25 ANIMAL EVOLUTION—THE INVERTEBRATES

Old Genes, New Drugs

Other than Samoans, few of us prize cone snails (*Conus*) as tasty treats. However, the intricate patterns of cone snail shells obviously have been prized down through the ages. Archaeologists digging up the remains of past cultures in Peru, Arizona, Micronesia, and Iran find bracelets, rings, and ritual objects made from *Conus* shells. Collectors still covet the shells, the most beautiful of which are still being used to make jewelry and other forms of decorative art.

Cone snails fascinate biologists for different reasons. More than 500 species of these predatory mollusks live in the seas. All subdue small prey with paralytic secretions called *conotoxins*. These secretions pack a wallop that can kill even large animals. Cone snails sometimes harpoon people who accidentally step on them. Seventy percent of those who did not seek prompt treatment ended up dead.

Conotoxins are peptides. They bind to channel proteins of cell membranes and shut them down. Any species of cone snail can make 100 to 300 conotoxins, each with a specific molecular target. What is so fascinating about toxin diversity and specificity of targets? It means that cone snails are potential sources of many new drugs.

One of the *C. magnus* conotoxins is a thousand times more potent than morphine—yet nonaddictive. It blocks the release of signaling molecules from nerve cells that can make neighboring cells change their activities. A synthetic version may shut down the neural pathway that gives rise to sensations of pain. It is now being tested in clinical trials. The test groups consist of cancer and AIDS patients who are in unbearable but otherwise untreatable pain.

C. geographicus, shown in Figure 25.1, secretes a toxin that one day might help epileptics. While studying this species, University of Utah researchers discovered a gene that has been conserved in the DNA of different species for a long, long time. In cone snails, the gene codes for an enzyme, gamma-glutamyl carboxylase (GGC), that catalyzes a step in the conotoxin synthesis pathway.

Oddly, humans make GGC, too, but it functions in blood clotting processes. Fruit flies also make it. To date, no one knows what GGC does in fruit flies.

Given its presence in mollusks, insects, and vertebrates, the GGC gene must have been around for at least the past 500 million years, before these lineages diverged from a common ancestor and started evolving independently of one another. Apparently the ancestral gene mutated in different ways in the three lineages, so that its enzyme product took on different functions.

This example leads us back to an organizing principle in the study of life. *Look back through time and you discover that all organisms interconnect*. At every branch point in the animal family tree, microevolutionary processes gave

Figure 25.1 *Conus geographicus* engulfing a small fish. This mollusk has a siphon, the tubelike structure extended straight up in this photograph. The siphon can detect disturbances in the water, which typically happen when small fishes and other prey swim within range. *C. geographicus* impaled this fish with a harpoon-like device. It then pumped paralyzing conotoxins into it. The photograph on the facing page shows a tiny sampling of the diverse patterns of *Conus* shells.

IMPACTS, ISSUES

Watch the video online!

rise to some novel change in biochemistry, body plans, or behavior. They were the source of unique traits that help define each lineage.

We have named more than a million kinds of animals that now share the planet with us. Researchers estimate there may be tens of millions more yet to be discovered. At least as many kinds appeared and disappeared in the past. Even though we devote two chapters to animals, we can scarcely do justice to those numbers.

The best we can do is to sketch what we know about the origin and evolution of animals and touch on trends that emerged among them. A quick reminder before you start reading: Do not assume the most ancient lineages are somehow stunted or "primitive." As you will see, even the simplest forms among them are exquisitely attuned to their environment.

How Would You Vote?

Cone snails are diverse, but most kinds have a limited geographic range, which makes them highly vulnerable to extinction. We do not know how many are harvested, because no one monitors the trade. Should the United States push to extend regulations on trade in endangered species to cover any species captured from the wild? See BiologyNow for details, then vote online.

Key Concepts

CHARACTERISTICS OF ANIMALS

Animals are multicelled heterotrophs that ingest other organisms, develop in a series of stages, and are motile during part or all of the life cyle. The cells of most kinds form tissues and extracellular matrixes.

Colonial flagellates may have started the animal lineage. The lineage as a whole reflects a trend toward increases in size, compartmentalization of tasks, then integration of activities of tissues and organs.

Animals differ in their structural organization. They do or do not have a symmetrical body, a cavity between the gut and body wall, a head, and a body divided into segments.

An early divergence gave rise to two major branches: the protostomes and deuterostomes. Sections 25.1, 25.2

STRUCTURALLY SIMPLE INVERTEBRATES

Sponges are the simplest animals, with no body symmetry and no tissues. Placozoans have two tissue layers but no symmetry. The radially symmetrical cnidarians have two tissue layers and cells carrying out specialized tasks in a gelatinous matrix between the two. Sections 25.3, 25.4

BILATERAL INVERTEBRATES

Bilateral symmetry evolved in almost all other branchings of the animal family tree. Bilateral animals have specialized tissues, organs, and organ systems that form from two or three germ layers in their embryos. Sections 25.5–25.10

THE MOST SUCCESSFUL ANIMALS

In terms of diversity, numbers, and distribution, arthropods are the most successful animals. On land, insects are the most successful arthropods. Sections 25.11–25.16

ON THE ROAD TO CHORDATES

The echinoderms are in the deuterostome branch of the family tree, which led to the chordates. Echinoderms have radial features but bilateral ancestors. Section 25.17

Links to Earlier Concepts

As you read about animal evolution, you will draw on your understanding of levels of organization in nature (Section 1.1), the surface-to-volume ratio (4.1), membrane proteins (5.2), and extracellular matrixes (4.9). You will see more outcomes of mutations that affected embryonic development (12.8, 15.1, 15.3, and 17.8). You also will see the impact of drifting and colliding of continents on the course of animal evolution (17.5, 17.6). You will come across more cases of pesticide resistance (18.4) and disease vectors (22.7).

25.1 Animal Origins

LINKS TO SECTIONS 4.1, 4.9, 5.2, 15.2, 22.12

Hundreds of millions of years ago, a flagellated cell founded a lineage that branched into perhaps as many as 30 million species of animals, most of which are far larger and more complex. Edward Ruppert makes the point nicely. If you could scale up a bacterium to the size of a mustard seed, you would have to make, say, a dinoflagellate as big as a grapefruit and a sea urchin as big as the Astrodome. How did such astounding changes come about?

WHAT IS AN ANIMAL?

Animals are multicelled heterotrophs that ingest other organisms or some portion of them. Most are motile, meaning they move about during one or more stages of the life cycle. They reproduce sexually and, often, asexually. Their embryos grow and develop through a series of orderly stages. Animal cells can make ATP by aerobic respiration, they are unwalled, and, in most species, they form tissues and organs.

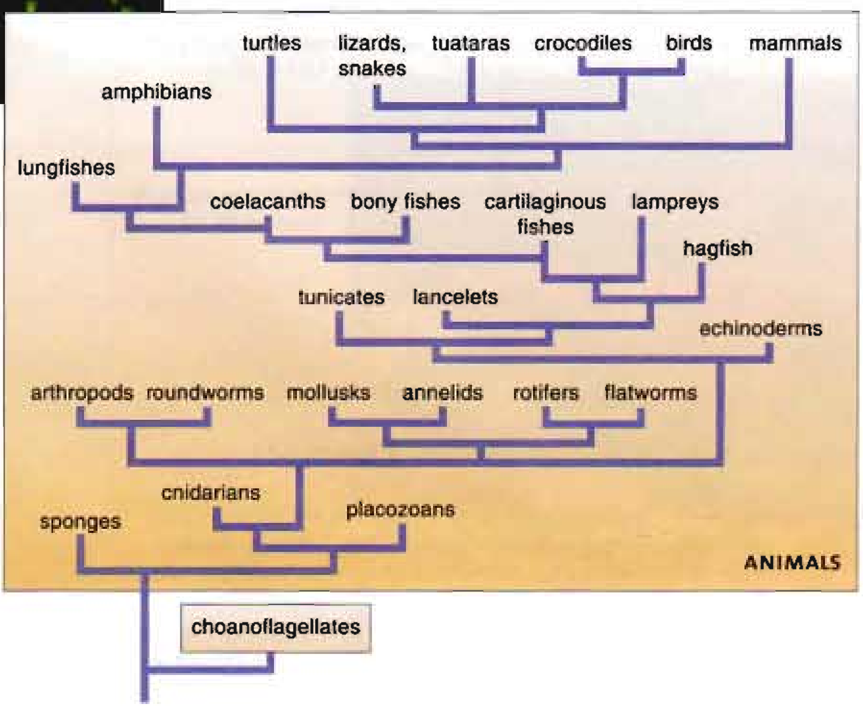
Animal Tissues Figure 25.2 shows an evolutionary tree for animals and lists the major groups mentioned in this book. All branches have living representatives. They all inherited many relatively unchanged genes from groups that preceded them, as well as mutated genes for unique traits that characterize their lineage alone. When considered as a whole, the tree reveals a trend toward increases in body size and complexity—toward added levels of organization. But this does not mean that the ancient groups are somehow inferior. They, too, have been successful in enduring over time.

Larger, more complex body plans became possible with a key innovation—*a capacity of cells to interact in functional units called epithelial and connective tissues.*

Each **epithelium** (singular, epithelia) is a sheetlike array of cells that covers the body surface or lines an inner cavity or a tube. Typically, many cells that make up the sheet function in absorption, secretion, sensory reception, and other specialized tasks. The first kind to evolve, epidermis, interacts directly with the outside world. Gastrodermis, the next to evolve, lines the **gut**, a cavity where food is digested and absorbed.

The forerunners of animals were no more than a layer of cells loosely arranged in a gelatinous matrix of their own secretions. In nearly all animals, epithelial cells secrete and rest on a thin basement membrane. Integrins, cadherins, and other adhesion proteins help anchor these cells to membrane components (Sections 4.9 and 5.2).

All animals contain **connective tissues**, most with a matrix in which living cells and protein fibers, such as collagen, are embedded. In many complex species, crosslinking fibers stiffened with mineral deposits are the structural materials for an internal skeleton.



Chordates	Vertebrate chordates:	
	Mammals	4,500
	Birds	8,600
	"Reptiles"	7,000
	Amphibians	4,900
	Jawed fishes	21,000
	Jawless fishes	84
	Invertebrate chordates (no backbone):	
	Tunicates, lancelets	2,100
Echinoderms	Sea stars, sea urchins	6,000
Arthropods	Crabs, spiders, insects	1,113,000*
Roundworms	Pinworms, hookworms	22,000
Mollusks	Snails, slugs, octopuses	100,000
Annelids	Leeches, earthworms, polychaetes	12,000
Rotifers	Bdelloids	2,000
Flatworms	Turbellarians, flukes, tapeworms	20,000
Cnidarians	Jellyfishes, hydras	10,000
Placozoans	*Trichoplax adhaerens*	1?
Poriferans	(Sponges)	9,000

Figure 25.2 Family tree for animals, and the number of species in major groups.

* More like tens of millions, by recent estimates.

As animal embryos are first forming, their cells are assigned specific addresses. At the least, they end up as part of two primary tissue layers, or *germ layers*—an outer **ectoderm** and an inner **endoderm** (Figure 25.3). Ectoderm is the start of the outer part of epidermis and the nervous system. Endoderm is the start of the gut's inner lining and organs derived from it. In all animals more complex than a jellyfish and its close relatives, a third primary tissue layer forms between the other two. This **mesoderm** gives rise to many internal organs. As you will see, it proved to have great potential in the evolution of large, internally complex animals.

After these layers form, master gene products help map out the basic body plan. As explained in Sections 15.1 and 15.3, they induce cells to differentiate in ways that fill in the details required for each body part.

Body Size Revisited Certain physical relationships constrain the size of cells and multicelled organisms. Given the surface-to-volume ratio, for instance, a solid ball of cells can only grow so large before its surface area will not be enough to service its volume (Section 4.1). That is why you find single-celled species having pseudopods and **microvilli**—filament-like absorptive structures. That is why the cells of structurally simple animals are in arranged like sheets or ribbons.

In most large-bodied animals, a circulatory system moves substances to and from cells much faster than diffusion would take them. The body must expend a great deal of energy to drive the flow, as by a beating muscular heart. Even so, for many species, the energy cost has been offset by the following advantages.

A big body shelters most cells from environmental threats, and it can survive the loss of some of its cells. Also, compared to a single predatory cell, large-bodied animals can handle bigger chunks of food. Advantages multiply when tasks that go into staying alive, such as processing food and escaping from predators, are divided among different cell types. *The ratio of energy spent to energy conserved is more advantageous when each cell type specializes in one task instead of having to build and maintain the structures required to perform all of them.*

In most big animals, epithelial sheets were the start of internal compartments that evolved into specialized organs. With this new level of organization, nervous and endocrine systems that could integrate activities throughout the body proved advantageous.

CLUES FROM CHOANOFLAGELLATES

So where did the animal lineage start? Molecular and morphological studies both support a *colonial theory,*

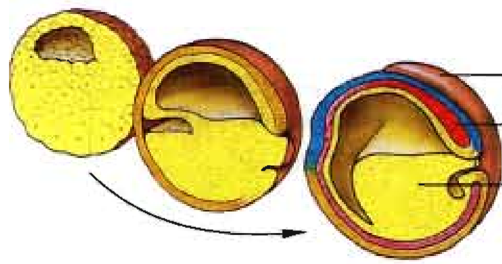


Figure 25.3 Location of three primary tissue layers that formed by way of mitotic cell divisions and cell migrations when the frog shown in Figure 25.2 was still a ball-shaped, multicelled embryo. Section 43.3 explains what goes on.

whereby the first animals evolved from a tiny colony of flagellated, amoebalike cells (Section 22.12).

Consider the **choanoflagellates**, the sister taxon of animals and fungi (Figure 25.2). At their anterior end, these heterotrophic cells have a "collar" of thirty to forty microvilli around a single flagellum. The whole array functions in feeding. The flagellum undulates, causing water to flow past the microvilli—which trap and absorb bacteria and other waterborne food.

Choanoflagellates are free-living, or anchored by a stalk to some substrate, or colonial. In *Proterospongia* colonies, flagellated collar cells are arrayed in a single layer at the surface of a gelatinous matrix of their secretions (Figure 25.4). The only cells that divide have no flagellum; they are under the surface layer, in the matrix. Epithelium and connective tissues may have evolved from such simple compartmentalization.

Most intriguingly, *choanoflagellates make signaling molecules and adhesion proteins which, in all multicelled animals, help cells form tissues and stick together!* They produce a variety of receptors, checkpoint proteins, epidermal growth factors, and cadherins. It appears that the key signaling pathways and adhesion genes necessary for the formation of tissues evolved many hundreds of millions of years ago, before multicelled animals did. What were their original functions? We do not know. But these proteins—and the existence of colonies of flagellated collar cells—support the view that choanoflagellates share a common ancestor with sponges. Sponges are at the base of the animal family tree, and they have flagellated collar cells.

Animals are multicelled heterotrophs, most of which form tissues. Taken as a whole, the groups reflect a trend toward increases in body size, compartmentalization of tasks, and integration. Colonial flagellates were their likely ancestors.

flagellated collar cell

Proterospongia

Figure 25.4 Flagellated collar cells, free-living and in a colony. This species is being studied as a model for the origin of animals.

25.2 Comparing Basic Body Plans

LINKS TO SECTIONS 4.11, 9.3, 12.8, 15.3

How can you get a conceptual handle on animals as diverse as flatworms, dinosaurs, and hummingbirds? You can start by comparing the similarities and differences in basic body plans and in certain internal and external features.

BODY SYMMETRY

Few animals have no polarity or symmetry. **Polarity** means that the body has a front-to-back axis, with an anterior or leading end and a posterior (trailing) end.

Many animals show **radial symmetry**. Body parts are organized around their main axis, like spokes of a bike wheel (Figure 25.5*a*). Radial animals live in water, and their body plan lets them capture food swimming or drifting toward them from any direction.

Most animals show **bilateral symmetry**, with more or less equivalent right and left halves along the main body axis (Figure 25.5*b*). Many have a *ventral* surface (underside) and a *dorsal* surface (upper side).

Did bilateral body plans start with the polarity of ancestral flagellates? A choanoflagellate, remember, has a leading end and trailing end (Figure 25.4). In certain animal eggs, a rudimentary flagellum and a collar of microvilli still starts to form at the top of what will be the body's anterior–posterior axis. Now consider this: Flagellated cells have receptors that detect gradients in oxygen, light, and nutrients. Did such environmental gradients promote the polarization of a whole colony of flagellated cells? If so, sensory receptors would have become concentrated at the colony's leading end, and motile or anchoring cells at the trailing end.

Whatever triggered it, **cephalization** did occur in the forerunners of bilateral animals. Their leading end evolved into a distinct *head*, with a concentration of sensory and nerve cells that responded more efficiently to environmental stimuli. Much later, sensory organs and a complex brain evolved in many lineages.

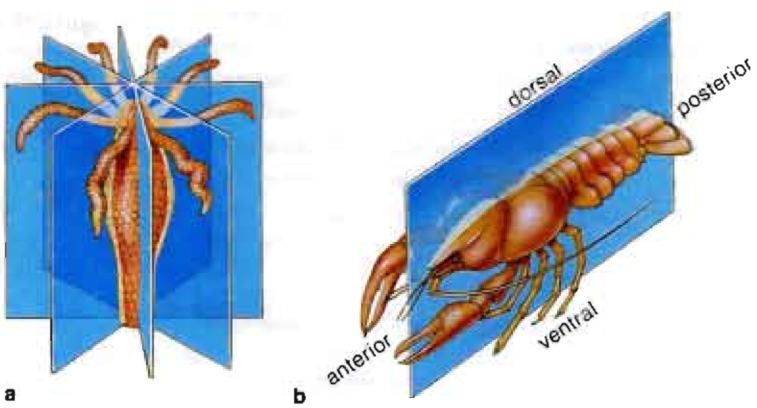


Figure 25.5 Simple way to think about (**a**) radial and (**b**) bilateral symmetry.

TYPE OF GUT AND BODY CAVITY

The type of gut and body cavity differ among animals (Figure 25.6). Either the gut is a sac with one opening or it is a tube with two openings to the outside. Food is digested in the gut, then absorbed into the internal environment. A saclike gut is an *incomplete* digestive system, and it was the first to evolve. A tubular gut is a *complete* digestive system. It starts at a mouth and ends at an anus. A tube has distinct advantages. Its mouth can have specialized feeding structures, such as teeth, instead of being a generic opening for taking in food and expelling residues. A long tube can be regionally modified for food breakdown, absorption of nutrients, storage, and elimination of undigestible wastes.

A complete digestive system forms in embryos of two major lineages of bilateral animals, but not in the

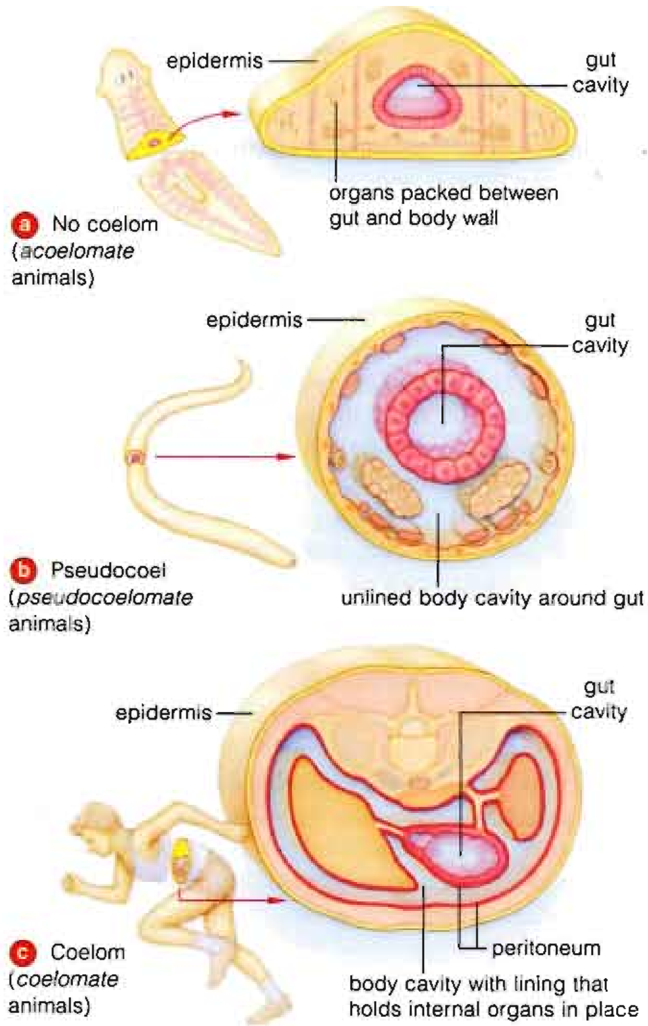


Figure 25.6 *Animated!* Type of animal body cavity (if any).

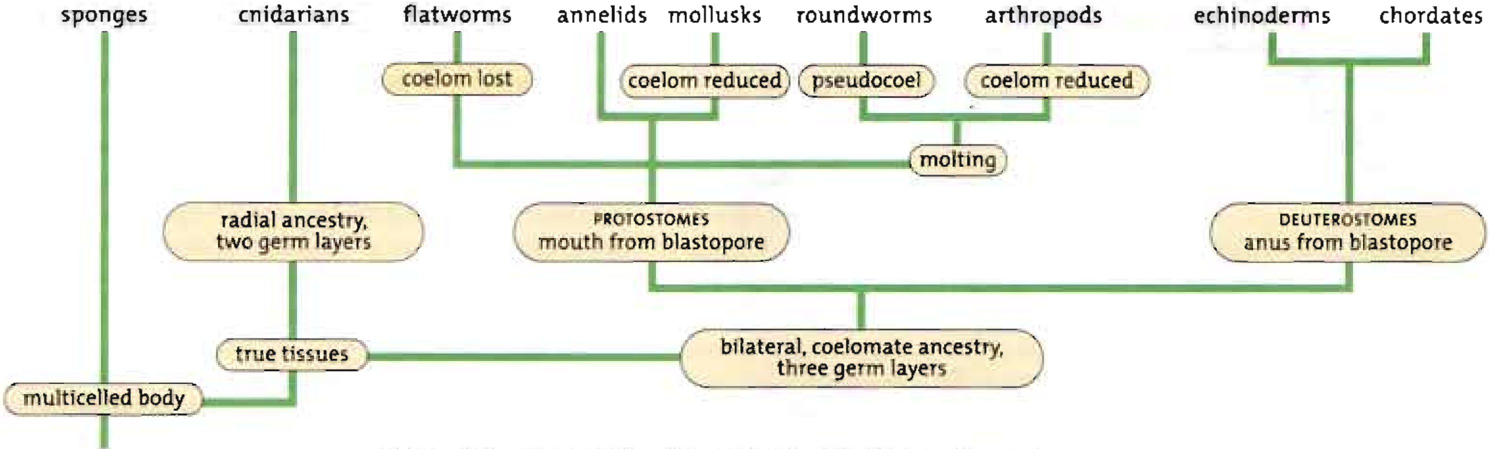


Figure 25.7 Some traits used to construct animal family trees. A blastopore forms in the early embryo; it is the first opening of the primitive gut. The segmentation of annelids, arthropods, and vertebrates might have arisen in a common ancestor or independently in all three lineages.

same way. It starts forming at or near the first opening to appear on an embryo's surface. In **protostomes**, such as flatworms, mollusks, annelids, roundworms, and arthropods, the opening becomes a mouth. That first opening becomes the anus in **deuterostomes**, which include echinoderms and chordates (Figure 25.7).

Flatworms and a few other invertebrates have no body cavity; tissues and organs fill the region between their gut and body wall (Figure 25.6*a*). Most animals have a **coelom**. This type of body cavity between the gut and body wall has a lining, a *peritoneum*, derived from mesoderm (Figure 25.6*c*). It does not develop the same way in protostome and deuterostome embryos, yet the coelom was a key innovation in both lineages. Organs that formed inside this cavity were cushioned in fluid, which helped protect them from jarring blows. The organs also were free to move, grow, and develop independently of the body wall.

Some protostomes have a small coelom or none at all. Their coelom became reduced or lost as a result of mutations in genes that affected early development. For instance, roundworms have a **pseudocoel**, a false coelom. This main body cavity is now only partially lined with mesoderm-derived tissue (Figure 25.6*b*).

REPEATING UNITS—THE START OF COMPLEXITY

Remember how chromosomes have repeats of genes, which favor structural and functional divergences in gene products (Section 12.8)? Repeats in body units have favored regional specializations in structure and function. Consider **segmentation**, which is obvious in annelids, arthropods, and vertebrates. As embryos of these animals develop, they get divided into a series of functionally connected units along the main body axis. Fossils show that segmented body plans emerged early in animal evolution, and regional specializations soon followed (Figure 25.8). Annelids still have many repetitive, similar units. In other groups, segments fused with one another and became adorned with a spectacular variety of specialized appendages. We see clues to our own segmented past in human embryos.

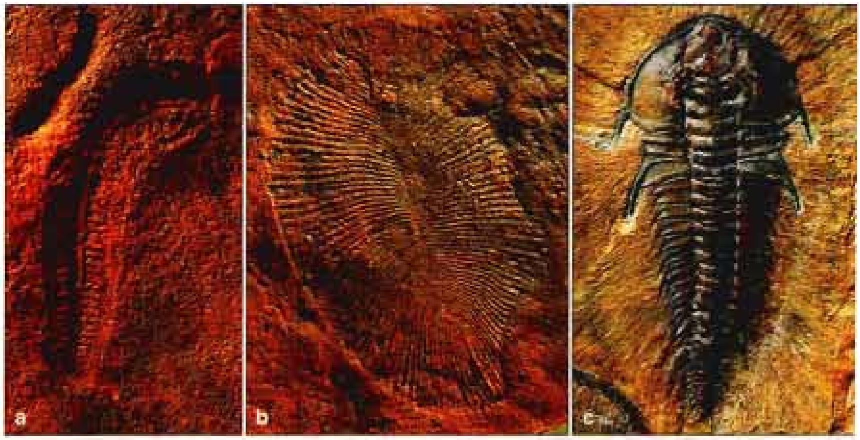


Figure 25.8 Unspecialized segmentation in two fossilized Ediacarans: (**a**) *Spriggina* and (**b**) *Dickensonia*. The oldest known Ediacarans lived between 610 million and 510 million years ago. (**c**) Fossil of one of the earliest trilobites, an early experiment in regional specializations.

Animals differ in body symmetry, cephalization, type of gut, type of body cavity, and segmentation. Most are bilateral, and collectively they show a stunning range of specializations along their main body axis.

25.3 Sponges and Placozoans

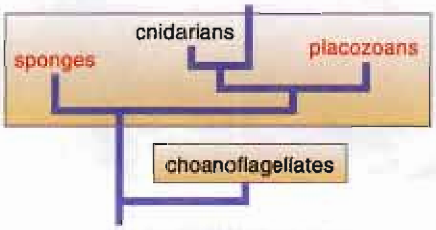
Yes, you can endure through time with simplicity, as demonstrated by the sponges and placozoans.

SPONGES—SUCCESS IN SIMPLICITY

Visualize great numbers of collar cells attached as a single-celled sheet to a matrix of their own secretions. Some amoeboid cells prowl about inside the matrix. The gelatinous matrix has enough tiny, sharp spikes (spicules) and protein fibers to act as a framework for thousands of collar cells. Also, a sheet of flattened, nonflagellated cells is attached to the framework, on the opposite side. That, basically, is the body plan of the asymmetrical animals called **sponges**.

Like the choanoflagellates, flagellated sponge cells draw food-laden water through a food-trapping collar of microvilli. In this case, there are so many cells that their beating flagella pull currents through tiny pores that riddle the body's framework. The cells filter food out of the water and pass on some of it to amoeboid cells in the matrix. The amoeboid cells process food and perform other compartmentalized tasks.

These "filter feeding" animals are composed of ten to twenty types of differentiated cells. Yet they have no symmetry and no epithelial or connective tissues. Only the sperm and larvae are motile. Once a larva has settled down and grows up to be an adult, the sponge can go nowhere else.



Nevertheless, sponges are one of nature's success stories. Their lineage has endured in mostly shallow, tropical seas since precambrian times. Different types live in deep-sea trenches, icy Antarctic seas, and fresh water. Some are big enough to sit in; others are small as a fingernail. They have flattened, sprawling, lobed, compact, or tubelike shapes. Simple sponges draw in water through pores in a tubular wall. Water that has already been filtered flows out through a big opening at the top of the tube (Figures 25.9 and 25.10).

Sea slugs are among the very few predators that eat sponges. As a group, sponges have an arsenal against predators, parasites, or pathogens. The protein fibers and spicules of calcium carbonate or silica that stiffen the body are deterrents. Predators learn that sampling a sponge is like eating a mouthful of glass splinters.

Some species secrete a slimy coating over the body. Others make toxins or smelly compounds that repel some (but not all) predators or competitors for living space. Some secretions might be sources of drugs to combat inflammations, viruses, microbes, and tumors.

Mature sponges don't move about, so how do they deal with sex? Some release sperm directly into water, as in Figure 25.9*a*, and currents may well carry them to another sponge. Sperm of some sponges fertilize eggs of the same species, which are kept in the body for a while. Each new zygote develops into a ciliated larva. A **larva** (plural, larvae) is a free-living, sexually immature stage in the development of many kinds of animals, one that precedes the adult form. The larvae

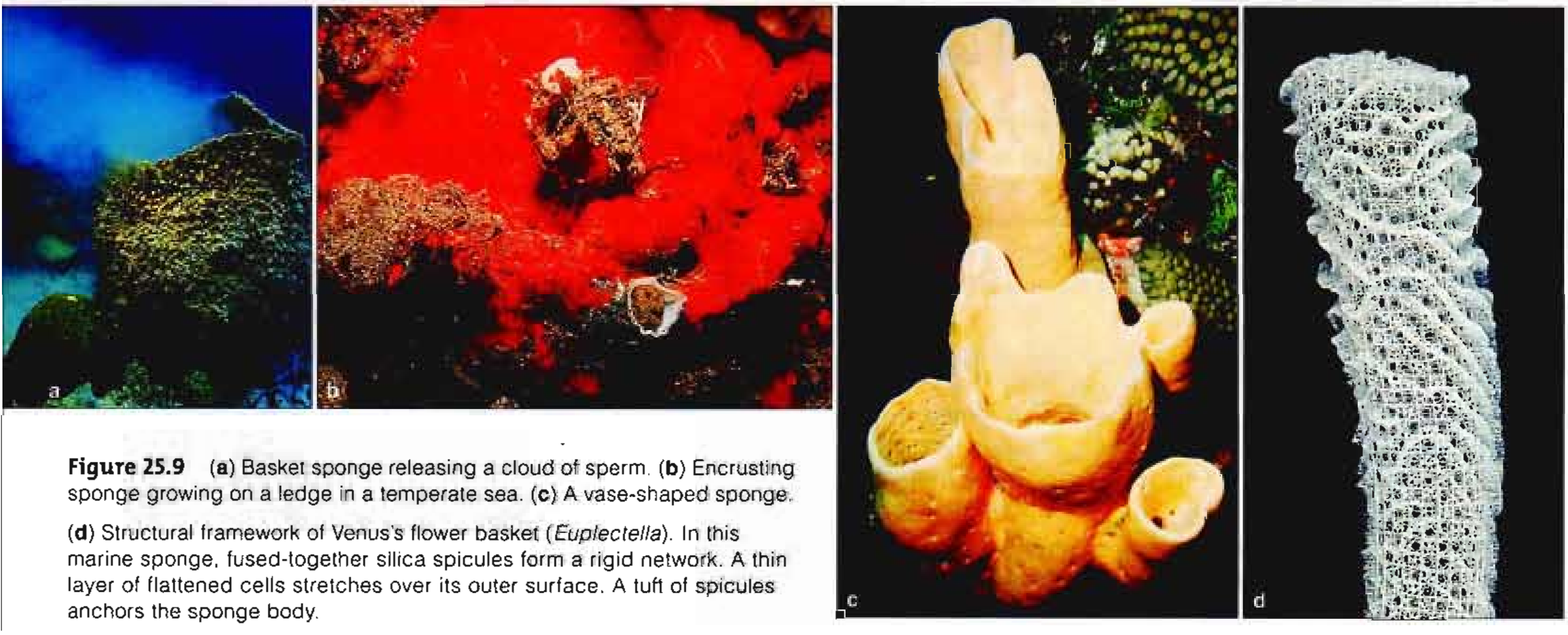


Figure 25.9 (**a**) Basket sponge releasing a cloud of sperm. (**b**) Encrusting sponge growing on a ledge in a temperate sea. (**c**) A vase-shaped sponge. (**d**) Structural framework of Venus's flower basket (*Euplectella*). In this marine sponge, fused-together silica spicules form a rigid network. A thin layer of flattened cells stretches over its outer surface. A tuft of spicules anchors the sponge body.

of sponges have flagella, which enable them to briefly swim about before settling down in a suitable place.

Many sponges reproduce asexually by budding or fragmentation. Small buds or pieces break away and grow into new sponges. Under stressful conditions, some freshwater species make gemmules; they encase clumps of cells in a hardened coat. Gemmules survive oxygen-poor water, drying out, and freezing. When conditions improve, each may grow as a new sponge.

THE IMPLACABLE PLACOZOANS

Placozoans, too, are asymmetrical animals. Their soft, flattened body has no more than a few thousand cells. But the cells do form two simple tissues, analogous to ectoderm and endoderm, around a thin, inner matrix. Molecular comparisons place the placozoans between sponges and cnidarians on the evolutionary tree.

Figure 25.11 shows *Trichoplax adhaerens*, which was discovered in a saltwater aquarium. Flattened cells, each with a single cilium, form a cover for its dorsal surface. Column-shaped cilated cells and gland cells make up the ventral side. *Trichoplax* glides about on the cilia. When it glides over food, the gland cells are stimulated to secrete digestive enzymes, and then the columnar cells absorb the breakdown products. Fiber cells that have thin, reinforced extensions interconnect through the matrix. These special cells have contractile properties. They probably are responsible for the way placozoans change shape, rather like an amoeba.

By 610 million years ago, soft-bodied animals as bloblike as *Trichoplax* were crawling on the seafloor or living in sediments. Others looked like exceedingly segmented fronds and disks (Figure 25.8*a,b*). We call them the **Ediacarans**. Like *Trichoplax*, they were tiny, and most had a flattened body suitable for absorbing dissolved organic compounds. So far, fossils show no evidence of predatory species.

Things got rougher in the Cambrian, when animals started a great adaptive radiation. Larger, multicelled predators as well as prey emerged, and they had true epithelial tissues. Before the Cambrian ended, all major groups of animals had originated in the seas.

What caused that Cambrian explosion of diversity? Changes in land masses, sea level, and climates may have triggered it (Sections 17.5 and 17.6). Besides that, remember the introduction to Chapter 10? Early on, predators and prey, and parasites and hosts, exerted selection pressure on each other every time a novel defense—or the means to overcome it—evolved. We turn now to outcomes of a coevolutionary arms race that has continued to the present.

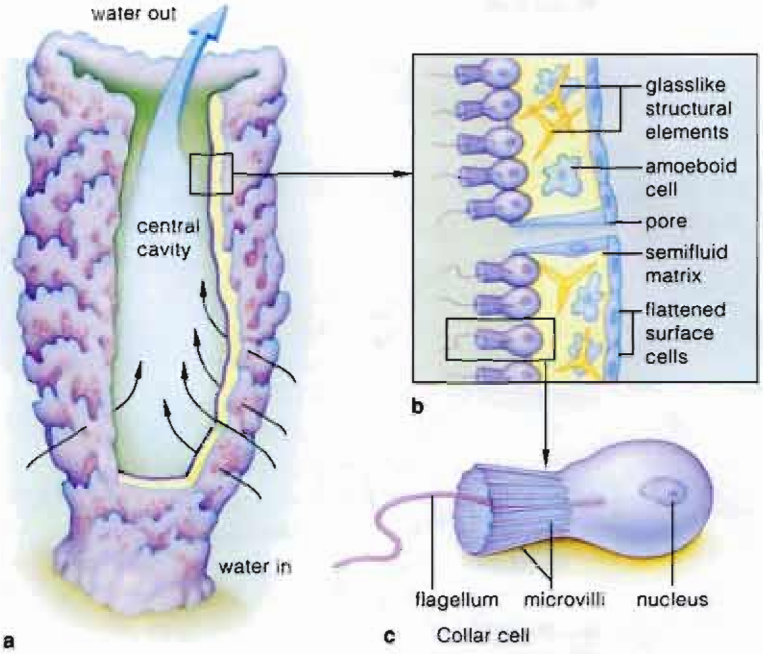


Figure 25.10 *Animated!* (**a,b**) Body plan of a simple sponge. Some cells in the outer lining contain contractile proteins. They encircle an opening at the top of the tubelike body. Their contractions help pull water into and out from the body. In the gelatinous matrix, amoeboid cells secrete materials that form spicules and fibers, which stiffen the matrix and support the body. Other amoeboid cells digest and transport food. They retain the capacity to divide, and their descendants differentiate into the other cell types. They also serve in asexual reproduction, as by gemmule formation.

(**c**) Thousands of phagocytic collar cells line the body's inner canals and chambers. Fine filaments connect the microvilli of one to those of its neighbors, forming a "sieve" that strains food from water. Cells at the collar's base engulf the filtered food.

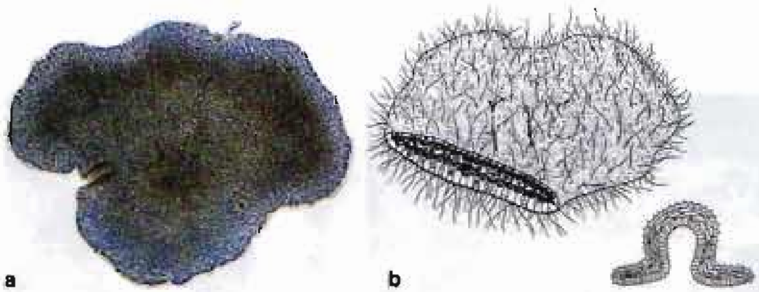


Figure 25.11 (**a**) Living specimen of the placozoan *Trichoplax adhaerens*. Its soft, two-layered body measures about three millimeters across. Of all animals, it has the smallest genome. (**b**) Cutaway views of its soft, flattened body, which humps over food. Gland cells in the bottom layer secrete digestive enzymes.

Sponges have no symmetry, tissues, or organs. Fibers and spicules in the body wall and chemical defenses help keep predators away. Placozoans appear to be the simplest existing animals at the tissue level of organization.

25.4 Cnidarians—Simple Tissues, No Organs

Cnidarians are at the tissue level of organization. Two radial body plans, the medusa and polyp, help characterize them.

Cnidarians are radial, tentacled animals. Fewer than 20 species live in fresh water; 10,000 others live in the seas. The *anthozoans*, or "flower animals," include soft corals, stony corals, sea fans, and sea anemones. The *medusazoans* include scyphozoans (big jellyfishes) and hydrozoans, which include the hydroids, reef-building corals, and siphonophores that cruise the open ocean. Figures 25.12 through 25.14 show examples.

Although cnidarians are known as the lovely flowers of the seas, they are aggressive carnivores. They alone have sensory cells that also function in prey capture and defense. Thick-walled **nematocysts** form in some of these cells. They are capsules with a dischargeable thread under a hinged lid, like a jack-in-the-box. Often the thread bears spines or barbs (Figure 25.13*a*). When something contacts the capsule's trigger, the lid pops open and the thread puts stinging barbs or toxins into whatever it hits. Most of the toxins are irritating but harmless to humans; a few are deadly (Figure 25.13*b*).

Cnidarians have two tissue layers but no internal organs. The most common body forms, the medusa

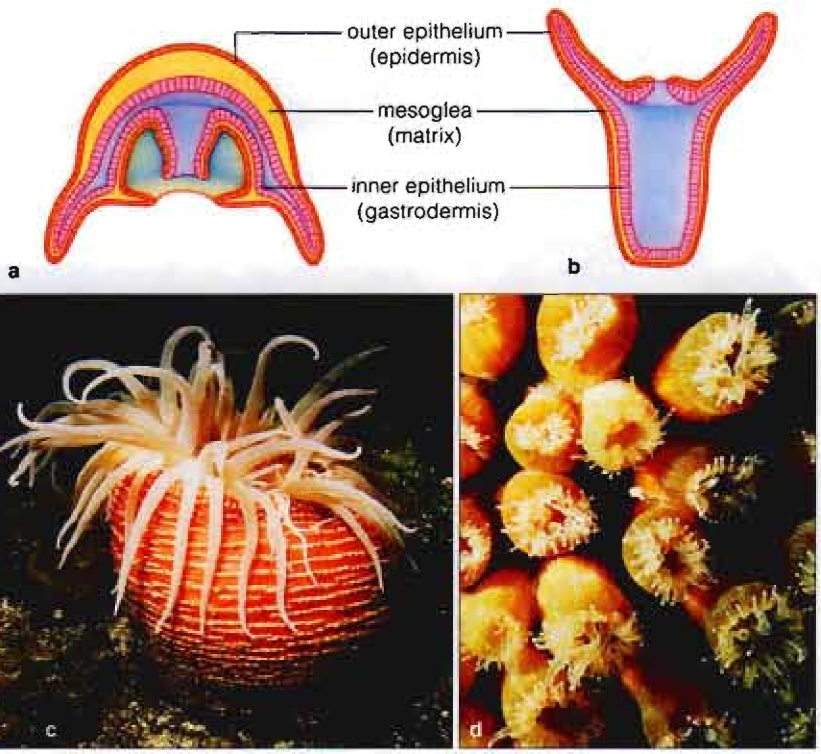


Figure 25.12 ***Animated!*** Cnidarian body plans: (**a**) medusa and (**b**) polyp, cutaway views. Sections 27.5, 34.1, and 37.2 offer other examples. (**c**) Sea anemone and (**d**) part of a colony of reef-building corals. The external walls of reef-building corals interconnect.

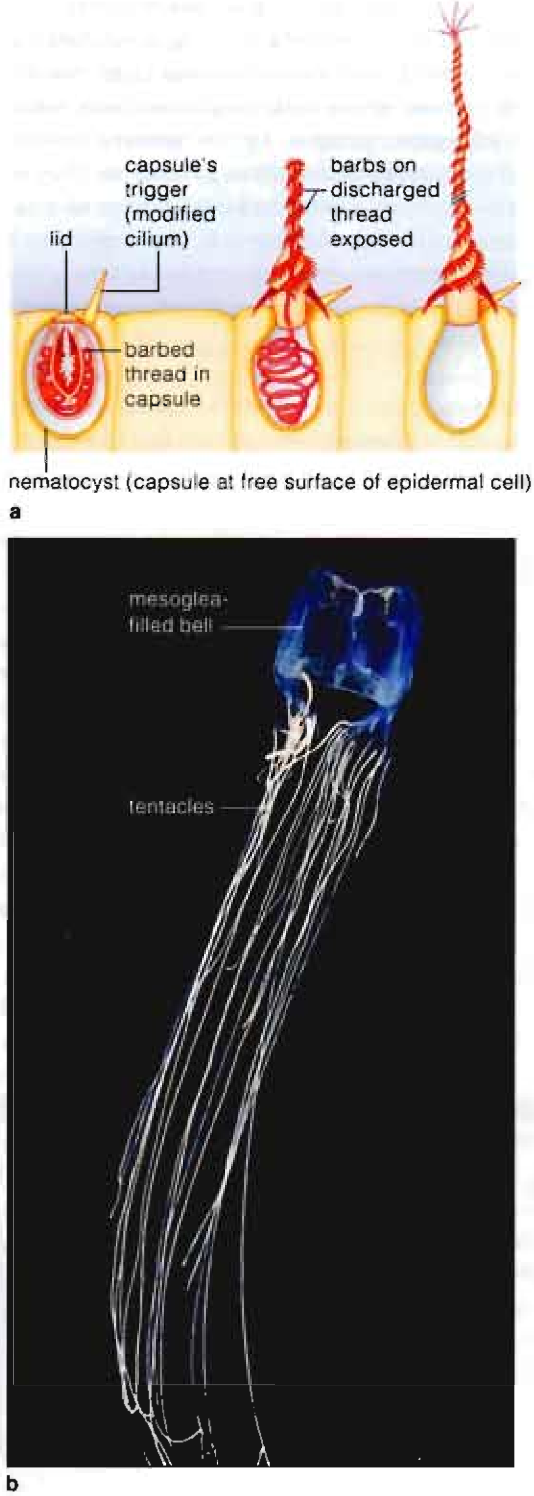


Figure 25.13 (**a**) Nematocyst before and after prey (not shown) touched its trigger and made the capsule "leakier" to water. As water diffused in, turgor pressure built up and forced the thread to turn inside out. Its barbed tip pierces prey. (**b**) All cnidarians, including this sea wasp (*Chironix*), make nematocysts. A sea wasp is a box jelly. Its nematocyst-studded tentacles can be as long as fifteen meters. They deliver a toxin that can kill you within minutes.

and polyp, have a saclike gut. Depending upon the group, medusae, polyps, or both form during the life cycle. Polyps form external or internal skeletons that vary tremendously in size and composition. Medusae look like bells or umbrellas with tentacles around the rim (Figure 25.12*a*). They move freely through water. Polyps are tubular, and usually one end attaches to a substrate. Tentacles ring the other end—the opening to the gut (Figures 25.12*b* and 25.13*b*). **Tentacles** are long, flexible, prey-capturing extensions of an animal body.

Cnidarians have two kinds of epithelia. Epidermis covers the body's outer surfaces and contains many nematocysts, especially on the tentacle. Gastrodermis lines the gut cavity. It incorporates gland cells, which secrete digestive enzymes.

Nerve cells threading through cnidarian epithelia form a *nerve net*. A later chapter illustrates this simple nervous system, which controls epithelial cells that have contractile filaments. By controlling contraction, the nerve net causes changes in shape that move the body. How? Between the inner and outer epithelia is a gelatinous matrix with only a few scattered cells. This **mesoglea** (or "middle glue") is a buoyant, deformable skeleton. Contractile cells work against it to squeeze water out from under a medusa and drive it forward. Any fluid-filled cavity or cell mass that contractile cells act against is a type of *hydrostatic* skeleton.

Cnidarians have extremely diverse life cycles. Only polyps develop in sea anemone life cycles, so gonads (gamete-producing reproductive organs) form only on polyps. The colonial hydroid *Obelia* produces polyps and medusae (its sexual stage), and planulas develop from zygotes (Figure 25.15). A planula is a bilateral, usually ciliated larva that moves about briefly before settling down and developing into an adult. Planulas form in all cnidarian groups.

Many other cnidarians are colonial. Polyps of some corals are cemented side by side in their own "houses" made of calcium carbonate secretions. Like many other cnidarians, the polyps have dinoflagellate symbionts. Their photoautotrophic partners get shelter and access to dissolved carbon dioxide and minerals. In return, they oxygenate host corals and cycle mineral wastes. Mineral ions often are scarce resources in tropical seas.

Another colonial form is the Portuguese man-of-war (*Physalia utriculus*). Figure 25.14*b* shows one of these siphonophores.

Cnidarians are the simplest living animals that have true epithelial tissues. All species are carnivores, and they alone make jack-in-the-box weapons called nematocysts.

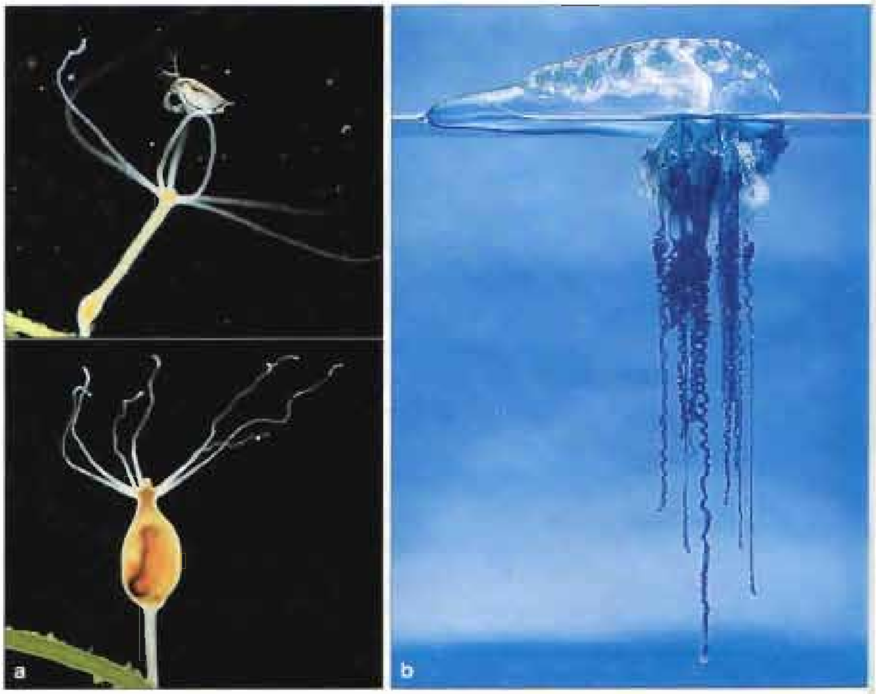


Figure 25.14 **(a)** A solitary hydroid (*Hydra*), feeding. *Hydra* is one of the few freshwater cnidarians. **(b)** Portuguese man-of-war (*Physalia utriculus*), a colonial siphonophore. A purplish-blue, air-filled float keeps the colony at the surface of warm seas. Beneath the float is a horizontal polyp, mouth forward. Tentacles as long as thirty-three meters are suspended below it. So are strands of polyps and medusae that are specialized for absorbing food, reproduction, and other tasks.

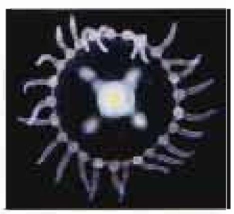


Figure 25.15 *Animated!* Life cycle of one colonial hydroid (*Obelia*). Medusae (*right*) make eggs or sperm. Zygotes develop into planulas, a type of ciliated larva that crawls briefly, then settles down and grows into a polyp. More polyps form by asexual reproduction. A colony often has thousands of feeding polyps and reproductive polyps that give rise to medusae.

25.5 Flatworms—The Simplest Organ Systems

LINKS TO SECTIONS 1.1, 9.1, 14.1

Beyond the cnidarians are animals ranging from simple worms to humans. Most are bilateral, with a distinct head and compartmentalization of functions into organs and organ systems along their anterior–posterior body axis.

Although cnidarians form tissues and some sensory structures, they do not have organs. **Organs**, recall, are structural units of two or more tissues that develop in predictable patterns and that interact in one or more tasks (Section 1.1). Each **organ system** consists of two or more organs interacting chemically, physically, or both as they carry out specialized tasks.

The 20,000 species of **flatworms** (platyhelminthes) are the simplest existing animals with organ systems that form from *three* primary tissue layers—ectoderm, endoderm, and mesoderm. These bilateral, cephalized animals have no coelom. They probably had coelomate ancestors that resembled cnidarian planulas. They can reproduce sexually, but most are hermaphrodites, with male *and* female gonads and a penis.

The major groups are free-living turbellarians and the parasitic flukes and tapeworms. **Parasites** feed on tissues of living hosts but typically do not kill them outright. They mature sexually in a *definitive* host, and immature stages live in one or more *intermediate* hosts.

TURBELLARIANS

Most turbellarians live in the seas. A few types live in fresh water, and one of the planarians lives on land. They ingest tiny animals or suck juices from dead or damaged ones. Figure 25.16 shows organ systems of a planarian. The saclike digestive system has a **pharynx**, a muscular tube between the mouth and gut. In this case, the pharynx sucks up food and expels wastes.

The head has light-detecting eyespots, nerve cords, and **ganglia** (singular, ganglion), or clusters of nerve cell bodies that can integrate communication signals. A system of tiny tubes (protonephridia) controls water and solute levels. The tubes extend from pores at the body surface to bulb-shaped flame cells, which collect excess water. A tuft of cilia "flickering" inside the bulb drives water out through the tubes (Figure 25.16*d–f*).

Planarians can reproduce asexually by *transverse* fission. The body splits in two somewhere near the midsection, and each piece regrows the missing parts. The same mechanism comes into play when you chop up a planarian; pieces may grow into new worms.

FLUKES AND TAPEWORMS

The life cycle of flukes, or trematodes, requires one to four different kinds of hosts and has sexual as well as asexual phases. Figure 25.17 shows the life cycle of one blood fluke (*Schistosoma*). This parasite requires a human definitive host, standing water for its larvae, and an aquatic snail as an intermediate host.

The ancestors of tapeworms, or cestodes, probably had a gut and a mouth but lost both as they evolved in a habitat rich in predigested food: the intestines of host vertebrates. Existing species latch on to the intestinal wall with a scolex, a structure at their anterior end that

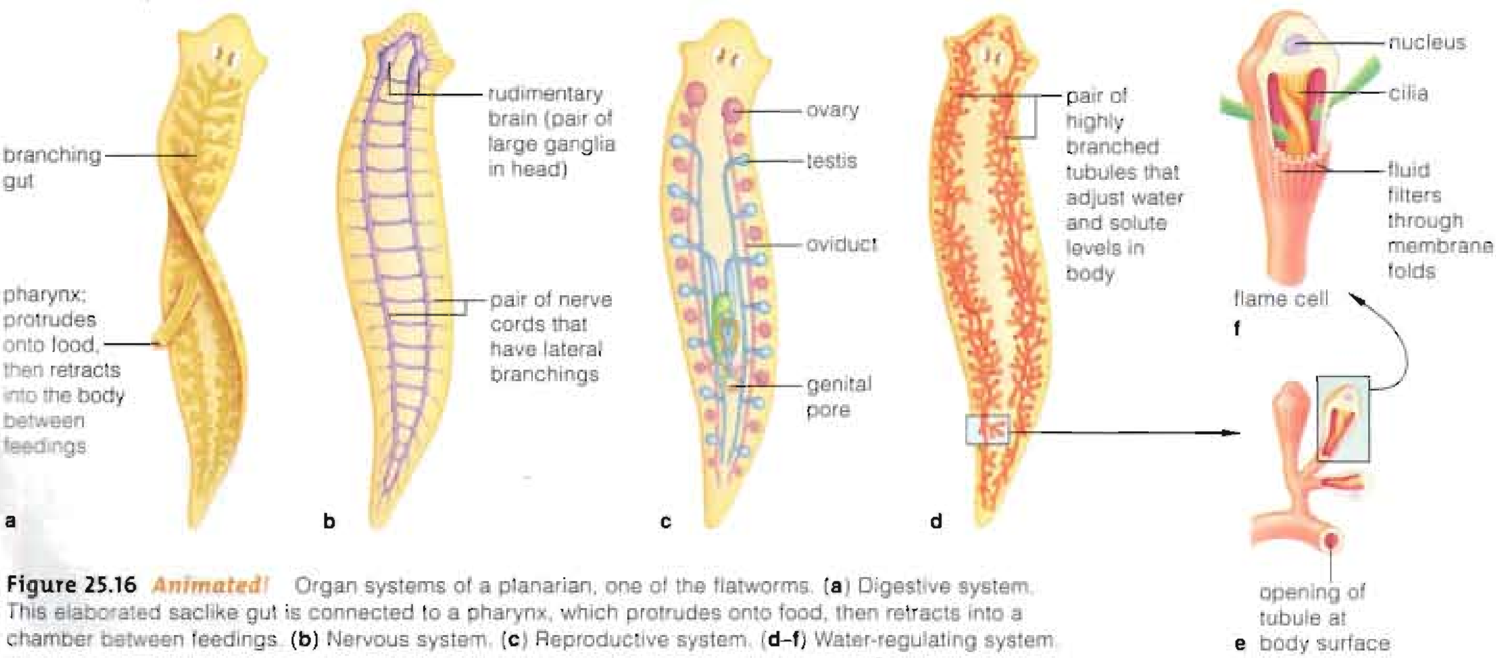


Figure 25.16 *Animated!* Organ systems of a planarian, one of the flatworms. (**a**) Digestive system. This elaborated saclike gut is connected to a pharynx, which protrudes onto food, then retracts into a chamber between feedings. (**b**) Nervous system. (**c**) Reproductive system. (**d–f**) Water-regulating system.

has barbs, hooks, or both. Nutrients diffuse across the tapeworm body wall. Some species secrete chemicals that slow muscle contraction in the intestinal wall and delay the propulsion of food through the host's gut. The slowdown prolongs the time that the worm is bathed in nutrients. How do tapeworms get into a host in the first place? Some larvae may be present in undercooked, raw, or improperly pickled pork, beef, or fish. They enter a host who eats the infected tissues. Figure 25.18 shows the life cycle of a beef tapeworm.

Proglottids bud behind a scolex. Each is a unit of a tapeworm body, and it is hermaphroditic. It produces sperm, which it transfers to others, and eggs. Older proglottids (farthest from the scolex) store fertilized eggs. They break off from younger ones, then exit the body in feces. Fertilized eggs can survive for months on their own, before reaching an intermediate host.

Flatworms are among the simplest bilateral, cephalized animals with organ systems. Organs arise from three primary tissue layers that form in their embryos.

Free-living turbellarians and some notorious parasitic flukes and tapeworms are in this group.

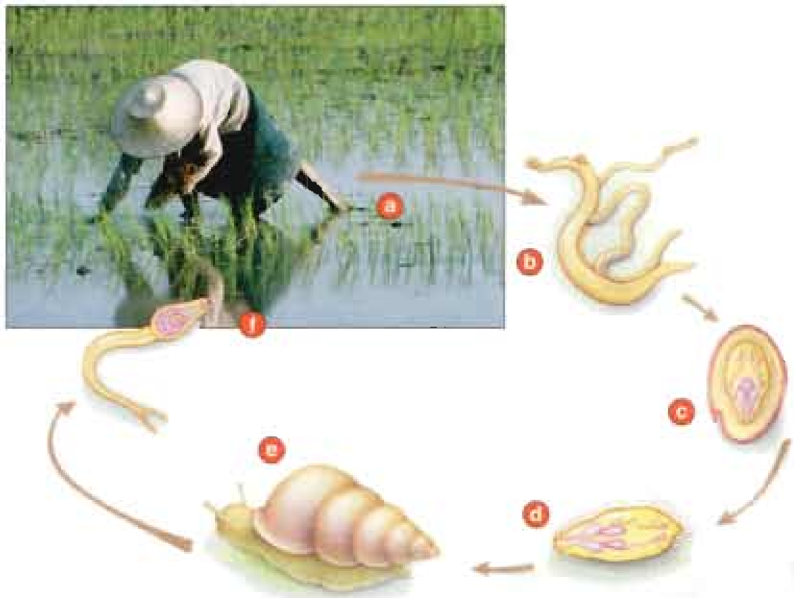


Figure 25.17 Life cycle of *Schistosoma japonicum*. **(a)** This blood fluke grows, matures, and mates in human hosts. **(b,c)** Fertilized eggs exit in feces and hatch as ciliated, swimming larvae. **(d)** Larvae burrow into an aquatic snail and multiply asexually inside it. **(e,f)** Fork-tailed, swimming larvae develop, depart from the snail, and bore into the skin of a human host. They enter thin-walled intestinal veins, and a new cycle starts. At first the resulting disease, *schistosomiasis*, does not cause obvious symptoms. Later, when white blood cells attack masses of fluke eggs, the liver, spleen, bladder, and kidneys can be damaged. About 200 million people are now infected.

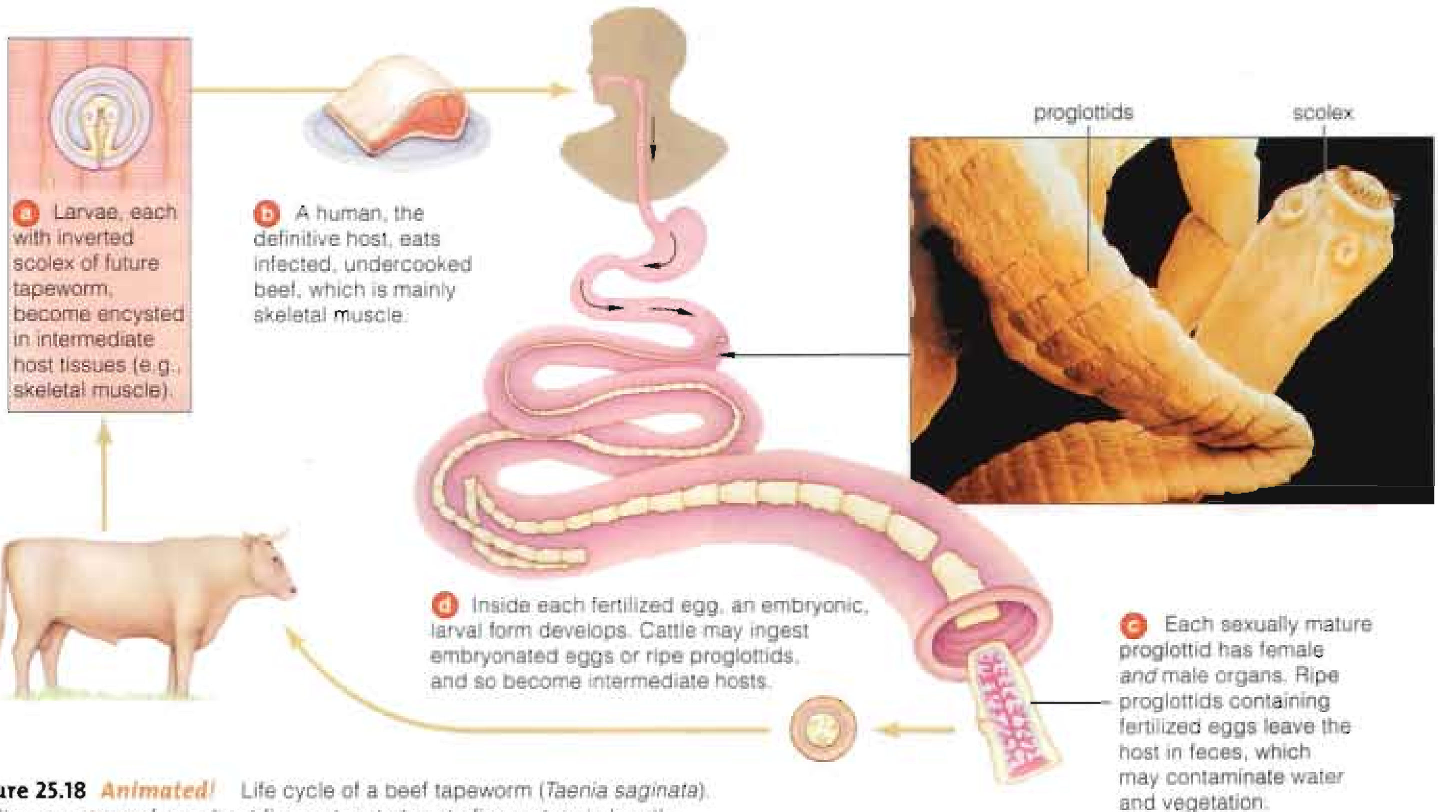


Figure 25.18 *Animated!* Life cycle of a beef tapeworm (*Taenia saginata*). Adult worms range from about five meters to twenty-five meters in length.

25.6 Annelids—Segments Galore

LINK TO SECTION 17.8

A master gene that induces appendages to form on body segments is exuberantly expressed in annelids (Section 17.8).

ADVANTAGES OF SEGMENTATION

Annelids are 12,000 or so species of bilateral animals that include polychaetes, leeches, and oligochaetes such as earthworms (Figures 25.19 through 25.21). Of all existing animals, annelids have the most segments. Except in leeches, nearly all segments have clusters or pairs of chitin-reinforced bristles called chaetae or setae. Hence the names oligochaete and polychaete (*oligo–*, few; *poly–*, many). Bristles shoved into soil or sediments afford traction for crawling or burrowing.

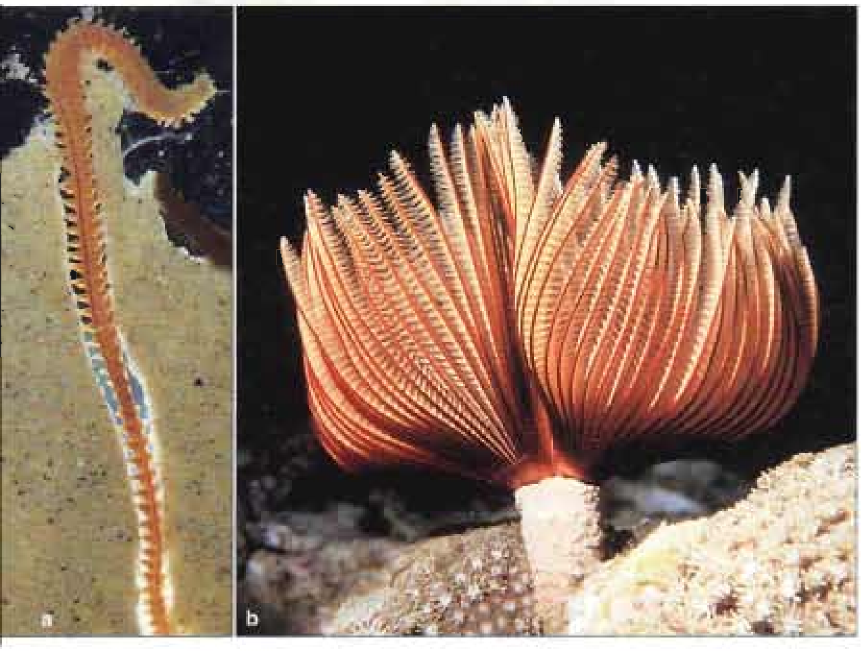
Some annelids show the evolutionary potential of segmentation. Most earthworm segments are similar. The segments at both ends of a leech have a sucker. Polychaetes have an elaborate head and fleshy-lobed parapods ("closely resembling feet"). Existing species hint at the modifications in body plans that favored increases in size, more complex internal organs, and segments adapted for specialized tasks.

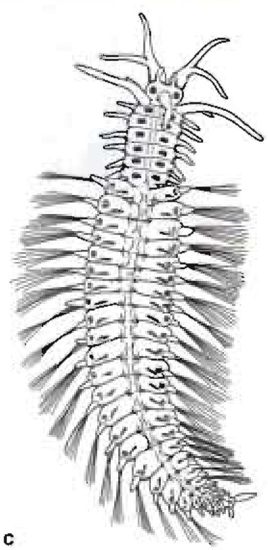
ANNELID ADAPTATIONS—A CASE STUDY

We can use an earthworm as a representative annelid. All earthworms are scavengers in moist habitats. Their flexible cuticle is permeable enough for gas exchange, so it cannot conserve body water. The segmented body has about 150 coelomic chambers, each with muscles, blood vessels, nerves, and other organs. A complete digestive system that has specialized regions extends through all the chambers, like a tube in a tube (Figure 25.21*a*). A muscular pharynx squeezes moist, detritus-rich soil down into the gut. **Detritus** means decaying particles of organic matter. An earthworm can eat the equivalent of its weight in detritus each day. As they burrow and feed, earthworms collectively aerate soil.

Like most annelids, earthworms also have a closed circulatory system with multiple hearts. Contractions of the heart and of muscularized blood vessels keep blood flowing in one direction. Smaller vessels service the gut, nerve cord, and body wall (Figure 25.21*b*).

An earthworm's head holds a fused pair of ganglia. Connected to this rudimentary "brain" are a pair of **nerve cords**: two lines of communication that extend down the length of the body. Signals from the brain travel along the cords and coordinate activities for the whole worm (Figure 25.21*c*). In each segment, both

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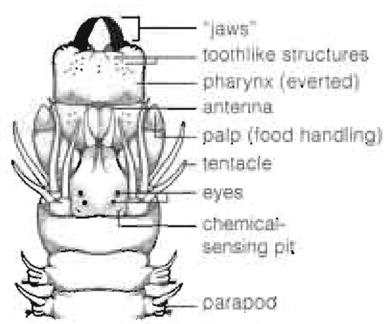
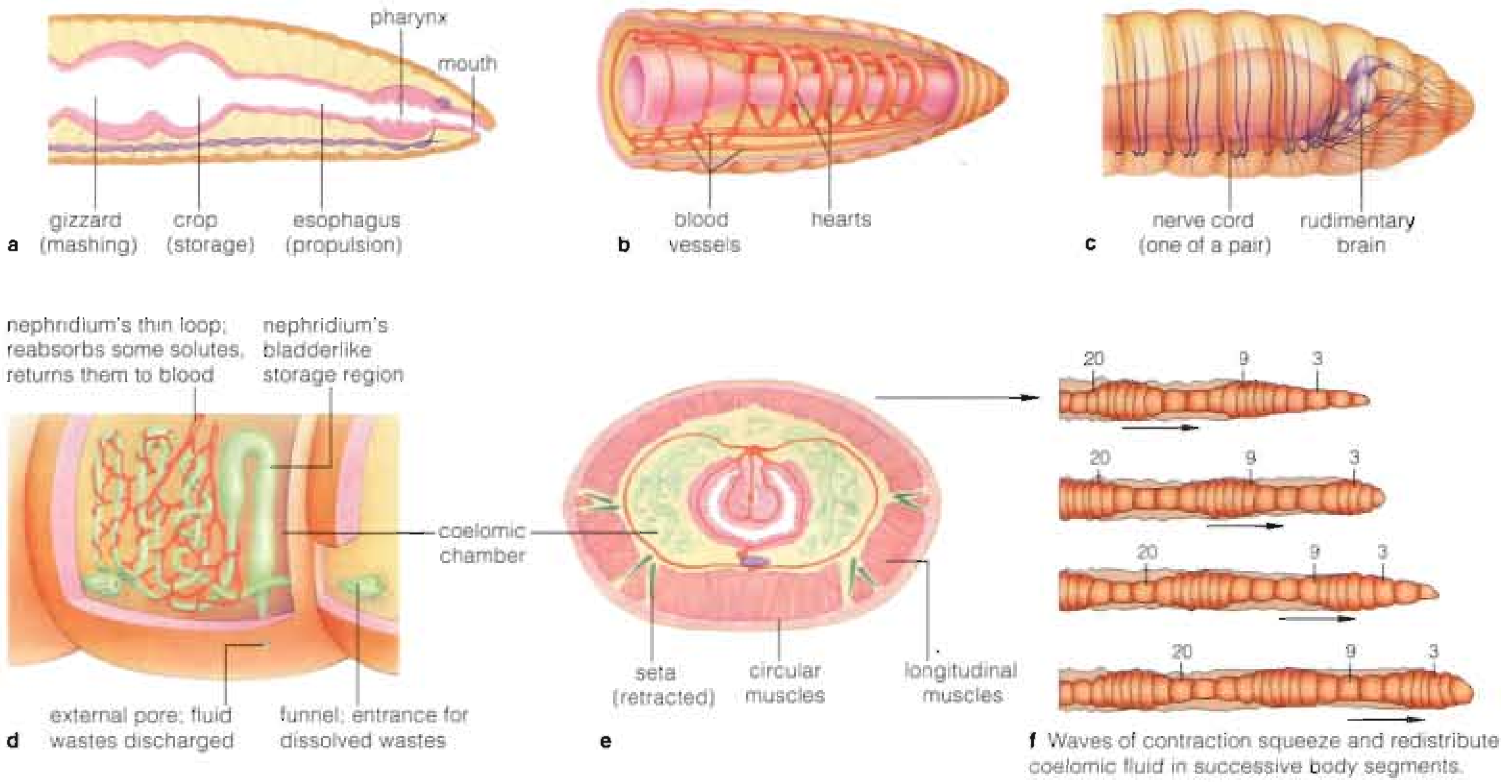


d

Figure 25.19 (**a**) Burrowing polychaete. (**b**) Tube-dwelling polychaete with featherlike, mucus-coated structures on its head. Polychaetes are common animals along coasts and by far the most diverse annelids, with stunning arrays of highly modified segments (**c**,**d**). Many types are predators or scavengers; others graze on algae.

Figure 25.20 Leeches. Most are aquatic scavengers or predators with sharp jaws and a blood-sucking device. Shown here, *Hirudo medicinalis*, a freshwater species used for at least 2,000 years as a blood-letting tool to "cure" nosebleeds, obesity, and some other conditions. Leeches are still used. They draw off pooled blood after a doctor reattaches a severed ear, lip, or fingertip. A patient's body cannot do this on its own until blood circulation routes are reestablished.



nerve cords connect with small, local ganglia, which help control activity in the immediate vicinity.

An organ system helps control the composition and volume of the coelomic fluids. Its units are **nephridia** (singular, nephridium). Each has a funnel that collects excess fluid from a coelomic chamber. The fluid drains into a tube in the chamber behind it (Figure 25.21*d*). It then enters a small bladder, which delivers it to a pore at the body surface of the next segment in line.

The coelomic chambers are a hydrostatic skeleton that interacts with muscle layers and setae in the body wall (Figure 25.21*e*). Like other burrowing animals, the worm anchors one part of its body so another part can advance. When a wave of contraction passes down the length of its body, longitudinal and circular muscles are alternately contracting and redistributing coelomic fluid. Where longitudinal muscles contract, that body region shortens and widens, so its setae plunge into soil and serve as anchors. Where circular muscles contract, that body region lengthens and narrows. Its setae are lifted, and the region pushes forward (Figure 25.21*f–h*).

Figure 25.21 *Animated!* Earthworm body plan. Externally, most body segments look alike but are regionally specialized inside, along the main body axis. Near the worm's head, part of the (**a**) digestive system, (**b**) closed circulatory system, and (**c**) nervous system. (**d**) A nephridium, one of many functional units that help maintain the volume and composition of body fluids. Nephridia are functionally linked with the circulatory system. (**e**) Muscle layers, transverse section. They function in locomotion (**f**). (**g**,**h**) Location of bristles that function in locomotion.

Annelids are bilateral, coelomate, segmented worms that have digestive, nervous, excretory, and circulatory systems. Diverse appendages on the segments of polychaetes are testimony to the stunning potential of segmentation.

25.7 Rotifers

Most rotifers are less than a millimeter long, yet they are packed with organs. They alone have a pair of ciliated lobes that rotate and waft food into the mouth.

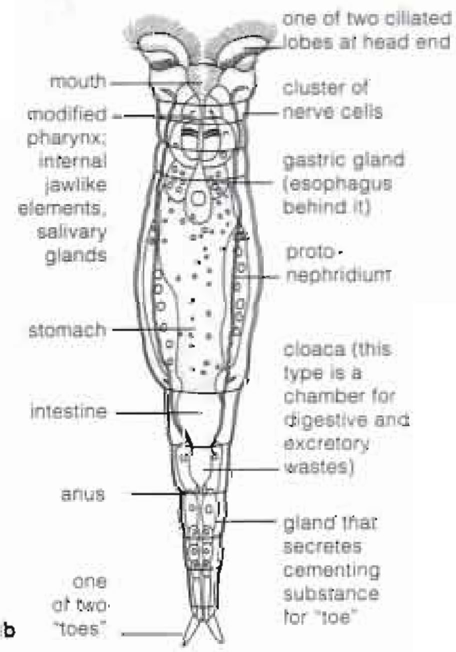
Rotifers share a common ancestor with the flatworms (Figure 25.2). They, too, are bilateral and cephalized, but they have a false coelom. All but 5 percent live in lakes, water droplets on plants, and other freshwater habitats. One liter of pondwater may hold 40 to 500 rotifers or, rarely, as many as 5,000. All rotifers prey on bacteria and tiny photoautotrophic algae.

Most species have a complete digestive system that has a pharynx, a jawlike structure that grinds food, an esophagus, a stomach and glands that secrete digestive enzymes, one intestine, and an anus. Protonephridia maintain the extracellular fluid by removing excess water and solutes. A ganglion in the head integrates body activities. Some rotifers have "eyes," clusters of light-sensitive pigments that keep the body oriented toward sunlit places where food is more likely to be. In certain species, two "toes" exude gluey substances that help anchor the body to substrates at feeding time (Figure 25.22). Rotifers do not have special circulatory or respiratory organs.

Males are unknown in some species (Figure 10.13). In others, they are dwarfed or short-lived.

Rotifers are bilateral, cephalized animals with ciliated lobes at their head end and a false coelom packed with organs.

a



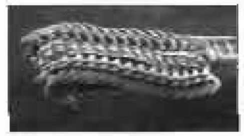
b

Figure 25.22 Bdelloid rotifers. (**a**) Micrograph of *Euchlanis*. (**b**) Body plan of *Philodina roseola*.

25.8 The Pliable Mollusks

Is there a "typical" mollusk? No. The group has more than 100,000 named species, including tiny snails in treetops, burrowing clams, and giant predators of the open ocean.

All **mollusks** are bilateral, soft-bodied animals with a reduced coelom. They alone have a **mantle**, a skirtlike extension of the body mass that drapes back on itself. Those with a head have tentacles and eyes, but not all have a head. Many have a shell or vestiges of one. Many have a food-rasping organ (radula), such as the one at right. A type of gill with thin-walled leaflets functions as the respiratory organ (Figure 25.23).



Mollusks include the gastropods, chitons, bivalves, and cephalopods. With 90,000 species, including snails, sea slugs, nudibranchs, and limpets, the gastropods are by far the largest group (Figure 25.24). Their name, which means "belly foots," refers to the bottom of the body mass. This muscular "foot" allows the animals to glide about over surfaces or to burrow.

EMBRYONIC TWISTING AND UNTWISTING

As a gastropod embryo develops, a cavity between its mantle and shell twists counterclockwise by 180°. So does most of the viscera: the gut, heart, gills, and other soft internal organs. This process—**torsion**—puts the anus near the mouth, and it occurs only in gastropods. Such a drastic rearrangement could have come about by mutations that affected muscles on the right side of

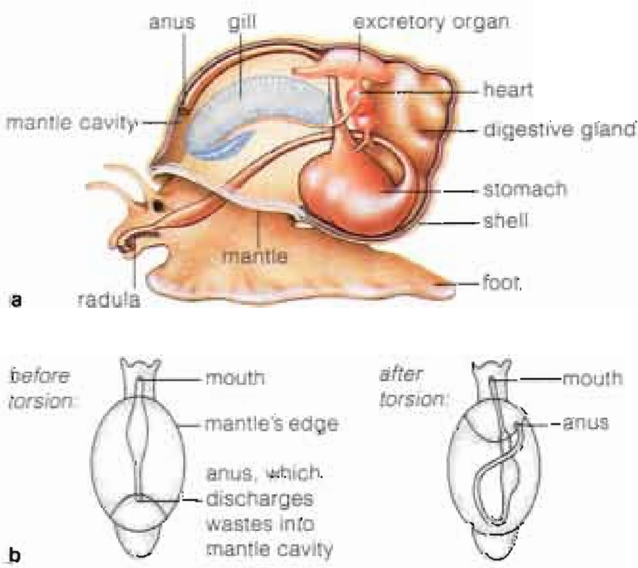


Figure 25.23 *Animated!* (**a**) Body plan of an aquatic snail. (**b**) Torsion, a developmental process unique to gastropods.

Figure 25.24 Mollusks. (**a**) Ventral view of an aquatic snail crawling on aquarium glass. (**b**) Chiton, with a shell divided into eight plates. (**c**) Land snail. (**d**) Octopus swimming. (**e**) Two Spanish shawl nudibranchs (*Flabellina iodinea*). Unlike other mollusks, which have males and females, nudibranchs are hermaphrodites; they exchange sperm and deposit chains of fertilized eggs into their partner. Their ancestors lost most of the mantle cavity and the respiratory organ. Most now have thin outgrowths that serve in gas exchange.

the body. They now form before those on the left, and they pull organs along with them when they grow.

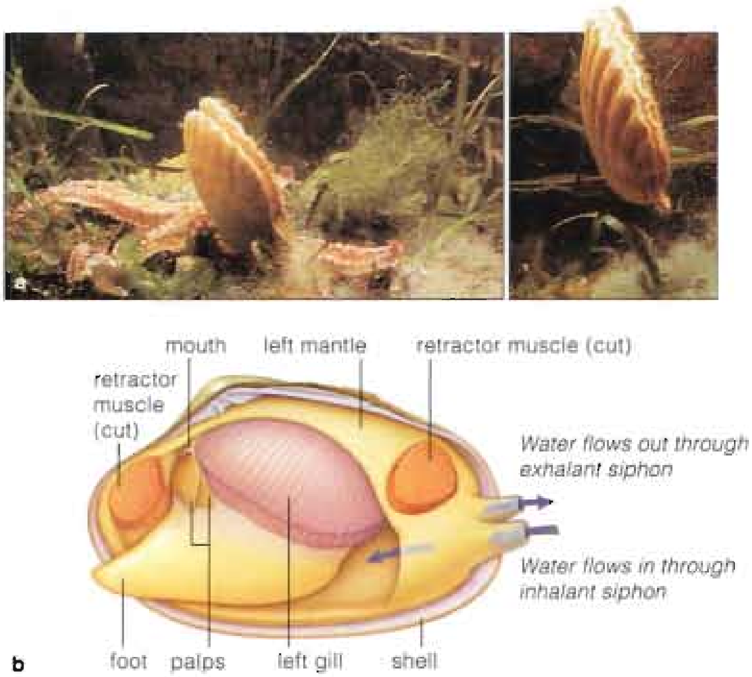
Was torsion—which put the anus above the mouth—a bad evolutionary experiment? Possibly, but lineages got around it. Often, cilia sweep out wastes. Sea slug and nudibranch larvae twist, but then they untwist.

HIDING OUT, OR NOT

Maybe it was their fleshy, soft bodies, so forgiving of chance evolutionary changes, that gave mollusks the potential to diversify so many ways. Consider a few examples. If you were small, soft of body, and *tasty*, a shell could discourage predators. For instance, when something disturbs it, a chiton contracts foot muscles that draw down its eight-piece shell, and its mantle is pressed like a suction cup against the substrate (Figure 25.24*b*). A shell protects scallops, oysters, mussels, and other bivalves. Its two hinged parts (valves) can snap shut. When a scallop claps the two together, it forces water out and propels itself backward, maybe enough to get away from a hungry sea star (Figure 25.25).

Finally, if you were small, soft of body, and *toxic* to a potential predator, a shell would be superfluous. Some nudibranchs secrete bad-tasting substances, such as sulfuric acid. Others graze on cnidarians and then incorporate ingested nematocysts into their tissues. The Spanish shawl nudibranchs flash red, nematocyst-studded respiratory organs while they mate (Figure 25.24*e*). Predators attracted to the colors get stung by nematocysts and learn to avoid the species.

Mollusks are bilateral, soft-bodied, coelomate animals, and only they form a mantle over the body mass.



b

Figure 25.25 Bivalves—clams, scallops, oysters, mussels, and other animals with a "two-valved shell." (**a**) A scallop escaping from a sea star by clapping its valves and producing a propulsive water jet. (**b**) Body plan of a clam, with half of its protective shell removed. In nearly all bivalves, gills collect food and exchange gases. As water moves through the mantle cavity, mucus on gills traps food. Cilia move the mucus and food to palps, where suitable bits are sorted out and driven to the mouth.

Some bivalves are 1 millimeter across. A few giant clams are more than 1 meter across and weigh 225 kilograms (close to 500 pounds). Humans have been eating one type of bivalve or another since prehistoric times.

25.9 On the Cephalopod Need for Speed

FOCUS ON EVOLUTION

LINK TO SECTION 17.5

Lively glimpses into the past emerge when evolutionary theory is enlisted to interpret the fossil record and the basis of existing species diversity.

Five hundred million years ago, the soft-bodied mollusks called **cephalopods** were supreme predators of the seas (Figure 25.26*a*). There were thousands of species with an elaborately chambered shell. All but one of their modern descendants have no shell at all or, at most, a shell that is extremely reduced in size (Figure 25.26*b*).

What happened? The loss or reduction of the shell correlates with the adaptive radiation of fishes during the Devonian, some 400 million years ago (Section 17.5). Among the fishes that hunted cephalopods or were competitors for the same prey, larger and swifter species emerged. In response, in what appears to have been a long-term race for speed and wits, most cephalopods lost the external shell and became active, streamlined and—for invertebrates—smart.

For cephalopods, jet propulsion became the name of the game. They now moved faster by forcing a water jet through a funnel-shaped siphon, out from beneath the mantle cavity. Modern species show how it works. Muscles in the mantle relax, which draws water into the cavity. They contract while the mantle's free edge closes over the head. The quick squeeze shoots water through the siphon. The brain controls the siphon's action, hence the direction of escape or pursuit. The increases in speed correlate with the evolution of complex eyes and far more efficient respiratory and circulatory systems. Cephalopods are the only mollusks with a closed circulatory system. Their heart pumps blood to two gills. Then two accessory (booster) hearts pump blood for oxygen uptake and carbon dioxide removal in metabolically active tissues, muscles especially.

Of all invertebrates, they became the fastest (squids), largest (giant squid), and smartest (octopuses). Of all mollusks, octopuses have the largest brain relative to body size, and they show the most complex behavior.

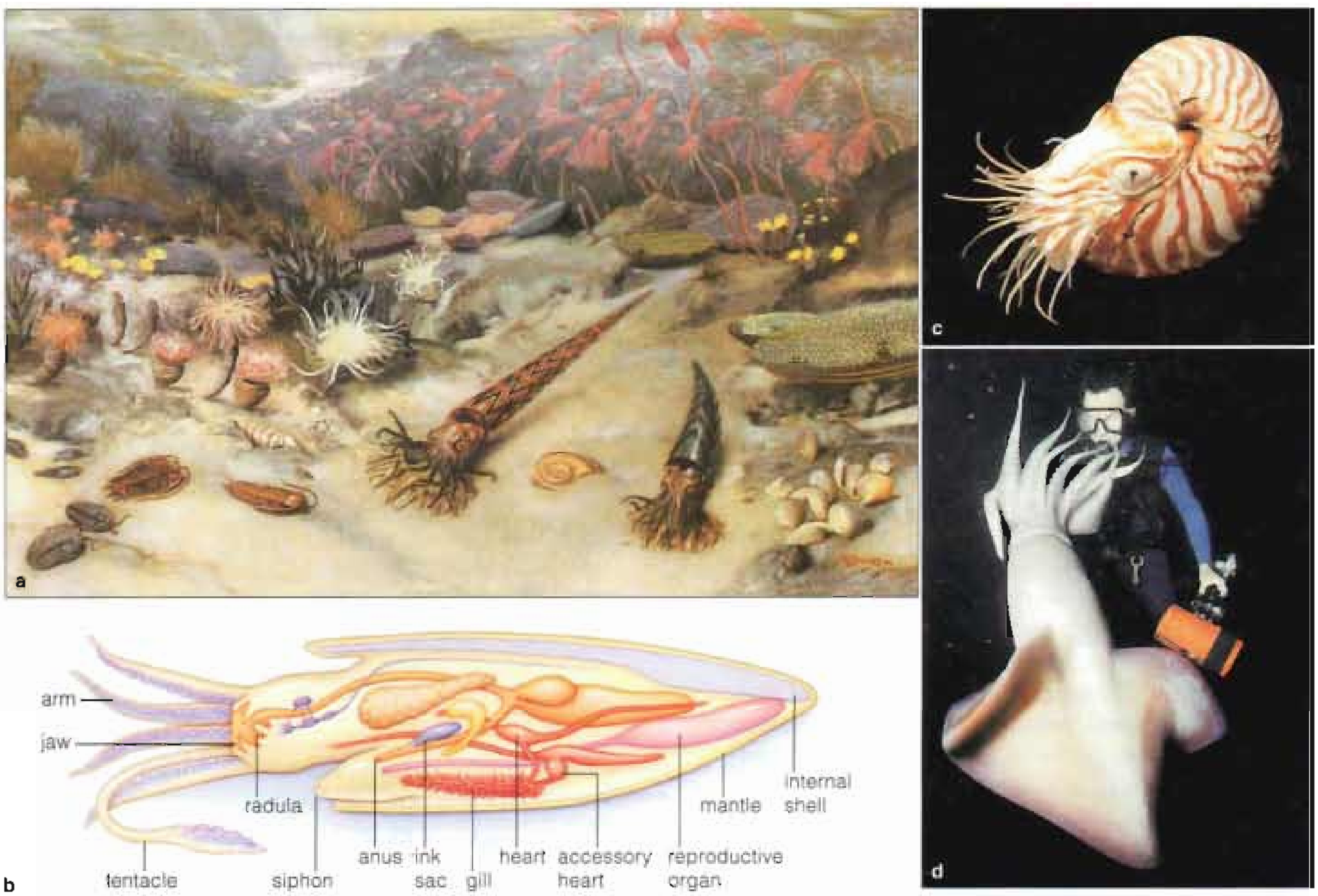


Figure 25.26 ***Animated!*** (**a**) Some animals of the vast, tropical seaways of the Ordovician: trilobites, the cephalopods called nautiloids, and crinoids that looked like stalked plants. (**b**) Generalized body plan of a cuttlefish, one of the cephalopods. (**c**) Chambered nautilus, a living descendant of Ordovician nautiloids. (**d**) Diver and squid (*Dosidicus*) inspecting each other.

25.10 Roundworms

Roundworms are among the most abundant living animals. Sediments in shallow water may hold a million per square meter; a cupful of topsoil teems with them.

The 22,000 or so kinds of roundworms, or nematodes, have a cylindrical body with bilateral features, tapered ends, a complete gut, and a false coelom packed mainly with reproductive organs (Figure 25.27). Roundworms shed their flexible cuticle during periodic molts. Many species are less than five millimeters long. Most are free-living decomposers that help cycle nutrients.

The free-living *Caenorhabditis elegans* is a cherished experimental organism among biologists. It has the same basic body plan and tissue types as far more complex animals, but it is transparent and tiny, with only 959 somatic cells. Researchers can monitor the developmental fate of each cell. Also, the generation time is short, and the genome is one-thirtieth the size of the human genome. Researchers also can enlist self-fertilizing hermaphroditic forms to get populations of offspring that are homozygous for desired alleles.

Many roundworms infect roots of crop plants; they are significant agricultural pests. Others are internal parasites of animals that include humans, dogs, and insects. *Ascaris lumbricoides*, a large roundworm, has now infected an estimated 1 billion people worldwide, mostly in Latin America and Asia (Figure 25.28*a*).

Pigs or game animals can carry *Trichinella spiralis*. Adults of this parasite lock on to the intestinal lining. Juveniles develop from eggs, travel the bloodstream to muscles, and form cysts (Figure 25.28*b*). The resulting disease, *trichinosis*, can be fatal. The encysted juveniles are hard to detect when inspecting fresh meat.

Repeated infections by the roundworm *Wuchereria bancrofti* can result in *elephantiasis*, a bad case of edema. Adult parasites in tissue fluid being sent back to the bloodstream get lodged inside lymph nodes (Section 38.10). There they obstruct the flow, so fluid backs up into tissue spaces. Increased fluid pressure makes the legs, feet, and other regions swell abnormally (Figure 25.28*c*). Mosquitoes serve as intermediate hosts.

The parasitic guinea worm makes thin, serpentlike ridges in human skin. For thousands of years, healers have extracted this "serpent" from infected people by very slowly winding it out around a stick. Pinworms (*Enterobius vermicularis*) are most commonly parasites of young children. At night, females migrate to the anal region and deposit eggs. When they thrash about, they make the infected person's skin itch.

Adult hookworms live inside the small intestine. Using toothlike devices or sharp ridges around their mouth, they cut into the intestinal wall, feed on blood and other tissues, and withdraw nutrients. Each day, adult females can release a thousand eggs, which exit in feces. When juveniles contact human skin, they cut their way inside, travel in blood to the lungs, and move up the windpipe. When the host swallows, they enter the stomach and then the small intestine, where they may mature and live for several years.

Roundworms are abundant bilateral animals with a false coelom and a complete digestive system. They include free-living decomposers and assorted parasites.

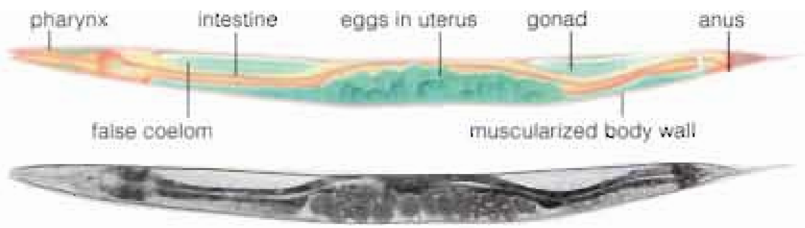


Figure 25.27 *Animated!* Body plan and micrograph of the roundworm *Caenorhabditis elegans*.

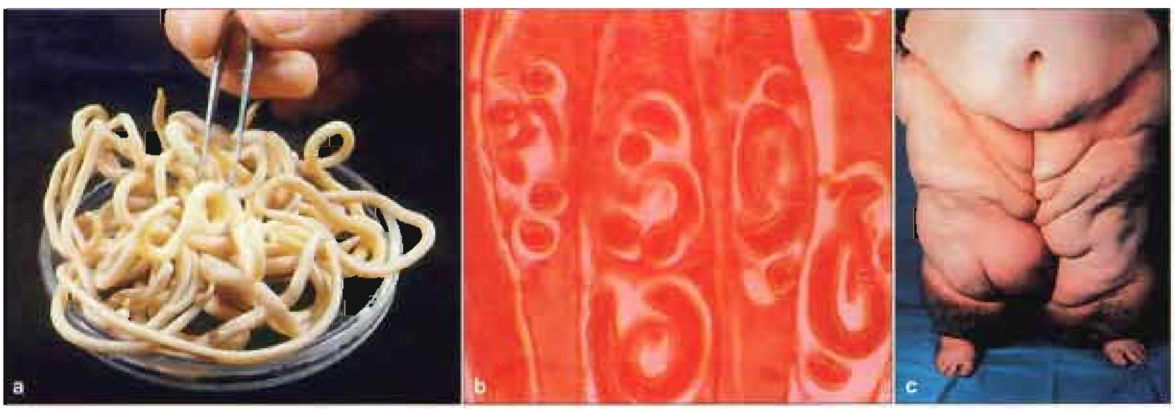


Figure 25.28 (**a**) Living roundworms (*Ascaris lumbricoides*). Infection by these intestinal parasites causes abdominal pain, vomiting, and appendicitis. (**b**) *Trichinella spiralis* juveniles in muscle tissue of a host animal. (**c**) One example of elephantiasis caused by the roundworm *Wuchereria bancrofti*.

25.11 Why Such Spectacular Arthropod Diversity?

LINKS TO SECTIONS 8.1, 15.1

Evolutionarily speaking, "success" means having the most species in the most habitats, fending off competition and threats efficiently, exploiting the greatest amounts and kinds of food, and producing the greatest number of offspring. These features characterize the arthropods.

Arthropods are bilateral animals that have a hardened, jointed exoskeleton and specialized appendages. They have a complete gut, a greatly reduced coelom, and an *open* circulatory system, in which blood flows out of small vessels or hearts, then flows back after trickling through tissues. One group, the trilobites (Figure 25.8), became extinct long ago. Chelicerates and crustaceans, insects, and myriapods are groups that endured. The last group includes millipedes and centipedes.

We consider representatives in sections that follow. For now, start thinking about six important arthropod adaptations. They contributed to the stunning success of arthropods in general and insects in particular.

A hardened exoskeleton. Arthropods have a cuticle of chitin, proteins, and waxes, often stiffened by calcium carbonate deposits. It is a type of protective external skeleton, or **exoskeleton**. The arthropod exoskeleton may have evolved as a deterrent to predators. It took on added functions when some groups invaded land. It restricts water loss, and it helps support the weight of a body removed from the buoyancy of water.

Such exoskeletons do not restrict increases in size, because arthropods molt after each spurt in growth. **Molting** is the periodic shedding of a too-small body covering (or hair, or feathers, or horns) during the life cycle. It is under hormonal control. In arthropods, the hormones trigger the formation of a soft, new cuticle beneath the old one, which is then shed, as in Figure 25.29. Before the new cuticle hardens, the body mass increases by way of the rapid uptake of air or water and continuous mitotic cell divisions.

Jointed appendages. If any cuticle were uniformly hardened, it would prevent movements. The arthropod cuticle thins where it spans *joints*—regions where two body parts abut. The contraction of adjoining muscles makes the cuticle bend at joints, which shifts the abutting body parts relative to one another. A jointed exoskeleton was a key innovation. It was like evolutionary clay that became molded into wings, antennae, legs, and other spectacularly diverse appendages. ("Arthropod" means jointed leg.)

Specialized and fused-together segments. Among the first arthropods, all of the body segments were more or less similar. However, in most lineages that made it to the present, some segments became fused together or modified in other specialized ways. As one example, compare the nearly identical segments of a centipede with the winged body of a butterfly.

Respiratory structures. Many freshwater and marine arthropods use a type of gill for gas exchange. Land-dwelling arthropods use a system of air-conducting tubes, called tracheas. Insect tracheas start at surface pores and branch into finer tubes that deliver oxygen into all internal tissues. Flight and other activities that use a great deal of ATP depend on the rapid uptake of oxygen in aerobically respiring tissues (Section 8.1).

Specialized sensory structures and organs. For many arthropods, diverse sensory structures contributed to their success. For example, each insect eye consists of many individual light-sensitive units that collectively sample the visual field in many directions.

Specialized stages of development. Many arthropods, especially insects, divide up the tasks of surviving and reproducing among different stages of development. For some species, the new individual is a juvenile, a miniaturized version of the adult that grows in size until sexually mature. Individuals of other species undergo **metamorphosis**. Between the embryonic and adult form, the body changes, often in drastic ways, as tissues get reorganized and remodeled. Hormones, recall, guide the developmental steps (Section 15.1).

Many immature stages in the life cycle specialize in eating and growing fast, whereas the adult specializes in reproduction and dispersal of the new generation. Think of caterpillars chewing leaves, then butterflies mating and depositing eggs. Differences in the stages of development are adaptations to specific conditions in the environment, including seasonal shifts in food sources, water, and availability of receptive mates.

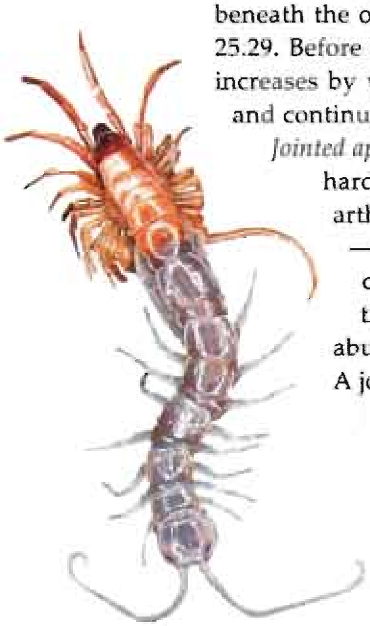


Figure 25.29 Example of molting. This red-orange centipede is busily wriggling out of its old exoskeleton.

As a group, the arthropods are abundant and widespread, with diverse life-styles. Their success correlates with their hardened, jointed exoskeleton, with modified and often fused segments, and with highly specialized appendages, respiratory structures, and sensory structures.

In many species—insects especially—success also arises from a division of labor among different stages of the life cycle, such as larvae, juveniles, and adults.

25.12 Spiders and Their Relatives

Chelicerates arose in shallow seas early in the Paleozoic. They are named for their first pair of feeding appendages (chelicerae). Horseshoe crabs are among the few living marine species. Of the familiar species on land—spiders, scorpions, ticks, and chigger mites—we might say this: Never have so many been loved by so few.

The body plan of horseshoe crabs (Figure 25.30*a*) has changed little since the Devonian. A horseshoe-shaped dorsal shield, or hardened carapace, protects the body from predators. The horseshoe crab's closest relatives on land are arachnids—spiders, scorpions, ticks, and chigger mites. Unlike arachnids, which have four pairs of legs, a horseshoe crab has five pairs. Its chelicerae move marine worms and scavenged food to its mouth.

All spiders and scorpions are aggressive predators (Figures 25.30*a* and 25.31*b*). Most spiders sting, bite, or stun prey before injecting venom into them. One spits glue and venom at prey. Another spins a thread with a ball of sticky material at the end, then uses one of its legs to swing the ball at insects passing by.

A spider's segments are fused into a forebody and hindbody. An open circulatory system extends through both regions. The heart pumps blood into tissues and takes it back through small openings in its wall. The respiratory organs are leaflike "book lungs" (Section 40.2). The paired, jointed forebody appendages include the legs, chelicerae that inflict wounds and discharge venom, and pedipalps that have mostly sensory roles (Figure 25.31). The spider's hindbody has one or more pairs of spinners, which put out silk threads for webs and egg cases. Most webs are netlike.

Figure 25.30 (**a**) Horseshoe crab (*Limulus*). Its long spine helps steer its body. (**b**) Fat-bodied scorpion of Australia.

Twenty-five or so kinds of spiders bite humans and other mammals when threatened or disturbed; Section 25.16 considers two of them. Unfortunately, they have given the whole group a bad name even though insects would overrun our world without spiders.

Mites, including the dust mites in Figure 25.31*c*, are among the smallest, most diverse, and widespread of all arachnids. Section 25.16 focuses on the direct and indirect impact of these parasites our lives.

Spiders, scorpions, and their relatives are predators or parasites. Their first pair of appendages, chelicerae, are structurally and functionally unique feeding structures.

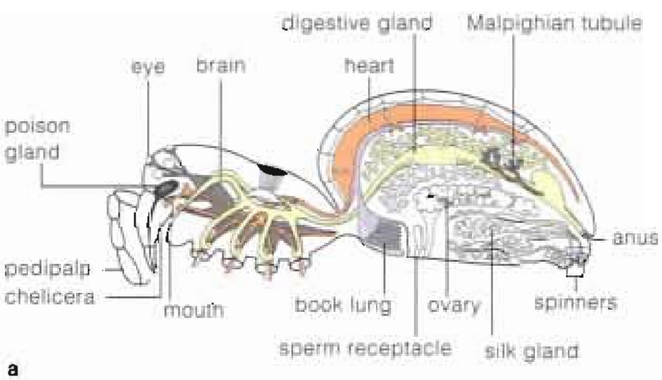


Figure 25.31 Arachnids. (**a**) A spider's internal organization. (**b**) Tarantula with a fearless female. Tarantulas, like other spiders help keep insects in check. Their bite does not harm humans. Section 25.16 describes two spiders that can be dangerous. (**c**) Dust mite. Mite feces and corpses often cause allergies in susceptible people.

25.13 A Look at the Crustaceans

LINK TO SECTION 7.8

The 35,000 or so species of ***crustaceans*** *got their name because they have a hard yet flexible "crust," an external skeleton, but so do nearly all arthropods. Nearly all live in marine habitats, where they are so abundant that they are dubbed "insects of the seas."*

Shrimps, lobsters, crabs, barnacles, and pillbugs are familiar crustaceans. The lobsters and crabs are the giants of the group; most species are less than a few centimeters long. All have major roles in food webs, and humans harvest many edible types.

In one respect, the simplest crustaceans display an ancient feature: They have pairs of similar appendages along most of their body length. In different lineages, unspecialized appendages evolved into many diverse structures of the sort shown in Figure 25.32. To give two examples, the strong claws of lobsters and crabs are used to collect food, intimidate other animals, and sometimes dig burrows. The feathery appendages of barnacles comb bits of food from the water.

Many crustaceans have sixteen to twenty segments; some have more than sixty. Their head has pairs of antennae, and jawlike and food-handling appendages. The lobsters, shrimps, and crabs have five pairs of walking legs. A dorsal cuticle extends back from the head like a shield over the thoracic segments, which are fused together (Figure 25.32*a*,*d*).

Of all arthropods, only barnacles have a calcium-hardened shell that they secrete around themselves. The shell protects them from predators, drying winds, and strong currents or surf (Figure 25.32*b*). The adult barnacles spend their lives cemented to piers, rocks, and even other animals, including whales. Once they are attached, they cannot move on, so you would

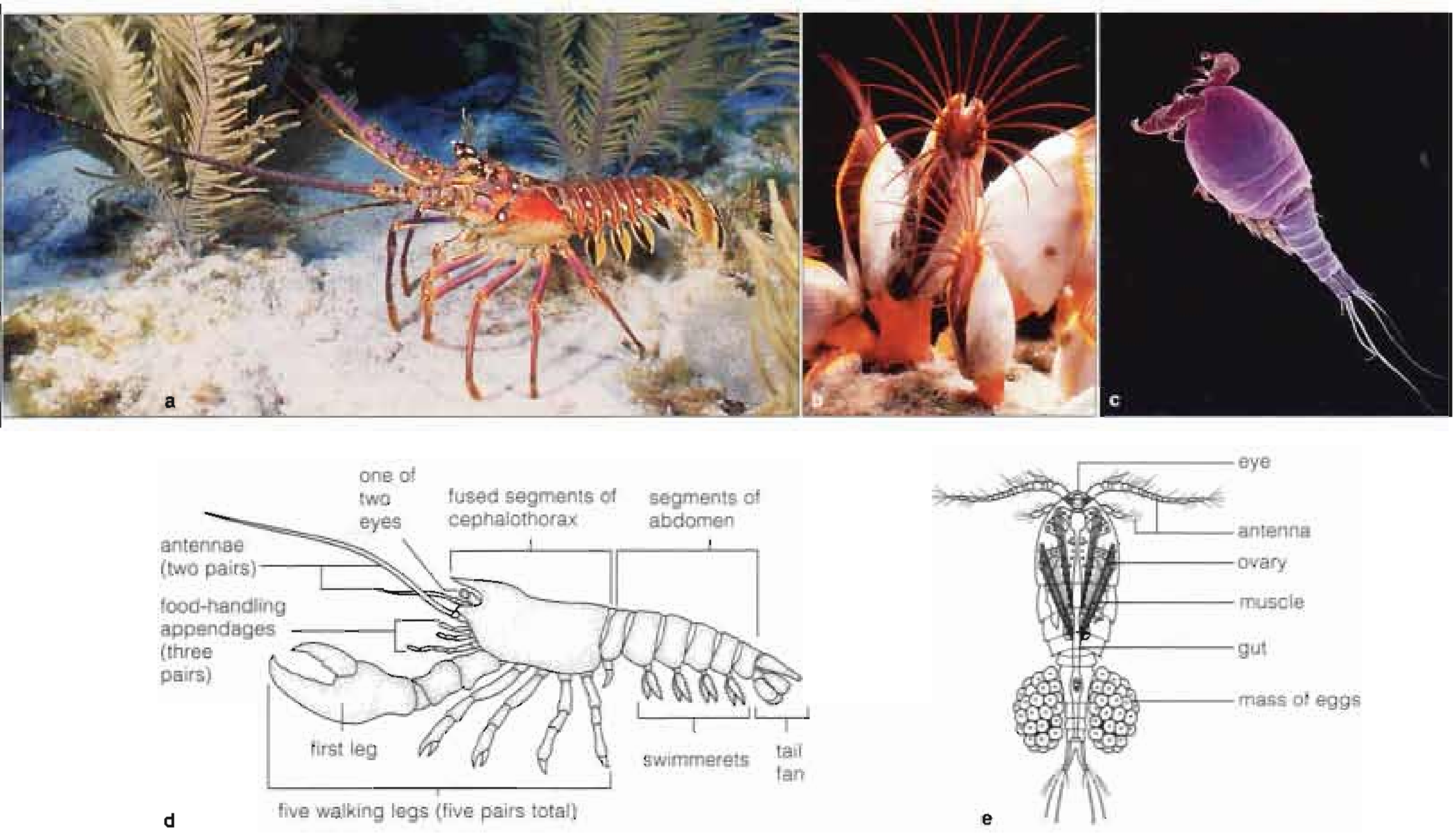


Figure 25.32 (**a**) Lobster in the Caribbean Sea, near Belize. (**b**) Goose barnacles. Adults are cemented to one spot. You might mistake them for mollusks until they open their hinged shell to filter-feed and you see jointed appendages—the hallmark of arthropods. (**c**) Copepod. Different kinds are free-living filter feeders, predators, and parasites. (**d**) Body plan of a lobster. The head has two pairs of antennae and pairs of food-handling appendages, including two jawlike mandibles. Lobsters, crayfish, crabs, shrimps, and their relatives have five pairs of walking legs. (**e**) Body plan of a copepod.

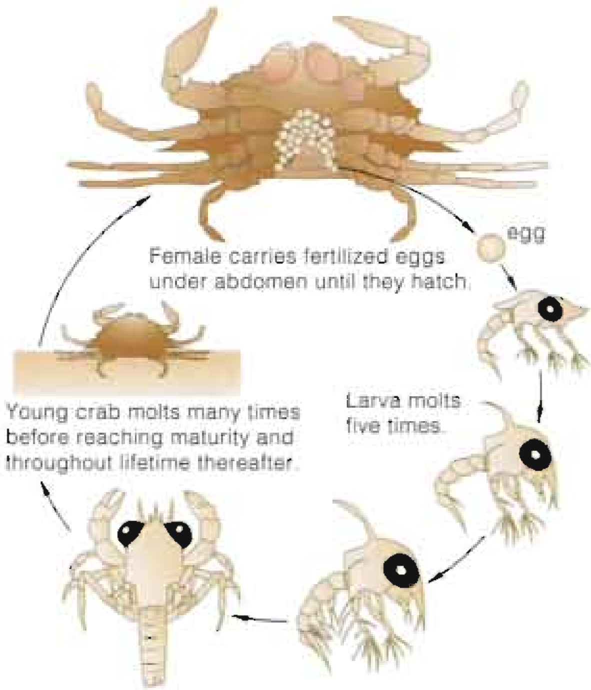


Figure 25.33 *Animated!* Life cycle of a crab. The larval and juvenile stages molt repeatedly and grow in size.

think that mating might be just a bit tricky for them. But barnacles tend to settle down and live in groups, and most species are hermaphrodites. One individual extends its penis, which can be several times its body length, out to neighboring barnacles.

Figure 25.32*c* shows a copepod. Copepods are less than two millimeters long and are the most numerous animals in aquatic habitats. They also are abundant on land. About 1,500 kinds parasitize invertebrates and fishes. However, the majority of copepods—8,000 species—eat phytoplankton, those aquatic "pastures" of photoautotrophs that you read about in Section 7.8. Some copepods prey on larvae or small invertebrates and fish eggs, which they grab with a pair of food-handling appendages. In turn, immense populations of copepods become food for different invertebrates, fishes, and baleen whales.

Like other arthropods, crustaceans repeatedly molt and shed the exoskeleton during the life cycle. Figure 25.33 shows larval stages of a crab as they periodically increase in size and molt their outgrown covering.

Crustaceans differ greatly in the number and kind of appendages. They grow in stages and periodically replace the hardened external skeleton by molting.

25.14 How Many Legs?

Millipedes and centipedes have a long, segmented body with many, many legs—a sure sign of that unfettered Dll gene you read about in Section 17.8.

LINK TO SECTION 17.8

Although millipedes do not have "a thousand" legs, as the name implies, most have about 100 pairs. One individual with an overexpressed *Dll* gene grew 752. Centipedes have between 15 and 177 pairs of legs, not a nicely rounded "one hundred."

As a millipede develops, its pairs of segments fuse, and each segment in its cylindrical body ends up with two pairs of legs (Figure 25.34*a*). Millipedes scavenge decaying plant material in soil and forest litter.

Centipedes have a flattened body, and all but two segments have a pair of walking legs. They are quick, aggressive predators with fangs and venom glands that subdue insects, earthworms, and snails. The one in Figure 25.34*b* hunts small lizards, toads, and frogs. A house centipede (*Scutigera*) often hides in buildings, where it hunts for cockroaches, flies, and other pests. Although helpful in this respect, most of us would rather do without its assistance.

Mild-mannered, scavenging millipedes and aggressive, predatory centipedes do not lend themselves to leg counts as they walk by.

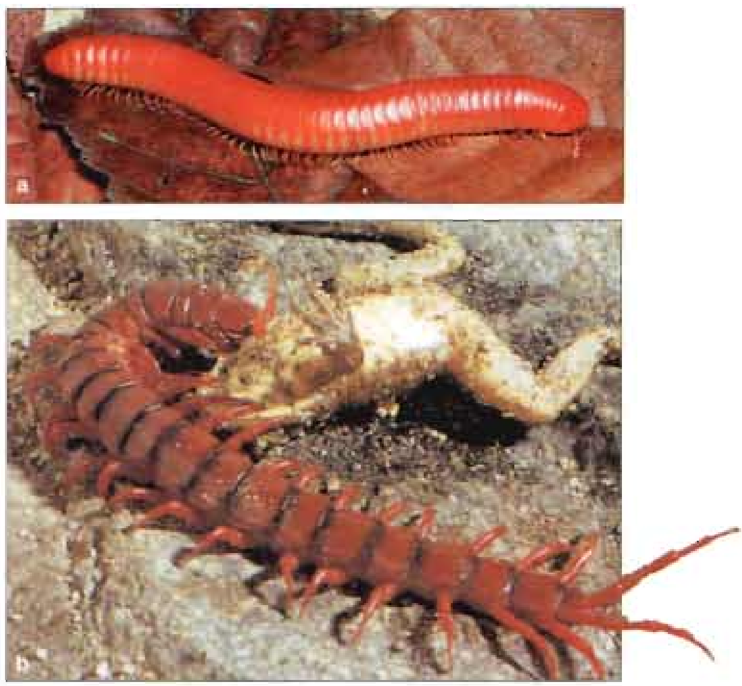


Figure 25.34 **(a)** Millipede. **(b)** A Southeast Asian centipede.