CHAPTER 28
THE ORIGINS OF EUKARYOTIC DIVERSITY

OUTLINE

I. Introduction to the Protists
  A. Protists are the most diverse of all eukaryotes
  B. Symbiosis was involved in the genesis of eukaryotes from prokaryotes

II. Protist Systematics and Phylogeny
  A. Monophyletic taxa are emerging from modern research in protist systematics
  B. Members of candidate kingdom Archaezoa lack mitochondria and may represent early eukaryotic lineages
  C. Candidate kingdom Euglenozoa includes both autotrophs and heterotrophic flagellates
  D. Surface cavities (alveoli) are diagnostic of candidate kingdom Alveolata
  E. A diverse assemblage of unicellular eukaryotes move by means of pseudopodia
  F. Slime molds have structural adaptations and life cycles that enhance their ecological role as decomposers
  G. Diatoms, golden algae, brown algae, and water molds are members of the candidate kingdom Stramenopila
  H. Structural and biochemical adaptations help seaweeds survive and reproduce at the ocean's margins
  I. Some algae have life cycles with alternating multicellular haploid and diploid generations
  J. Red algae (candidate kingdom Rhodophyta) lack flagella
  K. Green algae and plants probably had a common photoautotrophic ancestor
  L. Multicellularity originated independently many times

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

1. List the characteristics of protists.
2. Explain why some biologists prefer to use the term *undulipodia* for eukaryotic flagella and cilia.
3. Briefly summarize and compare the two major models of eukaryotic origins, the autogenous hypothesis and the endosymbiotic hypothesis.
4. Provide three major lines of evidence for the endosymbiotic hypothesis.
5. Explain why some critics are skeptical about the bacterial origins for chloroplasts and mitochondria.
6. Explain why modern biologists recommend expanding the original boundaries of the Kingdom Protista.

7. Explain what is meant by the statement that the Kingdom Protista is a polyphyletic group.
8. List five candidate kingdoms of protists and describe a major feature of each.
9. Describe amoeboid movement.
10. Outline the life cycle of *Plasmodium.*
11. Indicate the organism that causes African sleeping sickness and explain how it is spread and why it is difficult to control.
12. Describe the function of contractile vacuoles in freshwater ciliates.
13. Distinguish between macronuclei and micronuclei.
14. Using diagrams, describe conjugation in *Paramecium caudatum.*
15. Explain how accessory pigments can be used to classify algae and determine phylogenetic relationships among divisions.
16. Distinguish among the following algal groups based upon pigments, cell wall components, storage products, reproduction, number and position of flagella, and habitat:
    a. Dinoflagellata
    b. Bacillariophyta
    c. Chrysophyta
    d. Phaeophyta
    e. Rhodophyta
    f. Chlorophyta
17. Describe three possible evolutionary trends that led to multicellularity in the Chlorophyta.
18. Outline the life cycles of *Chlamydomonas*, *Ulva,* and *Laminaria* and indicate whether the stages are haploid or diploid.
19. Distinguish between isogamy and oogamy; sporophyte and gametophyte; and isomorphic and heteromorphic generations.
20. Compare the life cycles of plasmodial and cellular slime molds and describe the major differences between them.
21. Provide evidence that the oomycetes are not closely related to true fungi.
22. Give examples of oomycetes and describe their economic importance.
23. Explain the most widely accepted hypothesis for the evolution of multicellularity.

KEY TERMS

acritarchs	apicomplexans	Stramenopila	sporophyte
protozoa	sporozoites	diatoms	gametophyte
algae	ciliates	golden algae	heteromorphic
syngamy	conjugation	water mold	isomorphic
plankton	pseudopodia	white rust	red algae
serial endosymbiosis	detritus	brown algae	green algae
flagellates	amoebas	thallus	lichens
Euglenozoa	heliozoans	holdfast	diatoms
euglenoids	radiolarians	stipe	laminarin
kinetoplastids	forams	blades	isogamy
Alveolata	plasmodial slime molds	alternation of generations	anisogamy
dinoflagellates	cellular slime molds		oogamy

LECTURE NOTES

Using lenses he developed, Anton von Leeuwenhoek (17th century) was the first to describe the diversity of microscopic protists.

I. Introduction to the Protists

Protists are the earliest eukaryotic descendants of prokaryotes.

Protists arose a billion years before the emergence of other eukaryotes such as plants, fungi, and animals.

Precambrian rock dated to about 2.1 billion years of age contain *acritarchs*, the oldest commonly accepted fossils of protists.

- Remnants of the proper size and structure to be ruptured coats of cysts similar to those of extant protists.
- Adaptive radiation produced a diversity of protists over the next billion years.
- The variations present in these organisms were representative of the structure and function possible in eukaryotic cells.

A. Protists are the most diverse of all the eukaryotes

Because protists vary so much in structure and function, more so than any other group, few other general characteristics besides their being eukaryotes can be cited without exception.

There are about 60,000 extant species of protists.

- Most are unicellular, but colonial forms and even some simple multicellular forms exist.
- Their eukaryotic structure makes even the simplest protist more complex than prokaryotes.
- Primal eukaryotes not only gave rise to current protists, but also to plants, fungi, and animals.

Protists are considered the simplest eukaryotic organisms because most are unicellular.

- At the cellular level, protists are extremely complex.
- The unicellular protist is not analogous to a single plant or animal cell, but is a complete organism.
- The single cell of a protist must perform all the basic functions carried out by the specialized cells of plants and animals.

Protists are metabolically divers, and as a groups, they are the most nutritionally diverse of all eukaryotes.

- Almost all protists are aerobic, using mitochondria for cellular respiration.
- Anaerobic forms lack mitochondria and live in anaerobic environments or have mutualistic respiring bacteria.
- Some may be photoautotrophic, heterotrophic, or mixotrophic (combining photosynthesis and heterotrophy).
- The different modes of nutrition are used to separate protists into three categories: photosynthetic forms are typically referred to as algae, ingestive forms as protozoa, and absorptive protists. (Although the terms protozoa and algae are commonly used, they have no basis in phylogeny and no significance in taxonomy.)

Most protists have flagella or cilia (not homologous to prokaryotic flagella) at some time in life cycle.

- Eukaryotic cilia and flagella are extensions of the cytoplasm. (Prokaryotic flagella are attached to the cell surface.)
- These cilia and flagella have the same basic 9 + 2 microtubular ultrastructure, but cilia are shorter and more numerous.

The life cycles of protists are quite variable.

- Unique mitotic divisions occur in many groups.

- Some can reproduce asexually
- Some can also reproduce sexually or at least use *syngamy* (fusion of gametes) to trade genes between asexual reproductive episodes.
- Some form resistant cysts when stressed by harsh environments.

Protists are found in almost all moist environments: the seas, freshwater systems, and moist terrestrial habitats such as damp soil and leaf litter.

- They are important components of marine and freshwater plankton.
  - *Plankton* = Communities of organisms, mostly microscopic, that drift passively or swim weakly near the surface of oceans, ponds, and lakes
- Many are bottom dwellers in freshwater and marine habitats where they attach to rocks or live in the sand and silt.
- Photosynthetic species form mats at the still-water edges of lakes and ponds where they provide a food source for other protists.

Some protists are free-living, while others are symbiotic species found in the body fluids, tissues, or cells of host organisms.

- The nature of symbiosis ranges from mutualism to parasitism and many are important pathogens.

B. Symbiosis was involved in the genesis of eukaryotes from prokaryotes

There is a greater difference between prokaryotic and eukaryotic cells than between the cells of plants and animals.

During the genesis of eukaryotes, the following cellular structures and process unique to eukaryotes arose:

- A membrane-bound nucleus
- Mitochondria, chloroplasts, and the endomembrane system
- A cytoskeleton
- 9 + 2 flagella
- Multiple chromosomes consisting of linear DNA molecules compactly arranged with proteins
- Life cycles that involve mitosis, meiosis, and sex

The small size and simpler construction of the prokaryotic cell has many advantages but also imposes a number of limitations.

> Examples:
> - The number of metabolic activities that can occur at one time is smaller.
> - The smaller size of the prokaryotic genome limits the number of genes which code for enzymes controlling these activities.

While prokaryotes are extremely successful, natural selection resulted in increasing complexity in some groups, trending toward:

- Multicellular forms, such as the cyanobacteria, which have different cells types with specialized functions
- Evolution of complex prokaryotic communities in which each species benefits from the metabolic activities of other species
- Compartmentalization of different functions within single cells

  ⇒ The first eukaryotes resulted from this solution.

The evolution of the compartmentalized nature of eukaryotic cells may have resulted from two processes.

1. Specialization of plasma membrane invaginations

- Invaginations and subsequent specializations may have given rise to the nuclear envelope, endoplasmic reticulum, Golgi apparatus, and other components of the endomembrane system (see Campbell, Figure 28.2a).

2. Endosymbiotic associations of prokaryotes may have resulted in the appearance of some organelles.
   - Mitochondria, chloroplasts, and some other organelles evolved from prokaryotes living within other prokaryotic cells.

The hypothesis of *serial endosymbiosis* proposes that certain prokaryotic species, called *endosymbionts,* lived within larger prokaryotes. This theory was developed extensively by Lynn Margulis of University of Massachusetts (see Campbell, Figure 28.2b).

- Hypothesis focuses mainly on mitochondria and chloroplasts.
- Chloroplasts are descended from endosymbiotic photosynthesizing prokaryotes, such as cyanobacteria, living in larger cells.
- Mitochondria are postulated to be descendants of prokaryotic aerobic heterotrophs.
  - ⇒ May have been parasites or undigested prey of larger prokaryotes.
  - ⇒ The association progressed from parasitism or predation to mutualism.
  - ⇒ As the host and endosymbiont became more interdependent, they integrated into a single organism.
- Many extant organisms are involved in endosymbiotic relationships.

Evidence for the endosymbiotic origin of mitochondria and chloroplasts includes the similarities between these organelles and prokaryotes.

- Are of appropriate size to be descendants of bacteria
- Have inner membranes containing several enzymes and transport systems similar to those on prokaryotic plasma membranes
- Replicate by splitting processes similar to binary fission present in prokaryotes
- Have DNA that is circular and not associated with histones or other proteins, as in prokaryotes
- Contain their own tRNA, ribosomes, and other components for DNA transcription and translation into proteins
- Chloroplasts have ribosomes more similar to prokaryotic ribosomes (in size, biochemical characteristics, and antibiotic sensitivity) than to eukaryotic ribosomes.
- Mitochondrial ribosomes vary, but are also more similar to prokaryotic ribosomes.

Molecular systematics lends even more evidence to support the endosymbiotic theory.

- The rRNA of chloroplasts is more similar in base sequence to RNA from certain photosynthetic eubacteria than to rRNA in eukaryotic cytoplasm.
  - ⇒ Chloroplast rRNA is transcribed from genes in the chloroplast while eukaryotic rRNA is transcribed from nuclear DNA.
- Mitochondrial rRNA also has a base sequence which supports a prokaryotic origin.

A comprehensive theory for the origin of eukaryotic cells must also include the evolution of:

- 9 + 2 flagella and cilia, which are analogous, not homologous, to prokaryotic flagella.
- The origins of mitosis and meiosis which also utilize microtubules.
  - ⇒ Mitosis made it possible for large eukaryotic genomes to be reproduced.

⇒ Meiosis is essential to sexual reproduction.

⇒ Protists have the most varied sexual life histories of the eukaryotes.

II. Protist Systematics and Phylogeny

A. Monophyletic taxa are emerging from modern research in protist systematics

Classification schemes and the phylogeny they reflect are based on available information.

- These presentations are tentative and often change as additional information becomes available.

In 1969, Robert H. Whittaker popularized the five-kingdom taxonomic system and placed only unicellular eukaryotes in the kingdom Protista.

- During the 1970s and 1980s, the Kingdom Protista was expanded to include some multicellular organisms earlier classified as either plants or fungi.
- Studies of cell ultrastructure and life cycle details formed the basis for such taxonomic transfers.
  - ⇒ Seaweeds were found to exhibit characteristics which indicated a closer relationship with certain algae than to plants.
  - ⇒ Slime molds and water molds were found to be more closely related to certain protozoans than to fungi.
- The tendency was to place all eukaryotes that could not comfortably be fitted into the plants, fungi, or animals into this kingdom.

Molecular systematics, especially rRNA comparisons, have stimulated three main trends in eukaryotic systematics and taxonomy over the last decade.

1. Reassessment of the number and membership of protistan phyla
   - The phylum Sarcodina once housed all unicellular organisms that possessed pseudopodia, current classification splits these organisms into several phyla.
2. Arrangement of the phyla into a cladogram based largely on what molecular methods and cell structure comparisons reveal about evolutionary relationships of protists.
3. Reevaluation of the five-kingdom system and debate about the addition of new kingdoms.

At present, most systematists working on the origins of eukaryotes consider the Kingdom Protista and the five-kingdom system obsolete. This is based on the observation that the Kingdom Protista is polyphyletic.

The organization of protists into three groups as in the eight-kingdom system is still polyphyletic.

In light of current research, the organization of protists into five groups, candidate kingdoms (Archaezoa, Euglenozoa, Alveolata, Stramenopila, and Rhodophyta), is indicated. All but one of the five candidate kingdoms, Archaezoa, is monophyletic.

B. Members of candidate kingdom Archaezoa lack mitochondria and may represent early eukaryote lineages

An ancient lineage of eukaryotes branched away from the eukaryotic tree perhaps as early as two billion years ago (see Campbell, Figure 28.2). This group is referred to as the Archaezoa and contains only a few phyla.

- These organisms lack mitochondria and plastids and have relatively simple cytoskeletons.
- Their ribosomes have some characteristics more closely aligned with prokaryotes than with eukaryotes; rRNA sequencing indicates a closer relationship.

Giardia lamblia, a diplomonad, is a modern representative of the archaezoa (see Campbell, Figure 28.4).

- It is a flagellated, unicellular eukaryote that is parasitic in the human intestine.
- It is most commonly transmitted in the cyst form through water contaminated with human feces.

Giardia's importance to evolutionary biologists is related more to its characteristics than to its role as a human parasite.

- Diplomonads have two separate haploid nuclei which produce a "face-like" appearance.
  - Dual nuclei may be a vestige of early eukaryotic evolution.
- Prokaryotes have haploid genomes and some researchers postulate that early eukaryotes had a single haploid nucleus bounded by a nuclear envelope.
- In most modern eukaryotes, the diploid stages in the life cycle result from the fusion of haploid nuclei which form the diploid nucleus.
  - Diplomonads may represent an early mechanism in the evolution of diploidy in eukaryotes.

If the diplomonads diverged from the eukaryotic lineage before the process of nuclear fusion and meiosis evolved, their dual nuclei may be a clue to the past.

- This coupled with the absence of mitochondria in this group and other archaezoans is consistent with an origin occurring before the endosymbiotic relationships that gave rise to mitochondria in aerobic species.

C. Candidate kingdom Euglenozoa includes both autotrophic and heterotrophic flagellates

Protists with flagella are often informally referred to as *flagellates*.

Two groups of flagellates make up the monophyletic candidate kingdom Euglenozoa: euglenoids and kinetoplastids.

Euglenoids (e.g., *Euglena*) have the following characteristics:

- Anterior pocket or chamber from which one or two flagella project
- Production of paramylum, a glucose polymer
- Varying modes of nutrition depending on species
  - Autotrophic
  - Mixotrophic - chiefly autotrophic with some requirement for organic molecules (e.g., vitamins)
  - Heterotrophic

Kinetoplastids have the following characteristics:

- Possess a single large mitochondrion associated with a unique organelle, the kinetoplast, that contains extranuclear DNA
- Symbiotic; some are pathogenic to hosts
  - Species of *Trypanosoma* cause African sleeping sickness and are spread by the bite of the tsetse fly (see Campbell, Figure 28.5).

D. Subsurface cavities (alveoli) are diagnostic of candidate kingdom Alveolata

This candidate kingdom encompasses photosynthetic flagellates (dinoflagellates), a group of parasites (apicomplexans), and a distinctive group that move by means of cilia (ciliates).

All alveolates have small membrane-bound cavities, or alveoli, under their cell surfaces.

The function of alveoli is unknown; however, they may help to:

- Stabilize the cell surface

- Regulate water and ion transport

1. Dinoflagellates

Dinoflagellates are components of phytoplankton that provides the foundation of most marine food chains.

- May cause *red tides* by explosive growth (bloom)
  - ⇒ These dinoflagellates produce a toxin that is concentrated by invertebrates, including shellfish.
  - ⇒ The toxin is dangerous to humans consuming shellfish and causes the condition known as paralytic shellfish poisoning.
- Most are unicellular, some are colonial
- Cell surface is reinforced by cellulose plates with flagella in perpendicular grooves, creating its whirling movement and resulting in a characteristic shape (see Campbell, Figure 28.6)
- Some live as photosynthetic symbionts of the cnidarians that build coral reefs
- Some lack chloroplasts and live as parasites; a few carnivorous species are known
- Have brownish plastids containing chlorophyll *a*, chlorophyll *c* and a mix of carotenoids, including *peridinin* (found only in this phylum)
- Food is stored as starch
- Chromosomes lack histones and are always condensed
- Has no mitotic stages
- Kinetochores are attached to the nuclear envelope and chromosomes distributed to daughter cells by the splitting of the nucleus

2. Apicomplexans

All member of apicomplexans (formerly called sporozoans) are parasites of animals.

- The infectious cells produced in the life cycle are called *sporozoites*.
- The apex of sporozoites has organelles for penetrating host cells and tissues; the phylum is named for these apical organelles.
- Life cycles are intricate having both sexual and asexual reproduction, often requiring two or more different host species.

Several species of *Plasmodium* cause malaria (see Campbell, Figure 28.7).

- *Anopheles* mosquitoes serve as the intermediate host and humans as the final host.
- The incidence of malaria was greatly reduced by the use of insecticides against mosquitoes in the 1960s.
- More recently, incidence of malaria has increased due to insecticide-resistant strains of mosquitoes and drug-resistant strains of *Plasmodium*.
  - ⇒ This is a relatively common (300 million new cases per year) and potentially fatal tropical disease resulting in about two million deaths each year.

There has been little success in developing a vaccine against *Plasmodium*.

- The human immune system has little effect on the parasite.
  - ⇒ *Plasmodium* spends most of its life cycle in blood cells or liver cells.
  - ⇒ *Plasmodium* also has the ability to alter its surface proteins.
- The most promising treatment may lie in inhibiting the function of one or more processes in a *Plasmodium* plastid.

3. **Ciliates (Ciliophorans)**

Species within this group use cilia to move and feed.

- Most ciliates exist as solitary cells in fresh water.
- Cilia are relatively short and beat in synchrony.
- The cilia are associated with a submembranous system that coordinates the movement of thousands of cilia.
- Cilia may be dispersed over surface, or clustered in fewer rows or tufts.
- Some species move on leg-like *cirri* (many cilia bonded together).
- Other species have rows of tightly packed cilia that function together as locomotor membranelles (e.g., *Stentor*).

Ciliates are among the most complex of all cells (see Campbell, Figure 28.8).

They possess two types of nuclei: one large macronucleus and from one to several small micronuclei.

- Characteristics of the macronucleus:
  - ⇒ It is large and has over 50 copies of the genome.
  - ⇒ Genes are packaged in a large number of small units, each with hundreds of copies of just a few genes.
  - ⇒ It controls everyday functions of the cell by synthesizing RNA.
  - ⇒ It is also necessary for asexual reproduction during binary fission. The macronucleus elongates and splits instead of undergoing mitosis.
- Characteristics of the micronucleus:
  - ⇒ It is small and may number from 1 to 80 micronuclei, depending on the species.
  - ⇒ It does not function in growth, maintenance or asexual reproduction.
  - ⇒ It functions in *conjugation*, a sexual process which produces genetic variation (see Campbell, Figure 28.9).
- Note that in ciliates, meiosis and syngamy are separate from reproduction.

E. **A diverse assemblage of unicellular eukaryotes move by means of pseudopodia**

Three groups of unicellular eukaryotes move and feed by means of cellular extensions called *pseudopodia.*

The mode of nutrition among member groups varies:

- Most are heterotrophs.
  - Some actively seek and feed on bacteria, other protists, or *detritus* (dead organic matter)
  - Some are symbiotic species, including some parasites that cause human diseases

1. **Rhizopods (amoebas)**

This group (*Rhizopoda* = rootlike feet) includes the *amoebas* and their relatives.

- Simplest of protists; all are unicellular
- No flagellated stages in life cycle
- *Pseudopodia* form as cellular extensions and function in feeding and movement (see Campbell, Figure 28.10)
  - ⇒ The cytoskeleton of microtubules and microfilaments functions in amoeboid movement.
- All reproduction is by asexual mechanisms: no meiosis or sexual reproduction are known to occur.

- During mitosis, spindle fibers form, but typical stages of mitosis are not apparent in most species.
  - ⇒ The nuclear envelope persists during cell division in many genera.
- Rhizopods inhabit freshwater, marine, and soil habitats.
- Most are free-living, although some are parasitic.

2. Actinopods (heliozoans and radiozoans)

Actinopods (= ray feet) possess axopodia, a slender form of pseudopodia.

- *Axopodia* = Projections reinforced by bundles of microtubules thinly covered by cytoplasm
- Axopodia increase the surface area that comes into contact with the surrounding water.
- They help the organisms float and function in feeding.
- Small protists and other microorganisms stick to the axopodia and are phagocytized by the thin layer of cytoplasm. They are carried to the main portion of the cell by cytoplasmic streaming.

The two main groups of actinopods are the heliozoans and the radiolarians.

- Most are planktonic.
- *Heliozoans* live primarily in fresh water.
- *Radiolarians* are primarily marine and have delicate shells, usually made of silica.

3. Foraminiferans (forams)

Forams have porous, multi-chambered shells of organic material hardened by calcium carbonate.

- Forams are almost all marine with most living in the sand or attached to algae and rocks; some are planktonic.
- Cytoplasmic strands extend through the shell's pores and function in swimming, feeding, and shell formation.
- Many have symbiotic algae living beneath the shell that provide nourishment through photosynthesis.
- 90% of the described species are fossils.
- Foram shells are an important component of sediments and sedimentary rocks (see Campbell, Figure 28.12).

F. Slime molds have structural adaptations and life cycles that enhance their ecological role as decomposers

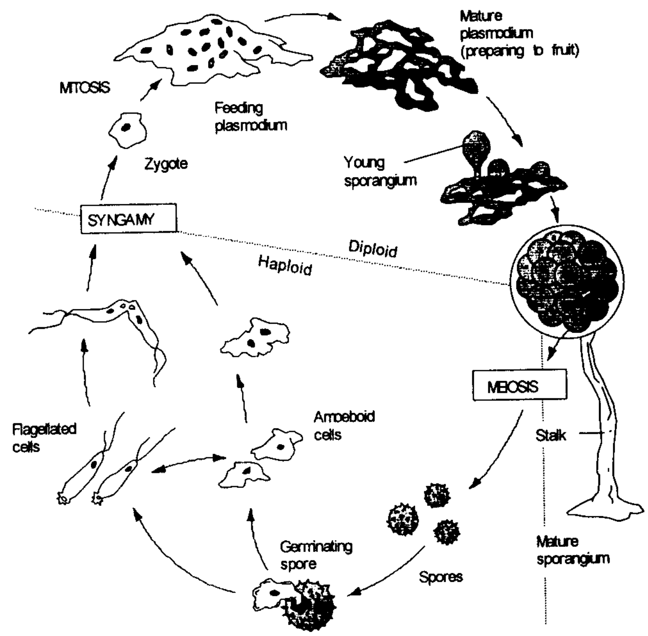
Two groups of protists called slime molds resemble fungi in appearance and lifestyle.

The resemblance of slime molds and water molds to true fungi is a result of convergent evolution of filamentous body structure.

- A filamentous body structure increases exposure to the environment and enhances their roles as decomposers.
- Slime molds differ from true fungi in their cellular organization, reproduction, and life cycles.

1. Plasmodial slime molds (Myxomycota)

The *plasmodial slime molds* are all heterotrophs and many are brightly pigmented.

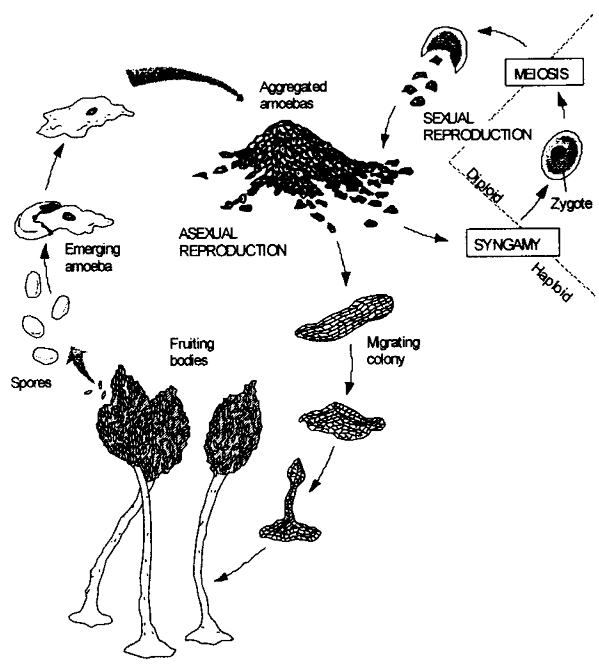


Plasmodium = Feeding stage of life cycle consisting of an amoeboid, coenocytic (multi-nucleated cytoplasm undivided by membranes) mass (see also Campbell, Figure 28.13).

- In most species, the nuclei of plasmodia are diploid and exhibit synchronous mitotic divisions.
- Cytoplasmic streaming within the plasmodium helps distribute nutrients and oxygen.
- Engulfs food by phagocytosis as it grows by extending pseudopodia.
- Live in moist soil, leaf mulch, and rotting logs.
- When stressed by drying or lack of food, the plasmodium ceases growth and forms sexually reproductive structures called fruiting bodies, or sporangia.

2. Cellular slime molds (Acrasiomycota)

This group possesses the following features:



- Feeding stage of life cycle consists of individual, solitary haploid cells.
- When the food supply is depleted, cells aggregate to form a mass similar to those of myxomycota but cells remain separate (not coenocytic) (see also Campbell, Figure 28.14).
- Fruiting bodies function in *asexual* reproduction (unlike plasmodial slime molds).
- Only a few have flagellated stages.

G. Diatoms, golden algae, brown algae, and water molds are members of the candidate kingdom Stramenopila

Stramenopila includes several groups of photosynthetic autotrophs (algae) and numerous heterotrophs.

The term "stramenopila" refers to numerous, fine, hairlike projections on the flagella, which is a characteristic feature of this group

1. Diatoms (Bacillariophyta)

- Diatoms are yellow or brown in color due to the presence of brown plastids.
- Many have a gliding movement produced by chemical secretions
- Usually reproduce asexually; sexual stages (egg and sperm production) are rare
- Some produce resistant cysts
- Mostly unicellular organisms with overlapping glasslike walls of hydrated silica in an organic matrix (see Campbell, Figure 28.15)
- Have the same photosynthetic pigments as in Chrysophyta
- Are components of freshwater and marine plankton
- Store food in laminarin (a glucose polymer) and in the form of oil
- Cellular regulation of ions counteracts weight of walls and maintains buoyancy

2. Golden algae (Chrysophyta)

- Algae named for their color, which results from accessory pigments (yellow and brown carotenoids and xanthophyll)
- Live among freshwater and marine plankton
- Most are unicellular, but some are colonial (see Campbell, Figure 28.16)
- Most are biflagellated, with both flagella attached near one end of the cell
- Survive environmental stress by forming resistant cysts
  - Microfossils resembling these cysts have been found in Precambrian rocks.

3. Water molds and their relatives (Oomycota)

This group includes water molds, white rusts, and downy mildews.

- All lack chloroplasts and are heterotrophic
- Have coenocytic hyphae (fine, branching filaments) that are analogous to fungal hyphae.
- Cell walls are made of cellulose rather than the chitin found in true fungi
- Diploid condition in the life cycle prevails in most species (see Campbell, Figure 28.17)
- Biflagellated cells are present in the life cycles, while fungi lack flagellated cells

In water molds:

- A large egg is fertilized by a smaller sperm cell to form a resistant zygote.
- These organisms are usually decomposers that grow on dead algae and animals in fresh water.
- Some are parasitic and grow on injured tissue, but they may also grow on the skin and gills of fish.

White rusts and downy mildews:

- Are usually parasitic on terrestrial plants

- Disperse by windblown spores, but also form flagellated zoospores at some point in their life cycle
- Some of the most important plant pathogens are members of this phylum.

4. **Brown algae (Phaeophyta)**

This is the largest and most complex of the algae. Color is due to accessory pigments.

- All are multicellular and most are marine inhabitants
- Have chlorophyll *a*, chlorophyll *c*, and the carotenoid pigment *fucoxanthin*
- Store carbohydrate food reserves in the form of laminarin
- Cell walls made of cellulose and *algin*

Many eukaryotes commonly called seaweeds are brown algae; however, red algae and green algae also are components of seaweeds.

H. Structural and biochemical adaptations help seaweeds survive and reproduce at the ocean's margins

Seaweeds are large, multicellular marine algae, which are found in the intertidal and subtidal zones of coastal waters.

- They are a diverse group and include members of the Phaeophyta (brown algae), Rhodophyta (red algae), and Chlorophyta (green algae).
- **The following emphasizes adaptations found in the red algae, however, many of these adaptations also apply to the brown algae and green algae seaweeds.**

The habitat of seaweeds, particularly the intertidal zone, poses several challenges to the survival of these organisms.

- Movement of the water due to wave action and winds produces a physically active habitat.
- Tidal rhythms result in the seaweeds being alternately covered by seawater and exposed to direct sunlight and the drying conditions of the air.

Seaweeds have evolved several unique structural and biochemical adaptations to survive the conditions of their habitats.

Structural adaptations found in seaweeds are a result of their complex multicellular anatomy. Some forms have differentiated tissues and organs analogous to those of plants.

- The body of a seaweed is called a *thallus*. It is plantlike in appearance but has no true roots, stems, or leaves.
- A thallus consists of a rootlike *holdfast* (maintains position), a stemlike *stipe* (supports the blades), and leaflike *blades* (large surfaces for photosynthesis) (see Campbell, Figure 28.18).
- Floats, which help suspend blades near the water surface, are present in some brown algae.
- Brown algae known as giant kelp occur beyond the intertidal zone where less harsh conditions exist and may have stipes which reach a length of up to 60 m (see Campbell, Figure 28.19).

Biochemical adaptations in some seaweeds reinforce the anatomical adaptations and enhance survival.

- Cellulose cell walls contain gel-forming polysaccharides (algin in brown algae; carageenan in red algae), which cushion the thalli against wave action and prevent desiccation during low tide.

- Some red algae retard grazing by marine invertebrates by incorporating large amounts of calcium carbonate into their cell walls, rendering them unpalatable.

Seaweeds are used by humans in a variety of ways:

- Brown and red alga are used as food in many parts of Asia.
- Algin, agar, and carageenan are extracted and used as thickeners for processed foods and lubricants in oil drilling.
- Agar is also used as a microbiological culture media.

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

A variety of life cycles in the brown algae, the most complex involve alternation of generations. Also found in certain groups of red algae and green algae.

Alternation of generations = Alternation between multicellular haploid forms and multicellular diploid forms in a life history

The life cycle of *Lamanaria* is an example of a complex life cycle with an alteration of generations (see Campbell, Figure 28.20).

- The diploid individual is called a *sporophyte* because it produces reproductive cells called spores.
- The haploid individual is called the *gametophyte* because it produces gametes.
- The sporophyte and gametophyte generations of the life cycle take turns producing one another.
  - Spores released from the sporophyte develop into gametophytes.
  - Gametophytes produce gametes which fuse (fertilization) to form a diploid zygote that develops into a sporophyte.
- In *Laminaria,* the sporophyte and gametophyte generations are said to be *heteromorphic,* because they are morphologically different.
- In *Ulva*, a green algae exhibiting alteration of generations, the generations are referred to as *isomorphic* because they look alike.

J. Red algae (candidate kingdom Rhodophyta) lack flagella

The defining characteristic of red algae is that they do not have flagella in any of their life cycle stages, unlike other eukaryotic algae

- Current data suggests that red algae aren't ancient, but that flagella were lost during their evolution.
- Red algae probably arose about the same time as Stamenopiles.

Red algae are primarily warm, tropical, marine inhabitants, although some are found in fresh water and soil. Other features include:

- Chlorophyll *a*, carotenoids, phycobilins, and chlorophyll *d* in some
- Red color of plastids due to the accessory pigment, phycoerythrin
  - ⇒ Phycoerythrin is a phycobilin, a pigment found only in red algae and cyanobacteria.
- Color of the thallus may vary (even in a single species) with depth, as pigmentation changes to optimize photosynthesis.
  - Deep water forms are almost black, moderate depth forms are red, and shallow water forms are green.
  - One species has been discovered near the Bahamas at a depth of 260 meters.
  - Some tropical species lack pigmentation and survive as parasites on other red algae.

- Carbohydrate food reserves stored as floridean starch (similar to glycogen).
- Cell walls are cellulose with agar and carageenan.
- Most red algae are multicellular and the largest are designated as seaweeds.
- Most thalli are filamentous and are often branched forming an interwoven lacy network (see Campbell, Figure 28.21)

All red algae reproduce sexually.

- Have no flagellated stages, unlike other algal protists
- Alternation of generations is common

K. Green algae and plants probably had a common photoautotrophic ancestor

Green algae (Chlorophyta) are named for their grass-green chloroplasts, which are similar in ultrastructure and pigment composition to the organelles of organism s traditionally referred to as plants.

Molecular and structural features suggest that green algae and plants are closely related and were derived from a common ancestor different from that giving rise to stramenopiles and red algae.

- Some systematists argue for the inclusion of green algae in the plant kingdom.

At least 7000 species of green algae are known; most are freshwater, some are marine.

- Many unicellular types live as plankton, inhabit damp soil, coat snow surfaces, or are symbionts with protozoa or invertebrates.
- When living mutualistically with fungi they form the association known as *lichens*.
- Colonial forms are often filamentous ("pond scum").
- Multicellular forms may have large, complex structures resembling true plants and comprise a group of seaweeds.

Evolutionary trends probably produced colonial and multicellular forms from flagellated unicellular ancestors.

1. Formation of colonies of individual cells, as seen in *Volvox* (see Campbell, Figure 28.22a)
2. Repeated division of nuclei with no cytoplasmic division, as in *Caulerpa* (see Campbell, Figure 28.22b)
3. Formation of true multicellular forms, as in *Ulva* (see Campbell, Figure 28.22c)

Most green algae have complex life histories involving sexual and asexual reproductive stages.

- Nearly all reproduce sexually by way of biflagellated gametes.
- Some are conjugating algae (e.g., *Spirogyra*), which produce amoeboid gametes (see Campbell, Figure 28.23).

The life cycle of *Chlamydomonas* is a good example of the life history of a unicellular chlorophyte. Note: a mature *Chlamydomonas* is a single haploid cell (see Campbell, Figure 28.24) .

- During asexual reproduction, the flagella are resorbed and the cell divides twice by mitosis to form four cells (more in some species).
  - ⇒ The daughter cells develop and emerge as swimming zoospores. Zoospore development includes formation of flagella and cell walls.
  - ⇒ Zoospores grow into mature cells, thus completing asexual reproduction.

Sexual reproduction is stimulated by environmental stress from such things as a shortage of nutrients, drying of the pond, or some other factor.

- ⇒ During sexual reproduction, many gametes are produced by mitotic division within the wall of the parent cell. The gametes escape the parent cell wall.
- ⇒ Gametes of opposite mating strains (+ and –) pair off and cling together by the tips of their flagella.
- ⇒ The gametes are morphologically indistinguishable and their fusion is known as *isogamy.*
- ⇒ The slow fusion of the gametes forms a diploid zygote which secretes a resistant coat that protects it from harsh environmental conditions.
- ⇒ When dormancy of the zygote is broken, four haploid individuals (two of each mating type) are produced by meiosis.
- ⇒ These haploid cells emerge from the coat and develop into mature cells, thus completing the sexual life cycle.

Many features of *Chlamydomonas* sex are believed to have evolved early in the chlorophyte lineage. Using this basic life cycle, many refinements that evolved among the chlorophytes have been identified.

- Some green algae produce gametes that differ from vegetative cells and, in some species, the male gamete differs in size or morphology from the female gamete (*anisogamy*).
- Many species exhibit *oogamy*, a type of anisogamy in which a flagellated sperm fertilizes a nonmotile egg.
- Some multicellular species also exhibit alternation of generations.
  - ⇒ *Ulva* produces isomorphic thalli for its diploid sphorophyte and haploid gametophyte (see Campbell, Figure 28.25).

L. Multicellularity originated independently many times

Early eukaryotes were more complex than prokaryotes and this increase in complexity allowed for greater morphological variations to evolve.

- Extant protists are more complex in structure and show a greater diversity of morphology than the simpler prokaryotes.
- The ancestral stock which gave rise to new waves of adaptive radiations were the protists with multicellular bodies.

Multicellularity evolved several times among the early eukaryotes and gave rise to the multicellular algae, plants, fungi, and animals.

Most researchers believe that the earliest multicellular forms arose from unicellular ancestors as colonies or loose aggregates of interconnected cells (see Campbell, Figure 28.26).

- Multicellular algae, plants, fungi, and animals probably evolved from several lineages of protists that formed by amalgamations of individual cells.
- Evolution of multicellularity from colonial aggregates involved cellular specialization and division of labor.
  - ⇒ The earliest specialization may have been locomotor capabilities provided by flagella.
  - ⇒ As cells became more interdependent, some lost their flagella and performed other functions.
- Further division of labor may have separated sex cells from somatic cells.
  - ⇒ This type of specialization and cooperation is seen today in colonial species such as *Volvox* (a green alga).
  - ⇒ Gametes specialized for reproduction are dependent on somatic cells while developing.

   - ⇒ The evolution of telomerase enzymes, which add nucleotides to the ends of DNA (telomeres; see chapter 19) and protects genes from degradation during DNA replication, may have been involved in gamete formation.
- Many additional steps were involved in the evolution of specialized somatic cells capable of performing all the nonreproductive function in a multicellular organism.
   - ⇒ Extensive division of labor exists among the different tissues that comprise the thalli of seaweeds.
- Multicellular forms more complex than filamentous algae appeared approximately 700 million years ago.
- A variety of animal fossils has been found in late Precambrian strata and many new forms evolved in the Cambrian period (about 570 million years ago).
- Seaweeds and other complex algae were also abundant during the Cambrian period.
- Primitive plants are believed to have evolved from certain green algae living in shallow waters about 400 million years ago.

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