

---

## 14. Fungal Phylogeny and Evolution

### Parimal Mandal

Associate Professor,  
Department of Botany, Raiganj University,  
West Bengal.

### Arka Pratim Chakraborty

Assistant Professor,  
Department of Botany, Raiganj University,  
West Bengal.

#### 14.1 Introduction:

India is rich in biodiversity. One-third of fungal diversity of the globe exists in India. The early fossil record of the fungi is poor, as unlike other organisms, fungal structures do not fossilize well. Fungi have ancient origins, with evidence indicating they likely first appeared about one billion years ago, though the fossil record of fungi is scanty. Fungal hyphae evident within the tissues of the oldest plant fossils confirm that fungi are an extremely ancient group. Indeed, some of the oldest terrestrial plant like fossils known, called Prototaxites, which were common in all parts of the world throughout the Devonian Period (419.2 million to 358.9 million years ago), are interpreted as large saprotrophic fungi. Fossils of *Tortotubus protuberans*, a filamentous fungus, date to the early Silurian Period (440 million years ago) and are thought to be the oldest known fossils of a terrestrial organism.

However, in the absence of an extensive fossil record, biochemical characters have served as useful markers in mapping the probable evolutionary relationships of fungi. From the beginning of the 20<sup>th</sup> century fungi were proposed to be monophyletic, assuming that all the fungi were derived from an algal ancestor that lost its ability to photosynthesize. This gave rise to the flagellate fungi, from which rest of the fungi evolved. The loss of flagella and the evolution of zygospore gave rise to the Zygomycotina. The uninucleate zygospores of the Edogonales gave rise to the Ascomycota. The link between them being a fungus resembles with Dipodascopsis (Ascomycota). The unicellular yeasts and complex filamentous Ascomycota members having extended dikaryotic stage evolved from it, believed to be similar to modern day Taphrina.

This Taphrina-like ancestor was believed to have given rise to the ancestral Basidiomycota. Monophyletic origin of fungi was followed by most of the mycologists till 1960s. Phylogeny of fungi on the basis of chemical characters can be related by cell wall composition (i.e., presence of both chitin and alpha-1, 3 and alpha-1, 6-glucan), organization of tryptophan enzymes, and synthesis of lysine (i.e., by the aminoadipic acid pathway). Molecular phylogenetic analyses that became possible during the 1990s have greatly contributed to the understanding of fungal origins and evolution. At first, these analyses generated evolutionary trees by comparing a single gene sequence, usually the small subunit ribosomal RNA gene (SSU rRNA).

Since then, information from several protein-coding genes has helped correct discrepancies, and phylogenetic trees of fungi are currently built using a wide variety of data largely, but not entirely, molecular in nature. Kingdom Fungi is a monophyletic group, meaning that all modern fungi can be traced to a single ancestral organism. In the middle of the 20<sup>th</sup> century, the three major kingdoms of multicellular eukaryotes, kingdom Plantae, kingdom Animalia, and kingdom Fungi, were recognized as being absolutely distinct.

The crucial character difference between kingdoms is the mode of nutrition: animals (whether single-celled or multicellular) engulf food; plants photosynthesize; and fungi excrete digestive enzymes and absorb externally digested nutrients. There are other notable differences between the kingdoms. For example, whereas animal cell membranes contain cholesterol, fungal cell membranes contain Ergosterol and certain other polymers. In addition, whereas plant cell walls contain cellulose (a glucose polymer), fungal cell walls contain chitin (a glucosamine polymer). One exception to this rule is a group of fairly ubiquitous microscopic fungi (referred to as the cryptomycota), members of which average about 3 to 5  $\mu\text{m}$  (1  $\mu\text{m}$  is about 0.000039 inch) in length, have cell walls lacking chitin, and possess a flagellum. Phylogenetic analyses of ribosomal RNA in this clade suggest that it is an ancient fungal group.

Genomic surveys show that plant genomes lack gene sequences that are crucial in animal development, animal genomes lack gene sequences that are crucial in plant development, and fungal genomes have none of the sequences that are important in controlling multicellular development in animals or plants. Such fundamental genetic differences imply that animals, plants, and fungi are very different cellular organisms. Molecular analyses indicate that plants, animals, and fungi diverged from one another almost one billion years ago. The phylogenetic classification of fungi is designed to group fungi on the basis of their ancestral relationships, also known as their phylogeny.

The genes possessed by organisms in the present day have come to them through the lineage of their ancestors. As a consequence, finding relationships between those lineages is the only way of establishing the natural relationships between living organisms. Phylogenetic relationships can be inferred from a variety of data, traditionally including fossils, comparative morphology, and biochemistry, although most modern phylogenetic trees (evolutionary trees, or cladograms) depend on molecular data coupled with these traditional forms of data.

Kingdom Fungi, one of the oldest and largest groups of living organisms, is a monophyletic group, meaning that all modern fungi can be traced back to a single ancestral organism. This ancestral organism diverged from a common ancestor with the animals about 800 million to 900 million years ago.

Today many organisms, particularly among the phycmycetes and slime molds, are no longer considered to be true fungi, even though mycologists might study them. Kingdom Fungi has gained several new members on the basis of molecular phylogenetic analysis, notably *Pneumocystis*, the *Microsporidia*, and *Hyaloraphidium*. *Pneumocystis jirovecii* causes pneumonia in mammals, including humans with weakened immune systems; pneumocystis pneumonia (PCP) is the most common opportunistic infection in people with human immunodeficiency virus (HIV) and has been a major cause of death in people with AIDS. *Pneumocystis* was initially described as a trypanosome, but evidence from sequence analyses of several genes places it in the fungal subphylum Taphrinomycotina in the phylum Ascomycota.

The Microsporidia were thought to be a unique phylum of protozoa for many years; however, molecular studies have shown that these organisms are fungi. The Microsporidia are obligate intracellular parasites of animals and lack mitochondria. Most infect insects, but they are also responsible for common diseases of crustaceans and fish and have been found in most other animal groups, including humans (probably transmitted through contaminated food or water). *Hyaloraphidium curvatum* was previously classified as a colorless green alga; however, it has since been recognized as a fungus on the basis of molecular sequence data, which show it to be a member of the order Monoblepharidales in the phylum Chytridiomycota. Based on 18S rDNA sequencing, the Ascomycota and Basidiomycota form monophyletic clades within the kingdom Mycobionta or chitinous Fungi, defined by a membrane-bounded nucleus, the kingdom Mycobionta is one of several kingdoms within the crown groups of the Eukarya or eukaryotes.

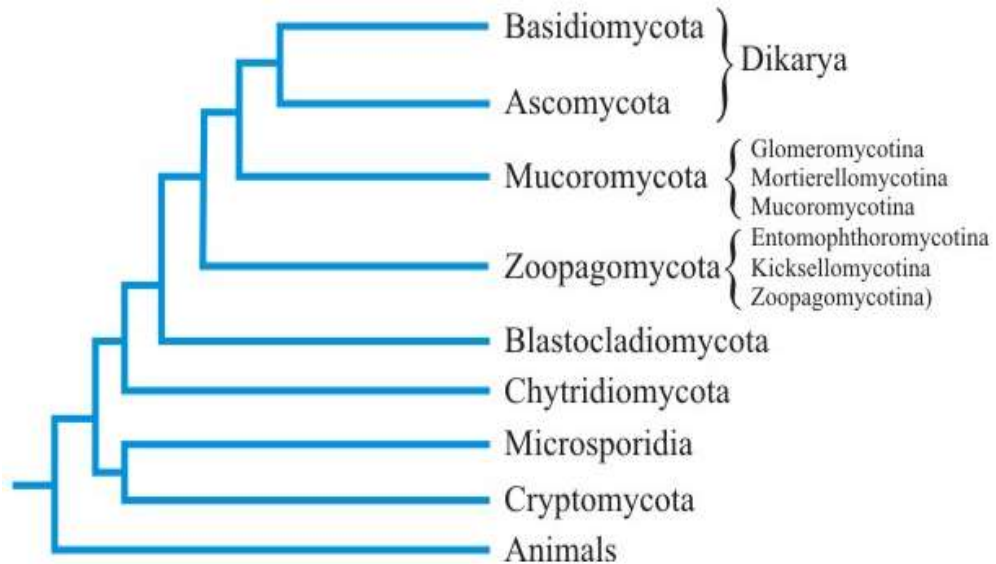
Some mycologists proposed polyphyletic origin, with red algae as origin of Ascomycota. In late 1960s Oomycota was separated from the fungi. Slime molds were also separated into a different kingdom as well. Fungi were separated into two kingdoms: All the flagellate fungi were placed in kingdom Protista (including Chytridiomycota and slime molds) and the remainder in kingdom Myceteae. Hypothesis of phylogeny of fungi has changed radically with the advent of molecular techniques, ultrastructural and biochemical studies. On the basis of these studies in the late 1980s chytridiomycetes, zygomycetes, ascomycetes and basidiomycetes were included in kingdom Fungi. Oomycota, hyphochytrids, labyrinthulids, thraustochytrids and slime molds were accommodated in pseudo fungi.

In 2007 a new classification of kingdom fungi-based on recent molecular phylogenetic analysis and morphotaxonomy was proposed, having one subkingdom – Dikarya and seven phyla. Recently in the 10th edition of Dictionary of the Fungi (2008) three kingdoms are accepted viz. Chromista, Fungi and Protozoa. True fungi belong to kingdom fungi having six phyla – Ascomycota, Basidiomycota, Chytridiomycota, Glomeromycota, Microsporidia and Zygomycota.

A global phylogeny of fungi first emerged using data from several gene regions: 18S rRNA, 28S rRNA, 5.8S rRNA, elongation factor-1 (EF1), and RNA polymerase II subunits (RPB1 and RPB2). Data for all these gene regions were combined (a total number of 6,436 aligned nucleotides) for 199 fungi (James *et al.*, 2006), and there have been several more genome level studies since this work was published, many of which were combined by McCarthy & Fitzpatrick (2017). The outcome is an enormous cladogram and highly simplified evolutionary tree (Figure 14.1).

Significantly, this extensive analysis generally supports the more traditional arrangement into Ascomycota, Basidiomycota, various zygomycetes and Chytridiomycota. Ascomycota and Basidiomycota are united as the Dikarya, fungi in which at least part of the life cycle is characterised by cells with paired nuclei.

The closest relatives of these two sister groups are the Glomeromycotina which was for a long time included as the Glomales within Zygomycota. Neither the Zygomycota nor the Chytridiomycota are monophyletic groups. They have representatives in different clades or branches of the tree that are grouped into those phyla by their shared primitive morphologies such groups are called paraphyletic.

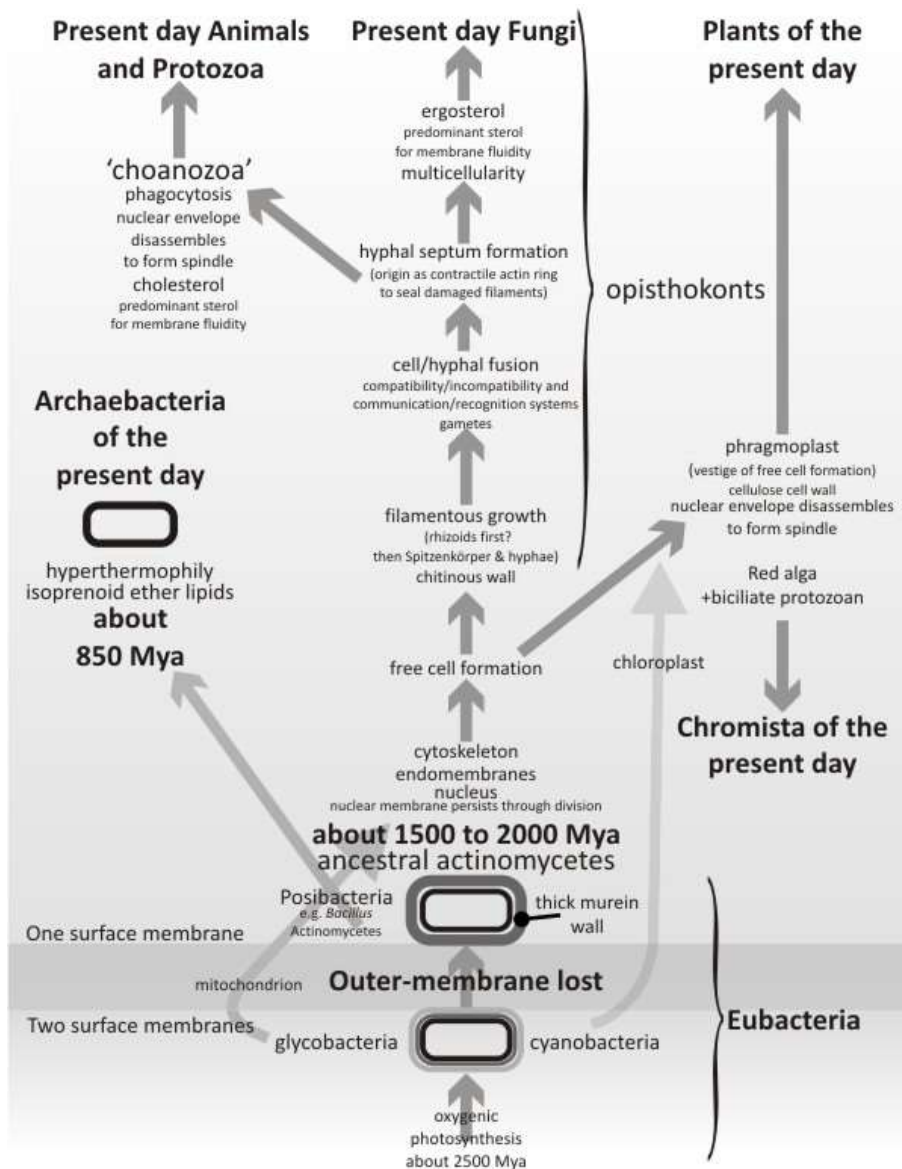


**Figure 14.1:** The main branches of the tree of life for Kingdom Fungi, as established by the AFTOL project and subsequent publications. All the traditional phyla are represented as Ascomycota, Basidiomycota, zygomycetes (as Mucoromycota, which includes Glomeromycotina, and Zoopagomycota), and Chytridiomycota. Ascomycota and Basidiomycota are united as the Dikarya, fungi in which at least part of the life cycle is characterised by cells with paired nuclei (i.e. dikaryons). The closest relatives of these two sister groups are the Glomeromycotina. The multigene phylogeny of fungi established by the AFTOL project placed the Glomeromycotina using the name Glomeromycota in a basal position as a sister group of Ascomycota and Basidiomycota, together is called Dikarya (Spatafora *et al.*, 2016).

Today's fungal kingdom is arguably the most abundant and diverse group of organisms on Earth. Fungi are found in every terrestrial ecosystem as mutualist partners, pathogens, parasites, or saprotrophs. It is estimated that the kingdom fungi contains 2.2 to 3.8 million species (Hawksworth & Lücking, 2017), but only about 3 to 8% of these have been described. If most of the unknowns are members of the traditional taxa, then current phylogenetic inferences will be unchallenged by additional discoveries. However, novel fungal groups could be awaiting discovery by DNA-based environmental sampling, which is already starting to reveal microscopic, undescribed, and unculturable fungi. Because unknowns are unknowns, we can't predict how such discoveries might affect our understanding of fungal origins and evolution.

An interesting development in the first few years of the 21st century was a trend to suggest that the first terrestrial eukaryotes might have been fungal. A few titles will illustrate this: *'Terrestrial life – fungal from the start?'* (Blackwell, 2000); *'Early cell evolution, eukaryotes, anoxia, sulfide, oxygen, fungi first (?)*, and *a Tree of Genomes revisited'* (Martin *et al.*, 2003); and *'Devonian landscape heterogeneity recorded by a giant fungus'* (Boyce *et al.*, 2007). For mycologists this was certainly a refreshing development because, prior to this, fungi have always been ignored when theorists pondered the origin and early emergence of life on this planet. The complete version of what we like to call 'The Mycologists' Tale' appeared in the book entitled *Fungal Biology in the Origin and Emergence of Life* (Moore, 2013).

This book offers a new interpretation (Figure 14.2) of the early radiation of eukaryotes based on the emergence of major innovations in cell biology that apply uniquely to present day fungi. These emphasised the increasingly detailed management of the positioning and distribution of membrane-bound compartments like vacuoles, vesicles and microvesicles by the filamentous components of the cytoskeleton (i.e. microfilaments, intermediate filaments and microtubules); culminating, as far as filamentous fungi are concerned, with emergence of the Spitzenkörper and apical hyphal extension.



**Figure 14.2:** The mycologist’s tree of life. The lower part of this diagram is based on Cavalier-Smith’s tree of life (Cavalier-Smith, 2010), which emphasises major evolutionary changes in membrane topology and chemistry, except that the most ancient bacteria are shown here to be heterotrophic descendants of LUCA (the last universal common ancestor of all current life on Earth). Eukaryotes diverge from actinobacterial ancestors about 1,500 million years ago and

the bulk of this illustration deals with eukaryote evolution. The most ancient stem eukaryotes are considered to exhibit characteristics that would today be thought of as applying to primitive fungi. Their evolution emphasises increasingly detailed management of the positioning and distribution of membrane-bound compartments like vacuoles, vesicles and microvesicles by the filamentous components of the cytoskeleton (such as microfilaments, intermediate filaments and microtubules); culminating, as far as filamentous fungi are concerned, with emergence of the Spitzenkörper and apical hyphal extension. Uniquely among present day eukaryotes, the fungi maintain their nuclear membrane intact as the nuclear division progresses.

## 14.2 References:

1. James, T.Y., Kauff, F., Schoch, C.L., Matheny, P.B., Hofstetter, V., Cox, C.J. and 65 others. (2006). Reconstructing the early evolution of Fungi using a six-gene phylogeny. *Nature*, 443: 818-822. DOI: <https://doi.org/10.1038/nature05110>.
2. McCarthy, C.G.P. & Fitzpatrick, D.A. (2017). Multiple approaches to phylogenomic reconstruction of the fungal kingdom. *Advances in Genetics*, 100: 211-266. DOI: <https://doi.org/10.1016/bs.adgen.2017.09.006>.
3. Spatafora, J.W., Chang, Y., Benny, G.L., Lazarus, K., Smith, M.E., Berbee, M.L., Bonito, G., Corradi, N., Grigoriev, I., Gryganskyi, A., James, T.Y. O'Donnell, K., Roberson, R.W., Taylor, T.N., Uehling, J., Vilgalys, R., White, M.M. & Stajich, J.E. (2016). A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. *Mycologia*, 108: 1028-1046. DOI: <https://doi.org/10.3852/16-042>.
4. Hawksworth, D.L. & Lücking, R. (2017). Fungal diversity revisited: 2.2 to 3.8 million species. In: *The Fungal Kingdom*, (Eds J. Heitman, B. Howlett, P. Crous, E. Stukenbrock, T. James & N. Gow), pp. 79-95. Washington, DC: ASM Press. DOI: <https://doi.org/10.1128/microbiolspec.FUNK-0052-2016>. VIEW on Amazon.
5. Blackwell, M. (2000). Terrestrial life - fungal from the start? *Science*, 289: 1884-1885. DOI: <https://doi.org/10.1126/science.289.5486.1884>.
6. Martin, W. Rotte, C., Hoffmeister, M., Theissen, U., Gelius-Dietrich, G., Ahr, S. & Henze, K. (2003). Early cell evolution, eukaryotes, anoxia, sulfide, oxygen, fungi first (?), and a Tree of Genomes revisited. *International Union of Biochemistry and Molecular Biology: Life*, 55: 193-204. DOI: <https://doi.org/10.1080/1521654031000141231>.
7. Boyce, C.K., Hotton, C.L., Fogel, M.L., Cody, G.D., Hazen, R.M., Knoll, A.H. & Hueber, F.M. (2007). Devonian landscape heterogeneity recorded by a giant fungus. *Geology*, 35: 399-402. DOI: <https://doi.org/10.1130/G23384A.1>.
8. Moore, D. (2013). *Fungal Biology in the Origin and Emergence of Life*. Cambridge, UK: Cambridge University Press. 230 pp. ISBN-10: 1107652774, ISBN-13: 978-1107652774. VIEW on Amazon.
9. Cavalier-Smith, T. (2010a). Deep phylogeny, ancestral groups and the four ages of life. *Philosophical Transactions of the Royal Society of London, series B*, 365: 111-132. DOI: <https://doi.org/10.1098/rstb.2009.0161>.