



# 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

DAVID MOORE is a retired Reader in Genetics and Honorary Reader in the Faculty of Life Sciences at the University of Manchester. He is a past President of the British Mycological Society and was Executive Editor of the international scientific journal *Mycological Research* for ten years. In recent years he has created the educational website [www.fungi4schools.org](http://www.fungi4schools.org) which provides resources for UK schools, sponsored by the British Mycological Society.

GEOFFREY D. ROBSON is Senior Lecturer in the Faculty of Life Sciences at the University of Manchester. He teaches undergraduate courses on 'Microbes, Man and the Environment', 'Fungal Ecology and Biotechnology' and 'Microbial Biotechnology' and is Programme Director for the Enterprise Biotechnology Course. He has served as General Secretary of the British Mycological Society and is currently President-Elect.

ANTHONY P. J. TRINCI was Barker Professor of Cryptogamic Botany and Dean of the School of Biological Sciences, and is now Emeritus Professor at the University of Manchester. His teaching at Manchester included undergraduate courses in microbiology, mycology and biotechnology, and postgraduate-level units in microbial biotechnology. He is a past President of both the Society for General Microbiology and the British Mycological Society.



*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.)

Cambridge University Press  
978-0-521-18695-7 - 21st Century: Guidebook to Fungi  
David Moore, Geoffrey D. Robson and Anthony P. J. Trinci  
Frontmatter  
[More information](#)



# 21st Century Guidebook to Fungi

David Moore  
Geoffrey D. Robson  
Anthony P. J. Trinci

Faculty of Life Sciences  
The University of Manchester



CAMBRIDGE  
UNIVERSITY PRESS

Cambridge University Press  
978-0-521-18695-7 - 21st Century: Guidebook to Fungi  
David Moore, Geoffrey D. Robson and Anthony P. J. Trinci  
Frontmatter  
[More information](#)

CAMBRIDGE  
UNIVERSITY PRESS

University Printing House, Cambridge CB2 8BS, United Kingdom

Published in the United States of America by Cambridge University Press,  
New York

Cambridge University Press is part of the University of Cambridge.

It furthers the University’s mission by disseminating knowledge in the  
pursuit of education, learning and research at the highest international  
levels of excellence.

[www.cambridge.org](http://www.cambridge.org)  
Information on this title: [www.cambridge.org/9781107006768](http://www.cambridge.org/9781107006768)

© The University of Manchester 2011

This publication is in copyright. Subject to statutory exception  
and to the provisions of relevant collective licensing agreements,  
no reproduction of any part may take place without  
the written permission of Cambridge University Press.

First published 2011  
3rd printing 2015

Printed in the United Kingdom by TJ International Ltd, Padstow, Cornwall

*A catalogue record for this publication is available from the British  
Library*

*Library of Congress Cataloging-in-Publication Data*

Moore, D. (David), 1942–  
21st century guidebook to fungi / David Moore, Geoff Robson,  
Tony Trinci.  
p. cm.  
ISBN 978-1-107-00676-8 (Hardback) – ISBN 978-0-521-18695-7  
(pbk.) 1. Fungi. 2. Fungal molecular biology. I. Robson, G. D.  
(Geoffrey D.) II. Trinci, A. P. J. III. Title. IV. Title: Twenty first  
century guidebook to fungi.  
QK603.M616 2011  
579.5–dc22 2010040920

ISBN 978-1-107-00676-8 Hardback  
ISBN 978-0-521-18695-7 Paperback

Cambridge University Press has no responsibility for the persistence or  
accuracy of URLs for external or third-party internet websites referred to  
in this publication, and does not guarantee that any content on such  
websites is, or will remain, accurate or appropriate.

CONTENTS

<i>Preface</i>	<i>page ix</i>	3.11 Ecosystem mycology	77
		3.12 References and further reading	79
<b>Part I Nature and origins of fungi</b>	<b>1</b>	<b>Part II Fungal cell biology</b>	<b>83</b>
<b>1 21st century fungal communities</b>	<b>3</b>	<b>4 Hyphal cell biology and growth on solid substrates</b>	<b>85</b>
1.1 What and where are fungi?	4	4.1 Mycelium: the hyphal mode of growth	86
1.2 Soil, the essential terrestrial habitat	5	4.2 Spore germination and dormancy	86
1.3 How much soil is there and where is it?	5	4.3 The fungal lifestyle: colony formation	86
1.4 The nature of soil and who made it	5	4.4 Mycelium growth kinetics	88
1.5 Soil biota are extremely varied and numerous	7	4.5 Colony growth to maturity	91
1.6 Microbial diversity in soil	7	4.6 Morphological differentiation of fungal colonies	92
1.7 Microbial diversity in general	8	4.7 Duplication cycle in moulds	92
1.8 Geomycology	9	4.8 Regulation of nuclear migration	93
1.9 The origins of agriculture and our dependence on fungi	10	4.9 Growth kinetics	94
1.10 References and further reading	15	4.10 Autotrophic reactions	96
<b>2 Evolutionary origins</b>	<b>18</b>	4.11 Hyphal branching	97
2.1 Life, the universe and everything	19	4.12 Septation	99
2.2 Planet Earth: your habitat	21	4.13 Ecological advantage of mycelial growth in colonising solid substrates	100
2.3 The Goldilocks planet	21	4.14 References and further reading	101
2.4 The tree of life has three domains	23	<b>5 Fungal cell biology</b>	<b>104</b>
2.5 The Kingdom Fungi	29	5.1 Mechanisms of mycelial growth	105
2.6 The opisthokonts	30	5.2 The fungus as a model eukaryote	105
2.7 Fossil fungi	31	5.3 The essentials of cell structure	107
2.8 The fungal phylogeny	35	5.4 Subcellular components of eukaryotic cells: the nucleus	108
2.9 References and further reading	38	5.5 The nucleolus and nuclear import and export	112
<b>3 Natural classification of fungi</b>	<b>41</b>	5.6 Nuclear genetics	114
3.1 The members of the Kingdom Fungi	42	5.7 Mitotic nuclear division	115
3.2 The chytrids	42	5.8 Meiotic nuclear division	117
3.3 More chytrids: the Neocallimastigomycota	45	5.9 Translation of mRNA and protein sorting	118
3.4 Blastocladiomycota	46	5.10 The endomembrane systems	121
3.5 Glomeromycota	50	5.11 Cytoskeletal systems	125
3.6 The traditional Zygomycota	52	5.12 Molecular motors	127
3.7 Ascomycota	55	5.13 Plasma membrane and signalling pathways	133
3.8 Basidiomycota	61	5.14 Fungal cell wall	136
3.9 The species concept in fungi	71		
3.10 The untrue fungi	75		



5.15	Cell biology of the hyphal apex	137	9.4	<i>Aspergillus</i> conidiophores	220
5.16	Hyphal fusions and mycelial interconnections	142	9.5	Conidiation in <i>Neurospora crassa</i>	223
5.17	Cytokinesis and septation	144	9.6	Conidiomata	223
5.18	Yeast–mycelial dimorphism	150	9.7	Linear structures: strands, cords, rhizomorphs and stipes	225
5.19	References and further reading	151	9.8	Globose structures: sclerotia, stromata, ascomata and basidiomata	227
6	<b>Structure and synthesis of fungal cell walls</b>	156	9.9	References and further reading	231
6.1	The fungal wall as a working organelle	157	<b>Part IV Biochemistry and developmental biology of fungi</b>		235
6.2	Fundamentals of wall structure and function	157	10	<b>Fungi in ecosystems</b>	237
6.3	Fundamentals of wall architecture	160	10.1	Contributions of fungi to ecosystems	238
6.4	The chitin component	160	10.2	Breakdown of polysaccharide: cellulose	239
6.5	The glucan component	162	10.3	Breakdown of polysaccharide: hemicellulose	240
6.6	The glycoprotein component	163	10.4	Breakdown of polysaccharide: pectins	241
6.7	Wall synthesis and remodelling	165	10.5	Breakdown of polysaccharide: chitin	241
6.8	On the far side	168	10.6	Breakdown of polysaccharide: starch and glycogen	241
6.9	The fungal wall as a clinical target	171	10.7	Lignin degradation	242
6.10	References and further reading	172	10.8	Digestion of protein	246
<b>Part III Fungal genetics and diversity</b>		177	10.9	Lipases and esterases	247
7	<b>From the haploid to the functional diploid: homokaryons, heterokaryons, dikaryons and compatibility</b>	179	10.10	Phosphatases and sulfatases	247
7.1	Compatibility and the individualistic mycelium	180	10.11	The flow of nutrients: transport and translocation	247
7.2	Formation of heterokaryons	181	10.12	Primary (intermediary) metabolism	251
7.3	Breakdown of a heterokaryon	183	10.13	Secondary metabolites, including commercial products like statins and strobilurins	257
7.4	The dikaryon	183	10.14	References and further reading	264
7.5	Vegetative compatibility	185	11	<b>Exploiting fungi for food</b>	266
7.6	Biology of incompatibility systems	188	11.1	Fungi as food	267
7.7	Gene segregation during the mitotic division cycle	189	11.2	Fungi in food webs	267
7.8	Parasexual cycle	194	11.3	Wild harvests: commercial mushroom picking	272
7.9	Cytoplasmic segregations: mitochondria, plasmids, viruses and prions	194	11.4	Cells and mycelium as human food	274
7.10	References and further reading	197	11.5	Fermented foods	274
8	<b>Sexual reproduction: the basis of diversity and taxonomy</b>	198	11.6	Industrial cultivation methods	275
8.1	The process of sexual reproduction	199	11.7	Gardening insects and fungi	279
8.2	Mating in budding yeast	200	11.8	Development of a fungal fruit body	280
8.3	Mating type switching in budding yeast	201	11.9	References and further reading	280
8.4	Mating types of <i>Neurospora</i>	203	12	<b>Development and morphogenesis</b>	282
8.5	Mating types in Basidiomycota	205	12.1	Development and morphogenesis	283
8.6	Biology of mating type factors	210	12.2	The formal terminology of developmental biology	283
8.7	References and further reading	211	12.3	The observational and experimental basis of fungal developmental biology	285
9	<b>Continuing the diversity theme: cell and tissue differentiation</b>	213	12.4	Ten ways to make a mushroom	286
9.1	What is diversity?	214	12.5	Competence and regional patterning	289
9.2	Mycelial differentiation	214			
9.3	Making spores	216			

12.6	The <i>Coprinopsis</i> fruit body: making hymenia	291	<b>14 Fungi as pathogens of plants</b>	367
12.7	<i>Coprinopsis</i> and <i>Volvariella</i> making gills (not forgetting how polypores make tubes)	295	14.1 Fungal diseases and loss of world agricultural production	368
12.8	The <i>Coprinopsis</i> fruit body: making stems	301	14.2 A few examples of headline crop diseases	370
12.9	Coordination of cell inflation throughout the maturing fruit body	304	14.3 The rice blast fungus <i>Magnaporthe grisea</i> (Ascomycota)	370
12.10	Mushroom mechanics	305	14.4 <i>Armillaria</i> (Basidiomycota)	370
12.11	Metabolic regulation in relation to morphogenesis	305	14.5 Pathogens that produce haustoria (Ascomycota and Basidiomycota)	371
12.12	Developmental commitment	308	14.6 <i>Cercospora</i> (Ascomycota)	372
12.13	Comparisons with other tissues and other organisms	310	14.7 <i>Ophiostoma</i> ( <i>Ceratocystis</i> ) <i>novo-ulmi</i> (Dutch elm disease or DED) (Ascomycota)	372
12.14	Classic genetic approaches to study development and the impact of genomic data mining	311	14.8 Black stem rust ( <i>Puccinia graminis</i> f. sp. <i>tritici</i> ) threatens global wheat harvest	373
12.15	Degeneration, senescence and death	315	14.9 Plant disease basics: the disease triangle	374
12.16	Basic principles of fungal developmental biology	316	14.10 Necrotrophic and biotrophic pathogens of plants	376
12.17	References and further reading	316	14.11 The effects of pathogens on their hosts	376
<b>Part V Fungi as saprotrophs, symbionts and pathogens</b>		323	14.12 How pathogens attack plants	379
<b>13 Ecosystem mycology: saprotrophs, and mutualisms between plants and fungi</b>		325	14.13 Host penetration through stomatal openings	379
13.1 Ecosystem mycology		326	14.14 Direct penetration of the host cell wall	382
13.2 Fungi as recyclers and saprotrophs		326	14.15 Enzymatic penetration of the host	382
13.3 Make the earth move		328	14.16 Preformed and induced defence mechanisms in plants	385
13.4 Fungal toxins: food contamination and deterioration (including mention of statins and strobilurins)		328	14.17 Genetic variation in pathogens and their hosts: co-evolution of disease systems	387
13.5 Decay of structural timber in dwellings		331	14.18 References and further reading	389
13.6 Using fungi to remediate toxic and recalcitrant wastes		334	<b>15 Fungi as symbionts and predators of animals</b>	392
13.7 Release of chlorohydrocarbons into the atmosphere by wood-decay fungi		336	15.1 Fungal co-operative ventures	393
13.8 Introduction to mycorrhizas		336	15.2 Ant agriculture	393
13.9 Types of mycorrhiza		337	15.3 Termite gardeners of Africa	398
13.10 Arbuscular (AM) endomycorrhizas		338	15.4 Agriculture in beetles	399
13.11 Ericoid endomycorrhizas		341	15.5 Anaerobic fungi and the rise of the ruminants	400
13.12 Arbutoid endomycorrhizas		343	15.6 Nematode-trapping fungi	405
13.13 Monotropoid endomycorrhizas		343	15.7 References and further reading	408
13.14 Orchidaceous endomycorrhizas		344	<b>16 Fungi as pathogens of animals, including humans</b>	411
13.15 Ectomycorrhizas		346	16.1 Pathogens of insects	412
13.16 Ectendomycorrhizas		351	16.2 Microsporidia	412
13.17 The effects of mycorrhizas and their commercial applications and the impact of environmental and climate changes		351	16.3 Trichomycetes	414
13.18 Introduction to lichens		356	16.4 Laboulbeniales	416
13.19 Introduction to endophytes		360	16.5 Entomogenous fungi	417
13.20 Epiphytes		361	16.6 Biological control of arthropod pests	421
13.21 References and further reading		361	16.7 Cutaneous chytridiomycosis: an emerging infectious disease of amphibians	422
			16.8 Aspergillosis disease of coral	424
			16.9 Mycoses: the fungus diseases of humans	424
			16.10 Clinical groupings for human fungal infections	426

16.11 Fungi within the home and their effects on health: allergens and toxins	432	<b>18 Molecular biotechnology</b>	511
16.12 Comparison of animal and plant pathogens and the essentials of epidemiology	436	18.1 Antifungal agents that target the membrane	512
16.13 Mycoparasitic and fungiculous fungi	439	18.2 Antifungal agents that target the wall	521
16.14 References and further reading	444	18.3 Clinical control of systemic mycoses at the start of the 21st century: azoles, polyenes and combinatorial therapy	522
<b>Part VI Fungal biotechnology and bioinformatics</b>	449	18.4 Agricultural mycocides at the start of the twenty-first century: strobilurins	526
<b>17 Whole organism biotechnology</b>	451	18.5 Understanding fungal genetic structure	529
17.1 Fungal fermentations in submerged liquid cultures	452	18.6 Sequencing fungal genomes	531
17.2 Culturing fungi	452	18.7 Annotating the genome	535
17.3 Oxygen demand and supply	456	18.8 Fungal genomes and their comparison	540
17.4 Fermenter engineering	458	18.9 Manipulating genomes: targeted gene disruption, transformation and vectors	547
17.5 Fungal growth in liquid cultures	460	18.10 Fungi as cell factories producing heterologous proteins	552
17.6 Fermenter growth kinetics	462	18.11 Recombinant protein production by filamentous fungi	554
17.7 Growth yield	464	18.12 Bioinformatics in mycology: manipulating very large data sets	557
17.8 Stationary phase	465	18.13 Genomic data mining supports the notion that there are different developmental control mechanisms in fungi, animals and plants	560
17.9 Growth as pellets	466	18.14 Effects of climate change on fungi revealed by analysis of large survey data sets	562
17.10 Beyond the batch culture	469	18.15 Cyber fungi: mathematical modelling and computer simulation of hyphal growth	563
17.11 Chemostats and turbidostats	470	18.16 References and further reading	567
17.12 Uses of submerged fermentations	473	<b>Part VII Appendices</b>	573
17.13 Alcoholic fermentations	474	Appendix 1 Outline classification of fungi	575
17.14 Citric acid biotechnology	477	Appendix 2 Mycelial and hyphal differentiation	589
17.15 Penicillin and other pharmaceuticals	478	<i>Index</i>	605
17.16 Enzymes for fabric conditioning and processing, and food processing	483	<i>Plate sections: Section 1 between pages 148 and 149</i>	
17.17 Steroids and use of fungi to make chemical transformations	486	<i>Section 2 between pages 340 and 341</i>	
17.18 The Quorn™ fermentation and evolution in fermenters	487		
17.19 Production of spores and other inocula	492		
17.20 Natural digestive fermentations in herbivores	493		
17.21 Solid state fermentations	494		
17.22 Digestion of lignocellulosic residues	497		
17.23 Bread: the other side of the alcoholic fermentation equation	499		
17.24 Cheese and salami manufacture	501		
17.25 Soy sauce, tempeh and other food products	504		
17.26 References and further reading	506		



## 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.<sup>1</sup> 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

<sup>1</sup> 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<sup>2</sup> 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

Université de Montréal; **Professor Mark Brundrett** University of Western Australia; **James Burn** emapsite.com sales team Reading; **Sheila and Jack Fisher** Chichester; **Forestry Images** <http://www.forestryimages.org>; **Dr Elizabeth Frieders** University of Wisconsin–Platteville; **Professor G. M. Gadd** FRSE University of Dundee; **Dr Daniel Henk** Medical School Imperial College London; **Professor David S. Hibbett** Clark University; **Dr Kentaro Hosaka** National Museum of Nature and Science Japan; **Dr Carol Hotton** National Museum of Natural History Washington DC; **Dr F. M. Hueber** National Museum of Natural History Washington DC; **Dr Timothy Y. James** University of Michigan; **Dr P. R. Johnston** Landcare Research New Zealand; **Tom Jorstad** Smithsonian Institution; **Pamela Kaminski** <http://pkaminski.homestead.com>; **Dr Bryce Kendrick** <http://www.mycolog.com>; **Geoffrey Kibby** *Field Mycology*; **Dr Cletus P. Kurtzman** USDA/ARS Peoria; **Dr Roselyne Labbé** Agriculture and Agri-Food Canada Ontario; **Dr Marc-André Lachance** Western Ontario University; **Professor Karl-Henrik Larsson** Göteborg University; **Dr Heino Lepp** Australian National Botanical Gardens; **Dr Peter M. Letcher** University of Alabama; **Professor Xingzhong Liu** Chinese Academy of Sciences Beijing; **Dr Mark Loftus** Lambert Spawn Co.; **Dr Joyce E. Longcore** University of Maine; **Dr P. Brandon Matheny** University of Tennessee; **Dr Audrius Meškauskas** Switzerland; **Professor Steven L. Miller** University of Wyoming; **Dr Randy Molina** *Mycorrhiza* and USDA Forest

Service; **Professor Dr H. Peter Molitoris** Regensburg; **Dr Jean-Marc Moncalvo** Royal Ontario Museum and University of Toronto; **Elizabeth Moore** Stockport; NASA's Space Telescope Science Institute; **Dr Stephen F. Nelsen** University of Wisconsin–Madison; **Professor Birgit Nordbring-Hertz** Lund University; **Dr Lily Novak Frazer** University Hospital of South Manchester; **Dr Ingo Nuss** Mintraching-Sengkofen Germany; **Dr Kerry O'Donnell** USDA/ARS Peoria; **Dr Fritz Oehl** ART Zürich; **Dr Lise Øvreås** University of Bergen; **Mary Parrish** Smithsonian Institution; **Dr Jens H. Petersen** University of Aarhus; **Professor Nick D. Read** Institute of Cell Biology University of Edinburgh; **Professeur Dirk Redecker** INRA/Université de Bourgogne; **Professor Karl Ritz** Cranfield University; **Dr Carmen Sánchez** Universidad Autónoma de Tlaxcala México; **Professeur Marc-André Selosse** Université Montpellier II; **Dr Sabrina Setaro** Wake Forest University; **Dr Karen Snetselaar** Managing Editor *Mycologia* Saint Joseph's University Philadelphia; **Malcolm Storey** <http://www.bioimages.org.uk>; **Professor Junta Sugiyama** TechnoSuruga Co. Ltd Tokyo; **Dr Sung-Oui Suh** American Type Culture Collection; **Mr John L. Taylor** Manchester; **Professor Vigdis Torsvik** University of Bergen; **Professor John Webster** University of Exeter; **Dr Alexander Weir** SUNY–ESF New York; **Professor Merlin M. White** Boise State University; **Alex Wild** Photography Illinois; **Ence Yang** Chinese Academy of Sciences Beijing.