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Perspectives in the new Russulales

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Abstract: The Russulales is one of 12 major lineages recently elucidated by molecular sequence data in the homobasidiomycetes. The order is morphologically most diverse, containing a remarkable variety of sporophore forms including resupinate, discoid, effused-reflexed, clavarioid, pileate, or gasteroid and hymenophore configurations from smooth, poroid, hydnoid, lamellate, to labyrinthoid. Functionally these fungi are primarily saprotrophs but others are ectomycorrhizal, root parasites and insect symbionts. A phylogenetic analysis of the nuclear 5.8S, ITS2 and large-subunit rDNA genes comprises the best information to date on relationships of taxa within the Russulales. Two large sister groups encompassing 11–13 major clades have been recovered within the Russulales. Based on molecular and morphological data 12 families and approximately 80 genera have been identified, although placement of many taxa has not yet been determined. The two clades containing ectomycorrhizal taxa, corresponding to the Russulaceae and the Albatrellaceae, represent the greatest diversity of sporophore morphologies. The primarily pileate lamellate family Russulaceae is nested with resupinate species and also contains pileate sequestrate, gasteroid annulate and pleurotoid forms. Albatrellaceae similarly contains resupinate poroid, pileate poroid and pileate labyrinthoid sporophores. Presence of gloeoplerous hyphae containing fluid that typically stains black in sulfoaldehyde compounds is a synapomorphy for the Russulales. Amyloid reactions in spore or hyphal walls that occur frequently throughout the Russulales often are perceived as an obvious synapomorphy but are inconsistent. Approaches including sequencing functional genes, analysis of gene expression and biochemical analysis across the entire order are needed.

Key words: fungi, homobasidiomycetes, russuloid

INTRODUCTION

Friesian concepts stressing macromorphological appearance of sporophores dominated classification systems in the homobasidiomycetes until the mid- to late 20th century. Before that time resupinate, agaric, coralloid and gasteromycete fungi were considered more closely related within each sporophore type and it was inconceivable that taxa with diverse sporophore morphologies could be classified together.

Donk (1971) recognized the possibility that the Hericiaceae was related to other basidiomycetes with a variety of sporophore types because these fungi all possess a system of gloeoplerous hyphae and amyloid ornamented spores. ''All these taxa may eventually be considered as part-chains of one big system without necessarily losing their status as distinct families,'' Donk said. ''They might appear to be members of one big order, but then certainly an order also containing quite a number of reduced species or genera in which the original, most prominent features chosen for its characterization have vanished.'' At about the same time Singer and Smith (1960) questioned the necessity of maintaining a separation between agarics and sequestrate or gasteroid taxa in the Hymenogastrales. Oberwinkler (1977) proposed the Russulales as an example of a closely knit group of fungi that included all possible types of sporocarps known among homobasidiomycetes. This concept has gained acceptance and underpins the classification used the Dictionary of Fungi (Kirk et al 2001).

Monophyly for the Russulales has been confirmed through DNA sequence analysis numerous times over the past decade (Hibbett and Donoghue 1995, Hibbett et al 1997, Bruns et al 1998, Hibbett and Binder 2002, Larsson and Larsson 2003, Larsson et al 2004, Binder et al 2005). Miller et al (2001) explored the molecular phylogeny of the agaricoid, gasteroid and pleurotoid taxa in the Russulales, now more appropriately called the Russulaceae. Larsson and Larsson (2003) provided a detailed study of russuloid aphyllophoralean taxa but included also representatives with most of the different sporophore morphologies. The goal of this paper is to present the most complete molecular data for the Russulales.

MATERIALS AND METHODS

Sampling of taxa for this analysis was guided by Miller et al (2001) and Larsson and Larsson (2003), recent sequencing efforts, and by sequence availability in GenBank. Taxon sampling included only OTUs with complete nLSU, 5.8s

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and ITS2 sequences. Sequence data from other gene regions were available for some taxa, however including these data would have resulted in an unacceptably large amount of missing data. Taxa sampled, GenBank accession numbers and morphological and cytological features, are provided (SUPPLEMENTARY TABLE I).

Molecular techniques and methods of phylogenetic analyses were essentially identical to those found in Miller et al (2001) and Larsson and Larsson (2003), and for the sake of brevity in this volume we direct the reader to those citations. The alignment for this study has been submitted to TreeBASE as No. SN3256. For discussion provisional names have been assigned to individual families, although these might not constitute formally valid names.

RESULTS AND DISCUSSION

Molecular analysis.—At present, based on molecular and morphological data, the Russulales comprises 12 families and approximately 80 genera (SUPPLEMENTARY TABLE II) and 4000 species worldwide. More than one-third of the species belong in two mainly pileate lamellate genera in the Russulaceae: *Russula* and *Lactarius*. Included in the 80 genera are many still poorly known fungi for which no sequence data are available and their placement in families has been difficult. Families include Albatrellaceae, Amylostereaceae, Auriscalpiaceae, Bondarzewiaceae, Echinodontiaceae, Gloeocystidiellaceae, Hericiaceae, Hybogasteraceae, Peniophoraceae, Russulaceae, Stereaceae and families containing *Aleurocystidiellum* and *Gloeodontia* that have not been described formally. Eleven to thirteen major well supported clades have been elucidated within the Russulales with 11 identified (FIG. 2). In a neighbor joining analysis Larsson and Larsson (2003) recovered a topology for the Russulales placing these major clades into two larger groups, the /peniophorales and the /eurussuloid clades, which could be considered suborders.

FAMILIES AND FAMILY CHARACTERISTICS

Peniophoraceae (bootstrap support 100%).—In the present analysis the Peniophoraceae, roughly equivalent to the /peniophorales recovered by Larsson and Larsson (2003), comprises primarily saprotrophic fungi with resupinate, discoid or clavarioid sporophores with smooth hymenophores (FIG. 1D, E) and weakly or nonamyloid spore walls. The insect symbiont *Entomocorticium* also has been tentatively placed here (Hsiau and Harrington 2003). The fresh sporophores can be monomitic or dimitic. Species that are dimitic typically are composed of or contain thick-walled dextrinoid dicho-, dendro- or asterohyphidia that are functionally equivalent to binding hyphae in the woody textured polypores. Some taxa form a typical palisade hymenium, while others form a catahymenium (Lemke 1964) where the basidia originate deeply within the thick-walled hyphidia and just reach the surface. These sporophores are adapted to resist drought and can quickly resume sporulation in favorable conditions. In the present study no clear topological break supported the /amylosteriaceae or /gloeocystidiellum II as separate from the Peniophoraceae. The remaining well supported clades corresponded to the /eurussuloid clade of Larsson and Larsson (2003).

Amylostereaceae (bootstrap support 100%).—The present analysis found strong support for the Amylostereaceae composed of three leathery effused-reflexed species with a smooth hymenophore. This differs dramatically from Larsson and Larsson (2003) who recovered a group composed of *Amylostereum* and *Artomyces*, which has a clavarioid sporophore. *Artomyces* in the present analysis was associated consistently with the Auriscalpiaceae, and this relationship has been observed in other molecular studies as well (Hibbett et al 1997, Hibbett et al 2000, Hibbett and Donoghue 2001).

Auriscalpiaceae (bootstrap support 65–90%).—The Auriscalpiaceae was erected by Maas Geesteranus (1963) to contain resupinate hydnoid (*Dentipratulum* and *Gloiodon*) and pileate hydnoid (*Auriscalpium*, FIG. 1A) taxa as well as pileate lamellate (both agaricoid and pleurotoid) taxa (*Lentinellus*, SUPPLEMENTARY FIGURE 1C). Most of the species with hydnoid hymenophores are moderately tough with dimitic hyphal systems and are sister to a clade containing the soft or slightly leathery *Lentinellus* spp., and it could be argued that these represent two closely related but distinct families.

The genus *Artomyces* (FIG. 1B) is composed of lignicolous, branched clavarioid taxa found throughout temperate regions of the northern hemisphere (Jülich 1981). A clade with several *Artomyces* species typically forms a sister clade with *Lentinellus*. If Artomyces is excluded from the clade support for the Auriscalpiaceae is 90%; if Artomyces is included bootstrap support falls to 65%.

Gloeodontia family (bootstrap support 100%).—The *Gloeodontia* family includes primarily resupinate fungi with tough dimitic hyphal systems and hydnoid hymenophores as well as at least one species with a monomitic hyphal system and smooth hymenophore. Dimitic taxa in the group have encrusted hyphoid cystidia, while this feature is lacking in the taxon with monomitic hyphal system.

The Aleurocystidiellum family (bootstrap support 100%).—The *Aleurocystidiellum* family has dimitic

FIG. 1. A–J. Sporophore morphology and hymenophore types in the Russulales. A. Pileate hydnoid sporophores of *Auriscalpium vulgare.* 2×. Photo courtesy Taylor F. Lockwood©. B. Clavarioid smooth sporophore of *Artomyces pyxidata.* 0.5×. Photo courtesy Taylor F. Lockwood©. C. Effused-reflexed smooth sporophores of *Stereum ostrea*, 3 oh tjv. 0.3×. Photo courtesy Tom Volk, University of Wisconsin at La Crosse. D. Discoid smooth sporophores of *Peniophora rufa*, sew Perot2. 0.5×. Photo

species with discoid sporophores and large verrucose amyloid spores. The prospective family has only two species and thus far shows no clear relationship to other clades.

Bondarzewiaceae and Echinodontiaceae (bootstrap support 70–100%).—*Bondarzewia*, *Heterobasidion* (SUPPLEMENTARY FIGURE 1E), *Laurilia* and *Echinodontium* frequently cluster together into a clade that has been circumscribed variously as the Bondarzewiaceae or the Echinodontiaceae. In the present analysis *Bondarzewia*, which includes species with dimitic pileate poroid sporophores, is separated from *Heterobasidion*, *Laurilia* and *Echinodontium* that form trimitic resupinate smooth, effused reflexed poroid, or pileate hydnoid sporophores, thus supporting both the Bondarzewiaceae (100% bootstrap support) and the Echinodontiaceae (90% bootstrap support). This placement also was recovered by Hibbett et al (1997). Others have found that *Bondarzewia* and *Heterobasidion* cluster together but are always separated from *Echinodontium* (Hibbett et al 2000, Hibbett and Donoghue 2001, Binder and Hibbett 2002, Hibbett and Binder 2002).

All species in this group cause a severe white rot, and *Bondarzewia berkeleyi*, *Echinodontium tinctorium* and *Heterobasidion annosum* can attack living trees. As indicated previously the biology of *H. annosum* is interesting because it has been observed both to have a mycorrhiza-like relationship with roots as well as being a devastating root pathogen (Stalpers 1996). Stalpers (1979) compared characteristics of *Heterobasidion* and *Bondarzewia* and found that both had amyloid ornamented basidiospores, absence of clamp connections in sporophores, a *Spiniger*-like anamorph, a parasitic habit, the production of laccase and a white rot. Based on these similarities Stalpers (1979) reduced both the Echinodontiaceae and the Amylariaceae into synonomy with the Bondarzewiaceae, and included *Amylaria*, a tropical genus with clavarioid sporophores, *Bondarzewia*, *Echinodontium*, *Heterobasidion*, *Laurilia* and *Wrightoporia* in the family. Judging from the molecular analyses *Wrightoporia* is a heterogeneous assemblage and the type species, *W. lenta*, shows no affinity to the other genera mentioned.

Singer (1975) placed the Bondarzewiaceae in the Agaricales because of a perceived alliance to *Lactarius* (SUPPLEMENTARY FIGURE 1A). Latex has been documented in *Bondarzewia mesenterica* (Redhead and Norvell 1993) and in reconstructing the taxonomic history surrounding *Bondarzewia* these authors highlighted the pivotal nature of *Bondarzewia* in leading taxonomists to accept the heretofore difficult linkages between the Bondarwewiaceae, Auriscalpiaceae and Russulaceae.

Stereaceae (bootstrap 100%).—The Stereaceae comprise species causing a white rot on hardwood and conifer trees. The effused-reflexed or discoid sporophores with smooth hymenophore often are produced in great numbers on dead but still attached branches and trunks of living trees. The leathery consistency in *Stereum* (FIGS. 1C; SUPPLEMENTARY FIGURE 1D, F) and catahymenium in *Aleurodiscus* have been interpreted as adaptations for resisting drought, as has been demonstrated in the Peniophoraceae.

Hericiaceae (bootstrap support 90–100%).—The Hericiaceae is composed of the well known choice edible genus *Hericium* with clavarioid sporophore (or pileate sporophore and hydnoid hymenophore), *Dentipellis* with effused-reflexed sporophore and hydnoid hymenophore and *Laxitextum* with effused-reflexed sporophore and smooth hymenophore. All are saprotrophic or parasitic and cause a white-rot. Spores and tissues in this family are largely amyloid (SUPPLEMENTARY FIGURE 3E, F). The genus *Hericium* alone has a bootstrap support of 100%, whereas including *Dentipellis* and *Laxitextum* results in a clade with 90% bootstrap support.

Gloeocystidiellaceae (bootstrap support 100%).—Larsson and Larsson (2003) identified two widely separated clades containing primarily *Gloeocystidiellum* species. In addition they found species that have been widely accepted in *Gloeocystidiellum* spread across at least seven of their well supported clades. Based on close relationships with species from other genera within clades they recommended several new combinations for several taxa. Bootstrap for the small clade containing the type of the genus is 100%.

Russulaceae (bootstrap support 100%).—The Russulaceae includes members with the most diverse sporophore morphology of any group, ranging from resupinate to pileate with poroid, lamellate (non-annulate, annulate and pleurotoid), and gasteroid

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courtesy Volk. E. Resupinate (= effused or corticioid) smooth sporophores of *Variaria investiens*, 2 ch WI tjv. 0.2×. Photo courtesy Volk. F. Pileate lamellate (= agaricoid) sporophores of *Russula discopus*, SLM 00-640. 0.5×. Additional photographic plates representing morphological diversity and microscopic features of the Russulales are available as SUPPLEMENTAL DOCUMENTS III, IV and V.

hymenophores (FIG. 1F; SUPPLEMENTARY FIGURE 1A, B). Their habits including ectomycorrhizal (*Russula*, *Lactarius* and sequestrate taxa) and putative wood-decaying species.

A synapomorphy for the pileate lamellate and labyrinthioid taxa in the Russulaceae is the presence of sphaerocytes, also known as ''sphaerocysts'' (Hawksworth et al 1995). These are large, isodiametric cells in the pileus, lamellar and stipe trama (SUPPLEMENTARY FIGURE 3K, L). The presence of sphaerocytes gives a gradation of fragility to the texture of most species of *Russula* and *Lactarius*, depending on the stage of development and the relative number of sphaerocytes present. It is interesting that sphaerocytes occur in this group of fungi and apparently nowhere else in the Russulales.

The pileus, stipe and frequently lamellar trama of members of the Russulaceae are called heteromerous because of the presence of sphaerocytes as well as cylindrical hyphae (SUPPLEMENTARY FIGURE 3K). The sphaerocytes frequently occur in clusters, known as nests or rosettes, which are formed in the mushroom primordia (SUPPLEMENTARY FIGURE 3L). Formation of the rosettes begins at the center of the pileus trama before the hymenium is developed and at the base of the stipe where they are arranged in columns (Reijnders 1976). Primary rosettes originate as a circle of small sphaerocytes around a central inductive hypha (SUPPLEMENTARY DOCUMENT VL). The inductive hypha degenerates quickly and frequently is difficult to observe.

Verbeken (1996) contrasted the development of sphaerocytes in *Russula* and *Lactarius* by observing that the complexes of sphaerocytes in *Lactarius* are composed mostly of only one primary rosette, while in *Russula* several primary rosettes agglomerate, resulting in much larger complexes of sphaerocytes. This difference in the number of sphaerocytes has been used as a key character in assigning new or unknown species to either *Lactarius* or *Russula*; however Henkel et al (2000) found this distinction tenuous in many tropical species. A more reliable difference is the presence of pseudocystidia in *Lactarius* and their absence in *Russula*.

The mainly tropical pleurotoid species in *Lactarius* and *Russula* originally were thought to be lignicolous, functioning either as deadwood decomposers or as parasites of living trees (Singer 1952, 1984; Dennis 1970; Pegler and Fiard 1979; Redhead and Norvell 1993; Verbeken 1998). This presumption was based on the observation that these fungi fruited from elevated positions on tree trunks and other woody substrates. However Henkel et al (2000) and Miller and Henkel (2004) matched sequences of sporophores of pleurotoid species of *Russula* and *Lactarius* with ectomycorrhizae found beneath the decorticated bark of standing trees and buried in well rotted wood, indicating that they were ectomycorrhizal and not wood decomposers. It should be noted that agaricoid representatives of *Lactarius* and *Russula* also can be observed to grow on wood while they have an ectomycorrhizal nutritional mode.

The reported saprotrophic nature of several resupinate taxa with amyloid ornamented spores that are sister to *Russula* and *Lactarius*, such as *Gloeocystidiellum* (*Boidinia*) *aculeatum*, *Gloeopeiophorella laxum* and *G. convolvens*, can be questioned. Gardes and Bruns (1996) and Lilleskov and Bruns (2005) have shown that basidiomycetes with frequently overlooked resupinate basidiomes can be important ectomycorrhizal symbionts.

Annulate species of *Russula* (FIG. 1F) and *Lactarius* as well as sequestrate forms, such as *Macowanites* (SUPPLEMENTARY FIGURE 3B), *Gymnomyces*, *Cystangium*, *Arcangeliella* and *Zelleromyces*, have been considered wildly different from agarioid species (Heim 1938, Singer and Smith 1960). However the present analysis, as well as Miller et al (2001), found that both annulate and gasteroid taxa were nested within established infrageneric taxa in both *Russula* and *Lactarius*, indicating multiple origins for the presence of an annulus and secotioid sporophores. The opinion on whether to include gasteroid and secotioid taxa in agaricoid genera is very differently approached by different authors. Recently some gasteroid species are described in the genus *Lactarius* (Desjardin 2003, Nuytinck et al 2003, Eberhardt and Verbeken 2004) and some of the known gasteroid taxa are conspecific with existing species of *Russula* and *Lactarius* (Martin et al 1999).

Albatrellaceae (bootstrap support 100%).—The genus *Albatrellus* (SUPPLEMENTARY FIGURE 2E) was shown by Bruns et al (1998) and Hibbett and Binder (2002) to be polyphyletic with some species related to the Polyporales and some closely aligned with the Russulales. The species of *Albatrellus* with relationships within the Russuloid clade form pileate poroid sporophores that are ectomycorrhizal with conifer trees (Agerer et al 1996, Ryvarden and Gilbertson 1986).

The taxonomic affinities of the pileate sequestrate taxa *Leucogaster*, *Leucophleps* and *Mycolevis* have long been a mystery. In the present analysis the clade containing *Albatrellus* also included additional resupinate poroid taxa such as *Byssoporia terrestris* (SUPPLEMENTARY FIGURE 2D) and the pileate poroid *Polyporoletus sublividus* (SUPPLEMENTARY FIGURE 2B–C), as well as *Mycolevis*, *Leucogaster* (SUPPLEMENTARY FIGURE 2A) and possibly *Leucophleps* (SUPPLEMENTARY

FIGURE 2E). A relationship between *Albatrellus* and *Byssoporia* also was recovered by Bruns et al (1998) using the mitochondrial LSU gene. Spores of *Leucophleps* and *Mycolevis* are unusual, being spiny with the spines embedded in an amyloid gel that readily dissipates in many mounting media (Fogel 1976). The spores of *Leucogaster* (SUPPLEMENTARY FIGURE 3J) are alveolate and enclosed in a separable perisporal sac and are unique in comparison to other sequestrate basidiomycetes (Fogel 1979).

The finding that *Polyporoletus* resides in this clade partially solves this mystery. Gilbertson and Ryvarden (1987) described the spores of *P. sublividus* as being ''ellipsoid, hyaline, appearing slightly rough, with a double wall separated by interwall pillars or partitions, the outer walls and pillars apparently sloughing off … quite unlike those of any other polypore.'' The spores of *Polyporoletus*, *Leucogaster* and *Leucophleps* therefore share many similarities but are not necessarily similar to species of *Albatrellus*, at least with inspection at the level of the light microscope. It might be speculated that examination of the spores with TEM and SEM will reveal similarities in tegumentation and cryptic ornamentation. All these taxa have been considered ectomycorrhizal or putatively ectomycorrhizal.

Poorly resolved taxa.—A number of other fungi in this analysis apparently were not closely related to any of the other taxa and ended up on terminal branches (FIG. 2). Larsson and Larsson (2003) suggested that, due to the possible influence of long branch problems, placement of these taxa must be approached with caution. Sampling of additional, putatively closely related taxa and creation of multigene phylogenies will be required to finally determine the affinities of these fungi. Another poorly known group, the Hybogasteraceae, is a monotypic family with *Hybogaster* as the sole genus. Singer (1964) described *Hybogaster* as a gasteroid polypore with amyloid basidiospores from the tropics. Although this genus has been mentioned many times in the literature it has been rarely, if ever, observed since the original collection, and no sequences exist for this elusive genus.

SYNAPOMORPHIES

A number of characters have been recognized as synapomorphies in the Russulales, including sporophore morphology, gloeopleurous systems and amyloid spores.

Sporophore morphology.—One of the hallmarks of the Russulales is the extensive morphological diversity in sporophore and hymenophore morphology (FIG. 1), yet little information is available on the biology or forces acting on evolution of sporophore morphology in this group. Miller (1971) found that *Lentinellus cochleatus* produced coralloid sporophores when fruited in culture at low temperatures. R.H. Petersen in the discussion after the Miller (1971) chapter reported that when *Sparassis crispa* was grown in culture a completely fertile layer of basidia was produced, resembling many of the resupinate species in the Russulales.

Using a molecular approach Hibbett and Binder (2002) examined the evolution of complex fruiting-body morphologies in homobasidiomycetes. Their ancestral state reconstruction based on binary characters showed that the ancestor of the homobasidiomycetes was likely resupinate and that there have been multiple gains and losses of complex forms in the homobasidiomycetes. Their models of morphological evolution indicated that the rate of transformations from simple to complex forms is about 3–6 times greater than the rate of transformations from complex to simple sporophore forms, suggesting to them that there was a driven trend toward evolution of complex forms in the homobasidiomycetes. However, using a multistate coding approach, Hibbett (2004) found that there is an active trend favoring the evolution of pileate-stipitate forms and that crustlike resupinate forms are not a particularly labile morphology, which contradicts the conclusions of the earlier study (Hibbett and Binder 2002).

Largely because the fungi in the Russulales are placed in the homobasidiomycetes, researchers have assumed that all sporophores are equatable to basidiomes and function to produce and deliver meiospores, namely basidiospores. However Stalpers (1996) pointed out that several fungi in the Russuloid clade (Bondarzewiaceae or Echinodontiaceae) produce an anamorphic stage including *Bondarzewia*, *Heterobasidion*, *Laurilia* and *Dichostereum*. The anamorph is known under the genus *Spiniger* (Stalpers 1974) and is characterized by clavate to rarely cylindrical sporophores (conidiophores) bearing blastic conidia on the apex, arising simultaneously from conical to cylindrical denticles similar to sterigmata. Stalpers (1987) contrasted development of the conidiophores of *Spiniger* with basidiospores and found that the shape of the anamorph is close to that of basidiospores; *Bondarzewia mesenterica* has globose basidiospores and conidia, *Heterobasidion annosum* has broadly ellipsoid spores and ovoid to pyriform conidia and *Laurilia sulcata* has subglobose basidiospores and ovoid to narrowly pyriform conidia. Petersen (1995) also reported several homobasidiomycetes that produce mitospores in what would appear otherwise normal ''basidiomata.''

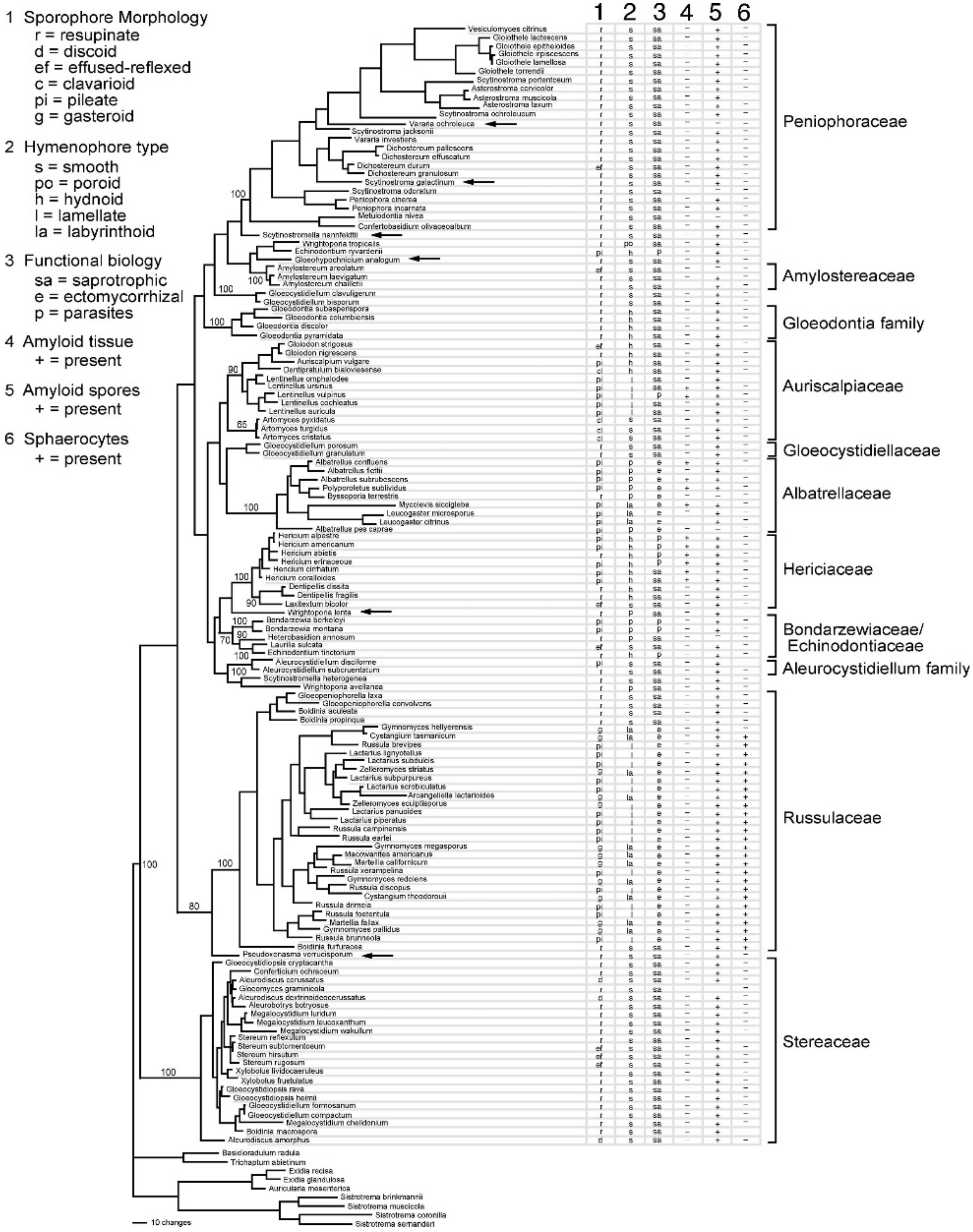

FIG. 2. Phylogeny of the Russulales inferred from unweighted parsimony analysis of 5.8S, ITS2 and nLSU nuclear rDNA sequence data. Best (-ln likelihood) of 6045 equally parsimonious trees depicted as a phylogram (tree length 3452, CI = 0.3002, RI = 0.7297). Families or prospective families are indicated with the brackets at the right. Individual taxa of uncertain placement are indicated with arrows. Characters mapped onto the phylogeny include sporophore morphology, hymenophore

Gloeoplerous system.—One of the good synapomorphies for the Russulales is the presence of a gloeoplerous hyphal system in the trama, hymenium, cuticle and even in cultured mycelium (Larsson and Larsson 2003) and the ectomycorrhizal sheath (Eberhardt 2000). Our knowledge of the gloeoplerous system in the Russulales and our ability to precisely use this information in a systematic fashion remains difficult for several reasons. One reason is imprecise usage of the terms and staining reactions used to distinguish the different types of gloeoplerous elements. The vascular or conducting nature of these hyphae was assumed because of the similarity of their appearance to the latex bearing lactifers found in plants. Fayod (1889) described two types of vascular hyphae, oleiferous vessels and laticiferous vessels. This was an early attempt to distinguish the fluid containing hyphae in *Russula* and *Lactarius* from other refractive or clear ''vascular'' hyphae found in many mushroom genera. In the Agaricales Singer (1975) distinguished five types of laticiferous hyphae, including ''lactifers'' and ''oleiferous hyphae''. Lactifers contain latex or are at least analogous to lactifers in plants, the fluid being a composite emulsion made up of several compounds. The oleiferous hyphae contain resinous substances that present an acrid flavor to the tissue, according to Singer. Romagnesi (1985) recognized two types of lactifers in *Russula*, one with a homogenous yellowish and oily content, similar to hyphae found in several other types of mushrooms, and another type with contents similar to that found in the macrocystidia of *Russula* and *Lactarius*. Stalpers (1996) defined 10 terms in connection with the gloeoplerous system. Clémençon et al (2004), in an attempt to add precision to the definitions, proposed the term secretional hyphae to replace vascular hyphae and found through the use of a variety of differential staining techniques that oleiferous hyphae did not contain oily material. He subsequently introduced the term ''thrombopleres''.

The primary means for distinguishing among the various types of gloeoplerous elements is differential staining. A variety of stains have been used, including general cytoplasmic stains and a plethora of putatively specific stains whose actions have been correlated with specific types of contents. Stearyl-velutinal has been shown to be responsible for the dark blue reaction of gloeoplerous elements when treated with sulfovanillin (Camazine and Lupo 1984), for example. Many of the stains are sulfoaldehyde compounds, such as sulfovanillin, sulfoformalin and sulfobenzaldehyde, that appear to indicate a variety of different hyphal contents (cf. SUPPLEMENTARY FIGURE 3B, C). However formulations and protocols for these stains are numerous, leading to confusion and frustration with their use and interpretation.

Relatively little is known regarding the chemical composition of the fluid present in the gloeoplerous hyphae across the Russulales, despite isolation of a number of novel compounds in the past decade. Many of the described compounds are sesquiterpenes with lactarane skeletons (Hansson and Sterner 1991). These compounds are largely cytotoxic and unstable, changing form rapidly upon disruption. Similar microscopic changes also have been noted by Verbeken (1997), who found that fresh latex from *Lactarius* appears as an emulsion containing numerous small guttules but upon drying changes into a dense mass of crystals. Staining reactions also are different in fresh and dried specimens. Larsson and Larsson (2003) discussed three categories of staining reactions in the Russulales. In most taxa the gloeoplerous system gives a positive reaction with sulfobenzaldehyde; in others it reacts positive only when fresh but loses this reaction after some period of storage, and some taxa never give a positive reaction. They suggested that sequence analysis and morphological features supported the hypothesis that all gloeoplerous systems within the Russulales are homologous.

Last there remains no clear consensus as to the function of these elements. Based on the chemistry of the fluid contained in hyphae from *Lactarius velutinus*, Camazine and Lupo (1984) suggested that the laticiferous hyphae functioned as a storage depot for precursors of pungent dialdehyde compounds. These compounds are largely unstable and change rapidly from nontoxic to toxic form, leading to the hypothesis that they are chemical defensive agents protecting the spore-producing structures from mycophagy.

Amyloidity.—Amyloidity, the dark blue to black staining of basidiospores or tissues in iodine reagents such as Melzer's solution, has been used as a taxonomic character in fungi for nearly 150 y (Dodd and McCracken 1972) and along with the gloeoplerous system has been used to identify members of the Russulales. Donk (1964) used amyloidity as a major character to unify what were at that time fairly

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type, life strategy, amyloidity of tissues, amyloidity of spores and presence or absence of sphaerocytes. Genera and family information is available in table format as SUPPLEMENTARY TABLE I. Character information is available in table format as SUPPLEMENTAL TABLE II.

disparate hydnoid, clavarioid and thelephoroid taxa into the aphyllophoralean family Hericiaceae. He also used amyloidity to infer relationships of the pileate lamellate genus *Lentinellus* and pileate poroid genus *Bondarzewia* to the Hericiaceae. Largely because of the relative importance and recognizability of the genera *Russula* and *Lactarius*, which are characterized by amyloid reticulate or warted basidiospores (SUPPLEMENTARY FIGURE 3H–I), the general view is that amyloidity is a synapomorphy for the Russulales. However the utility of visual observations of color change in iodine reagents as a synapomorphy is unresolved.

One strong argument against amyloidity as a synapomorphy is that it is a common phenomenon among homobasidiomycetes. Amyloid spore ornamentation is reported in 35 genera of the Agaricales (Singer 1975) and at least 20 genera of the Aphyllophorales (Donk 1964). Likewise, as Larsson and Larsson (2003) point out, within the Russulales the genus *Peniophora* lacks an amyloid reaction entirely while other genera (e.g. *Scytinostroma* and *Albatrellus*) contain both amyloid and nonamyloid species. Despite the occurrence of amyloidity in other groups, however, it might be unwise to dismiss amyloidity as a synapomorphy for the Russuloid clade altogether. In our analysis, of the 133 ingroup taxa for which we have sequence data, only 11 lack either an amyloid reaction of the spores or tissues or both. Reliance solely on color reactions, either macroscopic or microscopic, for detection of structural materials in spores and hyphae is an outdated approach unlikely to satisfactorily elucidate important biological functions. Exploration of the specific basis of amyloidity might be highly fruitful from a systematic perspective.

McCracken and Dodd (1971) and Dodd and McCracken (1972) first explored the chemical basis for the amyloid reaction. They traced the amyloid reaction in fungi to interactions of iodine with a short, straight-chained a-1,4 glucosidic-linked polysaccharide, namely the amylose form of starch. The presence of amylose in fungi is unusual for several reasons. In plants starch is considered to be a storage carbohydrate, whereas in fungi, amylose is primarily a structural cell (or spore) wall component. In plants the starch is primarily granular in nature and a mixture of amylose and amylopectin with much greater branching and subsequent higher molecular weight, whereas starch in fungi consists only of short-chained amylose. More recent studies have employed modern biochemical techniques to identify iodine staining compounds in fungi. Blackwell et al (2001) speculated that glycine betain, a compound found in fungi, and likely the material causing the dextrinoid (red) reaction in Melzer's reagent, might be an important osmolyte functioning to increase water activity in rapidly developing sporophores of polypores and agarics. De Gussem et al (2005), using Raman spectroscopy on *Lactarius* spores, which are strongly amyloid in Melzer's reagent, surprisingly determined that amylopectin is present in considerable amounts while amylose is at most present in very small amounts.

Future challenges.—Although the Russulales is comparatively well studied by molecular methods, many challenges remain. DNA sequences have been obtained only for relatively few species across the order. Many genera such as *Vararia* and *Stereum* are composed of many closely related species and the vast majority of them have not been sequenced. Likewise whole genera, such as *Hybogaster*, critical to our complete understanding of relationships in this group, have never been sequenced. To a large extent, homobasidiomycete systematists have accomplished the easy work of sampling and sequencing broadly across the Russulales with relatively few genes and few exemplar taxa compared to the diversity present in the order. The technology for sequencing has improved to the point where we now can easily generate multiple gene phylogenies. However, as important as molecular (DNA) approaches are to understanding evolutionary relationships in the Russulales, we cannot stop at sequencing. The hard work that lies ahead will be in documenting the diversity within each clade and deriving an appropriate and usable taxonomy.

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Supplementary Table I. Characteristics in the Russulales

	FB morph	Hym type	Biology	Amyloid tissue	Amyloid spor	Sphaerocytes
Albatrellus_confluens [Vamp101] [AF506393]	Pileate	Poroid	Ectomycorrhizal	+	+	−
Albatrellus_flettii [398IF62+398LS69]	Pileate	Poroid	Ectomycorrhizal	−	+	−
Albatrellus_pes_caprae [Vamp153][AF506394]	Pileate	Poroid	Ectomycorrhizal	−	−	−
Albatrellus_subrubescens [Vamp154][AF506395]	Pileate	Poroid	Ectomycorrhizal	+	+	−
Aleurobotrys_botryosus [T_637][AF506398]	Resupinate	smooth	Saprotrophic	−	+	−
Aleurocystidiellum_disciforme [2690_3][AF506402]	Resupinate	smooth	Saprotrophic	−	+	−
Aleurocystidiellum_subcruentatum [2615][AF506403]	Resupinate	smooth	Saprotrophic	−	+	−
Aleurodiscus_amorphus [KHL4240][AF506397]	Discoid	smooth	Saprotrophic	−	+	−
Aleurodiscus_cerussatus [2350][AF506399]	Discoid	smooth	Saprotrophic	−	+	−
Aleurodiscus_dextrinoideocerussatus [EL25][AF506401]	Discoid	smooth	Saprotrophic	−	+	−
Amylostereum_areolatum [1080][AF506405]	Effused-reflexed	smooth	Saprotrophic	−	+	−
Amylostereum_chailletii [1035][AF506406]	Resupinate	smooth	Saprotrophic	−	+	−
Amylostereum_laevigatum [2590][AF506407]	Resupinate	smooth	Saprotrophic	−	+	−
Arcangeliella_lactarioides [390IS61+LSU]	Pileate	Labyrinthioid	Ectomycorrhizal	−	+	+
Artomyces_cristatus [AF454421]	Clavarioid	smooth	Saprotrophic	−	+	−
Artomyces_pyxidatus [KGN941004][AF506] not RD818?!! not in GB?	Clavarioid	smooth	Saprotrophic	−	+	−
Artomyces_turgidus [AF454403]	Clavarioid	smooth	Saprotrophic	−	+	−
Asterostroma_cervicolor [KHL9239][AF506408]	Resupinate	smooth	Saprotrophic	−	+	−
Asterostroma_laxum [EL33.99][AF506410]	Resupinate	smooth	Saprotrophic	−	+	−
Asterostroma_muscicola [KHL9573][AF506409]	Resupinate	smooth	Saprotrophic	−	+	−
Auriscalpium_vulgare [2604][AF506375]=EL33-95?	Pileate	Hydnoid	Saprotrophic	−	+	−
Boidinia_aculeata [1485LSU]	Resupinate	smooth	Saprotrophic	−	+	−
Boidinia_furfuracea [JS16717][AF506376]	Resupinate	smooth	Saprotrophic	−	+	−
Boidinia_macrospora [2791][AF506377]	Resupinate	smooth	Saprotrophic	−	+	−
Boidinia_propinqua [KHL10931][AF506379]	Resupinate	smooth	Saprotrophic	−	+	−
Bondarzewia_berkeleyi [AF218563]	Pileate	Poroid	Parasitic	−	+	−
Bondarzewia_montana [DQ234539]	Pileate	Poroid	Parasitic	−	+	−
Byssoporia_terrestris [Hjm18172 not in GenBank]	Resupinate	Poroid	Ectomycorrhizal	−	−	−
Conferticium_ochraceum [1516][AF506383]	Resupinate	smooth	Saprotrophic	−	+	−
Confertobasidium_olivaceoalbum [Fp90196][AF511648]	Resupinate	smooth	Saprotrophic	−	+	−
Cystangium_tasmanicum [SLM46I83 - T14439]	Pileate	Labyrinthioid	Saprotrophic	−	+	−
Cystangium_theodorouii [SLM43I84 - H6145]	Pileate	Labyrinthioid	Saprotrophic	−	+	−
Dentipellis_dissita [581][AF506386]	Resupinate	Hydnoid	Saprotrophic	−	+	−
Dentipellis_fragilis [1755][AF506387]	Resupinate	Hydnoid	Saprotrophic	−	+	−
Dentipratulum_bialoviesense [G1645][AF506389]	Clavarioid	Hydnoid	Saprotrophic	−	+	−
Dichostereum_durum [1985F.Gallici][AF506429]	Effused-reflexed	smooth	Saprotrophic	−	+	−
Dichostereum_effuscatum [Gille930915][AF506390]	Resupinate	smooth	Saprotrophic	−	+	−
Dichostereum_granulosum [6961][AF506391]	Resupinate	smooth	Saprotrophic	−	+	−
Dichostereum_pallescens [673][AF506392]	Resupinate	smooth	Saprotrophic	−	+	−
Echinodontium_ryvardenii [LR43370][AF506431]	Pileate	Hydnoid	Parasitic	−	+	−

SUPPLEMENTARY TABLE I. Continued

	FB morph	Hym type	Biology	Amyloid tissue	Amyloid spor	Sphaerocytes
Echinodontium_tinctorium [500][AF506431]	Pileate	Hydnoid	Parasitic	−	+	−
Gloeocystidiellum_bisporum [KHL11135][AY048877]	Resupinate	smooth	Saprotrophic	−	+	−
Gloeocystidiellum_clavuligerum [2159][AF310088]	Resupinate	smooth	Saprotrophic	−	+	−
Gloeocystidiellum_compactum [2648][AF506434]	Resupinate	smooth	Saprotrophic	−	+	−
Gloeocystidiellum_formosanum [2651][AF506439]	Resupinate	smooth	Saprotrophic	−	+	−
Gloeocystidiellum_granulatum [2649][AF048880]	Resupinate	smooth	Saprotrophic	−	+	−
Gloeocystidiellum_porosum [1933][AF310094]	Resupinate	smooth	Saprotrophic	−	+	−
Gloeocystidiopsis_cryptacantha [KHL10334][AF506442]	Resupinate	smooth	Saprotrophic	−	+	−
Gloeocystidiopsis_heimii [2652][AF506381]=CBS321.66?	Resupinate	smooth	Saprotrophic	−	+	−
Gloeocystidiopsis_rava [Nisse][AF506382]=NH13291?	Resupinate	smooth	Saprotrophic	−	+	−
Gloeodontia_columbiensis [2133][AF506444]	Resupinate	Hydnoid	Saprotrophic	−	+	−
Gloeodontia_discolor [KHL10099][AF506445]	Resupinate	Hydnoid	Saprotrophic	−	+	−
Gloeodontia_pyramidata [LR15502][AF506446]	Resupinate	Hydnoid	Saprotrophic	−	+	−
Gloeodontia_subasperispora [KHL8695][AF506404]	Resupinate	Hydnoid	Saprotrophic	−	+	−
Gloeohypochnicium_analogum [NH12140][AF506447]	Resupinate	smooth	Saprotrophic	−	−	−
Gloeomyces_graminicola [2650][AF506448]	Resupinate	smooth	Saprotrophic	−	−	−
Gloeopeniophorella_convolvens [KHL10103][AF506435]	Resupinate	smooth	Saprotrophic	−	+	−
Gloeopeniophorella_laxa [2645][AF506440]	Resupinate	smooth	Saprotrophic	−	+	−
Gloiodon_nigrescens [Desj7287][AF506450]	Resupinate	Hydnoid	Saprotrophic	−	+	−
Gloiodon_strigosus [JS26147][AF506449]	Effused-reflexed	Hydnoid	Saprotrophic	−	+	−
Gloiothele_epitheloides [2656][AF506487]=CBS404.83?	Resupinate	smooth	Saprotrophic	−	+	−
Gloiothele_irpiscescens [LR35533][AF506452]	Resupinate	smooth	Saprotrophic	−	+	−
Gloiothele_lactescens [EL8.98][AF506453]	Resupinate	smooth	Saprotrophic	−	+	−
Gloiothele_lamellosa [KHL11031][AF506454]	Resupinate	smooth	Saprotrophic	−	+	−
Gloiothele_torrendii [JBoidin18615][AF506455]	Resupinate	smooth	Saprotrophic	−	+	−
Gymnomyces_hellyerensis [46IS83 + 46CY SLM]? 46 IS CYSTANGIUM?!!	Pileate	Labyrinthioid	Ectomycorrhizal	−	+	+
Gymnomyces_megasporus [SLM47GM SEQ2 9/27/99]	Pileate	Labyrinthioid	Ectomycorrhizal	−	+	+
Gymnomyces_pallidus [SLM44GM 28+27+ 33-SM17 1/22/99]	Pileate	Labyrinthioid	Ectomycorrhizal	−	+	+
Gymnomyces_redolens [SLM42GM]	Pileate	Labyrinthioid	Ectomycorrhizal	−	+	+
Hericium_abietis [663][AF506456]	Resupinate	Hydnoid	Saprotrophic	+	+	−
Hericium_alpestre [2754][AF506457]	Pileate	Hydnoid	Parasitic	+	+	−
Hericium_americanum [DAOM21467][AF506458]	Pileate	Hydnoid	Parasitic	+	+	−
Hericium_cirrhatum [F794][AF506385]	Pileate	Hydnoid	Parasitic	+	+	−
Hericium_coralloides [1229][AF506459]	Pileate	Hydnoid	Saprotrophic	+	+	−
Hericium_erinaceous [SLM164] USE HERS?	Pileate	Hydnoid	Parasitic	+	+	−
Heterobasidion_annosum [2450][AF347096]	Resupinate	Poroid	Saprotrophic	−	−	−
Lactarius_lignyotellus [SLM251]	Pileate	Lamellate	Ectomycorrhizal	−	+	+
Lactarius_panuoides [SLM395L]	Pileate	Lamellate	Ectomycorrhizal	−	+	+
Lactarius_piperatus [SLM116	Pileate	Lamellate	Ectomycorrhizal	−	+	+

SUPPLEMENTARY TABLE I. Continued

	FB morph	Hym type	Biology	Amyloid tissue	Amyloid spor	Sphaerocytes
Lactarius_scrobiculatus [SLM454] ?	Pileate	Lamellate	Ectomycorrhizal	−	+	+
Lactarius_subdulcis [SLM296]	Pileate	Lamellate	Ectomycorrhizal	−	+	+
Lactarius_subpurpureus [SLM90]	Pileate	Lamellate	Ectomycorrhizal	−	+	+
Laurilia_sulcata [2318][AF506414]=KHL8247?	Effused-reflexed	smooth	Saprotrophic	−	+	−
Laxitextum_bicolor [1350][AF310102]	Effused-reflexed	smooth	Saprotrophic	−	+	−
Lentinellus_auricula [KGN280994][AF506415]	Pileate	Lamellate	Saprotrophic	−	+	−
Lentinellus_cochleatus [KGN960928][AF506417]	Pileate	Lamellate	Saprotrophic	−	+	−
Lentinellus_omphalodes [JJ2077][AF506418]	Pileate	Lamellate	Saprotrophic	−	+	−
Lentinellus_ursinus [EL73][AF506]	Pileate	Lamellate	Saprotrophic	+	+	−
Lentinellus_vulpinus [KGN980825419]	Pileate	Lamellate	Parasitic	+	+	−
Leucogaster_citrinus [SLM2341ITS+2341LSU]	Pileate	Labyrinthioid	Ectomycorrhizal	−	+	−
Leucogaster_microsporus [SLM2340ITS+2340LSU]	Pileate	Labyrinthioid	Ectomycorrhizal	−	+	−
Macowanites_americanus [SLM480MC SEQ2 9/27/99]	Pileate	Labyrinthioid	Ectomycorrhizal	−	+	+
Martellia_californicum [SLM52MRLSU SEQ2 9/27/99]	Pileate	Labyrinthioid	Ectomycorrhizal	−	+	+
Martellia_fallax [SLM53]	Pileate	Labyrinthioid	Ectomycorrhizal	−	+	+
Megalocystidium_chelidonium [SJ110.1Lodge][AF506441]	Resupinate	smooth	Saprotrophic	−	+	−
Megalocystidium_leucoxanthum [19153][AF506420]	Resupinate	smooth	Saprotrophic	−	+	−
Megalocystidium_luridum [KHL8635][AF506422]	Resupinate	smooth	Saprotrophic	−	+	−
Megalocystidium_wakullum [52][AF506443]=OSLO-930107?	Resupinate	smooth	Saprotrophic	−	+	−
Metulodontia_nivea [2712][AF506423]	Resupinate	smooth	Saprotrophic	−	−	−
Mycolevis_siccigleba [AY963567+SLM380LS69]	Pileate	Labyrinthioid	Ectomycorrhizal	+	+	−
Peniophora_cinerea [1788][AF506424]	Resupinate	smooth	Saprotrophic	−	+	−
Peniophora_incarnata [1909][AF506425]	Resupinate	smooth	Saprotrophic	−	+	−
Polyporoletus_sublividus [JA030918 not in GenBank]	Pileate	Poroid				
Ectomycorrhizal?	+	+	−			
Pseudoxenasma_verrucisporum [97][AF506426]=EL34-95?	Resupinate	smooth	Saprotrophic	−	+	−
Russula_brevipes [SLM133]	Pileate	Lamellate	Ectomycorrhizal	−	+	+
Russula_brunneola [SLM]	Pileate	Lamellate	Ectomycorrhizal	−	+	+
Russula_campinensis [TH6844 +01-SM1]	Pileate	Lamellate	Ectomycorrhizal	−	+	+
Russula_discopus [SLM]	Pileate	Lamellate	Ectomycorrhizal	−	+	+
Russula_drimeia [SLM313LS69]	Pileate	Lamellate	Ectomycorrhizal	−	+	+
Russula_earlei [SLM]	Pileate	Lamellate	Ectomycorrhizal	−	+	+
Russula_foetentula [SLM38R]	Pileate	Lamellate	Ectomycorrhizal	−	+	+
Russula_xerampelina [SLM]	Pileate	Lamellate	Ectomycorrhizal	−	+	+
Scytinostroma_galactinum [1232][AF506466]	Resupinate	smooth	Saprotrophic	−	+	−
Scytinostroma_jacksonii [635][AF506467]	Resupinate	smooth	Saprotrophic	−	+	−
Scytinostroma_ochroleucum [TAA159869][AF506468]	Resupinate	smooth	Saprotrophic	−	+	−
Scytinostroma_odoratum [KHL8546][AF506469]	Resupinate	smooth	Saprotrophic	−	−	−
Scytinostroma_portentosum [EL1199][AF506470]	Resupinate	smooth	Saprotrophic	−	+	−
Scytinostromella_heterogenea [JS18244][AF506471]	Resupinate	smooth	Saprotrophic	−	+	−

Supplementary Table I. Continued

	FB morph	Hym type	Biology	Amyloid tissue	Amyloid spor	Sphaerocytes
Scytinostromella_nannfeldtii [1742][AF506472]	Resupinate	smooth	Saprotrophic	−	+	−
Sistrotrema_brinkmannii [2206][AF506473]	Resupinate	smooth	Saprotrophic	−	−	−
Sistrotrema_coronilla [785][AF506475]	Resupinate	smooth	Saprotrophic	−	−	−
Sistrotrema_muscicola [KHL8794][AF506474]	Resupinate	smooth	Saprotrophic	−	+	−
Sistrotrema_sernanderi [KHL8576?][AF506476]	Resupinate	smooth	Saprotrophic	−	−	−
Stereum_hirsutum [1022][AF506479]	Effused-reflexed	smooth	Saprotrophic	−	+	−
Stereum_reflexulum [EL48-97][AF506490]	Resupinate	smooth	Saprotrophic	−	+	−
Stereum_rugosum [2353][AF506481]	Effused-reflexed	smooth	Saprotrophic	−	+	−
Stereum_subtomentosum [EL1197][AF506482]	Effused-reflexed	smooth	Saprotrophic	−	+	−
Vararia_investiens [TAA164122][AF506484]	Resupinate	smooth	Saprotrophic	−	−+	−
Vararia_ochroleuca [JS24400][AF506485]	Resupinate	smooth	Saprotrophic	−	−	−
Vesiculomyces_citrinus [EL53.97][AF506486]	Resupinate	smooth	Saprotrophic	−	+	−
Wrightoporia_avellanea [LR41710][AF506488]	Resupinate	Poroid	Saprotrophic	−	+	−
Wrightoporia_lenta [KN150311][AF506489]	Resupinate	Poroid	Saprotrophic	−	+	−
Wrightoporia_tropicalis [LR40352][AF506490]	Resupinate	Poroid	Saprotrophic	−	+	−
Xylobolus_frustulatus [KGN980928][AF506491]	Resupinate	smooth	Saprotrophic	−	+	−
Xylobolus_lividocaeruleus [2001][AF506400]	Resupinate	smooth	Saprotrophic	−	+	−
Zelleromyces_sculptisporus [SLM]	Pileate	Labyrinthioid	Ectomycorrhizal	−	+	+
Zelleromyces_striatus [SLM57]	Pileate	Labyrinthioid	Ectomycorrhizal	−	+	+
Trichaptum_abietinum [2581][AF347104]						
Basidioradulum_radula [1706][AF347105]=NH9453?						
Exidia_glandulosa [EL399][AF506493]=EL3/97?						
Exidia_recisa [EL15_99][AF347112]=EL115-98?						
Auricularia_mesenterica [EL66_97][AF506492]						

Supplementary Table II. Genera of Russulales

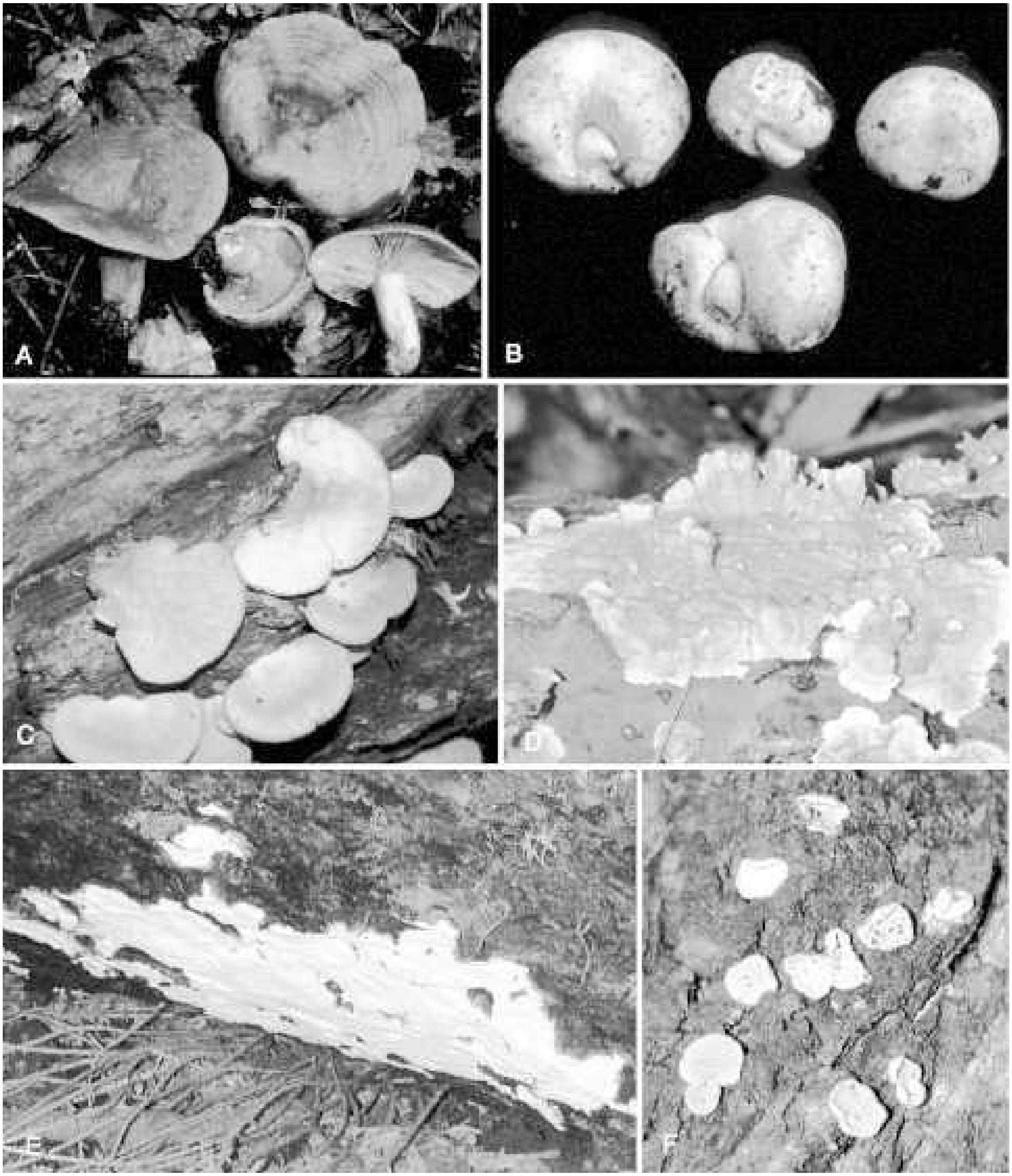
Genus	Family	Correct family	correct genus	correct order
Albatrellus		Albatrellaceae		
Byssoporia		Albatrellaceae		
Aleurocystidiellum	Stereaceae	Aleurocystidiellum family		
Artomyces	Auriscalpiaceae	Auriscalpiaceae		
Auriscalpium	Auriscalpiaceae	Auriscalpiaceae		
Gloiodon	Bondarzewiaceae	Auriscalpiaceae		
Dentipratulum	Hericiaceae	Auriscalpiaceae		
Bondarzewia	Bondarzewiaceae	Bondarzewiaceae		
Echinodontium	Echinodontiaceae	Echinodontiaceae		
Laurilia	Echinodontiaceae	Echinodontiaceae		
Amylostereum	Stereaceae	Echinodontiaceae ?		
Gloeocystidiellum	Gloeocystidiellaceae	Gloeocystidiellaceae		
Gloeodontia	Bondarzewiaceae	Gloeodontiaceae		
Creolophus	Hericiaceae	Hericiaceae		
Dentipellis	Hericiaceae	Hericiaceae		
Hericium	Hericiaceae	Hericiaceae		
Laxitextum	Stereaceae	Hericiaceae		
Amylodontia	Hericiaceae	Hericiaceae ?	Hericium ?	
Hybogaster	Hybogasteraceae	Hybogasteraceae	Hybogaster	
Stalpersia	Auriscalpiaceae	not known		
Amylaria	Bondarzewiaceae	not known		
Amylosporus	Bondarzewiaceae	not known		
Rigidoporopsis	Bondarzewiaceae	not known		
Steccherinum	Bondarzewiaceae	not known		
Wrightoporia	Bondarzewiaceae	not known		
Dextrinocystidium	Gloeocystidiellaceae	not known		
Myxomycidium	Hericiaceae	not known		
Dichantharellus	Lachnocladiaceae	not known		
Dichopleuropus	Lachnocladiaceae	not known		
Dichostereum	Lachnocladiaceae	not known		
Stelligera	Lachnocladiaceae	not known		
Amylohyphus	Stereaceae	not known		
Coniophorafomes	Stereaceae	not known		
Gloeosoma	Stereaceae	not known		
Scytinostromella	Stereaceae	not known		
Amylonotus	Auriscalpiaceae	not knwon		
Murrilloporus	Bondarzewiaceae	not knwon		
Amylofungus	Gloeocystidiellaceae	Peniophoraceae		
Asterostroma	Lachnocladiaceae	Peniophoraceae		
Lachnocladium	Lachnocladiaceae	Peniophoraceae		
Scytinostroma	Lachnocladiaceae	Peniophoraceae		

Supplementary Table II. Continued

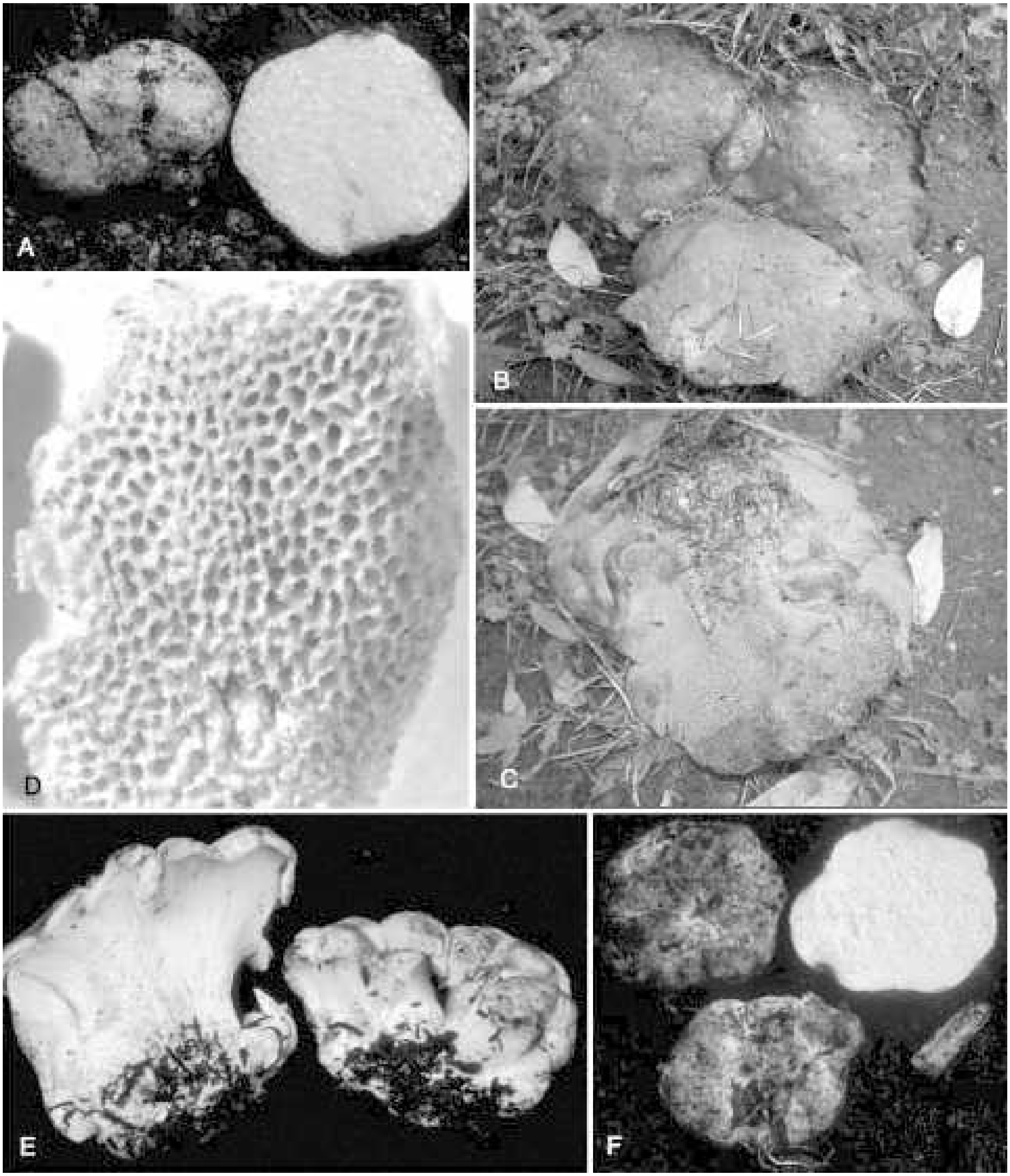
Genus	Family	Correct family	correct genus	correct order
Stereofomes	Lachnocladiaceae	Peniophoraceae		
Vararia	Lachnocladiaceae	Peniophoraceae		
Dendrophora	Peniophoraceae	Peniophoraceae		
Duportella	Peniophoraceae	Peniophoraceae		
Entomocorticium	Peniophoraceae	Peniophoraceae		
Peniophora	Peniophoraceae	Peniophoraceae		
Confertobasidium	Stereaceae	Peniophoraceae		
Gloiothele	Stereaceae	Peniophoraceae		
Vesiculomyces	Stereaceae	Peniophoraceae		
Metulodontia		Peniophoraceae		
Gloeopeniophorella	[incertae sedis]	Russulaceae		
Arcangeliella	Russulaceae	Russulaceae	Lactarius	
Cystangium	Russulaceae	Russulaceae	Russula	
Elasmomyces	Russulaceae	Russulaceae	Russula	
Gastrolactarius	Russulaceae	Russulaceae	Lactarius	
Gymnomyces	Russulaceae	Russulaceae	Russula	
Lactarius	Russulaceae	Russulaceae	Lactarius	
Macowanites	Russulaceae	Russulaceae	Russula	
Martellia	Russulaceae	Russulaceae	Russula	
Russula	Russulaceae	Russulaceae	Russula	
Zelleromyces	Russulaceae	Russulaceae	Lactarius	
Boidinia	Stereaceae	Russulaceae		
Pseudoxenasma	Stereaceae	Russulaceae		
Gloeomyces	Auriscalpiaceae	Stereaceae		
Acanthobasidium	Stereaceae	Stereaceae		
Acanthofungus	Stereaceae	Stereaceae		
Acanthophysellum	Stereaceae	Stereaceae		
Acanthophysium	Stereaceae	Stereaceae		
Aleurobotrys	Stereaceae	Stereaceae		
Aleurodiscus	Stereaceae	Stereaceae		
Conferticium	Stereaceae	Stereaceae		
Gloeocystidiopsis	Stereaceae	Stereaceae		
Megalocystidium	Stereaceae	Stereaceae	Megaliocystidium	
Stereum	Stereaceae	Stereaceae		
Xylobolus	Stereaceae	Stereaceae		
Aleurocystis	Stereaceae	Stereaceae ?		
Aleuromyces	Stereaceae	Stereaceae ?		
Hemicybe	Auriscalpiaceae			
Lentinellus	Auriscalpiaceae			
Heterobasidion	Bondarzewiaceae			
Buchholtzia	Russulaceae			
Dixophyllum	Russulaceae			

SUPPLEMENTARY TABLE II. Continued

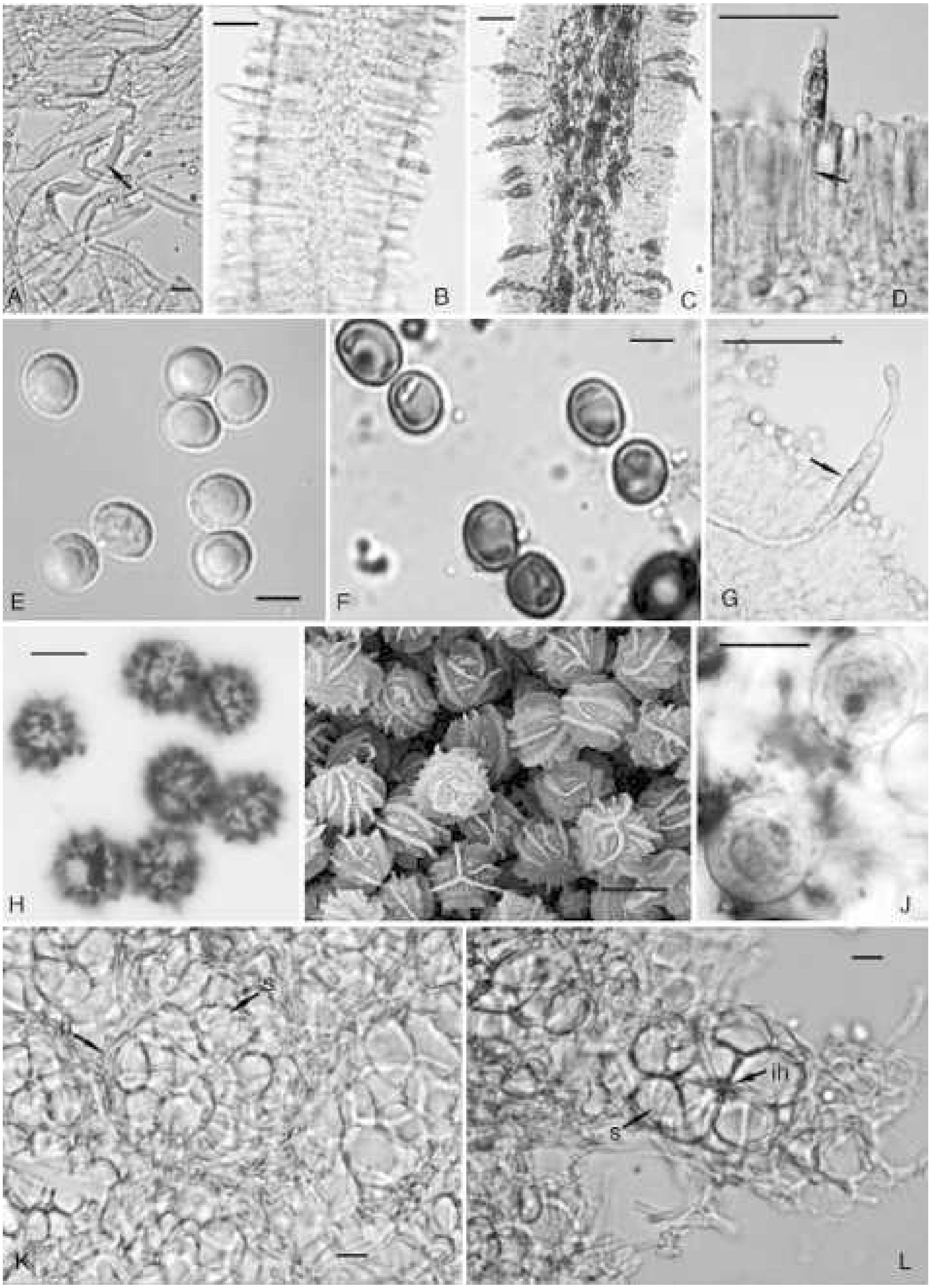
Genus	Family	Correct family	correct genus	correct order
Galorrheus	Russulaceae		Lactarius	
Gloeocybe	Russulaceae		Lactarius	
Hypochanum	Russulaceae			
Hypophyllum	Russulaceae			
Lactarelis	Russulaceae		Lactarius	
Lactaria	Russulaceae		Lactarius	
Lactariella	Russulaceae		Lactarius	
Lactariopsis	Russulaceae		Lactarius	
Lactifluus	Russulaceae		Lactarius	
Macowania	Russulaceae			
Omphalomyces	Russulaceae			
Phaeohygrocybe	Russulaceae			
Pleurogala	Russulaceae		Lactarius	
Russulina	Russulaceae			



SUPPLEMENTARY FIGURE I. A–J. Sporophore morphology and hymenophore types in the Russulales. A. Pileate lamellate (=agaricoid) sporophores of *Lactarius peckii*, SLM 9752. 0.3x. B. Pileate labyrinthioid (=sequestrate) sporophores of *Macowanites chlorinosmus*, SLM 1014. 0.7x. C. Pileate lamellate (pleurotoid) sporophores of *Lentinellus ursinus*, WI tjv1. 0.4x. Photo courtesy of Tom Volk, University of Wisconsin-La Crosse. D. Effused-reflexed smooth sporophores of *Stereum complicatum*, 3 IL 2000 tjv. 0.3x. Photo courtesy of Tom Volk, University of Wisconsin-La Crosse. E. Effused to effused-reflexed poroid sporophores of *Heterobasidion annosum*. 0.4x. Photo courtesy of Tom Volk, University of Wisconsin-La Crosse. F. Discoid smooth sporophores of *Aleurodiscus oakesii*, 2tjv. Photo courtesy of Tom Volk, University of Wisconsin-La Crosse. 0.5x.



Supplementary Figure II. A–F. Sporophore morphology and hymenophore types in the Russulales. A. Pileate labyrinthoid (=sequestrate) sporophores of *Leucogaster carolineana*, SLM 613. 1x. B. Pileate poroid sporophores of *Polyporoletus sublividus*, 2WAtjv (upper surface). 0.1x. Photo courtesy of Tom Volk, University of Wisconsin-La Crosse. C. Pileate poroid sporophores of *Polyporoletus sublividus*, 2WAtjv (lower surface). 0.1x. Photo courtesy of Tom Volk, University of Wisconsin-La Crosse. D. Effused poroid sporophores of *Byssoporia terrestris* 591, Photo courtesy of Karen Nakasone, USDA Forest Products Lab. 1x. E. Pileate poroid sporophores of Albatrellus ellsii. 0.25x. F. Pileate labyrinthoid (=sequestrate) sporophores of *Leucophleps spinispora*, SLM 1090. 1x.



SUPPLEMENTARY FIGURE III. A–L. Microscopic features of the Russulales. Bars = 10çm. A. Gloeopleurous hyphae (arrow) from trama of *Hericium erinaceous*. B. Lamellar trama from *Lactarius chrysorheus* mounted in KOH (compare with C). C. Lamellar trama from Lactarius chrysorheus mountedin sulfonvanillin. D. Pleuromacrocystidium (arrow) of *Russula* sp. mounted in KOH. Photo courtesy of Alejandro Kong Luz, University of Tlaxcala, Mexico. E. Basidiospores of *Hericium erinaceous* mounted in Melzer's iodine reagent. F. Basidiospores of *Hericium erinaceous* mounted in KOH. G. Pseudocystidium (arrow) of *Lactarius* sp. mounted in KOH. H. Basidiospores of *Lactarius lignyotellus* mounted in Melzer's iodine reagent. I. SEM of *Lactarius* sp. (rw22272) spores. J. Basidiospores of *Leucogaster carolineana* stained with iron hemotoxylin (note single nucleus present in each spores). K. Heteromerous pileus trama of *Russula* sp. Note nests of sphaerocytes (s) surrounded by organized cylindrical hyphae (h). L. Rosette of sphaerocytes (s) surrounding inductive hyphae (ih) in *Russula* sp.