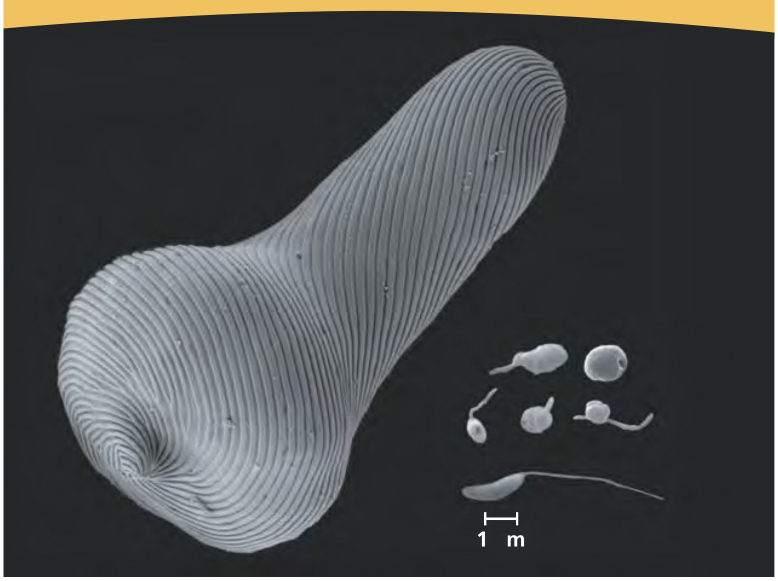
28

Protists



▲ **Figure 28.1 Which of these organisms are prokaryotes and which are eukaryotes?**

EVOLUTION

KEY CONCEPTS

28.1 Most eukaryotes are single-celled organisms
28.2 Excavates include protists with modified mitochondria and protists with unique flagella
28.3 Chromalveolates may have originated by secondary endosymbiosis
28.4 Rhizarians are a diverse group of protists defined by DNA similarities
28.5 Red algae and green algae are the closest relatives of land plants
28.6 Unikonts include protists that are closely related to fungi and animals
28.7 Protists play key roles in ecological communities

OVERVIEW

Living Small

Knowing that most prokaryotes are extremely small organisms, you might assume that **Figure 28.1** depicts six prokaryotes and one much larger eukaryote. But in fact, the only prokaryote is the organism immediately above the scale bar. The other six organisms are members of diverse, mostly unicellular groups of eukaryotes informally known as **protists**. Very small eukaryotes have intrigued scientists for more than 300 years, ever since the Dutch microscopist Antoni van Leeuwenhoek first laid eyes on them. As he discovered, viewing a drop of pond water under a light microscope can reveal a fascinating world of unicellular protists and prokaryotes. Some protists propel themselves with whipping flagella, while others creep along by means of blob-like appendages. Some are shaped like tiny trumpets; others resemble miniature jewelry. Recalling his observations, van Leeuwenhoek wrote, “No more pleasant sight has met my eye than this, of so many thousands of living creatures in one small drop of water.”

Until recently, biologists thought that 300 years of observation had uncovered a representative sample of living protist species. But in the last decade, genetic prospecting has turned up a treasure trove of previously unknown protists within the world of microscopic life. Many of these newly discovered organisms are just 0.5–2 μm in diameter—as small as many prokaryotes.

The surprising discovery of many species of minuscule protists followed close on the heels of recent findings regarding protist phylogeny. All protists were once classified in a single kingdom, Protista, but advances in eukaryotic systematics have caused the kingdom to crumble. It has become clear that the kingdom Protista is in fact polyphyletic (see Figure 26.10): Some protists are more closely related to plants, fungi, or animals than they are to other protists. As a result, the kingdom Protista has been abandoned, and various lineages of protists are now recognized as kingdoms in their own right. Most biologists still use the term *protist*, but only as a convenient way to refer to eukaryotes that are not plants, animals, or fungi.

In this chapter, you will become acquainted with some of the most significant groups of protists. You will learn about their structural and biochemical adaptations as well as their enormous impact on ecosystems, agriculture, industry, and human health.

CONCEPT **28.1**

Most eukaryotes are single-celled organisms

Protists, along with plants, animals, and fungi, are classified as eukaryotes; they are in domain Eukarya, one of the three domains of life. Unlike the cells of prokaryotes, eukaryotic cells have a nucleus and other membrane-bounded organelles, such as mitochondria and the Golgi apparatus. Such organelles provide specific locations in which particular cellular functions are accomplished, making the structure and organization of eukaryotic cells more complex than those of prokaryotic cells.

We'll survey the diversity of eukaryotes throughout the rest of this unit, beginning in this chapter with the protists. As you explore this material, bear in mind that

- the organisms in most eukaryotic lineages are protists, and
- most protists are unicellular.

Thus, life differs greatly from how most of us commonly think of it. The large, multicellular organisms that we know best (plants, animals, and fungi) are the tips of just a few branches on the great tree of life (see Figure 26.21).

Structural and Functional Diversity in Protists

Given the polyphyletic nature of the group once called Protista, it isn't surprising that few general characteristics of protists can be cited without exceptions. In fact, protists exhibit more structural and functional diversity than any other group of eukaryotes.

Most protists are unicellular, although there are some colonial and multicellular species. Single-celled protists are justifiably considered the simplest eukaryotes, but at the cellular level, many protists are very complex—the most elaborate of all cells. In multicellular organisms, essential biological functions are carried out by organs. Unicellular protists carry out the same essential functions, but they do so using subcellular organelles, not multicellular organs. The organelles that protists use are mostly those discussed in Chapter 6, including the nucleus, endoplasmic reticulum, Golgi apparatus, and lysosomes. Certain protists also rely on organelles not found in most other eukaryotic cells, such as contractile vacuoles that pump excess water from the protistan cell (see Figure 7.16).

Protists are more nutritionally diverse than other eukaryote groups. Some protists are photoautotrophs and contain chloroplasts. Some are heterotrophs, absorbing organic molecules or ingesting larger food particles. Still other protists, called **mixotrophs**, combine photosynthesis *and* heterotrophic nutrition. Photoautotrophy, heterotrophy, and mixotrophy have all arisen independently in many protist lineages.

Reproduction and life cycles also are highly varied among protists. Some protists are only known to reproduce asexually; others can also reproduce sexually or at least employ the sexual processes of meiosis and fertilization. All three basic types of sexual life cycles (see Figure 13.6) are represented among protists, along with some variations that do not quite fit any of these types. We will examine the life cycles of several protist groups later in this chapter.

Endosymbiosis in Eukaryotic Evolution

What gave rise to the enormous diversity of protists that exist today? There is abundant evidence that much of protist diversity has its origins in **endosymbiosis**, the process in which certain unicellular organisms engulf other cells, which become endosymbionts and ultimately organelles in the host cell. For example, as we discussed in Chapter 25, structural, biochemical, and DNA sequence data indicate that the first eukaryotes acquired mitochondria by engulfing an aerobic prokaryote (specifically, an alpha proteobacterium). The early origin of mitochondria is supported by the fact that all eukaryotes studied so far have either mitochondria or modified versions of them.

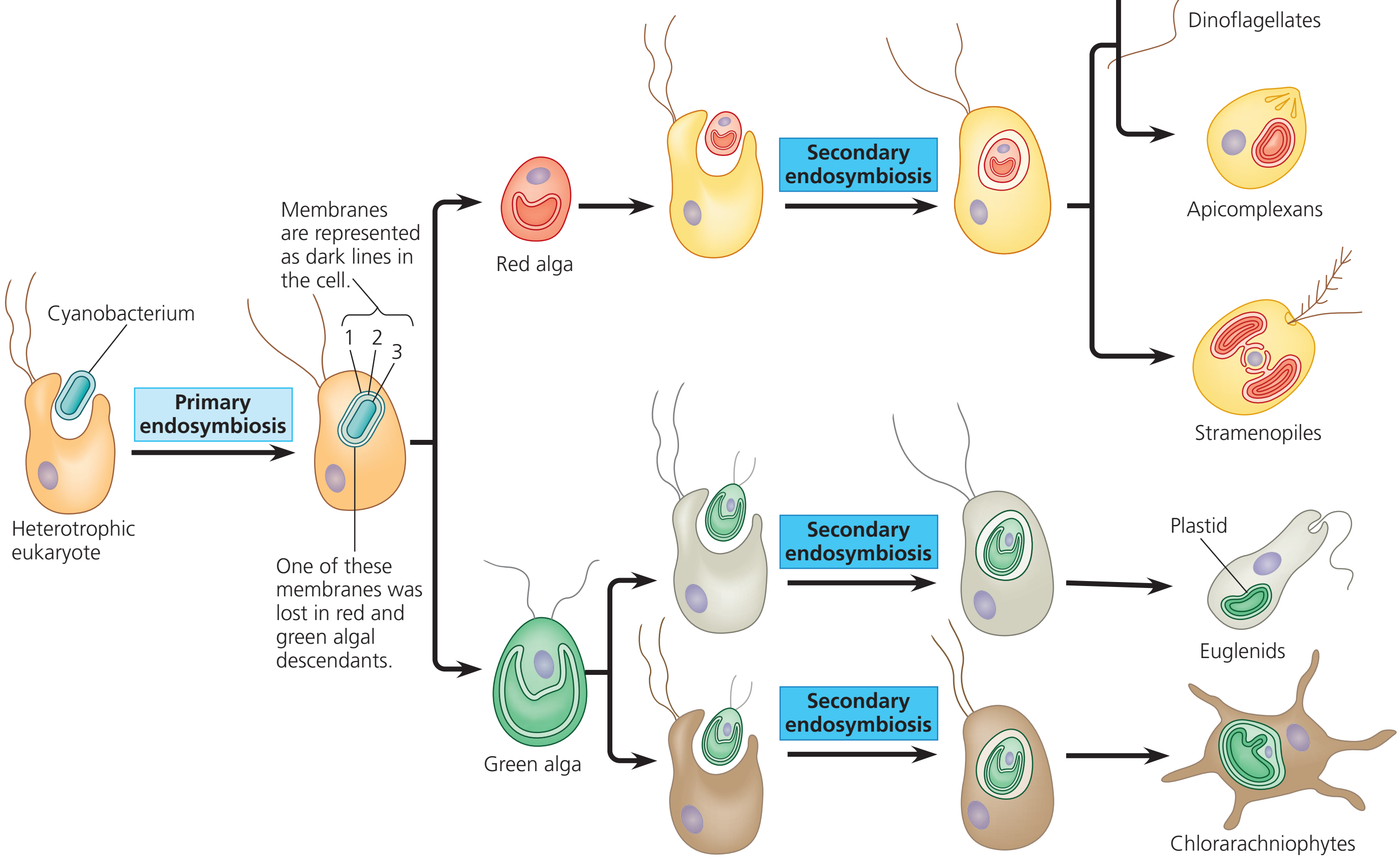
Much evidence also indicates that later in eukaryotic history, a lineage of heterotrophic eukaryotes acquired an additional endosymbiont—a photosynthetic cyanobacterium—that then evolved into plastids. As the hypothesis illustrated in **Figure 28.2** shows, this plastid-bearing lineage gave rise to two lineages of photosynthetic protists, or **algae:** red algae and green algae. This hypothesis is supported by the observation that the DNA of plastid genes in red algae and green algae closely resembles the DNA of cyanobacteria. In addition, plastids in red algae and green algae are surrounded by two membranes. Transport proteins in these membranes are homologous to proteins in the inner and outer membranes of cyanobacterial endosymbionts, providing further support for the hypothesis.

On several occasions during eukaryotic evolution, red algae and green algae underwent **secondary endosymbiosis**: They were ingested in the food vacuoles of heterotrophic eukaryotes and became endosymbionts themselves. For example, protists known as chlorarachniophytes likely evolved when a heterotrophic eukaryote engulfed a green alga. Evidence for this process can be found within the engulfed cell, which contains a tiny vestigial nucleus, called a *nucleomorph*. Genes from the nucleomorph are still transcribed, and their DNA sequences indicate the engulfed cell was a green alga. Also consistent with the hypothesis that chlorarachniophytes evolved from a eukaryote that engulfed another eukaryote, their plastids are surrounded by *four* membranes. The two inner membranes originated as the inner and outer membranes of the ancient cyanobacterium. The third membrane is derived from the engulfed alga's plasma membrane, and the outermost membrane is derived from the heterotrophic eukaryote's food vacuole. In some other protists, plastids acquired by secondary endosymbiosis are surrounded by three membranes, indicating that one of the original four membranes was lost during the course of evolution.

Five Supergroups of Eukaryotes

Our understanding of the evolutionary history of protists has been in a state of flux in recent years. Not only has kingdom Protista been abandoned, but a variety of other hypotheses have been discarded as well. For example, in the early 1990s,

▼ **Figure 28.2 Diversity of plastids produced by endosymbiosis.** Studies of plastid-bearing eukaryotes suggest that plastids evolved from a gram-negative cyanobacterium that was engulfed by an ancestral heterotrophic eukaryote (primary endosymbiosis). That ancestor then diversified into red algae and green algae, some of which were subsequently engulfed by other eukaryotes (secondary endosymbiosis).



many biologists thought that the oldest lineage of living eukaryotes consisted of the *amitochondriate protists*, organisms without conventional mitochondria and with fewer membrane-bounded organelles than other protist groups. But recent structural and DNA data have undermined this hypothesis. Many of the so-called amitochondriate protists have been shown to have mitochondria—though reduced ones—and some of these organisms are now classified in entirely different groups. For example, microsporidians, once considered amitochondriate protists, are now classified as fungi.

The ongoing changes in our understanding of the phylogeny of protists pose challenges to students and instructors alike. Hypotheses about these relationships are a focus of scientific activity, changing rapidly as new data cause previous ideas to be modified or discarded. In this chapter, our discussion is organized around one current hypothesis: the five supergroups of eukaryotes shown in **Figure 28.3**, on the next two pages. Because the root of the eukaryotic tree is not known, all five supergroups are shown as diverging simultaneously from a common ancestor. We know that is not correct, but we do not know which organisms were the first to diverge from the others. In addition, while some of the groups in Figure 28.3 are well supported by morphological and DNA data, others are more controversial. As you read this chapter, it may be helpful to focus less on the specific names of groups of organisms and more on why the organisms are important and how ongoing research is elucidating their evolutionary relationships.

CONCEPT CHECK 28.1

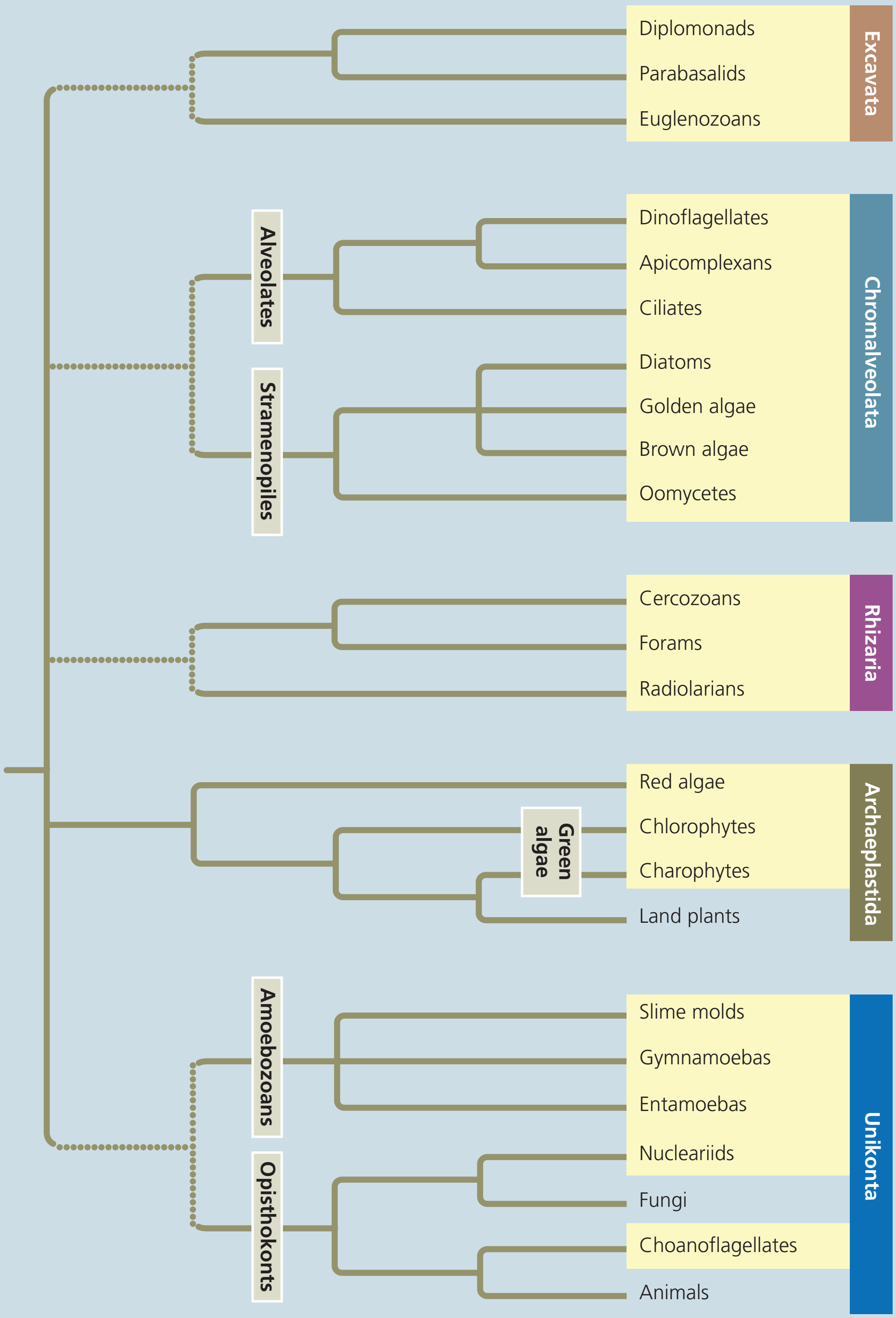
1. Cite at least four examples of structural and functional diversity among protists.
2. Summarize the role of endosymbiosis in eukaryotic evolution.
3. **WHAT IF?** After studying Figure 28.3, on the next two pages, draw a simplified version of the phylogenetic tree that shows only the five supergroups of eukaryotes. Now sketch how the tree would look if the unikonts were the first group of eukaryotes to diverge from other eukaryotes.

For suggested answers, see Appendix A.

▼ **Figure 28.3**

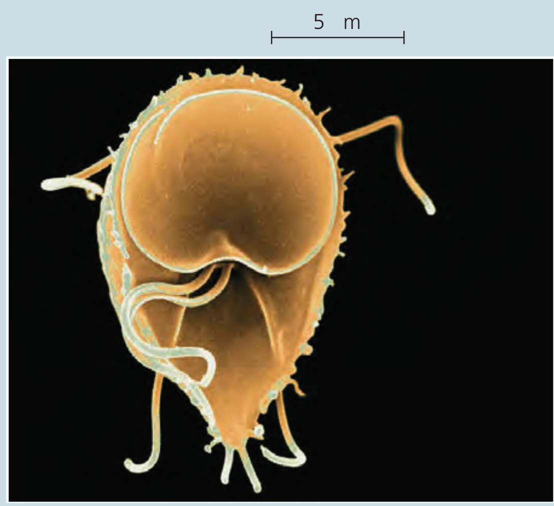
Exploring Protistan Diversity

The tree below represents a phylogenetic hypothesis for the relationships among all the eukaryotes on Earth today. The eukaryotic groups at the branch tips are related in larger "supergroups," labeled vertically at the far right of the tree. The kingdoms Plantae (land plants), Fungi, and Animalia (animals) have survived from the five-kingdom system of classification. Groups that were formerly classified in the kingdom Protista are listed in beige boxes. Dotted lines indicate evolutionary relationships that are uncertain and proposed clades that are under active debate.



Excavata

Some members of this supergroup have an "excavated" groove on one side of the cell body. Two major clades (the parabasalids and diplomonads) have modified mitochondria; others (the euglenozoans) have flagella that differ in structure from those of other organisms. Excavates include parasites such as *Giardia*, as well as many predatory and photosynthetic species.

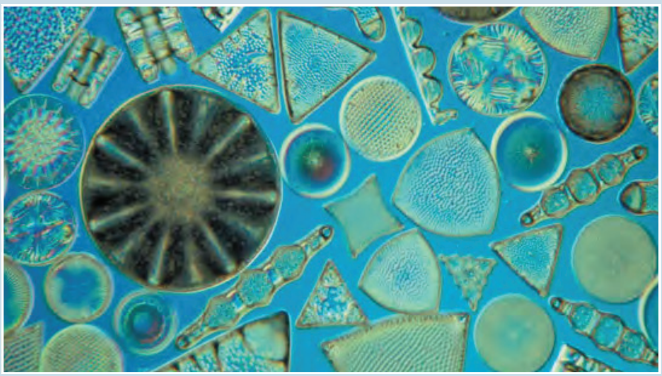


***Giardia intestinalis*, a diplomonad parasite.** This diplomonad (colorized SEM), which lacks the characteristic surface groove of the Excavata, can infect people when they drink water contaminated with feces containing *Giardia* cysts. Drinking such water—even from a seemingly pristine stream—can cause severe diarrhea. Boiling the water kills the parasite.

Chromalveolata

This group may have originated by an ancient secondary endosymbiosis event. Chromalveolates include some of the most important photosynthetic organisms on Earth, such as the diatoms shown here. The group also includes the brown algae that form underwater kelp "forests," as well as important pathogens, such as *Plasmodium*, which causes malaria, and *Phytophthora*, which caused the devastating potato famine in 19th-century Ireland.

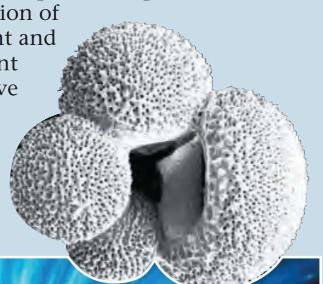
50 m



Diatom diversity. These beautiful single-celled protists are important photosynthetic organisms in aquatic communities (LM).

Rhizaria

This group contains many species of amoebas, most of which have pseudopodia that are threadlike in shape. Pseudopodia are extensions that can bulge from any portion of the cell; they are used in movement and in the capture of prey. Several recent molecular phylogenetic studies have suggested that Rhizaria should be nested within Chromalveolata; this hypothesis is currently being tested by other research groups.



100 m

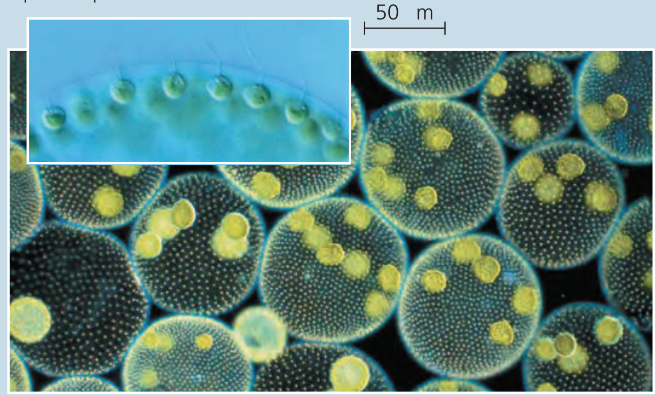
***Globigerina*, a foram in the supergroup Rhizaria.** Threadlike pseudopodia extend through pores in the shell, or *test* (LM). The inset SEM shows a foram test, which is hardened by calcium carbonate.

Archaeplastida

This group of eukaryotes includes red algae and green algae, along with land plants (kingdom Plantae, discussed in Chapters 29 and 30). Red algae and green algae include unicellular species, colonial species (such as the green alga *Volvox*), and multicellular species. Many of the large algae known informally as "seaweeds" are multicellular red or green algae. Protists in Archaeplastida include key photosynthetic species that form the base of the food web in some aquatic communities.

20 m

50 m



***Volvox*, a colonial freshwater green alga.** The colony is a hollow ball whose wall is composed of hundreds of biflagellated cells (see inset LM) embedded in a gelatinous matrix. The cells are usually connected by cytoplasmic strands; if isolated, these cells cannot reproduce. The large colonies seen here will eventually release the small "daughter" colonies within them (LM).

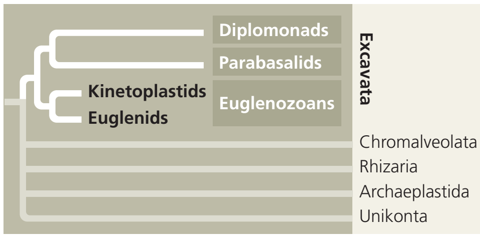
Unikonta

This group of eukaryotes includes amoebas that have lobe- or tube-shaped pseudopodia, as well as animals, fungi, and non-amoeba protists that are closely related to animals or fungi. According to one current hypothesis, the unikonts may have been the first group of eukaryotes to diverge from other eukaryotes (see Figure 28.23); however, this hypothesis has yet to be widely accepted.

A unikont amoeba. This amoeba (*Amoeba proteus*) is using its pseudopodia to move.

CONCEPT **28.2**

Excavates include protists with modified mitochondria and protists with unique flagella



Now that we have examined some of the broad patterns in eukaryotic evolution, we will look more closely at the five main groups of protists shown in Figure 28.3.

We begin this tour with **Excavata** (the excavates), a clade recently proposed based on morphological studies of the cytoskeleton. Some members of this diverse group also have an "excavated" feeding groove on one side of the cell body.

The excavates include the diplomonads, the parabasalids, and the euglenozoans. Molecular data indicate that each of these three groups is monophyletic, but the data have neither confirmed nor strongly refuted the monophyly of the excavate supergroup. Although many excavates share certain unique cytoskeletal features, we cannot yet tell whether that is because the excavates are monophyletic or because the common ancestor of eukaryotes had those features. Overall, support for the excavate clade is relatively weak, making it one of the more controversial of the five supergroups.

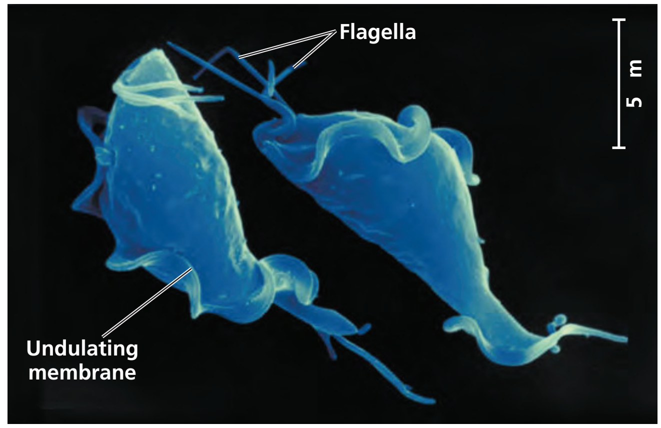
Diplomonads and Parabasalids

The protists in these two groups lack plastids and have modified mitochondria (until recently, they were thought to lack mitochondria altogether). Most diplomonads and parabasalids are found in anaerobic environments.

Diplomonads have modified mitochondria called *mitosomes*. These organelles lack functional electron transport chains and hence cannot use oxygen to help extract energy from carbohydrates and other organic molecules. Instead, diplomonads get the energy they need from anaerobic biochemical pathways.

Structurally, diplomonads have two equal-sized nuclei and multiple flagella. Recall that eukaryotic flagella are extensions of the cytoplasm, consisting of bundles of microtubules covered by the cell's plasma membrane (see Figure 6.24). They are quite different from prokaryotic flagella, which are filaments composed of the globular protein flagellin attached to the cell surface (see Figure 27.6).

Many diplomonads are parasites. An infamous example is *Giardia intestinalis* (also known as *Giardia lamblia*; see Figure 28.3), which inhabits the intestines of mammals.



▲ **Figure 28.4 The parabasalid *Trichomonas vaginalis*** (colorized SEM).

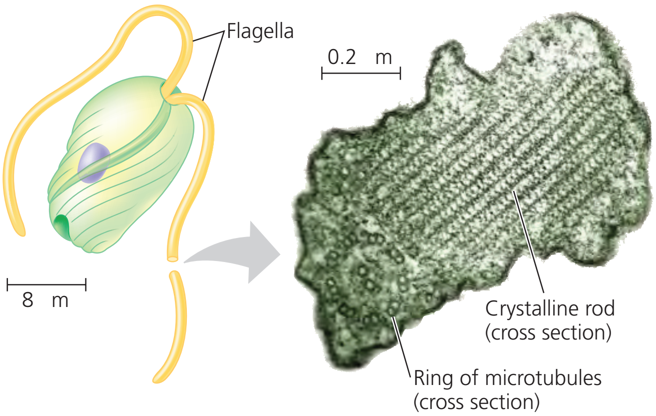
Parabasalids also have reduced mitochondria; called *hydrogenosomes*, these organelles generate some energy anaerobically, releasing hydrogen gas as a by-product. The best-known parabasalid is *Trichomonas vaginalis*, a sexually transmitted parasite that infects some 5 million people each year. *T. vaginalis* travels along the mucus-coated lining of the human reproductive and urinary tracts by moving its flagella and by undulating part of its plasma membrane **(Figure 28.4)**. In females, if the vagina's normal acidity is disturbed, *T. vaginalis* can outcompete beneficial microorganisms there and infect the vagina. (*Trichomonas* infections also can occur in the urethra of males, though often without symptoms.) *T. vaginalis* has a gene that allows it to feed on the vaginal lining, promoting infection. Studies suggest that the protist acquired this gene by horizontal gene transfer from bacterial parasites in the vagina.

Euglenozoans

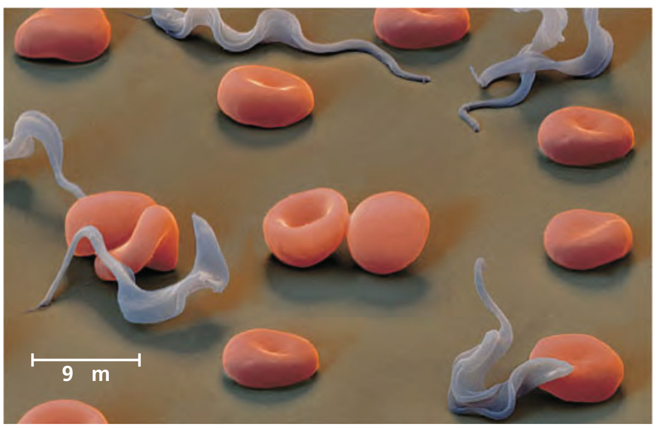
Protists called **euglenozoans** belong to a diverse clade that includes predatory heterotrophs, photosynthetic autotrophs, and parasites. The main morphological feature that distinguishes protists in this clade is the presence of a rod with either a spiral or a crystalline structure inside each of their flagella **(Figure 28.5)**. The two best-studied groups of euglenozoans are the kinetoplastids and the euglenids.

Kinetoplastids

Protists called **kinetoplastids** have a single, large mitochondrion that contains an organized mass of DNA called a *kinetoplast*. These protists include species that feed on prokaryotes in freshwater, marine, and moist terrestrial ecosystems, as well as species that parasitize animals, plants, and other protists. For example, kinetoplastids in the genus *Trypanosoma* infect humans and cause sleeping sickness, a neurological disease that is invariably fatal if not treated. The infection occurs via the bite of a vector (carrier) organism, the African tsetse fly **(Figure 28.6)**. Trypanosomes also cause Chagas' disease, which



▲ **Figure 28.5 Euglenozoan flagellum.** Most euglenozoans have a crystalline rod inside one of their flagella (the TEM is a flagellum shown in cross section). The rod lies alongside the 9 + 2 ring of microtubules found in all eukaryotic flagella (compare with Figure 6.24).



▲ **Figure 28.6 *Trypanosoma*, the kinetoplastid that causes sleeping sickness.** The purple, ribbon-shaped cells among these red blood cells are the trypanosomes (colorized SEM).

is transmitted by bloodsucking insects and can lead to congestive heart failure.

Trypanosomes evade immune responses with an effective "bait-and-switch" defense. The surface of a trypanosome is coated with millions of copies of a single protein. However, before the host's immune system can recognize the protein and mount an attack, new generations of the parasite switch to another surface protein with a different molecular structure. Frequent changes in the surface protein prevent the host from developing immunity (see Figure 43.24). About a third of *Trypanosoma*'s genome is dedicated to producing these surface proteins.

Euglenids

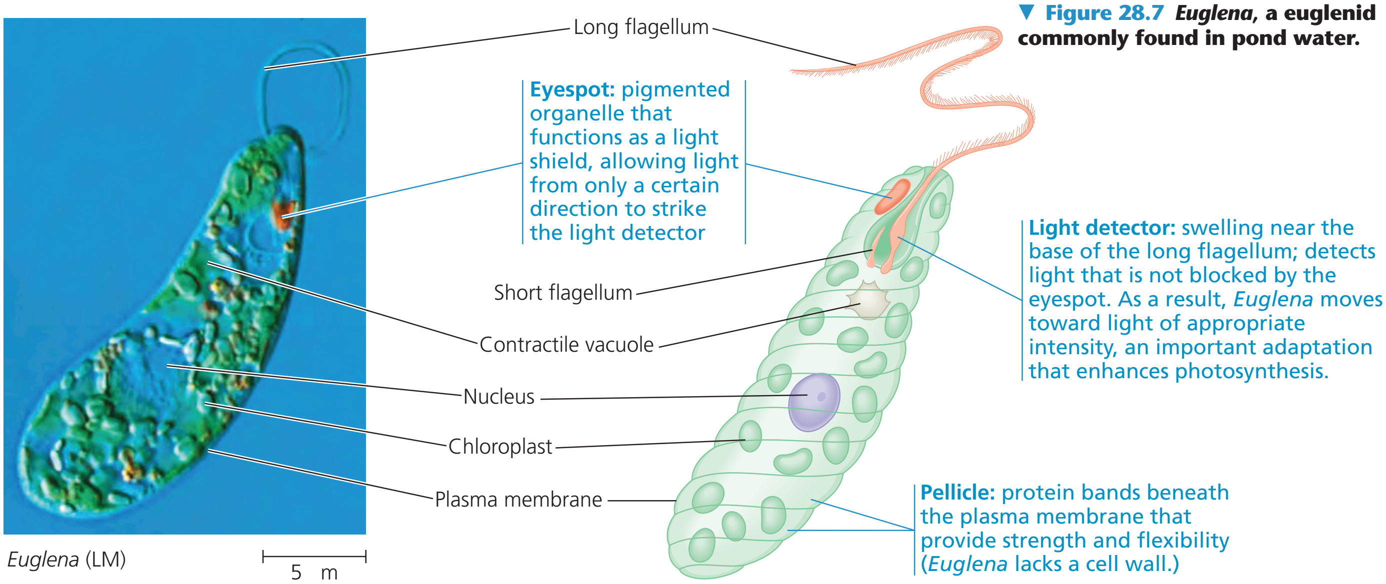
A **euglenid** has a pocket at one end of the cell from which one or two flagella emerge **(Figure 28.7)**. Many species of the euglenid *Euglena* are mixotrophs: In sunlight they are autotrophic, but when sunlight is unavailable, they can become heterotrophic, absorbing organic nutrients from their environment. Many other euglenids engulf prey by phagocytosis.

CONCEPT CHECK 28.2

1. Why do some biologists describe the mitochondria of diplomonads and parabasalids as "highly reduced"?
2. **WHAT IF?** DNA sequence data for a diplomonad, a euglenid, a plant, and an unidentified protist suggest that the unidentified species is most closely related to the diplomonad. Further studies reveal that the unknown species has fully functional mitochondria. Based on these data, at what point on the phylogenetic tree in Figure 28.3 did the mystery protist's lineage probably diverge from other eukaryote lineages? Explain.

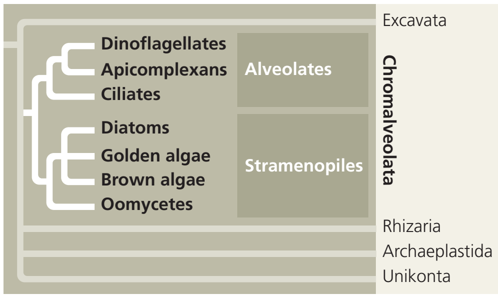
For suggested answers, see Appendix A.

▼ **Figure 28.7 *Euglena*, a euglenid commonly found in pond water.**



CONCEPT 28.3

Chromalveolates may have originated by secondary endosymbiosis



The supergroup **Chromalveolata** (the chromalveolates), a large, extremely diverse clade of protists, has recently been proposed based on two lines of evidence. First, some (though not all) DNA sequence data suggest that the chromalveolates form a monophyletic group. Second, some data support the hypothesis that the chromalveolates originated more than a billion years ago, when a common ancestor of the group engulfed a single-celled, photosynthetic red alga. Because red algae are thought to have originated by primary endosymbiosis (see Figure 28.2), such an origin for the chromalveolates is referred to as secondary endosymbiosis.

How strong is the evidence that the chromalveolates originated by secondary endosymbiosis? Many species in the clade have plastids whose structure and DNA indicate that they are of red algal origin. Others have reduced plastids that seem to be derived from a red algal endosymbiont. Still other species lack plastids altogether, yet some of these species have plastid genes in their nuclear DNA. Such data have led researchers to suggest that the common ancestor of the chromalveolates had plastids of red algal origin, but that later, some evolutionary lineages within the group lost the plastids. Others question this idea, based on the absence of plastid genes in the genomes of several chromalveolates that lack plastids. Overall, the endosymbiotic origin of the chromalveolates is an interesting idea, but like any scientific hypothesis, new data may show it to be incorrect.

The chromalveolates are perhaps the most controversial of the five supergroups we describe in this chapter. Even so, for many scientists, this supergroup represents the best current hypothesis for the phylogeny of the two large protist clades to which we now turn: the alveolates and the stramenopiles.

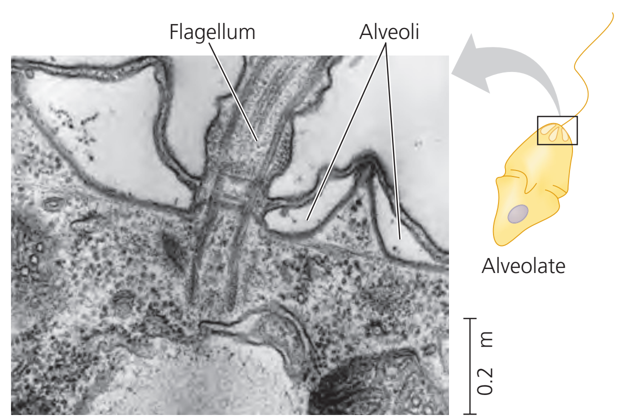
Alveolates

The **alveolates** are a group of protists whose monophyly is well supported by molecular systematics. Structurally, species in this group have membrane-bounded sacs (alveoli) just under the plasma membrane **(Figure 28.8)**. The function of the alveoli is unknown; researchers hypothesize that they may help stabilize the cell surface or regulate the cell's water and ion content.

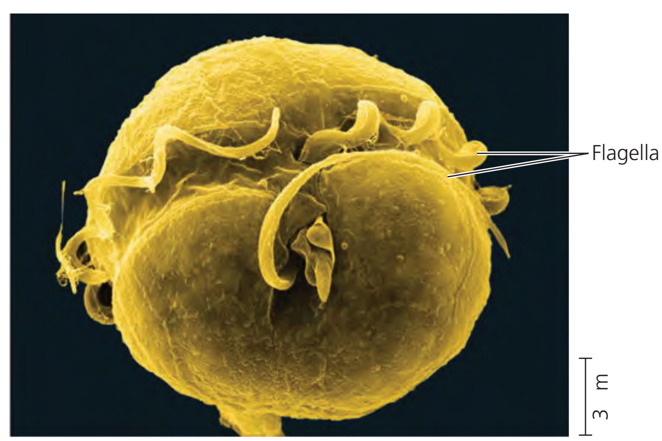
The alveolates include three subgroups: a group of flagellates (the dinoflagellates), a group of parasites (the apicomplexans), and a group of protists that move using cilia (the ciliates).

Dinoflagellates

The **dinoflagellates** are characterized by cells that are reinforced by cellulose plates. Two flagella located in grooves in this "armor" make dinoflagellates (from the Greek *dinos*, whirling) spin as they move through the water **(Figure 28.9)**. Dinoflagellates are abundant components of both marine and freshwater plankton, communities of mostly microscopic organisms that drift in currents near the water's surface. These dinoflagellates include some of the most important species of *phytoplankton* (photosynthetic plankton, which include photosynthetic bacteria as well as algae). However, many photosynthetic dinoflagellates are mixotrophic, and roughly half of all dinoflagellates are purely heterotrophic.



▲ **Figure 28.8 Alveoli.** These sacs under the plasma membrane are a characteristic that distinguishes alveolates from other eukaryotes (TEM).



▲ **Figure 28.9 *Pfiesteria shumwayae*, a dinoflagellate.** Beating of the spiral flagellum, which lies in a groove that encircles the cell, makes this alveolate spin (colorized SEM).

Episodes of explosive population growth, or *blooms*, in dinoflagellates sometimes cause a phenomenon called "red tide." The blooms make coastal waters appear brownish red or pink because of the presence of carotenoids, the most common pigments in dinoflagellate plastids. Toxins produced by certain dinoflagellates (such as *Karenia brevis*, which inhabits the Gulf of Mexico) have caused massive kills of invertebrates and fishes. Humans who eat molluscs that have accumulated the toxins are affected as well, sometimes fatally.

Apicomplexans

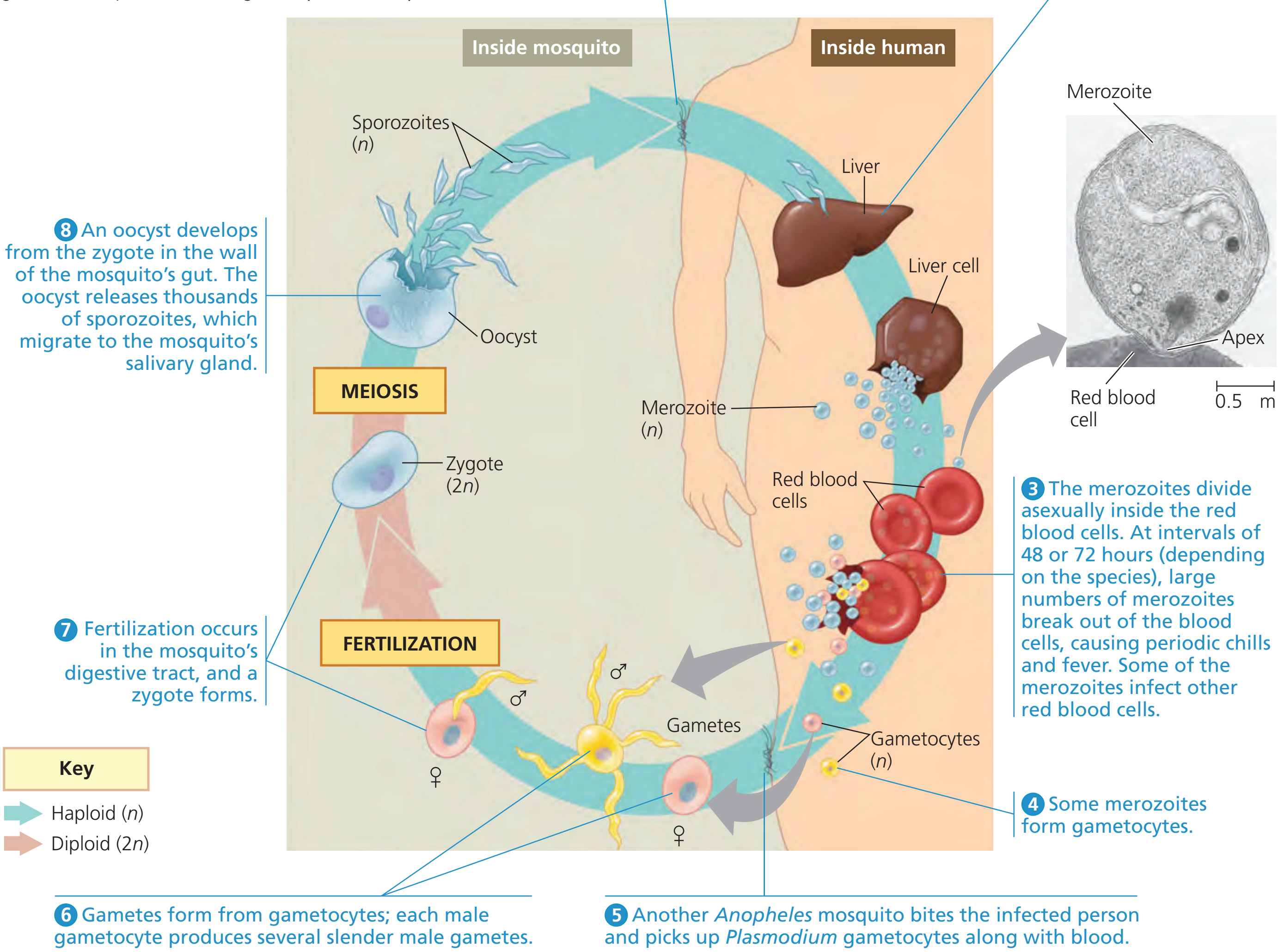
Nearly all **apicomplexans** are parasites of animals, and some cause serious human diseases. The parasites spread through their host as tiny infectious cells called *sporozoites*. Apicomplexans are so named because one end (the *apex*) of the sporozoite cell contains a *complex* of organelles specialized for penetrating host cells and tissues. Although apicomplexans are not photosynthetic, recent data show that they retain a modified plastid (apicoplast), most likely of red algal origin.

Most apicomplexans have intricate life cycles with both sexual and asexual stages. Those life cycles often require two or more host species for completion. For example, *Plasmodium*, the parasite that causes malaria, lives in both mosquitoes and humans **(Figure 28.10)**.

Historically, malaria has rivaled tuberculosis as the leading cause of human death by infectious disease. The incidence of malaria was greatly diminished in the 1960s by insecticides that reduced carrier populations of *Anopheles* mosquitoes and by drugs that killed *Plasmodium* in humans. But the emergence of resistant varieties of both *Anopheles* and *Plasmodium* has led

▼ **Figure 28.10 The two-host life cycle of *Plasmodium*, the apicomplexan that causes malaria.**

? *Are morphological differences between sporozoites, merozoites, and gametocytes caused by different genomes or by differences in gene expression? Explain.*



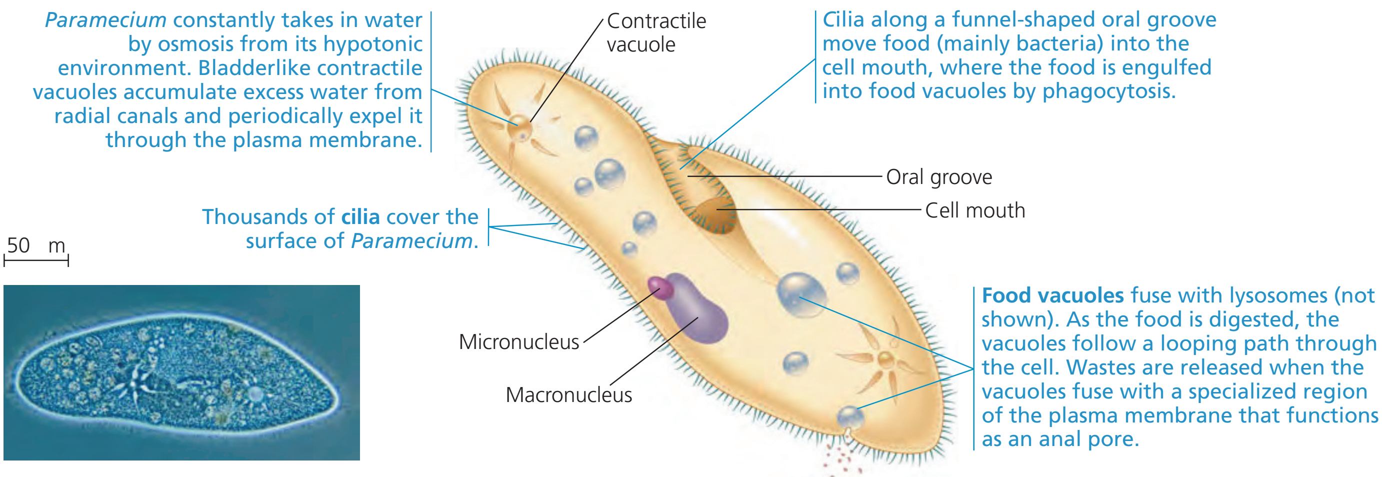
to a resurgence of malaria. About 250 million people in the tropics are currently infected, and 900,000 die each year.

The search for malarial vaccines has been hampered by the fact that *Plasmodium* lives mainly inside cells, hidden from the host's immune system. And, like trypanosomes, *Plasmodium* continually changes its surface proteins. The urgent need for treatments has inspired the sequencing of several *Plasmodium* genomes. Furthermore, researchers have now tracked the expression of most of the parasite's genes at numerous points in its life cycle. This research could help identify vaccine targets. Drugs that target the apicoplast are also in development. This approach may be effective because the apicoplast, derived by secondary endosymbiosis from a prokaryote, has metabolic pathways different from those in humans.

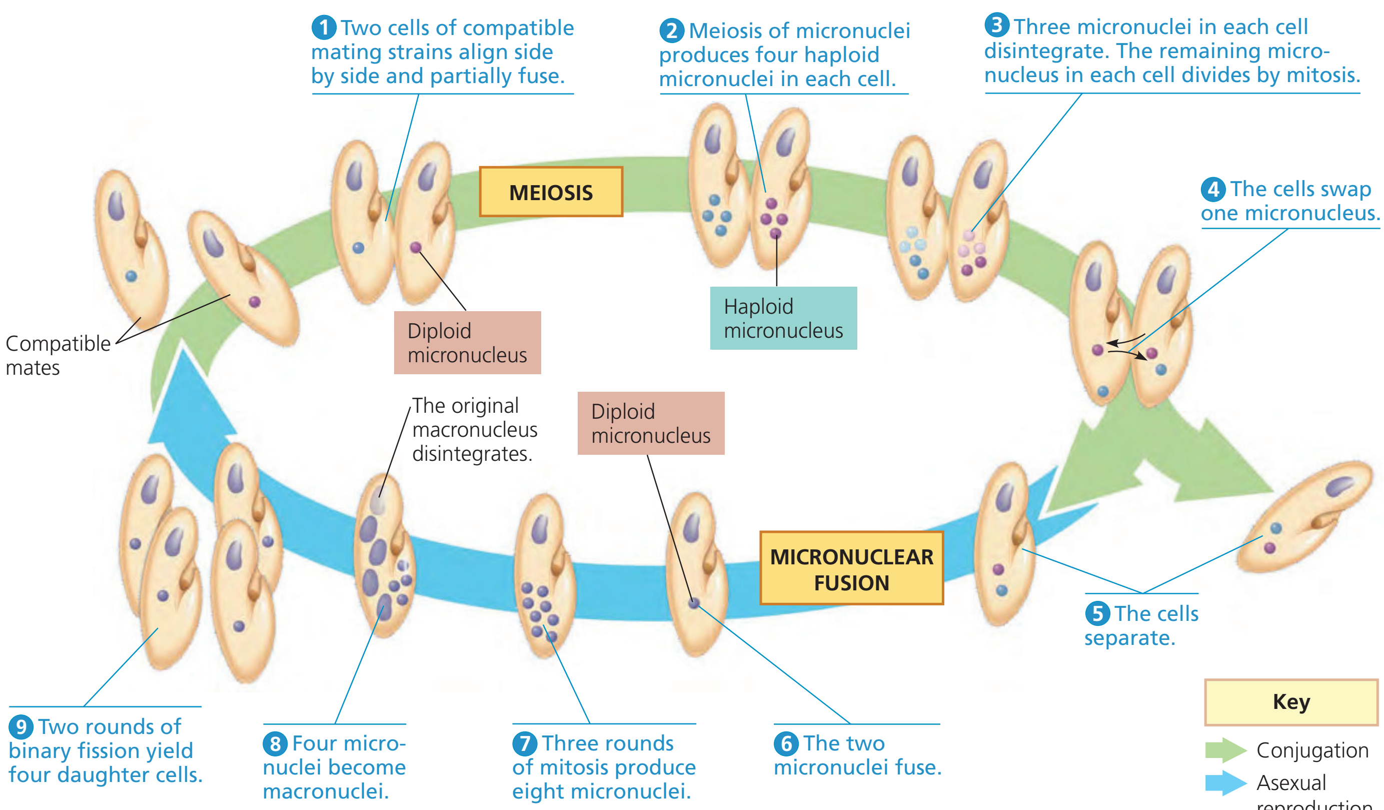
Ciliates

Ciliates are a large, varied group of protists named for their use of cilia to move and feed **(Figure 28.11a)**. The cilia may

▼ **Figure 28.11 Structure and function in the ciliate *Paramecium caudatum*.**



(a) Feeding, waste removal, and water balance.



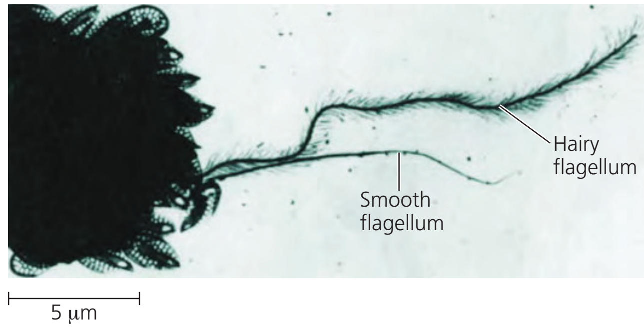
(b) Conjugation and reproduction.

completely cover the cell surface or may be clustered in a few rows or tufts. In certain species, rows of tightly packed cilia function collectively in locomotion. Other ciliates scurry about on leg-like structures constructed from many cilia bonded together.

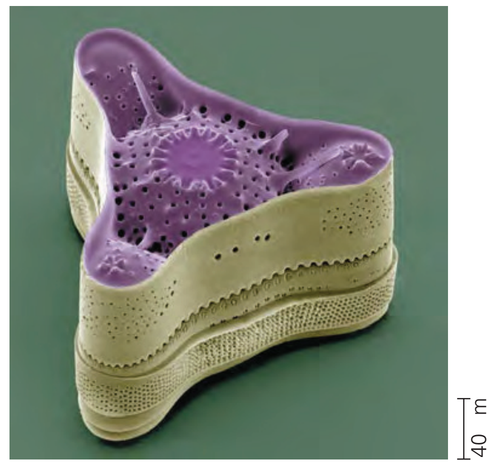
A distinctive feature of ciliates is the presence of two types of nuclei: tiny micronuclei and large macronuclei. A cell has one or more nuclei of each type. Genetic variation results from **conjugation**, a sexual process in which two individuals exchange haploid micronuclei but do not reproduce **(Figure 28.11b)**. Ciliates generally reproduce asexually by binary fission, during which the existing macronucleus disintegrates and a new one is formed from the cell's micronuclei. Each macronucleus typically contains multiple copies of the ciliate's genome. Genes in the macronucleus control the everyday functions of the cell, such as feeding, waste removal, and maintaining water balance (see Figure 28.11a).

Stramenopiles

Another major subgroup of the chromalveolates is the **stramenopiles**, protists that include some of the most important photosynthetic organisms on the planet, as well as several clades of heterotrophs. Their name (from the Latin *stramen*, straw, and *pilos*, hair) refers to their characteristic flagellum, which has numerous fine, hairlike projections. In most stramenopiles, this "hairy" flagellum is paired with a shorter "smooth" (nonhairy) flagellum **(Figure 28.12)**. Here we'll focus on four groups of stramenopiles: diatoms, golden algae, brown algae, and oomycetes.



▲ **Figure 28.12 Stramenopile flagella.** Most stramenopiles, such as *Synura petersenii*, have two flagella: one covered with fine, stiff hairs and a shorter one that is smooth.



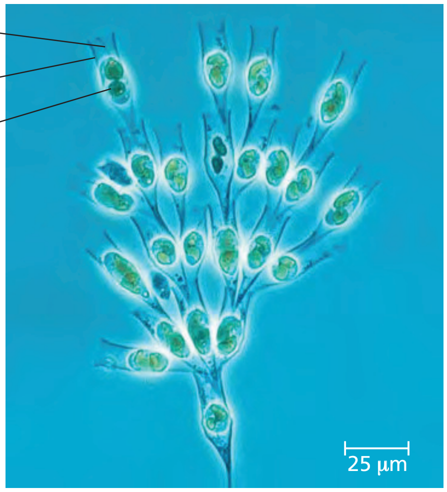
▲ **Figure 28.13 The diatom *Triceratium morlandii*** (colorized SEM).

Diatoms

Diatoms are unicellular algae that have a unique glass-like wall made of hydrated silica (silicon dioxide) embedded in an organic matrix. The wall consists of two parts that overlap like a shoe box and its lid. These walls provide effective protection from the crushing jaws of predators: Live diatoms can withstand pressures as great as 1.4 million kg/m^2, equal to the pressure under each leg of a table supporting an elephant! Much of the diatoms' strength comes from the delicate lacework of holes and grooves in their walls **(Figure 28.13)**; if the walls were smooth, it would take 60% less force to crush them.

With an estimated 100,000 living species, diatoms are a highly diverse group of protists (see Figure 28.3). They are a major component of phytoplankton both in the ocean and in lakes: One bucket of water scooped from the surface of the sea may contain millions of these microscopic algae. The abundance of diatoms in the past is also evident in the fossil record, where massive accumulations of fossilized diatom walls are major constituents of sediments known as *diatomaceous earth*. These sediments are mined for their quality as a filtering medium and for many other uses.

You might expect that since diatoms are so widespread and abundant, their photosynthetic activity would affect global carbon dioxide levels, and this is indeed the case. Diatoms have this effect in part because of the chain of events that follows their rapid population growth (a bloom) when ample nutrients are available. Typically, diatoms are eaten by a variety of protists and invertebrates, but during a bloom, many escape this fate. When these uneaten diatoms die, their bodies sink to the ocean floor. Diatoms that sink to the ocean floor are not very likely to be broken down by bacteria and other decomposers. Hence, the carbon in their bodies remains there, rather than being released as carbon dioxide as the decomposers respire. The overall effect of these events is that carbon dioxide absorbed by diatoms during photosynthesis is transported, or "pumped," to the ocean floor. With an eye toward reducing global warming by lowering atmospheric carbon dioxide levels, some scientists advocate promoting diatom blooms by fertilizing the ocean with essential nutrients such as iron. Other scientists question this strategy, noting that small-scale tests of this idea have yielded mixed results and that it is difficult to predict the effects of large-scale manipulations of ecological communities.



▲ **Figure 28.14** ***Dinobryon*, a colonial golden alga found in fresh water** (LM).

▲ **Figure 28.15** **Seaweeds: adapted to life at the ocean's margins.** The sea palm (*Postelsia*) lives on rocks along the coast of the northwestern United States and western Canada. The thallus of this brown alga is well adapted to maintaining a firm foothold despite the crashing surf.

Golden Algae

The characteristic color of **golden algae** results from their yellow and brown carotenoids. The cells of golden algae are typically biflagellated, with both flagella attached near one end of the cell.

Many golden algae are components of freshwater and marine plankton. While all golden algae are photosynthetic, some species are mixotrophic. These mixotrophs can absorb dissolved organic compounds or ingest food particles, including living cells, by phagocytosis. Most species are unicellular, but some, such as those in the freshwater genus *Dinobryon*, are colonial **(Figure 28.14)**. If environmental conditions deteriorate, many species form protective cysts that can survive for decades.

Brown Algae

The largest and most complex algae are **brown algae**. All are multicellular, and most are marine. Brown algae are especially common along temperate coasts, where the water is cool. They owe their characteristic brown or olive color to the carotenoids in their plastids.

Many of the species commonly called "seaweeds" are brown algae. (Some large, multicellular species of red and green algae are also referred to as seaweeds. We will examine them later in this chapter.) Brown algae include species that have the most complex multicellular anatomy of all algae; some even have specialized tissues and organs that resemble those in plants. But morphological and DNA evidence indicates that the similarities evolved independently in the algal and plant lineages and are thus analogous, not homologous.

The term **thallus** (plural, *thalli*; from the Greek *thallos*, sprout) refers to an algal body that is plantlike. Unlike the body of a plant, however, a thallus lacks true roots, stems, and leaves. A typical thallus consists of a rootlike **holdfast**, which anchors the alga, and a stemlike **stipe**, which supports leaflike **blades** **(Figure 28.15)**. The blades provide most of the alga's photosynthetic surface. Some brown algae are equipped with gas-filled, bubble-shaped floats, which help keep the blades up near the water surface. Beyond the intertidal zone in deeper waters live giant seaweeds known as kelps. The stipes of these brown algae may be as long as 60 m, more than half the length of a football field.

Brown algae that inhabit the intertidal zone must cope with water churned by waves and wind, along with low tides that expose the algae to the drying atmosphere and intense rays of the sun. Unique adaptations enable these seaweeds to survive. For example, their cell walls are composed of cellulose and gel-forming polysaccharides that help cushion the thalli from waves and reduce drying when the algae are exposed.

Brown algae are important commodities for humans. Some species are eaten, such as *Laminaria* (Japanese "kombu"), which is used in soups. In addition, the gel-forming substance in the cell walls of brown algae, called algin, is used to thicken many processed foods, including pudding and salad dressing.

Alternation of Generations

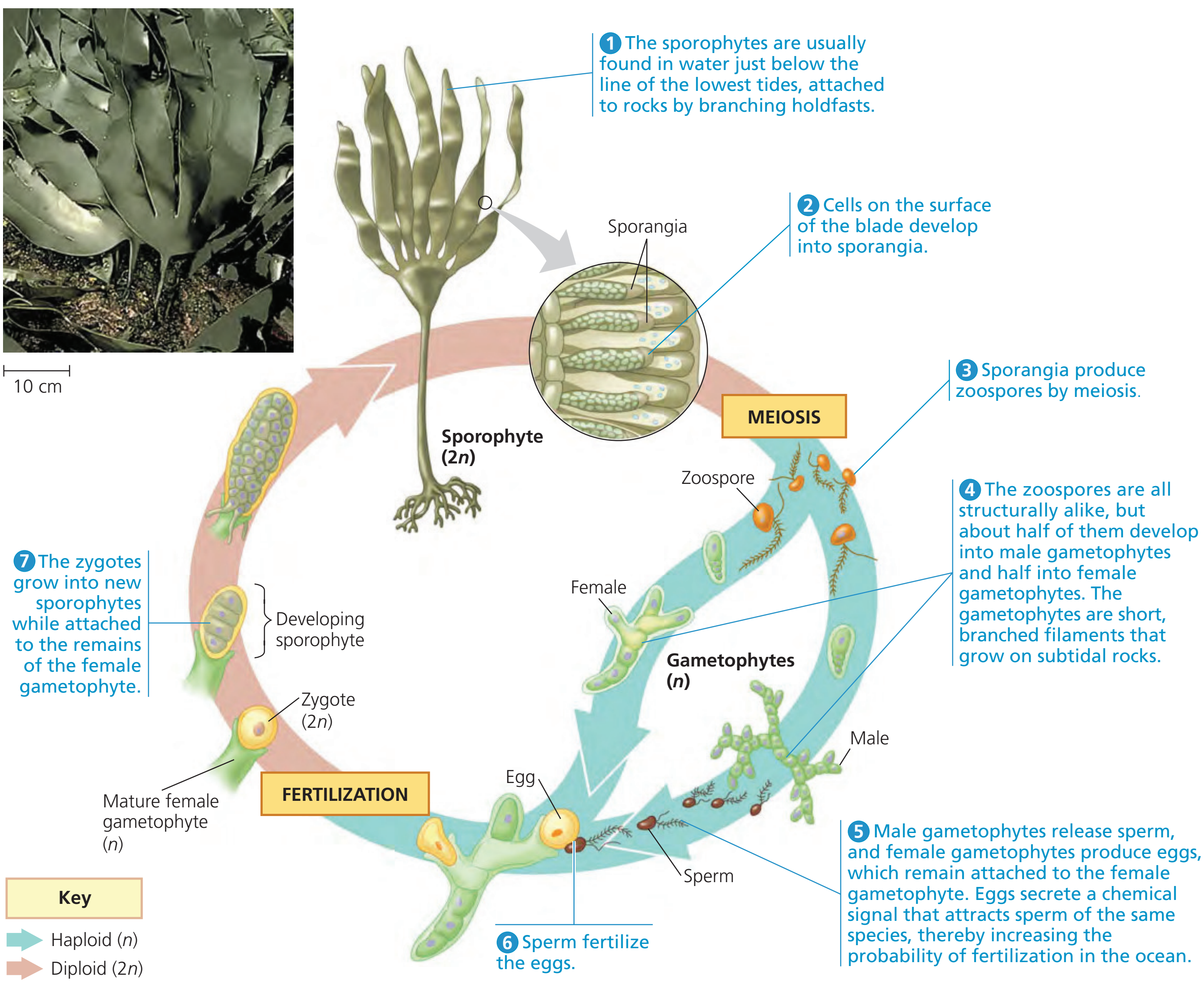
A variety of life cycles have evolved among the multicellular algae. The most complex life cycles include an **alternation of generations**, the alternation of multicellular haploid and diploid forms. Although haploid and diploid conditions alternate in *all* sexual life cycles—human gametes, for example, are haploid—the term *alternation of generations* applies only to life cycles in which both haploid and diploid stages are multicellular. As you will read in Chapter 29, alternation of generations also evolved in plants.

The complex life cycle of the brown alga *Laminaria* provides an example of alternation of generations **(Figure 28.16)**. The diploid individual is called the *sporophyte* because it produces spores. The spores are haploid and move by means of flagella; they are called zoospores. The zoospores develop into haploid, multicellular male and female *gametophytes*, which produce gametes. The union of two gametes (fertilization, or syngamy) results in a diploid zygote, which matures and gives rise to a new multicellular sporophyte.

In *Laminaria*, the two generations are **heteromorphic**, meaning that the sporophytes and gametophytes are structurally different. Other algal life cycles have an alternation of **isomorphic** generations, in which the sporophytes and gametophytes look similar to each other, although they differ in chromosome number.

Oomycetes (Water Molds and Their Relatives)

Oomycetes include the water molds, the white rusts, and the downy mildews. Based on their morphology, these organisms were previously classified as fungi (in fact, *oomycete* means



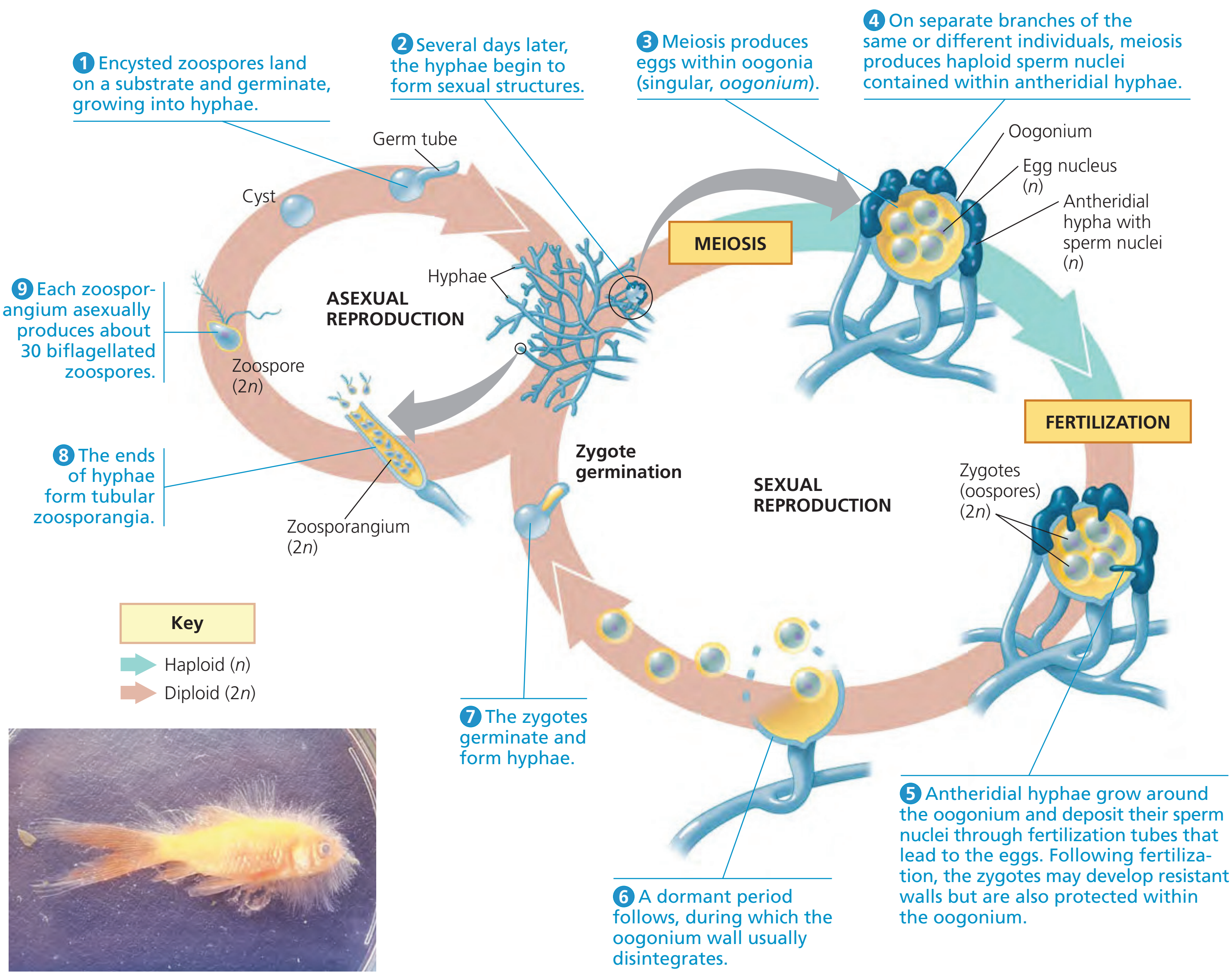
▲ **Figure 28.16 The life cycle of the brown alga *Laminaria*: an example of alternation of generations.**

? *Are the sperm shown in 5 genetically identical to one another? Are they genetically identical to the egg in 6? Explain.*

"egg fungus"). For example, many oomycetes have multinucleate filaments (hyphae) that resemble fungal hyphae **(Figure 28.17)**. However, there are key differences between oomycetes and fungi. Among the differences, oomycetes typically have cell walls made of cellulose, whereas the walls of fungi consist mainly of another polysaccharide, chitin. Data from molecular systematics have confirmed that oomycetes are not closely related to fungi. Their superficial similarity is a case of convergent evolution. In both oomycetes and fungi, the high surface-to-volume ratio of filamentous structures enhances the uptake of nutrients from the environment.

Although oomycetes descended from plastid-bearing ancestors, they no longer have plastids and do not perform photosynthesis. Instead, they typically acquire nutrients as decomposers or parasites. Most water molds are decomposers that grow as cottony masses on dead algae and animals, mainly in freshwater habitats (see Figure 28.17). White rusts and downy mildews generally live on land as plant parasites.

The ecological impact of oomycetes can be significant. For example, the oomycete *Phytophthora infestans* causes potato late blight, which turns the stalk and stem of potato plants to black slime. Late blight contributed to the devastating Irish famine of the 19th century, in which a million people died and at least that many were forced to leave Ireland. The disease remains a major problem today, causing crop losses of typically 15% in North America and as high as 70% in some parts of Russia where farmers cannot afford pesticides.



▲ **Figure 28.17 The life cycle of a water mold.** Water molds help decompose dead insects, fishes, and other animals in fresh water. (Note the hyphal mass growing on the goldfish in the photograph.)

To understand this pathogen better, molecular biologists have isolated DNA from a specimen of *P. infestans* preserved from the Irish potato blight of the 1840s. Genetic studies show that in recent decades, this oomycete has acquired genes that make it more aggressive and more resistant to pesticides. Scientists are looking within the genomes of both *Phytophthora* and potatoes to identify new weapons against the disease. Already, researchers have transferred genes from a blight-resistant strain of wild potato into domestic potatoes to produce a resistant crop strain.

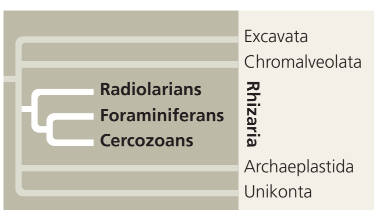
CONCEPT CHECK 28.3

1. Summarize the evidence for and against the hypothesis that the species currently classified as chromalveolates are members of a single clade.
2. **WHAT IF?** Would you expect the plastid DNA of photosynthetic dinoflagellates, diatoms, and golden algae to be more similar to the nuclear DNA of plants (domain Eukarya) or to the chromosomal DNA of cyanobacteria (domain Bacteria)? Explain.
3. **MAKE CONNECTIONS** Which of the three life cycles in Figure 13.6 (p. 252) exhibits alternation of generations? How does it differ from the other two?

For suggested answers, see Appendix A.

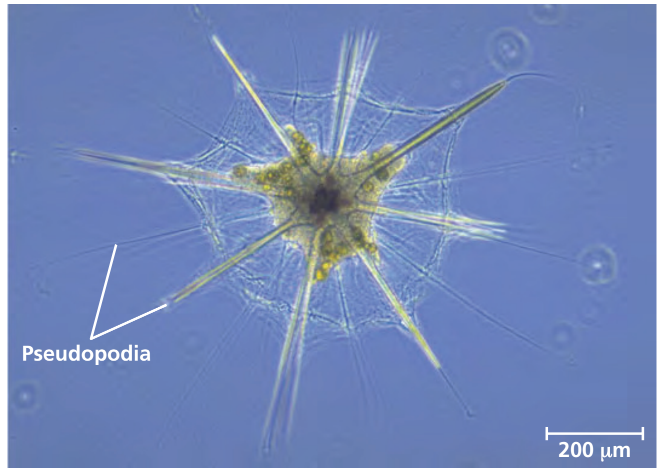
CONCEPT **28.4**

Rhizarians are a diverse group of protists defined by DNA similarities



The clade **Rhizaria** has recently been proposed based on results from molecular systematics. Although its members vary greatly in morphology, DNA evidence suggests that rhizarians are a monophyletic group. According to some recent phylogenetic studies, Rhizaria should be nested within Chromalveolata, as discussed in Figure 28.3.

Many species in Rhizaria are among the organisms referred to as amoebas. **Amoebas** were formerly defined as protists that move and feed by means of **pseudopodia**, extensions that may bulge from almost anywhere on the cell surface. An amoeba moves by extending a pseudopodium and anchoring the tip; more cytoplasm then streams into the pseudopodium. However, based on molecular systematics, it is now clear that amoebas do not constitute a monophyletic group but are dispersed across many distantly related eukaryotic taxa. Most of those that belong to the clade Rhizaria are distinguished morphologically from other amoebas by having threadlike pseudopodia.



▲ **Figure 28.18 A radiolarian.** Numerous threadlike pseudopodia radiate from the central body of this radiolarian, which is found in the Red Sea (LM).

Rhizarians include three groups that we'll examine here: radiolarians, forams, and cercozoans.

Radiolarians

The protists called **radiolarians** have delicate, intricately symmetrical internal skeletons that are generally made of silica. The pseudopodia of these mostly marine protists radiate from the central body **(Figure 28.18)** and are reinforced by bundles of microtubules. The microtubules are covered by a thin layer of cytoplasm, which engulfs smaller microorganisms that become attached to the pseudopodia. Cytoplasmic streaming then carries the captured prey into the main part of the cell. After radiolarians die, their skeletons settle to the seafloor, where they have accumulated as an ooze that is hundreds of meters thick in some locations.

Forams

The protists called **foraminiferans** (from the Latin *foramen*, little hole, and *ferre*, to bear), or **forams**, are named for their porous shells, called **tests** (see Figure 28.3). Foram tests consist of a single piece of organic material hardened with calcium carbonate. The pseudopodia that extend through the pores function in swimming, test formation, and feeding. Many forams also derive nourishment from the photosynthesis of symbiotic algae that live within the tests.

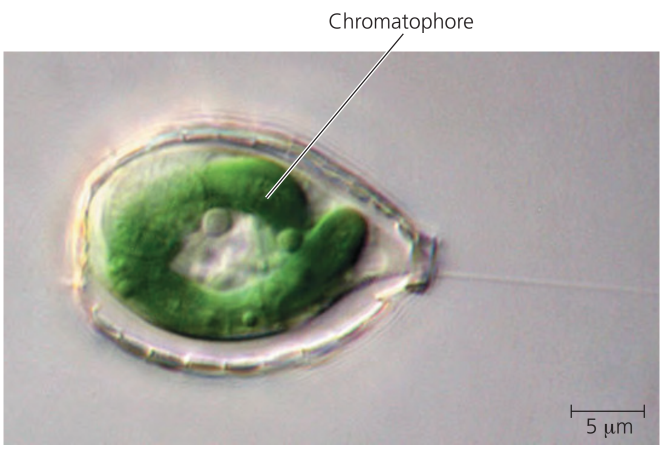
Forams are found in both the ocean and fresh water. Most species live in sand or attach themselves to rocks or algae, but some are abundant in plankton. The largest forams, though single-celled, grow to a diameter of several centimeters.

Ninety percent of all identified species of forams are known from fossils. Along with the calcium-containing remains of other protists, the fossilized tests of forams are part of marine sediments, including sedimentary rocks that are now land formations. Foram fossils are excellent markers for correlating the ages of sedimentary rocks in different parts of the world.

Cercozoans

First identified in molecular phylogenies, the **cercozoans** form a large group that contains most of the amoeboid and flagellated protists that feed with threadlike pseudopodia. Cercozoan protists are common in marine, freshwater, and soil ecosystems.

Most cercozoans are heterotrophs. Many are parasites of plants, animals, or other protists; many others are predators. The predators include the most important consumers of bacteria in aquatic and soil ecosystems, along with species that eat other protists, fungi, and even small animals. One small group of cercozoans, the chlorarachniophytes (mentioned earlier in the discussion of secondary endosymbiosis), are mixotrophic: These organisms ingest smaller protists and bacteria as well as perform photosynthesis. At least one other cercozoan, *Paulinella chromatophora*, is an autotroph, deriving its energy from light and its carbon from carbon dioxide. This species has a distinctive sausage-shaped internal structure where photosynthesis is performed **(Figure 28.19)**. Genetic and morphological analyses indicate that these structures were derived from a cyanobacterium, although not the same cyanobacterium from which all other plastids were derived. As such, *Paulinella* appears to represent an intriguing additional evolutionary example of a eukaryotic lineage that obtained its photosynthetic apparatus directly from a cyanobacterium.



▲ **Figure 28.19 A second case of primary endosymbiosis?** The cercozoan *Paulinella* conducts photosynthesis in a unique structure called a chromatophore (LM). Chromatophores are surrounded by a membrane with a peptidoglycan layer, suggesting that they are derived from a bacterium. DNA evidence indicates that chromatophores are derived from a different cyanobacterium than that from which other plastids are derived.

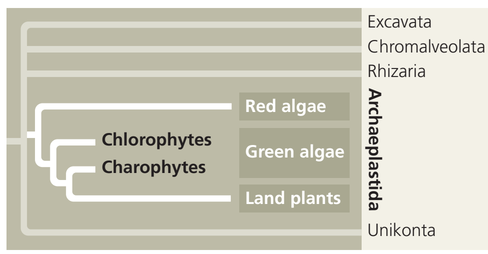
CONCEPT CHECK 28.4

1. Explain why forams have such a well-preserved fossil record.
2. **WHAT IF?** Suppose DNA evidence suggests that a newly discovered amoeba is in the clade Rhizaria, yet its morphology is more similar to amoebas in other eukaryotic groups. Suggest an explanation that could account for these conflicting observations.
3. **MAKE CONNECTIONS** Review Figures 9.2 (p. 163) and 10.6 (p. 188), and then summarize how CO_2 and O_2 are both used and produced by chlorarachniophytes and other aerobic algae.

For suggested answers, see Appendix A.

CONCEPT 28.5

Red algae and green algae are the closest relatives of land plants



As we described in Chapter 25, molecular systematics and studies of cell structure support the following scenario: More than a billion years ago, a heterotrophic protist acquired a cyanobacterial endosymbiont, and the photosynthetic descendants of this ancient protist evolved into red algae and green algae. At least 475 million years ago, the lineage that produced green algae gave rise to land plants. Together, red algae, green algae, and land plants make up the fourth eukaryotic supergroup, which is called **Archaeplastida**. Archaeplastida is a monophyletic group that descended from the ancient protist that engulfed a cyanobacterium. We will examine land plants in Chapters 29 and 30; here we will look at the diversity of their closest algal relatives, red algae and green algae.

Red Algae

Many of the 6,000 known species of **red algae** (rhodophytes, from the Greek *rhodos*, red) are reddish, owing to a photosynthetic accessory pigment called phycoerythrin, which masks the green of chlorophyll **(Figure 28.20)**. However, species adapted to more shallow water have less phycoerythrin. As a result, red algal species may be greenish red in very shallow

▶ ***Bonnemaisonia hamifera.*** This red alga has a filamentous form.

◀ **Dulse (*Palmaria palmata*).** This edible species has a "leafy" form.

▼ **Nori.** The red alga *Porphyra* is the source of a traditional Japanese food.

▲ **Figure 28.20 Red algae.**

water, bright red at moderate depths, and almost black in deep water. Some species lack pigmentation altogether and function heterotrophically as parasites on other red algae.

Red algae are the most abundant large algae in the warm coastal waters of tropical oceans. Their accessory pigments, including phycoerythrin, allow them to absorb blue and green light, which penetrate relatively far into the water. A species of red alga has been discovered near the Bahamas at a depth of more than 260 m. There are also a small number of freshwater and terrestrial species.

Most red algae are multicellular. Although none are as big as the giant brown kelps, the largest multicellular red algae are included in the informal designation "seaweeds." You may have eaten one of these multicellular red algae, *Porphyra* (Japanese "nori"), as crispy sheets or as a wrap for sushi (see Figure 28.20). Red algae have especially diverse life cycles, and alternation of generations is common. But unlike other algae, they have no flagellated stages in their life cycle and depend on water currents to bring gametes together for fertilization.

Green Algae

The grass-green chloroplasts of **green algae** have a structure and pigment composition much like the chloroplasts of land plants. Molecular systematics and cellular morphology leave little doubt that green algae and land plants are closely related. In fact, some systematists now advocate including green algae in an expanded "plant" kingdom, Viridiplantae (from the Latin *viridis*, green). Phylogenetically, this change makes sense, since otherwise the green algae are a paraphyletic group.

Green algae are divided into two main groups, the charophytes and the chlorophytes. The charophytes are the algae most closely related to land plants, and so we will discuss them along with plants in Chapter 29.

The second group, the chlorophytes (from the Greek *chloros*, green), includes more than 7,000 species. Most live in fresh water, but there are also many marine and some terrestrial species. The simplest chlorophytes are unicellular organisms such as *Chlamydomonas*, which resemble gametes or zoospores of more complex chlorophytes. Various species of unicellular chlorophytes live in aquatic habitats as phytoplankton or inhabit damp soil. Some live symbiotically within other eukaryotes, contributing part of their photosynthetic output to the food supply of their hosts. Some chlorophytes have even adapted to one of the last habitats you might expect to find them: snow. These chlorophytes carry out photosynthesis despite subfreezing temperatures and intense visible and ultraviolet radiation. They are protected by the snow itself, which acts as a shield, and by radiation-blocking compounds in their cytoplasm. Other chlorophytes contain similar protective compounds in their cell wall or in a durable coat that surrounds the zygote.

Larger size and greater complexity evolved in chlorophytes by three different mechanisms:

1. The formation of colonies of individual cells, as seen in *Volvox* (see Figure 28.3) and in filamentous forms that contribute to the stringy masses known as pond scum

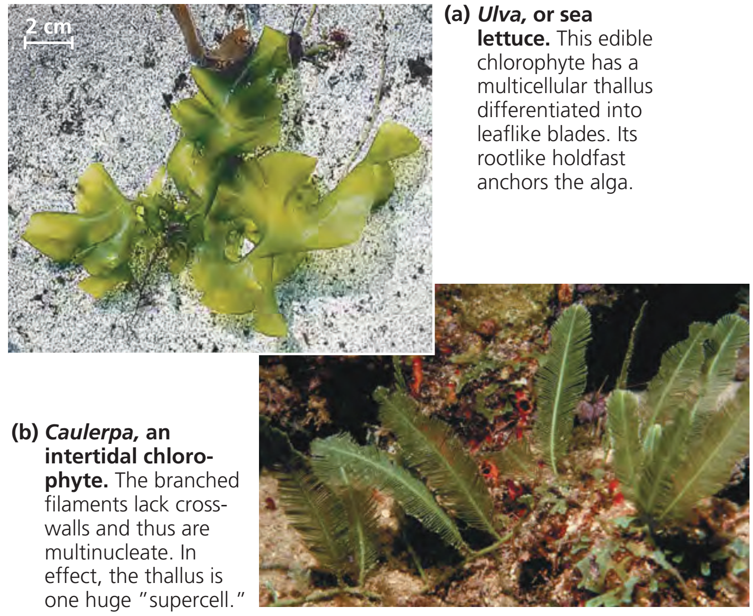
2. The formation of true multicellular bodies by cell division and differentiation, as in *Ulva* **(Figure 28.21a)**
3. The repeated division of nuclei with no cytoplasmic division, as in *Caulerpa* **(Figure 28.21b)**

Most chlorophytes have complex life cycles, with both sexual and asexual reproductive stages. Nearly all species of chlorophytes reproduce sexually by means of biflagellated gametes that have cup-shaped chloroplasts **(Figure 28.22)**. Alternation of generations has evolved in some chlorophytes, including *Ulva*.

CONCEPT CHECK 28.5

1. Contrast red algae and brown algae.
2. Why is it accurate to say that *Ulva* is truly multicellular but *Caulerpa* is not?
3. **WHAT IF?** Suggest a possible reason why species in the green algal lineage may have been more likely to colonize land than species in the red algal lineage.

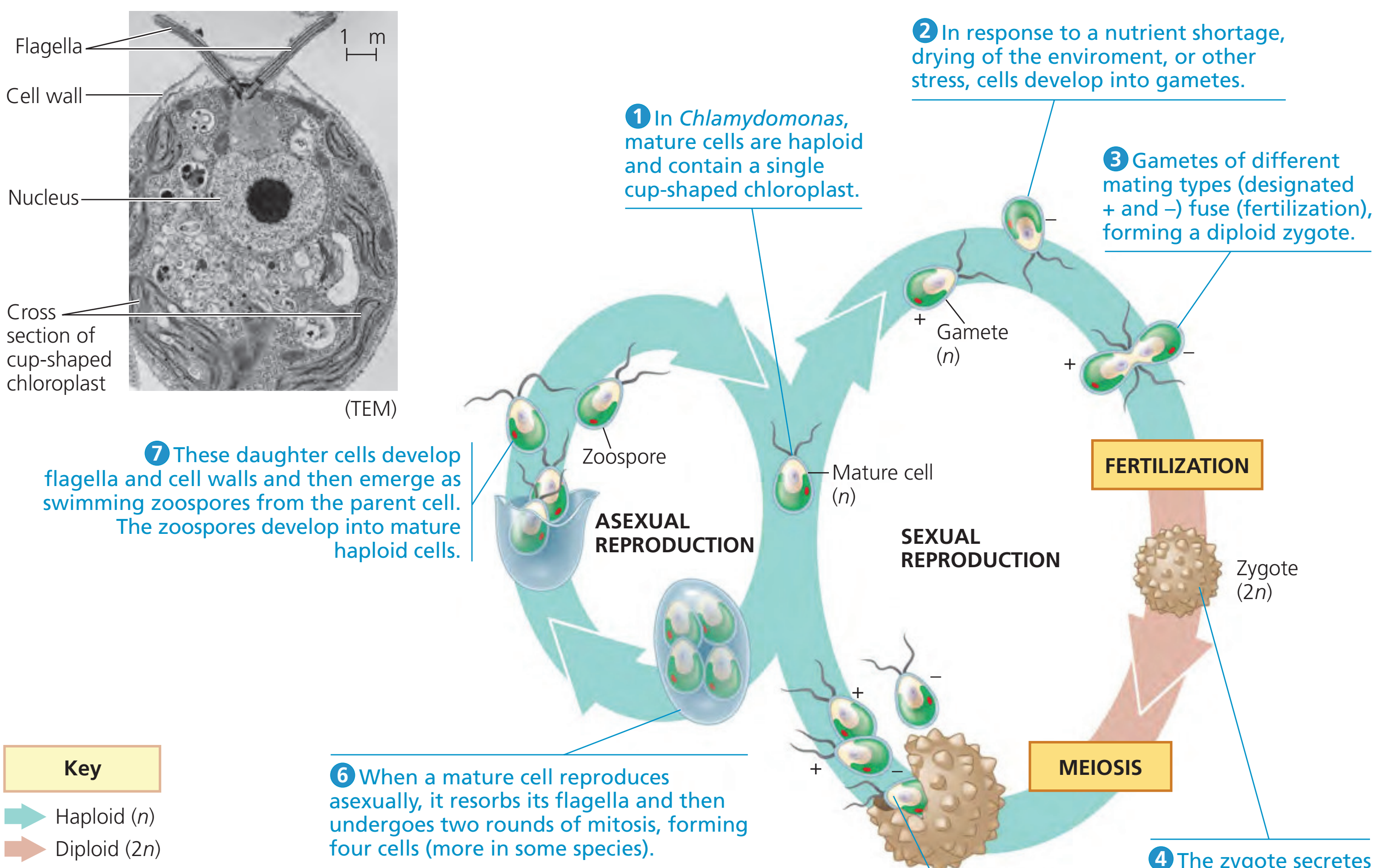
For suggested answers, see Appendix A.



(a) *Ulva*, or sea lettuce. This edible chlorophyte has a multicellular thallus differentiated into leaflike blades. Its rootlike holdfast anchors the alga.

(b) *Caulerpa*, an intertidal chlorophyte. The branched filaments lack cross-walls and thus are multinucleate. In effect, the thallus is one huge "supercell."

▲ **Figure 28.21 Multicellular chlorophytes.**

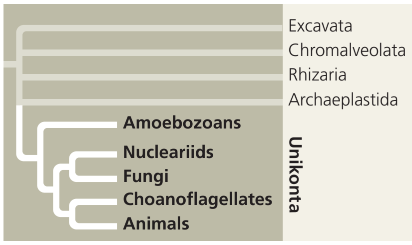


▲ **Figure 28.22 The life cycle of *Chlamydomonas*, a unicellular chlorophyte.**

DRAW IT *Circle the stage(s) in the diagram in which clones are formed, producing additional new daughter cells that are genetically identical to the parent cell(s).*

CONCEPT 28.6

Unikonts include protists that are closely related to fungi and animals



Unikonta is a recently proposed, extremely diverse supergroup of eukaryotes that includes animals, fungi, and some protists. There are two major clades of unikonts, the amoebozoans and the opisthokonts (animals, fungi, and closely related protist groups). Each of these two major clades is strongly supported by molecular systematics. The close relationship between amoebozoans and opisthokonts is more controversial. Support for this close relationship is provided by comparisons of myosin proteins and by several studies based on hundreds of genes, but not by other studies based on single genes.

Another controversy involving the unikonts concerns the root of the eukaryotic tree. Recall that the root of a phylogenetic tree anchors the tree in time: Branch points close to the root are the oldest. At present, the root of the eukaryotic tree is uncertain; thus, we do not know which group of eukaryotes was the first to diverge from other eukaryotes. Some hypotheses, such as the amitochondriate hypothesis described earlier, have been abandoned, but researchers have yet to agree on an alternative. If the root of the eukaryotic tree were known, scientists could infer characteristics of the common ancestor of all eukaryotes. Such information could help resolve some of the current debates about the five supergroups of eukaryotes.

In trying to determine the root of the eukaryotic tree, researchers have based their phylogenies on different sets of genes, producing conflicting results. Researchers at Oxford University have described a different approach, results from which support a radical new hypothesis about the root of the eukaryotic tree (**Figure 28.23**). According to their hypothesis, the unikonts were the first eukaryotes to diverge from other eukaryotes. This hypothesis proposes that animals and fungi belong to an early-diverging group of eukaryotes, while protists that lack typical mitochondria (such as the diplomonads and parabasalids) diverged much later in the history of life. This idea remains controversial and will require more supporting evidence to be widely accepted.

Amoebozoans

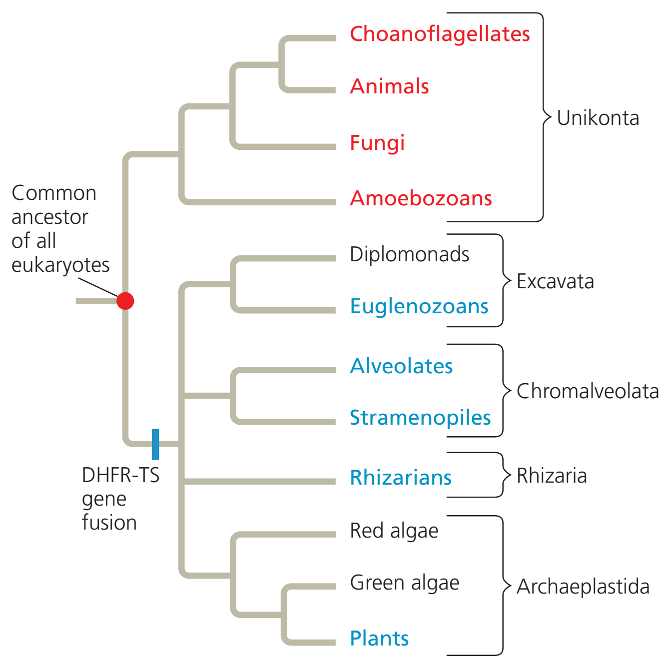
As already mentioned, **amoebozoans** form a clade that is well supported by molecular data. This clade includes many species

▼ **Figure 28.23** INQUIRY

What is the root of the eukaryotic tree?

EXPERIMENT Responding to the difficulty in determining the root of the eukaryotic phylogenetic tree, Alexandra Stechmann and Thomas Cavalier-Smith, of Oxford University, proposed a new approach. They studied two genes, one for the enzyme dihydrofolate reductase (DHFR), the other for the enzyme thymidylate synthase (TS). Their approach took advantage of a rare evolutionary event: In some organisms, the DHFR and TS genes have fused, leading to the production of a single protein with both enzyme activities. Stechmann and Cavalier-Smith amplified (using PCR; see Figure 20.8) and sequenced DHFR and TS genes in nine species (one choanoflagellate; two amoebozoans; one euglenozoan; two chromalveolates; and three rhizarians). They combined their data with previously published data for species of bacteria, animals, plants, and fungi.

RESULTS The bacteria studied all have separate DHFR and TS genes, suggesting that this is the ancestral condition (red dot on the tree below). Other taxa with separate genes are denoted by red type. Fused genes are a derived character, found in certain members (blue type) of the supergroups Excavata, Chromalveolata, Rhizaria, and Archaeplastida:



CONCLUSION These results support the hypothesis that the root of the tree is located between the unikonts and all other eukaryotes, suggesting that the unikonts were the first group of eukaryotes to diverge. Because support for this hypothesis is based on only one trait—the fusion of the DHFR and TS genes—more data are needed to evaluate its validity.

SOURCE A. Stechmann and T. Cavalier-Smith, Rooting the eukaryote tree by using a derived gene fusion, *Science* 297:89–91 (2002).

WHAT IF? Stechmann and Cavalier-Smith wrote that their conclusions are "valid only if the genes fused just once and were never secondarily split." Why is this assumption critical to their approach?

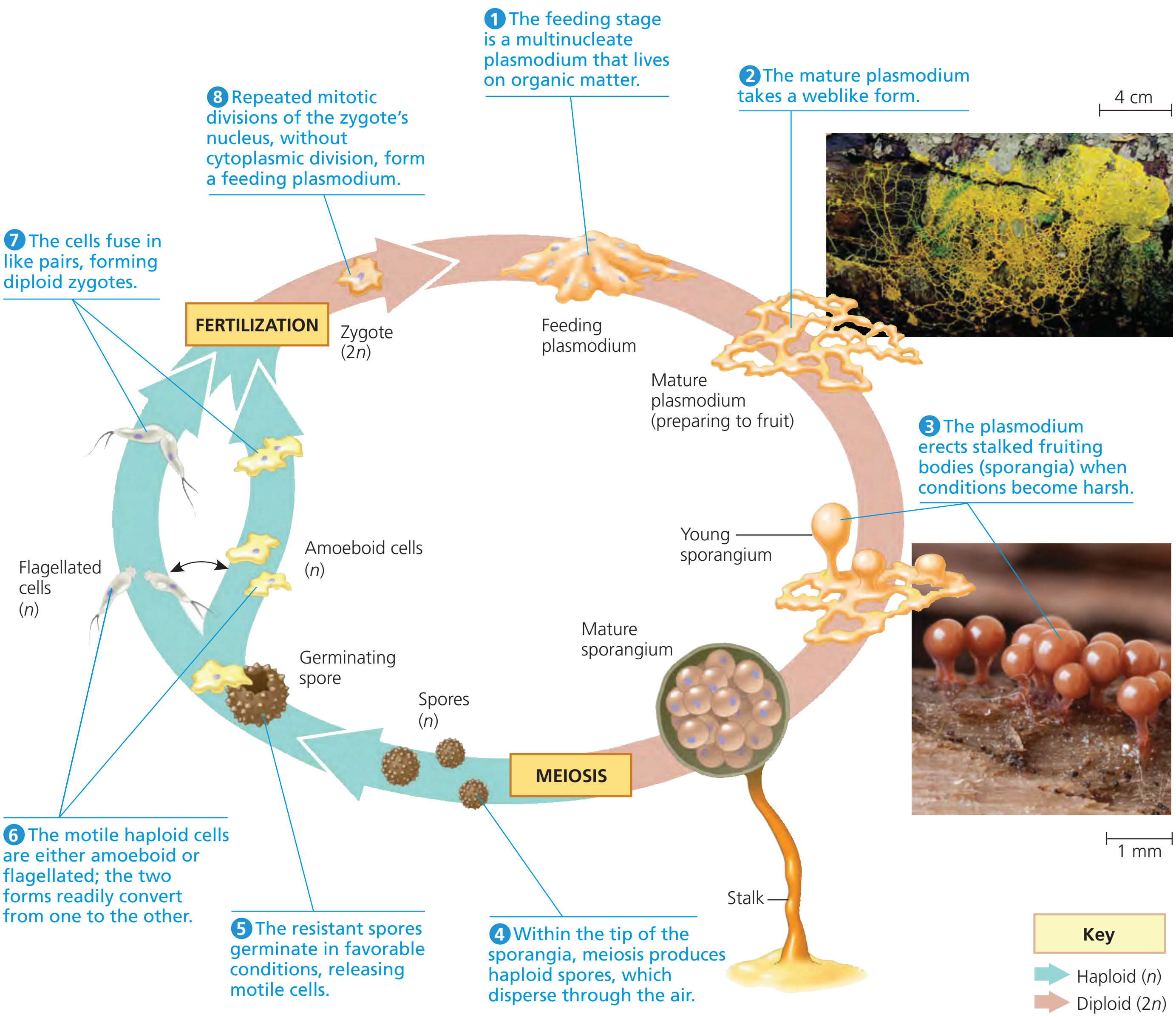
of amoebas that have lobe- or tube-shaped, rather than thread-like, pseudopodia. Amoebozoans include slime molds, gymnamoebas, and entamoebas.

Slime Molds

Slime molds, or mycetozoans (from the Latin, meaning "fungus animals"), were once thought to be fungi because, like fungi, they produce fruiting bodies that aid in spore dispersal. However, the resemblance between slime molds and fungi appears to be another example of evolutionary convergence. Molecular systematics places slime molds in Amoebozoa and suggests that they descended from unicellular ancestors. Slime molds have diverged into two main branches, plasmodial slime molds and cellular slime molds, distinguished in part by their unique life cycles.

Plasmodial Slime Molds Many **plasmodial slime molds** are brightly colored, often yellow or orange **(Figure 28.24)**. At one stage in their life cycle, they form a mass called a **plasmodium**, which may grow to a diameter of many centimeters. (Don't confuse a slime mold's plasmodium with the genus *Plasmodium*, which includes the parasitic apicomplexan that causes malaria.) Despite its size, the plasmodium is not multicellular; it is a single mass of cytoplasm that is undivided by plasma membranes and that contains many nuclei. This "supercell" is the product of mitotic nuclear divisions that are not followed by cytokinesis.

Within the plasmodium, cytoplasm streams first one way, then the other, in pulsing flows that are beautiful to watch through a microscope. This cytoplasmic streaming apparently helps distribute nutrients and oxygen. The plasmodium extends pseudopodia through moist soil, leaf mulch, or rotting

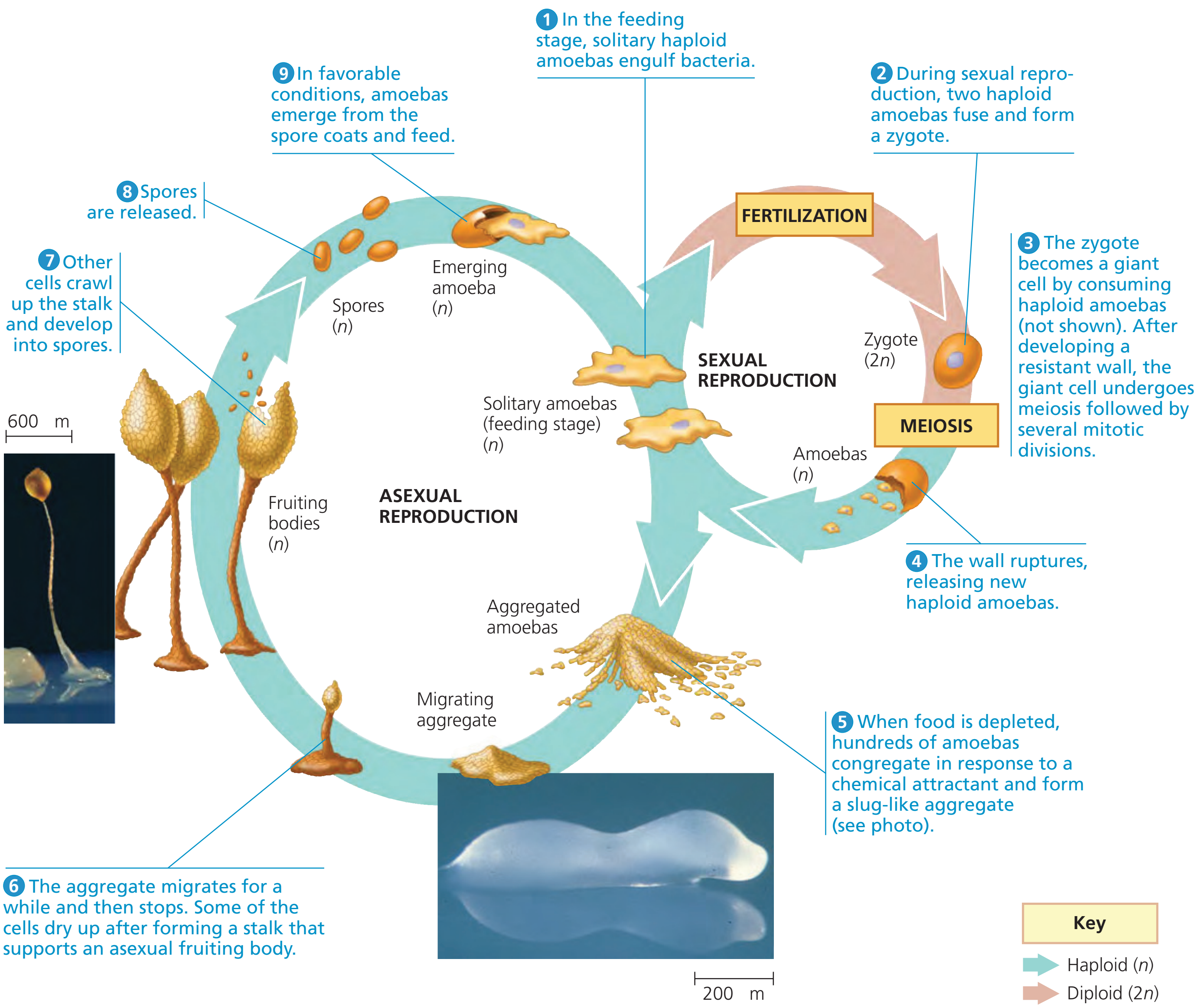


▲ **Figure 28.24 The life cycle of a plasmodial slime mold.**

logs, engulfing food particles by phagocytosis as it grows. If the habitat begins to dry up or there is no food left, the plasmodium stops growing and differentiates into fruiting bodies, which function in sexual reproduction.

Cellular Slime Molds The life cycle of the protists called **cellular slime molds** can prompt us to question what it means to be an individual organism. The feeding stage of these organisms consists of solitary cells that function individually, but when food is depleted, the cells form an aggregate that functions as a unit **(Figure 28.25)**. Although this mass of cells superficially resembles a plasmodial slime mold, the cells remain separated by their individual plasma membranes. Cellular slime molds also differ from plasmodial slime molds in being haploid organisms (only the zygote is diploid) and in having fruiting bodies that function in asexual rather than sexual reproduction.

Dictyostelium discoideum, a cellular slime mold commonly found on forest floors, has become a model organism for studying the evolution of multicellularity. One line of research has focused on the slime mold's fruiting body stage. During this stage, the cells that form the stalk die as they dry out, while the spore cells at the top survive and have the potential to reproduce. Scientists have found that mutations in a single gene can turn individual *Dictyostelium* cells into "cheaters" that never become part of the stalk. Because these mutants gain a strong reproductive advantage over noncheaters, why don't all *Dictyostelium* cells cheat?



▲ **Figure 28.25** **The life cycle of *Dictyostelium*, a cellular slime mold.**

Recent discoveries suggest an answer to this question. Cheating mutants lack a protein on their cell surface, and noncheating cells can recognize this difference. Noncheaters preferentially aggregate with other noncheaters, thus depriving cheaters of the opportunity to exploit them. Such a recognition system may have been important in the evolution of multicellular eukaryotes such as animals and plants.

Gymnamoebas

Gymnamoebas constitute a large and varied group of amoebozoans. These unicellular protists are ubiquitous in soil as well as freshwater and marine environments. Most are heterotrophs that actively seek and consume bacteria and other protists (see Figure 28.3). Some gymnamoebas also feed on detritus (nonliving organic matter).

Entamoebas

Whereas most amoebozoans are free-living, those that belong to the genus *Entamoeba* are parasites. They infect all classes of vertebrate animals as well as some invertebrates. Humans are host to at least six species of *Entamoeba*, but only one, *E. histolytica*, is known to be pathogenic. *E. histolytica* causes amebic dysentery and is spread via contaminated drinking water, food, or eating utensils. Responsible for up to 100,000 deaths worldwide every year, the disease is the third-leading cause of death due to eukaryotic parasites, after malaria (see Figure 28.10) and schistosomiasis (see Figure 33.11).

Opisthokonts

Opisthokonts are an extremely diverse group of eukaryotes that includes animals, fungi, and several groups of protists. We will discuss the evolutionary history of fungi and animals in Chapters 31–34. Of the opisthokont protists, we will discuss the nucleariids in Chapter 31 because they are more closely related to fungi than they are to other protists. Similarly, we will discuss choanoflagellates in Chapter 32, since they are more closely related to animals than they are to other protists. The nucleariids and choanoflagellates illustrate why scientists have abandoned the former kingdom Protista: A monophyletic group that included these single-celled eukaryotes would also have to include the multicellular animals and fungi that are closely related to them.

CONCEPT CHECK 28.6

1. Contrast the pseudopodia of amoebozoans and forams.
2. In what sense is "fungus animal" a fitting description of a slime mold? In what sense is it not fitting?
3. **WHAT IF?** If further evidence indicates that the root of the eukaryotic tree is as shown in Figure 28.23, would this evidence support, contradict, or have no bearing on the hypothesis that Excavata is monophyletic?

For suggested answers, see Appendix A.

CONCEPT **28.7**

Protists play key roles in ecological communities

Most protists are aquatic, and they are found almost anywhere there is water, including moist terrestrial habitats such as damp soil and leaf litter. In oceans, ponds, and lakes, many protists are bottom-dwellers that attach to rocks and other substrates or creep through the sand and silt. Other protists are important constituents of plankton. We'll focus here on two key roles that protists play in the varied habitats in which they live: that of symbiont and that of producer.

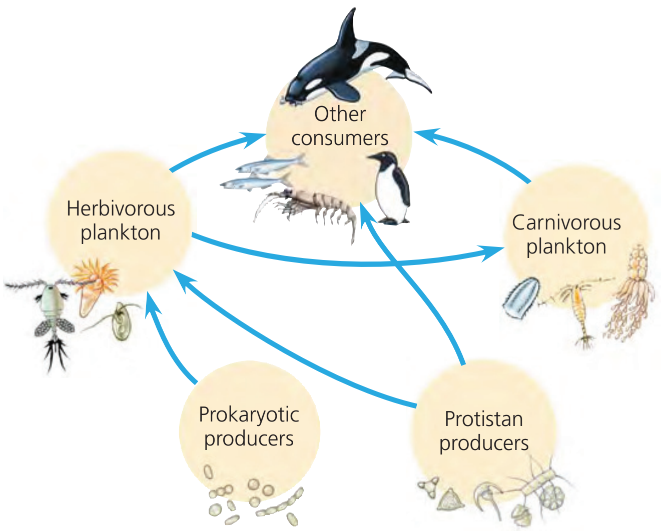
Symbiotic Protists

Many protists form symbiotic associations with other species. For example, photosynthetic dinoflagellates are food-providing symbiotic partners of the coral polyps that build coral reefs. Coral reefs are highly diverse ecological communities. That diversity ultimately depends on corals—and on the mutualistic protist symbionts that nourish them. Corals support reef diversity by providing food to some species and habitat to many others.

Another example is the wood-digesting protists that inhabit the gut of many termite species **(Figure 28.26)**. Unaided, termites cannot digest wood, and they rely on protistan or prokaryotic symbionts to do so. Termites cause over $3.5 billion in damage annually to wooden homes in the United States.

Symbiotic protists also include parasites that have compromised the economies of entire countries. Consider the malaria-causing protist *Plasmodium*: Income levels in countries hard hit by malaria are 33% lower than in similar countries free of the disease. Protists can have devastating effects on other species too. Massive fish kills have been attributed to *Pfiesteria shumwayae* (see Figure 28.9), a dinoflagellate parasite that attaches to its victims and eats their skin. Among species that parasitize plants, the oomycete protist *Phytophthora ramorum* has emerged as a major new forest pathogen. This species causes sudden oak death (SOD), a disease that has killed millions of oaks and other trees in California and Oregon (see Chapter 54).

▶ **Figure 28.26 A symbiotic protist.** This organism is a hypermastigote, a member of a group of parabasalids that live in the gut of termites and certain cockroaches and enable the hosts to digest wood (SEM).



▲ **Figure 28.27 Protists: key producers in aquatic communities.** Arrows in this simplified food web lead from food sources to the organisms that eat them.

Photosynthetic Protists

Many protists are important **producers**, organisms that use energy from light (or inorganic chemicals) to convert carbon dioxide to organic compounds. Producers form the base of ecological food webs. In aquatic communities, the main producers are photosynthetic protists and prokaryotes. All other organisms in the community depend on them for food, either directly (by eating them) or indirectly (by eating an organism that ate a producer; **Figure 28.27**). Scientists estimate that roughly 30% of the world's photosynthesis is performed by diatoms, dinoflagellates, multicellular algae, and other aquatic protists. Photosynthetic prokaryotes contribute another 20%, and land plants are responsible for the remaining 50%.

Because producers form the foundation of food webs, factors that affect producers can dramatically affect their entire community. In aquatic environments, photosynthetic protists are often held in check by low concentrations of nitrogen, phosphorus, or iron. Various human actions can increase the concentrations of these elements in aquatic communities. For example, when fertilizer is applied to a field, some of the fertilizer may be washed by rainfall into a river that drains into a lake or ocean. When people add nutrients to aquatic communities in this or other ways, the abundance of photosynthetic protists can increase spectacularly. Such increases can alter the abundance of other species in the community, as we'll see in Chapter 55.

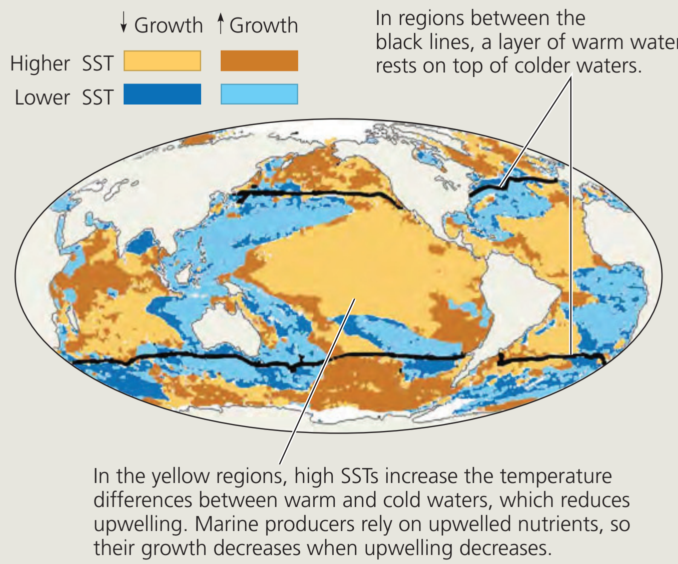
A pressing question is how global warming will affect protists and other producers. Satellite data indicate that the growth and biomass of photosynthetic protists and prokaryotes have declined in many regions as sea surface temperatures have increased **(Figure 28.28)**. If sustained, these changes would likely have far-reaching effects on marine ecosystems, fishery yields, and the global carbon cycle (see Chapter 55). Global warming can also affect producers on land, but there the base of food webs is occupied not by protists but by land plants, which we will discuss in Chapters 29 and 30.

▼ **Figure 28.28**

IMPACT

Marine Protists in a Warmer World

Photosynthetic protists are important components of marine food webs, each day converting millions of tons of carbon in CO_2 to organic molecules on which other organisms depend. How has global warming affected these key marine producers? Satellite data indicate that the growth and biomass of marine producers are negatively correlated to sea surface temperature (SST) across much of the tropical and midlatitude oceans (between the heavy black lines on the map below). In regions where SSTs have risen and growth has declined, the available nutrient supply may have been reduced by the formation of a light, warm layer of water that acts as a barrier preventing the rise, or upwelling, of cold, nutrient-rich waters from below.



WHY IT MATTERS Major changes to marine ecosystems are expected if the growth and biomass of producers decrease as SSTs increase due to global warming. A decrease in diatom biomass, for example, would likely reduce both the amount of carbon pumped to the ocean floor and the catch of economically important fishes such as salmon and anchovies that feed on phytoplankton.

FURTHER READING M. J. Behrenfeld et al., Climate-driven trends in contemporary ocean productivity, *Nature* 444:752–755 (2006).

WHAT IF? If diatom populations continue to drop as the oceans warm, how might climate be affected in the future?

CONCEPT CHECK 28.7

1. Justify the claim that photosynthetic protists are among the biosphere's most important organisms.
2. Describe three symbioses that include protists.
3. **WHAT IF?** High water temperatures and pollution can cause corals to expel their dinoflagellate symbionts. Predict how such "coral bleaching" would affect corals and other species in the community.

For suggested answers, see Appendix A.

28 CHAPTER REVIEW

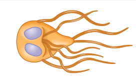
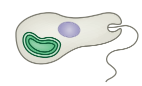
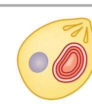
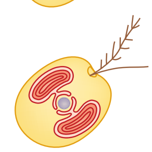
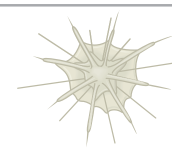
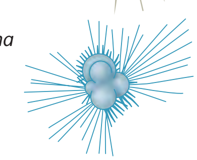
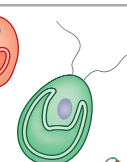
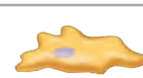
SUMMARY OF KEY CONCEPTS

CONCEPT 28.1

Most eukaryotes are single-celled organisms (pp. 575–579)

- Protists are more diverse than all other eukaryotes and are no longer classified in a single kingdom. Most are unicellular. Protists include photoautotrophs, heterotrophs, and mixotrophs. Protists are characterized by a wide diversity of life cycles.
- Mitochondria and plastids are thought to be descendants of bacteria that were engulfed by other cells and became endosymbionts. The plastid-bearing lineage eventually evolved into red algae and green algae. Other protist groups evolved from secondary endosymbiosis events in which red algae or green algae were themselves engulfed.
- In one hypothesis, eukaryotes are grouped into five supergroups, each a monophyletic clade: Excavata, Chromalveolata, Rhizaria, Archaeplastida, and Unikonta.

? *Describe similarities and differences between protists and other eukaryotes.*

Key Concept/Eukaryote Supergroup	Major Groups	Key Morphological Characteristics	Specific Examples
CONCEPT 28.2 **Excavates include protists with modified mitochondria and protists with unique flagella (pp. 580–581)** **?** *What evidence indicates that the excavates form a clade?*	**Diplomonads and parabasalids**	Modified mitochondria	*Giardia, Trichomonas* 
	Euglenozoans Kinetoplastids Euglenids	Spiral or crystalline rod inside flagella	*Trypanosoma, Euglena* 
CONCEPT 28.3 **Chromalveolates may have originated by secondary endosymbiosis (pp. 582–589)** **?** *If Chromalveolata originated by secondary endosymbiosis, what can be inferred about the plastids of its members? Explain.*	**Alveolates** Dinoflagellates Apicomplexans Ciliates	Membrane-bounded sacs (alveoli) beneath plasma membrane	*Pfiesteria, Plasmodium, Paramecium* 
	Stramenopiles Diatoms Golden algae Brown algae Oomycetes	Hairy and smooth flagella	*Phytophthora, Laminaria* 
CONCEPT 28.4 **Rhizarians are a diverse group of protists defined by DNA similarities (pp. 589–590)** **?** *What are the main subgroups of rhizarians, and what unites these subgroups as a clade?*	**Radiolarians**	Amoebas with threadlike pseudopodia radiating from central body	*Hexacontium* 
	Forams	Amoebas with threadlike pseudopodia and a porous shell	*Globigerina* 
	Cercozoans	Amoebas and flagellated protists with threadlike pseudopodia	*Paulinella*
CONCEPT 28.5 **Red algae and green algae are the closest relatives of land plants (pp. 590–592) (Archaeplastida)** **?** *On what basis do some systematists place land plants in the same supergroup (Archaeplastida) as red and green algae?*	**Red algae**	Phycoerythrin (accessory pigment)	*Porphyra* 
	Green algae	Plant-type chloroplasts	*Chlamydomonas, Ulva* 
	Land plants	(See Chapters 29 and 30.)	Mosses, ferns, conifers, flowering plants 
CONCEPT 28.6 **Unikonts include protists that are closely related to fungi and animals (pp. 593–596)** **?** *Describe a key feature for each of the main protist subgroups of Unikonta.*	**Amoebozoans** Slime molds Gymnamoebas Entamoebas	Amoebas with lobe-shaped pseudopodia	*Amoeba, Entamoeba, Dictyostelium* 
	Opisthokonts	(Highly variable; see Chapters 31–34.)	Nucleariids, choanoflagellates, animals, fungi 

CONCEPT 28.7

Protists play key roles in ecological communities (pp. 596–597)

- Protists form a wide range of mutualistic and parasitic relationships that affect their symbiotic partners and many other members of the community.
- Photosynthetic protists are among the most important producers in aquatic communities. Because they are at the base of the food web, factors that affect photosynthetic protists affect many other species in the community.

? *Describe several protists that are ecologically important.*

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Plastids that are surrounded by more than two membranes are evidence of
 a. evolution from mitochondria.
 b. fusion of plastids.
 c. origin of the plastids from archaea.
 d. secondary endosymbiosis.
 e. budding of the plastids from the nuclear envelope.

2. Biologists suspect that endosymbiosis gave rise to mitochondria before plastids partly because
 a. the products of photosynthesis could not be metabolized without mitochondrial enzymes.
 b. all eukaryotes have mitochondria (or their remnants), whereas many eukaryotes do not have plastids.
 c. mitochondrial DNA is less similar to prokaryotic DNA than is plastid DNA.
 d. without mitochondrial CO_2 production, photosynthesis could not occur.
 e. mitochondrial proteins are synthesized on cytosolic ribosomes, whereas plastids utilize their own ribosomes.

3. Which group is *incorrectly* paired with its description?
 a. rhizarians—morphologically diverse group defined by DNA similarities
 b. diatoms—important producers in aquatic communities
 c. red algae—acquired plastids by secondary endosymbiosis
 d. apicomplexans—parasites with intricate life cycles
 e. diplomonads—protists with modified mitochondria

4. Which protists are in the same eukaryotic supergroup as land plants?
 a. green algae
 b. dinoflagellates
 c. red algae
 d. brown algae
 e. both a and c

5. In life cycles with an alternation of generations, multicellular haploid forms alternate with
 a. unicellular haploid forms.
 b. unicellular diploid forms.
 c. multicellular haploid forms.
 d. multicellular diploid forms.
 e. multicellular polyploid forms.

LEVEL 2: APPLICATION/ANALYSIS

6. Based on the phylogenetic tree in Figure 28.3, which of the following statements is correct?
 a. The most recent common ancestor of Excavata is older than that of Chromalveolata.
 b. The most recent common ancestor of Chromalveolata is older than that of Rhizaria.
 c. The most recent common ancestor of red algae and land plants is older than that of nucleariids and fungi.
 d. The most basal (first to diverge) eukaryotic supergroup cannot be determined.
 e. Excavata is the most basal eukaryotic supergroup.

7. **EVOLUTION CONNECTION**

DRAW IT Medical researchers seek to develop drugs that can kill or restrict the growth of human pathogens yet have few harmful effects on patients. These drugs often work by disrupting the metabolism of the pathogen or by targeting its structural features.

Draw and label a phylogenetic tree that includes an ancestral prokaryote and the following groups of organisms: Excavata, Chromalveolata, Rhizaria, Archaeplastida, Unikonta, and, within Unikonta, amoebozoans, animals, choanoflagellates, fungi, and nucleariids. Based on this tree, hypothesize whether it would be most difficult to develop drugs to combat human pathogens that are prokaryotes, protists, animals, or fungi. (You do not need to consider the evolution of drug resistance by the pathogen.)

LEVEL 3: SYNTHESIS/EVALUATION

8. **SCIENTIFIC INQUIRY**

Applying the "If . . . then" logic of science (see Chapter 1), what are a few of the predictions that arise from the hypothesis that plants evolved from green algae? Put another way, how could you test this hypothesis?

9. **WRITE ABOUT A THEME**

Ecological Interactions Organisms interact with each other and the physical environment. In a short essay (100–150 words), explain how the response of diatom populations to a drop in nutrient availability can affect both other organisms and aspects of the physical environment (such as carbon dioxide concentrations).

For selected answers, see Appendix A.