33

An Introduction to Invertebrates

▲ **Figure 33.1 What function do the red whorls of this organism have?**

EVOLUTION

KEY CONCEPTS

- **33.1 Sponges are basal animals that lack true tissues**
- **33.2 Cnidarians are an ancient phylum of eumetazoans**
- **33.3 Lophotrochozoans, a clade identified by molecular data, have the widest range of animal body forms**
- **33.4 Ecdysozoans are the most species-rich animal group**
- **33.5 Echinoderms and chordates are deuterostomes**

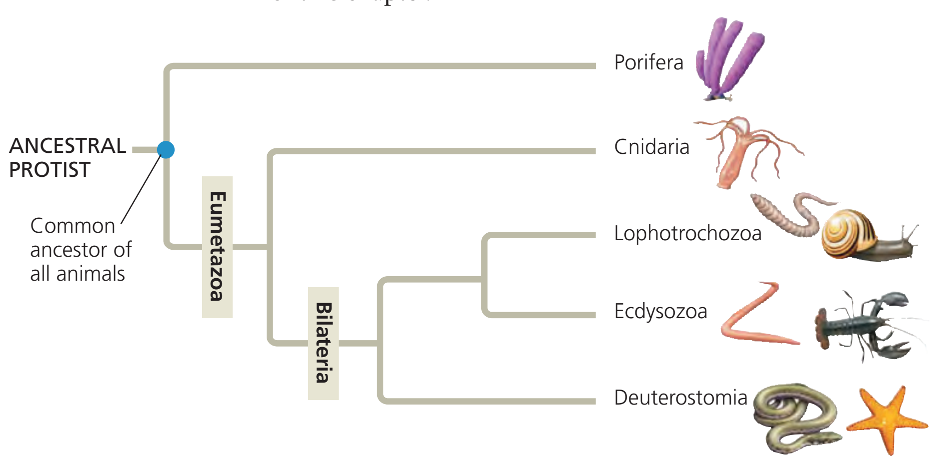
OVERVIEW

Life Without a Backbone

At first glance, you might mistake the organism shown in **Figure 33.1** for a type of seaweed. But this colorful inhabitant of coral reefs is actually an animal, not an alga. Specifically, it is a species of segmented worm known as a Christmas tree worm (*Spirobranchus giganteus*). The two tree-shaped whorls are tentacles, which the worm uses for gas exchange and for removing small food particles from the surrounding water. The tentacles emerge from a tube of calcium carbonate secreted by the worm that protects and supports its soft body. Light-sensitive structures on the tentacles can detect the shadow cast by a predator, triggering the worm to contract muscles that rapidly withdraw the tentacles into the tube.

Christmas tree worms are **invertebrates**—animals that lack a backbone. Invertebrates account for 95% of known animal species. They occupy almost every habitat on Earth, from the scalding water released by deep-sea hydrothermal vents to the rocky, frozen ground of Antarctica. Adaptation to these varied environments has produced an immense diversity of forms, ranging from a species consisting of a flat bilayer of cells to other species with features such as silk-spinning glands, pivoting spines, and tentacles covered with suction cups. Invertebrate species also show enormous variation in size, from microscopic organisms to organisms that can grow to 18 m long (1.5 times the length of a school bus).

In this chapter, we'll take a tour of the invertebrate world, using the phylogenetic tree in **Figure 33.2** as a guide. **Figure 33.3**, on the next three pages, surveys 23 invertebrate phyla. Serving as representatives of invertebrate diversity, many of those phyla are explored in more detail in the rest of this chapter.



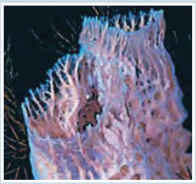
▲ **Figure 33.2 Review of animal phylogeny.** Except for sponges (basal animals in phylum Porifera) and a few other groups, all animals have tissues and are in the clade Eumetazoa. Most animals are in the diverse clade Bilateria. The evolutionary tree shown here provides an overview of material covered in Chapter 32 but omits many groups; for a more complete view of animal relationships, see Figure 32.11.

▼ Figure 33.3

Exploring Invertebrate Diversity

Kingdom Animalia encompasses 1.3 million known species, and estimates of total species range as high as 10–20 million species. Of the 23 phyla surveyed here, 12 are discussed more fully in this chapter, Chapter 32, or Chapter 34; cross-references are given at the end of their descriptions.

Porifera (5,500 species)


A sponge

Animals in this phylum are informally called sponges. Sponges are sessile animals that lack true tissues. They live as suspension feeders, trapping particles that pass through the internal channels of their body (see Concept 33.1).

Cnidaria (10,000 species)

Cnidarians include corals, jellies, and hydras. These animals have a diploblastic, radially symmetrical body plan that includes a gastrovascular cavity with a single opening that serves as both mouth and anus (see Concept 33.2).


A jelly

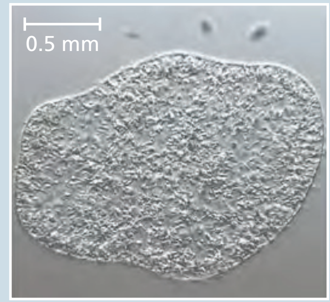
Acoela (400 species)

Acoel flatworms (LM)

Acoel flatworms have a simple nervous system and a saclike gut, and thus were once placed in phylum Platyhelminthes. Molecular analyses, however, indicate that Acoela is a separate lineage that diverged before the three main bilaterian clades (see Concept 32.4).

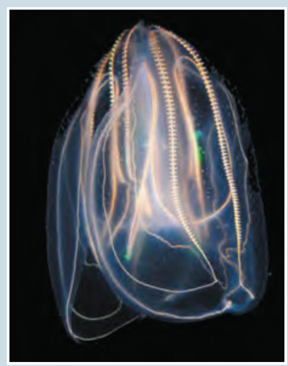
Placozoa (1 species)

The single known species in this phylum, *Trichoplax adhaerens*, doesn't even look like an animal. It consists of a simple bilayer of a few thousand cells. Placozoans are thought to be basal animals, but it is not yet known how they are related to other early-diverging animal groups such as Porifera and Cnidaria. *Trichoplax* can reproduce by dividing into two individuals or by budding off many multicellular individuals.



A placozoan (LM)

Ctenophora (100 species)


A ctenophore, or comb jelly

Ctenophores (comb jellies) are diploblastic and radially symmetrical like cnidarians, suggesting that both phyla diverged from other animals very early (see Figure 32.11). Comb jellies make up much of the ocean's plankton. They have many distinctive traits, including eight "combs" of cilia that propel the animals through the water. When a small animal contacts the tentacles of some comb jellies, specialized cells burst open, covering the prey with sticky threads.

Lophotrochozoa

Platyhelminthes (20,000 species)


A marine flatworm

Flatworms (including tapeworms, planarians, and flukes) have bilateral symmetry and a central nervous system that processes information from sensory structures. They have no body cavity or organs for circulation (see Concept 33.3).

Rotifera (1,800 species)

Despite their microscopic size, rotifers have specialized organ systems, including an *alimentary canal* (a digestive tract with both a mouth and an anus). They feed on microorganisms suspended in water (see Concept 33.3).

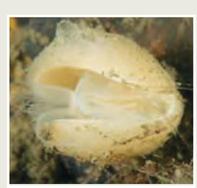
A rotifer (LM)

Ectoprocta (4,500 species)

Ectoprocts (also known as bryozoans) live as sessile colonies and are covered by a tough exoskeleton (see Concept 33.3).

Ectoprocts

Brachiopoda (335 species)


A brachiopod

Brachiopods, or lamp shells, may be easily mistaken for clams or other molluscs. However, most brachiopods have a unique stalk that anchors them to their substrate, as well as a crown of cilia called a lophophore (see Concept 33.3).

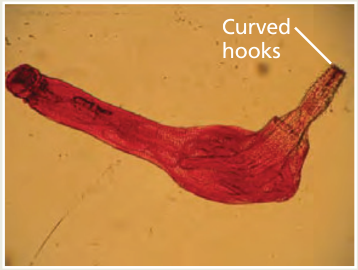
Continued on next page

▼ **Figure 33.3 (continued)**

Exploring Invertebrate Diversity

Lophotrochozoa (continued)

Acanthocephala (1,100 species)



An acanthocephalan (LM)

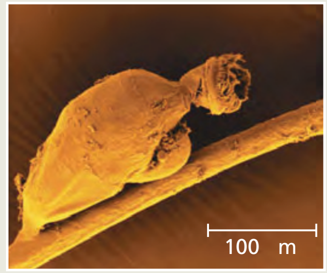
Acanthocephalans are called spiny-headed worms because of the curved hooks on the proboscis at the anterior end of their body. All species are parasites. Some acanthocephalans manipulate the behavior of their intermediate hosts (generally arthropods) in ways that increase their chances of reaching their final hosts (generally vertebrates). For example, acanthocephalans that infect New Zealand mud crabs force their hosts to move to more visible areas on the beach, where the crabs are more likely to be eaten by birds, the worms' final hosts. Some phylogenetic analyses place the acanthocephalans within Rotifera.

Nemertea (900 species)

A ribbon worm

Also called proboscis worms or ribbon worms, nemerteans swim through water or burrow in sand, extending a unique proboscis to capture prey. Like flatworms, they lack a true coelom. However, unlike flatworms, nemerteans have an alimentary canal and a closed circulatory system in which the blood is contained in vessels and hence is distinct from fluid in the body cavity.

Cycliophora (1 species)



A cycliophoran (colorized SEM)

The only known cycliophoran species, *Symbion pandora*, was discovered in 1995 on the mouthparts of a lobster. This tiny, vase-shaped creature has a unique body plan and a particularly bizarre life cycle. Males impregnate females that are still developing in their mothers' bodies. The fertilized females then escape, settle elsewhere on the lobster, and release their offspring. The offspring apparently leave that lobster and search for another one to which they attach.

Annelida (16,500 species)

Annelids, or segmented worms, are distinguished from other worms by their body segmentation. Earthworms are the most familiar annelids, but the phylum consists primarily of marine and freshwater species (see Concept 33.3).

A marine annelid

Mollusca (93,000 species)

Molluscs (including snails, clams, squids, and octopuses) have a soft body that in many species is protected by a hard shell (see Concept 33.3).

An octopus

Ecdysozoa

Loricifera (10 species)

Loriciferans (from the Latin *lorica*, corset, and *ferre*, to bear) are tiny animals that inhabit the deep-sea bottom. A loriciferan can telescope its head, neck, and thorax in and out of the lorica, a pocket formed by six plates surrounding the abdomen. Though the natural history of loriciferans is mostly a mystery, at least some species likely eat bacteria.

A loriciferan (LM)

Priapula (16 species)

A priapulan

Priapulans are worms with a large, rounded proboscis at the anterior end. (They are named after Priapos, the Greek god of fertility, who was symbolized by a giant penis.) Ranging from 0.5 mm to 20 cm in length, most species burrow through seafloor sediments. Fossil evidence suggests that priapulans were among the major predators during the Cambrian period.

Ecdysozoa (continued)

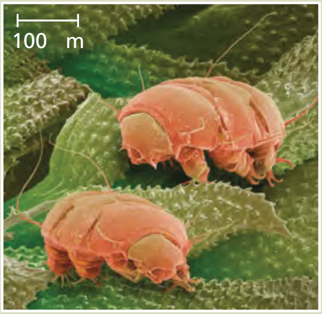
Onychophora (110 species)

An onychophoran

Onychophorans, also called velvet worms, originated during the Cambrian explosion (see Chapter 32). Originally, they thrived in the ocean, but at some point they succeeded in colonizing land. Today they live only in humid forests. Onychophorans have fleshy antennae and several dozen pairs of saclike legs.

Tardigrada (800 species)

Tardigrades (from the Latin *tardus*, slow, and *gradus*, step) are sometimes called water bears for their rounded shape, stubby appendages, and lumbering, bearlike gait. Most tardigrades are less than 0.5 mm in length. Some live in oceans or fresh water, while others live on plants or animals. As many as 2 million tardigrades can be found on a square meter of moss. Harsh conditions may cause tardigrades to enter a state of dormancy; while dormant, they can survive temperatures as low as −272°C, close to absolute zero!



Tardigrades (colorized SEM)

Nematoda (25,000 species)

A roundworm (colored SEM)

Also called roundworms, nematodes are enormously abundant and diverse in the soil and in aquatic habitats; many species parasitize plants and animals. Their most distinctive feature is a tough cuticle that coats the body (see Concept 33.4).

Arthropoda (1,000,000 species)

The vast majority of known animal species, including insects, crustaceans, and arachnids, are arthropods. All arthropods have a segmented exoskeleton and jointed appendages (see Concept 33.4).

A scorpion (an arachnid)

Deuterostomia

Hemichordata (85 species)

An acorn worm

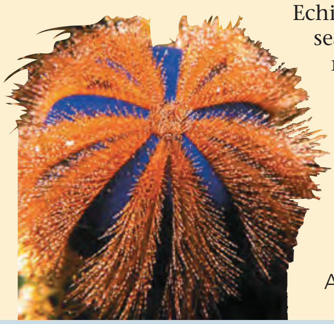
Like echinoderms and chordates, hemichordates are members of the deuterostome clade (see Chapter 32). Hemichordates share some traits with chordates, such as gill slits and a dorsal nerve cord. The largest group of hemichordates is the enteropneusts, or acorn worms. Acorn worms are marine and generally live buried in mud or under rocks; they may grow to more than 2 m in length.

Chordata (52,000 species)

More than 90% of all known chordate species have backbones (and thus are vertebrates). However, the phylum Chordata also includes three groups of invertebrates: lancelets, tunicates, and hagfishes. See Chapter 34 for a full discussion of this phylum.

A tunicate

Echinodermata (7,000 species)

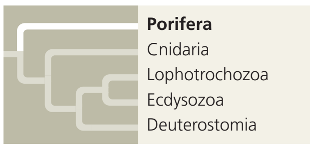


Echinoderms, such as sand dollars, sea stars, and sea urchins, are marine animals in the deuterostome clade that are bilaterally symmetrical as larvae but not as adults. They move and feed by using a network of internal canals to pump water to different parts of their body (see Concept 33.5).

A sea urchin

CONCEPT 33.1

Sponges are basal animals that lack true tissues

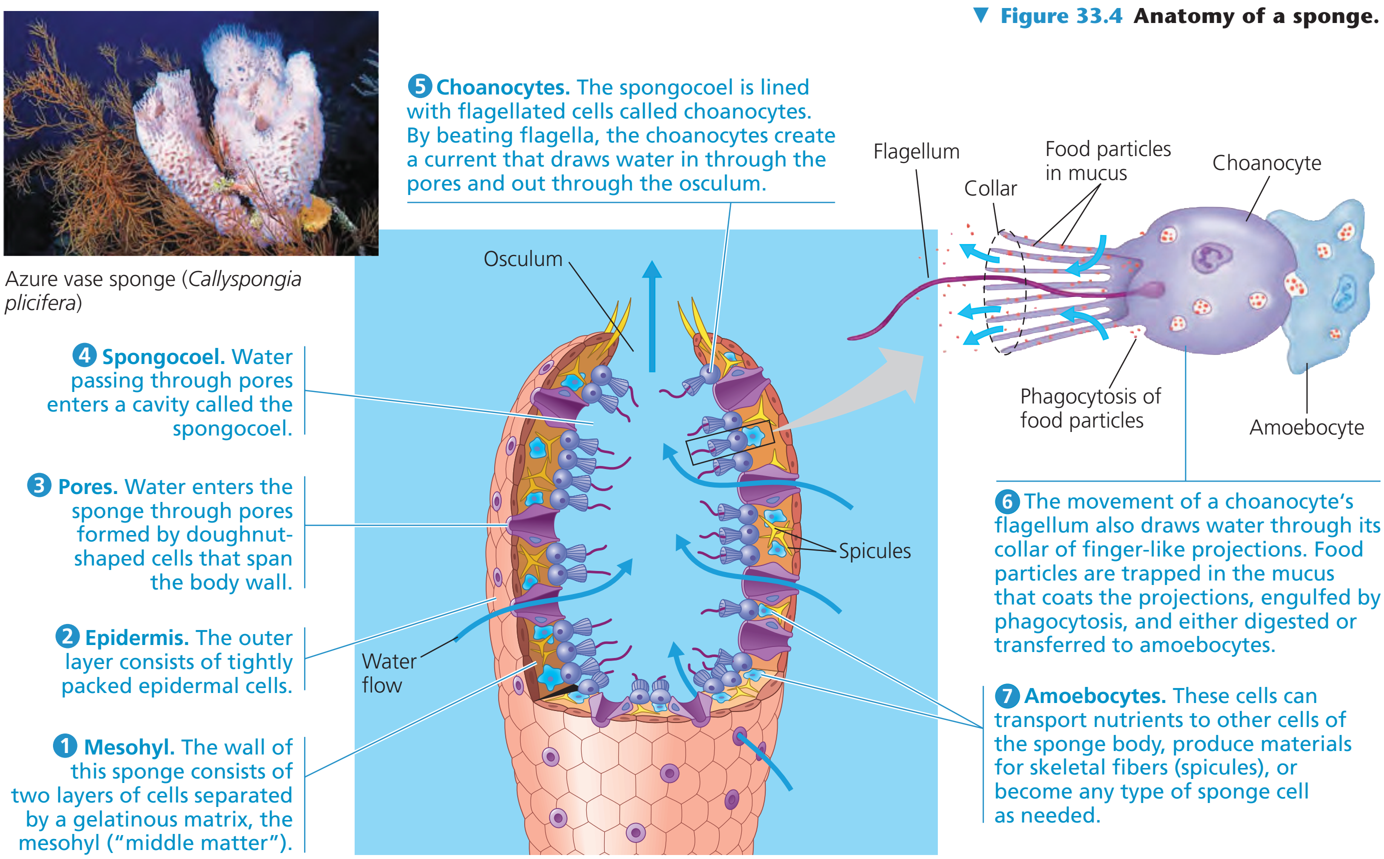


Animals in the phylum Porifera are known informally as sponges. (Recent molecular studies indicate that sponges are monophyletic, and that is the phylogeny we follow here; this remains under debate, however, as some studies suggest that sponges are paraphyletic.) Among the simplest of animals, sponges are sedentary and were mistaken for plants by the ancient Greeks. They range in size from a few millimeters to a few meters, and most species are marine, though a few live in fresh water. Sponges are **suspension feeders**: They capture food particles suspended in the water that passes through their body, which in some species resembles a sac perforated with pores. Water is drawn through the pores into a central cavity, the **spongocoel**, and then flows out of the sponge through a larger opening called the **osculum** **(Figure 33.4)**. More complex sponges have folded body walls, and many contain branched water canals and several oscula.

Sponges are basal animals; that is, they represent a lineage that originates near the root of the phylogenetic tree of animals. Unlike nearly all other animals, sponges lack true tissues, groups of similar cells that act as a functional unit and are isolated from other tissues by membranous layers. However, the sponge body does contain several different cell types. For example, lining the interior of the spongocoel are flagellated **choanocytes**, or collar cells (named for the finger-like projections that form a "collar" around the flagellum). These cells engulf bacteria and other food particles by phagocytosis. The similarity between choanocytes and the cells of choanoflagellates supports molecular evidence suggesting that animals evolved from a choanoflagellate-like ancestor (see Figure 32.3).

The body of a sponge consists of two layers of cells separated by a gelatinous region called the **mesohyl**. Because both cell layers are in contact with water, processes such as gas exchange and waste removal can occur by diffusion across the membranes of these cells. Other tasks are performed by cells called **amoebocytes**, named for their use of pseudopodia. These cells move through the mesohyl and have many functions. For example, they take up food from the surrounding water and from choanocytes, digest it, and carry nutrients to other cells. Amoebocytes also manufacture tough skeletal fibers within the mesohyl. In some sponges, these fibers are sharp spicules made from calcium carbonate or silica. Other sponges produce more flexible fibers composed of a protein called spongin; you may have seen these pliant skeletons

▼ **Figure 33.4 Anatomy of a sponge.**



being sold as brown bath sponges. Finally, and perhaps most importantly, amoebocytes are capable of becoming other types of sponge cells. This gives the sponge body remarkable flexibility, enabling it to adjust its shape in response to changes in its physical environment (such as the direction of water currents).

Most sponges are **hermaphrodites**, meaning that each individual functions as both male and female in sexual reproduction by producing sperm *and* eggs. Almost all sponges exhibit sequential hermaphroditism: They function first as one sex and then as the other.

Sponge gametes arise from choanocytes or amoebocytes. Eggs reside in the mesohyl, but sperm are carried out of the sponge by the water current. Cross-fertilization results from some of the sperm being drawn into neighboring individuals. Fertilization occurs in the mesohyl, where the zygotes develop into flagellated, swimming larvae that disperse from the parent sponge. After settling on a suitable substrate, a larva develops into a sessile adult.

Sponges produce a variety of antibiotics and other defensive compounds. Researchers are now isolating these compounds, which hold promise for fighting human diseases. For example, a compound called cribrostatin isolated from marine sponges can kill penicillin-resistant strains of the bacterium *Streptococcus*. Other sponge-derived compounds are being tested as possible anticancer agents.

CONCEPT CHECK 33.1

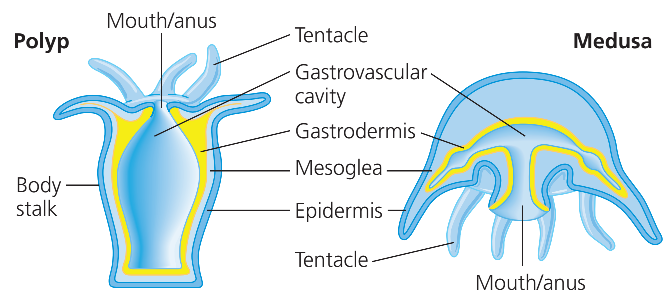
1. Describe how sponges feed.
2. **WHAT IF?** Some molecular evidence suggests that the sister group of animals is not the choanoflagellates, but rather a group of parasitic protists, Mesomycetozoa. Given that these parasites lack collar cells, can this hypothesis be correct? Explain.

For suggested answers, see Appendix A.

CONCEPT 33.2

Cnidarians are an ancient phylum of eumetazoans

All animals except sponges and a few other groups belong to the clade Eumetazoa, animals with true tissues (see Chapter 32). One of the oldest lineages in this clade is the phylum Cnidaria. Cnidarians have diversified into a wide range of sessile and motile forms, including hydras, corals, and jellies (commonly called "jellyfish"). Yet most cnidarians still exhibit the relatively simple, diploblastic, radial body plan that existed in early members of the group some 560 million years ago.

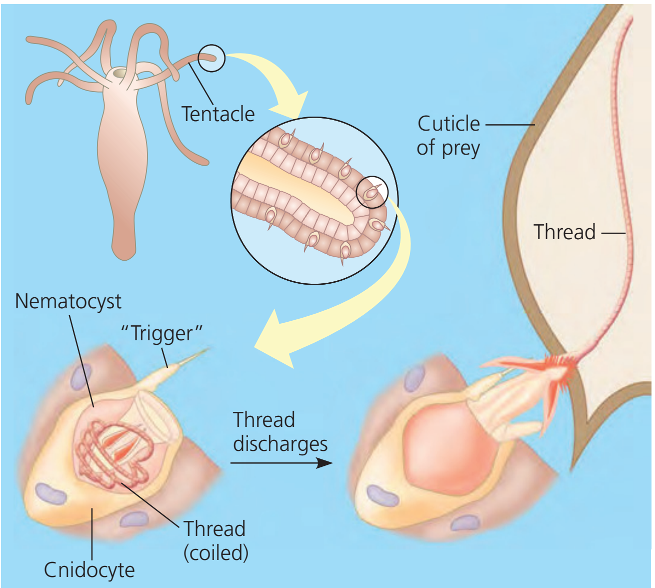


▲ **Figure 33.5 Polyp and medusa forms of cnidarians.** The body wall of a cnidarian has two layers of cells: an outer layer of epidermis (darker blue; derived from ectoderm) and an inner layer of gastrodermis (yellow; derived from endoderm). Digestion begins in the gastrovascular cavity and is completed inside food vacuoles in the gastrodermal cells. Flagella on the gastrodermal cells keep the contents of the gastrovascular cavity agitated and help distribute nutrients. Sandwiched between the epidermis and gastrodermis is a gelatinous layer, the mesoglea.

The basic body plan of a cnidarian is a sac with a central digestive compartment, the **gastrovascular cavity**. A single opening to this cavity functions as both mouth and anus. There are two variations on this body plan: the sessile polyp and the motile medusa **(Figure 33.5)**. **Polyps** are cylindrical forms that adhere to the substrate by the aboral end of their body (the end opposite the mouth) and extend their tentacles, waiting for prey. Examples of the polyp form include hydras and sea anemones. A **medusa** (plural, *medusae*) resembles a flattened, mouth-down version of the polyp. It moves freely in the water by a combination of passive drifting and contractions of its bell-shaped body. Medusae include free-swimming jellies. The tentacles of a jelly dangle from the oral surface, which points downward. Some cnidarians exist only as polyps or only as medusae; others have both a polyp stage and a medusa stage in their life cycle.

Cnidarians are carnivores that often use tentacles arranged in a ring around their mouth to capture prey and push the food into their gastrovascular cavity, where digestion begins. Enzymes are secreted into the cavity, thus breaking down the prey into a nutrient-rich broth. Cells lining the cavity then absorb these nutrients and complete the digestive process; any undigested remains are expelled through the mouth/anus. The tentacles are armed with batteries of **cnidocytes**, cells unique to cnidarians that function in defense and prey capture **(Figure 33.6)**. Cnidocytes contain *cnidae* (from the Greek *cnide*, nettle), capsule-like organelles that are capable of exploding outward and that give phylum Cnidaria its name. Specialized cnidae called **nematocysts** contain a stinging thread that can penetrate the body wall of the cnidarian's prey. Other kinds of cnidae have long threads that stick to or entangle small prey that bump into the cnidarian's tentacles.

Contractile tissues and nerves occur in their simplest forms in cnidarians. Cells of the epidermis (outer layer) and gastrodermis (inner layer) have bundles of microfilaments arranged into contractile fibers (see Chapter 6). The gastrovascular



▲ **Figure 33.6 A cnidocyte of a hydra.** This type of cnidocyte contains a stinging capsule, the nematocyst, which contains a coiled thread. When a "trigger" is stimulated by touch or by certain chemicals, the thread shoots out, puncturing and injecting poison into prey.

cavity acts as a hydrostatic skeleton (see Concept 50.6) against which the contractile cells can work. When a cnidarian closes its mouth, the volume of the cavity is fixed, and contraction of selected cells causes the animal to change shape. Movements are coordinated by a nerve net. Cnidarians have no brain, and the noncentralized nerve net is associated with sensory structures that are distributed around the body. Thus, the animal can detect and respond to stimuli from all directions.

The phylum Cnidaria is divided into four major clades: Hydrozoa, Scyphozoa, Cubozoa, and Anthozoa **(Figure 33.7)**.

Hydrozoans

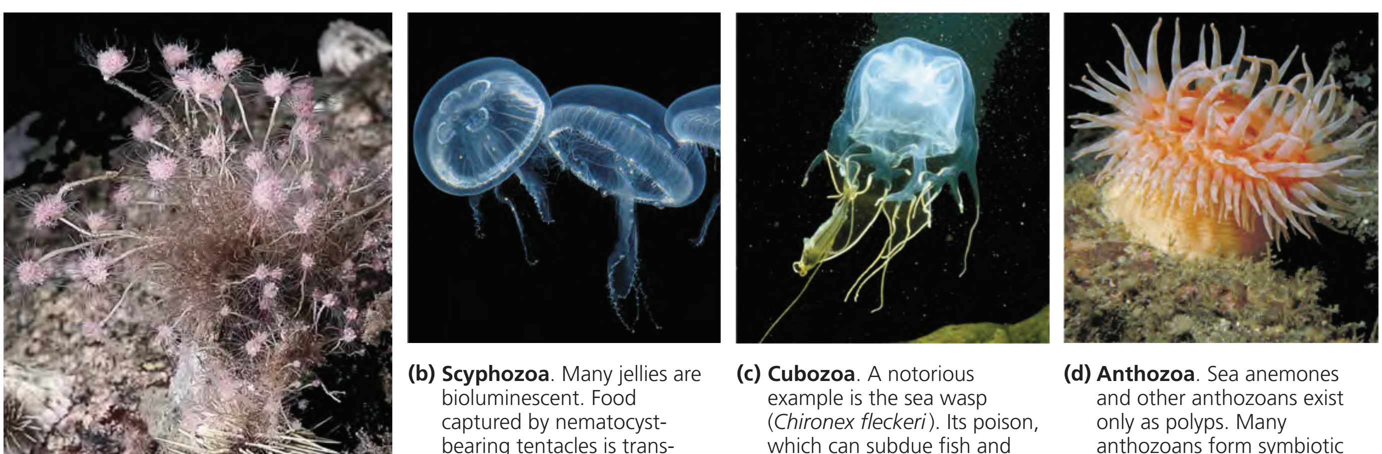
Most hydrozoans alternate between the polyp and medusa forms, as seen in the life cycle of *Obelia* **(Figure 33.8)**. The polyp stage, a colony of interconnected polyps in the case of *Obelia*, is more conspicuous than the medusa. Hydras, among the few cnidarians found in fresh water, are unusual hydrozoans in that they exist only in polyp form. When environmental conditions are favorable, a hydra reproduces asexually by budding, forming outgrowths that pinch off from the parent and live independently (see Figure 13.2). When conditions deteriorate, hydras can reproduce sexually, forming resistant zygotes that remain dormant until conditions improve.

Scyphozoans

The medusa is the predominant stage in the life cycle of most scyphozoans. The medusae of most species live among the plankton as jellies. Most coastal scyphozoans go through a stage as small polyps during their life cycle, whereas those that live in the open ocean generally lack the polyp stage altogether.

Cubozoans

As their name (which means "cube animals") suggests, cubozoans have a box-shaped medusa stage. Cubozoans can be distinguished from scyphozoans in other ways, such as having complex eyes embedded in the fringe of their medusae. They also are comparatively strong swimmers and as a result are less likely to be stranded on shore. Most cubozoans live in tropical oceans and are equipped with highly toxic cnidocytes. The sea wasp (*Chironex fleckeri*), a cubozoan that lives off the coast of northern Australia, is one of the deadliest organisms known: Its sting causes intense pain and can lead to respiratory failure, cardiac arrest, and death within minutes. The poison of sea wasps isn't universally fatal, however; sea turtles have defenses against it, allowing them to eat the cubozoan in great quantities.



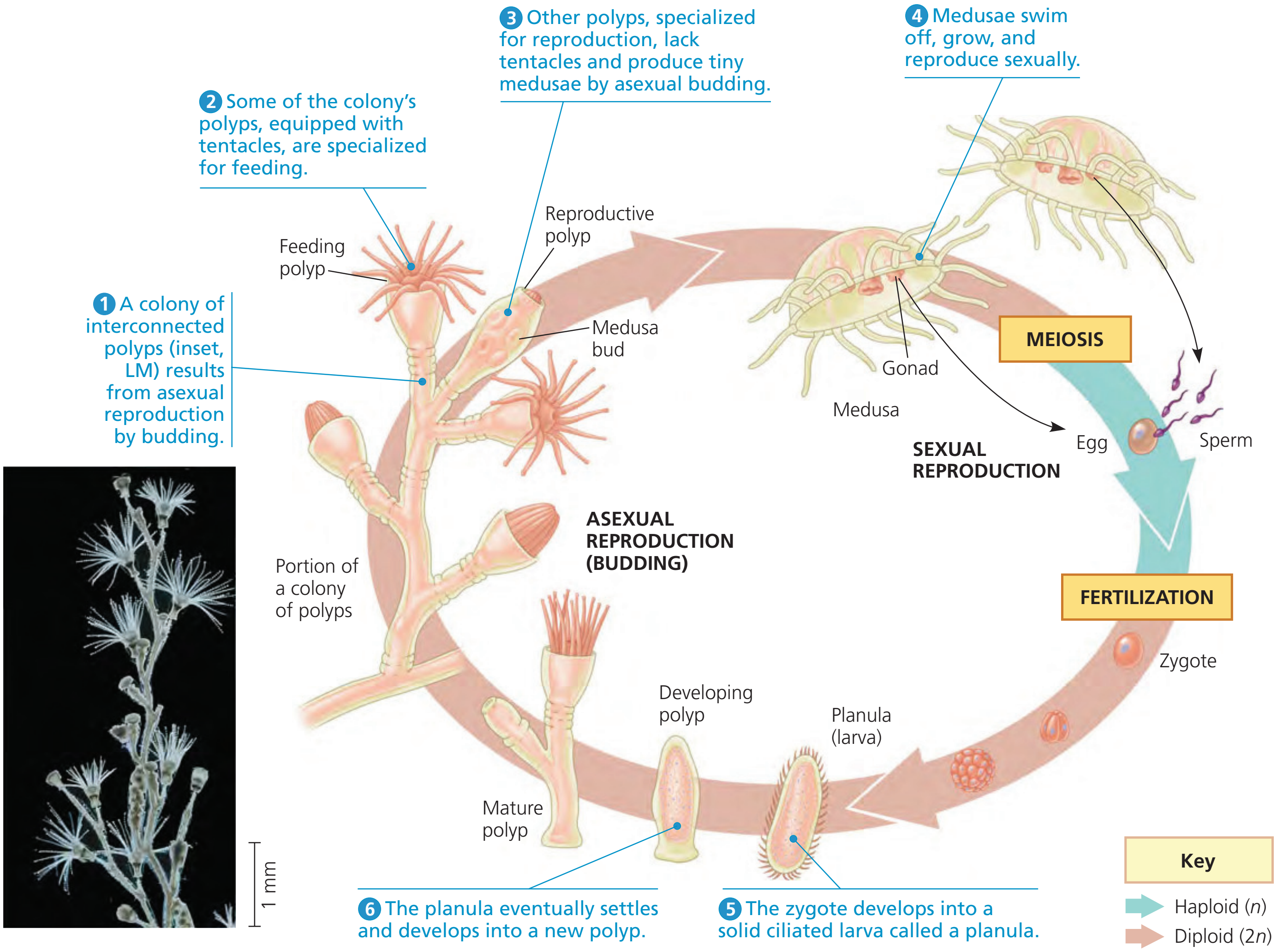
(a) Hydrozoa. Some species, such as this one, live as colonial polyps.

(b) Scyphozoa. Many jellies are bioluminescent. Food captured by nematocyst-bearing tentacles is transferred to specialized oral arms (that lack nematocysts) for transport to the mouth.

(c) Cubozoa. A notorious example is the sea wasp (*Chironex fleckeri*). Its poison, which can subdue fish and other large prey, is more potent than cobra venom.

(d) Anthozoa. Sea anemones and other anthozoans exist only as polyps. Many anthozoans form symbiotic relationships with photosynthetic algae.

▲ **Figure 33.7 Cnidarians.**



▲ **Figure 33.8 The life cycle of the hydrozoan *Obelia*.** The polyp is asexual, and the medusa is sexual, releasing eggs and sperm. These two stages alternate, one producing the other. Do not confuse this with the alternation of generations that occurs in plants and some algae: In *Obelia,* both the polyp and the medusa are diploid organisms. Typical of animals, only the single-celled gametes are haploid. By contrast, plants have a multicellular haploid generation and a multicellular diploid generation.

WHAT IF? *Suppose that* Obelia *medusae and gametes were haploid, but all other stages were diploid. What aspects of its actual life cycle would have to change for this to occur?*

Anthozoans

Sea anemones (see Figure 33.7d) and corals belong to the clade Anthozoa (meaning "flower animals"). These cnidarians occur only as polyps. Corals live as solitary or colonial forms, often forming symbioses with algae (see Chapter 28). Many species secrete a hard external skeleton of calcium carbonate. Each polyp generation builds on the skeletal remains of earlier generations, constructing "rocks" with shapes characteristic of their species. These skeletons are what we usually think of as coral.

Coral reefs are to tropical seas what rain forests are to tropical land areas: They provide habitat for many other species. Unfortunately, these reefs are being destroyed at an alarming rate. Pollution and overfishing are major threats, and global warming may also be contributing to their demise by raising seawater temperatures above the narrow range in which corals thrive.

CONCEPT CHECK 33.2

1. Compare and contrast the polyp and medusa forms of cnidarians.
2. Describe the structure and function of the stinging cells for which cnidarians are named.
3. **MAKE CONNECTIONS** As you read in Concept 25.3 (pp. 518–519), many new animal body plans emerged during and after the Cambrian explosion. In contrast, cnidarians today retain the same diploblastic, radial body plan found in cnidarians 560 million years ago. Are cnidarians therefore less successful or less "highly evolved" than other animal groups? Explain. (See also Concept 25.6, pp. 529–530.)

For suggested answers, see Appendix A.

CONCEPT 33.3

Lophotrochozoans, a clade identified by molecular data, have the widest range of animal body forms

The vast majority of animal species belong to the clade Bilateria, whose members exhibit bilateral symmetry and triploblastic development (see Chapter 32). Most bilaterians also have a digestive tract with two openings (a mouth and an anus) and a coelom. While the sequence of bilaterian evolution is a subject of active investigation, the most recent common ancestor of living bilaterians probably existed in the late Proterozoic eon (about 575 million years ago). Many of the major groups of bilaterians first appeared in the fossil record during the Cambrian explosion.

As you read in Chapter 32, molecular evidence suggests that there are three major clades of bilaterally symmetrical animals: Lophotrochozoa, Ecdysozoa, and Deuterostomia. This section will focus on the first of these clades, the lophotrochozoans. Concepts 33.4 and 33.5 will explore the other two clades.

Although the clade Lophotrochozoa was identified by molecular data, its name comes from features found in some of its members. Some lophotrochozoans develop a structure called a *lophophore*, a crown of ciliated tentacles that functions in feeding, while others go through a distinctive stage called the *trochophore larva* (see Figure 32.13). Other members of the group have neither of these features. Few other unique morphological features are widely shared within the group—in fact, the lophotrochozoans are the most diverse bilaterian clade in terms of body plan. This diversity in form is reflected in the number of phyla classified in the group: Lophotrochozoa includes about 18 phyla, more than twice the number in any other clade of bilaterians.

We'll now introduce six diverse lophotrochozoan phyla: the flatworms, rotifers, ectoprocts, brachiopods, molluscs, and annelids.

Flatworms

Flatworms (phylum Platyhelminthes) live in marine, freshwater, and damp terrestrial habitats. In addition to free-living species, flatworms include many parasitic species, such as flukes and tapeworms. Flatworms are so named because they have thin bodies that are flattened dorsoventrally (between the dorsal and ventral surfaces); the word *platyhelminth* means "flat worm." (Note that *worm* is not a formal taxonomic name but rather refers to a grade of animals with long, thin bodies.) The smallest flatworms are nearly microscopic free-living species, while some tapeworms are more than 20 m long.

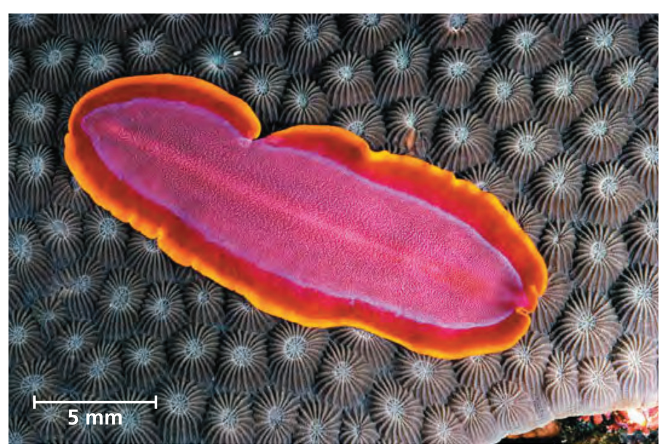
Although flatworms undergo triploblastic development, they are acoelomates (animals that lack a body cavity). Their flat shape places all their cells close to water in the surrounding environment or in their gut. Because of this proximity to water, gas exchange and the elimination of nitrogenous waste (ammonia) can occur by diffusion across the body surface. Flatworms have no organs specialized for gas exchange, and their relatively simple excretory apparatus functions mainly to maintain osmotic balance with their surroundings. This apparatus consists of **protonephridia**, networks of tubules with ciliated structures called *flame bulbs* that pull fluid through branched ducts opening to the outside (see Figure 44.11). Most flatworms have a gastrovascular cavity with only one opening. Though flatworms lack a circulatory system, the fine branches of the gastrovascular cavity distribute food directly to the animal's cells.

Early in their evolutionary history, flatworms separated into two lineages, Catenulida and Rhabditophora. Catenulida is a small clade of about 100 flatworm species, most of which live in freshwater habitats. Catenulids typically reproduce asexually by budding at their posterior end. The offspring often produce their own buds before detaching from the parent, thereby forming a chain of two to four genetically identical individuals—hence their informal name, "chain worms."

The other ancient flatworm lineage, Rhabditophora, is a diverse clade of about 20,000 freshwater and marine species, one example of which is shown in **Figure 33.9**. We'll explore this group in more detail, focusing on free-living and parasitic members of this clade.

Free-Living Species

Free-living rhabditophorans are important as predators and scavengers in a wide range of freshwater and marine habitats. The best-known members of this group are freshwater species in the genus *Dugesia*, commonly called **planarians**. Abundant in unpolluted ponds and streams, planarians prey on



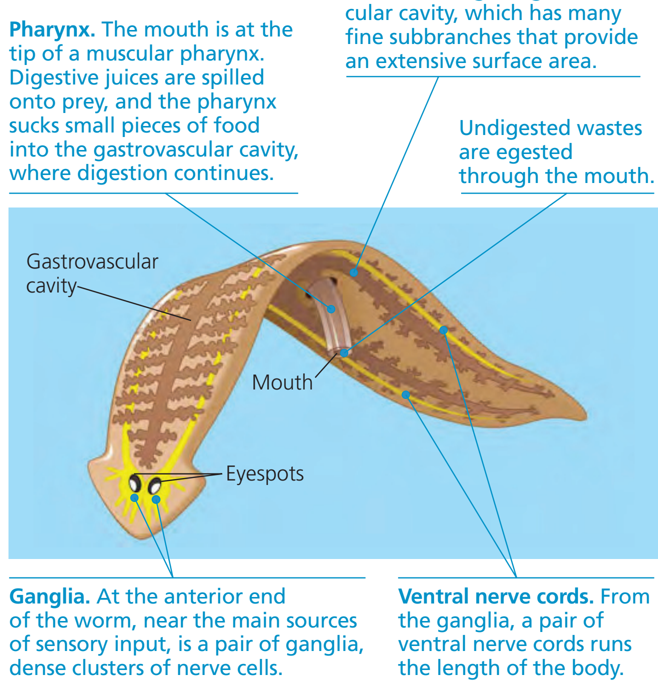
▲ **Figure 33.9 A free-living marine flatworm.**

smaller animals or feed on dead animals. They move by using cilia on their ventral surface, gliding along a film of mucus they secrete. Some other rhabditophorans also use their muscles to swim through water with an undulating motion.

A planarian's head is equipped with a pair of light-sensitive eyespots and lateral flaps that function mainly to detect specific chemicals. The planarian nervous system is more complex and centralized than the nerve nets of cnidarians **(Figure 33.10)**. Experiments have shown that planarians can learn to modify their responses to stimuli.

Some planarians can reproduce asexually through fission. The parent constricts roughly in the middle of its body, separating into a head end and a tail end; each end then regenerates the missing parts. Sexual reproduction also occurs. Planarians are hermaphrodites, and copulating mates typically cross-fertilize each other.

▼ **Figure 33.10 Anatomy of a planarian.**

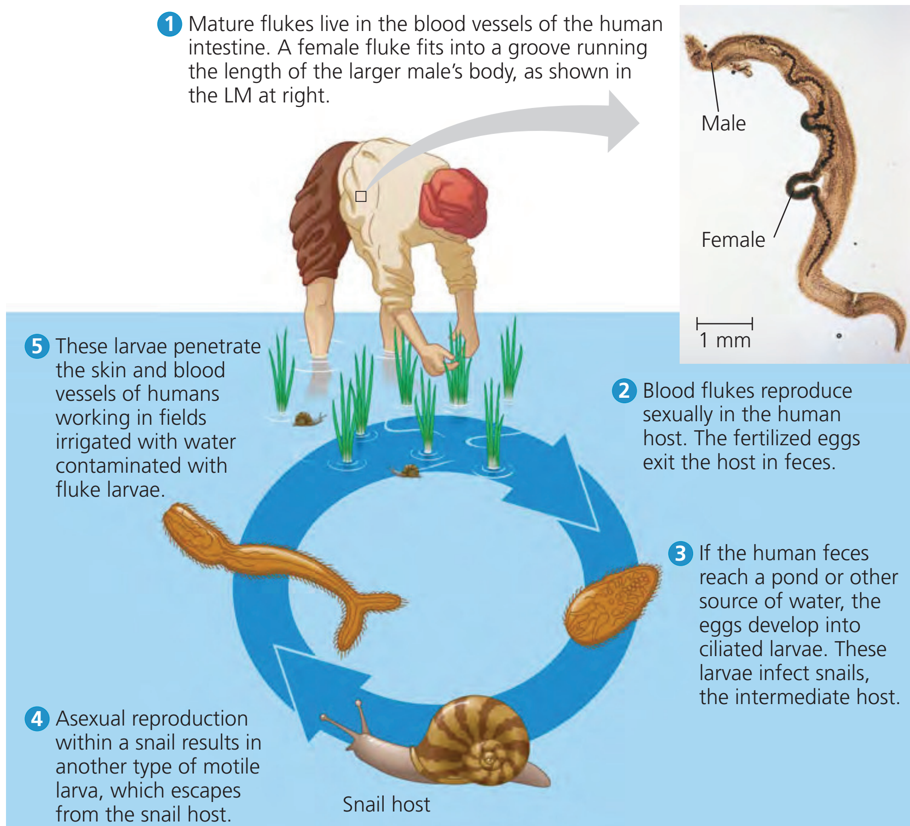


Parasitic Species

More than half of the known species of rhabditophorans live as parasites in or on other animals. Many have suckers that attach to the internal organs or outer surfaces of the host animal. In most species, a tough covering helps protect the parasites within their hosts. Reproductive organs occupy nearly the entire interior of these worms. We'll discuss two ecologically and economically important subgroups of parasitic rhabditophorans, the trematodes and the tapeworms.

Trematodes As a group, trematodes parasitize a wide range of hosts, and most species have complex life cycles with alternating sexual and asexual stages. Many trematodes require an intermediate host in which larvae develop before infecting the final host (usually a vertebrate), where the adult worms live. For example, trematodes that parasitize humans spend part of their lives in snail hosts **(Figure 33.11)**. Around the world, some 200 million people are infected with trematodes called blood flukes (*Schistosoma*) and suffer from schistosomiasis, a disease whose symptoms include pain, anemia, and diarrhea.

Living within different hosts puts demands on trematodes that free-living animals don't face. A blood fluke, for instance, must evade the immune systems of both snails and humans. By mimicking the surface proteins of its hosts, the blood fluke creates a partial immunological camouflage for itself. It



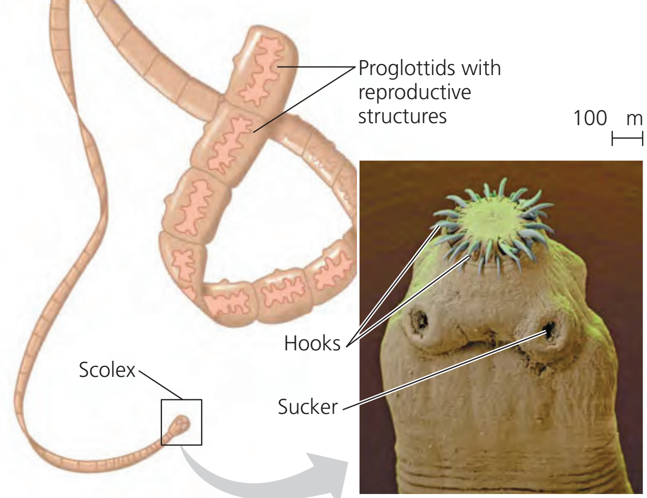
▲ **Figure 33.11 The life cycle of a blood fluke (*Schistosoma mansoni*), a trematode.**

WHAT IF? *Snails eat algae, whose growth is stimulated by nutrients found in fertilizer. How would the contamination of irrigation water with fertilizer likely affect the occurrence of schistosomiasis? Explain.*

also releases molecules that manipulate the hosts' immune systems into tolerating the parasite's existence. These defenses are so effective that individual blood flukes can survive in humans for more than 40 years.

Tapeworms The tapeworms are a second large and diverse group of parasitic rhabditophorans **(Figure 33.12)**. The adults live mostly inside vertebrates, including humans. In many tapeworms, the anterior end, or scolex, is armed with suckers and often hooks that the worm uses to attach itself to the intestinal lining of its host. Tapeworms lack a mouth and gastrovascular cavity; they simply absorb nutrients released by digestion in the host's intestine. Absorption occurs across the tapeworm's body surface.

Posterior to the scolex is a long ribbon of units called proglottids, which are little more than sacs of sex organs. After sexual reproduction, proglottids loaded with thousands of fertilized eggs are released from the posterior end of a tapeworm and leave the host's body in feces. In one type of life cycle, feces carrying the eggs contaminate the food or water of intermediate hosts, such as pigs or cattle, and the tapeworm eggs develop into larvae that encyst in muscles of these animals. A human acquires the larvae by eating undercooked meat containing the cysts, and the worms develop into mature adults within the human. Large tapeworms can block the intestines and rob enough nutrients from the human host to cause nutritional deficiencies. Doctors have patients take the drug niclosamide by mouth to kill the adult worms.

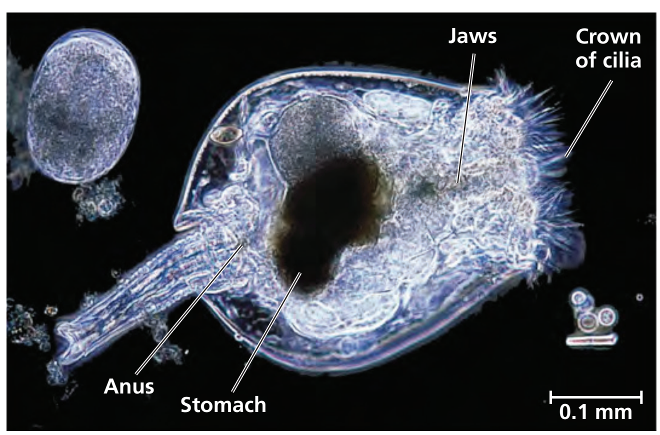
▲ **Figure 33.12 Anatomy of a tapeworm.** The inset shows a close-up of the scolex (colorized SEM).

Rotifers

Rotifers (phylum Rotifera) are tiny animals that inhabit freshwater, marine, and damp soil habitats. Ranging in size from about 50 μm to 2 mm, rotifers are smaller than many protists but nevertheless are multicellular and have specialized organ systems **(Figure 33.13)**. In contrast to cnidarians and flatworms, which have a gastrovascular cavity, rotifers have an **alimentary canal**, a digestive tube with two openings, a mouth and an anus. Internal organs lie within the pseudocoelom, a body cavity that is not completely lined by mesoderm (see Figure 32.8b). Fluid in the pseudocoelom serves as a hydrostatic skeleton. Movement of a rotifer's body distributes the fluid throughout the body, circulating nutrients.

The word *rotifer* is derived from the Latin meaning "wheel-bearer," a reference to the crown of cilia that draws a vortex of water into the mouth. Posterior to the mouth, a region of the digestive tract called the pharynx bears jaws called trophi that grind up food, mostly microorganisms suspended in the water. Digestion is then completed farther along the alimentary canal. Most other bilaterians also have an alimentary canal, which enables the stepwise digestion of a wide range of food particles.

Rotifers exhibit some unusual forms of reproduction. Some species consist only of females that produce more females from unfertilized eggs, a type of asexual reproduction called **parthenogenesis**. Some other invertebrates (for example, aphids and some bees) and even some vertebrates (for example, some lizards and some fishes) can also reproduce in this way. In addition to being able to produce females by parthenogeneis, some rotifers can also reproduce sexually under certain conditions, such as high levels of crowding. When this occurs, a female produces two types of eggs. Eggs



▲ **Figure 33.13 A rotifer.** These pseudocoelomates, smaller than many protists, are generally more anatomically complex than flatworms (LM).

of one type develop into females, and eggs of the other type develop into males. In some cases, the males do not feed and survive only long enough to fertilize eggs. The fertilized eggs develop into resistant embryos capable of remaining dormant for years. Once the embryos break dormancy, they develop into a new female generation that reproduces by parthenogenesis until conditions once again favor sexual reproduction.

It is puzzling that many rotifer species survive without males. The vast majority of animals and plants reproduce sexually at least some of the time, and sexual reproduction has certain advantages over asexual reproduction (see Concept 46.1). For example, species that reproduce asexually tend to accumulate harmful mutations in their genomes faster than sexually reproducing species. As a result, asexual species should experience higher rates of extinction and lower rates of speciation.

Seeking to understand this unusual group, researchers have been studying a clade of asexual rotifers named Bdelloidea. Some 360 species of bdelloid rotifers are known, and all of them reproduce by parthenogenesis without any males. Paleontologists have discovered bdelloid rotifers preserved in 35-million-year-old amber, and the morphology of these fossils resembles only the female form, with no evidence of males. By comparing the DNA of bdelloids with that of their closest sexually reproducing rotifer relatives, scientists have concluded that bdelloids have likely been asexual for 100 million years. How these animals manage to flout the general rule against long-lasting asexuality remains a puzzle.

Lophophorates: Ectoprocts and Brachiopods

Bilaterians in the phyla Ectoprocta and Brachiopoda are among those known as lophophorates. These animals have a *lophophore*, a crown of ciliated tentacles around their mouth (see Figure 32.13a). As the cilia draw water toward the mouth, the tentacles trap suspended food particles. Other similarities, such as a U-shaped alimentary canal and the absence of a distinct head, reflect these organisms' sessile existence. In contrast to flatworms, which lack a body cavity, and rotifers, which have a pseudocoelom, lophophorates have a true coelom that is completely lined by mesoderm (see Figure 32.8a).

Ectoprocts (from the Greek *ecto*, outside, and *procta*, anus) are colonial animals that superficially resemble clumps of moss. (In fact, their common name, bryozoans, means "moss animals.") In most species, the colony is encased in a hard **exoskeleton** (external skeleton) studded with pores through which the lophophores extend **(Figure 33.14a)**. Most ectoproct species live in the sea, where they are among the most widespread and numerous sessile animals. Several species are important reef builders. Ectoprocts also live in lakes and rivers. Colonies of the freshwater ectoproct *Pectinatella magnifica* grow on submerged sticks or rocks and can grow into a gelatinous, ball-shaped mass more than 10 cm across.

(a) Ectoprocts, such as this creeping bryozoan (*Plumatella repens*), are colonial lophophorates.

(b) Brachiopods, such as this lampshell (*Terebratulina retusa*), have a hinged shell. The two parts of the shell are dorsal and ventral.

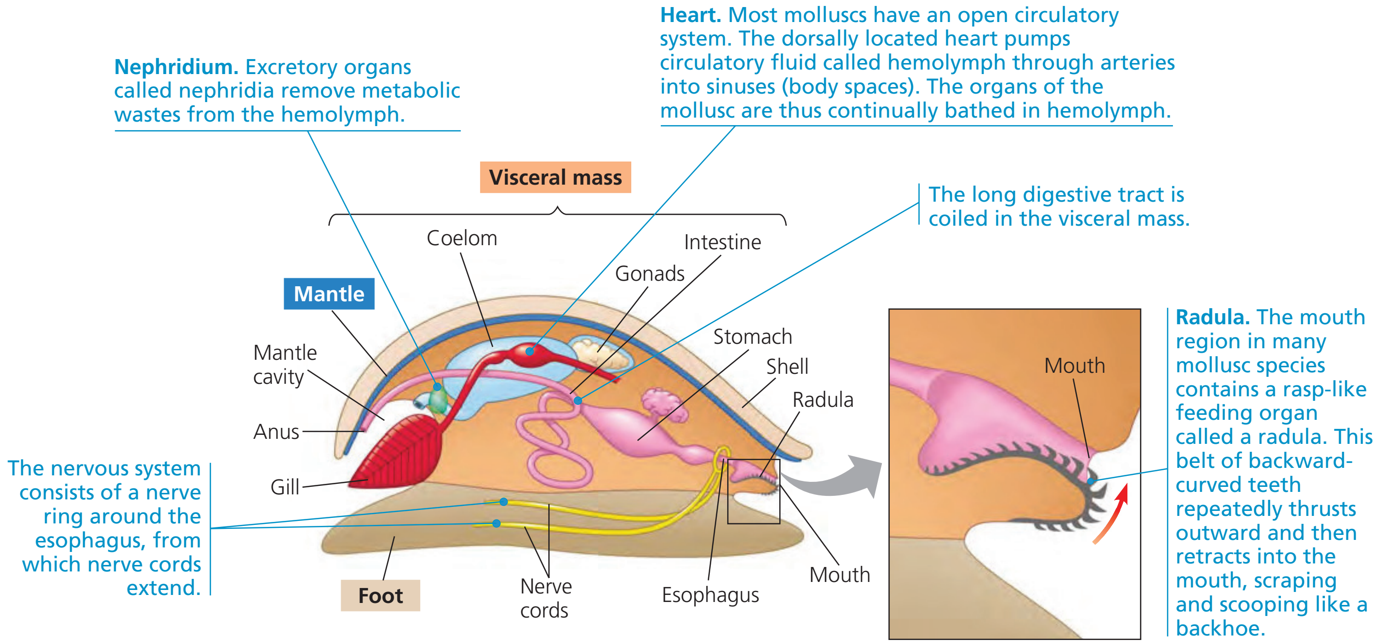
▲ **Figure 33.14 Lophophorates.**

Brachiopods, or lamp shells, superficially resemble clams and other hinge-shelled molluscs, but the two halves of the brachiopod shell are dorsal and ventral rather than lateral, as in clams **(Figure 33.14b)**. All brachiopods are marine. Most live attached to the seafloor by a stalk, opening their shell slightly to allow water to flow through the lophophore. The living brachiopods are remnants of a much richer past that included 30,000 species in the Paleozoic and Mesozoic eras. Some living brachiopods, such as those in the genus *Lingula*, appear nearly identical to fossils of species that lived 400 million years ago.

Molluscs

Snails and slugs, oysters and clams, and octopuses and squids are all molluscs (phylum Mollusca). There are 93,000 known species, making them the second most diverse phylum of animals (after the arthropods, discussed later). Although the majority of molluscs are marine, roughly 8,000 species inhabit fresh water, and 28,000 species of snails and slugs live on land. All molluscs are soft-bodied (from the Latin *molluscus*, soft), and most secrete a hard protective shell made of calcium carbonate. Slugs, squids, and octopuses have a reduced internal shell or have lost their shell completely during their evolution.

Despite their apparent differences, all molluscs have a similar body plan (**Figure 33.15**, on the next page). Molluscs are coelomates, and their bodies have three main parts: a muscular **foot**, usually used for movement; a **visceral mass** containing most of the internal organs; and a **mantle**, a fold of tissue that drapes over the visceral mass and secretes a shell (if one is present). In many molluscs, the mantle extends beyond the visceral mass, producing a water-filled chamber, the **mantle cavity**, which houses the gills, anus, and excretory pores. Many molluscs feed by using a straplike organ called a **radula** to scrape up food.



▲ **Figure 33.15 The basic body plan of a mollusc.**

Most molluscs have separate sexes, and their gonads (ovaries or testes) are located in the visceral mass. Many snails, however, are hermaphrodites. The life cycle of many marine molluscs includes a ciliated larval stage, the trochophore (see Figure 32.13b), which is also characteristic of marine annelids (segmented worms) and some other lophotrochozoans.

The basic body plan of molluscs has evolved in various ways in the phylum's seven or eight clades (experts disagree on the number). We'll examine four of those clades here: Polyplacophora (chitons), Gastropoda (snails and slugs), Bivalvia (clams, oysters, and other bivalves), and Cephalopoda (squids, octopuses, cuttlefishes, and chambered nautiluses). We will then focus on threats facing some groups of molluscs.

Chitons

Chitons have an oval-shaped body and a shell composed of eight dorsal plates **(Figure 33.16)**. The chiton's body itself, however, is unsegmented. You can find these marine animals clinging to rocks along the shore during low tide. If you try to dislodge a chiton by hand, you will be surprised at how well its foot, acting as a suction cup, grips the rock. A chiton can also use its foot to creep slowly over the rock surface. Chitons use their radula to scrape algae off the rock surface.

Gastropods

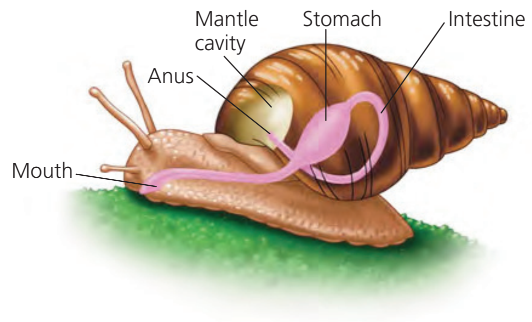
About three-quarters of all living species of molluscs are gastropods **(Figure 33.17)**. Most gastropods are marine, but there are also freshwater species. Still other gastropods have adapted to life on land, where snails and slugs thrive in habitats ranging from deserts to rain forests.

▲ **Figure 33.16 A chiton.** Note the eight-plate shell characteristic of molluscs in the clade Polyplacophora.

(a) A land snail

(b) A sea slug. Nudibranchs, or sea slugs, lost their shell during their evolution.

▲ **Figure 33.17 Gastropods.**



▲ **Figure 33.18 The results of torsion in a gastropod.** Because of torsion (twisting of the visceral mass) during embryonic development, the digestive tract is coiled and the anus is near the anterior end of the animal.

▲ **Figure 33.19 A bivalve.** This scallop has many eyes (dark blue spots) lining each half of its hinged shell.

Gastropods undergo a distinctive developmental process known as **torsion**. As a gastropod embryo develops, its visceral mass rotates up to 180°, causing the animal's anus and mantle cavity to wind up above its head **(Figure 33.18)**. After torsion, some organs that were bilateral may be reduced in size, while others may be lost on one side of the body. Torsion should not be confused with the formation of a coiled shell, which is a separate developmental process.

Most gastropods have a single, spiraled shell into which the animal can retreat when threatened. The shell is often conical but is somewhat flattened in abalones and limpets. Many gastropods have a distinct head with eyes at the tips of tentacles. Gastropods move literally at a snail's pace by a rippling motion of their foot or by means of cilia, often leaving a trail of slime in their wake. Most gastropods use their radula to graze on algae or plants. Several groups, however, are predators, and their radula has become modified for boring holes in the shells of other molluscs or for tearing apart prey. In the cone snails, the teeth of the radula act as poison darts that are used to subdue prey (see the Unit 7 interview with Baldomero Olivera on pp. 850–851 to learn more about cone snails and their venom).

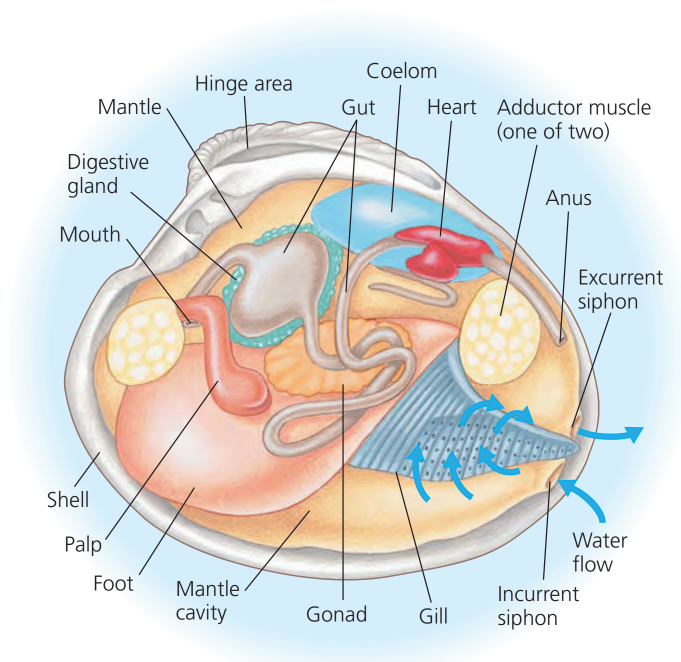
Terrestrial snails lack the gills typical of most aquatic gastropods. Instead, the lining of their mantle cavity functions as a lung, exchanging respiratory gases with the air.

Bivalves

The molluscs of the clade Bivalvia are all aquatic and include many species of clams, oysters, mussels, and scallops. Bivalves have a shell divided into two halves **(Figure 33.19)**. The halves are hinged, and powerful adductor muscles draw them tightly together to protect the animal's soft body. Bivalves have no distinct head, and the radula has been lost. Some bivalves have eyes and sensory tentacles along the outer edge of their mantle.

The mantle cavity of a bivalve contains gills that are used for gas exchange as well as feeding in most species **(Figure 33.20)**. Most bivalves are suspension feeders. They trap small food particles in mucus that coats their gills, and cilia then convey those particles to the mouth. Water enters the mantle cavity through an incurrent siphon, passes over the gills, and then exits the mantle cavity through an excurrent siphon.

Most bivalves lead sedentary lives, a characteristic suited to suspension feeding. Mussels secrete strong threads that tether them to rocks, docks, boats, and the shells of other animals. However, clams can pull themselves into the sand or mud, using their muscular foot for an anchor, and scallops can skitter along the seafloor by flapping their shells, rather like the mechanical false teeth sold in novelty shops.



▲ **Figure 33.20 Anatomy of a clam.** Food particles suspended in water that enters through the incurrent siphon are collected by the gills and passed via cilia and the palps to the mouth.

Cephalopods

Cephalopods are active marine predators **(Figure 33.21)**. They use their tentacles to grasp prey, which they then bite with beak-like jaws and immobilize with a poison present in their saliva. The foot of a cephalopod has become modified into a muscular excurrent siphon and part of the tentacles. Squids dart about by drawing water into their mantle cavity and then firing a jet of water through the excurrent siphon; they steer by pointing the siphon in different directions. Octopuses use a similar mechanism to escape predators.

The mantle covers the visceral mass of cephalopods, but the shell is generally reduced and internal (in most species) or missing altogether (in some cuttlefishes and some octopuses). One small group of cephalopods with external shells, the chambered nautiluses, survives today.

Cephalopods are the only molluscs with a *closed circulatory system*, in which the blood remains separate from fluid in the body cavity. They also have well-developed sense organs and a complex brain. The ability to learn and behave in a complex manner is probably more critical to fast-moving predators than to sedentary animals such as clams.

The ancestors of octopuses and squids were probably shelled molluscs that took up a predatory lifestyle; the shell was lost in later evolution. Shelled cephalopods called **ammonites**, some of them as large as truck tires, were the dominant invertebrate predators of the seas for hundreds of millions of years until their disappearance during the mass extinction at the end of the Cretaceous period, 65.5 million years ago (see Table 25.1).

◀ Squids are speedy carnivores with beak-like jaws and well-developed eyes.

▶ Octopuses are considered among the most intelligent invertebrates.

◀ Chambered nautiluses are the only living cephalopods with an external shell.

▲ **Figure 33.21 Cephalopods.**

Most species of squid are less than 75 cm long, but some are considerably larger. The giant squid *Architeuthis dux* was for a long time the largest squid known, with a mantle up to 2.25 m long and a total length of 18 m. In 2003, however, a specimen of the rare species *Mesonychoteuthis hamiltoni* was caught near Antarctica; its mantle was 2.5 m long. Some biologists think that this specimen was a juvenile and estimate that adults of its species could be twice as large! Unlike *A. dux*, which has large suckers and small teeth on its tentacles, *M. hamiltoni* has two rows of sharp hooks at the ends of its tentacles that can inflict deadly lacerations.

It is likely that *A. dux* and *M. hamiltoni* spend most of their time in the deep ocean, where they may feed on large fishes. Remains of both giant squid species have been found in the stomachs of sperm whales, which are probably their only natural predator. In 2005, scientists reported the first observations of *A. dux* in the wild, photographed while attacking baited hooks at a depth of 900 m. *M. hamiltoni* has yet to be observed in nature. Overall, these marine giants remain among the great mysteries of invertebrate life.

Protecting Freshwater and Terrestrial Molluscs

Species extinction rates have increased dramatically in the last 400 years, raising concern that a sixth, human-caused mass extinction may be under way (see Chapter 25). Among the many taxa under threat, molluscs have the dubious distinction of being the animal group with the largest number of documented extinctions **(Figure 33.22)**.

Threats to molluscs are especially severe in two groups, freshwater bivalves and terrestrial gastropods. The pearl mussels, a group of freshwater bivalves that can make natural pearls (gems that form when a mussel or oyster secretes layers of a lustrous coating around a grain of sand or other small irritant), are among the world's most endangered animals. Roughly 10% of the 300 pearl mussel species that once lived in North America have become extinct in the last 100 years, and over two-thirds of those that remain are threatened by extinction. Terrestrial gastropods, such as the snail in Figure 33.22, fare no better. Hundreds of Pacific island land snails have disappeared since 1800. Overall, more than 50% of the Pacific island land snails are extinct or under imminent threat of extinction.

Threats faced by freshwater and terrestrial molluscs include habitat loss, pollution, and competition or predation by non-native species introduced by people. Is it too late to protect these molluscs? In some locations, reducing water pollution and changing how water is released from dams have led to dramatic rebounds in pearl mussel populations. Such results provide hope that with corrective measures, other endangered mollusc species can be revived.

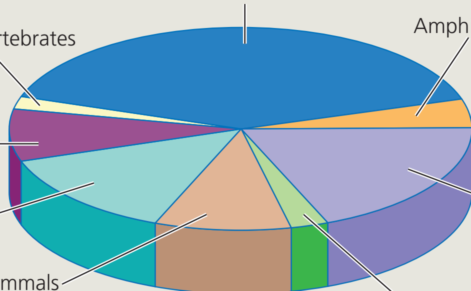
▼ **Figure 33.22**

IMPACT

Molluscs: The Silent Extinction

▲ An endangered Pacific island land snail, *Partula suturalis*

Molluscs account for a largely unheralded but sobering 40% of all documented extinctions of animal species. These extinctions have resulted from habitat loss, pollution, introduced species, overharvesting, and other human actions. Many pearl mussel populations, for example, were driven to extinction by overharvesting for their shells, which were used to make buttons and other goods. Today, remaining populations of these and other freshwater bivalves face threats from pollution and introduced species. Terrestrial gastropods such as the species pictured above are highly vulnerable to the same threats and are among the world's most imperiled animal groups.



▲ **Recorded extinctions of animal species.**
(Data: International Union for Conservation of Nature, 2008)

▲ Workers on a mound of pearl mussels killed to make buttons (ca. 1919)

WHY IT MATTERS The extinctions of molluscs represent an irreversible loss of biological diversity and greatly threaten other organisms, too. Land snails, for example, play a key role in nutrient cycling, while the filtering activities of freshwater bivalves purify the waters of streams, rivers, and lakes.

FURTHER READING C. Lydeard et al., The global decline of nonmarine mollusks, *BioScience* 54:321–330 (2004).

MAKE CONNECTIONS Freshwater bivalves feed on and can reduce the abundance of photosynthetic protists and bacteria. As such, would the extinction of freshwater bivalves likely have weak or strong effects on aquatic communities (see Concept 28.7, p. 597)? Explain.

◄ **Figure 33.23 A polychaete.** *Hesiolyra bergi* lives on the seafloor around deep-sea hydrothermal vents.

Annelids

Annelida means "little rings," referring to the annelid body's resemblance to a series of fused rings. Annelids are segmented worms that live in the sea, in most freshwater habitats, and in damp soil. Annelids are coelomates, and they range in length from less than 1 mm to more than 3 m, the length of a giant Australian earthworm.

The phylum Annelida can be divided into two main groups: Polychaeta (the polychaetes) and Oligochaeta (the earthworms and their relatives, and the leeches). Some recent phylogenetic analyses have suggested that the oligochaetes are actually a subgroup of the polychaetes. However, since this idea continues to be debated, we discuss polychaetes and oligochaetes separately.

Polychaetes

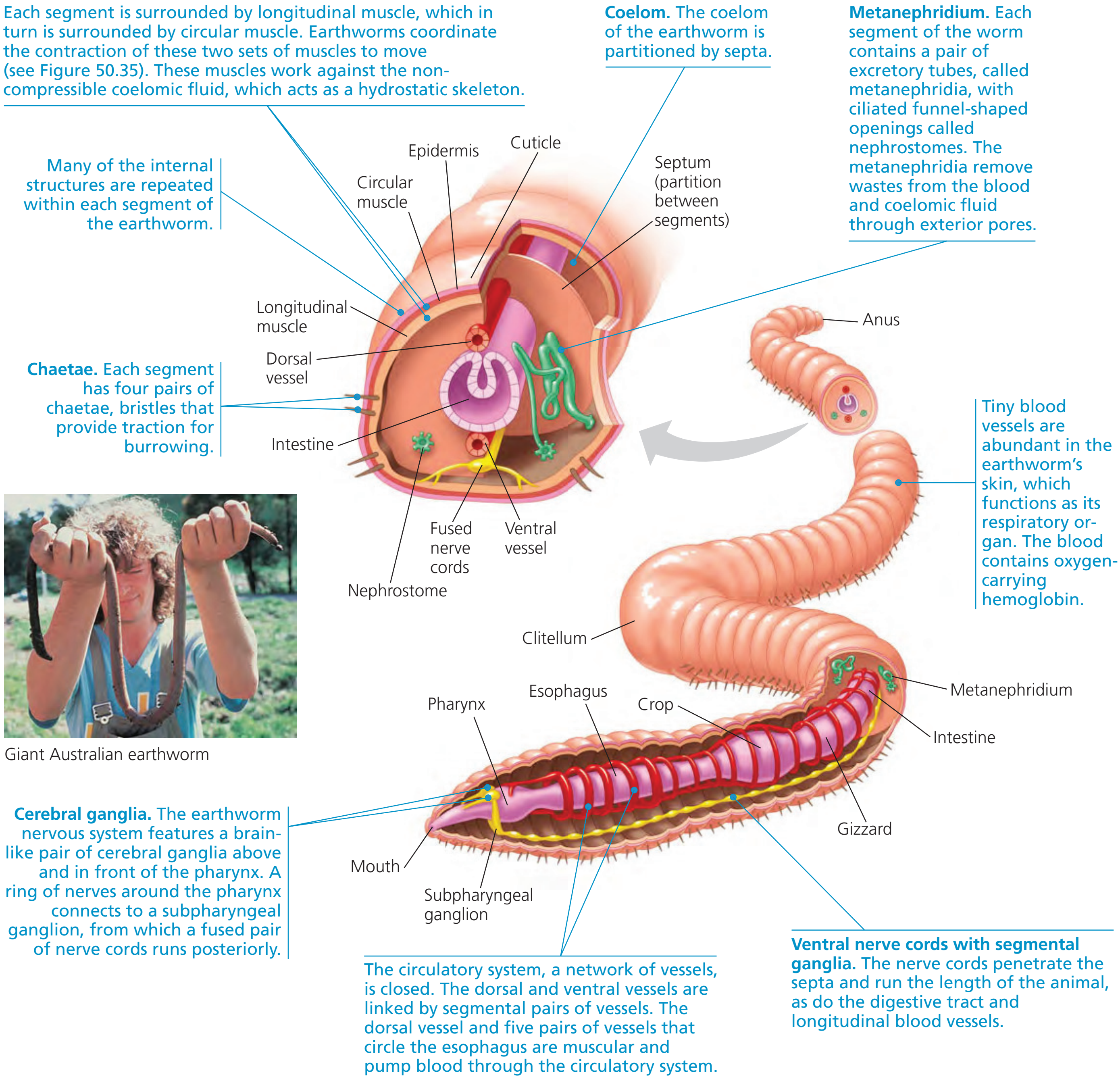
Each segment of a polychaete (from the Greek *poly*, many, and *chaitē*, long hair) has a pair of paddle-like or ridge-like structures called parapodia ("beside feet") that function in locomotion **(Figure 33.23)**. Each parapodium has numerous chaetae, bristles made of chitin. In many polychaetes, the parapodia are richly supplied with blood vessels and also function as gills.

Polychaetes make up a large and diverse group, most of whose members are marine. A few species drift and swim among the plankton, many crawl on or burrow in the seafloor, and many others live in tubes. Some tube-dwellers, such as the fan worms, build their tubes by mixing mucus with bits of sand and broken shells. Others, such as Christmas tree worms (see Figure 33.1), construct tubes using only their own secretions.

Oligochaetes

Oligochaetes (*oligos*, few, and *chaitē*, long hair) are named for their relatively sparse chaetae (far fewer per segment than in polychaetes). Molecular data indicate that these segmented worms form a diverse clade that includes the earthworms and their aquatic relatives, along with the leeches.

Earthworms Earthworms eat their way through the soil, extracting nutrients as the soil passes through the alimentary canal.



▲ **Figure 33.24 Anatomy of an earthworm, an oligochaete.**

Undigested material, mixed with mucus secreted into the canal, is eliminated as fecal castings through the anus. Farmers value earthworms because the animals till and aerate the earth, and their castings improve the texture of the soil. (Charles Darwin estimated that a single acre of British farmland contains about 50,000 earthworms, producing 18 tons of castings per year.)

A guided tour of the anatomy of an earthworm, which is representative of annelids, is shown in **Figure 33.24**. Earthworms are hermaphrodites, but they do cross-fertilize. Two earthworms mate by aligning themselves in opposite directions in such a way that they exchange sperm, and then they separate. The received sperm are stored temporarily while an organ called the clitellum secretes a cocoon of mucus. The cocoon slides along the worm, picking up the eggs and then the stored sperm. The cocoon then slips off the worm's head and remains in the soil while the embryos develop. Some earthworms can also reproduce asexually by fragmentation followed by regeneration.

Figure 33.25 A leech. A nurse applied this medicinal leech (*Hirudo medicinalis*) to a patient's sore thumb to drain blood from a hematoma (an abnormal accumulation of blood around an internal injury).

Leeches Most leeches inhabit fresh water, but there are also marine species and terrestrial leeches, which live in moist vegetation. Leeches range in length from 1 to 30 cm. Many are predators that feed on other invertebrates, but some are parasites that suck blood by attaching temporarily to other animals, including humans **(Figure 33.25)**. Some parasitic species use bladelike jaws to slit the skin of their host, whereas others secrete enzymes that digest a hole through the skin. The host is usually oblivious to this attack because the leech secretes an anesthetic. After making the incision, the leech secretes another chemical, hirudin, which keeps the blood of the host from coagulating near the incision. The parasite then sucks as much blood as it can hold, often more than ten times its own weight. After this gorging, a leech can last for months without another meal.

Until the 20th century, leeches were frequently used for bloodletting. Today they are used to drain blood that accumulates in tissues following certain injuries or surgeries. Researchers have also investigated the potential use of purified hirudin to dissolve unwanted blood clots that form during surgery or as a result of heart disease. Several forms of hirudin have been developed using recombinant DNA techniques; two of these were recently approved for clinical use.

As a group, Lophotrochozoa encompasses a remarkable range of body plans, as illustrated by members of such phyla as Rotifera, Ectoprocta, Mollusca, and Annelida. Next we'll explore the diversity of Ecdysozoa, a dominant presence on Earth in terms of sheer number of species.

CONCEPT CHECK 33.3

1. Explain how tapeworms can survive without a coelom, a mouth, a digestive system, or an excretory system.
2. Annelid anatomy can be described as "a tube within a tube." Explain.
3. **MAKE CONNECTIONS** Explain how the molluscan foot in gastropods and the excurrent siphon in cephalopods represent an example of descent with modification (see Concept 22.2, pp. 457–460).

For suggested answers, see Appendix A.

CONCEPT 33.4

Ecdysozoans are the most species-rich animal group

Although defined primarily by molecular evidence, the clade Ecdysozoa includes animals that shed a tough external coat (**cuticle**) as they grow; in fact, the group derives its name from this process, which is called *ecdysis*, or **molting**. Ecdysozoa consists of about eight animal phyla and contains more known species than all other animal, protist, fungus, and plant groups combined. Here we'll focus on the two largest ecdysozoan phyla, the nematodes and arthropods, which are among the most successful and abundant of all animal groups.

Nematodes

Among the most ubiquitous of animals, nematodes (phylum Nematoda), or roundworms, are found in most aquatic habitats, in the soil, in the moist tissues of plants, and in the body fluids and tissues of animals. In contrast to annelids, nematodes do not have segmented bodies. The cylindrical bodies of nematodes range from less than 1 mm to more than 1 m long, often tapering to a fine tip at the posterior end and to a blunter tip at the anterior end **(Figure 33.26)**. A nematode's body is covered by a tough cuticle (a type of exoskeleton); as the worm grows, it periodically sheds its old cuticle and secretes a new, larger one. Nematodes have an alimentary canal, though they lack a circulatory system. Nutrients are transported throughout the body via fluid in the pseudocoelom. The body wall muscles are all longitudinal, and their contraction produces a thrashing motion.

Nematodes usually reproduce sexually, by internal fertilization. In most species, the sexes are separate and females are larger than males. A female may deposit 100,000 or more fertilized eggs (zygotes) per day. The zygotes of most species are resistant cells that can survive harsh conditions.

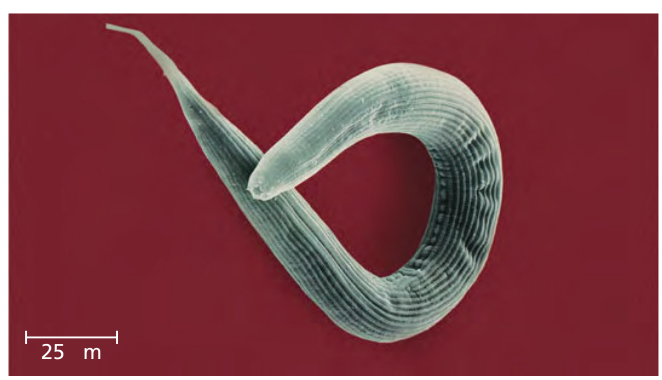
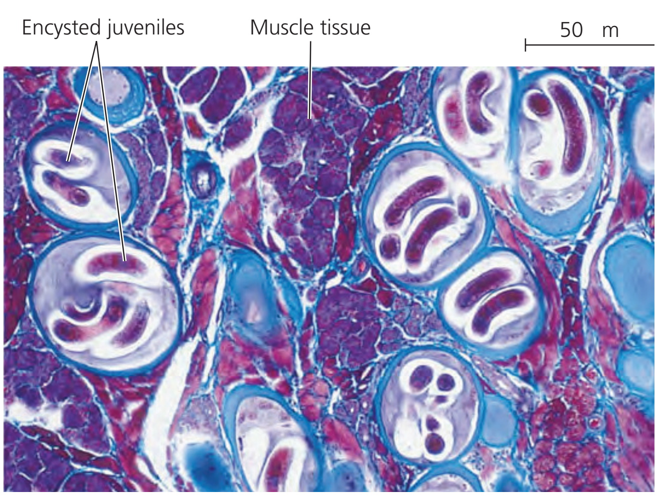


Figure 33.26 A free-living nematode (colorized SEM).

Multitudes of nematodes live in moist soil and in decomposing organic matter on the bottoms of lakes and oceans. While 25,000 species are known, perhaps 20 times that number actually exist. It has been said that if nothing of Earth or its organisms remained but nematodes, they would still preserve the outline of the planet and many of its features. These free-living worms play an important role in decomposition and nutrient cycling, but little is known about most species. One species of soil nematode, *Caenorhabditis elegans*, however, is very well studied and has become a model research organism in biology (see Chapter 47). Ongoing studies of *C. elegans* are revealing some of the mechanisms involved in aging in humans, among other findings.

Phylum Nematoda includes many species that parasitize plants, and some are major agricultural pests that attack the roots of crops. Other nematodes parasitize animals. Some of these species benefit humans by attacking insects such as cutworms that feed on the roots of crop plants. On the other hand, humans are hosts to at least 50 nematode species, including various pinworms and hookworms. One notorious nematode is *Trichinella spiralis*, the worm that causes trichinosis **(Figure 33.27)**. Humans acquire this nematode by eating raw or undercooked pork or other meat (including wild game such as bear or walrus) that has juvenile worms encysted in the muscle tissue. Within the human intestines, the juveniles develop into sexually mature adults. Females burrow into the intestinal muscles and produce more juveniles, which bore through the body or travel in lymphatic vessels to other organs, including skeletal muscles, where they encyst.

Parasitic nematodes have an extraordinary molecular toolkit that enables them to redirect some of the cellular functions of their hosts and thus evade their immune systems. Some species inject their plant hosts with molecules that induce the development of root cells, which then supply nutrients to the parasites. *Trichinella*, which parasitizes animals, controls the expression of specific muscle cell genes that code for proteins that make the cell elastic enough to house the nematode. Additionally, the infected muscle cell releases signals that promote the growth of new blood vessels, which then supply the nematode with nutrients.



▲ **Figure 33.27 Juveniles of the parasitic nematode *Trichinella spiralis* encysted in human muscle tissue** (LM).

Arthropods

Zoologists estimate that there are about a billion billion (10^{18}) arthropods living on Earth. More than 1 million arthropod species have been described, most of which are insects. In fact, two out of every three known species are arthropods, and members of the phylum Arthropoda can be found in nearly all habitats of the biosphere. By the criteria of species diversity, distribution, and sheer numbers, arthropods must be regarded as the most successful of all animal phyla.

Arthropod Origins

Biologists hypothesize that the diversity and success of **arthropods** are related to their body plan—their segmented body, hard exoskeleton, and jointed appendages (*arthropod* means "jointed feet"). The earliest fossils with this body plan are from the Cambrian explosion (535–525 million years ago), indicating that the arthropods are at least that old.

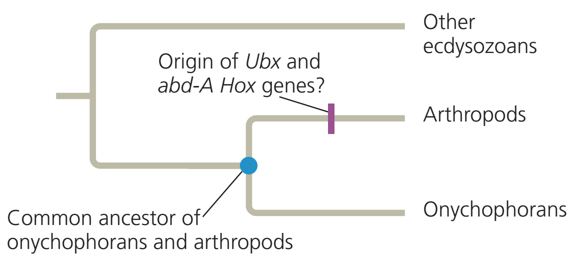
Along with arthropods, the fossil record of the Cambrian explosion contains many species of *lobopods*, an extinct group from which arthropods may have evolved. Lobopods such as *Hallucigenia* (see Figure 25.4) had segmented bodies, but most of their body segments were identical to one another. Early arthropods, such as the trilobites, also showed little variation from segment to segment **(Figure 33.28)**. As arthropods continued to evolve, the segments tended to fuse and become fewer, and the appendages became specialized for a variety of functions. These evolutionary changes resulted not only in great diversification but also in an efficient body plan that permits the division of labor among different body regions.

▶ **Figure 33.28 A trilobite fossil.** Trilobites were common denizens of the shallow seas throughout the Paleozoic era but disappeared with the great Permian extinctions about 250 million years ago. Paleontologists have described about 4,000 trilobite species.

▼ Figure 33.29 INQUIRY

Did the arthropod body plan result from new *Hox* genes?

EXPERIMENT How did the highly successful arthropod body plan arise? One hypothesis suggests that it resulted from the origin (by a gene duplication event) of two unusual *Hox* genes found in arthropods: *Ultrabithorax* (*Ubx*) and *abdominal-A* (*abd-A*). To test this hypothesis, Sean Carroll, of the University of Wisconsin, Madison, and colleagues turned to the onychophorans, a group of invertebrates closely related to arthropods. Unlike many living arthropods, onychophorans have a body plan in which most body segments are identical to one another. Thus, Carroll and colleagues reasoned that if the origin of the *Ubx* and *abd-A Hox* genes drove the evolution of body segment diversity in arthropods, these genes probably arose on the arthropod branch of the evolutionary tree:



According to this hypothesis, *Ubx* and *abd-A* would not have been present in the common ancestor of arthropods and onychophorans; hence, onychophorans should not have these genes. To find out whether this was the case, Carroll and colleagues examined the *Hox* genes of the onychophoran *Acanthokara kaputensis*.

RESULTS The onychophoran *A. kaputensis* has all arthropod *Hox* genes, including *Ubx* and *abd-A*.

Red indicates the body regions of this onychophoran embryo in which *Ubx* or *abd-A* genes were expressed. (The inset shows this area enlarged.)

Ant = antenna
J = jaws
L1–L15 = body segments

CONCLUSION Since *A. kaputensis*, an onychophoran, has the arthropod *Hox* genes, the evolution of increased body segment diversity in arthropods must not have been related to the origin of new *Hox* genes.

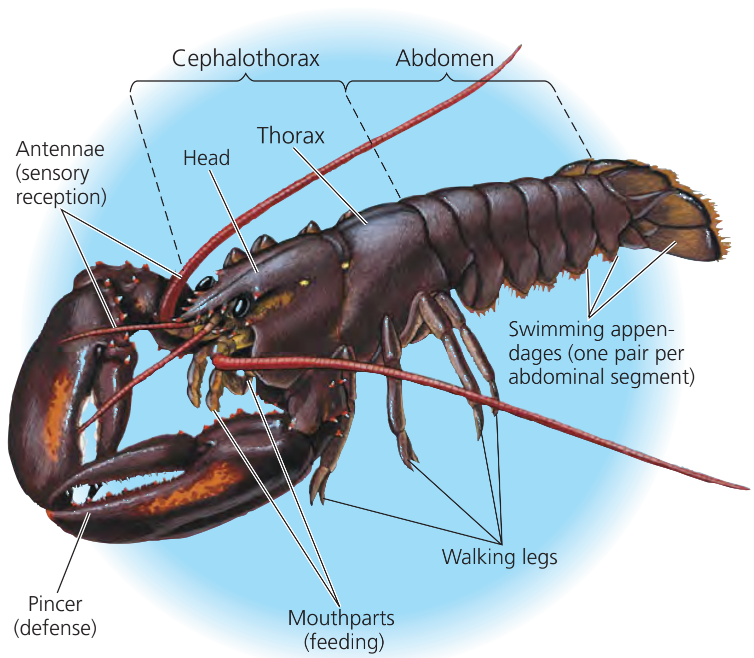
SOURCE J. K. Grenier, S. Carroll, et al., Evolution of the entire arthropod *Hox* gene set predated the origin and radiation of the onychophoran/arthropod clade, *Current Biology* 7:547–553 (1997).

WHAT IF? If Carroll and colleagues had found that *A. kaputensis* did *not* have the *Ubx* and *abd-A Hox* genes, how would their conclusion have been affected? Explain.

What genetic changes led to the increasing complexity of the arthropod body plan? Arthropods today have two unusual *Hox* genes, both of which influence segmentation. To test whether these genes could have driven the evolution of increased body segment diversity in arthropods, researchers studied *Hox* genes in onychophorans (see Figure 33.3), close relatives of arthropods **(Figure 33.29)**. Their results indicate that arthropod body plan diversity did *not* arise from the acquisition of new *Hox* genes. Instead, the evolution of body segment diversity in arthropods may have been driven by changes in the sequence or regulation of existing *Hox* genes. (See Chapter 25 for a discussion of how changes in form can result from changes in the sequence or regulation of developmental genes such as *Hox* genes.)

General Characteristics of Arthropods

Over the course of evolution, the appendages of some arthropods have become modified, specializing in functions such as walking, feeding, sensory reception, reproduction, and defense. Like the appendages from which they were derived, these modified structures are jointed and come in pairs. **Figure 33.30** illustrates the diverse appendages and other arthropod characteristics of a lobster.



▲ **Figure 33.30 External anatomy of an arthropod.** Many of the distinctive features of arthropods are apparent in this dorsal view of a lobster, along with some uniquely crustacean characteristics. The body is segmented, but this characteristic is obvious only in the abdomen. The appendages (including antennae, pincers, mouthparts, walking legs, and swimming appendages) are jointed. The head bears a pair of compound (multilens) eyes, each situated on a movable stalk. The whole body, including appendages, is covered by an exoskeleton.

The body of an arthropod is completely covered by the cuticle, an exoskeleton constructed from layers of protein and the polysaccharide chitin. The cuticle can be thick and hard over some parts of the body and paper-thin and flexible over others, such as the joints. The rigid exoskeleton protects the animal and provides points of attachment for the muscles that move the appendages. But it also means that an arthropod cannot grow without occasionally shedding its exoskeleton and producing a larger one. This molting process is energetically expensive. A molting or recently molted arthropod is also vulnerable to predation and other dangers until its new, soft exoskeleton hardens.

When the arthropod exoskeleton first evolved in the sea, its main functions were probably protection and anchorage for muscles, but it later enabled certain arthropods to live on land. The exoskeleton's relative impermeability to water helped prevent desiccation, and its strength solved the problem of support when arthropods left the buoyancy of water. Arthropods began to diversify on land following the colonization of land by plants in the early Paleozoic. Evidence includes a 428-million-year-old fossil of a millipede found in 2004 by an amateur fossil hunter in Scotland. Fossilized tracks of other terrestrial arthropods date from about 450 million years ago.

Arthropods have well-developed sensory organs, including eyes, olfactory (smell) receptors, and antennae that function in both touch and smell. Most sensory organs are concentrated at the anterior end of the animal, although there are interesting exceptions. Female butterflies, for example, "taste" plants using sensory organs on their feet.

Like many molluscs, arthropods have an **open circulatory system**, in which fluid called *hemolymph* is propelled by a heart through short arteries and then into spaces called sinuses surrounding the tissues and organs. (The term *blood* is generally reserved for fluid in a closed circulatory system.) Hemolymph reenters the arthropod heart through pores that are usually equipped with valves. The hemolymph-filled body sinuses are collectively called the *hemocoel*, which is not part of the coelom. Although arthropods are coelomates, in most species the coelom that forms in the embryo becomes much reduced as development progresses, and the hemocoel becomes the main body cavity in adults. Despite their similarity, phylogenetic analyses suggest that the open circulatory systems of molluscs and arthropods arose independently.

A variety of specialized gas exchange organs have evolved in arthropods. These organs allow the diffusion of respiratory gases in spite of the exoskeleton. Most aquatic species have gills with thin, feathery extensions that place an extensive surface area in contact with the surrounding water. Terrestrial arthropods generally have internal surfaces specialized for gas exchange. Most insects, for instance, have tracheal systems, branched air ducts leading into the interior from pores in the cuticle.

▲ **Figure 33.31 Horseshoe crabs (*Limulus polyphemus*).** Common on the Atlantic and Gulf coasts of the United States, these "living fossils" have changed little in hundreds of millions of years. They are surviving members of a rich diversity of chelicerates that once filled the seas.

Morphological and molecular evidence suggests that living arthropods consist of four major lineages that diverged early in the evolution of the phylum: **chelicerates** (sea spiders, horseshoe crabs, scorpions, ticks, mites, and spiders); **myriapods** (centipedes and millipedes); **hexapods** (insects and their wingless, six-legged relatives); and **crustaceans** (crabs, lobsters, shrimps, barnacles, and many others).

Chelicerates

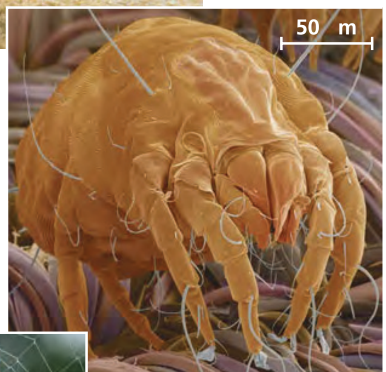
Chelicerates (subphylum Chelicerata; from the Greek *cheilos*, lips, and *cheir*, arm) are named for clawlike feeding appendages called **chelicerae**, which serve as pincers or fangs. Chelicerates have an anterior cephalothorax and a posterior abdomen. They lack antennae, and most have simple eyes (eyes with a single lens).

The earliest chelicerates were **eurypterids**, or water scorpions. These marine and freshwater predators grew up to 3 m long; it is thought that some species could have walked on land, much as land crabs do today. Most of the marine chelicerates, including all of the eurypterids, are extinct. Among the marine chelicerates that survive today are the sea spiders (pycnogonids) and horseshoe crabs **(Figure 33.31)**.

The bulk of modern chelicerates are **arachnids**, a group that includes scorpions, spiders, ticks, and mites **(Figure 33.32)**. Ticks and many mites are among a large group of parasitic arthropods. Nearly all ticks are bloodsucking parasites that live on the body surfaces of reptiles or mammals. Parasitic mites live on or in a wide variety of vertebrates, invertebrates, and plants.

Arachnids have a cephalothorax that has six pairs of appendages: the chelicerae; a pair of appendages called *pedipalps* that function in sensing, feeding, or reproduction; and four pairs of walking legs **(Figure 33.33)**. Spiders use their fang-like chelicerae, which are equipped with poison glands, to attack

▲ Scorpions have pedipalps that are pincers specialized for defense and the capture of food. The tip of the tail bears a poisonous stinger.



▲ Dust mites are ubiquitous scavengers in human dwellings but are harmless except to those people who are allergic to them (colorized SEM).

◀ Web-building spiders are generally most active during the daytime.

▲ **Figure 33.32 Arachnids.**

(a) Millipede

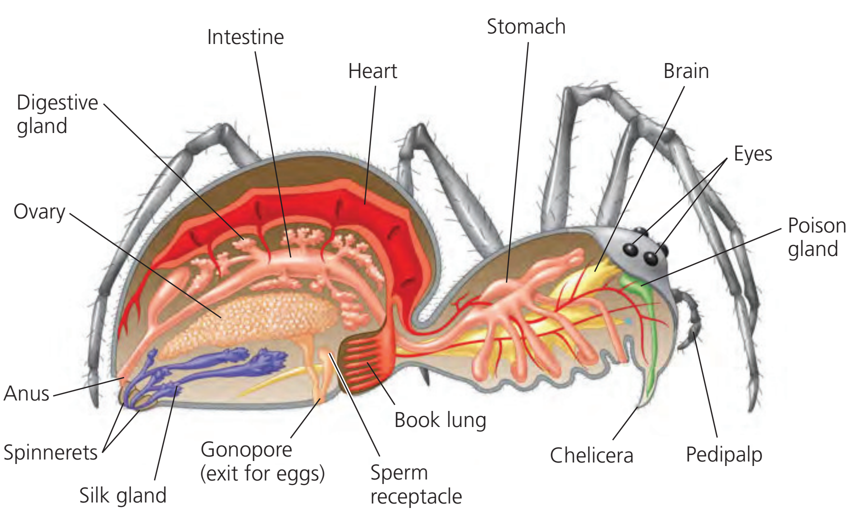
(b) Centipede

▲ **Figure 33.34 Myriapods.**

prey. As the chelicerae pierce the prey, the spider secretes digestive juices onto the prey's torn tissues. The food softens, and the spider sucks up the liquid meal.

In most spiders, gas exchange is carried out by **book lungs**, stacked platelike structures contained in an internal chamber (see Figure 33.33). The extensive surface area of these respiratory organs is a structural adaptation that enhances the exchange of O_2 and CO_2 between the hemolymph and air.

A unique adaptation of many spiders is the ability to catch insects by constructing webs of silk, a liquid protein produced by specialized abdominal glands. The silk is spun by organs called spinnerets into fibers that then solidify. Each spider engineers a web characteristic of its species and builds it perfectly on the first try, indicating that this complex behavior is inherited. Various spiders also use silk in other ways: as droplines for rapid escape, as a cover for eggs, and even as "gift wrap" for food that males offer females during courtship. Many small spiders also extrude silk into the air and let themselves be transported by wind, a behavior known as "ballooning."



▲ **Figure 33.33 Anatomy of a spider.**

Myriapods

Millipedes and centipedes belong to the subphylum Myriapoda **(Figure 33.34)**. All living myriapods are terrestrial. The myriapod head has a pair of antennae and three pairs of appendages modified as mouthparts, including the jaw-like **mandibles**.

Millipedes have a large number of legs, though fewer than the thousand their name implies. Each trunk segment is formed from two fused segments and bears two pairs of legs (see Figure 33.34a). Millipedes eat decaying leaves and other plant matter. They may have been among the earliest animals on land, living on mosses and early vascular plants.

Unlike millipedes, centipedes are carnivores. Each segment of a centipede's trunk region has one pair of legs (see Figure 33.34b). Centipedes have poison claws on their foremost trunk segment that paralyze prey and aid in defense.

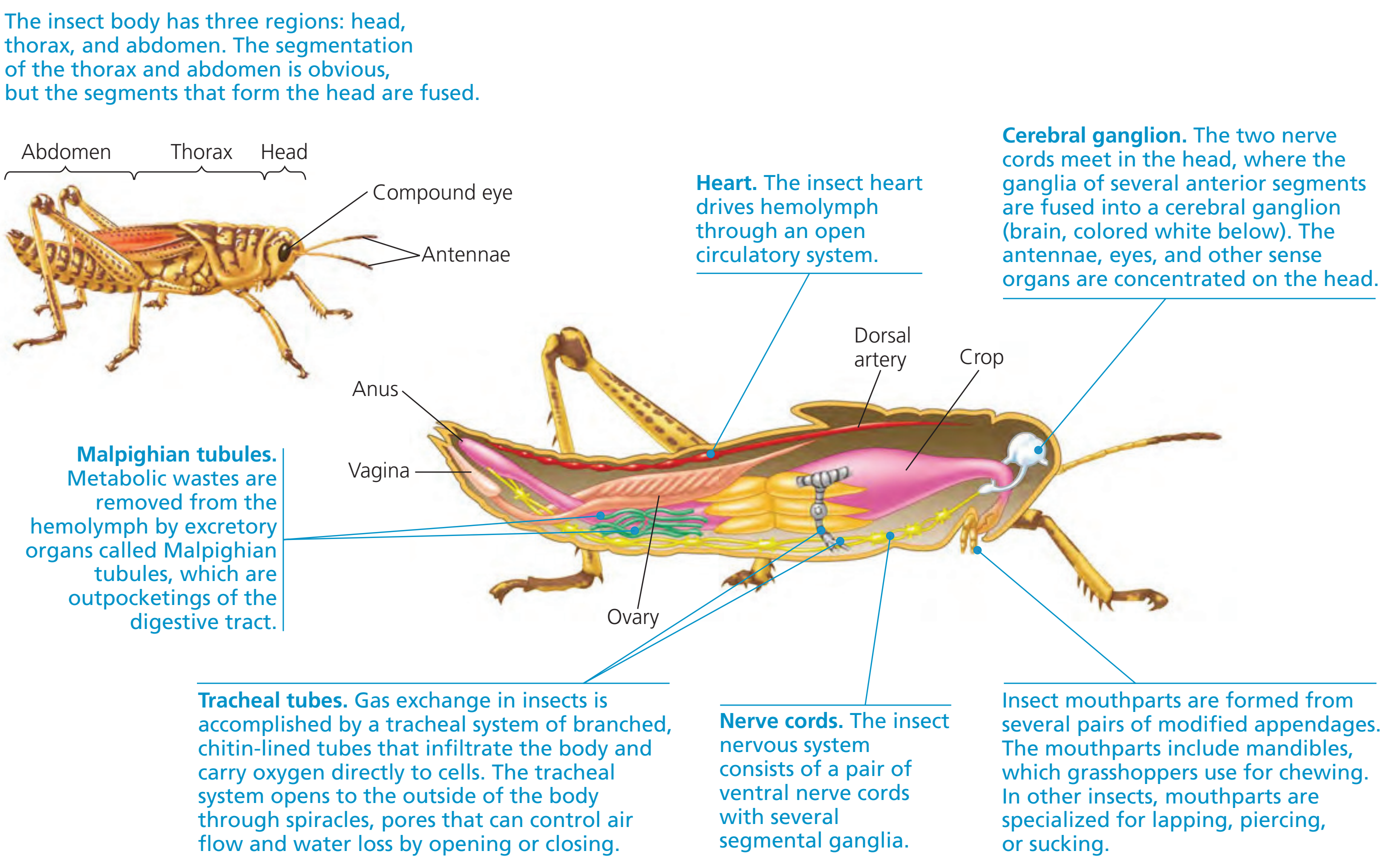
Insects

Insects and their relatives (subphylum Hexapoda) are more species-rich than all other forms of life combined. They live in almost every terrestrial habitat and in fresh water, and flying insects fill the air. Insects are rare, though not absent, in marine habitats, where crustaceans are the dominant arthropods. The internal anatomy of an insect includes several complex organ systems, which are highlighted in **Figure 33.35**.

The oldest insect fossils date from the Devonian period, which began about 416 million years ago. However, when insect flight evolved during the Carboniferous and Permian periods, it spurred an explosion in insect diversity. A fossil record of diverse insect mouthparts indicates that specialized feeding on gymnosperms and other Carboniferous plants also contributed to early adaptive radiations of insects. Later, a major increase in insect diversity appears to have been stimulated by the evolutionary expansion of flowering plants during the mid-Cretaceous period (about 90 million years ago). Although insect and plant diversity decreased during the Cretaceous mass extinction, both groups rebounded over the next 65 million years. Studies indicate that increases in the diversity of particular insect groups often were associated with radiations of the flowering plants on which they fed.

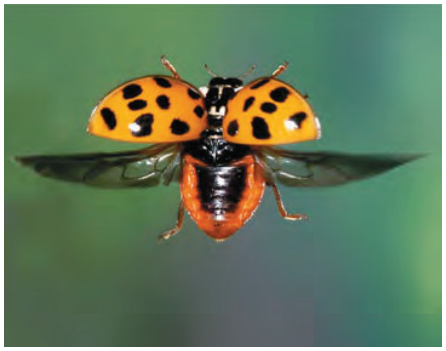
Flight is obviously one key to the great success of insects. An animal that can fly can escape many predators, find food and mates, and disperse to new habitats much faster than an animal that must crawl about on the ground. Many insects have one or two pairs of wings that emerge from the dorsal side of the thorax **(Figure 33.36)**. Because the wings are extensions of the cuticle and not true appendages, insects can fly without sacrificing any walking legs. By contrast, the flying vertebrates—birds and bats—have one of their two pairs of walking legs modified into wings, making some of these species clumsy on the ground.

Insect wings may have first evolved as extensions of the cuticle that helped the insect body absorb heat, only later becoming organs for flight. Other hypotheses suggest that wings allowed terrestrial insects to glide from vegetation to the ground or that they served as gills in aquatic insects. Still another hypothesis is that insect wings functioned for swimming before they functioned for flight.



▲ **Figure 33.35 Anatomy of a grasshopper, an insect.**

▶ **Figure 33.36** **Ladybird beetle in flight.**

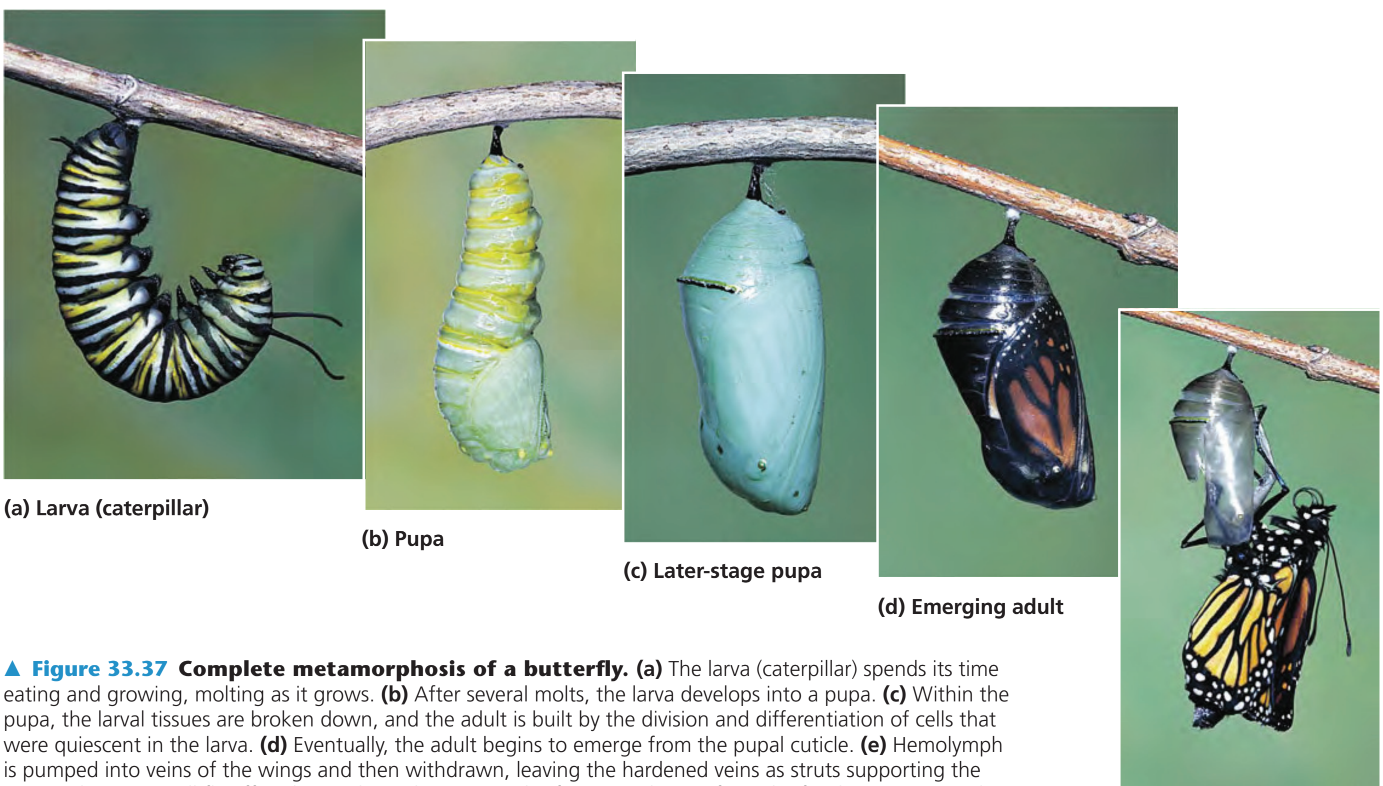


Morphological and molecular data indicate that wings evolved only once in insects. Dragonflies, which have two similar pairs of wings, were among the first insects to fly. Several insect orders that evolved later than dragonflies have modified flight equipment. The wings of bees and wasps, for instance, are hooked together and move as a single pair. Butterfly wings operate in a similar fashion because the anterior pair overlaps the posterior wings. In beetles, the posterior wings function in flight, while the anterior ones are modified as covers that protect the flight wings when the beetle is walking on the ground or burrowing.

Many insects undergo metamorphosis during their development. In the **incomplete metamorphosis** of grasshoppers and some other insect groups, the young (called nymphs) resemble adults but are smaller, have different body proportions, and lack wings. The nymph undergoes a series of molts, each time looking more like an adult. With the final molt, the insect reaches full size, acquires wings, and becomes sexually mature. Insects with **complete metamorphosis** have larval stages specialized for eating and growing that are known by such names as caterpillar, maggot, or grub. The larval stage looks entirely different from the adult stage, which is specialized for dispersal and reproduction. Metamorphosis from the larval stage to the adult occurs during a pupal stage (**Figure 33.37**).

Reproduction in insects is usually sexual, with separate male and female individuals. Adults come together and recognize each other as members of the same species by advertising with bright colors (as in butterflies), sounds (as in crickets), or odors (as in moths). Fertilization is generally internal. In most species, sperm are deposited directly into the female's vagina at the time of copulation, though in some species the male deposits a sperm packet outside the female, and the female picks it up. An internal structure in the female called the spermatheca stores the sperm, usually enough to fertilize more than one batch of eggs. Many insects mate only once in a lifetime. After mating, a female often lays her eggs on an appropriate food source where the next generation can begin eating as soon as it hatches.

Insects are classified in more than 30 orders, 8 of which are introduced in **Figure 33.38**.



(a) Larva (caterpillar)

(b) Pupa

(c) Later-stage pupa

(d) Emerging adult

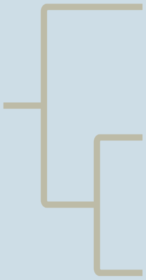
(e) Adult

▲ **Figure 33.37** **Complete metamorphosis of a butterfly.** **(a)** The larva (caterpillar) spends its time eating and growing, molting as it grows. **(b)** After several molts, the larva develops into a pupa. **(c)** Within the pupa, the larval tissues are broken down, and the adult is built by the division and differentiation of cells that were quiescent in the larva. **(d)** Eventually, the adult begins to emerge from the pupal cuticle. **(e)** Hemolymph is pumped into veins of the wings and then withdrawn, leaving the hardened veins as struts supporting the wings. The insect will fly off and reproduce, deriving much of its nourishment from the food reserves stored by the feeding larva.

▼ **Figure 33.38**

Exploring Insect Diversity

Although there are more than 30 orders of insects, we'll focus on just 8 here. Two early-diverging groups of wingless insects are the bristletails (Archaeognatha) and silverfish (Thysanura). Evolutionary relationships among the other groups discussed here are under debate and so are not depicted on the tree.



Archaeognatha (bristletails; 350 species)

These wingless insects are found under bark and in other moist, dark habitats such as leaf litter, compost piles, and rock crevices. They feed on algae, plant debris, and lichens.

Thysanura (silverfish; 450 species)

These small, wingless insects have a flattened body and reduced eyes. They live in leaf litter or under bark. They can also infest buildings, where they can become pests.

Winged insects (many orders; six are shown below)

Complete metamorphosis

Coleoptera (beetles; 350,000 species)

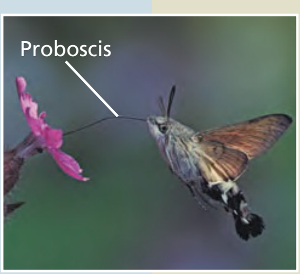
Beetles, such as this male snout weevil (*Rhiastus lasternus*), constitute the most species-rich order of insects. They have two pairs of wings, one of which is thick and stiff, the other membranous. They have an armored exoskeleton and mouthparts adapted for biting and chewing.

Diptera (151,000 species)

Dipterans have one pair of wings; the second pair has become modified into balancing organs called halteres. Their mouthparts are adapted for sucking, piercing, or lapping. Flies and mosquitoes are among the best-known dipterans, which live as scavengers, predators, and parasites. Like many other insects, flies such as this red tachinid (*Adejeania vexatrix*) have well-developed compound eyes that provide a wide-angle view and excel at detecting fast movements.

Hymenoptera (125,000 species)

Most hymenopterans, which include ants, bees, and wasps, are highly social insects. They have two pairs of membranous wings, a mobile head, and chewing or sucking mouthparts. The females of many species have a posterior stinging organ. Many species, such as this European paper wasp (*Polistes dominulus*), build elaborate nests.



Lepidoptera (120,000 species)

Butterflies and moths have two pairs of wings covered with tiny scales. To feed, they uncoil a long proboscis, visible in this photograph of a hummingbird hawkmoth (*Macroglossum stellatarum*). This moth's name refers to its ability to hover in the air while feeding from a flower. Most lepidopterans feed on nectar, but some species feed on other substances, including animal blood or tears.

Incomplete metamorphosis

Hemiptera (85,000 species)

Hemipterans include so-called "true bugs," such as stink bugs, bed bugs, and assassin bugs. (Insects in other orders are sometimes erroneously called bugs.) Hemipterans have two pairs of wings, one pair partly leathery, the other pair membranous. They have piercing or sucking mouthparts and undergo incomplete metamorphosis, as shown in this image of an adult stink bug guarding its offspring (nymphs).

Orthoptera (13,000 species)

Grasshoppers, crickets, and their relatives are mostly herbivorous. They have large hind legs adapted for jumping, two pairs of wings (one leathery, one membranous), and biting or chewing mouthparts. This aptly named spear-bearer katydid (*Cophiphora* sp.) has a threatening display. Male orthopterans commonly make courtship sounds by rubbing together body parts, such as ridges on their hind legs.

Animals as numerous, diverse, and widespread as insects are bound to affect the lives of most other terrestrial organisms, including humans. Insects consume enormous quantities of plant matter; play key roles as predators, parasites, and decomposers; and are an essential source of food for larger animals such as lizards, rodents, and birds. Humans depend on bees, flies, and many other insects to pollinate crops and orchards. In addition, people in many parts of the world eat insects as an important source of protein. On the other hand, insects are carriers for many diseases, including African sleeping sickness (spread by tsetse flies that carry the protist *Trypanosoma*; see Figure 28.6) and malaria (spread by mosquitoes that carry the protist *Plasmodium*; see Figure 28.10).

Insects also compete with humans for food. In parts of Africa, for instance, insects claim about 75% of the crops. In the United States, billions of dollars are spent each year on pesticides, spraying crops with massive doses of some of the deadliest poisons ever invented. Try as they may, not even humans have challenged the preeminence of insects and their arthropod kin. As Cornell University entomologist Thomas Eisner puts it: "Bugs are not going to inherit the Earth. They own it now. So we might as well make peace with the landlord."

(a) Ghost crabs live on sandy ocean beaches worldwide. Primarily nocturnal, they take shelter in burrows during the day.

(b) Planktonic crustaceans known as krill are consumed in vast quantities by some whales.

(c) The jointed appendages projecting from the shells of these barnacles capture organisms and organic particles suspended in the water.

▲ **Figure 33.39 Crustaceans.**

Crustaceans

While arachnids and insects thrive on land, crustaceans, for the most part, have remained in marine and freshwater environments. Crustaceans (subphylum Crustacea) typically have highly specialized appendages. Lobsters and crayfishes, for instance, have a toolkit of 19 pairs of appendages (see Figure 33.30). The anterior-most appendages are antennae; crustaceans are the only arthropods with two pairs. Three or more pairs of appendages are modified as mouthparts, including the hard mandibles. Walking legs are present on the thorax, and, unlike insects, crustaceans also have appendages on their abdomen. A lost appendage can be regenerated at the next molt.

Small crustaceans exchange gases across thin areas of the cuticle; larger species have gills. Nitrogenous wastes also diffuse through thin areas of the cuticle, but a pair of glands regulates the salt balance of the hemolymph.

Sexes are separate in most crustaceans. In the case of lobsters and crayfishes, the male uses a specialized pair of abdominal appendages to transfer sperm to the reproductive pore of the female during copulation. Most aquatic crustaceans go through one or more swimming larval stages.

One of the largest groups of crustaceans (numbering over 11,000 species) is the **isopods**, which include terrestrial, freshwater, and marine species. Some isopod species are abundant in habitats at the bottom of the deep ocean. Among the terrestrial isopods are the pill bugs, or wood lice, common on the undersides of moist logs and leaves.

Lobsters, crayfishes, crabs, and shrimps are all relatively large crustaceans called **decapods** **(Figure 33.39a)**. The cuticle of decapods is hardened by calcium carbonate; the portion that covers the dorsal side of the cephalothorax forms a shield called the carapace. Most decapod species are marine. Crayfishes, however, live in fresh water, and some tropical crabs live on land.

Many small crustaceans are important members of marine and freshwater plankton communities. Planktonic crustaceans include many species of **copepods**, which are among the most numerous of all animals. Some copepods are grazers that feed upon algae, while others are predators that eat small animals (including smaller copepods!). Copepods are rivaled in abundance by the shrimplike krill, which grow to about 5 cm long **(Figure 33.39b)**. A major food source for baleen whales (including blue whales, humpbacks, and right whales), krill are now being harvested in great numbers by humans for food and agricultural fertilizer. The larvae of many larger-bodied crustaceans are also planktonic.

With the exception of a few parasitic species, barnacles are a group of sessile crustaceans whose cuticle is hardened into a shell containing calcium carbonate **(Figure 33.39c)**. Most barnacles anchor themselves to rocks, boat hulls, pilings, and other submerged surfaces. Their natural adhesive is as strong as synthetic glues. These barnacles feed by extending appendages from their shell to strain food from the water. Barnacles were not recognized as crustaceans until the 1800s, when naturalists discovered that barnacle larvae resemble the larvae of other crustaceans. The remarkable mix of unique traits and crustacean homologies found in barnacles was a major inspiration to Charles Darwin as he developed his theory of evolution.

CONCEPT CHECK 33.4

1. How do nematode and annelid body plans differ?
2. Describe two adaptations that have enabled insects to thrive on land.
3. In contrast to mammalian jaws, which move up and down, the mouthparts of arthropods move side to side. Explain this feature of arthropods in terms of the origin of their mouthparts.
4. **MAKE CONNECTIONS** Traditionally, annelids and arthropods were viewed as closely related because both have body segmentation. Yet DNA sequence data indicate that annelids belong to one clade (Lophotrochozoa) and arthropods to another (Ecdysozoa). Could traditional and molecular hypotheses be tested by studying the expression of *Hox* genes that control body segmentation (see Concept 21.6, pp. 442–447)? Explain.

For suggested answers, see Appendix A.

CONCEPT 33.5

Echinoderms and chordates are deuterostomes

Sea stars, sea urchins, and other echinoderms (phylum Echinodermata) may seem to have little in common with vertebrates (animals that have a backbone) and other members of phylum Chordata. Nevertheless, DNA evidence indicates that echinoderms and chordates are closely related, with both phyla belonging to the Deuterostomia clade of bilaterian animals. Echinoderms and chordates also share features characteristic of a deuterostome mode of development, such as radial cleavage and formation of the anus from the blastopore (see Figure 32.9). As discussed in Chapter 32, however, some animal phyla with members that have deuterostome developmental features, including ectoprocts and brachiopods, are not in the deuterostome clade. Hence, despite its name, the clade Deuterostomia is defined primarily by DNA similarities—not developmental similarities.

Echinoderms

Sea stars (commonly called starfish) and most other **echinoderms** (from the Greek *echin*, spiny, and *derma*, skin) are slow-moving or sessile marine animals. A thin epidermis covers an endoskeleton of hard calcareous plates. Most echinoderms are prickly from skeletal bumps and spines. Unique to echinoderms is the **water vascular system**, a network of hydraulic canals branching into extensions called **tube feet** that function in locomotion and feeding **(Figure 33.40)**. Sexual reproduction of echinoderms usually involves separate male and female individuals that release their gametes into the water.

The internal and external parts of most adult echinoderms radiate from the center, often as five spokes. However, echinoderm larvae have bilateral symmetry. Furthermore, the symmetry of adult echinoderms is not truly radial. For example, the opening (madreporite) of a sea star's water vascular system is not central but shifted to one side.

Living echinoderms are divided into five clades.

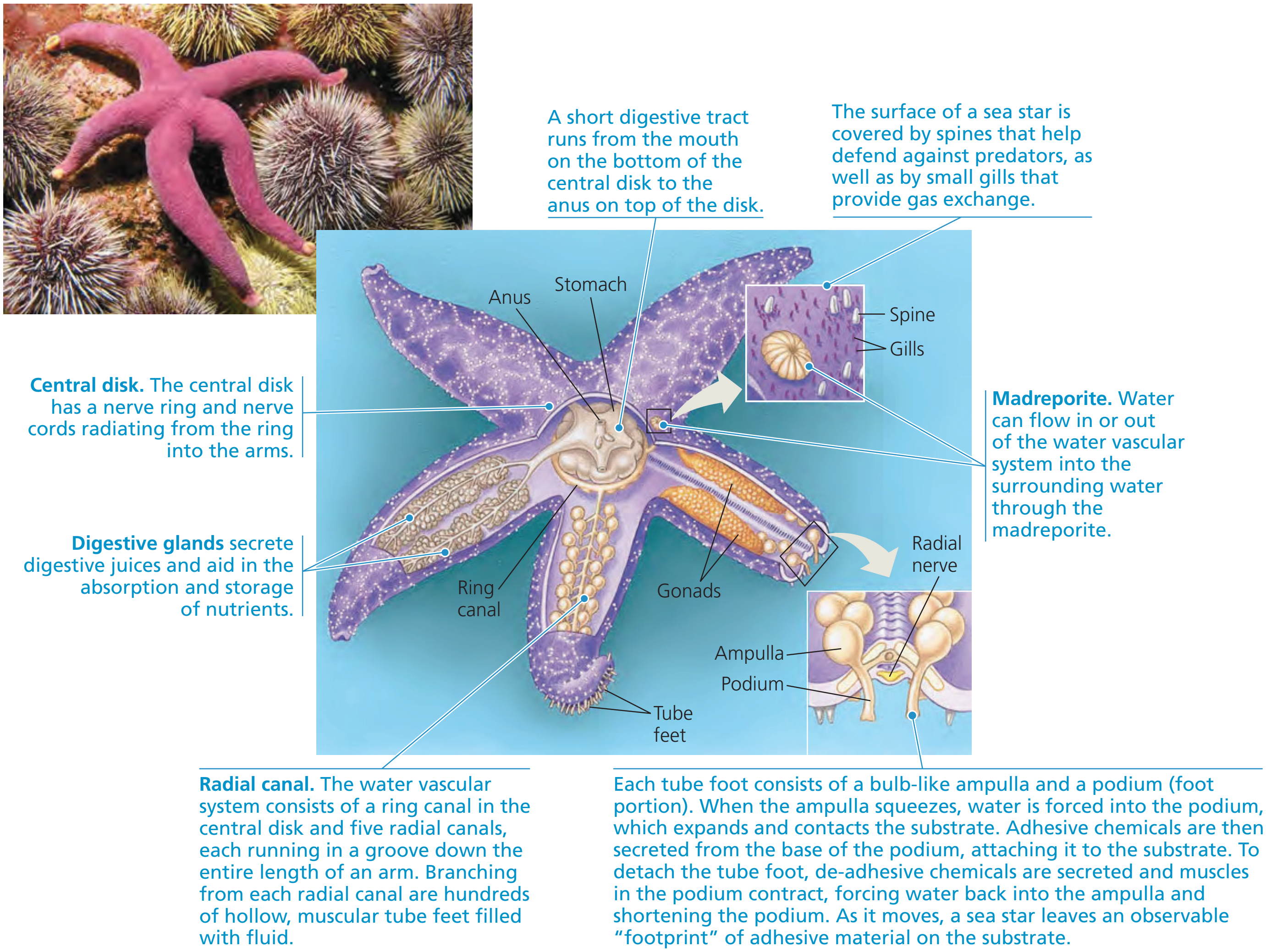
Asteroidea: Sea Stars and Sea Daisies

Sea stars have arms radiating from a central disk; the undersurfaces of the arms bear tube feet. By a combination of muscular and chemical actions, the tube feet can attach to or detach from a substrate. The sea star adheres firmly to rocks or creeps along slowly as its tube feet extend, grip, release, extend, and grip again. Although the base of the tube foot has a flattened disk that resembles a suction cup, the gripping action results from adhesive chemicals, not suction (see Figure 33.40).

Sea stars also use their tube feet to grasp prey, such as clams and oysters. The arms of the sea star embrace the closed bivalve, clinging tightly with their tube feet. The sea star then turns part of its stomach inside out, everting it through its mouth and into the narrow opening between the halves of the bivalve's shell. Next, the digestive system of the sea star secretes juices that begin digesting the mollusc within its own shell. The stomach is then brought back inside the seastar's body, where digestion of the mollusc's (now liquefied) body is completed. The ability to begin the digestive process outside of its body allows a sea star to consume bivalves and other prey species that are much larger than its mouth.

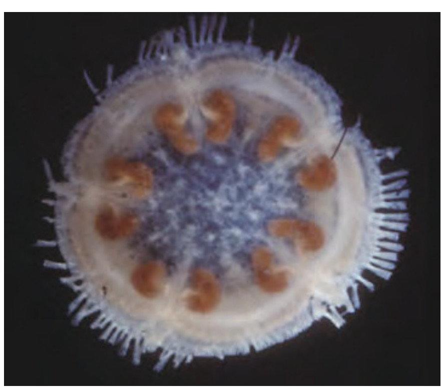
Sea stars and some other echinoderms have considerable powers of regeneration. Sea stars can regrow lost arms, and members of one genus can even regrow an entire body from a single arm if part of the central disk remains attached.

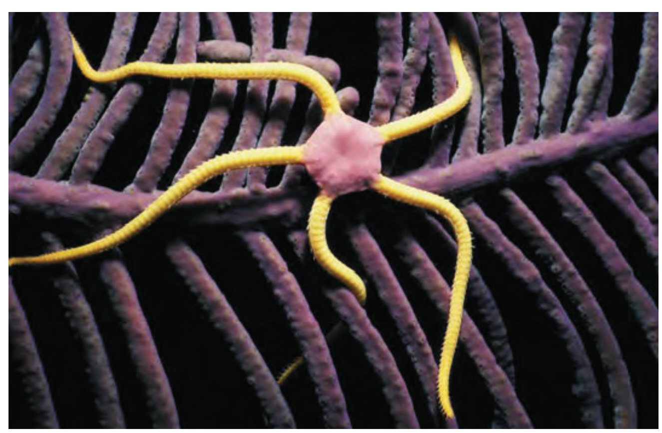
The clade Asteroidea, to which sea stars belong, also includes a small group of armless species, the *sea daisies*. Discovered in 1986, only three species of sea daisies are known, all of which live on submerged wood. A sea daisy's body is typically disk-shaped; it has a five-sided organization and measures less than a centimeter in diameter **(Figure 33.41)**. The edge of the body is ringed with small spines. Sea daisies absorb nutrients through a membrane that surrounds their body.



▲ **Figure 33.40 Anatomy of a sea star, an echinoderm.**

▶ **Figure 33.41 A sea daisy (clade Asteroidea).**

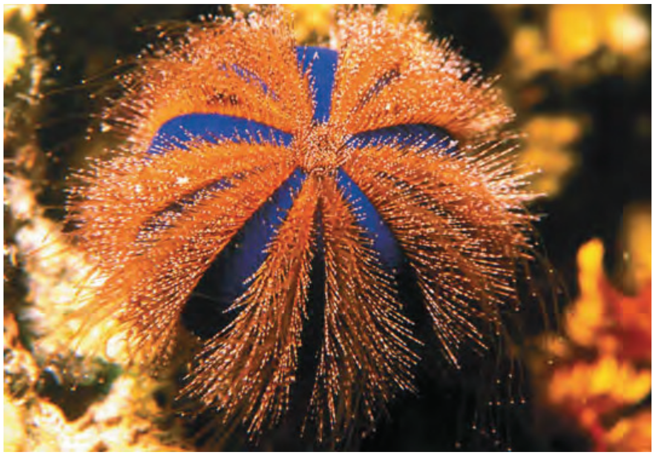




▲ **Figure 33.42 A brittle star (clade Ophiuroidea).**

Ophiuroidea: Brittle Stars

Brittle stars have a distinct central disk and long, flexible arms **(Figure 33.42)**. They move primarily by lashing their arms in serpentine movements. The base of a brittle star tube foot lacks the flattened disk found in sea stars but does secrete adhesive chemicals. Hence, like sea stars and other echinoderms, brittle stars can use their tube feet to grip substrates. Some species are suspension feeders; others are predators or scavengers.



▲ **Figure 33.43** **A sea urchin (clade Echinoidea).**

▲ **Figure 33.45** **A sea cucumber (clade Holothuroidea).**

Echinoidea: Sea Urchins and Sand Dollars

Sea urchins and sand dollars have no arms, but they do have five rows of tube feet that function in slow movement. Sea urchins also have muscles that pivot their long spines, which aid in locomotion as well as protection **(Figure 33.43)**. The mouth of a sea urchin is ringed by highly complex, jaw-like structures that are well adapted to eating seaweed. Sea urchins are roughly spherical, whereas sand dollars are flat disks.

Crinoidea: Sea Lilies and Feather Stars

Sea lilies live attached to the substrate by a stalk; feather stars crawl about by using their long, flexible arms. Both use their arms in suspension feeding. The arms encircle the mouth, which is directed upward, away from the substrate **(Figure 33.44)**. Crinoidea is an ancient group whose morphology has changed little over the course of evolution; fossilized sea lilies some 500 million years old are extremely similar to present-day members of the clade.

▲ **Figure 33.44** **A feather star (clade Crinoidea).**

Holothuroidea: Sea Cucumbers

On casual inspection, sea cucumbers do not look much like other echinoderms. They lack spines, and their endoskeleton is much reduced. They are also elongated in their oral-aboral axis, giving them the shape for which they are named and further disguising their relationship to sea stars and sea urchins **(Figure 33.45)**. Closer examination, however, reveals that sea cucumbers have five rows of tube feet. Some of the tube feet around the mouth are developed as feeding tentacles.

Chordates

Phylum Chordata consists of two subphyla of invertebrates, as well as the hagfishes and the vertebrates. Chordates are bilaterally symmetrical coelomates with segmented bodies. The close relationship between echinoderms and chordates does not mean that one phylum evolved from the other. In fact, echinoderms and chordates have evolved independently of one another for over 500 million years. We will trace the phylogeny of chordates in Chapter 34, focusing on the history of vertebrates.

CONCEPT CHECK 33.5

1. How do sea star tube feet attach to substrates?
2. **WHAT IF?** The insect *Drosophila melanogaster* and the nematode *Caenorhabditis elegans* are prominent model organisms. Are these species the most appropriate invertebrates for making inferences about humans and other vertebrates? Explain.
3. **MAKE CONNECTIONS** Describe how the features and diversity of echinoderms illustrate the unity of life, the diversity of life, and the match between organisms and their environments (see Concept 22.2, pp. 455–460).

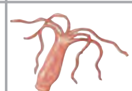
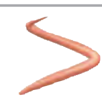
For suggested answers, see Appendix A.

33 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

The table below summarizes the groups of animals surveyed in this chapter.

Selected Animal Phyla

Key Concept		Phylum		Description
Concept 33.1 Sponges are basal animals that lack true tissues (pp. 670–671) ***?*** *Lacking tissues and organs, how do sponges accomplish tasks such as gas exchange, nutrient transport, and waste removal?*	Metazoa	Porifera (sponges)		Lack true tissues; have choanocytes (collar cells—flagellated cells that ingest bacteria and tiny food particles)
Concept 33.2 Cnidarians are an ancient phylum of eumetazoans (pp. 671–673) ***?*** *Describe the cnidarian body plan and its two major variations.*	Metazoa, Eumetazoa	Cnidaria (hydras, jellies, sea anemones, corals)		Unique stinging structures (nematocysts) housed in specialized cells (cnidocytes); diploblastic; radially symmetrical; gastrovascular cavity (digestive compartment with a single opening)
Concept 33.3 Lophotrochozoans, a clade identified by molecular data, have the widest range of animal body forms (pp. 674–683) ***?*** *Is the lophotrochozoan clade united by unique morphological features shared by all of its members? Explain.*	Metazoa, Eumetazoa, Bilateria, Lophotrochozoa	Platyhelminthes (flatworms)		Dorsoventrally flattened, unsegmented acoelomates; gastrovascular cavity or no digestive tract
	Metazoa, Eumetazoa, Bilateria, Lophotrochozoa	Rotifera (rotifers)		Pseudocoelomates with alimentary canal (digestive tube with mouth and anus); jaws (trophi) in pharynx; head with ciliated crown
	Metazoa, Eumetazoa, Bilateria, Lophotrochozoa	Lophophorates: Ectoprocta, Brachiopoda		Coelomates with lophophores (feeding structures bearing ciliated tentacles)
	Metazoa, Eumetazoa, Bilateria, Lophotrochozoa	Mollusca (clams, snails, squids)		Coelomates with three main body parts (muscular foot, visceral mass, mantle); coelom reduced; most have hard shell made of calcium carbonate
	Metazoa, Eumetazoa, Bilateria, Lophotrochozoa	Annelida (segmented worms)		Coelomates with segmented body wall and internal organs (except digestive tract, which is unsegmented)
Concept 33.4 Ecdysozoans are the most species-rich animal group (pp. 683–692) ***?*** *Describe ecological roles of nematodes and arthropods.*	Metazoa, Eumetazoa, Bilateria, Ecdysozoa	Nematoda (roundworms)		Cylindrical, unsegmented pseudocoelomates with tapered ends; no circulatory system; undergo ecdysis
	Metazoa, Eumetazoa, Bilateria, Ecdysozoa	Arthropoda (crustaceans, insects, spiders)		Coelomates with segmented body, jointed appendages, and exoskeleton made of protein and chitin
Concept 33.5 Echinoderms and chordates are deuterostomes (pp. 692–694) ***?*** *You've read that echinoderms and chordates are closely related and have evolved independently for over 500 million years. Explain how both of these statements can be correct.*	Metazoa, Eumetazoa, Bilateria, Deuterostomia	Echinodermata (sea stars, sea urchins)		Coelomates with bilaterally symmetrical larvae and five-part body organization as adults; unique water vascular system; endoskeleton
	Metazoa, Eumetazoa, Bilateria, Deuterostomia	Chordata (lancelets, tunicates, vertebrates)		Coelomates with notochord; dorsal, hollow nerve cord; pharyngeal slits; post-anal tail (see Chapter 34)

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. A land snail, a clam, and an octopus all share
a. a mantle.
b. a radula.
c. gills.
d. embryonic torsion.
e. distinct cephalization.

2. Which phylum is characterized by animals that have a segmented body?
a. Cnidaria
b. Platyhelminthes
c. Porifera
d. Arthropoda
e. Mollusca

3. The water vascular system of echinoderms
a. functions as a circulatory system that distributes nutrients to body cells.
b. functions in locomotion and feeding.
c. is bilateral in organization, even though the adult animal is not bilaterally symmetrical.
d. moves water through the animal's body during suspension feeding.
e. is analogous to the gastrovascular cavity of flatworms.

4. Which of the following combinations of phylum and description is *incorrect?*
a. Echinodermata—bilateral symmetry as a larva, coelom present
b. Nematoda—roundworms, pseudocoelomate
c. Cnidaria—radial symmetry, polyp and medusa body forms
d. Platyhelminthes—flatworms, gastrovascular cavity, acoelomate
e. Porifera—gastrovascular cavity, coelom present

LEVEL 2: APPLICATION/ANALYSIS

5. In Figure 33.2, which two main clades branch from the most recent common ancestor of the eumetazoans?
a. Porifera and Cnidaria
b. Lophotrochozoa and Ecdysozoa
c. Cnidaria and Bilateria
d. Rotifera and Deuterostomia
e. Deuterostomia and Bilateria

6. **MAKE CONNECTIONS** In Figure 33.8, assume that the two medusae shown at step 4 were produced by one polyp colony. Review Concept 12.1 (pp. 229–230) and Concept 13.4 (pp. 257–260), and then use your understanding of mitosis and meiosis to evaluate whether the following sentence is true or false. If false, select the answer that provides the correct reason.

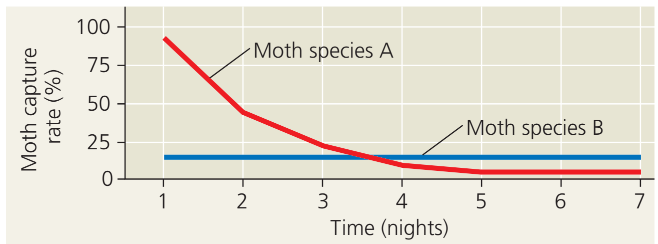
Although the two medusae are genetically identical, a sperm produced by one will differ genetically from an egg produced by the other.

a. F (the medusae are genetically identical, but so are the gametes)
b. F (neither the medusae or the gametes are genetically identical)
c. F (the medusae are not identical but the gametes are)
d. T

LEVEL 3: SYNTHESIS/EVALUATION

7. **EVOLUTION CONNECTION**
DRAW IT Draw a phylogenetic tree of Bilateria that includes the ten phyla of bilaterians discussed in detail in this chapter. Label each branch that leads to a phylum with a C, P, or A, depending on whether members of the phylum are coelomates (C), pseudocoelomates (P), or acoelomates (A). Use your labeled tree to answer the following questions:
a. For each of the three major clades of bilaterians, what (if anything) can be inferred about whether the common ancestor of the clade had a true coelom?
b. To what extent has the presence of a true coelom in animals changed over the course of evolution?

8. **SCIENTIFIC INQUIRY**
Bats emit ultrasonic sounds and then use the returning echoes of those sounds to locate and capture flying insects, such as moths, in the dark. In response to bat attacks, some tiger moths make ultrasonic clicks of their own. Researchers hypothesize that tiger moth clicks likely either (1) jam the bat's sonar or (2) warn the bat about the moth's toxic chemical defenses. The graph below shows two patterns observed in studies of moth capture rates over time.



Bats in these experiments were "naive," meaning that prior to the study the bats had not previously hunted tiger moths. Do the results support hypothesis (1), hypothesis (2), or both? Why did the researchers use naive bats? Explain.

9. **WRITE ABOUT A THEME**
Structure and Function Write a short essay (100–150 words) that explains how the structure of the digestive tract in different invertebrate groups affects the size of the organisms that they can eat.

For selected answers, see Appendix A.