Mycologia, 98(6), 2006, pp. 829–837.

Issued 19 April 2007

Research Coordination Networks: a phylogeny for kingdom Fungi (Deep Hypha)

Meredith Blackwell[1]
Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803

David S. Hibbett
Department of Biology, Clark University, Worcester, Massachusetts 01610

John W. Taylor
Department of Plant and Microbial Biology, University of California, Berkeley, California 94720

Joseph W. Spatafora
Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331

Abstract: Research in fungal phylogenetics and systematics progressed rapidly in the past decade due to advances in DNA sequencing technologies and analytical methods. A newfound wealth of sequence data acquired through community-wide initiatives has advanced the process of acquiring a stable phylogenetic classification of many fungal taxa. Financial support from the National Science Foundation Research Coordination Networks: a phylogeny for kingdom Fungi (Deep Hypha) for 5 y enabled more than 100 fungal systematists to assess the taxon sampling, molecular markers and analytical methods necessary to facilitate such a project. Later a second NSF program provided financial support for the Assembling the Fungal Tree of Life (AFTOL) project to accomplish much of the research. Deep Hypha may be viewed as an involved parent of AFTOL with a continuing role as coordinator of likeminded workers. Many questions posed at the beginning of the Deep Hypha project have been addressed, at least in part, although some details remain to be clarified. Many of the main branches of the fungal tree are stable and well supported, often as a result of multigene analyses that involved collaboration of many laboratories. More work is necessary, however, to resolve certain branching events near the base of the tree, as well as to reconstruct relationships in some terminal groups. The phylogenetic classification in this issue of *Mycologia* is a product of the AFTOL project and many other independent research initiatives, and it is an initial synthesis of a working classification designed to be used for all major publications that require a phylogenetic classification of fungi.

Key words: mycological community, mycota, systematics

Fungi have a profound impact on global ecosystems. They modify our habitats and are essential for many ecosystem functions. Fungi form soil, recycle nutrients, decay wood, enhance plant growth and cull plants from their environment. They feed us, poison us, parasitize us and cure us. They destroy our crops, homes and libraries, but they also produce valuable biochemicals, such as ethanol and antibiotics. For both practical and intellectual reasons it is important to provide a phylogeny of Fungi on which a classification can be firmly based. The Deep Hypha Research Coordination Network, supported by the United States National Science Foundation (NSF), promoted and facilitated the cooperation necessary for the mycological community to construct a comprehensive phylogeny of the Fungi. Although Deep Hypha did not support data collection, it provided an essential forum for fungal systematists to plan, coordinate and report their activities. One initiative that grew out of Deep Hypha was the NSF-supported Assembling the Fungal Tree of Life project (AFTOL), which provided money to develop multilocus molecular and morphological datasets for the entire kingdom. As the articles in this Deep Hypha issue of *Mycologia* attest, AFTOL and other recent independent projects, helped directly or indirectly by Deep Hypha, have dramatically enhanced our understanding of fungal phylogeny. In this mission, Deep Hypha has been a success. As a gauge of progress in the field one may consider the growth of fungal systematics through the latter half of the 20th century, as reflected in the successive volumes of *Introductory Mycology* by C.J. Alexopoulos and colleagues (Alexopoulos 1952, 1962; Alexopoulos and Mims 1979; Alexopoulos, Mims, Blackwell 1996).

The growth of fungal phylogenetics seen through Alexopoulos's Introductory Mycology.—The intent of Alexopoulos's *Introductory Mycology* has always been to be organized phylogenetically, as far as possible. The first edition (Alexopoulos 1952) began with bacteria, including actinomycetes, and a modern concept of prokaryotic cells and their structure was lacking. The second edition (Alexopoulos 1962) omitted bacteria but included for the first time Labyrinthulales, Hyphochytridiomycetes [sic] and Trichomycetes. These groups are still included in the latest edition of the text but mostly removed from

---

Accepted for publication 12 November 2006.

[1] Corresponding author. E-mail: mblackwell@lsu.edu

a monophyletic concept of fungi with the exception of some Trichomycetes. As will be seen below some members of these of groups have come back into consideration as protists that are in a position basal to fungi and animals. Alexopoulos was concerned particularly about the placement of slime molds, and although they are excluded from fungi their position continues to be somewhat unsettled. The third edition (Alexopoulos and Mims 1979) had a new look with the addition of electron micrographs, the revolutionary technique of the time. Classification, still problematic, included slime mold groups within Fungi but separated them in a different subdivision. Oomycetes and chytrids also were placed in separate subdivisions, and Deuteromycotina was a group equal to but distinct from zygomycetes, ascomycetes and basidiomycetes.

In 1993 Charles Mims and Meredith Blackwell revised the text to provide a fourth edition (1996). For a book with a phylogenetic arrangement the timing of the revision was arguably less than optimum, because results from DNA-based phylogenetic studies were just appearing. In fact the text was sent to the printer with a multitude of additions in the ''blue line'' stage because of the appearance of new papers and graciously contributed unpublished studies that helped to establish the bare bones of a molecular phylogeny, which endured fairly well despite heavy reliance on a single gene, SSU rDNA. A phylogeny was presented in a series of unresolved trees that required the use of informal names for numerous taxonomic groups. The text however did use for the first time the term ''phylum'', newly sanctioned by the revised International Code of Botanical Nomenclature from the Tokyo Botanical Congress, and as such served as a transition between the old and the new, with hints of many changes to come. The monophyly of Fungi was established by separating four phyla from a number of excluded groups (water molds, labyrinthulids and several types of slime molds). Chytrids were placed firmly among Fungi, and the heterokont flagellates were unquestionably excluded. There were surprises: *Pneumocystis* was determined to be a fungus, *Mixia* was recognized as a basidiomycete and *Saccharomyces* and *Schizosaccharomyces* were shown to be widely separated. Evidence was available to recognize the polyphyly of groups such as gasteromycetes and polypores, and perhaps most important of all there was no phylogenetically defensible use of the class Deuteromycetes (Taylor 1995, Taylor et al 1999). There were however many intriguing unresolved questions: Is it possible that *Basidiobolus* is not a zygomycete? Are smuts and rusts not monophyletic? Do animals represent the sister group of fungi, or is the relationship more removed with fungi and animals sharing common ancestors?

Phylogenetic status of kingdom Fungi at the time of writing the Deep Hypha proposal. A monophyletic kingdom Fungi had been defined when Deep Hypha began (Barr 1992, Bruns et al 1992) with our understanding of major subkingdom relationships summarized as follows:

- Four phyla generally were accepted in kingdom Fungi: Chytridiomycota, Zygomycota, Basidiomycota and Ascomycota (Alexopoulos et al 1996, Barr 1992, Bowman et al 1992, Bruns et al 1992, Hawksworth et al 1995).
- The phyla Chytridiomycota and Zygomycota were not supported as monophyletic and intergraded at several points based on analyses of the SSU rDNA (Nagahama et al 1995, James et al 2000).
- The Chytridiomycota was the only taxon within kingdom Fungi to include representatives with a flagellated stage at some point in their life cycle, and analyses agreed that some lineage of the Chytridiomycota occupied the most basal branch of kingdom Fungi, a finding consistent with a choanoflagellate ancestor; however there was conflict in the literature as to which group of the Chytridiomycota was most basal (James et al 2000).
- The Chytridiomycota was paraphyletic, largely defined by the ancestral character state of a smooth posterior flagellum. The Zygomycota was suspected of being polyphyletic with multiple origins within kingdom Fungi. Based on rDNA, at least one origin was derived from within the Chytridiomycota, representing the loss of the flagellum; however this was contradicted by analysis of β-tubulin sequences (Keeling et al 2000, James et al 2000).
- At the other extreme, the Glomerales (until then considered a member of Zygomycota) appeared more closely related to the Ascomycota/Basidiomycota clade (Simon et al 1993) based on rDNA.
- The larger clade comprising the Glomerales, Ascomycota and Basidiomycota was referred to as ''crown'' fungi; ''crown'' fungi were supported as a derived, higher monophyletic taxon within the Fungi, originated and diversified along with land plants (Redecker et al 2000, Simon et al 1993, Taylor et al 1995).
- The Basidiomycota and Ascomycota each were monophyletic and together formed the most derived fungal clade (Bowman et al 1992, Bruns et al 1992) that comprised more than 95% of all known fungi. Higher-level relationships within both the Ascomycota and Basidiomycota were tenuous.
- The Ascomycota generally was recognized to in-

clude the classes Euascomycetes (mostly filamentous, sporocarp-producing and mitosporic or conidial forms), Saccharomycetes (the true yeasts), and Archiascomycetes (a paraphyletic assemblage of basal taxa) (Nishida and Sugiyama 1994, Taylor et al 1993).
- The Basidiomycota generally was recognized to include three classes: Urediniomycetes (rusts and relatives), Ustilaginomycetes (smuts) and Hymenomycetes (mushrooms and relatives) (Swann and Taylor, 1995, Wells 1994).
- To that date, the lion's share of phylogenetic studies had been performed on nucleotide data determined from nuclear rDNA (Alexopoulos et al 1996).

Deep Hypha accomplishments.—Mycologists were primed for the first NSF Assembling the Tree of Life competition (2002) thanks to the community-wide discussions on taxon sampling and methodology that had been supported by Deep Hypha. Working with the AFTOL consortium (and with much overlap in membership) many Deep Hypha participants focused on the same major loci, including the well characterized nuclear rRNA genes, and the protein-coding loci *tef1* and *rpb1* and *rpb2*, which had been promoted as molecular phylogenetic markers in Fungi by Hall and colleagues (Liu et al 1999). The coordinated sampling enabled construction of kingdomwide multigene datasets (Lutzoni et al 2004, James et al 2006). Several Deep Hypha symposia and workshops were held in conjunction with other meetings during the AFTOL funding period. The symposia and workshops promoted multigene, collaborative research in fungal phylogenetics, the use of state-of-the-art phylogenetic algorithms and fungal biology in broader scientific and educational communities. This Deep Hypha issue of *Mycologia* presents phylogenetic analyses of most major fungal clades, including many studies that were aided by Deep Hypha and that use data obtained in the AFTOL project. The articles included in this issue provide summaries of the status of the phylogenetic reconstruction for most of the major fungal lineages, although some clades (e.g. Polyporales, Laboulbeniomycetes) have been omitted. Some highlights follow.

- Taylor and Berbee: Estimating the evolutionary age of Fungi and the origin of its phyla and subphyla remains an elusive goal, but new fossil findings and improved analytical methods support an origin of all extant phyla by the Devonian (Taylor et al 1995).
- Celio et al: Subcellular characters, especially associated with septal ultrastructure, while few in number, are providing important synapomorphies for deep nodes that have proved problematical (e.g. monophyly of Agaricomycotina plus Ustilaginomycotina, and monophyly of Dimargaritales plus Trichomycetes s.s.).
- James et al: The Chytridiomycota is not monophyletic. Fourteen clades, including a core group of the traditional chytrids, are defined; these clades have a paraphyletic relationship to other flagellated fungi, notably Blastocladiales, many of which have distinctive life cycles with sporic meiosis. *Olpidium* also falls outside the other chytrids.
- White et al: The Zygomycota as previously recognized is not a monophyletic group. Two trichomycete groups no longer are considered to be fungi and the remaining traditional members have a paraphyletic relationship. *Basidiobolus*, tentatively suggested to be a chytrid by SSU rDNA data, appears as a sister of the Entomophthorales with increased taxon sampling and use of a multigene dataset.
- Redecker and Raab: Glomeromycota is accepted as a sister group of Basidiomycota + Ascomycota within kingdom Fungi on the basis of rDNA analysis (Schüßler et al 2001). Some recent analyses including protein coding genes support monophyly of the phylum but also cast doubt on the sister group relationship of these fungi with Dikaryomycota. With a two-gene dataset the Glomeromycota is upheld as a monophyletic taxon with six major clades.
- Aime et al: Pucciniomycotina (=Urediniomycetes) comprises the rusts, Pucciniales (= Urediniales) and related teliospore-producing taxa (e.g. Septobasidiales, Sporidiales, etc.). The subphylum is defined with eight major clades ranked as classes (Agaricostilbomycetes, Atractiellomycetes, Classiculomycetes, Cryptomycocolacomycetes, Cystobasidiomycetes, Microbotryomycetes, Mixiomycetes and Pucciniomycetes) and eighteen orders.
- Begerow et al: Ustilaginomycotina (=Ustilaginomycetes) comprises the smuts, Ustilaginales and related taxa. Based on morphological, ultrastructural and molecular phylogenetic data, Ustilaginomycotina is defined with three classes, Entorrhizomycetes, Ustilaginomycetes and Exobasidiomycetes, which collectively comprise 11 orders.
- Hibbett: Agaricomycotina (=Hymenomycetes), one of the three main subphyla of Basidiomycota, includes Tremellomycetes, Dacrymycetes and Agaricomycetes. Phragmobasidia are present in all three classes with holobasidia restricted to the Agaricomycetes. The Agaricomycetes includes eight major subclades that are recognized as subclasses and orders and is characterized by high

levels of homoplasy associated with all major basidioma morphologies (e.g. mushrooms, crusts, etc.)

- Larsson et al: The Hymenochaetales (hymenochaetoid clade) is dominated by wood-decaying species previously classified in the artificial families Corticiaceae, Polyporaceae and Stereaceae. The majority of these species cause white rots. No unequivocal morphological synapomorphies are known for the hymenochaetoid clade. However, almost all species examined ultrastructurally have dolipore septa with continuous parenthesomes.
- Moncalvo et al: The Cantharellales (cantharelloid clade) includes the genera *Cantharellus, Craterellus, Hydnum, Clavulina, Membranomyces, Multiclavula, Sistotrema, Botryobasidium*, the family Ceratobasidiaceae and possibly *Tulasnella*. Numerous taxa within the clade are characterized by fast molecular evolution, especially rDNA sequences, which continue to complicate phylogenetic inference of this group.
- Hosaka et al: Phallomycetidae is proposed for the gomphoid-phalloid clade, which includes four well supported major subclades. Three of the four subclades (Geastrales, Hysterangiales and Phallales) are represented entirely by gastroid taxa. While the gastroid morphology is derived from epigeous, nongastroid taxa (e.g. *Ramaria*) in the Gomphales, the topology of the Phallales indicates that the truffle-like form is an ancestral morphology of the stinkhorn fruiting bodies.
- Miller et al: The Russulales contains a remarkable variety of sporophore forms, including resupinate, discoid, effused-reflexed, clavarioid, pileate or gasteroid. Based on molecular and morphological data, 12 families and approximately 80 genera have been identified, although placement of many taxa has not yet been determined. Presence of gloeoplerous hyphae containing fluid that stains black in sulfoaldehyde compounds is a synapomorphy for the Russulales, but amyloid reactions in spore or hyphal walls is an inconsistent trait for the order.
- Binder and Hibbett: Boletales includes six major lineages recognized at the subordinal level, Boletineae, Paxillineae, Sclerodermatineae, Suillineae, Tapinellineae and Coniophorineae. Analyses of the multigene dataset confirmed sister group relationships among Boletales, Agaricales and Atheliales, and ancestral state reconstruction suggests that the ancestor of the Boletales was a brown-rotting, resupinate or polyporoid, saprotrophic basidiomycete.
- Matheny et al: Multigene analyses support Agaricales comprising six major clades, the agaricoid, tricholomatoid, marasmioid, hygrophoroid, pluteoid and plicaturopsidoid. Ectomycorrhizae appear to have evolved at least 11 times in the Agaricales, nine of them in the agaricoid/tricholomatoid clade. A family-based phylogenetic classification is outlined for the six major clades in which 30 families, four autonomous tribes and two informally named clades are recognized.
- Sugiyama et al: The earliest diverging lineages of the Ascomycota include Neolectomycetes, Pneumocystidiomycetes, Schizosaccharomycetes and Taphrinomycetes. These taxa were classified formerly in the Taphrinomycotina (=Archiascomycetes), and while increased taxon and character sampling have resulted in increased support, the monophyly of the subphylum is debatable and its use remains controversial.
- Suh et al: Subphylum Saccharomycotina consists of a single order, Saccharomycetales. Although many close relatives of *Saccharomyces cerevisiae* are known from whole genome sequences, few protein-coding gene sequences are available for other species, especially basal members of the group. At least 12 clades based on rDNA analyses are strongly supported.
- Spatafora et al: Pezizomycotina includes the majority of filamentous, sporocarp-producing and mitosporic or conidial species of Ascomycota. The apothecial classes Pezizomycetes and Orbiliomycetes are supported as being the two most basal taxa of the subphylum. The remaining taxa form a well supported clade that includes the Arthoniomycetes plus Dothideomycetes, Eurotiomycetes, Lecanoromycetes plus Lichinomycetes and Leotiomycetes plus Sordariomycetes.
- Hansen and Pfister: Pezizomycetes comprise all Ascomycota that form operculate asci with the majority of species forming apothecial ascomata. The class includes three well supported subclades, all of which are classified currently in the Pezizales.
- Schoch et al: Dothideomycetes includes the majority of bitunicate ascostromatic species, excluding Chaetothyriales and related taxa. Support for the monophyly of the class and its sister group relationship with Arthoniomycetes is strengthened by the acquisition of protein coding data, and two new subclasses, Pleosporomycetidae and Dothideomycetidae, are described.
- Geiser et al: Eurotiomycetes includes two subclasses, Eurotiomycetidae and Chaetothyriomycetidae, which collectively include prototunicate, bitunicate and lichenized species. The monophyly of Eurotiomycetes has been debated, but new data provide strong support for the class as defined herein and for the inclusion of the Coryneliales in the Eurotiomycetidae.

- Wang et al: Leotiomycetes contains the majority of the inoperculate, apothecial fungi with the exception of Geoglossaceae, which is shown to represent a separate origin of the earth tongue morphology. Leotiomycetes contains the Helotiales, Rhytismatales, Erysiphales, Cyttariales and Myxotrichaceae, and proves to be one of the most diverse classes of Ascomycota with respect to ascomatal morphologies.
- Zhang et al: Sordariomycetes includes all nonlichenized perithecial species and related cleistothecial and anamorphic taxa. Multigene analyses support the recognition of three subclasses (Hypocreomycetidae, Sordariomycetidae and Xylariomycetidae), but placement of additional lineages within the class is undetermined.
- Miadilkowska et al: Lecanoromycetes includes most of the lichen-forming fungal species (>13 500). Three subclasses are recognized, including Acarosporomycetidae, Ostropomycetidae and Lecanoromycetidae, but support for Lecanoromycetidae is tenuous. Monophyly of several orders and families is not supported, and traditional use of ascus morphology in systematics of the class cannot be applied consistently.

The works described above will have a large impact on future textbooks and continuously updated Web-based educational materials, which will continue to increase in importance. Toward this end, Deep Hypha participants are involved in the Tree of Life Project <http://tolweb.org/tree/>, where biological information, including phylogenetic trees, soon will be available for each of the major fungal taxa discussed in this issue of *Mycologia.*

Work remaining.—The base of the tree and the bare branches. Questions about the base of the fungal tree remain, but fungi usually have been proposed to have a close relationship with animals (Baldauf et al 2000, Baldauf 2003, Baldauf and Palmer 1993, Embley and Martin 2006, Keeling 2003, Keeling et al 2000, Fast and Keeling 2005, Phillipe et al 2004, Ragan et al 1996, Steenkamp et al 2006, Wainright et al 1993), although the details of the basal radiation are not clear. When Deep Hypha began the major questions included: Is a choanoflagellate ancestor for fungi well supported? Where is the origin of DAP lysine biosynthesis in the fungal ancestry? Can character evolution (flagella, hyphae, etc.) be traced? Can we infer the general morphology of ''first fungus''? Are microsporidians fungi or merely closely related organisms?

Five years later these questions are only partially answered, largely because of long branches and incomplete taxon sampling. In addition, studies of physiology and biochemistry have not been addressed in a phylogenetic context. Members of Opistokontia (Animalia, Fungi and four protist allies, including Choanoflagellata, Ichthyosporea, Mesomycetozoea and *Corallochytrea, Nuclearia* and *Ministeria*) share an insertion of about 12 amino acids (positions 153–238) in the EF-1α protein sequence (Baldauf and Palmer 1993). Phylogenetic analysis of four combined nuclear protein-coding gene sequences includes opistokont protists as well as basal metazoans and fungi (Amaral- Zettler et al 2001, Medina et al 2003, Steenkamp 2006) and provides evidence that *Nuclearia* is the sister taxon of Fungi (Steenkamp 2006). Furthermore the establishment of the monophyly of Choanoflagellata indicates that these organisms could not have been an ancestor shared by animals and fungi, as has been suggested (Cavalier-Smith 1987). The data also reject other hypotheses, including groupings of plants and fungi (Philip et al 2005), and animals and plants (Löytynoja and Milinkovitch 2001).

Cienkowski (1865), who studied a number of problematic organisms, including species of *Amoebidium* and labyrinthulids, also described *Nuclearia.* This is a genus of amoeboid protists with spherical bodies and radiating, rigid, filose pseudopodia; many species form walled cysts (Patterson 1984). These species are known from freshwater where they ingest algae and might be associated with aquatic animals, including fish. Environmental DNA samples indicate that members of the genus also might be present in marine environments (Bhattacharya and Oliveira 2000). Are we close to inferring the morphology of ''first fungus''? If Steenkamp and colleagues (2006) are correct, we are getting close. One superficial problem however is the absence of a flagellum in *Nuclearia*, an apparent loss such as the one that has occurred within the main fungal lineage, or could the flagellum be present in an unconnected missing morphological state? Both possibilities were suggested.

The branch tips of the current tree are fairly bare and many taxa remain to be discovered and included in analyses. If the conservative estimate of 1 500 000 fungal taxa is used, as it continues to be, less than a 10th of the taxa in the kingdom have been discovered (Hawksworth 2004). Many of these taxa will come from field studies. Fungi from rapid radiations into a multitude of habitats continue to be discovered in large numbers in geographically distant localities or undercollected hidden habitats (Arnold et al 2001, Suh et al 2004, Vanderkoornhuyse et al 2002). Other taxa from previously described all inclusive taxa, especially those with few distinctive morphological traits, will be dissected out as cryptic taxa (Blackwell and Jones 1997, Fisher et al 2002,

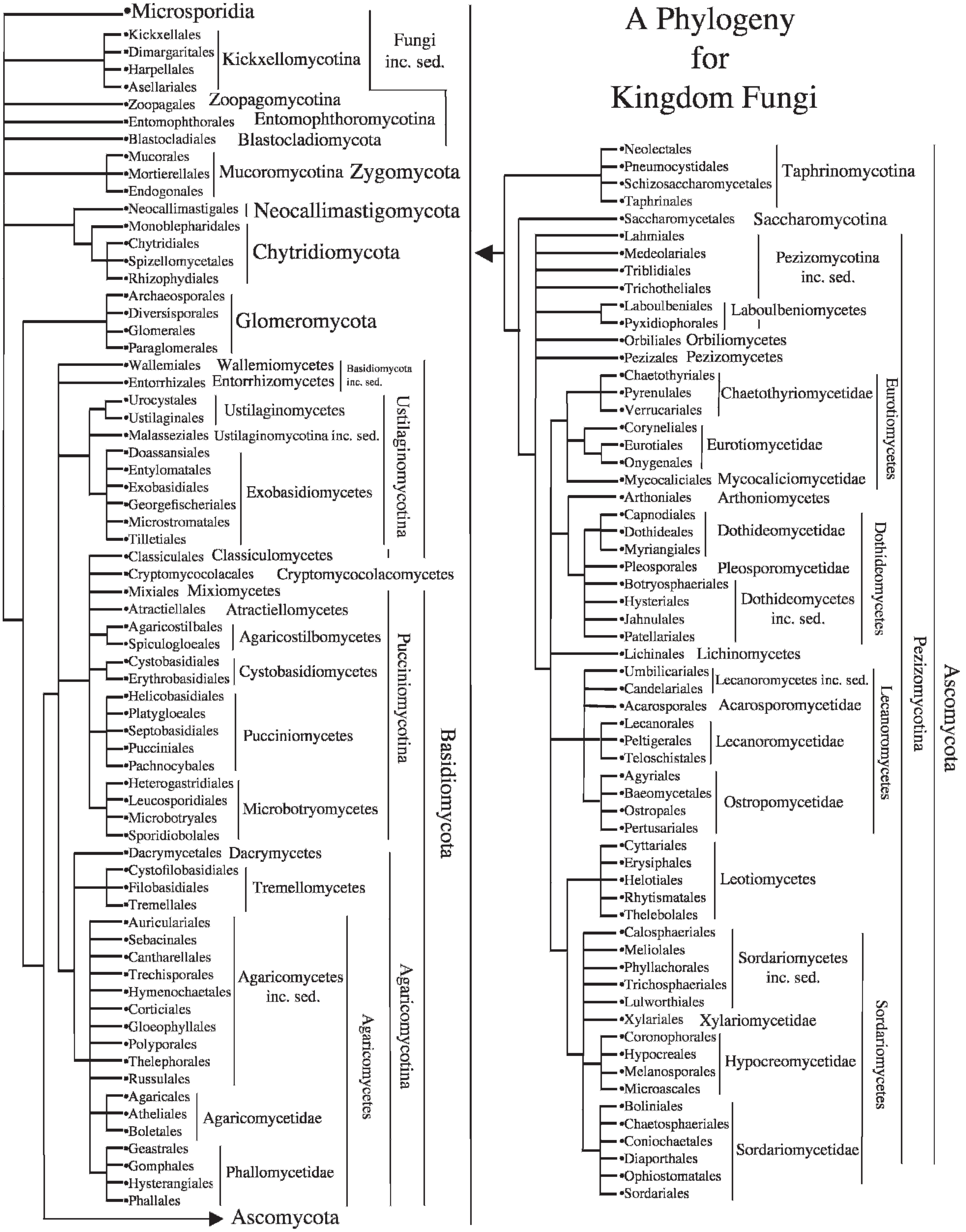

FIG 1. Phylogenetic tree diagram of members of kingdom Fungi. This tree is based on the phylogenetic studies of a number of mycologists. The project was originated by AFTOL and represents a first effort to provide an ordinal level phylogenetic classification to be used by all mycological publications. An expanded discussion of the classification is in preparation and will be published elsewhere. The most recent and archived earlier versions can be accessed at <http://www.clarku.edu/faculty/dhibbett/AFTOL/AFTOL.htm>. Also see the site for rules used in its construction.

Kurtzman 2003). One other way we are increasing numbers of taxa is by applying phylogenetic species concepts. Use of this concept results in a better understanding of the biology of organisms, including dispersal and geographical and host relations (Cassar and Blackwell 1996, Moncalvo 2005, Taylor et al 2000).

Classification.—The goal of synthesizing a uniform classification for kingdom Fungi was initiated at the Deep Hypha Arizona 2004 meeting and was designed as a collaborative effort with a number of mycologists. The authors of the *Dictionary of the Fungi*, individual authors of pages of the Tree of Life Web Project, the anticipated revision of the Alexopoulos textbook, GenBank and Myconet (www.fieldmuseum.org/myconet/) have agreed to use the classification. Many of the naming conventions applied to the classification of all fungi were those of Eriksson for Myconet. The overall goal of the classification was to produce a higher level phylogenetic classification of the Fungi by naming well supported clades. To do so, available higher level names sanctioned by the International Code of Botanical Nomenclature are employed for as many well supported clades as possible, and these names are used more consistently across the major phyla of Fungi (e.g. Ascomycota and Basidiomycota). The tree diagram (FIG. 1) is based on this classification and represents a working or draft consensus classification of the Fungi. A more complete classification is in preparation and will be published as a multi-authored manuscript (http://www.clarku.edu/faculty/dhibbett/AFTOL/AFTOL.htm). The classification presented here (FIG. 1) can be used as a guide to the groups discussed in this issue with the goal of producing a stable higher-level phylogenetic classification of Fungi.

ACKNOWLEDGMENTS

We thank all our collaborators who participated in the Deep Hypha project. We acknowledge financing from the National Science Foundation (Research Coordination Networks in Biological Sciences: a phylogeny for Kingdom Fungi, NSF- 0090301 to M. Blackwell, J.W. Spatafora and J.W. Taylor. We appreciate the commitment of James E. Rodman to promote systematics and encourage mycology for the past 25 y. We dedicate this paper to him.

LITERATURE CITED

Alexopoulos CJ. 1952. Introductory Mycology. New York: John Wiley & Sons.

———. 1962. Introductory Mycology. New York: John Wiley & Sons.

———, Mims CW. 1979. Introductory Mycology. New York: John Wiley & Sons.

———, ———, Blackwell M. 1996. Introductory Mycology. New York: John Wiley & Sons. 869 p.

Amaral-Zettler LA, Nerad TA, O'Kelly CJ, Sogin ML. 2001. The nucleariid amoebae: more protists at the animal-fungal boundary. J Euk Microbiol 48:293–297.

Arnold AE, Maynard Z, Gilbert GS. 2001. Fungal endophytes in dicotyledonous neotropical trees: patterns of abundance and diversity. Mycol Res 105:1502–1507.

Baldauf SL. 2003. The deep roots of eukaryotes. Science 300:1703–1706.

———, Palmer JD. 1993. Animal and fungi are each other's closest relatives: congruent evidence from multiple proteins. Proc Natl Acad Sci USA 90:11558–11562.

———, Roger AJ, Wenk-Siefert I, Doolittle WF. 2000. A kingdom-level phylogeny of eukaryotes based on combined protein data. Science 290:972–977.

Barr DJS. 1992. Evolution and kingdoms of organisms from the perspective of a mycologist. Mycologia 84:1–11.

Bhattacharya D, Oliveira MC. 2000. The SSU rDNA coding region of a filose amoeba contains a Group I Intron lacking the universally conserved G at the 3′-terminus. J Eukaryot Microbiol 47:585–589.

Blackwell M, Jones KG. 1997. Taxonomic diversity and interactions of insect-associated ascomycetes. Biodiver Conserv 6:689–699.

Bowman BH, Taylor JW, Brownlee AG, Lee J, Lu S-D, White TJ. 1992. Molecular evolution of the fungi: relationship of the Basidiomycetes, Ascomycetes and Chytridiomycetes. Mol Biol Evol 9:285–296.

Bruns TD, Vilgalys R, Barns SM, Gonzalez D, Hibbett DS, Lane DJ, Simon L, Stickel S, Szaro TM, Weisburg WG, Sogin ML. 1992. Evolutionary relationships within the Fungi: analyses of nuclear small subunit rRNA sequences. Mol Phylogen Evol 1:231–241.

Cassar SC, Blackwell M. 1996. Non-monophyly of ambrosia fungi in *Ambrosiella*. Mycologia 88:596–601.

Cavalier-Smith T. 1987. The origin of fungi and pseudofungi. In: Rayner ADM, Brasier CM, Moore D., eds. Evolutionary biology of fungi. Cambridge: Cambridge University Press. p 339–353.

Cienkowski L. 1865. Beiträge zur Kenntnis der Monaden. Ark Microsk Anat I:203–232. Pls. 12–14.

Embley TM, Martin W. 2006. Eukaryotic evolution, changes and challenges. Nature 440:623–630.

Fast NM, Keeling PJ. 2005. The fungal roots of microsporidian parasites. In: Vega FE, Blackwell M., eds. Insect-fungal associations. New York: Oxford Press. p 97–118.

Fischer MC, Koenig GL, White TJ, Taylor JW. 2002. Molecular and phenotypic description of *Coccidioides posadasii* sp. nov., previously recognized as the non-California population of *Coccidioides immitis*. Mycologia 94:73–84.

Hawksworth DL. 2004. Fungal diversity and its implications for genetic resource collections. Stud Mycol 50:9–18.

———, Kirk PM, Sutton BC, Pegler DM. 1995. Ainsworth & Bisby's dictionary of the fungi. 8th ed. Egham: CAB International. 616 p.

James TY, Porter D, Leander CA, Vilgalys R, Longcore JE.

2000. Molecular phylogenetics of the Chytridiomycota supports the utility of ultrastructural data in chytrid systematics. Can J Bot 78:336–350.

———, Kauff F, Schoch CL, Matheny PB, Hofstetter V, Cox CJ, Celio G, Gueidan C, Fraker E, Miadlikowska J, Lumbsch HT, Rauhut A, Reeb V, Arnold AE, Amtoft A, Stajich JE, Hosaka K, Sung G-H, Johnson D, O'Rourke B, Crockett M, Binder M, Curtis JM, Slot JC, Wang Z, Wilson AW, Schüßler A, Longcore JE, O'Donnell K, Mozley-Standridge S, Porter D, Letcher PM, Powell MJ, Taylor JW, White MM, Griffith GW, Davies DR, Humber RA, Morton JB, Sugiyama J, Rossman AY, Rogers JD, Pfister DH, Hewitt D, Hansen K, Hambleton S, Shoemaker RA, Kohlmeyer J, Volkmann-Kohlmeyer B, Spotts RA, Serdani M, Crous PW, Hughes KW, Matsuura K, Langer E, Langer G, Untereiner WA, Lücking R, Büdel B, Geiser DM, Aptroot A, Diederich P, Schmitt I, Schultz M, Yahr R, Hibbett DS, Lutzoni F, McLaughlin DJ, Spatafora JW, Vilgalys R. 2006. Reconstructing the early evolution of Fungi using a six-gene phylogeny. Nature 443:818–822.

Keeling PJ. 2003. Congruent evidence from a-tubulin and b-tubulin gene phylogenies for a zygomycete origin of microsporidia. Fungal Genet Biol 38:298–309.

———, Luker MA, Palmer JD. 2000. Evidence from beta-tubulin phylogeny that microsporidia evolved from within the fungi. Mol Biol Evol 17:23–31.

Kurtzman CP. 2003. Phylogenetic circumscription of *Saccharomyces, Kluyveromyces* and other members of the Saccharomycetaceae, and the proposal of the new genera *Lachancea, Nakaseomyces, Naumovia, Vanderwaltozyma* and *Zygotorulaspora*.. FEMS Yeast Res 4:233–245.

Liu Y, Whelen S, Hall BD. 1999. Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. Mol Biol Evol 16:1799–1808.

Löytynoja A, Milinkovitch MC. 2001. Molecular phylogenetic analysis of the mitochondrial ADP-ATP carriers: the Plantae/Fungi/Metazoa trichotomy revisited. Proc Natl Acad Sci USA 98:10202–10207.

Lutzoni F, Kauff F, Cox CJ, McLaughlin D, Celio G, Dentinger B, Padamsee M, Hibbett D, James TY, Baloch E, Grube M, Reeb V, Hofstetter V, Schoch C, Arnold AE, Miadlikowska J, Spatafora J, Johnson D, Hambleton S, Crockett M, Shoemaker R, Hambleton S, Crockett M, Shoemaker R, Sung GH, Lucking R, Lumbsch T, O'Donnell K, Binder M, Diederich P, Ertz D, Gueidan C, Hansen K, Harris RC, Hosaka K, Lim YW, Matheny B, Nishida H, Pfister D, Rogers J, Rossman A, Schmitt I, Sipman H, Stone J, Sugiyama J, Yahr R, Vilgalys R. 2004. Assembling the Fungal Tree of Life: progress, classification and evolution of subcellular traits. Am J Bot 91:1446–1480.

Medina M, Collins AG, Taylor JW, Valentine JW, Lipps JH, Amaral-Zettler L, Sogin ML. 2003. Phylogeny of Opisthokonta and the evolution of multicellularity and complexity in Fungi and Metazoa. Int J Astrobiol 2:203–211.

Moncalvo J-M. 2005. Molecular systematics: major fungal phylogenic groups and fungal species concepts. In: Xu JP, ed. Evolutionary genetics of Fungi. Norfolk: Horizon Scientific Press. p 1–33.

Nagahama T, Sato H, Shimazu M, Sugiyama J. 1995. Phylogenetic divergence of the entomophthoralean fungi: evidence from nuclear 18S ribosomal RNA gene sequences. Mycologia 87:203–209.

Nishida H, Sygiyama J. 1994. Archiascomycetes: detection of a major new lineage within the ascomycota. Mycoscience 35:361–366.

Patterson DJ. 1984. The genus *Nuclearia* (Sarcodina, Filosea) species composition and diagnoses of the taxa. Arch Protistenkd 128:127–139.

Philip GK, Creevey CF, McInerney JO. 2005. The Opisthokonta and the Ecdysozoa may not be clades: stronger support for the grouping of plant and animal than for animal and fungi and stronger support for the Coelomata than Ecdysozoa. Mol Biol Evol 22:1175–1184.

Philippe H, Snell EA, Bapteste E, Lopez P, Holland PWH, Casane D. 2004. Phylogenomics of eukaryotes: impact of missing data on large alignments. Mol Biol Evol 21: 1740–1752.

Ragan MA, Goggin CL, Cawthorn RJ, Cerenius L, Jamieson AVC, Plourd SM, Rand TG, Soderhall K, Gutell RR. 1996. A novel clade of protistan parasites near the animal-fungal divergence. Proc Natl Acad Sci USA 93: 11907–11912.

Redecker D, Morton JB, Bruns TD. 2000. Ancestral lineages of arbuscular mycorrhizal fungi (Glomales). Mol Phylogenet Evol 14:276–284.

Schüßler A, Scwarzott D, Walker C. 2001. A new fungal phylum, the Glomeromycota: phylogeny and evolution. Mycol Res 105:1414–1421.

Simon L, Bousquet L, Levesque RC, Lalonde M. 1993. Origin and diversification of endomycorrhizal fungi and coincidence with vascular plants. Nature 363:67–69.

Steenkamp ET, Wright J, Baldauf SL. 2006. The protistan origins of animals and fungi. Mol Biol Evol 23:93–106.

Suh S-O, McHugh JV, Blackwell M. 2004. Expansion of the *Candida tanzawaensis* yeast clade: 16 novel *Candida* species from basidiocarp-feeding beetles. Int J Syst Evol Microbiol 54:2409–2429.

Swann EC, Taylor JW. 1995. Phylogenetic perspectives on basidiomycete systematics: evidence from the 18S rRNA gene. Can J Bot 73:S862–S868.

Taylor JW. 1995. Making the Deuteromycota redundant: a practical integration of mitosporic and meiosporic fungi. Can J Bot 73S:S754–S759.

———, Bowman B, Berbee ML, White TJ. 1993. Fungal model organisms: phylogenetics of *Saccharomyces, Aspergillus* and *Neurospora.* System Biol 42:440–457.

———, Jacobson DJ, Fisher MC. 1999. The evolution of asexual fungi: reproduction, speciation and classification. An Rev Phytopathol 37:197–246.

———, Jacobson DJ, Kroken S, Kasuga T, Geiser DM, Hibbett DS, Fisher MC. 2000. Phylogenetic species recognition and concepts in Fungi. Fungal Genet Biol 31:21–32.

Taylor TN, Remy W, Hass H, Kerp H. 1995. Fossil arbuscular mycorrhizae from the lower Devonian. Mycologia 87: 560–573.

Vandenkoornhuyse P, Baldauf SL, Leyval C, Straczek J, Young JPJW. 2002. Extensive fungal diversity in plant roots. Science 295:2051.

Wainwright PO, Hinkle G, Sogin ML, Stickel SK. 1993. Monophyletic origins of the Metazoa: an evolutionary link with the Fungi. Science 260:340–342.

Wells K. 1994. Jelly fungi, then and now! Mycologia 86:18–48.