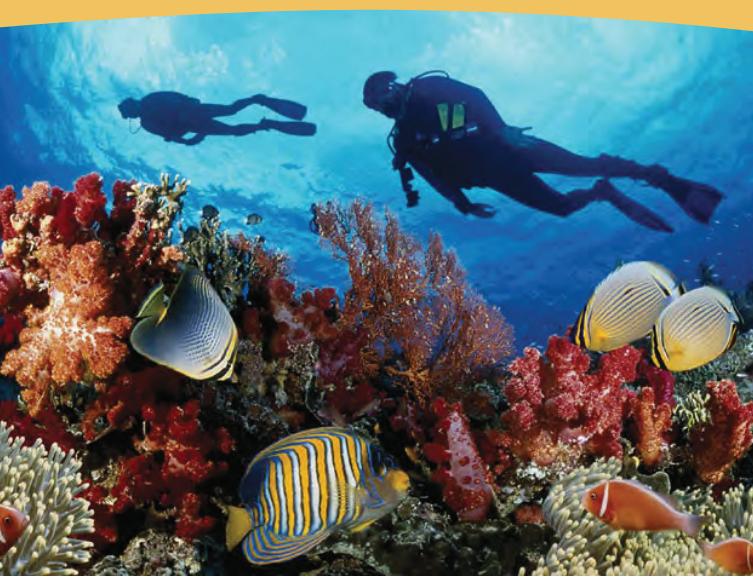


32

An Overview of Animal Diversity



▲ Figure 32.1 Which of these organisms are animals?

EVOLUTION

KEY CONCEPTS

- 32.1 Animals are multicellular, heterotrophic eukaryotes with tissues that develop from embryonic layers
- 32.2 The history of animals spans more than half a billion years
- 32.3 Animals can be characterized by “body plans”
- 32.4 New views of animal phylogeny are emerging from molecular data

OVERVIEW

Welcome to Your Kingdom

Reading the last few chapters, you may have felt like a tourist among some unfamiliar organisms, such as slime molds, whisk ferns, and sac fungi. You probably are more at home with the topic introduced in this chapter—the animal

kingdom, which of course includes yourself. But animal diversity extends far beyond humans and the dogs, cats, birds, and other animals we humans regularly encounter. For example, the diverse organisms in **Figure 32.1** are all animals, including those that appear to resemble lacy branches, thick stems, and curly leaves. To date, biologists have identified 1.3 million extant (living) species of animals. Estimates of the actual number of animal species run far higher. This vast diversity encompasses a spectacular range of morphological variation, from corals to cockroaches to crocodiles.

In this chapter, we embark on a tour of the animal kingdom that will continue in the next two chapters. We will consider the characteristics that all animals share, as well as those that distinguish various taxonomic groups. This information is central to understanding animal phylogeny, a topic that is a lively arena of biological research and debate, as you will read.

CONCEPT 32.1

Animals are multicellular, heterotrophic eukaryotes with tissues that develop from embryonic layers

Listing features shared by all animals is challenging, as there are exceptions to nearly every criterion for distinguishing animals from other life-forms. When taken together, however, several characteristics of animals sufficiently describe the group for our discussion.

Nutritional Mode

Animals differ from both plants and fungi in their mode of nutrition. Plants are autotrophic eukaryotes capable of generating organic molecules through photosynthesis. Fungi are heterotrophs that grow on or near their food and that feed by absorption (often after they have released enzymes that digest the food outside their bodies). Unlike plants, animals cannot construct all of their own organic molecules and so, in most cases, they ingest them—either by eating other living organisms or by eating nonliving organic material. But unlike fungi, most animals do not feed by absorption; instead, animals ingest their food and then use enzymes to digest it within their bodies.

Cell Structure and Specialization

Animals are eukaryotes, and like plants and most fungi, animals are multicellular. In contrast to plants and fungi, however, animals lack the structural support of cell walls. Instead, a variety of proteins external to the cell membrane provide structural support to animal cells and connect them to one another (see Figure 6.30). The most abundant of these proteins is collagen, which is found only in animals.

Many animals have two types of specialized cells not found in other multicellular organisms: muscle cells and nerve cells. In most animals, these cells are organized into **tissues**, groups of cells that have a common structure, function, or both. Muscle tissue and nervous tissue are responsible for moving the body and conducting nerve impulses, respectively. The ability to move and conduct nerve impulses underlies many of the adaptations that differentiate animals from plants and fungi. For this reason, muscle and nerve cells are central to the animal lifestyle.

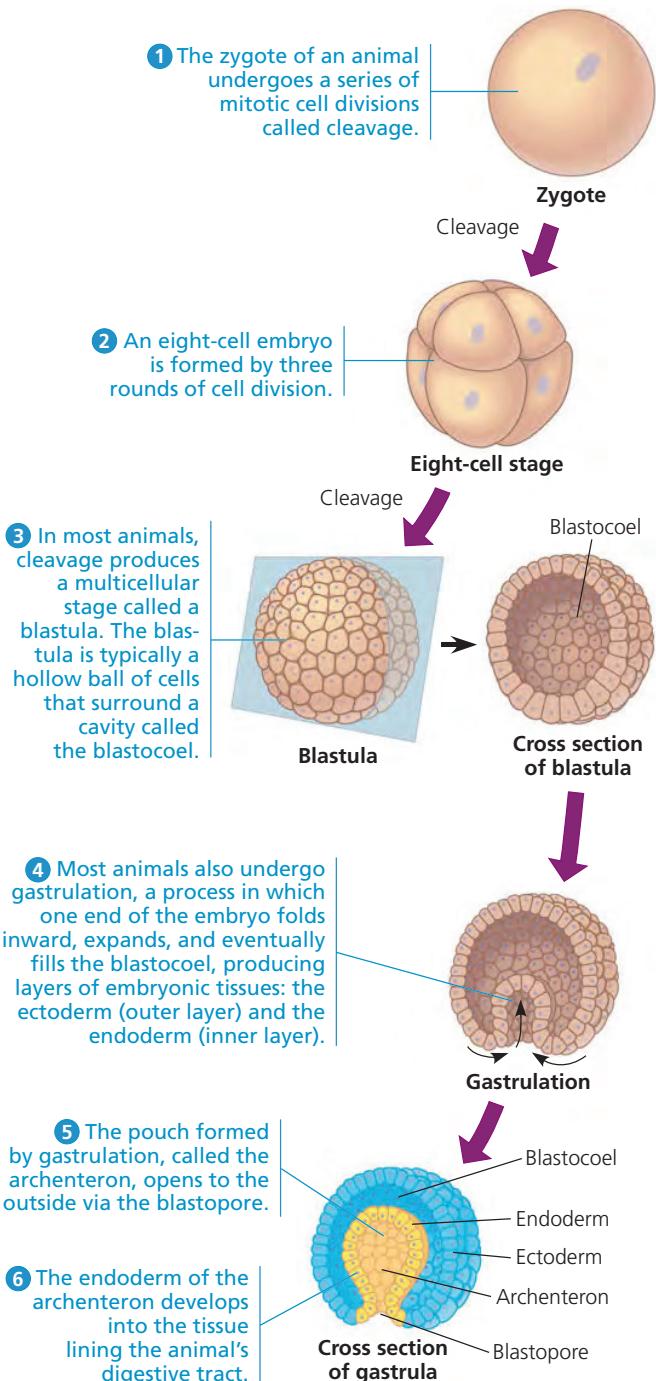
Reproduction and Development

Most animals reproduce sexually, and the diploid stage usually dominates the life cycle. In the haploid stage, sperm and egg cells are produced directly by meiotic division, unlike what occurs in plants and fungi (see Figure 13.6). In most animal species, a small, flagellated sperm fertilizes a larger, nonmotile egg, forming a diploid zygote. The zygote then undergoes **cleavage**, a succession of mitotic cell divisions without cell growth between the divisions. During the development of most animals, cleavage leads to the formation of a multicellular stage called a **blastula**, which in many animals takes the form of a hollow ball (Figure 32.2). Following the blastula stage is the process of **gastrulation**, during which the layers of embryonic tissues that will develop into adult body parts are produced. The resulting developmental stage is called a **gastrula**.

Although some animals, including humans, develop directly into adults, the life cycles of most animals include at least one larval stage. A **larva** is a sexually immature form of an animal that is morphologically distinct from the adult, usually eats different food, and may even have a different habitat than the adult, as in the case of the aquatic larva of a mosquito or dragonfly. Animal larvae eventually undergo **metamorphosis**, a developmental transformation that turns the animal into a juvenile that resembles an adult but is not yet sexually mature.

Although adult animals vary widely in morphology, the genes that control animal development are similar across a broad range of taxa. All animals have developmental genes that regulate the expression of other genes, and many of these regulatory genes contain sets of DNA sequences called *homeoboxes* (see Chapter 21). Most animals share a unique homeobox-containing family of genes, known as *Hox* genes. *Hox* genes play important roles in the development of animal embryos, controlling the expression of dozens or even hundreds of other genes that influence animal morphology (see Chapter 25).

Sponges, which are among the simplest extant animals, lack *Hox* genes. However, they have other homeobox genes that influence their shape, such as those that regulate the formation of water channels in the body wall, a key feature of sponge morphology (see Figure 33.4). In the ancestors of more complex animals, the *Hox* gene family arose via the duplication of



▲ **Figure 32.2** Early embryonic development in animals.

earlier homeobox genes. Over time, the *Hox* gene family underwent a series of duplications, yielding a versatile “toolkit” for regulating development. In vertebrates, insects, and most other animals, *Hox* genes regulate the formation of the anterior-posterior (front-to-back) axis, as well as other aspects of development. Similar sets of conserved genes govern the development of both flies and humans, despite their obvious differences and hundreds of millions of years of divergent evolution.

CONCEPT CHECK 32.1

- Summarize the main stages of animal development. What family of control genes plays a major role?
- WHAT IF?** What animal characteristics would be needed by an imaginary plant that could chase, capture, and digest its prey—yet could also extract nutrients from soil and conduct photosynthesis?
- MAKE CONNECTIONS** Humans have about the same number of protein-coding genes as do animals such as tunicates (see photograph) that have very simple body forms and few neurons. In contrast, humans have many more microRNA molecules (miRNAs) than these animals. Review Concept 18.3 (pp. 365–366); then suggest a possible reason for this observation.



For suggested answers, see Appendix A.

animal species are extinct.) Various studies suggest that this great diversity originated during the last billion years. For example, some estimates based on molecular clocks suggest that the ancestors of animals diverged from the ancestors of fungi about a billion years ago. Other such studies have estimated that the common ancestor of living animals lived sometime between 800 and 675 million years ago.

To learn what this common ancestor may have been like, scientists have sought to identify protist groups that are closely related to animals. As shown in **Figure 32.3**, a combination of morphological and molecular evidence indicates that choanoflagellates are among the closest living relatives of animals. Based on such evidence, researchers hypothesize that the common ancestor of living animals may have been a suspension feeder similar to present-day choanoflagellates. We will next survey the fossil evidence for how animals evolved from their distant common ancestor over four geologic eras (see Table 25.1 to review the geologic time scale).

Neoproterozoic Era (1 Billion–542 Million Years Ago)

Despite the molecular data indicating an earlier origin of animals, the first generally accepted macroscopic fossils of animals date from 565 to 550 million years ago. These fossils are members of an early group of soft-bodied multicellular eukaryotes, known collectively as the **Ediacaran biota**. The name comes from the Ediacara Hills of Australia, where these animals were first discovered (**Figure 32.4**). Similar fossils have since been found on other continents.

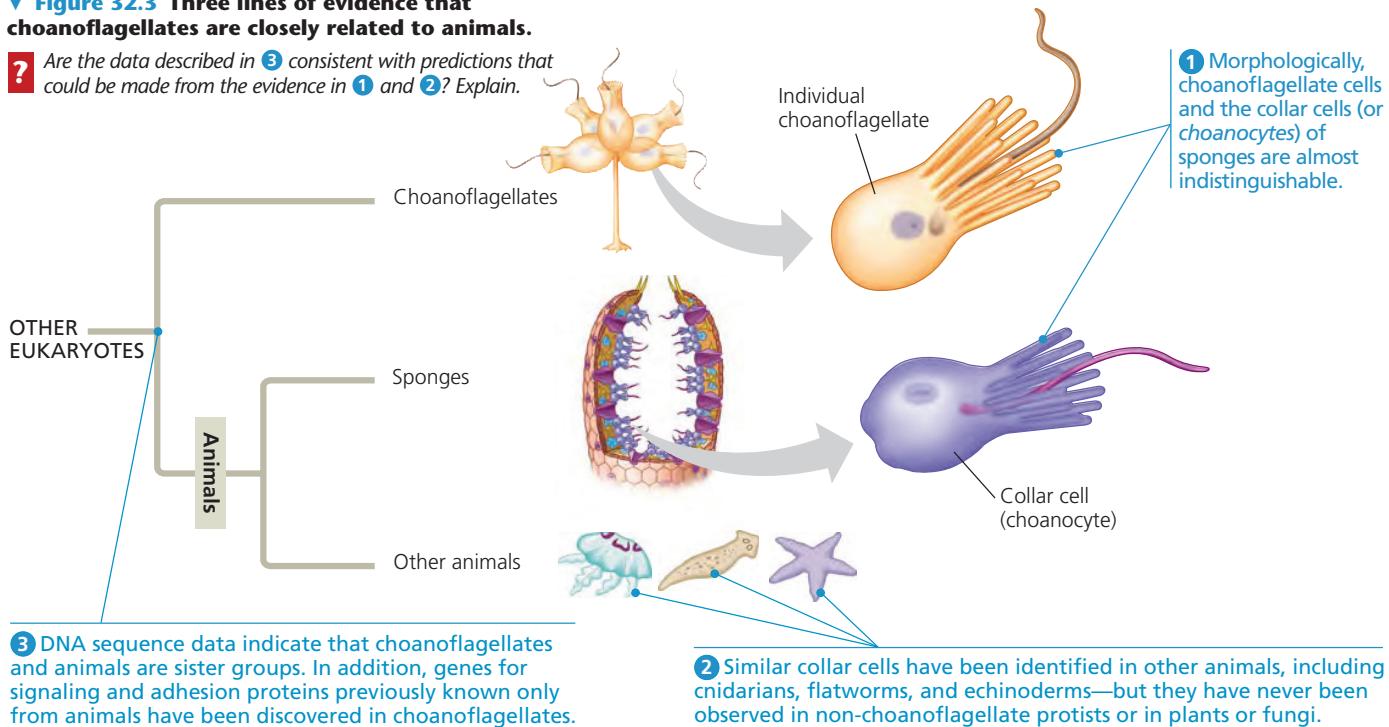
CONCEPT 32.2

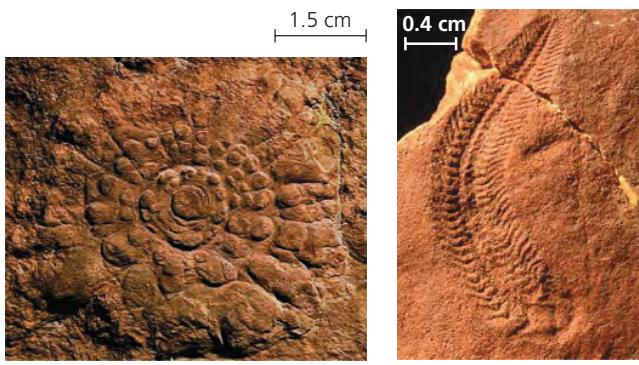
The history of animals spans more than half a billion years

The animal kingdom includes not only a great diversity of living species, but an even greater diversity of extinct ones. (Some paleontologists have estimated that over 99% of all

▼ **Figure 32.3** Three lines of evidence that choanoflagellates are closely related to animals.

? Are the data described in ③ consistent with predictions that could be made from the evidence in ① and ②? Explain.





(a) *Mawsonites spriggi*

(b) *Spriggina flindersi*

▲ **Figure 32.4 Ediacaran fossils.** Fossils dating to 565–550 million years ago include animals (a) with simple, radial forms and (b) with many body segments.

Some are sponges, while others may be related to living cnidarians. Still others of these fossil organisms have proved difficult to classify, as they do not seem to be closely related to any living animal or algal groups.

In addition to these macroscopic fossils, Neoproterozoic rocks have also yielded what may be microscopic signs of early animals. As you read in Chapter 25, 575-million-year-old microfossils discovered in China appear to exhibit the basic structural organization of present-day animal embryos. However, debate continues about whether the fossil embryos are animals or are members of extinct groups that are closely related to animals (but are not actually animals). Though older fossils of animals may be discovered in the future, the fossil record as it is known today shows that the late Neoproterozoic era was a time of increasing animal diversity.

Paleozoic Era (542–251 Million Years Ago)

Another wave of animal diversification occurred 535–525 million years ago, during the Cambrian period of the Paleozoic era—a phenomenon referred to as the **Cambrian explosion** (see Chapter 25). In strata formed before the Cambrian explosion, only a few animal phyla have been observed. But in strata that are 535–525 million years old, paleontologists have found the oldest fossils of about half of all extant animal phyla, including the first arthropods, chordates, and echinoderms. Many of these distinctive fossils, which include the first animals with hard, mineralized skeletons, look very different from most living animals (Figure 32.5). But for the most part, paleontologists have established that these Cambrian fossils are members of extant animal phyla, or at least are close relatives.

The increase in the diversity of animal phyla during the Cambrian was accompanied by a decline in the diversity of Ediacaran life-forms. What caused these trends? There are several current hypotheses. Some evidence suggests that during the Cambrian period, predators acquired novel adaptations,



▲ **Figure 32.5 A Cambrian seascape.** This artist's reconstruction depicts a diverse array of organisms found in fossils from the Burgess Shale site in British Columbia, Canada. The animals include *Pikaia* (eel-like chordate at top left), *Marella* (arthropod swimming at left), *Anomalocaris* (large animal with anterior grasping limbs and a circular mouth), and *Hallucigenia* (animal with toothpick-like spikes on the seafloor).

such as forms of locomotion that helped them catch prey, while prey species acquired new defenses, such as protective shells. As new predator-prey relationships emerged, natural selection may have led to the decline of some groups and the rise of others. Another hypothesis focuses on an increase in atmospheric oxygen that preceded the Cambrian explosion. More plentiful oxygen would have enabled animals with higher metabolic rates and larger body sizes to thrive, while potentially harming other species. A third hypothesis proposes that the origin of *Hox* genes and other genetic changes affecting the regulation of developmental genes facilitated the evolution of new body forms. These hypotheses are not mutually exclusive, however; predator-prey relationships, atmospheric changes, and changes in the regulation of development may each have played a role.

The Cambrian period was followed by the Ordovician, Silurian, and Devonian periods, when animal diversity continued to increase, although punctuated by episodes of mass extinction (see Figure 25.15). Vertebrates (fishes) emerged as the top predators of the marine food web. By 460 million years ago, groups that diversified during the Cambrian period were making an impact on land. Arthropods began to adapt to terrestrial habitats, as indicated by the appearance of millipedes and centipedes. Another clue is seen in fossilized fern galls—enlarged cavities that fern plants form in response to stimulation by resident insects, which then use the galls for protection. Fossils indicate that fern galls date back at least

302 million years, suggesting that insects and plants were influencing each other's evolution by that time.

Vertebrates made the transition to land around 365 million years ago and diversified into numerous terrestrial groups. Two of these survive today: the amphibians (such as frogs and salamanders) and the amniotes (reptiles, including birds, and mammals). We will explore these groups, known collectively as the tetrapods, in more detail in Chapter 34.

Mesozoic Era (251–65.5 Million Years Ago)

The animal phyla that had evolved during the Paleozoic now began to spread into new habitats. In the oceans, the first coral reefs formed, providing other marine animals with new habitats. Some reptiles returned to the water, leaving plesiosaurs (see Figure 25.4) and other large aquatic predators as their descendants. On land, descent with modification in some tetrapods led to the origin of wings and other flight equipment in pterosaurs and birds. Large and small dinosaurs emerged, both as predators and herbivores. At the same time, the first mammals—tiny nocturnal insect-eaters—appeared on the scene. In addition, as you read in Chapter 30, flowering plants (angiosperms) and insects both underwent dramatic diversifications during the late Mesozoic.

Cenozoic Era (65.5 Million Years Ago to the Present)

Mass extinctions of both terrestrial and marine animals ushered in a new era, the Cenozoic. Among the groups of species that disappeared were the large, nonflying dinosaurs and the marine reptiles. The fossil record of the early Cenozoic documents the rise of large mammalian herbivores and predators as mammals began to exploit the vacated ecological niches. The global climate gradually cooled throughout the Cenozoic, triggering significant shifts in many animal lineages. Among primates, for example, some species in Africa adapted to the open woodlands and savannas that replaced many of the former dense forests. The ancestors of our own species were among those grassland apes.

CONCEPT CHECK 32.2

- Put the following milestones in animal evolution in chronological order from oldest to most recent:
(a) origin of mammals, (b) earliest evidence of terrestrial arthropods, (c) Ediacaran fauna, (d) extinction of large, nonflying dinosaurs.
- WHAT IF?** Suppose the most recent common ancestor of fungi and animals lived 1 billion years ago. If the first fungi lived 990 million years ago, would animals also have been alive at that time? Explain.

For suggested answers, see Appendix A.

CONCEPT 32.3

Animals can be characterized by “body plans”

Animal species vary tremendously in morphology, but their great diversity in form can be described by a relatively small number of major “body plans.” A **body plan** is a particular set of morphological and developmental traits, integrated into a functional whole—the living animal. The term *plan* here does not imply that animal forms are the result of conscious planning or invention. But body plans do provide a succinct way to compare and contrast key animal features. They also are of interest in the study of *evo-devo*, the interface between evolution and development (see Chapters 21 and 25).

Like all features of organisms, animal body plans have evolved over time. Some of the evolutionary changes appear to have occurred early in the history of animal life. For example, recent research suggests that a key step in the molecular control of gastrulation has remained unchanged for more than 500 million years (Figure 32.6). This early evolutionary innovation was of fundamental importance: Gastrulation helps to explain why most animals are not a hollow ball of cells. As we'll discuss, however, other aspects of animal body plans have changed multiple times over the course of evolution. Thus, as we explore the major features of animal body plans, bear in mind that similar body forms may have evolved independently in different lineages. In addition, body features can be lost over the course of evolution, causing some closely related species to look very different from one another.

Symmetry

A basic feature of animal bodies is their type of symmetry—or absence of symmetry. (Many sponges, for example, lack symmetry altogether.) Some animals exhibit **radial symmetry**, the type of symmetry found in a flowerpot (Figure 32.7a). Sea anemones, for example, have a top side (where the mouth is located) and a bottom side. But they have no front and back ends and no left and right sides.

The two-sided symmetry seen in a shovel is an example of **bilateral symmetry** (Figure 32.7b). A bilaterally symmetrical animal has two axes of orientation: front to back and top to bottom. Such animals have a **dorsal** (top) side and a **ventral** (bottom) side, a left side and a right side, and an **anterior** (front) end and a **posterior** (back) end. Many animals with a bilaterally symmetrical body plan (such as arthropods and mammals) have sensory equipment concentrated at their anterior end, including a central nervous system (“brain”) in the head—an evolutionary trend called **cephalization** (from the Greek *kephale*, head).

The symmetry of an animal generally fits its lifestyle. Many radial animals are sessile (living attached to a substrate) or planktonic (drifting or weakly swimming, such as jellies,

▼ Figure 32.6

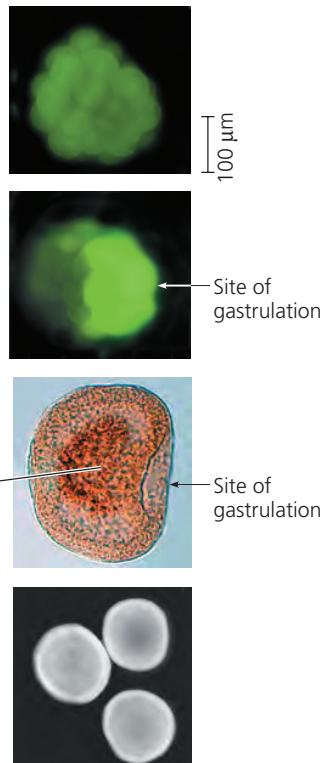
INQUIRY

Did β -catenin play an ancient role in the molecular control of gastrulation?

EXPERIMENT In most animals, gastrulation leads to the formation of three layers of embryonic cells. In some of these species, such as worms, sea urchins, and vertebrates, the protein β -catenin marks the site of gastrulation and activates the transcription of genes necessary for the process. Athula Wikramanayake and Mark Martindale, of the University of Hawaii, and colleagues tested whether β -catenin also helps to control gastrulation in the sea anemone *Nematostella vectensis*. This species is a member of the phylum Cnidaria, a group that predates the origin of animals whose embryos form three layers of cells.

RESULTS

- 1 In early stages of development, β -catenin (here labeled with green fluorescent protein) is found throughout the *N. vectensis* embryo.



- 2 By the 32-cell stage, β -catenin is concentrated on the side of the embryo where gastrulation will occur.

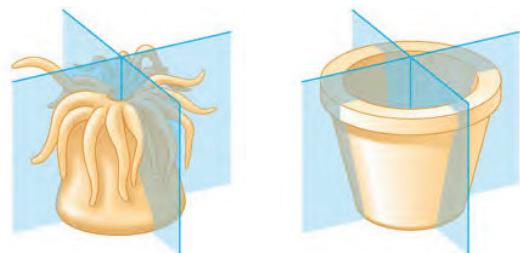
- 3 In the early gastrula stage, β -catenin activity (here stained a darker red) occurs in the inner layer of cells.

- 4 In embryos in which β -catenin activity is blocked (by a protein that binds to β -catenin), gastrulation does not occur.

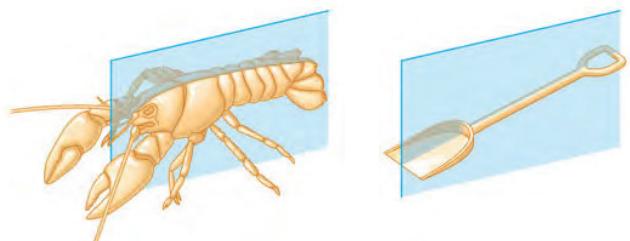
CONCLUSION In *N. vectensis*, β -catenin is required for gastrulation to occur and may help to determine the site of gastrulation. Since the fossil record indicates that cnidarians diverged more than 500 million years ago from species in which β -catenin is known to influence gastrulation, it seems likely that β -catenin played an ancient role in the molecular control of gastrulation.

SOURCE A. H. Wikramanayake et al., An ancient role for nuclear β -catenin in the evolution of axial polarity and germ layer segregation, *Nature* 426:446–450 (2003).

WHAT IF? β -catenin binds to DNA, thereby stimulating the transcription of genes necessary for gastrulation. Based on this information, suggest a different experiment that could be used to confirm the results in step 4. What would be the purpose of performing such an experiment?



(a) Radial symmetry. A radial animal, such as a sea anemone (phylum Cnidaria), does not have a left side and a right side. Any imaginary slice through the central axis divides the animal into mirror images.



(b) Bilateral symmetry. A bilateral animal, such as a lobster (phylum Arthropoda), has a left side and a right side. Only one imaginary cut divides the animal into mirror-image halves.

▲ **Figure 32.7 Body symmetry.** The flowerpot and shovel are included to help you remember the radial-bilateral distinction.

commonly called jellyfishes). Their symmetry equips them to meet the environment equally well from all sides. In contrast, bilateral animals typically move actively from place to place. Most bilateral animals have a central nervous system that enables them to coordinate the complex movements involved in crawling, burrowing, flying, or swimming. Fossil evidence indicates that these two fundamentally different kinds of symmetry have been present for at least 550 million years.

Tissues

Animal body plans also vary with regard to tissue organization. In animals, true tissues are collections of specialized cells isolated from other tissues by membranous layers. While sponges and a few other groups lack true tissues, in all other animals, the embryo becomes layered through the process of gastrulation (see Figure 32.2). As development progresses, these concentric layers, called *germ layers*, form the various tissues and organs of the body. **Ectoderm**, the germ layer covering the surface of the embryo, gives rise to the outer covering of the animal and, in some phyla, to the central nervous system. **Endoderm**, the innermost germ layer, lines the pouch that forms during gastrulation (the archenteron) and gives rise to the lining of the digestive tract (or cavity) and organs such as the liver and lungs of vertebrates.

Animals that have only these two germ layers are said to be **diploblastic**. Diploblasts include the animals called cnidarians (jellies and corals, for example) as well as the comb jellies (see Chapter 33). All bilaterally symmetrical animals have a third

germ layer, called the **mesoderm**, which fills much of the space between the ectoderm and endoderm. Thus, animals with bilateral symmetry are also said to be **triploblastic** (having three germ layers). In triploblasts, the mesoderm forms the muscles and most other organs between the digestive tract and the outer covering of the animal. Triploblasts include a broad range of animals, from flatworms to arthropods to vertebrates. (Although some diploblasts actually do have a third germ layer, it is not nearly as well developed as the mesoderm of animals considered to be triploblastic.)

Body Cavities

Most triploblastic animals have a **body cavity**, a fluid- or air-filled space located between the digestive tract and the outer body wall. This body cavity is also called a **coelom** (from the Greek *koilos*, hollow). A so-called “true” coelom forms from tissue derived from mesoderm. The inner and outer layers of tissue that surround the cavity connect and form structures that suspend the internal organs. Animals with a true coelom are known as **coelomates** (Figure 32.8a).

Some triploblastic animals have a body cavity that is formed from mesoderm and endoderm (Figure 32.8b). Such a cavity is called a “pseudocoelom” (from the Greek *pseudo*, false), and the animals that have one are called **pseudocoelomates**. Despite its name, however, a pseudocoelom is not false; it is a fully functional body cavity. Finally, some triploblastic animals lack a body cavity altogether (Figure 32.8c). They are known collectively as **acoelomates** (from the Greek *a-*, without).

A body cavity has many functions. Its fluid cushions the suspended organs, helping to prevent internal injury. In soft-bodied coelomates, such as earthworms, the coelom contains noncompressible fluid that acts like a skeleton against which muscles can work. The cavity also enables the internal organs to grow and move independently of the outer body wall. If it were not for your coelom, for example, every beat of your heart or ripple of your intestine would warp your body’s surface.

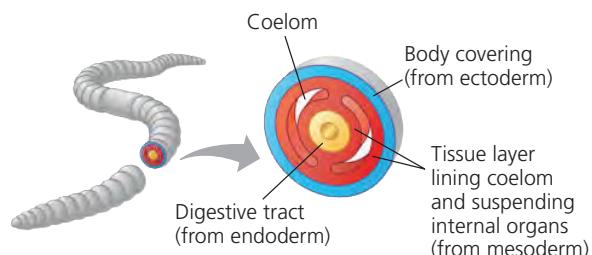
Terms such as *coelomates* and *pseudocoelomates* refer to organisms that have a similar body plan and hence belong to the same *grade* (a group whose members share key biological features). However, phylogenetic studies show that true coeloms and pseudocoeloms have been independently gained or lost multiple times in the course of animal evolution. As illustrated by this example, a grade is not necessarily equivalent to a *clade* (a group that includes an ancestral species and all of its descendants). Thus, while describing an organism as a coelomate or pseudocoelomate can be helpful in describing certain of its features, these terms must be interpreted with caution when seeking to understand evolutionary history.

Protostome and Deuterostome Development

Based on certain aspects of early development, many animals can be described as having one of two developmental modes: **protostome development** or **deuterostome**

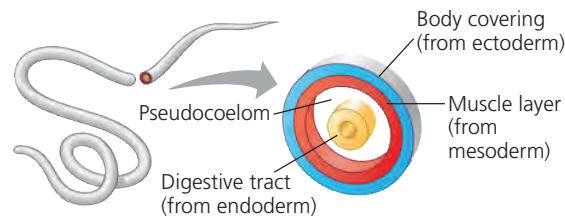
▼ Figure 32.8 Body cavities of triploblastic animals. The various organ systems of a triploblastic animal develop from the three germ layers that form in the embryo. Blue represents tissue derived from ectoderm, red from mesoderm, and yellow from endoderm.

(a) Coelomate



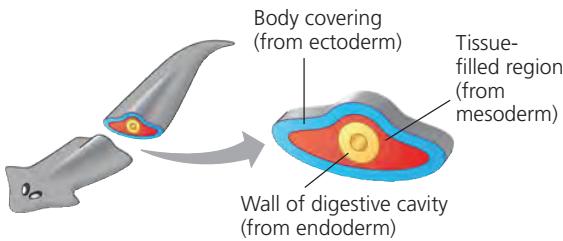
Coelomate, such as earthworms, have a true coelom, a body cavity completely lined by tissue derived from mesoderm.

(b) Pseudocoelomate



Pseudocoelomates, such as roundworms, have a body cavity lined in part by tissue derived from mesoderm, but also by tissue derived from endoderm.

(c) Acoelomate



Acoelomates, such as planarians, lack a body cavity between the digestive cavity and outer body wall.

development. These modes can generally be distinguished by differences in cleavage, coelom formation, and fate of the blastopore.

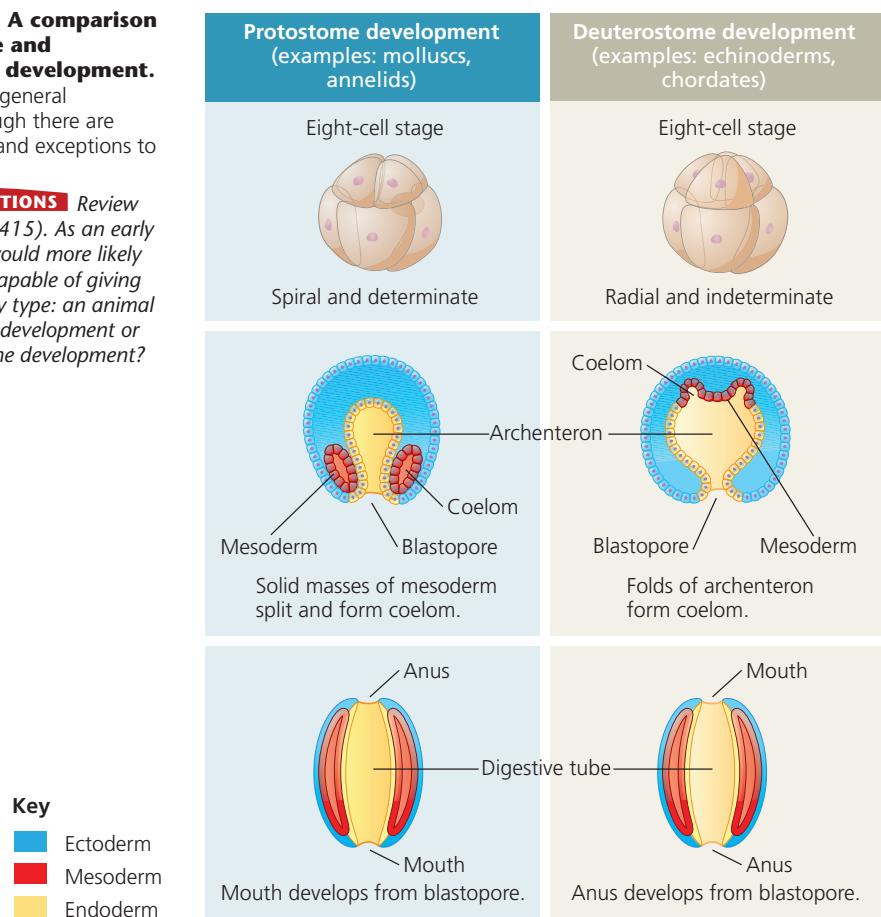
Cleavage

Many animals with protostome development undergo **spiral cleavage**, in which the planes of cell division are diagonal to the vertical axis of the embryo; as seen in the eight-cell stage of the embryo, smaller cells are centered over the grooves between larger, underlying cells (Figure 32.9a, left). Furthermore, the so-called **determinate cleavage** of some animals with protostome development rigidly casts (“determines”) the developmental fate of each embryonic cell very early. A cell

► **Figure 32.9 A comparison of protostome and deuterostome development.**

These are useful general distinctions, though there are many variations and exceptions to these patterns.

MAKE CONNECTIONS Review Figure 20.21 (p. 415). As an early embryo, which would more likely have stem cells capable of giving rise to cells of any type: an animal with protostome development or with deuterostome development? Explain.



isolated from a snail at the four-cell stage, for example, cannot develop into a whole animal. Instead, after repeated divisions, such a cell will form an inviable embryo that lacks many parts.

In contrast to the spiral cleavage pattern, deuterostome development is predominantly characterized by **radial cleavage**. The cleavage planes are either parallel or perpendicular to the vertical axis of the embryo; as seen at the eight-cell stage, the tiers of cells are aligned, one directly above the other (see Figure 32.9a, right). Most animals with deuterostome development also have **indeterminate cleavage**, meaning that each cell produced by early cleavage divisions retains the capacity to develop into a complete embryo. For example, if the cells of a sea urchin embryo are separated at the four-cell stage, each can form a complete larva. Similarly, it is the indeterminate cleavage of the human zygote that makes identical twins possible.

Coelom Formation

During gastrulation, an embryo's developing digestive tube initially forms as a blind pouch, the **archenteron**, which becomes the gut (Figure 32.9b). As the archenteron forms in protostome development, initially solid masses of mesoderm split and form the coelom. In contrast, in deuterostome development, the mesoderm buds from the wall of the archenteron, and its cavity becomes the coelom.

(a) Cleavage. In general, protostome development begins with spiral, determinate cleavage. Deuterostome development is characterized by radial, indeterminate cleavage.

(b) Coelom formation. Coelom formation begins in the gastrula stage. In protostome development, the coelom forms from splits in the mesoderm. In deuterostome development, the coelom forms from mesodermal outpocketings of the archenteron.

(c) Fate of the blastopore. In protostome development, the mouth forms from the blastopore. In deuterostome development, the mouth forms from a secondary opening.

Fate of the Blastopore

Protostome and deuterostome development often differ in the fate of the **blastopore**, the indentation that during gastrulation leads to the formation of the archenteron (Figure 32.9c). After the archenteron develops, in most animals a second opening forms at the opposite end of the gastrula. In many species, the blastopore and this second opening become the two openings of the digestive tube: the mouth and the anus. In protostome development, the mouth generally develops from the first opening, the blastopore, and it is for this characteristic that the term *protostome* derives (from the Greek *protos*, first, and *stoma*, mouth). In deuterostome development (from the Greek *deuteros*, second), the mouth is derived from the secondary opening, and the blastopore usually forms the anus.

CONCEPT CHECK 32.3

- Distinguish the terms *grade* and *clade*.
- Compare three aspects of the early development of a snail (a mollusc) and a human (a chordate).
- WHAT IF?** Evaluate this claim: Ignoring the details of their specific anatomy, worms, humans, and most other triploblasts have a shape analogous to that of a doughnut.

For suggested answers, see Appendix A.

CONCEPT 32.4

New views of animal phylogeny are emerging from molecular data

Zoologists currently recognize about three dozen animal phyla. But the boundaries of and relationships between these phyla continue to be debated. Although it might be frustrating that the phylogenies in textbooks cannot be memorized as set-in-stone truths, the uncertainty inherent in these diagrams is a healthy reminder that science is an ongoing, dynamic process of inquiry.

Researchers have long based their hypotheses about animal phylogeny on morphological data. Now biologists also reconstruct phylogenies using molecular data. Additional clues have come from studies of lesser-known animal phyla, along with fossil data that help clarify when key morphological traits arose in various groups.

Another important change has been the use of cladistics (see Chapter 26). Phylogenetic systematists seek to place organisms into clades, each of which includes an ancestral species and all of its descendants. Based on cladistic methods, a phylogenetic tree takes shape as a hierarchy of clades nested within larger clades—the finer and thicker branches of the tree, respectively. Clades are inferred from shared derived characters that are unique to members of the clade. For example, a clade might be inferred from key anatomical and embryological similarities that researchers conclude are homologous. Molecular data such as DNA sequences are another source of information for inferring common ancestry. But whether the data used are “traditional” morphological characters or “new” molecular sequences or a combination, the goal is the same: to reconstruct evolutionary history.

To get a sense of the debates in animal systematics, we’ll compare a traditional view of animal phylogeny, based primarily on morphological data (**Figure 32.10**), with a more current view, based mainly on molecular data (**Figure 32.11**).

Points of Agreement

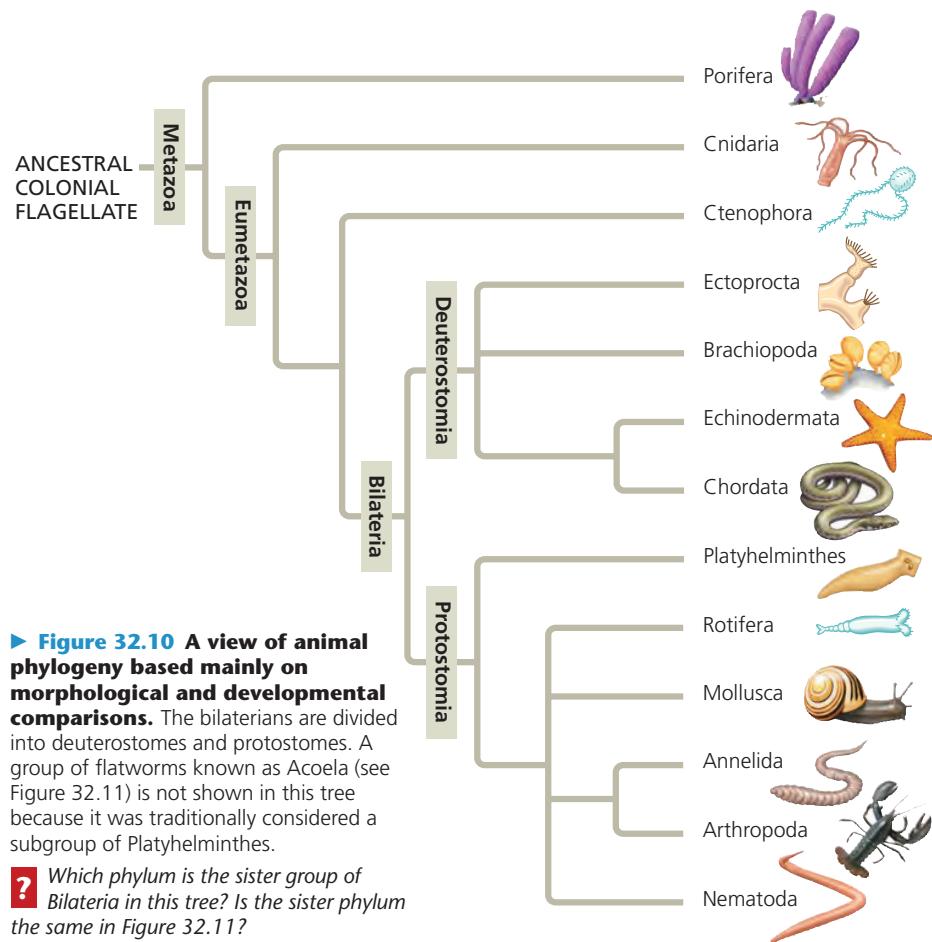
These two views agree on several significant aspects of animal phylogeny. Notice how the following points are reflected in Figures 32.10 and 32.11.

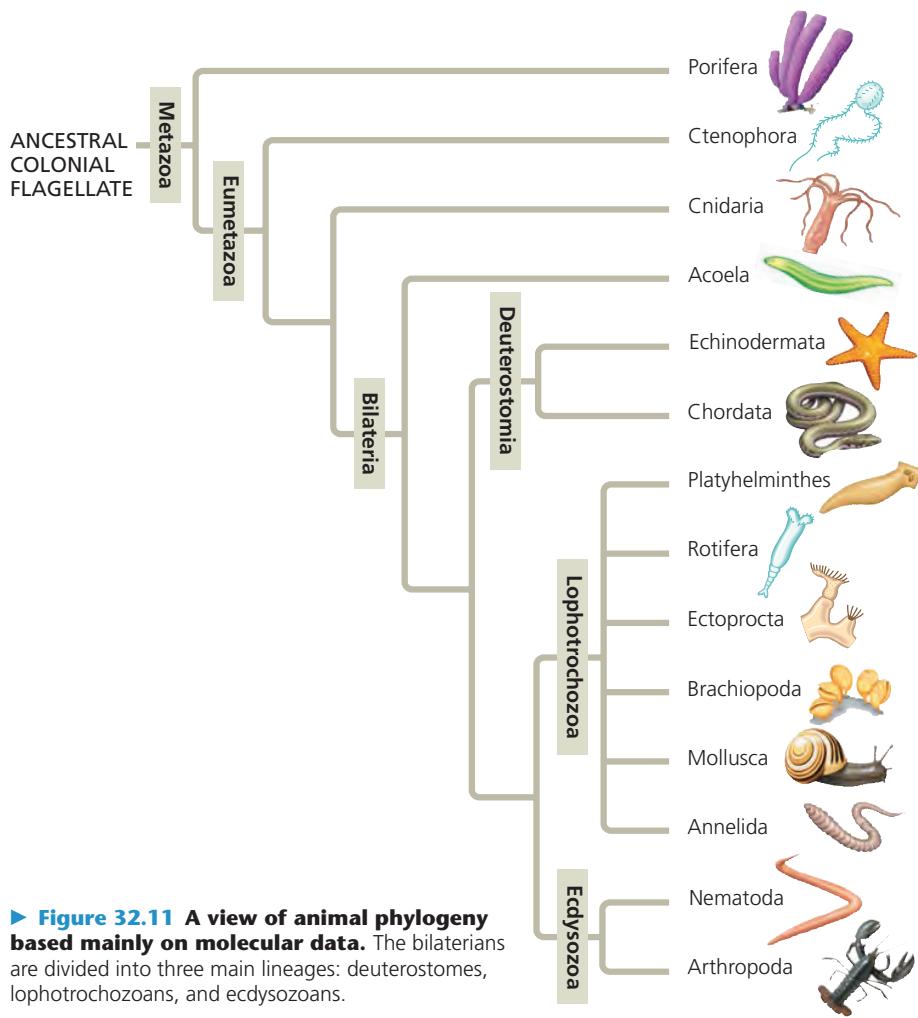
1. All animals share a common ancestor. Both trees indicate that animals are monophyletic, forming a clade called Metazoa. All extant and extinct animal lineages have descended from a common ancestor.

2. Sponges are basal animals. Among the extant taxa, sponges (phylum Porifera) branch from the base of both animal trees. Morphological and molecular analyses published in 2009 indicate that sponges are monophyletic, as shown here; some earlier studies had suggested that sponges are paraphyletic.

3. Eumetazoa is a clade of animals with true tissues. All animals except for sponges and a few others belong to a clade of **eumetazoans** (“true animals”). True tissues evolved in the common ancestor of living eumetazoans. Basal eumetazoans, which include the phyla Ctenophora (comb jellies) and Cnidaria, are diploblastic and generally have radial symmetry.

4. Most animal phyla belong to the clade Bilateria. Bilateral symmetry and the presence of three germ layers are shared derived characters that help define the clade Bilateria. This clade contains the majority of animal phyla, and its members are known as **bilaterians**. The Cambrian explosion was primarily a rapid diversification of bilaterians.





► Figure 32.11 A view of animal phylogeny based mainly on molecular data. The bilaterians are divided into three main lineages: deuterostomes, lophotrochozoans, and ecdysozoans.

5. Chordates and some other phyla belong to the clade Deuterostomia. The term *deuterostome* refers not only to a mode of animal development, but also to the members of a clade that includes vertebrates and other chordates. (Note, however, that the traditional and molecular views of animal phylogeny disagree as to which other phyla are also deuterostomes.)

Progress in Resolving Bilaterian Relationships

While evolutionary relationships inferred from morphological data and molecular data are similar in many respects, there are some differences. For example, the morphology-based tree in Figure 32.10 divides the bilaterians into deuterostomes and protostomes. This view assumes that these two modes of development reflect a phylogenetic pattern. Within the protostomes, arthropods (such as insects and crustaceans) are grouped with annelids. Both groups have segmented bodies (think of the tail of a lobster, which is an arthropod, and an earthworm, which is an annelid).

A different view has emerged from molecular phylogenies based on ribosomal genes, *Hox* genes, and dozens of other

protein-coding nuclear genes, as well as mitochondrial genes. Collectively, these studies indicate that there are three major clades of bilaterally symmetrical animals: the Deuterostomia, Lophotrochozoa, and Ecdysozoa (see Figure 32.11). In contrast to the traditional morphological view, the molecular phylogeny holds that the arthropods and annelids are not closely related to one another. Note also that Figure 32.11 includes a group of acoelomate flatworms (Acoela) not shown in Figure 32.10. Traditionally, acoelomate flatworms were classified with other flatworms in the phylum Platyhelminthes. However, recent research indicates that acoelomate flatworms are basal bilaterians, and not members of the phylum Platyhelminthes. Acoela's basal position suggests that the bilaterians may have descended from a common ancestor that resembled living acoelomate flatworms—that is, from an ancestor that had a simple nervous system, a saclike gut with a single opening (the “mouth”), and no excretory system.

As seen in Figure 32.11, the molecular phylogeny assigns the animal phyla that are not in Deuterostomia to two taxa rather than one: the

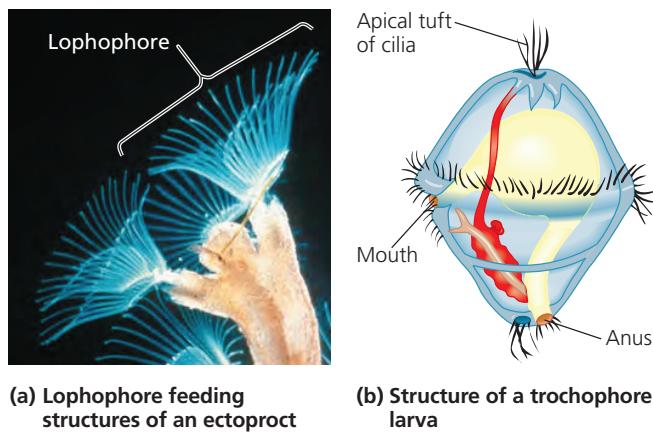
ecdysozoans and the **lophotrochozoans**. The clade name Ecdysozoa refers to a characteristic shared by nematodes, arthropods, and some of the other ecdysozoan phyla that are not included in our survey. These animals secrete external skeletons (exoskeletons); the stiff covering of a cicada or cricket is an example. As the animal grows, it molts, squirming out of its old exoskeleton and secreting a larger one. The process of shedding the old exoskeleton is called *ecdysis* (Figure 32.12). Though named for this characteristic, the



► Figure 32.12 Ecdysis. This molting cicada is in the process of emerging from its old exoskeleton. The animal will now secrete a new, larger exoskeleton.

clade was proposed mainly on the basis of molecular data that support the common ancestry of its members. Furthermore, some taxa excluded from this clade by their molecular data, such as certain species of leeches, do in fact molt.

The name Lophotrochozoa refers to two different features observed in some animals belonging to this clade. Some lophotrochozoans, such as ectoprocts, develop a structure called a **lophophore** (from the Greek *lophos*, crest, and *pherein*, to carry), a crown of ciliated tentacles that function in feeding (**Figure 32.13a**). Individuals in other phyla, including molluscs and annelids, go through a distinctive developmental stage called the **trochophore larva** (**Figure 32.13b**)—hence the name lophotrochozoan.



▲ Figure 32.13 Morphological characteristics of lophotrochozoans.

Future Directions in Animal Systematics

Like any area of scientific inquiry, animal systematics is a work in progress. At present, most systematists think that the tree shown in Figure 32.11 is more strongly supported than is the tree shown in Figure 32.10. Of course, as new information emerges, our understanding of the evolutionary relationships shown in these trees may change. Researchers continue to conduct large-scale analyses of multiple genes and morphological traits across a wide sample of animal phyla. A better understanding of the relationships between these phyla will give scientists a clearer picture of how the diversity of animal body plans arose. In Chapters 33 and 34, we will take a closer look at the diverse phyla of extant animals and their evolutionary history.

CONCEPT CHECK 32.4

- Describe the evidence that cnidarians share a more recent common ancestor with other animals than with sponges.
- How do the phylogenetic hypotheses presented in Figures 32.10 and 32.11 differ in structuring the major branches within the clade Bilateria?
- MAKE CONNECTIONS** Based on the phylogeny in Figure 32.11 and the information in Figure 25.10 (p. 518), evaluate this statement: “The Cambrian explosion actually consists of three explosions, not one.”

For suggested answers, see Appendix A.

32 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 32.1

Animals are multicellular, heterotrophic eukaryotes with tissues that develop from embryonic layers (pp. 654–656)

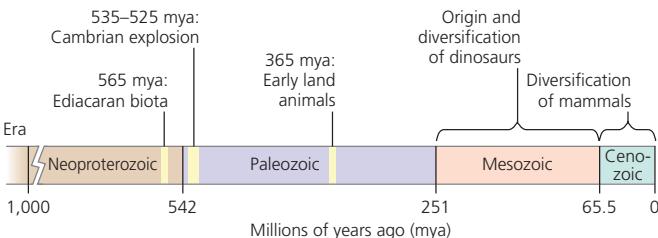
- Animals are heterotrophs that ingest their food.
- Animals are multicellular eukaryotes. Their cells are supported and connected to one another by collagen and other structural proteins located outside the cell membrane. Nervous tissue and muscle tissue are key animal features.
- In most animals, **gastrulation** follows the formation of the **blastula** and leads to the formation of embryonic tissue layers. All animals have *Hox* genes that regulate the development of body form. Although *Hox* genes have been highly conserved over the course of evolution, they can produce a wide diversity of animal morphology.

?

Describe key ways that animals differ from plants and fungi.

CONCEPT 32.2

The history of animals spans more than half a billion years (pp. 656–658)



?

What caused the Cambrian explosion? Describe current hypotheses.

CONCEPT 32.3

Animals can be characterized by “body plans” (pp. 658–661)

- Animals may lack symmetry or may have radial or bilateral symmetry. Bilaterally symmetrical animals have dorsal and ventral sides, as well as anterior and posterior ends.

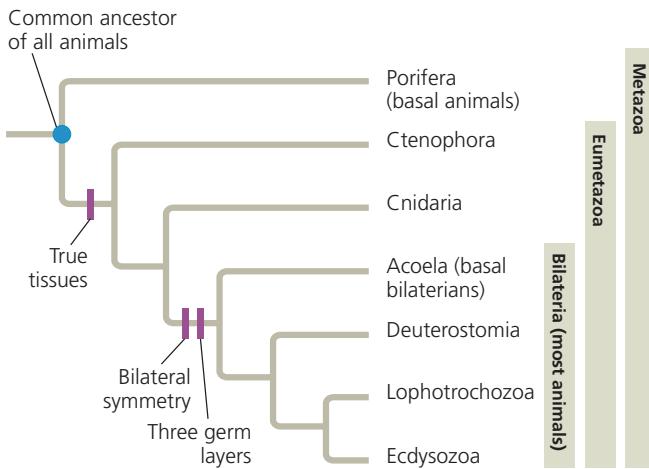
- Among eumetazoans (animals with true tissues), embryos may be **diploblastic** (having two germ layers) or **triploblastic** (having three germ layers).
- In triploblastic animals, a body cavity may be present or absent. A body cavity can be a **pseudocoelom** (derived from both mesoderm and endoderm) or a true **coelom** (derived only from mesoderm).
- Protostome** and **deuterostome** development often differ in patterns of cleavage, coelom formation, and blastopore fate.

? *Describe how body plans provide useful information yet should be interpreted cautiously when scientists are trying to understand evolutionary relationships.*

CONCEPT 32.4

New views of animal phylogeny are emerging from molecular data (pp. 662–664)

This phylogenetic tree shows key steps in animal evolution:



? *Describe the data and methods used today to reconstruct animal phylogeny.*

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

- Among the characteristics unique to animals is
 - gastrulation.
 - multicellularity.
 - sexual reproduction.
 - flagellated sperm.
 - heterotrophic nutrition.
- The distinction between sponges and other animal phyla is based mainly on the absence versus the presence of
 - a body cavity.
 - a complete digestive tract.
 - a circulatory system.
 - true tissues.
 - mesoderm.
- Acoelomates are characterized by
 - the absence of a brain.
 - the absence of mesoderm.
 - deuterostome development.
 - a coelom that is not completely lined with mesoderm.
 - a solid body without a cavity surrounding internal organs.
- Which of the following was probably the *least* important factor in bringing about the Cambrian explosion?
 - the emergence of predator-prey relationships among animals
 - the accumulation of diverse adaptations, such as shells and different modes of locomotion
 - the movement of animals onto land

- the origin of *Hox* genes and other genetic changes affecting the regulation of developmental genes
- the accumulation of sufficient atmospheric oxygen to support the more active metabolism of mobile animals

LEVEL 2: APPLICATION/ANALYSIS

- Which of these is a point of conflict between the phylogenetic analyses presented in Figures 32.10 and 32.11?
 - the monophyly of the animal kingdom
 - the relationship of taxa of segmented animals to taxa of nonsegmented animals
 - that sponges are basal animals
 - that chordates are deuterostomes
 - the monophyly of the bilaterians

LEVEL 3: SYNTHESIS/EVALUATION

6. EVOLUTION CONNECTION

A professor begins a lecture on animal phylogeny by saying, “We are all worms.” In this context, what did she mean?

7. SCIENTIFIC INQUIRY

DRAW IT Redraw the bilaterian portion of Figure 32.11 for the nine phyla in the table below. Consider these blastopore fates: protostomy (mouth develops from the blastopore), deuterostomy (anus develops from the blastopore), or neither (the blastopore closes and the mouth develops elsewhere). Depending on the blastopore fate of its members, label each branch that leads to a phylum with P, D, N, or a combination of these letters. What is the ancestral blastopore fate? How many times has blastopore fate changed over the course of evolution? Explain.

Blastopore Fate	Phyla
Protostomy (P)	Platyhelminthes, Rotifera, Nematoda; most Mollusca, most Annelida; few Arthropoda
Deuterostomy (D)	Echinodermata, Chordata; most Arthropoda; few Mollusca, few Annelida
Neither (N)	Acoela

Source: A. Hejnol and M. Martindale, The mouth, the anus, and the blastopore—open questions about questionable openings. In *Animal Evolution: Genomes, Fossils and Trees*, eds. D. T. J. Littlewood and M. J. Telford, Oxford University Press, pp. 33–40 (2009).

8. WRITE ABOUT A THEME

Feedback Regulation Animal life changed greatly during the Cambrian explosion, with some groups expanding in diversity and others declining. Write a short essay (100–150 words) interpreting these events as feedback regulation at the level of the biological community.

For selected answers, see Appendix A.

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