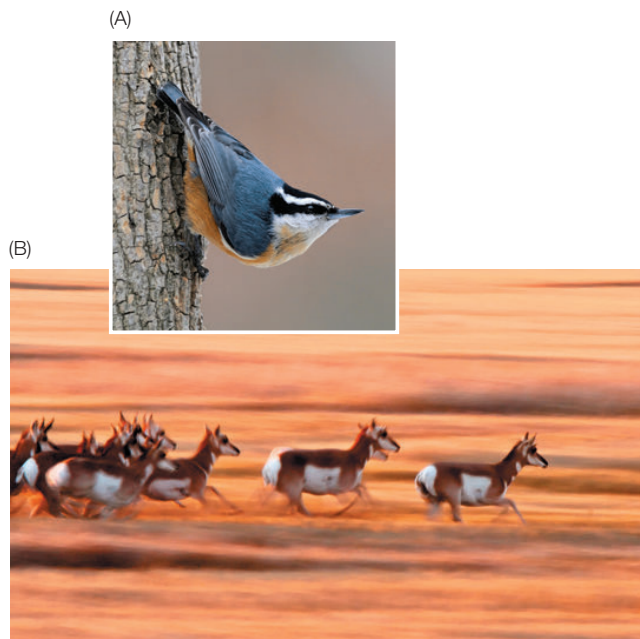
FIGURE 44.3 **Many Animals Are Associated with Habitats of a Particular Structure** (A) The legs and feet of the red-breasted nuthatch (*Sitta canadensis*) allow it to cling to the trunks, branches, and twigs of trees as it gleans small arthropods and seeds. It prefers conifer forests. (B) Pronghorn (*Antilocapra americana*), the fastest North American land mammal, uses speed to escape predators. It prefers open, flat habitats without obstacles to movement.

Rollers
Dweller
Dung
Tunneler

🟩	Rollers
🟥	Dwellers
🟦	Tunnelers

Species

Copris repertus
Drepanocerus setosus
Liatongus indicus
Sisyphus neglectus
Onitis subopacus
Onthophagus cervus
Onthophagus rectecormutus
Onthophagus falsus
Sisyphus longipes
Copris davisoni
Oniticellus cinctus
Copris signatus
Onitis siva

1   3   5   7   14   21
Dung age (days)
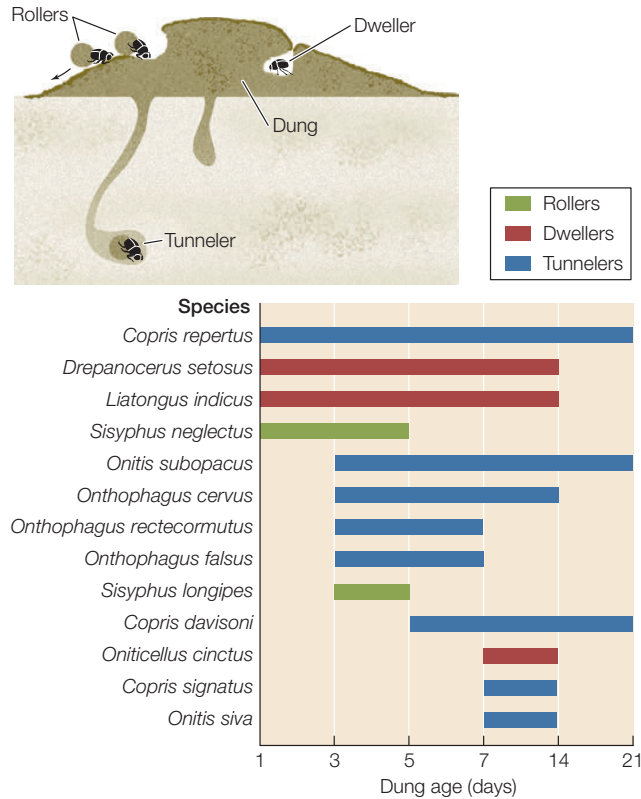
FIGURE 44.4 Dung Beetle Species Composition Changes over Time The Indian dung beetles represented in this diagram all consume elephant dung. Each bar indicates the time during which the species it represents is present. Whereas *Copris repertus* (top) colonizes newly produced dung and is still present 3 weeks later, other species enter and drop out of the community at various times, depending on their adaptations for finding dung and for using dung of different ages. Thus the composition of the beetle community changes over time. Notice also the different ways in which dung is used: some species roll balls of dung away and then bury them, some dwell in the dung, and some take bits of dung into chambers they dig under the dung pile.

environment that has changed not only because of physical processes, but also because of the activities of early-arriving species. The seeds of plants that colonized Krakatau after the forest canopy had closed had to germinate in the shade of other plants and compete successfully for water and nutrients in soils that earlier colonists had modified.

🔲 **Go to ANIMATED TUTORIAL 44.1**
Succession after Glacial Retreat
PoL2e.com/at44.1

When a disturbance damages or destroys a preexisting community, succession often leads in the end to a community that resembles the original one. On Krakatau, the tropical forests destroyed by the volcanic eruption eventually came back. Ecologists now realize, however, that a return to something like the original community is far from guaranteed. Instead, some disturbances may push the system past a threshold, or tipping point, so that there is an abrupt **ecological transition** to a distinctly different community. The

with wet conditions, whereas late-arriving species face a drier environment; pioneering species on Krakatau had to tolerate full sun and volcanic ash. Later-arriving species experience an

45°N
40°N
35°N

(A) 14,000 years ago

(B) Present

⬜	Desert
🟩	Grassland/shrubland
🟨	Piñon–juniper woodlands
🟩	Ponderosa pine forest
🟥	Mixed-conifer forest
🟦	Spruce–fir forest
🟦	Alpine
⬜	Pluvial lakes
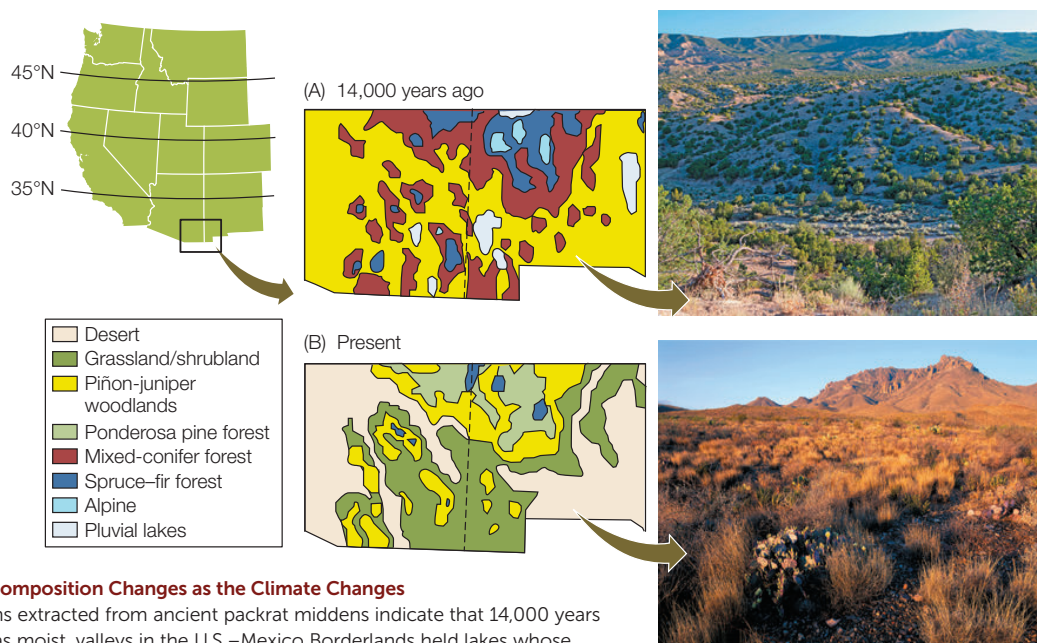
FIGURE 44.5 Species Composition Changes as the Climate Changes
(A) Fossilized plant remains extracted from ancient packrat middens indicate that 14,000 years ago, when the climate was moist, valleys in the U.S.–Mexico Borderlands held lakes whose shores were clothed in piñon–juniper woodland. (B) In today's more arid climate, the lakes have dried up and the woodland has given way to desert grassland—and more recently to shrubland, following human disturbance (see the opening story of Chapter 41).

system may then stay in this alternative state and not return to its original state, even when the factor that caused the disturbance is removed. For example, intensive cattle grazing led to an abrupt conversion of grasslands to shrublands in the U.S.–Mexico Borderlands (see the opening story of Chapter 41). Grasslands have not returned, even in places where cattle have been removed.

CLIMATE CHANGE   A final cause of temporal variation in communities is climate change. As physical conditions change, the geographic ranges of species necessarily change with them. One way in which ecologists have been able to reconstruct the history of such changes is by analyzing fossilized remains of plants found in middens—refuse piles—left by packrats (*Neotoma* spp.). These rodents bring plant material into their nests. When the material is preserved, it provides a record of the vegetation that was present when the animals were alive. By using carbon-14 (see Figure 18.1) to date packrat-midden fossils, biologists have been able to show how plant communities of the U.S.–Mexico Borderlands changed over the last 14,000 years as the climate became drier following the end of the last ice age (**FIGURE 44.5**).

> ### CHECKpoint   CONCEPT **44.2**
>
> ✓ Why are animal species often associated with particular plant communities?
>
> ✓ How does succession differ from species turnover that results from ongoing colonization and extinction?
>
> ✓ Give an example of an environmental gradient that you have observed yourself, explaining what factors change along it and what visible changes you see in the species present.

We saw in Concept 44.1 that species composition, species number, and species abundances all are aspects of community structure. How do these attributes affect the way a community functions?

> ### CONCEPT **44.3**   Community Structure Affects Community Function

It is useful to think of an ecological community as a dynamic system (see Concept 1.2) similar to a human-made machine, with inputs, "internal workings," and outputs. The inputs to a community are energy and materials from the surrounding abiotic environment. The "internal workings" of the community—the metabolism of its individuals, the dynamics of its populations, and the interactions among its species—produce an output of transformed energy and materials.

Energy flux is a critical aspect of community function

If we think of a community as a machine, we can measure **community function** as we would the function of a machine,

in terms of its inputs and outputs. Community function is measured by the amount of energy or matter that moves into and out of the community per unit of time. This **flux**, or flow rate, reflects an exchange between the community and its environment. We can also measure function for particular parts of the community. Wolves, for example, convert elk into new wolves—a conversion of primary consumers (an input) into secondary consumers (an output). The output of seeds and fruits by most flowering plants, including *Coffea arabica*, responds to visits by insect pollinators, a type of input. Retention of nutrients within an ecosystem is a function of the community's decomposers—the recyclers. Many community outputs affect not only species in the community, but also organisms in other ecosystems, including humans. These outputs represent "goods" and "services," which we will discuss in Concept 44.5.

> ### LINK
>
> The role of decomposers in recycling nutrients—particularly nitrogen—is described in **Concept 45.3**

To develop this idea of community function, let's first focus on how energy moves through communities. (The flux of matter through communities is coupled with that of energy, as will become more apparent in Chapter 45.) **FIGURE 44.6** shows, in simplified form, the flux of energy through the most common type of food web, in which the primary producers are photosynthetic organisms that use the sun's energy. The pattern of energy flux is similar in those rare communities (such as those in deep-sea hydrothermal vents) in which primary producers are chemoautotrophs.

Energy enters communities through primary producers; the total amount of energy that they capture and convert to chemical energy per unit of time is called **gross primary productivity** (**GPP**). Not all of the captured energy is available to primary consumers because primary producers use some of it to fuel cellular respiration and other catabolic processes. Ultimately this energy is lost as heat. The amount of energy stored in primary producer tissues per unit of time is called **net primary productivity** (**NPP**). GPP and NPP reflect two aspects of primary producer function: the rate at which primary producers capture energy, and the rate at which they convert it to forms available to other trophic levels. GPP can be measured from the rate with which primary producers take up carbon dioxide during photosynthesis, and NPP from the rate of CO_2 uptake minus its rate of release during respiration. New technologies allow us to measure such gas exchanges in nature, but it is often more convenient to use change in the **biomass** of primary producers (the dry mass of their tissues) per unit of time as an approximation for NPP.

The percentage of the energy contained in the biomass of one trophic level that is incorporated into biomass in the next trophic level is the **ecological efficiency** of energy transfer between those levels. Ecological efficiency of energy transfer averages only about 10 percent—the biomass of one trophic level is about 10 percent of that in the next lower level.
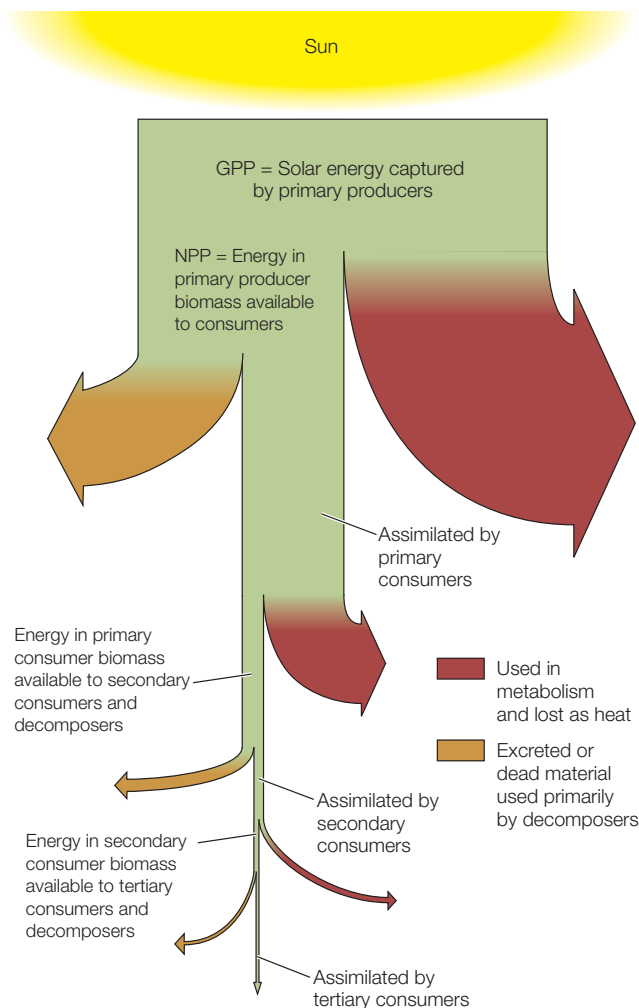
FIGURE 44.6 Energy Flow through Ecological Communities On average, the total amount of energy incorporated into the biomass of a trophic level per unit of time is about one-tenth that of the level it consumes. Of the 90 percent of energy *not* available to the next trophic level, some is waste or dead material used by decomposers, and some is lost during metabolism as heat.

Go to ACTIVITY 44.1
Energy Flow through an Ecological Community
PoL2e.com/ac44.1

LINK

Food-web structure is discussed in **Concept 43.3**; see especially **Table 43.1** and **Figure 43.6**. You can review photosynthesis and cellular respiration in **Chapter 6**; see especially **Concepts 6.2 and 6.5** and **Figure 6.14**

Just as NPP measures primary producer function, the biomass produced by primary consumers measures how well they function to convert primary producer tissue into their own tissue, and so on for secondary and tertiary consumers. The low efficiency of these energy transfers limits the number of trophic levels found

in a community—few contain more than four—because fewer and fewer individuals can be supported as one moves to higher trophic levels. This is one reason we sometimes are urged to "eat low on the food chain": more humans can be fed if we act as primary consumers than if we act as secondary consumers.

There are several reasons for low ecological efficiency. First, not all the biomass at one trophic level is ingested by the next one; for example, herbivores routinely miss hard-to-get plant parts or avoid eating plants that are chemically well defended. Second, some ingested matter is indigestible and is excreted as waste. Tree bark, for example, contains lignin and cellulose, which most herbivores cannot digest. Finally, and most important, consumers as well as primary producers use much of the energy they assimilate (the digested portion of what they ingest) to fuel aspects of their own metabolism that do not add new biomass through growth or reproduction. Energy used in metabolism does the work of assembling and disassembling biological molecules, moving the body, and so on, and heat is generated in the process. Except for the energy stored in the chemical bonds of assembled molecules, none of the energy used in metabolism is available to the next trophic level.

Community function is affected by species diversity

The structure of a community influences how much energy enters it and how much is transferred through the food web because each species has a unique **niche** that determines its function in the community. The niche is a central ecological concept with two important meanings. The first meaning refers to the physical and biological environments in which a species has a positive per capita growth rate—these are the environments where we expect to find that species. Figure 42.7 shows, for example, that the niche of the beetle *Rhyzopertha dominica* includes drier and warmer conditions than that of *Sitophilus oryzae*. Physical tolerances do not completely define a species' niche, however, because the biological environment—the presence of competitors, predators, and so on—also affects population growth. Figure 43.4 shows, for example, that low intertidal zones are included in the niche of stellate barnacles only where rock barnacles are absent.

A species' niche also refers to what the species does in the community—its functional role, or "profession." This role is largely defined by how it affects other species—what resources it uses and makes unavailable to other species, when and where it obtains them, how efficiently it does so, what it produces from them that other species can use, and whether it affects the physical environment. Many of these effects, but not all of them, are determined by the species' trophic interactions.

Once we think of functional roles, we can begin to see that community structure affects community function. Loss of wolves from Yellowstone National Park in the 1920s, for example, decreased the flux of energy from elk to secondary consumers and increased energy flux from aspen and willow to primary consumers (see Figures 43.6 and 43.7). But how do we go from specific examples like this to a more general understanding of how structure affects function? Ecologists have begun to tackle this problem by looking for broad patterns in structure–function

Community A

Community A is less diverse than community B because it contains three equally abundant species rather than four.

Community B

With four equally abundant species, community B is the most diverse.

Community C

Community C is less diverse than community B because it has an uneven distribution of the four species.
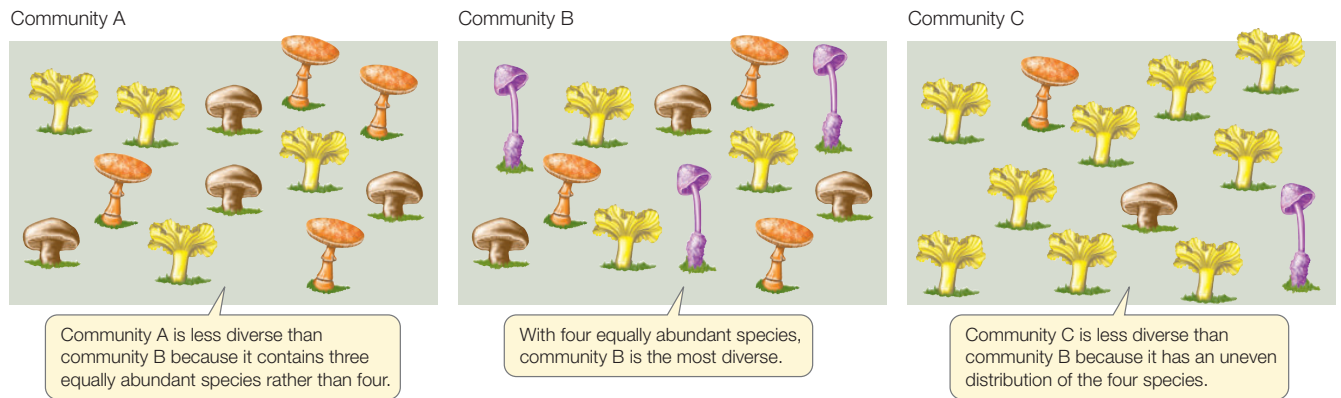
FIGURE 44.7 Species Richness and Species Evenness Contribute to Diversity   These hypothetical communities of fungi (mushrooms) are all the same size (12 individuals), but they differ in species richness (3 versus 4 species) and species evenness, both of which affect diversity.

Go to ACTIVITY 44.2 Measures of Species Diversity
PoL2e.com/ac44.2

relationships across communities. They have discovered that one important aspect of community structure—**species diversity**—influences community function.

Species diversity has two components, illustrated in **FIGURE 44.7**. One is simply the number of species in the community, called **species richness**. A community that contains more species is more diverse, all else being equal. The second component is how similar the species are in their abundances, a property called **species evenness**. A community that has four equally abundant species is more diverse than one in which 75 percent of the individuals belong to one species and the remaining 25 percent are spread among three other species. This second component may not be intuitive until we understand how it affects communities: the properties of a community with a few abundant species will be defined mostly by those species, whereas the properties of a community with equally abundant species will reflect the influence of all of them. Ecologists sometimes use species richness as a simple measure of diversity, but often prefer to use a mathematical diversity index that incorporates both richness and evenness.

Community outputs often vary with species diversity. In a long-term study of prairie plant communities, for instance, David Tilman and his colleagues at the University of Minnesota cleared outdoor plots into which they planted up to 32 native prairie species. After the plantings had reached maturity, they harvested the plants and measured their aboveground biomass. They found that this measure of NPP increased as the species richness of a plot increased (**FIGURE 44.8A**).

Two hypotheses have been proposed for such an increase. First, the relationship may come from "sampling": communities with more species may be more likely, just by chance, to include some "superspecies" that are exceptionally good at predation, or at photosynthesizing, or at whatever they do, and so have a strong influence on total community output.

(A)

Productivity increases, up to a point, when more species are present.

(B)

Productivity increases, up to a point, when more functional groups are present, filling more niches.
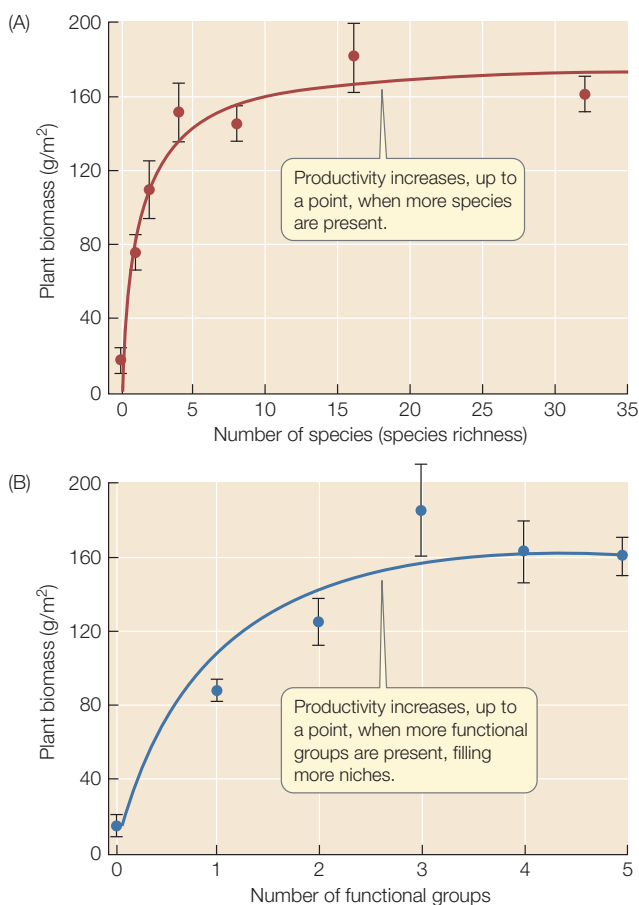
FIGURE 44.8 Species Richness and Number of Functional Groups Affect Primary Productivity   (A) In 289 experimental prairie plots, NPP (measured as aboveground plant biomass produced per square meter per year) increased with species richness. (B) When the researchers separated out the effects of the number of functional groups from those of species richness, they found that the number of functional groups was the key influence on production. These results suggest that primary productivity is enhanced by a greater variety of species with complementary niches. Error bars indicate $\pm$ 1 standard error of the mean. See Appendix B for review of statistical concepts.

Alternatively, the relationship may come from "niche complementarity": differences (often subtle) among species in how efficiently they use alternative resources under different conditions. (This idea is related to resource partitioning; see Figure 43.5). For example, "C_4" grasses, which have a special type of photosynthesis, grow better than "C_3" grasses in warm conditions but worse in cool conditions; symbiotic nitrogen-fixing bacteria give legumes a boost in nutrient-poor soils but are a drain in nutrient-rich soils; shrubs and trees can tap the nutrients and water in deeper soil layers than can herbaceous species. Species-rich communities may be more likely than species-poor communities to contain representatives of several such complementary "functional groups" that together make more complete use of available resources. (To see this idea, consider how total consumption of seed resources in Figure 43.5 would change if Species B were removed from the hypothetical community.) Tilman and colleagues could test these two hypotheses because they planted some species-rich plots with multiple species from only one functional group, and others with species from several functional groups. They found that NPP increased with the number of functional groups, and that the number of species within functional groups had no additional effect on NPP (**FIGURE 44.8B**). This result suggested that niche complementarity caused the relationship between species richness and NPP.

> **LINK**
>
> Some ways in which differences in resource use evolve and promote species coexistence are described in **Concepts 43.2 and 43.4**

NPP is not the only measure of community function that increases with species diversity. Control of agricultural pests by natural predators and parasites is enhanced when multiple crops are planted together or when a diverse natural plant community borders agricultural fields. And as we'll see at the end of this chapter, two recent studies of coffee pollination found that the production of seeds was higher, and pollination rates were less variable between years, in plantations that were close to natural tropical forests, which harbor a great diversity of coffee-visiting bee species.

> ### CHECKpoint CONCEPT 44.3
>
> ✓ What is the major source of energy for communities, and how does it enter them?
>
> ✓ What is ecological efficiency, and how does it influence the number of trophic levels in a community?
>
> ✓ Discuss parallels between the two components of species diversity and components of cultural and ethnic diversity in human societies.
>
> ✓ What would Tilman and colleagues have seen if "sampling" explained the relationship between species richness and NPP?

Species diversity is an important characteristic of communities because it affects how those communities function as ecological systems. But what factors determine species diversity in a particular community?

> ### CONCEPT 44.4 Diversity Patterns Provide Clues to What Determines Diversity

Species diversity is not uniform around the world. Geographic patterns in diversity shed light on factors that affect diversity by modifying the balance between processes that add species to and remove species from communities.

Species richness varies with latitude

When the German naturalist Alexander von Humboldt traveled around Central and South America, Europe, and Asia two centuries ago, he noted that "the nearer we approach the tropics, the greater the … variety of structure … of organic life." This recognition that species richness increases toward the equator has been amply confirmed since then. A 2-hectare plot of tropical forest in Malaysia, for example, can contain 227 tree species, whereas an equivalent plot of temperate forest in Michigan contains only 10 to 15. There are 56 bird species that breed in Greenland, 105 in New York State, 469 in Guatemala, and 1,395 in Colombia. And although some taxa appear not to follow the pattern—of some 20,000 known bee species on Earth, for instance, about half are found in temperate regions and half in the tropics—many other taxa do (**FIGURE 44.9**).

What is it about the tropics that supports such diversity? Over long time spans, climate conditions have been more stable in the tropics than in temperate regions. The tropics were never subjected to the dramatic glacial advances that caused massive shifts in the geographic ranges of species at higher latitudes and led to many extinctions. Tropical communities are certainly dynamic, and they are strongly influenced by disturbances (such as the death and fall of individual trees in rainforests), but the absence of disturbance at large spatial scales may have allowed these communities to retain more of their species than temperate communities, leaving them with higher species richness today.

We also know that climate changes with latitude. The tropics receive abundant solar energy input, which makes them warm and wet (see Concept 41.2). These conditions promote rapid growth of primary producers, so NPP, like diversity, increases toward the equator. High NPP can enhance diversity (as well as be enhanced by diversity; see Concept 44.3) if greater energy input into food webs allows species to maintain large population sizes, even if they are more specialized in their use of resources or habitats. In this way, greater energy flow through tropical communities could facilitate the coexistence of a greater number of species with narrow, specialized niches.

Variation in habitat structure could interact with greater niche specialization to amplify tropical diversity. In general, diversity is higher in more structurally complex habitats. Bird species diversity, for example, increases with the diversity of foliage height in deciduous forests. If tropical species have
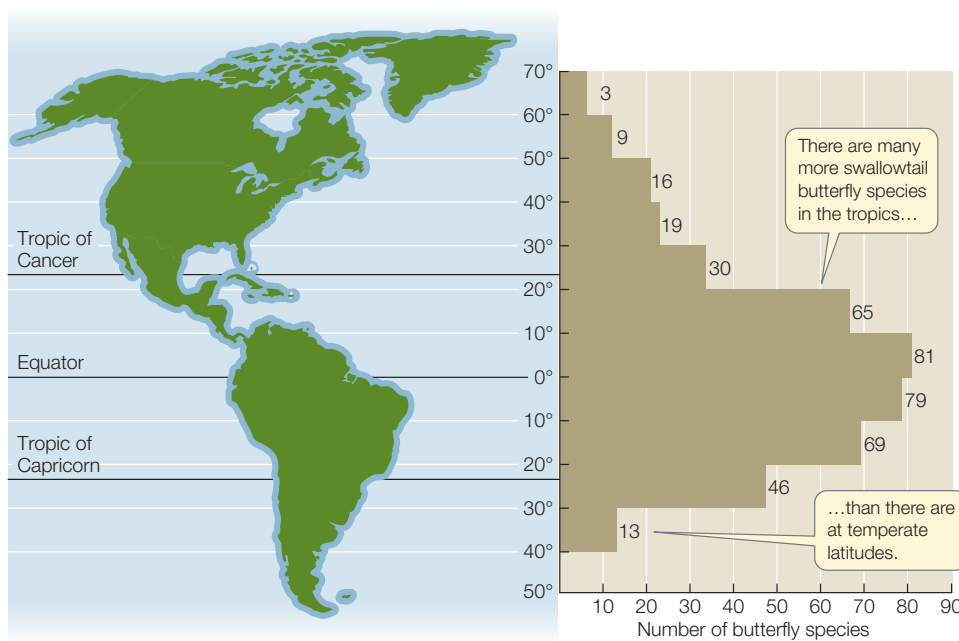
FIGURE 44.9 Species Richness Increases toward the Equator Among swallowtail butterflies (Papilionidae), species richness decreases with latitude both north and south of the equator. Similar latitudinal gradients of species richness have been observed in many other taxa.

more specialized habitat requirements, and if tropical vegetation is more structurally complex by virtue of greater plant species richness, then complex habitat structure and productivity may interact to increase tropical diversity.

Ecologists still have much to learn about the relative contributions of these various factors to the puzzle of tropical diversity, but the research stimulated by that puzzle has demonstrated that disturbance patterns, productivity, and habitat structure all affect species diversity.

Species richness varies with the size and isolation of oceanic islands

The numbers of species found on oceanic islands exhibit regular patterns that have long fascinated ecologists (**FIGURE**

44.10). First of all, species richness is greater on large than on small islands. And second, species richness is greater on islands near a mainland than on more distant islands. What can explain these differences?

As we saw in the case of Krakatau, communities are assembled by colonization, along with occasional extinctions. Just as a population reaches an equilibrium size when additions (births) and losses (deaths) are equal, it seems plausible that species richness on an island might ultimately represent an equilibrium between the rate at which new species colonize
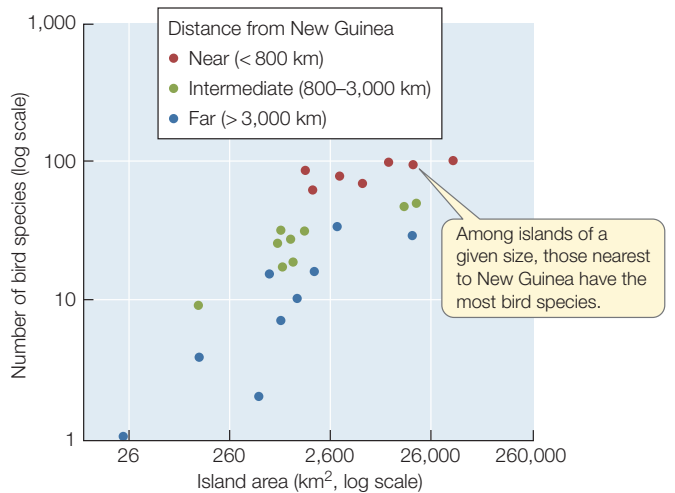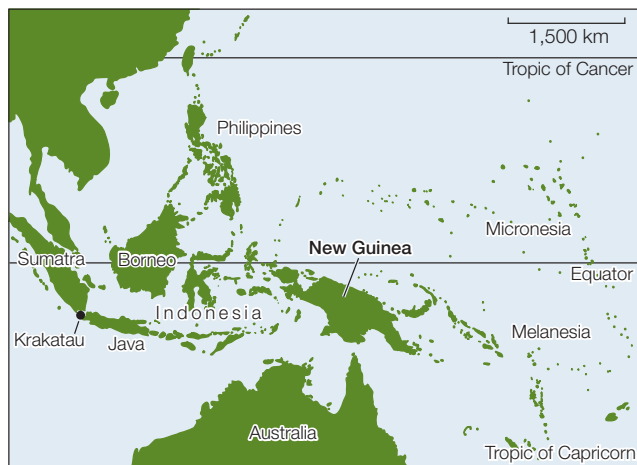
FIGURE 44.10 Area and Isolation Influence Species Richness on Islands On islands in the tropical eastern Pacific (left), species richness increases with island area and decreases with distance from New Guinea, the major source of colonists (right).
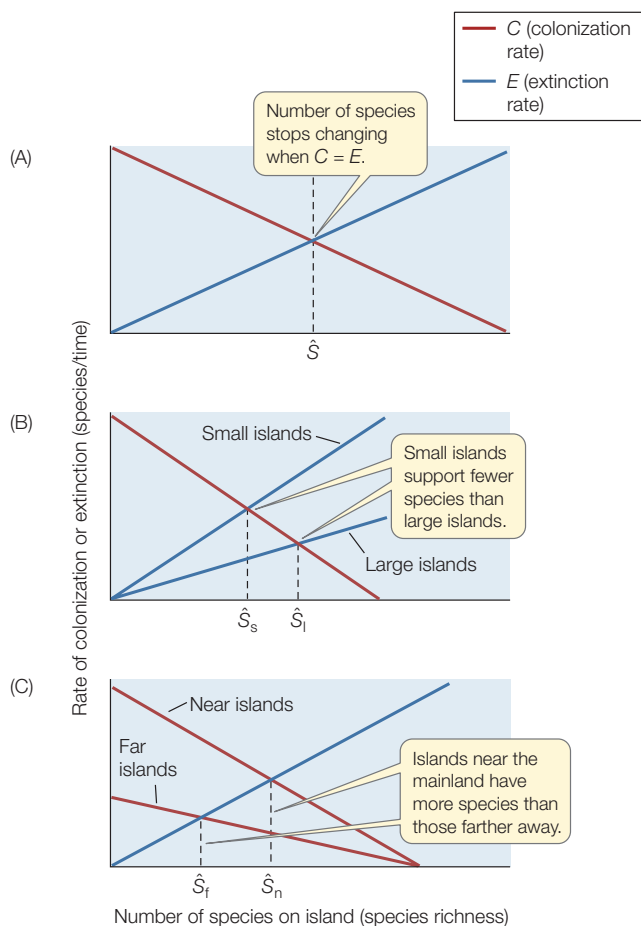
FIGURE 44.11 **MacArthur and Wilson's Theory of Island Biogeography**   (A) Species richness reaches a stable equilibrium ($\hat{S}$) when the colonization rate equals the extinction rate. (B) Smaller islands have larger per-species extinction rates, and hence lower equilibrium species richness. (C) Islands more distant from the mainland have lower colonization rates, and hence lower equilibrium species richness.

and the rate at which resident species go extinct. This idea forms the basis for the theory of **island biogeography**, proposed in 1963 by Robert H. MacArthur and Edward O. Wilson. The theory can be summarized as follows:

- An oceanic island gains species only if they colonize from elsewhere—usually from nearby islands or continents, whose communities make up the species pool of potential colonists.

- The rate at which new species arrive on an island declines as the island fills with species. At first, every immigrant represents a species new to the island, but as the island fills up, more and more of the arriving individuals represent species already resident there. (If all species in the mainland species pool were present on the island, the colonization rate would be zero.)

- The overall rate at which species are lost from the island—the extinction rate—increases as the island fills with species. In any time period, each species has some chance of going extinct from various causes, and as the number of species increases, so does the overall number of species that go extinct per unit of time.

- The number of species on an island—its species richness—stops changing if the colonization rate equals the extinction rate. When we plot colonization and extinction rates on a graph, this equilibrium species richness is represented by the point at which the two lines cross, $\hat{S}$ (**FIGURE 44.11A**).

- Population sizes will decline as island size decreases, and since small populations are more at risk of extinction, the extinction rate for small islands should rise more steeply than that of large islands as a function of total species on the islands. Thus the equilibrium species richness should be greater on large than on small islands (**FIGURE 44.11B**).

- Similarly, fewer wind- and water-borne seeds, and fewer dispersing animals, will encounter a distant island than one closer to the mainland species pool. As a result, the colonization rate, and thus the equilibrium species richness, will be higher on close islands than on distant ones (**FIGURE 44.11C**).

The theory of island biogeography successfully explains the patterns of species richness found not only on oceanic islands, but also on "islands" of one habitat type surrounded by a "sea" of a different habitat type. It has proved to be one of the most successful explanatory theories in ecology (**FIGURE 44.12**).

Go to ANIMATED TUTORIAL 44.2
Island Biogeography Simulation
PoL2e.com/at44.2

CHECKpoint   CONCEPT **44.4**

✓ Describe three factors that may contribute to the high species richness of tropical rainforests.

✓ Tropical coral reef communities are among the most species-rich of any on Earth. Speculate on factors that might explain their diversity.

✓ What do Figures 44.11B and C tell you about the predicted rate of change in species composition (species turnover rate) at equilibrium on small versus large islands and on islands distant from versus close to a mainland? (Hint: think of turnover rate as the number of new species that replace previous species in a period of time.)

Quantitative studies of species richness and the theory of island biogeography have contributed greatly to our knowledge of the structure and function of ecological communities. We will now turn to some ways in which this knowledge can be applied to conserving and restoring these communities.

INVESTIGATION

FIGURE 44.12 The Theory of Island Biogeography Can Be Tested
By experimentally defaunating (removing all the arthropods from) four small mangrove islands of equal size but at different distances from the mainland, Simberloff and Wilson were able to observe the process of recolonization and compare the results with the predictions of island biogeography theory.[a] See Apply the Concept on p. 910 for a test of a possible alternative explanation of the species diversity on the mangrove islands.

HYPOTHESIS

The number of species on an island before it is experimentally defaunated will decrease with distance from a mainland source of colonists, and this number will be reestablished after the island has been recolonized.

METHOD

1. Take a census of the terrestrial arthropod species on four small mangrove islands of equal size (11–12 m diameter) but at different distances from a mainland source of colonists.
2. Erect scaffolding and tent the islands. Fumigate with methyl bromide (a chemical that kills arthropods but does not harm plants).

3. Remove tenting. Monitor recolonization for the following 2 years, periodically taking a census of arthropod species.

RESULTS

The number of species present before defaunation decreased with distance from the mainland. Two years after defaunation, each island had about the same number of species it had before the experiment.

The number of species present before defaunation (dots) decreased with distance from the mainland (meters).

After 2 years, species richness on each island was close to what it was before defaunation.

Closest to mainland

Farthest from mainland
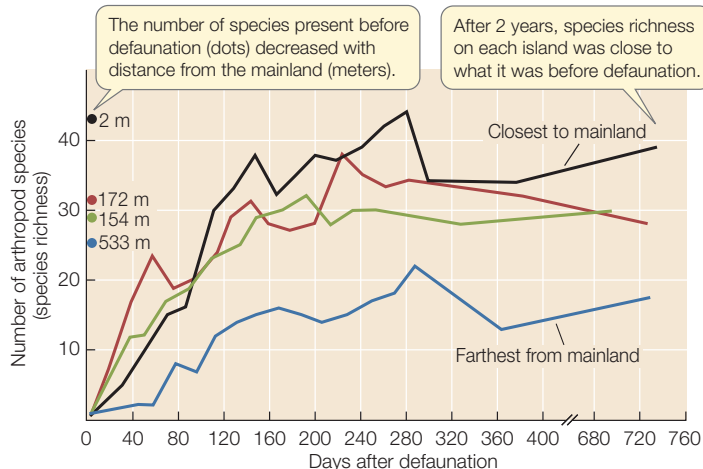
CONCLUSION

The results support predictions of island biogeography theory.

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]D. S. Simberloff and E. O. Wilson. 1970. *Ecology* 51(5): 934–937.

Community Ecology Suggests Strategies for Conserving Community Function

The ability of an ecological community to provide humans with critical goods and services often depends on its diversity. How can we use this knowledge to conserve community function?

Ecological communities provide humans with goods and services

Humans, like all species, depend on the ecological interactions that occur in communities and the interactions between communities and their physical environment. Although this seems obvious today, it was only in 1970 that ecosystems were first said to provide people with "goods and services." The goods include food, clean water, clean air, building materials, and fuel; the services include flood control, soil stabilization, pollination of plants, and climate regulation. Because many of these goods and services involve exchanges between communities and the abiotic environment, they are called **ecosystem services**; a short list of examples is given in **TABLE 44.1**.

Goods that are of direct biological origin are obvious: everybody knows that we get food from plants and animals, wood from trees, wool from sheep, and aesthetic enjoyment from flowers and birds. The roles of properly functioning communities in providing ecosystem services are less obvious, however, and we often take them for granted—until something goes wrong.

European settlers of Australia learned the hard way about the importance of the services provided by decomposers. When the first settlers arrived in 1788, they brought cattle with them. From the beginning, however, the Australian cattle industry ran into problems: native dung beetles, adapted as they were to the dry, fibrous dung of forest marsupials, shunned the wet manure produced by cattle in open pastures. As a consequence, manure piled up higher and deeper. The accumulated dung not only reduced pasture productivity (because the nitrogen in the dung was not being recycled, and because cattle do not eat fouled plant material), but also provided a perfect nursery for native bush flies and introduced blood-sucking buffalo flies. Populations of these pests exploded.

In 1964, Australia's national scientific research organization, CSIRO, finally tackled the problem. Insect biologists traveled the world to find dung beetles that could process cattle dung in Australian environments without disrupting native beetle communities—an important precaution, since many well-intended introductions have had unforeseen, detrimental impacts (see Concept 43.3). Between 1968 and 1984, CSIRO introduced more than 50 species of beetles. The project was successful: soil nitrogen content improved, pasture productivity

APPLY THE CONCEPT

Diversity patterns provide clues to what determines diversity

An alternative to MacArthur and Wilson's explanation for patterns of species richness on islands has been proposed: that any island has a particular mix of niches that support an island-specific community. For Simberloff and Wilson's mangrove islands (see Figure 44.12), this hypothesis would mean that each island gradually reassembled its original arthropod community, and that the number of species stopped changing when the full complement of species was restored. Review two additional results from the Simberloff and Wilson study shown below and answer the associated questions.[a]

1. Figure A shows the original community and post-defaunation census results for individual arthropod species on one mangrove island. Do these census results support or refute the alternative hypothesis? Explain your answer.

2. Figure B shows the accumulation of arthropod species in three functional groups—herbivores, carnivores, and parasites—for the same island. Did species in these three groups accumulate at the same rates? Why or why not?

[a]D. S. Simberloff and E. O. Wilson. 1969. *Ecology* 50(2): 278–296; J. W. Glasser. 1982. *American Naturalist* 119(3): 375–390.

(A)

(B)
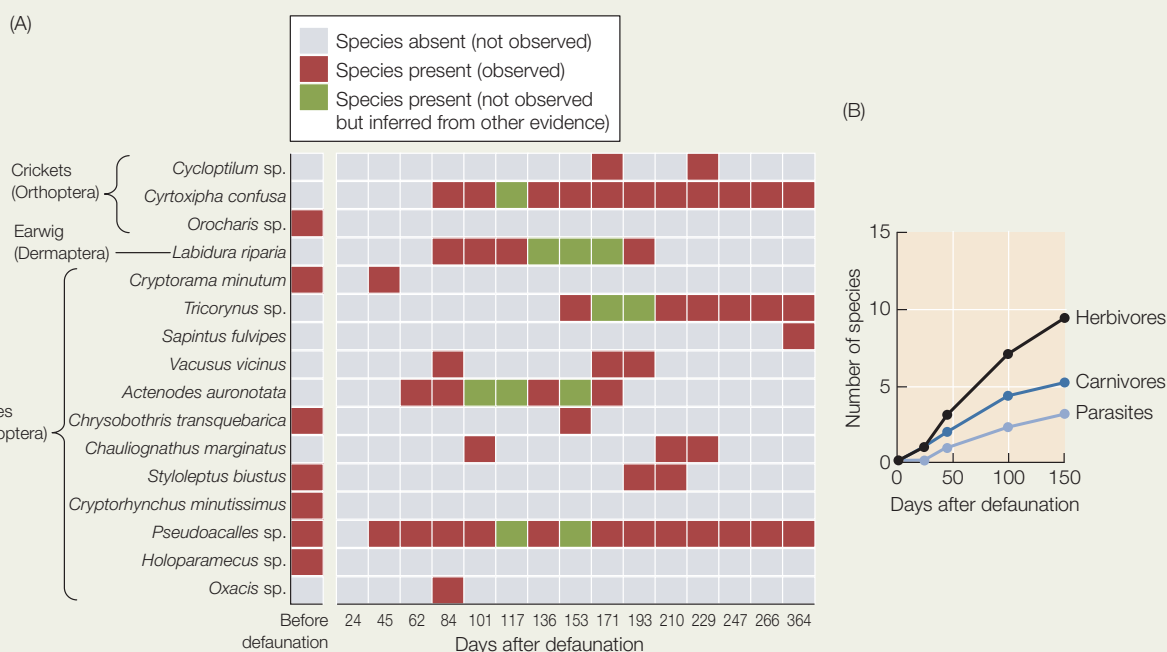
increased, fly numbers plummeted, cattle became healthier, and native dung beetles were unharmed.

Ecosystem services have economic value

Ecosystem services have economic value, as the Australian Dung Beetle Project shows. Some services related to food production are relatively straightforward to value because they are included in the price of the food. In the United States, for instance, wild native pollinating insects (not including domesticated honey bees) contribute $3 billion annually to crop production. Many other services—such as greenhouse gas regulation—are more difficult to value because they are not included in commercial markets, but that does not mean they lack value.

Consider the case of New York City's water, which comes from reservoirs in the Catskill Mountains. Natural ecosystems

in the Catskills provided the city with pure water for many years. But conversion of forests into agricultural fields and housing developments eventually began to decrease water infiltration into the soil, thus increasing the discharge of sewage, fertilizers, pesticides, and sediment into streams. New York was faced with the prospect of building a new $6–$8 billion water treatment facility. When the city considered alternatives, it realized that it could meet federal water quality standards by investing $1.5 billion in land protection and better sewage treatment in the Catskills. Although expensive, this natural alternative cost a lot less than the technological alternative! New York's Long-Term Watershed Protection Plan, completed in 2006, has been a complete success.

The New York example is not unique. Many ecosystems can provide more goods and services, at lower cost, than artificial substitutes can. But as we have seen, the community functions

TABLE 44.1	**Some Major Ecosystem Goods and Services**	
Good or service	**Community process**	**Examples**
Food production	Trophic interactions	Production of wild food; production of crops and livestock
Materials production	Trophic interactions	Production of lumber, fuel, fiber
Pollination and seed dispersal	Plant–pollinator and plant–disperser interactions	Plant reproduction and dispersal
Maintenance of fertile soil	Decomposition; composition of vegetation; plant- and animal-microbe mutualisms	Nitrogen fixation, nutrient recycling, erosion control
Waste treatment	Decomposition	Breakdown of toxins and wastes
Pest control	Predator–prey, host–parasite, and competitive interactions	Decreased pest abundance
Water supply	Regulation of water infiltration and runoff by vegetation structure and animal activity	Retention of water in watersheds, reservoirs, and aquifers
Climate regulation	Metabolic gas exchange	Regulation of greenhouse gases and cloud formation
Disturbance control	Composition and biomass of vegetation	Damping of storm winds and wave surges; flood control
Recreational and cultural opportunities	Ecological processes; species diversity	Ecotourism, outdoor recreation; aesthetic, educational, spiritual, scientific values

that deliver those goods and services depend on species diversity. Ecological communities can best meet our needs if we do not manage them so intensively, or disturb them so severely, that we lower their diversity.

Island biogeography suggests strategies for conserving community diversity

Concept 41.5 described how humans are converting natural communities into less diverse, human-managed communities such as croplands, pastures, and urban settlements. As a result, once-continuous areas of natural habitat are being reduced to scattered fragments—habitat islands embedded in human-modified landscapes (**FIGURE 44.13**). We expect such **fragmentation** of habitat to cause losses of species from communities for several reasons: the total amount of habitat decreases, the size of habitat patches decreases, and the patches become more isolated from one another. Given what you have learned about metapopulations (see Concept 42.5) and island biogeography, you now can predict the results. Subpopulations become smaller as habitat area shrinks and are therefore more prone to extinction. The human-dominated landscape surrounding the fragments may serve as a barrier to dispersal, decreasing colonization rates. The net consequence is lower species richness in the fragments than in the original habitat.

The insight that species richness reflects a balance between colonization and extinction suggests that the detrimental effects of fragmentation can be minimized by enhancing colonization and reducing extinction. Colonization rates can be

Green areas indicate dense forest cover.

1950

Belize
Honduras
15°N
Nicaragua
Guatemala
El Salvador
Costa Rica
Panama
9°N

1985

15°N

9°N

FIGURE 44.13 Habitat Fragmentation in Tropical Forests Less than half of the tropical forest that existed in Central America in 1950 (top) remained by 1985 (bottom), most of it in small patches. Although the rate of deforestation slowed somewhat after 1985, an additional 19 percent of the forest had disappeared by 2005.

increased by clustering habitat fragments close to one another or to a large "mainland" patch, or by connecting fragments with dispersal corridors (see Concept 42.6). Extinction rates can be minimized by retaining at least some large patches of the original habitat and by preserving the capacity of remaining patches to support healthy populations.

Several of these predictions have been tested in a remarkable large-scale experiment. Landowners in Brazil agreed to preserve tropical forest patches of certain sizes and configurations laid out by biologists (**FIGURE 44.14**), and they allowed the biologists to survey the parcels before and after the intervening forest was cleared for pasture. Species soon began to disappear from the patches. The first species lost were monkeys that travel over large areas of forest. Army ants and the birds that follow their columns also disappeared quickly. Species were lost more rapidly in isolated fragments than in fragments of equal area that were connected to nearby unfragmented forest, and small isolated fragments lost species more rapidly than larger isolates.

Results of studies such as these now guide land-use planning worldwide. They suggest that dispersal corridors and large habitat patches are necessary to maintain healthy, diverse communities.

Trophic cascades suggest the importance of conserving certain species

It is well and good to plan for dispersal corridors and large patches of habitat, but species differ considerably in their habitat area requirements and in the kinds of dispersal corridors they will use. How big should natural areas be? What constitutes an effective corridor? These decisions can often be facilitated if they target species that play particularly important roles in communities.

The wolves of Yellowstone National Park provide an example of a species whose presence has a major effect on community structure and function (see Concept 43.3). Wolves are crucial for maintaining healthy aspen forests and watersheds via trophic cascades that also involve elk, aspen and willow, and beavers. Conservation planning is now targeting such critical species. The Yellowstone to Yukon Conservation Initiative, for example, has the goal of maintaining a continuous corridor of wolf habitat between Yellowstone National Park and areas of similar habitat to the north, which should help maintain the Yellowstone wolf population and hence a healthy Yellowstone ecosystem.

The relationship of diversity to community function suggests strategies for restoring degraded habitats

We have seen that even highly disturbed communities, such as those on Krakatau or on experimentally defaunated mangrove islands, can recover. This insight from community ecology suggests that degraded ecosystems can often be restored—the goal of restoration ecology (see Concepts 41.5 and 43.3). The relationship between diversity and community function suggests that one of the best ways to improve the functioning of
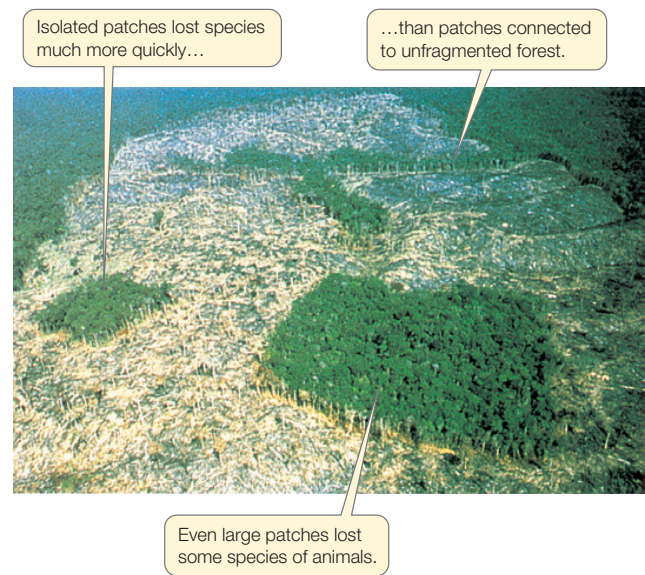
FIGURE 44.14 A Large-Scale Study of Habitat Fragmentation
Biologists studied patches of tropical evergreen forest near Manaus, Brazil, before and after the parcels were isolated by forest clearing. The results of the study demonstrated that small, isolated habitat fragments support fewer species than larger or less isolated patches of the same habitat.

Go to ANIMATED TUTORIAL 44.3
Fragmentation Effects
PoL2e.com/at44.3

a damaged system is to restore species diversity. To do so, restoration ecologists draw on their knowledge of the factors that shape diversity (**FIGURE 44.15**).

As we have also seen, however, disturbance sometimes results in an ecological transition to a community that is very different from the original community (see Concept 44.2). In such cases it may be difficult to find a way to reverse the transition and restore the function of the original community. This possibility is a sobering reminder that restoration is challenging and requires deep understanding of individual ecosystems.

CHECKpoint   CONCEPT 44.5

✓ Give two examples each of goods and services provided to humans by natural ecosystems and by ecosystems constructed and managed by humans.

✓ If you were working as a restoration ecologist to restore a certain community, what measures might you use to assess whether your efforts were successful?

In this chapter we have discussed factors that influence the structure of communities and the interactions that shape the flow of energy through them. We have seen how community

INVESTIGATION

FIGURE 44.15 Species Richness Can Enhance Wetland Restoration In one large-scale field experiment, ecologists compared different methods for restoring denuded areas of the Tijuana Estuary, a wetlands environment near San Diego, California. They found that several measures of community function improved more rapidly in species-rich than in species-poor plantings.[a]

HYPOTHESIS

Faster progress toward restoring the community's original function will be made by planting mixtures of species than by planting single species alone.

METHOD

1. In an area of wetland denuded of vegetation, mark off replicate small experimental plots, all of the same size.
2. Choose 8 native species typical of the region. Plant some plots with each of the 8 species by itself, others with different 3-species subsets, and others with different 6-species subsets.
3. Plant the same total number of seedlings per plot. Leave some plots unplanted as controls.
4. Return over the next 18 months to measure the vegetation and ecosystem nitrogen levels.

RESULTS

Vegetation covered the bare ground more quickly in those plots with higher species richness. Those same plots developed complex vertical structure more quickly and accumulated more nitrogen in plant roots per m² of area.
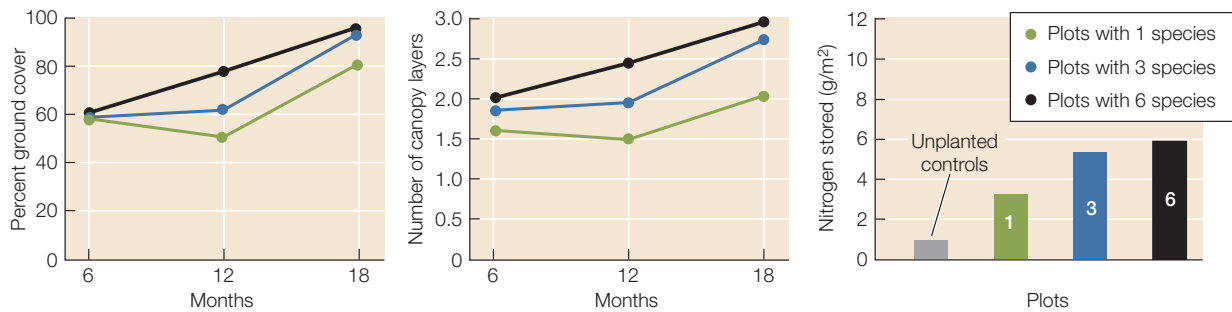
CONCLUSION

Planting more species into a community leads to more rapid restoration of wetland function.

ANALYZE THE DATA
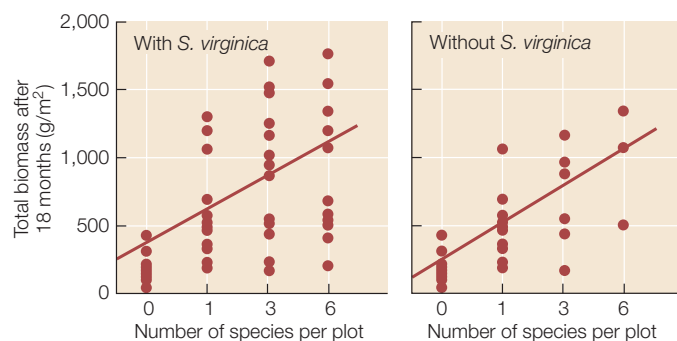
A. The unplanted control plots (above) showed nonzero values of stored nitrogen after 18 months. Is this a surprise? Why or why not?

B. One of the 8 species in the study, *Salicornia virginica*, contributed a disproportionate share of the biomass, cover, and nitrogen in mixtures in which it was included. In the two graphs at left, each circle represents the performance of a particular plot; the lines indicate best-fit regressions. Based on these two graphs, what do you conclude about the mechanism for the higher success of species-rich plantings? Is the greater chance of including *S. virginica* in species-rich plantings the likely explanation?

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]G. H. Keer and J. B. Zedler. 2002. *Ecological Applications* 12: 456–573; J. C. Callaway et al. 2003. *Ecological Applications* 13: 1626–1639.

structure affects a community's function, including its outputs of goods and services. But outputs are limited by inputs, and to understand what determines inputs to communities, we need to consider their abiotic environments. The next chapter will apply this ecosystem perspective and consider how humans are influencing the global ecosystem.

Q Can we use principles of community ecology to improve methods of coffee cultivation?

ANSWER   Croplands are ecological communities that are governed by the same factors that govern natural communities. We can therefore use our understanding of how natural communities function to improve the functioning of agricultural communities. For example, we know from studying natural communities that species diversity often enhances community function (Concept 44.3)—whether we are talking about pest control, pollination, or crop yield. We also know that species diversity is increased when colonization rates are high and extinction rates are low, and when complex habitat structure provides opportunities for species with diverse niches to coexist (Concept 44.4). We can use these ecological principles in many situations to produce more food at less cost and with fewer negative effects on the environment. For example, we can enhance crop production by growing crops in complementary functional groups together, a practice known as "intercropping." Planting coffee, which is shade-tolerant, in the shade of taller, timber-producing trees is an example of intercropping.

The desired output of coffee plantations is, of course, seeds (coffee "beans"). Although *Coffea arabica* flowers can pollinate themselves, seed production is enhanced when bees move pollen between individual plants. From our knowledge of community ecology, we might predict that diverse bee communities would provide the best pollination overall, because different bee species may pollinate in complementary ways. Recent research in Indonesia confirms this prediction: seed production was 50 percent higher, and varied less from year to year, in coffee plantations that hosted 20 wild bee species than in those that hosted 3 bee species.

We also know that wild species of insects are important for pollinating the flowers of most species of flowering plants. This knowledge suggests that embedding coffee plants in diverse natural communities of plants and animals might be an effective way to reap the benefits of better pollination. Research in both Costa Rica and Indonesia confirmed this

FIGURE 44.16 Traditional Coffee Cultivation and Community Diversity   Low-intensity, high-diversity coffee cultivation (the product of which is often marketed as "shade-grown organic coffee") results in lower yields, but can net a higher profit by avoiding the costs of fertilizers and other chemicals—with the added benefit of maintaining the services provided by natural forests.

prediction as well: planting coffee close to intact patches of forest and leaving flowering weeds in place (**FIGURE 44.16**) was all it took to attract a diverse bee community and thus increase production. This research is at the forefront of a new movement to enhance pollination and pest control services for crops by bordering croplands with species-rich and structurally diverse communities.

Traditional low-intensity cultivation methods therefore seem to be a cost-effective way to increase coffee production. Although traditional methods may not provide the highest yields per hectare, they may nevertheless be very profitable. A study of nine coffee plantations in Mexico reported that high-intensity sun cultivation produced more coffee per hectare, but that low-intensity plantations were more profitable because they reduced the costs of chemicals and labor. That low-intensity cultivation also avoids pollution and helps maintain diverse natural communities are added benefits of taking advantage of natural ecosystem services.

SUMMARY

CONCEPT 44.1   Communities Contain Species That Colonize and Persist

■ A **community** is a group of species that coexist and interact with one another within a defined geographic area.

■ A community is characterized by the particular mix of species it contains (**species composition**), by the number of species it contains, and by their abundances. Together these attributes of communities constitute **community structure**.

■ A community contains those species that are able to colonize an area and persist there.

CONCEPT 44.2   Communities Change over Space and Time

■ Spatial variation in physical conditions and in **habitat structure** is associated with predictable spatial variation in species composition. **Review Figure 44.2**

■ Even in a constant environment, ongoing extinction and colonization result in ongoing change, or **turnover**, in the species composition of communities over time.

■ After a sudden **disturbance**, species sometimes replace one another in a more or less predictable sequence called **succession**. Succession following a disturbance that removes the original community often results in a community that resembles the original one. **Review Figure 44.4 and ANIMATED TUTORIAL 44.1**

■ Some disturbances cause an **ecological transition** to a different type of community, and removal of the disturbance factor does not restore the original type of community.

■ Climate change can cause the species composition of a community to change over time. **Review Figure 44.5**

CONCEPT 44.3   Community Structure Affects Community Function

■ An ecological community is a dynamic system with inputs, internal workings, and outputs. A fundamental aspect of this **community function** is the flux of energy into and out of the community.

■ The total amount of energy that primary producers capture and convert into chemical energy per unit of time is called **gross primary productivity** (**GPP**). The amount of GPP that becomes available to consumers per unit of time is called **net primary productivity** (**NPP**). **Review Figure 44.6 and ACTIVITY 44.1**

■ The **ecological efficiency** of energy transfer from one trophic level to the next is only about 10 percent.

■ The term **niche** refers to the physical and biological environments in which a species has a positive per capita growth rate, as well as to the species' functional role in the community.

■ **Species diversity** has two components: the number of species in the community, called **species richness**, and the distribution of those species' abundances, called **species evenness**. **Review Figure 44.7 and ACTIVITY 44.2**

■ The outputs of a community are measures of its function. Community outputs increase with the species diversity of the community and the number of functional roles those species fill. **Review Figure 44.8**

CONCEPT 44.4   Diversity Patterns Provide Clues to What Determines Diversity

■ Species richness is greatest in the tropics and decreases with increasing latitude. Possible causes of this pattern include greater climate stability, greater energy input, and greater habitat complexity at lower latitudes. **Review Figure 44.9**

■ Species richness also varies among oceanic islands. Large islands support more species than small islands, and islands close to a mainland support more species than distant islands. **Review Figure 44.10**

■ The theory of **island biogeography** explains these island patterns as a balance between the rate at which new species colonize and the rate at which resident species go extinct. **Review Figures 44.11 and 44.12 and ANIMATED TUTORIAL 44.2**

CONCEPT 44.5   Community Ecology Suggests Strategies for Conserving Community Function

■ Ecosystems provide humans with a variety goods and services. These **ecosystem services** have economic value. **Review Table 44.1**

■ Production of ecosystem services is threatened by human activities, including the **fragmentation** of natural habitats, that reduce species diversity. The detrimental effects of habitat fragmentation can be mitigated by land-use management that minimizes extinction in each habitat "island" and maximizes dispersal among them. **Review Figures 44.13 and 44.14 and ANIMATED TUTORIAL 44.3**

■ Ecosystem function often can be preserved or restored by focusing on particular species that play especially important roles in the community, and by maintaining or restoring overall species diversity. **Review Figure 44.15**

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities
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45

The Global Ecosystem

The Mauna Loa observatory on the "Big Island" of Hawaii provides scientists with accurate data on the composition of Earth's atmosphere.

The nineteenth century was a golden age for Earth science. Geologists not only deduced the astonishing age of the planet, but also discovered that massive sheets of ice had covered much of Europe and North America only 15,000 years ago—Earth's climate was once much colder than it is today.

What could cause such dramatic climate change? One possibility, proposed in 1861, pointed to atmospheric gases such as carbon dioxide and water vapor, which by then were known to absorb infrared (heat) radiation. Scientists hypothesized that these gases might influence Earth's climate by trapping energy in the lower atmosphere. By the end of the nineteenth century, they had outlined a "carbon dioxide theory" to explain how fluctuating atmospheric CO_2 concentrations could change the strength of this "greenhouse effect" and explain past ice ages.

Scientists pursuing the carbon dioxide theory had an additional insight. They realized that coal and petroleum contained fossilized carbon from dead plants and animals. Since the Industrial Revolution, humans had been burning these fossil fuels, releasing their carbon as CO_2. Might fossil fuel combustion be increasing CO_2 in the atmosphere, thus magnifying the greenhouse effect? Some early skeptics felt that any effect of CO_2 would be insignificant because it constituted only about 300 parts per million (0.03 percent) of all molecules in the atmosphere. In the 1930s, however, physicists and chemists demonstrated that changes in atmospheric CO_2 could indeed affect Earth's climate. In the 1950s the American scientist Gilbert Plass estimated the rate at which atmospheric CO_2 was increasing and used one of the first electronic computers to predict that increased CO_2 concentrations could significantly raise the average global temperature.

The challenge now facing scientists was to see if the predicted rise in atmospheric CO_2 could be detected. But nobody had yet been able to measure atmospheric CO_2 with precision. A young American chemist, Dave Keeling, developed sensitive new instruments and set them up atop Mauna Loa in Hawaii, 4,000 meters above sea level and far from human-generated pollution. Pledging himself to a long-term study, he began taking measurements in 1957 as part of the International Geophysical Year (IGY), one of the first government-supported international scientific collaborations. But the IGY money soon dried up. Undaunted by periods of insufficient funding, Keeling continued his research on atmospheric CO_2 and the carbon cycle over the next four decades.

Q How did Keeling's research contribute to our understanding of the global ecosystem?

Climate and Nutrients Affect Ecosystem Function

As we learned in Concept 41.1, the term **ecosystem** is commonly applied to ecological communities plus the abiotic environments with which they exchange energy and materials. Most of the interactions among components of ecosystems happen at a local scale. A plant, for example, can absorb only those nitrate molecules that are in physical contact with its root hairs; an elk in Alberta cannot fall prey to a wolf living in Wyoming's Yellowstone National Park; and a raindrop interacts directly only with the soil particles it contacts. For this reason, most studies of ecosystems are done at relatively small spatial scales, such as a single river drainage, lake, or patch of forest.

Local ecosystems are linked, however, by slower exchanges of organisms, energy, and materials that occur on spatial scales ranging from tens of kilometers within regional landscapes to thousands of kilometers around the planet. These long-distance interactions occur when organisms move among communities and when energy and materials are transported by the physical circulation of the atmosphere and the oceans, by flowing water, and by geological processes that occur below Earth's crust. Large-scale patterns ultimately influence inputs to and losses from local ecosystems, making it impossible to understand a local ecosystem completely without considering it in the context of the larger systems of which it is a part. This chapter therefore takes both local and global perspectives.

NPP is a measure of ecosystem function

Ecosystems, like other biological systems (see Concept 1.2), can be characterized by their components and by patterns of interaction among those components. In ecosystem studies, the community as a whole is often treated as one component, and distinct portions of the abiotic environment, such as soil, atmosphere, or water, are treated as other components. The dynamic processes by which these components exchange and transform energy and materials are aspects of **ecosystem function**.

Ultimately, movements of materials between the abiotic and biotic components of ecosystems are tied to carbon. Primary producers combine inorganic carbon dioxide with inorganic water to make organic carbohydrates. Energy stored in the chemical bonds of those molecules fuels the synthesis of all the biomass in the bodies of organisms at every trophic level (see Concept 6.2). Most of the elemental constituents of that biomass enter communities through the primary producers as well. Calcium in the bones of a wolf, for example, came from the elk it ingested; the elk obtained calcium from the plants it ate; and the plants used energy from the breakdown of carbohydrates to extract inorganic calcium from the soil.

The rate at which a community makes primary producer biomass—its net primary productivity, or NPP (see Concept 44.3)—is therefore a measure of the flow of materials, as well as energy, into the biotic component of its ecosystem. This measure of ecosystem function does not incorporate all exchanges of materials between organisms and the abiotic environment:
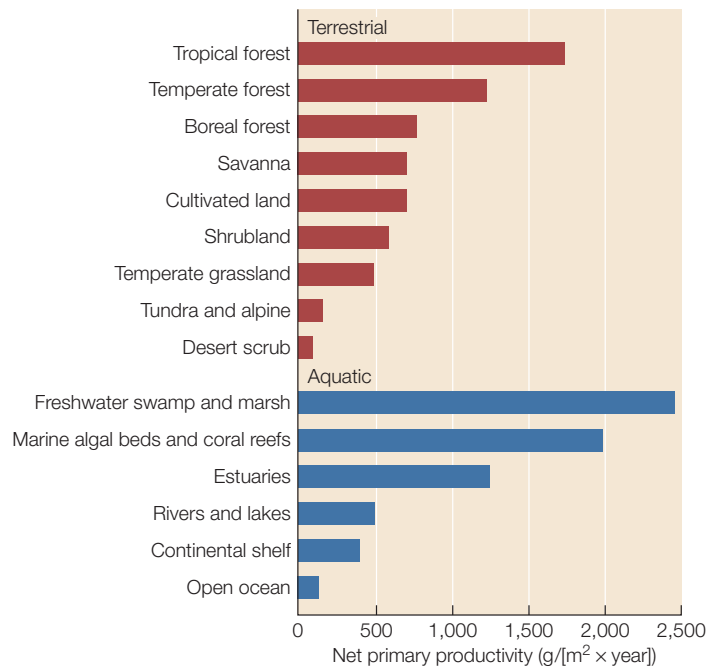
FIGURE 45.1 NPP Varies among Ecosystem Types Net primary productivity is expressed here as grams of biomass produced per square meter of area per year.

organisms, for example, also take in or excrete inorganic water or salts to maintain homeostasis. Such exchanges are nonetheless indirectly coupled with primary productivity because they are fueled by the energy that enters the community via primary producers.

Scientists are now able to estimate NPP with instruments, carried by orbiting satellites, that measure the reflection of different wavelengths of light by Earth's surface. This "view from space" allows them to calculate how much sunlight is absorbed by chlorophyll in different regions and thus to map the distribution of photosynthetic biomass—which is correlated with NPP—across the planet. These maps show that NPP is not the same everywhere. As we will see next, patterns of variation in NPP indicate factors that limit ecosystem function.

NPP varies predictably with temperature, precipitation, and nutrients

Net primary productivity varies considerably among ecosystem types. Among terrestrial ecosystems, tropical forests are the most productive per unit of area, followed by temperate forests, whereas tundra and deserts are the least productive (**FIGURE 45.1**). Among aquatic ecosystems, freshwater swamps and marshes and marine algal beds and coral reefs are the most productive, followed by estuarine habitats, whereas the open ocean is the least productive. Much of this pattern derives from variation in climate and nutrient availability.

Satellite images of terrestrial ecosystems show that NPP varies with latitude: highly productive areas are concentrated in the tropics, and higher latitudes are less productive (**FIGURE**
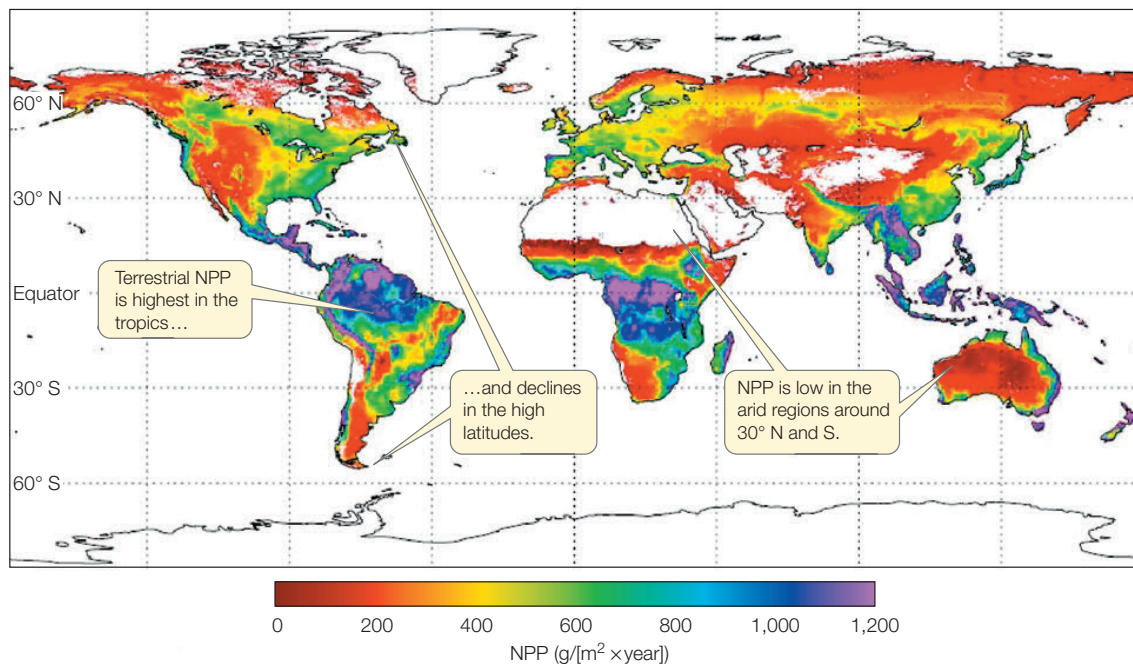
FIGURE 45.2 Terrestrial NPP Corresponds to Climate This map of estimated terrestrial NPP is based on satellite sensor data accumulated over the period 2000–2005. The white spaces on land represent unvegetated areas, including barren deserts and ice caps.

45.2). This pattern parallels latitudinal gradients in solar energy input (see Figure 41.3) and temperature, suggesting that NPP increases with temperature. Indeed, terrestrial NPP generally does increase with temperature (**FIGURE 45.3A**), which makes sense when we consider that the activity of photosynthetic enzymes, like that of other enzymes, increases up to the critical temperature at which enzymes denature (see Concept 3.4). This critical temperature varies among plant species that are adapted to different environments but is usually about 40°C–50°C.

The satellite images also show areas of low terrestrial NPP at 30° N and S latitude (see Figure 45.2), where deserts occur (see Figures 41.5 and 41.11). This pattern parallels gradients in precipitation, suggesting that moisture also affects NPP. Terrestrial NPP does increase with precipitation up to about 2,400 millimeters per year, then decreases at higher levels (**FIGURE**

FIGURE 45.3 Terrestrial NPP Varies with Temperature and Precipitation NPP is given in megagrams (1 Mg equals 10^6 g or 1 metric ton) per hectare per year.
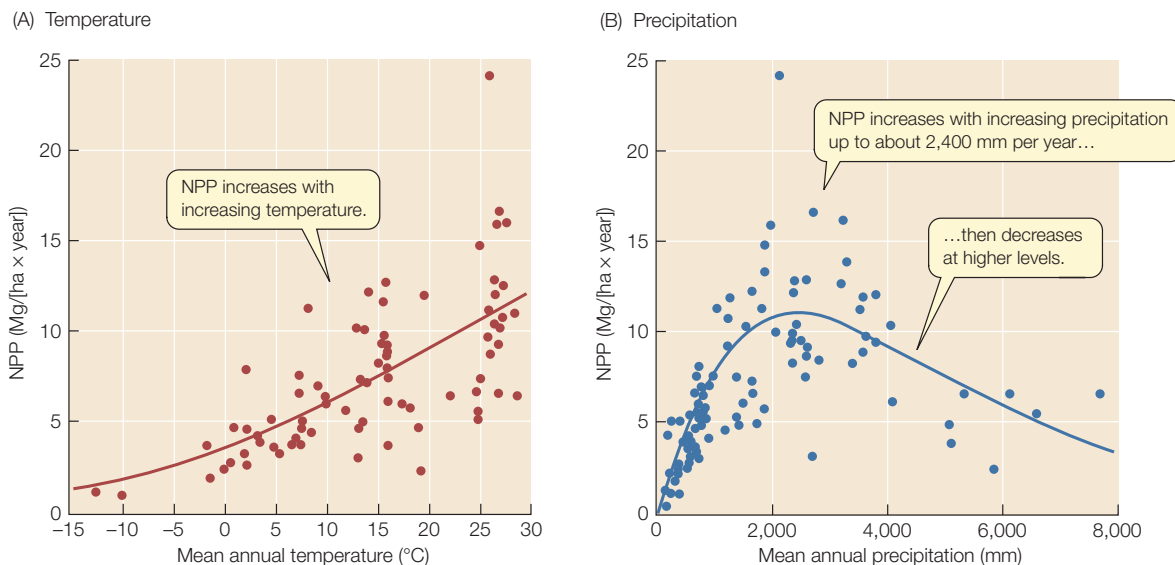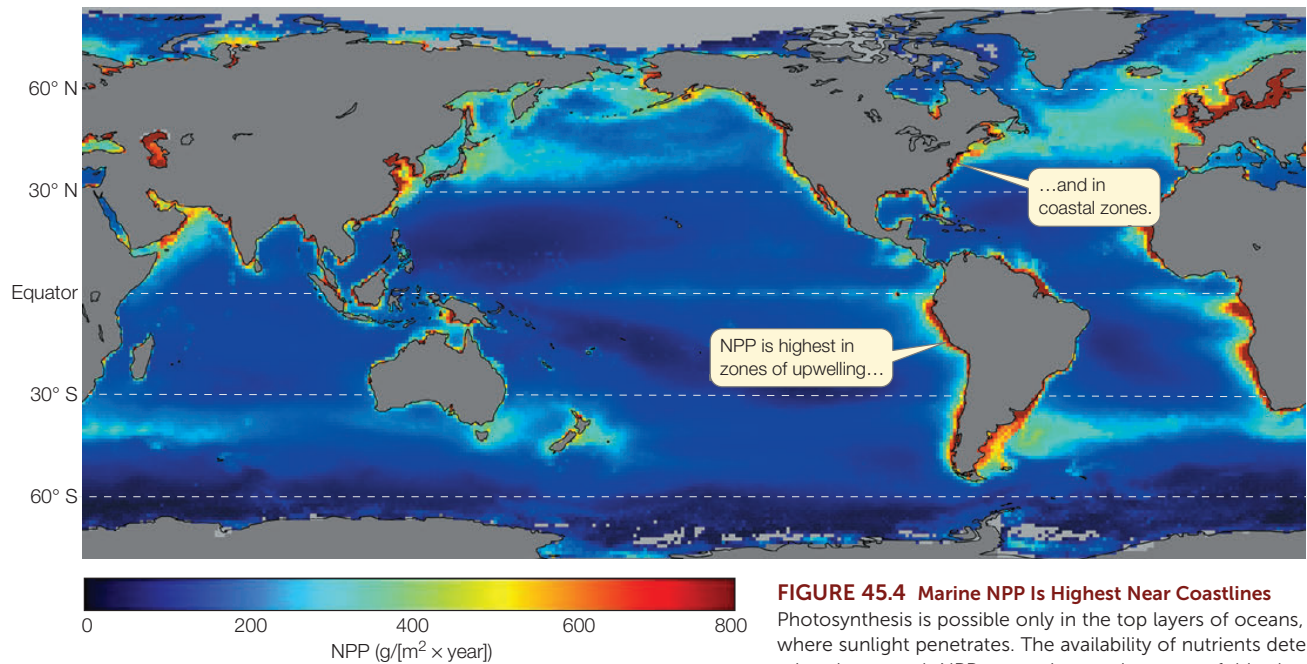
FIGURE 45.4 **Marine NPP Is Highest Near Coastlines**
Photosynthesis is possible only in the top layers of oceans, where sunlight penetrates. The availability of nutrients determines how much NPP occurs in any given part of this photic zone. Highest NPP occurs where runoff from land brings nutrients into shallow coastal waters, and where upwelling of deep waters brings nutrients from the benthic zone to the surface.

45.3B). This also makes physiological sense. Moist soil conditions facilitate water and nutrient uptake by roots and allow plants to maintain pressure within their cells without closing their stomata (leaf pores), thus facilitating CO_2 uptake (see Concept 25.3). The decrease in NPP in extremely moist climates may result from increased cloud cover and lower solar input or from a lack of oxygen in water-saturated soils.

Finally, we also know that elements such as nitrogen, phosphorus, and potassium, which are critical for plant growth (see Figure 25.1), can be in short enough supply to limit NPP in both natural and agricultural ecosystems. Soils in southwestern Australia, for example, are nutrient-poor because most nutrients have been washed (leached) out of the soil over hundreds of millions of years, during which there has been no nutrient-renewing geological uplift. As we saw in Concept 41.3, many plants in this region do not allocate their scarce nitrogen to defensive compounds; instead, they allocate it to proteins that are essential for metabolism and growth.

LINK

The principle of allocation of resources is discussed in **Concept 42.3**

In aquatic ecosystems, NPP is affected more strongly by light and nutrients than by temperature. Photosynthesis is restricted to surface waters where light can penetrate (the photic zone; see Figure 41.13). As a result, NPP is generally higher in surface than in deep waters; the only productive deep-water areas are hydrothermal vents, where chemoautotrophs (see Concept 19.3) generate new biomass by using chemical energy rather than sunlight. But not all surface waters are productive. The open ocean, for example (see Figure 45.1), is unproductive because dissolved nutrients are often

limited there—phytoplankton take up surface nutrients quickly and move them to deep waters when they (or the consumers that eat them) die and sink. Aquatic NPP is highest where nutrients are abundant—where rivers and streams discharge nutrients leached from terrestrial ecosystems into coastal marine areas, near-shore zones of lakes, and shallow freshwater wetlands (**FIGURE 45.4**). NPP is also high in areas of upwelling, where deep water from the bottom of an ocean or lake rises to the surface, bringing with it nutrients from benthic sediments.

CHECKpoint   CONCEPT 45.1

✓ NPP is generally higher in freshwater wetlands (swamps and marshes) than in shallow marine waters (algal beds, coral reefs, and estuaries; see Figure 45.1). Why might this be so?

✓ Why do you think NPP in human-cultivated land is lower than that in several natural ecosystem types such as temperate and tropical forest? (See Figure 45.1. Hint: See Concept 44.3.)

✓ Outline an experiment that would allow you to determine whether NPP in a grassland ecosystem is limited by the availability of water in the soil.

We now have an overview of global patterns of ecosystem function, as measured by NPP, and some of the factors that cause them. We have seen that nutrient availability plays an

important role in these patterns, which makes sense because nutrients are chemical elements that organisms require for their metabolism and as materials to build their bodies. What are the processes that affect the availability of nutrients?

> **CONCEPT 45.2** Biological, Geological, and Chemical Processes Move Materials through Ecosystems

The sun provides a steady input of radiant energy to Earth. A small amount of this radiant energy is captured by photosynthetic organisms and converted into chemical energy, as we saw in Concept 44.3. This energy fuels the metabolism of all organisms in the community and is ultimately transformed into waste heat. In contrast, the chemical elements that make up organisms come from within the Earth system itself. There is essentially a fixed amount of each element because little matter escapes Earth's gravity or enters the Earth system from space. Whereas Earth is an open system with respect to energy, it is a closed system with respect to matter. This does not mean that the distribution of matter is static, however: energy from the sun and heat from Earth's interior drive biological, geological, and chemical processes that transform matter and move it around the global ecosystem.

The forms and locations of elements determine their accessibility to organisms

Imagine an atom. At any time, this atom occurs in a particular molecular form and occupies a particular location in Earth's closed system. It might be part of a living organism or of dead organic matter. It might be part of a molecule in the atmosphere, in a body of fresh or salt water, or in soil, sediment, or rock. If in rock, it might be part of the surface crust of Earth or more deeply buried. These alternative forms and locations of matter can be thought of as **compartments**. Atoms cycle repeatedly among compartments when they are chemically transformed or physically moved. The atoms in Earth's crust, for example, have gone through repeated cycles of being buried, compressed, heated, uplifted, eroded, and deposited again in sediments (see Figure 18.2). The compartments of the global ecosystem, and the processes that cycle materials among them, can be depicted in a systems diagram (**FIGURE 45.5**; see also Figure 1.6).

The chemical form in which an atom exists determines whether it is accessible to life.

FIGURE 45.5 Chemical Elements and Compounds Cycle among Compartments of the Global Ecosystem The different chemical forms and locations of elements determine whether or not they are accessible to living organisms. These different forms and locations of matter represent compartments (boxes) in the diagram shown here. Biological (green arrows), geological, and chemical processes (brown arrows) cycle matter among the compartments.
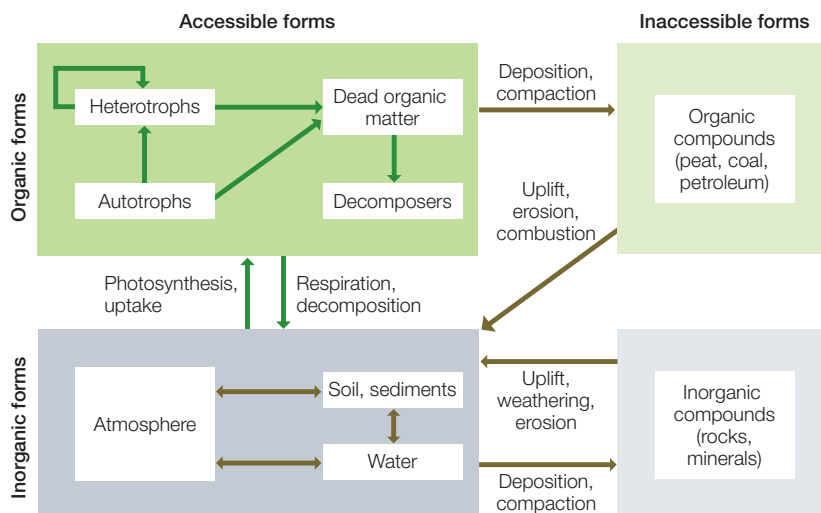
With rare exceptions, autotrophs take up carbon in the form of CO_2, and they absorb nutrients such as nitrogen, phosphorus, and potassium in the form of ions dissolved in water (see Concept 25.1). Heterotrophs (including decomposers) extract most of the materials they need from living or dead organic matter. But even when an atom is in the right chemical form, organisms cannot use it if it is in the wrong place. Matter that is buried too deeply, or that occurs in places that are too hot, too cold, or otherwise too hostile, is inaccessible to life.

The processes that supply matter to organisms occur in the **biosphere**, the thin skin at Earth's surface where atmosphere, land, and water are in contact with one another and where organisms live. The biosphere is only about 23 kilometers thick—a mere 1/277 of Earth's radius—extending up to the stratosphere and down to the abyssal zone of the oceans.

Movement of matter is driven by biogeochemical processes

Matter is moved among the compartments of the global ecosystem by processes that are biological, geological, and chemical; thus these movements are called **biogeochemical cycles**. Biological and abiotic chemical reactions combine elements with other elements and compounds, converting them between inorganic and organic forms or between oxidized and reduced states. Many of these reactions involve the abundant elements oxygen and hydrogen. Chemical reactions are also involved in the weathering of rock during soil formation. Physical processes—the circulation of air and water and convective flows within Earth's mantle—move matter through the Earth system, alternately exposing it to air, water, and solar radiation or to heat and pressure.

> **LINK**
>
> Oxidation–reduction ("redox") reactions are described in **Concept 6.1**, weathering and soil formation in **Concept 25.1**, plate tectonic processes in **Concept 18.2**, and circulation of the atmosphere and oceans in **Concept 41.2**

The total amount, or **pool**, of an element or molecule in a given compartment depends on its rate of movement into and out of that compartment. The rate of movement, or **flux**, from one compartment to another is measured in amount per unit of time. If the fluxes into and out of a compartment are not identical, the pool will grow or shrink. Oxidation of organic matter by respiration, wildfires, or fossil fuel combustion, for example, will increase the atmospheric pool of carbon unless photosynthesis and other biogeochemical processes remove carbon from the atmosphere at an identical or greater rate.

All of the materials contained in the bodies of living organisms are ultimately derived from abiotic sources, either atmospheric gases or materials dissolved in water. Primary producers (see Concept 44.3) take up elements from these inorganic compartments, accumulating them as biomass. Trophic interactions (see Concept 43.3) pass those elements on to heterotrophs, which also take in other inorganic materials such as oxygen and water as part of their metabolism. Eventually all of these materials enter the nonliving organic matter compartment. Decomposers break down the dead organic matter into simpler chemical compounds and elements that can be taken up by primary producers. Much of this recycling of materials occurs locally, but some occurs on a larger scale when materials diffuse away in gaseous form or are carried out of the local ecosystem by wind or water.

CHECKpoint   CONCEPT **45.2**

✓ What is the distinction between the concepts of pool and flux with regard to a given chemical element or compound?

✓ Explain the meaning of "closed system" in the statement that Earth is a closed system with respect to matter.

✓ Draw a systems diagram to show how energy from sunlight enters and flows through the global ecosystem. (Hint: See Concept 6.5 and Figures 44.6 and 45.5.)

We have now seen that the materials that make up living tissue—chemical elements and compounds—cycle through ecosystems. Let's next consider the cycles of three materials that are especially critical for ecosystem function.

CONCEPT 45.3   Certain Biogeochemical Cycles Are Especially Critical for Ecosystems

All biogeochemical cycles can be described in terms of compartments containing the material involved, amounts (pools) of the material contained in each compartment, and rates (fluxes) at which the material enters and leaves those compartments (see Figure 45.5). At the same time, the cycles of different materials vary in their spatial scales and in the processes that drive them. We will illustrate this variation by tracing the cycles for three essential materials: water, nitrogen, and carbon. We will point out how each cycle affects the global ecosystem, particularly the atmosphere, and is in turn affected by human activities.

Water transports materials among compartments

Water is a most remarkable molecule. It makes up more than 70 percent of living biomass. It is the medium for metabolism and the solvent in which biologically accessible forms of many nutrients are dissolved. Precipitation of water as rain or snow transports materials from the atmosphere to Earth's surface. Water weathers rock into soil. And as the primary agent of erosion and transport of dissolved ions and sediment, water is responsible for much of the physical movement of materials around the planet. By virtue of its high heat capacity and its ability to change between solid, liquid, and gaseous states at normal Earth temperatures, water redistributes heat around the planet as it circulates through the oceans and atmosphere. And, as we will soon see, water in the atmosphere is an important player in the global radiation balance.

> **LINK**
>
> The molecular nature of water and its crucial role in the evolution of life as we know it are covered in **Chapter 2**

The global ecosystem contains almost 1.4 billion cubic kilometers of water. About 96.5 percent of this water is in the oceans, which cover 71 percent of the planet's surface—making it obvious why Earth is sometimes called the "blue planet." Other compartments of water include ice and snow (1.76%), groundwater (1.70%), the atmosphere (0.001%), and fresh water in lakes and rivers (surface fresh water; 0.013%). Even though biomass is mostly water, only about 0.0001 percent of Earth's water is found in living organisms.

Some fluxes among these compartments (**FIGURE 45.6**) involve gravity-driven flows of water from the atmosphere to Earth's surface (precipitation) and from land to the oceans and other bodies of water (runoff). Other fluxes, however, are associated with changes in the physical state of water—from liquid to gas (evaporation), from gas to liquid (condensation), between liquid and solid (freezing and melting), and between solid and gas (sublimation and deposition).

The driving force of the water cycle is solar-powered evaporation, which transforms water from liquid to gas and, in the process, moves it into the atmosphere from oceans and other bodies of water, from the soil, and from plants (via transpiration; see Concept 25.3) and other organisms. It takes considerable energy—2.24 kJ (about the energy stored in one AA battery)—to evaporate 1 gram of water. On a global scale, the rate of evaporation is enormous, taking up about one-third of the total solar energy that reaches Earth's surface. This energy is released again as heat when the water vapor condenses to form precipitation. Fluxes of water from Earth's surface to the atmosphere and from the atmosphere to the surface are approximately equal on a global basis, although precipitation exceeds evaporation over land, and evaporation exceeds precipitation over the oceans.

Humans affect the global water cycle when they change the way land is used. Removing vegetation reduces the amount of precipitation that is retained by soil or groundwater and recycled locally, thereby increasing the amount that leaves the local ecosystem as surface runoff. As a result, deforestation, grazing, and crop cultivation all tend to dry out local
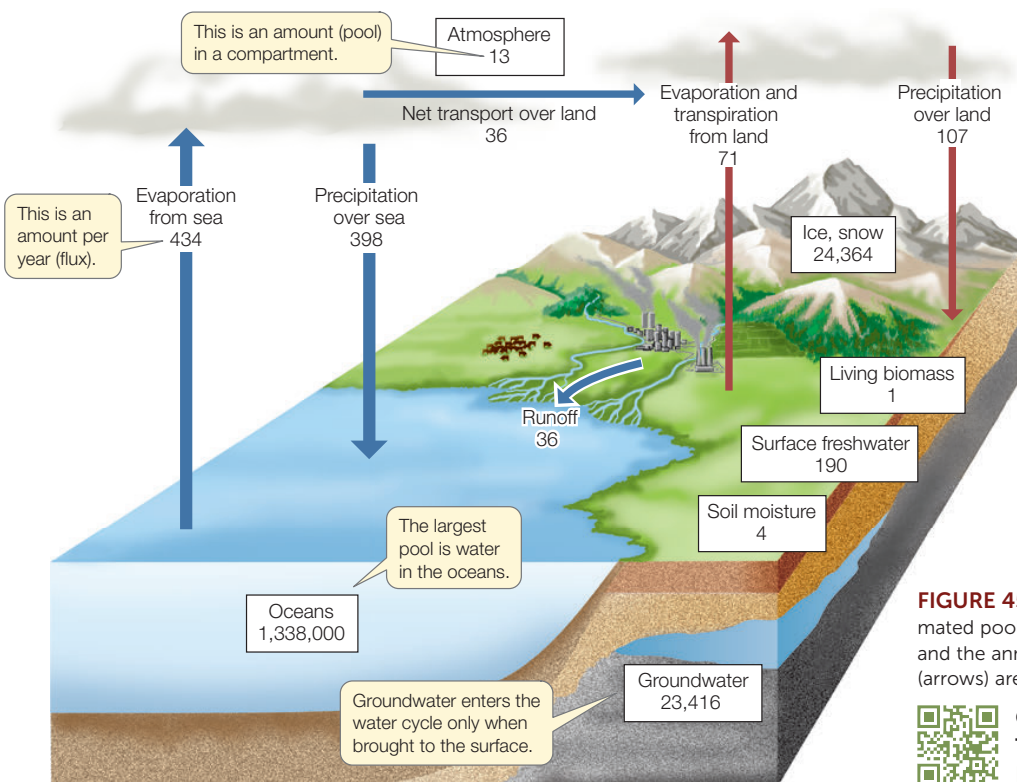
FIGURE 45.6 **The Global Water Cycle** The estimated pools in major compartments (white boxes) and the annual fluxes between compartments (arrows) are expressed in units of 10^{18} grams.

Go to ANIMATED TUTORIAL 45.1
The Global Water Cycle
PoL2e.com/at45.1

ecosystems. Pumping depletes groundwater, moving it to the surface, where it either evaporates or runs off into streams and, eventually, into oceans.

The water cycle also affects and is affected by the global climate. Warming of the climate is melting polar ice caps and glaciers, increasing the total amount of water in the oceans and causing sea level to rise. With more liquid water comes more evaporation, and thus more water entering the atmosphere and more precipitation globally. Water vapor absorbs infrared radiation—and thus contributes to the greenhouse effect—but it also forms clouds, which reflect incoming sunlight back into space. Scientists are working to predict the net effects on climate of these counterbalancing changes in the water cycle.

Within-ecosystem recycling dominates the global nitrogen cycle

Nitrogen is abundant on Earth, yet it is often in short supply in biological communities. Unlike water—whose availability to organisms depends only on where it occurs and its physical state—nitrogen's accessibility to life depends not only on where it occurs, but also on what other elements it is attached to. As a result, the nitrogen cycle, unlike the water cycle, involves chemical transformations (**FIGURE 45.7**).

The gas N_2 constitutes about 78 percent of the molecules in Earth's atmosphere, but most organisms cannot use nitrogen in this form because they cannot break the strong triple bond between the two nitrogen atoms. The exceptions are certain microbes that break the triple bond and attach hydrogen to make ammonium (NH_4^+)—which is usable by other

organisms—through a metabolic process called **nitrogen fixation**. In terrestrial ecosystems, nitrogen fixation is carried out mostly by free-living bacteria in the soil and by symbiotic bacteria associated with plant roots, but it also occurs in other places, such as the fungal gardens of leaf-cutter ants described in the opening story of Chapter 43 (**FIGURE 45.8**). Analogous biochemical processes in aquatic ecosystems are carried out by free-living microorganisms and by microbial symbionts of phytoplankton and other aquatic organisms. A small amount of nitrogen is fixed in the atmosphere by lightning. Diverse other microbial species in terrestrial and aquatic ecosystems convert ammonium into other accessible forms of nitrogen such as nitrate (NO_3^-). Nitrogen fixation is reversed by another group of microbes in a process called **denitrification**, which ultimately completes the cycle by returning N_2 gas to the atmosphere.

LINK

The metabolic processes by which microbes transform nitrogen are described in **Concepts 19.3 and 25.2**

Ammonium and nitrate are accessible to autotrophs because they dissolve in water and thus are easily taken up through cell membranes. Heterotrophs obtain nitrogen by breaking proteins down into amino acids, which can also be transported through cell membranes. Much of the nitrogen in terrestrial ecosystems is recycled locally as decomposition of dead organic matter releases accessible nitrogen into the soil. Some nitrogen, however, is lost to the atmosphere when biomass burns, or is leached from soils and carried away in streams, ultimately into lakes
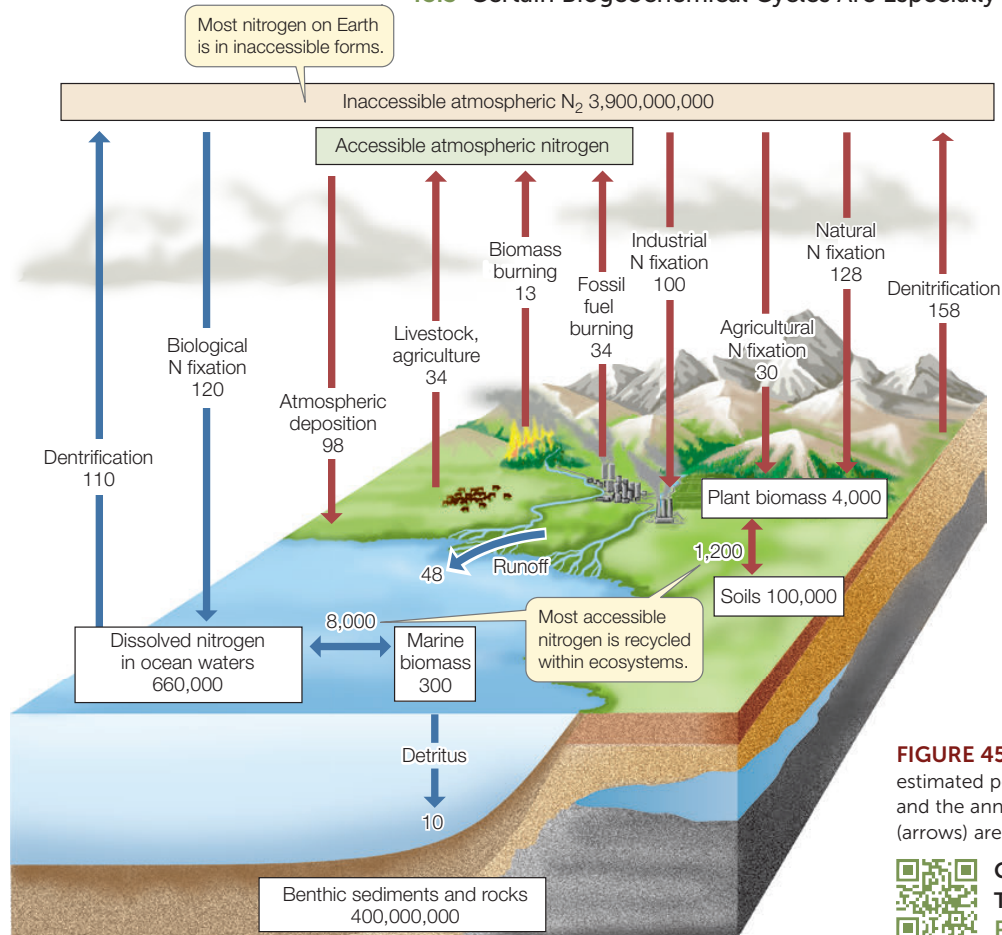
FIGURE 45.7 **The Global Nitrogen Cycle** The estimated pools in compartments (white boxes) and the annual fluxes between compartments (arrows) are expressed in units of 10^{12} grams.

Go to ANIMATED TUTORIAL 45.2
The Global Nitrogen Cycle
PoL2e.com/at45.2

and oceans. In aquatic systems, primary production occurs in surface waters, and some nitrogen is recycled there. However, much of it is recycled at greater depths in the water column as organisms in deep waters intercept and consume sinking organic matter. The nitrogen in this organic matter eventually accumulates in sediments. Some of it is returned to the surface by upwelling or, eventually, by tectonic processes followed by weathering of exposed rock.

Human activities are affecting nitrogen fluxes and pools. Cultivation of wetland crops (such as rice), livestock raising, and burning of plant material, coal, and petroleum release oxides of nitrogen and ammonia into the atmosphere. These molecules contribute to atmospheric smog and acid rain, and one of them, nitrous oxide (N_2O), absorbs infrared radiation. When they are eventually deposited on Earth's surface, sometimes far from their source, they can add as much nitrogen "fertilizer" as farmers place on their crops. Humans also alter the atmospheric pool of N_2 through the industrial process that fixes nitrogen to manufacture fertilizer and explosives. The rate of industrial fixation (see Concept 25.1) plus the rate of fixation by legume crops such as soybeans now adds up to more than the rate of natural terrestrial nitrogen fixation (see Figure 45.7). Transport of topsoil and dissolved nitrogen from fertilized croplands and deforested areas by wind or water runoff is increasingly exporting nitrogen from terrestrial to aquatic ecosystems.

Increased nitrogen inputs can increase primary production, but too much of a good thing can be a bad thing. In aquatic systems, nutrient-stimulated increases in primary productivity—a phenomenon called **eutrophication**—can result in rapid growth of phytoplankton (including cyanobacteria; see Figure 19.9C) and algae. Respiration by these primary producers and by the decomposers that process their dead bodies can reduce oxygen levels below the tolerances of many aquatic organisms, including fish and crustaceans. Eutrophication can lead to "dead zones" devoid of oxygen-requiring aquatic life, like that found where the Mississippi River discharges nutrient-rich agricultural runoff into the Gulf of Mexico (**FIGURE 45.9**). In nutrient-poor terrestrial ecosystems, excess nitrogen can change the species composition of plant communities. Species that are adapted to low nutrient levels grow slowly, even when fertilized, and thus are displaced by faster-growing species that can take advantage of the additional nutrient supply. In the Netherlands, nitrogen deposition from upwind industrial and agricultural regions has caused species-rich plant communities to give way to species-poor communities, contributing measurably to a recent loss of plant species diversity there.

Go to MEDIA CLIP 45.1
Tracking Dead Zones from Space
PoL2e.com/mc45.1

INVESTIGATION

FIGURE 45.8 Where Does the Extra Nitrogen Come From?   Leaf-cutter ants require more nitrogen than is contained in the fresh leaves that they supply to their fungal gardens. Perhaps the fungus concentrates nitrogen from the leaves into the special fungal structures that the ants eat. If so, then spent leaf material in the ants' refuse dumps (see Figure 43.12) should be lower in nitrogen than fresh leaves—but the opposite turns out to be true. One possible explanation for this enrichment of the discarded leaf material is that the ants eat protein-rich insects as well as the fungus and fertilize the fungal garden with their feces. Another is that the fungus absorbs nitrogen from the soil. A third possibility is that the fungus absorbs nitrogen from nitrogen-fixing organisms in the nest. Pinto-Tomás and colleagues tested this third hypothesis.[a]

HYPOTHESIS

Nitrogen-fixing organisms in leaf-cutter ant nests supply nitrogen to the ants.

METHOD

1. Bring ant colonies into the laboratory and allow them to function in an environ-ment with no other insects and no soil (that is, where the only non-atmospheric source of N is fresh leaves supplied by the researchers).
2. Measure the nitrogen content of leaves, fungus garden, ants, and leaf refuse.

RESULTS

The cultivated fungus, the bodies of worker ants, and the contents of the refuse dump all contained significantly more nitrogen than did the leaves.

Error bars indicate 1 standard error from the mean; bars with different letters are statistically different from one another. (See Appendix B for discussion of statistical concepts.)
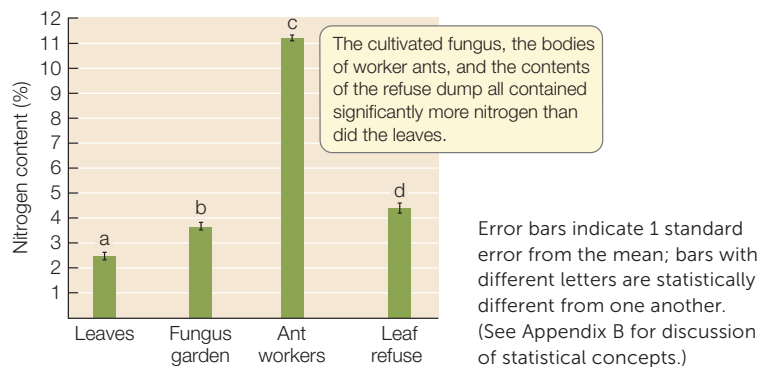
CONCLUSION

Nitrogen is being fixed within the ant nest.

ANALYZE THE DATA
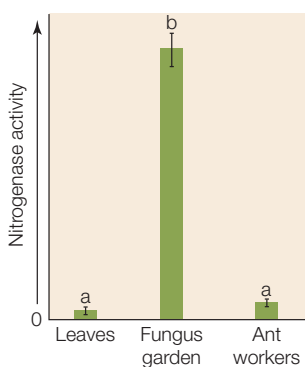
The researchers measured activity of nitro-genase, an enzyme in the bacterial metabolic pathway that fixes atmospheric nitrogen. The results are shown in the figure to the left. Error bars indicate 1 standard error from the mean; different letters indicate significant differences in nitrogenase activity.

A. Where in the nest is nitrogen fixation occurring?

B. How can the ant workers have a higher nitro-gen content than the fungus garden (see figure above)?

C. Can the researchers now conclude that the extra nitrogen comes from nitrogen-fixing bacteria living in the fungus gardens?

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

[a]A. A. Pinto-Tomás et al. 2009. *Science* 326: 1120–1123.

Movement of carbon is linked to energy flow through ecosystems

All the macromolecules that make up living or-ganisms contain carbon, and much of the energy that organisms use to fuel their metabolic activi-ties comes from the oxidation of organic carbon compounds. The movement of carbon into, through, and out of communities is therefore intimately linked to energy flow through eco-systems, and biomass is an important compart-ment of the carbon cycle (**FIGURE 45.10**). Most of the carbon in the atmosphere occurs as the gases CO_2 (carbon dioxide) and CH_4 (methane), which are mixed on a global scale by the solar-powered circulation of Earth's atmosphere (see Concept 41.2). These same forms are found dissolved in the oceans and in fresh water, and aquatic sys-tems also harbor carbonate (CO_3^{2-}). By far the largest pools of carbon occur in fossil fuels and in rocks containing carbonate compounds.

Fluxes of carbon are driven by biological, chemical, and physical processes. The bio-chemical process of photosynthesis moves carbon from inorganic compartments in the atmosphere and water into the organic com-partment; cellular respiration reverses this flux. Carbon dioxide and methane move from their atmospheric compartments into the much larger compartments in the oceans when they dissolve, and they are returned to the atmo-sphere by outgassing; both of these movements are purely physical processes. The rate at which CO_2 dissolves is slightly greater than the rate at which it is outgassed, for two reasons. First, some of the dissolved CO_2 is converted into organic compounds by marine primary pro-duction. Most of this carbon is then recycled through the trophic interactions of aquatic organisms, but gravity moves a steady rain of nonliving organic matter into sediments in the benthic zone, where geological processes transform it eventually into **fossil fuels** such as coal, natural gas, and petroleum. Second, some of the dissolved CO_2 is incorporated into relatively insoluble carbonate compounds, especially calcium carbonate. These also ulti-mately reach the sediments and form carbonate rocks such as limestone. The chemical reactions involved in carbonate formation are inorganic, but they are orchestrated by marine organisms when they form their shells (see Figure 20.10).

Human activities influence the carbon cycle in a number of ways. Anything that changes primary productivity, such as nitrogen de-position or altered land use, alters the move-ment of carbon between inorganic and organic compartments. Any activity that affects water
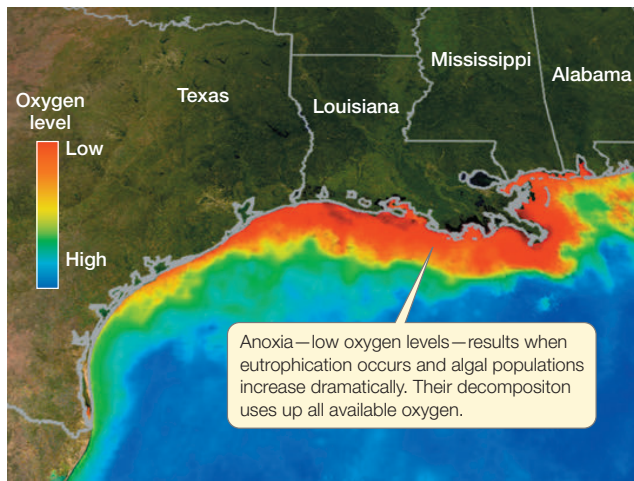
FIGURE 45.9 High Nutrient Input Creates Dead Zones   Runoff from agricultural lands in the midwestern United States carries nitrogen and phosphorus down the Mississippi River and into the Gulf of Mexico. The resulting eutrophication creates an oxygen-poor "dead zone" that few aquatic organisms other than microbes can tolerate.

Anoxia—low oxygen levels—results when eutrophication occurs and algal populations increase dramatically. Their decomposition uses up all available oxygen.

APPLY THE CONCEPT

Certain biogeochemical cycles are especially critical for ecosystems

Figure 45.10 depicts the global carbon cycle, showing organic and inorganic pools of carbon in various compartments as well as fluxes. Refer to that figure to answer the following questions.

1. What percentage of the flux of carbon from terrestrial ecosystems into the atmosphere is due to human activities?

2. What other flux of carbon from terrestrial ecosystems is being influenced by humans, and how?

3. Given the biogeochemical cycles we have discussed so far, which additional two cycles of materials would you wish to explore next in order to understand ecosystem function, and why? (Hint: Consider the major chemical constituents of living tissue, discussed in Concept 2.1.)

The atmosphere is the immediate source of inorganic carbon for terrestrial organisms.

Dissolved CO_2 in the photic zone is available for aquatic primary producers.

The two largest reservoirs of carbon are carbon-containing minerals in rocks and fossil fuels.
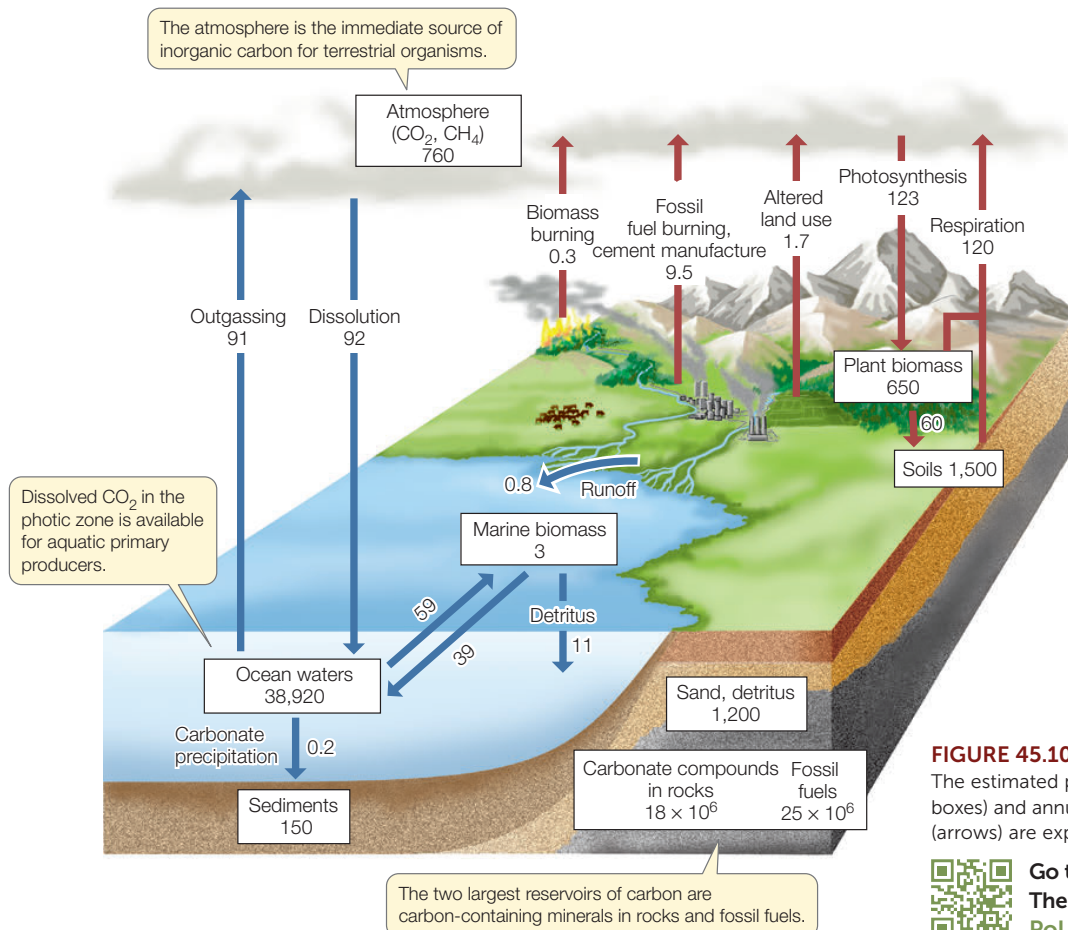
FIGURE 45.10 The Global Carbon Cycle
The estimated pools in compartments (white boxes) and annual fluxes between compartments (arrows) are expressed in units of 10^{15} grams.

**Go to ANIMATED TUTORIAL 45.3
The Global Carbon Cycle**
PoL2e.com/at45.3

runoff, such as deforestation or impoundment or alteration of river flows, affects the movement of carbon between the terrestrial and aquatic compartments. Burning of organic matter, whether biomass or fossil fuels, increases the atmospheric pool of CO_2, as does the heating of calcium carbonate in the manufacture of cement. The atmospheric pool of methane (CH_4) is increased by livestock production, rice cultivation, and water storage in reservoirs, because microbes in the guts of cattle and in waterlogged sediments break down organic compounds anaerobically to produce methane gas. Although the atmospheric pool of CH_4 is far smaller than that of CO_2, both are potent absorbers of infrared radiation and affect Earth's radiation balance, as we will soon see.

Biogeochemical cycles are not independent

The water, nitrogen, and carbon cycles illustrate the diversity of processes, relative sizes of pools and fluxes, and spatial and temporal scales that are involved in the cycling of materials within the Earth system. As you can imagine, there is even more variation if we consider other materials with different chemical and physical properties. For example, few forms of phosphorus are gases, and the phosphorus cycle lacks a significant atmospheric component. Similarly, sulfur released into the atmosphere by volcanic eruptions reacts with other gases to form tiny, airborne particles that affect Earth's radiation balance (See Concept 45.4).

Go to ACTIVITY 45.1 The Phosphorus and Sulfur Cycles
PoL2e.com/at45.1

This diversity does not mean that different biogeochemical cycles are entirely independent of one another, however. The cycles of many materials are at least partly linked, for several reasons.

First, the fluxes of different materials are linked if those fluxes share common physical or chemical processes. For example, many elements, including carbon, nitrogen, phosphorus, and sulfur, have water-soluble forms, which are transported together in precipitation and runoff. If runoff increases, the fluxes of all water-soluble materials from terrestrial to aquatic compartments will increase.

Second, the fluxes of different materials through communities are linked because the functional macromolecules in living tissue—proteins, nucleic acids, polysaccharides, and so forth—have a precise structure with fixed proportions of elemental building blocks. Thus when biomass is produced, there is coordinated movement of these building blocks into living organic compartments, and when biomass is decomposed or burned, they all move back into inorganic compartments.

Fluxes can also interact in more subtle ways. Increased atmospheric concentrations of CO_2, for example, can increase the water-use efficiency of many terrestrial plants. These plants obtain the CO_2 they need for photosynthesis by opening their stomata, which also leads to transpiration—the loss of water vapor from their tissues. In a high-CO_2 environment, these plants can leave their stomata open for a shorter time and therefore transpire less water, which slows the rate of water movement from soil to the atmosphere.

Biogeochemical cycles with significant atmospheric pools can be especially important for Earth's climate, as we will see next.

CONCEPT **Biogeochemical Cycles**
45.4 **Affect Global Climate**

Concept 41.2 discussed how latitudinal and seasonal variations in the input of solar radiation drive global climate patterns. Earth's climate is also influenced by the particular mix of gases that make up the atmosphere. As we saw in the opening story of this chapter, scientists have long known that some of these gases—particularly water vapor and carbon dioxide—absorb infrared radiation. Interactions of infrared-absorbing molecules with solar radiation have a profound effect on the radiation budget of the planet.

Earth's surface is warm because of the atmosphere

All objects that are warmer than absolute zero—our sun included—emit electromagnetic radiation (see Figure 6.16). The wavelengths emitted by an object depend on its temperature: hotter objects radiate at shorter, more energetic wavelengths. Because the surface of the sun is so hot—about 6,000°C—its radiation distribution peaks at wavelengths visible to the human eye. What happens to the incoming photons? Approximately 23 percent of them hit aerosols (tiny airborne particles and water droplets or ice crystals in clouds) and gas molecules in the atmosphere and are reflected back into space. Another 8 percent are reflected back into space when they hit Earth's surface. About 20 percent are absorbed, rather than reflected, by gas molecules in the atmosphere. Finally, about 49 percent of incoming solar energy (168 watts per square meter, averaged across day and night, all seasons, and all locations) is absorbed at Earth's surface (**FIGURE 45.11**).

The warmed surface of Earth in turn reemits photons, but at much longer, less energetic, infrared wavelengths (wavelengths beyond the red end of the visible spectrum, which we perceive as heat). Some of this infrared radiation is absorbed by greenhouse gas molecules rather than escaping immediately into space. Those molecules reradiate infrared photons back to Earth's surface, keeping the energy within the lower atmosphere. The additional warming of Earth caused by greenhouse gas molecules is called the **greenhouse effect**.

Reflected solar radiation
31

Reflected by clouds, aerosols, and atmospheric gases
23

Reflected by surface
8

Incoming solar radiation
100

Radiation absorbed by atmosphere
20

Absorbed by surface
49

Earth's surface is warmed by incoming solar radiation and by back radiation from greenhouse gases. This additional warming increases the outward radiation from the surface.

Infrared radiation lost to space
69

Emitted by atmosphere
48

Emitted by clouds
9

Atmospheric transmission
12

Outward radiation

Emitted by surface
114

Absorbed by surface
95

Greenhouse gases in the atmosphere absorb much of the surface reradiation…

Back radiation

…and radiate it back to the surface.

FIGURE 45.11 Earth's Radiation Budget   The average annual energy gain from incoming short-wave solar radiation that is absorbed by Earth's surface and atmosphere (left-hand portion of figure) is balanced by the average annual loss to outer space in the form of long-wave (infrared) radiation (right-hand portion of figure). Greenhouse gases in the lower atmosphere absorb some of the infrared radiation emitted by Earth's surface and radiate it back to the surface, adding to the warming caused by solar radiation. This "greenhouse effect" is sufficiently strong that the total infrared radiation emitted by the surface exceeds the average flux of incoming solar radiation at the top of the atmosphere (342 watts/m^2 averaged across day and night at all locations and over all seasons). All fluxes (arrows) are given as percentages of this average.

Go to ANIMATED TUTORIAL 45.4
Earth's Radiation Budget
PoL2e.com/at45.4

Water vapor, carbon dioxide, methane, nitrous oxide, and other molecules that absorb infrared radiation are referred to as **greenhouse gases**. The pools of these molecules in the atmosphere influence how much energy is retained in the lower atmosphere. Without its atmosphere, Earth's average surface temperature would be a frigid –18°C, about 34°C colder than it is at present. The greenhouse effect influences any planet with an atmosphere, but its magnitude depends on the amounts and types of materials in the atmosphere. Mars's thin atmosphere warms its surface by only 3°C, whereas the thick atmosphere of Venus warms that planet's surface by a whopping 468°C.

Recent increases in greenhouse gases are warming Earth's surface

Improved methods for measuring the content of air samples accurately—such as Dave Keeling's precise methods for measuring CO_2—show us that the composition of the atmosphere is changing. The measurements initiated by Keeling reveal a steady increase in atmospheric CO_2 over the last half century (**FIGURE 45.12A**). Analyses of air trapped in glacial ice demonstrate that CO_2 and other greenhouse gases have been increasing even longer—since about 1880 (**FIGURE 45.12B**).

Average annual global temperatures have followed suit (**FIGURE 45.13**).

This **global warming** is affecting patterns of climate worldwide. A warmer Earth means not only hotter air temperatures, but also more intense fluxes of water, with greater overall evaporation and precipitation. Hadley cells (see Concept 41.2) are expected to expand poleward because warmer tropical air will rise higher in the atmosphere and expand farther toward the poles before sinking. This expansion should cause precipitation to increase near the equator and at high latitudes and to decrease at middle latitudes. Global warming is uneven across Earth's surface—for instance, the tropical Pacific and western Indian Oceans are warming more than other waters, and high latitudes are warming faster than low latitudes. As a result, changes in precipitation will be season- and region-specific, but in general, wet regions are expected to get wetter and dry regions drier. Precipitation trends over the twentieth century appear to support these expectations (**FIGURE 45.14**). Global warming is also predicted to increase storm intensity and weather variability. Recent analyses indicate that hurricane numbers have not increased, but strong hurricanes (category 4 and 5) and "megastorms" such as 2012's Sandy have become more frequent since the 1970s.

(A)
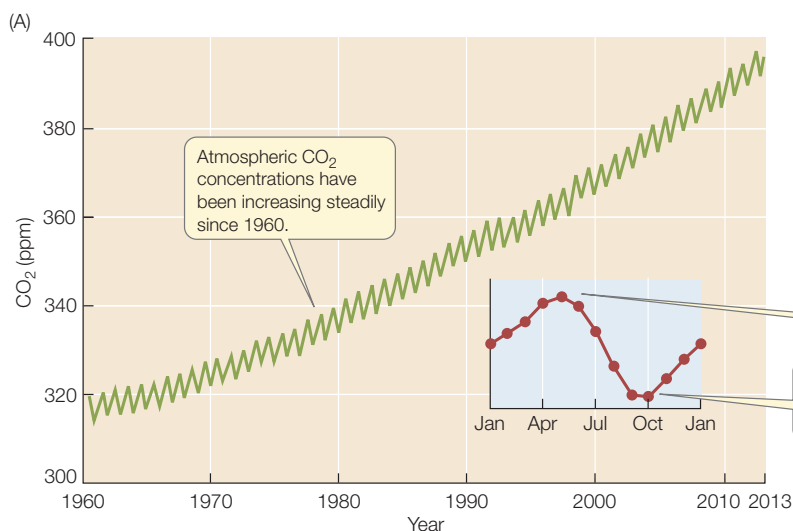
FIGURE 45.12 Atmospheric Greenhouse Gas Concentrations Are Increasing (A) The Keeling curve shows measurements of atmospheric CO_2 concentrations atop Mauna Loa, Hawaii, expressed as parts per million (ppm) by volume of dry air. (B) Measurements of air trapped in glacial ice have allowed researchers to extend our record of greenhouse gas concentrations back 2,000 years. Concentrations are expressed as parts per million (ppm) for CO_2 and parts per billion (ppb) for nitrous oxide (N_2O) and methane (CH_4).

Atmospheric CO_2 concentrations have been increasing steadily since 1960.

Each year CO_2 concentrations rise during the Northern Hemisphere winter, when respiration exceeds photosynthesis.

CO_2 concentrations then fall during the Northern Hemisphere summer, when photosynthesis exceeds respiration.

Go to MEDIA CLIP 45.2
Time-Lapse of Global CO_2 Emissions
PoL2e.com/mc45.2

(B)

Atmospheric concentration of N_2O and CH_4, as well as of CO_2, increased dramatically starting around 1880.

Carbon dioxide (CO_2)

Nitrous oxide (N_2O)

Methane (CH_4)
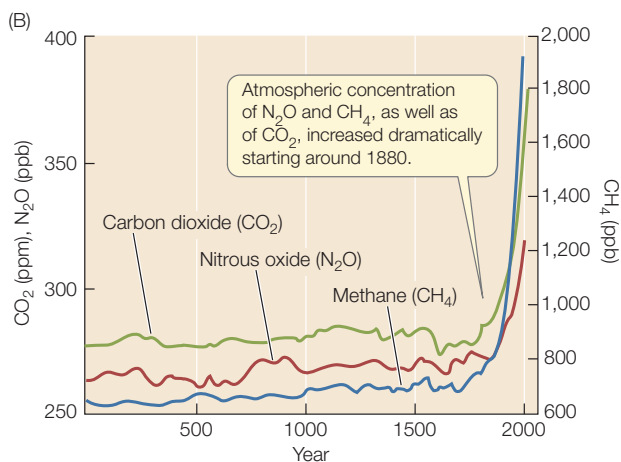
Human activities are contributing to changes in Earth's radiation budget

As we saw in Concept 45.3, human activities are affecting Earth's biogeochemical cycles. Fossil fuel burning, cement manufacture, and forest clearing are adding CO_2 to the atmosphere; expanded livestock production, water impoundment, and wetland crop cultivation are adding CH_4 and N_2O through anaerobic microbial metabolism. Other human activities are also influencing Earth's radiation budget. Expansion of livestock grazing, agriculture, and offroad vehicle traffic in arid regions is increasing airborne dust. Dust and dark-colored soot particles ("black carbon") from fossil fuel burning that are deposited on snow and ice increase absorption of incoming solar energy. The result is faster melting of persistent ice fields such as the Greenland ice sheet and Arctic sea ice, as well as advanced timing of spring snowmelt in temperate regions.

Other human activities have the potential to counteract these effects. Increasing amounts of aerosols in the atmosphere and land clearing, for example, increase the amount of solar radiation that is reflected. When climate scientists incorporate all of these effects into quantitative computer models of Earth's climate, however, they conclude that human activities are contributing significantly to global warming and all the aspects of climate change that go with it (see Apply the Concept, p. 930).

Average annual global temperatures have been increasing in concert with greenhouse gases.
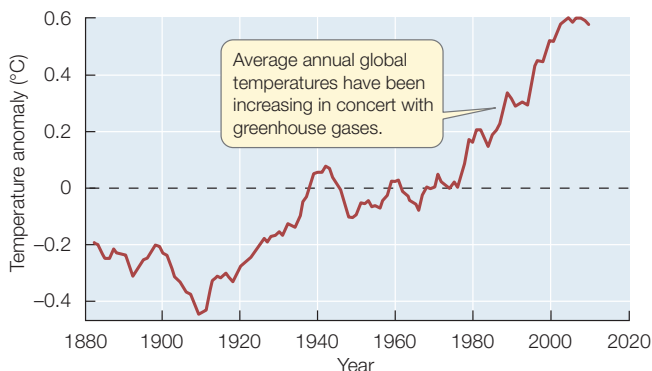
FIGURE 45.13 Average Annual Global Temperatures Are Increasing The curve shows the deviation from the average global temperature for the period 1951–1980 (indicated by 0).

CHECKpoint CONCEPT **45.4**

✓ What factors caused the dramatic increases in carbon dioxide and methane in the atmosphere that became apparent by the late 1800s? (See Figure 45.12B. Hint: See also Figure 42.9.)

✓ Is the greenhouse effect something that occurs without humans, or is it caused by humans?

✓ Why is global warming linked to a greater intensity of storms? (Hint: Consider Concept 41.2.)
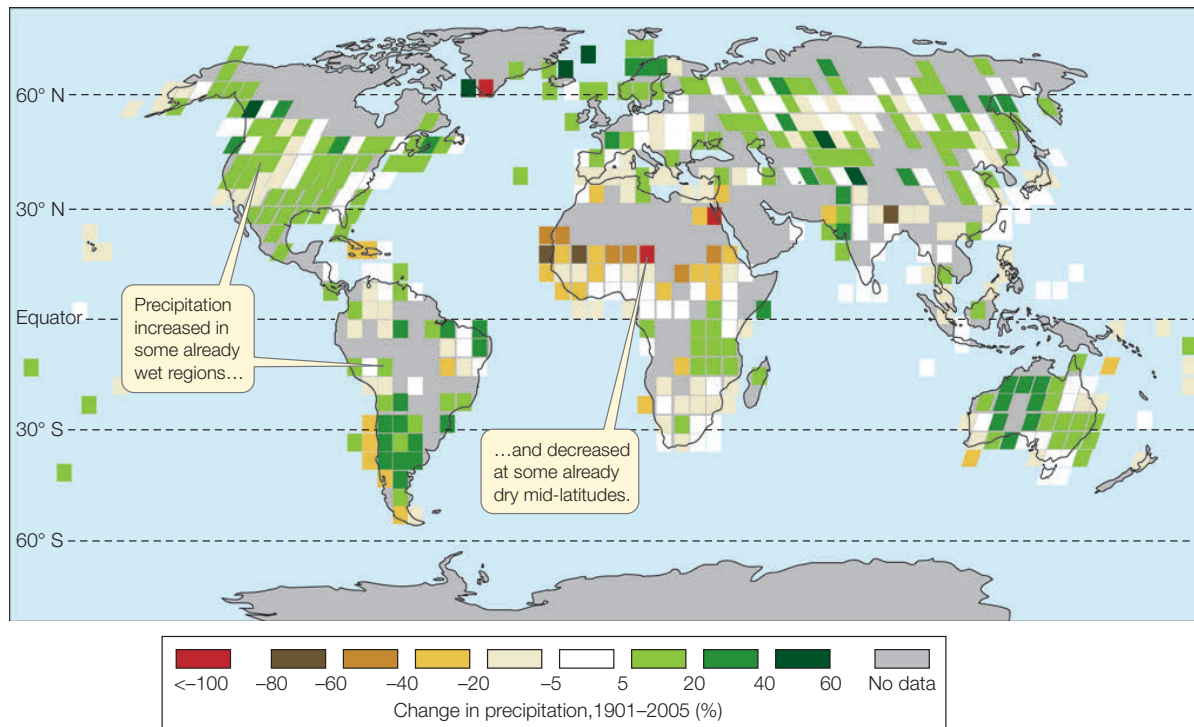
FIGURE 45.14 Global Precipitation Patterns Have Changed   Over the twentieth century, precipitation increased at high latitudes and in some tropical regions, but decreased at some already dry mid-latitudes. Note, however, that much regional variation is apparent.

Now that we have seen how human activities are changing Earth's radiation budget and climate, we can consider how ecological systems are responding.

> ## CONCEPT 45.5 Rapid Climate Change Affects Species and Communities

Climate change is not expected to affect all ecosystems in the same way because the changes are not distributed evenly around the globe or across the seasons. As we have seen, some parts of the planet are getting drier while others are getting wetter (see Figure 45.14), and some parts are warming much faster than others. In all cases, however, recent climate change has been far more rapid than what organisms have experienced in their evolutionary histories.

Rapid climate change presents ecological challenges

The life histories of organisms are shaped by their environment, as we saw in Concept 42.3. Thus organisms that live in seasonal environments have adaptations to ensure that crucial life events occur at favorable times of the year. Alpine plants, for example, start growing when the snow melts; seeds of desert plants germinate in response to certain combinations of soil temperature and moisture; changes in day length often trigger plant flowering, bird migration, and onset or cessation of insect dormancy. But climate change is altering the relative timing of many such environmental cues: in a warmer world, the day length that once signaled the start of good growing conditions may instead indicate the middle of the growing season. Although species' responses can evolve by natural selection, the rate of such evolution may be too slow, or available genetic variation may be too small, to keep up with an environment that changes too rapidly or that continues to change directionally for too long.

Over the short term, we have evidence that many species are continuing to track environmental changes so that events in their life histories remain within appropriate periods. For example, biological events that mark the end of the winter season in temperate ecosystems—such as the leafing out of trees— have generally been taking place at earlier dates as the climate has warmed. In Britain, the first flowers of a sample of 385 plant species have appeared, on average, 4.5 days earlier per 1°C increase in average temperature. However, this is an *average* value for advances in flowering, and not all species have responded in the same way—some did not shift their time of first flowering, and some now flower later in the spring rather than earlier. Thus some species may not be responding adaptively to climate change at all. Even for those that do, it is unclear that they can continue to track climate change over the long term.

Changes in seasonal timing can disrupt interspecific interactions

Not all environmental cues respond to the same degree, or in the same direction, to climate change, so relationships among

APPLY THE CONCEPT

Biogeochemical cycles affect global climate

The graphs below show the results of computer simulations of Earth's climate between 1850 and 2000. The blue-shaded regions indicate the range of average global temperatures produced by running the simulations many times (encompassing 95% of the outputs from the replicate simulations). The actual observed temperatures are shown by the red lines. The three graphs represent three different sets of assumptions used in the simulations: (A) only natural factors were included, such as solar radiation input, aerosols from volcanic eruptions, and oscillations in oceanic circulation; (B) only anthropogenic (human-generated) factors were included, such as land clearing, soot deposition, and emissions of aerosols and greenhouse gases; and (C) both natural and anthropogenic factors were included. Average global temperatures are expressed as deviation from the average global temperature of the last part of the nineteenth century (indicated by 0).[a] Using these graphs, answer the following questions, and explain your reasoning.
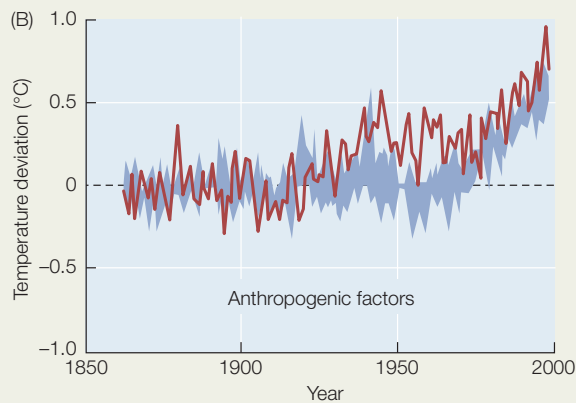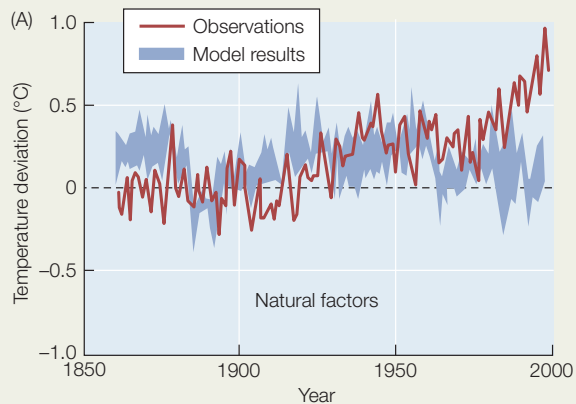
1. What aspects of the observed trends in global temperature are not accounted for by natural factors?

2. What aspects of the observed trends in global temperature are not accounted for by anthropogenic factors?

3. Which set of factors best accounts for the observed global temperature trends?

4. The arrows in panel (C) indicate five major volcanic eruptions. What effect did these natural events have on global temperatures?

[a]www.ipcc.ch/publications_and_data/ar4/wg1/en/contents.html
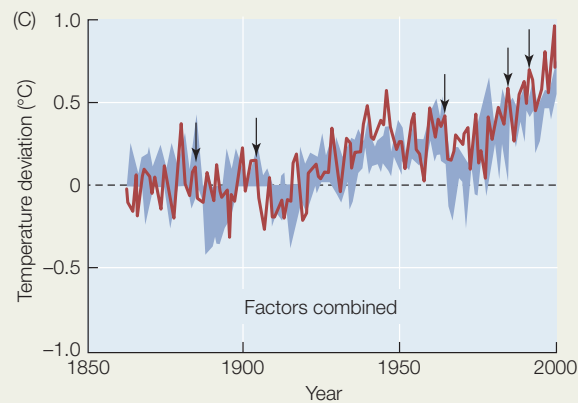
cues are shifting. Because different species make use of different cues, they may respond differently to climate change, as the different British plant species have done. This variation raises the possibility of mismatches in the timing of life history events among species that interact with one another.

Such mismatches are now becoming apparent in nature. In the Netherlands, for example, eggs of the winter moth (*Operophtera brumata*) hatch when temperatures warm after a fixed number of frosts, whereas the leaves of the oak trees on which the winter moth caterpillars feed (*Quercus robur*) emerge when warm days follow a certain number of cool days. The eggs have been hatching earlier, and oak leaves have been appearing earlier, in response to the earlier onset of warm temperatures in spring. The caterpillars do not use the same cues as the oaks, however, and they have been hatching too early and then starving. Great Tits (*Parus major*), which feed on winter moth caterpillars, are not nesting earlier because they use day length as the cue for egg laying (**FIGURE 45.15**). These birds now have less food for their nestlings not only because there are fewer caterpillars overall, but also because they are now feeding their nestlings after the peak in caterpillar abundance has passed. They are experiencing lower fecundity as a result.

Climate change can alter community composition by several mechanisms

If local populations cannot accommodate changing environmental conditions, they will go extinct, and their extinctions will change the species composition of their communities. As we saw in Figure 42.6, *Sceloporus* lizards in the Yucatán of Mexico are experiencing hotter temperatures during the spring

FIGURE 45.15 Climate Change Affects Life Histories   A long-term study in the Netherlands shows that warming temperatures have affected the seasonal cycle of the winter moth *Operophtera brumata*, whose caterpillars are now emerging before the leaves on which they feed have expanded, causing more caterpillars to starve. Great Tits (*Parus major*) are not laying eggs earlier. They now have difficulty finding enough caterpillars to feed their nestlings because they have missed the time of peak caterpillar abundance, and there are fewer caterpillars overall.

breeding season, and this warming restricts the time during which they can forage. The lizards have gone locally extinct where they have insufficient feeding time to support reproduction. Extrapolating to lizards worldwide, researchers predict that continued global warming will place most lizard populations at risk of extinction by the year 2080. Losses of lizards may affect populations of their insect prey, of the plants those insects feed on, and of other animals that also eat the insects. As we saw in Concept 44.3, loss of diversity in communities can lead to overall loss of community function.

Altered relationships between environmental cues can also change communities even if species do not go locally extinct. In southwestern North America, the winter rainy season now arrives later in the fall, after soil temperatures have cooled. This shift favors plant species whose seeds use cool-season moisture as the cue to germinate, at the expense of species whose germination is cued by warm-season moisture. Thus the relative abundance of the cool-season species is increasing in these communities.

Climate-caused shifts in environmental gradients can also lead to the assembly of novel communities (see Concept 44.2). Some species have moved up mountains as their low-elevation habitats become too warm and higher-elevation habitats become more favorable. Others have moved toward higher latitudes for similar reasons; such poleward shifts have been documented for numerous taxonomic groups. Different species shift to different degrees or not at all (as is true of shifts in timing of life history events), so the mixture of species at any place changes. These distributional shifts also influence species interactions. Warmer temperatures in western North America, for example, are speeding up the life history of the mountain

bark beetle (*Dendroctonus ponderosae*) and decreasing its winter mortality rate. As a result, beetle populations have increased and expanded, causing widespread tree mortality in pine and spruce forests from New Mexico to Alaska. Loss of the conifers has cascading effects on the consumers that depend on them, as well as on water runoff, wildfire frequency, and NPP.

Extreme weather events also have an impact

One of the predictions of climate models is that the frequency of extreme weather events will increase. Severe storms, flooding, droughts, heat waves, and other such events can elicit sudden shifts in species distributions and in community composition. For example, a brief but intense drought in the 1950s caused a ponderosa pine forest in northern New Mexico to shrink abruptly, and drought-adapted piñon–juniper woodland to expand, by more than 2 kilometers in less than 5 years. The new community boundary remained stable even after the drought ended. This is the most rapid shift in the boundary between two terrestrial plant communities so far documented at the scale of an entire landscape.

Such a response to an out-of-the-ordinary event might suggest that species are always able to change their geographic distributions rapidly in response to climate change. But as is true with shifts in timing, it remains virtually certain that many species will be left behind by continued shifts in environmental conditions, and that the number of species, their relative abundances, and their interactions will be altered in communities worldwide.

CHECKpoint   CONCEPT 45.5

✓ Extrapolating from the British plant data, what change might you anticipate in average first flowering date by the middle of this century, when atmospheric CO_2 is predicted to reach double its preindustrial concentration and the average temperature in Britain is expected to rise by an additional 3°C?

✓ How might changes in the seasonal timing of some events (such as the onset of warm weather at the end of winter) affect mutualistic interactions between plants and insect pollinators?

The changes that human activities are causing in Earth's biogeochemical cycles and in its climate have serious ecological implications. What can we do to address them?

CONCEPT 45.6   Ecological Challenges Can Be Addressed through Science and International Cooperation

The current period of climate change is not unprecedented. Throughout the history of life on Earth, wobble in the planet's orbit around the sun, continental drift, volcanic activity, sunspots, and even asteroid impacts have caused Earth's climates to change, precipitating five major episodes of mass extinction

(see Figure 18.12). There is even precedent for organism-caused change in the atmosphere. The first photosynthetic microbes increased atmospheric oxygen concentrations to a level that was toxic to the anaerobic prokaryotes that inhabited Earth at the time, and the first land plants raised oxygen concentrations even more about 250 million years ago. What is unprecedented about the present climate change is that it has been precipitated by diverse activities of a single species: *Homo sapiens*.

It is sobering to realize that one species can wield such power. However, it is encouraging to realize that, of all species on Earth, humans are uniquely able to address the problems they have caused—not only because science equips us to understand the natural world and to solve problems, but also because *Homo sapiens* has a remarkable capacity for cooperative action. We certainly are capable of selfishness and conflict too, but cooperative interactions are central features of all functional human societies. Other group-living animals cooperate as well, but scientific studies show that cooperation with unrelated individuals is especially highly developed in humans—even as infants we routinely offer help to another individual in need. We support cooperative societal ventures of all sorts, we police "bad" behaviors that can undermine cooperation—and we are unique, as far as we now know, in caring about the other species with which we share planet Earth.

The scale of cooperative human groups has gradually expanded through human history from prehistoric hunter–gatherer family groups to the United Nations, which spans the planet. It is encouraging that governments of separate nations have been cooperating in several global-scale initiatives to tackle complex environmental issues, from the IGY, which supported the first years of Dave Keeling's work, to the United Nations' Intergovernmental Panel on Climate Change and World Meteorological Organization, which operate today. Earth's nations have also negotiated international agreements to achieve environmental goals, including the Montreal Protocol to prevent depletion of UV-absorbing atmospheric ozone, the Kyoto Protocol to reduce emissions of greenhouse gases, and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which seeks to conserve species by eliminating the economic benefits of exploiting them.

Go to ACTIVITY 45.2 The Benefits of Cooperation
PoL2e.com/ac45.2

Nonetheless, humans face huge challenges to achieving effective cooperation on a global scale. A major challenge is that the economic policies of virtually every nation are structured to achieve continual economic growth—ever-increasing production and consumption of goods and services—despite the fact that Earth has a finite capacity to provide those goods and services. We will need to make the transition to sustainable, steady-state economies, and that will require an overhaul of economic models and institutions. Another, related, challenge is the continued multiplicative growth of the human population (see Concept 42.4). On a crowded planet, with competition among societies for limited resources, cooperation inevitably becomes more

difficult. Addressing both challenges will require us to devise international systems for establishing—and enforcing—rules of acceptable behavior among groups and nations.

Q How did Keeling's research contribute to our understanding of the global ecosystem?

ANSWER Dave Keeling's four decades of research left an important legacy, the Keeling curve (see Figure 45.12A), which documents the ongoing increase in atmospheric CO_2 (Concept 45.4). Almost immediately, Keeling discovered that CO_2 concentrations do not vary erratically, as earlier crude methods of measurement suggested, but instead change seasonally as summer warmth, and the primary productivity that goes with it, shifts from the Northern Hemisphere (where most of Earth's land mass lies) to the Southern Hemisphere (see Figure 45.12A inset).

Keeling's measurements quickly contributed to a better understanding of the pools and fluxes of the global carbon cycle (Concept 45.3), including the influence of fossil fuel burning and cement production (which together added 9.5×10^{15} g of carbon—and 34.7×10^{15} g of carbon dioxide—to the atmosphere in 2011). Measurements on Mauna Loa and elsewhere continue to the present day, and they show that CO_2 increased from 315 parts per million (ppm) in the atmosphere in 1958 to 399 ppm in July 2013. Better understanding of the carbon cycle has contributed to greatly improved global climate models.

Keeling's results were noticed almost immediately. In 1965 the U.S. President's Science Advisory Committee warned of the increasing greenhouse effect, and in 1966 the National Academy of Sciences issued a scholarly report on the topic. The first World Climate Conference was held in Geneva, Switzerland, in 1979, at a time when there was growing scientific consensus that climate change poses a critical environmental challenge (Concept 45.5). The number of scientists studying climate change, and the sophistication of their experiments and models, grew rapidly. At the end of the twentieth century, measurements showed that the average temperature of the planet had increased by 0.7°C since 1900—an increase very close to the predictions of global climate models.

The Keeling curve forms a crucial part of our understanding of the Earth system. It is an example of the carefully documented scientific information used by the Intergovernmental Panel on Climate Change (IPCC). The IPCC was formed in 1988 by another scientific collaboration of governments—a sort of "grandchild" of IGY—and its many scientists continue to summarize and report on the latest evidence for natural and human-caused climate change. The 2009 IPCC report predicted a further human-caused increase in the global average temperature of between 1.8°C and 4.0°C by the year 2100.

We have a civilization based on science and technology, and we've cleverly arranged things so that almost nobody understands science and technology. That is as clear a prescription for disaster as you can imagine. While we might get away with this combustible mixture of ignorance and power for a while, sooner or later it's going to blow up in our faces. The powers of modern technology are so formidable that it's insufficient just to say, 'Well, those in charge, I'm sure, are doing a good job.' This is a democracy, and for us to make sure that the powers of science and technology are used properly and prudently, we ourselves must understand science and technology. We must be involved in the decision-making process.

Carl Sagan

SUMMARY

CONCEPT 45.1 Climate and Nutrients Affect Ecosystem Function

■ The term **ecosystem** is commonly applied to ecological communities plus the abiotic environments with which they exchange energy and materials.

■ A community's net primary productivity (NPP) reflects the rate at which it exchanges energy and materials with its abiotic surroundings, and is thus a measure of **ecosystem function**.

■ NPP varies considerably among ecosystem types. **Review Figure 45.1**

■ The global pattern of variation in terrestrial NPP shows that it is influenced by temperature and precipitation. Soil nutrients also play a role in terrestrial NPP. **Review Figures 45.2 and 45.3**

■ Aquatic NPP varies most strongly with availability of light and nutrients. **Review Figure 45.4**

CONCEPT 45.2 Biological, Geological, and Chemical Processes Move Materials through Ecosystems

■ The chemical form in which an element exists and where it occurs on Earth determine whether the element is accessible to life. Alternative forms and locations of matter can be thought of as **compartments** of the global ecosystem

■ The chemical transformations and physical transport of elements or molecules that move them among compartments are called **biogeochemical cycles**. **Review Figure 45.5**

■ The **pool**, or amount, of an element or molecule in a compartment depends on its flows, or **fluxes**, into and out of that compartment.

CONCEPT 45.3 Certain Biogeochemical Cycles Are Especially Critical for Ecosystems

■ Solar-powered evaporation drives the water cycle, moving water into the atmosphere in gaseous form. Condensation and precipitation return water to Earth's surface. Gravity-driven flows move water from land to lakes and oceans. **Review Figure 45.6 and ANIMATED TUTORIAL 45.1**

■ The availability of nitrogen to living organisms depends on **nitrogen fixation** and other biochemical processes carried out by microbes. These processes convert gaseous N_2 into forms that other organ-

isms can use. Other microbial processes return N_2 to the atmosphere. **Review Figure 45.7 and ANIMATED TUTORIAL 45.2**

■ Human activities add various chemical forms of nitrogen to the atmosphere, where they contribute to smog and acid rain, to terrestrial systems, where they act as fertilizers, and to aquatic systems, where they cause **eutrophication**. **Review Figure 45.9**

■ Photosynthesis and respiration move carbon between inorganic and organic compartments. As a result, energy flow and the flux of carbon through biological communities are intimately linked.

■ Some carbon absorbed from the atmosphere by ocean waters is taken up through photosynthesis, some precipitates as carbonate compounds, and some sinks to the benthic zone as dead organic material. Carbonate compounds and organic material that accumulate in sediments and soils are transformed into carbonate rocks and **fossil fuels**.

■ Humans are increasing the carbon pool in the atmosphere by burning fossil fuels, manufacturing cement, raising livestock, and raising wetland crops. **Review Figure 45.10 and ANIMATED TUTORIAL 45.3**

■ The biogeochemical cycles of different materials are linked when the same physical, chemical, or biological processes drive their fluxes. **Review ACTIVITY 45.1**

CONCEPT 45.4 Biogeochemical Cycles Affect Global Climate

■ Earth absorbs incoming solar radiation and reemits it at infrared wavelengths. Some of this infrared radiation is absorbed by atmospheric gases and is reradiated back to Earth's surface. The resulting retention of heat energy within the Earth system is called the **greenhouse effect**. **Review Figure 45.11 and ANIMATED TUTORIAL 45.4**

■ Gases such as water vapor, carbon dioxide, methane, and nitrous oxide that absorb infrared radiation are called **greenhouse gases**. The pools of these molecules in the atmosphere influence Earth's radiation budget.

■ Atmospheric concentrations of CO_2 and other greenhouse gases have been increasing rapidly since about 1880, and average annual global temperatures have followed suit. **Review Figures 45.12 and 45.13**

(continued)

SUMMARY *(continued)*

- **Global warming** is changing Earth's climates. High latitudes are warming more than low latitudes, precipitation patterns are changing, and storm intensities are increasing. **Review Figure 45.14**

- Computer models of the Earth system show that human activities have contributed significantly to the recent warming of the climate.

CONCEPT 45.5 Rapid Climate Change Affects Species and Communities

- Climate change is altering the timing of some seasonal environmental cues but not others. Although species sometimes can evolve new responses to such cues, the rate of evolution will not keep up with an environment that changes too rapidly.

- Because different species respond to different seasonal cues, altered cues result in timing mismatches among species in a community and thus disrupt their interactions.

- Climate change is altering the distributions and abundances of species, resulting in the assembly of novel communities.

- Climate change is increasing the frequency of extreme weather events, which can cause sudden shifts in species distributions and in community composition.

CONCEPT 45.6 Ecological Challenges Can Be Addressed through Science and International Cooperation

- Humans are causing major changes in the biosphere and in other aspects of the Earth system. However, we are also uniquely equipped to address these changes, not only because science enables us to understand the natural world and to devise solutions to problems, but also because of our capacity for cooperative action. **Review ACTIVITY 45.2**

See **ACTIVITY 45.3** for a concept review of this chapter.

Go to the Interactive Summary to review key figures, Animated Tutorials, and Activities PoL2e.com/is45

Go to LaunchPad at **macmillanhighered.com/launchpad** for additional resources, including LearningCurve Quizzes, Flashcards, and many other study and review resources.

Appendix A   The Tree of Life

Phylogeny is the organizing principle of modern biological taxonomy. A guiding principle of modern phylogeny is monophyly. A monophyletic group is one that contains an ancestral lineage and all of its descendants. Any such group can be extracted from a phylogenetic tree with a single "cut" of the tree. The cut lineage, with all of its descendant taxa, is a monophyletic group. Biologists give names to the major monophyletic groups of life so that we may refer to them easily.

The tree shown here provides a guide to the relationships among the major groups of extant (living) organisms in the tree of life as we have presented them throughout this book. The position of the branching "splits" indicates the relative branching order of the lineages of life, but the time scale is not meant to be uniform. In addition, the groups appearing at the branch tips do not necessarily carry equal phylogenetic "weight." For example, the ginkgo [75] is indeed at the apex of its lineage; this gymnosperm group consists of a single living species. In contrast, a phylogeny of the eudicots [83] could continue on from this point to fill many more trees the size of this one.

The glossary entries that follow are informal descriptions of some major features of the organisms described in Part Four of this book. We show greater detail about the relationships and content of some groups than we have presented in this book so that this appendix may serve as a reference. Each entry gives the group's common name, followed by the formal scientific name of the group (in parentheses). Numbers in square brackets reference the location of the respective groups on the tree.

It is sometimes convenient to use an informal name to refer to a collection of organisms that are not monophyletic but nonetheless all share (or all lack) some common attribute. We call these "convenience terms"; such groups are indicated in these entries by quotation marks, and we do not give them formal scientific names. Examples include "prokaryotes," "protists," and "algae." Note that these groups cannot be removed with a single cut; they represent a collection of distantly related groups that appear in different parts of the tree.

A

acorn worms (*Enteropneusta*)   Benthic marine hemichordates [119] with an acorn-shaped proboscis, a short collar (neck), and a long trunk.

"algae"   Convenience term encompassing various distantly related groups of aquatic, photosynthetic eukaryotes [4].

alveolates (*Alveolata*) [5]   Unicellular eukaryotes with a layer of flattened vesicles (alveoli) supporting the plasma membrane. Major groups include the dinoflagellates [51], apicomplexans [50], and ciliates [49].

amborella (*Amborella*) [78]   An understory shrub or small tree found only on the South Pacific island of New Caledonia. Thought to be the sister group of the remaining living angiosperms [15].

ambulacrarians (*Ambulacraria*) [29]   The echinoderms [118] and hemichordates [119].

amniotes (*Amniota*) [36]   Mammals, reptiles, and their extinct close relatives. Characterized by many adaptations to terrestrial life, including an amniotic egg (with a unique set of membranes—the amnion, chorion, and allantois), a water-repellant epidermis (with epidermal scales, hair, or feathers), and, in males, a penis that allows internal fertilization.

amoebozoans (*Amoebozoa*) [84]   A group of eukaryotes [4] that use lobe-shaped pseudopods for locomotion and to engulf food. Major amoebozoan groups include the loboseans, plasmodial slime molds, and cellular slime molds.

amphibians (*Amphibia*) [128]   Tetrapods [35] with glandular skin that lacks epidermal scales, feathers, or hair. Many amphibian species undergo a complete metamorphosis from an aquatic larval form to a terrestrial adult form, although direct development is also common. Major amphibian groups include frogs and toads (anurans), salamanders, and caecilians.

amphipods (*Amphipoda*)   Small crustaceans [116] that are abundant in many marine and freshwater habitats. They are important herbivores, scavengers, and micropredators, and are an important food source for many aquatic organisms.

angiosperms (*Anthophyta* or *Magnoliophyta*) [15]   The flowering plants. Major angiosperm groups include the monocots [82], eudicots [83], and magnoliids [81].

animals (*Animalia* or *Metazoa*) [19]   Multicellular heterotrophic eukaryotes. The majority of animals are bilaterians [22]. Other groups of animals include the sponges [20], ctenophores [95], placozoans [96], and cnidarians [97]. The closest living relatives of the animals are the choanoflagellates [91].

annelids (*Annelida*) [105]   Segmented worms, including earthworms, leeches, and polychaetes. One of the major groups of lophotrochozoans [24].

anthozoans (*Anthozoa*)   One of the major groups of cnidarians [97]. Includes the sea anemones, sea pens, and corals.

anthropoids (*Haplorhini*)   A group of primate mammals [129] that consists of tarsiers, monkeys, and apes.

anurans (*Anura*)   Comprising the frogs and toads, this is the largest group of living amphibians [128]. They are tailless, with a shortened vertebral column and elongate hind legs modified for jumping. Many species have an aquatic larval form known as a tadpole.

apicomplexans (*Apicomplexa*) [50]   Parasitic alveolates [5] characterized by the possession of an apical complex at some stage in the life cycle.

arachnids (*Arachnida*)   Chelicerates [114] with a body divided into two parts: a cephalothorax that bears six pairs of appendages (four pairs of which are usually used as legs) and an abdomen that bears the genital opening. Familiar arachnids include spiders, scorpions, mites and ticks, and harvestmen.
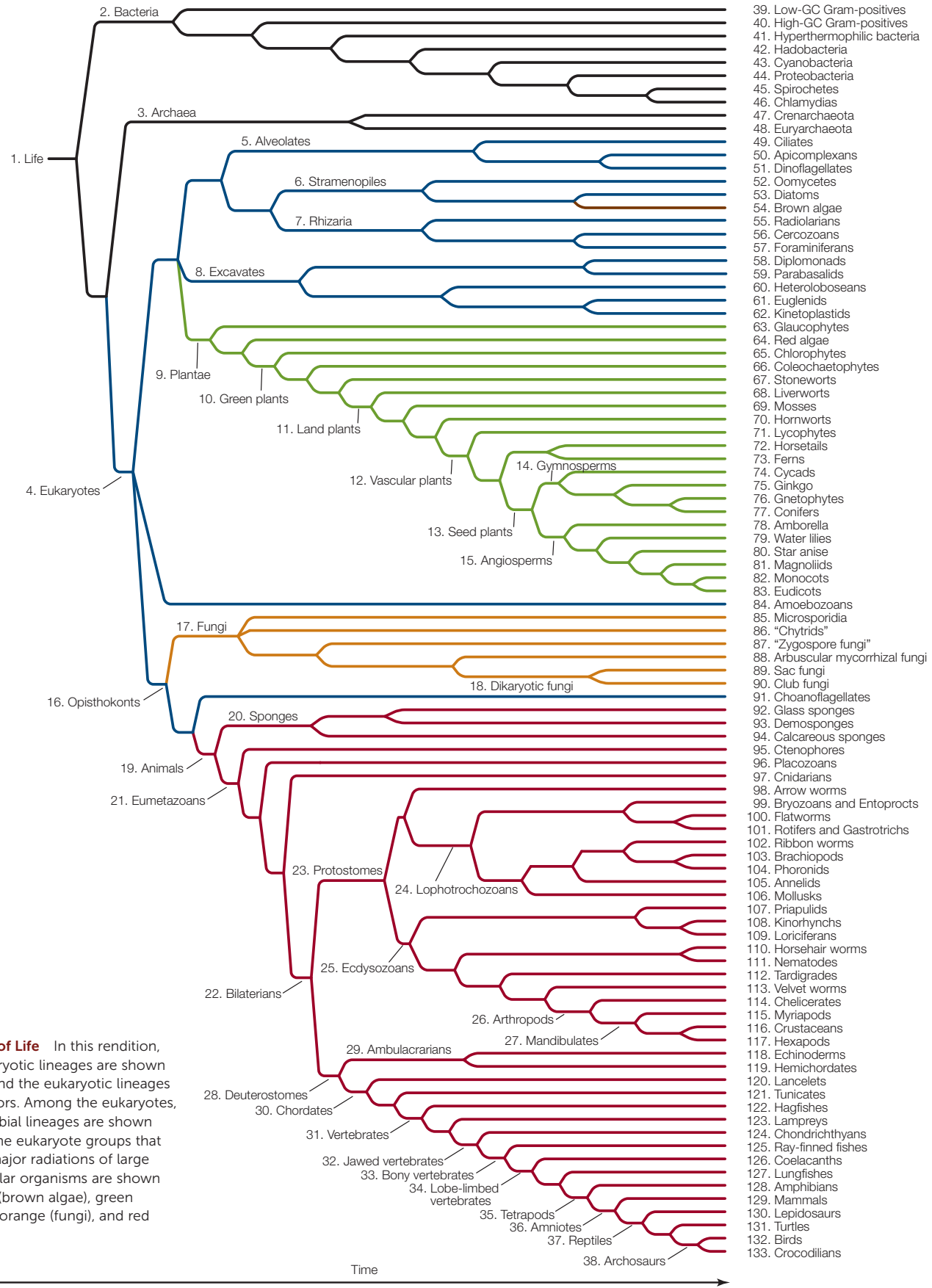
The Tree of Life In this rendition, the prokaryotic lineages are shown in black and the eukaryotic lineages are in colors. Among the eukaryotes, the microbial lineages are shown in blue. The eukaryote groups that contain major radiations of large multicellular organisms are shown in brown (brown algae), green (Plantae), orange (fungi), and red (animals).

1. Life
2. Bacteria
3. Archaea
4. Eukaryotes
5. Alveolates
6. Stramenopiles
7. Rhizaria
8. Excavates
9. Plantae
10. Green plants
11. Land plants
12. Vascular plants
13. Seed plants
14. Gymnosperms
15. Angiosperms
16. Opisthokonts
17. Fungi
18. Dikaryotic fungi
19. Animals
20. Sponges
21. Eumetazoans
22. Bilaterians
23. Protostomes
24. Lophotrochozoans
25. Ecdysozoans
26. Arthropods
27. Mandibulates
28. Deuterostomes
29. Ambulacrarians
30. Chordates
31. Vertebrates
32. Jawed vertebrates
33. Bony vertebrates
34. Lobe-limbed vertebrates
35. Tetrapods
36. Amniotes
37. Reptiles
38. Archosaurs

39. Low-GC Gram-positives
40. High-GC Gram-positives
41. Hyperthermophilic bacteria
42. Hadobacteria
43. Cyanobacteria
44. Proteobacteria
45. Spirochetes
46. Chlamydias
47. Crenarchaeota
48. Euryarchaeota
49. Ciliates
50. Apicomplexans
51. Dinoflagellates
52. Oomycetes
53. Diatoms
54. Brown algae
55. Radiolarians
56. Cercozoans
57. Foraminiferans
58. Diplomonads
59. Parabasalids
60. Heteroloboseans
61. Euglenids
62. Kinetoplastids
63. Glaucophytes
64. Red algae
65. Chlorophytes
66. Coleochaetophytes
67. Stoneworts
68. Liverworts
69. Mosses
70. Hornworts
71. Lycophytes
72. Horsetails
73. Ferns
74. Cycads
75. Ginkgo
76. Gnetophytes
77. Conifers
78. Amborella
79. Water lilies
80. Star anise
81. Magnoliids
82. Monocots
83. Eudicots
84. Amoebozoans
85. Microsporidia
86. "Chytrids"
87. "Zygospore fungi"
88. Arbuscular mycorrhizal fungi
89. Sac fungi
90. Club fungi
91. Choanoflagellates
92. Glass sponges
93. Demosponges
94. Calcareous sponges
95. Ctenophores
96. Placozoans
97. Cnidarians
98. Arrow worms
99. Bryozoans and Entoprocts
100. Flatworms
101. Rotifers and Gastrotrichs
102. Ribbon worms
103. Brachiopods
104. Phoronids
105. Annelids
106. Mollusks
107. Priapulids
108. Kinorhynchs
109. Loriciferans
110. Horsehair worms
111. Nematodes
112. Tardigrades
113. Velvet worms
114. Chelicerates
115. Myriapods
116. Crustaceans
117. Hexapods
118. Echinoderms
119. Hemichordates
120. Lancelets
121. Tunicates
122. Hagfishes
123. Lampreys
124. Chondrichthyans
125. Ray-finned fishes
126. Coelacanths
127. Lungfishes
128. Amphibians
129. Mammals
130. Lepidosaurs
131. Turtles
132. Birds
133. Crocodilians

Time

arbuscular mycorrhizal fungi (*Glomeromycota*) [88]   A group of fungi [17] that associate with plant roots in a close symbiotic relationship.

archaeans (*Archaea*) [3]   Unicellular organisms lacking a nucleus and lacking peptidoglycan in the cell wall. Once grouped with the bacteria, archaeans possess distinctive membrane lipids.

archosaurs (*Archosauria*) [38]   A group of reptiles [37] that includes dinosaurs and crocodilians [133]. Most dinosaur groups became extinct at the end of the Cretaceous; birds [132] are the only surviving dinosaurs.

arrow worms (*Chaetognatha*) [98]   Small planktonic or benthic predatory marine worms with fins and a pair of hooked, prey-grasping spines on each side of the head.

arthropods (*Arthropoda*)   The largest group of ecdysozoans [25]. Arthropods are characterized by a stiff exoskeleton, segmented bodies, and jointed appendages. Includes the chelicerates [114], myriapods [115], crustaceans [116], and hexapods (insects and their relatives) [117].

ascidians (*Ascidiacea*)   "Sea squirts"; the largest group of tunicates [121]. They are sessile (as adults), marine, saclike filter feeders.

B

bacteria (*Eubacteria*) [2]   Unicellular organisms lacking a nucleus, possessing distinctive ribosomes and initiator tRNA, and generally containing peptidoglycan in the cell wall. Different bacterial groups are distinguished primarily on nucleotide sequence data.

barnacles (*Cirripedia*)   Crustaceans [116] that undergo two metamorphoses—first from a feeding planktonic larva to a nonfeeding swimming larva, and then to a sessile adult that forms a "shell" composed of four to eight plates cemented to a hard substrate.

bilaterians (*Bilateria*) [22]   Those animal groups characterized by bilateral symmetry and three distinct tissue types (endoderm, ectoderm, and mesoderm). Includes the protostomes [23] and deuterostomes [28].

birds (*Aves*) [132]   Feathered, flying (or secondarily flightless) tetrapods [35].

bivalves (*Bivalvia*)   Major mollusk [106] group; clams and mussels. Bivalves typically have two similar hinged shells that are each asymmetrical across the midline.

bony vertebrates (*Osteichthyes*) [33]   Vertebrates [31] in which the skeleton is usually ossified to form bone. Includes the ray-finned fishes [125], coelacanths [126], lungfishes [127], and tetrapods [35].

brachiopods (*Brachiopoda*) [103]   Lophotrochozoans [24] with two similar hinged shells that are each symmetrical across the midline. Superficially resemble bivalve mollusks, except for the shell symmetry.

brittle stars (*Ophiuroidea*)   Echinoderms [118] with five long, whip-like arms radiating from a distinct central disk that contains the reproductive and digestive organs.

brown algae (*Phaeophyta*) [54]   Multicellular, almost exclusively marine stramenopiles [6] generally containing the pigment fucoxanthin as well as chlorophylls *a* and *c* in their chloroplasts.

bryozoans (*Ectoprocta* or *Bryozoa*) [99]   A group of marine and freshwater lophotrochozoans [24] that live in colonies attached to substrates; also known as ectoprocts or moss animals. They are the sister group of entoprocts.

C

caecilians (*Gymnophiona*)   A group of burrowing or aquatic amphibians [128]. They are elongate, legless, with a short tail (or none at all), reduced eyes covered with skin or bone, and a pair of sensory tentacles on the head.

calcareous sponges (*Calcarea*) [94]   Filter-feeding marine sponges with spicules composed of calcium carbonate.

cellular slime molds (*Dictyostelida*)   Amoebozoans [84] in which individual amoebas aggregate under stress to form a multicellular pseudoplasmodium.

cephalochordates (*Cephalochordata*) [120]   *See* lancelets.

cephalopods (*Cephalopoda*)   Active, predatory mollusks [106] in which the molluscan foot has been modified into muscular hydrostatic arms or tentacles. Includes octopuses, squids, and nautiluses.

cercozoans (*Cercozoa*) [56]   Unicellular eukaryotes [4] that feed by means of threadlike pseudopods. Group together with foraminiferans [57] and radiolarians [55] to comprise the rhizaria [7].

charophytes (*Charales*) [67]   *See* stoneworts.

chelicerates (*Chelicerata*) [114]   A major group of arthropods [26] with pointed appendages (chelicerae) used to grasp food (as opposed to the chewing mandibles of most other arthropods). Includes the arachnids, horseshoe crabs, pycnogonids, and extinct sea scorpions.

chimaeras (*Holocephali*)   A group of bottom-dwelling, marine, scaleless chondrichthyan fishes [124] with large, permanent, grinding tooth plates (rather than the replaceable teeth found in other chondrichthyans).

chitons (*Polyplacophora*)   Flattened, slow-moving mollusks [106] with a dorsal protective calcareous covering made up of eight articulating plates.

chlamydias (*Chlamydiae*) [46]   A group of very small Gram-negative bacteria; they live as intracellular parasites of other organisms.

chlorophytes (*Chlorophyta*) [65]   The most abundant and diverse group of green algae, including freshwater, marine, and terrestrial forms; some are unicellular, others colonial, and still others multicellular. Chlorophytes use chlorophylls *a* and *c* in their photosynthesis.

choanoflagellates (*Choanozoa*) [91]   Unicellular eukaryotes [4] with a single flagellum surrounded by a collar. Most are sessile, some are colonial. The closest living relatives of the animals [19].

chondrichthyans (*Chondrichthyes*) [124]   One of the two main groups of jawed vertebrates [32]; includes sharks, rays, and chimaeras. They have cartilaginous skeletons and paired fins.

chordates (*Chordata*) [30]   One of the two major groups of deuterostomes [28], characterized by the presence (at some point in development) of a notochord, a hollow dorsal nerve cord, and a post-anal tail. Includes the lancelets [120], tunicates [121], and vertebrates [31].

"chytrids" [86]   Convenience term used for a paraphyletic group of mostly aquatic, microscopic fungi [17] with flagellated gametes. Some exhibit alternation of generations.

ciliates (*Ciliophora*) [49]   Alveolates [5] with numerous cilia and two types of nuclei (micronuclei and macronuclei).

clitellates (*Clitellata*)   Annelids [105] with gonads contained in a swelling (called a clitellum) toward the head of the animal. Includes earthworms (oligochaetes) and leeches.

club fungi (*Basidiomycota*) [90]   Fungi [17] that, if multicellular, bear the products of meiosis on club-shaped basidia and possess a long-lasting dikaryotic stage. Some are unicellular.

club mosses (*Lycopodiophyta*) [71]   Vascular plants [12] characterized by microphylls. *See* lycophytes.

cnidarians (*Cnidaria*) [97]   Aquatic, mostly marine eumetazoans [21] with specialized stinging organelles (nematocysts) used for prey capture and defense, and a blind gastrovascular cavity. The sister group of the bilaterians [22].

coelacanths (*Actinista*) [126]   A group of marine lobe-limbed vertebrates [34] that was diverse from the Middle Devonian to the Cretaceous, but is now known from just two living species. The pectoral and anal fins are on fleshy stalks supported by skeletal elements, so they are also called lobe-finned fishes.

coleochaetophytes (*Coleochaetales*) [66]   Multicellular green algae characterized by flattened growth form composed of thin-walled cells. Thought to be the sister-group to the stoneworts [67] plus land plants [11].

conifers (*Pinophyta* or *Coniferophyta*) [77]   Cone-bearing, woody seed plants [13].

copepods (*Copepoda*)   Small, abundant crustaceans [116] found in marine, freshwater, or wet terrestrial habitats. They have a single eye, long antennae, and a body shaped like a teardrop.

craniates (*Craniata*)   Some biologist exclude the hagfishes [122] from the vertebrates [31], and use the term craniates to refer to the two groups combined.

crenarchaeotes (*Crenarchaeota*) [47]   A major and diverse group of archaeans [3], defined on the basis of rRNA base sequences. Many are extremophiles (inhabit extreme environments), but the group may also be the most abundant archaeans in the marine environment.

crinoids (*Crinoidea*)   Echinoderms [118] with a mouth surrounded by feeding arms, and a U-shaped gut with the mouth next to the anus. They attach to the substratum by a stalk or are free-swimming. Crinoids were abundant in the middle and late Paleozoic, but only a few hundred species have survived to the present. Includes the sea lilies and feather stars.

crocodilians (*Crocodylia*) [133]   A group of large, predatory, aquatic archosaurs [38]. The

closest living relatives of birds [132]. Includes alligators, caimans, crocodiles, and gharials.

crustaceans (*Crustacea*) [116] Major group of marine, freshwater, and terrestrial arthropods [26] with a head, thorax, and abdomen (although the head and thorax may be fused), covered with a thick exoskeleton, and with two-part appendages. Crustaceans undergo metamorphosis from a nauplius larva. Includes decapods, isopods, krill, barnacles, amphipods, copepods, and ostracods.

ctenophores (*Ctenophora*) [95] Radially symmetrical, diploblastic marine animals [19], with a complete gut and eight rows of fused plates of cilia (called ctenes).

cyanobacteria (*Cyanobacteria*) [43] A group of unicellular, colonial, or filamentous bacteria that conduct photosynthesis using chlorophyll *a*.

cycads (*Cycadophyta*) [74] Palmlike gymnosperms with large, compound leaves.

cyclostomes (*Cyclostomata*) This term refers to the possibly monophyletic group of lampreys [123] and hagfishes [122]. Molecular data support this group, but morphological data suggest that lampreys are more closely related to jawed vertebrates [32] than to hagfishes.

D

decapods (*Decapoda*) A group of marine, freshwater, and semiterrestrial crustaceans [116] in which five of the eight pairs of thoracic appendages function as legs (the other three pairs, called maxillipeds, function as mouthparts). Includes crabs, lobsters, crayfishes, and shrimps.

demosponges (*Demospongiae*) [93] The largest of the three groups of sponges [20], accounting for 90 percent of all sponge species. Demosponges have spicules made of silica, spongin fiber (a protein), or both.

deuterostomes (*Deuterostomia*) [28] One of the two major groups of bilaterians [22], in which the mouth forms at the opposite end of the embryo from the blastopore in early development (contrast with protostomes). Includes the ambulacrarians [29] and chordates [30].

diatoms (*Bacillariophyta*) [53] Unicellular, photosynthetic stramenopiles [6] with glassy cell walls in two parts.

dikaryotic fungi (*Dikarya*) [18] A group of fungi [17] in which two genetically different haploid nuclei coexist and divide within the same hypha; includes club fungi [90] and sac fungi [89].

dinoflagellates (*Dinoflagellata*) [51] A group of alveolates [5] usually possessing two flagella, one in an equatorial groove and the other in a longitudinal groove; many are photosynthetic.

dinosaurs (*Dinosauria*) A group of archosaurs [38] that includes birds [132] as well as many extinct groups from the Mesozoic era. Extinct Mesozoic dinosaurs included some of the largest terrestrial vertebrates that have ever lived. Informally, many people use the term to refer only to the extinct Mesozoic species.

diplomonads (*Diplomonadida*) [58] A group of eukaryotes [4] lacking mitochondria; most have two nuclei, each with four associated flagella.

E

ecdysozoans (*Ecdysozoa*) [25] One of the two major groups of protostomes [23], characterized by periodic molting of their cuticles. Nematodes [111] and arthropods [26] are the largest ecdysozoan groups.

echinoderms (*Echinodermata*) [118] A major group of marine deuterostomes [28] with fivefold radial symmetry (at some stage of life) and an endoskeleton made of calcified plates and spines. Includes sea stars, crinoids, sea urchins, sea cucumbers, and brittle stars.

elasmobranchs (*Elasmobranchii*) The largest group of chondrichthyan fishes [124]. Includes sharks, skates, and rays. In contrast to the other group of living chondrichthyans (the chimaeras), they have replaceable teeth.

embryophytes *See* land plants [11].

entoprocts (*Entoprocta*) [99] A group of marine and freshwater lophotrochozoans [24] that live as single individuals or in colonies attached to substrates. They are the sister group of bryozoans, from which they differ in having both their mouth and anus inside the lophophore (the anus is outside the lophophore in bryozoans).

eudicots (*Eudicotyledones*) [83] A group of angiosperms [15] with pollen grains possessing three openings. Typically with two cotyledons, net-veined leaves, taproots, and floral organs typically in multiples of four or five.

euglenids (*Euglenida*) [61] Flagellate excavates characterized by a pellicle composed of spiraling strips of protein under the plasma membrane; the mitochondria have disk-shaped cristae. Some are photosynthetic.

eukaryotes (*Eukarya*) [4] Organisms made up of one or more complex cells in which the genetic material is contained in nuclei. Contrast with archaeans [3] and bacteria [2].

eumetazoans (*Eumetazoa*) [21] Those animals [19] characterized by body symmetry, a gut, a nervous system, specialized types of cell junctions, and well-organized tissues in distinct cell layers (although there have been secondary losses of some or most of these characteristics in a few eumetazoan lineages).

euphyllophytes (*Euphyllophyta*) The group of vascular plants [12] that is sister to the lycophytes [71] and which includes all plants with megaphylls.

euryarchaeotes (*Euryarchaeota*) [48] A major group of archaeans [3], diagnosed on the basis of rRNA sequences. Includes many methanogens, extreme halophiles, and thermophiles.

eutherians (*Eutheria*) A group of viviparous mammals [129], eutherians are well developed at birth (contrast to prototherians and marsupials, the other two groups of mammals). Most familiar mammals outside the Australian and South American regions are eutherians (see Table 23.3).

excavates (*Excavata*) [8] Diverse group of unicellular, flagellate eukaryotes, many of which possess a feeding groove; some lack mitochondria.

F

ferns (*Pteridopsida* or *Polypodiopsida*) [73] Vascular plants [12] usually possessing large, frondlike leaves that unfold from a "fiddlehead." As used in this book, this name refers to a monophyletic clade, also known as the leptosporangiate ferns.

flatworms (*Platyhelminthes*) [100] A group of dorsoventrally flattened and generally elongate soft-bodied lophotrochozoans [24]. May be free-living or parasitic, found in marine, freshwater, or damp terrestrial environments. Major flatworm groups include the tapeworms, flukes, monogeneans, and turbellarians.

flowering plants *See* angiosperms [15].

flukes (*Trematoda*) A group of wormlike parasitic flatworms [100] with complex life cycles that involve several different host species. May be paraphyletic with respect to tapeworms.

foraminiferans (*Foraminifera*) [57] Amoeboid organisms with fine, branched pseudopods that form a food-trapping net. Most produce external shells of calcium carbonate.

fungi (*Fungi*) [17] Eukaryotic heterotrophs with absorptive nutrition based on extracellular digestion; cell walls contain chitin. Major fungal groups include the microsporidia [85], "chytrids" [86], "zygospore fungi" [87], arbuscular mycorrhizal fungi [88], sac fungi [89], and club fungi [90].

G

gastropods (*Gastropoda*) The largest group of mollusks [106]. Gastropods possess a well-defined head with two or four sensory tentacles (often terminating in eyes) and a ventral foot. Most species have a single coiled or spiraled shell. Common in marine, freshwater, and terrestrial environments.

gastrotrichs (*Gastrotricha*) [101] Tiny (0.06–3.0 mm), elongate acoelomate lophotrochozoans [24] that are covered in cilia. They live in marine, freshwater, and wet terrestrial habitats. They are simultaneous hermaphrodites.

ginkgo (*Ginkgophyta*) [75] A gymnosperm [14] group with only one living species. The ginkgo seed is surrounded by a fleshy tissue not derived from an ovary wall and hence not a fruit.

glass sponges (*Hexactinellida*) [92] Sponges [20] with a skeleton composed of four- and/or six-pointed spicules made of silica.

glaucophytes (*Glaucophyta*) [63] Unicellular freshwater algae with chloroplasts containing traces of peptidoglycan, the characteristic cell wall material of bacteria.

gnathostomes (*Gnathostomata*) *See* jawed vertebrates [32].

gnetophytes (*Gnetophyta*) [76] A gymnosperm [14] group with three very different lineages; all have wood with vessels, unlike other gymnosperms.

green plants (*Viridiplantae*) [10] Organisms with chlorophylls *a* and *b*, cellulose-containing cell walls, starch as a carbohydrate storage product, and chloroplasts surrounded by two membranes.

gymnosperms (*Gymnospermae*) [14]   Seed plants [13] with seeds "naked" (i.e., not enclosed in carpels). Probably monophyletic, but status still in doubt. Includes the conifers [77], gnetophytes [76], ginkgo [75], and cycads [74].

H

hadobacteria (*Hadobacteria*) [42]   A group of extremophilic bacteria [2] that includes the genera *Deinococus* and *Thermus*.

hagfishes (*Myxini*) [122]   Elongate, slimy-skinned vertebrates [31] with three small accessory hearts, a partial cranium, and no stomach or paired fins. *See also* craniates; cyclostomes.

hemichordates (*Hemichordata*) [119]   One of the two primary groups of ambulacrarians [29]; marine wormlike organisms with a three-part body plan.

heteroloboseans (*Heterolobosea*) [60]   Colorless excavates [8] that can transform among amoeboid, flagellate, and encysted stages.

hexapods (*Hexapoda*) [117]   Major group of arthropods [26] characterized by a reduction (from the ancestral arthropod condition) to six walking appendages, and the consolidation of three body segments to form a thorax. Includes insects and their relatives (see Table 23.2).

high-GC Gram-positives (*Actinobacteria*) [40]   Gram-positive bacteria with a relatively high (G+C)/(A+T) ratio of their DNA, with a filamentous growth habit.

hominid (*Hominidae*)   A group of primate mammals [129] that consists of the great apes (humans, chimpanzees, gorillas, orangutans, and their extinct close relatives).

hornworts (*Anthocerophyta*) [70]   Nonvascular plants with sporophytes that grow from the base. Cells contain a single large, platelike chloroplast.

horsehair worms (*Nematomorpha*) [110]   A group of very thin, elongate, wormlike freshwater ecdysozoans [25]. Largely nonfeeding as adults, they are parasites of insects and crayfish as larvae.

horseshoe crabs (*Xiphosura*)   Marine chelicerates [114] with a large outer shell in three parts: a carapace, an abdomen, and a tail-like telson. There are only five living species, but many additional species are known from fossils.

horsetails (*Sphenophyta* or *Equisetophyta*) [72]   Vascular plants [12] with reduced megaphylls in whorls.

hydrozoans (*Hydrozoa*)   A group of cnidarians [97]. Most species go through both polyp and mesuda stages, although one stage or the other is eliminated in some species.

hyperthermophilic bacteria [41]   A group of thermophilic bacteria [2] that live in volcanic vents, hot springs, and in underground oil reservoirs; includes the genera *Aquifex* and *Thermotoga*.

I

insects (*Insecta*)   The largest group within the hexapods [117]. Insects are characterized by exposed mouthparts and one pair of antennae containing a sensory receptor called a Johnston's organ. Most have two pairs of wings as adults.

There are more described species of insects than all other groups of life [1] combined, and many species remain to be discovered. The major insect groups are described in Table 23.2.

"invertebrates"   Convenience term encompassing any animal [19] that is not a vertebrate [31].

isopods (*Isopoda*)   Crustaceans [116] characterized by a compact head, unstalked compound eyes, and mouthparts consisting of four pairs of appendages. Isopods are abundant and widespread in salt, fresh, and brackish water, although some species (the sow bugs) are terrestrial.

J

jawed vertebrates (*Gnathostomata*) [32]   A major group of vertebrates [31] with jawed mouths. Includes chondrichthyans [124], ray-finned fishes [125], and lobe-limbed vertebrates [34].

K

kinetoplastids (*Kinetoplastida*) [62]   Unicellular, flagellate organisms characterized by the presence in their single mitochondrion of a kinetoplast (a structure containing multiple, circular DNA molecules).

kinorhynchs (*Kinorhyncha*) [108]   Small (< 1 mm) marine ecdysozoans [25] with bodies in 13 segments and a retractable proboscis.

korarchaeotes (*Korarchaeota*)   A poorly known group of Archaea [3] known only from DNA isolated from hot environments.

krill (*Euphausiacea*)   A group of shrimplike marine crustaceans [116] that are important components of the zooplankton.

L

lampreys (*Petromyzontiformes*) [123]   Elongate, eel-like vertebrates [31] that often have rasping and sucking disks for mouths.

lancelets (*Cephalochordata*) [120]   A group of weakly swimming, eel-like benthic marine chordates [30].

land plants (*Embryophyta*) [11]   Plants with embryos that develop within protective structures; also called embryophytes. Sporophytes and gametophytes are multicellular. Land plants possess a cuticle. Major groups are the liverworts [68], mosses [69], hornworts [70], and vascular plants [12].

larvaceans (*Larvacea*)   Solitary, planktonic tunicates [121] that retain both notochords and nerve cords throughout their lives.

lepidosaurs (*Lepidosauria*) [130]   Reptiles [37] with overlapping scales. Includes tuataras and squamates (lizards, snakes, and amphisbaenians).

leptosporangiate ferns (*Pteridopsida* or *Polypodiopsida*) [73]   Vascular plants [12] usually possessing large, frondlike leaves that unfold from a "fiddlehead," and possessing thin-walled sporangia.

life (*Life*) [1]   The monophyletic group that includes all known living organisms. Characterized by a nucleic-acid based genetic system (DNA or RNA), metabolism, and cellular structure. Some parasitic forms, such as viruses, have

secondarily lost some of these features and rely on the cellular environment of their host.

liverworts (*Hepatophyta*) [68]   Nonvascular plants lacking stomata; stalk of sporophyte elongates along its entire length.

lobe-limbed vertebrates (*Sarcopterygii*) [34]   One of the two major groups of bony vertebrates [33], characterized by jointed appendages (paired fins or limbs).

loboseans (*Lobosea*)   A group of unicellular amoebozoans [84]; includes the most familiar amoebas (e.g., *Amoeba proteus*).

"lophophorates"   Convenience term used to describe several groups of lophotrochozoans [24] that have a feeding structure called a lophophore (a circular or U-shaped ridge around the mouth that bears one or two rows of ciliated, hollow tentacles). Not a monophyletic group.

lophotrochozoans (*Lophotrochozoa*) [24]   One of the two main groups of protostomes [23]. This group is morphologically diverse, and is supported primarily on information from gene sequences. Includes bryozoans and entoprocts [99], flatworms [100], rotifers and gastrotrichs [101], ribbon worms [102], brachiopods [103], phoronids [104], annelids [105], and mollusks [106].

loriciferans (*Loricifera*) [109]   Small (< 1 mm) ecdysozoans [25] with bodies in four parts, covered with six plates.

low-GC Gram-positives (*Firmicutes*) [39]   A diverse group of bacteria [2] with a relatively low (G+C)/(A+T) ratio of their DNA, often but not always Gram-positive, some producing endospores.

lungfishes (*Dipnoi*) [127]   A group of aquatic lobe-limbed vertebrates [34] that are the closest living relatives of the tetrapods [35]. They have a modified swim bladder used to absorb oxygen from air, so some species can survive the temporary drying of their habitat.

lycophytes (*Lycopodiophyta*) [71]   Vascular plants [12] characterized by microphylls; includes club mosses, spike mosses, and quillworts.

M

magnoliids (*Magnoliidae*) [81]   A major group of angiosperms [15] possessing two cotyledons and pollen grains with a single opening. The group is defined primarily by nucleotide sequence data; it is more closely related to the eudicots and monocots than to three other small angiosperm groups.

mammals (*Mammalia*) [129]   A group of tetrapods [35] with hair covering all or part of their skin; females produce milk to feed their developing young. Includes the prototherians, marsupials, and eutherians.

mandibulates (*Mandibulata*) [27]   Arthropods [26] that include mandibles as mouth parts. Includes myriapods [115], crustaceans [116], and hexapods [117].

marsupials (*Marsupialia*)   Mammals [129] in which the female typically has a marsupium (a pouch for rearing young, which are born at an extremely early stage in development). Includes such familiar mammals as opossums, koalas, and kangaroos.

metazoans (*Metazoa*) *See* animals [19].

"methanogens" A convenience term for any of several groups of anaerobic Archaea [3] that produce methane as a metabolic biproduct.

microbial eukaryotes *See* "protists."

microsporidia (*Microsporidia*) [85] A group of parasitic unicellular fungi [17] that lack mitochondria and have walls that contain chitin.

mollusks (*Mollusca*) [106] One of the major groups of lophotrochozoans [24], mollusks have bodies composed of a foot, a mantle (which often secretes a hard, calcareous shell), and a visceral mass. Includes monoplacophorans, chitons, bivalves, gastropods, and cephalopods.

monilophytes (*Monilophyta*) A group of vascular plants [12], sister to the seed plants [13], characterized by overtopping and possession of megaphylls; includes the horsetails [72] and ferns [73].

monocots (*Monocotyledones*) [82] Angiosperms [15] characterized by possession of a single cotyledon, usually parallel leaf veins, a fibrous root system, pollen grains with a single opening, and floral organs usually in multiples of three.

monogeneans (*Monogenea*) A group of ectoparasitic flatworms [100].

monoplacophorans (*Monoplacophora*) Mollusks [106] with segmented body parts and a single, thin, flat, rounded, bilateral shell.

mosses (*Bryophyta*) [69] Nonvascular plants with true stomata and erect, "leafy" gametophytes; sporophytes elongate by apical cell division.

moss animals *See* bryozoans [99].

mycoplasmas (*Mycoplasma*) A group of tiny, low-GC Gram-positive bacteria [39] that lack a cell wall.

myriapods (*Myriapoda*) [115] Arthropods [26] characterized by an elongate, segmented trunk with many legs. Includes centipedes and millipedes.

N

nanoarchaeotes (*Nanoarchaeota*) Minute archaeans [3] that parasitize cells of crenarchaeotes.

nematodes (*Nematoda*) [111] A very large group of elongate, unsegmented ecdysozoans [25] with thick, multilayer cuticles. They are among the most abundant and diverse animals, although most species have not yet been described. Include free-living predators and scavengers, as well as parasites of most species of land plants [11] and animals [19].

neognaths (*Neognathae*) The main group of birds [132], including all living species except the ratites (ostrich, emu, rheas, kiwis, cassowaries) and tinamous. *See* palaeognaths.

neopterans (*Neoptera*) A group of hexapods [117] that includes all the winged insects that can flex their wings over their abdomens.

O

oligochaetes (*Oligochaeta*) Annelid [105] group whose members lack parapodia, eyes, and anterior tentacles, and have few setae. Earthworms are the most familiar oligochaetes.

onychophorans *See* velvet worms.

oomycetes (*Oomycota*) [52] Water molds and relatives; absorptive heterotrophs with nutrient-absorbing, filamentous hyphae.

opisthokonts (*Opisthokonta*) [16] A group of eukaryotes [4] in which the flagellum on motile cells, if present, is posterior. The opisthokonts include the fungi [17], animals [19], and choanoflagellates [91].

ostracods (*Ostracoda*) Marine and freshwater crustaceans [116] that are laterally compressed and protected by two clamlike calcareous or chitinous shells.

P

palaeognaths (*Palaeognathae*) A group of secondarily flightless or weakly flying birds [132]. Includes the flightless ratites (ostrich, emu, rheas, kiwis, cassowaries) and the weakly flying tinamous.

parabasalids (*Parabasalia*) [59] A group of unicellular eukaryotes [4] that lack mitochondria; they possess flagella in clusters near the anterior of the cell.

phoronids (*Phoronida*) [104] A small group of sessile, wormlike marine lophotrochozoans [24] that secrete chitinous tubes and feed using a lophophore.

placoderms (*Placodermi*) An extinct group of jawed vertebrates [32] that lacked teeth. Placoderms were the dominant predators in Devonian oceans.

placozoans (*Placozoa*) [96] A poorly known group of structurally simple, asymmetrical, flattened, transparent animals found in coastal marine tropical and subtropical seas. Most evidence suggests that placozoans are secondarily simplified eumetazoans [21].

Plantae (*Plantae* or *Archaeplastida*) [9] The most broadly defined plant group. In most parts of this book, we use the word "plant" as synonymous with "land plant" [11], a more restrictive definition.

plasmodial slime molds (*Myxogastrida*) Amoebozoans [84] that in their feeding stage consist of a coenocyte called a plasmodium.

pogonophorans (*Pogonophora*) Deep-sea annelids [105] that lack a mouth or digestive tract; they feed by taking up dissolved organic matter, facilitated by endosymbiotic bacteria in a specialized organ (the trophosome).

polychaetes (*Polychaeta*) A group of mostly marine annelids [105] with one or more pairs of eyes and one or more pairs of feeding tentacles; parapodia and setae extend from most body segments. May be paraphyletic with respect to the clitellates.

priapulids (*Priapulida*) [107] A small group of cylindrical, unsegmented, wormlike marine ecdysozoans [25] that takes its name from its phallic appearance.

primates (*Primates*) A group of mammals [129] that includes prosimians and anthropoids.

"prokaryotes" Not a monophyletic group; as commonly used, includes the bacteria [2] and archaeans [3]. A term of convenience encompassing all cellular organisms that are not eukaryotes.

prosimians (*Strepsirrhini*) A group of primate mammals [129] that includes lemurs, lorises, and galagos.

proteobacteria (*Proteobacteria*) [44] A large and extremely diverse group of Gram-negative bacteria that includes many pathogens, nitrogen fixers, and photosynthesizers. Includes the alpha, beta, gamma, delta, and epsilon proteobacteria.

"protists" This term of convenience is used to encompass a large number of distinct and distantly related groups of eukaryotes, many but far from all of which are microbial and unicellular. Essentially a "catch-all" term for any eukaryote group not contained within the land plants [11], fungi [17], or animals [19].

protostomes (*Protostomia*) [23] One of the two major groups of bilaterians [22]. In protostomes, the mouth typically forms from the blastopore (if present) in early development (contrast with deuterostomes). The major protostome groups are the lophotrochozoans [24] and ecdysozoans [25].

prototherians (*Prototheria*) A mostly extinct group of mammals [129], common during the Cretaceous and early Cenozoic. The five living species—four echidnas and the duck-billed platypus—are the only extant egg-laying mammals.

pterobranchs (*Pterobranchia*) A small group of sedentary marine hemichordates [119] that live in tubes secreted by the proboscis. They have one to nine pairs of arms, each bearing long tentacles that capture prey and function in gas exchange.

pterygotes (*Pterygota*) A group of hexapods [117] that includes all the winged insects.

pycnogonids (*Pycnogonida*) Treated in this book as a group of chelicerates [114], but sometimes considered an independent group of arthropods [26]. Pycnogonids have reduced bodies and very long, slender legs. Also called sea spiders.

R

radiolarians (*Radiolaria*) [55] Amoeboid organisms with needlelike pseudopods supported by microtubules. Most have glassy internal skeletons.

ray-finned fishes (*Actinopterygii*) [125] A highly diverse group of freshwater and marine bony vertebrates [33]. They have reduced swim bladders that often function as hydrostatic organs and fins supported by soft rays (lepidotrichia). Includes most familiar fishes.

red algae (*Rhodophyta*) [64] Mostly multicellular, marine and freshwater algae characterized by the presence of phycoerythrin in their chloroplasts.

reptiles (*Reptilia*) [37] One of the two major groups of extant amniotes [36], supported on the basis of similar skull structure and gene sequences. The term "reptiles" traditionally excluded the birds [132], but the resulting group is then clearly paraphyletic. As used in this book, the reptiles include turtles [131], lepidosaurs [130], birds [132], and crocodilians [133].

rhizaria (*Rhizaria*) [7]   Mostly amoeboid unicellular eukaryotes with pseudopods, many with external or internal shells. Includes the foraminiferans [57], cercozoans [56], and radiolarians [55].

rhyniophytes (*Rhyniophyta*)   A group of early vascular plants [12] that appeared in the Silurian and became extinct in the Devonian. Possessed dichotomously branching stems with terminal sporangia but no true leaves or roots.

ribbon worms (*Nemertea*) [102]   A group of unsegmented lophotrochozoans [24] with an eversible proboscis used to capture prey. Mostly marine, but some species live in fresh water or on land.

rotifers (*Rotifera*) [101]   Tiny (< 0.5 mm) lophotrochozoans [24] with a pseudocoelomic body cavity that functions as a hydrostatic organ, and a ciliated feeding organ called the corona that surrounds the head. Rotifers live in freshwater and wet terrestrial habitats.

roundworms (*Nematoda*) [111]   *See* nematodes.

S

sac fungi (*Ascomycota*) [89]   Fungi that bear the products of meiosis within sacs (asci) if the organism is multicellular. Some are unicellular.

salamanders (*Caudata*)   A group of amphibians [128] with distinct tails in both larvae and adults and limbs set at right angles to the body.

salps   *See* thaliaceans.

sarcopterygians (*Sarcopterygii*) [34]   *See* lobe-limbed vertebrates.

scyphozoans (*Scyphozoa*)   Marine cnidarians [97] in which the medusa stage dominates the life cycle. Commonly known as jellyfish.

sea cucumbers (*Holothuroidea*)   Echinoderms [118] with an elongate, cucumber-shaped body and leathery skin. They are scavengers on the ocean floor.

sea spiders   *See* pycnogonids.

sea squirts   *See* ascidians.

sea stars (*Asteroidea*)   Echinoderms [118] with five (or more) fleshy "arms" radiating from an indistinct central disk. Also called starfishes.

sea urchins (*Echinoidea*)   Echinoderms [118] with a test (shell) that is covered in spines. Most are globular in shape, although some groups (such as the sand dollars) are flattened.

"seed ferns"   A paraphyletic group of loosely related, extinct seed plants that flourished in the Devonian and Carboniferous. Characterized by large, frondlike leaves that bore seeds.

seed plants (*Spermatophyta*) [13]   Heterosporous vascular plants [12] that produce seeds; most produce wood; branching is axillary (not dichotomous). The major seed plant groups are gymnosperms [14] and angiosperms [15].

sow bugs   *See* isopods.

spirochetes (*Spirochaetes*) [45]   Motile, Gram-negative bacteria with a helically coiled structure and characterized by axial filaments.

sponges (*Porifera*) [20]   A group of relatively asymmetric, filter-feeding animals that lack a

gut or nervous system and generally lack differentiated tissues. Includes glass sponges [92], demosponges [93], and calcareous sponges [94].

springtails (*Collembola*)   Wingless hexapods [117] with springing structures on the third and fourth segments of their bodies. Springtails are extremely abundant in some environments (especially in soil, leaf litter, and vegetation).

squamates (*Squamata*)   The major group of lepidosaurs [130], characterized by the possession of movable quadrate bones (which allow the upper jaw to move independently of the rest of the skull) and hemipenes (a paired set of eversible penises, or penes) in males. Includes the lizards (a paraphyletic group), snakes, and amphisbaenians.

star anise (*Austrobaileyales*) [80]   A group of woody angiosperms [15] thought to be the sister-group of the clade of flowering plants that includes eudicots [83], monocots [82], and magnoliids [81].

starfish (*Asteroidea*)   *See* sea stars.

stoneworts (*Charales*) [67]   Multicellular green algae with branching, apical growth and plasmodesmata between adjacent cells. The closest living relatives of the land plants [11], they retain the egg in the parent organism.

stramenopiles (*Heterokonta* or *Stramenopila*) [6]   Organisms having, at some stage in their life cycle, two unequal flagella, the longer possessing rows of tubular hairs. Chloroplasts, when present, surrounded by four membranes. Major stramenopile groups include the brown algae [54], diatoms [53], and oomycetes [52].

streptophytes (*Streptophyta*)   All of the green plants [10] other than chlorophytes.

T

tapeworms (*Cestoda*)   Parasitic flatworms [100] that live in the digestive tracts of vertebrates as adults, and usually in various other species of animals as juveniles.

tardigrades (*Tardigrada*) [112]   Small (< 0.5 mm) ecdysozoans [25] with fleshy, unjointed legs and no circulatory or gas exchange organs. They live in marine sands, in temporary freshwater pools, and on the water films of plants. Also called water bears.

tetrapods (*Tetrapoda*) [35]   The major group of lobe-limbed vertebrates [34]; includes the amphibians [128] and the amniotes [36]. Named for the presence of four jointed limbs (although limbs have been secondarily reduced or lost completely in several tetrapod groups).

thaliaceans (*Thaliacea*)   A group of solitary or colonial planktonic marine tunicates [121]. Also called salps.

thaumarchaeotes (*Thaumarchaeota*)   A poorly known group of Archaea [3] that oxidize ammonia; known only from DNA isolated from hot environments.

therians (*Theria*)   Mammals [129] characterized by viviparity (live birth). Includes eutherians and marsupials.

theropods (*Theropoda*)   Archosaurs [38] with bipedal stance, hollow bones, a furcula ("wishbone"), elongated metatarsals with

three-fingered feet, and a pelvis that points backwards. Includes many well-known extinct dinosaurs (such as *Tyrannosaurus rex*), as well as the living birds [132].

tracheophytes   *See* vascular plants [12].

trilobites (*Trilobita*)   An extinct group of arthropods [26] related to the chelicerates [114]. Trilobites flourished from the Cambrian through the Permian.

tuataras (*Rhyncocephalia*)   A group of lepidosaurs [130] known mostly from fossils; there are only two living tuatara species. The quadrate bone of the upper jaw is fixed firmly to the skull. Sister group of the squamates.

tunicates (*Tunicata*) [121]   A group of chordates [30] that are mostly saclike filter feeders as adults, with motile larval stages that resemble tadpoles.

turbellarians (*Turbellaria*)   A group of free-living, generally carnivorous flatworms [100]. Their monophyly is questionable.

turtles (*Testudines*) [131]   A group of reptiles [37] with a bony carapace (upper shell) and plastron (lower shell) that encase the body in a fashion unique among the vertebrates.

U

urochordates (*Tunicata*) [121]   *See* tunicates.

V

vascular plants (*Tracheophyta*) [12]   Plants with xylem and phloem. Major groups include the lycophytes [71] and euphyllophytes.

velvet worms (*Onychophora*) [113]   Elongate, segmented ecdysozoans [25] with many pairs of soft, unjointed, claw-bearing legs. Also known as onychophorans.

vertebrates (*Vertebrata*) [31]   The largest group of chordates [30], characterized by a rigid endoskeleton supported by the vertebral column and an anterior skull encasing a brain. Includes hagfishes [122], lampreys [123], and the jawed vertebrates [32], although some biologists exclude the hagfishes from this group. *See also* craniates.

W

water bears   *See* tardigrades.

water lilies (*Nymphaeaceae*) [79]   A group of aquatic, freshwater angiosperms [15] that are rooted in soil in shallow water, with round floating leaves and flowers that extend above the water's surface. They are the sister-group to most of the remaining flowering plants, with the exception of the genus *Amborella* [78].

Y

"yeasts"   Convenience term for several distantly related groups of unicellular fungi [17].

Z

"zygospore fungi" (*Zygomycota*, if monophyletic) [87]   A convenience term for a probably paraphyletic group of fungi [17] in which hyphae of differing mating types conjugate to form a zygosporangium.

This appendix is designed help you understand the analysis of biological data in a statistical context. We outline major concepts involved in the collection and analysis of data, and we present basic statistical analyses that will help you interpret, understand, and complete the Apply the Concept and Analyze the Data problems throughout this book. Understanding these concepts will also help you understand and interpret scientific studies in general. We present formulas for some common statistical tests as examples, but the main purpose of this appendix is to help you understand the purpose and reasoning behind these tests. Once you understand the basis of an analysis, you may wish to use one of many free, online websites for conducting the tests (such as http://vassarstats.net).

Why Do We Do Statistics?

ALMOST EVERYTHING VARIES   We live in a variable world, but within the variation we see among biological organisms there are predictable patterns. We use statistics to find and analyze these patterns. Consider any group of common things in nature—all women aged 22, all the cells in your liver, or all the blades of grass in your yard. Although they will have many similar characteristics, they will also have important differences. Men aged 22 tend to be taller than women aged 22, but of course not every man will be taller than every woman in this age group.

Natural variation can make it difficult to find general patterns. For example, scientists have determined that smoking increases the risk of getting lung cancer. But we know that not all smokers will develop lung cancer and not all nonsmokers will remain cancer-free. If we compare just one smoker with just one nonsmoker, we may end up drawing the wrong conclusion. So how did scientists discover this general pattern? How many smokers and nonsmokers did they examine before they felt confident about the risk of smoking?

Statistics helps us find and describe general patterns in nature, and draw conclusions from those patterns.

AVOIDING FALSE POSITIVES AND FALSE NEGATIVES   When a woman takes a pregnancy test, there is some chance that it will be positive even if she is not pregnant, and there is some chance that it will be negative even if she is pregnant. We call these kinds of mistakes "false positives" and "false negatives."

Doing science is a bit like taking a medical test. We observe patterns in the world, and we try to draw conclusions about how the world works from those observations. Sometimes our observations lead us to draw the wrong conclusions. We might conclude that a phenomenon occurs, when it actually does not; or we might conclude that a phenomenon does not occur, when it actually does.

For example, planet Earth has been warming over the past century (see Concept 45.4). Ecologists are interested in whether plant and animal populations have been affected by global warming. If we have long-term information about the locations of species and about temperatures in certain areas, we can determine whether shifts in species distributions coincide with temperature changes. Such information, however, can be very complicated. Without proper statistical methods, one may not be able to detect the true impact of temperature, or instead may think a pattern exists when it does not.

Statistics helps us avoid drawing the wrong conclusions.

How Does Statistics Help Us Understand the Natural World?

Statistics is essential to scientific discovery. Most biological studies involve five basic steps, each of which requires statistics:

- **Step 1: Experimental Design**
  Clearly define the scientific question and the methods necessary to tackle the question.
- **Step 2: Data Collection**
  Gather information about the natural world through observations and experiments.
- **Step 3: Organize and Visualize the Data**
  Use tables, graphs, and other useful representations to gain intuition about the data.
- **Step 4: Summarize the Data**
  Summarize the data with a few key statistical calculations.
- **Step 5: Inferential Statistics**
  Use statistical methods to draw general conclusions from the data about the world and the ways it works.

Step 1: Experimental Design

We make observations and conduct experiments to gain knowledge about the world. Scientists come up with scientific ideas based on prior research and their own observations. These ideas start as a question such as "Does smoking cause cancer?" From prior experience, scientists then propose possible answers to the question in the form of hypotheses such as "Smoking increases the risk of cancer." Experimental design then involves devising comparisons that can test predictions of the hypotheses. For example, if we are interested in evaluating the hypothesis that smoking increases cancer risk, we might decide to compare the incidence of cancer in nonsmokers and smokers. Our hypothesis would predict that the cancer incidence is higher in smokers than in nonsmokers. There are various ways we could make that comparison. We could compare

the smoking history of people newly diagnosed with cancer with that of people whose tests came out negative for cancer. Alternatively, we could assess the current smoking habits of a sample of people and see whether those who smoke more heavily are more likely to develop cancer in, say, 5 years. Statistics provides us with tools for assessing which approach will provide us with an answer with smaller costs in time and effort in data collection and analysis.

We use statistics to guide us in planning exactly how to make our comparisons—what kinds of data and how many observations we will need to collect.

Step 2: Data Collection

TAKING SAMPLES   When biologists gather information about the natural world, they typically collect representative pieces of information, called **data** or observations. For example, when evaluating the efficacy of a candidate drug for medulloblastoma brain cancer, scientists may test the drug on tens or hundreds of patients, and then draw conclusions about its efficacy for all patients with these tumors. Similarly, scientists studying the relationship between body weight and clutch size (number of eggs) for female spiders of a particular species may examine tens to hundreds of spiders to make their conclusions.

We use the expression "sampling from a population" to describe this general method of taking representative pieces of information from the system under investigation (**FIGURE B1**). The pieces of information together make up a **sample** of the larger system, or **population**. In the cancer therapy example, each observation was the change in a patient's tumor size 6 months after initiating treatment, and the population of interest was all individuals with medulloblastoma tumors. In the spider example, each observation was a pair of measurements—body weight and clutch size—for a single female spider, and the population of interest was all female spiders of this species.

Sampling is a matter of necessity, not laziness. We cannot hope (and would not want) to collect and weigh *all* of the female spiders of the species of interest on Earth! Instead, we use statistics to determine how many spiders we must collect to confidently infer something about the general population and then use statistics again to make such inferences.
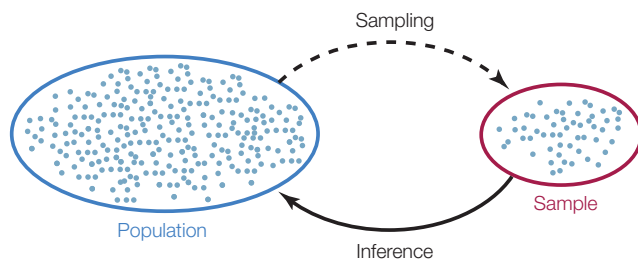
FIGURE B1 Sampling from a Population   Biologists take representative samples from a population, use descriptive statistics to characterize their samples, and then use inferential statistics to draw conclusions about the original population.

TABLE B1	Weight and Length Measurements for a Sample of *Abramis brama* from Lake Laengelmavesi	
Individual number	Fish weight (g)	Fish length (cm)
1	242	30.0
2	290	31.2
3	340	31.1
4	363	33.5
5	390	35.0
6	430	34.0
7	450	34.7
8	450	35.1
9	475	36.2
10	500	34.5
11	500	36.2
12	500	36.2
13	500	36.4
14	575	38.7
15	600	37.3
16	600	37.2
17	610	38.5
18	620	39.2
19	650	38.6
20	680	39.7
21	685	39.5
22	700	37.2
23	700	38.3
24	700	40.6
25	714	40.6
26	720	40.9
27	725	40.5
28	850	41.5
29	920	42.6
30	925	44.0
31	950	45.9
32	955	44.1
33	975	45.3
34	1,000	41.6

DATA COME IN ALL SHAPES AND SIZES   In statistics we use the word "variable" to mean a measurable characteristic of an individual component of a system. Some variables are on a numerical scale, such as the daily high temperature or the clutch size of a spider. We call these **quantitative variables**. Quantitative variables that take on only whole number values (such as spider clutch size) are called **discrete variables**, whereas variables that can also take on a fractional value (such as temperature) are called **continuous variables**.

TABLE B2	Summary of Fish Weights of *Abramis brama* from Lake Laengelmavesi	
Weight (g)	**Frequency**	**Relative frequency**
201–300	2	0.06
301–400	3	0.09
401–500	8	0.24
501–600	3	0.09
601–700	8	0.24
701–800	3	0.09
801–900	1	0.03
901–1,000	6	0.18
TOTAL	34	1.0

TABLE B3	Poinsettia Colors	
Color	**Frequency**	**Proportion**
Red	108	0.59
Pink	34	0.19
White	40	0.22
TOTAL	182	1.0

your data if you organize them. One way to do this is to group (or bin) your data into **classes**, and count up the number of observations that fall into each class. The result is a **frequency distribution**. **TABLE B2** shows the fish weight data as a frequency distribution. For each 100-gram weight class, Table B2 shows the number, or frequency, of observations in that weight class, as well as the relative frequency (proportion of the total) of observations in that weight class. Notice that the data take up much less space when organized in this fashion. Also notice that we can now see that most of the fish fall in the middle of the weight range, with relatively few very small or very large fish.

Go to MEDIA CLIP B1
Interpreting Frequency Distributions
PoL2e.com/mcB1

It is even easier to visualize the frequency distribution of fish weights if we graph them in the form of a **histogram** such as the one in **FIGURE B2**. When grouping quantitative data, it is necessary to decide how many classes to include. It is often useful to look at multiple histograms before deciding which grouping offers the best representation of the data.

Frequency distributions are also useful ways of summarizing categorical data. **TABLE B3** shows a frequency distribution of the colors of 182 poinsettia plants (red, pink, or white) resulting from an experimental cross between two parent plants. Notice that, as with the fish example, the table is a much more compact way to present the data than a list of 182 color observations would be. For categorical data, the possible values of the variable are the categories themselves, and the frequencies are the number of observations in each category. We can visualize frequency distributions of categorical data like this by constructing a **bar chart**. The heights of the bars indicate the number of observations in each category (**FIGURE B3**). Another way to display the

Other variables take categories as values, such as a human blood type (A, B, AB, or O) or an ant caste (queen, worker, or male). We call these **categorical variables**. Categorical variables with a natural ordering, such as a final grade in Introductory Biology (A, B, C, D, or F), are called **ordinal variables**.

Each class of variables comes with its own set of statistical methods. We will introduce a few common methods in this appendix that will help you work on the problems presented in this book, but you should consult a biostatistics textbook for more advanced tests and analyses for other data sets and problems.

Step 3: Organize and Visualize the Data

Your data consist of a series of values of the variable or variables of interest, each from a separate observation. For example, **TABLE B1** shows the weight and length of 34 fish (*Abramis brama*) from Lake Laengelmavesi in Finland. From this list of numbers, it's hard to get a sense of how big the fish in the lake are, or how variable they are in size. It's much easier to gain intuition about

FIGURE B2 Histograms Depict Frequency Distributions of Quantitative Data   This histogram shows the relative frequency of different weight classes of fish (*Abramis brama*).

FIGURE B3 Bar Charts Compare Categorical Data   This bar chart shows the frequency of three poinsettia colors that result from an experimental cross.
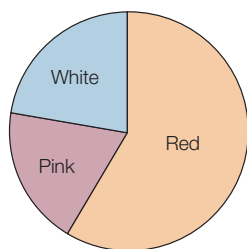
FIGURE B4 Pie Charts Show Proportions of Categories   This pie chart shows the proportions of the three poinsettia colors presented in Table B3.

same data is in a **pie chart**, which shows the proportion of each category represented like pieces of a pie (**FIGURE B4**).

Sometimes we wish to compare two quantitative variables. For example, the researchers at Lake Laengelmavesi investigated the relationship between fish weight and length, from the data presented in Table B1. We can visualize this relationship using a **scatter plot** in which the weight and length of each fish is represented as a single point (**FIGURE B5**). These two variables have a **positive relationship** since the slope of a line drawn through the points is positive. As the length of a fish increases, its weight tends to increase in an approximately linear manner.

Tables and graphs are critical to interpreting and communicating data, and thus should be as self-contained and understandable as possible. Their content should be easily understood simply by looking at them. Axes, captions, and units should be clearly labeled, statistical terms should be defined, and appropriate groupings should be used when tabulating or graphing quantitative data.

Step 4: Summarize the Data

A **statistic** is a numerical quantity calculated from data, whereas **descriptive statistics** are quantities that describe general patterns in data. Descriptive statistics allow us to make straightforward comparisons among different data sets and concisely communicate basic features of our data.
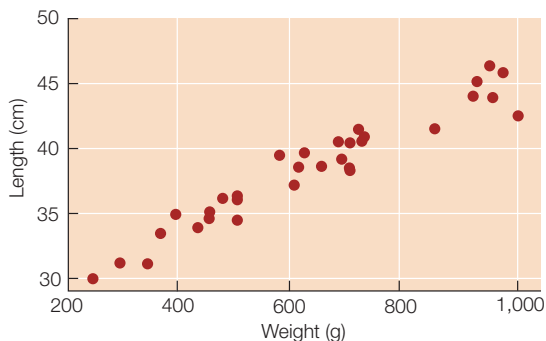
FIGURE B5 Scatter Plots Contrast Two Variables   Scatter plot of *Abramis brama* weights and lengths (measured from nose to end of tail). These two variables have a positive relationship since the slope of a line drawn through the points is positive.

DESCRIBING CATEGORICAL DATA   For categorical variables, we typically use proportions to describe our data. That is, we construct tables containing the proportions of observations in each category. For example, the third column in Table B3 provides the proportions of poinsettia plants in each color category, and the pie chart in Figure B4 provides a visual representation of those proportions.

DESCRIBING QUANTITATIVE DATA   For quantitative data, we often start by calculating **measures of center**, quantities that roughly tell us where the center of our data lies. There are three commonly used measures of center:

- The **mean**, or average value, of our sample is simply the sum of all the values in the sample divided by the number of observations in our sample (**FIGURE B6**).

- The **median** is the value at which there are equal numbers of smaller and larger observations.

- The **mode** is the most frequent value in the sample.

It is often just as important to quantify the variation in the data as it is to calculate its center. There are several statistics

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RESEARCH TOOLS

FIGURE B6   Descriptive Statistics for Quantitative Data

Below are the equations used to calculate the descriptive statistics we discuss in this appendix. You can calculate these statistics yourself, or use free internet resources to help you make your calculations.

Notation:
$x_1, x_2, x_3, \ldots x_n$ are the n observations of variable X in the sample.

$\sum_{i=1}^{n} x_i = x_1 + x_2 + x_3, \ldots + x_n$ is the sum of all of the observations. (The Greek letter sigma, $\sum$, is used to denote "sum of.")

In regression, the independent variable is X, and the dependent variable is Y. b_0 is the vertical intercept of a regression line. b_1 is the slope of a regression line.

Equations

1. Mean: $\bar{x} = \dfrac{\sum_{i=1}^{n} x_i}{n}$

2. Standard deviation: $s = \sqrt{\dfrac{\sum (x_i - \bar{x})^2}{n-1}}$

3. Correlation coefficient: $r = \dfrac{\sum (x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum (x_i - \bar{x})^2 (y_i - \bar{y})^2}}$

4. Least-squares regression line: $Y = b_0 + b_1 X$
   where $b_1 = \dfrac{\sum (x_i - \bar{x})(y_i - \bar{y})}{\sum (x_i - \bar{x})^2}$ and $b_0 = \bar{y} - b_1 \bar{x}$

5. Standard error of the mean: $SE_{\bar{x}} = \dfrac{s}{\sqrt{n}}$
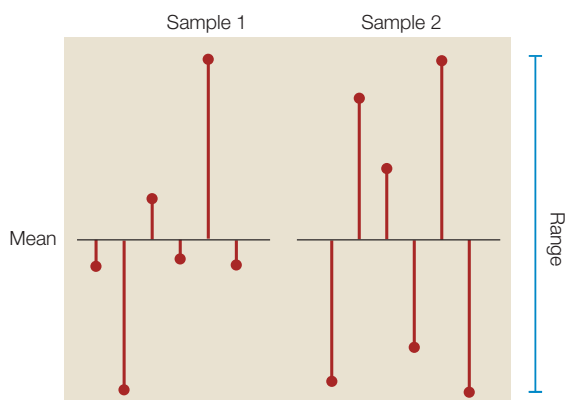
FIGURE B7 Measures of Dispersion   Two samples with the same mean (black horizontal lines) and range (blue vertical line). Red lines show the deviations of each observation from the mean. Samples with large deviations have large standard deviations. Sample 1 has a smaller standard deviation than sample 2.

that tell us how much the values differ from one another. We call these **measures of dispersion**. The easiest one to understand and calculate is the **range**, which is simply the largest value in the sample minus the smallest value. The most commonly used measure of dispersion is the **standard deviation**, which calculates the extent to which the data are spread out from the mean. A deviation is the difference between an observation and the mean of the sample. The standard deviation is a measure of how far the average observation in the sample is from the sample mean. Two samples can have the same range, but very different standard deviations if observations in one are clustered closer to the mean than in the other. In **FIGURE B7**, for example, sample 1 has a smaller standard deviation ($s =$ 2.6) than does sample 2 ($s = 3.6$), even though the two samples have the same means and ranges.

To demonstrate these descriptive statistics, let's return to the Lake Laengelmavesi study (see the data in Table B1). The mean weight of the 34 fish (see equation 1 in Figure B6) is:

$$\bar{x} = \frac{\text{sum of the weight of all fish in sample}}{\text{number of fish in sample}} = \frac{21,284\,\text{g}}{34} = 626\,\text{g}$$

Since there is an even number of observations in the sample, then the median weight is the value halfway between the two middle values:

$$\frac{610\,\text{g} + 620\,\text{g}}{2} = 615\,\text{g}$$

The mode of the sample is 500 g, which appears 4 times. The standard deviation (see equation 2 in Figure B6) is:

$$s = \sqrt{\frac{\sum (x_i - \bar{x})^2}{n - 1}} = 206.6\,\text{g}$$

and the range is 1,000 g – 242 g = 758 g.

DESCRIBING THE RELATIONSHIP BETWEEN TWO QUANTITATIVE VARIABLES   Biologists are often interested in understanding the relationship between two different quantitative variables: How does the height of an organism relate to its weight? How does air pollution relate to the prevalence of asthma? How does lichen abundance relate to levels of air pollution? Recall that scatter plots visually represent such relationships.

We can quantify the strength of the relationship between two quantitative variables using a single value called the Pearson product–moment **correlation coefficient** (see equation 3 in Figure B6). This statistic ranges between –1 and 1 and tells us how closely the points in a scatter plot conform to a straight line. A negative correlation coefficient indicates that one variable decreases as the other increases; a positive correlation coefficient indicates that the two variables increase together; and a correlation coefficient of zero indicates that there is no linear relationship between the two variables (**FIGURE B8**).

One must always keep in mind that *correlation does not mean causation*. Two variables can be closely related without one causing the other. For example, the number of cavities in a child's mouth correlates positively with the size of his or her feet. Clearly cavities do not enhance foot growth; nor does foot growth cause tooth decay. Instead the correlation exists because both quantities tend to increase with age.

Intuitively, the straight line that tracks the cluster of points on a scatter plot tells us something about the typical relationship between the two variables. Statisticians do not, however, simply eyeball the data and draw a line by hand. They often use a method called least-squares **linear regression** to fit a straight line to the data (see equation 4 in Figure B6). This method calculates the line that minimizes the overall vertical distances between the points in the scatter plot and the line itself. These distances are called **residuals** (**FIGURE B9**). Two parameters describe the regression line: b_0 (the vertical intercept of the line, or the expected value of variable Y when $X =$ 0), and b_1 (the slope of the line, or how much values of Y are expected to change with changes in values of X).
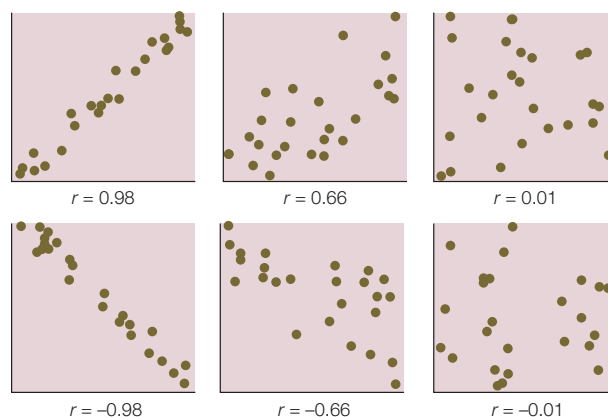
FIGURE B8 Correlation Coefficients   The correlation coefficient (r) indicates both the strength and the direction of the relationship.
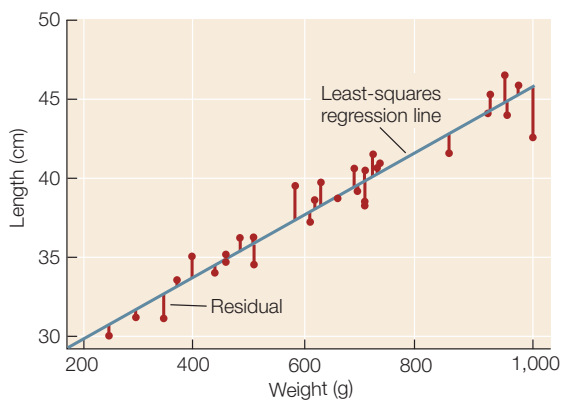
FIGURE B9 **Linear Regression Estimates the Typical Relationship between Two Variables** Least-squares linear regression line for *Abramis brama* weights and lengths (measured from nose to end of tail). The regression line (blue line) is given by the equation $Y = 26.1 + 0.02X$. It is the line that minimizes the sum of the squares of the residuals (red lines).

Step 5: Inferential Statistics

Data analysis often culminates with statistical inference—an attempt to draw general conclusions about the system under investigation—the larger population—from observations of a representative sample (see Figure B1). When we test a new medulloblastoma brain cancer drug on ten patients, we do not simply want to know the fate of those ten individuals; rather, we hope to predict the drug's efficacy on the much larger population of all medulloblastoma patients.

STATISTICAL HYPOTHESES Once we have collected our data, we want to evaluate whether or not they fit the predictions of our hypothesis. For example, we want to know whether or not cancer incidence is greater in our sample of smokers than in our sample of nonsmokers, whether or not clutch size increases with spider body weight in our sample of spiders, or whether or not growth of a sample of fertilized plants is greater than that of a sample of unfertilized plants.

Before making statistical inferences from data, we must formalize our "whether or not" question into a pair of opposing hypotheses. We start with the "or not" hypothesis, which we call the **null hypothesis** (denoted H_0) because it often is the hypothesis that there is no difference between sample means, no correlation between variables in the sample, or no difference between our sample and an expected frequency distribution. The **alternative hypothesis** (denoted H_A) is that there is a difference in means, that there is a correlation between variables, or that the sample distribution does differ from the expected one.

Suppose, for example, we would like to know whether or not a new vaccine is more effective than an existing vaccine at immunizing children against influenza. We have measured flu incidence in a group of children who received the new vaccine and want to compare it with flu incidence in a group of children who received the old vaccine. Our statistical hypotheses would be as follows:

H_0: Flu incidence was the same in both groups of children.

H_A: Flu incidence was different between the two groups of children.

In the next few sections we will discuss how we decide when to reject the null hypothesis in favor of the alternative hypothesis.

JUMPING TO THE WRONG CONCLUSIONS There are two ways that a statistical test can go wrong (**FIGURE B10**). We can reject the null hypothesis when it is actually true (**Type I error**), or we can accept the null hypothesis when it is actually false (**Type II error**). These kinds of errors are analogous to false positives and false negatives in medical testing, respectively. If we mistakenly reject the null hypothesis when it is actually true, then we falsely endorse the incorrect hypothesis. If we are unable to reject the null hypothesis when it is actually false, then we fail to realize a yet undiscovered truth.

Suppose we would like to know whether there are more females than males in a population of 10,000 individuals. To determine the makeup of the population, we choose 20 individuals randomly and record their sex. Our null hypothesis is that there are not more females than males; and our alternative hypothesis is that there are. The following scenarios illustrate the possible mistakes we might make:

- *Scenario 1*: The population actually has 40% females and 60% males. Although our random sample of 20 people is likely to be dominated by males, it is certainly possible that, by chance, we will end up choosing more females than males. If this occurs, and we mistakenly reject the null hypothesis (that there are not more females than males), then we make a Type I error.

- *Scenario 2*: The population actually has 60% females and 40% males. If, by chance, we end up with a majority of males in our sample and thus fail to reject the null hypothesis, then we make a Type II error.

Fortunately, statistics has been developed precisely to avoid these kinds of errors and inform us about the reliability of our conclusions. The methods are based on calculating the probabilities of different possible outcomes. Although you may have heard or even used the word "probability" on multiple

FIGURE B10 **Two Types of Errors** Possible outcomes of a statistical test. Statistical inference can result in correct and incorrect conclusions about the population of interest.

occasions, it is important that you understand its mathematical meaning. A **probability** is a numerical quantity that expresses the likelihood of some event. It ranges between zero and one; zero means there is no chance the event will occur, and one means the event is guaranteed to occur. This only makes sense if there is an element of chance, that is, if it is possible the event will occur and possible that it will not occur. For example, when we flip a fair coin, it will land on heads with probability 0.5 and land on tails with probability 0.5. When we select individuals randomly from a population with 60% females and 40% males, we will encounter a female with probability 0.6 and a male with probability 0.4.

Probability plays a very important role in statistics. To draw conclusions about the real world (the population) from our sample, we first calculate the probability of obtaining our sample if the null hypothesis is true. Specifically, statistical inference is based on answering the following question:

Suppose the null hypothesis is true. What is the probability that a random sample would, by chance, differ from the null hypothesis as much as our sample differs from the null hypothesis?

If our sample is highly improbable under the null hypothesis, then we rule it out in favor of our alternative hypothesis. If, instead, our sample has a reasonable probability of occurring under the null hypothesis, then we conclude that our data are consistent with the null hypothesis and we do not reject it.

Returning to the sex ratio example, let's consider two new scenarios:

- *Scenario 3*: Suppose we want to infer whether or not females constitute the majority of the population (our alternative hypothesis) based on a random sample containing 12 females and 8 males. We would calculate the probability that a random sample of 20 people includes at least 12 females assuming that the population, in fact, has a 50:50 sex ratio (our null hypothesis). This probability is 0.13, which is too high to rule out the null hypothesis.

- *Scenario 4*: Suppose now that our sample contains 17 females and 3 males. If our population is truly evenly divided, then this sample is much less likely than the sample in scenario 3. The probability of such an extreme sample is 0.0002, and would lead us to rule out the null hypothesis and conclude that there are more females than males.

This agrees with our intuition. When choosing 20 people randomly from an evenly divided population, we would be surprised if almost all of them were female, but would not be surprised at all if we ended up with a few more females than males (or a few more males than females). Exactly how many females do we need in our sample before we can confidently infer that they make up the majority of the population? And how confident are we when we reach that conclusion? Statistics allows us to answer these questions precisely.

STATISTICAL SIGNIFICANCE: AVOIDING FALSE POSITIVES Whenever we test hypotheses, we calculate the probability just discussed, and refer to this value as the **P-value** of our test.

Specifically, the *P*-value is the probability of getting data as extreme as our data (just by chance) if the null hypothesis is in fact true. In other words, it is the likelihood that chance alone would produce data that differ from the null hypothesis as much as our data differ from the null hypothesis. How we measure the difference between our data and the null hypothesis depends on the kind of data in our sample (categorical or quantitative) and the nature of the null hypothesis (assertions about proportions, single variables, multiple variables, differences between variables, correlations between variables, etc.).

For many statistical tests, *P*-values can be calculated mathematically. One option is to quantify the extent to which the data depart from the null hypothesis and then use look-up tables (available in most statistics textbooks or on the internet) to find the probability that chance alone would produce a difference of that magnitude. Most scientists, however, find *P*-values primarily by using statistical software rather than hand calculations combined with look-up tables. Regardless of the technology, the most important steps of the statistical analysis are still left to the researcher: constructing appropriate null and alternative hypotheses, choosing the correct statistical test, and drawing correct conclusions.

After we calculate a *P*-value from our data, we have to decide whether it is small enough to conclude that our data are inconsistent with the null hypothesis. This is decided by comparing the *P*-value to a threshold called the **significance level**, which is often chosen even before making any calculations. We reject the null hypothesis only when the *P*-value is less than or equal to the significance level, denoted α. This ensures that, if the null hypothesis is true, we have at most a probability α of accidentally rejecting it. Therefore the lower the value of α, the less likely you are to make a Type I error (see the lower left cell of Figure B10). The most commonly used significance level is $\alpha = 0.05$, which limits the probability of a Type I error to 5%.

If our statistical test yields a *P*-value that is less than our significance level α, then we conclude that the effect described by our alternative hypothesis is statistically significant at the level α and we reject the null hypothesis. If our *P*-value is greater than α, then we conclude that we are unable to reject the null hypothesis. In this case, we do not actually reject the alternative hypothesis, rather we conclude that we do not yet have enough evidence to support it.

POWER: AVOIDING FALSE NEGATIVES The **power** of a statistical test is the probability that we will correctly reject the null hypothesis when it is false (see the lower right cell of Figure B10). Therefore the higher the power of the test, the less likely we are to make a Type II error (see the upper right cell of Figure B10). The power of a test can be calculated, and such calculations can be used to improve your methodology. Generally, there are several steps that can be taken to increase power and thereby avoid false negatives:

- **Decrease the significance level, α**. The higher the value of α, the harder it is to reject the null hypothesis, even if it is actually false.

- **Increase the sample size**. The more data one has, the more likely one is to find evidence against the null hypothesis, if it is actually false.

- **Decrease variability in the sample**. The more variation there is in the sample, the harder it is to discern a clear effect (the alternative hypothesis) when it actually exists.

It is always a good idea to design your experiment to reduce any variability that may obscure the pattern you seek to detect. For example, it is possible that the chance of a child contracting influenza varies depending on whether he or she lives in a crowded (e.g., urban) environment or one that is less so (e.g., rural). To reduce variability, a scientist might choose to test a new influenza vaccine only on children from one environment or the other. After you have minimized such extraneous variation, you can use power calculations to choose the right combination of α and sample size to reduce the risks of Type I and Type II errors to desirable levels.

There is a trade-off between Type I and Type II errors: as α increases, the risk of a Type I error decreases but the risk of a Type II error increases. As discussed above, scientists tend to be more concerned about Type I than Type II errors. That is, they believe it is worse to mistakenly believe a false hypothesis than it is to fail to make a new discovery. Thus they prefer to use low values of α. However, there are many real-world scenarios in which it would be worse to make a Type II error than a Type I error. For example, suppose a new cold medication is being tested for dangerous (life-threatening) side effects. The null hypothesis is that there are no such side effects. A Type II error might lead regulatory agencies to approve a harmful medication that could cost human lives. In contrast, a Type I error would simply mean one less cold medication among the many that already line pharmacy shelves. In such cases, policymakers take steps to avoid a Type II error, even if, in doing so, they increase the risk of a Type I error.

STATISTICAL INFERENCE WITH QUANTITATIVE DATA   Statistics that describe patterns in our samples are used to estimate properties of the larger population. Earlier we calculated the mean weight of a sample of *Abramis brama* in Lake Laengelmavesi, which provided us with an estimate of the mean weight of all the *Abramis brama* in the lake. But how close is our estimate to the true value in the larger population? Our estimate from the sample is unlikely to exactly equal the true population value. For example, our sample of *Abramis brama* may, by chance, have included an excess of large individuals. In this case, our sample would overestimate the true mean weight of fish in the population.

The **standard error** of a sample statistic (such as the mean) is a measure of how close it is likely to be to the true population value. The **standard error of the mean**, for example, provides an estimate of how far we might expect a sample mean to deviate from the true population mean. It is a function of how much individual observations vary within samples (the standard deviation) and the size of the sample (n). Standard errors increase with the degree of variation within samples, and they decrease with the number of observations in a sample (because large samples provide better estimates about the underlying population than do small samples). For our sample of 34 *Abramis brama*, we would calculate the standard error of the mean using equation 5 in Figure B6:

$$SE_{\bar{x}} = \frac{s}{\sqrt{n}} = \frac{206.6\,\text{g}}{\sqrt{34}} = 35.4\,\text{g}$$

The standard error of a statistic is related to the **confidence interval**—a range around the sample statistic that has a specified probability of including the true population value. The formula we use to calculate confidence intervals depends on the characteristics of the data, and the particular statistic. For many types of continuous data, the bounds of the **95% confidence interval** of the mean can be calculated by taking the mean and adding and subtracting 1.96 times the standard error of the mean. Consider our sample of 34 *Abramis brama*, for example. We would say that the mean of 626 grams has a 95% confidence interval from 556.6 grams to 695.4 grams (626 ± 69.4 grams). If all our assumptions about our data have been met, we would expect the true population mean to fall in this confidence interval 95% of the time.

Researchers typically use graphs or tables to report sample statistics (such as the mean) as well as some measure of confidence in them (such as their standard error or a confidence interval). This book is full of examples. If you understand the concepts of sample statistics, standard errors, and confidence intervals, you can see for yourself the major patterns in the data, without waiting for the authors to tell you what they are. For example, if samples from two groups have 95% confidence intervals of the mean that do not overlap, then you can conclude that it is unlikely that the groups have the same true mean.

Go to ANIMATED TUTORIAL B1
Standard Deviations, Standard Errors, and Confidence Intervals
PoL2e.com/atB1

Biologists conduct statistical tests to obtain more precise estimates of the probability of observing a given difference between samples if the null hypothesis that there is no difference in the populations is true. The appropriate test depends on the nature of the data and the experimental design. For example, we might want to calculate the probability that the mean weights of two different fish species in Lake Laengelmavesi, *Abramis brama* and *Leusiscus idus*, are the same. A simple method for comparing the means of two groups is the *t*-test, described in **FIGURE B11**. We looked earlier at data for *Abramis brama*; the researchers who collected these data also collected weights for six individuals of *Leusiscus idus*: 270, 270, 306, 540, 800, and 1,000 grams. We begin by stating our hypotheses and choosing a significance level:

H_0: *Abramis brama* and *Leusiscus idus* have the same mean weight.

H_A: *Abramis brama* and *Leusiscus idus* have different mean weights.

α = 0.05

RESEARCH TOOLS

FIGURE B11   The *t*-test

What is the *t*-test? It is a standard method for assessing whether the means of two groups are statistically different from each another.

Step 1: State the null and alternative *hypotheses*:
H_0: The two populations have the same mean.
H_A: The two populations have different means.

Step 2: Choose a significance level, α, to limit the risk of a Type I error.

Step 3: Calculate the *test statistic*: $t_s = \dfrac{\bar{y}_1 - \bar{y}_2}{\sqrt{\dfrac{s_1^2}{n_1} + \dfrac{s_2^2}{n_2}}}$

Notation: $\bar{y}_1$ and $\bar{y}_2$ are the sample means; s_1 and s_2 are the sample standard deviations; and n_1 and n_2 are the sample sizes.

Step 4: Use the test statistic to assess whether the data are consistent with the null hypothesis:

Calculate the *P-value* (*P*) using statistical software or by hand using statistical tables.

Step 5: Draw conclusions from the test:

If $P \leq \alpha$, then reject H_0, and conclude that the population distribution is significantly different.

If $P > \alpha$, then we do not have sufficient evidence to conclude that the means differ.

The test statistic is calculated using the means, standard deviations, and sizes of the two samples:

$$t_s = \frac{626 - 531}{\sqrt{\dfrac{207^2}{34} + \dfrac{310^2}{6}}} = 0.724$$

We can use statistical software or one of the free statistical sites on the internet to find that the *P*-value for this result is $P = 0.497$. Since *P* is considerably greater than α, we fail to reject the null hypothesis and conclude that our study does not provide evidence that the two species have different mean weights.

You may want to consult an introductory statistics textbook to learn more about confidence intervals, *t*-tests, and other basic statistical tests for quantitative data.

STATISTICAL INFERENCE WITH CATEGORICAL DATA   With categorical data, we often wish to ask whether the frequencies of observations in different categories are consistent with a hypothesized frequency distribution. We can use a **chi-square goodness-of-fit** test to answer this question.

FIGURE B12 outlines the steps of a chi-square goodness-of-fit-test. As an example, consider the data described in Table B3. Many plant species have simple Mendelian genetic systems in which parent plants produce progeny with three different colors of flowers in a ratio of 2:1:1. However, a botanist believes that these particular poinsettia plants have a different genetic system that does not produce a 2:1:1 ratio of red, pink, and white plants. A chi-square goodness-of-fit can be used to assess whether or not the data are consistent with this ratio, and thus whether or not this simple genetic explanation is valid. We start by stating our hypotheses and significance level:

H_0: The progeny of this type of cross have the following probabilities of each flower color:

$\Pr\{\text{Red}\} = .50, \Pr\{\text{Pink}\} = .25, \Pr\{\text{White}\} = .25$

H_A: At least one of the probabilities of H_0 is incorrect.

$\alpha = 0.05$

We next use the probabilities in H_0 and the sample size to calculate the expected frequencies:

	Red	Pink	White
Observed	108	34	40
Expected	(.50)(182) = 91	(.25)(182) = 45.5	(.25)(182) = 45.5

Based on these quantities, we calculate the chi-square test statistic:

$$\chi_s^2 = \sum_{i=1}^{C} \frac{(O_i - E_i)^2}{E_i} = \frac{(108 - 91)^2}{91} + \frac{(34 - 45.5)^2}{45.5} + \frac{(40 - 45.5)^2}{45.5} = 6.747$$

RESEARCH TOOLS

FIGURE B12   The Chi-Square Goodness-of-Fit Test

What is the chi-square goodness-of-fit test? It is a standard method for assessing whether a sample came from a population with a specific distribution.

Step 1: State the null and alternative *hypotheses*:
H_0: The population has the specified distribution.
H_A: The population does not have the specified distribution.

Step 2: Choose a significance level, α, to limit the risk of a Type I error.

Step 3: Determine the *observed frequency* and *expected frequency* for each category:

The observed frequency of a category is simply the number of observations in the sample of that type.

The expected frequency of a category is the probability of the category specified in H_0 multiplied by the overall sample size.

Step 4: Calculate the *test statistic*: $\chi_s^2 = \sum_{i=1}^{C} \dfrac{(O_i - E_i)^2}{E_i}$

Notation: *C* is the total number of categories, O_i is the observed frequency of category *i*, and E_i is the expected frequency of category *i*.

Step 5: Use the test statistic to assess whether the data are consistent with the null hypothesis:

Calculate the *P-value* (*P*) using statistical software or by hand using statistical tables.

Step 6: Draw conclusions from the test:

If $P \leq \alpha$, then reject H_0, and conclude that the population distribution is significantly different than the distribution specified by H_0.

If $P > \alpha$, then we do not have sufficient evidence to conclude that population has a different distribution.

FIGURE B13 Some Common Methods of Statistical Inference
This flowchart shows some of the commonly used methods of statistical inference for different combinations of data. Detailed descriptions of these methods can be found in most introductory biostatistics textbooks.

We find the P-value for this result to be $P = 0.034$ using statistical software. Since P is less than α, we reject the null hypothesis and conclude that the botanist is likely correct: the plant color patterns are not explained by the simple Mendelian genetic model under consideration.

This introduction is meant to provide only a brief introduction to the concepts of statistical analysis, with a few example tests. **FIGURE B13** provides a summary of some of the commonly used statistical tests that you may encounter in biological studies.
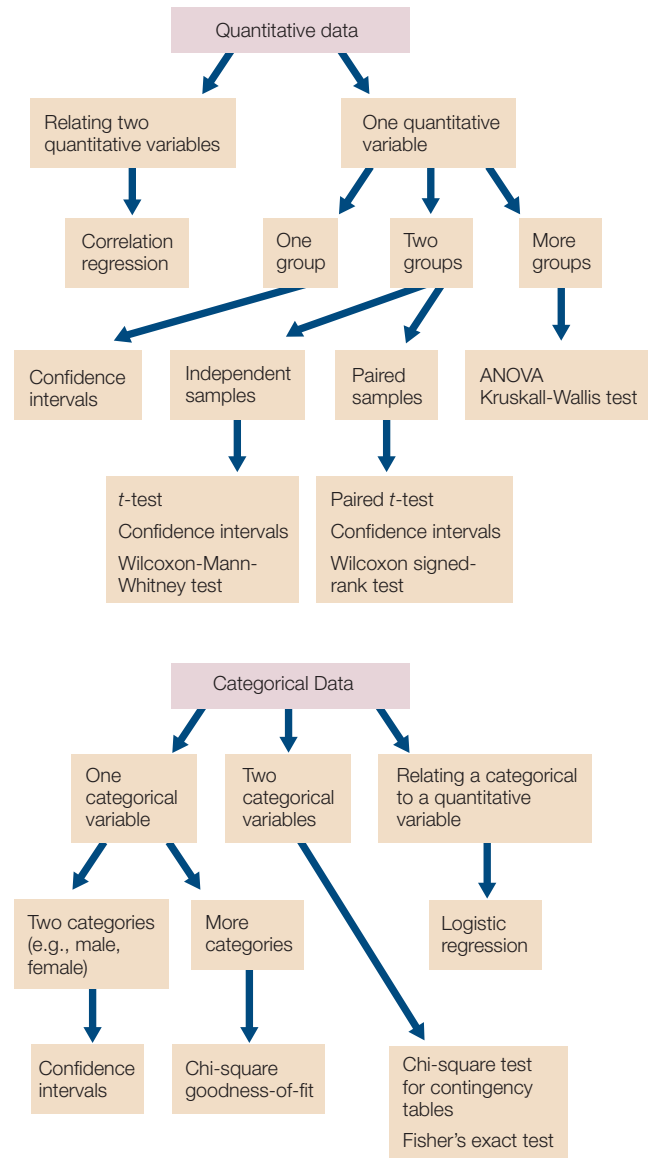
Appendix C Some Measurements Used in Biology

Measures of	Unit	Equivalents	Metric → English conversion
LENGTH			
	meter (m)	base unit	1 m = 39.37 inches = 3.28 feet = 1.196 yards
	kilometer (km)	1 km = 1,000 (10^3) m	1 km = 0.62 miles
	centimeter (cm)	1 cm = 0.01 (10^{-2}) m	1 cm = 0.39 inches
	millimeter (mm)	1 mm = 0.1 cm = 10^{-3} m	1 mm = 0.039 inches
	micrometer (μm)	1 μm = 0.001 mm = 10^{-6} m	
	nanometer (nm)	1 nm = 0.001 μm = 10^{-9} m	
AREA			
	square meter (m^2)	base unit	1 m^2 = 1.196 square yards
	hectare (ha)	1 ha = 10,000 m^2	1 ha = 2.47 acres
VOLUME			
	liter (L)	base unit	1 L = 1.06 quarts
	milliliter (ml)	1 ml = 0.001 L = 10^{-3} L	1 ml = 0.034 fluid ounces
	microliter (μl)	1 μl = 0.001 ml = 10^{-6} L	
MASS			
	gram (g)	base unit	1 g = 0.035 ounces
	kilogram (kg)	1 kg = 1,000 g	1 kg = 2.20 pounds
	metric ton (mt)	1 mt = 1,000 kg	1 mt = 2,200 pounds = 1.10 ton
	milligram (mg)	1 mg = 0.001 g = 10^{-3} g	
	microgram (μg)	1 μg = 0.001 mg = 10^{-6} g	
TEMPERATURE			
	degree Celsius (°C)	base unit	°C = (°F − 32)/1.8
			0°C = 32°F (water freezes)
			100°C = 212°F (water boils)
			20°C = 68°F ("room temperature")
			37°C = 98.6°F (human internal body temperature)
	Kelvin (K)*	K = °C − 273	0 K = −460°F
ENERGY			
	joule (J)		1 J ≈ 0.24 calorie = 0.00024 kilocalorie[†]

*0 K (–273°C) is "absolute zero," a temperature at which molecular oscillations approach 0—that is, the point at which motion all but stops.

[†]A *calorie* is the amount of heat necessary to raise the temperature of 1 gram of water 1°C. The *kilocalorie*, or nutritionist's calorie, is what we commonly think of as a calorie in terms of food.

Glossary

A

A horizon *See* topsoil.

abiotic (a′ bye ah tick) [Gk. *a*: not + *bios*: life] Nonliving. In ecology, the nonliving (physical and chemical) components of the environment of organisms. (Contrast with biotic.)

abscisic acid (ab sighs′ ik) A plant growth substance with growth-inhibiting action. Causes stomata to close; involved in a plant's response to salt and drought stress.

abscission (ab sizh′ un) [L. *abscissio*: break off] The process by which leaves, petals, and fruits separate from a plant.

absorption (1) Of light: complete retention (in contrast to reflection or transmission). (2) In the study of nutrition, the process of transporting molecules from the gut lumen into the blood.

absorption spectrum A graph of light absorption versus wavelength of light; shows how much light is absorbed at each wavelength.

absorptive heterotroph An organism (usually a fungus) that obtains its food by **absorptive heterotrophy**, i.e., by secreting digestive enzymes into the environment to break down large food molecules, then absorbing the breakdown products.

abyssal zone (uh biss′ ul) [Gk. *abyssos*: bottomless] The deepest portions of the oceans; characterized by extremely high pressures, low dissolved oxygen levels, and cold temperatures.

accessory fruit A fruit of a flowering plant in which the some of the flesh is derived from tissues other than the ovary; examples include apples and pears.

accessory reproductive organs Reproductive organs other than the gonads.

acclimation The change in an individual's phenotype that results from long-term exposure to a new environment. A form of phenotypic plasticity. Also called acclimatization.

acid growth hypothesis The hypothesis that auxin increases proton pumping, thereby lowering the pH of the cell wall and activating enzymes that loosen polysaccharides. Proposed to explain auxin-induced cell expansion in plants.

acoelomate An animal that does not have a coelom.

acquired immune deficiency syndrome (AIDS) A condition caused by human immunodeficiency virus (HIV) in which the body's T-helper cells are reduced, leaving the victim subject to opportunistic diseases.

ACTH *See* adrenocorticotropic hormone.

actin [Gk. *aktis*: ray] A protein that makes up the cytoskeletal microfilaments in eukaryotic cells and is one of the two contractile proteins in muscle. (*See also* myosin.)

actin filaments Chains of linked actin molecules. Also called thin filaments. (*See also* myosin filaments.)

action potential An impulse in a neuron taking the form of a brief, local, high-amplitude depolarization of the cell membrane. (Contrast with resting potential.)

action spectrum A graph of a biological process versus light wavelength; shows which wavelengths are involved in the process.

activation energy (E_a) The energy barrier that blocks the tendency for a chemical reaction to occur.

activator A transcription factor that stimulates transcription when it binds to a gene's promoter. (Contrast with repressor.)

active site The region on the surface of an enzyme or ribozyme where the substrate binds, and where catalysis occurs.

active transport The energy-dependent transport of a substance across a biological membrane against a concentration gradient—that is, from a region of low concentration (of that substance) to one of high concentration. (*See also* primary active transport, secondary active transport; contrast with facilitated diffusion, passive transport.)

adaptation (a dap tay′ shun) (1) In evolutionary biology, a particular structure, physiological process, or behavior that makes an organism better able to survive and reproduce. Also, the evolutionary process that leads to the development or persistence of such a trait. (2) In sensory neurophysiology, a sensory cell's loss of sensitivity as a result of repeated stimulation.

adaptive defenses In animals, one of two general types of defenses against

pathogens. Involves antibody proteins and other proteins that recognize, bind to, and aid in the destruction of specific viruses and bacteria. Present only in vertebrate animals. (Contrast with innate defenses.)

additive growth Population growth in which a constant number of individuals is added to the population during successive time intervals. (Contrast with multiplicative growth.)

adenine (A) (a′ den een) A nitrogen-containing base found in nucleic acids, ATP, NAD, and other compounds.

adenohypophysis *See* anterior pituitary gland.

adenosine triphosphate *See* ATP.

ADH *See* antidiuretic hormone.

adhesion Binding of one substance or structure to another, as in a cell binding to its extracellular matrix.

adiabatic (ad′ e uh bat′ ik) [Gk. *adiabatos*: impassable] Referring to a system that exchanges no heat with its surroundings. When such a "heat insulated" system—for example a parcel of air—contracts or expands, its temperature increases or decreases, respectively. This thermodynamic principle applies to the functioning of air conditioners and refrigerators.

adrenocorticotropic hormone (ACTH) A tropic hormone produced by the anterior pituitary gland that stimulates release of cortisol and certain other hormones from the adrenal cortex.

adventitious roots (ad ven ti′ shus) [L. *adventitius*: arriving from outside] Roots originating from the stem at ground level or below; typical of the fibrous root system of monocots.

aerenchyma In plants, parenchymal tissue containing air spaces.

aerobic (air oh′ bic) [Gk. *aer*: air + *bios*: life] Requiring molecular oxygen, O_2. (Contrast with anaerobic.)

aerotolerant anaerobes Organisms that tolerate the presence of oxygen, but do not use it for metabolism.

afferent neuron (af′ ur unt) [L. *ad*: toward + *ferre*: to carry] *See* sensory neuron.

aggregate fruit A fruit of a flowering plant that develops from the merger

of several different ovaries that were separate in the flower.

alcohol fermentation *See* fermentation.

aleurone layer In some seeds, a tissue that lies beneath the seed coat and surrounds the endosperm. Secretes digestive enzymes that break down macromolecules stored in the endosperm.

allantois (al' lun toh is) [Gk. *allant*: sausage] An extraembryonic membrane sac that stores the embryo's nitrogenous wastes; because it contains blood vessels, it provides the means for gas exchange. In eutherian mammals, forms part of the placenta.

allele (a leel') [Gk. *allos*: other] A specific form of a gene at a given locus on a chromosome, among multiple possible forms.

allergic reaction [Ger. *allergie*: altered] An overreaction of the immune system to amounts of an antigen that do not affect most people; often involves IgE antibodies.

allometry (1) In studies of animals of different sizes, nonproportional variation in relation to body size. (2) In studies of growth, a change in the proportions of various parts of an organism relative to one another as a consequence of unequal growth.

allopatric speciation (al' lo pat' rick) [Gk. *allos*: other + *patria*: homeland] The formation of two species from one when reproductive isolation occurs because of the interposition of (or crossing of) a physical geographic barrier such as a river. Also called geographic speciation. (Contrast with sympatric speciation.)

allopolyploidy The possession of more than two chromosome sets that are derived from more than one species.

allosteric regulation (al lo steer' ik) [Gk. *allos*: other + *stereos*: structure] Regulation of the activity of a protein (usually an enzyme) by the binding of an effector molecule to a site other than the active site.

α (alpha) helix A prevalent type of secondary protein structure; a right-handed spiral.

alternation of generations The succession of multicellular haploid and diploid phases in some sexually reproducing organisms, notably plants.

alternative hypothesis In statistical inference, the hypothesis that contrasts with the null hypothesis; typically the hypothesis of primary interest.

alternative splicing A process for generating different mature mRNAs from a single gene by splicing together different sets of exons during RNA processing.

altruism Behavior that benefits another individual at a cost of reduced fitness to the individual performing the behavior.

alveolar sac A blind sac found at the end of a branch of the lung airways in a mammal; consists of many alveoli

alveolus (al ve' o lus) (plural: alveoli) [L. *alveus*: cavity] A small, baglike cavity, especially a semispherical subpart of the wall of an alveolar sac in the mammalian lung

amensalism (a men' sul ism) A "–/0" interaction between individuals of two different species that harms one individual (i.e., it suffers reduced fitness) but does not affect the other. (Contrast with commensalism, mutualism.)

amine hormones Small hormone molecules synthesized from single amino acids (e.g., thyroxine and epinephrine). (Compare to peptide hormones, steroid hormones.)

amino acid An organic compound containing both NH_2 and COOH groups. Proteins are polymers of amino acids.

ammonotelic (am moan' o teel' ic) [Gk. *telos*: end] Pertaining to an organism (typically water-breathing aquatic animals) in which ammonia is the principal final product of breakdown of nitrogen-containing compounds (primarily proteins). (Contrast with ureotelic, uricotelic.)

amnion (am' nee on) The fluid-filled sac within which the embryos of reptiles (including birds) and mammals develop.

amniote egg A shelled egg surrounding four extraembryonic membranes and embryo-nourishing yolk. This evolutionary adaptation permitted mammals and reptiles to live and reproduce in drier environments than can most amphibians.

amphipathic (am' fi path' ic) [Gk. *amphi*: both + *pathos*: emotion] Of a molecule, having both hydrophilic and hydrophobic regions.

anabolic reaction (an uh bah' lik) [Gk. *ana*: upward + *ballein*: to throw] A synthetic reaction in which simple molecules are linked to form more complex ones; requires an input of energy and captures it in the chemical bonds that are formed. (Contrast with catabolic reaction.)

anaerobic (an ur row' bic) [Gk. *an*: not + *aer*: air + *bios*: life] Occurring without the use of molecular oxygen, O_2. (Contrast with aerobic.)

anaerobic glycolysis Glycolysis taking place in the absence of molecular oxygen, O_2. In animals, the most common process of anaerobic ATP production. In this process glucose is converted to lactic acid.

anaphase (an' a phase) [Gk. *ana*: upward] The stage in cell nuclear division at which the first separation of sister chromatids (or, in the first meiotic division, of paired homologs) occurs.

ancestral trait The trait originally present in the ancestor of a given group; may be retained or changed in the descendants of that ancestor.

androgen (an' dro jen) [Gk. *andros*: man + *genein*: to produce] Any of the several masculinizing steroid hormones (most notably testosterone).

aneuploidy (an' you ploy dee) A condition in which one or more chromosomes or pieces of chromosomes are either lacking or present in excess.

angiosperms Flowering plants; one of the two major groups of living seed plants. (*See also* gymnosperms.)

animal hemisphere The non-yolky upper portion of some animal eggs. (Contrast with vegetal hemisphere.)

anion (an' eye on) [Gk. *ana*: upward] A negatively charged ion. (Contrast with cation.)

annual A plant whose life cycle is completed in one growing season. (Contrast with biennial, perennial.)

ANS *See* autonomic nervous system.

antagonistic muscle pair Two muscles, or groups of muscles, that perform coordinated, opposing actions, thus allowing the bones at a joint to move in opposite directions. When one muscle contracts (to close the angle of a joint), its antagonist relaxes. To open the joint, the formerly relaxed muscle contracts and the formerly contracted muscle relaxes.

antenna system *See* light-harvesting complex.

anterior Toward or pertaining to the tip or headward region of the body axis. (Contrast with posterior.)

anterior pituitary gland The anterior portion of the vertebrate pituitary gland that is composed of nonneural endocrine cells and produces several hormones, including tropic hormones. Also called the adenohypophysis. (*See also* pituitary gland, posterior pituitary gland.)

anther (an' thur) [Gk. *anthos*: flower] A pollen-bearing portion of the stamen of a flower.

antheridium (an' thur id' ee um) [Gk. *antheros*: blooming] The multicellular structure that produces the sperm in nonvascular land plants and ferns.

antibody One of the myriad proteins produced by the immune system that specifically binds to a foreign substance in blood or other tissue fluids and initiates its removal from the body.

anticodon   The three nucleotides in transfer RNA that pair with a complementary triplet (a codon) in messenger RNA.

antidiuretic hormone (ADH)   A hormone that promotes water reabsorption by the kidney. ADH is produced by neurons in the hypothalamus and released from nerve terminals in the posterior pituitary gland. Also called vasopressin in mammals.

antigen   (an' ti jun) Any substance that stimulates the production of an antibody or antibodies in the body of a vertebrate.

antigen presentation   In cellular immunity, the process in which a cell ingests and digests an antigen, and then exposes fragments of that antigen, bound to a major histocompatibility complex (MHC) molecule, to the outside of the cell, where the antigen can be recognized by T cells.

antigenic determinant   The specific region of an antigen that is recognized and bound by a specific antibody. Also called an epitope.

antiparallel   Pertaining to molecular orientation in which a molecule or parts of a molecule have opposing directions.

antisense RNA   A single-stranded RNA molecule complementary to, and thus targeted against, an mRNA of interest to block its translation.

aphotic zone   The parts of lakes and oceans below the photic zone, where no sunlight penetrates.

apical–basal axis   Longitudinal definition of function in an adult organism or future function in an embryo, as in the root tip (apex).

apical dominance   In plants, inhibition by the apical bud of the growth of axillary buds.

apical hook   A form taken by the stems of many eudicot seedlings that protects the delicate shoot apex while the stem grows through the soil.

apical meristem   The meristem at the tip of a shoot or root; responsible for a plant's primary growth.

apomixis   (ap oh mix' is) [Gk. *apo*: away from + *mixis*: sexual intercourse] The asexual production of seeds.

apoplast   (ap' oh plast) In plants, the continuous meshwork of cell walls and extracellular spaces through which material can pass without crossing a plasma membrane. (Contrast with symplast.)

apoptosis   (ap uh toh' sis) A series of genetically programmed events leading to cell death.

aquaporin   [L. *aqua*: water + *porus*: pore] A transport protein in plant and animal cell membranes through which water passes by osmosis. Also called a water channel protein.

archegonium   (ar' ke go' nee um) The multicellular structure that produces eggs in nonvascular land plants, ferns, and gymnosperms.

arteriole   A small blood vessel with muscular walls that carries blood from an artery into a capillary bed.

artery   A muscular blood vessel carrying blood away from the heart to other parts of the body. (Contrast with vein.)

ascoma   The fruiting structure of sexually reproducing sac fungi; often a cup-shaped structure.

ascospores   Haploid spores contained with the sexual reproductive structure (the ascus) of sac fungi.

ascus   (ass' cus) (plural: asci) [Gk. *askos*: bladder] In sac fungi, the club-shaped sporangium within which spores (ascospores) are produced by meiosis.

asexual reproduction   The formation of new individuals without the union of genetic material from two different parents. Often takes place by budding or fragmentation. The offspring are genetically identical to their parent.

asynchronous muscle   A muscle in which each excitation results in multiple contractions.

atom   [Gk. *atomos*: indivisible] The smallest unit of a chemical element. Consists of a nucleus and one or more electrons.

atomic number   The number of protons in the nucleus of an atom; also equals the number of electrons around the neutral atom. Determines the chemical properties of the atom.

ATP (adenosine triphosphate)   An energy-storage compound containing adenine, ribose, and three phosphate groups. When it is formed from ADP, useful energy is stored; when it is broken down (to ADP or AMP), energy is released to drive endergonic reactions.

ATP synthase   An integral membrane protein that couples the transport of protons with the formation of ATP.

atrium   (a' tree um) [L. *atrium*: central hall] An internal chamber. In the hearts of vertebrates, the thin-walled chamber(s) entered by blood on its way to the ventricle(s).

autoimmune diseases   Diseases (e.g., rheumatoid arthritis) that result from failure of the immune system to distinguish between self and nonself, causing it to attack tissues in the organism's own body.

autoimmunity   An immune response by an organism to its own molecules or cells.

autonomic effector   An effector other than skeletal muscle; includes smooth and cardiac muscles, exocrine glands, and endocrine glands. Also called an internal effector.

autonomic nervous system (ANS)   The portion of the nervous system that controls autonomic effectors (effectors other than the skeletal muscles). Also called the involuntary nervous system.

autophagy   The programmed destruction of a cell's components.

autopolyploidy   The possession of more than two entire chromosomes sets that are derived from a single species.

autosome   Any chromosome (in a eukaryote) other than a sex chromosome.

autotroph   (au' tow trowf') [Gk. *autos*: self + *trophe*: food] An organism that is capable of living exclusively on inorganic materials, water, and an energy source other than the chemical bonds of organic compounds. Some autotrophs (photoautotrophs) use sunlight as their energy source. Others (chemoautotrophs) use oxidation of inorganic compounds. (Contrast with heterotroph.)

auxin   (awk' sin) [Gk. *auxein*: to grow] In plants, a substance (the most common being indoleacetic acid) that regulates growth and various aspects of development.

avirulence (*Avr*) genes   Genes in a pathogen that may trigger defenses in plants. (*See* gene-for-gene resistance.)

axis   In the study of endocrinology, a system in which several types of endocrine cells act on each other in sequence.

axon   [Gk. axle] The part of a neuron that conducts action potentials away from the cell body.

B

B horizon   *See* subsoil.

bacillus   (bah sil' us) [L: little rod] Any of various rod-shaped bacteria.

bacterial conjugation   *See* conjugation.

bacteriophage   (bak teer' ee o fayj) [Gk. *bakterion*: little rod + *phagein*: to eat] Any of a group of viruses that infect bacteria. Also called phage.

bacteroids   Nitrogen-fixing organelles that develop from endosymbiotic bacteria.

bar chart   A figure that displays frequency distributions of categorical data using bar lengths to represent relative frequency.

bark   All tissues external to the vascular cambium of a plant.

basal metabolic rate (BMR)   The minimum rate of energy use in an awake (but resting) bird or mammal. For measuring the BMR, the animal is resting, fasting, and in its thermoneutral zone (i.e., its metabolic rate is not elevated for thermoregulation).

base   In nucleic acids, the purine or pyrimidine that is attached to each sugar in the sugar–phosphate backbone.

base pair (bp)   In double-stranded DNA, a pair of nucleotides formed by the complementary base pairing of a purine on one strand and a pyrimidine on the other.

basidioma   (plural: basidiomata) A fruiting structure produced by club fungi.

basidium   (bass id' ee yum) In club fungi, the characteristic sporangium in which four **basidiospores** are formed by meiosis and then borne externally before being shed.

basilar membrane   A membrane in the human inner ear that flexes in response to sound waves and thereby activates hair cells; flexes at different locations in response to different pitches of sound.

BD model   A mathematical model that describes how Birth and Death rates affect the size and change in size (dynamics) of ecological populations.

bedrock   *See* parent rock.

behavioral imprinting   In animal behavior, a rapid form of learning in which an animal learns, during a brief critical period, to make a particular response, which is maintained for life, to some object or other organism.

benthic zone   [Gk. *benthos*: bottom] The substrate at the bottom of an ocean, lake, stream, or other body of water.

β (beta) pleated sheet   A type of protein secondary structure; results from hydrogen bonding between polypeptide regions running antiparallel to each other.

BIDE model   A mathematical model that describes how birth, immigration (movement of individuals into populations), death, and emigration (movement of individuals out of populations) affect the size and change in size (dynamics) of ecological populations.

biennial   A plant whose life cycle includes vegetative growth in the first year and flowering and senescence in the second year. (Contrast with annual, perennial.)

bilateral symmetry   The condition in which only the right and left sides of an organism, divided by a single plane through the midline, are mirror images of each other.

bilayer   A structure that is two layers in thickness. In biology, most often refers to

the phospholipid bilayer of membranes. (*See* phospholipid bilayer.)

binary fission   Reproduction of a prokaryote by division of a cell into two comparable progeny cells.

binomial nomenclature   A taxonomic naming system in which each species is given two names (a genus name followed by a species name).

biofilm   A community of microorganisms embedded in a polysaccharide matrix, forming a highly resistant coating on almost any moist surface.

biogeochemical cycle   A description of the cyclical pathways by which biological, geological, and chemical processes move a chemical element or molecule through biotic and abiotic compartments of planet Earth.

biogeographic region   A large, continental-scale region of planet Earth, encompassing multiple biomes, that contains a distinct assemblage of species, many of which are phylogenetically related. (Contrast with biome.)

biogeography   The spatial distribution of Earth's species.

bioinformatics   The use of computers and/or mathematics to analyze complex biological information, such as DNA sequences.

biological clock   A self-contained, metabolic mechanism that keeps track of time.

biological determination   As applied to behavior, the belief that genes completely determine an organism's behavior.

biological species concept   The definition of a species as a group of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups. (Contrast with lineage species concept, morphological species concept.)

biomass   The mass of a sample of biological tissue, living or dead. The term usually refers to the total mass of a designated group of organisms (or of certain of their tissues), and may be measured as the mass of their intact bodies or of their dried bodies.

biome   (bye' ome) A distinct abiotic environment that is found at different places on the planet and is inhabited in each of these locations by ecologically-similar organisms with convergent adaptations. (Contrast with biogeographic region.)

bioremediation   The use by humans of other organisms to remove contaminants from the environment.

biosphere   (bye' oh sphere) The region that supports living organisms on Earth, extending about 23 km from the abyssal

depths of the oceans into the stratosphere (an upper portion of the atmosphere).

biota   (bye oh' tah) All of the organisms—animals, plants, fungi, and microorganisms—found in a given area. (Contrast with flora, fauna.)

biotechnology   The use of cells or living organisms to produce materials useful to humans.

biotic   (bye ah' tick) [Gk. *bios*: life] Living. In ecology, the living components of the environment of organisms. (Contrast with abiotic.)

biotic interchange   The mixing of distinct groups of species that were isolated by physical or climatic barriers, after the barrier is removed.

bipedal locomotion   The act of walking or running on two appendages.

blade   The thin, flat portion of a leaf.

blastocyst   (blass' toe cist) A mammalian blastula. The sphere of cells formed by early cell divisions and composed of an inner cell mass that becomes the embryo and an outer layer of cells called the trophoblast.

blastodisc   (blass' toe disk) An embryo that forms as a disk of cells on the surface of a large yolk mass; comparable to a blastula, but occurring in animals such as birds and reptiles, in which the massive yolk restricts complete cleavage.

blastomere   Any of the cells produced by the early divisions of a fertilized animal egg.

blastula   (blass' chu luh) An early stage of the animal embryo; in many species, a hollow sphere of cells surrounding a central cavity, the blastocoel. (Compare with blastodisc.)

blood plasma   The watery solution in which red blood cells and/or other blood cells are suspended. The part of the blood other than cells.

blood pressure   The extent to which the pressure of the blood exceeds the pressure of the surrounding external environment.

BMR   *See* basal metabolic rate.

body cavity   An internal, fluid-filled space, enclosed by mesoderm in animals.

body plan   The general structure of an animal, the arrangement of its organ systems, and the integrated functioning of its parts.

Bohr model   A model for atomic structure that depicts the atom as largely empty space, with a central nucleus surrounded by electrons in orbits, or electron shells, at various distances from the nucleus.

bone   A rigid component of vertebrate skeletal systems that contains an extracellular matrix of insoluble calcium

phosphate crystals as well as collagen fibers.

bottleneck   *See* population bottleneck.

Bowman's capsule   An elaboration of the renal tubule, composed of podocytes, that surrounds and collects the filtrate from the glomerulus.

brain   The part of the central nervous system of greatest size.

brassinosteroids   Plant steroid hormones that mediate light effects promoting the elongation of stems and pollen tubes.

breathing   The exchange of O_2 and CO_2 between the environmental medium next to the gas exchange membranes and the outside world; often occurs by ventilation, but can occur entirely by diffusion. Also called external respiration.

breathing-organ circuit   In a circulatory system, the blood vessels that carry blood to and from the breathing organs. (Contrast with systemic circuit.)

breathing organs   Specialized organs involved in the exchange of O_2 and CO_2 between an organism and the external environment. Classified as either lungs or gills.

brown adipose tissue (BAT) A specialized fatty tissue, known only in mammals, that serves as the primary site of nonshivering thermogenesis.

bud   In plants, a small protuberance in the shoot that contains an undeveloped leaf, flower or shoot.

budding   Asexual reproduction in which a more or less complete new organism grows from the body of the parent organism, eventually detaching itself.

bulk flow   Mass movement of a fluid (gas or liquid) driven by a difference of pressure, from a region of high pressure to a region of low pressure.

C

C horizon   *See* parent rock.

calorie (cal)   [L. *calor*: heat] A unit of energy equal to the amount of heat required to raise the temperature of 1 gram of water by 1°C. Physiologists commonly use the kilocalorie (kcal) as a unit of energy (1 kcal = 1,000 calories). Nutritionists also use the kilocalorie, but refer to it as the *Calorie* (capital C).

Calvin cycle   The stage of photosynthesis in which CO_2 reacts with RuBP to form 3PG, 3PG is reduced to a sugar, and RuBP is regenerated, while other products are released to the rest of the plant. Also known as the Calvin–Benson cycle.

Cambrian explosion   The rapid diversification of multicellular life that took place during the Cambrian period.

cAMP (cyclic AMP)   A compound formed from ATP that acts as a second messenger.

5′ cap   *See* G cap.

capillary   [L. *capillaris*: hair] In the circulatory system, a microscopic blood vessel with walls composed of just a simple epithelium (called the capillary endothelium), one cell layer thick. Capillaries are the principal sites of exchange between blood and other tissues in animals with a closed circulatory system.

carbohydrates   Organic compounds containing carbon, hydrogen, and oxygen in the ratio 1:2:1 (i.e., with the general formula $C_nH_{2n}O_n$). Common examples are sugars, starch, and cellulose.

carbon-fixation reactions   The phase of photosynthesis in which chemical energy captured in the light reactions is used to drive the reduction of CO_2 to form carbohydrates.

cardiac cycle   Alternating contraction and relaxation of the heart. In a mammal, contraction of the two atria of the heart, followed by contraction of the two ventricles and then relaxation.

cardiac muscle   A type of muscle tissue that makes up the wall of the heart and is responsible for the beating of the heart. Characterized by branching, electrically coupled cells with single nuclei and a striated (striped) appearance. (Contrast with smooth muscle, skeletal muscle.)

cardiovascular system   [Gk. *kardia*: heart + L. *vasculum*: small vessel] The heart, and vessels of the circulatory system. Also called circulatory system.

carnivore   [L. *carn*: flesh + *vorare*: to devour] An organism that eats animal tissues. (*See* secondary consumer; contrast with omnivore, detritivore, herbivore.)

carpel   (kar′ pel) [Gk. *karpos*: fruit] The organ of the flower that contains one or more ovules.

carrier proteins   Membrane proteins that bind specific molecules and transport them through the membrane.

carrying capacity (*K*)   The maximum population size or density of a given species that a given unchanging environment can support indefinitely.

cartilage   In vertebrates, a tough connective tissue found in joints, the outer ear, part of the nose, and elsewhere. Forms the entire skeleton in some animal groups, notably sharks and their relatives.

Casparian strip   A band of cell wall containing suberin and lignin, found in the endodermis. Restricts the movement of water across the endodermis.

caspase   One of a group of proteases that catalyze cleavage of target proteins and are active in apoptosis.

catabolic reaction   (kat uh bah′ lik) [Gk. *kata*: to break down + *ballein*: to throw] A synthetic reaction in which complex molecules are broken down into simpler ones and energy is released. (Contrast with anabolic reaction.)

catalyst   (kat′ a list) [Gk. *kata*: to break down] A chemical substance that accelerates a reaction without itself being consumed in the overall course of the reaction. Catalysts lower the activation energy of a reaction. Enzymes are biological catalysts.

catch   A state in which some invertebrate muscles maintain a state of contraction over extended periods of time with minimal energy expenditure.

categorical variables   Variables that take on qualitative categories as values, such as human blood types (A, AB, B, or O).

cation   (cat′ eye on) An ion with one or more positive charges. (Contrast with anion.)

Cdk   *See* cyclin-dependent kinase.

cDNA library   A collection of complementary DNAs derived from mRNAs of a particular tissue at a particular time in the life cycle of an organism.

cDNA   *See* complementary DNA.

cell body   In a neuron, portion of the neuron that contains the cell nucleus and most of the neuron's other organelles.

cell cycle   The stages through which a cell passes between one division and the next. Includes all stages of interphase and mitosis.

cell cycle checkpoints   Points of transition between different phases of the cell cycle, which are regulated by cyclins and cyclin-dependent kinases (Cdk's).

cell division   The reproduction of a cell to produce two new cells. In eukaryotes, this process involves nuclear division (mitosis) and cytoplasmic division (cytokinesis).

cell fate   The type of cell that an undifferentiated cell in an embryo will become in the adult.

cell junctions   Specialized structures associated with the plasma membranes of epithelial cells. Some contribute to cell adhesion, others to intercellular communication.

cell membrane   Lipid bilayer also containing proteins and other molecules that encloses the cytoplasm of the cell and separates it from the surrounding environment.

cell potency   In multicellular organisms, an undifferentiated cell's potential to become a cell of a specific type. (*See* multipotent, pluripotent, totipotent.)

cell signaling   Communication between cells or within cells as they respond to specific cues.

cell theory   States that cells are the basic structural and physiological units of all living organisms, and that all cells come from preexisting cells.

cell wall   A relatively rigid structure that encloses cells of plants, fungi, many protists, and most prokaryotes, and which gives these cells their shape and limits their expansion in hypotonic media.

cellular immune response   Immune system response mediated by T cells and directed against parasites, fungi, intracellular viruses, and foreign tissues (grafts). (Contrast with humoral immune response.)

cellular respiration   The catabolic pathways by which electrons are removed from various molecules and passed through intermediate electron carriers to O_2, generating H_2O and releasing energy.

central nervous system (CNS)   Large structures composed principally of integrating neurons and associated glial cells, forming the site of most information processing, storage, and retrieval; in vertebrates, the brain and spinal cord. (Contrast with peripheral nervous system.)

centralization   (of the nervous system) Over the course of evolution, the tendency of neurons to become clustered into centralized, integrating organs.

centriole   (sen' tree ole) A paired organelle that helps organize the microtubules in animal and protist cells during nuclear division.

centromere   (sen' tro meer) [Gk. *centron*: center + *meros*: part] The region where sister chromatids join.

centrosome   (sen' tro soam) The major microtubule organizing center of an animal cell.

cephalization   (sef ah luh zay' shun) [Gk. *kephale*: head] The evolutionary trend toward increasing concentration of nervous tissue (e.g., the brain) and sensory organs at the anterior end of the animal.

cerebral cortex   The outer layer of the cerebral hemispheres in the vertebrate brain. Plays key roles in sensory perception, learning, memory, and motor control.

channel protein   An integral membrane protein that forms an aqueous passageway across the membrane in which it is inserted and through which specific solutes may pass.

character   In genetics, an observable feature, such as eye color. (Contrast with trait.)

chemical bond   An attractive force stably linking two atoms.

chemical reaction   The change in the composition or distribution of atoms of a substance with consequent alterations in properties.

chemical synapse   A point of contact between two neurons at which the neurons are separated by only a very narrow space and neurotransmitter molecules released from the presynaptic cell induce changes in ion flux and membrane potential in the postsynaptic cell. (Contrast with electrical synapse.)

chemiosmosis   Formation of ATP in mitochondria and chloroplasts, resulting from a pumping of protons across a membrane (against a gradient of electrical charge and of pH), followed by the return of the protons through a protein channel with ATP synthase activity.

chemoautotroph   An organism that uses carbon dioxide as a carbon source and obtains energy by oxidizing inorganic substances from its environment; also called chemolithotroph. (Contrast with chemoheterotroph, photoautotroph, photoheterotroph.)

chemoheterotroph   An organism that must obtain both carbon and energy from organic substances. (Contrast with chemoautotroph, photoautotroph, photoheterotroph.)

chemolithotroph   [Gk. *lithos*: stone, rock] *See* chemoautotroph.

chemoreceptor   A sensory receptor cell that senses specific molecules (such as CO_2 or O_2 internally or environmental odorant molecules externally).

chi-square goodness-of-fit
A statistical test used to assess whether the frequencies of observations in different categories are consistent with an hypothesized frequency distribution.

chitin   (kye' tin) [Gk. *kiton*: tunic] The characteristic tough but flexible organic component of the exoskeleton of arthropods, consisting of a complex, nitrogen-containing polysaccharide. Also found in cell walls of fungi.

chlorophyll   (klor' o fill) [Gk. *kloros*: green + *phyllon*: leaf] Any of several green pigments associated with chloroplasts or with certain bacterial membranes; responsible for trapping light energy for photosynthesis.

chloroplast   [Gk. *kloros*: green + *plast*: a particle] An organelle bounded by a double membrane containing the enzymes and pigments that perform photosynthesis. Chloroplasts occur only in eukaryotes.

choanocyte   (ko' an uh site) The collared, flagellated feeding cells of sponges.

chorion   (kor' ee on) [Gk. *khorion*: afterbirth] The outermost of the membranes protecting mammal and reptile (including bird) embryos; in mammals it forms part of the placenta.

chromatin   The nucleic acid–protein complex that makes up eukaryotic chromosomes.

chromatin remodeling   A mechanism for epigenetic gene regulation by the alteration of chromatin structure.

chromosomal mutation   Loss of or changes in position/direction of a DNA segment on a chromosome.

chromosome   (krome' o sowm) [Gk. *kroma*: color + *soma*: body] In bacteria and viruses, the DNA molecule that contains most or all of the genetic information of the cell or virus. In eukaryotes, a structure composed of DNA and proteins that bears part of the genetic information of the cell.

cilium   (sil' ee um) (plural: cilia) [L. eyelash] Hairlike organelle used for locomotion by many unicellular organisms and for moving water and mucus by many multicellular organisms. Generally shorter than a flagellum.

circadian clocks   A biological clock that has a free-running cycle of about 24 hours.

circadian rhythm   (sir kade' ee an) [L. *circa*: approximately + *dies*: day] A rhythm of growth or activity that recurs about every 24 hours.

circulatory system   A system consisting of a muscular pump (heart), a fluid (blood), and a series of conduits (e.g., blood vessels) that transports materials around the body by mass flow.

citric acid cycle   In cellular respiration, a set of chemical reactions whereby acetyl CoA is oxidized to carbon dioxide and hydrogen atoms are stored as NADH and $FADH_2$. Also called the Krebs cycle.

clade   [Gk. *klados*: branch] A monophyletic group made up of an ancestor and all of its descendants.

class   (1) In biological classification: A group of related orders. (2) Generally: a group of things defined by particular attributes.

class I MHC molecules   Cell surface proteins that are present on the surface of all nucleated cells. They present antigens to cytotoxic T (T_C) cells.

class II MHC molecules   Cell surface proteins that are present on the surface of macrophages, B cells, and dendritic cells. They present antigens to T-helper (T_H) cells.

cleavage   The first few cell divisions of an animal zygote. Cleavage divides the embryo without increasing its mass. (*See* complete cleavage, incomplete cleavage.)

climate   The long-term average state of the weather at a given place over a yearly cycle. (Contrast with weather.)

climate diagram   A way of summarizing the climate of a given location by superimposing graphs of average monthly temperature and precipitation through a year in a way that indicates periods that are favorable or unfavorable for plant growth.

clonal deletion   Inactivation or destruction of lymphocyte clones that would produce immune reactions against the animal's own body.

clonal lineages   Asexually reproduced groups of nearly identical organisms.

clonal selection   Mechanism by which exposure to antigen results in the activation of selected T- or B-cell clones, resulting in an immune response.

clone   [Gk. *klon*: twig, shoot] (1) Genetically identical cells or organisms produced from a common ancestor by asexual means. (2) To produce many identical copies of a DNA sequence by its introduction into, and subsequent asexual reproduction of, a cell or organism.

closed circulatory system   Circulatory system in which the circulating fluid is contained within a continuous system of vessels. (Contrast with open circulatory system.)

closed system   A system that isolated from, and does not interact with, its surroundings. (Contrast with open system.)

coccus   (kock′ us) (plural: cocci) [Gk. *kokkos*: berry, pit] Any of various spherical or spheroidal bacteria.

cochlea   (kock′ lee uh) [Gk. *kokhlos*: snail] A spiral tube in the inner ear of vertebrates; it contains the sensory cells involved in hearing.

cocurrent gas exchange   The exchange of gas between blood and water in a **cocurrent system** (a system in which the blood and water flow in the same direction along the gas exchange membrane of the animal; sometimes called a concurrent system).

coding region   Nucleotide sequences in a gene that directly specify amino acids in a protein.

coding strand   One of the two strand of DNA that for a particular gene specifies the amino acids in a protein.

codominance   A condition in which two alleles at a locus produce different phenotypic effects and both effects appear in heterozygotes.

codon   Three nucleotides in messenger RNA that direct the placement of a particular amino acid into a polypeptide chain. (Contrast with anticodon.)

coelom   (see′ loam) [Gk. *koiloma*: cavity] An animal body cavity completely enclosed by mesoderm.

coelomate   (see′ lo mate) An animal that contains a body cavity, the coelom, that develops within the mesoderm.

coenocyte   (see′ no site) An organism that contains many nuclei within each cell membrane.

coenocytic   (seen′ a sit ik) [Gk. *koinos*: common + *kytos*: container] Referring to the condition, found in some fungal hyphae, of "cells" containing many nuclei but enclosed by a single plasma membrane. Results from nuclear division without cytokinesis.

coenzyme A (CoA)   A coenzyme used in various biochemical reactions as a carrier of acyl groups.

cofactor   An inorganic ion that is weakly bound to an enzyme and required for its activity.

cohesion   The tendency of molecules (or any substances) to stick together.

cold-hardening   A process by which plants can acclimate to cooler temperatures; requires repeated exposure to cool temperatures over many days.

coleoptile   A sheath that surrounds and protects the shoot apical meristem and young primary leaves of a grass seedling as they move through the soil.

collagen   [Gk. *kolla*: glue] A fibrous protein found extensively in bone and connective tissue.

collecting duct   In mammals and birds, a tubule that receives urine produced in the nephrons of the kidney and delivers that fluid to the ureter for excretion. Concentration of the urine occurs in the collecting duct.

collenchyma   (cull eng′ kyma) [Gk. *kolla*: glue + *enchyma*: infusion] A type of plant cell, living at functional maturity, which lends flexible support by virtue of primary cell walls thickened at the corners. (Contrast with parenchyma, sclerenchyma.)

commensalism   [L. *com*: together + *mensa*: table] A "+/0" interaction between individuals of two different species that benefits one individual (i.e., increases its fitness) but does not affect the other. (Contrast with amensalism, mutualism.)

community   The assemblage of interacting individuals of different species within a particular geographic area.

community function   Any aspect of the interactions that occur within an ecological community that affects the rate

of input of energy and matter into the community and its output of transformed matter and energy.

community structure   The attributes used to characterize an ecological community, which usually include the number of species in the community, their identities, and their relative abundances. (*See* species composition, species diversity.)

companion cell   In angiosperms, a specialized cell found adjacent to a sieve tube element.

comparative genomics   Computer-aided comparison of DNA sequences between different organisms to reveal genes with related functions.

compartment   One of the interacting components of a system. Applied to the global ecosystem, the different forms and physical locations in which chemical elements or molecules may occur.

competition   In ecology, a "–/–" interaction between individuals of the same or different species that causes both individuals to lose fitness.

competitive inhibitor   A nonsubstrate that binds to the active site of an enzyme and thereby inhibits binding of its substrate. (Contrast with noncompetitive inhibitor.)

complementary base pairing   The AT (or AU), TA (or UA), CG, and GC pairing of bases in double-stranded DNA, in transcription, and between tRNA and mRNA.

complementary DNA (cDNA)   DNA formed by reverse transcriptase acting with an RNA template; essential intermediate in the reproduction of retroviruses; used as a tool in recombinant DNA technology; lacks introns.

complete cleavage   Pattern of cleavage that occurs in eggs that have little yolk. Early cleavage furrows divide the egg completely. (*See also* radial cleavage, spiral cleavage; contrast with incomplete cleavage.)

complete metamorphosis   A change of state during the life cycle of an organism in which the body is almost completely rebuilt to produce an individual with a very different body form. Characteristic of insects such as butterflies, moths, beetles, ants, wasps, and flies.

compound eye   An eye characteristic of arthropods, composed of many individual optical units called ommatidia.

condensation reaction   A chemical reaction in which two molecules become connected by a covalent bond and a molecule of water is released (AH + BOH → AB + H_2O.) (Contrast with hydrolysis reaction.)

conditional mutation   A mutation that results in a characteristic phenotype only under certain environmental conditions.

conducting airways   In the lungs of animals, the airways that do not participate in the exchange of respiratory gases between air and blood, but rather simply conduct air in and out of the lungs.

conducting system   In the vertebrate heart, a system of specialized muscle cells by which depolarization rapidly spreads throughout the heart muscle.

cone   (1) In conifers, a reproductive structure consisting of spore-bearing scales extending from a central axis. (Contrast with strobilus.) (2) In the vertebrate retina, a type of photoreceptor cell responsible for color vision.

confidence interval   A numerical interval that is calculated to contain the true value of some parameter of interest at a stated probability level.

conformer   An animal in which an internal condition (e.g., body temperature) adjusts to match an external condition (e.g., environmental temperature). (Contrast with regulators.)

conformity   The state in which an internal condition of an animal (e.g., body temperature) changes to match an external condition (e.g., environmental temperature). (Contrast with regulation.)

conidium   (ko nid' ee um) (plural: conidia) [Gk. *konis*: dust] A type of haploid fungal spore borne at the tips of hyphae, not enclosed in sporangia.

conjugation   (kon ju gay' shun) [L. *conjugare*: yoke together] (1) A process by which DNA is passed from one cell to another through a conjugation tube, as in bacteria. (2) A nonreproductive sexual process by which *Paramecium* and other ciliates exchange genetic material.

consensus sequences   Short stretches of DNA that appear, with little variation, in many different genes.

conservation ecology   The subdiscipline of ecology whose goal is to understand the processes of extinction of populations and species, and to devise ways to conserve species and the ecological systems of which they are a part.

constant region   The portion of an immunoglobulin molecule whose amino acid composition determines its class and does not vary among immunoglobulins in that class. (Contrast with variable region.)

constitutive   Always present; produced continually at a constant rate. (Contrast with inducible.)

constitutive genes   Genes that are expressed all the time. (Contrast with inducible genes.)

consumer–resource interactions   In ecology, a "+/−" interaction between individuals of different species in which one individual gains fitness by consuming part or all of another individual, which loses fitness from being consumed. Examples are predation, herbivory, and parasitism.

continental drift   The gradual movements of the world's continents that have occurred over billions of years.

continuous variables   Variables that can take on a continuous range of values.

contractile vacuole   (kon trak' tul) A specialized vacuole that collects excess water taken in by osmosis, then contracts to expel the water from the cell.

contraction   The condition in which a muscle produces force.

control mechanism   One of four essential elements of a control system; modifies a controlled variable by using information from sensors to determine which effectors to activate and how intense the activation needs to be.

controlled variable   One of four essential elements of a control system; the characteristic of a biochemical system, cell or animal that is being controlled.

convergent evolution   Independent evolution of similar features from different ancestral traits.

coral bleaching   A phenomenon in which corals lose their endosymbionts and become whitened as a result; leads to weakening, and sometimes death, of the coral.

corepressor   A molecule that binds to a bacterial repressor protein, altering its shape so that it binds to the operator sequence in DNA and prevents its transcription.

Coriolis effect   The apparent deflection of a moving body as viewed from a rotating frame of reference. In the system of the rotating Earth, an object (such as a packet of atmospheric gases) moving toward the Equator will appear to be deflected toward the west from the perspective of an observer on the surface; one moving toward a Pole will appear to be deflected toward the east.

cork   In plants, a protective outermost tissue layer composed of cells with thick walls waterproofed with suberin.

cork cambium   [L. *cambiare*: to exchange] In plants, a lateral meristem that produces secondary growth, mainly in the form of waxy-walled protective cells, including some of the cells that become bark.

cornea   In a vertebrate, the clear, transparent tissue that covers the forward-facing surface of the eye and allows light to pass through to the retina.

correlation coefficient   A measure of the strength of relationship between two quantitative variables, ranging from –1 (a perfect negative relationship) to 1 (a perfect positive relationship).

corolla   (ko role' lah) [L. *corolla*: a small crown] All of the petals of a flower, collectively.

coronary circulatory system   A system of blood vessels that carries blood to and from the heart muscle

corpus luteum   (kor' pus loo' tee um) (plural: corpora lutea) [L. yellow body] A hormone-producing (endocrine) structure formed from reorganization of the cells of an ovarian follicle that has undergone ovulation. In mammals, it secretes progesterone, estrogen, and inhibin. If fertilization occurs, it remains active during pregnancy; if not, it degenerates.

corpus luteum of pregnancy   A corpus luteum that functions for an extended period of time during pregnancy. Secretes hormones that are important for maintenance of pregnancy.

corpus luteum of the cycle   A corpus luteum that functions for a short time (e.g., about 10 days in humans) and then undergoes internally programmed degeneration.

cortex   [L. *cortex*: covering, rind] (1) In plants, the tissue between the epidermis and the vascular tissue of a stem or root. (2) In animals, the outer tissue of certain organs, such as the adrenal gland (adrenal cortex) and the brain (cerebral cortex).

cost–benefit approach   An approach to ecological and evolutionary analysis that assumes an animal has a limited amount of time and energy to devote to its activities, and accordingly activities will occur only if benefits exceed costs. (*See also* trade-off.)

cotyledon   (kot' ul lee' dun) [Gk. *kotyledon*: hollow space] A "seed leaf." An embryonic organ that stores and digests reserve materials; may expand when seed germinates.

countercurrent heat exchange   The exchange of heat that occurs between two closely juxtaposed fluid streams that are flowing in opposite directions (e.g. blood flowing in opposite directions in two juxtaposed blood vessels).

countercurrent gas exchange   The exchange of gas between blood and water in a **countercurrent system** (a system in which the blood and water flow in opposite directions along the gas exchange membrane of the animal).

countercurrent multiplication   The mechanism that increases the concentration of the interstitial fluids in the medulla of the mammalian kidney, permitting a mammal to

produce concentrated urine. During countercurrent multiplication, countercurrent flow in the loops of Henle multiplies effects of active ion transport.

covalent bond   Chemical bond based on the sharing of electrons between two atoms.

CpG islands   DNA regions rich in C residues adjacent to G residues. Especially abundant in promoters, these regions are where methylation of cytosine usually occurs.

cross-bridges   During muscle contraction, the links formed when the globular heads of myosin filaments bind to specific sites on actin filaments. The heads of a myosin molecule interact with actin molecules to produce contraction.

crossing over   The mechanism by which linked genes undergo recombination. In general, the term refers to the reciprocal exchange of corresponding segments between two homologous chromatids.

crustose   A growth form of organisms, such as lichens, in which the organism forms a thin, close, tight bond with the surface of a rock, tree, or other object.

cryptochromes   [Gk. *kryptos*: hidden + *kroma*: color] Photoreceptors mediating some blue-light effects in plants and animals.

ctene   (teen) [Gk. *cteis*: comb] In ctenophores, a comblike row of cilia-bearing plates. Ctenophores move by beating the cilia on their eight ctenes.

current   (1) Flow of a fluid (gas or liquid), for example in ocean waters or in the atmosphere. (2) The flow of electrical charge.

cuticle   (1) In plants, a waxy layer on the outer body surface that retards water loss. (2) In ecdysozoans, an outer body covering that provides protection and support and is periodically molted.

cyclic AMP   *See* cAMP.

cyclic electron transport   In photosynthetic light reactions, the flow of electrons that produces ATP but no NADPH or O_2.

cyclin   A protein that activates a cyclin-dependent kinase, bringing about transitions in the cell cycle.

cyclin-dependent kinase (Cdk)   A protein kinase whose target proteins are involved in transitions in the cell cycle and which is active only when complexed with additional protein subunits, called cyclins.

cytokine   A regulatory protein made by immune system cells that affects other target cells in the immune system.

cytokinesis   (sy′ toe kine ee′ sis) [Gk. *kytos*: container + *kinein*: to move] The division of the cytoplasm of a dividing cell. (Contrast with mitosis.)

cytokinin   (sy′ toe kine′ in) A member of a class of plant growth substances that plays roles in senescence, cell division, and other phenomena.

cytoplasm   The contents of the cell, excluding the nucleus.

cytoplasmic determinants   In animal development, materials in the cytoplasm, the spatial distribution of which may determine such things as embryonic axes and cell determination.

cytoplasmic segregation   The asymmetrical distribution of cytoplasmic determinants in a developing animal embryo.

cytoplasmic streaming   A form of amoeboid movement in which a fluid cytoplasm moves and stretches the organism's body in new directions.

cytosine (C)   (site′ oh seen) A nitrogen-containing base found in DNA and RNA.

cytoskeleton   The network of microtubules and microfilaments that gives a eukaryotic cell its shape and its capacity to arrange its organelles and to move.

cytosol   The fluid portion of the cytoplasm, excluding organelles and other solids.

cytotoxic T cells (T$_C$)   Cells of the cellular immune system that recognize and directly eliminate virus-infected cells. (Contrast with T-helper cells.)

D

data   Quantified observations about a system under study.

daughter chromosomes   During mitosis, the separated chromatids from the beginning of anaphase onward.

decomposer   An organism that obtains the energy and materials it needs to survive, grow, and reproduce from the waste products or dead bodies of other organisms.

defensin   A type of protein made by phagocytes that kills bacteria and enveloped viruses by insertion into their plasma membranes.

deficiency disease   A condition (e.g., scurvy) caused by chronic lack of any essential nutrient.

delayed implantation   Embryonic diapause in placental mammals. A state of arrested embryonic development that occurs after an embryo has arrived in the uterus but before it implants in the uterine wall.

deletion   A mutation resulting from the loss of a continuous segment of a gene or chromosome. Such mutations almost never revert to wild type. (Contrast with duplication, point mutation.)

demethylase   An enzyme that catalyzes the removal of the methyl group from cytosine, reversing DNA methylation.

demography   (Gk. *demos*: population + *graphia*: description) The quantitative study of the processes that determine the structure of populations (e.g., the relative proportions of individuals of different sizes, ages, stages, and genders), the size of populations, and the changes in these attributes.

denaturation   Loss of activity of an enzyme or a nucleic acid molecule as a result of structural changes induced by heat or other means.

dendrite   [Gk. *dendron*: tree] The receptive element of most neurons, which receives synaptic input from other neurons. Usually much branched and relatively short compared with the axon.

denitrification   The chemical process by which "fixed" (biologically-useable) nitrogen is converted back into N_2 gas. (Contrast with nitrogen fixation.)

denitrifiers   Bacteria that release nitrogen to the atmosphere as nitrogen gas (N_2).

density-dependent   Pertaining to any factor or interaction that varies with density. For example, individual survival or reproductive success often changes as population density changes.

deoxygenation   The release of O_2 from a combined state with a respiratory pigment such as hemoglobin.

deoxyribonucleic acid   *See* DNA.

deoxyribonucleoside triphosphates (dNTPs)   The raw materials for DNA synthesis: deoxyadenosine triphosphate (dATP), deoxythymidine triphosphate (dTTP), deoxycytidine triphosphate (dCTP), and deoxyguanosine triphosphate (dGTP). Also called deoxyribonucleotides.

deoxyribose   A five-carbon sugar found in nucleotides and DNA.

depolarization   A change in the membrane potential across a cell membrane so that the inside of the membrane becomes less negative, or even positive, compared with the outside of the membrane. (Contrast with hyperpolarization.)

derived trait   A trait that differs from the ancestral trait. (Contrast with synapomorphy.)

dermal tissue system   The outer covering of a plant, consisting of epidermis in the young plant and periderm in a plant with extensive secondary growth. (Contrast with ground tissue system, vascular tissue system.)

descent with modification Darwin's premise that all species share a common ancestor and have diverged from one another gradually over time.

descriptive statistics Quantitative measures that describe general patterns in data.

determinate growth A growth pattern in which the growth of an organism or organ ceases when an adult state is reached; characteristic of most animals and some plant organs. (Contrast with indeterminate growth.)

determination In development, the process whereby the fate of an embryonic cell or group of cells (e.g., to become epidermal cells or neurons) is set.

detritivore (di try′ ti vore) [L. *detritus*: worn away + *vorare*: to devour] An organism that obtains its energy from the dead bodies or waste products of other organisms. (Contrast with carnivore, herbivore, omnivore.)

development The process by which a multicellular organism, beginning with a single cell, goes through a series of changes, taking on the successive forms that characterize its life cycle.

diaphragm (dye′ uh fram) [Gk. *diaphrassein*: barricade] (1) A sheet of muscle that separates the thoracic and abdominal cavities, found only in mammals; helps drive air flow during breathing. (2) A birth control device in which a sheet of rubber is fitted over the woman's cervix, blocking the entry of sperm.

diastole (dye ass′ toll ee) [Gk. dilation] The portion of the cardiac cycle when the heart muscle relaxes. (Contrast with systole.)

dichotomous (dye cot′ oh mus) [Gk. *dichot*: split in two; *tomia*: removed] A branching pattern in which the shoot divides at the apex producing two equivalent branches that subsequently never overlap.

differentiation The process whereby originally similar cells follow different developmental pathways; the actual expression of determination.

diffusion Random movement of molecules or other particles, resulting in even distribution of the particles when no barriers are present.

digestion The breakdown (by hydrolysis) of ingested food molecules into smaller chemical components that an animal is capable of distributing to the tissues of its body.

digestive vacuole In protists, an organelle specialized for digesting food ingested by endocytosis.

dihybrid cross A mating in which the parents differ with respect to the alleles of two loci of interest.

dikaryon (di care′ ee ahn) [Gk. *di*: two + *karyon*: kernel] A cell or organism carrying two genetically distinguishable nuclei. Common in fungi.

dioecious (die eesh′ us) [Gk. *di*: two + *oikos*: house] Pertaining to organisms in which the two sexes are "housed" in two different individuals, so that eggs and sperm are not produced in the same individuals. Examples: humans, fruit flies, date palms. (Contrast with monoecious.)

diploblastic Having two cell layers. (Contrast with triploblastic.)

diploid (dip′ loid) [Gk. *diplos*: double] Having a chromosome complement consisting of two copies (homologs) of each chromosome. Designated $2n$. (Contrast with haploid.)

direct development Pattern of development in which the young resemble the adults. (Contrast with indirect development.)

directional selection Selection in which phenotypes at one extreme of the population distribution are favored. (Contrast with disruptive selection, stabilizing selection.)

disaccharide A carbohydrate made up of two monosaccharides (simple sugars).

discrete variables Quantitative variables that take on only whole number values.

dispersal corridor A continuous strip of habitat that connects larger pieces of habitat, thus facilitating movement of organisms between them.

disruptive selection Selection in which phenotypes at both extremes of the population distribution are favored. (Contrast with stabilizing selection.)

disturbance Events that cause sudden change in the environment and in ecological systems as a result. Examples include fire, landslides, floods, strong storms, and volcanic eruptions—as well as less obvious events such as the death and fall of a large tree that opens up the forest canopy.

disulfide bridge The covalent bond between two sulfur atoms (–S—S–) linking two molecules or remote parts of the same molecule.

DNA (deoxyribonucleic acid) The fundamental hereditary material of all living organisms. In eukaryotes, stored primarily in the cell nucleus. A nucleic acid using deoxyribose rather than ribose.

DNA fingerprint An individual's unique pattern of allele sequences, commonly short tandem repeats and single nucleotide polymorphisms.

DNA ligase Enzyme that unites broken DNA strands during replication and recombination.

DNA methyltransferase An enzyme that catalyzes the methylation of DNA.

DNA microarray A small glass or plastic square onto which thousands of single-stranded DNA sequences are fixed so that hybridization of cell-derived RNA or DNA to the target sequences can be performed.

DNA polymerase Any of a group of enzymes that catalyze the formation of DNA strands from a DNA template.

DNA replication The creation of a new strand of DNA in which DNA polymerase catalyzes the exact reproduction of an existing (template) strand of DNA.

DNA segregation The separation of two DNAs formed by replication into two new cells during cell division.

DNA transposons Mobile genetic elements that move without making an RNA intermediate. (Contrast with retrotransposons.)

dNTPs *See* deoxyribonucleoside triphosphates.

domain (1) An independent structural element within a protein. Encoded by recognizable nucleotide sequences, a domain often folds separately from the rest of the protein. Similar domains can appear in a variety of different proteins across phylogenetic groups (e.g., "homeobox domain"; "calcium-binding domain"). (2) In phylogenetics, the three monophyletic branches of life (Bacteria, Archaea, and Eukarya).

dominance In genetics, the ability of one allelic form of a gene to determine the phenotype of a heterozygous individual in which the homologous chromosomes carry both it and a different (recessive) allele. (Contrast with recessive.)

dominate In animal behavior, to have control over resources (e.g., food or mates) as a result of defeating challengers in one-on-one behavioral contests.

dormancy A condition in which normal activity is suspended, as in some spores, seeds, and buds.

dorsal [L. *dorsum*: back] Toward or pertaining to the back or upper surface. (Contrast with ventral.)

double fertilization In angiosperms, a process in which the nuclei of two sperm fertilize one egg. One sperm's nucleus combines with the egg nucleus to produce a zygote, while the other combines with the same egg's two polar nuclei to produce the first cell of the triploid endosperm (the tissue that will nourish the growing plant embryo).

doubling time   The time over which an ecological population doubles in size (number of individuals). Populations growing multiplicatively with a constant value of *r* have a constant doubling time, no matter what their current size is.

duplication   A mutation in which a segment of a chromosome is duplicated, often by the attachment of a segment lost from its homolog. (Contrast with deletion.)

dynamic   (Gk. *dunamikos*: powerful) Characterized by activity or change.

E

ecological efficiency   The transfer of energy from one trophic level to the next, often estimated as the ratio of dry biomass at the higher level to dry biomass at the lower level. Note that this use of "efficiency" as the ratio of energy output to input is similar to the measure of efficiency used for many human-made machines.

ecological system   One or more organisms and the abiotic and biotic environment with which they interact.

ecological transition   A transition from one ecological community to a different community following a disturbance. The transition is not easily reversible, and the new community persists even if original environmental conditions are restored; thus the two ecological communities are considered to be alternative stable states of the system. (Contrast with succession.)

ecology   [Gk. *oikos*: house] Defined by the German biologist Ernst Haeckel in 1866 as "the entire science of the relations of the organism to its external environment," by which he (and we) include both the biotic and abiotic environment.

ecosystem   (eek' oh sis tum) In general, shorthand for "ecological system." Often used more specifically to refer to an ecological community and its abiotic environmental context.

ecosystem function   Any aspect of the interactions that occur within an ecosystem that affects the rate of input of energy and matter into the ecosystem and its output of transformed matter and energy.

ecosystem services   Ecosystem outputs that benefit humans.

ectoderm   [Gk. *ektos*: outside + *derma*: skin] The outermost of the three embryonic germ layers first delineated during gastrulation. Gives rise to the skin, sense organs, and nervous system.

ectomycorrhizae   Mutualistic fungi that cover the roots of plants and assist in the uptake of water and minerals from the soil by the plant.

ectotherm   [Gk. *ektos*: outside + *thermos*: heat] An animal in which body temperature matches—and varies with—the external temperature. (*See also* poikilotherm.)

effector cells   In cellular immunity, B cells and T cells that attack an antigen, either by secreting antibodies that bind to the antigen or by releasing molecules that destroy any cell bearing the antigen.

effectors   One of four essential elements of a control system. A tissue, organ, or cell that performs actions ("carries out orders") under the direction of the nervous system or another physiological control system (e.g., the endocrine system).

efferent neurons   In a nervous system, nerve cells that carry commands from the central nervous system to physiological and behavioral effectors such as muscles and glands.

egg   In all sexually reproducing organisms, the female gamete (also called an ovum); in birds, reptiles, and some other animals, a structure within which the early embryonic development of a fertilized ovum occurs. (*See also* amniote egg.)

electrical synapse   A type of synapse at which there is direct continuity between the cytoplasms of the presynaptic and postsynaptic neurons and action potentials spread directly from presynaptic cell to postsynaptic cell. (Contrast with chemical synapse.)

electrocardiogram (ECG or EKG)   A graphic recording of electrical potentials that are measured on the body surface but originate from the heart.

electromagnetic radiation   A self-propagating wave that travels though space and has both electrical and magnetic properties.

electron   A subatomic particle outside the nucleus carrying a negative charge and very little mass.

electron shell   The region surrounding the atomic nucleus at a fixed energy level in which electrons orbit.

electron transport   The passage of electrons through a series of proteins with a release of energy which may be captured in a concentration gradient or in chemical form such as NADH or ATP.

electronegativity   The tendency of an atom to attract electrons when it occurs as part of a compound.

element   A substance that cannot be converted to simpler substances by ordinary chemical means.

elicitor   A substance that induces the synthesis of defensive molecules such as phytoalexins in higher plants.

elongation   (1) In molecular biology, the addition of monomers to make a longer RNA or protein during transcription or translation. (2) Growth of a plant axis or cell primarily in the longitudinal direction.

embryo   [Gk. *en*: within + *bryein*: to grow] A young animal, or young plant sporophyte, while it is still contained within a protective structure such as a seed, egg, or uterus.

embryo sac   In angiosperms, the female gametophyte. Found within the ovule, it consists of eight or fewer cells, membrane bounded, but without cellulose walls between them.

embryonic diapause   A programmed state of arrested or profoundly slowed embryonic development. (*See also* delayed implantation.)

embryonic stem cell (ESC)   A pluripotent cell in the blastocyst.

emigration   Movement of individual organisms out of a population.

3′ end   (3 prime) The end of a DNA or RNA strand that has a free hydroxyl group at the 3′ carbon of the sugar (deoxyribose or ribose).

5′ end   (5 prime) The end of a DNA or RNA strand that has a free phosphate group at the 5′ carbon of the sugar (deoxyribose or ribose).

endocrine cells   Cells that secrete hormones into the blood. (*See also* endocrine gland.)

endocrine gland   (en' doh krin) [Gk. *endo*: within + *krinein*: to separate] A gland or tissue , lacking ducts, in which endocrine cells secrete hormones into the blood. (Contrast with exocrine gland.)

endocytosis   A process by which liquids or solid particles are taken up by a cell through invagination of the plasma membrane. (Contrast with exocytosis.)

endoderm   [Gk. *endo*: within + *derma*: skin] The innermost of the three embryonic germ layers delineated during gastrulation. Gives rise to the digestive and respiratory tracts and structures associated with them.

endodermis   In plants, a specialized cell layer marking the inside of the cortex in roots and some stems. Frequently a barrier to free diffusion of solutes.

endogenous retroviruses   A DNA sequence derived from a retrovirus that persists in and is transmitted as part of the genome of a non-viral organism. Some endogenous retroviruses can become active and produce new viral infections.

endomembrane system   A system of intracellular membranes that exchange material with one another, consisting

of the Golgi apparatus, endoplasmic reticulum, and lysosomes when present.

endometrium The inner tissue layer of the uterus of a mammal. Embryos implant in the endometrium, which later helps form the placenta.

endophytic fungi Fungi that live within the aboveground portions of plants without causing obvious harm to the host plant.

endoplasmic reticulum (ER) [Gk. *endo*: within + L. *reticulum*: net] A system of membranous tubes and flattened sacs found in the cytoplasm of eukaryotes. Exists in two forms: rough ER, studded with ribosomes; and smooth ER, lacking ribosomes.

endoskeleton [Gk. *endo*: within + *skleros*: hard] An internal skeleton covered by other, soft body tissues. (Contrast with exoskeleton.)

endosome Membrane-enclosed compartment in a cell that is formed after endocytosis.

endosperm [Gk. *endo*: within + *sperma*: seed] A specialized triploid seed tissue found only in angiosperms; contains stored nutrients for the developing embryo.

endospore [Gk. *endo*: within + *spora*: to sow] In some bacteria, a resting structure that can survive harsh environmental conditions.

endotoxin A lipopolysaccharide that forms part of the outer membrane of certain Gram-negative bacteria that is released when the bacteria grow or lyse. (Contrast with exotoxin.)

end-product inhibition *See* feedback inhibition.

endurance exercise Exercise that consists of many repetitions of relatively low-intensity muscular actions over long periods of time. Also termed endurance training. (Contrast with resistance exercise.)

energy The capacity to create and maintain organization. More narrowly defined, the capacity do work or move matter against an opposing force.

enteric division One of three divisions of the vertebrate autonomic nervous system; composed of neurons located between the smooth muscle layers of the gut.

entropy (S) (en' tro pee) [Gk. *tropein*: to change] A measure of the degree of disorder in any system. Spontaneous reactions in a closed system are always accompanied by an increase in entropy.

environmental sex determination Mechanism in which the sex of an individual is determined by the temperature it experiences during embryonic development.

enzyme (en' zime) [Gk. *zyme*: to leaven (as in yeast bread)] A catalytic protein that speeds up a biochemical reaction.

enzyme–substrate complex (ES) An intermediate in an enzyme-catalyzed reaction; consists of the enzyme bound to its substrate(s).

eons The primary division of geologic time. The history of Earth is divided into four eons: Hadeon, Archean, Proterozoic, and Phanerozoic.

epi- [Gk. upon, over] A prefix used to designate a structure located on top of another; for example, epidermis, epiphyte.

epiblast The upper or overlying portion of the avian blastula which is joined to the hypoblast at the margins of the blastodisc.

epidermis [Gk. *epi*: over + *derma*: skin] In plants and animals, the outermost cell layers. (Only one cell layer thick in plants.)

epigenetics The scientific study of changes in the expression of a gene or set of genes that occur without change in the DNA sequence.

epistasis Interaction between genes in which the presence of a particular allele of one gene determines how another gene will be expressed.

epithelium (plural: epithelia) A sheet of cells that lines a body cavity or covers an organ or body surface; one of the major tissue types in multicellular animals.

epitope *See* antigenic determinant.

epoch A subdivision of geologic time that divides geologic periods.

EPSP *See* excitatory postsynaptic potential.

equilibrium The state of a system in which there is no net change through time.

equilibrium potential The membrane potential at which an ion is at electrochemical equilibrium, i.e., at which the concentration and electrical effects on diffusion of the ion are balanced so there is no net diffusion of the ion across the membrane.

ER *See* endoplasmic reticulum.

erythrocyte (ur rith' row site) [Gk. *erythros*: red + *kytos*: container] *See* red blood cell.

ES *See* enzyme–substrate complex.

ESC *See* embryonic stem cell.

essential amino acids Amino acids that an animal cannot synthesize for itself and must obtain from its food.

essential element A mineral nutrient required for normal growth and reproduction in plants and animals.

essential fatty acids Fatty acids that an animal cannot synthesize for itself and must obtain from its food.

essential mineral *See* essential nutrient.

essential nutrient A nutrient (e.g., amino acid, fatty acid, vitamin, mineral) that an animal cannot synthesize for itself and must obtain from its food.

ester linkage A condensation (water-releasing) reaction in which the carboxyl group of a fatty acid reacts with the hydroxyl group of an alcohol. Lipids, including most membrane lipids, are formed in this way. (Contrast with ether linkage.)

estrogens Any of several feminizing steroid sex hormones; produced chiefly by the ovaries in mammals, and by the placenta during pregnancy.

estrous cycle A cycle of behavioral readiness to copulate (called estrus and correlated with ovulation) in most female mammals.

estrus (es' trus) [L. *oestrus*: frenzy] The period of heat, or maximum sexual receptivity, observed in most female mammals at times correlated with ovulation.

ether linkage The linkage of two hydrocarbons by an oxygen atom (HC—O—CH). Ether linkages are characteristic of the membrane lipids of the Archaea. (Contrast with ester linkage.)

ethylene One of the plant growth hormones, the gas $H_2C=CH_2$. Involved in fruit ripening and other growth and developmental responses.

euchromatin Diffuse, uncondensed chromatin. Contains active genes that will be transcribed into mRNA. (Contrast with heterochromatin.)

eudicots Angiosperms with two embryonic cotyledons; one of the two largest clades of angiosperms. (*See also* monocots.)

eukaryotes (yew car' ree oats) [Gk. *eu*: true + *karyon*: kernel or nucleus] Organisms whose cells contain their genetic material inside a nucleus. Includes all life other than the viruses, archaea, and bacteria. (Contrast with prokaryotes.)

eusociality A type of social group in which some adults are infertile and provide services to other, fertile adults.

eutrophication (yoo trofe' ik ay' shun) [Gk. *eu*: truly + *trephein*: to flourish] Responses of aquatic ecosystems to excessive nutrient input, which include greatly increased primary productivity and resulting depletion of dissolved oxygen.

evolution Any gradual change. Most often refers to organic or Darwinian evolution, which is the genetic and

resulting phenotypic change in populations of organisms from generation to generation. (Contrast with speciation.)

evolutionary developmental biology (evo-devo)   The study of the interplay between evolutionary and developmental processes, with a focus on the genetic changes that give rise to novel morphology. Key concepts of evo-devo include modularity, genetic toolkits, genetic switches, and heterochrony.

evolutionary reversal   The reappearance of an ancestral trait in a group that had previously acquired a derived trait.

evolutionary theory   The understanding and application of the mechanisms of evolutionary change to biological problems.

excitable cell   A cell that can generate and propagate action potentials because its cell membrane contains voltage-gated channels, notably neurons and muscle cells.

excitation   In the study of muscle, the event in which a nerve impulse arrives at a neuromuscular junction and initiates an action potential in the cell membrane of a muscle cell.

excitation–contraction coupling   In a muscle cell, the process by which electrical excitation of the cell membrane leads to contractile activity by the contractile proteins (actin and myosin) in the cell. Key events occur at the transverse tubules and sarcoplasmic reticulum, and result in release of Ca^{2+} into the cytoplasm.

excitatory postsynaptic potential (**EPSP**)   At a chemical synapse (specifically, an excitatory synapse), a graded membrane depolarization produced in the postsynaptic cell by arrival of an impulse in the presynaptic cell. (Contrast with inhibitory postsynaptic potential.)

excitatory synapse   A synapse at which impulses in the presynaptic cell act to depolarize the postsynaptic cell.

exocrine gland   (eks′ oh krin) [Gk. *exo*: outside + *krinein*: to separate] Any gland, such as a salivary gland, that secretes to the outside of the body or into the gut. (Contrast with endocrine gland.)

exocytosis   A process by which a vesicle within a cell fuses with the plasma membrane and releases its contents to the outside. (Contrast with endocytosis.)

exon   A portion of a DNA molecule, in eukaryotes, that codes for part of a polypeptide. (Contrast with intron.)

exoskeleton   (eks′ oh skel′ e ton) [Gk. *exos*: outside + *skleros*: hard] A hard covering on the outside of the body to which muscles are attached. (Contrast with endoskeleton.)

exotoxin   A highly toxic, usually soluble protein released by living, multiplying bacteria. (Contrast with endotoxin.)

expression vector   A DNA vector, such as a plasmid, that carries a DNA sequence for the expression of an inserted gene into mRNA and protein in a host cell.

expressivity   The degree to which a genotype is expressed in the phenotype; may be affected by the environment.

external environment   The conditions of the surroundings outside an animal's body.

external fertilization   Fertilization that occurs after release of sperm and eggs into the external environment; typical of aquatic animals. Also called spawning. (Contrast with internal fertilization.)

external respiration   *See* breathing.

extracellular fluid   The aqueous solution (body fluid) outside cells (in the extracellular compartment). In animals with closed circulatory systems, subdivided into blood plasma and interstitial fluid.

extracellular matrix   A material of heterogeneous composition surrounding cells and performing many functions including adhesion of cells.

extraembryonic membranes   Four membranes that support but are not part of the developing embryos of reptiles, birds, and mammals, defining these groups phylogenetically as amniotes. (*See* amnion, allantois, chorion, and yolk sac.)

extrarenal salt excretion   Excretion of inorganic ions in concentrated solutions by structures other than the kidneys, such as the gills in marine fish and salt glands in marine birds and sea turtles.

extreme halophiles   A group of euryarchaeotes that live exclusively in very salty environments.

extremophiles   Archaea and bacteria that live and thrive under conditions (e.g., extremely high temperatures) that would kill most organisms.

F

F-box   A protein domain that facilitates protein–protein interactions necessary for protein degradation. Often involved in the regulation of gene expression (through the breakdown of regulatory proteins such as repressors), especially in plants.

F₁   The first filial generation; the immediate progeny of a parental (P) mating.

F₂   The second filial generation; the immediate progeny of a mating between members of the F_1 generation.

facilitated diffusion   Passive movement through a membrane involving a specific carrier protein; does not proceed against a concentration gradient. (Contrast with active transport, diffusion.)

facultative anaerobe   A prokaryote that can shift its metabolism between anaerobic and aerobic modes depending on the presence or absence of O_2. (Alternatively, facultative aerobe.)

facultative parasite   A organism that can parasitize other living organisms but is also capable of growing independently.

fallopian tube   *See* oviduct.

family   A group of related genera.

fast glycolytic cells   Muscle cells that are highly dependent on ATP production by anaerobic glycolysis and that contract and develop high tension rapidly, but fatigue quickly. Also called fast-twitch cells. (Compare to slow oxidative cells.)

fate map   A diagram of the blastula showing which cells (blastomeres) are "fated" to contribute to specific tissues and organs in the mature body.

fatty acid   A molecule made up of a long nonpolar hydrocarbon chain and a polar carboxyl group. Found in many lipids.

fauna   (faw′ nah) All the animals found in a given area. (Contrast with flora.)

fecundity   The average number of offspring produced by an individual female during a particular life stage, age, or period of time.

feedback inhibition   A mechanism for regulating a metabolic pathway in which the end product of the pathway can bind to and inhibit the enzyme that catalyzes the first committed step in the pathway. Also called end-product inhibition.

fermentation   (fur men tay′ shun) [L. *fermentum*: yeast] (1) Speaking specifically about energy metabolism, the anaerobic degradation of a substance such as glucose to smaller molecules such as lactic acid or alcohol with the extraction of energy. (2) Speaking generally, metabolic processes that occur in the absence of O_2.

fertilization   Union of gametes.

fertilizer   Any of a number of substances added to soil to improve the soil's capacity to support plant growth. May be organic or inorganic.

fetus   Medical and legal term for the stages of a developing human embryo from about the eighth week of pregnancy (the point at which all major organ systems have formed) to the moment of birth.

fiber   In angiosperms, an elongated, tapering sclerenchyma cell, usually with a thick cell wall, that serves as a support function in xylem. (*See also* muscle fiber.)

fibrous root system   A root system typical of monocots composed of

numerous thin adventitious roots that are all roughly equal in diameter. (Contrast with taproot system.)

Fick's law of diffusion   *See* law of diffusion for gases.

filament   In flowers, the part of a stamen that supports the anther.

filter feeder   (1) Speaking generally, an earlier term for a suspension feeder. (2) Speaking specifically, an organism that feeds by means of a straining or filtering device on organisms much smaller than itself that are suspended in water or air.

first filial generation   *See* F$_1$.

first law of thermodynamics   The principle that energy can be neither created nor destroyed.

fission   *See* binary fission.

fitness   An individual's contribution of genes to the next generation, as a consequence of its success in surviving and reproducing.

fixed   The condition in which a particular allele is the only allele present at a genetic locus within a population (i.e., there is no genetic variation at the locus).

fixed action pattern   In the study of animal behavior, a genetically determined behavior that is performed without learning, stereotypic (performed the same way each time), and not modifiable by learning.

flagellum   (fla jell' um) (plural: flagella) [L. *flagellum*: whip] Long, whiplike appendage that propels cells. Prokaryotic flagella differ sharply from those found in eukaryotes.

flora   (flore' ah) All of the plants found in a given area. (Contrast with fauna.)

floral meristem   In angiosperms, a meristem that forms the floral organs (sepals, petals, stamens, and carpels).

floral organ identity genes   In angiosperms, genes that determine the fates of floral meristem cells; their expression is triggered by the products of meristem identity genes.

florigen (FT)   A plant hormone involved in the conversion of a vegetative shoot apex to a flower.

flower   The sexual structure of an angiosperm.

fluid mosaic model   A molecular model for the structure of biological membranes consisting of a fluid phospholipid bilayer in which suspended proteins are free to move in the plane of the bilayer.

flux   The rate of movement of energy, or of matter (an element or a molecular compound), between two compartments of an ecosystem, or between the Earth system and space.

foliose   Having a leafy growth form.

follicle-stimulating hormone (FSH)   A hormone, produced by the anterior pituitary gland, that helps control secretion of hormones by the gonads (i.e., a gonadotropin).

food web   A diagrammatic representation of which organisms consume which other organisms in an ecological community, i.e., a diagram of trophic relationships.

foot   One of the three main body parts of a mollusk.

forebrain   The region of the vertebrate brain that comprises the cerebrum, thalamus, and hypothalamus.

foregut   The beginning of the digestive tract. Consists of the mouth, esophagus, and stomach, and in some animals, a crop or gizzard.

foregut fermenter   An animal that has a specialized, nonacidic foregut chamber housing a mixed microbial community composed of fermenting microbes that assist with the breakdown of food materials.

fossil fuels   Combustible materials, such as coal, natural gas, petroleum, and peat that are formed by geological processes over long periods of time from the remains of living organisms.

founder effect   Random changes in allele frequencies resulting from establishment of a population by a very small number of individuals.

fragmentation   In ecology, the subdivision of a larger piece of habitat into smaller pieces that are isolated from one another by a different habitat.

frame-shift mutation   The addition or deletion of a single or two adjacent nucleotides in a gene's sequence. Results in the misreading of mRNA during translation and the production of a nonfunctional protein. (Contrast with missense mutation, nonsense mutation, silent mutation.)

frequency distribution   A figure that displays the frequency of different classes of data.

free energy (*G*)   Energy that is available for doing useful work, after allowance has been made for the increase or decrease of disorder.

fruit   In angiosperms, a ripened and mature ovary (or group of ovaries) containing the seeds. Sometimes applied to reproductive structures of other groups of plants.

fruticose   Having a shrubby growth form.

FSH   *See* follicle-stimulating hormone.

FT   *See* florigen.

functional genomics   The assignment of functional roles to the proteins encoded by genes identified by sequencing entire genomes.

functional group   A characteristic combination of atoms that contribute specific properties when attached to larger molecules.

G

G cap   A chemically modified GTP added to the 5′ end of mRNA; facilitates binding of mRNA to ribosome and prevents mRNA breakdown. Also called 5′ cap.

G protein   A membrane protein involved in signal transduction; characterized by binding GDP or GTP.

G protein–linked receptors   A class of receptors that change configuration upon ligand binding such that a G protein binding site is exposed on the cytoplasmic domain of the receptor, initiating a signal transduction pathway.

G1   In the cell cycle, the gap between the end of mitosis and the onset of the S phase.

G1–S transition   In the cell cycle, the point at which G1 ends and the S phase begins.

G2   In the cell cycle, the gap between the S (synthesis) phase and the onset of mitosis.

gain of function mutation   A mutation that results in a protein with a new function. (Contrast with loss of function mutation.)

gametangium   (gam uh tan' gee um) (plural: gametangia) [Gk. *gamos*: marriage + *angeion*: vessel] Any plant or fungal structure within which a gamete is formed.

gamete   (gam' eet) [Gk. *gamete/gametes*: wife, husband] The mature sexual reproductive cell: the egg or the sperm.

gametogenesis   (ga meet' oh jen' e sis) The specialized series of cellular divisions, including meiosis, that leads to the formation of gametes.

gametophyte   (ga meet' oh fyte) In plants and photosynthetic protists with alternation of generations, the multicellular haploid phase that produces the gametes. (Contrast with sporophyte.)

ganglion   (gang' glee un) (plural: ganglia) [Gk. tumor] (1) In a vertebrate, a discrete cluster of neuron cell bodies in the peripheral nervous system. (2) In an arthropod, an enlarged part of the ventral nerve cord found in each body segment.

gap genes   In *Drosophila* (fruit fly) development, segmentation genes that

define broad areas along the anterior–posterior axis of the early embryo. Part of a developmental cascade that includes maternal effect genes, pair rule genes, segment polarity genes, and Hox genes.

gas exchange membranes   Thin layers of tissue (one or two cells thick) where respiratory gases move between the internal tissues of an animal and the animal's environmental medium.

gastrovascular cavity   Serving for both digestion (gastro) and circulation (vascular); in particular, the central cavity of the body of jellyfish and other cnidarians.

gastrula   The end product of gastrulation. At this point the embryo contains the forerunners of the three germ layers that will generate the entire body.

gastrulation   Development of a blastula into a gastrula. In embryonic development, the process by which a blastula is transformed by massive movements of cells, from the exterior to the interior, into a gastrula.

gated channel   A membrane protein that changes its three-dimensional shape, and therefore its ion conductance, in response to a stimulus. When open, it allows specific ions to move across the membrane.

gel electrophoresis   (e lek' tro fo ree' sis) [L. *electrum*: amber + Gk. *phorein*: to bear] A technique for separating molecules (such as DNA fragments) from one another on the basis of their electric charges and molecular weights by applying an electric field to a gel.

gene   [Gk. *genes*: to produce] A unit of heredity. Used here as the unit of genetic function which carries the information for a polypeptide or RNA.

gene family   A set of similar genes derived from a single parent gene; need not be on the same chromosomes. The vertebrate globin genes constitute a classic example of a gene family.

gene flow   Exchange of genes between populations through migration of individuals or movements of gametes.

gene-for-gene resistance   In plants, a mechanism of resistance to pathogens in which resistance is triggered by the specific interaction of the products of a pathogen's *Avr* genes and a plant's *R* genes.

general transcription factors   In eukaryotes, transcription factors that bind to the promoters of most protein-coding genes and are required for their expression. Distinct from transcription factors that have specific regulatory effects only at certain promoters or classes of promoters.

genetic drift   Changes in gene frequencies from generation to generation as a result of random (chance) processes.

genetic linkage   Association between genes on the same chromosome such that they do not show random assortment and seldom recombine; the closer the genes, the lower the frequency of recombination.

genetic screen   A technique for identifying genes involved in a biological process of interest. Involves creating a large collection of randomly mutated organisms and identifying those individuals that are likely to have a defect in the pathway of interest. The mutated gene(s) in those individuals can then be isolated for further study.

genetic structure   The frequencies of different alleles at each locus and the frequencies of different genotypes in a Mendelian population.

genetic switches   Mechanisms that control how the genetic toolkit is used, such as promoters and the transcription factors that bind them. The signal cascades that converge on and operate these switches determine when and where genes will be turned on and off.

genetic toolkit   A set of developmental genes and proteins that is common to most animals and is hypothesized to be responsible for the evolution of their differing developmental pathways.

genome   (jee' nome) The complete DNA sequence for a particular organism or individual.

genomic equivalence   The principle that no information is lost from the nuclei of cells as they pass through the early stages of embryonic development.

genomic imprinting   The form of a gene's expression is determined by parental source (i.e., whether the gene is inherited from the male or female parent).

genomic library   All of the cloned DNA fragments generated by the breakdown of genomic DNA into smaller segments.

genotype   (jean' oh type) [Gk. *gen*: to produce + *typos*: impression] An exact description of the genetic constitution of an individual, either with respect to a single trait or with respect to a larger set of traits. (Contrast with phenotype.)

genus   (jean' us) (plural: genera) [Gk. *genos*: stock, kind] A group of related, similar species recognized by taxonomists with a distinct name used in binomial nomenclature.

geographic range   The entire region in which a species occurs.

geographic speciation   *See* allopatric speciation.

geological time scale   The standardized scale accepted by geologists to mark the major divisions in the history of the Earth.

germ cells   [L. *germen*: to beget] Cells in the gonads that multiply mitotically and are capable of undergoing meiosis to produce gametes. (Contrast with somatic cell.)

germline mutation   Mutation in a cell that produces gametes (i.e., a germline cell). (Contrast with somatic mutation.)

germination   Sprouting of a seed or spore.

GFR   *See* glomerular filtration rate.

gibberellin   (jib er el' lin) A class of plant growth hormones playing roles in stem elongation, seed germination, flowering of certain plants, etc.

gill   A breathing organ that is evaginated (folded outward from the body) and surrounded by the environmental medium. The type of breathing organ found most commonly in water-breathers. (Contrast with lung.)

glial cells   One of the two major types of cells in the nervous system (the other being neurons); unlike neurons, glial cells are typically not excitable and do not conduct action potentials. Also called glia or neuroglia.

global warming   An increase through time in Earth's average annual surface temperature.

glomerular filtration rate (GFR)   The rate at which all the nephrons in the kidneys collectively produce primary urine by ultrafiltration of blood plasma.

glomerulus   (glo mare' yew lus) (plural: glomeruli) [L. *glomus*: ball] Vascular structure in the kidney where blood filtration takes place, forming primary urine. Each glomerulus consists of a knot of capillaries served by arterioles.

gluconeogenesis   The biochemical synthesis of glucose from other substances, such as amino acids, lactate, and glycerol.

glyceraldehyde 3-phosphate (G3P)   A phosphorylated three-carbon sugar; an intermediate in glycolysis and photosynthetic carbon fixation.

glycerol   (gliss' er ole) A three-carbon alcohol with three hydroxyl groups; a component of phospholipids and triglycerides.

glycosidic linkage   Bond between carbohydrate (sugar) molecules through an intervening oxygen atom (—O—).

glycolipid   A lipid to which sugars are attached.

glycolysis   (gly kol' li sis) [Gk. *gleukos*: sugar + *lysis*: break apart] The enzymatic breakdown of glucose to pyruvic acid.

glycoprotein   A protein to which sugars are attached.

glyoxysome   (gly ox' ee soam) An organelle found in plants, in which stored lipids are converted to carbohydrates.

Golgi apparatus   (goal' jee) A system of concentrically folded membranes found in the cytoplasm of eukaryotic cells; functions in secretion from the cell by exocytosis.

gonad   (go' nad) [Gk. *gone*: seed] An organ that produces gametes in animals: either an ovary (female gonad) or testis (male gonad). Certain of the tissues in a gonad secrete hormones.

gonadotropin   A type of tropic hormone that controls hormone secretion by gonadal endocrine cells, and that supports and maintains gonadal tissue, including gamete production. The two gonadotropins in vertebrates are follicle-stimulating hormone and luteinizing hormone, both secreted by the anterior pituitary gland.

gonadotropin-releasing hormone (GnRH)   In vertebrates, hormone produced by the hypothalamus that stimulates the anterior pituitary to secrete ("release") gonadotropins.

Gondwana   The large southern land mass that existed from the Cambrian (540 mya) to the Jurassic (138 mya). Present-day remnants are South America, Africa, India, Australia, and Antarctica.

GPP   *See* gross primary productivity.

graded membrane potentials   Small local changes in membrane potential caused by opening or closing of ion channels. They can be of any size (thus "graded").

grafting   Artificial transplantation of tissue from one organism to another. In horticulture, the transfer of a bud or stem segment from one plant onto the root of another as a form of asexual reproduction.

Gram-negative bacteria   Bacteria that appear red when stained using the Gram-staining technique. These bacteria have an outer membrane outside the relatively thin peptidoglycan layer of the cell wall.

Gram-positive bacteria   Bacteria that appear blue to purple when stained using the Gram-staining technique. These bacteria have an outer cell wall consisting of a thick layer of peptidoglycan.

Gram stain   A differential purple stain useful in characterizing bacteria. The peptidoglycan-rich cell walls of Gram-positive bacteria stain purple; cell walls of Gram-negative bacteria generally stain orange.

gravitropism   [Gk. *tropos*: to turn] A directed plant growth response to gravity.

gray crescent   In frog development, a band of diffusely pigmented cytoplasm on the side of the egg opposite the site of sperm entry. Arises as a result of cytoplasmic rearrangements that establish the anterior–posterior axis of the zygote.

greenhouse effect   The retention of heat energy near Earth's surface as a consequence of absorption and re-radiation of infrared radiation by certain gases (such as carbon dioxide and methane) in the atmosphere.

greenhouse gases   Gases in the atmosphere, such as carbon dioxide and methane, that absorb infrared radiation and thereby retain heat energy within Earth's lower atmosphere.

gross primary productivity (GPP)   The rate at which primary producers in a given area (or volume) capture energy from sunlight or other abiotic sources and convert it to chemical energy.

ground meristem   That part of an apical meristem that gives rise to the ground tissue system of the primary plant body.

ground tissue system   Those parts of the plant body not included in the dermal or vascular tissue systems. Ground tissues function in storage, photosynthesis, and support. (Contrast with dermal tissue system, vascular tissue system.)

growth   An increase in the size of the body and its organs by cell division and cell expansion. In ecology, change in size of the population of a species.

growth factor   A chemical signal that stimulates cells to divide.

growth hormone   A peptide hormone released by the anterior pituitary gland that stimulates many processes involved in tissue formation and growth.

guanine (G)   (gwan' een) A nitrogen-containing base found in DNA, RNA, and GTP.

guard cells   In plants, specialized, paired epidermal cells that surround and control the opening of a stoma (pore).

gut microbiome   Populations of microbes, consisting of many species of bacteria and other heterotrophic microbes, living in the gut lumen of an animal.

gymnosperms   Seed plants with seeds not enclosed in carpels. (*See also* angiosperms.)

gyre   Large-scale circular ocean currents caused by prevailing winds and Earth's rotation.

H

habitat patches   Areas of suitable habitat for a species that are separated by areas of unsuitable habitat.

habitat   The characteristic environment(s) occupied by a species.

habitat structure   The physical structure of a habitat, for example the horizontal and vertical distribution of objects (such as the stems and leaves of plants) in a habitat.

Hadley cells   Large-scale vertical patterns of atmospheric circulation in which warm rises near the Equator, moves toward the poles, and cools and sinks around 30 degrees N or S latitude.

half-life   The time required for half of a sample of a radioactive isotope to decay to its stable, nonradioactive form, or for a drug or other substance to reach half its initial dosage.

halophyte   (hal' oh fyte) [Gk. *halos*: salt + *phyton*: plant] A plant that grows in a saline (salty) environment.

haploid   (hap' loid) [Gk. *haploeides*: single] Having a chromosome complement consisting of just one copy of each chromosome; designated $1n$ or n. (Contrast with diploid.)

haplotype   Linked nucleotide sequences that are usually inherited as a unit (as a "sentence" rather than as individual "words").

Hardy–Weinberg equilibrium   The unchanging frequencies of alleles and genotypes in a population that is expected with random combination of gametes, in the absence of natural selection, mutation, migration, and genetic drift. The expectations of Hardy–Weinberg equilibrium can be used to calculate the expected frequencies of genotypes given the frequency of alleles, under the stated assumptions.

haustorium   (haw stor' ee um) (plural: haustoria) [L. *haustus*: draw up] A specialized hypha or other structure by which fungi and some parasitic plants draw nutrients from a host plant.

heart   In a circulatory system, a muscular pump that drives flow of blood around the body.

heat capacity   The ratio of energy absorbed by a substance the increase in temperature of that substance.

heat of vaporization   The energy that must be supplied to convert a molecule from a liquid to a gas at its boiling point.

heat shock proteins   Chaperone proteins expressed in cells exposed to high or low temperatures or other forms of environmental stress.

helical   Shaped like a screw or spring (helix); this shape occurs in DNA and proteins.

helicase   An enzyme that catalyzes the unwinding of a nucleic acid double helix.

helper T cell   *See* T-helper cell.

hemiparasite   A parasitic plant that can photosynthesize, but derives water and mineral nutrients from the living body of another plant. (Contrast with holoparasite.)

hemizygous   (hem′ ee zie′ gus) [Gk. *hemi*: half + *zygotos*: joined] In a diploid organism, having only one allele for a given trait, typically the case for X-linked genes in male mammals and Z-linked genes in female birds. (Contrast with homozygous, heterozygous.)

hemocyanin   A type of respiratory pigment found in arthropods and mollusks, consisting of a copper-based protein. Undergoes reversible combination with O_2 at copper-containing loci.

hemoglobin   (hee′ mo glow bin) [Gk. *heaema*: blood + L. *globus*: globe] A type of respiratory pigment consisting of an iron-containing protein. Undergoes reversible combination with O_2 at iron-containing loci called heme sites.

herbivore   (ur′ bi vore) [L. *herba*: plant + *vorare*: to devour] An animal that consumes plant tissues. *See* primary consumer. (Contrast with carnivore, detritivore, omnivore.)

herbivory   An interaction between individuals of two different species in which one individual, the herbivore, consumes all or part of the other individual, which is a plant.

heritability   The extent to which the value or expression of a trait of an organism is determined by genes transmitted from its parents.

hetero-   [Gk.: *heteros*: other, different] A prefix indicating two or more different conditions, structures, or processes. (Contrast with homo-.)

heterochromatin   Densely packed, dark-staining chromatin; any genes it contains are usually not transcribed. (Contrast with euchromatin.)

heterochrony   Alteration in the timing of developmental events, leading to different results in the adult organism.

heterocyst   A large, thick-walled cell type in the filaments of certain cyanobacteria that performs nitrogen fixation.

heteromorphic   (het′ er oh more′ fik) [Gk. *heteros*: different + *morphe*: form] Having a different form or appearance, as two heteromorphic life stages of a plant. (Contrast with isomorphic.)

heterosis   *See* hybrid vigor.

heterosporous   (het′ er os′ por us) Producing two types of spores, one of which gives rise to a female megaspore

and the other to a male microspore. (Contrast with homosporous.)

heterotopy   [Gk. different place] Spatial differences in gene expression during development, controlled by developmental regulatory genes and contributing to the evolution of distinctive adult phenotypes.

heterotroph   (het′ er oh trof) [Gk. *heteros*: different + *trophe*: feed] An organism that requires preformed organic molecules as sources of energy and chemical building blocks. (Contrast with autotroph.)

heterotypy   [Gk. different kind] Alteration in a developmental regulatory gene itself rather than the expression of the genes it controls. (Contrast with heterotopy.)

heterozygous   (het′ er oh zie′ gus) [Gk. *heteros*: different + *zygotos*: joined] In diploid organisms, having different alleles of a given gene on the pair of homologs carrying that gene. (Contrast with homozygous.)

heterozygous carrier   An individual that carries a recessive allele for a phenotype of interest (e.g., a genetic disease); the individual does not show the phenotype, but may have progeny with the phenotype if the other parent also carries the recessive allele.

hibernation   [L. *hibernum*: winter] In mammals, the state of inactivity of some species during winter, during which body temperature falls low enough to match ambient temperature and metabolic rate is prodoundly depressed.

high-throughput sequencing   Rapid DNA sequencing on a micro scale in which many fragments of DNA are sequenced in parallel.

highly repetitive sequences   Short (less than 100 bp), nontranscribed DNA sequences, repeated thousands of times in tandem arrangements.

hindbrain   The region of the developing vertebrate brain that gives rise to the medulla, pons, and cerebellum.

hindgut   The second part of the intestine; in mammals, the hindgut is also called the large intestine.

hindgut fermenters   An animal that has a specialized hindgut chamber housing mixed communities of fermenting microbes that assist with the breakdown of food materials.

histamine   (hiss′ tah meen) A substance released by damaged tissue, or by mast cells in response to allergens. Histamine increases vascular permeability, leading to edema (swelling).

histogram   A figure that displays frequencies of classes of quantitative data binned by ranges of a particular variable.

histone   Any one of a group of proteins forming the core of a nucleosome, the structural unit of a eukaryotic chromosome.

histone acetyltransferases   Enzymes involved in chromatin remodeling. Add acetyl groups to the tail regions of histone proteins. (Contrast with histone deacetylase.)

histone deacetylase   In chromatin remodeling, an enzyme that removes acetyl groups from the tails of histone proteins. (Contrast with histone acetyltransferases.)

HIV   *See* human immunodeficiency virus.

holometabolous   Undergoing complete metamorphosis.

holoparasite   A fully parasitic plant (i.e., one that does not perform photosynthesis).

home range   A region inhabited by an individual in which other individuals are not excluded. (Contrast with territory.)

homeobox   180-base-pair segment of DNA found in certain homeotic genes; regulates the expression of other genes and thus controls large-scale developmental processes.

homeostasis   (home′ ee o sta′ sis) [Gk. *homos*: same + *stasis*: position] Stability of the internal environment of an individual, such as a constant body temperature, and the physiological or behavioral feedback responses that maintain that stability. In the words of Walter Cannon, who coined the term, "the coordinated physiological processes which maintain most of the [constant] states in the organism."

homeotherm   An animal that maintains a relatively constant body temperature by physiological means, (e.g., changes in metabolic rate) rather than simply by behavior.

homeotic mutation   Mutation in a homeotic gene that results in the formation of a different organ than that normally made by a region of the embryo.

homo-   [Gk. *homos*: same] A prefix indicating two or more similar conditions, structures, or processes. (Contrast with hetero-.)

homologous pair   A pair of matching chromosomes made up of a chromosome from each of the two sets of chromosomes in a diploid organism.

homologous recombination   Exchange of segments between two DNA molecules based on sequence similarity between the two molecules. The similar sequences align and crossover. Used to create knockout mutants in mice and other organisms.

homology   (ho mol′ o jee) [Gk. *homologia*: of one mind; agreement] A similarity

between two or more features that is due to inheritance from a common ancestor. The structures are said to be **homologous**, and each is a *homolog* of the others.

homoplasy   (home′ uh play zee) [Gk. *homos*: same + *plastikos*: shape, mold] The presence in multiple groups of a trait that is not inherited from the common ancestor of those groups. Can result from convergent evolution, evolutionary reversal, or parallel evolution.

homosporous   Producing a single type of spore that gives rise to a single type of gametophyte, bearing both female and male reproductive organs. (Contrast with heterosporous.)

homozygous   (home′ oh zie′ gus) [Gk. *homos*: same + *zygotos*: joined] In diploid organisms, having identical alleles of a given gene on both homologous chromosomes. An individual may be a homozygote with respect to one gene and a heterozygote with respect to another. (Contrast with heterozygous.)

horizons   The horizontal layers of a soil profile, including the topsoil (A horizon), subsoil (B horizon) and parent rock or bedrock (C horizon).

hormone   (hore′ mone) [Gk. *hormon*: to excite, stimulate] A chemical substance produced in minute amounts by endocrine cells and transported in the blood to distant target cells, where it exerts regulatory influences on their function.

Human Genome Project   A publicly and privately funded research effort, successfully completed in 2003, to produce a complete DNA sequence for the entire human genome.

human immunodeficiency virus (HIV)   The retrovirus that causes acquired immune deficiency syndrome (AIDS).

humidic   Referring to terrestrial animals, those that are restricted to humid, water-rich microenvironments; unable to live steadily in the open air.

humoral immune response   The response of the immune system mediated by B cells that produces circulating antibodies active against extracellular bacterial and viral infections. (Contrast with cellular immune response.)

humus   (hew′ mus) The partly decomposed remains of plants and animals on the surface of a soil.

hybrid vigor   The superior fitness of heterozygous offspring as compared with that of their dissimilar homozygous parents. Also called heterosis.

hybrid zone   A region of overlap in the ranges of two closely related species where the species may hybridize.

hydrogen bond   A weak electrostatic bond which arises from the attraction between the slight positive charge on a hydrogen atom and a slight negative charge on a nearby oxygen or nitrogen atom.

hydrological cycle   The movement of water from the oceans to the atmosphere, to the soil, and back to the oceans.

hydrolysis reaction   (high drol′ uh sis) [Gk. *hydro*: water + *lysis*: break apart] A chemical reaction that breaks a bond by inserting the components of water (AB + $H_2O \rightarrow$ AH + BOH). (Contrast with condensation reaction.)

hydrophilic   (high dro fill′ ik) [Gk. *hydro*: water + *philia*: love] Having an affinity for water. (Contrast with hydrophobic.)

hydrophobic   (high dro foe′ bik) [Gk. *hydro*: water + *phobia*: fear] Having no affinity for water. Uncharged and nonpolar groups of atoms are hydrophobic. (Contrast with hydrophilic.)

hydroponic   Pertaining to a method of growing plants with their roots suspended in nutrient solutions instead of soil.

hydrostatic skeleton   Stiffness imparted to the body or part of the body of an animal by high blood pressure inside

hyper-   [Gk. *hyper*: above, over] Prefix indicating above, higher, more. (Contrast with hypo-.)

hyperaccumulators   Species of plants that store large quantities of heavy metals such as arsenic, cadmium, nickel, aluminum, and zinc.

hyperosmotic   In comparing two solutions, refers to the one having a higher osmotic pressure. The term is relative and has meaning only in comparing two specified solutions. (Compare with hyposmotic.)

hyperosmotic regulator   An aquatic animal that maintains a stable blood osmotic pressure higher than the osmotic pressure of the water in which it lives.

hyperpolarization   A change in the membrane potential across a cell membrane so that the inside of the membrane becomes more negative compared with the outside of the membrane. (Contrast with depolarization.)

hypersensitive response   A defensive response of plants to microbial infection in which phytoalexins and pathogenesis-related proteins are produced and the infected tissue undergoes apoptosis to isolate the pathogen from the rest of the plant.

hypertension   High blood pressure.

hypertonic   Having a greater solute concentration. Said of one solution

compared with another. (Contrast with hypotonic, isotonic.)

hypha   (high′ fuh) (plural: hyphae) [Gk. *hyphe*: web] In the fungi and oomycetes, any single filament.

hypo-   [Gk. *hypo*: beneath, under] Prefix indicating underneath, below, less. (Contrast with hyper-.)

hypophysis   *See* pituitary gland.

hyposmotic   In comparing two solutions, refers to the one having a lower osmotic pressure. The term is relative and has meaning only in comparing two specified solutions. The word is a contraction of *hypo-osmotic*. (Compare with hyperosmotic.)

hyposmotic regulator   An aquatic animal that maintains a stable blood osmotic pressure lower than the osmotic pressure of the water in which it lives.

hypothalamo–hypophysial portal system   In vertebrates, a system of blood vessels that connects capillaries in the hypothalamus to capillaries in the anterior pituitary gland; provides a direct pathway by which hypothalamic hormones can reach specific populations of cells in the anterior pituitary.

hypothalamus   A part of the forebrain lying below the thalamus and relatively near the base of the brain. It plays roles in learning, memory, spatial orientation, and control of water balance, reproduction, and temperature regulation.

hypotonic   Having a lesser solute concentration. Said of one solution in comparing it to another. (Contrast with hypertonic, isotonic.)

I

igneous   Rocks formed from the cooling and hardening of molten magma.

imbibition   Water uptake by a seed; first step in germination.

immunity   In animals, the ability to avoid disease when invaded by a pathogen by deploying various defense mechanisms.

immunoglobulins   A class of proteins containing a tetramer consisting of four polypeptide chains—two identical light chains and two identical heavy chains—held together by disulfide bonds; active as receptors and effectors in the immune system.

immunological memory   The capacity to more rapidly and massively respond to a second exposure to an antigen than occurred on first exposure.

imperfect flower   A flower lacking either functional stamens or functional carpels. (Contrast with perfect flower.)

implantation   The process by which the early mammalian embryo becomes

attached to and embedded in the endometrium (lining of the uterus).

imprinting *See* behavioral imprinting.

impulse *See* action potential.

in vitro evolution A method based on natural molecular evolution that uses artificial selection in the laboratory to rapidly produce molecules with novel enzymatic and binding functions.

inclusive fitness The sum of an individual's genetic contribution to subsequent generations both via production of its own offspring and via its influence on the survival of relatives who are not direct descendants.

incomplete cleavage A pattern of cleavage that occurs in many very yolky eggs, in which the cleavage furrows do not penetrate all of the cytoplasm. (Contrast with complete cleavage.)

incomplete dominance Condition in which the heterozygous phenotype is intermediate between the two homozygous phenotypes.

incomplete metamorphosis Insect development in which changes between instars are gradual.

independent assortment *See* law of independent assortment.

indeterminate growth A open-ended growth pattern in which an organism or organ continues to grow as long as it lives; characteristic of some animals and of plant shoots and roots. (Contrast with determinate growth.)

indirect development Development in which the young are morphologically very different than the adult. (Contrast with direct development.)

induced mutation A mutation resulting from exposure to a mutagen from outside the cell. (Contrast with spontaneous mutation.)

induced ovulation Ovulation (release of an egg from the ovaries of a female) triggered by the act of copulation. (Contrast with spontaneous ovulation.)

induced pluripotent stem cells (iPS cells) Multipotent or pluripotent animal stem cells produced from differentiated cells in vitro by the addition of several genes that are expressed.

induced responses Defensive responses that a plant produces only in the presence of a pathogen, in contrast to constitutive defenses, which are always present.

inducer (1) A compound that stimulates the synthesis of a protein. (2) In embryonic development, a substance that causes a group of target cells to differentiate in a particular way.

inducible enzyme An enzyme that is present in variable amounts, depending on the conditions to which a cell, tissue, or organism is exposed. Expression of an inducible enzyme depends on levels of specific inducing agents.

inducible genes Genes that are expressed only when their products are needed. (Contrast with constitutive genes.)

inducible Produced only in the presence of a particular compound or under particular circumstances. (Contrast with constitutive.)

induction In embryonic development, the process by which one cell population influences the fate of another cell population.

inflammation A nonspecific defense against pathogens; characterized by redness, swelling, pain, and increased temperature.

inflorescence A structure composed of several to many flowers.

inflorescence meristem A meristem that produces floral meristems as well as other small leafy structures (bracts).

infrared wavelengths Wavelengths in the electromagnetic spectrum that are too long to be seen by the human eye (i.e., greater than 0.7 μm).

ingroup In a phylogenetic study, the group of organisms of primary interest. (Contrast with outgroup.)

inhibiting hormones (IHs) Hormones, released by neurosecretory cells in the hypothalamus, that inhibit the secretion of hormones by the anterior pituitary gland. Each IH is specific for particular pituitary hormones. Also called release-inhibiting hormones.

inhibitory postsynaptic potential (IPSP) At a chemical synapse (specifically, an inhibitory synapse), a graded membrane hyperpolarization produced in the postsynaptic cell by arrival of an impulse in the presynaptic cell. (Contrast with excitatory postsynaptic potential.)

inhibitory synapse A synapse at which impulses in the presynaptic cell act to hyperpolarize the postsynaptic cell, thereby shifting the membrane potential of the postsynaptic cell away from the threshold for action potential production.

initiation complex In protein translation, a combination of a small ribosomal subunit, an mRNA molecule, and the tRNA charged with the first amino acid coded for by the mRNA; formed at the onset of translation.

innate defenses In animals, one of two general types of defenses against pathogens. Nonspecific and present in most animals. (Contrast with adaptive defenses.)

inner cell mass Part of the mammalian blastula (blastocyst), the inner cell mass will give rise to the embryo (via the epiblast) and the yolk sac, allantois, and amnion (via the hypoblast). (Contrast with trophoblast.)

innervate To provide neural input.

inorganic fertilizer A chemical or combination of chemicals applied to soil or plants to make up for a plant nutrient deficiency. Often contains the macronutrients nitrogen, phosphorus, and potassium (N-P-K).

instar (in' star) An immature stage of an insect between molts.

integral membrane proteins Proteins that are at least partially embedded in the plasma membrane. (Contrast with peripheral membrane proteins.)

integument [L. *integumentum*: covering] A protective surface structure. In gymnosperms and angiosperms, a layer of tissue around the ovule which will become the seed coat.

interference RNA (RNAi) *See* RNA interference.

interferon A glycoprotein produced by virus-infected animal cells; increases the resistance of neighboring cells to the virus.

intermediate filaments Components of the cytoskeleton whose diameters fall between those of the larger microtubules and those of the smaller microfilaments.

intermediate mesoderm The mesoderm that forms urinary and reproductive tissues.

internal effector *See* autonomic effector.

internal environment In multicellular organisms, the extracellular body fluids (interstitial fluids or tissue fluids), which bathe the cells of the body and therefore constitute the immediate environment of the cells.

internal fertilization Fertilization inside the body of the female that occurs because sperm are deposited into the female reproductive tract and encounter ova there (Contrast with external fertilization.)

internal membrane An intracellular membrane.

interneuron A neuron that communicates information between two other neurons.

interphase In the cell cycle, the period between successive nuclear divisions during which the chromosomes are diffuse and the nuclear envelope is intact. During interphase the cell is most active in transcribing and translating genetic information.

interspecific competition   A mutually detrimental (–/–) interaction between individuals of two different species that causes both to suffer reduced fitness. (Contrast with intraspecific competition.)

interspecific interactions   An interaction between individuals of different species that affects the per capita birth and/or death rate (or equivalently the fitness) of at least some of the individuals involved.

interstitial cells   Testosterone-secreting cells located in the tissue between the seminiferous tubules of the vertebrate testis. Also called Leydig cells.

interstitial fluid   Extracellular fluid that is found bathing the cells in tissues throughout the body. Also called tissue fluid.

intertidal zone   The nearshore region of oceans that lies between the level of the high and low tides, so that it is alternately inundated with water and exposed to air.

intracellular fluid   The aqueous solution inside a cell.

intraspecific competition   A mutually detrimental (–/–) interaction between individuals of the same species that causes both to suffer reduced fitness. (Contrast with interspecific competition.)

intron   Portion of a of a gene within the coding region that is transcribed into pre-mRNA but is spliced out prior to translation. (Contrast with exon.)

invasive species   A species that increases in abundance and spreads widely, often to the detriment of other species, when it is introduced to a new location.

invasiveness   The ability of a pathogen to multiply in a host's body. (Contrast with toxigenicity).

inversion   A rare 180° reversal of the order of genes within a segment of a chromosome.

involuntary nervous system   *See* autonomic nervous system.

ion   (eye′ on) [Gk. *ion*: wanderer] An electrically charged particle that forms when an atom gains or loses one or more electrons.

ion channel   An integral membrane protein that allows ions to diffuse across the membrane in which it is embedded.

ion exchange   A process by which protons produced by a plant root displace mineral cations from clay particles in the surrounding soil.

ionic attraction   An electrostatic attraction between positively and negatively ions.

ionotropic receptor   A receptor protein that is a ligand-gated ion channel and that therefore directly alters membrane ion permeability when it combines with its ligand.

ionotropic receptor cell   A sensory receptor cell that typically has an ionotropic receptor protein that is a stimulus-gated Na$^+$ channel. *See* ionotropic receptor.

iPS cells   *See* induced pluripotent stem cells.

iris   (eye′ ris) [Gk. *iris*: rainbow] The round, pigmented membrane that surrounds the pupil of the eye and adjusts its aperture to regulate the amount of light entering the eye.

island biogeography   Patterns in the spatial distribution of species among oceanic islands or "islands" of one kind of habitat surrounded by an "ocean" of a different habitat.

iso-   [Gk. *iso*: equal] Prefix used for two separate entities that share some element of identity.

isomorphic   (eye so more′ fik) [Gk. *isos*: equal + *morphe*: form] Having the same form or appearance, as when the haploid and diploid life stages of an organism appear identical. (Contrast with heteromorphic.)

isosmotic   Having the same osmotic pressure; said of a solution in comparison to another solution. The term is relative and has meaning only in comparing two specified solutions.

isotonic   Having the same solute concentration; said of two solutions. (Contrast with hypertonic, hypotonic.)

isotope   (eye′ so tope) [Gk. *isos*: equal + *topos*: place] Isotopes of a given chemical element have the same number of protons in their nuclei (and thus are in the same position on the periodic table), but differ in the number of neutrons.

iteroparity   [L. *itero*: to repeat + *pario*: to beget] A type of reproductive life history in which individuals are physiologically capable of reproducing multiple times in a lifetime. (Contrast with semelparity.)

iteroparous   Characterized by iteroparity.

J

jasmonate   Also called jasmonic acid, a plant hormone involved in triggering responses to pathogen attack as well as other processes.

jasmonic acid   *See* jasmonate.

jelly coat   The outer protective layer of a sea urchin egg, which triggers an acrosomal reaction in sperm.

joint   In skeletal systems, a junction between two or more bones.

joule (J)   A metric unit for measuring energy: 1 J = 0.24 calorie; 1 calorie = 4.2 joule.

K

karyogamy   The fusion of nuclei of two cells. (Contrast with plasmogamy.)

karyotype   The number, forms, and types of chromosomes in a cell.

kidney   An organ that regulates the composition and volume of the blood plasma by producing and eliminating from the body an aqueous solution (urine) derived from the blood plasma or other extracellular fluids.

kilocalorie (kcal)   *See* calorie.

kinase   *See* protein kinase.

kinetic energy   (kuh-net′ ik) [Gk. *kinetos*: moving] The energy associated with movement. (Contrast with potential energy.)

kinetochore   (kuh net′ oh core) Specialized structure on a centromere to which microtubules attach.

kingdom   A group of related phyla.

Koch's postulates   A set of rules for establishing that a particular microorganism causes a particular disease.

Krebs cycle   *See* citric acid cycle.

L

lactic acid fermentation   Anaerobic series of reactions that convert glucose to lactic acid, in some bacteria and animal cells.

lactifers   Plant cell or vessel that contains latex.

lagging strand   In DNA replication, the daughter strand that is synthesized in discontinuous stretches. *See* Okazaki fragments.

landscape   An ecological system consisting of multiple ecological communities within a geographical area larger than the area occupied by a single community.

lateral gene transfer   The transfer of genes from one species to another, common among bacteria and archaea.

lateral meristem   Either of the two meristems, the vascular cambium and the cork cambium, that give rise to a plant's secondary growth.

lateral plate mesoderm   One of three regions of mesoderm on either side of the notochord; encloses the coelom and gives rise to the heart, muscles of the digestive system, muscles of the outer body wall, and other tissues.

lateral root   A root extending outward from the taproot in a taproot system; typical of eudicots.

Laurasia   The northernmost of the two large continents produced by the breakup of Pangaea.

law of diffusion for gases   An equation that describes the factors that determine the rate of diffusion of gas molecules within a gas phase, liquid phase, or across the boundary between a gas phase and liquid phase; often called Fick's law.

law of independent assortment   During meiosis, the random separation of genes carried on nonhomologous chromosomes into gametes so that inheritance of these genes is random. This principle was articulated by Mendel as his second law

law of segregation   In genetics, the separation of alleles, or of homologous chromosomes, from each other during meiosis so that each of the haploid daughter nuclei produced contains one or the other member of the pair found in the diploid parent cell, but never both. This principle was articulated by Mendel as his first law.

laws of thermodynamics   [Gk. *thermos*: heat + *dynamis*: power] Laws derived from studies of the physical properties of energy and the ways energy interacts with matter. (*See also* first law of thermodynamics, second law of thermodynamics.)

LDP   *See* long-day plant.

leaching   In soils, a process by which mineral nutrients in upper soil horizons are dissolved in water and carried to deeper horizons, where they are unavailable to plant roots.

leading strand   In DNA replication, the daughter strand that is synthesized continuously. (Contrast with lagging strand.)

leaf   (plural: leaves) In plants, the chief organ of photosynthesis.

learning   The process of modifying an individual's behavior based on prior experiences of the individual.

leghemoglobin   In nitrogen-fixing plants, an oxygen-carrying protein in the cytoplasm of nodule cells that transports enough oxygen to the nitrogen-fixing bacteria to support their respiration, while keeping free oxygen concentrations low enough to protect nitrogenase.

lens   In an eye, a structure composed of transparent proteins that focuses images on the retina or other light-sensing structures.

leukocytes   *See* white blood cells.

Leydig cells   *See* interstitial cells.

LH   *See* luteinizing hormone.

lichen   (lie' kun) An organism resulting from the symbiotic association of a fungus and either a cyanobacterium or a unicellular alga.

life expectancy   The average time from birth to death of an individual organism.

life history   The sequence of key events, such as growth and development, reproduction, and death, that occur during the life of the average individual of a given species.

life-history tradeoffs   Negative relationships among growth, reproduction, and survival that occur because an individual cannot simultaneously allocate resources to such competing life functions as resource acquisition, maintenance, growth, defense, or reproduction.

ligand   (lig' and) Any molecule that binds to a receptor site of another (usually larger) molecule.

ligand-gated channel   A channel protein that can open and close and that opens to allow diffusion of a solute as a result of binding by a neurotransmitter (or other specific signaling molecule) to a receptor site on the channel protein.

light reactions   The initial phase of photosynthesis, in which light energy is converted into chemical energy.

light-harvesting complex   In photosynthesis, a group of different molecules that cooperate to absorb light energy and transfer it to a reaction center. Also called antenna system.

lignin   A complex, hydrophobic polyphenolic polymer in plant cell walls that crosslinks other wall polymers, strengthening the walls, especially in wood.

limiting resource   A resource that constrains the fitness of individuals at a given time and place because it is in short supply relative to demand.

limnetic zone   [Gk. *limn* : pool] The "open water" zone of freshwater lakes.

lineage   A series of populations, species, or genes descended from a single ancestor over evolutionary time.

lineage species concept   The definition of a species as a branch on the tree of life, which has a history that starts at a speciation event and ends either at extinction or at another speciation event. (Contrast with biological species concept, morphological species concept.)

linear regression   A statistical method of fitting a straight line to describe the relationship between two variables in a scatter plot.

linkage   *See* genetic linkage.

lipid   (lip' id) [Gk. *lipos*: fat] Nonpolar, hydrophobic molecules that include fats, oils, waxes, steroids, and the phospholipids that make up biological membranes.

lipid bilayer   *See* phospholipid bilayer.

littoral zone   The nearshore regions of lakes and oceans. In oceans this includes the intertidal zone.

loam   A type of soil consisting of a mixture of sand, silt, clay, and organic matter. One of the best soil types for agriculture.

locus   (low' kus) (plural: loci, low' sigh) In genetics, a specific location on a chromosome. May be considered synonymous with *gene*.

long-day plant (LDP)   A plant that requires long days (actually, short nights) in order to flower. (Compare to short-day plant.)

loop of Henle   (hen' lee) Long, hairpin loop in a mammalian nephron. The loop runs from the cortex of the kidney down into the medulla of the kidney and back to the cortex; creates a concentration gradient in the interstitial fluids in the medulla. Some nephrons in birds kidneys also have loops of Henle.

lophophore   A U-shaped fold of the body wall with hollow, ciliated tentacles that encircles the mouth of animals in several different groups. Used for filtering prey from the surrounding water.

loss of function mutation   A mutation that results in the loss of a functional protein. (Contrast with gain of function mutation.)

lung   A breathing organ that is invaginated (folded inward) into the body and contains the environmental medium. The most common type of breathing organ in terrestrial animals. (Contrast with gill.)

lung surfactant   A thin layer of lipids and proteins that coats the inside of a lung; decreases surface tension at the surfaces of the lung epithelium, which reduces the amount of work necessary to inflate the lung.

luteinizing hormone (LH)   A hormone, produced by the anterior pituitary gland, that helps control secretion of hormones by the gonads (i.e., a gonadotropin).

lymphatic system   An elaborate system of vessels, separate from the blood vascular system, that picks up excess interstitial fluid (lymph) and returns it to the blood.

lymphocyte   One of the two major classes of white blood cells; includes T cells, B cells, and other cell types important in the immune system.

lysogeny   A form of viral replication in which the virus becomes incorporated into the host chromosome and remains

inactive. Also called a lysogenic cycle. (Contrast with lytic cycle.)

lysosome (lie′ so soam) [Gk. *lysis*: break away + *soma*: body] A membrane-enclosed organelle originating from the Golgi apparatus and containing hydrolytic enzymes. (Contrast with secondary lysosome.)

lysozyme (lie′ so zyme) An enzyme in saliva, tears, and nasal secretions that hydrolyzes bacterial cell walls.

lytic cycle A viral reproductive cycle in which the virus takes over a host cell's synthetic machinery to replicate itself, then bursts (lyses) the host cell, releasing the new viruses. (Contrast with lysogeny.)

M

M phase The portion of the cell cycle in which mitosis takes place.

macromolecule A giant (molecular weight > 1,000) polymeric molecule. The macromolecules are the proteins, polysaccharides, and nucleic acids.

macronutrient In plants, a mineral element required in concentrations of at least 1 milligram per gram of plant dry matter; in animals, a mineral element required in large amounts. (Contrast with micronutrient.)

maintenance methyltransferase An enzyme that transfers methyl groups to DNA after DNA replication.

major histocompatibility complex (MHC) A complex of linked genes, with multiple alleles, that control a number of cell surface antigens that identify self and can lead to graft rejection.

malnutrition A condition caused by lack of adequate amounts of an essential nutrient.

Malpighian tubules (mal pee′ gy un) Fine tubules that initiate urine formation in insects. They empty their product into the gut at the junction of the midgut and hindgut.

mantle (1) In mollusks, a fold of tissue that covers the organs of the visceral mass and secretes the hard shell that is typical of many mollusks. (2) In geology, the Earth's crust below the solid lithospheric plates.

mass extinction A period of evolutionary history during which rates of extinction are much higher than during intervening times.

mass number The sum of the number of protons and neutrons in an atom's nucleus.

mast cells Cells, typically found in connective tissue, that release histamine in response to tissue damage.

maternal effect genes Genes coding for morphogens that determine the polarity of the egg and larva in fruit flies. Part of a developmental cascade that includes gap genes, pair rule genes, segment polarity genes, and Hox genes.

mating type A particular strain of a species that is incapable of sexual reproduction with another member of the same strain but capable of sexual reproduction with members of other strains of the same species.

maximum likelihood A statistical method of determining which of two or more hypotheses (such as phylogenetic trees) best fit the observed data, given an explicit model of how the data were generated.

mean The sum of all values in a sample divided by the number of observations in the sample.

measures of center Quantities that describe various aspects of the center of a group of observations.

measures of dispersion Measures that quantify the dispersion of observations in a sample of observations.

mechanoreceptor A sensory receptor cell that is sensitive to physical movement or physical distortion and generates action potentials in response.

median The value at which there are equal numbers of larger and smaller observations in a sample.

medusa (plural: medusae) In cnidarians, a free-swimming, sexual life cycle stage shaped like a bell or an umbrella.

megagametophyte In heterosporous plants, the female gametophyte; produces eggs. (Contrast with microgametophyte.)

megaphyll The generally large leaf of a fern, horsetail, or seed plant, with several to many veins. (Contrast with microphyll.)

megasporangia The structures on a heterosporous plant that produce a few large megaspores (which develop into female gametophytes).

megaspore [Gk. *megas*: large + *spora*: to sow] In plants, a haploid spore that produces a female gametophyte.

megastrobilus In conifers, the female (seed-bearing) cone. (Contrast with microstrobilus.)

meiosis (my oh′ sis) [Gk. *meiosis*: diminution] Division of a diploid nucleus to produce four haploid daughter cells. The process consists of two successive nuclear divisions with only one cycle of chromosome replication. In **meiosis I**, homologous chromosomes separate but retain their chromatids. The second division **meiosis II**, is similar to mitosis, in which chromatids separate.

membrane potential The difference in electrical charge (voltage) between the inside and the outside of a cell membrane, typically expressed in millivolts. The name derives from the fact that potential difference is a synonym for voltage.

memory cells In the immune system, long-lived lymphocytes produced after exposure to antigen. They persist in the body and are able to mount a rapid response to subsequent exposures to the antigen.

Mendel's laws *See* law of independent assortment, law of segregation.

menstrual cycle The cycle in which oocytes mature and are ovulated periodically in females of primates, including humans; one phase of each cycle is characterized by menstruation, the shedding of the uterine lining in a blood-tinged discharge from the vagina.

menstruation In humans and other primates, a process by which the lining of the uterus (the endometrium) breaks down (after a failure of pregnancy to occur), and the sloughed-off tissue, including blood, flows from the body.

meristem [Gk. *meristos*: divided] Plant tissue made up of undifferentiated actively dividing cells.

meristem culture A method for the asexual propagation of plants, in which pieces of shoot apical meristem are cultured to produce plantlets.

meristem identity genes In angiosperms, a group of genes whose expression initiates flower formation, probably by switching meristem cells from a vegetative to a reproductive fate.

mesoderm [Gk. *mesos*: middle + *derma*: skin] The middle of the three embryonic germ layers first delineated during gastrulation. Gives rise to the skeleton, circulatory system, muscles, excretory system, and most of the reproductive system.

mesoglea (mez′ uh glee uh) [Gk. *mesos*: middle + *gloia*, glue] A thick, gelatinous noncellular layer that separates the two cellular tissue layers of ctenophores, cnidarians, and scyphozoans.

mesophyll (mez′ uh fill) [Gk. *mesos*: middle + *phyllon*: leaf] Chloroplast-containing, photosynthetic cells in the interior of leaves.

messenger RNA (mRNA) Transcript of a region of one of the strands of DNA; carries information (as a sequence of codons) for the synthesis of one or more proteins.

meta- [Gk.: between, along with, beyond] Prefix denoting a change or a shift to a new form or level; for example, as used in metamorphosis.

metabolic pathway A series of enzyme-catalyzed reactions so arranged that the product of one reaction is the substrate of the next.

metabolic rate (**MR**) An animal's rate of energy consumption; the rate at which it converts chemical-bond energy to heat and external work.

metabolic water Water that is formed by oxidation of food during metabolism. For example, when glucose is oxidized, one of the products is H_2O that did not previously exist; this H_2O is metabolic water. Also called oxidation water.

metabolism (meh tab′ a lizm) [Gk. *metabole*: change] The sum total of the chemical reactions that occur in an organism, or some subset of that total (as in respiratory metabolism).

metabolome The quantitative description of all the small molecules in a cell or organism.

metabolomics The study of the metabolome as it relates to the physiological state of a cell or organism.

metabotropic receptor A receptor protein that is not an ion channel. Typically a G protein–linked receptor protein. (*See* G protein–linked receptors.)

metabotropic receptor cell A sensory receptor cell in which the sensory receptor protein is not an ion channel but typically instead is a G protein–linked receptor.

metagenomics The practice of analyzing DNA from environmental samples without isolating intact organisms.

metamorphosis (met′ a mor′ fo sis) [Gk. *meta*: between + *morphe*: form, shape] A change occurring between one developmental stage and another, as for example from a tadpole to a frog. (*See* complete metamorphosis, incomplete metamorphosis.)

metaphase (met′ a phase) The stage in nuclear division at which the centromeres of the highly supercoiled chromosomes are all lying on a plane (the metaphase plane or plate) perpendicular to a line connecting the division poles.

metapopulation A "population of populations"—the group of spatially-separated subpopulations that occurs within a defined geographic area.

MHC *See* major histocompatibility complex.

microbiomes The diverse communities of bacteria that live on or within the body and are essential to bodily function.

microcirculation The part of a closed circulatory system that consists of the smallest diameter blood vessels (i.e., arterioles, capillaries, and venules.)

microfilament In eukaryotic cells, a fibrous structure made up of actin monomers. Microfilaments play roles in the cytoskeleton, in cell movement, and in muscle contraction.

microgametophyte In heterosporous plants, the male gametophyte; produces sperm. (Contrast with megagametophyte.)

micronutrient In plants, a mineral element required in concentrations of less than 100 micrograms per gram of plant dry matter; in animals, a mineral element required in concentrations of less than 100 micrograms per day. (Contrast with macronutrient.)

microphyll A small leaf with a single vein, found in club mosses and their relatives. (Contrast with megaphyll.)

micropyle (mike′ roh pile) [Gk. *mikros*: small + *pylon*: gate] Opening in the integument(s) of a seed plant ovule through which pollen grows to reach the female gametophyte within.

microRNA A small, noncoding RNA molecule, typically about 21 bases long, that binds to mRNA to inhibit its translation.

microsporangia The structures on a heterosporous plant that produce many small microspores (which develop into male gametophytes).

microspore [Gk. *mikros*: small + *spora*: to sow] In plants, a haploid spore that produces a male gametophyte.

microstrobilus In conifers, male pollen-bearing cone. (Contrast with megastrobilus.)

microtubules Tubular structures found in centrioles, spindle apparatus, cilia, flagella, and cytoskeleton of eukaryotic cells. These tubules play roles in the motion and maintenance of shape of eukaryotic cells.

microvilli (sing.: microvillus) Minute, rod-shaped projections of epithelial cells, such as the cells lining the small intestine, that increase their surface area.

midbrain One of the three regions of the vertebrate brain. Part of the brainstem, it serves as a relay station for sensory signals sent to the cerebral hemispheres, in addition to other functions.

midgut The first part of the intestine. In mammals, the midgut is also called the small intestine.

midgut fermenter An animal that has a specialized midgut chamber housing mixed communities of fermenting microbes that assist with the breakdown of food materials

migrate To periodically move from one location to another, then, after a period of time, return to the original location.

missense mutation A change in a gene's sequence that changes the amino acid at that site in the encoded protein. (Contrast with frame-shift mutation, nonsense mutation, silent mutation.)

mitochondrion (my′ toe kon′ dree un) (plural: mitochondria) [Gk. *mitos*: thread + *chondros*: grain] An organelle in eukaryotic cells that contains the enzymes of the citric acid cycle, the respiratory chain, and oxidative phosphorylation.

mitosis (my toe′ sis) [Gk. *mitos*: thread] Nuclear division in eukaryotes leading to the formation of two daughter nuclei, each with a chromosome complement identical to that of the original nucleus.

mitosomes Reduced structures derived from mitochondria found in some organisms.

mode The most frequent value in a sample of observations.

moderately repetitive sequences DNA sequences repeated 10–1,000 times in the eukaryotic genome. They include the genes that code for rRNAs and tRNAs, as well as the DNA in telomeres.

molds Sac fungi composed of filamentous hyphae that do not form large ascomata.

molecular biology Study of the formation, structure and functions of nucleic acids and proteins.

molecular clock The approximately constant rate of divergence of macromolecules from one another over evolutionary time; used to date past events in evolutionary history.

molecular toolkit *See* genetic toolkit.

molecule A chemical substance made up of two or more atoms joined by covalent bonds or ionic attractions.

molting The process of shedding part or all of an outer covering, as the shedding of feathers by birds or of the entire exoskeleton by arthropods.

monocots Angiosperms with a single embryonic cotyledon; one of the two largest clades of angiosperms. (*See also* eudicots.)

monoecious (mo nee′ shus) [Gk. *mono*: one + *oikos*: house] Pertaining to organisms in which both sexes are "housed" in a single individual that produces both eggs and sperm. (In some plants, these are found in different flowers within the same plant.) Examples include corn, peas, earthworms, hydras. (Contrast with dioecious.)

monohybrid cross A mating in which the parents differ with respect to the alleles of only one locus of interest.

monomer [Gk. *mono*: one + *meros*: unit] A small molecule, two or more of which

can be combined to form oligomers (consisting of a few monomers) or polymers (consisting of many monomers).

monophyletic (mon' oh fih leht' ik) [Gk. *mono*: one + *phylon*: tribe] Pertaining to a group that consists of an ancestor and all of its descendants. (Contrast with paraphyletic, polyphyletic.)

monosaccharide A simple sugar. Oligosaccharides and polysaccharides are made up of monosaccharides.

morphogen A diffusible substance whose concentration gradient determines a developmental pattern in animals and plants.

morphogenesis (more' fo jen' e sis) [Gk. *morphe*: form + *genesis*: origin] The development of form; the overall consequence of determination, differentiation, and growth.

morphological species concept The definition of a species as a group of individuals that look alike. (Contrast with biological species concept, lineage species concept.)

morphology (more fol' o jee) [Gk. *morphe*: form + *logos*: study, discourse] The scientific study of organic form, including both its development and function.

mortality The average individual's chance of dying during a specified set of life stages, ages, or period of time. Mortality = 1 - survivorship (Contrast with survivorship.)

mosaic development Pattern of animal embryonic development in which each blastomere contributes a specific part of the adult body. (Contrast with regulative development.)

motor neuron A neuron that carries signals from the central nervous system to a skeletal muscle, stimulating the muscle to contract. A type of efferent neuron.

motor proteins Specialized proteins that use energy to change shape and move cells or structures within cells.

mRNA *See* messenger RNA.

mucus A slippery substance secreted by mucous membranes (e.g., mucosal epithelium). A barrier defense against pathogens in innate immunity in animals.

Muller's ratchet The accumulation—"ratcheting up"—of deleterious mutations in the nonrecombining genomes of asexual species.

multi-organ system A system in which multiple organs work together.

multiple fruit A fruit derived from carpels of several flowers. An example is a pineapple.

multiplicative growth In ecology, population growth in which a multiple of the current population size is added

to the population during each successive time interval. The multiple of growth may be a constant, or it may change. (Contrast with additive growth.)

multipotent Having the ability to differentiate into a limited number of cell types. (Contrast with pluripotent, totipotent.)

muscle fiber A single muscle cell. In the case of skeletal muscle, a multinucleate cell.

mutagen (mute' ah jen) [L. *mutare*: change + Gk. *genesis*: source] Any agent (e.g., a chemical, radiation) that increases the mutation rate.

mutation A change in the genetic material not caused by recombination.

mutualism A mutually beneficial (+/+) interaction between individuals of two different species that causes both to benefit, in terms of increased fitness. (Contrast with amensalism, commensalism.)

mutualistic A pair of symbiotic organisms in which both partners benefit from the interaction.

mycelium (my seel' ee yum) [Gk. *mykes*: fungus] In the fungi, a mass of hyphae.

mycorrhiza (my' ko rye' za) (plural: mycorrhizae) [Gk. *mykes*: fungus + *rhiza*: root] An association of the root of a plant with the mycelium of a fungus.

myelin (my' a lin) Concentric layers of cell membrane wrapped around some axons, forming a sheath around the axons; myelin provides an axon with electrical insulation and increases the rate of transmission of action potentials.

myocardium The muscle tissue of a heart.

MyoD The protein encoded by the *myo*blast *d*etermining gene. A transcription factor involved in the differentiation of myoblasts (muscle precursor cells).

myofibril (my' oh fy' bril) [Gk. *mys*: muscle + L. *fibrilla*: small fiber] A long, longitudinally oriented component of a striated muscle cell that consists of a series of sarcomeres and extends the length of the cell. A myofibril is composed principally of actin and myosin filaments. In cross section, a muscle cell consists of multiple myofibrils.

myogenic heart A heart in which the electrical impulse to contract during each beating cycle originates in muscle cells or modified muscle cells. (Contrast with neurogenic heart.)

myoglobin (my' oh globe' in) [Gk. *mys*: muscle + L. *globus*: sphere] An oxygen-binding molecule found in red muscle cells. A type of hemoglobin, consisting

of a single heme unit and a single globin chain per molecule

myosin One of the two contractile proteins of muscle. (*See also* actin.)

myosin filaments Bundles of linked myosin molecules. Also called thick filaments. (*See also* actin filaments.)

N

natural history An observation about nature, obtained outside of a formal hypothesis-testing context, that provides the basis for further investigation.

natural killer cell A type of lymphocyte that attacks virus-infected cells and some tumor cells as well as antibody-labeled target cells.

natural selection The differential contribution of offspring to the next generation by various genetic types belonging to the same population. The mechanism of evolution proposed by Charles Darwin.

navigation The act of moving on a particular course or toward a specific destination using sensory cues to determine direction and position.

necrosis (nec roh' sis) [Gk. *nekros*: death] Premature cell death caused by external agents such as toxins.

negative feedback In a regulatory system, a type of control that acts to reduce differences that arise between the level of a controlled variable and its set-point level. It tends to stabilize the controlled variable at a level close to the set-point level. (Contrast with positive feedback.)

negative-sense RNA RNA that is complementary to mRNA. Before it can be translated, it must be converted to positive-sense RNA by an RNA polymerase.

nematocyst (ne mat' o sist) [Gk. *nema*: thread + *kystis*: cell] An elaborate, threadlike structure produced by cells of jellyfishes and other cnidarians, used chiefly to paralyze and capture prey.

neoteny (knee ot' enny) [Gk. *neo*: new, recent; *tenein*: to extend] The retention of juvenile or larval traits by the fully developed adult organism.

nephron (nef' ron) [Gk. *nephros*: kidney] The functional unit of a vertebrate kidney, consisting of a structure for receiving a filtrate of blood plasma and a long tubule that modifies the filtrate by secretion and reabsorption.

Nernst equation A mathematical equation that calculates the electrical potential difference required for electrochemical equilibrium across a membrane that is permeable to a single type of ion, when the ion differs in

concentration on the two sides of the membrane.

nerve   A structure consisting of many neuronal axons bound together like wires in a telephone cable.

nerve impulse   *See* action potential.

nerve nets   Diffuse, loosely connected aggregations of nervous tissues in certain non-bilatarian animals such as cnidarians.

nervous tissue   Tissue specialized for processing and communicating information; one of the four major tissue types in multicellular animals.

net primary productivity (NPP)   The rate at which primary producers in a given area (or volume) convert energy they have captured from sunlight or other abiotic sources into energy stored in the molecules that make up their tissues, and which therefore is available for use by primary consumers. NPP is often estimated as the gain in biomass of primary producers in a unit of time.

neural crest cells   During vertebrate neurulation, cells that migrate outward from the neural plate; they are pluripotent cells that form the sensory nervous system, autonomic nervous system, many bones of the skull, pigment cells, and other tissues

neuroendocrine cells   *See* neurosecretory cells.

neurogenic heart   A heart in which the electrical impulse to contract during each beating cycle originate in neurons. (Contrast with myogenic heart.)

neuroglia   *See* glial cells.

neurohemal organ   A specialized organ in the circulatory system that is made up of axon terminals of neurosecretory cells in association with a well-developed bed of capillaries.

neuromuscular junction   Synapse (point of contact) where a motor neuron axon stimulates a muscle fiber (muscle cell).

neuron   (noor' on) [Gk. *neuron*: nerve] A nervous system cell that can generate and conduct action potentials along an axon to a synapse with another cell.

neurosecretory cells   Neurons that synthesize and release hormones into the blood. Also called neuroendocrine cells.

neurotransmitter   At a synapse, a substance produced and released by the presynaptic cell that diffuses across the synapse and excites or inhibits the postsynaptic cell.

neurulation   Stage in vertebrate development during which the nervous system begins to form.

neutron   (new' tron) One of the three fundamental particles of matter (along with protons and electrons), with mass

slightly larger than that of a proton and no electrical charge.

niche   (nitch) [L. *nidus*: nest] In ecology, the abiotic and biotic conditions under which a given species can persist, and the functional role of the species in its community.

nitrifiers   Chemoautotrophic bacteria that oxidize ammonia to nitrate in soil and in seawater.

nitrogen fixation   Conversion of atmospheric nitrogen gas (N_2) to a water-soluble, biologically-usable form (usually ammonium, NH_4^+), in nature by free-living or symbiotic microbes, but also by industrial processes. (Compare with denitrification.)

nitrogen fixers   Organisms that convert atmospheric nitrogen gas into a chemical form (ammonia) that is usable by the nitrogen fixers themselves as well as by other organisms.

nitrogenase   An enzyme complex found in nitrogen-fixing bacteria that mediates the stepwise reduction of atmospheric N_2 to ammonia and which is strongly inhibited by oxygen.

nitrogenous wastes   The potentially toxic nitrogen-containing end products resulting from the break down of proteins and nucleic acids. They are usually eliminated from the body by excretion.

node   [L. *nodus*: knob, knot] (1) In plants, a (sometimes enlarged) point on a stem where a leaf is or was attached. (2) In phylogenetics, a split in a phylogenetic tree when one lineage diverges into two.

node of Ranvier   In a myelinated axon, a gap in the myelin sheath where the axon cell membrane is not covered with myelin.

noncompetitive inhibitor   A nonsubstrate that inhibits the activity of an enzyme by binding to a site other than its active site. (Contrast with competitive inhibitor.)

nondisjunction   Failure of sister chromatids to separate in meiosis II or mitosis, or failure of homologous chromosomes to separate in meiosis I. Results in aneuploidy.

nonneural endocrine cells   Cells that secrete hormones into the blood and that are not neurons or derived from neurons. (*See* neurosecretory cells.)

nonsense mutation   Change in a gene's sequence that prematurely terminates translation by changing one of its codons to a stop codon.

nonshivering thermogenesis (NST)   In mammals and some birds, elevation of heat production for thermoregulation by means other than shivering.

nonsynonymous substitution   A change in a gene from one nucleotide to another that changes the amino acid specified by the corresponding codon (i.e., AGC → AGA, or serine → arginine). (Contrast with synonymous substitution.)

notochord   (no' tow kord) [Gk. *notos*: back + *chorde*: string] A flexible rod of gelatinous material serving as a support in the embryos of all chordates and in the adults of tunicates and lancelets.

NPP   *See* net primary productivity.

NST   *See* nonshivering thermogenesis.

nucleic acid   (new klay' ik) A polymer made up of nucleotides, specialized for the storage, transmission, and expression of genetic information. DNA and RNA are nucleic acids.

nucleic acid hybridization   A technique in which a single-stranded nucleic acid probe is made that is complementary to, and binds to, a target sequence, either DNA or RNA. The resulting double-stranded molecule is a hybrid.

nucleoid   (new' klee oid) The region that harbors the chromosomes of a prokaryotic cell. Unlike the eukaryotic nucleus, it is not bounded by a membrane.

nucleolus   (new klee' oh lus) A small, generally spherical body found within the nucleus of eukaryotic cells. The site of synthesis of ribosomal RNA.

nucleotide   The basic chemical unit in nucleic acids, consisting of a pentose sugar, a phosphate group, and a nitrogen-containing base.

nucleus   (new' klee us) [L. *nux*: kernel or nut] (1) In cells, the centrally located compartment of eukaryotic cells that is bounded by a double membrane and contains the chromosomes. (2) In the brain, an identifiable group of neurons that share common characteristics or functions.

null hypothesis   In statistics, the premise that any differences observed in an experiment are simply the result of random differences that arise from drawing two finite samples from the same population.

O

obligate aerobe   Organisms that require oxygen for metabolism.

obligate anaerobe   An anaerobic prokaryote that cannot survive exposure to O_2.

obligate parasites   Organisms that can only survive and grow in or on other living organisms, to the detriment of the host.

octet rule   Description of processes that atoms undergo whereby they obtain, give

up or share electrons such that their outer (valence) shell contains eight electrons.

Okazaki fragments Newly formed DNA making up the lagging strand in DNA replication. DNA ligase links Okazaki fragments together to give a continuous strand.

oligodendrocyte A type of glial cell that forms a myelin sheath on axons in the central nervous system.

oligopeptide Peptide made up of less than 20 amino acids.

oligosaccharide A polymer containing a small number of monosaccharides.

ommatidium (plural: ommatidia) [Gk. *omma*: eye] A single visual unit in the compound eye of an arthropod.

omnivore [L. *omnis*: everything + *vorare*: to devour] An organism that obtains the energy and materials it needs to survive, grow, and reproduce from a variety of trophic levels. (Contrast with carnivore, detritivore, herbivore.)

oncogene [Gk. *onkos*: mass, tumor + *genes*: born] A gene that codes for a protein product that stimulates cell proliferation. Mutations in oncogenes that result in excessive cell proliferation can give rise to cancer. (Contrast with tumor suppressor.)

one gene–one polypeptide The idea, since shown to be an oversimplification, that each gene in the genome encodes only a single polypeptide—that there is a one-to-one correspondence between genes and polypeptides.

oocyte The developing ovum.

open circulatory system Circulatory system in which the blood leaves blood vessels and travels through spaces (sinuses and lacunae) bounded by ordinary tissue cells as it flows through the body (Contrast with closed circulatory system.)

open system A system that is not isolated from, and interacts with, its surroundings. (Compare with closed system.)

open reading frames Sequences of DNA within genes that begin with an initiation codon and end with a stop codon.

operator The region of an operon that acts as the binding site for the repressor.

operon A genetic unit of transcription, typically consisting of several structural genes that are transcribed together; the operon contains at least two control regions: the promoter and the operator.

order A group of related families.

ordinal variables Categorical variables with a natural ordering, such as the grades A, B, C, D, and F.

organ [Gk. *organon*: tool] A body part, such as the heart, liver, brain, root, or leaf, that is composed of two or more tissues integrated to perform a distinct function.

organ identity genes In angiosperms, genes that specify the different organs of the flower. (Compare with homeotic genes.)

organelle (or gan el′) Any of the membrane-enclosed structures within a eukaryotic cell. Examples include the nucleus, endoplasmic reticulum, and mitochondria.

organic fertilizers Substances added to soil to improve the soil's fertility; derived from partially decomposed plant material (compost) or animal waste (manure).

organizer Region of the early amphibian embryo (the dorsal lip of the blastopore) that develops into the notochord and thus establishes the basic body plan. Also known as the primary embryonic inducer.

organogenesis The formation of organs and organ systems during development.

orientation A behavioral process in which an organism positions itself or moves in relation to environmental cues such as the sun.

origin of replication (*ori*) DNA sequence at which helicase unwinds the DNA double helix and DNA polymerase binds to initiate DNA replication.

orthologs Genes that are related by orthology.

osmoconformer *See* osmotic conformer.

osmolar (*Osm*) A unit of measure of osmotic pressure. A 1-osmolar solution is defined to be a solution that behaves osmotically as if it has one Avogadro's number (6×10^{23}) of independent dissolved entities per liter.

osmolarity The osmotic pressure of a solution expressed in osmolar units.

osmoregulator *See* osmotic regulator.

osmosis (oz mo′ sis) [Gk. *osmos*: to push] Movement of water across a differentially permeable membrane, from one region to another region where the water potential is more negative.

osmotic conformer An aquatic animal in which the osmotic pressure of the blood and other extracellular fluids matches the osmotic pressure of the external environment. Also called osmoconformer. (Contrast with osmotic regulator.)

osmotic regulator An aquatic animal that maintains a relatively constant osmotic pressure in its blood and other extracellular fluids regardless of changes in the osmotic pressure of its external environment. Also called osmoregulator. (Contrast with osmotic conformer.)

osmotic pressure Pressure exerted by the flow of water through a semipermeable membrane separating two solutions with different concentrations of solute.

outgroup In phylogenetics, a group of organisms used as a point of reference for comparison with the groups of primary interest (the ingroup).

ovarian follicle During gamete development in the ovary of a female animal, an oocyte (developing ovum) together with its support cells (theca and granulosa cells).

ovary (oh′ var ee) [L. *ovum*: egg] A female organ, in plants or animals, that produces ova (eggs).

overtopping Plant growth pattern in which one branch differentiates from and grows beyond the others.

oviduct In mammals, the tube serving to transport eggs from an ovary to the uterus. Also called a fallopian tube.

ovulation The process of releasing an ovum (egg) from the ovary.

ovule (oh′ vule) In plants, a structure comprising the megasporangium and the integument, which develops into a seed after fertilization.

ovum (plural: ova) *See* egg.

oxidation (ox i day′ shun) Relative loss of electrons in a chemical reaction; either outright removal to form an ion, or the sharing of electrons with substances having a greater affinity for them, such as oxygen. Most oxidations, including biological ones, are associated with the liberation of energy. (Contrast with reduction.)

oxidation water *See* metabolic water.

oxidative phosphorylation ATP formation in the mitochondrion, associated with flow of electrons through the respiratory chain.

oxidized Increase in positive charge of an element by removing electron(s); formation of an oxide by adding oxygen.

oxygenase An enzyme that catalyzes the addition of oxygen to a substrate from O_2.

oxygenation (1) Referring to water, the dissolution of O_2 in that water. (2) The combination of respiratory pigments with O_2; oxygenation of this sort is reversible and not equivalent to oxidation.

oxygen equilibrium curve A graph of the amount of O_2 per unit of blood volume as a function of the O_2 partial pressure of the blood (a measure of the concentration of O_2 dissolved in the blood plasma.)

oxytocin In mammals, a hormone released by the posterior pituitary gland;

its major functions are to stimulate contraction of the uterus and the flow of milk from mammary glands.

P

P-value   The calculated probability of observing a given result by chance sampling, given the null hypothesis is true.

pair rule genes   In *Drosophila* (fruit fly) development, segmentation genes that divide the early embryo into units of two segments each. Part of a developmental cascade that includes maternal effect genes, gap genes, segment polarity genes, and Hox genes.

paleomagnetic dating   A method for determining the age of rocks based on properties relating to changes in the patterns of Earth's magnetism over time.

Pangaea   (pan jee' uh) [Gk. pan: all, every] The single land mass formed when all the continents came together in the Permian period.

para-   [Gk. *para*: akin to, beside] Prefix indicating association in being along side or accessory to.

parallel phenotypic evolution   The repeated evolution of similar traits, especially among closely related species; facilitated by conserved developmental genes.

paraphyletic   (par' a fih leht' ik) [Gk. *para*: beside + *phylon*: tribe] Pertaining to a group that consists of an ancestor and some, but not all, of its descendants. (Contrast with monophyletic, polyphyletic.)

parasite   An organism that consumes parts of an organism much larger than itself (known as its host). Parasites sometimes, but not always, kill their host.

parasitism   A +/− interaction between individuals of two different species that causes one individual (the parasite) to benefit (it gains fitness) from consuming part or all of the other (the host), which suffers reduced fitness as a consequence of being consumed.

parasympathetic division   A division of the vertebrate autonomic nervous system that is connected to the central nervous system via cranial and sacral nerves; the parasympathetic and sympathetic divisions tend to exert opposing controls on autonomic effectors. (Contrast with sympathetic division.)

parenchyma   (pair eng' kyma) A plant tissue composed of relatively unspecialized cells without secondary walls.

parent rock   The soil horizon consisting of the rock that is breaking down to form the soil. Also called bedrock, or the C horizon.

parental (P) generation   The individuals that mate in a genetic cross. Their offspring are the first filial (F_1) generation.

parsimony principle   Principle that states that the preferred explanation of observed data is the simplest explanation.

parthenocarpy   Formation of fruit from a flower without fertilization.

passive transport   Diffusion across a membrane; may or may not require a channel or carrier protein. (Contrast with active transport.)

pathogen   (path' o jen) [Gk. *pathos*: suffering + *genesis:* source] An organism that causes disease.

pathogen associated molecular patterns (PAMPs)   The molecules recognized by pattern recognition receptors.

pathogenesis-related (PR) proteins   A component of the hypersensitive response of plants to pathogens. Some PR proteins function as direct defenses against pathogens, others initiate other defensive responses.

pattern formation   In animal embryonic development, the organization of differentiated tissues into specific structures such as wings.

pattern recognition receptors (PRRs)   Proteins made by cells that recognize molecular patterns on pathogens; part of innate immunity.

PCR   *See* polymerase chain reaction.

pedigree   The pattern of transmission of a genetic trait within a family.

pelagic zone   [Gk. *pelagos*: open sea] The "open water" zone of oceans that lies beyond the continental shelves.

penetrance   The proportion of individuals with a particular genotype that show the expected phenotype.

pentaradial symmetry   Symmetry in five or multiples of five; a feature of adult echinoderms.

peptidyl transferase   A catalytic function of the large ribosomal subunit that consists of two reactions: breaking the bond between an amino acid and its tRNA in the P site, and forming a peptide bond between that amino acid and the amino acid attached to the tRNA in the A site.

peptides   Molecule containing two or more amino acids.

peptide hormones   Hormone molecules made up of strings of amino acids. They are water soluble. (Compare to steroid hormones, amine hormones.)

peptide bond   The bond between amino acids in a protein; formed between a carboxyl group and amino group (—CO—NH—) with the loss of water molecules.

peptidoglycan   The cell wall material of many bacteria, consisting of a single enormous molecule that surrounds the entire cell.

per capita birth rate (*b*)   The number of offspring that the average individual produces in some specified interval of time.

per capita death rate (*d*)   The average individual's chance of dying in some specified interval of time.

per capita growth rate (*r*)   The average individual's contribution to total population growth rate in some specified interval of time, which equals per capita birth rate (*b*) minus per-capita death rate (*d*).

perennial   (per ren' ee al) [L. *per*: throughout + *annus*: year] A plant that survives from year to year. (Contrast with annual, biennial.)

perfect flower   A flower with both stamens and carpels; a hermaphroditic flower. (Contrast with imperfect flower.)

perfusion   The flow of blood through a tissue or organ.

pericycle   [Gk. *peri*: around + *kyklos*: ring or circle] In plant roots, tissue just within the endodermis, but outside of the root vascular tissue. Meristematic activity of pericycle cells produces lateral root primordia.

periderm   The outer tissue of the secondary plant body, consisting primarily of cork.

peripheral membrane proteins   Proteins associated with but not embedded within the plasma membrane. (Contrast with integral membrane proteins.)

peripheral nervous system (PNS)   The portion of the nervous system other than the central nervous system (CNS). It consists of neurons and parts of neurons located outside the CNS. (Contrast with central nervous system.)

peristalsis   (pair' i stall' sis) Wavelike muscular contractions proceeding along a tubular organ, propelling the contents along the tube.

peroxisome   An organelle that houses reactions in which toxic peroxides are formed and then converted to water.

petal   [Gk. *petalon*: spread out] In an angiosperm flower, a sterile modified leaf, nonphotosynthetic, frequently brightly colored, and often serving to attract pollinating insects.

petiole   (pet' ee ole) [L. *petiolus*: small foot] The stalk of a leaf.

P$_{fr}$ *See* phytochrome.

phage   (fayj) *See* bacteriophage.

phage therapy   A strategy for treating bacterial infections using bacteriophage.

phagocyte [Gk. *phagein*: to eat + *kystos*: sac] One of two major classes of white blood cells; one of the nonspecific defenses of animals; ingests invading microorganisms by phagocytosis.

phagocytosis Endocytosis by a cell of another cell or large particle.

phagosome Membrane-enclosed vesicle inside a cell that results from infolding of the cell membrane and enclosing a particle to be taken into the cell.

pharmacogenomics The study of how an individual's genetic makeup affects his or her response to drugs or other agents, with the goal of predicting the effectiveness of different treatment options.

pharming The use of genetically modified animals to produce medically useful products in their milk.

phenotype (fee' no type) [Gk. *phanein*: to show] The observable properties of an individual resulting from both genetic and environmental factors. (Contrast with genotype.)

phenotypic plasticity The ability of an individual animal to express two or more phenotypes during its life. (*See also* acclimation.)

pheromone (feer' o mone) [Gk. *pheros*: carry + *hormon*: excite, arouse] A chemical substance that is released into the external environment by an individual and that brings about specific behavioral responses in other individuals of the same species.

phloem (flo' um) [Gk. *phloos*: bark] In vascular plants, the vascular tissue that transports sugars and other solutes from sources to sinks.

phospholipid A lipid containing a phosphate group; an important constituent of cellular membranes. (*See* lipid.)

phospholipid bilayer The basic structural unit of biological membranes; a sheet of phospholipids two molecules thick in which the phospholipids are lined up with their hydrophobic "tails" packed tightly together and their hydrophilic, phosphate-containing "heads" facing outward. Also called lipid bilayer.

photic zone The surface zone of lakes or oceans that is penetrated by sunlight.

photoautotroph An organism that obtains energy from light and carbon from carbon dioxide. (Contrast with chemoautotroph, chemoheterotroph, photoheterotroph.)

photoheterotroph An organism that obtains energy from light but must obtain its carbon from organic compounds. (Contrast with chemoautotroph, chemoheterotroph, photoautotroph.)

photomorphogenesis In plants, a process by which physiological and developmental events are controlled by light.

photon (foe' ton) [Gk. *photos*: light] A quantum of visible radiation; a "packet" of light energy.

photoperiod Day length; the number of hours of daylight in a 24-hour day.

photoreceptor (1) In plants, a pigment that triggers a physiological response when it absorbs a photon. (2) In animals, a sensory receptor cell that senses and responds to light energy.

photosynthesis (foe tow sin' the sis) [literally, "synthesis from light"] Metabolic processes carried out by green plants and cyanobacteria, by which visible light is trapped and the energy used to convert CO_2 into organic compounds.

photosynthetic lamellae Elaborate internal membrane systems found in cyanobacteria that are used for photosynthesis.

photosystem [Gk. *phos*: light + *systema*: assembly] A light-harvesting complex in the chloroplast thylakoid composed of pigments and proteins.

photosystem I In photosynthesis, the complex that absorbs light at 700 nm, passing electrons to ferrodoxin and thence to NADPH.

photosystem II In photosynthesis, the complex that absorbs light at 680 nm, passing electrons to the electron transport chain in the chloroplast.

phototropins A class of blue light receptors that mediate phototropism and other plant responses.

phototropism [Gk. *photos*: light + *trope*: turning] A directed plant growth response to light.

phycoerythrin A red accessory photosynthetic pigment found in red algae.

phylogenetic tree A graphic representation of lines of descent among organisms or their genes.

phylogeny (fy loj' e nee) [Gk. *phylon*: tribe, race + *genesis*: source] The evolutionary history of a particular group of organisms or their genes.

phylum (plural: phyla) A group of related classes in biological classification.

physical geography The spatial distribution of Earth's climates and physical features.

phytoalexins Substances toxic to pathogens, produced by plants in response to fungal or bacterial infection.

phytochrome (fy' tow krome) [Gk. *phyton*: plant + *chroma*: color] A plant pigment regulating a large number of developmental and other phenomena in plants. It has two isomers: P_r, which absorbs red light, and P_{fr}, which absorbs far red light. P_{fr} is the active form.

phytomers In plants, the repeating modules that compose a shoot, each consisting of one or more leaves, attached to the stem at a node; an internode; and one or more axillary buds.

phytoplankton Photosynthetic plankton.

phytoremediation A form of bioremediation that uses plants to clean up environmental pollution.

pie chart A circular figure that displays proportions of different classes of data in an observed sample.

pigment A substance that absorbs visible light.

pinocytosis Endocytosis by a cell of liquid containing dissolved substances.

pistil [L. *pistillum*: pestle] The structure of an angiosperm flower within which the ovules are borne. May consist of a single carpel, or of several carpels fused into a single structure. Usually differentiated into ovary, style, and stigma.

pith In plants, relatively unspecialized tissue found within a cylinder of vascular tissue.

pituitary gland A small endocrine gland attached to the base of the brain in vertebrates. Many of its hormones control the activities of other endocrine glands. Also known as the hypophysis. (*See also* posterior pituitary gland, anterior pituitary gland.)

placenta (pla sen' ta) The organ in female mammals that provides for the nourishment of the fetus and elimination of the fetal waste products.

plankton Aquatic organisms that drift with the current. Photosynthetic members of the plankton are referred to as phytoplankton.

planula (plan' yew la) [L. *planum*: flat] A free-swimming, ciliated larval form typical of the cnidarians.

plasma (plaz' muh) The liquid portion of blood, in which blood cells are suspended. The part of the blood that is left after the blood cells are removed.

plasma cell An antibody-secreting cell that develops from a B cell; the effector cell of the humoral immune system.

plasmid A DNA molecule distinct from the chromosome(s); that is, an extrachromosomal element; found in many bacteria. May replicate independently of the chromosome.

plasmodesma (plural: plasmodesmata) [Gk. *plassein*: to mold + *desmos*: band]

A cytoplasmic strand connecting two adjacent plant cells.

plasmogamy   The fusion of the cytoplasm of two cells. (Contrast with karyogamy.)

plate tectonics   [Gk. *tekton*: builder] The scientific study of the structure and movements of Earth's lithospheric plates, which are the cause of continental drift.

platelet   In blood, a membrane-bounded body without a nucleus, arising as a fragment of a cell in the bone marrow of mammals. Important to blood-clotting action.

pluripotent   [L. *pluri*: many + *potens*: powerful] Having the ability to form all of the cells in the body. (Contrast with multipotent, totipotent.)

pneumatophores   Root, sometimes submerged, that function in gas exchange with the environment.

poikilotherm   An animal in which the body temperature matches the temperature of the external environment and varies as the external temperature varies. Also called an ectotherm.

point mutation   A mutation that results from the gain, loss, or substitution of a single nucleotide.

polar covalent bond   A covalent bond in which the electrons are drawn to one nucleus more than the other, resulting in an unequal distribution of charge.

polar nuclei   In angiosperms, the two nuclei in the central cell of the megagametophyte; following fertilization they give rise to the endosperm.

polarity   (1) In chemistry, the property of unequal electron sharing in a covalent bond that defines a polar molecule. (2) In development, the difference between one end of an organism or structure and the other.

pollen   [L. *pollin*: fine flour] In seed plants, microscopic grains that contain the male gametophyte (microgametophyte) and gamete (microspore).

pollen grain   *See* pollen.

pollen tube   A structure that develops from a pollen grain through which sperm are released into the megagametophyte.

pollination   The process of transferring pollen from an anther to the stigma of a pistil in an angiosperm or from a strobilus to an ovule in a gymnosperm.

poly A tail   A long sequence of adenine nucleotides (50–250) added after transcription to the 3′ end of most eukaryotic mRNAs.

poly-   [Gk. *poly*: many] A prefix denoting multiple entities.

polymer   [Gk. *poly*: many + *meros*: unit] A large molecule made up of similar or identical subunits called monomers. (Contrast with monomer.)

polymerase chain reaction (PCR)   An enzymatic technique for the rapid production of millions of copies of a particular stretch of DNA where only a small amount of the parent molecule is available.

polymorphic   (pol′ lee mor′ fik) [Gk. *poly*: many + *morphe*: form, shape] Coexistence in a population of two or more distinct traits.

polyp   (pah′ lip) [Gk. *poly*: many + *pous*: foot] In cnidarians, a sessile, asexual life cycle stage.

polypeptide   A large molecule made up of many amino acids joined by peptide linkages. Large polypeptides are called proteins.

polyphyletic   (pol′ lee fih leht′ ik) [Gk. *poly*: many + *phylon*: tribe] Pertaining to a group that consists of multiple distantly related organisms, and does not include the common ancestor of the group. (Contrast with monophyletic, paraphyletic.)

polyploidy   (pol′ lee ploid ee) The possession of more than two entire sets of chromosomes.

polyribosome (polysome)   A complex consisting of a threadlike molecule of messenger RNA and several (or many) ribosomes. The ribosomes move along the mRNA, synthesizing polypeptide chains as they proceed.

polysaccharide   A macromolecule composed of many monosaccharides (simple sugars). Common examples are cellulose and starch.

pool   In ecology, the total amount of any form of matter—of an element or a molecular compound—in a given compartment of an ecosystem.

population   A group of individuals of the same species that live, interact, and reproduce together in a particular geographic area.

population bottleneck   A period during which only a few individuals of a normally large population survive.

population density   The number of individuals in a population per unit of area (for organisms that live in two-dimensional habitats such as the land surface) or volume (for organisms that live in three-dimensional habitats such as air or water).

population size   The total number of individuals in an ecological population.

positional information   In development, the basis of the spatial sense that induces cells to differentiate as appropriate for their location within the developing organism; often comes in the form of a morphogen gradient.

positive feedback   In a regulatory system, a type of control that acts to increase differences that arise between the level of a controlled variable and its set-point level. The period of amplifying deviation is followed by a period in which stabilization is restored in most biological systems. (Contrast with negative feedback.)

positive relationship   A relationship in which two variables tend to vary among observations in the same direction.

positive selection   Natural selection that acts to establish a trait that enhances survival in a population. (Contrast with purifying selection.)

post-   [L. *postere*: behind, following after] Prefix denoting something that comes after.

posterior   Toward or pertaining to the rear. (Contrast with anterior.)

posterior pituitary gland   A portion of the pituitary gland that is derived from neural tissue. In mammals, it is involved in the release of antidiuretic hormone and oxytocin, both of which are synthesized by hypothalamic neurosecretory cells. (*See also* pituitary gland, anterior pituitary gland.)

postsynaptic cell   A neuron or effector cell that receives a signal (chemical or electrical) from a presynaptic cell at a synapse.

postzygotic isolating mechanisms   Barriers to the reproductive process that occur after the union of the nuclei of two gametes. (Contrast with prezygotic isolating mechanisms.)

potential difference   *See* voltage.

potential energy   Energy not doing work, such as the energy stored in chemical bonds. (Contrast with kinetic energy.)

power   In reference to statistical tests: refers to the probability of correctly rejecting a null hypothesis when it is false.

P_r   *See* phytochrome.

PR proteins   *See* pathogenesis-related proteins.

PRRs   *See* pattern recognition receptors.

Precambrian   The first and longest period of geological time, during which life originated.

precursor RNA (pre-mRNA)   Initial gene transcript before it is modified to produce functional mRNA. Also known as the primary transcript.

predator   An organism that kills and eats other organisms.

predation   A +/− interaction between individuals of two different species in which one individual (the predator) gains fitness by consuming the other individual (the prey), which of course loses fitness by being consumed.

pressure flow model   An effective model for phloem transport in angiosperms. It holds that sieve element transport is driven by an osmotically generated pressure gradient between source and sink.

pressure potential (Ψ_p)   The hydrostatic pressure of an enclosed solution in excess of the surrounding atmospheric pressure. (Contrast with solute potential, water potential.)

presynaptic axon terminal   One of the end processes of an axon, where the axon terminates at a synapse.

presynaptic cell   A neuron or other cell that transmits a signal to a postsynaptic cell at a synapse. (Contrast with postsynaptic cell.)

prey   [L. *praeda*: booty] An organism consumed by a predator as an energy source.

prezygotic isolating mechanisms Barriers to the reproductive process that occur before the union of the nuclei of two gametes (Contrast with postzygotic isolating mechanisms.)

primary active transport   Active transport in which ATP is hydrolyzed, yielding the energy required to transport an ion or molecule against its concentration gradient. (Contrast with secondary active transport.)

primary consumer   Organisms that consume primary producers.

primary embryonic inducer   *See* organizer.

primary endosymbiosis   The engulfment of a cyanobacterium by a larger eukaryotic cell that gave rise to the first photosynthetic eukaryotes with chloroplasts.

primary growth   In plants, growth that is characterized by the lengthening of roots and shoots and by the proliferation of new roots and shoots through branching. (Contrast with secondary growth.)

primary immune response   The first response of the immune system to an antigen, involving recognition by lymphocytes and the production of effector cells and memory cells. (Contrast with secondary immune response.)

primary lysosome   *See* lysosome.

primary meristem   Meristem that produces the tissues of the primary plant body.

primary producer   A photosynthetic or chemosynthetic organism that synthesizes complex organic molecules from simple inorganic ones.

primary reproductive organs   The gonads: the ovaries in females and the testes (or testicles) in males.

primary structure   The specific sequence of amino acids in a protein. (Contrast with secondary, tertiary, quaternary structure.)

primary transcript   *See* precursor RNA.

primase   An enzyme that catalyzes the synthesis of a primer for DNA replication.

primer   Strand of nucleic acid, usually RNA, that is the necessary starting material for the synthesis of a new DNA strand, which is synthesized from the 3′ end of the primer.

principle of allocation   The principle that a unit of resource (such as food) cannot be used simultaneously for multiple functions (such as growth and reproduction), but instead must be allocated to one or another function.

pro-   [L.: first, before, favoring] A prefix often used in biology to denote a developmental stage that comes first or an evolutionary form that appeared earlier than another. For example, prokaryote, prophase.

probability   A numerical quantity that expresses the likelihood of an event occurring on a scale from 0 (no chance of the event) to 1 (certainty of the event).

probe   A segment of single-stranded nucleic acid used to identify DNA molecules containing the complementary sequence.

proboscis   A hollow, muscular feeding organ.

procambium   Primary meristem that produces the vascular tissue.

processive   Pertaining to an enzyme that catalyzes many reactions each time it binds to a substrate, as DNA polymerase does during DNA replication.

products   The molecules that result from the completion of a chemical reaction.

progesterone   [L. *pro*: favoring + *gestare*: to bear] A female sex hormone that maintains pregnancy.

prokaryotes   Unicellular organisms that do not have nuclei. (Contrast with eukaryotes.)

prometaphase   The phase of nuclear division that begins with the disintegration of the nuclear envelope.

promoter   A DNA sequence to which RNA polymerase binds to initiate transcription.

prop roots   Adventitious roots in some monocots that function as supports for the shoot.

prophase   (pro′ phase) The first stage of nuclear division, during which chromosomes condense from diffuse, threadlike material to discrete, compact bodies.

prostaglandin   Any one of a group of specialized lipids with hormone-like functions. It is not clear that they act at any considerable distance from the site of their production.

proteasome   In the eukaryotic cytoplasm, a huge protein structure that binds to and digests cellular proteins that have been tagged by ubiquitin.

protein   (pro′ teen) [Gk. *protos*: first] Long-chain polymer of amino acids with twenty different common side chains. Occurs with its polymer chain extended in fibrous proteins, or coiled into a compact macromolecule in enzymes and other globular proteins.

protein kinase   (kye′ nase) An enzyme that catalyzes the addition of a phosphate group from ATP to a target protein.

proteoglycan   A glycoprotein containing a protein core with attached long, linear carbohydrate chains.

proteome   The set of proteins that can be made by an organism. Because of alternative splicing of pre-mRNA, the number of proteins that can be made is usually much larger than the number of protein-coding genes present in the organism's genome.

proteomics   The study of the proteome—the complete complement of proteins produced by an organism.

protocells   Ordered structures enclosed within a membrane that can be formed in the laboratory and are hypothesized to resemble cells when life originated.

protoderm   Primary meristem that gives rise to the plant epidermis.

proton   (pro′ ton) [Gk. *protos*: first, before] (1) A subatomic particle with a single positive charge. The number of protons in the nucleus of an atom determine its element. (2) A hydrogen ion, H^+.

proton pump   An active transport system that uses ATP energy to move hydrogen ions across a membrane, generating an electric potential.

provirus   Double-stranded DNA made by a virus that is integrated into the host's chromosome and contains promoters that are recognized by the host cell's transcription apparatus.

pseudocoelomate   (soo′ do see′ low mate) [Gk. *pseudes*: false + *koiloma*: cavity] Having a body cavity, called a

pseudocoel, consisting of a fluid-filled space in which many of the internal organs are suspended, but which is enclosed by mesoderm only on its outside.

pseudogene [Gk. *pseudes*: false] A DNA segment that is homologous to a functional gene but is not expressed because of changes to its sequence or changes to its location in the genome.

pseudoplasmodium An aggregate of individuals in cellular slime molds that act in a coordinated fashion to form a fruiting structure.

Punnett square Method of predicting the results of a genetic cross by arranging the gametes of each parent at the edges of a square.

pupil The opening in the vertebrate eye through which light passes from the outside to the retina.

purifying selection The elimination by natural selection of detrimental characters from a population. (Contrast with positive selection.)

purine (pure′ een) One of the two types of nitrogenous bases in nucleic acids. Each of the purines—adenine and guanine—pairs with a specific pyrimidine.

pyrimidine (per im′ a deen) One of the two types of nitrogenous bases in nucleic acids. Each of the pyrimidines—cytosine, thymine, and uracil—pairs with a specific purine.

pyruvate oxidation Conversion of pyruvate to acetyl CoA and CO_2 that occurs in the mitochondrial matrix in the presence of O_2.

Q

qualitative traits Traits that differ from one another by discrete qualities.

quantitative trait Phenotype determined by multiple genes.

quantitative variables Variables that can take on values along a numerical scale.

quaternary structure The specific three-dimensional arrangement of protein subunits. (Contrast with primary, secondary, tertiary structure.)

quorum sensing The use of chemical communication signals to trigger density-linked activities such as biofilm formation in prokaryotes.

R

R group The distinguishing group of atoms of a particular amino acid. Also known as a side chain.

radial axis Radial definition of function in an adult organism or future function in an embryo, as in the developing flower with organs in whorls.

radial cleavage Embryonic development in some deuterostomes in which the planes of cell division are parallel and perpendicular to the animal-vegetal axis of the embryo. Considered the basic deuterostome cleavage pattern. (Compare to spiral cleavage.)

radial symmetry The condition in which any two halves of a body are mirror images of each other, providing the cut passes through the center; a cylinder cut lengthwise down its center displays this form of symmetry.

radicle An embryonic root.

radiometric dating A method for determining the age of objects such as fossils and rocks based on the decay rates of radioactive isotopes.

rain shadow The relatively dry area on the down-wind side of a mountain range.

range The largest minus the smallest observed value for a variable in a sample.

rarity advantage Any situation in which individuals of a species lose less fitness from interspecific competition when they are rare than when they are common.

reactant A chemical substance that enters into a chemical reaction with another substance.

reaction center A group of electron transfer proteins that receive energy from light-absorbing pigments and convert it to chemical energy by redox reactions.

receptor *See* receptor protein, sensory receptor cell.

receptor endocytosis Endocytosis initiated by macromolecular binding to a specific membrane receptor. Also called receptor-mediated endocytosis.

receptor protein A protein that can bind to a specific molecule, or detect a specific stimulus, within the cell or in the cell's external environment.

recessive In genetics, an allele that does not determine phenotype in the presence of a dominant allele. (Contrast with dominance.)

recombinant Pertaining to an individual, meiotic product, or chromosome in which genetic materials originally present in two individuals end up in the same haploid complement of genes.

recombinant DNA A DNA molecule made in the laboratory that is derived from two or more genetic sources.

recombination frequency The proportion of offspring of a genetic cross that have phenotypes different from the parental phenotypes due to crossing over between linked genes during gamete formation.

red blood cell (**RBC**) A cell in the blood of an animal that contains hemoglobin and transports O_2. Also called an erythrocyte.

redox reaction A chemical reaction in which one reactant becomes oxidized and the other becomes reduced. Short for reduction–oxidation reaction.

reduction Gain of electrons by a chemical reactant; any reduction is accompanied by an oxidation. (Contrast with oxidation.)

regulation The maintenance of internal conditions at an approximately constant level while external conditions vary. (Contrast with conformity.)

regulative development A pattern of animal embryonic development in which the fates of the first blastomeres are not absolutely fixed. (Contrast with mosaic development.)

regulators Animals that maintain relatively constant internal conditions in the presence of changing external conditions (i.e., the animals exhibit regulation.) (Contrast with conformers.)

regulatory T cells (T$_{reg}$) The class of T cells that mediates tolerance to self antigens.

reinforcement The evolution of enhanced reproductive isolation between populations due to natural selection for greater isolation.

release-inhibiting hormones *See* inhibiting hormones.

releasing hormone (RH) A hormone secreted by neuroendocrine cells in the hypothalamus of a vertebrate that travels to the anterior pituitary gland through the hypothalamo–hypophysial portal system and stimulates the secretion of a hormone by a specific population of anterior pituitary endocrine cells.

replication fork A point at which a DNA molecule is replicating. The fork forms by the unwinding of the parent molecule.

reporter gene A genetic marker included in recombinant DNA to indicate the presence of the recombinant DNA in a host cell.

repressor A protein encoded by a regulatory gene that can bind to a promoter and prevent transcription of the associated gene. (Contrast with activator.)

reproductive isolation Condition in which two divergent populations are no longer exchanging genes. Can lead to speciation.

reproductive signals External cues that stimulate cells to divide or organisms to reproduce.

RER *See* rough endoplasmic reticulum.

residuals The deviations, along the y-axis from the linear regression line, of individual observations in a bivariate scatter plot.

resistance exercise Exercise that consists of relatively short periods of high-intensity muscular actions against a large load, often repeated with intervening interruptions. Also called resistance training. (Contrast with endurance exercise.)

resistance (R) genes Plant genes that confer resistance to specific strains of pathogens.

resource partitioning A situation in which competing organisms (usually of different species) differ in their use of resources.

resource In ecology, the materials (e.g., food, mineral nutrients), energy (e.g., photons of light), or favorable physical conditions, that organisms need to survive and reproduce, and that they make unavailable to other organisms when they use these resources.

respiratory airways Airways in the lungs where O_2 and CO_2 are exchanged between the air and blood.

respiratory chain The terminal reactions of cellular respiration, in which electrons are passed from NAD or FAD, through a series of intermediate carriers, to molecular oxygen, with the concomitant production of ATP.

respiratory gases Oxygen (O_2) and carbon dioxide (CO_2).

respiratory minute volume In an animal with lungs, the total volume of air inhaled and exhaled per minute.

respiratory pigments Any of the pigments that undergo reversible combination with O_2 and thus are able to pick up O_2 in certain places in an animal's body (e.g., the breathing organs) and release it in other places (e.g., systemic tissues). Respiratory pigments include hemoglobin and hemocyanin.

resting potential The potential difference (voltage) across the cell membrane of a living cell at rest. In cells at rest, the interior is negative to the exterior. (Contrast with action potential.)

restoration ecology The applied subdiscipline of ecology whose goal is to restore the function of damaged ecosystems.

restriction enzyme Any of a type of enzyme that cleaves double-stranded DNA at specific sites; extensively used in recombinant DNA technology. Also called a restriction endonuclease.

restriction site A specific DNA base sequence that is recognized and acted on by a restriction endonuclease.

retina (rett' in uh) [L. *rete*: net] The light-sensitive layer of cells in the vertebrate eye and some invertebrate eyes. In the vertebrate eye, it consists of photoreceptor cells and cells that process signals from the photoreceptor cells.

retrotransposons Mobile genetic elements that are reverse transcribed into RNA as part of their transfer mechanism. (Contrast with DNA transposons.)

retrovirus An RNA virus that contains reverse transcriptase. Its RNA serves as a template for cDNA production, and the cDNA is integrated into a chromosome of the host cell.

reverse transcriptase An enzyme that catalyzes the production of DNA (cDNA), using RNA as a template; essential to the reproduction of retroviruses.

rhizoids (rye' zoids) [Gk. root] Hairlike extensions of cells in mosses, liverworts, and a few vascular plants that serve the same function as roots and root hairs in vascular plants. The term is also applied to branched, rootlike extensions of some fungi and algae.

rhizome (rye' zome) An underground stem (as opposed to a root) that runs horizontally beneath the ground.

rhodopsin A visual pigment, found in many molecular forms in the animal kingdom, used in the process of transducing energy of photons of light into changes in the membrane potential of photoreceptor cells.

ribonucleic acid *See* RNA.

ribose A five-carbon sugar in nucleotides and RNA.

ribosomal RNA (rRNA) Several species of RNA that are incorporated into the ribosome. Involved in peptide bond formation.

ribosome A small particle in the cell that is the site of protein synthesis.

ribozyme An RNA molecule with catalytic activity.

ribulose bisphosphate carboxylase/ oxygenase *See* rubisco.

RNA (ribonucleic acid) An often single-stranded nucleic acid whose nucleotides use ribose rather than deoxyribose and in which the base uracil replaces thymine found in DNA. Serves as genome from some viruses. (*See* ribosomal RNA, transfer RNA, messenger RNA, ribozyme.)

RNA interference (RNAi) A mechanism for reducing mRNA translation whereby a double-stranded RNA, made by the cell or synthetically, is processed into a small, single-stranded RNA, whose binding to a target mRNA results in the latter's breakdown.

RNA polymerase An enzyme that catalyzes the formation of RNA from a DNA template.

RNA splicing The last stage of RNA processing in eukaryotes, in which the transcripts of introns are excised through the action of small nuclear ribonucleoprotein particles (snRNP).

rod cells Light-sensitive cells in the vertebrate retina; these sensory receptor cells are sensitive to extremely dim light and are responsible for dim-light, black and white vision.

root (1) In reference to phylogenetic trees: the base (oldest) part of the tree. (2) In reference to plants: the organ responsible for anchoring the plant in the soil, absorbing water and minerals, and producing certain hormones. Some roots are storage organs.

root apical meristem Undifferentiated tissue at theof the root that gives rise to the organs of the root.

root cap A thimble-shaped mass of cells, produced by the root apical meristem, that protects the meristem; the organ that perceives the gravitational stimulus in root gravitropism.

root system The organ system that anchors a plant in place, absorbs water and dissolved minerals, and may store products of photosynthesis from the shoot system.

rotational cleavage Cleavage pattern typical of eutherian mammals in which the first cleavage is meridional whereas in the second cleavage, one blastomere divides meridionally and the other equatorially.

rough endoplasmic reticulum (RER) The portion of the endoplasmic reticulum whose outer surface has attached ribosomes. (Contrast with smooth endoplasmic reticulum.)

rRNA *See* ribosomal RNA.

RT-PCR Determination of the quantity of an RNA by first converting to it to DNA by reverse transcriptase, and then amplifying the DNA by the polymerase chain reaction.

rubisco Contraction of ribulose bisphosphate carboxylase/oxygenase, the enzyme that combines carbon dioxide or oxygen with ribulose bisphosphate to catalyze the first step of photosynthetic carbon fixation or photorespiration, respectively.

S

S phase In the cell cycle, the stage of interphase during which DNA is replicated. (Contrast with G1, G2, M phase.)

salt glands   (1) In plants, glands on the leaves of some halophytic (salt-loving) plants that secrete salts onto the outer plant surfaces, thereby ridding the tissue fluids of the plants of excess salts. (2) In animals, organs other than kidneys that excrete concentrated salt solutions, thereby ridding the body fluids of excess salts.

sample   A set of observations made from a population.

saprobe   [Gk. *sapros*: rotten] An organism (usually a bacterium or fungus) that obtains its carbon and energy by absorbing nutrients from dead organic matter.

saprobic   Feeding on dead organic matter.

sarcomere   (sark′ o meer) [Gk. *sark*: flesh + *meros*: unit] The contractile unit of a skeletal muscle cell. Each myofibril in a muscle cell consists of a series of sarcomeres.

sarcoplasm   The cytoplasm of a muscle cell.

sarcoplasmic reticulum   The endoplasmic reticulum of a muscle cell.

saturated fatty acid   A fatty acid in which all the bonds between carbon atoms in the hydrocarbon chain are single bonds—that is, all the bonds are saturated with hydrogen atoms. (Contrast with unsaturated fatty acid.)

scaling relationships   The study of the relations between physiological (or morphological) characteristics and body size within sets of phylogenetically related species (e.g., the study of metabolism-weight relations among mammals of different sizes.)

scatter plot   A figure that displays the values of observations for two variables along perpendicular axes.

Schwann cell   A type of glial cell that forms a myelin sheath on axons in the peripheral nervous system.

scion   In horticulture, the bud or stem from one plant that is grafted to a root or root-bearing stem of another plant (the stock).

sclereid   One of the principle types of cells in sclerenchyma.

sclerenchyma   (skler eng′ kyma) [Gk. *skleros*: hard + *kymus*: juice] A plant tissue composed of cells with heavily thickened cell walls. The cells are dead at functional maturity. The principal types of sclerenchyma cells are fibers and sclereids.

scrotum   In most mammals, a pouch outside the body cavity that contains the testes (testicles).

SDP   *See* short-day plant.

seasonality   Predictable variation in the climate of a given place during the course of an annual cycle.

second filial generation   *See* F$_2$.

second law of thermodynamics   The principle that when energy is converted from one form to another, some of that energy becomes unavailable for doing work.

secondary active transport   A form of active transport that does not use ATP as an energy source; rather, transport is coupled to ion diffusion down a concentration gradient established by primary active transport. (Contrast with primary active transport.)

secondary consumer   An organism that consumes primary consumers.

secondary endosymbiosis   The engulfment of a photosynthetic eukaryote by another eukaryotic cell that gave rise to certain groups of photosynthetic eukaryotes (e.g., euglenids).

secondary growth   In plants, growth that contributes to an increase in girth. (Contrast with primary growth.)

secondary immune response   A rapid and intense response to a second or subsequent exposure to an antigen, initiated by memory cells. (Contrast with primary immune response.)

secondary lysosome   Membrane-enclosed organelle formed by the fusion of a primary lysosome with a phagosome, in which macromolecules taken up by phagocytosis are hydrolyzed into their monomers. (Contrast with lysosome.)

secondary metabolite   A compound synthesized by a plant that is not needed for basic cellular metabolism. Typically has an antiherbivore or antiparasite function.

secondary sexual characteristics   Sex-specific properties of nonreproductive tissues and organs.

secondary structure   Of a protein, localized regularities of structure, such as the α helix and the β pleated sheet. (Contrast with primary, tertiary, quaternary structure.)

secrete   To discharge a substance from a cell or gland.

sedimentary rock   Rock formed by the accumulation of sediment grains on the bottom of a body of water.

seed   A fertilized, ripened ovule of a gymnosperm or angiosperm. Consists of the embryo, nutritive tissue, and a seed coat.

seedling   A plant that has just completed the process of germination.

segment polarity genes   In *Drosophila* (fruit fly) development, segmentation genes that determine the boundaries and anterior–posterior organization of individual segments. Part of a developmental cascade that includes maternal effect genes, gap genes, pair rule genes, and Hox genes.

segmentation   Division of an animal body into segments.

segregation   *See* law of segregation.

selectable marker   A gene, such as one encoding resistance to an antibiotic, that can be used to identify (select) cells that contain recombinant DNA from among a large population of untransformed cells.

selective permeability   Allowing certain substances to pass through while other substances are excluded; a characteristic of membranes.

self-incompatability   In plants, the possession of mechanisms that prevent self-fertilization.

semelparity   A type of reproductive life history in which individuals are physiologically capable of reproducing only one time during their lives. In **semelparous** species, individuals are often programmed to die after reproducing once. (Contrast with iteroparity.)

semen   (see′ men) [L. *semin*: seed] The thick, whitish liquid produced by the male reproductive system in mammals, containing the sperm.

semiconservative replication   The way in which DNA is synthesized. Each of the two partner strands in a double helix acts as a template for a new partner strand. Hence, after replication, each double helix consists of one old and one new strand.

seminiferous tubules   The tubules within the testes (testicles) within which sperm production occurs.

sensor   One of four essential elements of a control system; an organ or cell that detects the current level of the controlled variable.

sensory neuron   A neuron that functions as a sensory receptor cell or that carries a signal from sensory cells or organs to the central nervous system. Also called an afferent neuron.

sensory receptor cell   A cell, typically a neuron, that is specialized to transform the energy of a stimulus into an electric signal. Each type is highly specific in the stimuli to which it ordinarily responds.

sensory receptor proteins   Proteins in sensory receptor cells that respond to sensory input, causing a receptor potential (a graded change of membrane potential) in the receptor cell.

sensory transduction   The transformation of environmental stimuli

into neural electric signals in a sensory receptor cell.

sepal (see' pul) [L. *sepalum*: covering] One of the outermost structures of the flower, usually protective in function and enclosing the rest of the flower in the bud stage.

sepsis Generalized inflammation caused by bacterial infection. Can cause a dangerous drop in blood pressure.

septate [L. wall] Divided, as by walls or partitions.

septum (plural: septa) (1) A partition or cross-wall appearing in the hyphae of some fungi. (2) The bony structure dividing the nasal passages.

sequential hermaphrodites Species in which an individual can be male at some times and female at other times during its lifespan

SER *See* smooth endoplasmic reticulum.

Sertoli cells Cells in the seminiferous tubules that nurture the developing sperm.

sex A process by which the genes of two individuals are combined to produce offspring.

sex chromosome In organisms with a chromosomal mechanism of sex determination, one of the chromosomes involved in sex determination.

sex determination The process by which the sex (male or female) of an individual becomes established during the conception and development of the individual.

sex pilus A thin connection between two bacteria through which genetic material passes during conjugation.

sex-linked inheritance Inheritance of a gene that is carried on a sex chromosome. Also called sex linkage.

sexual reproduction Reproduction in which the genes of two individuals are combined to produce offspring, typically involving the union of male and female gametes.

sexual selection Selection by one sex of characteristics in individuals of the opposite sex. Also, the favoring of characteristics in one sex as a result of competition among individuals of that sex for mates.

shared derived trait *See* synapomorphy.

shiver (1) In a mammal or bird, the subtle contraction and relaxation of skeletal muscles that produces heat rather than motion as the primary product. (2) In an insect, contraction of the flight muscles in a nonflying mode to generate heat rather than flight.

shoot apical meristem Undifferentiated tissue at the apex of the shoot that gives rise to the organs of the shoot.

shoot system In plants, the organ system consisting of the leaves, stem(s), and flowers.

short-day plant (SDP) A plant that flowers when nights are longer than a critical length specific for that plant's species. (Compare to long-day plant.)

short tandem repeat (STR) A short (1–5 base pairs), moderately repetitive sequence of DNA. The number of copies of an STR at a particular location varies between individuals and is inherited.

side chain *See* R group.

sieve tube element The characteristic cell of the phloem in angiosperms, which contains cytoplasm but relatively few organelles, and whose end walls (sieve plates) contain pores that form connections with neighboring cells.

sigma factor In prokaryotes, a protein that binds to RNA polymerase, allowing the complex to bind to and stimulate the transcription of a specific class of genes (e.g., those involved in sporulation).

signal sequence The sequence within a protein that directs the protein to a particular organelle.

signal transduction pathway The series of biochemical steps whereby a stimulus to a cell (such as a hormone or neurotransmitter binding to a receptor) is translated into a response of the cell.

significance level A particular threshold of making a Type I error (incorrectly rejecting a true null hypothesis) in a statistical test, selected a priori by the investigator.

silent mutation A change in a gene's sequence that has no effect on the amino acid sequence of a protein because it occurs in noncoding DNA or because it does not change the amino acid specified by the corresponding codon. (Contrast with frame-shift mutation, missense mutation, nonsense mutation.)

silent substitution *See* synonymous substitution.

simple diffusion Diffusion that doesn't involve a direct input of energy or assistance by carrier proteins.

simple epithelium An epithelium (sheet of cells that lines a body cavity or covers an organ or body surface) consisting of a single cell layer.

simple fruit A fruit derived from a single ovary; examples include grapes and tomatoes.

single nucleotide polymorphisms (SNPs) Inherited variations in a single nucleotide base in DNA that differ between individuals.

sink In plants, any organ that imports the products of photosynthesis, such as roots, developing fruits, and immature leaves. (Contrast with source.)

sister chromatid Each of a pair of newly replicated chromatids.

sister clades Two phylogenetic groups that are each other's closest relatives.

sister species Two species that are each other's closest relatives.

skeletal muscle A type of muscle tissue characterized by multinucleated cells containing highly ordered arrangements of actin and myosin microfilaments that give the tissue a striated appearance under a light microscope. Also called striated muscle. (Contrast with cardiac muscle, smooth muscle.)

sliding filament theory Mechanism of muscle contraction (use of ATP to produce contractile forces) based on the formation and breaking of crossbridges between actin and myosin filaments, causing the filaments to slide past each other.

slow oxidative cells Skeletal muscle cells specialized for sustained, relatively low-intensity, aerobic work; contain myoglobin and abundant mitochondria. Also called slow-twitch cells. (Compare to fast glycolytic cells.)

slug A worm-like organism or colony of organisms; used to refer to unshelled terrestrial mollusks as well as to the mobile, colonial stage of cellular slime molds.

small intestine *See* midgut.

small nuclear ribonucleoprotein particle (snRNP) A complex of an enzyme and a small nuclear RNA molecule, functioning in RNA splicing.

smooth endoplasmic reticulum (SER) Portion of the endoplasmic reticulum that lacks ribosomes and has a tubular appearance. (Contrast with rough endoplasmic reticulum.)

smooth muscle Muscle tissue consisting of small, mononucleated muscle cells innervated by the autonomic nervous system. (Contrast with cardiac muscle, skeletal muscle.)

social behavior Behavior that helps integrate individuals into social groups (societies), and the group behaviors of social groups. (*See also* society.)

society A group of individuals of a single species that exhibits some degree of cooperative action.

sodium–potassium (Na⁺–K⁺) pump A membrane protein (anti-porter) that carries out primary active transport of

ions; it uses energy from ATP to pump sodium ions out of a cell and potassium ions into the cell. Also called a sodium–potassium ATPase.

soil horizon   *See* horizons.

soil solution   The aqueous portion of soil, from which plants take up dissolved mineral nutrients.

solute potential (Ψ_s)   A property of any solution, resulting from its solute contents; it may be zero or have a negative value. The more negative the solute potential, the greater the tendency of the solution to take up water through a differentially permeable membrane. (Contrast with pressure potential, water potential.)

solvent   Liquid in which a substance (solute) is dissolved to form a solution.

somatic cell   [Gk. *soma*: body] All the cells of the body that are not specialized for reproduction. (Contrast with germ cell.)

somatic mutation   Permanent genetic change in a somatic cell. These mutations affect the individual only; they are not passed on to offspring. (Contrast with germline mutation.)

somite   (so' might) A segmental block of mesoderm; differentiates to form dermis, axial skeleton (vertebrae, ribs), and skeletal muscle.

soredia   (sing.: soredium) Propagules of lichens consisting of one or a few photosynthetic cells bound by fungal hyphae.

sori   Clusters of stalked sporangia that occur on the underside of fern fronds.

source   In plants, any organ that exports the products of photosynthesis in excess of its own needs, such as a mature leaf or storage organ. (Contrast with sink.)

spawning   *See* external fertilization.

speciation   (spee' see ay' shun) The process of splitting one biological lineage into two biological lineages that evolve independently from one another.

species   (spee' sees) [L. kind] The base unit of taxonomic classification, consisting of an ancestor–descendant group of populations of evolutionarily closely related, similar organisms. The more narrowly defined "biological species" consists of individuals capable of interbreeding with each other but not with members of other species.

species composition   The identities of all the species that make up a given ecological community.

species concepts   Ways that biologists think about the existence of species.

species diversity   In ecology, a measure of the chance that two individuals in a community are of the same species. Measures of species diversity include the number of distinct species in a community (species richness), and/or the relative abundances of different species (species evenness).

species evenness   A measure of the similarity in the abundances of species in a community. If species are equally abundant, evenness is at a maximum.

species richness   The total number of species in an ecological community.

sperm   [Gk. *sperma*: seed] *See* spermatozoa.

spermatozoa   Haploid gametes that are capable of swimming (usually by use of flagella), produced by spermatogenesis in the testis of a male animal. Also called sperm.

spicule   [L. arrowhead] A hard, calcareous skeletal element typical of sponges.

spinal reflex   In a vertebrate, the conversion of sensory neuronal signals to motor neuronal signals in the spinal cord without participation of the brain.

spindle   Array of microtubules emanating from both poles of a dividing cell during mitosis and playing a role in the movement of chromosomes at nuclear division. Named for its shape.

spiral cleavage   Embryonic development in many protostomes in which the plane of cell division is diagonal to the vertical axis of the embryo. (Compare to radial cleavage.)

spirillum   A bacterium that is shaped like a corkscrew.

spleen   Organ that serves as a reservoir for venous blood and eliminates old, damaged red blood cells from the circulation.

splicing   *See* RNA splicing.

spliceosome   RNA–protein complex that splices out introns from eukaryotic pre-mRNAs.

spontaneous mutation   A genetic change caused by internal cellular mechanisms, such as an error in DNA replication. (Contrast with induced mutation.)

spontaneous ovulation   Ovulation (release of an egg from the ovaries of a female) that results from endogenous processes (processes that originate within the animal), more or less independent of copulation. (Contrast with induced ovulation.)

sporangiophore   A stalked reproductive structure produced by zygospore fungi that extends from a hypha and bears one or many sporangia.

sporangium   (spor an' gee um) (plural: sporangia) [Gk. *spora*: seed + *angeion*: vessel or reservoir] In plants and fungi, any specialized structure within which one or more spores are formed.

spore   [Gk. *spora*: seed] (1) Any asexual reproductive cell capable of developing into an adult organism without gametic fusion. In plants, haploid spores develop into gametophytes, diploid spores into sporophytes. (2) In prokaryotes, a resistant cell capable of surviving unfavorable periods.

sporocyte   Specialized cells of the diploid sporophyte that will divide by meiosis to produce four haploid spores. Germination of these spores produces the haploid gametophyte.

sporulation   The formation of specialized cells (spores) that are capable of developing into new individuals.

sporophyte   (spor' o fyte) [Gk. *spora*: seed + *phyton*: plant] In plants and protists with alternation of generations, the diploid phase that produces the spores. (Contrast with gametophyte.)

stabilizing selection   Selection against the extreme phenotypes in a population, so that the intermediate types are favored. (Contrast with disruptive selection.)

stamen   (stay' men) [L. *stamen*: thread] A male (pollen-producing) unit of a flower, usually composed of an anther, which bears the pollen, and a filament, which is a stalk supporting the anther.

standard amino acid   One of the 20 amino acids that animals use to synthesize proteins.

standard deviation   A measure of the spread of observations in a sample. See Appendix B for the mathematical formula.

standard error   A measure of how close a sample statistic (such as the mean) is likely to be to the true population value.

standard error of the mean   A measure of how close a sample mean is likely to be to the true population value. Calculated by dividing the standard deviation of a sample by the square root of the sample size.

staphylococci   Bacteria of the genus *Staphylococcus*.

start codon   The mRNA triplet (AUG) that acts as a signal for the beginning of translation at the ribosome. (Contrast with stop codon.)

statistic   A numerical quantity calculated from data.

stele   (steel) [Gk. *stylos*: pillar] The central cylinder of vascular tissue in a plant stem.

stem   In plants, the organ that holds leaves and/or flowers and transports and

distributes materials among the other organs of the plant.

stem cell In animals, an undifferentiated cell that is capable of continuous proliferation. A stem cell generates more stem cells and a large clone of differentiated progeny cells. (*See also* embryonic stem cell.)

steroid hormones Lipid-soluble hormones synthesized from cholesterol. The chemical structure of a steroid hormone includes a distinctive subpart consisting of four interlinked rings. (Compare to peptide hormones, amine hormones.)

stigma [L. *stigma*: mark, brand] The part of the pistil at the apex of the style that is receptive to pollen, and on which pollen germinates.

stock In horticulture, the root or root-bearing stem to which a bud or piece of stem from another plant (the scion) is grafted.

stoma (plural: stomata) [Gk. *stoma*: mouth, opening] Small opening in the plant epidermis that permits gas exchange; bounded by a pair of guard cells whose osmotic status regulates the size of the opening.

stop codon Any of the three mRNA codons that signal the end of protein translation at the ribosome: UAG, UGA, UAA. (Contrast with start codon.)

STR *See* short tandem repeat.

stratigraphy The study of geological strata, or layers.

stratum (plural: strata) [L. *stratos*: layer] A layer of sedimentary rock laid down at a particular time in the past.

stretch-gated channel A membrane ion channel that opens and closes in response to local stretching or pulling forces applied to the cell membrane.

striated muscle *See* skeletal muscle.

strigolactones Signaling molecules produced by plant roots that attract the hyphae of mycorrhizal fungi.

strobilus (plural: strobili) One of several conelike structures in various groups of plants (including club mosses, horsetails, and conifers) associated with the production and dispersal of reproductive products.

structural gene A gene that encodes the primary structure of a protein not involved in the regulation of gene expression.

style [Gk. *stylos*: pillar or column] In the angiosperm flower, a column of tissue extending from the tip of the ovary, and bearing the stigma or receptive surface for pollen at its apex.

sub- [L. under] A prefix used to designate a structure that lies beneath another or is less than another. For example, subcutaneous (beneath the skin); subspecies.

subduction In plate tectonics, the movement of one plate under another.

subpopulation In ecology, the portion of a larger metapopulation that occupies a given piece of suitable habitat. *See* metapopulation.

subsoil The soil horizon lying below the topsoil and above the parent rock (bedrock); the zone of infiltration and accumulation of materials leached from the topsoil. Also called the B horizon.

substrate (sub' strayte) (1) The molecule or molecules on which an enzyme exerts catalytic action. (2) The base material on which a sessile organism lives.

succession A relatively predictable series of changes in the species composition of a community following a disturbance, that leads ultimately to a community that resembles the original, predisturbance community. (Contrast with ecological transition.)

succulence In plants, possession of fleshy, water-storing leaves or stems; an adaptation to dry environments.

surface area-to-volume ratio For any cell, organism, or geometrical solid, the ratio of surface area to volume; this is an important factor in setting an upper limit on the size a cell or organism can attain.

surface tension The attractive intermolecular forces at the surface of liquid; an especially important property of water.

survivorship The average individual's chance of surviving over a specified set of life stages, ages, or period of time—often from birth to a given stage or age. (Contrast with mortality.)

suspensor In the embryos of seed plants, the stalk of cells that pushes the embryo into the endosperm and is a source of nutrient transport to the embryo.

suspension feeder An aquatic animal that feeds on objects much smaller than itself that are suspended in water. (*See also* filter feeder.)

swim bladders Organs used to regulate buoyancy in fish.

symbiosis (sim' bee oh' sis) [Gk. *sym*: together + *bios*: living] The living together of two or more species in a prolonged, interactive relationship.

symbiotic A relationship in which two or more organisms live in close association with one another.

symmetry Pertaining to an attribute of an animal body in which at least one plane can divide the body into similar, mirror-image halves. (*See* bilateral symmetry, radial symmetry.)

sympathetic division A division of the vertebrate autonomic nervous system that is connected to the central nervous system via thoracic and lumbar spinal nerves; the sympathetic and parasympathetic divisions tend to exert opposing controls over autonomic effectors. (Contrast with parasympathetic division.)

sympatric speciation (sim pat' rik) [Gk. *sym*: same + *patria*: homeland] Speciation due to reproductive isolation without any physical separation of the subpopulation. (Contrast with allopatric speciation.)

symplast The continuous meshwork of the interiors of living cells in the plant body, resulting from the presence of plasmodesmata. (Contrast with apoplast.)

synapomorphy A trait that arose in the ancestor of a phylogenetic group and is present (sometimes in modified form) in all of its members, thus helping to delimit and identify that group. Also called a shared derived trait.

synapse (sin' aps) [Gk. *syn*: together + *haptein*: to fasten] A specialized type of junction where a neuron meets its target cell (which can be another neuron or some other type of cell) and neurotransmitter molecules serve to carry signals from the presynaptic neuron to the postsynaptic cell across the synaptic cleft.

synaptic plasticity The process by which synapses in the nervous system of an individual animal can undergo long-term changes in their functional properties.

synonymous (silent) substitution A change of one nucleotide in a sequence to another when that change does not affect the amino acid specified (i.e., UUA → UUG, both specifying leucine). (Contrast with nonsynonymous substitution, missense mutation, nonsense mutation.)

systematics The scientific study of the diversity and relationships among organisms.

systemic acquired resistance A general resistance to many plant pathogens following infection by a single agent.

systemic circuit In a circulatory system, the blood vessels that take blood to and from the systemic tissues. (Contrast with breathing-organ circuit.)

systemic tissues All tissues other than those of the breathing organs (lungs or gills).

systems biology The scientific study of an organism as an integrated and

interacting system of genes, proteins, and biochemical reactions.

systole (sis' tuh lee) [Gk. *systole*: contraction] During the cardiac cycle, the period of contraction of the chambers of the heart, which drives blood forward in the circulatory system. (Contrast with diastole.)

T

T tubules *See* transverse tubules.

T-helper (T$_H$) cell Type of T cell that stimulates events in both the cellular and humoral immune responses by binding to the antigen on an antigen-presenting cell; target of the HIV-I virus, the agent of AIDS. (Contrast with cytotoxic T cell.)

taproot The main root of a plant that is usually thick and grows down into the soil.

taproot system A root system typical of eudicots consisting of a primary root (taproot) that extends downward by tip growth and outward by initiating lateral roots. (Contrast with fibrous root system.)

target cell A cell with the appropriate receptor proteins to bind and respond to a particular hormone or other chemical mediator.

TATA box An eight-base-pair sequence, found about 25 base pairs before the starting point for transcription in many eukaryotic promoters, that binds a transcription factor and thus helps initiate transcription.

taxon (plural: taxa) [Gk. *taxis*: arrange, put in order] A biological group (typically a species or a clade) that is given a name.

telomerase An enzyme that catalyzes the addition of telomeric sequences lost from chromosomes during DNA replication.

telomeres (tee' lo merz) [Gk. *telos*: end + *meros*: units, segments] Repeated DNA sequences at the ends of eukaryotic chromosomes.

telophase (tee' lo phase) [Gk. *telos*: end] The final phase of mitosis or meiosis during which chromosomes become diffuse, nuclear envelopes re-form, and nucleoli begin to reappear in the daughter nuclei.

template A molecule or surface on which another molecule is synthesized in complementary fashion, as in the replication of DNA.

template strand In double-stranded DNA, the strand that is transcribed to create an RNA transcript that will be processed into a protein. Also refers to a strand of RNA that is used to create a complementary RNA.

tendon A collagen-containing band of tissue that connects a muscle with a bone.

termination In molecular biology, the end of transcription or translation.

territory A region that an individual occupies and defends against occupation by other individuals of the same species. (Compare with home range.)

tertiary consumers An organism that consumes secondary consumers.

tertiary endosymbiosis The mechanism by which some eukaryotes acquired the capacity for photosynthesis; for example, a dinoflagellate that apparently lost its chloroplast became photosynthetic by engulfing another protist that had acquired a chloroplast through secondary endosymbiosis.

tertiary structure In reference to a protein, the relative locations in three-dimensional space of all the atoms in the molecule. The overall shape of a protein. (Contrast with primary, secondary, quaternary structures.)

test cross Mating of a dominant-phenotype individual (who may be either heterozygous or homozygous) with a homozygous-recessive individual.

testis (tes' tis) (plural: testes) [L. *testis*: witness] The male gonad; the organ that produces the male gametes. Also sometimes called a testicle.

tetrad [Gk. *tettares*: four] During prophase I of meiosis, the association of a pair of homologous chromosomes or four chromatids.

thallus The vegetative body of a lichen.

thermoneutral zone (TNZ) [Gk. *thermos*: temperature] In a homeotherm, the range of ambient temperatures over which the animal is under neither heat nor cold stress and the metabolic rate is constant.

thermoregulation The maintenance of a relatively constant body temperature.

thick filaments *See* myosin filaments.

thin filaments *See* actin filaments.

thylakoid (thigh la koid) [Gk. *thylakos*: sack or pouch] A flattened sac within a chloroplast. Thylakoid membranes contain all of the chlorophyll in a plant, in addition to the electron carriers of photophosphorylation. Thylakoids stack to form grana.

thymine (T) Nitrogen-containing base found in DNA.

thyroid-stimulating hormone (TSH) A hormone, released by the anterior pituitary gland, that signals the thyroid gland to secrete its hormones.

tidal ventilation Bidirectional pumping of air in and out of lungs, during which air enters and leaves the lungs by the same route. (Contrast with unidirectional ventilation.)

tidal volume The volume of air that is breathed in and out of the lungs during each breath.

tissue A group of similar cells organized into a functional unit; usually integrated with other tissues to form part of an organ.

tissue fluid *See* interstitial fluid.

tissue system In plants, any of three organized groups of tissues—dermal tissue, vascular tissue, and ground tissue—that are established during embryogenesis and have distinct functions.

titin A giant, elongated, elastic protein molecule that in a striated muscle cell spans an entire half-sarcomere from the M band to the Z line.

TNZ *See* thermoneutral zone.

topography Variation in the elevation of Earth's surface, in the form of mountains, valleys, ocean basins, and so on.

topsoil The uppermost soil horizon; contains most of the organic matter of soil, but may be depleted of most mineral nutrients by leaching. Also called the A horizon.

totipotent [L. *toto*: whole, entire + *potens*: powerful] Possessing all the genetic information and other capacities necessary to form an entire individual. (Contrast with multipotent, pluripotent.)

toxigenicity The ability of some pathogenic bacteria to produce chemical substances that harm the host.

trachea (tray' kee ah) [Gk. *trakhoia*: tube] (1) In a vertebrate lung, the principal tube leading into the lungs from the mouth cavity. (2) One of the airways in the tracheal breathing system of an insect.

tracheal breathing system The type of breathing system found in insects, in which airways (called tracheae and tracheoles) branch throughout the animal's body so that airways are nearby all cells.

tracheid (tray' kee id) A type of tracheary element found in the xylem of nearly all vascular plants, characterized by tapering ends and walls that are pitted but not perforated. (Contrast with vessel element.)

tract A bundle of axons within a vertebrate central nervous system.

trade-off Any situation in which a gain in one function, outcome, aspect, or amount comes only at the cost of a loss in other functions, outcomes, aspects, or amounts.

trait In genetics, a specific form of a character: eye color is a character; brown eyes and blue eyes are traits. (Contrast with character.)

transcription   The synthesis of RNA using one strand of DNA as a template.

transcription factors   Proteins that assemble on a eukaryotic chromosome, allowing RNA polymerase II to perform transcription.

transcription initiation site   The part of a gene's promoter where synthesis of the gene's RNA transcript begins.

transfection   Insertion of recombinant DNA into animal cells.

transfer RNA (tRNA)   A family of folded RNA molecules. Each tRNA carries a specific amino acid and anticodon that will pair with the complementary codon in mRNA during translation.

transformation   (1) A mechanism for transfer of genetic information in bacteria in which pure DNA from a bacterium of one genotype is taken in through the cell surface of a bacterium of a different genotype and incorporated into the chromosome of the recipient cell. (2) Insertion of recombinant DNA into a host cell.

transgenic   Containing recombinant DNA incorporated into the genetic material.

transition state   In an enzyme-catalyzed reaction, the reactive condition of the substrate after there has been sufficient input of energy (activation energy) to initiate the reaction.

translation   The synthesis of a protein (polypeptide). Takes place on ribosomes, using the information encoded in messenger RNA.

translational repressor   A protein that blocks translation by binding to mRNAs and preventing their attachment to the ribosome. In mammals, the production of ferritin protein is regulated by a translational repressor.

translocation   (1) In genetics, a rare mutational event that moves a portion of a chromosome to a new location, generally on a nonhomologous chromosome. (2) In vascular plants, movement of solutes in the phloem.

transmembrane protein   An integral membrane protein that spans the phospholipid bilayer.

transpiration   [L. *spirare*: to breathe] The evaporation of water from plant leaves and stem, driven by heat from the sun, and providing the motive force to raise water (plus mineral nutrients) from the roots.

transpiration–cohesion–tension mechanism   Theoretical basis for water movement in plants: evaporation of water from cells within leaves (transpiration) causes an increase in surface tension, pulling water up through the xylem. Cohesion of water occurs because of hydrogen bonding.

transposon   Mobile DNA segment that can insert into a chromosome and cause genetic change.

transverse tubules (T tubules) Indentations of the cell membrane at regular intervals over the entire surface of a muscle cell. Transverse tubules conduct electrical excitation into the interior of the cell and thus play a key role in linking electrical excitation with contraction.

triglyceride   A simple lipid in which three fatty acids are combined with one molecule of glycerol.

triploblastic   Having three cell layers. (Contrast with diploblastic.)

tRNA   *See* transfer RNA.

trochophore   (troke' o fore) [Gk. *trochos*: wheel + *phoreus*: bearer] A radially symmetrical larval form typical of annelids and mollusks, distinguished by a wheel-like band of cilia around the middle.

trophic   [Gk *trophes*: nourishment] Referring to feeding.

trophic cascade   Effects of abundances of species at one trophic level on species at other trophic levels. For example, introduction of a tertiary consumer to a community may reduce the population sizes of secondary consumers which it eats, which in turn may increase the population sizes of primary consumers that the secondary consumers eat, which may reduce the population sizes of primary producers that the primary consumers eat.

trophic interactions   The consumer–resource relationships among species in a community.

trophic level   A group of organisms united by obtaining their energy from the same part of the food web of a biological community.

trophoblast   [Gk *trophes*: nourishment + *blastos*: sprout] In mammalian development, the outer group of cells of the blastocyst; will form the chorion and thus become part of the placenta, thereby helping to nourish the growing embryo. (Contrast with inner cell mass.)

tropic hormone   A hormone produced by one endocrine gland that controls the secretion of hormones by another endocrine gland. Also called a tropin.

tropics   The latitudes between the Tropic of Cancer and the Tropic of Capricorn (23.5° north and south, respectively), defined by the region of the planet in which the sun is directly overhead at least once during each annual cycle.

tropin   *See* tropic hormone.

tropomyosin   [troe poe my' oh sin] A muscle protein that controls the interactions of actin and myosin necessary for muscle contraction.

troponin   A muscle protein that controls the interactions of actin and myosin necessary for muscle contraction.

tube feet   A unique feature of echinoderms; extensions of the water vascular system, which functions in gas exchange, locomotion, and feeding.

tubular fluid   In a kidney, fluid flowing through the lumen of one of the tubular structures (e.g., a nephron) of which the kidney is composed.

tubulin   A protein that polymerizes to form microtubules.

tumor necrosis factor   A family of cytokines (growth factors) that causes cell death and is involved in inflammation.

tumor suppressor   A gene that codes for a protein product that inhibits cell proliferation; inactive in cancer cells. (Contrast with oncogene.)

turgor pressure   [L. *turgidus*: swollen] *See* pressure potential.

turnover   In ecology, the change through time or over space in the composition of an ecological community.

Type I error   The incorrect rejection of a true null hypothesis.

Type II error   The incorrect acceptance of a false null hypothesis.

U

ubiquitin   A small protein that is covalently linked to other cellular proteins identified for breakdown by the proteosome.

ultrafiltration   A process of primary urine formation during which fluid moves out of the blood plasma into tubules in the kidney, driven by the force of blood pressure.

ultraviolet wavelengths   Wavelengths in the electromagnetic spectrum that are too short to be seen by the human eye (i.e., shorter than 0.4 μm).

unidirectional ventilation   Forced flow (of water or air) over or through a breathing organ in a single direction from the point of intake to the point of outflow. (Contrast with tidal ventilation.)

unipotent   An undifferentiated cell that is capable of becoming only one type of mature cell. (Contrast with totipotent, multipotent, pluripotent.)

unsaturated fatty acid   A fatty acid whose hydrocarbon chain contains one or more double bonds. (Contrast with saturated fatty acid.)

uracil (U)   A pyrimidine base found in nucleotides of RNA.

ureotelic   Pertaining to an organism in which the principal final product of the breakdown of nitrogen-containing compounds (primarily proteins) is urea. Mammals and most amphibians are ureotelic. (Contrast with ammonotelic, uricotelic.)

uricotelic   Pertaining to an organism in which the principal final product of the breakdown of nitrogen-containing compounds (primarily proteins) is uric acid or other compounds closely related to uric acid. Insects, spiders, birds, and some other reptiles are uricotelic. (Contrast with ammonotelic, ureotelic.)

urine   (you′ rin) The fluid that the kidney produces and excretes from the body.

V

vacuole   (vac′ yew ole) Membrane-enclosed organelle in plant cells that can function for storage, water concentration for turgor, or hydrolysis of stored macromolecules.

van der Waals interactions   Weak attractions between atoms resulting from the interaction of the electrons of one atom with the nucleus of another. This type of attraction is about one-fourth as strong as a hydrogen bond.

variable region   The portion of an immunoglobulin molecule or T cell receptor that includes the antigen-binding site and is responsible for its specificity. (Contrast with constant region.)

vas deferens   (plural: vasa deferentia) In a male mammal, the duct that transfers sperm from the testis and epididymis to the urethra for ejaculation.

vascular bundle   In vascular plants, a strand of vascular tissue, including xylem and phloem as well as thick-walled fibers.

vascular cambium   (kam′ bee um) [L. *cambiare*: to exchange] In plants, a lateral meristem that gives rise to secondary xylem and phloem.

vascular endothelium   In the walls of all blood vessels, the layer of cells—a simple epithelium—that immediately surrounds the blood.

vascular system   All the blood vessels of the circulatory system. (*See also* cardiovascular system.)

vascular tissue system   The transport system of a vascular plant, consisting primarily of xylem and phloem. (Contrast with dermal tissue system, ground tissue system.)

vasomotor control   Related to changes in the inside (luminal) diameters of blood vessels mediated by contraction and relaxation of smooth muscles in the blood vessel walls. Changes in inside diameter have large effects on rate of blood flow through a vessel.

vasopressin   *See* antidiuretic hormone.

vector   (1) An agent, such as an insect, that carries a pathogen affecting another species. (2) A plasmid or virus that carries an inserted piece of DNA into a bacterium for cloning purposes in recombinant DNA technology.

vegetal hemisphere   The yolky portion of some animal eggs. (Contrast with animal hemisphere.)

vegetative cells   (1) Generally: non-reproductive cells. (2) The photosynthesizing cells of a cyanobacterial colony.

vegetative reproduction   Asexual reproduction through the modification of stems, leaves, or roots.

vein   [L. *vena*: channel] A blood vessel that returns blood to the heart. (Contrast with artery.)

ventilation   Forced flow of air or water over or through structures used for breathing (external respiration) or over body surfaces used for external respiration.

ventral   [L. *venter*: belly, womb] Toward or pertaining to the belly or lower side. (Contrast with dorsal.)

ventricle   In reference to a heart, the principal pumping chamber. The walls of the ventricle are highly muscular, composed of cardiac muscle.

vernalization   [L. *vernalis*: spring] Events occurring during a required chilling period, leading eventually to flowering.

vertebral column   [L. *vertere*: to turn] The jointed, dorsal column that is the primary support structure of vertebrates.

vesicle   Within the cytoplasm, a membrane-enclosed compartment that is associated with other organelles; the Golgi complex is one example.

vessel element   A type of tracheary element with perforated end walls; found only in angiosperms. (Contrast with tracheid.)

villus   (vil′ lus) (plural: villi) [L. *villus*: shaggy hair or beard] A hairlike projection from a membrane; for example, the gut wall is often covered with villi that increase its surface area.

virus   Any of a group of ultramicroscopic particles constructed of nucleic acid and protein (and, sometimes, lipid) that require living cells in order to reproduce. Viruses evolved multiple times from different cellular species.

visceral mass   A centralized, internal portion of a mollusk's body that contains the heart as well as digestive, excretory, and reproductive organs.

vitamin   [L. *vita*: life] A carbon compound that an organism cannot synthesize, but nevertheless requires in small quantities for normal growth and health.

voltage   A measure of the difference in electrical charge between two points. Also called potential difference.

voltage-gated channel   A type of gated channel protein, located in a cell membrane, that opens or closes in response to changes in the local membrane potential.

W

water channel protein   *See* aquaporin.

water potential (psi, Ψ)   In osmosis, the tendency for a system (a cell or solution) to take up water from pure water through a differentially permeable membrane. Water flows toward the system with a more negative water potential. (Contrast with solute potential, pressure potential.)

water vascular system   In echinoderms, a network of water-filled canals that functions in gas exchange, locomotion, and feeding.

wavelength   The distance between successive peaks of a wave train, such as electromagnetic radiation.

weather   The atmospheric conditions of temperature, humidity, precipitation, and wind speed and direction experienced at a given place and time. (Contrast with climate.)

white blood cells   Cells in the blood plasma that play defensive roles in the immune system. Also called leukocytes.

white matter   In the nervous system, tissue that is rich in myelinated axons and therefore has a glistening white appearance.

wild type   Geneticists' term for standard or reference type. Deviants from this standard, even if the deviants are found in the wild, are usually referred to as mutant. (Note that this terminology is not usually applied to human genes.)

wood   Secondary xylem tissue.

X

xeric   Referring to terrestrial animals, those that are able to live steadily in the open air and thus face the full drying power of the terrestrial environment.

xerophyte   (zee′ row fyte) [Gk. *xerox*: dry + *phyton*: plant] A plant adapted to an environment with limited water supply.

xylem   (zy′ lum) [Gk. *xylon*: wood] In vascular plants, the tissue that conducts water and minerals; xylem consists,

in various plants, of tracheids, vessel elements, fibers, and other highly specialized cells.

Y

yolk sac   In reptiles (including birds) and mammals, the extraembryonic membrane that forms from the endoderm and lateral plate mesoderm and surrounds the yolk. First source of blood and blood vessels. During development, the yolk sac digests the yolk, and its blood vessels carry products to the embryo.

Z

zeaxanthin   A blue-light receptor involved in the opening of plant stomata.

zone of cell division   The apical and primary meristems of a plant root; the source of all cells of the root's primary tissues.

zone of cell elongation   The part of a plant root, generally above the zone of cell division, where cells are expanding (growing), primarily in the longitudinal direction.

zone of cell maturation   The part of a plant root, generally above the zone of cell elongation, where cells are differentiating.

zygospore   Multinucleate, diploid cell that is a resting stage in the life cycle of zygospore fungi.

zygote   (zye' gote) [Gk. *zygotos*: yoked] The fertilized egg. The cell created by the union of two gametes, in which the gamete nuclei are fused. The earliest stage of the diploid generation.

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