

Molecular phylogenetics of the gomphoid-phalloid fungi with an establishment of the new subclass Phallomycetidae and two new orders

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Abstract: Molecular phylogenetic analyses for the gomphoid-phalloid fungi were conducted based on

the five gene dataset with extensive taxon sampling. The monophyly of the gomphoid-phalloid clade was strongly supported, and four well supported major subclades were recognized. Three of the four subclades were represented entirely by gastroid taxa, and only Gomphales contained both gastroid and non-gastroid taxa. While the gastroid morphology is derived from epigeous, nongastroid taxa in Gomphales, the topology of Phallales indicated that truffle-like form is an ancestral morphology of the stinkhorn fruiting bodies. Although basidiospore maturation occurs within the enclosed fruiting bodies of the stinkhorn, the elevation of the mature spore-producing tissue represents an independent origin of the stipe among Basidiomycota. Comparisons are made between previous and new classification schemes, which are based on the results of phylogenetic analyses. Based on the results of these analyses, a new subclass Phallomycetidae, and two new orders, Hysterangiales and Geastrales, are proposed.

Key words: *atp6*, *EF-1 α* , homobasidiomycetes, rDNA, *RPB2*, systematics

INTRODUCTION

The gomphoid-phalloid clade comprises a group of fungi that exhibits a considerable breadth of both morphological and ecological diversity. The fruiting body morphology includes earthstars (FIG. 1u), stinkhorns (FIGS. 1f–i), cannonball fungi (FIG. 1w), coral fungi (FIG. 1m), club fungi, gilled mushrooms, tooth fungi, resupinate fungi (FIG. 1p) and false truffles (FIGS. 1a–c, j, k, o, v). Both ectomycorrhizal and saprobic taxa are represented. Because of its diversity traditional morphology-based taxonomy has classified the fungi of the gomphoid-phalloid clade into several distantly related orders, including Lycoperdales, Phallales, Nidulariales and Gomphales (Zeller 1949, Jülich 1981).

Review of previous classifications.—The traditional classifications (e.g. Zeller 1949, Donk 1964) differ dramatically with the new classification scheme proposed herein (SUPPLEMENTARY FIG. 1). Many members of the gomphoid-phalloid clade can be broadly classified as gastroid fungi (e.g. *Hysterangium*, *Geastrum* and *Phallus*). Gastroid fungi traditionally were assigned to Gasteromycetes, which are now known to be an artificial assemblage (Hibbett et al 1997). The spores of these fungi develop and mature within an



FIG. 1. Macro- and microscopic characters of the gomphoid-phalloid fungi. a–e. Hysterangiales clade. a. *Hysterangium setchellii* (OSC122929). b. *Mesophellia castanea* (H1340). c. *Gallacea scleroderma* (PDD55140). d. Basidiospores of *H. inflatum* (H349). Note spores enclosed in utricle. e. Basidiospores of *Austrogautieria rodwayi* (L. Rodway 116). f–l. Phallales clade. f. *Phallus impudicus* (photo courtesy of Koukichi Maruyama). g. *Aseroë rubra* (PDD60341). h. *Ileodictyon cibarium* (PDD64844). i. *Lysurus mokusin* (photo courtesy of Ikuo Asai). j. *Claustula fischeri* (PDD87966). k. *Phallobata alba* (PDD56745, photo courtesy Peter Johnston). l. Basidiospores of *I. cibarium* (OSC122730). m–t. Gomphales clade. m. *Ramaria fennica* (photo courtesy Ikuo Asai). n. *Turbinellus (Gomphus) floccosus* (photo courtesy Ikuo Asai). o. *Gautieria* sp. (OSC122685). p. *Kavinia* sp. (RPL69050, photo courtesy Patrick Leacock). q. Basidiospores of *R. botrytis* (photo courtesy Koukichi Maruyama). Note cyanophilic ornamentation. r. Ampullate hypha of *R. eumorpha* (T25800, photo courtesy Efren Cazares). s. Acanthohypha of *R. cystidiophora* (Giachini 03) stained with cotton blue (photo courtesy Efren Cazares). t. Hyphal mat formed by *Ramaria* sp. Note sharp contrast in color between mat-soil (white) and non-mat-soil (black). u–z. Geastrales clade. u. *Geastrum fornicatum* (H.D. Thiers 24491). v. *Pyrenogaster pityophilus* (T11761). w. *Sphaerobolus stellatus* (SS13). x. Basidiospore of *G. coronatum* (AEF1443). y. Basidiospore of *Myriostoma coliforme* (AN014674). z. Basidiospores and germinating gemmae of *S. stellatus* (SS13). Bars: a, b, v = 5 mm; c, g, i–k, o, p, u = 1 cm; d, e, l, q–s, z = 5 μ m; f, h, m, n = 5 cm; t = 10 cm; w = 1 mm; x, y = 1 μ m.

enclosed spore-producing tissue or gleba; furthermore they lack a forcible spore discharge mechanism, termed statismosporic (Miller and Miller 1988). Nongastroid members of the gomphoid-phalloid clade (e.g. *Gomphus*, *Ramaria*) are found only within Gomphales. These fungi traditionally were classified in the family Gomphaceae within Aphyllophorales, along with distantly related taxa such as Cantharellaceae, Ganodermataceae and Polyporaceae (Donk 1964).

Phallales was described by Fischer (1898) to accommodate Phallaceae and Clathraceae. Cunningham (1931a, b) later added Claustulaceae. Hysterangiales initially was treated as a family of Hymenogastrales, along with Hymenogastraceae, which is distantly related to the gomphoid-phalloid fungi (Peintner et al 2001). Although this treatment has been widely used by subsequent authors (e.g. Cunningham 1944), some authors (e.g. Miller and Miller 1988) recognized the affinity of Hysterangiaceae to stinkhorns and included Hysterangiaceae in Phallales. Other authors (Zeller 1939, Jülich 1981) segregated Hysterangiales as an independent order from Phallales although they maintained the view that Hysterangiales is most closely related to Phallales. Three families, Hysterangiaceae, Protophallaceae and Gelopellaceae, were recognized in Hysterangiales (Zeller 1949, Jülich 1981). All members of this order are characterized by truffle-like (sequestrate) fruiting bodies, most of which are produced below ground.

The members of Geastrales have been classified into two orders, Lycoperdales and Nidulariales (Zeller 1949), both of which have been demonstrated to be polyphyletic (Hibbett et al 1997, Krüger et al 2001). Within Lycoperdales (*sensu* Zeller 1949) the close relationship between Lycoperdaceae and Geastraceae was long assumed. Kreisel (1969), however, segregated Geastraceae from Lycoperdales and recognized an independent order, Geastrales. Molecular phylogenetic studies revealed that Lycoperdaceae is nested within the euagarics clade and is related only distantly to Geastraceae (Hibbett et al 1997, Krüger et al 2001). Nidulariales contains two families, Nidulariaceae and Sphaerobolaceae. Although this ordinal concept was accepted by many authors (Zeller 1949, Jülich 1981, Miller and Miller 1988) the monophyly of the order has been rejected because it has been demonstrated that members of Nidulariaceae are nested within the euagarics clade while Sphaerobolaceae is allied with Geastraceae (Hibbett et al 1997).

Gautieria previously had been included in Hymenogastraceae, Hysterangiaceae (Cunningham 1944) and as an independent, monotypic order Gautieriales (Zeller 1948). Although its close relationship with Boletales also was suggested (Jülich 1981), molecular

phylogenetic studies revealed that *Gautieria* is nested within Gomphales (Humpert et al 2001). As mentioned above other members of Gomphales are nongastroid taxa, which previously were classified in Aphyllophorales (Donk 1964). Members of Gomphaceae (*sensu* Donk) later were divided into several smaller families and placed in a new order Gomphales (Jülich 1981). *Clavariadelphus* originally was included in Clavariaceae (Donk 1964), but the family was shown to be polyphyletic; *Clavariadelphus* is a member of Gomphales, whereas *Clavaria* and *Clavulina* are nested respectively within the euagarics and cantharelloid clade (Pine et al 1999).

MATERIALS AND METHODS

Taxa sampled, along with GenBank accession numbers are provided (SUPPLEMENTARY TABLE I). DNA sequence data were obtained from five independent loci: LR0R–LR3 region for nuclear large subunit ribosomal DNA (nuc-LSU-rDNA); MS1–MS2 region for mitochondrial small subunit ribosomal DNA (mt-SSU-rDNA); ATPase subunit 6 (*atp6*); bRPB2–6F–bRPB2–7R region for the second largest subunit of RNA polymerase (*RPB2*); EF1-983F–EF1-1567R region for translation elongation factor subunit 1 α (*EF-1 α*). The primers and PCR protocols have been described previously (summarized in Assembling the Fungal Tree of Life Website <http://aftol.org/primers.php>).

Phylogenetic analyses were conducted for the concatenated five locus dataset under Bayesian and parsimony criteria. Maximum parsimony analyses were conducted with PAUP*4.0b10 (Swofford 2002) with the heuristic search option (TBR and MULTTREES on) and 1000 replicates of random addition sequence. Nodal supports were tested by bootstrapping of 500 replicates with the heuristic search option (TBR and MULTTREES off) with five random addition sequences. Bayesian analysis was conducted with MrBayes ver. 3.0b4 (Huelsenbeck and Ronquist 2001) with 2 000 000 generations of MCMCMC by sampling every 100th tree. The GTR+G+I model was used for the nuc-LSU-rDNA, mt-SSU-rDNA, and each codon position for the remaining protein coding genes. The support of nodes was tested by posterior probabilities obtained from majority rule consensus after deleting the trees during burn-in.

Ancestral character state reconstructions of fruiting body morphologies under binary coding (sequestrate vs. non-sequestrate) were performed in the Geastrales, Gomphales and Phallales clades based on the tree topology and branch lengths are provided (SUPPLEMENTARY FIG. 2). In this paper the term “sequestrate” refers to the truffle-like fruiting body form and the “nonsequestrate” refers to the other gastroid forms, including stinkhorns, earthstars and cannonball fungi. Some taxa with uncertain fruiting body types (question marks in FIG. 2, SUPPLEMENTARY FIG. 2) were coded in alternative analyses as sequestrate, nonsequestrate or polymorphic (SUPPLEMENTARY TABLE II). Parsimony-based reconstructions were performed with MacClade ver. 4.06 (Maddison and Maddison 2003) without implementing

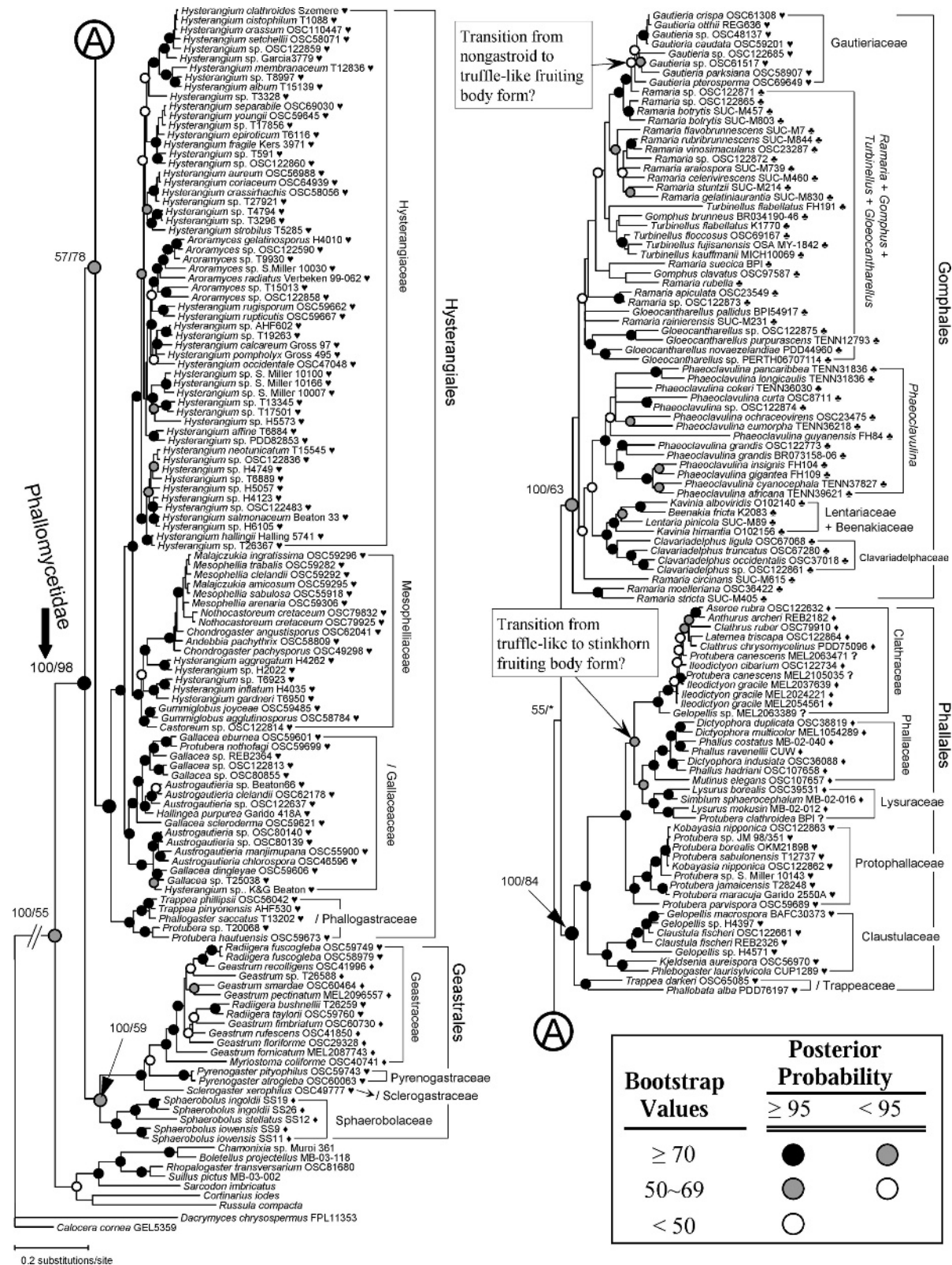


FIG. 2. Phylogeny of the gomphoid-phalloid fungi. Tree topology is based on the Bayesian analyses. Numbers on branches are Bayesian posterior probability/ maximum parsimony bootstrap values (shown as percentage). The provisional taxon names are indicated with a slash (/). Taxon names are followed by symbols indicating fruiting body forms: ♥ = sequestrate-gastroid (truffle-like), ♦ = nonsequestrate-gastroid (including stinkhorns, earthstars and cannonball fungi), ♣ = nongastroid.

character weighting. Likelihood-based reconstructions were performed with Multistate ver. 0.8 (Pagel 2003), and the significance of the difference in likelihood was determined by difference in 2 or more of $-\ln$ likelihood of each state, following Pagel (1999, also see Hibbett 2004 for analytical details).

RESULTS AND DISCUSSION

Both Bayesian and parsimony analyses showed strong support for the monophyly of the gomphoid-phalloid clade (“Phallomycetidae” in FIG. 2). No definitive synapomorphies have been identified for the gomphoid-phalloid fungi; however, some potential synapomorphic characters, including rhizomorph morphology (presence of ampullate hyphae and acanthohypha, Agerer and Iosifidou 2004; FIG. 1r, s), pistillarin content and structures of septal pore cap, have been proposed (Hibbett and Thorn 2001). In addition some members of the gomphoid-phalloid clade, such as *Gautieria*, *Hysterangium*, *Ramaria* and *Geastrum*, are known to produce thick hyphal mats in soil (Agerer and Iosifidou 2004, Nouhra et al 2005, Sunhede 1989; FIG. 1t). Although most of these characters are not exclusive to the gomphoid-phalloid fungi the yellowish filled acanthocystidia and associated “exuded drops of pigments” have been reported only from the gomphoid-phalloid fungi (e.g. *Geastrum*, *Gomphus*, *Phallogaster* and *Ramaria* [Agerer and Iosifidou 2004]). Four major clades were recognized within Phallomycetidae: Hysterangiales, Geastrales, Gomphales and Phallales. All four major clades were supported by 100% posterior probability although bootstrap values for these clades varied from 59% to 98% (FIG. 2).

Gomphales clade.—This clade corresponds to the order Gomphales (*sensu* Jülich 1981) with addition of Gautieriaceae and Clavariadelphaceae. The monophyly of Gomphales was consistent with previous studies (Villegas et al 1999). Fruiting body morphologies include coral fungi (e.g. *Ramaria* and Lentariaceae; FIG. 1m), club fungi (Clavariadelphaceae), gilled mushrooms (*Gloeocantharellus*), cantharelloid-gomphoid (e.g. *Gomphus* and *Turbinellus*, Giachini 2007; FIG. 1n), tooth fungi (*Beenakia*), resupinate fungi (*Kavinia*; FIG. 1p) and false truffles (Gautieriaceae; FIG. 1o). Despite their macromorphological variations the members of this clade share a number of microscopic and macrochemical characters, including cyanophilic spore ornamentation (FIG. 1q), hyphal

construction and positive hymenial reaction to ferric sulfate (Donk 1964, Villegas et al 1999).

Humpert et al (2001) suggested that branched coral fruiting bodies are ancestral forms for Gomphales. While lack of statistical support for some internal nodes within Gomphales in this study limits our inferences, the basal positions of some coral fungi, such as *Ramaria moelleriana* and *R. stricta*, are consistent with their conclusions (SUPPLEMENTARY TABLE VI). Gautieriaceae is the only false truffle taxon in Gomphales and it is restricted to a terminal clade, also indicating their derived form. This is consistent with the hypothesis that sequestrate fruiting bodies are derived forms from more complex, epigeous morphology (Thiers 1984, Peintner et al 2001). Gomphales also show heterogeneity in their ecological characters. Most species in Lentariaceae, Kaviniaaceae, Beenakiaceae, *Phaeoclavulina* and some species of *Ramaria*, such as *R. moelleriana*, *R. stricta*, and *R. circinans*, grow and fruit on woody debris, a trait that has led to their general categorization as saprobes. The other taxa of the order generally are considered ectomycorrhizal, and while the ectomycorrhizal status of many species of Gomphales is still unknown, the formation of ectomycorrhizae by *Turbinellus*, *Gomphus* and some *Ramaria* species has been confirmed (Agerer and Iosifidou 2001, Nouhra et al 2005).

Phallales clade.—It roughly corresponds to the order Phallales *sensu* Cunningham (1931a, b), with the results of molecular phylogenetic analyses (FIG. 2) suggesting the inclusion of more members to this order. Fruiting body morphologies include stink-horns (Phallaceae, FIG. 1f), lattice stinkhorns (Clathraceae and Lysuraceae, FIGS. 1g–i) and false truffles (Protophallaceae, Clautulaceae and Trappeaceae; FIGS. 1j, k). A few false truffle taxa also are observed in Clathraceae (*Protuberana canescens* and *Gelopellis* sp.) and Lysuraceae (*Protuberana clathroidea*). Based on tree topology and original descriptions of these taxa (Beaton and Malajczuk 1986, Malloch 1989) it is likely that these taxa are unopened stinkhorn fruiting bodies and therefore are considered as uncertain fruiting body forms (indicated by question marks in FIG. 2). *Gastrosporium* was shown to be the member of Phallales (Hibbett and Binder 2002) but it was not included in this study due to lack of a protein coding gene sequence. Zeller (1948) included Gastrosporaceae in Tremellogastrales, but *Tremellogaster* in Tremellogastraceae was demonstrated to be a member

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A few sequestrate taxa in the Phallales clade are indicated by question marks because of their uncertainty in fruiting body form (see text for details).

of Boletales (Binder and Hibbett 2006 this issue). The affinity of the remaining genus (*Clathrogaster*) to the gomphoid-phalloid fungi, however, is still unclear. Most taxa in this order are characterized by having fruiting bodies with a gelatinous layer and a gelatinous to mucilaginous gleba, but *Gastrosporium* has a powdery gleba (Domínguez de Toledo and Castellano 1997). Spores of most taxa are small, ellipsoid and smooth without ornamentation (FIG. 11) but a few taxa, such as *Kjeldsenia* and *Gastrosporium*, have warty spore surfaces (Colgan et al 1995, Domínguez de Toledo and Castellano 1997). Most taxa are believed to be saprobic due to their lignicolous habit, but at least one species (*Protuberana canescens*) has been reported to be ectomycorrhizal (Malajczuk 1988).

Lysuraceae was recognized as a separate family from Clathraceae by Corda (1842) but most subsequent authors treated them as a single family Clathraceae (e.g. Dring 1980, Jülich 1981). This study shows that Lysuraceae is more closely related to Phallaceae than it is to Clathraceae (FIG. 2). Fruiting bodies of Phallaceae are characterized by a single, unbranched receptacle and a gleba attached externally on the upper part of receptacle (FIG. 1f). Fruiting body morphologies of Lysuraceae are similar to Clathraceae in having a gelatinous layer divided by sutures but differ in having long, stipitate receptacles that are longer than the arms that arise from the receptacle (Dring 1980; FIG. 1i). Also the gleba of Lysuraceae tends to migrate to the exterior face of the arms (Dring 1980; FIG. 1i). Species in Clathraceae have gleba attached only to the interior face of the arms (Dring 1980; FIGS. 1g, h).

Protophallaceae traditionally has been classified in Hysterangiales, but this study shows that the family belongs to Phallales. *Protuberana* is polyphyletic in our analyses with species placed in at least three separate clades within Phallales, including Protophallaceae (and the type species, *P. maracuja*), Lysuraceae and Clathraceae. In addition some species of *Protuberana* were observed in Hysterangiales clade. Another member of this clade, *Kjeldsenia*, originally was described as a member of Cortinariaceae (Colgan et al 1995). It is noteworthy that three basal clades within Phallales (Protophallaceae, Claustulaceae and Trappeaceae) all were characterized by truffle-like taxa, while taxa with more complex, stinkhorn-like fruiting bodies are restricted to more terminal clades, indicating that stinkhorn-like fruiting bodies are derived morphologies in Phallales. The results of ancestral character state reconstruction were consistent, showing a single transition from sequestrate to stinkhorn fruiting body form (FIG. 2, also see SUPPLEMENTARY TABLE II-i), except when uncertain taxa were

coded as sequestrate, which showed ambiguous reconstructions for basal nodes. It is a rare example in the homobasidiomycetes showing that truffle-like fruiting bodies are ancestral morphologies. Unlike sequestrate taxa in Agaricales, however, the evolution of truffle-like fruiting bodies in Phallales does not require gains and/or losses of ballistospory because all taxa in Phallales are statismosporic.

Mycophagy (the use of fungi as food) by arthropods is well documented for many groups of Fungi (Martin 1979), and stinkhorn-like fungi are one of the prime examples (Nouhra and Domínguez 1994). On the other hand major mycophagous animals for truffle-like fungi are rodents and small marsupials, many of which eat significant amounts of truffle-like fungi in their diet (Lehmkuhl et al 2004). Spores of truffle-like taxa in Phallales, however, are not well documented from animal feces. Because many truffle-like fungi are known to emit chemical compounds to attract insects (Pacioni et al 1991) it is possible that spore dispersal of Phallales is entirely dependent on arthropods.

Hysterangiales clade.—It contains only sequestrate taxa although fruiting bodies of some taxa (e.g. *Phallogaster* and *Gallacea*) occasionally crack open and expose the gleba (Castellano and Beever 1994). While most taxa possess a gelatinous to cartilaginous gleba (FIGS. 1a, c) species in Mesophelliaceae clade are characterized by a powdery gleba (FIG. 1b). This feature is the reason why Mesophelliaceae has been classified in Lycoperdales, along with Lycoperdaceae and Geastraceae (Zeller 1949), and previous workers were not able to infer the close relationship of Mesophelliaceae and Hysterangiaceae. Mesophelliaceae *sensu* Zeller, however, is polyphyletic. The type genus *Mesophellia* belongs to Hysterangiales, but *Radiigera* belongs to Geastrales (FIG. 2) and *Abstoma* is most likely related to Lycoperdaceae. *Rhopalogaster* traditionally has been included in Hysterangiales (Zeller 1949), but this study clearly shows that it is nested within Boletales (FIG. 2).

Most taxa in Hysterangiales clade possess ellipsoidal spores that are smooth to minutely warted. One of the exceptions is observed in Gallaceaceae clade, where *Austrogautieria* possesses longitudinally ridged spores (FIG. 1e). Within Phallomycetidae *Austrogautieria* (FIG. 1e) and *Gautieria* (in Gomphales) share similar spore morphology and sequestrate habit, but the phylogenetic analysis shows these similarities are due to convergent evolution. Many taxa in Hysterangiaceae and Mesophelliaceae clade possess spores enveloped in a wrinkled to loose outer membrane (or utricle, FIG. 1d) whereas taxa in Gallaceaceae and Phallogastraceae clades do not (Stewart and Trappe 1985, Castellano and Beever 1994, Trappe et al 1996).

Taxa in Phallogastraceae clade are most likely saprobic (Miller and Miller 1988, Castellano 1990) whereas the rest of Hysterangiales all are ectomycorrhizal. Although ectomycorrhizal status has not been investigated for all taxa in Hysterangiales it was confirmed for some *Hysterangiium* spp. (Hysterangiaceae clade, Agerer and Iosifidou 2004), *Mesophellia* and *Castoreum* spp. (Mesophelliaceae clade, Dell et al 1990) and *Austrogautieria* spp. (Gallaceaceae clade, Lu et al 1999). In addition many ectomycorrhizal taxa in Hysterangiales form dense perennial hyphal mats, which often significantly change the soil chemistry and microorganism biomass (Griffiths et al 1994). Unlike sequestrate taxa in Phallales, mycophagy by small mammals and marsupials is well documented for Hysterangiales and they often occupy a significant portion of the diet for these animals (Lehmkuhl et al 2004).

Geastrales clade.—It contains cannonball fungi (Sphaerobolaceae, FIG. 1w), earthstars (Geastraceae, FIG. 1u) and false truffles (Pyrenogastraceae, Sclerogastraceae and *Radiigera*; FIG. 1v). The ancestral character reconstruction for fruiting body morphology did not show a clear pattern for the basal nodes of the Geastrales clade, but parsimony-based reconstruction indicated that there were at least two independent changes from nonsequestrate to sequestrate fruiting bodies at the nodes leading to *Radiigera* (TABLE III, SUPPLEMENTARY INFORMATION). This again is consistent with the hypothesis that truffle-like fruiting bodies are derived forms (Thiers 1984, Peintner et al 2001).

Zeller (1948) described Broomeiaceae in Lycoperdales, but it is unclear whether this family is more closely related to Geastrales than to other homobasidiomycetes. Likewise some genera such as *Phialastrum* and *Trichaster* were not included in this study although they traditionally have been placed in Geastraceae (Sunhede 1989). *Geastrum* and *Myriostoma* have fruiting bodies with multiple peridial layers. The exoperidium opens in a stellate manner as it matures, exposing the endoperidium with one (*Geastrum*) to multiple (*Myriostoma*) stomata, through which spores escape (FIG. 1u). *Radiigera* and Pyrenogastraceae both have truffle-like fruiting bodies, and their peridia do not open until they are naturally degraded or eaten by mycophagous animals. The gleba of Pyrenogastraceae is divided into multiple peridioles (FIG. 1v). Species within Geastraceae and Pyrenogastraceae have glebae that become brownish to blackish and powdery at maturity. Sclerogastraceae also have truffle-like fruiting bodies, but the mature gleba never becomes powdery and exhibits a yellowish to brownish color. Most taxa

described above possess globose spores with a warty surface (FIG. 1x), but *Myriostoma* possesses ornamentation that is fused into ramified ridge-like projections (Sunhede 1989; FIG. 1y).

The structure of the fruiting bodies of Sphaerobolaceae is unique for Geastrales. Although the outer peridium opens out stellately, similar to Geastraceae, the gleba is composed of a single peridiole (FIG. 1w), which never becomes powdery and contains numerous hyaline, smooth, subglobose to ellipsoid spores (FIG. 1z). The peridiole eventually is ejected forcibly (Ingold 1972). Members of Sphaerobolaceae are undoubtedly saprobic because they can easily produce fruiting bodies on artificial media (Flegler 1984), but the nutritional mode for the remaining taxa in Geastrales remains uncertain. Many species of *Geastrum* grow without obvious ectomycorrhizal plants, and some authors concluded that *Geastrum* is saprobic (Sunhede 1989, Kreisel 1969); however, at least one species, *G. fimbriatum*, is described as forming ectomycorrhizae (Agerer and Beenken 1998).

TAXONOMY

Based on the results of our phylogenetic analyses we propose a new subclass Phallomycetidae to include Gomphales and Phallales as well as two new orders, Hysterangiales and Geastrales.

Phallomycetidae Hosaka, Castellano et Spatafora, subclass. nov.

Basidiomata hypogaea vel epigaea, solitaria, gregaria vel caespitosa, sequestrata, resupinata, effuso-reflexa, pileata, turbinata, infundibuliformia, coralliformia, clavata, stellata vel receptacula singula vel irregulariter ramosa a volva basali exorienti. Rhizomorphae saepe conspicuae ad basim vel latera basidiomatum, tegetem densam hyphalem interdum producentes, interdum hyphis ampullaribus acanthocystidiis contentis luteolis. Hymenium interdum cum FeSO₄ coerulescens. Gleba taxorum gastroidum maturitate gelatinosa, mucilaginata, cartilaginea vel pulverea, grisea, viridis, olivacea, brunnea, cinnamomea vel nigra, saepe columella bene evoluta. Sporae in hymenio exposito enatae vel in gleba inclusae, ballistosporicae vel statismosporicae, symmetricae vel asymmetricae, globosae, subglobosae, ellipsoideae, elongatae, cylindricae vel fusiformes, laeves, verrucosae, echinatae vel porcatae, interdum utriculo vel vestigeis episporae, in KOH hyalinae vel brunneae, saepe cyanophilae. Ordo typus: Phallales. Ordines inclusi: Phallales, Gomphales, Hysterangiales, Geastrales.

Basidiomata hypogeous or epigeous, solitary, gregarious or caespitose, sequestrate or resupinate, effused-reflexed, pileate, turbinate, infundibuliform, coralliform, clavate, stellate or with a single to irregularly branched receptacle arising from a basal volva. Rhizomorphs often conspicuous at base or sides of basidiomata, occasionally producing dense hyphal mats in soil, sometimes with ampullate hyphae and acanthocystidia with yellowish contents. Hymenium sometimes turning blue with ferric sulfate. Gleba of gastroid taxa gelatinous, mucilaginous, cartilaginous or powdery at maturity, gray to green, olive, brown, cinnamon or black, often with a well developed columella. Spores borne on an exposed hymenium or enclosed within a gleba, statismosporic or ballistosporic, symmetrical or asymmetrical, globose, subglobose, ellipsoid, elongate, cylindrical to fusiform, smooth, verrucose, echinate or ridged, occasionally with a utricle or remnants of an epispore, hyaline to brown in KOH, often cyanophilic.

Type order. Phallales E. Fischer, in Engler and Prantl, *Die Natürlichen Pflanzenfamilien I (1**)*:276, 1898, "Phallineae".

Orders included. Phallales E. Fischer, Gomphales Jülich, Hysterangiales Hosaka et Castellano, ord. nov., Geastrales Hosaka et Castellano, ord. nov.

Remarks. This group is equivalent to Phallales in the Dictionary of the Fungi 9th edition (Kirk et al 2001) and the "gomphoid-phalloid clade" *sensu* Hibbett and Thorn (2001). Locquin (1984) used the term "Phallomycetidae" but did not provide a Latin diagnosis, and therefore it is considered invalid in accordance with Article 36.1 of the International Code of Botanical Nomenclature (ICBN). Furthermore Phallomycetidae *sensu* Locquin included only stinkhorn-like taxa and a few sequestrate taxa, which is roughly equivalent to Phallales clade in this study (FIG. 2). The results of our study strongly support the creation of the subclass Phallomycetidae to accommodate the four distinct but related clades (i.e. Phallales, Hysterangiales, Gomphales and Geastrales). This organization accommodates the two previously described orders, Phallales and Gomphales, with the numerous associated families.

On the other hand one could treat the entire gomphoid-phalloid clade as an order Phallales, following Kirk et al (2001). However this treatment would require the creation of four new suborders, or four major clades (Geastrales, Gomphales, Hysterangiales and Phallales; FIG. 2) would have to be recognized at the family level. This change forces the elimination of several widely recognized families, such as Clathraceae, Mesophelliaceae, Protophalla-ceae and Sphaerobolaceae, all of which are supported as monophyletic groups in this study (FIG. 2). In

addition the gomphoid-phalloid clade is potentially one of the basal clades within the homobasidiomycetes (Binder and Hibbett 2002, Lutzoni et al 2004), which further supports the recognition of the subclass status for this group. The use of subclass Phallomycetidae with four orders is the best reflection of the higher-level phylogeny and hence would provide a stable classification system of Basidiomycota.

Hysterangiales Hosaka et Castellano, ord. nov.

≡ Hysterangiales Zeller, *Mycologia* 31:29, 1939, nom. nud.

≡ Hysterangiales Locquin, *De Taxia Fungorum* 1:48, 1974, nom. nud.

Basidiomata hypogaea vel epigaea, solitaria vel gregaria, sequestrata, globosa vel irregulare, saepe basi contracta, cauloide, sterili, saepe arenaque solo adhaerenti tecta vel radicellis inclusa. Rhizomorphae ad basem vel latera basidiomatum conspicuae, tegetem densam hyphalem in solo saepe producentes, interdum crystallis calcis oxylatis affixis. Peridium e gleba interdum facile separabile, elasticum, glutinum vel durumque fragile, album, luteolum, brunneum, violaceum vel purpureum, interdum rubellescens, rubescens, brunnescens, purpurescens, lutescens ubi contusum, stratis 1–4, interdum subcute gelatinosa vel mycorrhizas includens. Gleba maturitate cartilaginea, gelatinosa vel pulverea, grisea, viridis, olivacea vel brunnea, saepe loculis labyrinthinis vel elongatis, saepe columella dendroideae, cartilagineae vel gelatinosa, vel nucleo molli vel cartilagineo vel structurata huius modi deficiens. Basidia 1–8-spora. Sporae statismosporicae, pro parte maxima symmetricae, ellipsoideae, oblongae vel fusioideae, laeves vel minute verrucosae vel interdum spinosae, saepe utriculo rugoso, inflato, vel ephemero, hyalinae, pallide virides vel brunneae in KOH, inamyloideae, interdum dilute dextrinoideae. Familia typica: Hysterangiaceae.

Basidiomata hypogeous or epigeous, solitary or gregarious, sequestrate, globose to irregular, with or without a tapering, stem-like sterile base, often covered with adhering sand and soil or encased in debris and rootlets. Rhizomorphs conspicuous at base or sides of basidiomata, often producing dense hyphal mats in the soil, occasionally with attached calcium oxalate crystals. Peridium sometimes readily separable from gleba, elastic, glutinous or hard and brittle, white to pale yellow, brown, violet, or purple, sometimes staining pink, red, brown, purple, yellow or brown when bruised, 1–4-layered, sometimes with a gelatinous subcutis containing sutures that divide the peridium into sections, sometimes incorporating mycorrhizae. Gleba at maturity cartilaginous to gelatinous or powdery, gray to green, olive or brown, often with labyrinthine to elongated locules, with

a dendroid, cartilaginous to gelatinous columella or a soft to rubbery central core or lacking such structures. Basidia 2–8-spored. Spores statismosporic, mostly symmetrical, ellipsoid, oblong to fusoid, smooth to minutely verrucose, or sometimes spinose, often with a wrinkled to inflated or ephemeral utricle, hyaline, pale green, or brown in KOH, inamyloid, sometimes weakly dextrinoid.

Type family. Hysterangiaceae E. Fischer, Die Natürlichen Pflanzenfamilien 1(1**):304, 1899.

Remarks. Several authors treated Hysterangiales as an independent order, segregated from Phallales (Zeller 1939, 1949; Jülich 1981; Locquin 1974, 1984). However, an extensive literature search revealed that the order had never been published with a Latin diagnosis and therefore it is considered invalid in accordance with Article 36.1 of the ICBN. Of interest, Hysterangiales *sensu* Zeller included Protophallaceae and Gelopellaceae, both of which were revealed to be members of Phallales (FIG. 2). Our study revealed several previously unrecognized relationships (i.e. Mesophelliaceae and *Austrogautieria*, which necessitate a redefinition of Hysterangiales as a new order). There are a few truffle-like genera in Gomphales and Geastrales but those that do occur in these two orders possess spores that have nonconvergent ridges with rounded margins or are distinctly warted, globose to subglobose with some tint of brown, which distinguish them from all members of Hysterangiales.

Geastrales Hosaka et Castellano, ord. nov.

- ≡ Geastrales Kreisel, Grundzüge eines natürlichen Systems der Pilze, 157, 1969, nom. nud.
- ≡ Geastrales Locquin, De Taxia Fungorum 1:57, 1974, nom. nud.

Basidiomata hypogaea vel epigaea, solitaria, gregaria vel caespitosa in stromate vel subiculo communi, maturitate sequestrata vel pro radiis stellatis vel irregularibus dehiscentia; corpus endoperidialis sessilis vel stipitatus. Rhizomorphae saepe conspicuae basem basidiomatium, interdum hyphis ampullaribus et acanthocystidiorum contentis luteolis. Peridium stratis 2–5. Si maturitate exoperidium aperit, tum corpus endoperidialis stoma unum vel stomata aliquot possedit vel irregulariter dehiscat vel peridiolum per vim mittit. Gleba patellis tramalibus a columella centrali radians vel in peridiolum unum vel peridiola aliquot dividens vel loculis sphaericis vel elongatis, lutea, aurantiaca, brunnea vel nigra, maturitate saepe pulveracea; capillitium praesens vel absens. Basidia globosa, clavata, pyriformes vel tubulares, saepe sub apice rotundato constricta, sporis 4–8. Sporae statismosporicae, symmetricae, globosae, subglobosae vel ellipsoideae, laeves, verrucosae, inamyloideae, nondextrinoideae. Familia typica: Geastraceae.

Basidiomata hypogeous or epigeous, solitary, gregarious or caespitose on a common stroma or subiculum, sequestrate or opening as stellate to irregular rays at maturity; endoperidial body sessile to stipitate. Rhizomorphs often conspicuous at base of basidiomata, sometimes of ampullate hyphae and acanthocystidia with yellowish contents. Peridium 2–5-layered; if the exoperidium opens at maturity, the endoperidial body possesses one to multiple stomata, or dehisces irregularly, or forcibly discharges a peridiole. Gleba of tramal plates radiating out from a central columella, or divided into one to multiple peridioles, or with spherical to elongate locules, yellow to orange, brown, or black, often powdery at maturity; capillitium present or absent. Basidia globose, clavate, pyriform to tubular, often constricted below the rounded apex, 4–8-spored. Spores statismosporic, symmetrical, globose, subglobose to ellipsoid, smooth to verrucose, echinulate or with ramified ridges, hyaline to brown in KOH, inamyloid, nondextrinoid.

Type family. Geastraceae Corda, Icones Fungorum 5:25, 1842, “Geastridae”.

Remarks. Geastrales was published by Kreisel (1969) without a Latin diagnosis and therefore it is considered invalid in accordance with Article 36.1 of the ICBN. Furthermore Kreisel (1969) recognized the order as monotypic, containing a single family Geastraceae, in which only *Geastrum* and *Myriostoma* were recognized. Our study revealed a broader concept of Geastrales, one that encompasses several previously unrecognized taxa in the order, such as Pyrenogastraceae, Sphaerobolaceae and *Sclerogaster*. For the most part Geastrales differs from other members of Phallomycetidae in having basidiomata that open stellately or irregularly and forcibly discharge a peridiole, or expose the endoperidial body with one to multiple stomata through which spores are released. The truffle-like taxa in Geastrales (e.g. Pyrenogastraceae, *Radiigera* and *Sclerogaster*) generally can be distinguished from the similar taxa in other orders of Phallomycetidae by the combination of their spore characters, including a globose to subglobose shape and verrucose to echinulate ornamentation. The order differs from Gasterosporiaceae by having a membranous endoperidium rather than a gelatinous one (Domínguez de Toledo and Castellano 1997).

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SUPPLEMENTARY TABLE I. Taxon list and associated GenBank accession numbers

Genus species	Herbarium	Specimen No.	GenBank No.				
			nuc-LSU- rDNA	mt-SSU- rDNA	atp6	RPB2	EF-1 α
OUTGROUP							
<i>Boletellus projectellus</i>	CUW	MB-03-118	AY684158	—	AFTOL ^b	AY787218	AY879116
<i>Calocera cornea</i>	—	—	AY701526	—	—	AY536286	AY881019
<i>Chamonixia</i> sp.	OSC	Muroi 361	DQ218598	DQ218741	DQ218885	DQ219046	DQ219224
<i>Cortinarius iodes</i>	—	—	AY702013	AF026675	AF388826	AY536285	AY881027
<i>Dacrymyces chrysospermus</i>	—	—	AF287855	AF026642	—	AY218480	—
<i>Rhopalogaster transversarium</i>	OSC	81680	DQ218599	DQ218742	DQ218886	DQ219047	DQ219225
<i>Russula compacta</i>	DUKE	s.n.	AF287888	U27074	—	AY218514	—
<i>Sarcodon imbricatus</i>	—	—	AY586711	—	AF002147	AY218528	—
<i>Suillus pictus</i>	CUW	MB-03-002	AY684154	—	AFTOL ^b	AY786066	AY883429
Geastrales clade							
<i>Geastrum fimbriatum</i>	OSC	60730	DQ218600	—	DQ218887	DQ219048	DQ219226
<i>Geastrum floriforme</i>	OSC	29328	DQ218485	DQ218660	DQ218769	DQ219049	DQ219227
<i>Geastrum fornicatum</i>	MEL	2087743	DQ218601	DQ218743	DQ218888	DQ219050	DQ219228
<i>Geastrum pectinatum</i>	MEL	2096557	DQ218602	—	DQ218889	DQ219051	DQ219229
<i>Geastrum recolligens</i>	OSC	41996	DQ218486	DQ218661	DQ218770	DQ219052	DQ219230
<i>Geastrum rufescens</i>	OSC	41850	DQ218603	DQ218744	DQ218890	DQ219053	—
<i>Geastrum smardae</i>	OSC	60464	DQ218604	—	DQ218891	DQ219054	—
<i>Geastrum</i> sp.	OSC	T26588	DQ218605	—	DQ218892	—	—
<i>Myriostoma coliforme</i>	OSC	40741	DQ218606	—	DQ218893	DQ219055	DQ219231
<i>Pyrenogaster atrogleba</i>	OSC	60063	DQ218607	—	DQ218894	DQ219056	—
<i>Pyrenogaster pityophilus</i>	OSC	59743	DQ218519	DQ218694	DQ218803	DQ219057	DQ219232
<i>Radiigera bushnellii</i>	OSC	T26259	DQ218608	DQ218745	DQ218895	DQ219058	DQ219233
<i>Radiigera fuscogleba</i>	OSC	58979	DQ218609	—	DQ218896	DQ219059	DQ219234
<i>Radiigera fuscogleba</i>	OSC	59749	DQ218610	—	DQ218897	—	—
<i>Radiigera taylorii</i>	OSC	59760	DQ218520	DQ218695	DQ218804	DQ219060	DQ219235
<i>Sclerogaster xerophilus</i>	OSC	49777	DQ218611	—	—	DQ219061	DQ219236
<i>Sphaerobolus ingoldii</i>	PSU ^a	SS19	AY439012	AY488015	—	—	AY487990
<i>Sphaerobolus ingoldii</i>	PSU ^a	SS26	AY439013	AY488022	—	—	AY487996
<i>Sphaerobolus iowensis</i>	PSU ^a	SS11	AY439014	AY488008	—	—	AY487984
<i>Sphaerobolus iowensis</i>	PSU ^a	SS9	AY439010	AY488006	—	—	AY487982
<i>Sphaerobolus stellatus</i>	PSU ^a	SS12	AF393077	AF026662	AY574789	DQ219062	DQ219237
Gomphales clade							
<i>Beenakia fricta</i>	K	2083	AY574693	AY574766	AY574833	—	DQ219238
<i>Clavariadelphus ligula</i>	OSC	67068	AY574650	AY574723	AY574793	DQ219063	DQ219239
<i>Clavariadelphus occidentalis</i>	OSC	37018	AY574648	AY574721	AY574791	—	—
<i>Clavariadelphus truncatus</i>	OSC	67280	AY574649	AY574722	AY574792	DQ219064	DQ219240
<i>Clavariadelphus</i> sp.	OSC	122861	DQ218612	—	DQ218898	DQ219065	DQ219241
<i>Gautieria caudata</i>	OSC	59201	DQ218483	DQ218658	DQ218767	DQ219066	DQ219242
<i>Gautieria crispa</i>	OSC	61308	DQ218484	DQ218659	DQ218768	DQ219068	DQ219244
<i>Gautieria otthii</i>	REG	636	AF393058	AF393085	—	AY218486	AY883434
<i>Gautieria parksiana</i>	OSC	58907	AY574652	AY574725	AY574795	—	DQ219245
<i>Gautieria pterosperma</i>	OSC	69649	DQ218614	DQ218747	DQ218900	DQ219069	DQ219246
<i>Gautieria</i> sp.	OSC	61517	DQ218613	DQ218746	DQ218899	DQ219067	DQ219243
<i>Gautieria</i> sp.	OSC	48137	DQ218615	DQ218748	DQ218901	DQ219070	DQ219247
<i>Gautieria</i> sp.	OSC	122685	DQ218616	DQ218749	DQ218902	DQ219071	DQ219248
<i>Gloeocantharellus novaezealandiae</i>	PDD	44960	AY574666	AY574739	AY574809	—	—
<i>Gloeocantharellus pallidus</i>	BPI	54917	AY574673	AY574746	AY574815	—	—

SUPPLEMENTARY TABLE I. Continued

Genus species	Herbarium	Specimen No.	GenBank No.				
			nuc-LSU- rDNA	mt-SSU- rDNA	atp6	RPB2	EF-1 α
<i>Gloeocantharellus purpurascens</i>	TENN	12793	AY574683	AY574756	AY574823	—	—
<i>Gloeocantharellus</i> sp.	PERTH	06707114	AY574667	AY574740	AY574810	—	—
<i>Gloeocantharellus</i> sp.	OSC	122875	DQ218617	—	DQ218903	DQ219072	DQ219249
<i>Gomphus brunneus</i>	BR	034190-46	AY574680	AY574753	AY574821	—	—
<i>Gomphus clavatus</i>	OSC	97587	DQ218487	DQ218662	DQ218771	—	—
<i>Kavinia alboviridis</i>	O	102140	AY574692	AY574765	AY574832	DQ219073	DQ219250
<i>Kavinia himantia</i>	O	102156	AY574691	AY574764	AY574831	—	—
<i>Lentaria pinicola</i>	SUC	M89	AY574688	AY574761	AY574828	—	DQ219251
<i>Phaeoclavulina africana</i>	TENN	39621	AY574653	AY574726	AY574796	—	—
<i>Phaeoclavulina cokeri</i>	TENN	36030	AY574701	AY574774	AY574843	—	—
<i>Phaeoclavulina curta</i>	OSC	8711	AY574713	—	AY574858	—	—
<i>Phaeoclavulina cyanocephala</i>	TENN	37827	AY574710	AY574779	AY574854	—	—
<i>Phaeoclavulina eumorpha</i>	TENN	36218	AY574712	AY574781	AY574856	—	—
<i>Phaeoclavulina gigantea</i>	FH	109	AY574703	AY574776	AY574845	—	—
<i>Phaeoclavulina grandis</i>	BR	073158-06	AY574678	AY574751	AY574820	—	—
<i>Phaeoclavulina grandis</i>	OSC	122773	DQ218618	—	DQ218904	DQ219074	DQ219252
<i>Phaeoclavulina guyanensis</i>	FH	84	AY574706	—	AY574848	—	—
<i>Phaeoclavulina insignis</i>	FH	104	AY574704	—	AY574846	—	—
<i>Phaeoclavulina longicaulis</i>	TENN	31836	AY574700	AY574773	AY574842	—	—
<i>Phaeoclavulina ochraceovirens</i>	OSC	23475	AY574714	—	AY574859	—	—
<i>Phaeoclavulina pancaribbea</i>	TENN	31836	AY574707	—	AY574849	—	—
<i>Phaeoclavulina</i> sp.	OSC	122874	—	—	DQ218905	DQ219075	DQ219253
<i>Ramaria apiculata</i>	OSC	23549	AY574695	AY574768	AY574836	—	—
<i>Ramaria araiospora</i>	SUC	M739	AF213068	AF213141	AY574838	DQ219076	DQ219254
<i>Ramaria botrytis</i>	SUC	M457	AY574698	AY574771	AY574840	—	—
<i>Ramaria botrytis</i>	SUC	M803	AF213058	—	DQ218906	—	—
<i>Ramaria celerivirescens</i>	SUC	M460	AF213073	—	DQ218907	DQ219077	DQ219255
<i>Ramaria circinans</i>	SUC	M615	AY574711	AY574780	AY574855	—	—
<i>Ramaria flavobrunnescens</i>	SUC	M7	AF213082	AF213140	DQ220790	DQ219045	DQ219223
<i>Ramaria gelatiniaurantia</i>	SUC	M830	AY574708	AY574777	AY574851	—	—
<i>Ramaria moelleriana</i>	OSC	36422	DQ218619	—	DQ218908	—	—
<i>Ramaria rainierensis</i>	SUC	M231	AF213115	AF213135	AY574834	—	—
<i>Ramaria rubella</i>	—	—	AY645057	—	—	AY786064	AY883435
<i>Ramaria rubribrunnescens</i>	SUC	M844	AF213098	AF213142	AY574852	—	—
<i>Ramaria stricta</i>	SUC	M405	AF213117	AF213138	DQ218805	DQ219078	DQ219256
<i>Ramaria stuntzii</i>	SUC	M214	AF213102	AF213134	AY574850	DQ219079	DQ219257
<i>Ramaria suecica</i>	BPI	s.n.	AY574705	—	AY574847	—	—
<i>Ramaria vinosimaculans</i>	OSC	23287	AY574709	AY574778	AY574853	—	—
<i>Ramaria</i> sp.	OSC	122865	DQ218620	—	DQ218909	—	—
<i>Ramaria</i> sp.	OSC	122871	DQ218621	—	DQ218910	—	—
<i>Ramaria</i> sp.	OSC	122873	DQ218622	—	DQ218911	DQ219080	—
<i>Ramaria</i> sp.	OSC	122872	DQ218623	—	DQ218912	—	DQ219258
<i>Turbinellus flabellatus</i>	FH	191	AY574674	AY574747	AY574816	—	—
<i>Turbinellus flabellatus</i>	K	1770	AY574681	AY574754	AY574822	—	—
<i>Turbinellus floccosus</i>	OSC	69167	AY574656	AY574729	AY574799	—	DQ219259
<i>Turbinellus fujisanensis</i>	OSA	MY-1842	AY574669	AY574742	AY574811	—	—
<i>Turbinellus kauffmanii</i>	MICH	10069	AY574671	AY574744	AY574813	—	—
Hysterangiales clade							
<i>Andebbia pachythrix</i>	OSC	58809	DQ218523	—	DQ218808	DQ218940	DQ219117
<i>Aroramycetes gelatinosporus</i>	OSC	H4010	DQ218524	DQ218698	DQ218809	DQ218941	DQ219118

SUPPLEMENTARY TABLE I. Continued

Genus species	Herbarium	Specimen No.	GenBank No.				
			nuc-LSU- rDNA	mt-SSU- rDNA	atp6	RPB2	EF-1 α
<i>Aroramyces radiatus</i>	OSC	Verbeken 99-062	DQ218525	DQ218699	DQ218810	DQ218942	DQ219119
<i>Aroramyces</i> sp.	OSC	122858	DQ218528	—	DQ218813	DQ218945	DQ219122
<i>Aroramyces</i> sp.	OSC	122590	DQ218529	DQ218701	DQ218814	DQ218946	DQ219123
<i>Aroramyces</i> sp.	RMS	S. Miller 10030	DQ218530	DQ218702	DQ218815	DQ218947	DQ219124
<i>Aroramyces</i> sp.	OSC	T15013	DQ218526	—	DQ218811	DQ218943	DQ219120
<i>Aroramyces</i> sp.	OSC	T9930	DQ218527	DQ218700	DQ218812	DQ218944	DQ219121
<i>Austrogautieria chlorospora</i>	OSC	46596	DQ218477	—	DQ218761	DQ218948	DQ219125
<i>Austrogautieria clelandii</i>	OSC	62178	DQ218531	—	DQ218816	DQ218949	DQ219126
<i>Austrogautieria manjimupana</i>	OSC	55900	DQ218533	—	DQ218818	DQ218951	DQ219128
<i>Austrogautieria</i> sp.	OSC	122637	DQ218534	—	DQ218819	DQ218955	DQ219132
<i>Austrogautieria</i> sp.	OSC	80139	DQ218479	DQ218654	DQ218763	DQ218953	DQ219130
<i>Austrogautieria</i> sp.	MELU	Beaton 66	DQ218535	—	DQ218820	—	DQ219133
<i>Austrogautieria</i> sp.	OSC	80140	DQ218480	DQ218655	DQ218764	DQ218954	DQ219131
<i>Castoreum</i> sp.	OSC	122814	DQ218536	—	DQ218821	DQ218956	DQ219134
<i>Chondrogaster angustisporus</i>	OSC	62041	DQ218537	DQ218703	DQ218822	DQ218957	DQ219135
<i>Chondrogaster pachysporus</i>	OSC	49298	DQ218538	DQ218704	DQ218823	DQ218958	DQ219136
<i>Gallacea dingleyae</i>	OSC	59606	DQ218539	DQ218705	DQ218824	DQ218959	DQ219137
<i>Gallacea eburnea</i>	OSC	59601	DQ218482	DQ218657	DQ218766	DQ218960	DQ219138
<i>Gallacea scleroderma</i>	OSC	59621	AY574645	AY574719	AY574787	DQ218961	DQ219139
<i>Gallacea</i> sp.	OSC	122813	DQ218543	DQ218709	DQ218829	DQ218966	DQ219144
<i>Gallacea</i> sp.	PDD	REB2364	DQ218540	DQ218706	DQ218825	DQ218962	DQ219140
<i>Gallacea</i> sp.	OSC	80855	—	DQ218707	DQ218827	DQ218964	DQ219142
<i>Gallacea</i> sp.	OSC	T25038	DQ218541	—	DQ218826	DQ218963	DQ219141
<i>Gummiglobus agglutinosporus</i>	OSC	58784	DQ218544	DQ218710	DQ218830	DQ218967	—
<i>Gummiglobus joyceae</i>	OSC	59485	DQ218488	DQ218663	DQ218772	DQ218968	—
<i>Hallingea purpurea</i>	OSC	Garido 418-A	DQ218545	—	—	DQ218969	DQ219145
<i>Hysterangium affine</i>	OSC	T6884	DQ218546	—	DQ218831	DQ218970	—
<i>Hysterangium aggregatum</i>	OSC	H4262	DQ218489	DQ218664	DQ218773	DQ218971	DQ219146
<i>Hysterangium album</i>	OSC	T15139	DQ218490	DQ218665	DQ218774	DQ218972	DQ219147
<i>Hysterangium aureum</i>	OSC	56988	DQ218491	DQ218666	DQ218775	DQ218973	DQ219148
<i>Hysterangium calcareum</i>	M	Gross 97	DQ218492	DQ218667	DQ218776	DQ218974	DQ219149
<i>Hysterangium cistophilum</i>	OSC	T1088	DQ218493	DQ218668	DQ218777	DQ218975	DQ219150
<i>Hysterangium clathroides</i>	MPU	Szemere 11- SEPT-1955	DQ218547	DQ218711	DQ218832	DQ218976	DQ219151
<i>Hysterangium coriaceum</i>	OSC	64939	AY574686	AY574759	AY574826	DQ218977	DQ219152
<i>Hysterangium crassirhachis</i>	OSC	58056	DQ218494	DQ218669	DQ218778	DQ218978	DQ219153
<i>Hysterangium crassum</i>	OSC	110447	AY574687	AY574760	AY574827	DQ218979	DQ219154
<i>Hysterangium epiroticum</i>	OSC	T6116	DQ218495	DQ218670	DQ218779	DQ218980	DQ219155
<i>Hysterangium fragile</i>	OSC	Kers 3971	DQ218496	DQ218671	DQ218780	DQ218981	DQ219156
<i>Hysterangium gardneri</i>	OSC	T6950	DQ218548	DQ218712	DQ218835	DQ218982	DQ219157
<i>Hysterangium hallingii</i>	OSC	Halling 5741	DQ218497	DQ218672	DQ218781	DQ218983	DQ219158
<i>Hysterangium inflatum</i>	OSC	H4035	DQ218549	—	DQ218836	DQ218984	DQ219159
<i>Hysterangium membranaceum</i>	OSC	T12836	DQ218498	DQ218673	DQ218782	DQ218985	DQ219160
<i>Hysterangium neotunicatum</i>	OSC	T15545	DQ218550	—	DQ218837	DQ218986	DQ219161
<i>Hysterangium occidentale</i>	OSC	47048	AY574685	AY574758	AY574825	DQ218987	DQ219162
<i>Hysterangium pompholyx</i>	OSC	Gross 495	DQ218499	DQ218674	DQ218783	—	DQ219163
<i>Hysterangium rugisporum</i>	OSC	59662	DQ218500	DQ218675	DQ218784	DQ218988	DQ219164
<i>Hysterangium rupticutis</i>	OSC	59667	DQ218551	DQ218713	DQ218838	—	—
<i>Hysterangium salmonaceum</i>	K	Beaton 33	DQ218501	DQ218676	DQ218785	DQ218989	DQ219165

SUPPLEMENTARY TABLE I. Continued

Genus species	Herbarium	Specimen No.	GenBank No.				
			nuc-LSU- rDNA	mt-SSU- rDNA	atp6	RPB2	EF-1 α
<i>Hysterangium separabile</i>	OSC	69030	DQ218502	DQ218677	DQ218786	DQ218990	DQ219166
<i>Hysterangium setchellii</i>	OSC	58071	DQ218552	—	DQ218839	DQ218991	DQ219167
<i>Hysterangium strobilus</i>	OSC	T5285	DQ218504	DQ218679	DQ218788	DQ218992	DQ219168
<i>Hysterangium youngii</i>	OSC	59645	DQ218505	DQ218680	DQ218789	DQ218993	DQ219169
<i>Hysterangium</i> sp.	OSC	AHF602	DQ218566	—	DQ218854	DQ219008	DQ219185
<i>Hysterangium</i> sp.	K	K. & G. Beaton	DQ218506	DQ218681	DQ218790	DQ218997	DQ219174
<i>Hysterangium</i> sp.	OSC	Garcia 3779	DQ218559	DQ218721	DQ218847	DQ219001	DQ219178
<i>Hysterangium</i> sp.	OSC	H2022	DQ218568	—	DQ218856	DQ219010	DQ219187
<i>Hysterangium</i> sp.	OSC	H4123	DQ218557	DQ218719	DQ218845	DQ218999	DQ219176
<i>Hysterangium</i> sp.	OSC	H4749	DQ218573	DQ218730	DQ218861	DQ219015	DQ219192
<i>Hysterangium</i> sp.	OSC	H5057	DQ218574	—	DQ218862	DQ219016	DQ219193
<i>Hysterangium</i> sp.	OSC	H5573	DQ218575	DQ218731	DQ218863	DQ219017	DQ219194
<i>Hysterangium</i> sp.	OSC	H6105	DQ218576	DQ218732	DQ218864	DQ219018	DQ219195
<i>Hysterangium</i> sp.	OSC	122859	DQ218571	—	DQ218859	DQ219013	DQ219190
<i>Hysterangium</i> sp.	OSC	122860	DQ218572	DQ218729	DQ218860	DQ219014	DQ219191
<i>Hysterangium</i> sp.	OSC	122836	DQ218577	—	DQ218865	DQ219019	DQ219196
<i>Hysterangium</i> sp.	OSC	122483	DQ218579	—	DQ218867	DQ219021	DQ219198
<i>Hysterangium</i> sp.	PDD	82853	DQ218580	DQ218734	DQ218868	DQ219022	DQ219199
<i>Hysterangium</i> sp.	RMS	S. Miller 10007	DQ218581	—	DQ218869	DQ219023	DQ219200
<i>Hysterangium</i> sp.	RMS	S. Miller 10100	DQ218582	DQ218735	DQ218870	DQ219024	DQ219201
<i>Hysterangium</i> sp.	RMS	S. Miller 10166	DQ218583	DQ218736	DQ218871	DQ219025	DQ219202
<i>Hysterangium</i> sp.	OSC	T13345	DQ218584	DQ218737	DQ218872	DQ219026	DQ219203
<i>Hysterangium</i> sp.	OSC	T17501	DQ218553	DQ218715	DQ218841	—	DQ219171
<i>Hysterangium</i> sp.	OSC	T17856	DQ218569	DQ218727	DQ218857	DQ219011	DQ219188
<i>Hysterangium</i> sp.	OSC	T19263	DQ218561	DQ218723	DQ218849	DQ219003	DQ219180
<i>Hysterangium</i> sp.	OSC	T26367	DQ218586	—	DQ218874	DQ219028	DQ219205
<i>Hysterangium</i> sp.	OSC	T27921	DQ218587	DQ218738	DQ218875	DQ219029	DQ219206
<i>Hysterangium</i> sp.	OSC	T3296	DQ218554	DQ218716	DQ218842	DQ218995	DQ219172
<i>Hysterangium</i> sp.	OSC	T3328	DQ218564	DQ218726	DQ218852	DQ219006	DQ219183
<i>Hysterangium</i> sp.	OSC	T4794	DQ218558	DQ218720	DQ218846	DQ219000	DQ219177
<i>Hysterangium</i> sp.	OSC	T591	—	DQ218714	DQ218840	DQ218994	DQ219170
<i>Hysterangium</i> sp.	OSC	T6889	DQ218570	DQ218728	DQ218858	DQ219012	DQ219189
<i>Hysterangium</i> sp.	OSC	T6923	DQ218567	—	DQ218855	DQ219009	DQ219186
<i>Hysterangium</i> sp.	OSC	T8997	DQ218588	—	DQ218876	—	DQ219207
<i>Malajczukia amicosum</i>	OSC	59295	DQ218508	DQ218683	DQ218792	DQ219030	DQ219208
<i>Malajczukia ingrattissima</i>	OSC	59296	DQ218509	DQ218684	DQ218793	DQ219031	DQ219209
<i>Mesophellia arenaria</i>	OSC	59306	DQ218589	—	DQ218877	DQ219032	DQ219210
<i>Mesophellia clelandii</i>	OSC	59292	DQ218511	DQ218686	DQ218795	DQ219033	DQ219211
<i>Mesophellia sabulosa</i>	OSC	55918	DQ218591	DQ218739	DQ218879	DQ219035	DQ219213
<i>Mesophellia trabalis</i>	OSC	59282	DQ218592	—	DQ218880	DQ219036	DQ219214
<i>Nothocastoreum cretaceum</i>	OSC	79832	DQ218593	—	DQ218881	—	DQ219215
<i>Nothocastoreum cretaceum</i>	OSC	79925	DQ218594	—	—	DQ219037	DQ219216
<i>Phallogaster saccatus</i>	OSC	T13202	DQ218595	DQ218740	DQ218882	DQ219038	DQ219217
<i>Protuberia hautuensis</i>	OSC	59673	DQ218517	DQ218692	DQ218801	DQ219039	DQ219218
<i>Protuberia nothofagi</i>	OSC	59699	AY574644	AY574718	AY574786	DQ219040	DQ219219
<i>Protuberia</i> sp.	OSC	T20068	DQ218596	—	DQ218883	DQ219041	DQ219220
<i>Trappea phillipsii</i>	OSC	56042	DQ218522	DQ218697	DQ218807	DQ219042	—
<i>Trappea pinyonensis</i>	OSC	AHF530	DQ218597	—	DQ218884	DQ219043	DQ219221

SUPPLEMENTARY TABLE I. Continued

Genus species	Herbarium	Specimen No.	GenBank No.				
			nuc-LSU- rDNA	mt-SSU- rDNA	atp6	RPB2	EF-1 α
Phallales clade							
<i>Anthurus archeri</i>	PDD	REB-2182	DQ218624	DQ218750	DQ218913	DQ219081	DQ219260
<i>Aseroe rubra</i>	OSC	122632	DQ218625	—	DQ218914	DQ219082	DQ219261
<i>Clathrus chrysomycelinus</i>	PDD	75096	DQ218626	—	DQ218915	DQ219083	DQ219262
<i>Clathrus ruber</i>	OSC	79910	—	—	DQ218916	DQ219084	—
<i>Claustula fischeri</i>	OSC	122661	—	—	—	DQ219085	DQ219263
<i>Claustula fischeri</i>	PDD	REB-2326	—	DQ218751	—	DQ219086	DQ219264
<i>Dictyophora duplicata</i>	OSC	38819	DQ218481	DQ218656	DQ218765	DQ219087	DQ219265
<i>Dictyophora indusiata</i>	OSC	36088	DQ218627	DQ218752	DQ218917	DQ219088	DQ219266
<i>Dictyophora multicolor</i>	MEL	1054289	DQ218628	DQ218753	DQ218918	DQ219089	DQ219267
<i>Gelopellis macrospora</i>	BAFC	30373	DQ218629	—	—	—	DQ219268
<i>Gelopellis</i> sp.	OSC	H4397	DQ218630	DQ218754	DQ218919	DQ219090	DQ219269
<i>Gelopellis</i> sp.	OSC	H4571	DQ218631	DQ218755	DQ218920	DQ219091	DQ219270
<i>Gelopellis</i> sp.	MEL	2063389	DQ218632	—	DQ218921	DQ219092	—
<i>Ileodictyon cibarium</i>	OSC	122734	DQ218633	DQ218756	DQ218922	DQ219093	—
<i>Ileodictyon gracile</i>	MEL	2024221	DQ218634	—	DQ218923	DQ219094	DQ219271
<i>Ileodictyon gracile</i>	MEL	2037639	DQ218635	DQ218757	DQ218924	DQ219095	DQ219272
<i>Ileodictyon gracile</i>	MEL	2054561	DQ218636	—	DQ218925	DQ219096	DQ219273
<i>Kjeldsenia aureispora</i>	OSC	56970	DQ218637	—	—	DQ219097	DQ219274
<i>Kobayasia nipponica</i>	OSC	122862	DQ218638	—	DQ218926	DQ219098	—
<i>Kobayasia nipponica</i>	OSC	122863	DQ218639	—	DQ218927	—	—
<i>Laternea triscapa</i>	OSC	122864	DQ218640	DQ218758	DQ218928	DQ219099	DQ219275
<i>Lysurus borealis</i>	OSC	39531	DQ218641	—	DQ218929	DQ219100	DQ219276
<i>Lysurus mokusin</i>	CUW	MB-02-012	DQ218507	DQ218682	DQ218791	DQ219101	DQ219277
<i>Mutinus elegans</i>	OSC	107657	AY574643	AY574717	AY574785	DQ219102	—
<i>Phallobata alba</i>	PDD	76197	DQ218642	—	DQ218930	DQ219103	DQ219278
<i>Phallus costatus</i>	CUW	MB-02-040	DQ218513	DQ218688	DQ218797	DQ219104	DQ219279
<i>Phallus hadriani</i>	OSC	107658	DQ218514	DQ218689	DQ218798	DQ219044	DQ219222
<i>Phallus ravenelii</i>	CUW	s.n.	DQ218515	DQ218690	DQ218799	DQ219105	DQ219280
<i>Phlebogaster laurisylvicola</i>	OSC	CUP1289	DQ218643	—	—	—	DQ219281
<i>Protuberata borealis</i>	OSC	OKM21898	DQ218516	—	DQ218800	DQ219106	DQ219282
<i>Protuberata canescens</i>	MEL	2063471	DQ218644	—	DQ218931	DQ219107	DQ219283
<i>Protuberata canescens</i>	MEL	2105035	DQ218645	DQ218759	DQ218932	DQ219108	DQ219284
<i>Protuberata clathroidea</i>	BPI	s.n.	DQ218646	—	—	DQ219109	DQ219285
<i>Protuberata jamaicensis</i>	OSC	T28248	DQ218647	DQ218760	DQ218933	DQ219110	DQ219286
<i>Protuberata maracuja</i>	OSC	Garido 2550-A	DQ218518	DQ218693	DQ218802	DQ219111	DQ219287
<i>Protuberata parvispora</i>	OSC	59689	DQ218648	—	DQ218934	DQ219112	DQ219288
<i>Protuberata sabulonensis</i>	OSC	T12737	DQ218649	—	DQ218935	DQ219113	DQ219289
<i>Protuberata</i> sp.	RMS	S. Miller 10143	DQ218650	—	DQ218936	DQ219114	DQ219290
<i>Protuberata</i> sp.	DUKE	JM 98/351	AF261555	—	DQ218937	—	DQ219291
<i>Simblum sphaerocephalum</i>	CUW	MB-02-016	DQ218521	DQ218696	DQ218806	DQ219115	—
<i>Trappea darkeri</i>	OSC	65085	DQ218651	—	DQ218938	DQ219116	DQ219292

^aThe Pennsylvania State University Mushroom Culture Collection.

^bSequences were obtained from Assembling the Fungal Tree of Life website (<http://aftol.org/data.php>).

SUPPLEMENTARY TABLE II. The results of the ancestral character state reconstructions of the fruiting body type for Phallales clade. i. Taxa with uncertain fruiting body type (? in FIG. 2, SUPPLEMENTARY FIG. 2) were coded as nonsequestrate. ii. Taxa with uncertain fruiting body type were coded as sequestrate

Character state	Ancestral states and $-\log L$								
	Node								
	A	B	C	D	E	F	G	H	I
[i]									
0 (= sequestrate)	5.012 ^d	4.720 ^d	4.189	5.608	5.221	10.486	4.881	4.021	4.161
1 (= nonsequestrate)	9.507	7.738	5.008	<0.001 ^d	<0.001 ^d	<0.001 ^d	<0.001 ^d	<0.001 ^d	<0.001 ^d
Probability ^a	0.989	0.989	0.962	0.070	0.002	<1.001	0.007	0.001	<0.001
Parsimony ^{b,c}	0	0	0	1	1	1	1	1	1
[ii]									
	Ancestral states and $-\log L$								
	Node								
	A	B	C	D	E	F	G	H	I
0 (= sequestrate)	19.765	19.374	18.662	18.357	11.287	17.946	7.756	4.475	2.428
1 (= nonsequestrate)	20.805	19.774	18.015	15.830 ^d	11.061	8.767 ^d	4.386 ^d	2.365 ^d	1.592
Probability ^a	0.739	0.745	0.634	0.330	0.403	<0.001	0.092	0.055	0.115
Parsimony ^b	0	0	0	E	E	1	1	1	1

^aProbabilities of state 0 (= sequestrate) obtained using the “testall” command of Multistate (Pagel 2003).

^bThe results from parsimony-based reconstruction using MacClade (Maddison and Maddison 2003); 0 = sequestrate, 1 = nonsequestrate, E = equivocal.

^cThe results were identical when taxa with uncertain fruiting body type were coded as polymorphic.

^dThe results were considered significant with a difference of two or more units in log-likelihood scores.

SUPPLEMENTARY TABLE III. The results of the ancestral character state reconstructions of the fruiting body type for Geastrales clade

Character state	Ancestral states and $-\log L$						
	Node						
	J	K	L	M	N	O	P
0 (= sequestrate)	10.788	8.763	8.168	7.541	6.872	1.982	1.998
1 (= nonsequestrate)	10.388	9.519	8.043	6.498	6.112	2.384	2.517
Probability ^a	0.401	0.588	0.576	0.222	0.136	0.198	0.159
Parsimony ^b	E	E	E	1	1	1	1

^aProbabilities of state 0 (= sequestrate) obtained using the “testall” command of Multistate (Pagel 2003).

^bThe results from parsimony-based reconstruction using MacClade (Maddison and Maddison 2003); 1 = nonsequestrate, E = equivocal.

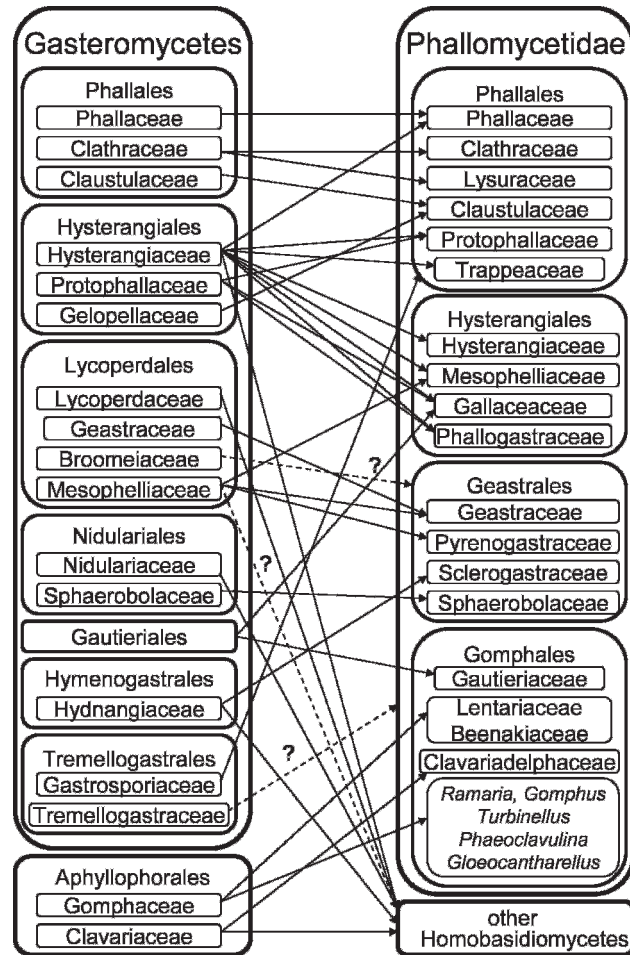
SUPPLEMENTARY TABLE IV. The results of the ancestral character state reconstructions of the fruiting body type for Gomphales clade

Character state	Ancestral states and $-\log L$					
	Node					
	Q	R	S	T	U	V
0 (= sequestrate)	10.505	10.377	9.282	6.258	3.601 ^c	<0.001 ^c
1 (= nongastroid)	7.278 ^c	6.733 ^c	6.504 ^c	6.300	6.279	10.613
Probability ^a	0.038	0.012	0.007	0.016	0.086	0.995
Parsimony ^b	1	1	1	1	1	0

^a Probabilities of state 0 (= sequestrate) obtained using the “testall” command of Multistate (Pagel 2003).

^b The results from parsimony-based reconstruction using MacClade (Maddison and Maddison 2003); 0 = sequestrate, 1 = nonsequestrate.

^c The results were considered significant with a difference of two or more units in log-likelihood scores.



SUPPLEMENTARY FIG. 1. Previous and new classification schemes for the representative gomphoid-phalloid fungi. Left: Classification schemes by Zeller (1949) for Gasteromycetes; by Donk (1964) for Aphylloporales. Right: Classification scheme based on this study. Taxa with dotted arrows and question marks are not included in this study. Multiple arrows arising from the single taxon indicate that the taxon as previously constituted was demonstrated to be polyphyletic.



SUPPLEMENTARY FIG. 2. Nodes used for the ancestral character state reconstructions of the fruiting body type. A. Phallales clade. B. Geastrales clade. C. Gomphales clade. Tree topology is from FIG. 3. The names of taxa and symbols correspond to those of FIG. 3. Polytomies in the Gomphales clade were arbitrarily resolved to bifurcations with branch lengths of 0.001.