

Figure 23.6 Secondary endosymbiosis. The hypothesized process of several endosymbiotic events leading to the evolution of chlorarachniophytes is shown. In a primary endosymbiotic event, a heterotrophic eukaryote consumed a cyanobacterium. In a secondary endosymbiotic event, the cell resulting from primary endosymbiosis was consumed by a second cell. The resulting organelle became a plastid in modern chlorarachniophytes.

Several lines of evidence support that chlorarachniophytes evolved from secondary endosymbiosis. The chloroplasts contained within the green algal endosymbionts still are capable of photosynthesis, making chlorarachniophytes photosynthetic. The green algal endosymbiont also exhibits a vestigial nucleus. In fact, it appears that chlorarachniophytes are the products of an evolutionarily recent secondary endosymbiotic event. The plastids of chlorarachniophytes are surrounded by *four membranes*: The first two correspond to the inner and outer membranes of the photosynthetic cyanobacterium, the third corresponds to plasma membrane of the green alga, and the fourth corresponds to the vacuole that surrounded the green alga when it was engulfed by the chlorarachniophyte ancestor. In other lineages that involved secondary endosymbiosis, only *three membranes* can be identified around plastids. This is currently interpreted as a sequential loss of a membrane during the course of evolution.

The process of secondary endosymbiosis is not unique to chlorarachniophytes. Secondary plastids are also found in the Excavates and the Chromalveolates. In the Excavates, secondary endosymbiosis of green algae led to euglenid protists, while in the Chromalveolates, secondary endosymbiosis of red algae led to the evolution of plastids in dinoflagellates, apicomplexans, and stramenopiles.

23.2 Characteristics of Protists

By the end of this section, you will be able to do the following:

- Describe the cell structure characteristics of protists
- Describe the metabolic diversity of protists
- Describe the life cycle diversity of protists

There are over 100,000 described living species of protists, and it is unclear how many undescribed species may exist. Since many protists live as commensals or parasites in other organisms and these relationships are often species-specific, there is a huge potential for protist diversity that matches the diversity of their hosts. Because the name "protist" serves as a catchall term for eukaryotic organisms that are not animal, plant, or fungi, it is not surprising that very few characteristics are common to all protists. On the other hand, familiar characteristics of plants and animals are foreshadowed in various protists.

Cell Structure

The cells of protists are among the most elaborate of all cells. Multicellular plants, animals, and fungi are embedded among the protists in eukaryotic phylogeny. In most plants and animals and some fungi, complexity arises out of *multicellularity*, *tissue specialization*, and subsequent interaction because of these features. Although a rudimentary form of multicellularity exists among some of the organisms labelled as "protists," those that have remained unicellular show how complexity can evolve in the absence of true multicellularity, with the differentiation of cellular morphology and function. A few protists live as colonies that behave in some ways as a group of free-living cells and in other ways as a multicellular organism. Some protists are composed of enormous, multinucleate, single cells that look like amorphous blobs of slime, or in other cases, like ferns. In some species of

protists, the nuclei are different sizes and have distinct roles in protist cell function.

Single protist cells range in size from less than a micrometer to three meters in length to hectares! Protist cells may be enveloped by animal-like cell membranes or plant-like cell walls. Others are encased in glassy silica-based shells or wound with **pellicles** of interlocking protein strips. The pellicle functions like a flexible coat of armor, preventing the protist from being torn or pierced without compromising its range of motion.

Metabolism

Protists exhibit many forms of nutrition and may be aerobic or anaerobic. Those that store energy by photosynthesis belong to a group of *photoautotrophs* and are characterized by the presence of chloroplasts. Other protists are *heterotrophic* and consume organic materials (such as other organisms) to obtain nutrition. Amoebas and some other heterotrophic protist species ingest particles by a process called *phagocytosis*, in which the cell membrane engulfs a food particle and brings it inward, pinching off an intracellular membranous sac, or vesicle, called a food vacuole (Figure 23.7). In some protists, food vacuoles can be formed anywhere on the body surface, whereas in others, they may be restricted to the base of a specialized feeding structure. The vesicle containing the ingested particle, the phagosome, then fuses with a lysosome containing hydrolytic enzymes to produce a **phagolysosome**, and the food particle is broken down into small molecules that can diffuse into the cytoplasm and be used in cellular metabolism. Undigested remains ultimately are expelled from the cell via *exocytosis*.

Phagocytosis Food particle Food vacuole Exocytic vesicle containing undigested material Phagocytosis Pseudopods Lysosome containing digestive enzymes

Figure 23.7 Phagocytosis. The stages of phagocytosis include the engulfment of a food particle, the digestion of the particle using hydrolytic enzymes contained within a lysosome, and the expulsion of undigested materials from the cell.

Subtypes of heterotrophs, called saprobes, absorb nutrients from dead organisms or their organic wastes. Some protists can function as **mixotrophs**, obtaining nutrition by photoautotrophic or heterotrophic routes, depending on whether sunlight or organic nutrients are available.

Motility

The majority of protists are motile, but different types of protists have evolved varied modes of movement (Figure 23.8). Some protists have one or more flagella, which they rotate or whip. Others are covered in rows or tufts of tiny cilia that they beat in a coordinated manner to swim. Still others form cytoplasmic extensions called *pseudopodia* anywhere on the cell, anchor the pseudopodia to a substrate, and pull themselves forward. Some protists can move toward or away from a stimulus, a movement referred to as taxis. For example, movement toward light, termed phototaxis, is accomplished by coupling their locomotion strategy with a light-sensing organ.

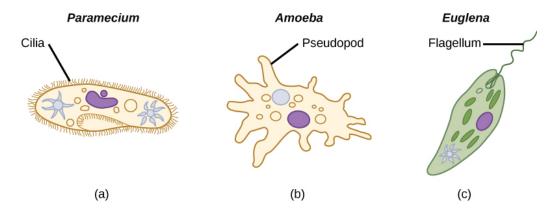


Figure 23.8 Locomotor organelles in protists. Protists use various methods for transportation. (a) *Paramecium* waves hair-like appendages called cilia to propel itself. (b) *Amoeba* uses lobe-like pseudopodia to anchor itself to a solid surface and pull itself forward. (c) *Euglena* uses a whip-like tail called a flagellum to propel itself.

Life Cycles

Protists reproduce by a variety of mechanisms. Most undergo some form of asexual reproduction, such as binary fission, to produce two daughter cells. In protists, binary fission can be divided into transverse or longitudinal, depending on the axis of orientation; sometimes *Paramecium* exhibits this method. Some protists such as the true slime molds exhibit multiple fission and simultaneously divide into many daughter cells. Others produce tiny buds that go on to divide and grow to the size of the parental protist.

Sexual reproduction, involving meiosis and fertilization, is common among protists, and many protist species can switch from asexual to sexual reproduction when necessary. Sexual reproduction is often associated with periods when nutrients are depleted or environmental changes occur. Sexual reproduction may allow the protist to recombine genes and produce new variations of progeny, some of which may be better suited to surviving changes in a new or changing environment. However, sexual reproduction is often associated with resistant **cysts** that are a protective, resting stage. Depending on habitat of the species, the cysts may be particularly resistant to temperature extremes, desiccation, or low pH. This strategy allows certain protists to "wait out" stressors until their environment becomes more favorable for survival or until they are carried (such as by wind, water, or transport on a larger organism) to a different environment, because cysts exhibit virtually no cellular metabolism.

Protist life cycles range from simple to extremely elaborate. Certain parasitic protists have complicated life cycles and must infect different host species at different developmental stages to complete their life cycle. Some protists are unicellular in the haploid form and multicellular in the diploid form, a strategy employed by animals. Other protists have multicellular stages in both haploid and diploid forms, a strategy called alternation of generations, analogous to that used by plants.

Habitats

Nearly all protists exist in some type of aquatic environment, including freshwater and marine environments, damp soil, and even snow. Several protist species are parasites that infect animals or plants. A few protist species live on dead organisms or their wastes, and contribute to their decay.

23.3 Groups of Protists

By the end of this section, you will be able to do the following:

- Describe representative protist organisms from each of the six presently recognized supergroups of eukaryotes
- Identify the evolutionary relationships of plants, animals, and fungi within the six presently recognized supergroups of eukaryotes
- Identify defining features of protists in each of the six supergroups of eukaryotes.

In the span of several decades, the Kingdom Protista has been disassembled because sequence analyses have revealed new genetic (and therefore evolutionary) relationships among these eukaryotes. Moreover, protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of