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ORIGINS, PHYLOGENIES AND RELATIONSHIPS IN THE FUNGAL KINGDOM

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The “true” fungi have been referred to as the Kingdom *Fungi,* the Kingdom *Eumyceteae,* or the *Eumycota* [1]. The fungi are eukaryotic organisms, characterized by: (i) a diversity of microbodies; (ii) cell walls that have a great similarity of architecture; (iii) hyphae that have a major chitin component, extended apically, and divide by centripetal invagination of the plasma membrane; (iv) lomasomes: sponge-like intumescences seen on the inside of the cell wall; (v) complete absence of the Golgi organelle in the terrestrial assemblages (zygomycetes, ascomycetes, and basidiomycetes) and some of the aquatic taxa; and (vi) nuclei in which most, if not all, gene products involved in mitosis probably have higher eukaryotic paramologues but which, in other ways, are exceptional [2]. Fungi are reproducing sexually or asexually, the diploid phase generally short-lived. Fungi parasitize a wide range of plants, animals, and other fungi [3].

The number of known species of fungi is about 70,000, but species of the fungal world are conservatively estimated to be 1.5 million [4]. The fungi are of great consequence agronomically, bioindustrially, medically, and biologically. In spite of their importance, their taxonomic inventory is poor. In addition, very little is known about the phylogeny and evolution of fungi and about the correlations between these and other organisms [1].

Sexual and asexual reproductive structures have provided important phenotypic characters to measure relatedness and evolutionary affinities among fungi. If they lose these structures, accurate taxonomic assignment is quite difficult.

To date, phylogenetic speculations and taxonomies for the fungi have been based mainly on analyses of morphological data sets. In the 1980s, development of molecular biological techniques (DNA:DNA hybridization, DNA fingerprinting, nucleic acid sequencing, isozyme analysis), proliferation of high performance computers, and improvement of molecular evolutionary analysis programs have extended studies of relatedness, phylogeny, and evolution of organisms, including fungi, at the molecular level [5–8]. Nucleic acid characters, as genotypic characters, are ubiquitous and are not dependent on the expression of reproductive structures. Nuclear DNA base composition

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and nuclear DNA relatedness, as nucleic acids characters resolve only to the genetic sibling species level [5].

Ribosomal RNA sequence comparisons, as a nucleic acid character, offer a means for estimating more distant relationships [9]. In recent years, molecular phylogenetic analysis of the fungi shifted to the small (18S) and large (23S to 28S) subunit rRNAs. Phylogenetic analysis among distantly related taxa, using 18S rRNA gene sequences, has contributed to well-resolved and statistically supported conclusions. In the early 1990s, such an approach has steered fungal taxonomy towards fungal molecular systematics [10–17]. Thus, studies on fungal phylogeny and evolution have entered a new era.

Among earlier phylogenetic speculations concerning the fungi and related organisms that have been made during the past ten years, Cavalier-Smith [1] provided a framework for a taxonomic system and phylogeny for the fungal kingdom. His system included only the *Chytridiomycetes, Zygomycetes, Ascomycetes,* and *Basidiomycetes* in the Kingdom *Fungi.* These four fungal groups are characterized by chitinous cell wall and the alpha-aminoadipic acid (AAA) lysine biosynthetic pathway. The *Oomycetes, Hyphochytrids, Labyrinthulida, Thraustochytrids,* and slime molds, which are cellulosic and have the diaminopimelic acid (DAP) lysine biosynthetic pathway, are excluded from the *Fungi.* The former four major groups have been accommodated in the *Pseudofungi* and the latter in the slime moulds in the kingdom *Protozoa* [18]. He concluded that all major eufungal taxa, e.g., the *Endomycota, Ascomycota,* and *Basidiomycota,* evolved from the *Entomophthorales* from a chytridiomycete ancestor by loss of cilia (flagella). Molecular phylogenetic analysis [19, 20] confirmed that the chytrids were true fungi and the true fungi, the ascomycetes, the basidiomycetes, the zygomycetes, and the chytridiomycetes, formed a monophyletic group, distinguished from slime molds and the oomycetes. On the basis of 18S rRNA sequence analysis, Hendriks et al. [21] indicated that the red algae and the higher fungi did not possess a common ancestor. Wainright et al. [22] suggested that animals and fungi share a unique evolutionary history and that their last common ancestor was a flagellated protist similar to extant choanoflagellates. According to the molecular evidence, the fungi may have originated from protozoan ancestors before the Kingdoms *Animalia* and *Plantae* split [23].

Berbee and Taylor [11] calculated that the three main fungal phyla diverged from the *Chytridiomycota* approximately 550 Myr ago, that the *Ascomycota/Basidiomycota* split occurred at about 400 Myr ago after plants invaded the land, and that many ascomycetous yeasts and moulds (e.g. *Eurotiales)* evolved after the origin of angiosperms in the last 200 Myr. These results are broadly supported by fossil evidence, the main difference being that remains of *Ascomycota* go back to the Silurian (c. 440 Myr ago) while the oldest definite *Basidiomycota* occurred at about 380 Myr ago [24].

Data of the latest molecular phylogenetic analysis, using 18S rDNA sequence divergence, shows that a monophyletic kingdom for the *Fungi* contains the *Chytridiomycetes* and the *Zygomycetes* as lower fungi, and the *Ascomycetes* and *Basidiomycetes* as higher fungi. They suggest great phylogenetic divergence among the chytrids and the entomophthoralean fungi of the lower fungi and loss of flagella within several lineages of the lower fungi. On the other hand, the molecular and morphological data set clearly indicate existence of two monophyletic Divisions, *Ascomycota* and *Basidiomycota.* The former comprises the *Archiascomycetes,* as a new concept, the

Hemiascomycetes (ascomycetous yeast), and the *Euascomycetes,* whereas the latter contains the *Ustilaginales* smut (or smut fungi), the simple septate *Basidiomycetes,* including most of the basidiomycetous yeasts, and the *Hymenomycetes.* Analyses of more taxa within these lineages and more sequence data are required to elucidate evolutionary relationships among the fungi, from the lower to higher fungi, in the light of the extensive fungal species diversity that has been revealed to date [13].

The other organisms previously regarded as "fungi" belong to Kingdom *Protista,* which for phylogenetic reasons should be divided into four separate kingdoms: *Archeozoa, Euglenozoa, Protozoa,* and *Chromista* [18].

In Kingdom *Euglenozoa* we find the *Acrasida* – a group of cellular slime moulds. Kingdom *Protozoa* contains two independent lineages of *fungus-like organisms.* One is phylum *Mycetozoa* encompassing class *Myxogastrea* (the true slime molds) and the small classes *Dictyostelea* (cellular slime moulds differ from *Acrasida)* and *Protostelea.* The other is the enigmatic phylum *Plasmodiophoromycota* which probably links with the *Ciliophora* in the alveolates. In Kingdom *Chromista* we also find two independent lineages. One leads to division *Labyrinthomorpha* comprising slime mould-like organisms. The other is the division *Pseudofungi* with the two classes *Oomycetes* and *Hyphochytridiomycetes.* Its closest relatives are probably yellow-green algae in *Xanthophyta* (25).

Out of the proposed classifications of higher categories including fungi and fungus-like organisms we cite the following [26]:

PROTOZOA
- Acrasiomycota
- Dictyosteliomycota
- Myxomycota
  - Myxomycetes
  - Protosteliomycetes
- Plasmodiophoromycota

CHROMISTA
- Hyphochytriomycota
- Labyrinthulomycota
- Oomycota

FUNGI
- Ascomycota
- Basidiomycota
  - Basidiomycetes
  - Teliomycetes
  - Ustomycetes
- Chytridiomycota
  - Zygomycota
  - Trychomycetes

Zygomycetes

The *Deuteromycota* (Mitosporic fungi) is not accepted as formal taxonomic category in this proposed classification; they are not a monophyletic unit, but are fungi which have either lost a sexual phase or which are anamorphs of other phyla (mainly *Ascomycota,* some *Basidiomycota).* Of the three kingdoms *(Chromista, Fungi, Protozoa)* only *Fungi* consist exclusively of fungi; the *Chromista* and *Protozoa* mainly comprise non-fungal phyla. Some authors unite the *Chromista* and *Protozoa* into a single highly polyphyletic Kingdom *Protoctista* (syn. *Protista),* but that conclusion is not supported by molecular, biochemical, and other evidence. Cavalier-Smith [18] and Corliss [27] both retain *Chromista* and *Protozoa* as separate kingdoms.

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