Preface

Life on Earth would look very different in the absence of Kingdom Fungi. Without wood-decomposing fungi, fallen timber would render forests impenetrable; without coprophilous fungi the landscape would be contoured by mountains of herbivore faeces, and without aquatic fungi, rivers and ponds would be clogged with plant debris. These dystopian fancies may be useful in pointing to the significance of fungi in the breakdown of biological debris, but they do not stand up to critical thinking for long. Without mycorrhizal fungi, there would be no forests in the first place, nor grasslands, herbivores, or herbivore faeces. Life on land has evolved with the participation of the fungi and would collapse without their continued activities. If fungi had not evolved, then their ecological roles might have been assumed by other groups of microorganisms, but this is the stuff of science fiction. Fungi did evolve and have diversified into a kingdom of more than 100,000 named species. The actual number of fungi is at least one order-of-magnitude higher. Fungi are a major component of the microbiome in almost every habitat.

A pair of familiar fungal species offers a study in contrasts that reflects the diversity of organisms within the kingdom: baker's yeast, *Saccharomyces cerevisiae*, and the button mushroom, *Agaricus bisporus*. Human civilisation would be inconceivable, or would require reconception, without our partnerships with *Saccharomyces*. The ease with which this yeast is cultured and its facility for metabolising glucose and producing carbon dioxide and alcohol has allowed humans to brew beer, make bread, and ferment wine for thousands of years. This single-celled fungus has been a model experimental organism for many decades, and the sequencing of its genome in 1996 was a landmark in modern biology. This was the first sequencing project for a eukaryote and revealed that the fungus housed 6000 genes on 16 chromosomes. More than one-fifth of these instructions match human genes, which is a persuasive reflection of the unity of all eukaryotes. Yeast cells grow by absorbing food and divide by creating buds on their surface. When sexually compatible strains of *Saccharomyces* mate, the resulting diploid cell divides by meiosis and produces four haploid ascospores.

It is difficult, at first glance, to equate *Agaricus bisporus* with yeast: one organism forms a gilled mushroom built from hundreds of thousands of filamentous cells, the other is a unicellular microbe. Like yeast, *Agaricus bisporus* is an organism that is partly a human invention. Wild versions of both species are different from cultivated strains. Untamed populations of the mushroom fruit beneath particular trees and shrubs, suggesting that they may be engaged in mutually beneficial symbioses with these plants. The farmed mushroom is grown as a saprotroph on compost. The fungus produces a colony of branching cells, called hyphae, which feed by secreting enzymes that decompose plant materials in the compost to release sugars and other small molecules that fuel their metabolism. Once the colony has accumulated sufficient biomass, and when the mushroom farmer manipulates the growth conditions, the colony undergoes the remarkable reorganisation that produces a flush of mushrooms.

Buttons develop from pinhead-sized groups of hyphae, and these inflate to form the familiar stem, cap, and gills of the fruit body or basidiome. Harvesting can occur early, before the gills are exposed, or later, when the mushroom has undergone a 1000-fold increase in volume. This hydraulic expansion process allows the wild mushroom to emerge from the ground and display its gills for the process of spore release. And what a marvel of natural engineering is the mushroom. Wild relatives of *Agaricusbisporus* can release an astonishing 31,000 spores per second, or 2.1 billion spores per day. The spores are shot from the gills by a catapult powered by the momentum of tiny droplets of fluid. Nothing like this happens in yeast.

Saccharomyces and *Agaricus* are members of the largest phyla of the fungi, respectively, the Ascomycota and the Basidiomycota, whose ancestral species began to diverge from one another 400 million years ago. These phyla are distinguished from one another by fundamental, or seemingly fundamental, differences in life cycles and developmental biology. If we adopt a broader view of fungal diversity, however, similarities between these great phyla are apparent, including commonalities in cell wall composition, trafficking of membranes within the cytoplasm, and features of metabolism and physiology. Once we recognise these characteristics, it becomes easier to embrace the fact that the single-celled yeast and the multicellular mushroom are different versions of the same kind of organism.

There is, of course, a great deal of subjectivity in organising the fungi, and the rest of life, into groups of taxonomic convenience. The scale of the inquiry is everything. After all, mushrooms and humans are different versions of the same kind of thing at the level of supergroupings of eukaryotes, because all animals and fungi are members of the Opisthokonta. This brief consideration of yeasts and mushrooms is useful because it indicates the breadth of morphological variation in the kingdom, but there is much more to the fungi besides yeasts and mushrooms. Fungal diversity and classification are introduced in Chapter 1.

Fungal cells are built from the same kinds of organelles as other eukaryotes, but possess many structures that are not encountered outside the kingdom. These include organelles involved in the hyphal mechanism of tip growth and plugs that protect wounded colonies from haemorrhaging cytoplasm. The mosaic of chitin and other polymers in the cell wall is another uniquely fungal attribute. Fungal cell biology and development are showcased in Chapter 2. Fungal developmental biology is a research arena that deserves greater attention. Despite tremendous advances in cell and molecular biology, we have very little information on the processes involved in the differentiation of root-like cords and rhizomorphs, resistant organs called sclerotia, and mushrooms. The puzzle of fungal multicellularity is one of the frontiers in mycology, and its solution requires the engagement of the brightest and most creative investigators.

Chapter 3 concerns the formation of microscopic spores, which is another unifying feature of the kingdom. Spores vary greatly in shape and size and help us to identify different groups of fungi, as well as individual species. They range from swimming cells, called zoospores, produced by the chytrids, to warty zygospores, multicelled conidia, and the beautiful spores of truffles patterned with delicate ridges. Within a single category of spores we see a range of dispersal mechanisms. Conidia of ascomycete fungi, for example, are dispersed passively by wind, rain, and insects, and by active mechanisms involving the explosive formation of gas bubbles and the elastic deformation of cell walls. Spore dispersal is a very important research area, because it affects fungal distribution and population biology, and the spread of plant and animal diseases (epidemiology). Airborne spores are a major cause of human allergy (Chapter 9), and there is growing evidence that the huge number of spores in the atmosphere influences cloud formation and rainfall patterns.

Genetic variation, sexuality, and evolution are discussed in Chapter 4. Researchers have turned a few fungi into model organisms for the study of genetics, including the aforementioned yeast, and the filamentous ascomycete, *Neurospora crassa*, which was instrumental in early research on gene expression. The life cycles of both species involve sexual reproduction in which pairs of compatible strains merge and form spores after sexual recombination. The notion of male and female is meaningless for fungi. Reproduction in some of the mushroom-forming basidiomycetes involves pairings between tens of thousands of different mating types. Fungal genetics is further complicated by difficulties in defining individual organisms. Should we regard two or more independent colonies that have separated from a parent mycelium as the same individual? Trickier still is the nature of the fungal species. Current work on these topics is informing wider questions on fungal variation, microevolution, gene flow, and other fundamental issues in evolutionary biology.

Fungal adaptation to the environment is the subject of Chapter 5. With the notable exception of aquatic species that form flagellate zoospores, fungi explore their environment through growth rather than motion. Growing fungi are at the mercy of the nutritional conditions in microscopic proximity to their cell surface. The expansion of a mycelium of interconnected hyphae allows the fungus to meet the challenges of localised nutrient depletion by transferring materials across the colony from regions where food is more plentiful. This adaptability allows fungi to travel through large volumes of soil and cope with exigencies of water and nutrient availability that exclude other microorganisms. Fungi are osmotrophs, absorbing nutrients from their surroundings using an array of secreted enzymes to decompose complex molecules and transport proteins to import the resulting harvest of small molecules through their cell membranes. The galaxy of proteins secreted by fungi is called the secretome, and its analysis is an exciting area of contemporary research. Fungal metabolism is another topic in Chapter 5. The primary metabolism of the fungi follows the same pathways that support other eukaryotes. Fungal secondary metabolism generates an incredible array of pharmacologically active compounds, mycotoxins and mushroom poisons, pigments, and volatile aromatic compounds.

Before the introduction of molecular methods to the study of fungal ecology, research on the roles of fungi in nutrient cycling and other ecological processes emphasised the importance of species made visible by their fruit bodies, or those that were amenable to pure culture. So much was missed. Molecular methods have changed our picture of microbial diversity in different habitats, and this work makes it clear that we have only begun to understand the ecological significance of the fungi. Metagenomic techniques and other methods used for environmental sampling and the analysis of ecosystem processes are introduced in Chapter 6.

The next four chapters (Chapters 7–10) cover interactions between fungi and other organisms. Fungi support plant productivity through mycorrhizal symbioses (Chapter 7) and damage and destroy plants through their activities as pathogens (Chapter 8). Mycorrhizal relationships include ectomycorrhizas, in which the colonies of mushroom-forming basidiomycetes, and a few ascomycetes, envelop the roots of trees and shrubs. These fungi expand into the surrounding soil, creating an absorptive network that supplies the plant host with water and dissolved minerals. The fungi benefit from these relationships by receiving carbohydrates from the plant. Arbuscular mycorrhizas are established by 200 species of Glomeromycota with 80% of the families of vascular plants. Fungi also engage in specialised kinds of mycorrhizal symbioses with orchids, species of parasitic plants, members of the Ericales, and bryophytes. Lichens and endophytic relationships are other examples of fungal mutualisms considered in Chapter 7. More than 18,000 ascomycete species and fewer than 50 basidiomycetes are lichenized; green algae and cyanobacteria are the photosynthetic partners in these intimate relationships. Pathogenic interactions with plants are introduced in Chapter 8. Plant pathogens include the rusts and smuts (Basidiomycota) and thousands of species of Ascomycota that infect every family of plants and cause billions of dollars of annual crop losses. Pathogens classified within the Oomycota (stramenopiles rather than fungi) have been studied by mycologists since the nineteenth century. *Phytophthora infestans* is the best known of these microorganisms, because it caused the potato famine in Ireland in the 1840s. The Oomycota, known as water moulds, are more closely related to brown algae and diatoms than they are to fungi. Functionally, however, they operate like fungi. Water moulds form branching colonies of tip-growing hyphae that penetrate their food sources, secrete digestive enzymes, and absorb small molecules to meet their nutritional needs. Similarities between the morphology, cellular organisation, and behaviour of the oomycetes and fungi offer a beautiful illustration of evolutionary convergence. Water moulds are included in this book, despite their lack of genealogical connection with the fungi.

Although fungal infections of humans are not as common as bacterial and viral diseases, human mycoses are widespread and are a significant cause of morbidity and mortality (Chapter 9). Most mycoses are opportunistic infections, stimulated by damage to the skin barrier, underlying metabolic problems, and compromised immune defenses. Fungal infections of the lung are established via the inhalation of infectious spores, and systemic infections can develop from normally harmless fungi that grow in the urogenital tract and gut, and on the skin. Fungal pathogens of other vertebrates and invertebrates are also addressed in this chapter. In recent decades a number of epidemic fungal diseases of animals have been recognised for the first time. These include: chytridiomycosis, caused by *Batrachochytrium dendrobatidis* (Chytridiomycota), which affects one-third of amphibian species; white-nose disease, caused by *Pseudogymnoascus destructans* (Ascomycota), which has killed 6 million bats in North America; and marine aspergillosis, caused by *Aspergillus sydowii* (Ascomycota), which threatens sea fan corals in the Caribbean. Mutualisms with animals include basidiomycetes farmed by ants and termites, and fungi that occupy the gut microbiome of vertebrates and invertebrates. Chapter 10 concerns interactions between fungi and other heterotrophic microorganisms. These include the competition for resources between different colonies of soil fungi, fungal parasitism of other fungi (mycoparasitism), and ecological relations between fungi and bacteria.

Mycological research has provided compelling illustrations of widespread biological responses to planetary warming. These investigations are the subject of Chapter 11. Changes in the prevalence of certain fungi can be tracked in the palynological record. A dramatic decrease in the prevalence of spores from dung fungi in the Pleistocene reflects the mass extinction of megaherbivores like the woolly mammoth and mastodon, resulting from human activity. In recent decades, alterations in the seasonality of mushroom fruiting have been measured in Europe that are linked to the extension of the growing season and delay in the first frost. Climate change is also affecting the distribution of lichens. Mathematical models predict an increase in the concentration of airborne allergenic spores and changes in the geographical distribution of plant diseases as warming proceeds.

Biotechnology is the subject of Chapter 12. The term biotechnology is often reserved for modern industrial processes involving genetically modified organisms, but a broader reading includes baking and brewing practices that originated in the ancient world. Mushroom cultivation on logs and horse dung are other examples of early biotechnology that has flavoured the omnivorous diet of our species. Methods for controlling fungal fermentations developed in parallel with progress in microbiology since the nineteenth century. The use of fungi to produce antibiotics and other pharmaceutical products is a more recent part of this endeavour and the introduction of molecular genetic manipulation of fungal strains has had a major impact on the business of biotechnology.

This book is written for undergraduates and graduate students, and will also be useful for professional biologists interested in familiarising themselves with specific topics in fungal biology. Few scientists identify themselves as fungal biologists or mycologists. This is a reflection of the ethos of modern biology that emphasises the study of questions about cell and molecular biology, genetics, ecological interactions, and so on, rather than encouraging societies of scientists to investigate all aspects of a particular group of organisms. In the last 50 years, academic departments have hired fewer and fewer mycologists, phycologists, entomologists, ornithologists, and so on. This is not necessarily a bad thing. There is a vibrant international community of cell biologists who study yeast, and none of these scientists call themselves mycologists. Filamentous fungi, including the ascomycete *Neurospora crassa*, have also attracted a good deal of attention from cell and molecular biologists, few of whom identify as mycologists. Ecological research is benefitting from more synthetic studies on interactions between groups of organisms, rather than the exclusive study of fungi or any other taxonomic category. Our growing recognition of the enormous breadth of biodiversity, the unifying molecular characteristics of all organisms, and the wealth and complexity of interactions between species may see the extinction of specialists in single groups of organisms. It will be interesting to see how the culture of biological research and education evolves.

The scope of mycological research has expanded in many areas in the 15 years since the publication of the second edition of this textbook. Molecular methods that seemed innovative in 2001 have been replaced with novel technologies, matched with increased computing power. For example, the laborious sequencing of short lengths of DNA, which was standard practice in 2001, has been supplanted by techniques that allow fast sequencing of genes and whole genomes. New techniques in light microscopy, including live-cell imaging, confocal microscopy, and high-speed video, have also had a huge impact on fungal biology. The resulting change of pace in many research areas presents a challenge for authors committed to covering the whole discipline of fungal biology. The variety of approaches necessitated by the diversity of topics has meant that the stylistic unity of previous editions is no longer feasible, and each of us has assumed responsibility for a subset of the chapters. Cross-referencing and a comprehensive index allow the reader to navigate between topics throughout the book.