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 Eumycetidae, 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 centriodal invagination of the plasma membrane; (iv) lomosomes: 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, biotechnologically, 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
and nuclear DNA relatedness, as nucleic acids characters resolve only to the generic 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 *Chytridomyces*, *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 cellulose 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 molds in the kingdom *Protozoa* [18]. He concluded that all major eufungal taxon, e.g., the *Endomycota*, *Ascomycota*, and *Basidiomycota*, evolved from the *Entomophthorales* from a chytridmycete 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 chytridomycetes, 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 *Chytridomyocota* approximately 550 Myr ago, that the *Ascomycota/Basidiomycota* split occurred at about 400 Myr ago after plants invaded the land, and that many ascomycete 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 *Chytridomyocetes* 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
Homiascomycetes (ascomyceteous yeasts), and the Euascomycetes, whereas the latter contains the Ustilaginales smut (or smut fungi), the simple sepiate Basidiomycetes, including most of the basidiomyceteous 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: Archaea, 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 moulds) and the small classes Dictyostelea (cellular slime moulds differ from Acrasida) and Protostelea. The other is the enigmatic phylum Plasmodiophoromyctes 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 Hyphochytriomyctes. 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
Acrasiomyctes
Dictyosteliomyctes
Myxomyctes

PROTOSTEI
Myxomyctes

HYDRA

HYMENOMYCETES

CHROMISTA
Hyphochytriomyctes
Labyrinthulomyctes
Oomycetes

FUNGI
Ascomycota
Basidiomycota

Basidiomycetes
Teliomyctes
Ustomyctes
Chytridiomycota
Zygomycota
Trychomycetes

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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 Protocista (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.

REFERENCES