
Series Preface

Mycology, the study of fungi, originated as a sub discipline of botany and was a descriptive discipline, largely neglected as an experimental science until the early years of this century. A seminal paper by Blakeslee in 1904 provided evidence for self incompatibility, termed “heterothallism”, and stimulated interest in studies related to the control of sexual reproduction in fungi by mating-type specificities. Soon to follow was the demonstration that sexually reproducing fungi exhibit Mendelian inheritance and that it was possible to conduct formal genetic analysis with fungi. The names Burgeff, Kniep and Lindegren are all associated with this early period of fungal genetics research.

These studies and the discovery of penicillin by Fleming, who shared a Nobel Prize in 1945, provided further impetus for experimental research with fungi. Thus began a period of interest in mutation induction and analysis of mutants for biochemical traits. Such fundamental research, conducted largely with *Neurospora crassa*, led to the one gene: one enzyme hypothesis and to a second Nobel Prize for fungal research awarded to Beadle and Tatum in 1958. Fundamental research in biochemical genetics was extended to other fungi, especially to *Saccharomyces cerevisiae*, and by the mid-1960s fungal systems were much favored for studies in eukaryotic molecular biology and were soon able to compete with bacterial systems in the molecular arena.

The experimental achievements in research on the genetics and molecular biology of fungi have benefited more generally studies in the related fields of fungal biochemistry, plant pathology, medical mycology, and systematics. Today, there is much interest in the genetic manipulation of fungi for applied research. This current interest in biotechnical genetics has been augmented by the development of DNA-mediated transformation systems in fungi and by an understanding of gene expression and regulation at the molecular level. Applied research initiatives involving fungi extend broadly to areas of interest not only to industry but to agricultural and environmental sciences as well.

It is this burgeoning interest in fungi as experimental systems for applied as well as basic research that has prompted publication of this series of books under the title *The Mycota*. This title knowingly relegates fungi into a separate realm, distinct from that of either plants, animals, or protozoa. For consistency throughout this Series of Volumes the names adopted for major groups of fungi (representative genera in parentheses) areas follows:

Pseudomycota

Division: Oomycota (*Achlya*, *Phytophthora*, *Pythium*)
Division: Hyphochytriomycota

Eumycota

Division:	Chytridiomycota (<i>Allomyces</i>)
Division:	Zygomycota (<i>Mucor</i> , <i>Phycomyces</i> , <i>Blakeslea</i>)
Division:	Dikaryomycota
Subdivision:	Ascomycotina
Class:	Saccharomycetes (<i>Saccharomyces</i> , <i>Schizosaccharomyces</i>)
Class:	Ascomycetes (<i>Neurospora</i> , <i>Podospora</i> , <i>Aspergillus</i>)
Subdivision:	Basidiomycotina
Class:	Heterobasidiomycetes (<i>Ustilago</i> , <i>Tremella</i>)
Class:	Homobasidiomycetes (<i>Schizophyllum</i> , <i>Coprinus</i>)

We have made the decision to exclude from *The Mycota* the slime molds which, although they have traditional and strong ties to mycology, truly represent nonfungal forms insofar as they ingest nutrients by phagocytosis, lack a cell wall during the assimilative phase, and clearly show affinities with certain protozoan taxa.

The Series throughout will address three basic questions: what are the fungi, what do they do, and what is their relevance to human affairs? Such a focused and comprehensive treatment of the fungi is long overdue in the opinion of the editors.

A volume devoted to systematics would ordinarily have been the first to appear in this Series. However, the scope of such a volume, coupled with the need to give serious and sustained consideration to any reclassification of major fungal groups, has delayed early publication. We wish, however, to provide a preamble on the nature of fungi, to acquaint readers who are unfamiliar with fungi with certain characteristics that are representative of these organisms and which make them attractive subjects for experimentation.

The fungi represent a heterogeneous assemblage of eukaryotic microorganisms. Fungal metabolism is characteristically heterotrophic or assimilative for organic carbon and some nonelemental source of nitrogen. Fungal cells characteristically imbibe or absorb, rather than ingest, nutrients and they have rigid cell walls. The vast majority of fungi are haploid organisms reproducing either sexually or asexually through spores. The spore forms and details on their method of production have been used to delineate most fungal taxa. Although there is a multitude of spore forms, fungal spores are basically only of two types: (i) asexual spores are formed following mitosis (mitospores) and culminate vegetative growth, and (ii) sexual spores are formed following meiosis (meiospores) and are borne in or upon specialized generative structures, the latter frequently clustered in a fruit body. The vegetative forms of fungi are either unicellular, yeasts are an example, or hyphal; the latter may be branched to form an extensive mycelium.

Regardless of these details, it is the accessibility of spores, especially the direct recovery of meiospores coupled with extended vegetative haploidy, that have made fungi especially attractive as objects for experimental research.

The ability of fungi, especially the saprobic fungi, to absorb and grow on rather simple and defined substrates and to convert these substances, not only into essential metabolites but into important secondary metabolites, is also noteworthy. The metabolic capacities of fungi have attracted much interest in natural products chemistry and in the production of antibiotics and other bioactive compounds. Fungi, especially yeasts, are important in fermentation processes. Other fungi are important in the production of enzymes, citric acid and other organic compounds as well as in the fermentation of foods.

Fungi have invaded every conceivable ecological niche. Saprobiotic forms abound, especially in the decay of organic debris. Pathogenic forms exist with both plant and animal hosts. Fungi even grow on other fungi. They are found in aquatic as well as soil environments, and their spores may pollute the air. Some are edible; others are poisonous. Many are variously associated with plants as copartners in the formation of lichens and mycorrhizae, as symbiotic endophytes or as overt pathogens. Association with animal systems varies; examples include the predaceous fungi that trap nematodes, the microfungi that grow in the anaerobic environment of the rumen, the many insect associated fungi and the medically important pathogens afflicting humans. Yes, fungi are ubiquitous and important. There are many fungi, conservative estimates are in the order of 100,000 species, and there are many ways to study them, from descriptive accounts of organisms found in nature to laboratory experimentation at the cellular and molecular level. All such studies expand our knowledge of fungi and of fungal processes and improve our ability to utilize and to control fungi for the benefit of humankind.

We have invited leading research specialists in the field of mycology to contribute to this Series. We are especially indebted and grateful for the initiative and leadership shown by the Volume Editors in selecting topics and assembling the experts. We have all been a bit ambitious in producing these Volumes on a timely basis and therein lies the possibility of mistakes and oversights in this first edition. We encourage the readership to draw our attention to any error, omission or inconsistency in this Series in order that improvements can be made in any subsequent edition.

Finally, we wish to acknowledge the willingness of Springer-Verlag to host this project, which is envisioned to require more than 5 years of effort and the publication of at least nine Volumes.

Bochum, Germany
Auburn, AL, USA
April 1994

KARL ESSER
PAUL A. LEMKE
Series Editors

Volume Preface to the Second Edition

There have been major changes in our knowledge of the systematics and evolution of fungi since the first edition of the *Mycota*, Vol. VII. These changes have been driven by an outpouring of molecular phylogenetic analyses at first based on one or a few genes but now by multiple conserved genes. The Assembling the Fungal Tree of Life projects have been a major contributor to the data needed to construct the molecular phylogenies along with work from many additional labs. The resulting phylogenies have made possible a new taxonomic outline for the Fungi (Hibbett D.S. et al., 2007, *Mycol. Res.* 111: 509–547), which has provided a more stable systematic treatment for this kingdom, although some of the basal groups of Fungi remain incompletely resolved (Table 1). Agreement among many mycologists on nomenclature is providing a stable framework for Fungi that has been incorporated into reference works and online databases (McLaughlin D. J. et al., 2009, *Trends Microbiol.* 17: 488–497), and has provided an escape from the conflicting phenetic classifications of the past. These nomenclatural changes are incorporated into these volumes along with much new information on the evolution and ecology of these organisms made possible by a variety of methods, including environmental sequencing and reevaluation of character evolution using molecular phylogenies.

While there is agreement on nomenclature within Kingdom Fungi, there is less agreement on the names for groups of fungus-like organisms, although these organisms remain a major interest of those who study fungi. Some of the confusion arises from the treatment of fungus-like organisms under two nomenclatural codes (Table 1). Of special concern has been the treatment of the oomycetes and their relatives with variant spellings of the kingdom and common name. The solution adopted by Beakes (Chap. 3, Vol. VII, Part A) reserves *Straminipila* for the kingdom and uses the widely cited *stramenopiles* for the common name.

Chapters in this edition of the *Mycota*, Vol. VII, vary from updates of chapters published in the first edition to new chapters. All systematic chapters treat monophyletic groups; clearly polyphyletic groups, such as those based on yeasts or asexual stages (anamorphs), have been omitted. While authors have been encouraged to provide illustrations of the diversity within each group, the results are somewhat uneven. Some authors have extensively illustrated the organisms, while others for reasons of time or access have provided limited illustrations. In the interest of getting these chapters to press in a not too tardy manner, the authors have not been unduly pressed to add illustrations. The reader's understanding is requested for the omissions, which is caused in part by the difficulty of getting all of the chapters needed to cover a wide spectrum of organisms.

Table 1 Taxonomic outline for Fungi and fungus-like organisms^a

<i>Fungus-like organisms</i>
Supergroup: Amoebozoa
Phylum: Dictyosteliomycota
Phylum: Myxomycota
Supergroup: Excavata
Phylum: Acrasiomycota
Supergroup: Sar ^b
Subgroup: Rhizaria
Phylum: Phytomyxea
Kingdom: Straminipila ^c
Phylum: Labyrinthulomycota
Phylum: Hyphochytriomycota
Phylum: Oomycota
<i>Fungi</i>
Supergroup: Opisthokonta
Kingdom: Fungi
<i>Basal fungi</i>
Phylum: Cryptomycota ^d
Phylum: Microsporidia
<i>Traditional Chytridiomycota</i>
Phylum: Chytridiomycota
Phylum: Monoblepharidomycota
Phylum: Neocallimastigomycota
Phylum: Blastocladiomycota
<i>Zygomycotan (Zygomycetous) Fungi</i>
Phylum: Entomophthoromycota
Phylum/a incertae sedis:
Subphylum: Kickxellomycotina
Subphylum: Mortierellomycotina
Subphylum: Mucoromycotina
Subphylum: Zoopagomycotina
Phylum: Glomeromycota
Subkingdom Dikarya
Phylum: Basidiomycota
Subphylum: Pucciniomycotina
Subphylum: Ustilaginomycotina
Subphylum: Agaricomycotina
Phylum: Ascomycota
Subphylum: Taphrinomycotina
Subphylum: Saccharomycotina
Subphylum: Pezizomycotina

^aNames for Fungi and fungus-like organisms traditionally studied by botanists are governed by the *International Code for Nomenclature of algae, fungi and plants (Melbourne Code)* (McNeil J. et al., 2012, Regnum Vegetabile 154, Koeltz Scientific Books). Multiple names exist for eukaryotic microorganisms that are treated under both the Melbourne Code and the International Code of Zoological Nomenclature, except for Microsporidia, which are classified under the zoological code

^bSar (Stramenopiles, Alveolata, and Rhizaria)

^cAlso known as Stramenopila or Stramenopiles. The latter is used by Adl et al. (2012, J. Eukaryot. Microbiol. 59: 429–493) and as a common name, stramenopiles, for Straminipila

^dAlso known as Rozellida and Rozellomycota

The Mycota, Vol. VII, includes treatments of the systematics and related topics for Fungi and fungus-like organisms in four eukaryotic supergroups (Table 1) as well as specialized chapters on nomenclature, techniques, and evolution. Most Fungi and fungus-like organisms are covered, including the Microsporidia. Chapter 1, Vol. VII, Part A, provides an overview of fungal origins and evolution.

Chapters 2–4, Vol. VII, Part A, cover the fungus-like organisms, and Chaps. 5 to 14, Vol. VII, Part A, and Chaps. 1–6, Vol. VII, Part B, cover the Fungi. Each of these chapters covers approximately the following topics: occurrence and distribution, economic importance, morphology and ultrastructure, development of the taxonomic theory, classification, and maintenance and culture. The fungus-like organisms are distributed in three distantly related supergroups (Table 1). The basal fungi and traditional Chytridiomycota are treated as six phyla and covered in four chapters, including Chap. 1, Vol. VII, Part A. The zygomycetous fungi, whose deeper relationships remain unresolved, and Glomeromycota are covered in two chapters. The Basidiomycota and Ascomycota, the largest groups of fungi, are treated in five or six chapters each. In the Basidiomycota two chapters cover Pucciniomycotina and Ustilaginomycotina, respectively, while three chapters are devoted to classes of the Agaricomycotina. In the Ascomycota a single chapter covers Taphrinomycotina and Saccharomycotina, while eight classes of the Pezizomycotina are covered in five chapters.

The following topics are treated in Chaps. 7–11 in Vol. VII, Part B: Chap. 7 deals with the nomenclatural changes necessitated by the recent changes to the International Code for Nomenclature of algae, fungi, and plants (Table 1), including the elimination of separate names for anamorphic fungi. Chapter 8 deals with methods for preservation of cultures and specimens, while Chap. 9 reviews the phylogenetic implications of subcellular and biochemical characters and methods for ultrastructural study. Chapter 10 deals with the fungal fossil record and Chap. 11 with the impact of the availability of whole genomes on studies of Fungi.

We are entering a new era in the study of fungi with whole genomes becoming available for an increasing number of species across all the known clades of Fungi. This genome-enabled mycology will utilize large numbers of genes in phylogenomic analyses to resolve difficult to determine relationships in fungi and to provide insights into fungal biology (Hibbett D.S. et al., 2013, *Mycologia* 106: 1339–1349). Initial studies are already having a significant impact on our understanding of biochemical processes and their ecological impacts. In time genomic studies may shed light on the genetic processes and the genes that control the great morphological diversity in Fungi from the subcellular to the macroscopic level. Thus, there is much new information on the systematics and evolution of fungi to be expected in the future.

We thank Meredith Blackwell for sharing unpublished manuscripts and discussions on the classification system, Esther G. McLaughlin for advice throughout the work, and the U.S. National Science Foundation for support to many labs for the AFTOL 1 and AFTOL 2 projects (including DEB-0732550 to DJM, and DEB-0732993 to JWS), and numerous scientists who have contributed to the work which has made the advances in these volumes possible.

St. Paul, MN
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22 May 2014

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Volume Preface to the First Edition

This is an exciting time to produce an overview of the systematics and evolution of the fungi. Homoplasmy is evident in all lineages, e.g., those based on the gross morphology of the chytrid zoospore, the perithecium and apothecium, the smut teliospore and the agaric fruiting body, and some classifications based on light microscope morphology have been shown to be unsound. Molecular and subcellular characters, aided by new methods of phylogenetic analysis, have allowed us to see through the conflicts between various phenetic classification schemes and have given us some confidence that we are beginning to achieve a true phylogeny of the fungi. Molecular data have both supported ultrastructural characters that first began to unravel the homoplasies unrecognized at the light microscopic level, and have also revealed the relationships of fungi to other eukaryotes. They continue to enlarge the scope of the fungi, e.g., with the recent addition of the Microsporidia (see Cavalier-Smith, Chap. 1, Vol. VII, Part A), and they have shown the need for more detailed chemical, subcellular, and developmental studies for a fuller understanding of these organisms and their relationships.

This volume is a mixture of phylogenetic and more classical systematics. Progress in knowledge of species and development of taxonomic characters is mixed. Groups with few species have been studied in great detail, while in groups with large numbers of species much effort is still needed to find and determine the taxa. Classical systematics groups organisms on a phenetic basis, then sets up a classification; phylogeny is a secondary consideration. Phylogenetic systematics first determines organism relationships, then constructs a systematic classification that reflects the phylogeny. Molecular characters have made possible the establishment of a monophyletic and, hopefully, more permanent classification for the fungi. Thus, Volume VII of *The Mycota* contains both classical and phylogenetic classifications, reflecting the available data and the orientation of different authors. The incompleteness of some classifications, e.g., those for the Urediniomycetes (Swann, Frieders, and McLaughlin, Chap. 2, Vol. VII, Part B) and Homobasidiomycetes (Hibbett and Thorn, Chap. 5, Vol. VII, Part B), demonstrates that we are in the early stages of a phylogenetic systematics for these groups.

The taxonomic outline used in *The Mycota*, Vol. VII, differs somewhat from that of other volumes in the series (Table 1), reflecting current mycological systematics. There is a lack of agreement on the naming of higher taxa, and the rules of nomenclature permit more than one name for these taxa. Cavalier-Smith (Chap. 1, Vol. VII, Part A) presents an alternative view to the taxonomic outline used for the remainder of the volume (Table 2). Some of the nomenclatural problems stem from a lack of resolution of deep branches in molecular evolutionary trees, a problem that appears likely to be resolved only with additional

Table 1 Taxonomic outline at the kingdom, phylum, and class levels as used in other volumes in the series and in this volume. The classification in this volume is necessarily confusing at this time because authors are using their own classifications rather than an imposed classification

Mycota, Vol. I	Mycota, Vol. VII
PSEUDOMYCOTA	PSEUDOMYCOTA ^{a,b}
Oomycota	Oomycota ^c
	Peronosporomycetes
Hyphochytriomycota	Hyphochytriomycota
	Hyphochytriomycetes
	Plasmodiophoromycota
	Plasmodiophoromycetes
EUMYCOTA	EUMYCOTA
Chytridiomycota	Chytridiomycota ^d
	Chytridiomycetes
Zygomycota	Zygomycota ^d
	Zygomycetes
	Trichomycetes
Dikaryomycota	
Ascomycotina	Ascomycota ^e
Saccharomycetes	Saccharomycetes
Ascomycetes	Plectomycetes
	Hymenoascomycetes ^a
	Loculoascomycetes ^a
Basidiomycotina	Basidiomycota
Heterobasidiomycetes	Urediniomycetes
	Ustilaginomycetes
	Heterobasidiomycetes ^{a,f}
Homobasidiomycetes	Homobasidiomycetes ^{a,f}

^aArtificial taxon

^bFor a natural classification for Oomycota and Hyphochytriomycota, kingdom Stramenopila (Stramenipila, Dick, Chap. 2, Vol. VII, Part A) or Chromista have been proposed, and for Plasmodiophoromycota, kingdom Protozoa (see Cavalier-Smith, Chap. 1, Vol. VII, Part A)

^cOr Heterokonta (see Cavalier-Smith, Chap. 1, and Dick, Chap. 2, Vol. VII, Part A)

^dProbably paraphyletic (see Cavalier-Smith, Chap. 1, Vol. VII, Part A, and Berbee and Taylor, Chap. 10, Vol. VII, Part B)

^eA phylogenetic classification for Ascomycota is not available. Current thinking among ascomycete scholars is that three classes should be recognized, as follows: “Archiascomycetes”, which may not be monophyletic, Hemiascomycetes (see Kurtzman and Sugiyama, Chap. 9, Vol. VII, Part A), and a filamentous group, Euascomycetes, that eventually will be subdividable, perhaps at the subclass level [M.E. Berbee and J.W. Taylor, 1995, Can J Bot 73 (Suppl. 1):S677, and Chap. 10, Vol. VII, Part B; J.W. Spatafora, 1995, Can J Bot 73 (Suppl. 1):S811]. Saccharomycetes as used here (see Barr, Chap. 8, Vol. VII, Part A) includes “Archiascomycetes” and Hemiascomycetes. See the relevant chapters for further speculation on the ultimate disposition of these groups

^fHeterobasidiomycetes as used in Vol. VIIB cannot be separated from Homobasidiomycetes. Hymenomycetes [E.C. Swann and J.W. Taylor, 1995, Can J Bot 73 (Suppl. 1):S862] has been proposed as a class for these groups (see Berbee and Taylor, Chap. 10, Vol. VII, Part B)

data from multiple genes and the addition of missing taxa to the analysis. Problems also arise from a difference of opinion among authors. The term *fungi* has assumed an ecological meaning for all organisms with a similar nutritional mode, and therefore, Eumycota, rather than Fungi, is less confusing for the members of the phylum that encompasses a monophyletic group of these organisms. *Pseudofungi* (Cavalier-Smith, Chap. 1, Vol. VII, Part A) implies that organisms that lie outside the Eumycota but possess the fungal lifestyle are not fungi, but in an ecological sense they are fungi. *Pseudomycota* is therefore used in this series for these fungal organisms that lie outside the Eumycota.

Table 2 Taxonomic outline at the kingdom, phylum, and class levels as used in the rest of this volume compared with that of Cavalier-Smith, Chap. 1, Vol. VII, Part A

Mycota, Vol. VII	Chapter 1, Vol. VII, Part A
PSEUDOMYCOTA ^a	CHROMISTA
Oomycota	Bigyra
Peronosporomycetes	Oomycetes
Hyphochytriomycota	
Hyphochytriomycetes	Hyphochytrrea
Plasmodiophoromycota	PROTOZOA
Plasmodiophoromycetes	Cercozoa
EUMYCOTA	Phytophyxea
Chytridiomycota	FUNGI
Chytridiomycetes	Archemycota
	Chytridiomycetes
	Allomycetes
Zygomycota	
Zygomycetes	Zygomycetes
	Bolomycetes
	Glomomycetes ^b
	Enteromycetes
Trichomycetes	Zoomycetes ^c
	Microsporidia
	Minisporea
	Microsporea
Ascomycota	Ascomycota
Saccharomycetes	Taphrinomycetes
	Geomycetes
	Endomycetes
Plectomycetes	Plectomycetes
Hymenoascomycetes	Discomycetes
	Pyrenomycetes
Loculoascomycetes	Loculomycetes
Basidiomycota	Basidiomycota
Urediniomycetes	Septomycetes
Ustilaginomycetes	Ustomycetes
Heterobasidiomycetes	Gelomycetes ^b
Homobasidiomycetes	Homobasidiomycetes

^aArtificial taxon^bProbably paraphyletic^cIncludes Zygomycetes, Ascomycetes, and Trichomycetes

The Mycota, Vol. VII, includes treatments of the systematics and related topics of the Eumycota and Pseudomycota as well as specialized chapters on nomenclature, techniques, and evolution. Certain groups are not treated in this volume: the Labyrinthulomycetes (Pseudomycota) and the slime molds. The evolutionary position of the slime molds has been controversial. Recent evidence suggests that most slime molds are more closely related to the Eumycota than previously believed (S.L. Baldauf and W.F. Doolittle, 1997, *Proc Natl Acad Sci USA* 94:12007), and they should continue to be of interest to those who study fungi for both ecological and phylogenetic reasons.

Chapters 2 to 4, Vol. VII, Part A, cover the Pseudomycota, and Chaps. 5–14, Vol. VII A, and Chaps. 1–5, Vol. VII, Part B, the Eumycota. The Pseudomycota contains distantly related groups of fungi (Table 1). The Chytridiomycota and

Zygomycota are treated in one and two chapters, respectively, while the Ascomycota and Basidiomycota are treated in five or six chapters each, with separate chapters for yeasts in each phylum, although the yeasts are not monophyletic groups. Chapter 14, Vol. VII, Part A, discusses the special problems of anamorphic genera and their relationships to the teleomorphic genera and describes the attempts being made to incorporate anamorphs into modern phylogenetic systematics. In Chap. 6, Vol. VII, Part B, Hawksworth discusses the development of a unified system of biological nomenclature. Chapters 7 and 8, Vol. VII, Part B, deal with techniques for cultivation and data analysis, respectively. The final two chapters in Vol. VII, Part B, consider speciation and molecular evolution.

The Mycota, Vol. VII, was originally intended to have been Vol. I in the series. Several changes in editors and the unfortunate death of Paul Lemke delayed its production. Added to these difficulties was the fact that these are tumultuous times in systematics because of the rapid development of molecular and phylogenetic analysis techniques and the explosive accumulation of data. As these techniques and new data are more broadly incorporated into systematics, a more stable and useful classification of the fungi will result.

We thank Heather J. Olson for her substantial efforts in compiling the indices.

St. Paul, MN
Minneapolis, MN
April 2000

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Systematics and Evolution

Part B

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2015, XXIII, 311 p. 33 illus., 3 illus. in color., Hardcover

ISBN: 978-3-662-46010-8