State of the World’s Fungi 2018

1. Definition and diversity

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What are fungi and why are they important? How many species, families and phyla are currently known to science and why is it so difficult to work these numbers out?

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In contrast, they can also cause devastating plant and animal diseases resulting from fungal pathogens such as mildews, rusts and chytrids.

Fungi were once regarded as merely simple or lower plants and were assigned fewer than fifty of the 1,200 pages in Linnaeus’ *Species Plantarum*. As time has moved on and more has been learned about fungi and their relationships to other forms of life, they are now rightly placed in their own kingdom (e.g. a leaf, a cheese, a lung). Thus, piecing together a fungal life cycle is complex and involves much detective work.

**WHAT ARE FUNGI?**

Fungi are distinctive organisms that digest their food externally by secreting enzymes into the environment and absorbing the dissolved organic matter back into their cells. Most have cell walls composed primarily of chitin (a substance that is also found in the animal kingdom, for example in the exoskeletons of insects and shells of crabs and lobsters). They also store food reserves as glycogen and lipids (not starch as in plants). Thus, despite the superficial resemblance of some fungi to plants (e.g. having rooted, stalked structures), their non-photosynthetic, absorptive method of feeding and their different cell walls, cell membrane chemistry, methods of food storage and DNA indicate that they form an independent kingdom (e.g. *S. cerevisiae*).

Some fungi exist as microscopic, single-celled yeasts (e.g. the bloom on the skin of a plum or grape), while the most complex forms have a far more elaborate multicellular body comprising an interconnected network, or mycelium, of minute, protoplasrn-filled tubes called hyphae. The individual thread-like tubes extend at their tips and form branches that explore their environment, fight with other fungi to occupy territory, or interact with other organisms. These activities can occur inside a few cells of a leaf, in a column of decay extending for several metres inside a tree trunk, or in the soil, for example forming a giant “fairy ring” of mushrooms in ancient grassland.

Other fungi live as lichens – a symbiotic association between a fungus (the mycobiont) and at least one photosynthetic partner (the photobiont), which can be an alga, a cyanobacterium or both. Lichens are often referred to as the ultimate example of mutualism (a type of symbiosis in which both partners benefit), given their ability to form distinct biological entities so well integrated that they resemble one single organism. They grow almost everywhere; they can be found in most terrestrial habitats, even in extreme conditions such as Antarctic deserts, growing on rocks, bark, soil, leaves, mosses, man-made materials and even on top of other lichens.

**FUNGAL NUTRITION AND NUTRIENT CYCLING**

Whereas human beings digest food within an internal tube (our alimentary tract) and absorb the resulting products into our blood to circulate throughout our bodies, fungal hyphae do it differently: enzymes produced inside the tubular hyphae are exuded into the surrounding environment, where they digest organic matter, and the nutrients are then absorbed back through the cell walls and membranes into the hyphae.

Fungi are associated with the roots of almost all plants, including forest trees and most food crops – the fungi act as living intermediaries between the plant and the surrounding soil. This type of root–fungus interaction is known as a mycorrhiza (see Chapter 5) and, like lichens, the partners engage in a mutualistic relationship. The plant benefits from the greater capacity of the fungus to absorb water and nutrients and to mobilise minerals that would otherwise be unavailable, and the fungus benefits from a steady source of carbohydrates from the plant.

Fungi are also the most significant organisms that break down cellulose, hemicellulose and lignin. These are the tough polymers in plant cell walls that give wood its great strength and durability. Their decomposition by wood-decaying fungi releases key plant nutrients back into the soil, thereby allowing the next generation of seedlings to grow. Without nutrient cycling, life on Earth as we know it would not exist; nutrients would be in such short supply that biological growth would be severely limited right across the globe.

**FUNGAL LIFE CYCLES**

Fungi have diverse, complex life cycles and can reproduce sexually, asexually and/or parasexually (which involves combining genes from different individuals without forming sexual cells and structures). They can do this through the production of different kinds of spores and/or through fragmenting hyphae. For most of their life cycles, the majority of animals and plants are built of diploid cells (i.e. combining one genome from each parent) and form bodies with determinate growth. In contrast, many fungal lineages are more complex, and for much of their life cycle their cells may be haploid (with just one genome), diploid, dikaryotic (two nuclei per cell) or multikaryotic (multiple nuclei per cell). In addition, many fungi have indeterminate growth, which means they can continue to grow as long as resources and conditions are suitable and enables them to take the shape of their environment (e.g. a leaf, a cheese, a lung). Thus, piecing together a fungal life cycle is complex and involves much detective work.
The interconnected network of hyphae is critically important for the life cycle of most fungi. It is usually hidden within soil or inside the tissues of living or dead plants, animals or other fungi and is often overlooked. However, once sufficient nutrients have been absorbed from the substrate, fungi usually reproduce and disperse to new sites by means of spores – it is at this point that they may become more visible to us. The spores themselves are usually microscopic and dust- or pollen-like, often measured in microns (thousandths of a millimetre). They may be formed asexually on specialised branches of the mycelium (as seen on mouldy food items or damp shower curtains) or after mating has occurred and elaborate spore-bearing reproductive structures have been developed, such as mushrooms. Mycologists sometimes refer to these as sporocarps, fruit bodies or fruiting bodies – in this report we use the term ‘spore-bearing structures’.

Fungi that produce spore-bearing structures visible to the naked eye are often referred to as macrofungi, and these structures are variously known as morels, mushrooms, brackets, puffballs, stinkhorns and earthstars to name just a few. Those that don’t produce spore-bearing structures at all, or where they are too small to be seen without a microscope, are often referred to as microfungi.

Evolutionary studies have shown that Fungi and Animalia are more closely related to each other than to any of the other kingdoms of life. The eight fungal phyla are shown here, along with estimates of the number of described species in each. Well-known examples of fungi from Ascomycota and Basidiomycota are also displayed. [Schematic based on [3,24,32]]
Hypocreopsis rhododendri, UK
Heterodermia sp., Bhutan
Umbilicaria cylindrica, UK
Ravenella macowaniana, South Africa
Sticta humboldtii, Ecuador
Letrouitia domingensis, Costa Rica
Microbotryum silenes-dioicae, UK
Phallus impudicus, UK
Scutellinia aff. scutellata, UK
Gomphus floccosus, Bhutan
Helvella lacunosa, Iceland
Myriostoma coliforme, UK
Clavariaceae, Bhutan
Fistulina hepatica, UK
Crucibulum laeve, USA
Ravenella macowaniana, South Africa
Heterodermia sp., Bhutan
Ravenella macowaniana, South Africa
Sticta humboldtii, Ecuador
Letrouitia domingensis, Costa Rica
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Clavariaceae, Bhutan
Fistulina hepatica, UK
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Ravenella macowaniana, South Africa
Heterodermia sp., Bhutan
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THE ORIGINS AND IMMENSE DIVERSITY OF FUNGI

Fungi have ancient origins, with evidence indicating they first appeared around 1 billion years ago\(^{[8-9]}\). Fossil fungi are difficult to find and study due to their perishable structure, but organisms recognisable as fungi (remarkably similar to modern species) are known from the Ordovician period around 450 million years ago (Mya)\(^{[9]}\) onwards, with evidence to modern species) are known from the Ordovician period around 450 million years ago (Mya)\(^{[9]}\) onwards, with evidence of lichens, plant and fungal parasites, and mycorrhiza-like associations\(^{[10]}\). A remarkable fossil is the late-Silurian (443–416 Mya) Prototaxites, which grew up to 8 m tall. It was originally assumed to have been a tree, but more recent analysis indicates that it was a fungus\(^{[11]}\).

Fungi and plants have been intricately linked through much of their evolutionary history. Without fungi, plants may have never colonised land. It is thought that the earliest rootless land plants evolved from freshwater algae, solving the problem of obtaining water and scarce mineral nutrients such as nitrogen and phosphorus in dry land masses by forming intimate associations with ground-dwelling filamentous fungi\(^{[12]}\). Exchanges of fungal-foraged minerals for plant photosynthetic products probably allowed land plants to dominate continents from around 450 Mya onwards, transforming the lithosphere (the Earth’s outer shell), biosphere (the Earth’s living systems) and atmosphere into what they are today.

Fungi are immensely diverse, with 144,000 species named and classified so far at a current rate of around 2,000 per year (see Chapter 3); this is comparable to the rate of species discovery of new plants\(^{[13]}\). However, it is estimated that the vast majority (over 93%) of fungal species are currently unknown to science. The latest best estimate suggests that the total number of fungal species on Earth is somewhere between 2.2 and 3.8 million, a number that exceeds the estimated number of plants by more than 6 times\(^{[14]}\). This broad range is based on extrapolations of plant/fungus species ratios supplemented by DNA studies of environmental samples (see Chapter 2: Box 4).

There were 536 accepted families of fungi in 2007\(^{[15]}\) and that number has risen to 886 in the last ten years. This reflects the large number of new taxa being recognised on a yearly basis (see Figure 2; see also Chapter 3), mainly as a result of the recent rapid increase in the availability, affordability and efficiency of DNA-based methods for detection and identification of fungi. Among the largest families are Mycosphaerellaceae with around 6,400 species (mainly facultative plant pathogens, i.e. those that don’t rely on infecting a host to complete their life cycle), and Pucciniaceae with around 5,000 species (obligate plant pathogens, i.e. those that must infect a host to survive and spread; see Box 1). Other large families include two that form mushroom-shaped spore-bearing structures (Agaricaceae and Cortinariaceae), each containing about 3,000 accepted species, and a further 32 families harbouring more than 1,000 species. Conversely, there are also 57 families that currently include only a single known species (known as monotypic families). Most are probably this way due to under-sampling, but some appear to be all that remain of an entire lineage – so-called ‘living fossils’.

Examples of the latter include Barbeletiaceae, with a single species restricted to leaves of another living fossil, the tree Ginkgo biloba\(^{[16,17]}\) (see Box 2), and Mixia osmundae, which only occurs in leaves of the fern genus Osmunda\(^{[18]}\).

Some families may be regarded as hyperdiverse partly because they have been sampled and studied more than others. This can be the case if the spore-bearing structures are large and conspicuous, such as those within Agaricaceae (mushrooms and allies), Polyporaceae (bracket fungi and allies) and the lichen family Parmeliaceae (see Box 3), or if the fungi are of economic importance, such as Aspergillaceae, whose members (including the familiar moulds Aspergillus and Penicillium) are important as producers of toxins and antibiotics (see Figure 2b).

BOX 1: PUCCINIACEAE (RUST FUNGI)

Pucciniaceae (Basidiomycota) is one of the most species-rich families of fungi and contains economically important plant pathogens, common in many crops including cereals and coffee. It has a widespread distribution across the globe. Many Pucciniaceae are the causal agents of disease epidemics, but they have also been tested as biological control agents of invasive species. Traditionally, they were classified based on their hosts, as many rust fungi are host specific, and on some morphological (physical) characteristics. DNA data suggest that the high species diversity we see today may have been facilitated by their ability to jump between hosts\(^{[33]}\). Rust fungi have very complex life cycles that can include up to five different spore stages, as in stem rust (Puccinia graminis). In some instances, two unrelated hosts are necessary for the different stages.
SHIFTING CLASSIFICATIONS AND NEW DISCOVERIES

The modern classification of fungi is mostly based on groups defined by the common descent of their DNA sequences, with other characteristics providing supporting evidence. Traditional classifications, however, were based purely on morphological and physiological characteristics that did not necessarily reflect evolutionary history. DNA analyses have therefore overturned traditional classification schemes, particularly with the finding that not all fungi with similar spore-bearing structures have evolved from the same ancestral lineages (convergent evolution; see Chapter 2: Box 1). A number of species that were once taxonomically ‘lumped’ together, due to the difficulties in distinguishing them using morphological characters, are also now known from DNA studies to be distinct species (so-called cryptic species because they appear identical). Similarly, fungal pathogens, such as rusts (Pucciniales), found on the same genus or species of host plant were often assumed to be members of the same species of fungus. However, this assumption is increasingly being challenged by molecular studies, which are detecting new species even in this relatively well-studied and species-rich group.

It seems likely that as molecular approaches are applied more widely, along with global sampling of fungal specimens, the number of cryptic species is likely to rise rapidly. Even further, along with global sampling of fungal specimens, relatively well-studied and species-rich group.

Aggregate sequence data started to become extensively used in species recognition from 2000 onwards. Nevertheless, it is also recognised that there are many potential issues that need to be addressed when dealing with these newly emerging molecular data, particularly in terms of reproducibility between environmental samples and protocols for naming species known only from DNA sequences. The challenge for the future will be to reach consensus across the community of scientists who work on fungi on how these exciting new discoveries of fungal diversity, based purely on DNA sequence data, are incorporated into existing fungal classification systems. Only then will it be possible to reach a truly comprehensive understanding of the full extent of global fungal diversity.

FIGURE 2: THE IMPACT OF DNA SEQUENCE-BASED CLASSIFICATION ON FUNGAL FAMILY AND SPECIES RECOGNITION

2a: Cumulative numbers of fungal families published each decade since 1800. [Data from Index Fungorum (indexfungorum.org)]

2b: The increase in numbers of accepted species from 1987 to 2017 for four economically important fungal genera. Molecular sequence data started to become extensively used in species recognition from 2000 onwards. [Data from Species Fungorum (speciesfungorum.org)]
BOX 2: THE MONOTYPIC FAMILY BARTHELETIACEAE
Many fungal families (as currently recognised) contain only a single species (i.e. they are monotypic), but in most cases it is suspected that this is due to under-sampling. *Bartheletia paradoxa*, however, is the only member of Bartheletiaceae and due to its ‘living fossil’ status it is likely that this family is genuinely monotypic.

BOX 3: THE LICHEN FAMILY PARMELIACEAE
Lichens are a symbiotic association between a fungus and at least one photosynthetic partner. Parmeliaceae is the largest and most morphologically diverse family of lichens, including around 2,750 species in 77 genera, with a single genus *Xanthoparmelia* currently containing about 820 species. The family has a worldwide distribution, occupying and sometimes dominating habitats as diverse as Antarctic rocks and tree bark in tropical montane forests, and is particularly prominent in southern hemisphere temperate regions. Species of Parmeliaceae contain a plethora of complex chemicals that may help to protect against UV radiation and predation, and they also play a part in human nutrition as one of the principal components of the spice mix garam masala. Their varied coloration partly reflects their internal chemistry, and some species are used in traditional fabric dyeing. Most species are foliose (leafy) in form, but many are shrubby in appearance and some have pendent, beard-like thalli, occasionally reaching several metres in length. The earliest-diverging lineages are crustose (resembling a crust).

BOX 4: SHAKING UP FUNGAL CLASSIFICATION
The last decade has seen a surge in production of fungal molecular data due to rapidly evolving DNA technologies, increasingly sophisticated methods of analysis and an improved ability to detect hitherto unsuspected levels of fungal diversity from environmental sequencing. Together, these studies are uncovering entirely new branches in the fungal tree of life (see Chapter 2: Box 4) and prompting novel and interesting proposals on how fungi are related to each other and how they should be classified. In one recent study, a group of intracellular parasites of microscopic algae, considered by some to be more closely related to animals and historically named in accordance with animal nomenclature, has been promoted to the rank of a fungal subkingdom (Aphelidiomycetap25].

It is still early days for assessing the acceptability of these new classifications, and further studies could result in even more upheaval. Nevertheless, they highlight how rapidly our understanding of what it means to be a fungus is changing and how new discoveries are shaking up fungal classification and the fungal tree of life. Truly, these are interesting times for fungal taxonomy!
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