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After the gold rush, or before the flood? Evolutionary morphology of mushroom-forming fungi (*Agaricomycetes*) in the early 21st century☆

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ABSTRACT

Mushroom-forming fungi (*Agaricomycetes*, approx. syn.: *Homobasidiomycetes*) produce a diverse array of fruiting bodies, ranging from simple crust-like forms to complex, developmentally integrated forms, such as stinkhorns and veiled agarics. The 19th century Friesian system divided the mushroom-forming fungi according to macromorphology. The Friesian taxonomy has long been regarded as artificial, but it continues to influence the language of mycology and perceptions of fungal diversity. Throughout the 20th century, the phylogenetic significance of anatomical features was elucidated, and classifications that departed strongly from the Friesian system were proposed. However, the anatomical studies left many questions and controversies unresolved, due in part to the paucity of characters, as well as the general absence of explicit phylogenetic analyses. Problems in fruiting body evolution were among the first to be addressed when molecular characters became readily accessible in the late 1980s. Today, GenBank contains about 108,000 nucleotide sequences of 'homobasidiomycetes', filed under 7300 unique names. Analyses of these data are providing an increasingly detailed and robust view of the phylogeny and the distribution of different fruiting body forms across the 14 major clades that make up the agaricomycetes. However, it would be wrong to suggest that all the important questions about fruiting body evolution have been resolved. Recent studies focusing on resupinate forms suggest that there may still be undetected major clades of agaricomycetes, which could have a significant impact on our estimates of the ancestral forms in this morphologically diverse group. Modern approaches, including comparative phylogenetic analyses and developmental studies, have the potential to yield novel insights into both the macroevolutionary processes and cellular mechanisms of fungal morphological evolution.

Introduction

Agaricomycetes (approx. syn. *Homobasidiomycetes sensu* Hibbett & Thorn 2001) produce a diverse array of fruiting bodies, including gilled mushrooms (agarics), chanterelles, stinkhorns, corticioid fungi, polypores, cyphelloid fungi, false truffles, coral fungi, bird's nest fungi, puffballs, and other forms that defy easy description (e.g. *Sparassis*). Reconstructing the evolution of fruiting body forms has been one of the major goals of fungal systematics for many generations. This review presents a synopsis of the development of our current understanding of phylogeny and morphological evolution in

☆ This paper is dedicated to Orson K. Miller, jr (1930–2006).

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Agaricomycetes. No attempt has been made to be comprehensive, and the selection of works cited is slanted towards my interests. With that caveat, this article is intended primarily for new students of mycology, who may be simultaneously searching for dissertation topics and grappling with the literature of the past.

Pre-molecular views on fruiting body evolution

Fruiting body form was the central organizing principle in the 19th century classification of Elias Fries (1874 and earlier publications; also see Persoon 1801). The Friesian classification, as it came to be interpreted by 20th century authors (e.g. Donk 1971), contains two classes, the *Hymenomycetes*, including fungi that produce spores on an exposed hymenium, and the *Gasteromycetes*, which produce spores internally. The *Hymenomycetes* were separated into two orders, the *Agaricales*, for all the gilled forms, and the *Aphyllophorales*, for all the non-gilled forms. The *Aphyllophorales* were further divided into six families based on the form of the hymenophore (e.g. *Polyporaceae* for poroid forms, *Hydnaceae* for toothed forms, etc.). Largely, the development of agaricomycete systematics from the time of Fries to the present, amounts to a decoupling of macromorphology and taxonomy with the successive introduction of anatomical, biochemical, and eventually, molecular characters. The Friesian higher taxa are now known to be polyphyletic, but we still talk about forms such as 'agarics', 'polypores', and 'hydnums', and these forms are used to organize field guides and introductory mycology courses. Thus, the Friesian view of fungal diversity remains influential.

The artificial nature of the Friesian system was evident long before the rise of molecular systematics. Indeed, as early as the beginning of the 20th century, Patouillard (1900) was using anatomical characters to arrange macrofungi into groups that were more 'natural' than the Friesian higher taxa. By the 1960s, many broad, intuitively derived evolutionary scenarios were being advanced for the agaricomycetes based on comparative anatomical studies (e.g. Savile 1955; Kreisel 1969; Corner 1972; Oberwinkler 1977; Jülich 1981; Parmasto 1986, and various authors in Petersen 1971a). It is fascinating now to look back on this literature and see how the ideas of one author, expressed in elegant prose, but generally without an accompanying cladogram, influenced those of another. For example, Corner (1972) suggested that the ancestral form of the *Agaricomycetes* was a simple clavarioid form, from which other more elaborate forms were derived, and this view was further developed by Jülich (1981), who placed the *Cantharellales* as the basal group in his comprehensive phylogeny of basidiomycetes.

One of the most influential works in evolutionary systematics of agaricomycetes was that of Donk (1964, 1971), who divided the *Aphyllophorales* into 23 families. Many of the 'modern' families recognized by Donk, such as the *Thelephoraceae*, *Gomphaceae*, and *Hymenochaetaceae*, were based on distinctive anatomical characters and they included taxa with highly divergent fruiting body forms (representing multiple Friesian families). These groups have remained largely intact in the light of modern molecular phylogenies. However, Donk's classification also included several residual families, including the *Clavariaceae*, *Corticiaceae*, *Hydnaceae*, *Stereaceae* and *Polyporaceae*, which Donk acknowledged—and molecular studies have confirmed—are artificial assemblages that are united only by gross morphology.

A complement to Donk's treatment of *Aphyllophorales* was Singer's (1986 and earlier editions) series of comprehensive publications on *Agaricales*, which he divided into three suborders, the *Agaricineae*, *Boletineae*, and *Russulineae*. The inclusion of the poroid members of the *Boletineae* in Singer's *Agaricales* was a departure from a strictly Friesian system, while the distribution of lamellate taxa in all three suborders reflected his view that there were multiple major groups of 'agarics'.

Gasteromycetes presented difficult challenges for pre-molecular fungal systematists. Some gasteroid taxa, such as stinkhorns and bird's nest fungi, are so highly modified at both the macro- and microscopic level that they cannot be linked to specific taxa of hymenomycetous forms based on morphology. However, other gasteroid forms, including 'secotioid' taxa, have obvious anatomical similarities to certain taxa of agarics and boletes (Heim 1971; Smith 1973; Thiers 1984; Singer 1986). To cite only two examples, false truffles in the genus *Zelleromyces* have amyloid ornamented spores and produce latex, which is strong evidence that they are related to agaricoid taxa in *Lactarius* of the *Russulaceae*, while another group of false truffles in *Rhizopogon* has fusiform to ellipsoid, pale to yellow–brown spores, which suggest a relationship to the *Boletales*. Workers such as Heim (1971); Smith (1973); Thiers (1984) and Singer (1986) all agreed that there must have been multiple evolutionary transitions between gasteroid and hymenomycetous forms *via* secotioid intermediates, but they disagreed about which forms were plesiomorphic and which were derived. Singer expressed the minority view that the gasteroid forms make up a paraphyletic assemblage that gave rise to agarics and boletes, whereas Thiers (1984) and others argued that it was more likely that gasteroid forms were derived repeatedly, because multiple origins of hymenomycetous forms would require repeated origins of the complex mechanism of ballistospory (forcible spore discharge). Thiers's essentially parsimony-based arguments would later be confirmed in multiple molecular studies.

The 'gasteromycetes early' *versus* 'gasteromycetes late' debate was just one of many cases where different workers viewing the same characters arrived at contradictory phylogenetic conclusions. Another example concerns the lentinoid fungi, a group of wood-decaying agarics placed in the genera *Lentinus*, *Panus*, and *Pleurotus* (and others). Lentinoid fungi have anatomical similarities to certain polypores, including thick-walled skeletal and binding hyphae in the fruiting body context, and hyphal pegs (fascicles of hyphae that protrude from the hymenium) in some species. Pegler (1983), Singer (1986), and Corner (1981) all agreed that the lentinoid fungi are closely related to polypores, but they disagreed about the polarity of the pore–gill transition, as well as the higher-level taxonomic placement of the lentinoid fungi. Pegler (1983: 10–11) suggested that *Lentinus* has 'an affinity with the *Aphyllophorales* rather than the *Agaricales*' and that it 'represents the most agaricoid development from a polyporoid ancestry'. In contrast, Singer (1986: 164) wrote that 'the lamellate genera (*Lentinieae*) of the *Polyporaceae*

have nothing in common with the *Aphyllophorales*', and he included the lentinoid fungi and a small number of polypores in the *Agaricales*. Yet another view was expressed by Corner (1981: 25), who suggested that the lentinoid fungi are 'rather primitive agarics' that were derived from hydnoid ancestors, and which gave rise to separate lineages of lignicolous polypores.

The controversy over the lentinoid fungi (as well as the debate over polarity of gasteroid-agaricoid transformations) illustrates both the strengths and weaknesses of fungal systematics in the pre-molecular era. Recognition of the phylogenetic significance of hyphal anatomy required keen observational skills and a broad, detailed knowledge of fungal diversity. At the same time, the absence of explicit analytical approaches made it difficult to resolve conflicting phylogenetic hypotheses. Unfortunately, mycologists were not among the early adopters of cladistic methods, as were some zoologists (Brundin 1965) and botanists (Wagner 1961). [However, see Petersen's (1971b) study using Wagner groundplan analysis to assess relationships of clavarioid and cantharelloid forms.] If mycologists had embraced Hennigian methods early, then perhaps that would have led to more critical analyses, with an emphasis on homology assessment in the context of multiple characters. Lacking such a conceptual framework, many mycologists viewed phylogenetic hypotheses as purely 'theoretical'. Such a sentiment was expressed by Heim (1971: 507), who wrote 'Phylogenesis in mycology is not yet a science. It is an intellectual game based on arguments that often escape rigorous control and that almost always escape the test of experiment'.

To summarize, fungal taxonomists working through the latter part of the 20th century resolved multiple clusters of agaricomycetes, many of which included diverse fruiting body forms that would have been placed in different families, orders, and even classes in the Friesian system. However, the placements of numerous taxa, such as many corticioid fungi and the more derived gasteroid forms, were obscure, and there was considerable ambiguity about the higher-order relationships of agaricomycetes. Compounding this uncertainty was the tendency to regard phylogenetic hypotheses as beyond the realm of objective evaluation. Perhaps for these reasons, the Friesian system, with its 'lure of simplicity' (Donk 1971: 5), continued to have a strong impact on taxonomy, even into the 1990s. For example, the 1996 edition of the major textbook of mycology by Alexopoulos, Mims & Blackwell (Alexopoulos *et al.* 1996) still divided the agaricomycetes into the *Agaricales*, *Aphyllophorales*, and *Gasteromycetes* (with an acknowledgement that these taxa are not monophyletic). A very different approach was taken in the 1995 (eighth) edition of the *Dictionary of the Fungi* by Hawksworth and colleagues, which divided the agaricomycetes (as *Holobasidiomycetidae*) into 27 orders, including a mixture of putatively monophyletic groups based on anatomy (e.g. *Hericiales*, *Hymenochaetales*), as well as residual 'garbage can' taxa based on macromorphology (e.g. *Hymenogastrales*, *Poriales*). Thus, in the 1990s agaricomycete taxonomy was in transition to a phylogenetic system. This process would be greatly accelerated by the advent of molecular characters, which became readily accessible after the development of PCR and, later, fluorescent automated DNA sequencing.

Molecular perspectives on morphological evolution in agaricomycetes

Early molecular studies—the gold rush

Anatomical studies in the pre-molecular era provided a wealth of detailed, explicit, and sometimes contradictory phylogenetic hypotheses. Understandably, the first problems to be explored with molecular data in the late 1980s and early 1990s involved morphologically dissimilar taxa that had been predicted to be closely related based on anatomical characters. Gasteroid forms were particularly attractive. A classic early study was that of Bruns *et al.* (1989), who confirmed that the false truffle *Rhizopogon* is derived from the boletoid *Suillus*, as predicted by Thiers (1984) and others. Other gasteroid forms that were the targets of the early molecular studies included the secotioid taxa *Podaxis* and *Montagnea*, which were shown to be closely related to certain coprinoid agarics (*Coprinus s. lat.*) (Hopple & Vilgalys 1994), the false truffle *Hydnangium*, which is related to the agaricoid *Laccaria* (Mueller & Pine 1994), and the secotioid *Gastrosuillus*, which is closely related to the boletoid *Suillus grevillei* (Baura *et al.* 1992). All of these studies used ribosomal genes, either of mitochondrial or nuclear origin (mt-rDNA, nu-rDNA), following the description of conserved primer sites by White *et al.* (1990). The early literature in fungal molecular systematics was reviewed by Bruns *et al.* (1991) and Hibbett (1992).

Lentinoid fungi were also among the first agaricomycetes to be studied with molecular approaches (Hibbett & Vilgalys 1991, 1993), and were found to represent four independent clades. *Lentinus s. str.* was shown to be closely related to *Polyporus arcularius*, which is a relatively ephemeral polypore with elongate, angular pores, binding hyphae, and hyphal pegs (Fig 1). Later, the lentinoid genera *Panus s. str.* and *Neolentinus* (Redhead & Ginns 1985) would be shown to be closely related to different groups of polypores (*Albatrellus syringae* and *Gloeophyllum*, respectively), while *Pleurotus* was shown to be among the *Agaricales* (Thorn *et al.* 2000). Thus, the general view that (some) lentinoid fungi and (some) polypores are closely related was upheld, although the extensive polyphyly of the lentinoid fungi, and their precise phylogenetic placements, had not been predicted.

The works cited above provided insight into the composition of relatively small terminal clades, and they highlighted individual cases of morphological transformations. These studies indicated the need for revision of major taxonomic groups, such as the *Agaricales sensu* Singer (1986) and the *Aphyllophorales sensu* Donk (1964, 1971), but they did not provide the comprehensive overview that could serve as the basis for such a revision.

Toward the end of the 1990s, phylogenetic studies with broad taxonomic sampling across the agaricomycetes began to appear, including works by Hibbett & Donoghue (1995), who sampled 62 species of agaricomycetes, with a focus on polypores, using partial mtSSU rDNA sequences; Boidin *et al.* (1998), who sampled 360 sequences of mostly *Aphyllophorales sensu* Donk, using the highly variable ITS of nu-rDNA; and Bruns *et al.* (1998), who examined 152 partial mtLSU rDNA sequences representing over 130 species, with a focus on

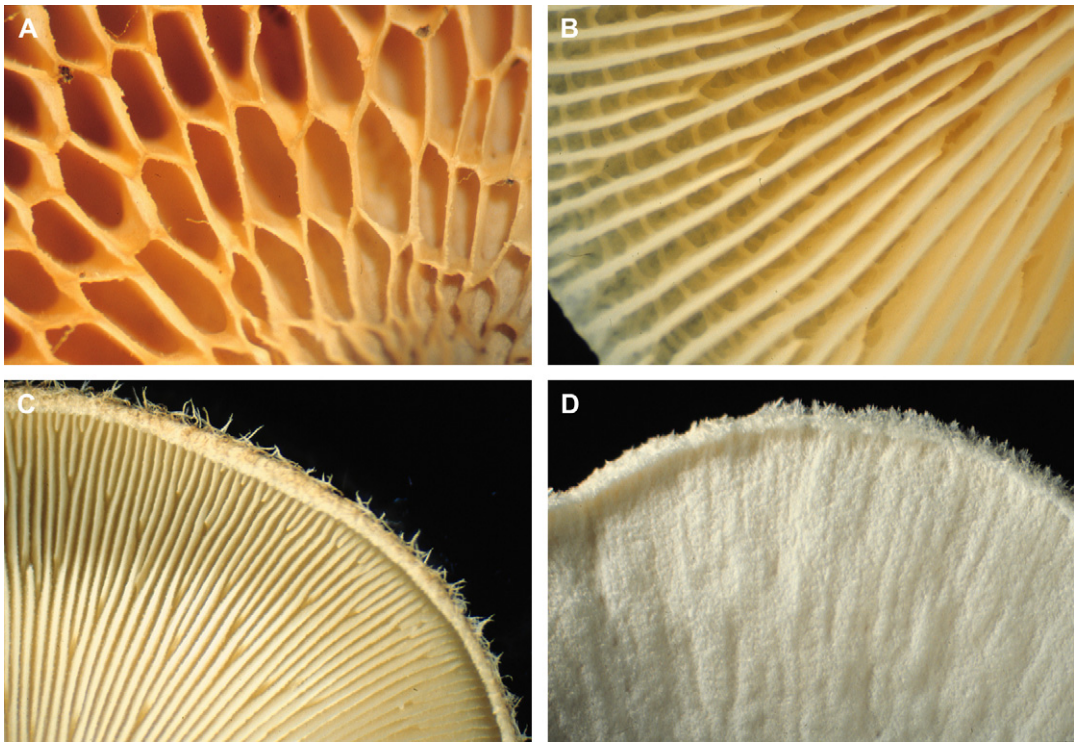


Fig 1 – Hymenophore transformations in *Lentinus* s. str. (A) *Polyporus arcularius*, which is closely related to *Lentinus*, has angular, radially elongate pores. (B) The typical agaricoid form of *L. tigrinus* has moderately crowded lamellae with tangential cross-bridges. (C) *L. crinitus* has crowded lamellae, with lamellulae of several lengths, and no cross-bridges. (D) The secotioid form of *L. tigrinus* has a hymenophore that is permanently covered by a layer of tissue derived from the margins of the lamellae.

ectomycorrhizal taxa. Each of these studies included what was for the time a large number of taxa, but owing to the limitations of the data, they did not resolve the deepest nodes in the agaricomycetes with confidence. Nevertheless, they resolved multiple terminal clades, many of which included taxa with highly divergent fruiting body forms. For example, Hibbett & Donoghue found support for a group including the polypore *Bjerkandera adusta* and the resupinate *Pulcherricium caeruleum*; while the tree of Boidin *et al.* resolved a clade of '*Hericiales*' including diverse resupinate forms along with the polypore *Heterobasidion annosum* and the pileate-stipitate hydnoid fungus *Auriscalpium vulgare* (among others); and Bruns *et al.* found strong support for a clade including the false truffle *Gautieria monticola*, the resupinate, hydnoid fungus *Kavinia alboviridis*, cantharelloid forms in *Gomphus*, and coralloid forms in *Ramaria*. Thus, through these studies a more detailed (if somewhat fragmentary and unresolved) picture of transformations in fruiting body forms began to appear.

One of the first multi-locus molecular studies that addressed the higher-level phylogenetic relationships of agaricomycetes was that of Hibbett *et al.* (1997), who combined mtSSU and nuSSU rDNA sequences of 81 species from across the traditional *Agaricales*, *Aphyllophorales*, and *Gasteromycetes*. A parsimony optimization of fruiting body forms on the resulting tree suggested that there have been at least six independent origins of the agaricoid habit. The vast majority of agaricoid forms were shown to be in a group that was labelled the 'euagarics', which corresponds in large part to the *Agaricales* suborder *Agaricineae* of Singer (1986). The *Boletales*, roughly equivalent to Singer's *Boletineae*, was placed as the sister group of the euagarics clade, but the gilled members of Singer's *Russulineae* were distantly related. Four independent origins of gasteroid forms were resolved. One remarkable clade of gasteroid forms was shown to contain stinkhorns (*Pseudocolus fusiformis*), earthstars (*Geastrum saccatum*), and the cannonball fungus (*Sphaerobolus stellatus*). In prior classifications of *Gasteromycetes* (Dring 1973; Hawksworth *et al.* 1995), these taxa were placed in three different orders (*Phallales*, *Lycoperdales*, and *Nidulariales* or *Sclerodermatales*, respectively), with no apparent relationship to any hymenomycetous forms. The mt/nuSSU rDNA data suggested that these gasteroid taxa form a clade that is the sister group of a clade that contains gomphoid, clavarioid, and coralloid forms (*Gomphus floccosus*, *Clavariadelphus pistillaris*, and *Ramaria stricta*).

Other studies in the 1990s were focused on boletes (Kretzer & Bruns 1997, Binder *et al.* 1997), agarics (Moncalvo *et al.* 2000), club and coral fungi (Pine *et al.* 1999), attine ant-associated fungi (Chapela *et al.* 1994), polypores (Ko *et al.* 1997), and other groups. Using the tree from Hibbett *et al.* (1997) as a framework, Hibbett & Thorn (2001) integrated the results of all the available published and unpublished studies on higher-level agaricomycete phylogeny produced from 1992 to 2000 (25 studies in all) to create a 'preliminary phylogenetic outline' that divided the agaricomycetes (as *Homobasidiomycetes*) into eight major clades

that were given informal names. In addition to the euagarics clade, these groups included the gomphoid-phalloid clade (described above), polyporoid clade, russuloid clade, thelephoroid clade, cantharelloid clade, hymenochaetoid clade, and bolete clade. Scoring fruiting body forms with seven states (agaricoid, poroid, hydnoid, clavarioid-coralloid, corticioid, epigeous-gasteroid, and hypogeous-gasteroid), Hibbett & Thorn suggested that each of the eight clades contains as few as four (cantharelloid clade) or as many as seven (russuloid clade) fruiting body forms (av. 5.75).

The eight-clade view of agaricomycete diversity was reflected in the ninth edition of the *Dictionary of the Fungi* by Kirk *et al.* (2001), who included eight orders of '*Agaricomycetidae*'. This was a bold move on the part of the authors, because not all of the clades proposed by Hibbett & Thorn were resolved with confidence by the molecular data available at the time, and the taxon sampling was still sparse. In particular, the polyporoid clade, which became the *Polyporales* in the *Dictionary*, had been very weakly supported. Also, the brown-rot polypore *Gloeophyllum sepiarium* could not be placed in any of the eight clades (Hibbett & Thorn 2001), which was an early indication that the eight-clade outline underestimated the actual phylogenetic diversity of agaricomycetes.

Recent molecular studies 1—resolving the major branches of agaricomycete phylogeny

Research in agaricomycete systematics has grown by leaps and bounds since 2001, with two general trends evident. One trend is a dramatic expansion in taxon sampling, which has been achieved primarily through studies using rDNA. The other trend is the rise of multi-locus analyses that combine rDNA with protein-coding genes, specifically RNA polymerase II subunits one and two (*rpb*1, *rpb*2), translation elongation factor (*tef*1-α), and ATP synthetase. The combined effect of this work has been the development of a robust, detailed understanding of agaricomycete phylogeny, which is now being used to construct a revised ordinal-level classification of agaricomycetes (and other fungi) by the Assembling the Fungal Tree of Life consortium (see http://www.clarku.edu/faculty/dhibbett/AFTOL/AFTOL.htm). Hereafter, the ordinal names used are those of this 'AFTOL classification'.

One of the major developments of recent years was the discovery of several new clades of agaricomycetes beyond the eight clades identifed by Hibbett & Thorn (2001). These groups, which are composed almost entirely of resupinate, crust-like forms, were independently discovered by several research groups (Lim 2001; Hibbett & Binder 2002; Langer 2002; Larsson *et al.* 2004; Binder *et al.* 2005). Multiple informal names were assigned to these clades in the original publications reporting their discovery. In the AFTOL classification they are called the *Corticiales*, *Trechisporales*, and *Atheliales* (Hibbett *et al.* 2007). In addition, studies on basal 'heterobasidiomycetes' have resulted in the discovery of another independent, major clade, the *Sebacinales*, which includes taxa with resupinate, coralloid, and encrusting fruiting bodies (Selosse *et al.* 2002; Weiss *et al.* 2004).

The studies cited in the preceding paragraph improved understanding of agaricomycete phylogeny by virtue of their intensive taxon sampling. However, they all used rDNA exclusively, and consequently, they all suffered from weak support for many of the 'backbone' nodes in the agaricomycetes, including the basal nodes that specify the relationships between the homobasidiomycetes and heterobasidiomycetes (Binder & Hibbett 2002). A recent multilocus study by Matheny *et al.* (2007b) provides much needed resolution of some of these problematical deep nodes. Matheny *et al.* sampled five genes (nuLSU, nuSSU, and 5.8S rDNA, *rpb*2, and *tef*1-α) in 119 species that represent all the major groups of agaricomycetes, except *Gloeophyllum* and its close relatives. Their analyses demonstrated with strong support that the agaricomycetes is a monophyletic group that includes the *Sebacinales* and the *Auriculariales*, which have gelatinous fruiting bodies and are traditionally recognized as heterobasidiomycetes (e.g., the cultivated 'wood-ear' jelly fungus, *Auricularia auricula-judae*). Other *heterobasidiomycetes* in the agaricomycetes include the *Tulasnellaceae* and *Ceratobasidiaceae*, which produce resupinate fruiting bodies and appear to be nested within the *Cantharellales*. However, the *Dacrymycetales* and *Tremellales*, which are heterobasidiomycetes with gelatinous fruiting bodies, were shown to be outside of the agaricomycetes. Thus, the homobasidiomycetes and heterobasidiomycetes are non-monophyletic groups, and these names should be used only as descriptive terms, in the same manner that the terms gasteromycetes and hymenomycetes are now used. The analysis of Matheny *et al.* also provided strong support for the *Polyporales*, and many other higher-order groupings within the agaricomycetes, including the sister-group relationship between the *Boletales*, which is dominated by pileate-stipitate forms, and the wholly resupinate *Atheliales*.

In short, the agaricomycetes is thought to contain at least 14 independent major clades, including three that are composed only of resupinate forms (*Atheliales*, *Corticiales*, *Trechisporales*), two that include only heterobasidiomycetes (*Auriculariales*, *Sebacinales*), and one that includes both heterobasidiomycetes and homobasidiomycetes (*Cantharellales*). The remaining eight clades contain only homobasidiomycetes and produce the vast majority of conspicuous mushroom fruiting bodies, as well as cryptic resupinate forms. One of these eight clades is the *Gloeophyllales*, which was represented by the lone taxon *Gleophyllum sepiarium* in the phylogenetic outline of Hibbett & Thorn (2001). The *Gloeophyllales* is now understood to contain polypores (*Gloeophyllum*), agarics (*Neolentinus, Heliocybe*), and resupinate forms (*Veluticeps*, and possibly others) (Thorn *et al.* 2000; Binder *et al.* 2005).

Recent molecular studies 2—reconstructing the fine branches of the tree

While the global studies described above have addressed the broad outlines of agaricomycete phylogeny, numerous analyses focused within individual clades have helped resolve patterns of evolution in terminal groups in detail. A summary of fruiting body forms across all 14 major clades of agaricomycetes (following the AFTOL classification; Hibbett *et al.* 2007) is presented in Table 1. For this purpose, fruiting body morphology has been coded with seven major forms [pileate-stipitate, pileate-sessile, resupinate, clavarioid (unbranched), coralloid (branched), cyphelloid, and gasteroid]. Pileate and resupinate forms are further divided according to the

Table 1 – Distribution of fruiting body forms across 14 major clades of agaricomycetes, with selected exemplars (names in parentheses deviate from typical forms)

	Agaricales	*Atheliales*	*Auriculariales*	*Boletales*	*Cantharellales*	*Corticiales*
Pileate-stipitate						
Lamellate	*Agaricus bisporus* *Amanita muscaria* *Coprinus comatus*			*Hygrophoropsis aurantiaca* *Phylloporus rhodoxanthus* *Tapinella atrotomentosa*	(*Cantharellus cibarius*)	
Poroid	*Poromycena manipularis*			*Boletus edulis* *Suillus pictus*		
Hydnoid					*Hydnum repdnum* *Sistotrema confluens*	
Smooth	*Marasmius meridionalis* *Physalacria inflata*		(*Tremiscus helvelloides*)		*Craterellus cornucopioides*	
Merulioid	*Arrhenia auriscalpium*			*Boletinellus merulioides*	*Craterellus tubaeformis*	
Pileate-sessile						
Lamellate	*Crepidotus mollis* *Panellus serotinus* *Pleurotus ostreatus* (*Schizophyllum commune*)			*Tapinella panuoides*		
Poroid	*Dictyopanus pusillus* *Favolaschia calocera* *(Fistulina hepatica)* *(Porodisculus pendulus)*			*Bondarcevomyces taxi*		
Hydnoid			*Pseudohydnum gelatinosum*	*Gyrodontium saccahri*		
Smooth	*Chondrostereum purpureum*		*Auricularia auricula-judae*			
Merulioid	*Gloiocephala rubescens* *Plicaturopsis crispa*			*(Pseudomerulius corticii)*		
Resupinate						
Poroid						
Hydnoid	*Deflexula subsimplex*		*Protodontia piceicola*	*Hydnomerulius pinastri*		

Table 1 – (*continued*)

Gloeophyllales	*Hymenochaetales*	*Phallomycetidae*	*Polyporales*	*Russulales*	*Sebacinales*	*Thelephorales*	*Trechisporales*
Heliocybe sulcata *Neolentinus lepideus*	*Omphalina brevibasidiata* *Rickenella fibula*	*Gloeocantharellus purpurascens*	*Lentinus tigrinus* *Panus rudis*	*Lentinellus omphalodes* *Russula compacta*			
	Coltricia perennis *Onnia tomentosa*		*Albatrellus syringae* *Phaeolus schweinitzii* *Polyporus squamosus* (*Polyporus umbellatus*)	*Albatrellus fletti* *Polyporoletus sublividus*		*Boletopsis leucomelaena*	
		Beenakia dacostae		*Auriscalpium vulgare*		*Hydnellum aurantiacum* *Phellodon confluens*	
	Cotylidia alba *Stipitochaete damaecornis*	*Clavariadelphus truncatus*	*Cymatoderma caperatum?* *Podoscypha petalodes*		*Tremelloscypha gelatinosa*		
		Gomphus floccosus				*Polyozellus multiplex* *Thelephora terrestris*	
Gloeophyllum sepiarium	(*Cyclomyces fuscus*)		*Lenzites betulina*	*Lactarius panuoides* *Lentinellus montanus*			
Gloeophyllum trabeum	*Oxyporus populinus* *Phellinus gilvus*		(*Daedalea quercina*) *Fomes fomentarius* *Ganoderma applanatum* *Piptoporus betulinus*	*Bondarzewia berkeleyi* *Heterobasidion annosum*			
	Trichaptum abietinum	*Beenakia informis*	*Climacodon septentrionale* *Spongipellis pachyodon*	*Creolophus cirrhatus* *Echinodontium tinctorium* (*Hericium coralloides*)			
Boreostereum radiatum				*Laxitextum bicolor* *Stereum hirsutum*			
			Phlebia tremellosa				
Donkioporia expansa	*Phellinus contiguus*		*Ceriporia purpurea* *Perenniporia medulla-panis*				*Porpomyces mucidus* *Trechispora hymenocystis*
	Hydnochaete olivacea *Schizopora paradoxa*	*Kavinia himantia*	*Mycoacia fuscoatra*	*Dentipellis separans*		*Tomentella crinalis*	*Trechispora lunata* (*Trechispora farinacea*)

Table 1 – (*continued*)

	Agaricales	*Atheliales*	*Auriculariales*	*Boletales*	*Cantharellales*	*Corticiales*
Smooth	*Cylindrobasidium evolvens*	*Athelia arachnoidea* *Piloderma fallax* *Tylospora asterophora*	*Basidiodendron caesiocinereum* *Eichleriella deglubens* *Exidia glandulosa*	*Coniophora puteana*	*Botryobasidium isabellinum* *Sistotrema sernanderi* *Tulasnella pruinosa*	*Dendrocorticium roseocarneum* *Galzinia incrustans* (*Laetisaria fuciformis*) *Vuilleminia comedens*
Merulioid			*Auricularia mesenterica*	*Pseudomerulius aureus* *Serpula lacrymans*		
Clavarioid	*Typhula phacorhiza*				*Multiclavula mucida*	
Coralloid	*Clavaria zollingeri* *Pterula multifida*				*Clavulina cinerea*	
Cyphelloid	(*Auriculariopsis ampla*) (*Caripia montagnei*) *Cyphella digitalis* *Henningsomyces candidus* *Stigmatolemma poriiforme*					
Gasteroid						
Epigeous	*Crucibulum laeve* *Lycoperdon pyriforme* (*Nia vibrissa*) *Thaxterogaster pingue* *Torrendia pulchella*			*Astraeus hygrometricus* *Calostoma cinnabarinum* *Gastrosuillus laricinus*		
Hypogeous	*Amarrendia gradnispora* *Hydnangium carneum* *Quadrispora oblongis-pora*			*Alpova trappei* *Melanogaster tuberiformis* *Rhizopogon rubescens*		

configuration of the hymenophore, and gasteroid forms are divided into epigeous and hypogeous forms, for 19 fruiting body forms. Scored in this manner, the most diverse clades are the *Agaricales*, *Polyporales*, *Russulales*, and *Phallomycetidae* (15, 13, 12, and 11 fruiting body forms, respectively), and the least diverse clades are the *Atheliales* and *Corticiales*, which have only resupinate forms with more or less smooth hymenophores. A similar chart (recognizing only eight clades, and divided primarily according to hymenophore configuration), with links to images, can be viewed at http://www.mykoweb.com/articles/Homobasidiomycete_chart.html.

It is clearly beyond the scope of this article to review the many recent phylogenetic studies in agaricomycetes that have contributed to the information in Table 1. A few selected works that illustrate interesting and occasionally surprising patterns of morphological evolution in the *Agaricales*, *Russulales*, and *Phallomycetidae* are discussed below.

Agaricales

This largest clade of agaricomycetes (*ca* 9400 spp., Kirk *et al.* 2001) has been intensively studied, perhaps most famously by Moncalvo *et al.* (2002), who sampled nuLSU rDNA in 877 species and resolved 117 clades of 'euagarics'. Another broad overview of the group was provided recently by Matheny *et al.* (in press-a), who performed a multi-locus analysis of *rpb*1, *rpb*2, nuLSU, nuSSU, and 5.8S rDNA sequences in 250 species, which added support for many backbone nodes that were not well resolved in the analysis of Moncalvo *et al.* (2002). Besides these comprehensive studies, there have been many analyses focused on individual families and genera of *Agaricales*, for which the reader should refer to Moncalvo *et al.* (2002) and Matheny *et al.* (in press-a). The *Agaricales* is dominated by gilled mushrooms, but every other major fruiting body morphotype has been derived within this group. The following paragraphs focus on the distribution of gasteroid, coralloid, cyphelloid, and marine forms in the *Agaricales*.

Gasteroid Agaricales. Gasteroid forms have evolved repeatedly in both saprotrophic and mycorrhizal groups of *Agaricales*. Studies in the *Agaricaceae* illustrate the phenomenon of gasteromycetation in saprotrophic lineages, and also exemplify the progress in agaricomycete systematics that has been achieved since the 1990s. Hopple & Vilgalys (1994) and Hibbett *et al.* (1997) established that the sessile and stalked puffballs *Calvatia*, *Lycoperdon*, and *Tulostoma*, and the secotioid taxa *Montagnea* and *Podaxis* are related to various *Agaricaceae*, including lepiotoid taxa and the 'shaggy mane' *Coprinus*

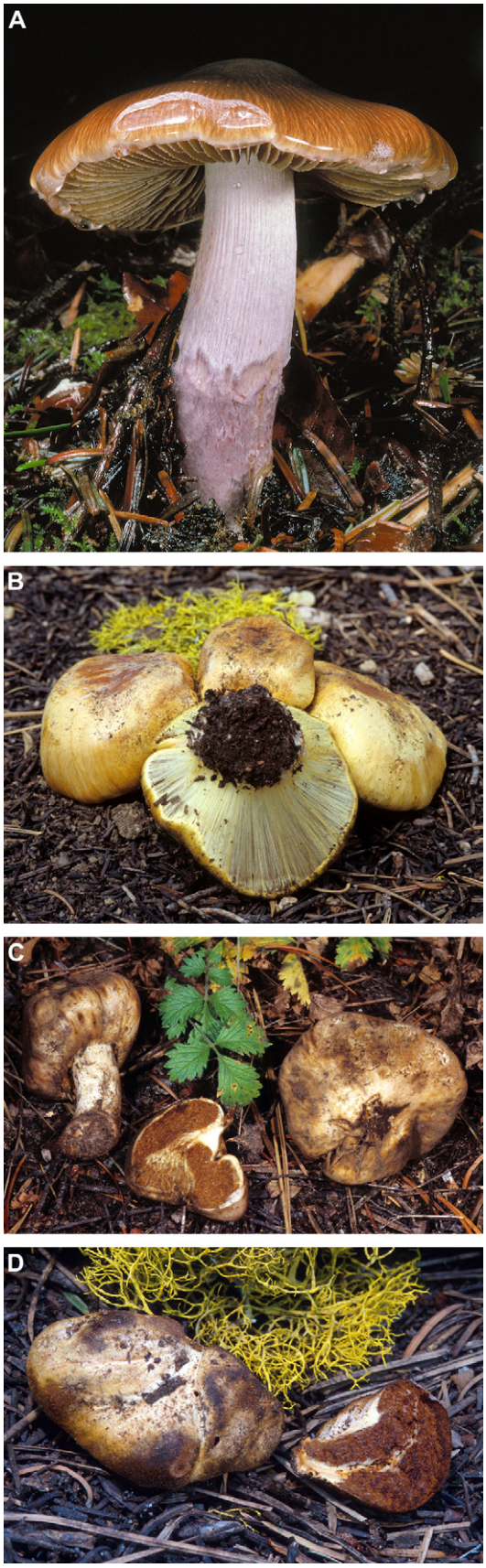
Table 1 – (*continued*)

Gloeophyllales	*Hymenochaetales*	*Phallomycetidae*	*Polyporales*	*Russulales*	*Sebacinales*	*Thelephorales*	*Trechisporales*
Veluticeps berkeleyi	*Basidioradulum radulum* *Hymenochaete tabacina* *Tublicrinis subulatus*	*Ramaricium alboflavescens*	*Dentocorticium sulphurellum* *Hypochnicium geogenium* *Phlebia radiata*	*Aleurodiscus amorphus* *Gloeocystidiellum porosum* *Peniophora nuda*	(*Craterocolla cerasi*) (*Sebacina incrustans*) *Serendipita vermifera*	*Tomentella sublilacina*	*Sistotremastrum niveocremeum* *Trechispora cohaerens* (*Trechispora fastidiosa*)
	Clavariachaete rubiginosa	*Clavariadelphus pistillaris* *Lentaria micheneri* *Ramaria stricta*	(*Sparassis crispa*)	*Clavicorona pyxidata*	*Tremellodendron pallidum*	*Thelephora palmata*	
		Geastrum saccatum *Phallus impudicus* *Sphaerobolus stellatus*	(*Lentinus tigrinus*)	*Arcangeliella parva* *Macowanites americanus*			
		Gautieria otthii *Protubera nothofagi*		*Gymnomyces megasporus* *Mycolevis siccigleba* *Zelleromyces striatus*			

comatus. Subsequent studies by Krüger *et al.* (2001), Moncalvo *et al.* (2002), Vellinga (2004), and Lebel *et al.* (2004) using rDNA expanded the sampling in this clade to include secotioid and puffball forms such as *Barcheria*, *Battaraea*, *Bovista*, *Endoptychum*, *Gyrophragmium*, *Longula*, *Mycenastrum*, and *Vascellum*, and many more species in agaricoid genera that had been sampled previously. Also, the secotioid *Galeropsis desertorum* is probably in this group (apparently close to *Lepiota* spp.), based on a BLAST search using a nuLSU rDNA sequence deposited by Hallen *et al.* (2003) as a query (D. S. H., unpubl.). Finally, the recent multi-locus analysis of Matheny *et al.* (2007a) suggests that the bird's nest fungi, *Cyathus* and *Crucibulum*, may be in the sister group of the *Agaricaceae*, along with the agaricoid *Cystoderma*. While the inclusion of *Cyathus* and *Crucibulum* in the *Agaricales* had been demonstrated previously (Hibbett *et al.* 1997), the study of Matheny *et al.* was the first to resolve their position with moderate confidence (supported by Bayesian PPs, if not parsimony BS values). Thus, the *Agaricaceae* and its relatives appear to contain a concentration of diverse, indpendently evolved gasteroid *Agaricales*. Other saprotrophic groups of *Agaricales* that have been shown to contain gasteroid forms based on molecular analyses include the agrocybe clade *sensu* Moncalvo *et al.* (2002), which contains *Leratiomyces smaragdina*, and the *Strophariaceae*, which contains the secotioid forms *Nivatogastrium nubigenum*, *Weraroa virescens*, and *W. erythrocephala*, and the puffball *Leratiomyces similis* (Binder *et al.* 1997; Moncalvo *et al.* 2002; Matheny *et al.* in press-a).

Ectomycorrhizal *Agaricales* have also produced gasteroid forms. Peintner *et al.* (2001) studied the origins of gasteroid forms in the *Cortinariaceae* using ITS sequences (also see Moncalvo *et al.* 2002). Fruiting bodies in this large group can be arranged in a series of intergrading forms, including (1) fully agaricoid forms with ephemeral veils and forcible spore discharge (e.g., *Cortinarius* spp., *Descolea* spp., *Hebeloma* spp.); (2) partially hypogeous 'emergent' agaricoid forms that have persistent veils and retain forcible spore discharge (e.g., *Cortinarius magnivelatus*); (3) epigeous secotioid forms with largely enclosed, contorted hymenophores, which lack ballistospory (*Thaxterogaster* spp., *Setchelliogaster* spp.); and (4) fully gasteroid forms with an enclosed gleba, including hypogeous false truffles (*Hymenogaster* spp., *Protoglossum* spp., *Quadrispora* spp.; Fig 2).

The trees that Peintner *et al.* (2001) obtained demonstrate that there have been many origins of gasteroid forms within the *Cortinariaceae*, including repeated origins of hypogeous



forms in *Hymenogaster* (which is polyphyletic) and *Descomyces*. However, the expected sequence of transitions from agaricoid and 'emergent' forms to secotioid, and finally fully gasteroid forms was not observed, with one exception in the clade '*Myxacium* I', in which two hypogeous *Quadrispora* strains were nested within a paraphyletic group of *Thaxterogaster* isolates. These findings suggested that the predicted intermediate forms have either gone extinct or, perhaps just as likely, have not been collected. Other ectomycorrhizal clades of *Agaricales* with gasteroid members that have been the subject of phylogenetic studies include the *Amanitaceae*, which contains the secotioid *Torrendia pulchella* and several hypogeous taxa in *Amarrendia* (Bougher & Lebel 2003), and the *Laccaria* clade, which contains the secotioid *Podohydnangium australe* and hypogeous *Hydnangium* species (Mueller & Pine 1994; Moncalvo *et al.* 2002).

Finally, an interesting reinterpretation of a gasteroid agaric was proposed by Hallen *et al.* (2003), who studied the 'secotioid' *Gastrocybe*, which produces a pileate-stipitate fruiting body. The cap of *Gastrocybe* becomes slimy and deliquescent, often toppling the stipe as it matures. Hallen *et al.* found strong support for a relationship between *Gastrocybe* and the saprotrophic lawn-inhabiting agarics *Conocybe,* as had been shown before (Moncalvo *et al.* 2002), but they suggested that the 'gelatinous-liquescent' fruiting body is actually caused by a bacterial infection, and that *Gastrocybe* is 'sick, not secotioid'.

Coralloid *Agaricales*. Coralloid forms, which Corner suggested represent the primitive state of basidiomycete fruiting bodies, are rare within the *Agaricales*. Several phylogenetic studies using rDNA have sampled club and coral forms in the *Agaricales*, including analyses by Hibbett *et al.* (1997), Pine *et al.* (1999), Moncalvo *et al.* (2002), Munkacsi *et al.* (2004), and Binder *et al.* (2005). Together, these studies suggested that there are about three groups of coralloid taxa in the *Agaricales*, including: (1) *Typhula* and *Macrotyphula*, which have slender clavarioid (unbranched) fruiting bodies; (2) *Pterula*, which has slender coralloid or clavarioid fruiting bodies, and *Deflexula*, which forms pendent, tooth-like fruiting bodies; and (3) *Clavaria* and *Clavulinopsis*, which form more robust clavarioid or coralloid fruiting bodies. The analysis of Moncalvo *et al.* (2002) provided weak (BS = 64 %) support for a close relationship between *Typhula phacorhiza* and the sessile, pleurotoid agarics *Phyllotopsis nidulans* and *Pleurocybella porrigens*, but the position of '*Clavaria*' *fusiformis* was unclear. Munkacsi *et al.* (2004) added sequences from ten species of *Deflexula* and *Pterula* to the dataset of Moncalvo *et al.* (2002), along with sequences from *Apterostigma* attine ant symbionts. Their

Fig 2 – Fruiting body forms in *Cortinariaceae*. (A) *Cortinarius vanduzerensis*, a fully epigeous agaricoid form with an ephemeral cortina (partial veil, not visible here). (B) *C. verrucisporus*, an 'emergent' agaricoid form with a persistent veil. (C) *Thaxterogaster pingue*, a secotioid form. (D) *Hymenogaster sublilacinus*, a hypogeous gasteroid form. (A) © Taylor Lockwood www.taylorlockwood.com; (B–D) © Michael Wood www.MykoWeb.com.

results suggested that the *Deflexula–Pterula* clade is the sister group of a clade of *Apterostigma* ant symbionts.

Several coralloid taxa were included in the multi-locus analysis of Matheny *et al.* (2007a). The beautiful coral fungi *Clavaria zollingeri* and *Clavulinopsis laeticolor* were strongly supported by both BS and Bayesian PPs as the sister group of the agaric *Camarophyllopsis hymenocephalum*. A second clade, supported only by Bayesian PPs, included *Phyllotopsis nidulans*, *Typhula phacorhiza*, and *Pterula echo*, which contrasts with the prior rDNA analyses that suggested the *Pterula–Deflexula* group is separate from the *Typhula–Macrotyphula* group. Thus, the results of Matheny *et al.* suggest a minimum of two origins of coral forms within the *Agaricales*. However, as Matheny *et al.* point out, the *Pterulaceae* and *Typhulaceae* contain over 200 species and are in need of further investigation. Moreover, analyses by Larsson *et al.* (2004) suggest that *Typhula* and *Macrotyphula* are closely related to certain resupinate forms, including *Coronicium alboglaucum*, which should be included in any study that seeks to understand the origins of coralloid *Agaricales*.

Cyphelloid and marine Agaricales. Scattered throughout the *Agaricales* are minute, cup or tube-shaped 'cyphelloid' forms, which have long been regarded as reduced agarics. A few cyphelloid taxa were included in studies by Binder *et al.* (2001), Hibbett & Binder (2001), Moncalvo *et al.* (2002), and Langer (2002), but the study of Bodensteiner *et al.* (2004) was the first to focus specifically on cyphelloid forms. Their analysis suggested that there have been roughly ten to 12 independent derivations of cyphelloid forms within the *Agaricales*, representing repeated instances of evolutionary reduction. However, Bodensteiner *et al.* sampled only 23 species of cyphelloid fungi, while it has been estimated that there may be as many as 400–500 cyphelloid species (Agerer, unpubl., fide Bodensteiner *et al.* 2004). Thus, cyphellization could be an even more common mode of morphological evolution than present datasets imply. All of the cyphelloid taxa studied by Bodensteiner *et al.* are nested within saprotrophic clades. The causal factors that have promoted the repeated evolution of these minute forms are unknown, but could be related to selection for spore production from minimal substrates.

As remarkable as cyphelloid fungi are, their close relatives are even more unusual. Binder *et al.* (2001) and Hibbett & Binder (2001) focused on the relationships between terrestrial cyphelloid forms and marine basidiomycetes. They found strong support for the existence of a '*Nia* clade', containing the terrestrial cyphelloid taxa *Henningsomyces candidus* and *Cyphellopsis anomala*, the mangrove-inhabiting cyphelloid taxa *Calathella mangrovei* and *Halocyphina villosa* (which are periodically submerged in seawater), and finally the fully marine (subtidal) *Nia vibrissa*, which forms tiny gasteroid fruiting bodies and has appendaged spores. The sister group of this clade includes the 'split-gill' fungus *Schizophyllum commune* and the 'beefsteak fungus' *Fistulina hepatica*, which looks like a fleshy polypore, but on closer inspection is found to have a hymenophore composed of many individually free tubes. *Schizophyllum* and *Fistulina* are morphological oddities that Donk (1971) placed in their own families. The finding that they may be closely related to cyphelloid forms raises the possibility that the unusual fruiting bodies of *Schizophyllum* and *Fistulina* retain features common to the precursors of cyphelloid forms, or they may represent aggregations of cyphelloid fruiting bodies. Other taxa in the *Schizophyllum* clade include the cupulate *Auriculariopsis ampla* (with a smooth hymenophore) and the minute pendent polypore *Porodisculus pendulus*.

The relationships between cyphelloid forms and marine basidiomycetes were further examined by Binder *et al.* (2006), who focused on another fully subtidal gasteromycete, *Mycaureola dilseae*, which is a parasite of the red alga *Dilsea carnosa*. *Mycaureola* superficially resembles *Nia*, in that it has a tiny gasteroid fruiting body, but it differs by the production of elongate, curved spores, as well as its habit as an algal parasite. Nonetheless, it was a surprise to find that *M. dilseae* is not related to *Nia* or its mangrove-inhabiting cyphelloid relatives, but rather is nested in a clade that contains typical agarics, such as *Flammulina velutipes* (the cultivated enokitake mushroom) and *Armillaria gallica* (the honey mushroom). Other taxa in this group include the highly reduced agarics *Gloiocephala* and *Physalacria*, and the resupinate *Cylindrobasidium laeve*. Binder *et al.* (2006) found strong support for this group (BS = 80 %, Bayesian PP = 1) and labelled it the *Physalacriaceae* clade. The multi-locus analysis of Matheny *et al.* (2007a) found weak support for the monophyly of a group that contains the *Physalacriaceae* clade, the *Nia* clade (as *Lachnellaceae*), and the *Schizophyllum* clade (as *Schizophyllaceae* and *Fistulinaceae*). This clade, if it is real, contains a collection of lineages that have undergone extensive diversification in fruiting body forms, and that deviate strongly from their agaricoid ancestors.

Russulales

Relationships among many of the morphologically diverse taxa that make up the *Russulales* have long been recognized, based on the irregular distribution of spores with varying degrees of amyloidity (often restricted to ornamentations) and 'gloeoplerous' hyphae and cystidia (with oily, refractive contents) (Donk 1971; Oberwinkler 1977). Sixteen species of *Russulales* formed a strongly supported clade in the analysis of Hibbett *et al.* (1997), including polypores (*Bondarzewia, Heterobasidion*), toothed fungi (*Auriscalpium, Hericium, Echinodontium*), agarics (*Lentinellus, Russula*), coral fungi (*Clavicorona*; syn. *Artomyces*), and resupinate and effused–reflexed forms (e.g. *Gloeocystidiellum, Stereum, Peniophora*). More comprehensive phylogenetic overviews of the entire clade were provided by Larsson & Larsson (2003) and Binder *et al.* (2005), which provided detailed views of possible patterns of morphological evolution. There have also been multiple studies focused on the *Russulaceae*, which includes the ectomycorrhizal agarics, *Russula* and *Lactarius*, and their gasteroid and pleurotoid derivatives (Miller *et al.* 2001; Miller & Buyck 2002; Eberhardt & Verbeken 2004).

One of the most striking results to come out of recent research on *Russulales* is the finding that the *Russulaceae* is nested within a paraphyletic group of resupinate forms in *Gloeocystidiellum*. Thus, these complex agarics, which Singer (1986) classified as a suborder of the *Agaricales*, may have been derived from simple crust-like ancestors. No intermediate forms are known. Pleurotoid taxa (with a short lateral stipe) occur in the *Russulaceae*, and these might be expected to be intermediates between centrally stipitate agarics and

resupinate forms. However, the pleurotoid forms have been shown to be nested within *Lactarius* and probably represent a derived condition, which may be an adaptation to fruiting on tree trunks and other elevated substrates in periodically flooded neotropical forests (Miller *et al.* 2001; Miller *et al.* 2002; Eberhardt & Verbeken 2004).

Epigeous secotioid forms and hypogeous false truffles have evolved repeatedly within the *Russulaceae* (Miller *et al.* 2001; Eberhardt & Verbeken 2004), as well as in the clade containing the ectomycorrhizal polypores *Albatrellus* and *Polyporoletus*, which are also members of the *Russulales*, but are not closely related to *Russulaceae* (Albee-Scott, 2007). There are several reports of gasteroid forms of *Russulales* that have retained forcible spore discharge (Miller & Miller 1988; Desjardin 2003). Based on the model of evolution of gasteroid forms proposed by Thiers (1984) and Bruns *et al.* (1989), such taxa may represent recently derived gasteroid forms that have not yet lost ballistospory.

Phallomycetidae

The 'gomphoid-phalloid clade' (Hibbett & Thorn 2001) was recognized based on rDNA sequences from only six species. Subsequent studies by Humpert *et al.* (2001) and Hosaka *et al.* (2007) have dramatically expanded the sampling of both genes and taxa, resulting in a robust, highly detailed phylogeny of this morphologically diverse group, now called the *Phallomycetidae*. Hosaka *et al.* sampled 222 species with five genes (nuSSU and LSU rDNA, mtSSU rDNA, *rpb*2, and *tef*1), and resolved four major clades of *Phallomycetidae*, which they called the *Phallales, Gomphales, Hysterangiales,* and *Geastrales*. Their analysis suggests that there have been multiple transitions between epigeous and hypogeous forms, as well as between mycorrhizal and saprotrophic nutritional modes in the *Phallomycetidae*.

Within the *Phallales*, the epigeous stinkhorns (*Phallaceae*, *Clathraceae*, *Lysuraceae*) are nested within a paraphyletic assemblage of false truffles (*Protophallaceae*, *Claustulaceae*, *Trappeaceae*) (Hosaka *et al.* 2007). This is the only well-supported case of a hypogeous-to-epigeous transformation in the agaricomycetes, and it is marked by the evolution of some of the most outlandish forms in all the *Fungi*. The showy fruiting bodies of epigeous *Phallales* are variously phalloid (sometimes also indusiate), cage-like, or stellate, often have bright red or yellow pigments, and present a highly aromatic gleba. They have apparently diversified in response to selection for insect spore dispersal, and are truly the 'flowers' of the fungi.

Hypogeous forms also occur in the *Gomphales*, *Geastrales*, and *Hysterangiales* (which is composed only of hypogeous taxa). According to Hosaka *et al.*, most hypogeous *Phallomycetidae* are probably mycorrhizal, including the *Gautieriaceae* (*Gomphales*), *Sclerogastraceae* (*Geastrales*), and most of the *Hysterangiales*. These results are consistent with observations in the *Agaricales*, *Boletales*, and *Russulales*, in which virtually all hypogeous forms are thought to be mycorrhizal. This apparent correlation led Thiers (1984) and others (e.g. Bruns *et al.* 1989) to suggest that mycorrhizal lifestyles promote the evolution of the false truffle habit. However, there are several other groups of hypogeous *Phallomycetidae,* which Hosaka *et al.* suggest are probably saprotrophic, including most of the hypogeous *Phallales* and the *Phallogastraceae* (*Hysterangiales*).

Recent molecular studies 3—assessing global patterns and trends in fruiting body evolution in agaricomycetes

Some of the most profound issues regarding fruiting body evolution in agaricomycetes, concern the ancestral fruiting body form of the agaricomycetes, and the existence of trends (general evolutionary tendencies) and causal factors in the evolution of fruiting bodies. As a number of authors have pointed out (e.g., Maddison 1990; Cunningham 1999), reconstruction of ancestral states and detection of trends are inherently linked to estimation of models of evolutionary processes. Under parsimony, for example, the patterns of reconstructed states depend heavily on the assigned costs of losses *versus* gains, which are based on assumptions regarding the relative probability of those events. A popular alternative method uses ML to estimate a model of evolution for a character, and then assesses support for alternative ancestral states under that model (Pagel 1997). The parameters of the model specify the rates of change between character states, which are assumed to be constant across the entire phylogeny. Felsenstein (2004) has questioned whether such models are appropriate for morphological characters, and has suggested that alternative models that do not follow a strict Markov process may be more realistic. Any probabilistic model of morpholgical evolution will surely oversimplify the actual process of fruiting body evolution. Nevertheless, the repeated evolution of strikingly similar forms in multiple clades of agaricomycetes suggests that there are general mechanisms at work, which validates a modelling approach.

Ancestral state reconstruction analyses have been performed in diverse groups of agaricomycetes, most often using equally-weighted parsimony optimization, as implemented in the program MacClade (Maddison & Maddison 2000) (e.g. Mueller & Pine 1994; Hibbett *et al.* 1997; Humpert *et al.* 2001), although the ML approach has been employed in both the *Boletales* (Binder & Hibbett 2007) and *Phallomycetidae* (Hosaka *et al.* 2007). In addition, Hibbett & Binder (2002) and Hibbett (2004) used parsimony and ML approaches to estimate patterns and processes of morphological evolution across the entire agaricomycetes. These studies, reviewed below, provide clues to the history and dynamics of fruiting body evolution, but they also illustrate pitfalls of the ML approach to studying character evolution.

Hibbett & Binder (2002) studied the evolution of fruiting body forms using a dataset of 481 species, which they coded in binary form as either 'resupinate' or 'pileate-erect' (i.e. all non-resupinate forms). Analyses using ML and parsimony on multiple tree topologies all suggested that the ancestral fruiting body form was resupinate, and that there have been multiple origins of pileate-erect forms, as well as some reversals to resupinate forms. Moreover, ML analyses suggested that the rate of change from resupinate to pileate-erect forms is significantly greater than changes in the reverse direction, which was interpreted as evidence of a 'driven' trend toward increasing morphological complexity.

Hibbett (2004) performed similar analyses to those of Hibbett & Binder (2002), using one of the trees from the earlier study. The major difference was that the 2004 study employed a character-coding regime with five states: resupinate,

pileate-sessile, pileate-stipitate, coralloid-clavarioid, and gasteroid (i.e. the pileate-erect character state from the binary coding regime was subdivided into four states). ML analyses under the five-state coding regime did not resolve the ancestral form of the agaricomycetes, although parsimony would still suggest that it was resupinate. Also, the models obtained under the five-state coding did not indicate that resupinate forms are particularly labile, and therefore did not support the prior conclusion that there is an active trend toward increasing complexity in fruiting body forms of agaricomycetes. Other aspects of the analyses under multistate coding are intuitively satisfying. For example, the irreversibility of gasteromycetation could not be rejected, which is consistent with the idea that once ballistospory has been lost, it can probably never be regained. Also, the pileate-stipitate form was found to be a relatively stable morphology, which is consistent with the prevalence of these forms among *Agaricales* and other clades of agaricomycetes, as well as the presence of ~94 million year old fossils that appear to be homologous to modern agaricoid forms (Hibbett *et al.* 1995).

The studies of Hibbett & Binder (2002) and Hibbett (2004) show that ML analyses of character evolution can be quite sensitive to character coding. The binary coding employed in the 2002 study is a relatively crude representation of morphological diversity, whereas the five-state coding is more descriptive and probably more biologically meaningful. Therefore, the models estimated with five-state coding may be more accurate representations of the actual dynamics of fruiting body evolution than those obtained under binary coding. However, even with appropriate character coding regimes, ML analyses of character evolution can yield surprising results. For example, Binder & Hibbett (2007) used multistate Bayesian ML methods to study evolution of fruiting body forms in the *Boletales*, which suggested that the ancestor of the *Suillineae* was a gasteroid form. The *Suillineae* includes false truffles in *Rhizopogon*, but it also contains pileate-stipitate forms with tubular hymenophores (*Suillus*) that are highly similar to boletoid forms in the *Sclerodermatinieae* (*Gyroporus*), *Boletineae* (e.g. *Boletus*), and *Paxillineae* (*Gyrodon*). It seems very unlikely that the boletoid forms in the *Suillineae* were derived from gasteroid ancestors, but this result was strongly supported by the ML analysis.

Conclusions and future directions

Phylogenetic analyses of molecular sequences have revealed 14 major independent clades of agaricomycetes, so far. Multigene studies are resolving the higher-order relationships among these groups, and studies with intensive sampling within the clades, still largely based on rDNA, are beginning to reconstruct the fine branches of the agaricomycete phylogeny. This review has emphasized research in the *Agaricales*, *Russulales*, *Phallomycetidae* and *Boletales*, but there has also been much recent activity in other groups, such as the *Hymenochaetales* (Wagner & Fischer 2002a,b; Larsson *et al.* 2007), *Thelephorales* (Kõljalg *et al.* 2002), and *Cantharellales* (Moncalvo *et al.* 2007). As a result, we now have a fairly detailed understanding of the phylogenetic distribution of different fruiting body forms across the agaricomycetes, albeit one that is based on a very incomplete sample of fungal diversity. The largest trees of agaricomycetes, constructed using automated phylogenetic methods and 'published' on the web (Hibbett *et al.* 2005), include over 2400 terminals representing about 1900 putative species, but this is still only about 10 % of the described species in the group (Kirk *et al.* 2001). The largest trees in print publications are much smaller, with 877 (Moncalvo *et al.* 2002) or 656 terminals (Binder *et al.* 2005). Resupinate taxa are especially in need of sampling. As the work of Larsson *et al.* (2004) and others indicates, these cryptic forms may harbour undiscovered major clades of agaricomycetes.

Simply increasing taxon sampling in phylogenetic studies will not lead, by itself, to significant advances in our understanding of morphological evolution, however. With further sampling, we will surely uncover additional instances of the kinds of transformations that have already been well documented, such as switches between poroid and gilled hymenophores, or derivations of false truffles and cyphelloid fungi from pileate-stipitate forms. To be certain, such discoveries will enrich our knowledge of fungal diversity. Nevertheless, if we do not go beyond simply describing the distribution of states at the tips of the tree, then our phylogenetic studies will yield only incremental advances (at best) in our understanding of evolutionary processes. This is not to say that phylogenies will not remain central to research in morphological evolution in agaricomycetes. Indeed, the next major advances in fungal evolutionary morphology may derive from two very different disciplines, both of which rely heavily on a phylogenetic perspective. These include evolutionary developmental biology (evo-devo), which addresses the genetic mechanisms of morphological transformations, and comparative phylogenetic analyses, which use phylogenies to address general trends and broad historical patterns in evolution.

Several methods for phylogenetic comparative analyses now exist, including the parsimony and ML approaches discussed previously (Maddison 1990; Pagel 1997) and more recent 'stochastic mapping' techniques that use Bayesian approaches (Huelsenbeck *et al.* 2003; Bollback 2006). These methods can be used not only to reconstruct ancestral states, but also to address correlations between characters, or to test key innovation hypotheses (Ree 2005). For example, correlation analyses could be used to test whether the occurrence of mycorrhizal symbioses promotes the evolution of false truffles, while key innovation tests could address whether evolution of agaricoid forms increases rates of speciation. None of the comparative methods that are currently available are completely satisfactory, and some prior results may reflect limitations of the methods [such as Hibbett's (2004) inability to determine the ancestral state of the agaricomycete using multi-state ML analyses], or may be artefacts [such as Binder & Hibbett's (2007) finding that the ancestor of the *Suillineae* was a gasteromycete]. Nevertheless, mycologists should cautiously embrace new phylogenetic comparative methods as they emerge, because these are the only approaches that permit statistical tests of hypotheses about processes of morphological evolution at a macroevolutionary scale.

ML and stochastic mapping methods circumvent some of the limitations of traditional parsimony methods, such as the reliance on a single-tree topology and character optimization, but they are sensitive to other factors, including taxon sampling. Large trees are necessary to estimate the

parameters of complex models, and bias in taxon sampling can skew results (Ree & Donoghue 1999; Hibbett 2004). Thus, to enable the most rigorous comparative analyses of morphological evolution, we should strive to construct comprehensive phylogenetic trees that include all the known species of agaricomycetes. An all-taxon phylogeny of agaricomycetes based on sequence data would also be invaluable for species discovery, biogeography, and molecular ecology, so assembling this resource should be a top priority.

Comparative analyses have the potential to resolve processes of morphological evolution that play out across clades over vast time scales. At the other extreme, there is much to be learned by studying the developmental processes that underlie individual character state changes. Like comparative analyses, mechanistic studies in evo-devo also rely on phylogenies, which are needed to pinpoint morphological transformations that can be studied using molecular approaches. Unfortunately, fungal evo-devo has lagged far behind its counterparts in animal and plant biology. While the mechanisms that trigger fruiting body initiation in the model systems *Schizophyllum commune* and *Coprinopsis cinereus* have been well characterized (Horton *et al.* 1999; Kües 2000), there is still very little known about pattern formation in agaricomycete fruiting bodies, or how those mechanisms might be modified through evolution.

The absence of a significant evo-devo enterprise in agaricomycetes is somewhat surprising, because fruiting body development has long been emphasized as a source of characters in fungal taxonomy (e.g. Kühner 1980; Singer 1986; Watling 1996; Reijnders & Stalpers 1992; Clemençon 2004). Now that there are robust phylogenies for many groups, it is possible to invert the traditional practices, and use phylogenies as tools for interpreting developmental evolution. This approach was taken in studies on the derivation of agaricoid forms in *Lentinus s. str.* from poroid forms in *Polyporus s. str.*, which was resolved using rDNA sequences (Hibbett & Vilgalys 1993). Using the rDNA-based phylogeny as a framework, Hibbett *et al.* (1993a) compared the ontogeny of *Lentinus* spp. and *P. arcularius* fruiting bodies using SEM. They interpreted the switch from pores to gills as being the result of a heterochronic shift in the development of radial *versus* tangential elements of the hymenophore, resulting in reduction of the tangential elements (Fig 1). These kinds of studies, which remain rare, are needed to characterize developmental phenotypes, and they provide a necessary precursor to genetic studies on the mechanisms of morphological transformations.

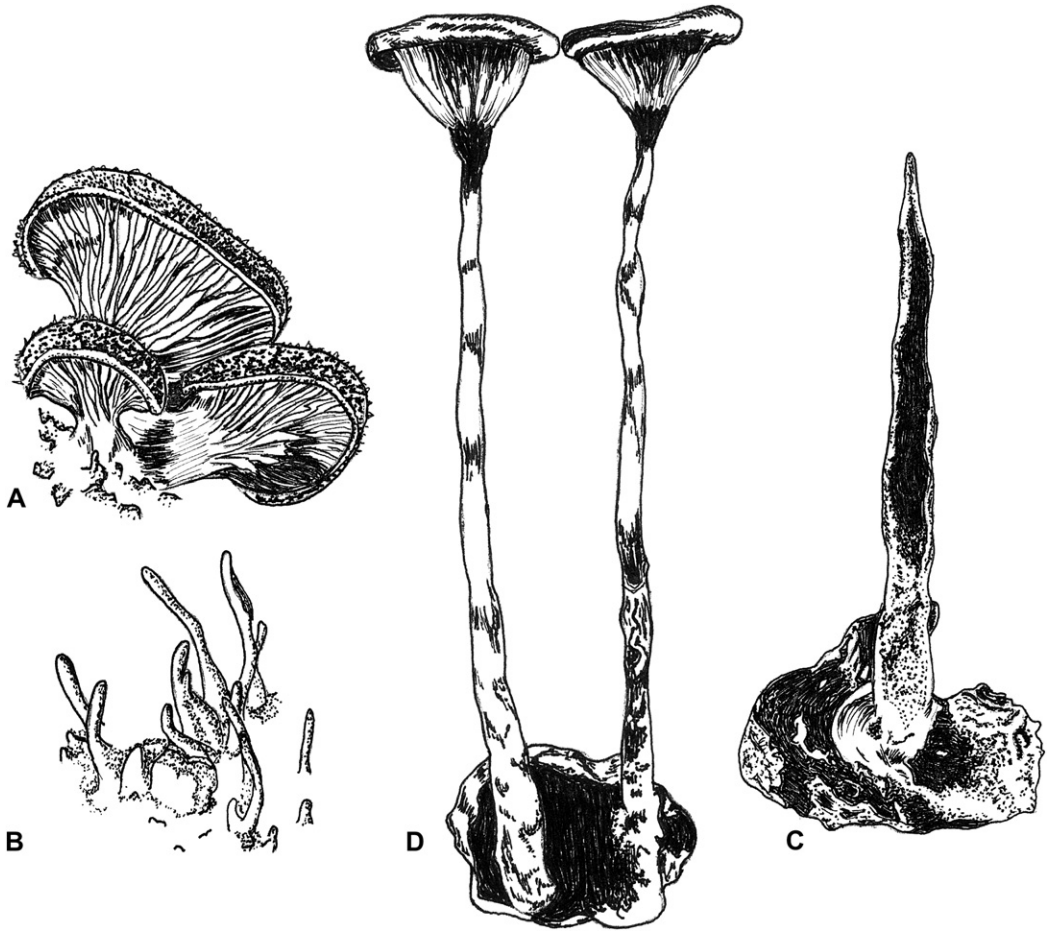


Fig 3 – Developmental plasticity and evolution in *Panus s. str.* (A) Typical form of *Panus rudis* (*P. lecomtei*) with a short, lateral stipe. (B) Developmental variant of *P. rudis* with elongate primordia produced under low-light conditions, after Miller (1967, fig 3). (C-D) *P. fulvus* has an elongate stipe and a prolonged primordial phase, after Hibbett *et al.* (1993a,b, figs 30–31). Drawings by Preethi S. Raj.

To advance the field of fungal evo-devo, mycologists need to team up with developmental biologists, both to draw on the molecular expertise that has been gained in laboratories devoted to animal and plant systems, and to lead developmental biologists to the most promising organisms. *Schizophyllum* and *Coprinus*, both members of the *Agaricales*, have yielded many insights, but it may be time to consider other candidate model systems from distantly-related lineages. In selecting new model organisms, several criteria should be considered. Of course, the organisms should be tractable and must fruit reliably in the laboratory, which probably means that they will be saprotrophic. Beyond that, taxa that contain naturally occurring developmental mutants with interesting phenotypes might be attractive. An example is *Lentinus tigrinus*, which is a predominantly agaricoid species in which there is a frequently collected 'secotoioid' form that has a gasteromycete-like enclosed hymenophore (but which retains ballistospory; Fig 1) (Hibbett *et al.* 1994). The secotioid morphology in *L. tigrinus* appears to be conferred by a recessive allele at a single locus and it closely resembles the predicted early stages of gasteromycetation based on the models proposed by Thiers (1984). Understanding the genetic basis of the secotioid morphology in *L. tigrinus* could provide insight into the general phenomenon of gasteromycetation in agaricomycetes.

Taxa that display developmental plasticity might also be informative subjects for evo-devo studies. One form of developmental plasticity that has been widely reported involves sensitivity to light, which appears to be required for induction of pileus formation in the agaricoid taxa *Neolentinus lepideus* and *Panus rudis*. *Neolentinus lepideus* produces antler-like 'carpophoroids' when growing in the dark on mine support timbers (Pegler 1983), and *P. rudis* was shown to produce elongate primordia when cultured under low-light conditions (Miller 1967) (Fig 3). It might be easy to dismiss these low-light forms as developmental aberrations with no evolutionary significance. However, in *Panus* there are both taxa with short lateral stipes, such as *P. rudis*, as well as taxa with very elongate stipes that develop through a prolonged primordial phase, including *P. fulvus* (Hibbett *et al.* 1993b) (Fig 3). It is conceivable that the same developmental mechanisms that are responsible for elongation of the primordia in low-light conditions in *P. rudis* are also involved in the hypermorphosis of the primordium/stipe in *P. fulvus*.

A final dramatic case of developmental plasticity is presented by *Lentinellus cochleatus*, which is an agaricoid form in the *Russulales*. Miller (1971) demonstrated that *L. cochleatus* produces coralloid fruiting bodies when it is cultured at low temperatures (Fig 4). Again, one might be tempted to regard this as an aberrant form, except that anatomical features and rDNA analyses have shown that *L. cochleatus* is closely related to the coralloid *Clavicorona* (syn. *Artomyces*), as well as the pileate, hydnoid *Auriscalpium vulgare*, as had been predicted by

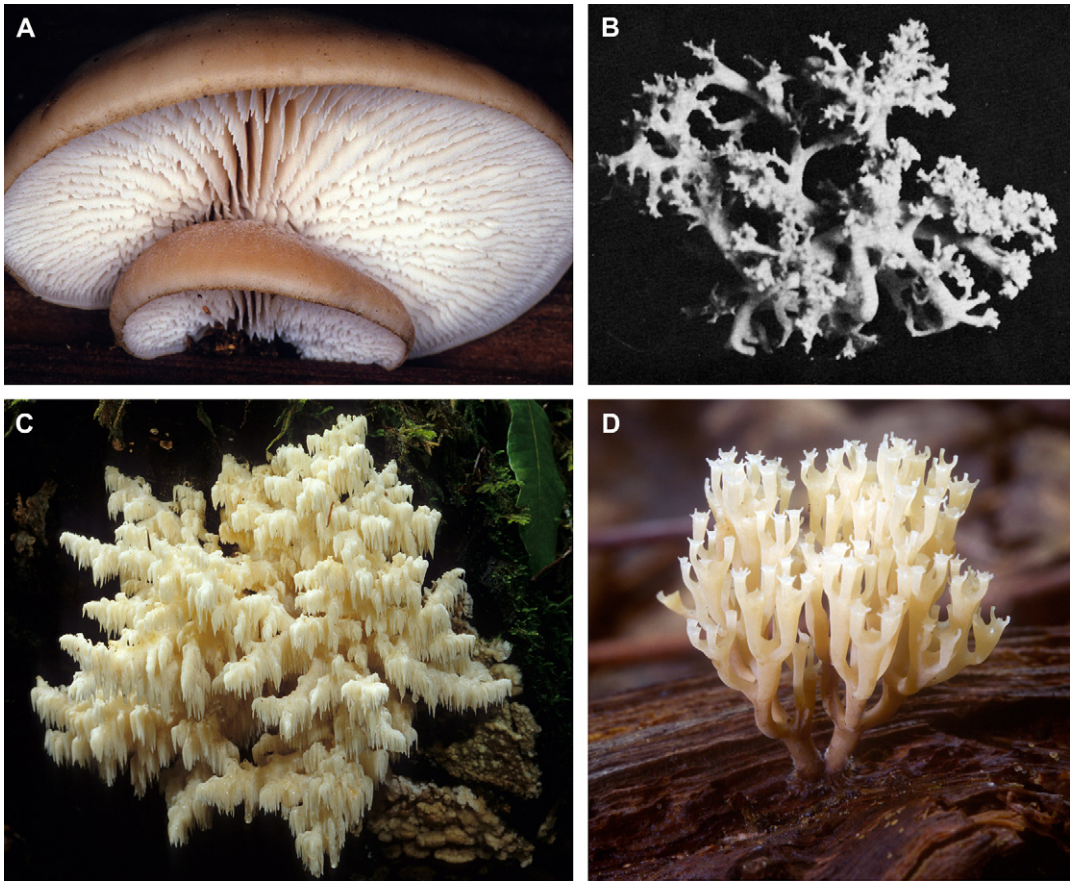


Fig 4 – Developmental plasticity and evolution in *Lentinellus* and related *Russulales*. (A) *Lentinellus montanus*, typical agaricoid form. (B) *L. pilatii*, coralloid form produced in culture (Miller 1971, fig 58). (C) *Hericium ramosum*. (D) *Clavicorona pyxidata* (syn. *Artomyces pyxidata*). (A, C–D) images from www.MykoWeb.com © Michael Wood. (B) © Orson K. Miller, jr.

Donk (1971) and others. The coralloid form of *L. cochleatus* is similar to *Clavicorona*, suggesting that the developmental shift in *Lentinellus* that is induced by low temperatures could involve modification of the same developmental programmes that are involved in the transformation from pileate to coralloid forms (or *vice versa*) within the *Russulales*.

In closing, agaricomycete evolutionary morphologists face several major challenges. Central among these is the need to construct a truly comprehensive phylogeny, with sampling approaching all the known species of agaricomycetes. However, it will not be enough just to build the tree. To achieve a deeper understanding of the history and the processes of morphological evolution, it will be necessary to use the tree as the basis for rigorous comparative analyses, including ancestral state reconstruction, tests of directionality in evolution, character correlation analyses, and tests of key innovation hypotheses. Finally, agaricomycete morphologists must work with developmental biologists to understand the molecular mechanisms that govern fruiting body formation, and how these mechanisms become modified through evolution. If these challenges are taken up, then the next 15 y promise to be just as exciting as the 'gold rush' period that followed the advent of molecular systematics in agaricomycetes.

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REFERENCES

Alexopoulos CJ, Mims CW, Blackwell M, 1996. *Introductory Mycology*, 4th ed. John Wiley and Sons, New York.

Albee-Scott SR, 2007. Does secotioid inertia drive the evolution of false truffles? *Mycological Research* **11**: 1032–1041.

Baura G, Szaro TM, Bruns TD, 1992. *Gastrosuillus laricinus* is a recent derivative of *Suillus grevillei*: molecular evidence. *Mycologia* **84**: 592–597.

Binder M, Hibbett DS, 2002. Higher-level phylogenetic relationships of homobasidiomycetes (mushroom-forming fungi) inferred from four rDNA regions. *Molecular Phylogenetics and Evolution* **22**: 76–90.

Binder M, Hibbett DS, 2007 [''2006'']. Molecular systematics and biological diversification of *Boletales*. *Mycologia* **98**: 971–983.

Binder M, Hibbett DS, Molitoris H-P, 2001. Phylogenetic relationships of the marine gasteromycete *Nia vibrissa*. *Mycologia* **93**: 679–688.

Binder M, Hibbett DS, Wang Z, Farnham W, 2006. Evolutionary origins of *Mycaureola dilseae*, a basidiomycete pathogen of the subtidal red alga *Dilsea carnosa*. *American Journal of Botany* **93**: 547–556.

Binder M, Besl H, Bresinsky A, 1997. *Agaricales* oder *Boletales?* Molekularbiologische Befunde zur Zuordnung einiger umstrittener Taxa. *Zeitschrift für Mykologie* **63**: 189–196.

Binder M, Hibbett DS, Larsson K-H, Larsson E, Langer E, Langer G, 2005. The phylogenetic distribution of resupinate forms in the homobasidiomycetes. *Systematics and Biodiversity* **3**: 113–157.

Bodensteiner P, Binder M, Agerer R, Moncalvo J-M, Hibbett DS, 2004. Phylogenetic diversity of cyphelloid forms in the homobasidiomycetes. *Molecular Phylogenetics and Evolution* **33**: 501–515.

Boidin J, Mugnier J, Canales R, 1998. Taxonomie moleculaire des *Aphyllophorales*. *Mycotaxon* **66**: 445–491.

Bollback JP, 2006. SIMMAP: Stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics* **7**: 88.

Bougher NL, Lebel T, 2003. Australasian sequestrate (truffle-like) fungi. XII *Ammarendia* gen. nov.: an astipitate, sequestrate relative of *Torrendia* and *Amanita (Amanitaceae)* from Australia. *Australian Systematic Botany* **15**: 513–525.

Brundin L, 1965. On the real nature of transantarctic relationships. *Evolution* **19**: 494–505.

Bruns TD, Fogel R, White TJ, Palmer JD, 1989. Accelerated evolution of a false truffle from a mushroom ancestor. *Nature* **339**: 140–142.

Bruns TD, White TJ, Taylor JW, 1991. Fungal molecular systematics. *Annual Reviews of Ecology and Systematics* **22**: 525–564.

Bruns TD, Szaro TM, Gardes M, Cullings KW, Pan JJ, Taylor DL, Horton DR, Kretzer A, Garbelotto M, Li Y, 1998. A sequence database for the identification of ectomycorrhizal basidiomycetes by phylogenetic analysis. *Molecular Ecology* **7**: 257–272.

Chapela IH, Rehner SA, Schultz TR, Mueller UG, 1994. Evolutionary history of the symbiosis between fungus-growing ants and their fungi. *Science* **266**: 1691–1694.

Clemençon H, 2004. Cytology and Plectology of the *Hymenomycetes*. *Bibliotheca Mycologica* **199** i-viii, 1–488.

Corner EJH, 1981. The agaric genera *Lentinus*, *Panus*, and *Pleurotus*. *Beiheft zur Nova Hedwigia* **69**: 1–169.

Corner EJH, 1972. Boletus *in Malaysia*. Singapore Botanic Gardens.

Cunningham CW, 1999. Some limitations of ancestral character-state reconstruction when testing evolutionary hypotheses. *Systematic Biology* **48**: 665–674.

Desjardin DE, 2003. A unique ballistosporic hypogeous sequestate *Lactarius* from California. *Mycologia* **95**: 148–155.

Donk MA, 1964. A conspectus of the families of *Aphyllophorales*. *Persoonia* **3**: 199–324.

Donk MA, 1971. Progress in the study of the classification of the higher basidiomycetes. In: Petersen RH (ed.), *Evolution in the Higher Basidiomycetes*. University of Tennessee Press, Knoxville, pp. 3–25.

Dring DM, 1973. *Gasteromycetes*. In: Ainsworth GC, Sparrow FK, Sussman AS (eds), *The Fungi: an advanced treatise*, Vol. IVB. Academic Press, New York, pp. 451–481.

Eberhardt U, Verbeken A, 2004. Sequestrate *Lactarius* species from tropical Africa: *L. angiocarpus* sp. nov. and *L. dolichocaulis* comb. nov. *Mycological Research* **108**: 1042–1052.

Felsenstein J, 2004. *Inferring Phylogenies*. Sinauer Associates, Sunderland, MA.

Fries, EM, (1874). *Hymenomycetes Europaei*. E. Berling, Uppsala.

Hallen HE, Watling R, Adams GC, 2003. Taxonomy and toxicity of *Conocybe lactea* and related species. *Mycological Research* **107**: 969–979.

Hawksworth DL, Kirk PM, Sutton BC, Pegler DN, 1995. *Ainsworth & Bisby's Dictionary of the Fungi*, 8th edn. CAB International, Wallingford.

Heim R, 1971. The interrelationships between the *Agaricales* and *Gasteromycetes*. In: Petersen RH (ed.), *Evolution in the Higher Basidiomycetes*. University of Tennessee Press, Knoxville, pp. 505–534.
Hibbett DS, 1992. Ribosomal RNA and fungal systematics. *Transactions of the Mycological Society of Japan* **33**: 533–556.
Hibbett DS, 2004. Trends in morphological evolution in homobasidiomycetes. *Systematic Biology* **53**: 889–903.
Hibbett DS, Binder M, 2001. Evolution of marine mushrooms. *Biological Bulletin* **201**: 319–322.
Hibbett DS, Binder M, 2002. Evolution of complex fruiting body morphologies in homobasidiomycetes. *Proceedings of the Royal Society of London, B* **269**: 1963–1969.
Hibbett DS, Donoghue MJ, 1995. Progress toward a phylogenetic classification of the *Polyporaceae* through parsimony analyses of ribosomal DNA sequences. *Canadian Journal of Botany* **73** (Suppl 1): S853–S861.
Hibbett DS, Grimaldi D, Donoghue MJ, 1995. Cretaceous mushrooms in amber. *Nature* **377**: 487.
Hibbett DS, Murakami S, Tsuneda A, 1993a. Hymenophore development and evolution in *Lentinus*. *Mycologia* **85**: 428–443.
Hibbett DS, Murakami S, Tsuneda A, 1993b. Sporocarp ontogeny in *Panus*: evolution and classification. *American Journal of Botany* **80**: 1336–1348.
Hibbett DS, Nilsson RH, Snyder M, Fonseca M, Costanzo J, Shonfeld M, 2005. Automated phylogenetic taxonomy: an example in the homobasidiomycetes (mushroom-forming fungi). *Systematic Biology* **54**: 660–668.
Hibbett DS, Pine EM, Langer E, Langer G, Donoghue MJ, 1997. Evolution of gilled mushrooms and puffballs inferred from ribosomal DNA sequences. *Proceedings of the National Academy of Sciences, USA* **94**: 12002–12006.
Hibbett DS, Thorn RG, 2001. Basidiomycota: Homobasidiomycetes. In: McLaughlin DJ, McLaughlin EG, Lemke PA (eds), *The Mycota*. Vol. II. Part B. *Systematics and Evolution*, Springer Verlag, Berlin, pp. 121–168.
Hibbett DS, Tsuneda A, Murakami S, 1994. The secotioid form of *Lentinus tigrinus*: genetics and development of a fungal morphological innovation. *American Journal of Botany* **81**: 466–478.
Hibbett DS, Vilgalys R, 1991. Evolutionary relationships of *Lentinus* to the *Polyporaceae*: evidence from restriction analysis of enzymatically amplified ribosomal DNA. *Mycologia* **83**: 425–439.
Hibbett DS, Vilgalys R, 1993. Phylogenetic relationships of *Lentinus* (*Basidiomycotina*) inferred from molecular and morphological characters. *Systematic Botany* **18**: 409–433.
Hibbett DS, Binder M, Bischoff JF, Blackwell M, Cannon PF, Eriksson OE, et al., 2007. A higher-level phylogenetic classification of the *Fungi*. *Mycological Research* **111**: 509–547.
Hopple JS, Vilgalys R, 1994. Phylogenetic relationships among coprinoid taxa and allies based on data from restriction site mapping of nuclear rDNA. *Mycologia* **86**: 96–107.
Horton JS, Palmer GE, Smith WJ, 1999. Regulation of dikaryon-expressed genes by FRT1 in the basidiomycete *Schizophyllum commune*. *Fungal Genetics and Biology* **26**: 33–47.
Hosaka K, Bates ST, Beever RT, Castellano MA, Colgan W III, Domínguez LS, Nouhra ER, Geml J, Giachini AJ, Kenney SR, Simpson NB, Trappe JM, 2007 [''2006'']. Molecular phylogenetics of the gomphoid-phalloid fungi with an establishment of the new subclass *Phallomycetidae* and two new orders. *Mycologia* **98**: 949–959.
Huelsenbeck JP, Nielsen R, Bollback JP, 2003. Stochastic mapping of morphological characters. *Systematic Biology* **52**: 131–159.
Humpert AJ, Muench EL, Giachini AJ, Castellano MA, Spatafora JW, 2001. Molecular phylogenetics of *Ramaria* and related genera: evidence from nuclear large subunit and mitochondrial small subunit rDNA sequences. *Mycologia* **93**: 465–477.
Jülich W, 1981. *Higher Taxa of Basidiomycetes*. Cramer, Lehre.
Kirk PM, Cannon PF, David JC, Stalpers JA, 2001. *Ainsworth & Bisby's Dictionary of the Fungi*, 9th edn. CABI Publishing, Wallingford.
Ko KS, Hong SG, Jung HS, 1997. Phylogenetic analysis of *Trichaptum* based on nuclear 18S, 5.8S and ITS ribosomal DNA sequences. *Mycologia* **89**: 727–734.
Kõljalg U, Tammi H, Timonen S, Agerer R, Sen R, 2002. ITS rDNA sequence-based phylogenetic analysis of *Tomentellopsis* species from boreal and temperate forests, and the identification of pink-type ectomycorrhizas. *Mycological Progress* **1**: 81–92.
Kreisel H, 1969. *Grunndzüge eines natürlichen Systems der Pilze*. J Cramer, Lehre.
Kretzer AM, Bruns TD, 1997. Use of *atp6* in fungal phylogenetics: an example from the *Boletales*. *Molecular Phylogenetics and Evolution* **13**: 483–492.
Krüger D, Binder M, Fischer M, Kreisel H, 2001. The *Lycoperdales*: a molecular approach to the systematics of some gasteroid mushrooms. *Mycologia* **93**: 947–957.
Kües U, 2000. Life history and developmental processes in the basidiomycete *Coprinus cinereus*. *Microbiology and Molecular Biology Reviews* **64**: 316–353.
Kühner R, 1980. Les *Hyménomycètes* agaricoïdes (*Agaricales*, *Tricholomatales*, *Pluteales*, *Russulales*). *Numéro spécial du Bulletin de la Société Linnéenne de Lyon*.
Langer E, 2002. *Phylogeny of non-gilled and gilled basidiomycetes: DNA sequence inference, ultrastructure and comparative morphology*. Habilitationsschrift, Universität Tübingen, Tübingen.
Larsson E, Larsson K-H, 2003. Phylogenetic relationships of russuloid basidiomycetes with emphasis on aphyllophoralean taxa. *Mycologia* **95**: 1037–1065.
Larsson K-H, Larsson E, Kõljalg U, 2004. High phylogenetic diversity among corticioid homobasidomycetes. *Mycological Research* **108**: 983–1002.
Larsson K-H, Parmasto E, Fischer M, Langer E, Nakasone KK, Redhead SA, 2007 [''2006'']. *Hymenochaetales*: a molecular phylogeny for the hymenochaetoid clade. *Mycologia* **98**: 926–936.
Lebel T, Thompson DK, Udovic F, 2004. Description and affinities of a new sequestrate fungus, *Barcheria willisiana* gen. et sp. nov. (*Agaricales*) from Australia. *Mycological Research* **108**: 206–213.
Lim YW, 2001. *Systematic study of corticioid fungi based on molecular sequence analyses*. PhD thesis, School of Biological Sciences, Seoul National University.
Maddison WP, 1990. A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* **44**: 539–557.
Maddison DR, Maddison WP, 2000. *MacClade*. Version 4. Sinauer Associates, Sunderland.
Matheny PB, Curtis JM, Hofstetter V, Aime MC, Moncalvo J-M, Ge Z-W, Yang Z-L, Slot JC, Ammirati JF, Baroni TJ, Bougher NL, Hughes KW, Lodge DJ, Kerrigan RW, Seidl MT, Aanen DK, DeNitis M, Daniele GM, Desjardin DE, Kropp BR, Norvell LL, Parker A, Vellinga EC, Vilgalys R, Hibbett DS, 2007a [''2006'']. Major clades of *Agaricales*: a multi-locus phylogenetic overview. *Mycologia* **98**: 984–997.
Matheny PB, Wang Z, Binder M, Curtis JM, Lim, Y-W, Nilsson RH, Hughes KW, Hofstetter V, Ammirati JF, Schoch CL, Langer GE, McLaughlin DJ, Wilson AW, Frøslev T, Ge Z-W, Kerrigan RW, Slot JC, Vellinga EC, Liang ZL, Baroni TJ, Fischer M, Hosaka K, Matsuura K, Seidl MT, Vaura J, Hibbett DS, 2007b [''2006'']. Contributions of rpb2 and tef1 to the phylogeny of mushrooms and allies (*Basidiomycota*, *Fungi*). *Molecular Phylogenetics and Evolution*, in press.
Miller jr OK, 1967. The role of light in the fruiting of *Panus fragilis*. *Canadian Journal of Botany* **45**: 1939–1943.
Miller jr OK, 1971. The relationship of cultural characters to the taxonomy of the agarics. In: Petersen RH (ed.), *Evolution in the*

Higher Basidiomycetes. University of Tennessee Press, Knoxville, pp. 197–215.
Miller SL, Aime MC, Henkel TW, 2002. *Russulaceae* of the Pakaraima mountains of Guyana. I. New species of pleurotoid *Lactarius*. *Mycologia* **94**: 545–553.
Miller SL, Buyck B, 2002. Molecular phylogeny of the genus *Russula* in Europe with a comparison of modern infrageneric classifications. *Mycological Research* **106**: 259–276.
Miller SL, McClean TM, Walker JF, Buyck B, 2001. A molecular phylogeny of the Russulales including agaricoid, gasteroid and pleurotoid taxa. *Mycologia* **93**: 344–354.
Miller SL, Miller Jr OK, 1988. Spore release in hypogeous, gasteroid, and agaricoid *Russulales*. *Transactions of the British Mycological Society* **90**: 513–526.
Moncalvo J-M, Nilsson RH, Koster B, Dunhma SM, Bernauer T, Matheny PB, McLenon T, Margaritescu S, Weiß M, Garnica S, Danell E, Langer G, Langer E, Larsson E, Larsson K-H, Vilgalys R, 2007 [''2006'']. The cantharelloid clade: dealing with incongruent gene trees and phylogenetic reconstruction methods. *Mycologia* **98**: 937–948.
Moncalvo J-M, Vilgalys R, Redhead SA, Johnson JE, James TY, Aime MC, Hofstetter V, Verduin SJW, Larsson E, Baroni TJ, Thorn RG, Jacobsson S, Clémençon H, Miller Jr OK, 2002. One hundred and seventeen clades of euagarics. *Molecular Phylogenetics and Evolution* **23**: 357–400.
Moncalvo J-M, Lutzoni FM, Rehner SA, Johnson J, Vilgalys R, 2000. Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. *Systematic Biology* **49**: 278–305.
Mueller GM, Pine EM, 1994. DNA data provide evidence on the evolutionary relationships between mushrooms and false truffles. *McIlvainea* **11**: 61–74.
Munkacsi AB, Pan JJ, Villesen P, Mueller UG, Blackwell M, McLaughlin DJ, 2004. Convergent coevolution in the domestication of coral mushrooms by fungus-growing ants. *Proceedings of the Royal Society, London, B* **271**: 1777–1782.
Oberwinkler F, 1977. Das neue System der Basidiomyceten. In: Frey H, Hurka H, Oberwinkler F (eds), *Beiträge zur Biologie der niederen Pflanzen*. G. Fischer, Stuttgart, pp. 59–105.
Pagel M, 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta* **26**: 331–348.
Parmasto E, 1986. On the origin of the *Hymenomycetes* (What are corticioid fungi?). *Windahlia* **16**: 3–19.
Patouillard NT, 1900. *Essai Taxonomique sur les Familles et les Genres des Hyménomycètes*. Declume, Lons-le-Saunier.
Pegler DN, 1983. The genus *Lentinus*, a world monograph. *Kew Bulletin Additional Series* **10**: 1–281.
Peintner U, Bougher NL, Castellano MA, Moncalvo J-M, Moser MM, Trappe JM, Vilgalys R, 2001. Multiple origins of sequestrate fungi related to *Cortinarius (Cortinariaceae)*. *American Journal of Botany* **88**: 2168–2179.
Persoon CH, 1801. *Synopsis methodica fungorum*. Henricus Dieterich, Göttingen.
Petersen RH (ed.), 1971a. *Evolution in the Higher Basidiomycetes*. University of Tennessee Press, Knoxville.
Petersen RH, 1971b. Interfamilial relationships in the clavarioid and cantharelloid fungi. In: Petersen RH (ed.), *Evolution in the Higher Basidiomycetes*. University of Tennessee Press, Knoxville, pp. 345–374.
Pine EM, Hibbett DS, Donoghue MJ, 1999. Evolutionary relationships of cantharelloid and clavarioid fungi. *Mycologia* **91**: 944–963.
Redhead SA, Ginns JH, 1985. A reappraisal of agaric genera associated with brown rots of wood. *Transactions of the Mycological Society of Japan* **26**: 349–381.
Ree R, 2005. Detecting the historical signature of key innovations using stochastic models of character evolution and cladogenesis. *Evolution* **59**: 257–265.
Ree R, Donoghue MJ, 1999. Inferring rates of change in flower symmetry in asterid angiosperms. *Systematic Biology* **48**: 633–641.
Reijnders AFM, Stalpers JA, 1992. The Development of the hymenophoral trama in the *Aphyllophorales* and the *Agaricales*. *Studies in Mycology* **34**: 1–109.
Savile DBO, 1955. A phylogeny of the *Basidiomycetes*. *Canadian Journal of Botany* **33**: 60–104.
Selosse MA, Bauer R, Moyersoen B, 2002. Basal hymenomycetes belonging to *Sebacinaceae* are ectomycorrhizal on temperate deciduous trees. *New Phytologist* **155**: 183–195.
Singer R, 1986. *The Agaricales in Modern Taxonomy*, 4th edn. Koeltz, Koenigstein.
Smith AH, 1973. *Agaricales* and related secotioid *Gasteromycetes*. In: Ainsworth GC, Sparrow FK, Sussman AS (eds), *The Fungi: an advanced treatise*, Vol. IVB. Academic Press, New York, pp. 421–450.
Thiers HD, 1984. The secotioid syndrome. *Mycologia* **76**: 1–8.
Thorn RG, Moncalvo J-M, Reddy CA, Vilgalys R, 2000. Phylogenetic analyses and the distribution of nematophagy support a monophyletic *Pleurotaceae* within the polyphyletic pleurotoid-lentinoid fungi. *Mycologia* **92**: 241–252.
Vellinga EC, 2004. Genera in the family *Agaricaceae*: evidence from nrITS and nrLSU sequences. *Mycological Research* **108**: 354–377.
Wagner T, Fischer M, 2002a. Classification and phylogenetic relationships of *Hymenochaete* and allied genera of the *Hymenochaetales*, inferred from rDNA sequence data and nuclear behaviour of vegetative mycelium. *Mycological Progress* **1**: 93–104.
Wagner T, Fischer M, 2002b. Proceedings towards a natural classification of the worldwide taxa *Phellinus* s.l. and *Inonotus* s.l., and phylogenetic relationships of allied genera. *Mycologia* **94**: 998–1016.
Wagner jr WH, 1961. Problems in the classification of ferns. *Recent Advances In Botany* **1**: 841–844.
Watling R, 1996. Patterns in fungal development—fruiting patterns in nature. In: Chiu S-W, Moore D (eds), *Patterns in Fungal Development*. Cambridge University Press, Cambridge, pp. 182–222.
Weiss M, Selosse M-A, Rexer K-H, Urban A, Oberwinkler F, 2004. Sebacinales: a hitherto overlooked cosm of heterobasidiomycetes with a broad mycorrhizal potential. *Mycological Research* **108**: 1003–1010.
White TJ, Bruns TD, Lee S, Taylor J, 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds), *PCR Protocols: a guide to methods and applications*. Academic Press, San Diego, pp. 315–322.