Chapter 28

Protists

Lecture Outline

Overview: Living Small

∞ The 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 mm in diameter.
∞ Although all protists were once classified in the single kingdom Protista, it is now clear that this kingdom is a paraphyletic group.
  ○ As a result, the kingdom Protista has been abandoned.
  ○ 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 are eukaryotes with a nucleus, membrane-bound organelles, and a complex cell organization.
∞ 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.
∞ 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 exclusively asexual, but most have life cycles that include meiosis and syngamy.
∞ Protists can be divided into three groups, based on their roles in biological communities: photosynthetic algal protists, ingestive protozoans, and absorptive protists.
  ○ These groups are not monophyletic.
∞ 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 had them in the past.

∞ Later in eukaryotic history, one 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.
  ○ Plastids in these algae are surrounded by two membranes, presumably derived from the cell membranes of host and endosymbiont.

∞ 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.

∞ A decade ago, biologists thought that the oldest lineage of living eukaryotes was the “amitochondriate” protists, a group that has 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.

**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 the excavates themselves represent a monophyletic taxon.

∞ Most diplomonads and parabasalids are found in anaerobic environments.

∞ These protists lack plastids and have modified mitochondria.
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 such as glycolysis.

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 travels 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 epithelial cells, resulting in infection.

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 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 parasitic species.
- Kinetoplastids are symbiotic and include 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 autotrophic but can become heterotrophic in the dark.
- Other euglenids can phagocytose prey.

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 flagellated protists (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.

Most dinoflagellates are unicellular, but some are colonial.

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 be deadly to humans as well.

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 300 million people are infected with malaria in the tropics, and 2 million 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, thereby changing its “face” to the human immune system.

The need for new treatments for malaria led to a major effort to sequence *Plasmodium*’s genome.
- By 2003, researchers had identified the expression of most of the parasite’s genes at specific points in its life cycle.
- This research could help scientists identify potential new targets for vaccines.
- In addition, antibiotics are being developed that target the apicoplast.
- Because the apicoplast was derived by secondary endosymbiosis from a prokaryotic ancestor, it has metabolic pathways that differ from those of the human host.

**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.
- A submembrane system of microtubules coordinates ciliary movements.

Ciliates have two types of nuclei: one or more large macronuclei and tiny micronuclei.
- Each macronucleus has dozens of copies of the ciliate’s genome.
- 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 sexual shuffling of genes occurs during **conjugation**, when two individuals exchange haploid micronuclei.

**The stramenopiles include both heterotrophic and photosynthetic protists.**
- 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 shoebox 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.
  - In 2003, German researchers discovered that live diatoms can withstand pressures of up to 1.4 million kg/m², equal to the pressure under each leg of a table supporting an elephant.
- Most of the year, diatoms reproduce asexually by mitosis, with each daughter cell receiving half of the parental cell wall and regenerating a new second half that fits inside it.
  - Some species form cysts as resistant stages.
  - Sexual stages are not common.

Diatoms are a highly diverse group of protists, with an estimated 100,000 species.
- Diatoms are abundant members of both freshwater and marine phytoplankton.
- Diatoms store food reserves as the glucose polymer laminarin or, in a few diatoms, as oil.
- Massive accumulations of fossilized diatoms are major constituents of diatomaceous earth, used as a filtering medium.
- Diatoms are also used in nanotechnology, where nano-engineers are studying the process by which diatoms self-assemble intricate three-dimensional components.
Diatom populations may bloom when nutrients are abundant.

During a bloom, many diatoms sink to the ocean floor after death, 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.”
- Brown algae include seaweeds that have a complex multicellular anatomy, with some differentiated 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 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 desiccation during exposure.
- Brown algae are important sources of food and commodities.
  - Many seaweeds are eaten by coastal people, including *Laminaria* (“kombu” in Japan) in soup.
  - A gel-forming substance (algae) 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 the life cycle of 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 many 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 hyphae enhances nutrient uptake.
- Although oomycetes descended from photosynthetic ancestors, they no longer have plastids or carry out photosynthesis.
- 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.
- Oomycetes are dispersed by windblown spores and form flagellated zoospores at another point in their life cycles.
- The ecological impact of oomycetes can be significant.
  - One species of downy mildew threatened French vineyards in the 1870s.
  - 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.
  - In 2003, a team of researchers produced resistant potatoes by transferring blight-resistant genes from wild potatoes.

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

- A newly proposed clade, **Rhizaria**, contains the amoebas.
  - DNA evidence indicates that Rhizarians are a monophyletic group, although many of its members differ in morphology.
• 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 chlorarachniophytes, forams, and radiolarians.

• *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 form symbioses with 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.
• More than 90% of the described forams are fossils.
  ○ The calcareous skeletons of forams are important components of marine sediments.
  ○ Fossil forams are often used as chronological markers to correlate the ages of sedimentary rocks from different parts of the world.

• *Radiolarians* are mostly marine protists that have 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 phagocytoses organisms that become attached to the pseudopodia.
• Cytoplasmic streaming carries the captured prey to the main part of the cell.
• After death, radiolarian tests accumulate as an ooze that may be hundreds of meters thick in some seafloor locations.

**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 parasites 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 thalli of many red algal species are filamentous and may be branched or interwoven.

The base of the thallus is usually differentiated into a simple holdfast.

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: chlorophytes and charophyceans.

Most of the 7,000 species of chlorophytes have been identified.

Most chlorophytes live in fresh water, but many are marine inhabitants.

The simplest chlorophytes are unicellular organisms such as *Chlamydomonas*, which resemble the gametes and zoospores of more complex green algae.

Some unicellular chlorophytes inhabit damp soil, while others are specialized to live on snow.

*Chlamydomonas nivalis* can form dense algal blooms on high-altitude glaciers and snowfields, where it carries out photosynthesis despite subfreezing temperatures and intense visible and ultraviolet radiation.

*C. nivalis* organisms are protected by radiation-blocking compounds in their cytoplasm and by the snow itself, which acts as a shield.

Some chlorophytes live symbiotically with fungi to form lichens, a mutualistic collective.

Large size and complexity in chlorophytes have evolved by three different mechanisms:

1. The formation of colonies of individual cells (for example, *Volvox*)
2. The repeated division of nuclei without cytoplasmic division to form multinucleate filaments (for example, *Caulerpa*)
3. The formation of true multicellular forms by cell division and cell differentiation (for example, the seaweed *Ulva*)

Some multicellular marine chlorophytes are large and complex enough to qualify as seaweeds.

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.

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 amoebozoans and the opisthokonts.
  - The existence of each of these clades is strongly supported by molecular systematics, but the close relationship between the two clades is more controversial.
  - Support for the divergence is provided by myosin proteins and 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.
  - Scientists do not agree on the root of the eukaryote tree. If the root were known, scientists could infer characteristics of the common ancestor of all eukaryotes.
- In attempts to root the eukaryote tree, phylogenies based on different genes provide conflicting results.
  - In 2002, Thomas Cavalier-Smith and Alexandra Stechmann proposed 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 in the Excavates) diverged much later in the history of life.
- **Amoebozoans** form a monophyletic clade that includes gymnamoebas, entamoebas, and slime molds.
  - Amoebozoans include many species of amoebas with lobe or tube-shapes pseudopodia.
  - 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 distinctive life cycles: plasmoidal slime molds and cellular slime molds.
  - The **plasmoidal 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 diploid nuclei.
  - The diploid 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 a stage of the life cycle that produces 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 (“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 investigating 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 to 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 do all Dictyostelium cells not cheat?
  - In 2003, a group of scientists found a possible 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 recognition systems 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, which causes amebic dysentery, 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.

Concept 28.7 Protists play key roles in ecological relationships.

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.

Termites cause more than $3.5 billion in damage to wood homes in the United States.
  - Termites can eat wood because they have large populations of wood-digesting protists 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.

∞ The oomycete protist *Phytophthora ramorum* causes Sudden Oak Death, a disease that has killed more than 100,000 oak trees in coastal California.

∞ Many protists are important **producers**.

∞ In aquatic communities, the main producers are photosynthetic protists and prokaryotes.
  ○ Up to one-quarter of the world’s photosynthesis is carried out by diatoms, dinoflagellates, multicellular algae, and other protists.

∞ Because producers form the foundation of food webs, factors that affect producers have dramatic effects on communities.
  ○ If human activities increase the availability of limiting nutrients in water bodies, the abundance of photosynthetic protists may increase dramatically, affecting the entire aquatic community.