

connections mark early basidiomycetes (4); basidia (smut-like, 5), asexual spores (6) and asci (7) probably evolved early in the major radiations of basidiomycetes and ascomycetes; filamentous ascomycetes diverged from the yeast lineage about 310 Mya, and fruiting bodies (8) presumably evolved before the Permian divergences because they are present in all the lineages today; mushroom fungi (9), with their characteristic holobasidium (10) probably radiated 130-200 Mya, soon after flowering plants became an important part of the flora.

It is interesting to note that coals deposited in the Cretaceous and Tertiary periods show much more evidence of fungal decay than the much older Carboniferous coals, reflecting the radiation of aggressive wood decay basidiomycetes from the Triassic onwards. Also note the relatively recent radiation of (anaerobic) chytrids as grasses and grazing mammals became more abundant.

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 (illustrated here in Fig. 2.12, below) 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:

- increasingly detailed management of the positioning and distribution of membrane-bound compartments (vacuoles, vesicles and microvesicles) by the filamentous components of the cytoskeleton (microfilaments, intermediate filaments and microtubules);
- culminating, as far as filamentous fungi are concerned, with emergence of the Spitzenkörper and apical hyphal extension.

These features of present day fungi are described in detail elsewhere in this book (Chapter 5, [Sections 5.10](#) and [5.11](#)) and we will reference where we describe other features as we mention them.

The interpretation suggests that the Last Universal Common Ancessor of all current life on Earth (usually known by the acronym **LUCA**) was a heterotrophic, mesophilic prokaryote, essentially a ‘bacterial’ cell with the cell enveloped by two distinct lipid bilayer membranes.

The earliest prokaryotes used prebiotically synthesised organic carbon compounds as nutrients but, as these supplies diminished, they were outstripped by the anoxygenically photosynthetic Chlorobacteria as the most primitive surviving prokaryotic phylum.

This interpretation follows the deep phylogeny of the tree of life published by Cavalier-Smith (2006, 2010a & b), who argued that thermophiles evolved late, making Archaeobacteria the youngest bacterial phylum and the *sisters, rather than ancestors* of eukaryotes (in contrast to the interpretations described in Section 2.4 above), which themselves diverged from actinobacterial ancestors.

Eukaryotes are generally thought to have appeared about 1.5 billion years ago, so, for a total of about 2 billion years the only living organisms on the planet were prokaryotes together, presumably, with their associated viruses (the full text PDF of our article entitled *‘A fungal root for the eukaryote tree’* is **attached as an appendix to this PDF**).

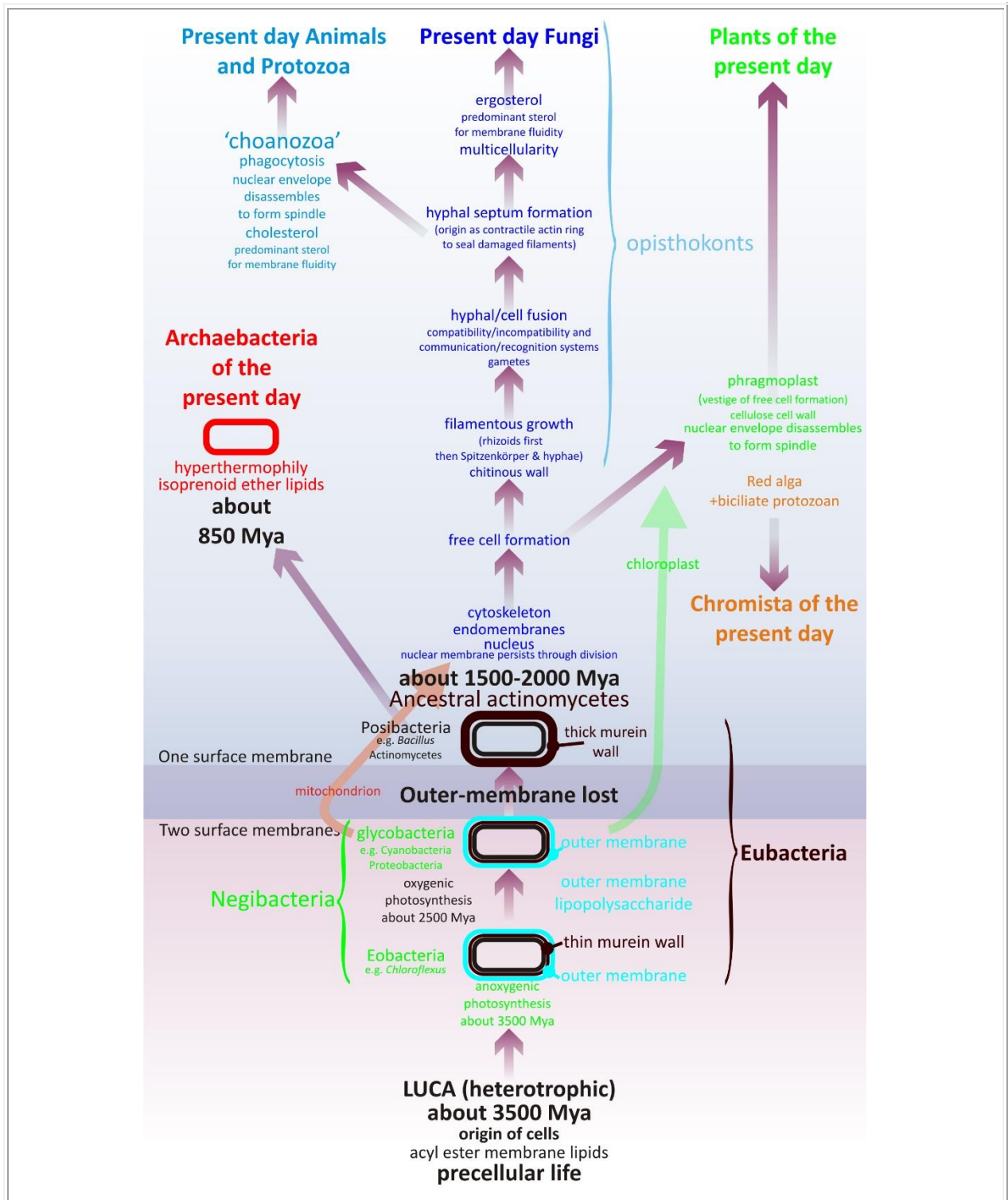


Fig. 2.12. The mycologist's tree of life. The lower part of this diagram is based on Cavalier-Smith's tree of life (Cavalier-Smith, 2010a; his Fig. 6), which emphasises major evolutionary changes in membrane topology and chemistry, except that the most ancient bacteria are shown here to be heterotrophic descendants of LUCA (the last universal common ancestor of all current life on Earth). Eukaryotes diverge from actinobacterial ancestors about 1,500 Mya (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 (vacuoles, vesicles and microvesicles) by the filamentous components of the cytoskeleton (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. The subsequent evolution of Kingdom Fungi has been outlined in Fig. 2.11, above.

The primitive eukaryotic stem featured primitive nuclear structures (including the nuclear membrane remaining intact as the nuclear division progresses, which is *a unique characteristic of present day fungi*) (Chapter 5, [Section 5.7](#)), added the mitochondrion by enslavement of a bacterium (Chapter 5, [Section 5.10](#)); and evolved those aspects of the endomembrane system and cytoskeletal architecture that are also unique characteristics of present day fungi, in the following probable temporal sequence:

- **Free cell formation**, ([Chapter 3](#)) by managing positioning of wall- and membrane-forming vesicles to enclose volumes of cytoplasm to subdivide sporangia into spores, with adoption of a chitinous cell wall, possibly as an adaptation of muramopeptide oligosaccharide synthesis from the wall of an actinobacterial ancestor. This is a possible branch point to plants if the phragmoplast is assumed to be a vestige of free cell formation and the cell wall was adapted to be a polymer of glucose rather than N-acetylglucosamine, possibly for economy in usage of reduced nitrogen in organisms abandoning heterotrophy. Plants also evolved a means to disassemble the nuclear envelope to form the division spindle.
- **Filamentous growth**, ([Chapter 4](#)) first to make rhizoids then apically-extending with the Spitzenkörper as the organising centre for hyphal extension and morphogenesis to make nucleated hyphae to explore and exploit the then extant biofilm and terrestrial debris that had accumulated during 2 billion years of prokaryote growth, life and death.
- **Hyphal/cell fusion**, ([Chapters 4 and 5](#), especially [Section 5.16](#)) with associated cytoplasmic (vegetative) and nuclear (sexual) compatibility/incompatibility systems, hypha to hypha communication/recognition systems, autotropism, gravitropism, and intrahyphal communication using secondary metabolites, including the evolution of gametes.
- **Hyphal septum formation**, (Chapter 4, [Section 4.12](#); and Chapter 5, [Section 5.17](#)) initially dependent on a contractile ring of actin to seal the membrane of damaged filaments rapidly, later developing ingressive wall synthesis to strengthen the seal, and ultimately cross-wall formation at regular intervals to *initiate multicellular development*. Possibly combined with the (accidental?) fixation on ergosterol as the quantitatively predominant sterol involved with controlling membrane fluidity in fungi.

This last is a possible branch point from chytrid level fungi to animals (of the sort presently called choanozoa). The animal stem gradually lost its wall and adapted cytoskeletal organisation/vesicle trafficking, originally used in wall synthesis, to the new function of phagocytosis. Animals also developed disassembly of the nuclear envelope as the division spindle forms; and adopted cholesterol as the predominant sterol for membrane fluidity, as well as equatorially contractile cell division.

Through this sequence of events filamentous fungi emerged 1.5 billion years ago as the *first* crown group of eukaryotes. They emerged to exploit the components of the biofilms in which they lived, and the debris left by 2 billion years of prokaryote growth, and they've been cleaning up the planet ever since (Moore, 2013).

Finally, to illustrate the ancient importance of fungi, and maybe suggest something that accounts for their success through the rest of geological time we offer a few quotations, which relate to

the Permian-Triassic (P-Tr) extinction event that occurred approximately 251 million years ago. The evolution of life on Earth has been interrupted by several mass extinction events. The P-Tr event, informally known as the Great Dying, was the Earth's most severe extinction event (so far!), with about 96% of all marine species and 70% of terrestrial vertebrates becoming extinct. This catastrophic ecological crisis was triggered by the effects of severe changes in atmospheric chemistry arising from the largest volcanic eruption in the past 500 million years of Earth's geological history, which formed what are now known as the Siberian Traps flood basalts. When first formed these are thought to have covered an area in Siberia about the size of the present continent of Australia.

Plants suffered massive extinctions as well as animals:

'...excessive dieback of arboreous vegetation, effecting destabilisation and subsequent collapse of terrestrial ecosystems with concomitant loss of standing biomass...' occurred 'throughout the world'.

However, the result of all this death and destruction is that

'...sedimentary organic matter preserved in latest Permian deposits is characterised by unparalleled abundances of fungal remains, irrespective of depositional environment (marine, lacustrine [= lake sediments], fluvialite [=river/stream deposits]), floral provinciality, and climatic zonation.' Both quotations were taken from Visscher *et al.* (1996).

The Cretaceous-Tertiary (K-T) extinction of 65 million years ago is another one that we all know a little bit about, because it was caused by an asteroid collision that caused the Chicxulub crater in Mexico and is blamed for the extinction of the dinosaurs. The K-T boundary is characterised by high concentration of the element iridium, which is rare on Earth but common in space debris, such as asteroids and meteors. Current understanding is that a meteor hit the Earth at the end of the Cretaceous and the iridium-rich layer was resulted as the world-wide dust cloud produced by the impact settled to the ground. As the Cretaceous is the last geological period in which dinosaur fossils are found, the belief is that the meteor collision at Chicxulub caused the extinction of the dinosaurs. There was also widespread deforestation right at the end of the Cretaceous, which is assumed to be due to post-impact conditions of high humidity (caused by widespread rain), decreased sunlight and cooler global temperatures resulting from increased atmospheric sulfur aerosols and dust.

However, coincident with all this death and destruction of animal and plant life at the K-T boundary there is a massive *proliferation* of fungal fossils. Vajda & McLoughlin (2004) put it like this:

'...This fungi-rich interval implies wholesale dieback of photosynthetic vegetation at the K-T boundary in this region. The fungal peak is interpreted to represent a dramatic increase in the available substrates for [saprotrophic] organisms (which are not dependent on photosynthesis) provided by global forest dieback after the Chicxulub impact.'

So, it is the same story as at the P-Tr extinction boundary: while the rest of the world was dying, the fungi were having a party!

But that might not be the full significance of this anecdote, because Casadevall (2005) suggests that the massive increase in the number of fungal spores in the atmosphere of the time caused fungal diseases that

'...could have contributed to the demise of dinosaurs and the flourishing of mammalian species...'

The impact of fungi on our own origins is as great as their impact on the world habitat.