the FUNGAL KINGDOM

Edited by
Joseph Heitman
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Eva H. Stukenbrock
Timothy Y. James
Neil A.R. Gow

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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.

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Preface

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 conservation 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.

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.

Joseph Heitman
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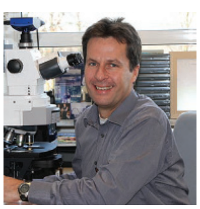
Editors

Joseph Heitman, M.D., Ph.D., is James B. Duke Professor and Chair, Department of Molecular Genetics and Microbiology, Duke University. His research focuses on model and pathogenic fungi, including mating-type locus evolution, transitions in sexual reproduction modes, fungal virulence, and genome evolution. His work discovered FKBP12 and TOR as the targets of rapamycin and unisexual reproduction. He is fellow of the American Society for Clinical Investigation, American Academy of Microbiology, AAAS, and Association of American Physicians and received Burroughs Wellcome, AMGEN, Squibb, and NIH MERIT awards. He is an editor or board member for numerous journals and has edited seven textbooks.

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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Professor Neil A. R. Gow, Ph.D., has research interests in medical mycology and in particular the structure and function of the fungal cell wall in relation to host-pathogen interactions. He is a founding member of the Aberdeen Fungal Group (AFG), which was established as the MRC Centre for Medical Mycology at the University of Aberdeen, United Kingdom. He has served as president of the British Mycological Society, the International Society for Human and Animal Mycology, and the Microbiology Society and has been elected as a FAAM, FRS, FRSE, and FMedSci.

Fungal Branches on the Eukaryotic Tree of Life

I

The Fungal Kingdom
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The Fungal Tree of Life: From Molecular Systematics to Genome-Scale Phylogenies

1

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INTRODUCTION

In 1996 the genome of *Saccharomyces cerevisiae* was published and marked the beginning of a new era in fungal biology (1). Since then, rapid advancements in both sequencing technologies and computational biology have resulted in the sequencing of genomes for more than 800 species (e.g., http://genome.jgi.doe.gov/fungi/). These genomes represent a windfall of data that are informing evolutionary studies of fungi and the search for biological solutions to alternative fuels, bioremediation, carbon sequestration, and sustainable agriculture and forestry (2). Indeed, the marriage between genomics and phylogenetics occurred early, both in the use of phylogenetic techniques to study genome evolution and in the use of genome-scale data to infer evolutionary relationships. In this article we will review the impact of genomic-scale phylogenies, along with standard molecular phylogenies, on our understanding of the evolution of the fungal tree of life and the classification that communicates it.

Genomic data provide the maximum amount of discrete genetic information available for phylogenetic analyses, and hundreds to thousands of genes have been identified as useful phylogenetic markers (3). Markov clustering algorithms have been proven powerful tools to identify orthologous clusters of proteins that can be filtered for single-copy clusters that are useful in phylogenetic analyses (4). This approach has transformed phylogenetics by no longer requiring selection of an *a priori* set of markers (e.g., rDNA, RPB2, etc.), but rather promotes the mining of a data set of genomes for the largest set of appropriate markers. Furthermore, hidden Markov models have proven to be valuable tools for identifying and retrieving these markers in newly sequenced genomes and rapidly growing genome-scale phylogenetic data sets (5).

The estimation of species trees from genome-scale data sets is not without challenges, however. Phylogenetic analyses of genomic data have revealed that different genes within a genome can have different evolutionary histories, i.e., phylogenetic conflict (6). Sources of conflict include incomplete lineage sorting (or deep coalescence), hybridization, and horizontal gene transfer, and the detection and characterization of this conflict in the context of phylogenetic inference are still in their infancy (7). The application of standard measures of topological support, such as the bootstrap partition, can also be difficult to interpret, due to the observation that nodes that resolve differently in different gene data sets can have high or maximum bootstrap partition values in a subset of analyses (e.g., 8, 9). At the time of the writing of this manuscript the majority of genome-scale phylogenetic analyses focus on the analysis of concatenated superalignments, but development and use of supertree methods, gene tree-species tree reconciliations, and alternative measures of nodal sup-

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port are increasing (e.g., 8, 10) and will be developed further over the coming years.

Despite the challenges mentioned above, phylogenetic analyses of genome-scale data sets, and more traditional multigene data sets, have greatly advanced our understanding of fungal evolution. Historically, the fungi were divided into more or less four groups—chytridiomycetes, zygomycetes, ascomycetes, and basidiomycetes—defined by morphological traits associated with reproduction. (Note: The suffix "-mycetes" is used to denote a class-level taxonomic group in fungal nomenclature, e.g., Agaricomycetes. Its use as a lowercase noun, however, signifies an informal name and not an explicit taxonomic rank.) The chytridiomycetes, or zoosporic fungi, were recognized based on their production of zoospores, characterized by a single posterior, smooth flagellum. The zygomycetes were characterized by gametangial conjugation and the production of zygospores, coenocytic hyphae, and typically asexual reproduction by sporangia. The ascomycetes and basidiomycetes were identified by the production of asci and basidia, respectively, possession of regularly septate hyphae, and a dikaryotic nuclear phase in their life cycle. The classification of the kingdom Fungi used here recognizes eight phyla (Fig. 1, Table 1), with the zoosporic fungi comprising the first three lineages of the kingdom—Cryptomycota/Microsporidia, Chytridiomycota, and Blastocladiomycota—since the divergence from the last universal common ancestor (LUCA) of Fungi.

The resolution of zoosporic fungi as paraphyletic rejects the flagellum as a diagnostic trait (synapomorphy) for a monophyletic group of flagellated fungi. Rather, it is an ancestral (symplesiomorphic) trait inherited from the LUCA of the kingdom Fungi. Most extant species of fungi are nonflagellated and are the result of multiple losses of the flagellum during fungal evolution. Two losses of the flagellum have occurred, giving rise to the Microsporidia and the most recent common ancestor (MRCA) of the remaining phyla of zygomycetes, ascomycetes, and basidiomycetes. Inferences of additional losses of the flagellum are required for the placement of nonflagellated species among the Chytridiomycota (11) and possibly for the placement of the enigmatic zoosporic genus *Olpidium* among zygomycetes (12), but the absolute number of losses is unclear. The zygomycetes are also paraphyletic and are classified in two phyla: Zoopagomycota and Mucoromycota (13). This classification rejects the zygospore as a synapomorphy for the zygomycetes; rather, it was inherited from the MRCA of terrestrial fungi and lost in the MRCA of ascomycetes and basidiomycetes. The monophyly of ascomycetes and basidiomycetes has been confirmed, and they are classified as the phyla Ascomycota and Basidiomycota, respectively, of the subkingdom Dikarya (14). More information on character evolution will be highlighted throughout this article.

One of the greatest challenges in evolutionary biology of fungi is accurately estimating geologic dates of the origin of the kingdom Fungi, emergence of the major phyla, and diversification of extant lineages (15). Our knowledge of the fossil record of fungi is less than that of plants and animals, but there does exist an increasing number of fossils that can be assigned to major groups of fungi based on their morphological similarity to extant taxa (16). An important observation is that morphologies associated with Blastocladiomycota, Chytridiomycota, Mucoromycota, and Ascomycota are present in the early Devonian and are associated with the earliest known land plant flora of the Rhynie chert. This observation, in combination with relaxed molecular clock analyses (e.g., 17, 18), suggests that the common ancestors of the phyla of Fungi are in fact old and may have been among the first terrestrial organisms. The interpretation of fungus-like fossils can be challenging, however, as it is difficult to interpret some morphologies that are not present among extant lineages as definitive representatives of the kingdom Fungi (19).

In this article we will highlight the major phyla of fungi based on the current understanding of the fungal tree of life. In doing so, we will outline their phylogenetic diversity and classification, provide examples of important taxa for each group, and discuss advancements in our understanding of morphological and ecological evolution through the analysis of genomic and molecular data. There are many specialized terms used in this article, and we are unable to fully define all of them here. However, Fig. 2 to 5 provide examples of taxa and morphologies discussed herein, but the reader is directed to more traditional textbooks in mycology for more detailed discussions.

ZOOSPORIC FUNGI (Fig. 2)

Before we consider zoosporic fungi, a brief discussion of some unique aspects of their development and morphology is necessary. The morphology of zoosporic fungi varies depending on the extent of their thallus development, number and position of reproductive structures, and position in the substrate. Thalli may exist as single cells with sparse rhizoidal systems to more extensive networks of rhizoids (rhizomycelia) and mycelial thalli. Endobiotic chytrids are partially or completely

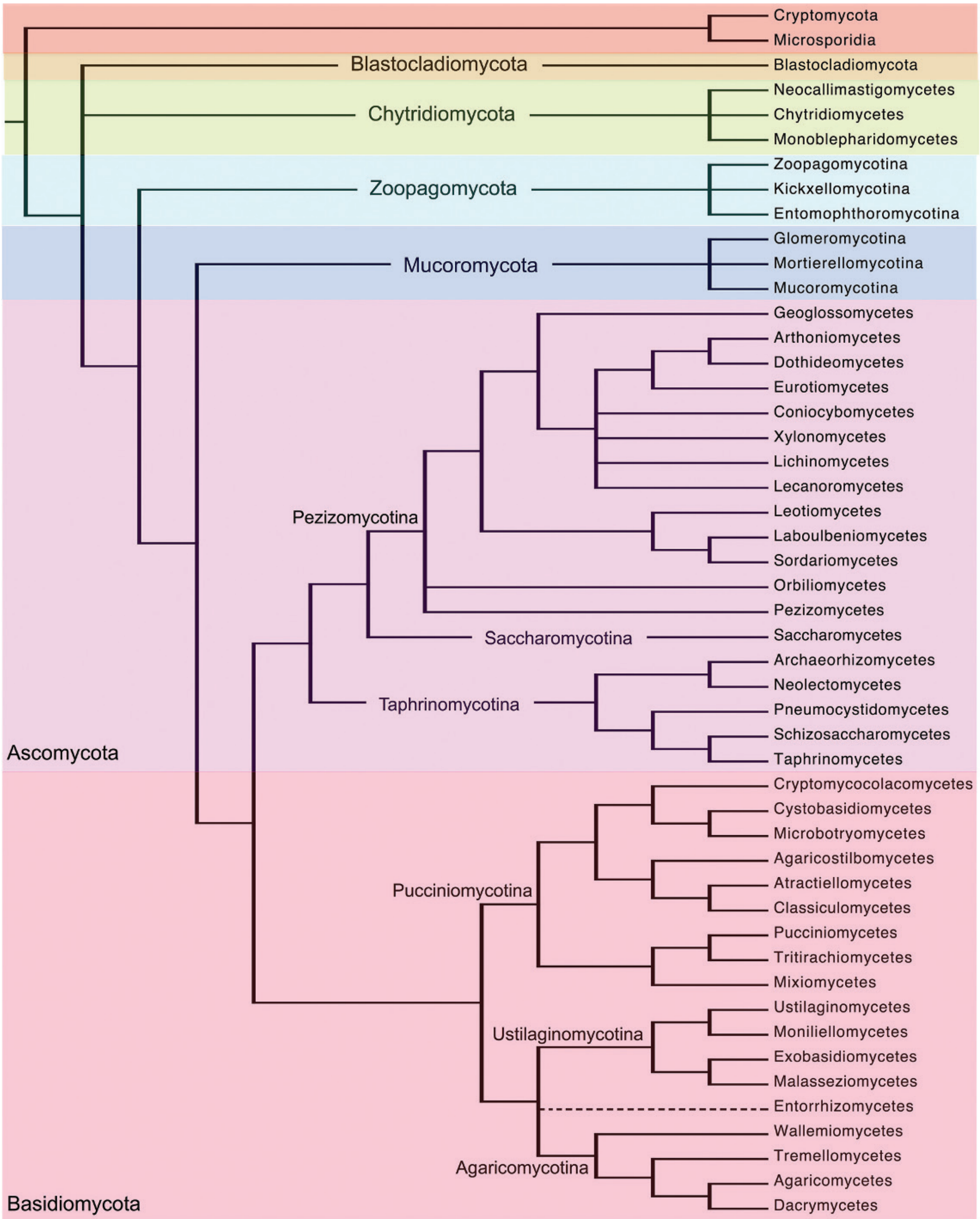

Figure 1 Fungal tree of life. Cladogram of the kingdom Fungi based on published multi-gene and genome-scale phylogenies (11–14, 17, 18, 32, 33, 83, 98, 109, 112, 167, 168). Polytomies represent regions of the tree currently unresolved by molecular and genomic data.

Table 1 Classification of the kingdom Fungi

- **Cryptomycota** M.D.M. Jones & T.A. Richards 2011 [=Rozellomycota Doweld (2011)]
- **Microsporidia**
- **Blastocladiomycota** T.Y. James (2007)
  - Blastocladiomycetes Doweld (2001)
- **Chytridiomycota** Hibbett et al. (2007)
  - Chytridiomycetes Caval.-Sm. (1998)
  - Monoblepharidomycetes J.H Schaffner (1909)
  - Neocallimastigomycetes M.J. Powell (2007)
- **Zoopagomycota** Gryganski et al. (2016)
  - Zoopagomycotina Benny (2007)
  - Kickxellomycotina Benny (2007)
  - Entomophthoromycotina Humber (2007)
    - Basidiobolomycetes Doweld (2001)
    - Neozygitomycetes Humber (2012)
    - Entomophthoromycetes Humber (2012)
- **Mucoromycota** Doweld (2001)
  - Glomeromycotina Spatafora & Stajich (2016)
    - Glomeromycetes Caval.-Sm. (1998)
  - Mortierellomycotina Hoffm., K. Voigt & P.M. Kirk (2011)
    - Moretierellomycetes Caval.-Sm. (1998)
  - Mucoromycotina Benny (2007)
- **Ascomycota** (Berk.) Caval.-Sm. (1998)
  - Pezizomycotina O.E. Erikss. & Winka (1997)
    - Arthoniomycetes O.E. Erikss. & Winka (1997)
    - Coniocybomycetes M. Prieto & Wedin (2013)
    - Dothideomycetes O.E. Erikss. & Winka (1997)
    - Eurotiomycetes O.E. Erikss. & Winka (1997)
    - Geoglossomycetes Zheng Wang, C.L. Schoch & Spatafora (2009)
    - Laboulbeniomycetes Engler (1898)
    - Lecanoromycetes O.E. Erikss. & Winka (1997)
    - Leotiomycetes O.E. Erikss. & Winka (1997)
    - Lichinomycetes Reeb, Lutzoni & Cl. Roux (2004)
    - Orbiliomycetes O.E. Erikss. & Baral (2003)
    - Pezizomycetes O.E. Erikss. & Winka (1997)
    - Sordariomycetes O.E. Erikss. & Winka (1997)
    - Xylonomycetes Gazis & P. Chaverri (2012)
  - Saccharomycotina O.E. Erikss. & Winka (1997)
    - Saccharomycetes G. Winter (1880)
  - Taphrinomycotina O.E. Erikss. & Winka (1997)
    - Archaeorhizomycetes Rosling & T.Y. James (2011)
    - Neolectomycetes O.E. Erikss. & Winka (1997)
    - Pneumocystidomycetes O.E. Erikss. & Winka (1997)
    - Schizosaccharomycetes O.E. Erikss. & Winka (1997)
    - Taphrinomycetes O.E. Erikss. & Winka (1997)
- **Basidiomycota** R.T. Moore (1980)
  - Agaricomycotina Doweld (2001)
    - Agaricomycetes Doweld (2001)
    - Dacrymycetes Doweld (2001)
    - Tremellomycetes Doweld (2001)
    - Wallemiomycetes Zalar, de Hoog & Schroers (2005)
  - Pucciniomycotina R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. (2006)
    - Agaricostilbomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. (2006)
    - Atractiellomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. (2006)
    - Classiculomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. (2006)
    - Cryptomycocolacomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. (2006)
    - Cystobasidiomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. (2006)
    - Microbotryomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. (2006)
    - Mixiomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. (2006)
    - Pucciniomycetes R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw. (2006)
    - Tritirachiomycetes Aime & Schell (2011)
  - Ustilaginomycotina Doweld (2001)
    - Exobasidiomycetes Begerow, M. Stoll & R. Bauer 2007
    - Malasseziomycetes Denchev & T. Denchev (2014)
    - Moniliellomycetes Q.M. Wang, F.Y. Bai & Boekhout (2014)
    - Ustilaginomycetes E. Warming (1884)
  - *Incertae sedis*
    - Entorrhizomycetes Begerow, Stoll & R. Bauer (2007)

immersed in their substrate, while only the rhizoids of epibiotic chytrids are immersed. Often, the thalli of single-celled chytrids are converted entirely to thin-walled zoosporangia or thick-walled resting sporangia (holocarpic condition), and others have thalli that are only partially converted to reproductive structures (eucarpic condition). Other terms describe the number of reproductive structures produced by an individual: a single sporangium on a thallus is a monocentric thallus, and multiple sporangia on a rhizomycelium or mycelium are termed polycentric. Zoosporangia, in which zoospores are produced, are asexual reproductive structures; resting sporangia that germinate by release of flagellated cells and resting spores that germinate by germ tubes may be asexual or sexual structures.

Cryptomycota/Microsporidia

Cryptomycota plus Microsporidia are sister to the remaining lineages of Kingdom Fungi. (Note: Rozellomycota [20] is another name for Cryptomycota [21] based on the genus *Rozella* and the principle of autotypification [14]. *Cryptomyces* is a genus in Ascomycota and cannot be used to typify Cryptomycota.) Cryptomycota consists of a handful of described taxa and taxa that are known only from environmental samples. One described taxon is *Rozella* (Fig. 2a), a biotrophic intracellular parasite of other zoosporic fungi