

35

Protists

Concept Outline

35.1 Eukaryotes probably arose by endosymbiosis.

Endosymbiosis. Mitochondria and chloroplasts are thought to have arisen by endosymbiosis from aerobic bacteria.

35.2 The kingdom Protista is by far the most diverse of any kingdom.

The Challenge of Classifying the Protists. There is no general agreement among taxonomists about how to classify the protists.

General Biology of the Protists. Protista contains members exhibiting a wide range of methods of locomotion, nutrition, and reproduction.

35.3 Protists can be categorized into five groups.

Five Groups of Protists. The 15 major phyla of protists can be conveniently discussed in seven general groups that share certain characteristics.

Heterotrophs with No Permanent Locomotor Apparatus. Amoebas and other sarcodines have no permanent locomotor apparatus.

Photosynthetic Protists. The flagellates are photosynthesizers that propel themselves through the water with flagella. Diatoms are photosynthesizers with hard shells of silica. Algae are photosynthetic protists, some are multicellular.

Heterotrophs with Flagella. Flagellates propel themselves through the water. Single cells with many cilia, the ciliates possess highly complex and specialized organelles.

Nonmotile Spore-Formers. The sporozoans are nonmotile parasites that spread by forming spores.

Heterotrophs with Restricted Mobility. Heterotrophs with restricted mobility, molds have cell walls made of carbohydrate.

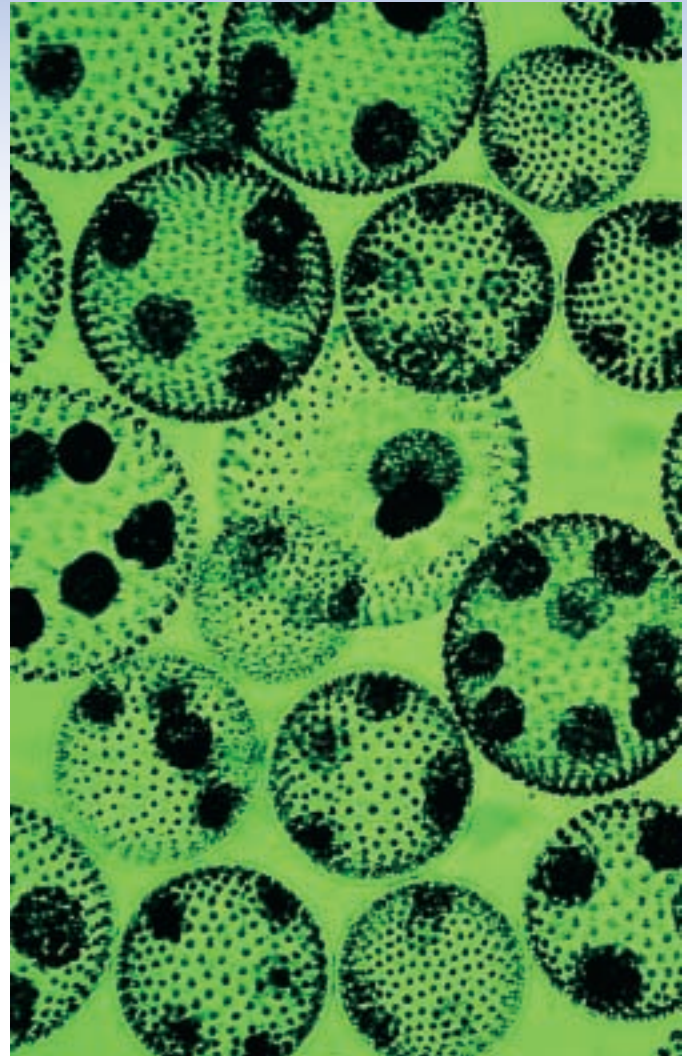


FIGURE 35.1

Volvox, a colonial protist. The protists are a large, diverse group of primarily single-celled organisms, a group from which the other three eukaryotic kingdoms each evolved.

For more than half of the long history of life on earth, all life was microscopic in size. The biggest organisms that existed for over 2 billion years were single-celled bacteria fewer than 6 micrometers thick. The first evidence of a different kind of organism is found in tiny fossils in rock 1.5 billion years old. These fossil cells are much larger than bacteria (some as big as 60 micrometers in diameter) and have internal membranes and what appear to be small, membrane-bounded structures. Many have elaborate shapes, and some exhibit spines or filaments. These new, larger fossil organisms mark one of the most important events in the evolution of life, the appearance of a new kind of organism, the eukaryote (figure 35.1). Flexible and adaptable, the eukaryotes rapidly evolved to produce all of the diverse large organisms that populate the earth today, including ourselves—indeed, all organisms other than bacteria are eukaryotes.

35.1 Eukaryotes probably arose by endosymbiosis.

Endosymbiosis

What was the first eukaryote like? We cannot be sure, but a good model is *Pelomyxa palustris*, a single-celled, nonphotosynthetic organism that appears to represent an early stage in the evolution of eukaryotic cells (figure 35.2). The cells of *Pelomyxa* are much larger than bacterial cells and contain a complex system of internal membranes. Although they resemble some of the largest early fossil eukaryotes, these cells are unlike those of any other eukaryote: *Pelomyxa* lacks mitochondria and does not undergo mitosis. Its nuclei divide somewhat as do those of bacteria, by pinching apart into two daughter nuclei, around which new membranes form. Although *Pelomyxa* cells lack mitochondria, two kinds of bacteria living within them may play the same role that mitochondria do in all other eukaryotes. This primitive eukaryote is so distinctive that it is assigned a phylum all its own, Caryoblastea.

Biologists know very little of the origin of *Pelomyxa*, except that in many of its fundamental characteristics it resembles the archaeobacteria far more than the eubacteria. Because of this general resemblance, it is widely assumed that the first eukaryotic cells were nonphotosynthetic descendants of archaeobacteria.

What about the wide gap between *Pelomyxa* and all other eukaryotes? Where did mitochondria come from? Most biologists agree with the theory of **endosymbiosis**, which proposes that mitochondria originated as symbiotic, aerobic (oxygen-requiring) eubacteria (figure 35.3). Symbiosis (Greek, *syn*, “together with” + *bios*, “life”) means living together in close association. Recall from chapter 5 that mitochondria are sausage-shaped organelles 1 to 3 micrometers long, about the same size as most eubacteria. Mitochondria are bounded by two membranes. Aerobic eubacteria are thought to have become mitochondria when they were engulfed by ancestral eukaryotic cells, much like *Pelomyxa*, early in the history of eukaryotes.

The most similar eubacteria to mitochondria today are the nonsulfur purple bacteria, which are able to carry out oxidative metabolism (described in chapter 9). In mitochondria, the outer membrane is smooth and is thought to be derived from the endoplasmic reticulum of the host cell, which, like *Pelomyxa*, may have already



FIGURE 35.2
Pelomyxa palustris. This unique, amoeba-like protist lacks mitochondria and does not undergo mitosis. *Pelomyxa* may represent a very early stage in the evolution of eukaryotic cells.

contained a complex system of internal membranes. The inner membrane of mitochondria is folded into numerous layers, resembling the folded membranes of nonsulfur purple bacteria; embedded within this membrane are the proteins that carry out oxidative metabolism. The engulfed bacteria became the interior portion of the mitochondria we see today. Host cells were unable to carry out the Krebs cycle or other metabolic reactions necessary for living in an atmosphere that contained increasing amounts of oxygen before they had acquired these bacteria.

During the billion and a half years in which mitochondria have existed as endosymbionts within eukaryotic cells, most of their genes have been transferred to the chromosomes of the host cells—but not all. Each mitochondrion still has its own genome, a circular, closed molecule of DNA similar to that found in eubacteria, on which is located genes encoding the essential proteins of oxidative metabolism. These genes are transcribed within the mitochondrion, using mitochondrial ribosomes that are smaller than those of eukaryotic cells, very much like bacterial ribosomes in size and structure. Mitochondria divide by simple fission, just as bacteria do, replicating and sorting their DNA much as bacteria do. However, nuclear genes direct the process, and mitochondria cannot be grown outside of the eukaryotic cell, in cell-free culture.

The theory of endosymbiosis has had a controversial history but has now been accepted by all but a few biologists. The evidence supporting the theory is so extensive that in this text we will treat it as established.

What of mitosis, the other typical eukaryotic process that *Pelomyxa* lacks? The mechanism of mitosis, now so common among eukaryotes, did not evolve all at once. Traces of very different, and possibly intermediate, mechanisms survive today in some of the eukaryotes. In fungi and some groups of protists, for example, the nuclear membrane does not dissolve and mitosis is confined to the nucleus. When mitosis is complete in these organisms, the nucleus divides into two daughter nuclei, and only then does the rest of the cell divide. This separate nuclear division phase of mitosis does not occur in most protists, or in plants or animals. We do not know if it represents an intermediate step on the evolutionary journey to the form of mitosis that is characteristic of most

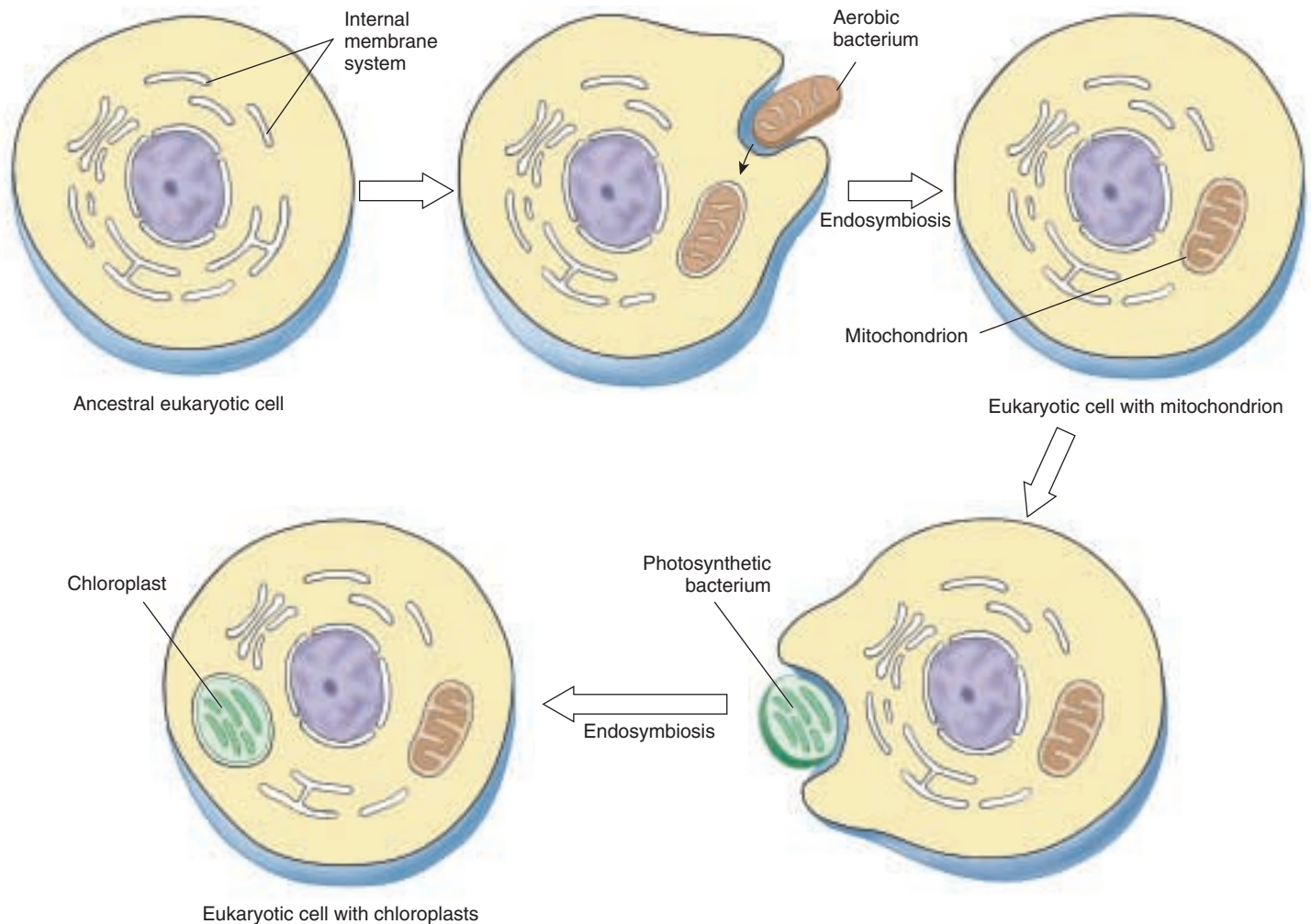


FIGURE 35.3

The theory of endosymbiosis. Scientists propose that ancestral eukaryotic cells, which already had an internal system of membranes, engulfed aerobic eubacteria, which then became mitochondria in the eukaryotic cell. Chloroplasts may also have originated this way, with eukaryotic cells engulfing photosynthetic eubacteria.

eukaryotes today or if it is simply a different way of solving the same problem. There are no fossils in which we can see the interiors of dividing cells well enough to be able to trace the history of mitosis.

Endosymbiosis Is Not Rare

Many eukaryotic cells contain other endosymbiotic bacteria in addition to mitochondria. Plants and algae contain chloroplasts, bacteria-like organelles that were apparently derived from symbiotic photosynthetic bacteria. Chloroplasts have a complex system of inner membranes and a circle of DNA. Centrioles, organelles associated with the assembly of microtubules, resemble in many respects spirochete bacteria, and they contain bacteria-like DNA involved in the production of their structural proteins.

While all mitochondria are thought to have arisen from a single symbiotic event, it is difficult to be sure with chloro-

plasts. Three biochemically distinct classes of chloroplasts exist, each resembling a different bacterial ancestor. Red algae possess pigments similar to those of cyanobacteria; plants and green algae more closely resemble the photosynthetic bacteria *Prochloron*; while brown algae and other photosynthetic protists resemble a third group of bacteria. This diversity of chloroplasts has led to the widely held belief that eukaryotic cells acquired chloroplasts by symbiosis at least three different times. Recent comparisons of chloroplast DNA sequences, however, suggest a single origin of chloroplasts, followed by very different postendosymbiotic histories. For example, in each of the three main lines, different genes became relocated to the nucleus, lost, or modified.

The theory of endosymbiosis proposes that mitochondria originated as symbiotic aerobic eubacteria.

35.2 The kingdom Protista is by far the most diverse of any kingdom.

The Challenge of Classifying the Protists

Protists are the most diverse of the four kingdoms in the domain Eukaryota. The kingdom Protista contains many unicellular, colonial, and multicellular groups. Probably the most important statement we can make about the kingdom Protista is that it is an artificial group; as a matter of convenience, single-celled eukaryotic organisms have typically been grouped together into this kingdom. This lumps many very different and only distantly related forms together. The “single-kingdom” classification of the Protista is not representative of any evolutionary relationships. The phyla of protists are, with very few exceptions, only distantly related to one another.

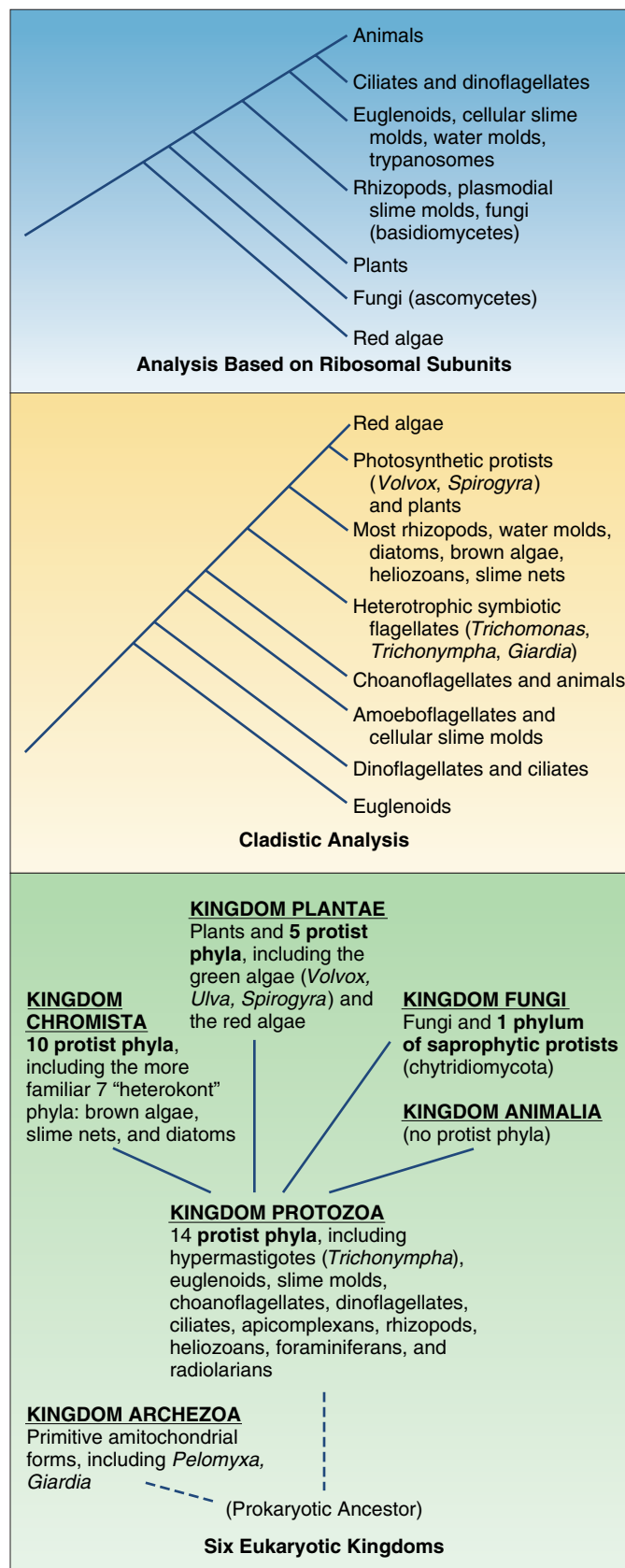
New applications of a wide variety of molecular methods are providing important insights into the relationships among the protists. Of all the groups of organisms biologists study, protists are probably in the greatest state of flux when it comes to classification. There is little consensus, even among experts, as to how the different kinds of protists should be classified. Are they a single, very diverse kingdom, or are they better considered as several different kingdoms, each of equal rank with animals, plants, and fungi?

Because the Protista are still predominantly considered part of one diverse, nonunified group, that is how we will treat them in this chapter, bearing in mind that biologists are rapidly gaining a better understanding of the evolutionary relationships among members of the kingdom Protista (figure 35.4). It seems likely that within a few years, the traditional kingdom Protista will be replaced by another more illuminating arrangement.

The taxonomy of the protists is in a state of flux as new information shapes our understanding of this kingdom.

FIGURE 35.4

The challenge of protistan classification. Three different suggestions for protistan classification are presented, each adapted from the work of an authority in the field. Their great differences attest to the wide divergence of opinion within the field itself. The classification on the top is based on molecular variation in ribosomal subunits. The classification in the middle presents a cladistic analysis of a broad range of characters (including ribosomal subunits). The classification on the bottom outlines a more revolutionary reevaluation of the protists. Comparison of the three schemes reveals that some groups are commonly recognized as related (like ciliates and dinoflagellates), while the classification of others (like *Giardia*) is clearly in a state of flux.



General Biology of the Protists

Protists are united on the basis of a single negative characteristic: they are not fungi, plants, or animals. In all other respects they are highly variable with no uniting features. Many are unicellular (figure 35.5), but there are numerous colonial and multicellular groups. Most are microscopic, but some are as large as trees. They represent all symmetries, and exhibit all types of nutrition.

The Cell Surface

Protists possess a varied array of cell surfaces. Some protists, like amoebas, are surrounded only by their plasma membranes. All other protists have a plasma membrane but some, like algae and molds, are encased within strong cell walls. Still others, like diatoms and forams, secrete glassy shells of silica.

Locomotor Organelles

Movement in protists is also accomplished by diverse mechanisms. Protists move chiefly by either flagellar rotation or pseudopodial movement. Many protists wave one or more flagella to propel themselves through the water, while others use banks of short, flagella-like structures called cilia to create water currents for their feeding or propulsion. Pseudopodia are the chief means of locomotion among amoeba, whose pseudopods are large, blunt extensions of the cell body called lobopodia. Other related protists extend thin, branching protrusions called filopodia. Still other protists extend long, thin pseudopodia called axopodia supported by axial rods of microtubules. Axopodia can be extended or retracted. Because the tips can adhere to adjacent surfaces, the cell can move by a rolling motion, shortening the axopodia in front and extending those in the rear.

Cyst Formation

Many protists with delicate surfaces are successful in quite harsh habitats. How do they manage to survive so well? They survive inhospitable conditions by forming **cysts**. A cyst is a dormant form of a cell with a resistant outer covering in which cell metabolism is more or less completely shut down. Not all cysts are so sturdy. Vertebrate parasitic amoebae, for example, form cysts that are quite resistant to gastric acidity, but will not tolerate desiccation or high temperature.

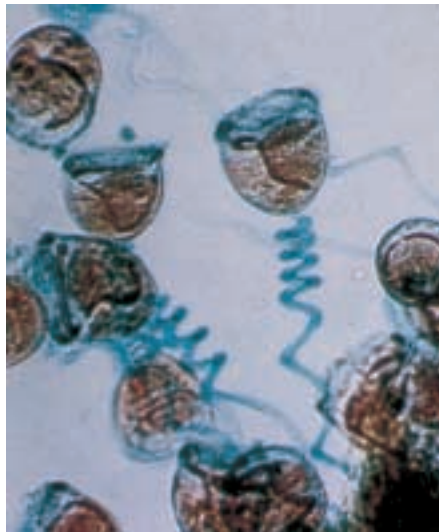


FIGURE 35.5
A unicellular protist. The protist kingdom is a catch-all kingdom for many different groups of unicellular organisms, such as this *Vorticella* (phylum Ciliophora), which is heterotrophic, feeds on bacteria, and has a retractable stalk.

Nutrition

Protists employ every form of nutritional acquisition except chemoautotrophic, which has so far been observed only in bacteria. Some protists are photosynthetic autotrophs and are called **phototrophs**. Others are heterotrophs that obtain energy from organic molecules synthesized by other organisms. Among heterotrophic protists, those that ingest visible particles of food are called **phagotrophs**, or **holozoic feeders**. Those ingesting food in soluble form are called **osmotrophs**, or **saprotrophic feeders**.

Phagotrophs ingest food particles into intracellular vesicles called **food vacuoles** or **phagosomes**. Lysosomes fuse with the food vacuoles, introducing enzymes that digest the food particles within. As the digested molecules are absorbed across the vacuolar membrane, the food vacuole becomes progressively smaller.

Reproduction

Protists typically reproduce asexually, reproducing sexually only in times of stress. Asexual reproduction involves mitosis, but the process is often somewhat different from the mitosis that occurs in multicellular animals. The nuclear membrane, for example, often persists throughout mitosis, with the microtubular spindle forming within it. In some groups, asexual reproduction involves spore formation, in others fission. The most common type of fission is **binary**, in which a cell simply splits into nearly equal halves. When the progeny cell is considerably smaller than its parent, and then grows to adult size, the fission is called **budding**. In multiple fission, or **schizogony**, common among some protists, fission is preceded by several nuclear divisions, so that fission produces several individuals almost simultaneously.

Sexual reproduction also takes place in many forms among the protists. In ciliates and some flagellates, **gametic meiosis** occurs just before gamete formation, as it does in metazoans. In the sporozoans, **zygotic meiosis** occurs directly *after* fertilization, and all the individuals that are produced are haploid until the next zygote is formed. In algae, there is **intermediary meiosis**, producing an alternation of generations similar to that seen in plants, with significant portions of the life cycle spent as haploid as well as diploid.

Protists exhibit a wide range of forms, locomotion, nutrition and reproduction.

35.3 Protists can be categorized into five groups.

Five Groups of Protists

There are some 15 major phyla of protists. It is difficult to encompass their great diversity with any simple scheme. Traditionally, texts have grouped them artificially (as was done in the nineteenth century) into photosynthesizers (algae), heterotrophs (protozoa), and absorbers (funguslike protists).

In this text, we will group the protists into five general groups according to some of the major shared characteristics (figure 35.6). These are characteristics that taxonomists are using today in broad attempts to classify the kingdom Protista. These include (1) the presence or absence and type of cilia or flagella, (2) the presence and kinds of pigments, (3) the type of mitosis, (4) the kinds of cristae present in the mitochondria, (5) the molecular genetics of the ribosomal “S” subunit, (6) the kind of inclusions the protist may have, (7) overall body form (amoeboid, coccoid, and so forth), (8) whether the protist has any kind of shell or other body “armor,” and

(9) modes of nutrition and movement. These represent only some of the characters used to define phylogenetic relationships.

The five criteria we have chosen to define groups are not the only ones that might be chosen, and there is no broad agreement among biologists as to which set of criteria is preferable. As molecular analysis gives us a clearer picture of the phylogenetic relationships among the protists, more evolutionarily suitable groupings will without a doubt replace the one represented here. Table 35.1 summarizes some of the general characteristics and groupings of the 15 major phyla of protists. It is important to remember that while the phyla of protists discussed here are generally accepted taxa, the larger groupings of phyla presented are functional groupings.

The 15 major protist phyla can be conveniently categorized into five groups according to major shared characteristics.

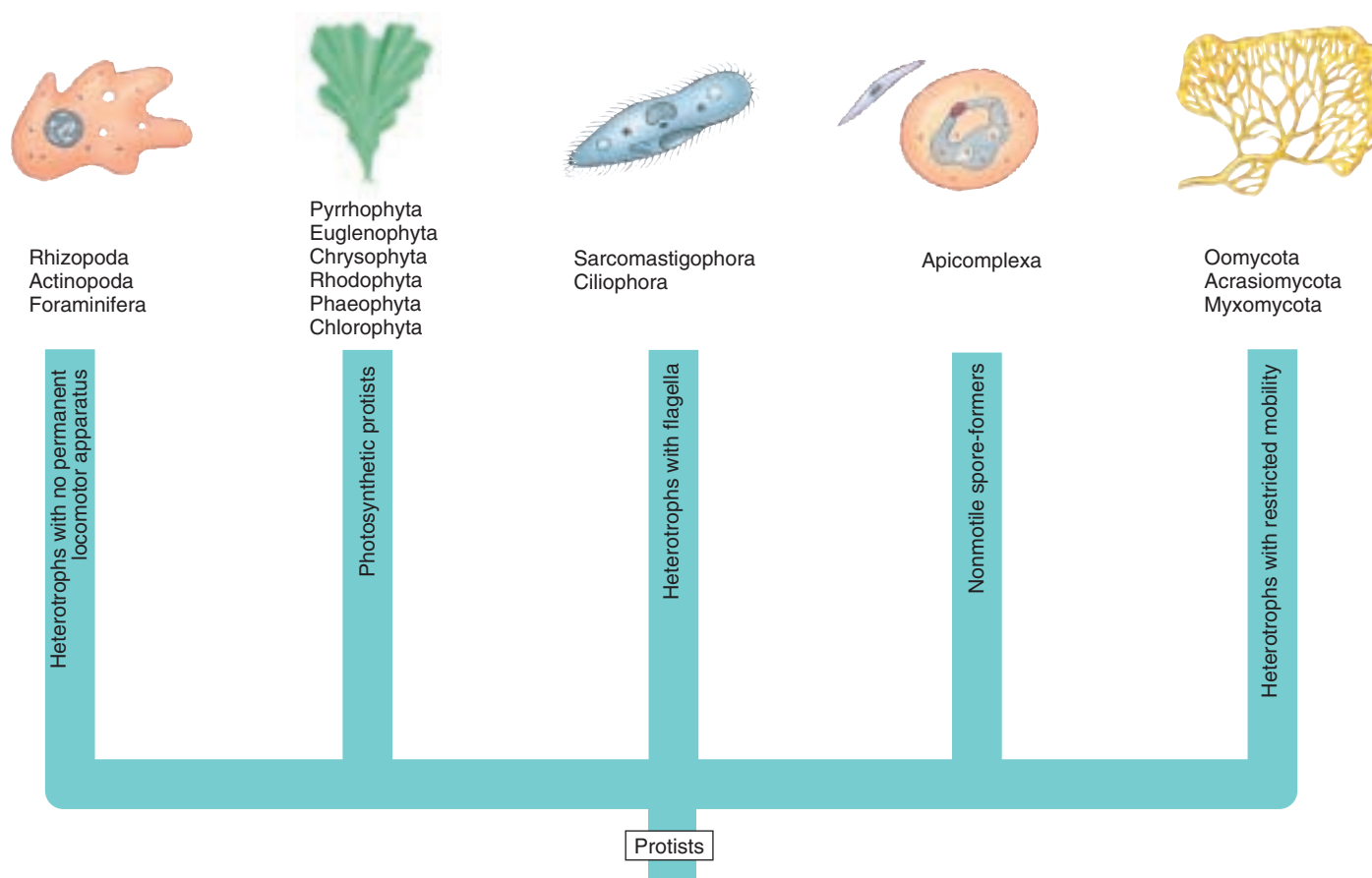
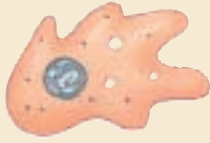

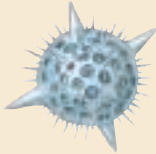



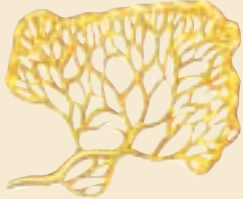


FIGURE 35.6
Five general groups of protists. This text presents the 15 major phyla of protists in five groups that share major characteristics.

Table 35.1 Kinds of Protists

Group	Phylum	Typical Examples		Key Characteristics
HETEROTROPHS WITH NO PERMANENT LOCOMOTOR APPARATUS				
Amoebas	Rhizopoda	<i>Amoeba</i>		Move by pseudopodia
Radiolarians	Actinopoda	Radiolarians		Glassy skeletons; needlelike pseudopods
Forams	Foraminifera	Forams		Rigid shells; move by protoplasmic streaming
PHOTOSYNTHETIC PROTISTS				
Dinoflagellates	Pyrrhophyta	Red tides		Photosynthetic; unicellular; two flagella; contain chlorophylls <i>a</i> and <i>b</i>
Euglenoids	Euglenophyta	<i>Euglena</i>		Some photosynthetic; others heterotrophic; unicellular; contain chlorophylls <i>a</i> and <i>b</i> or none
Diatoms	Chrysophyta	<i>Diatoma</i>		Unicellular; manufacture the carbohydrate chrysolaminarin; unique double shells of silica; contain chlorophylls <i>a</i> and <i>c</i>
Golden algae	Chrysophyta	Golden algae		Unicellular, but often colonial; manufacture the carbohydrate chrysolaminarin; contain chlorophylls <i>a</i> and <i>c</i>
Red	Rhodophyta	Coralline algae		Most multicellular; contain chlorophyll <i>a</i> and a red pigment
Brown	Phaeophyta	Kelp		Multicellular; contain chlorophylls <i>a</i> and <i>c</i>
Green	Chlorophyta	<i>Chlamydomonas</i>		Unicellular or multicellular; contain chlorophylls <i>a</i> and <i>b</i>
HETEROTROPHS WITH FLAGELLA				
Zoomastigotes	Sarcomastigophora	Trypanosomes		Heterotrophic; unicellular
Ciliates	Ciliophora	<i>Paramecium</i>		Heterotrophic unicellular protists with cells of fixed shape possessing two nuclei and many cilia; many cells also contain highly complex and specialized organelles
NONMOTILE SPORE-FORMERS				
Sporozoans	Apicomplexa	<i>Plasmodium</i>		Nonmotile; unicellular; the apical end of the spores contains a complex mass of organelles
HETEROTROPHS WITH RESTRICTED MOBILITY				
Water molds	Oomycota	Water molds, rusts, and mildew		Terrestrial and freshwater
Cellular slime molds	Acrasiomycota	<i>Dictyostelium</i>		Colonial aggregations of individual cells; most closely related to amoebas
Plasmodial slime molds	Myxomycota	<i>Fuligo</i>		Stream along as a multinucleate mass of cytoplasm

Heterotrophs with No Permanent Locomotor Apparatus

The largest of the five general groups of protists are primarily unicellular organisms with amoeboid forms. There are three principle phyla: the forams and the radiolarians have carbonate shells and the rhizopods lack shells.

Rhizopoda: The Amoebas

Hundreds of species of amoebas are found throughout the world in both fresh and salt waters. They are also abundant in soil. Many kinds of amoebas are parasites of animals. Reproduction in amoebas occurs by fission, or the direct division into two cells of equal volume. Amoebas of the phylum Rhizopoda lack cell walls, flagella, meiosis, and any form of sexuality. They do undergo mitosis, with a spindle apparatus that resembles that of other eukaryotes.

Amoebas move from place to place by means of their **pseudopods**, from the Greek words for “false” and “foot” (figure 35.7). Pseudopods are flowing projections of cytoplasm that extend and pull the amoeba forward or engulf food particles, a process called cytoplasmic streaming. An amoeba puts a pseudopod forward and then flows into it. Microfilaments of actin and myosin similar to those found in muscles are associated with these movements. The pseudopodia can form at any point on the cell body so that it can move in any direction.

Some kinds of amoebas form resistant cysts. In parasitic species such as *Entamoeba histolytica*, which causes amoebic dysentery, cysts enable the amoebas to resist digestion by their animal hosts. Mitotic division takes place within the cysts, which ultimately rupture and release four, eight, or even more amoebas within the digestive tracts of their host animals. The primary infection takes place in the intestine, but it often moves into the liver and other parts of the body. The cysts are dispersed in the feces and may be transmitted from person to person in infected food or water, or by flies. It is estimated that up to 10 million people in the United States have infections of parasitic amoebas, and some 2 million show symptoms of the disease, ranging from abdominal discomfort with

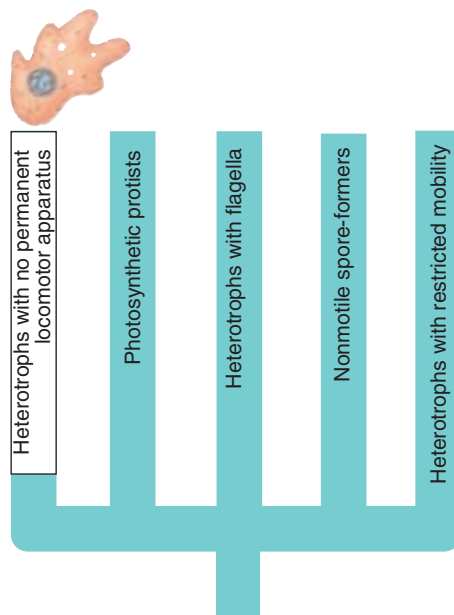


FIGURE 35.7
Amoeba proteus. This relatively large amoeba is commonly used in teaching and for research in cell biology. The projections are pseudopods; an amoeba moves by flowing into them. The nucleus of the amoeba is plainly visible.

slight diarrhea to much more serious conditions. In some tropical areas, more than half of the population may be infected. The spread of amoebic dysentery can be limited by proper sanitation and hygiene.

Actinopoda: The Radiolarians

The pseudopodia of amoeboid cells give them truly amorphous bodies. One group, however, have more distinct structures. Members of the phylum Actinopoda, often called radiolarians, secrete glassy exoskeletons made of silica. These skeletons give the unicellular organisms a distinct shape, exhibiting either bilateral or radial symmetry. The shells of different species form many elaborate and beautiful shapes and its pseudopodia extrude outward along spiky projections of the skeleton (figure 35.8). Microtubules support these cytoplasmic projections.

Foraminifera: Forams

Members of the phylum Foraminifera are heterotrophic marine protists. They range in diameter from about 20 micrometers to several centimeters. Characteristic of the group are pore-studded shells (called **tests**) composed of organic materials usually reinforced with grains of inorganic matter. These grains may be calcium carbonate, sand, or even plates from the shells of echinoderms or spicules (minute needles of calcium carbonate) from sponge skeletons. Depending on the building materials they use, foraminifera—often informally called “forams”—may have shells of very different appearance. Some of them are brilliantly colored red, salmon, or yellow-brown.

Most foraminifera live in sand or are attached to other organisms, but two families consist of free-floating planktonic organisms. Their tests may be single-chambered but more often are multichambered, and they sometimes have a spiral shape resembling that of a tiny snail. Thin cytoplasmic projections called **podia** emerge through openings in the tests (figure 35.9). Podia are used for swimming, gathering materials for the tests, and feeding. Forams eat a wide variety of small organisms.

The life cycles of foraminifera are extremely complex, involving an alternation between haploid and diploid generations (sporic meiosis). Forams have contributed massive

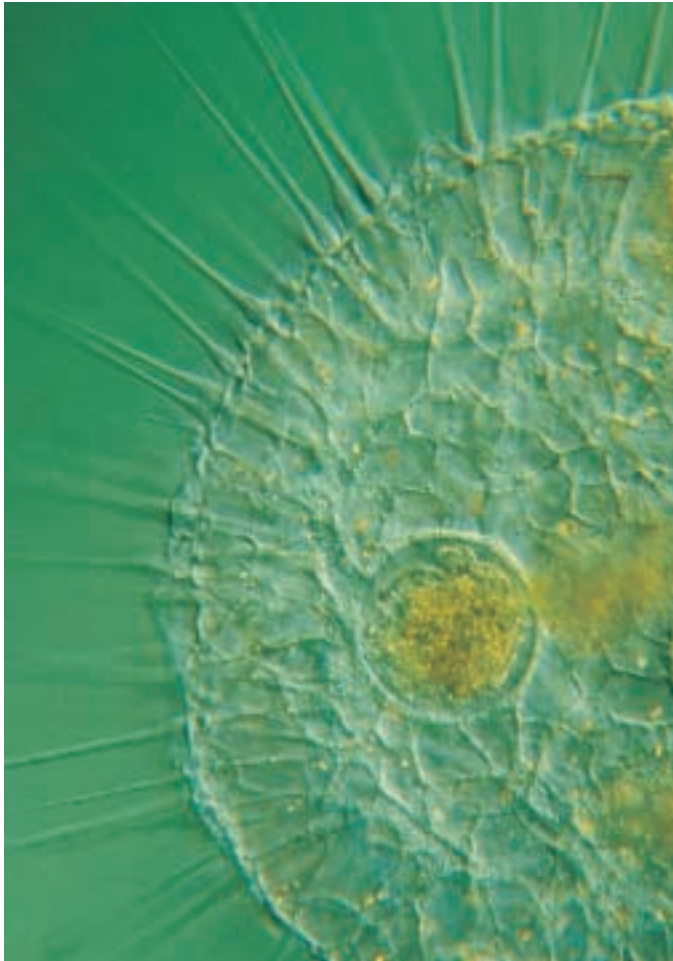


FIGURE 35.8
Actinosphaerium, a protist of the phylum Actinopoda (300×).
 This amoeba-like radiolarian has striking needlelike pseudopods.

accumulations of their tests to the fossil record for more than 200 million years. Because of the excellent preservation of their tests and the often striking differences among them, forams are very important as geological markers. The pattern of occurrence of different forams is often used as a guide in searching for oil-bearing strata. Limestones all over the world, including the famous white cliffs of Dover in southern England, are often rich in forams (figure 35.10).

Amoebas, radiolarians, and forams are unicellular, heterotrophic protists that lack cell walls, flagella, meiosis, and sexuality. Amoebas move from place to place by means of extensions called pseudopodia. The pore-studded tests, or shells, of the forams have openings through which podia extend that are used for locomotion.

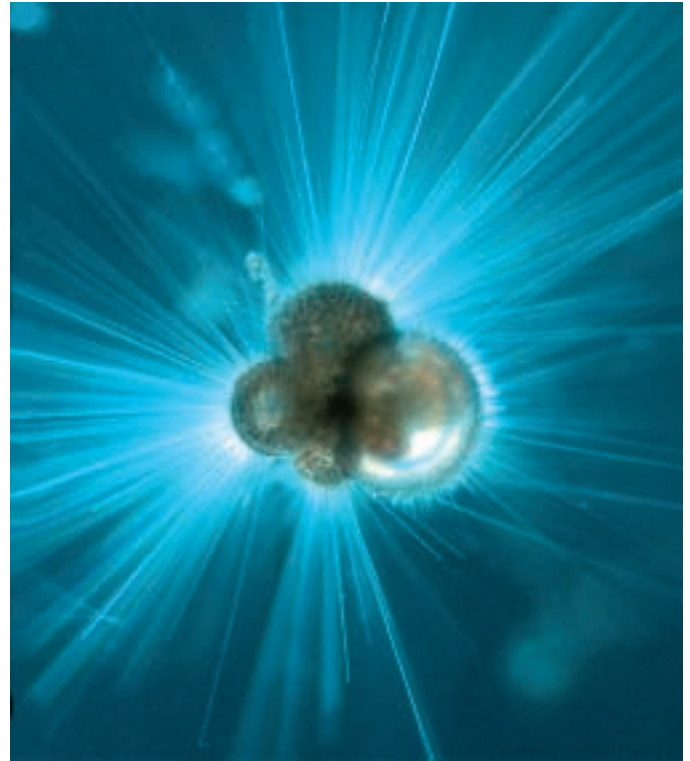


FIGURE 35.9
 A representative of the Foraminifera (90×). A living foram with podia, thin cytoplasmic projections that extend through pores in the calcareous test, or shell, of the organism.



FIGURE 35.10
 White cliffs of Dover. The limestone that forms these cliffs is composed almost entirely of fossil shells of protists, including coccolithophores (a type of algae) and foraminifera.

Photosynthetic Protists

Pyrrhophyta: The Dinoflagellates

The dinoflagellates consist of about 2100 known species of primarily unicellular, photosynthetic organisms, most of which have two flagella. A majority of the dinoflagellates are marine, and they are often abundant in the plankton, but some occur in fresh water. Some planktonic dinoflagellates are luminous and contribute to the twinkling or flashing effects that we sometimes see in the sea at night, especially in the tropics.

The flagella, protective coats, and biochemistry of dinoflagellates are distinctive, and they do not appear to be directly related to any other phylum. Plates made of a cellulose-like material encase the cells. Grooves form at the junctures of these plates and the flagella are usually located within these grooves, one encircling the body like a belt, and the other perpendicular to it. By beating in their respective grooves, these flagella cause the dinoflagellate to rotate like a top as it moves. The dinoflagellates that are clad in stiff cellulose plates, often encrusted with silica, may have a very unusual appearance (figure 35.11). Most have chlorophylls *a* and *c*, in addition to carotenoids, so that in the biochemistry of their chloroplasts, they resemble the diatoms and the brown algae, possibly acquiring such chloroplasts by forming endosymbiotic relationships with members of those groups.

Some dinoflagellates occur as symbionts in many other groups of organisms, including jellyfish, sea anemones, mollusks, and corals. When dinoflagellates grow as symbionts within other cells, they lack their characteristic cellulose plates and flagella, appearing as spherical, golden-brown globules in their host cells. In such a state they are called **zooxanthellae**. Photosynthetic zooxanthellae provide their hosts with nutrients. It is the photosynthesis conducted by zooxanthellae that

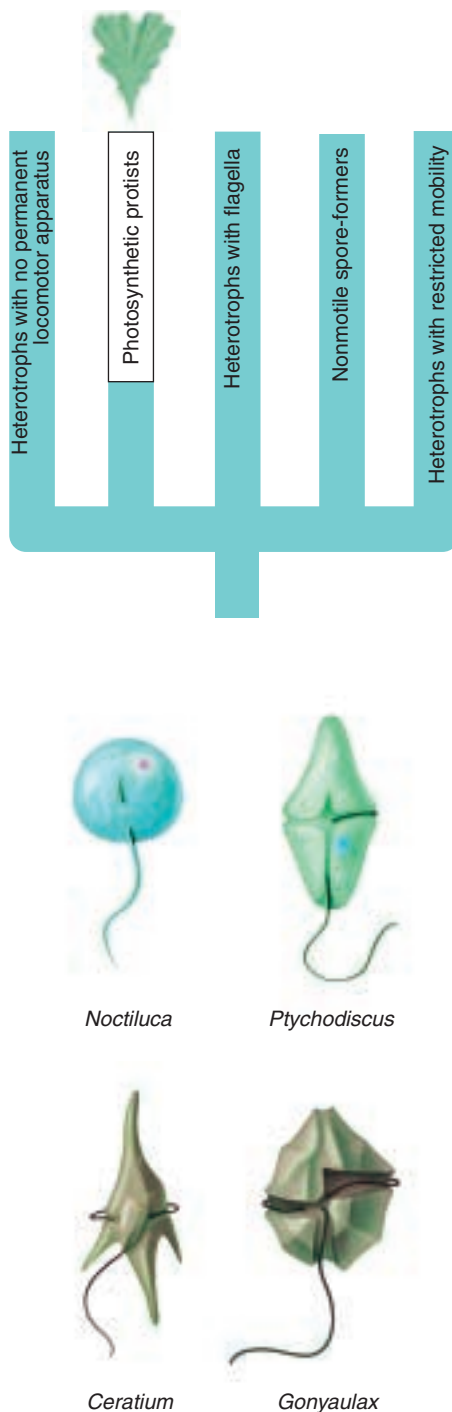


FIGURE 35.11
Some dinoflagellates: *Noctiluca*, *Ptychodiscus*, *Ceratium*, and *Gonyaulax*.

Noctiluca, which lacks the heavy cellulose armor characteristic of most dinoflagellates, is one of the bioluminescent organisms that causes the waves to sparkle in warm seas. In the other three genera, the shorter, encircling flagellum is seen in its groove, with the longer one projecting away from the body of the dinoflagellate. (Not drawn to scale.)

makes coral reefs one of the most productive ecosystems on earth. Corals primarily live in warm tropical seas that are typically extremely low in nutrients; without the aid of their photosynthetic endosymbionts, they would not be able to form large reefs in the nutrient-poor environment. Most of the carbon that the zooxanthellae fix is translocated to the host corals.

The poisonous and destructive “red tides” that occur frequently in coastal areas are often associated with great population explosions, or “blooms,” of dinoflagellates. The pigments in the individual, microscopic cells of the dinoflagellates are responsible for the color of the water. Red tides have a profound, detrimental effect on the fishing industry in the United States. Some 20 species of dinoflagellates are known to produce powerful toxins that inhibit the diaphragm and cause respiratory failure in many vertebrates. When the toxic dinoflagellates are abundant, fishes, birds, and marine mammals may die in large numbers.

More recently, a particularly dangerous toxic dinoflagellate called *Pfiesteria piscicida* is reported to be a carnivorous, ambush predator. During blooms, it stuns fish with its toxin and then feeds on the prey’s body fluids.

Dinoflagellates reproduce primarily by asexual cell division. But sexual reproduction has been reported to occur under starvation conditions. They have a unique form of mitosis in which the permanently condensed chromosomes divide longitudinally within the confines of a permanent nuclear envelope. After the numerous chromosomes duplicate, the nucleus divides into two daughter nuclei. Also the dinoflagellate chromosome is unique among eukaryotes in that the DNA is not complexed with histone proteins. In all other eukaryotes, the chromosomal DNA is complexed with histones to form nucleosomes, which represents the first order of DNA packaging in the nucleus. How dinoflagellates are able to maintain distinct chromosomes without histones and nucleosomes remains a mystery.

Euglenophyta: The Euglenoids

Most of the approximately 1000 known species of euglenoids live in fresh water. The members of this phylum clearly illustrate the impossibility of distinguishing “plants” from “animals” among the protists. About a third of the approximately 40 genera of euglenoids have chloroplasts and are fully autotrophic; the others lack chloroplasts, ingest their food, and are heterotrophic. These organisms are not significantly different from some groups of zoomastigotes (see next section), and many biologists believe that the two phyla should be merged into one.

Some euglenoids with chloroplasts may become heterotrophic if the organisms are kept in the dark; the chloroplasts become small and nonfunctional. If they are put back in the light, they may become green within a few hours. Normally photosynthetic euglenoids may sometimes feed on dissolved or particulate food.

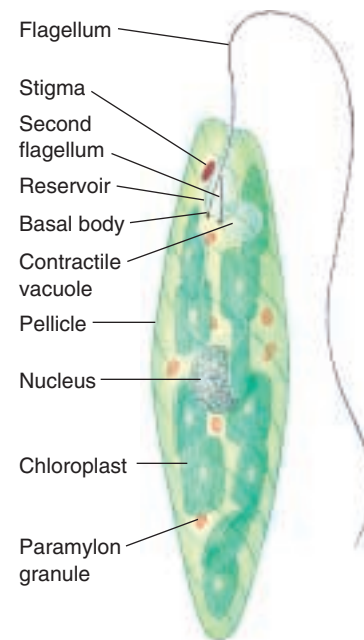
Individual euglenoids range from 10 to 500 micrometers long and are highly variable in form. Interlocking proteinaceous strips arranged in a helical pattern form a flexible structure called the **pellicle**, which lies within the cell membrane of the euglenoids. Because its pellicle is flexible, a euglenoid is able to change its shape. Reproduction in this phylum occurs by mitotic cell division. The nuclear envelope remains intact throughout the process of mitosis. No sexual reproduction is known to occur in this group.

In *Euglena* (figure 35.12), the genus for which the phylum is named, two flagella are attached at the base of a flask-shaped opening called the **reservoir**, which is located at the anterior end of the cell. One of the flagella is long and has a row of very fine, short, hairlike projections along one side. A second, shorter flagellum is located within the reservoir but does not emerge from it. Contractile vacuoles collect excess water from all parts of the organism and empty it into the reservoir, which apparently helps regulate the osmotic pressure within the organism. The **stigma**, an organ that also occurs in the green algae (phylum Chlorophyta), is light-sensitive and aids these photosynthetic organisms to move toward light.

Cells of *Euglena* contain numerous small chloroplasts. These chloroplasts, like those of the green algae and plants, contain chlorophylls *a* and *b*, together with carotenoids. Although the chloroplasts of euglenoids differ somewhat in structure from those of green algae, they probably had a common origin. It seems likely that euglenoid chloroplasts ultimately evolved from a symbiotic relationship through ingestion of green algae.



(a)



(b)

FIGURE 35.12

Euglenoids. (a) Micrograph of individuals of the genus *Euglena* (Euglenophyta). (b) Diagram of *Euglena*. Paramylon granules are areas where food reserves are stored.

Chrysophyta: The Diatoms and Golden Algae

The Diatoms. Diatoms, members of the phylum Chrysophyta, are photosynthetic, unicellular organisms with unique double shells made of opaline silica, which are often strikingly and characteristically marked. The shells of diatoms are like small boxes with lids, one half of the shell fitting inside the other. Their chloroplasts, with chlorophylls *a* and *c*, as well as carotenoids, resemble those of the brown algae and dinoflagellates. In other respects, however, there are few similarities between these groups, and they probably do not share an immediate common ancestor. Another member of the phylum Chrysophyta is the golden algae. Diatoms and golden algae are grouped together because they both produce a unique carbohydrate called chrysolaminarin.

There are more than 11,500 living species of diatoms, with many more known in the fossil record. The shells of fossil diatoms often form very thick deposits, which are sometimes mined commercially. The resulting “diatomaceous earth” is used as an abrasive or to add the sparkling quality to the paint used on roads, among other purposes. Living diatoms are often abundant both in the sea and in fresh water, where they are important food producers. Diatoms occur in the plankton and are attached to submerged objects in relatively shallow water. Many species are able to move by means of a secretion that is produced from a fine groove along each shell. The diatoms exude and perhaps also retract this secretion as they move.

There are two major groups of diatoms, one with radial symmetry (like a wheel) and the other with bilateral (two-sided) symmetry (figure 35.13). Diatom shells are rigid, and the organisms reproduce asexually by separating the two halves of the shell, each half then regenerating another half shell within it. Because of this mode of reproduction, there is a tendency for the shells, and consequently the individual diatoms, to get smaller and smaller with each asexual reproduction. When the resulting individuals have diminished to about 30% of their original size, one may slip out of its shell, grow to full size, and regenerate a full-sized pair of new shells.

Individual diatoms are diploid. Meiosis occurs more frequently under conditions of starvation. Some marine diatoms produce numerous sperm and others a single egg. If fusion occurs, the resulting zygote regenerates a full-sized individual. In some freshwater diatoms, the gametes are amoeboid and similar in appearance.

The Golden Algae. Also included within the Chrysophyta are the golden algae, named for the yellow and brown carotenoid and xanthophyll accessory pigments in their chloroplasts, which give them a golden color. Unicellular but often colonial, these freshwater protists typically have two flagella, both attached near the same end of the cell. When ponds and lakes dry out in summer, golden algae form resistant cysts. Viable cells emerge from these cysts when wetter conditions recur in the fall.

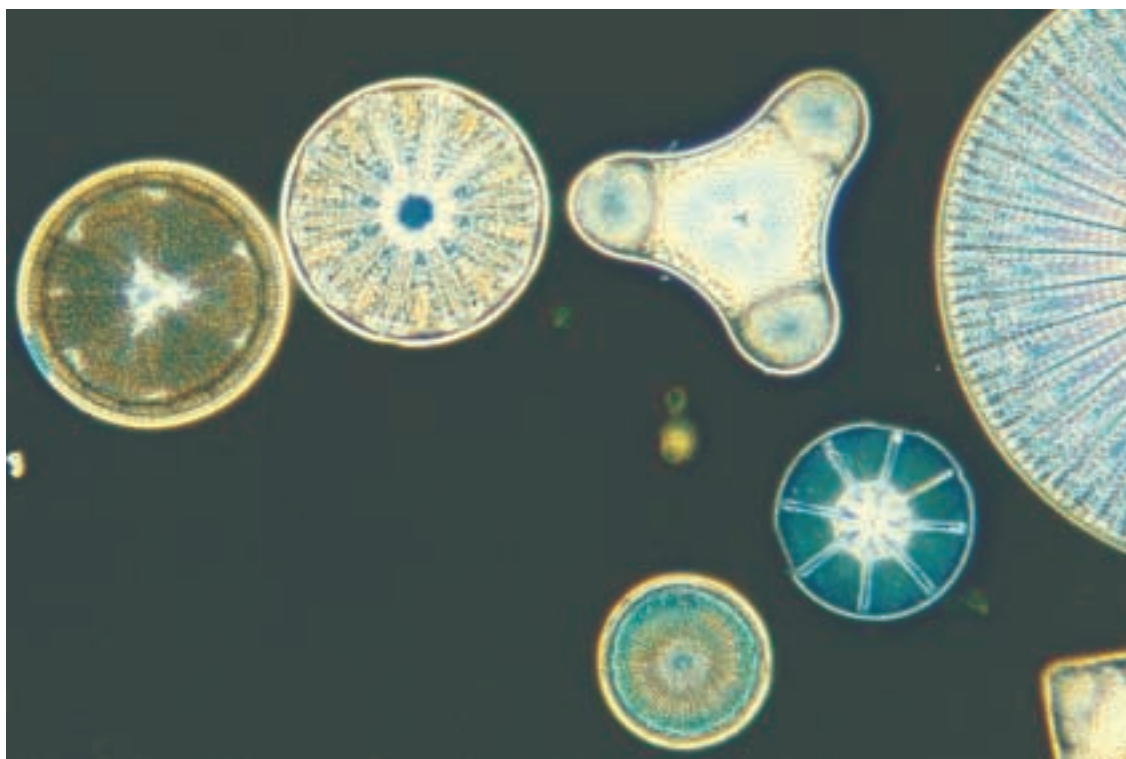


FIGURE 35.13
Diatoms (Chrysophyta). Several different centric (radially symmetrical) diatoms.

Rhodophyta: The Red Algae

Along with green algae and brown algae, red algae are the seaweeds we see cast up along shores and on beaches. Their characteristic colors result from phycoerythrin, a type of phycobilin pigment. Phycobilins are responsible for the colors of the cyanobacteria. Chlorophyll *a* also occurs with the phycobilins in red algae, just as it does in cyanobacteria. These similarities with cyanobacteria make it likely that the rhodophyta evolved when their heterotrophic eukaryotic ancestor developed an endosymbiotic relationship with a cyanobacteria which eventually gave rise to their chloroplasts.

The great majority of the estimated 4000 species of red algae occur in the sea, and almost all are multicellular.

Red algae have complex bodies made up of interwoven filaments of cells. In the cell walls of many red algae are sulfated polysaccharides such as agar and carrageenan, which make these algae important economically. Agar is used to make gel capsules, as material for dental impressions, and as a base for cosmetics. It is also the basis of the laboratory media on which bacteria, fungi, and other organisms are often grown. In addition, agar is used to prevent baked goods from drying out, for rapid-setting jellies, and as a temporary preservative for meat and fish in warm regions. Carrageenan is used mainly to stabilize emulsions such as paints, cosmetics, and dairy products such as ice cream. In addition to these uses, red algae such as *Porphyra*, called “nori,” are eaten and, in Japan, are even cultivated as a human food crop.

The life cycles of red algae are complex but usually involve an alternation of generations (sporic meiosis). None of the red algae have flagella or cilia at any stage in their life cycle, and they may have descended directly from ancestors that never had them, especially as the red algae also lack centrioles. Together with the fungi, which also lack flagella and centrioles, the red algae may be one of the most ancient groups of eukaryotes.

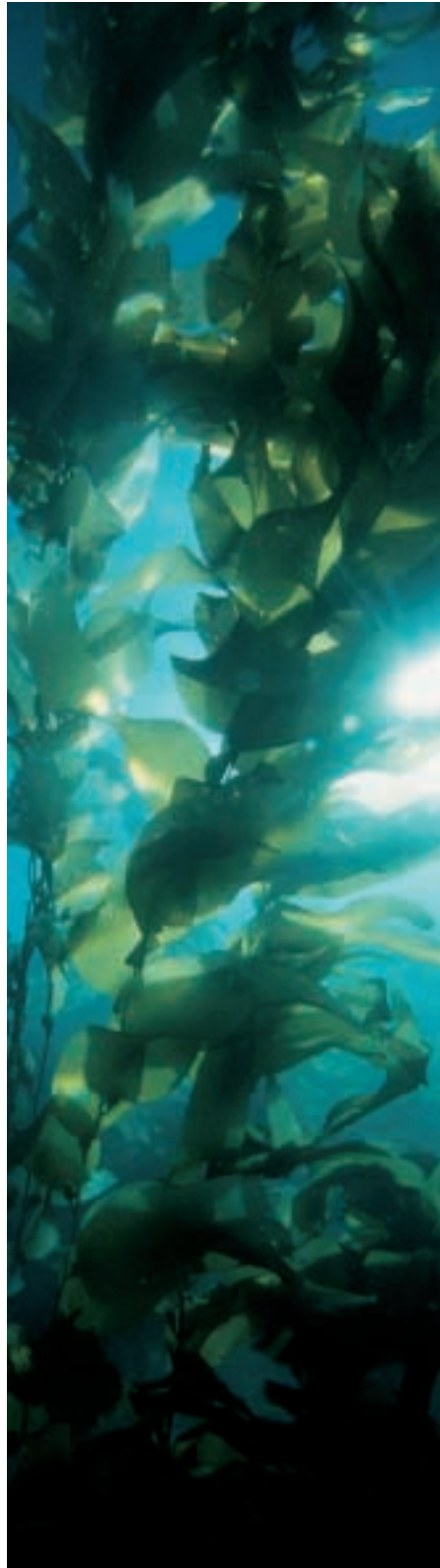


FIGURE 35.14
Brown algae (Phaeophyta). The massive “groves” of giant kelp that occur in relatively shallow water along the coasts of the world provide food and shelter for many different kinds of organisms.

Phaeophyta: The Brown Algae

The phaeophyta, or brown algae, consist of about 1500 species of multicellular protists, almost exclusively marine. They are the most conspicuous seaweeds in many northern regions, dominating rocky shores almost everywhere in temperate North America. In habitats where large brown algae known as **kelps** (order Laminariales) occur abundantly in so-called kelp forests (figure 35.14), they are responsible for most of the food production through photosynthesis. Many kelps are conspicuously differentiated into flattened blades, stalks, and grasping basal portions that anchor them to the rocks.

Among the larger brown algae are genera such as *Macrocystis*, in which some individuals may reach 100 meters in length. The flattened blades of this kelp float out on the surface of the water, while the base is anchored tens of meters below the surface. Another ecologically important member of this phylum is sargasso weed, *Sargassum*, which forms huge floating masses that dominate the vast Sargasso Sea, an area of the Atlantic Ocean northeast of the Caribbean. The stalks of the larger brown algae often exhibit a complex internal differentiation of conducting tissues analogous to that of plants.

The life cycle of the brown algae is marked by an alternation of generations between a sporophyte and a gametophyte. The large individuals we recognize, such as the kelps, are sporophytes. The gametophytes are often much smaller, filamentous individuals, perhaps a few centimeters across. Sporangia, which produce haploid, swimming spores after meiosis, are formed on the sporophytes. These spores divide by mitosis, giving rise to individual gametophytes. There are two kinds of gametophytes in the kelps; one produces sperm, and the other produces eggs. If sperm and eggs fuse, the resulting zygotes grow into the mature kelp sporophytes, provided that they reach a favorable site.

Chlorophyta: The Green Algae

Green algae are an extremely varied group of more than 7000 species. The chlorophytes have an extensive fossil record dating back 900 million years. They are mostly aquatic, but some are semiterrestrial in moist places, such as on tree trunks or in soil. Many are microscopic and unicellular, but some, such as sea lettuce, *Ulva* (see figure 35.16), are tens of centimeters across and easily visible on rocks and pilings around the coasts.

Green algae are of special interest, both because of their unusual diversity and because the ancestors of the plant kingdom were clearly multicellular green algae. Many features of modern green algae closely resemble plants, especially their chloroplasts which are biochemically similar to those of the plants. They contain chlorophylls *a* and *b*, as well as carotenoids. Green algae include a very wide array of both unicellular and multicellular organisms.

Among the unicellular green algae, *Chlamydomonas* (figure 35.15) is a well-known genus. Individuals are microscopic (usually less than 25 micrometers long), green, rounded, and have two flagella at the anterior end. They move rapidly in water by beating their flagella in opposite directions. Each individual has an eyespot, which contains about 100,000 molecules of rhodopsin, the same pigment employed in vertebrate eyes. Light received by this eyespot is used by the alga to help direct its swimming. Most individuals of *Chlamydomonas* are haploid. *Chlamydomonas* reproduces asexually (by cell division) as well as sexually.

In sexual reproduction, two haploid individuals fuse to form a four-flagellated zygote. The zygote ultimately enters a resting phase, called the **zygospore**, in which the flagella disappear and a tough protective coat is formed. Meiosis occurs at the end of this resting period and results in the production of four haploid cells.

Chlamydomonas probably represents a primitive state for green algae and several lines of evolutionary specialization have been derived from organisms like it. The first is the evolution of nonmotile, unicellular green algae. *Chlamydomonas* is capable of retracting its flagella and settling down as an immobile unicellular organism if the ponds in which it lives dry out. Some common algae of soil and bark, such as *Chlorella*, are essentially like *Chlamydomonas* in this

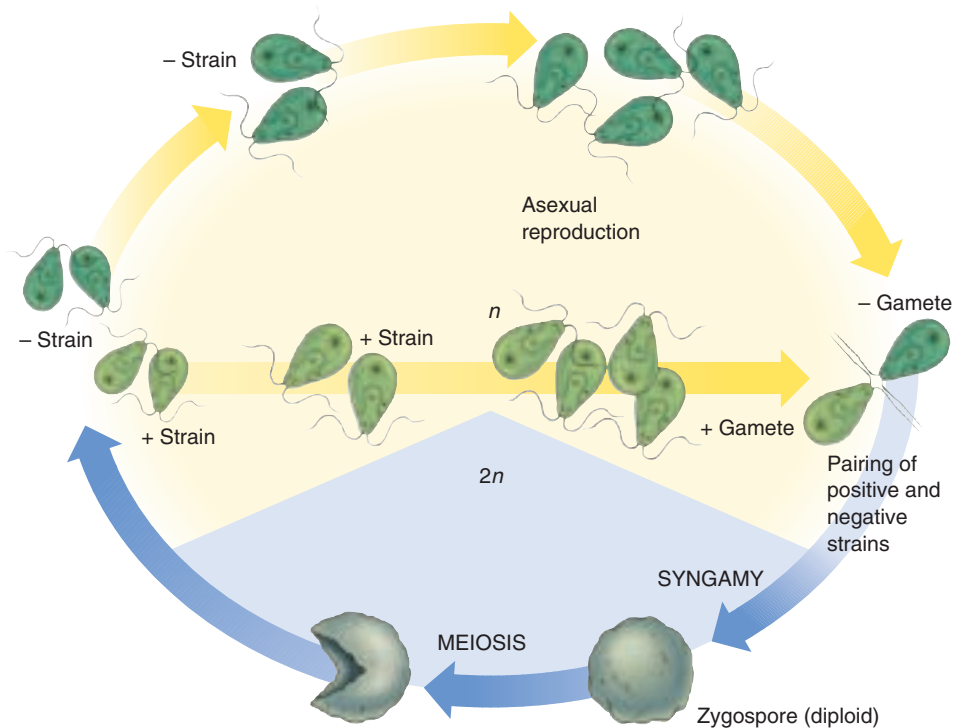


FIGURE 35.15

Life cycle of *Chlamydomonas* (Chlorophyta). Individual cells of this microscopic, biflagellated alga, which are haploid, divide asexually, producing identical copies of themselves. At times, such haploid cells act as gametes—fusing, as shown in the lower right-hand side of the diagram, to produce a zygote. The zygote develops a thick, resistant wall, becoming a zygospore; this is the only diploid cell in the entire life cycle. Within this diploid zygospore, meiosis takes place, ultimately resulting in the release of four haploid individuals. Because of the segregation during meiosis, two of these individuals are called the (+) strain, the other two the (–) strain. Only + and – individuals are capable of mating with each other when syngamy does take place, although both may divide asexually to reproduce themselves.

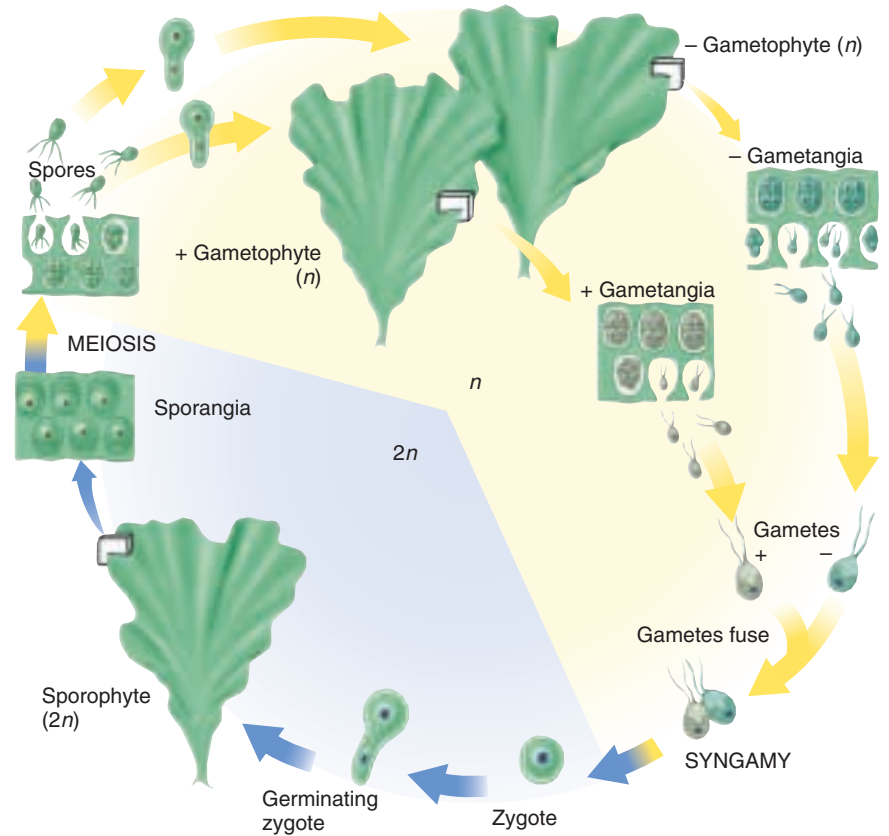
trait, but do not have the ability to form flagella. *Chlorella* is widespread in both fresh and salt water as well as soil and is only known to reproduce asexually. Recently, *Chlorella* has been widely investigated as a possible food source for humans and other animals, and pilot farms have been established in Israel, the United States, Germany, and Japan.

Another major line of specialization from cells like *Chlamydomonas* concerns the formation of motile, colonial organisms. In these genera of green algae, the *Chlamydomonas*-like cells retain some of their individuality. The most elaborate of these organisms is *Volvox* (see figure 35.1), a hollow sphere made up of a single layer of 500 to 60,000 individual cells, each cell with two flagella. Only a small number of the cells are reproductive. The colony has definite anterior and posterior ends, and the flagella of all of the cells beat in such a way as to rotate the colony in a clockwise direction as it moves forward through the water. The reproductive cells of *Volvox* are located mainly at the posterior end of the colony. Some may divide asexually, bulge inward, and give rise to new colonies that initially remain within the parent colony. Others produce gametes. In some species of



FIGURE 35.16

Life cycle of *Ulva*. In this green alga, the gametophyte and the sporophyte are identical in appearance and consist of flattened sheets two cells thick. In the haploid (n) gametophyte, gametangia give rise to haploid gametes, which fuse to form a diploid ($2n$) zygote. The zygote germinates to form the diploid sporophyte. Sporangia within the sporophyte give rise to haploid spores by meiosis. The haploid spores develop into haploid gametophytes.



Volvox, there is a true division of labor among the different types of cells, which are specialized in relation to their ultimate function throughout the development of the organism.

In addition to these two lines of specialization from *Chlamydomonas*-like cells, there are many other kinds of green algae of less certain derivation. Many filamentous genera, such as *Spirogyra*, with its ribbon-like chloroplasts, differ substantially from the remainder of the green algae in their modes of cell division and reproduction. Some of these genera have even been placed in separate phyla. The study of the green algae, involving modern methods of electron microscopy and biochemistry, is beginning to reveal unexpected new relationships within this phylum.

Ulva, or sea lettuce (figure 35.16), is a genus of marine green algae that is extremely widespread. The glistening individuals of this genus, often more than 10 centimeters across, consist of undulating sheets only two cells thick. Sea lettuce attaches by protuberances of the basal cells to rocks or other substrates. The reproductive cycle of *Ulva* involves an alternation of generations (sporic meiosis; figure 35.16) as is typical among green algae. Unlike most organisms that undergo sporic meiosis, however,

the **gametophytes** (haploid phase) and **sporophytes** (diploid phase) resemble one another closely.

The stoneworts, a group of about 250 living species of green algae, many of them in the genera *Chara* and *Nitella*, have complex structures. Whorls of short branches arise regularly at their nodes, and the gametangia (structures that give rise to gametes) are complex and multicellular. Stoneworts are often abundant in fresh to brackish water and are common as fossils.

Dinoflagellates are primarily unicellular, photosynthetic, and flagellated. Euglenoids (phylum Euglenophyta) consist of about 40 genera, about a third of which have chloroplasts similar biochemically to those of green algae and plants. Diatoms and golden algae are unicellular, photosynthetic organisms that produce a unique carbohydrate. Diatoms have double shells made of opaline silica. Nonmotile, unicellular algae and multicellular, flagellated colonies have been derived from green algae like *Chlamydomonas*—a biflagellated, unicellular organism. The life cycle of brown algae is marked by an alternation of generations between the diploid phase, or sporophyte, and the haploid phase, or gametophyte.

Heterotrophs with Flagella

The phylum Sarcomastigophora contains a diverse group of protists combined into one phylum because they all possess a single kind of nucleus and use flagella or pseudopodia (or both) for locomotion. We will focus on the class Zoomastigophora.

Zoomastigophora: The Zoomastigotes

The class Zoomastigophora is composed of unicellular, heterotrophic organisms that are highly variable in form (figure 35.17). Each has at least one flagellum, with some species having thousands. They include both free-living and parasitic organisms. Many zoomastigotes apparently reproduce only asexually, but sexual reproduction occurs in some species. The members of one order, the kinetoplastids, include the genera *Trypanosoma* (figure 35.17c) and *Crithidia*, pathogens of humans and domestic animals. The euglenoids could be viewed as a specialized group of zoomastigotes, some of which acquired chloroplasts during the course of evolution.

Trypanosomes cause many serious human diseases, the most familiar of which is trypanosomiasis also known as African sleeping sickness (figure 35.18). Trypanosomes cause many other diseases including East Coast fever, leishmaniasis, and Chagas' disease, all of great importance in tropical areas where they afflict millions of people each year. Leishmaniasis, which is transmitted by sand flies, afflicts about 4 million people a year. The effects of these diseases range from extreme fatigue and lethargy in sleeping sickness to skin sores and deep eroding lesions that can almost obliterate the face in leishmaniasis. The trypanosomes that cause these diseases are spread by biting insects, including tsetse flies and assassin bugs.

A serious effort is now under way to produce a vaccine for trypanosome-caused diseases. These diseases make it

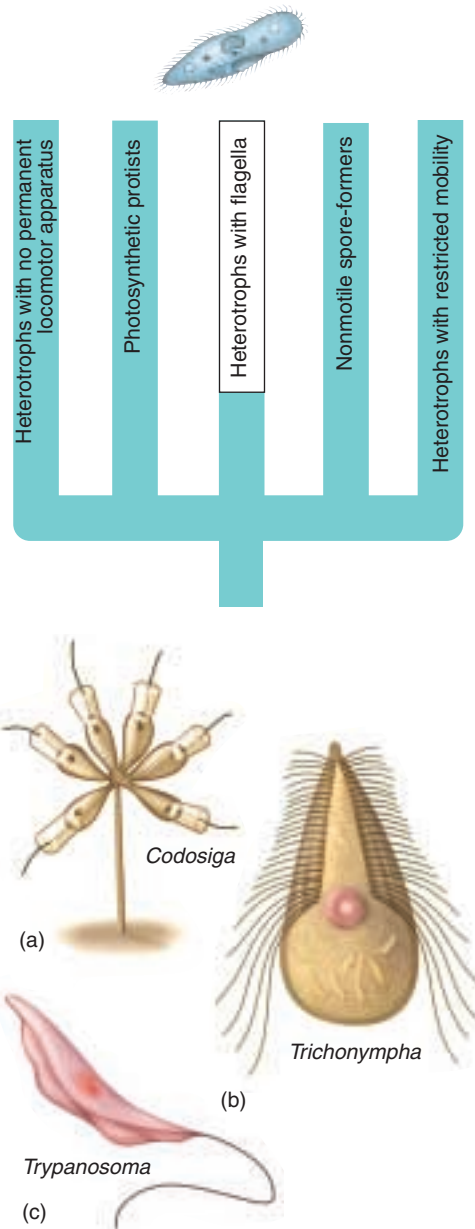


FIGURE 35.17
Three genera of zoomastigotes (Zoomastigophora), a highly diverse group. (a) *Codosiga*, a colonial choanoflagellate that remains attached to its substrate; other colonial choanoflagellates swim around as a colony, resembling the green alga *Volvox* in this respect. (b) *Trichonympha*, one of the zoomastigotes that inhabits the guts of termites and wood-feeding cockroaches and digests cellulose there. *Trichonympha* has rows of flagella in its anterior regions. (c) *Trypanosoma*, which causes sleeping sickness, an important tropical disease. It has a single, anterior flagellum.

impossible to raise domestic cattle for meat or milk in a large portion of Africa. Control is especially difficult because of the unique attributes of these organisms. For example, tsetse fly-transmitted trypanosomes have evolved an elaborate genetic mechanism for repeatedly changing the antigenic nature of their protective glycoprotein coat, thus dodging the antibodies their hosts produce against them (see chapter 57). Only a single one out of some 1000 to 2000 variable antigen genes is expressed at a time. Rearrangements of these genes during the asexual cycle of the organism allow for the expression of a seemingly endless variety of different antigen genes that maintain infectivity by the trypanosomes.

When the trypanosomes are ingested by a tsetse fly, they embark on a complicated cycle of development and multiplication, first in the fly's gut and later in its salivary glands. It is their position in the salivary glands that allows them to move into their vertebrate host. Recombination has been observed between different strains of trypanosomes introduced into a single fly, thus suggesting that mating, syngamy, and meiosis occur, even though they have not been observed directly. Although most trypanosome reproduction is asexual, this sexual cycle, reported for the first time in 1986, affords still further possibilities for recombination in these organisms.

In the guts of the flies that spread them, trypanosomes are noninfective. When they are ready to transfer to the skin or bloodstream of their host, trypanosomes migrate to the salivary glands and acquire the thick coat of glycoprotein antigens that protect them from the host's antibodies. When they are taken up by a fly, the trypanosomes again shed their coats. The production of vaccines against such a system is complex, but tests are underway. Releasing sterilized flies to impede the reproduction of populations is another technique used to try to control the fly population. Traps made of dark cloth and scented like cows, but

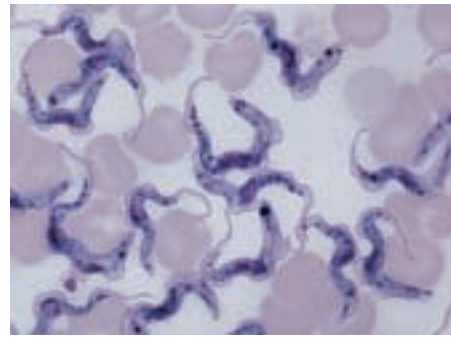
poisoned with insecticides, have likewise proved effective. Research is proceeding rapidly because the presence of tsetse flies with their associated trypanosomes blocks the use of some 11 million square kilometers of potential grazing land in Africa.

Some zoomastigotes occur in the guts of termites and other wood-eating insects. They possess enzymes that allow them to digest the wood and thus make the components of the wood available to their hosts. The relationship is similar to that between certain bacteria and protozoa that function in the rumens of cattle and related mammals (see chapter 51).

Another order of zoomastigotes, the choanoflagellates, is most likely the group from which the sponges (phylum Porifera) and probably all animals arose. Choanoflagellates have a single emergent flagellum surrounded by a funnel-shaped, contractile collar composed of closely placed filaments, a unique structure that is exactly matched in the sponges. These protists feed on bacteria strained out of the water by the collar.

Hiker's Diarrhea. *Giardia lamblia* is a flagellate protist (belonging to a small order called diplomonads) found throughout the world, including all parts of the United States and Canada (figure 35.19). It occurs in water, including the clear water of mountain streams and the water supplies of some cities. It infects at least 40 species of wild and domesticated animals in addition to humans. In 1984 in Pittsburgh, 175,000 people had to boil their drinking water for several days following the appearance of *Giardia* in the city's water system. Although most individuals exhibit no symptoms if they drink water infested with *Giardia*, many suffer nausea, cramps, bloating, vomiting, and diarrhea. Only 35 years ago, *Giardia* was thought to be harmless; today, it is estimated that at least 16 million residents of the United States are infected by it.

Giardia lives in the upper small intestine of its host. It occurs there in a motile form that cannot survive outside the host's body. It is spread in the feces of infected individuals in the form of dormant, football-shaped cysts—sometimes at levels as high as 300 million individuals per gram of feces. These cysts can survive at least two months in cool water, such as that of mountain streams. They are relatively resistant to the usual water-treatment agents such as chlorine and iodine but are killed at temperatures greater than about 65°C. Apparently, pollution by humans seems to be the main way *Giardia* is released into stream water. There are at least three species of *Giardia* and many distinct strains; how many of them attack humans and under what circumstances are not known with certainty.



(a)

20 μm



(b)

FIGURE 35.18

Trypanosoma is the zoomastigote that causes sleeping sickness. (a) *Trypanosoma* among red blood cells. The nuclei (dark-staining bodies), anterior flagella, and undulating, changeable shape of the trypanosomes are visible in this photograph (500 \times). (b) The tsetse



FIGURE 35.19

Giardia lamblia. *Giardia* are flagellated unicellular parasites that infect the human intestine. *Giardia* are very primitive, having only a rudimentary cytoskeleton and lacking mitochondria and chloroplasts. Sequencing of ribosomal RNA suggests that *Giardia* and *Pelomyxa*, the eukaryotes most closely related to prokaryotes, should be grouped together. The name Archezoa (Greek *arkhaios*, "ancient") has been suggested for the group, stressing its early divergence from bacteria as long as 2 billion years ago.

In the wilderness, good sanitation is important in preventing the spread of *Giardia*. Dogs, which readily contract and spread the disease, should not be taken into pristine wilderness areas. Drinking water should be filtered—the filter must be capable of eliminating particles as small as 1 micrometer in diameter—or boiled for at least one minute. Water from natural streams or lakes should never be consumed directly, regardless of how clean it looks. In other regions, good sanitation methods are important to prevent not only *Giardia* infection but also other diseases.

Ciliophora: The Ciliates

As the name indicates, most members of the Ciliophora feature large numbers of cilia. These heterotrophic, unicellular protists range in size from 10 to 3000 micrometers long. About 8000 species have been named. Despite their unicellularity, ciliates are extremely complex organisms, inspiring some biologists to consider them organisms without cell boundaries rather than single cells.

Their most characteristic feature, cilia, are usually arranged either in longitudinal rows or in spirals around the body of the organism (figure 35.20). Cilia are anchored to microtubules beneath the cell membrane, and they beat in a coordinated fashion. In some groups, the cilia have specialized locomotory and feeding functions, becoming fused into sheets, spikes, and rods which may then function as mouths, paddles, teeth, or feet. The ciliates have a tough but flexible outer covering called the pellicle that enables the organism to squeeze through or move around many kinds of obstacles.

All ciliates that have been studied have two very different types of nuclei within their cells, small **micronuclei** and larger **macronuclei** (figure 35.21). The micronuclei, which contain apparently normal diploid chromosomes, divide by meiosis and are able to undergo genetic recombination. Macronuclei are derived from certain micronuclei in a complex series of steps. Within the macronuclei are multiple copies of the genome, and the DNA is divided into small pieces—smaller than individual chromosomes. In one group of ciliates, these are equivalent to single genes. Macronuclei divide by elongating and constricting and play an essential role in routine cellular functions, such as the production of mRNA to direct protein synthesis for growth and regeneration.

Ciliates form vacuoles for ingesting food and regulating their water balance. Food first enters the gullet, which in the well-known ciliate *Paramecium* is lined with cilia fused into a membrane (figure 35.21). From the gullet, the food passes into food vacuoles, where enzymes and hydrochloric acid aid in its digestion. After the digested material has been completely absorbed, the vacuole empties its waste contents through a special pore in the pellicle known as the **cytoproct**. The cytoproct is essentially an exocytotic vesicle that appears periodically when solid particles are ready to be expelled. The contractile vacuoles, which function in the regulation of water balance, periodically expand and contract as they empty their contents to the outside of the organism.

Ciliates usually reproduce by transverse fission of the parent cell across its short axis, thus forming two identical individuals (figure 35.22a). In this process of cell division, the mitosis of the micronuclei proceeds normally, and the macronuclei divide as just described.

In *Paramecium*, the cells divide asexually for about 700 generations and then die if sexual reproduction has not occurred. Like most ciliates, *Paramecium* has a sexual process called **conjugation**, in which two individual cells remain



FIGURE 35.20
A ciliate (Ciliophora).
Stentor, a funnel-shaped ciliate, showing spirally arranged cilia (120 \times).

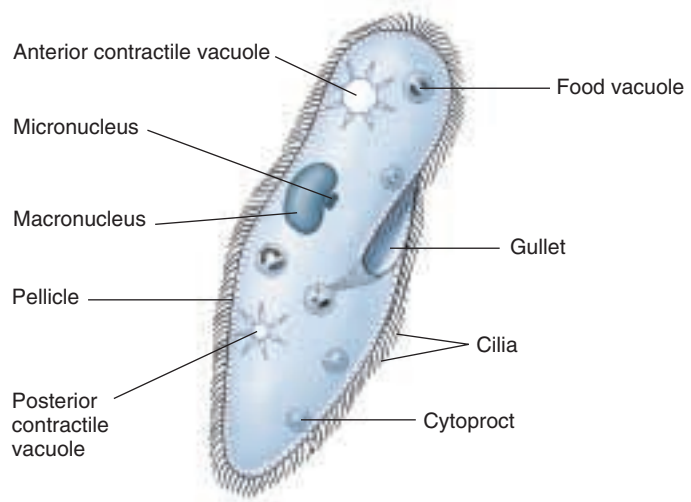


FIGURE 35.21
Paramecium. The main features of this familiar ciliate are shown.

attached to each other for up to several hours (figure 35.22b,c). Only cells of two different genetically determined mating types, *odd* and *even*, are able to conjugate. Meiosis in the micronuclei of each individual produces several haploid micronuclei, and the two partners exchange a pair of these micronuclei through a cytoplasmic bridge that appears between the two partners.

In each conjugating individual, the new micronucleus fuses with one of the micronuclei already present in that individual, resulting in the production of a new diploid micronucleus in each individual. After conjugation, the macronucleus in each cell disintegrates, while the new diploid micronucleus undergoes mitosis, thus giving rise to two new identical diploid micronuclei within each individual. One of these micronuclei becomes the precursor of the future micronuclei of that cell, while the other micronucleus undergoes multiple rounds of DNA replication, becoming the new macronucleus. This kind of complete segregation of the genetic material is a unique feature of the



(a)



(b)

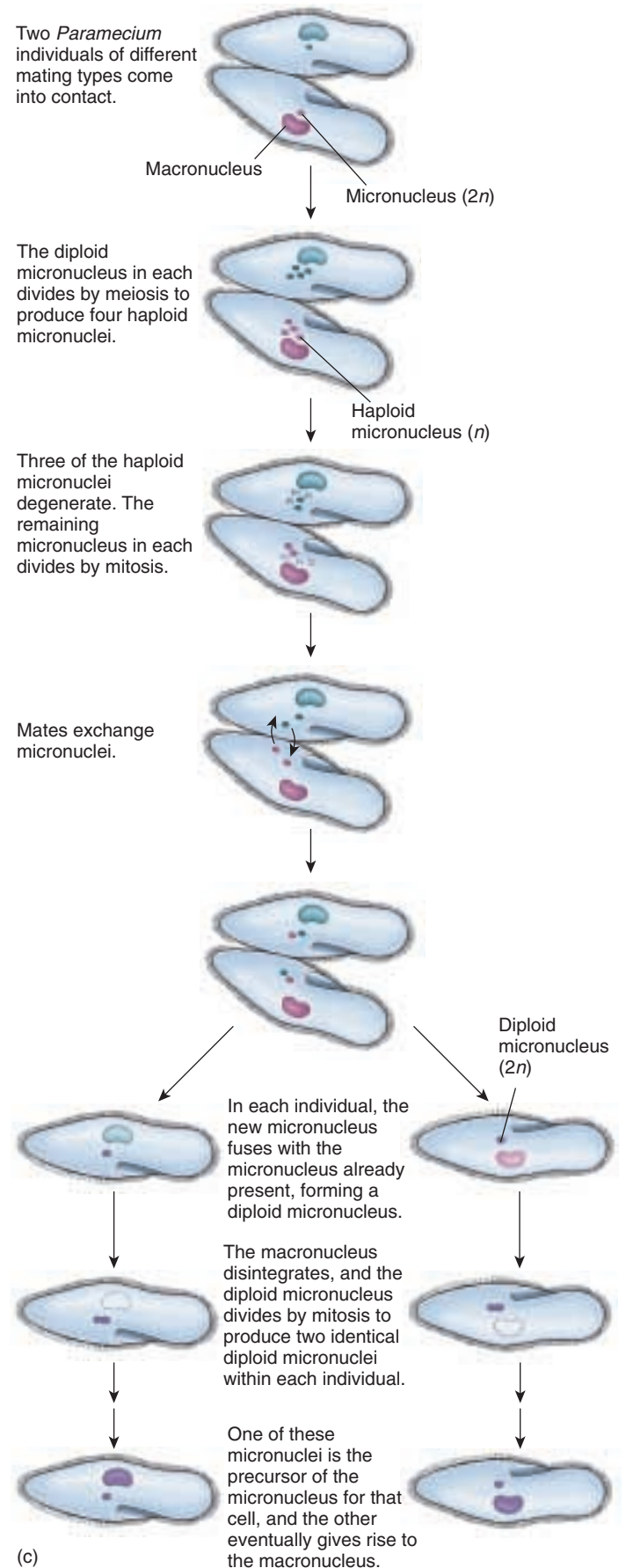
FIGURE 35.22

Life cycle of *Paramecium*. (a) When *Paramecium* reproduces asexually, a mature individual divides, and two complete individuals result. (b,c) In sexual reproduction, two mature cells fuse in a process called conjugation (100×).

ciliates and makes them ideal organisms for the study of certain aspects of genetics.

Progeny from a sexual division in *Paramecium* must go through about 50 asexual divisions before they are able to conjugate. When they do so, their biological clocks are restarted, and they can conjugate again. After about 600 asexual divisions, however, *Paramecium* loses the protein molecules around the gullet that enable it to recognize an appropriate mating partner. As a result, the individuals are unable to mate, and death follows about 100 generations later. The exact mechanisms producing these unusual events are unknown, but they involve the accumulation of a protein, which is now being studied.

The zoomastigotes are a highly diverse group of flagellated unicellular heterotrophs, containing among their members the ancestors of animals as well as the very primitive *Giardia*. Ciliates possess characteristic cilia, and have two types of nuclei. The macronuclei contain multiple copies of certain genes, while the micronuclei contain multigene chromosomes.



Nonmotile Spore-Formers

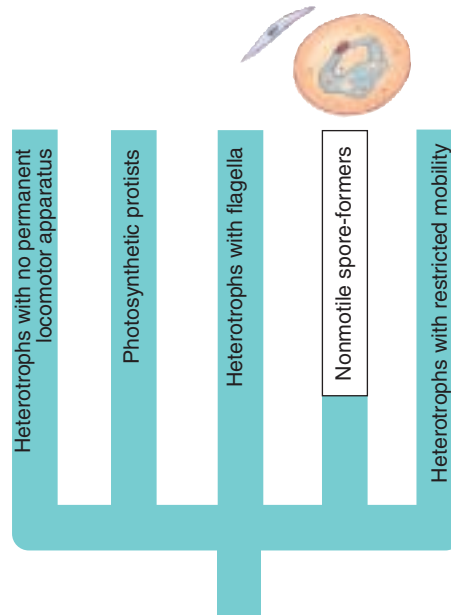
Apicomplexa: The Sporozoans

All sporozoans are nonmotile, spore-forming parasites of animals. Their spores are small, infective bodies that are transmitted from host to host. These organisms are distinguished by a unique arrangement of fibrils, microtubules, vacuoles, and other cell organelles at one end of the cell. There are 3900 described species of this phylum; best known among them is the malarial parasite, *Plasmodium*.

Sporozoans have complex life cycles that involve both asexual and sexual phases. Sexual reproduction involves an alternation of haploid and diploid generations. Both haploid and diploid individuals can also divide rapidly by mitosis, thus producing a large number of small infective individuals. Sexual reproduction involves the fertilization of a large female gamete by a small, flagellated male gamete. The zygote that results soon becomes an **oocyst**. Within the oocyst, meiotic divisions produce infective haploid spores called **sporozoites**.

An alternation between different hosts often occurs in the life cycles of sporozoans. Sporozoans of the genus *Plasmodium* are spread from person to person by mosquitoes of the genus *Anopheles* (figure 35.23); at least 65 different species of this genus are involved. When an *Anopheles* mosquito penetrates human skin to obtain blood, it injects saliva mixed with an anticoagulant. If the mosquito is infected with *Plasmodium*, it will also inject the elongated sporozoites into the bloodstream of its victim. The parasite makes its way through the bloodstream to the liver, where it rapidly divides asexually. After this division phase, **merozoites**, the next stage of the life cycle, form, either reinvading other liver cells or entering the host's bloodstream. In the bloodstream, they invade the red blood cells, dividing rapidly within them and causing them to become enlarged and ultimately to rupture. This event releases toxic substances throughout the body of the host, bringing about the well-known cycle of fever and chills that is characteristic of malaria. The cycle repeats itself regularly every 48 hours, 72 hours, or longer.

Plasmodium enters a sexual phase when some merozoites develop into **gametocytes**, cells capable of producing gametes. There are two types of gametocytes: male and female. Gametocytes are incapable of producing gametes within their human hosts and do so only when they are extracted from an infected human by a mosquito. Within the gut of the mosquito, the male and female gametocytes form sperm and eggs, respectively. Zygotes de-



velop within the mosquito's intestinal walls and ultimately differentiate into oocysts. Within the oocysts, repeated mitotic divisions take place, producing large numbers of sporozoites. These sporozoites migrate to the salivary glands of the mosquito, and from there they are injected by the mosquito into the bloodstream of a human, thus starting the life cycle of the parasite again.

Malaria. Malaria, caused by infections by the sporozoan *Plasmodium*, is one of the most serious diseases in the world. According to the World Health Organization, about 500 million people are affected by it at any one time, and approximately 2 million of them, mostly children, die each year. Malaria kills most children

under five years old who contract it. In areas where malaria is prevalent, most survivors more than five or six years old do not become seriously ill again from malaria infections. The symptoms, familiar throughout the tropics, include severe chills, fever, and sweating, an enlarged and tender spleen, confusion, and great thirst. Ultimately, a victim of malaria may die of anemia, kidney failure, or brain damage. The disease may be brought under control by the person's immune system or by drugs. As discussed in chapter 21, some individuals are genetically resistant to malaria. Other persons develop immunity to it.

Efforts to eradicate malaria have focused on (1) the elimination of the mosquito vectors; (2) the development of drugs to poison the parasites once they have entered the human body; and (3) the development of vaccines. The widescale applications of DDT from the 1940s to the 1960s led to the elimination of the mosquito vectors in the United States, Italy, Greece, and certain areas of Latin America. For a time, the worldwide elimination of malaria appeared possible, but this hope was soon crushed by the development of DDT-resistant strains of malaria-carrying mosquitoes in many regions; no fewer than 64 resistant strains were identified in a 1980 survey. Even though the worldwide use of DDT, long banned in the United States, nearly doubled from its 1974 level to more than 30,000 metric tons in 1984, its effectiveness in controlling mosquitoes is dropping. Further, there are serious environmental concerns about the use of this long-lasting chemical anywhere in the world. In addition to the problems with resistant strains of mosquitoes, strains of *Plasmodium* have appeared that are resistant to the drugs that have historically been used to kill them.

As a result of these problems, the number of new cases of malaria per year roughly doubled from the mid-1970s to

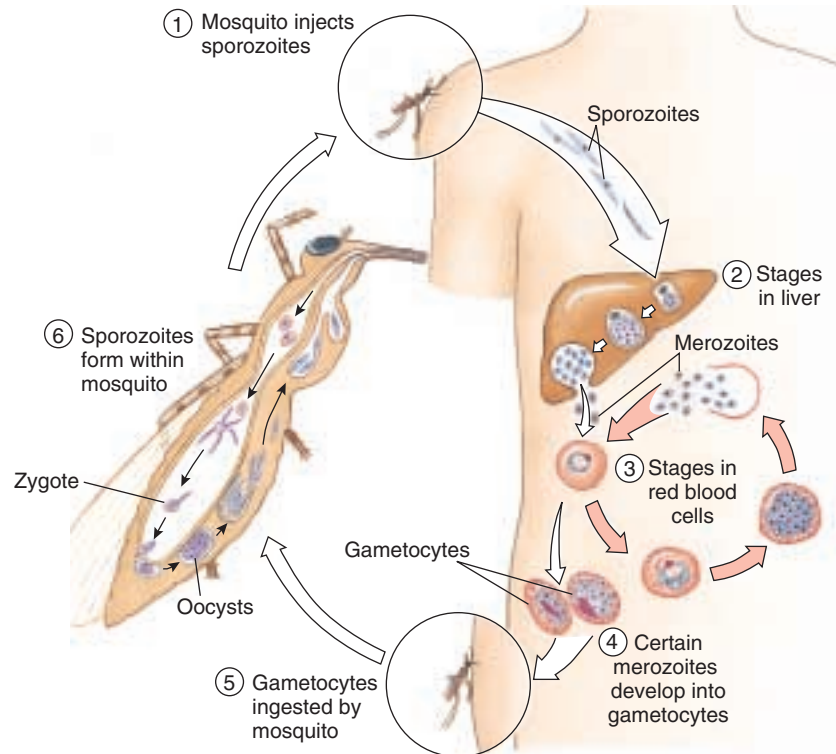


FIGURE 35.23

The life cycle of *Plasmodium*, the sporozoan that causes malaria. *Plasmodium* has a complex life cycle that alternates between mosquitoes and mammals.

the mid-1980s, largely because of the spread of resistant strains of the mosquito and the parasite. In many tropical regions, malaria is blocking permanent settlement. Scientists have therefore redoubled their efforts to produce an effective vaccine. Antibodies to the parasites have been isolated and produced by genetic engineering techniques, and they are starting to produce promising results.

Vaccines against Malaria. The three different stages of the *Plasmodium* life cycle each produce different antigens, and they are sensitive to different antibodies. The gene encoding the sporozoite antigen was cloned in 1984, but it is not certain how effective a vaccine against sporozoites might be. When a mosquito inserts its proboscis into a human blood vessel, it injects about a thousand sporozoites. They travel to the liver within a few minutes, where they are no longer exposed to antibodies circulating in the blood. If even one sporozoite reaches the liver, it will multiply rapidly there and cause malaria. The number of malaria parasites increases roughly eightfold every 24 hours after they enter the host's body. A compound vaccination against sporozoites, merozoites, and gameto-

cytes would probably be the most effective preventive measure, but such a compound vaccine has proven difficult to develop.

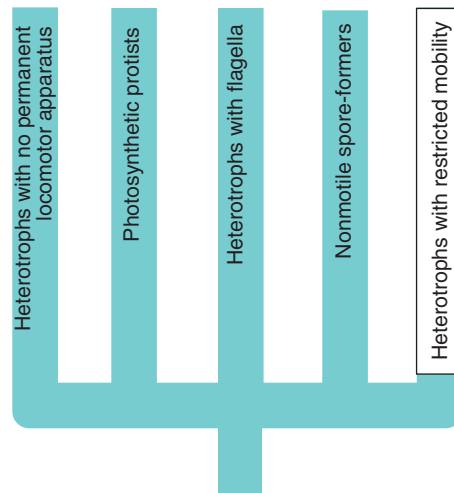
However, research completed in 1997 brings a glimmer of hope. An experimental vaccine containing one of the surface proteins of the disease-causing parasite, *P. falciparum*, seems to induce the immune system to produce defenses that are able to destroy the parasite in future infections. In tests, six out of seven vaccinated people did not get malaria after being bitten by mosquitoes that carried *P. falciparum*. Although research is still underway, many are hopeful that this new vaccine may be able to fight malaria, especially in Africa, where it takes a devastating toll.

The best known of the sporozoans is the malarial parasite *Plasmodium*. Like other sporozoans, *Plasmodium* has a complex life cycle involving sexual and asexual phases and alternation between different hosts, in this case mosquitoes and humans. Malaria kills about 2 million people each year.

Heterotrophs with Restricted Mobility

Oomycota

The oomycetes comprise about 580 species, among them the water molds, white rusts, and downy mildews. All of the members of this group are either parasites or **saprobies** (organisms that live by feeding on dead organic matter). The cell walls of the oomycetes are composed of cellulose or polymers that resemble cellulose. They differ remarkably from the chitin cell walls of fungi, with which the oomycetes have at times been grouped. Oomycete life cycles are characterized by gametic meiosis and a diploid phase; this also differs from fungi. Mitosis in the oomycetes resembles that in most other organisms, while mitosis in fungi has a number of unusual features, as you will see in chapter 36. Filamentous structures of fungi and, by convention, those of oomycetes, are called **hyphae**. Most oomycetes live in fresh or salt water or in soil, but some are plant parasites that depend on the wind to spread their spores. A few aquatic oomycetes are animal parasites.



Oomycetes are distinguished from other protists by the structure of their motile spores, or **zoospores**, which bear two unequal flagella, one of which is directed forward, the other backward. Such zoospores are produced asexually in a sporangium. Sexual reproduction in the group involves **gametangia** (singular, **gametangium**)—gamete-producing structures—of two different kinds. The female gametangium is called an **oogonium**, and the male gametangium is called an **antheridium**. The antheridia contain numerous male nuclei, which are the functional male gametes; the oogonia contain from one to eight eggs, which are the female gametes. When the contents of an antheridium flow into an oogonium, it leads to the individual fusion

of male nuclei with eggs. This is followed by the thickening of the cell wall around the resulting zygote or zygotes. This produces a special kind of thick-walled cell called an **oospore**, the structure that gives the phylum its name. Details from the life cycle of one of the oomycetes, *Saprolegnia*, are shown in figure 35.24.

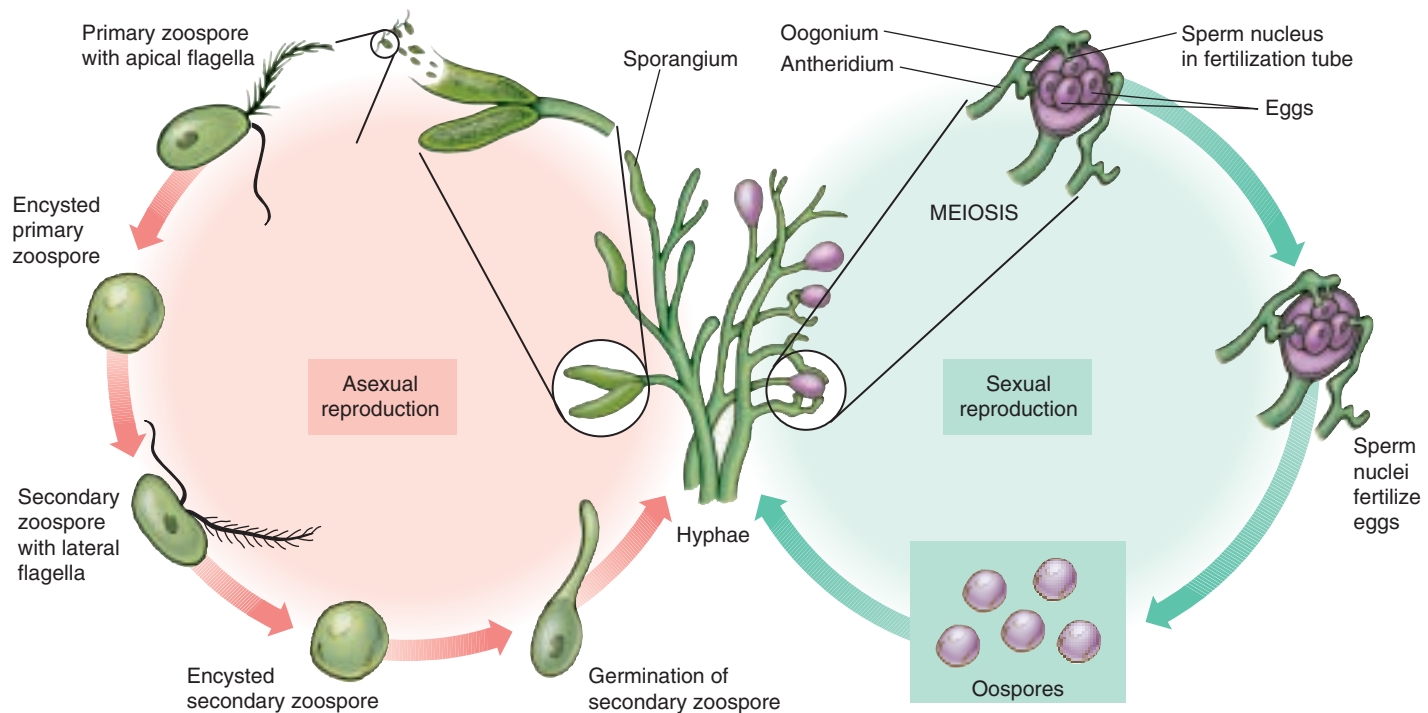


FIGURE 35.24 Life cycle of *Saprolegnia*, an oomycete. Asexual reproduction by means of flagellated zoospores is shown at left, sexual reproduction at right. Hyphae with diploid nuclei are produced by germination of both zoospores and oospores.

Aquatic oomycetes, or water molds, are common and easily cultured. Some water molds cause fish diseases, producing a kind of white fuzz on aquarium fishes. Among their terrestrial relatives are oomycetes of great importance as plant pathogens, including *Plasmopara viticola*, which causes downy mildew of grapes, and *Phytophthora infestans*, which causes the late blight of potatoes. This oomycete was responsible for the Irish potato famine of 1845 and 1847, during which about 400,000 people starved to death or died of diseases complicated by starvation. Millions of Irish people emigrated to the United States and elsewhere as a result of this disaster.

Acrasiomycota: The Cellular Slime Molds

There are about 70 species of cellular slime molds. This phylum has extraordinarily interesting features and was once thought to be related to fungi, “mold” being a general term for funguslike organisms. In fact, the cellular slime molds are probably more closely related to amoebas (phylum Rhizopoda) than to any other group, but they have many special features that mark them as distinct. Cellular slime molds are common in fresh water, damp soil, and on rotting vegetation, especially fallen logs. They have become one of the most important groups of organisms for studies of differentiation because of their relatively simple developmental systems and the ease of analyzing them (figure 35.25).

The individual organisms of this group behave as separate amoebas, moving through the soil or other substrate and ingesting bacteria and other smaller organisms. At a certain phase of their life cycle, the individual organisms aggregate and form a moving mass, the “slug,” that eventually transforms itself into a spore-containing mass, the **sorocarp**. In the sorocarp the amoebas become encysted as spores. Some of the amoebas fuse sexually to form **macro-cysts**, which have diploid nuclei; meiosis occurs in them after a short period (zygotic meiosis). The sporocarp develops a stalked structure with a chamber at the top which releases the spores. Other amoebas are released directly, eventually aggregating again to form a new slug.

The development of *Dictyostelium discoideum*, a cellular slime mold, has been studied extensively because of the implication its unusual life cycle has for understanding the developmental process in general. When the individual amoebas of this species exhaust the supply of bacteria in a given area and are near starvation, they aggregate and form a compound, motile mass. The aggregation of the individual amoebas is induced by pulses of cyclic adenosine monophosphate (cAMP), which the cells begin to secrete when they are starving. The cells form an aggregate organism that moves to a new area where food is more plentiful. In the new area, the colony differentiates into a multicellular sorocarp within which spores differentiate. Each of these spores, if it falls into a suitably moist habitat, releases a new amoeba, which begins to feed, and the cycle is started again.



FIGURE 35.25

Development in *Dictyostelium discoideum*, a cellular slime mold.

(a) First, a spore germinates, forming amoebas. These amoebas feed and reproduce until the food runs out. (b) The amoebas aggregate and move toward a fixed center. (c) Next, they form a multicellular “slug” 2 to 3 mm long that migrates toward light. (d) The slug stops moving and begins to differentiate into a spore-forming body, called a sorocarp (e). (f) Within heads of the sorocarps, amoebas become encysted as spores.

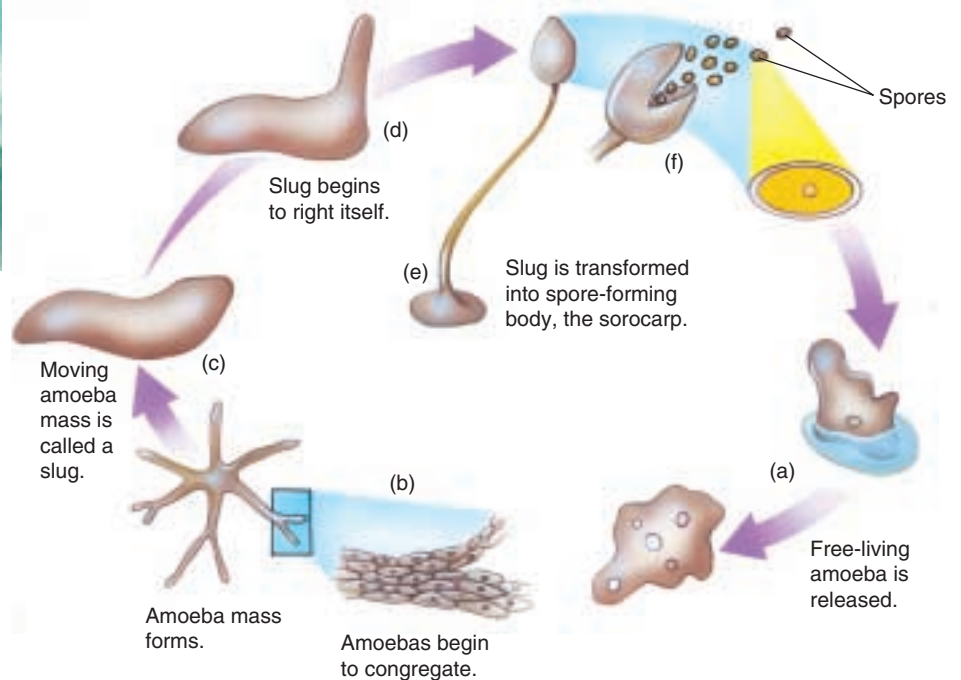




FIGURE 35.26

A plasmodial protist. This multinucleate plasmodium moves about in search of the bacteria and other organic particles that it ingests.

Myxomycota: The Plasmodial Slime Molds

Plasmodial slime molds are a group of about 500 species. These bizarre organisms stream along as a **plasmodium**, a nonwalled, multinucleate mass of cytoplasm, that resembles a moving mass of slime (figure 35.26). This is called the feeding phase, and the plasmodia may be orange, yellow, or another color. Plasmodia show a back-and-forth streaming of cytoplasm that is very conspicuous, especially under a microscope. They are able to pass through the mesh in cloth or simply flow around or through other obstacles. As they move, they engulf and digest bacteria, yeasts, and other small particles of organic matter. Plasmodia contain many nuclei (multinucleate), but these are not separated by cell membranes. The nuclei undergo mitosis synchronously, with the nuclear envelope breaking down, but only at late anaphase or telophase. Centrioles are lacking in cellular slime molds. Although they have similar common names, there is no evidence that the plasmodial slime molds are closely related to the cellular slime molds; they differ in most features of their structure and life cycles (figure 35.27).

When either food or moisture is in short supply, the plasmodium migrates relatively rapidly to a new area. Here it stops moving and either forms a mass in which spores differentiate or divides into a large number of small mounds, each of which produces a single, mature **sporangium**, the

structure in which spores are produced. These sporangia are often extremely complex in form and beautiful (figure 35.28). The spores can be either diploid or haploid. In most species of plasmodial slime molds with a diploid plasmodium, meiosis occurs in the spores within 24 hours of their formation. Three of the four nuclei in each spore disintegrate, leaving each spore with a single haploid nucleus.

The spores are highly resistant to unfavorable environmental influences and may last for years if kept dry. When conditions are favorable, they split open and release their protoplast, the contents of the individual spore. The protoplast may be amoeboid or bear two flagella. These two stages appear to be interchangeable, and conversions in either direction occur readily. Later, after the fusion of haploid protoplasts (gametes), a usually diploid plasmodium may be reconstituted by repeated mitotic divisions.

Molds are heterotrophic protists, many of which are capable of amoeba-like streaming. The feeding phase of plasmodial slime molds consists of a multinucleate mass of protoplasm; a plasmodium can flow through a cloth mesh and around obstacles. If the plasmodium begins to dry out or is starving, it forms often elaborate sporangia. Meiosis occurs in the spores once they have formed within the sporangium.

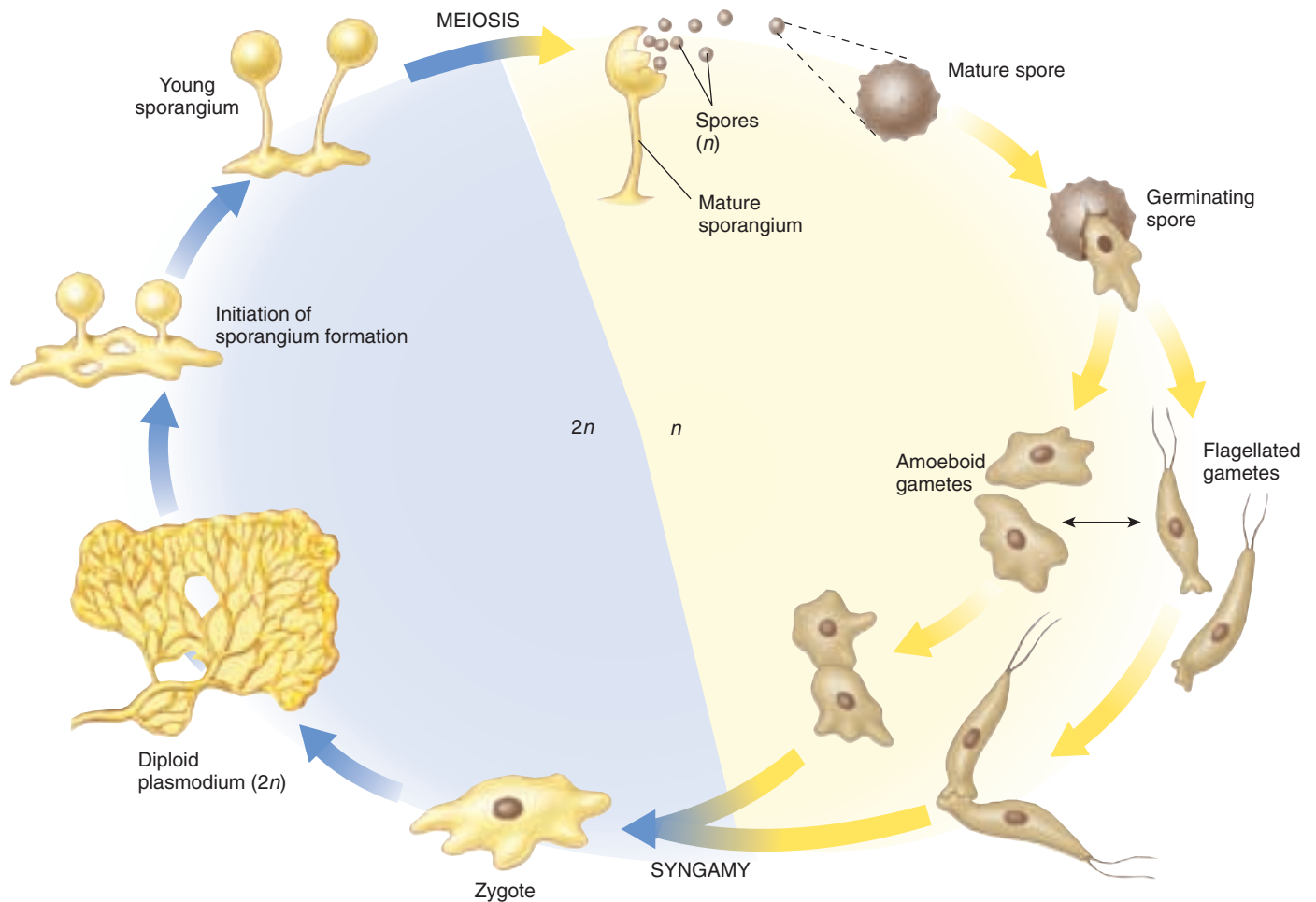


FIGURE 35.27

Life cycle of a plasmodial slime mold. When food or moisture is scarce, a diploid plasmodium stops moving and forms sporangia. Haploid spores form by meiosis. The spores wait until conditions are favorable to germinate. Spores can give rise to flagellated or amoeboid gametes; the two forms convert from one to the other readily. Fusion of the gametes forms the diploid zygote, which gives rise to the mobile, feeding plasmodium by mitosis.



FIGURE 35.28

Sporangia of three genera of plasmodial slime molds (phylum Myxomycota). (a) *Arcyria*. (b) *Fuligo*. (c) Developing sporangia of *Tubifera*.



Summary

Questions

Media Resources

35.1 Eukaryotes probably arose by endosymbiosis.

- The theory of endosymbiosis, accepted by almost all biologists, proposes that mitochondria and chloroplasts were once aerobic eubacteria that were engulfed by ancestral eukaryotes.
 - There is some suggestion that centrioles may also have an endosymbiotic origin.
1. What kind of bacteria most likely gave rise to the chloroplasts in the eukaryotic cells of plants and some algae?

35.2 The kingdom Protista is by far the most diverse of any kingdom.

- The kingdom Protista consists of predominantly unicellular phyla, together with three phyla that include large numbers of multicellular organisms.
 - The catch-all kingdom Protista includes all eukaryotic organisms except animals, plants, and fungi.
2. Why is the kingdom Protista said to be an artificial group? How is this different from the other kingdoms?



- Characteristics of Protists

35.3 Protists can be categorized into five groups.

- Dinoflagellates (phylum Dinoflagellata) are a major phylum of primarily unicellular organisms that have unique chromosomes and a very unusual form of mitosis. They are the only eukaryotes known to lack histones and nucleosomes.
 - Euglenoids (phylum Euglenophyta) have chloroplasts that share the biochemical features of those found in green algae and plants.
 - Diatoms (phylum Chrysophyta) are unicellular, photosynthetic protists with opaline silica shells. They include the golden algae.
 - Brown algae (phylum Phaeophyta) are multicellular, marine protists, some reaching 100 meters in length. The kelps contribute greatly to the productivity of the sea, especially along the coasts in relatively shallow areas.
 - The zoomastigotes (phylum Sarcomastigophora) are a group of heterotrophic, mostly unicellular protists that includes the organism responsible for sleeping sickness.
 - There are about 8000 named species of ciliates (phylum Ciliophora); these protists have a very complex morphology with numerous cilia.
 - The malarial parasite, *Plasmodium*, is a member of the phylum Apicomplexa. Carried by mosquitoes, it multiplies rapidly in the liver of humans and other primates and brings about the cyclical fevers characteristic of malaria by releasing toxins into the bloodstream of its host.
3. Why is mitosis in dinoflagellates unique? What are zooxanthellae?
 4. What determines whether a collection of individuals is truly multicellular?
 5. What unique characteristic differentiates the members of Ciliophora from other protists? What is the function of two vacuoles exhibited by most members of Ciliophora?
 6. Why has it been so difficult to produce a vaccine for trypanosome-caused diseases?
 7. What differentiates the oomycetes from the kingdom Fungi, in which they were previously placed? What is the feeding strategy of this phylum? Why are these organisms generally considered harmful?



- Protozoa
- Photosynthetic Protists
- Fungus-like Protists