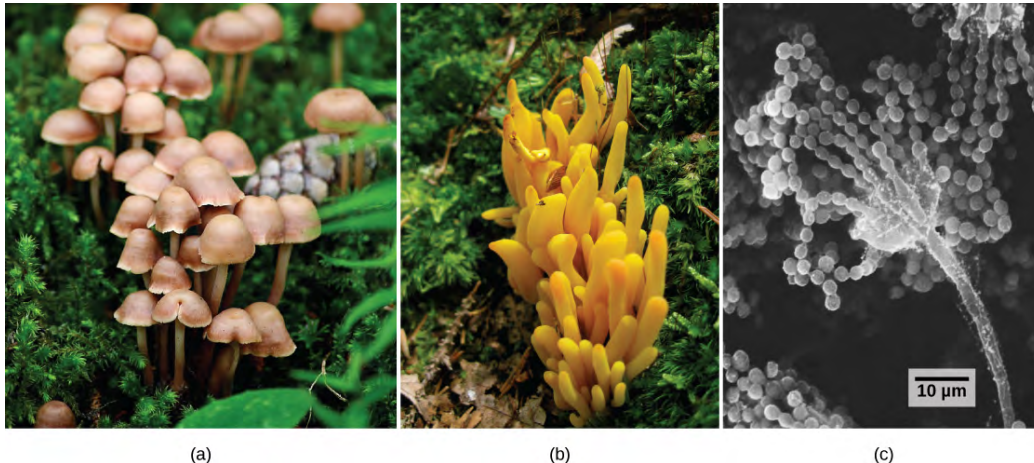


## 13.4 | Fungi

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

- List the characteristics of fungi
- Describe fungal parasites and pathogens of plants and infections in humans
- Describe the importance of fungi to the environment
- Summarize the beneficial role of fungi in food and beverage preparation and in the chemical and pharmaceutical industry



**Figure 13.20** The (a) familiar mushroom is only one type of fungus. The brightly colored fruiting bodies of this (b) coral fungus are displayed. This (c) electron micrograph shows the spore-bearing structures of *Aspergillus*, a type of toxic fungi found mostly in soil and plants. (credit a: modification of work by Chris Wee; credit b: modification of work by Cory Zanker; credit c: modification of work by Janice Haney Carr, Robert Simmons, CDC; scale-bar data from Matt Russell)

The word *fungus* comes from the Latin word for mushroom. Indeed, the familiar mushrooms are fungi, but there are many other types of fungi as well (Figure 13.20). The kingdom Fungi includes an enormous variety of living organisms collectively referred to as Eumycota, or true fungi. While scientists have identified about 100,000 species of fungi, this is only a fraction of the over 1 million species likely present on Earth. Edible mushrooms, yeasts, black mold, and *Penicillium notatum* (the producer of the antibiotic penicillin) are all members of the kingdom Fungi, which belongs to the domain Eukarya. As eukaryotes, a typical fungal cell contains a true nucleus and many membrane-bound organelles.

Fungi were once considered plant-like organisms; however, DNA comparisons have shown that fungi are more closely related to animals than plants. Fungi are not capable of photosynthesis: They use complex organic compounds as sources of energy and carbon. Some fungal organisms multiply only asexually, whereas others undergo both asexual reproduction and sexual reproduction. Most fungi produce a large number of spores that are disseminated by the wind. Like bacteria, fungi play an essential role in ecosystems, because they are decomposers and participate in the cycling of nutrients by breaking down organic materials into simple molecules.

Fungi often interact with other organisms, forming mutually beneficial or mutualistic associations. Fungi also cause serious infections in plants and animals. For example, Dutch elm disease is a particularly devastating fungal infection that destroys many native species of elm (*Ulmus* spp.). The fungus infects the vascular system of the tree. It was accidentally introduced to North America in the 1900s and decimated elm trees across the continent. Dutch elm disease is caused by the fungus *Ophiostoma ulmi*. The elm bark beetle acts as a vector and transmits the disease from tree to tree. Many European and Asiatic elms are less susceptible than American elms.

In humans, fungal infections are generally considered challenging to treat because, unlike bacteria, they do not respond to traditional antibiotic therapy since they are also eukaryotes. These infections may prove deadly for individuals with a compromised immune system.

Fungi have many commercial applications. The food industry uses yeasts in baking, brewing, and wine making. Many industrial compounds are byproducts of fungal fermentation. Fungi are the source of many commercial enzymes and antibiotics.

## Cell Structure and Function

Fungi are eukaryotes and as such have a complex cellular organization. As eukaryotes, fungal cells contain a membrane-bound nucleus. A few types of fungi have structures comparable to the plasmids (loops of DNA) seen in bacteria. Fungal cells also contain mitochondria and a complex system of internal membranes, including the endoplasmic reticulum and Golgi apparatus.

Fungal cells do not have chloroplasts. Although the photosynthetic pigment chlorophyll is absent, many fungi display bright colors, ranging from red to green to black. The poisonous *Amanita muscaria* (fly agaric) is recognizable by its bright red cap with white patches (Figure 13.21). Pigments in fungi are associated with the cell wall and play a protective role against ultraviolet radiation. Some pigments are toxic.



**Figure 13.21** The poisonous *Amanita muscaria* is native to the temperate and boreal regions of North America. (credit: Christine Majul)

Like plant cells, fungal cells are surrounded by a thick cell wall; however, the rigid layers contain the complex polysaccharides chitin and glucan and not cellulose that is used by plants. Chitin, also found in the exoskeleton of insects, gives structural strength to the cell walls of fungi. The cell wall protects the cell from desiccation and predators. Fungi have plasma membranes similar to other eukaryotes, except that the structure is stabilized by ergosterol, a steroid molecule that functions like the cholesterol found in animal cell membranes. Most members of the kingdom Fungi are nonmotile. Flagella are produced only by the gametes in the primitive division Chytridiomycota.

### Growth and Reproduction

The vegetative body of a fungus is called a **thallus** and can be unicellular or multicellular. Some fungi are dimorphic because they can go from being unicellular to multicellular depending on environmental conditions. Unicellular fungi are generally referred to as **yeasts**. *Saccharomyces cerevisiae* (baker's yeast) and *Candida* species (the agents of thrush, a common fungal infection) are examples of unicellular fungi.

Most fungi are multicellular organisms. They display two distinct morphological stages: vegetative and reproductive. The vegetative stage is characterized by a tangle of slender thread-like structures called hyphae (singular, **hypha**), whereas the reproductive stage can be more conspicuous. A mass of hyphae is called a **mycelium** (Figure 13.22). It can grow on a surface, in soil or decaying material, in a liquid, or even in or on living tissue. Although individual hypha must be observed under a microscope, the mycelium of a fungus can be very large with some species truly being “the fungus humongous.” The giant *Armillaria ostoyae* (honey mushroom) is considered the largest organism on Earth, spreading across over 2,000 acres of underground soil in eastern Oregon; it is estimated to be at least 2,400 years old.

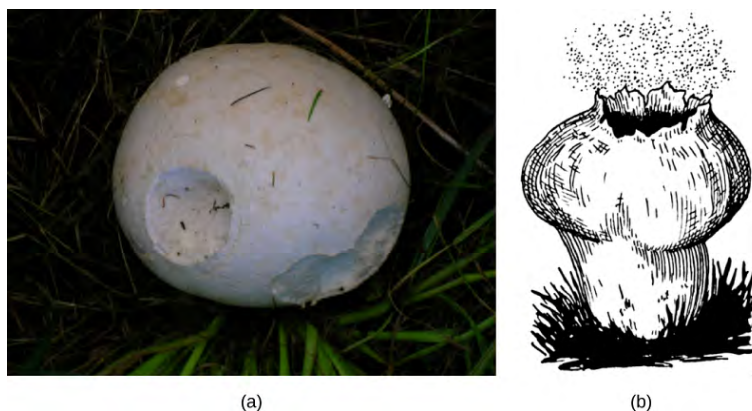


**Figure 13.22** The mycelium of the fungus *Neotestudina rosati* can be pathogenic to humans. The fungus enters through a cut or scrape and develops into a mycetoma, a chronic subcutaneous infection. (credit: CDC)

Most fungal hyphae are divided into separate cells by end walls called septa (singular, **septum**). In most divisions (like plants, fungal phyla are called *divisions* by tradition) of fungi, tiny holes in the septa allow for the rapid flow of nutrients and small molecules from cell to cell along the hyphae. They are described as perforated septa. The hyphae in bread **molds** (which belong to the division Zygomycota) are not separated by septa. They are formed of large cells containing many nuclei, an arrangement described as coenocytic hyphae.

Fungi thrive in environments that are moist and slightly acidic, and can grow with or without light. They vary in their oxygen requirements. Most fungi are obligate aerobes, requiring oxygen to survive. Other species, such as the Chytridiomycota that reside in the rumen of cattle, are obligate anaerobes, meaning that they cannot grow and reproduce in an environment with oxygen. Yeasts are intermediate: They grow best in the presence of oxygen but can use fermentation in the absence of oxygen. The alcohol produced from yeast fermentation is used in wine and beer production, and the carbon dioxide they produce carbonates beer and sparkling wine, and makes bread rise.

Fungi can reproduce sexually or asexually. In both sexual and asexual reproduction, fungi produce spores that disperse from the parent organism by either floating in the wind or hitching a ride on an animal. Fungal spores are smaller and lighter than plant seeds, but they are not usually released as high in the air. The giant puffball mushroom bursts open and releases trillions of spores: The huge number of spores released increases the likelihood of spores landing in an environment that will support growth (**Figure 13.23**).



**Figure 13.23** The (a) giant puffball mushroom releases (b) a cloud of spores when it reaches maturity. (credit a: modification of work by Roger Griffith; credit b: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation)

### How Fungi Obtain Nutrition

Like animals, fungi are heterotrophs: They use complex organic compounds as a source of carbon rather than fixing carbon dioxide from the atmosphere, as some bacteria and most plants do. In addition, fungi do not fix nitrogen from the atmosphere. Like animals, they must obtain it from their diet. However, unlike most animals that ingest food and then digest it internally in specialized organs, fungi perform these steps in the reverse order. Digestion precedes ingestion. First, exoenzymes, enzymes that catalyze reactions on compounds outside of the cell, are transported out of the hyphae where

they break down nutrients in the environment. Then, the smaller molecules produced by the external digestion are absorbed through the large surface areas of the mycelium. As with animal cells, the fungal storage polysaccharide is glycogen rather than starch, as found in plants.

Fungi are mostly saprobes, organisms that derive nutrients from decaying organic matter. They obtain their nutrients from dead or decomposing organic matter, mainly plant material. Fungal exoenzymes are able to break down insoluble polysaccharides, such as the cellulose and lignin of dead wood, into readily absorbable glucose molecules. Decomposers are important components of ecosystems, because they return nutrients locked in dead bodies to a form that is usable for other organisms. This role is discussed in more detail later. Because of their varied metabolic pathways, fungi fulfill an important ecological role and are being investigated as potential tools in bioremediation. For example, some species of fungi can be used to break down diesel oil and polycyclic aromatic hydrocarbons. Other species take up heavy metals such as cadmium and lead.

## Fungal Diversity

The kingdom Fungi contains four major divisions that were established according to their mode of sexual reproduction. Polyphyletic, unrelated fungi that reproduce without a sexual cycle, are placed for convenience in a fifth division, and a sixth major fungal group that does not fit well with any of the previous five has recently been described. Not all mycologists agree with this scheme. Rapid advances in molecular biology and the sequencing of 18S rRNA (a component of ribosomes) continue to reveal new and different relationships between the various categories of fungi.

The traditional divisions of Fungi are the **Chytridiomycota** (chytrids), the **Zygomycota** (conjugated fungi), the **Ascomycota** (sac fungi), and the **Basidiomycota** (club fungi). An older classification scheme grouped fungi that strictly use asexual reproduction into Deuteromycota, a group that is no longer in use. The **Glomeromycota** belong to a newly described group (**Figure 13.24**).



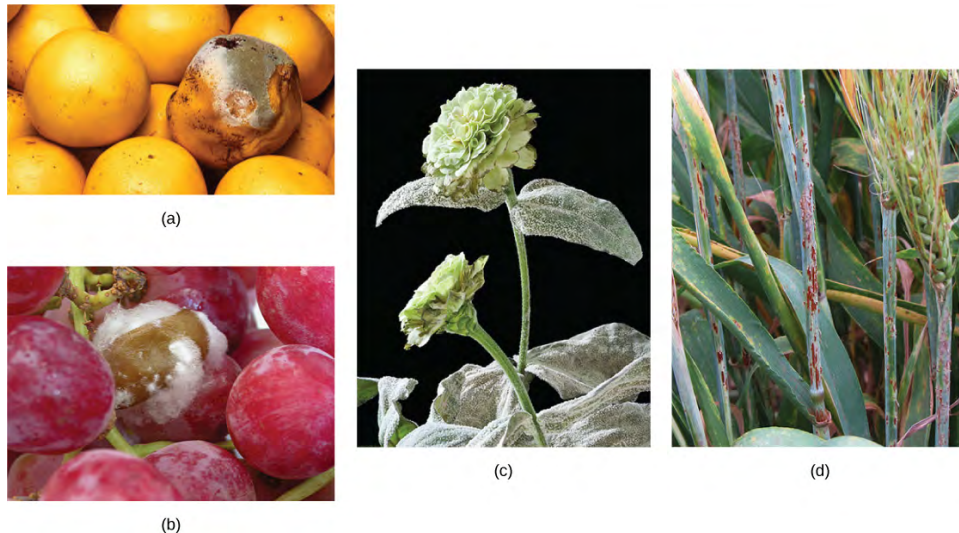
**Figure 13.24** Divisions of fungi include (a) chytrids, (b) conjugated fungi, (c) sac fungi, and (d) club fungi. (credit a: modification of work by USDA APHIS PPQ; credit c: modification of work by "icelight"/Flickr; credit d: modification of work by Cory Zanker.)

## Pathogenic Fungi

Many fungi have negative impacts on other species, including humans and the organisms they depend on for food. Fungi may be parasites, pathogens, and, in a very few cases, predators.

## Plant Parasites and Pathogens

The production of enough good-quality crops is essential to our existence. Plant diseases have ruined crops, bringing widespread famine. Most plant pathogens are fungi that cause tissue decay and eventual death of the host (**Figure 13.25**). In addition to destroying plant tissue directly, some plant pathogens spoil crops by producing potent toxins. Fungi are also responsible for food spoilage and the rotting of stored crops. For example, the fungus *Claviceps purpurea* causes ergot, a disease of cereal crops (especially of rye). Although the fungus reduces the yield of cereals, the effects of the ergot's alkaloid toxins on humans and animals are of much greater significance: In animals, the disease is referred to as ergotism. The most common signs and symptoms are convulsions, hallucination, gangrene, and loss of milk in cattle. The active ingredient of ergot is lysergic acid, which is a precursor of the drug LSD. Smuts, rusts, and powdery or downy mildew are other examples of common fungal pathogens that affect crops.



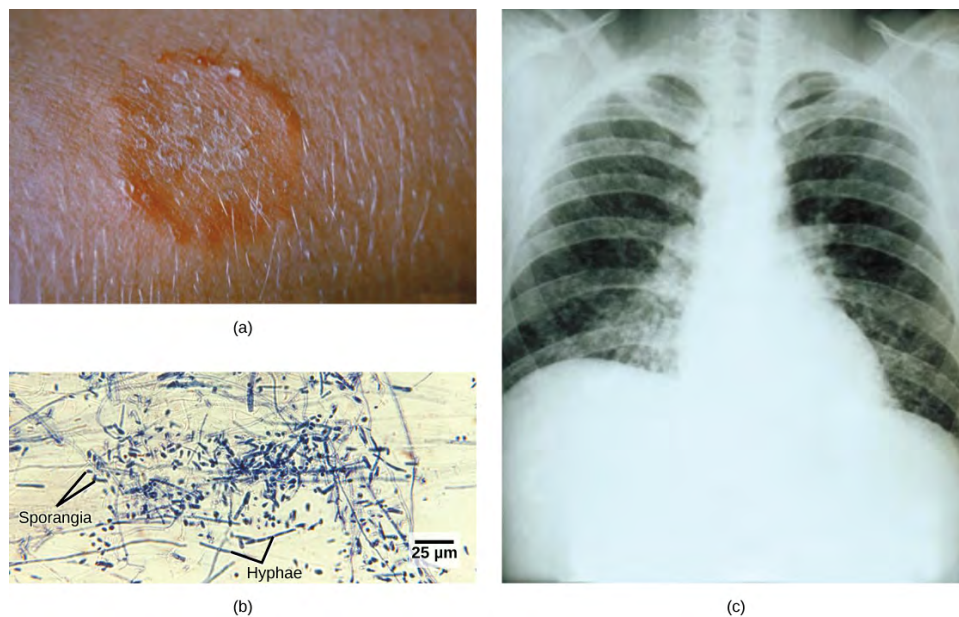
**Figure 13.25** Some fungal pathogens include (a) green mold on grapefruit, (b) fungus on grapes, (c) powdery mildew on a zinnia, and (d) stem rust on a sheaf of barley. Notice the brownish color of the fungus in (b) *Botrytis cinerea*, also referred to as the “noble rot,” which grows on grapes and other fruit. Controlled infection of grapes by *Botrytis* is used to produce strong and much-prized dessert wines. (credit a: modification of work by Scott Bauer, USDA ARS; credit b: modification of work by Stephen Ausmus, USDA ARS; credit c: modification of work by David Marshall, USDA ARS; credit d: modification of work by Joseph Smilanick, USDA ARS)

Aflatoxins are toxic and carcinogenic compounds released by fungi of the genus *Aspergillus*. Periodically, harvests of nuts and grains are tainted by aflatoxins, leading to massive recall of produce, sometimes ruining producers, and causing food shortages in developing countries.

## Animal and Human Parasites and Pathogens

Fungi can affect animals, including humans, in several ways. Fungi attack animals directly by colonizing and destroying tissues. Humans and other animals can be poisoned by eating toxic mushrooms or foods contaminated by fungi. In addition, individuals who display hypersensitivity to molds and spores develop strong and dangerous allergic reactions. Fungal infections are generally very difficult to treat because, unlike bacteria, fungi are eukaryotes. Antibiotics only target prokaryotic cells, whereas compounds that kill fungi also adversely affect the eukaryotic animal host.

Many fungal infections ( **mycoses** ) are superficial and termed cutaneous (meaning “skin”) mycoses. They are usually visible on the skin of the animal. Fungi that cause the superficial mycoses of the epidermis, hair, and nails rarely spread to the underlying tissue (**Figure 13.26**). These fungi are often misnamed “dermatophytes” from the Greek *dermis* skin and *phyte* plant, but they are not plants. Dermatophytes are also called “ringworms” because of the red ring that they cause on skin (although the ring is caused by fungi, not a worm). These fungi secrete extracellular enzymes that break down keratin (a protein found in hair, skin, and nails), causing a number of conditions such as athlete’s foot, jock itch, and other cutaneous fungal infections. These conditions are usually treated with over-the-counter topical creams and powders, and are easily cleared. More persistent, superficial mycoses may require prescription oral medications.



**Figure 13.26** (a) Ringworm presents as a red ring on the skin. (b) *Trichophyton violaceum* is a fungus that causes superficial mycoses on the scalp. (c) *Histoplasma capsulatum*, seen in this X-ray as speckling of light areas in the lung, is a species of Ascomycota that infects airways and causes symptoms similar to the flu. (credit a, b: modification of work by Dr. Lucille K. Georg, CDC; credit c: modification of work by M Renz, CDC; scale-bar data from Matt Russell)

Systemic mycoses spread to internal organs, most commonly entering the body through the respiratory system. For example, coccidioidomycosis (valley fever) is commonly found in the southwestern United States, where the fungus resides in the dust. Once inhaled, the spores develop in the lungs and cause signs and symptoms similar to those of tuberculosis. Histoplasmosis (**Figure 13.26c**) is caused by the dimorphic fungus *Histoplasma capsulatum*; it causes pulmonary infections and, in rare cases, swelling of the membranes of the brain and spinal cord. Treatment of many fungal diseases requires the use of antifungal medications that have serious side effects.

Opportunistic mycoses are fungal infections that are either common in all environments or part of the normal biota. They affect mainly individuals who have a compromised immune system. Patients in the late stages of AIDS suffer from opportunistic mycoses, such as *Pneumocystis*, which can be life threatening. The yeast *Candida* spp., which is a common member of the natural biota, can grow unchecked if the pH, the immune defenses, or the normal population of bacteria is altered, causing yeast infections of the vagina or mouth (oral thrush).

Fungi may even take on a predatory lifestyle. In soil environments that are poor in nitrogen, some fungi resort to predation of nematodes (small roundworms). Species of *Arthrobotrys* fungi have a number of mechanisms to trap nematodes. For example, they have constricting rings within their network of hyphae. The rings swell when the nematode touches it and closes around the body of the nematode, thus trapping it. The fungus extends specialized hyphae that can penetrate the body of the worm and slowly digest the hapless prey.

## Beneficial Fungi

Fungi play a crucial role in the balance of ecosystems. They colonize most habitats on Earth, preferring dark, moist conditions. They can thrive in seemingly hostile environments, such as the tundra, thanks to a most successful symbiosis with photosynthetic organisms, like lichens. Fungi are not obvious in the way that large animals or tall trees are. Yet, like bacteria, they are major decomposers of nature. With their versatile metabolism, fungi break down organic matter that is insoluble and would not be recycled otherwise.

### Importance to Ecosystems

Food webs would be incomplete without organisms that decompose organic matter and fungi are key participants in this process. Decomposition allows for cycling of nutrients such as carbon, nitrogen, and phosphorus back into the environment so they are available to living things, rather than being trapped in dead organisms. Fungi are particularly important because they have evolved enzymes to break down cellulose and lignin, components of plant cell walls that few other organisms are able to digest, releasing their carbon content.

Fungi are also involved in ecologically important coevolved symbioses, both mutually beneficial and pathogenic with organisms from the other kingdoms. **Mycorrhiza**, a term combining the Greek roots *myco* meaning fungus and *rhizo*

meaning root, refers to the association between vascular plant roots and their symbiotic fungi. Somewhere between 80–90 percent of all plant species have mycorrhizal partners. In a mycorrhizal association, the fungal mycelia use their extensive network of hyphae and large surface area in contact with the soil to channel water and minerals from the soil into the plant. In exchange, the plant supplies the products of photosynthesis to fuel the metabolism of the fungus. Ectomycorrhizae (“outside” mycorrhiza) depend on fungi enveloping the roots in a sheath (called a mantle) and a net of hyphae that extends into the roots between cells. In a second type, the Glomeromycota fungi form arbuscular mycorrhiza. In these mycorrhiza, the fungi form arbuscles, a specialized highly branched hypha, which penetrate root cells and are the sites of the metabolic exchanges between the fungus and the host plant. Orchids rely on a third type of mycorrhiza. Orchids form small seeds without much storage to sustain germination and growth. Their seeds will not germinate without a mycorrhizal partner (usually Basidiomycota). After nutrients in the seed are depleted, fungal symbionts support the growth of the orchid by providing necessary carbohydrates and minerals. Some orchids continue to be mycorrhizal throughout their lifecycle.

**Lichens** blanket many rocks and tree bark, displaying a range of colors and textures. Lichens are important pioneer organisms that colonize rock surfaces in otherwise lifeless environments such as are created by glacial recession. The lichen is able to leach nutrients from the rocks and break them down in the first step to creating soil. Lichens are also present in mature habitats on rock surfaces or the trunks of trees. They are an important food source for caribou. Lichens are not a single organism, but rather a fungus (usually an Ascomycota or Basidiomycota species) living in close contact with a photosynthetic organism (an alga or cyanobacterium). The body of a lichen, referred to as a thallus, is formed of hyphae wrapped around the green partner. The photosynthetic organism provides carbon and energy in the form of carbohydrates and receives protection from the elements by the thallus of the fungal partner. Some cyanobacteria fix nitrogen from the atmosphere, contributing nitrogenous compounds to the association. In return, the fungus supplies minerals and protection from dryness and excessive light by encasing the algae in its mycelium. The fungus also attaches the symbiotic organism to the substrate.

Fungi have evolved mutualistic associations with numerous arthropods. The association between species of Basidiomycota and scale insects is one example. The fungal mycelium covers and protects the insect colonies. The scale insects foster a flow of nutrients from the parasitized plant to the fungus. In a second example, leaf-cutting ants of Central and South America literally farm fungi. They cut disks of leaves from plants and pile them up in gardens. Fungi are cultivated in these gardens, digesting the cellulose that the ants cannot break down. Once smaller sugar molecules are produced and consumed by the fungi, they in turn become a meal for the ants. The insects also patrol their garden, preying on competing fungi. Both ants and fungi benefit from the association. The fungus receives a steady supply of leaves and freedom from competition, while the ants feed on the fungi they cultivate.

### Importance to Humans

Although we often think of fungi as organisms that cause diseases and rot food, fungi are important to human life on many levels. As we have seen, they influence the well-being of human populations on a large scale because they help nutrients cycle in ecosystems. They have other ecosystem roles as well. For example, as animal pathogens, fungi help to control the population of damaging pests. These fungi are very specific to the insects they attack and do not infect other animals or plants. The potential to use fungi as microbial insecticides is being investigated, with several species already on the market. For example, the fungus *Beauveria bassiana* is a pesticide that is currently being tested as a possible biological control for the recent spread of emerald ash borer. It has been released in Michigan, Illinois, Indiana, Ohio, West Virginia, and Maryland.

The mycorrhizal relationship between fungi and plant roots is essential for the productivity of farmland. Without the fungal partner in the root systems, 80–90% of trees and grasses would not survive. Mycorrhizal fungal inoculants are available as soil amendments from gardening supply stores and promoted by supporters of organic agriculture.

We also eat some types of fungi. Mushrooms figure prominently in the human diet. Morels, shiitake mushrooms, chanterelles, and truffles are considered delicacies (Figure 13.27). The humble meadow mushroom, *Agaricus campestris*, appears in many dishes. Molds of the genus *Penicillium* ripen many cheeses. They originate in the natural environment such as the caves of Roquefort, France, where wheels of sheep milk cheese are stacked to capture the molds responsible for the blue veins and pungent taste of the cheese.



**Figure 13.27** The morel mushroom is an ascomycete that is much appreciated for its delicate taste. (credit: Jason Hollinger)

Fermentation—of grains to produce beer, and of fruits to produce wine—is an ancient art that humans in most cultures have practiced for millennia. Wild yeasts are acquired from the environment and used to ferment sugars into CO<sub>2</sub> and ethyl alcohol under anaerobic conditions. It is now possible to purchase isolated strains of wild yeasts from different wine-making regions. Pasteur was instrumental in developing a reliable strain of brewer’s yeast, *Saccharomyces cerevisiae*, for the French brewing industry in the late 1850s. It was one of the first examples of biotechnology patenting. Yeast is also used to make breads that rise. The carbon dioxide they produce is responsible for the bubbles produced in the dough that become the air pockets of the baked bread.

Many secondary metabolites of fungi are of great commercial importance. Antibiotics are naturally produced by fungi to kill or inhibit the growth of bacteria, and limit competition in the natural environment. Valuable drugs isolated from fungi include the immunosuppressant drug cyclosporine (which reduces the risk of rejection after organ transplant), the precursors of steroid hormones, and ergot alkaloids used to stop bleeding. In addition, as easily cultured eukaryotic organisms, some fungi are important model research organisms including the red bread mold *Neurospora crassa* and the yeast, *S. cerevisiae*.



## KEY TERMS

**Amoebozoa** the eukaryotic supergroup that contains the amoebas and slime molds

**anaerobic** refers to organisms that grow without oxygen

**anoxic** without oxygen

**Archaeplastida** the eukaryotic supergroup that contains land plants, green algae, and red algae

**Ascomycota** (sac fungi) a division of fungi that store spores in a sac called ascus

**basidiomycota** (club fungi) a division of fungi that produce club shaped structures, basidia, which contain spores

**biofilm** a microbial community that is held together by a gummy-textured matrix

**bioremediation** the use of microbial metabolism to remove pollutants

**Black Death** a devastating pandemic that is believed to have been an outbreak of bubonic plague caused by the bacterium *Yersinia pestis*

**botulism** a disease produce by the toxin of the anaerobic bacterium *Clostridium botulinum*

**capsule** an external structure that enables a prokaryote to attach to surfaces and protects it from dehydration

**Chromalveolata** the eukaryotic supergroup that contains the dinoflagellates, ciliates, the brown algae, diatoms, and water molds

**Chytridiomycota** (chytrids) a primitive division of fungi that live in water and produce gametes with flagella

**commensalism** a symbiotic relationship in which one member benefits while the other member is not affected

**conjugation** the process by which prokaryotes move DNA from one individual to another using a pilus

**cyanobacteria** bacteria that evolved from early phototrophs and oxygenated the atmosphere; also known as blue-green algae

**Deuteromycota** a division of fungi that do not have a known sexual reproductive cycle (presently members of two phyla: Ascomycota and Basidiomycota)

**endosymbiosis** the engulfment of one cell by another such that the engulfed cell survives and both cells benefit; the process responsible for the evolution of mitochondria and chloroplasts in eukaryotes

**epidemic** a disease that occurs in an unusually high number of individuals in a population at the same time

**Excavata** the eukaryotic supergroup that contains flagellated single-celled organisms with a feeding groove

**extremophile** an organism that grows under extreme or harsh conditions

**foodborne disease** any illness resulting from the consumption of contaminated food, or of the pathogenic bacteria, viruses, or other parasites that contaminate food

**Glomeromycota** a group of fungi that form symbiotic relationships with the roots of trees

**Gram-negative** describes a bacterium whose cell wall contains little peptidoglycan but has an outer membrane

**Gram-positive** describes a bacterium that contains mainly peptidoglycan in its cell walls

**hydrothermal vent** a fissure in Earth's surface that releases geothermally heated water

**hypha** a fungal filament composed of one or more cells

**lichen** the close association of a fungus with a photosynthetic alga or bacterium that benefits both partners

**microbial mat** a multi-layered sheet of prokaryotes that may include bacteria and archaea

**mold** a tangle of visible mycelia with a fuzzy appearance

**MRSA** (methicillin-resistant *Staphylococcus aureus*) a very dangerous *Staphylococcus aureus* strain resistant to antibiotics

**mycelium** a mass of fungal hyphae

**mycorrhiza** a mutualistic association between fungi and vascular plant roots

**mycosis** a fungal infection

**Opisthokonta** the eukaryotic supergroup that contains the fungi, animals, and choanoflagellates

**pandemic** a widespread, usually worldwide, epidemic disease

**parasite** an organism that lives on or in another organism and feeds on it, often without killing it

**pathogen** an organism, or infectious agent, that causes a disease

**pellicle** an outer cell covering composed of interlocking protein strips that function like a flexible coat of armor, preventing cells from being torn or pierced without compromising their range of motion

**peptidoglycan** a material composed of polysaccharide chains cross-linked to unusual peptides

**phototroph** an organism that uses energy from sunlight

**plastid** one of a group of related organelles in plant cells that are involved in the storage of starches, fats, proteins, and pigments

**pseudopeptidoglycan** a component of some cell walls of Archaea

**Rhizaria** the eukaryotic supergroup that contains organisms that move by amoeboid movement

**saprobe** an organism that feeds on dead organic material

**septum** the cell wall division between hyphae

**stromatolite** a layered sedimentary structure formed by precipitation of minerals by prokaryotes in microbial mats

**thallus** a vegetative body of a fungus

**transduction** the process by which a bacteriophage moves DNA from one prokaryote to another

**transformation** a mechanism of genetic change in prokaryotes in which DNA present in the environment is taken into the cell and incorporated into the genome

**yeast** a general term used to describe unicellular fungi

**Zygomycota** (conjugated fungi) the division of fungi that form a zygote contained in a zygospore

## CHAPTER SUMMARY

### 13.1 Prokaryotic Diversity

Prokaryotes existed for billions of years before plants and animals appeared. Microbial mats are thought to represent the earliest forms of life on Earth, and there is fossil evidence, called stromatolites, of their presence about 3.5 billion years ago. During the first 2 billion years, the atmosphere was anoxic and only anaerobic organisms were able to live. Cyanobacteria began the oxygenation of the atmosphere. The increase in oxygen concentration allowed the evolution of other life forms.

Prokaryotes (domains Archaea and Bacteria) are single-celled organisms lacking a nucleus. They have a single piece of circular DNA in the nucleoid area of the cell. Most prokaryotes have cell wall outside the plasma membrane. Bacteria and Archaea differ in the compositions of their cell membranes and the characteristics of their cell walls.

Bacterial cell walls contain peptidoglycan. Archaeal cell walls do not have peptidoglycan. Bacteria can be divided into two major groups: Gram-positive and Gram-negative. Gram-positive organisms have a thick cell wall. Gram-negative organisms have a thin cell wall and an outer membrane. Prokaryotes use diverse sources of energy to assemble macromolecules from smaller molecules. Phototrophs obtain their energy from sunlight, whereas chemotrophs obtain it from chemical compounds.

Infectious diseases caused by bacteria remain among the leading causes of death worldwide. The excessive use of antibiotics to control bacterial infections has resulted in resistant forms of bacteria being selected. Foodborne diseases result from the consumption of contaminated food, pathogenic bacteria, viruses, or parasites that contaminate food. Prokaryotes are used in human food products. Microbial bioremediation is the use of microbial metabolism to remove pollutants. The human body contains a huge community of prokaryotes, many of which provide beneficial services such as the development and maintenance of the immune system, nutrition, and protection from pathogens.

### 13.2 Eukaryotic Origins

The first eukaryotes evolved from ancestral prokaryotes by a process that involved membrane proliferation, the loss of a cell wall, the evolution of a cytoskeleton, and the acquisition and evolution of organelles. Nuclear eukaryotic genes appear to have had an origin in the Archaea, whereas the energy machinery of eukaryotic cells appears to be bacterial in origin. The mitochondria and plastids originated from endosymbiotic events when ancestral cells engulfed an aerobic bacterium (in the case of mitochondria) and a photosynthetic bacterium (in the case of chloroplasts). The evolution of mitochondria likely preceded the evolution of chloroplasts. There is evidence of secondary endosymbiotic events in which plastids appear to be the result of endosymbiosis after a previous endosymbiotic event.

### 13.3 Protists

Protists are extremely diverse in terms of biological and ecological characteristics due in large part to the fact that they are an artificial assemblage of phylogenetically unrelated groups. Protists display highly varied cell structures, several types of reproductive strategies, virtually every possible type of nutrition, and varied habitats. Most single-celled protists are motile, but these organisms use diverse structures for transportation.

The process of classifying protists into meaningful groups is ongoing, but genetic data in the past 20 years have clarified many relationships that were previously unclear or mistaken. The majority view at present is to order all eukaryotes into six supergroups. The goal of this classification scheme is to create clusters of species that all are derived from a common ancestor.

### 13.4 Fungi

Fungi are eukaryotic organisms that appeared on land over 450 million years ago. They are heterotrophs and contain neither photosynthetic pigments such as chlorophylls nor organelles such as chloroplasts. Because they feed on decaying and dead matter, they are saprobes. Fungi are important decomposers and release essential elements into the environment. External enzymes digest nutrients that are absorbed by the body of the fungus called a thallus. A thick cell wall made of chitin surrounds the cell. Fungi can be unicellular as yeasts or develop a network of filaments called a mycelium, often described as mold. Most species multiply by asexual and sexual reproductive cycles, and display an alternation of generations.

The divisions of fungi are the Chytridiomycota, Zygomycota, Ascomycota, Basidiomycota, Glomeromycota, and the Deuteromycota, a polyphyletic group.

Fungi establish parasitic relationships with plants and animals. Fungal diseases can decimate crops and spoil food during storage. Compounds produced by fungi can be toxic to humans and other animals. Mycoses are infections caused by fungi. Superficial mycoses affect the skin, whereas systemic mycoses spread through the body. Fungal infections are difficult to cure.

Fungi have colonized all environments on Earth but are most often found in cool, dark, moist places with a supply of decaying material. Fungi are important decomposers because they are saprobes. Many successful mutualistic relationships involve a fungus and another organism. They establish complex mycorrhizal associations with the roots of plants. Lichens are a symbiotic relationship between a fungus and a photosynthetic organism, usually an alga or cyanobacterium.

Fungi are important to everyday human life. Fungi are important decomposers in most ecosystems. Mycorrhizal fungi are essential for the growth of most plants. Fungi, as food, play a role in human nutrition in the form of mushrooms and as

agents of fermentation in the production of bread, cheeses, alcoholic beverages, and numerous other food preparations. Secondary metabolites of fungi are used in medicine as antibiotics and anticoagulants. Fungi are used in research as model organisms for the study of eukaryotic genetics and metabolism.

## ART CONNECTION QUESTIONS

- 1. Figure 13.6** Which of the following statements is true?
- Gram-positive bacteria have a single cell wall formed from peptidoglycan.
  - Gram-positive bacteria have an outer membrane.
  - The cell wall of Gram-negative bacteria is thick, and the cell wall of Gram-positive bacteria is thin.
  - Gram-negative bacteria have a cell wall made of peptidoglycan, while Gram-positive bacteria have a cell wall made of phospholipids.

## REVIEW QUESTIONS

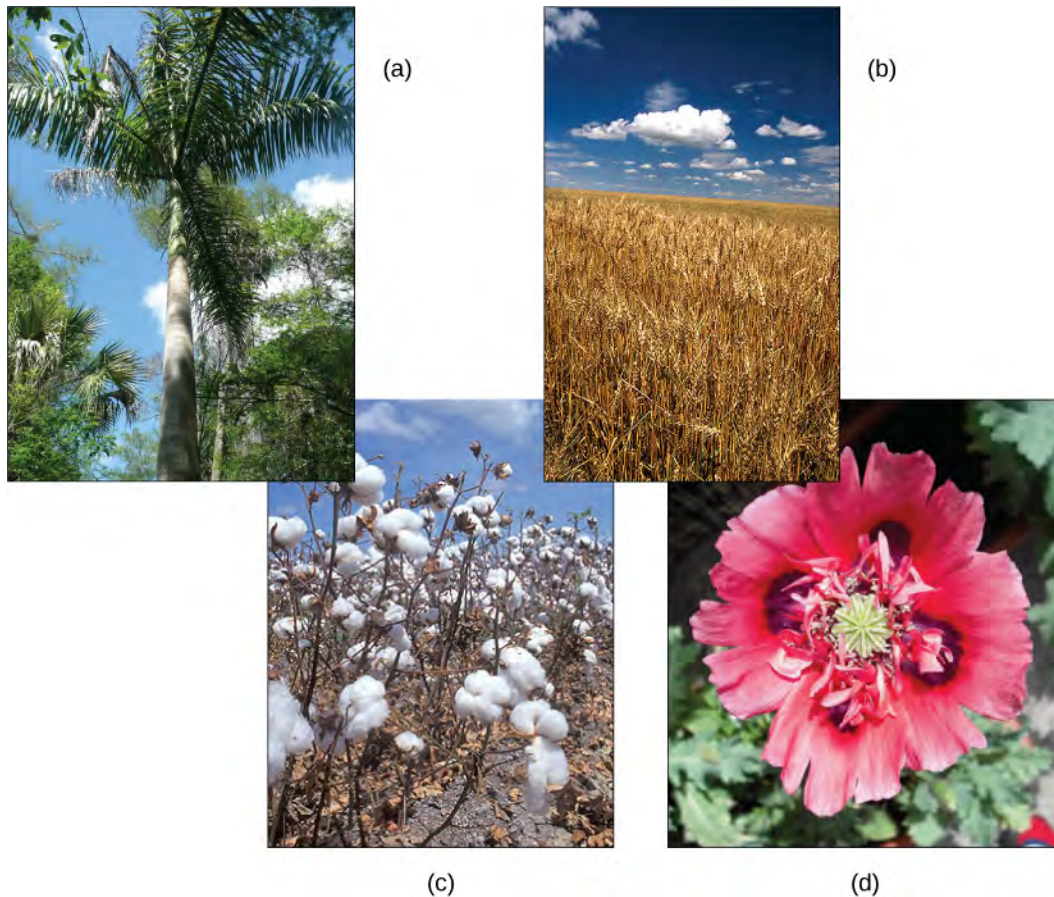
- 2.** The first forms of life on Earth were thought to be \_\_\_\_\_.
- single-celled plants
  - prokaryotes
  - insects
  - large animals such as dinosaurs
- 3.** The first organisms that oxygenated the atmosphere were \_\_\_\_\_.
- cyanobacteria
  - phototrophic organisms
  - anaerobic organisms
  - all of the above
- 4.** Which of the following consist of prokaryotic cells?
- bacteria and fungi
  - archaea and fungi
  - protists and animals
  - bacteria and archaea
- 5.** Prokaryotes stain as Gram-positive or Gram-negative because of differences in the \_\_\_\_\_.
- cell wall
  - cytoplasm
  - nucleus
  - chromosome
- 6.** Prokaryotes that obtain their energy from chemical compounds are called \_\_\_\_\_.
- phototrophs
  - auxotrophs
  - chemotrophs
  - lithotrophs
- 7.** Bioremediation includes \_\_\_\_\_.
- the use of prokaryotes that can fix nitrogen
  - the use of prokaryotes to clean up pollutants
  - the use of prokaryotes as natural fertilizers
  - All of the above
- 8.** What event is thought to have contributed to the evolution of eukaryotes?
- global warming
  - glaciation
  - volcanic activity
  - oxygenation of the atmosphere
- 9.** Mitochondria most likely evolved from \_\_\_\_\_.
- a photosynthetic cyanobacterium
  - cytoskeletal elements
  - aerobic bacteria
  - membrane proliferation
- 10.** Protists with the capabilities to absorb nutrients from dead organisms are called \_\_\_\_\_.
- photoautotrophs
  - autotrophs
  - saprobies
  - heterotrophs
- 11.** Which parasitic protist evades the host immune system by altering its surface proteins with each generation?
- Paramecium caudatum*
  - Trypanosoma brucei*
  - Plasmodium falciparum*
  - Phytophthora infestans*
- 12.** Which polysaccharide is usually found in the cell walls of fungi?
- starch
  - glycogen
  - chitin
  - cellulose
- 13.** What term describes the close association of a fungus with the root of a tree?
- a rhizoid
  - a lichen
  - a mycorrhiza
  - an endophyte

## CRITICAL THINKING QUESTIONS

- 14.** Explain the reason why the imprudent and excessive use of antibiotics has resulted in a major global problem.
- 15.** Your friend believes that prokaryotes are always detrimental and pathogenic. How would you explain to them that they are wrong?
- 16.** Describe the hypothesized steps in the origin of eukaryote cells.
- 17.** How does killing *Anopheles* mosquitoes affect the *Plasmodium* protists?
- 18.** Without treatment, why does African sleeping sickness invariably lead to death?
- 19.** Why can superficial mycoses in humans lead to bacterial infections?



# 14 | DIVERSITY OF PLANTS



**Figure 14.1** Plants dominate the landscape and play an integral role in human societies. (a) Palm trees grow in tropical or subtropical climates; (b) wheat is a crop in most of the world; the flower of (c) the cotton plant produces fibers that are woven into fabric; the potent alkaloids of (d) the beautiful opium poppy have influenced human life both as a medicinal remedy and as a dangerously addictive drug. (credit a: modification of work by “3BoysInSanDiego”/Wikimedia Commons”; credit b: modification of work by Stephen Ausmus, USDA ARS; credit c: modification of work by David Nance, USDA ARS; credit d: modification of work by Jolly Janner)

## Chapter Outline

- 14.1: The Plant Kingdom**
- 14.2: Seedless Plants**
- 14.3: Seed Plants: Gymnosperms**
- 14.4: Seed Plants: Angiosperms**

## Introduction

Plants play an integral role in all aspects of life on the planet, shaping the physical terrain, influencing the climate, and maintaining life as we know it. For millennia, human societies have depended on plants for nutrition and medicinal compounds, and for many industrial by-products, such as timber, paper, dyes, and textiles. Palms provide materials

including rattans, oils, and dates. Wheat is grown to feed both human and animal populations. The cotton boll flower is harvested and its fibers transformed into clothing or pulp for paper. The showy opium poppy is valued both as an ornamental flower and as a source of potent opiate compounds.

Current evolutionary thought holds that all plants are monophyletic: that is, descendants of a single common ancestor. The evolutionary transition from water to land imposed severe constraints on the ancestors of contemporary plants. Plants had to evolve strategies to avoid drying out, to disperse reproductive cells in air, for structural support, and to filter sunlight. While seed plants developed adaptations that allowed them to populate even the most arid habitats on Earth, full independence from water did not happen in all plants, and most seedless plants still require a moist environment.

## 14.1 | The Plant Kingdom

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

- Describe the major characteristics of the plant kingdom
- Discuss the challenges to plant life on land
- Describe the adaptations that allowed plants to colonize land

Plants are a large and varied group of organisms. There are close to 300,000 species of catalogued plants.<sup>[1]</sup> Of these, about 260,000 are plants that produce seeds. Mosses, ferns, conifers, and flowering plants are all members of the plant kingdom. The plant kingdom contains mostly photosynthetic organisms; a few parasitic forms have lost the ability to photosynthesize. The process of photosynthesis uses chlorophyll, which is located in organelles called chloroplasts. Plants possess cell walls containing cellulose. Most plants reproduce sexually, but they also have diverse methods of asexual reproduction. Plants exhibit indeterminate growth, meaning they do not have a final body form, but continue to grow body mass until they die.

### Plant Adaptations to Life on Land

As organisms adapt to life on land, they have to contend with several challenges in the terrestrial environment. Water has been described as “the stuff of life.” The cell’s interior—the medium in which most small molecules dissolve and diffuse, and in which the majority of the chemical reactions of metabolism take place—is a watery soup. Desiccation, or drying out, is a constant danger for an organism exposed to air. Even when parts of a plant are close to a source of water, their aerial structures are likely to dry out. Water provides buoyancy to organisms that live in aquatic habitats. On land, plants need to develop structural support in air—a medium that does not give the same lift. Additionally, the male gametes must reach the female gametes using new strategies because swimming is no longer possible. Finally, both gametes and zygotes must be protected from drying out. The successful land plants evolved strategies to deal with all of these challenges, although not all adaptations appeared at once. Some species did not move far from an aquatic environment, whereas others left the water and went on to conquer the driest environments on Earth.

To balance these survival challenges, life on land offers several advantages. First, sunlight is abundant. On land, the spectral quality of light absorbed by the photosynthetic pigment, chlorophyll, is not filtered out by water or competing photosynthetic species in the water column above. Second, carbon dioxide is more readily available because its concentration is higher in air than in water. Additionally, land plants evolved before land animals; therefore, until dry land was colonized by animals, no predators threatened the well-being of plants. This situation changed as animals emerged from the water and found abundant sources of nutrients in the established flora. In turn, plants evolved strategies to deter predation: from spines and thorns to toxic chemicals.

The early land plants, like the early land animals, did not live far from an abundant source of water and developed survival strategies to combat dryness. One of these strategies is drought tolerance. Mosses, for example, can dry out to a brown and brittle mat, but as soon as rain makes water available, mosses will soak it up and regain their healthy, green appearance. Another strategy is to colonize environments with high humidity where droughts are uncommon. Ferns, an early lineage of plants, thrive in damp and cool places, such as the understory of temperate forests. Later, plants moved away from aquatic environments using resistance to desiccation, rather than tolerance. These plants, like the cactus, minimize water loss to such an extent they can survive in the driest environments on Earth.

In addition to adaptations specific to life on land, land plants exhibit adaptations that were responsible for their diversity and predominance in terrestrial ecosystems. Four major adaptations are found in many terrestrial plants: the alternation of

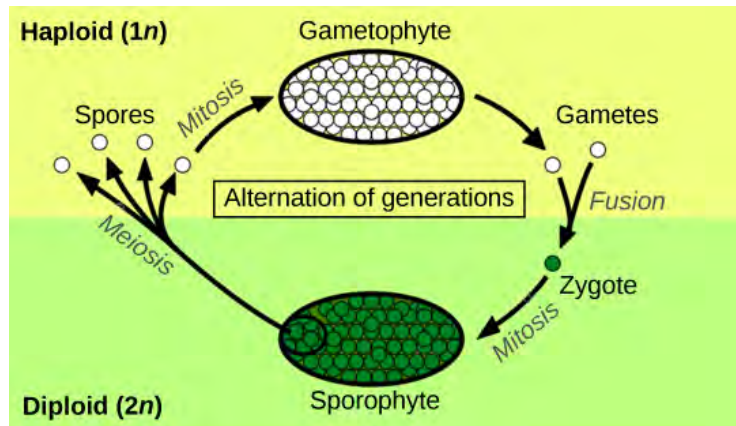
1. A.D. Chapman (2009) *Numbers of Living Species in Australia and the World*. 2nd edition. A Report for the Australian Biological Resources Study. Australian Biodiversity Information Services, Toowoomba, Australia. Available online at <http://www.environment.gov.au/biodiversity/abrs/publications/other/species-numbers/2009/04-03-groups-plants.html>.



generations, a sporangium in which spores are formed, a gametangium that produces haploid cells, and in vascular plants, apical meristem tissue in roots and shoots.

### Alternation of Generations

Alternation of generations describes a life cycle in which an organism has both haploid and diploid multicellular stages (Figure 14.2).



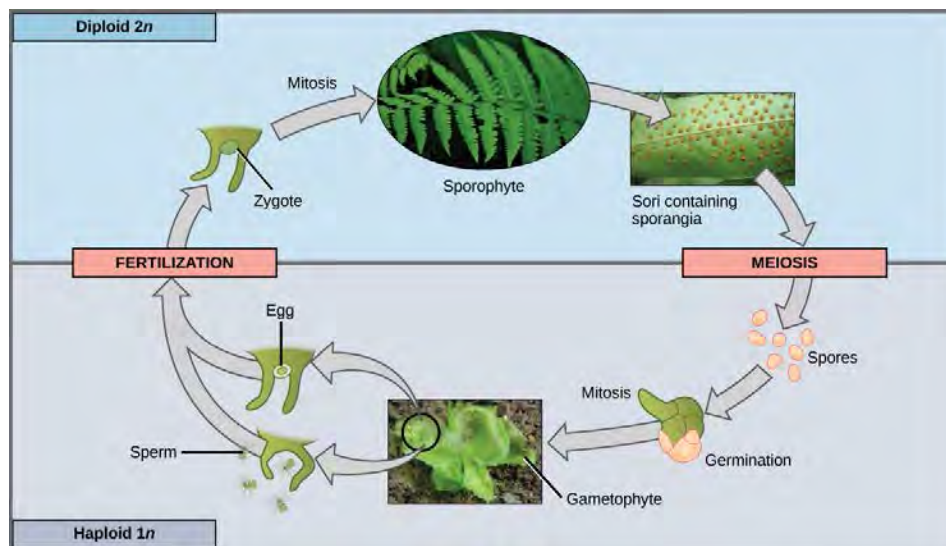
**Figure 14.2** Alternation of generations between the haploid ( $1n$ ) gametophyte and diploid ( $2n$ ) sporophyte is shown. (credit: modification of work by Peter Coxhead)

**Haplontic** refers to a life cycle in which there is a dominant haploid stage. **Diplontic** refers to a life cycle in which the diploid stage is the dominant stage, and the haploid chromosome number is only seen for a brief time in the life cycle during sexual reproduction. Humans are diplontic, for example. Most plants exhibit alternation of generations, which is described as **haplodiplontic**: the haploid multicellular form known as a gametophyte is followed in the development sequence by a multicellular diploid organism, the **sporophyte**. The **gametophyte** gives rise to the gametes, or reproductive cells, by mitosis. It can be the most obvious phase of the life cycle of the plant, as in the mosses, or it can occur in a microscopic structure, such as a pollen grain in the higher plants (the collective term for the vascular plants). The sporophyte stage is barely noticeable in lower plants (the collective term for the plant groups of mosses, liverworts, and hornworts). Towering trees are the diplontic phase in the lifecycles of plants such as sequoias and pines.

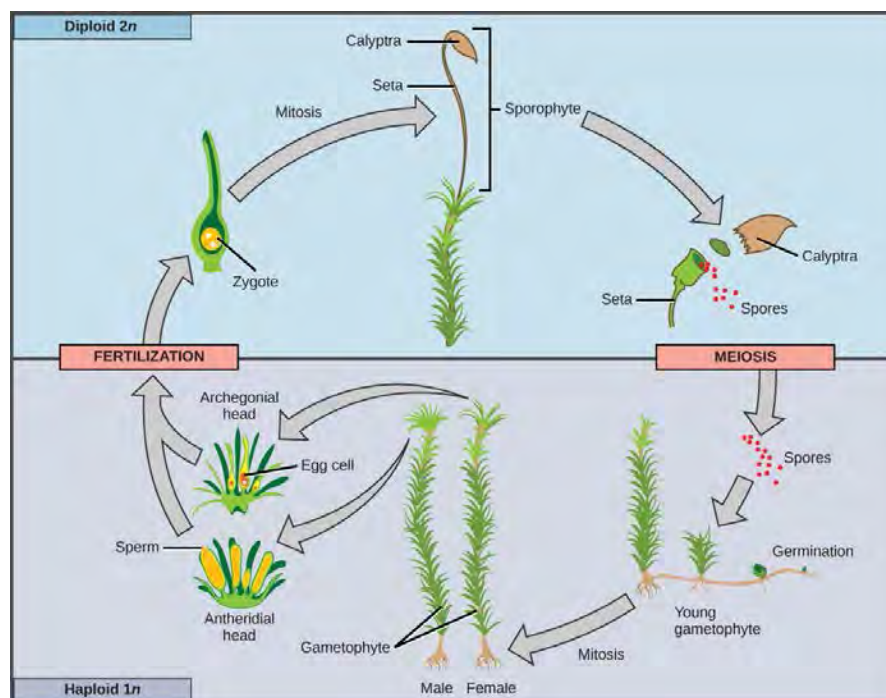
### Sporangia in the Seedless Plants

The sporophyte of seedless plants is diploid and results from **syngamy** or the fusion of two gametes (Figure 14.2). The sporophyte bears the **sporangia** (singular, sporangium), organs that first appeared in the land plants. The term “sporangia” literally means “spore in a vessel,” as it is a reproductive sac that contains spores. Inside the multicellular sporangia, the diploid sporocytes, or mother cells, produce haploid spores by meiosis, which reduces the  $2n$  chromosome number to  $1n$ . The spores are later released by the sporangia and disperse in the environment. Two different types of spores are produced in land plants, resulting in the separation of sexes at different points in the life cycle. Seedless nonvascular plants (more appropriately referred to as “seedless nonvascular plants with a dominant gametophyte phase”) produce only one kind of spore, and are called **homosporous**. After germinating from a spore, the gametophyte produces both male and female **gametangia**, usually on the same individual. In contrast, **heterosporous** plants produce two morphologically different types of spores. The male spores are called microspores because of their smaller size; the comparatively larger megaspores will develop into the female gametophyte. Heterospory is observed in a few seedless vascular plants and in all seed plants.

When the haploid spore germinates, it generates a multicellular gametophyte by mitosis. The gametophyte supports the zygote formed from the fusion of gametes and the resulting young sporophyte or vegetative form, and the cycle begins anew (Figure 14.3 and Figure 14.4).



**Figure 14.3** This life cycle of a fern shows alternation of generations with a dominant sporophyte stage. (credit "fern": modification of work by Cory Zanker; credit "gametophyte": modification of work by "Vlmastra"/Wikimedia Commons)



**Figure 14.4** This life cycle of a moss shows alternation of generations with a dominant gametophyte stage. (credit: modification of work by Mariana Ruiz Villareal)

The spores of seedless plants and the pollen of seed plants are surrounded by thick cell walls containing a tough polymer known as sporopollenin. This substance is characterized by long chains of organic molecules related to fatty acids and carotenoids, and gives most pollen its yellow color. Sporopollenin is unusually resistant to chemical and biological degradation. Its toughness explains the existence of well-preserved fossils of pollen. Sporopollenin was once thought to be an innovation of land plants; however, the green alga *Coleochaetes* is now known to form spores that contain sporopollenin.

Protection of the embryo is a major requirement for land plants. The vulnerable embryo must be sheltered from desiccation and other environmental hazards. In both seedless and seed plants, the female gametophyte provides nutrition, and in seed plants, the embryo is also protected as it develops into the new generation of sporophyte.

### Gametangia in the Seedless Plants

Gametangia (singular, gametangium) are structures on the gametophytes of seedless plants in which gametes are produced by mitosis. The male gametangium, the antheridium, releases sperm. Many seedless plants produce sperm equipped with flagella that enable them to swim in a moist environment to the archegonia, the female gametangium. The embryo develops inside the archegonium as the sporophyte.

### Apical Meristems

The shoots and roots of plants increase in length through rapid cell division within a tissue called the **apical meristem** (Figure 14.5). The apical meristem is a cap of cells at the shoot tip or root tip made of undifferentiated cells that continue to proliferate throughout the life of the plant. Meristematic cells give rise to all the specialized tissues of the plant. Elongation of the shoots and roots allows a plant to access additional space and resources: light in the case of the shoot, and water and minerals in the case of roots. A separate meristem, called the lateral meristem, produces cells that increase the diameter of stems and tree trunks. Apical meristems are an adaptation to allow vascular plants to grow in directions essential to their survival: upward to greater availability of sunlight, and downward into the soil to obtain water and essential minerals.



**Figure 14.5** This apple seedling is an example of a plant in which the apical meristem gives rise to new shoots and root growth.

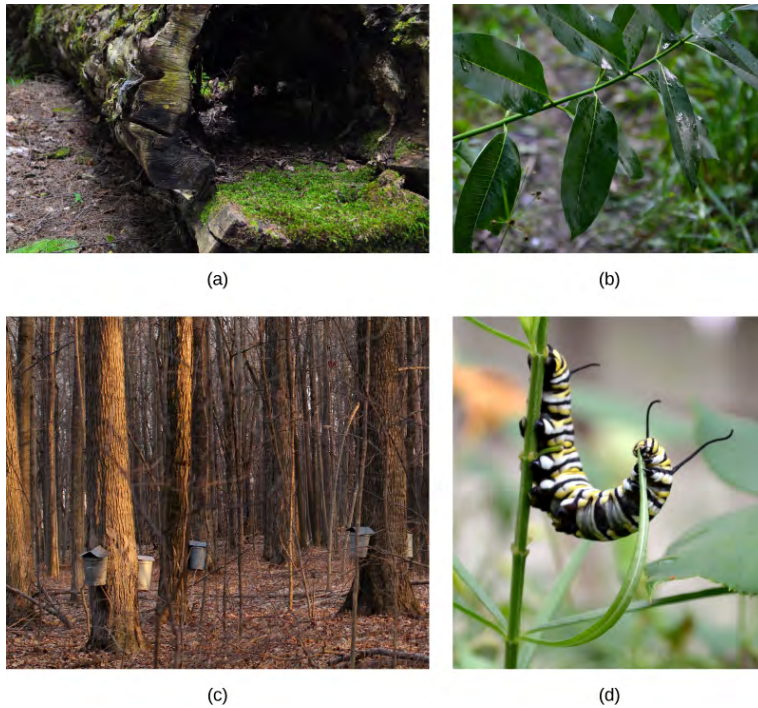
## Additional Land Plant Adaptations

As plants adapted to dry land and became independent of the constant presence of water in damp habitats, new organs and structures made their appearance. Early land plants did not grow above a few inches off the ground, and on these low mats, they competed for light. By evolving a shoot and growing taller, individual plants captured more light. Because air offers substantially less support than water, land plants incorporated more rigid molecules in their stems (and later, tree trunks). The evolution of vascular tissue for the distribution of water and solutes was a necessary prerequisite for plants to evolve larger bodies. The vascular system contains xylem and phloem tissues. Xylem conducts water and minerals taken from the soil up to the shoot; phloem transports food derived from photosynthesis throughout the entire plant. The root system that evolved to take up water and minerals also anchored the increasingly taller shoot in the soil.

In land plants, a waxy, waterproof cover called a cuticle coats the aerial parts of the plant: leaves and stems. The cuticle also prevents intake of carbon dioxide needed for the synthesis of carbohydrates through photosynthesis. Stomata, or pores, that open and close to regulate traffic of gases and water vapor therefore appeared in plants as they moved into drier habitats.

Plants cannot avoid predatory animals. Instead, they synthesize a large range of poisonous secondary metabolites: complex organic molecules such as alkaloids, whose noxious smells and unpleasant taste deter animals. These toxic compounds can cause severe diseases and even death.

Additionally, as plants coevolved with animals, sweet and nutritious metabolites were developed to lure animals into providing valuable assistance in dispersing pollen grains, fruit, or seeds. Plants have been coevolving with animal associates for hundreds of millions of years (Figure 14.6).



**Figure 14.6** Plants have evolved various adaptations to life on land. (a) Early plants grew close to the ground, like this moss, to avoid desiccation. (b) Later plants developed a waxy cuticle to prevent desiccation. (c) To grow taller, like these maple trees, plants had to evolve new structural chemicals to strengthen their stems and vascular systems to transport water and minerals from the soil and nutrients from the leaves. (d) Plants developed physical and chemical defenses to avoid being eaten by animals. (credit a, b: modification of work by Cory Zanker; credit c: modification of work by Christine Cimala; credit d: modification of work by Jo Naylor)

# evolution IN ACTION

## Paleobotany

How organisms acquired traits that allow them to colonize new environments, and how the contemporary ecosystem is shaped, are fundamental questions of evolution. Paleobotany addresses these questions by specializing in the study of extinct plants. Paleobotanists analyze specimens retrieved from field studies, reconstituting the morphology of organisms that have long disappeared. They trace the evolution of plants by following the modifications in plant morphology, and shed light on the connection between existing plants by identifying common ancestors that display the same traits. This field seeks to find transitional species that bridge gaps in the path to the development of modern organisms. Fossils are formed when organisms are trapped in sediments or environments where their shapes are preserved (**Figure 14.7**). Paleobotanists determine the geological age of specimens and the nature of their environment using the geological sediments and fossil organisms surrounding them. The activity requires great care to preserve the integrity of the delicate fossils and the layers in which they are found.

One of the most exciting recent developments in paleobotany is the use of analytical chemistry and molecular biology to study fossils. Preservation of molecular structures requires an environment free of oxygen, since oxidation and degradation of material through the activity of microorganisms depend on the presence of oxygen. One example of the use of analytical chemistry and molecular biology is in the identification of oleanane, a compound that deters pests and which, up to this point, appears to be unique to flowering plants. Oleanane was recovered from sediments dating from the Permian, much earlier than the current dates given for the appearance of the first flowering plants. Fossilized nucleic acids—DNA and RNA—yield the most information. Their sequences are analyzed and compared to those of living and related organisms. Through this analysis, evolutionary relationships can be built for plant lineages.

Some paleobotanists are skeptical of the conclusions drawn from the analysis of molecular fossils. For one, the chemical materials of interest degrade rapidly during initial isolation when exposed to air, as well as in further manipulations. There is always a high risk of contaminating the specimens with extraneous material, mostly from microorganisms. Nevertheless, as technology is refined, the analysis of DNA from fossilized plants will provide invaluable information on the evolution of plants and their adaptation to an ever-changing environment.



**Figure 14.7** This fossil of a palm leaf (*Palmacites* sp.) discovered in Wyoming dates to about 40 million years ago.

## The Major Divisions of Land Plants

Land plants are classified into two major groups according to the absence or presence of vascular tissue, as detailed in **Figure 14.8**. Plants that lack vascular tissue formed of specialized cells for the transport of water and nutrients are referred to as **nonvascular plants**. The bryophytes, liverworts, mosses, and hornworts are seedless and nonvascular, and likely appeared early in land plant evolution. **Vascular plants** developed a network of cells that conduct water and solutes through the plant body. The first vascular plants appeared in the late Ordovician (461–444 million years ago) and were probably similar to lycophytes, which include club mosses (not to be confused with the mosses) and the pterophytes (ferns, horsetails, and whisk ferns). Lycophytes and pterophytes are referred to as seedless vascular plants. They do not produce seeds, which are embryos with their stored food reserves protected by a hard casing. The seed plants form the largest group of all existing plants and, hence, dominate the landscape. Seed plants include gymnosperms, most notably conifers, which produce “naked

seeds,” and the most successful plants, the flowering plants, or angiosperms, which protect their seeds inside chambers at the center of a flower. The walls of these chambers later develop into fruits.

Embryophytes: The Land Plants						
Nonvascular Plants “Bryophytes”			Vascular Plants			
Liverworts	Hornworts	Mosses	Seedless Plants		Seed Plants	
			Lycophytes	Pterophytes	Gymno-sperms	Angio-sperms
			Club Mosses	Whisk Ferns		
			Quillworts	Horsetails		
Spike Mosses	Ferns					

**Figure 14.8** This table shows the major divisions of plants.

## 14.2 | Seedless Plants

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

- Describe the distinguishing traits of the three types of bryophytes
- Identify the new traits that first appear in seedless vascular plants
- Describe the major classes of seedless vascular plants

An incredible variety of seedless plants populates the terrestrial landscape. Mosses grow on tree trunks, and horsetails (**Figure 14.9**) display their jointed stems and spindly leaves on the forest floor. Yet, seedless plants represent only a small fraction of the plants in our environment. Three hundred million years ago, seedless plants dominated the landscape and grew in the enormous swampy forests of the Carboniferous period. Their decomposing bodies created large deposits of coal that we mine today.



**Figure 14.9** Seedless plants like these horsetails (*Equisetum* sp.) thrive in damp, shaded environments under the tree canopy where dryness is a rare occurrence. (credit: Jerry Kirkhart)

### Bryophytes

Bryophytes, an informal grouping of the nonvascular plants, are the closest extant relative of early terrestrial plants. The first bryophytes most probably appeared in the Ordovician period, about 490 million years ago. Because of the lack of lignin—the tough polymer in cell walls in the stems of vascular plants—and other resistant structures, the likelihood of bryophytes forming fossils is rather small, though some spores made up of sporopollenin have been discovered that have been attributed to early bryophytes. By the Silurian period (440 million years ago), however, vascular plants had spread throughout the continents. This fact is used as evidence that nonvascular plants must have preceded the Silurian period.

There are about 18,000 species of bryophytes, which thrive mostly in damp habitats, although some grow in deserts. They constitute the major flora of inhospitable environments like the tundra, where their small size and tolerance to desiccation offer distinct advantages. They do not have the specialized cells that conduct fluids found in the vascular plants, and generally lack lignin. In bryophytes, water and nutrients circulate inside specialized conducting cells. Although the name nontracheophyte is more accurate, bryophytes are commonly referred to as nonvascular plants.

In a bryophyte, all the conspicuous vegetative organs belong to the haploid organism, or gametophyte. The diploid sporophyte is barely noticeable. The gametes formed by bryophytes swim using flagella. The sporangium, the multicellular sexual reproductive structure, is present in bryophytes. The embryo also remains attached to the parent plant, which nourishes it. This is a characteristic of land plants.

The bryophytes are divided into three divisions (in plants, the taxonomic level “division” is used instead of phylum): the liverworts, or Marchantiophyta; the hornworts, or Anthocerotophyta; and the mosses, or true Bryophyta.

## Liverworts

**Liverworts** (Marchantiophyta) may be viewed as the plants most closely related to the ancestor that moved to land. Liverworts have colonized many habitats on Earth and diversified to more than 6,000 existing species (Figure 14.10a). Some gametophytes form lobate green structures, as seen in Figure 14.10b. The shape is similar to the lobes of the liver and, hence, provides the origin of the common name given to the division.



**Figure 14.10** (a) A 1904 drawing of liverworts shows the variety of their forms. (b) A liverwort, *Lunularia cruciata*, displays its lobate, flat thallus. The organism in the photograph is in the gametophyte stage.

## Hornworts

The **hornworts** (Anthocerotophyta) have colonized a variety of habitats on land, although they are never far from a source of moisture. There are about 100 described species of hornworts. The dominant phase of the life cycle of hornworts is the short, blue-green gametophyte. The sporophyte is the defining characteristic of the group. It is a long and narrow pipe-like structure that emerges from the parent gametophyte and maintains growth throughout the life of the plant (Figure 14.11).



**Figure 14.11** Hornworts grow a tall and slender sporophyte. (credit: modification of work by Jason Hollinger)

## Mosses

More than 12,000 species of **mosses** have been catalogued. Their habitats vary from the tundra, where they are the main vegetation, to the understory of tropical forests. In the tundra, their shallow rhizoids allow them to fasten to a substrate without digging into the frozen soil. They slow down erosion, store moisture and soil nutrients, and provide shelter for small animals and food for larger herbivores, such as the musk ox. Mosses are very sensitive to air pollution and are used to monitor the quality of air. The sensitivity of mosses to copper salts makes these salts a common ingredient of compounds marketed to eliminate mosses in lawns (**Figure 14.12**).



**Figure 14.12** This green feathery moss has reddish-brown sporophytes growing upward. (credit: "Lordgrunt"/Wikimedia Commons)

## Vascular Plants

The vascular plants are the dominant and most conspicuous group of land plants. There are about 275,000 species of vascular plants, which represent more than 90 percent of Earth's vegetation. Several evolutionary innovations explain their success and their spread to so many habitats.

### **Vascular Tissue: Xylem and Phloem**

The first fossils that show the presence of vascular tissue are dated to the Silurian period, about 430 million years ago. The simplest arrangement of conductive cells shows a pattern of xylem at the center surrounded by phloem. **Xylem** is the tissue responsible for long-distance transport of water and minerals, the transfer of water-soluble growth factors from the organs of synthesis to the target organs, and storage of water and nutrients.

A second type of vascular tissue is **phloem**, which transports sugars, proteins, and other solutes through the plant. Phloem cells are divided into sieve elements, or conducting cells, and supportive tissue. Together, xylem and phloem tissues form the vascular system of plants.



### Roots: Support for the Plant

Roots are not well preserved in the fossil record; nevertheless, it seems that they did appear later in evolution than vascular tissue. The development of an extensive network of roots represented a significant new feature of vascular plants. Thin rhizoids attached the bryophytes to the substrate. Their rather flimsy filaments did not provide a strong anchor for the plant; neither did they absorb water and nutrients. In contrast, roots, with their prominent vascular tissue system, transfer water and minerals from the soil to the rest of the plant. The extensive network of roots that penetrates deep in the ground to reach sources of water also stabilizes trees by acting as ballast and an anchor. The majority of roots establish a symbiotic relationship with fungi, forming mycorrhizae. In the mycorrhizae, fungal hyphae grow around the root and within the root around the cells, and in some instances within the cells. This benefits the plant by greatly increasing the surface area for absorption.

### Leaves, Sporophylls, and Strobili

A third adaptation marks seedless vascular plants. Accompanying the prominence of the sporophyte and the development of vascular tissue, the appearance of true leaves improved photosynthetic efficiency. Leaves capture more sunlight with their increased surface area.

In addition to photosynthesis, leaves play another role in the life of the plants. Pinecones, mature fronds of ferns, and flowers are all **sporophylls**—leaves that were modified structurally to bear sporangia. **Strobili** are structures that contain the sporangia. They are prominent in conifers and are known commonly as cones: for example, the pine cones of pine trees.

## Seedless Vascular Plants

By the Late Devonian period (385 million years ago), plants had evolved vascular tissue, well-defined leaves, and root systems. With these advantages, plants increased in height and size. During the Carboniferous period (359–299 million years ago), swamp forests of club mosses and horsetails, with some specimens reaching more than 30 meters tall, covered most of the land. These forests gave rise to the extensive coal deposits that gave the Carboniferous its name. In seedless vascular plants, the sporophyte became the dominant phase of the lifecycle.

Water is still required for fertilization of seedless vascular plants, and most favor a moist environment. Modern-day seedless vascular plants include club mosses, horsetails, ferns, and whisk ferns.

### Club Mosses

The **club mosses**, or Lycophyta, are the earliest group of seedless vascular plants. They dominated the landscape of the Carboniferous period, growing into tall trees and forming large swamp forests. Today's club mosses are diminutive, evergreen plants consisting of a stem (which may be branched) and small leaves called microphylls (**Figure 14.13**). The division Lycophyta consists of close to 1,000 species, including quillworts (*Isoetales*), club mosses (Lycopodiales), and spike mosses (Selaginellales): none of which is a true moss.



**Figure 14.13** *Lycopodium clavatum* is a club moss. (credit: Cory Zanker)

### Horsetails

Ferns and whisk ferns belong to the division Pterophyta. A third group of plants in the Pterophyta, the horsetails, is sometimes classified separately from ferns. **Horsetails** have a single genus, *Equisetum*. They are the survivors of a large group of plants, known as Arthrophyta, which produced large trees and entire swamp forests in the Carboniferous. The plants are usually found in damp environments and marshes (**Figure 14.14**).



**Figure 14.14** Horsetails thrive in a marsh. (credit: Myriam Feldman)

The stem of a horsetail is characterized by the presence of joints, or nodes: hence the name Arthrophyta, which means “jointed plant”. Leaves and branches come out as whorls from the evenly spaced rings. The needle-shaped leaves do not contribute greatly to photosynthesis, the majority of which takes place in the green stem (**Figure 14.15**).



**Figure 14.15** Thin leaves originating at the joints are noticeable on the horsetail plant. (credit: Myriam Feldman)

### **Ferns and Whisk Ferns**

Ferns are considered the most advanced seedless vascular plants and display characteristics commonly observed in seed plants. Ferns form large leaves and branching roots. In contrast, **whisk ferns**, the psilophytes, lack both roots and leaves, which were probably lost by evolutionary reduction. Evolutionary reduction is a process by which natural selection reduces the size of a structure that is no longer favorable in a particular environment. Photosynthesis takes place in the green stem of a whisk fern. Small yellow knobs form at the tip of the branch stem and contain the sporangia. Whisk ferns have been classified outside the true ferns; however, recent comparative analysis of DNA suggests that this group may have lost both vascular tissue and roots through evolution, and is actually closely related to ferns.

With their large fronds, **ferns** are the most readily recognizable seedless vascular plants (**Figure 14.16**). About 12,000 species of ferns live in environments ranging from tropics to temperate forests. Although some species survive in dry environments, most ferns are restricted to moist and shaded places. They made their appearance in the fossil record during

the Devonian period (416–359 million years ago) and expanded during the Carboniferous period, 359–299 million years ago (**Figure 14.17**).



**Figure 14.16** Some specimens of this short tree-fern species can grow very tall. (credit: Adrian Pingstone)

EON	ERA	PERIOD	MILLIONS OF YEARS AGO
Phanerozoic	Cenozoic	Quaternary	--- 1.6 ---
		Tertiary	--- 66 ---
	Mesozoic	Cretaceous	--- 138 ---
		Jurassic	--- 205 ---
		Triassic	--- 240 ---
	Paleozoic	Permian	--- 290 ---
		Carboniferous	--- 360 ---
		Devonian	--- 410 ---
		Silurian	--- 435 ---
		Ordovician	--- 500 ---
Proterozoic			--- 570 ---
Archean			--- 2500 ---
	Pre-Archean		--- 3800? ---

**Figure 14.17** This chart shows the geological time scale, beginning with the Pre-Archean eon 3800 million years ago and ending with the Quaternary period in present time. (credit: modification of work by USGS)



Go to this [website \(http://openstaxcollege.org/l/fern\\_life\\_cycl2\)](http://openstaxcollege.org/l/fern_life_cycl2) to see an animation of the lifecycle of a fern and to test your knowledge.

## careers IN ACTION

### Landscape Designer

Looking at the well-laid gardens of flowers and fountains seen in royal castles and historic houses of Europe, it is clear that the creators of those gardens knew more than art and design. They were also familiar with the biology of the plants they chose. Landscape design also has strong roots in the United States' tradition. A prime example of early American classical design is Monticello, Thomas Jefferson's private estate; among his many other interests, Jefferson maintained a passion for botany. Landscape layout can encompass a small private space, like a backyard garden; public gathering places, like Central Park in New York City; or an entire city plan, like Pierre L'Enfant's design for Washington, DC.

A landscape designer will plan traditional public spaces—such as botanical gardens, parks, college campuses, gardens, and larger developments—as well as natural areas and private gardens (**Figure 14.18**). The restoration of natural places encroached upon by human intervention, such as wetlands, also requires the expertise of a landscape designer.

With such an array of required skills, a landscape designer's education includes a solid background in botany, soil science, plant pathology, entomology, and horticulture. Coursework in architecture and design software is also required for the completion of the degree. The successful design of a landscape rests on an extensive knowledge of plant growth requirements, such as light and shade, moisture levels, compatibility of different species, and susceptibility to pathogens and pests. For example, mosses and ferns will thrive in a shaded area where fountains provide moisture; cacti, on the other hand, would not fare well in that environment. The future growth of the individual plants must be taken into account to avoid crowding and competition for light and nutrients. The appearance of the space over time is also of concern. Shapes, colors, and biology must be balanced for a well-maintained and sustainable green space. Art, architecture, and biology blend in a beautifully designed and implemented landscape.



**Figure 14.18** This campus garden was designed by students in the horticulture and landscaping department of the college. (credit: Myriam Feldman)

## 14.3 | Seed Plants: Gymnosperms

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

- Discuss the type of seeds produced by gymnosperms, as well as other characteristics of gymnosperms
- List the four groups of modern-day gymnosperms and provide examples of each

The first plants to colonize land were most likely closely related to modern-day mosses (bryophytes) and are thought to have appeared about 500 million years ago. They were followed by liverworts (also bryophytes) and primitive vascular plants,

the pterophytes, from which modern ferns are derived. The life cycle of bryophytes and pterophytes is characterized by the alternation of generations. The completion of the life cycle requires water, as the male gametes must swim to the female gametes. The male gametophyte releases sperm, which must swim—propelled by their flagella—to reach and fertilize the female gamete or egg. After fertilization, the zygote matures and grows into a sporophyte, which in turn will form sporangia, or "spore vessels," in which mother cells undergo meiosis and produce haploid spores. The release of spores in a suitable environment will lead to germination and a new generation of gametophytes.

## The Evolution of Seed Plants

In seed plants, the evolutionary trend led to a dominant sporophyte generation, in which the larger and more ecologically significant generation for a species is the diploid plant. At the same time, the trend led to a reduction in the size of the gametophyte, from a conspicuous structure to a microscopic cluster of cells enclosed in the tissues of the sporophyte. Lower vascular plants, such as club mosses and ferns, are mostly homosporous (produce only one type of spore). In contrast, all seed plants, or spermatophytes, are heterosporous, forming two types of spores: megaspores (female) and microspores (male). Megaspores develop into female gametophytes that produce eggs, and microspores mature into male gametophytes that generate sperm. Because the gametophytes mature within the spores, they are not free-living, as are the gametophytes of other seedless vascular plants. Heterosporous seedless plants are seen as the evolutionary forerunners of seed plants.

Seeds and pollen—two adaptations to drought—distinguish seed plants from other (seedless) vascular plants. Both adaptations were critical to the colonization of land. Fossils place the earliest distinct seed plants at about 350 million years ago. The earliest reliable record of gymnosperms dates their appearance to the Carboniferous period (359–299 million years ago). Gymnosperms were preceded by the progymnosperms ("first naked seed plants"). This was a transitional group of plants that superficially resembled conifers ("cone bearers") because they produced wood from the secondary growth of the vascular tissues; however, they still reproduced like ferns, releasing spores to the environment. In the Mesozoic era (251–65.5 million years ago), gymnosperms dominated the landscape. Angiosperms took over by the middle of the Cretaceous period (145.5–65.5 million years ago) in the late Mesozoic era, and have since become the most abundant plant group in most terrestrial biomes.

The two innovative structures of pollen and seed allowed seed plants to break their dependence on water for reproduction and development of the embryo, and to conquer dry land. The pollen grains carry the male gametes of the plant. The small haploid ( $1n$ ) cells are encased in a protective coat that prevents desiccation (drying out) and mechanical damage. Pollen can travel far from the sporophyte that bore it, spreading the plant's genes and avoiding competition with other plants. The seed offers the embryo protection, nourishment and a mechanism to maintain dormancy for tens or even thousands of years, allowing it to survive in a harsh environment and ensuring germination when growth conditions are optimal. Seeds allow plants to disperse the next generation through both space and time. With such evolutionary advantages, seed plants have become the most successful and familiar group of plants.

## Gymnosperms

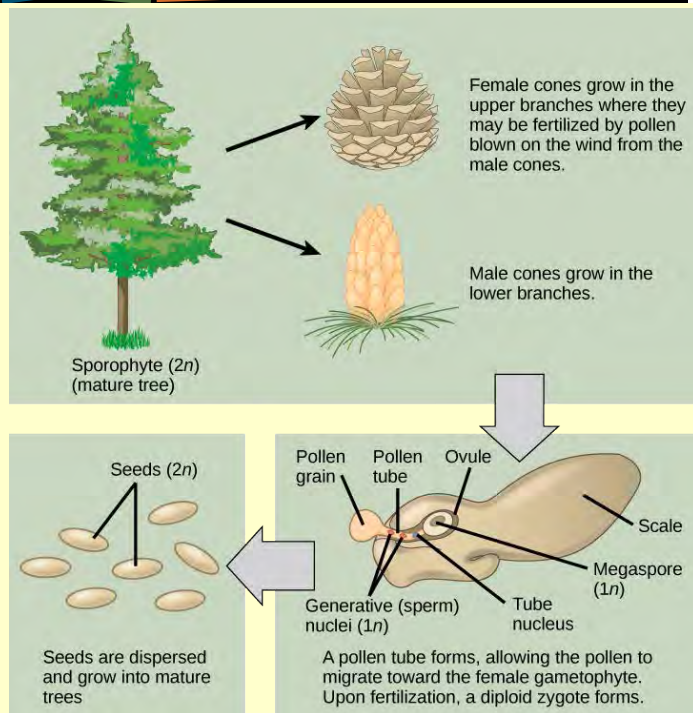
**Gymnosperms** ("naked seed") are a diverse group of seed plants and are paraphyletic. Paraphyletic groups do not include descendants of a single common ancestor. Gymnosperm characteristics include naked seeds, separate female and male gametes, pollination by wind, and tracheids, which transport water and solutes in the vascular system.

### Life Cycle of a Conifer

Pine trees are conifers and carry both male and female sporophylls on the same plant. Like all gymnosperms, pines are heterosporous and produce male microspores and female megaspores. In the male cones, or staminate cones, the **microsporocytes** give rise to microspores by meiosis. The microspores then develop into pollen grains. Each pollen grain contains two cells: one generative cell that will divide into two sperm, and a second cell that will become the pollen tube cell. In the spring, pine trees release large amounts of yellow pollen, which is carried by the wind. Some gametophytes will land on a female cone. The pollen tube grows from the pollen grain slowly, and the generative cell in the pollen grain divides into two sperm cells by mitosis. One of the sperm cells will finally unite its haploid nucleus with the haploid nucleus of an egg cell in the process of fertilization.

Female **cones**, or ovulate cones, contain two ovules per scale. One **megasporocyte** undergoes meiosis in each ovule. Only a single surviving haploid cell will develop into a female multicellular gametophyte that encloses an egg. On fertilization, the zygote will give rise to the embryo, which is enclosed in a seed coat of tissue from the parent plant. Fertilization and seed development is a long process in pine trees—it may take up to two years after pollination. The seed that is formed contains three generations of tissues: the seed coat that originates from the parent plant tissue, the female gametophyte that will provide nutrients, and the embryo itself. **Figure 14.19** illustrates the life cycle of a conifer.

# art CONNECTION



**Figure 14.19** This image shows the lifecycle of a conifer.

At what stage does the diploid zygote form?

- when the female cone begins to bud from the tree
- when the sperm nucleus and the egg nucleus fuse
- when the seeds drop from the tree
- when the pollen tube begins to grow

CONCEPT in ACTION



Watch this [video \(http://openstaxcollege.org/l/gymnosperm\)](http://openstaxcollege.org/l/gymnosperm) to see the process of seed production in gymnosperms.

## Diversity of Gymnosperms

Modern gymnosperms are classified into four major divisions and comprise about 1,000 described species. Coniferophyta, Cycadophyta, and Ginkgophyta are similar in their production of secondary cambium (cells that generate the vascular system of the trunk or stem) and their pattern of seed development, but are not closely related phylogenetically to each other. Gnetophyta are considered the closest group to angiosperms because they produce true xylem tissue that contains both tracheids and vessel elements.

### Conifers

**Conifers** are the dominant phylum of gymnosperms, with the most variety of species. Most are tall trees that usually bear scale-like or needle-like leaves. The thin shape of the needles and their waxy cuticle limits water loss through transpiration. Snow slides easily off needle-shaped leaves, keeping the load light and decreasing breaking of branches. These adaptations to cold and dry weather explain the predominance of conifers at high altitudes and in cold climates. Conifers include familiar evergreen trees, such as pines, spruces, firs, cedars, sequoias, and yews (**Figure 14.20**). A few species are deciduous and lose their leaves all at once in fall. The European larch and the tamarack are examples of deciduous conifers. Many coniferous trees are harvested for paper pulp and timber. The wood of conifers is more primitive than the wood of angiosperms; it contains tracheids, but no vessel elements, and is referred to as “soft wood.”



**Figure 14.20** Conifers are the dominant form of vegetation in cold or arid environments and at high altitudes. Shown here are the (a) evergreen spruce, (b) sequoia, (c) juniper, and (d) a deciduous gymnosperm: the tamarack *Larix laricina*. Notice the yellow leaves of the tamarack. (credit b: modification of work by Alan Levine; credit c: modification of work by Wendy McCormac; credit d: modification of work by Micky Zlimen)

### Cycads

**Cycads** thrive in mild climates and are often mistaken for palms because of the shape of their large, compound leaves. They bear large cones, and unusually for gymnosperms, may be pollinated by beetles, rather than wind. They dominated the landscape during the age of dinosaurs in the Mesozoic era (251–65.5 million years ago). Only a hundred or so cycad species persisted to modern times. They face possible extinction, and several species are protected through international conventions. Because of their attractive shape, they are often used as ornamental plants in gardens (**Figure 14.21**).



**Figure 14.21** This *Encephalartos ferox* cycad exhibits large cones. (credit: Wendy Cutler)

### Ginkgophytes

The single surviving species of **ginkgophyte** is the *Ginkgo biloba* (**Figure 14.22**). Its fan-shaped leaves, unique among seed plants because they feature a dichotomous venation pattern, turn yellow in autumn and fall from the plant. For centuries, Buddhist monks cultivated *Ginkgo biloba*, ensuring its preservation. It is planted in public spaces because it is unusually resistant to pollution. Male and female organs are found on separate plants. Usually, only male trees are planted by gardeners because the seeds produced by the female plant have an off-putting smell of rancid butter.



**Figure 14.22** This plate from the 1870 book *Flora Japonica, Sectio Prima (Tafelband)* depicts the leaves and fruit of *Ginkgo biloba*, as drawn by Philipp Franz von Siebold and Joseph Gerhard Zuccarini.

### Gnetophytes

**Gnetophytes** are the closest relatives to modern angiosperms, and include three dissimilar genera of plants. Like angiosperms, they have broad leaves. *Gnetum* species are mostly vines in tropical and subtropical zones. The single species of *Welwitschia* is an unusual, low-growing plant found in the deserts of Namibia and Angola. It may live for up to 2000



years. The genus *Ephedra* is represented in North America in dry areas of the southwestern United States and Mexico (**Figure 14.23**). *Ephedra*'s small, scale-like leaves are the source of the compound ephedrine, which is used in medicine as a potent decongestant. Because ephedrine is similar to amphetamines, both in chemical structure and neurological effects, its use is restricted to prescription drugs. Like angiosperms, but unlike other gymnosperms, all gnetophytes possess vessel elements in their xylem.



**Figure 14.23** *Ephedra viridis*, known by the common name Mormon tea, grows in the western United States. (credit: US National Park Service, USDA-NRCS PLANTS Database)



Watch this **BBC video** (<http://openstaxcollege.org/l/welwitschia>) describing the amazing strangeness of Welwitschia.

## 14.4 | Seed Plants: Angiosperms

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

- Describe the main parts of a flower and their purpose
- Detail the life cycle of an angiosperm
- Discuss the two main groups into which flower plants are divided, as well as explain how basal angiosperms differ from others

From their humble and still obscure beginning during the early Jurassic period (202–145.5 MYA), the angiosperms, or flowering plants, have successfully evolved to dominate most terrestrial ecosystems. Angiosperms include a staggering number of genera and species; with more than 260,000 species, the division is second only to insects in terms of diversification (**Figure 14.24**).



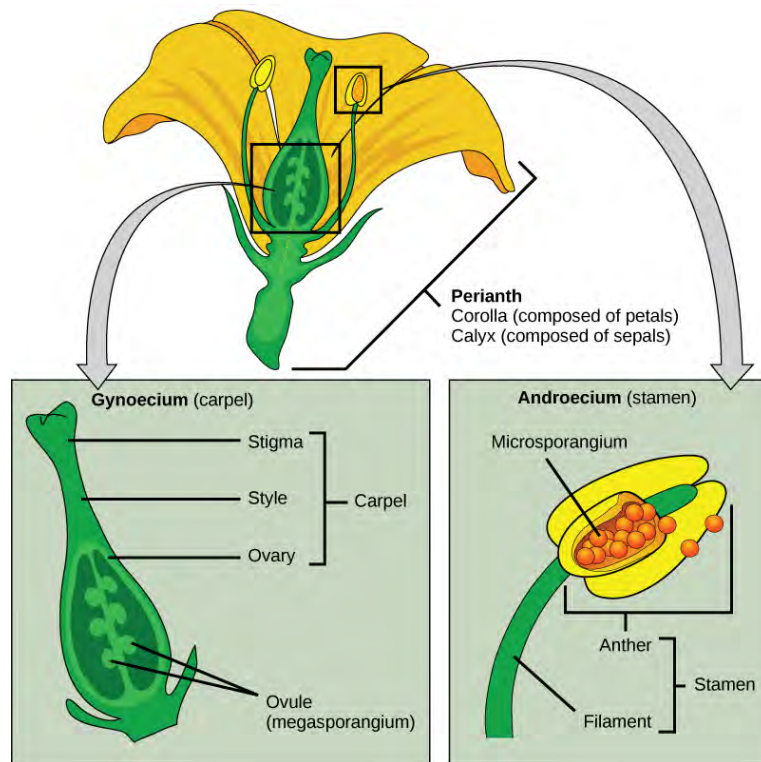
**Figure 14.24** These flowers grow in a botanical garden border in Bellevue, WA. Flowering plants dominate terrestrial landscapes. The vivid colors of flowers are an adaptation to pollination by insects and birds. (credit: Myriam Feldman)

Angiosperm success is a result of two novel structures that ensure reproductive success: flowers and fruit. Flowers allowed plants to form cooperative evolutionary relationships with animals, in particular insects, to disperse their pollen to female gametophytes in a highly targeted way. Fruit protect the developing embryo and serve as an agent of dispersal. Different structures on fruit reflect the dispersal strategies that help with the spreading of seeds.

## Flowers

Flowers are modified leaves or sporophylls organized around a central stalk. Although they vary greatly in appearance, all flowers contain the same structures: sepals, petals, pistils, and stamens. A whorl of **sepals** (the **calyx**) is located at the base of the peduncle, or stem, and encloses the floral bud before it opens. Sepals are usually photosynthetic organs, although there are some exceptions. For example, the corolla in lilies and tulips consists of three sepals and three petals that look virtually identical—this led botanists to coin the word tepal. **Petals** (collectively the **corolla**) are located inside the whorl of sepals and usually display vivid colors to attract pollinators. Flowers pollinated by wind are usually small and dull. The sexual organs are located at the center of the flower.

As illustrated in **Figure 14.25**, the stigma, style, and ovary constitute the female organ, the **carpel** or **pistil**, which is also referred to as the **gynoecium**. A gynoecium may contain one or more carpels within a single flower. The megaspores and the female gametophytes are produced and protected by the thick tissues of the carpel. A long, thin structure called a **style** leads from the sticky **stigma**, where pollen is deposited, to the **ovary** enclosed in the carpel. The ovary houses one or more ovules that will each develop into a seed upon fertilization. The male reproductive organs, the androecium or **stamens**, surround the central carpel. Stamens are composed of a thin stalk called a **filament** and a sac-like structure, the **anther**, in which microspores are produced by meiosis and develop into pollen grains. The filament supports the anther.



**Figure 14.25** This image depicts the structure of a perfect and complete flower. Perfect flowers carry both male and female floral organs. (credit: modification of work by Mariana Ruiz Villareal)

## Fruit

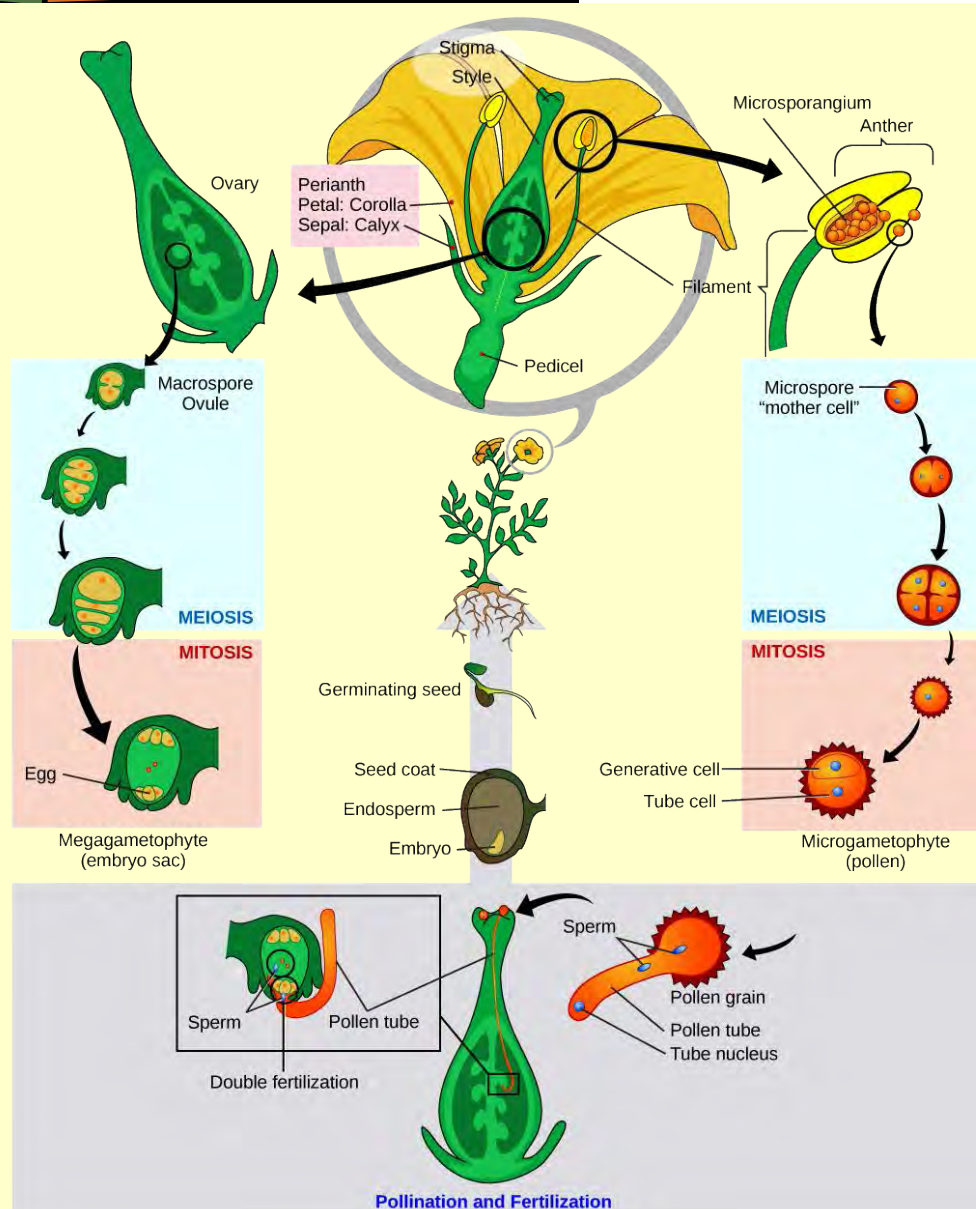
The seed forms in an ovary, which enlarges as the seeds grow. As the seed develops, the walls of the ovary also thicken and form the fruit. In botany, a fruit is a fertilized and fully grown, ripened ovary. Many foods commonly called vegetables are actually fruit. Eggplants, zucchini, string beans, and bell peppers are all technically fruit because they contain seeds and are derived from the thick ovary tissue. Acorns and winged maple keys, whose scientific name is a samara, are also fruit.

Mature fruit can be described as fleshy or dry. Fleshy fruit include the familiar berries, peaches, apples, grapes, and tomatoes. Rice, wheat, and nuts are examples of dry fruit. Another distinction is that not all fruits are derived from the ovary. Some fruits are derived from separate ovaries in a single flower, such as the raspberry. Other fruits, such as the pineapple, form from clusters of flowers. Additionally, some fruits, like watermelon and orange, have rinds. Regardless of how they are formed, fruits are an agent of dispersal. The variety of shapes and characteristics reflect the mode of dispersal. The light, dry fruits of trees and dandelions are carried by the wind. Floating coconuts are transported by water. Some fruits are colored, perfumed, sweet, and nutritious to attract herbivores, which eat the fruit and disperse the tough undigested seeds in their feces. Other fruits have burs and hooks that cling to fur and hitch rides on animals.

## The Life Cycle of an Angiosperm

The adult, or sporophyte, phase is the main phase in an angiosperm's life cycle. Like gymnosperms, angiosperms are heterosporous. They produce microspores, which develop into pollen grains (the male gametophytes), and megaspores, which form an ovule containing the female gametophytes. Inside the anthers' microsporangia (**Figure 14.26**), male microsporocytes divide by meiosis, generating haploid microspores that undergo mitosis and give rise to pollen grains. Each pollen grain contains two cells: one generative cell that will divide into two sperm, and a second cell that will become the pollen tube cell.

# art CONNECTION



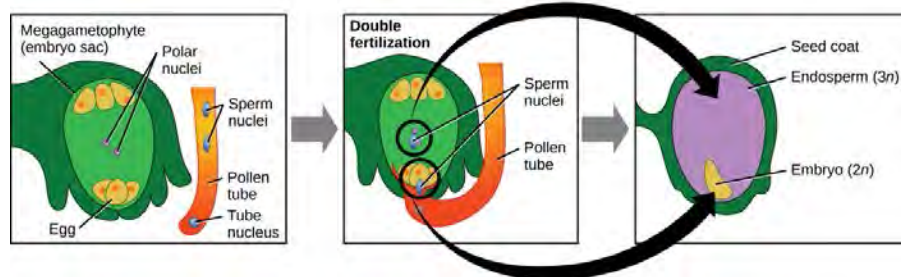
**Figure 14.26** This diagram shows the lifecycle of an angiosperm. Anthers and ovaries are structures that shelter the actual gametophytes: the pollen grain and embryo sac. Double fertilization is a process unique to angiosperms. (credit: modification of work by Mariana Ruiz Villareal)

If a flower lacked a megasporangium, what type of gamete would it not be able to form? If it lacked a microsporangium, what type of gamete would not form?

In the ovules, the female gametophyte is produced when a megasporocyte undergoes meiosis to produce four haploid megaspores. One of these is larger than the others and undergoes mitosis to form the female gametophyte or embryo sac. Three mitotic divisions produce eight nuclei in seven cells. The egg and two cells move to one end of the embryo sac (gametophyte) and three cells move to the other end. Two of the nuclei remain in a single cell and fuse to form a  $2n$  nucleus; this cell moves to the center of the embryo sac.

When a pollen grain reaches the stigma, a pollen tube extends from the grain, grows down the style, and enters through an opening in the integuments of the ovule. The two sperm cells are deposited in the embryo sac.

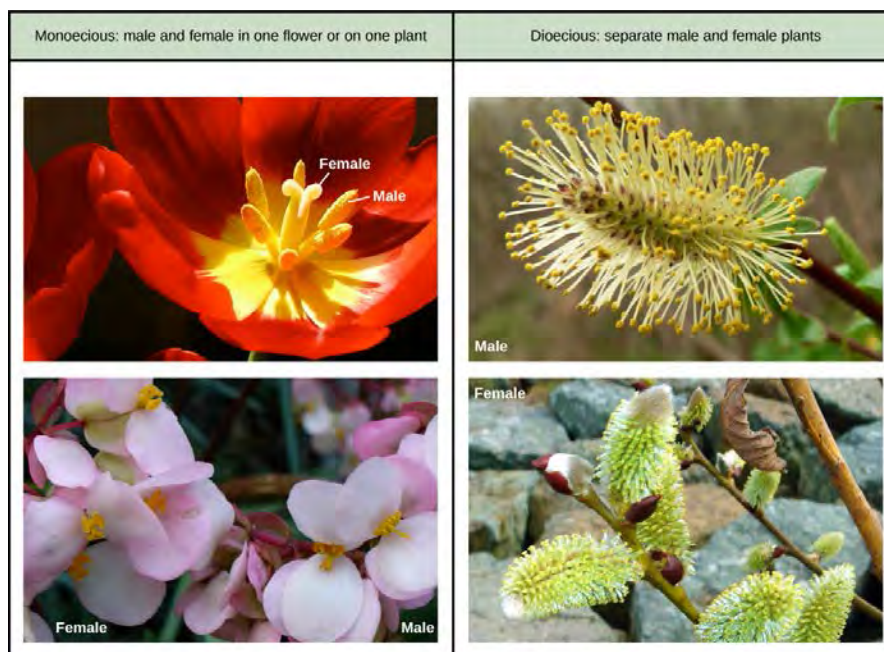
What occurs next is called a double fertilization event (**Figure 14.27**) and is unique to angiosperms. One sperm and the egg combine, forming a diploid zygote—the future embryo. The other sperm fuses with the diploid nucleus in the center of the embryo sac, forming a triploid cell that will develop into the endosperm: a tissue that serves as a food reserve. The zygote develops into an embryo with a radicle, or small root, and one or two leaf-like organs called **cotyledons**. Seed food reserves are stored outside the embryo, and the cotyledons serve as conduits to transmit the broken-down food reserves to the developing embryo. The seed consists of a toughened layer of integuments forming the coat, the endosperm with food reserves and, at the center, the well-protected embryo.



**Figure 14.27** Double fertilization occurs only in angiosperms. (credit: modification of work by Mariana Ruiz Villareal)

Most flowers carry both stamens and carpels; however, a few species self-pollinate. These are known as “perfect” flowers because they contain both types of sex organs (**Figure 14.25**). Biochemical and anatomical barriers to self-pollination promote cross-pollination. Self-pollination is a severe form of inbreeding, and can increase the number of genetic defects in offspring.

A plant may have perfect flowers, and thus have both genders in each flower; or, it may have imperfect flowers of both kinds on one plant (**Figure 14.28**). In each case, such species are called monoecious plants, meaning “one house.” Some botanists refer to plants with perfect flowers simply as hermaphroditic. Some plants are dioecious, meaning “two houses,” and have male and female flowers (“imperfect flowers”) on different plants. In these species, cross-pollination occurs all the time.



**Figure 14.28** Monoecious plants have both male and female reproductive structures on the same flower or plant. In dioecious plants, males and females reproductive structures are on separate plants. (credit a: modification of work by Liz West; credit c: modification of work by Scott Zona)

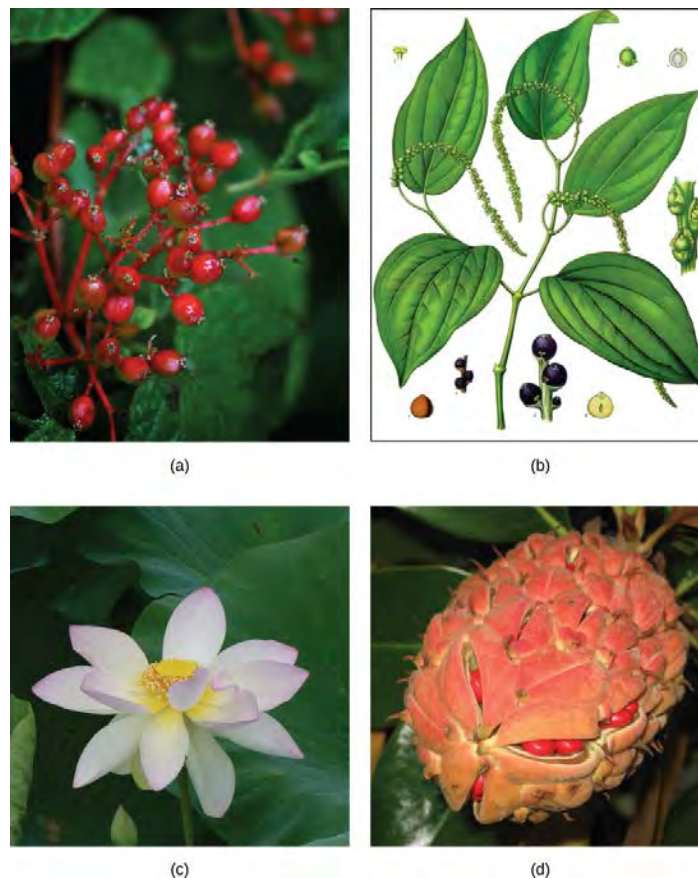
## Diversity of Angiosperms

Angiosperms are classified in a single division, the **Anthophyta**. Modern angiosperms appear to be a monophyletic group, which means that they originate from a single ancestor. Flowering plants are divided into two major groups, according to the structure of the cotyledons, the pollen grains, and other features: **monocots**, which include grasses and lilies, and **eudicots**

or **dicots**, a polyphyletic group. **Basal angiosperms** are a group of plants that are believed to have branched off before the separation into monocots and eudicots because they exhibit traits from both groups. They are categorized separately in many classification schemes, and correspond to a grouping known as the Magnoliidae. The Magnoliidae group is comprised of magnolia trees, laurels, water lilies, and the pepper family.

### Basal Angiosperms

The Magnoliidae are represented by the magnolias: tall trees that bear large, fragrant flowers with many parts, and are considered archaic (**Figure 14.29d**). Laurel trees produce fragrant leaves and small inconspicuous flowers. The Laurales are small trees and shrubs that grow mostly in warmer climates. Familiar plants in this group include the bay laurel, cinnamon, spice bush (**Figure 14.29a**), and the avocado tree. The Nymphaeales are comprised of the water lilies, lotus (**Figure 14.29c**), and similar plants. All species of the Nymphaeales thrive in freshwater biomes, and have leaves that float on the water surface or grow underwater. Water lilies are particularly prized by gardeners, and have graced ponds and pools since antiquity. The Piperales are a group of herbs, shrubs, and small trees that grow in tropical climates. They have small flowers without petals that are tightly arranged in long spikes. Many species are the source of prized fragrances or spices; for example, the berries of *Piper nigrum* (**Figure 14.29b**) are the familiar black pepper that is used to flavor many dishes.



**Figure 14.29** The (a) southern spicebush belongs to the *Laurales*, the same family as cinnamon and bay laurel. The fruit of (b) the *Piper nigrum* plant is black pepper, the main product that was traded along spice routes. Notice the small, unobtrusive clustered flowers. (c) Lotus flowers, *Nelumbo nucifera*, have been cultivated since antiquity for their ornamental value; the root of the lotus flower is eaten as a vegetable. The (d) red berries of a magnolia tree, characteristic of the final stage, are just starting to appear. (credit a: modification of work by Cory Zanker; credit b: modification of work by Franz Eugen Köhler; credit c: modification of work by "berduchwal"/Flickr; credit d: modification of work by "Coastside2"/Wikimedia Commons)

### Monocots

Plants in the monocot group have a single cotyledon in the seedling, and also share other anatomical features. Veins run parallel to the length of the leaves, and flower parts are arranged in a three- or six-fold symmetry. The pollen from the first angiosperms was monosulcate (containing a single furrow or pore through the outer layer). This feature is still seen in the modern monocots. True woody tissue is rarely found in monocots, and the vascular tissue of the stem is not arranged in any particular pattern. The root system is mostly adventitious (unusually positioned) with no major taproot. The monocots include familiar plants such as the true lilies (not to be confused with the water lilies), orchids, grasses, and palms. Many

important crops, such as rice and other cereals (**Figure 14.30a**), corn, sugar cane, and tropical fruit, including bananas and pineapple, belong to the monocots.



**Figure 14.30** The major crops in the world are flowering plants. One staple food, (a) rice, is a monocot, as are other cereals, while (b) beans are eudicots. Some popular flowers, such as this (c) lily are monocots; while others, such as this (d) daisy are eudicots. (credit a: modification of work by David Nance; credit b: modification of work by USDA, ARS; credit c: modification of work by “longhorndave”/Flickr; credit d: modification of work by “Cellulaer”/NinjaPhoto)

### Eudicots

Eudicots, or true dicots, are characterized by the presence of two cotyledons. Veins form a network in leaves. Flower parts come in four, five, or many whorls. Vascular tissue forms a ring in the stem. (In monocots, vascular tissue is scattered in the stem.) Eudicots can be **herbaceous** (like dandelions or violets), or produce woody tissues. Most eudicots produce pollen that is trisulcate or triporate, with three furrows or pores. The root system is usually anchored by one main root developed from the embryonic radicle. Eudicots comprise two-thirds of all flowering plants. Many species seem to exhibit characteristics that belong to either group; therefore, the classification of a plant as a monocot or a eudicot is not always clearly evident (**Table 14.1**).

### Comparison of Structural Characteristics of Monocots and Eudicots

Characteristic	Monocot	Eudicot
Cotyledon	One	Two
Veins in leaves	Parallel	Network ( branched)
Vascular tissue	Scattered	Arranged in ring pattern
Roots	Network of adventitious roots	Tap root with many lateral roots
Pollen	Monosulcate	Trisulcate
Flower parts	Three or multiple of three	Four, five, multiple of four or five and whorls

**Table 14.1**



Explore this **website** (<http://openstaxcollege.org/l/pollinators>) for more information on poillinators.



## KEY TERMS

**anther** a sac-like structure at the tip of the stamen in which pollen grains are produced

**Anthophyta** the division to which angiosperms belong

**apical meristem** the growing point in a vascular plant at the tip of a shoot or root where cell division occurs

**basal angiosperms** a group of plants that probably branched off before the separation of monocots and eudicots

**calyx** the whorl of sepals

**carpel** the female reproductive part of a flower consisting of the stigma, style, and ovary

**club moss** the earliest group of seedless vascular plants

**cone** the ovulate strobilus on gymnosperms that contains ovules

**conifer** the dominant division of gymnosperms with the most variety of species

**corolla** the collection of petals

**cotyledon** the one (monocot) or two (dicot) primitive leaves present in a seed

**cycad** a division of gymnosperms that grow in tropical climates and resemble palm trees

**dicot** a group of angiosperms whose embryos possess two cotyledons; also known as eudicot

**diplontic** describes a life cycle in which the diploid stage is the dominant stage

**eudicots** a group of angiosperms whose embryos possess two cotyledons; also known as dicot

**fern** a seedless vascular plant that produces large fronds; the most advanced group of seedless vascular plants

**filament** the thin stalk that links the anther to the base of the flower

**gametangium** (plural: gametangia) the structure within which gametes are produced

**gametophyte** the haploid plant that produces gametes

**gingkophyte** a division of gymnosperm with one living species, the *Ginkgo biloba*, a tree with fan-shaped leaves

**gnetophyte** a division of gymnosperms with varied morphological features that produce vessel elements in their woody tissues

**gymnosperm** a seed plant with naked seeds (seeds exposed on modified leaves or in cones)

**gynoecium** the group of structures that constitute the female reproductive organ; also called the pistil

**haplodiplontic** describes a life cycle in which the haploid and diploid stages alternate; also known as an alternation of generations life cycle

**haplontic** describes a life cycle in which the haploid stage is the dominant stage

**herbaceous** describes a plant without woody tissue

**heterosporous** having two kinds of spores that give rise to male and female gametophytes

**homosporous** having one kind of spore that gives rise to gametophytes that give rise to both male and female gametes

**hornwort** a group of non-vascular plants in which stomata appear

**horsetail** a seedless vascular plant characterized by a jointed stem

**liverwort** the most primitive group of non-vascular plants

**megasporocyte** a megaspore mother cell; larger spore that germinates into a female gametophyte in a heterosporous plant

**microsporocyte** smaller spore that produces a male gametophyte in a heterosporous plant

**monocot** a related group of angiosperms that produce embryos with one cotyledon and pollen with a single ridge

**moss** a group of plants in which a primitive conductive system appears

**nonvascular plant** a plant that lacks vascular tissue formed of specialized cells for the transport of water and nutrients

**ovary** the chamber that contains and protects the ovule or female megasporangium

**petal** a modified leaf interior to the sepal; colorful petals attract animal pollinator

**phloem** the vascular tissue responsible for transport of sugars, proteins, and other solutes

**pistil** the group of structures that constitute the female reproductive organ; also called the carpel

**sepal** a modified leaf that encloses the bud; outermost structure of a flower

**sporangium** (plural: sporangia) the organ within which spores are produced

**sporophyll** a leaf modified structurally to bear sporangia

**sporophyte** the diploid plant that produces spores

**stamen** the group of structures that contain the male reproductive organs

**stigma** uppermost structure of the carpel where pollen is deposited

**strobili** cone-like structures that contain the sporangia

**style** the long thin structure that links the stigma to the ovary

**syngamy** the union of two gametes in fertilization

**vascular plant** a plant in which there is a network of cells that conduct water and solutes through the organism

**whisk fern** a seedless vascular plant that lost roots and leaves by evolutionary reduction

**xylem** the vascular tissue responsible for long-distance transport of water and nutrients

## CHAPTER SUMMARY

### 14.1 The Plant Kingdom

Land plants evolved traits that made it possible to colonize land and survive out of water. Adaptations to life on land include vascular tissues, roots, leaves, waxy cuticles, and a tough outer layer that protects the spores. Land plants include nonvascular plants and vascular plants. Vascular plants, which include seedless plants and plants with seeds, have apical meristems, and embryos with nutritional stores. All land plants share the following characteristics: alternation of generations, with the haploid plant called a gametophyte and the diploid plant called a sporophyte; formation of haploid spores in a sporangium; and formation of gametes in a gametangium.

### 14.2 Seedless Plants

Seedless nonvascular plants are small. The dominant stage of the life cycle is the gametophyte. Without a vascular system and roots, they absorb water and nutrients through all of their exposed surfaces. There are three main groups: the liverworts, the hornworts, and the mosses. They are collectively known as bryophytes.

Vascular systems consist of xylem tissue, which transports water and minerals, and phloem tissue, which transports sugars and proteins. With the vascular system, there appeared leaves—large photosynthetic organs—and roots to absorb water from the ground. The seedless vascular plants include club mosses, which are the most primitive; whisk ferns, which lost leaves and roots by reductive evolution; horsetails, and ferns.

### 14.3 Seed Plants: Gymnosperms

Gymnosperms are heterosporous seed plants that produce naked seeds. They appeared in the Carboniferous period (359–299 million years ago) and were the dominant plant life during the Mesozoic era (251–65.5 million years ago). Modern-day gymnosperms belong to four divisions. The division Coniferophyta—the conifers—are the predominant woody plants at high altitudes and latitudes. Cycads resemble palm trees and grow in tropical climates. *Ginkgo biloba* is the only species of the division Ginkgophyta. The last division, the Gnetophytes, is a diverse group of species that produce vessel elements in their wood.

### 14.4 Seed Plants: Angiosperms

Angiosperms are the dominant form of plant life in most terrestrial ecosystems, comprising about 90 percent of all plant species. Most crop and ornamental plants are angiosperms. Their success results, in part, from two innovative structures: the flower and the fruit. Flowers are derived evolutionarily from modified leaves. The main parts of a flower are the sepals and petals, which protect the reproductive parts: the stamens and the carpels. The stamens produce the male gametes, which are pollen grains. The carpels contain the female gametes, which are the eggs inside ovaries. The walls of the ovary thicken after fertilization, ripening into fruit that can facilitate seed dispersal.

Angiosperms' life cycles are dominated by the sporophyte stage. Double fertilization is an event unique to angiosperms. The flowering plants are divided into two main groups—the monocots and eudicots—according to the number of cotyledons in the seedlings. Basal angiosperms belong to a lineage older than monocots and eudicots.

## ART CONNECTION QUESTIONS

- Figure 14.19** At what stage does the diploid zygote form?
  - When the female cone begins to bud from the tree
  - When the sperm nucleus and the egg nucleus fuse
  - When the seeds drop from the tree
  - When the pollen tube begins to grow
- Figure 14.26** If a flower lacked a megasporangium, what type of gamete would it not be able to form? If it lacked a microsporangium, what type of gamete would not form?

## REVIEW QUESTIONS

- The land plants are probably descendants of which of these groups?
  - green algae
  - red algae
  - brown algae
  - angiosperms
- The event that leads from the haploid stage to the diploid stage in alternation of generations is \_\_\_\_\_.
  - meiosis
  - mitosis
  - fertilization
  - germination
- Moss is an example of which type of plant?
  - haplontic plant
  - vascular plant
  - diplontic plant
  - seed plant
- Why do mosses grow well in the Arctic tundra?
  - They grow better at cold temperatures.
  - They do not require moisture.
  - They do not have true roots and can grow on hard surfaces.
  - There are no herbivores in the tundra.
- Which is the most diverse group of seedless vascular plants?
  - the liverworts
  - the horsetails
  - the club mosses
  - the ferns
- Which group are vascular plants?
  - liverworts
  - mosses
  - hornworts
  - ferns

- 9.** Which of the following traits characterizes gymnosperms?
- The plants carry exposed seeds on modified leaves.
  - Reproductive structures are located in a flower.
  - After fertilization, the ovary thickens and forms a fruit.
  - The gametophyte is longest phase of the life cycle.
- 10.** What adaptation do seed plants have in addition to the seed that is not found in seedless plants?
- gametophytes
  - vascular tissue
  - pollen
  - chlorophyll
- 11.** Pollen grains develop in which structure?
- the anther
  - the stigma
  - the filament
  - the carpel
- 12.** Corn develops from a seedling with a single cotyledon, displays parallel veins on its leaves, and produces monosulcate pollen. It is most likely:
- a gymnosperm
  - a monocot
  - a eudicot
  - a basal angiosperm

## CRITICAL THINKING QUESTIONS

- 13.** What adaptations do plants have that allow them to survive on land?
- 14.** What are the three classes of bryophytes?
- 15.** How did the development of a vascular system contribute to the increase in size of plants?
- 16.** What are the four modern-day groups of gymnosperms?
- 17.** Cycads are considered endangered species and their trade is severely restricted. Customs officials stop suspected smugglers, who claim that the plants in their possession are palm trees and not cycads. How would a botanist distinguish between the two types of plants?
- 18.** What are the two structures that allow angiosperms to be the dominant form of plant life in most terrestrial ecosystems?

# 15 | DIVERSITY OF ANIMALS



**Figure 15.1** The leaf chameleon (*Brookesia micra*) was discovered in northern Madagascar in 2012. At just over one inch long, it is the smallest known chameleon. (credit: modification of work by Frank Glaw, et al., PLOS)

## Chapter Outline

- 15.1: Features of the Animal Kingdom**
- 15.2: Sponges and Cnidarians**
- 15.3: Flatworms, Nematodes, and Arthropods**
- 15.4: Mollusks and Annelids**
- 15.5: Echinoderms and Chordates**
- 15.6: Vertebrates**

## Introduction

While we can easily identify dogs, lizards, fish, spiders, and worms as animals, other animals, such as corals and sponges, might be easily mistaken as plants or some other form of life. Yet scientists have recognized a set of common characteristics shared by all animals, including sponges, jellyfish, sea urchins, and humans.

The kingdom Animalia is a group of multicellular Eukarya. Animal evolution began in the ocean over 600 million years ago, with tiny creatures that probably do not resemble any living organism today. Since then, animals have evolved into a highly diverse kingdom. Although over one million currently living species of animals have been identified, scientists are continually discovering more species. The number of described living animal species is estimated to be about 1.4 million,<sup>[1]</sup> and there may be as many as 6.8 million.

Understanding and classifying the variety of living species helps us to better understand how to conserve and benefit from this diversity. The animal classification system characterizes animals based on their anatomy, features of embryological development, and genetic makeup. Scientists are faced with the task of classifying animals within a system of taxonomy that reflects their evolutionary history. Additionally, they must identify traits that are common to all animals as well as traits that can be used to distinguish among related groups of animals. However, animals vary in the complexity of their organization

1. "Number of Living Species in Australia and the World," A.D. Chapman, Australia Biodiversity Information Services, last modified August 26, 2010, <http://www.environment.gov.au/biodiversity/abrs/publications/other/species-numbers/2009/03-exec-summary.html>.

and exhibit a huge diversity of body forms, so the classification scheme is constantly changing as new information about species is learned.

## 15.1 | Features of the Animal Kingdom

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

- List the features that distinguish the animal kingdom from other kingdoms
- Explain the processes of animal reproduction and embryonic development
- Describe the hierarchy of basic animal classification
- Compare and contrast the embryonic development of protostomes and deuterostomes

Even though members of the animal kingdom are incredibly diverse, animals share common features that distinguish them from organisms in other kingdoms. All animals are eukaryotic, multicellular organisms, and almost all animals have specialized tissues. Most animals are motile, at least during certain life stages. Animals require a source of food to grow and develop. All animals are heterotrophic, ingesting living or dead organic matter. This form of obtaining energy distinguishes them from autotrophic organisms, such as most plants, which make their own nutrients through photosynthesis and from fungi that digest their food externally. Animals may be carnivores, herbivores, omnivores, or parasites (**Figure 15.2**). Most animals reproduce sexually: The offspring pass through a series of developmental stages that establish a determined body plan, unlike plants, for example, in which the exact shape of the body is indeterminate. The **body plan** refers to the shape of an animal.



**Figure 15.2** All animals that derive energy from food are heterotrophs. The (a) black bear is an omnivore, eating both plants and animals. The (b) heartworm *Dirofilaria immitis* is a parasite that derives energy from its hosts. It spends its larval stage in mosquitos and its adult stage infesting the hearts of dogs and other mammals, as shown here. (credit a: modification of work by USDA Forest Service; credit b: modification of work by Clyde Robinson)

### Complex Tissue Structure

A hallmark trait of animals is specialized structures that are differentiated to perform unique functions. As multicellular organisms, most animals develop specialized cells that group together into tissues with specialized functions. A tissue is a collection of similar cells that had a common embryonic origin. There are four main types of animal tissues: nervous, muscle, connective, and epithelial. Nervous tissue contains neurons, or nerve cells, which transmit nerve impulses. Muscle tissue contracts to cause all types of body movement from locomotion of the organism to movements within the body itself. Animals also have specialized connective tissues that provide many functions, including transport and structural support. Examples of connective tissues include blood and bone. Connective tissue is comprised of cells separated by extracellular material made of organic and inorganic materials, such as the protein and mineral deposits of bone. Epithelial tissue covers the internal and external surfaces of organs inside the animal body and the external surface of the body of the organism.



View this [video \(http://openstaxcollege.org/l/saving\\_life2\)](http://openstaxcollege.org/l/saving_life2) to watch a presentation by biologist E.O. Wilson on the importance of animal diversity.

## Animal Reproduction and Development

Most animals have diploid body (somatic) cells and a small number of haploid reproductive (gamete) cells produced through meiosis. Some exceptions exist: For example, in bees, wasps, and ants, the male is haploid because it develops from an unfertilized egg. Most animals undergo sexual reproduction, while many also have mechanisms of asexual reproduction.

### *Sexual Reproduction and Embryonic Development*

Almost all animal species are capable of reproducing sexually; for many, this is the only mode of reproduction possible. This distinguishes animals from fungi, protists, and bacteria, where asexual reproduction is common or exclusive. During sexual reproduction, the male and female gametes of a species combine in a process called fertilization. Typically, the small, motile male sperm travels to the much larger, sessile female egg. Sperm form is diverse and includes cells with flagella or amoeboid cells to facilitate motility. Fertilization and fusion of the gamete nuclei produce a zygote. Fertilization may be internal, especially in land animals, or external, as is common in many aquatic species.

After fertilization, a developmental sequence ensues as cells divide and differentiate. Many of the events in development are shared in groups of related animal species, and these events are one of the main ways scientists classify high-level groups of animals. During development, animal cells specialize and form tissues, determining their future morphology and physiology. In many animals, such as mammals, the young resemble the adult. Other animals, such as some insects and amphibians, undergo complete metamorphosis in which individuals enter one or more larval stages. For these animals, the young and the adult have different diets and sometimes habitats. In other species, a process of incomplete metamorphosis occurs in which the young somewhat resemble the adults and go through a series of stages separated by molts (shedding of the skin) until they reach the final adult form.

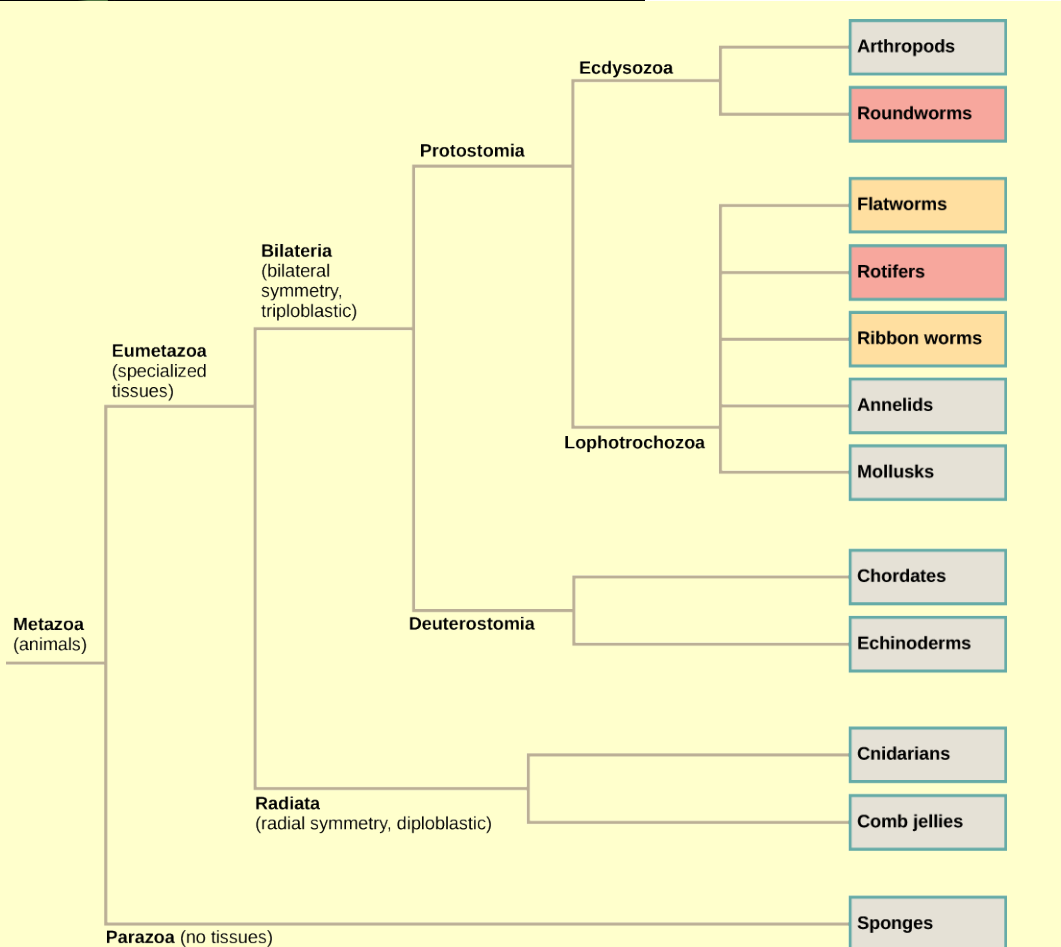
### *Asexual Reproduction*

Asexual reproduction, unlike sexual reproduction, produces offspring genetically identical to each other and to the parent. A number of animal species—especially those without backbones, but even some fish, amphibians, and reptiles—are capable of asexual reproduction. Asexual reproduction, except for occasional identical twinning, is absent in birds and mammals. The most common forms of asexual reproduction for stationary aquatic animals include budding and fragmentation, in which part of a parent individual can separate and grow into a new individual. In contrast, a form of asexual reproduction found in certain invertebrates and rare vertebrates is called parthenogenesis (or “virgin beginning”), in which unfertilized eggs develop into new offspring.

## Classification Features of Animals

Animals are classified according to morphological and developmental characteristics, such as a body plan. With the exception of sponges, the animal body plan is symmetrical. This means that their distribution of body parts is balanced along an axis. Additional characteristics that contribute to animal classification include the number of tissue layers formed during development, the presence or absence of an internal body cavity, and other features of embryological development.

# art CONNECTION



**Figure 15.3** The phylogenetic tree of animals is based on morphological, fossil, and genetic evidence.

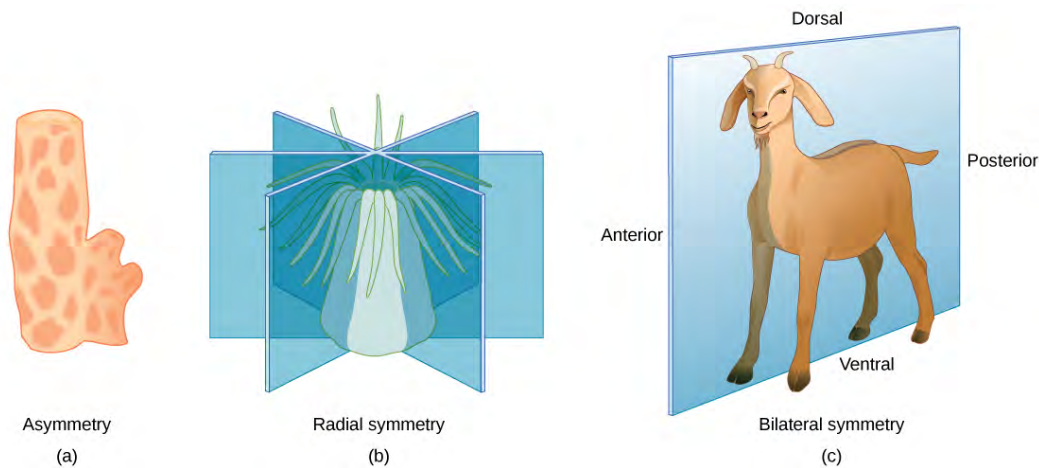
Which of the following statements is false?

- Eumetazoa have specialized tissues and Parazoa do not.
- Both acoelomates and pseudocoelomates have a body cavity.
- Chordates are more closely related to echinoderms than to rotifers according to the figure.
- Some animals have radial symmetry, and some animals have bilateral symmetry.

## Body Symmetry

Animals may be asymmetrical, radial, or bilateral in form (**Figure 15.4**). **Asymmetrical** animals are animals with no pattern or symmetry; an example of an asymmetrical animal is a sponge (**Figure 15.4a**). An organism with **radial symmetry** (**Figure 15.4b**) has a longitudinal (up-and-down) orientation: Any plane cut along this up-down axis produces roughly mirror-image halves. An example of an organism with radial symmetry is a sea anemone.





**Figure 15.4** Animals exhibit different types of body symmetry. The (a) sponge is asymmetrical and has no planes of symmetry, the (b) sea anemone has radial symmetry with multiple planes of symmetry, and the (c) goat has bilateral symmetry with one plane of symmetry.

**Bilateral symmetry** is illustrated in **Figure 15.4c** using a goat. The goat also has upper and lower sides to it, but they are not symmetrical. A vertical plane cut from front to back separates the animal into roughly mirror-image right and left sides. Animals with bilateral symmetry also have a “head” and “tail” (anterior versus posterior) and a back and underside (dorsal versus ventral).

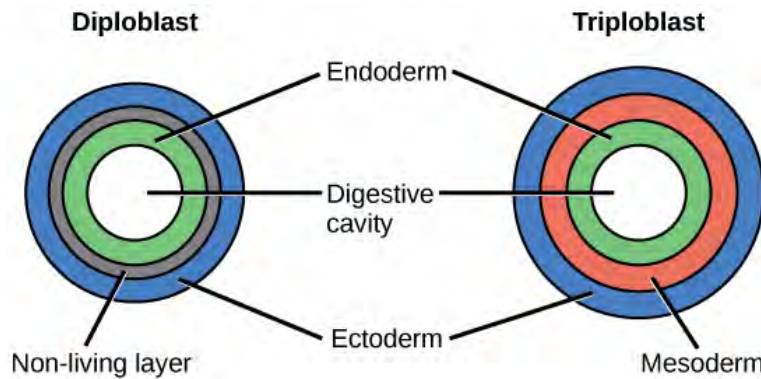
CONCEPT in ACTION



Watch this **video** (<http://openstaxcollege.org/l/symmetry2>) to see a quick sketch of the different types of body symmetry.

### Layers of Tissues

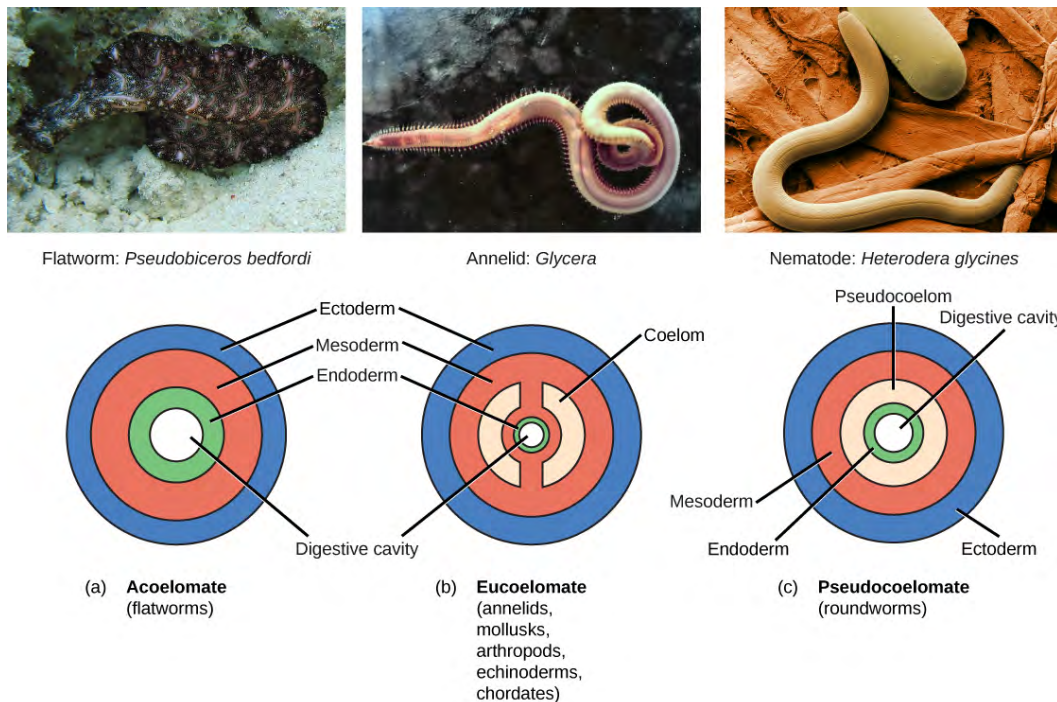
Most animal species undergo a layering of early tissues during embryonic development. These layers are called **germ layers**. Each layer develops into a specific set of tissues and organs. Animals develop either two or three embryonic germ layers (**Figure 15.5**). The animals that display radial symmetry develop two germ layers, an inner layer (endoderm) and an outer layer (ectoderm). These animals are called **diploblasts**. Animals with bilateral symmetry develop three germ layers: an inner layer (endoderm), an outer layer (ectoderm), and a middle layer (mesoderm). Animals with three germ layers are called **triploblasts**.



**Figure 15.5** During embryogenesis, diploblasts develop two embryonic germ layers: an ectoderm and an endoderm. Triploblasts develop a third layer—the mesoderm—between the endoderm and ectoderm.

### Presence or Absence of a Coelom

Triploblasts may develop an internal body cavity derived from mesoderm, called a **coelom** (pr. see-LŌM). This epithelial-lined cavity is a space, usually filled with fluid, which lies between the digestive system and the body wall. It houses organs such as the kidneys and spleen, and contains the circulatory system. Triploblasts that do not develop a coelom are called **acoelomates**, and their mesoderm region is completely filled with tissue, although they have a gut cavity. Examples of acoelomates include the flatworms. Animals with a true coelom are called **eucoelomates** (or coelomates) (Figure 15.6). A true coelom arises entirely within the mesoderm germ layer. Animals such as earthworms, snails, insects, starfish, and vertebrates are all eucoelomates. A third group of triploblasts has a body cavity that is derived partly from mesoderm and partly from endoderm tissue. These animals are called **pseudocoelomates**. Roundworms are examples of pseudocoelomates. New data on the relationships of pseudocoelomates suggest that these phyla are not closely related and so the evolution of the pseudocoelom must have occurred more than once (Figure 15.3). True coelomates can be further characterized based on features of their early embryological development.

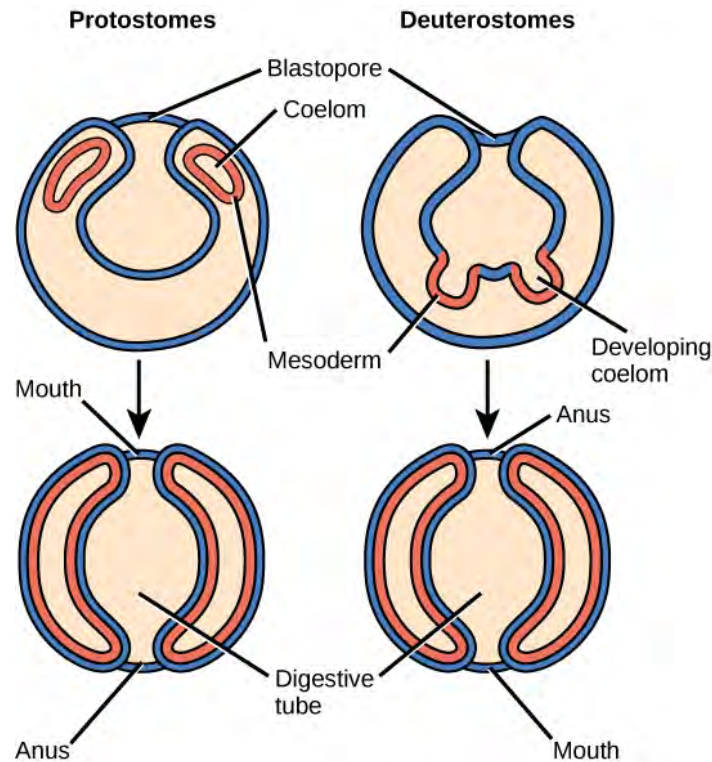


**Figure 15.6** Triploblasts may be acoelomates, eucoelomates, or pseudocoelomates. Eucoelomates have a body cavity within the mesoderm, called a coelom, which is lined with mesoderm tissue. Pseudocoelomates have a similar body cavity, but it is lined with mesoderm and endoderm tissue. (credit a: modification of work by Jan Derk; credit b: modification of work by NOAA; credit c: modification of work by USDA, ARS)

### Protostomes and Deuterostomes

Bilaterally symmetrical, triploblastic eucoelomates can be divided into two groups based on differences in their early embryonic development. **Protostomes** include phyla such as arthropods, mollusks, and annelids. **Deuterostomes** include

the chordates and echinoderms. These two groups are named from which opening of the digestive cavity develops first: mouth or anus. The word *protostome* comes from Greek words meaning “mouth first,” and *deuterostome* originates from words meaning “mouth second” (in this case, the anus develops first). This difference reflects the fate of a structure called the blastopore (Figure 15.7), which becomes the mouth in protostomes and the anus in deuterostomes. Other developmental characteristics differ between protostomes and deuterostomes, including the mode of formation of the coelom and the early cell division of the embryo.



**Figure 15.7** Eucoelomates can be divided into two groups, protostomes and deuterostomes, based on their early embryonic development. Two of these differences include the origin of the mouth opening and the way in which the coelom is formed.

## 15.2 | Sponges and Cnidarians

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

- Describe the organizational features of the simplest animals
- Describe the organizational features of cnidarians

The kingdom of animals is informally divided into invertebrate animals, those without a backbone, and vertebrate animals, those with a backbone. Although in general we are most familiar with vertebrate animals, the vast majority of animal species, about 95 percent, are invertebrates. Invertebrates include a huge diversity of animals, millions of species in about 32 phyla, which we can just begin to touch on here.

The sponges and the cnidarians represent the simplest of animals. Sponges appear to represent an early stage of multicellularity in the animal clade. Although they have specialized cells for particular functions, they lack true tissues in which specialized cells are organized into functional groups. Sponges are similar to what might have been the ancestor of animals: colonial, flagellated protists. The cnidarians, or the jellyfish and their kin, are the simplest animal group that displays true tissues, although they possess only two tissue layers.

### Sponges

Animals in subkingdom Parazoa represent the simplest animals and include the sponges, or phylum **Porifera** (Figure 15.8). All sponges are aquatic and the majority of species are marine. Sponges live in intimate contact with water, which plays a

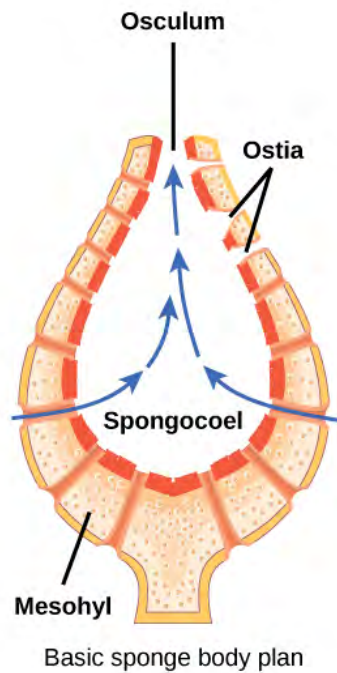
role in their feeding, gas exchange, and excretion. Much of the body structure of the sponge is dedicated to moving water through the body so it can filter out food, absorb dissolved oxygen, and eliminate wastes.



**Figure 15.8** Sponges are members of the phylum Porifera, which contains the simplest animals. (credit: Andrew Turner)

The body of the simplest sponges takes the shape of a cylinder with a large central cavity, the **spongocoel**. Water enters the spongocoel from numerous pores in the body wall. Water flows out through a large opening called the **osculum** (**Figure 15.9**). However, sponges exhibit a diversity of body forms, which vary in the size and branching of the spongocoel, the number of osculi, and where the cells that filter food from the water are located.

Sponges consist of an outer layer of flattened cells and an inner layer of cells called choanocytes separated by a jelly-like substance called **mesohyl**. The mesohyl contains embedded amoeboid cells that secrete tiny needles called **spicules** or protein fibers that help give the sponge its structural strength. The cell body of the **choanocyte** is embedded in mesohyl but protruding into the spongocoel is a mesh-like collar surrounding a single flagellum. The beating of flagella from all choanocytes moves water through the sponge. Food particles are trapped in mucus produced by the sieve-like collar of the choanocytes and are ingested by phagocytosis. This process is called **intracellular digestion**. **Amoebocytes** take up nutrients repackaged in food vacuoles of the choanocytes and deliver them to other cells within the sponge.



**Figure 15.9** The sponge's basic body plan is shown.

### Physiological Processes in Sponges

Despite their lack of complexity, sponges are clearly successful organisms, having persisted on Earth for more than half a billion years. Lacking a true digestive system, sponges depend on the intracellular digestive processes of their choanocytes for their energy intake. The limit of this type of digestion is that food particles must be smaller than individual cells. Gas exchange, circulation, and excretion occur by diffusion between cells and the water.

Sponges reproduce both sexually and asexually. Asexual reproduction is either by **fragmentation** (in which a piece of the sponge breaks off and develops into a new individual), or **budding** (an outgrowth from the parent that eventually detaches). A type of asexual reproduction found only in freshwater sponges occurs through the formation of **gemmules**, clusters of cells surrounded by a tough outer layer. Gemmules survive hostile environments and can attach to a substrate and grow into a new sponge.

Sponges are **monoecious** (or hermaphroditic), meaning one individual can produce both eggs and sperm. Sponges may be sequentially hermaphroditic, producing eggs first and sperm later. Eggs arise from amoebocytes and are retained within the spongocoel, whereas sperm arise from choanocytes and are ejected through the osculum. Sperm carried by water currents fertilize the eggs of other sponges. Early larval development occurs within the sponge, and free-swimming larvae are then released through the osculum. This is the only time that sponges exhibit mobility. Sponges are sessile as adults and spend their lives attached to a fixed substrate.

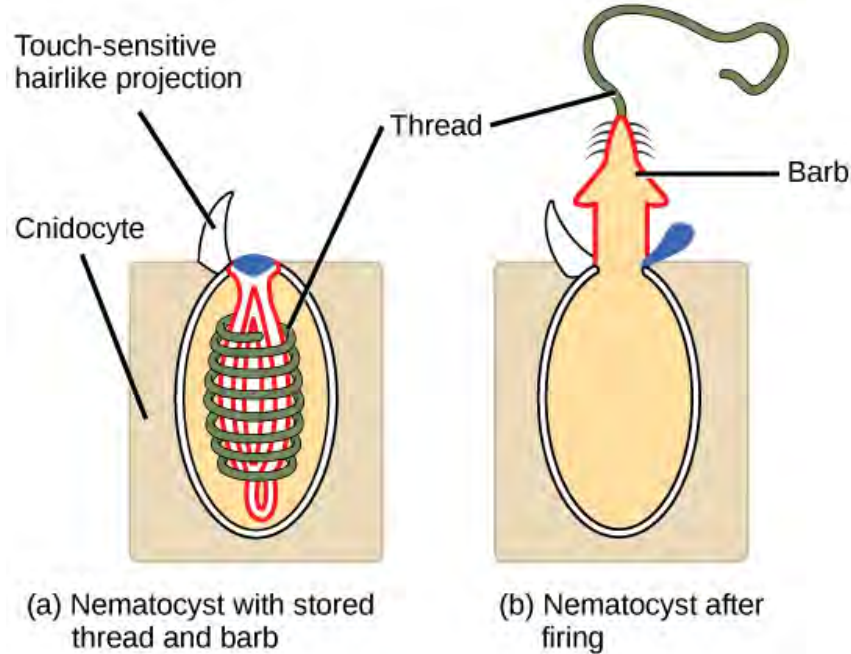


Watch this **video** ([http://openstaxcollege.org/l/sponge\\_feed](http://openstaxcollege.org/l/sponge_feed)) that demonstrates the feeding of sponges.

## Cnidarians

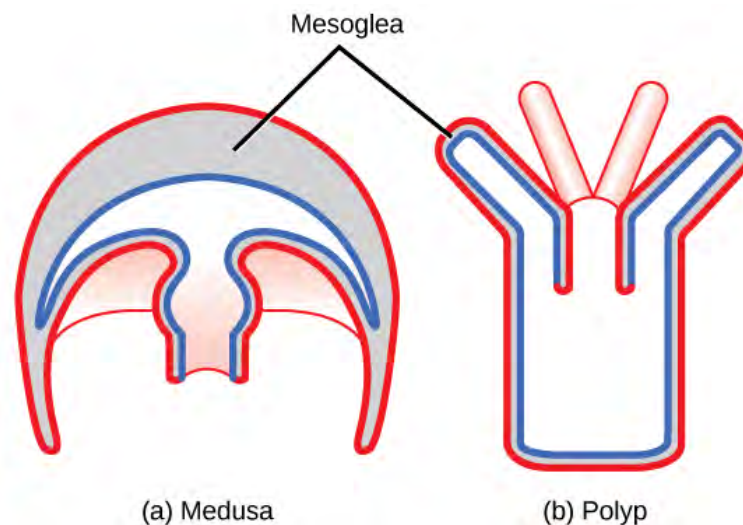
The phylum **Cnidaria** includes animals that show radial or biradial symmetry and are diploblastic. Nearly all (about 99 percent) cnidarians are marine species. Cnidarians have specialized cells known as **cnidocytes** (“stinging cells”) containing organelles called **nematocysts**. These cells are concentrated around the mouth and tentacles of the animal and

can immobilize prey with toxins. Nematocysts contain coiled threads that may bear barbs. The outer wall of the cell has a hairlike projection that is sensitive to touch. When touched, the cells fire the toxin-containing coiled threads that can penetrate and stun the predator or prey (see [Figure 15.10](#)).



**Figure 15.10** Animals from the phylum Cnidaria have stinging cells called cnidocytes. Cnidocytes contain large organelles called (a) nematocysts that store a coiled thread and barb. When hairlike projections on the cell surface are touched, (b) the thread, barb, and a toxin are fired from the organelle.

Cnidarians display two distinct body plans: **polyp** or “stalk” and **medusa** or “bell” ([Figure 15.11](#)). Examples of the polyp form are freshwater species of the genus *Hydra*; perhaps the best-known medusoid animals are the jellies (jellyfish). Polyps are sessile as adults, with a single opening to the digestive system (the mouth) facing up with tentacles surrounding it. Medusae are motile, with the mouth and tentacles hanging from the bell-shaped body. In other cnidarians, both a polyp and medusa form exist, and the life cycle alternates between these forms.



**Figure 15.11** Cnidarians have two distinct body plans, the (a) medusa and the (b) polyp. All cnidarians have two tissue layers, with a jelly-like mesoglea between them.

### Physiological Processes of Cnidarians

All cnidarians have two tissue layers. The outer layer is called the **epidermis**, whereas the inner layer is called the **gastrodermis** and lines the digestive cavity. Between these two layers is a non-living, jelly-like **mesoglea**. There are

differentiated cell types in each tissue layer, such as nerve cells, enzyme-secreting cells, and nutrient-absorbing cells, as well as intercellular connections between the cells. However, organs and organ systems are not present in this phylum.

The nervous system is primitive, with nerve cells scattered across the body in a network. The function of the nerve cells is to carry signals from sensory cells and to contractile cells. Groups of cells in the nerve net form nerve cords that may be essential for more rapid transmission. Cnidarians perform **extracellular digestion**, with digestion completed by intracellular digestive processes. Food is taken into the **gastrovascular cavity**, enzymes are secreted into the cavity, and the cells lining the cavity absorb the nutrient products of the extracellular digestive process. The gastrovascular cavity has only one opening that serves as both a mouth and an anus (an incomplete digestive system). Like the sponges, Cnidarian cells exchange oxygen, carbon dioxide, and nitrogenous wastes by diffusion between cells in the epidermis and gastrodermis with water.

### **Cnidarian Diversity**

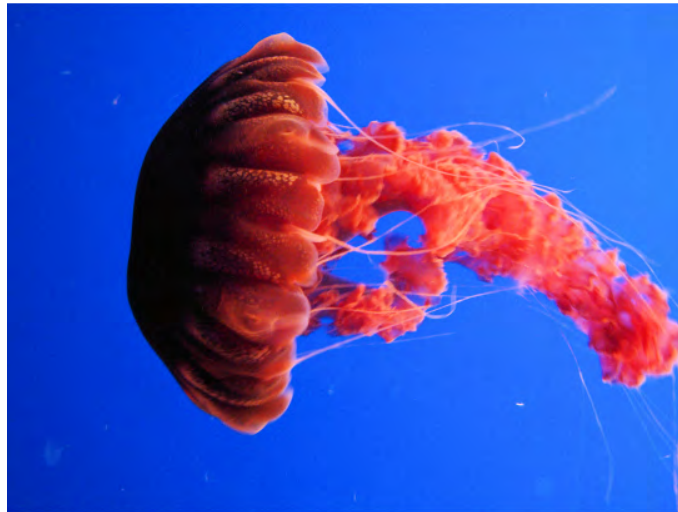
The phylum Cnidaria contains about 10,000 described species divided into four classes: Anthozoa, Scyphozoa, Cubozoa, and Hydrozoa.

The class Anthozoa includes all cnidarians that exhibit a sessile polyp body plan only; in other words, there is no medusa stage within their life cycle. Examples include sea anemones, sea pens, and corals, with an estimated number of 6,100 described species. Sea anemones are usually brightly colored and can attain a size of 1.8 to 10 cm in diameter. These animals are usually cylindrical in shape and are attached to a substrate. A mouth opening is surrounded by tentacles bearing cnidocytes (**Figure 15.12**).



**Figure 15.12** Sea anemones are cnidarians of class Anthozoa. (credit: "Dancing With Ghosts"/Flickr)

Scyphozoans include all the jellies and are motile and exclusively marine with about 200 described species. The medusa is the dominant stage in the life cycle, although there is also a polyp stage. Species range from 2 cm in length to the largest scyphozoan species, *Cyanea capillata*, at 2 m across. Jellies display a characteristic bell-like body shape (**Figure 15.13**).



**Figure 15.13** Scyphozoans include the jellies. (credit: "Jimg944"/Flickr)



Identify the life cycle stages of jellies using this **video animation game** ([http://openstaxcollege.org/l/amazing\\_jelly2](http://openstaxcollege.org/l/amazing_jelly2)) from the New England Aquarium.

The class Cubozoa includes jellies that are square in cross-section and so are known as “box jellyfish.” These species may achieve sizes of 15–25 cm. Cubozoans are anatomically similar to the jellyfish. A prominent difference between the two classes is the arrangement of tentacles. Cubozoans have muscular pads called pedalia at the corners of the square bell canopy, with one or more tentacles attached to each pedalium. In some cases, the digestive system may extend into the pedalia. Cubozoans typically exist in a polyp form that develops from a larva. The polyps may bud to form more polyps and then transform into the medusoid forms.

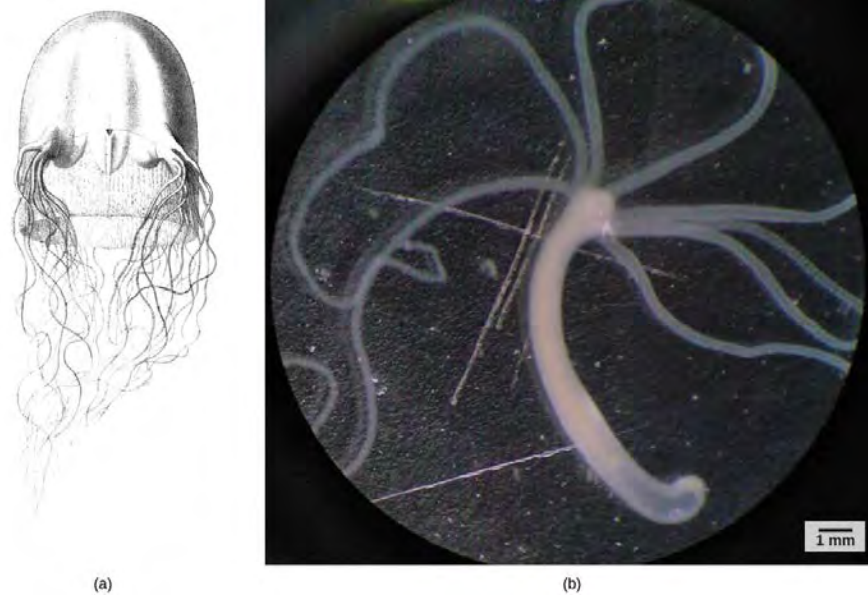


Watch this **video** ([http://openstaxcollege.org/l/box\\_jellyfish](http://openstaxcollege.org/l/box_jellyfish)) to learn more about the deadly toxins of the box jellyfish.

Hydrozoa includes nearly 3,500 species,<sup>[2]</sup> most of which are marine. Most species in this class have both polyp and medusa forms in their life cycle. Many hydrozoans form colonies composed of branches of specialized polyps that share a gastrovascular cavity. Colonies may also be free-floating and contain both medusa and polyp individuals in the colony, as in the Portuguese Man O’War (*Physalia*) or By-the-Wind Sailor (*Verella*). Other species are solitary polyps or solitary medusae. The characteristic shared by all of these species is that their gonads are derived from epidermal tissue, whereas in all other cnidarians, they are derived from gastrodermal tissue (**Figure 15.14ab**).

2. “The Hydrozoa Directory,” Peter Schuchert, Muséum Genève, last updated November 2012, <http://www.ville-ge.ch/mhng/hydrozoa/hydrozoa-directory.htm>.





**Figure 15.14** A (a) box jelly is an example from class Cubozoa. The (b) hydra is from class Hydrozoa. (credit b: scale-bar data from Matt Russell)

## 15.3 | Flatworms, Nematodes, and Arthropods

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

- Describe the structure and systems of flatworms
- Describe the structural organization of nematodes
- Compare the internal systems and the appendage specialization of arthropods

The animal phyla of this and subsequent modules are triploblastic and have an embryonic mesoderm sandwiched between the ectoderm and endoderm. These phyla are also bilaterally symmetrical, meaning that a longitudinal section will divide them into right and left sides that are mirror images of each other. Associated with bilateralism is the beginning of cephalization, the evolution of a concentration of nervous tissues and sensory organs in the head of the organism, which is where the organism first encounters its environment.

The flatworms are acoelomate organisms that include free-living and parasitic forms. The nematodes, or roundworms, possess a pseudocoelom and consist of both free-living and parasitic forms. Finally, the arthropods, one of the most successful taxonomic groups on the planet, are coelomate organisms with a hard exoskeleton and jointed appendages. The nematodes and the arthropods belong to a clade with a common ancestor, called Ecdysozoa. The name comes from the word *ecdysis*, which refers to the periodic shedding, or molting, of the exoskeleton. The ecdysozoan phyla have a hard cuticle covering their bodies that must be periodically shed and replaced for them to increase in size.

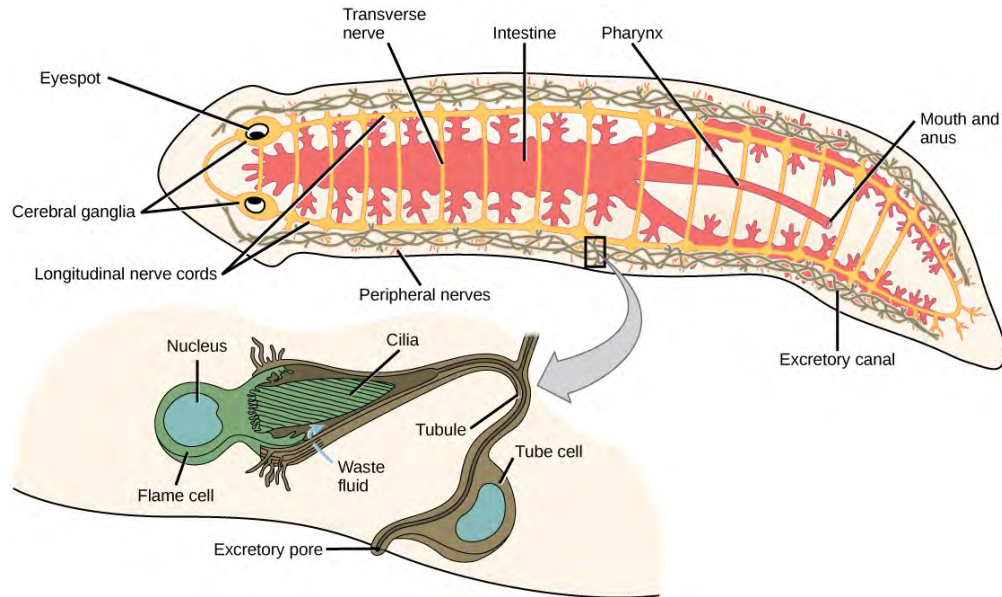
### Flatworms

The relationships among flatworms, or phylum Platyhelminthes, is being revised and the description here will follow the traditional groupings. Most flatworms are parasitic, including important parasites of humans. Flatworms have three embryonic germ layers that give rise to surfaces covering tissues, internal tissues, and the lining of the digestive system. The epidermal tissue is a single layer of cells or a layer of fused cells covering a layer of circular muscle above a layer of longitudinal muscle. The mesodermal tissues include support cells and secretory cells that secrete mucus and other materials to the surface. The flatworms are acoelomate, so their bodies contain no cavities or spaces between the outer surface and the inner digestive tract.

#### *Physiological Processes of Flatworms*

Free-living species of flatworms are predators or scavengers, whereas parasitic forms feed from the tissues of their hosts. Most flatworms have an incomplete digestive system with an opening, the “mouth,” that is also used to expel digestive

system wastes. Some species also have an anal opening. The gut may be a simple sac or highly branched. Digestion is extracellular, with enzymes secreted into the space by cells lining the tract, and digested materials taken into the same cells by phagocytosis. One group, the cestodes, does not have a digestive system, because their parasitic lifestyle and the environment in which they live (suspended within the digestive cavity of their host) allows them to absorb nutrients directly across their body wall. Flatworms have an excretory system with a network of tubules throughout the body that open to the environment and nearby flame cells, whose cilia beat to direct waste fluids concentrated in the tubules out of the body. The system is responsible for regulation of dissolved salts and excretion of nitrogenous wastes. The nervous system consists of a pair of nerve cords running the length of the body with connections between them and a large ganglion or concentration of nerve cells at the anterior end of the worm; here, there may also be a concentration of photosensory and chemosensory cells (**Figure 15.15**).

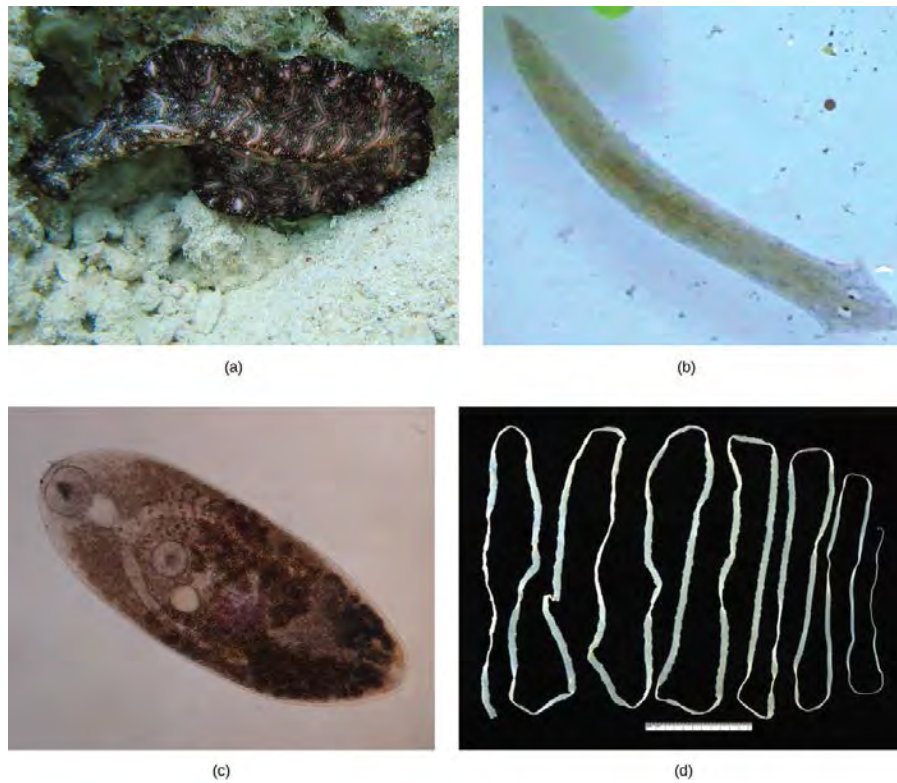


**Figure 15.15** This planarian is a free-living flatworm that has an incomplete digestive system, an excretory system with a network of tubules throughout the body, and a nervous system made up of nerve cords running the length of the body with a concentration of nerves and photosensory and chemosensory cells at the anterior end.

Since there is no circulatory or respiratory system, gas and nutrient exchange is dependent on diffusion and intercellular junctions. This necessarily limits the thickness of the body in these organisms, constraining them to be “flat” worms. Most flatworm species are monoecious (hermaphroditic, possessing both sets of sex organs), and fertilization is typically internal. Asexual reproduction is common in some groups in which an entire organism can be regenerated from just a part of itself.

### Diversity of Flatworms

Flatworms are traditionally divided into four classes: Turbellaria, Monogenea, Trematoda, and Cestoda (**Figure 15.16**). The turbellarians include mainly free-living marine species, although some species live in freshwater or moist terrestrial environments. The simple planarians found in freshwater ponds and aquaria are examples. The epidermal layer of the underside of turbellarians is ciliated, and this helps them move. Some turbellarians are capable of remarkable feats of regeneration in which they may regrow the body, even from a small fragment.



**Figure 15.16** Phylum Platyhelminthes is divided into four classes: (a) Bedford's Flatworm (*Pseudobiceros bedfordi*) and the (b) planarian belong to class Turbellaria; (c) the Trematoda class includes about 20,000 species, most of which are parasitic; (d) class Cestoda includes tapeworms such as this *Taenia saginata*; and the parasitic class Monogenea (not shown). (credit a: modification of work by Jan Derk; credit c: modification of work by "Sahaquiel9102"/Wikimedia Commons; credit d: modification of work by CDC)

The monogeneans are external parasites mostly of fish with life cycles consisting of a free-swimming larva that attaches to a fish to begin transformation to the parasitic adult form. They have only one host during their life, typically of just one species. The worms may produce enzymes that digest the host tissues or graze on surface mucus and skin particles. Most monogeneans are hermaphroditic, but the sperm develop first, and it is typical for them to mate between individuals and not to self-fertilize.

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

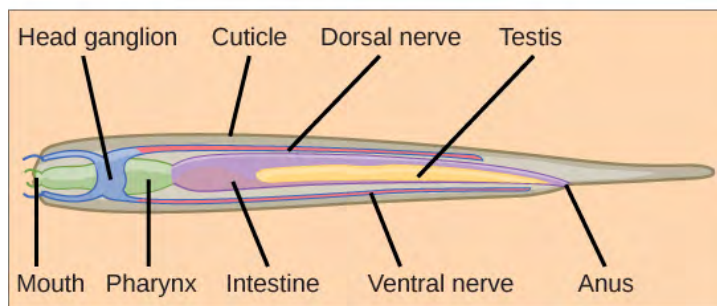
The cestodes, or tapeworms, are also internal parasites, mainly of vertebrates. Tapeworms live in the intestinal tract of the primary host and remain fixed using a sucker on the anterior end, or scolex, of the tapeworm body. The remaining body of the tapeworm is made up of a long series of units called proglottids, each of which may contain an excretory system with flame cells, but will contain reproductive structures, both male and female. Tapeworms do not have a digestive system, they absorb nutrients from the food matter passing them in the host's intestine. Proglottids are produced at the scolex and are pushed to the end of the tapeworm as new proglottids form, at which point, they are "mature" and all structures except fertilized eggs have degenerated. Most reproduction occurs by cross-fertilization. The proglottid detaches and is released in the feces of the host. The fertilized eggs are eaten by an intermediate host. The juvenile worms emerge and infect the intermediate host, taking up residence, usually in muscle tissue. When the muscle tissue is eaten by the primary host, the cycle is completed. There are several tapeworm parasites of humans that are acquired by eating uncooked or poorly cooked pork, beef, and fish.

## Nematodes

The phylum **Nematoda**, or roundworms, includes more than 28,000 species with an estimated 16,000 parasitic species. The name Nematoda is derived from the Greek word “nemos,” which means “thread.” Nematodes are present in all habitats and are extremely common, although they are usually not visible (**Figure 15.17**).



(a)



(b)

**Figure 15.17** (a) An scanning electron micrograph of the nematode *Heterodera glycines* and (b) a schematic representation of the anatomy of a nematode are shown. (credit a: modification of work by USDA, ARS; scale-bar data from Matt Russell)

Most nematodes look similar to each other: slender tubes, tapered at each end (**Figure 15.17**). Nematodes are pseudocoelomates and have a **complete digestive system** with a distinct mouth and anus.

The nematode body is encased in a cuticle, a flexible but tough exoskeleton, or external skeleton, which offers protection and support. The cuticle contains a carbohydrate-protein polymer called **chitin**. The cuticle also lines the pharynx and rectum. Although the exoskeleton provides protection, it restricts growth, and therefore must be continually shed and replaced as the animal increases in size.

A nematode's mouth opens at the anterior end with three or six lips and, in some species, teeth in the form of cuticular extensions. There may also be a sharp stylet that can protrude from the mouth to stab prey or pierce plant or animal cells. The mouth leads to a muscular pharynx and intestine, leading to the rectum and anal opening at the posterior end.

### Physiological Processes of Nematodes

In nematodes, the excretory system is not specialized. Nitrogenous wastes are removed by diffusion. In marine nematodes, regulation of water and salt is achieved by specialized glands that remove unwanted ions while maintaining internal body fluid concentrations.

Most nematodes have four nerve cords that run along the length of the body on the top, bottom, and sides. The nerve cords fuse in a ring around the pharynx, to form a head ganglion or “brain” of the worm, as well as at the posterior end to form the tail ganglion. Beneath the epidermis lies a layer of longitudinal muscles that permits only side-to-side, wave-like undulation of the body.



View this [video \(http://openstaxcollege.org/l/nematode\)](http://openstaxcollege.org/l/nematode) to see nematodes move about and feed on bacteria.

Nematodes employ a diversity of sexual reproductive strategies depending on the species; they may be monoecious, **dioecious** (separate sexes), or may reproduce asexually by parthenogenesis. *Caenorhabditis elegans* is nearly unique among animals in having both self-fertilizing hermaphrodites and a male sex that can mate with the hermaphrodite.

### Arthropoda

The name “arthropoda” means “jointed legs,” which aptly describes each of the enormous number of species belonging to this phylum. **Arthropoda** dominate the animal kingdom with an estimated 85 percent of known species, with many still undiscovered or undescribed. The principal characteristics of all the animals in this phylum are functional segmentation of the body and the presence of jointed appendages (**Figure 15.18**). As members of Ecdysozoa, arthropods also have an exoskeleton made principally of chitin. Arthropoda is the largest phylum in the animal world in terms of numbers of species, and insects form the single largest group within this phylum. Arthropods are true coelomate animals and exhibit prostostomic development.

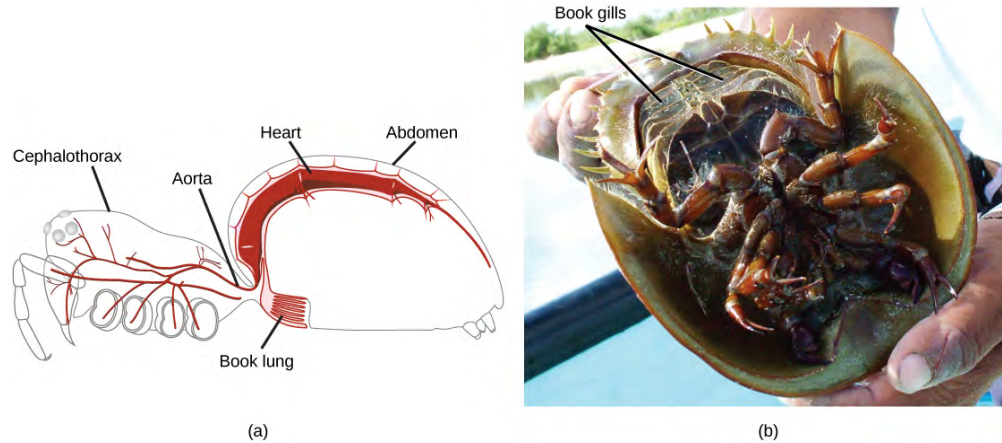


**Figure 15.18** Trilobites, like the one in this fossil, are an extinct group of arthropods. (credit: Kevin Walsh)

### Physiological Processes of Arthropods

A unique feature of arthropods is the presence of a segmented body with fusion of certain sets of segments to give rise to functional segments. Fused segments may form a head, thorax, and abdomen, or a cephalothorax and abdomen, or a head and trunk. The coelom takes the form of a **hemocoel** (or blood cavity). The open circulatory system, in which blood bathes the internal organs rather than circulating in vessels, is regulated by a two-chambered heart. Respiratory systems vary, depending on the group of arthropod: Insects and myriapods use a series of tubes ( **tracheae**) that branch throughout the body, open to the outside through openings called **spiracles**, and perform gas exchange directly between the cells and

air in the tracheae. Aquatic crustaceans use gills, arachnids employ “book lungs,” and aquatic chelicerates use “book gills.” The book lungs of arachnids are internal stacks of alternating air pockets and hemocoel tissue shaped like the pages of a book. The book gills of crustaceans are external structures similar to book lungs with stacks of leaf-like structures that exchange gases with the surrounding water (**Figure 15.19**).

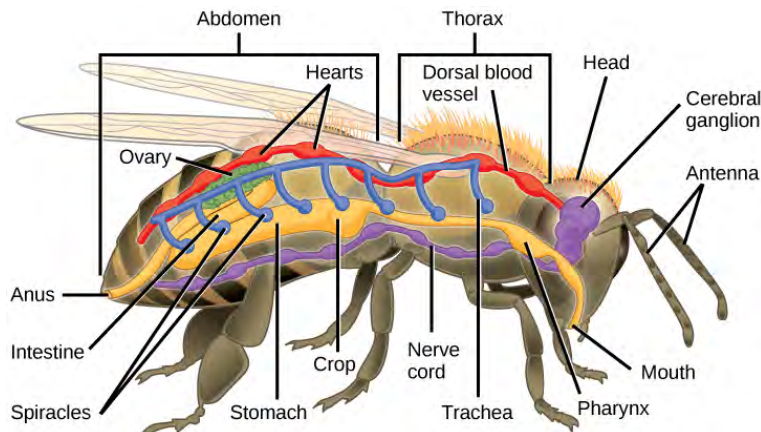


**Figure 15.19** The book lungs of (a) arachnids are made up of alternating air pockets and hemocoel tissue shaped like a stack of books. The book gills of (b) crustaceans are similar to book lungs but are external so that gas exchange can occur with the surrounding water. (credit a: modification of work by Ryan Wilson based on original work by John Henry Comstock; credit b: modification of work by Angel Schatz)

### Arthropod Diversity

Phylum Arthropoda includes animals that have been successful in colonizing terrestrial, aquatic, and aerial habitats. The phylum is further classified into five subphyla: Trilobitomorpha (trilobites), Hexapoda (insects and relatives), Myriapoda (millipedes, centipedes, and relatives), Crustacea (crabs, lobsters, crayfish, isopods, barnacles, and some zooplankton), and Chelicerata (horseshoe crabs, arachnids, scorpions, and daddy longlegs). Trilobites are an extinct group of arthropods found from the Cambrian period (540–490 million years ago) until they became extinct in the Permian (300–251 million years ago) that are probably most closely related to the Chelicerata. The 17,000 described species have been identified from fossils (**Figure 15.18**).

The Hexapoda have six legs (three pairs) as their name suggests. Hexapod segments are fused into a head, thorax, and abdomen (**Figure 15.20**). The thorax bears the wings and three pairs of legs. The insects we encounter on a daily basis—such as ants, cockroaches, butterflies, and bees—are examples of Hexapoda.



**Figure 15.20** In this basic anatomy of a hexapod, note that insects have a developed digestive system (yellow), a respiratory system (blue), a circulatory system (red), and a nervous system (purple).

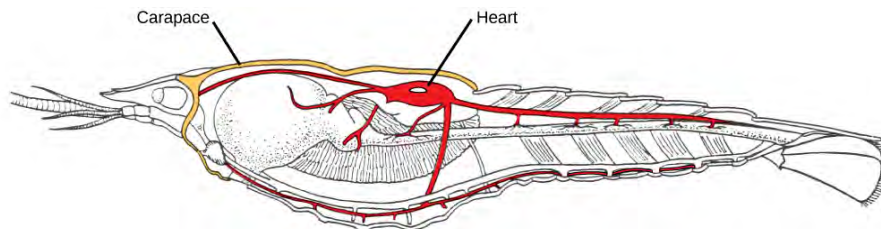
Subphylum Myriapoda includes arthropods with legs that may vary in number from 10 to 750. This subphylum includes 13,000 species; the most commonly found examples are millipedes and centipedes. All myriapods are terrestrial animals and prefer a humid environment (**Figure 15.21**).



**Figure 15.21** (a) The centipede *Scutigera coleoptrata* has up to 15 pairs of legs. (b) This North American millipede (*Narceus americanus*) bears many legs, although not one thousand, as its name might suggest. (credit a: modification of work by Bruce Marlin; credit b: modification of work by Cory Zanker)

Crustaceans, such as shrimp, lobsters, crabs, and crayfish, are the dominant aquatic arthropods. A few crustaceans are terrestrial species like the pill bugs or sow bugs. The number of described crustacean species stands at about 47,000.<sup>[3]</sup>

Although the basic body plan in crustaceans is similar to the Hexapoda—head, thorax, and abdomen—the head and thorax may be fused in some species to form a **cephalothorax**, which is covered by a plate called the carapace (**Figure 15.22**). The exoskeleton of many species is also infused with calcium carbonate, which makes it even stronger than in other arthropods. Crustaceans have an open circulatory system in which blood is pumped into the hemocoel by the dorsal heart. Most crustaceans typically have separate sexes, but some, like barnacles, may be hermaphroditic. Serial hermaphroditism, in which the gonad can switch from producing sperm to ova, is also found in some crustacean species. Larval stages are seen in the early development of many crustaceans. Most crustaceans are carnivorous, but detritivores and filter feeders are also common.



**Figure 15.22** The crayfish is an example of a crustacean. It has a carapace around the cephalothorax and the heart in the dorsal thorax area. (credit: Jane Whitney)

Subphylum Chelicerata includes animals such as spiders, scorpions, horseshoe crabs, and sea spiders. This subphylum is predominantly terrestrial, although some marine species also exist. An estimated 103,000<sup>[4]</sup> described species are included in subphylum Chelicerata.

The body of chelicerates may be divided into two parts and a distinct “head” is not always discernible. The phylum derives its name from the first pair of appendages: the **chelicerae** (**Figure 15.23a**), which are specialized mouthparts. The chelicerae are mostly used for feeding, but in spiders, they are typically modified to inject venom into their prey (**Figure 15.23b**). As in other members of Arthropoda, chelicerates also utilize an open circulatory system, with a tube-like heart that pumps blood into the large hemocoel that bathes the internal organs. Aquatic chelicerates utilize gill respiration, whereas terrestrial species use either tracheae or book lungs for gaseous exchange.

3. “Number of Living Species in Australia and the World,” A.D. Chapman, Australia Biodiversity Information Services, last modified August 26, 2010, <http://www.environment.gov.au/biodiversity/abrs/publications/other/species-numbers/2009/03-exec-summary.html>.

4. “Number of Living Species in Australia and the World,” A.D. Chapman, Australia Biodiversity Information Services, last modified August 26, 2010, <http://www.environment.gov.au/biodiversity/abrs/publications/other/species-numbers/2009/03-exec-summary.html>.



**Figure 15.23** (a) The chelicerae (first set of appendages) are well developed in the Chelicerata, which includes scorpions (a) and spiders (b). (credit a: modification of work by Kevin Walsh; credit b: modification of work by Marshal Hedin)



Click through (<http://openstaxcollege.org/l/arthropod2>) this lesson on arthropods to explore interactive habitat maps and more.

## 15.4 | Mollusks and Annelids

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

- Describe the unique anatomical features of mollusks
- Describe the features of an animal classified in phylum Annelida

The mollusks are a diverse group (85,000 described species) of mostly marine species. They have a variety of forms, ranging from large predatory squid and octopus, some of which show a high degree of intelligence, to small grazing forms with elaborately sculpted and colored shells. The annelids traditionally include the oligochaetes, which include the earthworms and leeches, the polychaetes, which are a marine group, and two other smaller classes.

The phyla Mollusca and Annelida belong to a clade called the **Lophotrochozoa**, which also includes the phylum Nemertea, or ribbon worms (**Figure 15.3**). They are distinct from the Ecdysozoa (nematodes and arthropods) based on evidence from analysis of their DNA, which has changed our views of the relationships among invertebrates.

### Phylum Mollusca

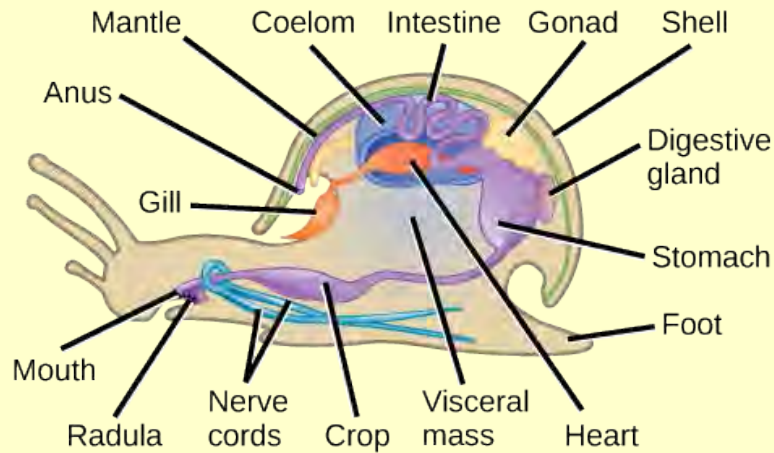
**Mollusca** is the predominant phylum in marine environments, where it is estimated that 23 percent of all known marine species belong to this phylum. It is the second most diverse phylum of animals with over 75,000 described species. The name “mollusca” signifies a soft body, as the earliest descriptions of mollusks came from observations of unshelled, soft-bodied cuttlefish (squid relatives). Although mollusk body forms vary, they share key characteristics, such as a ventral, muscular foot that is typically used for locomotion; the visceral mass, which contains most of the internal organs of the animal; and a dorsal mantle, which is a flap of tissue over the visceral mass that creates a space called the mantle cavity. The mantle may or may not secrete a shell of calcium carbonate. In addition, many mollusks have a scraping structure at the mouth, called a **radula** (**Figure 15.24**).

The muscular foot varies in shape and function, depending on the type of mollusk (described below in the section on mollusk diversity). It is a retractable as well as extendable organ, used for locomotion and anchorage. Mollusks are



eucoelomates, but the coelomic cavity is restricted to a cavity around the heart in adult animals. The mantle cavity, formed inside the **mantle**, develops independently of the coelomic cavity. It is a multi-purpose space, housing the gills, the anus, organs for sensing food particles in the water, and an outlet for gametes. Most mollusks have an open circulatory system with a heart that circulates the hemolymph in open spaces around the organs. The octopuses and squid are an exception to this and have a closed circulatory system with two hearts that move blood through the gills and a third, systemic heart that pumps blood through the rest of the body.

## art CONNECTION



**Figure 15.24** There are many species and variations of mollusks; the gastropod mollusk anatomy is shown here, which shares many characteristics common with other groups.

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

- Mollusks have a radula for scraping food.
- Mollusks have ventral nerve cords.
- The tissue beneath the shell is called the mantle.
- The mantle cavity contains hemolymph.

### Mollusk Diversity

This phylum is comprised of seven classes: Aplacophora, Monoplacophora, Polyplacophora, Bivalvia, Gastropoda, Cephalopoda, and Scaphopoda.

Class Aplacophora (“bearing no plates”) includes worm-like animals living mostly on deep ocean bottoms. These animals lack a shell but have aragonite spicules on their skin. Members of class Monoplacophora (“bearing one plate”) have a single, cap-like shell enclosing the body. The monoplacophorans were believed extinct and only known as fossils until the discovery of *Neopilina galathea* in 1952. Today, scientists have identified nearly two dozen living species.

Animals in the class Polyplacophora (“bearing many plates”) are commonly known as “chitons” and bear an armor-like, eight-plated shell (**Figure 15.25**). These animals have a broad, ventral foot that is adapted for attachment to rocks and a mantle that extends beyond the shell in the form of a girdle. They breathe with **ctenidia** (gills) present ventrally. These animals have a radula modified for scraping. A single pair of nephridia for excretion is present.



**Figure 15.25** This chiton from the class Polyplacophora has the eight-plated shell indicative of its class. (credit: Jerry Kirkhart)

Class Bivalvia (“two shells”) includes clams, oysters, mussels, scallops, and geoducks. They are found in marine and freshwater habitats. As the name suggests, bivalves are enclosed in a pair of shells (or valves) that are hinged at the dorsal side. The body is flattened on the sides. They feed by filtering particles from water and a radula is absent. They exchange gases using a pair of ctenidia, and excretion and osmoregulation are carried out by a pair of nephridia. In some species, the posterior edges of the mantle may fuse to form two siphons that inhale and exhale water. Some bivalves like oysters and mussels have the unique ability to secrete and deposit a calcareous **nacre** or “mother of pearl” around foreign particles that enter the mantle cavity. This property is commercially exploited to produce pearls.



Watch animations of **clams** (<http://openstaxcollege.org/l/clams2>) and **mussels** (<http://openstaxcollege.org/l/mussels2>) feeding to understand more about bivalves.

Gastropods (“stomach foot”) include well-known mollusks like snails, slugs, conchs, sea hares, and sea butterflies. Gastropods include shell-bearing species as well as species with a reduced shell. These animals are asymmetrical and usually present a coiled shell (**Figure 15.26**).

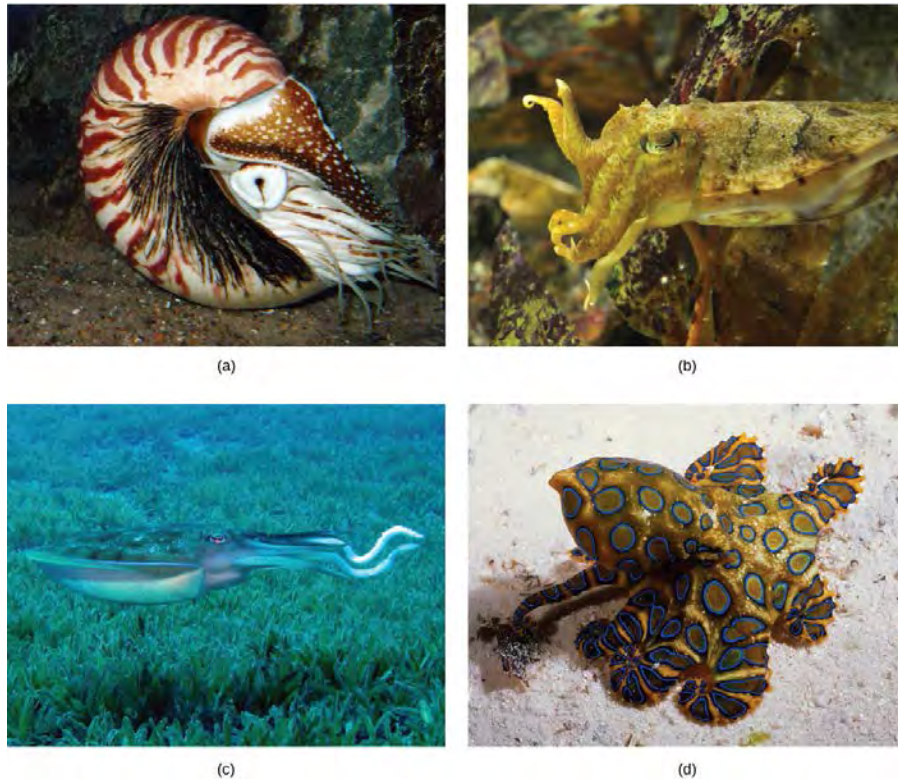


**Figure 15.26** (a) Like many gastropods, this snail has a stomach foot and a coiled shell. (b) This slug, which is also a gastropod, lacks a shell. (credit a: modification of work by Murray Stevenson; credit b: modification of work by Rosendahl)

The visceral mass in the shelled species is characteristically twisted and the foot is modified for crawling. Most gastropods bear a head with tentacles that support eyes. A complex radula is used to scrape food particles from the substrate. The mantle cavity encloses the ctenidia as well as a pair of nephridia.

The class Cephalopoda (“head foot” animals) includes octopuses, squids, cuttlefish, and nautilus. Cephalopods include shelled and reduced-shell groups. They display vivid coloration, typically seen in squids and octopuses, which is used for camouflage. The ability of some octopuses to rapidly adjust their colors to mimic a background pattern or to startle a predator is one of the more awe-inspiring feats of these animals. All animals in this class are predators and have beak-like jaws. All cephalopods have a well-developed nervous system, complex eyes, and a closed circulatory system. The foot is lobed and developed into tentacles and a funnel, which is used for locomotion. Suckers are present on the tentacles in octopuses and squid. Ctenidia are enclosed in a large mantle cavity and are serviced by large blood vessels, each with its own heart.

Cephalopods (**Figure 15.27**) are able to move quickly via jet propulsion by contracting the mantle cavity to forcefully eject a stream of water. Cephalopods have separate sexes, and the females of some species care for the eggs for an extended period of time. Although the shell is much reduced and internal in squid and cuttlefish, and absent altogether in octopus, nautilus live inside a spiral, multi-chambered shell that is filled with gas or water to regulate buoyancy.



**Figure 15.27** The (a) nautilus, (b) giant cuttlefish, (c) reef squid, and (d) blue-ring octopus are all members of the class Cephalopoda. (credit a: modification of work by J. Baecker; credit b: modification of work by Adrian Mohedano; credit c: modification of work by Silke Baron; credit d: modification of work by Angell Williams)

Members of the class Scaphopoda (“boat feet”) are known colloquially as “tusk shells” or “tooth shells.” Tooth shells are open at both ends and usually lie buried in sand with the front opening exposed to water and the reduced head end projecting from the back of the shell. Tooth shells have a radula and a foot modified into tentacles, each with a bulbous end that catches and manipulates prey (**Figure 15.28**).



**Figure 15.28** *Antalis vulgaris* shows the classic Dentaliidae shape that gives these animals their common name of “tusk shell.” (credit: Georges Jansoone)

## Annelida

Phylum **Annelida** are segmented worms found in marine, terrestrial, and freshwater habitats, but the presence of water or humidity is a critical factor for their survival in terrestrial habitats. The name of the phylum is derived from the Latin word

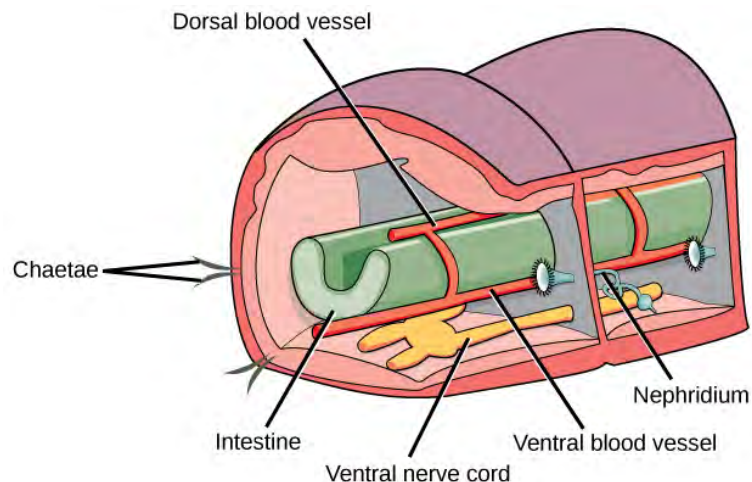
*annellus*, which means a small ring. Approximately 16,500 species have been described. The phylum includes earthworms, polychaete worms, and leeches. Like mollusks, annelids exhibit protostomic development.

Annelids are bilaterally symmetrical and have a worm-like appearance. Their particular segmented body plan results in repetition of internal and external features in each body segment. This type of body plan is called **metamerism**. The evolutionary benefit of such a body plan is thought to be the capacity it allows for the evolution of independent modifications in different segments that perform different functions. The overall body can then be divided into head, body, and tail.

## Physiological Processes of Annelida

The skin of annelids is protected by a cuticle that is thinner than the cuticle of the ecdysozoans and does not need to be molted for growth. Chitinous hairlike extensions, anchored in the skin and projecting from the cuticle, called **chaetae**, are present in every segment in most groups. The chaetae are a defining character of annelids. Polychaete worms have paired, unjointed limbs called parapodia on each segment used for locomotion and breathing. Beneath the cuticle there are two layers of muscle, one running around its circumference (circular) and one running the length of the worm (longitudinal). Annelids have a true coelom in which organs are distributed and bathed in coelomic fluid. Annelids possess a well-developed complete digestive system with specialized organs: mouth, muscular pharynx, esophagus, and crop. A cross-sectional view of a body segment of an earthworm is shown in **Figure 15.29**; each segment is limited by a membrane that divides the body cavity into compartments.

Annelids have a closed circulatory system with muscular pumping “hearts” in the anterior segments, dorsal and ventral blood vessels that run the length of the body with connections in each segment, and capillaries that service individual tissues. Gas exchange occurs across the moist body surface. Excretion is carried out by pairs of primitive “kidneys” called metanephridia that consist of a convoluted tubule and an open, ciliated funnel present in every segment. Annelids have a well-developed nervous system with two ventral nerve cords and a nerve ring of fused ganglia present around the pharynx.



**Figure 15.29** In this schematic showing the basic anatomy of annelids, the digestive system is indicated in green, the nervous system is indicated in yellow, and the circulatory system is indicated in red.

Annelids may be either monoecious with permanent gonads (as in earthworms and leeches) or dioecious with temporary or seasonal gonads (as in polychaetes).



This **video and animation** (<http://openstaxcollege.org/l/annelid2>) provides a close-up look at annelid anatomy.

## Annelid Diversity

Phylum Annelida includes the classes Polychaeta and Clitellata (**Figure 15.30**); the latter contains subclasses Oligochaeta, Hirudinoidea, and Branchiobdellida.

Earthworms are the most abundant members of the subclass Oligochaeta, distinguished by the presence of the **clitellum**, a ring structure in the skin that secretes mucus to bind mating individuals and forms a protective cocoon for the eggs. They also have a few, reduced chaetae (oligo- = “few”; -chaetae = “hairs”). The number and size of chaetae is greatly diminished in oligochaetes as compared to the polychaetes (poly- = “many”; -chaetae = “hairs”). The chaetae of polychaetes are also arranged within fleshy, flat, paired appendages on each segment called parapodia.

The subclass Hirudinoidea includes leeches. Significant differences between leeches and other annelids include the development of suckers at the anterior and posterior ends, and the absence of chaetae. Additionally, the segmentation of the body wall may not correspond to internal segmentation of the coelomic cavity. This adaptation may allow leeches to swell when ingesting blood from host vertebrates. The subclass Branchiobdellida includes about 150 species that show similarity to leeches as well as oligochaetes. All species are obligate symbionts, meaning that they can only survive associated with their host, mainly with freshwater crayfish. They feed on the algae that grows on the carapace of the crayfish.



**Figure 15.30** The (a) earthworm and (b) leech are both annelids. (credit a: modification of work by "schizoform"/Flickr; credit b: modification of work by "Sarah G..."/Flickr)

## 15.5 | Echinoderms and Chordates

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

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

Deuterostomes include the phyla Echinodermata and Chordata (which includes the vertebrates) and two smaller phyla. Deuterostomes share similar patterns of early development.

### Echinoderms

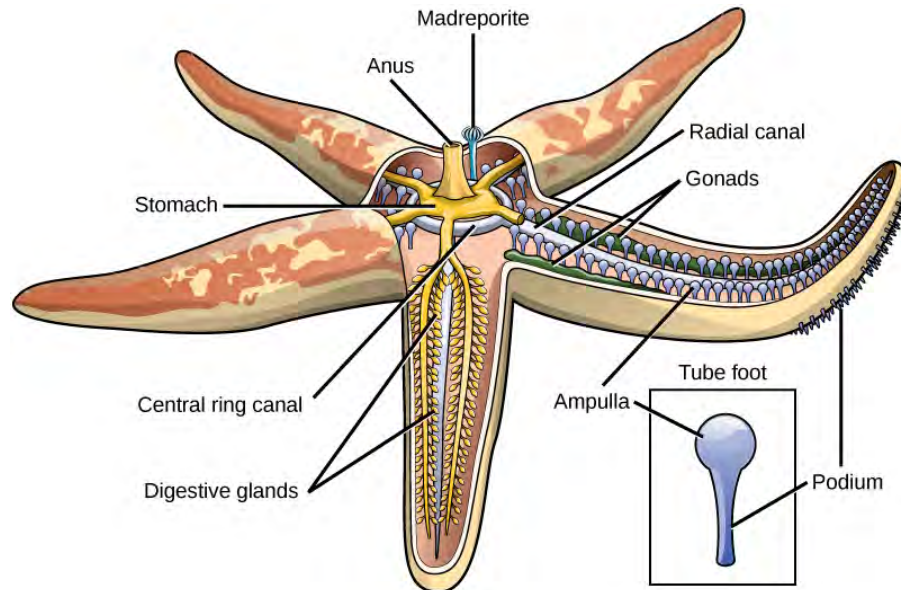
Echinodermata are named for their spiny skin (from the Greek “echinos” meaning “spiny” and “dermos” meaning “skin”). The phylum includes about 7,000<sup>[5]</sup> described living species, such as sea stars, sea cucumbers, sea urchins, sand dollars, and brittle stars. **Echinodermata** are exclusively marine.

Adult echinoderms exhibit pentaradial symmetry and have a calcareous endoskeleton made of ossicles (**Figure 15.31**), although the early larval stages of all echinoderms have bilateral symmetry. The endoskeleton is developed by epidermal cells, which may also possess pigment cells, giving vivid colors to these animals, as well as cells laden with toxins. These animals have a true coelom, a portion of which is modified into a unique circulatory system called a **water vascular system**. An interesting feature of these animals is their power to regenerate, even when over 75 percent of their body mass is lost.

5. “Number of Living Species in Australia and the World,” A.D. Chapman, Australia Biodiversity Information Services, last modified August 26, 2010, <http://www.environment.gov.au/biodiversity/abrs/publications/other/species-numbers/2009/03-exec-summary.html>.

## Physiological Processes of Echinoderms

Echinoderms have a unique system for gas exchange, nutrient circulation, and locomotion called the water vascular system. The system consists of a central ring canal and radial canals extending along each arm. Water circulates through these structures allowing for gas, nutrient, and waste exchange. A structure on top of the body, called the **madreporite**, regulates the amount of water in the water vascular system. “Tube feet,” which protrude through openings in the endoskeleton, may be expanded or contracted using the hydrostatic pressure in the system. The system allows for slow movement, but a great deal of power, as witnessed when the tube feet latch on to opposite halves of a bivalve mollusk, like a clam, and slowly, but surely pull the shells apart, exposing the flesh within.



**Figure 15.31** This diagram shows the anatomy of a sea star.

The echinoderm nervous system has a nerve ring at the center and five radial nerves extending outward along the arms. There is no centralized nervous control. Echinoderms have separate sexes and release their gametes into the water where fertilization takes place. Echinoderms may also reproduce asexually through regeneration from body parts.

## Echinoderm Diversity

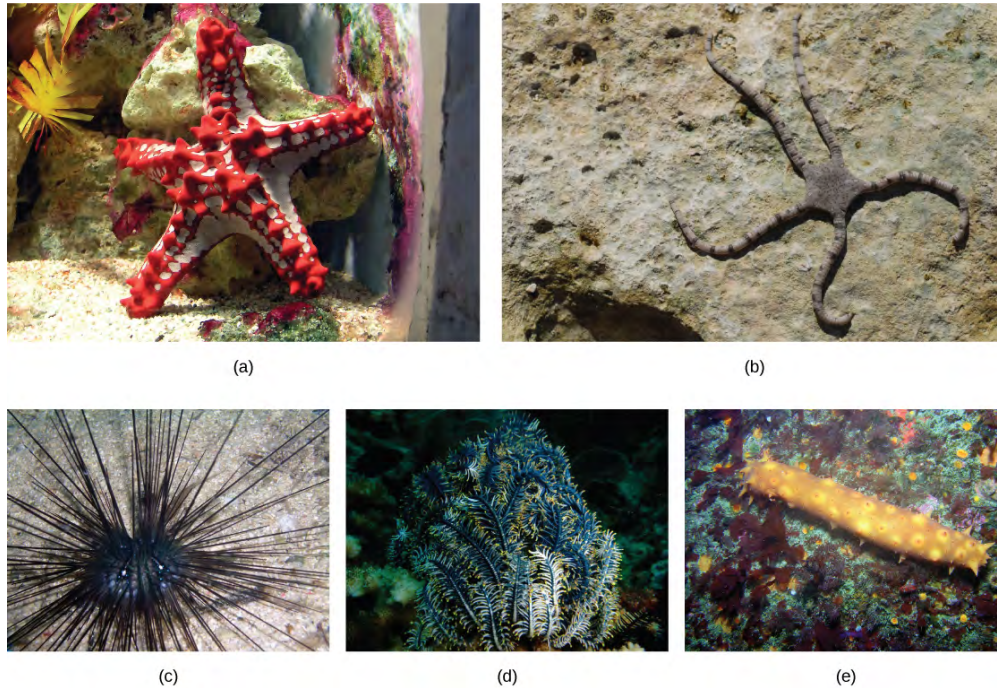
This phylum is divided into five classes: Asteroidea (sea stars), Ophiuroidea (brittle stars), Echinoidea (sea urchins and sand dollars), Crinoidea (sea lilies or feather stars), and Holothuroidea (sea cucumbers) (**Figure 15.32**).

Perhaps the best-known echinoderms are members of the class Asteroidea, or sea stars. They come in a large variety of shapes, colors, and sizes, with more than 1,800 species known. The characteristics of sea stars that set them apart from other echinoderm classes include thick arms that extend from a central disk where organs penetrate into the arms. Sea stars use their tube feet not only for gripping surfaces but also for grasping prey. Sea stars have two stomachs, one of which they can evert through their mouths to secrete digestive juices into or onto prey before ingestion. This process can essentially liquefy the prey and make digestion easier.



View this **video** (<http://openstaxcollege.org/l/echinoderm2>) to explore a sea star’s body plan up close, watch one move across the sea floor, and see it devour a mussel.

Brittle stars have long, thin arms that do not contain any organs. Sea urchins and sand dollars do not have arms but are hemispherical or flattened with five rows of tube feet, which help them in slow movement. Sea lilies and feather stars are stalked suspension feeders. Sea cucumbers are soft-bodied and elongate with five rows of tube feet and a series of tube feet around the mouth that are modified into tentacles used in feeding.



**Figure 15.32** Different members of Echinodermata include the (a) sea star in class Asterozoa, (b) the brittle star in class Ophiurozoa, (c) the sea urchins of class Echinozoa, (d) the sea lilies belonging to class Crinozoa, and (e) sea cucumbers representing class Holothurozoa. (credit a: modification of work by Adrian Pingstone; credit b: modification of work by Joshua Ganderson; credit c: modification of work by Samuel Chow; credit d: modification of work by Sarah Depper; credit e: modification of work by Ed Bierman)

## Chordates

The majority of species in the phylum Chordata are found in the subphylum Vertebrata, which include many species with which we are familiar. The vertebrates contain more than 60,000 described species, divided into major groupings of the lampreys, fishes, amphibians, reptiles, birds, and mammals.

Animals in the phylum **Chordata** share four key features that appear at some stage of their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail (**Figure 15.33**). In certain groups, some of these traits are present only during embryonic development.

The chordates are named for the **notochord**, which is a flexible, rod-shaped structure that is found in the embryonic stage of all chordates and in the adult stage of some chordate species. It is located between the digestive tube and the nerve cord, and provides skeletal support through the length of the body. In some chordates, the notochord acts as the primary axial support of the body throughout the animal's lifetime. In vertebrates, the notochord is present during embryonic development, at which time it induces the development of the neural tube and serves as a support for the developing embryonic body. The notochord, however, is not found in the postnatal stage of vertebrates; at this point, it has been replaced by the **vertebral column** (the spine).

The **dorsal hollow nerve cord** is derived from ectoderm that sinks below the surface of the skin and rolls into a hollow tube during development. In chordates, it is located dorsally to the notochord. In contrast, other animal phyla possess solid nerve cords that are located either ventrally or laterally. The nerve cord found in most chordate embryos develops into the brain and spinal cord, which compose the central nervous system.

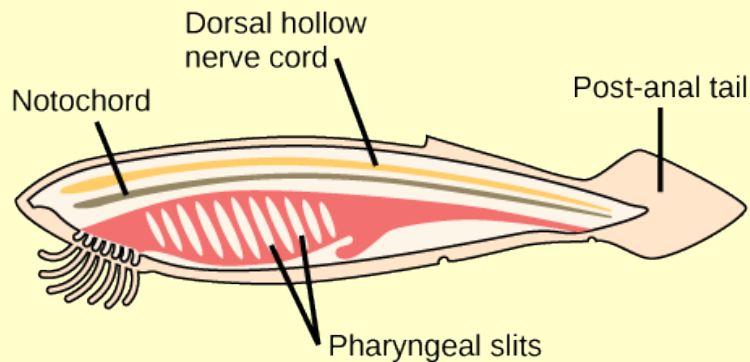
**Pharyngeal slits** are openings in the pharynx, the region just posterior to the mouth, that extend to the outside environment. In organisms that live in aquatic environments, pharyngeal slits allow for the exit of water that enters the mouth during feeding. Some invertebrate chordates use the pharyngeal slits to filter food from the water that enters the mouth. In fishes, the pharyngeal slits are modified into gill supports, and in jawed fishes, jaw supports. In tetrapods, the slits are further modified into components of the ear and tonsils, since there is no longer any need for gill supports in these air-breathing



animals. **Tetrapod** means “four-footed,” and this group includes amphibians, reptiles, birds, and mammals. (Birds are considered tetrapods because they evolved from tetrapod ancestors.)

The **post-anal tail** is a posterior elongation of the body extending beyond the anus. The tail contains skeletal elements and muscles, which provide a source of locomotion in aquatic species, such as fishes. In some terrestrial vertebrates, the tail may also function in balance, locomotion, courting, and signaling when danger is near. In many species, the tail is absent or reduced; for example, in apes, including humans, it is present in the embryo, but reduced in size and nonfunctional in adults.

## art CONNECTION



**Figure 15.33** In chordates, four common features appear at some point in development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. The anatomy of a cephalochordate shown here illustrates all of these features.

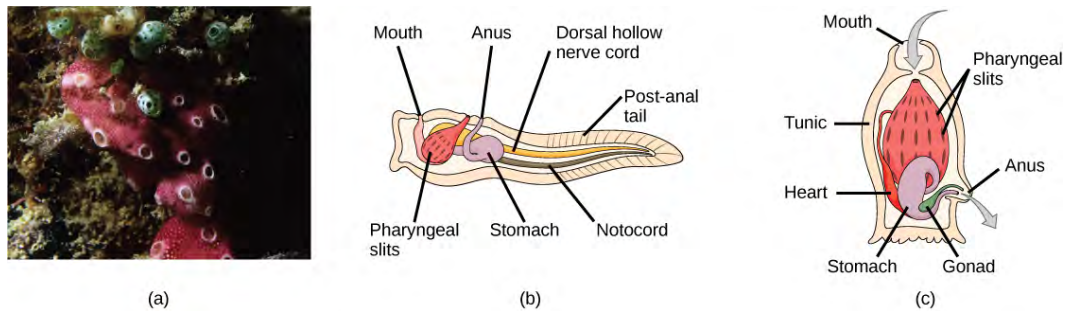
Which of the following statements about common features of chordates is true?

- The dorsal hollow nerve cord is part of the chordate central nervous system.
- In vertebrate fishes, the pharyngeal slits become the gills.
- Humans are not chordates because humans do not have a tail.
- Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

## Invertebrate Chordates

In addition to the vertebrates, the phylum Chordata contains two clades of invertebrates: **Urochordata** (tunicates) and **Cephalochordata** (lancelets). Members of these groups possess the four distinctive features of chordates at some point during their development.

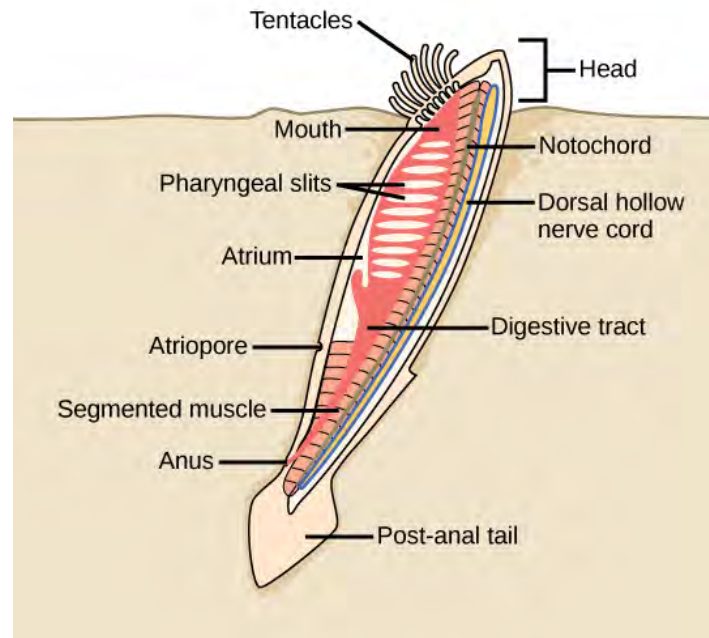
The **tunicates** (Figure 15.34) are also called sea squirts. The name tunicate derives from the cellulose-like carbohydrate material, called the tunic, which covers the outer body. Although tunicates are classified as chordates, the adult forms are much modified in body plan and do not have a notochord, a dorsal hollow nerve cord, or a post-anal tail, although they do have pharyngeal slits. The larval form possesses all four structures. Most tunicates are hermaphrodites. Tunicate larvae hatch from eggs inside the adult tunicate’s body. After hatching, a tunicate larva swims for a few days until it finds a suitable surface on which it can attach, usually in a dark or shaded location. It then attaches by the head to the substrate and undergoes metamorphosis into the adult form, at which point the notochord, nerve cord, and tail disappear.



**Figure 15.34** (a) This photograph shows a colony of the tunicate *Botrylloides violaceus*. In the (b) larval stage, the tunicate can swim freely until it attaches to a substrate to become (c) an adult. (credit a: modification of work by Dr. Dwayne Meadows, NOAA/NMFS/OPR)

Most tunicates live a sessile existence in shallow ocean waters and are suspension feeders. The primary foods of tunicates are plankton and detritus. Seawater enters the tunicate's body through its incurrent siphon. Suspended material is filtered out of this water by a mucus net (pharyngeal slits) and is passed into the intestine through the action of cilia. The anus empties into the excurrent siphon, which expels wastes and water.

**Lancelets** possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage (**Figure 15.35**). The notochord extends into the head, which gives the subphylum its name (Cephalochordata). Extinct fossils of this subphylum date to the middle of the Cambrian period (540–488 mya). The living forms, the lancelets, are named for their blade-like shape. Lancelets are only a few centimeters long and are usually found buried in sand at the bottom of warm temperate and tropical seas. Like tunicates, they are suspension feeders.



**Figure 15.35** Adult lancelets retain the four key features of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.