Protists are a **paraphyletic** group of eukaryotes that are **neither** plants, **nor** animals **nor** fungi. Most, but not all, are unicellular. Their descendants include plants (here labelled “green plants”), fungi and animals.
III.2 Protists: A Paraphyletic Group.

- Eukaryotes.
  1. Nucleus; organelles;
  2. Chromosomes;
  3. Cytoskeleton;
  4. Vesicles;
  5. Sex, etc.

- At or near the base of the food chain.

- Characteristics.
  1. Most live in aqueous environments.
  2. Most small; some large.
  3. Protists are
    a. Metabolically less diverse than prokaryotes;
    b. More diverse morphologically.

Top. A more detailed phylogeny. Bottom. Multicellular brown algae can be as large as a man and have differentiated tissues.
4. Protists reproduce **sexually and / or asexually**.

5. Some have **complex life cycles** life cycles involving **haploid** and **diploid** stages.

6. **Abundant.** Key **primary producers** in aquatic (marine and freshwater) habitats.

7. Some **cause diseases**, e.g., malaria and toxoplasmosis.

8. Within the “Protista”, **multicellularity evolved multiple times**.
Symbiogenesis and Organelles.

- **Mitochondria.**
  1. Double membranes of mitochondria remnants of engulfing “way back when.”
  2. Mitochondrial DNA groups with **Proteobacteria**.

- **Chloroplasts.**
  1. DNA groups chloroplasts with cyanobacteria.
  2. Multiple membranes in some photosynthetic protists reveal history of **multiple** engulfings in some species.
Sterols.

- Important components of eukaryotic cell membranes.
  
  1. Bind to hydrophilic heads / hydrophobic tails of membrane bilayer.
  
  2. Modulate flexibility, permeability.

- Biosynthesis
  
  1. Requires molecular oxygen – lots of it.
  
  2. Oxidant protection – an internal sink for oxygen.
  
  3. Made possible by accumulating oxygen in earth’s waters.
  
  4. May also have facilitated evolution of photosynthesis – *i.e.*, protected photosynthetic bacteria from poisoning themselves.
  
  5. Approximately coincident with evolution of multicellular cyanobacteria and / or origin of eukaryotes.
• **Sterol synthesis genes** recently found in **myxobacteria** (proteobacteria).

1. Did they get there by LGT from eukaryotes?

2. Is eukaryotic cell membrane descended (symbiogenesis) or borrowed (LGT) from myxobacteria?

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1.3.U3 Cholesterol is a component of animal cell membranes.

**Cholesterol**

Hydroxyl group makes the head polar and hydrophilic - attracted to the phosphate heads on the periphery of the membrane.

Carbon rings – it’s not classed as a fat or an oil, cholesterol is a steroid

Non-polar (hydrophobic) tail – attracted to the hydrophobic tails of phospholipids in the centre of the membrane.

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**Left.** Sterols are distinguished from other steroids by the presence of an OH group attached to the first of the four rings as shown in the figure. **Right.** The hydrophilic and hydrophobic ends of cholesterol are attracted to the corresponding constituents of membrane bilayers.
Sexual Reproduction.

- Gametes formed by meiosis.
  1. Chromosome number reduced from 2N to N.
  2. Recombination => new gene combinations.

- Haploid gametes fuse (fertilization) => diploid zygote.

- Offspring genetically distinct from parents and each other. Crossing over and recombination during meiosis.

- Contrast with mitosis.
  1. Daughter cells identical to each other and parent.
  2. **Both** haploid and diploid cells can reproduce by mitosis.

- **Sex ≠ Reproduction.** One can have
  1. **Sex without reproduction**, e.g., bacterial conjugation.
  2. **Reproduction without sex**, e.g., mitosis.
• **Proposed Advantages of Sex:**

  1. Production of genotypic **variability** via recombination.

  2. “**Hybrid vigor**” (consequent to heterozygous advantage)

  3. Facilitation of **DNA repair** when homologous chromosomes pair.

• **Inherent Cost:** A population of parthenogenetic females will increase twice as fast as a comparable population of males and females – “**cost of males**”.

• Many species **alternate** between sexual and asexual reproduction. In these cases,

  1. Asexual reproduction typically predominates when environmental conditions favorable.”

  2. Sexual reproduction often a response to **unfavorable** conditions.

  3. Sexual reproduction often entails production of **hardy**, e.g., temperature-resistant, **spores** that simultaneously constitute a **dispersal stage**.
Questions.

1. The chloroplasts of *Euglena* have three membranes. What do you conclude?

2. What are myxobacteria?

3. In species with complex life cycles, why should asexual reproduction be associated with “good times” and sexual reproduction with times of stress?
Protist Diversity.

• We consider four monophyletic groups plus with emphasis on evolutionary implications:

1. **Alveolates** – Apicomplexans, Dinoflagellates.

2. **Stramenopiles** – Brown algae.

3. **Chlorophytes** – Green algae; include ancestors of (land) plants.

4. **Choanoflagellates** – include ancestors of animals and fungi.

• We also consider amoebas, which are polyphyletic.
**Major Clades.**

**Principal protists.** Red and green-circled groups (plus polyphyletic amoebas) are those considered in this lecture. Red-circled groups multicellular protist descendants. Choanoflagellates the sister group to Animals; Chlorophytes to Plants.” Latter here defined to include only multicellular land (or land-derived) species such as water lilies.
Alveolates.

- Name refers to small vesicles (alveoli).

1. In or just below cell membrane.

2. May regulate ion transport and structural stabilization of the cell membrane.

3. Most are unicellular.

- Dinoflagellates.

  1. Two (transverse and longitudinal) flagella – permit forward and rotary motion.

  2. Some have a theca (protective covering composed of cellulose plates).
3. Nuclear structure **aberrant**.

   a. No histones / nucleosomes
   b. Chromosomes condensed during interphase.


5. **Bioluminescence**.

   a. Enzyme catalyzed production of light.
   b. Attracts secondary predators.
   c. Increases **predation** on dinoflagellate predators.
   d. Selects for flashing avoidance in same, *i.e.*, “police” on the way; so-called **“burglar alarm”** theory.

Time required by squid to strike mosquito fish in the presence of luminous and nonluminous dinoflagellates. Movement by mosquito fish stimulates bioluminescence, thereby increasing fish susceptibility to predation as predicted by burglar alarm hypothesis. From Fleisher and Case (1995).
6. **Red tides**

a. Consist of trillions of cells.

b. Induced by nutrient upwelling and warm temperatures.

c. Result is massive *fish kills* consequent to *oxygen depletion* and / or *neurotoxin production*.

d. Accumulation of dinoflagellate toxins in shellfish causes *paralytic shellfish poisoning* when eaten by humans.

Red tide off La Jolla, California. The reddish color is due to photosynthetic pigments called carotenoids. Not all red tides are red; the color depends instead on the species.
Apicomplexans.

1. Parasitic – includes the organisms that cause malaria.

2. Name refers **apical complex** (apical polar ring in the picture at right) that facilitates penetration of host cells.

   a. An associated structure, the **apicoplast**, is a **non-photosynthetic plastid** surrounded by four membranes.

   b. Killing the apicoplast does **not** kill the parasite, but **prevents penetration** of host cells.

   c. Promising target for new anti-malarial drugs because of **differing plastid** (prokaryote), mammalian cell sensitivities.

   d. Malaria caused by various species of **Falciparum**.

   e. **Extra-cellular** parasite of mosquitoes; an **intra-cellular** parasite of vertebrate (secondary) host.
Two apicomplexans: *Toxoplasma gondii* (left) and *Plasmodium falciparum* (right). The former causes toxoplasmosis; the latter, malaria. Toxoplasmosis is spread by contact with cat feces; malaria by mosquitoes of the genus *Anopheles*. 
Malaria life cycle. Gametes fuse in the mosquito gut, and the resulting ookinete inserts in the intestinal wall forming an oocyst. Haploid sporozoites form within the oocyst. When the latter ruptures, the sporozoites make their way to the salivary glands from which they are injected into the vertebrate host along with an anticoagulant that facilitates feeding. In the human host, the parasite infects both the liver and red blood cells. Eventually, male and female gametocytes are produced. When another female mosquito bites, it ingests gametocytes with the blood meal, and the cycle repeats. Malaria is an extra-cellular parasite of mosquitoes and an intra-cellular parasite of the secondary, vertebrate host.
Stramenopiles.

- **Brown algae.**
  1. Multicellular marine forms – giant kelp up to 60 m.

  2. Stem-like **stipes**, root-like **hold-fasts** and leaf-like **blades**.

  3. **Phloem-like** conducting cells distribute photosynthetic from “leaves” to “stems” & “roots.”

  4. Alternating generations

    a. Haploid **gametophyte**

    b. Diploid **sporophyte**.

      i. Both **multicellular**.

      ii. Grow **mitotically**.

      iii. Sporophyte produces **haploid cells** via **meiosis**.

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Top. *Fucus serratus*, a brown alga with differentiated parts. **Bottom.** Alternation of generations in brown algae. The sporophyte and gametophyte generations can be similar (**isomorphic**) or not (**heteromorphic**).
Green Algae and Plants.

- **Chlorophytes.**

  1. Contain the photosynthetic pigment used by plants to capture photons.

  2. Unicellular, colonial, and truly multicellular.

Multicellular green algae. **Left. Volvox**, a colonial form. **Right. Multicellular Ulva lactuca** (sea lettuce) attached to the substrate via a holdfast. The main part of the “plant” is two cell layers thick.
• **Chlorophyte Life Cycles.**

1. Like brown algae there are haploid (gametophyte) and diploid (sporophyte) “generations.”

2. Some **isomorphic**. Sporophyte and gametophyte similar.


4. Extreme cases:
   
   a. **Haplontic.** Immediate meiosis after fertilization. **No sporophyte.**
   
   b. **Diplontic** – gametes produced by sporophyte. **No gametophyte.**

• **Embryophytes** – (“green” / “land”) plants.¹

   1. Differentiation of cells/tissues – xylem, phloem, in particular.

   2. Differentiation of organs – true roots, stems, leaves, *etc.*

   ![Diagram of Life Cycle](image)

¹ The name refers to retention of an embryo protected by parental tissue.
3. Life Cycles.

a. Heteromorphic.

b. Embryophyte evolution marked by progressive **gametophyte reduction** and **sporophyte enlargement**.

*Ulothrix*, a filamentous green alga, has a haplontic life cycle. The diploid zygote undergoes meiosis to produce haploid zoospores that develop into the haploid “plant”, *i.e.*, the gametophyte. Zoospores, and hence new gametophytes, can also be produced asexually.
Opisthokonts.

- Name means posterior pole – the “pole” being the flagellum.

- Include

  1. **Fungi.**

  2. **Choanoflagellates.**

     a. Filter feeders – heterotrophs;

     b. Solitary or colonial.

     c. Similar to the **collar cells** of sponges and the **excretory (“flame”) cells** of flatworms and rotifers.

  3. **Animalia** – “Higher” animals.

A colonial choanoflagellate.
Amoebas.

- Polyphyletic – not a clade.

- Move / feed by pseudopods. Generally lack flagella.

- Some pathogens – e.g., Entamoeba causes amoebic dysentery.

- Foraminifera – calcareous shells; internal partitions.
  
  1. Include giant, multinucleate Xenophyophores – deep water, benthic deposit feeders.

  2. Late Precambrian “Ediacaran” biotas dominated by bacterial mats within which enigmatic “quilted” organisms believed by some to have been giant protozoans later exterminated by metazoans that ate them.

Top. Foraminiferan with protruding pseudopods. Bottom. Xenophyophore on the sea floor off the Galapagos Islands. Some species grow to over 20 cm. in diameter.
The “Garden of Ediacara”. So-called “frond animals” conjectured by Otto Seilacher to be giant protozoans.
• **Cellular slime molds** (social amoebae) – aggregating amoebae form multicellular fruiting bodies when bacteria on which they feed become scarce.

Aggregating “social amoebae” first form a motile “slug” and then a sessile fruiting body. The molecule inducing aggregation is cAMP – an important signaling molecule in **metazoans**.
Alternation of generations in social amoebae.
Recurrent Evolutionary Trends in Protists.

- Evolution of **complex life cycles**.
- Evolution of **multicellularity** and **cell differentiation**.

**Right.** Phylogenetic relations among unicellular, colonial and multicellular eukaryotes. Some lineages, e.g., animals, strictly multicellular (●); some, e.g., choanoflagellates, unicellular or colonial (○). Still others, e.g., fungi, a mix of unicellular / colonial and multicellular forms (□). From Abedin and King (2010).
Questions.

4. The organisms that produce malaria and sleeping sickness alternate between vertebrate and invertebrate hosts. What are the costs and benefits of such a life cycle as compared to one in which the pathogen completes its life cycle within a single host species? How might such a life cycle have evolved?

5. In response to diminished food availability, the amoeboae of cellular slime molds aggregate to form a multicellular “slug” that develops into a fruiting body. Only some of the original cells produce the spores that contribute to the next generation. The rest become the stalk and its base. This is shown schematically in the figure at the right. The cells at the front and back of the “slug” become the stalk, which dies, while the cells in the slug’s middle become spores. Being the first or the last cells to join a developing slug would thus appear to be an evolutionary dead end. Yet every slug has to have a front and a rear. Discuss.
III.3 Fungi: Life Between n and 2n.

Fungi, choanoflagellates and animals form a clade.
The Good, the Bad and the Ugly.

Phylogenetic Relationships.

- **Choanoflagellates, Fungi** and **Animalia** form a clade.

- Shared derived traits include:

  1. **Chitin**
     
     a. **Choanoflagellates**: Component of the surrounding **lorica** – most / mostly siliceous);
     
     b. **Fungi** – cell walls;
     
     c. **Metazoa** – exoskeletons.

  2. **Glycogen** – so-called “animal starch” (storage molecule).

  3. **Receptor tyrosine kinase** (RTK) – a signal receptor molecule.

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**Above.** A choanoflagellate and its lorica. **Next page.** Cladograms based on different proteins linking choanoflagellates (represented by *Monosiga*) to Metazoa. From King & Carroll (2001). Abbreviations MP, ME and QP, are measures of reconstruction reliability.
Extra-Cellular Digestion / Hyphae.

- Fungi **secrete enzymes** that break down living or dead organisms on which they grow.

- Multicellular fungi consist of branching, **thread-like hyphae** that absorb nutrients.

  1. Growth form maximizes surface area to volume ratio and absorption. Fungal mycelia are composed of hyphae.

  2. Hyphae organized into underground, vegetative **mycelia** and above ground **reproductive structures**.

**Left.** Both vegetative (mycelia) and reproductive parts of fungi composed of hyphae. **Right.** Partial division of hypha by septa.
• Extent of underground mycelium often enormous – can exceed a square mile.

• The same morphology that facilitates absorption of water and nutrients also increases vulnerability to environmental hazards.

• As the mycelium grows, its constituent hyphae

  Armillaria solidipes. Most of the fungus is underground. The enormous mycelium can be more than a thousand years old.

  1. Hunt for food by dispersing until they find it;

  2. Once found, food is exploited by mycelial proliferation

• Not all fungi multicellular – yeasts are unicellular.
Questions.

1. How do the cell walls of fungi differ from those of plants?

2. The thread-like structure (large surface area to volume ratio) of hyphae maximizes nutrient absorption. What structures in the human gut perform the same function?

3. Give other (at least two) examples from vertebrate anatomy in which increased surface area to volume ratio facilitates the exchange of materials.

4. What are receptor tyrosine kinases (RTKs)?
Nutrition.

1. Most fungi saprobes – feed on dead matter. Important decomposers.

2. Especially of cellulose (via cellulase) and lignin (via lignin peroxidase) – coevolved w. plants.

3. Recycle nutrients in terrestrial ecosystems.

- Some are parasites – feed on living tissue.
• **Pilobolus** – Cleaning Up After the Rhinos.

1. Lives on dung.

2. Has a light sensitive organ that points the fruiting body toward the light.

3. Hydrostatic pressure (up to 7 Atm) propels spores 2-3 meters.

4. Spores accelerated at 20,000 – 180,000 g – contrast w. maximum force (< 10 g) sustainable by WWII pilots.

*Pilobolus*. Sporangial vesicles (**left**), each with a single sporangium, orients toward the light and launches the spores (**right**).
• Some fungi are **predators**.

![Fungus “capturing” a nematode (round worm).](image)

• Some are parasites; a few are human pathogens. Fungal diseases include

  - Diaper rash;
  - Meningitis;
  - Pneumonia;
  - Ringworm;
  - Thrush;
  - Vaginitis
Fungi are important crop / food parasites.

(a) Parasitic fungi infect corn and other crop plants.

(b) Saprophytic fungi rot fruits and vegetables.
Symbioses.

- **Mycorrhizae**: Plant-fungus mutualisms.

1. Fungus obtains carbohydrates from the plant.

2. Plant obtains water and soil nutrients – principally **N** and **P**, from the fungus.

3. **Important** for plant growth since **N** and **P** often **limiting**.

Root tip, root hairs (arrows) and mycorrhizae.
• Gardeners often supplement (replace) conventional fertilizers with mycorrhizal spores.

Left. Conventional fertilizers contain nitrogen and phosphorus, the soil availability of which often limits plant growth. Right. A mycorrhizal fungal additive (spores).
Experiment using labeled CO$_2$, P and N establishing the mutualistic nature of plant-mycorrhizae associations. From Freeman, Ch. 32.
Lichens

1. Symbiotic associations of fungi and cyanobacteria or photosynthetic eukaryotes (algae).

2. “Pioneer” species; colonize bare rock, e.g., after volcanic eruptions.
Life Cycles.

- Life cycle is **haplontic**.

  1. Mycelial cells **haploid**.

  2. Nuclear fusion (zygote formation) followed by meiosis and production of haploid spores.

  3. Spores divide mitotically to form mycelia.

- Most fungal life cycles include a **dikaryon** (heterokaryon) stage where cells contain $n \geq 2$ haploid nuclei.

  1. Results from **hyphal fusion**.

  2. In septate fungi, hyphae partially divided by **septa**.

  3. If **no septa**, the structure is called a **coenocyte**.

- In most **organisms**, nuclear fusion (**karyogamy**) immediately follows cell fusion (**plasmogamy**) – e.g., when a sperm fertilizes an egg.
In fungi, karyogamy is delayed. Delayed karyogamy a derived trait, i.e., ancestral life cycle conventional alternation of generations.

1. No agreed-upon adaptive scenario.

2. Spatial separation of nuclei may facilitate independent nuclear response via up- / down- gene regulation to varying environmental circumstance encountered by spatially extensive mycelia.
Questions.

5. The large surface area to volume ratio of hyphae increases the absorption of water and nutrients from the soil. What’s a potential down side?

6. Name a common fungal disease in arid environments to which all of us have been exposed.

7. a. What are yeasts good for – besides rising dough? b. Name two fungal plant diseases that have resulted in the decimation / near extinction of important North American trees.

8. Why should *Pilobolus* discharge its spores away from the dung heap on which it’s growing?
Sex and Reproduction in Fungi.

- Recall.

1. **Sex**: Fusion of two nuclei followed by meiosis.

2. **Recombination** involves gene exchange.

3. **Reproduction**: Can be **sexual** or **asexual**.

- **Sexual reproduction in fungi** entails

  1. Fusion of flagellated gametes in chytrids – the ancestral reproductive mode.

  2. Fusion of hyphae of different mating types **except** in chytrids. Alternation of haploid (blue) and diploid (red) generations in chytrids. Note mycelium and heterokaryon absence.

  3. Production of spores by meiosis.
• **Asexual reproduction** in fungi entails

1. Mycelial fragmentation.

2. Spore production by **mitosis**.

3. Fission (equal sized products) and budding (small cell buds off from large) in yeasts.

• **Spores.**

1. Can be produced sexually (meiosis) or asexually (mitosis).

2. Typically small, tough cells that germinate upon exposure to favorable conditions.

3. Often long-lived, **resistant** to heat, cold, desiccation, etc.

4. Fungal spores are **everywhere** – $10^4$ per m$^3$ of air.

**Question.**

9. Approximately how many fungal spores do each of us inhale per minute? **Show your work.**