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Review:

Advances in the phylogenesis of Agaricales and its higher ranks and strategies for establishing phylogenetic hypotheses

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Abstract: We present an overview of previous research results on the molecular phylogenetic analyses in Agaricales and its higher ranks (Agaricomycetes/Agaricomycotina/Basidiomycota) along with the most recent treatments of taxonomic systems in these taxa. Establishing phylogenetic hypotheses using DNA sequences, from which an understanding of the natural evolutionary relationships amongst clades may be derived, requires a robust dataset. It has been recognized that single-gene phylogenies may not truly represent organismal phylogenies, but the concordant phylogenetic genealogies from multiple-gene datasets can resolve this problem. The genes commonly used in mushroom phylogenetic research are summarized.

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INTRODUCTION

Wherever we look in nature, we find a uniqueness of life that comprises biodiversity, e.g., in fungi (Ovrebo and Baroni, 2007; Noordeloos *et al*., 2007; Noordeloos and Hausknecht, 2007; Ortiz-Santana *et al*., 2007). To determine such uniqueness is the task of taxonomy. Presently, more than 1 million animal species and 500 000 plant and micro-organism species have been described, while the estimates of undescribed species range from 3~10 million or even higher. The amount of diversity is unmistakably immense (Mayr and Ashlock, 1991). In the case of fungi and even the larger basidiomycetes, the numbers of fungi being described are relatively immense (Lechner *et al*., 2006; Le *et al*., 2007a; 2007b; Tan *et al*., 2007).

The application of the terms, taxonomy and systematics, often overlaps, but they have a subtle difference in meaning: "taxonomy is the theory and practice of classifying organisms" (Mayr and Ashlock, 1991), whereas "systematics is the scientific study of the kinds and diversity of organisms and of any and all relationships among them" (Simpson, 1961). More simply, systematics is the science of diversity of organisms and deals with populations, species and higher taxa. It not only provides urgently needed information concerning these levels, but also, and more importantly, cultivates a way of thinking, a way of approaching biology as a whole (Mayr, 1968; 1982).

The major tasks of systematics are to determine by means of comparison what the unique properties of each species and higher taxa are, to determine what properties certain taxa have in common and establish the biological causes of the differences or shared

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characters, and to determine the variation within taxa (Mayr and Ashlock, 1991). The requirements of systematic study involve species recognition and arrangement of the different taxa into a classification that will show their natural relationships (Kaul, 1997).

Systematics is one of the major subdivisions of biology, and is as broad-based as genetics or molecular biology. It includes not only identification, but also the comparative study of all aspects of organisms as well as their evolutionary history. Based on the advance in DNA sequencing techniques and analytic methods in the last decade, the knowledge of molecular phylogenetics and systematics of fungi has progressed rapidly.

Basidiomycota are characterized by multi-layered cell walls, barrel-shaped structures or pulley wheel occlusions at the septa of hyphae (dolipore septa), an extended dikaryophase, clamp connections that often develop on septa, and the formation of meiosporangia (basidia) that produce meiospores (basidiospores) at the tips of sterigmata (Kendrick, 2000). Almost 30000 species had been described (Kirk *et al*., 2001).

Historically, Basidiomycota have been treated as a subphylum Basidiomycotina and comprise 3 classes: Teliomycetes (rust and smut fungi), Hymenomycetes (mostly gilled mushrooms) and Gasteromycetes (puffballs, bird's nest fungi, earth stars, stinkhorns) in a 5-subphyla classification system (Ainsworth *et al*., 1973). In the latest edition of *Dictionary of the Fungi*, Basidiomycota comprise 3 classes: (1) Basidiomycetes (including members of Hymenomycetes and Gasteromycetes), (2) Urediniomycetes, and (3) Ustilaginomycetes, and "hymenomycetes" and "gasteromycetes" taken as informal and not monophyletic categories (Kirk *et al*., 2001).

With the exception of Urediniomycetes and Ustilaginomycetes that contain important plant pathogens, the basidiomycetes mostly are saprobes and symbionts, and play ecologically important roles, such as oxygen, carbon and nitrogen cycling. Humans have been attracted by mushrooms since ancient times because of their edible or poisonous traits (Garibay-Orijel *et al*., 2006). Mushrooms are an important group in the biosphere and their significance in diversity and conservation issues has been recognized extensively.

ADVANCE OF PHYLOGENETIC SYSTEMATICS OF BASIDIOMYCOTA AND AGARICOMYCOTINA

Swann and Taylor (1993) conducted pioneering studies on the phylogeny of Basidiomycota by sequencing and analyzing the 18S rRNA gene of 19 species. They increased the number of species to 54 using the same gene (Swann and Taylor, 1995). Both publications revealed 3 major groups: Hymenomycetes, Ustilaginomycetes and Urediniomycetes in Basidiomycota. Subsequent researchers (James *et al*., 2006; Blackwell *et al*., 2006) have shown Swann and Taylor's classification to be remarkably stable, but the term of Hymenomycetes is no longer accepted because it is a homonym of "hymenomycetes" of Fries in 1874, which had been shown to be polyphyletic and should be used only informally.

The "Deep Hypha" project, which continued as the "Assembling the Fungal Tree of Life (AFTOL)" project, aims to establish the phylogeny of the entire fungal kingdom. Several publications, milestones in the classification of fungi, have been published as a result (James *et al*., 2006; Blackwell *et al*., 2006; Matheny *et al*., 2006). All publications consistently revealed similar major clades in the monophyletic fungal kingdom. These discoveries are summarized by Hibbett *et al*.(2007) as "the higher-level classification of fungi", which includes a comprehensive phylogenetic classification of the kingdom of fungi. The classification accepts 1 kingdom, 1 subkingdom, 7 phyla, 10 subphyla, 35 classes, 12 subclasses and 129 orders. Ascomycota and Basidiomycota constitute the subkingdom Dikarya, which comprises taxa with dikaryotic hyphae. The formerly named basidiomycetes, urediniomycetes and ustilaginomycetes (Kirk *et al*., 2001) are accepted as Agaricomycotina, Pucciniomycotina and Ustilaginomycotina, respectively.

The classification of major groups within the Agaricomycotina remains unsettled. It has been divided into Heterobasidiomycetes (jelly fungi) and Homobasidiomycetes (mushroom-forming fungi) based on the structure of the septal pore apparatus and the spindle pole body in GenBank 2006 and Mycota VIIb (Hibbett and Thorn, 2001), while they are called Tremellomycetidae and Agaricomycetidae under the class Basidiomycetes in the last edition of *Dictionary* *of the Fungi* (Kirk *et al*., 2001). In the Homobasidiomycetes, a preliminary phylogenetic outline with 8 major clades was revealed using nuc-ssu and mt-ssu rDNA sequences (Hibbett *et al*., 1997). These major clades coincided with Polyporoid, Euagarics, Bolete, Russuloid, Thelephoroid, Hymenochaetoid, Cantharelloid and Gomphoid-phalloid clades. This classification was not congruent with Swann and Taylor (1995)'s findings. Recently Homobasidiomycetes was shown to be polyphyletic (Binder *et al*., 2005; Moncalvo *et al*., 2006).

Presently, the most accepted classification of Agaricomycotina comprises 5 independent clades that are supported with Bayesian statistics (Hibbett, 2006), and they are recognized as the 5 classes, Agaricomycetes, Tremellomycetes, Dacrymycetes, Wallemiomycetes and Entorrhizomycetes (James *et al*., 2006; Hibbett *et al*., 2007; Matheny *et al*., 2007).

Lack of, or having septa within basidia, the type of basidia division and the basidiospore discharge mechanism were previously considered as important higher-level characters, but this is not reflected by phylogenetic reconstructions. Characters associated with the septal pore apparatus, nuclear division and the spindle pole body are in agreement with current molecular phylogenetic analyses (Celio *et al*., 2006) based on the structural and biochemical database for AFTOL.

ADVANCE OF PHYLOGENETIC SYSTEMATICS OF AGARICOMYCETES AND AGARICALES

The class Agaricomycetes is divided into 2 subclasses: Agaricomycetidae and Phallomycetidae (Binder *et al*., 2005; Matheny *et al*., 2007). Agaricomycetidae comprises 3 orders: Agaricales, Atheliales and Boletales, while Phallomycetidae comprises 13 orders (Matheny *et al*., 2006; 2007). In many orders, especially those representing larger groups, such as Agaricales, there is still not enough resolution or taxon sampling to develop comprehensive family-level classifications (Hibbett *et al*., 2007).

Agaricales comprises the so-called mushrooms and toadstools, and is the largest clade of mushroom-forming fungi (Kirk *et al*., 2001; Singer, 1986). More than 9000 species in more than 300 genera and 26 families had been described (Kirk *et al*., 2001). Mostly they are terrestrial, lignicolous and saprobic, and many are mycorrhizal.

An early classification of mushrooms was developed by Fries in 1874. In his classification 12 genera of gilled mushrooms (agarics) were recognized based on macroscopic features of basidiocarps and colors of spore prints (white, pink, brown, purple-brown and black). His system was widely used as it had the advantage that many genera could be identified on field characters. The system was relatively unchallenged until Fayod studied the anatomy and microscopic features of basidiocarps and consequently recognized 108 genera in 1889.

The most influential systematic treatment of the Agaricales is *The Agaricales in Modern Taxonomy* by Singer (1986; 1962). Singer utilized Fayod's anatomic characters and Fries's macroscopic characters in reorganizing families and genera. The term "Agaricales" in his scheme refers to the order containing the type genus *Agaricus* and the type family Agaricaceae. In his system there were 3 major groups in the order Agaricales s.l.: Agaricales s.str., Boletales, and Russulales. These 3 groups were accepted as the euagaric clades, bolete clade and russuloid clade based on molecular data (Hibbett and Thorn, 2001). Totally 18 families and 230 genera were distinguished in his system (Singer, 1986).

Recent molecular phylogenetic research has revealed that Singer's Agaricales roughly parallels the euagarics clade (Hibbett *et al*., 1997; Moncalvo *et al*., 2000; 2002). However, phylogenetic data have shown that an overemphasis on spore print color, fruit body formation and some anatomical and cytological traits has led to the establishment of many artificial groups, while some cyphelloid, aphyllophoralean and gasteroid fungi should be included. For example, Hibbett *et al*.(1997) constructed a comprehensive phylogenetic dataset using nuclear and mitochondrial ribosomal DNA sequences of representatives of Agaricales, Aphyllophorales and "gasteromycete" families (i.e., gilled, nongilled and puffballs). The data show that fruitbody form and hymenophore type did not reflect phylogenetic relationships well. Later research has also confirmed this (Hibbett, 2004). Moncalvo *et al*. (2000) investigated phylogenetic relationships within the order Agaricales with analysis of nuclear large subunit ribosomal DNA sequences. One of their discoveries was to reveal polyphyletic groups, such as in the families Tricholomataceae, Cortinariaceae and

Hygrophoraceae and the polyphyletic genera *Clitocybe*, *Omphalina* and *Marasmius*. Another phylogenetic study using a broader sampling in the euagaric clade (Moncalvo *et al*., 2002) analyzed nuclear large subunit ribosomal DNA sequences to reveal 117 monophyletics clades and at the same time showed that some traditional taxonomic groupings were artificial. Some non-gilled resupinate, cyphelloid and gasteroid taxa were found to be members of the Agaricales (Binder and Bresinsky, 2002; Binder *et al*., 2005; Bodensteiner *et al*., 2004; Larsson *et al*., 2004; Moncalvo *et al*., 2002; Hallen *et al*., 2003; Matheny and Bougher, 2006; Peintner *et al*., 2001). These discoveries indicate that ecological, biochemical, or tropic habits rather than morphological similarities should also be used as diagnostic characters to understand the natural groupings in this order (Moncalvo *et al*., 2002).

The most recent phylogenetic treatment within Agaricales was conducted by Matheny *et al*.(2006). In this study the dataset consisted of 146 genera and 238 species utilizing sequences from 6 gene regions: rpb1, rpb-intron2, rpb2, 18S, 25S and 5.8S rRNAs. Bayesian analysis revealed 6 clades labeled the Agaricoid, Tricholomatoid, Marasmioid, Pluteoid, Hygrophoroid and Plicaturopsidoid clades.

The Agaricoid clade (in Euagarics clade) comprised 14 families and tribes of primarily dark-spored agarics and gasteromycetes that clustered together with significant Bayesian support. The same group was also resolved in the maximum parsimony tree but with poor bootstrap support (Matheny *et al*., 2006). Nidulariaceae and Cystodermateae formed a subclade in the Agaricoid clade, thus the main group comprising 12 families.

RECOGNITION OF SPECIES AND ADVANCE IN STRATEGIES FOR ESTABLISHING PHYLOGENETIC HYPOTHESES

Speciation and recognition of species

Speciation is a process in which genetically cohesive groups diverge into two or more genetically distinct groups of individuals. This process is due to change and accumulation in genetic differences through the natural process of evolution, including mutation, selection and genetic drift. When the differences become sufficient, they are recognized as different species (Petersen and Hughes, 1999). Polyploidy or chromosomal rearrangement is the main way to form genetic differences and different species may arise from different populations in overlapping geographical ranges (Burnett, 2003). Speciation is a process that occurs with time, although there is uncertainty concerning the exact point in this process when a population becomes a species (Petersen and Hughes, 1999).

The species concept based on Darwinian evolution and speciation is known as the Evolutionary Species Concept (ESC), which defines a species as “a single lineage of ancestor-descendent populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate” (Wiley, 1978). However, this concept is difficult to operate in practice. Mayden (1997) proposed the Morphological Species Concept (MSC), Biological Species Concept (BSC), and Phylogenetic Species Concept (PSC) as secondary to the ESC, which can be used to diagnose or recognize species.

A species based on the MSC assesses overall similarities of morphological characters. MSC is in the most commonly used system for the identification of organisms. The recognition of species by MSC, however, often comprises more than one species (Taylor *et al*., 2000). In many cases, fruitbody phenotypic differences are subtle and there is disagreement as to whether two groups are different species or just local adaptations within a species. Evidence from fungi shows that genetic isolation precedes reproductive isolation and that morphological differentiation comes last. The rate of nucleotide substitution in fungi, a key factor in phylogenetics, has been shown to be similar to that in bacteria and macroscopic eukaryotes (Kasuga *et al*., 2002).

The BSC comprises “groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups” (Mayr, 1940). The greatest limitation of BSC is that it is impossible to apply this concept to all fungi as many lack meiospores or often cannot be cultivated to carry out mating tests. Furthermore, there is evidence (Hibbett *et al*., 1995; Hibbett and Donoghue, 1996) that the criterion of reproduction lumps together groups of fungi that are genetically isolated in nature (e.g., in *Lentinula edodes*). It has been argued that the BSC overemphasizes potential gene flow between populations, whereas the PSC can recognize as distinct species those groups or populations that are genetically isolated from other groups and, therefore, represent distinct evolutionary units (Harrison, 1998).

The PSC is "the smallest diagnosable cluster of individual organisms within which there is a pattern of ancestry and descent" (Mayr, 1940). PSC requires recognition of monophyletic groups of organisms that share at least one uniquely derived character, and this character is descended from a common ancestor (Taylor *et al*., 2000; Moncalvo, 2005). In fungi, applying the PSC in research concerning asexual organisms and in the detection of relationships between anamorphic and teleomorphic stages of a single species has an obvious advantage (Moncalvo, 2005).

Different attributes in a species have been regarded as being important, and thus some species have been defined differently. The most pragmatic way to proceed is therefore to continue to work with a morphospecies as the basic taxonomic unit, but to include additional supplementary material as supplied by other studies as a guide to both phylogenetic trends and the interpretation of evolutionary potentialities. In operational terms this could most easily be achieved by the use of the MSC, and supplementary reference to the entities defined as BSC or PSC (Burnett, 2003). There are many examples where new or old taxa are recognized based on morphological and molecular phylogenetic data (Blanco-Dios *et al*., 2006; Bruns *et al*., 1998; Buyck *et al*., 2006; Callac and Guinberteau, 2005; Capelari *et al*., 2006; Dai *et al*., 2006; Desjardin *et al*., 2004; Miller and Huhndorf, 2004; Minnis *et al*., 2006, Wang *et al*., 2002), but also where morphological data are only presented (Antonin and Buyck, 2006; Barrasa *et al*., 2006; Nuytinck *et al*., 2006) including occasionally with mating type studies (Tan *et al*., 2007).

Advance in strategies for establishing phylogenetic hypotheses

Statements such as "Phylogenetic methods come to age", "The use of molecular phylogenies to examine evolutionary questions has become commonplace with automation of DNA sequencing and availability of efficient computer programs to perform phylogenetic analysis" have evocated the use of sequencing in mushroom taxonomy (Huelsenbeck and Rannala, 1997). The goal of phylogenetics is to construct phylogenetic topologies that form assumptions concerning the natural evolutionary relationships of clades. There is an evident need to obtain a robust and accurate phylogeny from the data, and this can be achieved by extending the number of nucleotides sequenced and by choosing the appropriate genes. The use of more nucleotides in phylogenetic analysis has become commonplace (Berbee *et al*., 2000). It also been recognized that single-gene phylogenies may not truly represent organismal phylogenies, but the concordant phylogenetic genealogies from multi-gene sequences can solve this problem well (Doyle, 1992; Maddison, 1997; Taylor *et al*., 2000). Furthermore the use of different kinds of genes has been recommended, as the rDNA genes alone could not provide sufficient information to resolve a fungal phylogeny with a satisfactory level of confidence (Bruns *et al*., 1992; Sugiyama, 1998; Tehler *et al*., 2000; Berbee *et al*., 2000; Binder and Hibbett, 2002; Moncalvo *et al*., 2000; 2002). Multiple genes sequence data from both nuclear and mitochondrial rDNAs have been used in recent papers (Hibbett *et al*., 1997; Hibbett and Binder, 2002; Binder and Hibbett, 2002; Binder *et al*., 2005, Hughey *et al*., 2000; Wang *et al*., 2004). The use of data from protein-coding genes for a broad inference of fungal systematics has been hindered due to the difficulty in designing robust primers for PCR amplification across a broad range of diverse taxa, and the need to clone heterozygous loci in dikaryotic organisms (Moncalvo, 2005). However, progress has been made, as proposed in AFTOL (http://ocid.nacse.org/research/aftol/). The protein-coding genes frequently used in Basidiomycota are as follows: *RPB1*, the gene that encodes the largest subunit of RNA polymerase II (Kropp and Matheny, 2004; Matheny *et al*., 2002; Matheny, 2005); *RPB2*, the gene that encodes the second largest subunit of RNA polymerase II (Liu *et al*., 1999; Liu and Hall, 2004; Matheny, 2005; Reeb *et al*., 2004; Wang *et al*., 2004; Zhang and Blackwell, 2002); *tef1*, codes for translation elongation factor 1-α (Baldauf and Palmer, 1993; O′Donnell *et al*., 2001; Rehner and Buckley, 2005; Matheny *et al*., 2007); and *ATP6*, a mitochondrial gene (Kretzer and Bruns, 1999; Robison *et al*., 2001). In all this, the morphological characters must not be forgotten!

References

Ainsworth, G.C., Sparrow, F.K., Sussman, A.S. (Eds.), 1973. A Taxonomic Review with Keys: Basidiomycetes and Lower Fungi. *In*: The Fungi, an Advanced Treatise Volume IVB. Academic Press, New York and London.

Antonin, V., Buyck, B., 2006. *Marasmius* (Basidiomycota, Marasmiaceae) in Madagascar and the Mascarenes. *Fungal Diversity*, **23**:17-50.

Baldauf, S.L., Palmer, J.D., 1993. Animals and fungi are each others closest relatives: congruent evidence from multiple proteins. *Proc. Natl. Acad. Sci. USA*, **90**(24):11558-11562. [doi:10.1073/pnas.90.24.11558]

Barrasa, J.M., Esteve-Raventós, F., Dähncke, R.M., 2006. *Clitocybula canariensis* (Tricholomataceae), a new brown-rot fungus from the Canary Islands (Spain). *Fungal Diversity*, **22**:1-11.

Berbee, M.L., Carmean, D.A., Winka, K., 2000. Ribosomal DNA and resolution of branching order among the Ascomyceta: how many nucleotides are enough? *Mol. Phyl. Evol.*, **17**(3):337-344. [doi:10.1006/mpev.2000.0835]

Binder, M., Bresinsky, A., 2002. Derivation of a polymorphic lineage of Gasteromycetes from boletoid ancestors. *Mycologia*, **94**(1):85-98. [doi:10.2307/3761848]

Binder, M., Hibbett, D.S., 2002. Higher-level phylogenetic relationships of homobasidiomycetes (mushroom-forming fungi) inferred from four rDNA regions. *Mol. Phyl. Evol.*, **22**(1):76-90. [doi:10.1006/mpev.2001.1043]

Binder, M., Hibbett, D.S., Larsson, K.H., Larsson, E., Langer, E., Langer, G., 2005. The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi (Homobasidiomycetes). *Syst. Biodiv.*, **3**(2):113-157. [doi:10.1017/S1477200005001623]

Blackwell, M., Hibbett, D.S., Taylor, J.W., Spatafora, J.W., 2006. Research coordination networks: a phylogeny for kingdom fungi (Deep Hypha). *Mycologia*, **98**(6):829-837. [doi:10.3852/mycologia.98.6.829]

Blanco-Dios, J.B., Wang, Z., Binder, M., Hibbett, D.S., 2006. A new *Sparassis* from Spain described using morphological and molecular data. *Mycol. Res.*, **110**(10):1227-1231. [doi:10.1016/j.mycres.2006.07.012]

Bodensteiner, P., Binder, M., Agerer, R., Moncalvo, J.M., Hibbett, D.S., 2004. Phylogenetic diversity of cyphelloid forms in the homobasidiomycetes. *Mol. Phyl. Evol.*, **33**(2):501-515. [doi:10.1016/j.ympev.2004.06.007]

Bruns, T.D., Vilgalys, R., Barns, S.M., Gonzalez, D., Hibbett, D.S., Lane, D.J., Simon, L., Stickel, S., Szaro, T.M., Weisburg, W.G., Sogin, M.L., 1992. Evolutionary relationships within the fungi: analyses of nuclear small subunit rRNA sequences. *Mol. Phyl. Evol.*, **1**(3):231-241. [doi:10.1016/1055-7903(92)90020-H]

Bruns, T.D., Szaro, T.M., Gardes, M., Cullings, K.W., Pan, J.J., Taylor, D.L., Horton, T.R., Kretzer, A., Garbrlotto, M., Li, Y., 1998. A sequence database for the identification of ectomycorrhizal basidiamycetes by phylogenetic analysis. *Mol. Ecol.*, **7**(3):257-272. [doi:10.1046/j.1365-294X.1998.00337.x]

Burnett, J., 2003. Fungal Populations Species. Oxford University Press, London.

Buyck, B., Mitchell, D., Parrent, J., 2006. *Russula parvovirescens* sp. nov., a common but ignored species in the eastern Unoted States. *Mycologia*, **98**(4):612-615. [doi:10.3852/mycologia.98.4.612]

Callac, P., Guinberteau, J., 2005. Morphological and molecular characterization of two novel species of *Agaricus* section *Xanthodermatei*. *Mycologia*, **97**(2):416-424. [doi:10.3852/mycologia.97.2.416]

Capelari, M., Rosa, L.H., Lachance, M.A., 2006. Description and affinities of *Agaricus martineziensis*, a rare species. *Fungal Diversity*, **21**:11-18.

Celio, G.J., Padamsee, M., Dentinger, B.T.M., Bauer, R., McLaughlin, D.J., 2006. Assembling the fungal tree of life: constructing the structural and biochemical database. *Mycologia*, **98**(6):850-859. [doi:10.3852/mycologia.98.6.850]

Dai, Y.C., Wang, Z., Binder, M., Hibbett, D.S., 2006. Phylogeny and a new species of Sparassis (Polyporales, Basidiomycota): evidence from mitochondrial *atp6*, nuclear rDNA and *rpb2* genes. *Mycologia*, **98**(4):584-592. [doi:10.3852/mycologia.98.4.584]

Desjardin, D.E., Wang, Z., Binder, M., Hibbett, D.S., 2004. *Sparassis cystidiosa* sp. nov. from Thailand is described using morphological and molecular data. *Mycologia*, **96**(5):1010-1014.

Doyle, J.J., 1992. Gene trees and species trees: molecular systematics as one-character taxonomy. *Syst. Bot.*, **17**(1):144-163. [doi:10.2307/2419070]

Garibay-Orijel, R., Cifuentes, J., Estrada-Torres, A., Caballero, J., 2006. People using macro-fungal diversity in Oaxaca, Mexico. *Fungal Diversity*, **21**:41-67.

Hallen, H.E., Watling, R., Adams, G.C., 2003. Taxonomy and taxicity of Conocybe lacteal and related species. *Mycol. Res.*, **107**(8):969-979. [doi:10.1017/S0953756203008190]

Harrison, G.R., 1998. Linking evolutionary pattern and process. *In*: Howard, D.J., Berlocher, S.H. (Eds.), Endless Forms. Oxford University Press, Oxford.

Hibbett, D.S., 2004. Trends in morphological evolution in homobasidiomycetes inferred using maximum likelihood a comparison of binary and multistate approaches. *Syst. Biol.*, **53**(6):889-903. [doi:10.1080/10635150490522610]

Hibbett, D.S., 2006. A phylogenetic overview of the Agaricomycotina. *Mycologia*, **98**(6):917-925. [doi:10.3852/mycologia.98.6.917]

Hibbett, D.S., Donoghue, M.J., 1996. Implications of phylogenetic studies for conservation of genetic diversity in shiitake mushrooms. *Cons. Biol.*, **10**(5):1321-1327. [doi:10.1046/j.1523-1739.1996.10051321.x]

Hibbett, D.S., Thorn, R.G., 2001. Basidiomycota: Homobasidiomycetes. *In*: McLaughlin, D.J., McLaughlin, E.G., Lemke, R.A. (Eds.), The Mycota, Vol. 7B. Systematics and Evolution. Springer-Verlag, New York, p.121-168.

Hibbett, D.S., Binder, M., 2002. Evolution of complex fruiting body morphologies in homobasidiomycetes. *Proc. Roy. Soc. B Biol. Sci.*, **269**(1504):1963-1969. [doi:10.1098/

rspb.2002.2123]

Hibbett, D.S., Tsuneda, A., Fukumasa-Nakai, Y., Donoghue, M.J., 1995. Phylogenetic diversity in shiitake inferred from nuclear ribosomal DNA sequences. *Mycologia*, **87**(5):618-638. [doi:10.2307/3760806]

Hibbett, D.S., Pine, E.M., Langer, E., Langer, G., Donoghue, M.J., 1997. Evolution of gilled mushrooms and puffballs inferred from ribosomal DNA sequences. *Proc. Natl. Acad. Sci. USA*, **94**(22):12002-12006. [doi:10.1073/pnas.94.22.12002]

Hibbett, D.S., Binder, M., Bischoff, J.F., Blackwell, M., Cannon, P.F., Eriksson, O.E., Huhndorf, S., James, T., Kirk, P.M., Lücking, R., *et al.*, 2007. A higher-level phylogenetic classification of the fungi. *Mycol. Res.*, **111**(5):509-548. [doi:10.1016/j.mycres.2007.03.004]

Huelsenbeck, J.P., Rannala, B., 1997. Phylogenetic methods come of age: testing hypotheses in an evolutionary context. *Science*, **276**(5310):227-232. [doi:10.1126/science.276.5310.227]

Hughey, B.D., Adams, G.C., Bruns, T.D., Hibbett, D.S., 2000. Phylogeny of Calostoma, the gelatinous stalked puffball, based on nuclear and mitochondrial ribosomal DNA sequences. *Mycologia*, **92**(1):94-104. [doi:10.2307/3761453]

James, T.Y., Kauff, F., Schoch, C., Matheny, P.B., Hofstetter, V., Cox, C., Celio, G., Gueidan, C., Fraker, E., Miadlikowska, J., *et al.*, 2006. Reconstructing the early evolution of the fungi using a six gene phylogeny. *Nature*, **443**(7113):818-822. [doi:10.1038/nature05110]

Kasuga, T., White, T.J., Taylor, J.W., 2002. Estimation of nucleotide substitution rates in eurotiomycetes fungi. *Mol. Biol. Evol.*, **19**:2318-2324.

Kaul, T.N., 1997. Introduction to Mushroom Science (Systematics). Science Publishers Inc., New Hampshire.

Kendrick, B., 2000. The Fifth Kingdom, 3rd Ed. Focus Publishing, USA.

Kirk, P.M., Cannon, P.F., David, J.C., Stalpers, J.A., 2001. Dictionary of the Fungi, 9th Ed. CAB International, London.

Kretzer, A.M., Bruns, T.D., 1999. Use of *atp6* in fungal phylogenetics: an example from the boletales. *Mol. Phyl. Evol.*, **13**(3):483-492. [doi:10.1006/mpev.1999.0680]

Kropp, B.P., Matheny, P.B., 2004. Basidiospore homoplasy and variation in the lnocybe chelanensis group in North America. *Mycologia*, **96**(2):295-309. [doi:10.2307/3762065]

Larsson, K.H., Larsson, E., Köljalg, U., 2004. High phylogenetic diversity amony corticioid basidiomycetes. *Mycol. Res.*, **108**(9):983-1002. [doi:10.1017/S0953756204000851]

Le, H.T., Nuytinck, J., Verbeken, A., Lumyong, S., Desjardin, D.E., 2007a. *Lactarius* in northern Thailand: 1. *Lactarius* subgenus *Piperites*. *Fungal Diversity*, **24**:173-224.

Le, H.T., Stubbe, D., Verbeken, A., Nuytinck, J., Lumyong, S., Desjardin, D.E., 2007b. *Lactarius* in northern Thailand: 2. *Lactarius* subgenus *Plinthogali*. *Fungal Diversity*, **27**:61-94.

Lechner, B.E., Wright, J.E., Popoff, E., 2006. New taxa and new records of fungi for Argentina from Iguazú National Park, Misiones. *Fungal Diversity*, **21**:131-139.

Liu, Y.J., Hall, B.D., 2004. Body plan evolution of ascomycetes, as inferred from an RNA polymerase II phylogeny. *Proc. Natl. Acad. Sci. USA*, **101**(13):4507-4512. [doi:10.1073/pnas.0400938101]

Liu, Y.J., Whelen, S., Hall, B.D., 1999. Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. *Mol. Biol. Evol.*, **16**:1799-1808.

Maddison, W.P., 1997. Gene trees in species trees. *Syst. Biol.*, **46**(3):523-536. [doi:10.2307/2413694]

Matheny, P.B., 2005. Improving phylogenetic inference of mushrooms with RBP1 and RBP2 nucleotide sequences Inocybe, Agaricales. *Mol. Phyl. Evol.*, **35**(1):1-20. [doi:10.1016/j.ympev.2004.11.014]

Matheny, P.B., Bougher, N.L., 2006. The new genus *Auritella* from Africa and Australia (Inocybaceae, Agaricales): molecular systematics, taxonomy and historical biogeography. *Mycol. Prog.*, **5**(1):2-17. [doi:10.1007/s11557-005-0001-8]

Matheny, P.B., Liu, Y.J., Ammirati, J.F., Hall, B.D., 2002. Using RPB1 sequences to improve phylogenetic inference among mushrooms (*Inocebe*, Agaricales). *Am. J. Bot.*, **89**(4):688-698. [doi:10.3732/ajb.89.4.688]

Matheny, P.B., Curtus, J.M., Hofstetter, V., Aime, M.C., Moncalvo, J.M., Ge, Z.W., Yang, Z.L., Slot, J.C., Ammirati, J.F., Baroni, T.L., *et al.*, 2006. Major clades of Agaricales: a multilocus phylogenetic overview. *Mycologia*, **98**(6):982-995. [doi:10.3852/mycologia.98.6.982]

Matheny, P.B., Wang, Z., Binder, M., Curtis, J.M., Lim, Y.W., Nilsson, R.H., Hughes, K.W., Hofstetter, V., Ammirati, J.F., Schoch, C., *et al.*, 2007. Contributions of *rpb2* and *tef1* to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Mol. Phyl. Evol.*, **43**(2):430-451. [doi:10.1016/j.ympev.2006.08.024]

Mayden, R.L., 1997. A Hierarchy of Species Concepts: The DENOUEMENt in the Saga of the Species Problem. *In*: Claridge, M.F., Dawah, H.A., Wilson, M.P. (Eds.), The Units of Biodiversity. Chapman & Hall, London, p.381-424.

Mayr, E., 1940. Speciation phenomena in birds. *Am. Nat.*, **74**(752):249-278. [doi:10.1086/280892]

Mayr, E., 1968. The role of systematics in biology. *Science*, **159**(3815):595-599. [doi:10.1126/science.159.3815.595]

Mayr, E., 1982. The Growth of Biological Thought. Harvard University Press, Cambridge, MA.

Mayr, E., Ashlock, P.D., 1991. Principles of Systematic Zoology, 2nd Ed. McGraw-Hill, New York.

Miller, A.N., Huhndorf, S.M., 2004. Using phylogenetic species recognition to delimit species boundaries within *Lasiosphaeria*. *Mycologia*, **96**(5):1106-1127. [doi:10.2307/3762093]

Minnis, A.M., Sundberg, W.J., Nelsen, S.F., 2006. *Pluteus aurantipes* sp. nov. from Wisconsin, United States. *Mycologia*, **98**(4):659-661. [doi:10.3852/mycologia.98.4.659]

Moncalvo, J.M., 2005. Molecular Systematics: Major Fungal

Phylogenetic Groups and Fungal Species Concepts. *In*: Xu, J.P. (Ed.), Evolutionary Genetics of Fungi. Horizon Scientific Press, Norfolk.

Moncalvo, J.M., Lutzoni, F.M., Rehner, S.A., Johnson, J., Vilgalys, R., 2000. Phylogenetic relationships of Agaric fungi based on nuclear large subunit ribosomal DNA sequences. *Syst. Biol.*, **49**(2):278-305. [doi:10.1080/10635159950173852]

Moncalvo, J.M., Vilgalys, R., Redhead, S.A., Johnson, J.E., James, T.Y., Aime, M.C., Hofstetter, V., Verduin, S.J.W., Larsson, E., Baroni, T.J., *et al*., 2002. One hundred and seventeen clades of euagarics. *Mol. Phyl. Evol.*, **23**(3): 357-400. [doi:10.1016/S1055-7903(02)00027-1]

Moncalvo, J.M., Nilsson, R.H., Koster, B., Dunbam, S.M., Bernaruer, T., Matheny, P.B., Porter, T.M., Margaritescu, S., Weiß, M., Garnica, S., *et al*., 2006. The cantharelloid clade: dealing with incongruent gene trees and phylogenetic reconstruction methods. *Mycologia*, **98**(6):937-948. [doi:10.3852/mycologia.98.6.937]

Noordeloos, M.E., Hausknecht, A., 2007. The genus Entoloma (Basidiomycetes, Agaricales) of the Mascarenes and Seychelles. *Fungal Diversity*, **27**:111-144.

Noordeloos, M.E., Vrinda, K.B., Manimohan, P., 2007. On two remarkable brown-spored agarics from Kerala State, India. *Fungal Diversity*, **27**:145-155.

Nuytinck, J., Wang, X.H., Verbeken, A., 2006. Descriptions and taxonomy of the Asian representatives of *Lactarius* sect. *Deliciosi*. *Fungal Diversity*, **22**:171-203.

O′Donnell, K., Lutzoni, F., Ward, T.J., Benny, G.L., 2001. Evolutionary relationships among mucoralean fungi (Zygomecota): evidence for family polyphyly on a large scale. *Mycologia*, **93**(2):286-296. [doi:10.2307/3761650]

Ortiz-Santana, B., Lodge, D.J., Baroni, T.J., Both, E.E., 2007. Boletes from Belize and the Dominican Republic. *Fungal Diversity*, **27**:247-416.

Ovrebo, C.L., Baroni, T.J., 2007. New taxa of Tricholomataceae and Entolomataceae (Agaricales) from Central America. *Fungal Diversity*, **27**:157-170.

Peintner, U., Bougher, N.L., Castellano, M.A., Moncalvo, J.M., Moser, M.M., Trappe, J.M., Vilgalys, R., 2001. Multiple origins of sequestrate fungi related to *Cortinatius* (Cortinatiaceae). *Am. J. Bot.*, **88**(12):2168-2179. [doi:10.2307/3558378]

Petersen, R.H., Hughes, K.W., 1999. Species and speciation in mushrooms. *BioScience*, **49**(6):440-452. [doi:10.2307/1313552]

Reeb, V., Lutzoni, F., Roux, C., 2004. Contribution of RPB2 to multilocus phylogenetic studies of the euascomycetes (Pezizomycotina, Fungi) with special enphasis on the lichen-forming Acarosporaceae and evolution of pilyspory. *Mol. Phyl. Evol.*, **32**(3):1036-1060. [doi:10.1016/j.ympev.2004.04.012]

Rehner, S.A., Buckley, E., 2005. A Beauveria phylogeny inferred from nuclear ITS and EF1-α sequences: evidence for cryptic diversification and links to *Cordyceps teleomorphs*. *Mycologia*, **97**(1):84-98. [doi:10.3852/mycologia.97.1.84]

Robison, M.M., Chiang, B., Horgen, P.A., 2001. A phylogeny of the genus *Agaricus* based on mitochondrial *atp6* sequences. *Mycologia*, **93**(1):30-37. [doi:10.2307/3761603]

Simpson, G.G., 1961. Principles of Animal Taxonomy. Columbia University Press, New York.

Singer, R., 1962. The Agaricales in Modern Taxonomy, 2th Ed. Weinheim, J. Cramer, Germany, p.916.

Singer, R., 1986. The Agaricales in Modern Taxonomy, 4th Ed. Koeltz Scientific Books, Koenigsternm, Germany, p.981.

Sugiyama, J., 1998. Relatedness, phylogeny, and evolution of the fungi. *Mycoscience*, **39**(4):487-511. [doi:10.1007/BF02460912]

Swann, E.C., Taylor, J.W., 1993. Higher taxa of basidiomycetes: an 18S rRNA gene perspective. *Mycologia*, **85**(6): 923-936. [doi:10.2307/3760675]

Swann, E.C., Taylor, J.W., 1995. Phylogenetic perspective on basidiomycetes systematics: evidence from the 18S rRNA gene. *Can. J. Bot.*, **73**(Suppl. 1):S862-S868. [doi:10.1139/b95-332]

Tan, Y.S., Desjardin, D.E., Vikineswary, S., Abdullah, N., 2007. New species and mating studies of *Marasmius* from Malaysia. *Fungal Diversity*, **25**:187-217.

Taylor, J.W., Jacobson, D.J., Kroken, S., Kasuga, T., Geiser, D.M., Hibbett, D.S., Fisher, M.C., 2000. Phylogenetic species recognition and species concepts in fungi. *Fungal Genet. Biol.*, **31**(1):21-32. [doi:10.1006/fgbi.2000.1228]

Tehler, A., Farris, J.S., Lipscomb, D.L., Källersjo, M., 2000. Phylogenetic analyses of the fungi based on large rDNA data sets. *Mycologia*, **92**(3):459-474. [doi:10.2307/3761505]

Wang, Z., Binder, M., Hibbett, D.S., 2002. A new species of Cudonia based on morphological and molecular data. *Mycologia*, **94**(4):641-650. [doi:10.2307/3761715]

Wang, Z., Binder, M., Dai, Y.C., Hibbett, D.S., 2004. Phylogenetic relationships of *Sparassis* inferred from nuclear and mitochondrial ribosomal DNA and a protein-coding gene (*rpb2*). *Mycologia*, **96**(5):1013-1027. [doi:10.2307/3762086]

Wiley, E.O., 1978. The evolutionary species concept reconsidered. *Syst. Zool.*, **27**(1):17-26. [doi:10.2307/2412809]

Zhang, N., Blackwell, M., 2002. Molecular phylogeny of Melanospora and similar pyrenomycetous fungi. *Mycol. Res.*, **106**(2):148-155. [doi:10.1017/S0953756201005354]