

Structural Organization of fungi

Thallus

The coenocytic thallus of *chytrids* is considered as a distinct organization type. The multinuclear thalli have various forms in Chytridiomycota. The motile zoospores of chytrids develop in zoosporangia, and also the chytrids can form thick-walled resting structures. The entire thallus of some biotrophic chytrids resides within a cell of the host and has no separate vegetative and reproductive parts: the whole thallus will develop into a reproductive structure (zoospores, gametes or resting spore). In this case the thallus is **holocarpic**. Eucarpic thalli have a reproductive part and a vegetative, so-called rhizoid part serving for nutrient uptake and fixation of the fungi. The **eucarpic** thallus is monocentric when producing only one sporangium and polycentric when several sporangia develop on one thallus. The same chytrid species can develop both mono- and polycentric thalli. Monocentric thalli can develop completely in a host cell, or only the rhizoids colonize the cells, these are the endobiotic and epibiotic thalli, respectively.

Unicellular organization

Unicellular organization occurs in several fungal groups. The most widely known are the yeasts, a term used for a form-group of unicellular **coccal fungi** that reproduce by budding. Although the unicellular yeast form is discussed before hyphal organization it should be emphasized that the yeast form evolved from the hyphal form, so we consider hyphal organization to be an ancestral, plesiomorphic character. The best known yeasts belong to the Saccharomycotina subphylum of the Ascomycota, represented by fungi like the baker's yeast (*Saccharomyces cerevisiae*) and the human pathogenic *Candida albicans*. There are basidiomycetous yeasts as well, e.g. the important human pathogen *Cryptococcus neoformans*. This species belongs to the Tremellales (Agaricomycotina) together with mushrooms with macroscopic fruitbodies. This also shows that the yeast-form evolved in several fungal lineages.

Some fungi spend only a phase of their life cycle as yeasts. The meiospores (basidiospores) of the smut fungi could live and propagate as saprotrophic yeasts. They convert into the plant pathogenic phase when two compatible cells meet, fuse and form a dikaryotic hypha that colonizes the host plant. As mentioned previously, because of their special mitosis, the fission yeasts are distinguished from the budding yeasts. Nevertheless, both cellular organizations are coccal, as they cannot move by themselves. This feature fundamentally affects their nutrient uptake and their possibility to exhaust their environment on solid surfaces. They form similar colonies as bacteria, the size of the colony being determined and limited by exhaustion of the substrate.



Unicellular organization can be found in several fungi with motile zoospores in their life cycle. *In Kingdom Fungi only the chytrids have both sexual and asexual motile flagellar cells which are generally posterior whiplash opisthokonts* (cells with flagella inserted posteriorly). Oomycetes have one or two akrokont(cells with flagella inserted apically)or pleurokont (cell with flagella inserted laterally) flagella, at least one being a tinsel.

Unicellular forms were detected and visualized when the recently described basal lineage of *Regnum Fungi*, the Cryptomycota, was discovered. The spore-phase of the obligate endocellular parasite *Microsporidia* might be considered a special unicellular form as well, but it is beyond the scope of this chapter to discuss cellular organization of those highly specialized organisms.

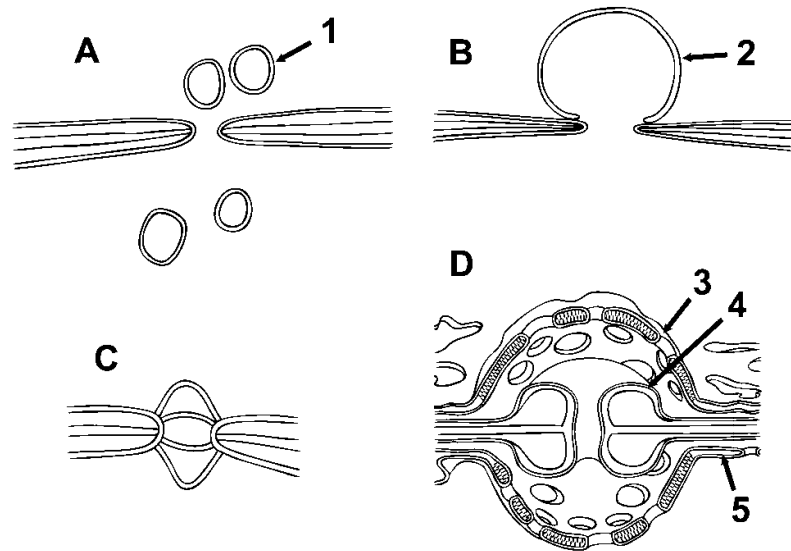
Hyphal organization

The hyphal organization of fungi is unique among the living organisms, there being few examples with similar growth and organization features, such as structures of some bacteria, the pollen tubes of plants, and some neuronal projections. Hyphae have a tubular structure, and those tubes can be divided by cross walls called septa. Septal hyphae are characteristic of the hyphalascmycetes and basidiomycetes but also can be found in some minor basal groups. Non-septate hyphae are characteristic of most Zygomycota and the arbuscularmycorrhizal fungi (Glomeromycota). Of course, these hyphae also develop cross walls when, for example, reproductive structures (e.g. sporangia) develop or to isolate damaged or senescent hyphal regions. The non-septate hyphae are coenocytic, so one continuous hyphal segment may contain multitudes of nuclei. Then there are **monokaryotic** hyphae, when one nucleus is in one hyphal segment or the special dikaryotic hyphae when two nuclei are in one segment. Such hyphae occur only in the phyla Ascomycota and Basidiomycota, as mentioned above, the reason why the clade of those two groups is called **Dikarya**.

The cross walls of the hyphae, the septa, can have different anatomies. Completely continuous septa with no pores do occur, but septa with some kind of pore are more general or even septa with several pores in some groups. The anatomy of the septal pore can be characteristic of different phylogenetic lineages. Although zygomycetes generally have coenocytic, i.e. nonseptate hyphae, some have characteristic septa with pores containing special plugs.

Ascomycetes generally have septa with simple pores, but the anatomy of those pores and the organization of organelles surrounding them may vary and be characteristic of some groups.





Structures of some septal pore types. A: Simple pore of a vegetative hyphae with Woronin bodies; B: Simple pore with pre-cap of a generative hypha. A-B: Ascomycota. C: Simple pores with different structures. D: dolipore with parenthesome. C-D: Basidiomycota.

1: Woronin-body; 2: pore-cap; 3: parenthesome; 4: dolipore; 5: wall-ER.

Membranous structures, special striate plugs in the pores or even pore-caps can cover the pore. The **Woronin-bodies** discussed above generally are detectable near the septal pores, too. The septal pore anatomy of vegetative and generative (ascogenous) hyphae of the same ascomycete species may differ significantly, and the pore organization of vegetative hyphae is generally more complex than that of generative hyphae.

Basidiomycete hyphae have diverse septal pore organization, too. Some smut fungi (in Ustilaginomycotina) have no septal pores. Several groups in Ustilaginomycotina and Pucciniomycotina have simple pores. A special pore anatomy, the **dolipore**, is exclusive to the phylum Basidiomycota. The border of this pore is swollen like a donut, and different structures (e.g. membrane-like bands) could occur in the tube of the pore. The dolipore can be covered by the **parenthesome**, a membrane organization continuous with the wall endoplasmatic reticulum (ER). The parenthesome can be sacculate, continuous or porate.

Bear in mind that the pores represent a direct physical connection of neighboring hyphal segments, their cytoplasm is continuous. Cellular organelles can migrate across the pores, even nuclei can sometimes migrate to neighbor segments. This is one reason why hyphal segments cannot be considered as analogous to the autonomous eukaryotic cell.



Mycelium, tissue

Fungal hyphae can group together to form a more or less organized multicellular structure resembling tissues of multicellular eukaryotes. However, these are not real tissues, but as the literature in English uses this term, we also do so, but bear in mind that fungal tissues do not fulfill the definition of real tissues.

We term the organized hyphal mass a mycelium. Although simple hyphae can usually be visible, the mycelial structures are the more obvious fungal parts. The several different types, forms and levels of mycelial organization have different functions. Characteristic structures include rhizomorphs, hyphae grouped together to form cord-like structures. **Rhizomorphs** help to find and exploit the nutrients of the environments of the fungi, but they can also serve as resting propagules and, being robust structures, they provide physical integrity for the fungi. They can grow to various distances but some are extremely effective, such as *Serpulalacrymans*, whose rhizomorphs can grow for several meters to find woody substrates, or members of the genus *Armillaria*, which includes the largest living organisms. The robust rhizomorphs of such species helps to preserve the multi-hectare-sized continuous genet of the *Armillariasolidipes*. Differentiated rhizomorphs have a thick-walled, compact rind covering their surface and the medial part consisting of hyphae with thinner walls and bigger lumina. Some ectomycorrhizal fungi have differentiated rhizomorphs with central hyphae of large diameter and partly or totally dissolved septa, making transport more effective. One concept uses the term rhizomorph only for differentiated structures and hyphal cords when there are no differentiated parts, only the cord-like organization of similar hyphae.

The hyphal mantle of ectomycorrhizae is another characteristic mycelial tissue that can even represent the main biomass of an ectomycorrhizal root tip. The two main anatomical types of those mantles are **plectenchymatous**, when the hyphae forming the mantle can be easily detected [The loosely woven tissue in which are closely packed, in the form of more or less parallel to one another is called **Prosenchyma**], or **pseudoparenchymatous** when it to be composed of nontubular cells such as inflated, polygonal or isodiametric in shape. We use the same terminology for other layer-like tissues formed by hyphae, e.g. the peridium (excipulum) enclosing sporocarps. Several subtypes of the two main types have been defined. For example, two main versions of the pseudoparenchymatous type are the angular and the epidermoid, depending if the cell walls are straight or wavy, respectively.

Sclerotia comprise other important mycelial structures, resting bodies which can tide the fungus over suboptimal periods. Their hyphal tissue is kept together by an extracellular glucan matrix as well. Sclerotia with differentiated tissue may have a melanized compact rind and a medular tissue with thinner walled hyaline hyphae. Similarly to rhizomorphs, sclerotia are defined in several different categories. *Botrytis cinerea*, a well known sclerotium-forming fungus, the plant pathogen casual agent of grey-rot, whose sclerotia overwinter on plant stems; the life cycle of the fungus starts from those sclerotia in the next vegetation period.



Another widely known sclerotium-forming fungus is the ergot (*Clavicepspurpurea*), which infects cereals and forms sclerotia in their spikes. These sclerotia contain the medically important ergot alkaloids in high concentration. The sclerotia overwinter and another mycelial structure, the stroma, develops from them during the spring. This stroma has a stem-like part and a head in which several **perithecia** develop to produce asci and ascospores.

Mycelial tissues form the fungal fruiting bodies, the sporocarps. The main functions of sporocarps are the support and development of spore producing structures, to hold and protect them and to help the spore dispersal. Sporocarps are sexual or asexual, depending on whether they produce sexual or asexual spores. Sexual sporocarps occur in the Ascomycota and are termed ascocarp or ascoma, and Basidiomycota (basidiocarp or basidioma). Some zygomycetes also form sexual sporocarps. The main characteristics of sporocarps will be discussed at the part dealing with sexual reproduction.

