structures produced by adult sponges (e.g., in the freshwater sponge *Spongilla*). In gemmules, an inner layer of archeocytes (amoebocytes) is surrounded by a pneumatic cellular layer that may be reinforced with spicules. In freshwater sponges, gemmules may survive hostile environmental conditions like changes in temperature, and then serve to recolonize the habitat once environmental conditions improve and 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. 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. 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. This temporal separation of gametes produced by the same sponge helps to encourage cross-fertilization and genetic diversity. 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 (such as flagellated *parenchymula*) 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*, i.e., rearranging their cells. 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, 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 do the following:

- Compare structural and organization characteristics of Porifera and Cnidaria
- Describe the progressive development of tissues and their relevance to animal complexity
- Identify the two general body forms found in the Cnidaria
- Describe the identifying features of the major cnidarian classes

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

Whereas the defining cell type for the sponges is the choanocyte, the defining cell type for the cnidarians is the **cnidocyte**, or stinging cell. These cells are located around the mouth and on the tentacles, and serve to capture prey or repel predators. Cnidocytes have large stinging organelles called **nematocysts**, which usually contain barbs at the base of a long coiled thread. The outer wall of the cell has a hairlike projection called a *cnidocil*, which is sensitive to tactile stimulation. If the cnidocils are touched, the hollow threads evert with enormous acceleration, approaching 40,000 times that of gravity. The microscopic threads then either entangle the prey or instantly penetrate the flesh of the prey or predator, releasing toxins (including neurotoxins and pore-forming toxins that can lead to cell lysis) into the target, thereby immobilizing it or paralyzing it (see **Figure 28.5**).

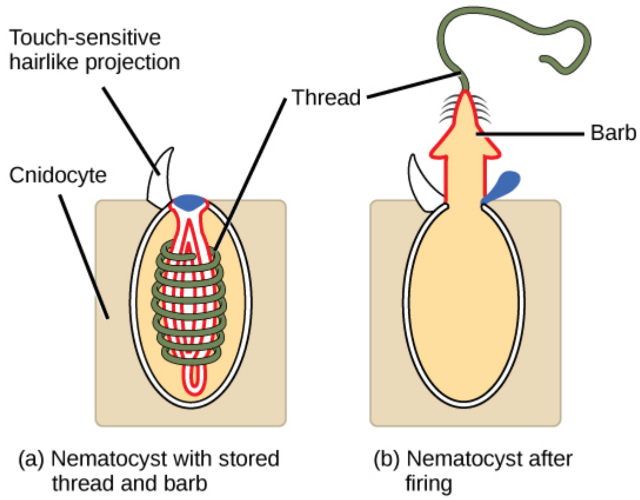


Figure 28.5 Cnidocytes. Animals from the phylum Cnidaria have stinging cells called cnidocytes. Cnidocytes contain large organelles called (a) nematocysts that store a coiled thread and barb, the nematocyst. When the hairlike cnidocil on the cell surface is touched, even lightly, (b) the thread, barb,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

LINK TO LEARNING

View this **video (https://www.openstaxcollege.org/l/nematocyst)** animation showing two anemones engaged in a battle.

Two distinct body plans are found in Cnidarians: the polyp or tuliplike "stalk" form and the medusa or "bell" form. (**Figure 28.6**). An example of the polyp form is found in the genus *Hydra*, whereas the most typical form of medusa is found in the group called the “sea jellies” (jellyfish). Polyp forms are sessile as adults, with a single opening (the mouth/anus) to the digestive cavity facing up with tentacles surrounding it. Medusa forms are motile, with the mouth and tentacles hanging down from an umbrella-shaped bell.

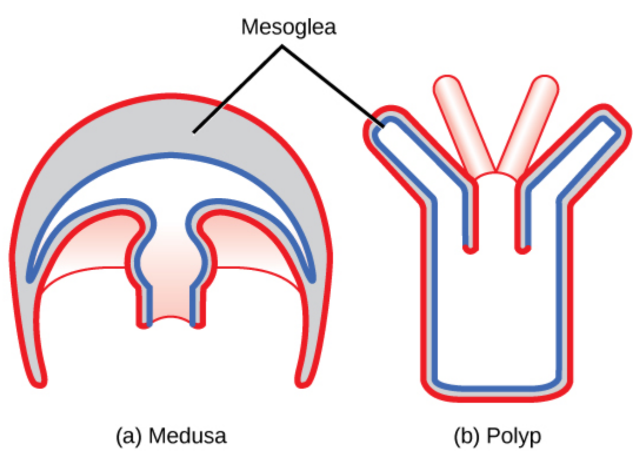


Figure 28.6 Cnidarian body forms. Cnidarians have two distinct body plans, the medusa (a) and the polyp (b). All cnidarians have two membrane layers, with a jelly-like mesoglea between them.

Some cnidarians are **dimorphic**, that is, they exhibit both body plans during their life cycle. In these species, the polyp serves as the asexual phase, while the medusa serves as the sexual stage and produces gametes. However, both body forms are diploid.

An example of cnidarian dimorphism can be seen in the colonial hydroid *Obelia*. The sessile asexual colony has two types of polyps, shown in **Figure 28.7**. The first is the *gastrozooid*, which is adapted for capturing prey and feeding. In *Obelia*, all polyps are connected through a common digestive cavity called a *coenosarc*. The other type of polyp is the *gonozooid*, adapted for the asexual budding and the production of sexual medusae. The reproductive buds from the gonozooid break off and mature into free-swimming medusae, which are either male or female (dioecious). Each medusa has either several testes or several ovaries in which meiosis occurs to produce sperm or egg cells. Interestingly, the gamete-producing cells do not arise within the gonad itself, but migrate into it from the tissues in the gonozooid. This separate origin of gonad and gametes is common throughout the eumetazoa. The gametes are released into the surrounding water, and after fertilization, the zygote develops into a blastula, which soon develops into a ciliated, bilaterally symmetrical planula larva. The planula swims freely for a while, but eventually attaches to a substrate and becomes a single polyp, from which a new colony of polyps is formed by budding.

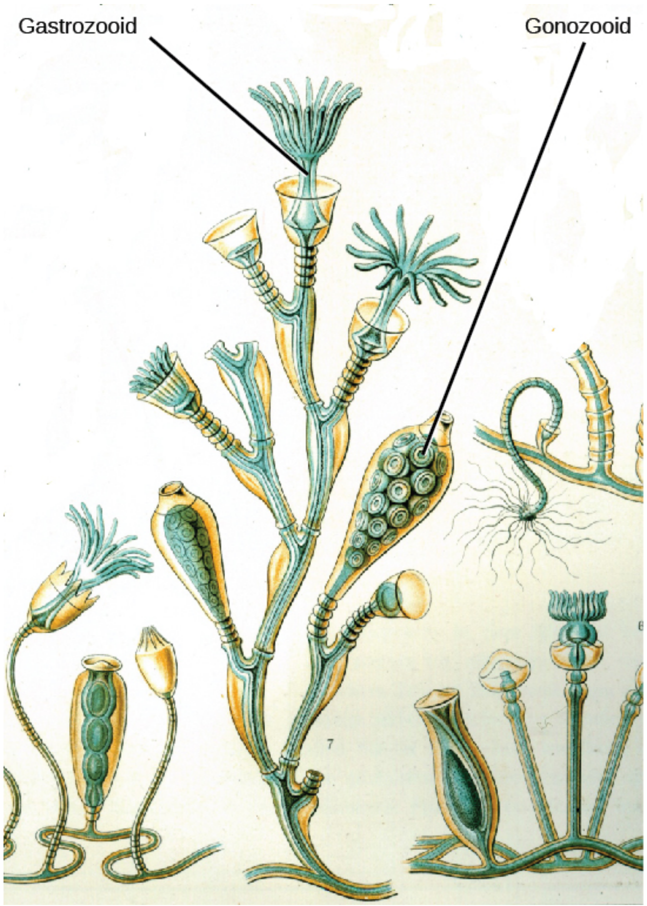


Figure 28.7 *Obelia*. The colonial sessile form of *Obelia geniculata* has two types of polyps: gastrozooids, which are adapted for capturing prey, and gonozooids, which asexually bud to produce medusae.

LINK TO LEARNING

Click here to follow an *Obelia* **life cycle (http://openstaxcollege.org/l/obelia)** animation and quiz.

All cnidarians are diploblastic and thus have two “epithelial” 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. In the planula larva, a layer of ectoderm surrounds a solid mass of endoderm, but as the polyp develops, the digestive or gastrovascular cavity opens within the endoderm. A non-living, jelly-like mesoglea lies between these two epithelial layers. 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, with a few notable exceptions such as *statocysts* and *rhopalia* (see below), the development of organs or organ systems is not advanced in this phylum.

The nervous system is rudimentary, with nerve cells organized in a network scattered across the body. This **nerve net** may show the presence of groups of cells that form nerve plexi (singular: plexus) or nerve cords. Organization of the nervous system in the motile medusa is more complex than that of the sessile polyp, with a nerve ring around the edge of the medusa bell that controls the action of the tentacles. Cnidarian nerve cells show mixed characteristics of motor and sensory neurons. The predominant signaling molecules in these primitive nervous systems are peptides, which perform both excitatory and inhibitory functions. Despite the simplicity of the nervous system, it is remarkable that it coordinates the complicated movement of the tentacles, the drawing of captured prey to the mouth, the digestion of food, and the expulsion of waste.

The gastrovascular cavity has only one opening that serves as both a mouth and an anus; this arrangement is called an incomplete digestive system. In the gastrovascular cavity, extracellular digestion occurs as food is taken into the gastrovascular cavity, enzymes are secreted into the cavity, and the cells lining the cavity absorb nutrients. However, some intracellular digestion also occurs. The gastrovascular cavity distributes nutrients throughout the body of the animal, with nutrients passing from the digestive cavity across the mesoglea to the epidermal cells. Thus, this cavity serves both digestive and circulatory functions.

Cnidarian cells exchange oxygen and carbon dioxide by diffusion between cells in the epidermis and water in the environment, and between cells in the gastrodermis and 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. In the cnidarians with a thicker mesoglea, a number of canals help to distribute both nutrients and gases. There is neither an excretory system nor organs, and nitrogenous wastes simply diffuse from the cells into the water outside the animal or into the gastrovascular cavity.

The phylum Cnidaria contains about 10,000 described species divided into two monophyletic clades: the Anthozoa and the Medusozoa. The Anthozoa include the corals, sea fans, sea whips, and the sea anemones. The Medusozoa include several classes of Cnidaria in two clades: The Hydrozoa include sessile forms, some medusoid forms, and swimming colonial forms like the Portuguese man-of-war. The other clade contains various types of jellies including both Scyphozoa and Cubozoa. The Anthozoa contain only sessile polyp forms, while the Medusozoa include species with both polyp and medusa forms in their life cycle.

Class Anthozoa

The class Anthozoa ("flower animals") includes 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. Individual animals are cylindrical in shape and are attached directly to a substrate.

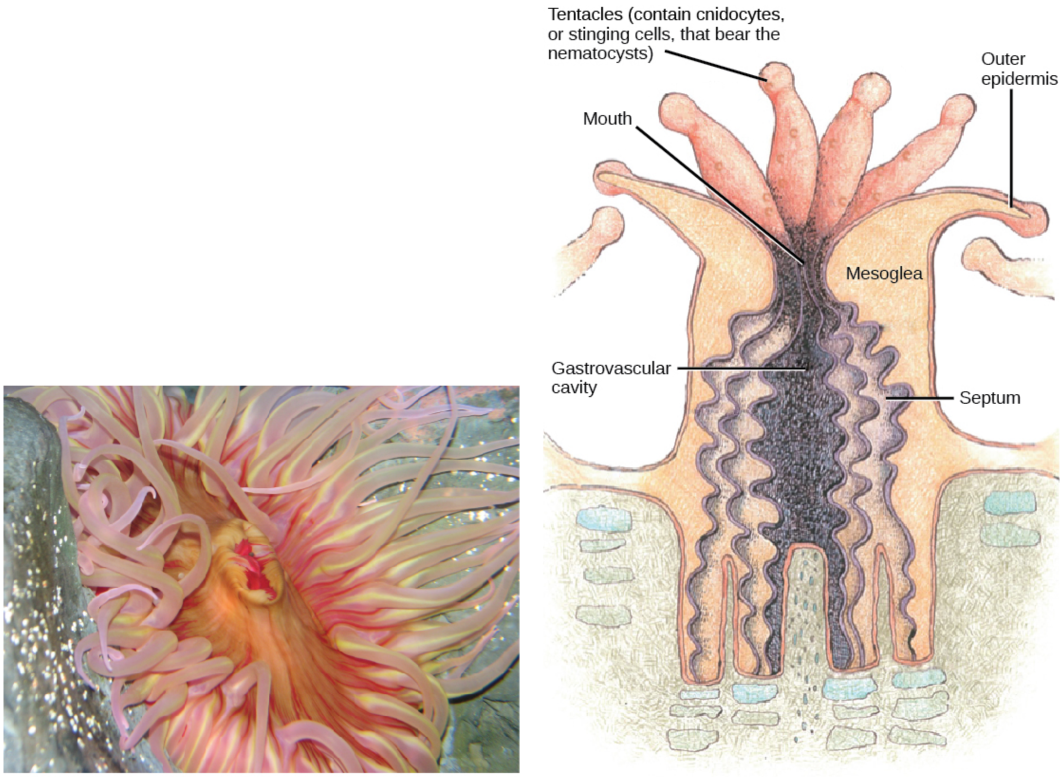


Figure 28.8 Sea anemone. The sea anemone is shown (a) photographed and (b) in a diagram illustrating its morphology. (credit a: modification of work by "Dancing With Ghosts"/Flickr; credit b: modification of work by NOAA)

The mouth of a sea anemone is surrounded by tentacles that bear cnidocytes. The slit-like mouth opening and flattened pharynx are lined with ectoderm. This structure of the pharynx makes anemones bilaterally symmetrical. A ciliated groove called a siphonoglyph is found on two opposite sides of the pharynx and directs water into it. 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 a fold of gastrodermal tissue with a layer of mesoglea between the sheets of gastrodermis. 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, as well as additional mechanical support for the body of the anemone.

Sea anemones feed on small fish and shrimp, usually by immobilizing their prey with nematocysts. Some sea anemones establish a mutualistic relationship with hermit crabs when the crab seizes and attaches them to their 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. Some species of anemone fish, or clownfish, are also able to live with sea anemones because they build up an acquired immunity to the toxins contained within the nematocysts and also secrete a protective mucus that prevents them from being stung.

The structure of coral polyps is similar to that of anemones, although the individual polyps are usually smaller and part of a colony, some of which are massive and the size of small buildings. Coral polyps feed on smaller planktonic organisms, including algae, bacteria, and invertebrate larvae. Some anthozoans have symbiotic associations with dinoflagellate algae called zooxanthellae. The mutually beneficial relationship between zooxanthellae and modern corals—which provides the algae with shelter—gives coral reefs their colors and supplies both organisms with nutrients. This complex mutualistic association began more than 210 million years ago, according to a new study by an international team of scientists. That this symbiotic relationship arose during a time of massive worldwide coral-reef expansion suggests that the interconnection of algae and coral is crucial for the health of coral reefs, which provide habitat for roughly one-fourth of all marine life. Reefs are threatened by a trend in ocean warming that has caused corals to expel their zooxanthellae algae and turn white, a process called coral bleaching.

Anthozoans remain *polypoid* (note that this term is easily confused with "polyploid") throughout their lives and can reproduce asexually by budding or fragmentation, or sexually by producing gametes. Male or female gametes produced by a polyp 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 ("cup animals") includes all (and only) the marine jellies, with about 200 known species. The medusa is the prominent stage in the life cycle, although there is a polyp stage in the life cycle of most species. Most jellies range from 2 to 40 cm in length but the largest scyphozoan species, *Cyanea capillata*, can reach a size of two meters in diameter. Scyphozoans display a characteristic bell-like morphology (**Figure 28.9**).

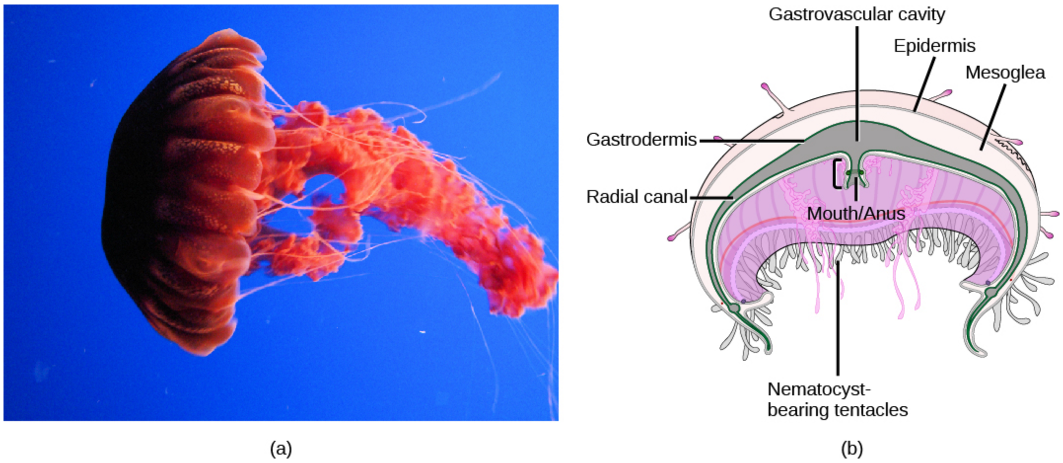


Figure 28.9 A sea jelly. A jelly is shown (a) photographed and (b) in a diagram illustrating its morphology. (credit a: modification of work by "Jimg944"/Flickr; credit b: modification of work by Mariana Ruiz Villareal)

In the sea jelly, a mouth opening is present on the underside of the animal, surrounded by hollow 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 branch further 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, and to support the body of the animal.

In scyphozoans, nerve cells are organized in a nerve net that extends over the entire body, with a nerve ring around the edge of the bell. Clusters of sensory organs called rhopalia may be present in pockets in the edge of the bell. Jellies have a ring of muscles lining the dome of the body, which provides the contractile force required to swim through water, as well as to draw in food from the water as they swim. Scyphozoans have separate sexes. 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. These polyps may bud to form additional polyps or begin immediately to produce medusa buds. In a few species, the planula larva may develop directly into the medusa. The life cycle (**Figure 28.10**) of most scyphozoans includes both sexual medusoid and asexual polypoid body forms.

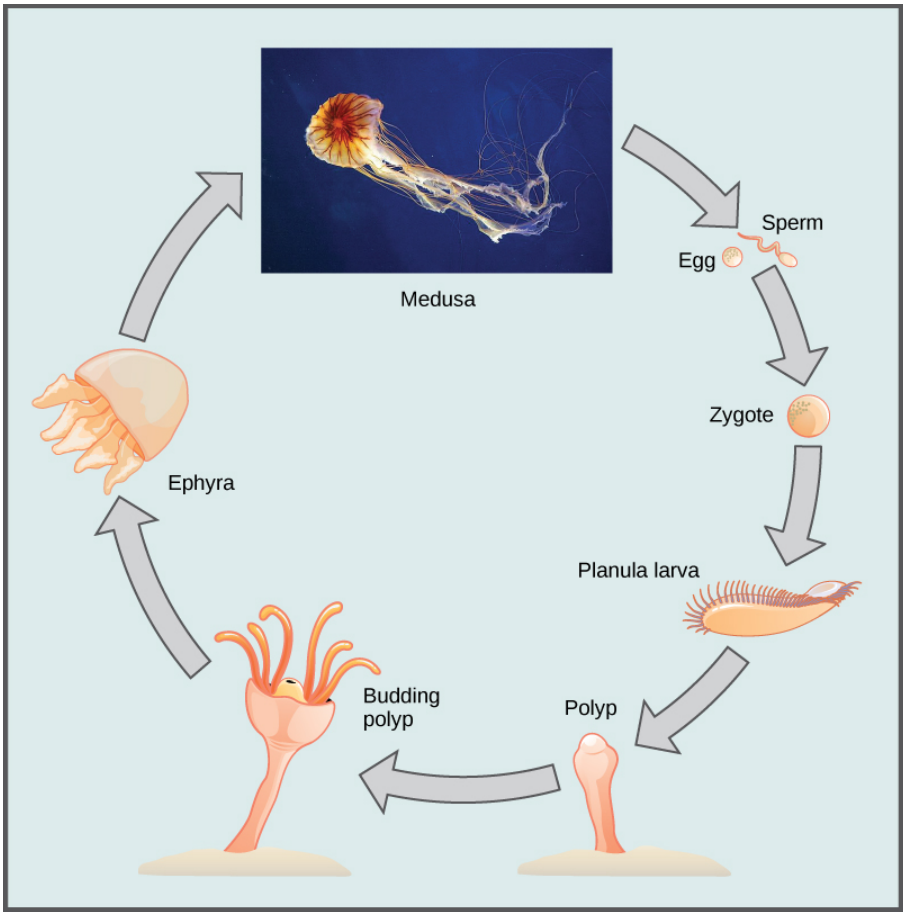


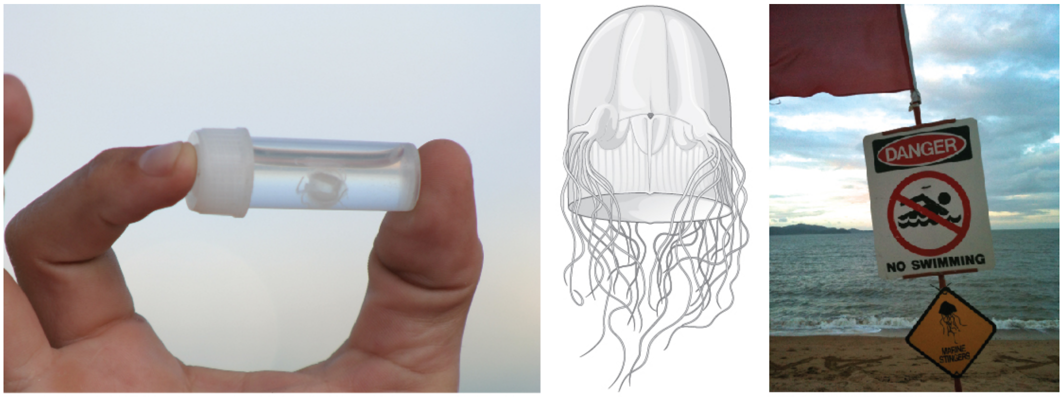
Figure 28.10 Scyphozoan life cycle. The lifecycle of most jellyfish includes two stages: the medusa stage and the polyp stage. The polyp reproduces asexually by budding, and the medusa reproduces sexually. (credit "medusa": modification of work by Francesco Crippa)

Class Cubozoa

This class includes jellies that have a box-shaped medusa, or a bell that is square in cross-section, and are colloquially known as “box jellyfish.” These species may achieve sizes of 15 to 25 cm, but typically members of the Cubozoa are not as large as those of the Scyphozoa. However, 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. The cubozoans contain muscular pads called **pedalia** at the corners of the square bell canopy, with one or more tentacles attached to each pedalium. 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 include the most venomous of all the cnidarians (**Figure 28.11**).

These animals are unusual in having image-forming eyes, including a cornea, lens, and retina. Because these structures are made from a number of interactive tissues, they can be called *true organs*. Eyes are located in four clusters between each pair of pedalia. Each cluster consists of four simple eye spots plus two image-forming eyes oriented in different directions. How images formed by these very complex eyes are processed remains a mystery, since cubozoans have extensive nerve nets but no distinct brain. Nontheless, the presence of eyes helps the cubozoans to be active and effective hunters of small marine animals like worms, arthropods, and fish.

Cubozoans have separate sexes and fertilization occurs inside the female. Planula larvae may develop inside the female or be released, depending on species. Each planula develops into a polyp. These polyps may bud to form more polyps to create a colony; each polyp then transforms into a single medusa.



(a) (b) (c)

Figure 28.11 A cubozoan. The (a) tiny cubozoan jelly *Malo kingi* is thimble-shaped and, like all cubozoan jellies, (b) 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. (c) A sign on a beach in northern Australia warns swimmers of the danger. (credit c: modification of work by Peter Shanks)

Class Hydrozoa

Hydrozoa is a diverse group that includes nearly 3,200 species; most are marine, although some freshwater species are known (**Figure 28.12**). Most species exhibit both polypoid and medusoid forms in their lifecycles, although the familiar *Hydra* has only the polyp form. The medusoid form has a muscular veil or **velum** below the margin of the bell and for this reason is called a *hydromedusa*. In contrast, the medusoid form of Scyphozoa lacks a velum and is termed a *scyphomedusa*.

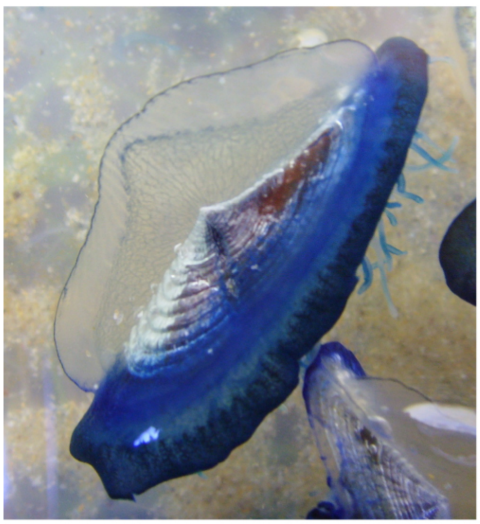
The polyp form in these animals often shows a cylindrical morphology with a central gastrovascular cavity lined by the gastrodermis. The gastrodermis and epidermis have a simple layer of mesoglea sandwiched between them. A mouth opening, surrounded by tentacles, is present at the oral end of the animal. Many hydrozoans form sessile, branched colonies of specialized polyps that share a common, branching gastrovascular cavity (coenosarc), such as is found in the colonial hydroid *Obelia*.

Free-floating colonial species called **siphonophores** contain both medusoid and polypoid individuals that are specialized for feeding, defense, or reproduction. The distinctive rainbow-hued float of the Portuguese man o' war (*Physalia physalis*) creates a pneumatophore with which it regulates buoyancy by filling and expelling carbon monoxide gas. At first glance, these complex superorganisms appear to be a single organism; but the reality is that even the tentacles are actually composed of zooids laden with nematocysts. Thus, although it superficially resembles a typical medusozoan jellyfish, *P. physalis* is a free-floating hydrozoan *colony*; each specimen is made up of many hundreds of organisms, each specialized for a certain function, including motility and buoyancy, feeding, reproduction and defense. Although they are carnivorous and feed on many soft bodied marine animals, *P. physalis* lack stomachs and instead have specialized polyps called gastrozooids that they use to digest their prey in the open water.

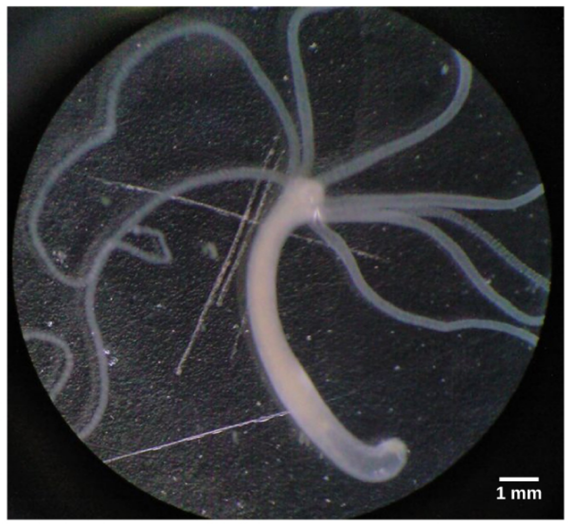
Physalia has male and female colonies, which release their gametes into the water. The zygote develops into a single individual, which then buds asexually to form a new colony. Siphonophores include the largest known floating cnidarian colonies such as *Praya dubia*, whose chain of zoids can get up to 50 meters (165 feet) long. Other hydrozoan species are solitary polyps (*Hydra*) or solitary hydromedusae (*Gonionemus*). One defining characteristic shared by the hydrozoans is that their gonads are derived from epidermal tissue, whereas in all other cnidarians they are derived from gastrodermal tissue.

(a) *Obelia*

(b) *Physalia physalis* (Portuguese Man O' War)



(c) *Velella bae*



(d) *Hydra*

Figure 28.12 Hydrozoans. The polyp colony *Obelia* (a), siphonophore colonies *Physalia* (b) *physalis*, known as the Portuguese man o' war and *Velella bae* (c), and the solitary polyp *Hydra* (d) 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: Flatworms, Rotifers, and Nemerteans

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

- Describe the unique anatomical and morphological features of flatworms, rotifers, and Nemertea
- Identify an important extracoelomic cavity found in Nemertea
- Explain the key features of Platyhelminthes and their importance as parasites

Animals belonging to superphylum Lophotrochozoa are triploblastic (have three germ layers) and unlike the cnidarians, they possess an embryonic mesoderm sandwiched between the ectoderm and endoderm. These phyla are also bilaterally symmetrical, meaning that a longitudinal section will divide them into right and left sides that are superficially symmetrical. In these phyla, we also see the beginning of cephalization, the evolution of a concentration of nervous tissues and sensory organs in the head of the organism—exactly where a mobile