

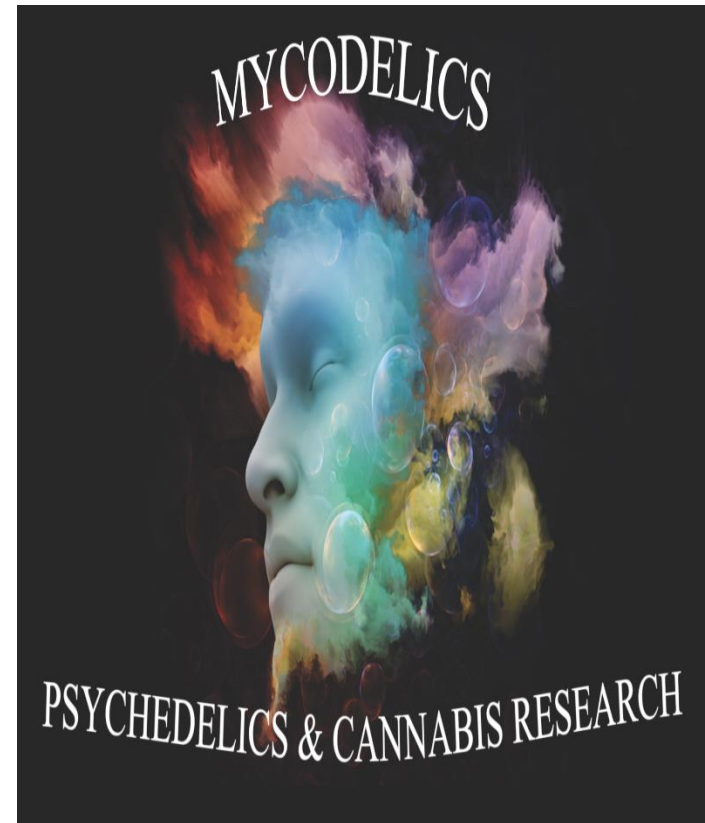


# BioX University of Botany Powered by J Gold

What are Fungi?



*J GOLD STANDARD*



# The Hidden Kingdom

Fungi are not plants. Living things are organized for study into large, basic groups called kingdoms. Fungi were listed in the Plant Kingdom for many years. Then scientists learned that fungi show a closer relation to animals but are unique and separate life forms. Now, Fungi are placed in their own Kingdom. It is a hidden kingdom. The part of the fungus that we see is only the fruit of the organism. The living body of the fungus is a mycelium made from a web of tiny filaments called hyphae. The mycelium is usually hidden in the soil, in wood, or another food source. A mycelium may fill a single ant or cover many acres. The branching hyphae can add over a half mile (1 km) of total length to the mycelium each day. These webs live unseen until they develop mushrooms, puffballs, truffles, brackets, cups, birds' nests, corals or other fruiting bodies. If the mycelium produces microscopic fruiting bodies, people may never notice the fungus.

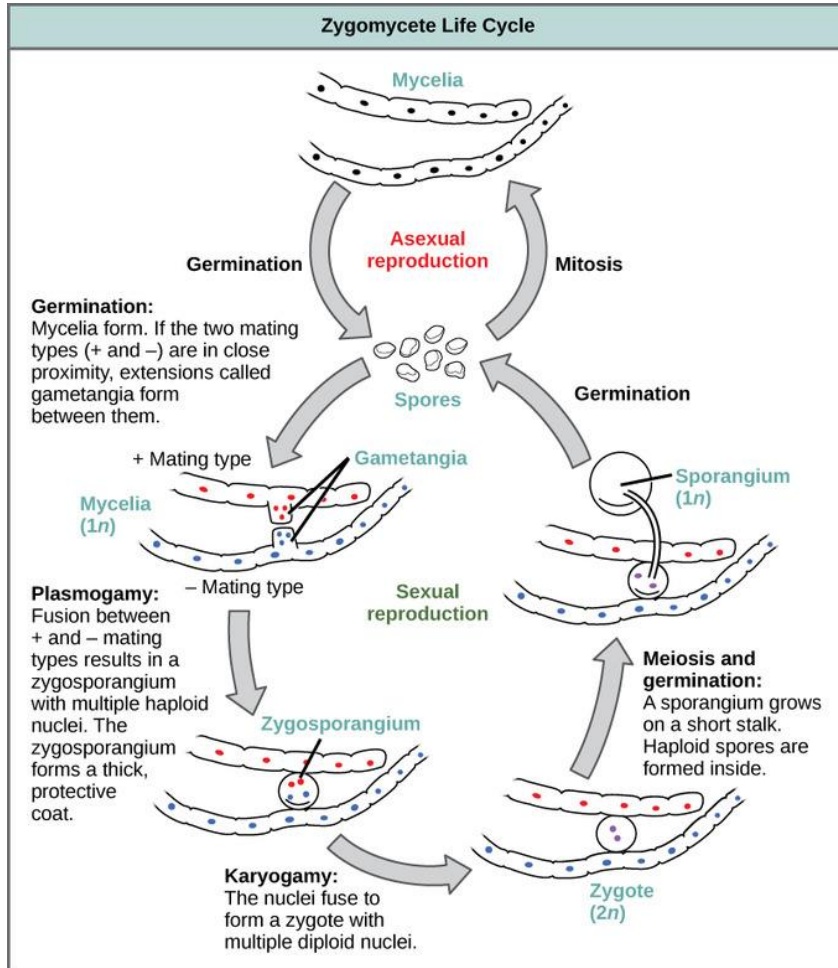
Most fungi build their cell walls out of chitin. This is the same material as the hard outer shells of insects and other arthropods. Plants do not make chitin. Fungi feed by absorbing nutrients from the organic material in which they live. Fungi do not have stomachs. They must digest their food before it can pass through the cell wall into the hyphae. Hyphae secrete acids and enzymes that break the surrounding organic material down into simple molecules they can easily absorb. Fungi have evolved to use a lot of different items for food. Some are decomposers living on dead organic material like leaves. Some fungi cause diseases by using living organisms for food. These fungi infect plants, animals and even other fungi. Athlete's foot and ringworm are two fungal diseases in humans. The mycorrhizal fungi live as partners with plants. They provide mineral nutrients to the plant in exchange for carbohydrates or other chemicals fungi cannot manufacture. You probably use fungal products every day without being aware of it. People eat mushrooms of all shapes, sizes and colors. Yeasts are used in making bread, wine, beer and solvents. Drugs made from fungi cure diseases and stop the rejection of transplanted hearts and other organs. Fungi are also grown in large vats to produce flavorings for cooking, vitamins and enzymes for removing stains.



About 80 000 to 120 000 species of fungi have been described to date, although the total number of species is estimated at around 1.5 million (Hawksworth, 2001; Kirk et al., 2001). This would render fungi one of the least-explored biodiversity resources of our planet. It is notoriously difficult to delimit fungi as a group against other eukaryotes, and debates over the inclusion or exclusion of certain groups have been going on for well over a century. In recent years, the main arguments have been between taxonomists striving towards a phylogenetic definition based especially on the similarity of relevant DNA sequences, and others who take a biological approach to the subject and regard fungi as organisms sharing all or many key ecological or physiological characteristics the 'union of fungi' (Barr, 1992). Being interested mainly in the way fungi function in nature and in the laboratory, we take the latter approach and include several groups in this book which are now known to have arisen independently of the monophyletic 'true fungi' (Eumycota) and have been placed outside them in recent classification schemes. The most important of these 'pseudofungi' are the Oomycota (see Chapter 5). Based on their lifestyle, fungi may be circumscribed by the following set of characteristics (modified from Ainsworth, 1973):

1. **Nutrition.** Heterotrophic (lacking photosynthesis), feeding by absorption rather than ingestion.
2. **Vegetative state.** On or in the substratum, typically as a non-motile mycelium of hyphae showing internal protoplasmic streaming. Motile reproductive states may occur.
3. **Cell wall.** Typically present, usually based on glucans and chitin, rarely on glucans and cellulose (Oomycota).
4. **Nuclear status.** Eukaryotic, uni- or multinucleate, the thallus being homo- or heterokaryotic, haploid, dikaryotic or diploid, the latter usually of short duration (but exceptions are known from several taxonomic groups).
5. **Life cycle.** Simple or, more usually, complex.





6. **Reproduction.** The following reproductive events may occur: sexual (i.e. nuclear fusion and meiosis) and/or parasexual (i.e. involving nuclear fusion followed by gradual de-diploidization) and/or asexual (i.e. purely mitotic nuclear division).

7. **Propagules.** These are typically microscopically small spores produced in high numbers. Motile spores are confined to certain groups.

8. **Sporocarps.** Microscopic or macroscopic and showing characteristic shapes but only limited tissue differentiation.

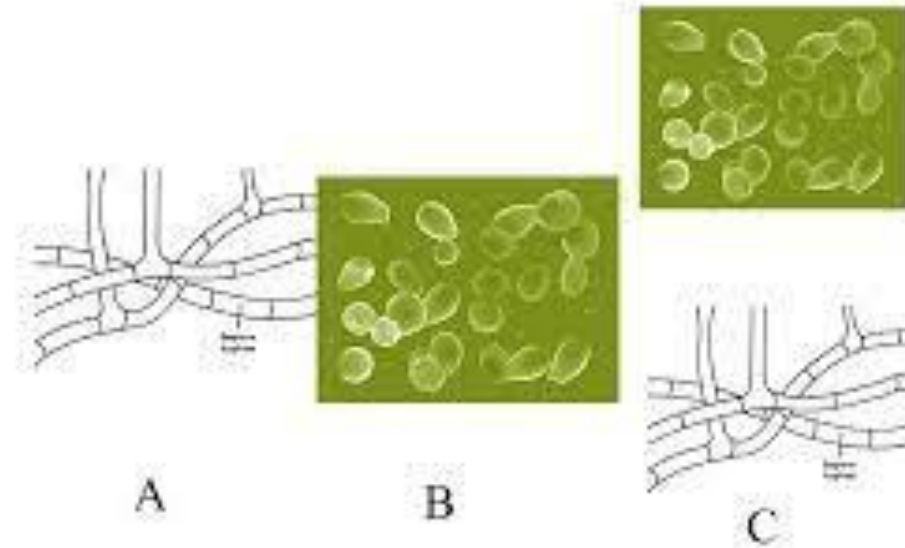
9. **Habitat.** Ubiquitous in terrestrial and freshwater habitats, less so in the marine environment.

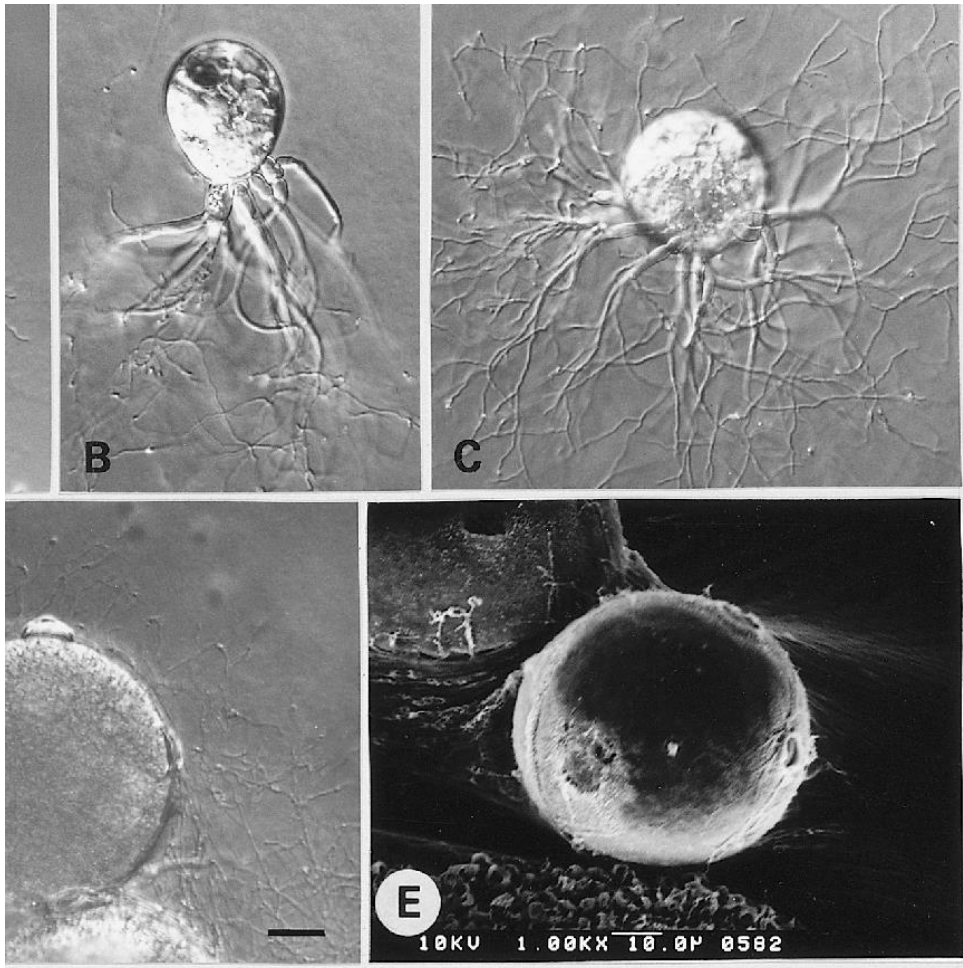
10. **Ecology.** Important ecological roles as saprotrophs, mutualistic symbionts, parasites, or hyperparasites.

11. **Distribution.** Cosmopolitan.

•With photosynthetic pigments being absent, fungi have a heterotrophic mode of nutrition. In contrast to animals which typically feed by ingestion, fungi obtain their nutrients by extracellular digestion due to the activity of secreted enzymes, followed by absorption of the solubilized breakdown products. The combination of extracellular digestion and absorption can be seen as the ultimate determinant of the fungal lifestyle. During evolution, fungi have conquered an astonishingly wide range of habitats, fulfilling important roles in diverse ecosystems (Dix & Webster, 1995). The conquest of new, often patchy resources is greatly facilitated by the production of numerous small spores rather than a few large propagules, whereas the colonization of a food source, once reached, is achieved most efficiently by growth as a system of branching tubes, the hyphae which together make up the mycelium.

## Growth Forms



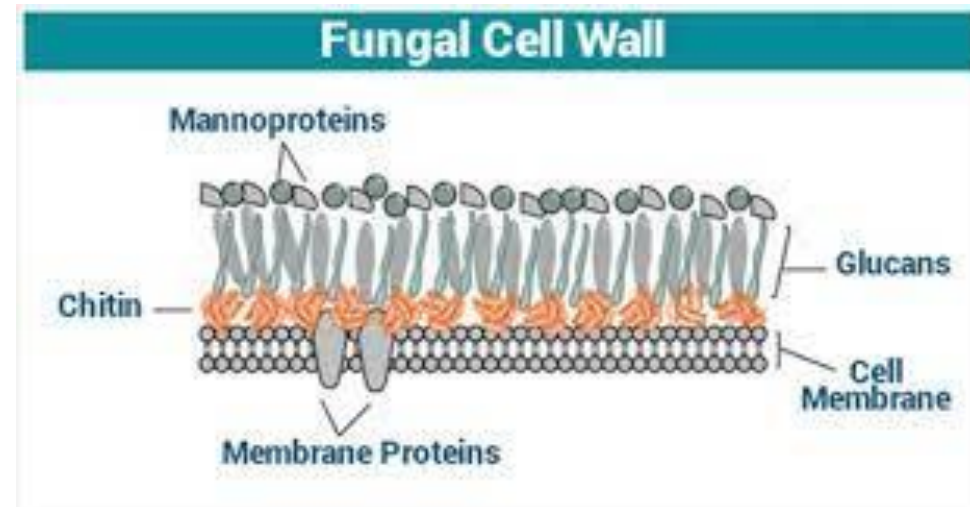


Hyphae are generally quite uniform in different taxonomic groups of fungi. One of the few features of distinction that they do offer is the presence or absence of cross-walls or septa. The Oomycota and Zygomycota generally have aseptate hyphae in which the nuclei lie in a common mass of cytoplasm. Such a condition is described as coenocytic (Gr. *koinos* ¼ shared, in common; *kytos* ¼ a hollow vessel, here meaning cell). In contrast, Asco- and Basidiomycota and their associated asexual states generally have septate hyphae in which each segment contains one, two or more nuclei. If the nuclei are genetically identical, as in a mycelium derived from a single uninucleate spore, the mycelium is said to be homokaryotic, but where a cell or mycelium contains nuclei of different genotype, e.g., as a result of fusion (anastomosis) of genetically different hyphae, it is said to be heterokaryotic. A special condition is found in the mycelium of many Basidiomycota in which each cell contains two genetically distinct nuclei. This condition is dikaryotic, to distinguish it from mycelia which are monokaryotic. It should be noted that septa, where present, are usually perforated and allow for the exchange of cytoplasm or organelles.

Not all fungi grow as hyphae. Some grow as discrete yeast cells which divide by fission or, more frequently, budding. Yeasts are common, especially in situations where efficient penetration of the substratum is not required, e.g., on plant surfaces or in the digestive tracts of animals (Carlile, 1995). A few species, including certain pathogens of humans and animals, are dimorphic, i.e. capable of switching between hyphal and yeast-like growth forms (Gow, 1995). Intermediate stages between yeast cells and true hyphae also occur and are termed pseudohyphae. Some lower fungi grow as a thallus, i.e., a walled structure in which the protoplasm is concentrated in one or more centers from which root-like branches (rhizoids) ramify. Certain obligately plant-pathogenic fungi and fungus-like organisms grow as a naked plasmodium, a uni- or multinucleate mass of protoplasm not surrounded by a cell wall of its own, or as a pseudoplasmodium of amoeboid cells which retain their individual plasma membranes. However, by far the most important device which accounts for the typical biological features of fungi is the hypha (Bartnicki-Garcia, 1996), which therefore seems an appropriate starting point for an exploration of these organisms.

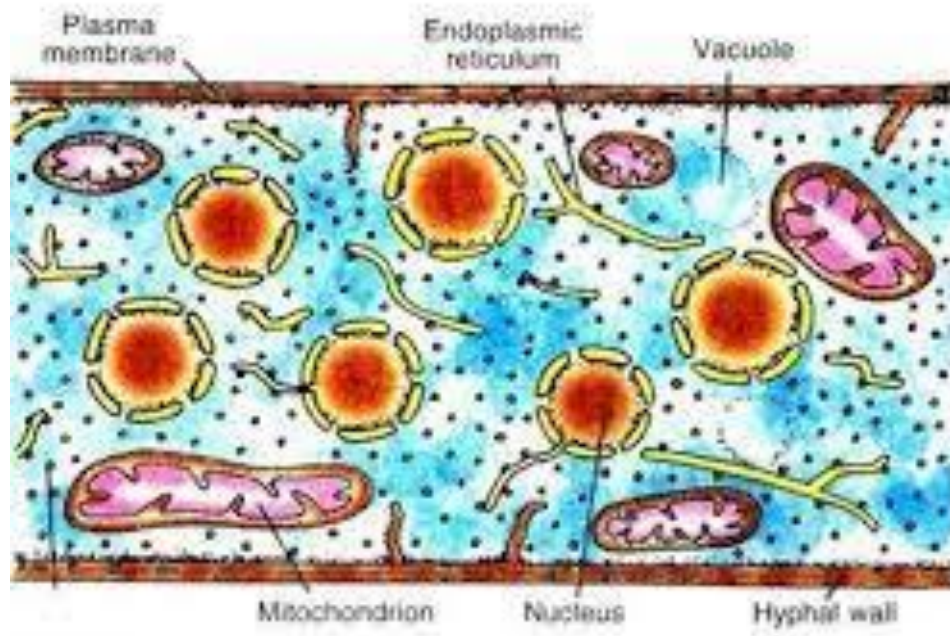
# Synthesis of the cell wall

•The synthesis of chitin is mediated by specialized organelles termed chitosomes (BartnickiGarcia et al., 1979; Sentandreu et al., 1994) in which inactive chitin synthases are delivered to the apical plasma membrane and become activated upon contact with the lipid bilayer (Montgomery & Gooday, 1985). Microvesicles, visible especially in the core region of the Spitzenkörper, are likely to be the ultrastructural manifestation of chitosomes (Fig. 1.6). In contrast, structural proteins and enzymes travel together in the larger secretory vesicles and are discharged into the environment when the vesicles fuse with the plasma membrane. Whereas most proteins are fully functional by the time they traverse the plasma membrane (see p. 10), the glucans are secreted by secretory vesicles as partly formed precursors (Wessels, 1993a) and undergo further polymerization in the nascent cell wall, or they are synthesized entirely at the plasma membrane (Sentandreu et al., 1994; de Nobel et al., 2001). Cross-linking of glucans with other components of the cell wall takes place after extrusion into the cell wall (Kolla' r et al., 1997; de Nobel et al., 2001).





# Architecture of the fungal cell wall

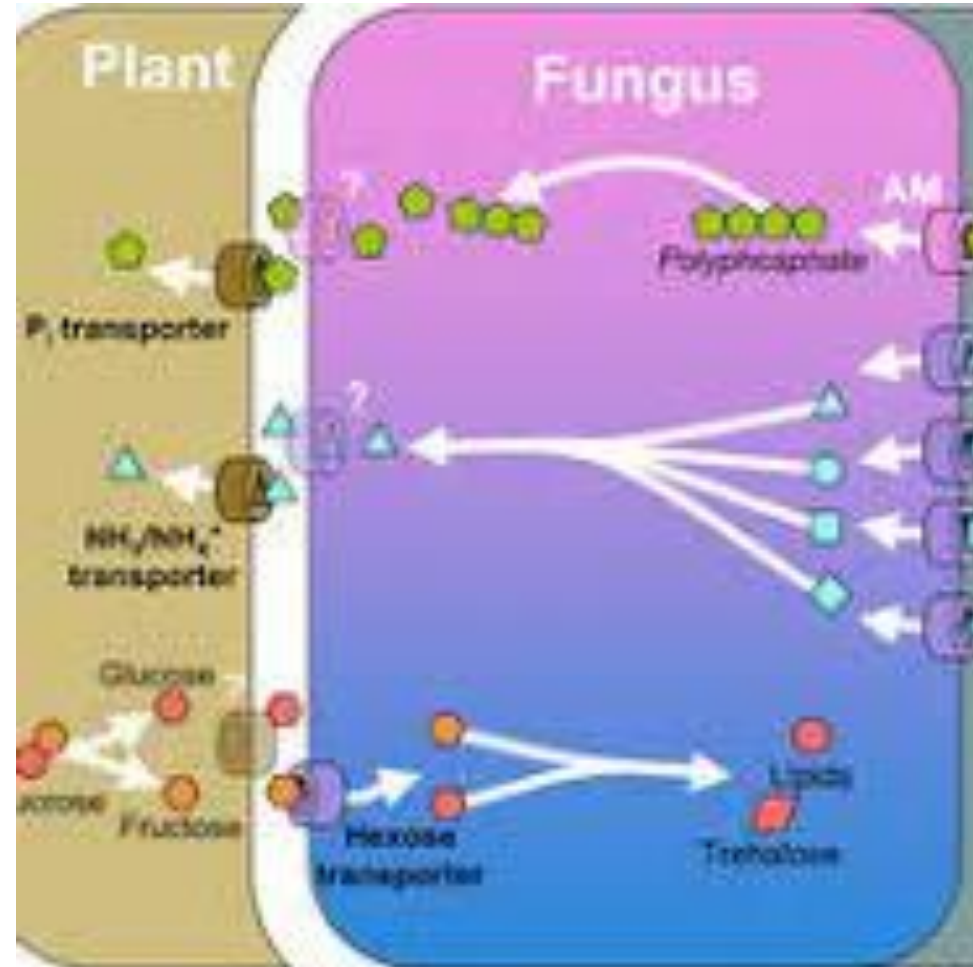


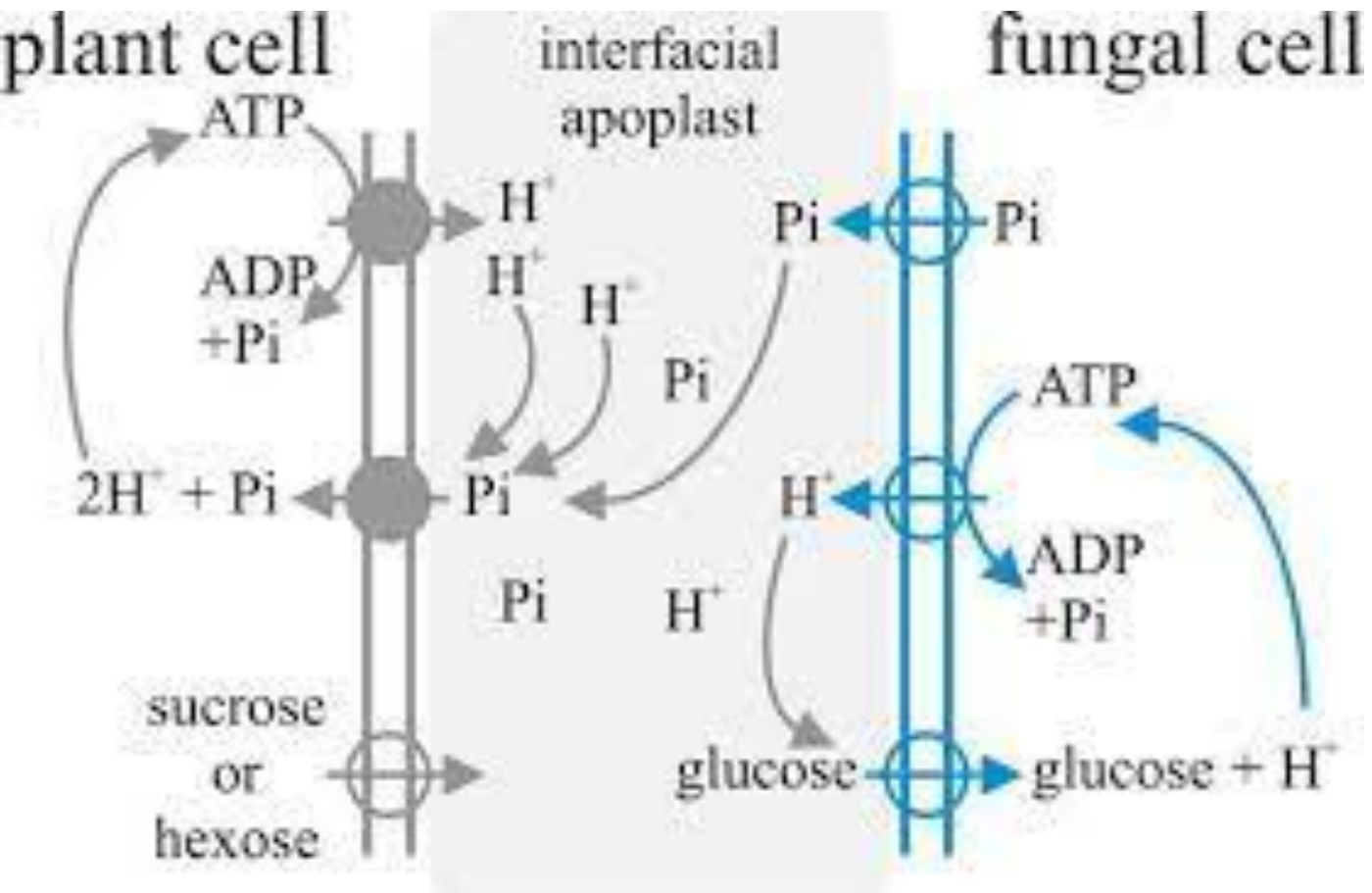
•Although the chemical composition of cell walls can vary considerably between and within different groups of fungi (Table 1.1), the basic design seems to be universal. It consists of a structural scaffold of fibres which are crosslinked, and a matrix of gel-like or crystalline material (Hunsley & Burnett, 1970; Ruiz-Herrera, 1992; Sentandreu et al., 1994). The degree of cross-linking will determine the plasticity (extensibility) of the wall, whereas the pore size (permeability) is a property of the wall matrix. The scaffold forms the inner layer of the wall and the matrix is found predominantly in the outer layer (de Nobel et al., 2001).

•In the Ascomycota and Basidiomycota, the fibers are chitin microfibrils, i.e. bundles of linear  $\beta$ -(1,4)-linked N-acetylglucosamine chains which are synthesized at the plasma membrane and extruded into the growing ('nascent') cell wall around the apical dome. The cell wall becomes rigid only after the microfibrils have been fixed in place by crosslinking. These cross-links consist of highly branched glucans (glucose polymers), especially those in which the glucose moieties are linked by  $\beta$ -(1,3)- and  $\beta$ -(1,6)-bonds (Suarit et al., 1988; Wessels et al., 1990; Sietsma & Wessels, 1994). Such  $\beta$ -glucans are typically insoluble in alkaline solutions (1 M KOH).

# Nutrient uptake

•One of the hallmarks of fungi is their ability to take up organic or inorganic solutes from extremely dilute solutions in the environment, accumulating them 1000-fold or more against their concentration gradient (Griffin, 1994). The main barrier to the movement of water-soluble substances into the cell is the lipid bilayer of the plasma membrane. Uptake is mediated by proteinaceous pores in the plasma membrane which are always selective for particular solutes. The pores are termed channels (system I) if they facilitate the diffusion of a solute following its concentration gradient whilst they are called porters (system II) if they use metabolic energy to accumulate the solute across the plasma membrane against its gradient (Harold, 1994). Fungi often possess one channel and one porter for a given solute. The high-affinity porter system is repressed at high external solute concentrations such as those found in most laboratory media (Scarborough, 1970; Sanders, 1988).





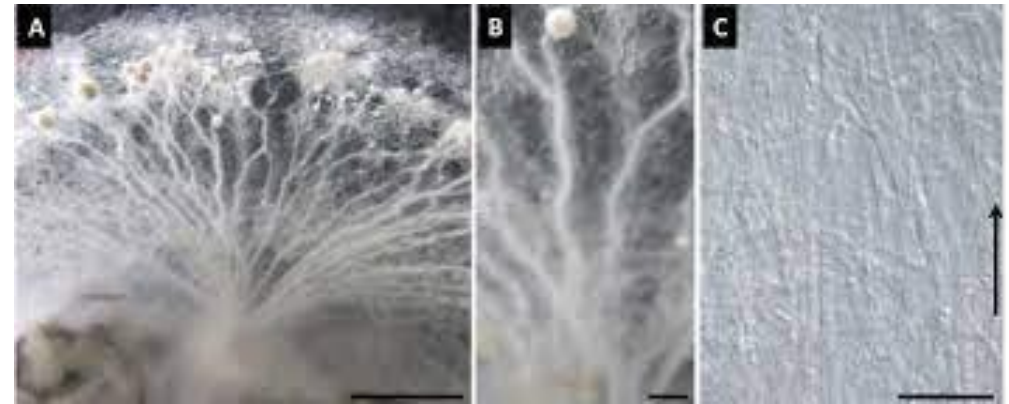
Media (Scarborough, 1970; Sanders, 1988). In nature, however, the concentration of nutrients is often so low that the porter systems are active. Porters do not directly convert metabolic energy (ATP) into the uptake of solutes; rather, ATP is hydrolysed by ATPases which pump protons ( $H^+$ ) to the outside of the plasma membrane, thus establishing a transmembrane pH gradient (acid outside). It has been estimated that one-third of the total cellular ATP is used for the establishment of the transmembrane  $H^+$  gradient (Gradmann et al., 1978). The inward movement of  $H^+$  following its electrochemical gradient is harnessed by the porters for solute uptake by means of soluteporter $H^+$  complexes (Slayman & Slayman, 1974; Slayman, 1987; Garrill, 1995). Different types of porter exist, depending on the charge of the desired solute. Uniport and symport carriers couple the inward movement of  $H^+$  with the uptake of uncharged or negatively charged solutes, respectively, whereas antiports harness the outward diffusion of cations such as  $K^+$  for the uptake of other positively charged solutes. Charge imbalances can be rectified by the selective opening of  $K^+$  channels. Porters have been described for  $NH_4^+$ ,  $NO_3^-$ , amino acids, hexoses, orthophosphate and other solutes (Garrill, 1995; Jennings, 1995).

# Mycelial strands

The formation of aggregates of parallel, relatively undifferentiated hyphae is quite common in the Basidiomycota and in some Ascomycota. For instance, mycelial strands form the familiar 'spawn' of the cultivated mushroom *Agaricus bisporus*. Strands arise most readily from a well-developed mycelium extending from an exhausted food base into nutrient-poor surroundings. When a strand encounters a source of nutrients exceeding its internal supply, coherence is lost, and a spreading assimilative mycelium regrows (Moore, 1994).

Alternatively, mycelial strands may be employed by fungi which produce their fructifications some distance away from the food base, as in the stinkhorn, *Phallus impudens*'s. Here the mycelial strand is more tightly aggregated and is referred to as a mycelial cord. The tip of the mycelial cord, which arises from a buried tree stump, differentiates into an egg-like basidiocarp initially upon reaching the soil surface.

The development of *A. bisporus* strands has been described by Mathew (1961). Robust leading hyphae extend from the food base and branch at fairly wide intervals to form finer laterals, most of which grow away from the parent hypha. A few branch hyphae, however, form at an acute angle to the parent hypha and tend to grow parallel to it. Hyphae of many fungi occasionally.





Grow alongside each other or another physical obstacle which they chance to encounter. A later and specific stage in strand development is characterized by the formation of numerous fine, aseptate 'tendrils' as branches from the older regions of the main hyphae. The tendrils, which may extend forwards or backwards, become appressed to the main hypha and branch frequently to form even finer tendrils which grow round the main hyphae and unsheath them. Major strands are consolidated by anastomoses between their hyphae, and they increase in thickness by the assimilation of minor strands. A similar development has been noted in the strands of *Serpula lacrymans*, the dryrot fungus which can extend for several metres across brickwork and other surfaces from a food base in decaying wood (Jennings & Watkinson, 1982; Nuss et al., 1991). By recovering the nutrients from obsolete strands and forming new strands, colonies can move about and explore their vicinity in the search for new food bases (Cooke & Rayner, 1984; Boddy, 1993). Mycelial strands are capable of translocating nutrients and water in both directions (Boddy, 1993; Jennings, 1995). This property is important not only for decomposer fungi, but also for species forming mycorrhizal symbioses with the roots of plants, many of which produce hyphal strands.

# Rhizomorphs

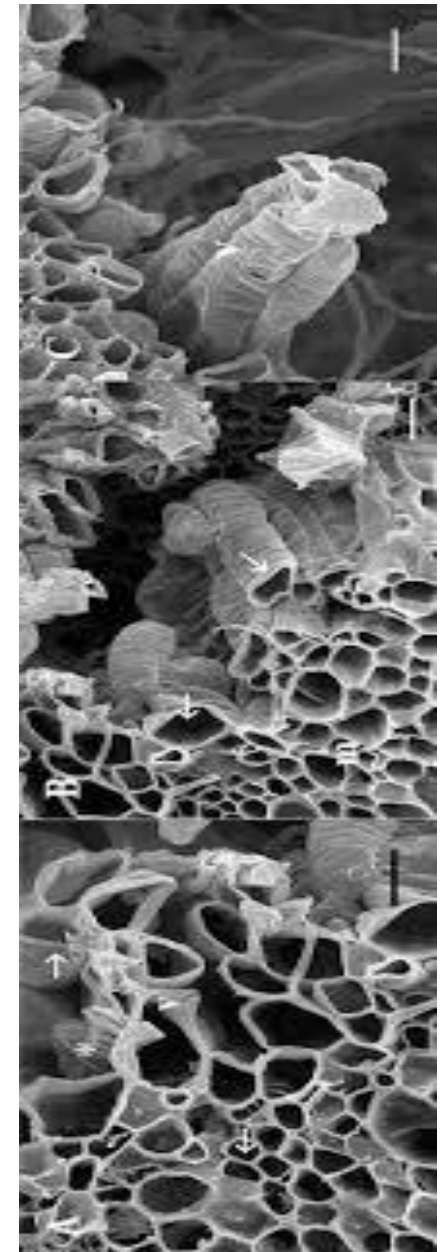
• In contrast to mycelial strands or cords which consist of relatively undifferentiated aggregations of hyphae and are produced by a great variety of fungi, rhizomorphs are found in only relatively few species and contain highly differentiated tissues. Well-known examples of rhizomorph-forming fungi are provided by *Armillaria* spp. which are serious parasites of trees and shrubs. In *Armillaria*, a central core of larger, thin-walled, elongated cells embedded in mucilage is surrounded by a rind of small, thicker-walled cells which are darkly pigmented due to melanin deposition in their walls. These root-like aggregations are a means for *Armillaria* to spread underground from one tree root system to another. In nature, two kinds are found a dark, cylindrical type and a paler, flatter type. The latter is particularly common beneath the bark of infected trees. Rhizomorphs on dead trees measure up to 4 mm in diameter. It has been estimated that a rhizomorph only 1 mm in diameter must contain over 1000 hyphae aggregated together. The development of rhizomorphs in agar culture has been described by Garrett (1953, 1970) and Snider (1959). Initiation of rhizomorphs can first be.





•Observed after about 7 days' mycelial growth on the agar surface as a compact mass of darkly pigmented hypertrophied cells. These pigmented structures have been termed microsclerotia. From white, non-pigmented points on their surface, the rhizomorphs develop. The growth of rhizomorphs can be several times faster than that of unorganized hyphae (Rishbeth, 1968). The most striking feature of the development of rhizomorphs is their compact growing point at the apex, which consists of small isodiametric cells protected by an apical cap of intertwined hyphae immersed in mucilage which they produce. Because of its striking similarity with a growing plant root, the rhizomorph tip was initially interpreted as a meristematic zone (Motta, 1967), but its hyphal nature can be demonstrated by careful ultrastructural observations (Powell & Rayner, 1983; Rayner et al., 1985). Behind the apex there is a zone of elongation. The centre of the rhizomorph may be hollow or solid. Surrounding the central lumen or making up the central medulla is a zone of enlarged hyphae 45 times wider than the vegetative hyphae (Fig. 1.14e). Possibly these vessel hyphae serve in translocation (Cairney, 1992; Jennings, 1995). Towards the periphery of the rhizomorph, the cells become smaller, darker, and thicker walled. Extending outwards between the outer cells of the rhizomorph, there may be a growth of vegetative hyphae somewhat resembling the root-hair zone in a higher plant. Rhizomorphs may develop on monokaryotic mycelia derived from single basidiospores, or on dikaryotic.

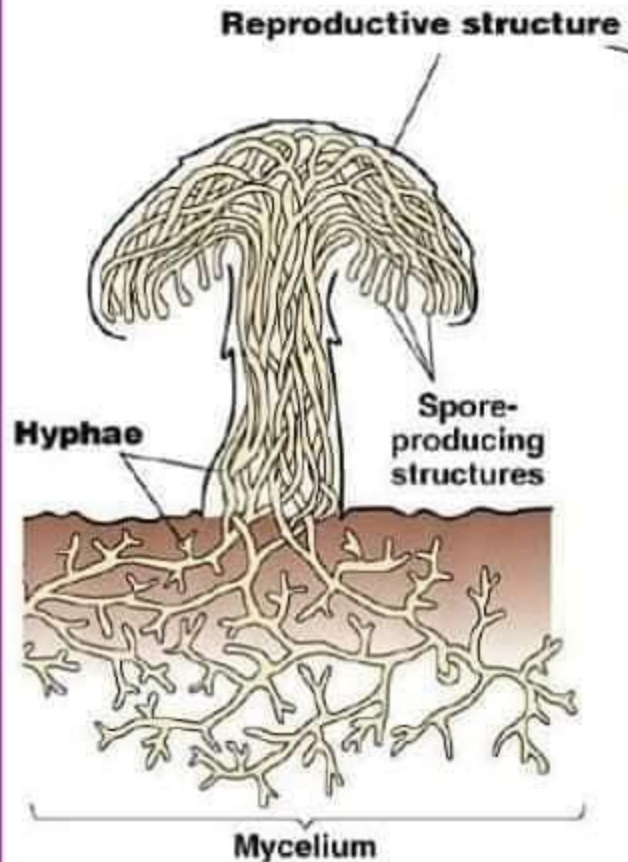
Mycelia following fusion of compatible monokaryotic hyphae. Dikaryotic rhizomorphs of *Armillaria* do not possess clamp connections (Hintikka, 1973). Rhizomorphs are also produced by another Basidiomycota and a few Ascomycota (Webster & Weber, 2000). They are mainly formed in soil. An interesting exception is presented by tropical *Marasmius* spp., which form a network of aerial rhizomorphs capable of intercepting falling leaves before they reach the ground (Hedger et al., 1993). Because these rhizomorphs have a rudimentary fruit body cap at their extending apex (Hedger et al., 1993), they have been interpreted as indefinitely extending fruit body stipes (Moore, 1994). Mycelial strands and rhizomorphs represent extremes in a range of hyphal aggregations, and several intergrading forms can be recognized (Rayner et al., 1985). protein, and lipid (Willetts & Bullock, 1992). The glucan matrix, too, may be utilized as a carbohydrate source during sclerotium germination (Backhouse & Willetts, 1985). Sclerotia may also have a reproductive role and are the only known means of reproduction in certain species. They are produced by a relatively small number of Asco- and Basidiomycota, especially plantpathogenic species such as *Rhizoctonia* spp. (p. 595), *Sclerotinia* spp. and *Claviceps purpurea* (p. 349). The form of sclerotia is very variable (Butler, 1966). The subterranean sclerotium of the Australian *Polyporus mylittae* can reach the size of a football and is known as native bread or blackfellow's bread. At the other extreme, they may be of microscopic dimensions consisting of a few cells only. Several kinds of development in sclerotia have been distinguished (Townsend & Willetts, 1954; Willetts, 1972).



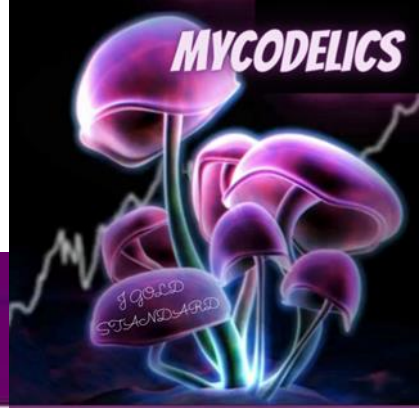




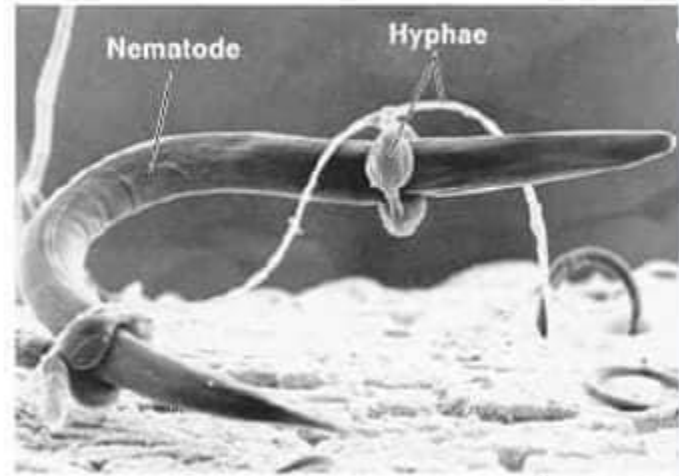
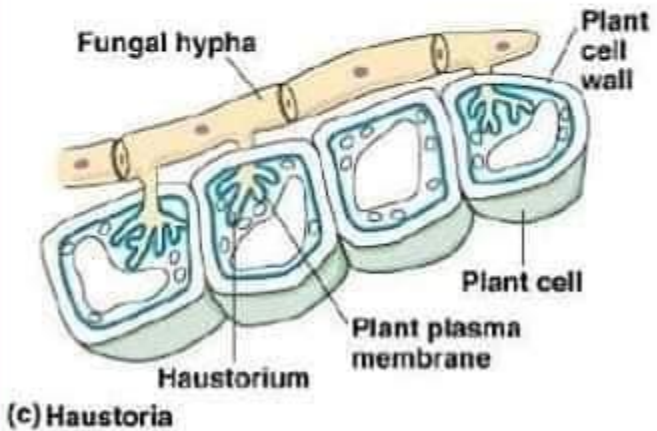
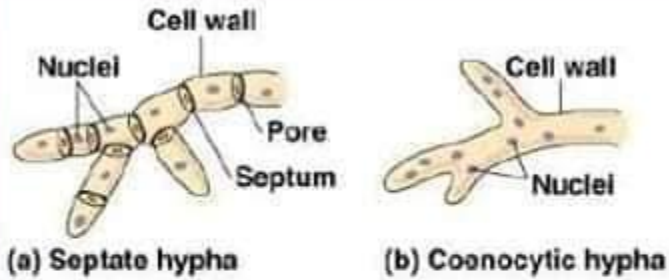
Fungal mycelia



Copyright © Pearson Education, Inc., publishing as Benjamin Cummings.

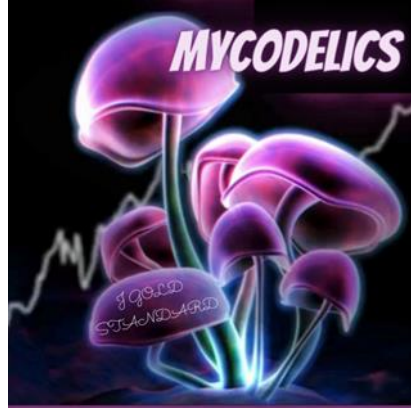


## Examples of fungal hyphae



**(d) Hyphae adapted for trapping and killing prey**

Copyright © Pearson Education, Inc., publishing as Benjamin Cummings.

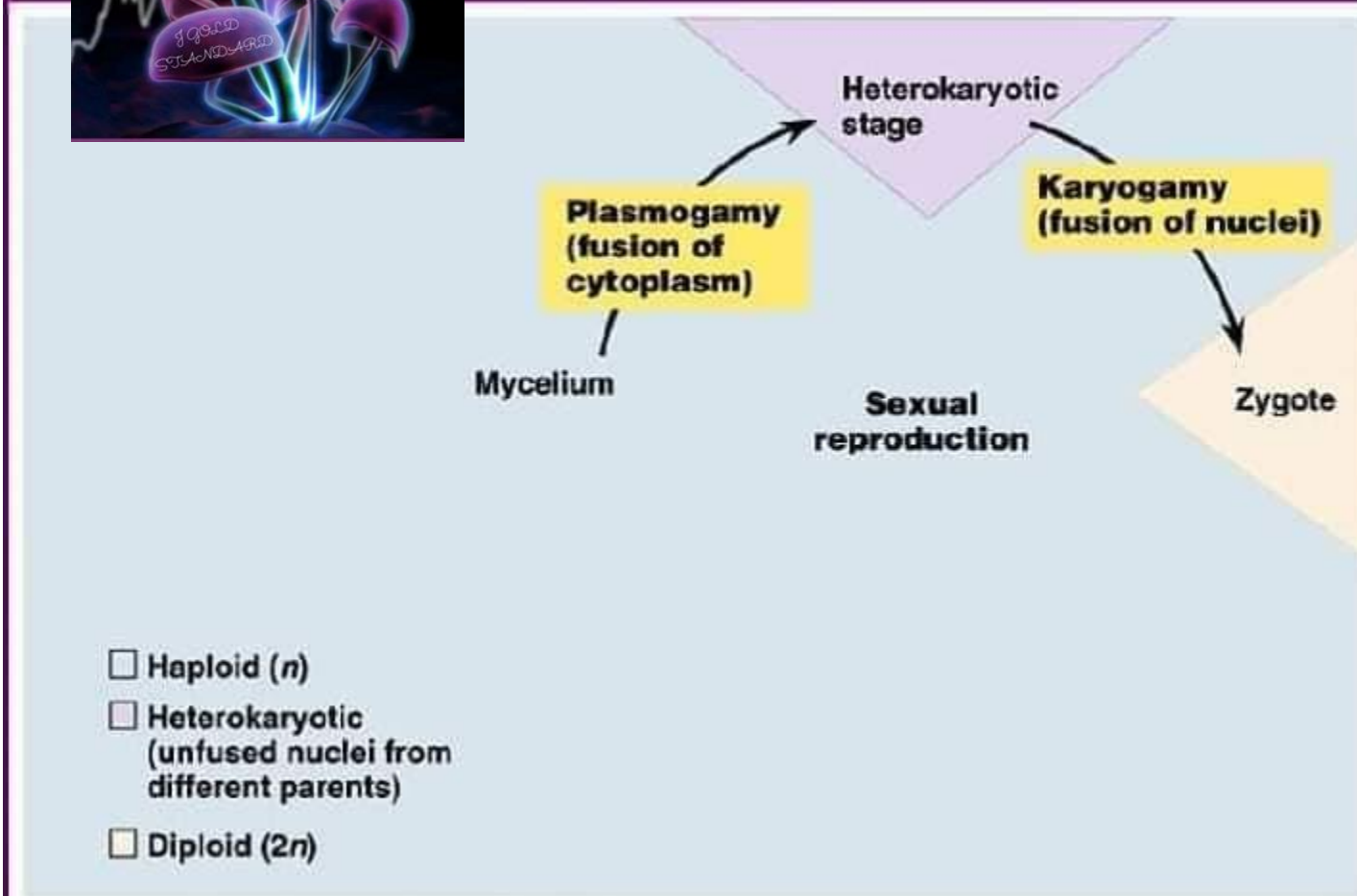


Septate hyphae (left) and nonseptate hyphae (right)





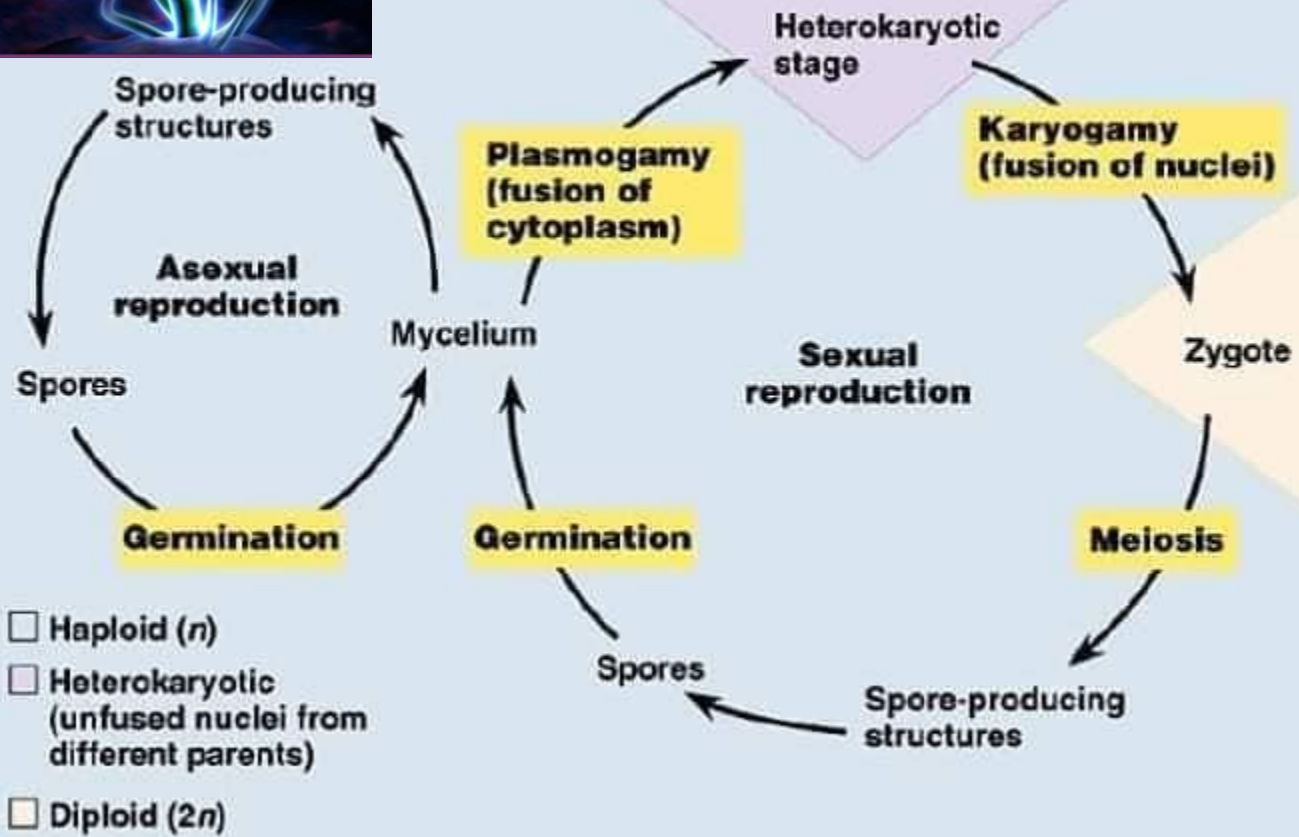
## Generalized life cycle of fungi (Layer 1)



Copyright © Pearson Education, Inc., publishing as Benjamin Cummings.



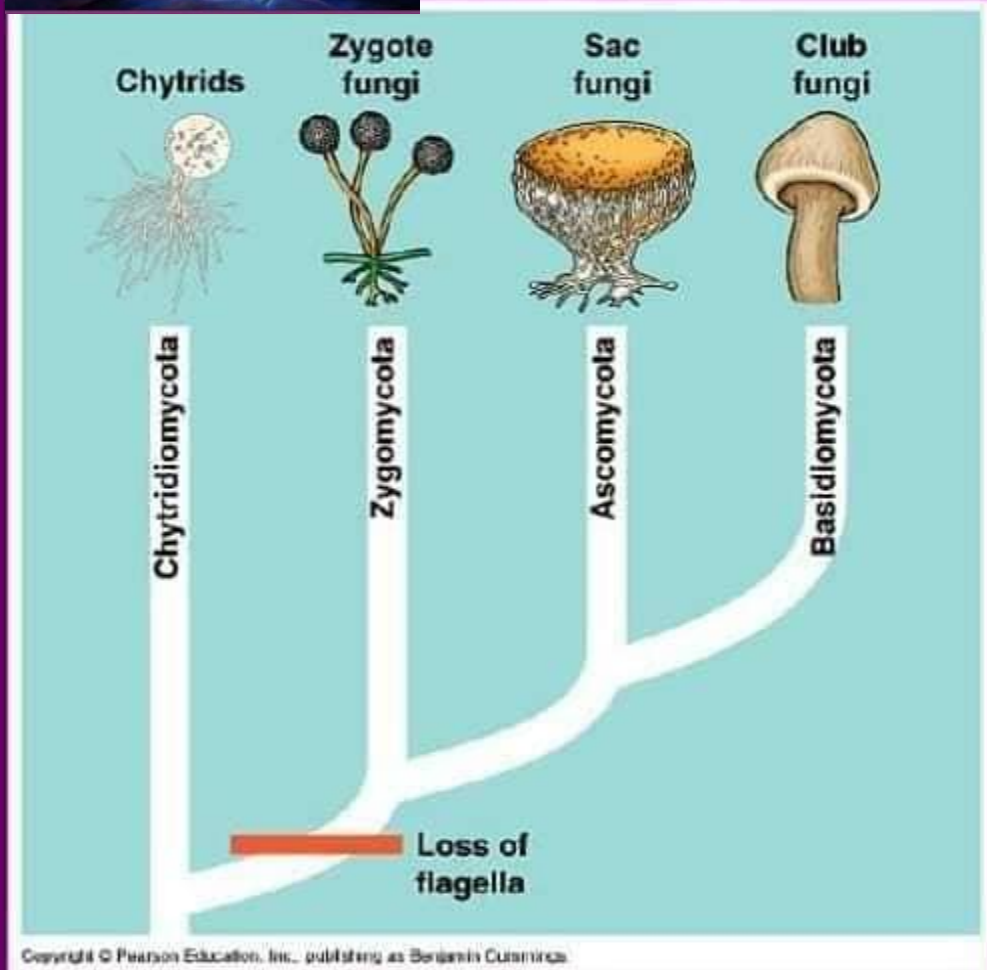
Generalized life cycle of fungi (Layer 3)



Copyright © Pearson Education, Inc., publishing as Benjamin Cummings.



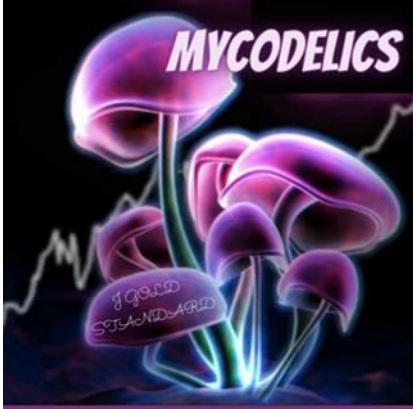
## Phylogeny of fungi





Chytridiomycota (chytrids)





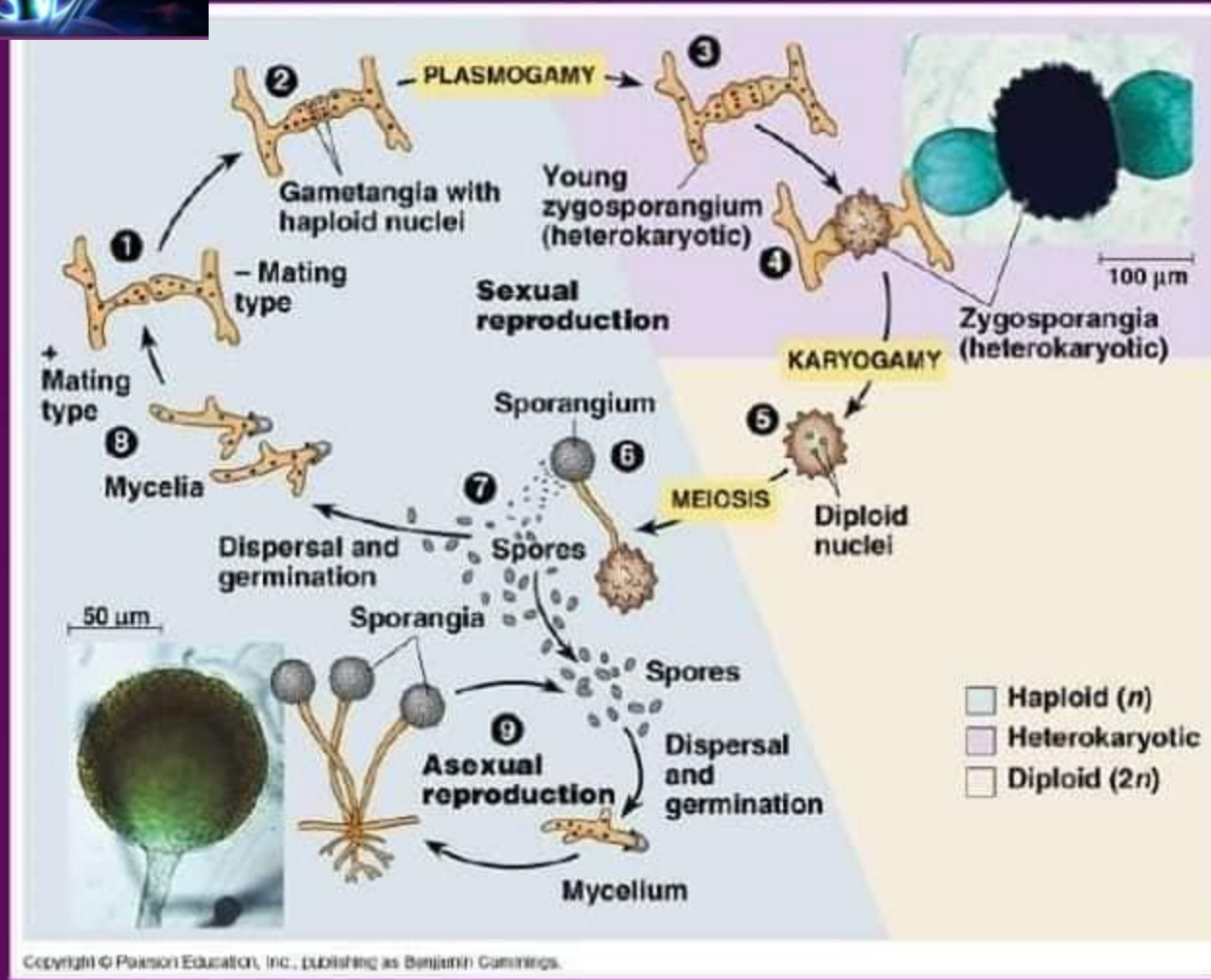
common mold *Rhizopus* decomposing strawberries





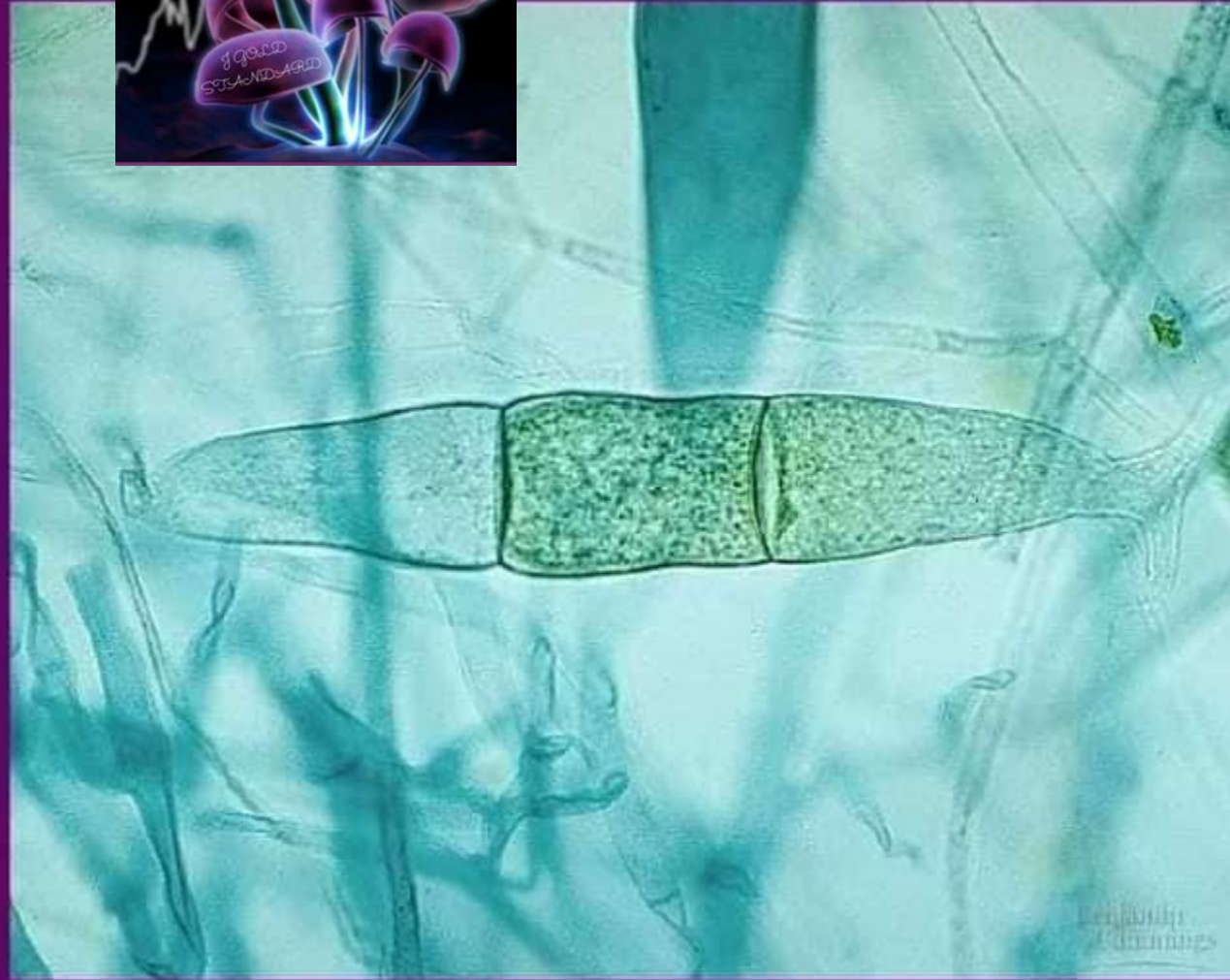


The life cycle of the zygomycete *Rhizopus* (black bread mold)





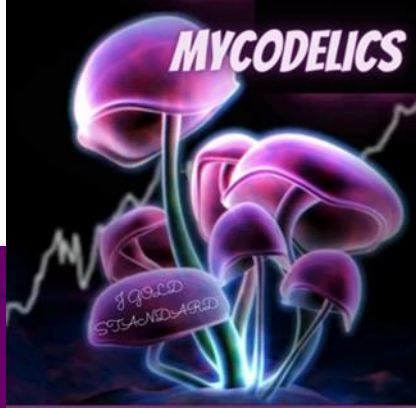
Young zygosporangium





Mature zygosporangium





*Pilobolus* aiming its sporangia





Ascomycetes (sac fungi): Scarlet cup (top left), truffles (bottom left), morel (right)





Carbon fungus



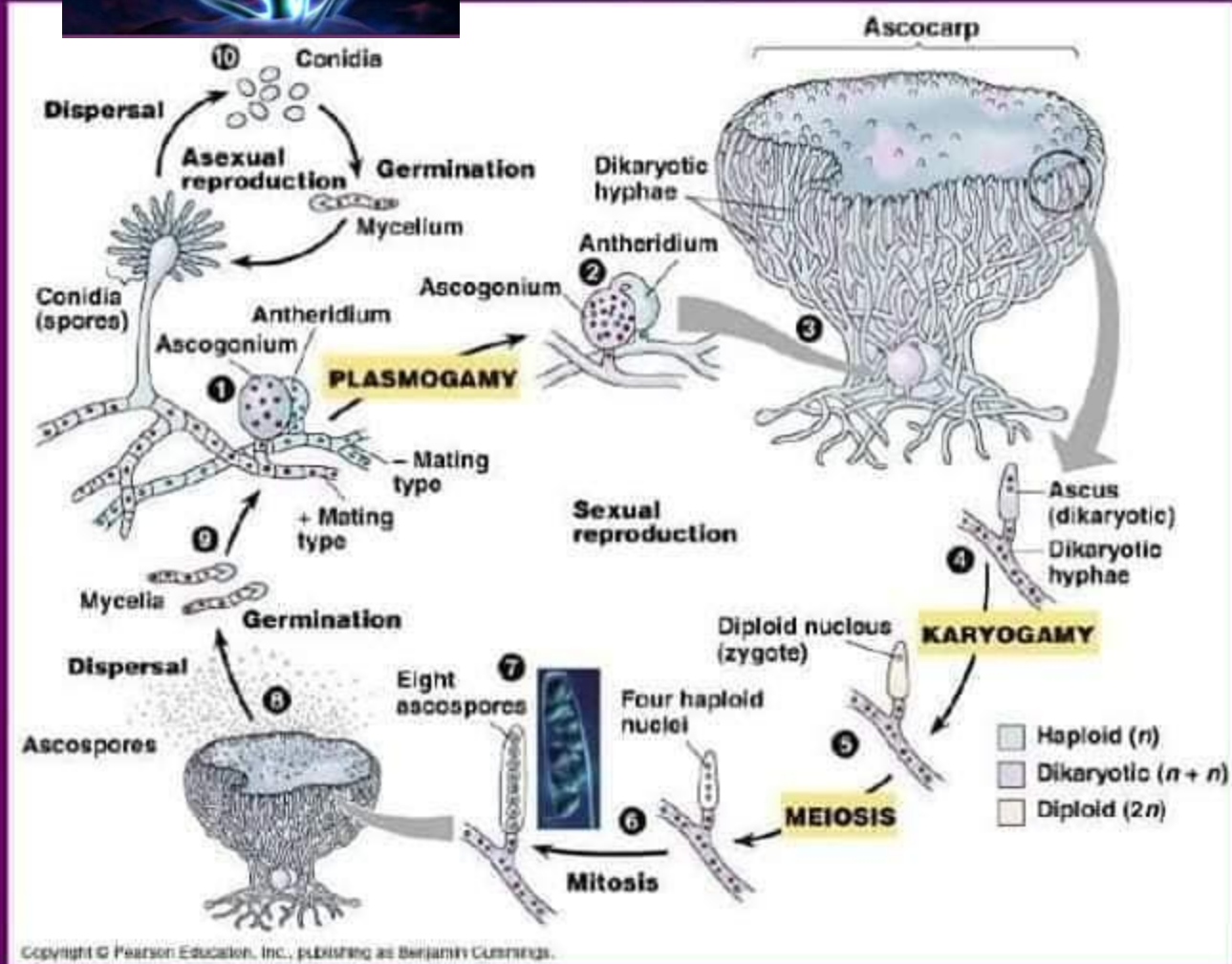


Aspergillus





## The life cycle of an ascomycete







## Life cycle of an ascomycete





Apothecium





Basidiomycetes (club fungi): Greville's bolete (top left), turkey tail (bottom left), stinkhorn (right)





*Coprinus comatus*, Shaggy Mane





*Geastrum triplex*





*Tremella messenterica*, Witch's Butter





Stinkhorn





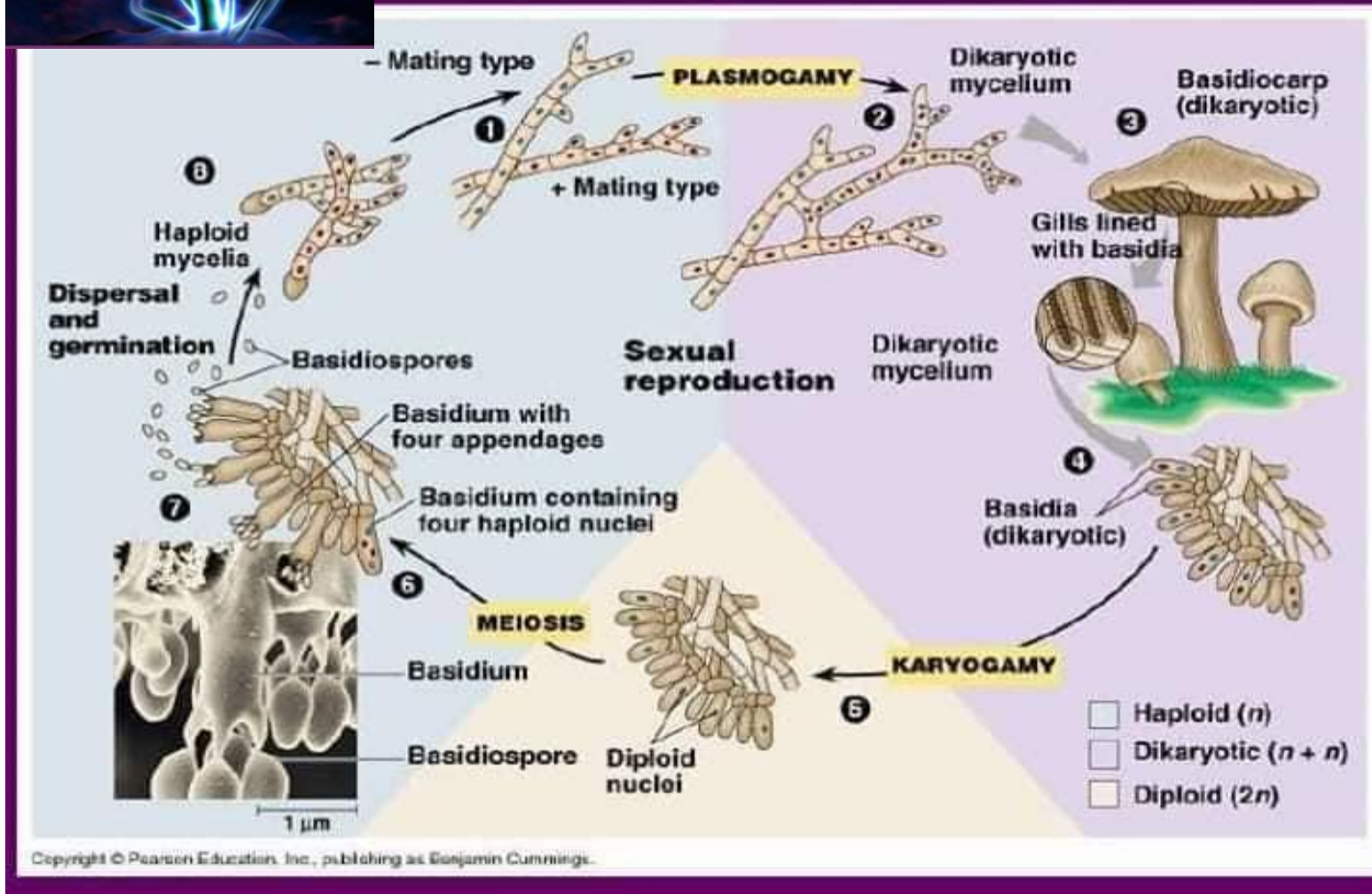
Amanita





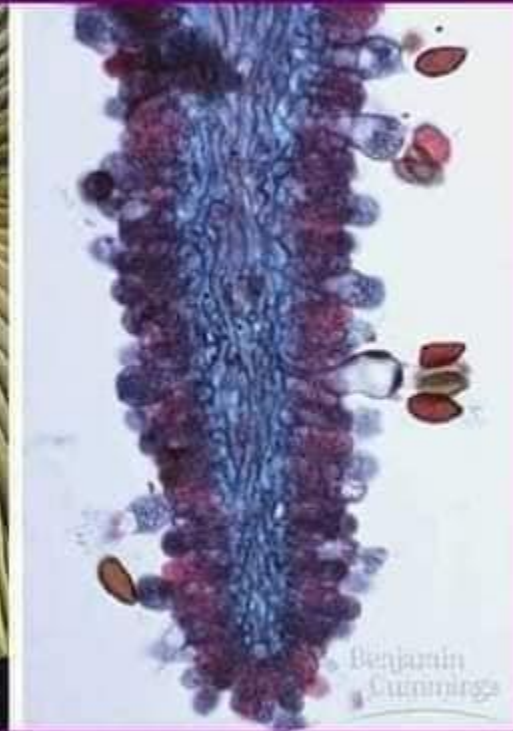


## The life cycle of a mushroom-forming basidiomycete





Gills













A fairy ring





## Review of Fungal Phyla

**Table 31.1 Review of Fungal Phyla**

Phylum	Key Reproductive Feature
Chytridiomycota (chytrids)	Motile spores with flagella
	
Zygomycota (zygote fungi)	Resistant zygosporangium as sexual stage
	
Ascomycota (sac fungi)	Sexual spores borne internally in sacs called asci
	
Basidiomycota (club fungi)	Sexual spores borne externally on club-shaped structures called basidia
	

Copyright © Pearson Education, Inc., publishing as Benjamin Cummings.

# References

1. Stajich, J.E. (2009). Fungal Genome Links: [http://fungalgenomes.org/wiki/Fungal\\_Genome\\_Links](http://fungalgenomes.org/wiki/Fungal_Genome_Links).
2. Liolios, K., Mavromatis, K., Tavernarakis, N., and Kyrpides, N.C. (2008). The Genomes On Line Database (GOLD). *Nucleic Acids Res.* 36, D475–D479.
3. Taylor, J.W., and Berbee, M.L. (2006). Dating divergences in the Fungal Tree of Life: review and new analyses. *Mycologia* 98, 838–849.
4. James, T.Y., Kauff, F., Schoch, C.L., Matheny, P.B., Hofstetter, V., Cox, C.J., Celio, G., Gueidan, C., Fraker, E., Miadlikowska, J., et al. (2006). Reconstructing the early evolution of Fungi using a six-gene phylogeny. *Nature* 443, 818–822.
5. Hibbett, D.S., Binder, M., Bischoff, J.F., Blackwell, M., Cannon, P.F., Eriksson, O.E., Huhndorf, S., James, T., Kirk, P.M., Luecking, R., et al. (2007). A higher-level phylogenetic classification of the Fungi. *Mycological Res.* 111, 509–547.
6. Multiple authors. (2006). A phylogeny for the Kingdom Fungi: Deep hyphae issue. *Mycologia* 98, 829–1103.
7. Alexopoulos, C.J., Mims, C.W., and Blackwell, M. (1996). *Introductory Mycology*, 4th Edition, (New York: John Wiley and Sons).
8. Carlile, M.J., Watkinson, S.C., and Gooday, G. (2001). *The Fungi*, 2nd Edition, (New York: Academic Press).
9. Keeling, P.J., and Fast, N.M. (2002). Microsporidia: Biology and evolution of highly reduced intracellular parasites. *Annu. Rev. Microbiol.* 56, 93–116.
10. James, T.Y., Letcher, P.M., Longcore, J.E., Mozley-Standridge, S.E., Porter, D., Powell, M.J., Griffith, G.W., and Vilgalys, R. (2006). A molecular phylogeny of the flagellated fungi (Chytridiomycota) and description of a new phylum (Blastocladiomycota). *Mycologia* 98, 860–871.
11. White, M.M., James, T.Y., O'Donnell, K., Cafaro, M.J., Tanabe, Y., and Sugiyama, J. (2006). Phylogeny of the Zygomycota based on nuclear ribosomal sequence data. *Mycologia* 98, 872–884.
12. Yafetto, L., Carroll, L., Cui, Y., Davis, D.J., Fischer, M.W., Henterly, A.C., Kessler, J.D., Kilroy, H.A., Shidler, J.B., Stolze-Rybczynski, J.L., et al. (2008). The fastest flights in nature: high-speed spore discharge mechanisms among fungi. *PLOS One* 3, e3237.
13. Genome websites (2009). <http://genome.jgi-psf.org/Phycomyces/>; [http://www.broad.mit.edu/annotation/genome/rhizopus\\_oryzae/](http://www.broad.mit.edu/annotation/genome/rhizopus_oryzae/); <http://mucorgen.um.es/>.
14. Redecker, D., and Raab, P. (2006). Phylogeny of the Glomeromycota (arbuscular mycorrhizal fungi): recent developments and new gene markers. *Mycologia* 98, 885–895.
15. Smith, S.E., and Read, D.J. (2008). *Mycorrhizal Symbiosis*, 3rd ed., (New York: Academic Press).
16. Heitman, J., Filler, S.G., and Mitchell, A.P. eds. (2006). *Molecular Principles of Fungal Pathogenesis* (Washington DC: ASM Press).
17. Sugiyama, J., Hosaka, K., and Suh, S.-O. (2006). Early diverging Ascomycota: phylogenetic divergence and related evolutionary enigmas. *Mycologia* 98, 996–1005.
18. Suh, S.-O., Blackwell, M., Kurtzman, C.P., and Lachance, M.-A. (2006). Phylogenetics of Saccharomycetales, the ascomycete yeasts. *Mycologia* 98, 1006–1017.
19. Spatafora, J.W., Sung, G.-H., Johnson, D., Hesse, C., O'Rourke, B., Serdani, M., Spotts, R., Lutzoni, F., Hofstetter, V., Miadlikowska, J., et al. (2006). A five-gene phylogeny of Pezizomycotina. *Mycologia* 98, 1018–1028.
20. James, T.Y., Stenlid, J., Olson, A., and Johannesson, H. (2008). Evolutionary significance of imbalanced nuclear ratios within heterokaryons of the basidiomycete fungus *Heterobasidion parviporum*. *Evolution* 62, 2279–2296.
21. Clark, T.A., and Anderson, J.B. (2004). Dikaryons of the basidiomycete fungus *Schizophyllum commune*: Evolution in longterm culture. *Genetics* 167, 1663–1675.
22. Pringle, A., Patek, S.N., Fischer, M., Stolze, J., and Money, N.P. (2005). The captured launch of a ballistospore. *Mycologia* 97, 866–871.
23. Aime, M.C., Matheny, P.B., Henk, D.A., Frieders, E.M., Nilsson, R.H., Piepenbring, M., McLaughlin, D.J., Szabo, L.J., Begerow, D., Sampaio, J.P., et al. (2006). An overview of the higher-level classification of Pucciniomycotina based on combined analyses of nuclear large and small subunit rDNA sequences. *Mycologia* 98, 896–905.
24. Begerow, D., Stoll, M., and Bauer, R. (2006). A phylogenetic hypothesis of Ustilaginomycotina based on multiple gene analyses and morphological data. *Mycologia* 98, 906–916.
25. Hibbett, D.S. (2006). A phylogenetic overview of the Agaricomycotina. *Mycologia* 98, 917–925.



**BIOX UNIVERSITY OF BOTANY**

*Powered by 7 Gold Fertilizer*

- <https://flow.page/horizonholdings>