Introduction

A brief look at any magazine pertaining to our natural world, such as *National Geographic*, would show a rich variety of vertebrates, especially mammals and birds. To most people, these are the animals that attract our attention. Concentrating on vertebrates, however, gives us a rather biased and limited view of biodiversity, because it ignores nearly 97 percent of the animal kingdom, namely the invertebrates. Invertebrate animals are those without a cranium and defined vertebral column or spine. In addition to lacking a spine, most invertebrates also lack an endoskeleton. A large number of invertebrates are aquatic animals, and scientific research suggests that many of the world’s species are aquatic invertebrates that have not yet been documented.

28.1 | Phylum Porifera

By the end of this section, you will be able to:

- Describe the organizational features of the simplest multicellular organisms
- Explain the various body forms and bodily functions of sponges
The invertebrates, or invertebrata, are animals that do not contain bony structures, such as the cranium and vertebrae. The simplest of all the invertebrates are the Parazoans, which include only the phylum Porifera: the sponges (Figure 28.2). Parazoans (“beside animals”) do not display tissue-level organization, although they do have specialized cells that perform specific functions. Sponge larvae are able to swim; however, adults are non-motile and spend their life attached to a substratum. Since water is vital to sponges for excretion, feeding, and gas exchange, their body structure facilitates the movement of water through the sponge. Structures such as canals, chambers, and cavities enable water to move through the sponge to nearly all body cells.

Figure 28.2 Sponges are members of the Phylum Porifera, which contains the simplest invertebrates. (credit: Andrew Turner)

Morphology of Sponges

The morphology of the simplest sponges takes the shape of a cylinder with a large central cavity, the spongocoel, occupying the inside of the cylinder. Water can enter into the spongocoel from numerous pores in the body wall. Water entering the spongocoel is extruded via a large common opening called the osculum. However, sponges exhibit a range of diversity in body forms, including variations in the size of the spongocoel, the number of osculi, and where the cells that filter food from the water are located.

While sponges (excluding the hexactinellids) do not exhibit tissue-layer organization, they do have different cell types that perform distinct functions. Pinacocytes, which are epithelial-like cells, form the outermost layer of sponges and enclose a jelly-like substance called mesohyl. Mesohyl is an extracellular matrix consisting of a collagen-like gel with suspended cells that perform various functions. The gel-like consistency of mesohyl acts like an endoskeleton and maintains the tubular morphology of sponges. In addition to the osculum, sponges have multiple pores called ostia on their bodies that allow water to enter the sponge. In some sponges, ostia are formed by porocytes, single tube-shaped cells that act as valves to regulate the flow of water into the spongocoel. In other sponges, ostia are formed by folds in the body wall of the sponge.

Choanocytes (“collar cells”) are present at various locations, depending on the type of sponge, but they always line the inner portions of some space through which water flows (the spongocoel in simple sponges, canals within the body wall in more complex sponges, and chambers scattered throughout the body in the most complex sponges). Whereas pinacocytes line the outside of the sponge, choanocytes tend to line certain inner portions of the sponge body that surround the mesohyl. The structure of a choanocyte is critical to its function, which is to generate a water current through the sponge and to trap and ingest food particles by phagocytosis. Note the similarity in appearance between the sponge choanocyte and choanoflagellates (Protista). This similarity suggests that sponges and choanoflagellates are closely related and likely share a recent common ancestry. The cell body is embedded in mesohyl and contains all organelles required for normal cell function, but protruding into the “open space” inside of the sponge is a mesh-like collar composed of microvilli with a single flagellum in the center of the column. The cumulative effect of the flagella from all choanocytes aids the movement of water through the sponge: drawing water into the sponge through the numerous ostia, into the spaces lined by choanocytes, and eventually out through the osculum (or osculi). In the meantime, food particles, including waterborne bacteria and algae, are trapped by the sieve-like collar of the choanocytes, slide down into the body of the cell, are ingested by phagocytosis, and become encased in a food vacuole. Lastly, choanocytes will differentiate into sperm for sexual reproduction, where they will become dislodged from the mesohyl and leave the sponge with expelled water through the osculum.
Watch this video (http://openstaxcollege.org/l/filter_sponges) to see the movement of water through the sponge body.

The second crucial cells in sponges are called amoebocytes (or archaeocytes), named for the fact that they move throughout the mesohyl in an amoeba-like fashion. Amoebocytes have a variety of functions: delivering nutrients from choanocytes to other cells within the sponge, giving rise to eggs for sexual reproduction (which remain in the mesohyl), delivering phagocytized sperm from choanocytes to eggs, and differentiating into more-specific cell types. Some of these more-specific cell types include collencytes and lophocytes, which produce the collagen-like protein to maintain the mesohyl, sclerocytes, which produce spicules in some sponges, and spongocytes, which produce the protein spongin in the majority of sponges. These cells produce collagen to maintain the consistency of the mesohyl. The different cell types in sponges are shown in Figure 28.3.

![Figure 28.3](image)

**Figure 28.3** The sponge’s (a) basic body plan and (b) some of the specialized cell types found in sponges are shown.

Which of the following statements is false?

a. Choanocytes have flagella that propel water through the body.

b. Pinacycites can transform into any cell type.

c. Lophocytes secrete collagen.

d. Porocytes control the flow of water through pores in the sponge body.

In some sponges, sclerocytes secrete small spicules into the mesohyl, which are composed of either calcium carbonate or silica, depending on the type of sponge. These spicules serve to provide additional stiffness to the body of the sponge.
Additionally, spicules, when present externally, may ward off predators. Another type of protein, spongin, may also be present in the mesohyl of some sponges.

**LINK TO LEARNING**

Take an up-close tour (http://openstaxcollege.org/l/sponge_ride) through the sponge and its cells.

The presence and composition of spicules/spongin are the differentiating characteristics of the three classes of sponges (Figure 28.4): Class Calcarea contains calcium carbonate spicules and no spongin, class Hexactinellida contains six-rayed siliceous spicules and no spongin, and class Demospongia contains spongin and may or may not have spicules; if present, those spicules are siliceous. Spicules are most conspicuously present in class Hexactinellida, the order consisting of glass sponges. Some of the spicules may attain giant proportions (in relation to the typical size range of glass sponges of 3 to 10 mm) as seen in *Monorhaphis chuni*, which grows up to 3 m long.

![Figure 28.4](https://openstaxcollege.org/l/image1)

**Figure 28.4** (a) *Clathrina clathrus* belongs to class Calcarea, (b) *Staurocalyptus* spp. (common name: yellow Picasso sponge) belongs to class Hexactinellida, and (c) *Acarnus erithacus* belongs to class Demospongia. (credit a: modification of work by Parent Géry; credit b: modification of work by Monterey Bay Aquarium Research Institute, NOAA; credit c: modification of work by Sanctuary Integrated Monitoring Network, Monterey Bay National Marine Sanctuary, NOAA)

**LINK TO LEARNING**

Use the Interactive Sponge Guide (http://openstaxcollege.org/l/id_sponges) to identify species of sponges based on their external form, mineral skeleton, fiber, and skeletal architecture.

**Physiological Processes in Sponges**

Sponges, despite being simple organisms, regulate their different physiological processes through a variety of mechanisms. These processes regulate their metabolism, reproduction, and locomotion.

**Digestion**

Sponges lack complex digestive, respiratory, circulatory, reproductive, and nervous systems. Their food is trapped when water passes through the ostia and out through the osculum. Bacteria smaller than 0.5 microns in size are trapped by choanocytes, which are the principal cells engaged in nutrition, and are ingested by phagocytosis. Particles that are larger than the ostia may be phagocytized by pinacocytes. In some sponges, amoebocytes transport food from cells that have
ingested food particles to those that do not. For this type of digestion, in which food particles are digested within individual cells, the sponge draws water through diffusion. The limit of this type of digestion is that food particles must be smaller than individual cells.

All other major body functions in the sponge (gas exchange, circulation, excretion) are performed by diffusion between the cells that line the openings within the sponge and the water that is passing through those openings. All cell types within the sponge obtain oxygen from water through diffusion. Likewise, carbon dioxide is released into seawater by diffusion. In addition, nitrogenous waste produced as a byproduct of protein metabolism is excreted via diffusion by individual cells into the water as it passes through the sponge.

**Reproduction**

Sponges reproduce by sexual as well as asexual methods. The typical means of asexual reproduction is either fragmentation (where a piece of the sponge breaks off, settles on a new substrate, and develops into a new individual) or budding (a genetically identical outgrowth grows from the parent and eventually detaches or remains attached to form a colony). An atypical type of asexual reproduction is found only in freshwater sponges and occurs through the formation of gemmules. **Gemmules** are environmentally resistant structures produced by adult sponges wherein the typical sponge morphology is inverted. In gemmules, an inner layer of amoebocytes is surrounded by a layer of collagen (spongin) that may be reinforced by spicules. The collagen that is normally found in the mesohyl becomes the outer protective layer. In freshwater sponges, gemmules may survive hostile environmental conditions like changes in temperature and serve to recolonize the habitat once environmental conditions stabilize. Gemmules are capable of attaching to a substratum and generating a new sponge. Since gemmules can withstand harsh environments, are resistant to desiccation, and remain dormant for long periods, they are an excellent means of colonization for a sessile organism.

Sexual reproduction in sponges occurs when gametes are generated. Sponges are monoecious (hermaphroditic), which means that one individual can produce both gametes (eggs and sperm) simultaneously. In some sponges, production of gametes may occur throughout the year, whereas other sponges may show sexual cycles depending upon water temperature. Sponges may also become sequentially hermaphroditic, producing oocytes first and spermatozoa later. Oocytes arise by the differentiation of amoebocytes and are retained within the spongocoel, whereas spermatozoa result from the differentiation of choanocytes and are ejected via the osculum. Ejection of spermatozoa may be a timed and coordinated event, as seen in certain species. Spermatozoa carried along by water currents can fertilize the oocytes borne in the mesohyl of other sponges. Early larval development occurs within the sponge, and free-swimming larvae are then released via the osculum.

**Locomotion**

Sponges are generally sessile as adults and spend their lives attached to a fixed substratum. They do not show movement over large distances like other free-swimming marine invertebrates. However, sponge cells are capable of creeping along substrata via organizational plasticity. Under experimental conditions, researchers have shown that sponge cells spread on a physical support demonstrate a leading edge for directed movement. It has been speculated that this localized creeping movement may help sponges adjust to microenvironments near the point of attachment. It must be noted, however, that this pattern of movement has been documented in laboratories, but it remains to be observed in natural sponge habitats.

**LINK TO LEARNING**

Watch this BBC video (http://openstaxcollege.org/l/sea_sponges) showing the array of sponges seen along the Cayman Wall during a submersible dive.
28.2 | Phylum Cnidaria

By the end of this section, you will be able to:

- Compare structural and organization characteristics of Porifera and Cnidaria
- Describe the progressive development of tissues and their relevance to animal complexity

Phylum **Cnidaria** includes animals that show radial or biradial symmetry and are diploblastic, that is, they develop from two embryonic layers. Nearly all (about 99 percent) cnidarians are marine species.

Cnidarians contain specialized cells known as **cnidocytes** (“stinging cells”) containing organelles called **nematocysts** (stingers). These cells are present around the mouth and tentacles, and serve to immobilize prey with toxins contained within the cells. Nematocysts contain coiled threads that may bear barbs. The outer wall of the cell has hairlike projections called cnidocils, which are sensitive to touch. When touched, the cells are known to fire coiled threads that can either penetrate the flesh of the prey or predators of cnidarians (see Figure 28.5) or ensnare it. These coiled threads release toxins into the target and can often immobilize prey or scare away predators.

![Figure 28.5](https://openstax.org/l/nematocyst) Animals from the phylum Cnidaria have stinging cells called cnidocytes. Cnidocytes contain large organelles called (a) nematocysts that store a coiled thread and barb. When hairlike projections on the cell surface are touched, (b) the thread, barb, and a toxin are fired from the organelle.

**Figure 28.5** Animals from the phylum Cnidaria have stinging cells called cnidocytes. Cnidocytes contain large organelles called (a) nematocysts that store a coiled thread and barb. When hairlike projections on the cell surface are touched, (b) the thread, barb, and a toxin are fired from the organelle.

View this [video](http://openstaxcollege.org/l/nematocyst) animation showing two anemones engaged in a battle.

Animals in this phylum display two distinct morphological body plans: **polyp** or “stalk” and **medusa** or “bell” (Figure 28.6). An example of the polyp form is *Hydra* spp.; perhaps the most well-known medusoid animals are the jellies (jellyfish). Polyp forms are sessile as adults, with a single opening to the digestive system (the mouth) facing up with tentacles surrounding it. Medusa forms are motile, with the mouth and tentacles hanging down from an umbrella-shaped bell.
Figure 28.6 Cnidarians have two distinct body plans, the medusa (a) and the polyp (b). All cnidarians have two membrane layers, with a jelly-like mesoglea between them.

Some cnidarians are polymorphic, that is, they have two body plans during their life cycle. An example is the colonial hydroid called an Obelia. The sessile polyp form has, in fact, two types of polyps, shown in Figure 28.7. The first is the gastrozooid, which is adapted for capturing prey and feeding; the other type of polyp is the gonozooid, adapted for the asexual budding of medusa. When the reproductive buds mature, they break off and become free-swimming medusa, which are either male or female (dioecious). The male medusa makes sperm, whereas the female medusa makes eggs. After fertilization, the zygote develops into a blastula, which develops into a planula larva. The larva is free swimming for a while, but eventually attaches and a new colonial reproductive polyp is formed.

Figure 28.7 The sessile form of Obelia geniculate has two types of polyps: gastrozoooids, which are adapted for capturing prey, and gonozooids, which bud to produce medusae asexually.
All cnidarians show the presence of two membrane layers in the body that are derived from the endoderm and ectoderm of the embryo. The outer layer (from ectoderm) is called the epidermis and lines the outside of the animal, whereas the inner layer (from endoderm) is called the gastrodermis and lines the digestive cavity. Between these two membrane layers is a non-living, jelly-like mesoglea connective layer. In terms of cellular complexity, cnidarians show the presence of differentiated cell types in each tissue layer, such as nerve cells, contractile epithelial cells, enzyme-secreting cells, and nutrient-absorbing cells, as well as the presence of intercellular connections. However, the development of organs or organ systems is not advanced in this phylum.

The nervous system is primitive, with nerve cells scattered across the body. This nerve net may show the presence of groups of cells in the form of nerve plexi (singular plexus) or nerve cords. The nerve cells show mixed characteristics of motor as well as sensory neurons. The predominant signaling molecules in these primitive nervous systems are chemical peptides, which perform both excitatory and inhibitory functions. Despite the simplicity of the nervous system, it coordinates the movement of tentacles, the drawing of captured prey to the mouth, the digestion of food, and the expulsion of waste.

The cnidarians perform extracellular digestion in which the food is taken into the gastrovascular cavity, enzymes are secreted into the cavity, and the cells lining the cavity absorb nutrients. The gastrovascular cavity has only one opening that serves as both a mouth and an anus, which is termed an incomplete digestive system. Cnidarian cells exchange oxygen and carbon dioxide by diffusion between cells in the epidermis with water in the environment, and between cells in the gastrodermis with water in the gastrovascular cavity. The lack of a circulatory system to move dissolved gases limits the thickness of the body wall and necessitates a non-living mesoglea between the layers. There is no excretory system or organs, and nitrogenous wastes simply diffuse from the cells into the water outside the animal or in the gastrovascular cavity. There is also no circulatory system, so nutrients must move from the cells that absorb them in the lining of the gastrovascular cavity through the mesoglea to other cells.

The phylum Cnidaria contains about 10,000 described species divided into four classes: Anthozoa, Scyphozoa, Cubozoa, and Hydrozoa. The anthozoans, the sea anemones and corals, are all sessile species, whereas the scyphozoans (jellyfish) and cubozoans (box jellies) are swimming forms. The hydrozoans contain sessile forms and swimming colonial forms like the Portuguese Man O’ War.

**Class Anthozoa**

The class Anthozoa includes all cnidarians that exhibit a polyp body plan only; in other words, there is no medusa stage within their life cycle. Examples include sea anemones (Figure 28.8), sea pens, and corals, with an estimated number of 6,100 described species. Sea anemones are usually brightly colored and can attain a size of 1.8 to 10 cm in diameter. These animals are usually cylindrical in shape and are attached to a substrate. A mouth opening is surrounded by tentacles bearing cnidocytes.
The mouth of a sea anemone is surrounded by tentacles that bear cnidocytes. The slit-like mouth opening and pharynx are lined by a groove called a siphonophore. The pharynx is the muscular part of the digestive system that serves to ingest as well as egest food, and may extend for up to two-thirds the length of the body before opening into the gastrovascular cavity. This cavity is divided into several chambers by longitudinal septa called mesenteries. Each mesentery consists of one ectodermal and one endodermal cell layer with the mesoglea sandwiched in between. Mesenteries do not divide the gastrovascular cavity completely, and the smaller cavities coalesce at the pharyngeal opening. The adaptive benefit of the mesenteries appears to be an increase in surface area for absorption of nutrients and gas exchange.

Sea anemones feed on small fish and shrimp, usually by immobilizing their prey using the cnidocytes. Some sea anemones establish a mutualistic relationship with hermit crabs by attaching to the crab’s shell. In this relationship, the anemone gets food particles from prey caught by the crab, and the crab is protected from the predators by the stinging cells of the anemone. Anemone fish, or clownfish, are able to live in the anemone since they are immune to the toxins contained within the nematocysts.

Anthozoans remain polypoid throughout their lives and can reproduce asexually by budding or fragmentation, or sexually by producing gametes. Both gametes are produced by the polyp, which can fuse to give rise to a free-swimming planula larva. The larva settles on a suitable substratum and develops into a sessile polyp.

**Class Scyphozoa**

Class Scyphozoa includes all the jellies and is exclusively a marine class of animals with about 200 known species. The defining characteristic of this class is that the medusa is the prominent stage in the life cycle, although there is a polyp stage present. Members of this species range from 2 to 40 cm in length but the largest scyphozoan species, *Cyanea capillata*, can reach a size of 2 m across. Scyphozoans display a characteristic bell-like morphology (Figure 28.9).
In the jellyfish, a mouth opening is present on the underside of the animal, surrounded by tentacles bearing nematocysts. Scyphozoans live most of their life cycle as free-swimming, solitary carnivores. The mouth leads to the gastrovascular cavity, which may be sectioned into four interconnected sacs, called diverticuli. In some species, the digestive system may be further branched into radial canals. Like the septa in anthozoans, the branched gastrovascular cells serve two functions: to increase the surface area for nutrient absorption and diffusion; thus, more cells are in direct contact with the nutrients in the gastrovascular cavity.

In scyphozoans, nerve cells are scattered all over the body. Neurons may even be present in clusters called rhopalia. These animals possess a ring of muscles lining the dome of the body, which provides the contractile force required to swim through water. Scyphozoans are dioecious animals, that is, the sexes are separate. The gonads are formed from the gastrodermis and gametes are expelled through the mouth. Planula larvae are formed by external fertilization; they settle on a substratum in a polypoid form known as scyphistoma. These forms may produce additional polyps by budding or may transform into the medusoid form. The life cycle (Figure 28.10) of these animals can be described as **polymorphic**, because they exhibit both a medusal and polypoid body plan at some point in their life cycle.
Figure 28.10 The lifecycle of a jellyfish includes two stages: the medusa stage and the polyp stage. The polyp reproduces asexually by budding, and the medusa reproduces sexually. (credit "medusa": modification of work by Francesco Crippa)

Identify the life cycle stages of jellies using this video animation quiz (http://openstaxcollege.org/l/amazing_jellies) from the New England Aquarium.

**Class Cubozoa**

This class includes jellies that have a box-shaped medusa, or a bell that is square in cross-section; hence, are colloquially known as “box jellyfish.” These species may achieve sizes of 15–25 cm. Cubozoans display overall morphological and anatomical characteristics that are similar to those of the scyphozoans. A prominent difference between the two classes is the arrangement of tentacles. This is the most venomous group of all the cnidarians (Figure 28.11).

The cubozoans contain muscular pads called pedalia at the corners of the square bell canopy, with one or more tentacles attached to each pedarium. These animals are further classified into orders based on the presence of single or multiple tentacles per pedarium. In some cases, the digestive system may extend into the pedalia. Nematocysts may be arranged in a spiral configuration along the tentacles; this arrangement helps to effectively subdue and capture prey. Cubozoans exist in a polypoid form that develops from a planula larva. These polyps show limited mobility along the substratum and, like scyphozoans, may bud to form more polyps to colonize a habitat. Polyp forms then transform into the medusoid forms.
The tiny cubozoan jelly *Malo kingi* is thimble shaped and, like all cubozoan jellies, has four muscular pedalia to which the tentacles attach. *M. kingi* is one of two species of jellies known to cause Irukandji syndrome, a condition characterized by excruciating muscle pain, vomiting, increased heart rate, and psychological symptoms. Two people in Australia, where Irukandji jellies are most commonly found, are believed to have died from Irukandji stings. A sign on a beach in northern Australia warns swimmers of the danger. (credit c: modification of work by Peter Shanks)

Class Hydrozoa

Hydrozoa includes nearly 3,200 species; most are marine, although some freshwater species are known (Figure 28.12). Animals in this class are polymorphs, and most exhibit both polypoid and medusoid forms in their lifecycle, although this is variable.

The polyp form in these animals often shows a cylindrical morphology with a central gastrovascular cavity lined by the gastrodermis. The gastrodermis and epidermis have a simple layer of mesoglea sandwiched between them. A mouth opening, surrounded by tentacles, is present at the oral end of the animal. Many hydrozoans form colonies that are composed of a branched colony of specialized polyps that share a gastrovascular cavity, such as in the colonial hydroid *Obelia*. Colonies may also be free-floating and contain medusoid and polypoid individuals in the colony as in *Physalia* (the Portuguese Man O’ War) or *Velella* (By-the-wind sailor). Even other species are solitary polyps (*Hydra*) or solitary medusae (*Gonionemus*). The true characteristic shared by all of these diverse species is that their gonads for sexual reproduction are derived from epidermal tissue, whereas in all other cnidarians they are derived from gastrodermal tissue.
Figure 28.12 (a) Obelia, (b) Physalia physalis, known as the Portuguese Man O’ War, (c) Velella bae, and (d) Hydra have different body shapes but all belong to the family Hydrozoa. (credit b: modification of work by NOAA; scale-bar data from Matt Russell)

28.3 | Superphylum Lophotrochozoa

By the end of this section, you will be able to:

- Describe the unique anatomical and morphological features of flatworms, rotifers, Nemertea, mollusks, and annelids
- Describe the development of an extracoelomic cavity
- Discuss the advantages of true body segmentation
- Explain the key features of Platyhelminthes and their importance as parasites
- Describe the features of animals classified in phylum Annelida

Animals belonging to superphylum Lophotrochozoa are protostomes, in which the blastopore, or the point of involution of the ectoderm or outer germ layer, becomes the mouth opening to the alimentary canal. This is called protostomy or “first mouth.” In protostomy, solid groups of cells split from the endoderm or inner germ layer to form a central mesodermal layer
of cells. This layer multiplies into a band and then splits internally to form the coelom; this protostomic coelom is hence termed **schizocoelom**.

As lophotrochozoans, the organisms in this superphylum possess either a lophophore or trochophore larvae. The lophophores include groups that are united by the presence of the lophophore, a set of ciliated tentacles surrounding the mouth. Lophophorata include the flatworms and several other phyla. These clades are upheld when RNA sequences are compared. Trochophore larvae are characterized by two bands of cilia around the body.

The lophotrochozoans are triploblastic and possess an embryonic mesoderm sandwiched between the ectoderm and endoderm found in the diploblastic cnidarians. These phyla are also bilaterally symmetrical, meaning that a longitudinal section will divide them into right and left sides that are symmetrical. It also means the beginning of cephalization, the evolution of a concentration of nervous tissues and sensory organs in the head of the organism, which is where it first encounters its environment.

**Phylum Platyhelminthes**

The flatworms are acoelomate organisms that include many free-living and parasitic forms. Most of the flatworms are classified in the superphylum Lophotrochozoa, which also includes the mollusks and annelids. The Platyhelminthes consist of two lineages: the Catenulida and the Rhabditophora. The Catenulida, or "chain worms" is a small clade of just over 100 species. These worms typically reproduce asexually by budding. However, the offspring do not fully attach from the parents and resemble a chain in appearance. All of the remaining flatworms discussed here are part of the Rhabditophora. Many flatworms are parasitic, including important parasites of humans. Flatworms have three embryonic tissue layers that give rise to surfaces that cover tissues (from ectoderm), internal tissues (from mesoderm), and line the digestive system (from endoderm). The epidermal tissue is a single layer cells or a layer of fused cells (syncytium) that covers a layer of circular muscle above a layer of longitudinal muscle. The mesodermal tissues include mesenchymal cells that contain collagen and support secretory cells that secrete mucus and other materials at the surface. The flatworms are acoelomates, so their bodies are solid between the outer surface and the cavity of the digestive system.

**Physiological Processes of Flatworms**

The free-living species of flatworms are predators or scavengers. Parasitic forms feed on the tissues of their hosts. Most flatworms, such as the planarian shown in Figure 28.13, have a gastrovascular cavity rather than a complete digestive system. In such animals, the “mouth” is also used to expel waste materials from the digestive system. Some species also have an anal opening. The gut may be a simple sac or highly branched. Digestion is extracellular, with digested materials taken in to the cells of the gut lining by phagocytosis. One group, the cestodes, lacks a digestive system. Flatworms have an excretory system with a network of tubules throughout the body with openings to the environment and nearby flame cells, whose cilia beat to direct waste fluids concentrated in the tubules out of the body. The system is responsible for the regulation of dissolved salts and the excretion of nitrogenous wastes. The nervous system consists of a pair of nerve cords running the length of the body with connections between them and a large ganglion or concentration of nerves at the anterior end of the worm, where there may also be a concentration of photosensory and chemosensory cells.

There is neither a circulatory nor respiratory system, with gas and nutrient exchange dependent on diffusion and cell-cell junctions. This necessarily limits the thickness of the body in these organisms, constraining them to be “flat” worms.

Most flatworm species are monoecious, and fertilization is typically internal. Asexual reproduction is common in some groups.
The planarian is a flatworm that has a gastrovascular cavity with one opening that serves as both mouth and anus. The excretory system is made up of tubules connected to excretory pores on both sides of the body. The nervous system is composed of two interconnected nerve cords running the length of the body, with cerebral ganglia and eyespots at the anterior end.

### Diversity of Flatworms

Platyhelminthes are traditionally divided into four classes: Turbellaria, Monogenea, Trematoda, and Cestoda (Figure 28.14). As discussed above, the relationships among members of these classes is being reassessed, with the turbellarians in particular now viewed as a paraphyletic group, a group that does not have a single common ancestor.
Figure 28.14 Phylum Platyhelminthes is divided into four classes. (a) Class Turbellaria includes the Bedford’s flatworm (*Pseudobiceros bedfordi*), which is about 8–10 cm in length. (b) The parasitic class Monogenea includes *Dactylogyrus* spp. *Dactylogyrus*, commonly called a gill fluke, is about 0.2 mm in length and has two anchors, indicated by arrows, that it uses to latch onto the gills of host fish. (c) The Trematoda class includes *Fascioloides magna* (right) and *Fasciola hepatica* (two specimens of left, also known as the common liver fluke). (d) Class Cestoda includes tapeworms such as this *Taenia saginata*. *T. saginata*, which infects both cattle and humans, can reach 4–10 meters in length; the specimen shown here is about 4 meters. (credit a: modification of work by Jan Derk; credit d: modification of work by CDC)

The class Turbellaria includes mainly free-living, marine species, although some species live in freshwater or moist terrestrial environments. The ventral epidermis of turbellarians is ciliated and facilitates their locomotion. Some turbellarians are capable of remarkable feats of regeneration in which they may regrow the body, even from a small fragment.

The monogeneans are ectoparasites, mostly of fish, with simple lifecycles that consist of a free-swimming larva that attaches to a fish to begin transformation to the parasitic adult form. The parasite has only one host and that host is usually only one species. The worms may produce enzymes that digest the host tissues or simply graze on surface mucus and skin particles. Most monogeneans are hermaphroditic, but the male gametes develop first and so cross-fertilization is quite common.

The trematodes, or flukes, are internal parasites of mollusks and many other groups, including humans. Trematodes have complex lifecycles that involve a primary host in which sexual reproduction occurs, and one or more secondary hosts in which asexual reproduction occurs. The primary host is almost always a mollusk. Trematodes are responsible for serious human diseases including schistosomiasis, a blood fluke. The disease infects an estimated 200 million people in the tropics, leading to organ damage and chronic symptoms like fatigue. Infection occurs when the human enters the water and a larva, released from the primary snail host, locates and penetrates the skin. The parasite infects various organs in the body and feeds on red blood cells before reproducing. Many of the eggs are released in feces and find their way into a waterway, where they are able to reinfect the primary snail host.

The cestodes, or tapeworms, are also internal parasites, mainly of vertebrates (Figure 28.15). Tapeworms live in the intestinal tract of the primary host and remain fixed using a sucker on the anterior end, or scolex, of the tapeworm body.
The remaining body of the tapeworm is made up of a long series of units called proglottids, each of which may contain an excretory system with flame cells, but contain reproductive structures, both male and female. Tapeworms do not possess a digestive system; instead, they absorb nutrients from the food matter passing them in the host’s intestine.

Proglottids are produced at the scolex and gradually migrate to the end of the tapeworm; at this point, they are “mature” and all structures except fertilized eggs have degenerated. Most reproduction occurs by cross-fertilization. The proglottid detaches from the body of the worm and is released into the feces of the organism. The eggs are eaten by an intermediate host. The juvenile worm infects the intermediate host and takes up residence, usually in muscle tissue. When the muscle tissue is eaten by the primary host, the cycle is completed. There are several tapeworm parasites of humans that are transmitted by eating uncooked or poorly cooked pork, beef, and fish.

![Figure 28.15 Tapeworm (Taenia spp.) infections occur when humans consume raw or undercooked infected meat. (credit: modification of work by CDC)](image)

**Phylum Rotifera**

The rotifers are a microscopic (about 100 µm to 30 mm) group of mostly aquatic organisms that get their name from the **corona**, a rotating, wheel-like structure that is covered with cilia at their anterior end (Figure 28.16). Although their taxonomy is currently in flux, one treatment places the rotifers in three classes: Bdelloidea, Monogononta, and Seisonidea. The classification of the group is currently under revision, however, as more phylogenetic evidence becomes available. It is possible that the “spiny headed worms” currently in phylum Acanthocephala will be incorporated into this group in the future.

The body form of rotifers consists of a head (which contains the corona), a trunk (which contains the organs), and the foot. Rotifers are typically free-swimming and truly planktonic organisms, but the toes or extensions of the foot can secrete a sticky material forming a holdfast to help them adhere to surfaces. The head contains sensory organs in the form of a bilobed brain and small eyespots near the corona.
Figure 28.16 Shown are examples from two of the three classes of rotifer. (a) Species from the class Bdelloidea are characterized by a large corona, shown separately from the whole animals in the center of this scanning electron micrograph. (b) Polyarthra, from the class Monogononta, has a smaller corona than Bdelloid rotifers, and a single gonad, which give the class its name. (credit a: modification of work by Diego Fontaneto; credit b: modification of work by U.S. EPA; scale-bar data from Cory Zanker)

The rotifers are filter feeders that will eat dead material, algae, and other microscopic living organisms, and are therefore very important components of aquatic food webs. Rotifers obtain food that is directed toward the mouth by the current created from the movement of the corona. The food particles enter the mouth and travel to the mastax (pharynx with jaw-like structures). Food then passes by digestive and salivary glands, and into the stomach, then onto the intestines. Digestive and excretory wastes are collected in a cloacal bladder before being released out the anus.

Watch this video (http://openstaxcollege.org/l/rotifers) to see rotifers feeding.

Rotifers are pseudocoelomates commonly found in fresh water and some salt water environments throughout the world. Figure 28.17 shows the anatomy of a rotifer belonging to class Bdelloidea. About 2,200 species of rotifers have been identified. Rotifers are dioecious organisms (having either male or female genitalia) and exhibit sexual dimorphism (males and females have different forms). Many species are parthenogenic and exhibit haplodiploidy, a method of gender determination in which a fertilized egg develops into a female and an unfertilized egg develops into a male. In many dioecious species, males are short-lived and smaller with no digestive system and a single testis. Females can produce eggs that are capable of dormancy for protection during harsh environmental conditions.
Phylum Nemertea

The Nemertea are colloquially known as ribbon worms. Most species of phylum Nemertea are marine, predominantly benthic or bottom dwellers, with an estimated 900 species known. However, nemertini have been recorded in freshwater and terrestrial habitats as well. Most nemerteans are carnivores, feeding on worms, clams, and crustaceans. Some species are scavengers, and some nemertini species, like Malacobdella grossa, have also evolved commensalistic relationships with some mollusks. Some species have devastated commercial fishing of clams and crabs. Nemerteans have almost no predators and two species are sold as fish bait.

Morphology

Ribbon worms vary in size from 1 cm to several meters. They show bilateral symmetry and remarkable contractile properties. Because of their contractility, they can change their morphological presentation in response to environmental cues. Animals in phylum Nemertea show a flattened morphology, that is, they are flat from front to back, like a flattened tube. Nemertea are soft and unsegmented animals (Figure 28.18).
Figure 28.18 The proboscis worm (Parborlasia corrugatus) is a scavenger that combs the sea floor for food. The species is a member of the phylum Nemertea. The specimen shown here was photographed in the Ross Sea, Antarctica. (credit: Henry Kaiser, National Science Foundation)

A unique characteristic of this phylum is the presence of a proboscis enclosed in a rhynchocoel. The proboscis serves to capture food and may be ornamented with barbs in some species. The rhynchocoel is a fluid-filled cavity that extends from the head to nearly two-thirds of the length of the gut in these animals (Figure 28.19). The proboscis may be extended or retracted by the retractor muscle attached to the wall of the rhynchocoel.

Figure 28.19 The anatomy of a Nemertean is shown.

Digestive System

The nemertini show a very well-developed digestive system. A mouth opening that is ventral to the rhynchocoel leads into the foregut, followed by the intestine. The intestine is present in the form of diverticular pouches and ends in a rectum that opens via an anus. Gonads are interspersed with the intestinal diverticular pouches and open outwards via genital pores. A circulatory system consists of a closed loop of a pair of lateral blood vessels. The circulatory system is derived from the coelomic cavity of the embryo. Some animals may also have cross-connecting vessels in addition to lateral ones. Although these are called blood vessels, since they are of coelomic origin, the circulatory fluid is colorless. Some species bear hemoglobin as well as other yellow or green pigments. The blood vessels are connected to the rhynchocoel. The flow of fluid in these vessels is facilitated by the contraction of muscles in the body wall. A pair of protonephridia, or primitive kidneys, is present in these animals to facilitate osmoregulation. Gaseous exchange occurs through the skin in the nemertini.

Watch this video (http://openstaxcollege.org/l/nemertean) to see a nemertean attack a polychaete with its proboscis.

This OpenStax book is available for free at http://cnx.org/content/col11448/1.10
**Nervous System**

Nemertini have a ganglion or “brain” situated at the anterior end between the mouth and the foregut, surrounding the digestive system as well as the rhynchocoel. A ring of four nerve masses called “ganglia” composes the brain in these animals. Paired longitudinal nerve cords emerge from the brain ganglia and extend to the posterior end. Ocelli or eyespots are present in pairs, in multiples of two in the anterior portion of the body. It is speculated that the eyespots originate from neural tissue and not from the epidermis.

**Reproduction**

Animals in phylum Nemertea show sexual dimorphism, although freshwater species may be hermaphroditic. Eggs and sperm are released into the water, and fertilization occurs externally. The zygote then develops into a **planuliform** larva.

In some nemertine species, a **pilidium** larva may develop inside the young worm, from a series of imaginal discs. This larval form, characteristically shaped like a deerstalker cap, devours tissues from the young worm for survival before metamorphosing into the adult-like morphology.

**Phylum Mollusca**

Phylum **Mollusca** is the predominant phylum in marine environments. It is estimated that 23 percent of all known marine species are mollusks; there are over 75,000 described species, making them the second most diverse phylum of animals. The name “mollusca” signifies a soft body, since the earliest descriptions of mollusks came from observations of unshelled cuttlefish. Mollusks are predominantly a marine group of animals; however, they are known to inhabit freshwater as well as terrestrial habitats. Mollusks display a wide range of morphologies in each class and subclass, but share a few key characteristics, including a muscular foot, a visceral mass containing internal organs, and a mantle that may or may not secrete a shell of calcium carbonate (Figure 28.20).

**Figure 28.20** There are many species and variations of mollusks; this illustration shows the anatomy of an aquatic gastropod.

Which of the following statements about the anatomy of a mollusk is false?

a. Mollusks have a radula for grinding food.

b. A digestive gland is connected to the stomach.

c. The tissue beneath the shell is called the mantle.

d. The digestive system includes a gizzard, a stomach, a digestive gland, and the intestine.

Mollusks have a muscular foot, which is used for locomotion and anchorage, and varies in shape and function, depending on the type of mollusk under study. In shelled mollusks, this foot is usually the same size as the opening of the shell. The foot is a retractable as well as an extendable organ. The foot is the ventral-most organ, whereas the mantle is the limiting dorsal organ. Mollusks are eucoelomate, but the coelomic cavity is restricted to a cavity around the heart in adult animals. The mantle cavity develops independently of the coelomic cavity.

The visceral mass is present above the foot, in the visceral hump. This includes digestive, nervous, excretory, reproductive, and respiratory systems. Mollusk species that are exclusively aquatic have gills for respiration, whereas some terrestrial species have lungs for respiration. Additionally, a tongue-like organ called a **radula**, which bears chitinous tooth-like...
ornamentation, is present in many species, and serves to shred or scrape food. The mantle (also known as the pallium) is the dorsal epidermis in mollusks; shelled mollusks are specialized to secrete a chitinous and hard calcareous shell.

Most mollusks are dioecious animals and fertilization occurs externally, although this is not the case in terrestrial mollusks, such as snails and slugs, or in cephalopods. In some mollusks, the zygote hatches and undergoes two larval stages—trochophore and veliger—before becoming a young adult; bivalves may exhibit a third larval stage, glochidia.

**Classification of Phylum Mollusca**

Phylum Mollusca is a very diverse (85,000 species) group of mostly marine species. Mollusks have a dramatic variety of form, ranging from large predatory squids and octopus, some of which show a high degree of intelligence, to grazing forms with elaborately sculpted and colored shells. This phylum can be segregated into seven classes: Aplacophora, Monoplacophora, Polyplacophora, Bivalvia, Gastropoda, Cephalopoda, and Scaphopoda.

Class Aplacophora (“bearing no plates”) includes worm-like animals primarily found in benthic marine habitats. These animals lack a calcareous shell but possess aragonite spicules on their epidermis. They have a rudimentary mantle cavity and lack eyes, tentacles, and nephridia (excretory organs). Members of class Monoplacophora (“bearing one plate”) possess a single, cap-like shell that encloses the body. The morphology of the shell and the underlying animal can vary from circular to ovate. A looped digestive system, multiple pairs of excretory organs, many gills, and a pair of gonads are present in these animals. The monoplacophorans were believed extinct and only known via fossil records until the discovery of *Neopilina galathaea* in 1952. Today, scientists have identified nearly two dozen extant species.

Animals in the class Polyplacophora (“bearing many plates”) are commonly known as “chitons” and bear an armor-like eight-plated shell (Figure 28.21). These animals have a broad, ventral foot that is adapted for suction to rocks and other substrates, and a mantle that extends beyond the shell in the form of a girdle. Calcareous spines may be present on the girdle to offer protection from predators. Respiration is facilitated by ctenidia (gills) that are present ventrally. These animals possess a radula that is modified for scraping. The nervous system is rudimentary with only buccal or “cheek” ganglia present at the anterior end. Eyespots are absent in these animals. A single pair of nephridia for excretion is present.

Figure 28.21 This chiton from the class Polyplacophora has the eight-plated shell that is indicative of its class. (credit: Jerry Kirkhart)

Class Bivalvia (“two shells”) includes clams, oysters, mussels, scallops, and geoducks. Members of this class are found in marine as well as freshwater habitats. As the name suggests, bivalves are enclosed in a pair of shells (valves are commonly called “shells”) that are hinged at the dorsal end by shell ligaments as well as shell teeth (Figure 28.22). The overall morphology is laterally flattened, and the head region is poorly developed. Eyespots and statocysts may be absent in some species. Since these animals are suspension feeders, a radula is absent in this class of mollusks. Respiration is facilitated by a pair of ctenidia, whereas excretion and osmoregulation are brought about by a pair of nephridia. Bivalves often possess a large mantle cavity. In some species, the posterior edges of the mantle may fuse to form two siphons that serve to take in and exude water.
One of the functions of the mantle is to secrete the shell. Some bivalves like oysters and mussels possess the unique ability to secrete and deposit a calcareous nacre or “mother of pearl” around foreign particles that may enter the mantle cavity. This property has been commercially exploited to produce pearls.

Watch the animations of bivalves feeding: View the process in clams (http://openstaxcollege.org/l/clams) and mussels (http://openstaxcollege.org/l/mussels) at these sites.

Animals in class Gastropoda (“stomach foot”) include well-known mollusks like snails, slugs, conchs, sea hares, and sea butterflies. Gastropoda includes shell-bearing species as well as species with a reduced shell. These animals are asymmetrical and usually present a coiled shell (Figure 28.23). Shells may be planospiral (like a garden hose wound up), commonly seen in garden snails, or conispiral, (like a spiral staircase), commonly seen in marine conches.

The visceral mass in the shelled species displays torsion around the perpendicular axis on the center of the foot, which is the key characteristic of this group, along with a foot that is modified for crawling (Figure 28.24). Most gastropods bear a
head with tentacles, eyes, and a style. A complex radula is used by the digestive system and aids in the ingestion of food. Eyes may be absent in some gastropods species. The mantle cavity encloses the ctenidia as well as a pair of nephridia.

**Figure 28.24** During embryonic development of gastropods, the visceral mass undergoes torsion, or counterclockwise rotation of anatomical features. As a result, the anus of the adult animal is located over the head. Torsion is an independent process from coiling of the shell.

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**Can Snail Venom Be Used as a Pharmacological Painkiller?**

Marine snails of the genus *Conus* ([Figure 28.25](#)) attack prey with a venomous sting. The toxin released, known as conotoxin, is a peptide with internal disulfide linkages. Conotoxins can bring about paralysis in humans, indicating that this toxin attacks neurological targets. Some conotoxins have been shown to block neuronal ion channels. These findings have led researchers to study conotoxins for possible medical applications.

Conotoxins are an exciting area of potential pharmacological development, since these peptides may be possibly modified and used in specific medical conditions to inhibit the activity of specific neurons. For example, these toxins may be used to induce paralysis in muscles in specific health applications, similar to the use of botulinum toxin. Since the entire spectrum of conotoxins, as well as their mechanisms of action, are not completely known, the study of their potential applications is still in its infancy. Most research to date has focused on their use to treat neurological diseases. They have also shown some efficacy in relieving chronic pain, and the pain associated with conditions like sciatica and shingles. The study and use of biotoxins—toxins derived from living organisms—are an excellent example of the application of biological science to modern medicine.

**Figure 28.25** Members of the genus *Conus* produce neurotoxins that may one day have medical uses. (credit: David Burdick, NOAA)
Class Cephalopoda (“head foot” animals), include octopi, squids, cuttlefish, and nautilus. Cephalopods are a class of shell-bearing animals as well as mollusks with a reduced shell. They display vivid coloration, typically seen in squids and octopi, which is used for camouflage. All animals in this class are carnivorous predators and have beak-like jaws at the anterior end. All cephalopods show the presence of a very well-developed nervous system along with eyes, as well as a closed circulatory system. The foot is lobed and developed into tentacles, and a funnel, which is used as their mode of locomotion. Suckers are present on the tentacles in octopi and squid. Ctenidia are enclosed in a large mantle cavity and are serviced by large blood vessels, each with its own heart associated with it; the mantle has siphonophores that facilitate exchange of water.

Locomotion in cephalopods is facilitated by ejecting a stream of water for propulsion. This is called “jet” propulsion. A pair of nephridia is present within the mantle cavity. Sexual dimorphism is seen in this class of animals. Members of a species mate, and the female then lays the eggs in a secluded and protected niche. Females of some species care for the eggs for an extended period of time and may end up dying during that time period. Cephalopods such as squids and octopi also produce sepia or a dark ink, which is squirted upon a predator to assist in a quick getaway.

Reproduction in cephalopods is different from other mollusks in that the egg hatches to produce a juvenile adult without undergoing the trochophore and veliger larval stages.

In the shell-bearing Nautilus spp., the spiral shell is multi-chambered. These chambers are filled with gas or water to regulate buoyancy. The shell structure in squids and cuttlefish is reduced and is present internally in the form of a squid pen and cuttlefish bone, respectively. Examples are shown in Figure 28.26.

![Figure 28.26](credit: modification of work by J. Baecker; credit b: modification of work by Adrian Mohedano; credit c: modification of work by Silke Baron; credit d: modification of work by Angell Williams)

Members of class Scaphopoda (“boat feet”) are known colloquially as “tusk shells” or “tooth shells,” as evident when examining Dentalium, one of the few remaining scaphopod genera (Figure 28.27). Scaphopods are usually buried in sand with the anterior opening exposed to water. These animals bear a single conical shell, which has both ends open. The head is rudimentary and protrudes out of the posterior end of the shell. These animals do not possess eyes, but they have a radula, as well as a foot modified into tentacles with a bulbous end, known as captaculae. Captaculae serve to catch and manipulate prey. Ctenidia are absent in these animals.
Phylum Annelida

Phylum Annelida includes segmented worms. These animals are found in marine, terrestrial, and freshwater habitats, but a presence of water or humidity is a critical factor for their survival, especially in terrestrial habitats. The name of the phylum is derived from the Latin word *annellus*, which means a small ring. Animals in this phylum show parasitic and commensal symbioses with other species in their habitat. Approximately 16,500 species have been described in phylum Annelida. The phylum includes earthworms, polychaete worms, and leeches. Annelids show protostomic development in embryonic stages and are often called “segmented worms” due to their key characteristic of metamerism, or true segmentation.

**Morphology**

Annelids display bilateral symmetry and are worm-like in overall morphology. Annelids have a segmented body plan wherein the internal and external morphological features are repeated in each body segment. Metamerism allows animals to become bigger by adding “compartments” while making their movement more efficient. This metamerism is thought to arise from identical teloblast cells in the embryonic stage, which give rise to identical mesodermal structures. The overall body can be divided into head, body, and pygidium (or tail). The *clitellum* is a reproductive structure that generates mucus that aids in sperm transfer and gives rise to a cocoon within which fertilization occurs; it appears as a fused band in the anterior third of the animal (Figure 28.28).

**Anatomy**

The epidermis is protected by an acellular, external cuticle, but this is much thinner than the cuticle found in the ecdysozoans and does not require periodic shedding for growth. Circular as well as longitudinal muscles are located interior to the epidermis. Chitinous hairlike extensions, anchored in the epidermis and projecting from the cuticle, called *setae/chaetae* are present in every segment. Annelids show the presence of a true coelom, derived from embryonic mesoderm and protostomy.
Hence, they are the most advanced worms. A well-developed and complete digestive system is present in earthworms (oligochaetes) with a mouth, muscular pharynx, esophagus, crop, and gizzard being present. The gizzard leads to the intestine and ends in an anal opening. A cross-sectional view of a body segment of an earthworm (a terrestrial type of annelid) is shown in Figure 28.29; each segment is limited by a membranous septum that divides the coelomic cavity into a series of compartments.

Annelids possess a closed circulatory system of dorsal and ventral blood vessels that run parallel to the alimentary canal as well as capillaries that service individual tissues. In addition, these vessels are connected by transverse loops in every segment. These animals lack a well-developed respiratory system, and gas exchange occurs across the moist body surface. Excretion is facilitated by a pair of metanephridia (a type of primitive “kidney” that consists of a convoluted tubule and an open, ciliated funnel) that is present in every segment towards the ventral side. Annelids show well-developed nervous systems with a nerve ring of fused ganglia present around the pharynx. The nerve cord is ventral in position and bears enlarged nodes or ganglia in each segment.

Figure 28.29 This schematic drawing shows the basic anatomy of annelids in a cross-sectional view.

Annelids may be either monoecious with permanent gonads (as in earthworms and leeches) or dioecious with temporary or seasonal gonads that develop (as in polychaetes). However, cross-fertilization is preferred in hermaphroditic animals. These animals may also show simultaneous hermaphroditism and participate in simultaneous sperm exchange when they are aligned for copulation.

Classification of Phylum Annelida

Phylum Annelida contains the class Polychaeta (the polychaetes) and the class Oligochaeta (the earthworms, leeches and their relatives).

Earthworms are the most abundant members of the class Oligochaeta, distinguished by the presence of the clitellum as well as few, reduced chaetae (“oligo- = “few”; -chaetae = “hairs”). The number and size of chaetae are greatly diminished in Oligochaeta compared to the polychaetes (poly = many, chaetae = hairs). The many chaetae of polychaetes are also arranged within fleshy, flat, paired appendages that protrude from each segment called parapodia, which may be specialized for different functions in the polychaetes. The subclass Hirudinea includes leeches such as Hirudo medicinalis and Hemiclepsis marginata. The class Oligochaeta includes the subclass Hirudinia and the subclass Brachiobdella. A significant difference between leeches and other annelids is the development of suckers at the anterior and posterior ends and a lack of chaetae.
Additionally, the segmentation of the body wall may not correspond to the internal segmentation of the coelomic cavity. This adaptation possibly helps the leeches to elongate when they ingest copious quantities of blood from host vertebrates. The subclass Brachiobdella includes species like Branchiobdella balcanica sketi and Branchiobdella astaci, worms that show similarity with leeches as well as oligochaetes.

![Figure 28.30](credit a: modification of work by S. Shepherd; credit b: modification of work by “Sarah G…”/Flickr; credit c: modification of work by Chris Gotschalk, NOAA)

### 28.4 | Superphylum Ecdysozoa

By the end of this section, you will be able to:

- Describe the structural organization of nematodes
- Understand the importance of Caenorhabditis elegans in research
- Compare the internal systems and appendage specializations of phylum Arthropoda
- Discuss the environmental importance of arthropods
- Discuss the reasons for arthropod success and abundance

#### Superphylum Ecdysozoa

The superphylum Ecdysozoa contains an incredibly large number of species. This is because it contains two of the most diverse animal groups: phylum Nematoda (the roundworms) and Phylum Arthropoda (the arthropods). The most prominent distinguishing feature of Ecdysozoans is their tough external covering called the cuticle. The cuticle provides a tough, but flexible exoskeleton that protects these animals from water loss, predators and other aspects of the external environment. All members of this superphylum periodically molt, or shed their cuticle as they grow. After molting, they secrete a new cuticle that will last until their next growth phase. The process of molting and replacing the cuticle is called ecdysis, which is how the superphylum derived its name.

### Phylum Nematoda

The Nematoda, like most other animal phyla, are triploblastic and possess an embryonic mesoderm that is sandwiched between the ectoderm and endoderm. They are also bilaterally symmetrical, meaning that a longitudinal section will divide them into right and left sides that are symmetrical. Furthermore, the nematodes, or roundworms, possess a pseudocoelom and consist of both free-living and parasitic forms.

It has been said that were all the non-nematode matter of the biosphere removed, there would remain a shadow of the former world in the form of nematodes. The arthropods, one of the most successful taxonomic groups on the planet, are coelomate organisms characterized by a hard exoskeleton and jointed appendages. Both the nematodes and arthropods belong to the superphylum Ecdysozoa that is believed to be a clade consisting of all evolutionary descendants from one common ancestor. The name derives from the word ecdysis, which refers to the shedding, or molting, of the exoskeleton. The phyla in this group have a hard cuticle that covers their bodies, which must be periodically shed and replaced for them to increase in size.

Phylum **Nematoda** includes more than 28,000 species with an estimated 16,000 being parasitic in nature. The name Nematoda is derived from the Greek word “Nemos,” which means “thread” and includes roundworms. Nematodes are

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present in all habitats with a large number of individuals of each species present in each. The free-living nematode, *Caenorhabditis elegans* has been extensively used as a model system in laboratories all over the world.

**Morphology**

In contrast with cnidarians, nematodes show a tubular morphology and circular cross-section. These animals are pseudocoelomates and show the presence of a complete digestive system with a distinct mouth and anus. This is in contrast with the cnidarians, where only one opening is present (an incomplete digestive system).

The cuticle of Nematodes is rich in collagen and a carbohydrate-protein polymer called chitin, and forms an external “skeleton” outside the epidermis. The cuticle also lines many of the organs internally, including the pharynx and rectum. The epidermis can be either a single layer of cells or a syncytium, which is a multinucleated cell formed from the fusion of uninucleated cells.

The overall morphology of these worms is cylindrical, as seen in Figure 28.31. The head is radially symmetrical. A mouth opening is present at the anterior end with three or six lips as well as teeth in some species in the form of cuticle extensions. Some nematodes may present other external modifications like rings, head shields, or warts. Rings, however, do not reflect true internal body segmentation. The mouth leads to a muscular pharynx and intestine, which leads to a rectum and anal opening at the posterior end. The muscles of nematodes differ from those of most animals: They have a longitudinal layer only, which accounts for the whip-like motion of their movement.

![Figure 28.31](image)

**Figure 28.31** Scanning electron micrograph shows (a) the soybean cyst nematode (*Heterodera glycines*) and a nematode egg. (b) A schematic representation shows the anatomy of a typical nematode. (credit a: modification of work by USDA ARS; scale-bar data from Matt Russell)

**Excretory System**

In nematodes, specialized excretory systems are not well developed. Nitrogenous wastes may be lost by diffusion through the entire body or into the pseudocoelom (body cavity), where they are removed by specialized cells. Regulation of water and salt content of the body is achieved by renette glands, present under the pharynx in marine nematodes.
Nervous system

Most nematodes possess four longitudinal nerve cords that run along the length of the body in dorsal, ventral, and lateral positions. The ventral nerve cord is better developed than the dorsal or lateral cords. All nerve cords fuse at the anterior end, around the pharynx, to form head ganglia or the “brain” of the worm (which take the form of a ring around the pharynx) as well as at the posterior end to form the tail ganglia. In *C. elegans*, the nervous system accounts for nearly one-third of the total number of cells in the animal.

Reproduction

Nematodes employ a variety of reproductive strategies that range from monoecious to dioecious to parthenogenic, depending upon the species under consideration. *C. elegans* is a monoecious species and shows development of ova contained in a uterus as well as sperm contained in the spermatheca. The uterus has an external opening known as the vulva. The female genital pore is near the middle of the body, whereas the male’s is at the tip. Specialized structures at the tail of the male keep him in place while he deposits sperm with copulatory spicules. Fertilization is internal, and embryonic development starts very soon after fertilization. The embryo is released from the vulva during the gastrulation stage. The embryonic development stage lasts for 14 hours; development then continues through four successive larval stages with ecdysis between each stage—L1, L2, L3, and L4—ultimately leading to the development of a young male or female adult worm. Adverse environmental conditions like overcrowding and lack of food can result in the formation of an intermediate larval stage known as the dauer larva.
C. elegans: The Model System for Linking Developmental Studies with Genetics

If biologists wanted to research how nicotine dependence develops in the body, how lipids are regulated, or observe the attractant or repellant properties of certain odors, they would clearly need to design three very different experiments. However, they might only need one object of study: C. elegans. The nematode Caenorhabditis elegans was brought into the focus of mainstream biological research by Dr. Sydney Brenner. Since 1963, Dr. Brenner and scientists worldwide have used this animal as a model system to study various physiological and developmental mechanisms.

C. elegans is a free-living organism found in soil. It is easy to culture this organism on agar plates (10,000 worms/plate), it feeds on Escherichia coli (another long-term resident of biological laboratories worldwide), and therefore, it can be readily grown and maintained in a laboratory. The biggest asset of this nematode is its transparency, which helps researchers to observe and monitor changes within the animal with ease. It is also a simple organism with fewer than 1,000 cells and a genome of 20,000 genes. It shows chromosomal organization of DNA into five pairs of autosomes plus a pair of sex chromosomes, making it an ideal candidate to study genetics. Since every cell can be visualized and identified, this organism is useful for studying cellular phenomena like cell-cell interactions, cell-fate determinations, cell division, apoptosis, and intracellular transport.

Another tremendous asset is the short life cycle of this worm (Figure 28.32). It takes only 3 days to achieve the “egg to adult to daughter egg;” therefore, tracking genetic changes is easier in this animal. The total life span of C. elegans is 2 to 3 weeks; hence, age-related phenomena are easy to observe. Another feature that makes C. elegans an excellent experimental model system is that the position and number of the 959 cells present in adult hermaphrodites of this organism is constant. This feature is extremely significant when studying cell differentiation, cell-cell communication, and apoptosis. Lastly, C. elegans is also amenable to genetic manipulations using molecular methods, rounding off its usefulness as a model system.

Biologists worldwide have created information banks and groups dedicated to research using C. elegans. Their findings have led, for example, to better understandings of cell communication during development, neuronal signaling and insight into lipid regulation (which is important in addressing health issues like the development of obesity and diabetes). In recent years, studies have enlightened the medical community with a better understanding of polycystic kidney disease. This simple organism has led biologists to complex and significant findings, growing the field of science in ways that touch the everyday world.

Figure 28.32 (a) This light micrograph shows Caenorhabditis elegans. Its transparent adult stage consists of exactly 959 cells. (b) The life cycle of C. elegans has four juvenile stages (L1 through L4) and an adult stage. Under ideal conditions, the nematode spends a set amount of time at each juvenile stage, but under stressful conditions, it may enter a dauer state that does not age. The worm is hermaphroditic in the adult state, and mating of two worms produces a fertilized egg. (credit a: modification of work by “snickclunk”/Flickr; credit b: modification of work by NIDDK, NIH; scale-bar data from Matt Russell)

A number of common parasitic nematodes serve as prime examples of parasitism. These animals exhibit complex lifecycles that involve multiple hosts, and they can have significant medical and veterinary impacts. Humans may become infected by Dracunculus medinensis, known as guinea worms, when they drink unfiltered water containing copepods (Figure 28.33).
Hookworms, such as *Ancyclostoma* and *Necator*, infest the intestines and feed on the blood of mammals, especially in dogs, cats, and humans. Trichina worms (*Trichinella*) are the causal organism of trichinosis in humans, often resulting from the consumption of undercooked pork; *Trichinella* can infect other mammalian hosts as well. *Ascaris*, a large intestinal roundworm, steals nutrition from its human host and may create physical blockage of the intestines. The filarial worms, such as *Dirofilaria* and *Wuchereria*, are commonly vectored by mosquitoes, which pass the infective agents among mammals through their blood-sucking activity. *Dirofilaria immitis*, a blood-infective parasite, is the notorious dog heartworm species. *Wuchereria bancrofti* infects the lymph nodes of humans, resulting in the non-lethal but deforming condition called elephantiasis, in which parts of the body become swelled to gigantic proportions due to obstruction of lymphatic drainage and inflammation of lymphatic tissues.

![Image of guinea worm](image)

**Figure 28.33** The guinea worm *Dracunculus medinensis* infects about 3.5 million people annually, mostly in Africa. (a) Here, the worm is wrapped around a stick so it can be extracted. (b) Infection occurs when people consume water contaminated by infected copepods, but this can easily be prevented by simple filtration systems. (credit: modification of work by CDC)

**Phylum Arthropoda**

The name “arthropoda” means “jointed legs” (in the Greek, “arthros” means “joint” and “podos” means “leg”); it aptly describes the enormous number of invertebrates included in this phylum. *Arthropoda* dominate the animal kingdom
with an estimated 85 percent of known species included in this phylum and many arthropods yet undocumented. The principal characteristics of all the animals in this phylum are functional segmentation of the body and presence of jointed appendages. Arthropods also show the presence of an exoskeleton made principally of chitin, which is a waterproof, tough polysaccharide. Phylum Arthropoda is the largest phylum in the animal world, and insects form the single largest class within this phylum. Arthropods are eucelomate, protostomic organisms.

Phylum Arthropoda includes animals that have been successful in colonizing terrestrial, aquatic, and aerial habitats. This phylum is further classified into five subphyla: Trilobitomorpha (trilobites, all extinct), Hexapoda (insects and relatives), Myriapoda (millipedes, centipedes, and relatives), Crustaceans (crabs, lobsters, crayfish, isopods, barnacles, and some zooplankton), and Chelicerata (horseshoe crabs, arachnids, scorpions, and daddy longlegs). Trilobites are an extinct group of arthropods found chiefly in the pre-Cambrian Era that are probably most closely related to the Chelicerata. These are identified based on fossil records (Figure 28.34).

Figure 28.34 Trilobites, like the one in this fossil, are an extinct group of arthropods. (credit: Kevin Walsh)

**Morphology**

A unique feature of animals in the arthropod phylum is the presence of a segmented body and fusion of sets of segments that give rise to functional body regions called tagma. Tagma may be in the form of a head, thorax, and abdomen, or a cephalothorax and abdomen, or a head and trunk. A central cavity, called the **hemocoel** (or blood cavity), is present, and the open circulatory system is regulated by a tubular or single-chambered heart. Respiratory systems vary depending on the group of arthropod: insects and myriapods use a series of tubes (tracheae) that branch through the body, open to the outside through openings called spiracles, and perform gas exchange directly between the cells and air in the tracheae, whereas aquatic crustaceans utilize gills, terrestrial chelicerates employ book lungs, and aquatic chelicerates use book gills (Figure 28.35). The book lungs of arachnids (scorpions, spiders, ticks and mites) contain a vertical stack of hemocoel wall tissue that somewhat resembles the pages of a book. Between each of the "pages" of tissue is an air space. This allows both sides of the tissue to be in contact with the air at all times, greatly increasing the efficiency of gas exchange. The gills of crustaceans are filamentous structures that exchange gases with the surrounding water. Groups of arthropods also differ in the organs used for excretion, with crustaceans possessing green glands and insects using Malpighian tubules, which work in conjunction with the hindgut to reabsorb water while ridding the body of nitrogenous waste. The cuticle is the covering of an arthropod. It is made up of two layers: the epicuticle, which is a thin, waxy water-resistant outer layer containing no chitin, and the layer beneath it, the chitinous procuticle. Chitin is a tough, flexible polysaccharide. In order to grow, the arthropod must shed the exoskeleton during a process called ecdisis (“to strip off”); this is a cumbersome method of growth, and during this time, the animal is vulnerable to predation. The characteristic morphology of representative animals from each subphylum is described below.
The book lungs of (a) arachnids are made up of alternating air pockets and hemocoel tissue shaped like a stack of books. The book gills of (b) crustaceans are similar to book lungs but are external so that gas exchange can occur with the surrounding water. (credit a: modification of work by Ryan Wilson based on original work by John Henry Comstock; credit b: modification of work by Angel Schatz)

Subphylum Hexapoda

The name Hexapoda denotes the presence of six legs (three pairs) in these animals as differentiated from the number of pairs present in other arthropods. Hexapods are characterized by the presence of a head, thorax, and abdomen, constituting three tagma. The thorax bears the wings as well as six legs in three pairs. Many of the common insects we encounter on a daily basis—including ants, cockroaches, butterflies, and flies—are examples of Hexapoda.

Amongst the hexapods, the insects (Figure 28.36) are the largest class in terms of species diversity as well as biomass in terrestrial habitats. Typically, the head bears one pair of sensory antennae, mandibles as mouthparts, a pair of compound eyes, and some ocelli (simple eyes) along with numerous sensory hairs. The thorax bears three pairs of legs (one pair per segment) and two pairs of wings, with one pair each on the second and third thoracic segments. The abdomen usually has eleven segments and bears reproductive apertures. Hexapoda includes insects that are winged (like fruit flies) and wingless (like fleas).
In this basic anatomy of a hexapod insect, note that insects have a developed digestive system (yellow), a respiratory system (blue), a circulatory system (red), and a nervous system (red).

Which of the following statements about insects is false?

a. Insects have both dorsal and ventral blood vessels.
b. Insects have spiracles, openings that allow air to enter.
c. The trachea is part of the digestive system.
d. Insects have a developed digestive system with a mouth, crop, and intestine.

Subphylum Myriapoda

Subphylum Myriapoda includes arthropods with numerous legs. Although the name is hyperbolic in suggesting that myriad legs are present in these invertebrates, the number of legs may vary from 10 to 750. This subphylum includes 13,000 species; the most commonly found examples are millipedes and centipedes. All myriapods are terrestrial animals and prefer a humid environment.

Myriapods are typically found in moist soils, decaying biological material, and leaf litter. Subphylum Myriapoda is divided into four classes: Chilopoda, Symphyla, Diplopoda, and Pauropoda. Centipedes like *Scutigera coleoptrata* (Figure 28.37) are classified as chilopods. These animals bear one pair of legs per segment, mandibles as mouthparts, and are somewhat dorsoventrally flattened. The legs in the first segment are modified to form forcipules (poison claws) that deliver poison to prey like spiders and cockroaches, as these animals are all predatory. Millipedes bear two pairs of legs per diplosegment, a feature that results from embryonic fusion of adjacent pairs of body segments, are usually rounder in cross-section, and are herbivores or detritivores. Millipedes have visibly more numbers of legs as compared to centipedes, although they do not bear a thousand legs (Figure 28.38).
Figure 28.37 (a) The *Scutigera coleoptrata* centipede has up to 15 pairs of legs. (b) This North American millipede (*Narceus americanus*) bears many legs, although not a thousand, as its name might suggest. (credit a: modification of work by Bruce Marlin; credit b: modification of work by Cory Zanker)

**Subphylum Crustacea**

Crustaceans are the most dominant aquatic arthropods, since the total number of marine crustacean species stands at 67,000, but there are also freshwater and terrestrial crustacean species. Krill, shrimp, lobsters, crabs, and crayfish are examples of crustaceans (Figure 28.38). Terrestrial species like the wood lice (*Armadillidium* spp.) (also called pill bugs, roly pollies, potato bugs, or isopods) are also crustaceans, although the number of non-aquatic species in this subphylum is relatively low.

Figure 28.38 The (a) crab and (b) shrimp krill are both crustaceans. (credit a: modification of work by William Warby; credit b: modification of work by Jon Sullivan)

Crustaceans possess two pairs of antennae, mandibles as mouthparts, and **biramous** (“two branched”) appendages, which means that their legs are formed in two parts, as distinct from the **uniramous** (“one branched”) myriapods and hexapods (Figure 28.39).
Arthropods may have (a) biramous (two-branched) appendages or (b) uniramous (one-branched) appendages. (credit b: modification of work by Nicholas W. Beeson)

Unlike that of the Hexapoda, the head and thorax of most crustaceans is fused to form a cephalothorax (Figure 28.40), which is covered by a plate called the carapace, thus producing a body structure of two tagma. Crustaceans have a chitinous exoskeleton that is shed by molting whenever the animal increases in size. The exoskeletons of many species are also infused with calcium carbonate, which makes them even stronger than in other arthropods. Crustaceans have an open circulatory system where blood is pumped into the hemocoel by the dorsally located heart. Hemocyanin and hemoglobin are the respiratory pigments present in these animals.

The crayfish is an example of a crustacean. It has a carapace around the cephalothorax and the heart in the dorsal thorax area. (credit: Jane Whitney)

Most crustaceans are dioecious, which means that the sexes are separate. Some species like barnacles may be hermaphrodites. Serial hermaphroditism, where the gonad can switch from producing sperm to ova, may also be seen in some species. Fertilized eggs may be held within the female of the species or may be released in the water. Terrestrial crustaceans seek out damp spaces in their habitats to lay eggs.

Larval stages—nauplius and zoea—are seen in the early development of crustaceans. A cypris larva is also seen in the early development of barnacles (Figure 28.41).
Crustaceans go through different larval stages. Shown are (a) the nauplius larval stage of a tadpole shrimp, (b) the cypris larval stage of a barnacle, and (c) the zoea larval stage of a green crab. (credit a: modification of work by USGS; credit b: modification of work by Mª. C. Mingorance Rodríguez; credit c: modification of work by B. Kimmel based on original work by Ernst Haeckel)

Crustaceans possess a tripartite brain and two compound eyes. Most crustaceans are carnivorous, but herbivorous and detritivorous species are also known. Crustaceans may also be cannibalistic when extremely high populations of these organisms are present.

**Subphylum Chelicerata**

This subphylum includes animals such as spiders, scorpions, horseshoe crabs, and sea spiders. This subphylum is predominantly terrestrial, although some marine species also exist. An estimated 77,000 species are included in subphylum Chelicerata. Chelicerates are found in almost all habitats.

The body of chelicerates may be divided into two parts: prosoma and opisthosoma, which are basically the equivalents of cephalothorax (usually smaller) and abdomen (usually larger). A “head” tagmum is not usually discernible. The phylum derives its name from the first pair of appendages: the chelicerae (Figure 28.42), which are specialized, claw-like or fang-like mouthparts. These animals do not possess antennae. The second pair of appendages is known as pedipalps. In some species, like sea spiders, an additional pair of appendages, called ovigers, is present between the chelicerae and pedipalps.

Chelicerae are mostly used for feeding, but in spiders, these are often modified into fangs that inject venom into their prey before feeding (Figure 28.43). Members of this subphylum have an open circulatory system with a heart that pumps blood into the hemocoel. Aquatic species have gills, whereas terrestrial species have either trachea or book lungs for gaseous exchange.
Most chelicerates ingest food using a preoral cavity formed by the chelicerae and pedipalps. Some chelicerates may secrete digestive enzymes to pre-digest food before ingesting it. Parasitic chelicerates like ticks and mites have evolved blood-sucking apparatuses.

The nervous system in chelicerates consists of a brain and two ventral nerve cords. These animals use external fertilization as well as internal fertilization strategies for reproduction, depending upon the species and its habitat. Parental care for the young ranges from absolutely none to relatively prolonged care.

Visit this [site](http://openstaxcollege.org/l/arthropodstory) to click through a lesson on arthropods, including interactive habitat maps, and more.

### 28.5 | Superphylum Deuterostomia

By the end of this section, you will be able to:

- Describe the distinguishing characteristics of echinoderms
- Describe the distinguishing characteristics of chordates

The phyla Echinodermata and Chordata (the phylum in which humans are placed) both belong to the superphylum Deuterostomia. Recall that protostome and deuterostomes differ in certain aspects of their embryonic development, and they are named based on which opening of the digestive cavity develops first. The word deuterostome comes from the Greek word meaning “mouth second,” indicating that the anus is the first to develop. There are a series of other developmental characteristics that differ between protostomes and deuterostomes, including the mode of formation of the coelom and the early cell division of the embryo. In deuterostomes, internal pockets of the endodermal lining called the archenteron fuse to form the coelom. The endodermal lining of the archenteron (or the primitive gut) forms membrane protrusions that bud off and become the mesodermal layer. These buds, known as coelomic pouches, fuse to form the coelomic cavity, as they eventually separate from the endodermal layer. The resultant coelom is termed an enterocoelom. The archenteron develops into the alimentary canal, and a mouth opening is formed by invagination of ectoderm at the pole opposite the blastopore of the gastrula. The blastopore forms the anus of the alimentary system in the juvenile and adult forms. The fates of embryonic cells in deuterostomes can be altered if they are experimentally moved to a different location in the embryo due to indeterminant cleavage in early embryogenesis.
Phylum Echinodermata

Echinodermata are so named owing to their spiny skin (from the Greek “echinos” meaning “spiny” and “dermos” meaning “skin”), and this phylum is a collection of about 7,000 described living species. Echinodermata are exclusively marine organisms. Sea stars (Figure 28.44), sea cucumbers, sea urchins, sand dollars, and brittle stars are all examples of echinoderms. To date, no freshwater or terrestrial echinoderms are known.

Morphology and Anatomy

Adult echinoderms exhibit pentaradial symmetry and have a calcareous endoskeleton made of ossicles, although the early larval stages of all echinoderms have bilateral symmetry. The endoskeleton is developed by epidermal cells and may possess pigment cells, giving vivid colors to these animals, as well as cells laden with toxins. Gonads are present in each arm. In echinoderms like sea stars, every arm bears two rows of tube feet on the oral side. These tube feet help in attachment to the substratum. These animals possess a true coelom that is modified into a unique circulatory system called a water vascular system. An interesting feature of these animals is their power to regenerate, even when over 75 percent of their body mass is lost.

Figure 28.44 This diagram shows the anatomy of a sea star.

Water Vascular System

Echinoderms possess a unique ambulacral or water vascular system, consisting of a central ring canal and radial canals that extend along each arm. Water circulates through these structures and facilitates gaseous exchange as well as nutrition, predation, and locomotion. The water vascular system also projects from holes in the skeleton in the form of tube feet. These tube feet can expand or contract based on the volume of water present in the system of that arm. By using hydrostatic pressure, the animal can either protrude or retract the tube feet. Water enters the madreporite on the aboral side of the echinoderm. From there, it passes into the stone canal, which moves water into the ring canal. The ring canal connects the radial canals (there are five in a pentaradial animal), and the radial canals move water into the ampullae, which have tube feet through which the water moves. By moving water through the unique water vascular system, the echinoderm can move and force open mollusk shells during feeding.

Nervous System

The nervous system in these animals is a relatively simple structure with a nerve ring at the center and five radial nerves extending outward along the arms. Structures analogous to a brain or derived from fusion of ganglia are not present in these animals.

Excretory System

Podocytes, cells specialized for ultrafiltration of bodily fluids, are present near the center of echinoderms. These podocytes are connected by an internal system of canals to an opening called the madreporite.
Reproduction

Echinoderms are sexually dimorphic and release their eggs and sperm cells into water; fertilization is external. In some species, the larvae divide asexually and multiply before they reach sexual maturity. Echinoderms may also reproduce asexually, as well as regenerate body parts lost in trauma.

Classes of Echinoderms

This phylum is divided into five extant classes: Asteroidea (sea stars), Ophiuroidea (brittle stars), Echinoidea (sea urchins and sand dollars), Crinoidea (sea lilies or feather stars), and Holothuroidea (sea cucumbers) (Figure 28.45).

The most well-known echinoderms are members of class Asteroidea, or sea stars. They come in a large variety of shapes, colors, and sizes, with more than 1,800 species known so far. The key characteristic of sea stars that distinguishes them from other echinoderm classes includes thick arms (ambulacra) that extend from a central disk where organs penetrate into the arms. Sea stars use their tube feet not only for gripping surfaces but also for grasping prey. Sea stars have two stomachs, one of which can protrude through their mouths and secrete digestive juices into or onto prey, even before ingestion. This process can essentially liquefy the prey and make digestion easier.

Explore the sea star’s body plan (http://openstaxcollege.org/l/sea_star) up close, watch one move across the sea floor, and see it devour a mussel.

Brittle stars belong to the class Ophiuroidea. Unlike sea stars, which have plump arms, brittle stars have long, thin arms that are sharply demarcated from the central disk. Brittle stars move by lashing out their arms or wrapping them around objects and pulling themselves forward. Sea urchins and sand dollars are examples of Echinoidea. These echinoderms do not have arms, but are hemispherical or flattened with five rows of tube feet that help them in slow movement; tube feet are extruded through pores of a continuous internal shell called a test. Sea lilies and feather stars are examples of Crinoidea. Both of these species are suspension feeders. Sea cucumbers of class Holothuroidea are extended in the oral-aboral axis and have five rows of tube feet. These are the only echinoderms that demonstrate “functional” bilateral symmetry as adults, because the uniquely extended oral-aboral axis compels the animal to lie horizontally rather than stand vertically.
Different members of Echinodermata include the (a) sea star of class Asteroidea, (b) the brittle star of class Ophiuroidea, (c) the sea urchins of class Echinoidea, (d) the sea lilies belonging to class Crinoidea, and (e) sea cucumbers, representing class Holothuroidea. (credit a: modification of work by Adrian Pingstone; credit b: modification of work by Joshua Ganderson; credit c: modification of work by Samuel Chow; credit d: modification of work by Sarah Depper; credit e: modification of work by Ed Bierman)

**Phylum Chordata**

Animals in the phylum **Chordata** share four key features that appear at some stage of their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. In some groups, some of these traits are present only during embryonic development. In addition to containing vertebrate classes, the phylum Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets). Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms.
KEY TERMS

amoebocyte  sponge cell with multiple functions, including nutrient delivery, egg formation, sperm delivery, and cell differentiation

Annelida  phylum of vermiform animals with metamerism

archenteron  primitive gut cavity within the gastrula that opens outwards via the blastopore

Arthropoda  phylum of animals with jointed appendages

biramous  referring to two branches per appendage

captacula  tentacle-like projection that is present in tusks shells to catch prey

cephalothorax  fused head and thorax in some species

chelicera  modified first pair of appendages in subphylum Chelicerata

choanocyte  (also, collar cell) sponge cell that functions to generate a water current and to trap and ingest food particles via phagocytosis

Chordata  phylum of animals distinguished by their possession of a notochord, a dorsal, hollow nerve cord, pharyngeal slits, and a post-anal tail at some point in their development

clitellum  specialized band of fused segments, which aids in reproduction

Cnidaria  phylum of animals that are diploblastic and have radial symmetry

nidocyte  specialized stinging cell found in Cnidaria

conispiral  shell shape coiled around a horizontal axis

corona  wheel-like structure on the anterior portion of the rotifer that contains cilia and moves food and water toward the mouth

ctenidium  specialized gill structure in mollusks

cuticle (animal)  the tough, external layer possessed by members of the invertebrate class Ecdysozoa that is periodically molted and replaced

cypris  larval stage in the early development of crustaceans

Echinodermata  phylum of deuterostomes with spiny skin; exclusively marine organisms

enterocoelom  coelom formed by fusion of coelomic pouches budded from the endodermal lining of the archenteron

epidermis  outer layer (from ectoderm) that lines the outside of the animal

extracellular digestion  food is taken into the gastrovascular cavity, enzymes are secreted into the cavity, and the cells lining the cavity absorb nutrients

gastrodermis  inner layer (from endoderm) that lines the digestive cavity

gastrovascular cavity  opening that serves as both a mouth and an anus, which is termed an incomplete digestive system

gemmule  structure produced by asexual reproduction in freshwater sponges where the morphology is inverted

hemocoel  internal body cavity seen in arthropods

hermaphrodite  referring to an animal where both male and female gonads are present in the same individual

invertebrata  (also, invertebrates) category of animals that do not possess a cranium or vertebral column
madreporite pore for regulating entry and exit of water into the water vascular system

mantle (also, pallium) specialized epidermis that encloses all visceral organs and secretes shells

mastax jawed pharynx unique to the rotifers

medusa free-floating cnidarian body plan with mouth on underside and tentacles hanging down from a bell

mesoglea non-living, gel-like matrix present between ectoderm and endoderm in cnidarians

mesohyl collagen-like gel containing suspended cells that perform various functions in the sponge

metamerism series of body structures that are similar internally and externally, such as segments

Mollusca phylum of protostomes with soft bodies and no segmentation

nacre calcareous secretion produced by bivalves to line the inner side of shells as well as to coat intruding particulate matter

nauplius larval stage in the early development of crustaceans

nematocyst harpoon-like organelle within cnidocyte with pointed projectile and poison to stun and entangle prey

Nematoda phylum of worm-like animals that are triploblastic, pseudocoelomates that can be free-living or parasitic

Nemertea phylum of dorsoventrally flattened protostomes known as ribbon worms

osculum large opening in the sponge’s body through which water leaves

ostium pore present on the sponge’s body through which water enters

oviger additional pair of appendages present on some arthropods between the chelicerae and pedipalps

parapodium fleshy, flat, appendage that protrudes in pairs from each segment of polychaetes

pedipalp second pair of appendages in Chelicerata

pilidium larval form found in some nemertine species

pinacocyte epithelial-like cell that forms the outermost layer of sponges and encloses a jelly-like substance called mesohyl

planospiral shell shape coiled around a vertical axis

planuliform larval form found in phylum Nemertea

polymorphic possessing multiple body plans within the lifecycle of a group of organisms

polyp stalk-like sessile life form of a cnidarians with mouth and tentacles facing upward, usually sessile but may be able to glide along surface

Porifera phylum of animals with no true tissues, but a porous body with rudimentary endoskeleton

radula tongue-like organ with chitinous ornamentation

rhynchocoel cavity present above the mouth that houses the proboscis

schizocoelom coelom formed by groups of cells that split from the endodermal layer

sclerocyte cell that secretes silica spicules into the mesohyl

seta/chaeta chitinous projection from the cuticle

siphonophore tubular structure that serves as an inlet for water into the mantle cavity
spicule  structure made of silica or calcium carbonate that provides structural support for sponges
spongocoel  central cavity within the body of some sponges
trochophore  first of the two larval stages in mollusks
uniramous  referring to one branch per appendage
veliger  second of the two larval stages in mollusks
water vascular system  system in echinoderms where water is the circulatory fluid
zoea  larval stage in the early development of crustaceans

CHAPTER SUMMARY

28.1 Phylum Porifera

Animals included in phylum Porifera are Parazoans because they do not show the formation of true tissues (except in class Hexactinellida). These organisms show very simple organization, with a rudimentary endoskeleton. Sponges have multiple cell types that are geared toward executing various metabolic functions. Although these animals are very simple, they perform several complex physiological functions.

28.2 Phylum Cnidaria

Cnidarians represent a more complex level of organization than Porifera. They possess outer and inner tissue layers that sandwich a noncellular mesoglea. Cnidarians possess a well-formed digestive system and carry out extracellular digestion. The cnidocyte is a specialized cell for delivering toxins to prey as well as warning off predators. Cnidarians have separate sexes and have a lifecycle that involves morphologically distinct forms. These animals also show two distinct morphological forms—medusoid and polypoid—at various stages in their lifecycle.

28.3 Superphylum Lophotrochozoa

Phylum Annelida includes vermiform, segmented animals. Segmentation is seen in internal anatomy as well, which is called metamerism. Annelids are protostomes. These animals have well-developed neuronal and digestive systems. Some species bear a specialized band of segments known as a clitellum. Annelids show the presence numerous chitinous projections termed chaetae, and polychaetes possess parapodia. Suckers are seen in order Hirudinea. Reproductive strategies include sexual dimorphism, hermaphroditism, and serial hermaphroditism. Internal segmentation is absent in class Hirudinea.

Flatworms are acoelomate, triploblastic animals. They lack circulatory and respiratory systems, and have a rudimentary excretory system. This digestive system is incomplete in most species. There are four traditional classes of flatworms, the largely free-living turbellarians, the ectoparasitic monogeneans, and the endoparasitic trematodes and cestodes. Trematodes have complex lifecycles involving a molluscan secondary host and a primary host in which sexual reproduction takes place. Cestodes, or tapeworms, infect the digestive systems of primary vertebrate hosts.

The rotifers are microscopic, multicellular, mostly aquatic organisms that are currently under taxonomic revision. The group is characterized by the rotating, ciliated, wheel-like structure, the corona, on their head. The mastax or jawed pharynx is another structure unique to this group of organisms.

The nemertini are the simplest eucoelomates. These ribbon-shaped animals bear a specialized proboscis enclosed within a rynchocoel. The development of a closed circulatory system derived from the coelom is a significant difference seen in this species compared to other pseudocoelomate phyla. Alimentary, nervous, and excretory systems are more developed in the nemertini than in less advanced phyla. Embryonic development of nemertine worms proceeds via a planuliform larval stage.

Phylum Mollusca is a large, marine group of invertebrates. Mollusks show a variety of morphological variations within the phylum. This phylum is also distinct in that some members exhibit a calcareous shell as an external means of protection. Some mollusks have evolved a reduced shell. Mollusks are protostomes. The dorsal epidermis in mollusks is modified to form the mantle, which encloses the mantle cavity and visceral organs. This cavity is quite distinct from the coelomic cavity, which in the adult animal surrounds the heart. Respiration is facilitated by gills known as ctenidia. A chitinously-toothed tongue called the radula is present in most mollusks. Early development in some species occurs via two larval
stages: trochophore and veliger. Sexual dimorphism is the predominant sexual strategy in this phylum. Mollusks can be divided into seven classes, each with distinct morphological characteristics.

28.4 Superphylum Ecdysozoa

Nematodes are pseudocoelomate animals akin to flatworms, yet display more advanced neuronal development, a complete digestive system, and a body cavity. This phylum includes free-living as well as parasitic organisms like Caenorhabditis elegans and Ascaris spp., respectively. They include dioecious as well as hermaphroditic species. Nematodes also possess an excretory system that is not quite well developed. Embryonic development is external and proceeds via three larval stages. A peculiar feature of nematodes is the secretion of a collagenous/chitinous cuticle outside the body.

Arthropods represent the most successful phylum of animal on Earth, in terms of the number of species as well as the number of individuals. These animals are characterized by a segmented body as well as the presence of jointed appendages. In the basic body plan, a pair of appendages is present per body segment. Within the phylum, traditional classification is based on mouthparts, number of appendages, and modifications of appendages present. Arthropods bear a chitinous exoskeleton. Gills, trachea, and book lungs facilitate respiration. Sexual dimorphism is seen in this phylum, and embryonic development includes multiple larval stages.

28.5 Superphylum Deuterostomia

Echinoderms are deuterostomial marine organisms. This phylum of animals bears a calcareous endoskeleton composed of ossicles. These animals also have spiny skin. Echinoderms possess water-based circulatory systems. A pore termed the madreporite is the point of entry and exit for water into the water vascular system. Osmoregulation is carried out by specialized cells known as podocytes.

The characteristic features of Chordata are a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets), together with the vertebrates in Vertebrata. Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms.

ART CONNECTION QUESTIONS

1. Figure 28.3 Which of the following statements is false?
   a. Choanocytes have flagella that propel water through the body.
   b. Pinacocytes can transform into any cell type.
   c. Lophocytes secrete collagen.
   d. Porocytes control the flow of water through pores in the sponge body.

2. Figure 28.20 Which of the following statements about the anatomy of a mollusk is false?
   a. Mollusks have a radula for grinding food.
   b. A digestive gland is connected to the stomach.
   c. The tissue beneath the shell is called the mantle.
   d. The digestive system includes a gizzard, a stomach, a digestive gland, and the intestine.

3. Figure 28.36 Which of the following statements about insects is false?
   a. Insects have both dorsal and ventral blood vessels.
   b. Insects have spiracles, openings that allow air to enter.
   c. The trachea is part of the digestive system.
   d. Insects have a developed digestive system with a mouth, crop, and intestine.

REVIEW QUESTIONS

4. Mesohyl contains:
   a. a polysaccharide gel and dead cells
   b. a collagen-like gel and suspended cells for various functions
   c. spicules composed of silica or calcium carbonate
   d. multiple pores

5. The large central opening in the Parazoan body is called the:
   a. gemmule
   b. spicule
   c. ostia
   d. osculum

6. Cnidocytes are found in _____.
   a. phylum Porifera
   b. phylum Nemertea
   c. phylum Nematoda
   d. phylum Cnidaria

7. Cubozaans are _____.
   a. polyps
   b. medusoids
   c. polymorphs
   d. sponges

8. Annelids have a:
   a. pseudocoelom
b. a true coelom  
c. no coelom  
d. none of the above

9. Which group of flatworms are primarily ectoparasites of fish?  
a. monogeneans  
b. trematodes  
c. cestodes  
d. turbellarians

10. A mantle and mantle cavity are present in:  
a. phylum Echinodermata  
b. phylum Adversoidea  
c. phylum Mollusca  
d. phylum Nemertea

11. The rhynchocoel is a ________.  
a. circulatory system  
b. fluid-filled cavity  
c. primitive excretory system  
d. proboscis

12. The embryonic development in nematodes can have up to ________ larval stages.  
a. one  
b. two  
c. three  
d. five

13. The nematode cuticle contains ________.

CRITICAL THINKING QUESTIONS

18. Describe the different cell types and their functions in sponges.
19. Describe the feeding mechanism of sponges and identify how it is different from other animals.
20. Explain the function of nematocysts in cnidarians.
21. Compare the structural differences between Porifera and Cnidaria.
22. Describe the morphology and anatomy of mollusks.
23. What are the anatomical differences between nemertines and mollusks?
24. Enumerate features of Caenorhabditis elegans that make it a valuable model system for biologists.
25. What are the different ways in which nematodes can reproduce?
26. Describe the various superclasses that phylum Arthropoda can be divided into.
27. Compare and contrast the segmentation seen in phylum Annelida with that seen in phylum Arthropoda.
28. Describe the different classes of echinoderms using examples.