32 Animal Origins and the Evolution of Body Plans

In 1822, nearly forty years before Darwin wrote *The Origin of Species*, a French naturalist, Étienne Geoffroy Saint-Hilaire, was examining a lobster. He noticed that when he turned the lobster upside down and viewed it with its ventral surface up, its central nervous system was located above its digestive tract, which in turn was located above its heart—the same relative positions these systems have in mammals when viewed *dorsally*. His observations led Geoffroy to conclude that the differences between arthropods (such as lobsters) and vertebrates (such as mammals) could be explained if the embryos of one of those groups were inverted during development.

Geoffroy's suggestion was regarded as preposterous at the time and was largely dismissed until recently. However, the discovery of two genes that influence a system of extracellular signals involved in development has lent new support to Geoffroy's seemingly outrageous hypothesis.

A vertebrate gene called *chordin* helps to establish cells on one side of the embryo as dorsal and on the other as ventral. A probably homologous gene in fruit flies, called *sog*, acts in a similar manner, but has the opposite effect. Fly cells where *sog* is active become ventral, whereas vertebrate cells where *chordin* is active become dorsal. However, when *sog* mRNA is injected into an embryo of the frog *Xenopus*, a vertebrate, it causes dorsal development. *Chordin* mRNA injected into fruit flies promotes ventral development. In both cases, injection of the mRNA promotes the development of the portion of the embryo that contains the central nervous system!

Chordin and *sog* are among many genes that regulate similar functions in very different organisms. Such genes are providing evolutionary biologists with information that can help them understand relationships among animal lineages that separated from one another in ancient times. As we saw in Chapter 25, new knowledge about gene functions and gene sequences is increasingly being used to infer evolutionary relationships.

In this chapter, we will apply the methods described in Chapter 25 to infer evolutionary relationships among the animals. First, we will review the defining characteristics of the animal way of life. Then we will describe several lineages of simple animals. Finally, we will describe the lophotro-

Genes that Control Development A human and a lobster carry similar genes that control the development of the body axis, but these genes position their body systems inversely. A lobster's nervous system runs up its ventral (belly) surface, whereas a vertebrate's runs down its dorsal (back) surface.

chozoans, one of the three great evolutionary lineages of animals. In the next two chapters, we will discuss the other two great animal lineages, the ecdysozoans and the deuterostomes.

Animals: Descendants of a Common Ancestor

Biologists have long debated whether animals arose once or several times from protist ancestors, but enough molecular and morphological evidence has now been assembled to indicate that, with the possible exception of sponges (Porifera), the Kingdom Animalia is a monophyletic group—that is, all animals are descendants of a single ancestral lineage. This conclusion is supported by the fact that all animals share several derived traits:

- Similarities in their small-subunit ribosomal RNAs (see Chapter 26)
- Similarities in their Hox genes (see Chapter 20)
- Special types of cell–cell junctions: tight junctions, desmosomes, and gap junctions (see Figure 5.6)
- A common set of extracellular matrix molecules, including collagen (see Figure 4.26)

Animals evolved from colonial flagellated protists as a result of division of labor among their aggregated cells. Within the ancestral colonies of cells—perhaps analogous to those still existing in the chlorophyte *Volvox* or some colonial choanoflagellates (see Figures 28.25*a* and 28.28)—some cells became specialized for movement, others became specialized for nutrition, and still others differentiated into gametes. Once this specialization by function had begun, working groups of cells continued to differentiate while improving their coordination with other groups of cells. Such coordinated groups of cells evolved into the larger and more complex organisms that we now call **animals**.

Animals are multicellular heterotrophs

What traits characterize the animals? In contrast to the Bacteria, Archaea, and most protists, all animals are *multicellular*. Unlike plants, animals must take in pre-formed organic molecules because they cannot synthesize them from inorganic chemicals. They acquire these organic molecules by ingesting other organisms or their products, either living or dead, and digesting them inside their bodies; thus animals are *heterotrophs*. Most animals have *circulatory systems* that take up O_2, get rid of CO_2, and carry nutrients from their guts to other body tissues.

To acquire food, animals must expend energy either to move through the environment and position themselves where food will pass close to them, or to move the environment and the food it contains to them. The foods animals ingest include most other members of the animal kingdom as well as members of all other kingdoms. Much of the diversity of animal sizes and shapes evolved as animals acquired the ability to capture and eat many different kinds of food and to avoid becoming food for other animals. The need to locate food has favored the evolution of sensory structures to provide animals with detailed information about their environment and nervous systems to receive and coordinate that information.

The accounts in this chapter and the following two chapters serve as an orientation to the major groups of animals, their similarities and differences, and the evolutionary pathways that resulted in the current richness of animal lineages and species. But how do biologists infer evolutionary relationships among animals?

Several traits show evolutionary relationships among animals

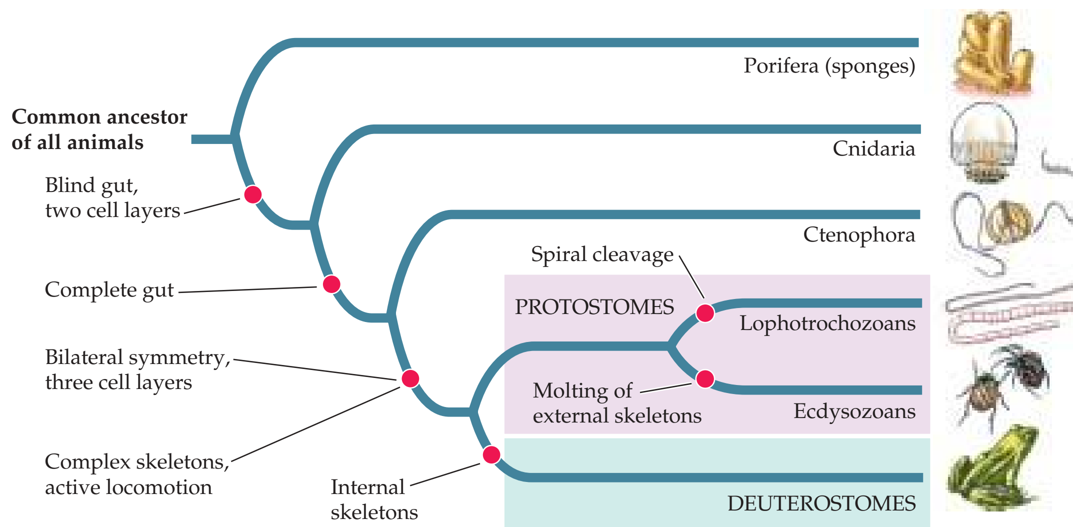
Biologists use a variety of traits in their efforts to infer animal phylogenies. Clues to these relationships are found in the fossil record, in patterns of embryonic development, in the comparative morphology and physiology of living and fossil animals, and in the structure of animal molecules, especially small subunit rRNAs and mitochondrial genes (see Chapters 25 and 26).

Using this wide variety of comparative data, zoologists concluded that sponges, cnidarians, and ctenophores separated from the remaining animal lineages early in evolutionary history. Biologists have divided the remaining animals into two major lineages: the protostomes and the deuterostomes. Figure 32.1 shows the postulated order of divergence of the major animal groups that we will use in these three chapters.

Several differences in patterns of embryonic development provide clues to animal phylogeny. During the development of an animal from a single-celled zygote to a multicellular adult, distinct layers of cells form. The embryos of **diploblastic** animals have only two of these cell layers: an outer *ectoderm* and an inner *endoderm*. The embryos of **triploblastic** animals have, in addition to ectoderm and endoderm, a third layer, the *mesoderm*, which lies between the ectoderm and the endoderm. The existence of three cell layers distinguishes the protostomes and deuterostomes from those groups of simple animals that diverged from them earlier.

During early development in many animals, a cavity forms in a spherical embryo. The opening of this cavity is called the *blastopore*. Among the **protostomes** (from the Greek, "mouth first"), the mouth arises from the blastopore; the anus forms later. Among the **deuterostomes** ("mouth second"), the blastopore becomes the anus; the mouth forms later.

In the common ancestor of the protostomes and deuterostomes, the pattern of early cleavage of the fertilized egg was



32.1 A Current Phylogeny of the Animals The phylogenetic tree used in this and the following two chapters assumes that the animals are monophyletic. The characters highlighted by red circles on the tree will be explained as we discuss the different phyla.

radial (see Figure 20.4). This cleavage pattern persisted during the evolution of the deuterostomes and in many protostomate lineages, but spiral cleavage evolved in one major protostomate lineage, as we will see.

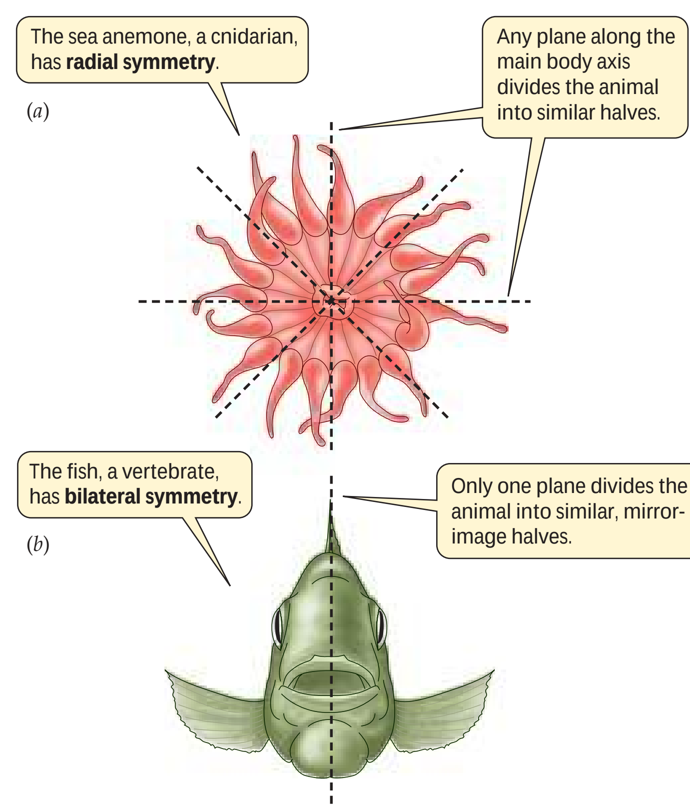
Body Plans: Basic Structural Designs

The general structure of an animal, its organ systems, and the integrated functioning of its parts are known as its **body plan**. A fundamental aspect of an animal's body plan is its overall shape, described in part by its **symmetry**. A symmetrical animal can be divided along at least one plane into similar halves. Animals that have no plane of symmetry are said to be **asymmetrical**. Many sponges are asymmetrical, but most animals have some kind of symmetry.

The simplest form of symmetry is **spherical symmetry**, in which body parts radiate out from a central point. An infinite number of planes passing through the central point can divide a spherically symmetrical organism into similar halves. Spherical symmetry is widespread among the protists, but most animals possess other forms of symmetry.

An organism with **radial symmetry** has one main axis around which its body parts are arranged. A perfectly radially symmetrical animal can be divided into similar halves by any plane that contains the main axis. Some simple sponges and a few other animals, such as sea anemones (Figure 32.2*a*), have radial symmetry. Most radially symmetrical animals are slightly modified so that fewer planes can divide them into identical halves. Two animal phyla—Cnidaria and Ctenophora—are composed primarily of radially symmetrical animals. These animals move slowly or not at all.

Bilateral symmetry is a common characteristic of animals that move rapidly through their environments. A bilaterally symmetrical animal can be divided into mirror images (left and right sides) by a single plane that passes through the dorsoventral midline of its body from the front (*anterior*) to the back (*posterior*) end (Figure 32.2*b*). A plane at right angles to the first one divides the body into two dissimilar sides; the back side of a bilaterally symmetrical animal is its *dorsal* surface; the belly side is its *ventral* surface.



32.2 Body Symmetry Most animals are either radially or bilaterally symmetrical.

Bilateral symmetry is strongly correlated with **cephalization**: the concentration of sensory organs and nervous tissues in a head at the anterior end of the animal. Cephalization is favored because the anterior end of a freely moving animal typically encounters new environments first.

Fluid-filled spaces, called **body cavities**, lie between the ectoderm and endoderm of most protostomes and deuterostomes. The type of body cavity an animal has strongly influences the way it moves.

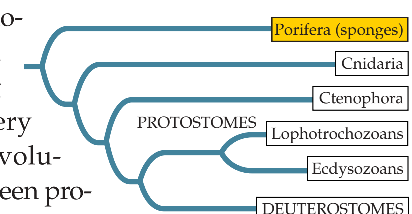
- Animals that lack an enclosed body cavity are called **acoelomates**. In these animals, the space between the gut and the body wall is filled with masses of cells called *mesenchyme* (Figure 32.3*a*).
- **Pseudocoelomate** animals have a body cavity called a *pseudocoel*, a liquid-filled space in which many of the internal organs are suspended. Their control over body shape is crude because the pseudocoel has muscles only on its outside; there is no inner layer of muscle surrounding the organs (Figure 32.3*b*).
- **Coelomate** animals have a *coelom*, a body cavity that develops within the mesoderm. It is lined with a special structure called the *peritoneum* and is enclosed on both the inside and the outside by muscles (Figure 32.3*c*).

The fluid-filled body cavities of simple animals function as **hydrostatic skeletons**. Because fluids are relatively incompressible, they move to another part of the cavity when the muscles surrounding them contract. If the body tissues around the cavity are flexible, fluids squeezed out of one region can cause some other region to expand. The moving fluids can thus move specific body parts. If a temporary attachment can be made to the substratum, the whole animals can move from one place to another.

In animals that have both circular muscles (encircling the body) and longitudinal muscles (running along the length of the body), the action of these antagonistic muscles on the fluid-filled body cavity gives the animal even greater control over its movement. A coelomate animal has better control over the movement of the fluids in its body cavity than does a pseudocoelomate animal, but its control is further improved if the coelom is separated into compartments or segments. Then muscles in each individual segment can change its shape independently of the other segments. Segmentation of the coelom evolved several different times among both protostomes and deuterostomes.

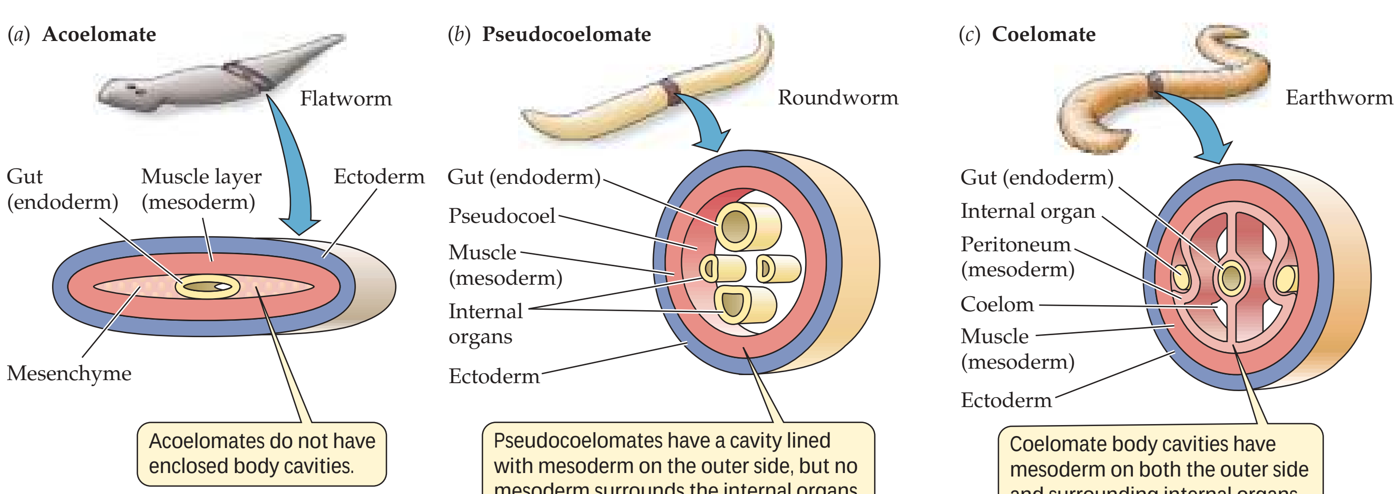
Other forms of skeletons developed in many animal lineages, either as substitutes for, or in combination with, hydrostatic skeletons. Some skeletons are internal (such as vertebrate bones); others are external (such as lobster shells). Some external skeletons consist of a single element (snail shells), others have two elements (clam shells), and still others have many elements (centipedes).

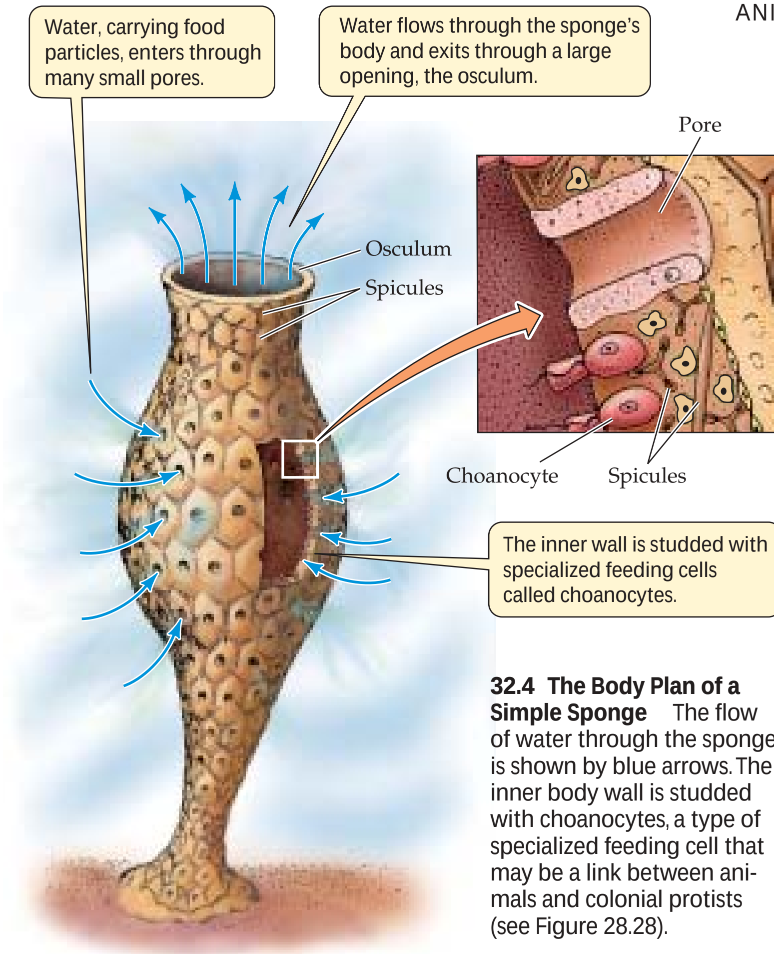
Sponges: Loosely Organized Animals



The lineage leading to modern sponges separated from the lineage leading to all other animals very early during animal evolution. The difference between protist colonies and simple multicellular animals is that the animal cells are differentiated and their activities are coordinated. However, sponge cells do not form true organs.

32.3 Animal Body Cavities There are three major types of body cavities among the animals. (*a*) Acoelomates do not have enclosed body cavities. (*b*) Pseudocoelomates have only one layer of muscle, and it lies outside the body cavity. (*c*) Coelomates have a peritoneum surrounding the internal organs. The body cavities of some coelomates, such as this earthworm, are segmented.





32.4 The Body Plan of a Simple Sponge The flow of water through the sponge is shown by blue arrows. The inner body wall is studded with choanocytes, a type of specialized feeding cell that may be a link between animals and colonial protists (see Figure 28.28).

Sponges (phylum **Porifera**, from the Latin, "pore bearers"), the simplest of animals, are **sessile**: They live attached to the substratum and do not move about. The body plan of all sponges—even large ones, which may reach more than a meter in length—is an aggregation of cells built around a water canal system. Feeding cells called *choanocytes* line the inside of the internal chambers. These cells, with a collar of microscopic villi and a single flagellum, bear a striking resemblance to choanoflagellates (see Figure 28.28). By beating their flagella, choanocytes cause the surrounding water to flow through the animal. The water, along with any food particles it contains, enters by way of small pores and passes into the water canals, where food particles are captured by the choanocytes. Water then exits through one or more larger openings called *oscula* (Figure 32.4).

Between the thin epidermis and the choanocytes is another layer of cells, some of which are similar to amoebas and move about within the body. A supporting skeleton is also present, in the form of simple or branching spines, called *spicules*, and often an elastic, complex, network of fibers. A few species of sponges are carnivores that trap prey on hook-shaped spicules that protrude from the body surface. Sponges also have an extracellular matrix, composed of collagens, adhesive glycoproteins, and other molecules, that holds the cells together. This molecular adhesion system may also be involved in cell–cell signaling.

Thus, sponges are functionally more complex than a superficial look at their morphology might suggest. Nonetheless, sponges are loosely organized. Even if a sponge is completely disassociated by being strained through a filter, its cells can reassemble into a new sponge.

Most of the 5,500 species of sponges are marine animals; only about 50 species live in fresh water. Sponges come in a wide variety of sizes and shapes that are adapted to different movement patterns of water (Figure 32.5). Sponges living in intertidal or shallow subtidal environments, where they are subjected to strong wave action, hug the substratum. Many sponges that live in calm waters are simple, with a single large osculum on top of the body. Most sponges that live in slowly flowing water are flattened and are oriented at right

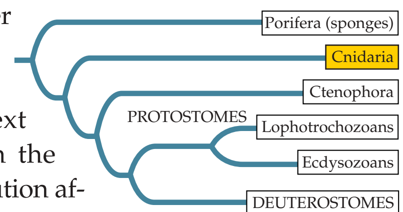
(*a*) *Euplectella aspergillum* (*b*) *Aplysina lacunosa* (*c*) *Asbestopluma* sp.

32.5 Sponges Differ in Size and Shape (*a*) Glass sponges are named after their glasslike spicules, which are formed of silicon. (*b*) The purple tube sponge is typical of many simple marine sponges. (*c*) This predatory sponge uses its hook-shaped spicules to capture small prey animals.

angles to the direction of current flow; they intercept water and the prey it contains as it flows past them.

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

Cnidarians: Two Cell Layers and Blind Guts



Animals in all phyla other than Porifera have distinct cell layers and symmetrical bodies. The next lineage to diverge from the main line of animal evolution after the sponges led to a phylum of animals called the **cnidarians** (phylum **Cnidaria**). These animals are *diploblastic* (have two cell layers) and have a blind gut with only one entrance (the mouth/anus). Despite their relative structural simplicity, cnidarians have structural molecules (such as collagen, actin, and myosin) and homeobox genes.

Cnidarians are simple but specialized carnivores

Cnidarians appeared early in evolutionary history and radiated in the late Precambrian. About 11,000 cnidarian species—jellyfish, sea anemones, corals, and hydrozoans—live today (Figure 32.6), all but a few in the oceans. The smallest cnidarians can hardly be seen without a microscope; the largest known jellyfish is 2.5 meters in diameter. All cnidarians are carnivores; some gain additional nutrition from photosynthetic endosymbionts. The cnidarian body plan combines a low metabolic rate with the ability to capture large prey. These traits allow cnidarians to survive in environments where encounters with prey are infrequent.

All cnidarians possess tentacles covered with *cnidocytes*, specialized cells that contain stinging organelles called *nematocysts*, which can inject toxins into their prey (Figure 32.7). Cnidocytes allow cnidarians to capture large and complex prey, which are carried into the mouth by retracting the tentacles. Nematocysts are responsible for the stings that some jellyfish inflict on human swimmers.

The cnidarian body is based on a "sac plan," in which the mouth is connected to a blind sac called the *gastrovascular cavity*. The sac functions in digestion, circulation, and gas exchange and acts as a hydrostatic skeleton. The single opening serves as both mouth and anus. Cnidarians also have epithelial cells with muscle fibers whose contractions enable the animals to move, as well as simple *nerve nets* that integrate their body activities.

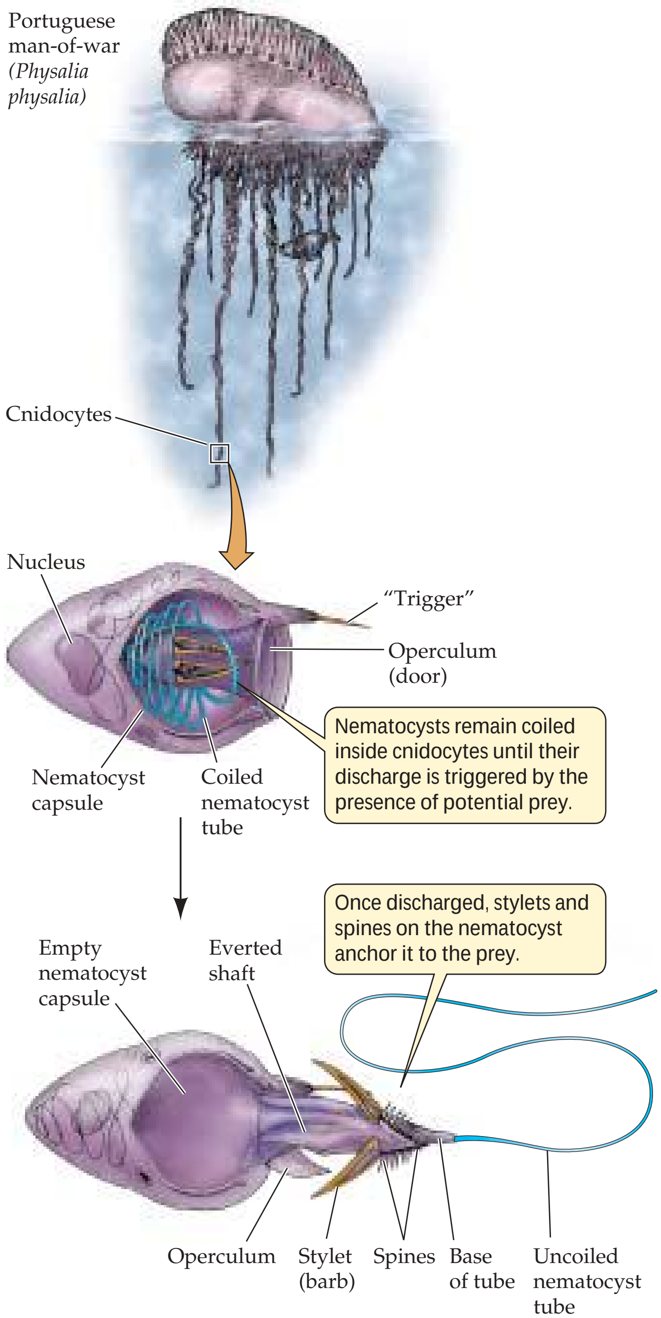
(*a*) *Anthopleura elegantissima*

(*b*) *Ptilosarcus gurneyi*

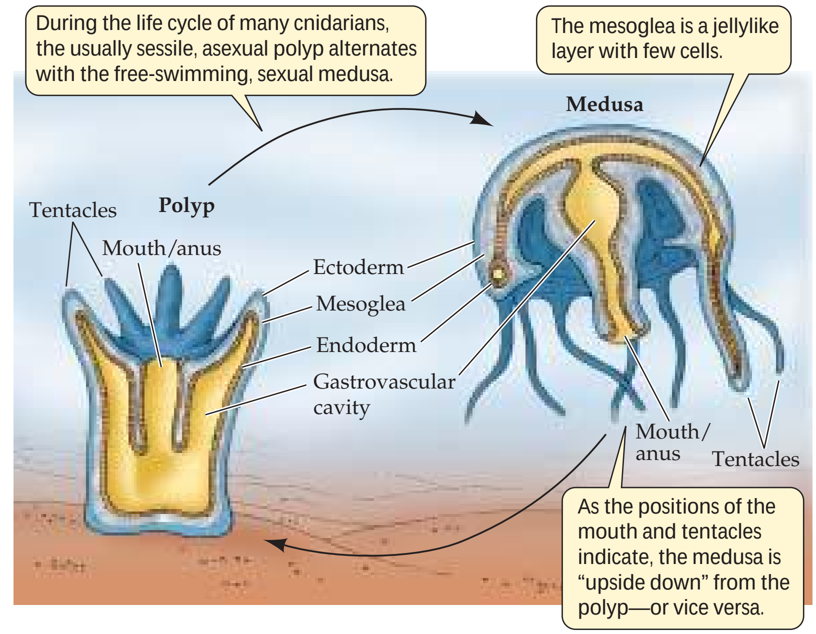
(*c*) *Pelagia panopyra*

(*d*) *Polyorchis penicillatus*

32.6 Diversity among Cnidarians (*a*) The nematocyst-studded tentacles of this sea anemone from British Columbia are poised to capture large prey carried to the animal by water movement. (*b*) The orange sea pen is a colonial cnidarian that lives in soft bottom sediments and projects polyps above the substratum. (*c*) This purple jellyfish illustrates the complexity of a scyphozoan medusa. (*d*) The internal structure of the medusa of a North Atlantic colonial hydrozoan is visible here.



32.7 Nematocysts Are Potent Weapons Cnidarians such as the Portuguese man-of-war, which possesses a large number of nematocysts, can subdue and consume very large prey.



32.8 A Generalized Cnidarian Life Cycle Cnidarians typically have two body forms, one asexual (the polyp) and the other sexual (the medusa).

Cnidarian life cycles have two stages

The generalized cnidarian life cycle has two distinct stages (Figure 32.8), although many species lack one of these stages:

- The sessile **polyp** stage has a cylindrical stalk attached to the substratum. Tentacles surround a mouth/anus located at the end opposite from the stalk. Individual polyps may reproduce by budding, thereby forming a colony.
- The **medusa** (plural, medusae) is a free-swimming stage shaped like a bell or an umbrella. It typically floats with its mouth and tentacles facing downward. Medusae of many species produce eggs and sperm and release them into the water. When an egg is fertilized, it develops into a free-swimming, ciliated larva called a **planula**, which eventually settles to the bottom and develops into a polyp.

Although the polyp and medusa stages appear very different, they share a similar body plan. A medusa is essentially a polyp without a stalk. Most of the outward differences between polyps and medusae are due to the *mesoglea*, an internal mass of jellylike material that lies between the two cell layers. The mesoglea contains few cells and has a low metabolic rate. In polyps, the mesoglea is usually thin; in medusae it is very thick, constituting the bulk of the animal.

ANTHOZOANS. All 6,000 species of sea anemones and corals that constitute the **anthozoans** (class **Anthozoa**) are marine animals. Evidence from morphology, rRNA, and mitochondrial genes suggests that the anthozoans, which lack the medusa stage, are sister to the other classes of cnidarians, and that the medusa stage evolved after the anthozoa diverged from those other lineages. In the anthozoans, the polyp produces eggs and sperm, and the fertilized egg develops into a planula that develops directly into another polyp. Many species can also reproduce asexually by budding or fission. Sea anemones (see Figure 32.6*a*) are solitary. They are widespread in both warm and cold ocean waters. Many sea anemones are able to crawl slowly on the discs with which they attach themselves to the substratum. A few species can swim and some can burrow.

Sea pens (see Figure 32.6*b*), by contrast, are sessile and colonial. Each colony consists of at least two different kinds of polyps. The primary polyp has a lower portion anchored in the bottom sediment and a branched upper portion that projects above the substratum. Along the upper portion, the primary polyp produces smaller secondary polyps by budding. Some of these secondary polyps can differentiate into feeding polyps, while others circulate water through the colony.

Corals also are usually sessile and colonial. The polyps of most corals form a skeleton by secreting a matrix of organic molecules upon which they deposit calcium carbonate, which forms the eventual skeleton of the coral colony. The forms of coral skeletons are species-specific and highly diverse. The common names of coral groups—horn corals, brain corals, staghorn corals, and organ pipe corals, among others—describe their appearance (Figure 32.9*a*).

As a coral colony grows, old polyps die, but their calcareous skeletons remain. The living members form a layer on top of a growing bank of skeletal remains, eventually forming chains of islands and reefs (Figure 32.9*b*). The Great Barrier Reef along the northeastern coast of Australia is a system of coral formations more than 2,000 km long and as wide as 150 km. A reef hundreds of kilometers long in the Red Sea has been calculated to contain more material than all the buildings in the major cities of North America combined.

Corals flourish in nutrient-poor, clear, tropical waters. They can grow rapidly in such environments because the photosynthetic dinoflagellates that live symbiotically within their cells provide them with products of photosynthesis and contribute to calcium deposition. In turn, the corals provide the dinoflagellates with a place to live and nutrients. This symbiotic relationship explains why reef-forming corals are restricted to clear surface waters, where light levels are high enough to allow photosynthesis.

Coral reefs throughout the world are being threatened both by global warming, which is raising the temperatures of shallow tropical ocean waters, and by polluted runoff from development on adjacent shorelines. An overabundance of nitrogen in the runoff gives an advantage to algae, which overgrow and eventually smother the corals.

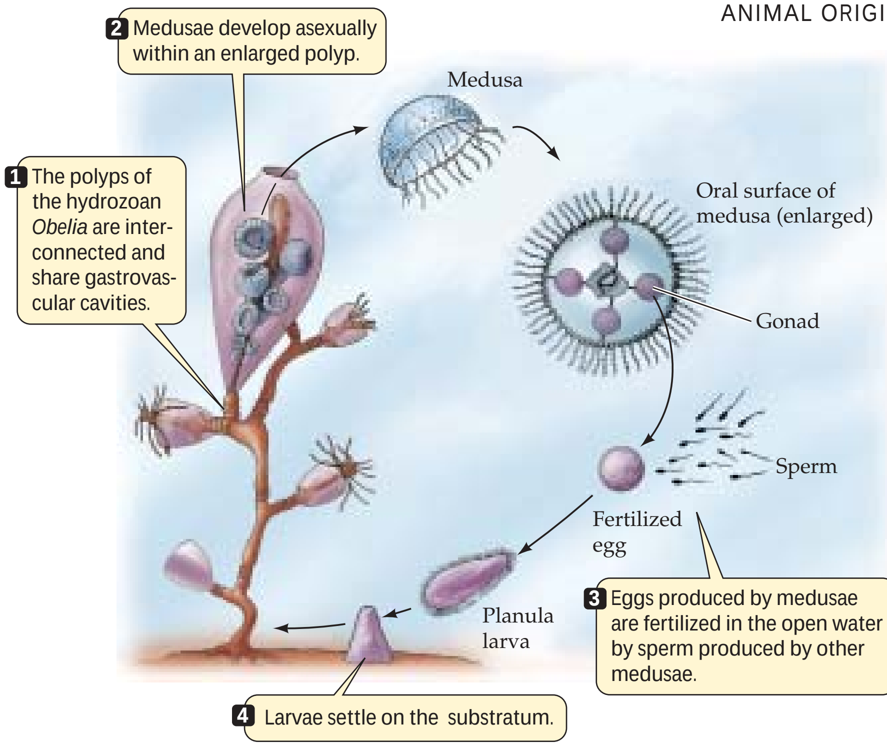
HYDROZOANS. Life cycles are diverse among the **hydrozoans** (class **Hydrozoa**). The polyp typically dominates the life cycle, but some species have only medusae and others only polyps. Most hydrozoans are colonial. A single planula eventually gives rise to a colony of many polyps, all interconnected and sharing a continuous gastrovascular cavity (Figure 32.10). Within such a colony (the man-of-war in Figure 32.7 is an example), some polyps have tentacles with many nematocysts; they capture prey for the colony. Others lack tentacles and are unable to feed, but are specialized for the production of medusae. Still others are fingerlike and defend the colony with their nematocysts.

SCYPHOZOANS. The several hundred species of **scyphozoans** (class **Scyphozoa**) are all marine. The mesoglea of their medusae is thick and firm, giving rise to their common names, jellyfish or sea jellies. The medusa, rather than the polyp, dominates the life cycle of scyphozoans. An indi-

32.9 Corals The South Pacific is home to many spectacular corals. (*a*) This unusually large formation of chalice coral was photographed off the coast of Fiji. (*b*) Many different species of corals and sponges grow together on this reef in Palau.

(*a*) *Montipora sp.*

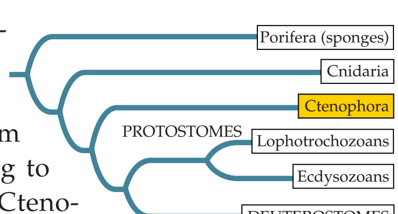
(*b*)



32.10 Hydrozoans Often Have Colonial Polyps The polyps within a hydrozoan colony may differentiate to perform specialized tasks. In the species whose life cycle is diagrammed here, the medusa is the sexual reproductive stage, producing eggs and sperm in organs called gonads.

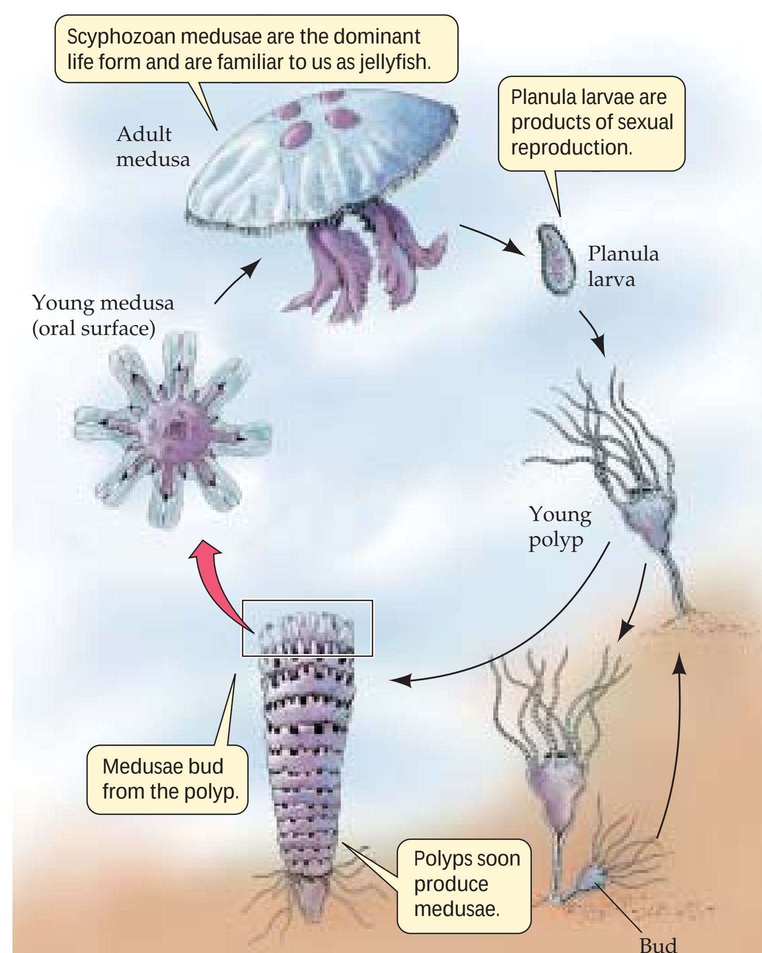
vidual medusa is male or female, releasing eggs or sperm into the open sea. The fertilized egg develops into a small planula that quickly settles on a substratum and develops into a small polyp. This polyp feeds and grows and may produce additional polyps by budding. After a period of growth, the polyp begins to bud off small medusae (Figure 32.11). These medusae feed, grow, and transform themselves into adult medusae, which are commonly seen during summer in harbors and bays.

Ctenophores: Complete Guts and Tentacles

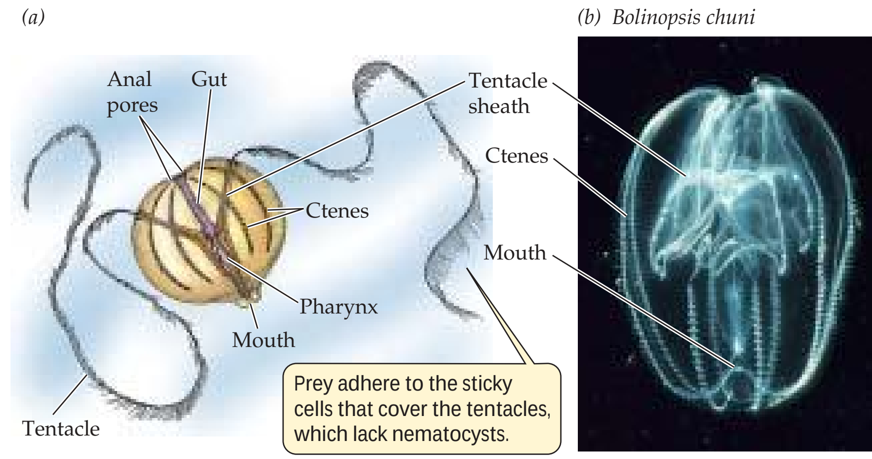


Ctenophores (phylum **Ctenophora**) were the next lineage to diverge from the lineage leading to all other animals. Ctenophores, also known as comb jellies, have body plans that are superficially similar to those of cnidarians. Both have two cell layers separated by a thick, gelatinous mesoglea, and both have radial symmetry and feeding tentacles. Like cnidarians, ctenophores have low metabolic rates because they are composed primarily of inert mesoglea. Unlike cnidarians, however, ctenophores have a complete gut. Food enters through a mouth, and wastes are eliminated through two anal pores.

Ctenophores have eight comblike rows of fused plates of cilia, called *ctenes* (Figure 32.12). Ctenophores move by beating these cilia rather than by muscular contractions. Ctenophoran tentacles do not have nematocysts; rather, they are covered with cells that discharge adhesive material when they contact prey. After capturing its prey, a ctenophore retracts its tentacles to bring the food to its mouth. In some species, the entire surface of the body is coated with sticky mucus that captures prey. All of the 100 known species of ctenophores eat small animals. They are common in open seas.



32.11 Medusae Dominate Scyphozoan Life Cycles Scyphozoan medusae are the familiar jellyfish of coastal waters. The small, sessile polyps quickly produce medusae (see Figure 32.6*c*).



32.12 Comb Jellies Feed with Tentacles (*a*) The body plan of a typical ctenophore. The long, sticky tentacles sweep through the water, efficiently harvesting small prey. (*b*) A comb jelly photographed in Sydney Harbour, Australia, has short tentacles.

Ctenophore life cycles are simple. Gametes are produced in structures called *gonads*, located on the walls of the gastrovascular cavity. The gametes are released into the cavity and then discharged through the mouth or the anal pores. Fertilization takes place in open seawater. In nearly all species, the fertilized egg develops directly into a miniature ctenophore that gradually grows into an adult.

The Evolution of Bilaterally Symmetrical Animals

The phylogenetic tree pictured in Figure 32.1 assumes that all bilaterally symmetrical animals share a common ancestor, but it does not tell us what that ancestor looked like. To infer the form of the earliest bilaterians, zoologists use evidence from the genes, development, and structure of existing animals. An important clue is provided by the fact that the development of all bilaterally symmetrical animals is controlled by homologous *Hox* and homeobox genes. Regulatory genes with similar functions are unlikely to have evolved independently in several different animal lineages.

Fossilized tracks from late Precambrian times provide additional clues to the nature of early bilaterians (Figure 32.13). The complexity of the movements recorded by these tracks suggests that early bilaterians had circulatory systems, systems of antagonistic muscles, and a tissue- or fluid-filled body cavity, structures that are also suggested by genetic data.

An early lineage split separated protostomes and deuterostomes

The next major split in the animal lineage after the divergence of the ctenophores occurred during the Cambrian period and separated two groups that have been evolving separately ever since. These two major lineages—the protostomes and the deuterostomes—dominate today's fauna. Members of both lineages are triploblastic (have three cell layers), bilaterally symmetrical, and cephalized. Because their skeletons and body cavities are more complex than those of the animals we have discussed so far, they are capable of more complex movements.

The most important shared, derived traits that unite the protostomes are

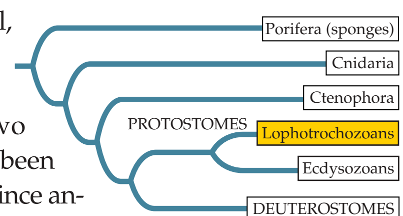
- An anterior brain that surrounds the entrance to the digestive tract
- A ventral nervous system consisting of paired or fused longitudinal nerve cords
- A free-floating larva with a food-collecting system consisting of compound cilia on multiciliate cells
- A blastopore that becomes the mouth
- Spiral cleavage (in some species)

32.13 The Trail of an Early Bilaterian These fossilized tracks indicate that their maker was able to crawl.

The major shared, derived traits that unite the deuterostomes are

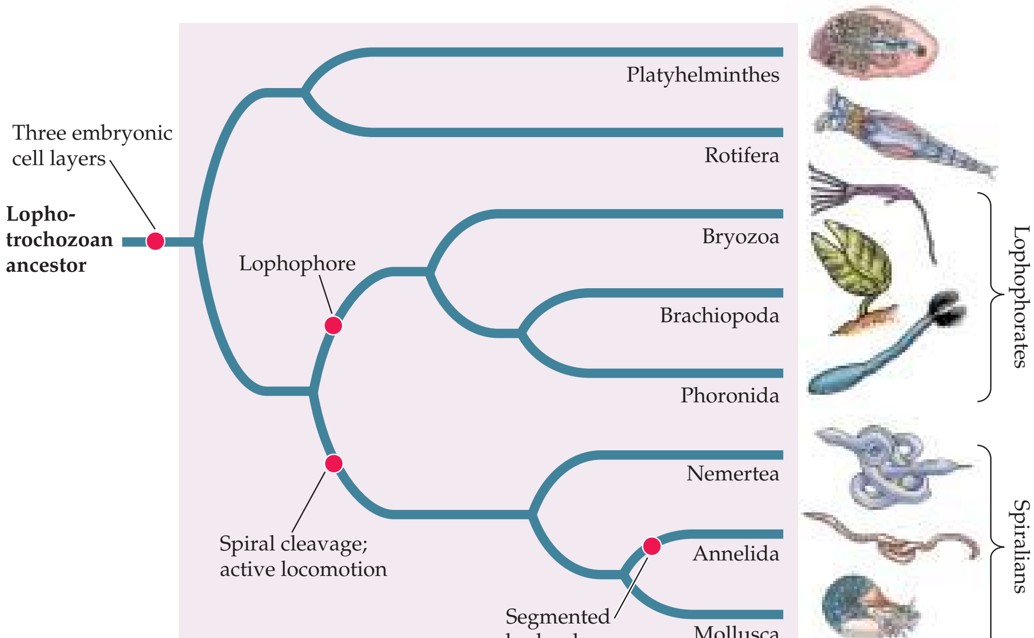
- A dorsal nervous system
- A larva, if present, that has a food-collecting system consisting of cells with a single cilium
- A blastopore that becomes the anus
- Radial cleavage

The protostomes split into two lineages



Developmental, structural, and molecular data all suggest that the protostomes soon split into two major lineages that have been evolving independently since ancient times: lophotrochozoans and ecdysozoans. **Lophotrochozoans**, the animals we will discuss in the remainder of this chapter, grow by adding to the size of their skeletal elements. Some of them use cilia for locomotion, and many lineages have a type of free-living larva known as a **trochophore** (see Figure 32.23) The phylogeny of lophotrochozoans we will use in this chapter is shown in Figure 32.14. In contrast, **ecdysozoans**, the animals we will discuss in the next chapter, increase in size by molting their external skeletons. They move by mechanisms other than ciliary action, and they all have a common set of homeobox genes.

32.14 A Current Phylogeny of Lophotrochozoans Three major lineages, including the lophophorate and spiralian phyla, dominate the tree. Some small phyla are not included here.



Simple Lophotrochozoans

The simplest lophotrochozoans—flatworms and rotifers—are small aquatic or parasitic animals. They move by rapidly beating cilia, and most have only simple organs.

Flatworms move by beating cilia

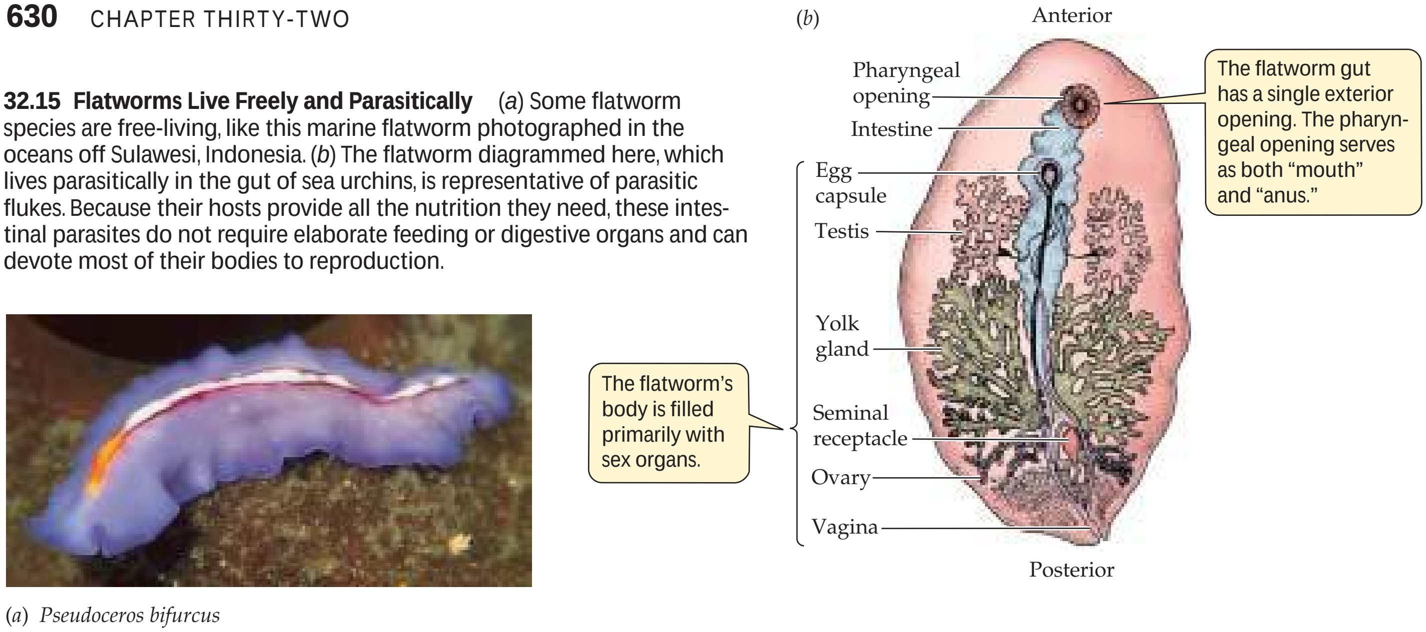
Members of the phylum **Platyhelminthes**, or **flatworms**, the simplest lophotrochozoans (Figure 32.15), are bilaterally symmetrical, unsegmented, acoelomate animals. They lack organs for transporting oxygen to internal tissues, and they have only simple cells for excreting metabolic wastes. Their lack of transport systems dictates that each cell must be near a body surface, a requirement met by their dorsoventrally flattened body form.

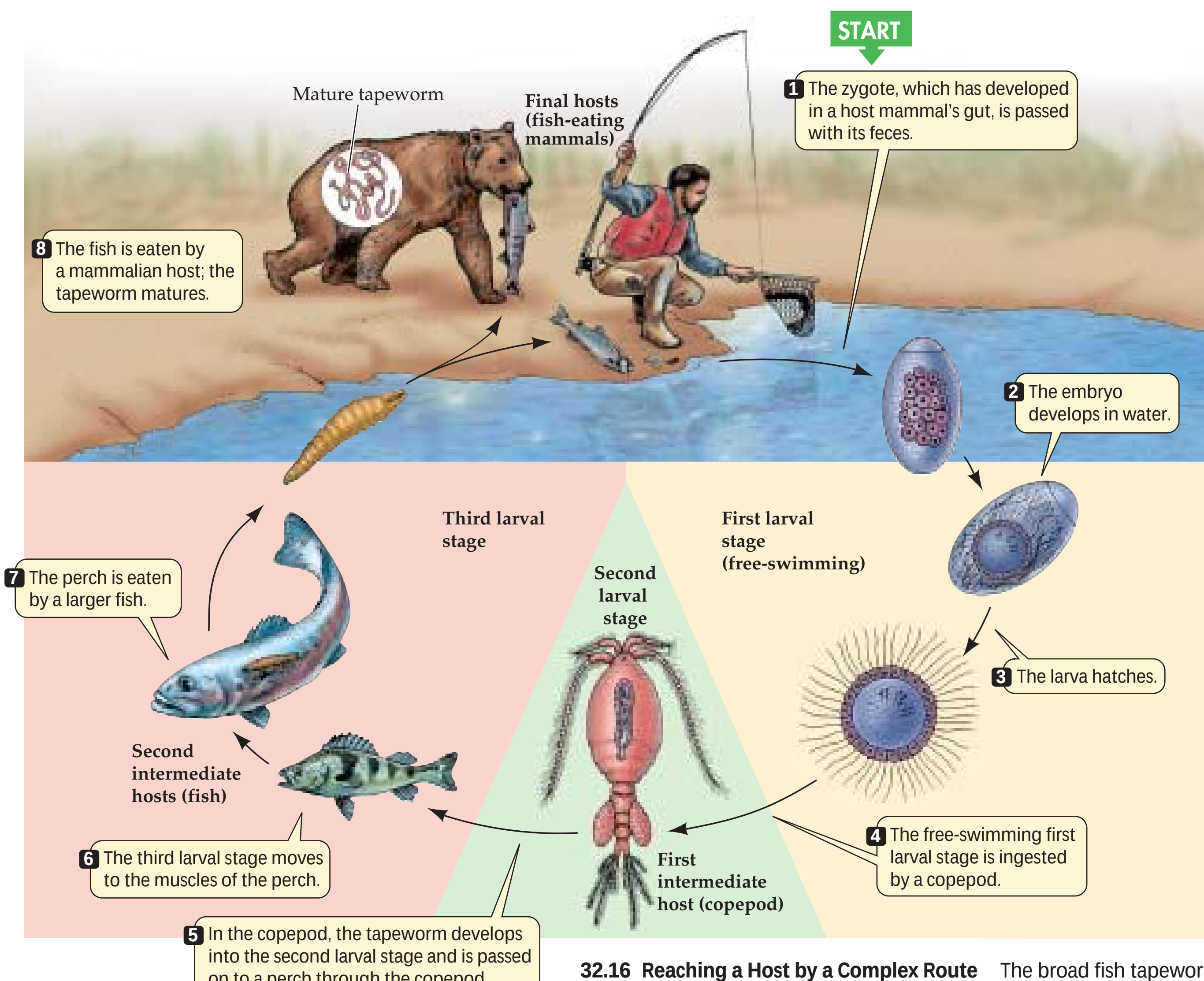
The digestive tract of a flatworm consists of a mouth opening into a blind sac. However, the sac is often highly branched, forming intricate patterns that increase the surface area available for the absorption of nutrients. Flatworms either feed on animal tissues (living or dead), or absorb nutients from a host's gut. Free-living flatworms glide over surfaces, powered by broad bands of cilia. This form of movement is very slow, but it is sufficient for small, scavenging animals.

The flatworms that are probably most similar to the ancestral bilaterians are the turbellarians (class **Turbellaria**), which are small, free-living marine and freshwater animals (a few live in moist terrestrial habitats). At one end they have a head with chemoreceptor organs, two simple eyes, and a tiny brain composed of anterior thickenings of the longitudinal nerve cords.

Although the earliest flatworms were free-living (Figure 32.15*a*), many species evolved a parasitic existence. A likely evolutionary transition was from feeding on dead organisms to feeding on the body surfaces of dying hosts to invading and consuming parts of living, healthy hosts. Most of the 25,000 species of living flatworms—including the tapeworms (class **Cestoda**) and flukes (class **Trematoda**; Figure 32.15*b*)—are internal parasites. These flatworms absorb digested food from the digestive tracts of their hosts, so many of them lack digestive tracts. They inhabit the bodies of many vertebrates; some cause serious human diseases, such as schistoso-

32.15 Flatworms Live Freely and Parasitically (*a*) Some flatworm species are free-living, like this marine flatworm photographed in the oceans off Sulawesi, Indonesia. (*b*) The flatworm diagrammed here, which lives parasitically in the gut of sea urchins, is representative of parasitic flukes. Because their hosts provide all the nutrition they need, these intestinal parasites do not require elaborate feeding or digestive organs and can devote most of their bodies to reproduction.





32.16 Reaching a Host by a Complex Route The broad fish tapeworm, *Diphyllobothrium latum*, must pass through the bodies of a copepod (a type of crustacean) and a fish before it can reinfect its primary host, a mammal. Such complex life cycles assist the flatworm's recolonization of hosts, but they also offer opportunities for humans to break the cycle with hygienic measures.

miasis. Monogeneans (class **Monogenea**) are external parasites of fishes and other aquatic vertebrates.

Parasites live in nutrient-rich environments where food is delivered to them, but they face other challenges. To complete their life cycle, parasites must overcome the defenses of their host. And because they die when their host dies, they must disperse their offspring to new hosts while their host is still living. The fertilized eggs of some parasitic flatworms are voided with the host's feces and later ingested directly by other host individuals. However, most parasitic species have complex life cycles involving one or more intermediate hosts and several larval stages (Figure 32.16). Such life cycles facilitate the transfer of individual parasites among hosts.

Rotifers are small but structurally complex

Rotifers (phylum **Rotifera**) are bilaterally symmetrical, unsegmented, pseudocoelomate lophotrochozoans. Most rotifers are tiny (50–500 μm long)—smaller than some ciliate protists—but they have highly developed internal organs (Figure 32.17). A complete gut passes from an anterior mouth to a posterior anus; the pseudocoel functions as a hydrostatic skeleton. Most rotifers propel themselves through the water by means of rapidly beating cilia rather than by muscular contraction. This type of movement is effective because rotifers are so small.

The most distinctive organs of rotifers are those they use to collect and process food. A conspicuous ciliated organ called the *corona* surmounts the head of many species. Coordinated beating of the cilia sweeps particles of organic matter from the water into the animal's mouth and down to a complicated structure called the *mastax*, in which food is ground into small pieces. By contracting the muscles around the pseudocoel, a few rotifer species that prey on protists and small animals can protrude the mastax through the mouth and seize small objects with it. Males and females are found in most species, but some species have only females that produce diploid eggs without being fertilized by a male.

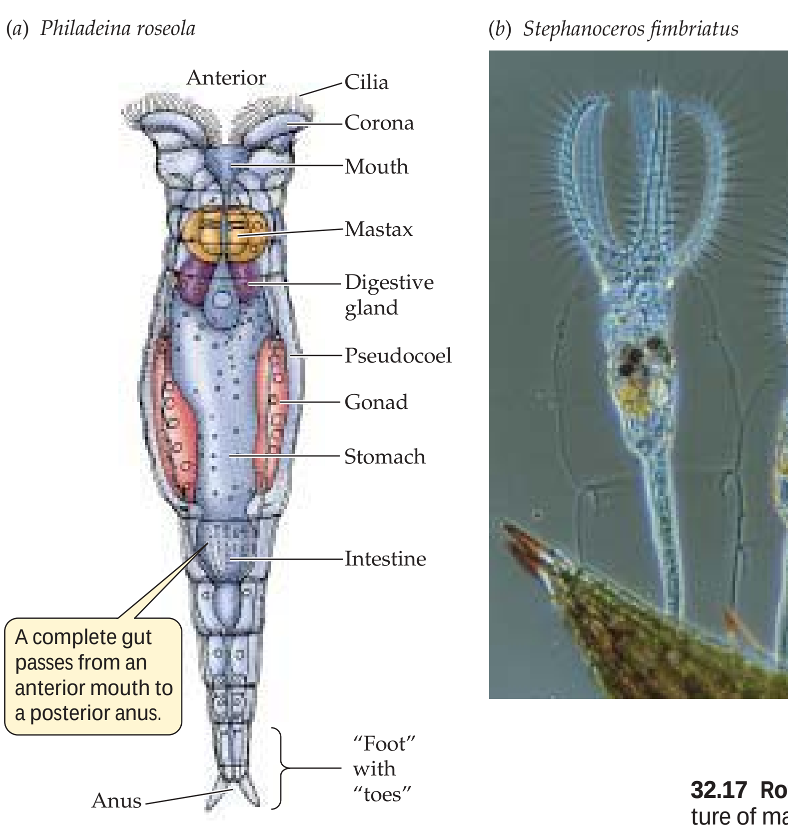
Some rotifers are marine, but most of the 1,800 known species live in fresh water. Members of a few species rest on the surface of mosses or lichens in a desiccated, inactive state until it rains. When rain falls, they absorb water and become mobile, feeding in the films of water that temporarily cover the plants. Most rotifers live no longer than 1 or 2 weeks.

Lophophorates: An Ancient Body Plan

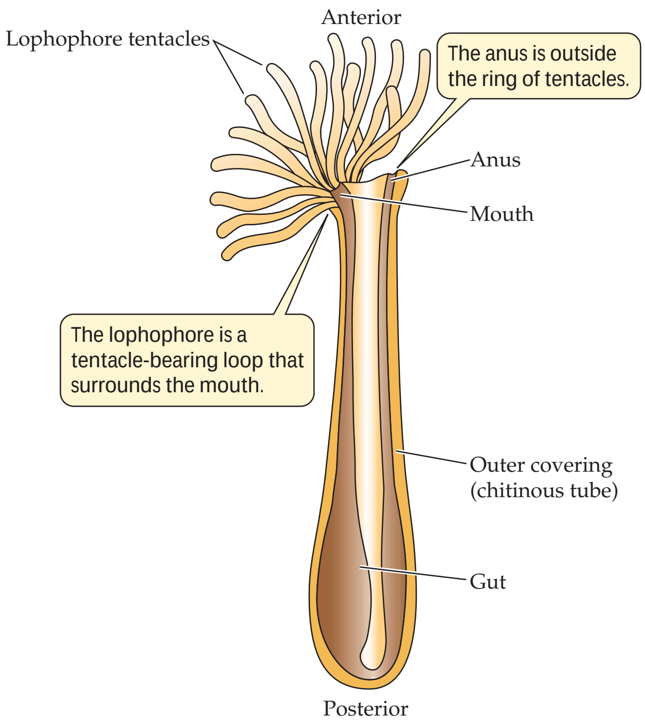
After the platyhelminthes and rotifers diverged from it, the lophotrochozoan lineage divided into two branches. The descendants of those branches became the modern **lophophorates**—the subject of this section—and the **spiralians**, which we will discuss in the following section.

About 4,850 living species of lophophorates are known, but many times that number of species existed during the Paleozoic and Mesozoic eras. Three lophophorate phyla survive today: Phoronida, Brachiopoda, and Ectoprocta. Nearly all members of these phyla are marine; only a few species of ectoprocts live in fresh water.

Lophophorate animals obtain food by filtering it from the surrounding water, a trait they share with many other protostomes. The most conspicuous feature of these animals is the **lophophore**, a circular or U-shaped ridge around the mouth that bears one or two rows of ciliated, hollow tentacles (Figure 32.18). This large and complex structure is an organ for both food collection and gas exchange. Nearly all adult lophophorate animals are sessile, and they use the tentacles and cilia of their lophophore to capture *plankton* (small floating organisms) from the water. Lophophorates also have a U-shaped gut; the anus is located close to the mouth, but outside the tentacles.



32.17 Rotifers (*a*) The rotifer diagrammed here reflects the general structure of many free-living species in the phylum. (*b*) A micrograph reveals the internal complexity of these living rotifers.



32.18 Lophophore Artistry The lophophore dominates the anatomy of this phoronid. The phoronid gut is U-shaped.

Phoronids are sedentary lophophorates

The 20 known species of **phoronids** (phylum **Phoronida**) are sedentary worms that live in muddy or sandy sediments or attached to a rocky substratum. Phoronids are found in marine waters ranging from intertidal zones to about 400 meters deep. They range in size from 5 to 25 cm in length. They secrete chitinous tubes, in which they live (Figure 32.18). The lophophore is the most conspicuous external feature of the phoronids. Cilia drive water into the top of the lophophore, and water exits through the narrow spaces between the tentacles. Suspended food particles are caught and transported to the mouth by ciliary action. In most species, eggs are released into the water, where they are fertilized, but some species produce large eggs that are fertilized internally, where they are brooded until they hatch.

Ectoprocts are colonial lophophorates

Ectoprocts (phylum **Ectoprocta**) are colonial lophophorates that live in a "house" made of material secreted by the external body wall. A colony consists of many small (1–2 mm) individuals connected by strands of tissue along which materials can be moved (Figure 32.19*a*). Most of the 4,500 species of ectoprocts are marine, but a few live in fresh water. They are able to oscillate and rotate the lophophore to increase contact with prey (Figure 32.19*b*) and can retract it into the tube.

A colony of ectoprocts is created by the asexual reproduction of its founding members. A single colony may contain as many as 2 million individuals. In some species, individual colony members are specialized for feeding, reproduction, defense, or support. Ectoprocts reproduce sexually by releasing sperm into the water, where they are collected by other individuals. Eggs are fertilized internally, and developing embryos are brooded before they exit as larvae to seek suitable sites for attachment to the substratum.

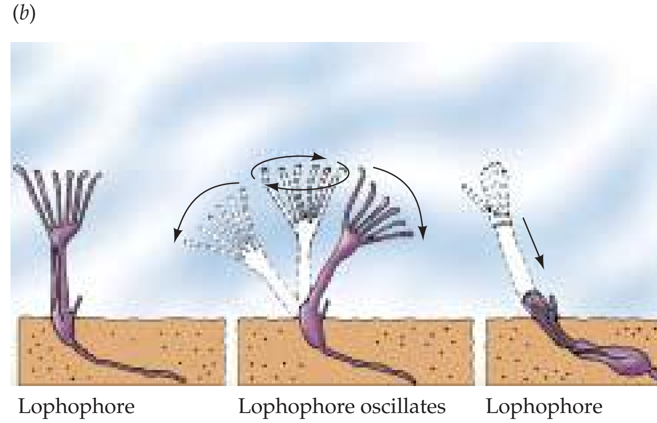
Brachiopods superficially resemble bivalve mollusks

Brachiopods (phylum **Brachiopoda**) are solitary marine lophophorate animals. Their shells are divided into two parts

(*a*) *Lophopus crystallinus*

32.19 Ectoprocts (*a*) Branching colonies of ectoprocts may appear plantlike. (*b*) Ectoprocts have greater control over the movement of their lophophores than members of other lophophorate phyla.

(*b*)



32.20 Brachiopods The lophophore of this North Pacific brachiopod can be seen between the valves of its shell.

that are connected by a ligament (Figure 32.20). The two halves can be pulled shut to protect the soft body. Brachiopods superficially resemble bivalve mollusks, but the brachiopod shell differs from that of mollusks in that the two halves are dorsal and ventral rather than lateral. The two-armed lophophore of a brachiopod is located within the shell. The beating of cilia on the lophophore draws water into the slightly opened shell. Food is trapped in the lophophore and directed to a ridge, along which it is transferred to the mouth. Most brachiopods are between 4 and 6 cm long, but some are as long as 9 cm.

Brachiopods live attached to a solid substratum or embedded in soft sediments. Most species are attached by means of a short, flexible stalk that holds the animal above the substratum. Gases are exchanged across body surfaces, especially the tentacles of the lophophore. Most brachiopods release their gametes into the water, where they are fertilized. The larvae remain among the plankton for only a few days before they settle and develop into adults.

Brachiopods reached their peak abundance and diversity in Paleozoic and Mesozoic times. More than 26,000 fossil species have been described. Only about 335 species survive, but they are common in some marine environments.

Spiralians: Spiral Cleavage and Wormlike Body Plans

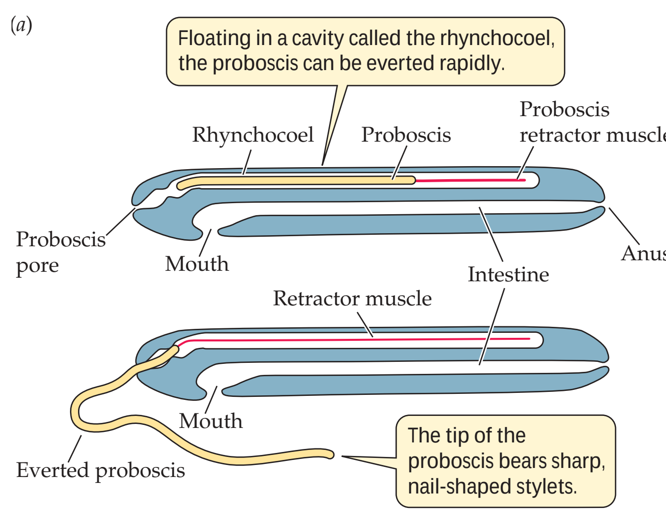
The spiralian lineage, containing animals that typically have spiral cleavage patterns, gave rise to many phyla. Members of more than a dozen of these phyla are *wormlike*; that is, they are bilaterally symmetrical, legless, soft-bodied, and at least several times longer than they are wide. This body form enables animals to move efficiently through muddy and sandy marine sediments. Most of these phyla have no more than several hundred species. The most species-rich spiralian phylum, the mollusks, shows significant modifications of the wormlike body plan.

Ribbon worms are unsegmented

The carnivorous **ribbon worms** (phylum **Nemertea**) are dorsoventrally flattened. They have nervous and excretory systems similar to those of flatworms, but unlike flatworms, they have a complete digestive tract with a mouth at one end and an anus at the other. Food moves in one direction through the digestive tract and is acted on by a series of digestive enzymes. Small ribbon worms move by beating their cilia. Larger ones employ waves of muscle contraction to move over the surface of sediments or to burrow. Movement by both of these methods is slow.

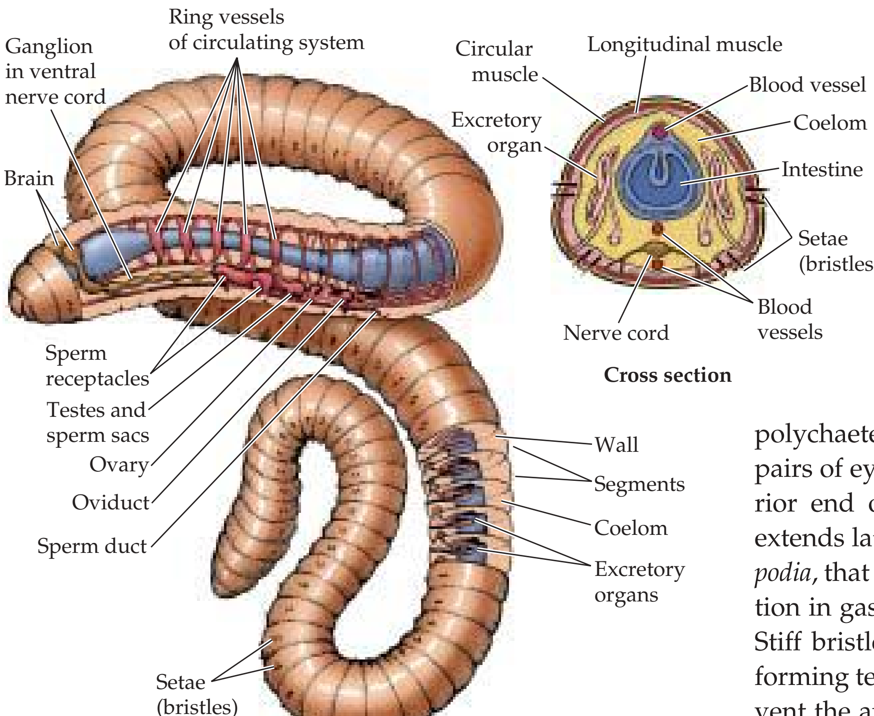
Within the body of nearly all of the 900 species of ribbon worms is a fluid-filled cavity called the *rhynchocoel*, within which lies a hollow, muscular *proboscis*. The proboscis, which is the feeding organ, may extend much of the length of the worm. Contraction of the muscles surrounding the rhynchocoel causes the proboscis to be everted explosively through an anterior opening (Figure 32.21) without moving the rest of the animal. The proboscis of most ribbon worms

(*a*)



(*b*) *Pelagonemertes* sp.

32.21 Ribbon Worms (*a*) The proboscis is the ribbon worm's feeding organ. (*b*) This deep-water nemertean displays an everted proboscis.



32.22 Annelids Have Many Body Segments The segmented structure of the annelids is apparent both externally and internally. Most organs of this earthworm are repeated serially.

is armed with a sharp stylet that pierces the prey. Paralysis-causing toxins produced by the proboscis are discharged into the wound. Reproduction and development in ribbon worms is highly varied.

Segmentation improved locomotion in the annelids

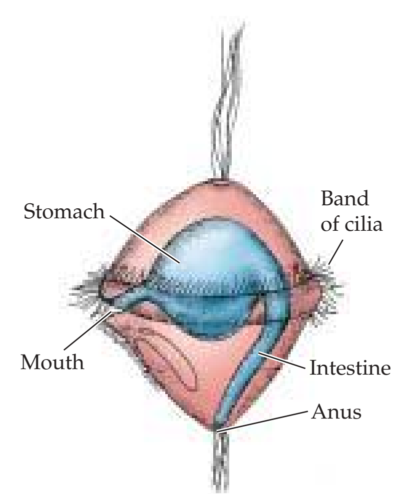
Segmentation allows an animal to alter the shape of its body in complex ways and to control its movements more precisely. Fossils of segmented worms are known from the middle Cambrian; the earliest forms are thought to have been burrowing marine animals. Segmentation evolved several times among spiralians; we will discuss only one of the phyla with segmented members: the annelids.

The **annelids** (phylum **Annelida**) are a diverse group of segmented spiralian worms (Figure 32.22). The coelom in each segment is isolated from those in other segments. A separate nerve center called a *ganglion* controls each segment, and the ganglia are connected by nerve cords that coordinate their functioning. Most annelids lack a rigid, external protective covering. The body wall serves as a general surface for gas exchange in most species, but this thin, permeable body surface restricts annelids to moist environments; they lose body water rapidly in dry air. The approximately 16,500 described species live in marine, freshwater, and terrestrial environments.

POLYCHAETES. More than half of all annelid species are members of the class **Polychaeta** ("many hairs"). Nearly all polychaetes are marine animals. Most have one or more pairs of eyes and one or more pairs of tentacles at the anterior end of the body. The body wall in most segments extends laterally as a series of thin outgrowths, called *parapodia*, that contain many blood vessels. The parapodia function in gas exchange, and some species use them to move. Stiff bristles called *setae* protrude from each parapodium, forming temporary attachments to the substratum that prevent the animal from slipping backward when its muscles contract.

Typically, males and female polychaetes release gametes into the water, where the eggs are fertilized and develop into trochophore larvae (Figure 32.23). The trochophore is a distinctive larval type found among polychaetes, mollusks, and several other marine lineages with spiral cleavage. The second half of the name "lophotrochozoans" is derived from this larva, which is believed by many researchers to represent an evolutionary link between the annelids and the mollusks.

As the polychaete trochophore develops, it forms body segments at its posterior end; eventually it becomes a small



32.23 The Trochophore Larva The trochophore ("wheel-bearer") is a distinctive larval form found in several animal lineages with spiral cleavage, most notably the marine polychaete worms and the mollusks.

(*a*) *Spirobranchus* sp.

(*b*) *Lumbricus* sp.

(*c*) *Microbdella* sp.

(*d*) *Riftia* sp.

32.24 Diversity among the Annelids
(*a*) The feather duster worm is a marine polychaete with striking feeding tentacles. (*b*) Earthworms are hermaphroditic (each individual is simultaneously both male and female). When they copulate, each individual donates and receives sperm. (*c*) This Australian tiger leech is attached to a leaf by its posterior sucker as it waits for a mammalian host. (*d*) Vestimentiferans live around hydrothermal vents deep in the ocean. Their skin secretes chitin and other substances, forming tubes.

adult worm. Many polychaete species live in burrows in soft sediments and filter prey from the surrounding water with elaborate, feathery tentacles (Figure 32.24*a*).

OLIGOCHAETES. More than 90 percent of the approximately 3,000 described species of **oligochaetes** (class **Oligochaeta**) live in freshwater or terrestrial habitats. Oligochaetes ("few hairs") have no parapodia, eyes, or anterior tentacles, and they have relatively few setae. Earthworms—the most familiar oligochaetes (see Figure 32.22)—are scavengers and ingesters of soil, from which they extract food particles.

Unlike polychaetes, all oligochaetes are *hermaphroditic:* that is, each individual is both male and female. Sperm are exchanged simultaneously between two copulating individuals (Figure 32.24*b*). Eggs are laid in a cocoon outside the adult's body. The cocoon is shed, and when development is complete, miniature worms emerge and begin independent life.

LEECHES. **Leeches** (class **Hirudinea**) probably evolved from oligochaete ancestors. Most species live in freshwater or terrestrial habitats and, like oligochaetes, lack parapodia and tentacles. Like oligochaetes, leeches are hermaphroditic. The coelom of leeches is not divided into compartments; the coelomic space is largely filled with undifferentiated tissue. Groups of segments at each end of the body are modified to form suckers, which serve as temporary anchors that aid the leech in movement (Figure 32.24*c*). With its posterior sucker attached to a substratum, the leech extends its body by contracting its circular muscles. The anterior sucker is then attached, the posterior one detached, and the leech shortens itself by contracting its longitudinal muscles.

Many leeches are external parasites of other animals, but some species also eat snails and other invertebrates. A leech makes an incision in its host, from which blood flows. It can ingest so much blood in a single feeding that its body may enlarge several times. An anticoagulant secreted by the leech into the wound keeps the host's blood flowing. For hundreds of years leeches were widely employed in medicine. Even today they are used to reduce fluid pressure and prevent blood clotting in damaged tissues and to eliminate pools of coagulated blood.

VESTIMENTIFERANS. Members of one lineage of annelids, the **vestimentiferans** (class **Pogonophora**), evolved burrowing forms with a crown of tentacles through which gases are exchanged; they entirely lost their digestive systems (Figure 32.24*d*). Vestimentiferans secrete chitin and other substances to form the tubes in which they live.

A vestimentiferan's coelom consists of an anterior compartment into which the tentacles can be withdrawn, and a long, subdivided cavity that extends much of the length of its body. The posterior end of the body is segmented. Experiments using radioactively labeled molecules have shown that vestimentiferans take up dissolved organic matter at high rates from either the sediments in which they live or the surrounding water.

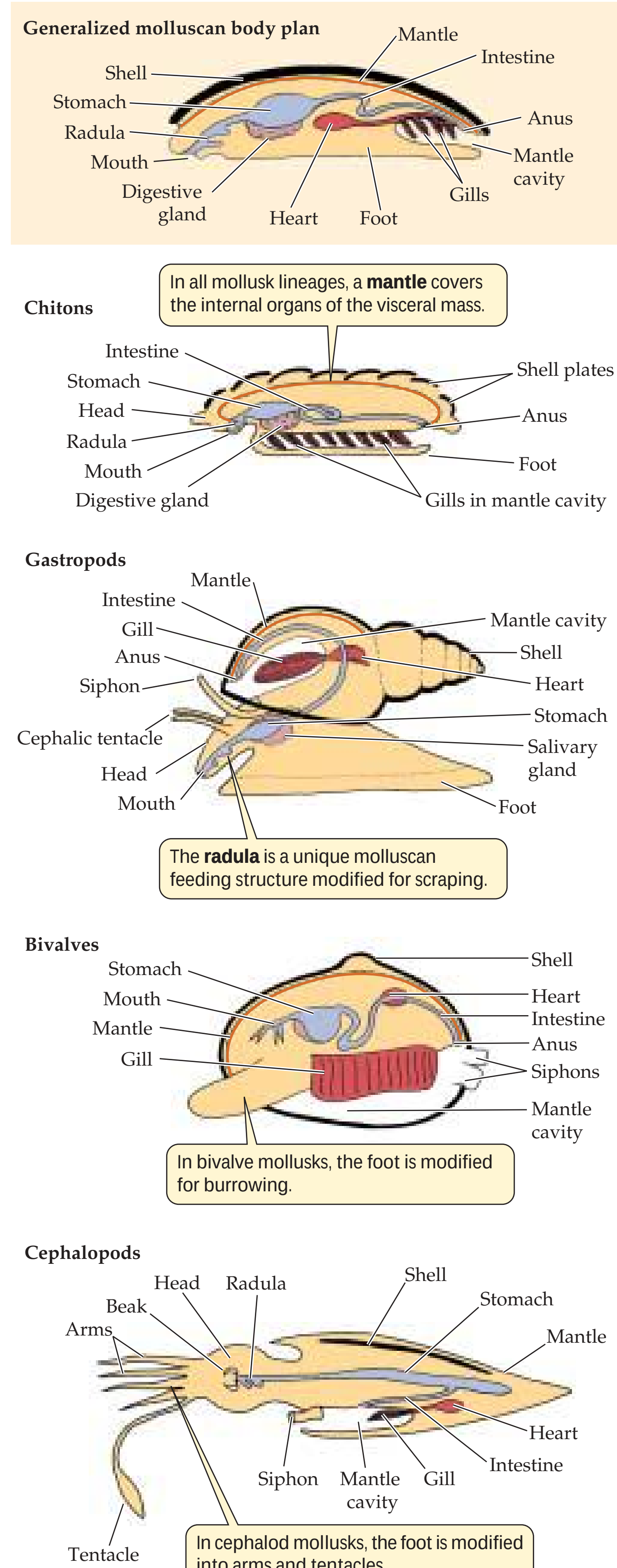
Vestimentiferans were not discovered until the twentieth century, when deep-sea exploration revealed them living many thousands of meters below the ocean surface. In these deep oceanic sediments, they are abundant, reaching densities of many thousands per square meter. About 145 species have been described. The largest and most remarkable vestimentiferans, which grow to 2 meters in length, live near deep-sea hydrothermal vents—volcanic openings in the sea floor through which hot, sulfide-rich water pours. The tissues of these species harbor endosymbiotic bacteria that fix carbon using energy obtained from oxidation of hydrogen sulfide (H_2S).

Mollusks evolved shells

Mollusks (phylum **Mollusca**) range in size from snails only a millimeter high to giant squids more than 18 meters long—the largest known invertebrates. Mollusks underwent one of the most dramatic of animal evolutionary radiations, based on a unique body plan with three major structural components: a foot, a mantle, and a visceral mass. Animals that appear very different, such as snails, clams, and squids, are all built from these components (Figure 32.25).

The molluscan *foot* is a large, muscular structure that originally was both an organ of locomotion and a support for the internal organs. In the lineage leading to squids and octopuses, the foot was modified to form arms and tentacles borne on a head with complex sense organs. In other groups, such as clams, the foot was transformed into a burrowing organ. In some lineages the foot is greatly reduced.

The *mantle* is a fold of tissue that covers the *visceral mass* of internal organs. In many mollusks, the mantle extends beyond the visceral mass to form a *mantle cavity*. The mantle secretes the hard, calcarous skeleton typical of most mollusks. The *gills*, which are used for gas exchange and, in some



32.25 Molluscan Body Plans The diverse modern mollusks are all variations on a general body plan that includes a foot, a mantle, and a visceral mass of internal organs.

species, for feeding, lie in this cavity. When the cilia on the gills beat, they create a flow of water over the gills. The tissue of the gills, which is highly *vascularized* (contains many blood vessels), takes up O_2 from the water and releases CO_2.

Mollusks have an *open circulatory system* that empties into large fluid-filled cavities, through which fluids move around the animal and deliver O_2 to internal organs. Mollusks also developed a rasping feeding structure known as the *radula*. The radula was originally an organ for scraping algae from rocks, a function it retains in many living mollusks. However, in some mollusks, it has been modified into a drill or poison dart. In others, such as clams, it is absent.

Although individual components have been lost in some lineages, these three unique, shared derived characteristics—the foot, the mantle, and the visceral mass—lead zoologists to believe that all 95,000 species of mollusks have a common ancestor. A small sample of these species is shown in Figure 32.26.

MONOPLACOPHORANS. **Monoplacophorans** (class **Monoplacophora**) were the most abundant mollusks during the Cambrian period, 550 million years ago, but today there are only a few surviving species. Unlike all other living mollusks, the surviving monoplacophorans have respiratory organs, muscles, and excretory pores that are repeated over the length of the body. The respiratory organs are located in a large cavity under the shell, through which oxygen-bearing water circulates.

CHITONS. **Chitons** (class **Polyplacophora**) have multiple gills and shell plates, but the body is not truly segmented (Figure 32.26*a*). The chiton body is bilaterally symmetrical, and its internal organs, particularly the digestive and nervous systems, are relatively simple. The larvae of chitons are almost indistinguishable from those of annelids. Most chitons are marine herbivores that scrape algae from rocks with their sharp radulae. An adult chiton spends most of its life clinging tightly to rock surfaces with its large, muscular, mucus-covered foot. It moves slowly by means of rippling waves of muscular contraction in the foot. Fertilization in most chitons takes place in the water, but in a few species fertilization is internal and embryos are brooded within the body.

BIVALVES. One lineage of early mollusks developed a hinged, two-part shell that extended over the sides of the body as well as the top, giving rise to the **bivalves** (class **Bivalvia**), which include the familiar clams, oysters, scallops, and mussels (Figure 32.26*b*). Bivalves are largely sedentary and have greatly reduced heads. The foot is compressed, and in many clams, it is used for burrowing into mud and sand. Bivalves feed by taking in water through an opening called an *incurrent siphon* and extracting food from the water with their large gills, which are also the main sites of gas exchange. Water and gametes exit through the *excurrent siphon*. Fertilization takes place in open water in most species.

GASTROPODS. Another lineage of early mollusks gave rise to the **gastropods** (class **Gastropoda**), which include snails, whelks, limpets, slugs, abalones, and the often brilliantly ornamented nudibranchs. Gastropods, unlike bivalves, have one-piece shells. Most gastropods are motile, using the large foot to move slowly across the substratum or to burrow through it. Gastropods are the most species-rich and widely distributed of the molluscan classes (Figure 32.26*c*,*d*). Most species move by gliding on the muscular foot, but in a few species—the sea butterflies and heteropods—the foot is modified into a swimming organ with which the animal moves through open ocean waters. The only mollusks that live in terrestrial environments—land snails and slugs—are gastropods. In these terrestrial species, the mantle tissue is modified into a highly vascularized lung. Fertilization is internal in most species.

CEPHALOPODS. In one lineage of mollusks, the cephalopods (class **Cephalopoda**), the excurrent siphon became modified to allow the animal to control the water content of the mantle cavity. Ultimately, the modification of the mantle into a device for forcibly ejecting water from the cavity enabled these animals to move rapidly through the water. Furthermore, many early cephalopods had chambered shells into which gas could be secreted to adjust buoyancy. Together, these adaptations allow cephalopods to live in open water.

The cephalopods include the squids, octopuses, and nautiluses (Figure 32.26*e*, *f*). They first appeared about 600 million years ago, near the beginning of the Cambrian period. By the Ordovician period a wide variety of types were present. With their greatly enhanced mobility, some cephalopods, such as squids, became the major predators in the open waters of the Devonian oceans.They remain important marine predators today. Cephalopods capture and subdue their prey with their tentacles; octopuses also use their tentacles to move over the substratum. As is typical of active predators, cephalopods have a head with complex sensory organs, most notably eyes that are comparable to those of vertebrates in their ability to resolve images. The head is closely associated with a large, branched foot that bears the tentacles and a siphon. The large muscular mantle provides a solid external supporting structure. The gills hang in the mantle cavity. As is typical of behaviorally complex animals, many cephalopods have elaborate courtship behavior, which may involve striking color changes.

(*a*) *Mopalia* sp.

(*b*) *Tridacna gigas*

(*c*) *Phidiana hiltoni*

(*d*) *Helminthoglypta walkeriana*

(*e*) *Octopus bimaculoides*

(*f*) *Nautilus pompilius*

32.26 Diversity among the Mollusks (*a*) Chitons are common in the intertidal zones of the temperate zone coasts. (*b*) The giant clam of Indonesia is among the largest of the bivalve mollusks. (*c*) Slugs are gastropods that have lost their shells; this shell-less sea slug is very conspicuously colored. (*d*) Land snails are shelled, terrestrial gastropods. (*e*) Cephalopods such as the octopus are active predators. (*f*) The boundaries of its chambers are clearly visible on the outer surface of this shelled *Nautilus*, another cephalopod.

The earliest cephalopod shells were divided by partitions penetrated by tubes through which liquids could be moved. Nautiloids (genus *Nautilus*) are the only cephalopods with external chambered shells that survive today (Figure 32.26*f*).

Mollusks and brachiopods are among the lophotrochozoans that evolved hard shells that help to protect them from predators and the physical environment. A sturdy outer covering is the main feature of the second protostomate lineage, the ecdysozoans—the subject of the next chapter.

Chapter Summary

Animals: Descendants of a Common Ancestor

▶ All members of the kingdom Animalia are believed to have a common ancestor, which was a colonial flagellated protist.

▶ The specialization of cells by function made possible the complex, multicellular body plan of animals.

▶ Animals are multicellular heterotrophs. They take in complex organic molecules, expending energy to do so.

▶ Morphological, developmental, and molecular data all support similar animal phylogenies.

▶ The two major animal lineages—protostomes and deuterostomes—are believed to have diverged early in animal evolution; they differ in several components of their early development. **Review Figure 32.1**

Body Plans Are Basic Structural Designs

▶ Most animals have either radial or bilateral symmetry. Radially symmetrical animals move slowly or not at all. Bilateral symmetry is strongly correlated with more rapid movement and the concentration of sense organs at the anterior end of the animal. **Review Figure 32.2**

▶ The body cavity of an animal is strongly correlated with its ability to move. On the basis of their body cavities, animals are classified as acoelomates, pseudocoelomates, or coelomates. **Review Figure 32.3**

Sponges: Loosely Organized Animals

▶ Sponges (phylum Porifera) are simple animals that lack cell layers and true organs, but have several different cell types.

▶ Sponges feed by means of choanocytes, feeding cells that draw water through the sponge body and filter out food particles. **Review Figure 32.4**

▶ Sponges come in a variety of sizes and shapes that are adapted to different movement patterns of water.

Cnidarians: Two Cell Layers and Blind Guts

▶ Cnidarians (phylum Cnidaria) are radially symmetrical and diploblastic, but with their nematocyst-studded tentacles, they can capture prey larger and more complex than themselves. **Review Figure 32.7**

▶ Most cnidarian life cycles have a sessile polyp stage and a free-swimming, sexual, medusa stage, but some species lack one of the stages. **Review Figures 32.8, 32.10, 32.11**

See Web/CD Tutorial 32.1

Ctenophores: Complete Guts and Tentacles

▶ Ctenophores (phylum Ctenophora) are diploblastic marine carnivores with a complete gut and simple life cycles. **Review Figure 32.12**

The Evolution of Bilaterally Symmetrical Animals

▶ All bilaterally symmetrical animals probably share a common ancestor.

▶ Protostomes and deuterostomes are each monophyletic lineages that have been evolving separately since the Cambrian period. Their members are structurally more complex than cnidarians and ctenophores.

▶ Protostomes have a ventral nervous system, paired nerve cords, and larvae with compound cilia.

▶ Deuterostomes have a dorsal nervous system and larvae with a single cilium per cell.

▶ The protostomes split into two major groups: lophotrochozoans and ecdysozoans. **Review Figure 32.14**

Simple Lophotrochozoans

▶ Flatworms (phylum Platyhelminthes) are acoelomate, lack organs for oxygen transport, have only one entrance to the gut, and move by beating their cilia. Many species are parasitic. **Review Figures 32.15, 32.16**

▶ Although they are no larger than many ciliated protists, rotifers (phylum Rotifera) have highly developed internal organs. **Review Figure 32.17**

Lophophorates: An Ancient Body Plan

▶ The lophotrochozoan lineage split into two branches, whose descendants became the modern lophophorates and the spiralians.

▶ The lophophore dominates the anatomy of many lophophorate animals. **Review Figure 32.18**

▶ Ectoprocts are colonial lophophorates that can move their lophophores. **Review Figure 32.19**

▶ Brachiopods, which superficially resemble bivalve mollusks, were much more abundant in the past than they are today.

Spiralians: Spiral Cleavage and Wormlike Body Plans

▶ The spiralian lineage gave rise to many phyla, most of whose members are wormlike.

▶ Ribbon worms (phylum Nemertea) have a complete digestive tract and capture prey with an eversible proboscis. **Review Figure 32.21**

▶ Annelids (phylum Annelida) are a diverse group of segmented worms that live in marine, freshwater, and terrestrial environments. **Review Figures 32.22**

▶ Mollusks (phylum Mollusca) have a body plan with three basic components: foot, mantle, and visceral mass. **Review Figure 32.25**

▶ The molluscan body plan has been modified to yield a diverse array of animals that superficially appear very different from one another.

See Web/CD Activities 32.1 and 32.3 for a concept review of this chapter

Self-Quiz

1. The body plan of an animal is
   a. its general structure.
   b. the integrated functioning of its parts.
   c. its general structure and the integrated functioning of its parts.
   d. its general structure and its evolutionary history.
   e. the integrated functioning of its parts and its evolutionary history.

2. A bilaterally symmetrical animal can be divided into mirror images by
   a. any plane through the midline of its body.
   b. any plane from its anterior to its posterior end.
   c. any plane from its dorsal to its ventral surface.
   d. any plane through the midline of its body from its anterior to its posterior end.
   e. a single plane through the midline of its body from its dorsal to its ventral surface.
3. Among protostomes, cleavage of the fertilized egg is
   a. delayed while the egg continues to mature.
   b. always radial.
   c. spiral in some species and radial in others.
   d. triploblastic.
   e. diploblastic.
4. The sponge body plan is characterized by
   a. a mouth and digestive cavity but no muscles or nerves.
   b. muscles and nerves but no mouth or digestive cavity.
   c. a mouth, digestive cavity, and spicules.
   d. muscles and spicules but no digestive cavity or nerves.
   e. no mouth, digestive cavity, muscles, or nerves.
5. Which are phyla of diploblastic animals?
   a. Porifera and Cnidaria
   b. Cnidaria and Ctenophora
   c. Cnidaria and Platyhelminthes
   d. Ctenophora and Platyhelminthes
   e. Porifera and Ctenophora
6. Cnidarians have the ability to
   a. live in both salt and fresh water.
   b. move rapidly in the water column.
   c. capture and consume large numbers of small prey.
   d. survive where food is scarce, because of their low metabolic rate.
   e. capture large prey and to move rapidly.
7. Many parasites evolved complex life cycles because
   a. they are too simple to disperse readily.
   b. they are poor at recognizing new hosts.
   c. they were driven to it by host defenses
   d. complex life cycles increase the probability of a parasite's transfer to a new host.
   e. their ancestors had complex life cycles and they simply retained them.
8. Members of which phyla have lophophores?
   a. Phoronida, Brachiopoda, and Nemertea
   b. Phoronida, Brachiopoda, and Ectoprocta
   c. Brachiopoda, Ectoprocta, and Platyhelminthes
   d. Phoronida, Rotifera, and Ectoprocta
   e. Rotifera, Ectoprocta, and Brachiopoda
9. Which of the following is not part of the molluscan body plan?
   a. Mantle
   b. Foot
   c. Radula
   d. Visceral mass
   e. Jointed skeleton
10. Cephalopods control their buoyancy by
    a. adjusting salt concentrations in their blood.
    b. forcibly expelling water from the mantle.
    c. pumping water in and out of internal chambers.
    d. using the complex sense organs in their heads.
    e. swimming rapidly.

For Discussion

1. Differentiate among the members of each of the following sets of related terms:
   a. radial symmetry/bilateral symmetry
   b. protostome/deuterostome
   c. diploblastic/triploblastic
   d. coelomate/pseudocoelomate/acoelomate
2. In this chapter we listed some of the traits shared by all animals that convince most biologists that all animals are descendants of a single common ancestral lineage. In your opinion, which of these traits provides the most compelling evidence that animals are monophyletic?
3. Describe some features that allow animals to capture prey that are larger and more complex than they themselves are.
4. Why is bilateral symmetry strongly associated with cephalization, the concentration of sense organs in an anterior head?
5. Why might mollusks not have evolved segmentation, given that a segmented body enables improved control over locomotion?