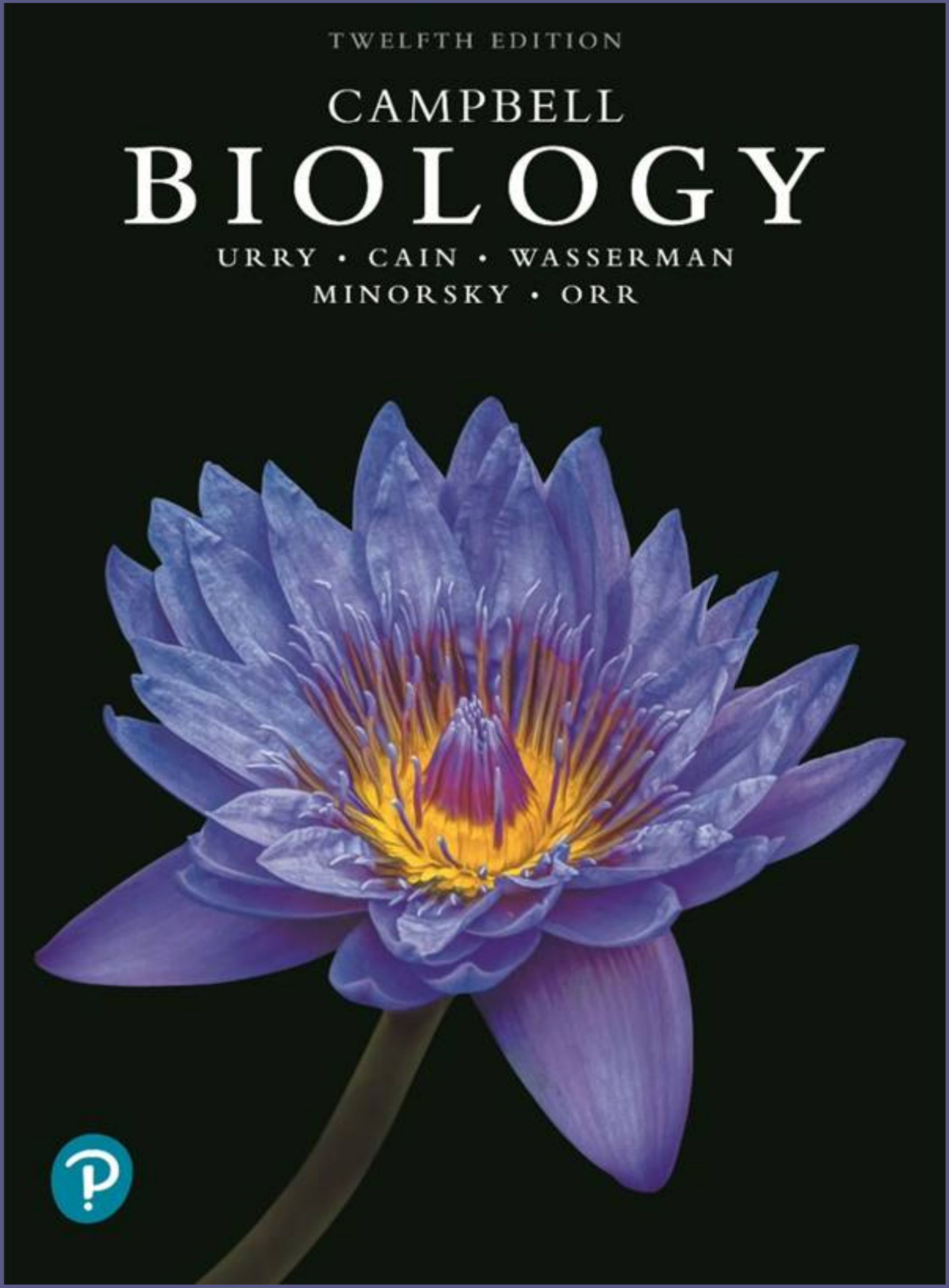


Chapter 31

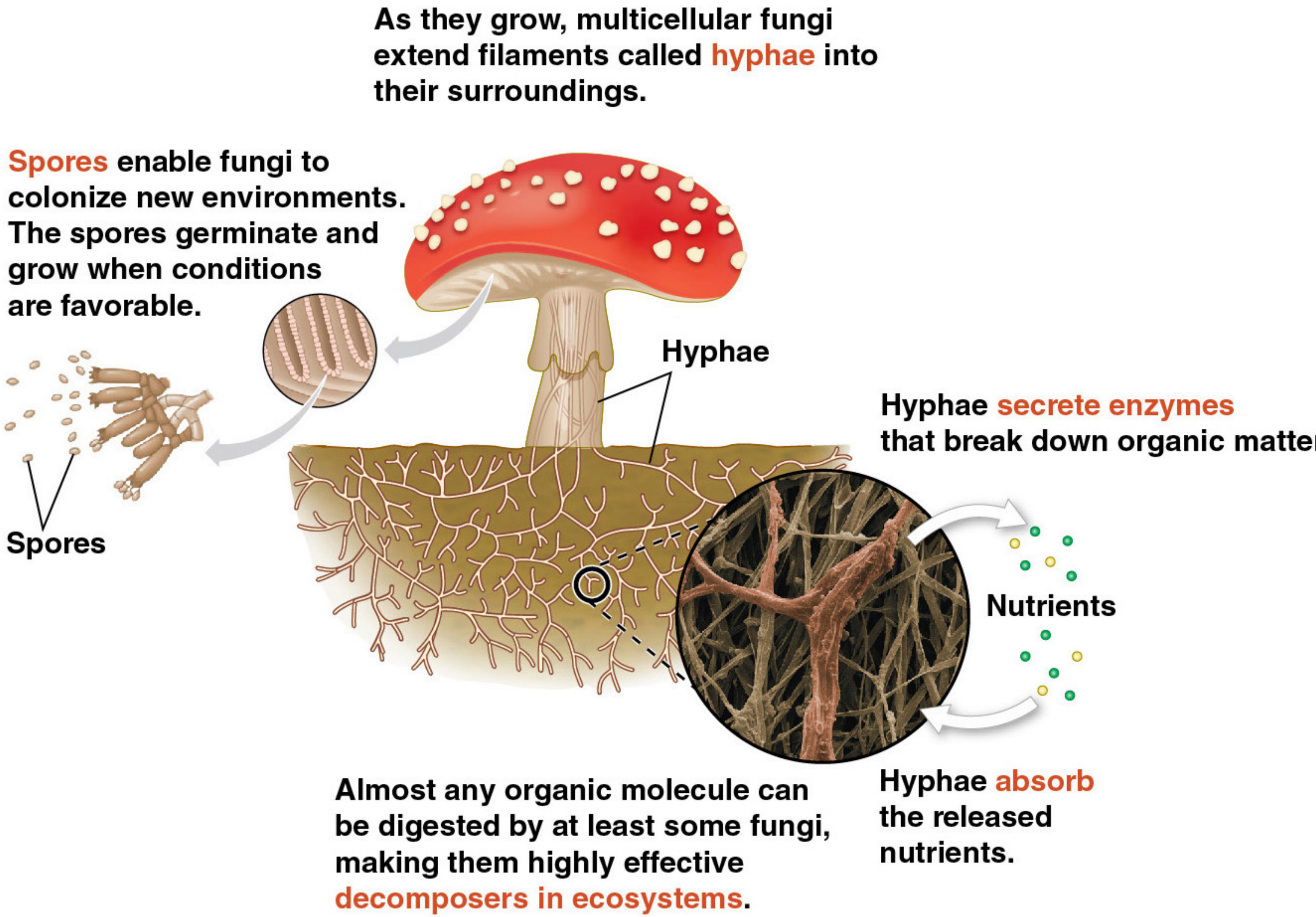
Fungi

Lecture Presentations by
Nicole Tunbridge and
Kathleen Fitzpatrick

Figure 31.1a

Figure 31.1b

How do structure and function in fungi relate to their role in ecosystems?



How do structure and function in fungi relate to their role in ecosystems?

- Fungi are diverse, widespread, and essential for the well-being of most ecosystems
- Some are single-celled, though most are complex multicellular organisms

CONCEPT 31.1: Fungi are heterotrophs that feed by absorption

- Despite their diversity, fungi share key traits, most importantly the way in which they derive nutrition

Nutrition and Ecology

- Fungi are heterotrophs that absorb nutrients from outside of their bodies
- Fungi use hydrolytic enzymes to break down complex molecules into smaller organic compounds
- These enzymes can digest compounds from from a wide range of sources, living or dead

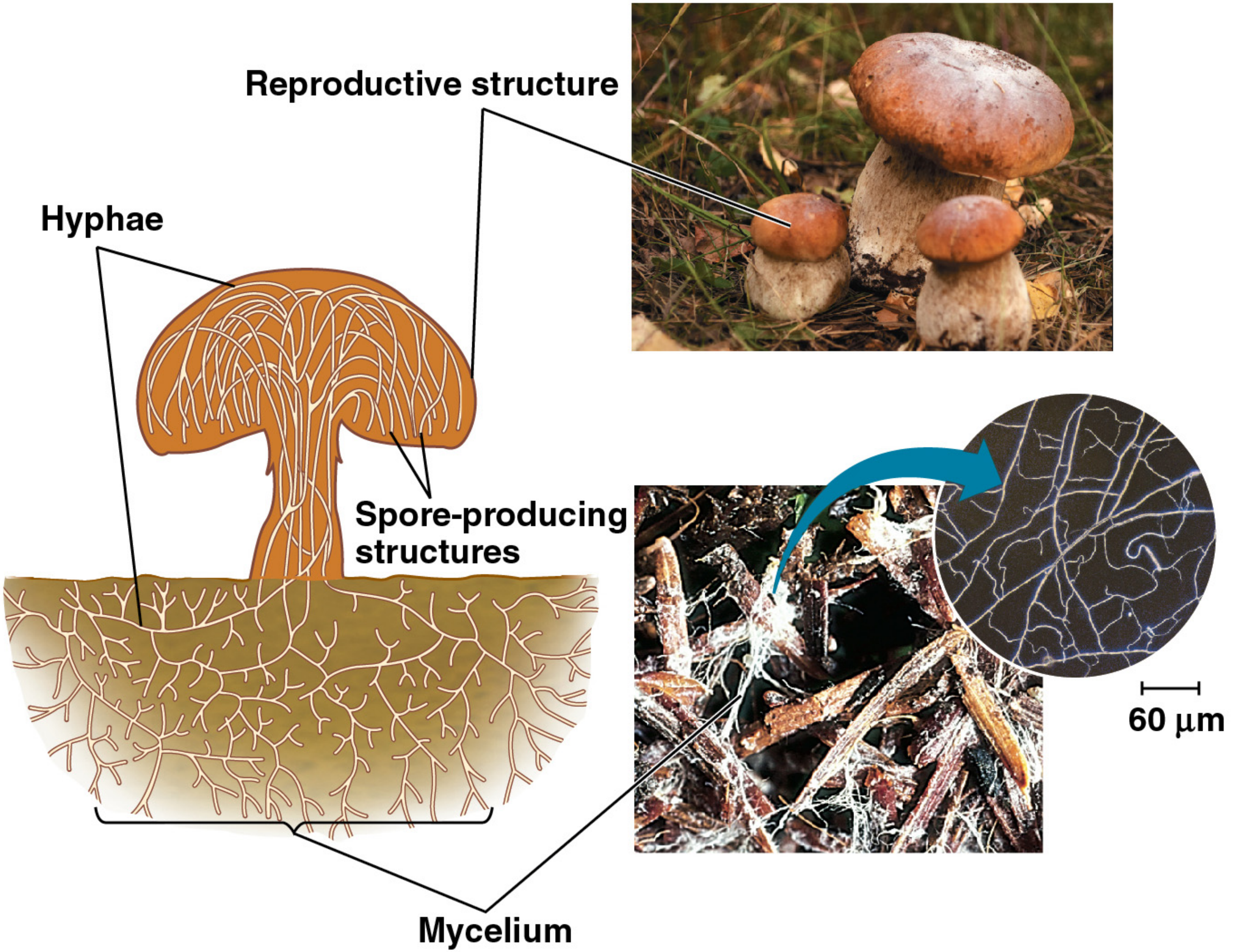
- Fungi exhibit diverse roles in the ecosystem:
  - Decomposers break down and absorb nutrients from nonliving organic material
  - Parasitic fungi absorb nutrients from living hosts
  - Mutualistic fungi absorb nutrients from hosts and reciprocate with actions that benefit the host

Body Structure

- The most common body structures are multicellular filaments and single cells (**yeasts**)
- Many grow as both, but most grow as only as filaments; relatively few grow as yeasts
- Yeasts inhabit moist environments with plentiful soluble nutrients, such as sugars or amino acids

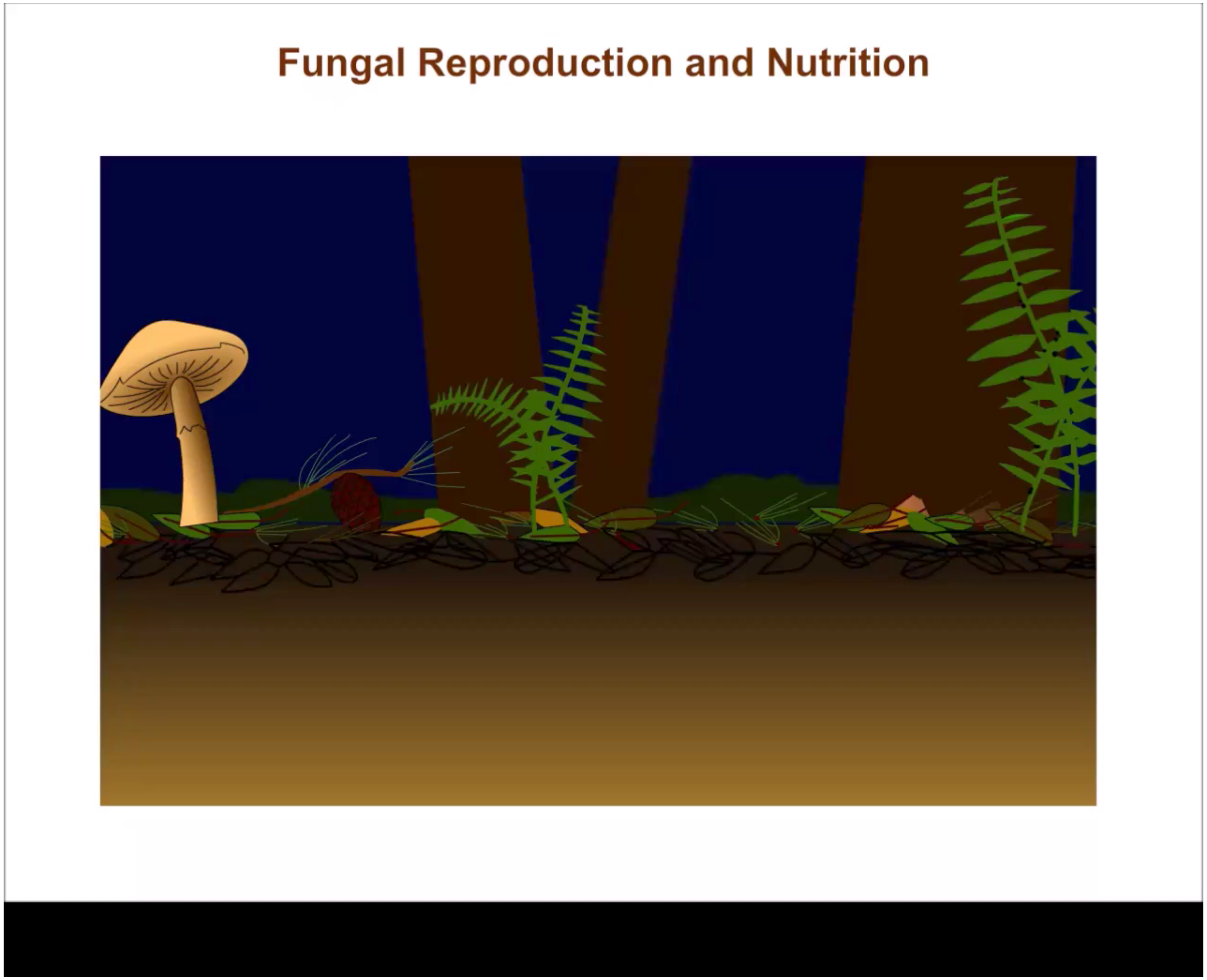
- Fungal bodies form networks of tiny filaments called **hyphae**
- Hyphae have tubular cell walls strengthened with **chitin**, a structural polymer
- Chitin-rich walls prevent cells from lysing due to the osmotic pressure that builds up during nutrient absorption

Figure 31.2



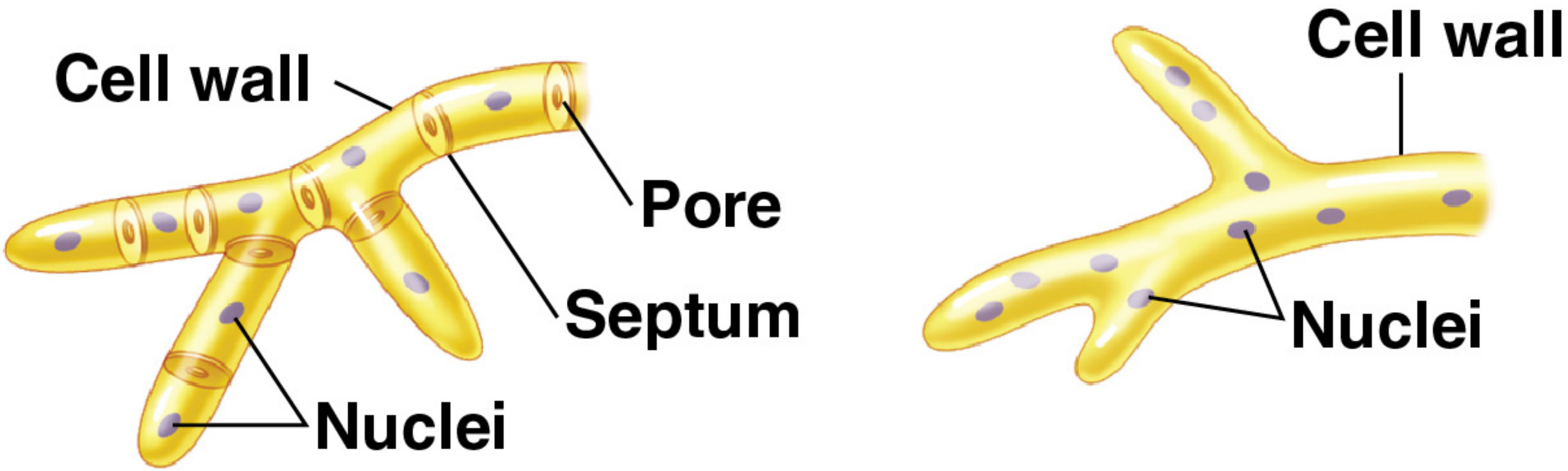
Reproductive structure
Hyphae
Spore-producing structures
60 µm
Mycelium

Animation: Fungal Growth and Nutrition



- In most fungi, hyphae are divided into cells by cross-walls, or **septa**
- Septa have pores large enough to enable cell-to-cell movement of organelles
- **Coenocytic fungi** lack septa; they have hundreds or thousands of nuclei in a continuous cytoplasmic mass

Figure 31.3



(a) Septate hypha

(b) Coenocytic hypha

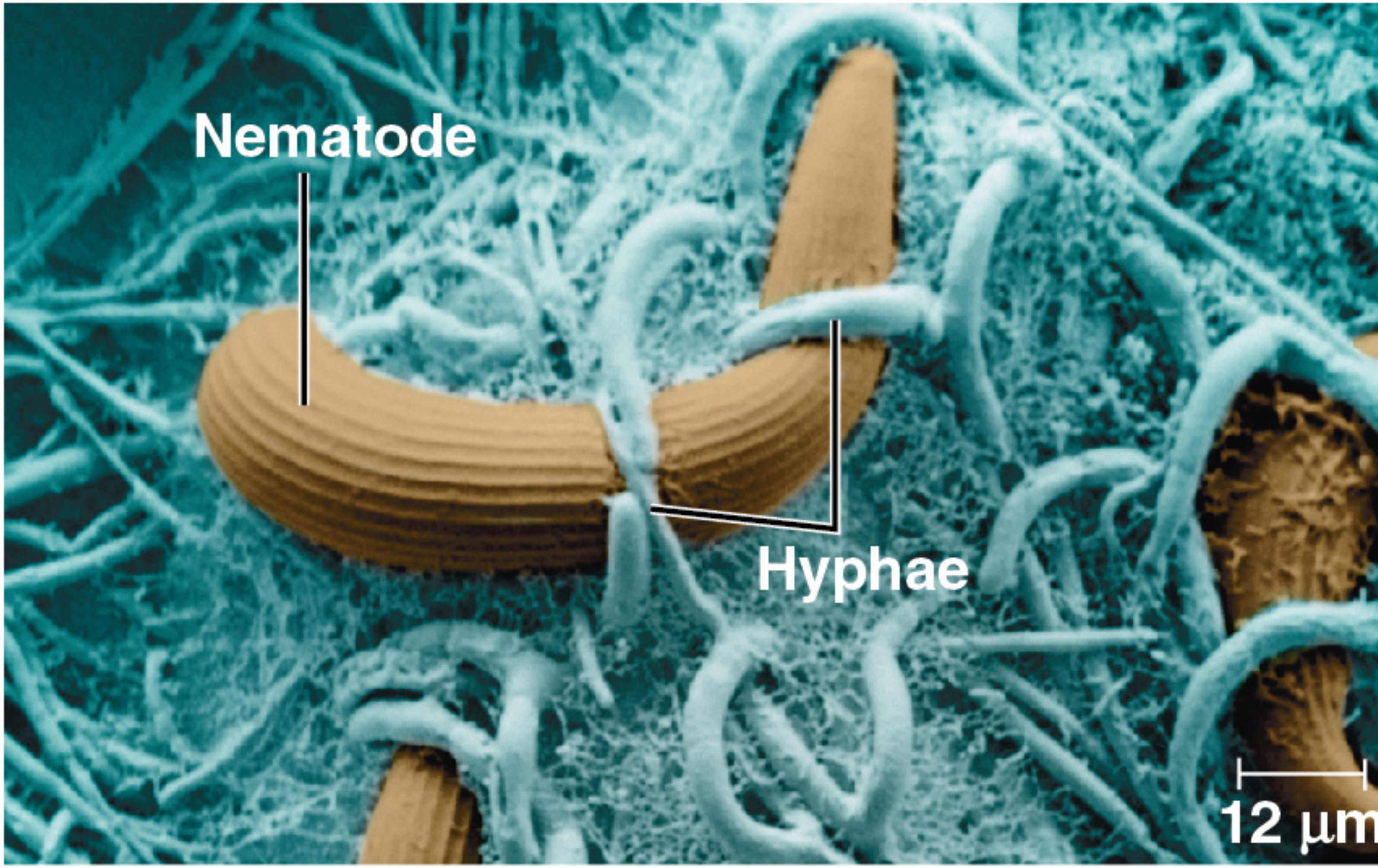
- Fungal hyphae form an interwoven mass called a **mycelium** that infiltrates the food source
- The structure of a mycelium maximizes surface-to-volume ratio, making absorption very efficient

- Hyphae grow primarily in length—not girth—using cytoplasmic streaming to move materials to the tips
- Multicellular fungi are not motile, but can colonize new territory through the growth of their hyphae

Specialized Hyphae in Mycorrhizal Fungi

- Some fungi have specialized hyphae for feeding on live animals
- Others have specialized hyphae called haustoria that allow them to extract nutrients from plants

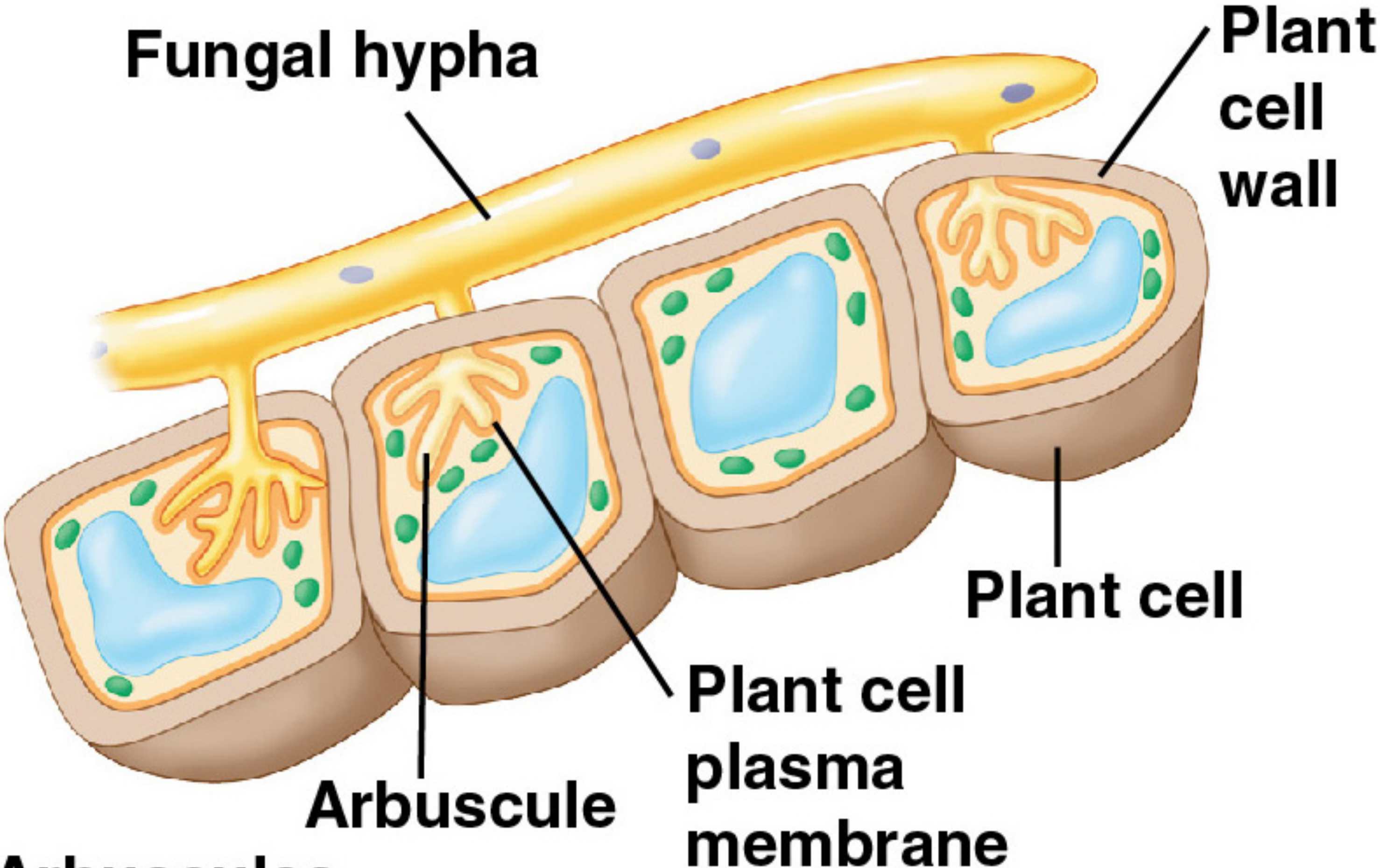
Figure 31.4a



(a) Hyphae adapted for trapping and killing prey

- Mutualistic fungi have specialized branching hyphae used to exchange nutrients with their plant hosts
  - For example, **arbuscules** are specialized hyphae that penetrate plant cell walls, but not the cell membrane

Figure 31.4b



(b) Arbuscules

- Mutually beneficial relationships between fungi and plant roots are called **mycorrhizae** (“fungus roots”)
- Mycorrhizal fungi deliver phosphate ions and minerals to plants
- In exchange, plants supply organic nutrients to the fungi

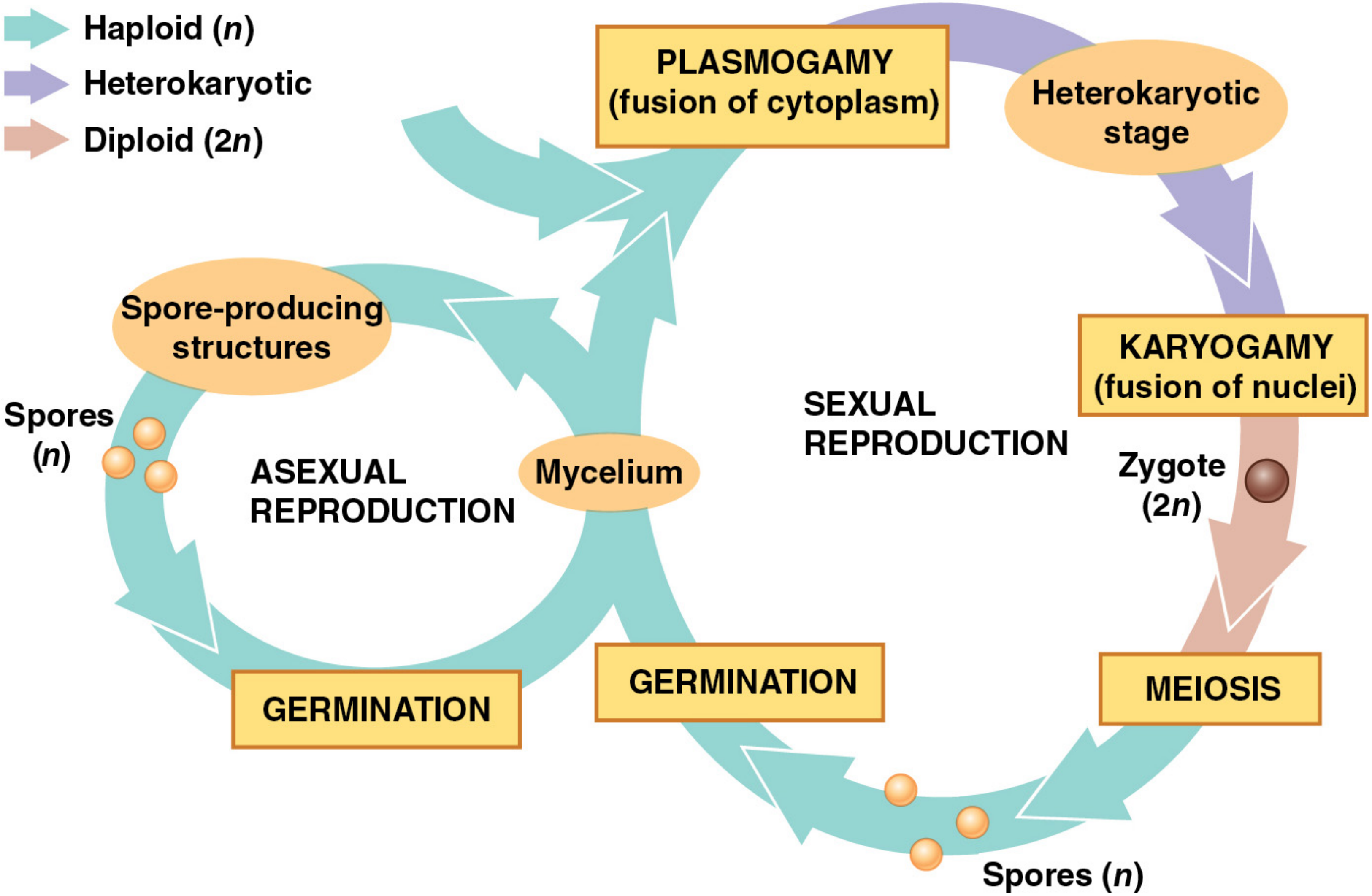
- There are two main types of mycorrhizal fungi
  - **Ectomycorrhizal fungi** form sheaths of hyphae over the root surface and extend into the extracellular spaces of the root cortex
  - **Arbuscular mycorrhizal fungi** extend arbuscules through the root cell wall and into tubes formed by invagination of the root cell plasma membrane

- Most vascular plants depend upon mycorrhizae
- Mycorrhizal fungi colonize soils by the dispersal of haploid cells called **spores**

CONCEPT 31.2: Fungi produce spores through sexual or asexual life cycles

- Fungi propagate themselves by producing vast numbers of spores, either sexually or asexually
- Spores are carried long distances by wind or water
- If they land in a moist place with food, they will germinate and form new mycelia

Figure 31.5


Haploid (n)
Heterokaryotic
Diploid (2n)
PLASMOGAMY (fusion of cytoplasm)
Heterokaryotic stage
KARYOGAMY (fusion of nuclei)
Zygote (2n)
SEXUAL REPRODUCTION
MEIOSIS
Spores (n)
GERMINATION
Mycelium
ASEXUAL REPRODUCTION
Spore-producing structures
Spores (n)
GERMINATION

Sexual Reproduction

- Fungal nuclei and spores are usually haploid
- Some species have transient diploid nuclei formed during the sexual life cycles
- Sexual reproduction requires the fusion of hyphae from different mating types
- Many fungi use sexual signaling molecules called **pheromones** to communicate their mating type

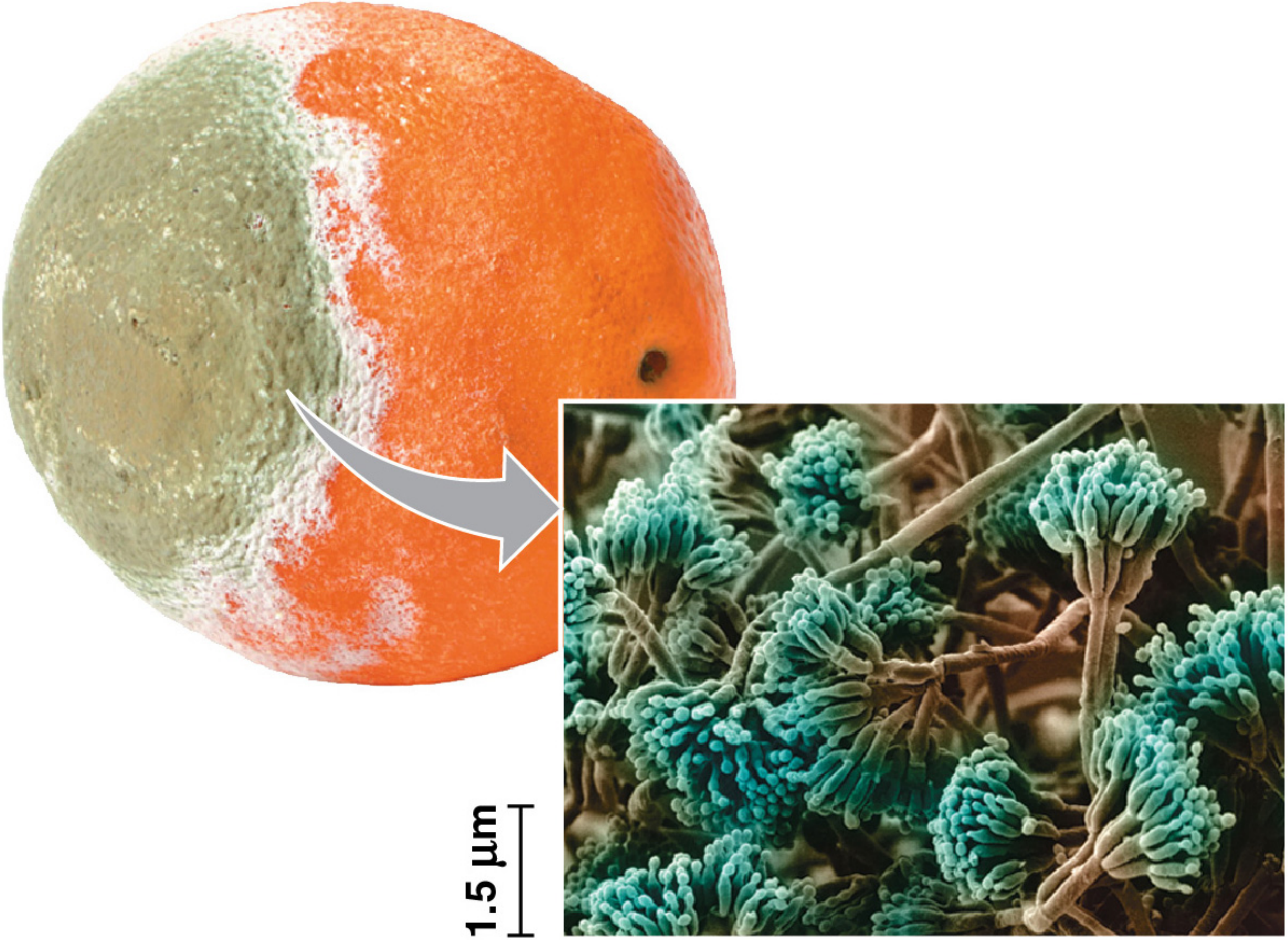
- **Plasmogamy** is the union of cytoplasm from two parent mycelia
- In most fungi, fusion between the haploid nuclei of the parents is delayed
- A mycelium that contains coexisting, genetically different nuclei is called a **heterokaryon**
- In some fungi, the haploid nuclei pair off two to a cell; such a mycelium is said to be **dikaryotic**

- Hours, days, or even centuries may pass before the nuclei fuse, a process called **karyogamy**
- When the haploid nuclei fuse, a diploid cell, such as a zygote, is produced
- The short-lived diploid cell undergoes meiosis, producing haploid spores
- The paired processes of karyogamy and meiosis produce genetic variation

Asexual Reproduction

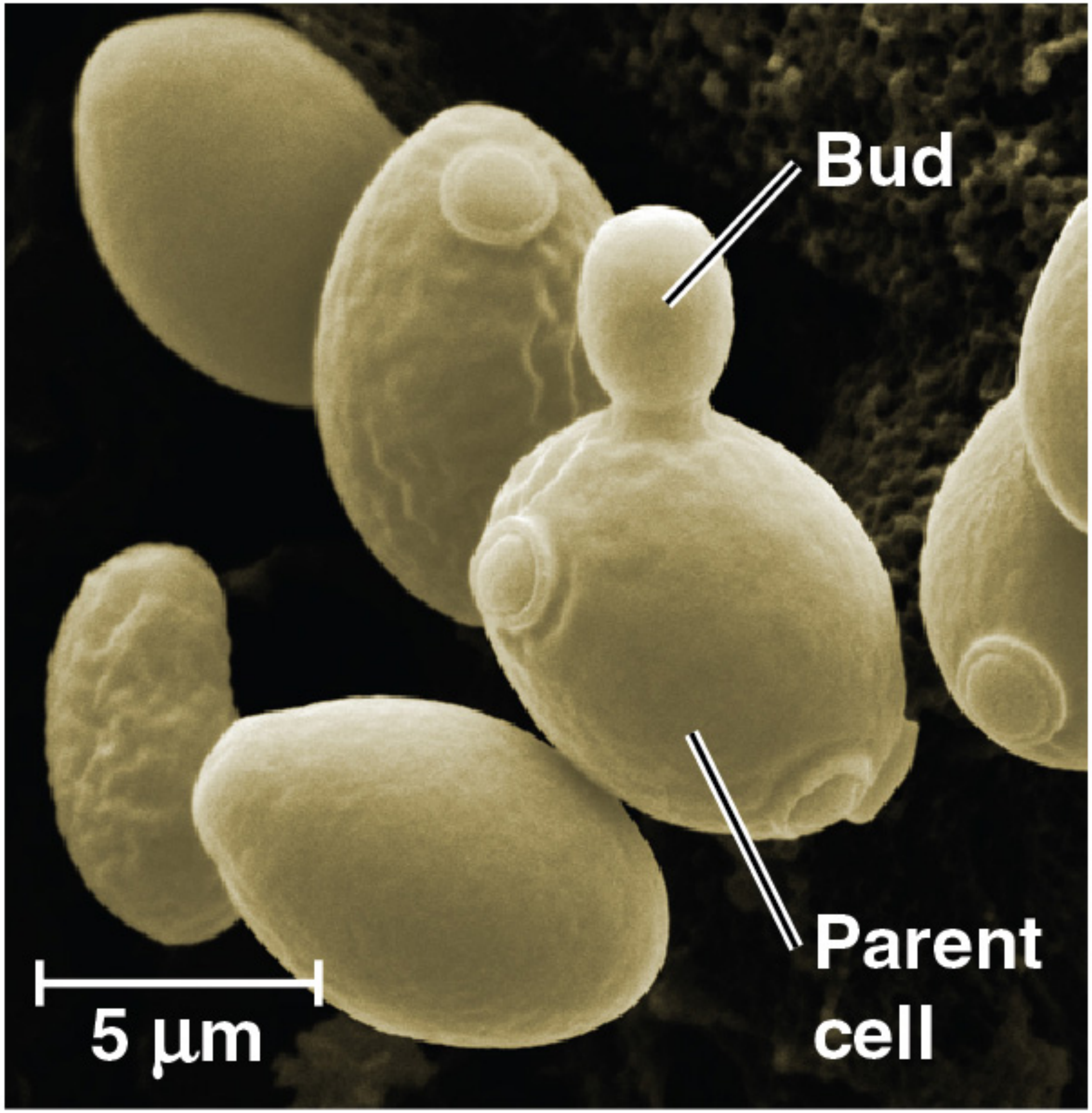
- Many fungi use both sexual and asexual reproduction, but others use only one or the other
- **Molds** produce haploid spores asexually by mitosis, and form visible, “furry” mycelia

Figure 31.6



- Single-celled yeasts reproduce asexually without producing spores
- Reproduction occurs through simple cell division or pinching of small “bud cells” off a parent cell

Figure 31.7



- Yeasts and filamentous fungi that have no known sexual stage form a group called **deuteromycetes**
- They are reclassified if a sexual stage is discovered
- Genomic techniques are also used to classify fungi

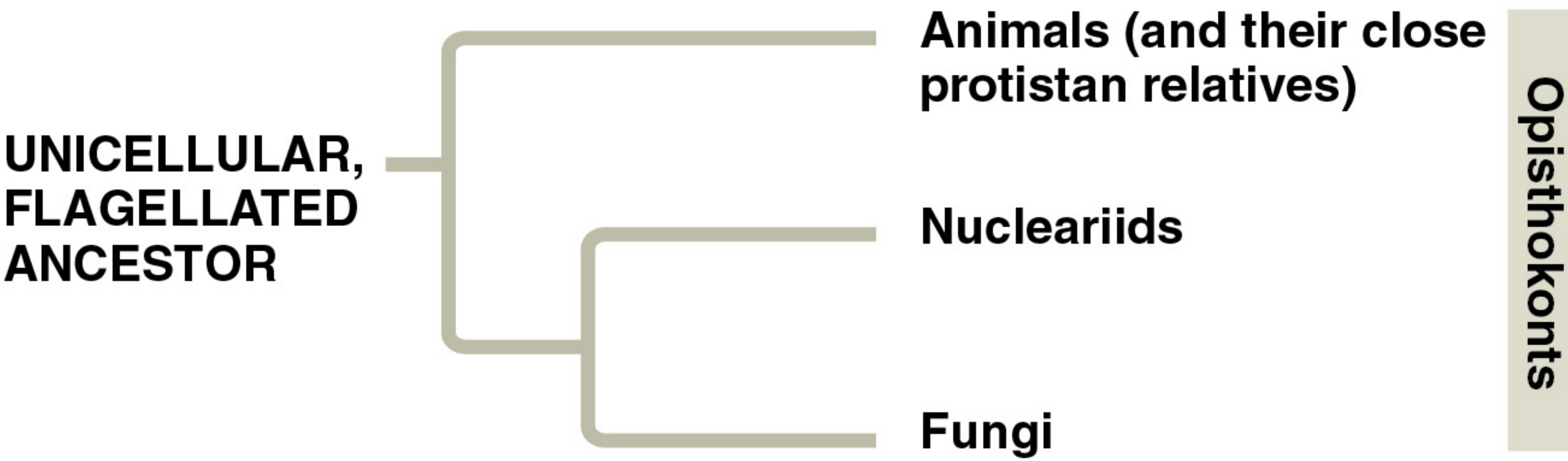
CONCEPT 31.3: The ancestor of fungi was an aquatic, single-celled, flagellated protist

- Fungi and animals are more closely related to each other than either group is to plants or most other eukaryotes

The Origin of Fungi

- The **opisthokonts** clade includes fungi, animals, and their protistan relatives
- Opisthokonts evolved from a unicellular flagellated ancestor

Figure 31.8


UNICELLULAR, FLAGELLATED ANCESTOR
Animals (and their close protistan relatives)
Nucleariids
Fungi
Opisthokonts

- Fungi are most closely related to several groups of single-celled protists
  - For example, **nucleariids** are closely related amoebas that feed on algae and bacteria
- Animals are most closely related to a different group of protists called choanoflagellates
- Multicellularity likely evolved independently in fungi and animals

- Molecular clock analysis indicates that animals and fungi diverged more than a billion years ago
- Fungi likely originated in aquatic habitats, but the oldest widely accepted fossils are of terrestrial species from 440 million years ago
- Fungi may have colonized land as early as 505 million years ago

Figure 31.9

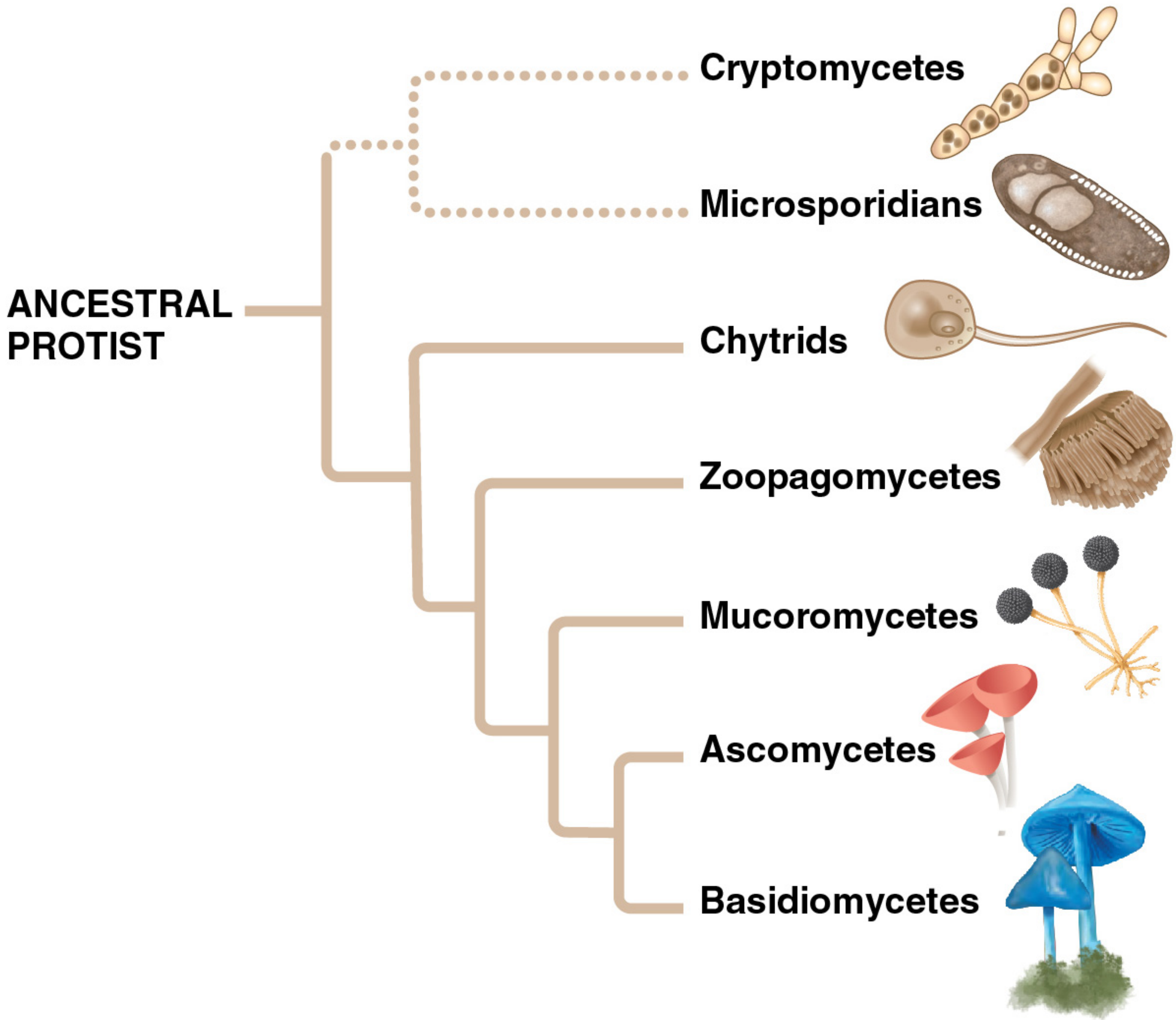
The Move to Land

- Fungi were among the earliest colonizers of land
- Fossil evidence supports the formation of mutualistic relationships between fungi and early plants
- Molecular analysis indicates that *sym* genes required for mycorrhizal formation were present in early plants

CONCEPT 31.4: Fungi have radiated into a diverse set of lineages

- Molecular analyses have helped clarify evolutionary relationships among fungal groups
- Metagenomic studies have led to the discovery of entirely new groups
- There are 145,000 known species of fungi; estimates of the actual number lie between 2.2 and 3.8 million

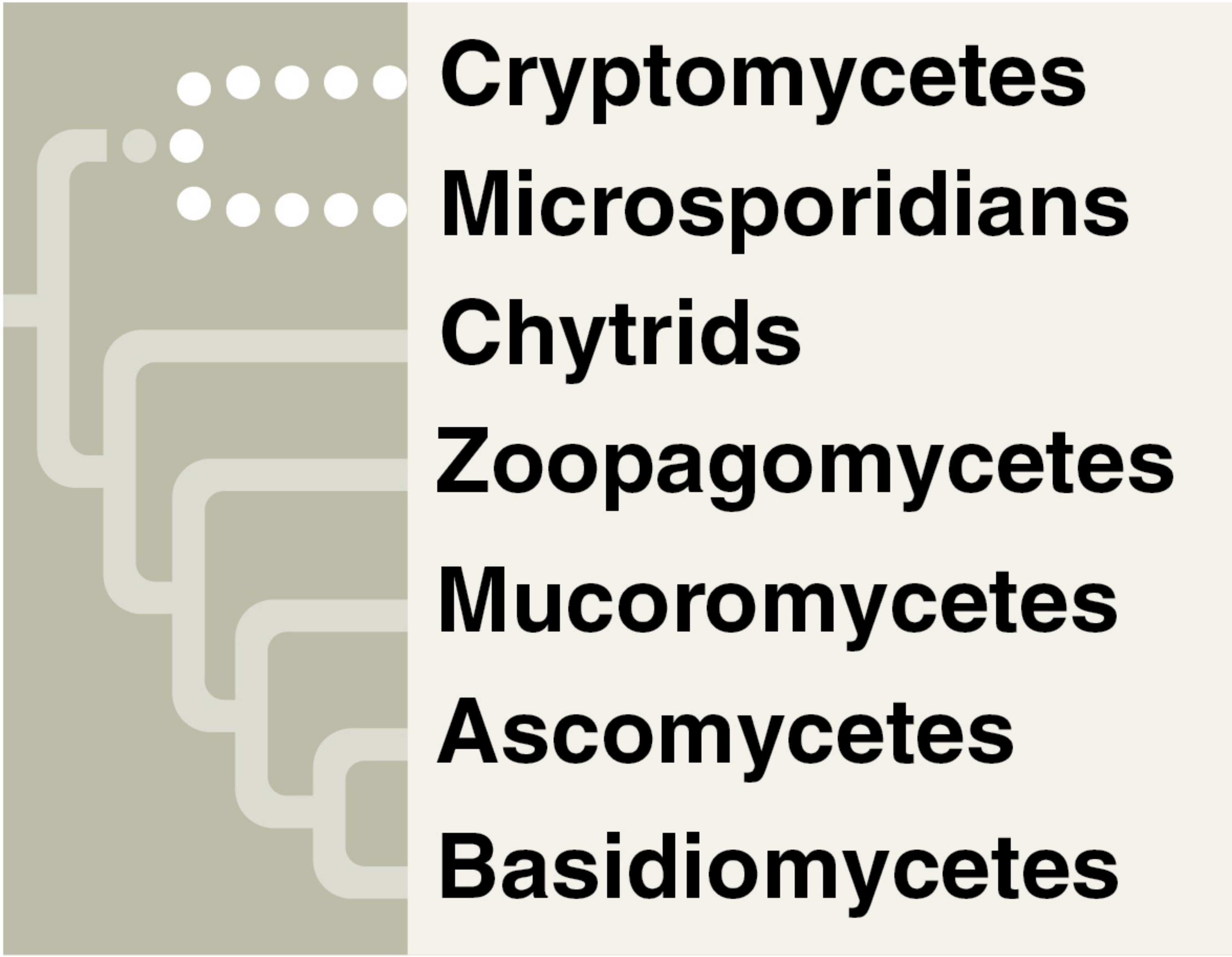
Figure 31.10


Cryptomycetes
Microsporidians
ANCESTRAL PROTIST
Chytrids
Zoopagomycetes
Mucoromycetes
Ascomycetes
Basidiomycetes

Cryptomycetes and Microsporidians

- **Cryptomycetes** (phylum Cryptomycota) and **microsporidians** (phylum Microsporidia) form a sister group and are a basal fungal lineage

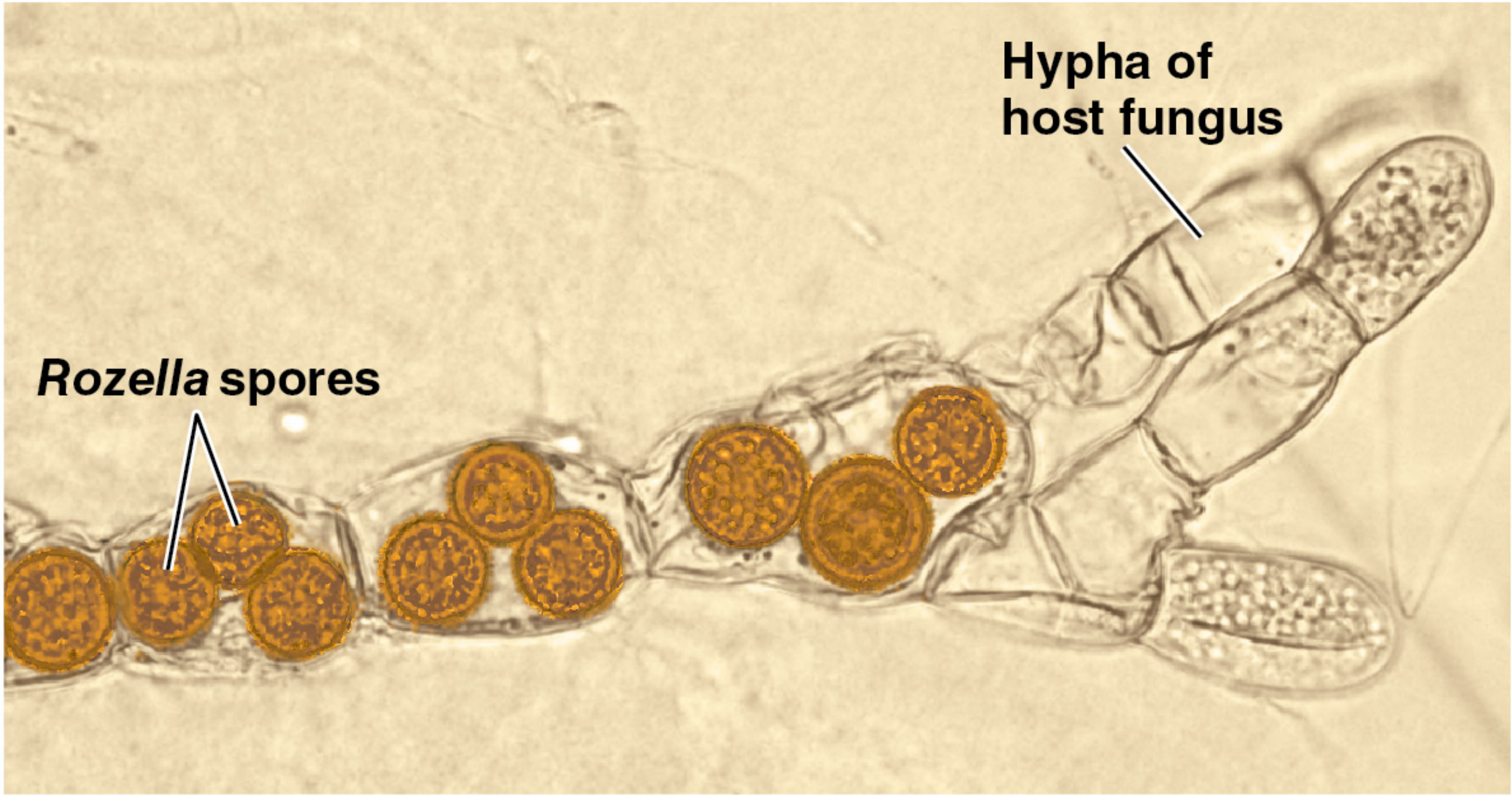
Figure 31.UN01



Cryptomycetes

- Only 30 species are known, but genetic data suggest cryptomycetes are a large, diverse group
- They are found globally in soils, and marine and freshwater habitats
- There are both aerobic and anaerobic species
- Many species are parasites of protists and other fungi

Figure 31.11

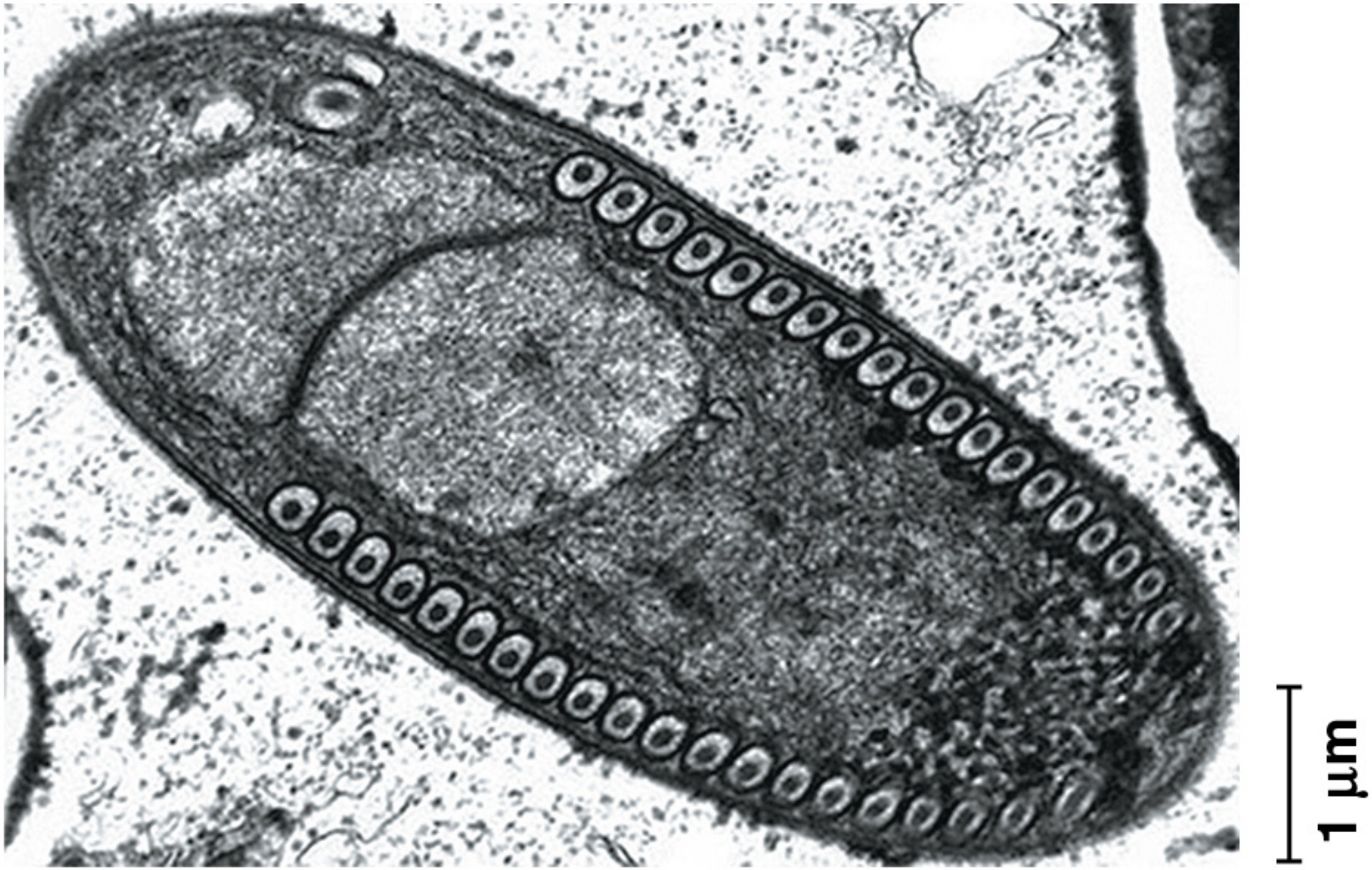


- Cryptomycetes are unicellular and have flagellated spores
- Like other fungi, they can synthesize a chitin-rich cell wall

Microsporidians

- The 1,300 known species of microsporidians are unicellular parasites of protists and animals, including humans
  - For example, *Nosema ceranae* is a parasite of honeybees that may contribute to Colony Collapse Disorder

Figure 31.12

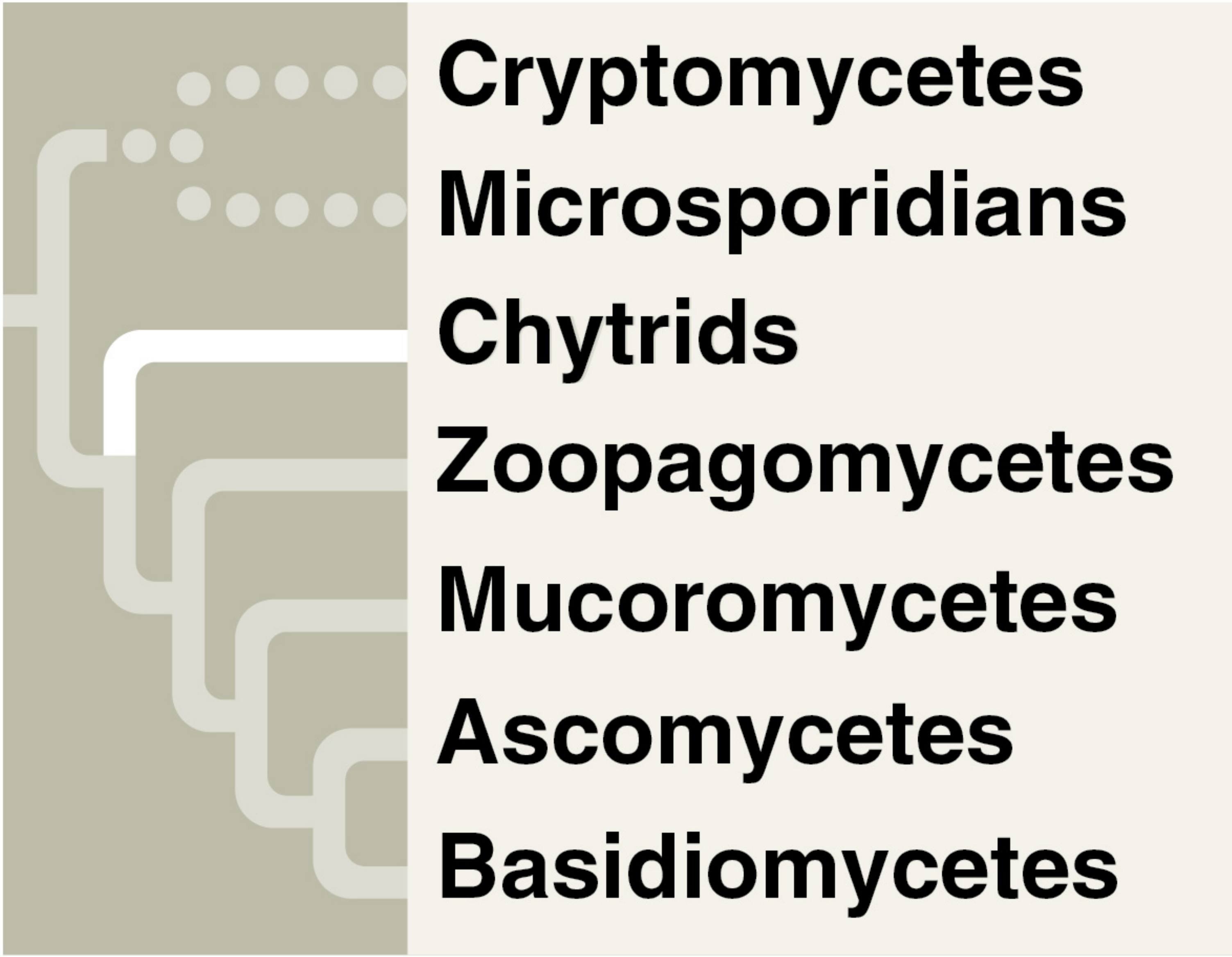


- Microsporidians can synthesize a chitin-rich cell wall
- They have highly reduced mitochondria and small genomes with as few as 2,000 genes
- Instead of flagellated spores, they produce spores that infect host cells via a harpoon-like organelle

Chytrids

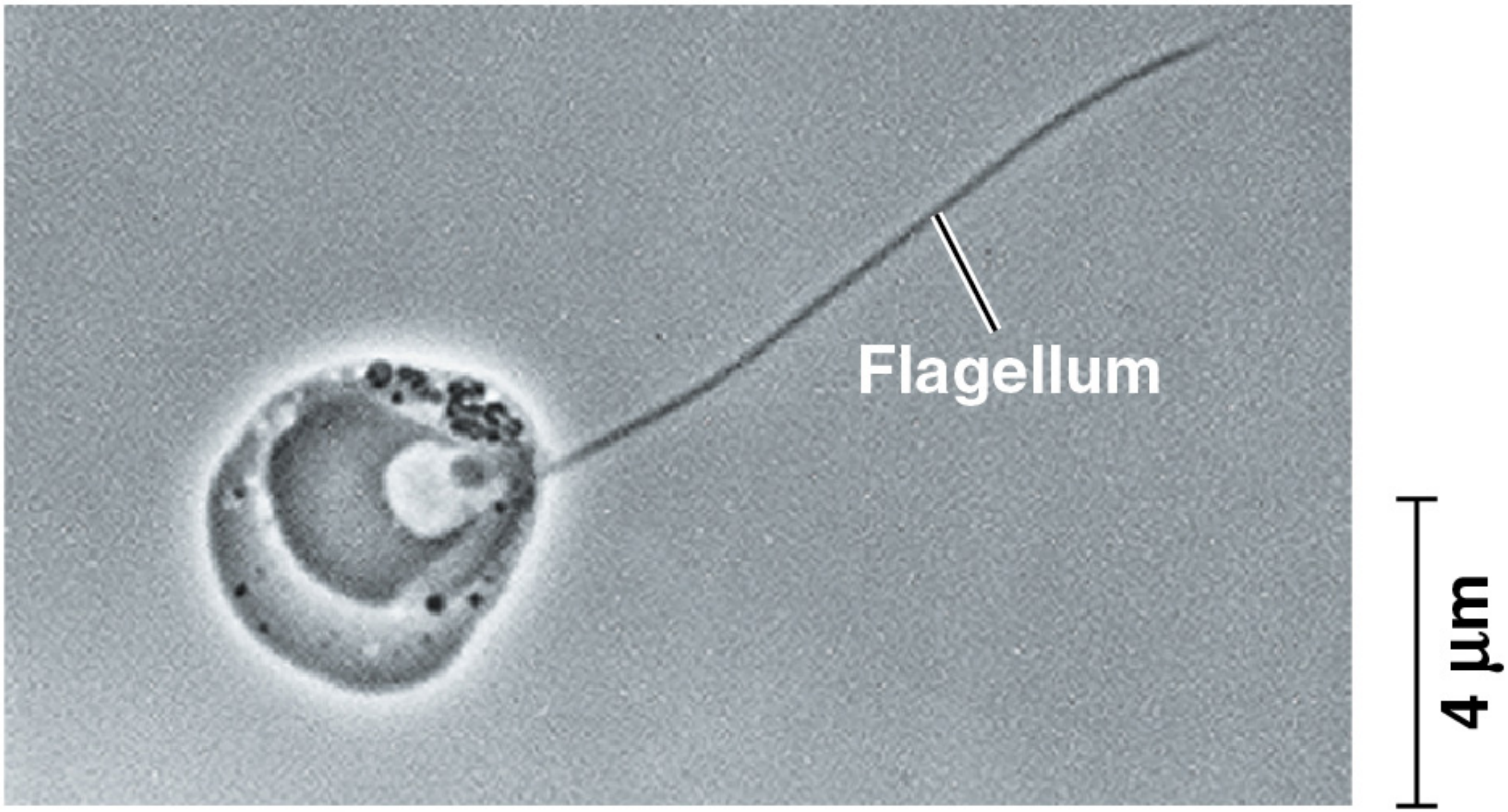
- There are about 1,000 known species of **chytrids** (phylum Chytridiomycota)
- They are found in lakes, soil, and marine habitats including hydrothermal vents
- They include species that function as decomposers, parasites, and mutualists

Figure 31.UN02



- Nearly all chytrids have flagellated spores, called **zoospores**
- Like other fungi, the cell walls are made of chitin
- Some are single-celled; others form colonies

Figure 31.13

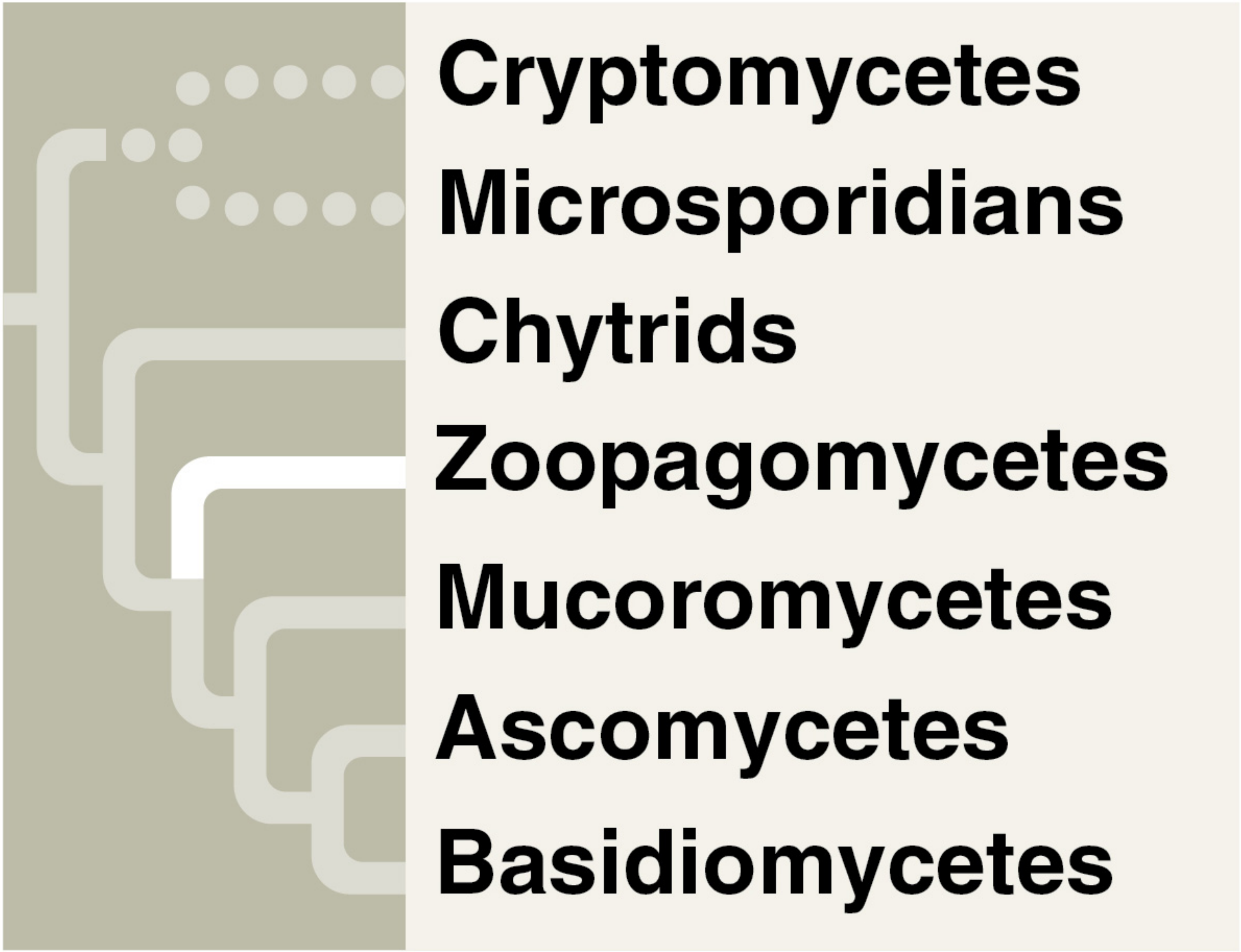


Video: *Phlyctochytrium* Zoospore Release

Zoopagomycetes

- There are about 900 known species of **zoopagomycetes** (phylum Zoopagomycota)
- They live as parasites or commensal symbionts of animals, or as parasites of other fungi or protists
- Zoopagomycetes form filamentous hyphae and reproduce asexually via nonflagellated spores

Figure 31.UN03

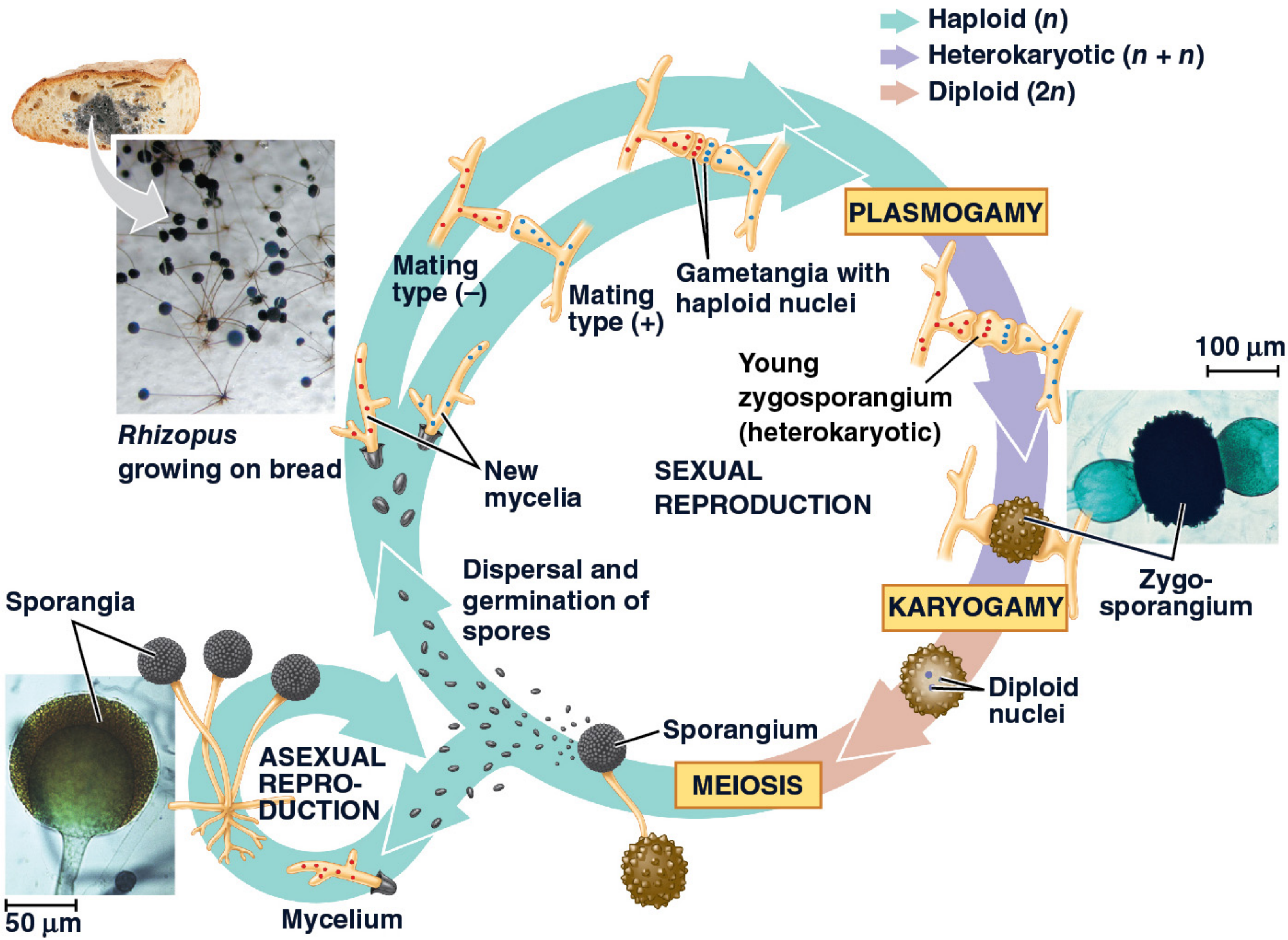


- Some species induce behavioral changes in the insects they parasitize

Figure 31.14

- Those that reproduce sexually form a durable structure called a zygosporangium
- The zygosporangium houses and protects the zygote
- This structure is also produced by some mucoromycete species

Figure 31.15



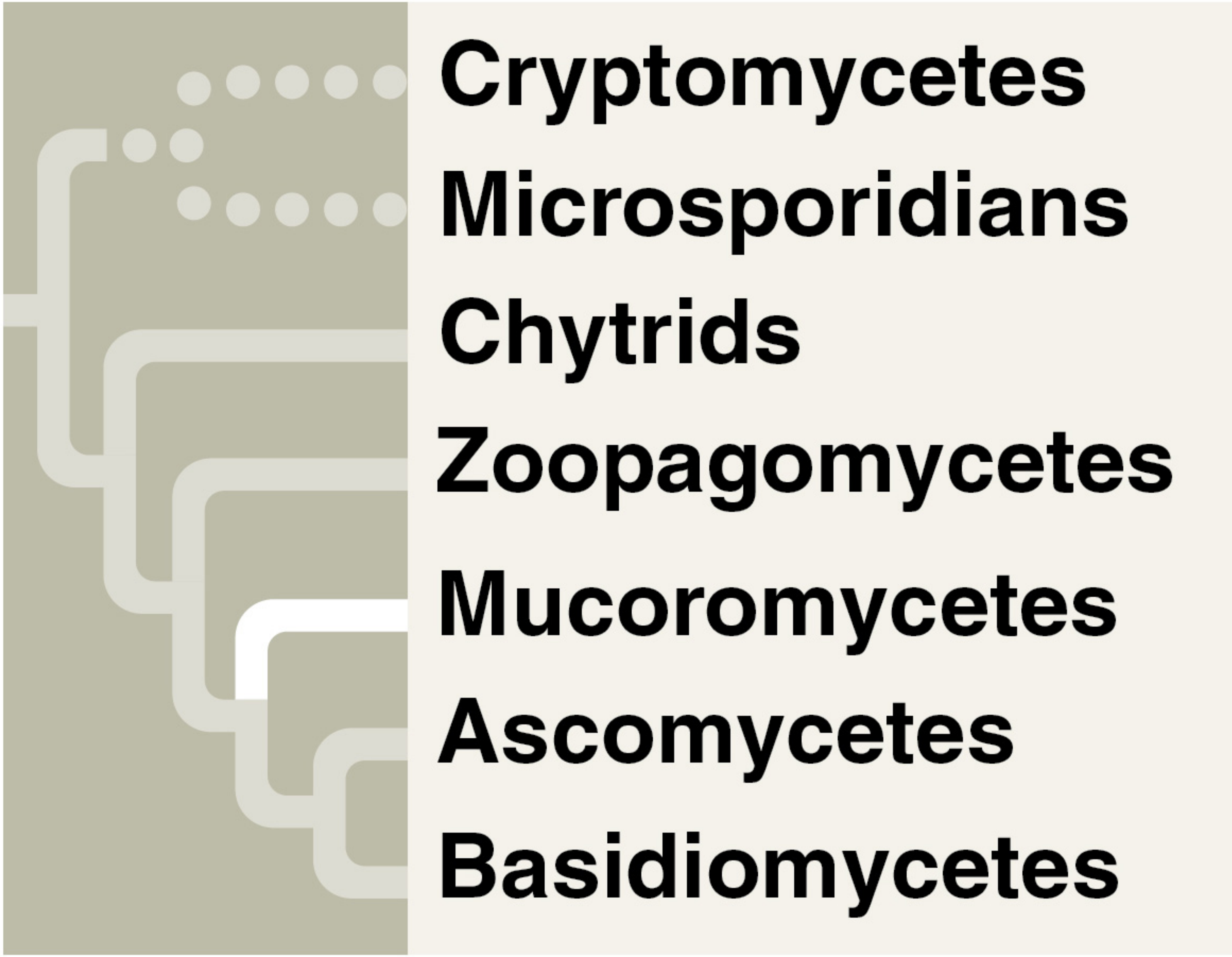
Haploid (n)
Heterokaryotic (n + n)
Diploid (2n)
PLASMOGAMY
Gametangia with haploid nuclei
Mating type (–)
Mating type (+)
Young zygosporangium (heterokaryotic)
100 µm
Rhizopus growing on bread
New mycelia
SEXUAL REPRODUCTION
Zygo-sporangium
KARYOGAMY
Dispersal and germination of spores
Sporangia
Diploid nuclei
Sporangium
MEIOSIS
ASEXUAL REPRO-DUCTION
50 µm
Mycelium

- Unlike more basal species, zoopagomycetes and their close relatives have nonflagellated, wind dispersed spores
- This change was likely associated with the transition from aquatic habitats to life on land

Mucoromycetes

- There are about 750 known species of **mucoromycetes** (phylum Mucoromycota)
- Molds in this group include important decomposers
  - For example, *Rhizopus stolonifer* is the mold responsible for breaking down bread
- Many others live as parasites, pathogens, or mutualists with plants (including some mycorrhizae)

Figure 31.UN04



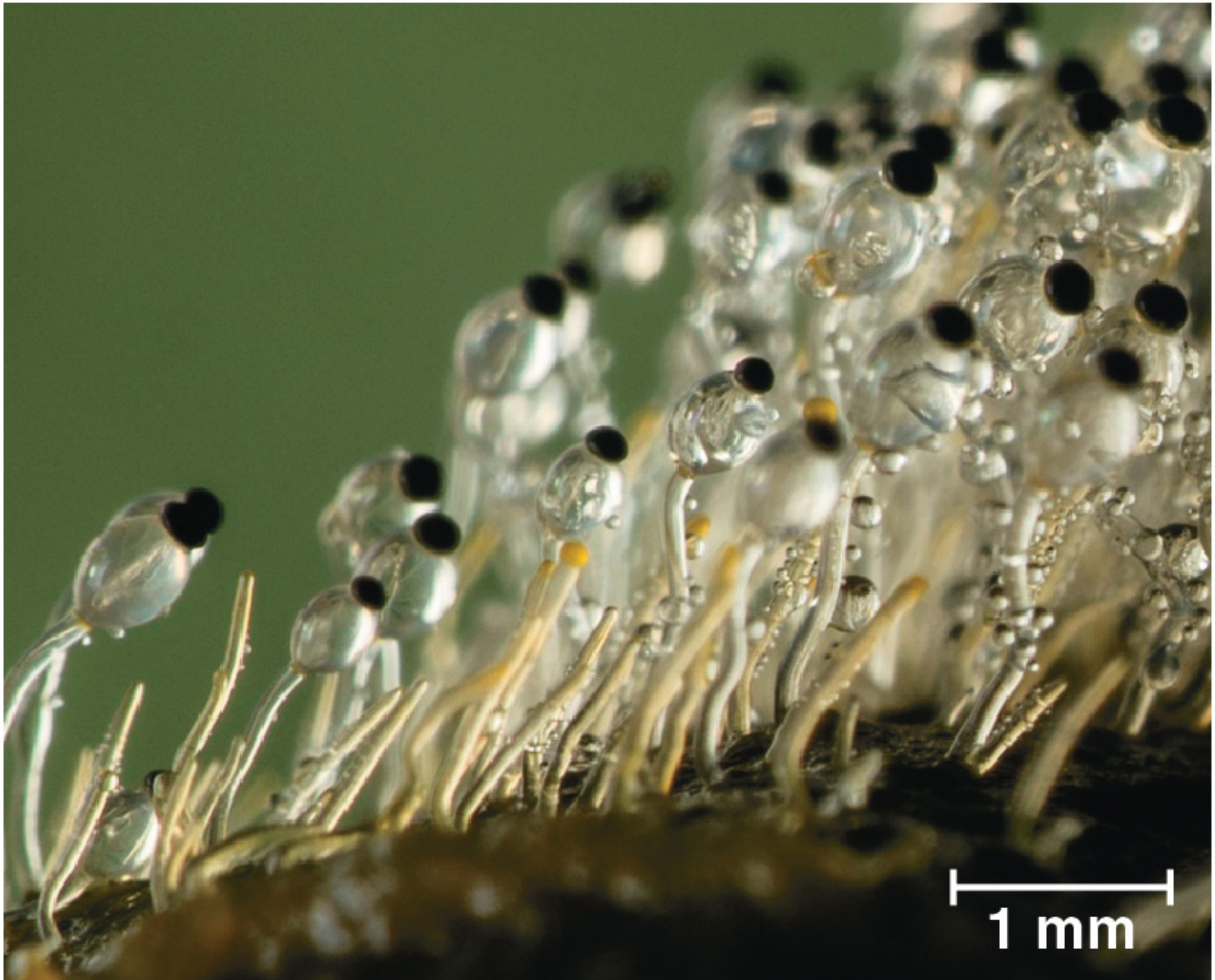
- In deteriorating conditions—for instance, most of the food is consumed—sexual reproduction may occur
- Fusion between mycelia of different mating types (plasmogamy) produces a **zygosporangium**
- Nuclei fusion (karyogamy) and then meiosis occur within the zygosporangium

- The life cycle of *Rhizopus stolonifer* (black bread mold) is fairly typical of mucoromycetes
- Coenocytic hyphae spread and penetrate the surface, absorbing nutrients from the rotting food
- Sporangia develop at the tips of upright hyphae, and asexually produce hundreds of air-dispersed spores

- Zygosporangia are metabolically inactive and resistant to freezing and drying
- When conditions improve, meiosis occurs and the zygosporangium germinates into a sporangium
- The sporangium releases genetically diverse haploid spores

- Some mucoromycetes, such as *Pilobolus*, can “aim” and shoot their sporangia toward bright light

Figure 31.16

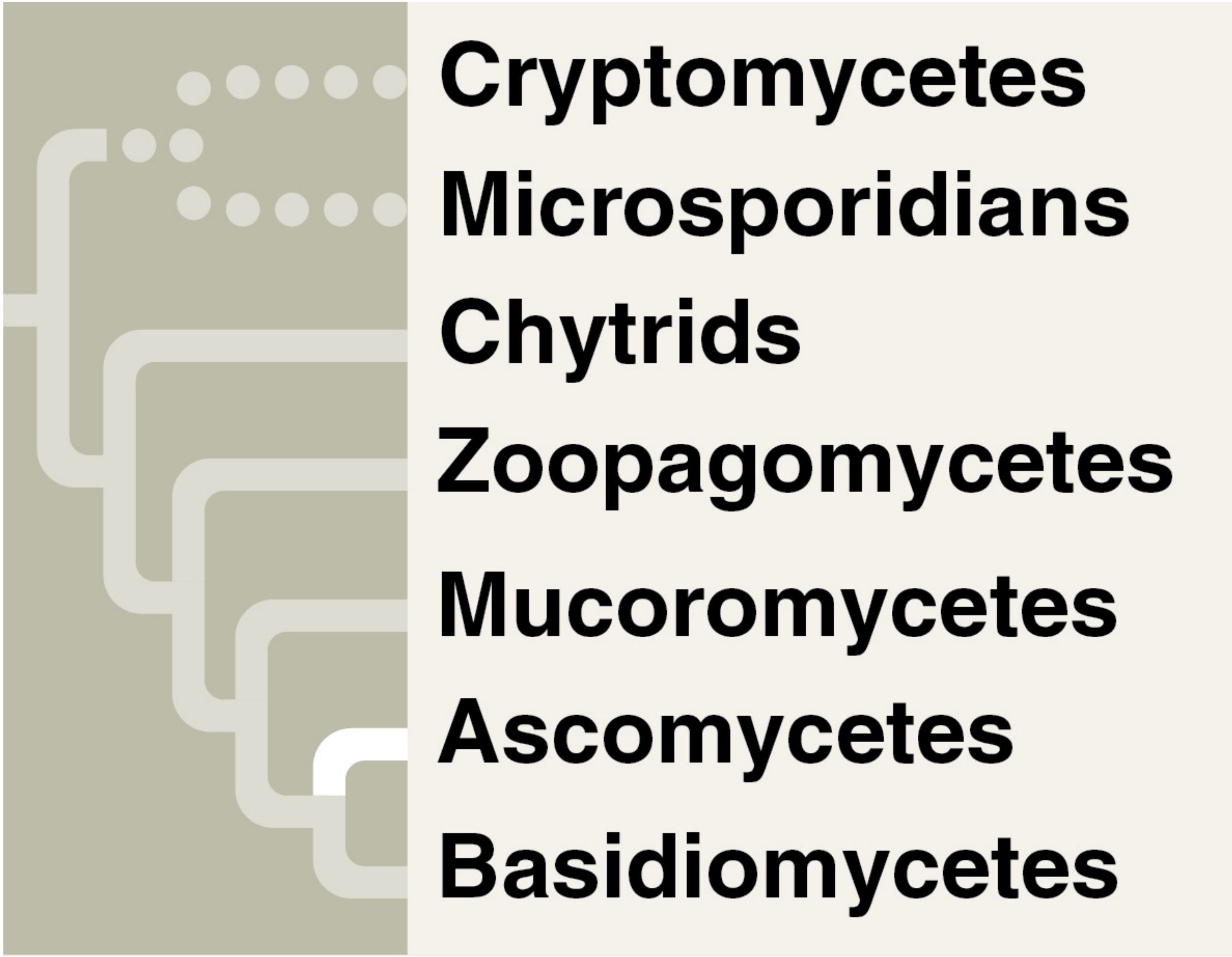


- Phylum Mucoromycota also includes an arbuscular forming clade of fungi called glomeromycetes
- About 85% of all plant species have mutualistic partnerships with arbuscular mycorrhizae

Ascomycetes

- There are about 90,000 known species of **ascomycetes** (phylum Ascomycota)
- They live in a variety of marine, freshwater, and terrestrial habitats
- They vary in size and complexity from unicellular yeasts to elaborate cup fungi and morels

Figure 31.UN05



- Ascomycetes are often called sac fungi, named for the saclike **asci**, in which spores are produced
- During the sexual stage, ascomycetes produce fruiting bodies called **ascocarps**
- The ascocarps contain the spore-forming asci

Figure 31.17

Morchella esculenta

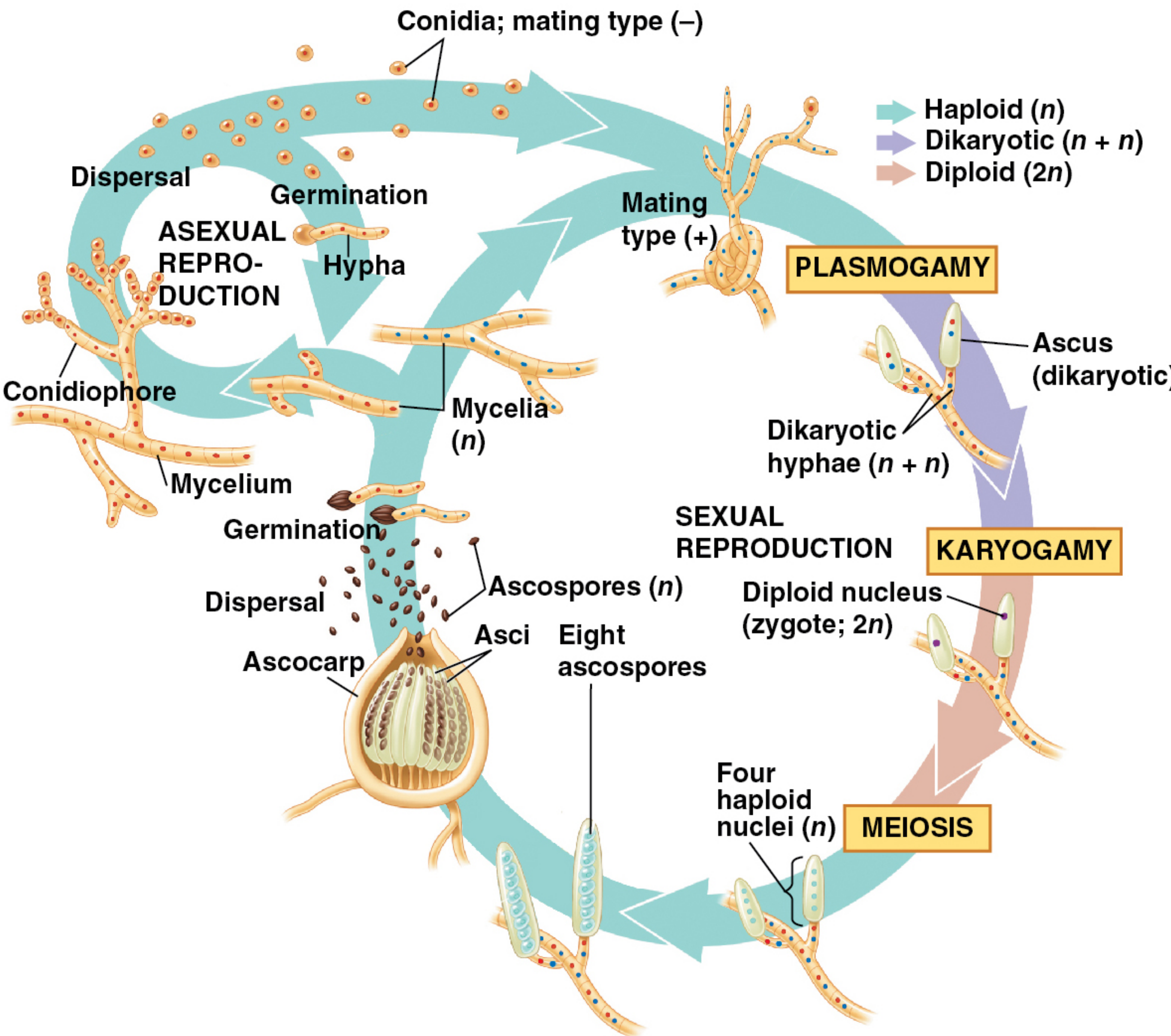
Tuber melanosporum

- Ascomycetes include plant pathogens, decomposers, and symbionts
- More than 25% of all ascomycete species form lichens, symbiotic associations with green algae or cyanobacteria
- Some form mycorrhizae with plants; others live within plant leaves and produce compounds toxic to insects

- Ascomycetes reproduce asexually by enormous numbers of asexual spores called **conidia**
- Conidia are produced at the tips of specialized hyphae called conidiophores

- In sexual reproduction, conidia fuse with the hyphae of a mycelium from a different mating type
- Dikaryotic cells are formed, each containing two haploid nuclei, one from each parent
- Asci form at the tips of dikaryotic hyphae, and karyogamy and meiosis occur within the asci
- Ascospores develop and are discharged from the ascocarp

Figure 31.18



Conidia; mating type (–)
Haploid (n)
Dikaryotic (n + n)
Diploid (2n)
Dispersal
Germination
ASEXUAL REPRO-DUCTION
Hypha
Mating type (+)
PLASMOGAMY
Ascus (dikaryotic)
Conidiophore
Mycelia (n)
Dikaryotic hyphae (n + n)
Mycelium
Germination
SEXUAL REPRODUCTION
KARYOGAMY
Ascospores (n)
Diploid nucleus (zygote; 2n)
Dispersal
Asci
Eight ascospores
Ascocarp
Four haploid nuclei (n)
MEIOSIS

- *Neurospora crassa*, a bread mold, is a model research organism
- Its entire genome was published in 2003
- *Neurospora* has about three-fourths as many genes as the fruit fly *Drosophila* and about half as many as a human

Table 31. 1 Comparison of Gene Density in *Neurospora, Drosophila*, and *Homo sapiens*

	Genome Size (million base pairs)	Number of Genes	Gene Density (genes per million base pairs)
Neurospora crassa **(ascomycete fungus)**	41	9,700	236
Drosophila melanogaster **(fruit fly)**	165	14,000	85
Homo sapiens **(human)**	3,000	<21,000	7

Basidiomycetes

- There are about 50,000 known species of **basidiomycetes** (phylum Basidiomycota) including mushrooms, puffballs, and shelf fungi
- Some are mutualists that form mycorrhizae
- Others are destructive plant parasites: rusts and smuts

Figure 31.UN06

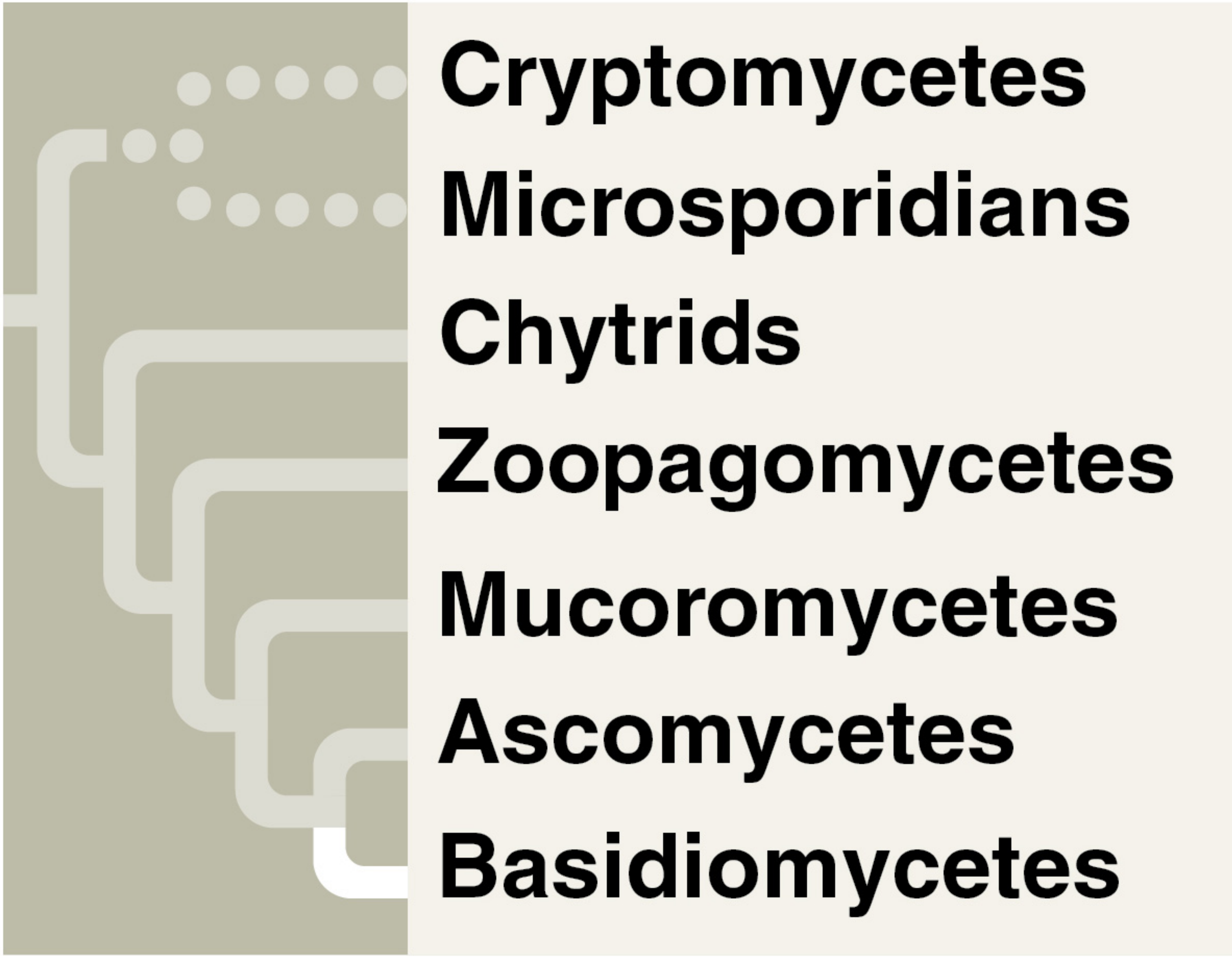


Figure 31.19

Puffballs

Shelf fungi

Maiden veil fungus

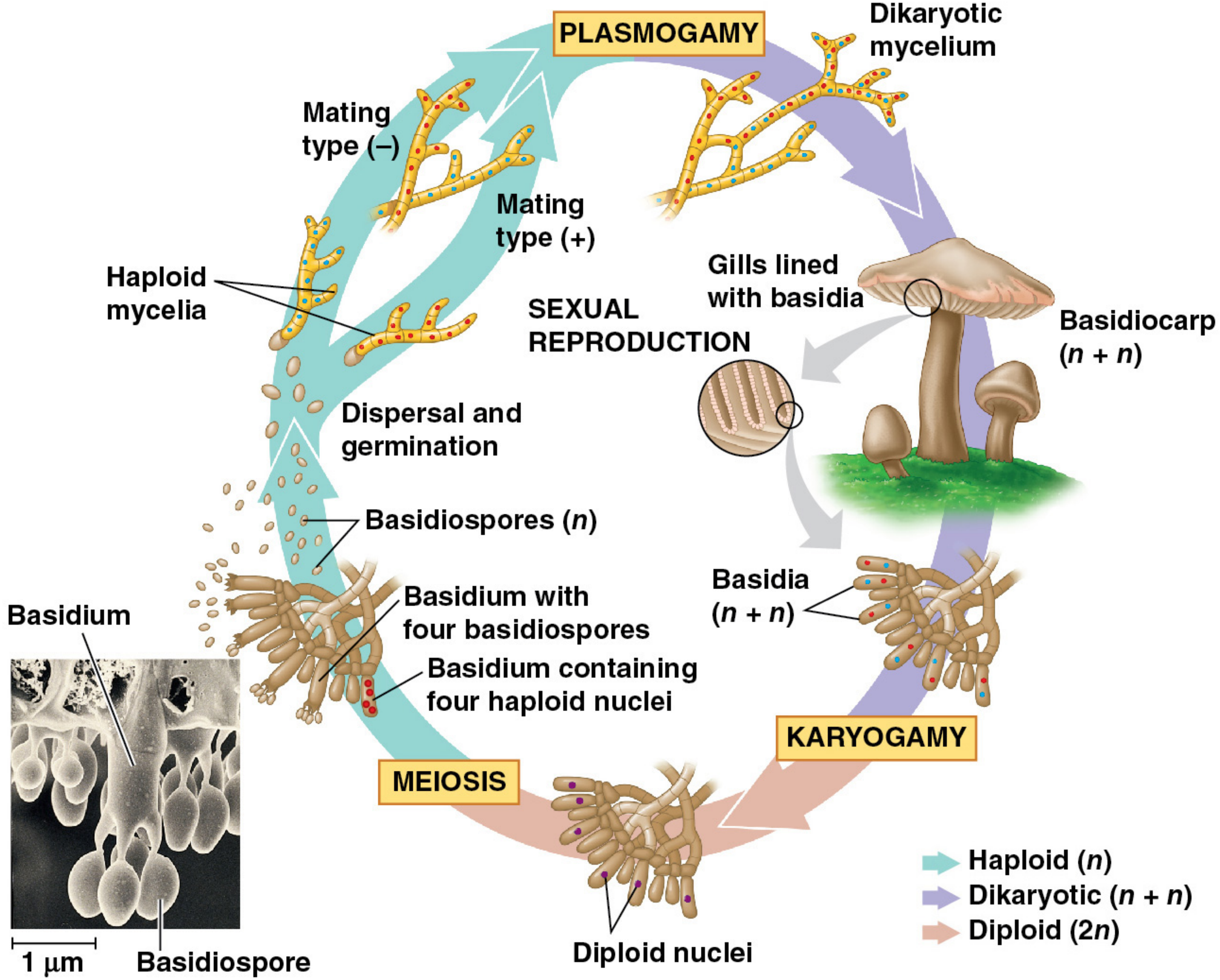
- The phylum is named for the **basidium**, a cell in which karyogamy and meiosis occur
- The club-like shape of the basidium gives rise to the common name club fungus

- Basidiomycetes are important decomposers of wood
- Certain basidiomycetes are the best at decomposing lignin, a complex polymer abundant in wood

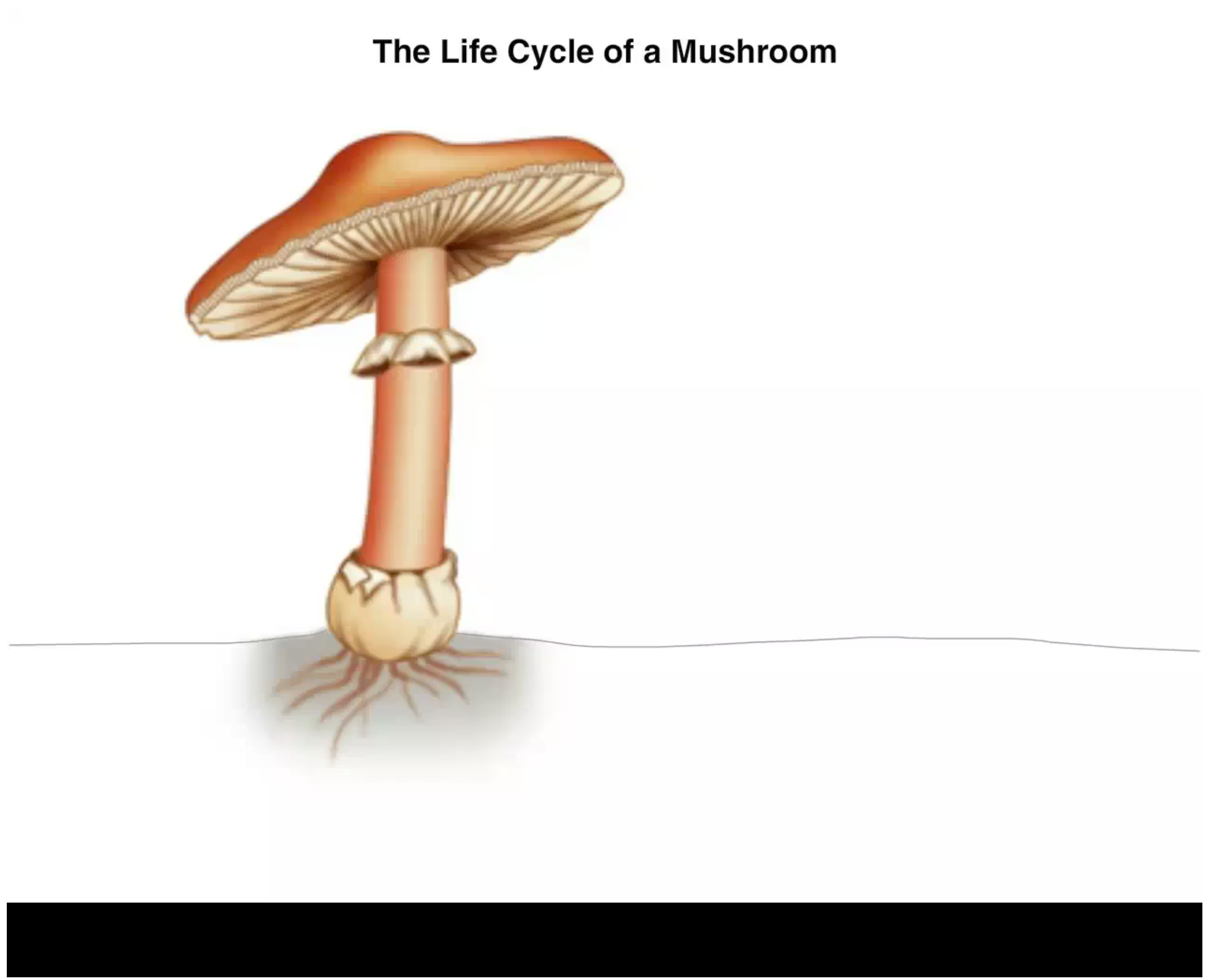
- The life cycle of a basidiomycete usually includes a long-lived dikaryotic mycelium
- The mycelium can reproduce sexually by producing fruiting bodies called **basidiocarps**
  - For example, the common white mushrooms found in supermarkets are basidiocarps

- A mushroom results from a concentrated growth of hyphae that forms from the dikaryotic mycelium
- The cap of the mushroom supports and protects a large surface area of dikaryotic basidia on gills
- Karyogamy occurs within the basidia, immediately followed by meiosis
- Sexually produced basidiospores are ejected and dispersed by wind

Figure 31.20


PLASMOGAMY
Dikaryotic mycelium
Mating type (–)
Mating type (+)
Haploid mycelia
SEXUAL REPRODUCTION
Gills lined with basidia
Basidiocarp (n + n)
Dispersal and germination
Basidiospores (n)
Basidium
Basidium with four basidiospores
Basidium containing four haploid nuclei
Basidia (n + n)
KARYOGAMY
MEIOSIS
Diploid nuclei
1 µm
Basidiospore
Haploid (n)
Dikaryotic (n + n)
Diploid (2n)

Animation: Life Cycle of a Mushroom



- Some species produce rings of mushrooms called "fairy rings" that may appear literally overnight
- The underlying mycelium expands outward by 30 cm per year, causing the diameter of the fairy ring to expand with it

Figure 31.21

CONCEPT 31.5: Fungi play key roles in nutrient cycling, ecological interactions, and human welfare

- Fungi interact with other organisms as decomposers, mutualists, and pathogens

Fungi as Decomposers

- Fungi are efficient decomposers of organic material including cellulose and lignin
- Together, fungi and bacteria perform essential recycling of chemical elements between the living and nonliving world
- Without these critical decomposers, life as we know it would cease

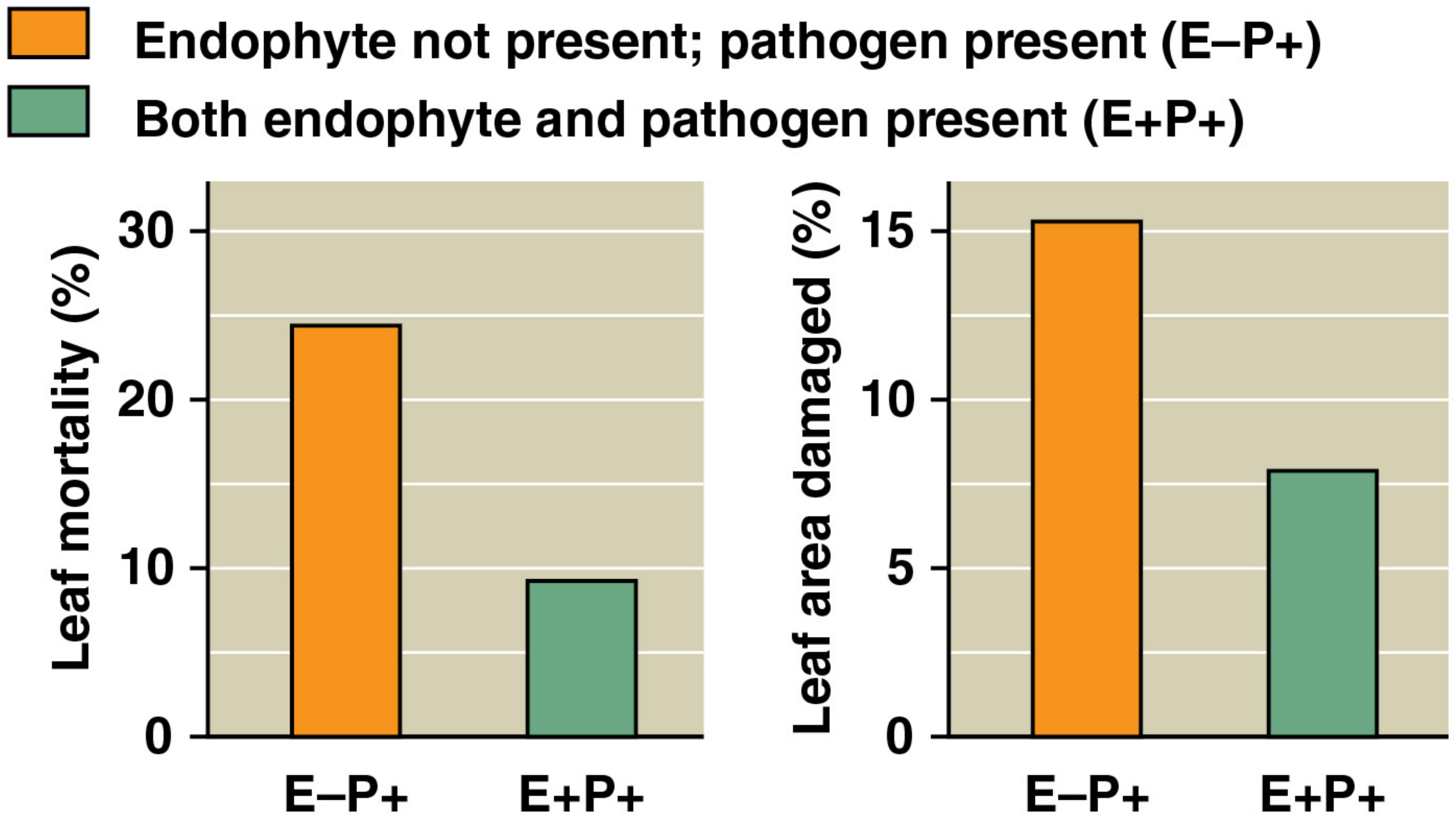
Fungi as Mutualists

- Fungi form mutualistic relationships with plants, algae, cyanobacteria, and animals
- Mutualistic fungi absorb nutrients from a host, but reciprocate with actions that benefit the host

Fungus-Plant Mutualisms

- All plant species harbor symbiotic **endophytes**, fungi (or bacteria) that live inside leaves or other plant parts without causing harm
- Most endophytes are ascomycetes
- Some make toxins to defend the host plant; others help the plant tolerate heat, drought, or heavy metals

Results



Data from A. E. Arnold et al., Fungal endophytes limit pathogen damage in a tropical tree, *Proceedings of the National Academy of Sciences USA* 100:15649–15654 (2003).

Fungus-Animal Mutualisms

- Some fungi share digestive services with animals
- They help break down plant material in the guts of cattle and other grazing mammals
- Many species of ants use the digestive power of fungi by raising them in "farms"
  - For example, leaf-cutter ants provide leaves to feed fungi that grow in their nests; in return, the ants feed on the nutrient-rich tips of the fungal hyphae

Figure 31.23

Lichens

- **Lichens** are symbiotic associations between photosynthetic microorganisms and fungi
- Millions of photosynthetic cells are held in a mass of fungal hyphae
- They grow on the surfaces of rocks, rotting logs, trees, and roofs in various forms

Figure 31.24

A fruticose (shrublike) lichen

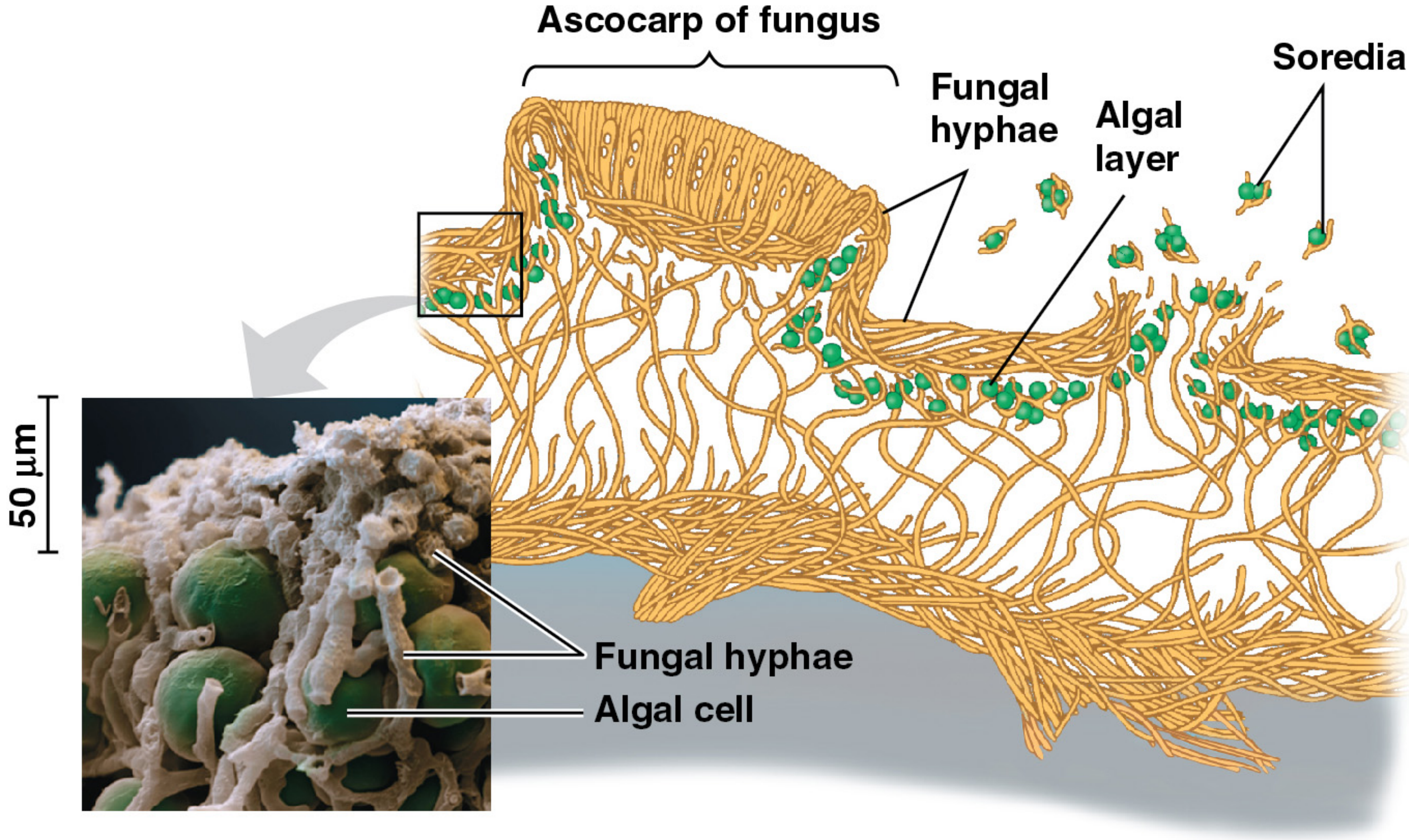
A foliose (leaflike) lichen

Crustose (encrusting) lichens

- The fungal partners are most often ascomycetes
- The photosynthetic partners are unicellular or filamentous green algae or cyanobacteria
- Many lichens also have a basidiomycete yeast as a second fungal component, but its role is unknown

- The fungus usually gives a lichen its overall shape and structure, and forms most of its mass
- Cells of the algae or cyanobacteria usually occupy an inner layer below the surface
- The symbioses are so complete that lichens are given scientific names, like single organisms

Figure 31.25



Ascocarp of fungus
Soredia
Fungal hyphae
Algal layer
50 µm
Fungal hyphae
Algal cell

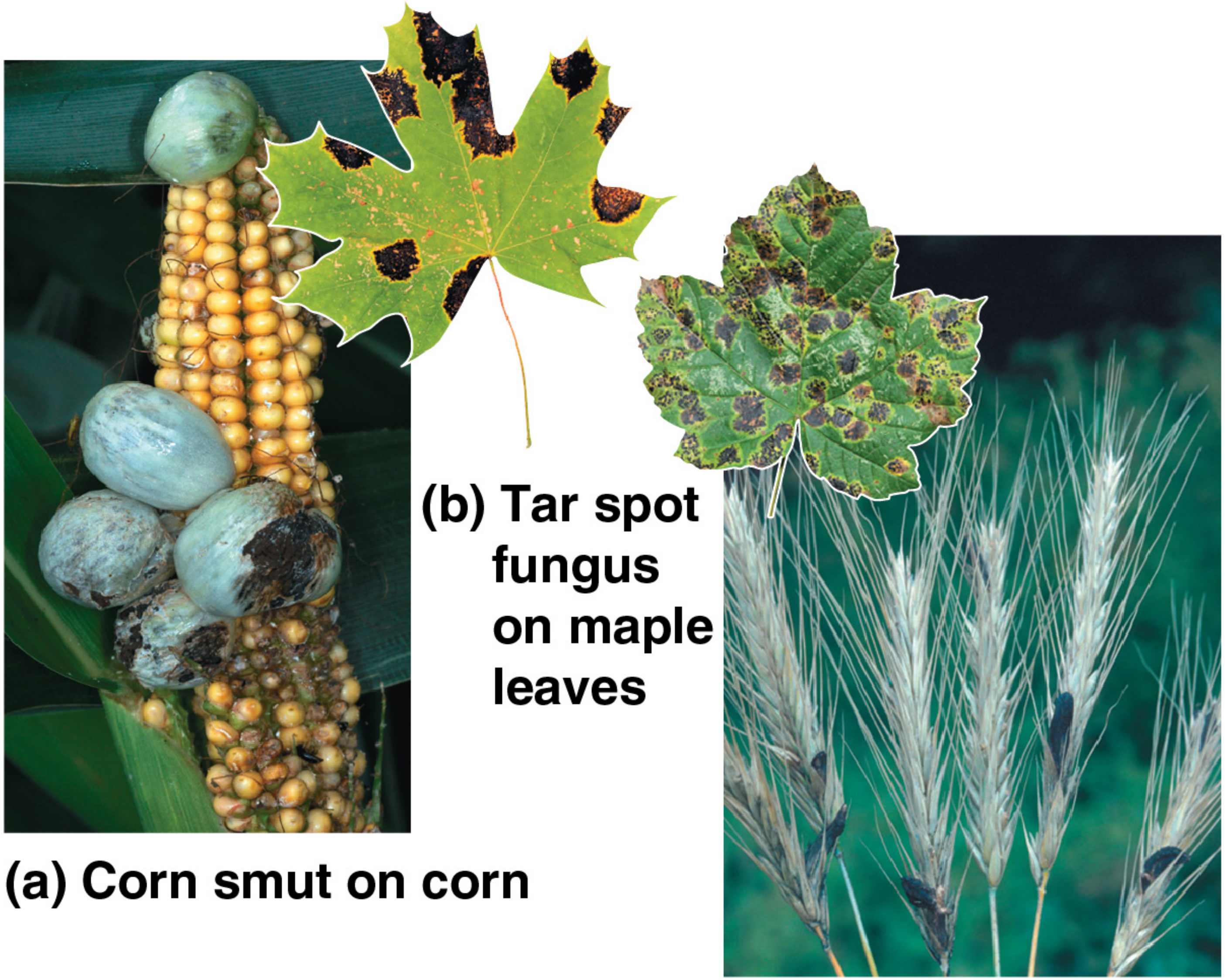
- Lichens reproduce asexually by fragmentation or by formation of **soredia**, small clusters of hyphae with embedded algae
- The fungal partner of many lichens can also reproduce sexually

- The fungal partner provides the photosynthetic partner with a suitable environment for growth
- The alga or cyanobacterium provides carbon compounds to the fungus
- Cyanobacteria also fix nitrogen and provide organic nitrogen compounds to the fungus

- Lichens are important pioneers on new rock and soil surfaces, such as volcanic flows or burned forests
- They physically penetrate the surface and break it down chemically; some also fix nitrogen
- Early lichens likely modified the land, helping to pave the way for early plants

Fungi as Parasites

- About 30% of known fungal species are parasites or pathogens, mostly on or in plants
- Each year, 10% to 50% of the world's fruit harvest is lost annually due to fungi; grain crops also suffer major annual losses



(a) Corn smut on corn

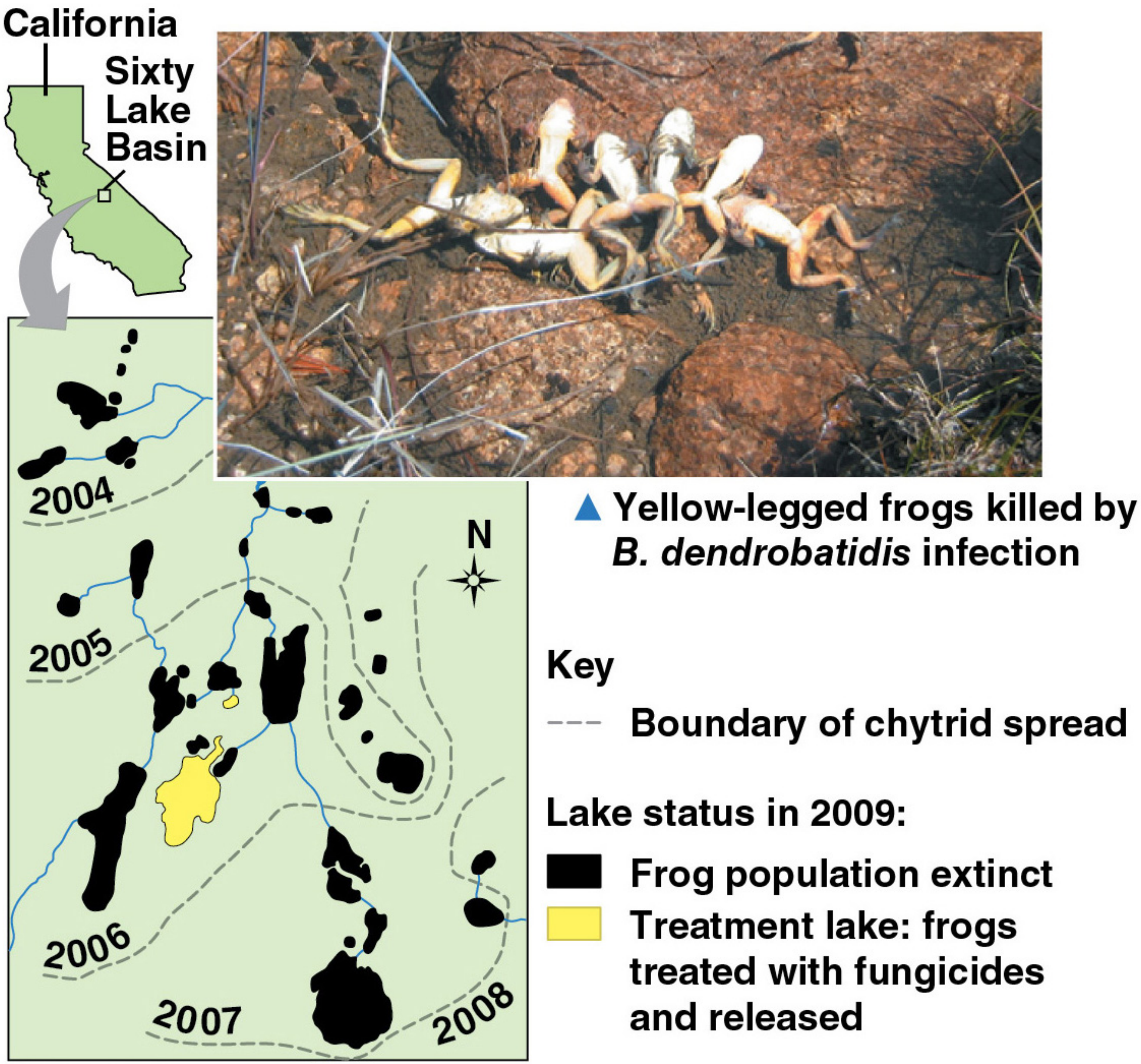
(b) Tar spot fungus on maple leaves

(c) Ergots on rye

- Some fungal parasites of food crops produce toxins
  - For example *Claviceps purpurea* is an ascomycete that causes ergots to grow on rye
  - Toxins from the ergots cause severe symptoms including gangrene, nervous spasms, burning sensations, hallucinations, and temporary insanity
  - An epidemic of ergotism around 944 CE killed up to 40,000 people in France

- Animals are much less susceptible to parasitic fungi than are plants
- Two chytrid species have been implicated in the decline or extinction of about 500 species of amphibians worldwide
- They cause sever skin infections, leading to massive die-offs

Figure 31.27


California
Sixty Lake Basin
2004
2005
2006
2007
2008
N
▲ Yellow-legged frogs killed by *B. dendrobatidis* infection
Key
Boundary of chytrid spread
Lake status in 2009:
Frog population extinct
Treatment lake: frogs treated with fungicides and released

- The general term for fungal infection in animals is **mycosis**
  - For example, a skin mycosis in humans is ringworm, which commonly grows on feet causing athlete's foot
  - Ringworm infections can be treated with fungicidal lotions and powders

- Systemic mycoses spread through the body and usually cause serious illnesses
  - For example, coccidioidomycosis is a potentially fatal systemic mycosis that produces tuberculosis-like symptoms in the lungs

- Some mycoses are opportunistic, occurring only when the body is vulnerable to infection
  - For example, *Candida albicans* is a normal inhabitant of moist epithelia, such as the vaginal lining
  - Under certain conditions, it can grow rapidly and become pathogenic, causing “yeast infections”

Practical Uses of Fungi

- Humans eat many fungi and use others to make cheeses, alcoholic beverages, and bread
- Some fungi have great medical value as well
  - For example, the ascomycete *Penicillium* produces penicillin, an antibiotic used to treat bacterial infections
  - For example, a compound extracted from ergot is used to reduce high blood pressure and stop maternal bleeding after childbirth

- Genetic research on fungi is leading to medical applications in biotechnology
  - For example, the yeast *Saccharomyces cerevisiae* has been genetically modified to produce human glycoproteins, including insulin-like growth factor

- Genetic research is also targeting fungi for use in the production of biofuels
  - For example, researchers are sequencing the genome of *Gliocladium roseum*, a fungus that produces hydrocarbons similar to those in diesel fuel

Figure 31.28

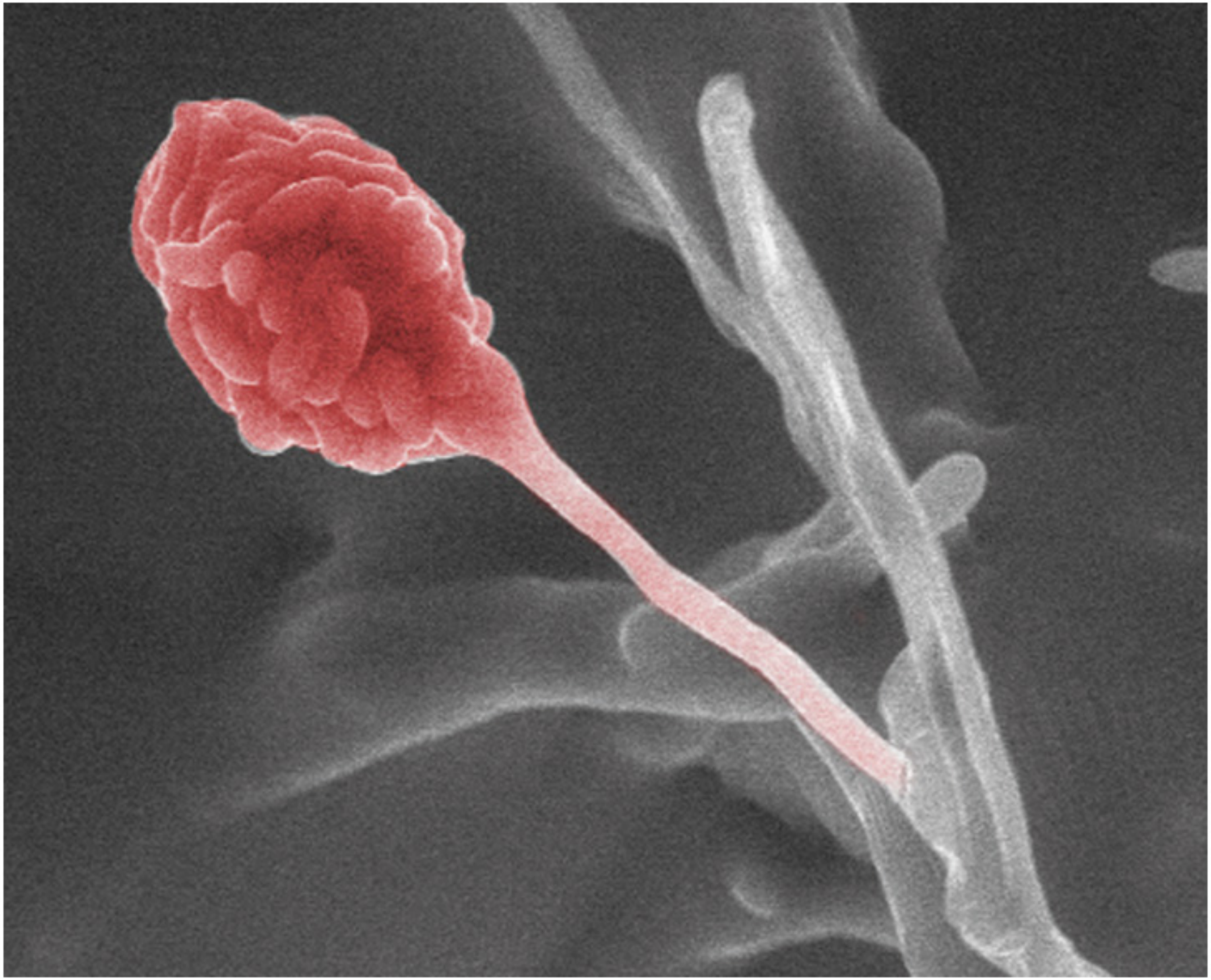


Figure 31.UN07a

Table 1 Numbers of Genes in *L. bicolor* and Four Nonmycorrhizal Fungal Species

	L. bicolor	1	2	3	4
Protein-coding genes	20,614	13,544	10,048	7,302	6,522
Genes for membrane transporters	505	412	471	457	386
Genes for small secreted proteins (SSPs)	2,191	838	163	313	58

Data from F. Martin et al., The genome of *Laccaria bicolor* provides insights into mycorrhizal symbiosis, *Nature* 452:88–93 (2008).

Figure 31.UN07b

Table 2 ***L. bicolor*** **Genes Most Highly Upregulated in Ectomycorrhizal Mycelium (ECM) of Douglas Fir or Poplar Versus Free-Living Mycelium (FLM)**

Protein ID	Protein Feature or Function	Douglas Fir ECM/FLM Ratio	Poplar ECM/FLM Ratio
298599	SSP	22,877	12,913
293826	Enzyme inhibitor	14,750	17,069
333839	SSP	7,844	1,931
316764	Enzyme	2,760	1,478

Data from F. Martin et al., The genome of *Laccaria bicolor* provides insights into mycorrhizal symbiosis, *Nature* 452:88–93 (2008).

Figure 31.UN07c

Figure 31.UN08

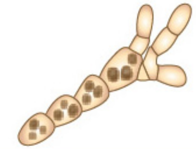
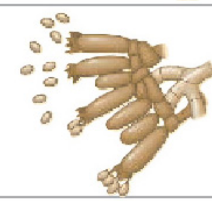
Fungal Phylum	Distinguishing Features
Cryptomycota (cryptomycetes)	Parasites with flagellated spores 
Microsporidia (microsporidians)	Parasitic cells that form resistant spores 
Chytridiomycota (chytrids)	Flagellated spores 
Zoopagomycota (zoopagomycetes)	Resistant zygosporangium as sexual stage 
Mucuromycota (mucuromycetes)	Include fungi that form arbuscular mycorrhizae with plants 
Ascomycota (ascomycetes)	Sexual spores (ascospores) borne internally in sacs called asci; vast numbers of asexual spores (conidia) produced 
Basidiomycota (basidiomycetes)	Elaborate fruiting body (basidiocarp) containing many basidia that produce sexual spores (basidiospores) 

Figure 31.UN09

Soil Temp.	*Curvularia* + or –	Plant Mass (g)	No. of New Shoots
30°C	E–	16.2	32
	E+	22.8	60
35°C	E–	21.7	43
	E+	28.4	60
40°C	E–	8.8	10
	E+	22.2	37
45°C	E–	0	0
	E+	15.1	24

Data from R. S. Redman et al., Thermotolerance generated by plant/fungal symbiosis, *Science* 298:1581 (2002).

Figure 31.UN10