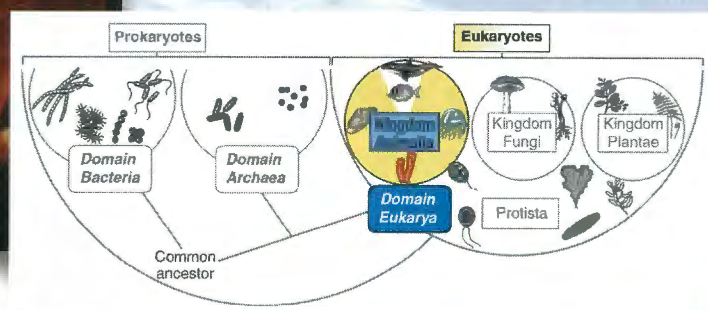
The crab *Trapezia flavopunctata* and its coral host, *Pocillopora*.

CHAPTER 7

Marine Animals Without a Backbone



Most species of multicellular organisms inhabiting our planet are **animals** (kingdom **Animalia**). In contrast to photosynthetic organisms like algae and plants, we animals cannot manufacture our own food and must therefore obtain it from others. The need to eat has resulted in the evolution of myriad ways of obtaining and processing food, as well as equally diverse ways of avoiding being eaten.

The colorful crab in the photo on this page is a good example. It inhabits reef-building corals, relying on them for food and shelter. The crabs feed on mucus, which the coral produces to keep its surface free from debris. The coral is also an animal, though it may not look like one. It gets some of its food from **zooxanthellae** that live in its tissues. The coral also eats small planktonic organisms that it captures by using stinging structures in its tentacles. Though an absent-minded crab is occasionally captured by a fish or an octopus, the crabs are usually safe among the coral branches. The crabs repay the favor by using their claws to drive away other animals that have a taste for coral tissue.

Our survey of the many kinds of marine animals follows the traditional classification into two major groups: the **vertebrates,** which have a **backbone** (a row of bones called **vertebrae**), and the **invertebrates,** animals without a backbone.

At least 97% of all species of animals are invertebrates. All major groups of invertebrates have marine representatives, and many are exclusively marine. Only a few groups have successfully invaded land. Were it not for one of these groups, the insects, we could boast without hesitation that most invertebrate species, and therefore most animals, are marine.

Zooxanthellae Dinoflagellates (single-celled algae) that live within animal tissues.
• Chapter 5, p. 96 Figure 14.1

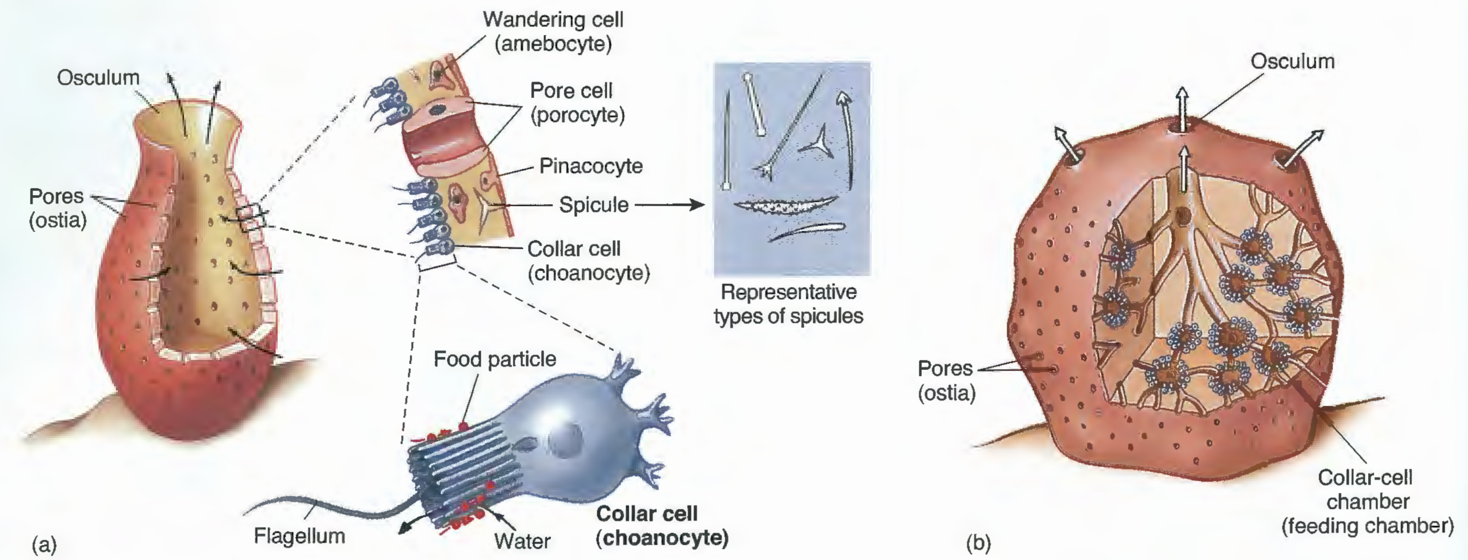


FIGURE 7.1 Sponges consist of complex aggregations of cells that carry out specific functions. Collar cells trap food particles in both (*a*) simple and (*b*) complex sponges.

SPONGES

Sponges are best described as aggregations of specialized cells. Sponges have a cellular level of organization, meaning that the cells are largely independent of each other and do not form true **tissues** and **organs** (see Table 7.1, p. 148). Sponges are among the structurally simplest multicellular animals (see Fig. 7.54).

Nearly all sponges are marine. All are **sessile,** living permanently attached to the bottom or some other surface. They show an amazing variety of shapes, sizes, and colors but share a relatively simple body plan. Numerous tiny pores, or **ostia,** on the surface allow water to enter and circulate through a series of canals where **plankton** and organic particles are filtered out and eaten (Fig. 7.1*a*). This network of canals and a relatively flexible skeletal framework give most sponges a characteristic spongy texture. Because of this unique body plan, sponges are classified as the phylum **Porifera,** or "pore bearers."

Sponges may be similar to the first multicellular animals, which were probably simple colonies in which some cells became specialized for such functions as feeding and protection. Sponge cells are very plastic and easily change from one type to another. If experimentally separated, the cells can even regroup and form a new sponge (Fig. 7.2).

The architecture of sponges is best understood by examining the simplest kind of sponge (Fig. 7.1*a*). The outer surface is covered with flat cells called **pinacocytes** and occasional tube-like **pore cells,** or **porocytes,** through which a microscopic canal allows water to enter. Water is pumped into a larger feeding chamber lined with **collar cells,** or **choanocytes.** Each choanocyte has a flagellum that creates currents and a thin collar that traps food particles, which are then ingested by the body of the cell. Water then leaves through the **osculum,** a large opening on top of the sponge.

Sponges are an example of **suspension feeders,** animals that eat food particles suspended in the water. Because sponges actively filter the food particles, they are a type of suspension feeder known as **filter feeders** (Fig. 7.3). In contrast, **deposit feeders** eat **detritus** that settles on the bottom.

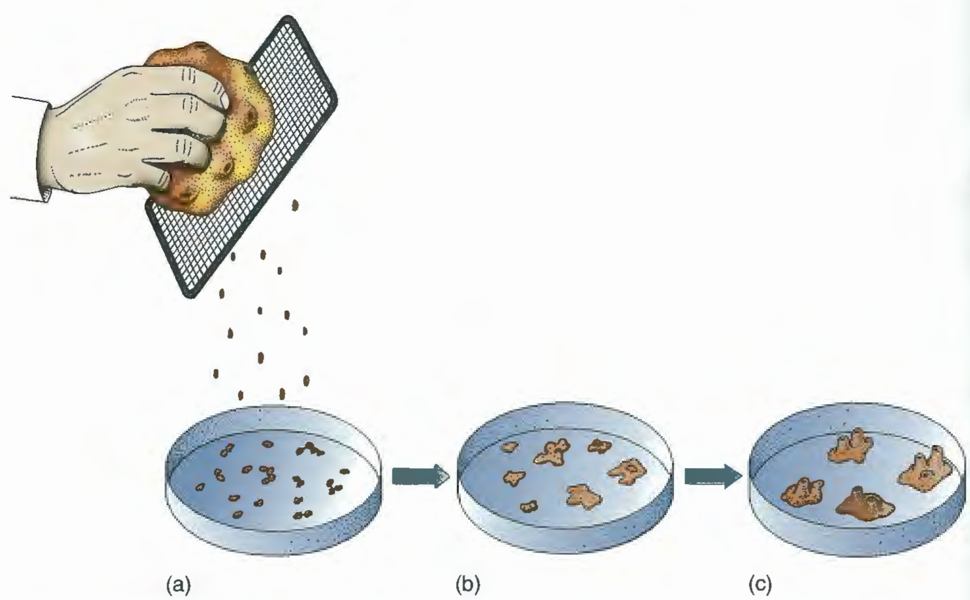


FIGURE 7.2 Some sponges form new individuals after their cells are separated from one another. The cells can be separated by squeezing pieces through a very fine sieve (*a*). In a matter of hours, the cells begin to aggregate and reorganize (*b*) and eventually form new sponges (*c*). When cells of different species are mixed, they generally reaggregate into their individual species.

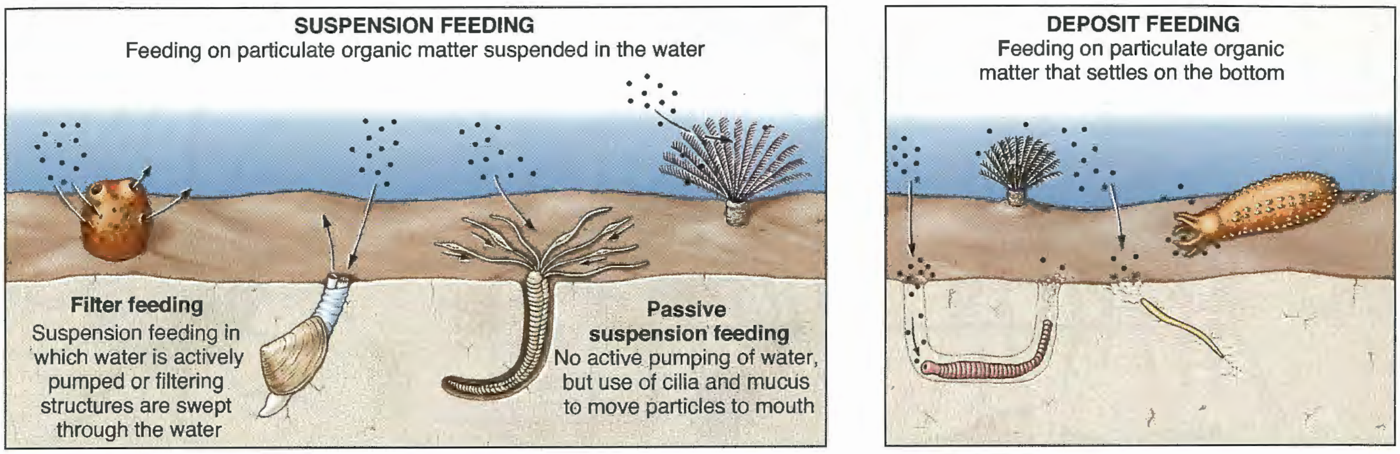


FIGURE 7.3 Feeding on particulate organic matter can be classified as suspension or deposit feeding. The difference between these two types of feeding is not always well defined. Fanworms, for instance, are tube-dwelling polychaetes that switch back and forth between suspension and deposit feeding, depending on the strength of the water current.

Most marine sponges show a more complex arrangement in which the collar cells are restricted to chambers connected to the outer pores by a network of canals (Fig. 7.1*b*). Water exits not through a single osculum but through several oscula, each of which serves as the exit for many canals. This increased complexity is associated with increased size, which demands higher water flow through the sponge and therefore a larger surface area of collar cells.

Sponges are among the structurally simplest multicellular animals, lacking true tissues and organs. They are mostly marine, living as attached filter feeders.

As sponges get larger, they need structural support. Most have **spicules,** transparent **siliceous** or **calcareous** supporting structures of different shapes and sizes (Fig. 7.1*a*). Many also have a skeleton of tough, elastic fibers made of a protein called **spongin.** Spongin may be the only means of support, or it may be found together with spicules. When present, spongin and spicules are mostly between the outer and inner layers of cells. Wandering cells, or **amebocytes,** secrete the spicules and spongin. Some of these wandering cells also transport and store food particles. Some can even transform themselves into other types of cells, quickly repairing any damage to the sponge.

Many sponges reproduce **asexually** when branches or buds break off (see Fig. 4.19*a*) and grow into separate sponges identical to the original one. Sponges also reproduce **sexually** by producing **gametes.** Unlike most animals, sponge gametes are not produced by **gonads.** Instead, specialized collar cells or amebocytes develop into gametes (Fig. 7.4). The gametes are like those of other animals: large, nutrient-rich eggs and smaller sperm cells that have a flagellum. Most sponges are **hermaphrodites,** animals in which individuals have both male and female gonads. Some species, however, have separate males and females, which is the case in many other invertebrates. Sponges typically release sperm into the water. The release of gametes into the water is called **broadcast spawning.** The eggs, however, are usually retained inside the body and fertilization takes place internally after sperm enter the sponge.

The early stages of development take place inside the sponge. Eventually, a tiny, flagellated sphere of cells is released into the water (Fig. 7.4). This planktonic **larva,** called the parenchymula larva in most sponges, is carried by currents until it settles on the bottom and develops into a minute sponge. Most marine invertebrates have characteristic larvae that eventually change into juveniles that resemble adults. This drastic change from the larva to the adult is called **metamorphosis** (Fig. 7.4).

Almost all the approximately 6,000 known species of sponges are marine. Sponges live from the poles to the tropics, but the largest number of species inhabits shallow tropical waters. Sponges may grow into branching, tubular (Fig. 7.5*a*), round, or volcano-like masses that sometimes reach a huge size. **Encrusting** sponges form thin, sometimes brightly colored growths on rocks or dead coral (Fig. 7.5*b*).

Glass sponges, such as the Venus flower basket sponge (*Euplectella*), live anchored in deep-water sediments and have a lace-like skeleton of fused siliceous spicules. **Boring sponges** (*Cliona*) bore thin channels through calcium carbonate, such as oyster shells

Tissues Specialized, coordinated groups of cells.
Organs Structures consisting of several types of tissues grouped together to carry out particular functions.
• Chapter 4, p. 70

Plankton Organisms that drift with the currents.
• Chapter 10, p. 220; Figure 10.11

Detritus Particles of dead organic matter.
• Chapter 10, p. 223

Siliceous Made of silica (SiO_2).
Calcareous Made of calcium carbonate ($CaCo_3$).
• Chapter 2, p. 32

Gametes Specialized reproductive cells with half the genetic complement of each parent, usually produced by organs called *gonads: sperm* (male gametes produced by the *testes*) and eggs (female gametes produced by the *ovaries*).
• Chapter 4, p. 77

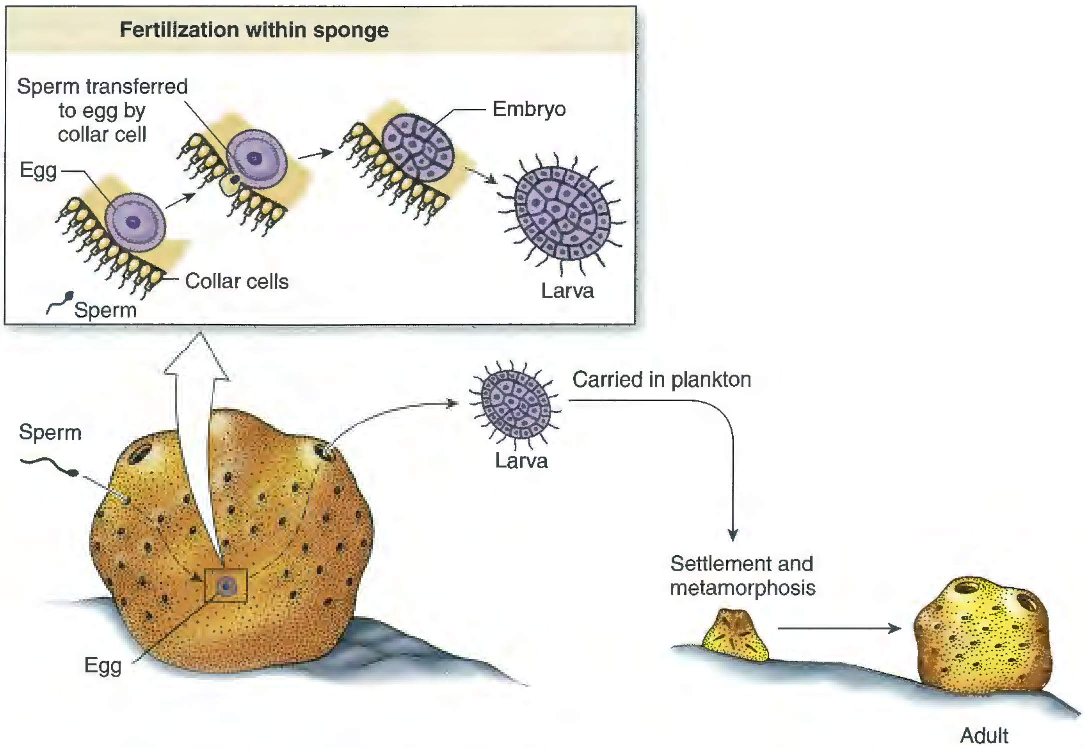
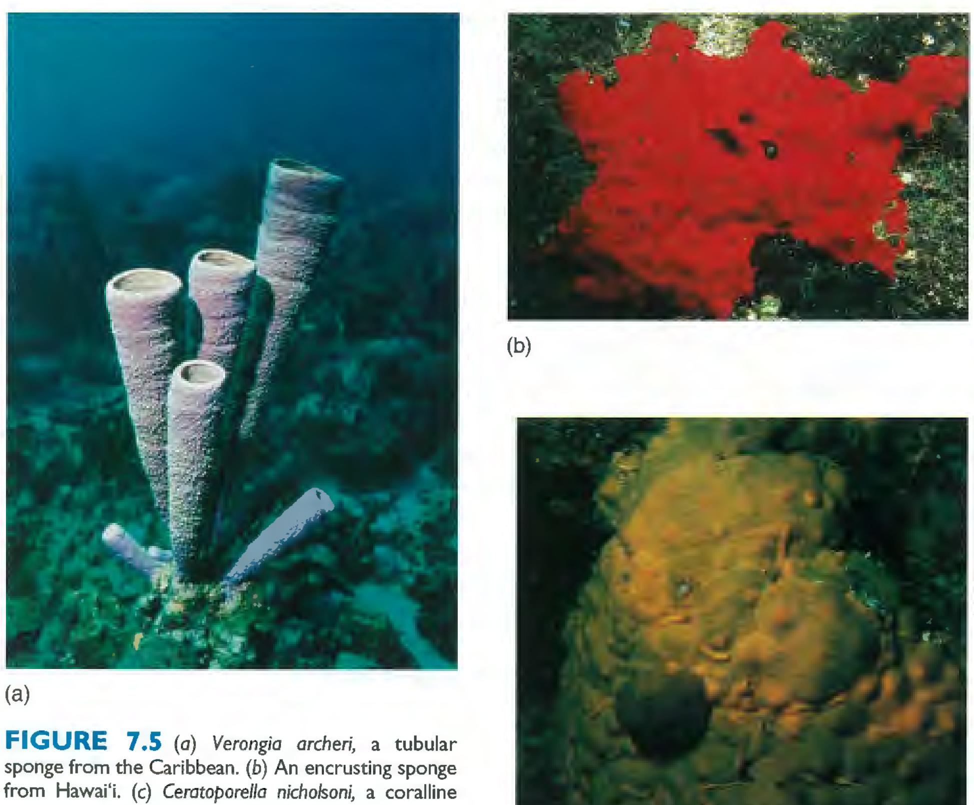


FIGURE 7.4 Sexual reproduction in many marine sponges involves fertilization within the sponge, development of the embryo into a larva, the release of a planktonic larva, and its eventual settlement and metamorphosis into a new sponge on the bottom.



(a)

(b)

(c)

FIGURE 7.5 (*a*) *Verongia archeri,* a tubular sponge from the Caribbean. (*b*) An encrusting sponge from Hawai'i. (*c*) *Ceratoporella nicholsoni,* a coralline sponge, or sclerosponge, photographed at a depth of 52 m (170 ft) in Puerto Rico. Also see Fig. 4.9.

and corals. In the **sclerosponges,** or **coralline sponges** (*Ceratoporella;* Fig. 7.5*c*), a calcium carbonate skeleton forms beneath the body of the sponge, which also contains siliceous spicules and spongin. Sclerosponges were first known as fossils, but living specimens were discovered in underwater caves and on steep coral reef slopes after the advent of scuba diving.

Some marine sponges are of commercial importance. Bath sponges (*Spongia*) are still harvested in a few locations in the Gulf of Mexico and the eastern Mediterranean in what remains of a once-flourishing industry. Bath sponges, not to be confused with synthetic sponges, consist of the spongin fibers remaining after cells and debris are washed away. Some marine sponges produce potentially useful chemicals (see "Take Two Sponges and Call Me in the Morning," p. 397).

CNIDARIANS: RADIAL SYMMETRY

The next level of organizational complexity among animals after the sponges involves quite a big step: the evolution of multicellular animals with tissues that perform specific functions. This development makes it possible for organisms to swim, respond to external stimuli, and engulf prey, among other things. **Cnidarians,** sometimes called **coelenterates** (phylum **Cnidaria**), include the sea anemones, jellyfishes, corals, and their relatives.

Besides having a tissue level of organization, cnidarians display **radial symmetry,** where similar parts of the body are arranged and

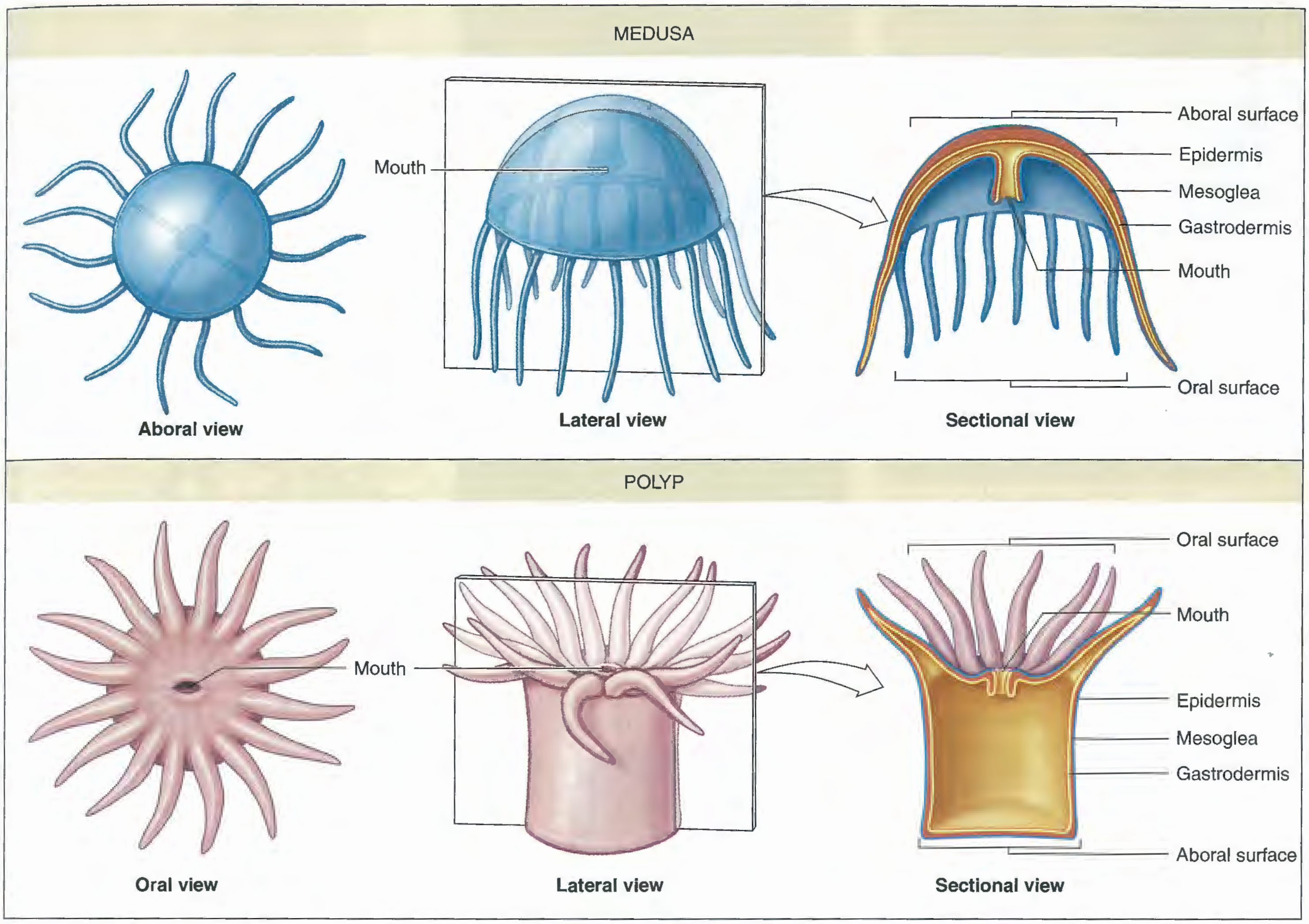


FIGURE 7.6 The flower-like appearance of many cnidarians is a consequence of their radial symmetry. In both the medusa and polyp, tentacles are arranged and repeated around a central axis that runs through the mouth.

repeated around a central axis (Figs. 7.6 and 7.13*a*). If a radially symmetrical animal were cut like a pizza, all the resulting slices would be similar. Animals with radial symmetry look the same from all sides and have no head, front, or back. They do, however, have an **oral surface,** where the mouth is, and an **aboral surface** on the opposite side (Fig. 7.6).

Cnidarians have a centrally located mouth surrounded by **tentacles,** slender, finger-like extensions used to capture and handle food. The mouth opens into a **gut,** where food is digested. The cnidarian gut is a blind cavity with only one opening, the mouth. Cnidarians capture small prey by discharging their **nematocysts** (or cnidae), unique stinging structures found within **cnidocytes,** specialized cells in the tentacles (see Fig. 7.8).

Cnidarians occur in two basic forms (Fig. 7.6): a **polyp,** a sac-like attached stage with the mouth and tentacles oriented upward, and a bell-like **medusa,** or jellyfish, which is like an upside-down polyp adapted for swimming. The life history of some cnidarians includes both polyp and medusa stages. Others spend their entire lives as either polyp or medusa.

The characteristic larva of most cnidarians is the **planula,** a cylindrical, ciliated stage consisting of two layers of cells. After a time in the plankton, the planula settles on the bottom and metamorphoses into a polyp or develops into a medusa.

The radially symmetrical cnidarians have unique stinging structures, nematocysts, that are used to capture prey. Cnidarians exist as either polyps or medusae, or both in alternation. Most have a planula larva.

Two layers of cells form the body wall of cnidarians. One of these, the **epidermis** (see Figs. 7.6 and 7.9), is external, whereas the other, the **gastrodermis,** lines the gut. There is also a narrow, gelatinous middle layer, or **mesoglea,** that usually doesn't contain cells. In medusae this layer is expanded to form a gelatinous, domed bell, hence their common name of jellyfish.

Types of Cnidarians

The basic cnidarian body plan, though structurally simple, has been very successful. Some 10,000 species are known, almost all of which are marine.

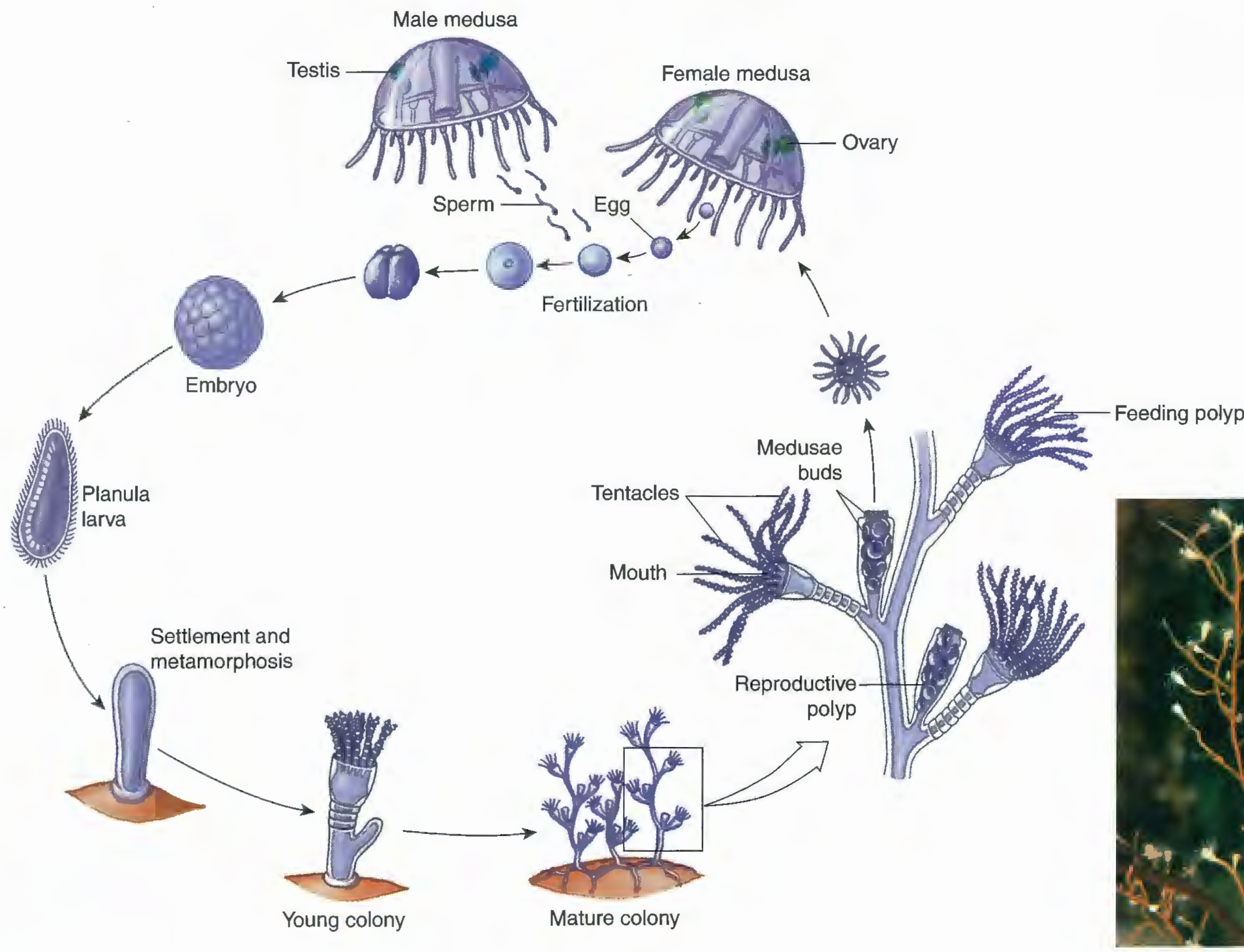
Hydrozoans The **hydrozoans** (class **Hydrozoa**) have a wide range of forms and life histories. Many consist of feathery or bushy colonies of tiny polyps. They attach to pilings, shells, seaweeds, and other surfaces (Fig. 7.7). The polyps may be specialized for feeding, defense, or reproduction.

Reproductive polyps produce minute, transparent medusae (Fig. 7.8). These medusae, usually planktonic, release gametes into the water. The fertilized eggs develop into free-swimming planula larvae. Each planula settles on the bottom and develops into a polyp. This first polyp divides repeatedly and develops into a colony of many interconnected polyps. There are, however, several variations of this life cycle. For instance, some hydrozoans lack a polyp stage, and instead their planula develops into a medusa. A few lack a medusa stage, and instead the polyp produces gametes directly.

FIGURE 7.7 Colonial hydrozoans include this feather-like colony of the hydroid *Macrorhynchia phillipina.* It is a common species in warm and some temperate waters around the world.

Siphonophores are hydrozoans that form drifting colonies of polyps. Some polyps in a siphonophore colony may be specialized as floats, which may be gas-filled, as in the Portuguese man-of-war (*Physalia physalis;* Fig. 7.9), or contain droplets of oil. Other siphonophore polyps form long tentacles used to capture prey. Toxins from the nematocysts can produce painful reactions in swimmers or divers.

Scyphozoans The larger jellyfishes common in all oceans are quite different from the often tiny hydrozoan medusae. These large medusae (Fig. 7.10) are the dominant stage of the life cycle of **scyphozoans** (class **Scyphozoa**). The polyps of scyphozoans are very small and release juvenile medusae. A few species lack a polyp stage altogether. The rounded body, or **bell,** of some scyphozoan medusae may reach a diameter of 3 m (10 ft) across in a recently discovered



Eudendrium, worldwide

FIGURE 7.8 The life cycles of hydrozoans follow different patterns. A common one involves a sessile, asexually reproducing colony of polyps that releases planktonic, sexually reproducing medusae.

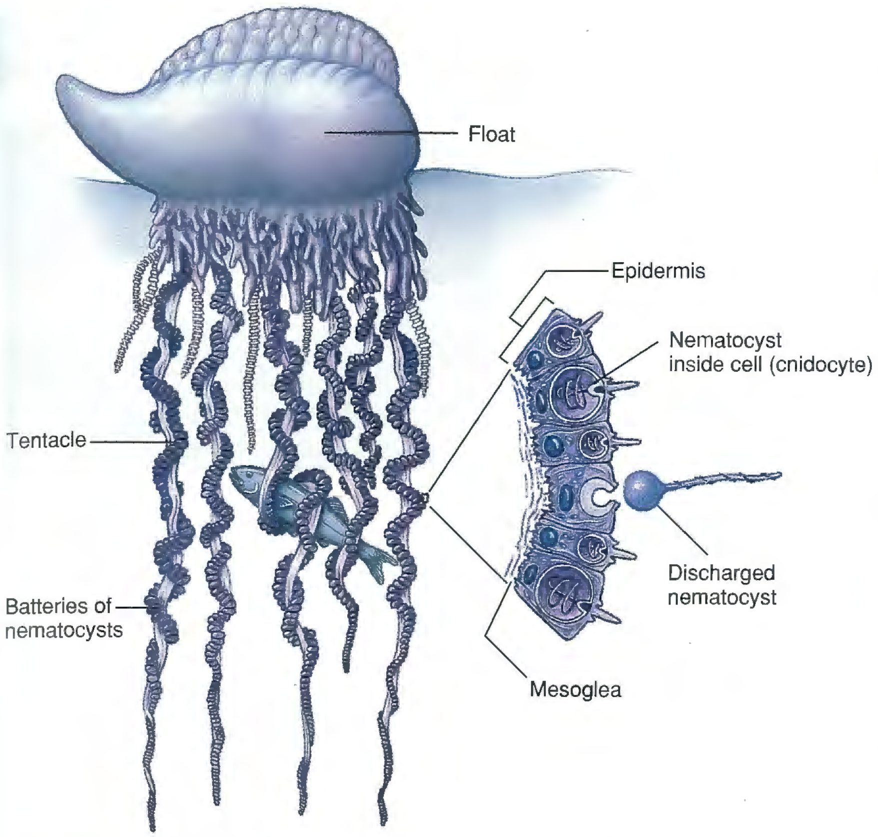


FIGURE 7.9 A diagrammatic representation of the Portuguese man-of-war (*Physalia physalis*). It consists of a colony of specialized polyps, one of which forms a gas-filled float that may reach 30 cm (12 in) in length. The long tentacles, here contracted, are armed with nematocysts notorious for their ability to sting swimmers.

FIGURE 7.10 Scyphozoan medusae are larger and more complex than hydrozoan medusae. This example is the sea nettle (*Chrysaora quinquecirrha*), which is found from Cape Cod to the Gulf of Mexico. It is especially common in Chesapeake Bay.

deep-water species. Scyphozoans swim with rhythmic contractions of the bell, but their swimming ability is limited and they are easily carried by currents. Some scyphozoan medusae are among the most dangerous marine animals known, giving extremely painful and sometimes fatal stings. This is particularly true of cubomedusae, once classified as scyphozoans but now placed in their own group, the class **Cubozoa** (see "The Case of the Killer Cnidarians," p. 122).

Anthozoans Most cnidarian species are **anthozoans** (class **Anthozoa**), solitary or colonial polyps that lack a medusa stage. The anthozoan polyp is more complex than hydrozoan or scyphozoan polyps. The gut, for instance, contains several thin partitions, or **septa** (see Fig. 14.2), which provide additional surface area for the digestion of large prey. Septa also provide support, which allows the polyp to be larger than the polyps of other cnidarians. **Sea anemones** are common and colorful anthozoans that often have large polyps (see Fig. 11.26). Colonial anthozoans occur in an almost infinite variety of shapes. **Corals** include various groups of mostly colonial anthozoans (see Table 14.1, p. 304). Many of these have calcium carbonate skeletons and, though such corals occur in cold waters, in tropical waters they often form **coral reefs. Gorgonians,** such as sea fans (Fig. 7.11), are colonial anthozoans that secrete a tough, branching skeleton made in part of protein. **Precious corals** are gorgonians with fused red or pink calcareous spicules in addition to the protein skeleton. **Black corals,** which are neither gorgonians nor stony corals, secrete a hard, black, protein skeleton. Both precious and black corals are carved into jewelry. Some anthozoans form fleshy colonies with large polyps and no hard skeletons. Examples of these are the soft corals, sea pens (see Fig. 13.13), and sea pansies.

FIGURE 7.11 Sea fans are gorgonians with branches that grow in only one plane and have many cross-connections.

Biology of Cnidarians

The presence of tissues allows cnidarians to perform more complex functions than sponges can. In particular, cnidarians display advances in feeding and can sense and respond to their environment.

Feeding and Digestion Practically all cnidarians are **carnivores,** animals that prey on other animals. Many capture and digest prey much bigger than that of filter feeders such as sponges. Cnidarians use their nematocysts primarily to capture prey. Each nematocyst consists of a fluid-filled capsule containing a thread that can be quickly ejected (see Fig. 7.9). The thread may be sticky or armed with spines, or it may be a long tube that wraps around parts of the prey. Some nematocysts contain toxins.

The Case of the Killer Cnidarians

The stings of most cnidarians are harmless to humans, but there are exceptions. Delicate and innocent-looking, some cnidarians are among the most dangerous marine animals. The sinister side of these creatures is due to the potent toxins released by their nematocysts.

The Portuguese man-of-war (*Physalia*), a siphonophore, is found in warm waters around the world. Though its blue, sail-like float can be seen fairly easily, its long tentacles are nearly invisible. Armed with thick batteries of nematocysts, these tentacles may reach 50 m (165 ft) in length. Portuguese men-of-war may occur by the thousands, sometimes forcing the closure of beaches. Pieces of tentacle that wash ashore can be as nasty as the whole animal.

Physalia stings are very painful, like being repeatedly burned with a hot charcoal. The pain may last for hours, especially if sensitive areas of the body are affected. Red lines appear wherever tentacles have touched the skin, and welts usually follow. Both of the authors have had encounters with *Physalia*, painful but fortunately less severe than the experiences of others. One of us saw a man get stung on the hand. When the wave of intense pain reached his armpit, the man passed out. Even more severe reactions may occur. There can be nausea and difficulty in breathing. Contact of tentacles with the eye may damage the cornea. Allergic reactions to the toxin may cause shock and even death, and swimmers may drown because of pain or shock.

If you are stung, the best thing to do is not to panic. Carefully wash the area with seawater, but don't rub the area or wash with fresh water because this stimulates firing of the nematocysts. Vinegar and alcohol will inactivate the nematocysts. Urine may be useful if nothing else is available. The toxin is a protein, and some recommend papain, a protein-digesting enzyme found in meat tenderizer. The meat tenderizer is of little help, however, because the poison is injected into the skin while the meat tenderizer remains on the surface. Severe reactions should be treated in a hospital.

A group of medusae, the cubomedusae, release even more powerful toxins. The sea wasp, or box jellyfish, *Chironex fleckeri*, of northern Australia, Southeast Asia, and the Indian Ocean, has been responsible for many known deaths. Its stings cause immediate, extreme pain. Death due to heart failure may follow within minutes, especially in children. Skin that touches the tentacles swells up, and the purple or dark brown lines that are left are slow to heal. Fortunately, an antivenin ("antivenom") has been developed. Otherwise, the recommended first aid is to dowse the sting with vinegar.

The sting of *Chiropsalmus*, a cubomedusa.

There are other tropical cubomedusae that give severe stings, particularly in Australia and the West Indies. The irukandji (*Carukia barnesi*) of northern Australia have caused several deaths in recent years. Unlike the sea wasp, irukandji normally live offshore but currents occasionally sweep them into shallow water.

Cubomedusae are more common along the shore during summer. Their transparent, almost square bells are difficult to see in the water. Most are small, but in the sea wasp the bell may reach 25 cm (almost 10 in) in diameter, and the tentacles may stretch to 4.5 m (15 ft). Irukandji have a bell only 2.5 cm (1 in) in diameter and four tentacles of about the same length, so they are almost impossible to spot in the water.

After ingestion, food passes into the gut, where it is digested. The initial phase of digestion is said to be **extracellular** because it takes place outside cells. **Intracellular digestion** within cells lining the gut completes the breakdown of food.

Behavior Though cnidarians lack a brain or true nerves, they do have specialized **nerve cells.** These cells interconnect to form a **nerve net** that transmits impulses in all directions. This simple nervous system can produce some relatively sophisticated behaviors. Some anemones can tell whether other members of the same species are also members of the same clone, a group of genetically identical individuals. They are known to attack and even kill anemones from other clones using special nematocysts. Some medusae have primitive eyes. Medusae also have **statocysts,** small, calcareous bodies in fluid-filled chambers surrounded by sensitive hairs. Statocysts give medusae a sense of balance.

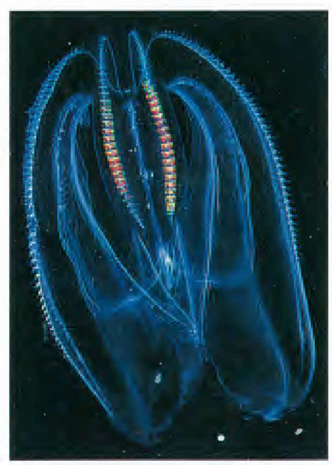


FIGURE 7.12 This comb jelly (*Mnemiopsis leidyi*) displays the rows of ciliary combs characteristic of the group. Four rows are visible here, the middle ones appearing as multicolored bands. The species is common along the Atlantic coast of North America but it has been accidentally introduced into other locations.

COMB JELLIES: RADIAL SYMMETRY REVISITED

The **comb jellies,** or **ctenophores** (phylum **Ctenophora**), are an exclusively marine group of about 100 species. Their radially symmetrical and gelatinous body resembles that of a medusa (Fig. 7.12), but a closer look reveals some unique traits. Ctenophores swim with eight rows of **ciliary combs,** long cilia fused at the base, like combs, that beat in waves. The continuous beating of the ciliary combs refracts light, creating a prism-like, multicolor effect. Body length varies from a few millimeters in the sea gooseberry (*Pleurobrachia*) to 2 m (6.6 ft) in the elongated Venus's girdle (*Cestum;* see Fig. 15.12*c*).

Comb jellies, or ctenophores, are radially symmetrical and similar in appearance to cnidarians but possess eight rows of ciliary combs.

Comb jellies are common in both warm and cold waters. They are carnivores with a voracious appetite. Swarms of comb jellies may consume large numbers of fish larvae and other plankton (see "Biological Invasions: The Uninvited Guests," p. 414). Many capture their prey using two long tentacles armed with sticky cells named **colloblasts.** A few species have nematocysts, possibly obtained by eating jellyfishes or siphonophores.

BILATERALLY SYMMETRICAL WORMS

Radial symmetry works fairly well in animals that attach to surfaces or drift in currents, but animals that crawl or swim in one direction have different needs. Most animals show **bilateral symmetry,** the arrangement of body parts in such a way that there is only one way to cut the body and get two identical halves (Fig. 7.13*b*). Bilaterally symmetrical animals, including humans, have a front, or **anterior,** end and a rear, or **posterior,** end. At the anterior end is a head with a brain, or at least an accumulation of nerve cells, and sensory organs such as eyes. Similarly, bilaterally symmetrical animals have a back, or **dorsal** surface, that is different from the belly, or **ventral** surface. Bilateral symmetry allows animals to be more active in the pursuit of prey and to develop more sophisticated behaviors than those of radially symmetrical animals.

Flatworms

The structurally simplest bilaterally symmetrical body plan is seen in the **flatworms** (phylum **Platyhelminthes**), so called because they are dorsoventrally flattened—that is, they have flat backs and bellies. Flatworms also are the simplest animals in which tissues are organized into real organs and organ systems.

The presence of a **central nervous system** in which information is stored and processed is of special significance. In flatworms it typically consists of a simple **brain,** which is just an aggregation of nerve cells in the head. There are also several nerve cords running from the brain through the length of the worm. The nervous system coordinates the movements of a well-developed muscular system. The gut is similar to those of cnidarians and ctenophores in having only one opening to the outside, the mouth. The space between the outer and inner tissue layers, however, is no longer thin or gelatinous as in cnidarians and ctenophores but is filled with tissue. In developing embryos this middle layer of tissue, the **mesoderm,** gives rise to muscles, the reproductive system, and other organs—not only in flatworms but also in structurally more complex animals. The gut and other internal organs are surrounded by tissue, since there is no body cavity.

Flatworms are bilaterally symmetrical invertebrates typically flattened in appearance. They have true organs and organ systems, including a central nervous system.

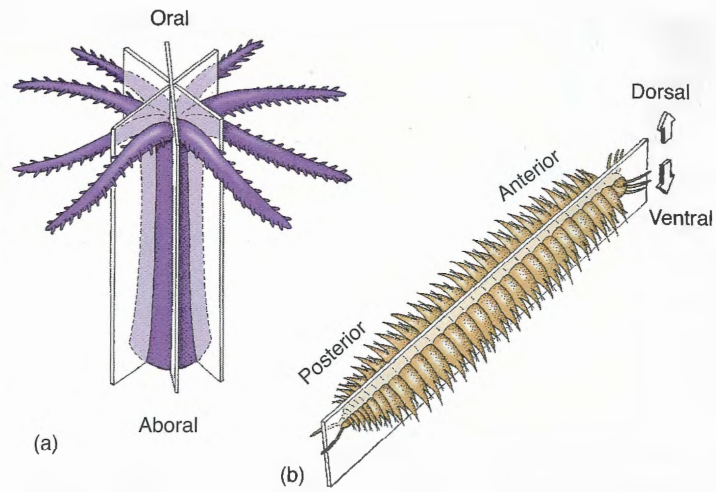


FIGURE 7.13 The radial symmetry of a soft coral's polyp (*a*) in contrast to the bilateral symmetry of a worm (*b*). Bilateral symmetry implies the development of an anterior end with a head, a brain, eyes, and all the other features demanded by more complex behaviors.

There are some 20,000 known species of flatworms. The most commonly seen marine flatworms are the **turbellarians,** a group that consists mostly of free-living carnivores. Most are small, but some are obvious because of their striking color patterns (Fig. 7.14). Some turbellarians live inside or on the surface of oysters, crabs, and other invertebrates.

Flukes, or **trematodes,** are the largest group of flatworms, with more than 6,000 species. All flukes are **parasites,** which live in close association with other animals and feed on their tissues, blood, or intestinal contents. Like most parasites, flukes have complex life histories with amazing reproductive abilities, a key to their success. Adult flukes always live in a vertebrate. The larvae may inhabit invertebrates like snails or clams or vertebrates like fish. The larva must then be eaten by the vertebrate destined to harbor the adult. Flukes are common in fishes, seabirds, and whales.

Tapeworms, or **cestodes,** are parasitic flatworms that, with a few exceptions, have a long body consisting of repeated units. These unique worms live inside the intestine of most species of vertebrates, including marine ones. The head of the worm attaches to the walls of the gut by suckers, hooks, or other structures. Tapeworms lack a gut or mouth. They absorb nutrients from their host's intestinal contents directly across the body wall. Their larvae are found in invertebrates or vertebrates. Tapeworms may reach a prodigious length. The record appears to be a species found in sperm whales that is 15 m (50 ft) long!

Ribbon Worms

Though they look like long flatworms, **ribbon,** or **nemertean, worms** (phylum **Nemertea**) show several features that indicate a more complex degree of organization. Their digestive tract is complete, with a gut that includes a mouth and an anus to get rid of undigested material. They also have a **circulatory system,** by which blood transports nutrients and oxygen to tissues. The most distinctive feature of ribbon worms, however, is their **proboscis**

(a)

(b)

FIGURE 7.14 (*a*) A turbellarian flatworm (*Pseudobiceros gratus*) from Australia's Great Barrier Reef. (*b*) Turbellarian flatworms (*Pseudoceros bifurcus*) joust in a mating ritual known as penis fencing. The worms are hermaphrodites, and each tries to penetrate the skin of the other with its needle-like penis to inject its sperm. The first to succeed acts as the male and avoids the energy costs of healing the wound and developing eggs.

FIGURE 7.15 Ribbon, or nemertean, worms use a proboscis to entangle prey. The proboscis secretes toxins and may be armed at the tip with a spine. Once the prey is captured, the proboscis is pulled back and it's dinnertime.

(Fig. 7.15), a long, fleshy tube used to entangle prey. It is everted from a cavity above the mouth like the finger of a glove. All ribbon worms are predators that feed on worms and crustaceans.

There are approximately 900 species of ribbon worms, most of which are marine. They are found in all oceans but are most common in shallow temperate waters. Some are nocturnal and not easily seen; others are brightly colored and may be found under rocks at low tide. Ribbon worms are incredibly elastic, and the proboscis may extend a meter or more beyond the body. One species reaches 30 m (100 ft) long, which makes it the longest invertebrate on earth.

Nematodes

Nematodes (phylum **Nematoda**), some of which are known as **roundworms,** are hardly ever seen, but their numbers in sediments, particularly those rich in organic matter, can be staggering. Many species are parasitic, and most groups of marine organisms have nematode parasites. Nematodes are perfectly adapted to live in sediments or the tissues of other organisms. They are mostly small, with slender and cylindrical bodies that are typically pointed at both ends (see the figure in "Life in Mud and Sand," p. 291). Nematodes that inhabit sediments feed mostly on bacteria and organic matter. The gut, which ends in an anus, lies within a **body cavity** filled with fluid that transports nutrients. A layer of muscles in the tough but flexible body wall pushes and squeezes against the fluid, which acts as a **hydrostatic skeleton** that provides support and aids in locomotion.

Nematodes are very common inhabitants of marine sediments and are widespread parasites of most groups of marine animals.

The actual number of species of nematodes is debatable. Estimates vary between 10,000 and 25,000 species, but some biologists believe there may be as many as half a million remaining to be discovered.

The adults of *Anisakis* and a few related nematodes inhabit the intestine of seals and dolphins. Their larvae, however, are found in the flesh of many types of fish and may infect humans who eat raw or poorly cooked fish. Often the larvae are vomited or coughed up without further complications. Sometimes, however, larvae penetrate into the walls of the stomach or intestine, causing symptoms similar to those of ulcers. It is a risk that lovers of raw fish dishes such as *sashimi* and *ceviche* must take.

Segmented Worms

A large group of perhaps as many as 20,000 species, the **segmented worms,** or **annelids** (phylum **Annelida**), includes earthworms and many marine worms. Their body plan includes innovations that have been incorporated in some of the more structurally complex groups of animals. The body consists of a series of similar compartments, or **segments,** a condition known as **segmentation.** Segmentation can be clearly seen in the rings of the familiar earthworm. The gut goes through all the segments and lies in a cavity known as a **coelom** (Fig. 7.16*c*). The coelom is entirely surrounded by a different type of tissue, which develops from mesoderm in contrast to the simpler body cavity of nematodes. It is present in all of the remaining structurally complex phyla. The coelom of segmented worms is filled with fluid and divided by partitions that correspond to the external segments. The segments act as a hydrostatic skeleton and can be contracted in sequence by means of muscles in the body wall. **Longitudinal muscles** (Fig. 7.16*c*) lengthen and shorten the segments, whereas **circular muscles** increase or reduce their diameter. These movements, plus the flexibility given by segmentation, make annelids efficient crawlers and burrowers.

Polychaetes Almost all marine annelids are **polychaetes** (class **Polychaeta**), which are common and important in many environments. Each of the body segments of most polychaetes has a pair of flattened extensions, or **parapodia,** which are provided with stiff and sometimes sharp bristles, or **setae** (Fig. 7.16).

Annelids have a body consisting of similar segments and a coelom. Most marine annelids are polychaetes, segmented worms that have parapodia.

Like all annelids, polychaetes have a circulatory system that transports nutrients, oxygen, and carbon dioxide. Circulating blood always remains within distinct blood vessels (Fig. 7.16*c*), making it a **closed circulatory system.** Muscular contraction of vessels helps in the circulation of blood. Wastes from the coelom are removed by a pair of **excretory organs** in each segment (Fig. 7.16*c*).

In small animals, oxygen—essential in the release of energy through **respiration**—can easily move from the water across the body wall to all the tissues. In the larger and relatively more active polychaetes, however, obtaining enough oxygen from the water is

Respiration
organic matter + $O_2 \rightarrow CO_2 + H_2O$ + energy
(glucose)
• Chapter 4, p. 67

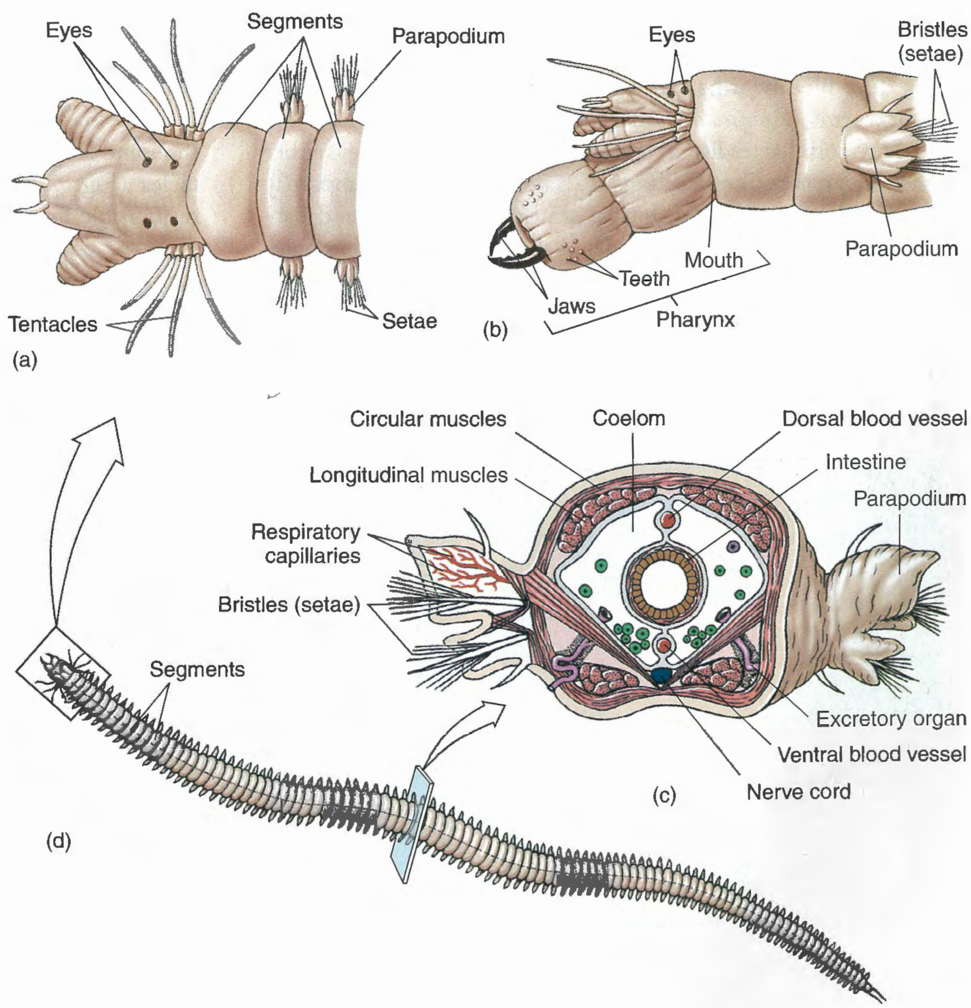


FIGURE 7.16 This sandworm (*Nereis*) illustrates the meaning of the name polychaetes—"many setae, or bristles." (*a*) Dorsal view of the head, with the pharynx retracted, showing the sensory tentacles and eyes. (*b*) Side view of the head, showing the large pharynx in an extended position. (*c*) Section across a segment. (*d*) Dorsal view of the worm.

a potential problem. Polychaetes have solved this problem by evolving **gills** on the parapodia or elsewhere (Fig. 7.16*a*). The gills are thin-walled extensions of the body wall that have many blood vessels called **capillaries,** which allow for the easy absorption of oxygen. Capillaries may also be found on the walls of the parapodia (Fig. 7.16*c*). This absorption of oxygen, along with the elimination of carbon dioxide, is known as **gas,** or **respiratory, exchange.**

The life history of many polychaetes involves a planktonic larval stage known as the **trochophore,** which has a band of cilia around the body (see Fig. 15.11*d*). The trochophore is of considerable interest because it is also one of the larval stages in some other groups of invertebrates. The types of larvae, among other characters, are used by biologists to deduce evolutionary relationships among different groups of invertebrates.

The more than 10,000 species of polychaetes are almost entirely marine. Length varies a great deal but is typically 5 to 10 cm (2 to 4 in). Many polychaetes crawl on the bottom, hiding under rocks or coral. These crawling worms, such as most sandworms (*Nereis*), are mostly carnivores. They feature heads provided with several pairs of eyes and other sense organs (see Fig. 7.16) used to search for small invertebrates. A proboscis, often armed with jaws, is used to capture prey. The parapodia are well developed and are used in locomotion.

Other polychaetes burrow in mud or sand (see Fig. 11.31). Many, like bloodworms (*Glycera*), capture small prey. Others, like lugworms (*Arenicola*), are deposit feeders (see Fig. 7.3).

Many polychaetes live in temporary or permanent tubes, either singly or in aggregations (see Figs. 12.11 and 13.6). The tubes may be made of mucus, protein, bits of seaweed, cemented mud particles, sand grains, or tiny fragments of shells. Tube-dwelling polychaetes usually have reduced parapodia. Some, such as *Terebella* and related forms (see Fig. 13.11), are suspension feeders. Their tentacles have cilia and mucus that catch organic particles in the water and move them to the mouth (see Fig. 7.3). Fanworms, or feather-duster worms (*Sabella;* Fig. 7.17*b*), use feathery tentacles covered with cilia to capture, sort, and transport particles. Serpulids (*Serpula*) and spirorbids (*Spirorbis*), also suspension feeders, extend feather-like tentacles from calcium carbonate tubes they build on rocks and other surfaces (see Fig. 13.17).

Polychaetes are also successful at other lifestyles. Species of *Tomopteris* are planktonic throughout life. Their parapodia are flat and expanded to help in swimming (see Fig. 15.12*d*). In the tropical Pacific the bodies of the Palolo worm (*Eunice*) periodically break off, and the posterior half swims up to the surface to spawn. This behavior, known as **swarming,** is timed in some areas with the phases of the moon, reaching its peak just after full moon. This bit of information is useful because in some places people gather the worms for food.

Some polychaetes live on the external surface of such invertebrates as sea stars and sea urchins. Several species live in the burrows of other invertebrates or inhabit shells occupied by hermit crabs.

Beard worms, or **pogonophorans,** are highly specialized annelids. They lack a mouth and gut. Except for sponges and tapeworms, this phenomenon is uncommon in animals. A tuft of one to many thousand long tentacles (Fig. 7.18), responsible for the group's common name, appears to be involved in absorbing nutrients

FIGURE 7.17 Polychaetes are common inhabitants of most marine bottoms. (*a*) The anterior end of a free-living polychaete (*Hermodice carunculata*), a fireworm that feeds on corals. The bright red structures are gills. (*b*) *Sabella melanostigma,* a feather-duster worm, inhabits leathery tubes.

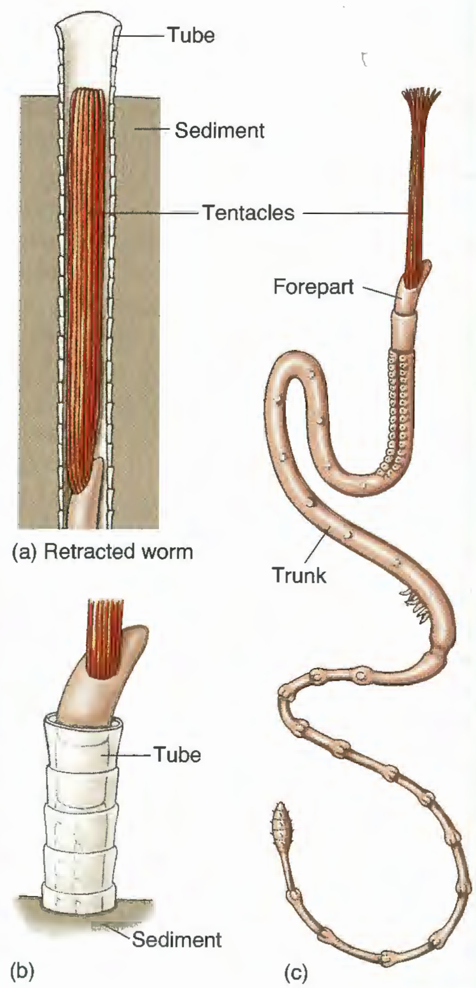


FIGURE 7.18 Diagrammatic representation of a beard worm, or pogonophoran. (*a*) Most secrete and live in tubes buried in the soft sediment. (*b*) Only the upper end of the tube protrudes, with the tentacle or tentacles extending from it. (*c*) Worm removed from its tube.

dissolved in the water. Some beard worms have **symbiotic** bacteria that use the nutrients to manufacture food, which in turn is used by the worms.

Approximately 135 species of beard worms are known. They are mostly restricted to deep water, which helps explain why they remained unknown until 1900. Beard worms were once grouped as a separate phylum (see "How to Discover a New Phylum," p. 128). The total length of the worms ranges from 10 cm to 2 m (4 in. to 7 ft). A group related to beard worms, the **vestimentiferans,** are even longer. Large numbers of these worms have been found at hydrothermal vents (see Figs. 16.28 and 16.29).

Oligochaetes **Oligochaetes** are small worms found in mud and sand (see "Life in Mud and Sand," p. 291), where they feed on detritus. They are the marine relatives of earthworms. Some species may be very abundant. Unlike most polychaetes, oligochaetes lack parapodia.

Leeches Bloodsucking **leeches** (class **Hirudinea**) live mostly in fresh water, but marine species can be found attached to marine fishes and invertebrates. Leeches are highly specialized annelids distinguished by a sucker at each end and no parapodia.

Peanut Worms

Often called **peanut worms,** the **sipunculans** (phylum **Sipuncula**) have soft, unsegmented bodies with a coelom. They burrow in muddy bottoms, rocks, and corals or hide in empty shells. All are marine, living mostly in shallow water. The long anterior portion contains a mouth and a set of small lobes or branching tentacles (Fig. 7.19). These can be pulled into the remaining portion of the body, and the worm then becomes a compact bundle that looks like a large peanut. Peanut worms are 1 to 35 cm (0.4 to 14 in) long. Approximately 320 species are known, all deposit feeders.

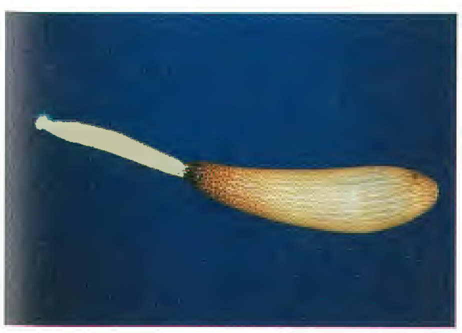


FIGURE 7.19 *Antillesoma antillarum*, a peanut worm (or sipunculan), burrows in coral and rocks in the Caribbean. The anterior portion, which is extended in this specimen, can be retracted.

Echiurans

All of the 135 known species of **echiurans** (phylum **Echiura**) are marine. They look like soft, unsegmented sausages buried in the mud or in coral. They are similar to peanut worms in shape and size except for having a non-retractable, spoon-like or forked proboscis (see Fig. 13.9). Some biologists consider them to be annelids. Echiurans are deposit feeders that use the proboscis to gather organic matter. The "fat innkeeper" (*Urechis caupo*) of the western coast of North America lives in **U**-shaped tubes in mud (see Fig. 12.11).

MOLLUSCS: THE SUCCESSFUL SOFT BODY

Snails, clams, octopuses, and other familiar forms are members of the phylum **Mollusca. Molluscs** have been very successful: there are more species of molluscs in the ocean than of any other animal group. There may be as many as 200,000 species of molluscs, which are surpassed only by the arthropods as the largest phylum of animals.

Most molluscs have a soft body enclosed in a calcium carbonate shell (Fig. 7.20). The body is covered by a **mantle,** a

Symbiosis The living together in close association of two different species.
• Chapter 10, p. 218

Littorina obtusata, North Atlantic Ocean

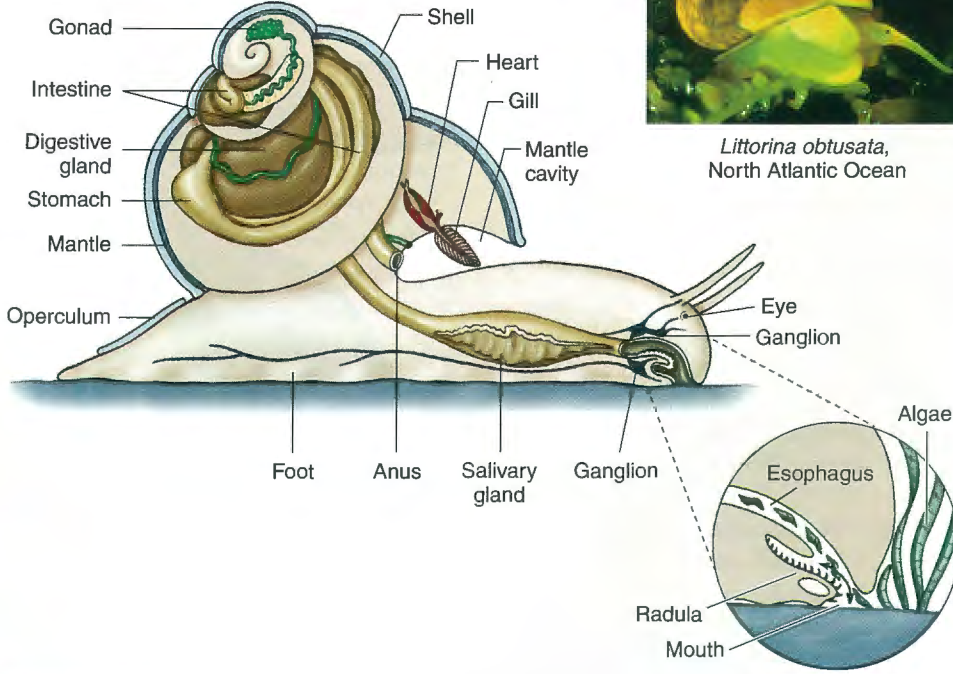


FIGURE 7.20 The general body plan of a gastropod, indicating the most important internal structures. In many species the head and foot can be retracted into the shell, leaving a tough operculum blocking the shell opening.

How to Discover a New Phylum

It is not very difficult to discover a new marine invertebrate species. Small animals living in sediments, among rocky shore seaweeds, in crevices or holes in coral, or in deep water are good candidates. Discovering a new phylum of invertebrates, however, is a different story.

The founding species of three phyla escaped description until relatively recently. All three are exclusively marine.

The first species of what eventually became the new phylum **Gnathostomulida** was not officially described until 1956. Gnathostomulids are a group of about 100 species of minute worms living among sediment particles around the world (see the figure in "Life in Mud and Sand," p. 291). They are similar to the flatworms but possess unique features, including a set of toothed jaws to scrape bacteria, diatoms, and other organisms from sand grains.

The next of the new phyla has a short but turbulent history. In 1961 Robert Higgins, then at the Smithsonian Institution in Washington, D.C., predicted the existence of a group that lived in the spaces between clean, coarse sediment particles in deep water. He actually found a specimen in 1974 but, unfortunately, did not realize it was something new.

One year later, in 1975, Reinhardt Kristensen of the University of Copenhagen, Denmark, collected a specimen, but it was destroyed while being prepared for microscopic examination. Kristensen later found larvae of the elusive animal in coarse sediments from western Greenland and the Coral Sea. In 1982 he was working with a large sample off the coast of Brittany in France. It was his last day at the Roscoff Biological Station, and to save time he washed the sample with fresh water instead of following the standard but more time-consuming method. It happened to loosen the grip of the animals on the sediment particles, and Kristensen got a complete series of larval and adult specimens.

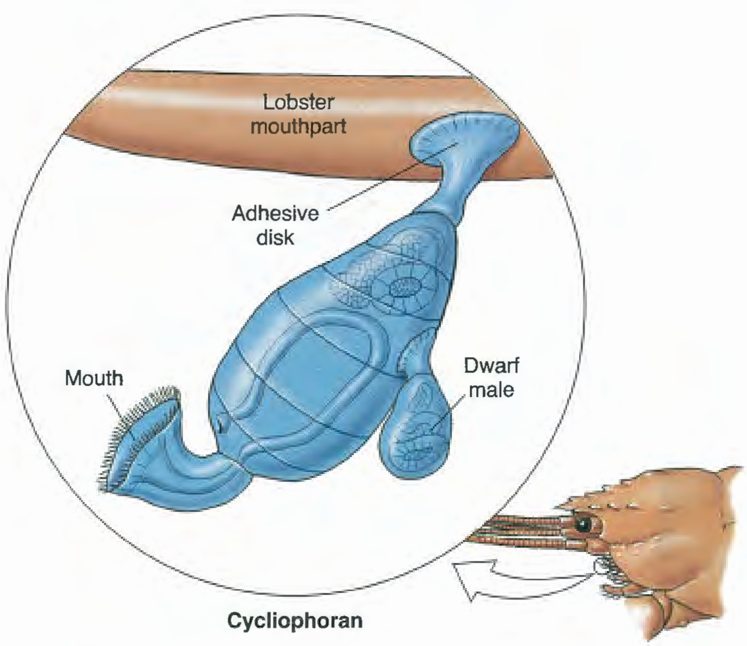
The microscopic animals Kristensen found have a body encased by six plates. The head, which can be retracted, bears a set of spines and a mouth at the end of a cone. Kristensen got together with Higgins, and they concluded that the specimens Higgins examined in 1974 and those subsequently found by Kristensen were members of a new phylum. They found additional adults in eastern Florida, which further confirmed the new status of the group.

The new phylum **Loricifera** (meaning "armor bearer") was officially born in 1983 when Kristensen published a paper in a German scientific journal. The first species was named *Nanaloricus mysticus* ("mystic, or enigmatic, dwarf armor"), and the larva was baptized the Higgins larva in honor of Higgins—a nice consolation prize, indeed! Some 20 additional species have so far been described. About 100 new species have been collected but not yet officially described.

The latest new phylum comes from another unexpected location: the hairs around a Norway lobster's mouth. Though first observed in the 1960s, the phylum **Cycliophora** was not described until 1995. So far it consists of one species, *Symbion pandora*, a tiny, bottle-shaped sac with a disk-like mouth. Cilia around the mouth sweep food particles that come off the lobster's mouth at mealtime.

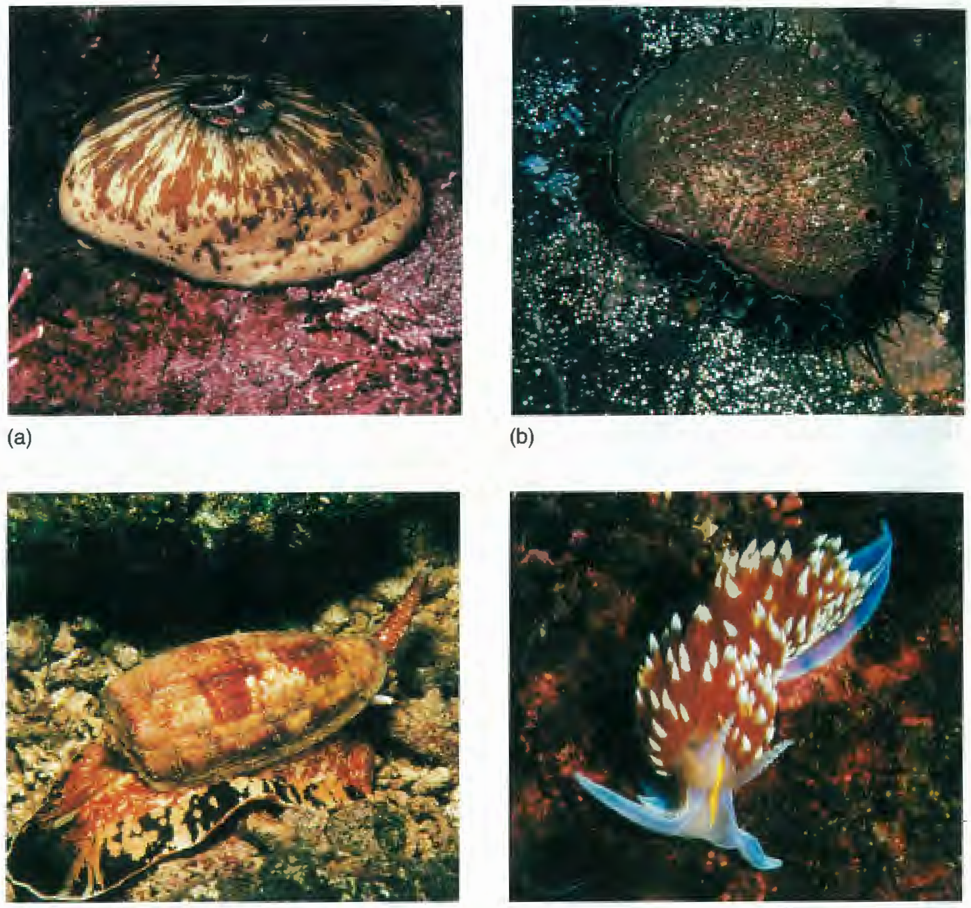
This strange lifestyle coincides with a bizarre life cycle. The minute but multicellular animal—hundreds often live on a lobster—alternates sexual and asexual generations. Dwarf males, which live attached to females, exist only to produce sperm. Females also reproduce asexually, but they produce only females that develop inside box-like structures inside their mothers. The new generation of females is set free from the boxes as it bursts out from the mothers. The Greek myth of a box that Pandora (and hence the name of the first cycliophoran) opened to allow all human ills to escape is thus re-created around a lobster's mouth.

A second species of *Symbion* was described from the American lobster. A third species, not yet described, has been discovered on the European lobster.



Cycliophoran

FIGURE 7.21 The Cooper's nutmeg snail (*Cancellaria cooperi*) seeks out electric rays, which rest partially buried in sand. It then extends its long proboscis, makes a tiny cut in the ray's skin with the radula at the end of the proboscis, and then sucks the ray's blood. A high-magnification photo (inset) shows the teeth of the radula.



(a) (b) (c) (d)

FIGURE 7.22 Gastropods come in all shapes, colors, and habits. (*a*) The giant keyhole limpet (*Megathura crenulata*), from the Pacific coast of North America, photographed on a bottom covered by encrusting red coralline algae. (*b*) The red abalone (*Haliotis rufescens*) is much sought after for food and is now rare in some areas. (*c*) Cone shells, such as *Conus geographus*, are carnivorous snails that bury themselves in sand, waiting for prey such as small fishes. Their radula is modified into a dart-like tooth that is shot—together with a poison—into the unsuspecting prey, which is eaten whole, very much as in snakes (also see Fig. 10.7). (*d*) A flashy nudibranch (*Phidiana crassicornis*).

thin layer of tissue that secretes the shell. The unsegmented body is typically bilaterally symmetrical. There is a ventral, muscular **foot,** usually used in locomotion. Most molluscs have a head that normally includes eyes and other sensory organs. A feature unique to molluscs is the **radula,** a ribbon of small teeth that is used to feed, usually by rasping food from surfaces (Fig. 7.20). The radula is modified in carnivorous molluscs (Figs. 7.21 and 10.7). The radula is made largely of **chitin,** a highly resistant carbohydrate also found in other invertebrates. Gas exchange is through paired gills. The body cavity, a coelom, is much reduced, being restricted to small cavities around the heart and a few other organs.

All molluscs have this basic body plan, but it is often greatly modified. The shell, for example, is internal in squids and absent in octopuses and a few other groups. In snails portions of the body are coiled and asymmetrical. In some molluscs the radula is modified or even absent.

The molluscs constitute the largest group of marine animals. Their body is soft with a muscular foot. They usually have a shell and a radula, a rasping "tongue" unique to the group.

Types of Molluscs

Molluscs exhibit an immense diversity of structure and habit. They occupy all marine environments from the wave-splashed zone of rocky shores to hydrothermal vents in the deep sea. They thrive on practically every conceivable type of diet. For all their diversity, though, most molluscs belong to one of three major groups.

Gastropods The **gastropods** (class **Gastropoda**), are the largest, most common, and most varied group of molluscs. Snails are the most familiar gastropods, but the group includes other forms such as limpets, abalones, and nudibranchs (Fig. 7.22). There are perhaps 75,000 species, mostly marine. A typical gastropod can best be described as a coiled mass of vital organs enclosed by a dorsal shell (see Fig. 7.20). The shell rests on a ventral creeping foot (the term "gastropod" means "stomach footed") and is usually coiled.

Most gastropods use their radula to scrape algae from rocks, as in periwinkles (*Littorina;* see Fig. 11.2), limpets (*Fissurella, Lottia;* Fig. 7.22*a*), and abalones (*Haliotis;* Fig. 7.22*b*). Some, like mud snails (*Hydrobia*), are deposit feeders on soft bottoms. Whelks (*Nucella, Buccinum;* see Fig. 11.21), oyster drills (*Murex, Urosalpinx*), and cone shells (*Conus;* Fig. 7.22*c*), are carnivores. They prey on clams, oysters, worms, and even small fishes. The violet snail *Janthina* has a thin shell and produces a bubble raft out of mucus to float on the surface, looking for siphonophores, its prey (see Fig. 15.15). Sea hares (*Aplysia*), whose shells are small, thin, and buried in tissue, graze on seaweeds.

Nudibranchs, or **sea slugs,** are gastropods that have lost the shell altogether. Colorful branches of the gut or exposed gills make nudibranchs among the most beautiful of all marine animals (Fig. 7.22*d*). They prey on sponges, hydroids, and other invertebrates. As a defensive mechanism, nudibranchs often produce noxious chemicals or retain undischarged nematocysts taken undigested from their prey.

Bivalves **Bivalves** (class **Bivalvia**) are clams, mussels, oysters, and similar molluscs. In bivalves the body is laterally compressed (that is, flattened sideways) and enclosed in a shell with two parts, or **valves** (Fig. 7.23). The **umbo,** the upper hump near the hinge of each shell, is the oldest part of the shell. Growth from the umbo proceeds in the form of concentric growth lines. There is no head to speak of, and no radula. The gills, expanded and folded, are used not only to obtain oxygen but also to filter and sort small food particles from the water. The inner surface of the shell is lined by the mantle, so that the whole body lies in the **mantle cavity,** a large space between the two halves of the mantle. Strong muscles, the **adductor muscles,** are used to close the valves.

Clams (*Macoma, Mercenaria*) use their shovel-shaped foot to burrow in sand or mud (see Figs. 11.30 and 12.11). When the clam is buried, water is drawn in and out of the mantle cavity through **siphons** formed by the fusion of the edge of the mantle (Fig. 7.23*a* and *d*). This allows clams to feed and obtain oxygen while buried in sediment.

Not all bivalves are burrowers. Mussels (*Mytilus;* see Fig. 11.4), for instance, secrete strong **byssal threads** that attach them to rocks and other surfaces. Oysters (*Ostraea, Crassostrea;* Fig. 7.24*a*) cement their left shell to a hard surface, often the shell of another oyster. Aphrodisiac or not, they have been lustfully swallowed by lovers of good food for thousands of years. Pearl oysters (*Pinctada*) are the source of most commercially valuable pearls. Pearls are formed when the oyster secretes shiny layers of calcium carbonate to coat irritating particles or parasites lodged between the mantle and the iridescent inner surface of the shell, which is called mother-of-pearl. Cultured pearls are obtained by carefully inserting a tiny bit of shell or plastic into the mantle. Some scallops (*Pecten, Lima;* Fig. 7.24*b*) live unattached and can swim for short distances by rapidly ejecting water from the mantle cavity and clapping the valves. The largest bivalve is the giant clam (*Tridacna;* see Fig. 14.34), which grows to more than 1 m (3 ft) in length.

Many bivalves bore in coral, rock, or wood. The shipworm (*Teredo*) bores in mangrove roots, driftwood, and wooden structures such as boats and pilings. They use their small valves to excavate the wood, which is eaten. Symbiotic bacteria in the shipworm's gut digest the wood. The rasping valves lie at the inner end of a tunnel lined with calcium carbonate, and a tiny siphon protrudes from the entrance at the other end. Shipworms are an example of a **fouling organism,** one that settles on the bottoms of boats, pilings, and other submerged structures.

Cephalopods The **cephalopods** (class **Cephalopoda**), predators that are specialized for locomotion, include the octopuses, squids, cuttlefishes, and other fascinating creatures. Cephalopods adapt the molluscan body plan to an active way of life. Nearly all are agile swimmers with a complex nervous system and a reduction or loss of the shell. All 650 living species are marine. A cephalopod (the name means "head-footed") is like a gastropod with its head pushed down toward the foot. The foot is modified into arms and tentacles, usually equipped with suckers that are used

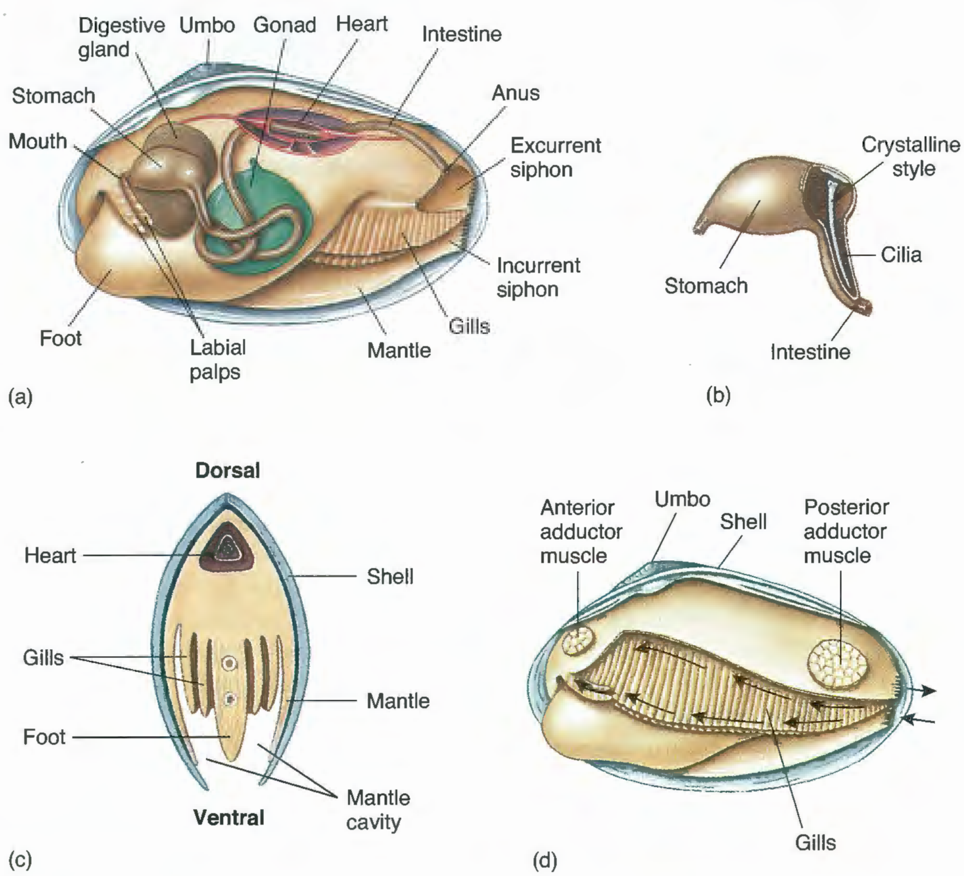


FIGURE 7.23 A laterally compressed body is the most distinctive feature of bivalves, illustrated here by a clam. The gills, which hang on both sides of the body (*a, c*), sort out food particles and transport them to the mouth with the help of cilia and mucus. The palps then push the food into the mouth. Food is digested in the stomach with the help of the crystalline style (*b*). The path of the particles from the incurrent siphon to the mouth is indicated by arrows (*d*).

FIGURE 7.24 Oysters such as *Crassostrea virginica* (*a*) are harvested commercially around the world (see Fig. 17.15). Some bivalves, like scallops and the file clam (*Lima scabra, b*) live free on the bottom. Others bury themselves in sand or mud.

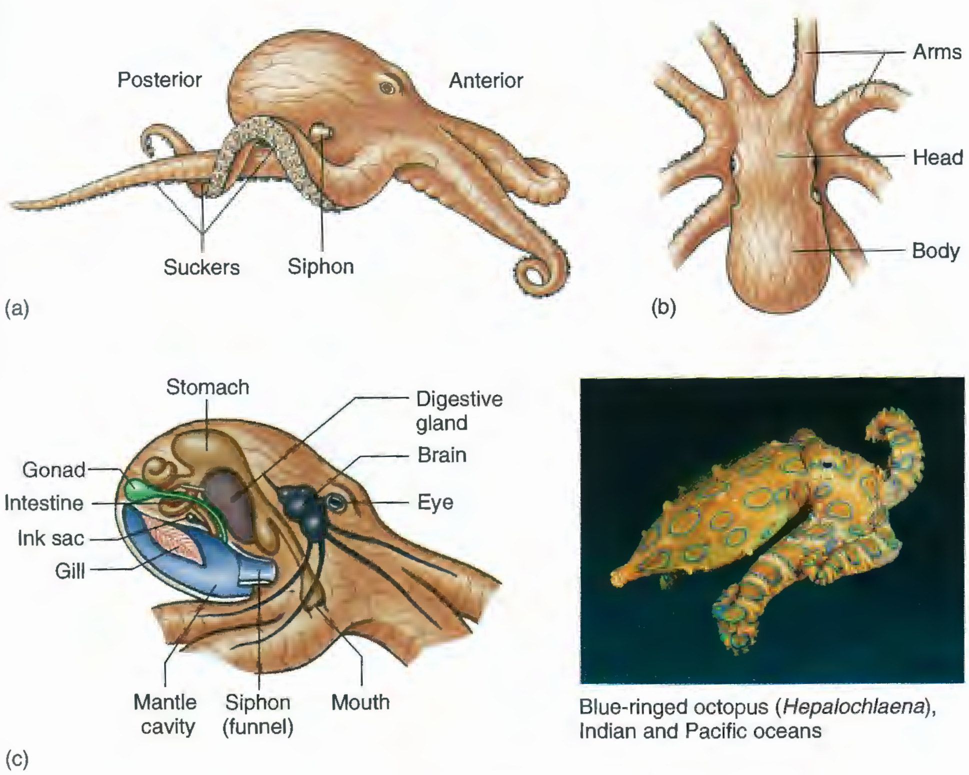


FIGURE 7.25 External (*a* and *b*) and internal (*c*) structure of the octopus. In the male the tip of the third right arm is modified to transfer packets of sperm from his siphon into the mantle cavity of the female. Copulation is preceded by courtship behavior that includes intricate color changes.

to capture prey (Fig. 7.25) The large eyes, usually set on the sides of the head, are remarkably like ours. The body, rounded in octopuses and elongated in squids, is protected by a thick and muscular mantle. The mantle forms a mantle cavity behind the head that encloses two or four gills. Water enters through the free edge of the mantle and leaves through the **siphon,** or **funnel,** a muscular tube formed by what remains of the foot, which projects under the head. Cephalopods swim by forcing water out of the mantle cavity through the siphon. The flexible siphon can be moved around, allowing the animal to move in practically any direction, an example of jet propulsion in nature.

Octopuses (*Octopus*)—not "octopi"—have eight long arms and lack a shell (Fig. 7.25). They are common bottom dwellers. Including arms, the size varies from 5 cm (2 in) in the dwarf octopus (*Octopus joubini*) to a record of 9 m (30 ft) in the Pacific giant octopus (Fig. 7.26*a*).

Octopuses are efficient hunters, with crabs, lobsters, and shrimps among their favorite dishes. They bite their prey with a pair of beak-like jaws. The radula may help rasp away flesh. They also secrete a paralyzing substance, and some have a highly toxic bite. Most, however, are harmless. They use crevices in rocks, and even discarded bottles and cans, as homes. Their shelters are given away by the presence of rocks, which they move around, and by the remains of crabs. Like most other cephalopods, they can distract potential predators by emitting a cloud of dark fluid produced by the **ink sac** (Fig. 7.27).

FIGURE 7.26 (*a*) The Pacific giant octopus (*Enteroctopus dofleini*). (*b*) Mating squids (*Loligo opalescens*). Notice the masses of white, gelatinous egg cases on the bottom.

Squids (*Loligo;* Figs. 7.26*b* and 7.27) are better adapted for swimming than are octopuses. The body is covered by the mantle, which has two triangular fins (Fig. 7.27). The arrangement of the internal organs is similar to that of the octopus (see Fig. 7.25*c*), except that the squid's body is elongated. Squids can remain motionless in one place or move backward or forward just by changing the direction of the siphon. Eight arms and two tentacles, all with suckers, circle the mouth. The tentacles are long and retractable and have suckers only at the broadened tips. They can be swiftly shot out to catch prey. The shell is reduced to a stiff **pen** embedded in the upper surface of the mantle. Adult size varies from tiny individuals of a few centimeters in length to the largest living invertebrate, the deep-sea colossal squid (*Mesonychoteuthis*). Very few specimens have been caught, but the largest, caught in 2007, had a total length of about 10 m (33 ft). The giant squid (*Architeuthis*) is another deep-sea squid. It may grow to 20 m (60 ft) in length but weighs less than the colossal squid.

Cuttlefishes (*Sepia*) resemble squids in having eight arms and two tentacles, but the body is flattened and has a fin running along the sides. Cuttlefishes, which are not fish at all, have a calcified internal shell that aids in buoyancy. This shell is the "cuttlebone" sold as a source of calcium for cage birds.

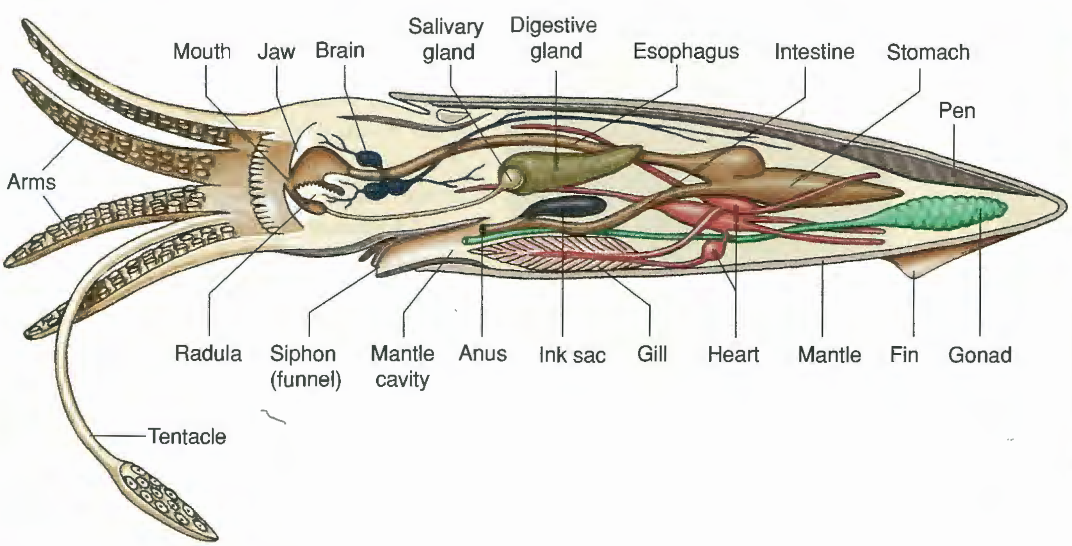
The chambered nautilus (*Nautilus;* see "The Chambered Nautilus," p. 360) has a coiled external shell containing a series of gas-filled chambers that serve as a buoyancy organ. The shell may be up to 25 cm (10 in.) in diameter. The body—which occupies the outer, largest chamber—has 60 to 90 short, suckerless tentacles used to capture prey.

Other Molluscs About 800 species of **chitons** (class **Polyplacophora**) are known, all marine. They can be readily identified by the eight overlapping shell plates that cover their slightly arched dorsal surface (Fig. 7.28). Their internal organs are not coiled as in snails.

Most chitons live on shallow, hard bottoms where they use a rasping radula to feed on algae. Many of them return to a homesite after feeding. One species, however, captures small crustaceans and other invertebrates with a flap-like extension of the mantle that surrounds the mouth.

The **monoplacophorans** (class **Monoplacophora**) are represented by only a handful of species of limpet-like molluscs. They were known only as fossils until the discovery of live individuals in 1952. They have now been collected, mostly from deep water, in scattered locations around the world. Monoplacophorans are peculiar because their gills and other organs are repeated along the body, which is reminiscent of the segmentation of annelids.

The 350 or so species of **tusk shells,** or **scaphopods** (class **Scaphopoda**), have an elongated shell, open at the top and tapered like an elephant tusk. They live in sandy or muddy bottoms. The narrow top end of the shell protrudes from the bottom, while the foot projects from the wide end. Many species



Juvenile *Illex illecebrosus*, Atlantic coast of North America

FIGURE 7.27 Section across a squid, showing its internal anatomy and only half the number of arms and tentacles.

EYE ON SCIENCE

The Sea Hare's Giant Nerve Cells

Aplysia californica, the California sea hare, has been used to study how the nervous system works. Humans and other vertebrates have billions of microscopic nerve cells, or neurons, electrically excitable cells involved in the transmission and storage of information. The sea hare, a shell-less gastropod, has only about 10,000, but they are giant-sized, and aggregate to form equally even larger ganglia. This is handy because it allows neurobiologists to easily identify and stimulate the sea here's individual nerve cells with microelectrodes or neurotransmitters. This makes it much easier to map the role of single nerve cells in specific functions in the nervous system than in the complex brain of vertebrates like rats and humans. The large size and simple organization of the sea hare's nerve cells have also helped in the study of the molecular events that take place during the transmission of nerve impulses.

Research on *Aplysia* has been particularly useful in understanding the biological basis of learning and memory in which nerve cells play fundamental roles. Although its nervous system and behavior are relatively simple, *Aplysia* can learn simple tasks, and stores this information in nerve cells just as we do. In fact, Dr. Eric Kandel of Columbia University earned a share of the 2000 Nobel Prize in Medicine by using *Aplysia* for his research on the neurological basis of memory in the human brain.

Scientists have determined many of the *Aplysia* genetic sequences that control specific nerve cell functions, providing exciting links between gene expression, behavior, and learning. Researchers from the University of Florida and Columbia University analyzed gene expression in relation to nerve connections that control specific feeding and defensive behaviors. They discovered that more than 10,000 of the sea here's genes are active in a single nerve cell at any given time. This suggests that memory does not take place in isolation from other cellular functions. Most of these genes are unique to *Aplysia*, but surprisingly more than 100 are similar to genes associated with major neurological diseases in humans. These findings strongly suggest that the molecular and genetic basis for function of nerve cells in behavior and learning evolved early in animal evolution, and have remained relatively unchanged in diverse groups like molluscs and vertebrates, including humans.

Research is underway to complete sequencing the genome of *Aplysia californica*. The genome will reveal the complete set of genes that control or influence how nerve cells work. Since humans share some of these genes, application of this research may ultimately improve understanding of human learning and memory. It could also lead to treatments for Alzheimer's disease, some types of mental retardation, and at least some brain injuries.

For more information, explore the links provided on the Marine Biology *Online Learning Center.*

FIGURE 7.28
Chitons such as *Tonicella lineata* use their strong foot and the flexibility provided by the eight articulated shells to fit tightly to the irregular surface of rocky shores.

have thin tentacles with adhesive tips. They are used to capture **foraminiferans,** young bivalves, and other small organisms from the sediment. Tusk shells are most common in deep water, but empty shells sometimes wash ashore.

Biology of Molluscs

The body structure and organ systems of molluscs show a complexity that parallels their abundance and diversity.

Feeding and Digestion The molluscan gut has a separate mouth and anus. Digestion involves **salivary** and **digestive glands** (see Figs. 7.20 and 7.27) that release digestive **enzymes,** which break down food into simpler molecules. Other aspects of the digestive system differ among groups and according to diet.

Grazers such as chitons, limpets, and many snails have a rasping radula that removes minute algae from surfaces or cuts through large seaweeds. Their relatively simple digestive system can efficiently process large amounts of hard-to-digest plant material. Digestion is partly extracellular in the gut cavity and partly intracellular in the digestive glands. Some shell-less gastropods that feed on seaweeds keep the seaweeds' **chloroplasts** intact. The chloroplasts are kept in the digestive gland, where they can photosynthesize and provide nourishment for the gastropod.

Foraminiferans or Forams Protozoans with tiny calcareous shells.
- Chapter 5, p. 97; Figure 5.11

Enzymes Substances that speed up specific chemical reactions.
- Chapter 4, p. 65

Chloroplasts Cell organelles in plants and other primary producers in which the process of photosynthesis takes place.
- Chapter 4, p. 69; Figure 4.8b

Carnivorous snails have a radula modified to drill, cut, or even capture prey. The radula and mouth are contained in a proboscis that can be protruded to strike the prey (see Fig. 7.21). Jaws may even be present. In these snails digestion is extracellular and takes place in the stomach.

Bivalves ingest food particles that are filtered and sorted out by the cilia on the gills. The radula is absent, and food enters the mouth trapped in long strings of mucus. An enzyme-secreting rod in the stomach, the **crystalline style** (see Fig. 7.23*b*), continually rotates the food to help in its digestion. The stomach contents eventually pass into a large digestive gland for intracellular digestion. Giant clams not only filter food but also obtain nutrients from zooxanthellae living in tiny branches of the gut that extend into the clam's expanded mantle (see Fig. 14.34). This extra nourishment may allow the clams to attain their giant size.

All cephalopods are carnivores that have to digest large prey. The stomach is sometimes connected to a sac in which digestion is rapidly and efficiently completed. It is entirely extracellular.

Molluscs have a circulatory system that transports nutrients and oxygen. A dorsal, muscular heart pumps blood to all tissues. Most molluscs have an **open circulatory system** in which blood flows out of vessels into open blood spaces. Cephalopods, on the other hand, have a closed circulatory system in which the blood always remains in vessels and can be more effectively directed to oxygen-demanding organs such as the brain.

Nervous System and Behavior The nervous system of molluscs varies in complexity. Gastropods and bivalves do not have a single brain but, rather, several sets of **ganglia,** or "local brains," clusters of nerve cells located in different parts of the body (see Fig. 7.20; "The Sea Hare's Giant Nerve Cells," p. 133).

Cephalopods have the most complex nervous system not just of molluscs but of all invertebrates. Some of the separate local brains of other molluscs are fused into a single, large brain (see Figs. 7.25*c* and 7.27) that coordinates and stores information received from the environment. Different functions and behaviors of cephalopods are controlled by particular regions of the brain, as in humans. Giant nerve fibers rapidly conduct impulses, allowing cephalopods to capture prey or escape at amazing speeds. The strikingly complex eyes of cephalopods reflect the development of their nervous system. Octopuses and cuttlefishes have a remarkable capacity for learning. Most cephalopods, especially cuttlefishes, display color changes correlated with particular behaviors and moods, from intricate sexual displays to camouflage. Some cuttlefishes flash two large, black spots resembling eyes, perhaps to fool potential predators. Some octopuses even change color and behavior to mimic, or imitate, poisonous fishes and sea snakes!

Reproduction and Life History Most molluscs have separate sexes, but some species are **hermaphrodites,** animals in which individuals have both male and female gonads. In bivalves, chitons, tusk shells, and some gastropods, sperm and eggs are released into the water and fertilization is external (see Fig. 4.21*a*). Fertilization is internal in cephalopods and most gastropods. When cephalopods mate, the male uses a modified arm to transfer a **spermatophore,** an elongated packet of sperm, to the female. Males of gastropods that copulate have a long, flexible penis.

Some molluscs have a trochophore larva like polychaetes, a characteristic often used as evidence for close affinities among molluscs, the segmented worms, and other groups. In gastropods and bivalves the trochophore usually develops into a **veliger,** a planktonic larva that has a tiny shell (see Fig. 15.11*a*). In many gastropods, however, part or all of development takes place within strings or capsules of eggs. Cephalopods lack larvae, and the young develop from large, yolk-filled eggs. Female octopuses protect their eggs, which are often attached to crevices or holes in rocks, until they hatch. The female usually dies afterward because she eats little or nothing while guarding the eggs.

ARTHROPODS: THE ARMORED ACHIEVERS

Arthropods (phylum **Arthropoda**) make up the largest phylum of animals, with more than a million known species and several million remaining undiscovered. Of all the animals on earth, three out of four are arthropods. The largest group of arthropods by far, however, are the insects, which though the dominant arthropods on land are rare in the sea. The overwhelming majority of marine arthropods are **crustaceans** (subphylum **Crustacea**), a group that includes barnacles, shrimps, lobsters, crabs, and a huge variety of less familiar animals.

The arthropod body is segmented and bilaterally symmetrical. In addition to a flexible, segmented body arthropods have jointed appendages, such as legs and mouthparts, that are moved by sets of attached muscles. Another characteristic of arthropods is a tough, non-living external skeleton, or **exoskeleton,** composed of chitin and secreted by the underlying layer of tissue. The exoskeleton and jointed appendages provide protection, support, flexibility, and increased surface area for muscle attachment.

To grow, arthropods must **molt,** or shed their exoskeleton (Fig. 7.29). A new shell develops under the old one prior to molting, then hardens after the old skeleton is discarded and the animal takes in water to expand itself. Most arthropods are small because the rigid exoskeleton imposes limitations on size. We will never see arthropods as big as giant squids or whales, but the legs of a giant spider crab (*Macrocheira*) may reach 3 m (10 ft) long.

More species belong to the arthropods than to any other animal group. Most arthropods on land are insects, but crustaceans are the dominant arthropods in the sea. Arthropods have a segmented and bilaterally symmetrical body. Their success in adapting to all types of environments is due in part to a protective exoskeleton and jointed appendages.

FIGURE 7.29 This is not really a live Galápagos shore crab (*Grapsus grapsus*) but its exoskeleton, or molt. The old exoskeleton covered the entire external surface of the crab, even its mouthparts and eyes. After molting, which is regulated by hormones, the soft, helpless crab must find shelter for a few days until its new, larger skeleton hardens.

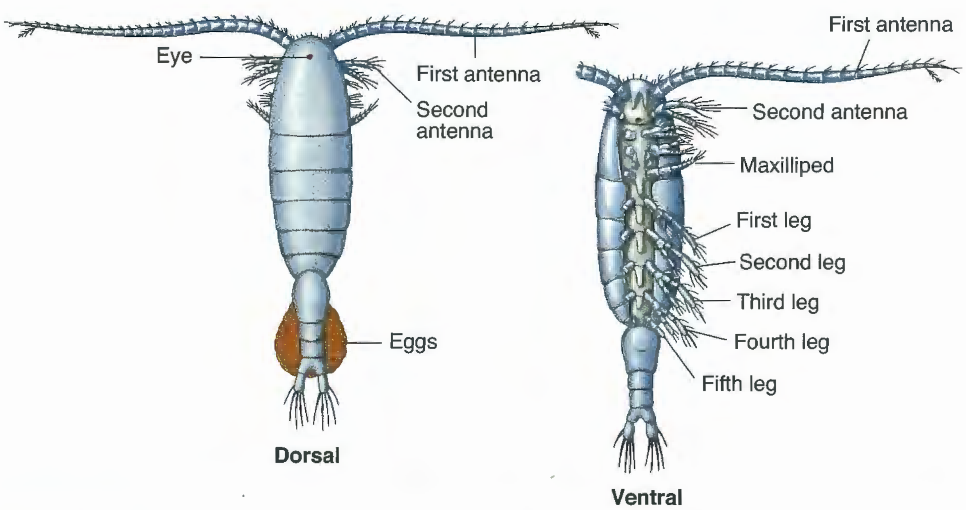


FIGURE 7.30 The structurally simplest crustaceans, like this planktonic copepod, tend to be small and have appendages that are similar to each other—that is, less specialized. One exception here is the first antenna, which is specialized for swimming (also see Figs. 15.6 and 15.7). All appendages are paired, but the ventral view shows only those on one side.

Crustaceans

There are approximately 68,000 known species of crustaceans, but there may be as many as 150,000 undescribed species. Most are marine.

Crustaceans are specialized for life in water, and most possess gills to obtain oxygen. Their chitinous skeleton is usually hardened by calcium carbonate. The appendages are specialized for swimming, crawling, attaching to other animals, mating, and feeding. Crustaceans possess two pairs of **antennae** (Figs. 7.30, 7.32, and 7.34), which are usually involved in sensing the surroundings. The crustacean body plan is repeated in myriad forms, from the familiar to the not-so-familiar.

Crustaceans are arthropods adapted for life in water. They have two pairs of antennae, gills, and a calcified exoskeleton.

The Small Crustaceans Small crustaceans are everywhere: in the plankton, on the bottom, among sediments, on and in other animals, and among seaweeds.

Copepods are extremely abundant and important in the plankton (see "Copepods," p. 332). They use their mouthparts to filter out or capture food. Some species are so common that they are among the most abundant animals on earth. Many planktonic species keep from sinking by using their enlarged first pair of antennae (Fig. 7.30) to swim. Many species are parasitic, some being so simplified that they look like little more than small bags of tissue.

Barnacles are filter feeders that usually live attached to surfaces, including living surfaces like whales and crabs. Many are very particular about the type of surface on which they live. Some are among the most important types of fouling organisms.

Common barnacles look almost like molluscs because their bodies are enclosed by heavy, calcareous plates (Fig. 7.31). The plates on the upper surface open to allow the feathery filtering appendages **(cirri),** which are actually the legs, to sweep the water. Some barnacles have become highly modified parasites and lack plates. All barnacles, however, have typical crustacean larvae, which swim and attach to surfaces before metamorphosing into adults (see Fig. 7.39).

Amphipods are small crustaceans with a curved body that is flattened sideways (Fig. 7.32). Most amphipods are under 2 cm (3/4 in) in length, but some deep-water species are much larger (see Fig. 16.26). The head and tail typically curve downward, and the appendages are specialized according to function. Beach hoppers, common in shore debris, are strong jumpers that spring about by briskly stretching their curved bodies. Other amphipods crawl among seaweeds. Burrowing in the skin of whales (as whale lice; see Fig. 10.9) and living as part of the plankton are some other lifestyles of this large, mostly marine group of over 5,000 species.

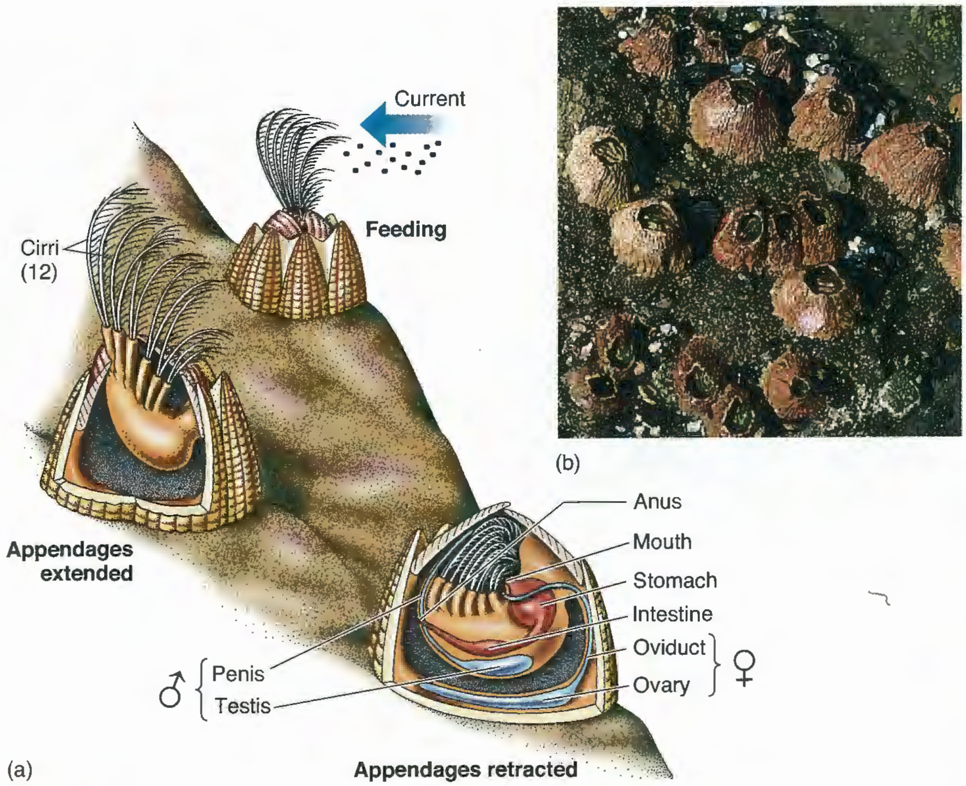


FIGURE 7.31 (*a*) Barnacles conceal a crustacean body beneath thick plates. They lie on their backs and use their legs to filter feed. Note that barnacles are hermaphrodites. Individuals, however, mate with each other, alternatively taking different sex roles. One individual may act as "male" by inserting its extended penis into a nearby "female." It may then turn into a "female" by accepting the penis of a neighbor. (*b*) The thatched barnacle (*Tetraclita squamosa*) from the Pacific coast of North America.

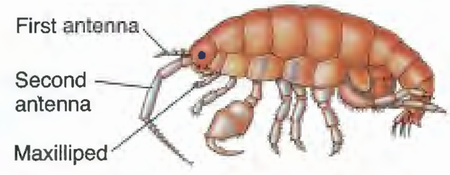


FIGURE 7.32 Most amphipods, like this beach hopper (*Orchestoidea*), can be recognized by a body that is curved and flattened sideways. The skeleton shrimps common among seaweeds and hydroids, however, are amphipods with bizarre skinny bodies. A giant deep-sea amphipod is illustrated in Figure 16.24.

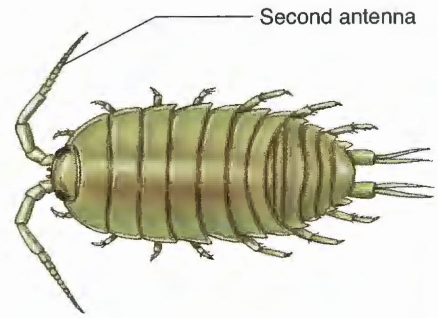


FIGURE 7.33 The sea louse, or sea roach (*Ligia oceanica*), is neither a louse nor a roach but an isopod. It feeds mainly on decaying seaweeds carried in to shore by the waves. Some isopods live as parasites on fishes (see Fig. 10.10).

Isopods are found in many of the same environments as amphipods. They are about the same size as amphipods, but isopods are easily identifiable because the main part of the body has legs that are similar to each other and the body is dorsoventrally flattened and thus has a flat back (Fig. 7.33). Pill bugs are common land isopods that are similar to many marine species. **Fish lice** (no relation to lice of birds and land mammals, which are insects) and other isopods are parasites of fishes (see Fig. 10.10) and other crustaceans.

Krill, or **euphausiids,** are planktonic, shrimp-like crustaceans up to 6 cm (2.5 in) long. The head is fused with some of the body segments to form a distinctive **carapace** that covers the anterior half of the body like armor (see Fig. 17.12). Most krill are filter feeders that feed on diatoms and other plankton. Krill are extremely common in polar waters, aggregating in gigantic schools of billions of individuals. They are an almost exclusive food source for many Antarctic whales, penguins, and fishes (see Fig. 10.14). Other species of krill live in the deep sea (see Fig. 16.2).

Shrimps, Lobsters, and Crabs With around 10,000 species, the **decapods** (the term means "10 legs") are the largest group of crustaceans. They include the shrimps, lobsters, and crabs. Decapods are also the largest crustaceans in size. Many are prized as food and are of great commercial importance.

Decapods feature five pairs of legs, or **pereopods,** the first of which is heavier and usually has claws used for feeding and defense (Fig. 7.34). Decapods also have three pairs of **maxillipeds,** which are closer to the mouth, turned forward, and specialized to sort out food and push it toward the mouth. Maxillipeds are used as filtering devices in decapods that eat small food particles. The carapace is well developed and encloses the part of the body known as the **cephalothorax.** The rest of the body is called the **abdomen.**

Shrimps and **lobsters** tend to have laterally compressed bodies with distinct and elongated abdomens, the "tails" we like to eat so much. Shrimps are typically **scavengers,** specialists in feeding on bits of detritus on the bottom. They also have other lifestyles. Many colorful shrimps, particularly in the tropics, live on the surface of other invertebrates (Fig. 7.35) or remove parasites from the skin of fish (see "Cleaning Associations," p. 218). Other shrimps live in deep water (see Fig. 16.2). Ghost and mud shrimps burrow in muddy bottoms (see Fig. 12.11). Lobsters, such as the American, or Maine, lobster (*Homarus;* Fig. 7.34) and the clawless spiny lobster (*Panulirus;* see Fig. 4.22) are mostly nocturnal and hide during the day in rock or coral crevices. They are scavengers and predators that crush molloscs and sea urchins.

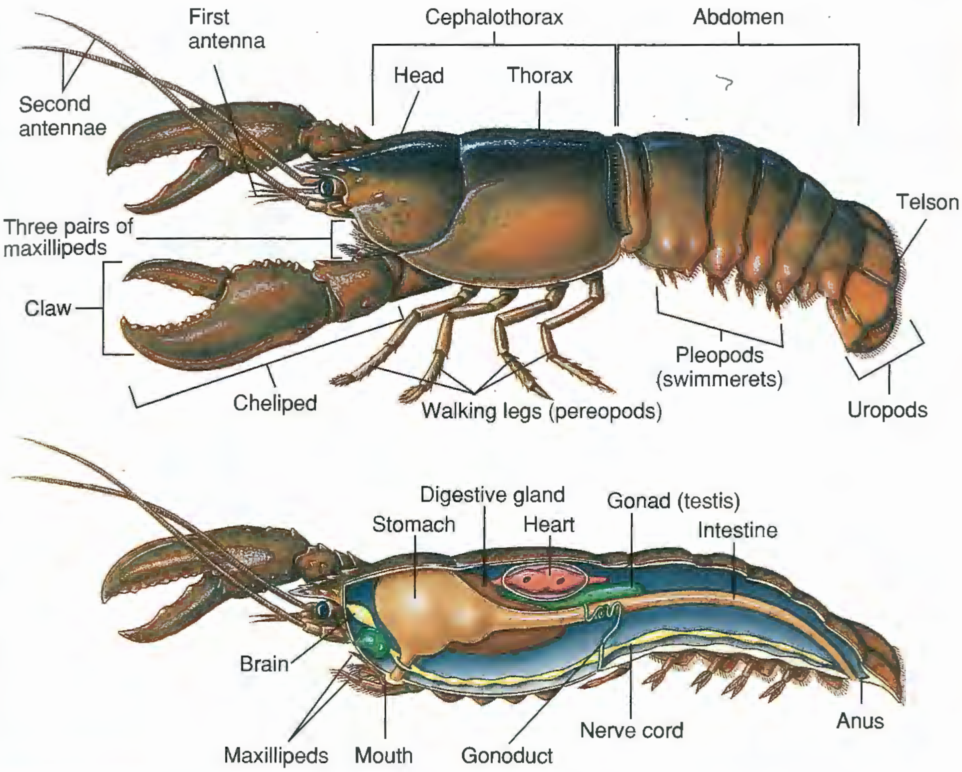


FIGURE 7.34 The American lobster (*Homarus americanus*) illustrates the basic body plan of decapod crustaceans. One significant omission from this drawing is the feathery gills, which lie in a chamber on each side of the cephalothorax. The ducts from the gonads, the gonoducts, open at the base of the last pair of walking legs in males and at the base of the second pair in females. Be sure to check next time you eat a lobster.

FIGURE 7.35 This shrimp (*Periclimenes*) is camouflaged to live on the branching arms of crinoids (see Fig. 7.47) in the tropical Pacific.

FIGURE 7.36 Hermit crab (*Dardanus* sp.) with sea anemones living on its shell. The hermit crab is protected by the nematocysts on the sea anemone's tentacles, and the sea anemones get to eat food particles that are let loose when the hermit crab feeds.

Hermit crabs, which are not true crabs, are also scavengers. They hide their long, soft abdomens in empty gastropod shells (see Fig. 10.5). Some hermit crabs cover their shells with sea anemones (Fig. 7.36) or sponges for added protection and camouflage. One type, however, doesn't hide its abdomen (Fig. 7.37).

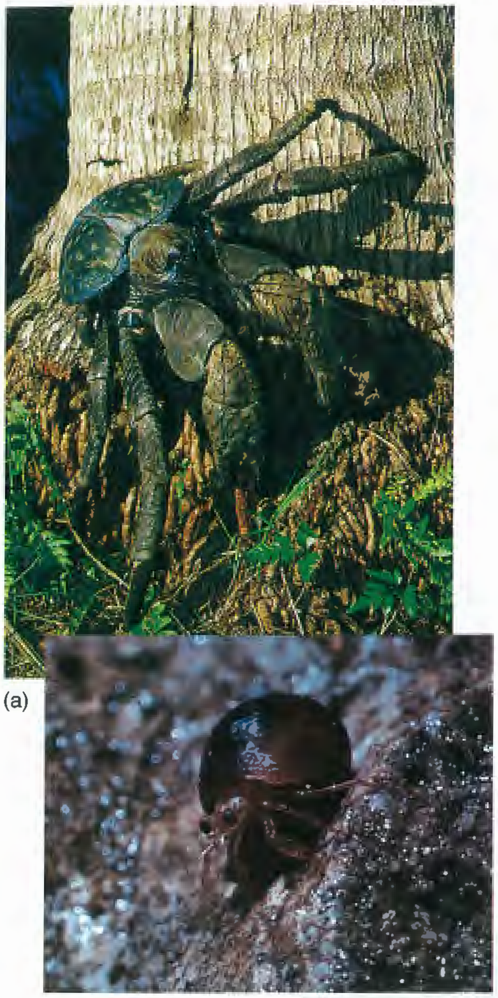
In the **true crabs** the abdomen is small and tucked under the compact and typically broad cephalothorax. The abdomen is visible as a flat, **V**-shaped plate in males; in females it is expanded and **U**-shaped for carrying eggs (Fig. 7.38). Crabs may be highly mobile, and most can easily move sideways when in a hurry. They make up the largest and most diverse group of decapods, more than 4,500 species strong. Most are scavengers or predators, but some have specialized diets such as seaweeds, organic matter in mud, or even coral mucus (see the photo on page 115). Many crabs live along rocky shores or sandy beaches, exposed to air much of the time. Land crabs spend most of their lives on land, returning to the sea only to release their eggs.

Biology of Crustaceans

The diversity of forms among crustaceans is paralleled by equally diverse functional features.

Feeding and Digestion Filter feeding is very common in copepods and many of the small planktonic crustaceans (see Fig. 15.7). Stiff, hair-like bristles on some appendages are used to catch food particles in the water. Particles are carried to the bristles by currents induced by the beating of other appendages. Still other specialized appendages move food from the bristles to the mouth. Appendages are adapted for piercing and sucking in parasitic copepods and isopods.

Food passes to a stomach that typically has chitinous teeth or ridges for grinding and bristles for sifting. The stomach,



(a)

(b)

FIGURE 7.37
The coconut crab (*Birgus latro*) is a large, land-dwelling hermit crab that does not use a shell as an adult (*a*). Females return to seawater only to release their eggs. After a planktonic existence, the young settle on the bottom and use shells for a home (*b*) as they crawl out of the sea to begin life on land. Coconut crabs, so called because they often eat coconuts, are found in the tropical Pacific and Indian oceans. They have been known to reach 13.5 kg (30 lb) in weight and are thus the largest and heaviest of all land arthropods.

FIGURE 7.38
The abdomen is V-shaped in male crabs (top) and larger and U-shaped in females (bottom). This is the European, or shore, crab (*Carcinus maenas*), an introduced pest on the Atlantic and Pacific coasts of North America and other regions around the world.

two-chambered in decapods, is connected to digestive glands that secrete digestive enzymes and absorb nutrients. Digestion is essentially extracellular. The intestine ends in an anus.

As in molluscs, absorbed nutrients are distributed by an open circulatory system. Gas exchange is typically carried out by gills attached to some of the appendages. In most decapods the gills lie in a chamber under the carapace, where they are constantly bathed by water. In land crabs, however, the gill chamber, though moistened, is filled with air and acts almost as our lungs do.

Nervous System and Behavior The nervous system of the structurally simplest crustaceans is ladder-like, but it is more centralized in decapods. Crustaceans have a small, relatively simple brain (see Fig. 7.34) but well-developed sensory organs. Most have **compound eyes,** which consist of a bundle of up to 14,000 light-sensitive units grouped in a mosaic. In decapods the compound eyes are at the end of movable stalks and can be used as periscopes. Crustaceans have a keen sense of "smell"—that is, they are very sensitive to chemicals in the water. Many crustaceans have a pair of statocysts for balance.

Crustaceans are among the most behaviorally complex invertebrates. They use a variety of signals to communicate with each other. Many of these signals involve special body postures or movements of the legs and antennae, which are often distinctively marked or colored to make the signals more conspicuous. This type of communication has been shown to be very important in settling disputes between neighbors and in courtship. Courtship behavior can be especially elaborate (see "Fiddler on the Mud," p. 273).

Reproduction and Life History The sexes are separate in most crustaceans. Gametes are rarely shed into the water. Instead, males use specialized appendages to transfer sperm directly to the female. Even hermaphroditic species transfer sperm between individuals. Barnacles, for instance, have a penis that can stretch to reach other barnacles in the neighborhood. Mating in decapods usually takes place immediately after the female molts, while the exoskeleton is still soft. Females of many species can store sperm for long periods and use it to fertilize separate batches of eggs. In amphipods and isopods eggs are brooded in a chamber formed by lateral extensions of the body. In decapods and other groups females carry their eggs using **pleopods,** or swimmerets, specialized appendages beneath the body (see Fig. 7.34).

Most crustaceans have planktonic larvae that look nothing like the adult. Probably the most characteristic crustacean larva is the **nauplius,** but the type and number of larval stages vary widely from group to group (Fig. 7.39).

Other Marine Arthropods

Very few arthropods other than crustaceans are common in the ocean. Most belong to two small and entirely marine groups. A third group, huge and mostly terrestrial, includes a few shy invaders of the sea.

Horseshoe Crabs The **horseshoe crabs** are the only surviving members of a group (class **Merostomata**) that is widely represented in the fossil record. The five living species of horseshoe crabs are not true crabs but "living fossils," not unlike forms that became extinct long ago. Horseshoe crabs live on soft bottoms in shallow water on the Atlantic and Gulf coasts of North

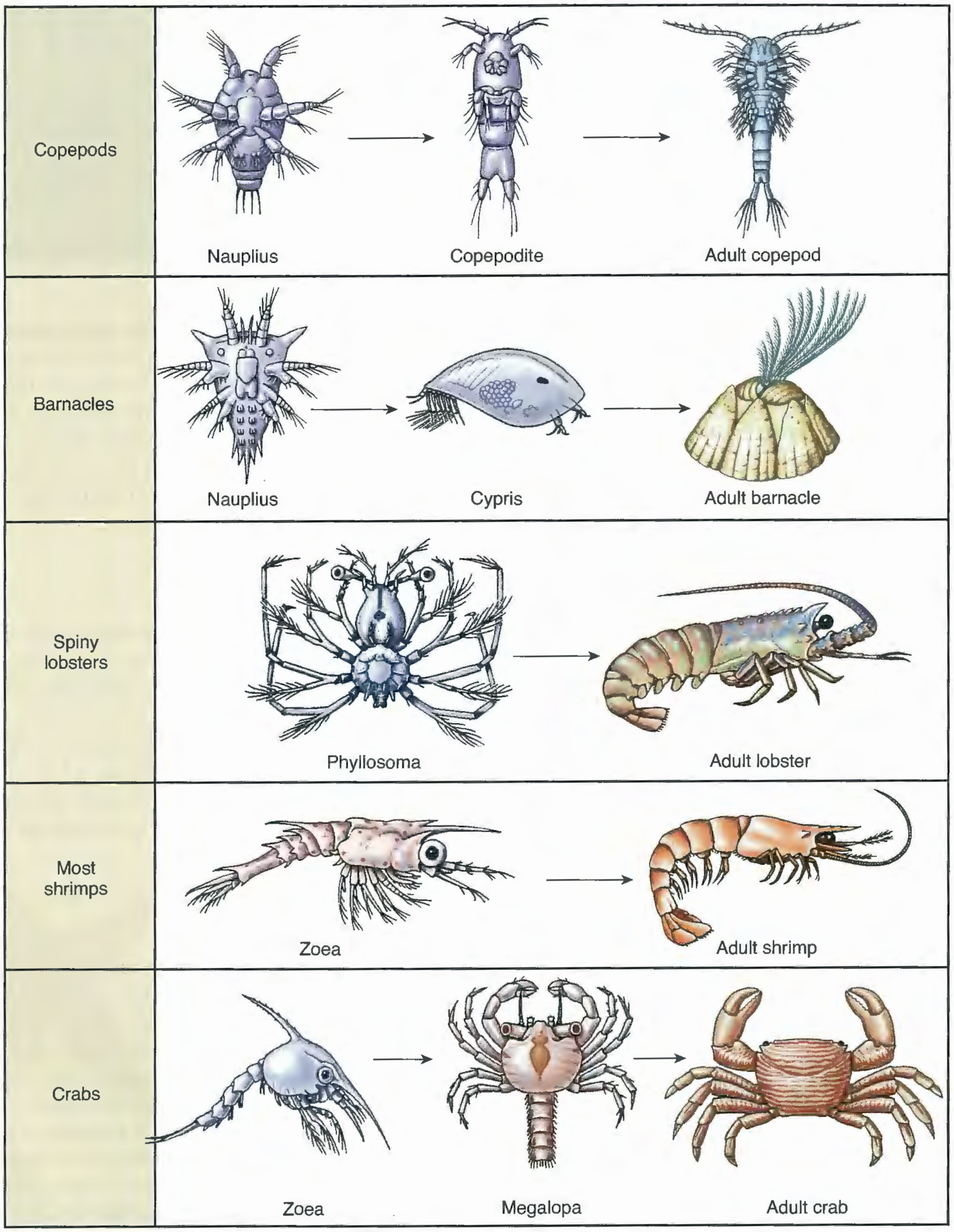


FIGURE 7.39 The eggs of marine crustaceans hatch into planktonic larvae that undergo consecutive molts. Each molt adds a new pair of appendages, with the ones already present becoming more specialized. The last larval stage eventually metamorphoses into a juvenile (see Fig. 13.5). The larvae and adults shown here are not drawn to scale. In most cases, each arrow represents several molts. Other crustacean larvae are shown in Figure 15.13.

America (*Limulus*) and Southeast Asia (*Carcinoscorpius*). Their most distinctive feature is a horseshoe-shaped carapace that encloses a body with five pairs of legs (Fig. 7.40). They emerge on beaches to reproduce.

Sea Spiders **Sea spiders** (class **Pycnogonida**) only superficially resemble true spiders. Four or more pairs of jointed legs stretch from a small body (Fig. 7.41). A large proboscis with the mouth at the tip is used to feed on soft invertebrates such as sea anemones and hydrozoans. Sea spiders are most common in cold waters, but they occur throughout the oceans.

Insects **Insects** (class **Insecta**) are distinguished from other arthropods by having only three pairs of legs as adults. They are

FIGURE 7.40
Limulus polyphemus is a horseshoe crab that grows as long as 60 cm (2 ft), including the tail. It feeds on clams and other small, soft-bottom invertebrates.

FIGURE 7.42
Canda simplex and many other bryozoans form crusty, lace-like colonies.

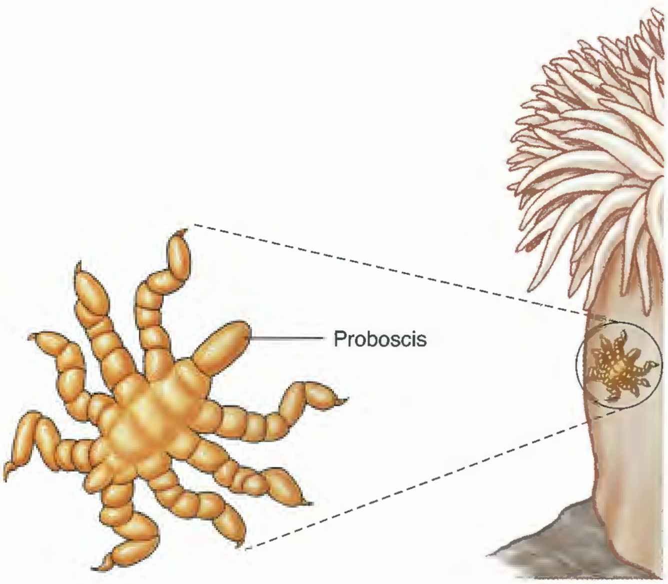


FIGURE 7.41 Sea spiders, or pycnogonids, are often found on soft-bodied invertebrates such as sponges, sea anemones, jellyfishes, and bryozoans. Most shallow-water species are small, with body length rarely over 1 cm (about ½ in.). Some deep-sea sea spiders are bigger, as are species in Arctic and Antarctic waters.

the most diverse group of animals on earth but are rare in the sea. Most marine insects live at the water's edge, where they scavenge among seaweeds, barnacles, and rocks. Many inhabit the decaying seaweed that accumulates at the high tide mark. One marine insect that is found far from shore is the marine water strider (*Halobates;* see Fig. 15.17).

LOPHOPHORATES

Three groups of marine invertebrates have a unique feeding structure, the **lophophore.** It consists of a set of ciliated tentacles arranged in a horseshoe-shaped, circular, or coiled fashion. Lophophorates are suspension feeders, using their cilia to create feeding currents. They share other important traits: lack of segmentation, bilateral symmetry, a coelom, and a **U**-shaped gut.

Bryozoans

Bryozoans ("moss animals") form colonies on seaweed, rocks, and other surfaces. Approximately 4,500 species, almost all marine, are grouped in the phylum **Ectoprocta.** Bryozoan colonies consist of minute interconnected individuals, called **zooids,** that secrete skeletons of a variety of shapes. The colonies may be encrusting or take an upright form that looks like tufts of crusty lace (Fig. 7.42). A close look reveals the rectangular, round, or vase-like compartments occupied by zooids (see Fig. 13.17). The lophophore is retractable. The **U**-shaped gut ends in an anus outside the edge of the lophophore.

Phoronids

At first sight, **phoronids** (phylum **Phoronida**) may be easily confused with polychaetes. They are worm-like and build tubes made in part of sand grains. They have a horseshoe-shaped or circular lophophore, however, and their gut is **U**-shaped, in contrast to the straight gut of polychaetes. All 20 known species are marine, burrowing in sand or attaching their tubes to rocks and other hard surfaces in shallow water. Though one Californian species may reach 25 cm (10 in.), most phoronids are only a few centimeters long.

Lamp Shells

There are close to 350 living species of **lamp shells,** or **brachiopods** (phylum **Brachiopoda**). Thousands of other species are known only as fossils. Lamp shells have a shell with two valves, like the unrelated clams. The two valves are dorsal and ventral to the body, in contrast to the lateral (right and left) valves of clams. When the valves are opened, another major difference between lamp shells and clams is apparent. Lamp shells have a conspicuous lophophore, consisting of at least two coiled and ciliated arms, that occupies most of the space between the valves. Most brachiopods are found attached to rocks or burrowing in soft sediments.

ARROW WORMS

In terms of number of species, the **arrow worms,** or **chaetognaths** (phylum **Chaetognatha**), rank among the smallest animal phyla. Only about 100 species, all marine, are known. They are nevertheless one of the most common and important members of the plankton. They are almost transparent, streamlined, with fish-like fins and tail (Fig. 7.43). The head has eyes, grasping spines, and teeth. Total length ranges from a few millimeters to 10 cm (up to 4 in).

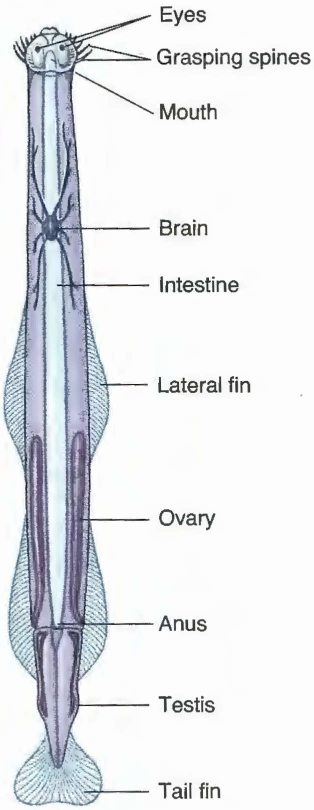


FIGURE 7.43 Arrow worms, or chaetognaths, have a transparent, fish-like body, an adaptation to living as planktonic predators. *Sagitta elegans* ("elegant arrow"), illustrated here, is widely distributed. Notice that individuals have both testes and ovaries.

Arrow worms are voracious carnivores with efficient sensory structures to detect their prey. They prey on small crustaceans, the eggs and larvae of fishes and other animals, other arrow worms, and practically anything else that is small. They spend most of their time motionless in the water but will swim in rapid, darting movements to grab their prey.

ECHINODERMS: FIVE-WAY SYMMETRY

Sea stars, sea urchins, sea cucumbers, and several other forms make up the **echinoderms** (phylum **Echinodermata**). Echinoderms are radially symmetrical, like cnidarians and comb jellies. The radial symmetry of echinoderms, however, is only a secondary development. Their planktonic larvae are bilaterally symmetrical (see Fig. 15.11*c*), and only the adults develop radial symmetry. Unlike cnidarians and comb jellies, echinoderms have **pentamerous** radial symmetry—that is, symmetry based on five parts (Fig. 7.44). As might be expected in a radially symmetrical animal, echinoderms lack a head. They have no anterior or posterior end or dorsal or ventral side. It is useful instead to refer to one surface of echinoderms as oral, because that is where the mouth is located, and the opposite surface as aboral (Fig. 7.44*a* and *b*).

Echinoderms typically have a complete digestive tract, a well-developed coelom, and an internal skeleton. This skeleton,

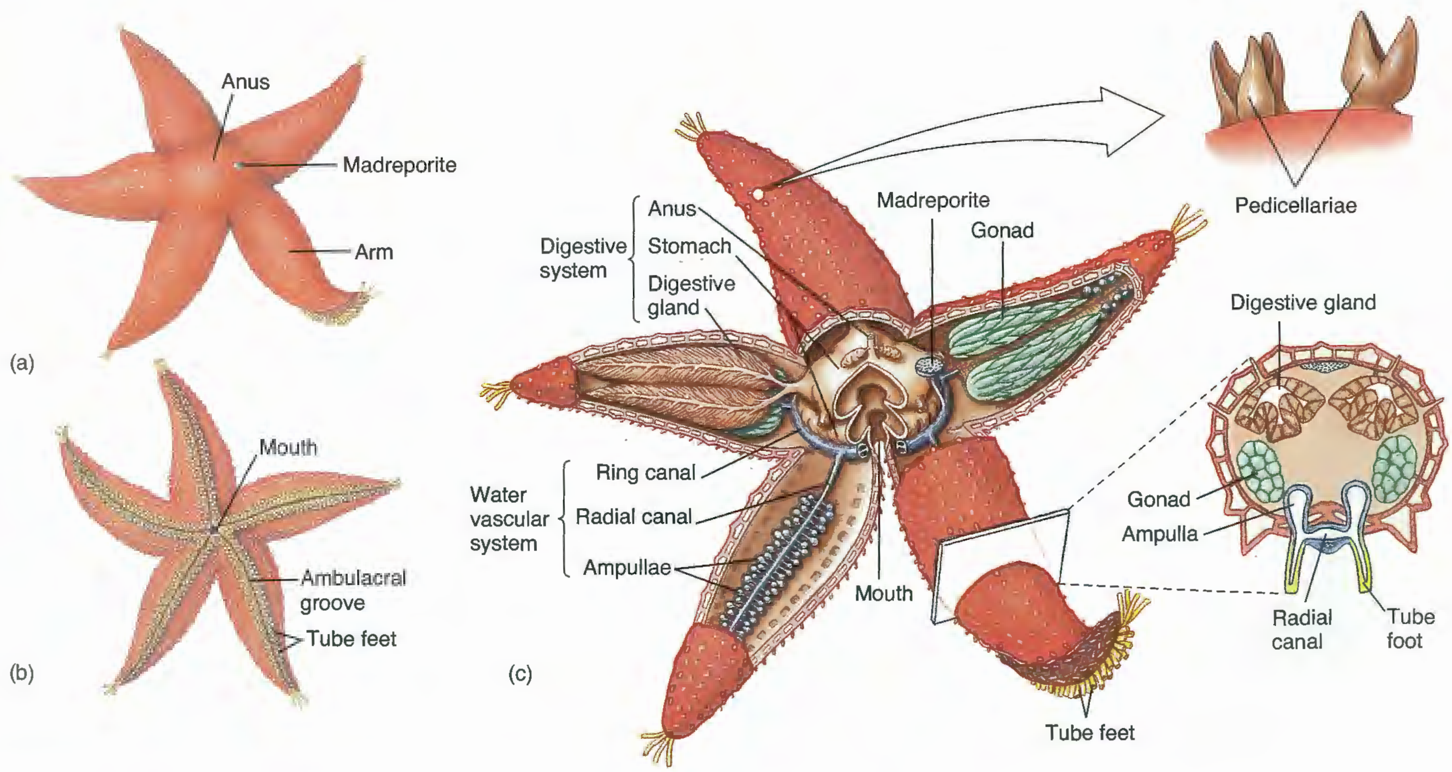


FIGURE 7.44 (*a*) Aboral and (*b*) oral surfaces of a sea star (*Asterias vulgaris*) common on the Atlantic and Gulf coasts of North America. (*c*) Internal structure, with an arm cut across to show the relationship between tube feet, the internal sacs (ampullae), and the canals that make up the water vascular system. This and other carnivorous sea stars evert their thin-walled stomach and begin digesting prey without having to eat it.

like ours, is an **endoskeleton.** It is secreted within the tissues, rather than externally, like the exoskeleton of arthropods. Though sometimes it looks external, as in the spines of sea urchins, the endoskeleton is covered by a thin layer of ciliated tissue. Spines and pointed bumps give many echinoderms a spiny appearance—hence the name Echinodermata, meaning "spiny-skinned."

Unique to echinoderms is the **water vascular system,** a network of water-filled canals (Fig. 7.44*c*). **Tube feet** are muscular extensions of these canals. They are extended when filled with water, sometimes by the action of muscular sacs, the **ampullae,** that extend inside the body opposite the tube feet. Tube feet often end in a sucker and are used for attachment, locomotion, and the reception of chemical and mechanical stimuli. In sea stars and sea urchins (see Fig. 7.48) the system connects to the outside through the **madreporite,** a porous plate on the aboral surface.

(a)

(b)

FIGURE 7.45 (*a*) The giant spined sea star (*Pisaster giganteus*) from the Pacific coast of North America. (*b*) *Linckia guildingi*, from the Caribbean, shows a remarkable ability for regeneration; here the larger arm regenerated the central disk and four small arms to form a complete individual.

Echinoderms are radially symmetrical as adults. They are characterized by an endoskeleton and a unique water vascular system.

Types of Echinoderms

The echinoderms are a large group of about 7,000 known species, all marine. They are important members of bottom communities from the poles to the tropics.

Sea Stars **Sea stars** (class **Asteroidea**), sometimes called starfishes, clearly display the distinctive echinoderm body plan (Fig. 7.44). Most species have five arms that radiate from a central disk, though some have more than five, sometimes close to 50. Hundreds of tube feet protrude from the oral surface along radiating channels on each arm called **ambulacral grooves** (Fig. 7.44*b*). Sea stars can move in any direction, though usually slowly, by reaching out their tube feet and pulling themselves along.

The endoskeleton of sea stars consists of interconnected calcium carbonate plates that form a relatively flexible framework. This allows their arms to be somewhat flexible. The aboral surface of many sea stars is often covered with spines modified into minute, pincer-like organs called **pedicellariae** (Fig. 7.44*c*). They help keep the surface clean.

FIGURE 7.46 *Ophiothrix oerstedii* is a brittle star typically found on sponges and other habitats in the Caribbean.

Most sea stars are predators of bivalves, snails, barnacles, and other attached or slow-moving animals. Typical examples include *Asterias* (Fig. 7.44), common on rocky shores from the North Atlantic to the Gulf of Mexico, and *Pisaster* (Fig. 7.45*a*), its counterpart on the North Pacific.

Brittle Stars **Brittle stars** (class **Ophiuroidea**) also have a star-shaped body architecture. The five arms, however, are long, very flexible, and sharply demarcated from the central disk (Fig. 7.46). The swift, snake-like movements of the arms are used in locomotion. The tube feet, which lack suckers, are used in feeding. Unlike sea stars, the gonads and other internal organs of brittle stars are contained within the central disk and do not extend into the arms.

Most brittle stars eat detritus and small animals they pick up from the bottom of the water. Particles are collected by the tube feet and passed from foot to foot to the mouth. They lack an anus. There are more species of brittle stars, around 2,000, than of any other group of echinoderms. Brittle stars are widely distributed but not always visible, often hiding under rocks and corals or covering themselves with mud or sand.

Sea Urchins In **sea urchins** (class **Echinoidea**) the endoskeleton forms a round, rigid, shell-like test with movable spines and pedicellariae (Figs. 7.47 and 7.48). Locomotion is achieved by the movable spines, jointed to sockets in the test, and the sucker-tipped tube feet. The flat and radiating body plan of sea stars can be transformed into a sea urchin by dropping the arms and pulling the oral and aboral surfaces to form a sphere. The five rows of ambulacral grooves with their tube feet now extend along the outer surface of the sphere (Fig. 7.48). The mouth is on the bottom and the anus on top. The plates that make up the test can be seen in a sea urchin cleaned of spines


(a)


(b)

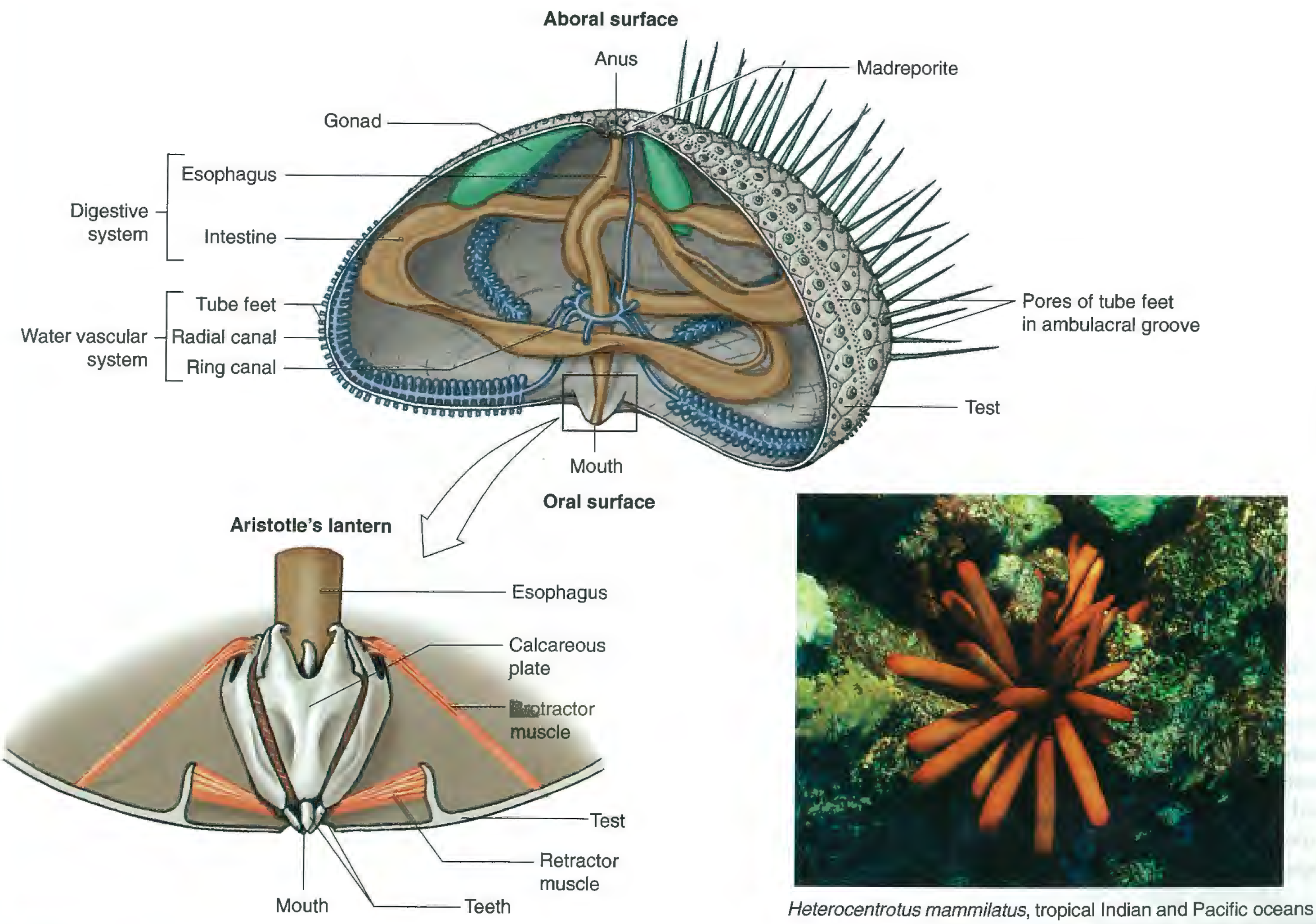
FIGURE 7.47 (*a*) The green sea urchin (*Strongylocentrotus droebachiensis*) is found on rocky shores and kelp forests on the Atlantic, Arctic, and Pacific coasts of North America. (*b*) *Mellita sexiesperforata*, the six-hole sand dollar from sandy bottoms along the southern United States and the Caribbean. The five-part pattern characteristic of all echinoderms can be seen in the light star pattern in the center of the sand dollar.

and tissue. Bands of pores along the ambulacral grooves correspond to the bands of tube feet.

Sea urchins graze on attached or drifting seaweeds and seagrasses. In the process they also ingest detritus and encrusting animals such as sponges and bryozoans. The mouth, directed downward, has an intricate system of jaws and muscles called **Aristotle's lantern** (Fig. 7.48), which is used to bite off algae and other bits of food from the bottom.

Sea urchins are a common sight on rocky shores throughout the world. Examples are species of *Arbacia* from the Atlantic Ocean and Gulf of Mexico and *Strongylocentrotus* from most North Atlantic and Pacific coasts (Figs. 7.47*a* and 13.19). Sea urchins in the tropics show an even richer variety of shapes and sizes, particularly on coral reefs (*Echinometra, Diadema;* see Fig. 14.33).

Not all of the approximately 1,000 species in the class Echinoidea have round tests with prominent spines. **Heart urchins** (see Fig. 13.7) and **sand dollars** (Figs. 7.47*b* and 13.8) are adapted to live in soft bottoms by having flattened bodies and short spines. They are deposit feeders that use their tube feet and sometimes strands of mucus to pick up organic particles.



Heterocentrotus mammilatus, tropical Indian and Pacific oceans

FIGURE 7.48 Internal structure of a typical sea urchin, with a simplified diagram of the Aristotle's lantern. Five pairs of protactor muscles push the lantern down, exposing the teeth; five pairs of retractor muscles move the lantern and teeth in. Additional muscles are responsible for grasping and other movements of the teeth.

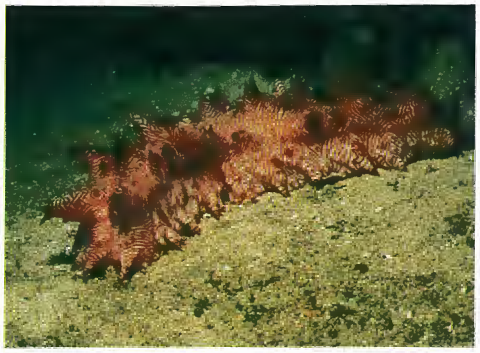


FIGURE 7.49 A sea cucumber (*Thelenota rubralineata*) from Papua New Guinea. Sea cucumbers in general are among the largest echinoderms, reaching 2 m (6.6 ft) in length.

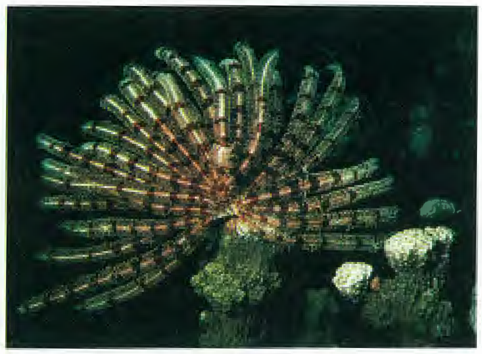


FIGURE 7.50 A feather star, or crinoid, photographed at night at Kwajalein atoll, Marshall Islands. The outstretched arms of feeding individuals can reach a diameter of 70 cm (more than 2 ft). See Figure 7.35 for a close-up of arms.

Sea Cucumbers In yet another modification of the echinoderm body plan, **sea cucumbers** (class **Holothuroidea**) are superficially worm-like (Fig. 7.49). They do not have spines and lack an obvious radial symmetry. The basic body plan of sea urchins appears to have been elongated along the oral-aboral axis, as if they were pulled from the mouth and anus and stretched. The animal lies on one side, where the five rows of tube feet are concentrated. The oral and aboral surfaces are at the ends. The endoskeleton consists of microscopic, calcareous spicules scattered throughout the warty, often tough skin. Like sea urchins, most species have five rows of tube feet extending from mouth to anus.

Many sea cucumbers are deposit feeders. The tube feet around the mouth are modified into branched tentacles that are used to pick up organic matter from the bottom or scoop sediment into the mouth (see Fig. 7.3). Some sea cucumbers burrow or hide and extend only their tentacles to obtain food directly from the water.

Many sea cucumbers have evolved novel defensive mechanisms that compensate for the lack of a test and spines. Some secrete toxic substances. When disturbed, some species discharge sticky, sometimes toxic filaments through the anus to discourage potential predators. Others resort to a startling response, the sudden expulsion of the gut and other internal organs through the mouth or anus, a response known as **evisceration.** It is assumed that evisceration distracts the offender while the sea cucumber, which will eventually grow back the lost organs, escapes—messy, perhaps, but effective.

Crinoids Crinoids (class **Crinoidea**) are suspension feeders that use outstretched, feathery arms to obtain food from the water. Crinoids are represented by close to 600 species of **feather stars** (Fig. 7.50) and **sea lilies.** Sea lilies are restricted to deep water and attach permanently to the bottom. Feather stars perch and crawl on hard bottoms in both shallow and deep waters, especially in the tropical Pacific and Indian oceans. They are also capable of graceful swimming.

The body plan of crinoids is best described as an upside-down brittle star with the ambulacral grooves and mouth directed upward. The mouth and larger organs are restricted to a small, cup-shaped body from which the arms radiate. Some crinoids have only five arms but most have many—up to 200—because of branching of the initial five. The arms also have small side branches (see Fig. 7.35). Tiny tube feet along these side branches secrete mucus, which aids in catching food particles. Food makes its way into the mouth by way of ciliated ambulacral grooves. These appendages tilt the body, so that the extended arms orient to currents for efficient suspension feeding.

Biology of Echinoderms

Radial symmetry is associated with sedentary lifestyles. With the exception of limited swimming in some feather stars and some deep-water sea cucumbers, adult echinoderms are relatively slow bottom crawlers. But do they need to be fast to be successful? Certainly not.

Feeding and Digestion The digestive system of echinoderms is relatively simple. Most sea stars are carnivorous. Many feed by extending, or everting, part of their stomach inside out through the mouth to envelop the food. The stomach then secretes digestive enzymes produced by large digestive glands that extend into the arms (Fig. 7.44*c*). The digested food is carried into the glands for absorption and the stomach pulled back inside the body. The intestine is short or missing. Brittle stars and crinoids also have simple, short guts. Brittle stars lack an anus.

The gut of sea urchins and sea cucumbers is long and coiled (Fig. 7.48). In sea urchins this is an adaptation for the lengthier digestion needed for the breakdown of plant material. A long gut also is advantageous to sea cucumbers because they need to process large amounts of sediment to obtain enough organic matter.

In all echinoderms nutrients are transported in the fluid that fills the extensive body cavity. The fluid is called **coelomic fluid** because the body cavity of echinoderms is a coelom.

The coelomic fluid also transports oxygen because most echinoderms lack a distinct circulatory system. In sea stars and sea urchins gas exchange takes place across small, branched projections of the body wall connected at the base to the coelomic cavity. In sea cucumbers water is drawn in through the anus into a pair of thin, branched tubes called **respiratory trees.** The respiratory trees are extensions of the gut and are suspended in the body cavity, surrounded by coelomic fluid. They provide a large surface area in close proximity to the coelomic fluid, thus allowing considerable gas exchange.

Nervous System and Behavior Our knowledge of the nervous system of echinoderms is rather limited. The presence of a nerve net is reminiscent of cnidarians. The nervous system coordinates movements of tube feet and spines in the absence of a brain. Nevertheless, more complex behaviors, such as the righting of the body after being turned over and camouflaging with bits of debris by sea urchins, are evidence that the nervous system may not be as simple as it looks.

Reproduction and Life History The sexes are separate in most echinoderms. In most groups, 5, 10, or more gonads shed sperm or eggs directly into the water. The gonads are usually located in the body cavity and open to the outside by way of a duct (see Figs. 7.44*c* and 7.48). Gametes do not survive long in the water, so in many species individuals spawn all at once to ensure fertilization.

Development of the fertilized egg proceeds in the plankton and typically results in a ciliated larva characteristic of each group (see Fig. 15.11*b* and *c*). Echinoderm larvae are bilaterally symmetrical and it is not until metamorphosis that radial symmetry develops. Some echinoderms do not have planktonic larvae and brood their offspring in special pouches or under the body.

Some sea stars, brittle stars, and sea cucumbers regularly reproduce asexually by the separation of the central disk or body into two pieces. The resulting halves then grow into complete individuals. **Regeneration,** the ability to grow lost or damaged body parts, is highly developed in echinoderms. Sea stars, brittle stars, and crinoids regenerate lost arms. In some sea stars a severed arm can grow into a new individual (see Fig. 7.45*b*). Efforts to control sea stars that prey on oyster beds or corals by cutting them up and throwing the pieces back into the water have failed miserably. In most sea stars, however, only arms that include portions of the central disk can regenerate.

HEMICHORDATES: A "MISSING LINK"?

The search for evolutionary links between the chordates—our own phylum—and other groups of animals (see Fig. 7.54) has been a provocative challenge, and several explanations have been proposed. As strange as it may seem, echinoderms and chordates share several features related to the development of our embryos. The wide evolutionary gap between echinoderms and chordates, however, may be filled by a small and infrequently seen group of worms, the **hemichordates** (phylum **Hemichordata**). Hemichordates share the same basic developmental characteristics of chordates and echinoderms. Some hemichordates also have a larva similar to that of some echinoderms. Hemichordates share with us chordates some of the features used to define our phylum. These characteristics—a dorsal, hollow nerve cord and openings along the anterior part of the gut—will be discussed in the following section.

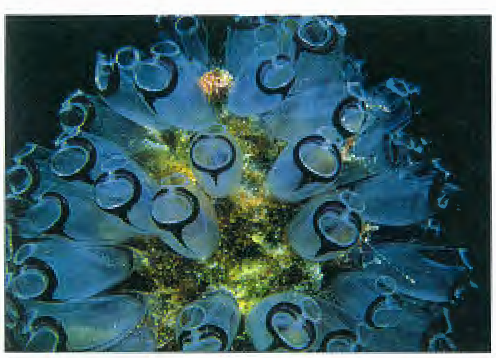
The hemichordates include 85 known species. Most of these are **acorn worms,** or **enteropneusts,** worm-like deposit feeders that live free or in **U**-shaped tubes. Some acorn worms have been found around hydrothermal vents, often in large numbers. They generally range in length from about 8 to 45 cm (3 to 18 in) but some reach 2.5 m (more than 8 ft). Like sea cucumbers, practically all acorn worms ingest sediment, using a thick, mucus-secreting proboscis to collect organic material, which is then swept toward the mouth.

CHORDATES WITHOUT A BACKBONE

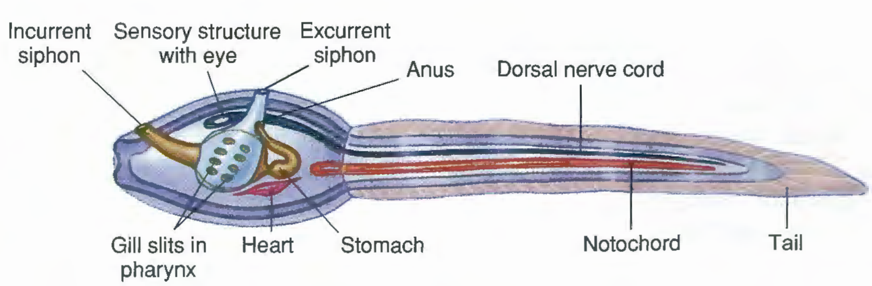
The **chordates** (phylum **Chordata**) are divided into three major groups, or subphyla. Two of these lack a backbone and are discussed here with the invertebrates. These invertebrate chordates are collectively called **protochordates.** The third and by far the largest chordate subphylum comprises the vertebrates, the subject of Chapters 8 and 9.

The estimated 49,000 living species of chordates share many characteristics, but four stand out. During at least part of their development, all chordates, including humans, have (1) a single, hollow **nerve cord** that runs along the dorsal length of the animal, (2) **gill** (or **pharyngeal) slits,** small openings along the anterior part of the gut (or **pharynx**), (3) a **notochord,** a flexible rod for support that lies between the nerve cord and the gut, and (4) a **post-anal tail**—that is, a tail that extends beyond the anus (Figs. 7.51*b* and 7.53). All chordates also have a ventral heart. In vertebrates the notochord is surrounded or replaced by a series of articulating bones, the **backbone,** or vertebral column.

All chordates possess—at least during part of their lives—a dorsal nerve cord, gill slits, a notochord, and a post-anal tail. Vertebrate chordates also have a backbone.



(a)



(b)

FIGURE 7.51 (*a*) *Clavelina picta* is a colonial sea squirt, or ascidian. Its outer covering, the tunic, contains cellulose, a substance typical of plants. (*b*) The tadpole larva of ascidians exhibits all the distinguishing characteristics of chordates. Some of these characteristics, however, are missing in the adults.

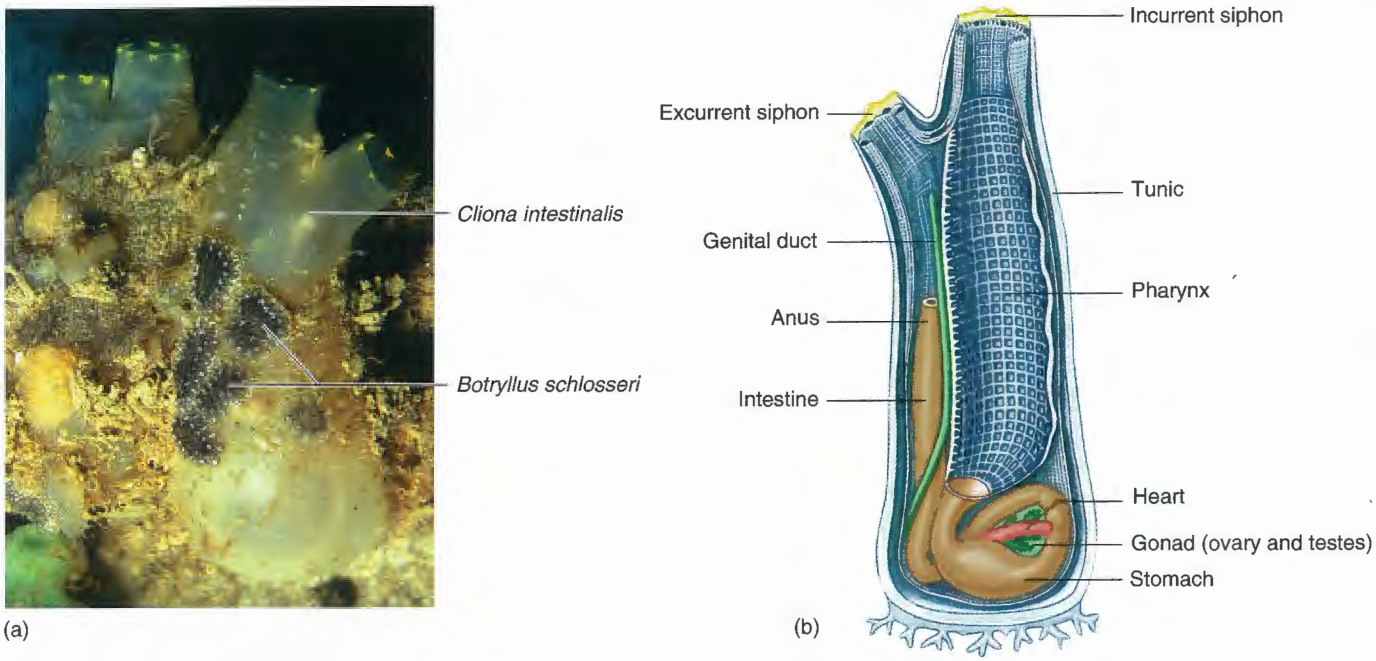


FIGURE 7.52 *Ciona intestinalis* is a shallow-water sea squirt that has become a common fouling animal in many parts of the world. A colonial sea squirt (*Botryllus schlosseri*) can be seen on the outer covering, or tunic, of *Ciona* (*a*).

Tunicates

The largest group of protochordates is the **tunicates** (subphylum **Urochordata**). All 3,000 known species are marine. Those we are most apt to see are the **sea squirts, or ascidians** (class **Ascidiacea**). Their sac-like bodies are attached to hard surfaces, often as fouling organisms (Fig. 7.52*a*), or anchored in soft sediments. They are the only sessile, or permanently attached, chordates. To the inexperienced eye, some sea squirts may be confused with sponges because of their general appearance. The body of the sea squirt, however, is protected by a **tunic,** a leathery or gelatinous outer covering that often has a different texture than that of sponges, and the internal structure is completely different (Fig. 7.52*b*).

Sea squirts are filter feeders. Water typically flows through the mouth, or **incurrent siphon,** and is filtered by a ciliated, sieve-like sac. This sac represents the pharynx, and the openings are derived from the gill slits. Food is filtered from the water and passed into a U-shaped gut. Filtered water is expelled through a second opening, the **excurrent siphon.** When disturbed or expelling debris, ascidians force a jet of water out of both siphons, giving them their common name of sea squirts. Some sea squirts are colonial, some consisting of clumps of separate individuals (Fig. 7.51*a*) and others of a circular, flower-like arrangement of individuals having a common tunic and excurrent siphon (Figs. 7.52*a* and 13.17).

Were it not for their planktonic larvae, the headless, attached sea squirts could easily pass as anything but chordates. The adults possess neither a notochord nor a dorsal nerve cord (Fig. 7.52*b*). Ascidian larvae are known as **tadpole larvae** because of their superficial resemblance to the tadpoles of frogs (Fig. 7.51*b*). Tadpole larvae clearly display the fundamental chordate traits. They have gill slits, a dorsal nerve cord, a notochord, and a well-developed post-anal tail. They also have an eye. Tadpole larvae do not feed; their only purpose is to find a suitable surface on which to settle. During metamorphosis of a tadpole larva into a juvenile ascidian, the notochord and tail are reabsorbed and free existence is no more.

Some tunicates lead a planktonic existence throughout their lives. **Salps** (class **Thaliacea**) have a transparent, barrel-shaped body with muscle bands for locomotion (see Fig. 15.8). Water enters through the anterior mouth, or incurrent siphon, and is forced out through the excurrent siphon on the posterior end. Salps can be extremely abundant, particularly in warm water. Some are colonial, much like floating colonies of sea squirts, and may reach several meters in length. **Larvaceans,** or **appendicularians** (class **Larvacea**) are another group of planktonic tunicates. They retain the body of a tadpole larva through life. Each tiny individual secretes a complex but delicate gelatinous "house" for protection and to filter water for food (see Fig. 15.9).

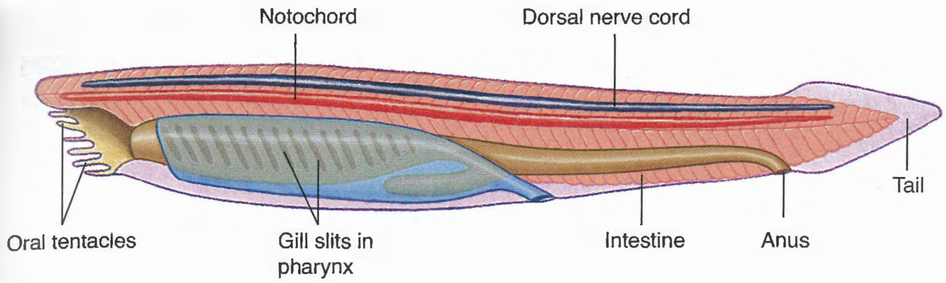


FIGURE 7.53 Though it looks like a fish, the lancelet (*Branchiostoma*) is an invertebrate because it lacks a backbone. The notochord, dorsal nerve cord, and gill slits show it is a chordate.

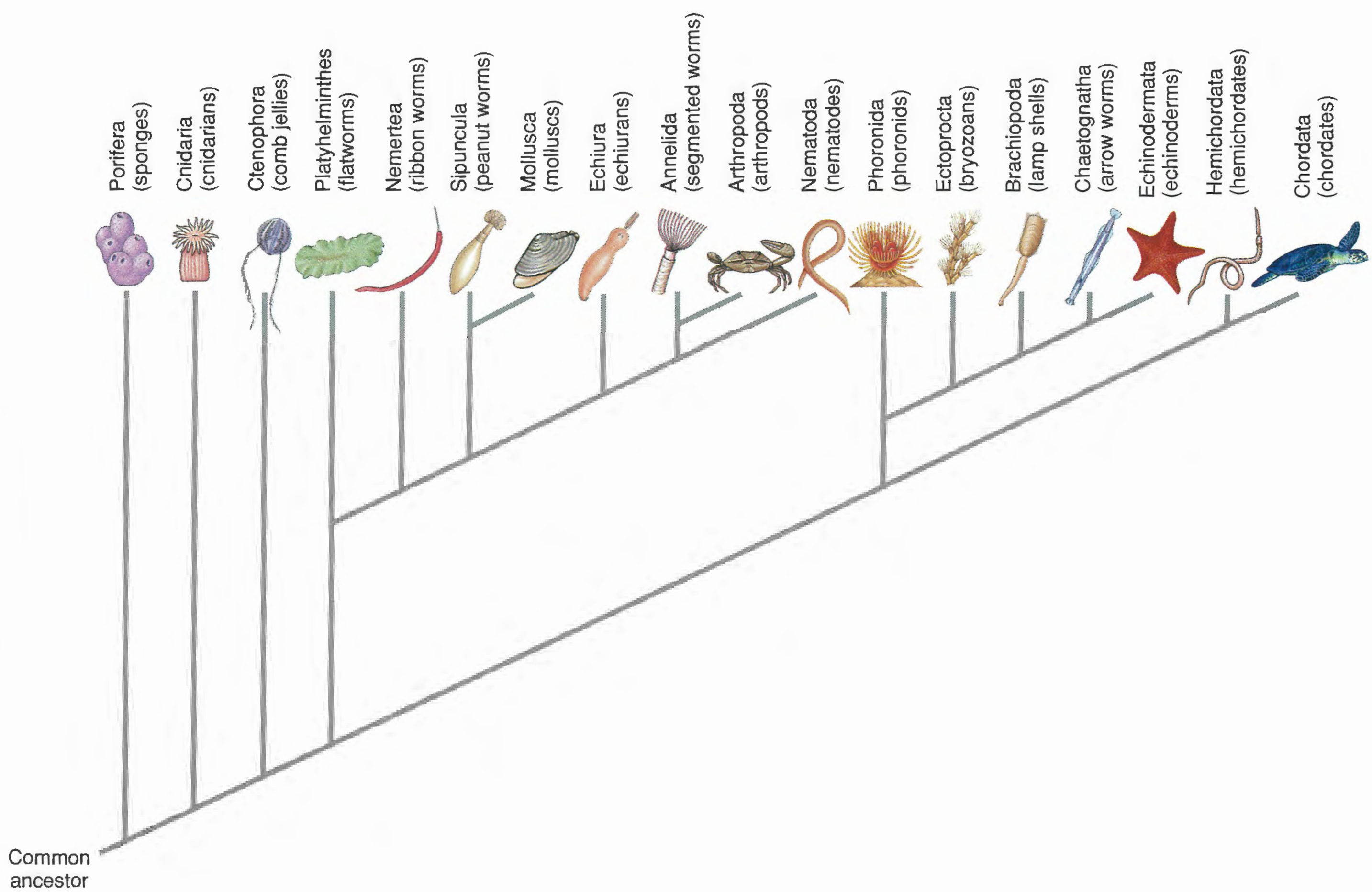
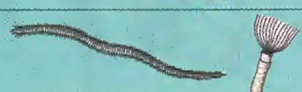
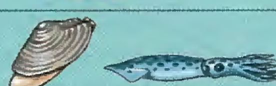
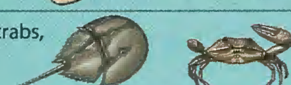
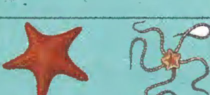


FIGURE 7.54 Phylogenetic relationships among the major animal phyla. This scheme is based on many characters, including morphology, embryological development, and types of larvae. Alternative schemes based on other information have been proposed.

Lancelets

The second group of invertebrate chordates consists of 23 known species of **lancelets** (subphylum **Cephalochordata**). The body, up to 7 cm (close to 3 in) long, is laterally compressed and elongated like that of a fish (Fig. 7.53). The basic chordate characteristics are well developed throughout life. Only the lack of a backbone separates lancelets from vertebrates. Lancelets are inhabitants of soft bottoms. They are filter feeders, using the gill slits to capture and concentrate organic particles.

Table 7.1 Some of the Most Important Characteristics of the Major Animal Phyla

Phylum	Representative Groups	Distinguishing Features	General Habitat	Significance in the Marine Envionment
Porifera (sponges)	Sponges 	Collar cells (choanocytes)	Benthic	Filter feeders
Cnidaria (cnidarians)	Jellyfishes, sea anemones, corals 	Nematocysts	Benthic, pelagic	Predators, passive suspension feeders; corals are important reef builders
Ctenophora (comb jellies)	Comb jellies 	Ciliary combs, colloblasts	Mostly pelagic	Predators
Platyhelminthes (flatworms)	Turbellarians, flukes, tapeworms 	Flattened body	Mostly benthic, many parasitic	Predators, many parasitic
Nemertea (ribbon worms)	Ribbon worms 	Long proboscis	Mostly benthic	Predators
Nematoda (nematodes)	Nematodes, roundworms 	Body round in cross section	Mostly benthic, many parasitic	Many parasitic, deposit feeders
Annelida (segmented worms)	Polychaetes, oligochaetes, leeches 	Segmentation	Mostly benthic	Predators, deposit feeders, passive suspension feeders
Sipuncula (peanut worms)	Peanut worms 	Long, retractable anterior end	Benthic	Predators
Echiura (echiurans)	Echiurans 	Non-retractable proboscis	Benthic	Predators
Mollusca (molluscs)	Snails, clams, oysters, octopuses, chitons 	Foot, mantle, radula (absent in some groups)	Benthic, pelagic	Predators, grazers, filter feeders, some parasitic
Arthropoda (arthropods)	Crustaceans (crabs, shrimps), insects 	Exoskeleton, jointed legs	Benthic, pelagic, some parasitic	Predators, grazers, filter feeders, some parasitic
Ectoprocta (bryozoans)	Bryozoans 	Lophophore, colonial	Benthic	Filter feeders
Phoronida (phoronids)	Phoronids 	Lophophore, worm-like body	Benthic	Filter feeders
Brachiopoda (lamp shells)	Lamp shells 	Lophophore, clam-like shells	Benthic	Filter feeders
Chaetognatha (arrow worms)	Arrow worms 	Transparent body with fins	Filter feeders	Predators
Echinodermata (echinoderms)	Sea stars, brittle stars, sea urchins, sea cucumbers 	Tube feet, five-way radial symmetry, water vascular system	Predators	Predators, deposit feeders, passive suspension feeders
Hemichordata (hemichordates)	Acorn worms 	Dorsal, hollow nerve cord, gill slits	Mostly benthic	Deposit feeders
Chordata (chordates)	Tunicates, vertebrates (fishes, reptiles, birds, mammals) 	Dorsal, hollow nerve cord, gill slits, notochord	Benthic, pelagic	Predators, grazers, filter feeders

Level of Organization	Symmetry	Segmentation	Body Cavity	Digestive Tract	Respiratory Exchange	Circulatory System
Cellular	Asymmetrical	No	None	None	Body surface	None
Tissue	Radial	No	None	Incomplete	Body surface	None
Tissue	Radial	No	None	Incomplete	Body surface	None
	Bilateral	No	None	Incomplete or absent	Body surface	None
	Bilateral	No	Proboscis cavity	Complete	Body surface	Closed
	Bilateral	No	Pseudocoelom	Complete	Body surface	None
	Bilateral	Yes		Complete or absent	Gills or body surface	Closed
	Bilateral	No			Body surface	None
	Bilateral	No			Body surface	Closed
	Bilateral	No			Gills	Open or closed
Organ system	Bilateral	Yes			Gills (in many crustaceans)	Open
	Bilateral	No	Coelom		Body surface	None
	Bilateral	No		Complete	Body surface	Closed
	Bilateral	No			Body surface	Open
	Bilateral	No			Body surface	None
	Radial (adults) Bilateral (larvae)	No			Body surface	None
	Bilateral	Reduced			Body surface	Part closed, part open
	Bilateral	Reduced			Gills, lungs	Closed

Interactive Exploration

The *Marine Biology* Online Learning Center is a great place to check your understanding of chapter material. Visit **www.mhhe.com/castrohuber7e** for access to interactive chapter summaries, chapter quizzing, and more! Further enhance your knowledge with videoclips and web links to chapter-related material.

Critical Thinking

1. If bilateral symmetry were to evolve among cnidarians, in which group or groups would you expect it to occur? Why?
2. Cephalopods, the squids, octopuses, and allies, show a much higher degree of structural and behavioral complexity than the other groups of molluscs. What factors triggered the evolution of these changes? A rich fossil record among cephalopods shows that once they were very common and even dominant in some marine environments. Now there are only about 650 living species of cephalopods, far fewer than gastropods. In the end, were cephalopods successful? What do you think happened along the way?
3. A new class of echinoderms, the sea daisies, or concentricycloids, was discovered in 1986. They are deep-water animals living on sunken wood. They are flat and round, looking very much like a small sea star without arms. They also lack a gut. Without ever having seen them, why do you think they were classified as echinoderms, not as members of a new phylum? Do you have any hypotheses as to how they feed or move around?

For Further Reading

Some of the recommended readings may be available online. Look for live links on the *Marine Biology* Online Learning Center.

General Interest

Bottjer, D. J., 2005. The early evolution of animals. *Scientific American*, vol. 293, no. 2, August, pp. 42–47. The discovery of an invertebrate fossil pushes back the origins of complex animals by at least 50 million years.

Duffy, J. E., 2003/2004. Underwater urbanites. *Natural History*, vol. 112, no. 10, December/January, pp. 40–45. Snapping, or pistol, shrimps that live in sponges have evolved complex societies similar to those of bees.

Fortey, R. A., 2004. The lifestyles of the trilobites. *American Scientist*, vol. 92, no. 5, September/October, pp. 446–453. A surprisingly high number of species of trilobites, a group of extinct arthropods, inhabited the oceans 450 million years ago.

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Levy, S., 2004. Crabs in space. *New Scientist*, vol. 181, no. 2438, 13 March, pp. 42–43. Cells in the blood of horseshoe crabs help space scientists detect earth microbes in space probes.

Mather, A., 2007. Eight arms, with attitude. *Natural History*, vol. 116, no. 1, February, pp. 30–36. The fascinating behavior of octopuses never fails to amaze.

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In Depth

Anderson, P., 2004. Cnidarian neurobiology: what does the future hold? *Hydrobiologia*, vol. 530, pp. 107–116.

Collins, M. A. and P. G. K. Rodhouse, 2006. Southern ocean cephalopods. *Advances in Marine Biology*, vol. 50, pp. 191–265.

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Nielsen, C., 2005. Larval and adult brains. *Evolution & Development*, vol. 7, pp. 483–489.

Sotka, E. E., 2005. Local adaptation in host use among marine invertebrates. *Ecology Letters*, vol. 8, pp. 448–459.

Waloszek, D. and A. Maas, 2005. The evolutionary history of crustacean segmentation: a fossil-based perspective. *Evolution & Development*, vol. 7, pp. 515–527.