Fungi

Brian Spooner and Peter Roberts

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EDITORS

The aim of this series is to interest the general reader in the wildlife
of Britain by recapturing the enquiring spirit of the old naturalists.
The editors believe that the natural pride of the British public
in the native flora, fauna and fungi, to which must be added
concern for their conservation, is best fostered
by maintaining a high standard of accuracy
combined with clarity of exposition
in presenting the results
of modern scientific
research.

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Editors' Preface

IT IS NOW more than 50 years since John Ramsbottom's *Mushrooms and Toadstools* first appeared as Volume 7 in the New Naturalist series. It fast became one of the most prominent of the early titles, running to a total of six impressions before finally going out of print in 1983. The Editors have long planned a successor which would present an up-to-date account of fungal natural history that took into account all the developments in the subject over the past half-century. Thus it is with particular satisfaction that we welcome *Fungi* as Volume 96, written by two of the country's leading mycologists.

Brian Spooner is Head of Mycology at the Royal Botanic Gardens, Kew, where he has worked since 1975, and is an authority on the British Ascomycetes. Peter Roberts also works at Kew as a Senior Mycologist with a particular interest in the non-agaricoid Basidiomycetes.

In 1953, the Editors wrote in the preface to *Mushrooms and Toadstools*, 'Dr. Ramsbottom could undoubtedly have written – in fact, did, in the first place, write – a book more than double the present length; and even then, he complained that much had to be omitted!' Honesty compels us to record that the present authors had to be no less curtailed and no doubt harbour a similar grumble about the Editors! It is now generally accepted that the original view that the living world could be conveniently divided into plants and animals, albeit with the bacteria constituting an awkward anomaly, is no longer adequate to describe the diversity of the planet. The fungi are now recognised as a separate Kingdom of their own, but back in the early 1950s, this view was only just beginning to be universally accepted. Indeed, one of the questions that John Ramsbottom rather coyly skirted around was 'What is a fungus?'.

Fungi contain some of the most beautiful, bizarre and grotesque products of evolution on the planet. Among them can be found some of the largest and long-lived organisms on earth. There is probably no corner of the globe that is without them. Most importantly, they form intimate associations with other organisms, enabling them to live in conditions from which they would otherwise be excluded. The partnerships between fungi and green algae, or cyanobacteria, that produce lichens are well known, but it is now recognised that, among the higher plants, those without a fungal partner are the exception rather than the rule. Indeed, it may well be that the invasion of the land itself was crucially facilitated by the evolution of these plant-fungal partnerships. Finally, fungi touch our own lives as causers of crop diseases and, more positively, from the yeast that provides our daily bread to the antibiotics on which modern medicine depends. Some of these aspects have already been covered in recent New Naturalist volumes such as David Ingram's and Noel Robertson's *Plant Disease* (85) and Oliver Gilbert's *Lichens* (86), but for the rest, we confidently leave the reader to discover in the following pages.

Authors' Foreword and Acknowledgements

IT IS NOW more than half a century since John Ramsbottom's classic *Mushrooms and Toadstools* was published in the New Naturalist series. It was the first of the series to deal with fungi and contained a wealth of information, focused particularly on the development of mycology and the ecology of fungi, which helped bring both subjects to the wider audience they deserve.

The succeeding 50 years has seen immense progress in the study of fungi, establishing even more firmly the major role they play in the environment and in our day-to-day lives, and highlighting the extraordinary diversity of these ancient and ubiquitous organisms. Gone are the days when fungi were treated as an obscure subset of 'lower plants' studied mainly as unwanted causers of disease. They are now understood to form intimate and beneficial partnerships with almost every form of life, from bacteria and algae to flowering plants, insects and even mammals, while also providing the vital service of decay, decomposition and nutrient recycling on which all terrestrial life depends.

So integral are fungi to the health and wealth of mankind that nobody can escape their influence even on a daily basis. It is true we still suffer the unwanted effects of fungal decay – from moulds and crop diseases to dry rot and athlete's foot – but increasingly we are discovering the many and varied benefits of fungi, in new and traditional foods and drinks, in pharmaceuticals, in forest and agricultural management, in biological pest-control and in the bioremediation of oil spills and waste pollution.

The fungi themselves have finally been recognised as forming their own kingdom distinct from animals and plants. It is no small kingdom either. The mushrooms and toadstools of Ramsbottom's book, as diverse and numerous as they are, are just a small part of the vast assemblage of fungi, probably amounting to well over a million species worldwide, the majority of which remain as yet undescribed and still unknown to science.

It is clearly impossible to cover all aspects of modern mycology in a single volume, and our aims have therefore been to look at the ecology and influence of fungi, to give some idea of their diversity and importance, and to outline their main characteristics. A lot more could be said about their structure, biology and physiology, but these topics are already well covered in student and academic texts. A lot more could also be said about recognising and identifying fungi in the field but, fortunately, today's forayers can choose from a wide selection of well-illustrated field guides – an indication of the growing popularity of fungi as a worthwhile subject to explore. We hope this new book will be a complementary volume to such field guides, giving the interested naturalist a few extra insights into what is going on behind the scenes in the fungal world.

The writing of this work has proved to be a far longer and more involved exercise than was originally envisaged, and we owe considerable thanks to our publishers for their patience in allowing it to develop over several more years than were initially planned. It has also been the source of endless surprise and learning, with many of the subjects covered proving far more complex and far-reaching than we ever imagined, leading us not only into byways but also some major highways of research of which we previously knew little. Keeping up with the constant flow of new papers, new discoveries and information has also been a challenge, albeit an exciting one, and we have tried our best to keep pace. We would like to acknowledge all the mycologists and other researchers who, through their many and various papers and books, have unwittingly helped us create this book. Our initial hope was to list all our sources and references, but when the working bibliography started heading for the 100-page mark, common-sense (and our publishers) dictated a substantial cut-back. The references that remain will, we hope, still be of use for exploring many topics further.

It is a big book, but the kingdom of the fungi is an even bigger subject. We trust that you may find at least a few new, interesting, remarkable and entertaining things inside.

The broad scope of the book has required an equally broad search for photographs and images to illustrate the many different kinds of fungi involved. The authors are indebted to the following generous individuals, who responded so promptly and positively to our requests for help in sourcing illustrations, and for kindly giving permission to use their photographs and images. Additional thanks are due to Paul Bridge and Julian Mitchell and also to Lynton Mclain who supplied further information on some specialist topics.

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CHAPTER 1
Neither Animals nor Plants

ANIMAL, vegetable, or mineral? For centuries, this simple system of classification happily divided the natural world into three great, god-given categories. Fungi, if considered at all, were normally placed in the 'vegetable' category or occasionally (as 'excrescences of the earth') in amongst the minerals.

We now know that fungi are neither plants nor animals, and are certainly not earthy outgrowths. But if not these, then what exactly are they? The question sounds simple, but proves in fact to be a highly complex one, with many aspects still not fully understood. The enormous diversity of the fungi, not just the larger and more obvious species, but the innumerable microfungi and 'fungus-like' organisms, presents an immense challenge in clarifying their interrelationships and defining their characters. Nevertheless, remarkable progress in recent years, due not least to the advent of molecular systematics, has painted a much clearer picture and allows a fuller answer to the question 'What are fungi?'.

In this first chapter, we consider this question and say something about the distinguishing characters of fungi, their classification, and main groups.

Hyphae: the threads of fungal life

Scoop up a handful of old, damp, woodland leaf litter and you will probably find that it is bound together with a cobweb-like mat of fungal strands. The same thing can be found in the compost of a mushroom bed or in a crumbling piece of rotten wood. Under a microscope, mushrooms themselves, the moulds on rotting food, and the hard brackets on a tree stump are all seen to be composed of these same fine strands. These are 'hyphae' (Fig. 1), the building blocks of all filamentous fungi. They are essentially hollow tubes, the living parts of which contain nuclei, mitochondria, and other organelles, just as do animal and plant cells. In most fungi, the hyphae are divided into compartments by cross-walls (septa), keeping the organelles separate in cell-like units, the septa themselves having microscopic pores, allowing movement of water and nutrients from one compartment to another.

Fungi absorb nutrients through the walls of the hyphae, 'feeding' in much the same way as plant roots. All species can absorb small molecules such as amino acids and simple sugars, particularly glucose, but many produce digestive enzymes which can attack more complex substances such as cellulose and starch, breaking them down into simpler components. Wood-rotting fungi, for example, can break down cellulose and sometimes lignin, whilst others can break down keratin (found in hair and feathers), chitin (found in insects and other fungi), and various more surprising substances, including kerosene. This method of nutrition is the main reason why fungi are the principal agents of natural decay and nutrient recycling (Chapter Three).
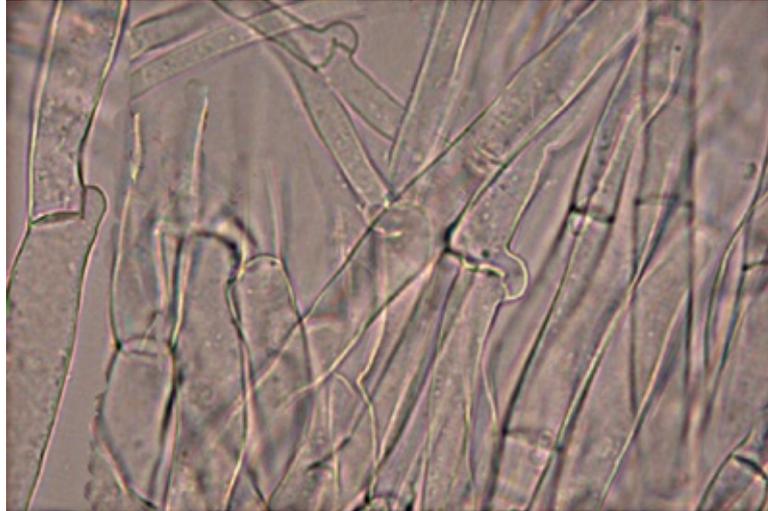
FIG 1. Hyphae from the agaric *Leucopaxillus giganteus* showing septa (cross-walls) and swollen clamp connections (see also Fig. 4) which are typical of basidiomycetes (RBG Kew).
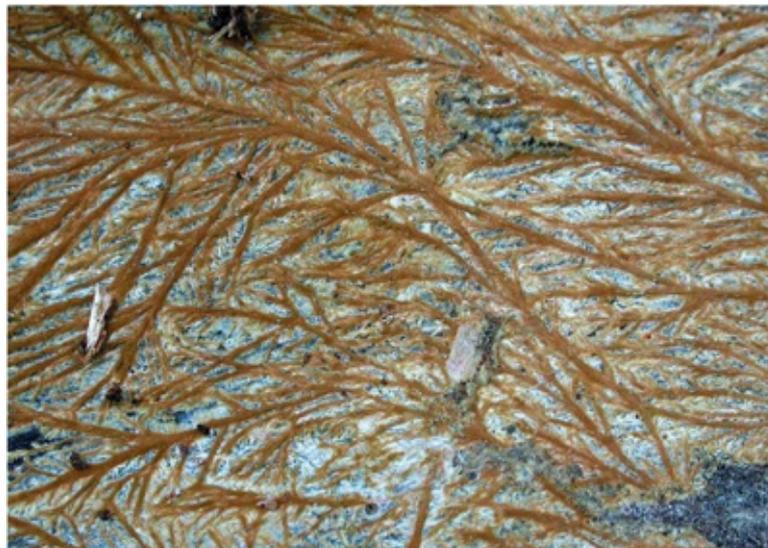

FIG 2. Mycelium of a corticioid fungus spreading over the underside of a log. The hyphae show a tendency to clump together, forming visible branches and fronds (S. Evans).

Individual hyphae are microscopically small, typically around 5–20 µm wide (a micrometre (µm) or 'micron' is one millionth of a metre), but when branched and growing together they can easily be seen as a cobwebby, mould-like growth (Fig. 2). This is termed the 'mycelium' (or 'spawn' in cultivated mushrooms) and is how most filamentous fungi grow through a nutrient-rich substratum, be it rotten wood, dung, damp leaf litter, or a long-forgotten sandwich. Each hypha branches and grows from the tip, spreading indefinitely as long as there is a food source. Components needed to synthesise new walls are produced throughout the hypha and actively transported to the growing tip. Branching commonly occurs, usually behind a septum, by thinning of the hyphal wall and extension of a new growing tip. This method of growth can be extremely efficient in appropriate conditions, with growth rates in some fungi, such as the common ascomycete *Neurospora crassa*, as high as 6 mm per hour. This is one reason why moulds are such rapid and effective colonisers. It also explains why some fungi have become very large (the biggest living organisms on the planet, in fact) and

also very old (potentially, perhaps even immortal).

Fruitbodies: from mushrooms to moulds

Hyphae become most visible when they combine to produce complex spore-bearing structures or 'fruitbodies'. These fruitbodies include the mushrooms and toadstools, brackets, puffballs, truffles, cup fungi, morels, and so on, which most people think of as 'fungi'.

Examination of sections of any fruitbody under a microscope will demonstrate that it is almost entirely composed of hyphae. In fleshy species, like mushrooms, the hyphae are generally distinct and easily visible but in many fungi the hyphae are variously modified by being swollen, thick-walled, gelatinised, compacted, pigmented, ornamented, or any combination of these. From these structural hyphae, which comprise the bulk of any fruitbody, specialised spore-bearing hyphae arise, capable of releasing the spores by which the fungus reproduces and forms new colonies.

An ordinary cultivated mushroom provides a familiar example. The fruitbodies arise from the mycelium in soil or compost, once it has reached a certain age and bulk. Their development is triggered by various factors, including temperature, humidity, aeration, nutrient availability, and the presence of physical constraints (many larger fungi fruit where mycelial growth is checked, often by compacted earth at the edge of a path). Though mushrooms famously grow in the dark, other fungi may need light to initiate fruiting. However, this can be astonishingly brief, an exposure of just 12 seconds being sufficient for *Neurospora crassa*. Blue light at the right intensity is required for this species, whilst others prefer near-ultraviolet light, or varying periods of light and darkness. The effects of light on fruitbody development can be quite complex, stimulating the development of some species but inhibiting others. In some cases, fruitbodies developed in dark conditions exhibit weird and monstrous forms (Chapter 13).
Many species of dung-inhabiting fungi are 'phototropic', actively growing towards a light source in order to discharge their spores most efficiently into the air stream.

The young mushroom fruitbody or 'primordium' initially resembles little more than a knot of hyphae, but quickly grows and differentiates below the soil surface. At the 'button' stage it is effectively fully formed and (if conditions, particularly humidity, are right) is ready to expand, breaking the surface and becoming visible as a fresh mushroom. It continues to expand and mature until the spores are released. This expansion phase, effectively using hydraulic pressure, is rapid and extremely powerful, generating a considerable force. Mushrooms developing below paving stones, for example, will readily lift the stones as they expand and mature. Buller (1931) showed that the delicate ink-cap toadstool *Coprinus sterquilinus* can raise a weight of over 200 grams during the development of its fruitbody, without breaking its stem. Spore production in the cultivated mushroom typically continues for several days (if left unpicked), after which the fruitbody collapses and rots away. A single mycelium will produce many such mushrooms, both simultaneously and in succession, during the fruiting season. In the wild state, further crops will be produced the following year, and so on indefinitely, as long as nutrients are available.

The mushroom itself has three main parts: the stem (or 'stipe'), which lifts the

fertile part into the air; the cap (or 'pileus') which covers and supports the fruiting surface; and the gills (or 'lamellae'), on which the spores are produced. In addition, protective membranes (or veils) are present in many mushroom and toadstool species. These may enclose the entire developing fruitbody (a universal veil) or cover just the developing gills (a partial veil). At maturity, these veils rupture and leave either a sac-like 'volva' at the base of the stem and scale-like remnants on the cap (universal veil), or a ring on the stem (partial veil) (Fig. 3).

Though mushrooms and toadstools are ephemeral, lasting only for a few hours or at most for a few days, some of the wood-rotting bracket fungi have tough, long-lasting fruitbodies which allow a much longer period of spore release but represent a substantial investment for the fungus concerned. As a result, many brackets are perennial, some persisting for twenty years or more, producing a new spore-producing layer each year. It is often possible to count these, like tree rings, if the bracket is damaged or cut through vertically. The structural hyphae in such fruitbodies are unusually thick-walled (so-called 'skeletal' hyphae) and in the toughest fruitbodies are further strengthened by being interwoven with equally thick-walled 'binding' hyphae. The result may be a bracket that feels as hard and solid as the wood on which it is growing.
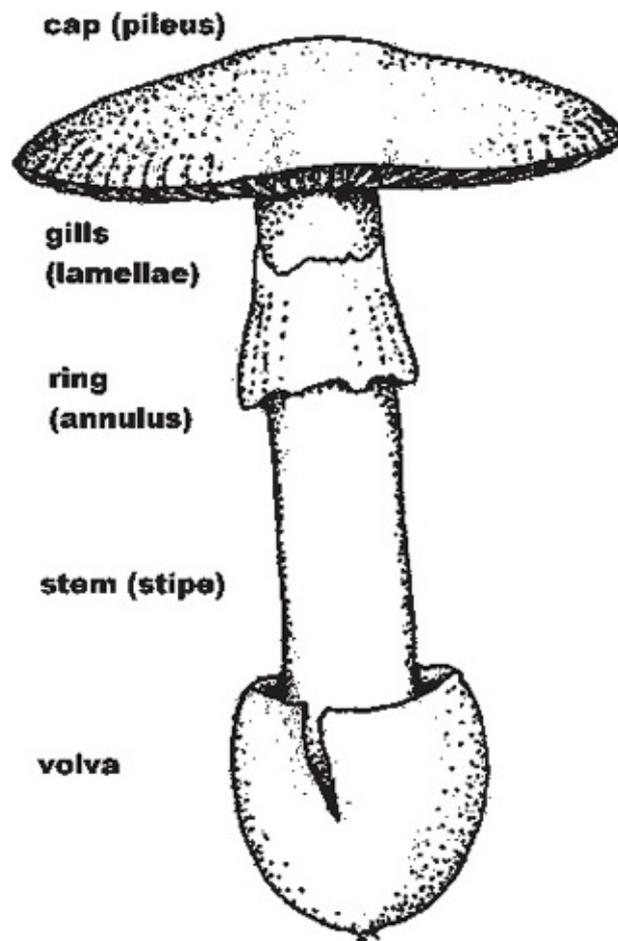

FIG 3. Features of a typical agaric fruitbody (*Amanita* species). The ring and volva are remnants of veils that rupture as the toadstool expands (P. Roberts).

Most moulds, mildews, and other microfungi produce small, often microscopic

fruitbodies, or have no specialised structures. Typically, a mould produces a felty colony of modified surface hyphae which produce asexual spores (or 'conidia') on specialised cells. These conidia, often produced in vast quantities, serve to colonise new and often ephemeral substrata.

Sex and spores

Sex, as we know it, is a very different process in the fungi. Indeed, some species, mainly moulds and yeasts, manage without it, and populations are essentially clones. In others, both sexual and asexual reproductive stages occur at different points in their life cycle, each stage producing a distinct and usually independent fruitbody, known as the 'anamorph' (asexual fruitbody) and 'teleomorph' (sexual fruitbody). In addition, a mechanism termed 'heterokaryosis', which also leads to genetic diversification, may occur in asexual stages. This follows fusion of different hyphae, which results in two or more genetically slightly different nuclear types in the same mycelium, providing some genetic mixing despite the lack of sex.

In general, however, sexual reproduction is as important to fungi as to other organisms. Typically it involves the union of hyphae (or yeast cells) containing nuclei with a single set of chromosomes (i.e. haploid, with half the full complement), the resulting hypha (or cell) being then 'dikaryotic', containing nuclei of two different types. In basidiomycetes (the large group which includes mushrooms and toadstools) proliferation of dikaryotic hyphae usually occurs through the formation of 'clamp connections', unique structures found in no other group of fungi. After division of each nucleus, one nucleus migrates into a bulge in the wall of the hypha and, after formation of a septum, is transferred to the newly formed uninucleate adjacent cell, so maintaining the dikaryotic condition (Fig. 4). Sooner or later, the haploid nuclei in dikaryotic hyphae will fuse to produce a diploid nucleus with two sets of chromosomes. In due course, this nucleus undergoes 'meiosis', a division process which effectively restores the haploid condition, but combines in each resulting cell chromosomes from two different sources. Following meiosis, haploid spores are produced, allowing dispersal to occur (Fig. 5). A few species of fungi produce morphologically distinct reproductive cells, roughly the equivalent of sperm and ova, but since both can arise from the same parent fungus there is no real differentiation between 'male' and 'female'.
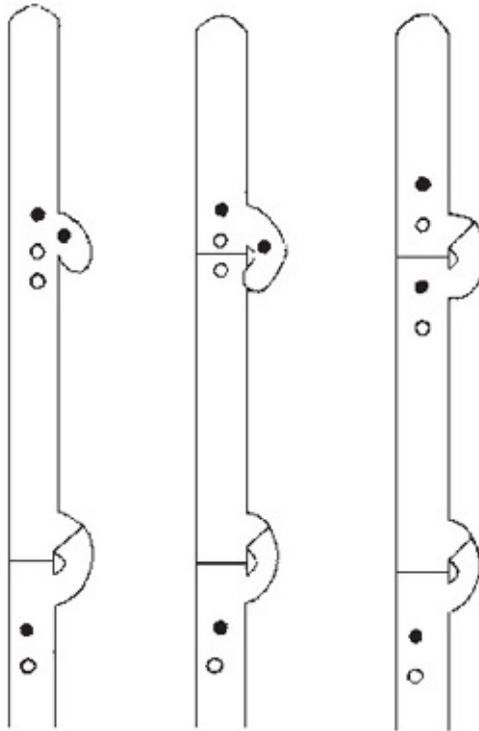
FIG 4. How clamp connections are formed in basidiomycetes. Hyphae are typically dikaryotic (with two genetically distinct nuclei in each hyphal cell, represented by black and white dots). When the nuclei divide and new cells start to form, there is a danger that two of the same nuclei may enter the new cell. But the process of clamp formation, shown here in three very simplified stages, ensures that the dikaryotic condition is maintained (P. Roberts).

Inbreeding within a population in general decreases its adaptive potential. In many fungi, populations are therefore self-sterile and can 'mate' only with adjacent populations. Such fungi are termed 'heterothallic'. Others, in contrast, are self-fertile and these are known as 'homothallic'. Heterothallism is due to the existence of 'alleles' (different types of a single gene) which effectively produce different strains of the same fungus, commonly referred to as 'plus' and 'minus'. A plus strain cannot mate with another plus strain, but can do so with any minus strain. Such different mating types, morphologically indistinguishable, occur in the majority of fungi. The existence in many species of multiple alleles, present in different populations, can lead to highly complex situations with large numbers of mating types. The ink cap *Coprinus cinereus*, for example, has been shown to have at least 1,152 different mating types, whilst other fungi may have even more!
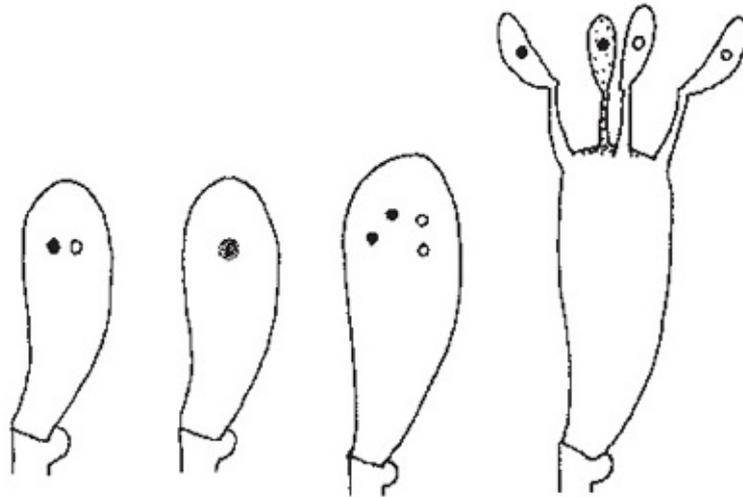
FIG 5. Meiosis in typical basidiomycetes. The young basidium is dikaryotic, containing two genetically distinct haploid nuclei. These fuse to form a single diploid nucleus which then undergoes meiosis, forming four new haploid nuclei. Each of the new nuclei then migrates into a developing haploid spore (P. Roberts).
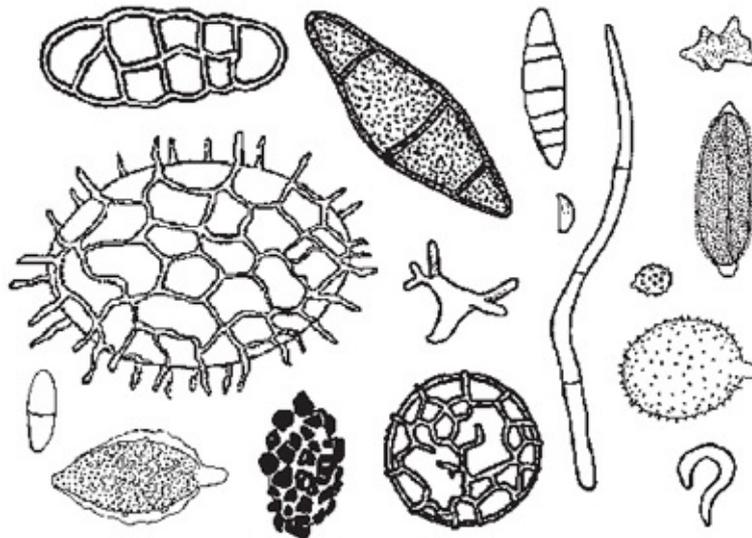

FIG 6. A selection of fungal spores to give a flavour of the enormous diversity of size, shape, pigmentation, ornamentation and septation that they exhibit. Spores may be simple or multicellular, and many bear appendages or a mucilaginous coat, all adaptations to particular ecologies. Others may have complex coils and branches, as shown in Fig. 103 depicting spores of aquatic fungi (P. Roberts & B. Spooner).

Most fungi produce some kind of spores, individually microscopic but varying enormously in size. The smallest, no more than about 2 or 3 µm across, are hardly larger than bacteria, whereas the largest may reach almost 500 µm (0.5 mm) in length (Fig. 6). In mushrooms and toadstools, spores are normally around 5–20 µm long, depending on species. They are typically produced in vast quantities, often in billions. To see them, take a mature mushroom, remove the stalk, place the cap on a piece of white paper or glass, cover with a glass to prevent drying out, and leave overnight. The result will be an attractive chocolate-brown spore deposit comprising several million spores (Fig. 7). Each spore is capable of germination, but clearly very, very few ever encounter precisely the right conditions to form a new mycelium and continue the
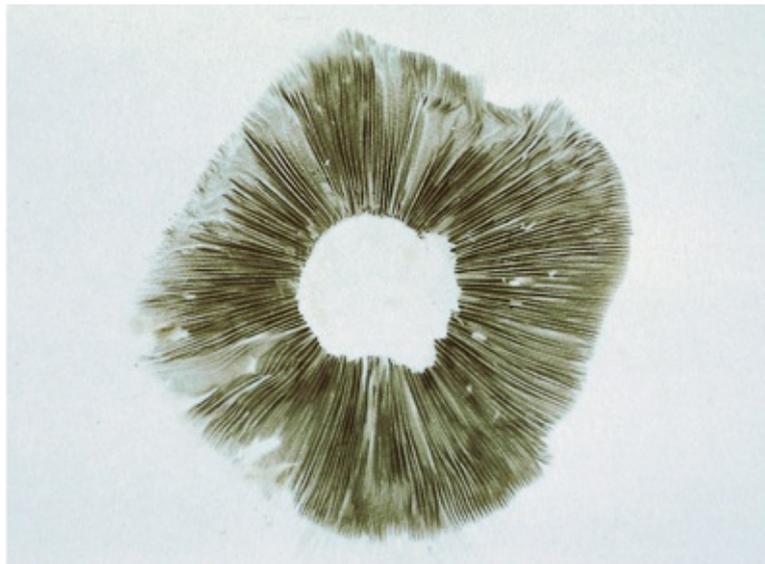
species.

FIG 7. Spore deposit or 'print' of the commercial mushroom (*Agaricus bisporus*). As well as forming attractive patterns reflecting gill arrangement, spore deposits have scientific value in showing precise spore colour and in comprising fully mature spores (RBG Kew).

A KINGDOM APART

Fungi are clearly a very distinctive group of organisms, but just where do they fit into the grand scheme of things?

All life on Earth can be classified into a number of separate, major units known as 'kingdoms', each representing an ancient lineage that has evolved into a multiplicity of modern species. Just how many kingdoms are required to encompass this multiplicity is, however, uncertain. The simplistic view recognised just two, 'animals' and 'plants', following classical beliefs established long before the foundation of modern systematics by Linnaeus in the mid 18th century. This comfortable tradition continued almost unchallenged for close on three centuries, and not until the latter part of the 20th century has it been radically reviewed and replaced. This change has largely reflected progress in the study of micro-organisms, involving ultrastructural and biochemical characters and especially the application of molecular systematics, advances which have finally shown that a two-kingdom system is hopelessly inadequate to encompass the huge diversity of life on Earth. A several-kingdom structure of life is now not in dispute.

Although fungi, as well as protozoa and bacteria, had occasionally been considered separate kingdoms at various times since the 17th century, no consensus on this view was held until comparatively recently. Margulis & Schwartz (1982) were the first to propose the classification of living organisms into five kingdoms, following earlier suggestions by Whittaker (1969). More recently, a six kingdom system has been suggested (Cavalier-Smith, 1998), although it now seems that Woese *et al*. (1990) were correct in splitting one of these kingdoms (the *Prokaryota* or bacteria) into two, the *Archaea* and the *Bacteria*. Prokaryotes are single-celled structures, the most ancient of all organisms, with which life on Earth began. Their cells lack nuclei or other subcellular structures (organelles) such as mitochondria, and their DNA is

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dispersed. Prokaryotes probably evolved at least 4,000,000,000 years ago and were for an immense period of time the only life forms on the planet. Eventually, after at least two billion years of slow evolution, they gave rise to the more complex 'eukaryotes', organisms with sophisticated cells containing separate organelles. The most important of these are the 'nucleus', which governs the cell and in which the DNA is packaged, and the 'mitochondria', which provide energy.

All life other than bacteria is eukaryotic, highly evolved and diversified over the last two billion years into five separate kingdoms. These are the plants (kingdom *Plantae*), the animals (kingdom *Animalia*), the true fungi (kingdom *Fungi*), and the less well-known kingdoms *Chromista* and *Protozoa* which both contain some fungus-like organisms. *Protozoa* is probably the most ancient of the eukaryotic kingdoms and includes a total of thirteen 'phyla' (the next main unit (or taxon) below kingdom), a level which distinguishes human beings (phylum *Chordata*) from jellyfish (phylum *Cnidaria*). *Animalia* comprises 23 phyla, *Plantae* and *Chromista* each have five, and four phyla make up the *Fungi*. In this system, most of the organisms traditionally called 'fungi' belong within the kingdom *Fungi*, but some are placed within the *Protozoa* and *Chromista*. Although this seven-kingdom system is not yet fully accepted, it seems to be gaining favour as the current standard model. Nonetheless, significant changes are still being proposed and it seems likely that even the highest levels in the classification of life will remain in a state of flux for a long time to come.

Defining the fungi

Each of the seven kingdoms, as with all taxa, has its own unique features. In the old two-kingdom view of life, fungi were placed with plants mainly because, unlike animals, they do not move around. This is undeniably true, but is hardly a good scientific definition. The fungal mode of nutrition, for example, is quite different from that of plants. Like animals, they are 'heterotrophs', unable to make their own food and requiring organic carbon derived from plants or other organisms. Unlike animals, however, which ingest their food, fungi digest and absorb nutrients externally. Plants, in contrast, are 'autotrophs', making their food by photosynthesis, their cells containing chlorophyll and able to use sunlight to convert carbon dioxide into sugars. Fungi also differ structurally from plants, in particular lacking cellulose which is characteristic of plant cell walls. Instead, fungi are mainly composed of chitin, the same basic material that makes up insect exoskeletons.

Recognition of a separate kingdom for fungi was a major advance, although it was soon evident that the kingdom was not yet homogeneous but included organisms placed there because of similarities in their mode of nutrition, now known to have arisen independently from a different ancestor. As long ago as 1864, de Bary had proposed that slime moulds were not fungi but actually protozoa, a conclusion which, because of the fungus-like nature of their fruitbodies, only recently received acceptance. Slime moulds (*Myxomycota*) are actually 'phagotrophs', ingesting bacteria and fungi by means of amoeboid stages, typical of protozoa. Again, the filamentous nature and mode of nutrition of the 'actinomycetes' placed them with the fungi until it was realised that they were actually prokaryotic and belonged instead with the bacteria. Their fungus-like characters were evolved quite independently, and the same

has been found to apply to some other fungus-like organisms. As a result, definition of the 'true fungi' cannot be simply stated but relies on characters such as mode of nutrition, chemistry of the cell wall, biosynthetic pathways and ultrastructure of the mitochondria. The taxonomic value of this last character, first suggested in the 1960s, has now become firmly established (Cavalier-Smith, 2001). Mitochondrial cristae, essentially folds of the inner membrane of the mitochondrion, are flattened in *Fungi* but tubular in other groups, providing a major (but not the only) distinction between *Fungi* and other heterotrophs. On this basis, the kingdom can be technically defined as follows:

> "*The* Fungi *comprise non-photosynthetic eukaryotes with an absorptive nutrition that do not have an amoeboid pseudopodial stage, and may occur as both single celled and multicelled organisms. The cell walls contain chitin and ß-glucans, and their mitochondria have flattened cristae.*"

FROM MOULDS TO MUSHROOMS: A GUIDE TO THE MAJOR GROUPS

The classification adopted for fungi in this book recognises the three kingdoms (*Fungi, Chromista,* and *Protozoa*) noted above and broadly follows that given in the most recent edition of the 'Dictionary of the Fungi' (Kirk *et al*., 2001), with some modifications based on recent findings. However, with continued rapid development of techniques such as molecular analysis it seems unlikely that the system suggested here will yet prove a stable one. Nevertheless, the following brief guide should help place the fungi discussed throughout this book into appropriate context.

KINGDOM FUNGI: ASCOMYCOTA

The *Ascomycota,* the largest of the fungal phyla, contains not only the more visible cup-fungi, morels and truffles, but also the ubiquitous and often microscopic flask fungi, most of the lichens, and many of the asexual yeasts and moulds. Ascomycetes occur worldwide, and exhibit an enormous range of life styles and forms. Currently, the phylum is divided into seven classes, 56 orders, and well over 200 families. Total species numbers are difficult to estimate, but it seems that at least 40,000 ascomycetes are known worldwide, with several times that number yet to be described. About 5,500 ascomycetes (excluding asexual stages likely to belong within this phylum) have been recorded from Britain, including around 1,800 lichenised species.

Ascomycetes are characterised by the possession of 'asci', microscopic club-shaped cells in which sexual spores ('ascospores'), are developed. Asci themselves are extremely diverse in structure and provide the basis for the current classification of these fungi (Fig. 8). In many species, including most of the larger ascomycetes, asci are simple structures which have a single, one-layer wall and are therefore referred to as 'unitunicate'. However, many other ascomycetes have asci with complex wall structures involving more than one layer. These are termed 'bitunicate' but are themselves diverse in their microanatomy and method of functioning for spore discharge. Ascomycetes are also characterised by the structure of their hyphal walls

which involve two layers of differing density to electrons. It is this character which can be used to determine the ascomycetous affinities of most asexual fungi in which the ascus stage is lacking.
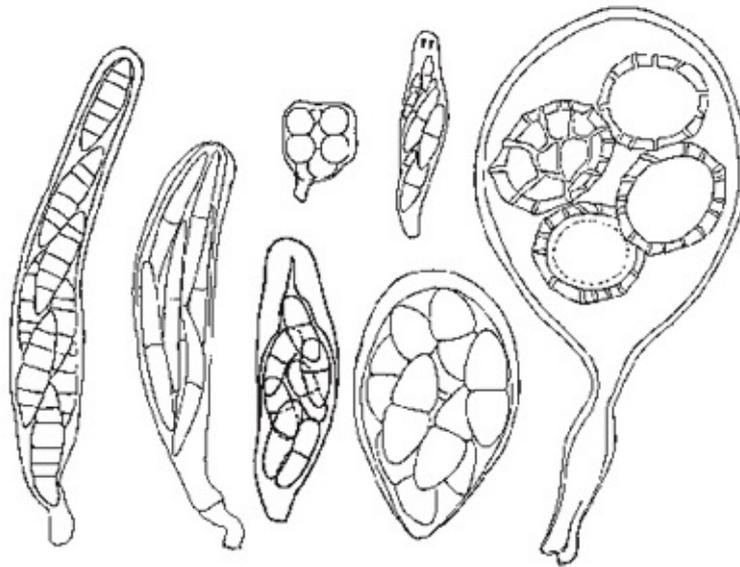

FIG 8. Examples of different types of asci, the cells in which the spores of ascomycetes are produced. They exhibit immense diversity in shape, size, wall structure and method of spore release, providing a basis for classification of these fungi (B. Spooner).

Two main forms of fruitbody provide convenient if artificial groupings for the bulk of species. These are the cup-fungi, or 'discomycetes', and the flask fungi, or 'pyrenomycetes'. In addition, there are the ascomycetous yeasts together with the anamorphic stages of ascomycetes, usually known as 'hyphomycetes' and 'coelomycetes'.

Cup-fungi or discomycetes

Cup-fungi are virtually cosmopolitan in distribution and occur in all habitat types. Although most are saprobes (living off dead matter), they also include mycorrhizal species (symbiotically associated with plant roots) as well as many parasites and pathogens. Some of the larger cup-fungi, particularly truffles and morels, are edible and sought after.

The term 'cup fungus' refers only to a general design and has little taxonomic value in itself. The fruitbodies (known as 'apothecia') of most species take the form of miniature cups, goblets, or discs, with the spore-bearing layer on the inner surface. However, some have diverged markedly from this basic design, and form complex, compound structures, as in the honeycomb-like morels (*Morchella* species), or have become totally enclosed and chambered, as in the truffles and other subterranean species.

Most apothecia are small, only a millimetre or so across and sometimes much smaller, but they often occur in swarms on rotting stems or leaves. Many are highly attractive, especially when examined with a lens, displaying a range of colours and often delicately ornamented with hair-like structures. Most of the smaller species have

characteristic asci termed 'inoperculate' (lacking a lid) referring to their mode of spore discharge through an apical pore (as in the genus *Bisporella*, Fig. 9). They belong mainly to the order *Helotiales* and are the most numerous of the cup-fungi with perhaps 1,500 species known from Britain and 4,000 or so worldwide.

FIG 9. *Bisporella citrina*, one of the smaller inoperculate discomycetes, often found in swarms on dead wood and stems. The distinctive bright yellow fruitbodies are fairly common on rotten logs (B. Spooner).

Fundamentally distinct from the *Helotiales* are the cup-fungi that belong to the *Pezizales*. These are distinguished by their asci being 'operculate', releasing their spores through an apical lid or 'operculum'. Most *Pezizales* have easily visible fruitbodies often several centimetres across or more, and most of the larger cup fungi belong here. They include the striking orange-peel fungus *Aleuria aurantia*, the equally flamboyant scarlet elf-cups in the genus *Sarcoscypha*, and a range of variously coloured *Otidea* and *Peziza* species. More complex in form and among the largest of the *Pezizales* are the spring-fruiting morels (*Morchella* species) and autumn-fruiting saddle-fungi (*Helvella* species; Fig. 10). Though less numerous than the *Helotiales*, there are nevertheless over 300 species of *Pezizales* known in Britain and almost 1,200 worldwide. Closely related to them are the truffles (*Tuber* species) and others which have evolved underground fruitbodies adapted to their unique ecology and quite unlike typical discomycetes. They include some of the most sought after edible fungi.

Disc-like fruitbodies are also produced by many lichens, these belonging mainly in the *Lecanorales*, distinguished not just by their mode of life but by the structure of their asci. This is the largest order of ascomycetes, comprising a huge range of forms currently divided into more than 40 families and including some 5,500 species worldwide, more than 1,000 of which occur in Britain.

Although more than 11,000 cup-fungi (including lichenised species) have been described world-wide, they remain little known. New species are frequently encountered, and their ecology and life histories, physiology and chemistry are, for the most part, little-studied. Their bewildering diversity provides a seemingly endless challenge, even within the British Isles.

FIG 10. *Helvella crispa*, one of the larger operculate discomycetes which have become modified into a stalk and a saddle-shaped cap. This whitish species is common in woodlands (B. Spooner).

Flask fungi or pyrenomycetes

The second big group of ascomycetes has flask-shaped fruitbodies ('perithecia'), fully enclosing the asci except, in most cases, for an apical pore ('ostiole') through which the spores are liberated. These fungi are even more diverse than the discomycetes, and are almost ubiquitous in their distribution. They include parasites as well as saprobes and symbionts, many of which are lichenised.

The flask fungi have tiny fruitbodies, some less than a tenth of a millimetre wide and none exceeding about two millimetres across. Most are dark-walled, appearing black to the eye, although some, such as coral spot, *Nectria cinnabarina*, are bright red or orange. The fruitbodies are usually gregarious but often developed inside plant tissue and largely hidden from view with only the ostioles breaking the surface. Others, however, develop conspicuous and sometimes massive areas of sterile tissue in which numerous perithecia are immersed. Since this tissue, known as a 'stroma', is typically black, many of these flask fungi appear burnt or carbonised, hence the term 'pyrenomycetes' (literally 'fire fungi'). Stromatic tissue varies greatly in structure and extent. At its simplest it merely comprises dark hyphae in the epidermal cells of the host, covering just a single perithecium, as in species of *Anthostomella* (*Xylariaceae*). In other cases, including most *Diatrypaceae*, it may blacken the host surface over extensive areas, or become crust-like or cushion-like with numerous embedded perithecia. Discrete, often massive, fruitbodies are formed in some pyrenomycetes, particularly in the *Xylariaceae* and *Hypocreaceae*. Amongst the largest of these are *Daldinia* species, called 'cramp balls' or 'King Alfred's cakes', common in Britain, and species of *Xylaria* (Fig. 11), a genus which includes the familiar black and white candlesnuff fungus, *Xylaria hypoxylon*, and dead man's fingers, *X. polymorpha*, on old stumps and logs. Cutting open one of these blackened 'fingers' reveals a core of whitish, sterile tissue with a multitude of tiny flask-shaped perithecia embedded in the surface layer.

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