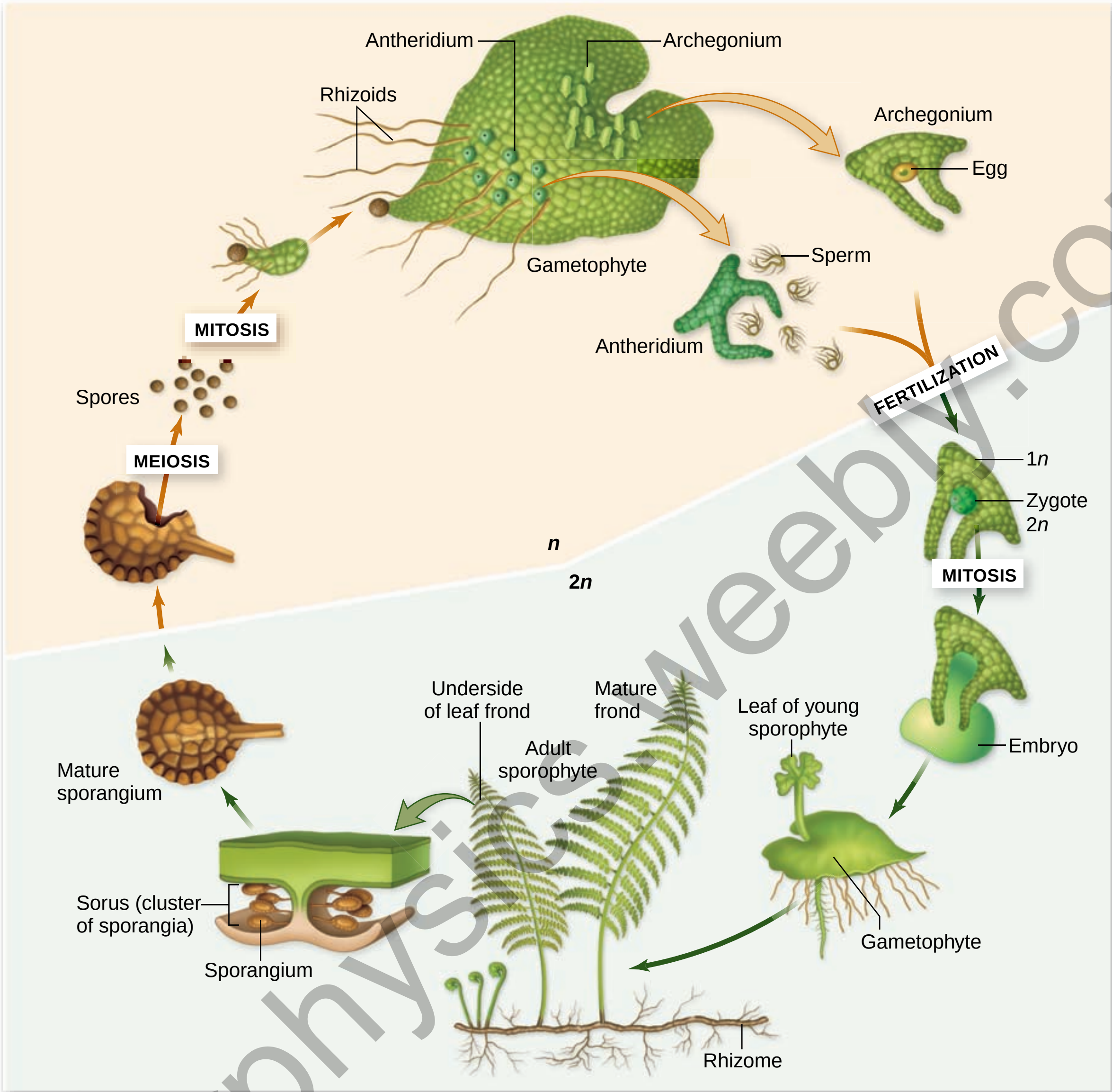


Figure 30.19 Life cycle of a typical fern. Both the gametophyte and sporophyte are photosynthetic and can live independently. Water is necessary for fertilization. Sperm are released on the underside of the gametophyte and swim in moist soil to neighboring gametophytes. Spores are dispersed by wind.

gametophytes, which rarely reach 6 mm in diameter, are both photosynthetic.

The fern life cycle (figure 30.19) differs from that of a moss primarily in the much greater development, independence, and dominance of the fern's sporophyte. The fern sporophyte is structurally more complex than the moss sporophyte, having vascular tissue and well-differentiated roots, stems, and leaves. The gametophyte, however, lacks the vascular tissue found in the sporophyte.

Fern morphology

Fern sporophytes, like horsetails, have rhizomes. Leaves, referred to as *fronds*, usually develop at the tip of the rhizome as tightly rolled-up coils ("fiddleheads") that unroll and expand (figure 30.20). Fiddleheads are considered a delicacy in several cuisines, but some species contain secondary compounds linked to stomach cancer.

Many fronds are highly dissected and feathery, making the ferns that produce them prized as ornamental garden plants. Some ferns, such as *Marsilea*, have fronds that resemble a four-leaf clover, but *Marsilea* fronds still begin as coiled fiddleheads. Other ferns produce a mixture of photosynthetic fronds and nonphotosynthetic reproductive fronds that tend to be brownish in color.

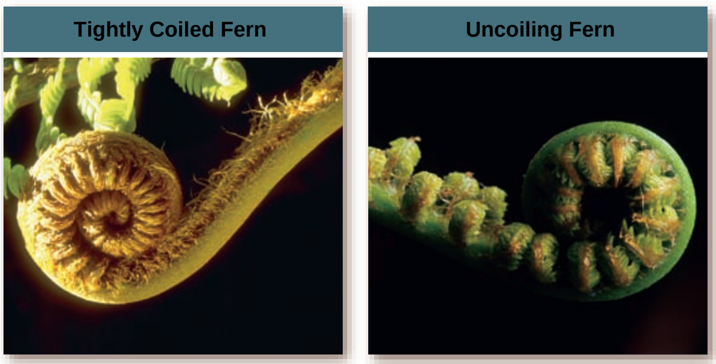


Figure 30.20 Fern "fiddlehead." Fronds develop in a coil and slowly unfold on ferns, including the tree fern fronds in these photos.

Fern reproduction

Ferns, produce distinctive sporangia, usually in clusters called **sori** (singular, *sorus*), typically on the underside of the fronds. Sori are often protected during their development by a transparent, umbrella-like covering. (At first glance, one might mistake the sori for an infection on the plant.) Diploid spore mother cells in each sporangium undergo meiosis, producing haploid spores.

At maturity, the spores are catapulted from the sporangium by a snapping action, and those that land in suitable damp locations may germinate, producing gametophytes that are often heart-shaped, are only one cell layer thick (except in the center), and have rhizoids that anchor them to their substrate. These rhizoids are not true roots because they lack vascular tissue, but they do aid in transporting water and nutrients from the soil. Flask-shaped archegonia and globular antheridia are produced on either the same or a different gametophyte. The multicellular archegonia provide some protection for the developing embryo.

The sperm formed in the antheridia have flagella, with which they swim toward the archegonia when water is present, often in response to a chemical signal secreted by the archegonia. One sperm unites with the single egg toward the base of an archegonium, forming a zygote. The zygote then develops into a new sporophyte, completing the life cycle (see figure 30.19).

The developing fern embryo has substantially more protection from the environment than a charophyte zygote, but it cannot enter a dormant phase to survive a harsh winter the way a seed plant embryo can. Although extant ferns do not produce seeds, seed fern fossils have been found that date back 365 million years. The seed ferns are not actually pterophytes, but gymnosperms. Of the seven tracheophyte phyla (table 30.1), only two—gymnosperms and angiosperms—produce seeds.

Learning Outcomes Review 30.6

Ferns and their relatives have a large and conspicuous sporophyte with vascular tissue. Many have well-differentiated roots, stems, and leaves (fronds). The gametophyte generation is small and lacks vascular tissue.

- ***What would be the advantage of silica deposits in stems, as is found in horsetails?***

TABLE 30.1 The Seven Phyla of Extant Vascular Plants

Phylum	Examples		Key Characteristics	Approximate Number of Living Species
SEEDLESS VASCULAR PLANTS				
Lycophyta	Club mosses		Homosporous or heterosporous. Sperm motile. External water necessary for fertilization. About 12–13 genera.	1150
Pterophyta	Ferns		Primarily homosporous (a few heterosporous). Sperm motile. External water necessary for fertilization. Leaves uncoil as they mature. Sporophytes and virtually all gametophytes are photosynthetic. About 365 genera.	11,000
	Horsetails		Homosporous. Sperm motile. External water necessary for fertilization. Stems ribbed, jointed, either photosynthetic or nonphotosynthetic. Leaves scalelike, in whorls; nonphotosynthetic at maturity. One genus.	15
	Whisk ferns		Homosporous. Sperm motile. External water necessary for fertilization. No differentiation between root and shoot. No leaves; one of the two genera has scalelike extensions and the other leaflike appendages.	6

(Continued on next page)

TABLE 30.1 The Seven Phyla of Extant Vascular Plants, *continued*

Phylum	Examples		Key Characteristics	Approximate Number of Living Species
S E E D P L A N T S				
Coniferophyta	Conifers (including pines, spruces, firs, yews, redwoods, and others)		Heterosporous seed plants. Sperm not motile; conducted to egg by a pollen tube. Leaves mostly needlelike or scalelike. Trees, shrubs. About 50 genera. Many produce seeds in cones.	601
Cycadophyta	Cycads		Heterosporous. Sperm flagellated and motile but confined within a pollen tube that grows to the vicinity of the egg. Palmlike plants with pinnate leaves. Secondary growth slow compared with that of the conifers. Ten genera. Seeds in cones.	206
Gnetophyta	Gnetophytes		Heterosporous. Sperm not motile; conducted to egg by a pollen tube. The only gymnosperms with vessels. Trees, shrubs, vines. Three very diverse genera *(Ephedra, Gnetum, Welwitschia).*	65
Ginkgophyta	*Ginkgo*		Heterosporous. Sperm flagellated and motile but conducted to the vicinity of the egg by a pollen tube. Deciduous tree with fan-shaped leaves that have evenly forking veins. Seeds resemble a small plum with fleshy, foul-smelling outer covering. One genus.	1
Anthophyta	Flowering plants (angiosperms)		Heterosporous. Sperm not motile; conducted to egg by a pollen tube. Seeds enclosed within a fruit. Leaves greatly varied in size and form. Herbs, vines, shrubs, trees. About 14,000 genera.	250,000

30.7 *The Evolution of Seed Plants*

Learning Outcomes

1. ***List the evolutionary advantages of seeds.***
2. ***Distinguish between pollen and sperm in seed plants.***

The history of the land plants is replete with evolutionary innovations allowing the ancestors of aquatic algae to colonize the harsh and varied terrestrial terrains. Early innovations made survival on land possible, later followed by an explosion of plant life that continues to change the land and atmosphere, and support terrestrial animal life. Seed-producing plants have come to dominate the terrestrial landscape over the last several hundred million years. Much of the remarkable success of seed plants, both gymnosperms and angiosperms, can be attributed to the evolution of the seed, an innovation that protects and provides food for delicate embryos. Seeds allow embryos to "stop the clock" and germinate after a harsh winter or extremely dry season has passed. Fruits, a later innovation, enhanced the dispersal of embryos across a broader landscape.

Seed plants, which have additional embryo protection, first appeared about 305 to 465 MYA and were the ancestors of gymnosperms and angiosperms. Seed plants appear to have evolved from spore-bearing plants known as **progymnosperms.** Progymnosperms shared several features with modern gymnosperms, including secondary vascular tissues (which allow for an increase in girth later in development). Some progymnosperms had leaves. Their reproduction was very simple, and it is not certain which particular group of progymnosperms gave rise to seed plants.

The seed protects the embryo

From an evolutionary and ecological perspective, the seed represents an important advance. The embryo is protected by an extra layer or two of sporophyte tissue called the **integument,** creating the **ovule** (figure 30.21). Within the ovule, the megasporangium divides meiotically, producing a haploid megaspore. The megaspore produces the egg that combines with the sperm, resulting in the zygote. Seeds also contain a food supply for the developing embryo.

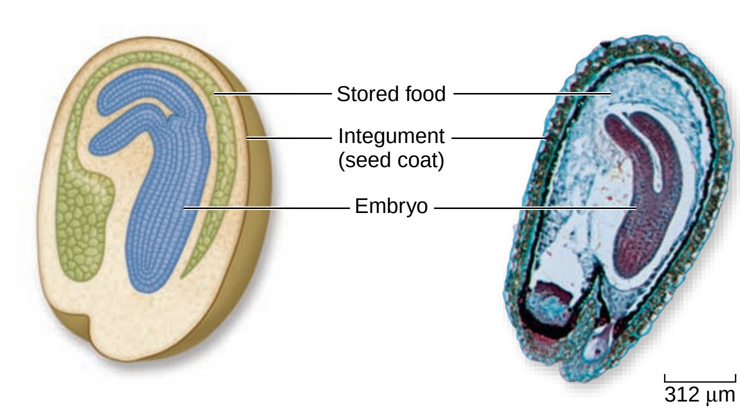


Figure 30.21 Cross-section of an ovule.

During development, the integuments harden to produce the seed coat. In addition to protecting the embryo from drought, the seed can be easily dispersed. Perhaps even more significantly, the presence of seeds introduces into the life cycle a dormant phase that allows the embryo to survive until environmental conditions are favorable for further growth.

A pollen grain is the male gametophyte

Seed plants produce two kinds of gametophytes—male and female—each of which consists of just a few cells. Pollen grains, multicellular male gametophytes, are conveyed to the egg in the female gametophyte by wind or by a pollinator. In some seed plants, the sperm moves toward the egg through a growing **pollen tube.** This eliminates the need for external water. In contrast to the seedless plants, the whole male gametophyte, rather than just the sperm, moves to the female gametophyte.

A female gametophyte forms within the protection of the integuments, collectively forming the ovule. In angiosperms, the ovules are completely enclosed within additional diploid sporophyte tissue. The ovule and the surrounding, protective tissue are called the ovary. The ovary develops into the fruit.

Learning Outcomes Review 30.7

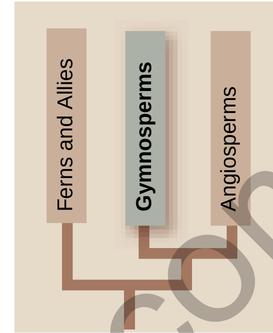
A common ancestor that had seeds gave rise to the gymnosperms and the angiosperms. Seeds protect the embryo, aid in dispersal, and can allow for an extended pause in the life cycle. Seed plants produce male and female gametophytes; the male gametophyte is a pollen grain, which is carried to the female gametophyte by wind or other means. The sperm is within the pollen grain.

- ***Why is water not essential for fertilization in seed plants?***

30.8 *Gymnosperms: Plants with "Naked Seeds"*

Learning Outcomes

1. *Describe the distinguishing features of a gymnosperm.*
2. *List the four groups of living gymnosperms.*



Seeds distinguish the gymnosperms from the pterophytes. There are four groups of living **gymnosperms,** namely coniferophytes, cycadophytes, gnetophytes, and ginkgophytes, all of which lack the flowers and fruits of angiosperms. In all of them, the ovule, which becomes a seed, rests exposed on a scale (a modified shoot or leaf) and is not completely enclosed by sporophyte tissues at the time of pollination. The name *gymnosperm* literally means "naked seed." Although the ovules are naked at the time of pollination, the seeds of gymnosperms are sometimes enclosed by other sporophyte tissues by the time they are mature.

Details of reproduction vary somewhat in gymnosperms, and their forms vary greatly. For example, cycads and *Ginkgo* have motile sperm, whereas conifers and gnetophytes have sperm with no flagella. All sperm are carried within a pollen tube. The female cones range from tiny, woody structures weighing less than 25 g and having a diameter of a few millimeters, to massive structures produced in some cycads, weighing more than 45 kg and growing to lengths of more than a meter.

Conifers are the largest gymnosperm phylum

The most familiar gymnosperms are **conifers** (phylum Coniferophyta), which include pines (figure 30.22), spruces, firs, cedars, hemlocks, yews, larches, cypresses, and others. The coastal redwood *(Sequoia sempervirens)*, a conifer native to northwestern California and southwestern Oregon, is the tallest living vascular plant; it may attain a height of nearly 100 m (300 ft). Another conifer, the bristlecone pine *(Pinus longaeva)* of the White Mountains of California, is the oldest living tree; one specimen is 4900 years of age.

Conifers are found in the colder temperate and sometimes drier regions of the world. Various species are sources of timber, paper, resin, taxol (used to treat cancer), and other economically important products.

Pines are an exemplary conifer genus

More than 100 species of pines exist today, all native to the northern hemisphere, although the range of one species does extend a

Figure 30.22 Conifers. Longleaf pines, *Pinus palustris*, in Florida are representative of the Coniferophyta, the largest phylum of gymnosperms.

little south of the equator. Pines and spruces, which belong to the same family, are members of the vast coniferous forests that lie between the arctic tundra and the temperate deciduous forests and prairies to their south. During the past century, pines have been extensively planted in the southern hemisphere.

Pine morphology

Pines have tough, needlelike leaves produced mostly in clusters of two to five. Among the conifers, only pines have clustered leaves. The leaves, which have a thick cuticle and recessed stomata, represent an evolutionary adaptation for retarding water loss. This strategy is important because many of the trees grow in areas where the topsoil is frozen for part of the year, making it difficult for the roots to obtain water.

The leaves and other parts of the sporophyte have canals into which surrounding cells secrete resin. The resin deters insect and fungal attacks. The resin of certain pines is harvested commercially for its volatile liquid portion, called *turpentine*, and for the solid *rosin*, which is used on bowed stringed instruments. The wood of pines lacks some of the more rigid cell types found in other trees, and it is considered a "soft" rather than a "hard" wood. The thick bark of pines is an adaptation for surviving fires and subzero temperatures. Some cones actually depend on fire to open them, releasing seeds to reforest burned areas.

Reproductive structures

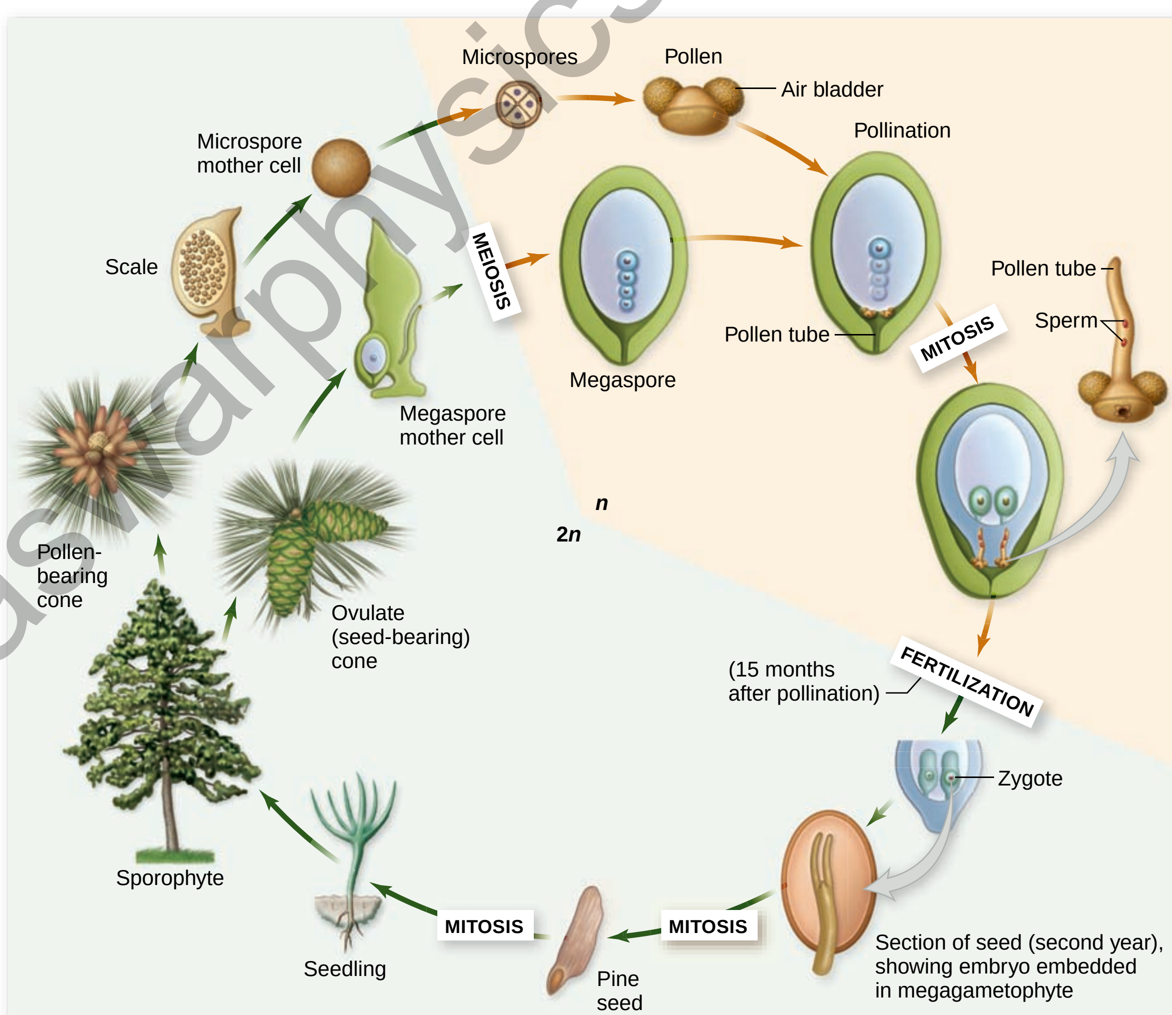
All seed plants produce two types of spores that give rise to two types of gametophytes (figure 30.23). The male gametophytes (pollen grains) of pines develop from microspores, which are produced in male cones that develop in clusters of 30 to 70, typically at the tips of the lower branches; there may be hundreds of such clusters on any single tree.

The male pine cones generally are 1 to 4 cm long and consist of small, papery scales arranged in a spiral or in whorls. A pair of microsporangia form as sacs within each scale. Numerous microspore mother cells in the microsporangia undergo meiosis, each becoming four microspores. The microspores develop into four-celled pollen grains with a pair of air sacs that give them added buoyancy when released into the air. A single cluster of male pine cones may produce more than a million pollen grains.

Female pine cones typically are produced on the upper branches of the same tree that produces male cones. Female cones are larger than male cones, and their scales become woody.

Two ovules develop toward the base of each scale. Each ovule contains a megasporangium called the **nucellus.** The nucellus itself is completely surrounded by a thick layer of cells called the integument that has a small opening (the **micropyle**) toward one end. One of the layers of the integument later

Figure 30.23
Life cycle of a typical pine. The male and female gametophytes are dramatically reduced in size in these plants. Wind generally disperses the male gametophyte (pollen), which produces sperm. Pollen tube growth delivers the sperm to the egg on the female cone. Additional protection for the embryo is provided by the integument, which develops into the seed coat.



becomes the seed coat. A single megaspore mother cell within each megasporangium undergoes meiosis, becoming a row of four megaspores. Three of the megaspores break down, but the remaining one, over the better part of a year, slowly develops into a female gametophyte. The female gametophyte at maturity may consist of thousands of cells, with two to six archegonia formed at the micropylar end. Each archegonium contains an egg so large it can be seen without a microscope.

Fertilization and seed formation

Female cones usually take two or more seasons to mature. At first they may be reddish or purplish in color, but they soon turn green, and during the first spring, the scales spread apart. While the scales are open, pollen grains carried by the wind drift down between them, some catching in sticky fluid oozing out of the micropyle. The pollen grains within the sticky fluid are slowly drawn down through the micropyle to the top of the nucellus, and the scales close shortly thereafter.

The archegonia and the rest of the female gametophyte are not mature until about a year later. While the female gametophyte is developing, a pollen tube emerges from a pollen grain at the bottom of the micropyle and slowly digests its way through the nucellus to the archegonia. During growth of the pollen tube, one of the pollen grain's four cells, the *generative cell*, divides by mitosis, with one of the resulting two cells dividing once more. These last two cells function as sperm. The germinated pollen grain with its two sperm is the mature male gametophyte, a very limited haploid phase compared with fern gametophytes.

About 15 months after pollination, the pollen tube reaches an archegonium and discharges its contents into it. One sperm unites with the egg, forming a zygote. The other sperm and cells of the pollen grain degenerate. The zygote develops into an embryo within the seed. After dispersal and germination of the seed, the young sporophyte of the next generation develops into a tree.

Cycads resemble palms, but are not flowering plants

Cycads (phylum Cycadophyta) are slow-growing gymnosperms of tropical and subtropical regions. The sporophytes of most of the 100 known species resemble palm trees (figure 30.24*a*) with trunks that can attain heights of 15 m or more. Unlike palm trees, which are flowering plants, cycads produce cones and have a life cycle similar to that of pines.

The female cones, which develop upright among the leaf bases, are huge in some species and can weigh up to 45 kg. The sperm of cycads, although formed within a pollen tube, are released within the ovule to swim to an archegonium. These sperm are the largest sperm cells among all living organisms. Several species of cycads are facing extinction in the wild and soon may exist only in botanical gardens.

Gnetophytes have xylem vessels

There are three genera and about 65 living species of gnetophytes (phylum Gnetophyta). They are the only gymnosperms with vessels in their xylem. **Vessels** are a particularly efficient conducting cell type that is a common feature in angiosperms.

The members of the three genera differ greatly from one another in form. One of the most bizarre of all plants is *Welwitschia*, which occurs in the Namib and Mossamedes deserts of southwestern Africa (figure 30.24*b*). The stem is shaped like a large, shallow cup that tapers into a taproot below the surface. It has two strap-shaped, leathery leaves that grow continuously from their base, splitting as they flap in the wind. The reproductive structures of *Welwitschia* are conelike, appear toward the bases of the leaves around the rims of the stems, and are produced on separate male and female plants.

More than half of the gnetophyte species are in the genus *Ephedra*, which is common in arid regions of the western United States and Mexico. Species are found on every continent except Australia. The plants are shrubby, with stems that superficially resemble those of horsetails, being jointed and having tiny, scalelike leaves at each node. Male and female reproductive structures may be produced on the same or different plants.

The drug ephedrine, widely used in the treatment of respiratory problems, was in the past extracted from Chinese species of *Ephedra*, but it has now been largely replaced with synthetic preparations (pseudoephedrine). Because ephedrine found in herbal remedies for weight loss was linked to strokes and heart attacks, it was withdrawn from the market in April of 2004. Sales restrictions were placed on pseudoephedrine-containing products in 2006 because it can be used to manufacture the illegal drug methamphetamine.

a. ***b.*** ***c.***

Figure 30.24 Three phyla of gymnosperms. ***a.*** A cycad, *Cycas circinalis.* ***b.*** *Welwitschia mirabilis* represents one of the three genera of gnetophytes. ***c.*** Maidenhair tree, *Ginkgo biloba*, the only living representative of the phylum Ginkgophyta.

The best known species of the third genus, *Gnetum*, is a tropical tree, but most species are vinelike. All species have broad leaves similar to those of angiosperms. One *Gnetum* species is cultivated in Java for its tender shoots, which are cooked as a vegetable.

Only one species of the ginkgophytes remains extant

The fossil record indicates that members of the ginkgophytes (phylum Ginkgophyta) were once widely distributed, particularly in the northern hemisphere; today, only one living species, *Ginkgo biloba*, remains (figure 30.24*c*). This tree, which sheds its leaves in the fall, was first encountered by Europeans in cultivation in Japan and China; it apparently no longer exists in the wild.

Like the sperm of cycads, those of *Ginkgo* have flagella. The ginkgo is **dioecious**—that is, the male and female reproductive structures are produced on separate trees. The fleshy outer coverings of the seeds of female ginkgo plants exude the foul smell of rancid butter, caused by the presence of butyric and isobutyric acids. As a result, male plants vegetatively propagated from shoots are preferred for cultivation. Because of its beauty and resistance to air pollution, *Ginkgo* is commonly planted along city streets.

Learning Outcomes Review 30.8

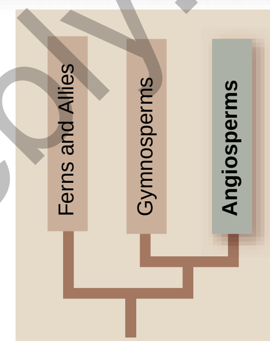
Gymnosperms are mostly cone-bearing seed plants. In gymnosperms, the ovules are not completely enclosed by sporophyte tissue at pollination, and thus have "naked seeds." The four groups of gymnosperms are conifers, cycads, gnetophytes, and ginkgophytes.

- *What adaptation do conifers exhibit to capture wind-borne pollen?*

30.9 *Angiosperms: The Flowering Plants*

Learning Outcomes

1. *List the defining features of angiosperms.*
2. *Describe the roles of some animals in the angiosperm life cycle.*
3. *Explain double fertilization and its outcome.*



The 270,000 known species of flowering plants are called **angiosperms** because their ovules, unlike those of gymnosperms, are enclosed within diploid tissues at the time of pollination. The *carpel*, a modified leaf that encapsulates seeds, develops into the fruit, a unique angiosperm feature (figure 30.25). Although some gymnosperms, including the yew (*Taxus* spp.), have fleshlike tissue around their seeds, it is of a different origin and not a true fruit.

Angiosperm origins are a mystery

The origins of the angiosperms puzzled even Darwin (he referred to their origin as an "abominable mystery"). Recent fossil pollen and plants accompanied by molecular sequence data have provided exciting clues about basal angiosperms, indicating origins as early as 145 to 208 MYA.

In the remote Liaoning province of China, a complete angiosperm fossil that is at least 125 million years old has been found (figure 30.26). The fossil may represent a new, basal, and

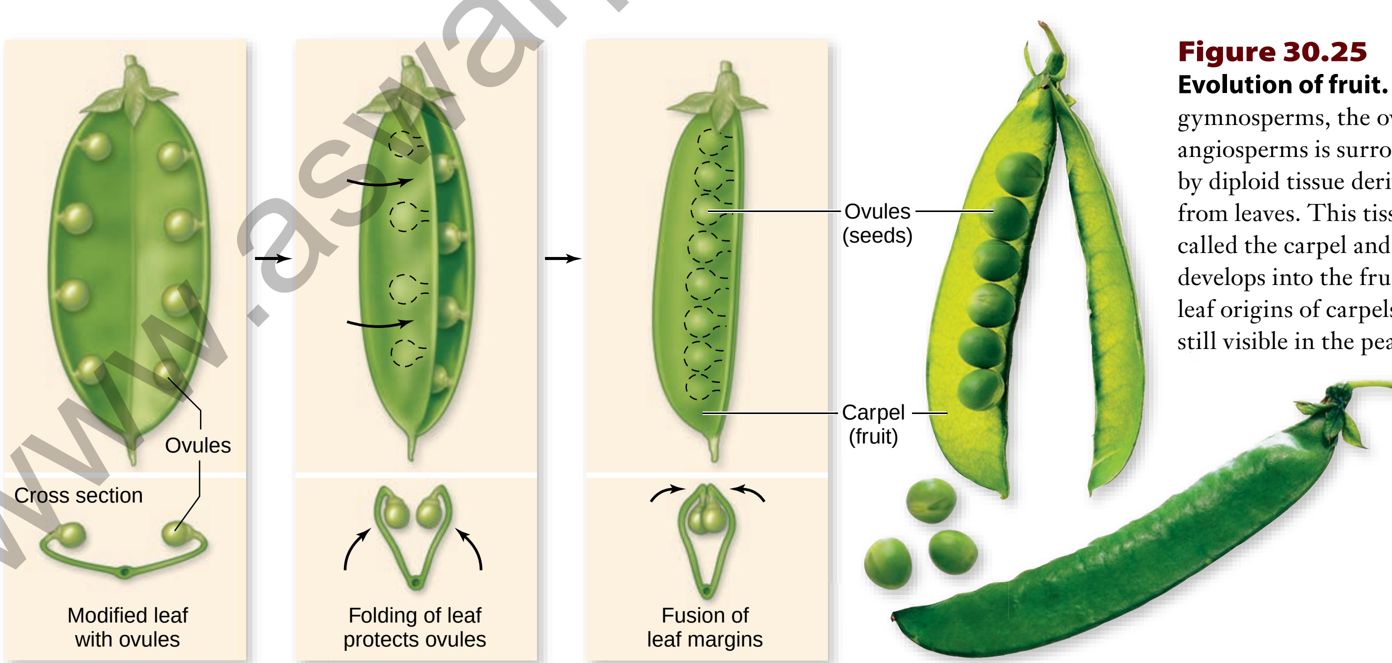


Figure 30.25
Evolution of fruit. Unlike gymnosperms, the ovule of angiosperms is surrounded by diploid tissue derived from leaves. This tissue is called the carpel and develops into the fruit. The leaf origins of carpels are still visible in the pea pod.

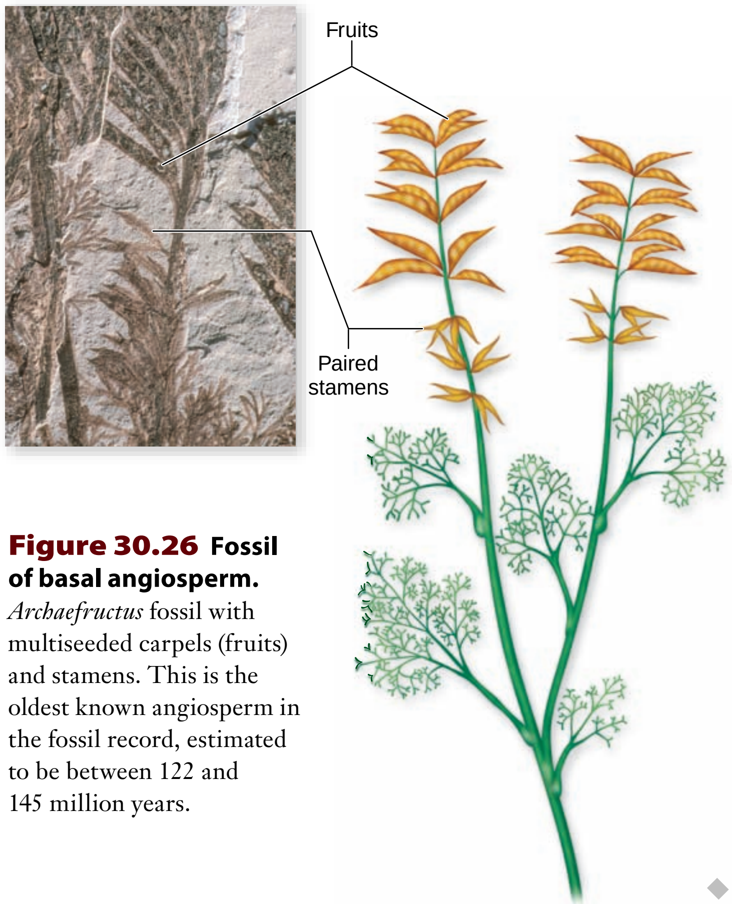


Figure 30.26 Fossil of basal angiosperm. *Archaefructus* fossil with multiseeded carpels (fruits) and stamens. This is the oldest known angiosperm in the fossil record, estimated to be between 122 and 145 million years.

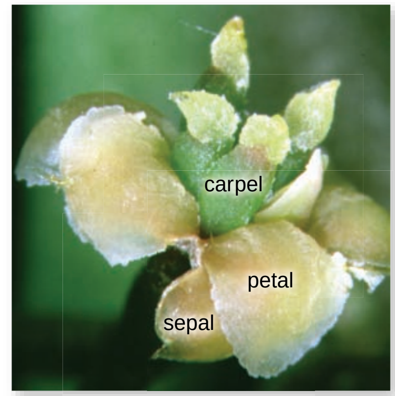


Figure 30.27 An ancient living angiosperm, *Amborella trichopoda*. This plant is believed to be the closest living relative to the original angiosperm.

extinct angiosperm family, Archaefructaceae, with two species: *Archaefructus liaoningensis* and *A. sinensis*. *Archaefructus* was an herbaceous, aquatic plant. This family is proposed to be the sister clade to all other angiosperms, but there is a lively debate about the validity of this claim.

Archaefructus fossils have both male and female reproductive structures; however, they lack the sepals and petals that evolved in later angiosperms to attract pollinators. The fossils were so well preserved that fossil pollen could be examined using scanning electron microscopy. Although *Archaefructus* is ancient, it is unlikely to be the very first angiosperm. Still, the incredibly well-preserved fossils provide valuable detail on angiosperms in the Upper Jurassic to Lower Cretaceous period, when dinosaurs roamed the Earth.

Consensus has also been growing on the most basal living angiosperm—*Amborella trichopoda* (figure 30.27). *Amborella*, with small, cream-colored flowers, is even more primitive than water lilies. This small shrub, found only on the island of New Caledonia in the South Pacific, is the last remaining species of the earliest extant lineage of the angiosperms that arose about 135 MYA.

Although *Amborella* is not the original angiosperm, it is sufficiently close that studying its reproductive biology may help us understand the early radiation of the angiosperms. The angiosperm phylogeny reflects an evolutionary hypothesis that is driving new research on angiosperm origins (figure 30.28).

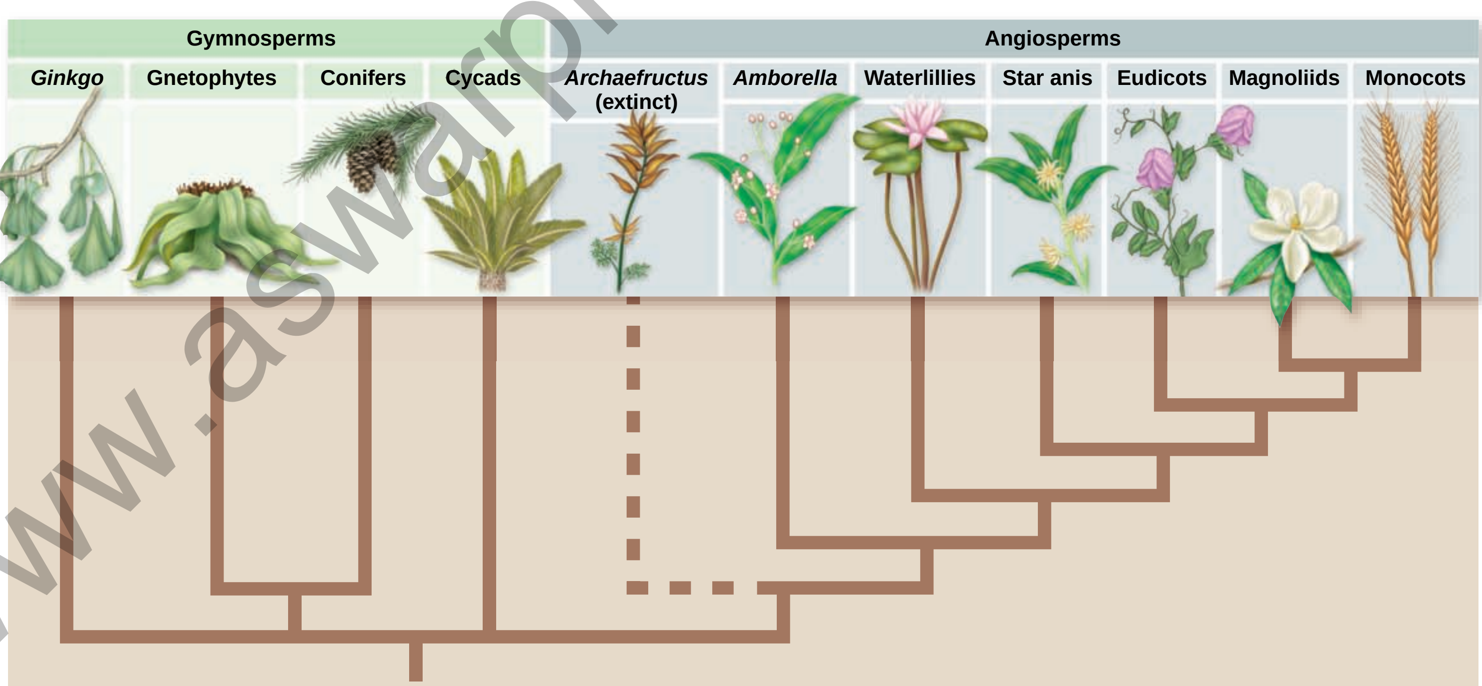


Figure 30.28 *Archaefructus* may be the sister clade to all other angiosperms. All members of the *Archaefructus* lineage are extinct, leaving *Amborella* as the most basal, living angiosperm. Gymnosperms species labels are shaded green.

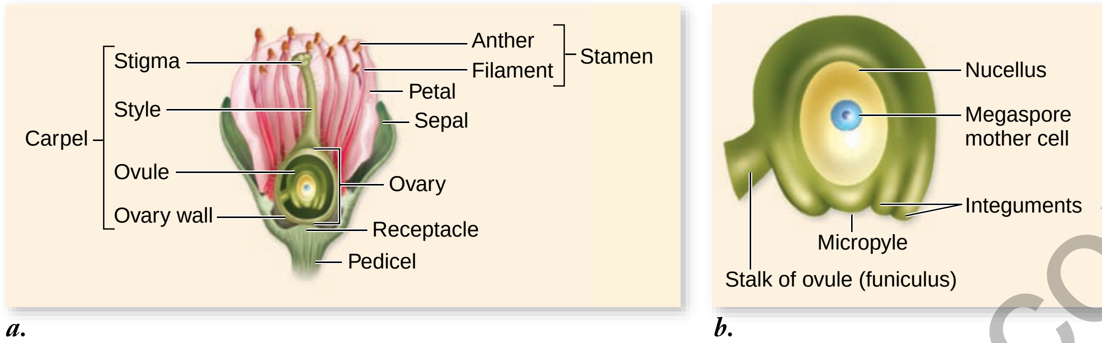


Figure 30.29 Diagram of an angiosperm flower. ***a.*** The main structures of the flower are labeled. ***b.*** Details of an ovule. The ovary as it matures will become a fruit; as the ovule's outer layers (integuments) mature, they will become a seed coat.

Flowers house the gametophyte generation of angiosperms

Flowers are considered to be modified stems bearing modified leaves. Regardless of their size and shape, they all share certain features (figure 30.29). Each flower originates as a **primordium** that develops into a bud at the end of a stalk called a pedicel. The pedicel expands slightly at the tip to form the receptacle, to which the remaining flower parts are attached.

Flower morphology

The other flower parts typically are attached in circles called **whorls.** The outermost whorl is composed of **sepals.** Most flowers have three to five sepals, which are green and somewhat leaflike. The next whorl consists of **petals** that are often colored, attracting pollinators such as insects, birds, and some small mammals. The petals, which also commonly number three to five, may be separate, fused together, or missing altogether in wind-pollinated flowers.

The third whorl consists of **stamens** and is collectively called the androecium. This whorl is where the male gametophytes, pollen, are produced. Each stamen consists of a pollen-bearing **anther** and a stalk called a **filament,** which may be missing in some flowers.

At the center of the flower is the fourth whorl, the **gynoecium,** where the small female gametophytes are housed; the gynoecium consists of one or more **carpels.** The first carpel is believed to have been formed from a leaflike structure with ovules along its margins. Primitive flowers can have several to many separate carpels, but in most flowers, two to several carpels are fused together. Such fusion can be seen in an orange sliced in half; each segment represents one carpel.

Structure of the carpel

A carpel has three major regions (see figure 30.29*a*). The **ovary** is the swollen base, which contains from one to hundreds of ovules; the ovary later develops into a **fruit.** The tip of the carpel is called a **stigma.** Most stigmas are sticky or feathery, causing pollen grains that land on them to adhere. Typically, a neck or stalk called a **style** connects the stigma and the ovary; in some flowers, the style may be very short or even missing.

Many flowers have nectar-secreting glands called *nectaries*, often located toward the base of the ovary. Nectar is a fluid containing sugars, amino acids, and other molecules that attracts insects, birds, and other animals to flowers.

Most species use flowers to attract pollinators and reproduce

Eudicots (about 175,000 species) include the great majority of familiar angiosperms—almost all kinds of trees and shrubs, snapdragons, mints, peas, sunflowers, and other plants. Monocots (about 65,000 species) include the lilies, grasses, cattails, palms, agaves, yuccas, orchids, and irises and share a common ancestor with the eudicots (see figure 30.28). Some of the monocots, including maize, rely on wind rather than pollinators to reproduce.

The angiosperm life cycle includes double fertilization

During development of a flower bud, a single megaspore mother cell in the ovule undergoes meiosis, producing four megaspores (figure 30.30). In most flowering plants, three of the megaspores soon disappear; the nucleus of the remaining megaspore divides mitotically, and the cell slowly expands until it becomes many times its original size.

The female gametophyte

While the expansion of the megaspore is occurring, each of the daughter nuclei divides twice, resulting in eight haploid nuclei arranged in two groups of four. At the same time, two layers of the ovule, the integuments, differentiate and become the *seed coat* of a seed. The integuments, as they develop, form the micropyle, a small gap or pore at one end that was described earlier (see figure 30.29b).

One nucleus from each group of four migrates toward the center, where they function as polar nuclei. Polar nuclei may fuse together, forming a single diploid nucleus, or they may form a single cell with two haploid nuclei. Cell walls also form around the remaining nuclei. In the group closest to the micropyle, one cell functions as the egg; the other two nuclei are called synergids. At the other end, the three cells are now called antipodals; they have no apparent function and eventually break down and disappear.

The large sac with eight nuclei in seven cells is called an embryo sac; it constitutes the female gametophyte. Although it is completely dependent on the sporophyte for nutrition, it is a multicellular, haploid individual.

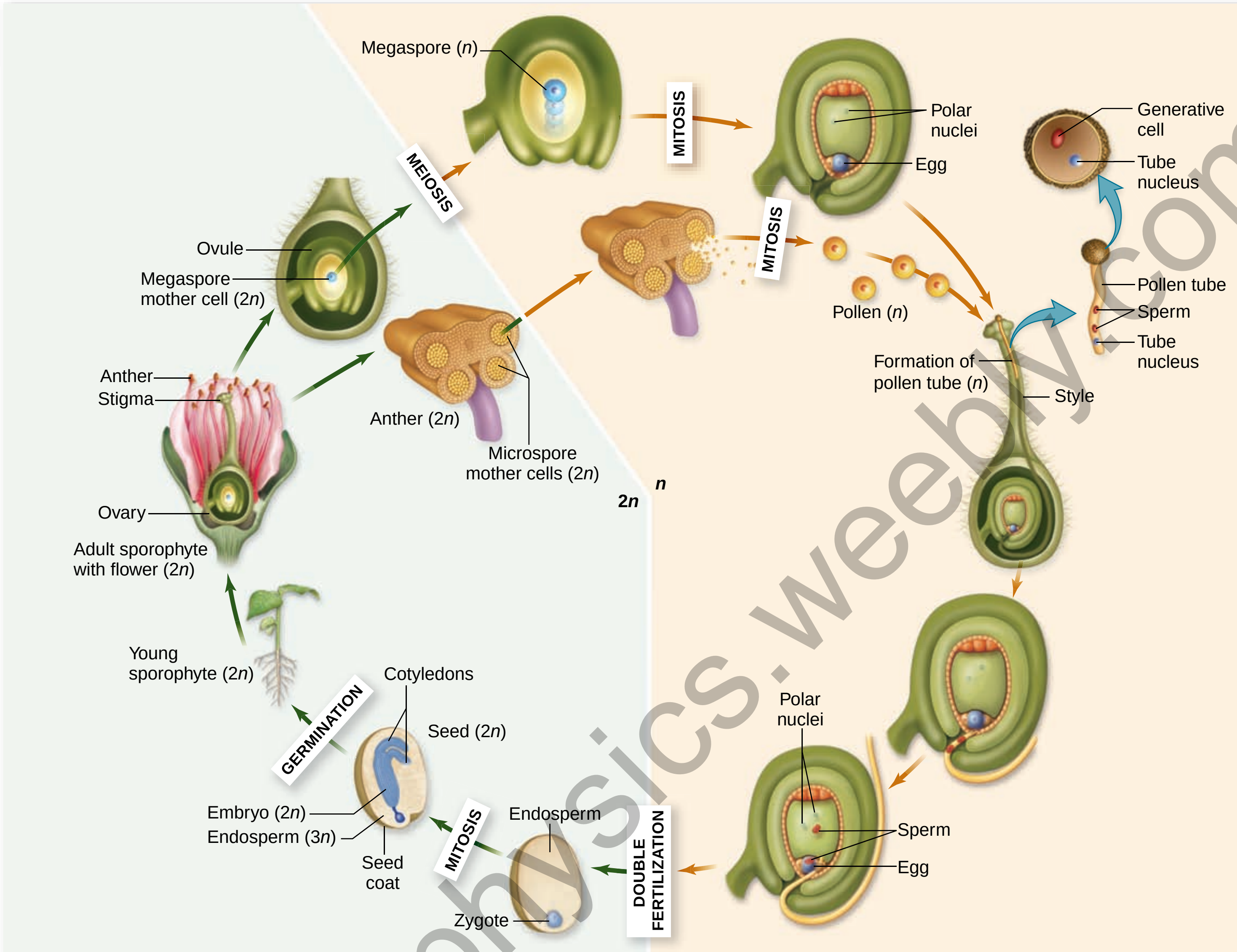


Figure 30.30 Life cycle of a typical angiosperm. As in pines, external water is no longer required for fertilization. In most species of angiosperms, animals carry pollen to the carpel. The outer wall of the carpel forms the fruit, which often entices animals to disperse the seed.

Pollen production

While the female gametophyte is developing, a similar but less complex process takes place in the anthers (see figure 30.30). Most anthers have patches of tissue (usually four) that eventually become chambers lined with nutritive cells. The tissue in each patch is composed of many diploid microspore mother cells that undergo meiosis more or less simultaneously, each producing four microspores.

The four microspores at first remain together as a quartet, or tetrad, and the nucleus of each microspore divides once; in most species, the microspores of each quartet then separate. At the same time, a two-layered wall develops around each microspore. As the microspore-containing anther continues to mature, the wall between adjacent pairs of chambers breaks down, leaving two larger sacs. At this point, the binucleate microspores have become pollen grains.

The outer pollen grain wall layer often becomes beautifully sculptured, and it contains chemicals that may react with others in a stigma to signal whether development of the male gametophyte should proceed to completion. The pollen grain has areas called *apertures*, through which a pollen tube may later emerge.

Pollination and the male gametophyte

Pollination is simply the mechanical transfer of pollen from its source (an anther) to a receptive area (the stigma of a flowering plant). Most pollination takes place between flowers of different plants and is brought about by insects, wind, water, gravity, bats, and other animals. In as many as one-quarter of all angiosperms, however, a pollen grain may be deposited directly on the stigma of its own flower, and self-pollination occurs. Pollination may or may not be followed by *fertilization*, depending on the genetic compatibility of the pollen grain and the flower on whose stigma it has landed.

If the stigma is receptive, the pollen grain's dense cytoplasm absorbs substances from the stigma and bulges through an aperture. The bulge develops into a pollen tube that responds to chemical and mechanical stimuli that guide it to the embryo sac. It follows a diffusion gradient of the chemicals and grows down through the style and into the micropyle. The pollen tube usually takes several hours to two days to reach the micropyle, but in a few instances, the journey may take up to a year. Pollen tube growth is more rapid in angiosperms than gymnosperms. Rapid pollen tube growth rate is an innovation that is believed to have preceded fruit development and been essential in the origins of angiosperms (see figure 30.31)

One of the pollen grain's two cells, the *generative cell*, lags behind. Its nucleus divides in the pollen grain or in the pollen tube, producing two sperm cells. Unlike sperm in mosses, ferns, and some gymnosperms, the sperm of flowering plants have no flagella. At this point, the pollen grain with its tube and sperm has become a mature male gametophyte.

Double fertilization and seed production

As the pollen tube enters the embryo sac, it destroys a synergid in the process and then discharges its contents. Both sperm are functional, and an event called **double fertilization** follows. One sperm unites with the egg and forms a zygote, which develops into an embryo sporophyte plant. The other sperm and the two polar nuclei unite, forming a triploid primary endosperm nucleus.

The primary endosperm nucleus begins dividing rapidly and repeatedly, becoming triploid endosperm tissue that may soon consist of thousands of cells. Endosperm tissue can become an extensive part of the seed in grasses such as corn, and it provides nutrients for the embryo in most flowering plants (see figure 37.11).

Until recently, the nutritional, triploid endosperm was believed to be the ancestral state in angiosperms. A recent analysis of extant, basal angiosperms revealed that diploid endosperms were also common. The female gametophyte in these species has four, not eight nuclei. At the moment, it is unclear whether diploid or triploid endosperms are the most primitive.

Inquiry question

? **If the endosperm failed to develop in a seed, how do you think the fitness of that seed's embryo would be affected? Explain your answer.**

Germination and growth of the sporophyte

As mentioned earlier, a seed may remain dormant for many years, depending on the species. When environmental conditions become favorable, the seed undergoes germination, and the young sporophyte plant emerges. Again depending on the species, the sporophyte may grow and develop for many years before becoming capable of reproduction, or it may quickly grow and produce flowers in a single growing season.

We present a more detailed description of reproduction in plants in chapter 42.

Learning Outcomes Review 30.9

Angiosperms are characterized by ovules that at pollination are enclosed within an ovary at the base of a carpel, a structure unique to the phylum; a fruit develops from the ovary. Evolutionary innovations of angiosperms include flowers to attract pollinators, fruits to protect embryos and aid in their dispersal, and double fertilization, which provides endosperm to help nourish the embryo.

- ***What advantage does an angiosperm gain by producing a fruit that animals eat?***

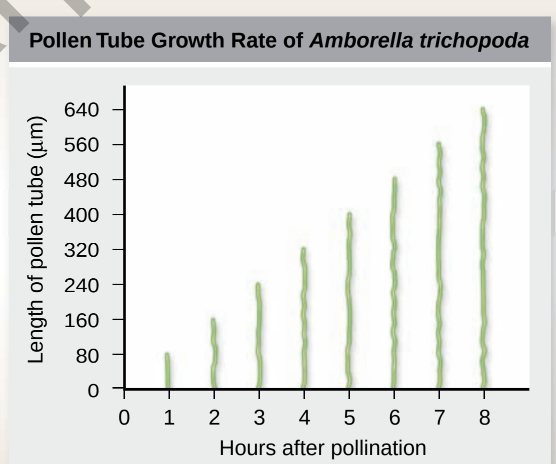
SCIENTIFIC THINKING

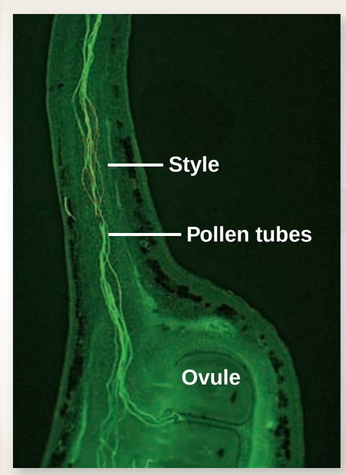
Hypothesis: *An increase in pollen tube growth accompanied angiosperm origins.*

Prediction: *The time from pollination to fertilization will be greater in gymnosperms than angiosperms that are sister to the ancestral angiosperm and also more derived angiosperms.*

Test: *Pollinate three angiosperm species, including* Amborella, *that are most closely related to the first angiosperm. At different time intervals, cut sections of the carpel and observe pollen tube position under a fluorescent microscope. Calculate and compare the rate of pollen tube growth with results published for gymnosperms and more derived angiosperms.*

Species	Pollen Tube Growth Rate (μm/hour)
Close relatives of ancestral angiosperm	
Amborella trichopoda	80
Nuphar polysepala	589
Austrobaileya scandens	271
Derived angiosperms	
Petunia inflata	900
Zea mays (maize)	10,000
Gymnosperms	
Gnetum gnemon	6
Ginkgo biloba	0.31





Conclusion: *An increase in pollen tube growth rate is found in angiosperms most closely related to the ancestral angiosperm, supporting the hypothesis.*

Further Experiments: *Develop a hypothesis to explain the difference in pollen tube growth rates among the tested angiosperms. Is there a correlation between the distance a pollen tube must travel to fertilize an egg and the rate of growth? How could you test your hypothesis?*

Figure 30.31 Rapid pollen tube growth accompanied the origin of angiosperms.

Chapter Review

30.1 Defining Plants

Land plants evolved from freshwater algae.

All green plants arose from a single freshwater green algal species (see figure 30.1). The charophytes are the sister clade of the land plants.

Green algae and the land plants are placed in the kingdom Viridiplantae.

Land plants have adapted to terrestrial life.

Land plants have two major characteristics: protected embryos and multicellular haploid and diploid phases. A waxy cuticle, stomata, and specialized cells for transport of water and minerals enhance survival.

Most multicellular Viridiplantae have haplodiplontic life cycles.

Plants have a haplodiplontic life cycle with multicellular diploid sporophytes and haploid gametophytes (see figure 30.2).

The haplodiplontic cycle produces alternation of generations.

The relative sizes of haploid and diploid generations vary.

As some plants became more complex, the sporophyte stage became the dominant phase.

30.2 Chlorophytes and Charophytes: Green Algae (see figure 30.5)

The chlorophytes gave rise to aquatic algae; the streptophytes include the group that gave rise to land plants.

Chlorophytes can be unicellular.

Unicellular chlorophytes include *Chlamydomonas*, which has two flagella, and *Chlorella*, which has no flagella and reproduces asexually.

Colonial chlorophytes have some cell specialization.

Volvox is an example of a colonial green alga; some cells specialize for producing gametes or for asexual reproduction.

Multicellular chlorophytes can have haplodiplontic life cycles.

Ulva has sporophyte and gametophyte generations; however, the chlorophytes did not give rise to land plants.

Charophytes are the closest relatives to land plants.

Both candidate Streptophyta clades—Charales and Coleochaetales—exhibit plasmodesmata, cytoplasmic links between cells. They also undergo mitosis and cytokinesis like terrestrial plants.

30.3 Bryophytes: Dominant Gametophyte Generation

Bryophytes are unspecialized but successful in many environments.

Bryophytes consist of three distinct clades: liverworts, mosses, and hornworts. Bryophytes do not have true roots or tracheids, but do have conducting cells for movement of water and nutrients.

In liverworts and mosses, the nonphotosynthetic sporophyte is nutritionally dependent on the gametophyte.

Liverworts are an ancient phylum.

The gametophyte of some liverworts is flattened and has lobes that resemble those of the liver. They produce upright structures that contain the gametangia.

Mosses have rhizoids and water-conducting tissue.

Mosses exhibit alternation of generations and have widespread distribution. Many are able to withstand droughts.

Hornworts developed stomata.

Stomata in the sporophyte can open and close to regulate gas exchange. The sporophyte is also photosynthetic.

30.4 Tracheophyte Plants: Roots, Stems, and Leaves (see table 30.1)

Vascular tissue allows for distribution of nutrients.

The evolution of tracheids allowed more efficient vascular systems to develop. This vascular tissue develops in the sporophyte.

Vascular plants have a much reduced gametophyte.

Tracheophytes include seven extant phyla grouped in three clades.

The vascular plants found today exist in three clades: lycophytes, pterophytes, and seed plants.

Stems evolved prior to roots.

Roots provide structural support and transport capability.

Leaves evolved more than once.

Lycophytes have small leaves called lycophylls that lack vascularization.

True leaves (euphylls) are found only in ferns and seed plants and have origins different from lycophylls.

Seeds are another innovation in some phyla.

Seeds are resistant structures that protect the embryo from desication and to some extent from predators.

30.5 Lycophytes: Dominant Sporophyte Generation and Vascular Tissue

Lycophyte ancestors were the earliest vascular plants and were among the first plants to have a dominant sporophyte generation.

30.6 Pterophytes: Ferns and Their Relatives (see figure 30.17)

Ancestors of the pterophytes gave rise to two clades: one line of ferns and horsetails, and a second line of ferns and whisk ferns.

Pterophytes require water for fertilization and are seedless.

Whisk ferns lost their roots and leaves secondarily.

The sporophyte of a whisk fern consists of evenly forking green stems without roots.

Horsetails have jointed stems with brushlike leaves.

Scalelike leaves of horsetail sporophytes emerge in a whorl. The stems have silica deposits in epidermal cells of their ribs.

Ferns have fronds that bear sori.

The leaves of ferns, called fronds, develop as tightly rolled coils that unwind to expand. Sporangia called sori develop on the underside of the fronds. The gametophyte is often heart shaped and can live independently.

30.7 The Evolution of Seed Plants

The seed protects the embryo.

An extra layer of sporophyte tissue surrounds the embryo, creating the ovule, which later hardens. The seed protects the embryo, helps it resist drying out, and allows a dormant stage that pauses the life cycle until environmental conditions are favorable.

A pollen grain is the male gametophyte.

The gametophytes of seed plants consist of only a few cells. Pollen grains are male gametophytes; each pollen grain contains sperm cells. Water is not required for fertilization. The female gametophyte develops within an ovule that forms the seed.

30.8 Gymnosperms: Plants with "Naked Seeds" (see figure 30.23)

Gymnosperms have ovules that are not completely enclosed in sporophyte (diploid) tissue at the time of pollination.

The four groups of gymnosperms are coniferophytes, cycadophytes, gnetophytes, and ginkgophytes; all lack flowers and true fruits.

Conifers are the largest gymnosperm phylum.

Conifers include pines, spruces, firs, cedars, and many other groups. Both the tallest and the oldest vascular plants are conifers.

Pines are an exemplary conifer genus.

Pines have tough, needlelike leaves in clusters of two to five. They produce male and female cones.

In the male cones, microspore mother cells in the microsporangia give rise to microspores that then develop into four-celled pollen grains, the male gametophytes.

In the female cones, a megasporangium (nucellus) produces a single megaspore mother cell that becomes four megaspores; three of these break down, and the remaining one develops into a female gametophyte, which produces archegonia that carry eggs.

Upon fertilization, a pollen tube emerges from the pollen grain and grows through the nucellus. Eventually two sperm cells migrate through the tube, and one unites with the egg; the other disintegrates.

Cycads resemble palms, but are not flowering plants.

Most cycads can reach heights of 15 m or more. Cycads, unlike palms, produce cones; in some species the female cones are huge. Their life cycle is like that of conifers.

Gnetophytes have xylem vessels.

Xylem vessels, a common feature in angiosperms, are highly efficient conducting cells. Gnetophytes are the only gymnosperms that have them.

This group includes the strange *Welwitschia* genus of southwestern Africa and the numerous worldwide *Ephedra* species.

Only one species of the ginkgophytes remains extant.

Ginkgo biloba is a gymnosperm with broad leaves that it sheds in the fall. It is dioecious, and the fleshy seeds of the female tree have a foul odor.

30.9 Angiosperms: The Flowering Plants (see figure 30.28)

Angiosperms are distinct from gymnosperms and other plants because their ovules are enclosed within diploid tissue called the ovary at the time of fertilization, and they form fruits.

Angiosperm origins are a mystery.

No one is certain how the angiosperms arose, although the extinct family Archaefructaceae may have been a sister clade. The earliest extant angiosperm appears to be *Amborella trichopoda*, found on the island of New Caledonia.

Flowers house the gametophyte generation of angiosperms.

Flowers are considered to be modified stems that bear modified leaves. Flower parts are organized into four whorls: sepals, petals, androecium, and gynoecium (see figure 30.29*a*).

The male androecium consists of the stamens where haploid pollen, the male gametophyte, is produced.

The female gynoecium consists of one or more carpels that contain the female gametophyte. The carpel has three major regions: the ovary, which later becomes the fruit; the stigma, which is the tip of the carpel; and the style, a stalk that connects the stigma and ovary.

Most species use flowers to attract pollinators and reproduce.

Many angiosperm flowers have nectaries near the base of the ovary that produce nectar containing nutrients and other molecules. Nectar and scent attracts animal pollinators, which carry pollen from one flower to another; some angiosperms are wind pollinated, however.

The angiosperm life cycle includes double fertilization.

The megaspore produces eight haploid nuclei. The female gametophyte consists of a large embryo sac with the eight nuclei in seven cells. The egg and the two polar nuclei (in a single cell) are most important.

After landing on a receptive stigma, a pollen grain develops a pollen tube that grows toward the embryo sac. Eventually, two sperm pass through this tube. One fuses with the egg to form a zygote, and the other unites with the polar bodies to form a triploid endosperm nucleus that develops into endosperm to nourish the embryo.

Review Questions

UNDERSTAND

1. Which of the following plant structures is not matched to its correct function?
   a. Stomata—allow gas transfer
   b. Tracheids—allow the movement of water and minerals
   c. Cuticle—prevents desication
   d. All of the above are matched correctly.
2. Which of the following genera most likely directly gave rise to the land plants?
   a. *Volvox*
   b. *Chlamydomonas*
   c. *Ulva*
   d. *Chara*
3. Which of the following would not be found in a bryophytes?
   a. Mycorrhizal associations
   b. Rhizoids
   c. Tracheid cells
   d. Photosynthetic gametophytes
4. Which of the following statements is correct regarding the bryophytes?
   a. The bryophytes represent a monophyletic clade.
   b. The sporophyte stage of all bryophytes is photosynthetic.
   c. Archegonium and antheridium represent haploid structures that produce reproductive cells.
   d. Stomata are common to all bryophytes.

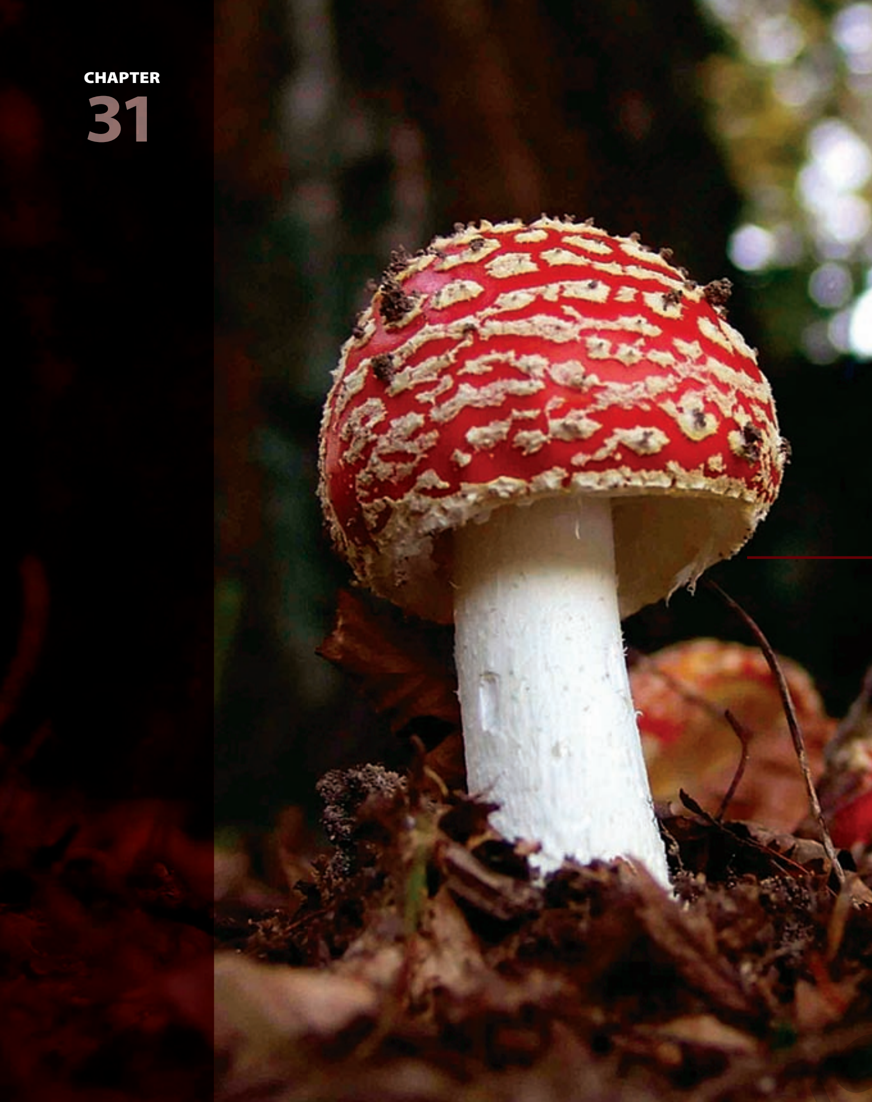
5. The lack of seeds is a characteristic of all
   a. lycophytes.
   b. conifers.
   c. tracheophytes.
   d. gnetophytes.
6. Which of the following adaptations allows plants to pause their life cycle until environmental conditions are optimal?
   a. Stomata
   b. Phloem and xylem
   c. Seeds
   d. Flowers
7. Which of the following gymnosperms possesses a form of vascular tissue that is similar to that found in the angiosperms?
   a. Cycads
   b. Gnetophytes
   c. Ginkgophytes
   d. Conifers
8. In a pine tree, the microspores and megaspores are produced by the process of
   a. fertilization.
   b. mitosis.
   c. fusion.
   d. meiosis.
9. Which of the following terms is *not* associated with a male portion of a plant?
   a. Megaspore
   b. Antheridium
   c. Pollen grains
   d. Microspore
10. Which of the following potentially represents the oldest known living species of angiosperm?
   a. *Cooksonia*
   b. *Chlamydomonas*
   c. *Archaefructus*
   d. *Amborella*

APPLY

1. Compare what happens to a spore mother cell as it gives rise to a spore with what happens to a spore as it gives rise to a gametophyte.
   a. The spore mother cell and the spore both go through meiosis.
   b. The spore mother cell and the spore both go through mitosis.
   c. The spore mother cell goes through mitosis and the spore goes through meiosis.
   d. The spore mother cell goes through meiosis and the spore goes through mitosis.
2. How could a plant without roots obtain sufficient nutrients from the soil?
   a. It cannot, all land plants have roots.
   b. Mychorrizal fungi associate with the plant and assist with the transfer of nutrients.
   c. Charophytes associate with the plant and assist with the transfer of nutrients.
   d. It relies on its xylem in the absence of a root.
3. A major innovation of land plants is embryo protection. How is a moss embryo protected from desication?
   a. By the seed
   b. By the antheridium
   c. By the archegonium
   d. By the lycophyll
4. Reproduction in angiosperms can occur more quickly than in gymnosperms because
   a. gymnosperm sperm requires water to swim to the egg.
   b. flowers always increase the rate of reproduction.
   c. angiosperm pollen tubes grow more quickly than gymnosperm pollen tubes.
   d. angiosperms have nectaries.
5. In double fertilization, one sperm produces a diploid ________, and the other produces a triploid ___________.
   a. zygote; primary endosperm
   b. primary endosperm; microspore
   c. antipodal; zygote
   d. polar nuclei; zygote
6. Apply your understanding of angiosperms to identify which innovations likely contributed to the tremendous success of angiosperms.
   a. Homospory in angiosperms
   b. Fruits that attract animal dispersers
   c. Cones that protect the seed
   d. Dominant gametophyte generation
7. Comparing stems of two plant specimens under the microscope, you identify vessels in one sample and conclude the specimen
   a. with vessels must be an angiosperm.
   b. with vessels is either *Ephedra* or a cycad.
   c. without vessels is a pterophyte.
   d. without vessels must be a tracheophyte.
8. In a flower after fertilization, the following tissues are diploid:
   a. carpel, integuments, and megaspore mother cell.
   b. carpel, integuments, and megaspore.
   c. carpel, megaspore, and zygote.
   d. carpel, megaspore mother cell, and endosperm.

SYNTHESIZE

1. You have access to the sequenced genomes for moss and the lycophyte *Selaginella*. Your goal in analyzing the data is to write a ground-breaking paper that answers an important question about the evolution of plants. What question would you try to answer?
2. You have been hired as a research assistant to investigate the origins of the angiosperms, specifically the boundary between a gymnosperm and an angiosperm. Which characteristics would you use to clearly define a new fossil as a gymnosperm? An angiosperm?
3. Assess the benefits and drawbacks of self-pollination for a flowering plant? Explain your answer.
4. The relationship between flowering plants and pollinators is often used as an example of coevolution. Many flowering plant species have flower structures that are adaptive to a single species of pollinator. Evaluate the benefits and drawbacks of using such a specialized relationship.



Chapter 31

Fungi

Chapter Outline

Introduction

The fungi, an often overlooked group of unicellular and multicellular organisms, have a profound influence on ecology and human health. Along with bacteria, they are important decomposers and disease-causing organisms. Fungi are found everywhere—from the tropics to the tundra and in both terrestrial and aquatic environments. Fungi made it possible for plants to colonize land by associating with rootless stems and aiding in the uptake of nutrients and water. Mushrooms and toadstools are the multicellular spore-producing part of fungi that grow rapidly under proper conditions. A single Armillaria *fungus can cover 15 hectares underground and weigh 100 tons, making it the largest organism in the world based on area. Some puffball fungi are almost a meter in diameter and may contain 7 trillion spores—enough to circle the Earth's equator!*

Yeasts are used to make bread and beer, but other fungi cause disease in plants and animals. These fungal killers are particularly problematic because fungi are animals' closest relatives. Drugs that can kill fungi often have toxic effects on animals, including humans. In this chapter we present the major groups of this intriguing life form.

31.1 Defining Fungi

Learning Outcomes

1. *Identify characteristics that distinguish fungi from other eukaryotes.*
2. *Compare mitosis in fungi and animals.*
3. *Explain why fungi are useful for bioremediation.*

Mycologists, scientists who study fungi as well as fungi-like protists, believe there may be as many as 1.5 million fungal species. Fungi exist either as single-celled yeasts or in multicellular form with several different cell types. Their reproduction may be either sexual or asexual, and they exhibit an unusual form of mitosis. They are specialized to extract and absorb nutrients from their surroundings through external secretion of enzymes. Recent phylogenetic analysis of DNA sequences and protein sequences indicates that fungi are more closely related to animals than to plants. Fossils and molecular data indicate that animals and fungi last shared a common ancestor at least 460 MYA, but inconsistencies remain. The oldest

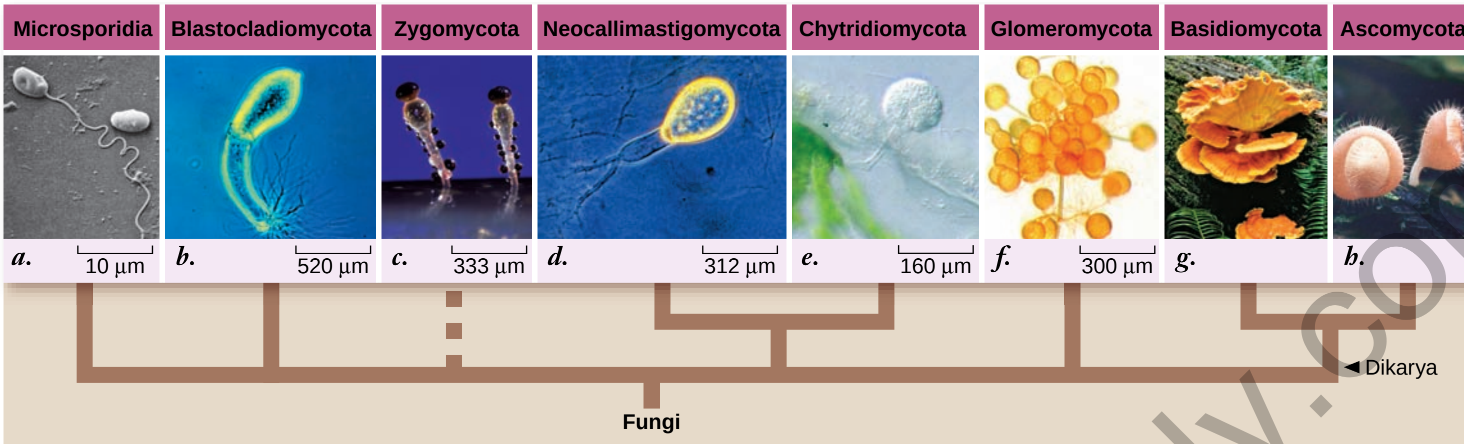


Figure 31.1 Seven major phyla of fungi. All phyla, except Zygomycota, are monophyletic. ***a.*** Microsporidia, including *Encephalitozoon cuniculis*, are animal parasites. ***b.*** *Allomyces arbuscula*, a water mold, is a blastocladiomycete. ***c.*** *Pilobolus*, a zygomycete, grows on animal dung and also on culture medium. Stalks about 10 mm long contain dark, spore-bearing sacs. ***d.*** Neocallimastigales, including *Piromyces communis*, decompose cellulose in the rumens of herbivores. ***e.*** Some chytrids, including members of the genus *Rhizophydium*, parasitize green algae. ***f.*** Spores of *Glomus intraradices*, a glomeromycete associated with roots. ***g.*** *Amanita muscaria*, the fly agaric, is a toxic basidiomycete. ***h.*** The cup fungus *Cookeina tricholoma* is an ascomycete from the rain forest of Costa Rica. In the cup fungi, the spore-producing structures line the cup; in basidiomycetes that form mushrooms such as *Amanita*, they line the gills beneath the cap of the mushroom. All visible structures of fungi, including the ones shown here, arise from an extensive network of filamentous hyphae that penetrates and is interwoven with the substrate on which they grow.

fossil resembles extant members of the genus *Glomus* that arose within the Glomeromycota. One DNA analysis placed the animal/fungal divergence at 1.5500 BYA. This latter estimate is not generally accepted, but many researchers believe that the last common ancestor existed around close to 670 MYA based on an analysis of multiple genes. The last common ancestor with animals was a single cell, and unique solutions to multicellularity evolved both in fungi and in animals.

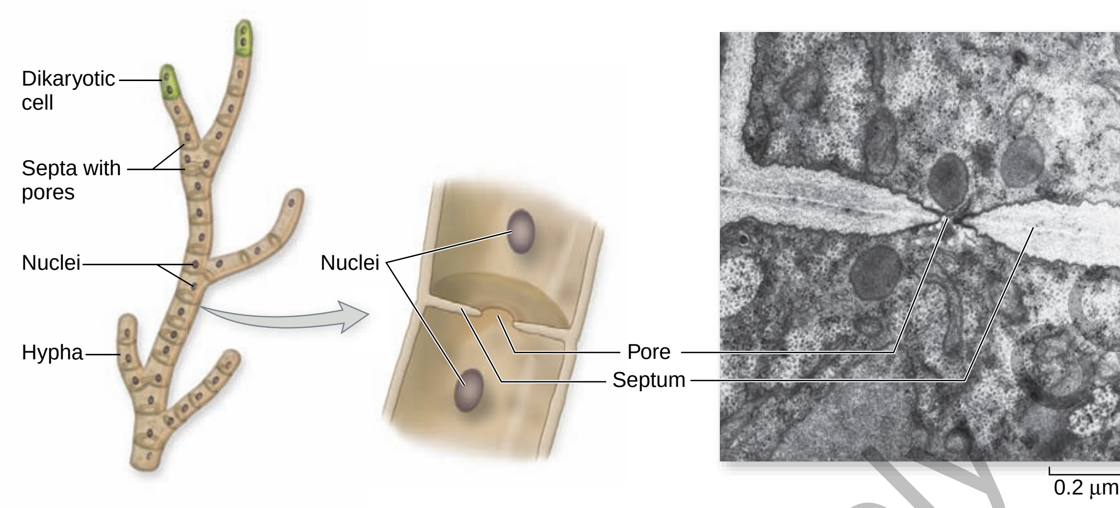
The phylogenetic relationships among fungi have been the cause of much debate. Traditionally, four fungal phyla were recognized, based primarily on characteristics of the cells undergoing meiosis: Chytridiomycota ("chytrids"), Zygomycota ("zygomycetes"), Ascomycota ("ascomycetes"), and Basidiomycota ("basidiomycetes"). The chytrids and zygomycetes are not monophyletic. The understanding of fungal phylogeny is going through rapid and exciting changes, aided by increasing molecular sequence data (figure 31.1 and table 31.1). In 2007, mycologists agreed on seven monophyletic phyla: Microsporidia, Blastocladiomycota, Neocallismastigomycota, Chytridiomycota, Glomeromycota, Basidiomycota, and Ascomycota (see figure 31.1). Blastomycetes and neocallistmastigamycetes were formerly grouped with the chytrids. The Microsporidia are sister to all other fungi, but there is disagreement as to whether or not they are true fungi.

In reading the chapter you will find that phyla with common characteristics are sometimes grouped under one heading. Phylogenies are included as reminders of the evolutionary relationships among phyla. Not all fungi are currently assigned to a monophyletic clade, yet their biology is fascinating.

TABLE 31.1 Fungi

Group	Typical Examples	Key Characteristics	Approximate Number of Living Species
Chytridiomycota	*Allomyces*	Aquatic, flagellated fungi that produce haploid gametes in sexual reproduction or diploid zoospores in asexual reproduction.	1000
Zygomycota	*Rhizopus, Pilobolus*	Multinucleate hyphae lack septa, except for reproductive structures; fusion of hyphae leads directly to formation of a zygote in zygosporangium, in which meiosis occurs just before it germinates; asexual reproduction is most common.	1050
Glomeromycota	*Glomus*	Form arbuscular mycorrhizae. Multinucleate hyphae lack septa. Reproduce asexually.	150
Ascomycota	Truffles, morels	In sexual reproduction, ascospores are formed inside a sac called an ascus; asexual reproduction is also common.	45,000
Basidiomycota	Mushrooms, toadstools, rusts	In sexual reproduction, basidiospores are borne on club-shaped structures called basidia; asexual reproduction occurs occasionally.	22,000

Figure 31.2 A septum. This transmission electron micrograph of a section through a hypha of an ascomycete shows a pore through which the cytoplasm streams.



The body of a fungus is a mass of connected hyphae

Some hyphae are continuous or branching tubes filled with cytoplasm and multiple nuclei. Other hyphae are typically made up of long chains of cells joined end-to-end and divided by cross-walls called septa (singular, *septum*). The septa rarely form a complete barrier, except when they separate the reproductive cells. Even fungi with septa can be considered one long cell.

Cytoplasm characteristically flows or streams freely throughout the hyphae, passing through major pores in the septa (figure 31.2). Because of this streaming, proteins synthesized throughout the hyphae may be carried to their actively growing tips. As a result, fungal hyphae may grow very rapidly when food and water are abundant and the temperature is optimum. For example, you may have seen mushrooms suddenly appear in a lawn overnight after a rain in summer.

The mycelium

A mass of connected hyphae is called a **mycelium** (plural, *mycelia*). (This word and the term mycology, the study of fungi, are both derived from the Greek word *mykes*, meaning fungi.) The mycelium of a fungus (figure 31.3) constitutes a system that may, in the aggregate, be many meters long. This mycelium grows into the soil, wood, or other material and digestion of the material begins quickly. In two of the four major groups of fungi, reproductive structures formed of interwoven hyphae, such as mushrooms, puffballs, and morels, are produced at certain stages of the life cycle. These structures expand rapidly because of rapid inflation of the hyphae.

Cell walls with chitin

The cell walls of fungi are formed of polysaccharides, including chitin. In contrast, cell walls of plants and many protists contain cellulose, not chitin. Chitin is a modified cellulose consisting of linked glucose units to which nitrogen groups have been added; this polymer is then cross-linked with proteins. Chitin is the same material that makes up the major portion of the hard shells, or exoskeletons, of arthropods, a group of animals that includes insects and crustaceans (chapter 34). Chitin is one of the shared traits that has led scientists to believe that fungi and animals are more closely related than fungi and plants.

Fungal cells may have more than one nucleus

Fungi are different from most animals and plants in that each cell (or hypha) can house one, two, or more nuclei. A hypha that has only one nucleus is called **monokaryotic;** a cell with two nuclei is **dikaryotic.** In a dikaryotic cell, the two haploid nuclei exist independently. Dikaryotic hyphae have some of the genetic properties of diploids, because both genomes are transcribed.

Sometimes, many nuclei intermingle in the common cytoplasm of a fungal mycelium, which can lack distinct cells. If a dikaryotic or multinucleate hypha has nuclei that are derived from two genetically distinct individuals, the hypha is called **heterokaryotic.** Hyphae whose nuclei are genetically similar to one another are called **homokaryotic.**

Mitosis is not followed by cell division

Mitosis in multicellular fungi differs from that in most other organisms. Because of the linked nature of the cells, the cell

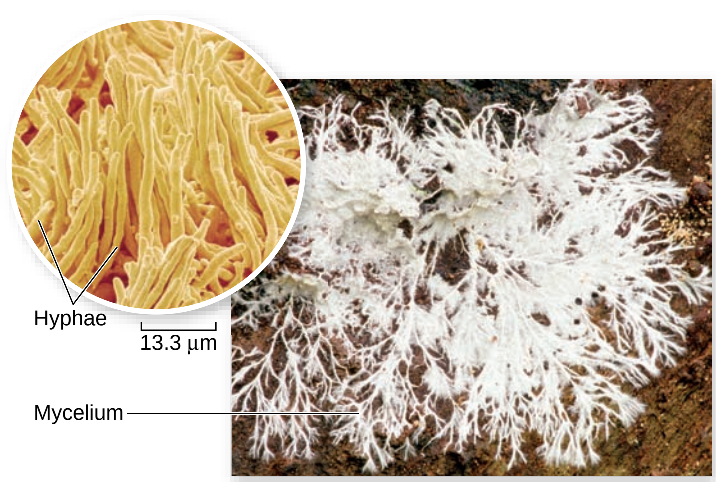


Figure 31.3 Fungal mycelium. This mycelium, composed of hyphae, is growing through leaves on the forest floor in Maryland.

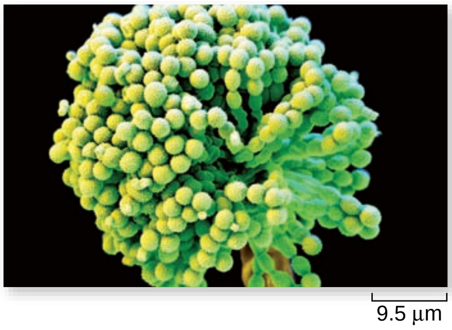


Figure 31.4 Fungal spores. Scanning electron micrograph of fungal spores from *Aspergillus.*

itself is not the relevant unit of reproduction; instead, the nucleus is. The nuclear envelope does not break down and re-form; instead, the spindle apparatus is formed *within* it.

Centrioles are absent in all fungi except chytrids; instead, fungi regulate the formation of microtubules during mitosis with small, relatively amorphous structures called *spindle plaques.* This unique combination of features strongly suggests that fungi originated from some unknown group of single-celled eukaryotes with these characteristics.

Fungi can reproduce both sexually and asexually

Many fungi are capable of producing both sexual and asexual spores. When a fungus reproduces sexually, two haploid hyphae of compatible mating types may come together and fuse.

The dikaryon stage

In animals, plants, and some fungi, the fusion of two haploid cells during reproduction immediately results in a diploid cell ($2n$). But in other fungi, namely basidiomycetes and ascomycetes, an intervening dikaryotic stage ($1n + 1n$) occurs before the parental nuclei fuse and form a diploid nucleus. In ascomycetes, this dikaryon stage is brief, occurring in only a few cells of the sexual reproductive structure. In basidiomycetes, however, it can last for most of the life of the fungus, including both the feeding and sexual spore-producing structures.

Reproductive structures

Some fungal species produce specialized mycelial structures to house the production of spores. Examples are the mushrooms we see above ground, the "shelf" fungus that appears on the trunks of dead trees, and puffballs, which can house billions of spores.

As noted previously, the cytoplasm in fungal hyphae normally flows through perforated septa or moves freely in their absence. Reproductive structures are an important exception to this general pattern. When reproductive structures form, they are cut off by complete septa that lack perforations or that have perforations that soon become blocked.

Spores

Spores are the most common means of reproduction among fungi. They may form as a result of either asexual or sexual processes, and they are often dispersed by the wind. When spores land in a suitable place, they germinate, giving rise to a new fungal mycelium.

Because the spores are very small, between 2 and 75 μm in diameter (figure 31.4), they can remain suspended in the air for a long time. Unfortunately, many of the fungi that cause diseases in plants and animals are spread rapidly by such means. The spores of other fungi are routinely dispersed by insects or other small animals. A few fungal phyla retain the ancestral flagella and have motile zoospores.

Biologists had believed for a long time that the worldwide presence of fungal species could be accounted for, on an evolutionary timescale, by the almost limitless, long-distance dispersal of fungal spores. Recent biogeographic studies, however, have examined the phylogenetic relationships among fungi in distant parts of the world and disproved this long-held assumption.

Fungi are heterotrophs that absorb nutrients

All fungi obtain their food by secreting digestive enzymes into their surroundings and then absorbing the organic molecules produced by this external digestion. The fungal body plan reflects this approach. Unicellular fungi have the greatest surface area-to-volume ratio of any fungus, maximizing the surface area for absorption. Extensive networks of hyphae also provide an enormous surface area for absorptive nutrition in a fungal mycelium.

Many fungi are able to break down the cellulose in wood, cleaving the linkages between glucose subunits and then absorbing the glucose molecules as food. Most fungi also digest lignin, an insoluble organic compound that strengthens plant cell walls. The specialized metabolic pathways of fungi allow them to obtain nutrients from dead trees and from an extraordinary range of organic compounds, including tiny roundworms called nematodes (figure 31.5*a*).

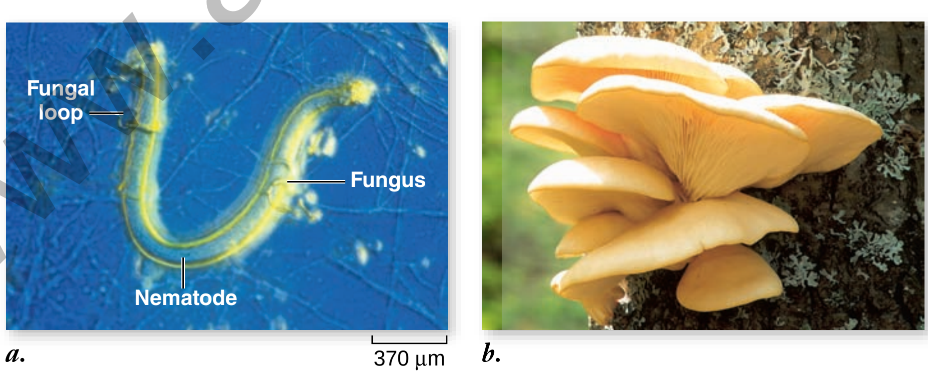


Figure 31.5 Carnivorous fungi. ***a.*** Fungus obtaining nutrients from a nematode. ***b.*** The oyster mushroom *Pleurotus ostreatus* not only decomposes wood but also immobilizes nematodes, which the fungus uses as a source of nitrogen.

The mycelium of the edible oyster mushroom *Pleurotus ostreatus* (figure 31.5*b*) excretes a substance that paralyzes nematodes that feed on the fungus. When the worms become sluggish and inactive, the fungal hyphae envelop and penetrate their bodies. Then the fungus secretes digestive juices and absorbs the nematode's nutritious contents, just like it would from a plant source.

This fungus usually grows within living trees or on old stumps, obtaining the bulk of its glucose through the enzymatic digestion of cellulose and lignin from plant cell walls. The nematodes it consumes apparently serve mainly as a source of nitrogen—a substance almost always in short supply in biological systems. Other fungi are even more active predators than *Pleurotus*, snaring, trapping, or firing projectiles into nematodes, rotifers, and other small animals on which they prey.

Because of their ability to break down almost any carbon-containing compound—even jet fuel—fungi are of interest for use in bioremediation, using organisms to clean up soil or water that is environmentally contaminated. As one example, some fungal species can remove selenium, an element that is toxic in high accumulations, from soils by combining it with other harmless volatile compounds.

Learning Outcomes Review 31.1

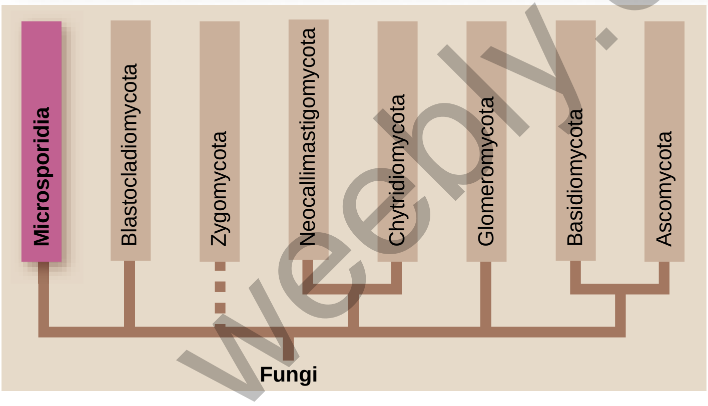
Fungi are more closely related to animals than to plants. Many, but not all, fungi form seven monophyletic phyla. A fungus consists of a mass of hyphae (cells) termed a mycelium; cell walls contain the polysaccharide chitin. Mitosis in fungi divides the nucleus but not the hypha itself. Sexual reproduction may occur when hyphae of two different mating types fuse. Haploid nuclei from each type may persist separately in some groups, termed a dikaryon stage. Spores are produced sexually or asexually and are spread by wind or animals. Fungi secrete digestive enzymes externally and then absorb the products of the digestion. Fungi can break down almost any organic compound.

- ***What differentiates fungi from animals, since both are heterotrophs?***
- ***What protects hyphae from being digested by the fungus's own secreted enzymes?***

31.2 Microsporidia: Unicellular Parasites

Learning Outcomes

1. ***Explain characteristics that led microsporidians to be classified as protists.***
2. ***Describe evidence for placing microsporidians with fungi.***



Microsporidia are obligate, intracellular, animal parasites, long thought to be protists. The lack of mitochondria led biologists to believe that microsporidians were in a deep branch of protists that diverged before endosymbiosis led to mitochondria. Genome sequencing of the microsporidian *Encephalitozoon cuniculi* revealed genes related to mitochondrial functions within the tiny 2.9-Mb genome. Finding mitochondrial genes led to the hypothesis that microsporidia ancestors had mitochondria, and that greatly reduced, mitochondrion-derived organelles exist in microsporidia. Coupled with phylogenies derived from analyses of new sequence data, microsporidia have been tentatively moved from the protists to the fungi.

E. cuniculi and other microsporidia commonly cause disease in immunosuppressed patients, such as those with AIDS and people who have received organ transplants. Microsporidians infect hosts with their spores, which contain a polar tube (figure 31.6). The polar tube extrudes the contents of the spore

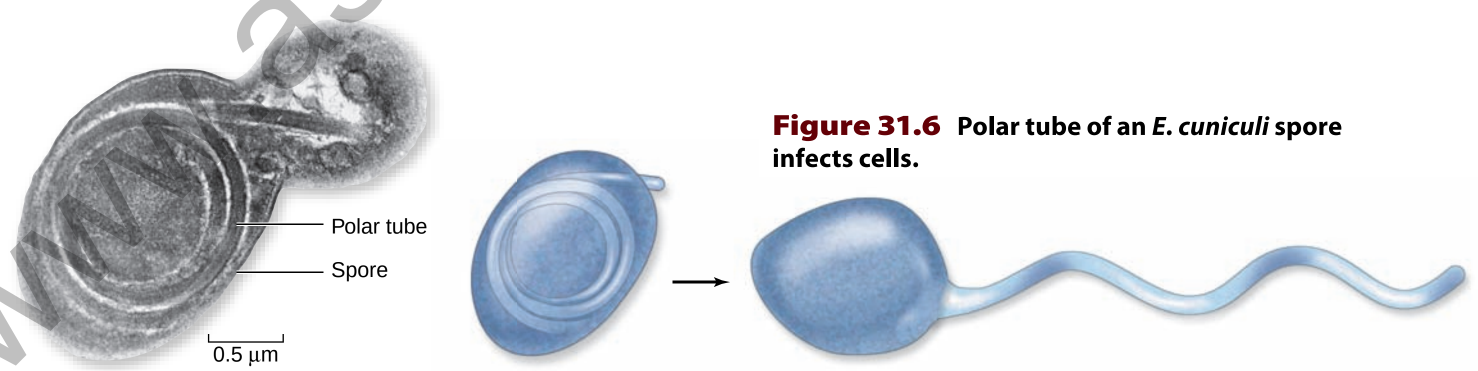


Figure 31.6 Polar tube of an *E. cuniculi* spore infects cells.

into the cell and the parasite sets up housekeeping in a vacuole. *E. cuniculi* infects intestinal and neuronal cells, leading to diarrhea and neurodegenerative disease. Understanding the phylogenetic placement of the microsporidia is important in identifying effective disease treatments.

Learning Outcomes Review 31.2

Microsporidia lack mitochondria; however, the presence of mitochondrial genes indicates that at one time an ancestral form possessed them. As obligate parasites, microsporidia cause diseases in animals, including humans.

- *How would you distinguish a microsporidian from the parasitic protistan* Plasmodium?

31.3 *Chytridiomycota and Relatives: Fungi with Flagellated Zoospores*

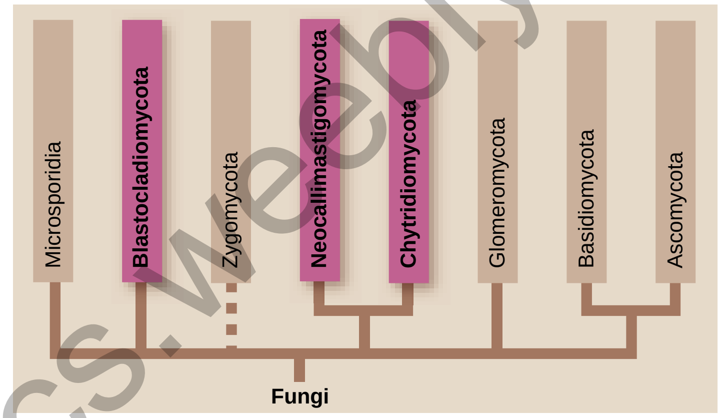
Learning Outcomes

1. *Distinguish between blastocladiomycetes and microsporidians.*
2. *Explain the meaning of "chytrid."*
3. *Discuss possible uses of neocallimastigomycetes.*

Members of phylum Chytridiomycota, the **chitridiomycetes** or **chytrids,** are aquatic, flagellated fungi that are closely related to ancestral fungi. Motile zoospores are a distinguishing character of this fungal group. Chytrid has its origins in the Greek word *chytridion*, meaning "little pot," referring to the structure that releases the flagellated zoospores (figure 31.7).

Chytrids include *Batrachochytrium dendrobatidis*, which has been implicated in the die-off of amphibians. Other chytrids have been identified as plant pathogens (figure 31.8). Traditionally the blastocladiomycetes and the neocallimastigomycetes have been grouped with the chytrids. Recent phylogenetic inferences have accorded the two groups their own phyla. Both proposed phyla are discussed here because of their many similarities with the chytrids.

Blastocladiomycota have single flagella



Blastocladiomycetes have uniflagellated zoospores. Blastocladiomycetes, neocallimastigomycetes, and chytridiomycetes were originally grouped as a single phylum because they all have flagella that have been lost in other groups, except the microsporidians. Inclusion of multiple genes in phylogenetic analyses has established that the three groups form three separate, monophyletic phyla.

Figure 31.7 Zoospore release. The potlike structure (*chytridion* in Greek) containing the zoospores gives chytrids their name.

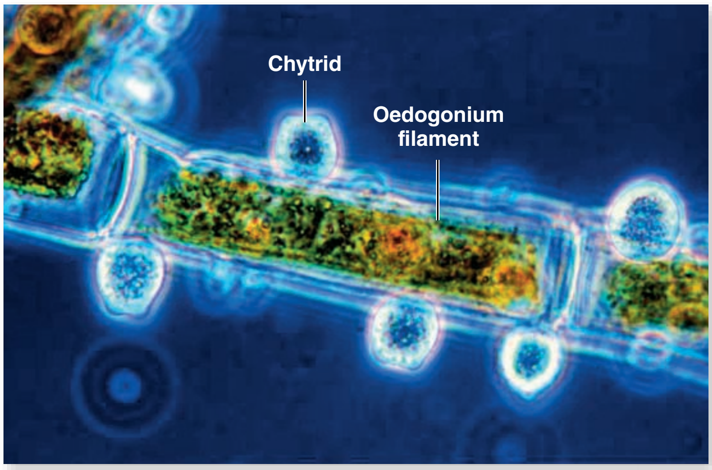
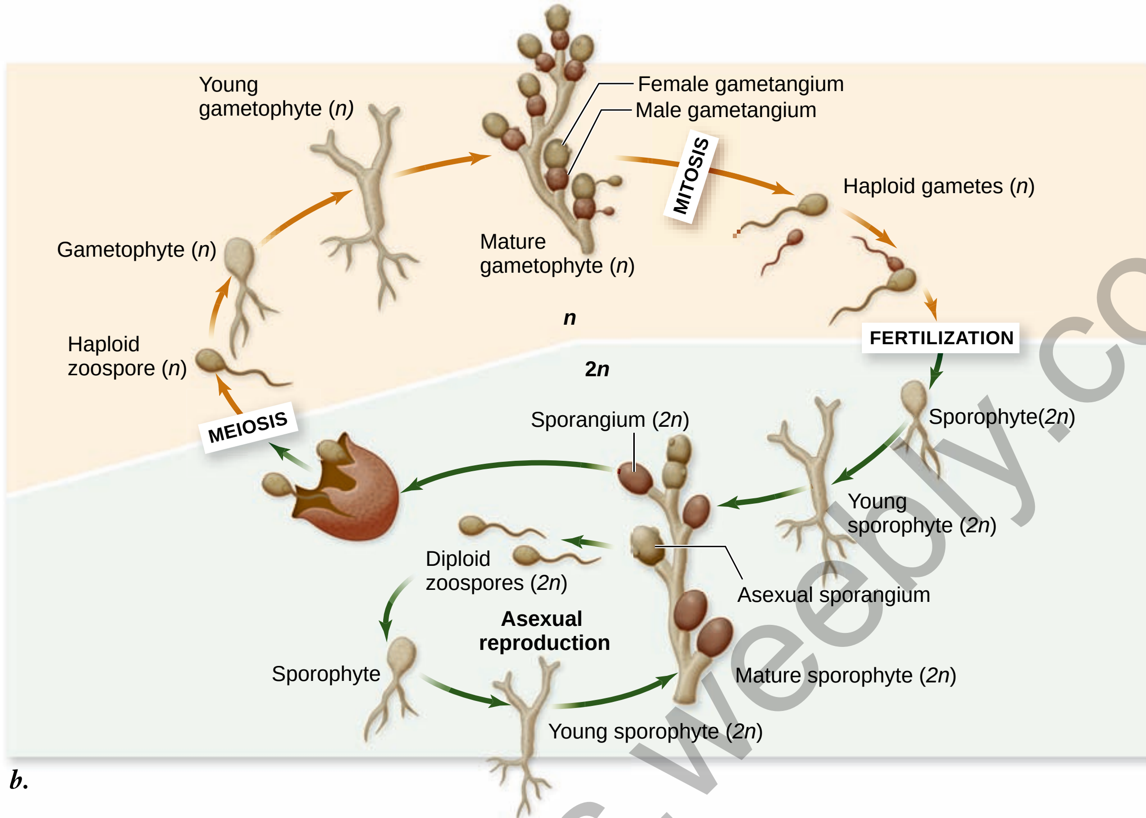


Figure 31.8 Chytridiomycota can be plant pathogens. *Rhizophydium granulosporum* sporangia on a filament of the green algae *Oedogonium.*

Figure 31.9 ***Allomyces*, a blastocladiomycete that grows in the soil.** ***a.*** The spherical sporangia can produce either diploid zoospores via mitosis or haploid zoospores via meiosis. ***b.*** Life cycle of *Allomyces*, which has both haploid and diploid multicellular stages (alternation of generations).

a. 100 µm



b.

Allomyces is a typical blastocladiomycete genus. A water mold, it exhibits a true haplodiplontic life cycle (figure 31.9). Reproduction in *Allomyces* species is enhanced by the secretion of a pheromone, a long-distance chemical signal, from the female gametes that attracts male gametes. Pheromones are similar to hormones, but work between organisms, rather than within organisms. The *Allomyces* pheromone is called sirenin (after the Sirens in Greek mythology) and was the first fungal sex hormone to be identified chemically.

Unlike microsporidia, which lack mitochondria, *A. macrogynus* has giant mitochondria in its zoospores. Each flagellated zoospore contains a single giant mitochondrion that is fragmented into several normal-sized organelles in vegetative cells.

Neocallimastigomycota digest cellulose in ruminant herbivores

Within the rumens of mammalian herbivores, **neocallimastigomycetes** enzymatically digest the cellulose and lignin of the plant biomass in their grassy diet. Sheep, cows, kangaroos, and elephants all depend on these fungi to obtain sufficient calories. These anaerobic fungi have greatly reduced mitochondria that lack cristae. Their zoospores have multiple flagella. "Mastig" in Neocalli*mastigo*mycota is Latin for "whips," referencing the multiple flagella.

The genus *Neocallimastix* can survive on cellulose alone. Genes encoding digestive enzymes such as cellulase made their way into the *Neocallimastix* genomes via horizontal gene transfer from bacteria. Horizontal gene transfer is covered in chapter 26.

The many enzymes that neocallimastigamycetes use to digest cellulose and lignin in plant cell walls may be useful in biofuel production from cellulose. Although it is possible to obtain ethanol from cellulose, breaking down the cellulose is a major technical hurdle. The use of neocallimastigamycetes fungi to produce cellulosic ethanol is a promising, cost-effective approach.

Learning Outcomes Review 31.3

Three closely related phyla, Chytridiomycota, Blastocladiomycota, and Neocallimastigomycota have flagellated zoospores. Chytrid refers to the potlike shape of the structure releasing the zoospores. *Allomyces,* a representative blastocladiomycete, has uniflagellated zoospores with giant mitochondria, and a haplodiplontic life cycle. Neocallimastigamycetes acquired cellulases from bacteria. They aid ruminant animals in digesting cellulose from plants and may be useful in production of biofuels.

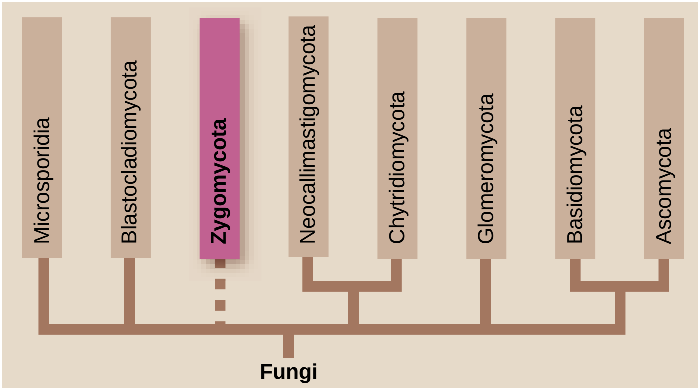
- ***What two features differentiate blastocladiomycetes from microsporidians?***

31.4 *Zygomycota: Fungi That Produce Zygotes*

Learning Outcomes

1. *Describe the defining feature of the zygomycetes.*
2. *Explain the advantage of zygospore formation.*

Zygomycetes (phylum Zygomycota) include only about 1050 named species, but they are incredibly diverse. The zygomycota are not monophyletic, but are included in this chapter as a group while research on their evolutionary history continues. Among them are some of the more common bread molds, which have been assigned to the monophyletic subphylum Mucoromycotina (figure 31.10), as well as a variety of others



found on decaying organic material, including strawberries and other fruits. A few human pathogens are in this group.

In sexual reproduction, zygotes form inside a zygosporangium

The zygomycetes lack septa in their hyphae except when they form sporangia or gametangia (structures in which spores or gametes are produced). The group is named after a characteristic feature of the sexual phase of the life cycle, the formation of diploid zygote nuclei.

Sexual reproduction begins with the fusion of gametangia, which contain numerous nuclei. The gametangia are cut off from the hyphae by complete septa. These gametangia may be formed on hyphae of different mating types or on a single hypha.

The haploid nuclei fuse to form a diploid zygote nucleus, a process called karyogamy. The area where the fusion has taken place develops into a zygosporangium (figure 31.10*b*), within which a **zygospore** develops. The zygospore, which may contain one or more diploid nuclei, acquires a thick coat that helps the fungus survive conditions not favorable for growth.

Meiosis, followed by mitosis, occurs during the germination of the zygospore, which releases haploid spores. Haploid hyphae grow when these haploid spores germinate. Except for the zygote nuclei, all nuclei of the zygomycetes are haploid.

Asexual reproduction is more common

Asexual reproduction occurs much more frequently than sexual reproduction in the zygomycetes. During asexual reproduction, hyphae produce clumps of erect stalks, called **sporangiophores.** The tips of the sporangiophores form sporangia, which are separated by septa. Thin-walled haploid spores are produced within the sporangia. These spores are shed above the food substrate, in a position where they may be picked up by the wind and dispersed to a new food source.

Learning Outcomes Review 31.4

Zygomycetes are named for the production of diploid zygote nuclei by fusion of haploid nuclei, a process called karyogamy. The hyphae of zygomycetes are multinucleate, with septa only where gametangia or sporangia are separated. Many zygomycetes form characteristic resting structures called zygosporangia, which contain zygospores that are able to withstand harsh conditions.

- ***Under what conditions would you expect a zygomycete to produce zygospores rather than haploid spores?***

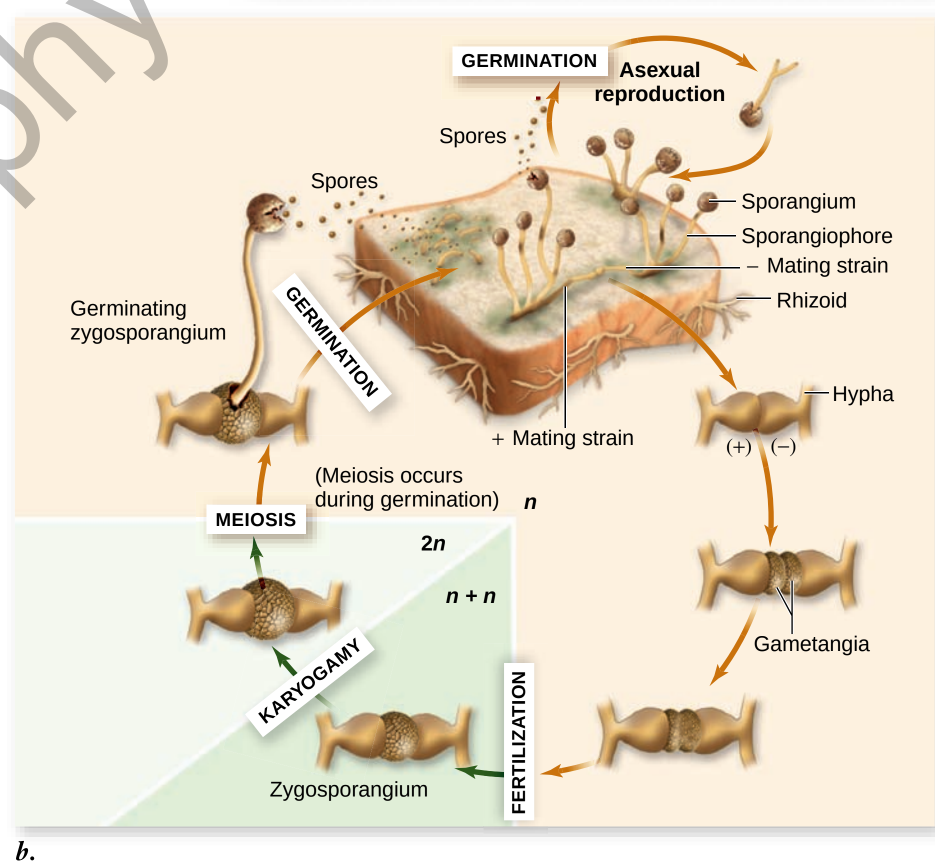
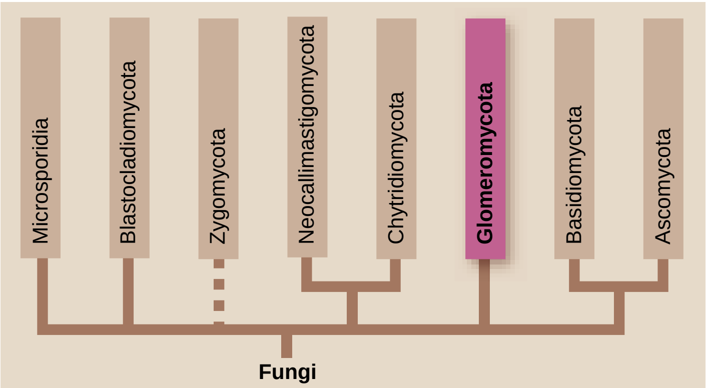


Figure 31.10 ***Rhizopus*, a zygomycete that grows on simple sugars.** This fungus is often found on moist bread or fruit. ***a.*** The dark, spherical, spore-producing sporangia are on hyphae about 1 cm tall. The rootlike hyphae (rhizoids) anchor the sporangia. ***b.*** Life cycle of *Rhizopus.* The Zygomycota group is named for the zygosporangia characteristic of *Rhizopus.* The (+) and (-) denote mating types.

31.5 Glomeromycota: Asexual Plant Symbionts

Learning Outcome

1. *Explain why Glomeromycota is now considered separate from Zygomycota.*



The glomeromycetes, a tiny group of fungi with approximately 150 described species, likely made the evolution of terrestrial plants possible. Tips of hyphae grow within the root cells of most trees and herbaceous plants, forming a branching structure that allows nutrient exchange. The intracellular associations with plant roots are called **arbuscular mycorrhizae.** The specifics of arbuscular mycorrhizal associations and other forms of mycorrhizal interactions are detailed in section 31.8.

Glomeromycetes cannot survive in the absence of a host plant. The symbiotic relationship is mutualistic, with the glomeromycetes providing essential minerals, especially phosphorous, and the plants providing carbohydrates.

The glomeromycetes are challenging to characterize, in part, because there is no evidence of sexual reproduction. These fungi exemplify our emerging understanding of fungal phylogeny. Like zygomycetes, glomeromycetes lack septae in their hyphae and were once grouped with the zygomycetes. However, comparisons of DNA sequences of small-subunit rRNAs reveal that glomeromycetes are a monophyletic clade that is phylogenetically distinct from zygomycetes. Unlike zygomycetes, glomeromycetes lack zygospores. Glomeromycota originated at least 600 to 620 MYA, well before the split of the Ascomycota and Basidiomycota, which we will consider next.

Learning Outcome Review 31.5

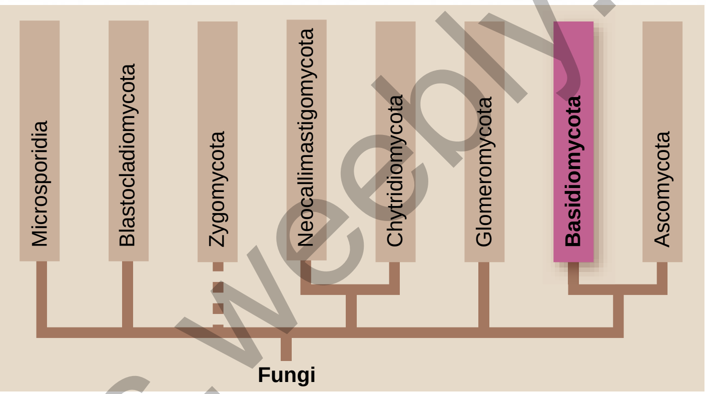
Glomeromycetes are a monophyletic fungal lineage based on analysis of small-subunit rRNAs. Their obligate symbiotic relationship with the roots of many plants appears to be ancient and may have made it possible for terrestrial plants to evolve.

- *Why do glomeromycetes require a host plant?*

31.6 Basidiomycota: The Club (Basidium) Fungi

Learning Outcomes

1. *Explain which cells in the life cycle of a basidiomycete are diploid.*
2. *Distinguish between primary and secondary mycelium in basidiomycetes.*



The basidiomycetes (phylum Basidiomycota) include some of the most familiar fungi. Among the basidiomycetes are not only the mushrooms, toadstools, puffballs, jelly fungi, and shelf fungi, but also many important plant pathogens, including rusts and smuts (figure 31.11*a*). Rust infections resemble rusting metals, and smut infections appear black and powdery due to the spores. Many mushrooms are used as food, but others are hallucinogenic or deadly poisonous.

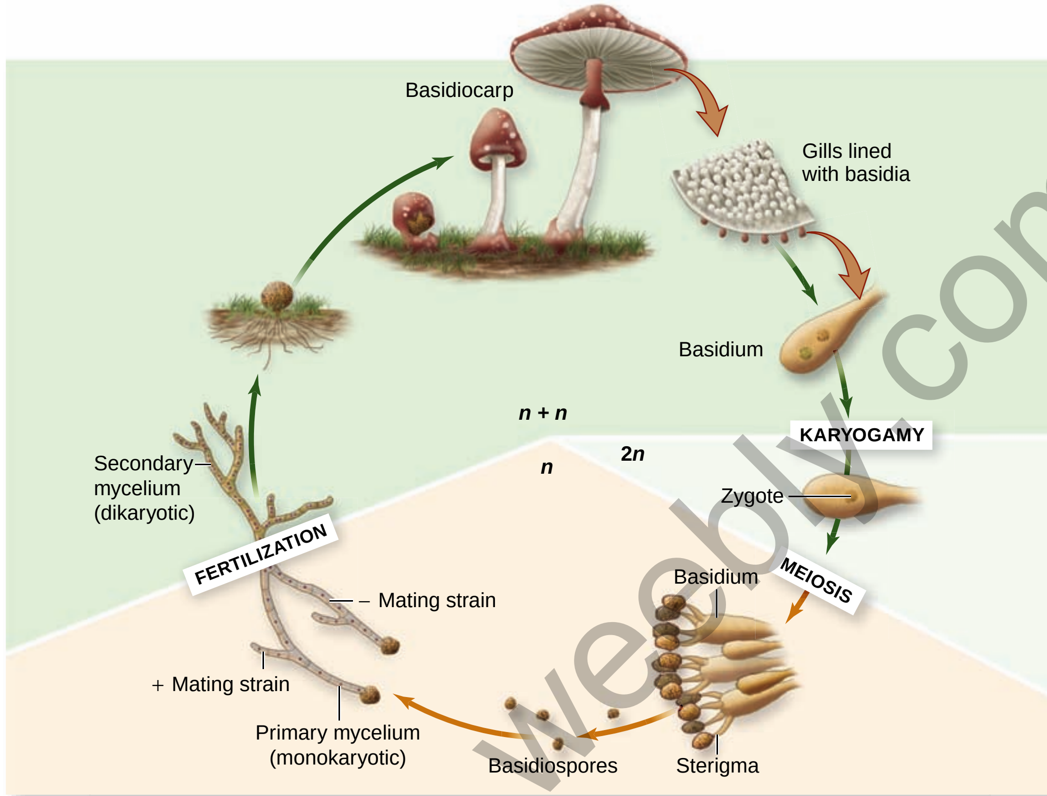
Basidiomycetes sexually reproduce within basidia

Basidiomycetes are named for their characteristic sexual reproductive structure, the club-shaped **basidium** (plural, *basidia*). Karyogamy (fusion of two nuclei) occurs within the basidium, giving rise to the only diploid cell of the life cycle (figure 31.11*b*). Meiosis occurs immediately after karyogamy. In the basidiomycetes, the four haploid products of meiosis are incorporated into **basidiospores.** In most members of this phylum, the basidiospores are borne at the end of the basidia on slender projections (sterigmata).

The secondary mycelium of basidiomycetes is heterokaryotic

The life cycle of a basidiomycete continues with the production of monokaryotic hyphae after spore germination. These hyphae lack septa early in development. Eventually, septa form between the nuclei of the monokaryotic hyphae. A basidiomycete mycelium made up of monokaryotic hyphae is called a *primary mycelium.*

a.



b.

Figure 31.11 Basidiomycetes. ***a.*** The death cap mushroom, *Amanita phalloides.* When eaten, these mushrooms are usually fatal. ***b.*** Life cycle of a basidiomycete. The basidium is the reproductive structure.

Different mating types of monokaryotic hyphae may fuse, forming a dikaryotic mycelium, or *secondary mycelium.* Such a mycelium is heterokaryotic, with two nuclei representing the two different mating types, between each pair of septa. This stage is the dikaryon stage described earlier as being a distinguishing feature of fungi. It is found in both the ascomycetes and the basidiomycetes. The two phyla are grouped as the subkingdom Dikarya because of this commonality. The maintenance of two genomes in the heterokaryon allows for more genetic plasticity than in a diploid cell with one nucleus. One genome may compensate for mutations in the other.

The **basidiocarps,** or mushrooms, are formed entirely of secondary (dikaryotic) mycelium. Gills, sheets of tissue on the undersurface of the cap of a mushroom, produce vast numbers of minute spores. It has been estimated that a mushroom with a cap measuring 7.5 cm in diameter produces as many as 40 million spores per hour!

Learning Outcomes Review 31.6

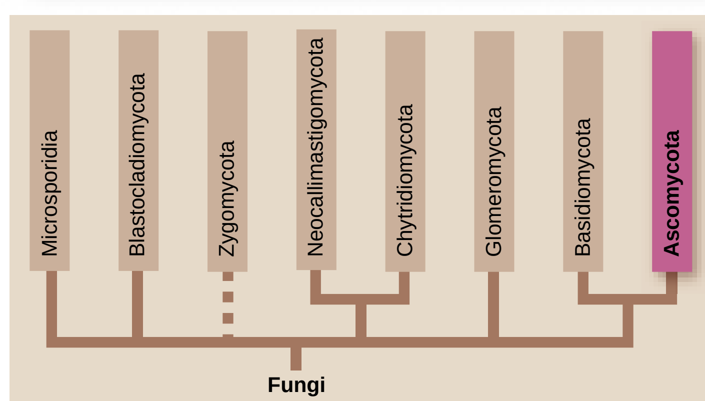
Basidiomycetes undergo karyogamy, after which meiosis occurs within club-shaped basidia. The primary mycelium consists of monokaryotic hyphae resulting from spore germination. The secondary mycelium of basidiomycetes is the dikaryon stage, in which two nuclei exist within a single hyphal segment.

- ***What distinguishes a dikaryotic cell from a diploid cell?***

31.7 *Ascomycota: The Sac (Ascus) Fungi*

Learning Outcomes

1. ***Compare the ascomycetes and the basidiomycetes***
2. ***List the ways ascomycetes affect humans.***



The phylum **Ascomycota** contains about 75% of the known fungi. Among the ascomycetes are such familiar and economically important fungi as bread yeasts, common molds, morels (figure 31.12*a*), cup fungi (figure 31.12*b*), and truffles. Also included in this phylum are many serious plant pathogens, including those that produce chestnut blight, *Cryphonectria parasitica*, and Dutch elm disease, *Ophiostoma ulmi*. Penicillin-producing ascomycetes are in the genus *Penicillium*.

Sexual reproduction occurs within the ascus

The ascomycetes are named for their characteristic reproductive structure, the microscopic, saclike **ascus** (plural, *asci*). Karyogamy, the production of the only diploid nucleus of the ascomycete life cycle (figure 31.12*c*), occurs within the ascus. The structure of an ascus differs from that of a basidium, although functionally the two are identical.

Asci are differentiated within a structure made up of densely interwoven hyphae, corresponding to the visible portions of a morel or cup fungus, called the **ascocarp.** Meiosis immediately follows karyogamy, forming four haploid daughter nuclei. These usually divide again by mitosis, producing eight haploid nuclei that become walled **ascospores.** The ascospores of the ascomycetes are borne internally in asci instead of externally as in basidiospores.

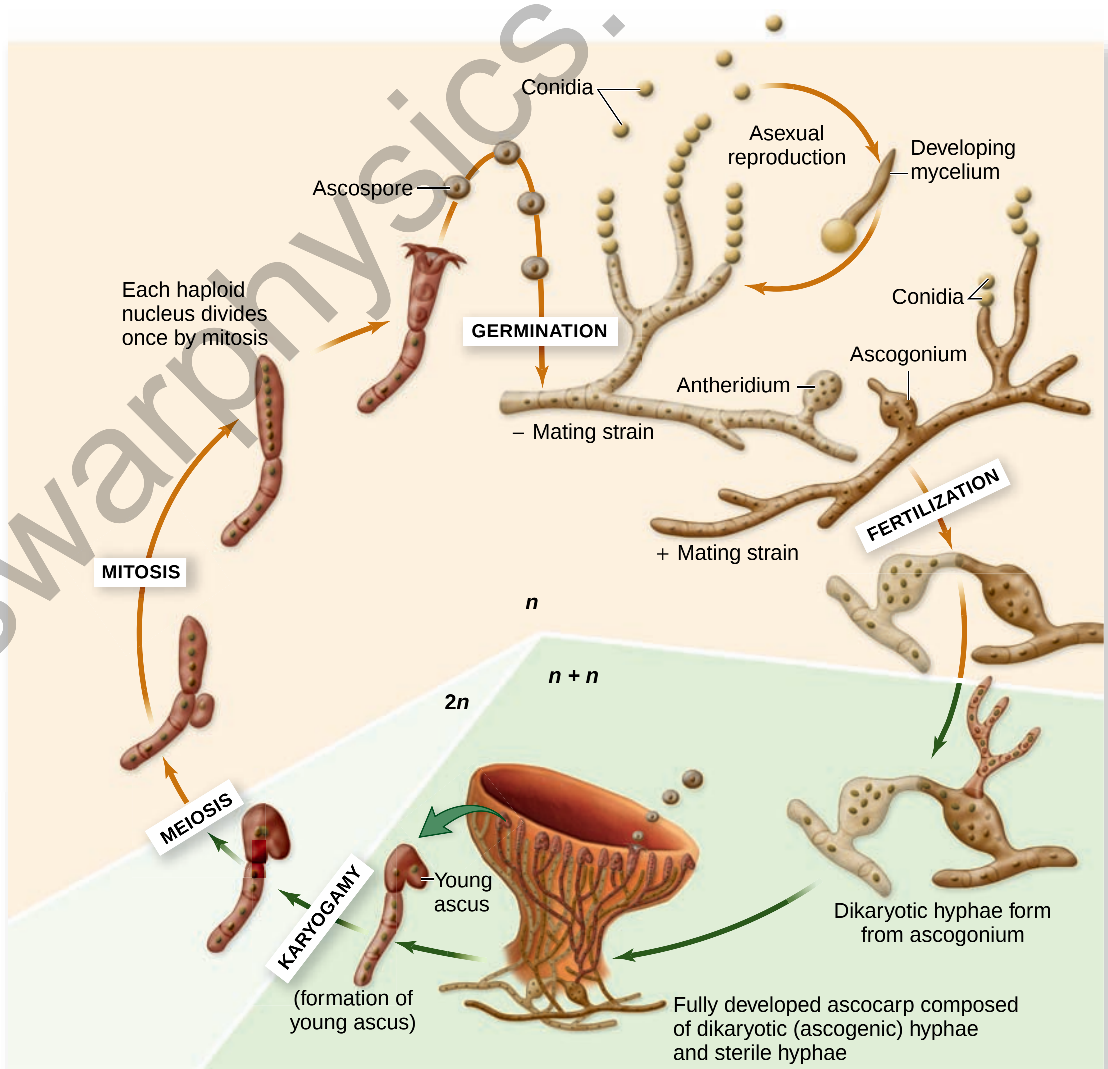
In many ascomycetes, the ascus becomes highly turgid at maturity and ultimately bursts, often at a preformed area. When this occurs, the ascospores may be thrown as far as 31 cm, an amazing distance considering that most ascospores are only about 10 μm long. This would be equivalent to throwing a baseball (diameter 7.5 cm) 1.25 km—about 10 times the length of a home run!

Asexual reproduction occurs within conidiophores

Asexual reproduction is very common in the ascomycetes. It takes place by means of **conidia** (singular, *conidium*), asexual spores cut off by septa at the ends of modified hyphae called conidiophores. Conidia allow for the rapid colonization of a new food source. Many conidia are multinucleate. The hyphae of ascomycetes are divided by septa, but the septa are perforated, and the cytoplasm flows along the length of each hypha. The septa that cut off the asci and conidia are initially perforated, but later become blocked.

a.

b.



c.

Figure 31.12 Ascomycetes. ***a.*** This morel, *Morchella esculenta*, is a delicious edible ascomycete that appears in early spring. ***b.*** A cup fungus. ***c.*** Life cycle of an ascomycete. Haploid ascospores form within the ascus.

Some ascomycetes have yeast morphology

Most yeasts are ascomycetes with a single-celled lifestyle. Most of yeasts' reproduction is asexual and takes place by cell fission or budding, when a smaller cell forms from a larger one (figure 31.13). Sometimes two yeast cells fuse, forming one cell containing two nuclei. This cell may then function as an ascus, with karyogamy followed immediately by meiosis. The resulting ascospores function directly as new yeast cells.

The ability of yeasts to ferment carbohydrates, breaking down glucose to produce ethanol and carbon dioxide, is fundamental in the production of bread, beer, and wine. About four billion of these tiny, powerful organisms can fit in a teaspoon. Many different strains of yeast have been domesticated and selected for these processes, using the sugars in rice, barley, wheat, and corn. Wild yeasts—ones that occur naturally in the areas where wine is made—were important in wine making historically, but domesticated cultured yeasts are normally used now.

Wild yeast, often *Candida milleri*, is still important in making sourdough bread. Unlike most breads that are made with pure cultures of yeast, sourdough uses an active culture of wild yeast and bacteria that generate acid. This culture is maintained, and small amounts—"starter" cultures—are used for each batch of bread. The combination of yeast and acid-producing bacteria is needed for fermentation and gives sourdough bread its unique flavor.

The most important yeast in baking, brewing, and wine making is *Saccharomyces cerevisiae*. This yeast has been used by humans throughout recorded history. Yeast is also employed as a nutritional supplement because it contains high levels of B vitamins and because about 50% of yeast is protein.

Ascomycete genetics and genomics have practical applications

Yeast is a long-standing model system for genetic research. It was the first eukaryote to be manipulated extensively by the techniques of genetic engineering, and they still play the leading role as models for research in eukaryotic cells. In 1996, the genome sequence of *S. cerevisiae*, the first eukaryote to be sequenced entirely, was completed. The yeast two-hybrid system has been an important component of research on protein interactions (see chapter 17).

The fungal genome initiative is now under way to provide sequence information on other fungi. More than 25 fungi have been or are being sequenced. These fungi were selected based on their effects on human health, including plant pathogens that threaten our food supply.

The ascomycetes *Coccidioides posadasii* and its relative *C. immitis* were included because they are endemic in soil in the southwestern portion of the United States, can cause a fatal infection called coccidioidomycosis ("valley fever"), and have been considered a possible bioterrorism threat. In the United States the annual infection rate is about 100,000 individuals, although only a small percentage of infected individuals die.

A second important criterion in selecting which fungi to sequence was the potential to provide information on fungal evolution. This new information will complement and expand our understanding of the diverse fungal kingdom.

Figure 31.13 Budding in *Saccharomyces*. As shown in this scanning electron micrograph, the cells tend to hang together in chains, a feature that calls to mind the derivation of single-celled yeasts from multicellular ancestors.

Learning Outcomes Review 31.7

Ascomycetes undergo karyogamy within a characteristic saclike structure, the ascus. The function of the ascus is therefore identical to that of the basidium, although they are structurally different. Meiosis follows, resulting in the production of ascospores. Yeasts within this group generally reproduce asexually by budding. Ascomycetes include both beneficial forms used as foods, and in the production of foods, and harmful forms responsible for diseases and spoilage. Many ascomycetes are employed in scientific research.

- ***Coccidioidomycosis is caused by inhaling spores; it often occurs in farmworkers in the Southwest United States. What would help prevent this disease?***

31.8 Ecology of Fungi

Learning Outcomes

1. ***Identify a trait that contributes to the value of fungi in symbiotic relationships.***
2. ***Describe the living components of a lichen.***
3. ***List examples of fungal associations with different organisms.***

Fungi, together with bacteria, are the principal decomposers in the biosphere. They break down organic materials and return the substances locked in those molecules to circulation in the ecosystem. Fungi can break down cellulose and lignin, an insoluble organic compound that is one of the major constituents of wood. By breaking down such substances, fungi release carbon, nitrogen, and phosphorus from the bodies of living or dead organisms and make them available to other organisms.

In addition to their role as decomposers, fungi have entered into fascinating relationships with a variety of life forms. Interactions between different species are described in chapter 57 where we discuss community ecology, but we cover fungal relationships briefly here because of their unique character.

Fungi have a range of symbioses

The interactions, or symbioses, between fungi and other living organisms fall into a broad range of categories. In some cases, the symbiosis is an **obligate symbiosis** (essential for survival), and in other cases it is a **facultative symbiosis** (the fungus can survive without the host). Within a group of closely related fungi, several different types of symbiosis can be found.

First, here is a summary of ways in which living things can interact. **Pathogens** and **parasites** gain resources from their host, but they have a negative effect on the host that can even lead to death. The difference between pathogens and parasites is that pathogens cause disease, but parasites do not, except in extreme cases.

Commensal relationships benefit one partner but do not harm the other. Fungi that are in a **mutualistic** relationship benefit both themselves and their hosts. Many of these relationships are described in the discussion that follows.

Endophytes live inside plants and may protect plants from parasites

Endophytic fungi live inside plants, actually in the intercellular spaces. Found throughout the plant kingdom, many of these relationships may be examples of parasitism or commensalism.

There is growing evidence that some of these fungi protect their hosts from herbivores by producing chemical toxins or deterrents. Most often, the fungus synthesizes alkaloids that protect the plant. As you will learn in chapter 40, plants also synthesize a wide range of alkaloids, many of which serve to defend the plant.

One way to assess whether an endophyte is enhancing the health of its host plant is to grow plots of plants with and without the same endophyte. An experiment with perennial ryegrass, *Lolium perenne*, demonstrated that it is more resistant to aphid feeding when an endophytic fungus, *Neotyphodium*, is present (figure 31.14).

Lichens are an example of symbiosis between different kingdoms

Lichens (figure 31.15) are symbiotic associations between a fungus and a photosynthetic partner. Although many lichens are excellent examples of mutualism, some fungi are parasitic on their photosynthetic host.

Composition of a lichen

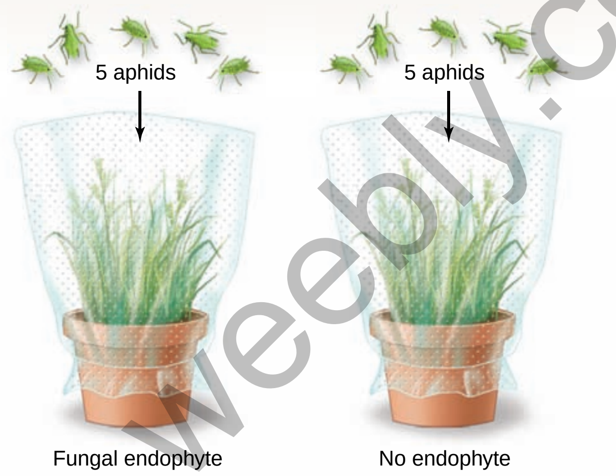
Ascomycetes are the fungal partners in all but about 20 of the approximately 15,000 species of lichens estimated to exist. Most of the visible body of a lichen consists of its fungus, but between

SCIENTIFIC THINKING

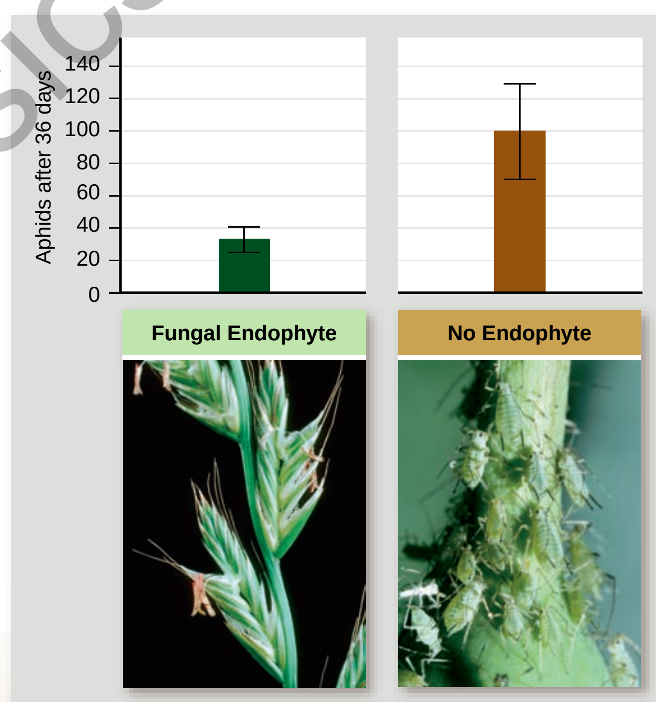
Hypothesis: *Endophytic fungi can protect their host from herbivory.*

Prediction: *There will be fewer aphids* (Rhopalosiphum padi, *an herbivore) on perennial ryegrass* (Lolium perenne) *infected with endophytic fungi than on uninfected ryegrass.*

Test: *Place five adult aphids on each pot of 2-week-old grass plants with and without endophytic fungi. Place pots in perforated bags and grow for 36 days. Count the number of aphids in each pot.*



Result: *Significantly more aphids were found on the uninfected grass plants.*



Conclusion: *Endophytic fungi protect host plants from herbivory.*

Further Experiments: *How do you think the fungi protect the plants from herbivory? If they secrete chemical toxins, could you use this basic experimental design to test specific fungal compounds?*

Figure 31.14 Effect of the fungal endophyte *Neotyphodium* on the aphid population living on perennial ryegrass *(Lolium perenne)*.

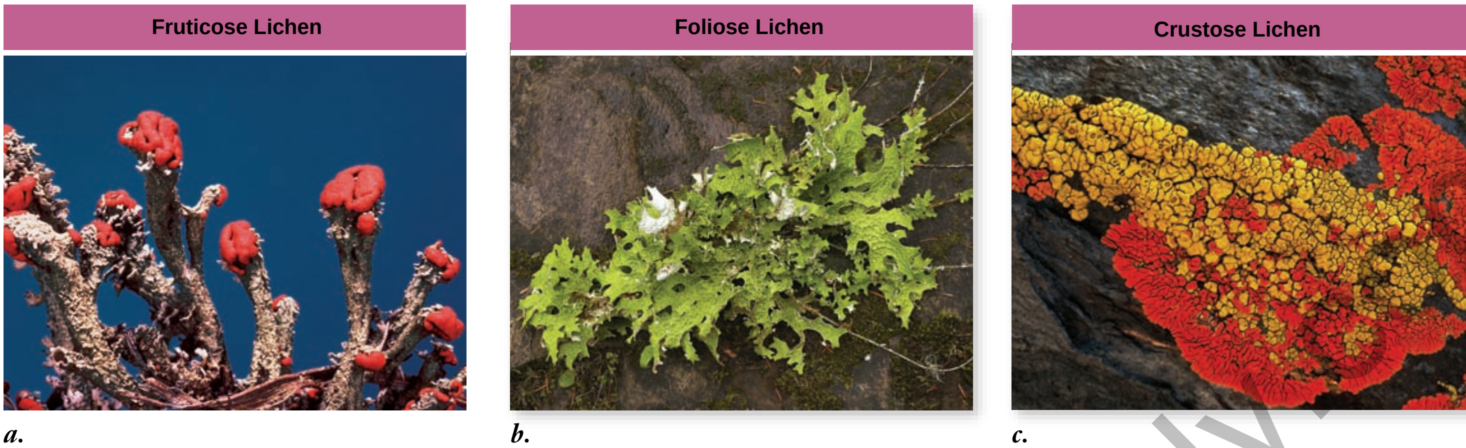


Figure 31.15 Lichens are found in a variety of habitats. *a.* A fruticose lichen, growing in the soil. *b.* A foliose ("leafy") lichen, growing on the bark of a tree in Oregon. *c.* A crustose lichen, growing on rocks leading to the breakdown of rock into soil.

the filaments of that fungus are cyanobacteria, green algae, or sometimes both (figure 31.16).

Specialized fungal hyphae penetrate or envelop the photosynthetic cell walls within them and transfer nutrients directly to the fungal partner. Note that although fungi penetrate the cell wall, they do not penetrate the plasma membrane. Biochemical signals sent out by the fungus apparently direct its cyanobacterial or green algal component to produce metabolic substances that it does not produce when growing independently of the fungus.

The fungi in lichens are unable to grow normally without their photosynthetic partners, and the fungi protect their partners from strong light and desiccation. When fungal components of lichens have been experimentally isolated from their photosynthetic partner, they survive, but grow very slowly.

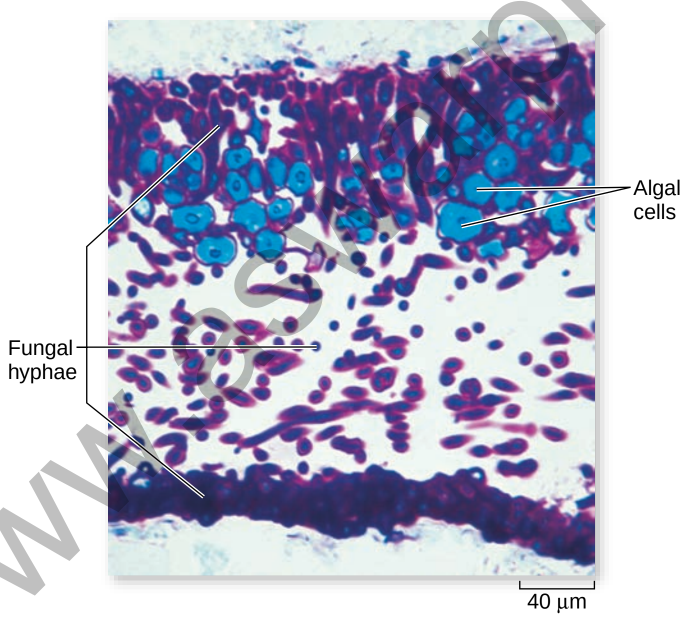


Figure 31.16 Stained section of a lichen. This section shows fungal hyphae *(purple)* more densely packed into a protective layer on the top and, especially, the bottom layer of the lichen. The blue cells near the upper surface of the lichen are those of a green alga. These cells supply carbohydrate to the fungus.

Ecology of lichens

The durable construction of the fungus combined with the photosynthetic properties of its partner have enabled lichens to invade the harshest habitats—the tops of mountains, the farthest northern and southern latitudes, and dry, bare rock faces in the desert. In harsh, exposed areas, lichens are often the first colonists, breaking down the rocks and setting the stage for the invasion of other organisms.

Lichens are often strikingly colored because of the presence of pigments that probably play a role in protecting the photosynthetic partner from the destructive action of the sun's rays. These same pigments may be extracted from the lichens and used as natural dyes. The traditional method of manufacturing Scotland's famous Harris tweed used fungal dyes.

Lichens vary in sensitivity to pollutants in the atmosphere, and some species are used as bioindicators of air quality. Their sensitivity results from their ability to absorb substances dissolved in rain and dew. Lichens are generally absent in and around cities because of automobile traffic and industrial activity, but some are adapted to these conditions. As pollution decreases, lichen populations tend to increase.

Mycorrhizae are fungi associated with roots of plants

The roots of about 90% of all plant families have species that are involved in mutualistic symbiotic relationships with certain kinds of fungi. It has been estimated that these fungi probably amount to 15% of the total weight of the world's plant roots. Associations of this kind are termed **mycorrhizae,** from the Greek words for fungus and root.

The fungi in mycorrhizal associations function as extensions of the root system. The fungal hyphae dramatically increase the amount of soil contact and total surface area for absorption. When mycorrhizae are present, they aid in the direct transfer of phosphorus, zinc, copper, and other mineral nutrients from the soil into the roots. The plant, on the other hand, supplies organic carbon to the fungus, so the system is an example of mutualism.

There are two principal types of mycorrhizae (figure 31.17). In arbuscular mycorrhizae, the fungal hyphae penetrate the outer cells of the plant root, forming coils, swellings, and minute branches; they also extend out into the surrounding soil. In **ectomycorrhizae,** the hyphae surround but do not penetrate the cell walls of the roots. In both kinds of mycorrhizae, the mycelium extends far out into the soil. A single root may associate with many fungal species, dividing the root at a millimeter-by-millimeter level.

Arbuscular mycorrhizae

Arbuscular mycorrhizae are by far the more common of the two types, involving roughly 70% of all plant species (figure 31.17*a*). The fungal component in them are glomeromycetes, a monophyletic group that arose within one of the zygomycete lineages. The glomeromycetes are associated with more than 200,000 species of plants.

Unlike mushrooms, none of the glomeromycetes produce aboveground fruiting structures, and as a result, it is difficult to arrive at an accurate count of the number of extant species. Arbuscular mycorrhizal fungi are being studied intensively because they are potentially capable of increasing crop yields with lower phosphate and energy inputs.

The earliest fossil plants often show arbuscular mycorrhizal roots. Such associations may have played an important role in allowing plants to colonize land. The soils available at such times would have been sterile and lacking in organic matter. Plants that form mycorrhizal associations are particularly successful in infertile soils; considering the fossil evidence, it seems reasonable that mycorrhizal associations helped the earliest plants succeed on such soils. In addition, the closest living relatives of early vascular plants surviving today continue to depend strongly on mycorrhizae.

Some nonphotosynthetic plants also have mycorrhizal associations, but the symbiosis is one-way because the plant has no photosynthetic resources to offer. Instead of a two-partner symbiosis, a tripartite symbiosis is established. The fungal mycelium extends between a photosynthetic plant and a nonphotosynthetic, parasitic plant. This third, nonphotosynthetic member of the symbiosis is called an *epiparasite.* Not only does it obtain phosphate from the fungus, but it uses the fungus to channel carbohydrates from the photosynthetic plant to itself. Epiparasitism also occurs in ectomycorrhizal symbiosis.

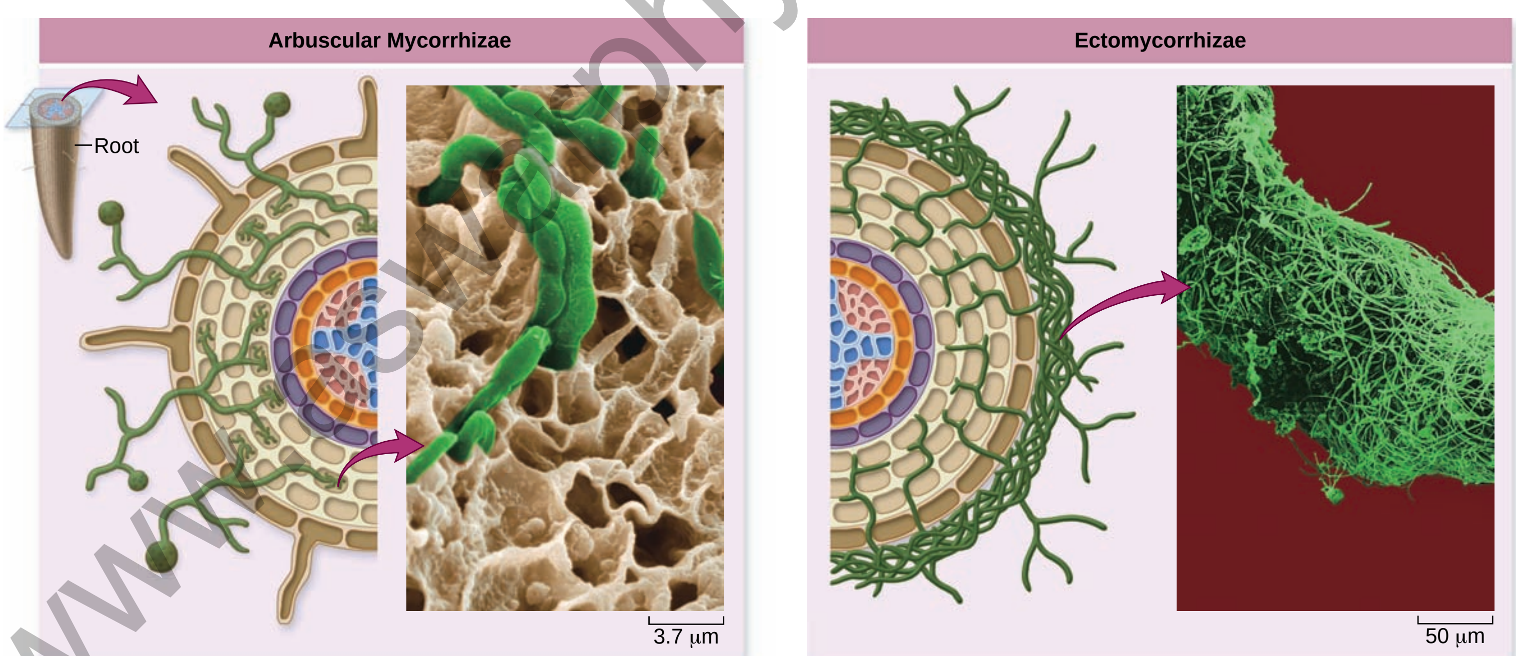
Ectomycorrhizae

Ectomycorrhizae (see figure 31.17*b*) involve far fewer kinds of plants than do arbuscular mycorrhizae—perhaps a few thousand. Most ectomycorrhizal hosts are forest trees, such as pines, oaks, birches, willows, eucalyptus, and many others. The fungal components in most ectomycorrhizae are basidiomycetes, but some are ascomycetes.

Most ectomycorrhizal fungi are not restricted to a single species of plant, and most ectomycorrhizal plants form associations with many ectomycorrhizal fungi. Different combinations have different effects on the physiological characteristics of the plant and its ability to survive under different environmental conditions. At least 5000 species of fungi are involved in ectomycorrhizal relationships.

Fungi also form mutual symbioses with animals

A range of mutualistic fungal–animal symbioses has been identified. Ruminant animals host neocallimastigomycete fungi in



a. *b.*

Figure 31.17 Arbuscular mycorrhizae and ectomycorrhizae. ***a.*** In arbuscular mycorrhizae, fungal hyphae penetrate the root cell wall of plants but not the plant membranes. ***b.*** Ectomycorrhizae on the roots of a *Eucalyptus* tree do not penetrate root cells, but grow around and extend between the cells.

Figure 31.18 Ant–fungal symbiosis. Ants farming their fungal garden.

their gut. The fungus gains a nutrient-rich environment in exchange for releasing nutrients from grasses with high cellulose and lignin content.

One tripartite symbiosis involves ants, plants, and fungi. Leaf-cutter ants are the dominant herbivore in the New World tropics. These ants, members of the phylogenetic tribe Attini, have an obligate symbiosis with specific fungi that they have domesticated and maintain in an underground garden. The ants provide fungi with leaves to eat and protection from pathogens and other predators (figure 31.18). The fungi are the ants' food source.

Depending on the species of ant, the ant nest can be as small as a golf ball or as large as 50 cm in diameter and many feet deep. Some nests are inhabited by millions of leaf-cutter ants that maintain fungal gardens. These social insects have a caste system, and different ants have specific roles. Traveling on trails as long as 200 m, leaf-cutter ants search for foliage for their fungi. A colony of ants can defoliate an entire tree in a day. This ant farmer–fungi symbiosis has evolved multiple times and may have occurred as early as 50 MYA.

Learning Outcomes Review 31.8

Fungi are the primary decomposers in ecosystems. A range of symbiotic relationships have evolved between fungi and plants. Endophytes live inside tissues of a plant and may protect it from parasites. Lichens are a complex symbiosis between fungal species and cyanobacteria or green algae. Mycorrhizal associations between fungi and plant roots are mutually beneficial and in some cases are obligate symbioses. Fungi have also coevolved with animals in mutualistic relationships.

- ***How might the symbiosis between fungi and ants have evolved?***

31.9 *Fungal Parasites and Pathogens*

Learning Outcomes

1. ***Review the pathogenic effects of fungi and the targets they affect.***
2. ***Explain why treating fungal disease in animals is particularly difficult.***

Fungi can destroy a crop of plants and create significant problems for human health. A major problem in treatment and prevention is that fungi are eukaryotes, as are plants and animals. Understanding how fungi are distinct from these other two eukaryotic kingdoms may lead to safer and more efficient means of treating diseases caused by fungal parasites and pathogens.

Fungal infestation can harm plants and those who eat them

Fungal species cause many diseases in plants (figure 31.19), and they are responsible for billions of dollars in agricultural losses

Figure 31.19 World's largest organism? ***a.*** *Armillaria*, a pathogenic fungus shown here afflicting three discrete regions of coniferous forest in Montana, grows out from a central focus as a single, circular clone. The large patch at the bottom of the picture is almost 8 hectares. ***b.*** Closeup of tree destroyed by *Armillaria*. ***c.*** *Armillaria* growing on a tree.

every year. Not only are fungi among the most harmful pests of living plants, but they also spoil food products that have been harvested and stored. In addition, fungi often secrete substances into the foods they are infesting that make these foods unpalatable, carcinogenic, or poisonous.

Pathogenic fungal–plant symbioses are numerous, and fungal pathogens of plants can also harm the animals that consume the plants. *Fusarium* species growing on spoiled food produce highly toxic substances, including vomitoxin, which has been implicated in brain damage in humans and animals in the southwestern United States.

Aflatoxins, which are among the most carcinogenic compounds known, are produced by some *Aspergillus flavus* strains growing on corn, peanuts, and cotton seed (figure 31.20). Aflatoxins can also damage the kidneys and the nervous system of animals, including humans. Most developed countries have legal limits on the concentration of aflatoxin permitted in different foods. More recently, aflatoxins have been considered as possible bioterrorism agents.

In contrast, corn smut is a maize fungal disease that is harmful to the plant, but not animals that consume it (figure 31.20). Corn smut is caused by the basidiomycete *Ustilago maydi* and is edible.

Fungal infections are difficult to treat in humans and other animals

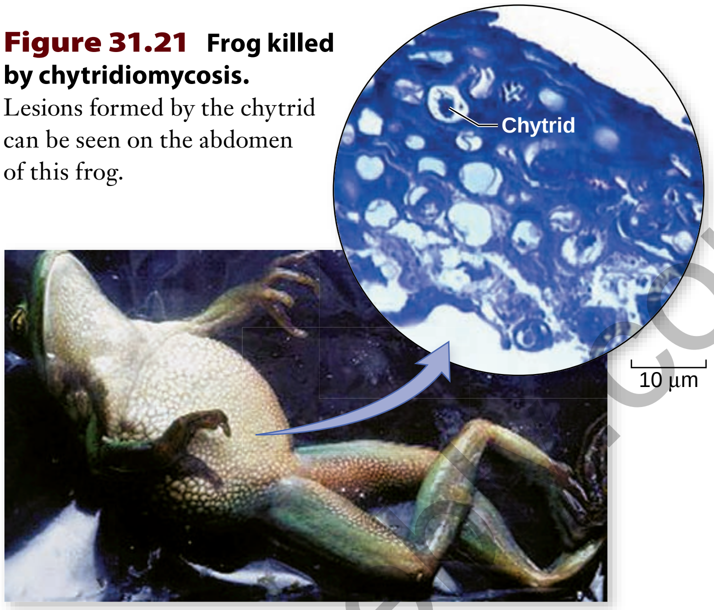
Human and animal diseases can also be fungal in origin. Some common diseases, such as ringworm (which is not a worm but a fungus), athlete's foot, and nail fungus, can be treated with topical antifungal ointments and in some cases with oral medication.

Fungi can create devastating human diseases that are often difficult to treat because of the close phylogenetic relationship between fungi and animals. Yeast ascomycetes are important pathogens that cause diseases such as thrush, an infection of the mouth; the yeast *Candida* causes common oral or vaginal infections. *Pneumocystis jiroveci* (formerly *P. carinii*) invades the lungs, disrupting breathing, and can spread to other organs. In immunesuppressed AIDS patients, this infection can lead to death.

a. **b.**

Figure 31.20 Maize (corn) fungal infections. ***a.*** *Ustilago maydis* infections of maize are a delicacy in Hispanic cuisine. ***b.*** A photomicrograph of *Aspergillus flavus* conidia. *Aspergillus flavus* infects maize and can produce aflatoxins that are harmful to animals.

Figure 31.21 Frog killed by chytridiomycosis. Lesions formed by the chytrid can be seen on the abdomen of this frog.



Mold allergies are common, and mold-infested "sick" buildings pose concerns for inhabitants. Individuals with suppressed immune systems and people undergoing steroid treatments for inflammatory disorders are particularly at risk for fungal disease.

An example of a parasitic fungal–animal symbiosis is **chytridiomycosis**, first identified in 1998 as an emerging infectious disease of amphibians. Amphibian populations have been declining worldwide for over three decades. The many possible causes for the decline in amphibian numbers are covered in chapter 60. In this chapter, a primary causative agent, fungal infection, is explored. The decline correlates with the presence of the chytrid *Batrachochytrium dendrobatidis encased in the skin* (figure 31.21), identified after extensive studies of frog carcasses. Sick and dead frogs were more likely than healthy frogs to have flasklike structures encased in their skin, which proved to be associated with chytrid spore production (see figure 31.21).

The connection with *B. dendrobatidis* has been supported by DNA sequence data, by isolating and culturing the chytrid, and by infecting healthy frogs with the organism and replicating disease symptoms. The *B. dendrobatidis* genome has now been sequenced. The infection reduces sodium and potassium transport across the skin, altering electrolyte balance which leads to cardiac arrest. Bathing frogs in antifungal drugs can halt the disease or even eliminate the chytrids.

How the disease emerged simultaneously on different continents is a yet unsolved mystery. Both environmental change and carriers are being considered.

Learning Outcomes Review 31.9

Fungi can severely harm or kill both plants and animals, either by direct infection or by secretion of toxins and carcinogens. Treatment of fungal disease and parasitism in animals is made difficult by the close relationship between fungi and animals; what is damaging to the fungus may also have ill effects on the host.

- ***What is likely to be the most common mechanism for the spread of fungal disease?***

Chapter Review

31.1 Defining Fungi

Fungi are more closely related to animals than to plants and form seven monophyletic phyla (see figure 31.1).

Fungi are heterotrophic and have hyphal cells; their cell walls contain chitin. They may have a dikaryon stage and undergo nuclear mitosis.

The body of a fungus is a mass of connected hyphae.

A mass of connected hyphae is termed a mycelium. Hyphae can be continuous and multinucleate, or they may be divided into long chains of cells separated by cross-walls called septa.

The chitin found in fungi cell walls is the same material found in the exoskeletons of arthropods.

Fungal cells may have more than one nucleus.

A hypha with only one nucleus is monokaryotic; a hypha with two nuclei is dikaryotic. The two haploid nuclei exist independently, but both genomes are transcribed so that some properties of diploids may be observed.

Mitosis is not followed by cell division.

Because cells are linked, the cell is not the relevant unit of reproduction, but rather the nucleus is. The spindle forms inside the nuclear envelope, which does not break down and re-form.

Fungi can reproduce both sexually and asexually.

Fungi can reproduce sexually by fusion of hyphae from two compatible mating types or hyphae from the same fungus. Spores can form either by asexual or sexual reproduction and are usually dispersed by the wind.

Fungi are heterotrophs that absorb nutrients.

Fungi obtain their nutrients through excreting enzymes for external digestion and then absorbing the products.

31.2 Microsporidia: Unicellular Parasites

Microsporidia are obligate cellular parasites that lack mitochondria but may have had them at one time; they were previously classed with the protists.

31.3 Chytridiomycota and Relatives: Fungi with Flagellated Zoospores

Chytrids form symbiotic relationships; they have been implicated in the decline of amphibian species.

Blastocladiomycota have single flagella.

Allomyces, a blastocladiomycete, is an example of a fungus with a haplodiplontic life cycle.

Neocallimastigomycota digest cellulose in ruminant herbivores.

Neocallimastigomycetes have enzymes that can digest cellulose and lignin; they may have uses in production of biofuels.

31.4 Zygomycota: Fungi That Produce Zygotes

In sexual reproduction, zygotes form inside a zygosporangium.

Zygomycetes all produce a diploid zygote. In sexual reproduction, fusion (karyogamy) of the haploid nuclei of gametangia produces diploid zygote nuclei. These become zygospores.

Asexual reproduction is more common.

Sporangia produce haploid spores that are airborne; bread mold is a common example of a zygomycete.

31.5 Glomeromycota: Asexual Plant Symbionts

Glomeromycete hyphae form intracellular associations with plant roots and are called arbuscular mycorrhizae.

The glomeromycetes show no evidence of sexual reproduction.

31.6 Basidiomycota: The Club (Basidium) Fungi

The basidiocarp is the visible reproductive structure of this group, which includes mushrooms, toadstools, puffballs, and others.

Basidiomycetes sexually reproduce within basidia (see figure 31.11).

Karyogamy occurs within the basidia, giving rise to a diploid cell. Meiosis then ultimately results in four haploid basidiospores.

The secondary mycelium of basidiomycetes is heterokaryotic.

Primary mycelium is monokaryotic, but different mating types may fuse to form the secondary mycelium. Maintenance of two haploid genomes allows greater genetic plasticity.

31.7 Ascomycota: The Sac (Ascus) Fungi

***Sexual reproduction occurs within the ascus* (see figure 31.12).**

Karyogamy occurs only in the ascus and results in a diploid nucleus. Meiosis and mitosis then result in eight haploid nuclei in walled ascospores.

Asexual reproduction occurs within conidiophores.

Asexual reproduction is very common and occurs by means of conidia formed at the end of modified hyphae called conidiophores.

Some ascomycetes have yeast morphology.

Yeasts usually reproduce by cell fission or budding.

Ascomycete genetics and genomics have practical applications.

31.8 Ecology of Fungi

Fungi are organisms capable of breaking down cellulose and lignin.

Fungi have a range of symbioses.

Fungi can be pathogenic or parasitic, commensal or mutualistic.

Endophytes live inside plants and may protect plants from parasites.

Lichens are an example of symbiosis between different kingdoms.

A lichen is composed of a fungus, usually an ascomycete, along with cyanobacteria, green algae, or both.

Mycorrhizae are fungi associated with roots of plants.

Arbuscular mycorrhizae are common and involve glomeromycetes; ectomycorrhizae are primarily found in forest trees and involve basidiomycetes and a few ascomycetes.

Fungi also form mutual symbioses with animals.

Some ants grow "farms" of fungi by providing plant material.

31.9 Fungal Parasites and Pathogens

Fungal infestation can harm plants and those who eat them.

Fungi spread via spores and can secrete chemicals that make food unpalatable, carcinogenic, or poisonous.

Fungal infections are difficult to treat in humans and other animals.

Treatment of fungal diseases in animals is difficult because of the similarities between the two kingdoms.

Review Questions

UNDERSTAND

1. Which of the following is not a characteristic of a fungus?
   a. Cell walls made of chitin
   b. A form of mitosis different from plants and animals
   c. Ability to conduct photosynthesis
   d. Filamentous structure
2. A fungal cell that contains two genetically different nuclei would be classified as
   a. monokaryotic.
   b. bikaryotic.
   c. homokaryotic.
   d. heterokaryotic.
3. Which of the following groups of fungi is *not* monophyletic?
   a. Zygomycota
   b. Basidiomycota
   c. Glomeromycota
   d. Ascomycota
4. Based on physical characteristics, the __________ represent the most ancient phylum of fungi.
   a. Basidiomycota
   b. Zygomycota
   c. Ascomycota
   d. Chytridiomycota
5. The early evolution of terrestrial plants was made possible by mycorrhizal relationships with the
   a. Zygomycetes.
   b. Glomeromycota.
   c. Ascomycota.
   d. Basidiomycota.
6. Symbiotic relationships occur between the fungi and
   a. plants.
   b. bacteria.
   c. animals.
   d. all of the above.
7. Which of the following species of fungi is not associated with diseases in humans?
   a. *Pneumocystis jiroveci*
   b. *Aspergillus flavus*
   c. *Candida albicans*
   d. *Batrachochytrium dendrobatidis*

APPLY

1. In a culture of hyphae of unknown origin you notice that the hyphae lack septa and that the fungi reproduce asexually by using clumps of erect stalks. However, at times sexual reproduction can be observed. To what group of fungi would you assign it?
   a. Chytridiomycota
   b. Basidiomycota
   c. Ascomycota
   d. Zygomycota
2. Examine the life cycle of a typical basidiomycetes and determine where you would expect to find a dikaryotic cell.
   a. Primary mycelium
   b. Secondary mycelium
   c. In the basidiospores
   d. In the zygote
3. Determine which of the following is correct regarding the yeast *Saccharomyces cerevisiae*.
   a. It reproduces asexually by a process called budding.
   b. It produces an ascocarp during reproduction.
   c. It belongs in the group Zygomycota.
   d. All of the above are correct.
4. Appraise the fungal relationship between a forest tree and a basidiomycetes and determine the most suitable classification for the symbiosis.
   a. Parasitism only
   b. An arbuscular mycorrhizae
   c. Ectomycorrhizae
   d. A lichen
5. Choose which of the following best reflects the symbiotic relationships between animals and fungi.
   a. Protection from bacteria
   b. Colonization of land
   c. Protection from desiccation
   d. Exchange of nutrients

SYNTHESIZE

1. Historically fungi have been classified as being more plantlike despite their lack of photosynthetic ability. Although we now know that fungi are more closely related to the animals than the plants, review characteristics that initially led scientists to place them closer to the plants.
2. The importance of fungi in the evolution of terrestrial life is typically understated. Evaluate the importance of fungi in the colonization of land.
3. Based on your understanding of fungi, hypothesize why antibiotics won't work in the treatment of a fungal infection.

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Chapter 32

Overview of Animal Diversity

Chapter Outline

Introduction

We now explore the great diversity of modern animals, the result of a long evolutionary history. Animals are among the most abundant living organisms. Found in almost every habitat, they bewilder us with their diversity in form, habitat, behavior, and lifestyle. About a million and a half species have been described, and several million more are thought to await discovery. Despite their great diversity, animals have much in common. For example, locomotion is a distinctive characteristic, although not all animals can move about. Early naturalists thought that sponges and corals were plants because the adults are attached to the surface on which they live.

32.1 Some General Features of Animals

Learning Outcome

1. *Identify three features that characterize all animals and three that characterize only some types of animals.*

Animals are so diverse that few criteria fit them all. But some, such as animals being eaters, or consumers, apply to all. Others, such as their being mobile (they can move about) have exceptions. Taken together, the universal characteristics and other features of major importance that have exceptions are convincing evidence that animals are monophyletic—that they descended from a common ancestor. Table 32.1 describes the general features of animals.

Learning Outcome Review 32.1

All animals are multicellular and heterotrophic, and their cells lack cell walls. Most animals can move from place to place, can reproduce sexually, and possess unique tissues. Animals can be found in almost all habitats.

- *What evidence is there that animals could not have been the first type of life to have evolved?*

TABLE 32.1 General Features of Animals

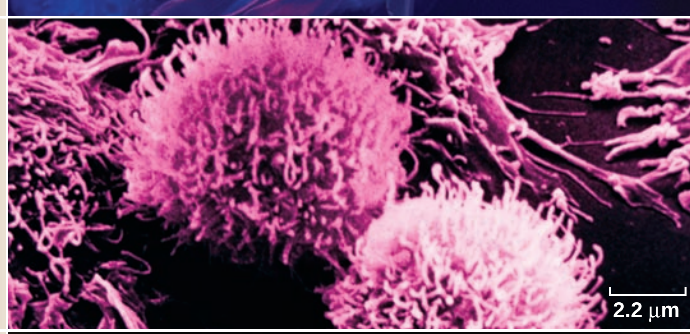
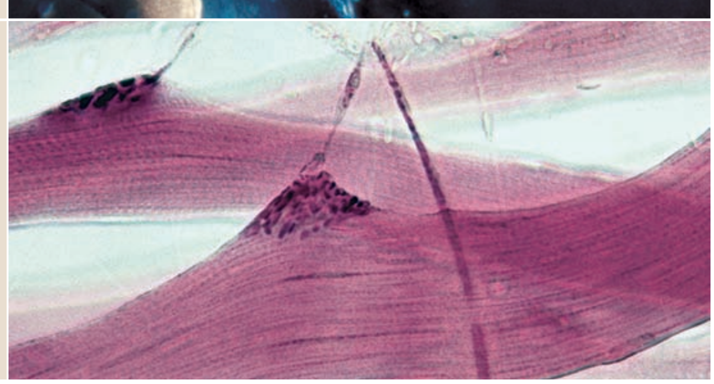
Heterotrophy. All animals are heterotrophs—that is, they obtain energy and organic molecules by ingesting other organisms. Unlike autotrophic plants and algae, animals cannot construct organic molecules from inorganic chemicals. Some animals (herbivores) consume autotrophs; other animals (carnivores) consume heterotrophs; some animals (omnivores) consume both autotrophs and heterotrophs; and still others (detritivores) consume decomposing organisms.	
Multicellularity. All animals are multicellular; many have complex bodies like that of this jellyfish (phylum Cnidaria). The unicellular heterotrophic organisms called Protozoa, which were at one time regarded as simple animals, are now considered members of the large and diverse kingdom Protista, discussed in chapter 29.	
No Cell Walls. Animal cells differ from those of other multicellular organisms: they lack rigid cell walls and are usually quite flexible. The many cells of animal bodies are held together by extracellular frames of structural proteins such as collagen. Other proteins form unique intercellular junctions between animal cells.	
Active Movement. Animals move more rapidly and in more complex ways than members of other kingdoms—this ability is perhaps their most striking characteristic, one directly related to the flexibility of their cells and the evolution of nerve and muscle tissues. A remarkable form of movement unique to animals is flying, a capability that is well developed among vertebrates and insects such as this butterfly (phylum Arthropoda). Many animals cannot move from place to place (they are sessile) or do so rarely or slowly (they are sedentary) although they have muscles or muscle fibers that allow parts of their bodies to move. Sponges, however, have little capacity for movement.	

TABLE 32.1 General Features of Animals, *continued*

Diversity in Form. Animals vary greatly in form, ranging in size from organisms too small to see with the unaided eye to enormous whales and giant squids. Almost all animals, like this millipede (phylum Arthropoda), lack a backbone—they are therefore called invertebrates. Of the million known living animal species, only 42,500 have a backbone—they are therefore referred to as **vertebrates.** Probably most of the many millions of animal species awaiting discovery are invertebrates.	
Diversity in Habitat. The animal kingdom is divided into 35–40 phyla, most of which have members that occur only in the sea like this brittlestar (phylum Echinodermata). Members of fewer phyla occur in fresh water, and members of fewer still occur on land. Members of three phyla that are successful in the marine environment—Arthropoda, Mollusca, and Chordata—also dominate animal life on land. Only one animal phylum, Onychophora (velvet worms) is entirely terrestrial.	
Sexual Reproduction. Most animals reproduce sexually; these tortoises (phylum Chordata) are engaging in the first step of that process. Animal eggs, which are nonmobile, are much larger than the small, usually flagellated sperm. In animals, cells formed in meiosis function as gametes. These haploid cells do not divide by mitosis first, as they do in plants and fungi, but rather fuse directly with each other to form the zygote. Consequently, there is no counterpart among animals to the alternation of haploid (gametophyte) and diploid (sporophyte) generations characteristic of plants. Some individuals of some species and all individuals of a very few animal species are incapable of sexual reproduction.	
Embryonic Development. An animal zygote first undergoes a series of mitotic divisions, called *cleavage,* and like this dividing frog's egg, that produces a ball of cells, the **blastula.** In most animals, the blastula folds inward at one point to form a hollow sac with an opening at one end called the **blastopore.** An embryo at this stage is called a **gastrula.** The subsequent growth and movement of the cells of the gastrula differ from one group of animals to another, reflecting the evolutionary history of the group. Embryos of most kinds of animals develop into a larva, which looks unlike the adult of the species, lives in a different habitat, and eats different sorts of food; in most groups, it is very small. A larva undergoes metamorphosis, a radical reorganization, to transform into the adult body form.	
Tissues. The cells of all animals except sponges are organized into structural and functional units called **tissues,** collections of cells that together are specialized to perform specific tasks. Animals are unique in having two tissues associated with movement: (1) muscle tissue, which contracts, and (2) nervous tissue, which conducts signals among cells. Neuromuscular junctions, where nerves connect with muscle tissue, are shown here.	

32.2 Evolution of the Animal Body Plan

Learning Outcomes

1. *Differentiate between a pseudocoelom and a coelom.*
2. *Explain the difference between protostomes and deuterostomes.*
3. *Describe the advantages of segmentation.*

The features described in the preceding section evolved over the course of millions of years. We can understand how the history of life has proceeded by examining the types of animal bodies and body plans present in fossils and in existence today.

Five key innovations can be noted in animal evolution:

1. The evolution of symmetry
2. The evolution of tissues, allowing specialized structures and functions
3. The evolution of a body cavity
4. The evolution of various patterns of embryonic development
5. The evolution of segmentation, or repeated body units

These innovations are explained in the sections that follow. Some innovations appear to have evolved only once, some twice or more. Scientists use an innovation that evolved once as evidence that all the animals possessing it are more closely related to one another than they are to any animal lacking the innovation. The animals with the innovation and their ancestor in which the innovation arose are said to constitute a clade—an evolutionarily coherent group (see chapter 23). On the other hand, some innovations evolve more than once in different clades. This is the phenomenon of convergent evolution (see chapter 23). Although not indicative of close evolutionary relationship, convergently evolved innovations may be important to how species have adapted to their environments.

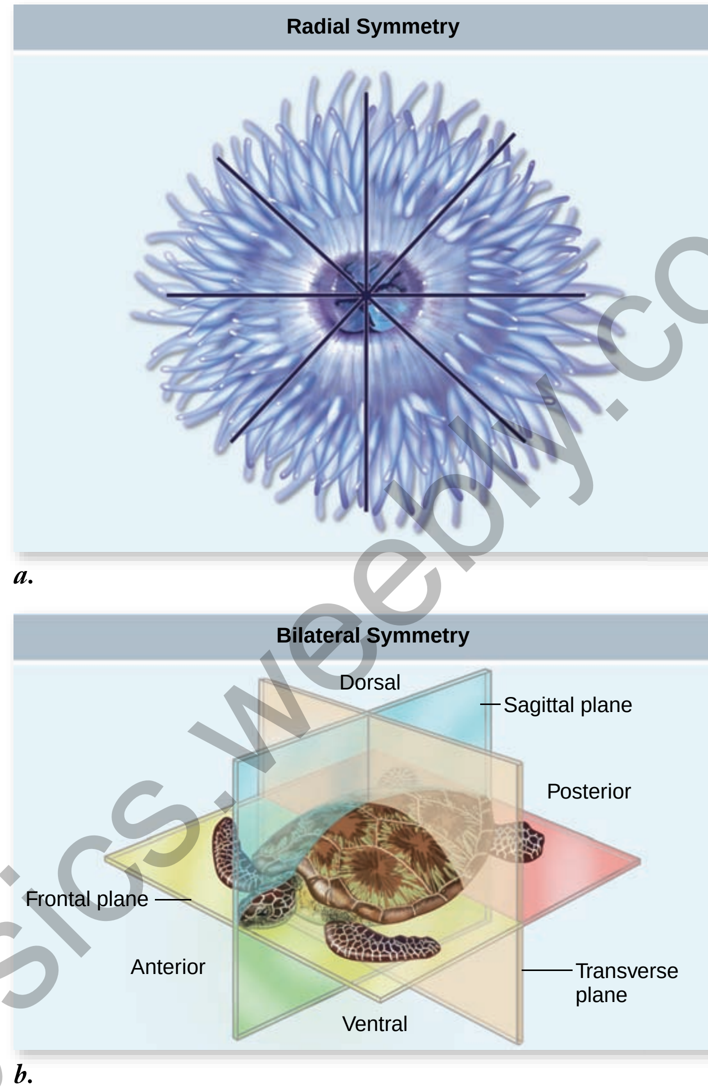


Figure 32.1 A comparison of radial and bilateral symmetry. ***a.*** Radially symmetrical animals, such as this sea anemone (phylum Cnidaria), can be bisected into equal halves by any longitudinal plane that passes through the central axis. ***b.*** Bilaterally symmetrical animals, such as this turtle (phylum Chordata), can only be bisected into equal halves in one plane (the sagittal plane).

Most animals exhibit radial or bilateral symmetry

A typical sponge lacks definite symmetry, growing as an irregular mass. Virtually all other animals have a definite shape and symmetry that can be defined along an imaginary axis drawn through the animal's body. The two main types of symmetry are radial and bilateral.

Radial symmetry

The body of a member of phylum Cnidaria (jellyfish, sea anemones, and corals: the C of Cnidaria is silent; see chapter 34) exhibits **radial symmetry.** Its parts are arranged in such a way that any longitudinal plane passing through the central axis divides the organism into halves that are approximate mirror images (figure 32.1*a*). A pie, for example, is radially symmetrical. In cnidarians such as corals and sea anemones, the mouth is not circular, but oval, because it opens into a sort of throat that is like a flattened sleeve. Thus there are two planes that divide the body into mirror-image halves, one along the mouth and one perpendicular to it; these animals are actually biradially symmetrical (figure 32.1*b*).

Bilateral symmetry

The bodies of most animals other than sponges and cnidarians exhibit **bilateral symmetry,** in which the body has right and left halves that are mirror images of each other. Animals with this body plan are collectively termed the Bilateria. The sagittal plane defines these halves. A bilaterally symmetrical body has, in addition to left and right halves, dorsal and ventral portions, which are divided by the frontal plane, and anterior (front) and posterior (rear) ends, which are divided by the transverse plane (in an animal that walks on all fours, dorsal is the top side). In echinoderms (sea stars and their relatives), adults are radially symmetrical (actually pentaradially symmetrical, because the body has five clear sections), but the larvae are bilaterally symmetrical.

Bilateral symmetry constitutes a major evolutionary advance in the animal body plan. Bilaterally symmetrical animals have the ability to move through the environment in a consistent direction (typically with the anterior end leading)—a feat that is difficult for radially symmetrical animals. Associated with directional movement is the grouping of nerve cells into a brain, and sensory structures, such as eyes and ears, at the anterior end of the body. This concentration of nervous tissue at the anterior end, which appears to have occurred early in evolution, is called **cephalization.** Much of the layout of the nervous system in bilaterally symmetrical animals is centered on one or more major longitudinal nerve cords that transmit information from the anterior sense organs and brain to the rest of the body. Cephalization is often considered a consequence of the development of bilateral symmetry.

The evolution of tissues allowed for specialized structures and functions

The zygote (a fertilized egg), has the capability to give rise to all the kinds of cells in an animal's body. That is, it is totipotent (all powerful). During embryonic development, cells specialize to carry out particular functions. In all animals except sponges, the process is irreversible: once a cell differentiates to serve a function, it and its descendants can never serve any other.

A sponge cell that had specialized to serve one function (such as lining the cavity where feeding occurs) can lose the special attributes that serve that function and change to serve another function (such as being a gamete). Thus a sponge cell can dedifferentiate and redifferentiate. Cells of all other animals are organized into tissues, each of which is characterized by cells of particular morphology and capability. But their competence to dedifferentiate prevents sponge cells from forming clearly defined tissues (and therefore, of course, organs, which are composed of tissues).

Because cells differentiate irreversibly in all animals except sponges, scientists infer that bodies containing cells specialized to serve particular functions have an advantage compared to those with cells that potentially have multiple functions. Judging by the relative diversity of animals with specialized tissues and those lacking them, tissues are a favorable adaptation. Presumably the advantage to the animal is embodied in the old adage "Jack of all trades, master of none."

A body cavity made possible the development of advanced organ systems

In the process of embryonic development, the cells of animals of most groups organize into three layers (called germ layers): an outer **ectoderm,** an inner **endoderm,** and an intermediate **mesoderm.** Animals with three embryonic cell layers are said to be triploblastic. Part of the maturation from the embryo is that certain organs and organ systems develop from each germ layer. The ectoderm gives rise to the outer covering of the body and the nervous system; the endoderm gives rise to the digestive system, including the intestine; and the skeleton and muscles develop from the mesoderm. Cnidarians have only two layers (thus they are diplobastic), the endoderm and the ectoderm, and lack organs. Sponges lack germ layers altogether; they, of course, have no tissues or organs. All triploblastic animals are members of the Bilateria.

A key innovation in the body plan of some bilaterians was a body cavity isolated from the exterior of the animal. This is different from the digestive cavity, which is open to the exterior at least through the mouth, and in most animals at the opposite end as well, via the anus. The evolution of efficient organ systems within the animal body was not possible until a body cavity evolved for accommodating and supporting organs (such as our heart and lungs), distributing materials, and fostering complex developmental interactions. The cavity is filled with fluid: in most animals, the fluid is liquid, but in vertebrates, it is gas—the body cavity of humans filling with liquid is a life-threatening condition. A very few types of bilaterians have no body cavity, the space between tissues that develop from the mesoderm and those that develop from the endoderm being filled with cells and connective tissue. These are the so-called acoelomate animals (figure 32.2).

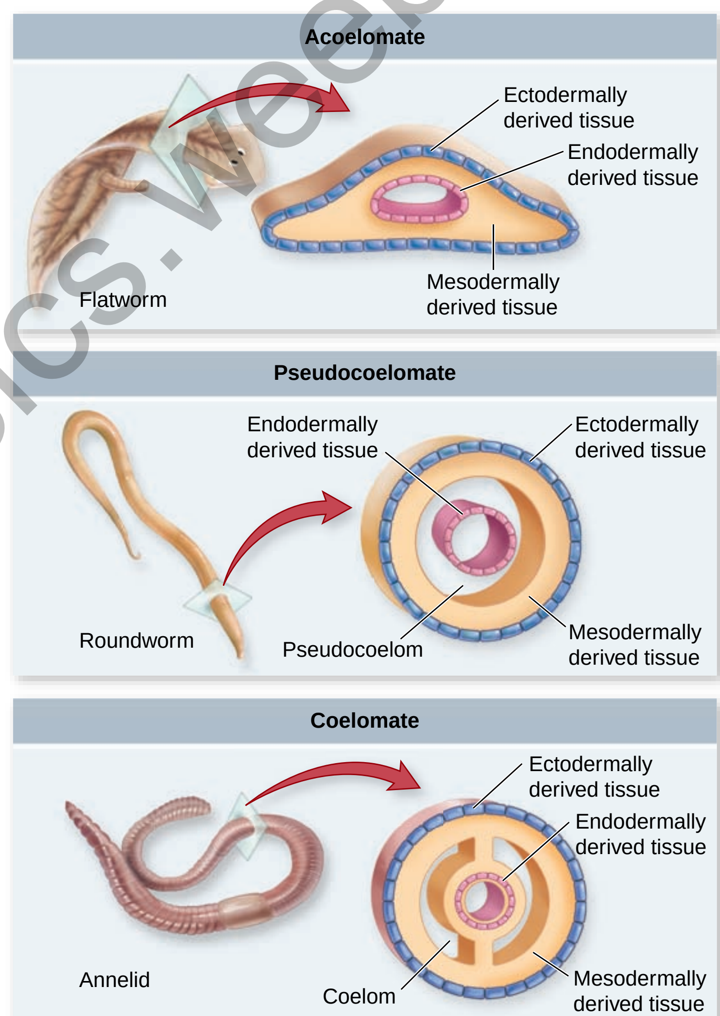


Figure 32.2 Three body plans for bilaterally symmetrical animals. Acoelomates, such as flatworms, have no body cavity between the digestive tract (derived from the endoderm) and the musculature layer (derived from the mesoderm). Pseudocoelomates have a body cavity, the pseudocoelom, between tissues derived from the endoderm and those derived from the mesoderm. Coelomates have a body cavity, the coelom, that develops entirely within tissues derived from the mesoderm, and so is lined on both sides by tissue derived from the mesoderm.

Body cavities

Body cavities appear to have evolved multiple times in the Bilateria (see figure 32.2). A body cavity called the **pseudocoelom** develops embryologically between mesoderm and endoderm, so occurs in the adult between tissues derived from the mesoderm and those derived from endoderm; animals with this type of body cavity are termed pseudocoelomates. Although the word *pseudocoelom* means "false coelom," this is a true body space and characterizes many successful groups of animals. A **coelom** is a cavity that develops entirely within the mesoderm. The coelom is surrounded by a layer of epithelial cells derived from the mesoderm and termed the peritoneum.

Zoologists previously inferred that the first animals were acoelomate, that some of their descendants evolved a pseudocoelom, and that some pseudocoelomate descendants evolved the coelom. However, as you saw in chapter 21, evolution rarely occurs in such a linear and directional way. Rather, pseudocoeloms seem to have evolved several times, and some animals have lost the body space, becoming acoelomate secondarily. However, a coelom appears to have evolved just once. Thus, species possessing a coelom form a clade, but those with a pseudocoelom do not.

The circulatory system

In many small animals, nutrients and oxygen are distributed and wastes are removed by fluid in the body cavity. Most larger animals, in contrast, have a **circulatory system,** a network of vessels that carry fluids to and from the parts of the body distant from the sites of digestion (gut) and gas exchange (gills or lungs). The circulating fluid carries nutrients and oxygen to the tissues and removes wastes, including carbon dioxide, by diffusion between the circulatory fluid and the other cells of the body.

In an **open circulatory system,** the blood passes from vessels into sinuses, mixes with body fluid that bathes the cells of tissues, then reenters vessels in another location. In a **closed circulatory system,** the blood is entirely confined to blood vessels, so is physically separated from other body fluids. Blood moves through a closed circulatory system faster and more efficiently than it does through an open system; open systems are typical of animals that are relatively inactive and so do not have a high demand for oxygen. In small animals, blood can be pushed through a closed circulatory system by movement of the animal. In larger animals, the body musculature does not provide enough force, so the blood must be propelled by contraction of one or more hearts, which are specialized, muscular parts of the blood vessels.

Bilaterians have two main types of development

The processes of embryonic development in animals is discussed fully in chapter 54. Briefly, development of a bilaterally symmetrical animal begins with mitotic cell divisions (called cleavages) of the egg that lead to the formation of a hollow ball of cells, which subsequently indents to form a two-layered ball. The internal space that is created through such indentation (figure 54.11) is the **archenteron** (literally the "primitive gut"); it communicates with the outside by a **blastopore.**

In a protostome, the mouth of the adult animal develops from the blastopore or from an opening near the blastopore (protostome means "first mouth"—the first opening becomes the mouth). **Protostomes** include most bilaterians, including flatworms, nematodes, mollusks, annelids, and arthropods. In some protostomes, both mouth and anus form from the embryonic blastopore; in other protostomes, the anus forms later in another region of the embryo. Two outwardly dissimilar groups, the echinoderms and the chordates, together with a few other small phyla, constitute the **deuterostomes,** in which the mouth of the adult animal does not develop from the blastopore. The deuterostome blastopore gives rise to the organism's anus, and the mouth develops from a second pore that arises later in development (deuterostome means "second mouth"). Protostomes and deuterostomes differ in several other aspects of embryology too, as discussed later.

Cleavage patterns

The cleavage pattern relative to the embryo's polar axis determines how the resulting cells lie with respect to one another. In some protostomes, each new cell cleaves off at an angle oblique to the polar axis. As a result, a new cell nestles into the space between the older ones in a closely packed array. This pattern is called **spiral cleavage** because a line drawn through a sequence of dividing cells spirals outward from the polar axis (figure 32.3 top). Spiral cleavage is characteristic of annelids, mollusks, nemerteans, and related phyla; the clade of animals with this cleavage pattern is therefore known as the Spiralia.

In all deuterostomes, by contrast, the cells divide parallel to and at right angles to the polar axis. As a result, the pairs of cells from each division are positioned directly above and below one another, a process that gives rise to a loosely packed ball. This pattern is called **radial cleavage** because a line drawn through a sequence of dividing cells describes a radius outward from the polar axis (figure 32.3 bottom).

Determinate versus indeterminate development

Many protostomes exhibit **determinate development,** in which the type of tissue each embryonic cell will form in the adult is determined early, in many lineages even before cleavage begins, when the molecules that act as developmental signals are localized in different regions of the egg. Consequently, the cell divisions that occur after fertilization segregate molecular signals into different daughter cells, specifying the fate of even the very earliest embryonic cells. Each embryonic cell is destined to occur only in particular parts of the adult body, so if the cells are separated, development cannot proceed.

Deuterostomes, on the other hand, display **indeterminate development.** The first few cell divisions of the zygote produce identical daughter cells. If the cells are separated, any one can develop into a complete organism because the molecules that signal the embryonic cells to develop differently are not segregated in different cells until later in the embryo's development. (This is how identical twins are formed.) Thus, each cell remains totipotent and its fate is not determined for several cleavages.

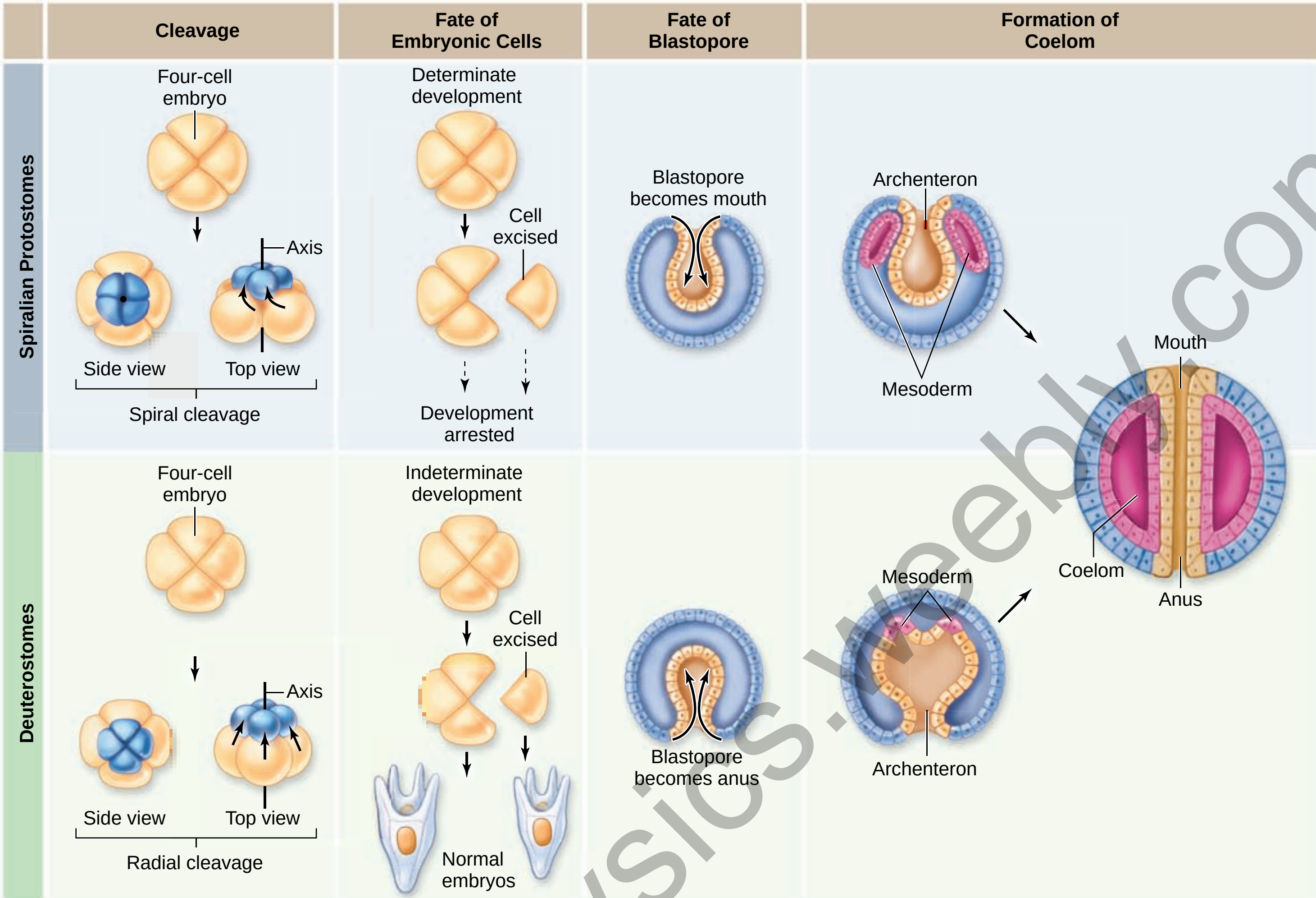


Figure 32.3 Embryonic development in protostomes and deuterostomes. In spiralian protostomes, embryonic cells cleave in a spiral pattern and exhibit determinate development; the blastopore becomes the animal's mouth, and the coelom originates from a split among endodermal cells. In deuterostomes, embryonic cells cleave radially and exhibit indeterminate development; the blastopore becomes the animal's anus, and the coelom originates from an invagination of the archenteron.

Formation of the coelom

The coelom arises within the mesoderm. In protostomes, cells simply move apart from one another to create an expanding coelomic cavity within the mass of mesodermal cells. In deuterostomes, groups of cells pouch off the end of the archenteron, which you will recall is the primitive gut—the hollow in the center of the developing embryo that is lined with endoderm.

The consistency of deuterostome development and its distinctiveness from that of the protostomes suggest that it evolved once, in the ancestor of the deuterostome phyla. The mode of development in protostomes is more diverse, but because of the distinctiveness of spiral development, scientists infer it also evolved once, in the common ancestor to all spiralian phyla.

Segmentation allowed for redundant systems and improved locomotion

Segmented animals consist of a series of linearly arrayed compartments that typically look alike (see figure 34.14), at least early in development, but that may have specialized functions. Development of segmentation is mediated at the molecular level by *Hox* genes (see chapters 19 and 25, and in section 32.4). During early development, segments first are obvious in the mesoderm but later are reflected in the ectoderm and endoderm. Two advantages result from early embryonic segmentation:

1. In highly segmental animals, such as earthworms (phylum Annelida), each segment may develop a more or less complete set of adult organ systems. Because these are redundant systems, damage to any one segment need not be fatal because other segments duplicate the damaged segment's functions.
2. Locomotion is more efficient when individual segments can move semi-independently. Because partitions isolate the segments, each can contract or expand autonomously. Therefore, a long body can move in ways that are often quite complex.

Segmentation underlies the organization of body plans of the most morphologically complex animals. In some adult arthropods, the segments are fused, but segmentation is usually apparent in embryological development. In vertebrates, the backbone and muscle blocks are segmented, although segmentation is often disguised in the adult form.

Previously, zoologists considered that true segmentation was found only in annelids, arthropods, and chordates, but segmentation is now recognized to be more widespread. Animals such as onychophorans (velvet worms), tardigrades (water bears), and kinorhynchs (mud dragons) are also segmented.

Learning Outcomes Review 32.2

Animals are distinguished on the basis of symmetry, tissues, type of body cavity, sequence of embryonic development, and segmentation. A pseudocoelom is a space that develops between the mesoderm and endoderm; a coelom develops entirely within mesoderm. In bilaterians, protostomes develop the mouth prior to the anus; deuterostomes develop the mouth after the anus has formed. Segmentation allows redundant systems and more efficient locomotion.

- ***How is cephalization related to body symmetry?***

32.3 *The Classification of Animals*

Learning Outcomes

1. ***List the major criteria scientists have used to distinguish animal phyla.***
2. ***Distinguish between spiralian and ecdysozoan organisms.***
3. ***Identify the placement of humans among the animal phyla.***

Multicellular animals, or metazoans, are traditionally divided into 35 to 40 phyla (singular, *phylum*). There is little disagreement among biologists about the placement of most animals in phyla, although zoologists disagree on the status of some, particularly those with few members or recently discovered ones. The diversity of animals is obvious in tables 32.2 and 32.3, which describe key characteristics of 20 of the phyla.

Traditionally, the phylogeny of animals has been inferred using features of anatomy and aspects of embryological development, as discussed earlier, from which a broad consensus emerged over the last century concerning the main branches of the animal tree of life. In the past 30 years, data derived from molecular features have been added, leading to some rethinking of classification schemes. Depending on the features compared, biologists may draw quite different family trees—although, of course, there is only one way that evolution actually occurred, and the goal of phylogeny is to detect that history.

Whether morphological or molecular characters (or both) are used, the underlying principle is the same: systematists use features they assume to have evolved only once, so the animals sharing such a feature are inferred to be more closely related to one another than they are to animals not sharing the feature. The shared derived characters unique to a group and its ancestors define a monophyletic assemblage termed a clade (see chapter 23). The animal phylogenetic tree viewed in these terms is a hierarchy of clades nested within larger clades, and containing smaller clades.

Tissues and symmetry separate the Parazoa and Eumetazoa

Systematists traditionally divided the kingdom Animalia (also termed Metazoa) into two main branches. Parazoa ("near animals") comprises animals that, for the most part, lack definite symmetry, and that do not possess tissues. These are the sponges, phylum Porifera. Because they are so different in so many ways from other animals, some scientists inferred that sponges were not closely related to other animals, which would mean that what we consider animals had two separate origins. Eumetazoa ("true animals") are animals that have a definite shape and symmetry. All have tissues, and most have organs and organ systems. Now most systematists agree that Parazoa and Eumetazoa are descended from a common ancestor, so animal life had a single origin. And although most trees constructed including molecular data consider Parazoa to be at the base of the animal tree of life, some do not.

Further divisions are based on other key features, as discussed previously. Bilaterally symmetrical animals (which are also triploblastic) are divided into the groups Protostomia and Deuterostomia depending on whether the embryonic blastopore (see figure 32.3) becomes the mouth or the anus (or both), respectively, in the adult animal.

Animals are traditionally classified into 35 to 40 phyla. The evolutionary relationships among the animal phyla are based on the inference that phyla sharing certain fundamental morphological and molecular characters are more closely related to one another than they are to phyla not sharing those characters. Phylogenetically informative characters are inferred to have arisen only once.

Molecular data help reveal evolutionary relationships

Gene sequence data are accumulating at an accelerating pace for all animal groups. Phylogenies developed from different molecules sometimes suggest quite different evolutionary relationships among the same groups of animals. However, combining data from multiple genes has resolved the relationships of most phyla. Current studies are using sequences from hundreds of genes to try to fully resolve the animal tree of life.

Molecular data are helping to resolve some problems with the traditional phylogeny, such as puzzling groups that did not fit well into the widely accepted phylogeny. These data may be especially helpful in clarifying relationships that conventional data cannot, as, for example, in animals such as parasites. Through dependence on their host, the anatomy, physiology, and behavior of parasites tends to be greatly altered, so features that may reveal the phylogenetic affinities of free-living animals can be highly modified or lost.

TABLE 32.2 Animal Phyla with the Most Species

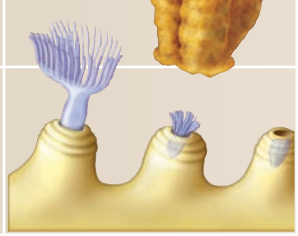
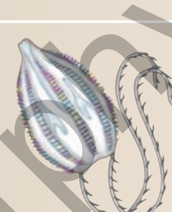
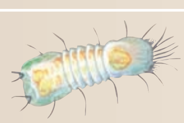
Phylum	Typical Examples		Key Characteristics	Approximate Number of Named Species
Arthropoda (arthropods)	Beetles, other insects, crabs, spiders, krill, scorpions, centipedes, millipedes		Chitinous exoskeleton covers segmented, coelomate body. With paired, jointed appendages; many types of insects have wings. Occupy marine, terrestrial, and freshwater habitats. Most arthropods are insects (as are most animals!).	1,000,000
Mollusca (mollusks)	Snails, oysters, clams, octopuses, slugs		Coelomate body of many mollusks is covered by one or more shells secreted by a part of the body termed the mantle. Many kinds possess a unique rasping tongue, a radula. Members occupy marine, terrestrial, and freshwater habitats (35,000 species are terrestrial).	110,000
Chordata (chordates)	Mammals, fish, reptiles, amphibians		Each coelomate individual possesses a notochord, a dorsal nerve cord, pharyngeal slits, and a postanal tail at some stage of life. In vertebrates, the notochord is replaced during development by the spinal column. Members occupy marine, terrestrial, and freshwater habitats (20,000 species are terrestrial).	56,000
Platyhelminthes (flatworms)	Planarians, tapeworms, liver and blood flukes		Unsegmented, acoelomate, bilaterally symmetrical worms. Digestive cavity has only one opening; tapeworms lack a gut. Many species are parasites of medical and veterinary importance. Members occupy marine, terrestrial, and freshwater habitats (as well as the bodies of other animals)	20,000
Nematoda (roundworms)	*Ascaris,* pinworms, hookworms, filarial worms		Pseudocoelomate, unsegmented, bilaterally symmetrical worms; tubular digestive tract has mouth and anus. Members occupy marine, terrestrial, and freshwater habitats; some are important parasites of plants and animals, including humans.	25,000 (but it is thought by some that the number of nematode species may be much greater)
Annelida (segmented worms)	Earthworms, polychaetes, tube worms, leeches		Segmented, bilaterally symmetrical, coelomate worms with a complete digestive tract; most have bristles (chaetae) on each segment that anchor them in tubes or aid in crawling. Occupy marine, terrestrial, and freshwater habitats.	16,000
Cnidaria (cnidarians)	Jellyfish, *Hydra,* corals, sea anemones, sea fans		Radially symmetrical, acoelomate body has tissues but no organs. Mouth opens into a simple digestive sac and is surrounded by tentacles armed with stinging capsules (nematocysts). In some groups, individuals are joined into colonies; some can secrete a hard exoskeleton. The very few nonmarine species live in fresh water.	10,000
Echinodermata (echinoderms)	Sea stars, sea urchins, sand dollars, sea cucumbers		Adult body pentaradial (fivefold) in symmetry. Water-vascular system is a coelomic space; endoskeleton of calcium carbonate plates. Many can regenerate lost body parts. Fossils are more diverse in body plan than extant species. Exclusively marine.	7000
Porifera (sponges)	Barrel sponges, boring sponges, basket sponges, bath sponges		Bodies of most asymmetrical: defining "an individual" is difficult. Body lacks tissues or organs, being a meshwork of cells surrounding channels that open to the outside through pores, and that expand into internal cavities lined with food-filtering flagellated cells (choanocytes). Most species are marine (150 species live in fresh water).	7000
Bryozoa (moss animals) (also called Polyzoa and Ectoprocta)	Sea mats, sea moss		The only exclusively colonial phylum; each colony comprises small, coelomate individuals (zooids) connected by an exoskeleton (calcareous in marine species, organic in most freshwater ones). A ring of ciliated tentacles (lophophore) surrounds the mouth of each zooid; the anus lies beyond the lophophore.	4500

TABLE 32.3 Some Important Animal Phyla with Fewer Species—and Three Recently Discovered Ones

Phylum	Typical Examples		Key Characteristics	Approximate Number of Named Species
Rotifera (wheel animals)	Rotifers		Small pseudocoelomates with a complete digestive tract including a set of complex jaws. Cilia at the anterior end beat so they resemble a revolving wheel. Some are very important in marine and freshwater habitats as food for predators such as fishes.	2000
Nemertea (ribbon worms) (also called Rhynchocoela)	*Lineus*		Protostome worms notable for their fragility—when disturbed, they fragment in pieces. Long, extensible proboscis occupies a coelomic space; that of some tipped by a spearlike stylet. Most marine, but some live in fresh water, and a few are terrestrial.	900
Tardigrada (water bears)	*Hypsibius*		Microscopic protostomes with five body segments and four pairs of clawed legs. An individual lives a week or less but can enter a state of suspended animation ("cryptobiosis") in which it can survive for many decades. Occupy marine, freshwater, and terrestrial habitats.	800
Brachiopoda (lamp shells)	*Lingula*		Protostomous animals encased in two shells that are oriented with respect to the body differently than in bivalved mollusks. A ring of ciliated tentacles (lophophore) surrounds the mouth. More than 30,000 fossil species are known.	300
Onychophora (velvet worms)	*Peripatus*		Segmented protostomous worms resembling tardigrades; with a chitinous soft exoskeleton and unsegmented appendages. Related to arthropods. The only exclusively terrestrial phylum, but what are interpreted as their Cambrian ancestors were marine.	110
Ctenophora (sea walnuts)	Comb jellies, sea walnuts		Gelatinous, almost transparent, often bioluminescent marine animals; eight bands of cilia; largest animals that use cilia for locomotion; complete digestive tract with anal pore.	100
Chaetognatha (arrow worms)	*Sagitta*		Small, bilaterally symmetrical, transparent marine worms with a fin along each side, powerful bristly jaws, and lateral nerve cords. Some inject toxin into prey and some have large eyes. It is uncertain if they are coelomates, and, if so, whether protostomes or deuterostomes.	100
Loricifera (loriciferans)	*Nanaloricus mysticus*		Tiny marine pseudocoelomates that live in spaces between grains of sand. The mouth is borne on the tip of a flexible tube. Discovered in 1983.	10
Cycliophora (cycliophorans)	*Symbion*		Microscopic animals that live on mouthparts of claw lobsters. Discovered in 1995.	3
Micrognathozoa (micrognathozoans)	*Limnognathia*		Microscopic animals with complicated jaws. Discovered in 2000 in Greenland.	1

Morphology- and molecule-based phylogenies agree on many major groupings

Although they differ from one another in some respects, phylogenies incorporating molecular data or based entirely on them share some deep structure with the traditional animal tree of life. Figure 32.4 is a summary of animal phylogeny developed from morphological, molecular, life-history, and other types of relevant data. Some aspects of this view have been contradicted by studies based on particular characters or using particular analytical methods. It is an exciting time to be a systematist, but shifts in understanding of relationships among groups of animals can be frustrating to some! Like any scientific idea, a phylogeny is a hypothesis, open to challenge and to being revised in light of additional data.

One consistent result is that Porifera (sponges) constitutes a monophyletic group that shares a common ancestor with other animals. Some systematists had considered sponges to comprise two (or three) groups that are not particularly closely related, but molecular data support what had been the majority view, that phylum Porifera is monophyletic. And, as mentioned earlier, all animals are found to be monophyletic.

Among eumetazoans, molecular data are in accord with the traditional view that cnidarians (hydras, sea jellies, and corals) branch off the tree before the origin of animals with bilateral symmetry. Our understanding of the phylogeny of the deuterostome branch of Bilateria (discussed in chapter 34) has not changed much, but our understanding of the phylogeny of protostomes has been altered by molecular data.

Most revolutionary is that annelids and arthropods, which had been considered closely related based on the occurrence of segmentation in both, belong to separate clades. Now arthropods are grouped with protostomes that molt their cuticles at least once during their life. These are termed ecdysozoans, which means "molting animals" (see chapter 34). Molecular sequence data can help test our ideas of which morphological features reveal evolutionary relationships best; in this case, molecular data allowed us to see that, contrary to our hypothesis, segmentation seems to have evolved convergently, but molting did not.

But not all features are easy to diagnose, and molecular data do not resolve all uncertainties. The enigmatic phylum Ctenophora (comb jellies)—pronounced with a silent C—has been considered both diploblastic and triploblastic and has been thought to have both a complete gut and a blind gut. Likewise the enigmatic phylum Chaetognatha (arrow worms) has been considered both coelomate and pseudocoelomate, and if coelomate, both protostome and deuterostome (as reflected in figure 32.4). Their placement in phylogenies varies, seeming to depend on the features and methods used to construct the tree. Further research is needed to resolve these uncertainties.

Molecular data are contributing to our understanding of relationships among animal phyla. Animals are monophyletic, as are sponges—relationships that were uncertain using only morphological data. Molecular data confirm that cnidarians branched off from the rest of animals before bilaterial symmetry evolved. Although the position of ctenophores has not been resolved, molecular data have significantly altered some ideas of protostome evolution.

Morphology-based phylogeny focused on the state of the coelom

In the morphology-based animal family tree, bilaterally symmetrical animals comprised three major branches. If the body has no cavity (other than the gut), the animal is said to be acoelomate; members of phylum Platyhelminthes are acoelomates.

A body cavity not lined with tissue derived from mesoderm is a pseudocoelom; members of the phylum Nematoda are pseudocoelomate. A body cavity lined with tissue derived from mesoderm is a coelom; we and members of the phylum Annelida are coelomate. All acoelomates and pseudocoelomates are protostomes; some coelomates are protostomes and some are deuterostomes.

Protostomes consist of spiralians and ecdysozoans

Two major clades of protostomes are recognized as having evolved independently since ancient times: the spiralians and the ecdysozoans (see figure 32.4).

Spiralia

Spiralian animals grow by gradual addition of mass to the body. Most live in water, and propel themselves through it using cilia or contractions of the body musculature. Spiralians undergo spiral cleavage (see figure 32.3).

There are two main groups of spiralians: Lophotrochozoa and Platyzoa. Lophotrochozoa includes most coelomate protostome phyla; those animals move by muscular contractions. Most platyzoans are acoelomates; these animals are tiny or flat, and move by ciliary action. Some platyzoans (such as rotifers, gnathostomulids, and the recently discovered phylum Micrognathozoa have a set of complicated jaws. The most prominent group is phylum Platyhelminthes; a flatworm has a simple body with no circulatory or respiratory system but a complex reproductive system. This group includes marine and freshwater planarians as well as the parasitic flukes and tapeworms.

Lophotrochozoa consists of two major phyla and several smaller ones. Many of the animals have a type of free-living larva known as a **trochophore,** and some have a feeding structure termed a **lophophore,** a horseshoe-shaped crown of ciliated tentacles around the mouth used in filter-feeding. The phyla characterized by a lophophore are Bryozoa and Brachiopoda. Lophophorate animals are sessile (anchored in place).

Among the lophotrochozoans with a trochophore are phyla Mollusca and Annelida. Mollusks are unsegmented, and their coelom is reduced to a hemocoel (open circulatory space) and some other small body spaces. This phylum includes animals as diverse as octopuses, snails, and clams. Annelids are segmented coelomate worms, the most familiar of which is the earthworm, but also includes leeches and the largely marine polychaetes.

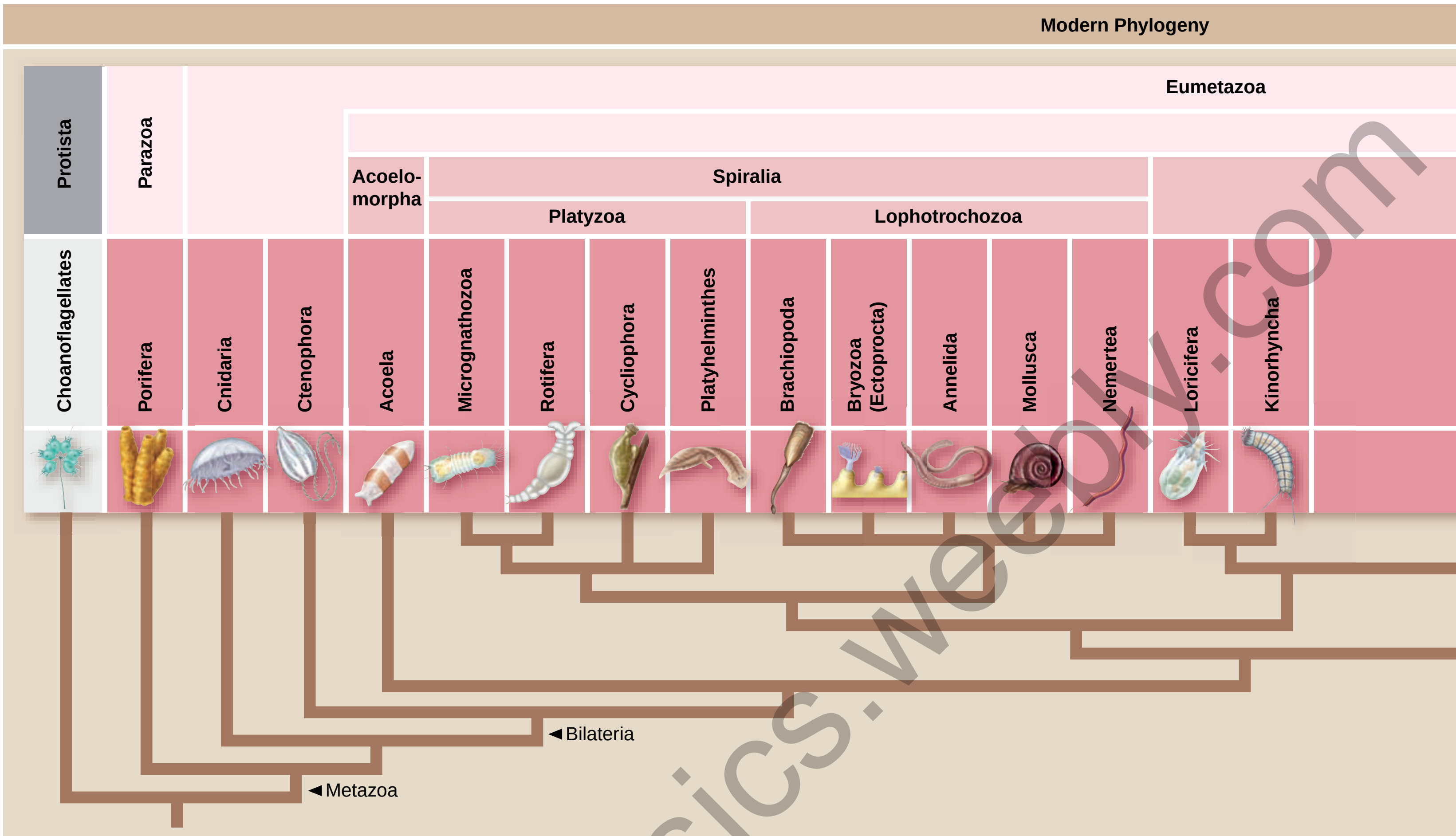


Figure 32.4 Proposed revision of the animal tree of life. A phylogeny of many of the 35–40 phyla reflects the consensus as of 2005 based on interpretation of anatomical and developmental data as well as results derived from molecular phylogenetic studies. Whether Chaetognatha is a protostome or a deuterostome is unclear.

Ecdysozoa

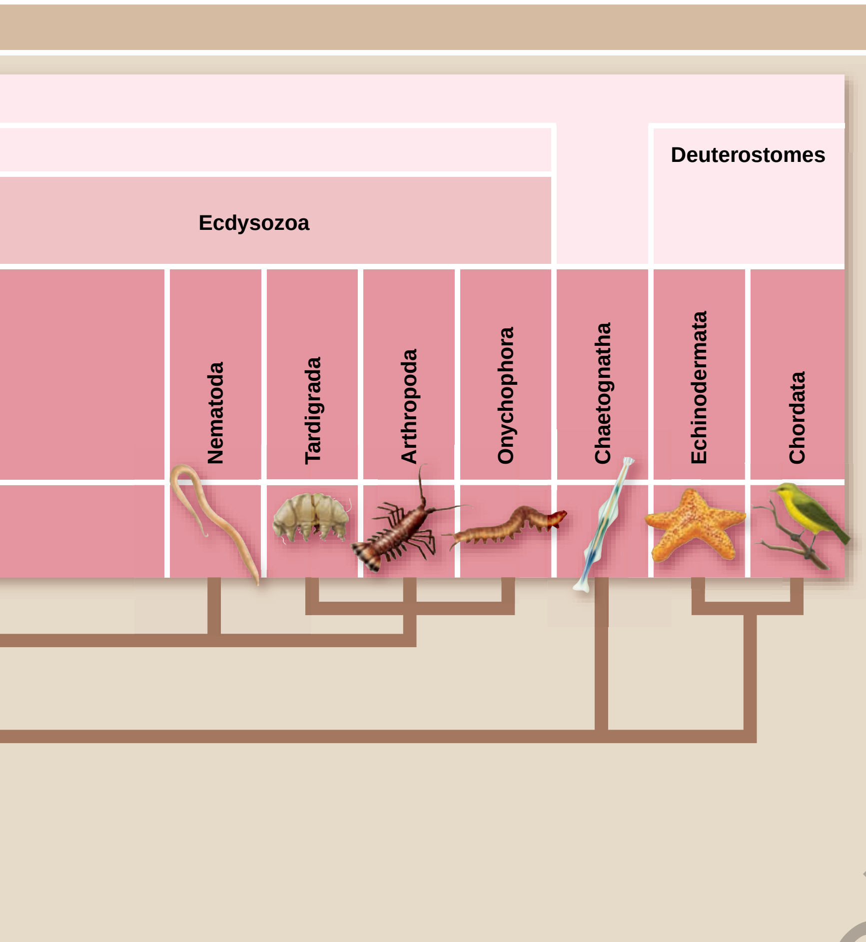
The other major clade of protosomes is the Ecdysozoa. Ecdysozoans are animals that molt, a phenomenon that seems to have evolved only once in the animal kingdom. When an animal grows large enough that it completely fills its hard external skeleton, it must lose that skeleton (by molting, a process also called ecdysis). While the animal grows, it forms a new exoskeleton underneath the existing one. The first step in molting is for the body to swell until the existing exoskeleton cracks open and is shed (figure 32.5). Upon molting that skeleton, the animal inflates the soft, new one, expanding it using body fluids (and, in many insects and spiders, air as well). When the new one hardens, it is larger than the molted one had been and has room for growth. Thus, rather than being continuous, as in other animals, the growth of ecdysozoans is step-wise.

Of the numerous phyla of protostomes assigned to the Ecdysozoa, Arthropoda contains the largest number of described species of any phylum. Each phylum contains one of the model organisms used in laboratory studies that have informed much of our current understanding of genetics and development: the fruit fly *Drosophila melanogaster* and the roundworm *Caenorhabditis elegans.*

Arthropods are coelomate animals with jointed appendages and segmented external skeletons composed of chitin. Arthropods include insects, spiders, crustaceans, and centipedes, among many others. Arthropods have colonized almost all habitats, being found from the ocean floor to the air and in all terrestrial and freshwater environments.

Roundworms are pseudocoelomate worms that lack circulatory or gas exchange structures, and their bodies have only longitudinal muscles. Nematodes inhabit marine, freshwater, and terrestrial environments, and many species are parasitic in

Figure 32.5 Blue crab undergoing ecdysis (molting). Members of Ecdysozoa grow step-wise because their external skeleton is rigid.



plants or animals. It is said that if everything in the world except nematodes were to disappear, an outline of what had been there would be visible in the remaining nematodes!

Deuterostomes include chordates and echinoderms

Deuterostomes consist of fewer phyla and species than protostomes, and are more uniform in many ways, despite great differences in appearance. Echinoderms such as sea stars, and chordates such as humans, share a mode of development that is evidence of their evolution from a common ancestor, and separates them clearly from other animals.

Learning Outcomes Review 32.3

Scientists have defined phyla based on tissues, symmetry, characteristics such as presence or absence of a coelom or pseudocoelom, protostome versus deuterostome development, growth pattern and larval stages, and molecular data. Among protostomes, spiralian organisms have a growth pattern in which their body size simply increases; ecdysozoans must molt in order to grow larger. Among the deuterostome phyla are Echinodermata and Chordata, which includes humans.

- *Why do systematists attempt to characterize each group of animals by one or more features that have evolved only once?*

32.4 *The Roots of the Animal Tree of Life*

Learning Outcomes

1. *Explain the colonial flagellate hypothesis of metazoan origin and why it is now favored.*
2. *Describe the possible role of* Hox *genes in the Cambrian explosion.*

Some of the most exciting contributions of molecular systematics are being made to our understanding of the base of the animal family tree—the origins of the major clades of animals.

Metazoans appear to have evolved from colonial protists

The ancestor to all animals was presumably a protist (see chapter 29), but it is not clear from which line of protists animals evolved. Evidence is available to support two major hypotheses.

- The multinucleate hypothesis is that metazoans arose from a multinuclear protist similar to today's ciliates. Each nucleus became compartmentalized into a cell, resulting in the multicellular condition.
- The **colonial flagellate hypothesis,** first proposed by Ernst Haeckel in 1874, is that metazoans descended from colonial protists. Each colony is a hollow sphere composed of flagellated cells. Some of the cells of sponges are strikingly like those of choanoflagellate protists.

Molecular data based on ribosomal RNA sequences favor the colonial flagellate hypothesis, and reject the multinucleate ciliate hypothesis based on evidence that metazoans are more closely related to eukaryotic algae than to ciliates.

Molecular analysis may explain the Cambrian explosion

Most major animal body plans can be seen in fossils of Cambrian age, dating from 543 to 525 MYA. Although fossil cnidarians are found in rocks from the Ediacaran period, as old as 565 million years, along with what appear to be fossil mollusks and the burrows of worms, the great diversity of animals evolved quite rapidly in geological terms around the beginning of the Cambrian period—an event known as the **Cambrian explosion.** Biologists have long debated what caused this enormous expansion of animal diversity (figure 32.6). Many have argued that the emergence of new body plans was biological—the consequence of the evolution of predation, which encouraged an arms race between defenses, such as armor, and innovations that improved mobility and hunting success. Others have attributed the rapid diversification in body plans to physical factors—such as the build-up of dissolved oxygen and minerals in the oceans.

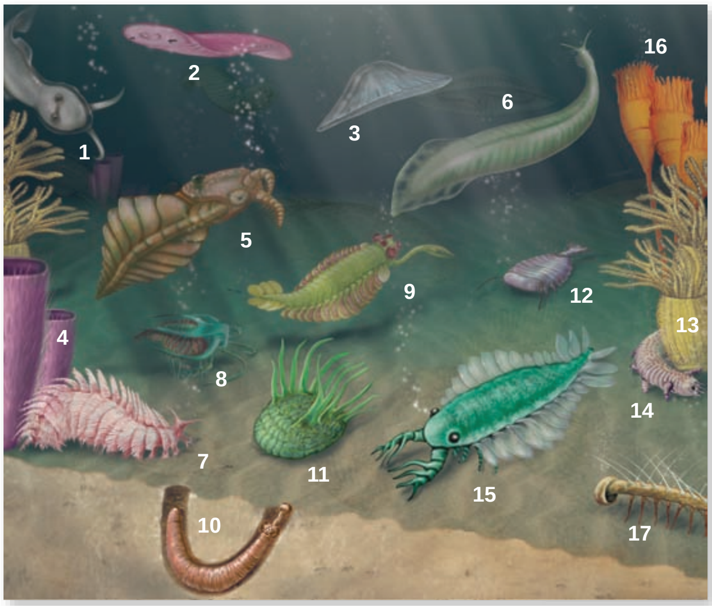


Figure 32.6 Diversity of animals that evolved during the Cambrian explosion. The Cambrian saw an astonishing variety of body plans, many of which gave rise to the animals we find today. The natural history of these species is open to speculation.

Whether these causes or others are at the heart of the Cambrian explosion, molecular studies in the field of evolutionary developmental biology may provide a mechanism for the emergence of so many body plans. Much of the variation in animal body plans is associated with changes in the location or time of expression of *homeobox* genes (*Hox* genes) in embryos (see chapters 19 and 25). *Hox* genes specify the identity of developing body parts, such as the legs, thorax, and antennae. Perhaps the Cambrian explosion reflects the evolution of the *Hox* developmental gene complex, which provides a mechanism for producing rapid changes in body plan.

Learning Outcomes Review 32.4

The hypothesis of evolution of metazoans from colonial flagellates is favored because of the similarity between flagellate colonies and metazoan sponges, and because of molecular data based on ribosomal RNA sequences. Animal fossils become highly abundant in the Cambrian period in what is known as the Cambrian explosion. *Hox* genes, which control development of body shape and parts, may be responsible for the diversity found in this period.

- ***What alternative interpretations are there for the fossils that have led to the idea of the Cambrian explosion?***

Chapter Review

32.1 Some General Features of Animals

Features common to all animals are multicelluarity, heterotrophic lifestyle, and lack of a cell wall. Other features include specialized tissues, ability to move, and sexual reproduction.

32.2 Evolution of the Animal Body Plan

Most animals exhibit radial or bilateral symmetry.

Most sponges are asymmetrical, but other animals are bilaterally or radially symmetrical at some time during their life. The body parts of radially symmetrical animals are arranged around a central axis. The body of a bilaterally symmetrical animal has left and right halves. Most bilaterally symmetrical organisms are cephalized and can move directionally.

The evolution of tissues allowed for specialized structures and functions.

Each tissue consists of differentiated cells that have characteristic forms and functions.

A body cavity made possible the development of advanced organ systems.

Most bilaterian animals possess a body cavity other than the gut. A coelom is a cavity that lies within tissues derived from mesoderm. A pseudocoelom lies between tissues derived from mesoderm and the gut (which develops from endoderm). The acoelomate condition and the pseudocoelom appear to have evolved more than once, but the coelom evolved only once.

A circulatory system is an example of a specialized organ system that assists with distribution of nutrients and removal of wastes.

Bilaterians have two main types of development.

In a protostome, the mouth develops from or near the blastopore. A protostome has determinate development, and many have spiral cleavage.

In a deuterostome, the anus develops from the blastopore. A deuterostome has indeterminate development and radial cleavage.

Segmentation allowed for redundant systems and improved locomotion.

Segmentation, which evolved multiple times, allows for efficient and flexible movement because each segment can move somewhat independently. Another advantage to segmentation is redundant organ systems.

32.3 The Classification of Animals

Animals are classified into 35 to 40 phyla based on shared characteristics. Systematists attempt to use features assumed to have evolved only once.

Tissues and symmetry separate the Parazoa and Eumetazoa.

With the exception of sponges, animals exhibit embryonic germ layers and differentiated cells that form tissues. These characteristics lead to most animals being termed collectively the Eumetazoa; other animals, including the sponges, are Parazoa.

Molecular data help reveal evolutionary relationships.

By incorporating molecular data into phylogenetic analyses, major alterations have been made to the traditional view of how members of these phyla are related.

Morphology- and molecule-based phylogenies agree on many major groupings.

Porifera (sponges) constitutes a monophyletic group that shares a common ancestor with other animals. Cnidarians (hydras, sea jellies, and corals) evolved before the origin of bilaterally symmetrical animals.

Annelids and arthropods had been considered closely related based on segmentation, but now arthropods are grouped with protostomes that molt their cuticles at least once during their life.

Morphology-based phylogeny focused on the state of the coelom.

The two groups of bilaterally symmetrical animals (the Bilateria)—protostomes and deuterostomes—differ in embryology. All acoelomates and pseudocoelomates are protostomes; some coelomates are protostomes and some are deuterostomes.

Protostomes consist of spiralians and ecdysozoans.

Spiralia comprises the clades Lophotrochozoa and Platyzoa. Spiralian animals grow by gradual addition of mass to the body and undergo spiral cleavage. Examples of Lophotrochozoa include annelids and mollusks. Examples of Platyzoa are rotifers and platyhelminthine worms.

Ecdysozoans grow by molting the external skeleton; Ecdysozoa includes many varied species, ranging from the pseudocoelomate, unsegmented Nematoda to the coelomate, segmented Arthropoda.

Deuterostomes include chordates and echinoderms.

The major groups of deuterostomes are the echinoderms, which include animals such as sea stars and sea urchins, and the chordates, which include vertebrates.

Deuterostome development indicates that echinoderms and chordates evolved from a common ancestor, distinguishing them clearly from other animals.

32.4 The Roots of the Animal Tree of Life

Metazoans appear to have evolved from colonial protists.

Systematics based on ribosomal RNA supports the hypothesis that the Eumetazoa are monophyletic and arose from colonial flagellates.

Molecular analysis may explain the Cambrian explosion.

Molecular analysis suggests that the rapid diversification during the Cambrian explosion may have been due to evolution of the *Hox* genes.

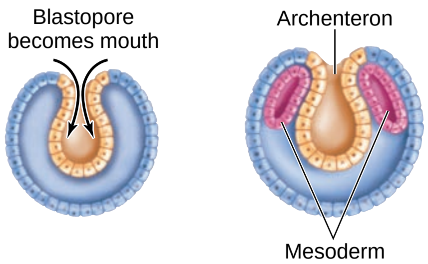
Review Questions

UNDERSTAND

1. Which of the following characteristics is unique to all members of the animal kingdom?
   a. Sexual reproduction
   b. Multicellularity
   c. Lack of cell walls
   d. Heterotrophy
2. Animals are unique in the fact that they possess _______ for movement and _______ for conducting signals between cells.
   a. brains; muscles
   b. muscle tissue; nervous tissue
   c. limbs; spinal cords
   d. flagella; nerves
3. In animal sexual reproduction the gametes are formed by the process of
   a. meiosis.
   b. mitosis.
   c. fusion.
   d. binary fission.
4. The evolution of bilateral symmetry was a necessary precursor for the evolution of
   a. tissues.
   b. segmentation.
   c. a body cavity.
   d. cephalization.
5. A fluid-filled cavity that develops completely within mesodermal tissue is a characteristic of a
   a. coelomate.
   b. pseudocoelomate.
   c. acoelomate.
   d. all of the above
6. Which of the following statements is not true regarding segmentation?
   a. Segmentation allows the evolution of redundant systems.
   b. Segmentation is a requirement for a closed circulatory system.
   c. Segmentation enhances locomotion.
   d. Segmentation represents an example of convergent evolution.
7. Which of the following characteristics is used to distinguish between a parazoan and a eumetazoan?
   a. Presence of a true coelom
   b. Segmentation
   c. Cephalization
   d. Tissues
8. With regard to classification in the animals, the study of which of the following is changing our understanding of the organization of the kingdom?
   a. Molecular systematics
   b. Origin of tissues
   c. Patterns of segmentation
   d. Evolution of morphological characteristics
9. The _______ contain the greatest number of known species.
   a. Chordata
   b. Arthropoda
   c. Porifera
   d. Mollusca
10. The evolution of which of the following occurred after the Cambrian explosion?
    a. Cephalization
    b. Coelom
    c. Segmentation
    d. None of the above
11. A coelomate organism may have which of the following characteristics?
    a. Circulatory system
    b. Internal skeleton
    c. Larger size than a pseudocoelomate
    d. All of the above

APPLY

1. The following diagram is of the blastopore stage of embryonic development. Based on the information in the diagram, which of the following statements is correct?
   a. It is a diagram of a protostome.
   b. It would have formed by radial cleavage.
   c. It would exhibit determinate development.
   d. All of the above are correct.



2. Which of the following characteristics would not apply to a species in the Ecdysozoa?
   a. Bilateral
   b. Indeterminate cleavage
   c. Molt at least once in their life cycle
   d. Metazoan
3. In the rain forest you discover a new species that is terrestrial, has determinate development, molts during its lifetime, and possesses jointed appendages. To which phylum of animals should it be assigned?

SYNTHESIZE

1. Worm evolution represents an excellent means of understanding the evolution of a body cavity. Using the phyla of worms Nematoda, Annelida, Platyhelminthes, and Nemetera, construct a phylogenetic tree based only on the form of body cavity (refer to figure 32.2 and table 32.2 for assistance). How does this relate to the material in figure 32.4? Should body cavity be used as the sole characteristic for classifying a worm?
2. Most students find it hard to believe that Echinodermata and Chordata are closely related phyla. If it were not for how their members form a body cavity, where would you place Echinodermata in the animal kingdom? Defend your answer.

Chapter 33

Noncoelomate Invertebrates

Chapter Outline

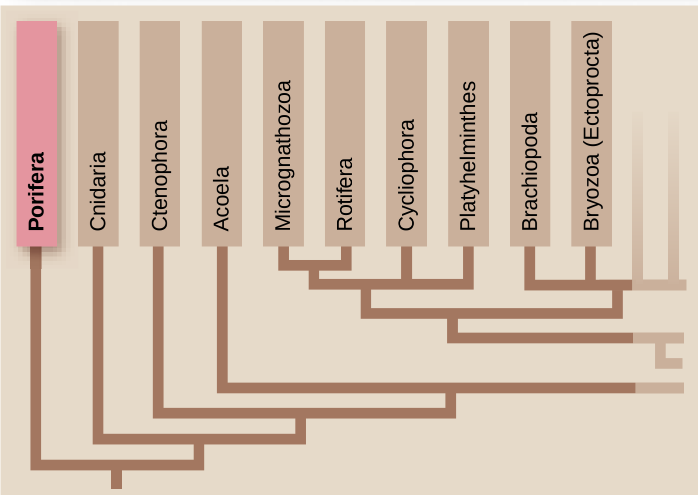
Introduction

Our exploration of the great diversity of animals starts with the morphologically simplest members of the animal kingdom—sponges, jellyfish, and some of the worms (fully a third of animal phyla are based on a "wormy" body plan!). Despite their simplicity, these animals can carry out all the essential functions of life, just as do more morphologically complex animals—eating, respiring, reproducing, and protecting themselves. These animals lack a coelom, so we refer to them as noncoelomates, but many have a body space called a pseudocoelom. The major organization of the animal body first evolved in these animals, the basic body plan from which that of all the rest of animals evolved. In chapter 34, we consider the invertebrate animals that have a coelom, and in chapter 35 the vertebrates. You will see that all animals, despite their great variation, have much in common.

33.1 *Parazoa: Animals That Lack Specialized Tissues*

Learning Outcomes

1. *Describe the different types of cells in the sponge body.*
2. *Explain the function of choanocytes.*



Parazoans are animals lacking tissues (and therefore organs) and a definite symmetry. The major group of parazoans is phylum **Porifera,** the sponges. Despite their morphological simplicity, like all animals, sponges are truly multicellular.

The sponges, phylum Porifera, have a loose body organization

Nearly 7000 species of sponges live in the sea, and perhaps 150 species live in fresh water. Marine sponges occur at all depths, and may be among the most abundant animals in the deepest part of the oceans. Although some sponges are small (no more than a few millimeters across), some may reach 2 m or more in diameter.

A few small sponges are radially symmetrical, but most members of this phylum lack symmetry. Some have a low and encrusting form and grow covering various sorts of surfaces; others are erect and lobed, some in complex patterns (figure 33.1*a*).

As is true of many marine invertebrate animals, larval sponges are free-swimming. After a sponge larva attaches to an appropriate surface, it metamorphoses into an adult and remains attached to that surface for the rest of its life. Thus adult sponges are sessile; that is, they are anchored, immobile, on rocks or other submerged objects. Sponges defend themselves by producing chemicals that repel potential predators and organisms that might overgrow them.

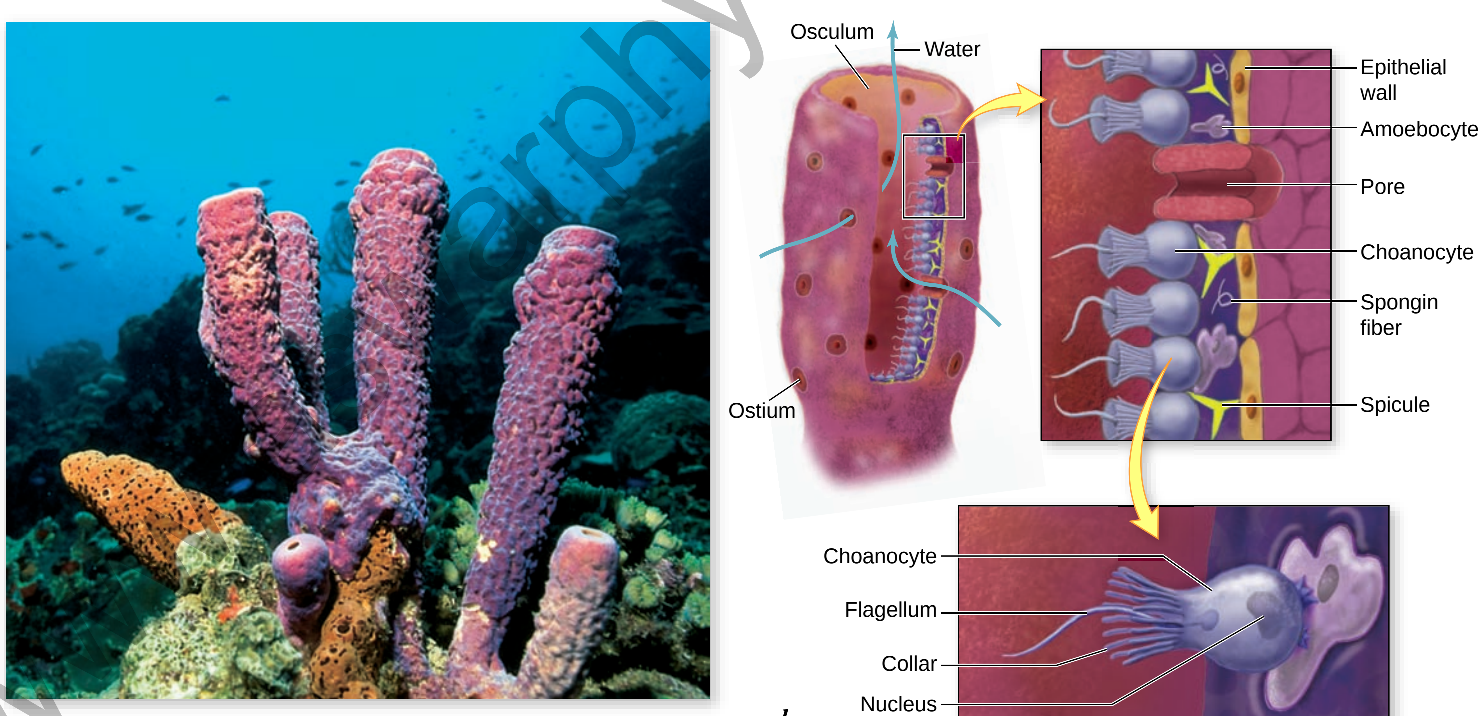


Figure 33.1 Phylum Porifera: Sponges. ***a.*** *Aplysina longissima.* This beautiful, bright orange and purple elongated sponge is found on deep coral reefs. ***b.*** Diagrammatic drawing of the simplest type of sponge. Sponges are composed of several distinct cell types, the activities of which are coordinated. The sponge body has no organized tissues, and most are not symmetrical.

As a result, pharmaceutical companies are interested in possibly using these chemicals for human applications.

The sponge body is composed of several cell types

Lacking head or appendages, mouth or anus, and the organized internal structure characteristic of all other animals, at first sight a sponge seems to be little more than a mass of cells embedded in a gelatinous matrix. In fact, a sponge contains several cell types (figure 33.1*b*), each with specialized functions. If a sponge is put through a fine sieve or coarse cloth so that the cells are separated, they will seek one another out and reassemble the entire sponge—a phenomenon that does not occur in any other animal.

As mentioned in chapter 32, a unique feature of sponge cells is their ability to differentiate from one type to another, and to dedifferentiate from a specialized state to an unspecialized one. Activities of the cells are loosely coordinated to perform functions such as synchronizing reproduction and building the complex skeletal meshwork. This distinguishes sponges as truly multicellular, by contrast with colonial protists, which may form aggregates of cells, but all are functionally identical (except for the reproductive cells).

A small, anatomically simple sponge has a vaselike shape. The walls of the "vase" have three functional layers. Facing the internal cavity are flagellated cells called **choanocytes,** or collar cells (see figure 33.1*b*). A larger and more complex sponge has many small chambers connected by channels rather than a single chamber. Once water has passed through a flagellated chamber, it travels through channels that converge at a large opening called an **osculum** (plural, *oscula*), through which water is expelled from the sponge.

The body of a sponge is bounded by an outer epithelium consisting of flattened cells somewhat like those that make up the outer layers of animals in other phyla. Pores on the sponge allow water to enter the channels that course through its body, leading to and from the flagellated chambers. The name of the phylum, Porifera, refers to these pores, the ostia (singular, ostium); a large sponge has multiple oscula, but they are far, far fewer than the number of ostia.

Some epithelial cells are specialized to surround the ostia; they can contract when touched or exposed to appropriate stimuli, causing the ostia to close and thereby protecting the delicate inner cells from the entry of potentially harmful substances such as sand and noxious chemicals. Cells surrounding individual ostia operate independently of one another; because a sponge has no nervous system, actions cannot be coordinated across large distances.

Between the outer and inner layers of cells, sponges consist mainly of a gelatinous, protein-rich matrix called the **mesohyl,** which contains various types of amoeboid cells (and eggs). In many kinds of sponges, some of these cells secrete needles of calcium carbonate or silica known as **spicules,** or fibers of a tough protein called **spongin.** Spicules and spongin form the skeleton of the sponge, strengthening its body. The siliceous spicules of some deep-sea sponges can reach a meter in length! A genuine bath sponge is the spongin skeleton of a marine sponge; artificial sponges made of cellulose or plastic are modeled on the body design of this animal, with a porous body adapted to contain large amounts of water. The three classes of sponges—Hexactinellida, Demospongiae, and Calcarea—are distinguished in part by the mineral form of their spicules.

Choanocytes help circulate water through the sponge

Each choanocyte resembles a protist with a single flagellum (plural, flagella) (see figure 33.1*b*), a similarity that may reflect its evolutionary derivation. The pressure created by the beating flagella in the cavity contributes to circulating the water that brings in food and oxygen and carries out wastes. In large sponges, the inner wall of the body interior is convoluted, increasing the surface area and, therefore, the number of flagella. In such a sponge, 1 cm^3 of sponge can propel more than 20 L of water per day. Choanocytes also capture food particles from the passing water, engulfing and digesting them. Obviously, this arrangement restricts a sponge to feeding on particles considerably smaller than choanocytes—largely bacteria.

Sponges reproduce both asexually and sexually

Some sponges can reproduce asexually simply by breaking into fragments. Each fragment is able to continue growing as a new individual. Whether a sponge should be considered colonial is an illustration of the limitations of human language. A colony of invertebrate animals, such as coral, is generally defined as a group of individuals that are physically connected (and may be physiologically connected as well), all having been produced by asexual reproduction (such as budding or dividing) from a single progenitor that arose by sexual reproduction. Nearly all sponges grow by multiplying the number of flagellated chambers connected to a single osculum, but whether these units can be considered "individuals" is debatable.

Sponge sperm are created by the transformation of choanocytes, which are then released into the water where they may be carried into another sponge of the same species. When a sperm is captured by a choanocyte, it is carried to an egg cell, which is in the mesohyl (and in some sponges is also a transformed choanocyte). In many sponges, development of the externally ciliated larva occurs within the mother. In sponges of other species, the fertilized egg is released into the water, where development occurs. Whether a fertilized egg or a ciliated larva is released, after a short planktonic (drifting) stage, the larva settles on a suitable substrate where it transforms into an adult.

Learning Outcomes Review 33.1

Sponges possess multicellularity but have neither tissue-level development nor body symmetry. Cells that compose a sponge include a layer of choanocytes, a layer of epithelial cells, and amoeboid cells in the mesohyl between the two layers. Choanocytes have flagella that beat to circulate water through the sponge body.

- ***What features of a sponge make it seem to be a colony, and what features make it seem to be a single organism?***

33.2 Eumetazoa: Animals with True Tissues

Learning Outcomes

1. *Explain the defining feature of cnidarians.*
2. *Differentiate between cnidarians and ctenophores.*
3. *Discuss the question of symmetry of ctenophores.*

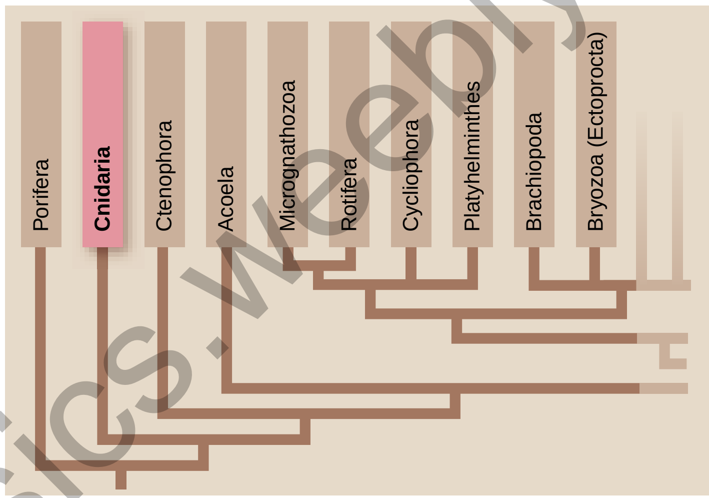
The Eumetazoa contains animals that evolved the first key transition in the animal body plan: distinct tissues. The embryonic cell layers differentiate into the tissues of the adult body, giving rise to the body plan characteristic of each group of animals.

Recall that the outer covering of the body (the epidermis) and the nervous system develop from the embryonic ectoderm, and the digestive tissue (called the **gastrodermis**) develops from the embryonic endoderm. In the Bilateria, the embryonic mesoderm, which lies between endoderm and ectoderm, forms the muscles.

Eumetazoans also evolved body symmetry. Metazoans living sessile on the ocean floor or free-living in the water may be radially symmetrical. One phylum consisting of pentaradially symmetrical animals (those with fivefold symmetry), the Echinodermata, are dealt with in chapter 34. Some animals of the phylum Cnidaria, comprising hydroids, jellyfish, sea anemones, and corals, are clearly radially symmetrical and some are biradially symmetrical (see chapter 32). Members of the phylum Ctenophora, the comb jellies, are considered by some people to be radially symmetrical but by others to be bilaterally symmetrical.

All cnidarians, phylum Cnidaria, are carnivores

Most of the 10,000 species of cnidarians are marine; a very few live in fresh water. The bodies of these fascinating and simply constructed diploblastic animals are made of distinct tissues, although they do not have organs. Despite having no reproductive, circulatory, digestive, or excretory systems, cnidarians reproduce, exchange gas, capture and digest prey, and distribute the resulting organic molecules to all their cells. A cnidarian has no concentration of nervous tissue that could be considered a brain or even a ganglion. Rather, its nervous system is a latticework, the cells having junctions like those of bilaterians. All cnidarians have nervous receptors sensitive to touch, and some have gravity and light receptors, which include, in a few species, image-forming eyes.



Cnidarians capture their prey (which includes fishes, crustaceans, and many other kinds of animals) with nematocysts (figure 33.2), microscopic intracellular structures unique

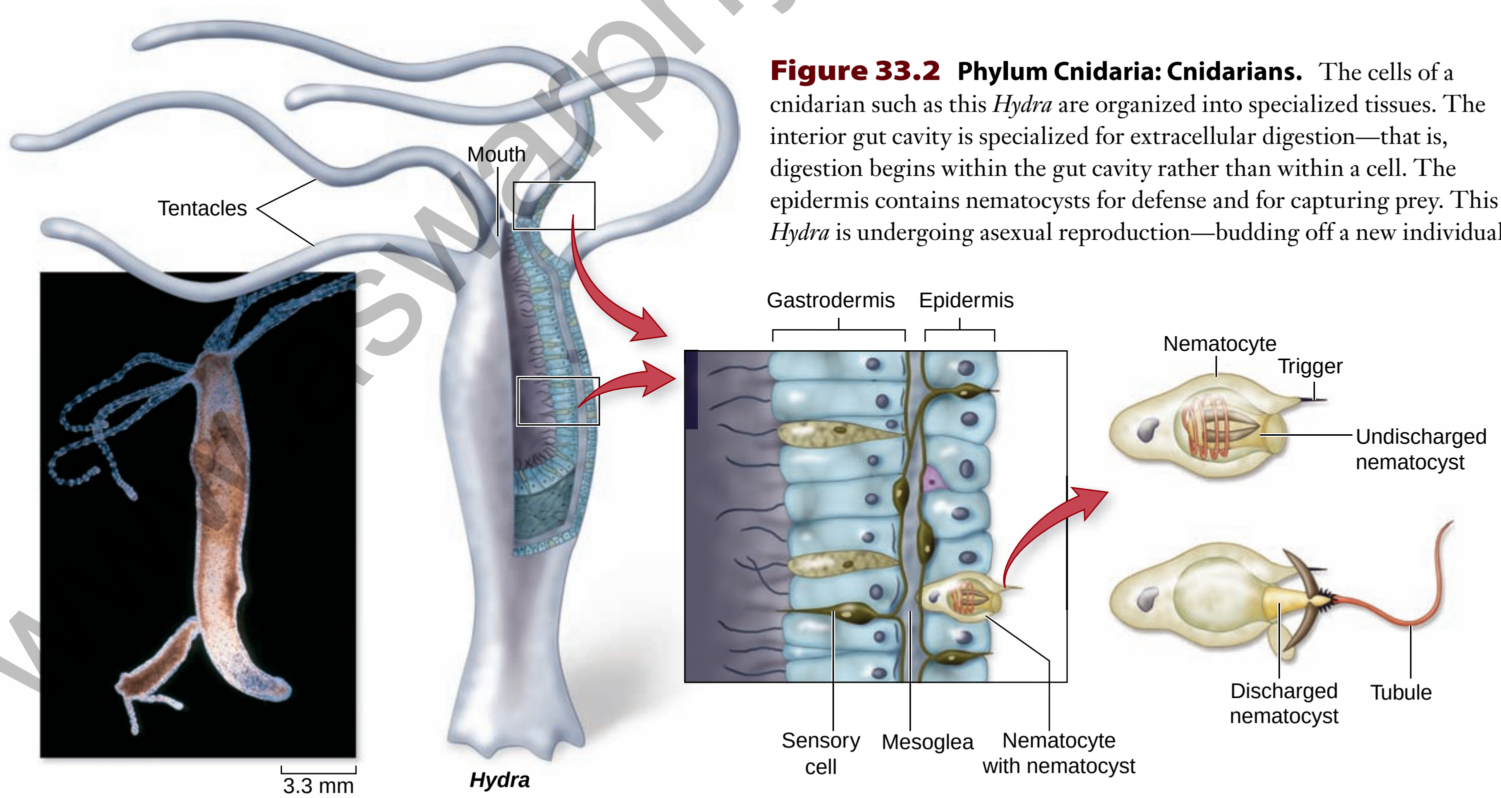


Figure 33.2 Phylum Cnidaria: Cnidarians. The cells of a cnidarian such as this *Hydra* are organized into specialized tissues. The interior gut cavity is specialized for extracellular digestion—that is, digestion begins within the gut cavity rather than within a cell. The epidermis contains nematocysts for defense and for capturing prey. This *Hydra* is undergoing asexual reproduction—budding off a new individual.

to the phylum. Food captured by a cnidarian is brought to the mouth by the tentacles that ring the mouth.

Basic body plans

A cnidarian exhibits one of two body forms: the polyp and the medusa (figure 33.3). A **polyp** is cylindrical, with a mouth surrounded by tentacles at the end of the cylinder opposite where it is attached. Attachment in most solitary polyps is to a firm substratum, but in those that are part of a colony, it is to the mass of common colonial tissue. A **medusa** is discoidal or umbrella-shaped, with a mouth surrounded by tentacles on one side; most live free in the water. These two seemingly quite different body forms share the same morphology—the mouth opens into a saclike gastrovascular cavity and is surrounded by tentacles.

The cnidarian body plan has a single opening leading to the gastrovascular space, which is the site of digestion, most gas exchange, waste discharge, and, in many cnidarians, formation of gametes. The body wall is composed of two layers: the epidermis, which covers the surfaces in contact with the outside environment, and the gastrodermis, which covers the gastrovascular cavity. Between these two layers is the **mesoglea,** which varies from acellular, being no more than a glue holding gastrodermis to epidermis in *Hydra,* to thick and rubbery with many cells in large medusae called jellyfish (see figures 33.2, 33.3).

The gastrovascular space also serves as a hydrostatic skeleton (see chapter 47). A hydrostatic skeleton serves two of the roles that a skeleton made of bone or shells does: it provides a rigid structure against which muscles can operate, and it gives the animal shape. For muscles to operate against it, the fluid-filled space must be closed sufficiently tightly so the fluid is under pressure and does not escape when muscles contract around the space. Think of the gastrovascular space of a cnidarian full of water like an inflated, elongated, air-filled balloon. Because it is firm, muscles that shorten it cause it to broaden, and muscles that decrease its diameter lengthen it. However, if you inflate the balloon with air, but then do not hold the opening closed, the air will escape and the balloon will become flaccid. Similarly, when a cnidarian contracts greatly, it must open its mouth so water can escape. However, the mouth can close sufficiently tightly to retain water in the gastrovascular cavity, so the animal is turgid and can bend and extend its tentacles.

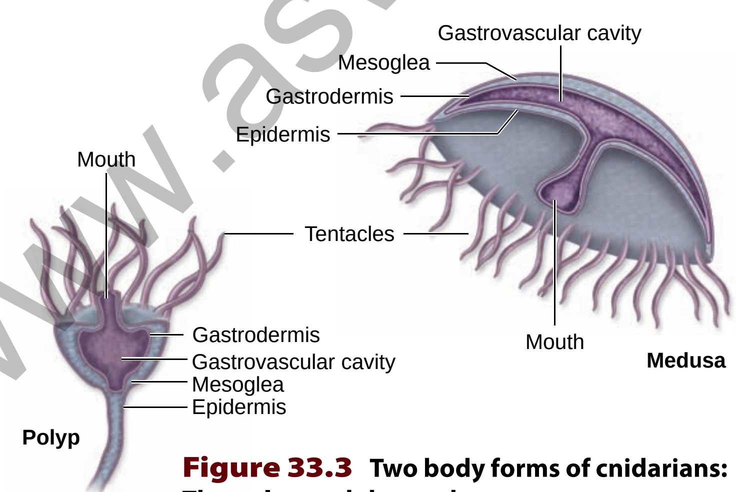


Figure 33.3 Two body forms of cnidarians: The polyp and the medusa.

In addition to the hydrostatic skeleton of all polyps, those of many species build an exoskeleton of chitin or calcium carbonate around themselves; in many colonial species, the skeleton links the members of the colony. The polyps of a smaller number of species secrete internal skeletal elements. Polyps of some groups of cnidarians, such as sea anemones, have no skeleton at all. All medusae are solitary (that is, they do not form colonies) and form no skeleton.

The cnidarian life cycle

Some cnidarians occur only as polyps, and others exist only as medusae, but many alternate between these two phases (see figure 33.3); both phases consist of diploid individuals. In general, in species having both polyp and medusa in the life cycle, the medusa forms gametes. The sexes are separate; this condition, known as gonochorism, means an individual is either male or female. An egg and a sperm unite to form a zygote, which develops into a planktonic ciliated **planula** larva that metamorphoses into a polyp. The polyp produces medusae asexually. Dispersal occurs in both medusa and larvae. In most species with such a life cycle, a polyp may also produce other polyps asexually; if they remain attached to one other, the resulting group is referred to as a colony.

In a small number of species, the planula produced by medusae may develop directly or indirectly into another medusa without passing through the polyp stage. More commonly, there is a polyp but no medusa in the life cycle. In such cnidarians, the polyp can form gametes, and the resulting planula will develop into another polyp. In some, but by no means all, of these species, the polyp can also produce other polyps asexually, by dividing, budding, or breaking off bits of itself that regenerate (grow the missing parts).

Digestion

A major evolutionary innovation in cnidarians is extracellular digestion of food inside the animal. Recall that in a sponge, digestion occurs within choanocytes, so food particles must be small enough to be engulfed by a choanocyte. In a cnidarian, digestion takes place partly in the gastrovascular cavity. Digestive enzymes, released from cells lining the cavity, partially break down food. Other cells lining the space engulf those food fragments by phagocytosis. This allows a cnidarian to feed on prey larger than a sponge can handle.

Nematocysts

Cnidarians capture food with the aid of **nematocysts,** microscopic stinging capsules unique to the phylum (see figure 33.2). Although often referred to as "stinging cells," they are capsules, each secreted within a cell called a nematocyte. Cnidarians may be morphologically simple, but nematocysts are the most complex structures secreted by single animal cells. When appropriately stimulated, the closure at the end of the capsule springs open, and a tubule is emitted. Nematocyst discharge is one of the fastest cellular processes in nature. The mechanism of discharge of a nematocyst is unknown—several hypotheses for it have been proposed. Although the action of a nematocyst is often described as harpoon-like, the tubule actually everts (turns inside-out). It may penetrate or wrap around an object; the tubules of some nematocysts are barbed and some carry venom. In a very few species, the venoms are strong enough to kill a human.

Many thousand nematocytes typically are part of the epidermis of each tentacle. Each one can be used only once. In some types of cnidarians, nematocysts occur in parts of the body other than the tentacles, including in the gastrovascular cavity, where they may aid in digestion. In addition to being used offensively, nematocysts are the only defense of cnidarians—they are the reason jellyfish and fire coral sting. Some cnidarians have stinging capsules of types other than nematocysts, which are termed cnidae—hence the name of the phylum, Cnidaria.

Cnidarians are grouped into four—or five—classes

Traditionally, three classes of Cnidaria were recognized: Anthozoa (sea anemones, corals, sea fans), Hydrozoa (hydroids, Hydra, Portuguese man-of-war), and Scyphozoa (jellyfish). Now nearly all biologists accept that some scyphozoans are sufficiently distinct in life cycle and morphology that they constitute their own class, Cubozoa (box jellies), some of which have a sting sufficiently toxic to kill humans. Less widely accepted is the separation of some other scyphozoans into their own class, Staurozoa (star jellies).

Class Anthozoa: Sea anemones and corals

The largest class of Cnidaria is **Anthozoa,** consisting of approximately 6200 species of solitary and colonial polyps. They include stony corals (figure 33.4), soft-bodied sea anemones (figure 33.5), and other groups known by such fanciful names as sea pens, sea pansies, sea fans, and sea whips. Many of these names reflect the plantlike appearance of the individual polyps or colonies.

Figure 33.4 Stony corals. *Tubastraea aurea*, a non-reef building species from Malaysia.

Figure 33.5 Class Anthozoa. Crimson anemone, *Cribrinopsis fernaldi*.

An anthozoan polyp differs from a polyp of the other classes in its gastrovascular cavity being compartmentalized by radially arrayed, longitudinal sheets of tissue called mesenteries. The way they are arranged imparts the biradial symmetry to these animals mentioned in chapter 32. The gametes of an anthozoan develop in the mesenteries. The tentacles of an anthozoan are hollow, whereas those of many other cnidarians are solid.

Sea anemones (see figure 33.5) constitute a group of just over 1000 species of highly muscular and relatively complex soft-bodied anthozoans. Living in waters of all depths throughout the world, they range from a few millimeters to over a meter in diameter, and many are equally long.

Most corals are anthozoans, and most hard corals (about 1400 species, see figure 33.4) are closely related to sea anemones. The polyp of a coral secretes an exoskeleton of calcium carbonate around and under itself (this is the same material of which chalk is composed); as the individual or colony grows upward, dead skeleton accumulates below it. In shallow water of the tropics, these accumulations form coral reefs. Most waters in which coral reefs develop are nutrient-poor, but the corals are able to grow well because they contain within their cells symbiotic dinoflagellates (zooxanthellae) that photosynthesize and provide energy for the animals. Obviously coral reefs are restricted to water sufficiently shallow for sunlight to reach the living animals (typically no more than 100 m), but corals that do not form reefs can grow deeper—to about 5000 m. Only about half the species of hard corals participate in forming reefs.

Coral reefs are economically important, serving as refuges for the young of many species of crustaceans and fishes that are eaten by humans, as well as protecting coasts of many tropical islands. But they are threatened by global climate change. Water warmer than usual can cause the symbiosis with zooxanthellae to break down, a phenomenon known as "coral bleaching" because the underlying white skeleton of the animal becomes visible through its body in the absence of the symbionts. Bleaching does not always kill a coral, but it is stressful. As carbon dioxide in the atmosphere rises, it dissolves in water, forming carbonic acid, which lowers the pH of the water. This makes calcium carbonate less available; some species of calcifying marine plants and animals, including corals, have been shown to form less robust skeletons, and to form them more slowly, as pH drops.

Some "soft corals" secrete needles of calcium carbonate much like sponge spicules; these sclerites form a case around the polyp or are embedded in their tissues, presumably providing protection against predation. Some of these animals also secrete a horny rod that provides flexible support to the members of the colony growing around it (sea fans are such colonies).

Figure 33.6
Class Cubozoa. *Chironex fleckeri*, a box jelly.

Figure 33.8
Class Scyphozoa. *Aurelia aurita*, a jellyfish.

Class Cubozoa: The box jellies

As their name implies, medusae of class **Cubozoa** are box-shaped, with a tentacle or group of tentacles hanging from each corner of the box (figure 33.6). Most of the 40 or so species are only a few centimeters in height, although some reach 25 cm. Box jellies are strong swimmers and voracious predators of fish in tropical and subtropical waters; both of these facts are related to some cubozoans having image-forming eyes! The stings of some species can be fatal to humans. The polyp stage is inconspicuous and in many cases unknown.

Class Hydrozoa: The hydroids

Most of the approximately 2700 species of class **Hydrozoa** have both polyp and medusa stages in their life cycle (see figure 33.3). The polyp stage of most species is colonial. The polyps of a colony may not be identical in structure or function: some may be specialized to feed but be unable to reproduce, whereas the opposite may be true of others (they are nourished by material transported from feeding polyps through the gastrovascular space connecting members of the colony). The Portuguese man-of-war (figure 33.7) is not a jellyfish, but is a floating colony of highly integrated polypoid and medusoid individuals! Some marine hydroids and medusae are bioluminescent.

Hydrozoa is the only class of Cnidaria with freshwater members. A well-known hydroid is the freshwater *Hydra*, which is exceptional not only in its habitat, but in having no medusa stage and being solitary (see figure 33.2). Each polyp attaches by a basal disk, on which it can glide, aided by mucous secretions. It can also somersault—by bending over and attaching to the substrate by its tentacles, then looping over to a new location. If the polyp detaches from the substrate, it can float to the surface.

Class Scyphozoa: The jellyfish

In the approximately 200 species of class **Scyphozoa,** the medusa is much more conspicuous and complex than the polyp. Although many scyphomedusae are essentially colorless (figure 33.8), some are a striking orange, blue, or pink. The polyp is small, inconspicuous, simple in structure, and typically white in color, but is entirely lacking in a few scyphozoans that live in the open ocean.

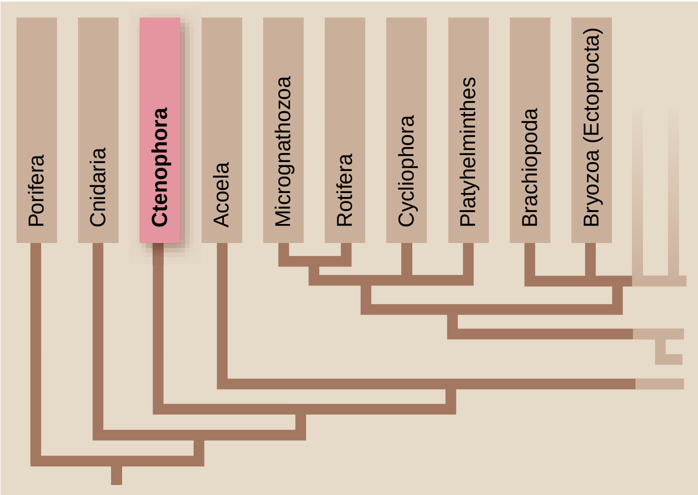
The epithelium around the margin of a jellyfish contains a ring of muscle cells that can contract rhythmically to propel the animal through the water by jetting water from the gastrovascular cavity or space beneath it; by contracting those on just one side, the animal can steer. A scyphomedusa *(Cyanea capilata)* was the killer in the Sherlock Holmes tale "The Lion's Mane," but, although some can inflict pain on humans, they are unlikely to be capable of killing.

Class Staurozoa: The star jellies

Among the reasons the 50 species of this group were separated from the Scyphozoa and placed in their own class (Staurozoa) is that the animal resembles a medusa in most ways but is attached to the substratum by a sort of stalk that emerges from the side opposite the mouth (figure 33.9). In addition, in all staurozoans known, the planula larva creeps rather than swims or drifts.

Figure 33.7
Portuguese man-of-war *(Physalia physalis).* This species has a very painful sting.

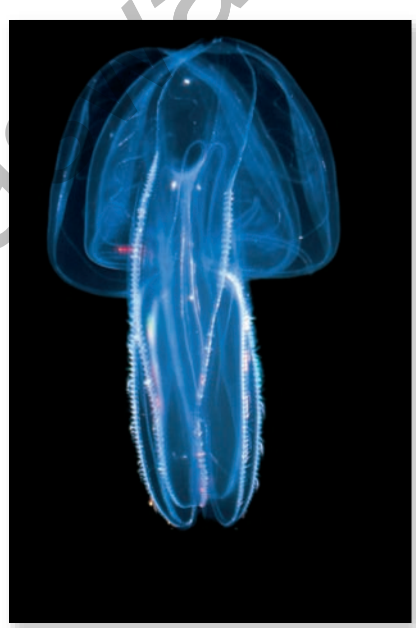
Figure 33.9
Star jelly. Stalked jellyfish *(Haliclystus auricula).*



The comb jellies, phylum Ctenophora, use cilia for movement

Pelagic members of the small marine phylum **Ctenophora** range from spherical to ribbon-like and are known as comb jellies, sea walnuts, or sea gooseberries. Abundant in the open ocean, most of these animals are transparent and only a few centimeters long, but rare ones are deeply pigmented and reach 1 m in length. They propel themselves through the water with eight rows of comblike plates of fused cilia that beat in a coordinated fashion, scattering light so they appear like rainbows (figure 33.10). Ctenophores are the largest animals that use cilia for locomotion. Many ctenophores are bioluminescent, giving off bright flashes of light that are particularly evident in the deep sea or on the surface of the ocean at night. Most ctenophores have two long, retractable tentacles used in prey capture. The epithelium of the tentacles contains **colloblasts,** a type of cell that bursts to discharge a strong adhesive material on contact with animal prey.

Figure 33.10
A comb jelly (phylum Ctenophora). Note the iridescent rows of comblike plates of fused cilia.



The phylogenetic position of Ctenophora is unclear. It was formerly considered closely related to Cnidaria because of the gelatinous, medusa-like form of most species. However, ctenophores lack nematocysts and are structurally more complex than cnidarians. They have anal pores through which water and other substances can exit the body. Although ctenophores have been considered diploblasts with radial symmetry, recent developmental studies have demonstrated them to have muscle cells derived from mesoderm, which means they should be considered triploblasts, like bilaterians. The two tentacles placed on opposite sides of a ctenophore's body impart some bilaterality to them, but whether their symmetry should be considered biradial, like that of sea anemones, is unclear. A recent molecular phylogeny places ctenophores at the base of the animal tree of life, as the sister group to all other metazoans. If this is borne out, it implies that the ancestral animal was triploblastic and bilaterally symmetrical.

Learning Outcomes Review 33.2

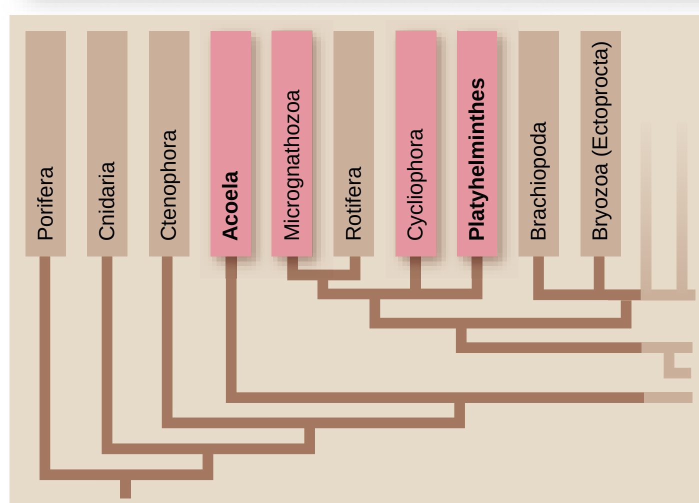
Members of phylum Cnidaria have nematocysts, capsules used in defense and prey capture, and are radially symmetrical. Members of phylum Ctenophora lack nematocysts; they propel themselves by means of eight rows of comblike plates of fused cilia. Ctenophores have cells called colloblasts that assist in prey capture. The symmetry of ctenophores is a subject of debate.

- ***Why would triploblasty be important to phylogeny?***

33.3 *The Bilaterian Acoelomates*

Learning Outcomes

1. ***List the distinguishing features of bilaterian flatworms.***
2. ***Explain why the scolex of a tapeworm is not a head.***



The Bilateria is characterized by a key transition in the animal body plan—bilateral symmetry—which allowed animals to achieve high levels of specialization within parts of their bodies, such as the concentration of sensory structures at the anterior. (Even if ctenophores are truly bilateral as just mentioned, they lack these other specializations.)

As discussed in chapter 32, bilaterians are traditionally divided into acoelomates, pseudocoelomates, and coelomates. The acoelomate and pseudocoelomate conditions appear to have evolved multiple times; thus these conditions are convergent and not homologous and do not necessarily indicate close evolutionary relationship among the animals sharing that anatomy. Nonetheless, the state of the internal part of the animal's body does provide information about how the animals are constructed and how they live. In this chapter, we cover acoelomates and pseudocoelomates; in the next chapter we cover coelomates, which are probably monophyletic.

Structurally, the simplest bilaterians are the acoelomates, which lack an internal cavity other than the digestive tract. The largest phylum of the group is the Platyhelminthes.

The flatworms, phylum Platyhelminthes, have an incomplete gut

The phylum Platyhelminthes consists of some 20,000 species. These ciliated, soft-bodied animals are flattened dorsoventrally, the anatomy that gives them the name flatworms. Flatworm bodies are solid aside from an incomplete digestive cavity (figure 33.11). Although among the morphologically simplest of bilaterally symmetrical animals, they have some complex structures, like their reproductive apparatus, and they have the most complex life cycles among animals.

Free-living flatworms occur in a wide variety of marine, freshwater, and even moist terrestrial habitats. They are carnivores and scavengers, eating small animals and bits of organic debris. They move around by means of ciliated epithelial cells, which are particularly concentrated on their ventral surfaces, but they also have well-developed musculature. By contrast, many species of flatworms are parasitic, living inside the bodies of other animals. Flatworms range in length from 1 mm or less to many meters (some tapeworms).

Digestion in flatworms

Most flatworms have only a single opening for their digestive cavity, a mouth located on the bottom side of the animal at midbody. A flatworm ingests its food and tears it into small bits using muscular contractions in the upper end of the gut, the pharynx.

Like sponges, cnidarians, and ctenophores, a flatworm lacks a circulatory system for the transport of oxygen and food molecules. The thin body of a flatworm allows gas to diffuse between its cells and the air (oxygen diffuses in and carbon dioxide diffuses out). Branches of the gut extend throughout the body, so the gut functions in both digestion and distribution of food. Cells that line the gut engulf most of the food particles by phagocytosis and digest them; but, as in cnidarians and most bilaterians, some particles are partly digested extracellularly. Tapeworms, which are parasitic, have a mouth at the front of their body and no digestive cavity at all; they absorb food directly through the body wall.

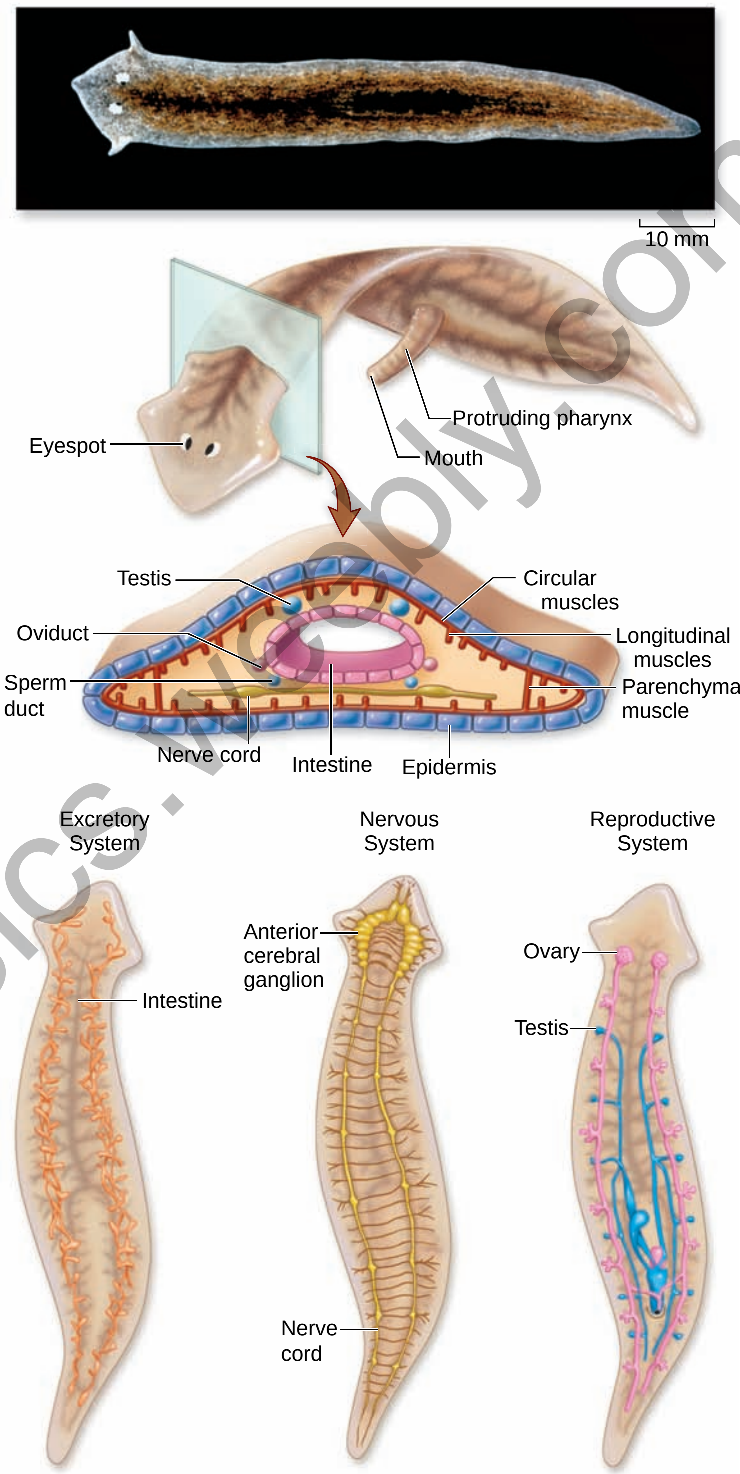


Figure 33.11 Architecture of a flatworm. A photo and an idealized diagram of the genus *Dugesia*, the familiar freshwater planarian of ponds and rivers. Upper schematic shows a whole animal and a transverse section through the anterior part of the body. Schematics below show the digestive, central nervous, and reproductive systems.

Excretion and osmoregulation

Unlike cnidarians and ctenophores, flatworms have an excretory system, which consists of a network of fine tubules that run throughout the body. Bulblike **flame cells,** so named because of the flickering movements of the flagella beating inside them, are located on the side branches of the tubules. Flagella in the flame cells move water and excretory substances into the tubules and then to pores located between the epidermal cells through which the liquid is expelled. Flame cells primarily regulate water balance of the organism; the excretory function appears to be secondary, and much of the metabolic waste of a flatworm diffuses into the gut and is eliminated through the mouth.

Nervous system and sensory organs

The flatworm nervous system comprises an anterior cerebral ganglion and nerve cords that run down the body, with cross-connections that give it a ladder-like shape (see figure 33.11). Free-living flatworms are poorly cephalized, with eyespots on their heads (see figure 33.11). These inverted, pigmented cups, which contain light-sensitive cells connected to the nervous system, enable a worm to distinguish light from dark: most flatworms tend to move away from strong light.

Flatworm reproduction

The reproductive systems of flatworms are complex. Most are **hermaphroditic,** each individual containing both male and female sexual structures (see figure 33.11). In many of members of Platyhelminthes, copulation is required between two individuals, and fertilization is internal, each partner depositing sperm in the copulatory sac of the other. The sperm travel along special tubes to reach the eggs.

In most freshwater flatworms, fertilized eggs are laid in cocoons strung in ribbons and hatch into miniature adults. In contrast, some marine species develop indirectly, the fertilized egg undergoing spiral cleavage, and the embryo giving rise to a larva that swims or drifts until metamorphosing, when it settles in an appropriate habitat.

Flatworms are known for their regenerative capacity: when a single individual of some species is divided into two or more parts, an entirely new flatworm can regrow what is missing from each bit.

Flatworms comprise two major groups

Most flatworms are parasitic; those that are not are referred to as free-living. There is strong morphological and molecular evidence that the parasitic lifestyle evolved only once in platyhelminths, from free-living ancestors.

Turbellaria: Free-living flatworms

Flatworm phylogeny is in a state of flux. The group of free-living flatworms, Turbellaria, has been considered a class, but recent studies show it is not monophyletic so it is likely to be divided into several classes. One of the most familiar members of this group are freshwater members of the genus *Dugesia*, the common planarian used in biology laboratories.

Neodermata: Parasitic flatworms

All parasitic flatworms are placed in the subphylum Neodermata. That name means "new skin" and refers to the animal's outer surface. All neodermatans live as ectoparasites or endoparasites on or in the bodies of other animals for some period of their lives. The neodermis is resistant to the digestive enzymes and immune defenses produced by the animals parasitized by these flatworms. These animals also lack other features of free-living flatworms such as eyespots, which are of no adaptive value to an organism living inside the body of another animal. Neodermata contains two subgroups: Trematoda, the flukes, and Cercomeromorpha, the tapeworms and their relatives.

Trematoda: The flukes

There are more than 10,000 named species of flukes, ranging in length from less than 1 mm to more than 8 cm. Flukes attach themselves within the bodies of their hosts by means of suckers, anchors, or hooks. A fluke takes in food (cells or fluids of the host) through its mouth, like its free-living relatives. The life cycle of some species involves only one host, usually a fish, but the life cycle of most flukes involves two or more hosts. The first intermediate host is almost always a snail, and the final host (in which the adult fluke lives and reproduces sexually) is almost always a vertebrate; in between there may be other intermediate hosts. Although the life of a parasite is secure within a host, which provides food and shelter, getting from one host to another is extremely risky, and most individuals die in the transition.

Flukes that cause disease in humans

The oriental liver fluke, *Clonorchis sinensis*, is an example of a flatworm that parasitizes humans, living in the bile duct of the liver (as well as that of cats, dogs, and pigs) (figure 33.12). It is especially common in Asia. Each worm is 1 to 2 cm long and, like all flukes, has a complex life cycle. A fertilized egg containing a ciliated first-stage larva, the **miracidium,** is passed in the feces. If the larva reaches water, it may be ingested by an aquatic snail (but most do not reach water and most that do are not ingested. The prodigious number of eggs a parasitic flatworm produces is an adaptation to this life-cycle full of risks). Within the snail, the ciliated larva transforms into a **sporocyst,** a bag-like structure containing embryonic germ cells, each of which develops into a **redia** (plural, *rediae*), an elongated, nonciliated larva. Each of these larvae grows within the snail, then gives rise to several individuals of the next larval stage, the tadpole-like **cercaria** (plural, *cercariae*).

Cercariae escape into the water, where they swim about freely. When one encounters a fish of the family Cyprinidae—the family that includes carp and goldfish—it bores into the muscles, loses its tail, and encysts, transforming into a metacercaria. If a human or other mammal eats raw fish containing metacercariae, the cyst dissolves in the intestine, and the young fluke migrates to the bile duct, where it matures, thereby completing the cycle. Even if infected fish is cooked, the parasite can be transmitted if metacercariae stuck to cutting boards or the hands of a person handling the raw fish flesh are ingested. An individual fluke may live for 15 to 30 years in the liver; a heavy infection of liver flukes may cause cirrhosis of the liver and death in humans.

Perhaps the most important trematodes to human health are blood flukes of the genus *Schistosoma*. They afflict about 5%

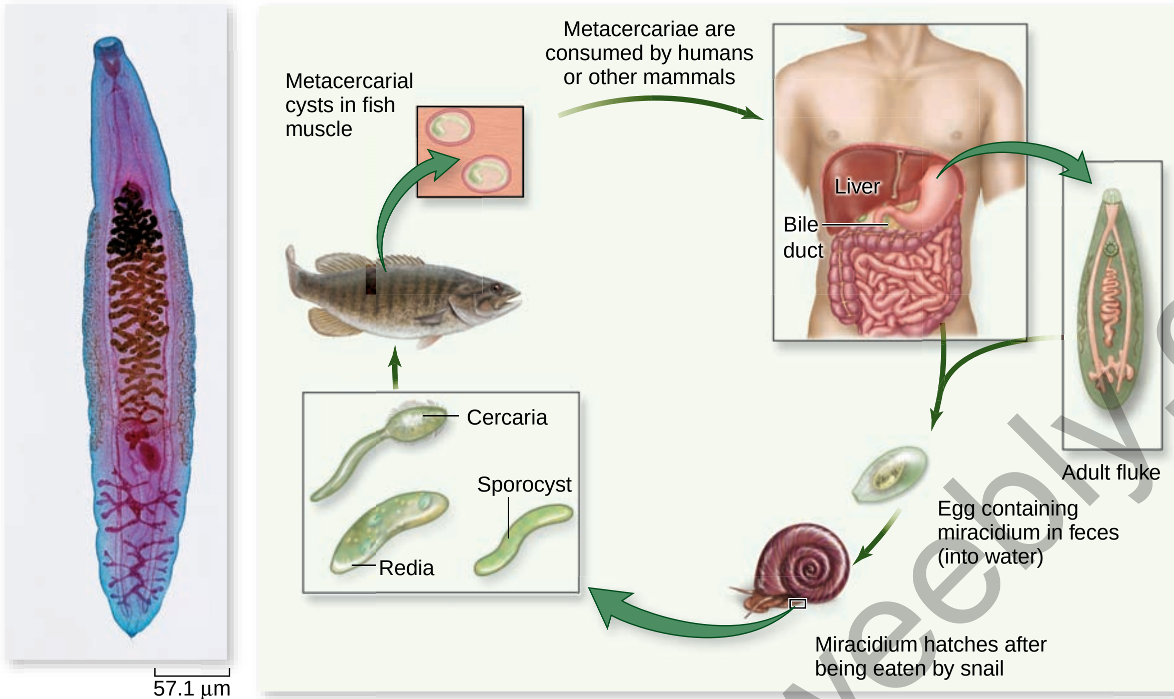


Figure 33.12 **Life cycle of the oriental liver fluke, *Clonorchis sinensis*.**

of the world's population, or more than 200 million people, in tropical Asia, Africa, Latin America, and the Middle East. About 800,000 people die each year from the disease called **schistosomiasis,** or bilharzia.

Schistosomes live in blood vessels associated with the intestine or the urinary bladder, depending on the species (figure 33.13). Thus if the worm is killed, it cannot be washed out of the host, unlike parasites that live in the gut or associated organs such as the liver. Nor do its fertilized eggs have that easy route out of the body. Instead, a fertilized egg must break through the wall of the blood vessel to get into either the intestine or the urinary bladder (depending on the species). The damage done to the blood vessels and gut or bladder wall is considerable, especially considering that an individual worm may release 300 to 3000 eggs per day and live for many years.

Great effort is being made to control schistosomiasis. The worms protect themselves from the body's immune system in part by coating themselves with some of the host's own antigens that effectively render the worm immunologically invisible (see chapter 52). The search is on for a vaccine that would cause the host to develop antibodies to one of the antigens of young worms before they can protect themselves.

Cercomeromorpha: The tapeworms and their relatives

An adult tapeworm hangs onto the inner wall of its host's intestine by means of a terminal attachment structure. It lacks a digestive cavity as well as digestive enzymes, absorbing food from the host's gut through its outer surface. Most species of tapeworm occur in the intestines of vertebrates; about a dozen of them regularly occur in humans.

The long, flat body of a tapeworm is divided into three zones: the **scolex,** or attachment structure; the neck; and a series of repetitive sections, the **proglottids** (figure 33.14). The scolex of many species bears four suckers and may also have hooks. The scolex is not a head: it has neither concentrated nervous tissue nor a mouth. Each proglottid is a complete hermaphroditic unit, containing both male and female

Figure 33.13 **Schistosomes.** The male lies within the groove on the female's ventral side, with its front and hind ends protruding.

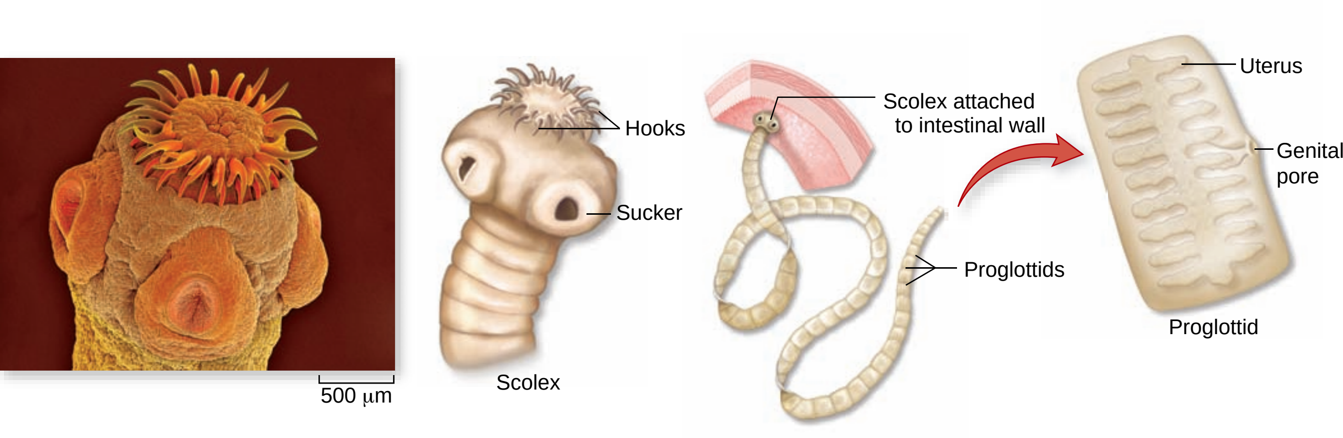


Figure 33.14 Tapeworms. Flatworms such as this beef tapeworm, *Taenia saginata*, live parasitically in the intestine of mammals.

reproductive organs. Proglottids are formed continuously in a growth zone at the base of the neck, with maturing ones being pushed posteriorly as new ones are formed. The gonads in the proglottids progressively mature away from the neck, fertilization occurs, and the embryos form, the proglottids nearer the end of the body being more mature. The most terminal proglottid, filled with embryonated eggs, breaks off; either it ruptures and the embryos, each surrounded by a shell, are carried out with the host's feces, or the entire proglottid is carried out, where the embryos emerge from it through a pore or the ruptured body wall. Embryos are scattered in the environment, on leaves, in water, or in other places where they may be picked up by another animal.

The beef tapeworm, *Taenia saginata*, occurs as a juvenile in the intermuscular tissue of cattle; as an adult, it inhabits the intestines of human beings, where a mature worm may reach a length of 10 m or more. A worm attaches itself to the intestinal wall of the host by a scolex with four suckers. Shed proglottids pass from the human in the feces and may crawl onto vegetation, a favorable place to be picked up by cattle; they may remain viable for up to five months. If one is ingested by cattle, the larva burrows through the wall of the intestine and ultimately reaches muscle tissues through the blood or lymph vessels. About 1% of cattle in the United States are infected, and because some 20% of the beef consumed is not federally inspected, when humans eat infected beef that is cooked "rare," infection by these tapeworms can occur. As a result, the beef tapeworm is a frequent parasite of humans.

Acoel flatworms appear to be distinct from Platyhelminthes: A case study

An acoel flatworm (figure 33.15) has a nervous system that consists of a simple network of nerves with a minor concentration of neurons in the anterior body end. It lacks a permanent digestive cavity, so the mouth leads to a solid digestive syncytium (a mass of cells that have no cell membranes separating them).

These characteristics had been used to place the acoels at the base of phylum Platyhelminthes and that phylum at the base of the Bilateria. However, based on molecular evidence, scientists have concluded that acoels are not closely related to members of phylum Platyhelminthes—similarities between the two groups are convergent. They belong in their own phylum, Acoela, or are members of the phylum Acoelomorpha, which includes another group of simple bilaterians once considered to be flatworms. Their precise position in the phylogenetic tree differs depending on the features used to construct it; one hypothesis is they evolved before the phylogenetic split between protostomes and deuterostomes.

Phylum Cycliophora was discovered relatively recently

In December 1995, Danish biologists Peter Funch and Reinhardt Kristensen reported the discovery of a strange new kind of acoelomate creature about the size of a period on a printed page. The tiny organism has a striking circular mouth surrounded by a ring of cilia, and its anatomy and life cycle are so unusual that their discoverers assigned it to an entirely new phylum, Cycliophora (figure 33.16).

The newest phylum to be named before Cycliophora, the Loricifera, was discovered also by Reinhardt Kristensen in 1983, and he and Peter Funch discovered yet another new phylum in 2000, the Micrognathozoa.

Cycliophorans live on the mouthparts of claw lobsters on both sides of the North Atlantic. When the lobster to which they are attached starts to molt, the tiny cycliophoran undergoes sexual reproduction. Each male, which consists of nothing but brains and reproductive organs, seeks out a female on the molting lobster and fertilizes her eggs, generating free-swimming larvae that can seek out another lobster and continue the life cycle.

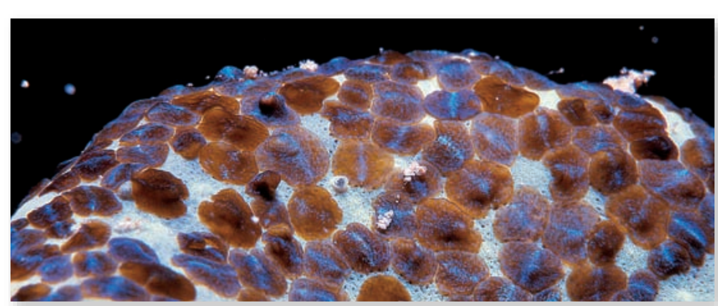


Figure 33.15 Phylum Acoela. An acoel flatworm of the genus *Waminoa*. These flatworms, long thought to be relatives of the Platyhelminthes, have a primitive nervous system and lack a permanent digestive cavity.

Figure 33.16
Phylum Cycliophora. About the size of the period at the end of this sentence, these acoelomates live on the mouthparts of claw lobsters. One feeding stage (and part of a second one) of *Symbion pandora* are shown attached to the mouthpart of a lobster.

Learning Outcomes Review 33.3

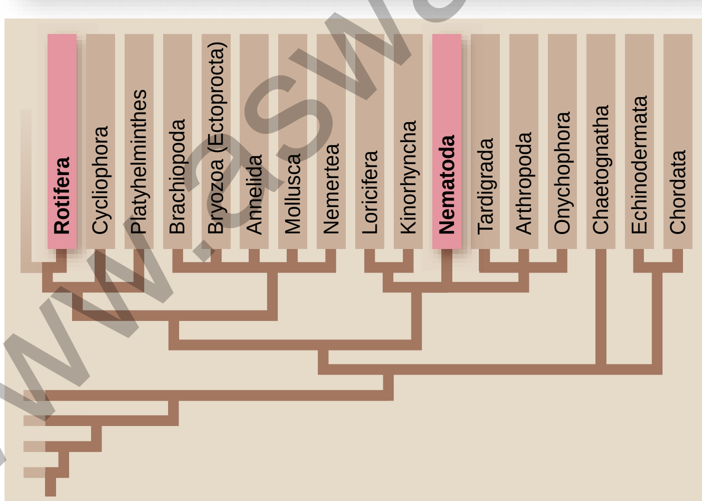
The acoelomates, typified by flatworms, are compact, bilaterally symmetrical animals. Most have a blind digestive cavity with only one opening; they also have an excretory system consisting of flame cells within tubules that run throughout the body. Many are free-living, but some cause human diseases. The scolex of a tapeworm is not a head, but simply an anchoring device to hold the animal in the intestine where it acts as a parasite.

- ***How does the anatomy of a tapeworm relate to its way of life?***

33.4 *The Pseudocoelomates*

Learning Outcomes

1. ***Describe the distinguishing features of pseudocoelomates.***
2. ***Describe the musculature of a nematode that allows it to wriggle in a highly characteristic manner.***
3. ***Explain why rotifers are referred to as "wheel animals."***



All bilaterians except acoelomates possess an internal body cavity. One type of cavity is a pseudocoelom, which, you will recall, lies between tissues derived from the mesoderm and those derived from the endoderm (chapter 32; see figure 32.2). The pseudocoelomic fluid performs the functions carried out by a circulatory system in most coelomate animals. The pseudocoelom also serves as a hydrostatic skeleton. The hydrostatic skeleton of both pseudocoelomates and coelomates is an improvement on the one supporting cnidarian polyps and medusae because, not being the digestive cavity, it is entirely isolated from the environment. The movement of these animals with a hydrostatic skeleton is more efficient than that of the solid acoelomates.

Recall that pseudocoelomates are not monophyletic. Most belong to the Ecdysozoa, which includes phyla Nematoda, Kinorhyncha, and Loricifera. Other pseudocoelomates, such as the rotifers, belong to the Platyzoa. In this section, we focus on two significant pseudocoelomate phyla.

The roundworms, phylum Nematoda, are ecdysozoans comprising many species

Vinegar eels, eelworms, and other roundworms constitute a large phylum, **Nematoda,** with some 20,000 recognized species; scientists estimate that the actual number might approach 100 times that many. Nematodes are abundant and diverse in marine and freshwater habitats, and many members of this phylum are parasites of animals (figure 33.17) and plants. Many nematodes are microscopic and live in soil. A spadeful of fertile soil may contain, on the average, a million nematodes.

Nematode structure

Nematodes are bilaterally symmetrical, unsegmented worms covered by a flexible, thick cuticle that is molted as they grow—parasitic nematodes molt four times. Lacking specialized respiratory organs, nematodes exchange oxygen and carbon dioxide through their cuticles. Muscles beneath the epidermis, which underlies the cuticle, extend longitudinally, from anterior to posterior. Nematodes are unusual among worms in that they lack circular musculature, so they can shorten but not change

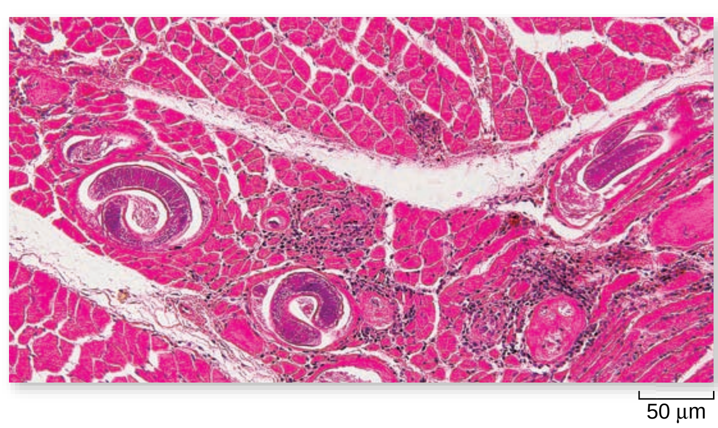


Figure 33.17 ***Trichinella*** **nematode encysted in pork.** The serious disease trichinosis can result from eating undercooked pork or bear meat containing such cysts.

diameter. The pulling of these longitudinal muscles against both the cuticle and the pseudocoelom produces the characteristic wriggling motion of nematodes.

Nematodes possess a well-developed digestive system and feed on a diversity of food sources. Near the mouth, at the anterior end, are hairlike sensory structures. The mouth may be equipped with piercing organs called **stylets.** Food passes into the mouth as a result of the sucking action produced by the rhythmic contraction of a muscular pharynx and continues through the intestine; waste is eliminated through the anus (figure 33.18).

Reproduction and development

Reproduction in nematodes is sexual; most nematodes are gonochoric. Nematode males and females differ in form, a state known as **sexual dimorphism** (meaning "two bodies"): the tail end of the smaller male is hooked (see figure 33.18), whereas that of a female is straight. Fertilization is internal, the male using its hooked end and associated structure to help inseminate the female. Development is indirect, meaning that an egg hatches into a larva, which does not grow directly into an adult, but must pass through several molts and, in parasitic species, transfer from one host to another.

The adults of some species consist of a fixed number of cells, a phenomenon known as eutely. For this reason, nematodes have become extremely important subjects for genetic and developmental studies (see chapter 19). The 1 mm long *Caenorhabditis elegans* matures in three days; its body is transparent, and it has precisely 959 cells. It is the only animal whose complete developmental cellular anatomy is known.

Nematode lifestyles

Many nematodes are active hunters, preying on protists and other small animals. Many are parasites of plants or live within the bodies of larger animals. Almost every species of plant and animal that has been studied has been found to have at least one parasitic species of nematode. The largest known nematode, which can attain a length of 9 m, parasitizes the placenta of sperm whales.

Nematode-caused human diseases

About 50 species of nematodes, including several that are rather common in the United States, regularly parasitize human beings. Hookworms, most of the genus *Necator*, can be common in southern states. By sucking blood through the intestinal wall, they can produce anemia.

The most serious and common nematode-caused disease in temperate regions is trichinosis. Worms of the genus *Trichinella* (see figure 33.17) live in the small intestine of some mammals, especially pigs and bears, where fertilized females burrow through the intestinal wall and release live young (as many as 1500 per female). The young enter the lymph channels, which transport them to muscles throughout the body. There they mature and form highly resistant, calcified cysts. Eating undercooked or raw pork or bear in which cysts are present transmits the worm. Fatal infections, which can occur if the worms are abundant, are rare: in the United States, only about 20 deaths have been attributed to trichinosis during the past decade.

It is estimated that pinworms, *Enterobius vermicularis*, infect about 30% of children and 16% of adults in the United States. Adult pinworms live in the human rectum where they

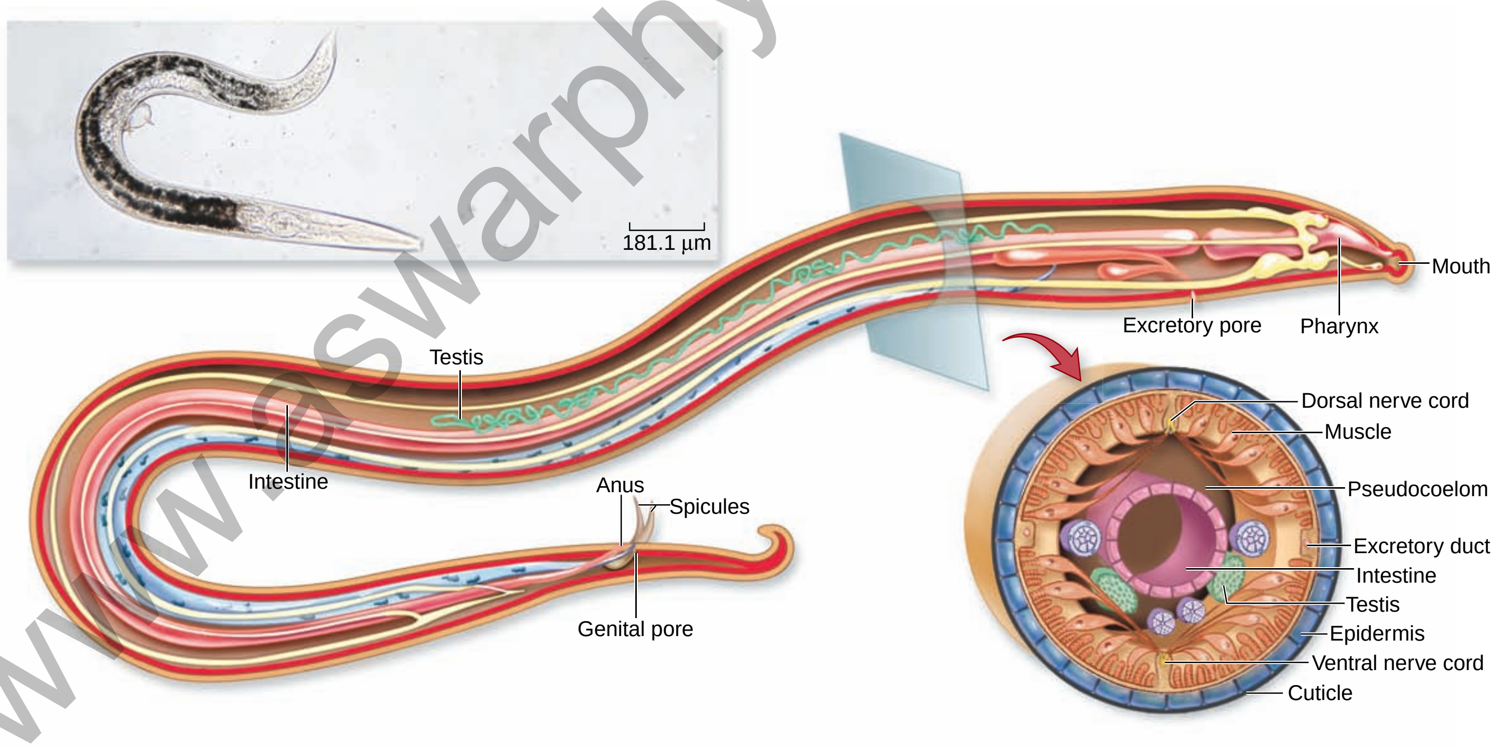


Figure 33.18 Phylum Nematoda: Roundworms. Roundworms such as this male nematode possess a body cavity between the gut and the body wall called the pseudocoelom. It allows nutrients to circulate throughout the body and prevents organs from being deformed by muscle movements.

usually cause nothing more serious than itching of the anus; large numbers, however, can lead to prolapse of the rectum. The worms can easily be killed by drugs.

The intestinal roundworm *Ascaris lumbricoides* infects approximately one of six people worldwide, but is rare in areas with modern plumbing. An adult female, which can be as much as 30 cm long, can release as many as 20,000 fertilized eggs each day into the gut of its host. The eggs, are carried from the body in the host's feces, and can remain viable for years in the soil; dust may carry them onto food, eating implements, or lips. Because the embryo has developed in each egg before it is shed, once it is ingested, it hatches. The larva follows a circuitous path through the body, and metamorphoses into an adult, which lives in the human intestine.

Some nematode-caused diseases are extremely serious in the tropics. Filariasis is caused by several species of nematodes that infect at least 250 million people worldwide. Filarial worms of some species live in the circulatory system. Infection by *Wuchereria bancrofti* may produce the condition known as elephantiasis, in which the lower extremities may swell to disfiguring proportions. This occurs because worms clog the lymph nodes, causing severe inflammation and resulting in swelling by preventing the lymph from circulating. The larval filarial worms are transmitted by an intermediate host, typically a bloodsucking insect such as a mosquito.

The rotifers, phylum Rotifera, are tiny

Rotifers (phylum **Rotifera**) are bilaterally symmetrical, unsegmented pseudocoelomates (figure 33.19) that look nothing like nematodes. Several features suggest their ancestors may have resembled flatworms, with which they are classified in the spiralian Platyzoa.

At 50 to 500 μm long, rotifers are smaller than some ciliate protists. But they have complex bodies with three cell layers, highly developed internal organs, and a complete gut. An extensive pseudocoelom acts as a hydrostatic skeleton; the cytoskeleton provides rigidity. A rotifer has a rigid external covering, but its body can lengthen and shorten greatly because the posterior part is tapered so it can fold up like a telescope. Many have adhesive toes used for clinging to vegetation and other such objects.

Diversity and distribution

About 1800 species are known, most of which occur in fresh water; a few rotifers live in soil, the capillary water in cushions of mosses, and the ocean. The lifespan of a rotifer is typically no longer than 1 or 2 weeks, but some species can survive in a desiccated, inactive state on the leaves of plants; when rain falls, the rotifers become active and feed in the film of water that temporarily covers the leaf.

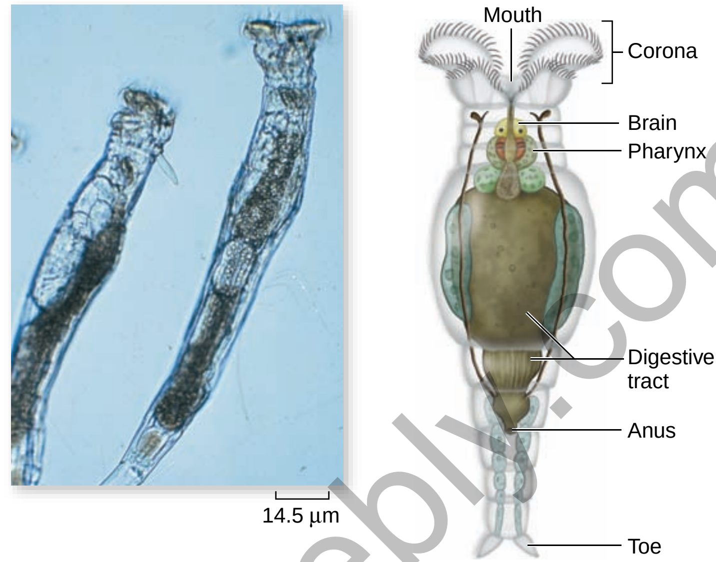


Figure 33.19 Phylum Rotifera. Microscopic in size, rotifers are smaller than some ciliate protists, and yet have complex internal organs.

Food gathering

The corona, a conspicuous ring of cilia at the anterior end (see figure 33.19), is the source of the common name "wheel animals" for rotifers because its beating cilia make it appear that a wheel is rotating around the head of the animal. The corona is used for locomotion, but its cilia also sweep food into the rotifer's mouth. Once food is swallowed, it is crushed with a complex jaw in the pharynx.

Learning Outcomes Review 33.4

Pseudocoelomates have fluid-filled body cavities lined by endoderm and mesoderm. Nematodes are bilaterally symmetrical, unsegemented worms that have longitudinal muscle, but not muscle in a circle around the body. Aside from the many free-living species, some nematodes are parasites of animals and plants. Rotifers are extremely small but with highly complex body structure; the name "wheel animals" comes from the apparent motion of their beating cilia.

- ***What modern development is most effective in combating the spread of intestinal roundworms?***

Chapter Review

33.1 Parazoa: Animals That Lack Specialized Tissues

The sponges, phylum Porifera, have a loose body organization.

Sponges lack tissues and organs and a definite symmetry, but they do have a complex multicellularity. Larval sponges are free-swimming, and the adults are anchored onto submerged objects.

The sponge body is composed of several cell types.

Sponges are composed of three layers: an external protective epithelial layer; a central protein-rich matrix called mesohyl with amoeboid cells; and an inner layer of choanocytes that circulate water and capture food particles (see figure 33.1*b*).

Choanocytes help circulate water though the sponge.

The mesohyl may contain spicules and/or fibers of a tough protein called spongin that strengthen the body of the sponge.

Sponges reproduce both asexually and sexually.

Fragments of a sponge are able to grow into complete individuals. Sperm and eggs may be produced by mature individuals; these undergo fertilization to form zygotes that develop into free-swimming larvae that eventually become sessile adults.

33.2 Eumetazoa: Animals with True Tissues

All cnidarians, phylum Cnidaria, are carnivores.

Members of the carnivorous and radially (or biradially) symmetrical Cnidaria have distinct tissues but no organs. They are diploblastic and have two body forms: a sessile, cylindrical polyp and a free-floating medusa (see figure 33.3).

Cnidarians are distinguished by capsules called nematocysts that are used in offense and defense.

Cnidarians have no circulatory, excretory, or respiratory systems. They have a latticework of nerve cells and are sensitive to touch; some have gravity receptors and light receptors.

Cnidarians are grouped into four—or five—classes.

The five classes of Cnidaria are the Anthozoa (sea anemones, corals, seafans); Cubozoa (box jellies); Hydrozoa (hydroids, Hydra), Scyphozoa (jellyfish); and Staurozoa (star jellies). The Staurozoa class is not accepted by all scientists.

The comb jellies, phylum Ctenophora, use cilia for movement.

Ctenophora (comb jellies) is a small phylum of medusa-like animals that propel themselves with bands of fused cilia. They may be triploblastic. They capture prey with colloblasts, cells that release an adhesive.

33.3 The Bilaterian Acoelomates

The Bilateria are characterized by bilateral symmetry, which allows for functional specialization such as having nerve receptors at the anterior end of the body.

The flatworms, phylum Platyhelminthes, have an incomplete gut.

Free-living flatworms, phylum Platyhelminthes, move by muscles and ciliated epithelial cells. They also exhibit a head and an incomplete gut (see figure 33.11).

Flatworms have an excretory system containing a fine network of tubules with flame cells. The primary function of this system is water balance.

Flatworms reproduce sexually and are hermaphroditic. They also have the capacity for asexual regeneration.

Flatworms comprise two major groups.

Free-living flatworms belong to the groups Turbellaria, which is likely not to be monophyletic.

Parasitic flatworms belong to the group Neodermata, of which there are two groups: the flukes (Trematoda), and the tapeworms and their relatives (Cercomeromorpha). Flukes and tapeworms can cause disease in humans.

Acoel flatworms appear to be distinct from Platyhelminthes: A case study.

Acoel flatworms, phylum Acoela, were once considered basal to the phylum Platyhelminthes, but they may have evolved before the split between protostomes and deuterostomes.

Phylum Cycliophora was discovered relatively recently.

Cycliophorans are tiny organisms that live on the mouthparts of claw lobsters. They undergo sexual reproduction that coincides with the lobsters' molts.

33.4 The Pseudocoelomates

A pseudocoelom is a cavity between tissues derived from mesoderm and tissues derived from endoderm. The pseudocoelomate animals do not represent a clade.

The roundworms, phylum Nematoda, are ecdysozoans comprising many species.

Nematodes, which are ecdysozoans, reproduce sexually and exhibit sexual dimorphism. More species of nematodes may exist than species of arthropods.

Some important human, veterinary, and plant diseases are caused by nematodes, including hookworm, pinworm, trichinosis, intestinal roundworm, and filariasis.

The rotifers, phylum Rotifera, are tiny.

The tiny rotiferans are spiralian, and belong to the Platyzoa.

Rotifers propel themselves and gather food with cilia and break down food with a complex jaw located in the pharynx. They are either free-swimming or sessile.

Review Questions

UNDERSTAND

1. In modern phylogenetic analysis of the animals, the protostomes are divided into two major groups based on what characteristic?
   a. Their symmetry
   b. Having a head
   c. Their ability to molt
   d. The presence or absence of vertebrae
2. Which of the following cell types of a sponge possesses a flagellum?
   a. Choanocyte
   b. Amoebocyte
   c. Epithelial
   d. Spicules
3. Spicules and spongin are found _______ of a sponge.
   a. within the osculum
   b. within the mesohyl
   c. within the choanocytes
   d. outside of the epithelial cells
4. The larval stage of a cnidarian is known as a
   a. medusa.
   b. planula.
   c. polyp.
   d. cnidocyte.
5. In the flatworm, flame cells are involved in what metabolic process?
   a. Reproduction
   b. Digestion
   c. Locomotion
   d. Osmoregulation
6. Which of the following nematodes cause disease?
   a. Filarial worms
   b. Pinworms
   c. Trichina worms
   d. All of the above
7. Which of the following have a complete gut?
   a. Tapeworms
   b. Medusae
   c. Nematodes
   d. None of the above

APPLY

1. All animals have which of the following characteristics?
   a. Body symmetry
   b. Tissues
   c. Multicellularity
   d. Body cavity
2. Which of the following cell layers is not necessary to be considered a eumetazoan?
   a. Ectoderm
   b. Endoderm
   c. Mesoderm
   d. All of the above are found in all eumetazoans.
3. Which of the following would be considered a neodermatan?
   a. Earthworm
   b. Fluke
   c. Tapeworm
   d. Both b and c

SYNTHESIZE

1. What do the phyla Acoela and Cycliophora tell you about our understanding of noncoelomate invertebrates? Do you think that the phylogeny presented in section 33.2 is complete? Explain your answer.
2. What benefit would being a hermaphrodite confer on a parasitic species?
3. Does the lack of a digestive system in tapeworms indicate that it is a primitive, ancestral form of platyhelminthes? Explain your answer.

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Chapter 34

Coelomate Invertebrates

Chapter Outline

Introduction

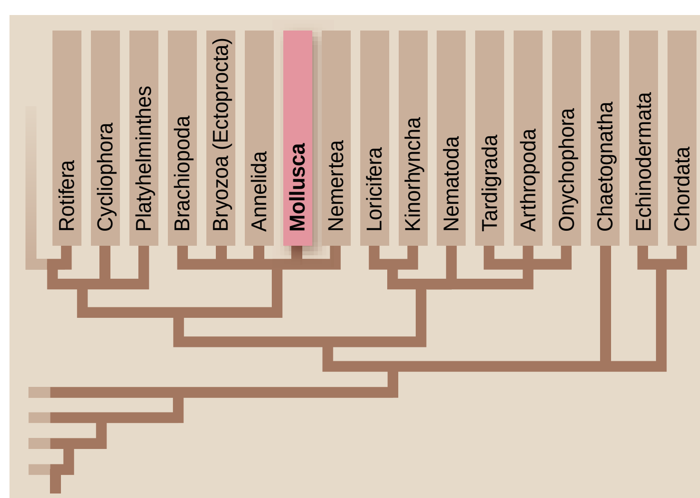
The body cavity of some animals is a coelom. As described in chapter 32, a coelom is an internal space lined with tissue derived from mesoderm. Clades of coelomate animals can be recognized by details of how the coelom develops and other features such as whether the body is segmented or the skeleton is internal or external. Some animals with a coelom are protostomes; all deuterostomes have a coelom. Among coelomate protostomes are mollusks, annelids, and arthropods. Deuterostomes include echinoderms, which are exclusively marine animals, and chordates (the subject of chapter 35).

34.1 *Phylum Mollusca: The Mollusks*

Learning Outcomes

1. *List the defining features of phylum Mollusca.*
2. *Describe representatives of the four best-known groups of mollusks.*
3. *Explain the distinguishing features of cephalopods.*

Mollusks (phylum Mollusca) are diverse morphologically and live in many types of environments. With more than 110,000 described species, the phylum is second only to arthropods. Mollusks include snails, slugs, clams, scallops,



a. *b.* *c.* *d.*

Figure 34.1 Mollusk diversity. Mollusks exhibit a broad range of variation. ***a.*** The flame scallop, *Lima scabra*, is a filter feeder. ***b.*** The blue-ringed octopus, *Hapalochlaena maculosa*, is one of the few mollusks dangerous to humans. Strikingly beautiful, it is equipped with a sharp beak that can deliver a poisonous bite! ***c.*** Nautiluses, such as this chambered nautilus, *Nautilus pompilius*, have been around since before the age of the dinosaurs. ***d.*** The banana slug, *Ariolimax columbianus*, native to the Pacific Northwest, is the second largest slug in the world, attaining a length of 25 cm.

oysters, cuttlefish, octopuses, and many other familiar animals (figures 34.1 and 34.2). The shells of many mollusks are beautiful and elegant; they have long been collected, preserved, and studied by professional scientists and amateurs. Some mollusks, however, lack a shell.

Mollusks are extremely diverse—and important to humans

Mollusks range in size from almost microscopic to huge. Although most measure a few millimeters to centimeters in their largest dimension, the giant squid may grow to more than 15 m long and weigh as much as 250 kg. It is therefore one of the heaviest invertebrates (although nemerteans can be longer, as discussed later). Other large mollusks are the giant clams of the genus *Tridacna*, which may be as long as 1.5 m and may weigh as much as 270 kg (see figure 34.2).

Figure 34.2 Giant clam. Second only to the arthropods in number of described species, members of the phylum Mollusca occupy almost every habitat on Earth. This giant clam, *Tridacna maxima*, contains symbiotic dinoflagellates (zooxanthellae) as do reef-forming corals. Through photosynthesis, the dinoflagellates probably contribute to the food of the clam, although it is a filter feeder like most bivalves. Some individual giant clams may be nearly 1.5 m long and weigh as much as 270 kg.

Like all major animal groups, mollusks evolved in the oceans, and most groups have remained there. Marine mollusks are widespread and many are abundant. Snails and slugs have invaded freshwater and terrestrial habitats, and freshwater mussels live in lakes and streams (the flat foot of a snail or slug allows it to crawl, but the foot of clams, mussels, and other bivalved mollusks is adapted to digging, so they cannot move about on land). Some places where terrestrial mollusks live, such as crevices of desert rocks, may appear dry, but if mollusks live there, the habitat has at least a temporary supply of water.

Mollusks—including oysters, clams, scallops, mussels, octopuses, and squids—are an important source of food for humans. They are also economically significant in other ways. For example, the material called mother-of-pearl (nacre), which is used for jewelry and other decorative objects, and formerly for buttons, comes from mollusk shells, most notably that of the abalone. Mollusks can also be pests. Bivalves called ship-worms burrow through wood exposed to the sea, damaging boats, docks, and pilings. The zebra mussel (*Dreissena polymorpha*) (see figure 60.16) has recently invaded many North American freshwater ecosystems. Many slugs and snails damage flowers, vegetable gardens, and crops. Other mollusks serve as hosts to the larval stages of many serious parasites, as discussed in chapter 33.

The mollusk body plan is complex and varied

Some mollusk body plans are illustrated in figure 34.3. The **mantle,** a thick epidermal sheet, covers the dorsal side of the body, and bounds the mantle cavity. The mantle secretes the calcium carbonate of the shell in those mollusks with a shell. The muscular foot is the primary means of locomotion in mollusks other than cephalopods (octopuses, squid, and

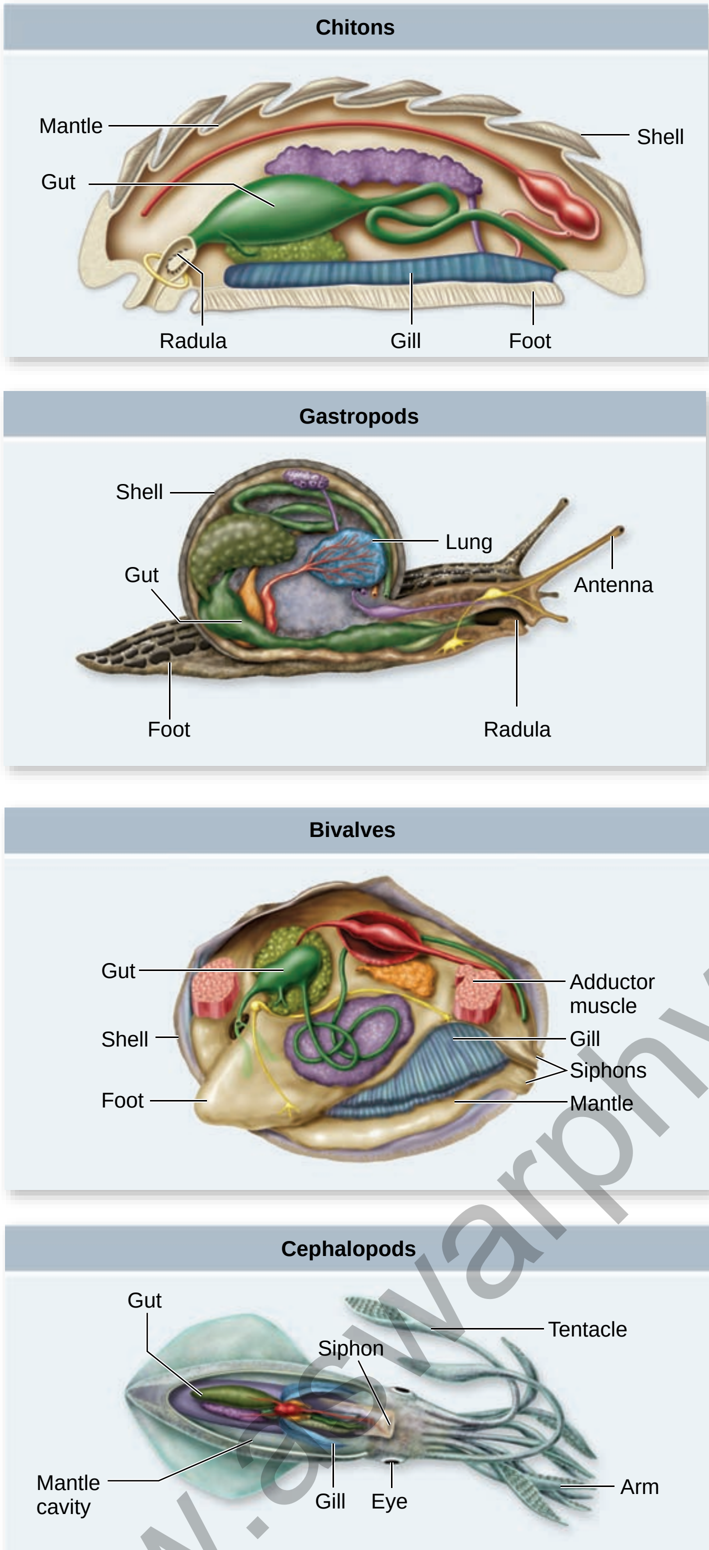


Figure 34.3 **Body plans of some mollusks.**

chambered nautilus). The head may be well developed or not. Like all coelomates, mollusks are bilaterally symmetrical, but this symmetry is modified during development of many gastropods (snails and their relatives), which undergo torsion (a twisting of the body discussed in detail later on).

The muscular foot is variously adapted for locomotion, attachment, food capture, digging, or combinations of these functions. The foot of slugs and snails secretes mucus, forming a path that it glides along. In cephalopods, the foot is divided into tentacles and, in some cephalopods, arms. Clams burrow into mud and sand using their hatchet-shaped foot. In some mollusks that live in the open ocean, the foot is modified into winglike projections, the large surface area of which serves to slow its sinking. The feet of these mollusks can beat like wings.

Internal organs

In all mollusks, the coelom is highly reduced, being limited to small spaces around the excretory organs, heart, and part of the intestine. An important role of the coelom in some other invertebrates (that is, forming the hydrostatic skeleton) is served in mollusks by the shell. The digestive, excretory, and reproductive organs are concentrated in a **visceral mass.**

In aquatic mollusks, the **ctenidia** (or gills, the respiratory structures) project into the mantle cavity (see figure 34.3). They consist of filaments rich in blood vessels that greatly increase the surface area and capacity for gas exchange. The continuous stream of water that passes through the mantle cavity, propelled by cilia on the gills of all mollusks except cephalopods, carries oxygen in and carbon dioxide away. Mollusk ctenidia are so efficient that they can extract 50% or more of the dissolved oxygen from the water that passes through the mantle cavity. In addition to extracting oxygen from incoming water, the gills of most bivalves filter out food. Because the outlets from the excretory, reproductive, and digestive organs open into the mantle cavity, wastes and gametes are carried away from a mollusk's body with the exiting water stream.

Shells

One of the best known characters of the phylum is the shell. A mollusk shell, which is secreted by the outer surface of the mantle, protects against predators and adverse environmental conditions. However, a shell is clearly not essential: reduction, internalization, and loss of the shell have evolved repeatedly. Examples of shell-less mollusks are cuttlefish, squids, and octopuses (cephalopods) as well as slugs (gastropods).

A typical mollusk shell consists of two layers of calcium carbonate, which is precipitated extracellularly. The outer layer consists of densely packed crystals. In some species, the inner layer is pearly in appearance, and is called mother-of-pearl or nacre. Particularly in freshwater mollusks, the mineralic layers are covered by a thin organic coating rich in the protein conchiolin that protects the shell from dissolving. Pearls are formed when a foreign object, such as a grain of sand, becomes lodged between the mantle and the inner shell layer. The mantle coats the object with layer upon layer of nacre to reduce the irritation caused by the object. The most beautiful and highly valued pearls are produced by oysters.

Feeding and prey capture: Radula

A characteristic feature of most mollusks is the **radula** (plural, *radulae*), a rasping, tonguelike structure used in feeding. It consists of dozens to hundreds of microscopic, chitinous teeth arranged in rows on an underlying membrane and lies in a chamber at the anterior end of the gut (figure 34.4). The

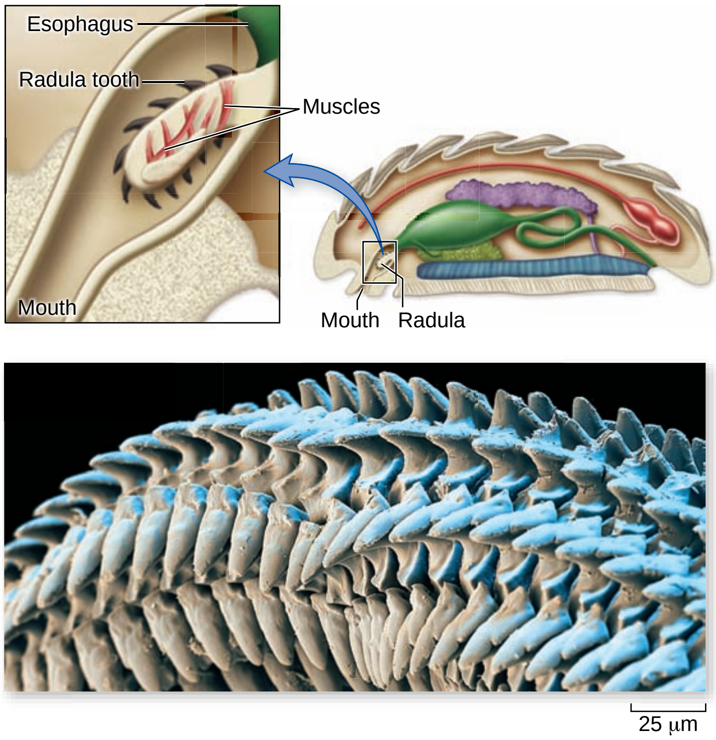


Figure 34.4 Structure of the radular apparatus in a chiton. The radula consists of rows of teeth made of chitin. As the animal feeds, its mouth opens, and the radula is thrust out to scrape food off surfaces.

membrane wraps around a muscular support structure so the radula can be protruded through the mouth and move something like a sanding belt over what is being rasped. Benthic mollusks use their radulae to scrape up algae and other food materials.

In some predatory gastropods (such as moon snails), the radula is modified to drill through clam shells so the snail can eat the clams. In snails of the genus *Conus*, the radula has been transformed into a harpoon that is associated with a venom gland; cone snails use this harpoon to capture prey such as fish, and some cone snails can harm—or even kill—humans.

Bivalves are the only mollusks that have no radula. The gills of most bivalves are adapted to filter food particles from the water, although primitive bivalves pick up bits of food from soft sediments (this is, they are deposit feeders) using appendages around the mouth.

Removal of wastes

Nitrogenous wastes are removed from the mollusk body by the **nephridium** (plural, *nephridia*), a sort of kidney. A typical nephridium has an open funnel, the nephrostome, which is lined with cilia. A coiled tubule runs from the **nephrostome** into a bladder, which in turn connects to an excretory pore. Wastes are gathered by the nephridia from the coelomic cavity and discharged into the mantle cavity. Sugars, salts, water, and other materials are reabsorbed by the walls of the nephridia and returned to the animal's body as needed to maintain osmotic balance.

The circulatory system

The main coelomic cavity of a mollusk is a hemocoel, which comprises several sinuses and a network of vessels in the gills, where gas exchange takes place. Except for cephalopods, all mollusks have such an open circulatory system; blood (technically termed "hemolymph") is propelled by a heart through the aorta vessel that empties to the hemocoel. The blood moves through the hemocoel being recaptured by other venous vessels before re-entering the heart (see chapter 50). The heart of most, but not all mollusks has three chambers, two that collect aerated blood from the gills, and a third that pumps it into the hemocoel. The blood of the closed circulatory system of cephalopods is contained in a continuous system of vessels, so it does not contact other tissues directly.

Reproduction

Most mollusks have separate sexes although a few bivalves and many freshwater and terrestrial gastropods are hermaphroditic. Most hermaphroditic mollusks engage in cross-fertilization. Some oysters are able to change sex.

As is typical of animals living in the sea, many marine mollusks have external fertilization: gametes are released by males and females into the water where fertilization occurs. Most gastropods, however, have internal fertilization, with the male inserting sperm directly into the female's body (not, that is, into a preformed channel). Internal fertilization, a foot, and an efficient excretory system that prevents desiccation are some of the key adaptations that allowed gastropods to colonize the land.

A mollusk zygote undergoes spiral cleavage (thus Mollusca is part of the Spiralia; see chapter 32). The embryo develops into a free-swimming larva called a trochophore (figure 34.5*a*) that closely resembles the larval stage of many marine annelids and other lophotrochozoans. A trochophore swims by means of cilia that encircle the middle of its body.

In most marine snails and in bivalves, the trochophore develops into a second free-swimming stage, the **veliger.** The veliger forms the beginnings of a foot, shell, and mantle (figure 35.5*b*). Trochophores and veligers drift widely in the ocean, dispersing these otherwise sedentary mollusks.

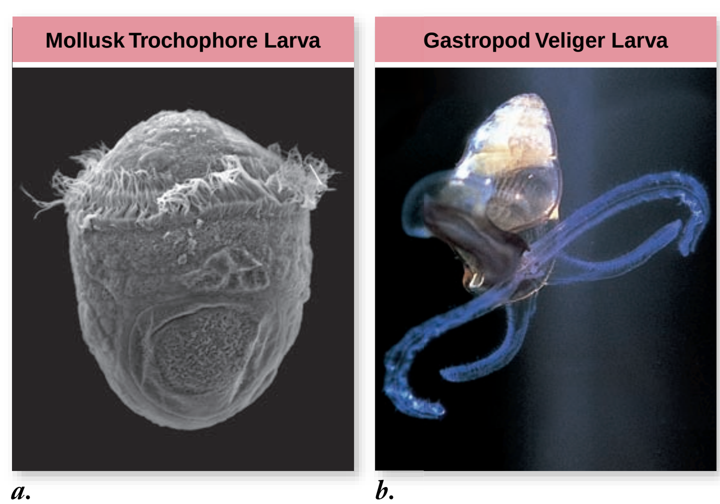


Figure 34.5 Stages in the molluskan life cycle. ***a.*** The trochophore larva. Similar larvae are characteristic of some annelid worms as well as a few other phyla. ***b.*** The veliger stage of a gastropod.

Four classes of mollusks show the diversity of the phylum

We examine four of the seven or eight recognized classes of mollusks: (1) Polyplacophora—chitons; (2) Gastropoda—limpets, snails, slugs, and their relatives; (3) Bivalvia—clams, oysters, scallops, and their relatives; and (4) Cephalopoda—squids, octopuses, cuttlefishes, and the chambered nautilus.

By studying living mollusks and the fossil record, some scientists have deduced that the ancestral mollusk was probably a bilateral, dorsoventrally flattened, unsegmented, wormlike animal that glided on its ventral surface. This animal may have had a chitinous cuticle that secreted calcareous spicules. Other scientists infer that mollusks arose from segmented ancestors and became unsegmented secondarily.

Class Polyplacophora: Chitons

Chitons are exclusively marine; there are perhaps 1000 species. The oval body is covered dorsally with eight overlapping dorsal calcareous plates (figure 34.6). The body is not segmented, but chitons do have eight sets of dorsoventral pedal retractor muscles and serially repeated gills. The broad, flat ventral foot, on which the animal creeps, is surrounded by a groove, the mantle cavity, in which the gills are suspended. Most chitons are grazing herbivores, and live in shallow marine habitats, but chitons occur to depths of more than 7000 m.

Class Gastropoda: Snails and slugs

The 40,000 or so species of limpets, snails and slugs belong to this class, which is primarily marine. However, this group contains many freshwater species and the only terrestrial mollusks (figure 34.7). Most gastropods have a single shell, but some, such as slugs and nudibranchs (or sea slugs), have lost the shell through the course of evolution. Most gastropods creep on a foot, but in some it is modified for swimming.

The head of most gastropods has a pair of tentacles, which serve as chemo- or mechanoreceptors, with eyes at the base. A typical garden snail may have two sets of tentacles, one of them bearing eyes at the ends (see figure 34.7).

Uniquely among animals, gastropods undergo torsion during larval life. **Torsion** involves twisting of the body so the

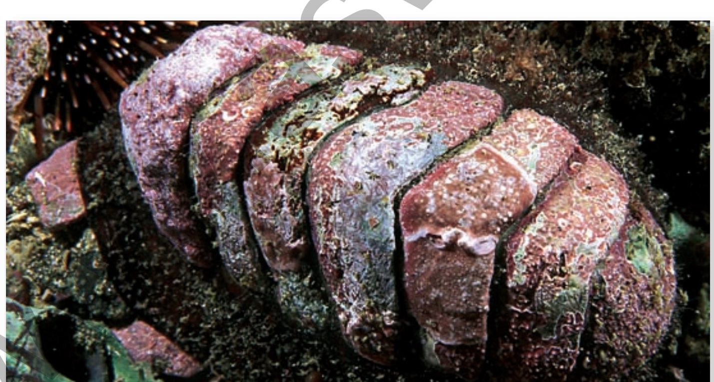


Figure 34.6 The noble chiton, *Eudoxochiton nobilis*, from New Zealand. The foot of the chiton can grip the substrate very strongly, making chitons hard to dislodge by waves or predators.

Figure 34.7 A Gastropod mollusk. The terrestrial Oregon forest snail *Allogona townsendiana*.

mantle cavity and anus are moved from a posterior location to the front of the body. Torsion may lead to the reduction or disappearance of the nephridium, gonad, or other internal organs on one side. Most adult gastropods are therefore not bilaterally symmetrical. Torsion should not be confused with coiling, the spiral winding of the shell. Coiling also occurs in cephalopods. The fossil record suggests that the first gastropods were coiled but did not undergo torsion.

Like many gastropods, nudibranchs (sea slugs) are active predators. Nudibranchs get their name from their gills, which, instead of being enclosed within the mantle cavity, are exposed along the dorsal surface (figure 34.8). Nudibranchs would seem vulnerable to predation, but many secrete distasteful chemicals. They prey on animals that are avoided by other predators. Some are specialist feeders on sponges, most species of which form spicules and noxious chemicals. Other nudibranchs specialize in feeding on cnidarians, which are protected from most predators by their nematocysts. Some of these nudibranchs have the extraordinary ability to extract the

Figure 34.8 A nudibranch (or sea slug). The bright colors of many nudibranchs such as this alert predators to their repulsive taste.

nematocysts undischarged, transfer them through their digestive tract to the surface of their bodies, and use them for their own protection.

In terrestrial gastropods, the mantle cavity, which is occupied by gills in aquatic snails, is extremely rich in blood vessels and serves as a lung. This lung absorbs oxygen from the air much more effectively than a gill could; however, a snail will drown if its lung fills with water; for this reason, terrestrial gastropods can close the opening of the lung to the outside.

Class Bivalvia: Clams, mussels, and cockles

Most of the 10,000 species of bivalves are marine, but some live in fresh water. More than 500 species of pearly freshwater mussels, or naiads, occur in the rivers and lakes of North America.

Unlike other mollusks, a bivalve does not have a radula or distinct head (figure 34.9). The foot of most is wedge-shaped, adapted for burrowing or anchoring the animal in its burrow. Some species of clams can dig into sand or mud very rapidly by means of muscular contractions of their foot. Some species of scallops and file clams can move swiftly by clapping their shells rapidly together (although they cannot control the direction of their movement); the adductor muscle that allows this clapping is the part of a scallop eaten by humans. Projecting from the edge of a scallop's mantle are tentacle-like projections having complex eyes between them.

Bivalves, as their name implies, have two shells (valves) that are hinged dorsally so the shells are oriented laterally (left and right). A ligament lying along the hinge is structured so it causes the shells to gape open. One or two large adductor muscles link the shells internally (see figure 34.9), and when they contract, they counteract the hinge ligament to draw the shells together. The mantle covers the internal surface of the shells, enveloping the visceral mass on its inner side and secreting the shells on its outer side. As is typical of mollusks, the respiratory structures, a set of complexly folded gills on each side of the visceral mass, lie in the mantle cavity.

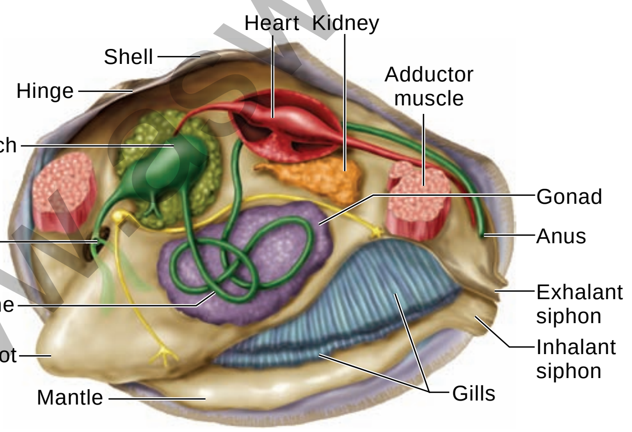


Figure 34.9 Diagram of a clam. The left shell and mantle are removed to show the internal organs and the foot. Bivalves such as this clam circulate water across their gills and filter out food particles.

The edges of the mantle may be partly fused. In bivalves in which this is the case, typically two areas are not fused, and may be drawn out to form tubes called siphons (see figure 34.9). Water enters the mantle chamber through the **inhalant siphon** bringing oxygen and food, and water exits through the **exhalant siphon,** taking wastes and gametes with it. In bivalves that live buried deeply in mud or burrow into rock, the siphons allow the animals to eat and breathe, functioning essentially as snorkels.

Class Cephalopoda: Octopuses, squids, and nautiluses

The more than 600 species of cephalopods are strictly marine. They are active predators that swim, often swiftly, and they are the only mollusks with a closed circulatory system. The foot has evolved into a series of arms equipped with suction cups, adhesive structures, or hooks that seize prey. Octopuses, as their name suggests, have eight arms; squids have eight arms and two tentacles; and the chambered nautilus has 80 to 90 tentacles (which lack suckers). After snaring prey with its arms, a cephalopod bites the prey with its strong, beak-like jaws, then pulls it into its mouth by the action of the radula. The salivary gland of many cephalopods secretes a toxin that can be injected into prey; the tiny blue-ringed octopus of Australia (see figure 34.1*b*) can kill a human with its deadly bite.

Cephalopods have the largest relative brain sizes among invertebrates and highly developed nervous systems. Many exhibit complex patterns of behavior and are highly intelligent (figure 34.10); octopuses can be easily trained to distinguish

Figure 34.10 Problem-solving by an octopus. This two-month-old common octopus *(Octopus vulgaris)* was presented with a crab in a jar. It tried to unscrew the lid to get to the crab. Although it failed in this attempt, in some cases it was successful.

among classes of objects and are capable of leaving one tank to seize prey in another, then returning to their original one. Cephalopod eyes are much like those of vertebrates, although they evolved independently (see chapter 45).

Aside from the chambered nautiluses, living cephalopods lack an external shell. Shelled cephalopods were formerly far more diverse, as evidenced by the many fossil cephalopods such as ammonites and belemnites. These cephalopods were extraordinarily successful because they could move in open water instead of on the sea bottom like other mollusks. However, once the more maneuverable fishes evolved,shelled mollusks declined, some dying out, others experiencing evolutionary reduction and eventual loss of their heavy shells. The cuttlebone of cuttlefish and the pen of squids are internal shells that support these animals and give them some buoyancy. Even the internal shell has disappeared in the lineage that gave rise to octopuses.

As in other mollusks, water passes through the mantle cavity. In a cephalopod, it is pumped in by muscles and exits through a siphon, which allows the animal to move by jet propulsion, and which can be directed to steer. The ink sac of cephalopods, which typically contains a purplish fluid, can eject its contents through the siphon as a cloud that may hide the cephalopod and confuse predators (figure 34.11).

Most octopuses and squids are capable of changing skin color and texture to match their background or to communicate with one another. They do so using chromatophores, epithelial cells that contain pigments. Some deep-sea squids harbor symbiotic luminescent bacteria. These may be emitted with the ink to produce a glimmering cloud (ink would not be seen at depths where sunlight cannot penetrate) or they may inhabit cells like chromatophores so they can light up the surface of the animal.

Another difference with many other mollusks is that cephalopods have direct development, that is, they lack a larval stage, hatching as miniature adults.

Figure 34.11 Ink defense by a giant Pacific octopus *(Octopus dofleini).* When threatened, octopuses and squids expel a dark cloudy liquid.

Learning Outcomes Review 34.1

Mollusks are coelomates with a coelom surrounding the heart. Most have efficient excretory systems, ctenidia for respiration, and a rasping structure, the radula, for gathering food. The mantle of mollusks not only secretes their protective shell but also forms structures essential to body functions. Chitons, gastropods, bivalves, and cephalopods are the four best-known groups. Cephalopods lack cilia on their ctenidia and have a closed circulatory system.

- ***Why might a closed circulatory system be necessary in a cephalopod?***

34.2 *Phylum Nemertea: The Ribbon Worms*

Learning Outcome

1. ***Describe the two characteristics that place nemerteans with mollusks in the lophotrochozoa.***

Nemerteans (phylum Nemertea) consist of about 900 species of cylindrical to flattened very long worms (figure 34.12). Most nemerteans are marine; a few species live in fresh water and humid terrestrial habitats. An individual may reach 10 to 20 cm in length, although the animals are difficult to measure because they can stretch, and many species break into pieces when disturbed or handled. The species *Lineus longissimus* has been reported to measure 60 m in length—the longest animal known!

The nemertean body plan resembles that of a flatworm (see chapter 33), with networks of fine tubules constituting the excretory system, and with internal organs not lying in a body cavity. A bit of cephalization is present, with two lateral nerve cords extending posteriorly from an anterior ganglion; some animals have eyespots on the head. But, by contrast with a platyhelminth, a nemertean has a complete gut, with both mouth and anus, connected by a straight tube. Nemerteans also possess a fluid-filled cavity called a rhynchocoel. This sac serves

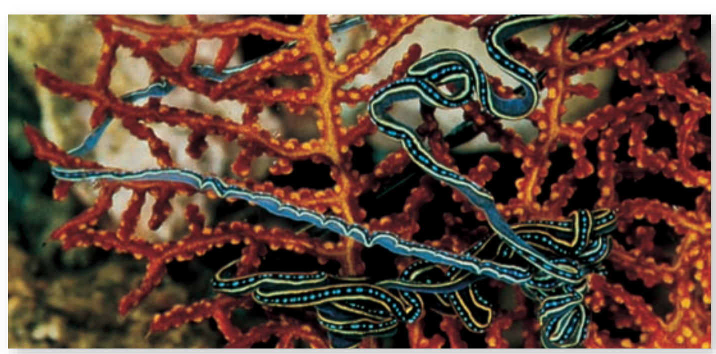


Figure 34.12 Phylum Nemertea: A ribbon worm of the genus *Lineus*. Some nemerteans can stretch to several meters in length.

as a hydraulic power source for the proboscis, a long muscular tube that can be thrust out quickly from a sheath to capture animal prey.

Nemerteans are gonochoric, and all reproduce sexually. Some are capable of asexual reproduction by fragmentation. However, in most species, most fragments resulting from disturbance die, so nemertean regenerative powers may not be as great as is sometimes stated.

Blood of nemerteans flows entirely in vessels that are derived from the coelom. That and the rhynchocoel are good evidence that nemerteans are not related to flatworms, which they resemble superficially, but belong to the Lophotrochozoa, along with mollusks.

Learning Outcome Review 34.2

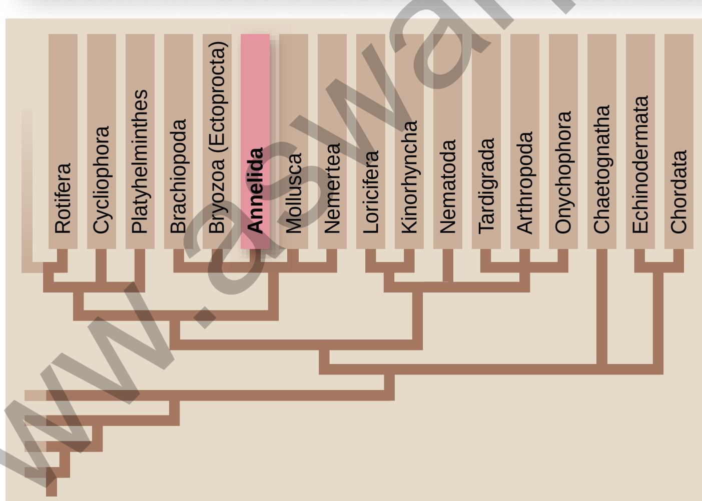
Nemerteans are very long worms that have a coelomic cavity and blood vessels derived from the coelom. They capture prey with a muscular proboscis. Unlike the acoelomate flatworms, nemerteans have a complete gut with mouth and anus.

- ***What would be some advantages of a flow-through digestive tract?***

34.3 Phylum Annelida: The Annelids

Learning Outcomes

1. *Explain how circular and longitudinal muscles in a segmented body facilitate movement.*
2. *Distinguish between the classes Polychaeta and Clitellata.*
3. *Describe adaptations in leeches for feeding on the blood of animals.*



An important innovation in the animal body plan was segmentation, the building of a body from a series of repeated units (see chapter 32), which has evolved multiple times. Worms of the phylum Annelida (figure 34.13) are segmented. One advantage of a segmented body is that the development and function of individual segments or groups of segments can differ. For example, some segments may be specialized for reproduction, whereas others are adapted for locomotion or excretion.

Figure 34.13 A polychaete annelid. *Nereis virens* is a wide-ranging, predatory, marine polychaete worm equipped with feathery parapodia for movement and respiration, as well as jaws for hunting. You may have purchased *Nereis* as fishing bait!

All animals that have been regarded as annelids are segmented, so the animals were considered to constitute a natural group, but the monophyly of Annelida is being reconsidered because some unsegmented worms may belong to this clade.

The annelid body is composed of ringlike segments

The head, which contains a well-developed cerebral ganglion, or brain, and sensory organs occurs at the anterior end (front) of a series of ringlike segments that resemble a stack of coins (figure 34.14). Many species have eyes, which in some species have lenses and retinas. Technically the head is not a segment,

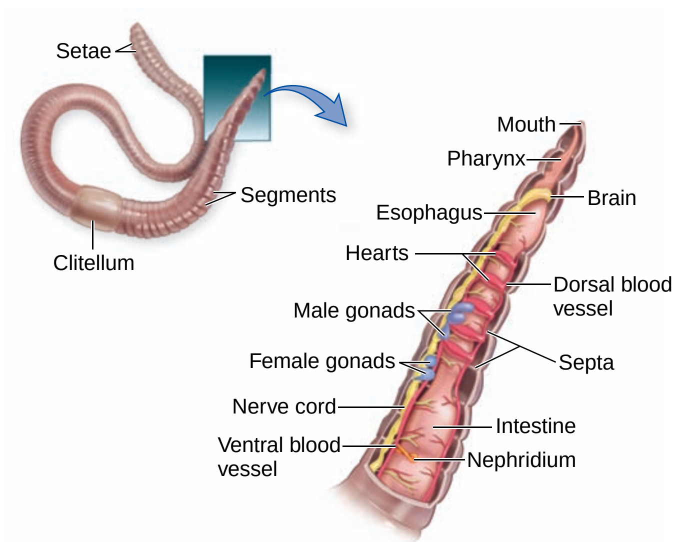


Figure 34.14 Phylum Annelida: An oligochaete. The earthworm body plan is based on repeated body segments. Segments are separated internally from each other by septa.