The Mycota

Edited by
K. Esser

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The Mycota

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The Mycota

A Comprehensive Treatise on Fungi as Experimental Systems for Basic and Applied Research

Edited by K. Esser

II *Genetics and Biotechnology*

2nd Edition

Volume Editor:
U. Kück

With 62 Figures, 6 in Color, and 35 Tables

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Karl Esser

(born 1924) is retired Professor of General Botany and Director of the Botanical Garden at the Ruhr-Universität Bochum (Germany). His scientific work focused on basic research in classical and molecular genetics in relation to practical application. His studies were carried out mostly on fungi. Together with his collaborators he was the first to detect plasmids in higher fungi. This has led to the integration of fungal genetics in biotechnology. His scientific work was distinguished by many national and international honors, especially three honorary doctoral degrees.

Ulrich Kück

(born 1950) completed his studies in biology and chemistry in 1977 and wrote his dissertation (Ph.D.) under the supervision of Karl Esser at the Ruhr-Universität Bochum, Germany, in 1981. He was awarded a post-doctoral fellow at Harvard University, USA (1982/1983). This was followed by his post-doctoral dissertation (habilitation) and permission to teach at the university level (venia legendi) in botany at the Ruhr-Universität Bochum in 1986. He became professor of botany at the Johann-Wolfgang-Goethe Universität Frankfurt, Germany, in 1990/1991. Since 1991, he has held the Chair for General and Molecular Biology, Ruhr-Universität Bochum. His research focuses on biogenesis of plant cell organelles and molecular biology of complex functions in filamentous fungi.

Series Preface

Mycology, the study of fungi, originated as a subdiscipline 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) are as follows:

Pseudomycota

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

Eumycota

Division:	Chytridiomycota (*Allomyces*)
Division:	Zygomycota (*Mucor*, *Phycomyces*, *Blakeslea*)
Division:	Dikaryomycota

Subdivision:	Ascomycotina
Class:	Saccharomycetes (*Saccharomyces*, *Schizosaccharomyces*)
Class:	Ascomycetes (*Neurospora*, *Podospora*, *Aspergillus*)
Subdivision:	Basidiomycotina
Class:	Heterobasidiomycetes (*Ustilago*, *Tremella*)
Class:	Homobasidiomycetes (*Schizophyllum*, *Coprinus*)

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. Saprobic 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

insectassociated 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

Addendum to the Series Preface

In early 1989, encouraged by Dieter Czeschlik, Springer-Verlag, Paul A. Lemke and I began to plan *The Mycota*. The first volume was released in 1994, 11 volumes followed in the subsequent years. Unfortunately, after a long and serious illness, Paul A. Lemke died in November 1995. Thus, it was my responsibility to proceed with the continuation of this series, which was supported by Joan W. Bennett for Volumes X–XII.

The series was evidently accepted by the scientific community, because some of the first volumes are out of print. Therefore, Springer-Verlag has decided to publish completely revised and updated new editions of Volumes II and III. I am glad that the volume editors and most of the authors have agreed to join our project again.

I would like to take this opportunity to thank Dieter Czeschlik, his colleague, Andrea Schlitzberger, and Springer-Verlag for their help in realizing this enterprise and for their excellent cooperation for many years.

Bochum, Germany
August 2003

KARL ESSER

Volume Preface to the Second Edition

Since the first edition of Volume II of *The Mycota*, several developments in fungal molecular biology have progressed tremendously and thus have affected fundamental genetics as well as biotechnology. A major impact, for example, comes from fungal genome projects which provide a huge amount of sequencing data which will be used subsequently in further functional genomic studies. Therefore, the time point to publish a second edition of Volume II of *The Mycota* appears appropriate since genomic and postgenomic research in the fungal field extends substantially the potency of molecular genetics in manipulating fungal organisms. Five out of 19 articles are new contributions to this volume. All remaining articles were rewritten and new information gathered in recent years have been introduced to provide updated and concise overviews.

This volume is divided into three parts. The first one considers fungal model systems of nuclear (Chaps. 1–3) and extranuclear genetics (Chaps. 5 and 6) and current developments stimulated through genomic sequencing projects have been introduced. This part is completed by Chapter 4 about electrophoretic karyotyping.

Part two gathers articles dealing with the molecular genetics of yeast and mycelial fungi. Functional genomics investigates gene function through the parallel expression measurements of genomes. Most commonly, array techniques or serial analyses of gene expression are used to answer questions of basic as well as applied research. This novel development in fungal molecular biology is summarized in a new article (Chap. 7). Chapters 8 and 9 deal with our current knowledge of gene expression in yeast and mycelial fungi and are complemented by a new contribution (Chap. 13) on the regulation of amino acid biosynthesis in both yeast and filamentous fungi. Finally, this part also (Chaps. 10–12) deals with fungal extranuclear genetic elements which have been studied extensively by both conventional as well as molecular genetics. Chapter 10 can be considered an encyclopedia about fungal mobile elements including transposons, plasmids and intronic sequences.

The final part contains reviews with relevance for fungal biotechnology. Yeast and mycelial fungi are of increasing importance as expression platforms for the synthesis of heterologous proteins. This aspect has been addressed in two new contributions (Chaps. 14 and 15). Moreover, fungal organisms have a constant and outstanding position in applied and environmental mycology as producers of primary or secondary metabolites (Chaps. 15–19).

I am grateful to all authors who have made the production of this second edition possible. All are experts in their respective fields. Their contributions should be useful references for all scientists interested in fungal genetics and biotechnology.

Bochum, Germany
August 2003

ULRICH KÜCK
Volume Editor

Volume Preface to the First Edition

The discovery of sexuality in fungi during the second half of the 19th century contributed substantially to an understanding of karyogamy and meiosis in eukaryotic organisms. The subsequent discovery that Mendelian inheritance could be studied in fungal organisms made them preferred objects for conventional genetic analyses. Later, fungal genetics was extended by extrachromosomal genetics, stimulated profoundly by the observation that the "petite" phenotype was inherited in a non-Mendelian fashion in the yeast *Saccharomyces cerevisiae*.

While initial molecular genetic techniques were developed mainly from studies involving the prokaryotic *Escherichia coli*, fungi were first among eukaryotic organisms for which it was possible to apply such techniques. Consequently, molecular biology has had considerable influence upon the study of fungi, especially biotechnically important fungi, as this group is traditionally of wide industrial and economic significance. The objective of Volume II of *The Mycota* is to provide overviews on fungal systems which have been used extensively for conventional genetic analyses as well as for molecular genetic study. The latter is extended by review chapters on aspects of fungal biotechnology, which provide representative examples for the contribution of genetics to applied mycology.

The lead chapters of this volume (1–3) represent overviews on Mendelian genetics in *Neurospora*, *Aspergillus* and *Coprinus*, which can be considered as prototypes for genetic study with mycelial fungi. This is followed by Chapter 4, that deals with protoplast fusion as a tool for non-sexual or parasexual genetics in strain manipulation.

Conventional genetic techniques usually result in the generation of linkage maps indicative of karyotype. In recent years, this type of mapping has been enhanced and confirmed by electrophoretic karyotyping, the subject of Chapter 5.

The following chapters (6, 7) summarize current knowledge on mitochondrial genetics in *Saccharomyces* and *Neurospora*. In these reviews the impact of molecular biology becomes especially evident through substantial contribution of genetics to the understanding of extrachromosomally inherited phenomena such as respiratory deficiency and mycelial aging.

While conventional genetic techniques are dependent on recombination events during meiotic or mitotic processes, genetic manipulation through DNA-mediated transformation relies on in vitro recombinant DNA molecules. Chapter 8 is devoted to transformation procedures now applicable to a wide variety of fungi. These techniques have contributed significantly to our current understanding of gene regulation in unicellular as well as in mycelial fungi and are discussed in successive chapters (9, 10).

In addition to the mitochondrial genome, extranuclear genetic deteriminants may be represented in fungi by plasmid DNAs and/or viral-like genomes. The diversity of plasmid DNAs and their contribution to transformation systems in mycelial fungi is described in Chapter 11, and the two following chapters (12, 13) deal with the killer phenotype in different yeasts which is caused by small viral-like DNA and RNA genomes, respectively.

Many yeasts and mycelial fungi provide powerful experimental systems, allowing the investigation of truly basic biological phenomena. This has led to the discovery of

genetic elements with reverse transcriptase activities in yeast as well as in various filamentous fungi. Chapter 14 describes exclusively retrotransposons from yeast, while Chapter 15 deals with retro-like elements discovered recently in other fungi.

The final five contributions (16–20) summarize genetic work with fungi having industrial or economic significance. Molecular techniques are now being used to establish genetic systems for biotechnically important fungi and this is exemplified by the description of biotechnical genetics on fungi involved with antibiotic synthesis, lignin degradation and cellulolytic processes. In Chapter 19, the influence of molecular genetics on conventional breeding strategies is demonstrated with *Agaricus*. The last chapter (20) highlights the role of lipids in fungal biotechnology and the need to involve genetic study to improve upon lipid production.

Finally, I wish to express may gratitude to all contributors to this volume, and to acknowledge the organizational help of Ms. H. Heming and J. Beal.

Bochum, Germany
January 1995

ULRICH KÜCK
Volume Editor

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Biotechnology

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