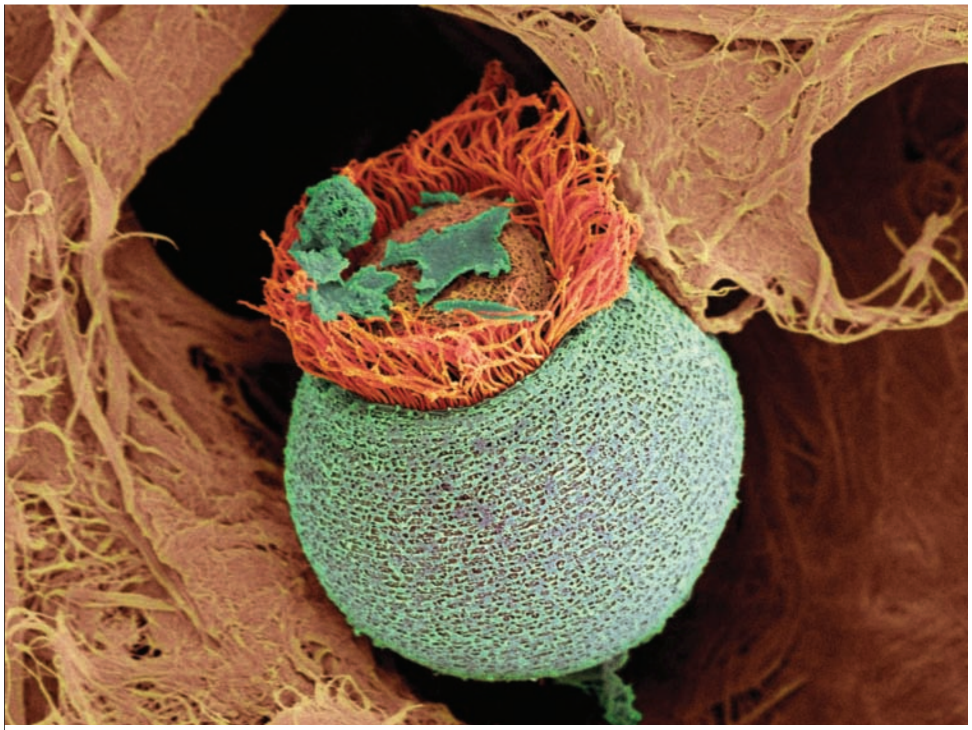
A ciliated protozoan, a type of protist (colorized SEM). This protozoan lives in water, feeding on bacteria and decaying organic matter.

Steve Gschmeissner/SPL/Photo Researchers, Inc.



26 Protists

Study Plan

26.1 What Is a Protist?

Protists are most easily classified by what they are not

Protist diversity is reflected in their metabolism, reproduction, structure, and habitat

26.2 The Protist Groups

The Excavates lack mitochondria

The Discicristates include the euglenoids and kinetoplastids, which are motile protists

The Alveolates have complex cytoplasmic structures and use flagella or cilia to move

The Heterokonts include the largest protists, the brown algae

The Cercozoa are amoebas with filamentous pseudopods

The Amoebozoa includes most amoebas and two types of slime molds

The Archaeplastida include the red and green algae, and land plants

The Opisthokonts include the choanoflagellates, which may be the ancestors of animals

In several protist groups, plastids evolved from endosymbionts

Why It Matters

Go for a swim just about anywhere in the natural world and you will share the water with multitudes of diverse organisms called protists. Like their most ancient ancestors, almost all of these eukaryotic species are aquatic. Structurally, single-celled protists are the simplest of all eukaryotes. Although most are microscopic in size, many have had or have a significant impact on the world. For example, the protist *Phytophthora infestans,* a water mold also referred to as a downy mildew, infects valuable crop plants such as potatoes. Pototoes were the main food staple in Europe in the nineteenth century, and *P. infestans* destroyed potato crops, causing potato famines that spread across Europe; millions died in these famines. In Ireland, for instance, the growing seasons between 1845 and 1860 were cool and damp. Year after year, *P. infestans* spores spread along thin films of water on the plants. Late blight, a rotting of plant parts, became epidemic. One-third of the Irish population starved to death, died of typhoid fever (a secondary effect), or fled to other countries.

Today, related species threaten forests in the United States, Europe, and Australia. For example, when conditions favored its growth, *Phytophthora ramorum,* started an epidemic of sudden oak death in California, during which tens of thousands of oak trees have died. As the name suggests, infected trees die rapidly. The first sign of infection is a dark red-to-black sap oozing from the bark surface. The pathogen has now jumped to madrones, redwoods, and certain other trees and shrubs. Cascading ecological changes resulting from tree death caused by this pathogen will reduce sources of food and shelter for forest species.

Protists are the subject of this chapter. Also known as *protoctists,* they are members of the kingdom **Protoctista.** Protists are the results of the varied early branching of eukaryotic evolution. They are abundant on Earth and play key ecological, economic, and medical roles in the world's biological communities.

We begin this chapter with a discussion of the identity of the protists. As our discussion will show, the members of the kingdom Protoctista are so diverse that they are best defined as what they are not—that is, by contrasting them with other kingdoms.

26.1 What Is a Protist?

Protists are easily the most varied of all Earth's creatures. **Figure 26.1** shows a number of protists, illustrating their great diversity. Protists include both microscopic single-celled and large multicellular organisms. They may inhabit aquatic environments, moist soils, or the bodies of animals and other organisms, and they may live as predators, photosynthesizers, parasites, or decomposers. The extreme diversity of the group has made the protists so difficult to classify that their status as a kingdom remains highly unsettled.

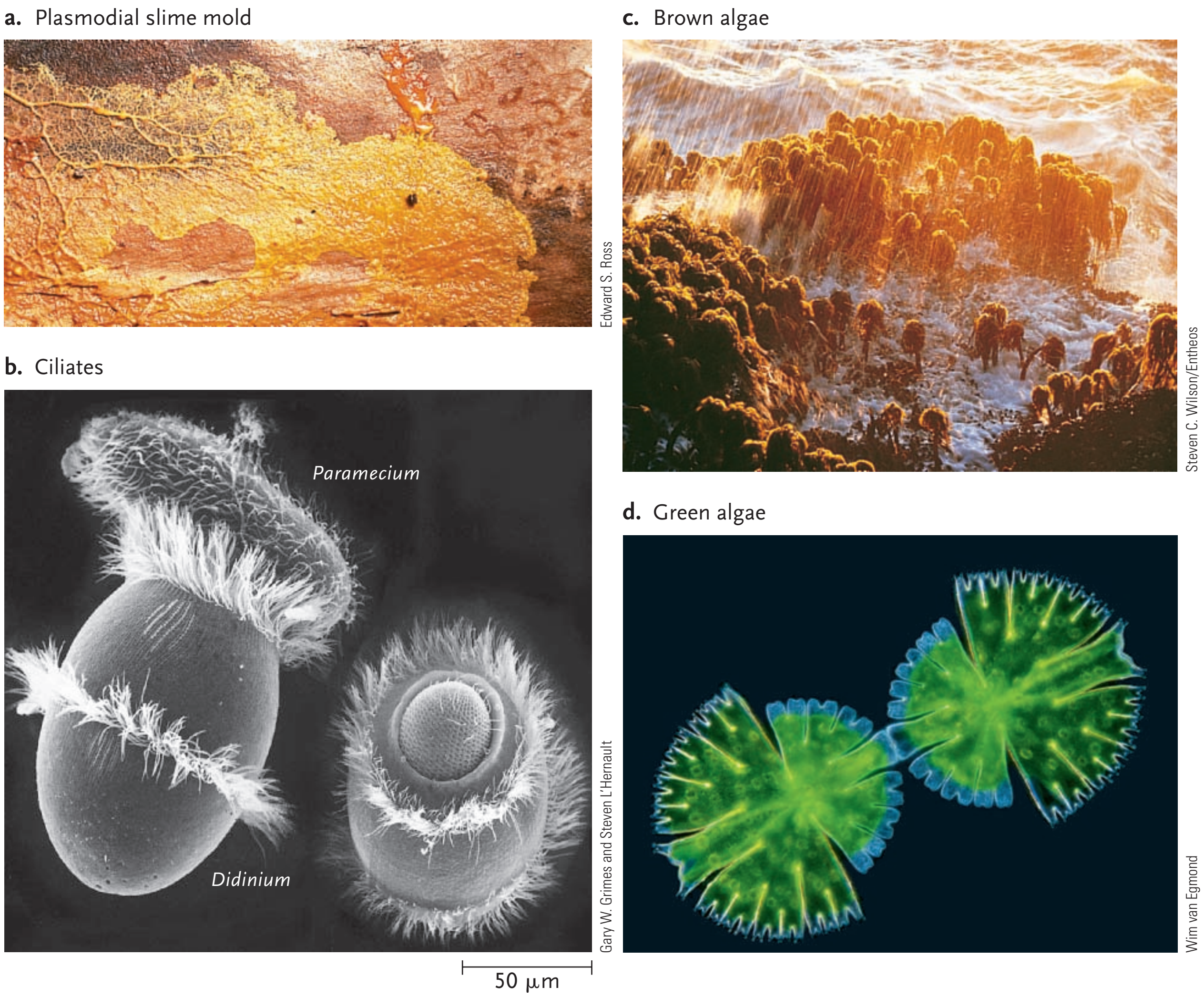


Figure 26.1
A sampling of protist diversity. **(a)** *Physarum,* a plasmodial slime mold (yellow shape, lower part of figure) migrating over a rotting log. **(b)** *Didinium,* a ciliate, consuming another ciliate, *Paramecium.* **(c)** *Postelsia palmaeformis* (the sea palm), a brown alga, thriving in the surf pounding a California coast. **(d)** *Micrasterias,* a single-celled green alga, here shown dividing in two.

Protists Are Most Easily Classified by What They Are Not

The one reasonable certainty about protist classification is that the organisms lumped together in the kingdom Protoctista are not prokaryotes, fungi, plants, or animals.

Because protists are eukaryotes, the boundary between them and prokaryotes is clear and obvious. Unlike prokaryotes, protists have a true nucleus, with multiple, linear chromosomes. In addition to cytoplasmic organelles—including mitochondria (in most but not all species), endoplasmic reticulum, Golgi complex, and chloroplasts (in some species)—protists and other eukaryotes have microtubules and microfilaments, which provide motility and cytoskeletal support. They reproduce asexually by mitosis or sexually by meiosis and union of sperm and egg cells, rather than by binary fission as do prokaryotes.

The phylogenetic relationship between protists and other eukaryotes is more complex **(Figure 26.2).** From its beginning, the eukaryotic family tree branched out in many directions. All of the organisms in the eukaryotic lineages consist of protists except for three groups, the animals, land plants, and fungi, which arose from protist ancestors. Although some protists have features that resemble those of the fungi, plants, or animals, several characteristics are distinctive. For instance, cell wall components in protists differ from those of the fungi (molds and yeasts, for example). In contrast to land plants, protists lack highly differentiated structures equivalent to true roots, stems, and leaves; they also lack the protective structures that encase developing embryos in plants. Protists are distinguished from animals by their lack of highly differentiated structures such as limbs and a heart, and by the absence of features such as nerve cells, complex developmental stages, and an internal digestive tract. Pro-

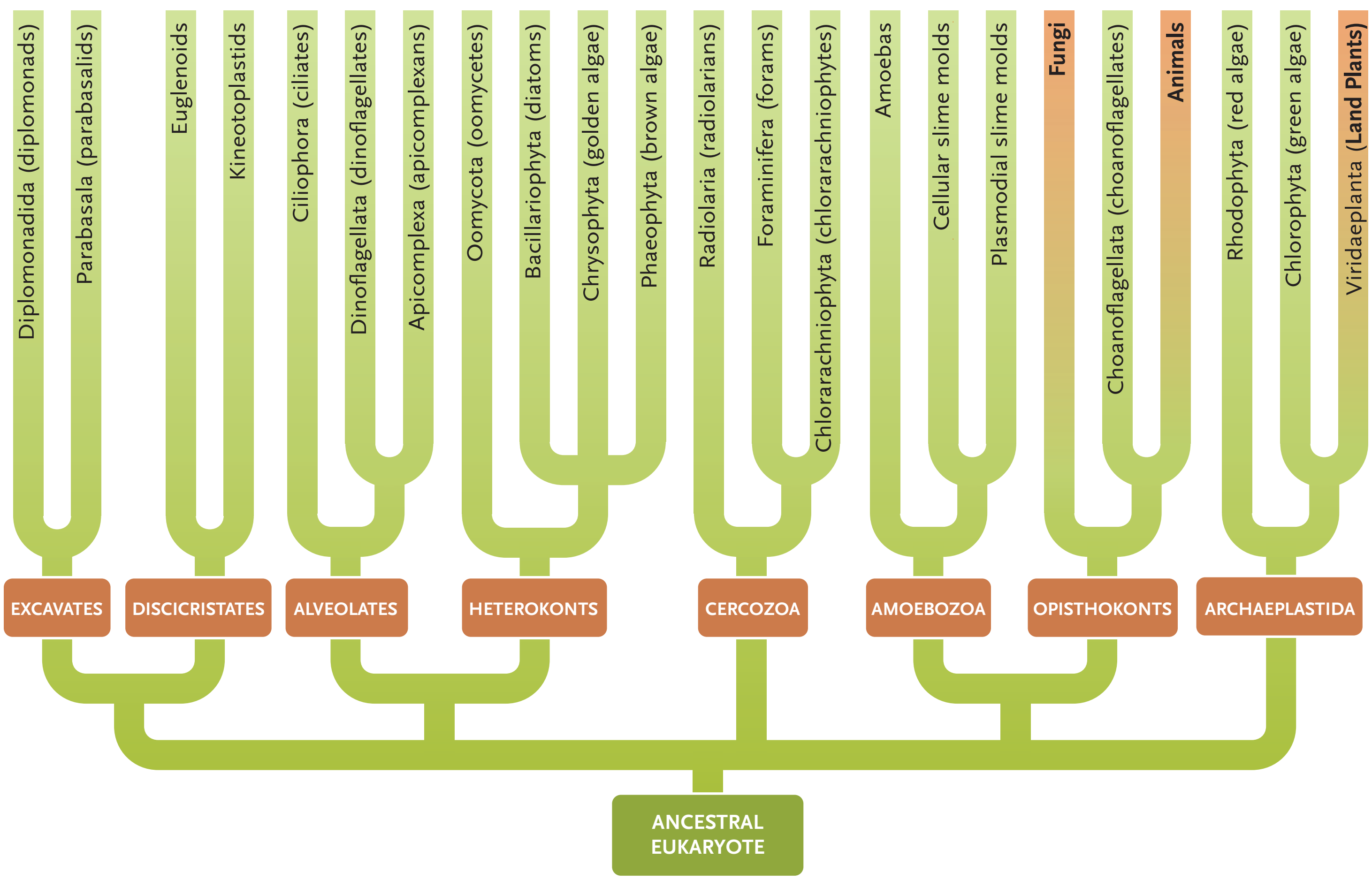


Figure 26.2
The phylogenetic relationship between the evolutionary groups within the kingdom Protoctista and the other eukaryotes. The Archaeplastida include the land plants of the kingdom Plantae (boxed), and the Opisthokonts include the animals of the kingdom Animalia and the fungi of the kingdom Fungi (boxed). The tree was constructed based on a consensus of molecular and ultrastructural data.

tists also lack collagen, the characteristic extracellular support protein of animals. Thus, the kingdom Protoctista is a catchall group that includes all the eukaryotes that are not fungi, plants, or animals.

Until recently, the protists were classified into phyla according to criteria such as body form, modes of nutrition and movement, and forms of meiosis and mitosis. However, comparisons of nucleic acid and amino acid sequences, now considered the most informative method for determining the evolutionary relationships of protists, show that most of the organisms previously grouped together do not share a common lineage. Further, many organisms within the phyla are no more closely related to each other than they are to the fungi, plants, or animals.

Given the extreme diversity of the protists, some evolutionists maintain that the kingdom Protoctista is actually a collection of many kingdoms—as many as 30, depending on differing evaluations of the lineages indicated by the sequence comparisons. Evolutionary lineages within the kingdoms are variously described as clades, subkingdoms, or phyla, and the existing schemes are constantly revised as new information is obtained.

For simplicity, we retain the Protoctista as a single kingdom in this book, with the understanding that it is a collection of largely unrelated organisms placed together for convenience. We will refer to the major evolutionary clusterings indicated by molecular and structural comparisons as groups (see Figure 26.2).

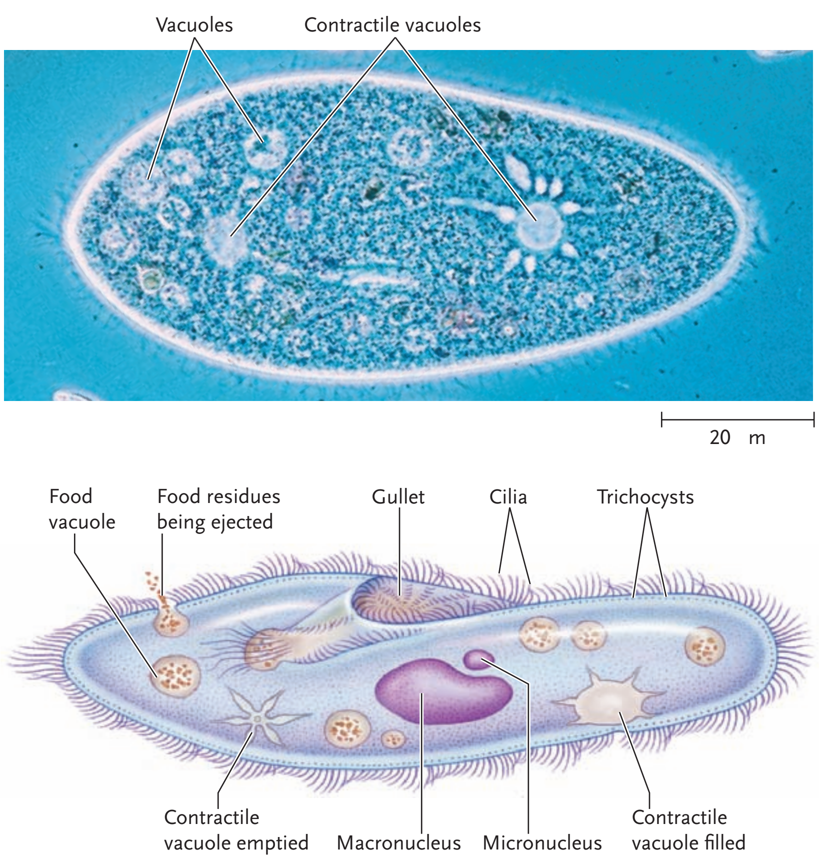


Figure 26.3
A ciliate, *Paramecium*, showing the cytoplasmic structures typical of many protists.
(Top: Frieder Sauer/Bruce Coleman Ltd.; bottom: Redrawn from V. & J. Pearse and M. & R. Buchsbaum, Living Invertebrates, The Boxwood Press, 1987.)

Protist Diversity Is Reflected in Their Metabolism, Reproduction, Structure, and Habitat

As you might expect from the broad range of organisms included in the kingdom, protists are highly diverse in metabolism, reproduction, structure, and habitat.

Metabolism. Almost all protists are aerobic organisms that live either as heterotrophs—by obtaining their organic molecules from other organisms—or as autotrophs—by producing organic molecules for themselves by photosynthesis. Among the heterotrophs, some protists obtain organic molecules by directly ingesting part or all of other organisms and digesting them internally. Others absorb organic molecules from their environment. A few protists can live as either heterotrophs or autotrophs.

Reproduction. Reproduction may be asexual by mitosis or sexual by meiotic cell division and formation of gametes. In protists that reproduce by both mitosis and meiosis, the two modes of cell division are combined into a **life cycle** that is highly distinctive among the different protist groups.

Structure. Many protists live as single cells or as **colonies** in which individual cells show little or no differentiation and are potentially independent. Within colonies, individuals use cell signaling to cooperate on tasks such as feeding or movement. Some protists are large multicellular organisms, in which cells are differentiated and completely interdependent. For example, seaweeds are multicellular marine protists that include the largest and most differentiated organisms of the group; their structures include a hodlfast to secure the organism to the rocks, leaflike fronds, and, in some cases, an air bladder for flotation. The giant kelp of coastal waters rival forest trees in size.

Some single-celled and colonial protists have complex intracellular structures, some found nowhere else among living organisms **(Figure 26.3).** For example, many freshwater protists have a mechanism to maintain water balance in and out of the cell to prevent lysis. Excess water entering cells by osmosis (see Section 6.3) is handled using a specialized cytoplasmic organelle, the **contractile vacuole.** The contractile vacuole gradually fills with water; when it reaches maximum size it moves to the plasma membrane and forcibly contracts, expelling the water to the outside through a pore in the membrane. Many protists also have **food vacuoles** that digest prey or other organic material engulfed by the cells. Enzymes secreted into the food vacuoles digest the organic molecules; any remaining undigested matter is expelled to the outside by a mechanism similar to the expulsion of water by contractile vacuoles.

The cells of some protists are supported by an external cell wall, or by an internal or external shell built up from organic or mineral matter; in some, the shell takes on highly elaborate forms. Other protists have a **pellicle**, a layer of supportive protein fibers located inside the cell, just under the plasma membrane, providing strength and flexibility instead of a cell wall (see Figure 26.5).

Almost all protists have structures providing motility at some time during their life cycle. Some move by amoeboid motion, in which the cell extends one or more lobes of cytoplasm called **pseudopodia** ("false feet"; see Figure 26.15). The rest of the cytoplasm and the nucleus then flow into a pseudopodium, completing the movement. Other protists move by the beating of flagella or cilia (see Section 5.3; cilia are essentially the same as flagella, except that cilia are often shorter and occur in greater numbers on a cell). In some protists, cilia are arranged in complex patterns, with an equally complex network of microtubules and other cytoskeletal fibers supporting the cilia under the plasma membrane. Among the protists are the most complex single cells known because of the wide variety of cytoplasmic structures they have.

Habitat. Protists live in aqueous habitats, including aquatic or moist terrestrial locations such as oceans, freshwater lakes, ponds, streams, and moist soils, and within host organisms. In bodies of water, small photosynthetic protists collectively make up the **phytoplankton** (*phytos* = plant; *planktos* = drifting), the abundant organisms that capture the energy of sunlight in nearly all aquatic habitats. These photosynthetic protists provide organic substances and oxygen for heterotrophic bacteria and protists and for the small crustaceans and animal larvae that are the primary constituents of **zooplankton** (*zoe* = life, usually meaning animal life); although protists are not animals, biologists often include them among the zooplankton. The phytoplankton and the larger multicellular protists forming seaweeds collectively account for about half of the total organic matter produced by photosynthesis.

In the moist soils of terrestrial environments, protists play important roles among the detritus feeders that recycle matter from organic back to inorganic form. In their roles in phytoplankton, zooplankton, and as detritus feeders, protists are enormously important in the world ecosystem.

Protists that live in host organisms are parasites, obtaining nutrients from the host. Indeed, many of the parasites that have significant effects on human health are protists, causing diseases such as malaria, sleeping sickness, and giardiasis.

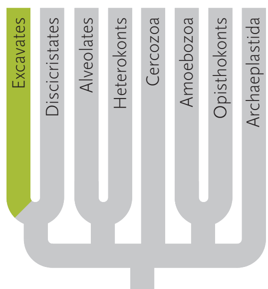
Study Break

What distinguishes protists from prokaryotes? What distinguishes them from fungi, plants, and animals?

26.2 The Protist Groups

This section considers the biological features of each of the groups of protists included in Figure 26.2. This taxonomic tree represents a current consensus, based both on molecular data, such as comparative genomics, and on fine structures that have a distinctive form in a particular group.

The Excavates Lack Mitochondria

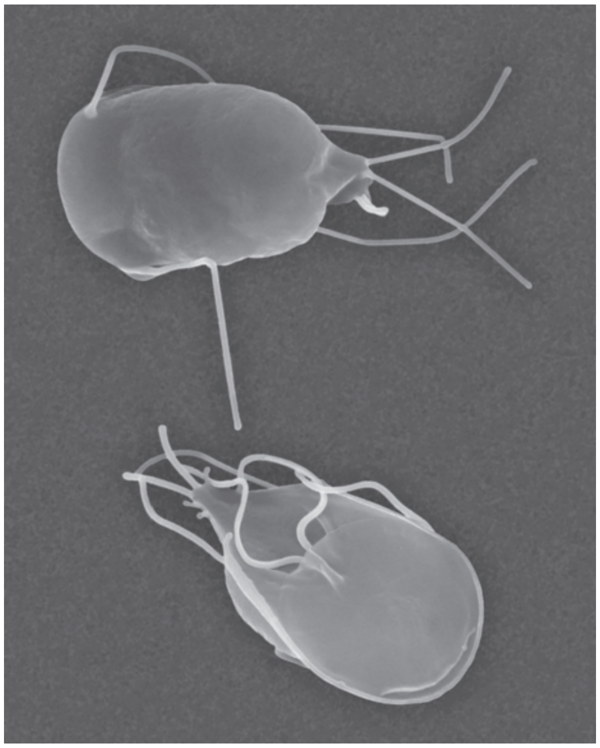


All members of the Excavates are single-celled animal parasites that lack mitochondria and move by means of flagella; most have a hollow (excavated) ventral feeding groove. Because they lack mitochondria, they are limited to glycolysis as an ATP source. However, the nuclei of Excavates contain genes derived from mitochondria, meaning that the ancestors of these protists probably had mitochondria. They may have lost their mitochondria as an adaptation to the parasitic way of life, in which oxygen is in short supply. We consider two groups here, the Diplomonadida and the Parabasala.

Diplomonadida. Diplomonad cells have two nuclei and move by means of multiple freely beating flagella. In addition to lacking mitochondria, they also lack a clearly defined endoplasmic reticulum and Golgi complex. The best-known representative of the group, *Giardia lamblia* **(Figure 26.4a),** infects the mammalian intestinal tract, inducing severe diarrhea and abdominal cramps. *Giardia* is spread by contamination of water with feces, in which resistant cysts of the protist can be present in large numbers. So many streams and lakes in wilderness areas of the United States have become contaminated with *Giardia* cysts that hikers must boil water from these sources before drinking it, or pass it through filters able to remove particles as small as 1 μm. Treating water with chemicals such as chlorine or iodine does not kill the cysts.

Parabasala. In addition to freely beating flagella, species among the Parabasala have a sort of fin called an **undulating membrane**, formed by a flagellum buried in a fold of the cytoplasm. The buried flagellum allows parabasalans to move through thick and viscous fluids. Among the Parabasala are the trichomonads, including *Trichomonas vaginalis* **(Figure 26.4b),** a worldwide nuisance responsible for infections of the urinary and reproductive tracts in both men and women. The infective trichomonad is passed from person to person primarily, but not exclusively, by sexual intercourse. It lives in the vagina in women and in the urethra of both sexes. The

a. *Giardia lamblia*



b. *Trichomonas vaginalis*

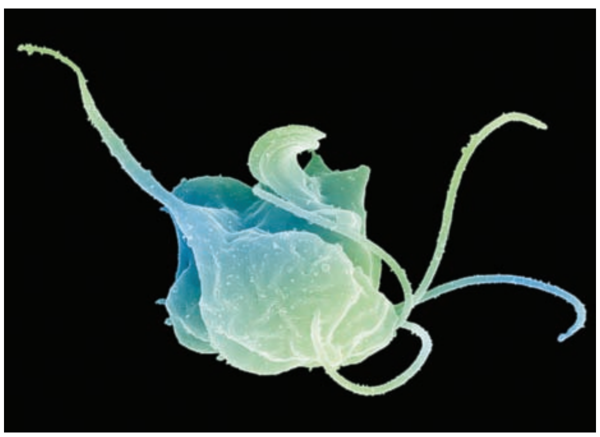
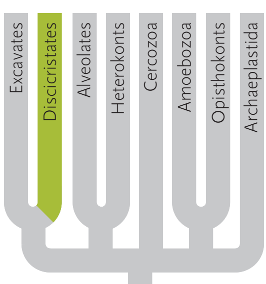


Figure 26.4
The Diplomonadida and Parabasala of the Excavates. **(a)** A diplomonad, *Giardia lamblia*, that causes intestinal disturbances. **(b)** A parabasalid, *Trichomonas vaginalis*, that causes a sexually transmitted disease, trichomoniasis.

infection is usually symptomless in men, but in women *T. vaginalis* can cause severe inflammation and irritation of the vagina and vulva. It is easily cured by drugs.

The Discicristates Include the Euglenoids and Kinetoplastids, Which Are Motile Protists



The **Discicristates** are named for their disc-shaped mitochondrial cristae (inner mitochondrial membranes). The group includes about 1800 species, almost all single-celled, highly motile cells that swim by means of flagella. While most are photosynthetic, some are facultative heterotrophs; some can even alternate between photosynthesis and life as a heterotroph. The best-known members of this group are the euglenoids, with *Euglena gracilis* **(Figure 26.5)** as the best-known species. Another group, the parasitic kinetoplastids, includes some organisms responsible for human diseases. A commonly used nontaxonomic name for protists of the Discicristates is *protozoa* ("first animal"), referring to their similarity to animals with respect to ingesting food and moving by themselves.

Euglenoids. With the exception of a few marine species, the euglenoids inhabit freshwater ponds, streams, and lakes. Most are autotrophs that carry out photosynthesis by the same mechanisms as plants, using the same photosynthetic pigments, including chlorophylls *a* and *b* and β-carotene. Many of the photosynthetic euglenoids, including *E. gracilis,* can also live as heterotrophs by absorbing organic molecules through the plasma membrane. Some euglenoids lack chloroplasts and live entirely as heterotrophs.

Euglena gracilis and other euglenoids have a profusion of cytoplasmic organelles, including a contractile vacuole and, in photosynthetic species, chloroplasts (see Figure 26.5). Rather than an external cell wall, the euglenoids have a spirally grooved pellicle formed from transparent, protein-rich material. Most of the photosynthetic euglenoids, including *E. gracilis,* have an *eyespot* containing carotenoid pigment granules in association with a light-sensitive structure. The eyespot is part of a sensory mechanism that stimulates cells to swim toward moderately bright light or away from intensely bright light so that the organism is in light conditions for optimal photosynthetic activity. The cells swim by whiplike movements of flagella that extend from a pocketlike depression at one end of the cell. Most have two flagella, one rudimentary and short, the other long.

Kinetoplastids. The kinetoplastids are a group of nonphotosynthetic, heterotrophic cells that live as animal parasites **(Figure 26.6).** Their name reflects the structure of the single mitochondrion in a cell of this group, which contains a large DNA-protein deposit called a *kinetoplast.* Most kinetoplastids have a leading and a trailing flagellum, which are used for movement. In some cases, the trailing flagellum is attached to the side of the cell, forming an undulating membrane that is often used to enable the organism to glide along or attach to surfaces.

The kinetoplastids include the trypanosomes, responsible for several diseases afflicting millions of humans in tropical regions. *Trypanosoma brucei* (see Figure 26.6) causes African sleeping sickness, transmitted from one host to another by bites of the tsetse fly. Early symptoms include fever, headaches, rashes, and anemia. Untreated, the disease damages the cen-

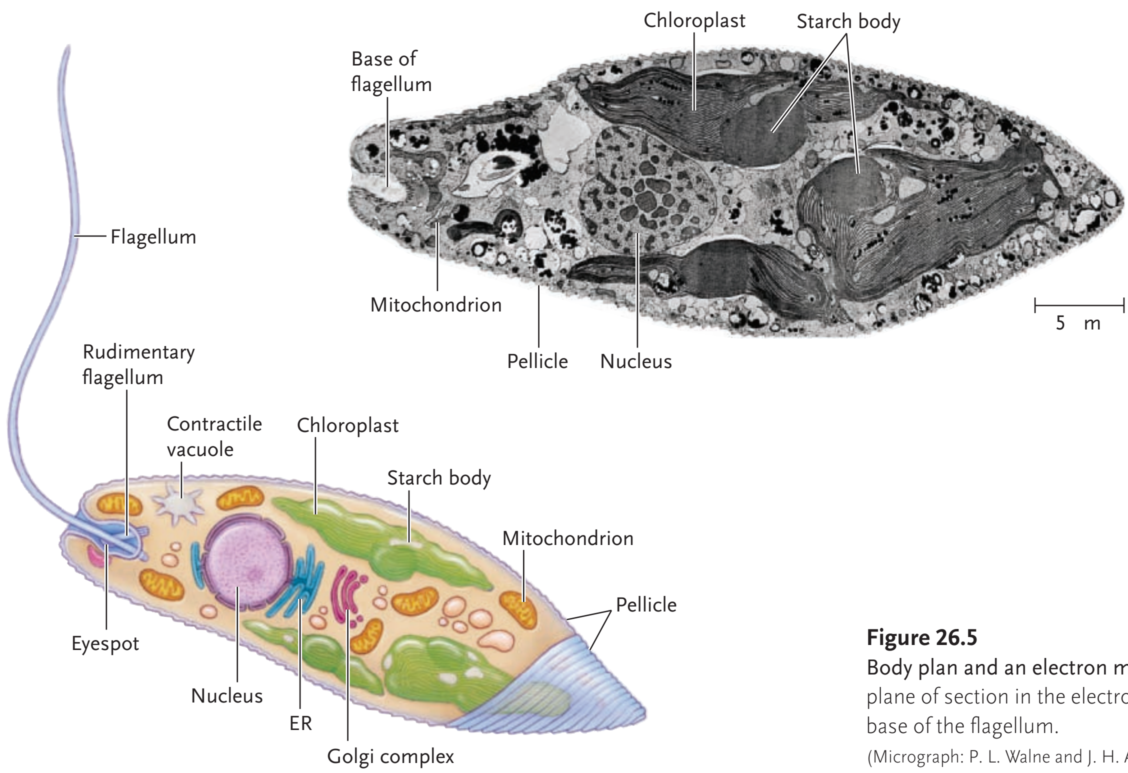
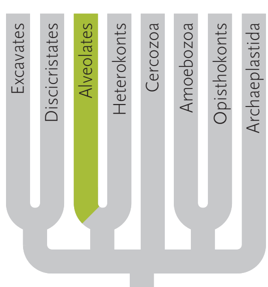


Figure 26.5
Body plan and an electron micrograph of *Euglena gracilis.* The plane of section in the electron micrograph has cut off all but the base of the flagellum.
(Micrograph: P. L. Walne and J. H. Arnott, Planta, 77:325–354, 1967.)

tral nervous system, leading to a sleeplike coma and eventual death. The disease has proved difficult to control because the same trypanosome infects wild mammals, providing an inexhaustible reservoir for the parasite. Other trypanosomes, also transmitted by insects, cause Chagas disease in the southwestern United States and Central and South America, and leishmaniasis in the tropics. Humans with Chagas disease have an enlarged liver and spleen and may experience severe brain and heart damage; people with leishmaniasis have skin sores and ulcers that may become very deep and disfiguring, particularly to the face.

The Alveolates Have Complex Cytoplasmic Structures and Use Flagella or Cilia to Move

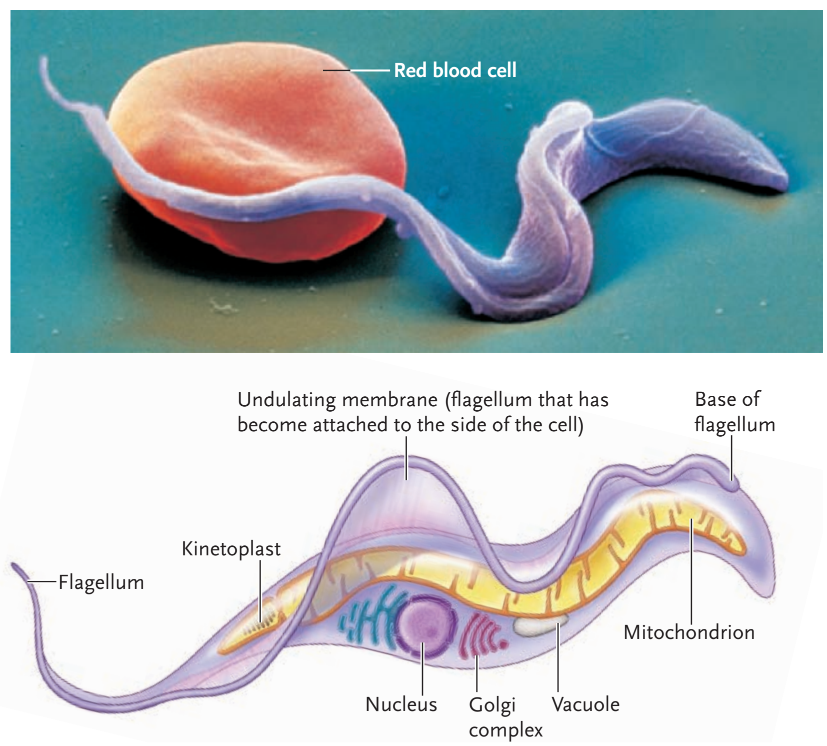


The Alveolates are so called because they have small, membrane-bound vesicles called *alveoli* (*alvus* = belly) in a layer just under the plasma membrane. The Alveolates include two motile, primarily free-living groups, the Ciliophora and Dinoflagellata, and a nonmotile, parasitic group, the Apicomplexa.

Ciliophora: The Ciliates. The Ciliophora—the ciliates—includes nearly 10,000 known species of primarily single-celled but highly complex heterotrophic organisms that swim by means of cilia (see Figures 26.1b and 26.3). Ciliates were among the first organisms observed in the seventeenth century by the pioneering microscopist Anton van Leeuwenhoek. Essentially any sample of pond water or bottom mud contains a wealth of these creatures.

The organisms in the Ciliophora have many highly developed organelles, including a mouthlike gullet lined with cilia; structures that exude mucins, toxins, or other defensive and offensive materials from the cell surface; contractile vacuoles; and complex systems of

Figure 26.6
Trypanosoma brucei, the parasitic kinetoplastid that causes African sleeping sickness.



food vacuoles. A pellicle reinforces cell shape. A complex cytoskeletal network of microtubules and other fibers anchors the cilia just below the pellicle and coordinates the ciliary beating. The cilia can stop and reverse their beating in synchrony, allowing ciliates to stop, back up, and turn if they encounter negative stimuli. Evidence that the cytoskeletal network organizes ciliary beating comes from microsurgical experiments in which a segment of the body surface was cut out and reinserted in the opposite direction. The cilia in the reversed segment beat in the opposite direction to those on the rest of the organism.

The ciliates are the only eukaryotes that have two types of nuclei in each cell: one or more small nuclei called *micronuclei,* and a single larger *macronucleus* (see Figure 26.3b). A **micronucleus** is a diploid nucleus that contains a complete complement of genes. It functions primarily in cellular reproduction, which may be asexual or sexual. The number of micronuclei present depends on the species. The **macronucleus** develops from a micronucleus, but loses all genes except those required for basic "housekeeping" functions of the cell and for ribosomal RNAs. These DNA sequences are duplicated many times, greatly increasing its capacity to transcribe the mRNAs needed for these functions, and the rRNAs needed to make ribosomes.

In asexual reproduction by mitosis, both types of nuclei replicate their DNA, divide, and are passed on to daughter cells. In sexual reproduction of *Paramecium,* for example, two cells **conjugate** by first forming a cytoplasmic bridge **(Figure 26.7).** Next, the micronucleus in each cell undergoes meiosis, producing four haploid micronuclei. In a series of steps, three of the four micronuclei in each cell degenerate, and the macronucleus also begins degenerating. The remaining micronucleus divides by mitosis, and one of the two micronuclei in each cell then passes through the cytoplasmic bridge into the other cell (step 5). The two haploid micronuclei in each cell now fuse to form a diploid micronucleus, with pairs of homologous chromosomes, one from each of the original parents. The two cells then separate. Through a further series of divisions, the micronucleus in each cell gives rise to two micronuclei and two macronuclei. Finally, each cell divides to produce two daughter cells, completing sexual reproduction.

Ciliates abound in freshwater and marine habitats, where they feed voraciously on bacteria, algae, and each other. *Paramecium* is a typical member of the group (see Figure 26.3). Its rows of cilia drive it through its watery habitat, rotating the cell on its long axis while it moves forward, or backs and turns. The cilia also sweep water laden with prey and food particles into the gullet, where food vacuoles form. The ciliate digests food in the vacuoles and eliminates indigestible material through an anal pore. Contractile vacuoles with elaborate, raylike extensions remove excess water from the cytoplasm and expel it to the outside. When under attack or otherwise stressed, *Paramecium* discharges many dartlike protein threads from surface organelles called **trichocysts.**

Some ciliates live individually while others are colonial. Certain ciliates are animal parasites; others live and reproduce in their hosts as mutually beneficial symbionts. (*Symbiosis* is the interaction between two organisms living together in close association, sometimes one inside another.) A compartment of the stomach of cattle and other grazing animals contains large numbers of symbiotic ciliates that digest the cellulose in their host's plant diet. The animals then digest the excess ciliates.

One ciliate, *Balantidium coli,* is a human intestinal parasite that causes diarrhea, with stools typically containing blood and pus. It is passed on when humans eat food contaminated by the feces of animals infected by *Balantidium,* particularly pigs. Less than 1% of the human population is infected worldwide.

Dinoflagellata: The Dinoflagellates. Of over 4000 known dinoflagellate species, most are single-celled organisms in marine phytoplankton. They live as heterotrophs or autotrophs; many can carry out both modes of nutrition. Some contain algae as symbionts. Typically, they have a shell formed from cellulose plates **(Figure 26.8).** The beating of flagella, which fit into grooves in the plates, makes dinoflagellates spin like a top (*dinos* = spinning).

The cytoplasmic structures of dinoflagellates include mitochondria, chloroplasts in photosynthetic species, and other internal membrane systems characteristic of eukaryotes. The photosynthetic dinoflagellates contain chlorophylls *a* and *c* along with accessory pigments that make them golden-brown or brown; algal symbionts give some a green, blue, or red color.

Their abundance in phytoplankton makes dinoflagellates a major primary producer of ocean ecosystems. Some species live as symbionts in the tissues of other marine organisms such as jellyfish, sea anemones, corals, and mollusks. For example, dinoflagellates in coral use the coral's carbon dioxide and nitrogenous waste, while supplying 90% of the coral's nutrition. The vast numbers of dinoflagellates living as photosynthetic symbionts in tropical coral reefs allow the reefs to reach massive size; without the dinoflagellates many coral species would die.

Some dinoflagellates are **bioluminescent**—they glow or release a flash of light, particularly when disturbed. The production of light depends on the enzyme *luciferase* and its substrate *luciferin,* in forms similar to the system that produces light in fireflies. Dinoflagellate fluorescence can make the sea glow in the wake of a boat at night and coat nocturnal surfers and swimmers with a ghostly light.

At times dinoflagellate populations grow to such large numbers that they color the seas red, orange, or brown. The resulting **red tides** are common in spring and summer months along the warmer coasts of the world, including all the U.S. coasts. Some red-tide dinoflagellates produce a toxin that interferes with nerve

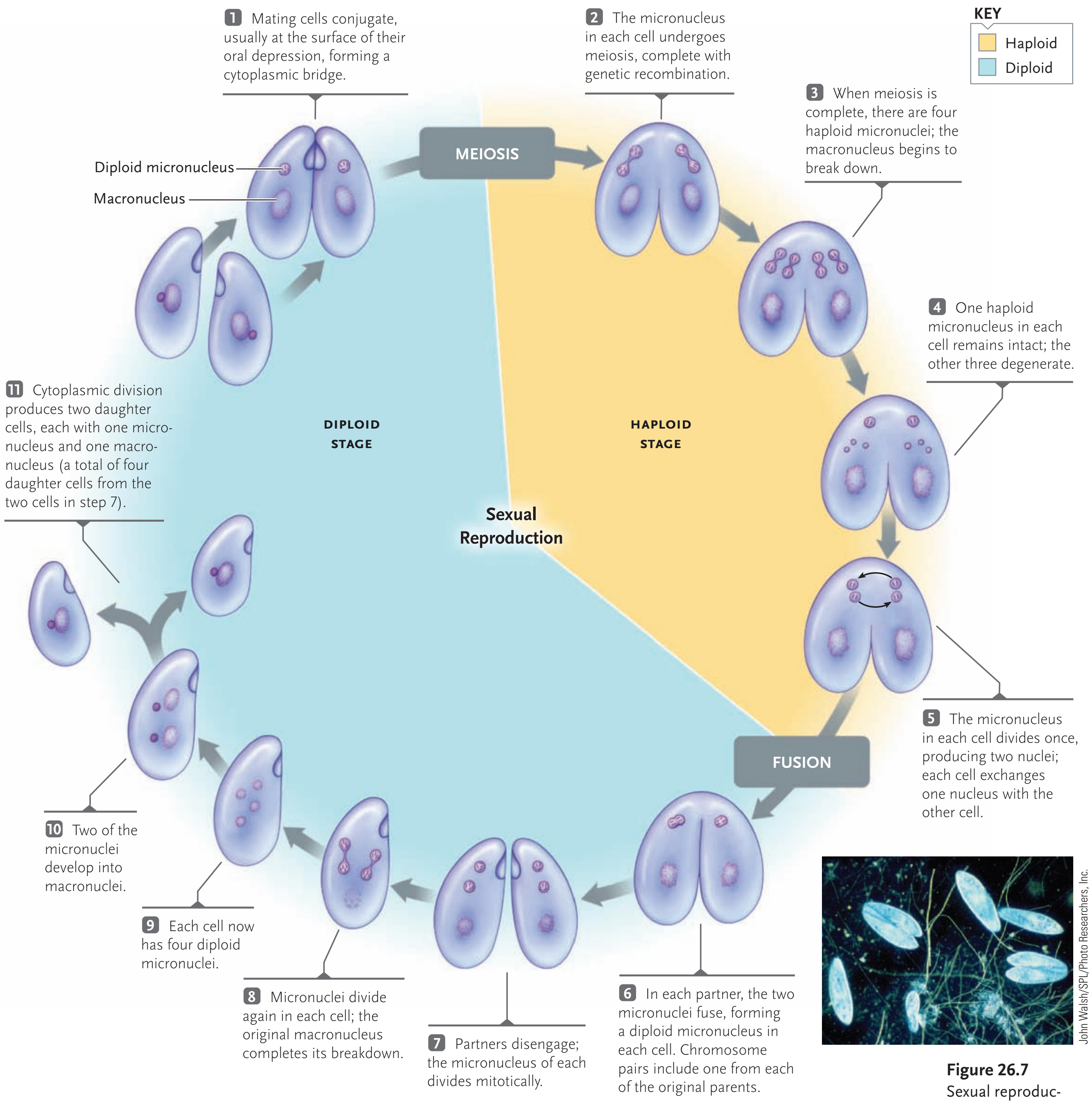


Figure 26.7
Sexual reproduction by conjugation in a ciliate, *Paramecium.*

function in animals that ingest these protists. Fish that feed on plankton, and birds that feed on the fish, may be killed in huge numbers by the toxin. Dinoflagellate toxin does not noticeably affect clams, oysters, and other mollusks, but it becomes concentrated in their tissues. Eating the tainted mollusks can cause respiratory failure and death for humans and other animals. The toxin is especially deadly for mammals because it paralyzes the diaphragm and other muscles required for breathing.

Apicomplexa. The apicomplexans are all nonmotile parasites of animals. They absorb nutrients through their plasma membranes rather than by engulfing food particles, and they lack food vacuoles. They get their name from the *apical complex,* a group of organelles at one end of the cell that functions in attachment and invasion of host cells.

Typically, apicomplexan life cycles involve both asexual and sexual reproduction. All the apicomplexans, which includes almost 4000 known species, pro-

Figure 26.8
Karenia brevis, a toxin-producing dinoflagellate.

duce infective sporelike stages called *sporozoites*. The sporozoites reproduce asexually in cells they infect, eventually bursting them, which releases the progeny to infect new cells. At some point they generate specialized cells that form gametes; fusion of gametes produces resistant cells known as *cysts*. Usually, a host is infected by ingesting cysts, which divide to produce sporozoites. This basic life cycle pattern varies considerably among the apicomplexans, and many of these organisms use more than one host species for different stages of their life cycle.

One apicomplexan genus, *Plasmodium,* is responsible for malaria, one of the most widespread and debilitating diseases of humans. The disease is transmitted by the bite of 60 different species of mosquitoes, all members of the genus *Anopheles*. Although the disease is now rare in the United States, *Anopheles* mosquitoes are common enough to spread malaria if *Plasmodium* is introduced by travelers from other countries. The infective cycle of *Plasmodium,* described in *Focus on Research,* is representative of the complex life cycles of apicomplexans.

Another organism in this group, *Toxoplasma,* has a sexual phase of its life cycle in cats and asexual phases in humans, cattle, pigs, and other animals. Cysts of the parasite in the feces of infected cats are spread in household and garden dust. Humans ingesting or inhaling the cysts develop toxoplasmosis, a disease that is usually mild in adults but can cause severe brain damage or even death to a fetus. Because of the danger of toxoplasmosis, pregnant women should avoid emptying litter boxes or otherwise cleaning up after a cat.

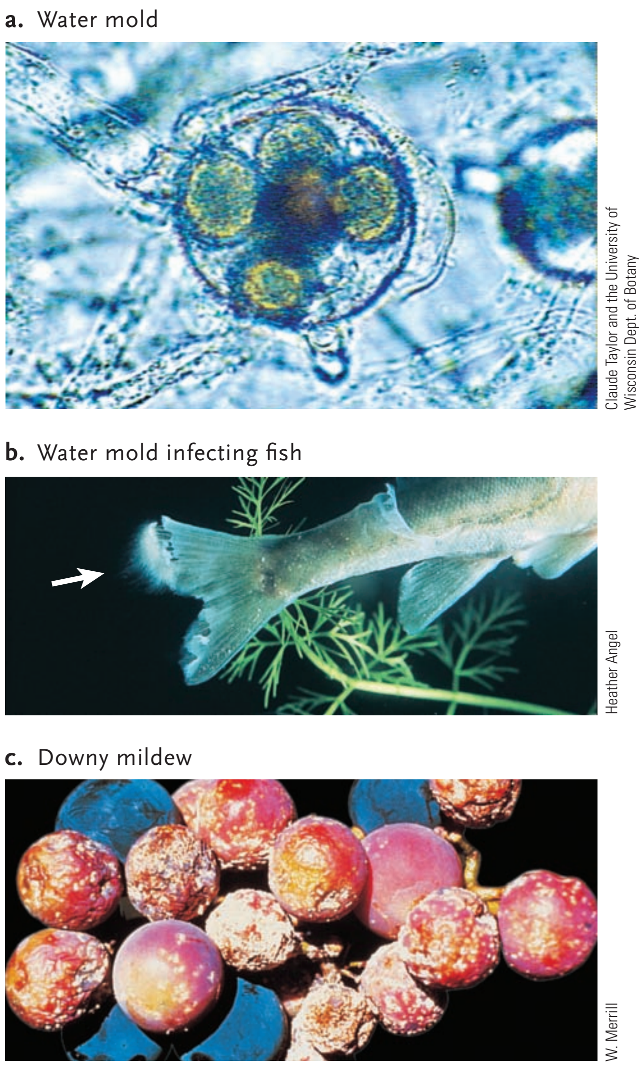
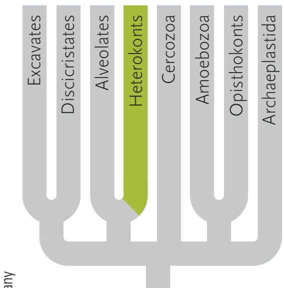


Figure 26.9
Oomycota. **(a)** The water mold *Saprolegnia parasitica.* **(b)** *S. parasitica* growing as cottony white fibers on the tail of an aquarium fish. **(c)** A downy mildew, *Plasmopara viticola*, growing on grapes. At times it has nearly destroyed vineyards in Europe and North America.

The Heterokonts Include the Largest Protists, the Brown Algae



The Heterokonts (*hetero* = different; *kontos* = pole, referring to the flagellum) are named for their two different flagella: one with hollow tripartite hairs that give the flagellum a "hairy" appearance and a second one that is plain. The flagella occur only on reproductive cells such as eggs and sperm, except in the golden algae, in which cells are flagellated in all stages. The heterokonts include the Oomycota (water molds, white rusts, and mildews—formerly classified as fungi), Bacillariophyta (diatoms), Chrysophyta (golden algae), and Phaeophyta (brown algae).

Oomycota: Water Molds, White Rusts, and Downy Mildews. The Oomycota **(Figure 26.9)** are funguslike heterokonts that lack chloroplasts and live as heterotrophs. Like fungi, they secrete enzymes that digest the complex molecules of surrounding dead or alive organic matter into simpler substances small enough to be absorbed into their cells. The water molds live almost exclusively in freshwater lakes and streams or moist terrestrial habitats; the white rusts and downy mildews are parasites of plants. Oomycota may reproduce asexually or sexually.

Like fungi, many Oomycota grow as microscopic, nonmotile filaments called **hyphae** (singular, hypha), which form a network called a **mycelium (Figure 26.10).** Other features, however, set the Oomycota apart from the fungi; chief among them are differences in nucleotide sequence, which clearly indicate close evolutionary relationships to the heterokonts rather than to the fungi. Further, nuclei in hyphae are diploid in the Oomycota, rather than haploid as in the fungi, and repro-

Focus on Research

Applied Research: Malaria and the *Plasmodium* Life Cycle

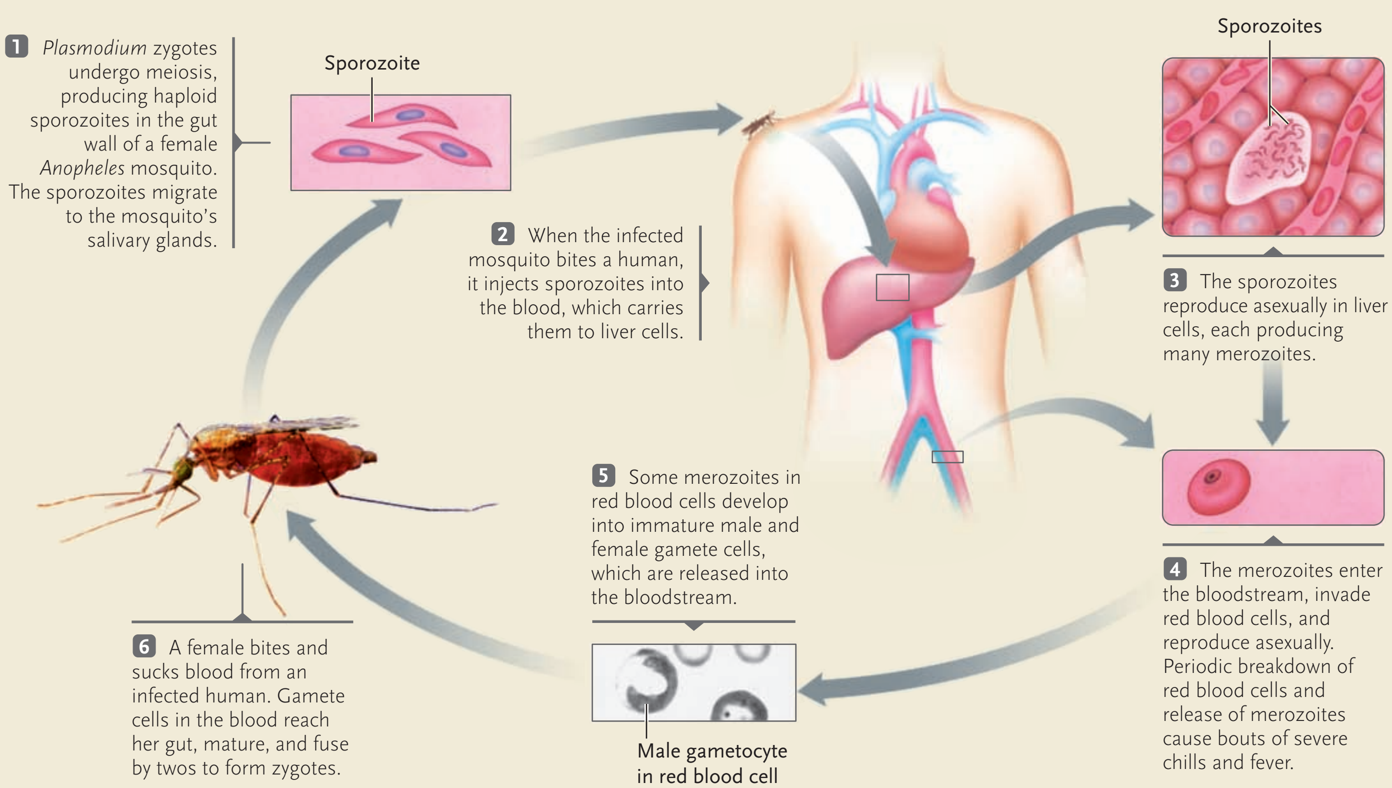
Although malaria is uncommon in the United States, it is a major epidemic in many other parts of the world. From 300 million to 500 million people become infected with malaria each year in tropical regions, including Africa, India, southeast Asia, the Middle East, Oceania, and Central and South America. Of these, about 2 million die each year, twice as many as from AIDS worldwide. It is particularly deadly for children younger than 6. In many countries where malaria is common, people are often infected repeatedly, with new infections occurring alongside preexisting infections.

Four different species of the apicomplexan genus *Plasmodium* cause malaria. In the life cycle of the parasites (see **figure**), sporozoites develop in the female *Anopheles* mosquito, which transmits them by its bite to human or bird hosts. The infecting parasites divide repeatedly in their hosts, initially in liver cells and then in red blood cells. Their growth causes red blood cells to rupture in regular cycles every 48 or 72 hours, depending on the *Plasmodium* species. The ruptured red blood cells clog vessels and release the parasite's metabolic wastes, causing cycles of chills and fever.

The victim's immune system is ineffective because, during most of the infective cycle, the parasite is inside body cells and thus "hidden" from antibodies. Further, *Plasmodium* regularly changes its surface molecules, continually producing new forms that are not recognized by antibodies developed against a previous form. In this way, the parasite keeps one step ahead of the immune system, often making malarial infections essentially permanent.

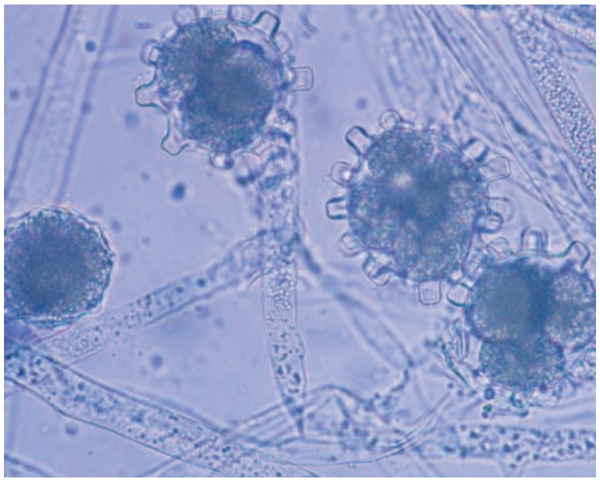
Travelers in countries with high rates of malaria are advised to use antimalarial drugs such as chloroquine, quinine, or quinidine as a preventative. However, many *Plasmodium* strains in Africa, India, and southeast Asia have developed resistance to the drugs. Vaccines have proved difficult to develop; because vaccines work by inducing the production of antibodies that recognize surface groups on the parasites, they are defeated by the same mechanisms the parasite uses inside the body to keep one step ahead of the immune reaction.

While in a malarial region, travelers should avoid exposure to mosquitoes by remaining indoors from dusk until dawn and sleeping inside mosquito nets treated with insect repellent. When out of doors, travelers should wear clothes that expose as little skin as possible and are thick enough to prevent mosquitoes from biting through the cloth. An insect repellent containing DEET should be spread on any skin that is exposed.



Life cycle of a *Plasmodium* species that causes malaria.

(Photo: Sinclair Stammers/Photo Researchers, Inc.; micrograph: Steven L'Hernault.)



Dr. John Cunningham/Visuals Unlimited

Figure 26.10
The funguslike body form of the Oomycota, consisting of filaments called hyphae, which grow into a network called a mycelium.

ductive cells are flagellated and motile; fungi have no motile stages. Finally, the cell walls of most Oomycota contain cellulose (see Figure 3.7c); fungal cell walls instead contain a different polysaccharide, chitin (see Figure 3.7d).

Most water molds are key decomposers of both aquatic and moist terrestrial habitats. Dead animal or plant material immersed in water commonly becomes coated with cottony water molds. Other water molds parasitize living aquatic animals, such as the mold growing on the fish shown in Figure 26.9a. The white rusts and downy mildews are parasites of land plants (see Figure 26.9c).

Some water molds have had drastic effects on human history. *P. infestans,* a water mold that causes rotting of potato and tomato plants, was responsible for the Irish potato famine of 1845 to 1860. In this famine more than a million people, a third of Ireland's population, starved to death. Many of the survivors migrated in large numbers to other countries, including the United States and Canada.

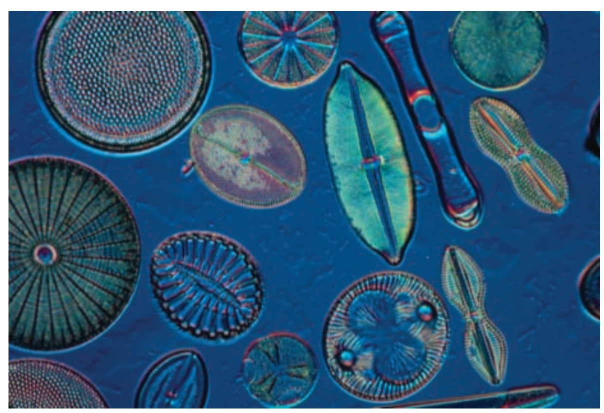
Bacillariophyta: Diatoms. The Bacillariophyta, or diatoms, are single-celled organisms that are covered by a glassy silica shell, which is intricately formed and beautiful in many species. The two halves of the shell fit together like the top and bottom of a candy box **(Figure 26.11).** Substances move to and from the plasma membrane through elaborately patterned perforations in the shell. Although flagella are present only in gametes, many diatoms move by an unusual mechanism in which a secretion released through grooves in the shell propels them in a gliding motion.

Diatoms are autotrophs that carry out photosynthesis by pathways similar to those of plants. The primary photosynthetic organisms of marine plankton, they fix more carbon into organic material than any other planktonic organism. They are also abundant in freshwater habitats as both phytoplankton and bottom-dwelling species. Although most diatoms are free living, some are symbionts inside other marine protists. One diatom, *Pseudonitzschia,* produces a toxic amino acid that can accumulate in shellfish. The amino acid, which acts as a nerve poison, causes amnesic shellfish poisoning when ingested by humans; the poisoning can be fatal.

Asexual reproduction in diatoms occurs by mitosis followed by a form of cytoplasmic division in which each daughter cell receives either the top or bottom half of the parent shell. The daughter cell then secretes the missing half, which becomes the smaller, inside shell of the box. The daughter cell receiving the larger top half grows to the same size as the parent shell, but the cell receiving the smaller bottom half is limited to the size of this shell. As asexual divisions continue, the cells receiving bottom halves become progressively smaller. Very small diatoms may switch to a sexual mode of reproduction; they enter meiosis and produce flagellated gametes, which lose their shells and fuse in pairs to form a zygote. The zygote grows to normal size before secreting a completely new shell with full-size top and bottom halves.

The shells of diatoms are common in fossil deposits. In fact, more diatoms are known as fossils than as living species—some 35,000 extinct species have been described as compared with 7000 living species. For about 180 million years the shells of diatoms have been accumulating into thick layers of sediment at the bottom of lakes and seas. Since diatoms store food as oil, fossil diatoms may be a source of oil in many oil deposits.

Grinding the fossilized shells into a fine powder produces *diatomaceous earth,* which is used in abra-



Jan Hinsch/SPL/Photo Researchers, Inc.

Figure 26.11
Diatom shells. Depending on the species, the shells are either radially or bilaterally symmetrical, as seen in this sample.

a. Golden alga

b. Brown alga, *Macrocystis*

c. Brown alga, *Postelsia palmaeformis*

Ron Hoham, Dept. of Biology, Colgate University

Lewis Trusty/Animals, Animals

Jeffrey Levinton, State University of New York, Stony Brook

Figure 26.12

Golden and brown algae. **(a)** A microscopic, swimming colony of *Synura,* a golden alga. Each cell bears two flagellae, which are not visible in this light micrograph. **(b)** A brown alga, *Macrocystis.* Note the whitish gas bladders that keep the blades floating. **(c)** The holdfast, stemlike stipes, and leaflike blades, as seen in another brown alga, the sea palm *Postelsia palmaeformis.*

sives and filters, as an insulating material, and as a pesticide. Diatomaceous earth kills crawling insects by abrading their exoskeleton, causing them to dehydrate and die. Insect larvae are killed in the same way. Insects also die when they eat the powder but larger animals, including humans, are unaffected by it.

Chrysophyta: Golden Algae. Most golden algae **(Figure 26.12a)** are colonial forms in which each cell of the colony bears a pair of flagella. The golden algae have glassy shells, but in the form of plates or scales rather than in the candy-box form of the diatoms.

Nearly all chrysophytes are autotrophs and carry out photosynthesis using pathways similar to those of plants. Their color is due to a brownish carotenoid pigment, fucoxanthin, which masks the green color of the chlorophylls. Golden algae are important in freshwater habitats and in "nanoplankton," a community of marine phytoplankton composed of huge numbers of extremely small cells. During the spring and fall, "blooms" of golden algae can give a fishy taste and brownish color to the water.

Phaeophyta: Brown Algae. The brown algae (*phaios* = brown) are photosynthetic autotrophs that range from microscopic forms to giant kelps reaching lengths of 50 m or more (Figure 26.1c and **Figure 26.12b** and **c**). Their color is also due to fucoxanthin. Their cell walls contain cellulose and a mucilaginous polysaccharide, alginic acid.

Nearly all of the 1500 known phaeophyte species inhabit temperate or cool coastal marine waters. The kelps form vast underwater forests; fragments of these algae litter the beaches in coastal regions where they grow. Great masses of another brown alga, *Sargassum,* float in an area of the mid-Atlantic Ocean called the Sargasso Sea, which covers millions of square kilometers between the Azores and the Bahamas.

Kelps are the largest and most complex of all protists. Their tissues are differentiated into leaflike *blades,* stalklike *stipes,* and rootlike *holdfasts* that anchor them to the bottom. Hollow, gas-filled bladders give buoyancy to the stipes and blades and help keep them upright. The stalks of some kelps contain tubelike vessels, similar to the vascular elements of plants, which rapidly distribute dissolved sugars and other products of photosynthesis throughout the body of the alga.

Life cycles among the brown algae are typically complex and in many species consist of alternating haploid and diploid generations **(Figure 26.13).** The large structures that we recognize as kelps and other brown seaweeds are diploid **sporophytes,** so called because they give rise to haploid spores by meiosis. The spores, which are flagellated swimming cells, germinate and divide by mitosis to form an independent, haploid **gametophyte** generation. The gametophytes give rise to haploid gametes, the egg and sperm cells. Most brown algal gametophytes are multicellular structures only a few centimeters in diameter. Cells in the gametophyte, produced by mitosis, differentiate to form flagellated, swimming sperm cells or nonmotile eggs. Fusion of a sperm and an egg cell gives rise to a diploid zygote, which grows by mitotic divisions into the sporophyte generation. Other variations occur in smaller brown algae, including some life cycles in which the sporophytes and gametophytes are the same size and some in which the gametophyte is larger than the sporophyte.

The alginic acid in brown algal cell walls, called **algin** when extracted, is an essentially tasteless and nontoxic substance used to thicken such diverse prod-

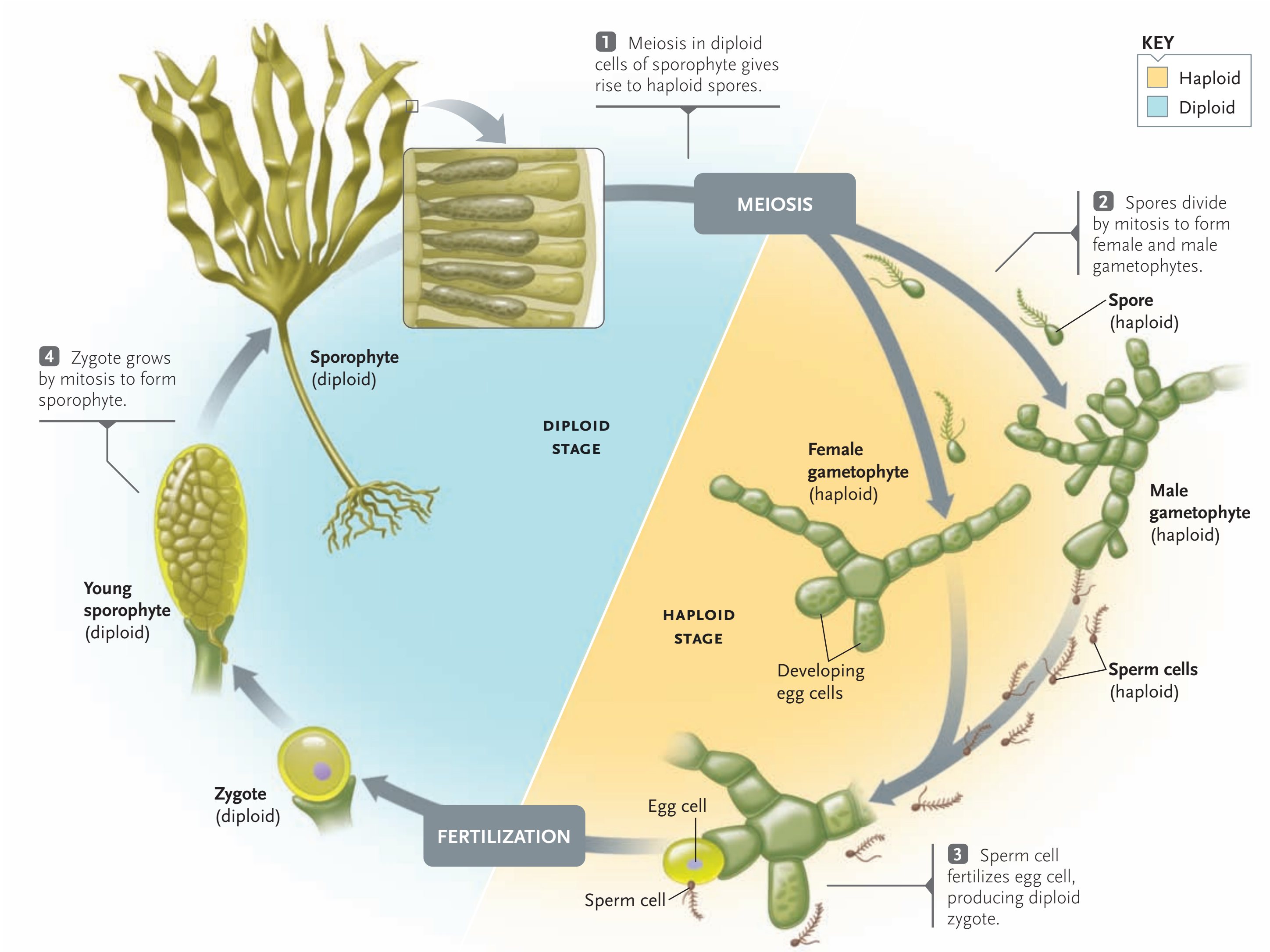
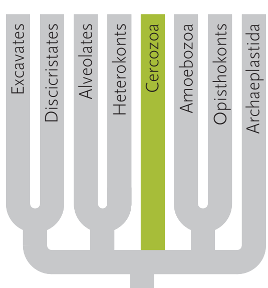


Figure 26.13
The life cycle of the brown alga *Laminaria*, which alternates between a diploid sporophyte stage and a haploid gametophyte stage.

ucts as ice cream, pudding, salad dressing, jellybeans, cosmetics, paper, and floor polish. Brown algae are also harvested as food crops and fertilizers.

The Cercozoa Are Amoebas with Filamentous Pseudopods



Amoeba is a descriptive term for a single-celled protist that moves by means of temporary cellular projections called pseudopods. Several major groups of protists contain amoebas, which are similar in form but are not all closely related. The amoebas classified in cercozoa produce stiff, filamentous pseudopodia, and many produce hard outer shells, also called *tests*. We consider here two heterotrophic groups of cercozoan amoebae, the Radiolaria and the Foraminifera, and a third, photosynthesizing group, the Chlorarachniophyta.

Radiolaria. Radiolarians are distinguished by axopods, slender, raylike strands of cytoplasm supported internally by long bundles of microtubules. They engulf prey organisms that stick to the axopods and digest them in food vacuoles.

Radiolarians live in marine environments. They secrete a glassy internal skeleton from which the axopods project (**Figure 26.14a** and **b**). Just outside the skeleton, the cytoplasm is crowded with frothy vacuoles and lipid droplets, which provide buoyancy.

The skeletons of dead radiolarians sink to the bottom and become part of the sediment. Over time, they harden into sedimentary rocks that form an important part of the geological record.

Foraminifera: Forams. Foraminifera, or forams, live in marine environments. Their shells consist of organic matter reinforced by calcium carbonate **(Figure**

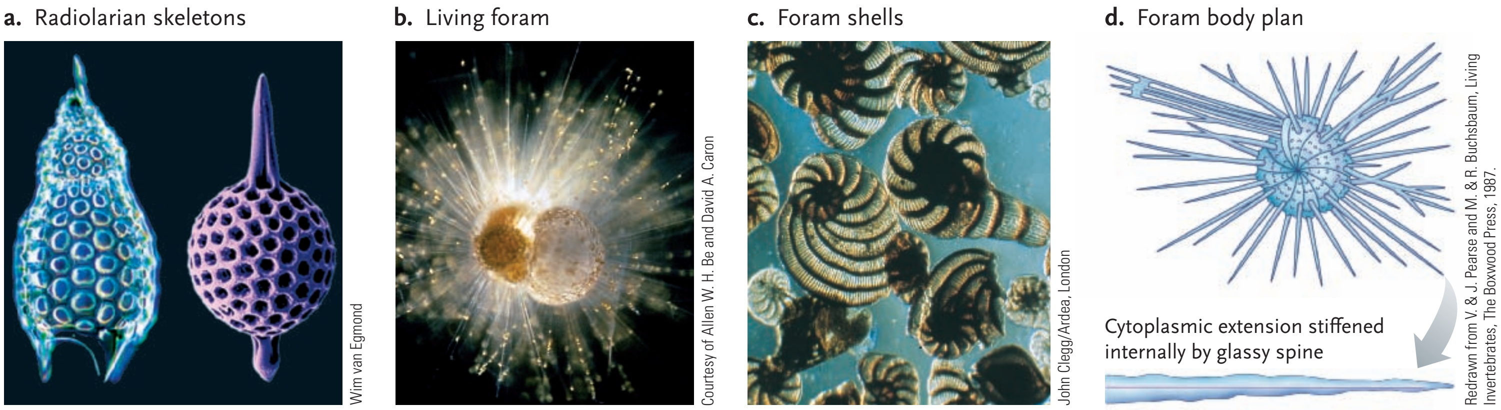


Figure 26.14

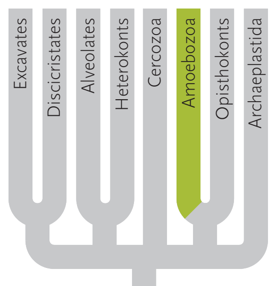
Radiolarians and forams. **(a)** The internal skeletons of two radiolarian species, possibly *Pterocorys* and *Stylosphaera.* Bundles of microtubules support the cytoplasmic extensions of the radiolarians. **(b)** A living foram, showing the cytoplasmic strands extending from its shell. **(c)** Empty foram shells. **(d)** The body plan of a foram. Needlelike, glassy spines support the cytoplasmic extensions of the forams.

26.14c–d). Most foram shells are chambered, spiral structures that, although microscopic, resemble those of mollusks. Forams are identified and classified primarily by the form of the shell; about 250,000 species are known. Some species are planktonic, but they are most abundant on sandy bottoms and attached to rocks along the coasts. Their name comes from the perforations in their shells (*foramen* = little hole), through which extend long, slender strands of cytoplasm supported internally by a network of needlelike spines. The forams engulf prey that adhere to the strands and conduct them through the holes in the shell into the central cytoplasm, where they are digested in food vacuoles. Some forams have algal symbionts that carry out photosynthesis, allowing them to live as both heterotrophs and autotrophs.

Marine sediments are typically packed with the shells of dead forams. The sediments may be hundreds of feet thick; the White Cliffs of Dover in England are composed primarily of the shells of ancient forams. Most of the world's deposits of limestone and marble contain foram shells; the great pyramids and many other monuments of ancient Egypt are built from blocks cut from fossil foram deposits. Because distinct species lived during different geological periods, they are widely used to establish the age of sedimentary rocks containing their shells. They, along with radiolarian species, are also used as indicators by oil prospectors because layers of forams often overlie oil deposits.

Chlorarachniophyta. Chloroarachniophytes are green, photosynthetic amoebas that also engulf food. They contain chlorophylls *a* and *b,* but they are phylogenetically distinct from other chlorophyll *b*–containing eukaryotes. Many filamentous pseudopodia extend from the cell surface.

The Amoebozoa Includes Most Amoebas and Two Types of Slime Molds



The Amoebozoa includes most of the amoebas (others are in the Cercozoa) as well as the cellular and plasmodial slime molds. All members of this group use pseudopods for locomotion and feeding for all or part of their life cycles.

Amoebas. Amoebas of the Amoebozoa are single-celled organisms that are abundant in marine and freshwater environments and in the soil. They use pseudopods for locomotion and feeding. The pseudopods extend and retract at any point on their body surface and are unsupported by any internal cellular organization. This type of pseudopod—called a *lobose* ("lobelike") *pseudopod*—distinguishes these amoebas from those in the Cercozoa, which have stiff, supported pseudopods. As a result of their pseudopod activity, and the ability to flatten or round up, these amoebas have no fixed body shape. A number of species are parasites, but most species feed on algae, bacteria, other protists, and bits of organic matter. The ingested matter is enclosed in food vacuoles and digested by enzymes secreted into the vacuoles. Any undigested matter is expelled to the outside by fusion of the vacuole with the plasma membrane. Their reproduction is entirely asexual, through mitotic divisions.

The most-studied amoebozoan is *Amoeba proteus* **(Figure 26.15).** Its natural habitat is in freshwater ponds and streams. Another member, *Acanthamoeba,* which lives in the soil, is widely used as a source of actin and

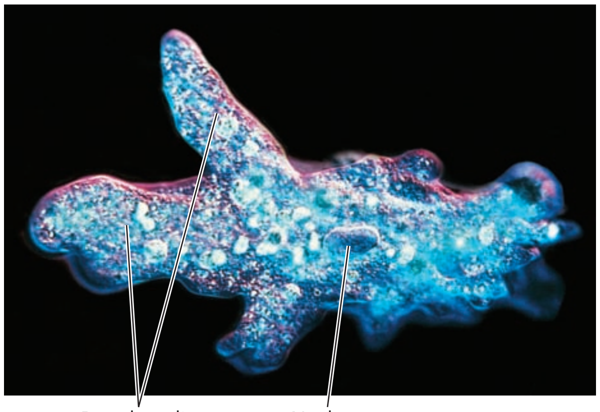


Figure 26.15 *Amoeba proteus* of the Amoebozoa is perhaps the most familiar protist of all.

myosin for scientific studies of amoeboid motion and cytoplasmic streaming.

The parasitic amoebas include some 45 species that infect the human digestive tract, one in the mouth and the rest in the intestine. One of the intestinal parasites, *Entamoeba histolytica,* causes amoebic dysentery. Cysts of this amoeba contaminate water supplies and soil in regions with inadequate sewage treatment. When ingested, a cyst breaks open to release an amoeba that feeds and divides rapidly in the digestive tract. Enzymes released by the amoebas destroy cells lining the intestine, producing the ulcerations, painful cramps, and debilitating diarrhea characteristic of the disease. Amoebic dysentery afflicts millions of people worldwide; in less-developed countries, it is a leading cause of death among infants and small children. Other parasitic amoebas cause less severe digestive upsets.

Slime Molds. Slime molds are heterotrophic protists that, at some stage of their life cycle, exist as individuals that move by amoeboid motion but the remainder of the time exist in more complex forms. They live on moist, rotting plant material such as decaying leaves and bark. The cells engulf particles of dead organic matter, and also bacteria, yeasts, and other microorganisms, and digest them internally. At one stage of their life cycles, they differentiate into a funguslike, stalked structure called a **fruiting body,** which forms spores by either asexual or sexual reproduction. Some species are brightly colored in hues of yellow, green, red, orange, brown, violet, or blue. The two major evolutionary lineages of slime molds, the cellular slime molds and the plasmodial slime molds, differ in cellular organization.

The Cellular Slime Molds. **Cellular slime molds** exist primarily as individual cells, either separately or as a coordinated mass. Among the 70 or so species of cellular slime molds, *Dictyostelium discoideum* is best known; its genome sequence was reported in May 2005. Its life cycle begins when a haploid spore lands in a suitably moist environment containing decaying organic matter **(Figure 26.16).** The spore germinates into an amoeboid cell that grows and divides mitotically into separate haploid cells as long as the food source lasts. When the food supply dwindles, some of the cells release a chemical signal (cyclic AMP; see Section 7.4) in pulses; in response, the amoebas move together and form a sausage-shaped mass that crawls in coordinated fashion like a slug. Some "slugs," although not much more than a millimeter in length, contain more than 100,000 individual cells. At some point the slug stops moving and differentiates into a stalked fruiting body, with cell walls reinforced by cellulose. When mature, the head of the fruiting body bursts, releasing spores that are carried by wind, water, or animals to new locations. Because the cells forming the slug and fruiting body are all products of mitosis, this pattern of reproduction is asexual.

Cellular slime molds also reproduce sexually by a pattern in which two haploid cells fuse to form a diploid zygote (also shown in Fig. 26.16) that enters a dormant stage. Eventually, the zygote undergoes meiosis, producing four haploid cells that may multiply inside the spore by mitosis. When conditions are favorable, the spore wall breaks down, releasing the cells. These grow and divide into separate amoeboid cells.

The Plasmodial Slime Molds. **Plasmodial slime molds** exist primarily as a large composite mass, the **plasmodium,** in which individual nuclei are suspended in a common cytoplasm surrounded by a single plasma membrane. (This is not to be confused with *Plasmodium,* the genus of apicomplexans that causes malaria.) There are about 500 known species of plasmodial slime molds. The main phase of the life cycle, the plasmodium (see Figure 26.1a), flows and feeds as a single huge amoeba—a single cell that contains thousands to millions or even billions of diploid nuclei surrounded by a single plasma membrane. Typically, a plasmodium, which may range in size from a few centimeters to more than a meter in diameter, moves in thick, branching strands connected by thin sheets. The movements occur by cytoplasmic streaming, driven by actin microfilaments and myosin (see Section 5.3). You may have seen one of these slimy masses crossing a lawn, moving over a mat of dead leaves, climbing a tree, or even in the movies—a slime mold in effect stars as a monster in the science fiction movie *The Blob.*

At some point, often in response to unfavorable environmental conditions, fruiting bodies form at sites on the plasmodium. At the tips of the fruiting bodies, nuclei become enclosed in separate cells, each surrounded by its own plasma membrane and cell wall. Depending on the species, either chitin or cellulose may reinforce the walls. These cells undergo meiosis, forming haploid, resistant spores that are released from the fruiting bodies and carried about by water or wind. If they reach a favorable environment, the spores germinate to form flagellated or unflagellated gametes, depending on the species, that fuse to form a diploid

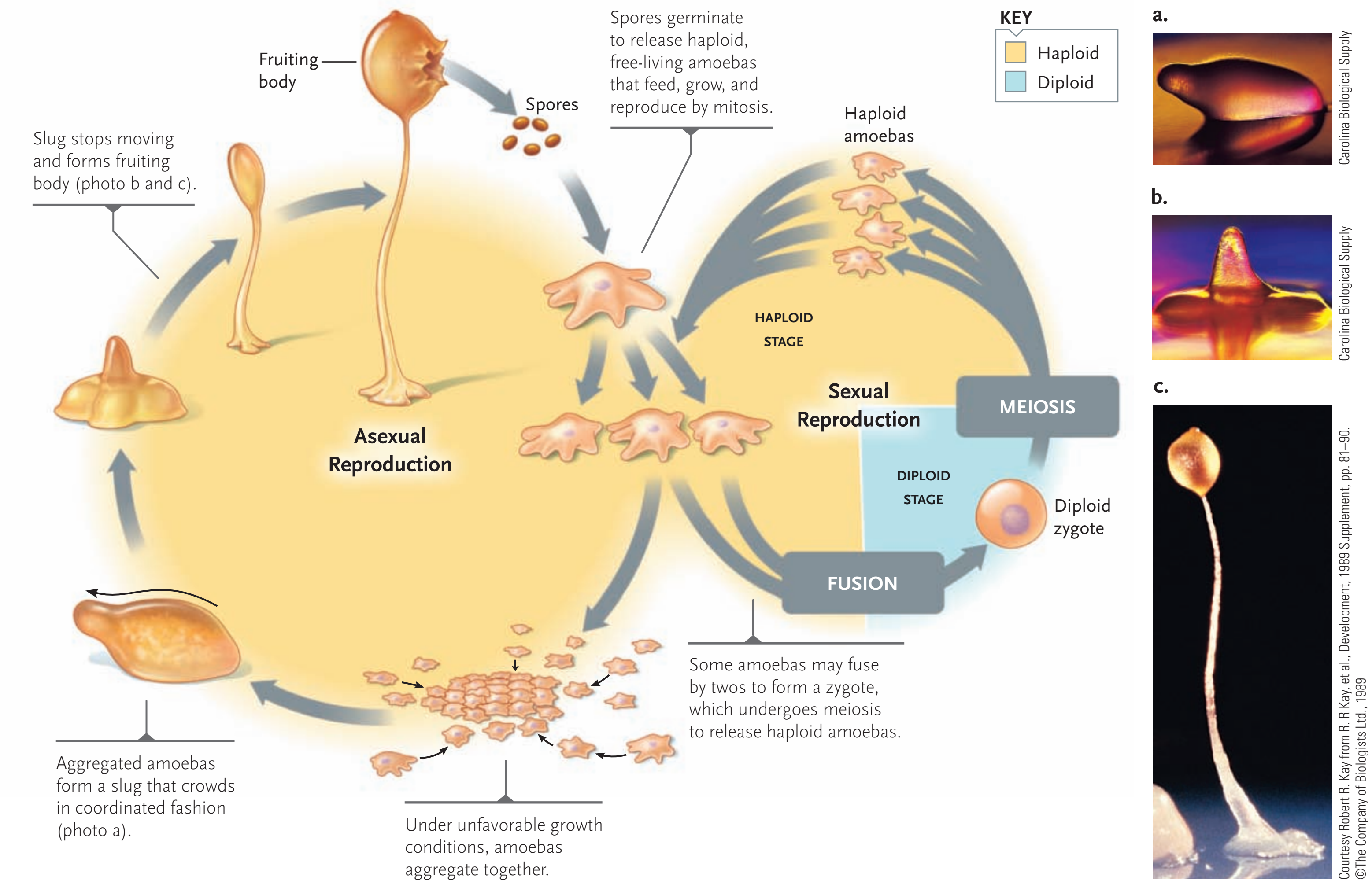


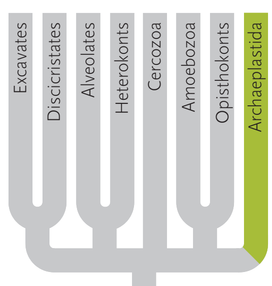
Figure 26.16 Life cycle of the cellular slime mold *Dictyostelium discoideum.* The light micrographs show **(a)** a migrating slug, **(b)** an early stage in fruiting body formation, and **(c)** a mature fruiting body.

zygote. The zygote nucleus then divides repeatedly without an accompanying division of the cytoplasm, forming many diploid nuclei suspended in the common cytoplasm of a new plasmodium.

The Slime Molds in Science. Both the cellular and plasmodial slime molds, particularly *Dictyostelium* (cellular) and *Physarum* (plasmodial; see Figure 26.1a), have been of great interest to scientists because of their ability to differentiate into fruiting bodies with stalks and spore-bearing structures. This differentiation is much simpler than the complex developmental pathways of other eukaryotes, providing a unique opportunity to study cell differentiation at its most fundamental level. One such study, examining the role of cyclic AMP in differentiation, is described in *Insights from the Molecular Revolution.*

The plasmodial slime molds are particularly useful in this kind of research because they become large enough to provide ample material for biochemical and molecular analyses. Actin and myosin extracted from *Physarum polycephalum,* for example, have been much used in studies of actin-based motility. A further advantage of plasmodial slime molds is that the many nuclei of a plasmodium usually replicate and pass through mitosis in synchrony, making them useful in research tracking the changes that take place in the cell cycle.

The Archaeplastida Include the Red and Green Algae, and Land Plants



The Archaeplastida consist of the red and green algae, which are protists, and the land plants (the *viridaeplantae,* or "true plants"), which comprise the kingdom Plantae. These three groups have a common evolutionary origin, and they are all photosynthesizers. Here we describe the two types of algae; we discuss land plants in Chapter 27.

Rhodophyta: The Red Algae. Nearly all the 4000 known species of red algae, which are also known as the Rhodophyta (*rhodon* = rose), are small marine seaweeds **(Figure 26.17).** Fewer than 200 species are found in freshwater lakes and streams or in soils. Most red algae grow

Insights from the Molecular Revolution

Getting the Slime Mold Act Together

Development of differentiated structures can be followed at its simplest level in slime molds. In the cellular slime mold *Dictyostelium discoidium*, the aggregation of individual cells leading to differentiation begins when unfavorable living conditions induce some cells to secrete cyclic AMP (cAMP). Other *Dictyostelium* cells move toward the regions of highest cAMP concentration and aggregate into the slug stage. Further pulses of cAMP trigger differentiation into a stalk and spores.

Within the aggregating cells, the cAMP activates a cAMP-dependent protein kinase (PKA; see Section 7.4). The PKA, which is active only when cAMP is present, adds phosphate groups to target proteins in the cells. The target proteins, activated or deactivated by addition of the phosphate groups, trigger cellular developmental processes that lead to slug formation and differentiation of the stalk and spores.

These observations prompt several questions about development in *Dictyostelium*. Which is more important to the process, cAMP or the PKA? Is the PKA the only enzyme activated by the cAMP signal, or are other cAMP-activated pathways also essential to cell differentiation in the slime mold?

Adam Kuspa and his graduate student Bin Wang at Baylor College of Medicine in Houston, Texas, set out to answer these questions. They were aided by the availability of a mutant strain of *Dictyostelium* that lacks a normal form of *adenylyl cyclase*, the enzyme that converts ATP into cAMP.

Kuspa and Wang constructed an artificial gene by linking the promoter of an actin gene to the protein-encoding portion of a gene for the PKA. They chose the actin promoter because it is highly active and would induce essentially continuous transcription of the gene to which it is attached. The enzyme encoded in the artificial PKA gene was a modified form that does not require cAMP to be active, making it a *cAMP-independent* protein kinase. The researchers induced the mutant cells to take up the artificial gene by exposing them to Ca^{2+} ions (see Section 17.1). Once inside the cells, the actin promoter resulted in transcription of the artificial PKA gene, raising internal PKA concentration to levels about 1.6 times the amount in normal cAMP-activated cells.

Kuspa and Wang found that the cells with the artificial PKA gene aggregated into slugs when their cultures were deprived of food (in this case, bacteria). Moreover, the slugs differentiated normally into fruiting bodies. Tests for cAMP failed to detect the signal molecule, indicating that activated PKA by itself can trigger all the steps in the developmental pathway. Thus the requirement for cAMP in normal slime mold development is primarily or exclusively to stimulate the PKA. And, because development can proceed with active PKA alone, this protein kinase is probably more central to the growth and differentiation processes of the slime mold than is cAMP. Further, it appears from the results that no essential developmental pathways other than those involving PKA are triggered by cAMP.

These results are of more than passing interest because both cAMP and cAMP-dependent protein kinases are also active in animal development and intercellular signaling, including that of humans and other mammals. They also show that in *Dictyostelium*, a single molecule, the PKA normally activated by cAMP, can trigger all stages of development and differentiation.

attached to sandy or rocky substrates, but a few occur as plankton. Although most are free-living autotrophs, some are parasites that attach to other algae or plants.

Red algae are typically multicellular organisms, with plantlike bodies composed of interwoven filaments. The base of the body is differentiated into a holdfast, which anchors it to the bottom or other solid substrate, and into stalks with leaflike plates. Their cell walls contain cellulose and mucilaginous pectins that give them a slippery texture. In some species, the walls

a. Filamentous red alga

b. Sheetlike red alga

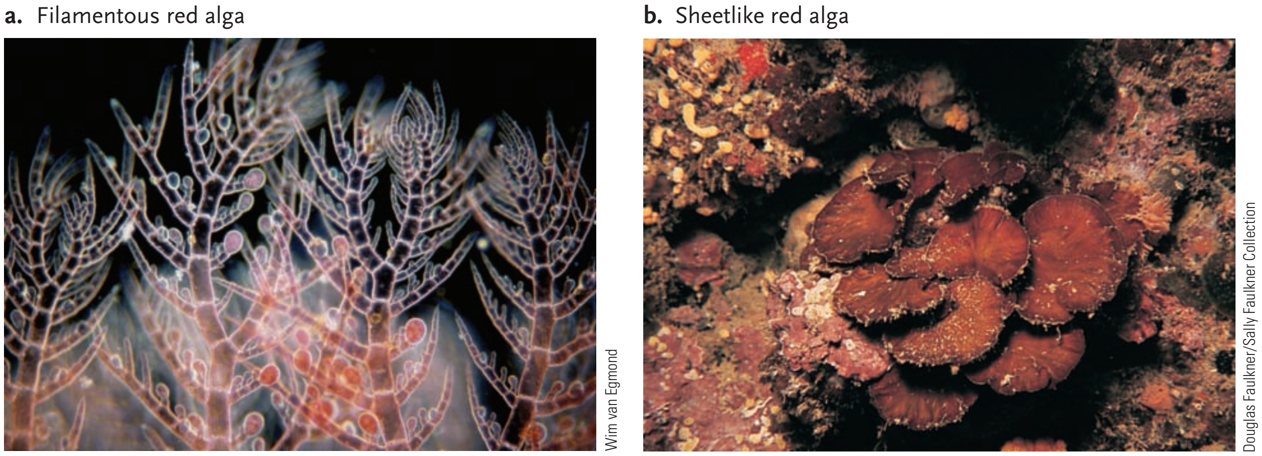


Figure 26.17 Red algae. **(a)** *Antithamnion plumula*, showing the filamentous and branched body form most common among red algae. **(b)** A sheetlike red alga growing on a tropical reef.

are hardened with stonelike deposits of calcium carbonate. Many of the red algae with stony cell walls resemble corals and occur with corals in reefs and banks.

Although most red algae are reddish in color, some are greenish purple or black. The color differences are produced by accessory pigments, mainly *phycobilins,* which mask the green color of their chlorophylls. The phycobilins are unusual photosynthetic pigments with structures related to the ring structure of hemoglobin. The accessory pigments of some red algae make them highly efficient in absorbing the shorter wavelengths of light that penetrate to the ocean depths, allowing them to grow at deeper levels than any other algae. Some red algae live at depths to 260 m if the water is clear enough to transmit light to these levels.

Red algae have complex reproductive cycles involving alternation between diploid sporophytes and haploid gametophytes. No flagellated cells occur in the red algae; instead, gametes are released into the water to be brought together by random collisions in currents.

Extracts containing the mucilaginous pectins of red algal cell walls are widely used in industry and science. Extracted **agar** is used as a moisture-preserving, inert agent in cosmetics and baked goods, as a setting agent for jellies and desserts, and as a culture medium in the laboratory. **Carrageenan,** extracted from the red alga *Eucheuma,* is used to thicken and stabilize paints, dairy products such as pudding and ice cream, and many other creams and emulsions.

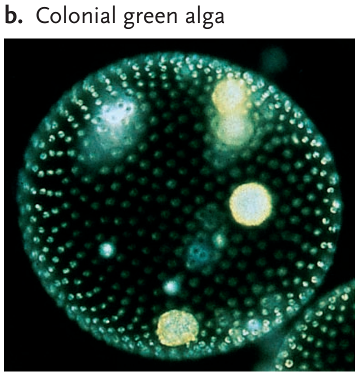
Some red algae are harvested as food in Japan and China. *Porphyra,* one of these harvested algae, is used in sushi bars as the *nori* wrapped around fish and rice. Different *Porphyra* species have different flavors; all are nutritious.

Chlorophyta: The Green Algae. The green algae or Chlorophyta (*chloros* = green) are autotrophs that carry out photosynthesis using the same pigments as plants. They include single-celled, colonial, and multicellular species (**Figure 26.18;** see also Figure 26.1d). Most green algae are microscopic, but some range upward to the size of small seaweeds. Although the multicellular green algae have bodies that are filamentous, tubular, or leaflike, there is relatively little cellular differentiation as compared with the brown algae. However, the most complex green algae, such as the sea lettuce *Ulva* (see Figure 26.18c), have tissues differentiated into a leaflike body and a holdfast.

a. Single-celled green alga

Linda Sims/Visuals Unlimited

b. Colonial green alga



Brian Parker/Tom Stack and Associates

c. Multicellular green alga

Manfrage Kage/Peter Arnold, Inc.

Figure 26.18
Green algae. **(a)** A single-celled green alga, *Acetabularia,* which grows in marine environments. Each individual in the cluster is a large single cell with a rootlike base, stalk, and cap. **(b)** A colonial green alga, *Volvox.* Each green dot in the spherical wall of the colony is a potentially independent, flagellated cell. Daughter colonies can be seen within the parent colony. **(c)** A multicellular green alga, *Ulva,* common to shallow seas around the world.

With at least 16,000 species, green algae show more diversity than any other algal group. Most live in freshwater aquatic habitats, but some are marine, or live on rocks and soil surfaces, on tree bark, or even on snow. The green, slimy mat that grows profusely in stagnant pools and ponds, for example, consists of filaments of a green alga. A few species live as symbionts in other protists or in fungi and animals. Lichens (see Figure 28.14) are the primary example of a symbiotic relationship between green algae and fungi. Many animal phyla, including some marine snails and sea anemones, contain green algal chloroplasts, or entire green algae, as symbionts in their cells.

Life cycles among the green algae are as diverse as their body forms. Many can reproduce either sexually or asexually, and some alternate between haploid and diploid generations. Gametes in different species may be undifferentiated flagellated cells, or differentiated as a flagellated sperm cell and a nonmotile egg cell. Most common is a life cycle with a multicellular haploid phase and a single-celled diploid phase **(Figure 26.19).**

Among all the algae, the nucleic acid sequences of green algae are most closely related to those of land plants. In addition, as we have noted, green algae use the same photosynthetic pigments as plants, including chlorophylls *a* and *b,* and have the same complement of carotenoid accessory pigments. In some green algae, the thylakoid membranes within chloroplasts are arranged into stacks resembling the grana of plant chloroplasts (see Section 5.4). As storage reserves,

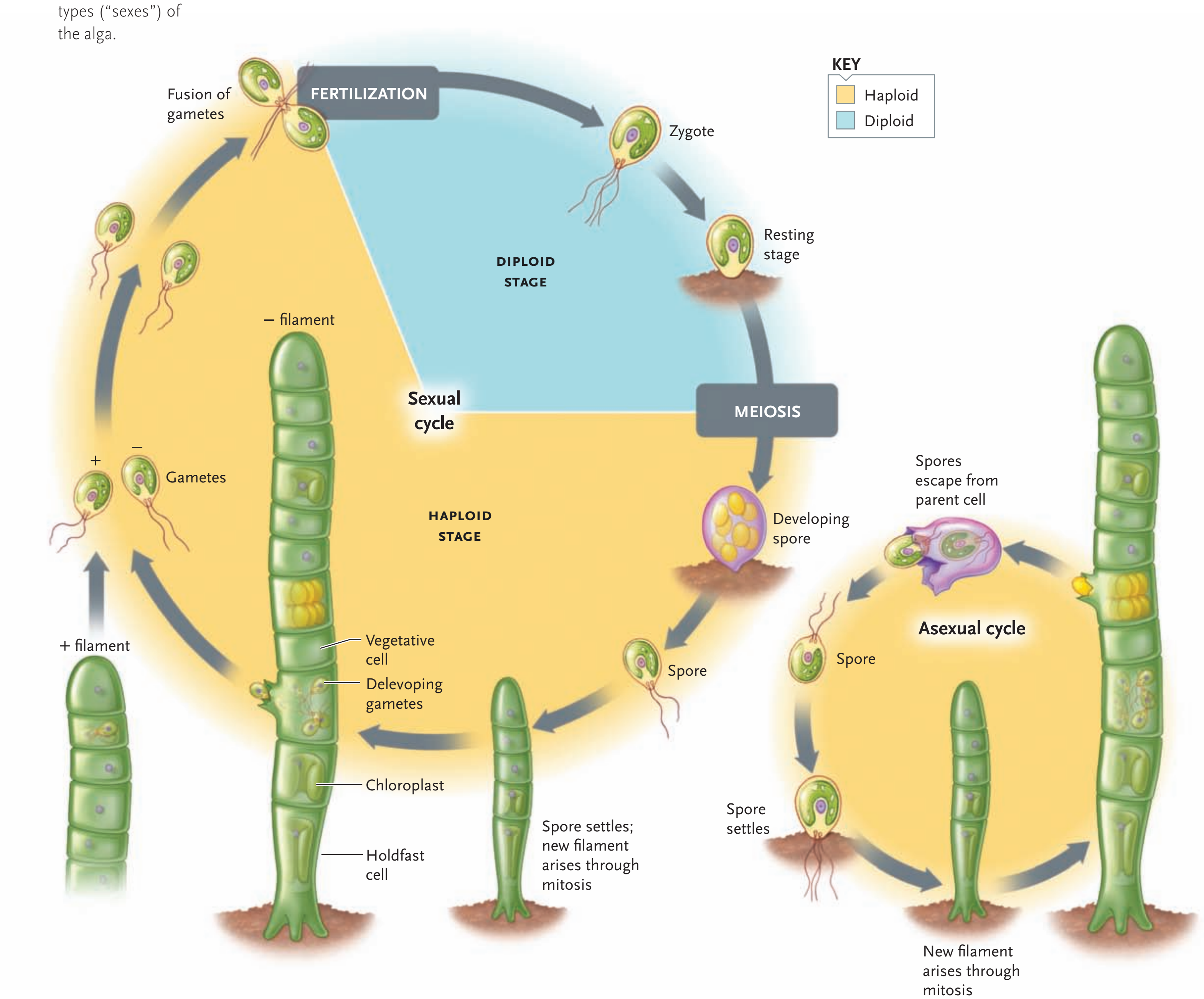


Figure 26.19
The life cycle of the green alga *Ulothrix,* in which the haploid stage is multicellular and the diploid stage is a single cell, the zygote. "+" and "−" are morphologically identical mating types ("sexes") of the alga.

green algae contain starches of the same types as plants, and the cell walls of some green algal species contain cellulose, pectins, and other polysaccharides like those of plants. On the basis of these similarities, many biologists propose that some ancient green algae gave rise to the evolutionary ancestors of modern-day plants.

What green alga might have been the ancestor of modern land plants? Many biologists consider a group known as the **charophytes** to be most similar to the algal ancestors of land plants. These organisms, including *Chara* **(Figure 26.20),** *Spirogyra, Nitella,* and *Coleochaete,* live in freshwater ponds and lakes. Their ribosomal RNA and chloroplast DNA sequences are more closely related to plant sequences than those of any other green alga. Further, the new cell wall separating daughter cells in charophytes is formed through development of a cell plate, by a mechanism closely similar to that of plants (see Section 10.2). The body form is distinctly plantlike, with a stemlike axis upon which whorls of leaflike blades occur at intervals.

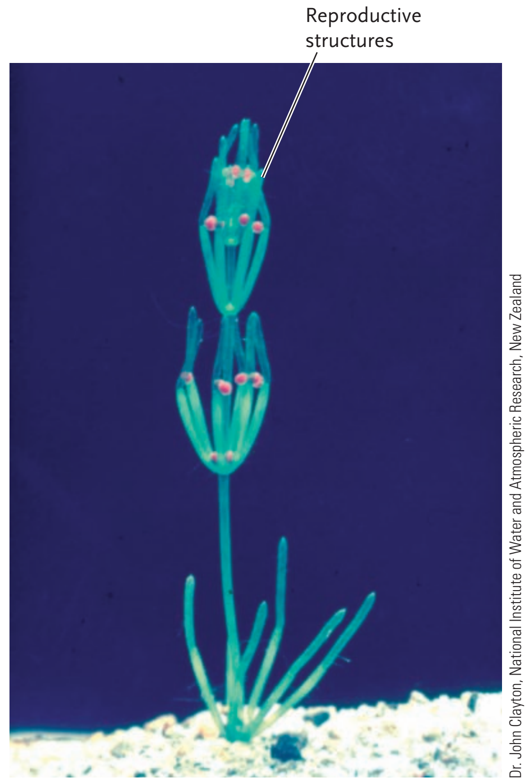
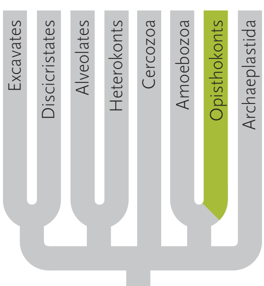


Figure 26.20 The charophyte *Chara*, representative of a group of green algae that may have given rise to the plant kingdom.

The Opisthokonts Include the Choanoflagellates, Which May Be the Ancestors of Animals



Opisthokonts (*opistho* = posterior) are a broad group of eukaryotes that includes the choanoflagellates, protists thought to be the ancestors of fungi and animals. A single posterior flagellum is found at some stage in the life cycle of these organisms; sperm in animals is an example.

Choanoflagellata (*choanos* = collar) are named for a collar of closely packed microvilli that surrounds the single flagellum by which these protists move and take in food **(Figure 26.21).** The collar resembles an upside-down lampshade. There are about 150 species of choanoflagellates. They live in fresh and marine waters. Some species are mobile, with the flagellum pushing the cells along, as is the case with animal sperm, in contrast to most flagellates, which are pulled by their flagella. Most choanoflagellates, though, are *sessile;* that is, attached via a stalk to a surface. A number of species are colonial with a cluster of cells on a single stalk.

Choanoflagellates have the same basic structure as choanocytes (collar cells) of sponges, and they are similar to collared cells that act as excretory organs in organisms such a the flatworms and rotifers. These morphological similarities, as well as molecular sequence comparison data, indicate that a choanoflagellate type of protist is likely to have been the ancestor of animals and, of course, of present-day choanoflagellates.

In Several Protist Groups, Plastids Evolved from Endosymbionts

We have encountered chloroplasts in a number of eukaryotic organisms in this chapter: red algae, green algae, land plants, euglenoids, dinoflagellates, heterokonts, and chlorarachniophytes. How did these chloroplasts evolve?

In Section 24.3 we discussed the endosymbiont hypothesis for the origin of eukaryotes. In brief, an anaerobic prokaryote ingested an aerobic prokaryote, which survived as an endosymbiont (see Figure 24.7). Over time, the endosymbiont became an organelle, the mitochondrion, which was incapable of free living, and the result was a true eukaryotic cell. Cells of animals,

Figure 26.21 A choanoflagellate.

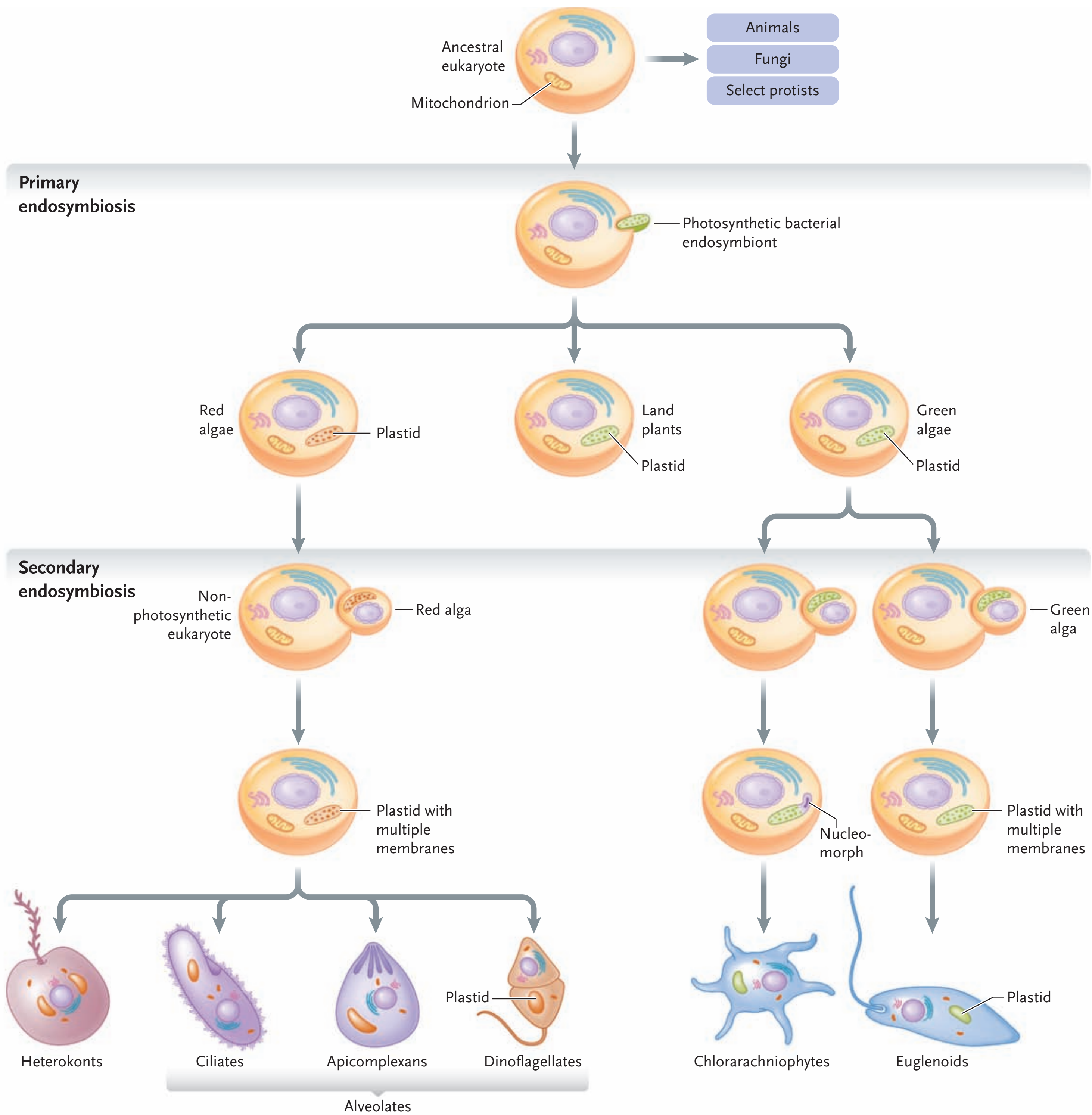


Figure 26.22 The origin and distribution of plastids among the eukaryotes by primary and secondary endosymbiosis.

fungi, and some protists derive from this ancestral eukaryote. The addition of plastids (the general term for chloroplasts and related organelles) through further endosymbiotic events produced the cells of all photosynthetic eukaryotes, including land plants, algae, and some other protists.

Figure 26.22 presents a model for the origin of plastids in eukaryotes through two major endosymbiosis events. First, in a single **primary endosymbiosis** event perhaps 600 million years ago, a eukaryotic cell engulfed a photosynthetic cyanobacterium (a photosynthetic prokaryote, remember). In some such cells, the cyanobacterium was not digested, but instead formed a symbiotic relationship with the engulfing host cell—it become an endosymbiont. Over time the symbiont lost genes no longer required for independent existence, and most of the remaining genes migrated from the prokaryotic genome to the host's nuclear genome.

The symbiont had become an organelle—a chloroplast. All plastids subsequently evolved from this original chloroplast. Evidence for the single origin of plastids comes from a variety of sequence comparisons, including recent sequencing of the genomes of key protists, a red alga and a diatom.

The first photosynthesizing eukaryote was essentially an ancestral single-celled alga. The chloroplasts of the Archaeplastida—the red algae, green algae, and land plants—result from evolutionary divergence of this organism. Their chloroplasts, which originate from primary endosymbiosis, have two membranes, one from the plasma membrane of the engulfing eukaryote and the other from the plasma membrane of the cyanobacterium.

At least three **secondary endosymbiosis** events led to the plastids in other protists (see Figure 26.22). In each case, a nonphotosynthetic eukaryote engulfed a photosynthetic eukaryote, and new evolutionary lineages were produced. In one of these events, a red alga ancestor was engulfed and became an endosymbiont. In models accepted by a number of scientists, the transfer of functions that occurred over evolutionary time led to the chloroplasts of the heterokonts and the dinoflagellates. And, from the same photosynthetic ancestor, loss of chloroplast functions occurred

Unanswered Questions

What was the first eukaryote?

Since prokaryotes precede eukaryotes in the fossil record, we assume that eukaryotes arose after prokaryotes. The first eukaryote would have been some sort of protist—a single-celled organism with a nucleus and some rudimentary organelles, perhaps even a half-tamed mitochondrion. One approach to identifying which of the surviving protists is the most ancient has been to infer evolutionary trees from gene sequence data. To determine the earliest branching eukaryote, these trees need to include the prokaryotes. But herein lies the problem—prokaryotes are very distant, evolutionarily speaking, from even the simplest eukaryotes, and the mathematical models used to construct evolutionary trees are not yet up to the job. Initially, these models suggested that some protist parasites, like the excavates *Giardia* and *Trichomonas,* might be the most ancient eukaryotes, and this idea fit nicely with the fact that these protists lacked mitochondria. Indeed, for a time it was thought that the excavates might actually have diverged from the eukaryotic branch of life before the establishment of mitochondria. Nowadays, we know that *Giardia* and *Trichomonas* did initially have mitochondria. The latest research shows that they even have a tiny relic of the mitochondrion, though exactly what it does in these oxygen-shunning parasites remains to be figured out. Thus, trees depicting *Giardia* and *Trichomonas* at the base of the great expansion of eukaryotic life must be viewed with some caution—these protists might be the surviving representatives of the earliest cells with a nucleus, but they might not be. We simply need better methods for identifying just what the first eukaryotes were like.

How many times did plastids arise by endosymbioses?

For many years researchers thought that the green algae, plants, and red algae were the only organisms to have primary endosymbiosis-derived plastids. However, a second, independent primary endosymbiosis has been recently discovered in which a shelled amoeba has captured and partially domesticated a cyanobacterium. This organism, known as *Paulinella,* is a vital window into the process by which autotrophic eukaryotes first arose some 600 million years. *Paulinella* has tamed the cyanobacterium sufficiently to have it divide and segregate in coordination with host cell division, but the endosymbiont is still very much a cyanobacterium and has undergone little of the modification and streamlining we see in the red or green algal plastids.

After a primary endosymbiosis was established, the second chapter in plastid acquisition could take place. Secondary endosymbiosis involves a eukaryotic host engulfing and retaining a eukaryotic alga. Essentially, secondary endosymbiosis can convert a heterotrophic organism into an autotroph by hijacking a photosynthetic cell and putting it to work as a solar-powered food factory. Secondary endosymbiosis results in plastids with three or four membranes, and we know that it occurred at least three times—once for the euglenoids, once for the chlorarachniophytes, and once for the chromalveolates (a proposed grouping of heterokonts and alveolates). We can even tell what kind of endosymbiont was involved by the biochemistry and genetic makeup of the plastid: a green alga for euglenoids and chlorarachniophytes, and a red alga for chromalveolates. The number of secondary endosymbioses is hotly debated, largely because not all protistologists support the existence of chromalveolates. Some contend that there were multiple, independent enslavements of different red algae to produce the dinoflagellates, heterokonts, and apicomplexans. Understanding these events is crucial to confirming or refuting the proposed chromalveolate "supergroup."

A nice example of secondary endosymbiosis-in-action was recently discovered by Japanese scientists who found a flagellate, *Hatena,* with a green algal endosymbiont. *Hatena* hasn't yet assumed control of endosymbiont division and has to get new symbionts each time it divides, so it appears to be at a very early stage in establishing a relationship. We also want to know how secondary endosymbioses proceed because they have been a major driver in eukaryotic evolution. The heterokonts, for instance, are the most important ocean phytoplankton and are key to ocean productivity and global carbon cycling. Knowing exactly how they got to be autotrophs in the first place is fundamental to understanding the world we live in.

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in the lineage of the Apicomplexa, which have a remnant plastid. In an independent event, a nonphotosynthetic eukaryote engulfed a green alga ancestor. Subsequent evolution in this case produced the euglenoids. In a different event, a similar endosymbiosis involving a green alga led to the chlorarachniophytes. In these protists, the chloroplast is contained still within the remnants of the original symbiont cell, with a vestige of the original nucleus (the nucleomorph) also present.

Note that secondary endosymbiosis has produced plastids with additional membranes acquired from the new host, or series of hosts. For example, euglenoids have plastids with three membranes, while chlorarachniophytes have plastids with four membranes (see Figure 26.22). Sequencing the genomes of the chlorarachniophyte's nucleus, chloroplast, and vestigial nucleus is providing interesting information about the early endosymbiosis event that generated these organisms.

In sum, the protists are a highly diverse and ecologically important group of organisms. Their complex evolutionary relationships, which have long been the subject of contention, are now being revised as new information is discovered, including more complete genome sequences. A deeper understanding of protists is also contributing to a better understanding of their recent descendents, the fungi, plants, and animals. We turn to these descendents in the next four chapters, beginning with the fungi.

Study Break

1. What is the evidence that the Excavates, which lack mitochondria, derive from ancestors that had mitochondria rather than from ancestors that were in lineages that never contained mitochondria?
2. In primary endosymbiosis, a nonphotosynthetic eukaryotic cell engulfed a photosynthetic cyanobacterium. How many membranes surround the chloroplast that evolved?

Review

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26.1 What Is a Protist?

- Protists are eukaryotes that differ from fungi in having motile stages in their life cycles and distinct cell wall molecules. Unlike plants, they lack true roots, stems, and leaves. Unlike animals, protists lack collagen, nerve cells, and an internal digestive tract, and they lack complex developmental stages (Figures 26.1 and 26.2).
- Protists are aerobic organisms that live as autotrophs or heterotrophs, or by a combination of both nutritional modes. Some are parasites or symbionts living in or among the cells of other organisms.
- Protists live in aquatic or moist terrestrial habitats, or as parasites within animals as single-celled, colonial, or multicellular organisms, and range in size from microscopic to some of Earth's largest organisms.
- Reproduction may be asexual by mitotic cell divisions, or sexual by meiosis and union of gametes in fertilization.
- Many protists have specialized cell structures including contractile vacuoles, food vacuoles, eyespots, and a pellicle, cell wall, or shell. Most are able to move by means of flagella, cilia, or pseudopodia (Figure 26.3).

26.2 The Protist Groups

- The Excavates, exemplified by the Diplomonadida and Parabasala are flagellated, single cells that lack mitochondria (Figure 26.4).
- The Discicristates are almost all single-celled, autotrophic or heterotrophic (some are both), motile protists that swim using flagella. The free-living, photosynthetic forms—the euglenoids—typically have complex cytoplasmic structures, including eyespots (Figures 26.5 and 26.6).
- Alveolates include the ciliates, dinoflagellates, and apicomplexans. The ciliates swim using cilia and have complex cytoplasmic structures and two types of nuclei, the micronucleus and macronucleus. The dinoflagellates swim using flagella and are primarily marine organisms; some are photosynthetic. The apicomplexans are nonmotile parasites of animals (Figures 26.7 and 26.8).
- Heterokonts include the funguslike Oomycota, which live as saprophytes or parasites, and three photosynthetic groups, the diatoms, golden algae, and brown algae. For most heterokonts, flagella occur only on reproductive cells. Many Oomycota grow as masses of microscopic hyphal filaments and secrete enzymes that digest organic matter in their surroundings. Diatoms are single-celled organisms covered by a glassy silica shell; golden algae are colonial forms; brown algae are primarily multicellular marine forms that include large seaweeds with extensive cell differentiation (Figures 26.9–26.13).
- Cercozoa are amoebas with filamentous pseudopods supported by internal cellular structures. Many produce hard outer shells. Radiolara (radiolarians) are primarily marine organisms that secrete a glassy internal skeleton. They feed by engulfing prey that adhere to their axopods. Foraminifera (forams) are marine, single-celled organisms that form chambered, spiral shells containing calcium. They engulf prey that adhere to the strands of cytoplasm extending from their shells. Chlorarachniophytes engulf food using their pseudopodia (Figure 26.14).
- The Amoebozoa includes most amoebas and two heterotrophic slime molds, cellular (which move as individual cells) and plasmodial (which move as large masses of nuclei sharing a common cytoplasm). The amoebas in this group are heterotrophs abundant in marine and freshwater environments and in the soil. They move by extending pseudopodia (Figures 26.15 and 26.16).
- The Archaeplastida include the red and green algae, as well as the land plants that comprise the kingdom Plantae. The red algae are typically multicellular, primarily photosynthetic organisms of marine environments, with plantlike bodies composed of interwoven filaments. They have complex life cycles including alternation of generations, with no flagellated cells at any stage. The green algae are single-celled, colonial, and multicel-

lular species that live primarily in freshwater habitats and carry out photosynthesis by mechanisms like those of plants; all produce flagellated gametes (Figures 26.17–26.20).

- The Opisthokonts are a broad group of eukaryotes that includes the choanoflagellates. These protists are characterized by a collar of microvilli surrounding a single flagellum. A choanoflagellate type of protist is considered likely to have been the ancestor of animals (Figure 26.21).
- Several groups of protists, as well as land plants, contain chloroplasts. Present-day chloroplasts and other plastids result from endosymbiosis events that took place millions of years ago: In a primary endosymbiosis event, a eukaryotic cell engulfed a cyanobacterium, which became an endosymbiont. Over time, the symbiont became an organelle, the chloroplast. This first photosynthesizing organism was a green alga. Evolutionary divergence produced the red algae, green algae, and land plants. By secondary endosymbiosis, in which a nonphotosynthetic eukaryote engulfed a photosynthetic eukaryote, the various photosynthetic protists were produced (Figure 26.22).

Animation: Body plan of Euglena

Animation: Paramecium body plan

Animation: Ciliate conjugation

Animation: Apicomplexan life cycle

Animation: Red alga life cycle

Animation: Green alga life cycle

Animation: Amoeboid motion

Animation: Cellular slime mold life cycle

Questions

Self-Test Questions

1. Protists are characterized by:
   a. division by binary fission.
   b. multicellular structures.
   c. complex digestive systems.
   d. peptidoglycan cell walls.
   e. organelles and reproduction by meiosis/mitosis.
2. Which of the following is *not* found among the protist groups?
   a. life cycles
   b. contractile vacuoles
   c. pellicles
   d. collagen
   e. pseudopodia
3. Freely beating flagella buried in a fold of cytoplasm moving through viscous fluids of humans and commonly found as an infective agent in U.S. college health centers describes a member of:
   a. Ciliophora.
   b. Discicristates.
   c. Diplomonadida.
   d. Parabasala.
   e. Alveolates.
4. When *Paramecium* conjugate:
   a. cytoplasmic division produces four daughter cells, each having two micronuclei and two macronuclei.
   b. one haploid micronucleus in each cell remains intact; the other three degenerate. The micronucleus of each cell divides once, producing two nuclei, and each cell exchanges one nucleus with the other cell. In each partner the two micronuclei fuse, forming a diploid zygote micronucleus in each cell.
   c. and the partners disengage, the micronucleus of each divides meiotically. Macronuclei divide again in each cell and the original micronucleus breaks down. Each cell has two haploid micronuclei; one of the macronuclei develops into a micronucleus.
   d. the mating cells join together at opposite sites of their oral depression.
   e. the micronucleus in each cell undergoes mitosis. When mitosis is complete there are four diploid macronuclei; the micronucleus then breaks down.
5. The protist group Diplomonadida is characterized by:
   a. a mouthlike gullet and hairlike surface. *Paramecium* is an example.
   b. flagella and a lack of mitochondria. *Giardia* is an example.
   c. nonmotility, parasitism, and sporelike infective stages. *Toxoplasma* is an example.
   d. switching between autotrophic and heterotrophic life styles. *Euglena* is an example.
   e. large protein deposits. Movement is by two flagella, which are part of an undulating membrane. *Trypanosoma* is an example.
6. The greatest contributors to protist fossil deposits are:
   a. Oomycota.
   b. Chrysophyta.
   c. Bacillariophyta.
   d. Sporophyta.
   e. Alveolates.
7. The group with the distinguishing characteristic of gas-filled bladders and a cell wall composed of alginic acid is:
   a. Chrysophyta.
   b. Phaeophyta.
   c. Oomycota.
   d. Bacillariophyta.
   e. none of the preceding.
8. *Plasmodium* is transmitted to humans by the bite of a mosquito *(Anopheles)* and engages in a life cycle with infective spores, gametes, and cysts. This infective protist belongs to the group:
   a. Apicomplexa.
   b. Heterokonts.
   c. Dinoflagellata.
   d. Oomycota.
   e. Ciliophora.
9. Tripping on a rotten log, a hunter notices a mucus-looking mass moving slowly toward brightly colored fruiting bodies. The organisms in the mass are:
   a. amoebas in the group Cercozoa.
   b. slime molds.
   c. red algae.
   d. green algae.
   e. charophytes.
10. The latest stage for evolving the double membrane seen in modern day algal chloroplasts is thought to be the combining of:
    a. two ancestral nonphotosynthetic prokaryotes.
    b. two ancestral photosynthetic prokaryotes.
    c. a nonphotosynthetic eukaryote with a photosynthetic eukaryote.
    d. a photosynthetic prokaryote with a nonphotosynthetic eukaryote.
    e. mitochondria with an already established plastid.

Questions for Discussion

1. You decide to vacation in a developing country where sanitation practices and standards of personal hygiene are inadequate. Considering the information about protists covered in this chapter, what would you consider safe to drink in that country? What treatments could make the water safe to drink? What kinds of foods might be best avoided? What kinds of preparation might make foods safe to eat?
2. The overreproduction of dinoflagellates, producing red tides, is sometimes caused by fertilizer runoff into coastal waters. The red tides kill countless aquatic species, birds, and other wildlife. Would you consider drastic cutbacks in the use of fertilizers as a means to lessen the red tides? Why?

Experimental Analysis

Design an experiment to demonstrate whether the flagellated protist *Euglena* is phototropic, that is, is attracted to and moves toward light. Also propose a follow-up experiment (on the assumption of a positive result) to determine the wavelength range and light intensity range sufficient to cause phototropic movement.

Evolution Link

Use the Internet to research why studies of a molecular sensor, receptor tyrosine kinase (see Section 7.3), supports the hypothesis that a choanoflagellate type of protist is the ancestor of animals. Summarize your findings.

How Would You Vote?

The pathogen that causes sudden oak death has already infected 26 kinds of plants in California and Oregon. Some infected species are commonly sold as nursery stock. Should the states that are free of this pathogen be allowed to prohibit shipping of all plants from the states that are affected? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.