Chapter 28

Protists

Lecture Outline

Overview: Living Small

- **Protists** are an informal set of kingdoms of diverse, mostly unicellular eukaryotes.
- During the last decade, genetic prospecting has turned up a number of ultra-small protists, in the size range of many prokaryotes—0.5 to 2 µm in diameter.
- Although all protists were once classified in the single kingdom Protista, it is now clear that this kingdom is a polyphyletic group.
    - As a result, the kingdom Protista has been abandoned and various lineages of protists are recognized as kingdoms in their own right.
- Scientists still use the convenient term *protist* informally to refer to eukaryotes that are not plants, animals, or fungi.

Concept 28.1 Most eukaryotes are single-celled organisms.

- Protists belong to the Domain Eukarya.
    - Unlike prokaryotes, eukaryotes have a nucleus, membrane-bound organelles, and a complex cell organization.
- The organisms in most eukaryotic lineages are protists.
- Protists exhibit more structural and functional diversity than any other group of eukaryotes.
- Most protists are unicellular, although some are colonial and multicellular.
- At the cellular level, many protists are very complex.
    - Complexity is necessary for a single cell that must carry out the basic functions performed by all the specialized cells in a multicellular organism.
    - Protists carry out their essential biological functions using subcellular organelles.
    - In addition to the nucleus, endoplasmic reticulum, Golgi apparatus, and lysosomes, some protists also have organelles not found in most other eukaryotic cells, such as contractile vacuoles to pump excess water from the cell.
- Protists are the most nutritionally diverse of all eukaryotes.
    - Some protists are photoautotrophs, containing chloroplasts.
    - Some are heterotrophs, absorbing organic molecules or ingesting food particles.
    - Some are **mixotrophs**, combining photosynthesis *and* heterotrophic nutrition.
- The life cycles of protists vary greatly. Some are only known to reproduce asexually, but most have life cycles that include meiosis and fertilization.

- Much of protist diversity is the result of *endosymbiosis*, a process in which unicellular organisms engulf other cells that evolve into organelles in the host cell.
- The earliest eukaryotes acquired mitochondria by engulfing alpha proteobacteria.
  - This origin of mitochondria is supported by the fact that all eukaryotes studied so far either have mitochondria or modified versions of them.
- Later in eukaryotic history, a lineage of heterotrophic eukaryotes acquired an additional endosymbiont—a photosynthetic cyanobacterium—that evolved into plastids.
  - This lineage gave rise to red and green algae.
- This hypothesis is supported by the observation that the DNA of plastids in red and green algae closely resembles the DNA of cyanobacteria.
  - Also, plastids in these algae are surrounded by two membranes. Transport proteins in these membranes are homologous to proteins in the inner and outer membranes of cyanobacterial endosymbionts.
- On several occasions during eukaryotic evolution, red and green algae underwent **secondary endosymbiosis**.
- The algae were ingested in the food vacuole of a heterotrophic eukaryote and became endosymbionts themselves.
  - For example, algae known as chlorarachniophytes evolved when a heterotrophic eukaryote engulfed a green alga.
  - This secondary endosymbiosis likely occurred relatively recently in evolutionary time because the engulfed green alga still carries out photosynthesis with its plastids and contains a tiny, vestigial nucleus called a *nucleomorph*.
- *Four* membranes surround the plastids of chlorarachniophytes.
  - 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 other protists, plastids acquired by secondary endosymbiosis are surrounded by three membranes, indicating that one of the original four membranes has been lost.
- Scientists' understanding of the evolutionary history of protists has recently been in a state of flux.
- In the early 1990s, biologists thought that the oldest lineage of living eukaryotes was the *amitochondriate protists*, organisms that have few membrane-bound organelles and lacks conventional mitochondria.
  - Recent structural and DNA data have undermined this hypothesis.
  - Many of the amitochondriate protists are shown to have reduced mitochondria.
  - The microsporidians, once considered amitochondriate protists, are now classified as fungi.
- One current hypothesis organizes protist diversity into five supergroups: Excavata, Chromalveolata, Rhizaria, Archaeplastida, and Unikonta.
  - Because the root of the eukaryotic tree is not known, all five supergroups are shown as diverging simultaneously from a common ancestor.
  - This is not correct, but reflects uncertainty about which organisms were the first to diverge from the others.

Concept 28.2 Excavates include protists with modified mitochondria and protists with unique flagella.

- The **Excavata** are a recently proposed clade that has emerged from morphological studies of the cytoskeleton.
    - Some members of this diverse group have an "excavated" feeding groove on one side of the cell body.
- The excavates include the diplomonads, the parabasalids, and the euglenozoans.
- Molecular data suggest that each of these three groups is monophyletic.
    - It is not yet clear, however, whether excavates themselves represent a monophyletic taxon.

Diplomonads and parabasalids lack plastids and have modified mitochondria.

- Most diplomonads and parabasalids are found in anaerobic environments.
- **Diplomonads** have modified mitochondria called *mitosomes*.
    - Mitosomes lack functional electron transport chains and cannot use oxygen to extract energy from carbohydrates.
    - The diplomonads obtain energy from anaerobic biochemical pathways.
- Diplomonads have two equal-sized nuclei and multiple flagella.
- Many diplomonads are parasites.
    - *Giardia intestinalis* is an infamous diplomonad parasite that lives in the intestines of mammals.
- **Parabasalids** have reduced mitochondria called *hydrogenosomes* that generate energy anaerobically, releasing hydrogen gas as a by-product.
- The best-known parabasalid species, *Trichomonas vaginalis*, is a sexually transmitted parasite that uses its flagella and undulating plasma membrane to travel along the mucus-coated lining of the human reproductive and urinary tracts.
    - If the normal acidity of the vagina is disturbed, *T. vaginalis* can outcompete beneficial microbes and infect the vaginal lining.
    - The male urethra may also be infected, but without symptoms.
- Genetic studies of *T. vaginalis* suggest that the species became pathogenic after some individuals acquired a particular gene through horizontal gene transfer from other vaginal bacteria.
    - The gene allows *T. vaginalis* to feed on the vaginal lining, aiding the infection process.
- **Euglenozoans** are a diverse clade that includes predatory heterotrophs, photosynthetic autotrophs, and pathogenic parasites.
- Members of this group are distinguished by the presence of a spiral or crystalline rod inside their flagella. The function of this rod is unknown.

The best-studied groups of euglenozoans are the kinetoplastids and euglenids.

- The **kinetoplastids** have a single large mitochondrion that contains an organized mass of DNA called a *kinetoplast*.
- Kinetoplastids include free-living consumers of prokaryotes in freshwater, marine, and moist terrestrial ecosystems, as well as some pathogenic parasites.
    - For example, *Trypanosoma* causes sleeping sickness, a neurological disease spread by the African tsetse fly, and Chagas' disease, which is transmitted by bloodsucking insects.
- Trypanosomes evade immune detection by switching surface proteins from generation to generation, preventing the host from developing immunity.
    - One-third of *Trypanosoma*'s genome codes for these surface proteins.
- **Euglenids** have an anterior pocket from which one or two flagella emerge.

- Many species of the euglenid *Euglena* are mixotrophic: they are autotrophic in sunlight but can become heterotrophic in the dark.
- Other euglenids engulf prey by phagocytosis.

Concept 28.3 Chromalveolates may have originated by secondary endosymbiosis.

- **Chromalveolata** is a large, extremely diverse clade of protists.
- Some (but not all) DNA data suggest that chromalveolates form a monophyletic group.
- Some data support the hypothesis that the chromalveolates originated by an ancient secondary endosymbiosis event.
    - According to this hypothesis, a common ancestor of the group engulfed a single-celled red alga more than a billion years ago.
- How strong is the evidence for the origin of chromalveolates by secondary endosymbiosis?
    - Many species in the clade have plastids whose structure and DNA indicate they are of red algal origin.
    - Other species have reduced plastids that seem to be derived from a red algal endosymbiont.
    - Still other species lack plastids yet have plastid genes in their nuclear DNA.
- These findings suggest that the common ancestor of chromalveolates had plastids of red algal origin and that some evolutionary lineages within the group lost the plastids.
    - Some scientists challenge this hypothesis, noting that several chromalveolates lack plastids and show no evidence of plastid genes.

The alveolates have membrane-bound sacs just under the plasma membrane.

- **Alveolates** have alveoli, small membrane-bound cavities under the plasma membrane.
    - The function of these cavities is not known, but they may help stabilize the cell surface or regulate the cell's water and ion content.
- Alveolata includes flagellates (dinoflagellates), parasites (apicomplexans), and ciliates.
- **Dinoflagellates** include species characterized by cells that are reinforced by internal plates of cellulose.
    - Two flagella sit in perpendicular grooves in this "armor" and produce a spinning movement.
- Dinoflagellates are abundant components of marine and freshwater phytoplankton.
    - Dinoflagellates and other phytoplankton form the foundation of most marine and many freshwater food chains.
- Many of the photosynthetic species are mixotrophic, and half are fully heterotrophic.
- Dinoflagellate *blooms*, characterized by explosive population growth, can cause "red tides" in coastal waters.
    - The blooms are brownish red or pinkish orange because of the carotenoids in dinoflagellate plasmids.
    - Toxins produced by some red-tide organisms (such as *Pfiesteria shumawayae*) have produced massive invertebrate and fish kills. These toxins can also be deadly to humans.
- Nearly all **apicomplexans** are parasites of animals, and some cause serious human diseases.
- The parasites disseminate as tiny infectious cells (*sporozoites*) that have a *complex* of organelles within the cell *apex*, specialized for penetrating host cells and tissue.

- Apicomplexans have a nonphotosynthetic plasmid called the apicoplast, most likely of red algal origin.
- Most apicomplexans have intricate life cycles with both sexual and asexual stages, and they often require two or more different host species for completion.
  - *Plasmodium,* the parasite that causes malaria, spends part of its life in mosquitoes and part in humans.
- The incidence of malaria was greatly diminished in the 1960s by the use of insecticides against the *Anopheles* mosquitoes, which spread the disease, and by drugs that killed the parasites in humans.
  - However, resistant varieties of *Anopheles* and *Plasmodium* have caused a malarial resurgence.
  - About 250 million people are infected with malaria in the tropics, and 900,000 die each year.
- The search for malarial vaccines has had little success because *Plasmodium* lives mainly inside human cells, hidden from the host's immune system.
  - Like trypanosomes, *Plasmodium* continually changes its surface proteins.
- The need for new treatments for malaria led to a major effort to sequence *Plasmodium*'s genome.
  - Researchers had identified the expression of most of the parasite's genes at numerous points in its life cycle. This research could help scientists identify potential new targets for vaccines.
  - Drugs are being developed that target the apicoplast. Because the apicoplast was derived by secondary endosymbiosis from a prokaryote, it has metabolic pathways that differ from those of humans.
- **Ciliates** are a diverse group of protists, named for their use of cilia to move and feed.
  - The cilia may cover the cell surface or be clustered in rows or tufts.
  - Some ciliates scurry about on leg-like structures constructed from many cilia.
- Ciliates have two types of nuclei: one or more large macronuclei and tiny micronuclei.
- The sexual shuffling of genes occurs during **conjugation,** when two individuals exchange haploid micronuclei.
- 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 contains multiple copies of the ciliate's genome.
  - Macronuclear genes control the everyday functions of the cell, such as feeding, waste removal, and water balance.

The stramenopiles include both heterotrophic and photosynthetic chromalveolates.

- The name *stramenopile* is derived from the numerous fine, hairlike projections on the flagella.
  - In most cases, a "hairy" flagellum is paired with a shorter, smooth flagellum.
- **Diatoms** are unicellular algae with unique glass-like walls composed of hydrated silica embedded in an organic matrix.
  - The wall is divided into two parts that overlap like a shoe box and lid.
- The lacey network of holes and grooves in diatom walls enable live diatoms to withstand immense pressure, providing a defense for them from the crushing jaws of predators.
  - Live diatoms can withstand pressures of up to 1.4 million kg/m^2, equal to the pressure under each leg of a table supporting an elephant!
- Diatoms are a highly diverse group of protists, with an estimated 100,000 species.
- Diatoms are abundant members of both freshwater and marine phytoplankton.

- Massive accumulations of fossilized diatoms are major constituents of *diatomaceous earth*, mined for their quality as a filtering medium.
- Diatom populations may *bloom* when nutrients are abundant.
    - During a bloom, many diatoms sink to the ocean floor after death, and most are not broken down by bacteria or other decomposers.
    - The carbon in their bodies remains, effectively "pumping" carbon dioxide to the ocean bottom.
- Some scientists have suggested fertilizing the ocean with limiting nutrients such as iron to promote diatom blooms, sequestering carbon dioxide on the ocean bottom, and thus reducing global warming.
    - Other scientists note that it is difficult to predict the effects of such large-scale manipulations of ecological communities.
- **Golden algae** are named for their yellow and brown carotenoids.
- The cells of golden algae are biflagellated, with both flagella attached near one end of the cell.
- Although all golden algae are photosynthetic, some species are mixotrophic, absorbing organic molecules or ingesting living cells by phagocytosis.
- Most golden algae are unicellular, but some are colonial.
- At high densities, they can form resistant cysts that remain viable for decades.

Brown algae, or phaeophytes, are the largest and most complex protists known.

- All **brown algae** are multicellular, and most species are marine.
    - Brown algae are especially common along temperate coasts in areas of cool water and adequate nutrients.
- Brown algae owe their characteristic brown or olive color to carotenoids in their plastids.
- Brown algae include many of the species known as "seaweeds." These phaeophytes have a complex multicellular anatomy, with specialized tissues and organs that resemble those in plants.
    - These analogous features include the **thallus**, or body, of the seaweed, which lacks true roots, stems, and leaves.
    - The thallus typically consists of a rootlike **holdfast** and a stemlike **stipe**, which supports leaflike photosynthetic **blades**.
    - Some brown algae are equipped with gas-filled floats to keep the blades near the water surface.
- The giant seaweeds known as kelps live in deep water beyond the intertidal zone.
    - The stipes of these algae may be as long as 60 m.
- Brown algae living in the intertidal zone must cope with rough water as well as twice-daily low tides that expose the algae to hot sun and the risk of desiccation.
- Unique adaptations allow these seaweeds to survive.
    - For example, their cell walls are composed of cellulose and gel-forming polysaccharides that cushion the thalli from wave action and reduce drying during exposure.
- Brown algae are important commodities for humans.
    - Many seaweeds are eaten by coastal people, including *Laminaria* ("kombu" in Japan) in soup.
    - A gel-forming substance (algin) from the cell walls of brown algae is used to thicken processed foods.

Some algae have life cycles with alternating multicellular haploid and diploid generations.

- Many multicellular algae show complex life cycles with alternation of multicellular haploid and multicellular diploid forms.

- A similar **alternation of generations** evolved convergently in plants.

- The complex life cycle of the kelp *Laminaria* provides an example of alternation of generations.
  - The diploid individual, the *sporophyte*, produces haploid flagellated zoospores by meiosis.
  - The zoospores develop into haploid male and female *gametophytes*, which produce gametes (sperm and eggs) by mitosis.
  - The fertilization, or syngamy, of two gametes forms a diploid zygote, which gives rise to a new sporophyte.
- In *Laminaria*, the sporophyte and gametophyte are structurally different or **heteromorphic.**
  - In other algae, the alternating generations look alike (**isomorphic**) but differ in the chromosome number.

Oomycetes include water molds, white rusts, and downy mildews.

- The **oomycetes** were once classified as fungi.
  - Many oomycetes have multinucleate filaments that resemble fungal hyphae.
- However, there are key differences between oomycetes and fungi.
  - Oomycetes have cell walls made of cellulose, whereas fungal walls are made of chitin.
- Molecular systematics has confirmed that oomycetes are not closely related to fungi.
  - Their superficial similarity is a case of convergent evolution.
  - In both groups, the high surface-to-volume ratio of filamentous structures enhances nutrient uptake.
- Although oomycetes descended from plastid-bearing ancestors, they no longer have plastids or carry out photosynthesis.
  - Instead, oomycetes acquire nutrients as decomposers or parasites.
- Water molds are important decomposers, mainly in fresh water. They form cottony masses on dead algae and animals.
  - White rusts and downy mildews are parasites of terrestrial plants.
- The ecological impact of oomycetes can be significant.
  - The oomycete *Phytophthora infestans* causes potato late blight, which contributed to the Irish famine in the 19th century. At least a million people died, and another million were forced to leave Ireland.
  - Late blight continues to cause crop losses today. Up to 70% of crops may be lost in areas without pesticides.
- Researchers 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, the oomycete has acquired genes that make it more aggressive and resistant to pesticides.
- Scientists are examining the genomes of both *Phytophthora* and potatoes to develop new weapons against the disease.
  - A team of researchers has transferred blight-resistant genes from wild potatoes into domestic potatoes to produce a resistant crop strain.

Concept 28.4 Rhizarians are a diverse group of protists defined by DNA similarities.

- The clade **Rhizaria** has been proposed based on evidence from molecular systematics.

- DNA evidence indicates that rhizarians are a monophyletic group, although many of its members differ in morphology.
- According to some phylogenetic studies, rhizarians should be nested within Chromalveolata.

Many species of rhizarians are amoebas with thread-like pseudopodia.

- The term **amoeba** used to refer to protists that move and feed by means of **pseudopodia,** cellular extensions that bulge from the cell surface.
  - When an amoeba moves, it extends a pseudopodium and anchors the tip. Cytoplasm then streams into the pseudopodium.
- It is now clear that amoebas are not a monophyletic group but are dispersed across many distantly related eukaryotic taxa.
  - Amoebas that belong to the clade Rhizaria are distinguished by their threadlike pseudopodia.
- Rhizarians include radiolarians, forams, and cercozoans.
- **Radiolarians** are mostly marine protists that have delicate, intricately symmetrical internal skeletons made of silica.
- Pseudopodia radiate from the central body of radiolarians and are reinforced by microtubules.
  - The microtubules are covered by a thin layer of cytoplasm, which engulfs organisms that become attached to the pseudopodia.
  - Cytoplasmic streaming carries the captured prey into the main part of the cell.
- After death, radiolarian skeletons accumulate as an ooze that may be hundreds of meters thick in some seafloor locations.
- **Foraminiferans**, **or forams**, have multichambered, porous shells called **tests**.
  - Foram tests consist of a single piece of organic material hardened with calcium carbonate.
  - Pseudopodia extend through the pores for swimming, test formation, and feeding.
- Many forams obtain nutrients from the photosynthesis of symbiotic algae that live within the test.
- Forams live in marine and freshwater environments.
  - Most live in sand or attach to rocks or algae, but some are abundant in the plankton.
- The largest forams, though single-celled, grow to a diameter of several centimeters.
- More than 90% of all described forams are known from fossils.
  - The calcareous skeletons of forams are important components of marine sediments.
  - Fossil forams are often used as markers to correlate the ages of sedimentary rocks in different parts of the world.
- **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, including many parasites of plants, animals, and protists, and many 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, are mixotrophic, ingesting bacteria and small protists as well as performing photosynthesis.
- *Paulinella chromatophora* is an autotroph, deriving its energy from light and its carbon from carbon dioxide.

- This species has a distinctive sausage-shaped structure where photosynthesis is performed.
- 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.
- The lineage represented by *Paulinella* appears to have obtained its photosynthetic apparatus directly from a cyanobacterium.

Concept 28.5 Red algae and green algae are the closest relatives of land plants.

- More than a billion years ago, a heterotrophic protist acquired a cyanobacterial endosymbiont.
  - The photosynthetic descendents of this ancient protist evolved into the red and green algae.
  - At least 475 million years ago, the lineage that produced green algae gave rise to the land plants.
- Together, red algae, green algae, and land plants make up the fourth eukaryotic supergroup, the **Archaeplastida**.
  - Archaeplastida is a monophyletic group, descended from the ancient protist that engulfed a cyanobacterium.
- There are more than 6,000 known species of **red algae**, which owe their red color to the accessory pigment phycoerythrin.
  - Coloration varies among species and depends on the depth that they inhabit.
  - Some species lack pigmentation and are parasitic on other red algae.
- Red algae are the most abundant large algae in the warm coastal waters of tropical oceans.
- Red algae inhabit deeper waters than other photosynthetic eukaryotes.
  - Their accessory pigments allow them to absorb blue and green wavelengths that penetrate down to deep water.
  - One red algal species has been discovered off the Bahamas at a depth of more than 260 m.
- A few red algae live in fresh water or on land.
- Most red algae are multicellular, with some reaching a size large enough to be called "seaweeds."
- Humans eat the red alga *Porphyra* as crispy sheets or as sushi wrap.
- The life cycles of red algae are especially diverse, and alternation of generations is common.
  - Unlike other algae, they lack flagellated stages in their life cycle. In the absence of flagella, fertilization depends entirely on water currents.
- **Green algae** are named for their grass-green chloroplasts.
  - These chloroplasts are similar in ultrastructure and pigment composition to those of plants.
- Molecular systematics and cellular morphology provide considerable evidence that green algae and land plants are closely related.
  - In fact, some systematists advocate the inclusion of green algae in an expanded "plant" kingdom, Viridiplantae.
  - Phylogenetically, this makes sense. Otherwise, the green algae are a paraphyletic group.
- Green algae are divided into two main groups: charophytes and chlorophytes.
- There are more than 7,000 species of chlorophytes.
  - Most live in fresh water, but many are marine inhabitants and a few are terrestrial.

- The simplest chlorophytes are unicellular organisms such as *Chlamydomonas*, which resemble the gametes or zoospores of more complex green algae.
- Unicellular chlorophytes live as plankton or inhabit damp soil, while others are specialized to live on snow.
    - These chlorophytes carry out photosynthesis despite subfreezing temperatures and intense visible and ultraviolet radiation.
    - They are protected by the snow, 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.
- Large size and complexity in chlorophytes have evolved by three different mechanisms:
    1. The formation of colonies of individual cells, as seen in *Volvox* and in the filaments that form pond scum
    2. The formation of true multicellular forms by cell division and cell differentiation, as in *Ulva*
    3. The repeated division of nuclei without cytoplasmic division to form multinucleate filaments, as in *Caulerpa*
- Most chlorophytes have complex life cycles, with both sexual and asexual reproductive stages.
    - Most sexual species have biflagellated gametes with cup-shaped chloroplasts.
    - Alternation of generations evolved in the life cycles of some green algae, including *Ulva*.
- The other main group of green algae, the charophyceans, is most closely related to land plants.

Concept 28.6 Unikonts include protists that are closely related to fungi and animals.

- The **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 amoeobozoans and the opisthokonts.
    - The opisthokonts include animals, fungi, and closely related protist groups.
- The existence of these two major clades is strongly supported by molecular systematics, but the close relationship between amoeobozoans and opisthokonts is more controversial.
    - Support for the divergence is provided by comparisons of myosin proteins and by several studies based on hundreds of genes.
    - Other studies based on single genes do not provide support for this divergence.
- Another controversy involving unikonts concerns the root of the eukaryotic tree.
    - 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: Scientists do not know which group of eukaryotes was the first to diverge from other eukaryotes.
    - If the root were known, scientists could infer characteristics of the common ancestor of all eukaryotes.
- In attempts to determine the root of the eukaryotic tree, phylogenies based on different genes provide conflicting results.
- Thomas Cavalier-Smith and Alexandra Stechmann propose that the unikonts were the first eukaryotes to diverge from other eukaryotes.

- This controversial hypothesis proposes that animals and fungi belong to an early-diverging group of eukaryotes, while protists that lack typical mitochondria (such as diplomonads and parabasalids) diverged much later in the history of life.

Amoebozoans include amoebas with lobe- or tube-shaped pseudopodia.

- **Amoebozoans** form a monophyletic clade that includes gymnamoebas, entamoebas, and slime molds.
- Slime molds, or mycetozoans, were once classed as fungi because they produce fruiting bodies that aid in spore dispersal.
    - However, this resemblance is due to evolutionary convergence.
- Slime molds have diverged into two lineages with unique life cycles: plasmodial slime molds and cellular slime molds.
- The **plasmodial slime molds** are brightly pigmented, heterotrophic organisms.
    - The feeding stage is an amoeboid mass, the **plasmodium,** which may be several centimeters in diameter.
- The plasmodium is not multicellular but rather a single mass of cytoplasm with multiple nuclei.
    - The nuclei undergo synchronous mitotic divisions, thousands at a time. Mitosis is not followed by cytokinesis.
- Within the cytoplasm, cytoplasmic streaming distributes nutrients and oxygen throughout the plasmodium.
    - The plasmodium extends pseudopodia that phagocytose food particles from moist soil, leaf mulch, or rotting logs.
- If the habitat begins to dry or if food levels drop, the plasmodium stops growing and differentiates into fruiting bodies, which function in sexual reproduction.
- **Cellular slime molds** straddle the line between individuality and multicellularity.
    - The feeding stage consists of solitary cells that feed and divide mitotically as individuals.
    - When food is scarce, the cells form an aggregate called a slug that functions as a unit.
    - Each cell remains separated by its membrane and retains its identity in the aggregate.
- The dominant stage in a cellular slime mold is the haploid stage. Only the zygote is diploid.
    - The fruiting bodies of cellular slime molds function in asexual, rather than sexual, reproduction.
- *Dictyostelium discoideum* is a common cellular slime mold that has become a model organism for studying the evolution of multicellularity.
    - As the fruiting body forms, cells that form the stalk dry out and die. Cells at the top survive, form spores, and have the potential for future reproduction.
- Scientists have found that mutations in a single gene can turn individual *Dictyostelium* cells into "cheaters" that never become part of the stalk.
    - Since these mutants gain a strong reproductive advantage over noncheaters, why don't all *Dictyostelium* cells cheat? 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, depriving cheaters of the opportunity to exploit them.
    - Such a recognition system may have been important in the evolution of multicellular animals and plants.
- **Gymnamoebas** are a large and varied group of amoebozoans.

- Gymnamoebas are common in soil as well as in freshwater and marine environments.
- Most gymnamoebas are heterotrophs that actively seek and consume bacteria and protists, while some feed on detritus.
- **Entamoebas** include free-living and parasitic species.
- Humans host at least six species of *Entamoeba*.
    - One, *E. histolytica*, causes amebic dysentery. This disease spreads through contaminated drinking water and food.
    - Amebic dysentery kills 100,000 people each year and is the third-leading cause of death due to eukaryotic parasites, after malaria and schistosomiasis.
- **Opisthokonts** are an extremely diverse group of eukaryotes that include animals, fungi, and several groups of protists.
    - The protists within this taxon include nucleariids, which are closely related to fungi, and choanoflagellates, which are closely related to animals.
- The nucleariids and choanoflagellates illustrate why scientists no longer consider Protista to be a valid taxon: 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 28.7 Protists play key roles in ecological communities.

- Most protists are aquatic. They are found almost anywhere there is water, including damp soil and leaf litter.
- Many protists attach to rocks, sand, or silt in aquatic habitats. Others live in the plankton.

Many protists form symbiotic associations with other species.

- In corals, photosynthetic dinoflagellates provide nourishment to their hosts, the coral polyps that build coral reefs.
    - Coral reefs are highly diverse ecological communities that ultimately depend on protist symbionts.
    - Corals support reef diversity by providing food to some species and habitat to many others.
- Termites cause more than $3.5 billion in damage to wood homes in the United States.
    - Termites can digest wood only because they have large populations of wood-digesting protists or prokaryotes in their gut.
- Other symbiotic protists include pathogenic parasites such as *Plasmodium*, which has an enormous impact on human health and regional economies.
    - Incomes in countries hard-hit by malaria are 33% lower than incomes in similar countries free of the disease.
- Massive fish kills have been attributed to *Pfiesteria shumwayae*, a dinoflagellate parasite that attaches to its victims and eats their skin.
- The oomycete protist *Phytophthora ramorum* causes Sudden Oak Death, a disease that has killed millions of oaks and other trees in California and Oregon.

Many protists are important producers.

- In aquatic communities, the main **producers** are photosynthetic protists and prokaryotes.
    - Up to 30% of the world's photosynthesis is carried out 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 have dramatic effects on communities.
    - For example, when fertilizer is applied to a field, some may be washed by rainfall into a river that drains into a lake or ocean and the abundance of photosynthetic protists may increase dramatically, affecting the entire aquatic community.
- 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.
    - If sustained, these changes would likely have far-reaching effects on marine ecosystems, fishery yields, and the global carbon cycle.
- Global warming also affects producers on land, but there the base of food webs is occupied not by protists but by land plants.