The Fungi

```
Archaea
|--Eubacteria
`--Eukarya
   |--Chlorobionta
   `--+--Fungi
      |  |--Chytridomycota
      |  `--+--+--Zygomycota
      |     |  `--Trichomycota
      |     `--+--Basidiomycota
      |        |  |--Ustilaginomycetes
      |        |  `--Hymenomycetes
      |        `--Ascomycota
      |           |--Saccharomycotina
      |           `--Pezizomycotina
      `--Metazoa
         |--Deuterostomia
         `--Protostomia
```


Ganoderma applanatum (Basidiomycota, Homobasidiomycetes, Polyporales, Ganodermataceae)

photo by Eric Steinert in Munich, Germany, GNU Free Documentation License, Wikipedia

Lists

A. Glossary of terms and abbreviations.

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

B. Taxon Index: alphabetical list of taxa.

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

C. References: literature citations by author.

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

The Fungi are one of the three major kingdoms of multicelluar eukaryotes. For a long time classified with plants (for example, like plants but unlike animals, their cells of fungi have cell walls), they are now recognised as a distinct major group of organisms. in the Whittaker-Marguelis system of classification of life they are one of the five kingdoms (along with paraphyletic Monera and Protista, as well as plants and animals).

Although superficially resembling plants, in that they are immobile, rooted in place, lacking organs, senses, circulatory, nervous, and other such systems and so on, they feed in a very different way. Unlike plants, fungi do not make their own food through photosynthesis, but like animals derive nutrients from their environment (heterotrophy). Fungi absorb their food while animals ingest it; and rather than feeding on other living organisms, most fungi are decomposers of dead organic matter (like most bacteria).

Evolutionarily, Fungi are now considered to be more closely related to animals than to plants, both are included in a group called Opisthokonta. They seem to have been insignificant before the rise of terrestrial ecosystems in the Silurian and Devonian, but soon made up for that shortcoming by becoming ubiquitious in most terrestrial ecosystems, with many species having an essential symbiotic relationship with plants (Mycorrhizal symbiosis). MAK061005

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The Fungi

```
Archaea
|--Eubacteria
`--Eukarya
   |--Chlorobionta
   `--+--Fungi
      |  |--Chytridomycota
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      |     |  `--Trichomycota
      |     `--+--Basidiomycota
      |        |  |--Ustilaginomycetes
      |        |  `--Hymenomycetes
      |        `--Ascomycota
      |           |--Saccharomycotina
      |           `--Pezizomycotina
      `--Metazoa
         |--Deuterostomia
         `--Protostomia
```

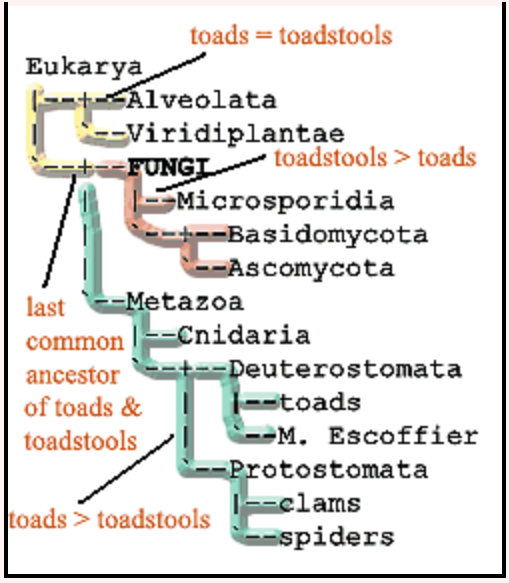

What are the Fungi?

The Fungi are the great *saprophytes*, the master recyclers. They are the black rot, the dry rot, and the white rot, the colorful fate of last week's lasagna left too long in the 'fridge, and the great, grey walls of stinking mould that can destroy whole buildings. But, they are also the baker's yeast and the brewer's yeast. They are the difference between grape juice and Chateauneuf du Pape. They are the portobellos and the morels and the cloud ears and the truffles. In fact, the French could not be half so obnoxious about their cuisine were it not for the Fungi. But, then again, perhaps they could **[1]**.

Auguste Escoffier

We leave that conundrum for another day. The first order of business ought to be the matter of definition. How do we define this group? We have found no hint that anyone is using a workable *phylogenetic* definition of the Fungi. A phylogenetic definition, for those who have somehow managed to escape our interminable, high-pitched whining on the subject, is a definition based on some explicit hypothesis about a group's relative position in phylospace. For example, dinosauria is defined as the last common ancestor of *Triceratops* and birds and all descendants of that ancestor. This may be conveniently abbreviated: "*Triceratops* + birds". Such a definition is quite different from a definition based on some arbitrary set of characteristics which approximate an implicit, unstated, and therefore untestable notion of what a dinosaur "ought" to look like. That second type of definition is referred to as an "*apomorphy*-based" definition. It is properly viewed with the same derisive contempt with which M. Auguste Escoffier (at right) would regard the use of corn starch to thicken a demi-glace **[3]**.

Were we in a position to impose a phylogenetic definition on the Fungi,



our leading candidate would be the stem group "toadstools > toads" (all organisms more closely related to Basidiomycota than to Tetrapoda **[2]**). That definition presupposes a close relationship between Metazoa and Fungi. However, such an assumption shouldn't slow us up much. The Metazoa-Fungi connection now seems quite secure. This definition would, however, require us to gather the Microsporidia into the brotherhood of the Fungi. Microsporidia *could* be Fungi under many definition of the taxon, but they are certainly closer to Fungi than to toads. Such a definition would also dispense with meaningless arguments about the inclusion of the Chytridiomycota within Fungi.

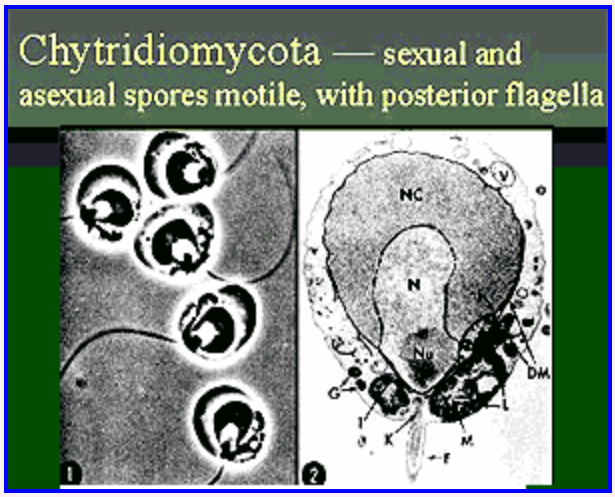
To our discredit, the foregoing discussion may serve as a useful study in the use of the English conditional mode for advanced students of the language, but it ignores the realities of fungal phylogeny. That reality is illustrated in the following examples.

The "fungi contain cell walls and produce *spores*." Madigan *et al*. (2003). So ferns are Fungi?


"Fungus," *sensu* Madigan *et al.* (2003).

The Tree of Life will not venture even this far. It contents itself with a list of common names: "The organisms of the fungal lineage include mushrooms, rusts, smuts, puffballs, truffles, morels, molds, and yeasts, as well as many less well-known organisms." In other words, the fungi are defined by listing a number of vague, vernacular terms with a completely indefinite catch-all category at the end.

"What is Fungi? Fungi are a group of organisms and micro-organisms that are classified within their own kingdom, the fungal kingdom, as they are neither plant nor animal. Fungi draw their nutrition from decaying organic matter, living plants and even animals. They do not photosynthesize as they totally lack the green pigment chlorophyll, present in green plants. Many play an important role in the natural cycle as decomposers and return nutrients to the soil, they are not all destructive."WHAT IS FUNGI? But this description would apply equally as well to most bacteria.



"These nonmotile eukaryotes lack *flagella* and develop from spores." Dr. Fungus- Fungi, Fungus, Fungal. But see the image.

We could beat this drum for quite a long time. The point is that, of the hundreds of references and sites on the web which purport to discuss the Fungi, not one of the many we have reviewed supplies a reasonable definition. Some sources are very useful in listing numerous characteristics of Fungi. But, the more characters listed, the more Fungi (in any phylogenetic sense) they exclude. A substantial majority of sources simply dodge the issue.

Ultimately, we are left in the untenable position of admitting that there is *no* definition in general use for the word "fungus." Happily, this yawning gap at the threshold of mycology seems to bother mycologists even less than it bothers the Fungi themselves. Thus, in a manner sanctioned by the universal practice of man and mushroom alike, we will pointedly ignore the yawning abyss at our feet, and move on to other matters.

Characteristics of the Fungi

We never eat bread cookies
For cookies have yeast,
And one little bite
Turns a man to a beast
O, can you imagine
A sadder disgrace
Than a man in the gutter
With crumbs on his face?

-- *Song of the Salvation Army* (trad.)

So, what about all those characteristics mentioned in the last section? The following is a list of the most commonly cited characters shared by most Fungi:

- The Fungi are eukayotes, which may exist in nature as either single and multi-celled organisms, or in both at different points in the the life cycle.
- Fungi are avascular -- no specialized respiratory, digestive or transport systems beyond the hyphae themselves.
- Most fungi grow as tubular filaments called *hyphae*. A connected mass of hyphae is a *mycelium*.
- Fungi have a vegetative body called a *thallus*, composed of hyphae.
- The walls of hyphae are often reinforced with *chitin*, a polymer of N-acetylglucosamine.
- Fungal cell membranes contain *ergosterol*, rather than cholesterol.
- The Fungi have a unique biosynthetic pathway for lysine.
- Fungi produce a unique form of tubulin in connection with nuclear division.
- Fungi have small nuclei with very little repetitive DNA
- Mitosis occcurs without dissolution of the nuclear membrane.
- Fungi are never *autotrophs*. No fungus has chlorophyll or chloroplasts.
- Fungi are usually found either as opportunistic *saprophytes* (living on dead organic matter) or in some parasitic or symbiotic relationship with plants or other autotroph.
- Fungi digest food outside their bodies: they release enzymes into the surrounding environment (exoenzymes), breaking down organic matter into a form the fungus can absorb
- food reserves stores as glycogen (like animals), not starch (like plants).
- Fungi reproduce by means of *spores*, *budding*, or *fragmentation*.
- Spores may be either sexual or aesexual.
- Spores may be used as a dormant, resting phase, like bacterial spores

In short, Fungi are a rather odd, and distinctly different, part of the tree of life.

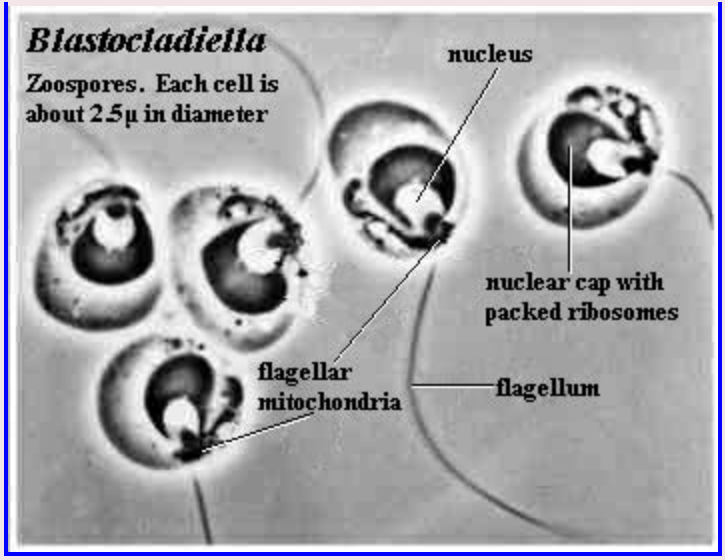
Diversity of the Fungi

The following is our usual diversity table, which somewhat overemphasizes the basal Fungi. Recent work suggests that fungal diversity may be undersampled even at the highest taxonomic levels. Specifically, a taxonomic survey of alpine fungal communities which flourished under snow cover suggests that there may be 1-2 high-level fungal taxa between Basidiomycota and Ascomycota. Schadt *et al.* (2003).

Fungi

Chytridomycota

The chytridomycotes, or "chytrids," are usually aquatic, either marine or freshwater. Presumably this is the



original domain of the chytrids, and of all Fungi, but chytrids are also found in terrestrial communities almost as soon as there were terrestrial communities to be found in. So, for example, several different groups of chytrids are known from the Early Devonian Rhynie Chert. The implication is that they had begun to radiate even before the Devonian. They are a remarkably diverse lot, as one might expect from a basal radiation of the Fungi, and there is some possibility that the Chytridomycota may be paraphyletic, *i.e.* that all Fungi are descended from chytrids.

The chytrids are mostly single-celled forms, traditionally classified as protists. In fact, some sources *still* classify them with the Chromista, even though, so far as we can tell, chytrids have no light-sensitive pigments at all. What chytrids *do* have is a single- celled *zoospore* with an anterior flagellum, which is distinctly odd for a fungus. In fact, chytrids are the only large taxon of Fungi which produces a zoospore of *any* kind.

However, there's no real doubt about their position any more. For example Borneman & Hartin (2000) showed that rDNA primers from all of four basic fungal phyla (Trichomycota was not included) permit amplification of rDNA in the other fungal groups, including Chytridomycota, but don't amplify anything else. This strongly suggests that that rDNA from all four groups was very similar and that all are closely related.

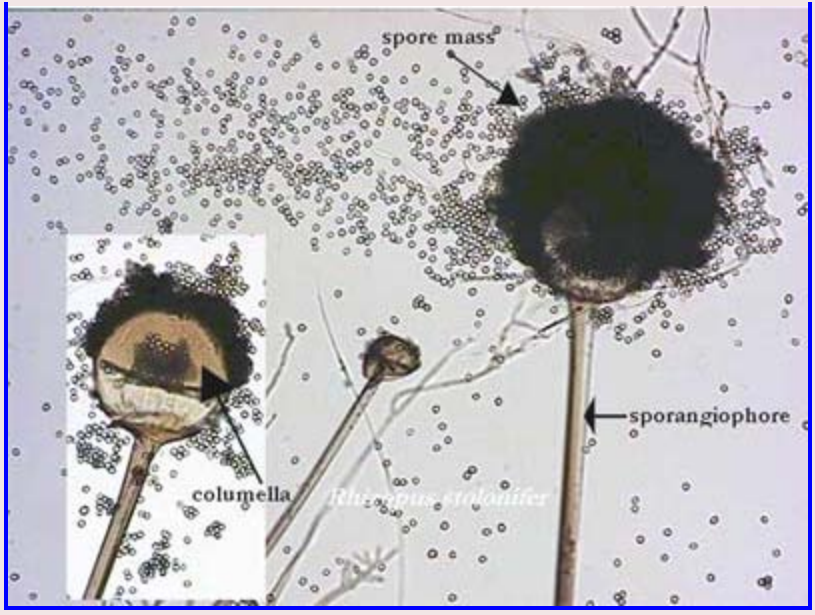
That same conclusion can be reached for any number of other reasons. Chytrids have an absorptive mode of nutrition, like other Fungi. Chytrids have cell walls composed of *chitin*. Chytrids form *hyphae*. They share, with the other Fungi, key enzymes and metabolic pathways that are not found in other fungus-like protozoans (slime molds and water molds), in addition to oddities of molecular structure. Alkemar & Nygard (2003). The chytrids are surely the most basal Fungi, but Fungi they are.

Image Credit: The Microbial World.

Zygomycota

Unnamed Clade

This group is sometimes referred to as Zygomycota, with Zygomycetes and Trichomycetes treated as included taxa.



Zygomycotes, like chytrids, are known from the Rhynie Chert, although, in this case, the identification is more tentative. What are actually seen are fungal hyphae which appear to pierce other cells, a characteristic of many zygomycotes. Definitive zygomycotes are found in Carboniferous exposures. A more familiar present-day example of a zygomycote is *Rhizopus*, the black bread mold.

The Zygomycota are named for their characteristic *teleomorph*, which is referred to as a *zygosporangium*. The images at the glossary entry for *gametangium* are of *Phycomyces* and *Rhizopus*, both zygomycotes. They illustrate how the zygosporangium is formed from the head-on meeting of two *hyphae* whose ends have specialized as gametangia. The contents of the gametangia are mixed in the zygosporangium, which develops between them. The haploid nuclei from the gametangia then fuse. The zygosporangium develops a hard, thick chitin shell, which is frequently ornamented and may bear spines or other appendages. The remains of the gametangia protrude from the sides and are referred to as *suspensors*. The zygosporangium also serves as a resting phase, which will develop when conditions are favorable.

Zygomycotes also reproduce asexually. The haploid spores develop in a bulbous *mitosporangium* at the tips of specialized vertical hyphae referred to as *sporangiophores*.

Image: Dr. Paul Davis, Univ. N. Alabama.

Trichomycota

From time to time we find a web resource that is so comprehensive well-organized that there is no point in providing a summary here. That is the case with the Trichomycota. We happily defer to **The Trichomycetes: Fungal Associates of Arthropods**. The authors' own summary of their work is Chapter 1 of the treatise. Trichomycotes are obligate commensals (sometimes parasites) of insects and are thought to have developed with neopteran insects in the Mississippian.

Basidiomycota

The basidiomycotes are the rusts, smuts, gilled mushrooms, puffballs, stinkhorns, and club, shelf or coral fungi. They are one of the two major divisions of Fungi, the other being the Ascomycota. Definitive Basidiomycote fossils are known from the Late Devonian, although there has been a recent report of a possible Early Devonian lichen incorporating a probable basidiomycote fungus.

The Basidiomycota is such a large and diverse group, that the living members have little in common. The basidiomycote life cycle has a four unique properties which are probably synapomorphies, but which are no longer shared by all members of the group:

(1) The taxon is named for the *basidium* where sexual spores are produced.

(2) The life cycle generally includes a persistent *dikaryon*, frequntly large (e.g., a mushroom) in which each cell in the *thallus* contains two haploid nuclei, typically as the resulting of a mating event

(3) *Clamp connections* (explained at the glossary entry) are unique to Basidiomycota and are used to maintain the dikaryon state during *hyphal* division.

(4) Many basidiomycotes can launch spores into the air in a process referred to as *ballistospory*.

The *basidiospores* bear a single haploid nucleus. They germinate into hyphae with a single nucleus in each compartment, a *monokaryon*. A mating event results from end-to-end fusion of hyphae, as in Zygomycota, or fusion of a hypha with an *oidium*, a specialized mating spore. Then the resulting dikaryon divides through clamp connections so that the dikaryon state is maintained. Many basidiomycotes remain in the dikaryon state indefinitely. Under appropriate conditions, the dikaryon will produce *fruiting bodies*. Some of these hyphae produce *basidia*, such as the cells lining the "gills" under the cap of gilled mushrooms. Ultimately, the two haploid nuclei in each basidium fuse (*karyogamy*) to form a diploid nucleus. This then undergoes meiosis to produce four haploid nuclei whch migrate into the basidiospores and are dispersed into the environment.

Ascomycota

The Ascomycota are the largest and most diverse group of Fungi. They include the yeasts, most of the fungal elements of lichen, and such famous Fungi as *Saccharomyces*, *Aspergillus*, *Candida* and *Neurospora*, as well as morels, truffles and similar delicacies. The current understanding is that supposed pre-Devonian (even

Proterozoic!) lichens are probably artifacts, making the earliest known ascomycote of Carboniferous age.

The Ascomycota are united by the presence of *asci* (*see* glossary entry). Like Basidiomycota, ascomycotes remain indefinitely in the *dikaryon* state, with the fungal filaments (*hyphae*) partitioned into cells each containing two haploid nuclei -- one from each parent. Also as in basidiomycotes, nuclear fusion (*karyogamy*) occurs only in connection with the formation of sexual spores. At that time the newly diploid nucleus undergoes one (sometimes more) round of mitosis, followed by *meiosis*, to yield eight (or a multiple of eight) haploid nuclei. The nuclei are then partitioned by internal membranes into individual *ascospores*. The Ascomycota also share with Basidiomycota the use of *conidia* for the development of asexual spores.

Another unique character (but not present in all ascomycotes) is the presence of *Woronin bodies* on each side of the septa separating the hyphal segments. The septae are pierced by pores which allow most cytoplasmic constituents (but not nuclei) to travel freely between hyphae. However, if an adjoining hypha is ruptured, the Woronin bodies block the pore to prevent loss of cytoplasm into the ruptured compartment.

For more information, see **Ascomycota**.

Top Level Dendrogram

```
Archaea
|--Eubacteria
`--Eukarya
   |--Chlorobionta
   `--+--Fungi
      |  |--Chytridomycota
      |  `--+--Zygomycota
      |     `--+--Basidiomycota
      |        |  |--Ustilaginomycetes
      |        |  `--Hymenomycetes
      |        `--Ascomycota
      |           |--Saccharomycotina
      |           `--Pezizomycotina
      `--Metazoa
         |--Deuterostomia
         `--Protostomia
```


Introduction

This page is written near the beginning of our fungal enterprise, and without sufficient research to justify any claim to independent judgment in the matter. Accordingly, we have taken the **Tree of Life** phylogeny more or less as given. ToL's arrangement is moderately complete for the Basidiomycota, but short-changes the Ascomycota, or sac fungi. Since the ascomycotes represent 75% of known fungal species, we feel constrained to do better. Fortunately, the online journal **Myconet** is devoted to the precise subject of ascomycote phylogeny. Unlike most journals, it attempts to build a consensus, and a consensus tree, in a progressive fashion. Theirs is a somewhat Linnean tree, but we have arranged things to correspond to the trees reported in **Mycophylogeny** by Derek Peršoh. Additional bits and pieces were assembled from Vandenkoornhuyser *et al*. (2002). We've made a completely unsupported guess as to the branching order of Christianseniales and Trichosporonales within Tremellomycetidae. Recently, we rearranged the Ascomycetes following Liu & Hall (2004). When these ingredients are thoroughly mixed and incubated for 600 My at about 293° K, the result looks a like this.

Top-Level Dendrogram

```
Fungi
|--Chytridomycota
`--+--+--Zygomycota
   |  |  |--Mucorales
   |  |  `--Mortierellales
   |  `--Trichomycota
   `--+--Basidiomycota
      |  |--Urediniomycetes
      |  `--+--Ustilaginomycetes
```

```
|      |  |--Entorrhizomycetidae
|      |  `--+--Ustilaginomycetidae
|      |     `--Exobasidiomycetidae
|      `--Hymenomycetes
|         |--Tremellomycetidae
|         |  |--Christianseniales
|         |  `--+--Trichosporonales
|         |     `--+--Filobasidiales
|         |        `--+--Cystofilobasidiales
|         |           `--Tremallales
|         `--+--Dacrymycetales
|            `--+--Auriculariales
|               `--Homobasidomycetes
`--Ascomycota
   |--Taphrinomycotina (= Archaeoascomycetes)
   `--+--Saccharomycotina (= Hemiascomycetes)
      `--Pezizomycotina (= Euascomycetes)
         |--Pezizomycetes (paraphyletic)
         `--+--Hymenascomycetes
            |  |--+--Leotiomycetes
            |  |  `--Sordariomycetes
            |  `--+--Lecanoromycetes
            |     `--Eurotiomycetes
            `--Loculoascomycetes
               |--Dothideomycetes
               `--Chaetothyriales
```


Clades, Culture, and Collaboration

"Do you have any hobbies?"
"I collect mold, spores, and fungus."

-- **Ghostbusters** (1984)

The fungal cladogram brings home the point that each of the major regions of phylospace has created its own scientific culture. Our brief encounter with fungal phylogeny suggests that mycologists are very polite to one another. Nowhere else would an entire scientific community attempt to construct a phylogeny on a collaborative basis. Phylogenetic discussions among mycologists seem to go out of their way to mix concepts from Linnean, cladistic, and molecular phylogenies in an effort to show that all paradigms can be reconciled.

Protistologists also tend to be quite accommodating in phylogenetic matters. However, that is the courtesy of indifference. Many protistologists either don't care about phylogenetic matters, or don't believe that the major phylogenetic issues have any solution in their part of phylospace. Sadly, they may be correct. Mycologists, however, *do* seem to care about phylogeny. Yet the dynamic among mycologists is nothing like the eternal, vicious rapier duel of vertebrate workers, who are inclined to shift paradigms aggressively every few months just to keep each other off balance. Nor yet are the mycologists like the paleobotanists. The plant folk tend to be rather ... vague. Their writing often suggests an underlying vitalism, as if the evolution of plants were some semi- conscious, concerted effort by the entire chlorophyll *b* community to advance from grade to grade. No, the mycologists can't be accused of that philosophical bent. Yet the idea that "if we all agree, we must have the right answer," also seems passing strange.

This mind-set, and the passion for consensus, becomes more understandable in historical perspective. Mycology was historically a minor branch of botany, and most fungi were classified in form-taxa, without even the pretense of phylogeny. Furthermore, since these were utilitarian form-taxa, overlapping and inconsistent systems of nomenclature were introduced freely. Thus, by the time that mycology finally obtained its long and messy divorce from the botany, fungal taxonomy was in a state of near chaos. A system of collective decision-making was necessary to bring scientific rationality to the subject. It will be interesting to see how that cultural influence plays out, now that the main outlines of fungal phylogeny are almost complete.

"Back off, man! I'm a scientist!"

-- **Ghostbusters** (1984)

We have, of course, grossly exaggerated some minor peculiarities of mycology in order to make an interesting essay out of a few cheap shots at people we don't even know. Fortunately, there is one good thing that can be said for consensus phylogenies. They certainly make life easier for those of us who normally must struggle to chose from among competing trees. So, who are we to question this good fortune?

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Taxon Index

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

-A-

Ascomycota: sac fungi

-B-

Basidiomycota: rusts, smuts, gilled mushrooms, puffballs, stinkhorns, and club, shelf or coral fungi.

-C-

Chytridomycota: very primitive fungi with flagellate zoospores

-F-

Fungi: toadstools > toads

-P-

Pezizomycotina: same as Euascomycetes

-S-

Saccharomyces: (Ascomycota: Saccharomycotina) *see also* The Cell Wall.
Saccharomycotina: yeasts

-T-

Taphrinomycotina: paraphyletic basal ascomycetes
Trichomycota: specialized commensals and parasites of insects.

-Z-

Zygomycota: bread moulds and relatives

---

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Glossary A-F

The initial entries in this glossary were assembled in considerable haste. I tender my apologies to **Jonathan Dixon**, late of the University of Manchester, from whose glossary I borrowed liberally. Various other gleanings are credited individually.

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

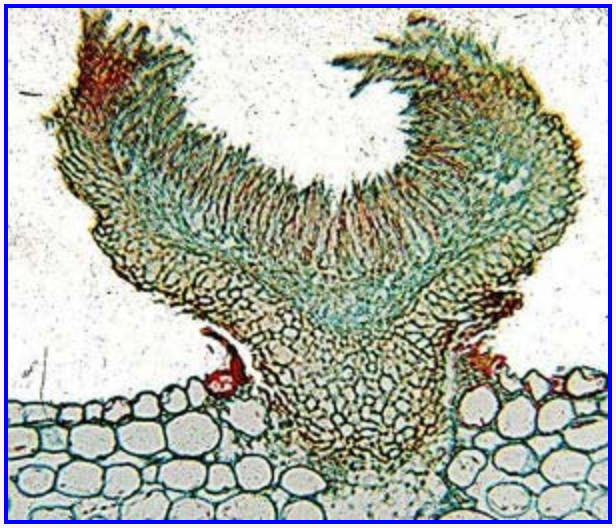
-A-

Anamorph: the asexual reproductive or propogative manifestation of a fungus.

Anomer: *See*, The Cell Wall.

Apomorphy: a character state which is unique to a single, terminal taxon. Example: amongprimates, complex grammar is an apomorphy of human beings. It is quite diagnostic of humans, but useless in determining phylogenetic relationships because it is not a shared, derived characteristic, or synapomorphy, of any larger group.

Apothecial: pertaining to apothecia



Apothecium: a disk-shaped or cup-shaped ascocarp (fruiting body) of a lichen or non-lichenized ascomycete. In an apothecium, the asci are born in a single, orderly layer on an open, fairly flat surface. Image of apothecium from *Mollisia dehnii* from the **Univ. of Wisconsin -- Madison Botany Department** web site.

Arthrospore: A spore resulting from the fragmentation of a hypha.

Ascocarp: the fruiting body of an ascomycete; the multicellular structure that produces asci, and acts as the platform from which the spores are launched.

Ascohymenial: relating to an ascocarp which forms after nuclear

pairing. The ascocarps produced by ascohymenial development extend out into the medium, as in the image at apothecium, and the asci are unitunicate. *Comapare* ascolocular.

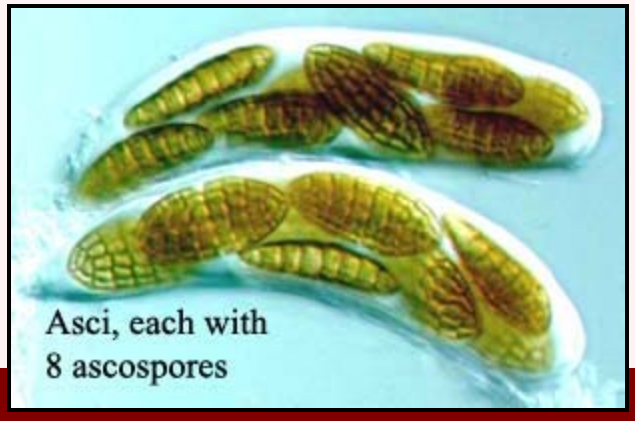
Ascolocular: relating to a mode of ascocarp growth in which a perithecium develops within a cushioning hollow of cells (the stroma) which is nested in a depression of the hymenium (a locule). The ascocarps produced by ascolocular growth do not grow into the medium, and the asci are usually bitunicate. *Compare* ascohymenial.

Ascoma: (pl. *ascomata*) (1) same as ascocarp (2) "an ascocarp having the spore-bearing layer of cells (the hymenium) on a broad disklike receptacle." This latter definition is frequently cited but appears to be either incorrect or useless. For our purposes, *ascoma* and *ascocarp* will be treated as synonymous.

Ascospore: A meiospore borne in an ascus

Ascus: a sac-like cell containing the ascospores cleaved from within by free cell formation after karyogamy (nuclear fusion) and meiosis. Eight ascospores typically are formed within the ascus, but this number may vary considerably.

Autotroph: an organism which obtains energy from inorganic sources, sunlight or the oxidation of inorganic chemicals.



-B-

Ballistospory: the ability to launch spores into the air. The mechanism of ballistospory is not fully understood. This ability is common in Basiodiomycota and is also known in some Ascomycota.

Basidiospore: a meiospore borne on the outside of a basidium.

Basidium: structure produced by basidiomycetes on which sexual spore formation occurs.

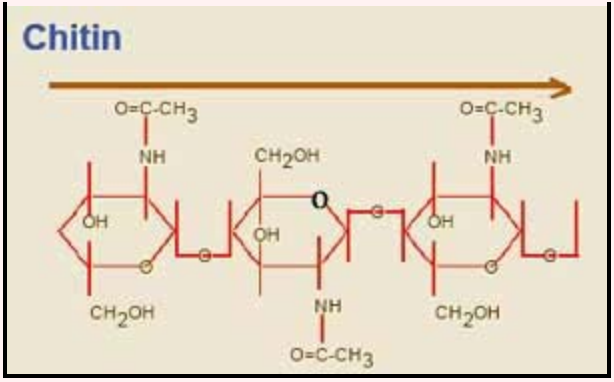
Binding hyphae: thick walled, typically aseptate, highly branched vegetative hyphae.

Bitunicate: an ascus with differentiated inner and outer walls is said to be *bitunicate*. *See also*, fissitunicate.

Budding: reproduction by binary fission, a characteristic form of propogation in yeasts. "The onset of the cellular events is accompanied by the nuclear events of mitosis. ... The initial events of budding can be seen as the development of a ring of chitin around the point where the bud is about to appear. This reinforces and stabilizes the cell wall. Enzymatic activity and turgor pressure the act to weaken and extrude the cell wall. New cell wall material is incorporated during this phase. Cell contents are forced into the progeny cell, and as the final phase of mitosis ends a cell plate, the point at which a new cell wall will grow inwards from, forms." http://www micro.msb.le.ac.uk/224/mycology/2.html (former site)

-C-

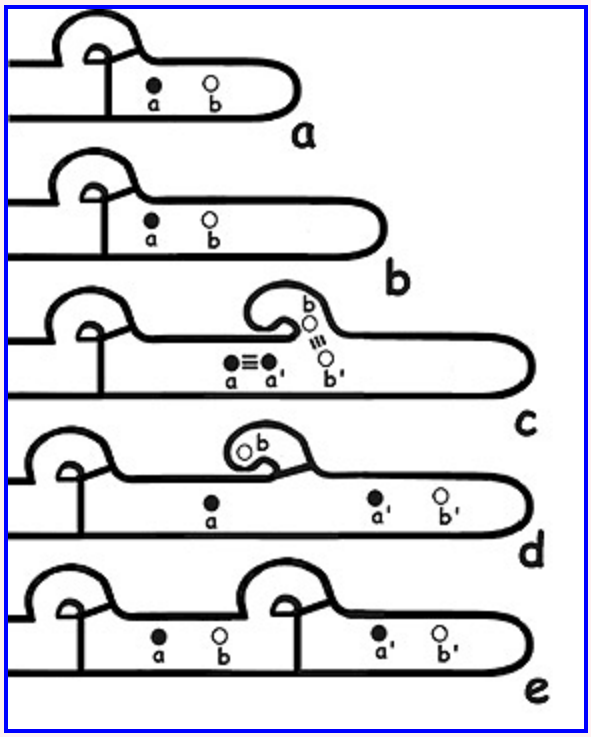
Chitin: a polymer of repeating sugar molecules (a slightly modified glucose, poly-N-acetyl-D-glucosamine). See image. Chitin is the material which makes up the exoskeleton of insects and, in more or less modified form, in almost all arthropods. In arthropods, chitin occurs in a crosslinked form, a-chitin. Significantly, it is also found in the radular "teeth" of molluscs, the setae (bristles) and jaws of annelid worms, and the cell walls of Fungi. So, this is exceedingly ancient stuff, possibly predating the split between bacteria and metazoans. [What may be of sociological interest is that the 1,5 aldose linkage was missing



from the middle glucose in this diagram and no one spotted it for over a year ....]

Chitosan: Chitosan (poly-**D**-glucosamine) is one of the most common polymers found in nature. Structurally, it is related to cellulose, which consists of long chains of glucose molecules linked to each other. Chitosan is chitin with acetic acid amide linkage hydrolyzed from the 2-amino group. In fact, this is exactly how chitosan is commercially prepared.

Clade: a "natural group" or phylogenetically defined group of organisms. A clade is usually defined as a particular organism "and all of its descendants." This apparantly innocuous concept, introduced to systematics by Willi Hennig, has completely changed the way systematics is done and has fundamentally altered the way we view evolutionary change. To understand why, see Dendrograms.



Clamp connection: a bridge-like hyphal connection involved in maintaining the dikaryotic condition. There's a great animation of this process at Forest and Shade Tree Pathology. Another explanation, from Prof. George Wong's site at the University of Hawaii (see image): "a. Terminal cell of hypha. Growth only takes place at hyphal tips; b. Hyphal tip elongating. c. Synchronous division of nuclei and the beginning of hyphal branch that will become the clamp connection. One nucleus (b) migrates into the new clamp. d. Septum forms at base of the clamp trapping nucleus b. Nuclei a' and b' migrate to the hyphal tip, while nucleus a migrates away from the tip. e. Septum forms below clamp forming new cell at hyphal tip. Fusion of the clamp to the adjacent cell releases nucleus b to the adjacent cell. Now both the terminal and subterminal are binucleate, each with a compatible pair of nuclei."

Cleistocarp: same as cleistothecium

Cleistothecial: of an ascocarp (especially Aspergillaceae and Erysiphaceae), have a closed spore-bearing structure without a pore (ostiole) for spore release, and from which spores are released only by decay or disintegration.

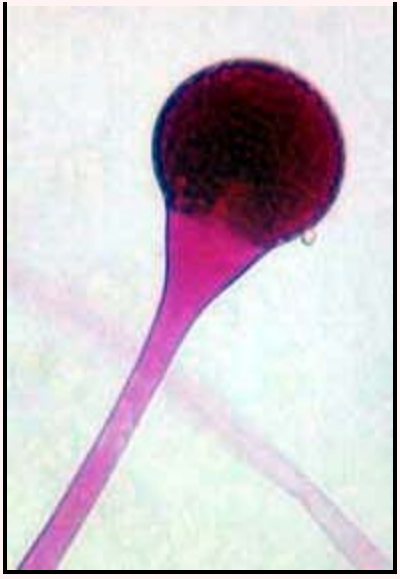
Cleistothecium: a cleistothecial ascocarp.

Coenocytic: only divisions (septa) are formed between the nuclei of the hypha when reproductive cells develop.

Columella: the swollen tip of the sporangiophore (the stalk) on which mitospores develop. The image shows an intact columella, with spores attaches. When the spores have dispersed, the columella collapses into a structure that looks remarkably like a microscopic mushroom.

Colony: coherent mycelium or mass of cells, like yeast cells, of one origin.

Conidium: Conidia are sporangia grown on elaborate structures called conidiophores. These are usually stalked, lifting the conidia off the substrate for better dispersal and to avoid microscopic grazing animals. They are often produced hundreds or thousands of at a time.



Crista: (pl. *cristae*) **(1)** of mitochondria, folds in the internal membrane of the mitochondrion which gives the organelle its characteristic appearance. This is the site of the electron transport chain in oxidative metabolism. The cristae, therefore, serve as the physical link between the tricarboxylic acid cycle and oxidative phosphorylation (ATP synthesis). *See also* Mitochondrion - Wikipedia. **(2)** more generally, a crest (its literal meaning in Latin) or ridge.

-D-

Dehiscence: the process of releasing spores. That is actually the botanical definition, although it is widely used in mycology. *Dehiscence* is also used in a more restricted, mycological sense to mean a process for realsing all of the spores in an ascocarp simultaneously, or in some coordinated manner.

Deuteromycetes: Fungi that can only reproduce asexually.

Dikaryon: a pair of closely associated, sexually compatible nuclei, may or may not be derived from a different parent hypha or cell. Occasionally, polykaryons are produced with nuclei from more than two individuals.

Diploid: a nucleus is dipploid if it contains two copies of each non-redundant gene. In Fungi, it is necessary to distinguish between diploid nuclei and diploid cells. A hypha may contain several haploid nuclei (either identical or from different individuals). Technically, the cell is diploid or polyploid. However, there may be no diploid nuclei.

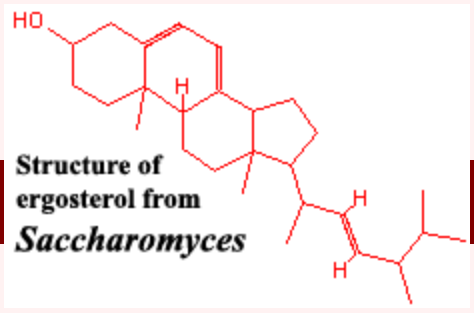
Diploidization: The process which occurs when compatible haploid hyphae from different individuals exchange nuclei. This does not necessarily result in the formation of diploid nuclei, meiosis, or genetic exchange. In fact, some fungi can maintain populations of nuclei from up to six independent individuals in a single hypha.

-E-

Enantiomer: *see* The Cell Wall

Endomycorrhiza: mycorrhiza in which the fungal hyphae penetrate cell walls of host plant.

Endophyte: a fungus living within plants, often without causing visible symptoms.



Structure of ergosterol from *Saccharomyces*

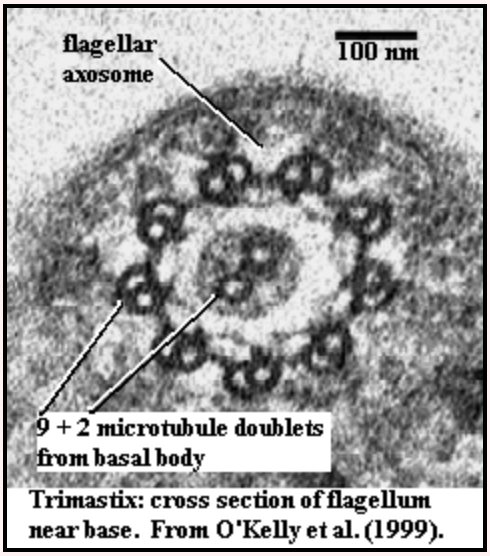
Ergosterol: a sterol lipid which occurs in fungal cell membranes, apparently in place of cholesterol. It is found in metazoans as a precursor to vitamin D2.

-F-

Fission: cytoplasmic division of a cell to form two cells, a form of asexual reproduction.

Fissitunicate: A bitunicate "ascus has a distinctly bilayered wall, with the outer layer being rigid and the inner layer being expandable. As it matures, the thin outer layer splits and the thick inner layer absorbs water and expands upward. The ascus stretches up into the narrow neck of the ascoma, and the ascospores are expelled. These asci with a 'jack-in-the-box' design are also called fissitunicate." Guarro *et al*. (1999).

Flagellum: (pl. *flagella*) A eukaryotic flagellum is a bundle of nine fused pairs of microtubules called "doublets" surrounding two central single microtubules (the so-called 9+1 structure of paired microtubules; also called the "axoneme"). At the base of a eukaryotic flagellum is a microtubule organizing center about 500 nm long, called the basal body or kinetosome. The flagellum is encased within the cell's plasma membrane, so that the interior of the flagellum is accessible to the cell's cytoplasm. This is necessary because the flagellum's flexing is driven by the protein dynein bridging the microtubules all along its length and forcing them to slide relative to each other, and ATP must be transported to them for them to function. This extension of the cytoplasm is called the *axosome*. **Important note:** The eukaryotic flagellum is completely different from the prokaryote flagellum in structure and in evolutionary origin. The only thing that the bacterial, archaeal, and eukaryotic flagella have in common is that they stick outside of the cell and wiggle to produce propulsion. From Flagellum - Wikipedia. Image: O'Kelly *et al*. (1999).



Trimastix: cross section of flagellum near base. From O'Kelly et al. (1999).

Fragmentation: "Many fungi can reproduce by fragmentation. Any mycelium that is fragmented or disrupted, provided that the fragment contains the equivalent of the peripheral growth zone, can grow into a new colony. Many fungi are sub-cultured using this hyphal fragment technique. All of this weeks practical plates have been inoculated in this way with a cork bore taken from a colonized donor plate. Cut mycelial tips do not regenerate, but branches can form some distance from the damage point." Reproduction in the fungi.

Fruiting body: any complex fungal structure that contains or bears spores.

Furanose: *see* The Cell Wall.

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Glossary G

The initial entries in this glossary were assembled in considerable haste. I tender my apologies to **Jonathan Dixon**, late of the University of Manchester, from whose glossary I borrowed liberally. Various other gleanings are credited individually.

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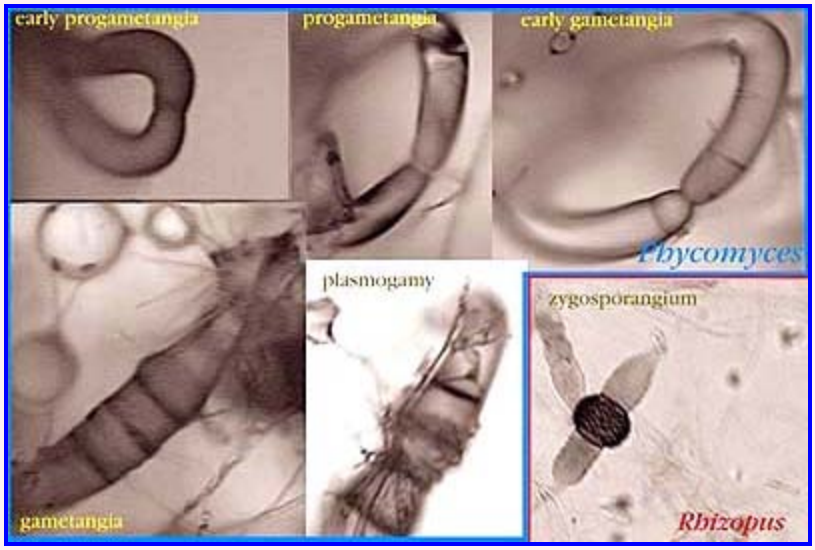
-G-



Gametangium: a single-celled structure producing gametes (sex cells) or gametic nuclei.

Ghost lineage: a period of time during which a clade is inferred to exist, but is not known in the fossil record. As discussed in the text, Ascomycota and Basidiomycota are sister groups. Basidiomycota is known from the Early Devonian. This means that Ascomycota must have diverged from Basidiomycota at least this early. However, no definitive ascomycete remains are known older than the Missisippian. Thus, Ascomycota has a ghost lineage spanning the 60 My between these two periods.

Gleba: fleshy spore-producing inner mass of a clestothecium (enclosed ascocarp), *e.g*. a puffball or stinkhorn. A gleba on the *outside* of an *open* ascocarp is referred to as a hymenium. The term is also used in a slightly different sense to mean the mass of spores left as the asci disintegrate.

Glucan: a polysaccharide composed of repeating units of glucose.

Glucan, beta: b-Glucans consist of linear unbranched polysaccharides of linked b-(1®3)- and b-(1®4)-**D**-glucopyranose units. They are (together with chitin) an important component of the cell wall in Basidiomycota and Ascomycota. See image at Ascomycota.

Glucose: *see* The Cell Wall.

Glycoprotein: a protein to which sugar molecules are bound, often in short chains ("oligosaccharides"). The free hydroxyl groups on the sugar molecules are often strongly hydrated, resulting in a matrix which contains considerable water and a surface with low friction. The hydroxyl groups also form hydrogen bonds with other sugars, creating a complex of flexible cross-links between individual protein molecules. Animal "gristle" is a good example of a glycoprotein matrix.

Glycoside: *see* The Cell Wall.

-H-

Haploid: a nucleus is haploid if it contains only one copy of each non-redyndant gene. In Fungi, it is necessary to distinguish between haploid nuclei and haploid cells. A hypha may contain several haploid nuclei (either identical or from different individuals). Technically, the cell is diploid or polyploid. However, there may be no diploid nuclei.

Haworth diagram: *See*, The Cell Wall.

Hemiacetal: *See*, The Cell Wall.

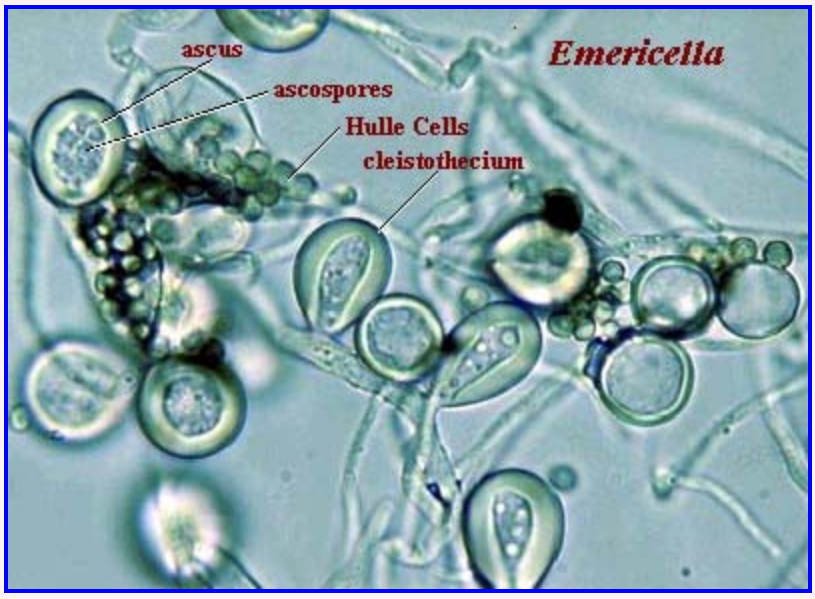
Heterogametes: male and female gametes that are morphologically distinguishable.

Heterothallic: describes fungi in which two genetically distinct but compatible mycelia must meet before sexual reproduction can take place

Heterotroph: an organism which obtains energy from the oxidation of organic matter.

Homing Endonuclease: an enzyme which catalyzes the insertion of an intron into chromosomal DNA. Homing enzymes may be coded by the intron itself, or may come from elsewhere. Homing enzymes may work in a variety of ways. For example they may act as, or work with, a reverse transcriptase to create a DNA copy of an intron RNA. Alternatively, they may directly ligate the intron transcript (RNA) into the DNA od the "host," relying on the host DNA repair machinery to convert the inserted sequence into double-stranded DNA.

Homothallic: describes fungi in which a single strain can undertake sexual reproduction; self-compatible.



Hülle Cell: in some ascomycetes, "thick-walled globose cells (Hülle cells) develop by budding at the tips of specialized hyphae. Hülle cells envelop the developing cleistothecium and may serve as nurse cells." Wu & Miller (1997). Image by David Geiser from a Ball State University site.

Hydroxyl group: *see* The Cell Wall.

Hymenium: "The hymenium is the layer of cells containing the spore-bearing cells (usually basidia or asci) of the fungus. The **hymenophore** is a collective term for the fleshy structures that bear the hymenium. Thus, in a gilled mushroom, all the gills constitute the hymenophore, and the hymenium is the layer of cells on the surface of those gills. Although the hymenophore may be convoluted and enclosed within the fruiting body, the hymenium still has to be, in some sense, on the 'outside' of the hymenophore in order for either of these structure to qualify for their names. Otherwise, you have a gleba, inside a peridium." hymenium.

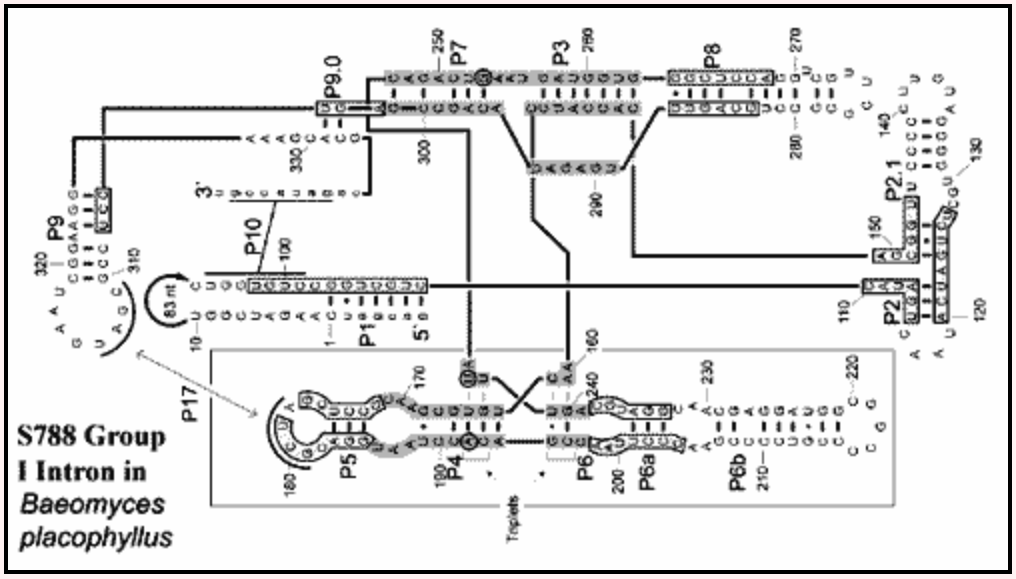
Hypha: "(plural *hyphae*) is a long, branching filament that, with other hyphae, forms the feeding thallus of a fungus

called the mycelium. Hyphae are also found enveloping the gonidia in lichens, making up a large part of their structure. A typical hypha consists of a tubular wall, usually made of chitin, which surrounds, supports, and protects the cellss that compose a hypha. For most fungi, a cell within a hyphal filament is separated from other cells by internal cross-walls called septa (singular septum). Some forms of parasitic fungi have a portion of their hyphae modified to form haustoria that are able to penetrate the tissues of a host organism. Similar, yet mutualistic forms of penetrating hyphae are called mycorrhizae and are important in assisting nutrient and water absorption by plants." Hypha

Hyphal body: portion of mycelium that becomes separated from remainder of thallus.

-I-

Imperfect state: asexual state of a fungus, also known as an anamorph in a life cycle.



Intron: An intron, generically, is a piece of DNA which is transcribed into RNA but does not form part of the final gene product. In one fashion or another, it must be spliced out of the RNA before the RNA can be used for translation, ribosome formation, etc. **Group I introns** are large introns whose RNA product has an extremely complex secondary structure. *See* image from Haugen *et al*. (2004). The RNA itself (with or without cofactors such as nucleotides or metal ions) catalyzes its *own* removal from the initial RNA transcript. That is, it functions as a ribozyme, an enzyme made up of RNA. Most Group I introns then catalyze their own circularization. *See*, generally, Hemiascomycetous Yeast Spliceosomal Introns. Mobile Group I elements may also encode a *homing endonuclease*, or use an endonuclease native to the host, to insert a DNA copy of the transcribed intron into the homologous location on a sister chromosome, or into another copy of the "home" gene in the case of genes present in multiple copies. The point of insertion is never random, and tends to be quite specific to a particular gene. A **Spliceosomal Intron**, at the opposite extreme, is a short (c. 40 bp) intron which serves as a substrate for splicing enzymes which remove the intron and probably also perform various regulatory roles, including adding the 3'-poly(A) "tail" which acts as a shipping label, specifying that the nuclear RNA is a messenger RNA which can be exported to the cytoplasm for translation. Various regulatory roles and one possible template for the evolution of the system are reviewed by Lynch & Kewalramani (2003). Group I and spliceosomal introns are likely to be related, with Group I introns gradually becoming simplified and more dependent on the host cell until they are eventually reduced to spliceosomal introns or disappear altogether.

-K-

Karyogamy: fusion of two (haploid) nuclei.

-L-

Ligand: *see* The Cell Wall.

Locule: generally, in botany, a locule is a small chamber in which

a reproductive structure develops. In the ascomycetes, it refers to a small chamber in the hymenium (generalized reproductive tissue) in which a perithecium develops.

LUCA: Last Universal Common Ancestor. The last common ancestor of all extant species: Eubacteria, Archaea, and Eukarya.

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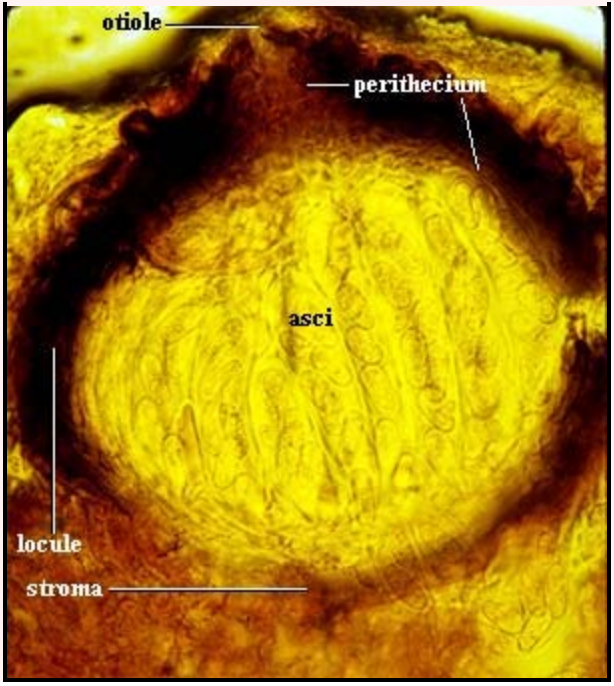

Glossary M

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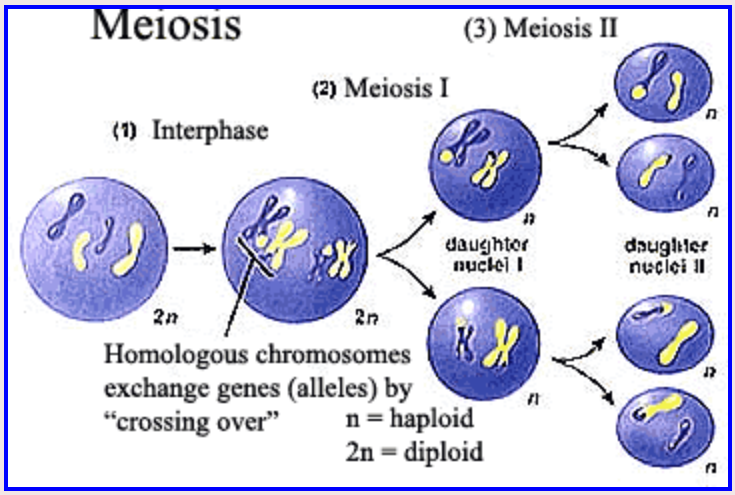
A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

-M-

Mannose: *see* The Cell Wall.

Meiosis: A process common to almost sexual reproduction in eukaryotic cells. The homologous chromosomes of a diploid nucleus first exchange homologous genes (alleles) on a roughly random basis, so that the resulting chromosomes carry a mixture of genes from each parent. The nucleus then divides normally (by mitosis) to yield two diploid daughter nuclei. Finally, the nuclei divide again, but now without DNA replication, to yield four haploid cells.



Meiospore: a spore formed after meiosis; a spore produced by sexual reproduction.

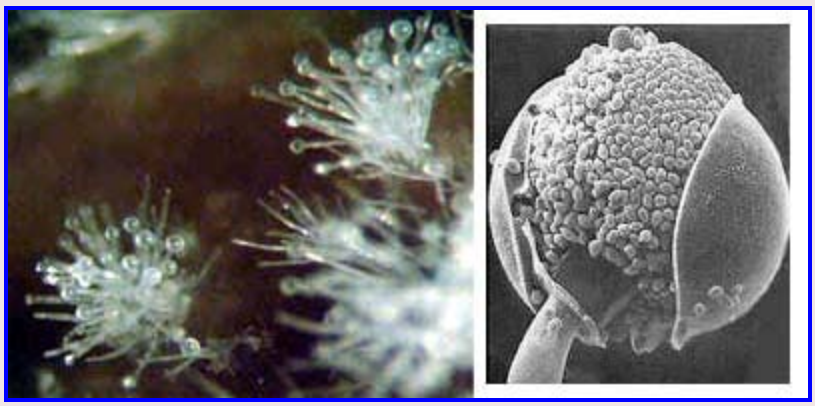
Meiosporangium: a sporangium in which meiosis occurs (reference to certain Chytrids).

Microtubule: Microtubules are protein structures found within cells. They are generally long and form a structural network (the cytoskeleton) within the cell's cytoplasm, but in addition to structural support microtubules are used in many other processes as well. They form a substrate on which other cellular chemicals can interact, they are used in intracellular transport, and are involved in cell motility. The assembly and disassembly of microtubules into their subcomponent tubulin is one way in which cells can change their shape. A notable structure involving microtubules is the mitotic spindle used by eukaryotic cells to segregate their chromosomes correctly during cell division. Microtubules are also responsible for the flagella of eukaryotic cells (prokaryote flagella are entirely different). From

Microtubule - Wikipedia; *see also,* Structure and Function of Microtubules. Microtubules are straight, hollow cylinders have a diameter of about 25 nm are variable in length but can grow 1000 times as long as they are thick. Microtubules are built by the assembly of dimers of alpha tubulin and beta tubulin. Microtubules grow at each end by the polymerization of tubulin dimers (powered by the hydrolysis of GTP), and shrink at each end by the release of tubulin dimers (depolymerization). However, both processes always occur more rapidly at one end, called the plus end. The other, less active, end is the minus end. Microtubules participate in a wide variety of cell activities. Most involve motion. The motion is provided by protein "motors" that use the energy of ATP to move along the microtubule. From The Cytoskeleton.

Mitochondrion: an organelle responsible for most of the oxidative metabolism in the cell. There is far too much to cover in a glossary definition. See Mitochondrion - Wikipedia for a relatively brief introduction.

Mitosporangium: a fungal organ which develops spores by mitosis, *i.e.* asexual spores. Image from Mycolog.com.



Monokaryon: a hypha having only a single, haploid nucleus.

Monophyletic: a group of organisms is said to be monophyletic if it consists of only an ancestral organism and *all* descendants of that organism. If the group does not contain the last common ancestor of its members, it is *polyphyletic*. If it contains the last common ancestor of all members, but not *all* of the descendants, it is termed *paraphyletic*. A monophyletic group is called a *clade*. The significance of all this is explained at Dendrograms.

mtDNA: each mitochondrion has its own small DNA genome which does not undergo recombination. In higher plants and in animals, both of which have well-differentiated microgametes (sperm) and macrogametes (eggs), the mitochondria of offspring are all decended from the mitochondria in the macrogamete. It is not obvious that this should be the case in Fungi, given their more egalitarian mating practices; and we are unsure if the same rule applies.

Mushroom: fleshy, sometimes tough, umbrella like basidiocarp of certain Basidiomycota.

Mycelium: a network of numerous hyphae which develop within or along the substrate. "The spore and initial hyphae are haploid; that is, they contain only one copy of each chromosome. When a haploid mycelium meets another haploid mycelium of the same species, and they are sexually compatible, the two mycelia join together and each cell receives a nucleus from the other mycelium. This process is called diploidization. Some authors seem to want to reserve the term mycelium for hyphae that have undergone diploidization (the earlier, haploid stuff is just hyphae), but most people seem to use it for both phases." hypha.

Mycorrhizal association: a symbiotic relationship between fungus and plant in which the fungus interpenetrates the roots, mobilizing soil nutrients for the plant and absorbing complex organics produced by the plant.

-N-

Necrotrophic: growing by first killing the host organism or mycelium.

-O-

Oidium: a small, specialized haploid mating spore which fuses with a haploid hypha to produce a dikaryon.

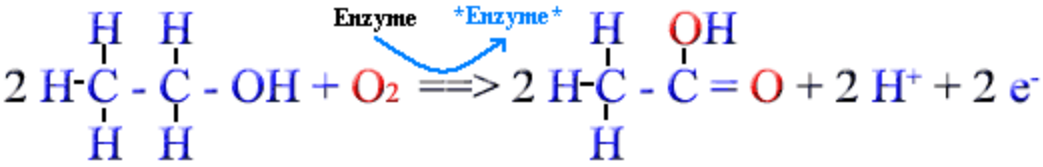
Operculum: a lid. Thus, for example, the asci of some pezizomycotines have a sort of lid at the distal end which opens and releases the spores at maturity. In the image, the opercula are stained blue. Image from North Carolina State Univ., College of Agriculture & Life Sciences.

Osmotic pressure: Most biological membranes are impermeable to many of the solutes found in the cell. If this were not so, all of the valuable biomolecules in the cell would simply diffuse out and be lost. However, the same membranes are often more or less permeable to water. Since there are many solutes trapped in the cell, the "concentration" of water is lower in the cell than outside, *i.e.*, there are more water molecules per unit volume outside the cell than inside. Diffusion of water through the membrane works both ways and is completely random. However, water "concentration" is higher outside the cell. That is, there are more water molecules in contact with the membrane on the outside than on the inside. So, there will be a net flux of water into the cytoplasm until the concentrations equalize. The ***osmotic potential*** is the measure of the net tendency of water to enter the cell. Real cells can't usually behave in this fashion, since the cell will expand and ultimately burst. The problem is handled in numerous different ways, depending on the cell type. In fungal cells (and various others), the cell membrane is confined within a semi-rigid cell wall. Water enters the cell only until the elastic reaction force of the cell wall equals the outward force caused by water molecules crowding into the cell. At steady state, the cell then maintains a rather high internal pressure, referred to as ***turgor pressure***. Turgor pressure serves as a sort of internal hydrostatic skeleton which helps to support -- and even move -- fungal structures.

Ostiole: a pore or hole in an enclosing ascocarp for the release of spores.

Oxidation: in the sense used by chemists, this means the removal of electrons from an outer electron shell. Oxidation often involves the use of oxygen, but oxygen is not necessarily required. As a practical matter, the removed electrons have to go somewhere, so biological oxidation is a matter of coupling the oxidation of one chemical with the reduction of another. So, what does this accomplish? The trick here is that the resulting product(s) may have lower energy than the starting products. The energy released by the reaction is used by the organism for its own nefarious purposes.

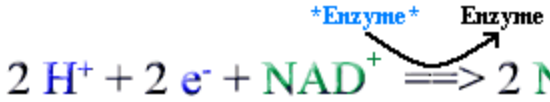
Oxidation Reaction



$$2\ H\text{-}\underset{H}{\overset{H}{C}}\text{-}\underset{H}{\overset{H}{C}}\text{-}OH + O_2 \Longrightarrow 2\ H\text{-}\underset{H}{\overset{H}{C}}\text{-}\overset{OH}{C}=O + 2\ H^+ + 2\ e^-$$

Here, ethanol is oxidized to form acetic acid, resulting in the liberation of two protons and two electrons. The electrons are not actually free but are held for, at most, picoseconds by an enzyme which catalyzes the reaction. This puts the enzyme in an unstable, high-energy state.

Reduction Reaction



$$2\ H^+ + 2\ e^- + NAD^+ \Longrightarrow 2\ NADH + H^+$$

The energy stored in the enzyme's excited state is then released by the reduction of NAD+ to its reduced form, NADH. NADH is used by other enzymes as a reducing agent to power other reactions. Note that the process also produces a proton (H+). As oxidation continues, the medium becomes more acid. In the mitochondria, this causes a proton gradient to build up. The gradient is another form of stored energy, used to power other reactions. That mechanism is discussed at length in connection with the Eubacteria.

Typically, in biological systems, oxidation of chemicals from a food item is coupled with reduction of a special-purpose carrier molecule. That carrier can then dock with any number of enzymes, proteins that perform all the chemical chores needed by a living cell. The enzymes then use the energy stored in the carrier by coupling oxidation of the carrier with a reduction reaction which performs the job the enzyme was evolved to accomplish. Examples from real life tend to be complex, so we'll use a simplified and somewhat unrealistic example involving the carrier nicotinamide- adenine dinucleotide (NAD), a common carrier in the metabolic reactions handled by enzymes in mitochondria. In this example, the energy released by oxidation is stored in three different ways, all of which are important to biological systems. (1) the energy is first stored in the form of an excited intermediate state of an enzyme. This typically involves a slight change in the shape of the protein. As the protein drops back to its normal state, the change in shape drives the next reaction. (2) The energy is stored by reducing a carrier molecule, here the coenzyme NAD^+, as discussed above. (3) The reaction produces an ion, here H^+. Over many such reactions inside a membrane system (from an entire cell to a single mitochondrial crista), a gradient develops across the membrane. This can be used to drive other types of reactions as discussed elsewhere.

-P-

Palisade: series of parallel hyphae having the appearance of a wall or fence -- or even a palisade.

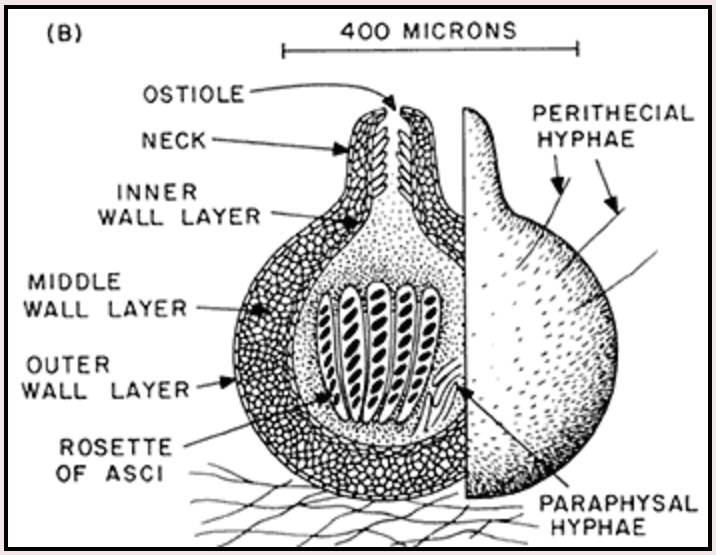
Paraphysis: (pl. *paraphyses*) a poorly-constrained term which seems to include every sort of generally elongate cell in a perithecium (or similar structure) which is not actually an ascus.

Perfect state: sexual state of a fungus, also known as the teleomorph in a life cycle.

Peridium: the outer membrane of a mitospore. See image at mitosporangium. In that image, the peridia are the two structures which look a bit like compound eyes in the electron micrograph. A more familiar example of a peridium may be the outer sac visible on fungal puffballs. The term is not restricted to strictly cleistothecial (completely enclosed) ascocarps (spore organs). Any outer membrane which encloses spores, even if not completely, is a peridium. The image here shows a peridium in the process of dehiscence. I have lost the source of this image.

Periphysis: a paraphysis (elongate sterile cell) which grows into the neck of a perithecium. *See* image at perithecium.

Perithecial: relating to a perithecium.



Perithecium: A form of ascocarp in which the peridium (outer membrane) is almost closed but for an ostiole (pore) at the distal end. Image from Johnson (1978).

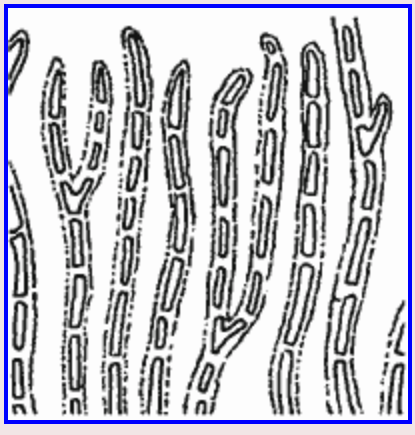
Phylogenetic: relating to the evolution of a taxon or, more specifically, the particular evolutionary context of a taxon. Thus, a **phylogenetic definition** is one which defines a taxon by its evolutionary path, *e.g.*, Archosauria = crocs + rocs. This is shorthand for "Archosauria is defined as the last common ancestor of crocodiles and birds and all descendants of that ancestor." This is discussed in connection with the Fungi on the opening page.

Phylospace: a portmanteau word used to describe the placement of organisms in space, time and phylogeny. It is an evolving concept, so to speak.

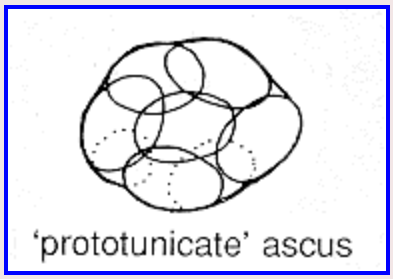
Plasmodium: a naked, multinucleate mass of protoplasm that moves and feeds in a amoeboid fashion.

Plasmogamy: fusion of two cell cytoplasms.

Plectenchymatous: having strongly parallel oriented hyphae (a palisade) which rarely branch or overlap one another, as in the image.



Polysaccharide: *see* The Cell Wall.



Prototunicate: "Some asci have no active spore-shooting mechanism. These asci are usually more or less spherical, and are found in cleistothecial (occasionally perithecial), and hypogeous ascomata. Sometimes the wall of this kind of ascus dissolves at maturity and releases the ascospores, which can then ooze, rather than be shot, out of the ascoma; or they may wait inside until it decays or is ruptured. These asci are often called

prototunicate. ... [T]hey are found in several otherwise rather different orders, [and] it seems likely that they represent a secondary condition, [which has] evolved several times from unitunicate asci." Ascomycetes and anamorphs. The term may be used simply to mean spores withoutany mechanism for ballistospory. Such spores typically have a fragile membrane which disintegrates spontaneously at maturity or breaks open with very slight mechanical stress. Image from **Mycolog.com**.

Pseudoparaphysis: pseudoparaphyses are long, hair-like cells which grow down from the roof of the locule and often attach to its base. *See* image at pseudothecium.

Pseudoparenchyma: thin-walled, usually angular, randomly-arranged cells in fungi, which are tightly packed. Often used to form walls in specialized structures such as ascocarps. They are similar in appearance to the *parenchyma* cells of plants and have some of the same functions, *i.e.* as a population of undifferentiated cells competent to form various different types of specialized tissues.

Pseudothecium of ***Venturia inaequalis***

Pseudothecium: perithecium-like fruiting body containing asci and ascospores dispersed rather than in an organized hymenium; an ascostroma with a locule or cavity and containing bitunicate asci.

Pyranose: *see* The Cell Wall.

-R-

rDNA: the DNA which codes for ribosomal RNA. If that term isn't familiar, see the Cell Biology summary at Eubacteria. However, there are some significant differences. In contrast to prokaryotes, the four RNAs contained in eukaryotic ribosomes are coded by two types of genetic units which are generally not linked. Each type occurs in its own randomly repeated clusters. The larger unit, the rDNA, is transcribed by RNA polymerase I as a single precursor containing the small subunit (18S) rRNA, 5.8S rRNA and the large subunit (28S) rRNA, each bracketed with spacer sequences. The second type of unit codes for 5S rRNA and is transcribed by RNA polymerase III. Peyretaillade *et al*. (1998).

Reverse transcriptase: an enzyme so called because it operates in a manner which reverses normal transcription. That is, a reverse transcriptase uses RNA as a template to create a complementary single-stranded DNA molecule.

Rhizoid: a short, thin branch of thallus, superficially resembling a root.

Ribozyme: an RNA molecule with catalytic properties, typically in association with a cofactor such as a neucleotide or metal ion.

Rust fungus: fungus belonging to the Uredinales.

-S-

Saprobe: same as *saprophyte*

Saprophyte: an organism which feeds on dead organic matter.

Septal pore: a possible synapomorphy of the Ascomycota. The hyphae of ascomycetes are partitioned off into compartments by septal walls. The septae are bridged by pores which provide controlled cytoplasmic continuity throughout the hypha. See Woronin body for image and additional information.

Septate: with more or less regularly occurring cross-walls.

Septum: a cross-wall in a hypha that develops centripetally.

Slime mould: common term for members of Dictyosteliomycota, Acrasiomycota, Plasmodiophoromycota and Myxomycota.

Smut fungi: fungus belonging to the Ustilaginomycetes.

Soma: same as thallus.

Spliceosome: a nuclear ribonucleoprotein complex which (usually along with other functions) removes intron transcripts from newly synthesized RNA.

Sporangiophore: sporangia borne on stalks, or the specialized hyphae which bear sporangia.

Sporangiospore: a spore with a nucleus formed by mitosis, an asexual spore. There seem to be an unreasonable number of names for this concept.

Sporangium: a structure in which spores are created and released into the environment.

Spore: "Biologically speaking, a fungal spore is a microscopic reproductive unit one or multicelled, used by fungi and other organisms on dispersal of new individuals. Spores contains some food reserve, usually oil or glycogen, they can be produced by meiosis or not. Even if spores are mostly dispersive units, some act as resting structures over unfavorable conditions as intense cold or prorogated [sic] drought. The great majority of spores posses firm cell walls. The most recognizable characteristics used to identify spores are color, size, shape, septation and surface characteristics (e.g. ornamentation). However all of them should be very variable even for a genus alone." MycoSpora - generalities. "By wet weight spores generally contain 25% protein and 20% fat, and they have a low water content relative to vegetative mycelium. Cell walls of spores are generally not fibrillar, but they are multi-layered and often contain melanin and have ornamentations. Spores contain all normal mycelial organelles. Respiratory reserves include lipids, glycogen, phospholipids and polysaccharides that can include sugar alcohols like Trehalose). Respiration rates in spores are only 1-4% those of vegetative mycelium, but obviously the more reserves a spore has, the longer it will survive." Reproduction in the fungi (former site). Image from Steve Newell, Univ. Georgia.

Stereochemistry: *see* The Cell Wall.

Stroma: (pl. *stromata*) fungal tissue mass of pseudoparenchyma in or on which the reproductive structures (perithecia) are formed in some sac fungi. More generally, a mass or matrix of vegetative hyphae, with or without tissue of the host or substrate, in or on which spores are produced.

Suspensor: in Zygomycota, the remains of the gametangia that project from the sides of the zygosporangium which has developed between them. See the image at gametangium.

Synapomorphy: a character which is shared by all basal members of a clade and is derived from their common ancestor. A synapomorphy may be secondarily lost in later descendants. Only a synapomorphy may be used to infer phylogeny.

-T-

Teleomorph: the sexual form of a fungus; unknown in many taxa (*see also* anamorph).

Thallus: Fungi have a vegetative body normally located above the substrate called a thallus or soma, composed of hyphae. In botany, a thallus is a relatively simple plant body devoid of stems, leaves and roots. In fungi, it is the somatic phase.

Toadstool: a member of the "Agaricales" or "Boletales" (both probably polyphyletic) with an inedible fruiting body.

Transcript: one nucleic acid is the transcript of another if it was synthesized using the original nucleic acid as a template, so that the base sequence of the transcrip is comlementary to the base sequence of the template. By far the most common transcription is the synthesis of RNA in the nucleus by an RNA polymerase, using the organism's DNA as a template. Thus the DNA sequence AAAGGTTCAGT is transcribed as an RNA with sequence UUUCCAAGUCA (RNA contains **U**racil bases where DNA has **T**hymidine). In cell biology and biochemistry, transcription is contrasted with *translation*, the process in which the base sequence of messenger RNA (*mRNA*) is used as a template to create proteins.

Turgor pressure: see osmotic pressure.

Type: in systematics, a group defined by a set of physical characteristics, rather than by phylogeny. Compare clade.

-U-

Unitunicate: an ascus without differentiated inner and outer walls is said to be *unitunicate*. "The unitunicate ascus sometimes has an operculum (a small lid), which opens to liberate the ascospores when the ascus is mature. These asci are called **unitunicate-operculate**. ... Other asci have no operculum but have an apical pore and/or a ring-like structure at the tip, acting as a valve, or sphincter, through which the ascospores are violently discharged and are dispersed by the air. Such asci are called **unitunicate-inoperculate** ... There are still other perithecial fungi with unitunicate asci which have no obvious mechanism for ascospore release. In this case, the ascospores are released into the cavity of the ascomata, when the ascus wall disintegrates." Guarro *et al*. (1999: 467).

Uredospore: dikaryotic spore of rust fungi produced in the second host and capable of reinfecting it.

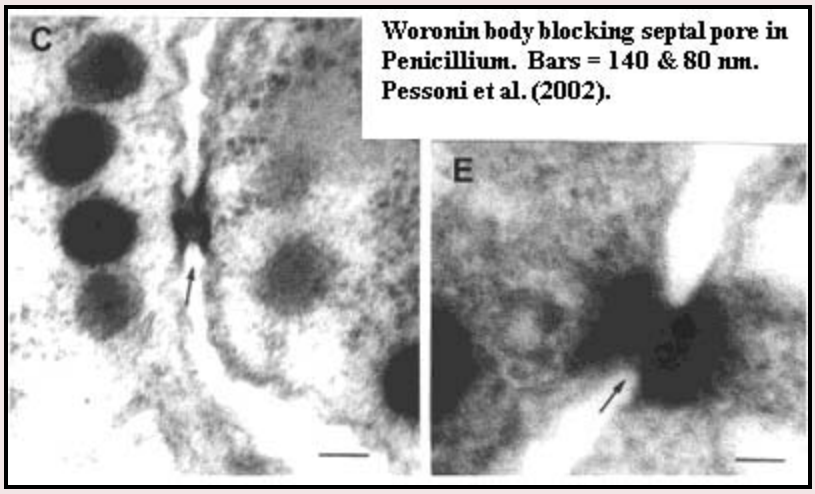
-V-

Vegetative: assimilative phase in fungi, structure or function as distinguished from the reproductive.

-W-

White rot: fungal decay of wood in which both cellulose and lignin are broken down.

Woronin body: Woronin bodies are highly refractive, electron dense, membrane bound particles found on either side of septae that divide hyphal compartments in filamentous fungi. One current theory is that Woronin bodies are peroxisomes that function to maintain cellular integrity. The septae separate hyphal compartments are pierced by pores which allow most cytoplasmic constituents (but not nuclei) to travel freely between hyphae. However, if an adjoining hypha is ruptured, the Woronin bodies block the pore to prevent loss of cytoplasm into the ruptured compartment. Image: Pessoni *et al.* (2002).



Woronin body blocking septal pore in Penicillium. Bars = 140 & 80 nm. Pessoni et al. (2002).

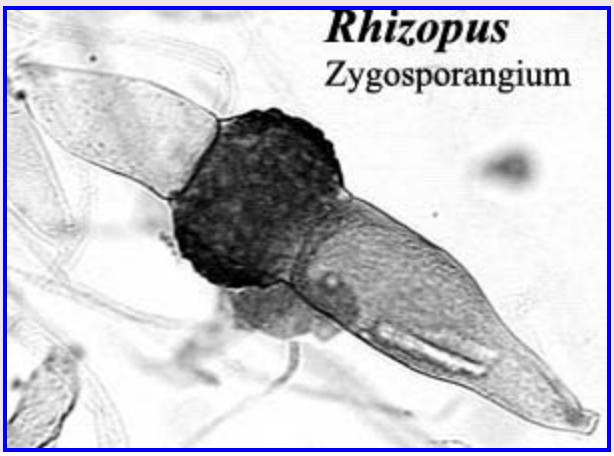
-Y-

Yeast: single-celled ascomycete fungus that reproduces by budding or fission. The "true yeasts" are the Saccharomycotina.

-Z-

Zoospores: a motile, asexually produced spore.

Zygosporangium: the teleomorph of the Zygomycetes; a usually thick-walled, often ornamented, multinucleate resting sporangium formed following anastomosis of gametangia arising from compatible mycelia (in heterothallic species) or from the same mycelium (in homothallic species).



Zygote: a diploid cell resulting from the union of two haploid cells.

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Footnotes

[1] *C.f.*, " ... [L]a science culinaire, c'est de pallier, dans la mesure du possible, par la perfection de ses produits, les imprudences des hommes." Auguste Escoffier (1912).

[2] If you're unsure how these definitions work, see The Dendrograms: Introduction.

[3] "On peut et on doit déplorer de telles habitudes. Ne serait-ce qu'au point de vue de la santé des convives, dont l'estomac est appelé à en supporter les conséquences, elles sont absolument blâmables." Auguste Escoffier (1912).

[4] Two relatively recent sources have given opposite indications about the relative proportions of chitin and glycoprotein -- one stating that the wall is "mostly chitin" and the other stating that very little chitin is present. As in many areas of ascomycete biology, the degree of variation within this diverse group of fungi probably makes any generalization impossible.

[5] Note, once again, traditional mycology's fixation on sexual reproduction. Not only are fungi with no known *teleomorphs* excluded from the Ascomycota, but they are referred to as "imperfect." This would simply be a source of amusement, but it led to a corresponding lack of interest in matters of great importance in the vegetative state, such as the mechanisms of the ecologically critical "rots," intercellular transport and signaling, vegetative growth habits and structural biology, and so on.

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References

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

-A-

Adams, DJ (2004), *Fungal cell wall chitinases and glucanases*. **Microbiology** 150: 2029-2035. Cell Wall.

Alkemar, G & O Nygård (2003), *A possible tertiary rRNA interaction between expansion segments ES3 and ES6 in eukaryotic 40S ribosomal subunits*. **RNA** 9:20–24.

An, K-D, H Nishida, Y Miura & A Yokota (2002), *Aminoadipate reductase gene: a new fungal-specific gene for comparative evolutionary analyses*. **BMC Evol. Biol.** 2: 6 Cell Wall.

-B-

Baker, BJ, MA Lutz, SC Damson, PL Bond & JF Banfield (2004), *Metabolically active eukaryotic communities in extremely acidic mine drainage*. **Appl. Environ. Microbiol.** 70: 6264-6271. Pezizomycotina.

Bhattacharya, D, F Lutzoni, V Reeb, D Simon, J Nason, & F Fernandez (2000), *Widespread occurrence of spliceosomal introns in the rDNA genes of Ascomycetes*. **Mol. Biol. Evol.** 17: 1971–1984. Pezizomycotina.

Bold, HC (1973), **Morphology of Plants** [3rd ed.]. Harper & Row, 668 pp.

Borneman, J & RJ Hartin (2000), *PCR primers that amplify fungal rRNA genes from environmental samples*. **Appl. & Env. Microbiol.** 66: 4356-4360.

Bullerwell, CE, J Leigh, L Forget & BF Lang (2003), *A comparison of three fission yeast mitochondrial genomes*, **Nucl. Acids Res.** 31: 759-768 Ascomycota.

-C-

Cabib, E, D-H Roh, M Schmidt, LB Crotti & A Varma (2001), *The yeast cell wall and septum as paradigms of cell growth and morphogenesis*. **J. Biol. Chem.** 276: 19679-19682. Cell Wall.

Cannone JJ, S Subramanian, MN Schnare, JR Collett, LM D'Souza, Y Du, B Feng, N Lin, LV Madabusi, KM Muller, N Pande, Z Shang, N Yu, & RR Gutell (2002),*The comparative RNA web (CRW) site: An online database of comparative sequence and structure information for ribosomal, intron, and other RNAs*. **BioMed Central Bioinformatics** 3:15. Pezizomycotina.

Cooper, S & K Shedden (2003), *Microarray analysis of gene expression during the cell cycle*. **Cell & Chromosome** 2:1. Pezizomycotina.

-D-

Durán, A & C Nombela (2004), *Fungal cell wall biogenesis: building a dynamic interface with the environment*. **Microbiology** 150: 3099-3103. Cell Wall.

-F-

Ferreiro, JA, NG Powell, N Karabetsou, NA Kent, J Mellor & R Waters (2004), *Cbf1p modulates chromatin structure, transcription and repair at the **Saccharomyces cerevisiae MET16** locus*. **Nuc. Acids Res.** 32: 1617-1626. Pezizomycotina.

Filley, TR, RA Blanchette, E Simpson & ML Fogel (2001), *Nitrogen cycling by wood decomposing soft-rot fungi in the "King Midas tomb," Gordion, Turkey*. **Proc. Nat. Acad. Sci. (USA)** 98: 13346–13350. Ascomycota.

-G-

Gaillardin, C, G Duchateau-Nguyen, F Tekaia, B Llorente, S Casaregola, C Toffano-Nioche, M Aigle, F Artiguenave, G Blandin, M Bolotin-Fukuhara, E Bon, P Brottier, J deMontigny, B Dujon, P Durrens, A Lépingle, A Malpertuy, C Neuvéglise, O Ozier-Kalogéropoulos, S Potier, W Saurin, M Termier, M Wésolowski-Louvel, P Wincker, J-L Souciet & J Weissenbach (2000), *Genomic exploration of the hemiascomycetous yeasts: 21. Comparative functional classification of genes*. **FEBS Let.** 487: 134-149 Ascomycota.

García, R, C Bermejo, C Grau, R Pérez, JM Rodríguez-Peña, J Francois, C Nombela & J Arroyo (2004), *The global transcriptional response to transient cell wall damage in **Saccharomyces cerevisiae** and its regulation by the cell integrity signaling pathway*. **J. Biol. Chem.** 279: 15183–15195. Cell Wall.

Gasch AP, AM Moses, DY Chiang, HB Fraser, M Berardini & MB Eisen (2004), *Conservation and evolution of cis-regulatory systems in ascomycete fungi*. **PLoS Biol** 2: e398. Pezizomycotina.

Grün, CH (2003), **Structure and Biosynthesis of Fungal a-Glucans**. Ph.D. dissertation, Univ. Utrcht. **WWW**. Cell Wall.

Guarro, J, J Gené & AM Stchigel (1999), *Developments in fingal taxonomy*. **Clin. Microbiol. Rev.** 12: 454-500.

-H-

Haugen, P & D Battacharya (2004), *The spread of LAGLIDADG homing endonuclease genes in rDNA*. **Nucleic Acids Res.** 32: 2049-2057. Group I Introns.

Haugen, P, V Reeb, F Lutzoni & D Bhattacharya (2004a), *The evolution of homing endonuclease genes and Group I introns in nuclear rDNA*. **Mol. Biol. Evol.** 21: 129–140. Pezizomycotina.

Haugen, P, HJ Runge & D Bhattacharya (2004), *Long-term evolution of the S788 fungal nuclear small subunit rRNA group I introns*. **RNA** 10: 1084–1096. Pezizomycotina.

Hinnebusch, AG & K Natarajan (2002), *Gcn4p, a master regulator of gene expression, is controlled at multiple levels by diverse signals of starvation and stress*. **Eukar. Cell** 1: 22-32. Pezizomycotina.

-I-

-J-

Johnson, TE (1978), *Isolation and characterization of perithecial development mutants in **Neurospora***. **Genetics** 88: 27-47.

-K-

Kuras, L, R Barbey & D Thomas (1997), *Assembly of a bZIP-bHLH transcription activation complex: formation of the yeast Cbf1-Met4-Met28 complex is regulated through Met28 stimulation of Cbf1 DNA binding*. Pezizomycotina.

-L-

Lesage, G, A-M Sdicu, P Ménard, J Shapiro, S Hussein & H Bussey (2004), *Analysis of ß-1,3-glucan assembly in **Saccharomyces cerevisiae** using a synthetic interaction network and altered sensitivity to caspofungin*. **Genetics** 167: 35-49. Cell Wall.

Liu, Y-JJ & BD Hall (2004), *Body plan evolution of ascomycetes, as inferred from an RNA polymerase II phylogeny*. **Proc. Nat. Acad. Sci. (USA)** 101: 4507-4512. Ascomycota, Pezizomycotina.

Liu, Y-JJ, S Whelan & BD Hall (1999), *Phylogenetic relationships among Ascomycetes: Evidence from an RNA polymerse II subunit*. **Mol. Biol. Evol.** 16: 1799–1808. Cell Wall.

Llorente, B, P Durrens, A Malpertuy, M Aigle, F Artiguenave, G Blandin, M Bolotin-Fukuhara, E Bon, P Brottier, S Casaregola, B Dujon, J deMontigny, A Lépingle, C Neuvéglise, O Ozier-Kalogeropoulos, S Potier, W Saurin, F Tekaia, C Toffano-Nioche, M Wésolowski-Louvel, P Wincker, J Weissenbach, J-L Souciet & C Gaillardin (2000), *Genomic exploration of the hemiascomycetous yeasts: 20. Evolution of gene redundancy compared to **Saccharomyces cerevisiae***. **FEBS Let.** 487: 122-133. Ascomycota.

Llorente, B, A Malpertuy, C Neuvéglise, J deMontigny, M Aigle, F Artiguenave, G Blandin, M Bolotin-Fukuhara, E Bon, P Brottier, S Casaregola, P Durrens, C Gaillardin, A Lépingle, O Ozier-Kalogéropoulos, S Potier, W Saurin, F Tekaia, C Toffano-Nioche, M Wésolowski-Louvel, P Wincker, J Weissenbach, J-L Souciet & B Dujon (2000), *Genomic exploration of the hemiascomycetous yeasts: 18. Comparative analysis of chromosome maps and synteny with **Saccharomyces cerevisiae***. **FEBS Let.** 487: 101-112. Ascomycota.

Lutzoni, F, F Kauff, CJ Cox, D Mclaughlin, G Celio, B Dentinger, M Padamsee, D Hibbett, TY James, E Baloch, M Grube, V Reeb, V Hofstetter, C Schoch, AE Arnold, J Miadlikowska, J Spatafora, D Johnson, S Hambleton, M Crockett, R Shoemaker, G-H Sung, R Lücking, T Lumbsch, K O'donnell, M Binder, P Diederich, D Ertz, C Gueidan, K Hansen, RC Harris, K Hosaka, Y-W Lim, B Matheny, H Nishida, D Pfister, J Rogers, A Rossman, I Schmitt, H

Sipman, J Stone, J Sugiyama, R Yahr, & R Vilgalys (2004). *Assembling the fungal tree of life: Progress, classification, and evolution of subcellular traits*. **Amer. J. Bot.** 91: 1446-1480. Pezizomycotina.

Lynch, M & A Kewalramani (2003), *Messenger RNA surveillance and the evolutionary proliferation of introns*. **Mol. Biol. Evol.** 20:563-571.

-M-

Machado, AK, BA Morgan & GF Merrill (1997), *Thioredoxin reductase-dependent inhibition of MCB Cell Cycle Box activity in **Saccharomyces cerevisiae***. **J. Biol. Chem.** 272: 17045-17054. Pezizomycotina.

Madigan, MT, JM Martinko & J Parker (2003), **Brock: Biology of Microorganisms, [10th ed.]**. Prentice-Hall. 1019+ pp.

Malpertuy, A, F Tekaia, S Casarégola, M Aigle, F Artiguenave, G Blandin, M Bolotin-Fukuhara, E Bon, P Brottier, J deMontigny, P Durrens, C Gaillardin, A Lépingle, B Llorente, C Neuvéglise, O Ozier-Kalogeropoulos, S Potier, W Saurin, C Toffano-Nioche, M Wésolowski-Louvel, P Wincker, J Weissenbach, J-L Souciet & B Dujon (2000), *Genomic exploration of the hemiascomycetous yeasts: 19. Ascomycetes-specific genes*. **FEBS Let.** 487: 113-121. Ascomycota.

Muller, KM, JJ Cannone, RR Gutell, & RG Sheath (2001), *A structural and phylogenetic analysis of the Group IC1 Introns in the Order Bangiales (Rhodophyta)*. **Mol. Biol. Evol.** 18: 1654–1667. Group I Introns.

-N-

Natarajan, K, MR Meyer, BM Jackson, D Slade, C Roberts, AG Hinnebusch & MJ Marton (2001), *Transcriptional profiling shows that Gcn4p is a master regulator of gene expression during amino acid starvation in yeast*. **Mol. & Cell. Biol.** 21: 4347-4368. Pezizomycotina.

-P-

Pessoni, RAB, G Freshour, R deCássia, L Figueiredo-Ribeiro, MG Hahn & MR Braga (2002), *Woronin bodies in **Penicillium janczewskii** Zaleski*. **Brazil. J. Microbiol.** 33(2). **WWW**.

Pilpel, Y, P Sudarsanam & GM Church (2001), *Identifying regulatory networks by combinatorial analysis of promoter elements*. **Nature Genetics** 29: 1-7. Pezizomycotina.

Pitarch, A, M Sánchez, C Nombela & C Gil (2002) *Sequential fractionation and two-dimensional gel analysis unravels the complexity of the dimorphic fungus **Candida albicans** cell wall proteome*. **Molec. & Cell. Proteomics** 1.12: 967-982. Cell Wall.

-R-

Redecker, D (2002), *New views on fungal evolution based on DNA markers and the fossil record*. **Res. Microbiol.** 153: 125-130. Pezizomycotina.

Redecker, D, R Kodner & LE Graham (2000), *Glomalean fungi from the Ordovician*. **Science** 289: 1920-1921. Pezizomycotina.

Reeb, V, F Lutzoni & C Roux (2004), *Contribution of RPB2 to multilocus phylogenetic studies of the Euascomycetes (Pezizomycotina, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory*. **Mol. Phylog. & Evol.** 32: 1036-1060. Pezizomycotina.

Remy, W, TN Taylor, H Hass & H Kerp (1994), *Four hundred-million-year-old vesicular arbuscular mycorrhizae*. **Proc. Nat. Acad. Sci. (USA)** 91: 11841-11843. Pezizomycotina.

Rooney, AP & TJ Ward (2005), *Evolution of a large ribosomal RNA multigene family in filamentous fungi: Birth and death of a concerted evolution paradigm*. **Proc. Nat. Acad. Sci. (USA)** 102: 5084-5089. Pezizomycotina.

-S-

Schadt, CW, AP Martin, DA Lipson & SK Schmidt (2003), *Seasonal dynamics of previously unknown fungal lineages in tundra soils*. **Science** 301: 1359-1361. Pezizomycotina.

-U-

-V-

Vandenkoornhuyse, P SL Baldauf, C Leyval, J Straczek, & JPW Young (2002), *Extensive fungal diversity in plant roots*. **Science** 295: 2051

-W-

Wu, J-G & BL Miller (1997), ***Aspergillus*** *asexual reproduction and sexual reproduction are differentially affected by transcriptional and translational mechanisms regulating* ***stunted*** *gene expression*. **Mol. Cell. Biol.** 17: 6191–6201. Ascomycota.

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Pieces

This section contains discussions of individual proteins, organelles or other subcellular components. To put the matter plainly, we frequently get side-tracked by brief discussions of non-germane topics. For the most part, these random remarks are shunted off into the glossary, where they can be safely ignored and forgotten. Sometimes, however, we not only get off-topic, but ramble on for several hundred words about some dull and completely inconsequential point. Eventually, we run out of steam and realize we've blundered far off the path; but, by then, the screen is full of words and pictures. Like so many clay objects made by small children, we're reluctant to simply discard the results of such earnest effort, however inartful and misguided. We have instead chosen to pack them away in this deep recess where they are unlikely to be found. Thus far, we have pondered:

The Cell Wall (with introduction to sugar chemistry)

Group I Introns

The Cell Wall

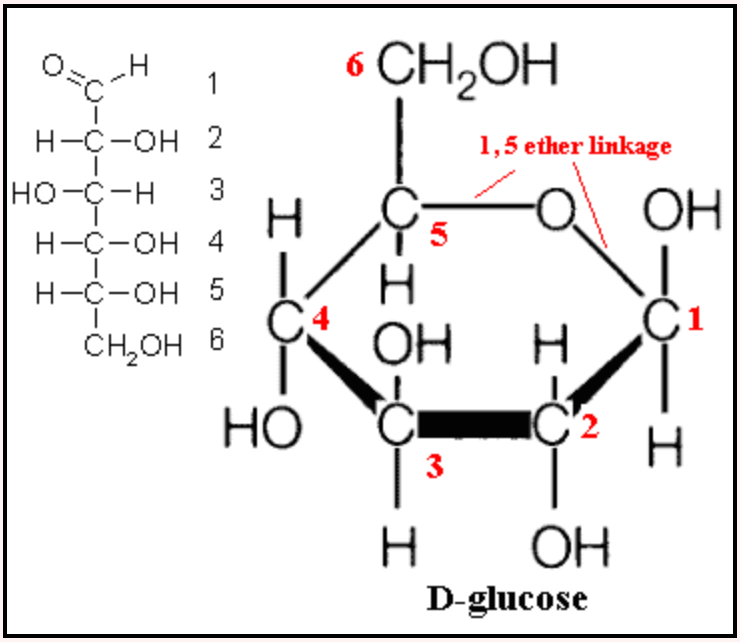
A Spoonful of Sugars

Terms defined on this page:	
anomer	**hemiacetal**
enantiomer	**hydroxyl group**
furanose	**ligand**
glucan	**mannose**
glucose	**polysaccharide**
glycoside	**pyranose**
Haworth diagram	**stereochemistry**
These would be on the test, if we gave one.	

Since we haven't done this elsewhere, it's time we provided the rudiments of sugar (saccharide) chemistry, so that we can make useful noises about *polysaccharides* (sugar polymers) -- easily the most common class of biopolymers on the planet. A more extensive and far better introduction may be found at **Natural Products**.

All sugar monomers of biological importance have structural formulas which looks something like this: $CH_2OH\text{-}(CHOH)_n\text{-}CHO$. In other words, they consist of a chain of carbon atoms, in which each carbon atom has a *hydroxyl* (-OH) group attached to it, except for C1 (sometimes C2) which has an aldehyde or keto (=O) group. In living organisms, the chain is generally 3-7 carbons long. In biologically important polysaccharides, the monomers are almost always 5- or 6-carbon sugars.

We have only reluctantly provided a reference graphic of a sugar monomer in linear form because, in life, 5- and 6-carbon sugars rarely occur as straight chains. The carbon atoms with the aldehyde (or keto) group reversibly bonds to one of the other carbons by "sharing" a hydroxyl oxygen, forming a C-O-C linkage. This is known as an *hemiacetal* linkage. Typically, the result is a 5- or 6-member ring -- four or five carbon atoms plus the linking oxygen. A five-member form (*e.g.* a C1→C4 linkage) form is called a *furanose*. A six-member ring (*e.g.* C1→C5 linkage) is a *pyranose*. A simple example, and perhaps the most common sugar monomer, is *glucose*. Its usual (pyranose) ring form is shown in the image. It can also occur as a furanose. In fact, the two forms are in equilibrium. Under biologically relevant conditions, the equilibrium so strongly favors the pyranose form of glucose that we can ignore the furanose. However, this is not necessarily the case for all sugars.



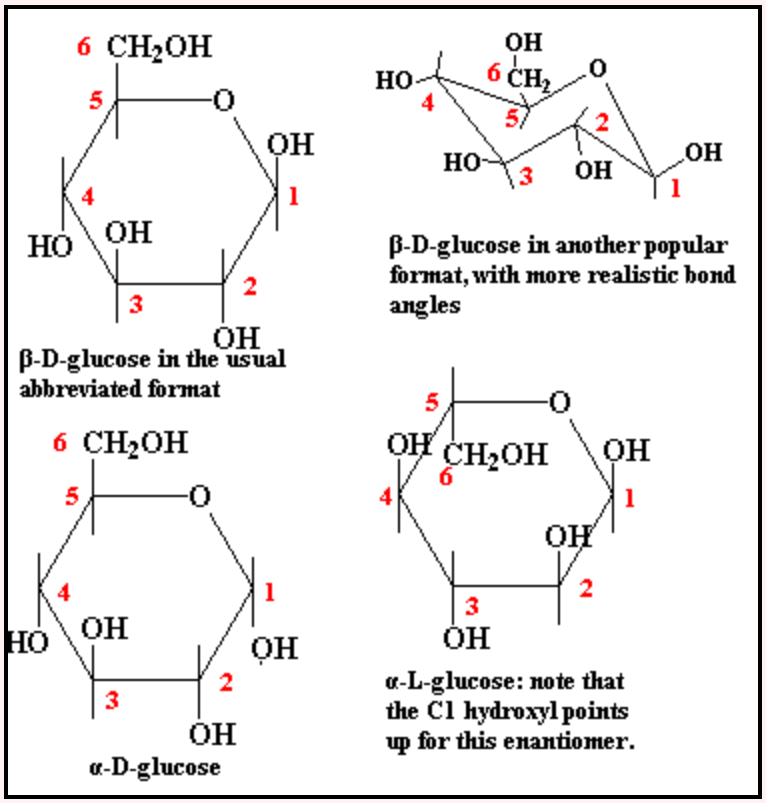
This is also the last time we will show the ring carbons. By the universal convention of biochemists, carbon atoms forming part of a ring structure are not shown with a 'C' symbol. They are simply indicated by the intersection of the bonds from the various groups (*ligands*) to which the carbon atom is attached. Very frequently, hydrogen ligands (H-) are not shown either. A line with nothing at the end means a hydrogen ligand,

and an unlabelled intersection of bonds means a carbon atom. See examples below.

Sugar monomers are not always quite this simple. Each of the hydroxyl ligands is moderately chemically active, and all kinds of variants exist. An example, of particular relevance to fungi, is chitin. Chitin is a polymer of N-acetly-2-glucosamine, *i.e.*, a glucose derivative in which the ligand CH_3-CH_2-NH- substitutes for the OH-group on C2. See the *chitin* glossary entry for an image.

In most of these examples, we have shown the structure of sugars using a *Haworth Diagram*. These are easy to draw and to understand, but they are rather crude tools because the bond angles are grossly distorted. Carbonnormally forms tetrahedral structures, with the bonds about 108° apart. However, Haworth diagrams will do for our purposes, so long as we don't take them too seriously.

Stereochemistry



The figure above is labeled "**D**"-glucose for an important reason: it gives us an excuse to discuss three quick points about *stereochemistry*. Stereochemistry relates to the properties of compounds which are chemically identical, except that they are asymmetrical, and differ in the arrangement of ligands about one or more asymmetrical backbone atoms.

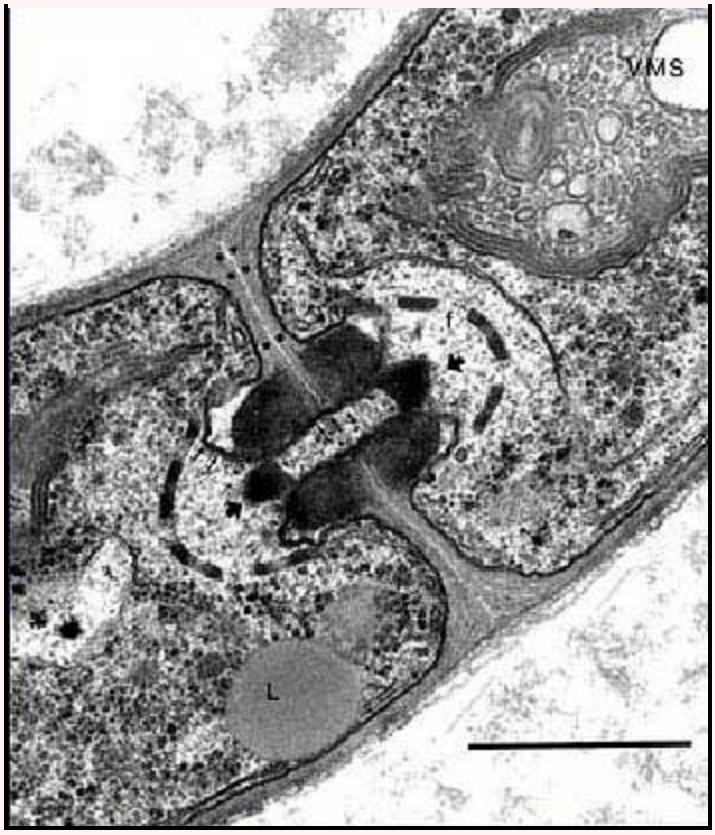
(1) Note that carbons 1 through 5 are asymmetrical in glucose. Each of these carbons is attached to four *different* ligands. Thus, the relative positions of the groups attached to the carbon atoms makes a difference. If, for example, we flipped the hydroxyl group on C2 so that it was *above* the ring, this would no longer be glucose. It would be *mannose*, a sugar with rather different chemical properties.

(2) If we took the mirror image of the *entire* molecule, all of the bonds would be in the same relative position. Thus we would have a molecule that ought to have exactly the same chemical properties as glucose, which it does -- sort of. The difficulty is that, when this reversed glucose interacts with some other asymmetrical biochemical, the two molecules no longer mesh in the same way. Consequently, we must distinguish between **D**-glucose and its mirror image (*enantiomer*), **L**-glucose. Don't worry about telling the difference. The biologically relevant form for sugars is usually the **D**-enantiomer. You can assume a figure shows the **D**-enantiomer unless someone tells you differently.

(3) C1 is a special case. In the linear form, C1 is not asymmetrical because it has only three ligands. However, when the C1 forms a pyranose linkage to C5, it becomes asymmetrical. In terms of our diagram, the -OH group on C1 might point down or up. Free glucose in solution is, once again, in equilibrium between the two forms, referred to as a- and ß-**D**-glucose. These alternate forms of the hemiacetal are referred to as *anomers*. However, this time, neither form is strongly favored. (This is also not like the glucose-mannose example, since the two forms freely interconvert.) For free glucose, the exact form at any given time is unimportant. However, when glucose is linked to another sugar through the C1 hydroxyl group, the conformation becomes "frozen." Consequently, for glucose *polymers*, we need to distinguish between a (hydroxyl down) and ß (hydroxyl up) linkages (*glycoside bonds*). Incidentally, the alpha-down/beta-up convention is reversed for **L**-enantiomers or, naturally enough, when the sugar monomer is represented upside-down.

General Features

Fungal cells maintain a very high turgor pressure, so the integrity of the cell wall is a critical matter. Cabib *et al*. (2001). The composition of the fungal cell wall is rather variable. The variability appears to have phylogenetic significance, but few, to our knowledge, have followed that trail (*but see* Grun, 2003). In general, mycology has leapt directly from the ponderous fallacies of classical typological systematics to the facile, but sometimes equally fallacious, paradigms of molecular systematics. Consequently, there is remarkably little honest biology and biochemistry being applied to phylogenetic issues.

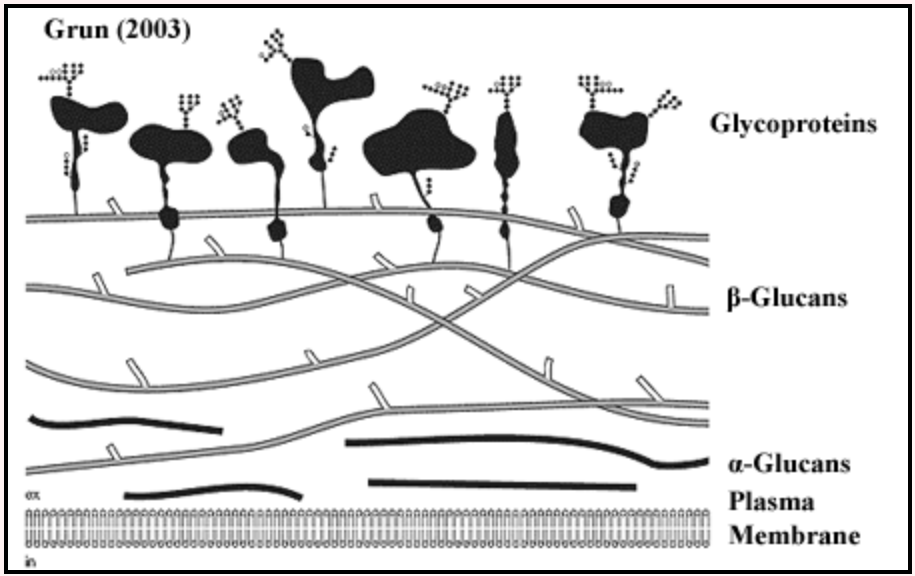


The situation is not improved by the usual non-specialist texts which characterize the fungal cell wall as a relatively simple structure made up of "cellulose" and chitin. Consider that the fungal cell wall can make up 30% or more of the dry weight of the fungus, and that the fungi are characterized by external digestion of food followed by selective absorption of the digestion products. Clearly, we can expect that the fungal cell wall will be a complex, specialized system.

It is all that; and, in addition, it is a highly dynamic system, constantly being regenerated and remodeled according to the needs of the moment. Adams (2004). Thus, many of the cell wall-associated proteins are enzymes whose function is to hydrolyze chitin and polysaccharides. The lesson is that this type of cell wall is, from a metabolic point of view, very different from insect exoskeletons or a plant cell walls, which are terminally differentiated structures.

Not unexpectedly, attempts to understand the biosynthesis of cell wall components have run into a maze of regulatory pathways which are difficult to sort out. García *et al*. (2004) applied brute force genomics methods to analyze gene responses to several different physical and chemical agents affecting cell wall integrity. The genetic responses in each case involved on the order of 100 different genes, with a significant different cohort of genes activated by each agent. Similarly, Lesage *et al*. (2004) identified 135 genes involved in the synthesis and regulation of the ß-(1→3)-glucan component (*see infra*) alone (*see also* several similar studies cited by these authors). In fact, it has been estimated that 20% of the *Saccharomyces* genome is involved with cell wall biosynthesis. Durán & Nombela (2004). Some efforts are being made to pare these lists down to some "core" group of pathways. However, the magnitude of the problem has only become clear in the last few years, and it is much too early to say anything useful.

Structure

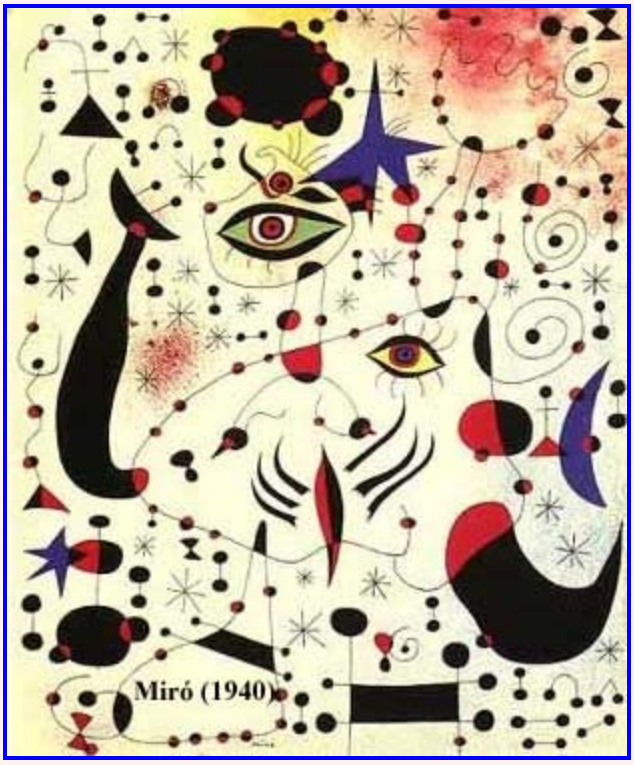


We include two diagrams of the fungal cell wall by Grün (2003) and Cabib *et al*. (2001). We've also thrown in Joan Miró's (1940) *Chiffres et Constellations* just because it has somewhat the same feel to it.

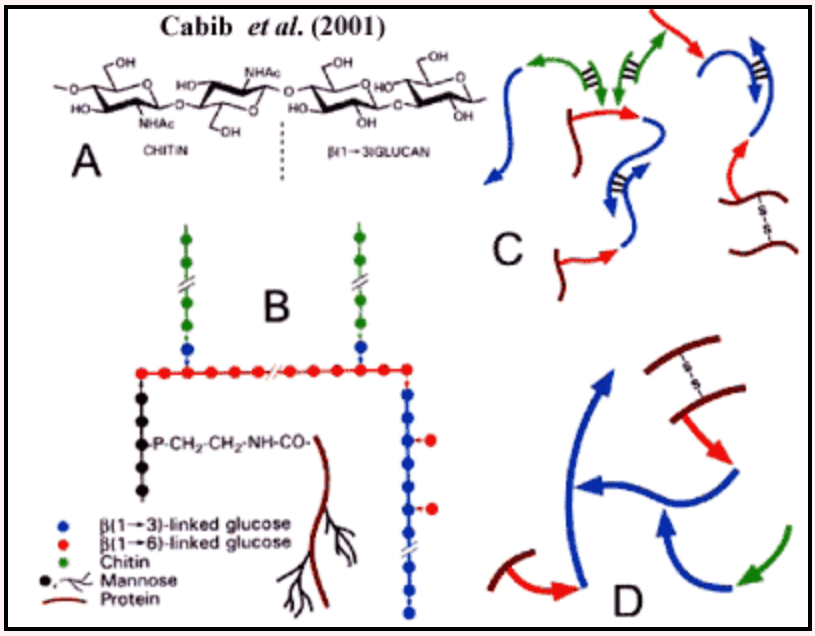
While each of these images speaks to us in its own way, we will work primarily with Grün's concept. The cell wall is generally constructed of three layers: (1) an a-glucan layer (a *glucan* is a polymer of glucose), (2) a ß-glucan layer, and (3) an outer layer of glycoprotein. In addition, *chitin* may be a significant component of certain cell wall structures.

The a-glucan layer, if present, is generally composed of the a(1→3)-glucan polymer. However, a(1→4) glycosides are variably present. *Compare* glycogen, which is a(1→4)-glucan with (1→6) side chains. Where present, the a-glucan material appears as a fibrillar layer adjacent to the plasma membrane and is thought to serve a largely structural role, stiffening the basal layer of the cell wall.

The a-glucan layer is rarely represented in diagrams of the fungal cell wall because it does not occur in *Saccharomyces*, which is the usual model system. In fact, it has a rather peculiar phylogenetic distribution. Among ascomycetes, the alpha glucan is found in *Schizosaccharomyces*, but is not known from any other yeasts. The material is common among all groups in the Pezizomycotina. However, in Lecanoromycetes, a very large proportion tends to be in the a(1→4) form. Alpha glucans also form a significant, sometimes even dominant, part of the cell wall in many basidiomycetes, but are completely absent outside the Hymenomycetes. Grün (2003). Although *Schizosaccharomyces* is often classified with the yeasts, its position is probably more basal. A number of studies show it branching with (paraphyletic) taphrinomycotines. *See, e.g.*, Liu *et al*. (1999), An *et al*. (2002). We tend to prefer the methodology of these studies, which are neither biased by the superficial similarities of "yeast" forms nor confused by the usual problems with *rDNA* and *mtDNA*. Thus, it appears likely that the alpha glucan layer is primitive for all higher fungi, or at least for Ascomycota, with subsequent multiple losses.



The bulk material of the cell wall is usually in the form of ß(1→3)-glucan. This forms a very stable hydrogen-bonded triple helix in solution, and probably *in vivo*. The packing of these triple helix structures appears to be controlled by the size and frequency of very short (1→6) side chains, sometimes consisting of only a single glucose monomer. Grün (2003). If so, this clearly provides a method for controlling the structure and conformation of the cell wall very simply and with very fine, localized control. However, essentially no work appears to have been done in this area. If anyone out there is looking for a potentially elegant and informative dissertation topic in a virtual research vacuum, this is it.



In addition to ß(1→3)-glucan, the cell wall contains ß(1→6)-glucan. We emphasize that this is not simply a ß(1→3)-glucan with big side-chains, but a polysaccharide with a true ß(1→6) backbone. This material may be peripheral to the bulk ß(1→3)-glucan and is, in any case, strongly involved in cross-linking the various components of the cell wall, as shown in the figure from Cabib *et al*. (2001).

The outermost layer of the cell wall is composed of diverse proteins bearing polysaccharide side chains composed of mannose. The usual explanation is that these are attached through their mannan side chains via a (1→3) linkage with the ß(1→6)-glucan. However, this is only a model. Real life appears to be very much more complex, involving a wide variety of different interactions between glycoproteins and bulk cell wall materials. Pitarch *et al*. (2002).

Finally, the fungal cell wall contains variable amounts of *chitin*. In many systems chitin is a major constituent of the cell wall. In others, it is involved only in cell division or reproductive structures and is virtually absent otherwise. Again. we are reluctant to say much about it, absent more detailed, phylogenetically-grounded studies of the actual

ultrastructure in particular cases.

In general, the study of the fungal cell wall tends to be strong on models and somewhat weaker on data. One virtue of the brute force genomic and proteomic studies now being produced is that they clearly confront us with the scope of the problem. Fungal cells probably lack the diversity of metazoan tissues. However, each fungal cell must, for that very reason, be competent to perform a much wider variety of functions than a typical terminally-differentiated metazoan cell. Consequently, their superficial similarity and simplicity are likely to mask a very complex, plastic biochemical repertoire. Perhaps, after all, the Miró is the best representation, given the current state of our knowledge. ATW051113.

Group I Introns

Coopting Cthulhu

We live on a placid island of ignorance in the midst of black seas of infinity, and it was not meant that we should voyage far. The sciences, each straining in its own direction, have hitherto harmed us little; but some day the piecing together of dissociated knowledge will open up such terrifying vistas of reality, and of our frightful position therein, that we shall either go mad from the revelation or flee from the deadly light into the peace and safety of a new dark age."

The Call of Cthulhu
HP Lovecraft (1927)

Cthulhu

If you have not encountered the strange world of *spliceosomes* and semi-autonomous RNA snippets, a quick introduction may be found at Hemiascomycetous Yeast Spliceosomal Introns. Some of the information at that site seems a bit dated, but it covers the essentials almost painlessly.

An *intron*, generically, is a piece of DNA which is transcribed into RNA but does not form part of the final gene product. In one fashion or another, the intron must be spliced out of the RNA before the RNA can be used for translation, ribosome formation, etc. Almost all introns are tiny and innocuous, or even beneficial, since they play a part in the regulation of transcription. They are routinely removed from the initial RNA transcript by *spliceosomes* and are thus known as *spliceosomal introns*.

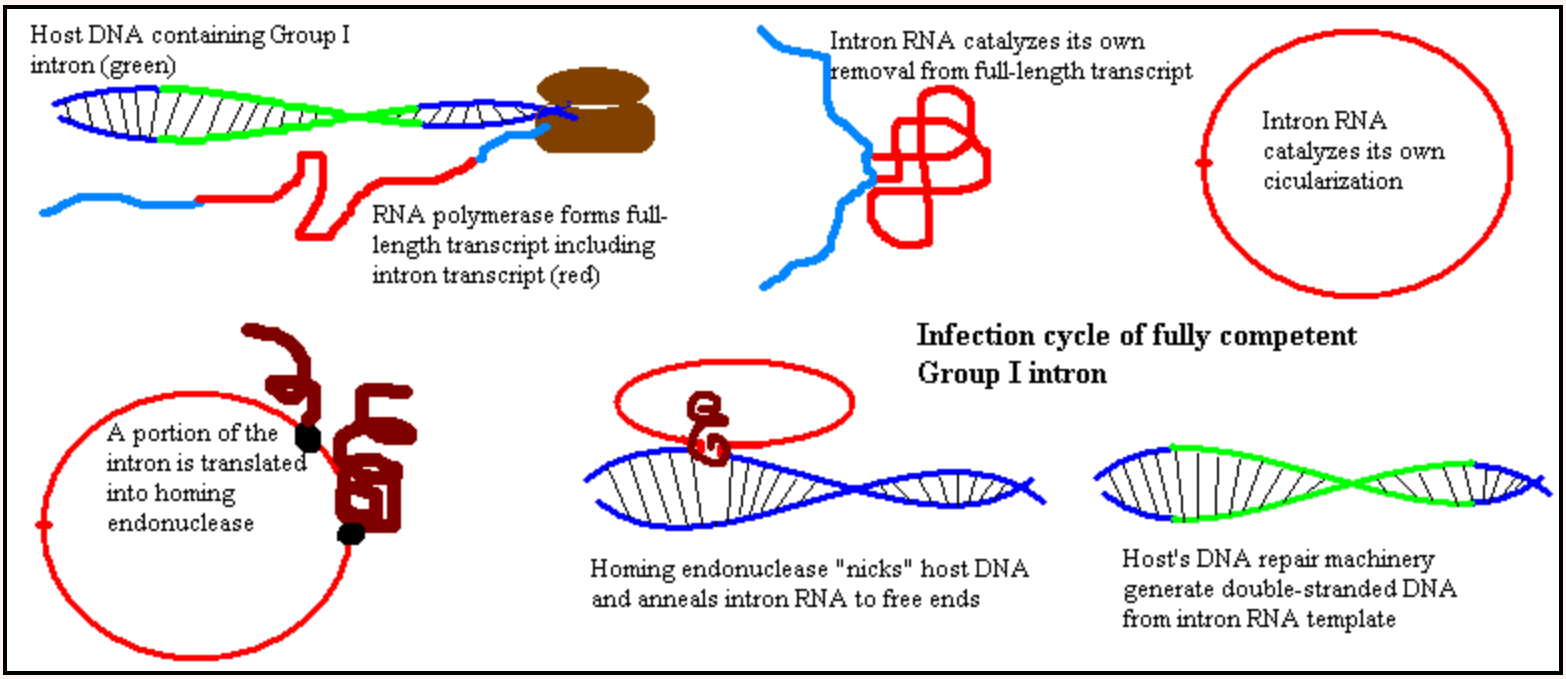
However, some bacteria and basal Eukarya (*Tetrahymena* is the usual example) are host to *Group I introns*. These are a hulking, sinister lot. Group I introns are very large introns whose RNA transcript has an extremely complex secondary structure (*see* image at glossary entry for *intron*). The RNA transcript from such an intron is capable of catalyzing its *own* removal from the initial transcript of the host's gene. That is, it functions as a *ribozyme*, an enzyme made up of RNA. Most Group I introns then simply catalyze their own circularization.

Group I introns may also contain sequences coding for a *homing endonuclase*. Such an enzyme allows the RNA transcipt to insert itself into the DNA of an uninfected allele -- that is, into the homologous chromosome of diploid cells -- at the same or, sometimes, a different position. The cell's own DNA repair system then generates a double-stranded DNA copy of the single-stranded RNA. Alternatively, the intron may spread to new cells, or even to cells of

a different organism. More commonly, Group I introns lose the ability to code homing endonucleases and rely instead on homing enzymes enzymes produced by other introns, or on association with other henchmen. Underfavorable conditions they may still perform a variety of evil tasks, such as spreading through the genome somewhat in the manner of an RNA virus.

This evolutionary attempt to parasitize, not only the host cell, but also other introns, seems to have led to a gradual decline in the significance of Group I introns. As in all free rider phenomena, the most succesful parasite is the one who does the least work. However, this selects against fully competent introns so that there are fewer and fewer introns capable of expressing homing enzyme. When homing endonucleases become unavailable, Group I introns in the phylogenetic neighborhood rely exclusively on vertical transmission through the host cell line. Under those conditions, the sites responsible for interaction with the endonuclease become a neutral or negative selective factor, and the introns gradually lose even the ability to respond to homing endonuclease. At that point, it no longer serves any purpose for the intron to self-splice and circularize and the fragment ceases to be a Group I intron. Eventually, the theory goes, they are reduced to small (c. 50 bp) fragments and coopted to serve as spliceosomal introns. Thus, beginning as dangerous parasites, they end among the happy legion of the cell's own loyal regulatory agents.

At least we hope so. The picture may be complicated by, for example, the ability of homing endonuclease sequences to insert into introns previously incapable of expressing homing endonuclease. Haugen & Bhattacharya (2004).



In the deep past, fully competent Group I introns were likely much more common. In fact, this may have been the way genes normally conducted business -- as semiautonomous units. But, these days, and so far as we know, Group I introns in multi-cellular organisms are rare. Those that remain have reached the stage at which they splice themselves out of the initial transcript, circularlize, then simply wait, patiently, for an ancient call which never comes, like Deep Ones awaiting the **Call of Cthulhu**.

Eukaryotic Group I introns are often found today in Rhodophyta and other Eukarya, largely confined to mitochondrial genes. *See, e.g.*, Muller *et al*. (2001). They are most abundantly present in Fungi, particularly in yeasts. In fact, one suspects that this contributes to the yeasts' inability to form multi-cellular systems. Pezizomycotina contain relatively fewer Group I introns, but numerous spliceosomal introns -- presumably the debased remnants of a once virulent culture of parasitic Group I introns. Haugen *et al*. (2004).

The evolutionary implications of this theory of intron evolution are enormous. Unfortunately, they also tend to be completely speculative, pending additional work on the distribution and evolution of the type. At a minimum, Group I introns give us a possible glimpse into the nature of life before *LUCA*, when genes may have been semi-autonomous units. Group I introns may explain why multicellular eukaryotes were so slow to develop at all. And, since we rarely shy from speculation -- it's more fun than real work -- we also provide the following:

Disquieting Speculation

Biochemistry in the Style of H.P. Lovecraft

Mankind, indeed all higher life, takes happy pride in that singular construct, the eukaryotic cell, whose many inner chambers are bounded by twisting membranes of alien geometry. We are accustomed to say, in our ignorance, that "this is Golgi" or "this is nucleus" while, in reality, we know nothing of the flowing, unnameable shapes which form the fundamental architecture of our own tissues. Within this labyrinth, doors and archways open suddenly, hinting of lofty passages which, however, fade like fevered dreams, leaving faceless walls with no escape. Hither and yon rush the servitors of the cell, appearing suddenly and vanishing as quickly through hitherto seamless barriers, all intent on the manifold errands of metabolism. It is well that they move briskly about their tasks. Everywhere also are guardians, vigilant agents meting out unquestioning destruction to any who deviate in the merest trifle from a rigid code of chemistry, conformation and location.

But from whence might such a closed and closely guarded system have arisen? Earth's most ancient life, the bacterium, exhibits little need for a system such as this: one resembling a windowless mountain fastness built by a terrified populace to baffle inmates of vast intellect, but posessed of a mad and malicious spirit. What twisted genius might abide, chained and gibbering, confined within the inner fabric of our own organs, awaiting the slightest chance to bring holocaust to the higher life of this small planet?

The answer, even were it to fall withing the narrow confines of human comprehension, is surely lost forever in the gray, primordial oceans of the distant past. Yet, we may speculate; or we may do so until our minds can no longer bear the weight of the those nameless eons. It may be, for example, that those very introns of which we have lately spoken, take a not inconsiderable part on that forgotten stage. There they twist and turn, making and unmaking, in mindless dance to unheard flutes, a slithering nest of obscene genetic parasites, spawning endlessly, feeding on each other.

It is best not to consider the matter overlong. Indeed, it is best to wall such unwholesome things away in sinuous sheets of shapeless membrane, to guard scrupulously against their escape, and to allow only a few, carefully chosen products of the Crawling Chaos within to enter into the larger business of the cell. Thus the peculiar compartmentalized geometry of the eukaryotic cell, far from expressing some decent inner order and efficiency, may have evolved from antique horror and revulsion -- the final, desperate attempt to stem a swarming tide of genetic vermin at the core of our own cells.

ATW051105

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References

Adams, DJ (2004), *Fungal cell wall chitinases and glucanases*. **Microbiology** 150: 2029-2035. Cell Wall.

An, K-D, H Nishida, Y Miura & A Yokota (2002), *Aminoadipate reductase gene: a new fungal-specific gene for comparative evolutionary analyses*. **BMC Evol. Biol.** 2: 6 Cell Wall.

Cabib, E, D-H Roh, M Schmidt, LB Crotti & A Varma (2001), *The yeast cell wall and septum as paradigms of cell growth and morphogenesis*. **J. Biol. Chem.** 276: 19679-19682. Cell Wall.

Durán, A & C Nombela (2004), *Fungal cell wall biogenesis: building a dynamic interface with the environment*. **Microbiology** 150: 3099-3103. Cell Wall.

García, R, C Bermejo, C Grau, R Pérez, JM Rodríguez-Peña, J Francois, C Nombela & J Arroyo (2004), *The global transcriptional response to transient cell wall damage in* ***Saccharomyces cerevisiae*** *and its regulation by the cell integrity signaling pathway*. **J. Biol. Chem.** 279: 15183–15195. Cell Wall.

Grün, CH (2003), **Structure and Biosynthesis of Fungal a-Glucans**. Ph.D. dissertation, Univ. Utrcht. **WWW**. Cell Wall.

Haugen, P & D Battacharya (2004), *The spread of LAGLIDADG homing endonuclease genes in rDNA*. **Nucleic Acids Res.** 32: 2049-2057. Group I Introns.

Haugen, P, HJ Runge & D Bhattacharya (2004), *Long-term evolution of the S788 fungal nuclear small subunit rRNA group I introns*. **RNA** 10: 1084–1096. Group I Introns.

Lesage, G, A-M Sdicu, P Ménard, J Shapiro, S Hussein & H Bussey (2004), *Analysis of ß-1,3-glucan assembly in* ***Saccharomyces cerevisiae*** *using a synthetic interaction network and altered sensitivity to caspofungin*. **Genetics** 167: 35-49. Cell Wall.

Liu, Y-JJ, S Whelan & BD Hall (1999), *Phylogenetic relationships among Ascomycetes: Evidence from an RNA polymerse II subunit*. **Mol. Biol. Evol.** 16: 1799–1808. Cell Wall.

Muller, KM, JJ Cannone, RR Gutell, & RG Sheath (2001), *A structural and phylogenetic analysis of the Group IC1 Introns in the Order Bangiales (Rhodophyta)*. **Mol. Biol. Evol.** 18: 1654–1667. Group I Introns.

Pitarch, A, M Sánchez, C Nombela & C Gil (2002) *Sequential fractionation and two-dimensional gel analysis unravels the complexity of the dimorphic fungus* ***Candida albicans*** *cell wall proteome*. **Molec. & Cell. Proteomics** 1.12: 967-982. Cell Wall.

The Ascomycota

```
Fungi
|--Chytridomycota
`--+--Zygomycota
   `--+--Basidiomycota
      `--ASCOMYCOTA
         |--Taphrinomycotina
         `--+--Saccharomycotina
            `--Pezizomycotina
```


The 73rd plate from Ernst Haeckel's *Kunstformen der Natur* (Artforms in Nature), depicting Ascomycetes.

The Ascomycota are the largest division/phylum of Fungi, with over 64,000 species. They are also known as the Sac fungi, so-called because of the presence of microscopic spore- producing organ called an "*ascus*" (or *askos*, if you want to get into the ancient Greek for "sac" or "wineskin"), hence the name.

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The Ascomycota - 1

```
Fungi
|--Chytridomycota
`--+--Zygomycota
   `--+--Basidiomycota
      `--ASCOMYCOTA
         |--Taphrinomycotina
         `--+--Saccharomycotina
            `--Pezizomycotina
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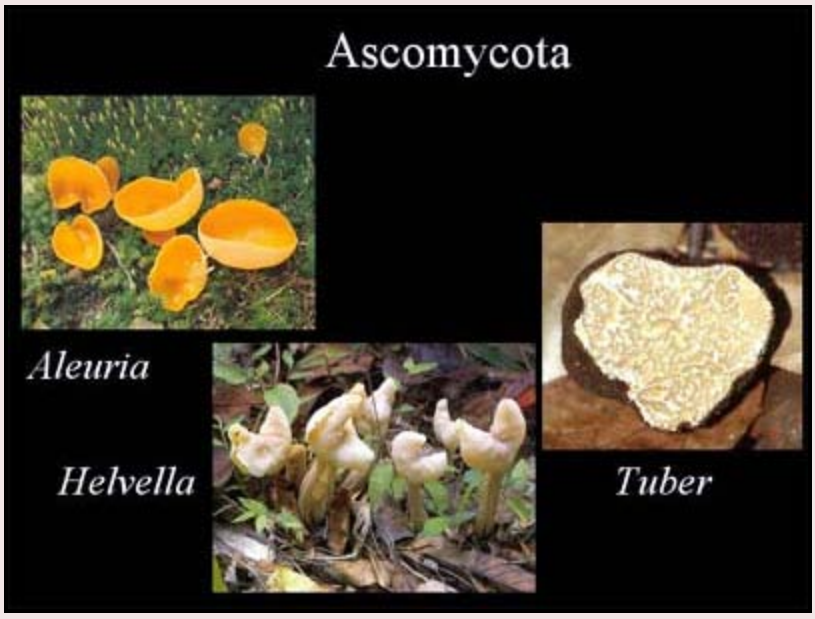
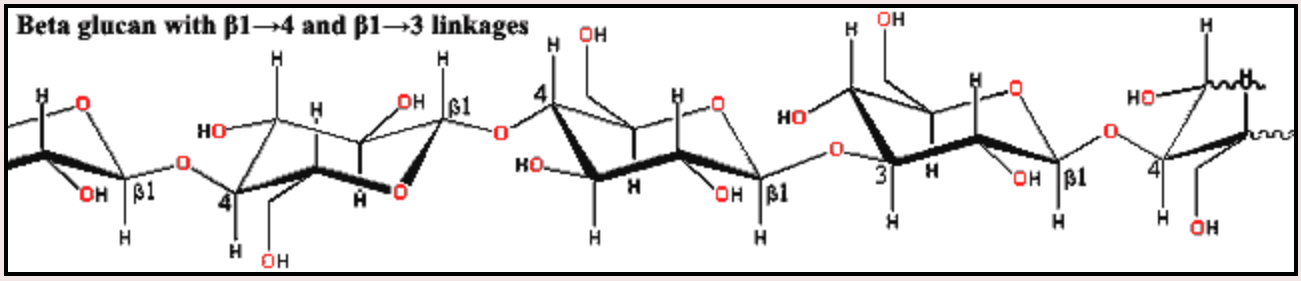
Introduction to the Ascomycota



The Ascomycota are the largest and most diverse group of Fungi. They include the yeasts, most of the fungal elements of lichen, and such famous Fungi as *Saccharomyces*, *Aspergillus*, *Candida* and *Neurospora*, as well as morels, truffles and similar delicacies. The current understanding is that supposed pre-Devonian (even Proterozoic!) lichens are probably artifacts, making the earliest known ascomycote of Carboniferous age.

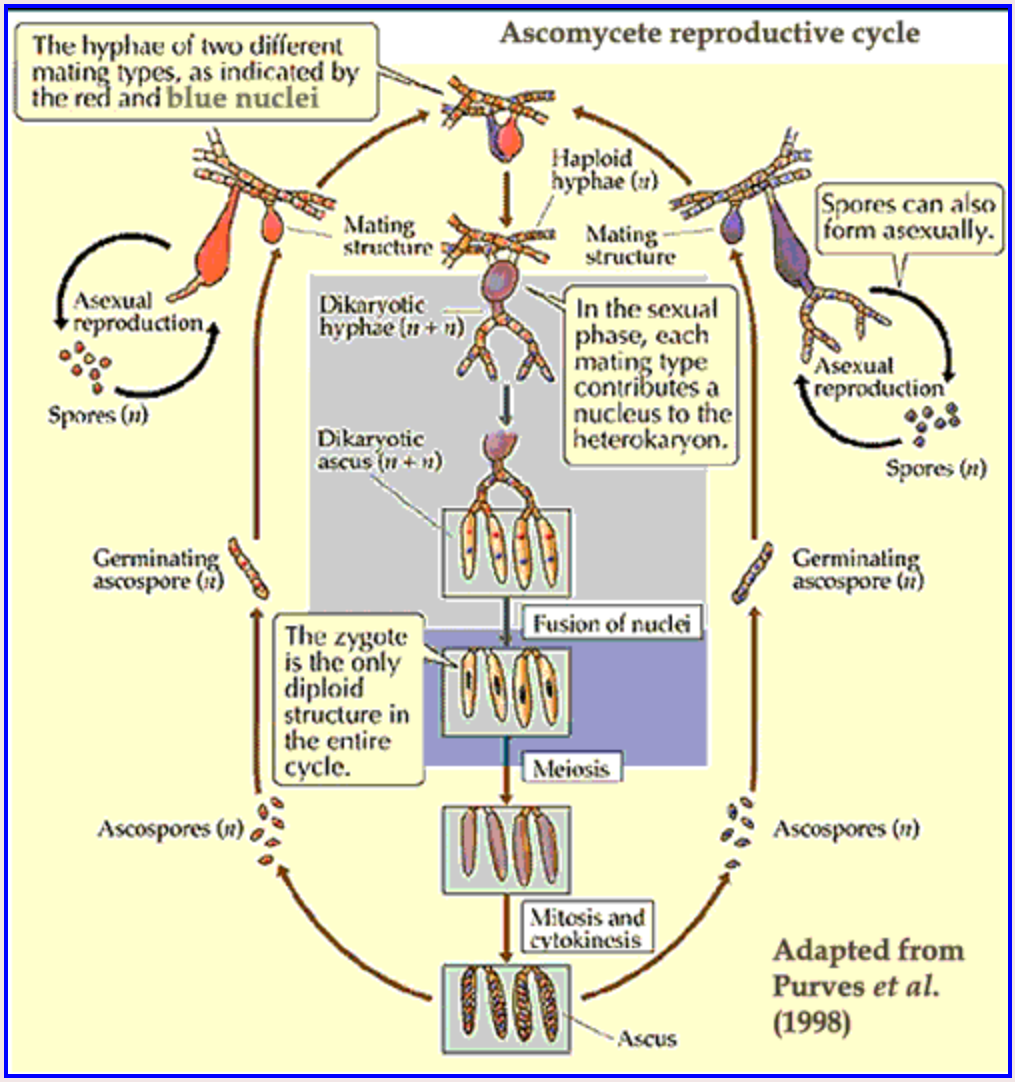
Ascomycetes are united by the presence of *asci* (*see* glossary entry). Like Basidiomycota, ascomycetes remain indefinitely in the *dikaryon* state, with the fungal filaments (*hyphae*) partitioned into cells each containing two haploid nuclei -- one from each parent. Also as in basidiomycotes, nuclear fusion (*karyogamy*) occurs only in connection with the formation of sexual spores. At that time the newly diploid nucleus undergoes one (sometimes more) round of mitosis, followed by *meiosis*, to yield eight (or a multiple of eight) haploid nuclei. The nuclei are then partitioned by internal membranes into individual *ascospores*. The Ascomycota also share with Basidiomycota the use of *conidia* for the development of asexual spores.

Characteristics



Other than the *ascus*, not a great deal unites the Ascomycota. Almost all ascomycetes are terrestrial or parasitic. However, a few have adapted to marine or freshwater environments. The cell walls of the hyphae are variably composed of *chitin* and ß-glucans, just as in Basidiomycota. However, these fibers are set in a matrix of *glycoproteins* containing the sugars galactose and mannose, rather than xylose and mannose as in Basidiomycota **[4]**.

The *mycelium* of ascomycetes is usually made up of *septate hyphae*. However, there is not necessarily any fixed number of nuclei in each of the divisions. The septal walls have *septal pores* which provide cytoplasmic continuity throughout the individual hyphae. Under appropriate conditions, nuclei may also migrate between septal compartments through the septal pores.

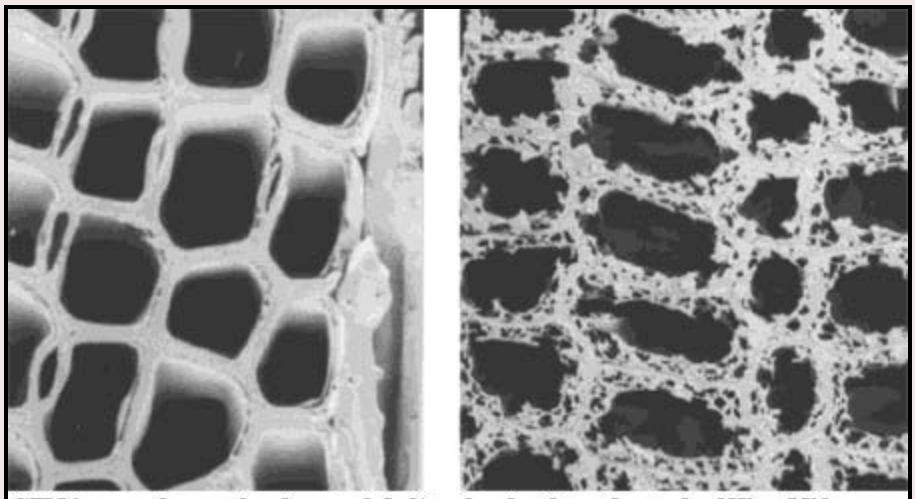


A unique character of the Ascomycota (but not present in all ascomycetes) is the presence of *Woronin bodies* on each side of the septa separating the hyphal segments which control these septal pores. If an adjoining hypha is ruptured, the Woronin bodies block the pores to prevent loss of cytoplasm into the ruptured compartment. The Woronin bodies are spherical, hexagonal, or rectangular membrane bound structures with a crystalline protein matrix. More derived ascomycetes may have, in addition, septal pore organelles which isolate portions of the mycelium which are undergoing sexual reproduction.

Mycologists long ago learned the same trick which has more recently been discovered by television programming executives. The secret is this: regardless of phylogenetic position, reproductive behavior and physiology lend themselves to the creation of strong and attractive images which enable one to go on for hours without really having to communicate a great deal of substance. In addition, ascomycetes, like the characters in situation comedies, seem to lead sex lives of utterly unreasonable complexity. Sadly, the resemblance ends there, or mycology would be considerably more popular than it is. Quite aside from issues of physical aesthetics, Fungi simply lack the native ability to make us identify with their unrequited yearnings for hyphae of the opposite mating type. Even such dramatic events as *ballistospory* (quite common among ascomycetes) cannot disguise the fact that this is, fundamentally, a rather tedious business once we get past the usual colorful diagram.

At any rate, we have now provided a suitably edifying chart with which to illumine the dark night of ignorance, etc. So, our work here is done; and we may return to matters of more intrinsic interest, secure in the knowledge that our duty to a century of mycological tradition has been fully performed.

It is worth noting that ascomycetes tend to have special relationships with insects. Some are "farmed" by beetles and social insects, while others are parasitic on insects. Yet others produce powerful toxins which are relatively specific to insects. Since both insects and ascomycetes are largely terrestrial and both experienced their first major radiation in the Mississippian, it may be that they shared some significant resource or niche. However, the great expansion of insect life probably took place in the Serpukhovian, quite late in the Mississippian, and was most closely related to the evolution of flight.



SEM image of normal cedar wood (left) and cedar from the tomb of King Midas which was subject to soft rot deterioration. Filley et al. (2001).

Another notable ecological link is the relationship between ascomycetes and plant life. Both basidiomycetes and ascomycetes developed the ability to digest plant tissues early on. This was a critical development, since the explosive spread of land plants in the Late Devonian and Mississippian was burying atmospheric carbon dioxide at a ferocious rate and increasing oxygen to the point that it became -- explosive. Basidiomycetes and ascomycetes evolved a sort of division of labor in handling this important bit of recycling. Basidiomycetes do most of the heavy lifting by digesting cellulose (brown rot) and lignin (white rot). However, ascomycetes do their bit by digesting the other glucans which hold the other plant materials together (soft rot). The effects of soft rot are shown -- from a most unusual source -- in the image. Filley *et al*. (2001). Thus the ascomycetes are important in making plant tissues accessible to attack by basidiomycetes. It seems we have the fungi to thank for saving us from a world caught in an unstable alternation between frozen wastes and exploding forests.

Links: Ascomycota; Mycology - Structure and Function - Wall Composition; 561- Lecture#13

Phylogeny

It is now generally accepted that Ascomycota and Basidiomycota are sister clades, since they share a number of synapomorphies, including *septate mycelia*, a *dikaryotic* stage in the life cycle, *plectenchymatous* structures associated with spore production, and *conidia*. The only weak spot in this reasoning is that the yeasts, which are rather basal ascomycetes, are secondarily (probably) unicellular and lack some of these multicellular *synapomorphies*. However, both molecular and morphological comparisons place the yeasts comfortably within the Ascomycota, and most workers are willing to accept that they derived from a yet more basal multicellular ascomycete ancestor with the appropriate characteristics. A certain amount of this sort of thing is likely, given that Ascomycota has a *ghost lineage* of about 60 My, *i.e.*, the time between the first known appearance of Basidiomycota and the first clear remains of Ascomycota.

The ascomycetes were traditionally divided into the Hemiascomycetes and the Euascomycetes, sometimes with the addition of a probably paraphyletic basal group called Archaeascomycetes. Bold (1973). More recently, mycology was seduced by the spell of the Svengalis of Sequencing, with the usual disastrous abandonment of useful nomenclature. We often resist using molecular nomenclature because it is only useful when discussing sequence data and seems to represent a willful rejection of everything else. Like the "Newspeak" of George Orwell's **1984**, molecular nomenclature tends to make certain thoughts impossible by denying them a convenient linguistic point of reference. However, at least for the Fungi, we acknowledge the superior pressure of competing considerations, discussed elsewhere. For those reasons we have adopted the new words. For those who wish to mentally translate:

Taphrinomycotina = Archaeascomycetes
Saccharomycotina = Hemiascomycetes
Pezizomycotina = Euascomycetes

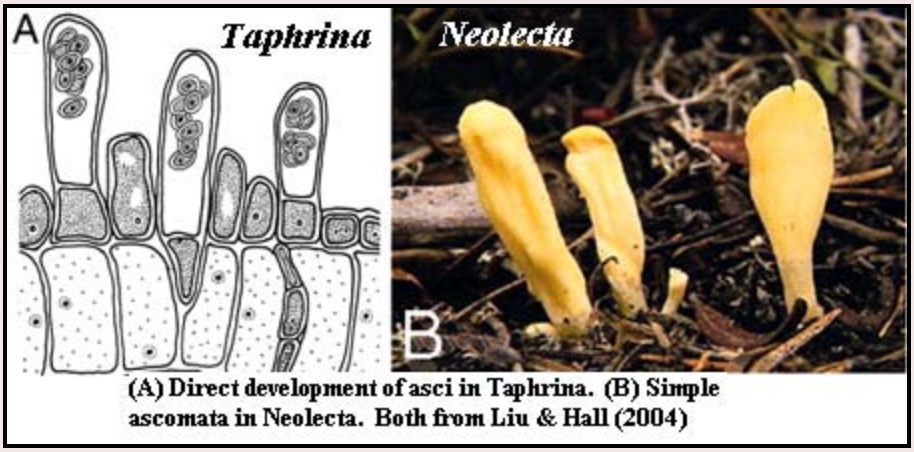
In even older literature, the ascomycetes, as we presently understand them, were divided between two groups, the Ascomycota and the Deuteromycota. The latter were often referred to as *fungi imperfecti*, *i.e.*, species of fungi for which no sexual stage was known. It is now known that these "imperfect fungi", formerly Class Hyphomycetes in the Deuteromycota, are *anamorphs* (asexual forms) of the ascomycetes **[5]**.

Diversity of the Ascomycota

As mentioned above, the Ascomycota are very unevenly divided into Taphrinomycotina, Saccharomycotina, and Pezizomycotina.

Taphrinomycotina

This is almost certainly a paraphyletic basal radiation of ascomycetes. Some may even be more closely related to true yeasts than to pezizomycotines. Bullerwell *et al*. (2003). Typical members include *Neolecta*, the fission yeast *Schizosaccharomyces*, the human pathogen *Pneumocystis carinii*, and the plant pathogen *Taphrina*. As might be expected, body forms are particularly diverse among the Taphrinomycotina, ranging from relatively complex filamentous forms to single-celled yeast-like growths.



(A) Direct development of asci in Taphrina. (B) Simple ascomata in Neolecta. Both from Liu & Hall (2004)

Generally, two simple body plans are found for the production of asci: uncovered asci with unicellular growth, or a rudimentary *ascocarp* with hyphal growth. That is, these fungi grow either unicellularly or with a sparse mycelium, and their sexual phase normally produces naked asci directly from the ascogenous cells. Only *Neolecta* produces a (primitive) enclosing ascocarp. Liu & Hall (2004).

Saccharomycotina

These are the true yeasts, including the *Saccharomyces cereviseae* of college genetics classes, and the human pathogen *Candida*. Domestication of *Saccharomyces* for fermentation of beer goes back at least 9000 years, and probably predates human cultivation of most other plants and animals. This group appears to be monophyletic and to have abandoned multicellularity independently of the yeast like genera in Taphrinomycotina. Basal members of Saccharomycotina still retain a mycelial growth habit. However, none of the Saccharomycotina produces an *ascocarp*.

Saccharomyces became the first eukaryote to have its genome completely sequenced in 1996. Shortly

afterwards, a dozen other saccharomycotine genomes were partially sequenced, creating the first opportunity to look seriously at the comparative genomics and evolution of an entire eukaryotic class. So far as we know, this remains the only study of this scope as of this date (041231). The results of this analysis were reported in a series of papers published in **FEBS Letters** in 2000, all of which are now available at the **Génolevures** website. *See*, especially, Gaillardin *et al*. (2000), Llorente *et al*. (2000a), Llorente *et al*. (2000), and Malpertuy *et al*. (2000). A brief diversity summary, such as the present section, is not the place to take on such a massive body of data. However, we cannot resist the temptation to mention a few of the gems to be found in this gigantic dragon-hoard of information.

First, it appears that yeast evolution is driven by a dynamic balance between gene duplication and deletion. It appears that genes are constantly being shuffled around the genome, with chromosome fragments frequently being duplicated and inserted elsewhere, often as additions to the ends of chromosomes -- the peculiarly labile regions near the telomeres. In most cases, the resulting copies are simply deleted. However, over geological time, the entire genome is shuffled with considerable regularity.

Second, the number of orthologs (copies, but not necessarilly exact copies) of each gene is more stable than one might expect from this mode of evolution. It seems that unnecessary gene copies are deleted rather quickly. This conclusion is also fortified by the observation that genes involved in unused metabolic pathways are almost entirely absent. Thus, for example, *Saccharomyces*, which feeds solely by fermentation, has no genes orthologous to those coding for enzymes involved in oxidative metabolism.

Finally, and most significantly, yeasts show a strong correlation between the age of a gene and its stability. So, for example, the ancient genes coding for proteins involved in the basic work of transcription and translation are quite stable. By contrast, genes related to cell wall synthesis -- functions unique to the fungi and to particular groups within the fungi -- change quite quickly. This particular study needs to be done at a much higher level of resolution, but the tentative conclusion one may draw is that long-term selective pressures are a significant part of the evolutionary picture. If so, this data may settle an important and contentious point about the process of evolution.

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The Ascomycota - 2

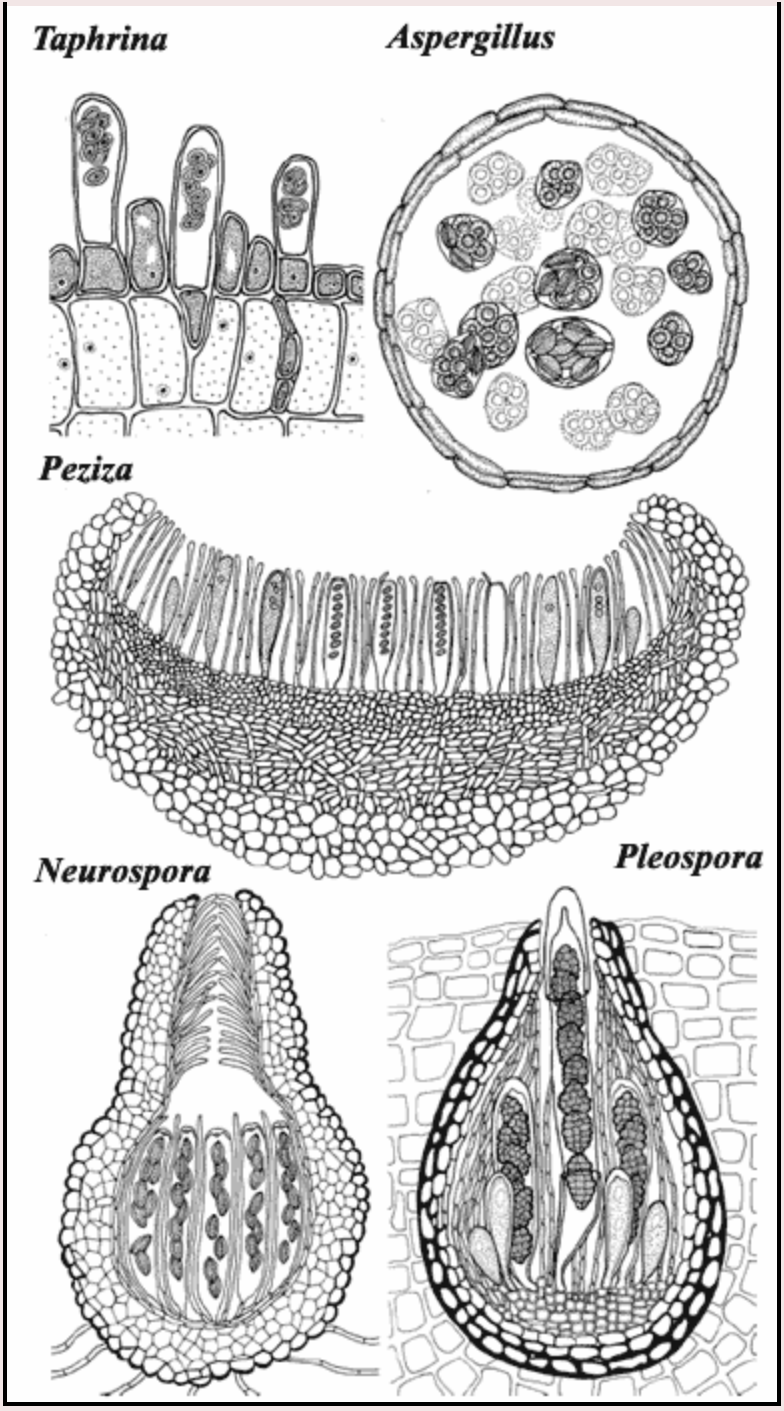
```
Fungi
|--Chytridomycota
`--+--Zygomycota
   `--+--Basidiomycota
      `--ASCOMYCOTA
         |--Taphrinomycotina
         `--+--Saccharomycotina
            `--Pezizomycotina
```


Pezizomycotina

And a thousand thousand slimy things
Lived on; and so did I.
-- Samuel Taylor Coleridge
The Rime of the Ancient Mariner

The Pezizomycotina are the euascomycetes of traditional mycology. The older name is perhaps more descriptive. The other groups of ascomycetes are special cases. The great majority of ascomycetes fall into the Pezizomycotina. Nonetheless, we're not going to say too much about them, since they will have their own page soon enough.

The euascomycetes have traditionally been characterized by the growth of an *ascocarp* within which the *asci* develop. The problem here is that *Neolecta*, a taphrinomycotine (very basal acomycete) also has an ascocarp. *See* image on previous page. This structure is believed to be homologous to the ascocarps of Pezizomycotina. An even more disturbing problem is that euascomycetes have traditionally been classified by reference to details of ascus formation. As usual, the classical phylogenies are not all that far off the mark. Unless we are to adopt the newspeak of the Molecullariat and ignore everything that isn't a DNA sequence, we're going to have to tackle these details. This job involves a good



bit of particularly weird and obscure terminology. While the prospect of explaining this stuff fills us with a deep sense of foreboding, we may as well get it over with.

Most of the necessary information can be excavated from the figure, which we have borrowed from Liu & Hall (2004). Their notions of ascomycete evolution are a bit heterodox, but phylogeny is not our concern here. Let us take a walk through this field of fertile fungi simply to see what there is by way of anatomy.

Taphrina we have already encountered amongst the Taphrinomycotina. *Taphrina* has no ascocarp at all. The asci simply grow out of the normal somatic tissue of the fungus. This is, presumably, the primitive condition. It is simple, but inefficient. The asci have no protection during development. Since the asci are naked, their walls need to be relatively thick, which is inconvenient when it comes time to release the spores. Further, there is no convenient way to send the *ascospores* on their way into the world.

Aspergillus is presumed by many to represent the primitive condition among pezizomycotes. It is said to have a *cleistothecial* ascoma (or cleistothecium), because the ascii are completely enclosed. The cleistothecium is formed by fusion of vegetative hyphae. In *Aspergillus*, the fused hyphae harden into a hard, red pigmented shell at maturity. This is an example of a *peridium*, a rather vague term that includes any shell or membrane that encloses spores -- for example, the visible outer membrane of a puffball. *Hülle cells* may be associated with the peridium. These thick-walled, globular cells develop by budding from the tips of specialized hyphae. Hülle cells can envelope the entire developing cleistothecium and may serve as nurse cells. Wu & Miller (1997).

Since the asci are completely enclosed, they are well protected, but the spores can only be released by the decay or mechanical breach of the peridium. As we might expect, the walls of the asci are thin and fragile, designed to fall apart spontaneously, or at the slightest mechanical stress. Such walls are said to be *prototunicate*.

Peziza has an open or *apothecial* ascocarp. This makes it much easier to release the spores, but leaves the asci with much less protection during maturation than in cleistothecial forms. In *Peziza*, the individual asci are thus stronger and *unitunicate*, meaning that they are formed with a single, relatively stout membrane. In order for the spores to be

released, some different mechanism is required. Consequently, *Peziza* and other forms have evolved asci which are *operculate*, meaning that they have a sort of lid on the end. As the spores grow, fluid pressure builds up in the ascus until the operculum bursts open and the ascospores are blown out into the environment.

Neurospora develops a *perithecial* ascocarp. In other words, the ascocarp is closed but for an *ostiole* (pore) at the distal end. The ostiole is blocked by elongate sterile cells, known generically as *paraphyses*. "Ingold (1965) studied ascospore discharge in Sordaria. He found that the perithecial necks are positively phototropic. As the asci mature they swell and fill the upper part of the perithecium. One of the asci stretches and pushes through the ostiolar opening while its base remains attached to the perithecial wall. As the ascus tip protrudes, it discharges all of its spores explosively, collapses, and disintegrates, to be followed by each of the other asci in succession. This method of ascospore discharge is probably not confined to Sordaria, but may be the pattern of other members of this family." BOT 461/561: Lecture#17. Since the perithecium grows out into the medium from the hymenium after nuclear pairing, this is *ascohymenial* development. As in other ascohymenial forms, the asci produced are unitunicate.

Pleospora, by contrast, exhibits *ascolocular* development. Here, the asci develop in a *locule*, a small hollow in the generalized reproductive tissue of the *hymenium* (a/k/a *stroma* or *ascostroma*) **[1]**. As this is not typical perithecial development, the structure is referred to as a *pseudothecium*. By contrast to ascohymenial development, only the tip of the otiole is exposed. In *Pleospora*, the asci develop last -- in contrast to ascohymenial development, in which everything grows up around the developing asci. In *Pleospora*, the asci develop in a matrix of *pseudoparaphyses*, long, hair-like cells which grow down from the roof of the locule and often attach to its base. The asci in *Pleospora* are *bitunicate*.

And that, we are happy to report, is all the jargon we feel moved to impart on this subject, and doubtless more than the reader wished to absorb.

He went like one that hath been stunned,
And is of sense forlorn :
A sadder and a wiser man,
He rose the morrow morn.

Links: Ascomycetes and anamorphs; BOT 461/561: Lecture#17

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[1] On the difference between the stroma and hymenium: "It may seem obnoxious of me to dredge up this obsolete controversy when no one really cares about any more; but you may run across it in the older literature, and I believe that it is the source of the similar, stupid, and continuing controversy over names for hymenial cells." Illinois Mycological Association

---

Pezizomycotina (Euascomycetes)

```
ASCOMYCOTA
|--Taphrinomycotina
`--+--Saccharomycotina
   `--Pezizomycotina
      `--Pezizomycetes
         |--Hymenoascomycetes
         `--Loculoascomycetes
```


Introduction

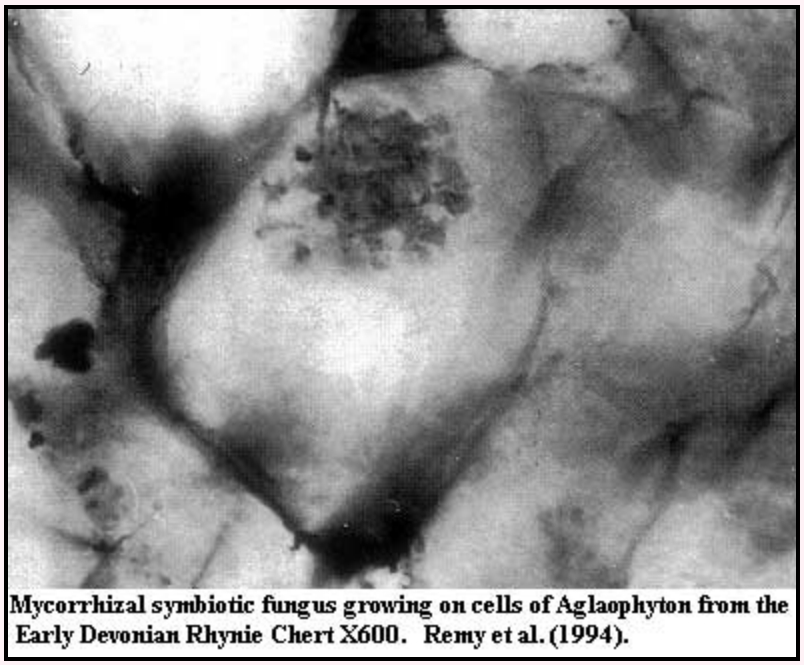
In our general section on Ascomycota, it was our unfortunate duty to describe some aspects of the sexual reproductive cycle of the Pezizomycotina. That discussion may be found on another page. Having discharged this obligation, we decline to repeat the performance here. It is still necessary for the reader to know the general outlines of this stuff in order to make much sense of ascomycete phylogeny, so the reader is referred to that earlier discussion -- with our sincere condolences.

Truthfully, there is not all that much to say about Pezizomycotina as a taxonomic entity separate from Ascomycota. Euascomycetes, as Pezizomycotina was traditionally known, is a sort of inverse garbage taxon. As the old name implies, all ascomycetes which fit the classical concept of a well-behaved fungus of the general ascomycete type were called euascomycetes. Everyone else got put in a some special box. This is exactly the opposite of the way things tend to work in zoology. In zoology, well-behaved taxa are zealously packaged into innumerable, tightly-constrined systematic containers, while non-conforming animals tend to be lumped into broad garbage taxa. However, as we have mentioned elsewhere, the culture of mycology is unique. We will see more evidence of this below. In any event, the attention of mycology has been focused at other taxonomic levels, with Pezizomycotina simply serving as a general umbrella.

This is not to say that the taxon Pezizomycotina fails the test of *monophyly*. One of the reasons for the change of

name was, presumably, to celebrate the taxon's graduation from a botanical *type* to a mycological *clade*. Nevertheless, although it is a phylogenetic entity, Pezizomycotina does not yet seem to have acquired a suitable phylogenetic *definition*, and its boundaries are a little unclear. As a result, although Pezizomycotina is evidently intended as a natural group of some sort, it is somewhat difficult to pin synapomorphies on it.

Early Evolution



Mycorrhizal symbiotic fungus growing on cells of Aglaophyton from the Early Devonian Rhynie Chert X600. Remy et al. (1994).

Pezizomycotines are first known in the fossil record from the Early Devonian Rhynie Chert. Certain remains from the Swedish Silurian may also represent Pezizomycotina. Redecker (2002). Claims for an ascomycete divergence date anywhere from 600 to 1200 Mya (*id.*), based on "molecular clock" models, currently lack substantiation. It may be significant that the fungi which accompanied the first land plants in the Ordovician were neither ascomycetes nor basidiomycetes, but basal to both. Redecker *et al*. (2000). This suggests that the evolution of these key groups, or at least their widespread radiation, had not yet occurred. Note also that both Ascomycota and Basidiomycota are characterized by the absence of any type of cell motility, and by unique reproductive characters which do not seem well designed for a marine environment.

Nevertheless, the Rhynie Chert fossils probably represent (at least) Sordariomycetes and some sort of loculoascomycete -- *i.e.* highly derived pezizomycotines. Remy *et al*. (1994). Redecker (2002). Therefore, if the Pezizomycotina were not present in the Ordovician, they must have developed very rapidly in the following 50 My. The presence of possible lichenized forms with filamentous hyphae from c. 650 Mya are also evidence suggesting, but not requiring, the evolution of pezizomycotines by that date.

Symbiotic Associations

Pezizomycotina is notable for its association with plants, animals and protists. Redecker *et al*. (2000). One interesting example comes from recent studies attempting to characterize the mixed fungal/microbial/algal communities responsible for acid mine drainage. Baker *et al*. (2004) recently examined the phylogenetic composition of fungi in the mixed communities inhabiting this hostile environment: pH 1, 30-50° C., and containing about 0.3 M metal salts (mostly iron, but with significant amounts of, *e.g.*, arsenic and copper). All of the fungi appeared to be pezizomycotines -- in particular, eurotiomycetes and dothidiomycetes. The fungi appear to play a structural role in the community, anchoring the biofilm to the underlying pyrite matrix. Baker *et al*. also speculate that they control the population structure of the community by selective grazing on the prokaryotic population.

The Cell Wall

This section, like the one on introns (below) has spawned a Pieces page on sugar chemistry and the fungal cell wall. As noted there, the cell wall is complex, with a poorly understood structure. The phylogenetic signal, particularly in the a(1→3)-glucan layer is obscure. However, the size and importance of a(1→4) side chains seems to increase over the course of pezizomycotine evolution, particularly in the Lecanoromycetes.

Phylogeny

We approach this section with great trepidation. The phylogeny of the Pezizomycotina is fraught with contradictions and inconsistency. Worse, we have reluctantly reached the conclusion that we're going to have to endorse a minority view. Specifically, we will reject the results of Prof. François Lutzoni and the AFTOL (Assembling the Fungal Tree of Life) Project and follow the phylogeny of Liu & Hall (2004). We have bent and stretched nomenclature to the breaking point in order to force both phylogenies into a head-to-head comparison, and into as close a correspondence as possible. However, as the table shows, the results of these studies are fundamentally dissonant.

Standardized Dendrograms

Liu & Hall (2004)

```
Pezizomycotina
`--Pezizomycetes*
   |--B--Chaetothyriales
   |   `--Dothidiomycetes*
   |      `--Arthoniomycetes
   `--A--Eurotiomycetes
      |--+--Sordariomycetes
      |   `--Leotiomycetes
      `--Lecanoromycetes
```

A = Hymenoascomycetes
B = Loculoascomycetes

Lutzoni *et al*. (2004)

```
Pezizomycotina
`--Pezizomycetes*
   |--+--Sordariomycetes
   |   `--+--Dothidiomycetes
   |      `--Arthoniomycetes
   `--Leotiomycetes*
      |--Eurotiomycetes
      |   `--Chaetothyriales
      `--Lecanoromycetes
```

* = Paraphyletic

The AFTOL approach combines truly massive amounts of rDNA and mtDNA data with sequence data from genes coding for RNA polymerase. Reeb *et al*. (2004); Lutzoni *et al*. (2004). Liu & Hall use only RNA polymerase amino acid sequence data, and a considerably smaller sample of taxa. However, it is likely that neither study uses a representative sample of euascomycete diversity, for the simple reason that only a small fraction of actual fungal diversity has been described. *See*, e.g., Schadt *et al*. (2003). In any case, this factor is slightly outweighed by the following considerations:

(1) Because of its history of generating bizarre phylogenies, we don't trust ribosomal DNA phylogenies, when there is anything else to rely on. In addition, they suffer from many of the same problems as mtDNA phylogenies. We don't trust mtDNA phylogenies under *any* circumstances, for reasons detailed elsewhere.

(2) There are particular reasons to be cautious when using fungal rDNA sequences.

(3) The AFTOL phylogeny has a slightly greater tendency to break up classical taxa into clumps that don't make any obvious biological sense; whereas

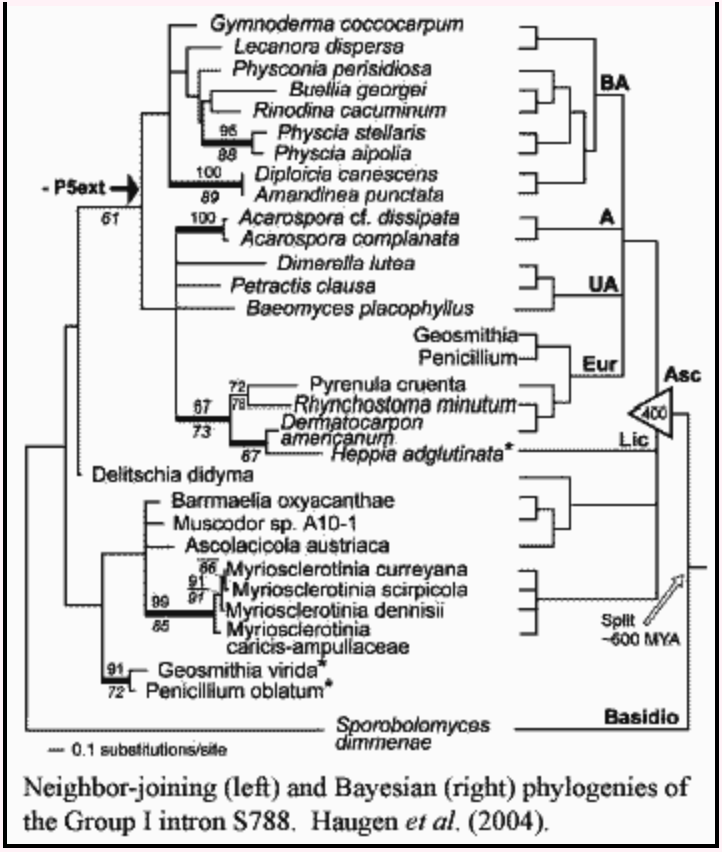
(4) Liu & Hall's phylogeny makes excellent biological sense. This, by a considerable margin, is the most important factor.

Fungal rDNA

Ascomycete rDNA is, quite literally, pathological. At some point, probably about the time that Ascomycota and Basidiomycota diverged, the ascomycetes (and to a far lesser extent, the Basidiomycetes) were attacked by a sort of RNA parasite, the Group I introns. The background material on Group I introns refused to confine itself to a brief paragraph or two, so we have moved it to Pieces. This is unlikely to do you much good, since you are probably not on a first name basis with *pAco.S788* and its relatives (Haugen *et al*., 2004). Accordingly, you will have to read the explanation anyway in order to make sense of what follows. Nonetheless, we derive a certain amount of wholly unmerited personal satisfaction from the superficial efficiency of referring you to this conveniently packaged discussion.

Unlike all other higher organisms, fungi contain a "vast array" of both Group I and *spliceosomal introns* in their rDNA. Haugen *et al*. (2004). Spliceosomal introns are found *only* in Pezizomycotina, and in fact, only in derived pezizomycotines. They are absent in the basal Pezizomycetes. Bhattacharya *et al*. (2000).

The Group I introns are somewhat more widely distributed. As of this writing (051105), 2696 Group I introns have been identified and sequenced. Of these, 1984 (74%) were isolated from eukaryotic nuclei, the remainder being from bacteria (3%) or organelles (23%). Of the roughly 2000 nuclear Group I introns, 67% are from Fungi generally and 61% from the Ascomycetes alone. Essentially all of the remaining Group I introns are from protists, with a handful known in land plants. No Group I introns have been isolated from metazoans. Cannone *et al*. (2002). Thus, unless the sampling has been extraordinarily poor, ascomycetes are peculiarly vulnerable to intron insertion. (Indeed, Haugen *et al*., 2004a report the bizarre case of an ascomycete with a Group I intron containing an internal spliceosomal intron).



Neighbor-joining (left) and Bayesian (right) phylogenies of the Group I intron S788. Haugen *et al*. (2004).

It is not clear whether this chronic infestation is the result of a single event in the distant past, or whether entirely new infections have occurred at intervals. The S788 family of introns, for example, appears to have been vertically transmitted (with a few exceptions) since Precambrian times, since one, highly divergent, member of the family is found among the basidiomycetes. Haugen *et al*. (2004). On the other hand, a few Group I introns are known in *all* major fungal groups except the Microsporidia **[1]**. Cannone *et al*. (2002). At any rate, the ascomycetes have been infected and periodically cross-infected with these rDNA parasites for their entire history.

It is difficult to tell what effects this may have had on the underlying rDNA sequences. In all likelihood, there has been irregular selection against intron splicing sites, irregular insertions of partial intron copies or degraded spliceosomal intron sequences. The real point is that we just don't know what effects this pathology may have had; but the effects, whatever they may have been, are likely to have included irregular jumps and twists in the rDNA family tree.

Euascomycete rDNA is also unusual in another way. It has recently been discovered that the multiple copies of the genes coding for the 5S rRNA of ascomycetes are not identical. Not only may a single organism contain many different 5S "alleles," but it may also contain 5S pseudogenes and incomplete copies. Rooney & Ward (2005). For a number of reasons, we would not expect to see this kind of *gross* sequence heterogeneity in other rDNA species. However, we know to a certainty that other fungal rDNA repeats contain some sequence heterogeneity due to the variable presence and variable sequence of introns. So, how certain can we be that these rDNA phylogenetic probes are not also, to some degree, heterogeneous mixtures of independently evolving genes?

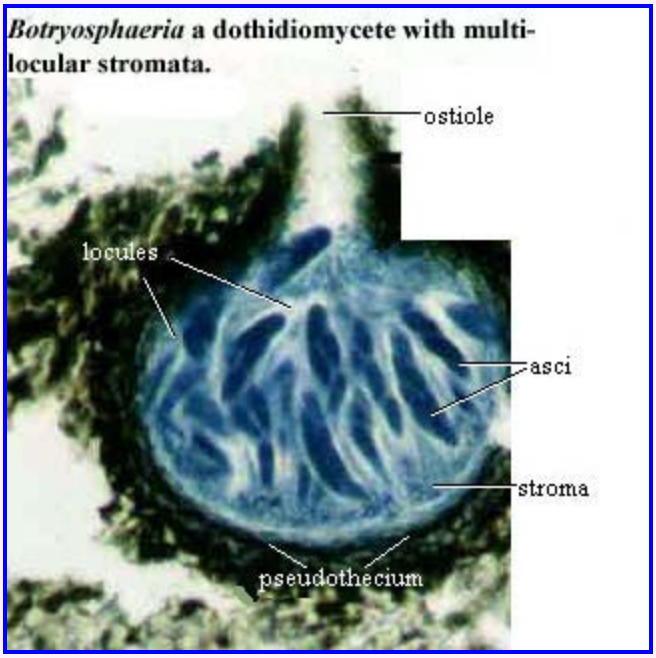
On the whole, we have reason to be particularly suspicious of rDNA phylogenies among the Ascomycota. Thus, the absence of rDNA data from the Liu & Hall study is likely to be a point in its favor.

Classical Taxa

Each generation of scientists tends to believe, in its heart, that all previous generations suffered from moderately severe brain damage. Mycologists are, on the whole, less subject to this prejudice than most. Yet, some of this prejudice is also present in mycology. However, as cladistic and molecular methods have matured, we are finding with astonishing frequency that the Ancients weren't idiots after

all. The astonishing thing is that they were able to accomplish so much accurate phylogeny with nothing more than intuition and gross morphology. Some key mistakes were made -- in mycology, the unfortunate absorption with botanical concepts, and the inclusion of the oomycetes among fungi, to name two. Nevertheless, previous generations of systematists were, on the average, keener observers then we are today because phyletic observation was essentially the only tool they had. Consequently, absent convincing evidence to the contrary, we ought to prefer a phylogeny which preserves the traditional taxa.

Neither the Lutzoni nor the Liu & Hall phylogenies invariably preserves the classical taxa, although both make claims to classical antecedents. However, Liu & Hall score slightly better. Both find that Pezizomycetes is paraphyletic. Liu & Hall also take the entire Chaetothyriales out of Eurotiomycetes and make it sister to Dothidiomycetes -- but so do a good many classical mycologists. Finally, they slip *Baeomyces*, a lichenized dothidiomycete, in with the Lecanoromycetes by relabelling the group with the unlatinized term "Lichenized."



On the other hand, the AFTOL phylogenies tend to fragment both Dothidiomycetes and Leotiomycetes each into several parts. The Leotiomycetes are a vague lot, and even Liu & Hall insist only on the monophyly of one portion, the Heliotiales. However, the Dothidiomycetes are a reasonably distinct and specialized bunch. They include the Pleosporales, such as *Pleospora*, which was described previously. As in *Pleospora*, development is *ascolocular* and the *asci* are usually associated with *pseudoparaphyses* in a *pseudothecium* and are *bitunicate*. (Look, we *told* you that you were going to have to review the page on pezizomycotine reproduction. But did you heed this warning? Of course not!) We are uncomfortable breaking up this kind of taxon, absent more compelling reasons to do so.

Finally, a prior paper by the Lutzoni group, Reeb *et al*. (2004) introduces and circumscribes several novel large taxa which are carried forward into Lutzoni *et al*. (2004). It is hard to know what to make of these taxa without a more specialized knowledge of fungal anatomy than we yet possess. Yet, the circumscriptions these taxa are couched in phrases such as "ascomata immersed, sessile or pedunculate in form of apothecia (cryptolecanorine, lecanorine, rarely lecideine-immersed) or in form of perithecia." Reeb *et al*. (2004: 1055). This is an intimidating barrage of terminology. But the bottom line, we suspect, is that not much is excluded when so many possibilities are included, and the morphological criteria thus look suspiciously uninformative.

Biological Reasonableness

Here is where Liu & Hall sharply differ from Lutzoni *et al*. Putting together a nice molecular phylogeny is like winning at solitaire. To do either one consistently takes an understanding of the rules and a command of a large, but sharply delimited, set of data. But neither feat means anything by itself, because there is no real-world connection. To graduate from being an interesting, but pointless, expenditure of computing power, molecular phylogenetics has to make sense in terms of real-world biology. Liu & Hall do a spectacular job of showing why and how their phylogeny relates to biology. Lutzoni *et al*. don't. We do not say that the AFTOL group *could* not do so, but they have not done

so yet.

Liu & Hall Phylogeny

(rearranged to emphasize evolution of developmental characters)

```
Pezizomycotina: unitunicate, apothecial
`--Pezizomycetes: no change
   |--Hymenoascomycetes: no change
   |  |--+--Leotiomycetes: no change
   |  |  `--Sordariomycetes: unitunicate, perithecial
   |  |--Lecanoromycetes: no change
   |  `--Eurotiomycetes: unitunicate, cleistothecial
   `--Loculoascomycetes: bitunicate, locular
      |--Dothidiomycetes: no change
      `--Chaetothyriales: same, pseudoparaphyses
```

At this point we ought to summarize Liu & Hall's discussion of biological correspondences in some detail. However, their paper is a short one, and it can be found on the web at the PNAS web site – to be precise, **here**. Thus, unlike many papers on the web, Liu & Hall (2004) is likely to be available indefinitely. We will therefore leave the reader to her own devices, except for the sections of the paper concerning the evolution and initial diversification of the Pezizomycotina.

Like Lutzoni *et al*., Liu & Hall find that *Neolecta* and yeasts (Saccharomycotina) are the sister groups of Pezizomycotina. As noted earlier, *Neolecta* has a basic form of ascus. This makes it likely that the euascomycete ascus is directly inherited from a *Neolecta*-like taphrinomycote. The yeasts therefore represent a side branch of development from ancestors who were multicellular and already possessed mycelial growth, specialized tissues, and even some of the basic euascomycete reproductive equipment. However, *Neolecta* lacks paraphyses, and the croziers do not develop until the ascus is formed. These characteristics probably represent the primitive state.

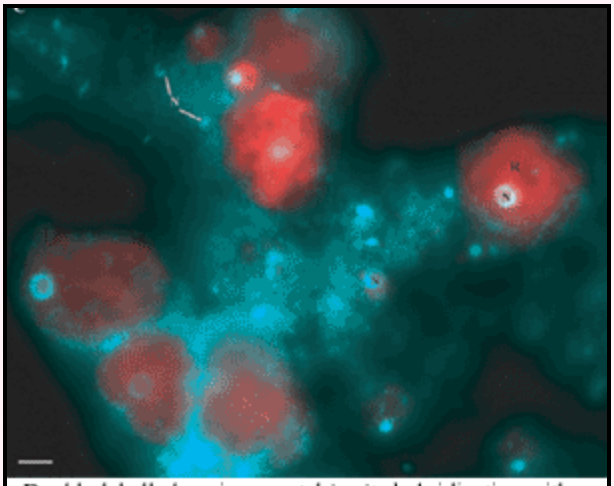
Also like the AFTOL group, Liu & Hall find that Pezizomycetes, the basal taxon of Pezizomycotina, is paraphyletic, with *Peziza* the most basal member of the series. Since *Peziza* and other basal pezizomycetes show *ascohymenial* development (as opposed to development in a locule), an *apothecium*, and *unitunicate* asci, these appear to constitute the primitive state within Pezizomycotina. Thus the unitunicate ascohymenial growth form is basal and we would expect it to have a parpaphyletic distribution. This is exactly what Liu & Hall find.

However, for the same reasons, we would expect *monophyletic* distribution of the *ascolocular*, *bitunicate* mode of development. This is exactly where Liu & Hall's phylogeny differs from the AFTOL tree. In the AFTOL tree, ascolocular development is either independently developed three times, or developed twice and reversed once. Nearly anything is possible to evolution, given enough time; but this is not exactly a parsimonious solution. Liu & Hall's phylogeny, by contrast, requires monophyletic development of these highly specialized tissues. This happens mainly because, compared to the scheme of Lutzoni *et al*., the Chaetothyriales switch places with the Sordariomycetes. This switch creates three different molecular lineages within the ascolocular clade; and each of these molecular lineages corresponds to one of three identifiable, morphological variations on ascolocular development -- a really wonderful result.

The purpose of a phylogeny is to explain the evolution of organisms. With sufficiently sophisticated numerical methods, and a judicious selection of assumptions, even the most chaotic data can be rearranged to form some kind of statistically coherent pattern -- but that isn't the point of the exercise. Molecular methods merely maximize particular measures of internal statistical consistency. The idea is that such measures serve as numerical proxies for the life, death, reproduction and change of real organisms. However, there are no guarantees: that these measures are an adequate proxy, that the assumptions made are correct, or that the particular genes examined have evolved in a manner consistent with the assumptions and the statistical metric. A phylogeny is a hypothesis; and, in science, a hypothesis must be testable and should be tested. That can only be done by comparing a phylogeny with what we know about biology, chemistry, the fossil record -- whatever may be available.

Liu & Hall's phylogeny has passed one such test with a very high score. That's a good start.

The Phylogeny of Gene Regulation



Double-labelled environmental *in situ* hybridization with fluorescent probes. Blue is non-specific DNA probe. Red is eukaryotic rRNA. Bar = 5 microns. Baker *et al*. (2004).

In addition to the usual molecular phylogenetic trees, the full sequencing of several fungal genomes has permitted other types of phylogenetic exploration. A particularly interesting series of experiments was recently reported by Gasch *et al*. (2004). These workers chose a number of short DNA sequence motifs which have been identified as regulatory binding sites in the yeast genome. Thus, for example, the sequence TCACGTG is a binding site for centromere binding factor 1p ("Cbf1p"). In *Saccharomyces cerevisiae*, Cbf1p sites are important in the regulation of genes involved in methionine biosynthesis **[2]**. Gasch & Co. then located the orthologous genes in a number of other ascomycete species and tested to see whether their upstream regulatory regions contained the same binding site.

Not surprisingly, the results indicated that other *Saccharomyces* species and other closely related yeasts had substantially the same regulatory motifs in the same places. The phylogenetically interesting result was the rate at which this similarity fell away. *Candida*, a less closely related saccharomycotine, shared barely a third of these regulatory sites. The Pezizomycotina and Taphrinomycotina outgroup members shared only a very few regulators. The retained motifs corresponded to a small handful of very high level regulators at the top of extensive regulatory cascades **[3]**.

These results fit a developing pattern with at least two important consequences for the way evolution works. First, it suggests that gene regulation -- at least in eukaryotes -- is hierarchical, rather than reticulated (net-like). Thus, evolution can take place by adding or tuning successively finer and more localized levels of control. This has the consequence of (a) creating a long-term trend toward higher complexity and (b) creating an environment which permits cellular specialization. By contrast, in a reticulated system, any change in one regulatory system will tend to affect all other systems. The probability of introducing a lethal side-effect goes up exponentially with complexity, so that the evolutionary potential of a reticulated system is limited. This is precisely the reason that other large, interacting systems, such as computer programs, must be built in a hierarchical, modular fashion.

Second, what the specific results of Gasch *et al*. (2004) also tell us is that, at least in fungi, this process is not overly conservative. That is, evolution doesn't simply continue to add more layers of control. Only thevery highest level controllers are conserved in ascomycete evolution. Thus, the observed progressive evolution at low regulatory levels is eventually capable of re-engineering everything else in the organism, as localized changes incrementally affect higher levels of regulation. Ultimately, only the very highest levels of regulation are conserved.

In conceptual terms, Gasch *et al*. provide the beginnings of a precise answer to the noisy, but data-poor, debates about "micro-evolution" vs. "macro-evolution."

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[1] Recall that Microsporidia have minimal genomes, probably due to their mode of infecting metazoan cells. Any unnecessary code would have been eliminated during the process of genome miniaturization.

[2] One problem with Gasch *et al*. (2004) is that the paper grossly oversimplifies the specificity of the DNA binding factors. In this example, Cbf1p binding is not only involved in methionine biosynthesis, but also in cysteine synthesis, as well as in completely unrelated activities such as DNA repair. Ferreiro *et al*. (2004); Kuras *et al*. (1997). Sure, a more complete description would make the paper five times longer; but, for an on-line journal like **PLoS Biology**, why is that a problem?

[3] Examples include the *Mlu1* cell cycle box (MCB) and General Control Nondepressible Factor 4 (Gcn4p). MCB sits at the top of a cascade which promotes vegetative cell growth and nucleotide synthesis. Machado *et al*. (1997); Pilpel *et al*. (2001). Gcn4p may be even more general. It not only serves as a master switch to promote at least 12 different amino acid synthesis pathways, but also serves as a high-level regulator of glycolysis and other elements of

vegetative metabolism. Hinnebusch & Natarajan (2002); Natarajan *et al*. (2001).

Ascomycota References

Baker, BJ, MA Lutz, SC Damson, PL Bond & JF Banfield (2004), *Metabolically active eukaryotic communities in extremely acidic mine drainage*. **Appl. Environ. Microbiol.** 70: 6264-6271. Pezizomycotina.

Bhattacharya, D, F Lutzoni, V Reeb, D Simon, J Nason, & F Fernandez (2000), *Widespread occurrence of spliceosomal introns in the rDNA genes of Ascomycetes*. **Mol. Biol. Evol.** 17: 1971–1984. Pezizomycotina.

Bold, HC (1973), **Morphology of Plants** [3rd ed.]. Harper & Row, 668 pp. Ascomycota.

Bullerwell, CE, J Leigh, L Forget & BF Lang (2003), *A comparison of three fission yeast mitochondrial genomes*, **Nucl. Acids Res.** 31: 759-768 Ascomycota.

Cannone JJ, S Subramanian, MN Schnare, JR Collett, LM D'Souza, Y Du, B Feng, N Lin, LV Madabusi, KM Muller, N Pande, Z Shang, N Yu, & RR Gutell (2002),*The comparative RNA web (CRW) site: An online database of comparative sequence and structure information for ribosomal, intron, and other RNAs*. **BioMed Central Bioinformatics** 3:15. Pezizomycotina.

Cooper, S & K Shedden (2003), *Microarray analysis of gene expression during the cell cycle*. **Cell & Chromosome** 2:1. Pezizomycotina.

Ferreiro, JA, NG Powell, N Karabetsou, NA Kent, J Mellor & R Waters (2004), *Cbf1p modulates chromatin structure, transcription and repair at the **Saccharomyces cerevisiae MET16** locus*. **Nuc. Acids Res.** 32: 1617-1626. Pezizomycotina.

Filley, TR, RA Blanchette, E Simpson & ML Fogel (2001), *Nitrogen cycling by wood decomposing soft-rot fungi in the "King Midas tomb," Gordion, Turkey*. **Proc. Nat. Acad. Sci. (USA)** 98: 13346–13350. Ascomycota.

Gaillardin, C, G Duchateau-Nguyen, F Tekaia, B Llorente, S Casaregola, C Toffano-Nioche, M Aigle, F Artiguenave, G Blandin, M Bolotin-Fukuhara, E Bon, P Brottier, J deMontigny, B Dujon, P Durrens, A Lépingle, A Malpertuy, C Neuvéglise, O Ozier-Kalogéropoulos, S Potier, W Saurin, M Termier, M Wésolowski-Louvel, P Wincker, J-L Souciet & J Weissenbach (2000), *Genomic exploration of the hemiascomycetous yeasts: 21. Comparative functional classification of genes*. **FEBS Let.** 487: 134-149 Ascomycota.

Gasch AP, AM Moses, DY Chiang, HB Fraser, M Berardini & MB Eisen (2004), *Conservation and evolution of cis-regulatory systems in ascomycete fungi*. **PLoS Biol** 2: e398. Pezizomycotina.

Haugen, P, V Reeb, F Lutzoni & D Bhattacharya (2004a), *The evolution of homing endonuclease genes and Group I introns in nuclear rDNA*. **Mol. Biol. Evol.** 21: 129–140. Pezizomycotina.

Haugen, P, HJ Runge & D Bhattacharya (2004), *Long-term evolution of the S788 fungal nuclear small subunit rRNA group I introns*. **RNA** 10: 1084–1096. Pezizomycotina.

Hinnebusch, AG & K Natarajan (2002), *Gcn4p, a master regulator of gene expression, is controlled at multiple levels by diverse signals of starvation and stress*. **Eukar. Cell** 1: 22-32. Pezizomycotina.

Kuras, L, R Barbey & D Thomas (1997), *Assembly of a bZIP-bHLH transcription activation complex: formation of the yeast Cbf1-Met4-Met28 complex is regulated through Met28 stimulation of Cbf1 DNA binding*. Pezizomycotina.

Liu, Y-JJ & BD Hall (2004), *Body plan evolution of ascomycetes, as inferred from an RNA polymerase II phylogeny*. **Proc. Nat. Acad. Sci. (USA)** 101: 4507-4512. Ascomycota, Pezizomycotina.

Llorente, B, P Durrens, A Malpertuy, M Aigle, F Artiguenave, G Blandin, M Bolotin-Fukuhara, E Bon, P Brottier, S Casaregola, B Dujon, J deMontigny, A Lépingle, C Neuvéglise, O Ozier-Kalogeropoulos, S Potier, W Saurin, F Tekaia, C Toffano-Nioche, M Wésolowski-Louvel, P Wincker, J Weissenbach, J-L Souciet & C Gaillardin (2000), *Genomic exploration of the hemiascomycetous yeasts: 20. Evolution of gene redundancy compared to **Saccharomyces cerevisiae***. **FEBS Let.** 487: 122-133. Ascomycota.

Llorente, B, A Malpertuy, C Neuvéglise, J deMontigny, M Aigle, F Artiguenave, G Blandin, M Bolotin-Fukuhara, E Bon, P Brottier, S Casaregola, P Durrens, C Gaillardin, A Lépingle, O Ozier-Kalogéropoulos, S Potier, W Saurin, F Tekaia, C Toffano-Nioche, M Wésolowski-Louvel, P Wincker, J Weissenbach, J-L Souciet & B Dujon (2000), *Genomic exploration of the hemiascomycetous yeasts: 18. Comparative analysis of chromosome maps and synteny with **Saccharomyces cerevisiae***. **FEBS Let.** 487: 101-112. Ascomycota.

Lutzoni, F, F Kauff, CJ Cox, D Mclaughlin, G Celio, B Dentinger, M Padamsee, D Hibbett, TY James, E Baloch, M Grube, V Reeb, V Hofstetter, C Schoch, AE Arnold, J Miadlikowska, J Spatafora, D Johnson, S Hambleton, M Crockett, R Shoemaker, G-H Sung, R Lücking, T Lumbsch, K O'donnell, M Binder, P Diederich, D Ertz, C Gueidan, K Hansen, RC Harris, K Hosaka, Y-W Lim, B Matheny, H Nishida, D Pfister, J Rogers, A Rossman, I Schmitt, H Sipman, J Stone, J Sugiyama, R Yahr, & R Vilgalys (2004). *Assembling the fungal tree of life: Progress, classification, and evolution of subcellular traits*. **Amer. J. Bot.** 91: 1446-1480. Pezizomycotina.

Machado, AK, BA Morgan & GF Merrill (1997), *Thioredoxin reductase-dependent inhibition of MCB Cell Cycle Box activity in **Saccharomyces cerevisiae***. **J. Biol. Chem.** 272: 17045-17054. Pezizomycotina.

Malpertuy, A, F Tekaia, S Casarégola, M Aigle, F Artiguenave, G Blandin, M Bolotin-Fukuhara, E Bon, P Brottier, J deMontigny, P Durrens, C Gaillardin, A Lépingle, B Llorente, C Neuvéglise, O Ozier-Kalogeropoulos, S Potier, W Saurin, C Toffano-Nioche, M Wésolowski-Louvel, P Wincker, J Weissenbach, J-L Souciet & B Dujon (2000), *Genomic exploration of the hemiascomycetous yeasts: 19. Ascomycetes-specific genes*. **FEBS Let.** 487: 113-121. Ascomycota.

Natarajan, K, MR Meyer, BM Jackson, D Slade, C Roberts, AG Hinnebusch & MJ Marton (2001), *Transcriptional profiling shows that Gcn4p is a master regulator of gene expression during amino acid starvation in yeast*. **Mol. & Cell. Biol.** 21: 4347-4368. Pezizomycotina.

Pilpel, Y, P Sudarsanam & GM Church (2001), *Identifying regulatory networks by combinatorial analysis of promoter elements*. **Nature Genetics** 29: 1-7. Pezizomycotina.

Redecker, D (2002), *New views on fungal evolution based on DNA markers and the fossil record*. **Res. Microbiol.** 153: 125-130. Pezizomycotina.

Redecker, D, R Kodner & LE Graham (2000), *Glomalean fungi from the Ordovician*. **Science** 289: 1920-1921. Pezizomycotina.

Reeb, V, F Lutzoni & C Roux (2004), *Contribution of RPB2 to multilocus phylogenetic studies of the Euascomycetes (Pezizomycotina, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory*. **Mol. Phylog. & Evol.** 32: 1036-1060. Pezizomycotina.

Remy, W, TN Taylor, H Hass & H Kerp (1994), *Four hundred-million-year-old vesicular arbuscular mycorrhizae*. **Proc. Nat. Acad. Sci. (USA)** 91: 11841-11843. Pezizomycotina.

Rooney, AP & TJ Ward (2005), *Evolution of a large ribosomal RNA multigene family in filamentous fungi: Birth and death of a concerted evolution paradigm*. **Proc. Nat. Acad. Sci. (USA)** 102: 5084-5089. Pezizomycotina.

Schadt, CW, AP Martin, DA Lipson & SK Schmidt (2003), *Seasonal dynamics of previously unknown fungal lineages in tundra soils*. **Science** 301: 1359-1361. Pezizomycotina.

Wu, J-G & BL Miller (1997), ***Aspergillus*** *asexual reproduction and sexual reproduction are differentially affected by transcriptional and translational mechanisms regulating* ***stunted*** *gene expression*. **Mol. Cell. Biol.** 17: 6191–6201. Ascomycota.

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