

7



chapter
seven

Radiate Animals

Cnidarians and Ctenophores

A Fearsome Tiny Weapon

Although members of phylum Cnidaria are more highly organized than sponges, they are still relatively simple animals. Most are sessile; those that are unattached, such as jellyfish, can swim only feebly. None can chase their prey. Indeed, we might easily get the false impression the cnidarians were placed on earth to provide easy meals for other animals. The truth is, however, many cnidarians are very effective predators that are able to kill and eat prey that are much more highly organized, swift, and intelligent. They manage these feats because they possess tentacles that bristle with tiny, remarkably sophisticated weapons called nematocysts.

As it is secreted within the cell that contains it, a nematocyst is endowed with potential energy to power its discharge. It is as though a factory manufactured a gun, cocked and ready with a bullet in its chamber, as it rolls off the assembly line. Like the cocked gun, the completed nematocyst requires only a small stimulus to make it fire. Rather than a bullet, a tiny thread bursts from the nematocyst. Achieving a velocity of 2 m/sec and an acceleration of $40,000 \times$ gravity, it instantly penetrates its prey and injects a paralyzing toxin. A small animal unlucky enough to brush against one of the tentacles is suddenly speared with hundreds or even thousands of nematocysts and quickly immobilized. Some nematocyst threads can penetrate human skin, resulting in sensations ranging from minor irritation to great pain, even death, depending on the species. A fearsome, but wondrous, tiny weapon.



Tentacles of a Caribbean sea anemone, *Condylactis gigantea*.

Phylum Cnidaria

Phylum Cnidaria (ny-dar´e-a) (Gr. *knidē*, nettle, + L. *aria* [pl. suffix]; like or connected with) is an interesting group of more than 9000 species. It takes its name from cells called **cnidocytes**, which contain the stinging organelles (**nematocysts**) characteristic of the phylum. Nematocysts are *formed and used* only by cnidarians. Another name for the phylum, Coelenterata (se-len´te-ra´ta) (Gr. *koilos*, hollow, + *enteron*, gut, + L. *ata* [pl. suffix], characterized by), is used less commonly than formerly, and it sometimes now refers to both radiate phyla, since its meaning is equally applicable to both.

Cnidarians are generally regarded as originating close to the basal stock of the metazoan line. They are an ancient group with the longest fossil history of any metazoan, reaching back

more than 700 million years. Although their organization has a structural and functional simplicity not found in other metazoans, they form a significant proportion of the biomass in some locations. They are widespread in marine habitats, and there are a few in fresh water. Although they are mostly sessile or, at best, fairly slow moving or slow swimming, they are quite efficient predators of organisms that are much swifter and more complex. The phylum includes some of nature's strangest and loveliest creatures: branching, plantlike hydroids; flowerlike sea anemones; jellyfishes; and those architects of the ocean floor, horny corals (sea whips, sea fans, and others), and stony corals whose thousands of years of calcareous house-building have produced great reefs and coral islands (p. 131).

We recognize four classes of Cnidaria: Hydrozoa (the most variable class, including hydroids, fire corals, Portuguese

position of radiates in animal kingdom

The two phyla Cnidaria and Ctenophora make up the radiate animals, which are characterized by **primary radial** or **biradial symmetry**, which we believe is ancestral for eumetazoans. Radial symmetry, in which body parts are arranged concentrically around an oral-aboral axis, is particularly suitable for sessile or sedentary animals and for free-floating animals because they approach their environment (or it approaches them) from all sides equally. Biradial symmetry is basically a type of radial symmetry in which only

two planes through the oral-aboral axis divide the animal into mirror images because of the presence of some part that is paired. All other eumetazoans have a primary bilateral symmetry; that is, they are bilateral or were derived from an ancestor that was bilateral.

Neither phylum has advanced generally beyond the **tissue level of organization**, although a few organs occur. In general, ctenophores are structurally more complex than cnidarians.

biological contributions

- Both phyla have developed two well-defined **germ layers**, ectoderm and endoderm; a third, or mesodermal, layer, which is derived embryologically from ectoderm, is present in some. The body plan is saclike, and the body wall is composed of two distinct layers, epidermis and gastrodermis, derived from ectoderm and endoderm, respectively. The gelatinous matrix, mesoglea, between these layers may be structureless, may contain a few cells and fibers, or may be composed largely of mesodermal connective tissue and muscle fibers.
- An internal body cavity, the **gastrovascular cavity**, is lined by gastrodermis and has a single opening, the mouth, which also serves as the anus.
- Extracellular digestion** occurs in the gastrovascular cavity, and intracellular digestion takes place in gastrodermal cells. Extracellular digestion allows ingestion of larger food particles.
- Most radiates have **tentacles**, or extensible projections around the oral end, that aid in capturing food.
- Radiates are the simplest animals to possess true **nerve cells** (protoneurons), but nerves are arranged as a nerve net, with no central nervous system.
- Radiates are the simplest animals to possess sense organs, which include well-developed statocysts (organs of equilibrium) and ocelli (photosensitive organs).
- Locomotion in free-moving forms is achieved by either **muscular contractions** (cnidarians) or **ciliary comb plates** (ctenophores). However, both groups are still better adapted to floating or being carried by currents than to strong swimming.
- Polymorphism**¹ in cnidarians has widened their ecological possibilities. In many species the presence of both a polyp (sessile and attached) stage and a medusa (free-swimming) stage permits occupation of a benthic (bottom) and a pelagic (open-water) habitat by the same species. Polymorphism also widens the possibilities of structural complexity.
- Some unique features are found in these phyla, such as **nematocysts** (stinging organelles) in cnidarians and **colloblasts** (adhesive organelles) and **ciliary comb plates** in ctenophores.

¹Note that polymorphism here refers to more than one structural form of individual within a species, as contrasted with the use of the word in genetics, in which it refers to different allelic forms of a gene in a population.

characteristics of phylum cnidaria

1. Entirely aquatic, some in fresh water but mostly marine
2. **Radial symmetry** or biradial symmetry around a longitudinal axis with **oral** and **aboral** ends; no definite head
3. Two basic types of individuals: **polyps** and **medusae**
4. Exoskeleton or endoskeleton of chitinous, calcareous, or protein components in some
5. Body with two layers, epidermis and gastrodermis, with mesoglea (**diploblastic**); mesoglea with cells and connective tissue (ectomesoderm) in some
6. **Gastrovascular cavity** (often branched or divided with septa) with a single opening that serves as both mouth and anus; extensible tentacles usually encircling the mouth or oral region
7. Special stinging-cell organelles called **nematocysts** in either epidermis or gastrodermis or in both; nematocysts abundant on tentacles, where they may form batteries or rings
8. **Nerve net** with symmetrical and asymmetrical synapses; with some sensory organs; diffuse conduction
9. Muscular system (epitheliomuscular type) of an outer layer of longitudinal fibers at base of epidermis and an inner one of circular fibers at base of gastrodermis; modifications of this plan in some cnidarians, such as separate bundles of independent fibers in mesoglea
10. Asexual reproduction by budding (in polyps) or sexual reproduction by gametes (in all medusae and some polyps); sexual forms monoecious or dioecious; **planula larva**; holoblastic indeterminate cleavage
11. No excretory or respiratory system
12. No coelomic cavity

man-of-war, and others), Scyphozoa (“true” jellyfishes), Cubozoa (cube jellyfishes), and Anthozoa (the largest class, including sea anemones, stony corals, soft corals, and others).

Ecological Relationships

Cnidarians are found most abundantly in shallow marine habitats, especially in warm temperatures and tropical regions. There are no terrestrial species. Colonial hydroids are usually found attached to mollusc shells, rocks, wharves, and other animals in shallow coastal water, but some species are found at great depths. Floating and free-swimming medusae are found in open seas and lakes, often far from shore. Floating colonies such as the Portuguese man-of-war and *Velella* (*L. velum*, veil, + *ellus*, dim. suffix) have floats or sails by which the wind carries them.

Some ctenophores, molluscs, and flatworms eat hydroids bearing nematocysts and use these stinging structures for their own defense. Some other animals, such as some molluscs and fishes, feed on cnidarians, but cnidarians rarely serve as food for humans.

Cnidarians sometimes live symbiotically with other animals, often as commensals on the shell or other surface of their host. Certain hydroids (figure 7.1) and sea anemones commonly live on snail shells inhabited by hermit crabs, providing the crabs some protection from predators. Algae frequently live as mutuals in tissues of cnidarians, notably in some freshwater hydras and in reef-building corals. The presence of algae in reef-building corals limits the occurrence of coral reefs to relatively shallow, clear water where sunlight is sufficient for photosynthetic requirements of the algae. These corals are an essential component of coral reefs, and reefs are extremely important habitats in tropical waters. Coral reefs are discussed further later in the chapter.

Although many cnidarians have little economic importance, reef-building corals are an important exception. Fish and other animals associated with reefs provide substantial amounts of food for humans, and reefs are of economic value as tourist attractions. Precious coral is used for jewelry and ornaments, and coral rock serves for building purposes.

Planktonic medusae may be of some importance as food for fish that are of commercial value; the reverse is also true— young fish fall prey to cnidarians.

Form and Function

Dimorphism and Polymorphism in Cnidarians

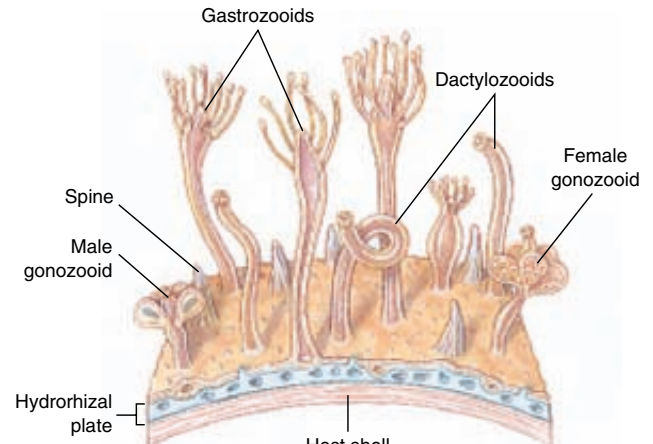
One of the most interesting—and sometimes puzzling— aspects of this phylum is the dimorphism and often polymorphism displayed by many of its members. All cnidarian forms fit into one of two morphological types (dimorphism): a **polyp**, or hydroid form, which is adapted to a sedentary or sessile life, and a **medusa**, or jellyfish form, which is adapted for a floating or free-swimming existence (figure 7.2).

Most polyps have tubular bodies with a mouth at one end surrounded by tentacles. The aboral end is usually attached to a substratum by a pedal disc or other device. Polyps may live singly or in colonies. Colonies of some species include morphologically differing individuals (polymorphism), each specialized for a certain function, such as feeding, reproduction, or defense (see figure 7.1).

The name “medusa” was suggested by a fancied resemblance to the Gorgon Medusa, a mythological lass with snake tresses that turned to stone any who gazed upon her.



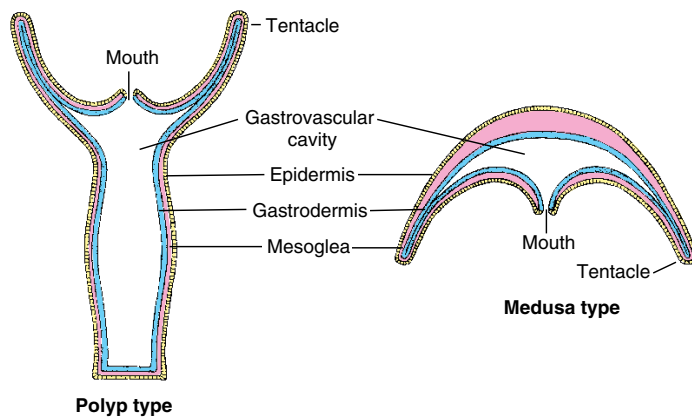
A



B

figure 7.1

A, A hermit crab with its cnidarian mutuals. The shell is blanketed with polyps of the hydrozoan *Hydractinia milleri*. The crab gets some protection from predation by the cnidarians, and the cnidarians get a free ride and bits of food from their host's meals. **B**, Portion of a colony of *Hydractinia*, showing the types of zooids and the stolon (hydrorhiza) from which they grow.



Polyp type

Medusa type

figure 7.2

Comparison between the polyp and medusa types of individuals.

Medusae are usually free swimming and have bell-shaped or umbrella-shaped bodies and tetramerous symmetry (body parts arranged in fours). The mouth is usually centered on the concave side, and tentacles extend from the rim of the umbrella.

Sea anemones and corals (class Anthozoa) are all polyps; hence, they are not dimorphic. The true jellyfishes (class Scyphozoa) have a conspicuous medusoid form, but many have a polypoid larval stage. Colonial hydroids of class Hydrozoa, however, sometimes have life histories that feature both a polyp stage and a free-swimming medusa stage—rather like a Jekyll-and-Hyde existence. A species that has both an attached polyp and a floating medusa within its life history can take advantage of the feeding and distribution possibilities of both pelagic (open-water) and benthic (bottom) environments.

Many hydrozoans are also polymorphic, with several distinct types of polyps in a colony.

Superficially polyps and medusae seem very different. But actually each has retained the saclike body plan that is basic to the phylum (figure 7.2). A medusa is essentially an unattached polyp with the tubular portion widened and flattened into the bell shape.

Both polyp and medusa possess the three body wall layers typical of cnidarians, but the jellylike layer of mesoglea is much thicker in a medusa, constituting the bulk of the animal and making it more buoyant. Because of this mass of mesoglea (“jelly”), medusae are commonly called jellyfishes.

Nematocysts: Stinging Organelles

One of the most characteristic structures in the entire cnidarian group is the stinging organelle called a **nematocyst** (figure 7.3). Over 20 different types of nematocysts (figure 7.4) have been described in cnidarians so far; they are important in taxonomic determinations. The nematocyst is a tiny capsule composed of material similar to chitin and containing a coiled tubular “thread” or filament, which is a continuation of the narrowed end of the capsule. This end of the capsule is covered by a little lid, or **operculum**. The inside of the undischarged thread may bear tiny barbs, or spines.

A nematocyst is enclosed in the cell that has produced it, the cnidocyte (during its development, a cnidocyte is properly called a **cnidoblast**). Except in Anthozoa, cnidocytes are equipped with a triggerlike **cnidocil**, which is a modified cilium. Anthozoan cnidocytes have a somewhat different ciliary mechanoreceptor. In some sea anemones, and perhaps other cnidarians, small organic molecules from a prey “tune” the mechanoreceptors, sensitizing them to the

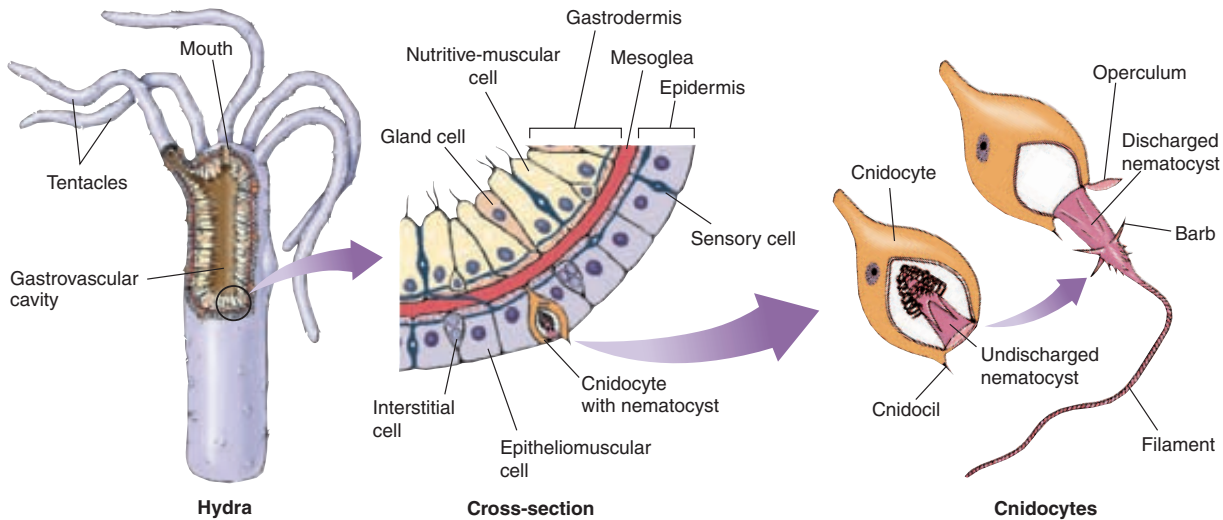


figure 7.3

At right, structure of a stinging cell. Center, portion of the body wall of a hydra. Cnidocytes, which contain the nematocysts, arise in the epidermis from interstitial cells.

frequency of vibration caused by the prey swimming. Tactile stimulation causes a nematocyst to discharge. Cnidocytes are borne in invaginations of ectodermal cells and, in some forms, in gastrodermal cells, and they are especially abundant on the tentacles. When a nematocyst has discharged, its cnidocyte is absorbed and a new one replaces it. Not all nematocysts have barbs or inject poison. Some, for example, do not penetrate prey but rapidly recoil like a spring after discharge, grasping and holding any part of a prey caught in the coil (figure 7.4). Adhesive nematocysts generally are not used to capture food.

The mechanism of nematocyst discharge is remarkable. Present evidence indicates that discharge is due to a combination of tensional forces generated during nematocyst formation and also to an astonishingly high osmotic pressure within the nematocyst: 140 atmospheres. When stimulated to discharge, permeability of the nematocyst changes, and the high internal osmotic pressure causes water to rush into the capsule. The operculum opens, and the rapidly increasing *hydrostatic pressure* within the capsule forces the thread out with great force, the thread turning inside out as it goes. At the everting end of the thread, the barbs flick to the outside like tiny switchblades. This minute but awesome weapon then injects poison when it penetrates prey.

Note the distinction between osmotic and hydrostatic pressure. A nematocyst is never required actually to contain 140 atmospheres of hydrostatic pressure within itself; such a hydrostatic pressure would doubtless cause it to explode. As water rushes in during discharge, osmotic pressure falls rapidly, while hydrostatic pressure rapidly increases.

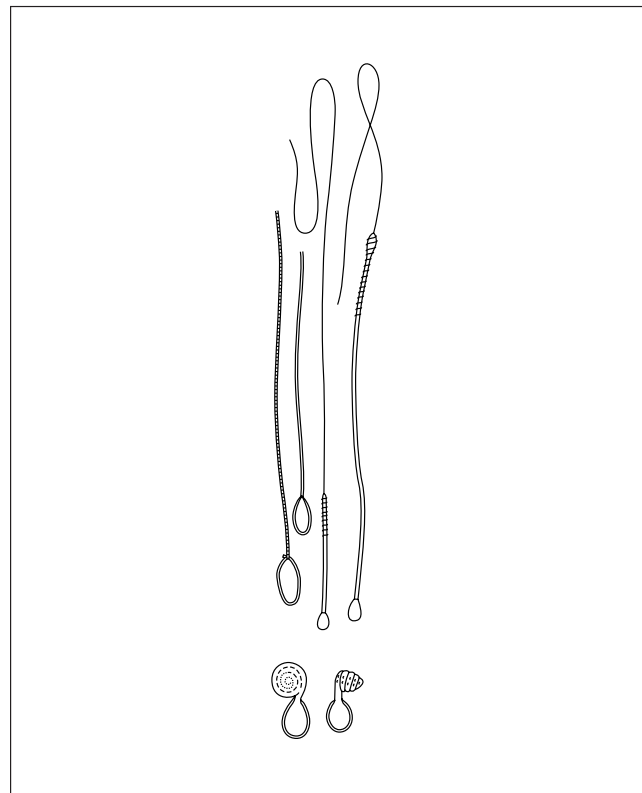


figure 7.4

Several types of nematocysts shown after discharge. At bottom are two views of a type that does not impale the prey; it recoils like a spring, catching any small part of the prey in the path of the recoiling thread.

Nematocysts of most cnidarians are not harmful to humans and are a nuisance at worst. However, stings of the Portuguese man-of-war (see figure 7.12) and certain jellyfish are quite painful and sometimes dangerous.

Nerve Net

The nerve net of the cnidarians is one of the best examples of a diffuse nervous system in the animal kingdom. This plexus of nerve cells is found both at the base of the epidermis and at the base of the gastrodermis, forming two interconnected nerve nets. Nerve processes (axons) end on other nerve cells at synapses or at junctions with sensory cells or effector organs (nematocysts or epitheliomuscular cells). Nerve impulses are transmitted from one cell to another by release of a neurotransmitter from small vesicles on one side of the synapse or junction. One-way transmission between nerve cells in higher animals is ensured because the vesicles are located on only one side of the synapse. However, cnidarian nerve nets are peculiar in that many of the synapses have vesicles of neurotransmitters on both sides, allowing transmission across the synapse in either direction. Another peculiarity of cnidarian nerves is the absence of any sheathing material (myelin) on the axons.

There is no concentrated grouping of nerve cells to suggest a “central nervous system.” Nerves are grouped, however, in the “ring nerves” of hydrozoan medusae and in the marginal sense organs of scyphozoan medusae. In some cnidarians the nerve nets form two or more systems: in Scyphozoa there is a fast conducting system to coordinate swimming movements and a slower one to coordinate movements of tentacles.

Note that there is little adaptive value for a radially symmetrical animal to have a central nervous system with a brain. The environment approaches from all sides equally, and there is no control over the direction of approach to a prey organism.

Nerve cells of the net have synapses with slender sensory cells that receive external stimuli, and the nerve cells have junctions with epitheliomuscular cells and nematocysts. Together with the contractile fibers of epitheliomuscular cells, the sensory cell and nerve net combination is often referred to as a **neuromuscular system**, an important landmark in the evolution of nervous systems. The nerve net arose early in metazoan evolution, and it has never been completely lost phylogenetically. Annelids have it in their digestive systems. In the human digestive system it is represented by nerve plexuses in the musculature. The rhythmical peristaltic movements of the stomach and intestine are coordinated by this counterpart of the cnidarian nerve net.

Body Structure

The mouth opens into the **gastrovascular cavity** (coelenteron), which communicates with cavities in the tentacles. The mouth may be surrounded by an elevated **manubrium** or by elongated **oral lobes**.

Body Wall The body wall surrounding the gastrovascular cavity consists of an outer **epidermis** (ectodermal) and an inner **gastrodermis** (endodermal) with **mesoglea** between them (see figure 7.3).

Epidermis The epidermal layer contains epitheliomuscular, interstitial, gland, cnidocyte, and sensory and nerve cells.

Epitheliomuscular cells (figure 7.5) make up most of the epidermis and serve both for covering and for muscular contraction. The bases of most of these cells are extended parallel to the tentacle or body axis and contain myofibrils, thus forming a layer of longitudinal muscle next to the mesoglea. Contraction of these fibrils shortens the body or tentacles.

Interstitial cells are undifferentiated stem cells found among the bases of the epitheliomuscular cells. Differentiation of interstitial cells gives rise to cnidoblasts, sex cells, buds, nerve cells, and others, but generally not to epitheliomuscular cells (which reproduce themselves).

Gland cells are tall cells particularly abundant around the mouth and in the pedal disc of hydra. They secrete mucus or adhesive material.

Cnidocytes containing nematocysts are found throughout the epidermis. They may be between the epitheliomuscular cells or housed in invaginations of these cells, and they are most abundant on the tentacles. There are three functional types of nematocysts in hydras: those that penetrate prey and inject poison (penetrants, see figure 7.3); those that recoil and entangle prey (volvents, see figure 7.4); and those that secrete an adhesive substance used in locomotion and attachment (glutinants).

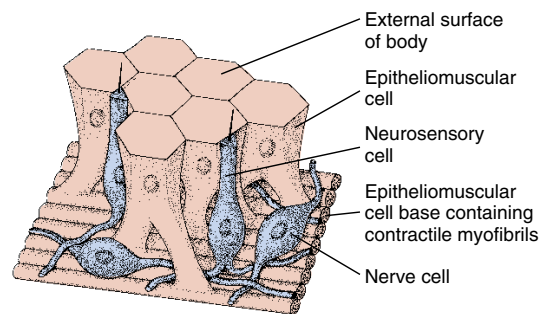


figure 7.5

Epitheliomuscular and nerve cells in hydra.

Sensory cells are scattered among the other epidermal cells, especially around the mouth and tentacles. The free end of each sensory cell bears a flagellum, which is the sensory receptor for chemical and tactile stimuli. The other end branches into fine processes, which synapse with nerve cells.

Nerve cells of the epidermis are often multipolar (have many processes), although in more highly organized cnidarians the cells may be bipolar (with two processes). Their processes (axons) form synapses with sensory cells and other nerve cells, and junctions with epitheliomuscular cells and cnidocytes. Both one-way and two-way synapses with other nerve cells are present.

Gastrodermis The gastrodermis, a layer of cells lining the gastrovascular cavity, is made up chiefly of large, ciliated, columnar epithelial cells with irregular flat bases. Cells of the gastrodermis include nutritive-muscular, interstitial, and gland cells and, in classes other than Hydrozoa, cnidocytes.

Nutritive-muscular cells are usually tall columnar cells that have laterally extended bases containing myofibrils. In hydrozoans the myofibrils run at right angles to the body or tentacle axis and so form a circular muscle layer. However, this muscle layer is very weak, and longitudinal extension of the body and tentacles is brought about mostly by increasing the volume of water in the gastrovascular cavity. Water is brought in through the mouth by the beating of cilia on the nutritive-muscular cells in hydrozoans or by ciliated cells in the pharynx of anthozoans. Thus, water in the gastrovascular cavity serves as a **hydrostatic skeleton**. The two cilia on the free end of each cell also serve to circulate food and fluids in the digestive cavity. The cells often contain large numbers of food vacuoles. Gastrodermal cells of green hydras (*Chlorohydra* [Gr. *chlōros*, green, + *hydra*, a mythical nine-headed monster slain by Hercules]), bear green algae (**zoochlorellae**), but in marine cnidarians they are a type of dinoflagellate (p. 98) (**zooxanthellae**). Both are cases of mutualism, with the algae furnishing organic compounds they have synthesized to their cnidarian hosts.

Interstitial cells scattered among the bases of the nutritive cells can transform into other cell types. **Gland cells** secrete digestive enzymes.

Mesoglea Mesoglea lies between the epidermis and gastrodermis and adheres to both layers. It is gelatinous, or jellylike, and has no fibers or cellular elements in hydrozoan polyps. It is thicker in medusae and has elastic fibers, and in scyphozoan medusae it has ameboid cells. The mesoglea of anthozoans is a mesenchyme containing ameboid cells.

Locomotion

Colonial polyps are permanently attached, but hydras can move about freely by gliding on their basal disc, aided by mucus secretions. Sea anemones can move similarly on their basal discs. Hydras can also use a “measuring worm” movement, loop-

ing along by bending over and attaching their tentacles to the substratum. They may even turn handsprings or detach and, by forming a gas bubble on the basal disc, float to the surface.

Most medusae can move freely, and they swim by contracting the bell, expelling water from the concave, oral side. The muscular contractions are antagonized by the compressed mesoglea and elastic fibers within it. Usually, they contract several times and move generally upward, then sink slowly. Cubozoan medusae, however, can swim strongly.

Feeding and Digestion

Cnidarians prey on a variety of organisms of appropriate size; larger species are usually capable of killing and eating larger prey. Normally prey organisms are drawn into the gastrovascular cavity into which gland cells discharge enzymes. Digestion is started in the gastrovascular cavity (**extracellular digestion**), but nutritive-muscular cells phagocytize many food particles for **intracellular digestion**. Ameboid cells may carry undigested particles to the gastrovascular cavity, where they are eventually expelled with other indigestible matter.

Reproduction

Most cnidarians are dioecious, and many shed their gametes directly into the water. Zygotes may be retained by the female and brooded for some period. Gonads are epidermal in hydrozoans and gastrodermal in the other groups. The embryo characteristically develops into a free-swimming **planula** larva (see figure 7.9).

Cnidarians are capable of asexual reproduction, usually by budding, but sea anemones commonly practice a peculiar form of fission known as **pedal laceration** (p. 130).

Class Hydrozoa

Most Hydrozoa are marine and colonial in form, and the typical life cycle includes both an asexual polyp and a sexual medusa stage. Some, however, such as the freshwater hydras, have no medusa stage. Some marine hydroids do not have free medusae (figure 7.6), whereas some hydrozoans occur only as medusae and have no polyp.

Hydras, although not typical hydrozoans, have become favorites as an introduction to Cnidaria because of their size and ready availability. Combining study of a hydra with that of a representative colonial marine hydroid such as *Obelia* (Gr. *obelias*, round cake) gives an excellent idea of class Hydrozoa.

Hydra: A Freshwater Hydrozoan

The common freshwater hydra (figure 7.7) is a solitary polyp and one of the few cnidarians found in fresh water. Its normal habitat is the underside of aquatic leaves and lily pads in cool, clean fresh water of pools and streams. The hydra family is found throughout the world, with 16 species occurring in North America.



figure 7.6

In some hydroids, such as this *Tubularia crocea*, medusae are reduced to gonadal tissue and do not detach. These reduced medusae are known as gonophores.

Over 230 years ago, Abraham Trembley was astonished to discover that isolated sections of the stalk of hydra could regenerate and each become a complete animal. Since then, over 2000 investigations of hydra have been published, and the organism has become a classic model for the study of morphological differentiation. The mechanisms governing morphogenesis have great practical importance, and the simplicity of hydra lends itself to these investigations. Substances controlling development (morphogens), such as those determining which end of a cut stalk will develop a mouth and tentacles, have been discovered, and they may be present in the cells in extremely low concentrations (10^{-10}M).

The body of a hydra can extend to a length of 25 to 30 mm or can contract to a tiny, jellylike mass. It is a cylindrical tube with the lower (aboral) end drawn out into a slender stalk, ending in a **basal** (or pedal) **disc** for attachment. This basal disc has gland cells that enable a hydra to adhere to a substratum and also to secrete a gas bubble for floating. In the center of the disc there may be an excretory pore. The **mouth**, located on a conical elevation called the **hypostome**, is encircled by six to ten hollow tentacles that, like the body, can greatly extend when the animal is hungry.



figure 7.7

Hydra with developing bud and ovary.



figure 7.8

Hydra catches an unwary water flea with the nematocysts of its tentacles. This hydra already contains one water flea eaten previously.

The mouth opens into the gastrovascular cavity, which communicates with the cavities in the tentacles. In some individuals **buds** may project from the sides, each with a mouth and tentacles like the parent. Testes or ovaries, when present, appear as rounded projections on the surface of the body (figure 7.7).

Hydras feed on a variety of small crustaceans, insect larvae, and annelid worms. The hydra awaits its prey with tentacles extended (figure 7.8). A food organism that brushes against its tentacles may find itself harpooned by scores of

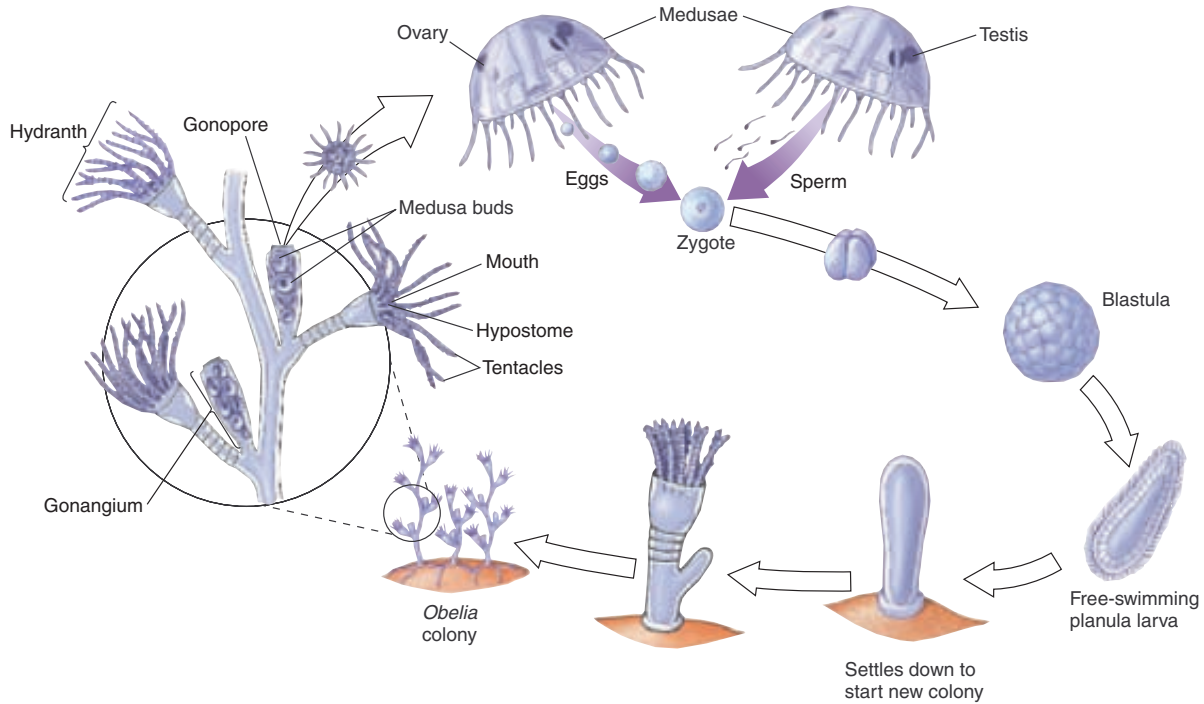


figure 7.9

Life cycle of *Obelia*, showing alternation of polyp (asexual) and medusa (sexual) stages. *Obelia* is a calyptoblastic hydrozoan; that is, its polyps as well as its stems are protected by continuations of the nonliving covering.

nematocysts that render it helpless, even though it may be larger than the hydra. The tentacles move the prey toward the mouth, which slowly widens. Well moistened with mucous secretions, the mouth glides over and around the prey, totally engulfing it.

The activator that actually causes the mouth to open is the reduced form of **glutathione**, which is found to some extent in all living cells. Glutathione is released from the prey through the wounds made by the nematocysts, but only animals releasing enough of the chemical to activate a feeding response are eaten by a hydra. This explains how a hydra distinguishes between *Daphnia*, which it relishes, and some other forms that it refuses. If we place glutathione in water containing hydras, each hydra will go through the motions of feeding, even though no prey is present.

In asexual reproduction, buds appear as outpocketings of the body wall and develop into young hydras that eventually detach from the parent. In sexual reproduction, temporary gonads (see figure 7.7) usually appear in autumn, stimulated by lower temperatures and perhaps also by reduced aeration of stagnant waters. Eggs in the ovary usually mature one at a time and are fertilized by sperm shed into the water. A cyst forms around the embryo before it breaks loose from the parent, enabling it to survive the winter. Young hydras hatch out in spring when the weather is favorable.

Hydroid Colonies

Far more representative of class Hydrozoa than hydras are those hydrozoans that have a medusa stage in their life cycle. *Obelia* is often used in laboratory exercises for beginning students to illustrate the hydrozoan type (figure 7.9).

A typical hydrozoan has a base, a stalk, and one or more terminal polyps (zooids). The base by which colonial hydrozoans are attached to the substratum is a rootlike stolon, which gives rise to one or more stalks. The living cellular part of the stalks secretes a nonliving chitinous sheath. Attached to the ends of the branches of the stalks are individual zooids. Most zooids are feeding polyps called **hydranths**, or **gastrozooids**. They may be tubular, bottle shaped, or vase-like, but all have a terminal mouth and a circlet of tentacles. In some forms, such as *Obelia*, the chitinous sheath continues as a protective cup around the polyp into which the polyp can withdraw for protection (figure 7.9). In others the polyp is naked. **Dactylozooids** are polyps specialized for defense.

Hydranths, much like hydras, capture and ingest prey, such as tiny crustaceans, worms, and larvae, thus providing nutrition for the entire colony. After partial digestion in a hydranth, the digestive broth passes into the common gastrovascular cavity where intracellular digestion occurs.

Circulation within the gastrovascular cavity is a function of the ciliated gastrodermis, but rhythmic contractions and

pulsations of the body, which occur in many hydroids, also aid circulation.

In contrast to hydras, new individuals that bud do not detach from the parent; thus the size of the colony increases. New polyps may be hydranths or reproductive polyps known as **gonangia**. Medusae are produced by budding within the gonangia. Young medusae leave the colony as free-swimming individuals that mature and produce gametes (eggs and sperm) (figure 7.9). In some species medusae remain attached to the colony and shed their gametes there. In other species medusae never develop, gametes being shed by male and female gonophores. Development of a zygote results in a ciliated planula larva that swims about for a time. Then it settles down to a substratum to develop into a minute polyp that gives rise, by asexual budding, to the hydroid colony, thus completing the life cycle.

Hydroid medusae are usually smaller than their scyphozoan counterparts, ranging from 2 or 3 mm to several centimeters in diameter (figure 7.10). The margin of the bell projects inward as a shelllike **velum**, which partly closes the open side of the bell and is used in swimming (figure 7.11). Muscular pulsations that alternately fill and empty the bell propel the animal forward, aboral side first, with a sort of “jet propulsion.” Tentacles attached to the bell margin are richly supplied with nematocysts.

The mouth opening at the end of a suspended **manubrium** leads to a stomach and four radial canals that connect with a ring canal around the margin. This in turn connects with the hollow tentacles. Thus the coelenteron is continuous from mouth to tentacles, and the entire system is lined with gastrodermis. Nutrition is similar to that of hydranths.

The nerve net is usually concentrated into two nerve rings at the base of the velum. The bell margin is liberally supplied with sensory cells. It usually also bears two kinds of specialized sense organs: **statocysts**, which are small organs of equilibrium (figure 7.11), and **ocelli**, which are light-sensitive organs.

Other Hydrozoans

Some hydrozoans form floating colonies, such as *Physalia* (Gr. *physallis*, bladder), the Portuguese man-of-war (figure 7.12). These colonies include several types of modified medusae and polyps. *Physalia* has a rainbow-hued float, probably a modified polyp, which carries it along at the mercy of winds and currents. It contains an air sac filled with secreted gas and acts as a carrier for the generations of individuals that bud from it and hang suspended in the water. There are several types of individuals, including feeding polyps, reproductive polyps, long stinging tentacles, and so-called jelly polyps. Many swimmers have experienced the uncomfortable sting that these colonial floaters can inflict. The pain, along with the panic of the swimmer, can increase the danger of drowning.

Other hydrozoans secrete massive calcareous skeletons that resemble true corals (figure 7.13). They are sometimes called **hydrocorals**.



figure 7.10

Bell medusa, *Polyorchis penicillatus*, medusa stage of an unknown attached polyp.

Class Scyphozoa

Class Scyphozoa (si-fo-zo´a) (Gr. *skyphos*, cup) includes most of the larger jellyfishes, or “cup animals.” A few, such as *Cyanea* (Gr. *kyanos*, dark-blue substance), may attain a bell diameter exceeding 2 m and tentacles 60 to 70 m long (figure 7.14). Most scyphozoans, however, range from 2 to 40 cm in diameter. Most are found floating in the open sea, some even at depths of 3000 m, but one unusual order is sessile and attaches by a stalk to seaweeds and other objects on the sea bottom (figure 7.15). Their coloring may range from colorless to striking orange and pink hues.

Scyphomedusae, unlike hydromedusae, have no velum. Bells of different species vary in depth from a shallow saucer shape to a deep helmet or goblet shape, and in many the margin is scalloped, each notch bearing a sense organ called a **rhopalium** and a pair of lobelike projections called lappets. *Aurelia* (L. *aurum*, gold) has eight such notches (figures 7.16 and 7.17); others may have four or sixteen. Each rhopalium bears a statocyst for balance, two sensory pits containing concentrations of sensory cells, and sometimes an ocellus (simple eye) for photoreception. The mesoglea is thick and contains cells as well as fibers. The stomach is usually divided into pouches containing small tentacles with nematocysts.

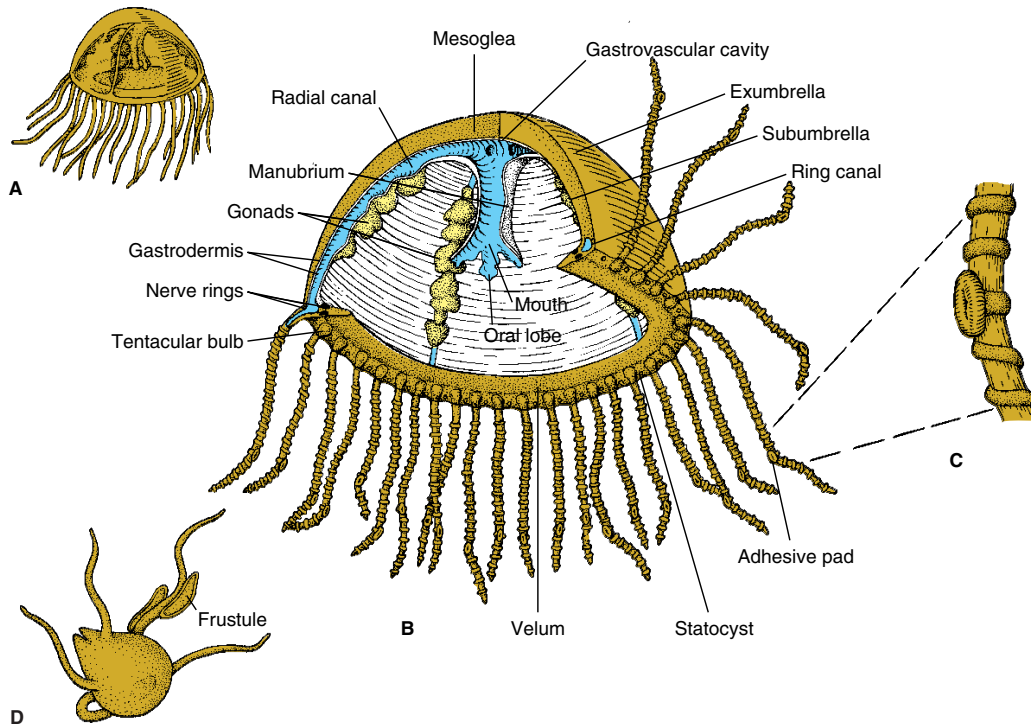


figure 7.11

Structure of *Gonionemus*. **A**, Medusa with typical tetramerous arrangement. **B**, Cutaway view showing morphology. **C**, Portion of a tentacle with its adhesive pad and ridges of nematocysts. **D**, Tiny polyp, or hydroid stage, that develops from the planula larva. It can produce more polyps by budding (frustules) or produce medusa buds.



figure 7.12

A Portuguese man-of-war colony, *Physalia physalis* (order Siphonophora, class Hydrozoa). Colonies often drift onto southern ocean beaches, where they are a hazard to bathers. Each colony of medusa and polyp types is integrated to act as one individual. As many as a thousand zooids may be found in one colony. The nematocysts secrete a powerful neurotoxin.

The mouth is centered on the subumbrellar side. The manubrium is usually drawn out into four frilly **oral lobes** used in food capture and ingestion. Marginal tentacles may be many or few and may be short, as in *Aurelia*, or long, as in *Cyanea*. Tentacles, manubrium, and often the entire body surface of scyphozoans are well supplied with nematocysts. Scyphozoans feed on all sorts of small organisms, from protozoa to fishes. Capture of prey involves stinging and manipulation with tentacles and oral arms, but methods vary. *Aurelia* feeds on small planktonic animals. These are caught in mucus of the umbrella surface, carried to “food pockets” on the umbrella margin by cilia, and picked up from the pockets by the oral lobes whose cilia carry the food to the gastrovascular cavity. Cilia on the gastrodermis keep a current of water moving to bring food and oxygen into the stomach and carry out wastes.

Internally four **gastric pouches** containing nematocysts connect with the stomach in scyphozoans, and a complex system of **radial canals** that branch from the pouches to the **ring canal** (see figure 7.16) completes the gastrovascular cavity, through which nutrients circulate.

Sexes are separate, with gonads located in the gastric pouches. Fertilization is internal, with sperm being carried by ciliary currents into the gastric pouch of the female. Zygotes



A



B

figure 7.13

These hydrozoans form calcareous skeletons that resemble true coral. **A**, *Stylaster roseus* (order Stylasterina) occurs commonly in caves and crevices in coral reefs. These fragile colonies branch in only a single plane and may be white, pink, purple, red, or red with white tips. **B**, Species of *Millepora* (order Milleporina) form branching or platelike colonies and often grow over the horny skeleton of gorgonians. They have a generous supply of powerful nematocysts that produce a burning sensation on human skin, justly earning the common name fire coral.

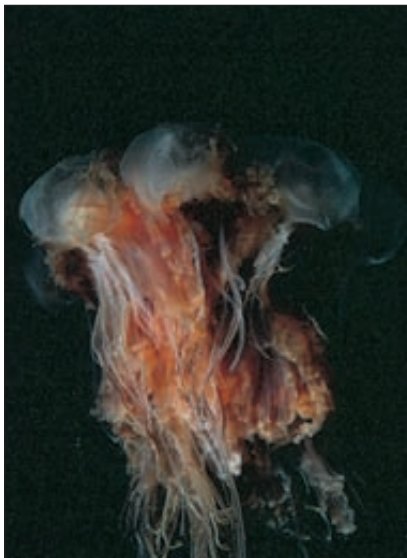


figure 7.14

Giant jellyfish, *Cyanea capillata* (order Semeaeostomeae, class Scyphozoa). A North Atlantic species of *Cyanea* reaches a bell diameter exceeding 2 m. It is known as “sea blubber” by fishermen.

may develop in seawater or may be brooded in folds of the oral arms. The ciliated planula larva becomes attached and develops into a **scyphistoma**, a hydralike form (figure 7.16). By a process of **strobilation** the scyphistoma of *Aurelia* forms a series of saucerlike buds, **ephyrae**, and is now called a **strobila** (figure 7.16). When the ephyrae break loose, they grow into mature jellyfish.

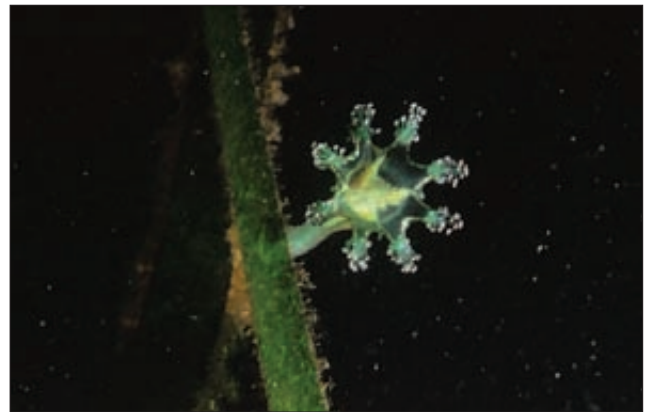


figure 7.15

Thaumatoscyphus hexaradiatus (order Stauromedusae, class Scyphozoa). Members of this order are unusual scyphozoans in that the medusae are sessile and attached to seaweed or other objects.

Class Cubozoa

Cubozoa formerly were considered an order (Cubomedusae) of Scyphozoa. The medusa is the predominant form (figure 7.18); the polyp is inconspicuous and in most cases unknown. In transverse section the bells are almost square. A tentacle or group of tentacles is found at each corner of the square at the umbrella margin. The base of each tentacle is differentiated into a flattened, tough blade called a **pedalium** (figure 7.18). Rhopalia are present. The umbrella margin is not scalloped, and the subumbrella edge turns inward to form a **velarium**. The velarium functions as a velum does in hydrozoan

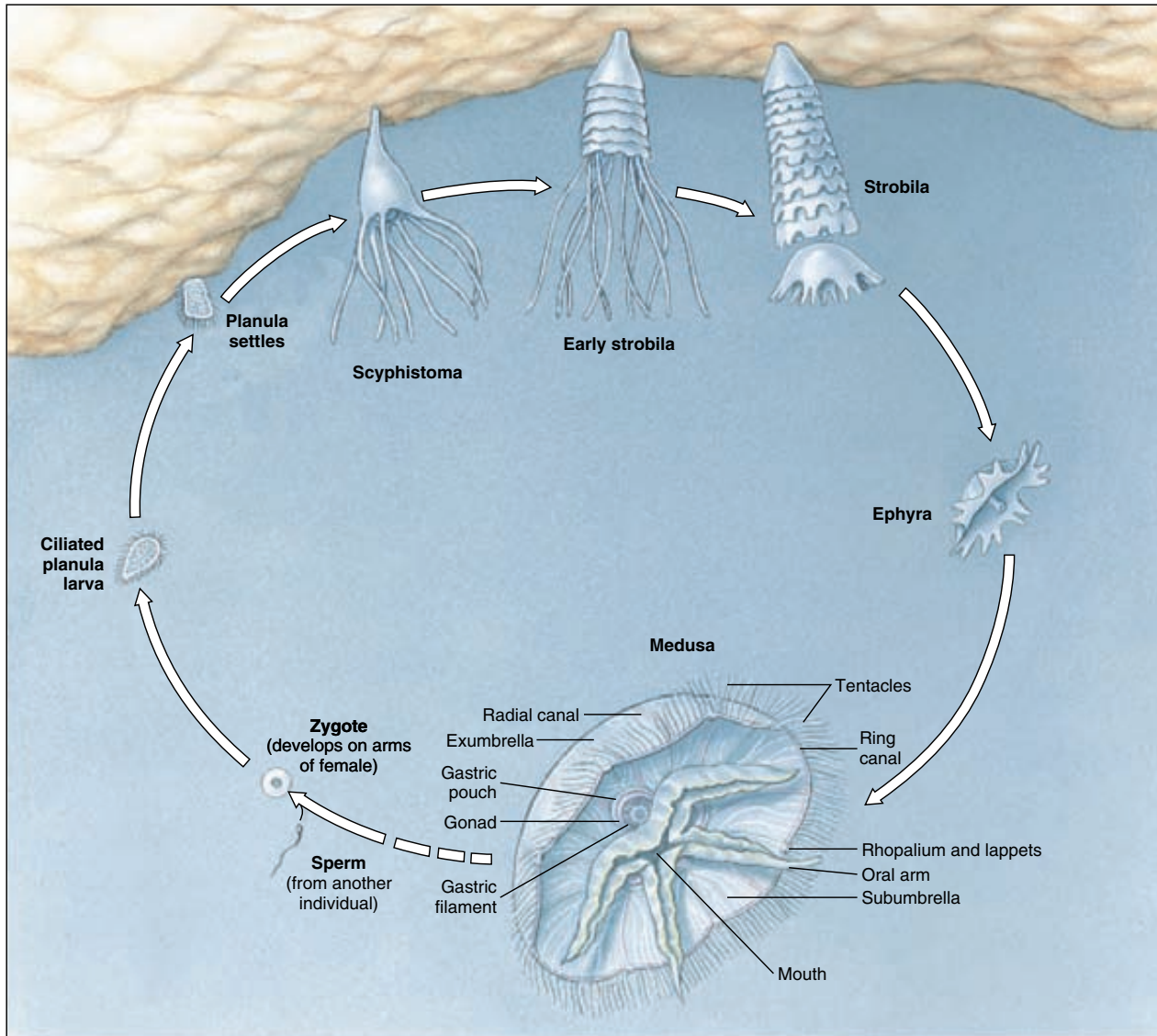


figure 7.16

Life cycle of *Aurelia*, a marine scyphozoan medusa.

medusae, increasing swimming efficiency, but it differs structurally. Cubomedusae are strong swimmers and voracious predators, feeding mostly on fish.

Class Anthozoa

Anthozoans, or “flower animals,” are polyps with a flowerlike appearance (figure 7.19). There is no medusa stage. Anthozoa are all marine and are found in both deep and shallow water and in polar seas as well as tropical seas. They vary greatly in size and may be solitary or colonial. Many are supported by skeletons.

Chironex fleckeri (Gr. *cheir*, hand, + *nexis*, swimming) is a large cubomedusa known as the sea wasp. Its stings are quite dangerous and sometimes fatal. Most fatal stings have been reported from tropical Australian waters, usually following quite massive stings. Witnesses have described victims as being covered with “yards and yards of sticky wet string.” Stings are very painful, and death, if it is to occur, ensues within a matter of minutes. If death does not occur within 20 minutes after stinging, complete recovery is likely.

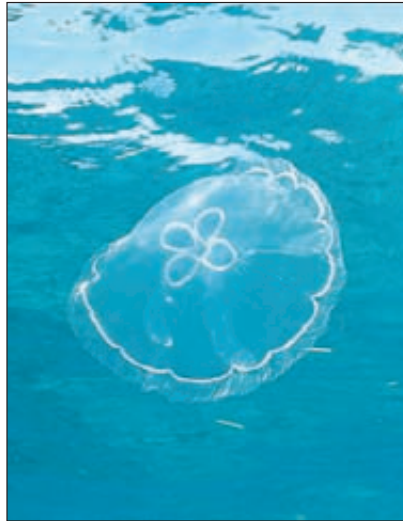
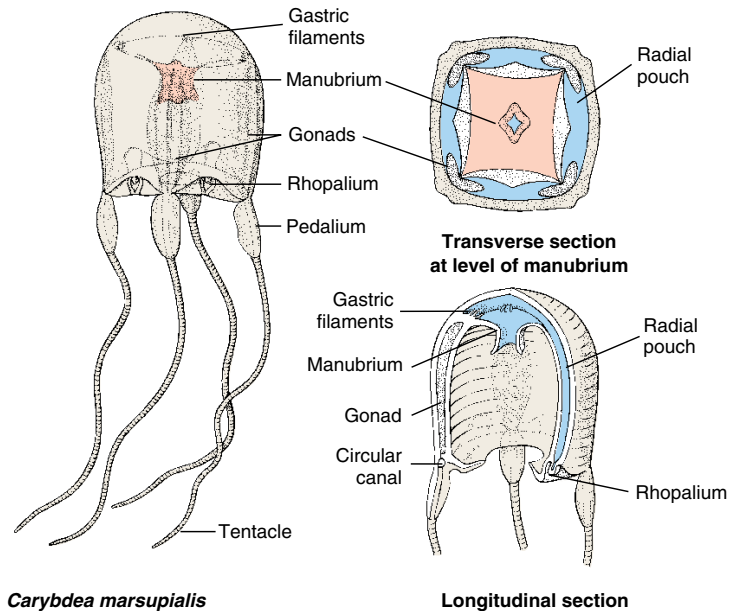


figure 7.17

Moon jellyfish *Aurelia aurita* (class Scyphozoa) is cosmopolitan in distribution. It feeds on planktonic organisms caught in mucus on its umbrella.



Carybdea marsupialis

figure 7.18

Carybdea, a cubozoan medusa.



figure 7.19

Sea anemones (order Actiniaria, subclass Zoantharia) are the familiar and colorful “flower animals” of tide pools, rocks, and pilings of the intertidal zone. Most, however, are subtidal, their beauty seldom revealed to human eyes. These are rose anemones, *Tealia piscivora*.

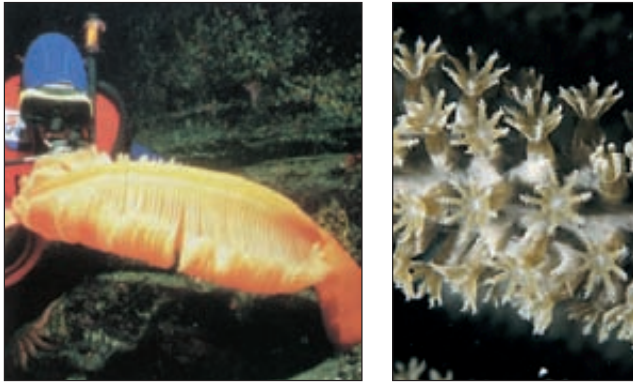
The class has three subclasses: **Zoantharia** (or **Hexacorallia**), made up of the sea anemones, hard corals, and others; **Ceriantipatharia**, which includes only tube anemones and thorny corals; and **Octocorallia** (or **Alcyonaria**), containing soft and horny corals, such as sea fans, sea pens, sea pansies, and others. Zoantharians and ceriantipatharians have a **hexamerous** plan (of six or multiples of six) or polymerous symmetry and have simple tubular tentacles arranged in one or

more circlets on the oral disc. Octocorallians are **octomerous** (built on a plan of eight) and always have eight pinnate (featherlike) tentacles arranged around the margin of the oral disc (figure 7.20).

The gastrovascular cavity is large and partitioned by septa, or mesenteries, that are inward extensions of the body wall. Where one septum extends into the gastrovascular cavity from the body wall, another extends from the diametrically opposite side; thus, they are said to be **coupled**. In Zoantharia, septa are not only coupled, they are also **paired** (figure 7.21). The muscular arrangement varies among different groups, but there are usually circular muscles in the body wall and longitudinal and transverse muscles in the septa.

Subclass Ceriantipatharia has been created from the Ceriantharia and Antipatharia, formerly considered orders of Zoantharia. Ceriantarians are tube anemones and live in soft bottom sediments, buried to the level of the oral disc. Antipatharians are thorny or black corals. They are colonial and have a skeleton of a horny material. Both of these groups are small in numbers of species and are limited to warmer waters of the sea.

The mesoglea is a mesenchyme containing ameboid cells. There is a general tendency towards biradial symmetry in the septal arrangement and in the shape of the mouth and pharynx. There are no special organs for respiration or excretion.



A

B

figure 7.20

A, Orange sea pen *Ptilosarcus gurneyi* (order Pennatulacea, subclass Octocorallia, class Anthozoa). Sea pens are colonial forms that inhabit soft bottoms. The base of the fleshy body of the primary polyp is buried in sediment. It gives rise to numerous secondary, branching polyps.

B, Close-up of a gorgonian. The pinnate tentacles characteristic of the subclass Octocorallia are apparent.

Sea Anemones

Sea anemone polyps (subclass, Zoantharia, order Actiniaria) are larger and heavier than hydrozoan polyps (figures 7.19 and 7.21). Most range from 5 mm or less to 100 mm in diameter, and from 5 mm to 200 mm long, but some grow much larger. Some are quite colorful. Anemones are found in coastal areas all over the world, especially in warmer waters, and they attach by means of their pedal discs to shells, rocks, timber, or whatever submerged substrata they can find. Some burrow in mud or sand.

Sea anemones are cylindrical with a crown of tentacles arranged in one or more circles around the mouth on the flat **oral disc** (figure 7.21). The slit-shaped mouth leads into a **pharynx**. At one or both ends of the mouth is a ciliated groove called a **siphonoglyph**, which extends into the pharynx. Siphonoglyphs create water currents directed into the pharynx. Cilia elsewhere on the pharynx direct water outward. Currents thus created carry in oxygen and remove wastes. They also help maintain an internal fluid pressure providing a hydrostatic skeleton that serves as a support for opposing muscles.

The pharynx leads into a large gastrovascular cavity divided into radial chambers by pairs of septa that extend vertically from the body wall toward the pharynx (figure 7.21). These chambers communicate with each other and are open below the pharynx. In many anemones the lower ends of the septal edges are prolonged into **acontia threads**, also provided with nematocysts and gland cells, that can be protruded through the mouth or through pores in the body wall to help overcome prey or provide defense. The pores also aid in the rapid discharge of water from the body when the animal is endangered and contracts to a small size.

Anemones form some interesting mutualistic relationships with other organisms. Many anemones house unicellular algae in their tissues (as do reef-building corals), from which they undoubtedly derive some nutrients. Some hermit crabs place anemones on the snail shells in which the crabs live, gaining some protection from predators by the presence of the anemone, while the anemone dines on particles of food dropped by the crab. Anemone fishes (figure 7.22) of the tropical Indo-Pacific form associations with large anemones. An unknown property of the skin mucus of the fish causes the anemone's nematocysts not to discharge, but if some other fish is so unfortunate as to brush the anemone's tentacles, it is likely to become a meal.

Sea anemones are carnivorous, feeding on fish or almost any live animals of suitable size. Some species live on minute forms caught by ciliary currents.

Sexes are separate in some sea anemones, and some are hermaphroditic. Gonads are arranged on the margins of the septa. Fertilization is external in some species, whereas in others the sperm enter the gastrovascular cavity to fertilize eggs. The zygote develops into a ciliated larva. Asexual reproduction commonly occurs by pedal laceration. Small pieces of the pedal disc break off as the animal moves, and each of these regenerates a small anemone. Asexual reproduction by transverse fission also has been reported.

Zoantharian Corals

Zoantharian corals belong to order Scleractinia of subclass Zoantharia, sometimes known as the true or stony corals. Stony corals might be described as miniature sea anemones that live in calcareous cups they themselves have secreted (figures 7.23 and 7.24). Like that of anemones, a coral polyp's gastrovascular cavity is subdivided by septa arranged in multiples of six (hexamerous) and its hollow tentacles surround the mouth, but there is no siphonoglyph.

Instead of a pedal disc, the epidermis at the base of the column secretes a limy skeletal cup, including sclerosepta, which project up into the polyp between its true septa (figure 7.24). Living polyps can retract into the safety of their cup when not feeding. Since the skeleton is secreted below the living tissue rather than within it, the calcareous material is an exoskeleton. In many colonial corals, the skeleton may become massive, building up over many years, with the living coral forming a sheet of tissue over the surface (figure 7.25). The gastrovascular cavities of the polyps are all connected through this sheet of tissue.

Octocorallian Corals

Octocorals include soft corals, sea pansies, sea pens, and sea fans and other gorgonian corals (horny corals). They have strict octomerous symmetry, with eight pinnate tentacles and

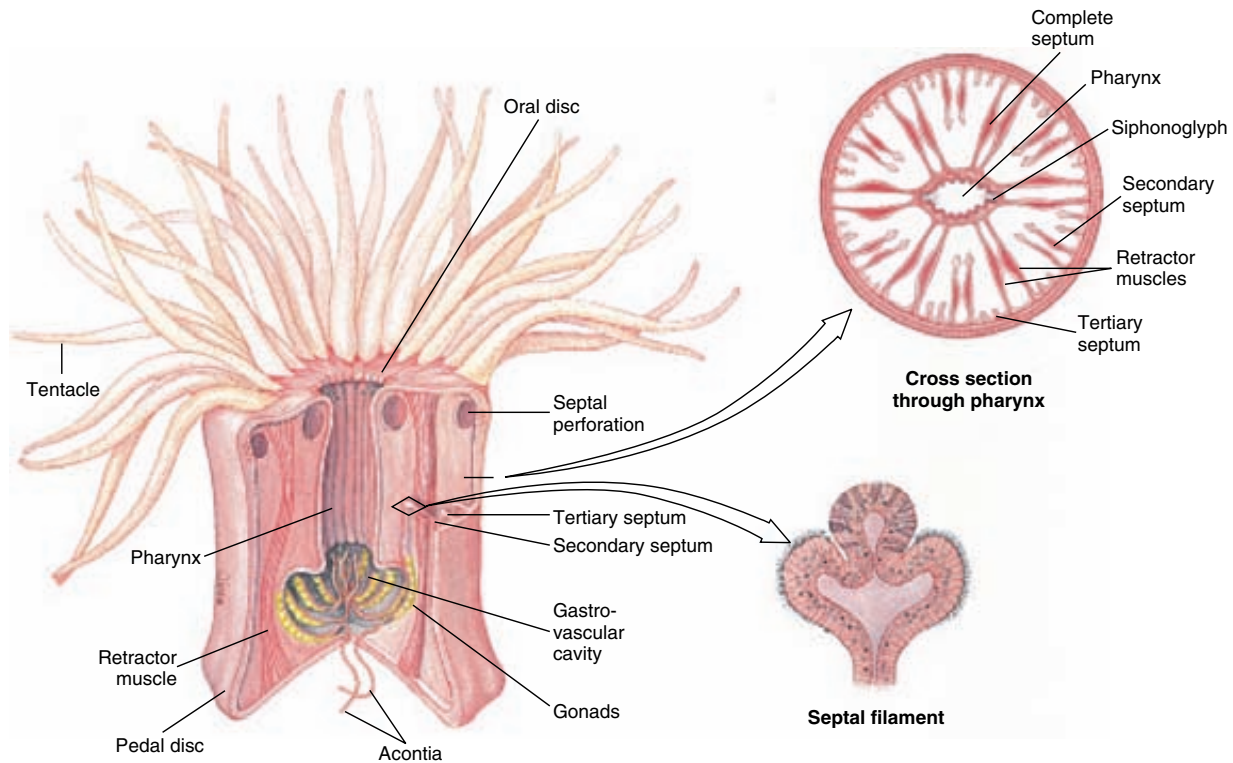


figure 7.21

Structure of the sea anemone. The free edges of the septa and the acontia threads are equipped with nematocysts to complete the paralysis of prey begun by the tentacles.



figure 7.22

Orangefin anemone fish (*Amphiprion chrysopterus*) nestles in the tentacles of its sea anemone host. Anemone fishes do not elicit stings from their hosts but may lure unsuspecting other fish to become meals for the anemone.

eight unpaired, complete septa (figure 7.26). They are all colonial, and the gastrovascular cavities of the polyps communicate through a system of gastrodermal tubes called **solenia**. The tubes run through an extensive mesoglea in most octocorals, and the surface of the colony is covered by epidermis.

Their skeleton is secreted within the mesoglea and consists of limy spicules, fused spicules, or a horny protein, often in combination. Thus the skeletal support of most octocorals is an endoskeleton. The variation in pattern among the species of octocorals lends great variety to the form of the colonies.

The graceful beauty of octocorals—in hues of yellow, red, orange, and purple—helps create the “submarine gardens” of coral reefs (figure 7.27).

Coral Reefs

Coral reefs are among the most productive of all ecosystems, and their diversity of life forms is rivaled only by tropical rain forests. Coral reefs are large formations of calcium carbonate (limestone) in shallow tropical seas laid down by living organisms over thousands of years; living plants and animals are confined to the top layer of reefs where they add more calcium carbonate to that deposited by their predecessors. The most important organisms that take dissolved calcium and carbonate ions from seawater and precipitate it as limestone to form reefs are **reef-building corals** and **coralline algae**. Reef-building corals have mutualistic algae (zooxanthellae) living in their tissues. Coralline algae are several types of red algae, and they may be encrusting or form upright, branching growths. Not only do they contribute to the total mass of calcium carbonate, but



figure 7.23
A, Cup coral *Tubastrea* sp. The polyps form clumps resembling groups of sea anemones. Although often found on coral reefs, *Tubastrea* is not a reef-building coral (ahermatypic) and has no symbiotic zooxanthellae in its tissues. **B**, The polyps of *Montastrea cavernosa* are tightly withdrawn in the daytime but open to feed at night, as in **C** (order Scleractinia, subclass Zoantharia).

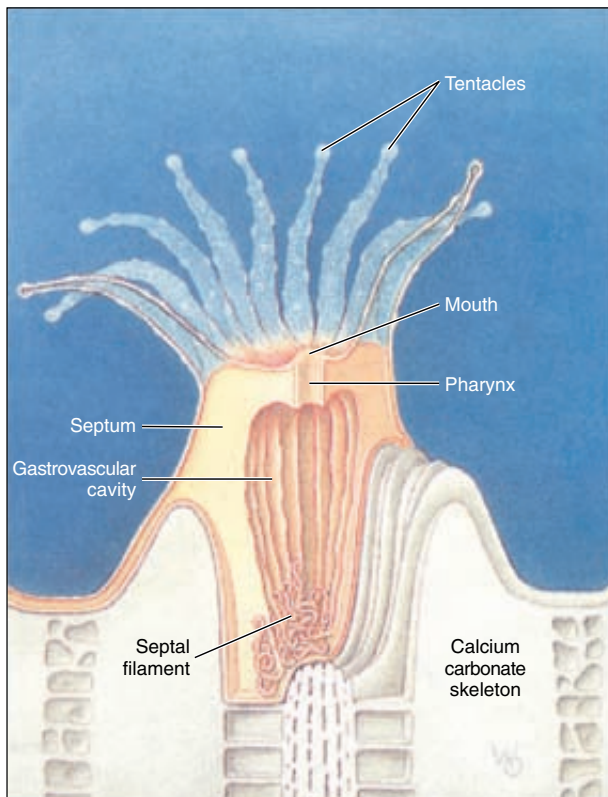


figure 7.24
 Polyp of a zoantharian coral (order Scleractinia) showing calcareous cup (exoskeleton), gastrovascular cavity, sclerosepta, septa, and septal filaments.



figure 7.25
 Boulder star coral, *Montastrea annularis* (subclass Zoantharia, class Anthozoa). Colonies can grow up to 10 feet (3 m) high.

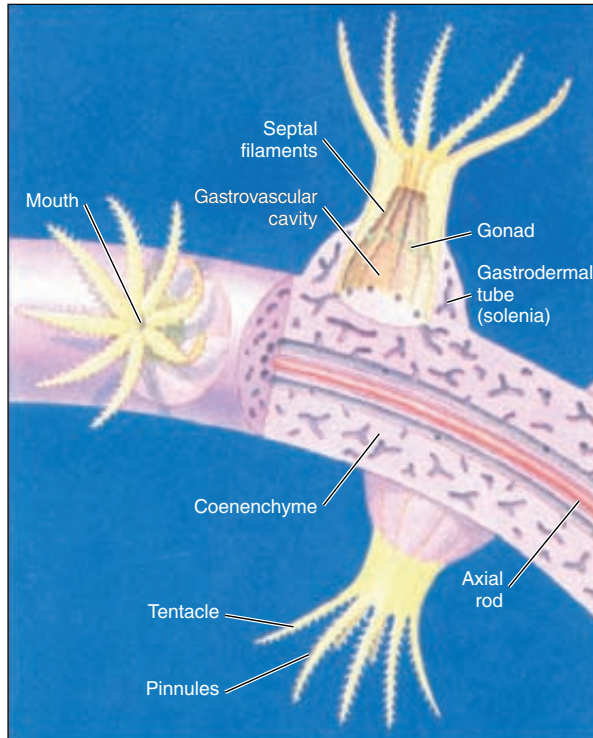


figure 7.26

Polyps of an octocorallian coral. Note the eight pinnate tentacles, coenenchyme, and solenia. They have an endoskeleton of limy spicules often with a horny protein, which may be in the form of an axial rod.

their deposits help to hold the reef together. Some octocorals and hydrozoans (especially *Millepora* [*L. mille*, a thousand, + *porus*, pore] spp., the “fire coral,” see figure 7.13) contribute in some measure to the calcareous material, and an enormous variety of other organisms contributes small amounts. However, reef-building corals seem essential to the formation of large reefs, since such reefs do not occur where these corals cannot live.

Because zooxanthellae are vital to reef-building corals, and water absorbs light, reef-building corals rarely live below a depth of 30 m (100 feet). Interestingly, some deposits of coral reef limestone, particularly around Pacific islands and atolls, reach great thickness—even thousands of feet. Clearly the corals and other organisms could not have grown from the bottom in the abyssal blackness of the deep sea and reached shallow water where light could penetrate. Charles Darwin was the first to realize that such reefs began their growth in shallow water around volcanic islands; then, as the islands slowly sank beneath the sea, growth of the reefs kept up with the rate of sinking, thus accounting for the depth of the deposits.



figure 7.27

A soft coral, *Dendronephthya* sp. (order Alcyonacea, subclass Octocorallia, class Anthozoa), on a Pacific coral reef. The showy hues of this soft coral vary from pink and yellow to bright red and contribute much color to Indo-Pacific reefs.

The distribution of coral reefs in the world is limited to locations that offer optimal conditions for their zooxanthellae. They require warmth, light, and the salinity of undiluted seawater, thus limiting coral reefs to shallow waters between 30° N and 30° S latitude and excluding them from areas with upwelling of cold water or areas near major river outflows with attendant low salinity and high turbidity. Photosynthesis and fixation of carbon dioxide by the zooxanthellae furnish food molecules for their hosts. Zooxanthellae recycle phosphorus and nitrogenous waste compounds that otherwise would be lost, and they enhance the ability of the coral to deposit calcium carbonate.

Despite their great intrinsic and economic value, coral reefs in many areas are threatened by a variety of factors, mostly of human origin. These include overenrichment with nutrients (from sewage and runoff of agricultural fertilizer from nearby land) and overfishing of herbivorous fishes, both of which contribute to overgrowth of multicellular algae. Agricultural pesticides, sediment from tilled fields and dredging, and oil spills contribute to reef degradation. When such environmental stresses do not kill corals directly, they may make the organisms more susceptible to the numerous coral diseases that have been observed in recent years. Coral reefs are apparently suffering from effects of global warming. When their surrounding water becomes too warm, corals expel their zooxanthellae (coral “bleaching”) for reasons that are not yet clear. Instances of coral bleaching are becoming increasingly common around the world. Furthermore, higher atmospheric concentrations of carbon dioxide (from burning hydrocarbon fuels) tends to acidify ocean water, which makes precipitation of CaCO₃ by corals more difficult metabolically.

classification of phylum cnidaria

Class Hydrozoa (hi-dro-zo´a) (Gr. *hydra*, water serpent, + *zōon*, animal). Solitary or colonial; asexual polyps and sexual medusae, although one type may be suppressed; hydranths with no mesenteries; medusae (when present) with a velum; both fresh water and marine. Examples: *Hydra*, *Obelia*, *Physalia*, *Tubularia*.

Class Scyphozoa (si-fo-zo´a) (Gr. *skyphos*, cup, + *zōon*, animal). Solitary; polyp stage reduced or absent; bell-shaped medusae without velum; gelatinous mesoglea much enlarged; margin of bell or umbrella typically with eight notches that are provided with sense organs; all marine. Examples: *Aurelia*, *Cassiopeia*, *Rhizostoma*.

Class Cubozoa (ku´bo-zo´a) (Gr. *kybos*, a cube, + *zōon*, animal). Solitary; polyp stage reduced; bell-shaped medusae square in cross section, with tentacle or group of tentacles hanging from a bladelike pedalum at each corner of the umbrella; margin of umbrella entire, without velum but with velarium; all marine. Examples: *Tripedalia*, *Carybdea*, *Chironex*, *Chiropsalmus*.

Class Anthozoa (an-tho-zo´a) (Gr. *anthos*, flower, + *zōon*, animal). All polyps; no medusae; solitary or colonial; enteron subdivided by mesenteries or septa bearing nematocysts; gonads endodermal; all marine.

Subclass Zoantharia (zo´an-tha´re-a) (N.L. from Gr. *zōon*, animal, + *anthos*, flower, + L. *aria*, like or connected with) (**Hexacorallia**). With simple unbranched tentacles; mesenteries in pairs, in multiples of six; sea anemones, hard corals, and others. Examples: *Metridium*, *Anthopleura*, *Tealia*, *Astrangia*, *Acropora*.

Subclass Ceriantipatharia (se´re-ant-ip´a-tha´re-a) (N.L. combination of Ceriantharia and Antipatharia). With simple unbranched tentacles; mesenteries unpaired, initially six; tube anemones and black or thorny corals. Examples: *Cerianthus*, *Antipathes*, *Stichopathes*.

Subclass Octocorallia (ok´to-ko-ral´e-a) (L. *octo*, + Gr. *korallion*, coral) (**Alcyonaria**). With eight pinnate tentacles; eight complete, unpaired mesenteries; soft and horny corals. Examples: *Tubipora*, *Alcyonium*, *Gorgonia*, *Plexaura*, *Renilla*.

Phylum Ctenophora

Ctenophora (te-nof´o-ra) (Gr. *kteis*, *ktenos*, comb, + *phora*, pl. of bearing) is composed of fewer than 100 species. All are marine forms occurring in all seas but especially in warm waters. They take their name from the eight rows of comblike plates they bear for locomotion. Common names for ctenophores are “sea walnuts” and “comb jellies.” Ctenophores, along with cnidarians, represent the only two phyla having primary radial symmetry, in contrast to other metazoans, which have primary bilateral symmetry.

Ctenophores do not have nematocysts, except in one species (*Haeckelia rubra*, after Ernst Haeckel, nineteenth-century German zoologist) that carries nematocysts on certain regions of its tentacles but lacks colloblasts. These nematocysts are apparently appropriated from cnidarians on which it feeds.

In common with cnidarians, ctenophores have not advanced beyond the tissue grade of organization. There are no definite organ systems in the strict meaning of the term.

Except for a few creeping and sessile forms, ctenophores are free-swimming. Although they are feeble swimmers and are more common in surface waters, ctenophores are sometimes found at considerable depths. Highly modified forms such as *Cestum* (L. *cestus*, girdle) use sinuous body movements as well as their comb plates in locomotion (figure 7.28).

The fragile, transparent bodies of ctenophores are easily seen at night when they emit light (luminesce).

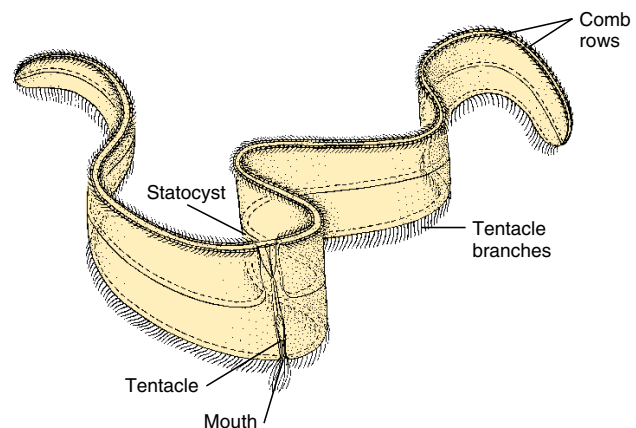
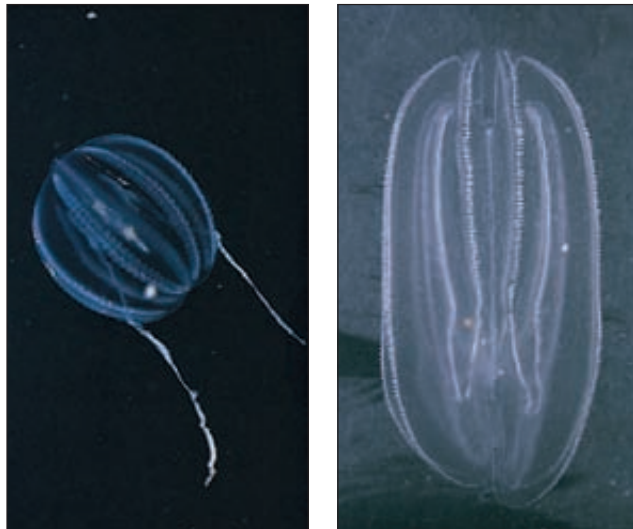


figure 7.28

Venus' girdle (*Cestum* sp.), a highly modified ctenophore. It may reach a length of 5 feet but is usually much smaller.

Form and Function

Pleurobrachia (Gr. *pleuron*, side, + L. *brachia*, arms), is a representative ctenophore (figure 7.29). Its surface bears eight longitudinal rows of transverse plates bearing long fused cilia and called **comb plates**. The beating of the cilia in each row starts at the aboral end and proceeds along the rows to the oral end, thus propelling the animal forward. All rows beat in



A

B

figure 7.29

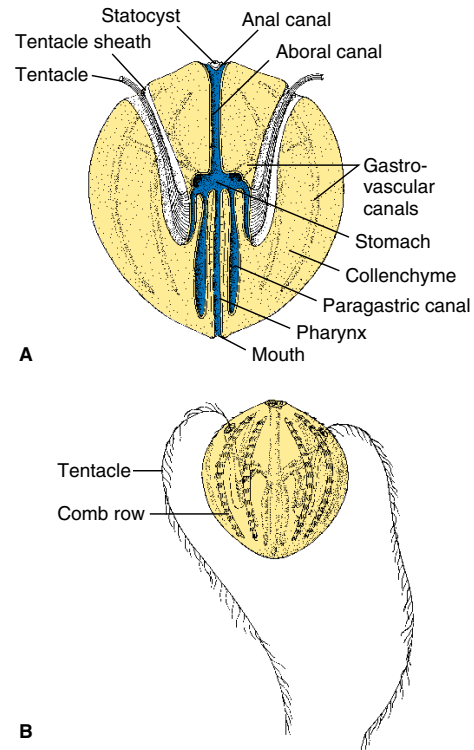
A, Comb jelly *Pleurobrachia* sp. (order Cydippida, class Tentaculata). Its fragile beauty is especially evident at night when it luminesces from its comb rows. **B**, *Mnemiopsis* sp. (order Lobata, class Tentaculata).

unison. A reversal of the wave direction drives the animal backward. Ctenophores may be the largest animals that swim exclusively by cilia.

Two long tentacles are carried in a pair of tentacle sheaths (figure 7.30) from which they can stretch to a length of perhaps 15 cm. The surface of the tentacles bears specialized glue cells called **colloblasts**, which secrete a sticky substance that facilitates catching small prey. When covered with food, the tentacles contract and food is wiped onto the mouth. The gastrovascular cavity consists of a pharynx, stomach, and a system of gastrovascular canals. Rapid digestion occurs in the pharynx; then partly digested food circulates through the rest of the system where digestion is completed intracellularly. Residues are regurgitated or expelled through small pores in the aboral end.

A nerve net system similar to that of the cnidarians includes a subepidermal plexus concentrated under each comb plate.

Since the 1980s population explosions of *Mnemiopsis leidyi* in the Black and Azov Seas have led to catastrophic declines in fisheries there. Inadvertently introduced from the coast of the Americas with ballast water of ships, the ctenophores feed on zooplankton, including small crustaceans and eggs and larvae of fish. The normally inoffensive *M. leidyi* is kept in check in the Atlantic by certain specialized predators, but introduction of such predators into the Black Sea carries its own dangers.



A

B

figure 7.30

The comb jelly *Pleurobrachia*, a ctenophore. **A**, Hemisection. **B**, External view.

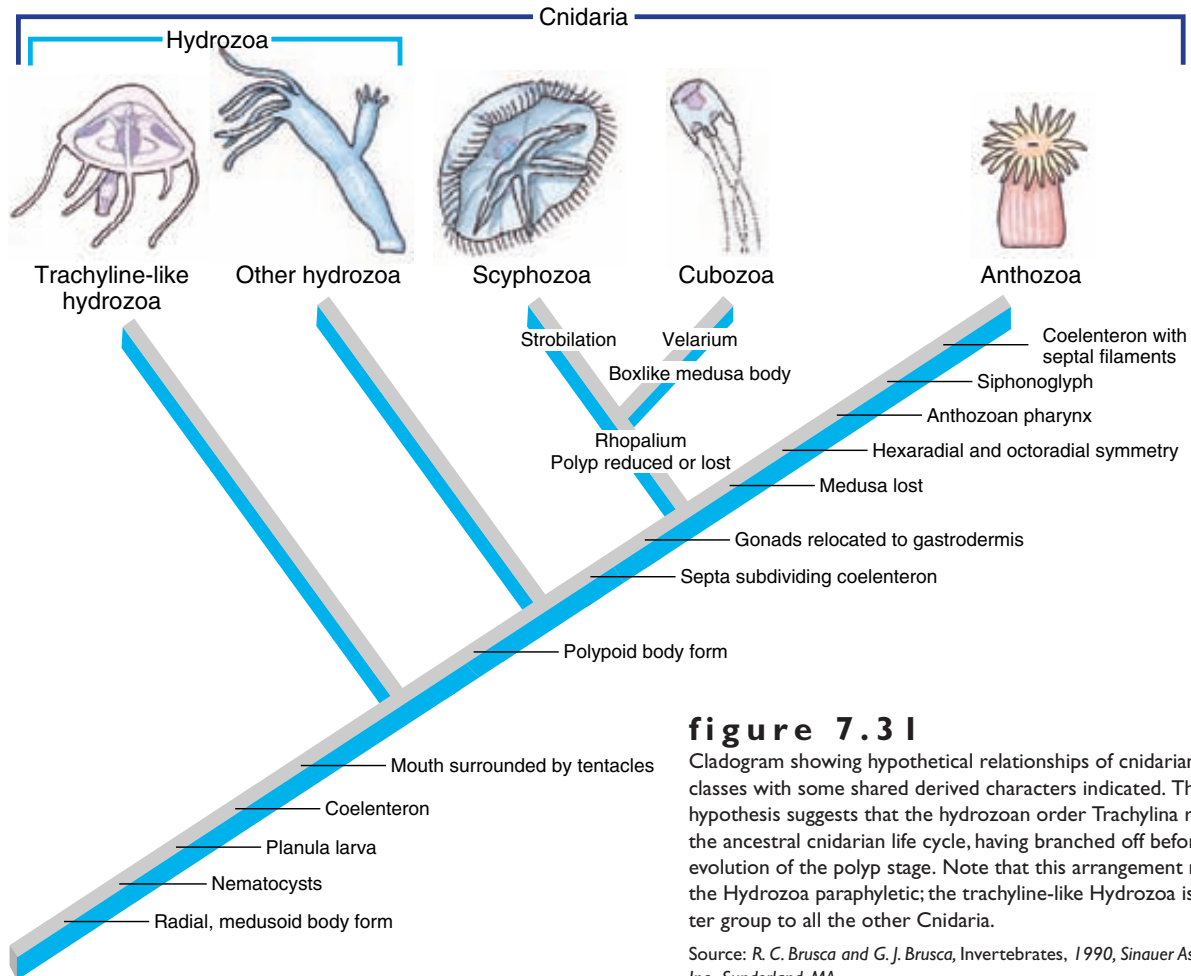
The sense organ at the aboral pole is a **statocyst**, or organ of equilibrium, and is also concerned with beating of the comb rows but does not trigger their beat. Other sensory cells are abundant in the epidermis.

All ctenophores are monoecious, bearing both an ovary and a testis. Gametes are shed into the water, except in a few species that brood their eggs, and there is a free-swimming larva.

Phylogeny and Adaptive Radiation

Phylogeny

Although the origin of the cnidarians and ctenophores is obscure, the most widely supported hypothesis today is that the radiate phyla arose from a radially symmetrical, planula-like ancestor. Such an ancestor could have been common to the radiates and to higher metazoans, the latter having been derived from a branch whose members habitually crept about on the sea bottom. Such a habit would select for bilateral symmetry. Others became sessile or free floating, conditions for which radial symmetry is a selective advantage. A planula larva in which an invagination formed to become the gastrovascular



cavity would correspond roughly to a cnidarian with an ectoderm and an endoderm.

Some researchers believe trachylina medusae (an order of class Hydrozoa) resemble the ancestral cnidarian in their direct development from planula and actinula larvae to medusae (figure 7.31). The trachylina-like ancestor would have given rise to other cnidarian lines after evolution of the polyp stage and alternation of sexual (medusa) and asexual (polyp) generations. Subsequently, the medusa was completely lost in the anthozoan line. If order Trachylina is retained within class Hydrozoa, however, then Hydrozoa becomes paraphyletic. Future investigators may resolve this problem.

In the past it was assumed that ctenophores arose from a medusoid cnidarian, but this assumption has been questioned recently. Similarities between the groups are mostly of a general nature and do not seem to indicate a close relationship. Some molecular evidence suggests that ctenophores branched off the metazoan line after sponges but before cnidarians. Ctenophores have a more derived and stereotypical cleavage

pattern than cnidarians. Other analyses indicate a nearest common ancestor of ctenophores and cnidarians, which together would form the sister taxon to bilateral metazoans.

Adaptive Radiation

In their evolution neither phylum has deviated far from its basic structure. In Cnidaria, both polyp and medusa are constructed on the same scheme. Likewise, ctenophores have adhered to the arrangement of the comb plates and their biradial symmetry.

Nonetheless, cnidarians have achieved large numbers of individuals and species, demonstrating a surprising degree of diversity considering the simplicity of their basic body plan. They are efficient predators, many feeding on prey quite large in relation to themselves. Some are adapted for feeding on small particles. The colonial form of life is well explored, with some colonies growing to great size among corals, and others, such as siphonophores, showing astonishing polymorphism and specialization of individuals within the colony.

summary

Phyla Cnidaria and Ctenophora have a primary radial symmetry; radial symmetry is an advantage for sessile or free-floating organisms because environmental stimuli come from all directions equally. Cnidaria are surprisingly efficient predators because they possess stinging organelles called nematocysts. Both phyla are essentially diploblastic, with a body wall composed of epidermis and gastrodermis and a mesoglea between. The digestive-respiratory (gastrovascular) cavity has a mouth and no anus. Cnidarians are at the tissue level of organization. They have two basic body types (polyp and medusa), and in many hydrozoans and scyphozoans the life cycle involves both an asexually reproducing polyp and a sexually reproducing medusa.

That unique organelle, the nematocyst, is produced by a cnidoblast (which becomes the cnidocyte) and is coiled within a capsule. When discharged, some types of nematocysts

penetrate prey and inject poison. Discharge is effected by a change in permeability of the capsule and an increase in internal hydrostatic pressure because of high osmotic pressure within the capsule.

Most hydrozoans are colonial and marine, but the freshwater hydras are commonly demonstrated in class laboratories. They have a typical polypoid form but are not colonial and have no medusoid stage. Most marine hydrozoans are in the form of a branching colony of many polyps (hydranths). Hydrozoan medusae may be free-swimming or remain attached to the colony.

Scyphozoans are typical jellyfishes, in which the medusa is the dominant body form, and many have an inconspicuous polypoid stage. Cubozoans are predominantly medusoid. They include the dangerous sea wasps.

Anthozoans are all marine and are polypoid; there is no medusoid stage. The most important subclasses are Zoantharia (with

hexamerous or polymerous symmetry) and Octocorallia (with octomerous symmetry). The largest zoantharian orders contain sea anemones, which are solitary and do not have a skeleton, and stony corals, which are mostly colonial and secrete a calcareous exoskeleton. Stony corals are the critical component in coral reefs, which are habitats of great beauty, productivity, and ecological and economic value. Octocorallia contain the soft and horny corals, many of which are important and beautiful components of coral reefs.

Ctenophora are biradial and swim by means of eight comb rows. Colloblasts, with which they capture small prey, are characteristic of the phylum.

Cnidaria and Ctenophora are probably derived from an ancestor that resembled the planula larva of the cnidarians. Despite their relatively simple level of organization, cnidarians are an important phylum economically, environmentally, and biologically.

review questions

1. Explain the selective advantage of radial symmetry for sessile and free-floating animals.
2. What characteristics of phylum Cnidaria do you think are most important in distinguishing it from other phyla?
3. Name and distinguish the classes in phylum Cnidaria.
4. Distinguish between polyp and medusa forms.
5. Explain the mechanism of nematocyst discharge. How can a hydrostatic pressure of one atmosphere be maintained within a nematocyst until it receives an expulsion stimulus?
6. What is an unusual feature of the nervous system of cnidarians?
7. Diagram a hydra and label the main body parts.
8. Name and give the functions of the main cell types in the epidermis and in the gastrodermis of hydra.
9. What stimulates feeding behavior in hydras?
10. Give an example of a highly polymorphic, floating, colonial hydrozoan.
11. Distinguish the following from each other: statocyst and rhopalium; scyphomedusae and hydromedusae; scyphistoma, strobila, and ephyrae; velum, velarium, and pedaliium; Zoantharia and Octocorallia.
12. Define the following with regard to sea anemones: siphonoglyph; primary septa or mesenteries; incomplete septa; septal filaments; acontia threads; pedal laceration.
13. Describe three specific interactions of anemones with nonprey organisms.
14. Contrast the skeletons of zoantharian and octocorallian corals.
15. Coral reefs generally are limited in geographic distribution to shallow marine waters. How do you account for this?
16. Specifically, what kinds of organisms are most important in deposition of calcium carbonate on coral reefs?
17. How do zooxanthellae contribute to the welfare of reef-building corals?
18. What characteristics of Ctenophora do you think are most important in distinguishing it from other phyla?
19. How do ctenophores swim, and how do they obtain food?
20. What is a widely held hypothesis on the origin of the radiate phyla?

selected references

- See also general references on page 406.
- Brown, B. E., and J. C. Ogden. 1993. Coral bleaching. *Sci. Am.* **268**:64–70 (Jan.). *Abnormally warm water is apparently the cause of reef corals losing their zooxanthellae.*
- Buddemeier, R. W., and S. V. Smith. 1999. Coral adaptation and acclimatization: a most ingenious paradox. *Amer. Zool.* **39**:1–9. *First of a series of papers in this issue dealing with effects of climatic and temperature changes on coral reefs.*
- Crossland, C. J., B. G. Hatcher, and S. V. Smith. 1991. Role of coral reefs in global ocean production. *Coral Reefs* **10**:55–64. *Because of extensive recycling of nutrients within reefs, their net energy production for export is relatively minor. However, they play a major role in inorganic carbon precipitation by biologically-mediated processes.*
- Humann, P. 1992. Reef creature identification. Florida, Caribbean, Bahamas. Jacksonville, Florida, New World Publications, Inc. *This is the best field guide available for identification of “non-coral” cnidarians of the Caribbean.*
- Humann, P. 1993. Reef coral identification. Florida, Caribbean, Bahamas. Jacksonville, Florida, New World Publications, Inc. *Superb color photographs and accurate identifications make this by far the best field guide to corals now available; includes sea grasses and some algae.*
- Kennington, R., and G. Kelleher. 1992. Crown-of-thorns starfish management conundrums. *Coral Reefs* **11**:53–56. *The first article of an entire issue on the starfish: Acanthaster planci, a predator of corals. Another entire issue was devoted to this predator in 1990.*
- Lesser, M. P. 1997. Oxidative stress causes coral bleaching during exposure to elevated temperatures. *Coral Reefs* **16**:187–192. *Evidence that reactive types of oxygen molecules, perhaps produced by the zooxanthellae in response to increased temperatures, cause cell damage and expulsion of zooxanthellae.*
- Pennisi, E. 1998. New threat seen from carbon dioxide. *Science* **279**:989.
- Increase in atmospheric CO₂ is acidifying ocean water, making it more difficult for corals to deposit CaCO₃. If CO₂ doubles in the next 70 years, as expected, reef formation will decline by 40%, and by 75% if CO₂ doubles again.*
- Rosenberg, W., and Y. Loya. 1999. *Vibrio shiloi* is the etiological (causative) agent of *Oculina patagonica* bleaching: general implications. *Reef encounter* **25**:8–10. *These investigators believe all coral bleaching is due to bacteria, not just that of O. patagonica. The bacterium that they report (Vibrio shiloi) needs high temperatures to thrive.*
- Winnepenninckx, B. M. H., Y. Van de Peer, and T. Backeljau. 1998. Metazoan relationships on the basis of 18S rRNA sequences: a few years later . . . *Amer. Zool.* **38**:888–906. *Some analyses suggest that sponges and ctenophores form a clade that branched from their common ancestor with cnidarians, all of them forming a sister group to bilateral metazoans.*

custom website

Visit this textbook’s Custom Website at www.mhhe.com/zoology (click on this book’s cover) to access these interactive study tools, and more:

Key Terms Flashcards

All of the key terms in this chapter are available as study flashcards, for your review of important terms.

Links to the Internet

Explore live links for these topics:

[Classification and Phylogeny of Animals](#)
[Radiate Animals](#)
[Phylum Cnidaria](#)
[Class Hydrozoa](#)
[Class Scyphozoa](#)
[Class Anthozoa](#)
[Coral Reefs](#)
[Coral Bleaching](#)
[Class Cubozoa](#)
[Phylum Ctenophora](#)

Self-Test

Take the online quiz for this chapter to test your knowledge.