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Foreword

Studies attempting to estimate fungal biodiversity mainly serve to underscore the limitations of our current awareness of the likely total number of species—currently estimated to be around 5 million. As environmental organisms, fungi influence the global ecology and the recycling of nutrients in the biosphere and also, both positively and negatively, the viability of many plants and animals. As simple eukaryotes that can be facilely studied and experimentally manipulated, fungi serve as important models that have profoundly influenced our understanding of life by enabling the identification and analysis of conserved mechanisms underpinning the growth, cell division, and death of all eukaryotic cells.

Fungal research is a vibrant and exciting area, but it is often dispersed among distinct scientific communities with different cultures and traditions. The objective of bringing together this broad research portfolio into a book and collection of contemporary reviews is therefore a useful, important, but challenging objective. This ASM-sponsored volume is unusual in uniting a community of mycologists and cell biologists with the common objective of illustrating the state of our understanding of both model fungi and organisms with specific environmental, pathogenic, or biological relevance. The book includes chapters where the focus is at the molecular, cellular, or organismal levels of spatial organization and includes fungi from all the major phylogenetic groupings. The result is an anthology of articles that defines the current trajectory of current research and questions for the next generation of investigators. The authors are leaders in their respective fields, and the editorial style is such that the work has achieved an overview of the field as a whole in a form that is useful both for the specialist and for those seeking understanding in areas in which they may be unfamiliar.

Some of the most profoundly important questions in biology have been explored using fungi, yeasts, and molds—and it is likely that this paradigm will continue into the future. This book should serve to stimulate a new generation of mycologically inclined scientists to investigate the extraordinary diversity and experimental accessibility of members of the mycobiota.

Sir Paul Nurse
The Francis Crick Institute,
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Our fascination with the Fungal Kingdom is a natural and ancient one and based on (i) the roles of fungi in the production of a variety of foods and beverages, and even as a source of food themselves; (ii) their global ecological impact, especially as the cause of devastating infections of humans and other animals and of plants, including many crops grown around the world; and (iii) their roles as fundamental model systems in genetics and biological research.

The earliest fascination with fungi likely began with humans across the globe foraging for food sources, often in the context of forests, and the prominent role of mushroom fruiting bodies associated with trees, either as mycorrhizal species on roots of living trees or as wood-degrading fungi on dead plant materials. These mushroom species include popular and delicious edible ones such as porcini, chanterelles, and truffles as well as shiitake, oyster, portobello, and more. In aggregate, the global commercial mushroom market was ~$35 billion US in 2015 and is anticipated to grow to as much as ~$60 billion by 2021. The species named are representatives of just one phylum (the Basidiomycota) within the broader Fungal Kingdom, which is now estimated to include as many as 2.2 to 3.8 million or more distinct species and at least seven phyla (Ascomycota, Basidiomycota, Mucoromycota, Zoopagomycota, Blastocladiomycota, Chytridiomycota, and the Cryptomycota/Rozellomycota).

Interest in fungi also derives from their key roles in the production of other foods and beverages, including the prominent role of the yeast *Saccharomyces cerevisiae* (Ascomycota) in production of beer, wine, Champagne, and bread. Yet other fungi such as *Penicillium chrysogenum* produce natural products like the antibiotic penicillin, which revolutionized medicine and health care and contributed to dramatically prolong the human lifespan by enabling effective treatment of infectious diseases. Finally, pathogenic fungi cause (i) devastating, life-threatening systemic infections of humans and also other diseases including allergies, blindness, vaginitis, and common skin infections including dandruff and athlete’s foot; (ii) widespread infections of animals including the ones that are devastating bat populations in North America and causing extinctions in frog species around the world; and (iii) the majority of infections that occur in plants, including many crop species, which lead to famines and disruptions of food supply with billions of dollars lost in agriculture annually. Whatever your vantage point, the impact of fungi on the biology of our planet, the development of human civilization, and our daily lives and health is writ large.

A few decades ago the position of the Fungal Kingdom within the broader eukaryotic tree of life was unclear, and in many instances it was thought and even taught that the fungi were more closely related to plants than to animals. The overt morphological features of mushrooms likely contributed to this view, along with uncertainty about where to place unicellular microbes within the context of complex multicellular organisms such as animals. But with the advent of molecular phylogenetic studies, the placement of fungi within the eukaryotic tree of life came into sharper focus, and we now appreciate that fungi are much more closely related to animals than they are to plants. This evolutionary kinship is in fact so certain that the Animal Kingdom and the Fungal Kingdom are now appreciated to be sister groups within the broader Opisthokonta supergroup of eukaryotes. This revised phylogenetic placement reveals much about the con-
ervation of molecular mechanisms of life and contributes to making fungi exceptional models to understand the form and function of other eukaryotes, including the Animal Kingdom.

In concert with these advances in molecular phylogenetics and taxonomy, two other fields have revolutionized our understanding of the Fungal Kingdom. First, advances in genetics of fungi have contributed to illuminate their unique and conserved biological properties. Studies on fungi have contributed profound insights as models for all of biology, such as the discovery of RNA interference (RNAi) pathways and how they operate to silence transgenes and protect genome integrity; the detailed mechanisms and operation of a biological clock and the key concept that this involves a molecular oscillator; the first experimental demonstration of DNA sequences that can function as telomeres, centromeres, and eukaryotic origins of replication; the discovery of the first components of the nuclear pore; the description of the secretory pathway and discovery of autophagy; the elucidation of how the cell cycle is orchestrated; the understanding of the impact of both ploidy and aneuploidy on cell functions; insights into how species evolve and species boundaries operate; and the discovery that the mismatch repair system is required for the stability of DNA repeats, leading to insights into how similar mutations lead to colon cancer in humans. Taken together, genetic, genomic, and cell biological studies have brought representatives of the entire Fungal Kingdom of life into focus and thereby made an invaluable contribution to our understanding of how eukaryotic organisms evolved and function. Indeed, seven Nobel prizes have been awarded to scientists studying yeasts and molds as model organisms that explain fundamental aspects of cell biology. These were awarded to Alexander Fleming, Ernst Chain, and Howard Florey in 1945 for the discovery of penicillin by *Penicillium notatum*; to George Beadle and Edward Tatum in 1958 for their One Gene = One Enzyme hypothesis in *Neurospora crassa*; to Paul Nurse and Leland Hartwell in 2001 for cell division and cancer in *Schizosaccharomyces pombe* and *Saccharomyces cerevisiae*; to Roger Kornberg in 2006 for eukaryotic gene transcription in *S. cerevisiae*; to Jack W. Szostak (shared) in 2009 for chromosome telomeres in *S. cerevisiae*; to Randy Schekman in 2013 (shared) for machinery regulating vesicle traffic in *S. cerevisiae*; and to Yoshinori Ohsumi in 2016 for autophagy in *S. cerevisiae*.

In concert with advances in genetics, subsequent advances in genome sciences have provided the complete genome sequences for an increasing number of fungal species, now >1,000, and in some species a staggering number of individual representative genomes (500 or more). In fact, a fungal species was the first eukaryotic organism to have its genome completely sequenced (the model budding yeast *S. cerevisiae*). Second, advances in genetics and cell biology have contributed to provide a detailed view of how the genome contributes to the functions of the cell and of the organism. Together, these advances in genomics and genetics provide a “blueprint” for how these species operate and have evolved at a cellular level, and consequently they offer a wealth of knowledge about how representative species in the fungal kingdom function and the diversity that lies within. This diversity spans from the most basic way that a fungal cell is organized, either as a yeast or as a filamentous hypha, to the myriad ways these species interact with their environment, from the aquatic basal fungi (Chytridiomycota, Cryptomycota), to fungi that are associated with plants and were critical for their emergence from the oceans and colonization of the planet, to fungi that are pathogens of plants or animals. This diversity also extends to the biological behavior and cell biology of fungi, including for example fungi that can sense light and those that have evolved to be insensitive to light (blind), the modes of sexual reproduction including heterothallism and homothallism, the loss and retention of RNAi pathways, the replacement of regional centromeres by point centromeres, and the retention of flagella in basal fungi versus their loss in fungal branches that evolved the ability to be aerially dispersed.

Given the rapidly advancing fields of fungal genetics and genomics, and mycology more generally, we increasingly found ourselves in need of a compendium to organize this information and to serve as a reference to guide both our own efforts and those of others whose research focuses on or interfaces with fungi. We have assembled a team of six editors with complementary and diverse interests and enlisted a cadre of 170 experts in the field who as authors have contributed the 54 chapters that comprise The Fungal Kingdom. We have organized the book into nine different sections to present related material together and provide a framework for organization. Each chapter is designed to be self-contained, such that any reader may choose to read any given chapter in isolation or a series of related chapters from one section. At the same time, the book has a coherent theme of focusing on the diversity, importance, impact, dangers, and beauty of the fungi and could therefore be read as a continuous text. As modes of publication have advanced, this book is also an experiment in that it is available as a hard copy printed volume, as an electronic book, and as individual chapters available electronically or in their published form as part of the Microbiology Spectrum journal from ASM Press.
Preface

It is our hope, and our goal and intention, that this book both takes stock of the current state of knowledge in the field and also spurs further investigations into topics of interest that stem from the information contained herein. We invite you to peruse the current state of knowledge here and hope these musings spur you to join us in further advancing the field. We also invite you to communicate to us your experiences with the book. It is our fervent hope that advances over the next several decades will ultimately render this book out of date, and therefore in need of revision or replacement, as the field advances.

In closing, we would like to thank the numerous individuals who have contributed to advance our understanding of the Fungal Kingdom and, by extension, to the stimulation and realization of this text. We wish to dedicate this effort to the scientific mentors who trained and inspired us, and also to our significant others, children, and families, without whose forbearance and tolerance this effort would not have been possible. Finally, we thank our tireless ASM editors, Greg Payne, Lauren Luethy, and Ellie Tupper, who with administrative assistance from Melissa Palmer made this text possible through their indefatigable and enthusiastic efforts.

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Barbara Howlett, Ph.D., is an Honorary Professor in the School of BioSciences, the University of Melbourne. She studies blackleg, a fungal disease of canola. She has exploited a “genome to paddock” approach: identifying fungal genes and genetic mechanisms crucial for disease, and developing disease management strategies that are now implemented by Australian canola growers. She also has discovered biosynthetic pathways for fungal toxins involved in diseases of both plants and animals. Howlett is a Fellow of the American Academy of Microbiology, the Australian Academy of Science, and the Australasian Plant Pathology Society and an Honorary Member of the American Mycological Society.

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