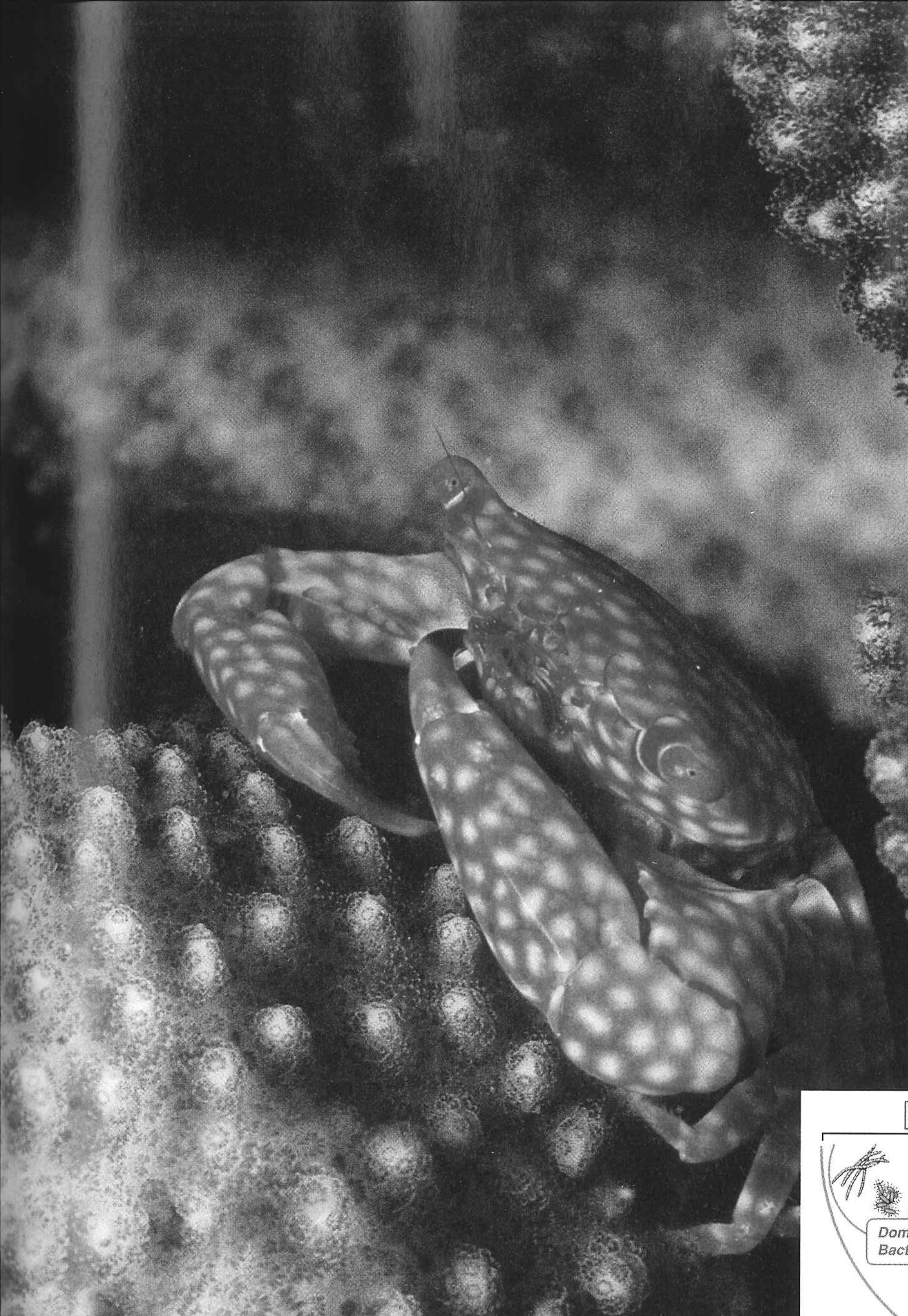
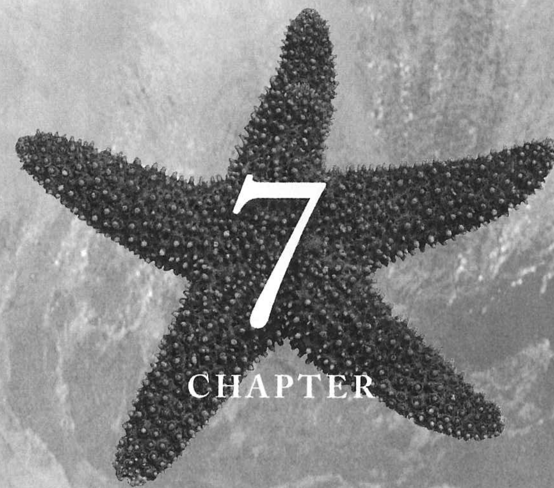
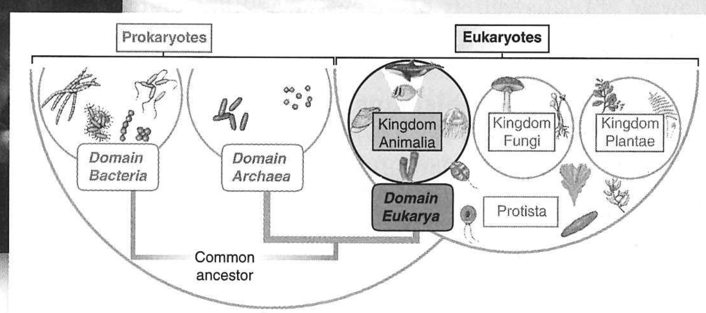


The crab *Trapezia flavopunctata* and its coral host, *Pocillopora*.



7 CHAPTER

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

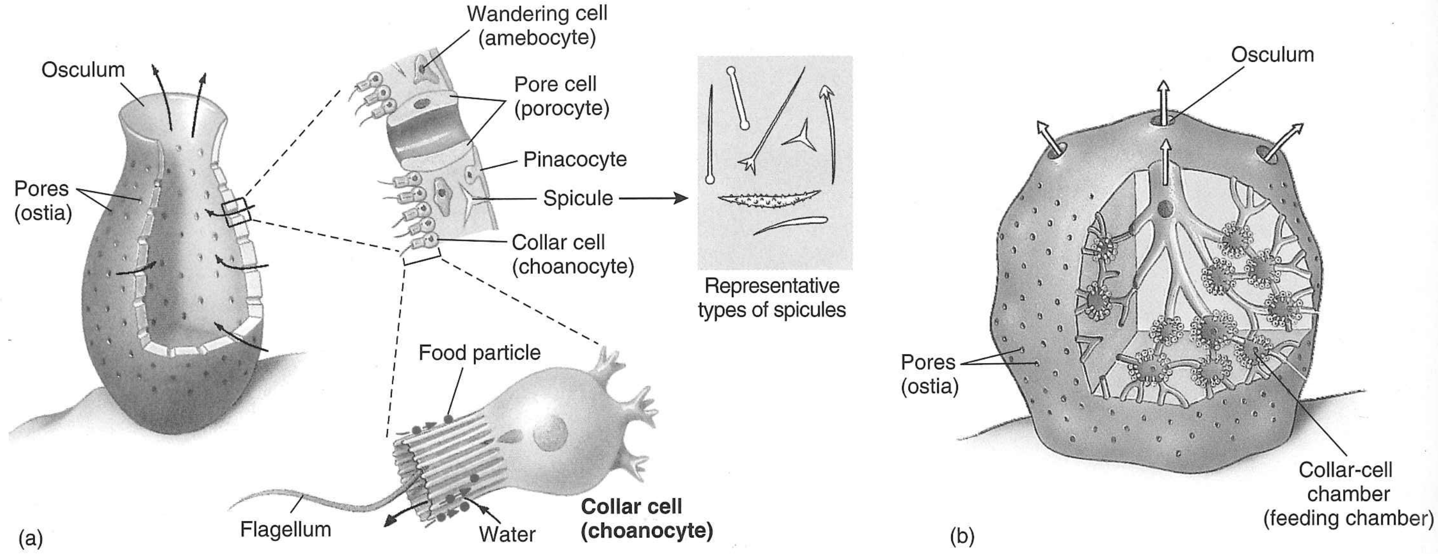


FIGURE 7.1 Sponges consist of complex aggregations of cells that carry out specific functions. Collar cells trap food particles in both (*a*) simple and (*b*) complex sponges.

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.

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

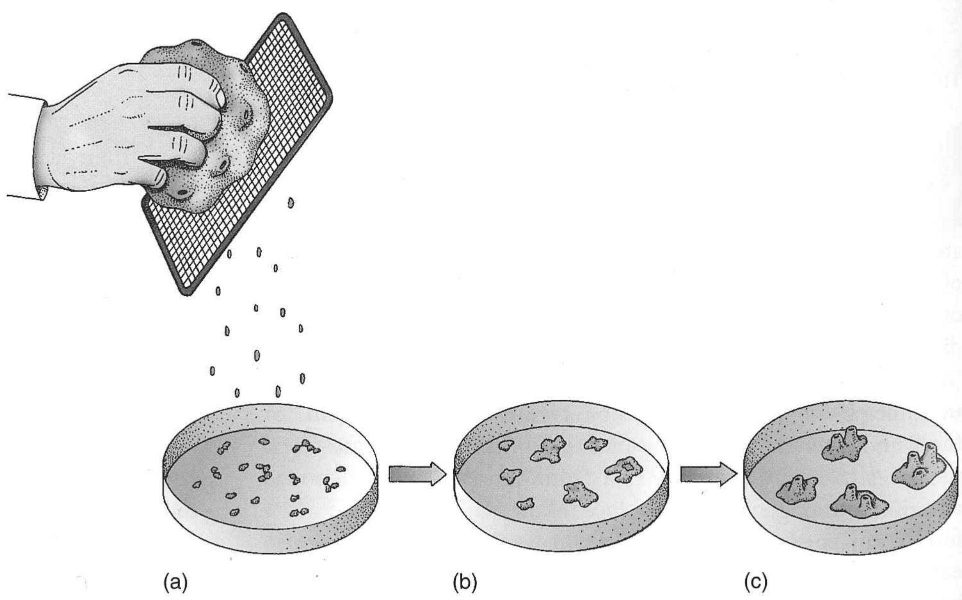


FIGURE 7.2 Some sponges form new individuals after their cells are separated from one another. The cells can be separated by squeezing pieces through a very fine sieve (*a*). In a matter of hours, the cells begin to aggregate and reorganize (*b*) and eventually form new sponges (*c*). When cells of different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

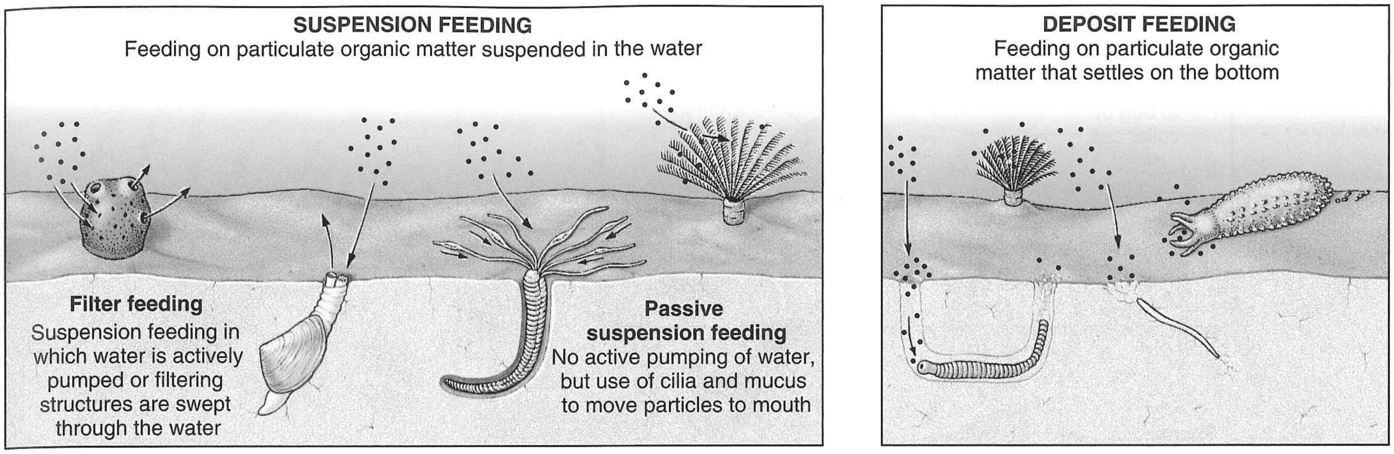


FIGURE 7.3 Feeding on particulate organic matter can be classified as suspension or deposit feeding. The difference between these two types of feeding is not always well defined. Fanworms, for instance, are tube-dwelling polychaetes that switch back and forth between suspension and deposit feeding, depending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

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 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 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

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. 31

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

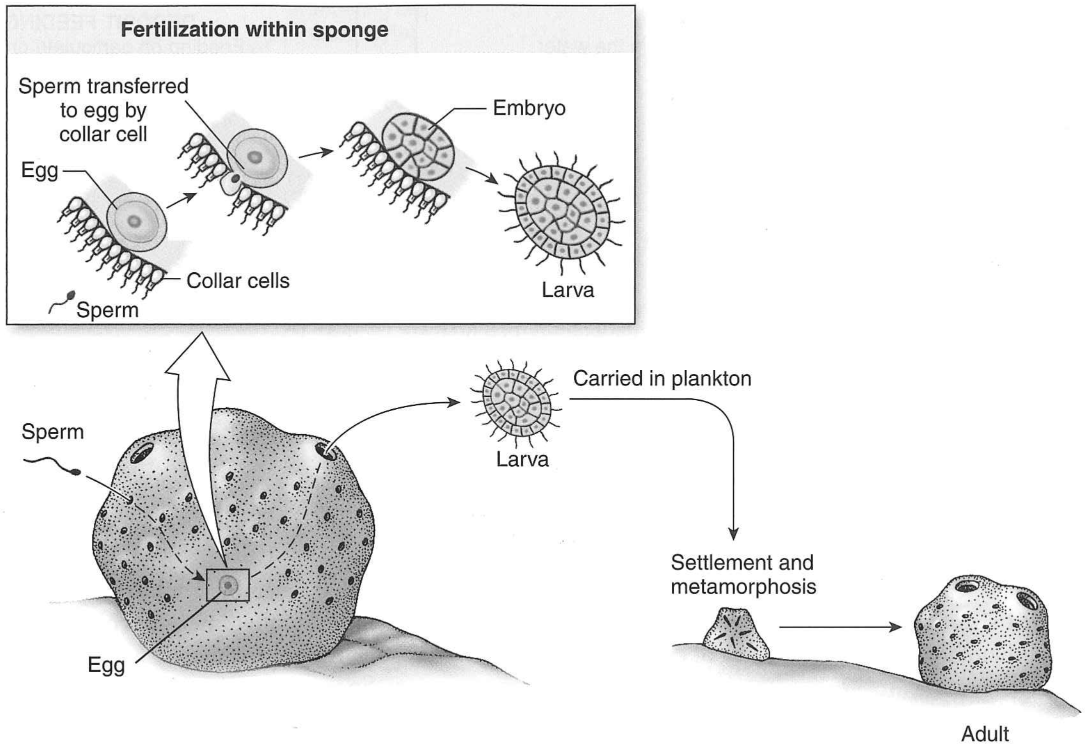


FIGURE 7.4 Sexual reproduction in many marine sponges involves fertilization within the sponge, development of the embryo into a larva, the release of a planktonic larva, and its eventual settlement and metamorphosis into a new sponge on the bottom.

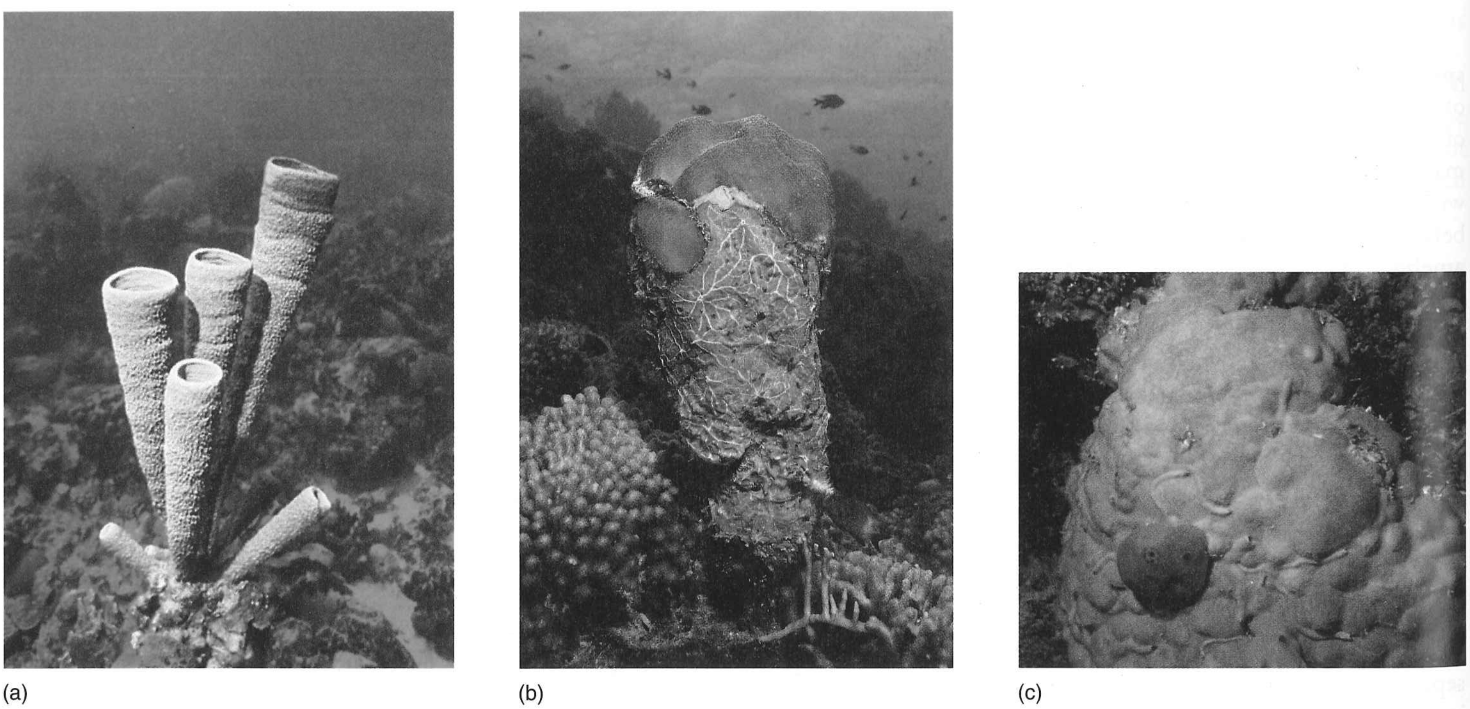


FIGURE 7.5 (*a*) *Aplysina archeri*, a tubular sponge from the Caribbean. (*b*) An encrusting sponge from Hawai'i. (*c*) *Ceratoporella nicholsoni*, a coralline sponge, or sclerosponge, photographed at a depth of 52 m (170 ft) in Puerto Rico. Also see Fig. 4.9.

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. 401).

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

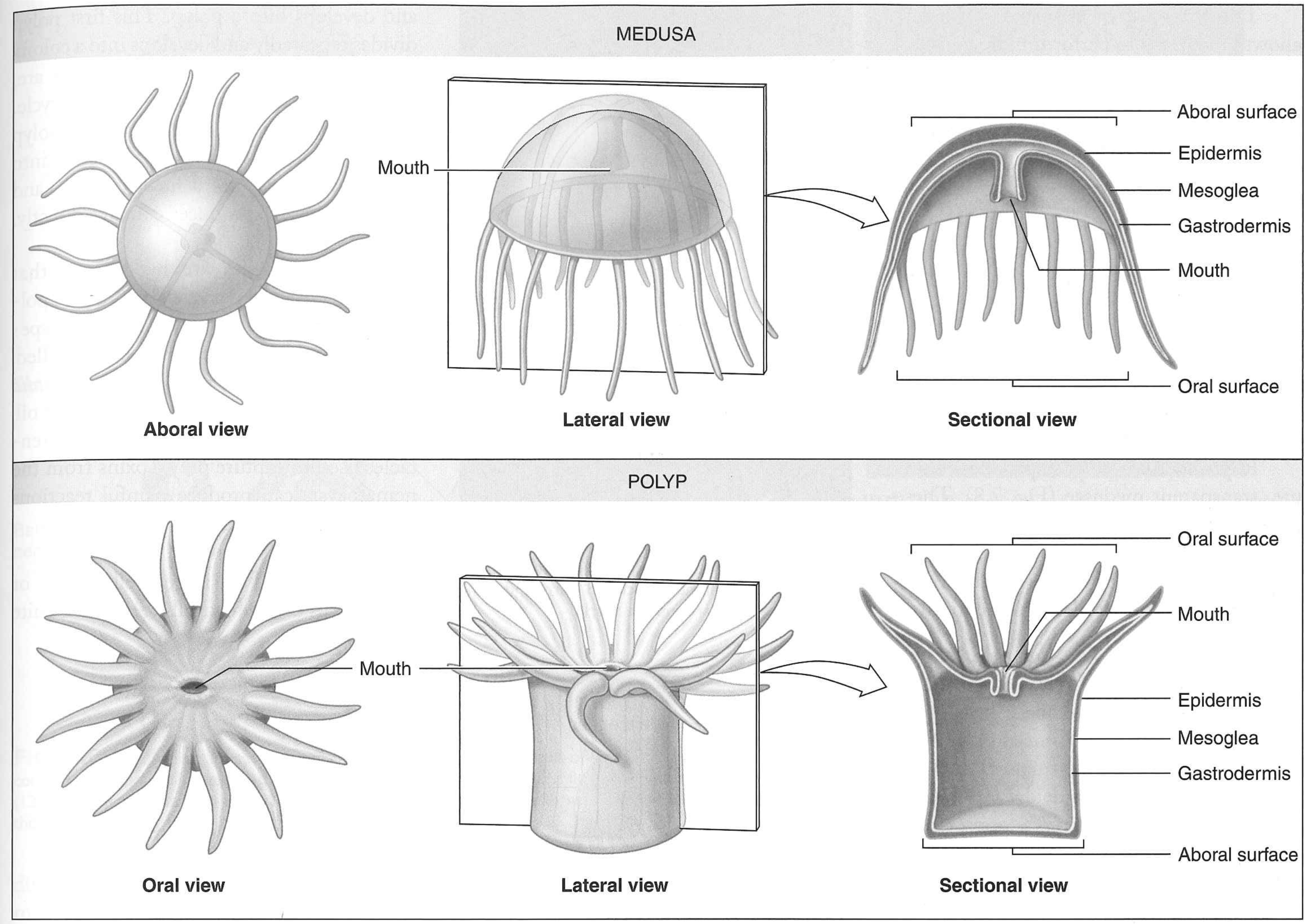


FIGURE 7.6 The flower-like appearance of many cnidarians is a consequence of their radial symmetry. In both the medusa and polyp, tentacles are arranged and repeated around a central axis that runs through the mouth.

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 (or sea jellies), corals, and their relatives.

Besides having a tissue level of organization, cnidarians display **radial symmetry,** where similar parts of the body are arranged and 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. 7.9).

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** (commonly known as jellyfish, or sea jelly), 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, or sea jelly.

The presence of tissues nevertheless allows cnidarians to perform more complex functions than sponges can. Their basic body plan, though structurally simple, has been very successful. Some 10,000 species are known, almost all of which are marine.

Types of Cnidarians

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.

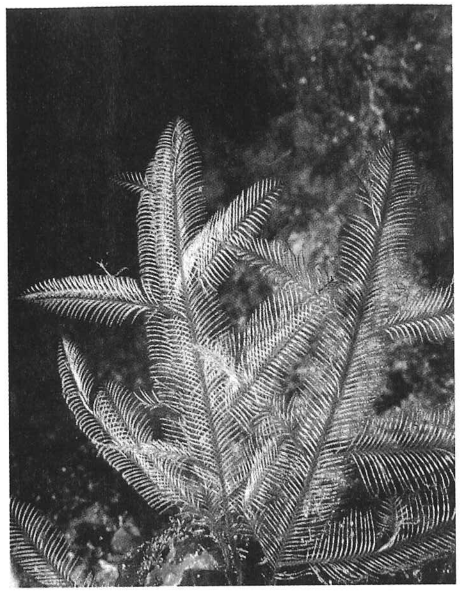


FIGURE 7.7 Colonial hydrozoans include this feather-like colony of the hydroid *Macrorhynchia phillipina*. It is a common species in warm and some temperate waters around the world.

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, or sea jellies, common in all oceans are quite

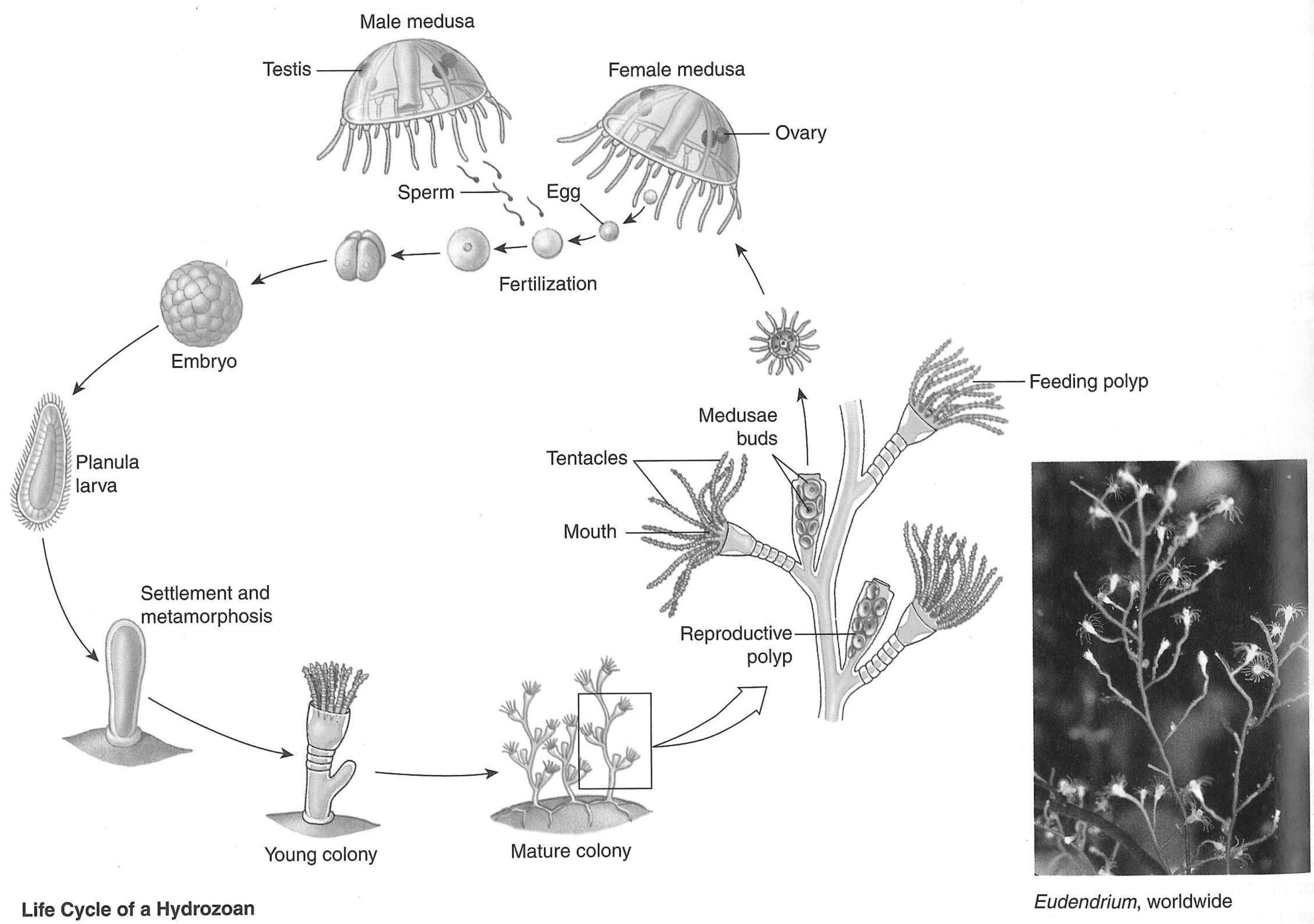


FIGURE 7.8 The life cycles of hydrozoans follow different patterns. A common one involves a sessile, asexually reproducing colony of polyps that releases planktonic, sexually reproducing medusae.

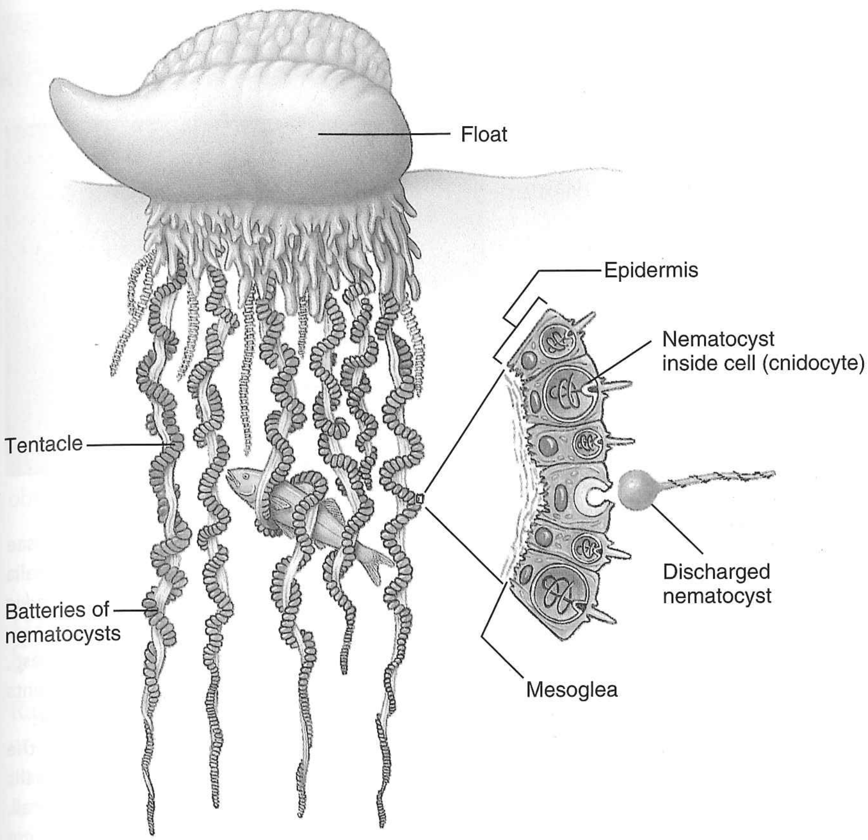


FIGURE 7.9 A diagrammatic representation of the Portuguese man-of-war (*Physalia physalis*). It consists of a colony of specialized polyps, one of which forms a gas-filled float that may reach 30 cm (12 in) in length. The long tentacles, here contracted, are armed with nematocysts notorious for their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

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**). Scyphozoan polyps 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 some 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 can sting swimmers. Jellyfishes in general have become more common and widespread worldwide in recent years, an indication of the declining health of the oceans or perhaps a natural fluctuation in numbers.

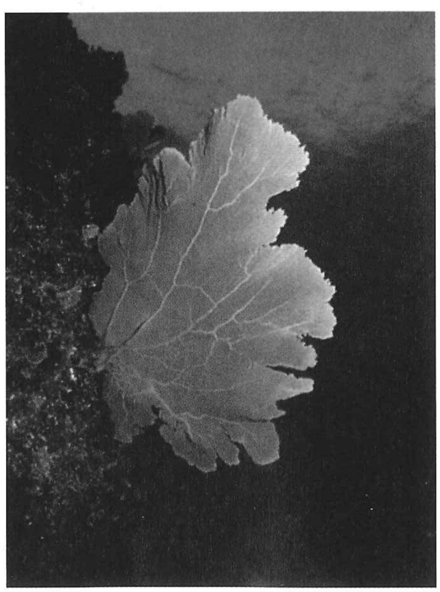


FIGURE 7.11 Sea fans are gorgonians with branches that grow in only one plane and have many cross-connections.

Cubomedusae The **cubomedusae,** or box jellyfishes (class **Cubozoa**), are cnidarians that have a small, mostly transparent, cube-shaped medusa that has only four tentacles, one on each corner. The life cycle includes a minute polyp as in scyphozoans. Box jellyfishes, particularly the sea wasp, are among the most dangerous marine animals known, giving extremely painful and sometimes fatal stings (see "The Case of the Killer Cnidarians," p. 122).

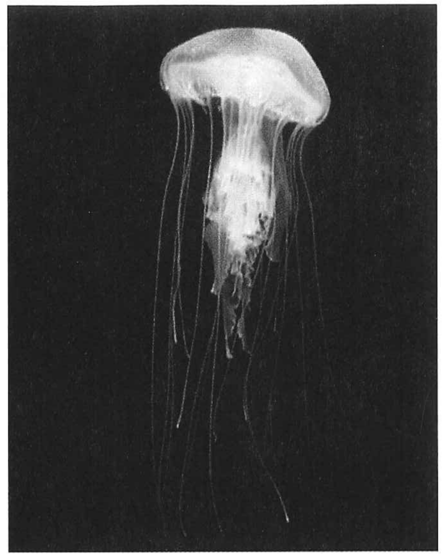


FIGURE 7.10 Scyphozoan medusae are larger and more complex than hydrozoan medusae. This example is the sea nettle (*Chrysaora quinquecirrha*), which is found from Cape Cod to the Gulf of Mexico. It is especially common in the Chesapeake Bay.

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. 11.25). Colonial anthozoans occur in an almost infinite variety of shapes. **Corals** include various groups of mostly colonial anthozoans (see Table 14.1, p. 308). 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.

Biology of Cnidarians

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

The Case of the Killer Cnidarians

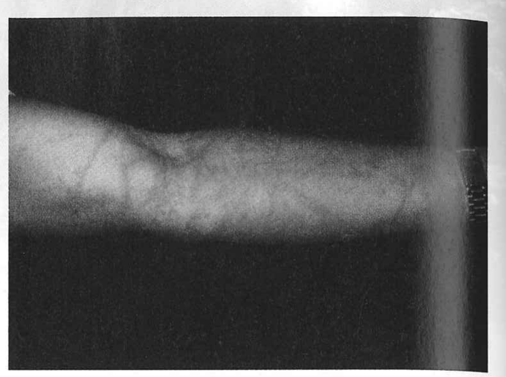
The stings of most cnidarians are harmless to humans, but there are exceptions. Delicate and innocent-looking, some cnidarians are among the most dangerous marine animals. The sinister side of these creatures is due to the potent toxins released by their nematocysts.

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 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. 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, releases even more powerful toxins. The sea wasp, *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 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.

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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.

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**, or **neurons.** 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 scyphozoan medusae have primitive eyes, but the eyes of cubomedusae are known to form images. Medusae also have **statocysts,** small, calcareous bodies in fluid-filled chambers surrounded by sensitive hairs. Statocysts give medusae a sense of balance.

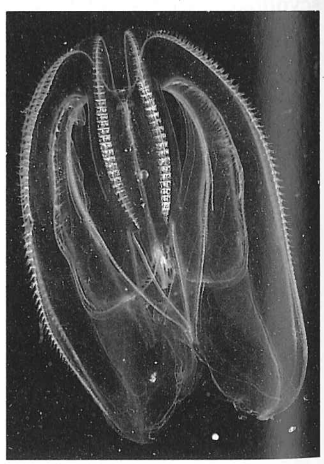


FIGURE 7.12 This comb jelly (*Mnemiopsis leidyi*) displays the rows of ciliary combs characteristic of the group. Four rows are visible here, the middle ones appearing as multicolored bands. The species is common along the Atlantic coast of North America but it has been accidentally introduced into other 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. 418). 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.

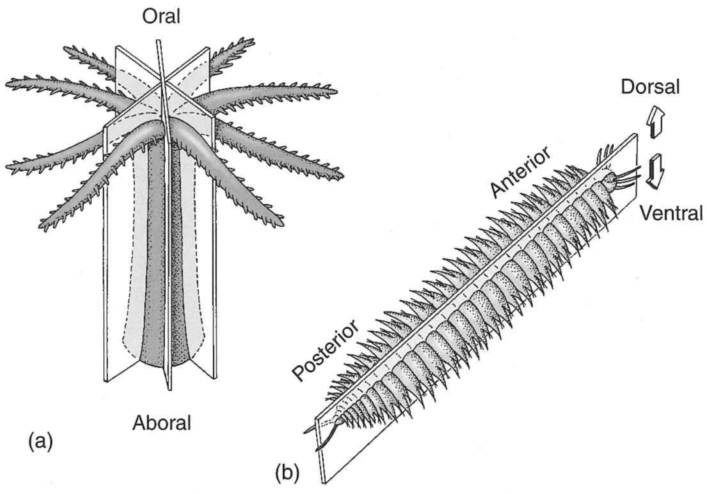


FIGURE 7.13 The radial symmetry of a soft coral's polyp (*a*) in contrast to the bilateral symmetry of a worm (*b*). Bilateral symmetry implies the development of an anterior end with a head, a brain, eyes, and all the other features demanded by more complex behaviors.

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.

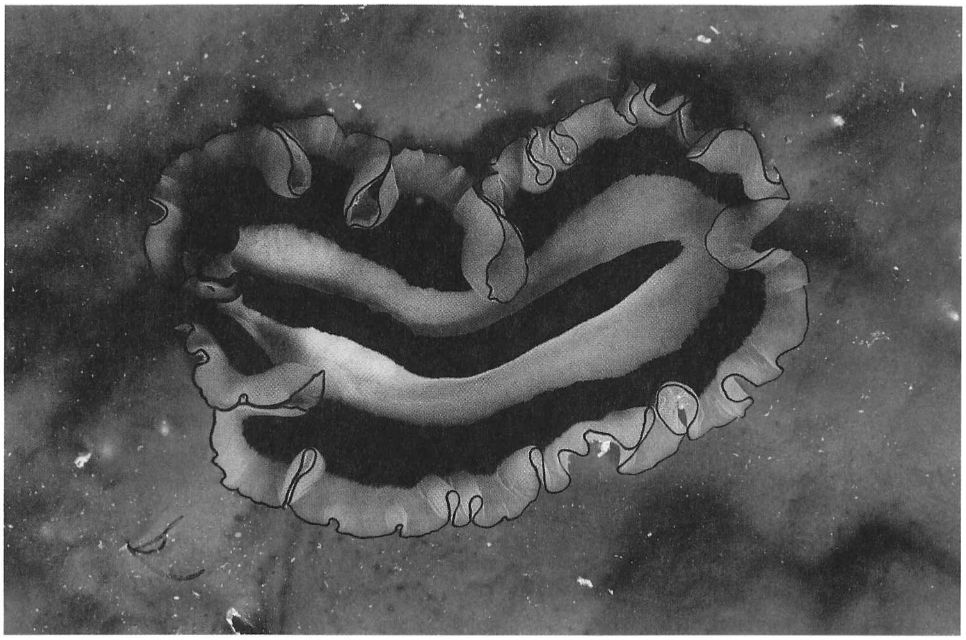
There are some 20,000 known species of flatworms. The most commonly seen marine flatworms are the **turbellarians,** a group that consists mostly of free-living carnivores. Most are small, but some are obvious because of their striking color patterns (Fig. 7.14). Some turbellarians live inside or on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

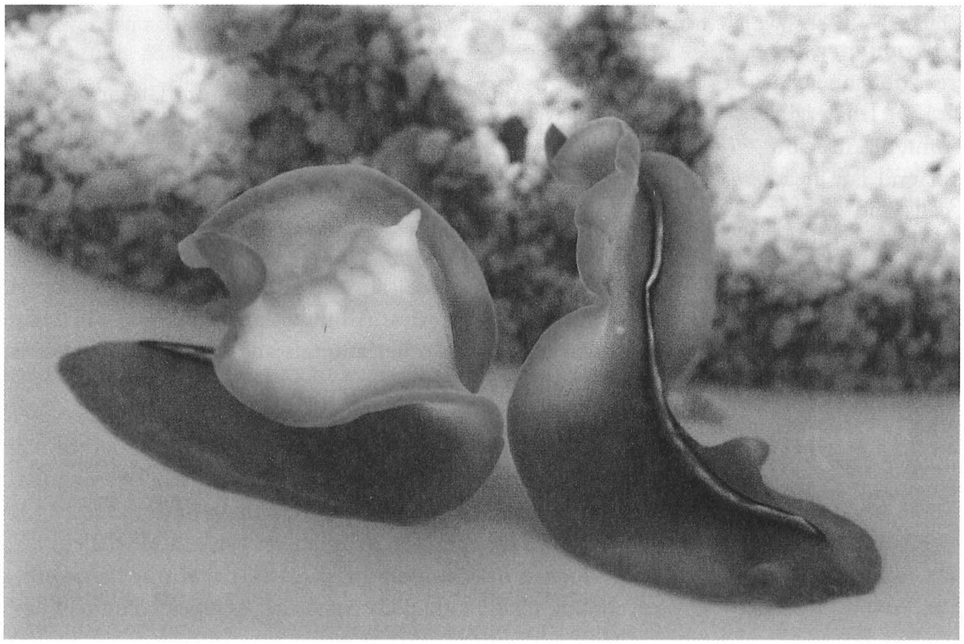
Tapeworms, or **cestodes,** are parasitic flatworms that, with a few exceptions, have a long body consisting of repeated units. These unique worms live inside the intestine of most species of vertebrates, including marine ones. The head of the worm attaches to the walls of the gut by suckers, hooks, 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 whales known to reach 40 m (130 ft), which makes it the longest invertebrate!

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 reduced **body cavity** and



(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.

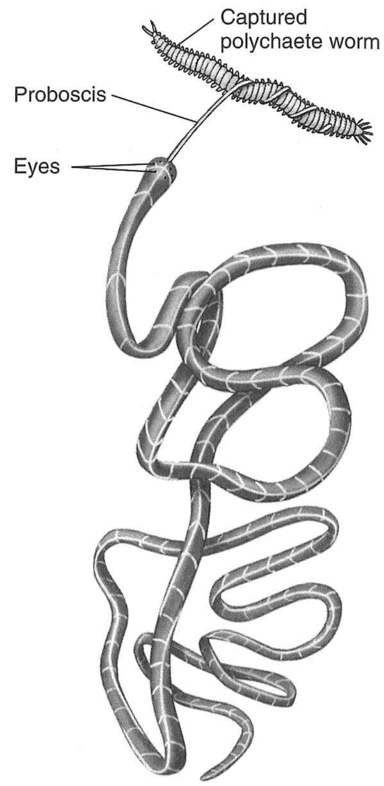


FIGURE 7.15 Ribbon, or nemertean, worms use a proboscis to entangle prey. The proboscis secretes toxins and may be armed at the tip with a spine. Once the prey is captured, the proboscis is pulled back and it's dinnertime.

a **circulatory system,** by which blood transports nutrients and oxygen to tissues. The most distinctive feature of ribbon worms, however, is their **proboscis** (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.

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. 295). Nematodes that inhabit sediments feed mostly on bacteria and organic matter. The gut, which ends in an anus, lies within a well-developed 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 are found 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

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

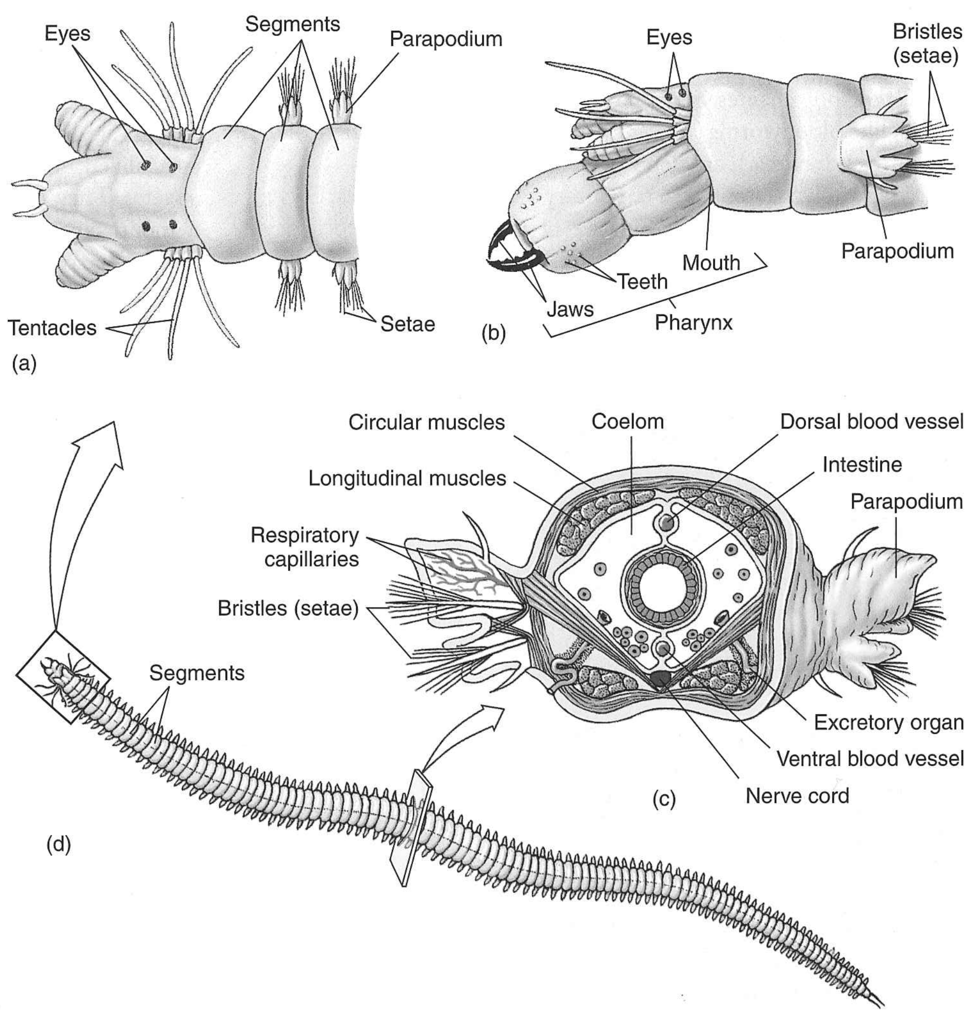


FIGURE 7.16 This sandworm (*Nereis*) illustrates the meaning of the name polychaetes—"many setae, or bristles." (*a*) Dorsal view of the head, with the pharynx retracted, showing the sensory tentacles and eyes. (*b*) Side view of the head, showing the large pharynx in an extended position. (*c*) Section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

polychaetes, however, obtaining enough oxygen from the water is 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.

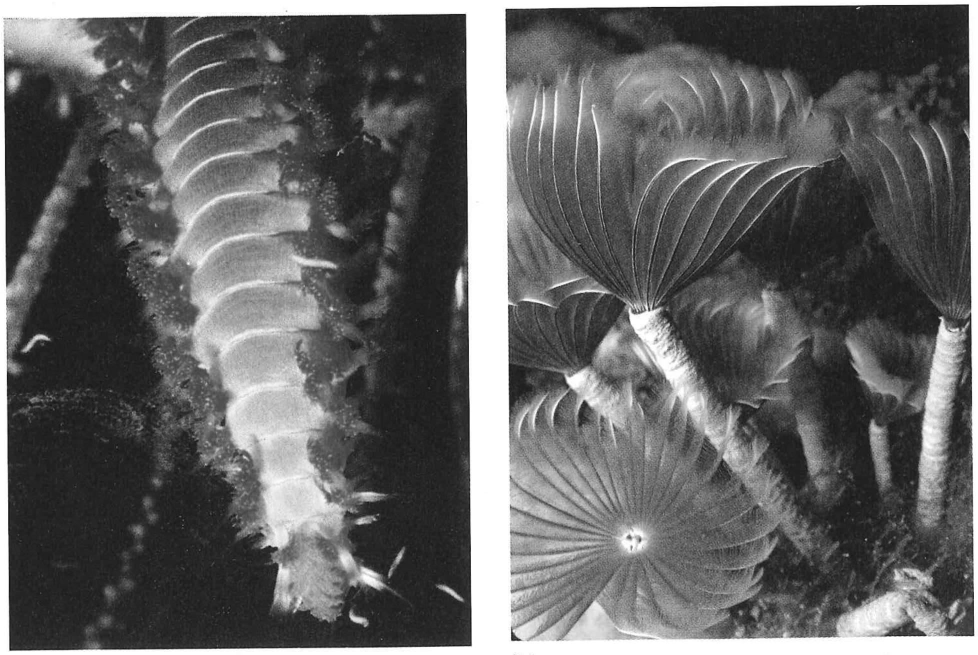
Other polychaetes burrow in mud or sand (see Fig. 11.30). Many, like bloodworms (*Glycera*), capture small prey. Others, like lugworms (*Arenicola*), are deposit feeders (see Fig. 7.3).

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, also known as **pogonophorans,** and **vestimentiferans** are highly specialized polychaetes. They lack a mouth and gut. Except for sponges and tapeworms, this phenomenon



(a) (b)

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.

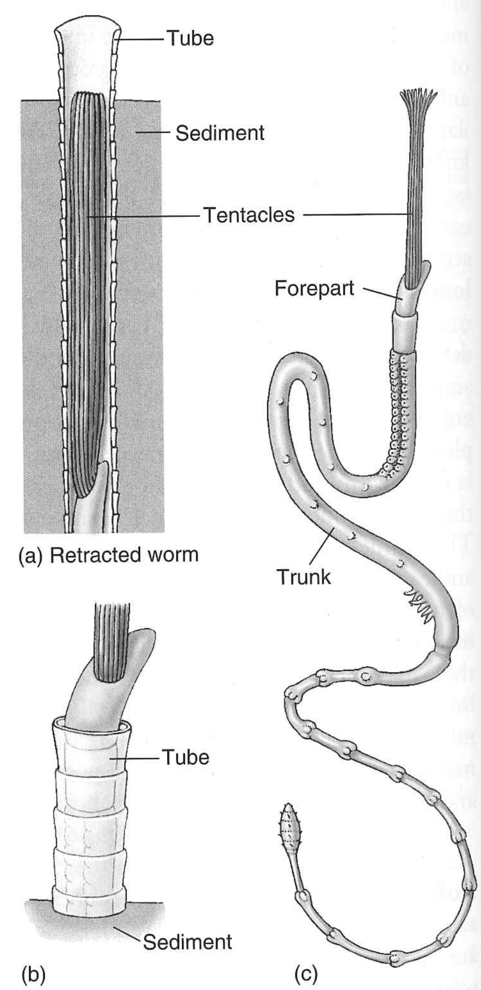


FIGURE 7.18 Diagrammatic representation of a beard worm, or pogonophoran. (*a*) Most secrete and live in tubes buried in the soft sediment. (*b*) Only the upper end of the tube protrudes, with the tentacle or tentacles extending from it. (*c*) Worm removed from its tube.

is uncommon in animals. A tuft of one to many thousand long tentacles characterize beard worms (Fig. 7.18), the tentacles being responsible for the group's common name. The tentacles appear to be involved in absorbing nutrients 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.

Close to 150 species of beard worms are known. They are mostly restricted to deep water, which helps explain why they remained unknown until 1900. Beard worms and vestimentiferans were once grouped as separate phyla. The total length of beard worms ranges from 10 cm to 2 m (4 in to 7 ft).

Large numbers of nearly 20 species of vestimentiferans are found at hydrothermal vents and deep-sea whale remains. These tubeworms depend on symbiotic bacteria to obtain nutrients (see "Hot Springs, Cold Seeps, and Dead Bodies," p. 379).

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.

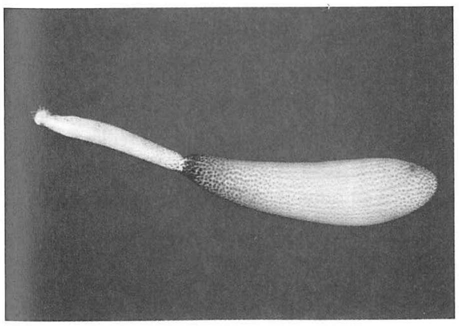


FIGURE 7.19 *Antillesoma antillarum,* a peanut worm (or sipunculan), burrows in coral and rocks in the Caribbean. The anterior portion, which is extended in this specimen, can be retracted.

Echiurans

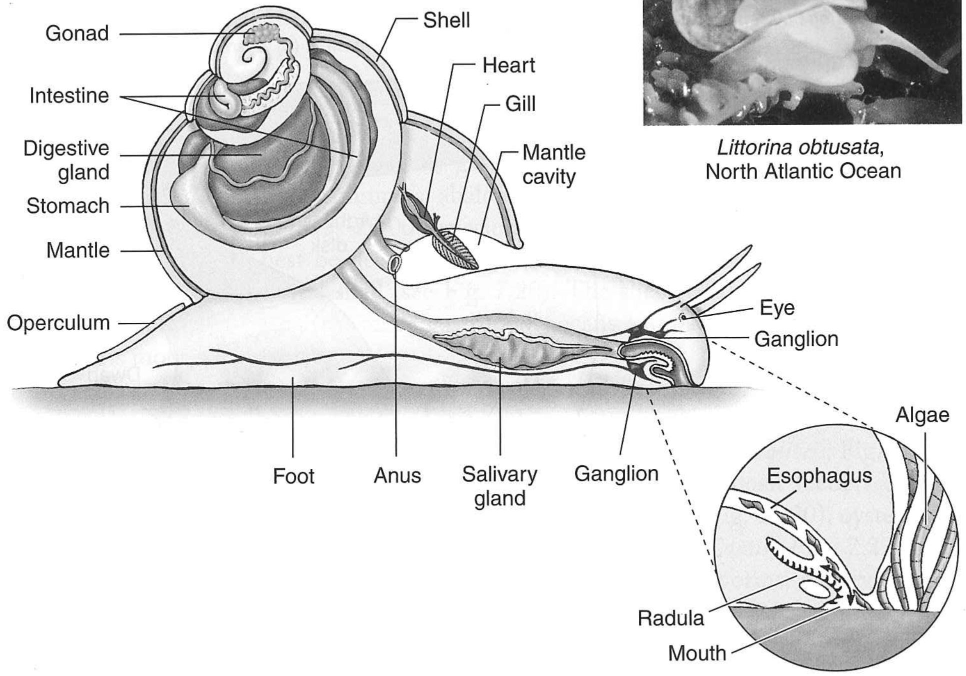
All of the 135 known species of **echiurans** (phylum **Echiura**) are marine. They look like soft, unsegmented sausages buried in the mud or in coral. They are similar to peanut worms in shape and size except for having a non-retractable, spoon-like or forked proboscis (see Fig. 13.9). Some biologists 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).

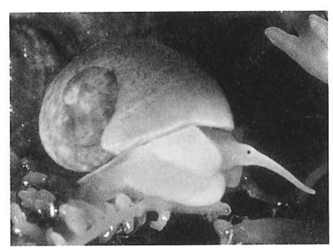
MOLLUSCS: THE SUCCESSFUL SOFT BODY

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. They exhibit an immense diversity of structures and habits, thrive on practically every conceivable type of diet, and occupy all marine environments, from the wave-splashed zone of rocky shores to hydrothermal vents in the deep sea. 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 thin layer

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. 295). 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.

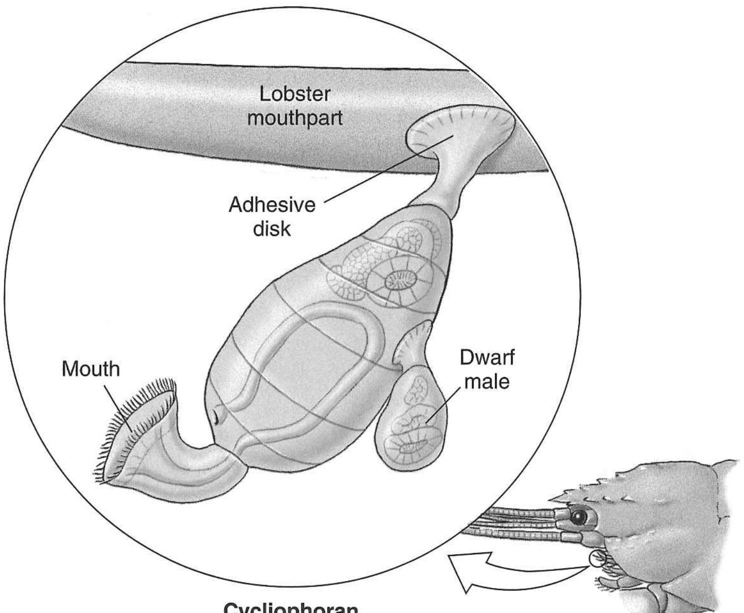
The microscopic animals Kristensen found have a body encased by six plates. The head, which can be retracted, bears a set of spines and a mouth at the end of a cone. Kristensen got together with Higgins, and they concluded that the specimens Higgins examined in 1974 and those subsequently found by Kristensen 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 was discovered on the European lobster.



Cycliophoran

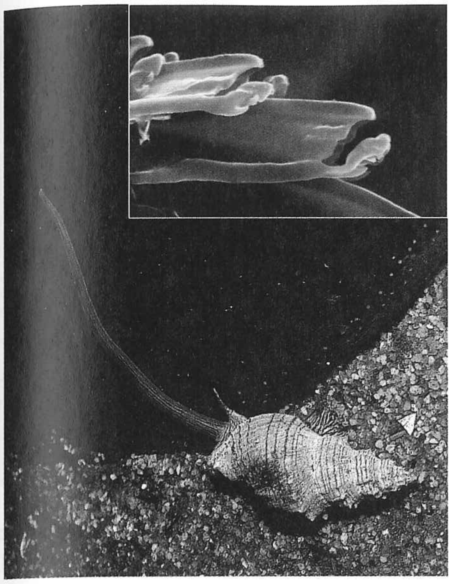


FIGURE 7.21 The Cooper's nutmeg snail (*Cancellaria cooperi*) seeks out electric rays, which rest partially buried in sand. It then extends its long proboscis, makes a tiny cut in the ray's skin with the radula at the end of the proboscis, and then sucks the ray's blood. A high-magnification photo (inset)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

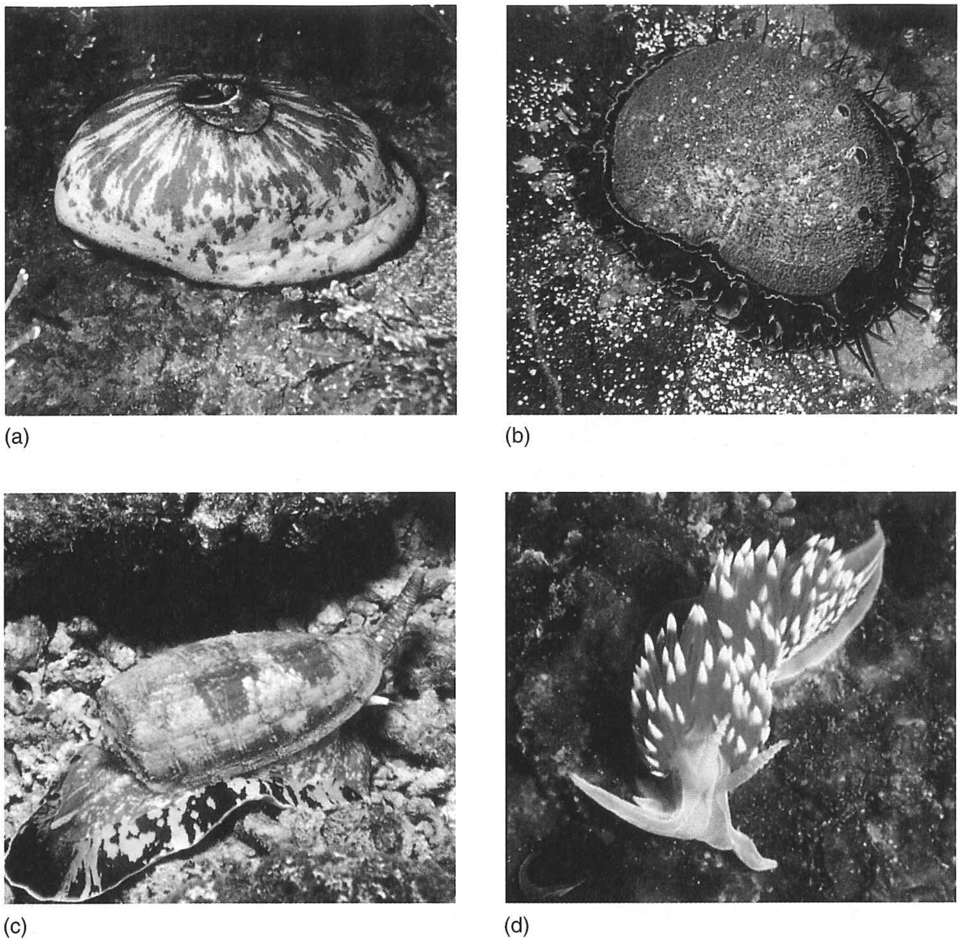


FIGURE 7.22 Gastropods come in all shapes, colors, and habits. (*a*) The giant keyhole limpet (*Megathura crenulata*), from the Pacific coast of North America, photographed on a bottom covered by encrusting red coralline algae. (*b*) The red abalone (*Haliotis rufescens*) is much sought after for food 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). The poison is now used as a painkiller in humans. (*d*) A flashy nudibranch (*Phidiana crassicornis*).

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

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. 11.20), oyster drills (*Murex, Urosalpinx*), and cone shells (*Conus;* Fig. 7.22*c*), are carnivores. They prey on clams, oysters, worms, and even small fishes (see Fig. 10.7). 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. 11.29 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 photo on p. 262), for instance, secrete strong **byssal threads** that attach them to rocks and other surfaces. Oysters (*Ostrea, 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, Chlamus;* 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 **biofouling,** the undesirable accumulation of organisms that settle on the bottoms of boats, pilings, and other submerged structures.

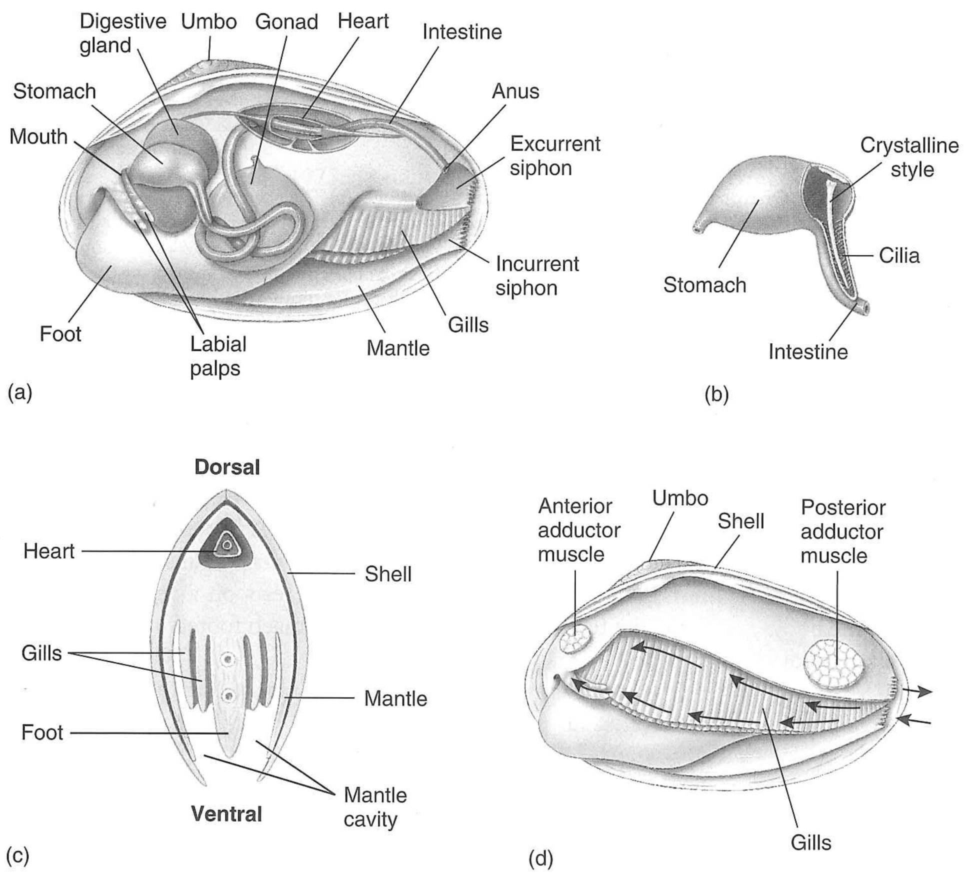


FIGURE 7.23 A laterally compressed body is the most distinctive feature of bivalves, illustrated here by a clam. The gills, which hang on both sides of the body (*a, c*), sort out food particles and transport them to the mouth with the help of cilia and mucus. The palps then push the food into the mouth. 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*).

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 to

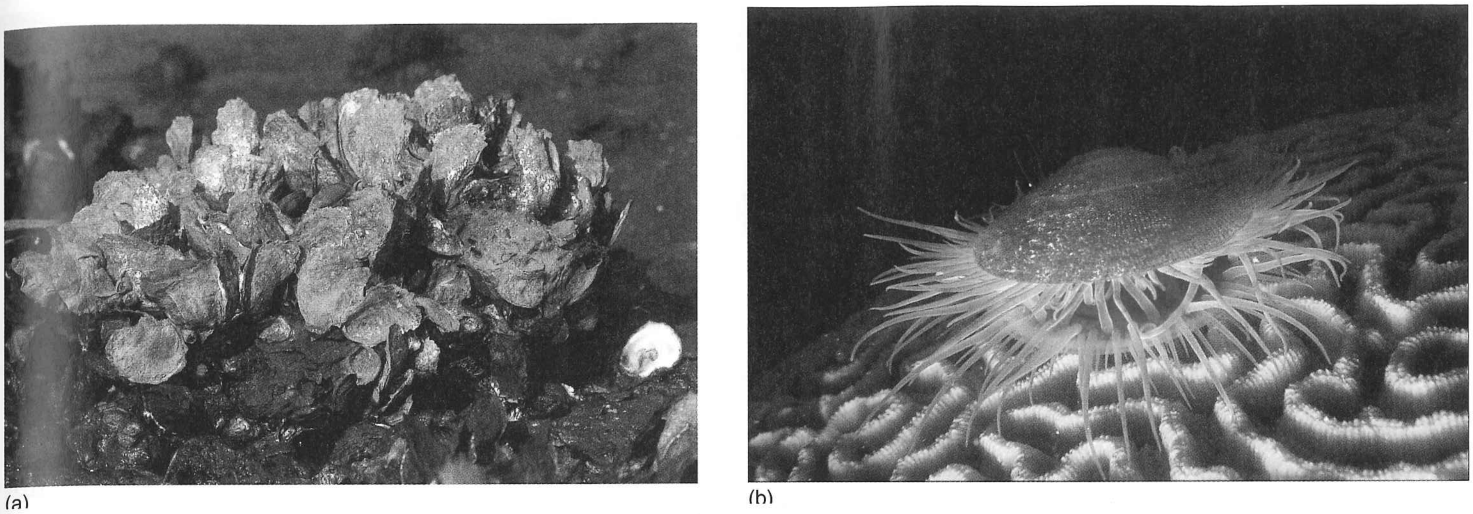
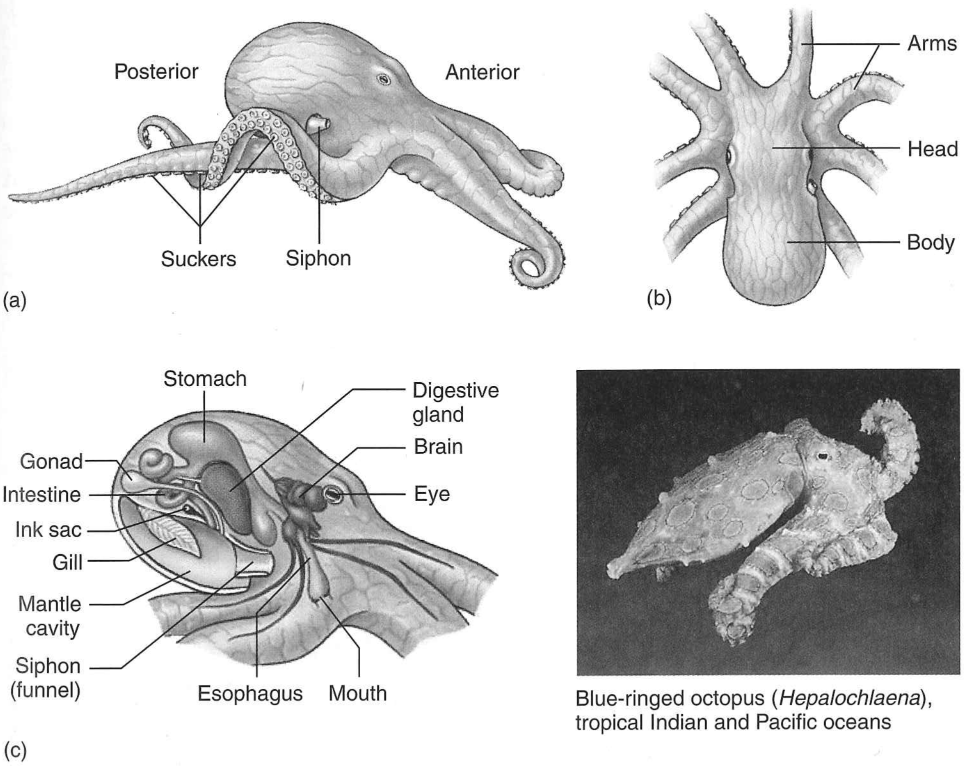


FIGURE 7.24 Oysters such as *Crassostrea virginica* (*a*) are harvested commercially around the world (see Fig. 17.15). Some bivalves, like scallops and the file clam (*Lima scabra, b*), live free on the bottom and can swim by clapping their shells. Others bury themselves in sand or mud.



Blue-ringed octopus (*Hepalochlaena*), tropical Indian and Pacific oceans

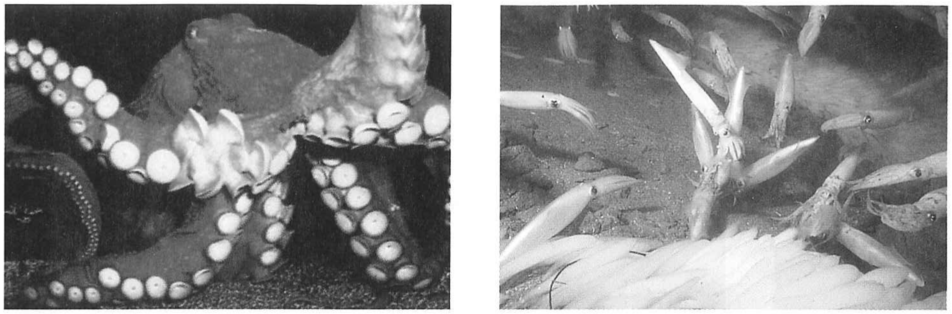
FIGURE 7.25 External (*a* and *b*) and internal (*c*) structure of the octopus. In the male the tip of the third right arm is modified to transfer packets of sperm from his siphon into the mantle cavity of the female. Copulation is preceded by courtship behavior that includes intricate color changes.

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).

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



(a) (b)

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.

arms and two tentacles, all with suckers, circle the mouth (see the photo on page 361). 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 hamiltoni*). Very few specimens have been caught, but the largest, caught in 2007, had a total length of about 10 m (33 ft). The giant squids (*Architeuthis*) are also found in deep water. One species supposedly grows to 20 m (66 ft) in length but weighs less than the colossal squid. Although not as large, the Humboldt, or jumbo, squid (*Dosidicus gigas*) may reach 1.8 m (6 ft). Once found from Baja California, Mexico, to southern South America, it has been gradually extending its range as far north as Alaska. A voracious predator, the invading squid may threat northern Pacific fisheries.

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. 364) 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.

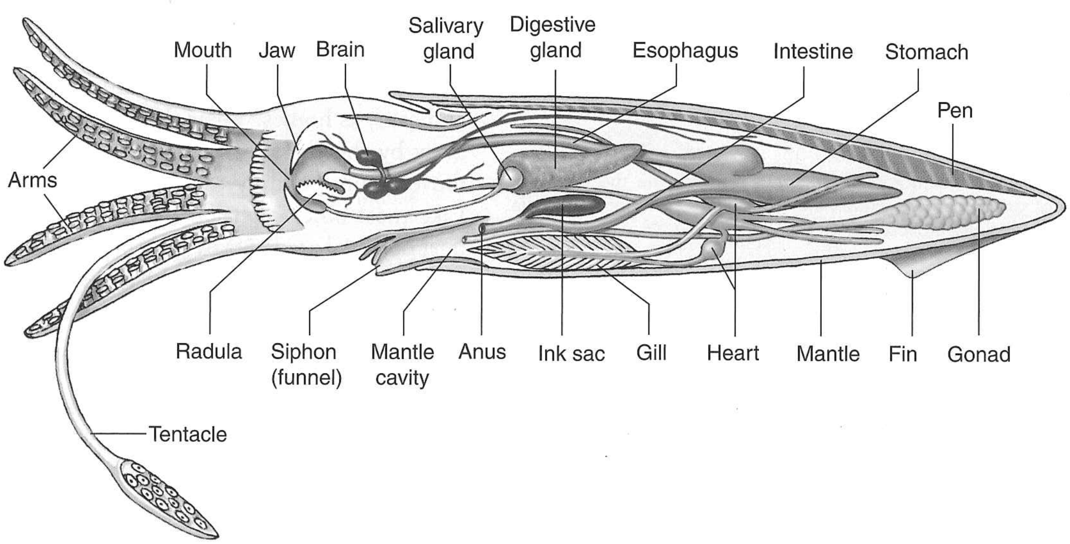
Most chitons live on shallow, hard bottoms where they use a rasping radula to feed on algae. Many of them return to a homesite after feeding. One species, however, captures small crustaceans and other invertebrates with a flap-like extension of the mantle that surrounds the mouth.

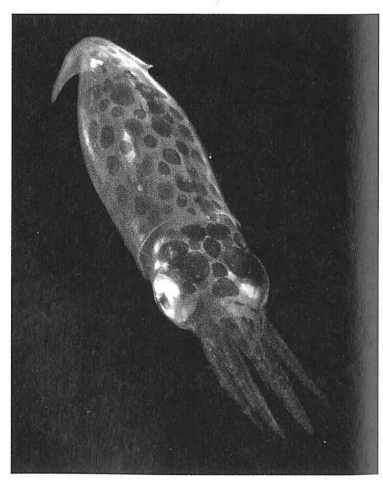
The **monoplacophorans** (class **Monoplacophora**) are represented by only a handful of species of limpet-like molluscs. They were known only as fossils until the discovery of live individuals in 1952. They have now been collected, mostly from deep water, in scattered locations around the world. Monoplacophorans 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 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

Feeding and Digestion The molluscan gut has a separate mouth and anus. Digestion involves **salivary** and **digestive**





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.

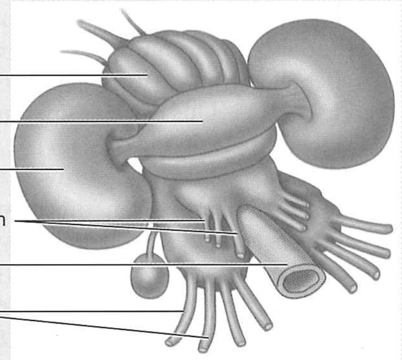
EYE ON SCIENCE

The Octopus Complex Brain

The remarkable complexity of the nervous system and behavior of octopuses and their kin is well known (see "Nervous System and Behavior," p. 134). Key to this complexity is a centralized and complex brain unique among invertebrates.

Comparisons of the octopus brain with that of vertebrates, particularly the human brain, are intriguing and almost inevitable. The octopus brain, like the vertebrate brain, consists of two major halves connected by nerve fibers. The brain, which surrounds the esophagus, is made of ganglia, clusters of neurons (nerve cells) that form lobes known to control particular functions. Some of the lobes, such as the vertical lobe, are folded to increase their surface area and therefore their potential functions, a trait shared with mammals like humans and cetaceans (see Fig. 9.27). Another similarity is that some of the lobes have miniaturized neurons, which allow concentrating more of them per volume. There are between 300 to 500 million neurons in the brain of some octopuses, comparable to the number in the cat's brain. The number of neurons in some parts of the brain actually increases as the octopus grows in size. There are even additional neurons concentrated outside the brain, in the arms and eye region, suggesting limited brain control for the use of the arms and perhaps visual memory outside the brain.

The cephalopod and vertebrate brains evolved independently from each other. Their development in different but remarkably parallel paths, however, has stimulated the search for the origin of complex behavior and intelligence among animals, and that includes us. The mapping of nerve impulses in the octopus brain, for instance, has demonstrated that the lobe where memory and learning takes place is organized very much like the region of the vertebrate brain devoted to these functions. Because the cephalopod neurons are simpler than those in vertebrates (lacking, for example, the outer sheath that speeds up impulses in vertebrates), these results suggest that what is important is how the brain is organized, not the relative complexity of its components.



The Octopus Connectome Project, which involves a team of neurobiologists from several nations, is mapping out the neurons in the octopus brain to find out how they are connected. Researchers slice brain tissue and obtain images of individual neurons using a knife-edge scanning electron microscope that, with the help of computers, provides amazing tridimensional details. The study of the octopus **connectome**, a detailed map of the neural connections in the brain (a field known as "connectomics") hopes to unravel the detailed structure of individual neurons in the octopus brain and relate such information to how the brain works. Our understanding of neuronal function and, particularly, its firing patterns (known as nerve impulses or action potentials) found its beginnings in studies of the nervous system of another cephalopod, the squid. For years, and even to some extent today, the squid giant nerve fibers served as the model for studying the nerve impulse. It may just be that the relatively simpler brain of the octopus can enable us to better understand neuronal connections and how information processing in these connectomes leads to higher-level nervous functions such as learning and problem solving.

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

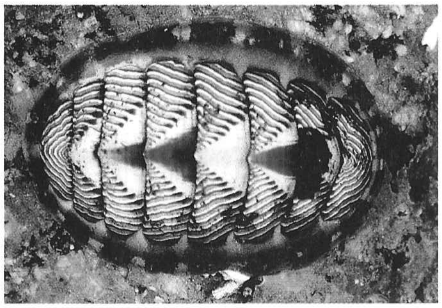


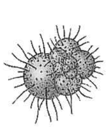
FIGURE 7.28 Chitons such as *Tonicella lineata* use their strong foot and the flexibility provided by the eight articulated shells to fit tightly to the irregular surface of rocky shores.

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.

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.

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 4.8*b*

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).

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 (see "The Octopus Complex Brain," p. 133). 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 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. Octopuses are known to use tools and even show play behavior. Some species 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.

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