21st Century
Guidebook to **Fungi**

Fungi have their own unique cell biology and life cycle, but also play critical roles in wider biological systems. This textbook provides an all-round view of fungal biology, ranging in scope from the evolutionary origins of fungi and other eukaryotes more than a billion years ago, to the impact fungi have on our current, everyday lives. Bringing mycology teaching right up to date, this integrative approach gives students a broader understanding of fungal biology than traditional textbooks and provides the tools to incorporate fungi into wider biology teaching.

- Unique systems biology approach emphasises interactions between fungi and other organisms to illustrate the critical roles that fungi play in every ecosystem and food web
- Highlights the importance of fungi in 'new' biology, including genomics and bioinformatics, with examples of computational modelling
- Over 20 resource boxes spread throughout the text point the reader towards external resources that provide further information
- Companion CD features a hyperlinked version of the book, the fully integrated *World of Cyberfungi* website and the *Neighbour-Sensing* interactive fungal growth simulator program

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Psathyrella multipedata (crowded brittlestem) photographed by David Moore at Harlow Carr Gardens. 'A thousand mushrooms crowd to a keyhole ... They lift frail heads in gravity and good faith ... They are begging us, you see, in their wordless way ... To do something, to speak on their behalf ... Or at least not to close the door again.' (Lines from Derek Mahon's poem 'A disused shed in County Wexford' In: *Collected Poems*, Gallery Press, 1999.)

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PREFACE

Why write a textbook? That's a question we've asked ourselves several times over the past few years; sometimes with exasperation, often in dismay at the mountain of tasks that remained to be completed. The authors have taught a general mycology course in the University of Manchester for many years. From the year 2000 increasing emphasis was given to Internet/Intranet-delivered modules for this course, providing students with yearly-enhanced resources in the form of PDF downloads of lecture notes, PowerPoint presentations as Flash movies, broadcast video and audio files streamed to the registered student end-user, and an extensive resource of reference material provided as full-text PDF for download from the Faculty Intranet. By the 2008/9 session these resources were distilled into a completely new online textbook: the first draft of *21st Century Guidebook to Fungi*.

So we didn't actually make a decision to write a textbook; rather it emerged from our everyday (and every year) teaching. For something like 20 years our course portrayed Kingdom Fungi as a major eukaryotic Kingdom in its own right. Fungi have their own unique cell biology, their own unique developmental biology and their own unique lifestyle, and play critical roles in every ecosystem and every food web, and we thought it essential that biology undergraduates should be given the opportunity to understand all this.

In adapting these resources to a print-format manuscript we have taken the opportunity to structure the manuscript in a way that satisfies the various definitions of the phrase ***systems biology***:

- we emphasise ***interactions*** between fungi and other organisms to bring out the functions and behaviours of biological systems;
- we concentrate on ***integration*** rather than reduction, which satisfies those who would see systems biology as a paradigm of scientific method, and we show original research data and how interpretations are drawn from them;
- we include all sorts of ***computational modelling*** and ***bioinformatics*** for those who view systems biology in terms of operational research protocols;
- and we bring together data about the biological systems from diverse ***interdisciplinary sources***, from astrophysics to zoology;
- finally, we make it all computer friendly with an accompanying CD which features a hyperlinked version of the entire book, the fully integrated World of Cyberfungi website and the Neighbour-Sensing interactive fungal growth simulator program.

This makes *21st Century Guidebook to Fungi* unique for a textbook of fungal biology, and other unique features include the fact that this book has been written in ***this*** century and gives a 'new-millennium' treatment to Kingdom Fungi as a ***biological system*** with its own intrinsic interest rather than as a diverse group of individually fascinating, but still separate, organisms. We call this a *Guidebook* because we have always been aware of the impossibility of writing a comprehensive, monographic treatment of an entire Kingdom, so we decided to follow the model of a tourist guide to a holiday destination. These do not attempt a comprehensive depiction of a location, but they bring attention to a broad range of places you might find interesting, describe enough for you to decide if you ***are*** interested, and tell you how to get there. Each section of your *Guidebook to Fungi* directs you to an interesting aspect of fungal biology and, perhaps unusually for a textbook, provides references to external resources that will provide more information. Some of those references are to Internet resources, particularly videos; others are to reprinted papers and articles. If you are fortunate enough to take the course as a registered student at the University of Manchester, just a click of your mouse will immediately download a PDF full-text version of over 700 such articles from the Faculty's Intranet.

Here, we cannot provide another 7000 or so pages of reprint collection, but we can give you the means to access them quickly and you will find that the vast majority of our references include a DOI number (indeed the complete DOI URL). The acronym DOI stands for Digital Object Identifier, which uniquely identifies where an electronic document (or other electronic object) can be found on the Internet and remains fixed. Other information about a document may change over time, including where to find it, but its DOI name will not change and will always direct you to the original electronic document. To access one of these references using the printed information enter the DOI URL into your browser and you will be taken to the document on the website of the original publisher. Alternatively, the DOI references on the accompanying CD version of the book are live hyperlinks so, providing you have a live Internet connection, just a click of your mouse will take you to the original publisher's website. Almost always you will have free access to the abstract or summary of the article, but if your institution maintains a subscription to the products of that publisher you may be able to download the complete text of the article. Save the downloaded document to your hard disk to build your own reprint collection.

There is a broader reason why we have written ***this*** textbook, which is that mycology teaching needs some tender, loving care. It's in danger of disappearing altogether.

Over the last 25 years there has been a large increase in the number of students proceeding to university but this has been accompanied by a substantial decrease in the funding provided per student. Change in teaching provision has been accompanied by a narrowing of biological sciences research, which has become increasingly focussed on the more biomedical aspects of the subject, resulting in a consequential narrowing in the scope of biological science subjects taught in universities, both in the UK and worldwide.

These changes in biological sciences teaching and research have been encouraged by several features. Universities have sought economies of scale by merging Biological Science departments. For example, the University of Manchester merged **eleven** Biological Science departments into a single Department of Biological Sciences.[1] This Department became the Faculty of Life Sciences in the new institution formed when UMIST and the Victoria University of Manchester merged in 2004.

With most other UK universities following Manchester's lead, only the Universities of Oxford and Cambridge now have Departments of Botany, the traditional host department for mycology teaching and research. This reduction in the scope of biological sciences teaching intensified as many staff in traditional areas of biology, for example, taxonomy and ecology, failed to appreciate the importance of molecular biology and the influence it would have on their subject areas. Indeed, in the 1980s some biological science staff viewed molecular biology as a self-contained discipline that had little or no relevance to their work. Unfortunately, many mycologists were among those who held this view. So, one purpose of the present text is to dispel lingering doubts about the importance of molecular biology to all aspects of mycology by illustrating from the start how the molecule-level perspective improves our understanding of fungi.

Inevitably, the natural importance that governments attach to health care has caused funding bodies to focus support on biomedical research at the expense of other areas of the subject, including mycology. During the latter part of the twentieth century, reduced funding for biological science teaching and channelling of funding to biomedical research strongly influenced the way in which universities redeveloped their biological science departments. Today, some such departments largely serve the perceived needs of teaching and research in medicine, that is, they mainly support or underpin medical activities. In our opinion, this type of interdepartmental relationship is unlikely to generate high-quality research in either biological sciences or medicine. Would the research of George Beadle and Edward Tatum, working with *Neurospora crassa,* or Paul Nurse, working with *Schizosaccharomyces pombe* or Lee Hartwell (who worked with *Saccharomyces cerevisiae*) flourish in such an environment? When Beadle and Tatum, and Nurse and Hartwell initiated the research that eventually resulted in their becoming Nobel laureates, they were almost certainly unaware of the relevance of their work to medicine. It is our view that, although biological sciences and medical departments should collaborate closely, each should be independent of the other, and, to a greater or lesser extent, each should foster all aspects of its subject area. If evolution has taught us anything it is about the advantage gained by populations that have large gene pools, and there's not much academic diversity in a Department of Human Biology.

In view of all this, an underlying purpose of the present text is to emphasise the broad importance of fungi to man and the economy. Every hour of our day depends on the activities of fungi. The feature which has figured most in our decision to write on this topic is that although fungi comprise

[1] Wilson, D. (2008). *Reconfiguring Biological Sciences in the Late Twentieth Century: A Study of the University of Manchester.* Manchester, UK: Centre for the History of Science, Technology and Medicine. ISBN-10: 095589719X, ISBN-13: 978–0955897191.

what is arguably the most crucial kingdom of organisms on the planet, these organisms are often bypassed and ignored by the majority of biologists. We use the word 'crucial' in the previous sentence because molecular phylogenies place animals and fungi together at the root of evolutionary trees. It is likely that the first eukaryotes would have been recognised as 'fungal in nature' by features presently associated with that kingdom. So in a sense, those primitive 'fungi' effectively ***invented*** the lifestyle of so-called higher organisms. Fungi remain crucial to life on Earth because animal life depends on plant life for continued existence and plants depend on fungi (over 95% of terrestrial plants require fungal infection of their roots by mycorrhizas for adequate root function; Section 13.8). The number of fungal species has been conservatively put at 1.5 million, though the true number may be much higher than this. Among this number is included the largest organism on Earth; one individual mycelium of *Armillaria gallica* covering some 8.9 km^2 in the Malheur National Forest, Oregon (see Section 14.4). Fungi also include some of the most rapidly moving organisms on Earth, because when some fungal spores are discharged they can be subjected to forces of acceleration several thousand times greater than that experienced by astronauts during the launch of the Space Shuttle (Section 9.8)! Fungi also provide an essential service to the planet by being responsible for the majority of the biomass recycling, particularly the decomposition of dead plants. Saprotrophic degradation is the characteristic lifestyle of the majority of fungi, and without this activity we would be buried under dead plant litter (see Chapter 10).

The contribution that fungi make to human existence is close to crucial, too. Imagine life without bread, without alcohol, without antibiotics, without soft drinks (citric acid), coffee or chocolate, without cheese (fungal rennet), salami or soy sauce, or without cyclosporine, which prevents organ rejection by suppressing the immune response in transplant patients, without the statins, which keep so many people alive these days by controlling cholesterol levels, and even without today's most widely used agricultural fungicides, the strobilurins, and you are imagining a much less satisfactory existence than we currently enjoy.

But fungi are not always benevolent. There are fungal diseases of all our crops, and in many cases crop losses of 20% to 50% are *expected* by the industry. And there is more to fungal infection of humans than athlete's foot; the majority of AIDS patients now die of fungal infections, and opportunistic fungal infections of patients with chronic immunodeficiency is an increasing clinical challenge.

Unfortunately, even though fungi make up such a large group of higher organisms, most current biology teaching, from school level upwards, concentrates on animals, with a trickle of information about plants. School curricula around the world are almost completely silent about fungal biology as most school curricula persist with the Victorian obsession to compare animals with plants. But fungi are not plants, and are so different from plants that no amount of plant biology will give an adequate understanding of any fungus. Similarly, although more closely related, in molecular terms, to animals, fungi are not animals and a deficiency of fungal biology cannot be compensated by more zoology. Yet none of the school science curricula we have examined (not even those claiming to specialise in 'biology') give adequate accounts of ***all*** the different sorts of organisms that exist on Earth. The result is that the majority of school and college students (and, since they've been through the same system, most current university academics) are ignorant of fungal biology and therefore of their own dependence on fungi in everyday life. This is a self-sustaining cycle of ignorance that results in institutions being oblivious to fungi; all generated by the lack of an even-handed treatment of fungal biology in national school curricula. It seems to apply throughout Europe, North and South America, and Australasia; indeed, through most of the English-speaking world.

We believe, though we have small hope of seeing it, that biological science departments need to guard against overspecialisation, particularly as most universities are following an identical strategy of focussing on biomedical activities. We fear that emerging concerns about food security will result in the UK regretting its lack of mycologists and plant scientists, as it presently regrets its lack of nuclear engineers. It is important for Europe to maintain a critical mass of mycologists in both universities and research institutes; and we've written this book to educate them.

We want to end by proffering our sincere thanks to those students of ours who have made constructive comments on this *Guidebook* as it developed over the years. We also thank our families for their help and understanding while we produced this text. And finally, we give our thanks to the many friends and colleagues who provided information ahead of publication and devoted their time and effort to supplying us with illustrations used in this book: **Professor M. Catherine Aime** Louisiana State University; **Dr G. W. Beakes** University of Newcastle upon Tyne; **Professor Meredith Blackwell** Louisiana State University; **Dr Manfred Binder** Clark University; **Professor C. Kevin Boyce** University of Chicago; **Professeur Jacques Brodeur**

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