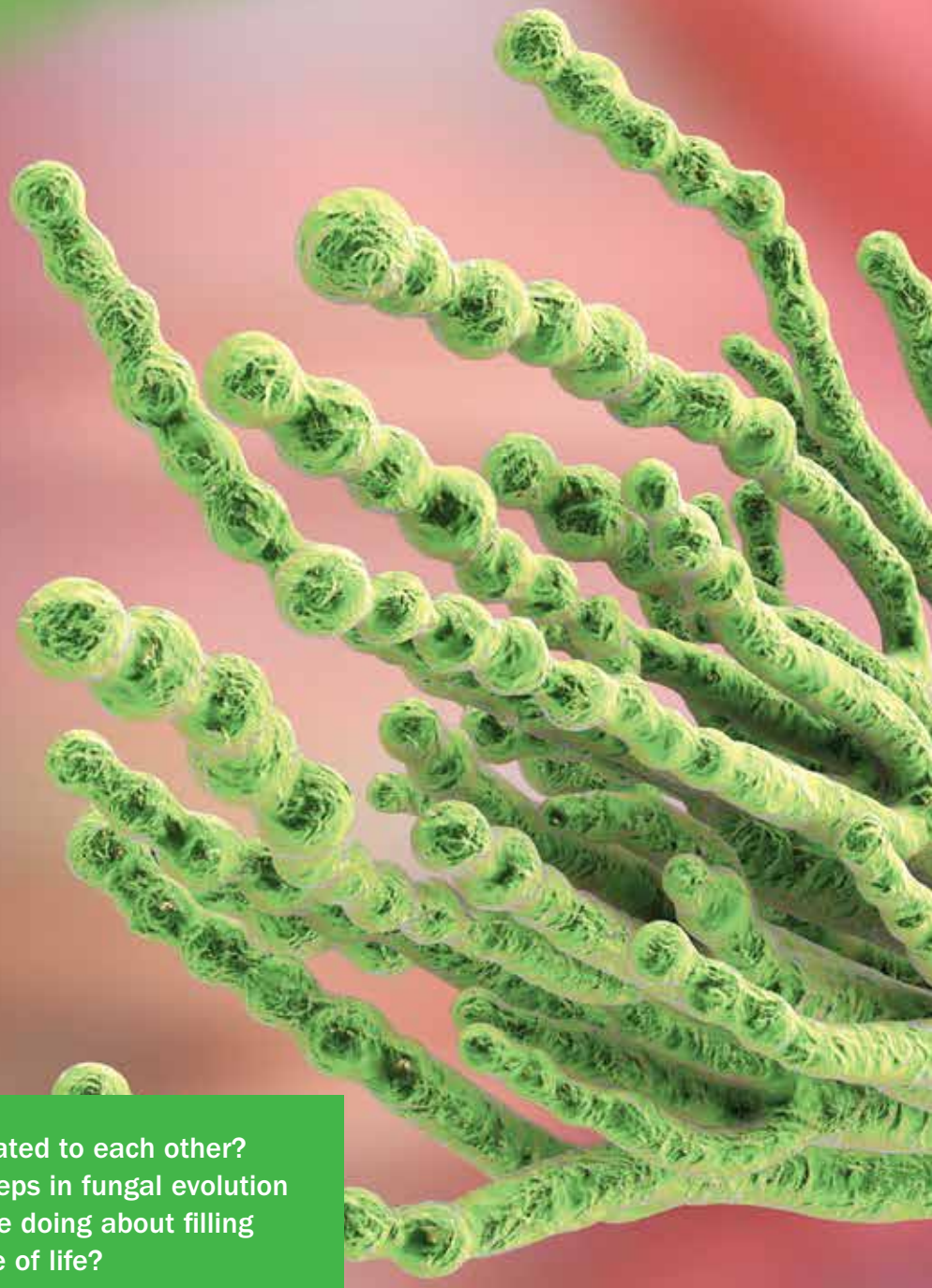
FUNGAL TREE OF LIFE



How are different species of fungi related to each other? What do we know about the major steps in fungal evolution and when they occurred? What are we doing about filling the knowledge gaps in the fungal tree of life?

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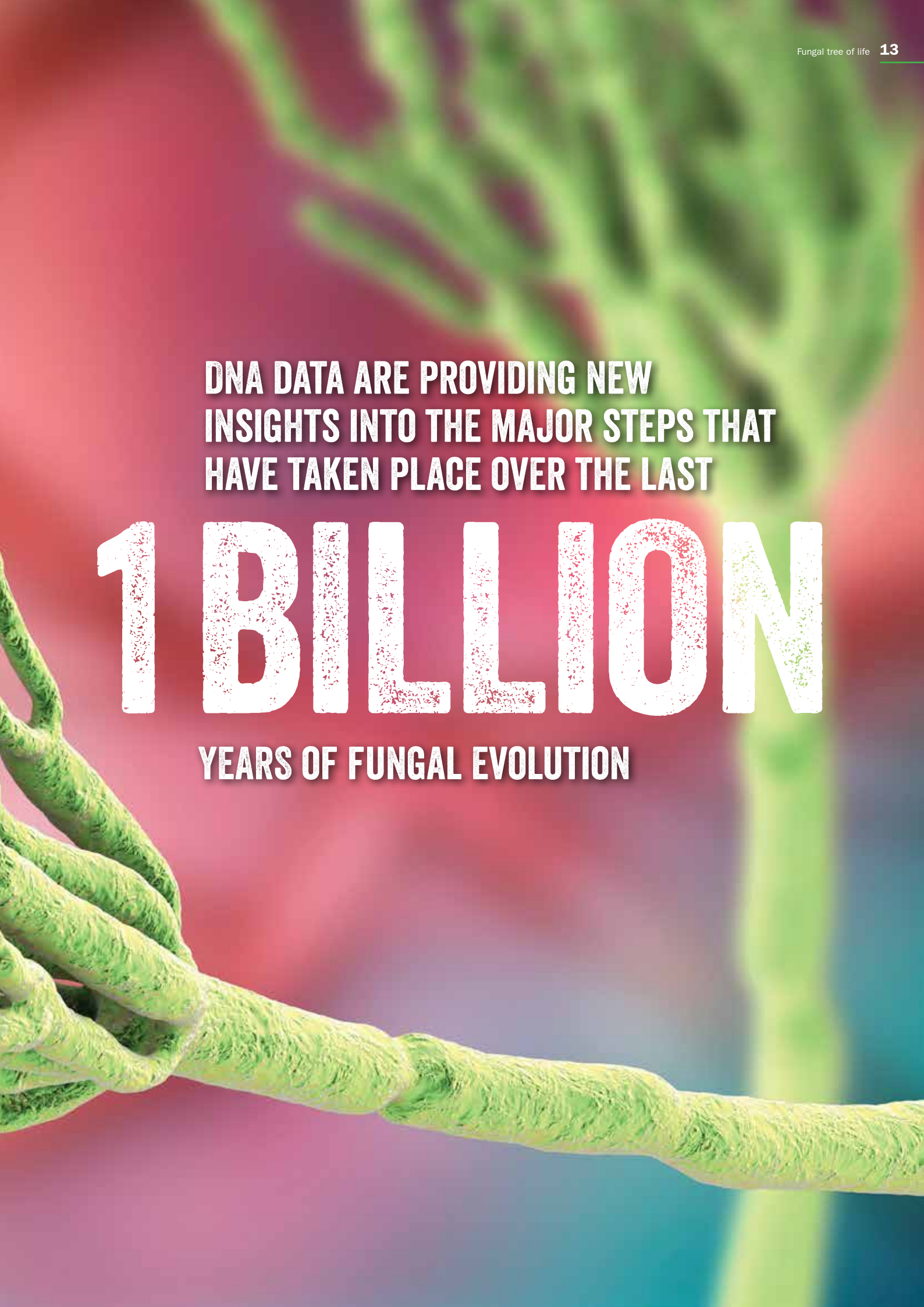

DNA DATA ARE PROVIDING NEW INSIGHTS INTO THE MAJOR STEPS THAT HAVE TAKEN PLACE OVER THE LAST
1 BILLION
YEARS OF FUNGAL EVOLUTION

HOW ARE DIFFERENT SPECIES RELATED TO EACH OTHER? THIS SIMPLE YET CRITICALLY IMPORTANT QUESTION, WHICH IS ROUTINELY ASKED ABOUT SPECIES IN ALL KINGDOMS OF LIFE, IS ONE OF THE MOST DIFFICULT TO ANSWER FOR FUNGI.

This is because building the fungal tree of life has several significant challenges. First, similarities in the physical features of fungi, such as the shape of the spore-bearing structures (e.g. mushrooms), can be misleading – species that occupy similar habitats or adopt a similar life strategy can evolve to look superficially similar even though they are not (see Box 1). Second, many fungi live unseen underground or within the cells of plants, animals or other fungi for most, or all, of their lives, often without visible reproductive structures or mycelium. It is therefore often hard, if not impossible, to find distinctive physical features to use. In this chapter, we address this question by examining the increasing evidence emerging from the rapid advances being made in DNA sequencing technologies (see also Chapter 6).

UNCOVERING THE MAJOR STEPS IN THE EVOLUTION OF FUNGI

Identifying similarities and differences in DNA sequences between fungi is helping us to understand how the branches of the fungal tree of life fit together – i.e. the evolutionary relationships between species and how they are grouped together into higher levels of classification (e.g. orders, classes and phyla)[1–5]. This has given rise to many new classifications, including a recent recognition of eight fungal phyla[5], which we follow in this volume. In addition, these data are providing new insights into the major steps that have taken place over the last 1 billion years of fungal evolution[5–7] (see Figure 1).

1. The earliest fungi. The earliest fungi are thought to have evolved around 1 billion years ago and to have been simple, single-celled organisms living in water and reproducing using motile asexual spores (zoospores) propelled by a posterior whip-like structure called the flagellum[8,9]. Indeed, these earliest fungi may well have been similar to the modern-day fungi that have been placed in the early-diverging branches of the fungal tree of life (i.e. the phyla Cryptomycota, Chytridiomycota and Blastocladiomycota; see Figure 1) because they also produce motile spores and predominantly adopt an aquatic life (see Box 2). However, while the phylum Microsporidia is also placed among these early diverging branches[5], all known species lack motile spores.

Despite their simplicity, these phyla include species capable of causing diseases not only in humans but also in many other organisms. For example, at least 15 species of Microsporidia cause a diverse set of symptoms in humans collectively known as microsporidiosis, resulting in reduced longevity, weight loss and a general reduction in health and well-being. Another microsporidian, *Nosema ceranae,* is a globally widespread parasite of honey bees that not only shortens the life of individuals but may well be a key player in the devastating Colony Collapse Disorder of beehives around the world[10]. Perhaps even more devastating is a fungus belonging to the phylum Chytridiomycota, *Batrachochytrium dendrobatidis*, which is responsible for the death of many amphibians. Indeed, it is estimated that over 30% of amphibian species across the globe may suffer extinction or severe decline, with no known treatment in sight[11,12].

BOX 1: APPEARANCES CAN BE DECEPTIVE

When studying evolution, scientists distinguish between convergent evolution (where distantly related species look similar) and divergent evolution (where closely related species look different). Spore-bearing structures of fungi come in many different shapes and forms and confusion can arise when convergent evolution results in similar shapes and forms in distantly related fungi. When that happens, the appearance of the spore-bearing structure can be misleading for taxonomists aiming to predict the relationships between fungi. For example, the black truffle or Périgord truffle (*Tuber melanosporum*), one of the most expensive edible mushrooms in the world and from the phylum Ascomycota, has a spore-bearing structure that resembles the false truffle (*Melanogaster tuberiformis*), which belongs to the phylum Basidiomycota. However, these two species are separated by over 600 million years of evolution.

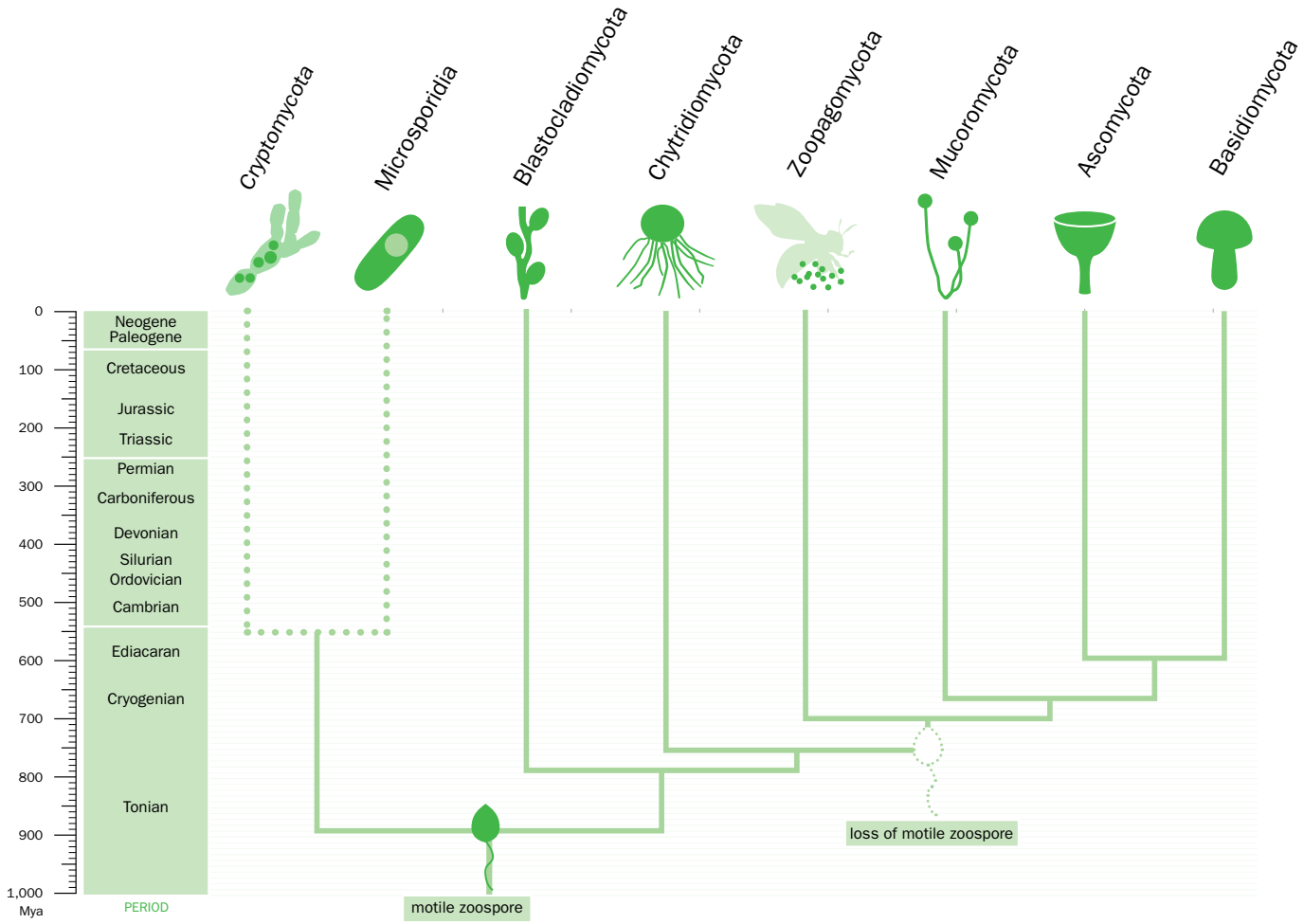
In contrast, divergent evolution occurs when the appearance of the spore-bearing structure evolves so rapidly between closely related groups, that they no longer look similar. This gives the erroneous impression that such species are distantly related. For example, three distinctive types of mushroom can be found in relatively closely related species belonging to the family Agaricaceae (Basidiomycota). These are: i) the agaricoid or parasol-shaped mushrooms; ii) the gasteroid or puffball-shaped mushrooms; and iii) mushrooms shaped like a bird's nest (e.g. fluted bird's nest, *Cyathus striatus*).

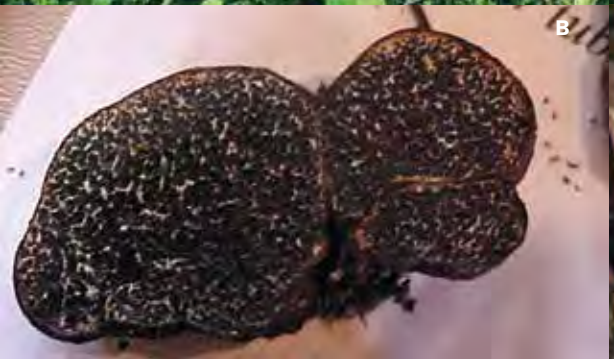
Convergent evolution: the black truffle (*Tuber melanosporum*; Ascomycota) **(A)** and false truffle (*Melanogaster tuberiformis*; Basidiomycota) **(B)** have a similar appearance despite belonging to different phyla.

Divergent evolution: three different spore-bearing structures in Agaricaceae (Basidiomycota). Field mushroom (*Agaricus campestris*) **(C)**, giant puffball (*Calvatia gigantea*) **(D)** and fluted bird's nest (*Cyathus striatus*) **(E)**.

FIGURE 1: THE FUNGAL TREE OF LIFE

The figure shows the order in which the major fungal phyla are considered to have appeared over evolutionary time[5]. The divergence times of the branches are approximations based on fossil and molecular data, as there is considerable uncertainty over the precise timings of these events[6,7].





2. The evolution of land-dwelling fungi. The evolutionary transition from predominantly aquatic to land-dwelling fungi is estimated to have taken place around 700 million years ago (Mya)[7]. The first two groups of fungi to evolve that lacked motile spores were the Zoopagomycota and Mucoromycota. Both of these are characterised by the production of a unique thick-walled spore called the zygospore[13].

The fungi belonging to the phylum Zoopagomycota are almost exclusively pathogens, parasites or living on or within animals and other fungi[14]. In contrast, Mucoromycota almost exclusively obtain their nutrition by plant associations and include those species that live inside plant cells (i.e. endophytes; see Chapter 5)[15–17], those that decompose common foods[18], such as the all-too-familiar black bread mould (*Rhizopus stolonifer*) that also attacks a broad array of fruits and vegetables, and those that form underground root associations (mycorrhizas; see Chapter 5)[19,20]. Indeed, the discovery of c. 400-million-year-old fossils that have mycorrhizal-like structures similar to Mucoromycota species living today, has led to the suggestion that fungi may well have been essential for enabling the successful transition of plants onto land[6,7,19,21] (see Box 3 and also Chapter 1).

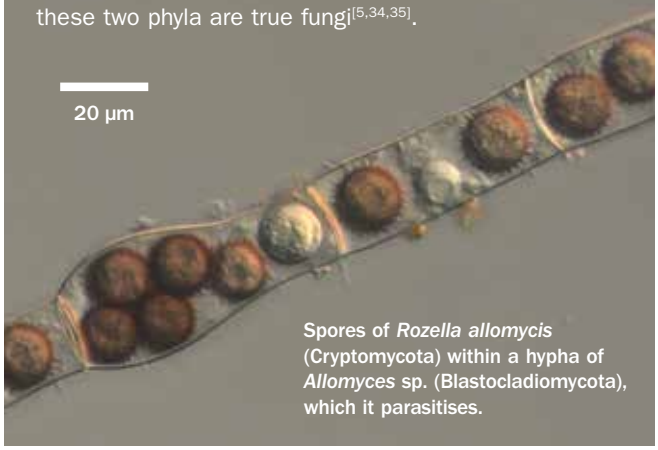
3. Evolution of complexity in body structure. The evolution of the two fungal groups that contain species capable of forming highly complex spore-bearing structures (i.e. Ascomycota and Basidiomycota) is considered to have occurred around 600–700 Mya. Together they contain the vast majority of known fungal species diversity – c. 90,000 species in Ascomycota and c. 50,000 species in Basidiomycota. They contain not only most of the more familiar groups of fungi with visible spore-bearing structures, but also the single-celled yeasts and other microscopic fungi (see Chapter 1).

The phylum Ascomycota includes species that were among the first to be domesticated by humans. For example, there is evidence to suggest that yeasts were being used to produce the alcoholic drink mead as far back as 9,000 years ago[22]. Most medicines of fungal origin are also found in this group (see Chapter 4), as are some of the most expensive foods on Earth, the white truffle (*Tuber magnatum*) and the black truffle (*Tuber melanosporum*)[23]. Yet there is another side to this phylum since it also contains some of the most economically damaging pathogens; these can bring devastation to farms and threaten food security (e.g. *Fusarium* wilt diseases[24]) or transform entire ecosystems (e.g. *Hymenoscyphus fraxineus,* which is the fungus responsible for ash dieback[25], a destructive disease of ash trees (*Fraxinus* spp.) in Europe; see Chapter 8).

The phylum Basidiomycota also includes a diverse array of species that have a major impact on humanity. Among them are some of the major players that perform a vital role in decomposing and recycling wood and leaf litter[26], unlocking and releasing the stored carbon and other nutrients back into the environment. Basidiomycota, like Ascomycota, includes species that are devastating plant pathogens, such as those belonging to the rusts and allies (Pucciniomycotina) and smuts (Ustilaginomycotina). Basidiomycota also includes the iconic mushroom-forming fungi (Agaricomycotina) that are consumed in large quantities by humans, such as the familiar button mushroom (*Agaricus bisporus*) as well as the shiitake mushroom (*Lentinula edodes*) and chanterelle (*Cantharellus cibarius*).

BOX 2: FUNGI OR NOT FUNGI?

One of the characters that is widely used to define a fungus is the presence of chitin (a carbohydrate) in the cell walls (see Chapter 1). Thus, the absence of chitin in most stages of the life cycle in members of Cryptomycota and Microsporidia led to a debate as to whether these species were actually fungi. Nevertheless, genomic data have now revealed that Cryptomycota and Microsporidia contain the genes needed for making chitin, while anatomical analyses show that chitin can be detected in their resting spores. It is now, therefore, generally accepted that these two phyla are true fungi[5,34,35].



Spores of *Rozella allomycis* (Cryptomycota) within a hypha of *Allomyces* sp. (Blastocladiomycota), which it parasitises.

CHALLENGES AND OPPORTUNITIES IN COMPLETING THE FUNGAL TREE OF LIFE

Although there is now a reasonably good understanding of the evolutionary relationships between the fungal phyla (even if the naming of the different lineages is still much debated – see Chapter 1: Box 4), relationships at the family, genus and species levels are still largely unresolved. In addition, while the technology for generating molecular data continues to advance[27–29], there are still many issues arising from the ever-increasing rate at which fungal species are being discovered from environmental sequencing (see Box 4). These approaches are revealing a whole new 'invisible dimension of fungal diversity' in our soils, bodies and waterways[30].

The challenge for the future will be not only to continue to enhance the understanding of evolutionary relationships based on currently described species but also to see how the full diversity of fungal species, including the so-called dark taxa (see Box 4), fits onto the branches of the fungal tree of life. With advances in DNA sequencing technologies, opportunities to exploit the vast archives in fungaria around the world[31], and projects focused specifically on building the fungal tree of life (e.g. the *Plant and Fungal Trees of Life*[32] and the *1000 Fungal Genomes* project[33]), our understanding of the tree of life for all fungi is likely to improve significantly and rapidly in the near future. This will provide us with exciting and unparalleled opportunities to predict the fungal properties that will enable them to be best utilised, exploited and conserved.

Retesporangicus lyonii (Holotype), a 407-million-year-old fossil from the Rhynie chert rocks with affinities to Blastocladiomycota. Image showing thallus with hyphae and swellings. This fossil is the earliest known to develop hyphae that probably served as a saprotrophic adaptation[40].

BOX 3: DATING THE FUNGAL TREE OF LIFE AND THE DEARTH OF FUNGAL FOSSILS

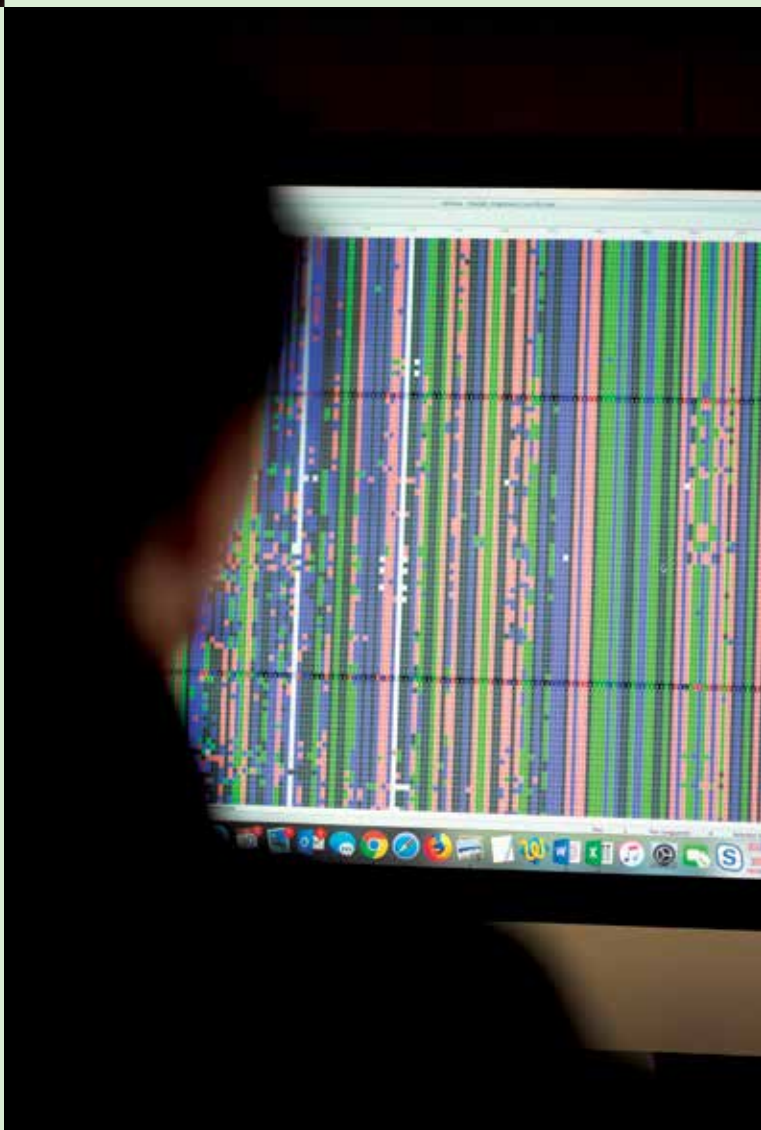
Estimating when fungal lineages diverged on the fungal tree of life is not an easy task. The estimates require the conversion of the rate at which molecular changes take place in the DNA sequence (=mutation rate) into measures of geological time (called molecular clocks). However, since the mutation rate can vary considerably between fungal lineages, fungal fossils are also critical to the analysis, as the age of the rock in which the fossil is found provides an estimate of the minimum age of the fungus within[36].

Unfortunately, the fungal fossil record is not as extensive as for plants and animals and this has led to far greater uncertainty in establishing when the major events of fungal evolution took place. Nevertheless, new fungal fossil discoveries are continually being made[6,21,37,38]. For example, several exquisitely preserved fossils from the c. 400-million-year-old Rhynie chert rocks in Scotland appear to show fungi associated with some of the earliest known land plants[39]. Such discoveries, combined with molecular clock analyses[7,26], suggest that some of the fungal lineages we find today were already present with the earliest land plants; indeed they may well have played an essential role in the early colonisation of land.

BOX 4: THE DARK TAXA – IMPLICATIONS OF ENVIRONMENTAL SEQUENCING FOR THE FUNGAL TREE OF LIFE

In recent years, there has been a huge increase in the amount of data generated from sequencing DNA present in environmental samples (e.g. soil, water, air or tissues of other organisms) rather than individual fungi. This approach is revealing a hitherto unsuspected level of fungal diversity, with the identification of potentially thousands to hundreds of thousands of new species[30,41–43] (see also Chapters 1 and 3). For example, a study of dust samples across the USA recovered nearly 40,000 distinct molecular signatures, of which around 40% could not be correlated with known species in gene bank databases[43,44]. These 'dark taxa' are only known from their DNA sequence and as yet have no known physical specimen for reference.

While these new data are enhancing our understanding of fungal diversity, they are also opening up new challenges – how do we place hundreds or thousands of fungal sequences into the fungal tree of life? While the analytical methods that can cope with these data are still being developed, it is already clear that many of the newly identified fungi are so distinctive that they are being assigned to entirely new orders and classes across the fungal tree of life[42,43,45]. For example, a recent analysis of soil samples from a broad geographical range detected over 40 previously unrecognised major lineages and even a new phylum[42,46]. These new discoveries will not only substantially impact estimates of the total number of fungal species on Earth (see Chapter 1) but will also considerably modify the current fungal tree of life[30,43,47,48].



Contributors and references

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2. Fungal tree of life

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[For fungal tree of life]

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J. Eden, a fungus from the family Psathyrellaceae decomposing bark chippings near the Sackler crossing at Kew, cover; A. Pouliot, *Omphalotus nidiformis*, inside cover (front); Kurinui, bush fungi, Coromandel Forest Park, New Zealand, inside cover (back); B. Spragg, *Favolaschia calocera*, 3; P. F. Cannon, *Caloplaca cerina*, 4–5, and 8 except R. Lücking, *Sticta humboldtii* and *Letrouitia domingensis*; P. F. Cannon, 9, 11 (Boxes 2 & 3); G. Griffith, 11 (Box 4); Katerynakon, *Penicillium* sp., 12–13; E. Regina, 15 (A); D. B. Wheeler, 15 (B); Byrain@mushroomobserver, 15 (C); H. Krisp, 15 (D); Björn S, 15 (E); T. James, 16; C. Strullu-Derrien, 17 (Box 3); J. Eden, 17 (Box 4); M. Sandoval-Denis, *Umbelopsis wiegerinckiae*, 18–19; R. Lücking, 20 (top left); Y. Liang and C. Tian, 20 (top right); A. Spielman, 20 (2nd row, left); L. Quijada, 20 (2nd row, right); S.-H. He, 20 (bottom left); P. B. Matheny, P. Crous, P. Crous, P. Crous, 20 (bottom right – clockwise from top left image); P. Sandoval-Leiva, 22; A. Pouliot, *Agaricus*, 24–25; C. Mueller, 29 (A); N. Schorr, 29 (B); L. Hercigonja, 29 (C); Picture Partners, 29 (D); AmyLv, 29 (E); R. Thongdumhyu, 30 (main); RBG Kew, 30 (Box 1); L. M. Suz, *Xerocomellus pruinatus*, 32–33; A. Alvarez-Lafuente, 37 (A); A. J. Elliott, 37 (B); J. Kowal, 37 (C); E. Schofield, 37 (D); R. Gargiulo, *Cypripedium calceolus*, 39 (Box 2); J. Duckett, restored heathland after fire, 39 (Box 3); K. Findlay, *Puccinia striiformis* var. *tritici*, 40–41; R. Thongdumhyu, yeast under a microscope, 43 (main); C. S. Hoffman, V. Wood, & P. A. Fantes (2015), *Genetics* 201: 403–423, 43 (Box 1); J. Seaman 46–47 (main); G. Strobel, 47 (Box 3); Tkavc et al. (2018). *Frontiers in Microbiology* 8: 2528, 47 (Box 4); T.-H. Li (李泰辉), *Phallus indusiatus*, 48–49; Y. Li, 50; Y. Li (李玉) & X. Li (李晓), 51; X.-L. He (何晓岚), 52; S.-P. Wan (万山平), 54 (Box 1); T.-H. Li (李泰辉), 54 (bottom); L. Fan (范黎), 55 (Box 2); F. Wu (吴芳), 55 (bottom left); Q. Zhao (赵琪), 55 (bottom right); J. Eden, *Gymnosporangium sabinae*, 56–57; Robert L. Anderson, USDA Forest Service, Bugwood.org, 58 (Box 1); Joseph OBrien, USDA Forest Service, Bugwood.org, 58 (Box 2); US Forest Service, 59 (Box 3); A. Pouliot, *Rhizocarpon geographicum*, 62–63; L. Elcova, 65; C. Andrew, 67 (Box 1); K. D. Fetzer, 67 (Box 2); C. Ellis, 67 (Box 3); E. Gaya, *Xanthoria elegans*, 69; A. M. Ainsworth, *Hericium erinaceus*, 70–71; P. F. Cannon, 73 (Box 1); A. M. Ainsworth, 75 (Box 2); N. Siegel, 75 (Box 3); G. Katinas, 76–77 (main); G. Furci, 77 (Box 5).