Chapter 28

Protists

Key Concepts

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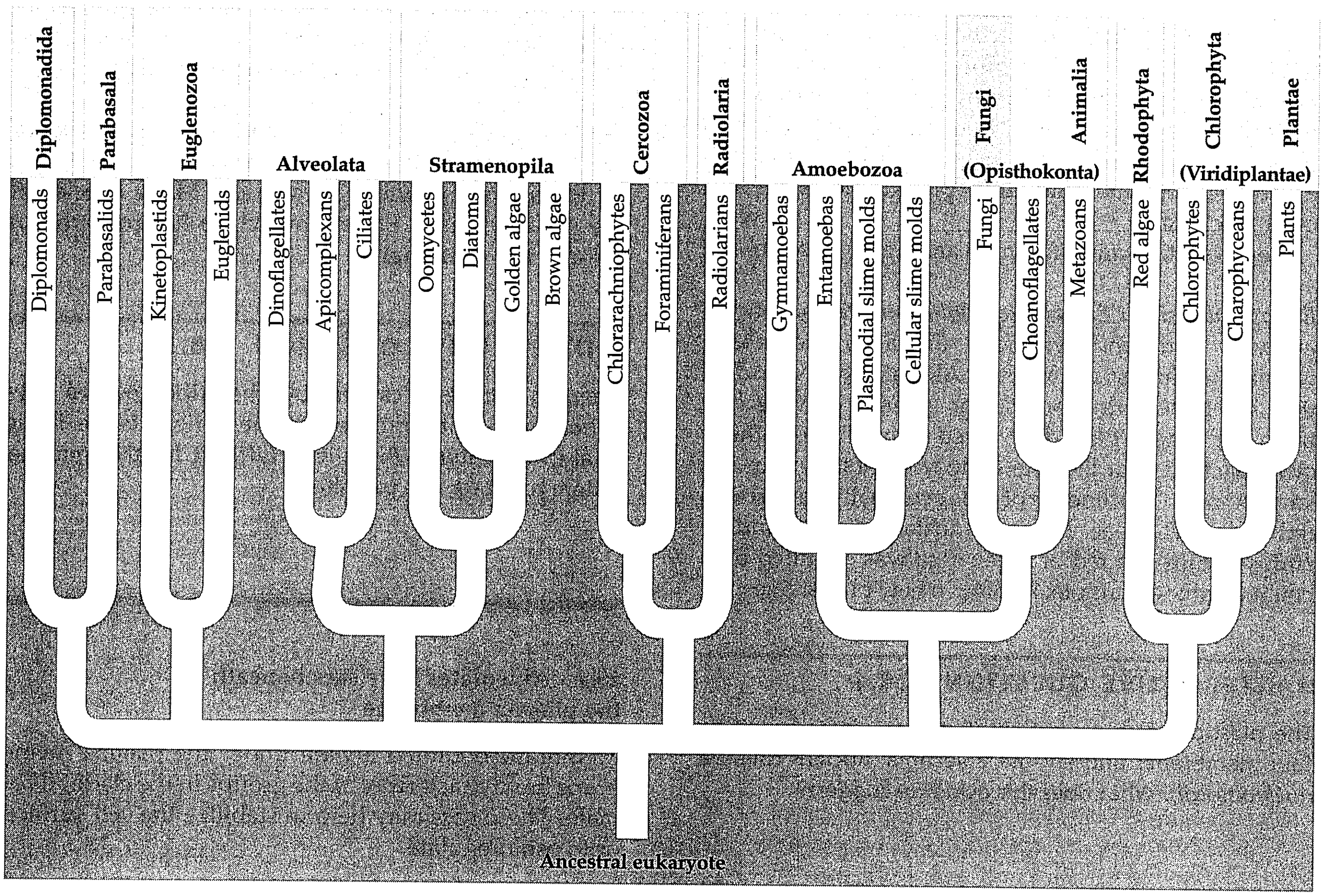
Framework



This chapter surveys the incredible diversity of protists—eukaryotes that are not fungi, plants, or animals. Below is a tentative phylogeny of eukaryotes.

Chapter Review

The traditional kingdom Protista has been abandoned; many lineages of this paraphyletic group may be recognized as their own kingdoms. The informal term *protist* is still used for eukaryotes that are not plants, animals, or fungi.

28.1 Protists are an extremely diverse assortment of eukaryotes

Protists include eukaryotic primarily unicellular organisms, with a few multicellular forms. Nutritionally, protists can be photoautotrophs, heterotrophs, or **mixotrophs,** which are both photosynthetic and heterotrophic. These modes of nutrition are spread throughout the various protist lineages. Based on their nutrition and not phylogeny, protists are often grouped for convenience into three categories: photosynthetic, plant-like protists (algae); ingestive, animal-like protists (protozoans); and absorptive, funguslike protists.

Protists abound almost anywhere there is water—they occupy freshwater, marine, and moist terrestrial habitats or live symbiotically within the bodies of hosts. They form an important part of plankton, the drifting community of mostly microscopic organisms found in bodies of water. Most aquatic food chains are based on phytoplankton, planktonic algae and cyanobacteria.

Reproduction and life cycles are highly diverse.

Endosymbiosis in Eukaryote Evolution Mitochondria evolved from endosymbiotic alpha proteobacteria within the earliest eukaryotes. All eukaryotes studied thus far have mitochondria, or signs of having had them in the past. Plastids evolved from photosynthetic cyanobacteria that became endosymbionts within eukaryotic cells. This lineage of cells eventually gave rise to red and green algae. In several instances of **secondary endosymbiosis,** a red or green alga was engulfed by a heterotrophic eukaryote, leading to new protist lineages.

INTERACTIVE QUESTION 28.1

The plastids of chlorarachniophytes are surrounded by four membranes and enclose a vestigial nucleus called a *nucleomorph.* What does this evidence suggest?

28.2 Diplomonads and parabasalids have modified mitochondria

Diplomonads and parabasalids are found in anaerobic environments. They do not have plastids and their reduced mitochondria lack DNA, electron transport chains, and enzymes of the citric acid cycle.

Diplomonads **Diplomonads,** such as the intestinal parasite *Giardia intestinalis,* have two nuclei and multiple flagella.

Parabasalids The **parabasalids** include protists called trichomonads, of which *Trichomonas vaginalis* is the best known. This common vaginal inhabitant moves with flagella and an undulating part of its plasma membrane.

28.3 Euglenozoans have flagella with a unique internal structure

The diverse clade Euglenozoa includes predatory heterotrophs, autotrophs, and pathogenic parasites, all of which have a spiral or crystalline rod inside their flagella. Most have disk-shaped mitochondrial cristae.

Kinetoplastids A single large mitochondrion containing a mass of DNA called a kinetoplast is characteristic of the group named **kinetoplastids.** These protists include free-living heterotrophs as well as a number of parasites of plants, animals, and other protists.

Euglenids The **euglenids** are characterized by one or two flagella that emerge from an anterior pocket and by the storage polymer paramylon. Many species of the photosynthetic *Euglena* switch to heterotrophy in the absence of sunlight.

INTERACTIVE QUESTION 28.2

Sleeping sickness, caused by the kinetoplastid *Trypanosoma* and transmitted by the African tsetse fly, is fatal if untreated. Why is it so difficult for the immune system to attack this parasite?

28.4 Alveolates have sacs beneath the plasma membrane

Membrane-bounded alveoli under the plasma membrane are characteristic of the groups in the clade Alveolata. These sacs may help to stabilize the cell surface or to osmoregulate.

Dinoflagellates Most species of **dinoflagellates** are unicellular, each with a characteristic shape. The beating of two flagella in perpendicular grooves on the cell surface between the internal cellulose plates of the cell produces a characteristic spinning movement.

Dinoflagellates make up a large proportion of marine and freshwater phytoplankton. Blooms of some populations are responsible for the often-harmful red tides. Photosynthesis by symbiotic dinoflagellates, living in small coral polyps, provides the main food source for coral reef communities.

Apicomplexans All **apicomplexans** are animal parasites, and most have complex life cycles that often include sexual and asexual stages and several host species. The parasites spread by tiny infectious cells called **sporozoites.** They have an apical complex of organelles specialized for invading host cells and a nonphotosynthetic plastid called an apicoplast.

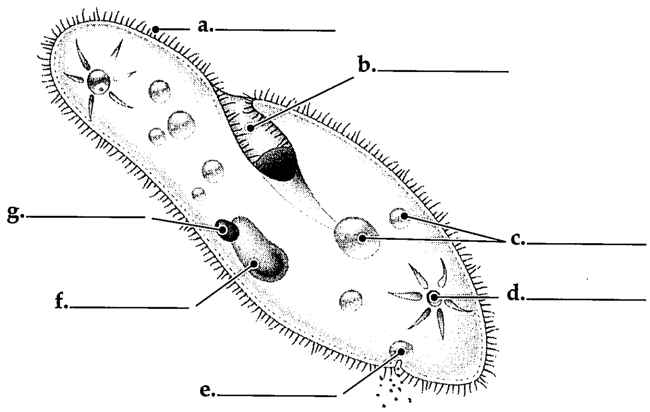
The control of malaria, caused by *Plasmodium,* is complicated by the multiple factors: development of insecticide resistance in *Anopheles* mosquitoes, which spread the disease; drug resistance in *Plasmodium;* the sequestering of the parasite within human liver and blood cells; and the ability of the parasite to change its surface proteins. The genome of *Plasmodium* has been sequenced and the expression of most genes has been tracked. These developments may help development of vaccines.

Ciliates These protists are characterized by the cilia they use to move and feed. Their numerous cilia, coordinated by a submembrane system of microtubules, may be widespread or clumped.

Ciliates have two types of nuclei: Large macronuclei control everyday functions of the cell, have multiple copies of the genome, and split during binary fission (asexual reproduction); small micronuclei are exchanged in a process called **conjugation,** which provides for genetic recombination. Foreign genetic material is also excised from the genome during conjugation.

■ INTERACTIVE QUESTION 28.3

Label the indicated structures in this diagram of a Paramecium. To which group and protist clade does this organism belong?



28.5 Stramenopiles have "hairy" and smooth flagella

The clade Stramenopila includes several heterotrophic groups and various groups of algae, all characterized by hairlike projections on a flagellum. In some cases, only reproductive cells are flagellated, having one smooth and one "hairy" flagellum.

Oomycetes (Water Molds and Their Relatives) **Oomycetes** include water molds, white rusts, and downy mildews. Although many resemble fungi in appearance, oomycetes have cell walls made of cellulose, as well as a predominant diploid stage and flagellated cells in their life cycles. Molecular systematics confirms that oomycetes and fungi are not closely related.

The large egg cell of a water mold is fertilized by a smaller sperm nucleus. Zygotes, following dormancy, germinate to form hyphae, which are tipped by zoosporangia that asexually produce biflagellated zoospores. Water molds are important decomposers in aquatic ecosystems. White rusts and downy mildews can be destructive parasites of land plants. Genetic studies of *Phytophthora infestans,* the oomycete that causes potato late blight, indicate that it has acquired genes in recent decades that make it more aggressive and resistant to pesticides.

Diatoms **Diatoms** (baccilariophytes) are a major component of marine and freshwater phytoplankton with unique, protective, boxlike silica walls. These unicellular protists usually reproduce asexually, although eggs and sperm may be produced. Food reserves are in the form of laminarin, a glucose polymer. Massive quantities of fossilized diatom walls make up diatomaceous earth. Diatoms may make a contribution to the field of nanotechnology as nanoengineers study the self-assembly of their intricate shells.

Golden Algae The color of **golden algae** (chrysophytes) results from yellow and brown carotenoids. Most golden algae are unicellular, biflagellated, and found among marine and freshwater plankton. Some species are mixotrophic. Many species form long-lasting resistant cysts when population densities become too high.

Brown Algae The mostly marine **brown algae** (phaeophytes) include some of the largest and most complex algae. Their color is due to accessory pigments in their plastids, which are homologous to the plastids of golden algae and diatoms.

Large marine brown algae (and some red and green algae) are called seaweeds. Some seaweeds have tissues and organs that are analogous to those found in plants. Seaweeds may have a plantlike **thallus,** or body, consisting of a rootlike **holdfast** and a stemlike **stipe** that supports leaflike **blades.** Some brown algae have floats, which keep the photosynthesizing blades near the surface. The giant, fast-growing brown algal kelps live in deeper waters. Humans use some seaweeds for food and as thickeners in processed foods.

Some algae have an **alternation of generations.** The multicellular, haploid gametophyte produces gametes. After syngamy, the diploid zygote grows into the multicellular sporophyte, which then produces spores by meiosis. The gametophyte and sporophyte may be similar in appearance **(isomorphic)** or distinct **(heteromorphic).**

■ INTERACTIVE QUESTION 28.4

What adaptations help brown algal seaweeds inhabit intertidal zones?

28.6 Cercozoans and radiolarians have threadlike pseudopodia

Amoebas, originally defined on the basis of their cellular extensions called **pseudopodia,** are spread across many eukaryotic taxa. Cercozoa, a newly recognized clade, contains species of amoebas that have threadlike pseudopodia. Chlorarachniophytes and foraminiferans are cercozoans; radiolarians, also with threadlike pseudopodia, are closely related.

Foraminiferans (Forams) **Foraminiferans,** or **forams,** are known for their porous, multichambered shells, called **tests,** made of organic material and calcium carbonate. Pseudopodia extending through the pores function in swimming, test formation, and feeding. Many forams obtain nourishment from symbiotic algae.

Radiolarians Slender pseudopodia called axopodia help these organisms phagocytize microscopic food organisms. **Radiolarians** are primarily marine and have delicate silica shells.

■ INTERACTIVE QUESTION 28.5

How are foram fossils used?

28.7 Amoebozoans have lobe-shaped pseudopodia

Gymnamoebas Most amoebas of the diverse group gymnamoebas are found free-living in freshwater, marine, or soil habitats, where they consume bacteria and other protists.

Entamoebas Amoebas of the genus *Entamoeba* are parasites of vertebrates and some invertebrates. *E. histolytica* causes amebic dysentery in humans.

Slime Molds The resemblance of the slime molds (or mycetozoans) to fungi is the result of convergent evolution to similar lifestyles. Molecular comparisons place them in the clade Amoebozoa.

Plasmodial Slime Molds **Plasmodial slime molds** engulf food particles by phagocytosis as they grow through leaf litter or rotting logs. This multinucleate mass called a **plasmodium** is the feeding stage. Under harsh conditions, sporangia on erect stalks produce resistant spores by meiosis. Spores germinate, the amoeboid or flagellated haploid cells fuse, and the diploid nucleus repeatedly divides to form a new plasmodium.

Cellular Slime Molds During the feeding stage of the life cycle, **cellular slime molds** consist of haploid solitary amoeboid cells. As food is depleted, the individual cells congregate into a mass. Asexual fruiting bodies produce resistant spores. In sexual reproduction, two amoebas fuse to form a zygote that develops into a giant cell enclosed in a protective wall. Following meiosis and mitosis, haploid amoebas are released. The cellular slime mold *Dictyostelium discoideum* is an experimental model for studying the evolution of multicellularity. Research indicates that a recognition system allows noncheater cells to aggregate differentially from "cheater" cells (mutant cells that always become spore cells).

■ INTERACTIVE QUESTION 28.6

Compare the following aspects of the life cycles of plasmodial slime molds and cellular slime molds.

Phylum	Haploid or Diploid	Common Body Form	Gametes or Sexual Cells
Plasmodial slime molds	a.	b.	c.
Cellular slime molds	d.	e.	f.

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

Descendants of the heterotrophic protist that acquired a cyanobacterium endosymbiont evolved into red algae and green algae more than a billion years ago. Land plants arose from the green algal lineage at least 475 million years ago.

Red Algae The accessory pigment phycoerythrin produces the color of **red algae,** and allows them to absorb the wavelengths of light that penetrate into deep water. Most red algae species are marine and multicellular, often with filamentous, delicately branched thalli. Some coralline algae have cell walls hardened by calcium carbonate and are members of coral reef communities. Alternation of generations is common, although life cycles are diverse and they have no flagellated stages in their life cycle.

Green Algae The chloroplasts of **green algae** resemble those of plants, and molecular systematics indicates that green algae and plants share a common ancestor. Some systematists favor including green algae in an extended kingdom, Viridiplantae. The two main green algal groups are chlorophytes and charophyceans. The charophyceans are very closely related to land plants.

Most chlorophytes live in fresh water, although many are marine. Unicellular forms may be planktonic, inhabitants of damp soil, symbionts in other eukaryotes, or mutualistic partners with fungi—forming associations known as lichens.

Size and complexity have increased in the green algae in three ways: the formation of colonies; repeated nuclear divisions to produce multinucleated filaments; and cell division and differentiation to produce true multicellular forms. Some large marine forms are considered seaweeds.

The life cycles of most green algae include sexual (with biflagellated gametes) and asexual stages. Some multicellular green algae have an alternation of generations, as in the seaweed *Ulva.*

Word Roots

-phyte = plant (*gametophyte:* the multicellular haploid form in organisms undergoing alternation of generations)

con- = with, together (*conjugation:* in ciliates, the transfer of micronuclei between two cells that are temporarily joined)

hetero- = different; **-morph** = form (*heteromorphic:* a condition in the life cycle of all modern plants in which the sporophyte and gametophyte generations differ in morphology)

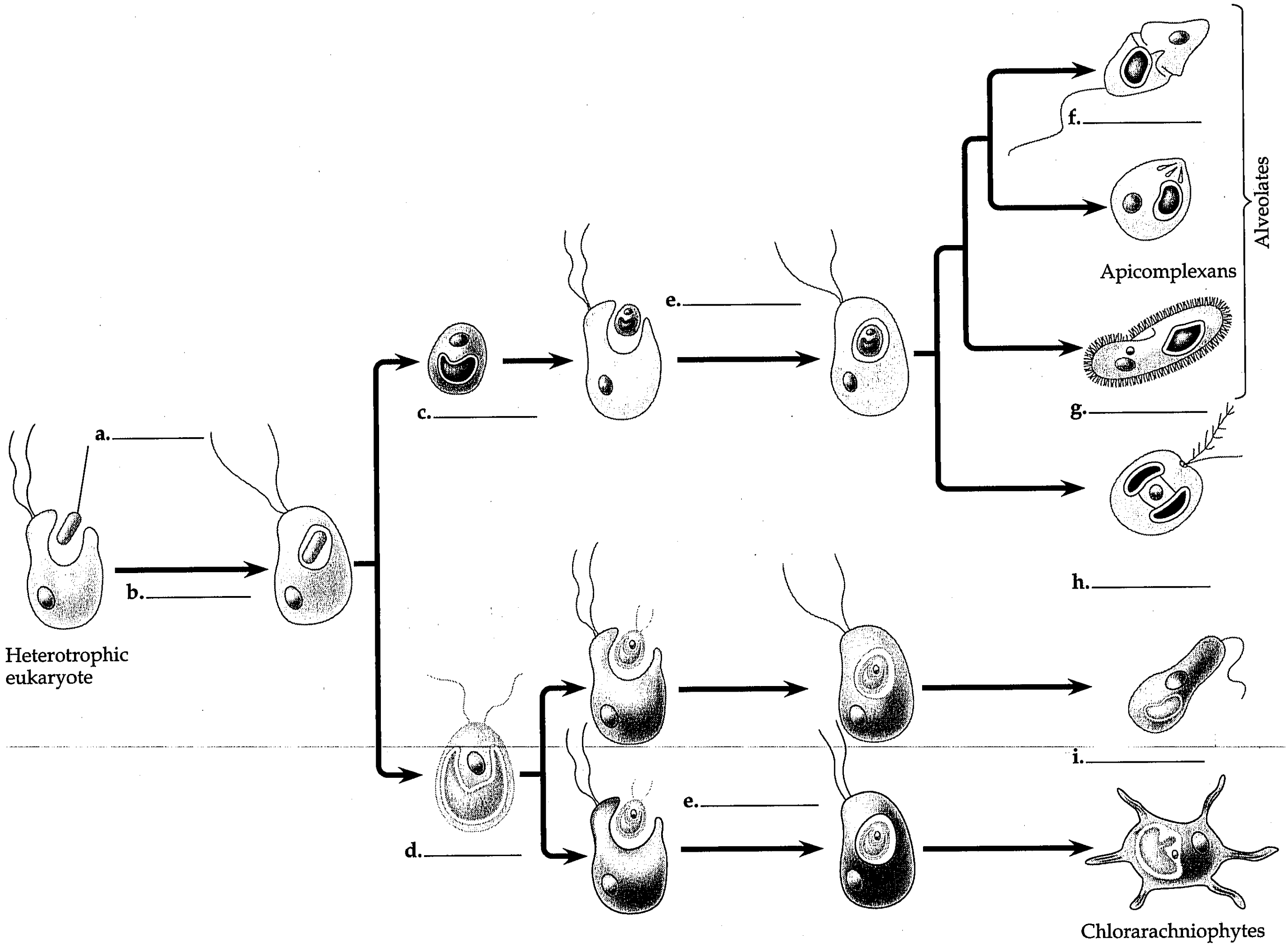
iso- = same (*isomorphic:* alternating generations in which the sporophytes and gametophytes look alike, although they differ in chromosome number)

pseudo- = false; **-podium** = foot (*pseudopodium:* a cellular extension of amoeboid cells used in moving and feeding)

thallos- = sprout (*thallus:* a seaweed body that is plantlike but lacks true roots, stems, and leaves)

Structure Your Knowledge

1. Evidence indicates that all plastids evolved from a cyanobacterium that was engulfed by an ancestral heterotrophic eukaryote. Fill in the blanks in the figure below, which diagrams the diversification of this ancestral eukaryote into red algae and green algae as well as several instances of secondary endosymbiosis that led to various protist groups.



Test Your Knowledge

MATCHING: *Match the protist clades with their characteristics and examples.*

_________ **1.** modified mitochondria, two nuclei; *Giardia*

_________ **2.** plant-type chloroplasts; *Chlamydomonas, Ulva*

_________ **3.** lobe-shaped pseudopodia; free-living amoeba, parasites, slime molds

_________ **4.** phycoerythrin, no flagellated stage; red algae

_________ **5.** hairy and smooth flagella; water molds, diatoms, golden and brown algae

_________ **6.** amoebas with threadlike pseudopodia; forams, radiolarians

_________ **7.** subsurface sacs; dinoflagellates, apicomplexans, ciliates

_________ **8.** flagella with spiral or crystalline rod; *Trypanosoma, Euglena*

_________ **9.** undulating membrane, modified mitochondria; *Trichomonas*

A. Alveolata

B. Amoebozoa

C. Cercozoa & Radiolaria

D. Chlorophyta

E. Diplomonadida

F. Euglenozoa

G. Parabasala

H. Rhodophyta

I. Stramenopila

MULTIPLE CHOICE: *Choose the one best answer.*

1. Mixotrophs are
   a. plasmodial slime molds.
   b. cellular slime molds.
   c. gametophyte and sporophyte generations that differ in morphology.
   d. organisms that can be both heterotrophic and autotrophic.
   e. organisms that can be both parasitic and free-living.

2. Phytoplankton
   a. form the basis of most marine food chains.
   b. include the multicellular green, red, and brown algae.
   c. are mutualistic symbionts that provide food for coral reef communities.
   d. are unicellular heterotrophs that float near the ocean surface.
   e. Both a and d are correct.

3. According to the theory of secondary endosymbiosis,
   a. multicellularity evolved when primitive cells incorporated prokaryotic cells that then took on specialized functions.
   b. the symbiotic associations found in lichens resulted from the incorporation of algal protists into the ancestors of fungi.
   c. cells that had obtained their plastids through endosymbiosis were engulfed and themselves became plastids in heterotrophic eukaryotic cells.
   d. the infoldings and specializations of the plasma membrane led to the evolution of the endomembrane system.
   e. the nuclear membrane evolved first, then mitochondria, and then plastids.

4. The diplomonads and parabasalids are unique among eukaryotes in that
   a. they lack nuclear membranes, even though diplomonads have two nuclei.
   b. they lack ribosomes.
   c. they lack plastids, and all other protist lineages have at least some members that are autotrophic.
   d. they have modified mitochondria that lack electron transport chains and Krebs-cycle enzymes.
   e. they were an early branch from the bacteria rather than the archaea.

5. Genetic variation is generated in the ciliate *Paramecium* when
   a. a micronucleus replicates its genome many times and becomes a macronucleus.
   b. zoospores, which are gametes, fuse.
   c. micronuclei are exchanged in conjugation.
   d. mutations occur in the many copies of the genome contained in the macronucleus and are passed on to offspring.
   e. plasmids are exchanged in conjugation.

6. The Chlorophyta, or green algae, are believed to share a common ancestor with plants because
   a. they are the only multicellular algal protists.
   b. they do not have flagellated gametes.
   c. they are the only protists whose plastids evolved from cyanobacteria.
   d. their chloroplasts are similar in ultrastructure and pigment composition to those of plants.
   e. they are the only algae that exhibit alternation of generations.

7. Which of the following is *not* true of seaweeds?
   a. They are found in the red, green, and brown algal groups.
   b. They have true roots that anchor them tightly to withstand the turbulence of waves.
   c. They are a source of food and commercial products.
   d. The gel-forming polysaccharides in their cell walls protect them from the abrasive action of waves.
   e. They are multicellular photoautotrophs.

8. Examples of mutualistic symbiotic relationships include
   a. dinoflagellates producing red tides.
   b. dinoflagellates living within cnidarians in coral reefs.
   c. sporozoans in their multiple hosts.
   d. lichens.
   e. both b and d.

9. The protist clade Alveolata includes
   a. the diatoms, golden algae, and brown algae.
   b. the dinoflagellates, apicomplexans, and ciliates.
   c. the slime molds and water molds that are the ancestors of fungi.
   d. the diplomonads and parabasalids.
   e. the amoebas and other protists that move using pseudopods.

10. Which of the following is *not* an autotroph?
   a. dinoflagellate
   b. diatom
   c. kinetoplastid
   d. brown algae
   e. chlorarachniophyte