CHAPTER 31
FUNGI

OUTLINE

I. Introduction to Fungi
   A. Absorptive nutrition enables fungi to live as decomposers and symbionts
   B. Extensive surface area and rapid growth adapt fungi for absorptive nutrition
   C. Fungi reproduce by releasing spores that are produced either sexually or asexually

II. Diversity of Fungi
   A. Division Chytridiomycota: chytrids may provide clues about fungal origins
   B. Division Zygomycota: zygote fungi form resistant dikaryotic structures during sexual reproduction
   C. Division Ascomycota: sac fungi produce sexual spores in saclike asci
   D. Division Basidiomycota: club fungi have long-lived dikaryotic mycelia and a transient diploid stage
   E. Molds, yeasts, lichens, and mycorrhizae represent unique lifestyles that evolved independently in three fungal divisions

III. Ecological Impacts of Fungi
   A. Ecosystems depend on fungi as decomposers and symbionts
   B. Some fungi are pathogens
   C. Many animals, including humans, eat fungi

IV. Phylogenetic Relationships of Fungi
   A. Fungi and animals probably evolved from a common protistan ancestor

OBJECTIVES

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

1. List characteristics that distinguish fungi from organisms in other kingdoms.
2. Explain how fungi acquire their nutrients.
3. Explain how non-motile fungi seek new food sources and how they disperse.
4. Describe the basic body plan of a fungus.
5. Distinguish between septate and aseptate (coenocytic) fungi.
6. Describe some advantages to the dikaryotic state.
7. Distinguish among fungi and list some common examples of each.
8. Describe asexual and sexual reproduction in Zygomycota, Ascomycota, and Basidiomycota, and the sexual structure that characterizes each group.
9. Explain the difference between conidia and ascospores.
10. Explain why ascomycetes can be useful to geneticists studying genetic recombination.
11. Explain why the Deuteromycota are called imperfect fungi.

12. Describe the anatomy of lichens and explain how they reproduce.
13. Provide evidence for both sides of the debate on whether symbiosis in lichens is parasitic or mutualistic.
14. Describe the ecological importance of lichens.
15. Explain why fungi are ecologically and commercially important.
16. Describe how the mutualistic relationship in mycorrhizae is beneficial to both the fungus and the plant, and explain its importance to natural ecosystems and agriculture.
17. Describe a scenario for fungal phylogeny and list two possible ancestors of Zygomycota.

KEY TERMS

absorption	plasmogamy	asci	imperfect fungi
hyphae	karyogamy	ascocarp	yeast
mycelium	dikaryon	conidia	lichen
septa	chytrids	basidium	soredia
chitin	zygote fungi	club fungus	
coenocytic	mycorrhizae	basidiocarps	
haustoria	sac fungi	mold	

LECTURE NOTES

I. Introduction to the Fungi

Fungi are eukaryotes, and nearly all are multicellular (although yeasts are unicellular). Their nutrition, structural organization, growth, and reproduction distinguish them from organisms in other kingdoms.

A. Absorptive nutrition enables fungi to live as decomposers and symbionts

Fungi are heterotrophs that acquire nutrients by *absorption.*

- They secrete hydrolytic enzymes and acids to decompose complex molecules into simpler ones that can be absorbed.
- Fungi are specialized into three main types:
  1. Saprobes, which absorb nutrients from dead organic material
  2. Parasitic fungi, which absorb nutrients from the cells of living hosts; some are pathogenic
  3. Mutualistic fungi, which absorb nutrients from a host, but reciprocate to benefit the host.

Fungi exist in diverse habitats and form symbioses with many organisms.

> For example, fungi are found in:
> - Terrestrial habitats
> - Aquatic habitats, both freshwater and marine
> - Symbiotic relationships with algae to form lichens

B. Extensive surface area and rapid growth adapt fungi for absorptive nutrition

The basic structural unit of a fungal vegetative body (*mycelium*) is the *hypha*. Except for yeasts, fungal bodies are diffuse, intertwining mats of hyphae that are organized around and within their food source (see Campbell, Figure 31.1).

These hyphae:

- Are composed of tubular walls containing *chitin*, a strong, flexible nitrogen-containing polysaccharide similar to that found in arthropod exoskeletons
- Provide enormous surface area for the absorptive mode of nutrition. Parasitic fungi have modified hyphae called *haustoria*, which are nutrient absorbing hyphae that penetrate host tissue, but remain outside the host cell membrane (see Campbell, Figure 31.2c).

Fungal hyphae may be aseptate or septate.

- Hyphae of aseptate fungi lack cross-walls and are *coenocytic*, formed from repeated nuclear division without cytokinesis (see Campbell, Figure 31.2b).
- Hyphae of septate fungi are divided into cells by crosswalls called *septa*. Pores in the septa allow organelles to move from cell to cell.

True fungi have no flagellated stages in their life cycle. This characteristic is partly why the Chytridiomycota and Oomycota have been moved to the Protista.

C. Fungi reproduce by releasing pores that are produced either sexually or asexually

Mycelial growth is adapted to the absorptive node of nutrition.

- Mycelia grow in length, not girth, which maximizes the surface area for absorption.
- Mycelia grow rapidly, as much as a kilometer of hyphae each day. Fast growth can occur because cytoplasmic streaming carries molecules synthesized by the mycelium to the growing hyphal tips.
- Since fungi are nonmotile, they cannot search for food or mates. Instead, they grow in hyphal length to reach new food sources and territory.

Fungal chromosomes and nuclei are relatively small, and the nuclei divide differently from most other eukaryotes.

- During mitosis, the nuclear envelope remains intact from prophase to anaphase; the spindle is inside the nuclear envelope.
- After anaphase, the nuclear envelope pinches in two, and the spindle disappears.

Fungi reproduce by releasing spores that are:

- Usually unicellular, haploid, and of various shapes and sizes.
- Produced either sexually (by meiosis) or asexually (by mitosis). In favorable conditions, fungi generally produce enormous numbers of spores asexually. For many fungi (not all), sexual reproduction occurs only as a contingency for stressful environmental conditions.
- The agent of dispersal responsible for the wide geographic distribution of fungi. Carried by wind or water, spores germinate if they land in a moist place with an appropriate substratum.

Except for transient diploid stages in sexual life cycles, fungal hyphae and spores are haploid. Some mycelia may, however, be genetically heterogeneous resulting from fusion of hyphae with different nuclei.

- The different nuclei may stay in separate parts of the same mycelium.
- Alternatively, the different nuclei may mingle and even exchange genes in a process similar to crossing over.

The sexual cycle in fungi differs from other eukaryotic organisms in that syngamy occurs in two stages that are separated in time.

Syngamy = The sexual union of haploid cells from two individuals. In fungi, syngamy occurs in two stages:

1. *Plasmogamy*, the fusion of cytoplasm
2. *Karyogamy*, the fusion of nuclei

After plasmogamy, haploid nuclei from each parent pair up, forming a *dikaryon*, but they do not fuse.

- Nuclear pairs in dikaryons may exist and divide synchronously for months or years.
- The dikaryotic condition has some advantages of diploidy; one haploid genome may compensate for harmful mutations in the other nucleus.
- Eventually, the haploid nuclei fuse forming a diploid cell that immediately undergoes meiosis.

II. Diversity of Fungi

There are four divisions of fungi (see Campbell, Figure 31.4). They differ in the:

- Structures involved in plasmogamy
- Length of time spent as a dikaryon
- Location of karyogamy; the fungal divisions are named for the sexual structures in which karyogamy occurs.

A. Division Chytridiomycota: chytrids may provide clues about fungal origins

The Chytridiomycota and Fungi may share a protistan ancestor.

- Chytrids were placed in the Kingdom Protista because they form flagellated zoospores and gametes—a protistan characteristic.
- However, chytrids and fungi share many characteristics, such as:
  - ⇒ An absorptive mode of nutrition
  - ⇒ Cell walls of chitin
  - ⇒ Most form hyphae
  - ⇒ Key enzymes and metabolic pathways that are not found in the other fungus-like protists (slime molds and water molds)
  - ⇒ Similar sequences of proteins and nucleic acids
- This evidence lends support for
  - ⇒ Combining the chytrids with fungi as a monophyletic group
  - ⇒ The hypothesis that chytrids are the most primitive fungi, diverging earliest in fungal phylogeny.
  - ⇒ The hypothesis that fungi evolved from protists with flagella, a feature retained by the chytrids.

B. Division Zygomycota: zygote fungi form resistant dikaryotic structures during sexual reproduction

Fungi in the division Zygomycota are characterized by the presence of dikaryotic *zygosporangia*, resistant structures formed during sexual reproduction.

- Zygomycetes are mostly terrestrial and live in soil or on decaying organic material.
- Some form *mycorrhizae*, mutualistic associations with plant roots (see Campbell, Figure 31.16).
- Zygomycete hyphae are coenocytic; septa are found only in reproductive cells.

See Campbell, Figure 31.6 for the life cycle of the zygomycete, *Rhizopus stolonifer*, a common bread mold.

- The mycelium consists of horizontal hyphae that spread out and penetrate the food source.
- Under favorable environmental conditions, *Rhizopus* reproduces asexually:
  - ⇒ Sporangia develop at the tips of upright hyphae.
  - ⇒ Mitosis produces hundreds of haploid spores that are dispersed through the air.
  - ⇒ If they land in a moist, favorable environment, spores germinate into new mycelia.
- In unfavorable conditions, *Rhizopus* begins its sexual cycle of reproduction:
  - ⇒ Mycelia of opposite mating types (+ and –) form gametangia that contain several haploid nuclei walled off by the septum.
  - ⇒ Plasmogamy of the + and – gametangia occurs, and the haploid nuclei pair up forming a dikaryotic zygosporangium that is metabolically inactive and resistant to desiccation and freezing.
  - ⇒ When conditions become favorable, karyogamy occurs between paired nuclei; the resulting diploid nuclei immediately undergo meiosis producing genetically diverse haploid spores.
  - ⇒ The zygosporangium germinates a sporangium that releases the genetically recombined haploid spores.
  - ⇒ If they land in a moist, favorable environment, spores germinate into new mycelia.

Even though air currents are not a very precise way to disperse spores, *Rhizopus* releases so many that enough land in hospitable places. Some zygomycetes, however, can actually aim their spores.

- For example, *Pilobolus*, a fungus that decomposes animal dung, bends sporangium-bearing hyphae toward light, where grass is likely to be growing.
- The sporangium is shot out of the hypha, dispersing spores away from the dung and onto surrounding grass. If an herbivore eats the grass and consumes the spores, the asexual life cycle is completed when the animal disperses the spores in its feces.

C. Division Ascomycota: sac fungi produce sexual spores in saclike asci

Ascomycetes include unicellular yeasts and complex multicellular cup fungi (see Campbell, Figure 31.7).

- Hyphae are septate.

- In asexual reproduction, the tips of specialized hyphae form *conidia*, which are chains of haploid, asexual spores that are usually wind dispersed.
- In sexual reproduction, haploid mycelia of opposite mating strains fuse. One acts as "female" and produces an ascogonium which receives haploid nuclei from the antheridium of the "male" (see Campbell, Figure 31.8).

The ascogonium grows hyphae with dikaryotic cells. Syngamy is delayed.

↓

In terminal cells of dikaryotic hyphae, syngamy occurs.

↓

Meiosis forms four haploid nuclei which undergo mitotic division to yield eight haploid nuclei.

↓

The nuclei form walls and become ascospores within an *ascus*, the sac of sexually produced spores. Multiple asci may form an ascocarp.

Ascocarps = Fruiting structures of many asci packed together

- The ascospores of each ascus are lined up in a row in the order in which they formed from a single zygote, allowing geneticists to study genetic recombination.
- Unicellular yeasts appear dissimilar, but produce the equivalent of an ascus during sexual reproduction and bud during asexual reproduction in a manner similar to the formation of conidia. Thus, they are classified as ascomycetes.
- Includes important decomposers and both mutualistic and parasitic symbionts
- Many live symbiotically with algae as lichens.

D. Division Basidiomycota: club fungi have long-lived dikaryotic mycelia and a transient diploid stage

The division Basidiomycota, or *club fungi*, includes mushrooms, shelf fungi, puffballs, and stinkhorns (see Campbell, Figure 31.9).

Basidiomycetes:

- Are named for a transient diploid stage called the *basidium*, a club-shaped spore-producing structure.
- Are important decomposers of wood and other plant material. Saprobic basidiomycetes can decompose the complex polymer lignin, an abundant component of wood.
- Include mycorrhiza-forming mutualists and plant parasites. Many shelf fungi are tree parasites that function later as saprobes after the trees die.

- Include mushroom-forming fungi, only a few of which are strictly parasitic. About half are saprobic and the other half form mycorrhizae.
- Include the rusts and smuts, which are plant parasites.

Basidiomycete life cycles are characterized by a long-lived *dikaryotic* mycelium that reproduces sexually by producing fruiting bodies called *basidiocarps*. Refer to Campbell, Figure 31.10 for the life cycle of a mushroom-forming basidiomycete.

- Haploid basidiospores grow into short-lived haploid mycelia. Under certain environmental conditions, *plasmogamy* occurs between two haploid mycelia of opposite mating types (+ and –).
- The resulting dikaryotic mycelium grows; depending upon the species, it may form mycorrhizae with trees. Certain environmental cues stimulate the mycelium to produce mushrooms (basidiocarps). A "fairy ring" is an expanding ring of living mycelium that produces mushrooms above it; it slowly increases in diameter, about 30 cm per year.
- The mushroom cap supports and protects a large surface area of gills; karyogamy in the terminal, dikaryotic cells lining the gills produces diploid basidia.
- Each basidium immediately undergoes meiosis producing four haploid basidiospores. When mature, these sexual spores drop from the cap and are dispersed by wind.

Asexual reproduction occurs less often than in ascomycetes, but also results in conidia formation.

E. Molds, yeasts, lichens, and mycorrhizae represent unique lifestyles that evolved independently in three fungal divisions

1. Molds

Mold = A rapidly growing, asexually reproducing fungus

Molds may be saprobes or parasites on a great variety of substrates.

Molds only include asexual stages; they may be zygomycetes, ascomycetes, basidiomycetes or fungi with no known sexual stage.

Since molds are classified by their sexual stages (zygosporangium, ascogonium or basidium), molds with no known sexual stage cannot be classified as zygomycetes, ascomycetes, or basidiomycetes.

Molds with no known sexual stages are classified as Deuteromycota or *imperfect fungi*.

- Imperfect fungi reproduce asexually by producing spores.
- Deuteromycetes are sources of antibiotics. Penicillin is produced by some species of *Penicillium,* which are ascomycetes.
- Other commercial uses of imperfect fungi include flavoring for cheeses, such as blue cheese, Brie, Camembert and Roquefort; fermenting food products such as soybeans; and providing pharmaceuticals such as cyclosporine.
- Some deuteromycetes are predatory soil fungi that kill small animals such as soil nematodes (see Campbell, Figure 31.12).

2. Yeasts

Yeasts are unicellular fungi that inhabit liquid or moist habitats; some can alternate between mycelium or yeast, depending on the amount of liquid in the environment.

Yeasts reproduce:

- Asexually by simple cell division or by budding off from a parent cell; some are classified as Deuteromycota, if no sexual stages are known.
- Sexually by forming asci (Ascomycota) or basidia (Basidiomycota)

Though humans have used yeasts to raise bread and ferment alcoholic beverages for thousands of years, only recently have they been separated into pure culture for more controlled human use.

- *Saccharomyces cerevisiae* is the most important of all domesticated fungi (see Campbell, Figure 31.13). Highly active metabolically, this ascomycete is available as baker's and brewer's yeast.
- In an aerobic environment, baker's yeast respires, releasing small bubbles of carbon dioxide that leaven dough; cultured anaerobically, *Saccharomyces* ferments sugars to alcohol.
- Researchers use *Saccharomyces* to study eukaryotic molecular genetics because it is easy to culture and manipulate.

Some yeasts cause problems for humans.

- *Rhodotorula*, a pink yeast, grows on shower curtains and other moist surfaces.
- *Candida*, a normal inhabitant of moist human tissues, can become pathogenic when there is a change in pH or other environmental factor; or when an individual's immune system is compromised.

3. Lichens

Lichen = Highly integrated symbiotic association of algal cells (usually filamentous green algae or blue-green algae) with fungal hyphae (usually ascomycetes)

Though lichens vary in shape and physiology, some shared general features characterize the symbiotic relationship.

The alga, which is below the lichen's surface (see Campbell, Figure 31.15),

- Always provides the fungus with food
- May fix nitrogen (e.g.,. cyanobacteria)

The fungus provides a suitable environment for algal growth:

The hyphal mass:

- Absorbs needed minerals from airborne dust or rain
- Retains water and minerals
- Allows gas exchange
- Protects the algae

The fungus produces unique organic compounds with several functions.

- Fungal pigments shade the algae from intense sunlight.
- Toxic fungal compounds prevent lichens from being eaten by consumers.
- Fungal acid secretion aids the uptake of minerals.

Most of the lichen's mass is hyphal tissue which gives the lichen its shape and structure. Named for their fungal component, lichens are informally categorized as:

- Foliose (leafy)
- Fruticose (shrubby)

- Crustose (crusty)

Lichen reproduction occurs as a combined unit or as independent reproduction of the symbionts.

- Many lichen fungi reproduce sexually by forming ascocarps or rarely, basidiocarps.
- Lichen algae reproduce independently by asexual cell division.
- Symbiotic units commonly reproduce asexually by:
  - ⇒ Fragmentation of the parental lichen
  - ⇒ Formation of *soredia*, specialized reproductive structures that are small clusters of hyphae with embedded algae.

Though most evidence points to a mutualistic symbiosis, some debate that the relationship may actually be parasitic.

- The argument for mutualism is that fungi benefit the algae and that lichens can survive in habitats that are inhospitable to either organism alone.
- The argument for "controlled parasitism" is based on the fact that the fungus actually kills some algal cells, though not as fast as the algae replenishes itself.

Lichens are important pioneers, breaking down rock and allowing for colonization by other plants.

- Some can tolerate severe cold.
- Photosynthesis occurs when lichen water content is 65-75%.

Lichens are sensitive to air pollution due to their mode of mineral uptake.

4. Mycorrhizae

Mycorrhizae are specific, mutualistic associations of plant roots and fungi (see Campbell, Figure 31.16).

- The fungi increase the absorptive surface of roots and exchanges soil minerals.

Mycorrhizae are seen in 95% of all vascular plants.

They are necessary for optimal plant growth.

III. Ecological Impacts of Fungi

A. Ecosystems depend on fungi as decomposers and symbionts

Fungi and bacteria are the principal decomposers in ecosystems. Decomposition allows for the recycling of nutrients between biotic and abiotic components.

Fungi decompose food, wood, and even certain plastics.

Between 10% - 50% of the world's fruit harvest is lost each year to fungal attack.

B. Some fungi are pathogens

Many fungi are pathogenic (e.g., athletes foot, ringworm, and yeast infections).

Plants are particularly susceptible. For example, Dutch elm disease, caused by an ascomycete, drastically changed the landscape of northeastern United States.

Ergots = Purple structure on rye caused by an ascomycete

- Causes gangrene, hallucinations, and burning sensations (St. Anthony's fire).
- Produces lysergic acid, from which LSD is made.

Toxins from fungi may be used in weak doses for medical purposes such as treating high blood pressure.

C. Many animals, including humans, eat fungi

Fungi are consumed as food by a variety of animals, including humans.

- In the U.S., mushroom (basidiomycete) consumption is usually restricted to one species of *Agaricus*, which is cultivated commercially on compost in the dark.
- In many other countries, however, people eat a variety of cultivated and wild mushrooms.
- Truffles prized by gourmets are underground ascocarps of mycelia that are mycorrhizal on tree roots (see Campbell, Figure 31.17). The fruiting bodies (ascocarps) release strong odors that attract mammals and insects—consumers that excavate the truffles and disperse their spores.
- Since it is difficult for novices to distinguish between poisonous and edible mushrooms, only qualified experts at identification should collect wild mushrooms for eating.

IV. Phylogenetic Relationships of Fungi

A. Fungi and animals probably evolved from a common protistan ancestor

The presence of flagella in the most primitive group of fungi, the chytrids, suggests that the ancestors of fungi were flagellated and that the lack of flagella in the other fungi divisions is a secondary condition.

There is compelling evidence that animals and fungi diverged from a common protistan ancestor.

- Animals also probably evolved from flagellated protists.
- Proteins and rRNA comparisons indicate that fungi and animals are more closely related to each other than either is to plants. Molecular systematists believe the most likely protistan ancestor common to fungi and animals was a choanoflagellate.

Perhaps the fungi are a consequence of adaptive radiation when life began to colonize land.

- The oldest undisputed fossils are 450-500 million years old.
- All major groups of fungi evolved by the end of the Carboniferous period (approximately 300 million years ago).
- Plants and fungi moved from water to land together. Fossils of the first vascular plants have mycorrhizae.

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