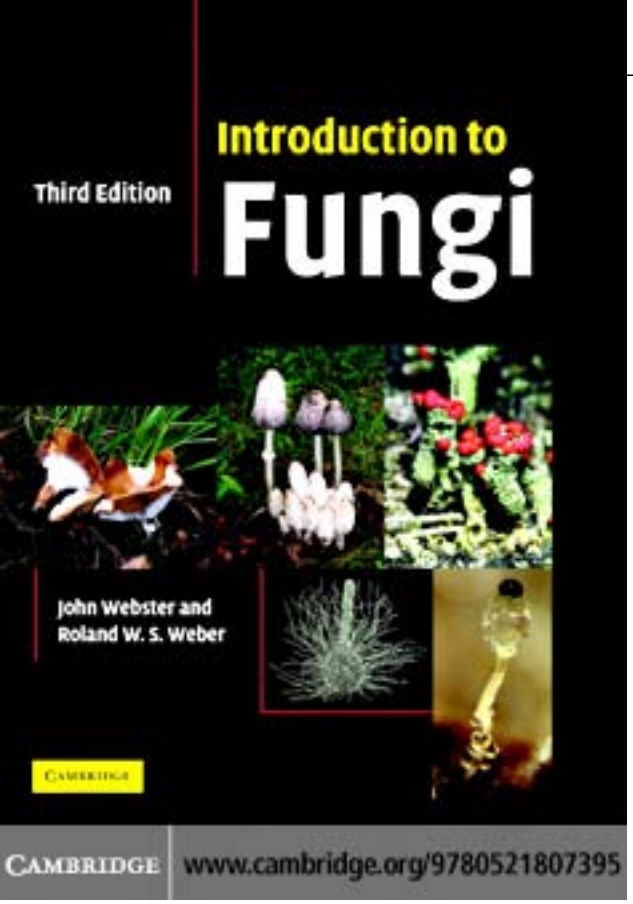
Introduction to
Third Edition
Fungi
John Webster and
Roland W. S. Weber
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Introduction to Fungi

This new edition of the universally acclaimed and widely used textbook on fungal biology has been completely rewritten, drawing directly on the authors' research and teaching experience. The text takes account of the rapid and exciting progress that has been made in the taxonomy, cell and molecular biology, biochemistry, pathology and ecology of the fungi. Features of taxonomic significance are integrated with natural functions, including their relevance to human affairs. Special emphasis is placed on the biology and control of human and plant pathogens, providing a vital link between fundamental and applied mycology. The book is richly illustrated throughout with specially prepared drawings and photographs, based on living material. Illustrated life cycles are provided, and technical terms are clearly explained. Extensive reference is made to recent literature and developments, and the emphasis throughout is on whole-organism biology from an integrated, multi-disciplinary perspective.

John Webster is Professor Emeritus of the School of Biosciences at the University of Exeter, UK.

Roland W.S. Weber was a Lecturer in the Department of Biotechnology at the University of Kaiserslautern, Germany, and is currently at the Fruit Experiment station (OVB) in Jork, Germany.

Introduction to Fungi

John Webster
University of Exeter
and
Roland Weber
University of Kaiserslautern

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To Philip M. Booth

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Colour plate section appears between pages 412 and 413

Preface to the first edition

There are several available good textbooks of mycology, and some justification is needed for publishing another. I have long been convinced that the best way to teach mycology, and indeed all biology, is to make use, wherever possible, of living material. Fortunately with fungi, provided one chooses the right time of the year, a wealth of material is readily available. Also by use of cultures and by infecting material of plant pathogens in the glasshouse or by maintaining pathological plots in the garden, it is possible to produce material at almost any time. I have therefore tried to write an introduction to fungi which are easily available in the living state, and have tried to give some indication of where they can be obtained. In this way I hope to encourage students to go into the field and look for fungi themselves. The best way to begin is to go with an expert, or to attend a Fungus Foray such as those organized in the spring and autumn by mycological and biological societies. I owe much of my own mycological education to such friendly gatherings. A second aim has been to produce original illustrations of the kind that a student could make for himself from simple preparations of living material, and to illustrate things which he can verify for himself. For this reason I have chosen not to use electron micrographs, but to make drawings based on them.

The problem of what to include has been decided on the criterion of ready availability. Where an uncommon fungus has been included this is because it has been used to establish some important fact or principle. A criticism which I must accept is that no attempt has been made to deal with Fungi Imperfecti as a group. This is not because they are not common or important but that to have included them would have made the book much longer. To mitigate this shortcoming I have described the conidial states of some Ascomycotina rather fully, to include reference to some of the form-genera which have been linked with them. A more difficult problem has been to know which system of classification to adopt. I have finally chosen the 'General Purpose Classification' proposed by Ainsworth, which is adequate for the purpose of providing a framework of reference. I recognize that some might wish to classify fungi differently, but see no great merit in burdening the student with the arguments in favour of this or that system.

Because the evidence for the evolutionary origins of fungi is so meagre I have made only scant reference to the speculations which have been made on this topic. There are so many observations which can be verified, and for this reason I have preferred to leave aside those which never will.

The literature on fungi is enormous, and expanding rapidly. Many undergraduates do not have much time to check original publications. However, since the book is intended as an introduction I have tried to give references to some of the more recent literature, and at the same time to quote the origins of some of the statements made.

Exeter, 27 April 1970 J.W.

Preface to the second edition

In revising the first edition, which was first published about ten years ago, I have taken the opportunity to give a more complete account of the Myxomycota, and to give a more general introduction to the Eumycota. An account has also been given of some conidial fungi, as exemplified by aquatic Fungi Imperfecti, nematophagous fungi and seed-borne fungi. The taxonomic framework has been based on Volumes IVA and IVB of Ainsworth, Sparrow and Sussman's *The Fungi: An Advanced Treatise* (Academic Press, 1973).

Exeter, January 1979 J.W.

Preface to the third edition

Major advances, especially in DNA-based technology, have catalysed a sheer explosion of mycological knowledge since the second edition of *Introduction to Fungi* was published some 25 years ago. As judged by numbers of publications, the field of molecular phylogeny, i.e. the computer-aided comparison of homologous DNA or protein sequences, must be at the epicentre of these developments. As a result, information is now available to facilitate the establishment of taxonomic relationships between organisms or groups of organisms on a firmer basis than that previously assumed from morphological resemblance. This has in turn led to revised systems of classification and provided evidence on which to base opinions on the possible evolutionary origin of fungal groups. We have attempted to reflect some of these advances in this edition. In general we have followed the outline system of classification set out in *The Mycota* Volume VII (Springer-Verlag) and the *Dictionary of the Fungi* (ninth edition, CABI Publishing). However, the main emphasis of our book remains that of presenting the fungi in a sensible biological context which can be understood by students, and therefore some fungi have been treated along with taxonomically separate groups if these share fundamental biological principles. Examples include *Microbotryum*, which is treated together with smut fungi rather than the rusts to which it belongs taxonomically, or *Haptoglossa*, which we discuss alongside *Plasmodiophora* rather than with the Oomycota.

Molecular phylogeny has been instrumental in clarifying the relationships of anamorphic fungi (fungi imperfecti), presenting an opportunity to integrate their treatment with sexually reproducing relatives. There are only a few groups such as nematophagous fungi and the aquatic and aero-aquatic hyphomycetes which we continue to treat as ecological entities rather than scattered among ascomycetes and basidiomycetes. Similarly, the gasteromycetes, clearly an unnatural assemblage, are described together because of their unifying biological features. However, in all these cases taxonomic affinities are indicated where known. We have also included several groups now placed well outside the Fungi, such as the Oomycota (Straminipila) and Myxomycota and Plasmodiophoromycota (Protozoa). This is because of their biological and economic importance and because they have been and continue to be studied by mycologists.

There have been major advances in other areas of research, notably the molecular cell biology of the two yeasts *Saccharomyces* and *Schizosaccharomyces*, 'model organisms' which have a bearing far beyond mycology. Further, much exciting progress is being made in elucidating the molecular aspects of the infection biology of human and plant pathogens, and in developing fungi for biotechnology. These trends are represented in the current edition. Nevertheless, the fundamental concept of *Introduction to Fungi* remains that of the previous two editions: to place an organism in its taxonomic context while discussing as many relevant aspects of its biology as possible in a holistic manner. Many of the illustrations are based on original line drawings because we believe that these can readily portray an understanding of structure and that drawing as a record of interpretation is a good discipline. However, we have also extended the use of photographs, and we now provide illustrated life cycles because these are more easily understood. As before, our choice of illustrated species has been influenced by the ready availability of material, enabling students and their teachers to examine living fungi, which is a cornerstone of good teaching. At their first introduction most technical terms have been printed in bold, their meanings explained and their derivations given. The page numbers where these definitions are given have been highlighted in the index.

The discipline of mycology has evolved and diversified so enormously in recent decades that it is now a daunting task for individual authors to give a balanced, integrated account of the fungi. Of course, there will be omissions or

misrepresentations in a work of this scale, and we offer our apologies to those who feel that their work or that of others has not been adequately covered. At the same time, it has been a fascinating experience for us to write this book, and we have thoroughly enjoyed the immense diversity of approaches and ideas which make mycology such a vibrant discipline at present. We hope to have conveyed some of its fascination to the reader in the text and by referring to as many original publications as possible.

Exeter and Kaiserslautern, 1 March 2006

J.W. and R.W.S.W.

Acknowledgements

We are indebted to many people who have helped us in our extensive revisions to *Introduction to Fungi*. This edition is dedicated to Mr Philip M. Booth in profound gratitude for his financial support and his encouragement over many years. We have acknowledged in the figure legends the many friends and colleagues who have responded so enthusiastically to our call for help by providing us with illustrations, sometimes previously unpublished, and we thank numerous publishing houses for permission to include published figures. We thank Caroline Huxtable and Rob Ford (Exeter University Library) and Jennifer Mergel and Petra Tremmel (Kaiserslautern University Library) for help beyond the call of duty in obtaining interlibrary loans. Dr Wolf-Rüdiger Arendholz and Dr Roger T.A. Cook have read the entire manuscript or parts of it, and their feedback and corrections have been most valuable to us. We are immensely grateful to Professors Heidrun and Timm Anke (Kaiserslautern) for their support of this project, their encouragement and for providing such a stimulating environment for research and teaching of fungal biology.

By far the heaviest toll has been paid by our families and friends who have had only cursory sightings of us during the past six years. We owe a debt of gratitude to them for their patient forbearance and unwavering support.

1

Introduction

1.1 What are fungi?

About 80 000 to 120 000 species of fungi have been described to date, although the total number of species is estimated at around 1.5 million (Hawksworth, 2001; Kirk *et al*., 2001). This would render fungi one of the least-explored biodiversity resources of our planet. It is notoriously difficult to delimit fungi as a group against other eukaryotes, and debates over the inclusion or exclusion of certain groups have been going on for well over a century. In recent years, the main arguments have been between taxonomists striving towards a phylogenetic definition based especially on the similarity of relevant DNA sequences, and others who take a biological approach to the subject and regard fungi as organisms sharing all or many key ecological or physiological characteristics – the 'union of fungi' (Barr, 1992). Being interested mainly in the way fungi function in nature and in the laboratory, we take the latter approach and include several groups in this book which are now known to have arisen independently of the monophyletic 'true fungi' (**Eumycota**) and have been placed outside them in recent classification schemes (see Fig. 1.25). The most important of these 'pseudofungi' are the Oomycota (see Chapter 5). Based on their lifestyle, fungi may be circumscribed by the following set of characteristics (modified from Ainsworth, 1973):

1. *Nutrition*. Heterotrophic (lacking photosynthesis), feeding by absorption rather than ingestion.
2. *Vegetative state*. On or in the substratum, typically as a non-motile mycelium of hyphae showing internal protoplasmic streaming. Motile reproductive states may occur.
3. *Cell wall*. Typically present, usually based on glucans and chitin, rarely on glucans and cellulose (Oomycota).
4. *Nuclear status*. Eukaryotic, uni- or multinucleate, the thallus being homo- or heterokaryotic, haploid, dikaryotic or diploid, the latter usually of short duration (but exceptions are known from several taxonomic groups).
5. *Life cycle*. Simple or, more usually, complex.
6. *Reproduction*. The following reproductive events may occur: sexual (i.e. nuclear fusion and meiosis) and/or parasexual (i.e. involving nuclear fusion followed by gradual de-diploidization) and/or asexual (i.e. purely mitotic nuclear division).
7. *Propagules*. These are typically microscopically small spores produced in high numbers. Motile spores are confined to certain groups.
8. *Sporocarps*. Microscopic or macroscopic and showing characteristic shapes but only limited tissue differentiation.
9. *Habitat*. Ubiquitous in terrestrial and freshwater habitats, less so in the marine environment.
10. *Ecology*. Important ecological roles as saprotrophs, mutualistic symbionts, parasites, or hyperparasites.
11. *Distribution*. Cosmopolitan.

With photosynthetic pigments being absent, fungi have a heterotrophic mode of nutrition. In contrast to animals which typically feed by ingestion, fungi obtain their nutrients by extracellular digestion due to the activity of secreted enzymes, followed by absorption of the solubilized breakdown products. The combination of extracellular digestion and absorption can be seen as the ultimate determinant of the fungal lifestyle. In the course of evolution, fungi have conquered an astonishingly wide range of habitats, fulfilling important roles in diverse ecosystems (Dix & Webster, 1995). The conquest of new, often patchy resources is greatly facilitated by the production of numerous small spores rather than a few large propagules, whereas the colonization of a food source, once reached, is achieved most efficiently by growth as a system of branching tubes, the **hyphae** (Figs. 1.1a,b), which together make up the **mycelium**.

Hyphae are generally quite uniform in different taxonomic groups of fungi. One of the few features of distinction that they do offer is the presence or absence of cross-walls or **septa**. The Oomycota and Zygomycota generally have aseptate hyphae in which the nuclei lie in a common mass of cytoplasm (Fig. 1.1a). Such a condition is described as **coenocytic** (Gr. *koinos* = shared, in common; *kytos* = a hollow vessel, here meaning cell). In contrast, Asco- and Basidiomycota and their associated asexual states generally have septate hyphae (Fig. 1.1b) in which each segment contains one, two or more nuclei. If the nuclei are genetically identical, as in a mycelium derived from a single uninucleate spore, the mycelium is said to be **homokaryotic**, but where

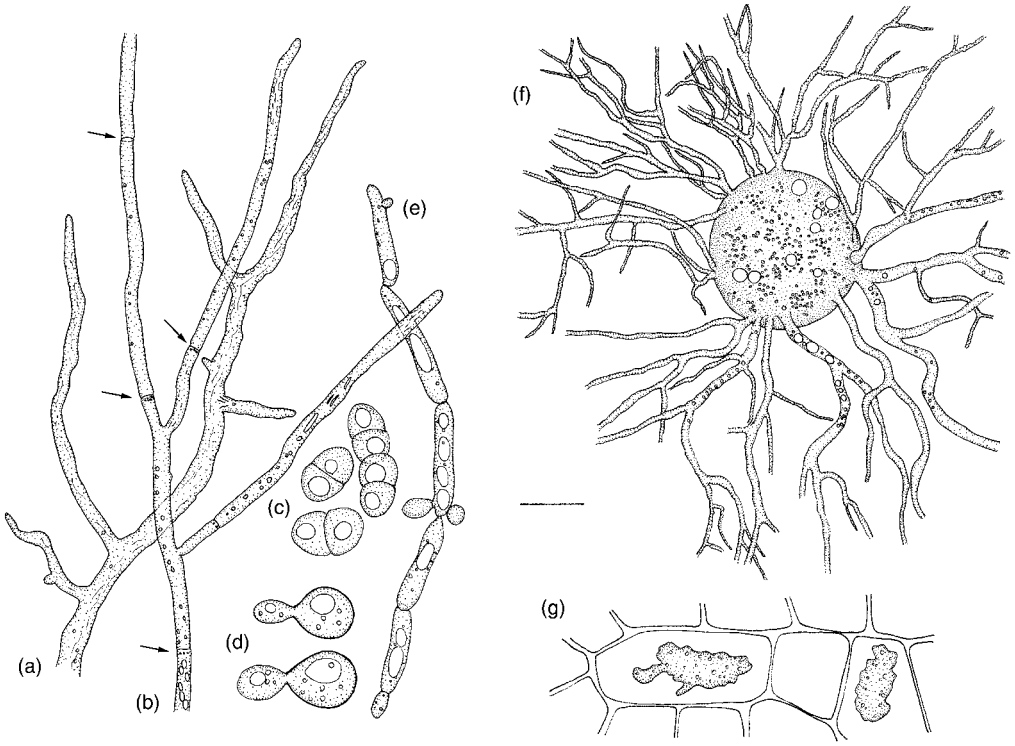

Fig 1.1 Various growth forms of fungi. (a) Aseptate hypha of *Mucor mucedo* (Zygomycota). The hypha branches to form a mycelium. (b) Septate branched hypha of *Trichoderma viride* (Ascomycota). Septa are indicated by arrows. (c) Yeast cells of *Schizosaccharomyces pombe* (Ascomycota) dividing by binary fission. (d) Yeast cells of *Dioszegia takashimae* (Basidiomycota) dividing by budding. (e) Pseudohypha of *Candida parapsilosis* (Ascomycota), which is regarded as an intermediate stage between yeast cells and true hyphae. (f) Thallus of *Rhizophlyctis rosea* (Chytridiomycota) from which a system of branching rhizoids extends into the substrate. (g) Plasmodia of *Plasmodiophora brassicae* (Plasmodiophoromycota) inside cabbage root cells. Scale bar = 20 μm (a,b,f,g) or 10 μm (c–e).