

Classification of the Fungi

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CHARACTERISTICS OF THE FUNGI

The fungi (also commonly called molds, mildews, yeasts, mushrooms, truffles, and so on) are ubiquitous in nature. Fungi, like plants, are generally nonmotile and have rigid cell walls. Unlike plants, the fungi never have chlorophyll; like animals, the fungi must obtain ready-made carbohydrates from their environment. Fungi are considered evolutionarily distinct from both plants and animals, primarily because they use a unique method for synthesizing lysine. Although both plants and fungi produce lysine, plants use pathways that differ in every step from those used by fungi. Animals cannot synthesize lysine; they must obtain it from their food.

The primary role of fungi in the natural environment is to facilitate aerobic decay of nonliving organic material. Some fungi, called parasites, obtain nourishment from living organic material. A few fungi have developed a cooperative life style, called symbiosis, with other kinds of organisms. A lichen, for example, is the symbiotic association of a fungus and an alga.

Fungi affect and are used by people in many ways. For example, such fungi as *Histoplasma* and *Coccidioides* are primary human pathogens. Fungal antigens cause diseases, such as allergic rhinitis, allergic asthma, and hypersensitivity pneumonitis. Many fungi produce toxic metabolites that cause serious acute and/or chronic human health effects (1). Fungi are used in industry to produce a

wide range of useful chemicals, including most antibiotics, many organic acids, and ethanol (which is generated in the production of beer and wine). People use fungi for food (mushrooms, truffles), or to process other materials to make them more easily digestible (e.g., tempeh, which is a soybean curd infected with *Rhizopus*).

Fungal organisms can exist as single cells, simple chains of cells called hyphae, undifferentiated masses of hyphae called mycelia, or differentiated masses of hyphae that form sclerotia (resting structures) or fruiting bodies (e.g., mushrooms or truffles). Most fungi exhibit complex life cycles; they reproduce both sexually and asexually. Sex is controlled by a single gene with two alleles in all fungi except the higher basidiomycetes. These more advanced fungi have multiple alleles that may occur on one gene (bipolar) or on two genes (tetrapolar). This multiple allelic situation determines the numerous mating types that occur within each taxon. These complex systems allow for nearly 100% compatibility between strains. In the Holobasidiomycetes, sexually produced spores are the primary mode of reproduction and dissemination. On the other hand, in the plant rusts (Teliomycetes), both sexual and asexual spores are necessary for completion of life cycles in the environment. The best known of the allergenic fungi (e.g., *Alternaria*) reproduce primarily by means of asexual or "clone" spores. These fungi rely on a high rate of somatic mutation and the production of heterokaryons by hyphal fusion to produce new gene combinations that allow them to adapt to changes in the environment.

Fungus spores can be thick-walled, dry, pigmented, and hydrophobic, thus favoring long-range transport through dry air. On the other hand, fungus spores can be colorless and "slimy," with modes of dispersal depending on water. Both spore types are common in indoor and outdoor air. Spores are considered the most important mode of human exposure to fungal materials.

Biochemically, the fungi are complex and variable. The fungal cell wall is usually composed of an acetyl glucosamine polymer (chitin), although mannans, glucans, and cellulose can also be present. The principal sterol of the fungus membrane system is ergosterol. The DNA content of fungi is very low, and ratios of guanine + cytosine have been reported in the range of 38–63%. RNA content may be as high as 10% dry wt and is primarily present as ribosomal RNA. The principal storage carbohydrate is glycogen (tre-

halose and mannitol may also be used). The fungi metabolize glucose via aerobic respiration into CO₂ and water, or via fermentation into CO₂ and alcohol or lactic acid.

The fungi produce many enzymes. Some of these enzymes (such as proteases) are produced by other organisms, but some enzymes are unique to the fungi. These unique enzymes allow fungi to degrade unusually resistant substrates, such as cellulose, lignin, and even polyethylene (2).

Secondary metabolites are produced by some fungi. The value of these compounds to the fungi is unclear; however, their impact on humanity can be dramatic. Among these secondary metabolites are many of the commonly used antibiotics (e.g., penicillin, cyclosporin), some of the most potent known toxins (e.g., aflatoxin, trichothecenes), and many psychoactive substances (e.g., psilocybin).

CLASSIFICATION SYSTEMS

Biologists use classification systems to facilitate the study of groups of organisms. Some of these systems are called “natural” and are based on taxonomic studies that have traced evolutionary relationships among the organisms. Others are “file drawer” systems that provide a convenient way of thinking about subgroups of organisms or some given aspect of the organisms.

Classification of the Biological World

As new information regarding evolutionary relationships has become available, the living organisms of earth have been classified and reclassified. Initially, all organisms were considered “plants” or “animals.” Fungi were considered plants because they were apparently immobile. However, biochemical, physiological, morphological, and reproductive studies of living organisms have resulted in the evolutionary classification of the five kingdoms of life outlined in Table 1.

Organisms that have been called fungi are now included in the Monera (actinomycetes), and in the Protocista (slime molds, downy mildews). Most of the well-known allergenic fungi are in the kingdom “Fungi.”

Table 1
The Kingdoms of Life

Kingdom	Major characteristics	Representatives
Monera	Prokaryotic, heterotrophic (a few autotrophs), DAP synthesis	bacteria, actinomycetes, blue-green algae
Protoctista	Eukaryotic, heterotrophic or autotrophic, DAP lysine synthesis	protozoans, slime molds, algae, Oomycetes (e.g., downy mildews)
Fungi	Eukaryotic, heterotrophic, AAA lysine synthesis	most "fungi" (e.g., molds, mushrooms, lichens)
Plantae	Eukaryotic, autotrophic, DAP lysine synthesis	mosses, ferns, seed plants
Animalia	Eukaryotic, heterotrophic, no lysine synthesis	jellyfish, mollusks, insects, birds, mammals

Classification of the Fungi

The fungi have been classified in many ways by nonmycologists. Table 2 summarizes a few of these systems.

Sexual reproductive attributes are "conservative" (i.e., they change slowly) and are therefore ideal bases for classification systems. This conservatism is a result of the fact that mutations and recombinations that change sexual characteristics tend to be lethal. The "true" fungi (Kingdom Fungi) are classified into two major phyla, based on patterns of sexual reproduction:

1. The Zygomycota, in which cytoplasmic fusion and nuclear fusion occur in the same cell (the zygote) and
2. The Dikaryomycota, in which cytoplasmic fusion occurs, the binucleate cell divides to produce a multicellular dikaryotic state, and nuclear fusion occurs later.

These major divisions based on reproductive characters are supported by biochemical differences. The Dikaryomycota is further subdivided into two subphyla based on the morphology of sexual spore production:

Table 2
Some Common “Lay” Methods for Classifying Fungi

Method	Category	Examples
Gross morphology	Yeasts	<i>Saccharomyces</i> , <i>Candida</i>
	Molds	<i>Rhizopus</i> , <i>Penicillium</i>
	Mushrooms	<i>Coprinus</i> , <i>Agaricus</i>
	Toadstools	<i>Amanita</i> , <i>Galerina</i>
Fungus life style	Plant pathogens	<i>Puccinia</i> , <i>Ustilago</i>
	Human pathogens	<i>Histoplasma</i> , <i>Candida</i>
Effect on humans	Poisonous	<i>Amanita</i> , <i>Claviceps</i>
	Edible	<i>Morchella</i> , <i>Tuber</i>
	Toxic	<i>Aspergillus</i> , <i>Fusarium</i>
Color	Pink mold	<i>Monilia</i>
	Black mold	<i>Rhizopus</i>
Economic status	Wood rotters	<i>Ganoderma</i>
	Food production	<i>Penicillium roqueforti</i> , <i>Saccharomyces</i>
	Antibiotics	<i>Penicillium</i>

- 1. The Ascomycotina (sexual spores borne in an ascus) and
- 2. The Basidiomycotina (sexual spores borne on a basidium).

Further divisions, based on modes of sexual reproduction within the Dikaryomycota, are presented in Table 3.

The classification system presented in Table 3 is that described by Kendrick (3). Other authors have interpreted available information differently. For example, Tubaki (4) places the sexual stages of *Alternaria* and *Stemphylium* in the Pleosporales instead of the Dothidiales.

Systems based on modes of sexual reproduction should allow one to predict the degree of difference between individual taxa based on their position within subphyla, classes, series, orders, and the like. *Alternaria* and *Stemphylium*, both asexual stages of members of the Dothidiales, do appear to contain crossreacting antigens (5). However, many studies of crossreactivity have relied on single-batch/single-strain preparations. Because batch and strain variability has been found to be significant in the fungi, such studies are valuable

Table 3
Classification of the True Fungi

Group	Examples
Phylum Zygomycota	<i>Rhizopus</i> , <i>Mucor</i>
Phylum Dikaryomycota	
Subphylum Ascomycotina	
Series Prototunicatae	
Order Onygenales	Sexual stages of <i>Histoplasma</i> , dermatophytes
Order Eurotiales	Sexual stages of <i>Aspergillus</i> , <i>Penicillium</i>
Series Unitunicatae operculate	Morels, truffles
Series Unitunicatae inoperculate	
Order Sphaeriales	Sexual stages of <i>Aureobasidium</i> , <i>Drechslera</i> , <i>Curvularia</i> , <i>Helminthosporium</i>
Order Hypocreales	<i>Chaetomium</i> , <i>Neurospora</i> , sexual stages of <i>Fusarium</i> , <i>Trichoderma</i>
Order Diaporthales	<i>Endothia</i> (Chestnut blight)
Order Helotiales	Sexual stages of <i>Botrytis</i> and <i>Monilia</i>
Order Clavicipitales	<i>Claviceps</i> (ergot)
Series Bitunicatae	
Order Dothidiales	Sexual stages of <i>Alternaria</i> , <i>Stemphylium</i> , and <i>Cladosporium</i>
Order Erysiphales	Powdery mildews
Series Hemiascomycetes	Ascosporogenous yeasts
Subphylum Basidiomycotina	
Class Holobasidiomycetes	
Order Exobasidiales	<i>Exobasidium</i>
Order Dacrymycetales	<i>Dacrymyces</i>
Order Aphyllophorales	"Bracket" fungi
Order Agaricales	Mushrooms
Order Lycoperdales	Puffballs
Class Phragmobasidiomycetes	Jelly fungi, ear fungi
Class Teliomycetes	Rusts, smuts

only when they demonstrate clear crossreactivity between taxa (6). Purification and characterization of specific fungal allergens, and production of relevant monoclonal antibodies against these allergens, will be required for accurate assessment of relationships among the fungi (7).

Table 4
The Saccardo Classification for Asexual Fungi

Taxon	Major character	Example
Order		
Mucorales	Mycelium without septae	<i>Rhizopus</i> , <i>Mucor</i>
Sphaeropsidales	Spores in fruiting bodies: pycnidia	<i>Phoma</i>
Melanconiales	Spores in acervuli	<i>Pestalotia</i>
Moniliales	Spores produced on the mycelium	Most asexual fungi
Family		
Tuberculariaceae	Spore-bearing structures in sporodochia	<i>Fusarium</i>
Stilbaceae	Spore-bearing structures in synnemata	<i>Graphium</i>
Moniliaceae	Spore-bearing structures scattered; spores colorless or bright	<i>Aspergillus</i>
Dematiaceae	Spore-bearing structures scattered; spores brown to black	<i>Alternaria</i>
Mycelia Sterilia	No spores produced	<i>Rhizoctonia</i>

Many fungi rarely produce their sexual phase, and rely, therefore, on asexual processes for reproduction and dissemination. For these fungi, classification systems have been developed that focus on the production of asexual spores. Although based on characters less evolutionarily stable than those connected with sexual reproduction, some of these systems tend to group organisms in ways that often parallel groups based on sexual relationships.

The asexual system best known to nonmycologists is the Saccardo system, which is truly a "file drawer" system. It is not based on natural relationships, and divides the spore-bearing fungi into five orders, as shown in Table 4.

Pycnidia are flask-shaped, microscopic fruiting bodies within which spores and spore-bearing structures are compacted. Acervuli are flattened fruiting bodies with a broad, open top. These are often very difficult to separate from sporodochia (compact collections of spore-bearing structures not surrounded by fruiting-body tissue) in culture. Synnemata are ropy agglomerations of hyphae with spore-

bearing structures. The formation of these structures may be strongly dependent on nutritional factors in the substrate. Recently, the asexual fungi have been divided into two general groups, based on whether or not asexual spores are produced in a fruiting body. Those in which spores are produced directly on the mycelium are termed Hyphomycetes, those with fruiting bodies, Coelomycetes. Another method for classifying asexual fungi depends on the type of spore produced. Some common spore types are

Amerosporae	Spores one-celled	<i>Aspergillus</i>
Didymosporae	Spores two-celled	<i>Trichothecium</i>
Phragmosporae	Spores with transverse septa only	<i>Fusarium</i>
Dictyosporae	Spores with both transverse and longitudinal septa	<i>Alternaria</i>

Although these spore categories are descriptive, they are of limited use. Many fungi produce spores with variable septation. *Cladosporium*, for example, produces amerospores, didymospores, and phragmospores. *Pithomyces* produces phragmospores or dictyospores, depending on the species.

The Hughes-Tubaki-Barron system of classification divides the Moniliales into sections based on developmental stages during the formation of conidia (8). This is a more "natural" (evolutionarily relevant) system than Saccardo's, but it is more difficult for the nonmycologist to use. Some major subdivisions in the system are summarized in Table 5.

Above are presented a few of the systems that have been developed to attempt to organize the thousands of fungi that have been described. However, by using only these three systems, one can identify most fungi and make some hypotheses as to relationships.

FUNGAL NOMENCLATURE

Compounding the problems caused by the existence of both sexual and asexual names for each fungus and of multiple modes of classification, the established rules for naming the fungi are often misused or ignored (especially by nonmycologists). Regardless of

Table 5
The Hughes-Tubaki-Barron Classification of Asexual Fungi

Series	Characteristics	Examples
Arthrospora	Segmentation of vegetative hyphae	<i>Geotrichum</i>
Aleuriospora	Transformation of hyphal tip into single spore	<i>Pithomyces</i> , <i>Nigrospora</i>
Annellospora	Formation of successive spores by percurrent proliferation	<i>Scopulariopsis</i>
Blastospora	Budding to produce spore chains	<i>Cladosporium</i> , <i>Monila</i>
Botryoblastospora	Blastospores produced simultaneously on swollen head	<i>Botrytis</i>
Porospora	Formation of spores through pores in mycelial wall	<i>Alternaria</i> , <i>Stemphylium</i>
Symptodulospora	Successive spores produced sympodially on pegs as hyphae tip elongates	<i>Sporothrix</i> <i>Tritarachium</i>
Phialospora	Successive spores produced through open tip of hyphae which does not elongate	<i>Aspergillus</i> , <i>Penicillium</i> , <i>Fusarium</i>

which classification system you use, each fungus must be assigned a Latin binomial (a genus name and a species name). Note that when one uses a genus name without a species name, one refers to the entire genus (i.e., all the species). The rules further state that the first person to describe a particular fungus is entitled to name it, and that person's name is attached to the fungus name as the authority (e.g., *Stemphylium botryosum* Wallroth). The authority is necessary because the same name could have been (illegally) used by more than one mycologist to apply to completely different organisms.

Inconsistent application of the rules for fungal nomenclature has resulted in several kinds of problems with respect to fungal allergens.

1. Use of genus-only designations: *Monilia albicans* is a name that has been incorrectly applied to the fungus *Candida albicans*. *Monilia* is actually a mycelial fungus that rarely, if ever, colonizes human tissue. *Candida albicans* is a yeast-like human pathogen. As a consequence, the term *Monilia* when used alone may refer to a mycelial fungus (e.g., *Monilia sitophila*) or the yeastlike *Candida albicans*.
2. Use of outdated generic names: *Cladosporium* is one of the most common airborne fungal genera. Unfortunately, for many years, several of the common species of *Cladosporium* were assigned to the genus *Hormodendron*. At least 30 years ago, the two genera were found to be identical. Some allergists and allergen suppliers continue to use the outdated name.
3. Use of incorrect species names: *Epicoccum* is a monospecific genus with only one species. In the past, several species have been described, but all have been found to be identical. Currently, allergen suppliers provide three different *Epicoccum* species, which are, in reality, all actually *Epicoccum nigrum*. Studies that make comparisons between these "species" are comparing strains of a single species.

A similar problem involves using fungus names without specifying authorities or discussing synonymy. *Alternaria tenuis* C. G. Nees is considered synonymous with *Alternaria alternata* (Fr.) Keissler. Published research on this fungus has used both names, usually without pointing out that they are identical (5,9).

SUGGESTIONS

1. When choosing fungi for use in diagnosis, treatment, or research, one should insist on strains labeled with a legal binomial that includes an authority.
2. One should seek a person who is an authority in the specific group of fungi of interest to verify the identification and nomenclature.
3. If confusion exists regarding nomenclature within a taxon, one should discuss the nomenclature in publications resulting from research.
4. One should deposit fungi used in research in recognized culture collections so that your research can be precisely duplicated by others in the scientific community.
5. When designing studies that seek to examine antigenic or allergenic relationships within the fungal kingdom, one should try to

use sexual reproductive characters in choosing fungi for comparison. If sexual characters are not available, use the Hughes-Tubaki-Barron system to select taxa for study.

6. One should always use multiple batches and strains of each fungus species.

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