

28.1 Evolution of Animals

Animals can be contrasted with plants and fungi. Like both of these, animals are multicellular eukaryotes, but unlike plants, which make their food through photosynthesis, they are heterotrophs, and must acquire nutrients from an external source. Fungi digest their food externally and absorb the breakdown products. Animals ingest (eat) whole food and digest it internally.

Animals have the diploid life cycle (see Fig. 21Ac). They usually carry on sexual reproduction and begin life only as a fertilized diploid egg. From this starting point, they undergo a series of developmental stages to produce an organism that has specialized tissues, usually within organs that carry on specific functions. Two types of tissues in particular—muscle and nerve—characterize animals. The evolution of these tissues allows an animal to exhibit motility and a variety of flexible movements. They enable many types of animals to search actively for their food and to prey on other organisms. Coordinated movements also allow animals to seek mates,

shelter, and a suitable climate—behaviors that have resulted in the vast diversity of animals. Animals are monophyletic; and both invertebrates and vertebrates can trace their ancestry to the same ancestor. Adult **vertebrates** have a spinal cord (or backbone) running down the center of the back, while **invertebrates**, the topic of this chapter, do not have a backbone. The frog in Figure 28.1 is a vertebrate, while the damselfly it is devouring is an invertebrate.

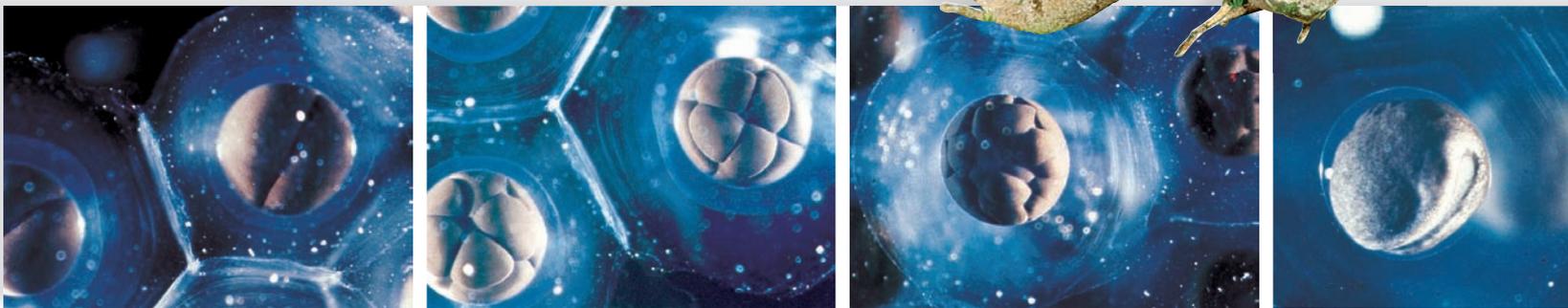
Figure 28.1 illustrates the characteristics of a complex animal, using the frog as an example. A frog goes through a number of embryonic stages to become a larval form (the tadpole) with many specialized tissues. A larva is an immature stage that typically lives in a different habitat and feeds on different foods than the adult. By means of a change in body form called metamorphosis, the larva, which typically swims, turns into a sexually mature adult frog that swims and hops. The tadpole lives on tiny aquatic organisms, and the terrestrial adult typically feeds on insects and worms. A large African bullfrog will try to eat just about anything, including other frogs, as well as small fish, reptiles, and mammals.

FIGURE 28.1 Animals—multicellular, heterotrophic eukaryotes.

Animals begin life as a $2n$ zygote that undergoes development to produce a multicellular organism that has specialized tissues. Animals depend on a source of external food to carry on life's processes. This series of images shows the development and metamorphosis of the frog, a complex animal.



Adult frog



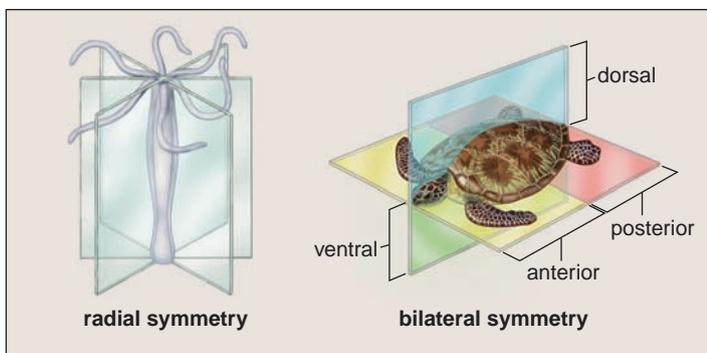
Stages in development, from zygote to embryo.



Stages in metamorphosis, from hatching to tadpole.

Ancestry of Animals

In Chapter 23, we discussed evidence that plants most likely share a green algal ancestor with the charophytes. What about animals? Did they also evolve from a protist, most likely a particular motile protozoan? The *colonial flagellate hypothesis* states that animals are descended from an ancestor that resembled a hollow spherical colony of flagellated cells. Figure 28.2 shows how the process would have begun with an aggregate of a few flagellated cells. From there a larger number of cells could have formed a hollow sphere. Individual cells within the colony would have become specialized for particular functions, such as reproduction. Two tissue layers could have arisen by an infolding of certain cells into a hollow sphere. Tissue layers do arise in this manner during the development of animals today. The colonial flagellate hypothesis is also attractive because it implies that **radial symmetry** preceded **bilateral symmetry** in the history of animals, as is probably the case. In a radially symmetrical animal, any longitudinal cut produces two identical halves; in a bilaterally symmetrical animal, only one longitudinal cut yields two identical halves:

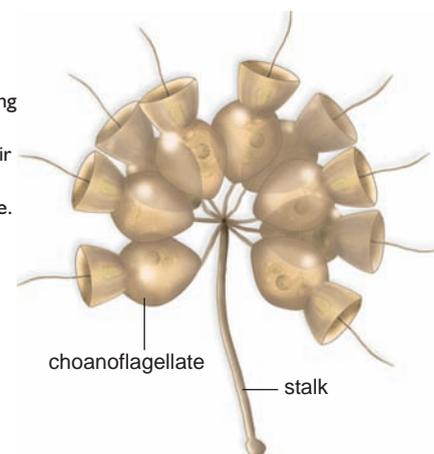


Among the protists, the choanoflagellates (collared flagellates) most likely resemble the last unicellular ancestor of animals, and molecular data tells us that they are the closest living relatives of animals! A choanoflagellate is a single cell, 3–10 μm

FIGURE 28.3

Choanoflagellate.

The choanoflagellates are the living protozoans most closely related to animals and may resemble their immediate unicellular ancestor. Some live as a colony like this one.



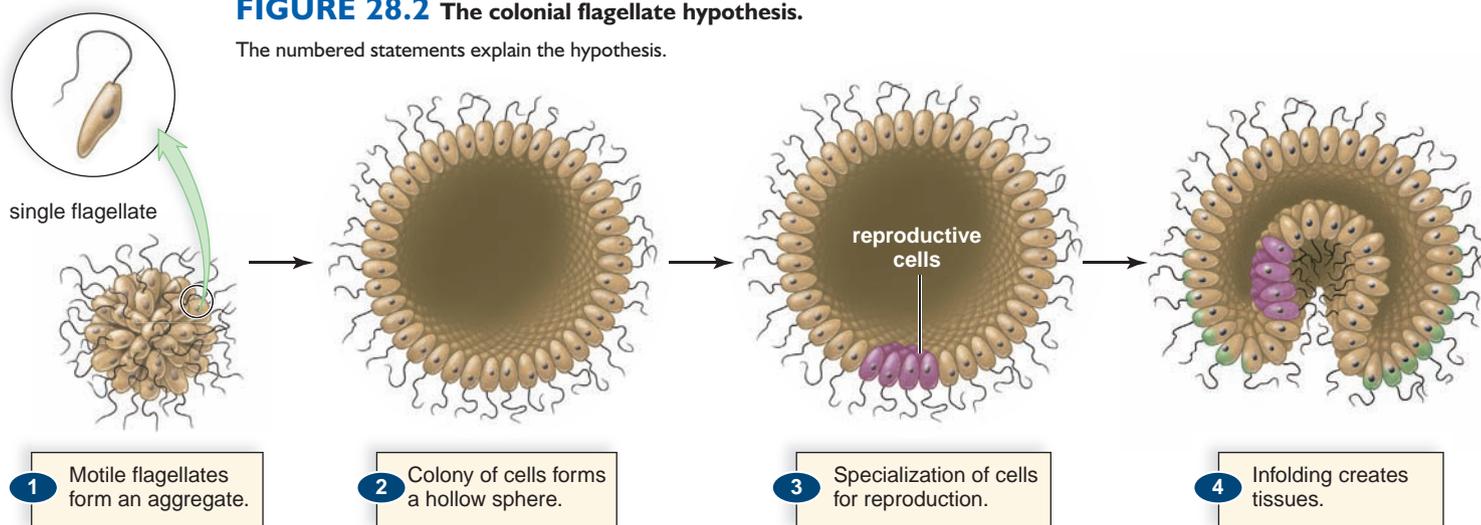
in diameter, with a flagellum surrounded by a collar of 30–40 microvilli. Movement of the flagellum creates water currents that pull the protist along. As the water moves through the microvilli, they engulf bacteria and debris from the water. Interesting to our story, choanoflagellates also exist as a colony of cells (Fig. 28.3). Several can be found together at the end of a stalk or simply clumped together like a bunch of grapes.

Evolution of Body Plans

As we discussed in the Science Focus on page 308, all of the various animal body plans were present by the Cambrian period. How could such diversity have arisen within a relatively short period of geological time? As an animal develops, there are many possibilities regarding the number, position, size, and patterns of its body parts. Different combinations could have led to the great variety of animal forms in the past and present. We now know that slight shifts in genes called *Hox* (homeotic) genes are responsible for the major differences between animals that arise during development. Perhaps changes in the expression of *Hox* developmental genes explain why all the animal groups of today had representatives in the Cambrian seas.

FIGURE 28.2 The colonial flagellate hypothesis.

The numbered statements explain the hypothesis.



The Phylogenetic Tree of Animals

There is no adequate fossil record by which to trace the early evolution of animals. Therefore, the phylogenetic tree of animals shown in Figure 28.4 is based on molecular and morphological data, including homologies that become apparent during the development of animals. When utilizing molecular data, it is assumed that the more closely related two organisms, the more rRNA nucleotide sequences they will have in common. Molecular data have resulted in a phylogenetic tree that is quite different from one based only on morphological characteristics.

Morphological Data

Refer to the tree in Figure 28.4 as we discuss the anatomical characteristics substantiating the molecular data used to construct the tree.

Type of Symmetry. Three types of symmetry exist in the animal world. *Asymmetrical symmetry* is seen in sponges that have no particular body shape. The cnidarians and comb jellies are *radially symmetrical*—they are organized circularly, similar to a wheel, and two identical halves are obtained, no matter how the animal is sliced longitudinally. The rest of the

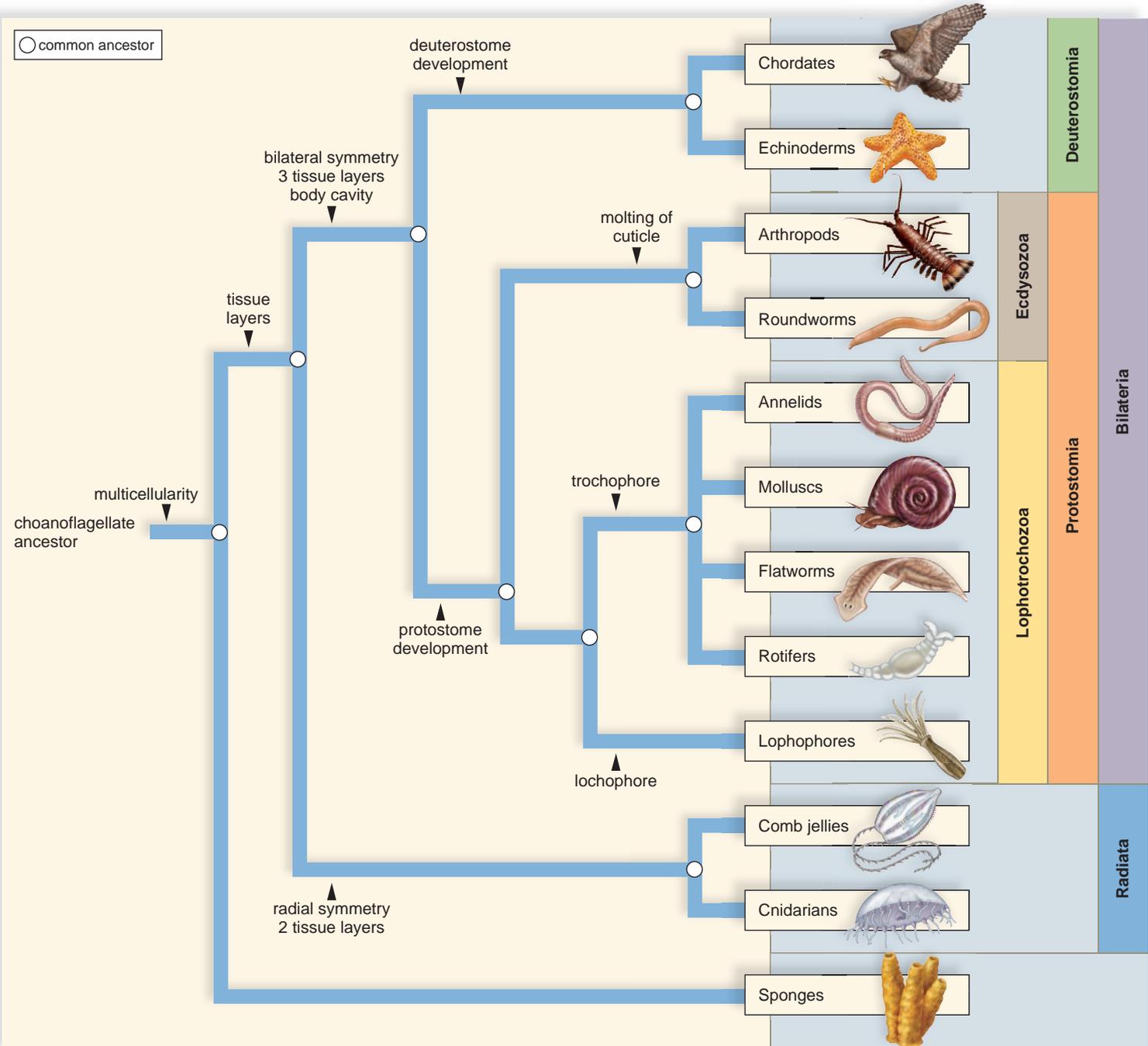


FIGURE 28.4 Phylogenetic tree of animals.

All animal phyla living today are most likely descended from a colonial flagellated protist living about 600 million years ago, and this accounts for their motility. This phylogenetic (evolutionary) tree uses morphological and molecular data (rRNA sequencing) to determine which phyla are most closely related to one another.

animals are *bilaterally symmetrical* as adults, and they have a definite left and right half, and only a longitudinal cut down the center of the animal will produce two equal halves.

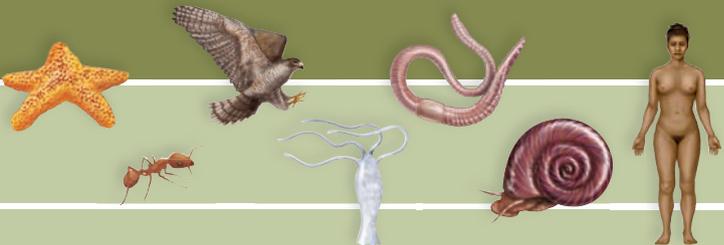
Radially symmetrical animals are sometimes attached to a substrate—that is, they are **sessile**. This type of symmetry is useful because it allows these animals to reach out in all directions from one center. This advantage also applies to floating animals with radial symmetry, such as jellyfish. Bilaterally symmetrical animals tend to be active and to move forward with an anterior end. During the evolution of animals, bilateral symmetry is accompanied by **cephalization**, localization of a brain and specialized sensory organs at the anterior end of an animal.

Embryonic Development. Like all animals, sponges are multicellular but they do not have true tissues. There-

fore, sponges have the cellular level of organization. True tissues appear in the other animals as they undergo embryological development. The first three tissue layers are often called **germ layers** because they give rise to the organs and organ systems of complex animals. Animals such as the cnidarians, which have only two tissue layers (ectoderm and endoderm) as embryos, are *diploblastic* with the tissue level of organization. Those animals that develop further and have all three tissue layers (ectoderm, mesoderm, and endoderm) as embryos are *triploblastic* and have the organ level of organization. Notice in the phylogenetic tree that the animals with three tissue layers are either **protostomes** [Gk. *proto*, first; *stoma*, mouth] or **deuterostomes** [Gk. *deuter*, second; *stoma*, mouth].

DOMAIN: Eukarya
KINGDOM: Animals

CHARACTERISTICS
Multicellular, usually with specialized tissues; ingest or absorb food; diploid life cycle



INVERTEBRATES

Sponges (bony, glass, spongin):* Asymmetrical, saclike body perforated by pores; internal cavity lined by choanocytes; spicules serve as internal skeleton. 5,150⁺

Radiata

Cnidarians (hydra, jellyfish, corals, sea anemones): Radially symmetrical with two tissue layers; sac body plan; tentacles with nematocysts. 10,000⁺

Comb jellies: Have the appearance of jellyfish; the “combs” are eight visible longitudinal rows of cilia that can assist locomotion; lack the nematocysts of cnidarians but some have two tentacles. 150⁺

Protostomia (Lophotrochozoa)

Lophophorates (lampshells, bryozoa): Filter feeders with a circular or horseshoe-shaped ridge around the mouth that bears feeding tentacles. 5,935⁺

Flatworms (planarians, tapeworms, flukes): Bilateral symmetry with cephalization; three tissue layers and organ systems; acoelomate with incomplete digestive tract that can be lost in parasites; hermaphroditic. 20,000⁺

Rotifers (wheel animals): Microscopic animals with a corona (crown of cilia) that looks like a spinning wheel when in motion. 2,000⁺

Molluscs (chitons, clams, snails, squids): Coelom, all have a foot, mantle, and visceral mass; foot is variously modified; in many, the mantle secretes a calcium carbonate shell as an exoskeleton; true coelom and all organ systems. 110,000⁺

Annelids (polychaetes, earthworms, leeches): Segmented with body rings and setae; cephalization in some polychaetes; hydroskeleton; closed circulatory system. 16,000⁺

Protostomia (Ecdysozoa)

Roundworms (*Ascaris*, pinworms, hookworms, filarial worms): Pseudocoelom and hydroskeleton; complete digestive tract; free-living forms in soil and water; parasites common. 25,000⁺

Arthropods (crustaceans, spiders, scorpions, centipedes, millipedes, insects): Chitinous exoskeleton with jointed appendages undergoes molting; insects—most have wings—are most numerous of all animals. 1,000,000⁺

Deuterostomia

Echinoderms (sea stars, sea urchins, sand dollars, sea cucumbers): Radial symmetry as adults; unique water-vascular system and tube feet; endoskeleton of calcium plates. 7,000⁺

Chordates (tunicates, lancelets, vertebrates): All have notochord, dorsal tubular nerve cord, pharyngeal pouches, and postanal tail at some time; contains mostly vertebrates in which notochord is replaced by vertebral column. 56,000⁺

VERTEBRATES

Fishes (jawless, cartilaginous, bony): Endoskeleton, jaws, and paired appendages in most; internal gills; single-loop circulation; usually scales. 28,000⁺

Amphibians (frogs, toads, salamanders): Jointed limbs; lungs; three-chambered heart with double-loop circulation; moist, thin skin. 5,383⁺

Reptiles (snakes, turtles, crocodiles): Amniotic egg; rib cage in addition to lungs; three- or four-chambered heart typical; scaly, dry skin; copulatory organ in males and internal fertilization. 8,000⁺

Birds (songbirds, waterfowl, parrots, ostriches): Endothermy, feathers, and skeletal modifications for flying; lungs with air sacs; four-chambered heart. 10,000⁺

Mammals (monotremes, marsupials, placental): Hair and mammary glands. 4,800⁺

*After a character is listed, it is present in the rest, unless stated otherwise.
*Number of species.

Figure 28.5 shows that protostome and deuterostome development are differentiated by three major events:

1. Cleavage, the first event of development, is cell division without cell growth. In protostomes, spiral cleavage occurs, and daughter cells sit in grooves formed by the previous cleavages. The fate of these cells is fixed and determinate in protostomes; each can contribute to development in only one particular way. In deuterostomes, radial cleavage occurs, and the daughter cells sit right on top of the previous cells. The fate of these cells is indeterminate—that is, if they are separated from one another, each cell can go on to become a complete organism.
2. As development proceeds, a hollow sphere of cells, or blastula, forms and the indentation that follows produces an opening called the blastopore. In protostomes, the mouth appears at or near the blastopore, hence the origin of their name; in deuterostomes, the anus appears at or near the blastopore, and only later does a second opening form the mouth, hence the origin of their name.
3. Certain of the protostomes and all deuterostomes have a body cavity completely lined by mesoderm, called a **true coelom** [Gk. *koiloma*, cavity]. However, a true coelom develops differently in the two groups. In protostomes, the mesoderm arises from cells located near the embryonic blastopore, and a splitting occurs that produces the coelom. In deuterostomes, the coelom arises as a pair of mesodermal pouches from the wall of the primitive gut. The pouches enlarge until they meet and fuse.

The deuterostomes include the echinoderms and the chordates, two groups of animals that will be examined in detail later. The protostomes are divided into the two groups: the **ectdysozoa** [Gk. *ecdysis*, stripping off] and the **lophotrochozoa**. The ectdysozoans include the roundworms and arthropods. Both of these types of animals **molt**; they shed their outer covering as they grow. Ectdysozoa means molting animals. The lophotrochozoa contain two groups: the **lophophores** [Gk. *lophos*, crest; *phoros*, bearing] and the **trochophores** [Gk. *trochos*, wheel]. All the lophophores have the same type of feeding apparatus. The trochophores either have presently or their ancestors had a trochophore larva (see page 520).

Check Your Progress

28.1

1. State three characteristics that all animals have in common.
2. Explain the colonial flagellate hypothesis about the origin of animals.
3. Refer to Figure 28.4 and state the characteristics that pertain to arthropods.

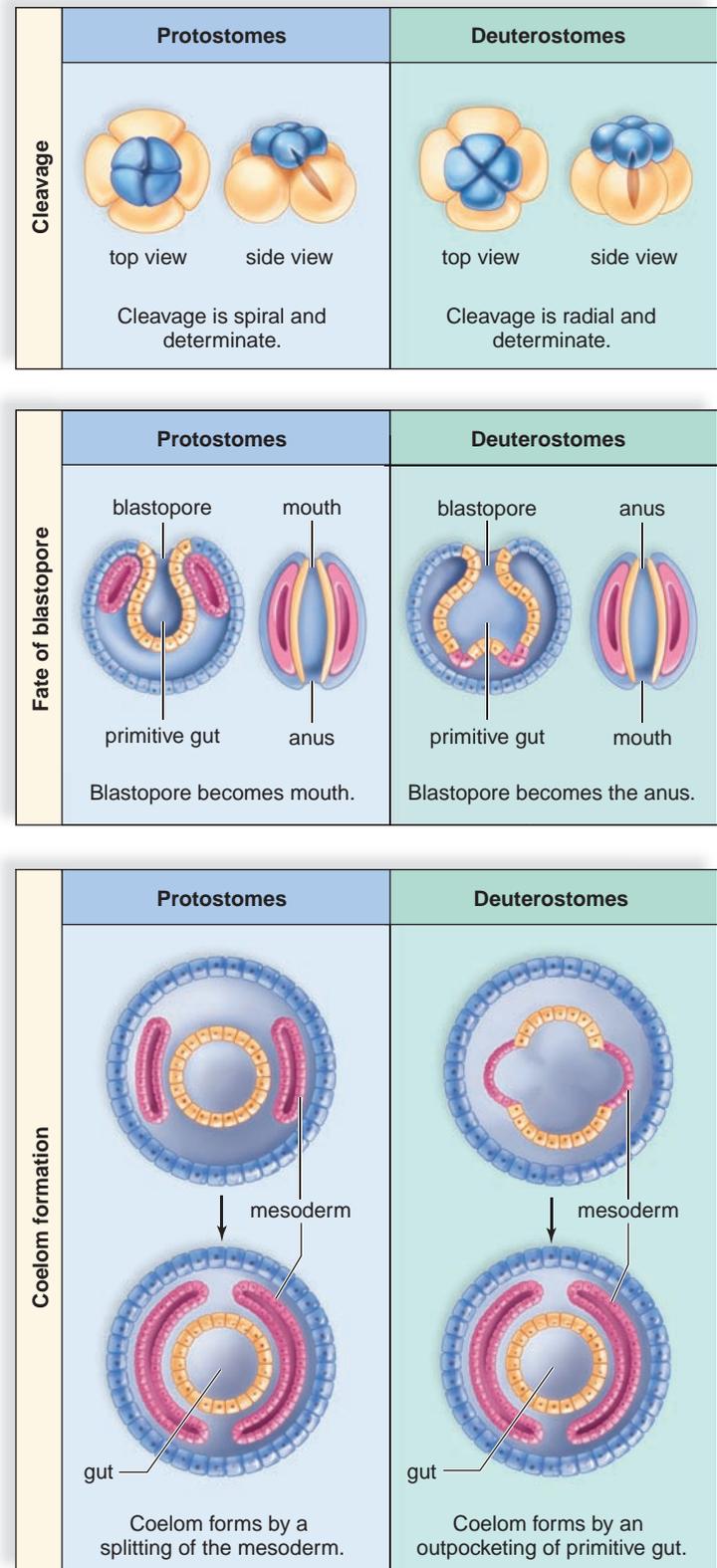


FIGURE 28.5 Protostomes compared to deuterostomes.

Left: In the embryo of protostomes, cleavage is spiral—new cells are at an angle to old cells—and each cell has limited potential and cannot develop into a complete embryo; the blastopore is associated with the mouth; and the coelom, if present, develops by a splitting of the mesoderm. *Right:* In deuterostomes, cleavage is radial—new cells sit on top of old cells—and each one can develop into a complete embryo; the blastopore is associated with the anus; and the coelom, if present, develops by an outpocketing of the primitive gut.

28.2 Introducing the Invertebrates

Sponges, cnidarians, and comb jellies are the least complex of the animals we will study.

Sponges

While all animals are multicellular, **sponges** (phylum Porifera [L. *porus*, pore, and *ferre*, to bear]) are the only animals to lack true tissues and to have a cellular level of organization. Actually, they have few cell types and no nerve or muscle cells to speak of. Still, molecular data show that they are at the base of the evolutionary tree of animals.

The saclike body of a sponge is perforated by many pores (Fig. 28.6). Sponges are aquatic, largely marine animals that vary greatly in size, shape, and color. But, they all have a canal system of varying complexity that allows water to move through their bodies.

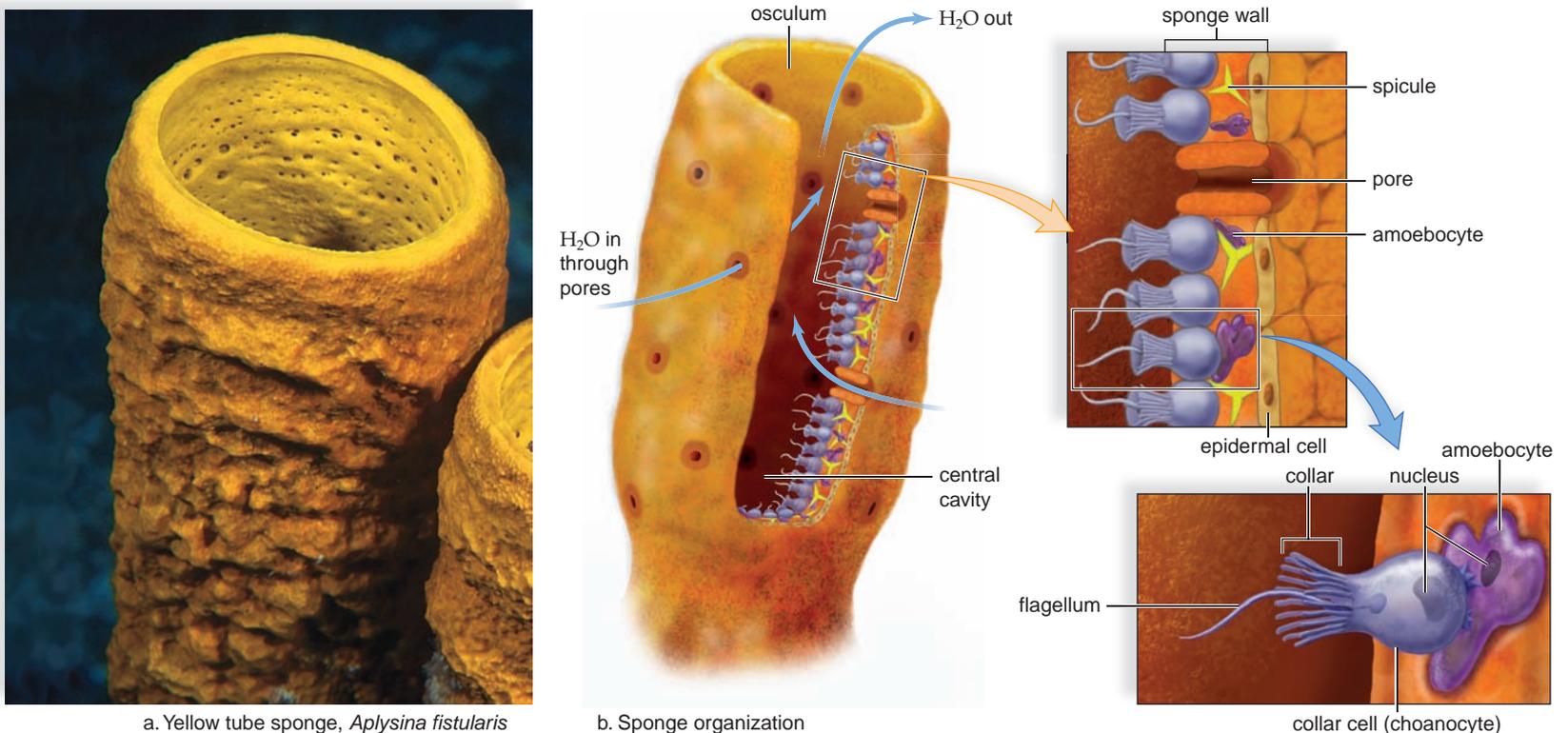
The interior of the canals is lined with flagellated cells that resemble a choanoflagellate. In a sponge, these cells are called collar cells, or choanocytes. The beating of the flagella produces water currents that flow through the pores into the central cavity and out through the osculum, the upper opening of the body. Even a simple sponge only 10 cm tall is estimated to filter as much as 100 L of water each day. It takes this much water to supply the needs of the sponge. A sponge is a stationary filter feeder, also called a suspension feeder, because it filters suspended particles from the water by means of a straining device—in this case,

the pores of the walls and the microvilli making up the collar of collar cells. Microscopic food particles that pass between the microvilli are engulfed by the collar cells and digested by them in food vacuoles.

The skeleton of a sponge prevents the body from collapsing. All sponges have fibers of spongin, a modified form of collagen; a bath sponge is the dried spongin skeleton from which all living tissue has been removed. Today, however, commercial “sponges” are usually synthetic. Typically, the endoskeleton of sponges also contains **spicules**—small, needle-shaped structures with one to six rays. Traditionally, the type of spicule has been used to classify sponges, in which case there are bony, glass, and spongin sponges. The success of sponges—they have existed longer than many other animal groups—can be attributed to their spicules. They have few predators because a mouth full of spicules is an unpleasant experience. Also, they produce a number of foul-smelling and toxic substances that discourage predators.

Sponges can reproduce both asexually and sexually. They reproduce asexually by fragmentation or by budding. During budding, a small protuberance appears and gradually increases in size until a complete organism forms. Budding produces colonies of sponges that can become quite large. During sexual reproduction, eggs and sperm are released into the central cavity, and the zygote develops into a flagellated larva that may swim to a new location. If the cells of a sponge are mechanically separated, they will reassemble into a complete and functioning organism! Like many less specialized organisms, sponges are also capable of regeneration, or growth of a whole from a small part.

FIGURE 28.6 Simple sponge anatomy.



a. Yellow tube sponge, *Aplysina fistularis*

b. Sponge organization

collar cell (choanocyte)

Comb Jellies and Cnidarians

These two groups of animals (Fig. 28.7) have true tissues and, as embryos, they have the two germ layers ectoderm and endoderm. They are radially symmetrical as adults, a type of symmetry with the advantages discussed on page 515.

Comb Jellies

Comb jellies (phylum Ctenophora) are solitary, mostly free-swimming marine invertebrates that are usually found in warm waters. Ctenophores represent the largest animals propelled by beating cilia and range in size from a few centimeters to 1.5 m in length. Their body is made up of a transparent jellylike substance called **mesoglea**. Most ctenophores do not have stinging cells and capture their prey by using sticky adhesive cells called colloblasts. Some ctenophores are bioluminescent, capable of producing their own light.

Cnidarians

Cnidarians (phylum Cnidaria) are tubular or bell-shaped animals that reside mainly in shallow coastal waters; however, there are some freshwater, brackish, and oceanic forms. The term *cnidaria* is derived from the presence of specialized stinging cells called cnidocytes. Each cnidocyte has a fluid-filled capsule called a **nematocyst** [Gk. *nema*, thread, and *kystis*, bladder] that contains a long, spirally coiled hollow thread. When the trigger of the cnidocyte is touched, the nematocyst is discharged. Some threads merely trap a prey, and others have spines that penetrate and inject paralyzing toxins.

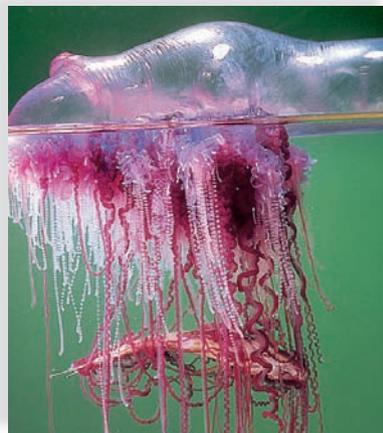
The body of a cnidarian is a two-layered sac. The outer tissue layer is a protective epidermis derived from ectoderm. The inner tissue layer, which is derived from endoderm, secretes



a. Sea anemone, *Corynactis*



b. Cup coral, *Tubastrea*



c. Portuguese man-of-war, *Physalia*



d. Jellyfish, *Crambionella*

FIGURE 28.8 Cnidarian diversity.

a. The anemone, which is sometimes called the flower of the sea, is a solitary polyp. b. Corals are colonial polyps residing in a calcium carbonate or proteinaceous skeleton. c. The Portuguese man-of-war is a colony of modified polyps and medusae. d. True jellyfishes undergo the complete life cycle; this is the medusa stage. The polyp is small.

digestive juices into the internal cavity, called the **gastrovascular cavity** [Gk. *gastros*, stomach; L. *vasculum*, dim. of *vas*, vessel] because it serves for digestion of food and circulation of nutrients. The fluid-filled gastrovascular cavity also serves as a supportive **hydrostatic skeleton**, so called because it offers some resistance to the contraction of muscle but permits flexibility. The two tissue layers are separated by mesoglea.

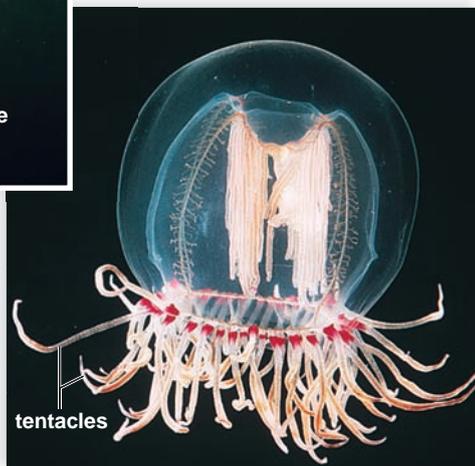
Two basic body forms are seen among cnidarians. The mouth of a **polyp** is directed upward, while the mouth of a jellyfish, or **medusa**, is directed downward. The bell-shaped medusa has more mesoglea than a polyp, and the tentacles are concentrated on the margin of the bell. At one time, both body forms may have been a part of the life cycle of all cnidarians. When both are present, the animal is dimorphic: The sessile polyp stage produces medusae by asexual budding, and the motile medusan stage produces egg and sperm. In some cnidarians, one stage is dominant and the other is reduced; in other species, one form is absent altogether.



a.

FIGURE 28.7 Comb jelly compared to cnidarian.

a. *Pleurobrachia pileus*, a comb jelly.
b. *Polyorchis penicillatus*, medusan form of a cnidarian. Both animals have similar symmetry, diploblastic organization, and gastrovascular cavities.



b.

Cnidarian Diversity

Sea anemones (Fig. 28.8a) are sessile polyps that live attached to submerged rocks, timbers, or other substrate. Most sea anemones range in size from 0.5–20 cm in length and 0.5–10 cm in diameter and are often colorful. Their upward-turned oral disk that contains the mouth is surrounded by a large number of hollow tentacles containing nematocysts.

Corals (Fig. 28.8b) resemble sea anemones encased in a calcium carbonate (limestone) house. The coral polyp can extend into the water to feed on microorganisms and retreat into the house for safety. Some corals are solitary, but the vast majority live in colonies that vary in shape from rounded to branching. Many corals exhibit elaborate geometric designs and stunning colors and are responsible for the building of coral reefs. The slow accumulation of limestone can result in massive structures, such as the Great Barrier Reef along the eastern coast of Australia. Coral reef ecosystems are very productive, and a diverse group of marine life call the reef home.

The hydrozoans have a dominant polyp. *Hydra* (see Fig. 28.9) is a hydrozoan, and so is a Portuguese man-of-war. You might think the Portuguese man-of-war is an odd-shaped medusa, but actually it is a colony of polyps (Fig. 28.8c). The original polyp becomes a gas-filled float that provides buoyancy, keeping the colony afloat. Other polyps, which bud from this one, are specialized for feeding or for reproduction. A long, single tentacle armed with numerous nematocysts arises from the base of each feeding polyp. Swimmers who accidentally come upon a Portuguese man-of-war can receive painful, even serious, injuries from these stinging tentacles.

In true jellyfishes (Fig. 28.8d), the medusa is the primary stage, and the polyp remains small. Jellyfishes are zooplankton and depend on tides and currents for their primary means of movement. They feed on a variety of invertebrates and fishes and are themselves food for marine animals.

Hydra. The body of a hydra [Gk. *hydra*, a many-headed serpent] is a small tubular polyp about one-quarter inch in length. Hydroids are often studied as an example of a cnidarian. Hydroids are likely to be found attached to underwater plants or rocks in most lakes and ponds. The only opening (the mouth) is in a raised area surrounded by four to six tentacles that contain a large number of nematocysts.

Figure 28.9 shows the microscopic anatomy of *Hydra*. The cells of the epidermis are termed epitheliomuscular cells because they contain muscle fibers. Also present in the epidermis are nematocyst-containing cnidocytes and sensory cells that make contact with the nerve cells within a **nerve net**. These interconnected nerve cells allow transmission of impulses in several directions at once. The body of a hydra can contract or extend, and the tentacles that ring the mouth can reach out and grasp prey and discharge nematocysts.

Hydras reproduce asexually by forming buds, small outgrowths that develop into a complete animal and then detach. Interstitial cells of the epidermis are capable of becoming other types of cells such as an ovary and/or a testis. When hydras reproduce sexually, sperm from

a testis swim to an egg within an ovary. The embryo is encased within a hard, protective shell that allows it to survive until conditions are optimum for it to emerge and develop into a new polyp. Like the sponges, cnidarians have great regenerative powers, and hydras can grow an entire organism from a small piece.

Check Your Progress

28.2

1. In what ways are cnidarians more complex than the sponges?

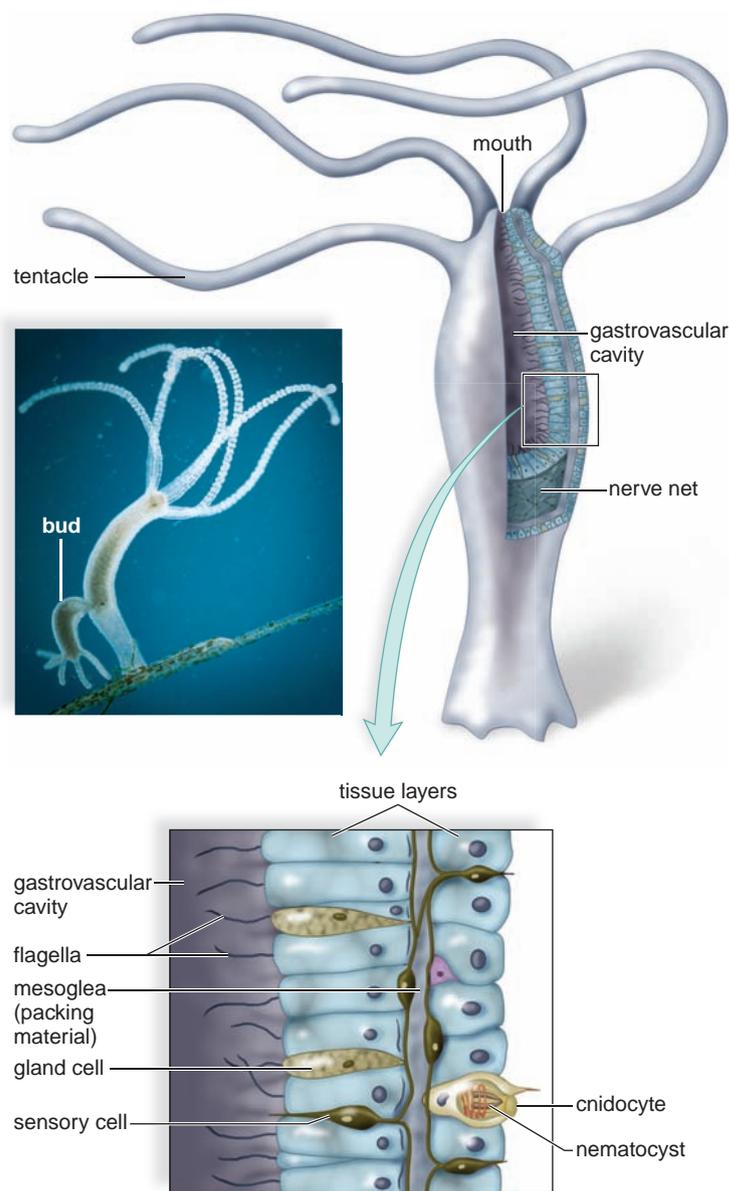


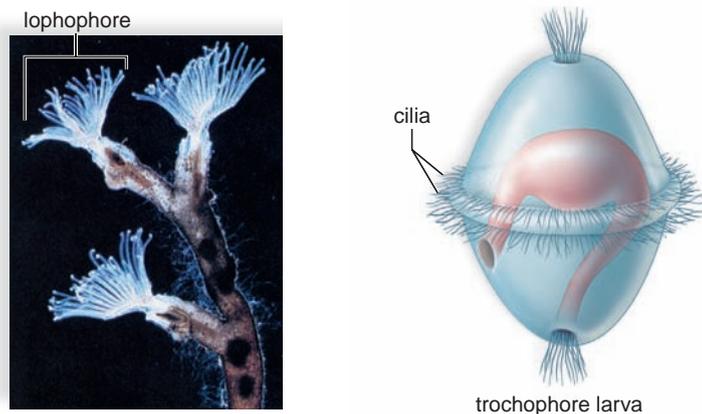
FIGURE 28.9 Anatomy of *Hydra*.

Above: The body of *Hydra* is a small tubular polyp that reproduces asexually by forming outgrowths called buds. The buds develop into a complete animal. Below: The body wall contains two tissue layers separated by mesoglea. Cnidocytes are cells that contain nematocysts.

28.3 Variety Among the Lophotrochozoans

The lophotrochozoa encompass several groups of animals. These animals are bilaterally symmetrical at least in some stage of their development. As embryos, they have three germ layers, and as adults, they have the organ level of organization. As discussed on page 516, lophotrochozoans have the protostome pattern of development. Some have a true coelom, as exemplified best in the annelids.

The lophotrochozoans can be divided into two groups: the lophophores (e.g., bryozoans and brachiopods) and the trochophores (flatworms, rotifers, molluscs, and annelids). The lophophores may not be closely related, but they all have a feeding apparatus called the lophophore. The trochophores either have a trochophore larva today (molluscs and annelids), or an ancestor had one some time in the past (flatworms and rotifers).



Flatworms

Flatworms (phylum Platyhelminthes) are trochozoans rightly named because they are worms with an extremely flat body. Like the cnidarians, flatworms have a sac body plan and only one opening, the mouth. When one opening is present, the digestive tract is said to be *incomplete*, and when two openings are present, the digestive tract is *complete*. Also, flatworms have no body cavity, and instead the third germ layer, mesoderm, fills the space between their organs.

Among flatworms, planarians are free-living; flukes and tapeworms are parasitic.

Free-living Flatworms

Dugesia is a planarian that lives in freshwater lakes, streams, and ponds, where it feeds on small living or dead organisms. A planarian captures food by wrapping itself around the prey, entangling it in slime, and pinning it down. Then a muscular pharynx is extended through the mouth and a sucking motion takes pieces of the prey into the pharynx. The pharynx leads into a three-branched gastrovascular cavity in which digestion is both extracellular and intracellular (Fig. 28.10a). The digestive system delivers nutrients and oxygen to the cells, and there is no circulatory system nor respiratory system. Waste molecules exit through the mouth.

Planarians have a well-developed excretory system (Fig. 28.10b). The excretory organ functions in osmotic regulation,

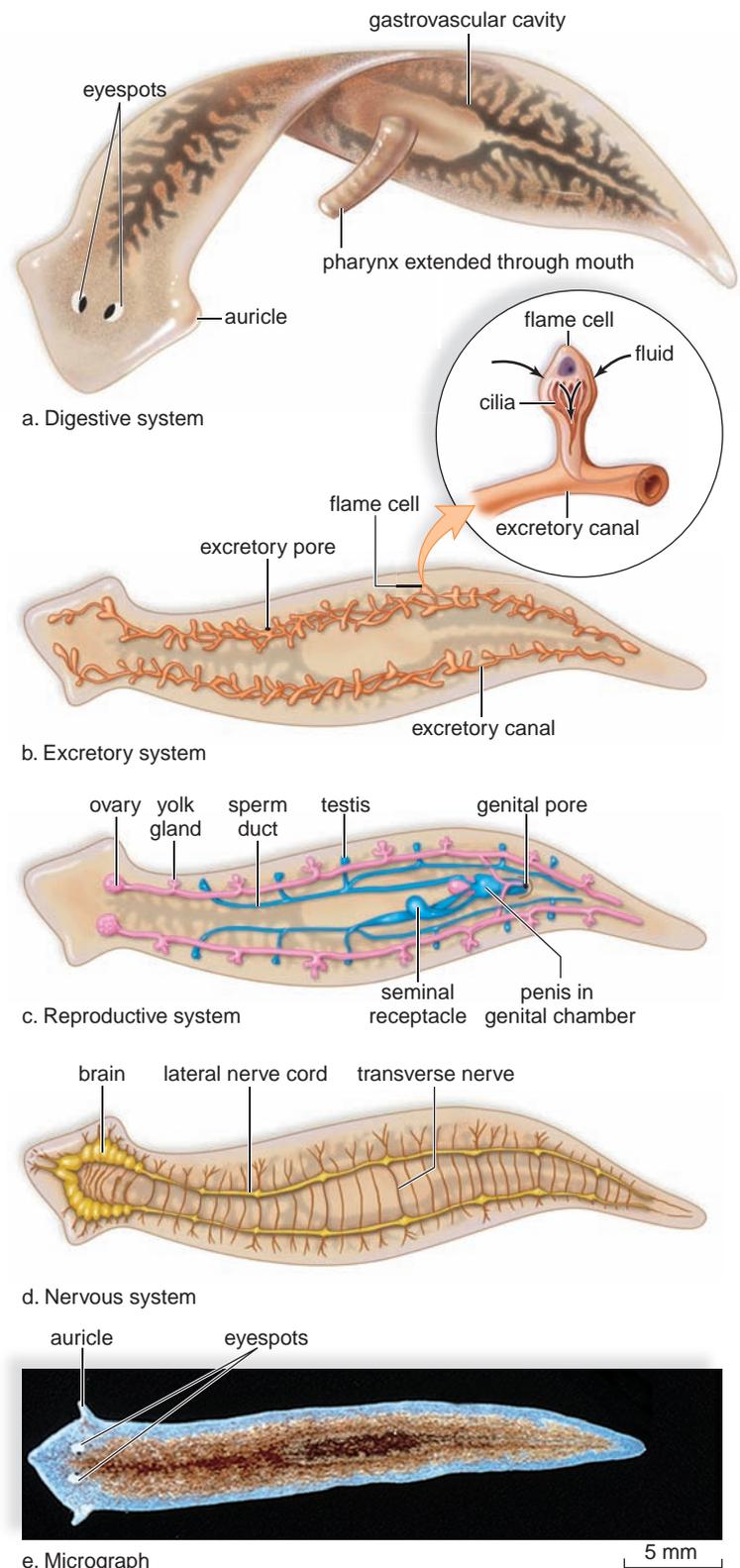


FIGURE 28.10 Planarian anatomy.

a. When a planarian extends the pharynx, food is sucked up into a gastrovascular cavity that branches throughout the body. **b.** The excretory system with flame cells is shown in detail. **c.** The reproductive system (shown in pink and blue) has both male and female organs. **d.** The nervous system has a ladderlike appearance. **e.** The photograph shows that a planarian, *Dugesia*, is bilaterally symmetrical and has a head region with eyespots.

as well as in water excretion. The organ consists of a series of interconnecting canals that run the length of the body on each side. Bulblike structures containing cilia are at the ends of the side branches of the canals. The cilia move back and forth, bringing water into the canals that empty at pores. The excretory system often functions as an osmotic-regulating system. The beating of the cilia reminded an early investigator of the flickering of a flame, and so the excretory organ of the flatworm is called a flame cell.

Planarians can reproduce asexually. They constrict beneath the pharynx, and each part grows into a whole animal again. Because planarians have the ability to regenerate, they have been the subject of much research. Planarians also reproduce sexually. They are **hermaphroditic** or monoecious, which means that they possess both male and female sex organs (Fig. 28.10c). The worms practice cross-fertilization when the penis of one is inserted into the genital pore of the other. The fertilized eggs are enclosed in a cocoon and hatch in two or three weeks as tiny worms.

The nervous system is called a *ladder-type* because the two lateral nerve cords plus transverse nerves look like a ladder (Fig. 28.10d). Paired ganglia (collections of nerve cells) function as a brain in the head region. Planarians are bilaterally symmetrical and they undergo cephalization. The head of a planarian is bluntly arrow shaped, with lateral extensions called auricles that contain chemosensory cells and tactile cells used to detect potential food sources and enemies. The pigmentation of the two light-sensitive eyespots causes the worm to look cross-eyed (Fig. 28.10e).

Three kinds of muscle layers—an outer circular layer, an inner longitudinal layer, and a diagonal layer—allow for quite varied movement. In larger forms, locomotion is accomplished by the movement of cilia on the ventral and lateral surfaces. Numerous gland cells secrete a mucus upon which the animal moves.

Parasitic Flatworms

Flukes (trematodes) and tapeworms (cestodes) are parasitic flatworms. Both are highly modified for the parasitic mode of life, losing some of the attributes of free-living flatworms and gaining others. Flukes and tapeworms are covered by a protective tegument, which is a specialized body covering resistant to host digestive juices. Associated with the loss of a predatory lifestyle is an absence of cephalization. The head with sensory structures is replaced by an anterior end with hooks and/or suckers for attachment to the host. They no longer hunt for prey and the nervous system is not well developed. On the other hand, a well-developed reproductive system helps ensure transmission to a new host.

Both flukes and tapeworms utilize a secondary, or intermediate, host to transmit offspring from primary host to primary host. The primary host is infected with the sexually mature adult; the secondary host contains the larval stage or stages.

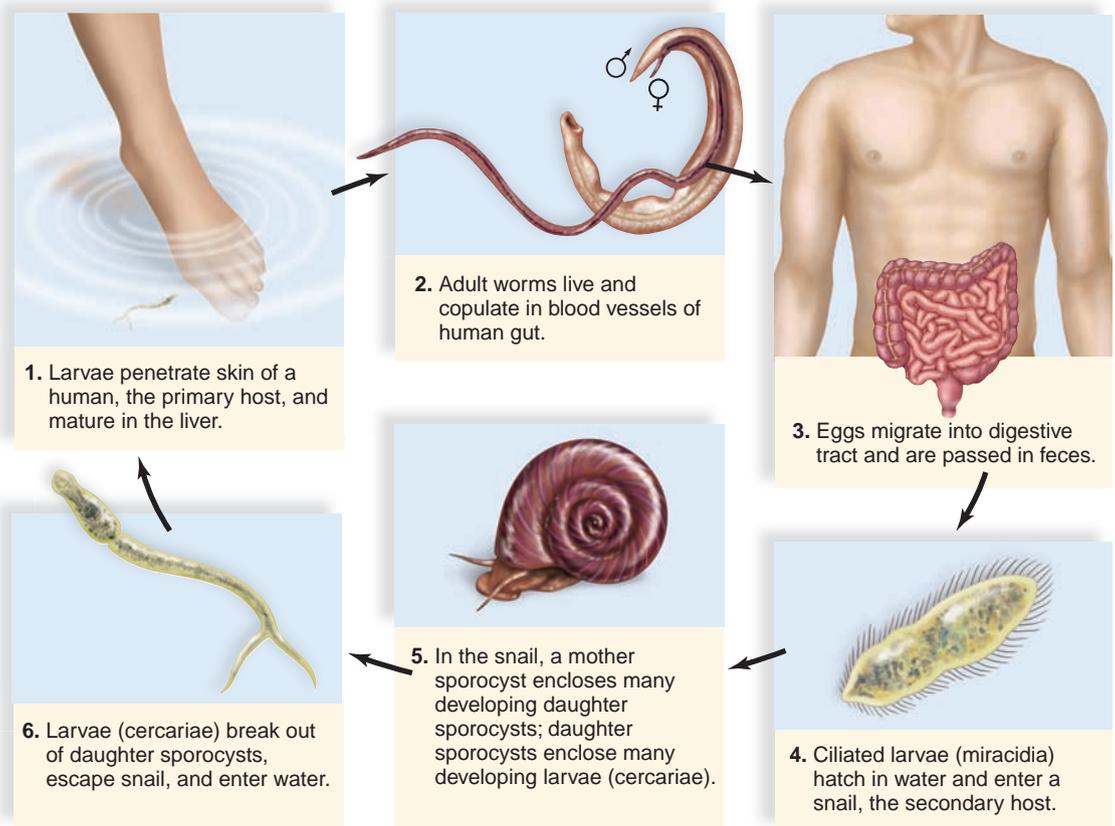
Flukes. Flukes are named for the organ they inhabit; for example, there are liver, lung, and blood flukes (Fig. 28.11). The almost 11,000 species have an oval to more elongated

FIGURE 28.11 Life cycle of a blood fluke, *Schistosoma*.

a. Micrograph of *Schistosoma*.
b. *Schistosomiasis*, an infection of humans caused by the blood fluke *Schistosoma*, is an extremely prevalent disease in Egypt—especially since the building of the Aswan High Dam. Standing water in irrigation ditches, combined with unsanitary practices, has created the conditions for widespread infection.



a.



b.

flattened body about 2.5 cm long. At the anterior end is an oral sucker surrounded by sensory papilla and at least one other sucker used for attachment to a host. The blood fluke (*Schistosoma*) occurs predominantly in the Middle East, Asia, and Africa where 200,000 infected persons die each year from *schistosomiasis*. In this disease, female flukes deposit their eggs in small blood vessels close to the lumen of the intestine, and the eggs make their way into the digestive tract by a slow migratory process (Fig. 28.11). After the eggs pass out with the feces, they hatch into tiny larvae that swim about in rice paddies and elsewhere until they enter a particular species of snail. Within the snail, asexual reproduction occurs; sporocysts, which are spore-containing sacs, eventually produce new larval forms that leave the snail. If the larvae penetrate the skin of a human, they begin to mature in the liver and implant themselves in the blood vessels of the small intestine. The flukes and their eggs can cause dysentery, anemia, bladder inflammation, brain damage, and severe liver complications. Infected persons usually die of secondary diseases brought on by their weakened condition.

The Chinese liver fluke, *Clonorchis sinensis*, is a parasite of cats, dogs, pigs, and humans and requires two secondary hosts: a snail and a fish. The adults reside in the liver and deposit their eggs in bile ducts, which carry them to the intestines for elimination in feces. Nonhuman species generally become infected through the fecal route, but humans usually become infected by eating raw fish. A heavy *Clonorchis* infection can cause severe cirrhosis of the liver and death.

Tapeworms. Tapeworms vary in length from a few millimeters to nearly 20 m. They have a highly modified head region called the scolex that contains hooks for attachment to the intestinal wall of the host and suckers for feeding. Behind the **scolex**, a series of reproductive units called **proglottids** are found that contain a full set of female and male sex organs. The number of proglottids may vary depending on the species. After fertilization, the organs within a proglottid disintegrate and the proglottids become filled with mature eggs. These egg-filled proglottids are called gravid, and in some species may contain 100,000 eggs. Once mature, depending on the species, the eggs may be released through a pore into the host's intestine, where they exit with the feces. In other species, the gravid proglottids break off and are eliminated with the feces.

Most tapeworms have complicated life cycles that usually involve several hosts. Figure 28.12 illustrates the life cycle of the pork tapeworm, *Taenia solium*, which involves the human as the primary host and the pig as the secondary host. After a pig feeds on feces-contaminated food, the larvae are released. They burrow through the intestinal wall and travel in the bloodstream to finally lodge and encyst in muscle. This **cyst** is a small, hard-walled structure that contains a larva called a bladder worm. When humans eat infected meat that has not been thoroughly cooked, the bladder worms break out of the cysts, attach themselves to the intestinal wall, and grow to adulthood. Then the cycle begins again. Generally, tapeworm infections cause diarrhea, weight loss, and fatigue in the primary host.

FIGURE 28.12 Life cycle of a tapeworm, *Taenia*.

The life cycle includes a human (primary host) and a pig (secondary host). The adult worm is modified for its parasitic way of life. It consists of a scolex and many proglottids, which become bags of eggs.

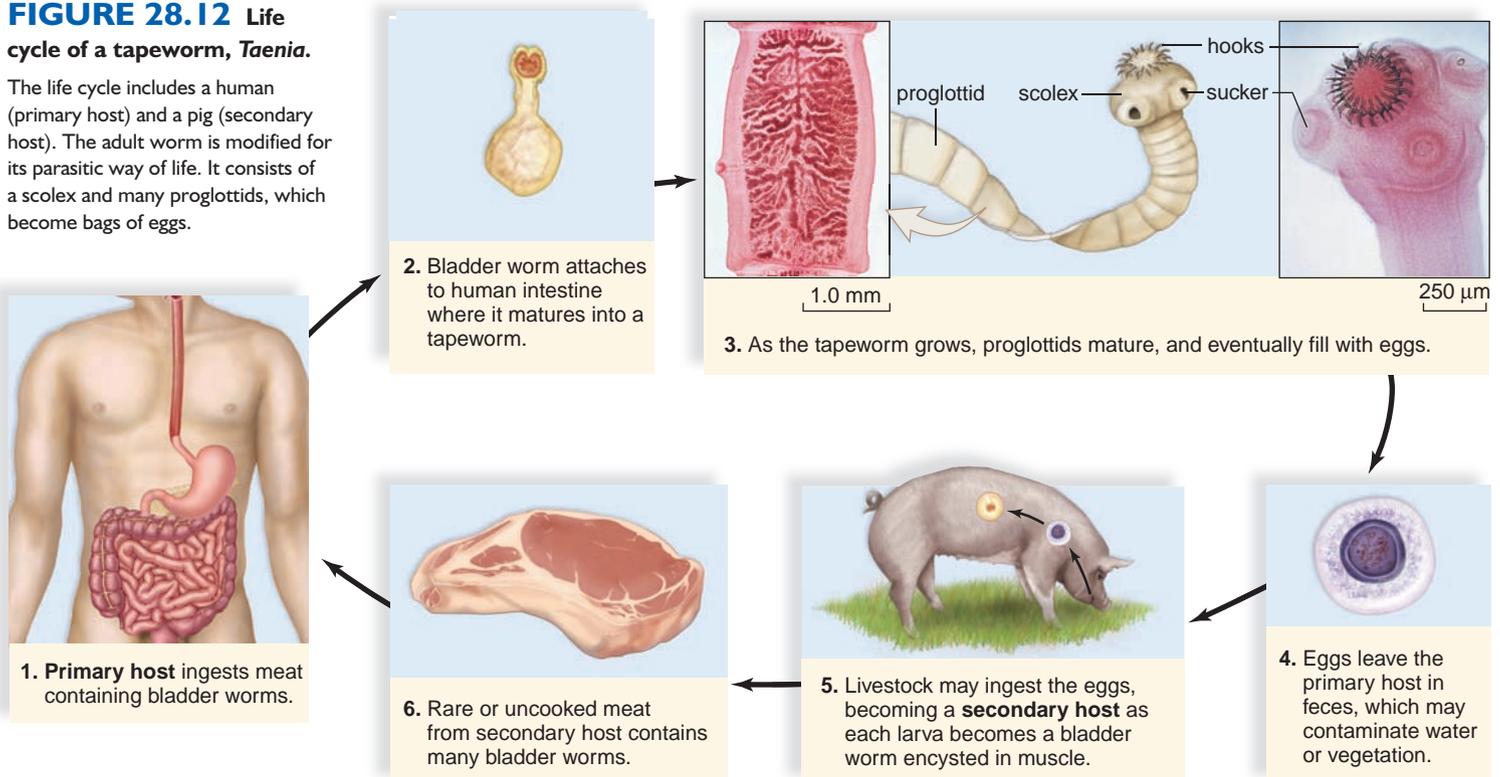
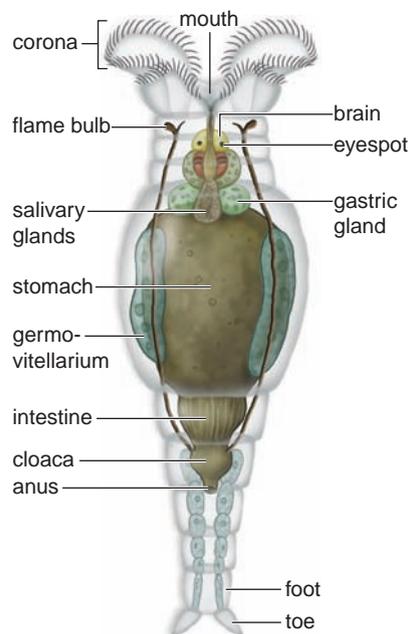


FIGURE 28.13**Rotifer.**

Rotifers are microscopic animals only 0.1–3 mm in length. The beating of cilia on two lobes at the anterior end of the animal gives the impression of a pair of spinning wheels

**Rotifers**

Rotifers (phylum Rotifera) are related to the flatworms and both are trochozoans. Anton von Leeuwenhoek viewed rotifers through his microscope and called them the “wheel animacules.” Rotifers have a crown of cilia, known as the corona, on their heads (Fig. 28.13). When in motion, the corona, which looks like a spinning wheel, serves as an organ of locomotion and also directs food into the mouth. The approximately 2,000 species primarily live in fresh water; however, some marine and terrestrial forms exist. The majority of rotifers are transparent, but some are very colorful. Many species of rotifers can desiccate during harsh conditions and remain dormant for lengthy periods of time. This characteristic has earned them the title “resurrection animacules.”

Molluscs

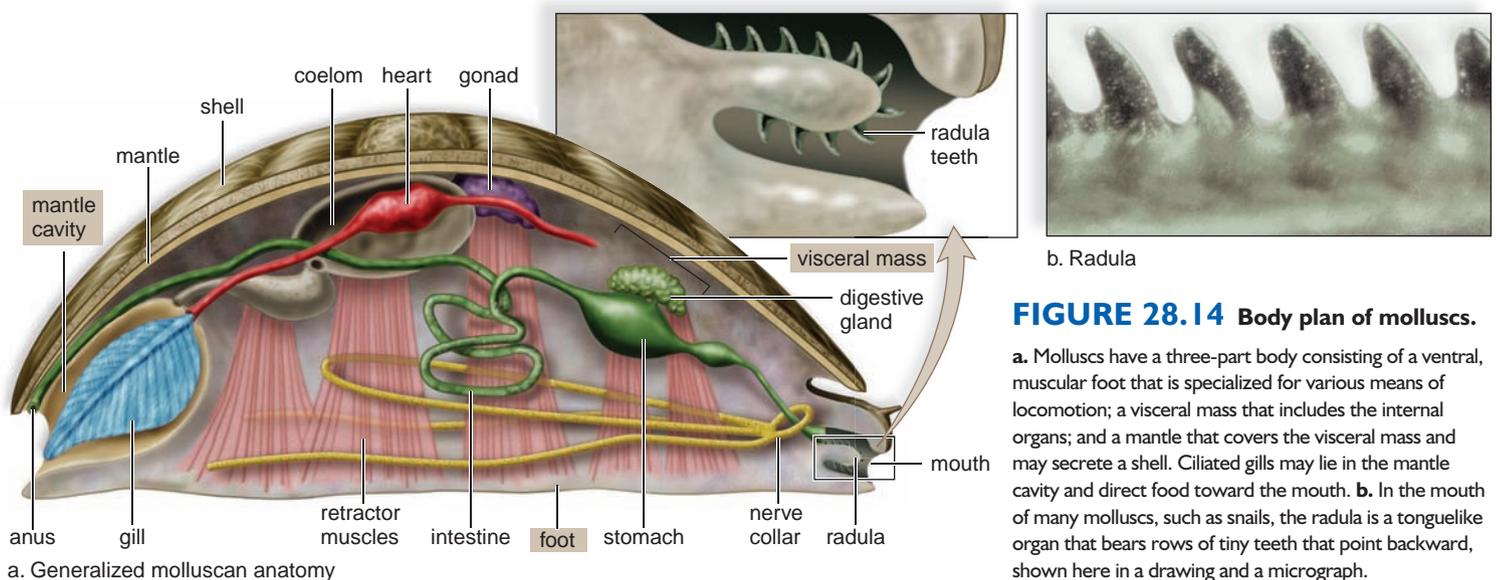
The **molluscs** (phylum Mollusca), the second most numerous group of animals, inhabit a variety of environments,

including marine, freshwater, and terrestrial habitats. This diverse phylum includes chitons, limpets, slugs, snails, abalones, conchs, nudibranchs, clams, scallops, squid, and octopuses. Molluscs vary in size from microscopic to the giant squid, which can attain lengths of over 20 m and weigh over 450 kg. The group includes herbivores, carnivores, filter feeders, and parasites.

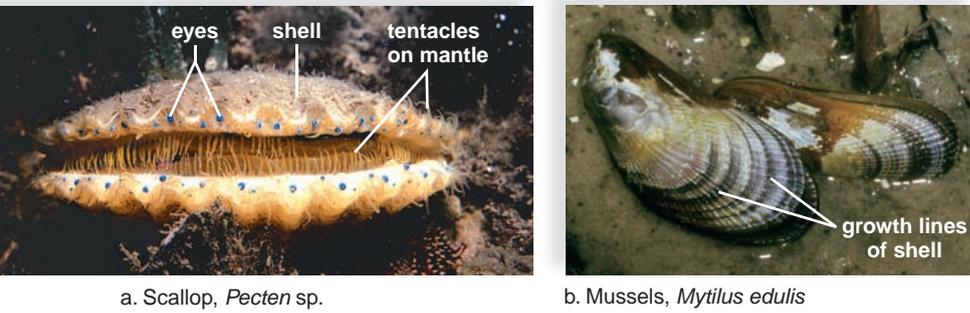
Although diverse, molluscs share a three-part body plan consisting of the visceral mass, mantle, and foot (Fig. 28.14a). The visceral mass contains the internal organs, including a highly specialized digestive tract, paired kidneys, and reproductive organs. The **mantle** is a covering that lies to either side of, but does not completely enclose, the visceral mass. It may secrete a shell and/or contribute to the development of gills or lungs. The space between the folds of the mantle is called the mantle cavity. The foot is a muscular organ that may be adapted for locomotion, attachment, food capture, or a combination of functions. Another feature often present in molluscs is a rasping, tonguelike **radula**, an organ that bears many rows of teeth and is used to obtain food (Fig. 28.14b).

The true coelom is reduced and largely limited to the region around the heart in molluscs. Most molluscs have an open circulatory system. The heart pumps blood, more properly called hemolymph, through vessels into sinuses (cavities) collectively called a **hemocoel** [Gk. *haima*, blood, and *koiloma*, cavity]. Blue hemocyanin, rather than red hemoglobin, is the respiratory pigment. Nutrients and oxygen diffuse into the tissues from these sinuses instead of being carried into the tissues by capillaries, microscopic blood vessels present in animals with closed circulatory systems.

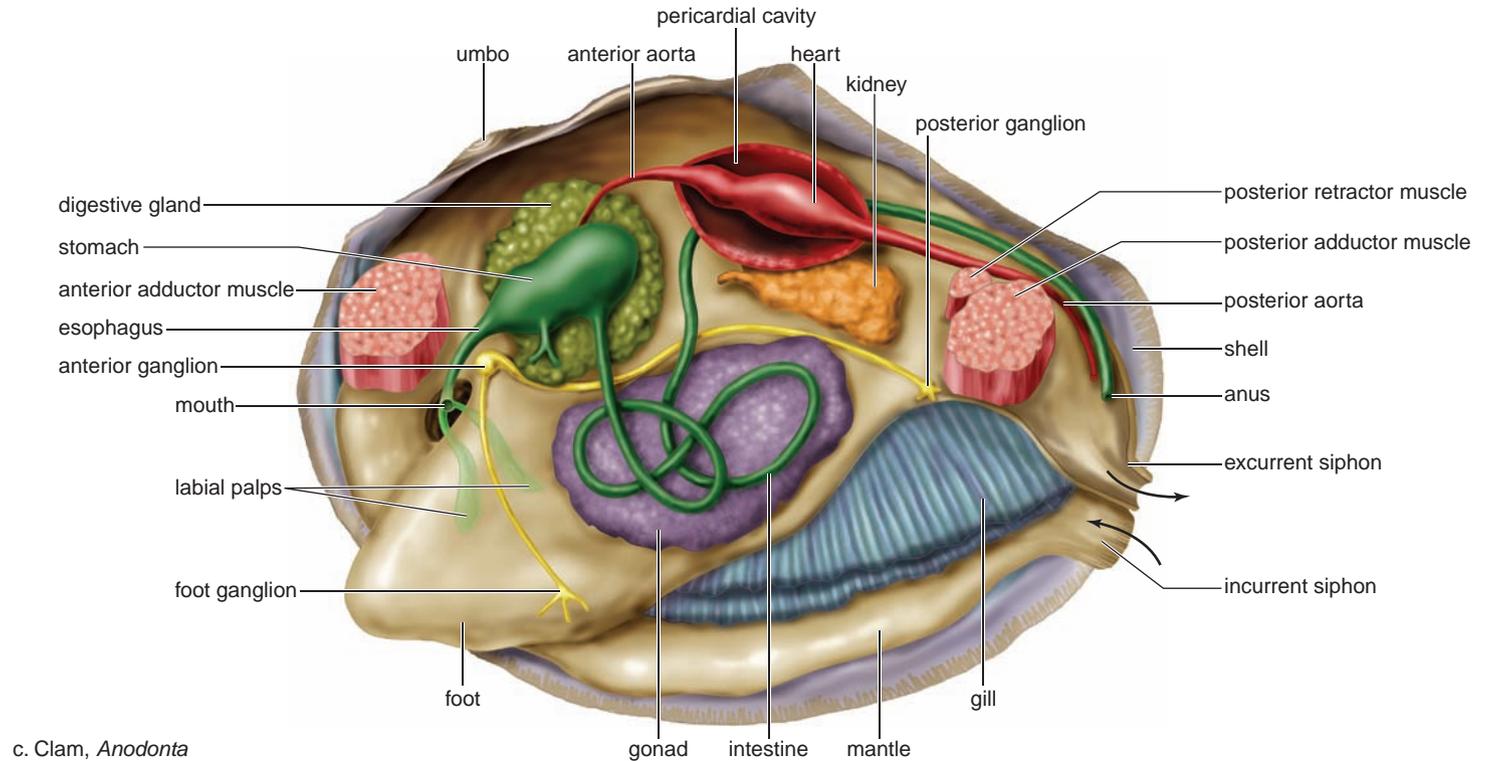
The nervous system of molluscs consists of several ganglia connected by nerve cords. The amount of cephalization and sensory organs varies from nonexistent in clams to complex in squid and octopi. The molluscs also exhibit variations in mobility. Oysters are sessile, snails are extremely slow moving, and squid are fast-moving, active predators.

**FIGURE 28.14** Body plan of molluscs.

a. Molluscs have a three-part body consisting of a ventral, muscular foot that is specialized for various means of locomotion; a visceral mass that includes the internal organs; and a mantle that covers the visceral mass and may secrete a shell. Ciliated gills may lie in the mantle cavity and direct food toward the mouth. **b.** In the mouth of many molluscs, such as snails, the radula is a tonguelike organ that bears rows of tiny teeth that point backward, shown here in a drawing and a micrograph.

a. Scallop, *Pecten* sp.b. Mussels, *Mytilus edulis***FIGURE 28.15 Bivalve diversity.**

Bivalves have a two-part shell. **a.** Scallops clap their valves and swim by jet propulsion. This scallop has sensory organs consisting of blue eyes and tentacles along the mantle edges. **b.** Mussels form dense beds in the intertidal zone of northern shores. **c.** In this drawing of a clam, the mantle has been removed from one side. Follow the path of food from the incurrent siphon to the gills, the mouth, the stomach, the intestine, the anus, and the excurrent siphon. Locate the three ganglia: anterior, foot, and posterior. The heart lies in the reduced coelom.

c. Clam, *Anodonta***Bivalves**

Clams, oysters, shipworms, mussels, and scallops are all **bivalves** (class Bivalvia) with a two-part shell that is hinged and closed by powerful muscles (Fig. 28.15). They have no head, no radula, and very little cephalization. Clams use their hatchet-shaped foot for burrowing in sandy or muddy soil, and mussels use their foot to produce threads that attach them to nearby objects. Scallops both burrow and swim; rapid clapping of the valves releases water in spurts and causes the animal to move forward in a jerky fashion for a few feet.

In freshwater clams such as *Anodonta* (Fig. 28.15c), the shell, secreted by the mantle, is composed of protein and calcium carbonate with an inner layer, called mother of pearl. If a foreign body is placed between the mantle and the shell, pearls form as concentric layers of shell are deposited about the particle. The compressed muscular foot of a clam projects ventrally from the shell; by expanding the tip of the foot and pulling the body after it, the clam moves forward.

Within the mantle cavity, the ciliated gills hang down on either side of the visceral mass. The beating of the cilia causes water to enter the mantle cavity by way of the incurrent siphon and to exit by way of the excurrent siphon. The clam is a filter feeder; small particles in this constant stream of water adhere to the gills, and ciliary action sweeps them toward the mouth.

The mouth leads to a stomach and then to an intestine, which coils about in the visceral mass before going right through the heart and ending in an anus. The anus empties at the excurrent siphon. There is also an accessory organ of digestion called a digestive gland. The heart lies just below the hump of the shell within the pericardial cavity, the only remains of the coelom. The circulatory system is open; the heart pumps hemolymph into vessels that open into the *hemocoel*. The nervous system is composed of three pairs of ganglia (located anteriorly, posteriorly, and in the foot), which are connected by nerves.

There are two excretory kidneys, which lie just below the heart and remove waste from the pericardial cavity for excretion into the mantle cavity. The clam excretes ammonia (NH_3), a toxic substance that requires the excretion of water at the same time.

In freshwater clams, the sexes are separate, and fertilization is internal. Fertilized eggs develop into specialized larvae and are released from the clam. Some larvae attach to the gills of a fish and become a parasite before they sink to the bottom and develop into a clam. Certain clams and annelids have the same type of larva (see page 520), and this reinforces their evolutionary relationship between molluscs and annelids.

Other Molluscs

The **gastropods** [Gk. *gastros*, stomach, and *podos*, foot], the largest class of molluscs, include slugs, snails, whelks, conchs, limpets, and nudibranchs. While most are marine, slugs and garden snails are adapted to terrestrial environments (Fig. 28.16c).

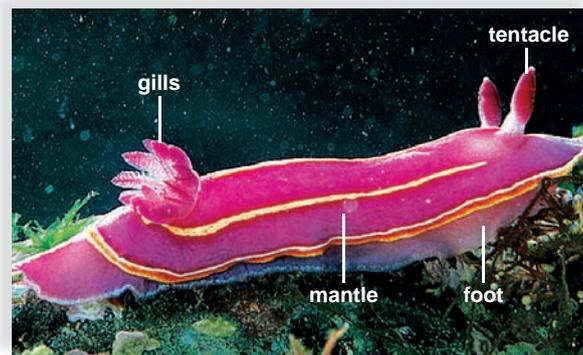
Gastropods have an elongated, flattened foot and most, except for slugs and nudibranchs, have a one-piece coiled

shell that protects the visceral mass. The anterior end bears a well-developed head region with a cerebral ganglion and eyes on the ends of tentacles. Land snails are hermaphroditic; when two snails meet, they shoot calcareous darts into each other's body wall as a part of premating behavior. Then each inserts a penis into the vagina of the other to provide sperm for the future fertilization of eggs, which are deposited in the soil. Development proceeds directly without the formation of larvae.

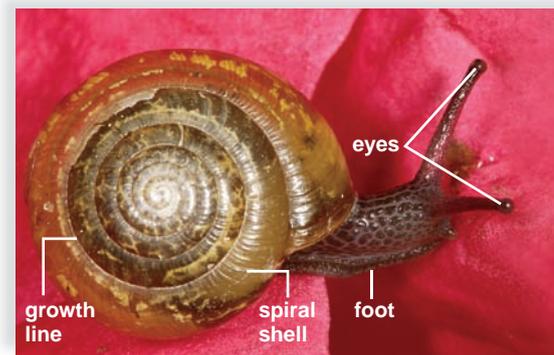
Cephalopods [Gk. *kaphale*, head, and *podos*, foot] range in length from 2 cm to 20 m as in the giant squid, *Architeuthis*. Cephalopod means head footed; both squids and octopi can squeeze their mantle cavity so that water is forced out through a funnel, propelling them by jet propulsion (Fig. 28.16). Also, the tentacles and arms that circle the head capture prey by adhesive secretions or by suckers. A powerful, parrotlike beak is used to tear prey apart. They have well-developed sense organs, including eyes that are similar to those of vertebrates and focus like a camera. Cephalopods, particularly octopi, have well-developed brains and show a remarkable capacity for learning.



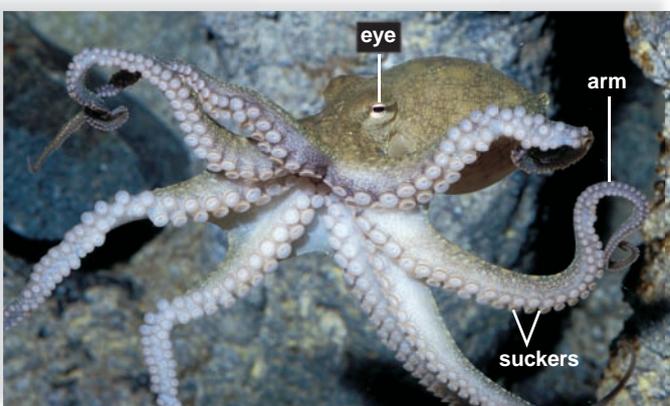
a. Flamingo tongue shell, *Cyphoma gibbosum*



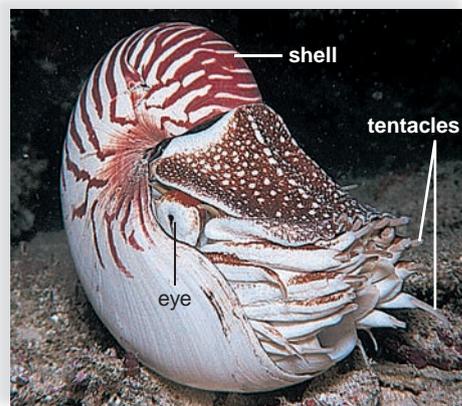
b. Nudibranch, *Glossodoris macfarlandi*



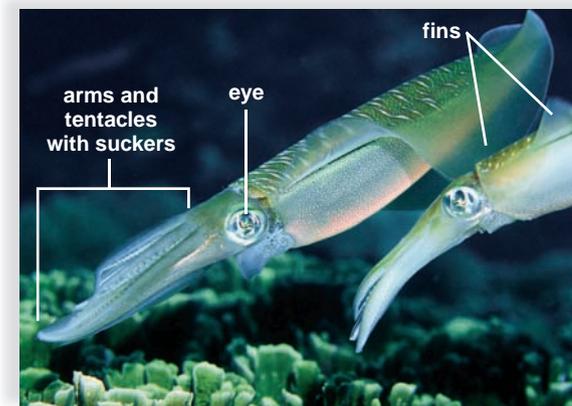
c. Land snail, *Helix aspersa*



d. Two-spotted octopus, *Octopus bimaculatus*



e. Chambered nautilus, *Nautilus belauensis*



f. Bigfin reef squid, *Sepioteuthis lessoniana*

FIGURE 28.16 Gastropod and cephalopod diversity.

a–c. Gastropods have the three parts of a mollusc, and the foot is muscular, elongated, and flattened. Nudibranchs have no shell, as do the other two shown.

d–f. Cephalopods have tentacles and/or arms in place of a head. Speed suits their predatory lifestyle, and only the chambered nautilus has a shell among those shown.

Annelids

Annelids (phylum Annelida [*L. anellus*, little ring]), which are sometimes called the segmented worms, vary in size from microscopic to tropical earthworms that can be over 4 m long. The most familiar members of this group are earthworms, marine worms, and leeches.

Annelids are the only trochozoan with segmentation and a well-developed coelom. **Segmentation** is the repetition of body parts along the length of the body. The well-developed coelom is fluid-filled and serves as a supportive *hydrostatic skeleton*. A hydrostatic skeleton, along with partitioning of the coelom, permits independent movement of each body segment. Instead of just burrowing in the mud, an annelid can crawl on a surface.

Setae [*L. seta*, bristle] are bristles that protrude from the body wall, can anchor the worm, and help it move. The *oligochaetes* are annelids with few setae, and the *polychaetes* are annelids with many setae.

Earthworms

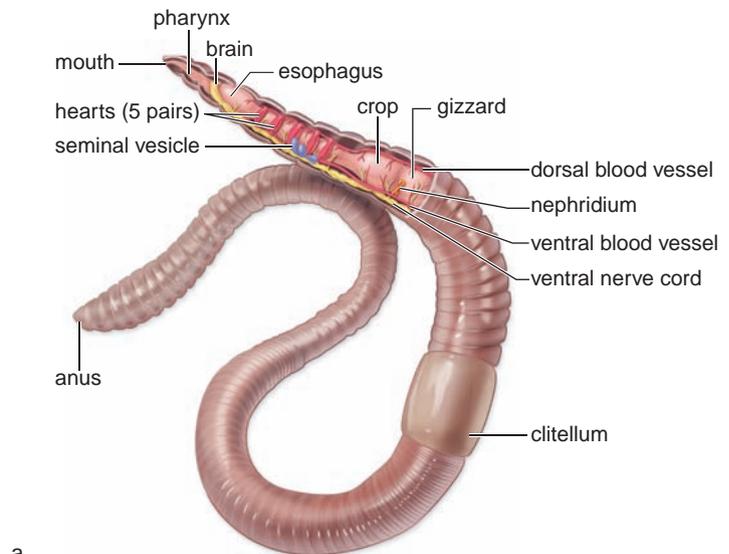
The common earthworm, *Lumbricus terrestris*, is an oligochaete (Fig. 28.17). Earthworm setae protrude in pairs directly from the surface of the body. Locomotion, which is accomplished section by section, uses muscle contraction and the setae. When longitudinal muscles contract, segments bulge and their setae protrude into the soil; then, when circular muscles contract, the setae are withdrawn, and these segments move forward.

Earthworms reside in soil where there is adequate moisture to keep the body wall moist for gas exchange. They are scavengers that feed on leaves or any other organic matter conveniently taken into the mouth along with dirt. Segmentation and a complete digestive tract have led to increased specialization of parts. Food drawn into the mouth by the action of the muscular pharynx is stored in a crop and ground up in a thick, muscular gizzard. Digestion and absorption occur in a long intestine whose dorsal surface has an expanded region called a **typhlosole** that increases the surface for absorption. Waste is eliminated through the anus.

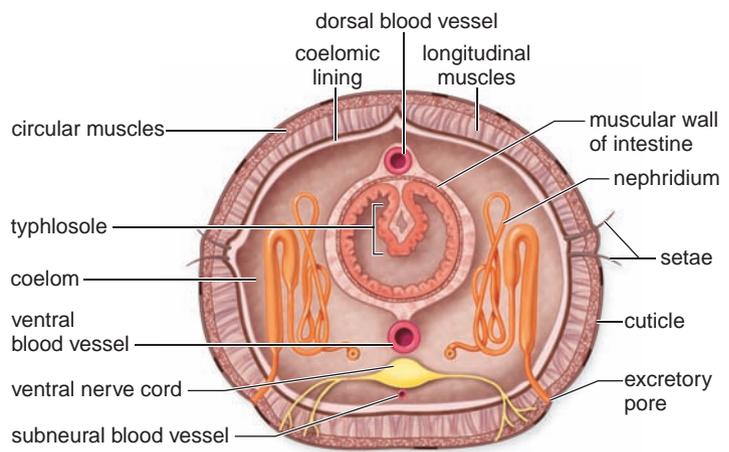
Earthworm segmentation, which is obvious externally, is also internally evidenced by septa that occur between segments. The long, ventral nerve cord leading from the brain has ganglionic swellings and lateral nerves in each segment. The excretory system consists of paired **nephridia** [Gk. *nephros*, kidney], which are coiled tubules in each segment. A nephridium has two openings: One is a ciliated funnel that collects coelomic fluid, and the other is an exit in the body wall. Between the two openings is a convoluted region where waste material is removed from the blood vessels about the tubule.

Annelids have a *closed circulatory system*, which means that the blood is always contained in blood vessels that run the length of the body. Red blood moves anteriorly in the dorsal blood vessel, which connects to the ventral blood vessel by five pairs of muscular vessels called “hearts.” Pulsations of the dorsal blood vessel and

the five pairs of hearts are responsible for blood flow. As the ventral vessel takes the blood toward the posterior regions of the worm’s body, it gives off branches in every segment.



a.



b.



c.

FIGURE 28.17 Earthworm, *Lumbricus terrestris*.

a. In the longitudinal section, note the specialized parts of the digestive tract. b. In cross section, note the spacious coelom, the paired setae and nephridia, and a ventral nerve cord that has branches in each segment. c. When earthworms mate, they are held in place by a mucus secreted by the clitellum. The worms are hermaphroditic, and when mating, sperm pass from the seminal vesicles of each to the seminal receptacles of the other.

Earthworms are *hermaphroditic*; the male organs are the testes, the seminal vesicles, and the sperm ducts, and the female organs are the ovaries, the oviducts, and the seminal receptacles. During mating, two worms lie parallel to each other facing in opposite directions (Fig. 28.17c). The fused midbody segment, called a clitellum, secretes mucus, protecting the sperm from drying out as they pass between the worms. After the worms separate, the clitellum of each produces a slime tube, which is moved along over the anterior end by muscular contractions. As it passes, eggs and the sperm received earlier are deposited, and fertilization occurs. The slime tube then forms a cocoon to protect the worms as they develop. There is no larval stage in earthworms.

Other Annelids

Approximately two-thirds of annelids are marine polychaetes. In polychaetes, the setae are in bundles on parapodia [Gk. *para*, beside, and *podos*, foot], which are paddlelike appendages found on most segments. These are used not only in swimming but also as respiratory organs, where the expanded surface area allows for exchange of gases. Some polychaetes are free-swimming, but the majority live in crevices or burrow into the ocean bottom. Clam worms, such as *Nereis* (Fig. 28.18a), are predators. They prey on crustaceans and other small animals, which are captured by a pair of strong chitinous jaws that extend with a part of the pharynx when the animal is feeding. Associated with its way of life, *Nereis* is cephalized, having a head region with eyes and other sense organs.

Other marine polychaetes are sedentary (sessile) tube worms, with radioles (ciliated mouth appendages) used to gather food (Fig. 28.18b). Christmas tree worms, fan worms, and featherduster worms all have radioles. In featherduster worms, the beautiful radioles cause the animal to look like an old fashioned feather duster.

Polychaetes have breeding seasons, and only during these times do the worms have sex organs. In *Nereis*, many worms simultaneously shed a portion of their bodies containing either eggs or sperm, and these float to the surface where fertilization takes place. The zygote rapidly develops into the trochophore larva, similar to that of the marine clam.

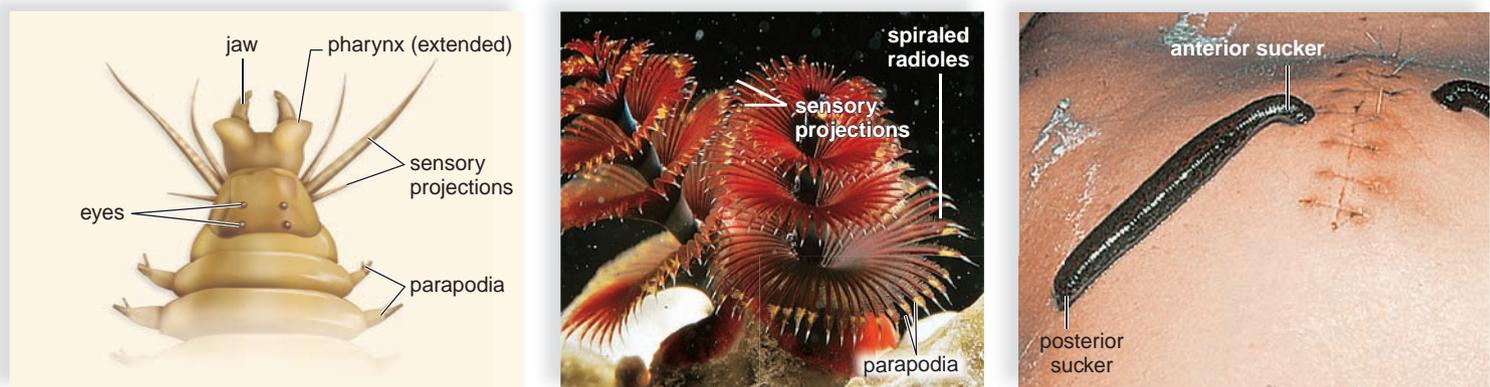
Leeches are annelids that normally live in freshwater habitats. They range in size from less than 2 cm to the medicinal leech, which can be 20 cm in length. They exhibit a variety of patterns and colors but most are brown or olive green. The body of a leech is flattened dorsoventrally. They have the same body plan as other annelids, but they have no setae and each body ring has several transverse grooves.

While some are free-living, most leeches are fluid feeders that attach themselves to open wounds. Among their modifications are two suckers, a small oral one around the mouth and a posterior one. Some bloodsuckers, such as the medicinal leech, can cut through tissue. Leeches are able to keep blood flowing by means of hirudin, a powerful anticoagulant in their saliva. Medicinal leeches have been used for centuries in blood-letting and other procedures. Today, they are used in reconstructive surgery for severed digits and in plastic surgery (Fig. 28.18c).

Check Your Progress

28.3

1. Even though flatworms, molluscs, and annelids are very different, they are all considered lophotrochozoans. What characteristic(s) unite(s) these three phyla?
2. Compare these three groups with regard to body cavity, digestive tract, and circulatory system.
3. Briefly describe any parasites that occur among these three groups.



a. Clam worm, *Nereis succinea*

b. Christmas tree worm, *Spirobranchus giganteus*

c. Medicinal leech, *Hirudo medicinalis*

FIGURE 28.18 Polychaete diversity.

a. Clam worms are predaceous polychaetes that undergo cephalization. Note also the parapodia, which are used for swimming and as respiratory organs. b. Christmas tree worms (a type of tube worm) are sessile feeders whose radioles (ciliated mouth appendages) spiral as shown here. c. Medical leech is a blood sucker.

28.4 Quantity Among the Ecdysozoans

The ecdysozoans are protostomes, as are the lophotrochozoans. The term *ecdysis* means molting, and both roundworms and arthropods, which belong to this group, periodically shed their outer covering.

Roundworms

Roundworms (phylum Nematoda) are nonsegmented worms that are prevalent in almost any environment. Generally, nematodes are colorless and range in size from microscopic to exceeding 1 m in length. The internal organs, including the tubular reproductive organs, lie within the pseudocoelom. A **pseudocoelom** [Gk. *Pseudes*, false, and *koiloma*, cavity] is a body cavity that is incompletely lined by mesoderm. In other words, mesoderm occurs inside the body wall but not around the digestive cavity (gut).

Nematodes have developed a variety of lifestyles from free-living to parasitic. One species, *Caenorhabditis elegans*, a free-living nematode, is a model animal used in genetics and developmental biology.

Parasitic Roundworms

An *Ascaris* infection is common in humans, cats, dogs, pigs, and a number of other vertebrates. As in other nematodes, *Ascaris* males tend to be smaller (15–31 cm long) than females (20–49 cm long) (Fig. 28.19a). In males, the posterior end is curved and comes to a point. Both sexes move by means of a characteristic whiplike motion because only longitudinal muscles lie next to the body wall. A typical female *Ascaris* is very prolific, producing over 200,000 eggs daily. The eggs are eliminated with the host's feces and can remain viable in the soil for many months. Eggs enter the body via uncooked vegetables, soiled fingers, or ingested fecal material and hatch in the intestines. The juveniles make their way into the veins and lymphatic vessels and are carried to the

heart and lungs. From the lungs, the larvae travel up the trachea, where they are swallowed and eventually reach the intestines. There, the larvae mature and begin feeding on intestinal contents.

The symptoms of an *Ascaris* infection depend on the stage of the infection. Larval *Ascaris* in the lungs can cause pneumonia-like symptoms. In the intestines, *Ascaris* can cause malnutrition; blockage of the bile duct, pancreatic duct, and appendix; and poor health.

Trichinosis, caused by *Trichinella spiralis*, is a serious infection that humans can contract when they eat rare pork containing encysted *Trichinella* larvae. After maturation, the female adult burrows into the wall of the small intestine and produces living offspring that are carried by the bloodstream to the skeletal muscles, where they encyst (Fig. 28.19b). Heavy infections can be painful and lethal.

Filarial worms, a type of roundworm, cause various diseases. In the United States, mosquitoes transmit the larvae of a parasitic filarial worm to dogs. Because the worms live in the heart and the arteries that serve the lungs, the infection is called *heartworm disease*. The condition can be fatal; therefore, heartworm medicine is recommended as a preventive measure for all dogs.

Elephantiasis is a disease of humans caused by the filarial worm, *Wuchereria bancrofti*. Restricted to tropical areas of Africa, this parasite also uses a mosquito as a secondary host. Because the adult worms reside in lymphatic vessels, collection of fluid is impeded, and the limbs of an infected person may swell to a monstrous size (Fig. 28.19c). Elephantiasis is treatable in its early stages but usually not after scar tissue has blocked lymphatic vessels.

Pinworms are the most common nematode parasite in the United States. The adult parasites live in the cecum and large intestine. Females migrate to the anal region at night and lay their eggs. Scratching the resultant itch can contaminate hands, clothes, and bedding. The eggs are swallowed, and the life cycle begins again.

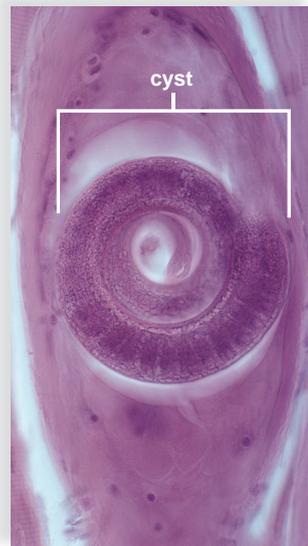
FIGURE 28.19

Roundworm diversity.

a. *Ascaris*, a common cause of a roundworm infection in humans. **b.** Encysted *Trichinella* larva in muscle. **c.** A filarial worm infection causes elephantiasis, which is characterized by a swollen body part when the worms block lymphatic vessels.



a.



b.

SEM 400×



c.

Arthropods

The **arthropods** (phylum Arthropoda [Gk. *arthron*, joint, and *podos*, foot]) vary greatly in size. The parasitic mite measures less than 0.1 mm in length, while the Japanese crab measures up to 4 m in length. Arthropods, which also occupy every type of habitat, are considered the most successful group of all the animals. The remarkable success of arthropods is dependent on five characteristics:

1. A rigid but jointed **exoskeleton** (Fig. 28.20a, b). The exoskeleton is composed primarily of **chitin** [Gk. *chiton*, tunic], a strong, flexible, nitrogenous polysaccharide. The exoskeleton serves many functions, including protection, attachment for muscles, locomotion, and prevention of desiccation. However, because it is hard and nonexpandable, arthropods must molt, or shed, the exoskeleton as they grow larger. Arthropods have this in common with other ecdysozoans. Before molting, the body secretes a new, larger exoskeleton, which is soft and wrinkled, underneath the old one. After enzymes partially dissolve and weaken the old exoskeleton, the animal breaks it open and wriggles out. The new exoskeleton then quickly expands and hardens (Fig. 28.20c).
2. Segmentation. Segmentation is readily apparent because each segment has a pair of jointed appendages, even though certain segments are fused into a head, thorax, and abdomen. The jointed appendages of arthropods are basically hollow tubes moved by muscles. Typically, the appendages are highly adapted for a particular function, such as food gathering, reproduction, and locomotion. In addition, many appendages are associated with sensory structures and used for tactile purposes.

3. Well-developed nervous system. Arthropods have a brain and a ventral nerve cord. The head bears various types of sense organs, including eyes of two types—simple and compound. The compound eye is composed of many complete visual units, each of which operates independently (Fig. 28.20d). The lens of each visual unit focuses an image on the light-sensitive membranes of a small number of photoreceptors within that unit. The simple eye, like that of vertebrates, has a single lens that brings the image to focus onto many receptors, each of which receives only a portion of the image. In addition to sight, many arthropods have well-developed touch, smell, taste, balance, and hearing. Arthropods display many complex behaviors and methods of communication.
4. Variety of respiratory organs. Marine forms use gills, which are vascularized, highly convoluted, thin-walled tissue specialized for gas exchange. Terrestrial forms have book lungs (e.g., spiders) or air tubes called **tracheae** [L. *trachia*, windpipe]. Tracheae serve as a rapid way to transport oxygen directly to the cells.
5. Reduced competition through **metamorphosis** [Gk. *meta*, implying change, and *morphe*, shape, form]. Many arthropods undergo a drastic change in form and physiology that occurs as an immature stage, called a larva, becomes an adult. Among arthropods, the larva eats different food and lives in a different environment than the adult. For example, larval crabs live among and feed on plankton, while adult crabs are bottom dwellers that catch live prey or scavenge dead organic matter. Among insects, such as butterflies, the caterpillar feeds on leafy vegetation, while the adult feeds on nectar.

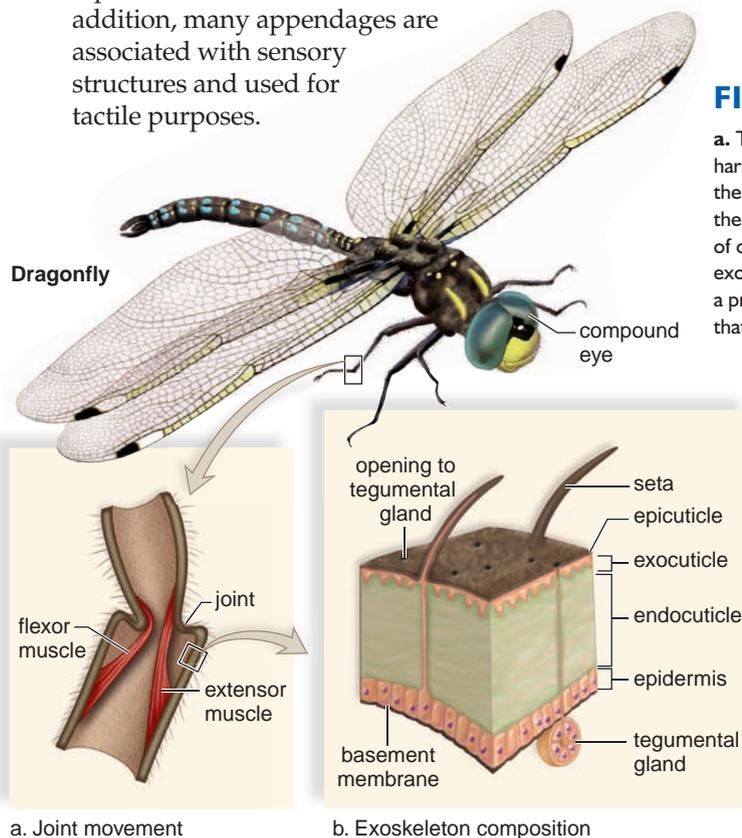
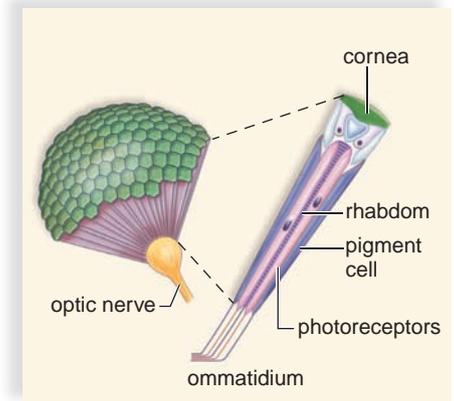


FIGURE 28.20 Arthropod skeleton and eye.

a. The joint in an arthropod skeleton is a region where the cuticle is thinner and not as hard as the rest of the cuticle. The direction of movement is toward the flexor muscle or the extensor muscle, whichever one has contracted. **b.** The exoskeleton is secreted by the epidermis and consists of the endocuticle; the exocuticle, hardened by the deposition of calcium carbonate; and the epicuticle, a waxy layer. Chitin makes up the bulk of the exo- and endocuticles. **c.** Because the exoskeleton is nonliving, it must be shed through a process called molting for the arthropod to grow. **d.** Arthropods have a compound eye that contains many individual units, each with its own lens and photoreceptors.



c. Molting



d. Compound eye

Crustaceans

The name **crustacean** is derived from their hard, crusty exoskeleton, which contains calcium carbonate in addition to the typical chitin. Although crustaceans are extremely diverse, the head usually bears a pair of compound eyes and five pairs of appendages. The first two pairs, called antennae and antennules, lie in front of the mouth and have sensory functions. The other three pairs (mandibles, first and second maxillae) lie behind the mouth and are mouthparts used in feeding. Biramous [Gk. *bis*, two, and *ramus*, a branch] appendages on the thorax and abdomen are segmentally arranged; one branch is the gill branch, and the other is the leg branch.

The majority of crustaceans live in marine and aquatic environments (Fig. 28.21). **Decapods**, which are the most familiar and numerous crustaceans, include lobsters, crabs, crayfish, hermit crabs, and shrimp. These animals have a thorax that bears five pairs of walking appendages. Typically, the gills are positioned above the walking legs. The first pair of walking legs may be modified as claws.

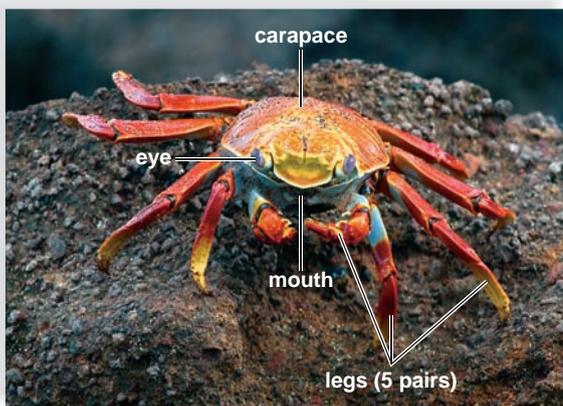
Copepods and krill are small crustaceans that live in the water, where they feed on algae. In the marine environment, they serve as food for fishes, sharks, and whales. They are so numerous that, despite their small size, some believe they are harvestable as food. Barnacles are also crustaceans, but they have a thick, heavy shell as befits their inactive lifestyle. Barnacles can live on wharf pilings, ship hulls, seaside rocks, and even the bodies of whales. They begin life as free-swimming larvae, but they undergo a metamorphosis that transforms their swim-

ming appendages to cirri, feathery structures that are extended and allow them to filter feed when they are submerged.

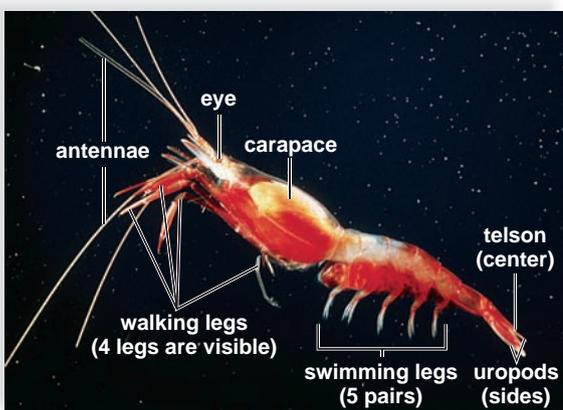
Anatomy of a Crayfish. Figure 28.22a gives a view of the external anatomy of the crayfish. The head and thorax are fused into a cephalothorax, which is covered on the top and sides by a nonsegmented carapace. The abdominal segments are equipped with swimmerets, small paddlelike structures. The first two pairs of swimmerets in the male, known as claspers, are quite strong and are used to pass sperm to the female.

The last two segments bear the uropods and the telson, which make up a fan-shaped tail. Ordinarily, a crayfish lies in wait for prey. It faces out from an enclosed spot with the claws extended, and the antennae moving about. The claws seize any small animal, either dead or living that happens by, and carry it to the mouth. When a crayfish moves about, it generally crawls slowly, but may swim rapidly by using its heavy abdominal muscles and tail.

The respiratory system consists of gills that lie above the walking legs protected by the carapace. As shown in Figure 28.22b, the digestive system includes a stomach, which is divided into two main regions: an anterior portion called the gastric mill, equipped with chitinous teeth to grind coarse food, and a posterior region, which acts as a filter to prevent coarse particles from entering the digestive glands, where absorption takes place. Green glands lying in the head region, anterior to the esophagus, excrete metabolic wastes through a duct that opens externally at the base of the antennae. The coelom, which



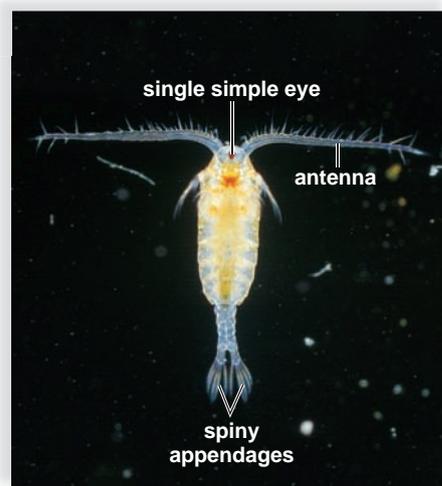
a. Sally lightfoot crab, *Grapsus grapsus*



b. Red-backed cleaning shrimp, *Lysmata grasbhami*

FIGURE 28.21 Crustacean diversity.

The crayfish on the next page, crabs (a), and shrimp (b) are decapods—they have five pairs of walking legs. Shrimp resemble crayfish more closely than crabs, which have a reduced abdomen. Pelagic shrimp feed on copepods, such as the one seen from below in (c). A copepod has long antennae used for floating, and feathery maxillae used for filter feeding. Barnacles have no abdomen and a reduced head; the thoracic legs project through a shell to filter feed. Barnacles often live on human-made objects such as ships, buoys, and cables. The gooseneck barnacle (d) is attached to an object by a long stalk.



c. Copepod, *Diaptomus*



d. Gooseneck barnacles, *Lepas anatifera*

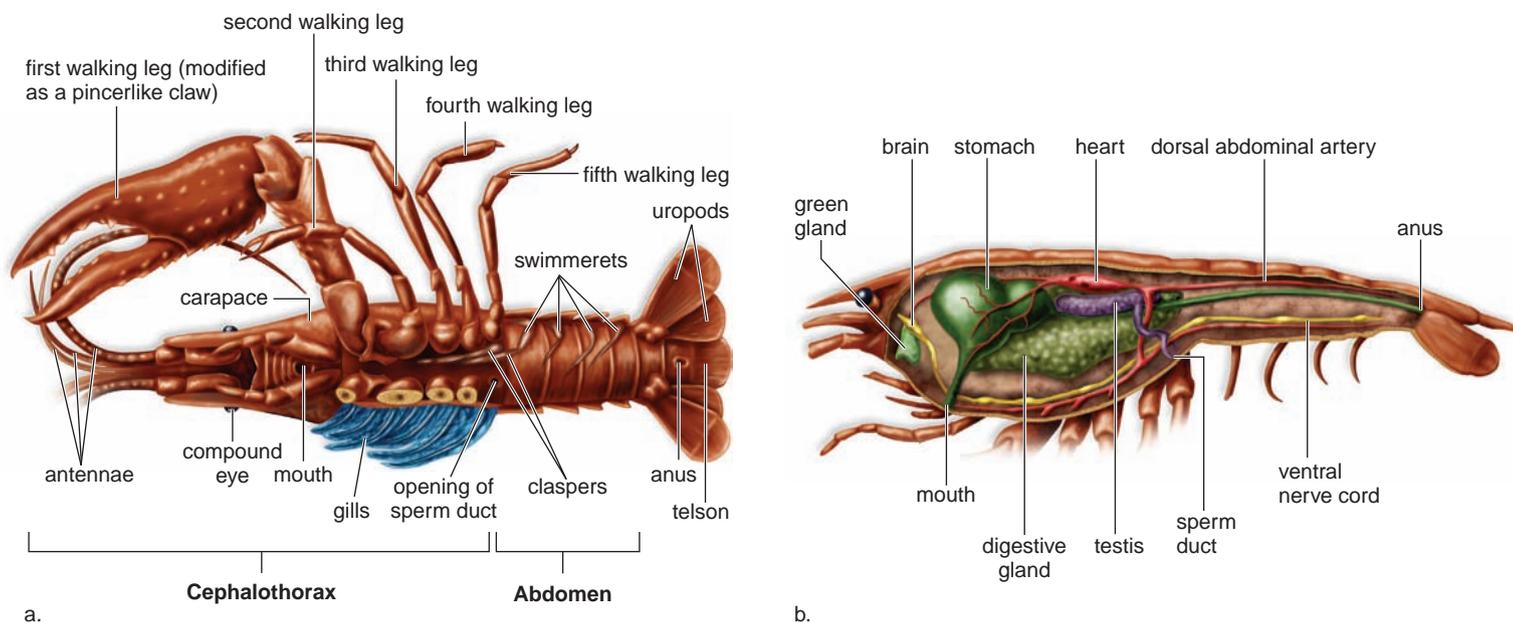


FIGURE 28.22 Male crayfish, *Cambarus*.

a. Externally, it is possible to observe the jointed appendages, including the swimmerets, and the walking legs, which include the claws. These appendages, plus a portion of the carapace, have been removed from the right side so that the gills are visible. **b.** Internally, the parts of the digestive system are particularly visible. The circulatory system can also be clearly seen. Note the ventral nerve cord.

is so well developed in the annelids, is reduced in the arthropods and is composed chiefly of the space about the reproductive system. A heart pumps hemolymph containing the blue respiratory pigment hemocyanin into a *hemocoel* consisting of sinuses (open spaces), where the hemolymph flows about the organs. As in the molluscs, this is an open circulatory system because blood is not contained within blood vessels.

The crayfish nervous system is well developed. Crayfish have a brain and a ventral nerve cord that passes posteriorly. Along the length of the nerve cord, periodic ganglia give off lateral nerves. Sensory organs are well developed. The compound eyes are found on the ends of movable eye stalks. These eyes are accurate and can detect motion and respond to polarized light. Other sensory organs include tactile antennae and chemosensitive setae. Crayfish also have statocysts that serve as organs of equilibrium.

The sexes are separate in the crayfish, and the gonads are located just ventral to the pericardial cavity. In the male, a coiled sperm duct opens to the outside at the base of the fifth walking leg. Sperm transfer is accomplished by the modified first two swimmerets of the abdomen. In the female, the ovaries open at the bases of the third walking legs. A stiff

fold between the bases of the fourth and fifth pairs serves as a seminal receptacle. Following fertilization, the eggs are attached to the swimmerets of the female. Young hatchlings are miniature adults, and no metamorphosis occurs.

Centipedes and Millipedes

The centipedes and millipedes are known for their many legs (Fig. 28.23a). In **centipedes** (“hundred-leggers”), each of their many body segments has a pair of walking legs. The approximately 3,000 species prefer to live in moist environments such as under logs, in crevices, and in leaf litter, where they are active predators on worms, small crustaceans, and insects. The head of a centipede includes paired antennae and jawlike mandibles. Appendages on the first trunk segment are clawlike venomous jaws that kill or immobilize prey, while mandibles chew.

In **millipedes** (“thousand leggers”), each of four thoracic segments bears one pair of legs (Fig. 28.23b), while abdominal segments have two pairs of legs. Millipedes live under stones or burrow in the soil as they feed on leaf litter. Their cylindrical bodies have a tough chitinous exoskeleton. Some secrete hydrogen cyanide, a poisonous substance.



a.



b.

FIGURE 28.23

Centipede and millipede.

a. A centipede has a pair of appendages on almost every segment. **b.** A millipede has two pairs of legs on most segments.

Insects

Insects are adapted for an active life on land, although some have secondarily invaded aquatic habitats. The body of an insect is divided into a head, a thorax, and an abdomen. The head bears the sense organs and mouthparts (Fig. 28.24). The thorax bears three pairs of legs and possibly one or two pairs of wings; and the abdomen contains most of the internal organs. Wings enhance an insect's ability to survive by providing a way of escaping enemies, finding food, facilitating mating, and dispersing offspring.

In the grasshopper (Fig. 28.25), the third pair of legs is suited to jumping. There are two pairs of wings. The forewings are tough and leathery, and when folded back at rest, they protect the broad, thin hindwings. On each lateral surface, the first abdominal segment bears a large tympanum for the reception of sound waves. The posterior region of the exoskeleton in the female has an ovipositor, used to dig a hole in which eggs are laid.

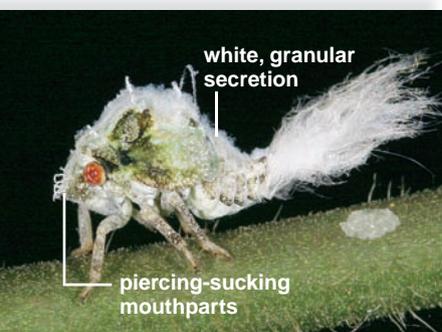
The digestive system is suitable for a herbivorous diet. In the mouth, food is broken down mechanically by mouthparts and enzymatically by salivary secretions. Food is temporarily stored in the crop before passing into the gizzard, where it is finely ground. Digestion is completed in the stomach, and nutrients are absorbed into the hemocoel from outpockets called gastric ceca (*cecum*, a cavity open at one end only). The excretory system consists of **Malpighian tubules**, which extend into a hemocoel and collect nitrogenous wastes that are concentrated and excreted into the digestive tract. The formation of a solid nitrogenous waste, namely uric acid, conserves water.

The respiratory system begins with openings in the exoskeleton called spiracles. From here, air enters small tubules called tracheae (Fig. 28.25a). The tracheae branch and rebranch, finally ending in moist areas where the actual exchange of gases takes place. No individual cell is very far from a site of gas exchange. The movement of air through this complex of tubules is not a passive process; air is pumped through by a series of bladderlike structures (air sacs) attached to the tracheae near the spiracles. Air enters the anterior four spiracles and exits by the posterior six spiracles. Breathing by tracheae may account for the small size of insects (most are less than 6 cm in length), since the tracheae are so tiny and fragile that they would be crushed by any amount of weight.

The circulatory system contains a slender, tubular heart that lies against the dorsal wall of the abdominal exoskeleton and pumps hemolymph into the hemocoel, where it circulates before returning to the heart again. The hemolymph is colorless and lacks a respiratory pigment, and so transports nutrients and wastes. The highly efficient tracheal system transports respiratory gases.

Grasshoppers undergo *incomplete metamorphosis*, a gradual change in form as the animal matures. The immature grasshopper, called a nymph, is recognizable as a grasshopper, even though it differs in body proportions from the adult. Other insects, such as butterflies, undergo *complete metamorphosis*, involving drastic changes in form. At first, the animal is a wormlike larva (caterpillar) with chewing mouthparts. It then forms a case, or cocoon, about itself and becomes a pupa. During this stage, the body parts are completely reorganized;

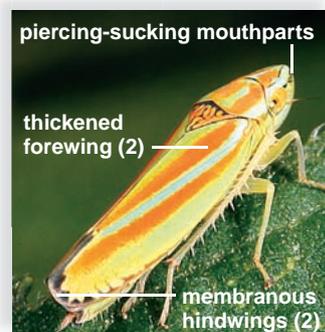
FIGURE 28.24 Insect diversity.



Mealybug, order Homoptera



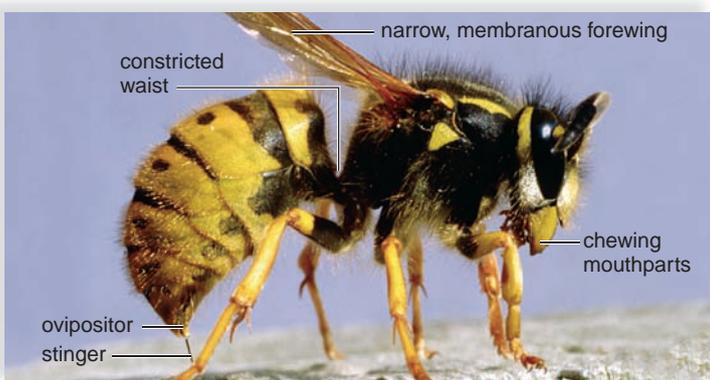
Beetle, order Coleoptera



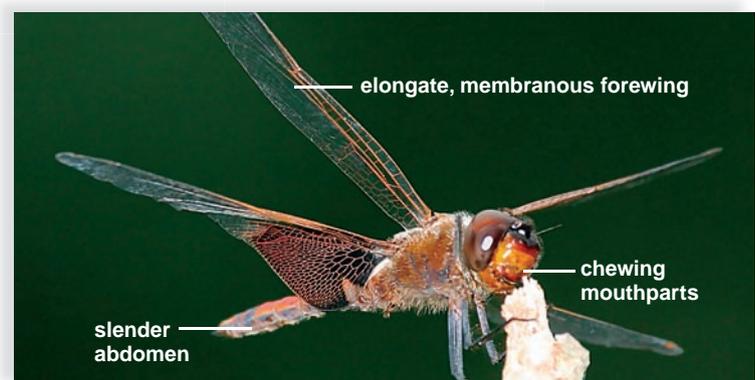
Leafhopper, order Homoptera



Head louse, order Anoplura



Wasp, order Hymenoptera



Dragonfly, order Odonata

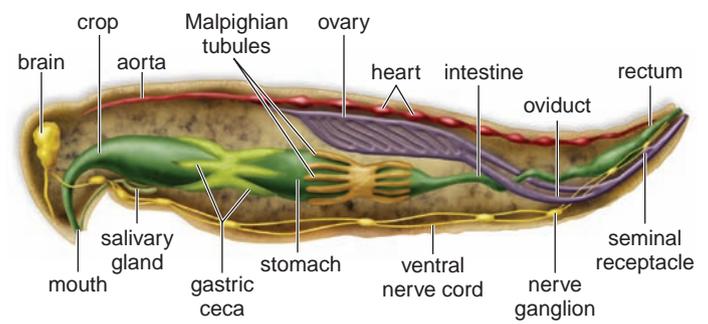
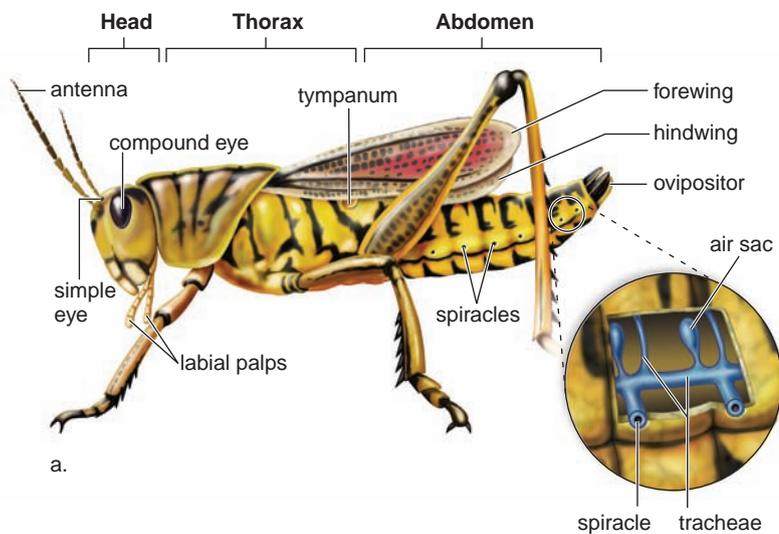


FIGURE 28.25 Female grasshopper, *Romalea*.

a. Externally, the body of a grasshopper is divided into three sections and has three pairs of legs. The tympanum receives sound waves, and the jumping legs and the wings are for locomotion. **b.** Internally, the digestive system is specialized. The Malpighian tubules excrete a solid nitrogenous waste (uric acid). A seminal receptacle receives sperm from the male, which has a penis.

the adult then emerges from the cocoon. This life cycle allows the larvae and adults to use different food sources.

Insects show remarkable behavior adaptations. Bees, wasps, ants, termites, and other colonial insects have complex societies.

Chelicerates

The **chelicerates** live in terrestrial, aquatic, and marine environments. The first pair of appendages is the pincerlike chelicerae, used in feeding and defense. The second pair is the pedipalps, which can have various functions. A *cephalothorax* [Gk. *kephale*, head, and *thorax*, breastplate] (fused head and thorax) is followed by an abdomen that contains internal organs.

Horseshoe crabs of the genus *Limulus* are familiar along the east coast of North America. The body is covered by exoskeletal shields. The anterior shield is a horseshoe-shaped carapace, which bears two prominent compound eyes (Fig. 28.26a). Ticks, mites, scorpions, spiders, and harvestmen are all arachnids. Over 25,000 species of mites and ticks have been classified, some of which are parasitic on a variety of other animals. Ticks are ectoparasites of various vertebrates, and they are carriers for such diseases as Rocky Mountain spotted fever and Lyme disease. When not attached to a host, ticks hide on plants and in the soil.

Scorpions can be found on all continents except Antarctica (Fig. 28.26b). North America is home to approximately 1,500 species. Scorpions are nocturnal and spend most of the day hidden under a log or a rock. Their pedipalps are large pincers, and their long abdomen ends with a stinger that contains venom.

Presently, over 35,000 species of spiders have been classified (Fig. 28.26c). Spiders, the most familiar chelicerates, have a narrow waist that separates the cephalothorax from the abdomen. Spiders do not have compound eyes; instead, they have numerous simple eyes that perform a similar function. The chelicerae are modified as fangs, with ducts from poison glands, and the pedipalps are used to hold, taste, and chew food. The abdomen often contains silk glands, and spiders spin a web in which to trap their prey.

Check Your Progress

28.4

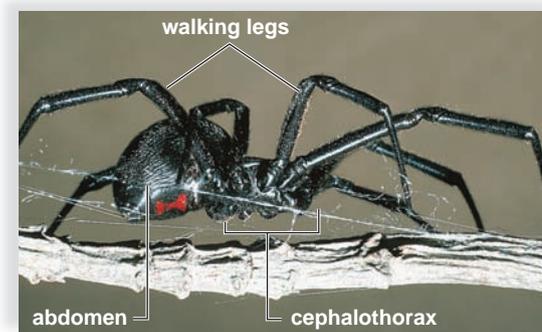
1. Name two ways the roundworms are anatomically similar to the arthropods.
2. Name two ways crustaceans are adapted to an aquatic life and insects are adapted to living on land.
3. What feature do the chelicerates have in common?



a. Horseshoe crab, *Limulus*



b. Kenyan giant scorpion, *Pandinus*



c. Black widow spider, *Latrodectus*

FIGURE 28.26 Chelicerate diversity.

a. Horseshoe crabs are common along the east coast. **b.** Scorpions are more common in tropical areas. **c.** The black widow spider is a poisonous spider that spins a web.

28.5 Invertebrate Deuterostomes

Molecular data tell us that echinoderms and chordates are closely related. Morphological data indicate that these two groups share the deuterostome pattern of development, which was described on page 516. The echinoderms and a few chordates are invertebrates; the echinoderms are discussed in this chapter and the invertebrate chordates are discussed in Chapter 29. Most of the chordates are vertebrates, as will become apparent.

Echinoderms

Echinoderms (phylum Echinodermata [Gk. *echinos*, spiny, and *derma*, skin]) are primarily bottom-dwelling marine animals. They range in size from brittle stars less than 1 cm in length to giant sea cucumbers over 2 m long. The most striking feature of echinoderms is their 5-pointed radial symmetry, as illustrated by a sea star. Although echinoderms are radially symmetrical as adults, their larvae are free-swimming filter feeders with bilateral symmetry. Echinoderms have an endoskeleton of spiny calcium-rich plates called ossicles. The spines protruding from their skin account for the phylum name Echinodermata. Another innovation is their unique **water vascular system** consisting of canals and appendages that function in locomotion, feeding, gas exchange, and sensory reception.

The more familiar of the echinoderms are the Asterozoa containing the sea stars (Fig. 28.27*a, b*), which are studied here; the Holothurians, including the sea cucumbers, which have long leathery bodies and resemble a cucumber (Fig. 28.27*c*); and the Echinozoa, including the sea urchin and sand dollar, both of which use their spines for locomotion, defense, and burrowing

(Fig. 28.27*d*). Less familiar are the Ophiurozoa, which includes the brittle stars, with a central disk surrounded by radially flexible arms, and the Crinozoa, the oldest group, which includes the stalked feather stars and the motile feather stars.

Sea Stars

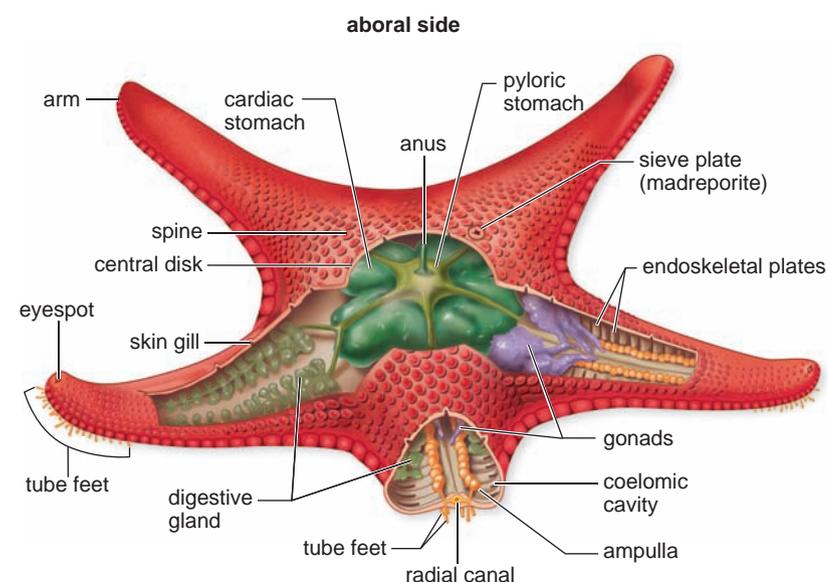
Sea stars number about 1,600 species that are commonly found along rocky coasts, where they feed on clams, oysters, and other bivalve molluscs. Various structures project through the body wall: (1) spines from the endoskeletal plates offer some protection; (2) pincerlike structures around the bases of spines keep the surface free of small particles; and (3) skin gills, tiny fingerlike extensions of the skin, are used for respiration. On the oral surface, each arm has a groove lined by little **tube feet** (Fig. 28.27).

To feed, a sea star positions itself over a bivalve and attaches some of its tube feet to each side of the shell. By working its tube feet in alternation, it pulls the shell open. A very small crack is enough for the sea star to evert its cardiac stomach and push it through the crack, so that it contacts the soft parts of the bivalve. The stomach secretes enzymes, and digestion begins, even while the bivalve is attempting to close its shell. Later, partly digested food is taken into the sea star's body, where digestion continues in the pyloric stomach using enzymes from the digestive glands found in each arm. A short intestine opens at the anus on the aboral side (side opposite the mouth).

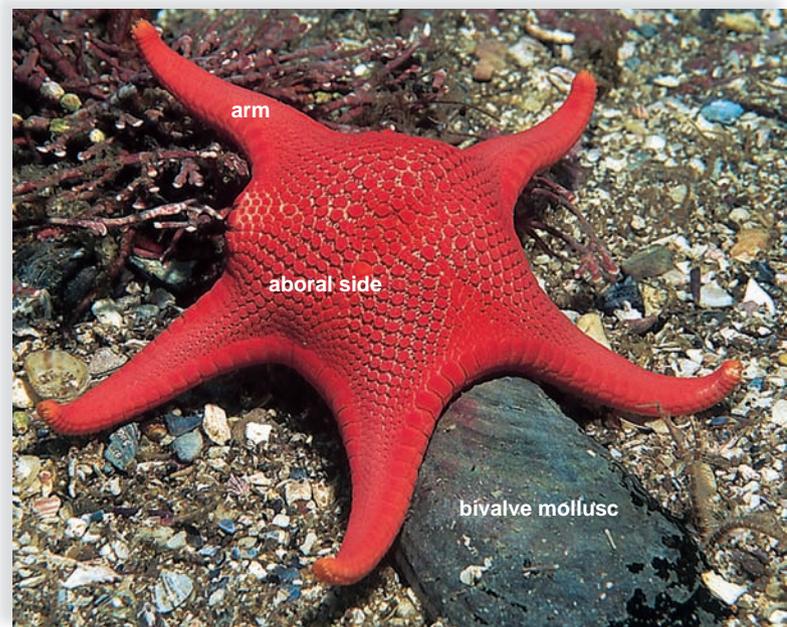
In each arm, the well-developed coelom contains a pair of digestive glands and gonads (either male or female) that open on the aboral surface by very small pores. The nervous system consists of a central nerve ring that gives off radial nerves in each arm. A light-sensitive eyespot is at the tip of each arm.

FIGURE 28.27 Echinoderms.

a. Sea star (starfish) anatomy. Like other echinoderms, sea stars have a water vascular system that begins with the sieve plate and ends with expandable tube feet. **b.** The red sea star, *Mediastar*, uses the suction of its tube feet to open a clam, a primary source of food. **c.** Sea cucumber, *Pseudocolochirus*. **d.** Sea urchin, *Strongylocentrotus*.



a.



b. Red sea star, *Mediastar*

Locomotion depends on the water vascular system. Water enters this system through a structure on the aboral side called the *sieve plate*, or *madreporite*. From there it passes through a stone canal to a ring canal, which circles around the central disc, and then to a radial canal in each arm. From the radial canals, many lateral canals extend into the tube feet, each of which has an ampulla. Contraction of an ampulla forces water into the tube foot, expanding it. When the foot touches a surface, the center is withdrawn, giving it suction so that it can adhere to the surface. By alternating the expansion and contraction of the tube feet, a sea star moves slowly along.

Echinoderms do not have a respiratory, excretory, or circulatory system. Fluids within the coelomic cavity and the water vascular system carry out many of these functions. For example, gas exchange occurs across the skin gills and the tube feet. Nitrogenous wastes diffuse through the coelo-

mic fluid and the body wall. Cilia on the peritoneum lining the coelom keep the coelomic fluid moving.

Sea stars reproduce asexually and sexually. If the body is fragmented, each fragment can regenerate a whole animal as long as a portion of the central disc is present. Sea stars spawn and release either eggs or sperm at the same time. The bilateral larva will undergo a metamorphosis to become the radially symmetrical adult.

Check Your Progress

28.5

1. What evidence do we have that echinoderms evolved from bilaterally symmetrical animals?
2. Describe the functions of the water vascular system in sea stars.

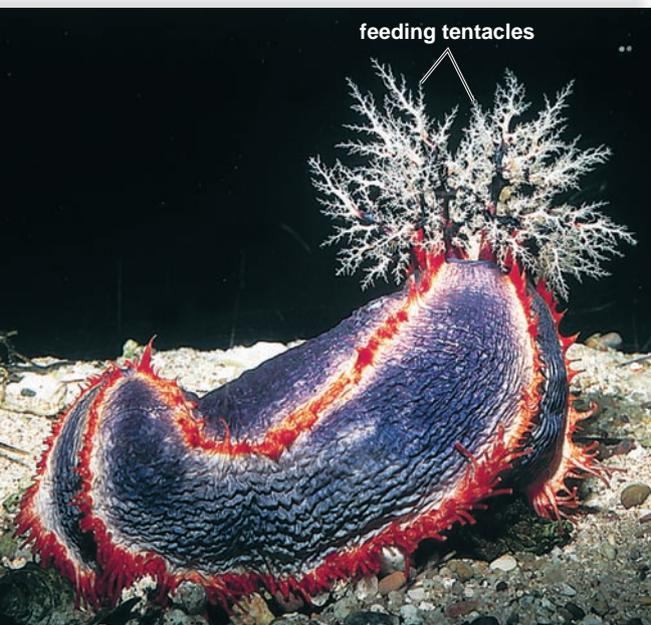
Connecting the Concepts

About 90% of all animal species have a coelom and are in the phyla Mollusca, Annelida, Arthropoda, Echinodermata, and Chordata. (The chordates, which include the vertebrates, will be studied in Chapter 29.) This indicates that there are some adaptive advantages to having a coelom, or perhaps a combination of bilateral symmetry and the complexity made possible by the presence of a coelom. Most animals with a coelom have both circulatory and respiratory systems, which permit them to be active. The echinoderms are an anomaly because they lack these systems and have radial symmetry.

Some of the coelomate phyla are protostomes (molluscs, annelids, and arthropods) and some are deuterostomes (echinoderms and chordates) on the basis of embryological development. However, it is interesting that both lines of descent have representatives that are segmented. Based on the current phylogenetic tree, segmentation must have evolved three separate times in the annelids, arthropods, and chordates. Segmentation of the annelids and many arthropods is obvious because the body has demarcations that can be seen externally. The repeating vertebrae of the backbone in vertebrates signal that they, too, are segmented. Was a coelom present

before the evolution of segmentation? Perhaps it was. Later, a partitioned coelom may have provided a hydrostatic skeleton that enabled a worm to burrow more efficiently in the soil. In other words, there was a selective advantage to having a segmented coelom in organisms that lacked limbs. The later evolution of limbs in jointed arthropods (e.g., insects) and vertebrates (e.g., frogs, lizards, horses) was even more adaptive for locomotion on land.

Animals that live on land must also have a means of reproduction that allows fertilization and development to take place without requiring external water.



c. Sea cucumber, *Pseudocolochirus*



d. Purple sea urchin, *Strongylocentrotus*

summary

28.1 Evolution of Animals

Animals are multicellular organisms that are heterotrophic and ingest their food. They have the diploid life cycle. Typically, they have the power to move by means of contracting fibers. It is hypothesized that animals evolved from a protist that resembles the choanoflagellates of today. Molecular data used to construct an evolutionary tree of the animals can be substantiated by morphological data.

28.2 Introducing the Invertebrates

Sponges resemble colonial protozoans. They have the cellular level of organization, lack tissues, and have various symmetries. Sponges are sessile filter feeders and depend on a flow of water through the body to acquire food, which is digested in vacuoles within collar cells that line a central cavity.

Comb jellies and cnidarians have two tissue layers derived from the germ layers ectoderm and endoderm. They are radially symmetrical.

Cnidarians have a sac body plan. They exist as either polyps or medusae, or they can alternate between the two. Hydras and their relatives—sea anemones and corals—are polyps; in jellyfishes, the medusan stage is dominant. In *Hydra* and other cnidarians, an outer epidermis is separated from an inner gastrodermis by mesoglea. They possess tentacles to capture prey and cnidocytes armed with nematocysts to stun it. A nerve net coordinates movements.

28.3 Variety Among the Lophotrochozoans

Free-living flatworms (planarians) exemplify that flatworms have three tissue layers and no coelom. Planarians have muscles and a ladder-type nervous system, and they show cephalization. They take in food through an extended pharynx leading to a gastrovascular cavity, which extends throughout the body. There is an osmotic-regulating organ that contains flame cells. Flukes and tapeworms are parasitic. Flukes have two suckers by which they attach to and feed from their hosts. Tapeworms have a scolex with hooks and suckers for attaching to the host intestinal wall. The body of a tapeworm is made up of proglottids, which, when mature, contain thousands of eggs. If these eggs are taken up by pigs or cattle, larvae become encysted in their muscles. If humans eat this meat, they too may become infected with a tapeworm.

Rotifers are microscopic and have a corona that resembles a spinning wheel when in motion.

The body of a mollusc typically contains a visceral mass, a mantle, and a foot. Many also have a head and a radula. The nervous system consists of several ganglia connected by nerve cords. There is a reduced coelom and an open circulatory system. Clams (bivalves) are adapted to a sedentary coastal life, squids (cephalopods) to an active life in the sea, and snails (gastropods) to life on land.

Annelids are segmented worms. They have a well-developed coelom divided by septa, a closed circulatory system, a ventral solid nerve cord, and paired nephridia. Earthworms are oligochaetes (“few bristles”) that use the body wall for gas exchange. Polychaetes (“many bristles”) are marine worms that have parapodia. They may be predators, with a definite head region, or they may be filter feeders, with ciliated tentacles to filter food from the water. Leeches also belong to this phylum.

28.4 Quantity Among the Ecdysozoans

Roundworms have a pseudocoelom. Roundworms are usually small and very diverse; they are present almost everywhere in great numbers. Many are significant parasites of humans. The parasite *Ascaris* is representative of the group. Infections can also be caused

by *Trichinella*, whose larval stage encysts in the muscles of humans. Elephantiasis is caused by a filarial worm that blocks lymphatic vessels.

Arthropods are the most varied and numerous of animals. Their success is largely attributable to a flexible exoskeleton, specialized body regions, and jointed appendages. Also important are a high degree of cephalization, a variety of respiratory organs, and reduced competition through metamorphosis. Crustaceans (crayfish, lobsters, shrimps, copepods, krill, and barnacles) have a head that bears compound eyes, antennae, antennules, and mouthparts. Crayfish illustrate other features, such as an open circulatory system, respiration by gills, and a ventral solid nerve cord. Insects include butterflies, grasshoppers, bees, and beetles. The anatomy of the grasshopper illustrates insect anatomy and the ways they are adapted to life on land. Like other insects, grasshoppers have wings and three pairs of legs attached to the thorax. Grasshoppers have a tympanum for sound reception, a digestive system specialized for a grass diet, Malpighian tubules for excretion of solid nitrogenous waste, tracheae for respiration, internal fertilization, and incomplete metamorphosis.

Chelicerates (horseshoe crabs, spiders, scorpions, ticks, and mites) have chelicerae, pedipalps, and four pairs of walking legs attached to a cephalothorax.

28.5 Invertebrate Deuterostomes

Echinoderms (e.g., sea stars, sea urchins, sea cucumbers, and sea lilies) have radial symmetry as adults (not as larvae) and internal calcium-rich plates with spines. Typical of echinoderms, sea stars have tiny skin gills, a central nerve ring with branches, and a water vascular system for locomotion. Each arm of a sea star contains branches from the nervous, digestive, and reproductive systems.

understanding the terms

annelid	526	medusa	518
arthropod	529	mesoglea	518
bilateral symmetry	513	metamorphosis	529
bivalve	524	millipede	531
centipede	531	mollusc	523
cephalization	515	molt	516
cephalopod	525	nematocyst	518
chelicerate	533	nephridium (pl., nephridia)	526
chitin	529	nerve net	519
cnidarian	518	polyp	518
comb jelly	518	proglottid	522
crustacean	530	protostome	515
cyst	522	pseudocoelom	528
decapod	530	radial symmetry	513
deuterostome	515	radula	523
ecdyszoa	516	rotifer	523
echinoderm	534	roundworm	528
exoskeleton	529	scolex	522
flatworm	520	sea star	534
gastropod	525	segmentation	526
gastrovascular cavity	518	sessile	515
germ layer	515	seta (pl., setae)	526
hemocoel	523	spicule	517
hermaphroditic	521	sponge	517
hydra	519	trachea (pl., tracheae)	529
hydrostatic skeleton	518	trochophore	516
insect	532	true coelom	516
invertebrate	512	tube foot	534
lophophore	516	typhlosole	526
lophotrochozoa	516	vertebrate	512
Malpighian tubule	532	water vascular system	534
mantle	523		

Match the terms to these definitions:

- _____ Blind digestive cavity that also serves a circulatory (transport) function in animals lacking a circulatory system.
- _____ Body cavity lying between the digestive tract and body wall that is completely lined by mesoderm.
- _____ Change in shape and form that some animals, such as insects, undergo during development.
- _____ System of canals and appendages used for movement in echinoderms.

reviewing this chapter

1. What does the phylogenetic tree (see Fig. 28.4) tell you about the evolution of the animals studied in this chapter? 514–15
2. What features make sponges different from the other organisms placed in the animal kingdom? 517
3. What are the two body forms found in cnidarians? Explain how they function in the life cycle of various types of cnidarians. 518–19
4. Describe the anatomy of *Hydra*, pointing out those features that typify cnidarians. 519
5. Describe the anatomy of a free-living planarian, and how it differs from the parasitic flatworms. 520–22
6. What are the general characteristics of molluscs and the specific features of bivalves, cephalopods, and gastropods? 523–25
7. What are the general characteristics of annelids and the specific features of earthworms? 526–27
8. Describe the anatomy of *Ascaris*, pointing out those features that typify roundworms. 528
9. What are the general characteristics of arthropods, specifically crustaceans and insects? 529–33
10. What other types of arthropods were discussed in the chapter? 531–33
11. What are the general characteristics of echinoderms? Explain how the water vascular system works in sea stars. 534–35

testing yourself

Choose the best answer for each question.

1. Which of these is not a characteristic of animals?
 - heterotrophic
 - diploid life cycle
 - have contracting fibers
 - single cells or colonial
 - lack of chlorophyll
2. The phylogenetic tree of animals shows that
 - three germ layers evolved before a coelom.
 - both molluscs and annelids are protostomes.
 - some animals have radial symmetry.
 - sponges were the first to evolve from an ancestral protist.
 - All of these are correct.
3. Which of these descriptions does not pertain to both protostomes and deuterostomes?
 - three germ layers, bilateral symmetry, first opening is mouth
 - bilateral symmetry, first opening is mouth, all have a true coelom
 - spiral cleavage, first opening is anus, true coelom develops by a splitting of mesoderm
 - bilateral symmetry, three germ layers, second opening is mouth
 - None pertain to both protostomes and deuterostomes.
4. Which of these sponge characteristics is not typical of animals?
 - They practice sexual reproduction.
 - They have the cellular level of organization.
 - They have various symmetries.
 - They have flagellated cells.
 - Both b and c are not typical.
5. Which of these pairs is mismatched?
 - sponges—spicules
 - tapeworms—proglottids
 - cnidarians—nematocysts
 - roundworms—cilia
 - cnidarians—polyp and medusa
6. Flukes and tapeworms
 - show cephalization.
 - have well-developed reproductive systems.
 - have well-developed nervous systems.
 - are free-living.
7. *Ascaris* is a parasitic
 - roundworm.
 - flatworm.
 - hydra.
 - sponge.
 - comb jelly.
8. The phylogenetic tree of animals shows that
 - cnidarians evolved directly from sponges.
 - flatworms evolved directly from roundworms.
 - rotifers are closely related to flatworms.
 - coelomates gave rise to the acoelomates.
 - All of these are correct.
9. Comb jellies are most closely related to
 - cnidarians.
 - sponges.
 - flatworms.
 - roundworms.
 - Both a and b are correct.
10. Write the correct type of animal beside each of the following terms.
 - proglottids:
 - mantle cavity:
 - collar cells:
 - cnidocytes:
 - crown of cilia:
 - branched gastrovascular cavity:
 - exoskeleton contains chitin:
11. Which of these does not pertain to a protostome?
 - spiral cleavage
 - blastopore is associated with the anus
 - coelom, splitting of mesoderm
 - annelids, arthropods, and molluscs
 - mouth is associated with first opening
12. Which of these best shows that snails are not closely related to crayfish?
 - Snails are terrestrial, and crayfish are aquatic.
 - Snails have a broad foot, and crayfish have jointed appendages.
 - Snails are hermaphroditic, and crayfish have separate sexes.
 - Snails are insects, but crayfish are fishes.
 - Snails are bivalves, and crayfish are chelicerates.
13. Which of these pairs is mismatched?
 - clam—gills
 - lobster—gills
 - grasshopper—book lungs
 - polychaete—parapodia
14. A radula is a unique organ for feeding found in
 - molluscs.
 - annelids.
 - arthropods.
 - only insects.
 - All of these are correct.

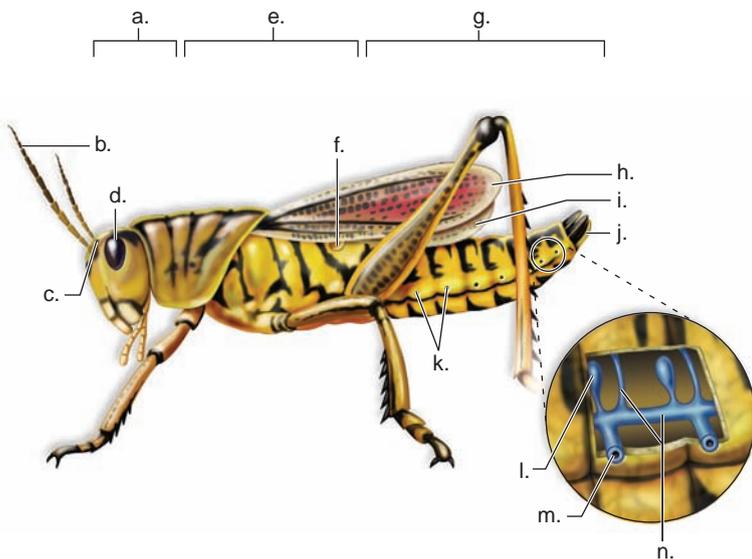
15. Which of these pairs is mismatched?
- crayfish—walking legs
 - clam—hatchet foot
 - grasshopper—wings
 - earthworm—many cilia
 - squid—jet propulsion
16. Associate each of these terms to annelids, to arthropods, and/or to molluscs.

Terms:

- organ system level of organization _____
 - segmentation _____
 - true coelom _____
 - cephalization in some representatives _____
 - bilateral symmetry _____
 - complete gut _____
 - jointed appendages _____
 - three-part body plan _____
17. Associate each of these terms to clams and/or to earthworms.

Terms:

- annelid _____
 - mollusc _____
 - three ganglia _____
 - gills _____
 - closed circulatory system _____
 - setae _____
 - open circulatory system _____
 - hatchet foot _____
 - hydrostatic skeleton _____
 - ventral nerve cord _____
18. Label this diagram.



For questions 19–23, match the description to a body system in the key.

KEY:

- | | |
|-----------------------|--------------------------|
| a. respiratory system | c. cardiovascular system |
| b. digestive system | d. nervous system |
- particles adhere to labial palps
 - passes through the heart
 - has three pairs of ganglia
 - hemocoel
 - gills

For questions 24–27, match the classification to an animal in the key.

KEY:

- | | |
|-----------|--------------|
| a. shrimp | c. earthworm |
| b. squid | d. spider |
- molluscan cephalopod
 - annelid oligochaete
 - arthropod crustacean
 - arthropod chelicerate
 - Segmentation in the earthworm is not exemplified by
 - body rings.
 - coelom divided by septa.
 - setae on most segments.
 - nephridia interior in most segments.
 - tympanum exterior to segments.
 - Which of these is an incorrect difference between clam and squid?

Clam	Squid
------	-------

 - filter feeder—active predator
 - hatchet foot—jet propulsion
 - brain and nerves—three separate ganglia
 - open circulation—closed circulation
 - no cephalization—marked cephalization
 - Which characteristic accounts for the success of arthropods?
 - jointed exoskeleton
 - well-developed nervous system
 - segmentation
 - respiration adapted to environment
 - All of these are correct.
 - Sea stars
 - have no respiratory, excretory, or circulatory systems.
 - usually reproduce asexually.
 - are protostomes.
 - can evert their stomach to digest food.
 - Both a and d are correct.
 - The tube feet of echinoderms
 - are their head.
 - are a part of the water vascular system.
 - are found in the coelom.
 - help pass sperm to females during reproduction.
 - All of these are correct.

thinking scientifically

- How is the lifestyle of radially symmetrical animals different from that of bilaterally symmetrical animals? Explain.
- Animals, like other life-forms, evolved in the ocean. What made water a better nursery than land for the evolution of animals?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

<http://www.mhhe.com/maderbiology10>

29

Vertebrate Evolution

The New Guinea (NG) singing dog lives on the island of New Guinea, but it doesn't actually sing. It yelps, whines, and howls at different pitches unlike other dogs. The howl is eerie to the point of causing goose bumps when one tone blends with the next. The evolutionary history of the NG singing dog is a matter of debate. Is it a unique species, a type of gray wolf, or is it related to the dingo, the nonbarking canine that lives in Australia? Some suggest that the NG singing dog might be the most primitive known "breed" of domestic dog because Stone Age people brought it to New Guinea 6,000 years ago! Living on an island, it has remained geographically and reproductively isolated ever since. Therefore, it could be a living fossil, an organism with the same genes and characteristics as its original ancestor. If so, the NG singing dog offers an opportunity to study not only why it "sings" but also what the first domesticated dog was like.

However, like many other vertebrates, the topic of this chapter, the NG singing dog is threatened with extinction. Expeditions into the highlands of New Guinea have only yielded a few droppings, tracks, and haunting howls in the distance.

New Guinea singing dog, *Canis familiaris hallstromi*.



29.1 THE CHORDATES

- Lancelets are nonvertebrate chordates with the four chordate characteristics as adults: notochord, a dorsal tubular nerve cord, pharyngeal pouches, and a postanal tail. 540–41

29.2 THE VERTEBRATES

- In vertebrates, the notochord is replaced by the vertebral column. Most vertebrates also have a head region, an endoskeleton, and paired appendages. 542

29.3 THE FISHES

- There are three main groups of fishes: jawless (hagfishes and lampreys), cartilaginous (e.g., sharks and rays), and bony (ray-finned and lobe-finned). Ancestral lobe-finned fishes gave rise to modern-day lobe-finned fishes and to the amphibians. 543–45

29.4 THE AMPHIBIANS

- Amphibians (e.g., frogs and salamanders) are partially adapted to living on land. Ancestral amphibians gave rise to modern-day amphibians and to the reptiles. 546–47

29.5 THE REPTILES

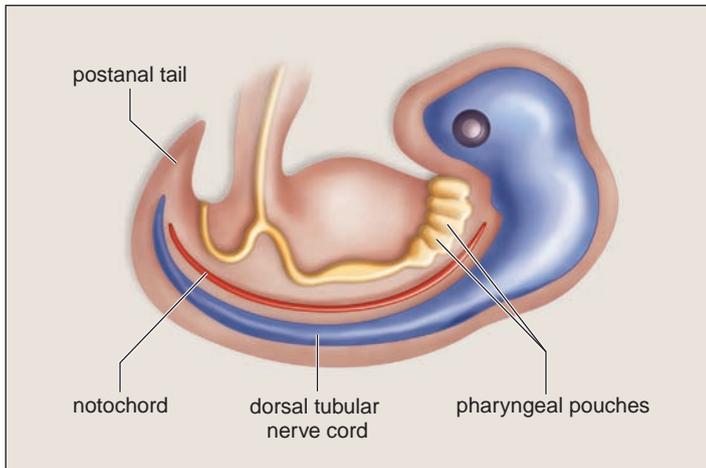
- Reptiles are completely adapted to life on land. 548
- The shelled egg of reptiles, which contains extraembryonic membranes, is an adaptation for reproduction on land. 548
- Modern-day reptiles include the turtles, the lizards, snakes, and the archosaurs (crocodilians, dinosaurs, and birds). 548–50
- Birds have feathers and skeletal adaptations that enable them to fly. 552–53

29.6 THE MAMMALS

- Mammals, which have derived traits not seen in reptiles, were present when the dinosaurs existed. They did not diversify until the dinosaurs became extinct. 554
- Mammals are vertebrates with hair and mammary glands. Hair helps them maintain a constant body temperature. 554
- Mammals are classified according to methods of reproduction: Monotremes lay eggs; marsupials have a pouch into which the newborn crawls and develops further; and placental mammals retain offspring in a uterus for development until birth. 554–56

29.1 The Chordates

Chordates (phylum Chordata), like echinoderms, have the deuterostome pattern of development. However, the **chordates** have a different type of skeleton compared to the invertebrates. In invertebrates, the skeleton is external, and the muscles are attached to its inner surface. In chordates, the skeleton is internal, and the muscles are attached to the outer surface. This allows the chordates to enjoy freedom of movement and attainment of a larger size than invertebrates. These four basic characteristics occur during the life history of all chordates:



Notochord [Gk. *notos*, back, and *chorde*, string]. A dorsal supporting rod; the notochord is located just below the nerve cord. The majority of vertebrates have an embryonic notochord that is replaced by the vertebral column during development.

Dorsal tubular nerve cord. The anterior portion becomes the brain in most chordates. In vertebrates, the nerve cord, often called the spinal cord, is protected by vertebrae.

Pharyngeal pouches. These are seen only during embryonic development in most vertebrates. In the nonvertebrate chordates, the fishes, and amphibian larvae, the pharyngeal pouches become functioning **gills** (respiratory organs of aquatic vertebrates). Water passing into the mouth and the pharynx goes through the gill slits, which are supported by gill arches. In terrestrial vertebrates, the pouches are modified for various purposes. For example, in humans the first pair of pouches become the auditory tubes.

Postanal tail. A tail—in the embryo, if not in the adult—extends beyond the anus. In other groups of animals, the anus is terminal.

Nonvertebrate Chordates

The nonvertebrate chordates are divided into two groups: the cephalochordates and the urochordates. Lancelets (genus *Branchiostoma*) are the **cephalochordates**. (The former genus for these organisms, *Amphioxus*, is now sometimes

used as a common name also.) These marine chordates, which are only a few centimeters long, are named for their resemblance to a lancet—a small, two-edged surgical knife (Fig. 29.1). Lancelets are found in the shallow water along most coasts, where they usually lie partly buried in sandy or muddy substrates with only their anterior mouth and gill apparatus exposed. They feed on microscopic particles filtered out of the constant stream of water that enters the mouth and passes through the gill slits into an atrium that opens at the atriopore.

Lancelets retain the four chordate characteristics as an adult and for that reason lancelets are important in comparative anatomy and evolutionary studies. In lancelets, the notochord extends from the tail to the head, and this accounts for their group name, the cephalochordates. In addition to the four features of all chordates, segmentation is present, as witnessed by the fact that the muscles are segmentally arranged, and the dorsal tubular nerve cord has periodic branches. Segmentation may not be an important feature in lancelets, but it is in the vertebrates where it leads

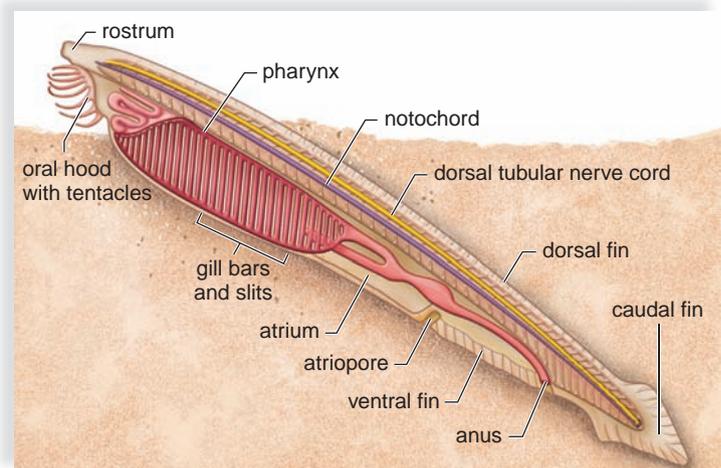


FIGURE 29.1 Lancelet, *Branchiostoma*.

Lancelets are filter feeders. Water enters the mouth and exits at the atriopore after passing through the gill slits.

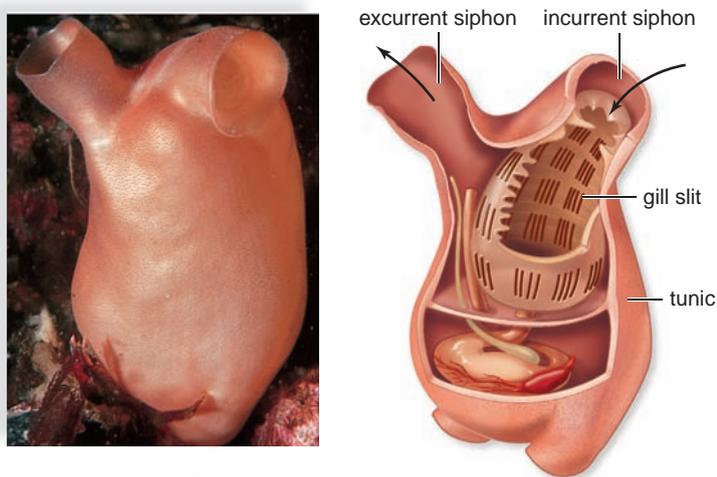


FIGURE 29.2 Sea squirt, *Halocynthia*.

Note that the only chordate characteristic remaining in the adult is gill slits.

to specialization of parts, as we also witnessed in the annelids and arthropods.

Sea squirts, the **urochordates**, live on the ocean floor, where they squirt out water from their excurrent siphon when disturbed. They are also called tunicates because they

have a tunic that makes them look like thick-walled, squat sacs. The sea squirt larva is bilaterally symmetrical and has the four chordate characteristics. Metamorphosis produces the sessile adult with an incurrent and excurrent siphon (Fig. 29.2). The pharynx is lined by numerous cilia whose beating creates a current of water that moves into the pharynx and out the numerous gill slits, the only chordate characteristic that remains in the adult.

Many evolutionary biologists hypothesize that the sea squirts are directly related to the vertebrates. It has been suggested that a larva with the four chordate characteristics may have become sexually mature without developing the other adult sea squirt characteristics. Then it may have evolved into a fishlike vertebrate. Figure 29.3 shows how the main groups of chordates may have evolved.

Check Your Progress

29.1

1. Would you predict that humans have the four chordate characteristics as embryos? Why or why not?
2. Adult sea squirts look like thick-walled, squat sacs. Why are they classified as chordates?

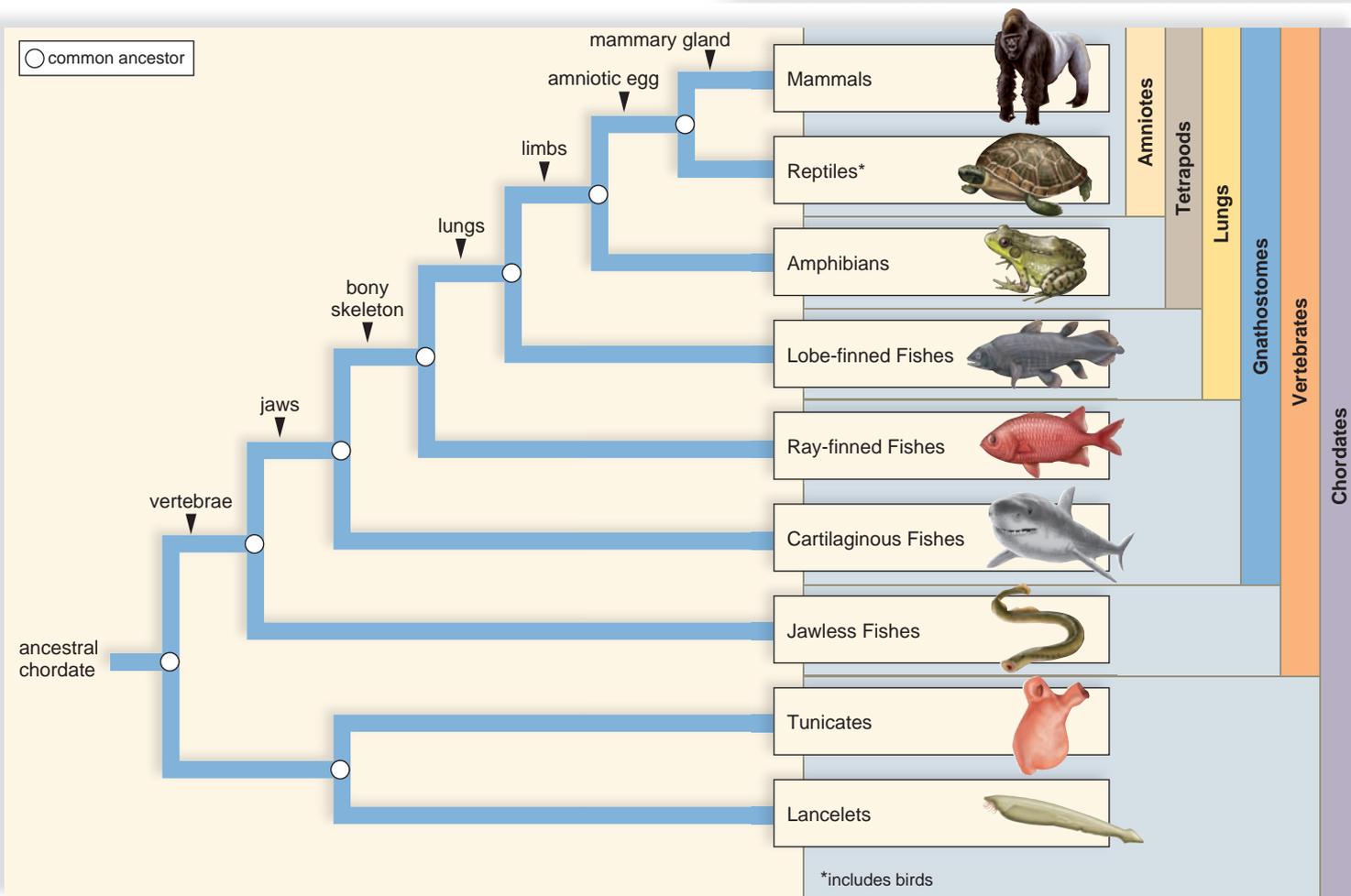


FIGURE 29.3 Phylogenetic tree of the chordates.

The evolution of vertebrates is marked by at least seven derived characteristics.

29.2 The Vertebrates

As embryos, vertebrates have the four chordate characteristics. In addition, vertebrates have these features:

Vertebral column. The embryonic notochord is generally replaced by a vertebral column composed of individual vertebrae (Fig. 29.4). Remnants of the notochord are seen in the intervertebral discs, which are compressible cartilaginous pads found between the vertebrae. The vertebral column, which is a part of the flexible but strong endoskeleton, gives evidence that vertebrates are segmented.

Skull. The main axis of the internal skeleton consists of not only the vertebral column, but also a skull that encloses and protects the brain. During vertebrate evolution, the brain increases in complexity, and specialized regions developed to carry out specific functions. The high degree of cephalization is accompanied by complex sense organs. The eyes develop as outgrowths of the brain. The ears are primarily equilibrium devices in aquatic vertebrates, but they also function as sound-wave receivers in land vertebrates. In addition, many vertebrates possess well-developed senses of smell and taste.

Endoskeleton. The vertebrate skeleton (either cartilage or bone) is a living tissue that grows with the animal. It also protects internal organs and serves as a place of attachment for muscles. Together, the skeleton and muscles form a system that permits rapid and efficient movement. Two pairs of appendages are characteristic. Fishes typically have pectoral and pelvic fins, while terrestrial tetrapods have four limbs.

Internal organs. Vertebrates have a large coelom and a complete digestive tract. The blood in vertebrates is contained entirely within blood vessels. Therefore, the circulatory system is called closed. The respiratory system consists of gills or lungs, which are used to obtain oxygen from the environment. The kidneys are important excretory and water-regulating organs that conserve or rid the body of water as necessary. The sexes are generally separate, and reproduction is usually sexual.

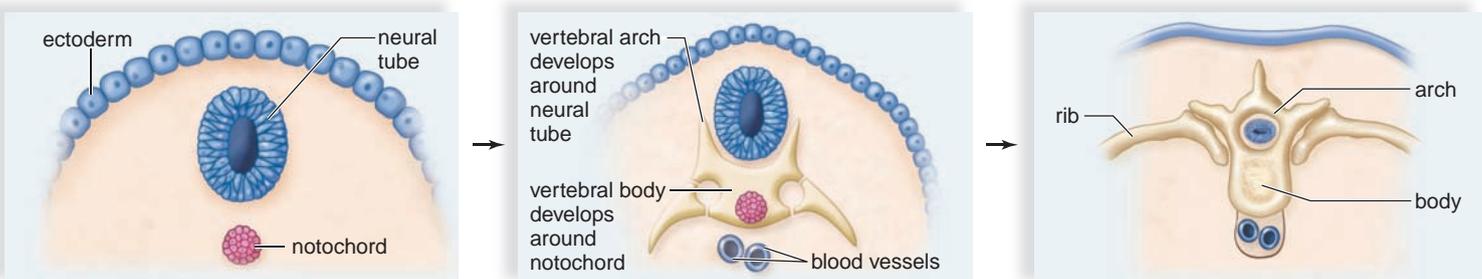


FIGURE 29.4 Replacement of notochord by the vertebrae.

During vertebrate development, the vertebrae replace the notochord and surround the neural tube. The result is the flexible vertebral column, which protects the nerve cord. The term spine refers to the vertebral column plus the nerve cord.

Vertebrate Evolution

Chordates, including vertebrates, appear on the scene suddenly at the start of the Cambrian period (see page 327). Even though we do not know the origin of vertebrates, we can trace their later evolution, as shown in Figure 29.3. The earliest vertebrates were fishes, organisms that are abundant both in marine and freshwater habitats. A few of today's fishes lack jaws and have to suck and, otherwise, engulf their prey. Most fishes have jaws, which are a more efficient means of gasping and eating prey. The jawed fishes and all the other vertebrates are **gnathostomes**—animals with jaws.

Certain of the early fishes not only had jaws, they also had a bony skeleton, lungs, and fleshy fins. These characteristics were preadaptive for a land existence, and the amphibians, the first vertebrates to live on land, evolved from these fishes. The amphibians were the first vertebrates to have limbs. The terrestrial vertebrates are **tetrapods** because they have four limbs. Some, such as the snakes, no longer have four limbs, but their evolutionary ancestors had four limbs.

Many amphibians, such as the frog, reproduce in an aquatic environment. This means that, in general, amphibians are not fully adapted to living on land. Reptiles are fully adapted to life on land because, among other features, they produce an amniotic egg. The amniotic egg is so named because the embryo is surrounded by an amniotic membrane that encloses the amniotic fluid. Therefore, it is obvious that **amniotes** develop within an aquatic environment but of their own making. In placental mammals, such as ourselves, the fertilized egg develops inside the female, where it is surrounded by an amniotic membrane. A watertight skin, which is seen among the reptiles and mammals, is also a good feature to have when living on land.

Check Your Progress

29.2

1. Which vertebrate characteristic shows that they are segmented? Explain.
2. With few exceptions, all vertebrates develop in an aquatic environment. Explain.

29.3 The Fishes

Fishes are the largest group of vertebrates with nearly 28,000 recognized species. They range in size from a few millimeters in length to the whale shark, which may reach lengths of 12 m. The fossil record of the fishes is extensive.

Jawless Fishes

The earliest fossils of Cambrian origin were the small, filter-feeding, jawless and finless **ostracoderms**. Several groups of ostracoderms developed heavy dermal armor for protection.

Today's **jawless fishes**, or **agnathans**, have a cartilaginous skeleton and persistent notochord. They are cylindrical, up to a meter long, and have smooth, nonscaly skin (Fig. 29.5). The hagfishes are exclusively marine scavengers that feed on soft-bodied invertebrates and dead fishes. Many species of lampreys are filter feeders like their ancestors. Parasitic lampreys have a round, muscular mouth used to attach themselves to another fish and suck nutrients from the host's cardiovascular system. The parasitic sea lamprey gained access to the Great Lakes in 1829 and by 1950 had almost demolished the resident trout and whitefish populations.

Fishes with Jaws

Fishes with jaws have these characteristics:

Ectothermy. Like all fishes, jawed fishes are **ectotherms** [Gk. *ekto*, outer, and *therme*, heat], which means that they depend on the environment to regulate their temperature.

Gills. Like all fishes, jawed fishes breathe with gills and have a single-looped, closed circulatory system with a heart that pumps the blood first to the gills. Then, oxygenated blood passes to the rest of the body.

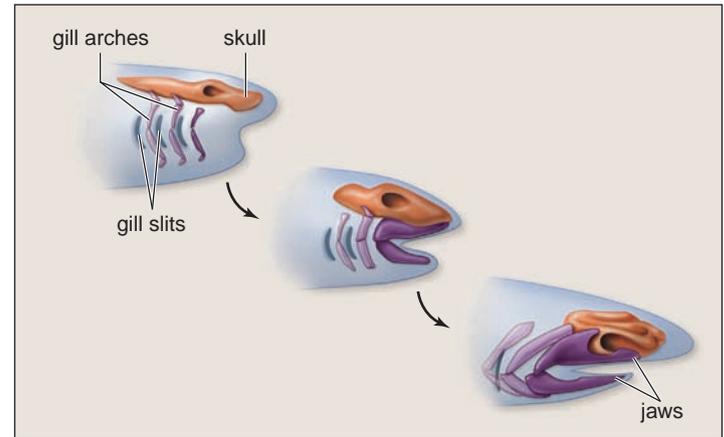


FIGURE 29.5 Lamprey, *Petromyzon*.

Lampreys, which are agnathans, have an elongated, rounded body and nonscaly skin. Note the lamprey's toothed oral disk, which is attached to the aquarium glass.

Cartilaginous or bony endoskeleton. The endoskeleton of jawed fishes includes the vertebral column, a skull with jaws, and paired pectoral and pelvic fins. The large muscles of the body actually do most of the work of locomotion, but the fins help with balance and turning.

Jaws evolved from the first pair of gill arches present in ancestral agnathans. The second pair of gill arches became support structures for the jaws:



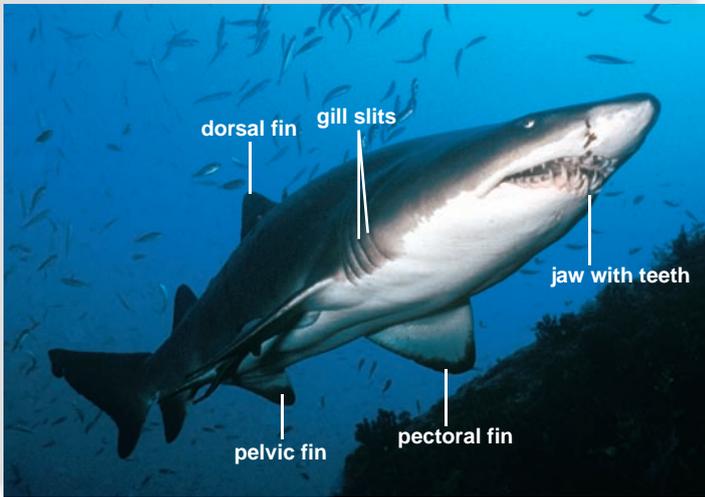
Scales. The skin of the jawed fishes is covered by scales, therefore, it is not exposed to the environment. A scientist can tell the age of a fish from examining the growth of the scales.

The **placoderms**, extinct jawed fishes of the Devonian period, are probably the ancestors of early sharks and bony fishes. Placoderms were armored with heavy, bony plates and had strong jaws. Like modern-day fishes, they also had paired pectoral and pelvic fins (see Fig. 29.6).

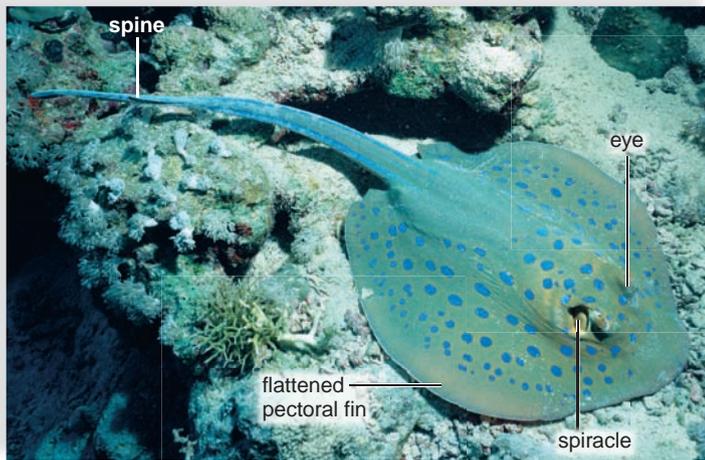
Cartilaginous Fishes

Sharks, rays, skates, and chimaeras are marine **cartilaginous fishes (Chondrichthyes)**. The cartilaginous fishes have a skeleton composed of cartilage instead of bone; have five to seven gill slits on both sides of the pharynx; and lack the gill cover of bony fishes. In addition, many have openings to the gill chamber located behind the eyes called spiracles. Their body is covered with dermal denticles, tiny teethlike scales that project posteriorly, which is why a shark's skin feels like sandpaper. The menacing teeth of sharks and their relatives are simply larger, specialized versions of these scales. At any one time, a shark such as the great white shark may have up to 3,000 teeth in its mouth, arranged in 6 to 20 rows. Only the first row or two are actively used for feeding; the other rows are replacement teeth.

Three well-developed senses enable sharks and rays to detect their prey. They have the ability to sense electric currents in water—even those generated by the muscle movements of animals. They have a lateral line system, a series of pressure-sensitive cells that lie within canals along both sides of the body, which can sense pressure caused by a fish or other animal swimming nearby. They also have a very



a. Sand tiger shark, *Carcharias taurus*



b. Blue-spotted stingray, *Taeniura lymma*

FIGURE 29.6 Cartilaginous fishes.

a. Sharks are predators or scavengers that move gracefully through open ocean waters. b. Most stingrays grovel in the sand, feeding on bottom-dwelling invertebrates. This blue-spotted stingray is protected by the spine on its whiplike tail.

keen sense of smell; the part of the brain associated with this sense is very well developed. Sharks can detect about one drop of blood in 115 liters of water.

The largest sharks are filter feeders, not predators. The basking sharks and whale sharks ingest tons of small crustaceans, collectively called krill. Many sharks are fast-swimming predators in the open sea (Fig. 29.6a). The great white shark, about 7 m in length, feeds regularly on dolphins, sea lions, and seals. Humans are normally not attacked except when mistaken for sharks' usual prey. Tiger sharks, so named because the young have dark bands, reach 6 m in length and are unquestionably one of the most predaceous sharks. As it swims through the water, a tiger shark will swallow anything, including rolls of tar paper, shoes, gasoline cans, paint cans, and even human parts. The number of bull shark attacks has increased in the Gulf of Mexico

in recent years. This is due to more swimmers in the shallow waters and loss of the sharks' natural food supply.

In rays and skates (Fig. 29.6b), the pectoral fins are greatly enlarged into a pair of large, winglike fins, and the bodies are dorsoventrally flattened. The spiracles are enlarged and allow them to move water over the gills while resting on the bottom, where they feed on organisms such as crustaceans, small fishes, and molluscs.

Stingrays have a whiplike tail that has serrated spines with venom glands at the base. These animals can deliver a painful "sting." Manta rays are harmless oceanic filter-feeding giants with a fin span of up to 6 m and a weight of 2,000 kg. Sawfish rays are named for their large, protruding anterior "saw." Some species of stingrays can deliver an electric shock. Their large electric organs, located at the base of their pectoral fins, can discharge over 300 volts. Skates resemble stingrays but possess two dorsal fins and a caudal fin.

The chimaeras, or ratfishes, are a group of cartilaginous fishes that live in cold marine waters. They are known for their unusual shape and iridescent colors.

Bony Fishes

The majority of living vertebrates, approximately 25,000 species, are **bony fishes (Osteichthyes)**. The bony fishes range in size from gobies, which are less than 7.5 mm long, to the giant sturgeons, which can obtain a length of 4 m.

The majority of fish species are **ray-finned bony fishes** with fan-shaped fins supported by a thin, bony ray. These fishes are the most successful and diverse of all the vertebrates (Fig. 29.7). Some, such as herrings, are filter feeders; others, such as trout, are opportunists; and still others are predaceous carnivores, such as piranhas and barracudas.

Despite their diversity, bony fishes have many features in common. They lack external gill slits and, instead, their gills are covered by an **operculum**. Many bony fishes have a **swim bladder**, a gas-filled sac into which they can secrete gases or from which they can absorb gases, altering its pressure. This results in a change in the fishes' buoyancy and, therefore, their depth in the water. Bony fishes have a single-loop, closed cardiovascular system (see Fig. 29.9a). The nervous system and brain in bony fishes are well developed, and complex behaviors are common. Bony fishes have separate sexes, and the majority of species undergo external fertilization after females deposit eggs and males deposit sperm into the water.

Lobe-Finned Fishes **Lobe-finned fishes** possess fleshy fins supported by bones. Ancestral lobe-finned fishes gave rise to modern-day lobe-finned fishes, the lungfishes, and the amphibians. **Lungfishes** have lungs and also gills for gas exchange. The lobe-finned fishes and lungfishes are grouped together as the **Sarcopterygii**. Today, there are only two species of lobe-finned fishes (the coelacanths) and six species of lungfish. Lungfishes live in Africa, South America, and Australia, either in stagnant fresh water or in ponds that dry up annually.