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Re-thinking the classification of corticioid fungi

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ABSTRACT

Corticioid fungi are basidiomycetes with effused basidiomata, a smooth, merulioid or hydnoid hymenophore, and holobasidia. These fungi used to be classified as a single family, *Corticiaceae*, but molecular phylogenetic analyses have shown that corticioid fungi are distributed among all major clades within *Agaricomycetes*. There is a relative consensus concerning the higher order classification of basidiomycetes down to order. This paper presents a phylogenetic classification for corticioid fungi at the family level. Fifty putative families were identified from published phylogenies and preliminary analyses of unpublished sequence data. A dataset with 178 terminal taxa was compiled and subjected to phylogenetic analyses using MP and Bayesian inference. From the analyses, 41 strongly supported and three unsupported clades were identified. These clades are treated as families in a Linnean hierarchical classification and each family is briefly described. Three additional families not covered by the phylogenetic analyses are also included in the classification. All accepted corticioid genera are either referred to one of the families or listed as *incertae sedis*.

Introduction

Corticioid fungi are homobasidiomycetes with effused, resupinate fruiting structures that usually develop on the underside of decaying wood. As they are effused they do not have a definite form and extend over the substrate until they are checked by competition or unsuitable growth conditions. Resupinate means that basidiomata are fully attached to the substrate and not revolved or reflexed at the margin. None of these definitions are absolute as some corticioid fungi form a disc-like basidioma instead of being effused (for example *Aleurodiscus amorphous*) and some species have developed more or less erect fruiting structures (for example *Sistotrema confluens*).

The connection to dead wood has two explanations. Most species are true wood decayers and extend their vegetative mycelium inside the slowly degrading wood resource. Other species live in soil but need a firm structure upon which to develop a downward-facing basidioma. Dead wood on the ground serves that purpose well and such species were earlier falsely designated as wood-decaying.

The name corticioid means 'resembling a [member of the genus] *Corticium*', the type genus for the family *Corticiaceae*. Donk (1964) tried to create well-defined families for homobasidiomycetes without gills (*Aphyllophorales*). His paper was an important step towards a natural classification for fungi, but he admittedly failed to find a reliable system for the corticioid fungi. Still the family name *Corticiaceae* has found wide application as a convenient label for an assemblage of morphologically similar fungi much in the same way as *Polyporaceae* has been used for all polypores.

A change of term from *Corticiaceae* to 'corticioid fungi' reflects the radically increased knowledge of fungal evolution gained from molecular phylogenetic analyses (e.g. Larsson *et al.* 2004; Binder *et al.* 2005). As these analyses now make it possible to define *Corticiaceae* in a strict sense, its use as

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a classification label for all corticioid fungi should be abandoned. The same phylogenetic analyses have also shown that the term 'corticioid fungi' refers to a highly polyphyletic group, even more so than anticipated by Donk in 1964. Not only are they distributed over all currently identified evolutionary lineages among the *Agaricomycetes* (syn. *Homobasidiomycetes*) but they also blend with nearly all other morphogroups from the Friesian classification. With such a ubiquitous presence corticioid fungi emerge as a key group for understanding homobasidiomycete evolution, and at least some ancestral character state analyses favour a corticioid-like fungus as the ancestor of all homobasidiomycetes (Hibbett & Binder 2002; but see Hibbett 2004).

Early classifications of larger basidiomycetes placed the main emphasis either on basidioma construction or on hymenophore configuration, or a combination of both. Persoon (1801), for example, kept all species with a toothed hymenophore in *Hydnoidei* (*Sistotrema, Hydnum, Odontia*) and those with a smooth hymenophore in *Gymnodermata* (*Thelephora, Stereum, Corticium*). The last classification to be published by Fries (1874) comprised two main groups for the *Hymenomycetes*: (1) hymenial surface uneven; (2) hymenial surface even. The former group contained three subgroups based on hymenophore configuration: *Agaricini, Polyporei*, and *Hydnei*. In the latter group, species were divided according to hymenial position in *Thelephorei* (hymenium horizontal, below), *Clavariei* (hymenium vertical, amphigenous), and *Tremellinei* (hymenium above, gelatinous).

Berkeley (1860) divided *Hymenomycetes* into six 'orders', among them *Hydnei* (*Hydnum, Sistotrema, Irpex, Radulum, Phlebia, Grandinia, Odontia, Kneiffia*) and *Auricularini* (*Craterellus, Thelephora, Stereum, Hymenochaete, Auricularia, Corticium, Cyphella*). His classification also gives a glimpse of what genera were most widely used during the 19th century. In mycology the entrance of a new century was marked by the extraordinary publication *Essai taxonomique des Hyménomycètes* (Patouillard 1900). This book presented a new classification that broke with the Friesian tradition and introduced many of the concepts still widely used. For example, Patouillard divided the *Hymenomycetes* into *Hetero*- and *Homobasidiomycetes* and divided the latter into 'Agaricacés' and 'Aphyllophoracés'. Patouillard's classification became the foundation for taxonomic mycology for almost 100 y. When Donk published his conspectus of the families of *Aphyllophorales* (Donk 1964) he quoted Patouillard as the prime inspiration. Donk (1964) tried to carve out 'natural groups' using all the information on morphology and cytology available at that time. He preferred evolution rather than revolution and accepted 21 families but still he had to leave the bulk of aphyllophoralean species in four artificial groups: *Corticiaceae, Hydnaceae, Polyporaceae*, and *Stereaceae*.

In an attempt to create an alternative higher order classification for basidiomycetes Jülich (1982) introduced numerous new orders and families. His ideas were not generally accepted but because the new names were validly published they must be considered when reorganising the basidiomycetes. The most comprehensive and up-to-date classification for all fungi is presented in *Ainsworth & Bisby's Dictionary of the Fungi* (Kirk *et al.* 2001). The latest version has incorporated some of the results generated by molecular phylogenetic investigations but is still somewhat outdated.

The foundation of contemporary corticiology can be traced back to Bourdot, who, together with his friend and colleague Galzin, published numerous new species and finally summarized his knowledge in the monumental *Hyménomycètes de France* (Bourdot & Galzin 1928). This book enabled, for the first time, the identification of corticioid fungi with at least acceptable accuracy. In fact, no alternative handbooks were available until the publication of *The Corticiaceae of North Europe* (Eriksson & Ryvarden 1973, 1975, 1976; Eriksson *et al.* 1978, 1981, 1984; Hjortstam *et al.* 1988a,b), although *Danish Resupinate Fungi* (Christiansen 1960) must be mentioned as a remarkable achievement.

Bourdot & Galzin used the old traditional genera for corticioid fungi, e.g. *Corticium, Peniophora*, and *Gloeocystidium*, but sorted species in sections that they perceived as natural groups, thus initiating the splitting of the Friesian genera. The challenge was adopted first and foremost by Donk who, in a series of influential papers, introduced new genera or emended long-forgotten, but valid, genus names (Donk 1931, 1956, 1957, 1958). Other important contributions were made by Eriksson (1958), Oberwinkler (1965), and Parmasto (1968). The latter publication also introduced a classification for all corticioid fungi. Parmasto basically followed Donk (1964) but restricted *Corticiaceae* to monomitic species and created *Steccherinaceae* for dimitic corticioid species. Each family was further divided into subfamilies and tribes, and some of the genera were divided into subgenera. Several of the new taxa introduced by Parmasto have later been raised to family and genus level.

Among the many contemporary mycologists who have studied the taxonomy of corticioid fungi two in particular must be mentioned. Jacques Boidin has added valuable characters for taxonomy through his studies of culture characteristics, mating systems, and nuclear behaviour. Kurt Hjortstam has followed Donk and Eriksson, and contributed numerous new genera. Boidin and Hjortstam have also pioneered the contemporary exploration of tropical corticioid diversity by collecting and describing new species and by reviving many old and ignored names introduced by 19th century mycologists.

A new classification for the fungi down to order is now available as the result of an international cooperation, and that unified classification is fully adopted here (Hibbett *et al.* 2007). The object of the present paper is to elaborate on a classification for corticioid fungi at family level, drawing on recent achievements through molecular phylogenetic analyses and taking into account only monophyletic groups. It is my hope that the hypotheses put forward here, subjective as they may be, will stimulate further investigations and encourage students of other groups of basidiomycetes to include corticioid fungi in future projects.

Materials and methods

Numerous published phylogenies were screened and compared (Binder & Hibbett 2002; Binder *et al.* 2005; Bodensteiner *et al.* 2004; Boidin *et al.* 1998; Bresinsky *et al.* 1999; Bruns *et al.* 1998; de Koker *et al.* 2003; Hallenberg & Parmasto 1998; Hibbett & Binder 2002; Hibbett & Donoghue 1995, 2001; Hibbett *et al.* 2000; Hibbett *et al.* 1997; Hibbett & Thorn 2001; Hsiau & Harrington 2003; Jarosch & Besl 2001; Kim & Jung 2000; Kottke *et al.* 2003; Langer 1998, 2002; Larsson & Larsson 2003; Larsson *et al.* 2004; Lee & Jung 1997; Lim 2001; Moncalvo *et al.* 2002; Parmasto & Hallenberg 2000; Redhead *et al.* 2002; Taylor *et al.* 2003; Wang *et al.* 2004; Weiss & Oberwinkler 2001; Wu *et al.* 2001; Yoon *et al.* 2003). A great number of unpublished nuLSU rDNA sequences were analysed separately and together with selected GenBank sequences in order to track additional support for a putative family classification. From these analyses and the aforementioned publications, 50 groups containing corticioid fungi were identified as potential families and served as a template for a sequence sampling that covered 47 of the groups. The non-sampled groups were *Physalacriaceae* (*Agaricales*), possibly the correct family for the corticioid genus *Cylindrobasidium* (Binder *et al.* 2005), *Schizophyllaceae* (*Agaricales*) that includes *Auriculariopsis* (Bodensteiner *et al.* 2004), and *Ceratobasidiaceae* (*Cantharellales*). A minimum of two species from each group were selected together with three representatives from *Auriculariales,* an order that constitutes a suitable outgroup (Weiss & Oberwinkler 2001). The final dataset included 178 species of which 138 have corticioid basidiomata. The set of publications on fungal phylogeny recently published in *Mycologia* (vol. 98(6), 2007) were not available at the time the dataset was compiled and analysed.

Protocols for DNA extraction, PCR, and sequencing followed Larsson & Larsson (2003) and Larsson *et al.* (2004). For each specimen nu-rDNA sequences covering 5.8S, ITS2, and *ca* 1000 bp of 28S (LSU) were combined and manually aligned using the data editor of PAUP 4.0 (Swofford 1999). The dataset was complete except for eight species that only have the LSU gene (*Dendrothele acerina, D. griseo-cana, Serpula incrassata, Sistotrema eximum, Veluticeps berkeleyi, Phellinus chrysoloma, Inonotus radiatus, Kavinia alboviridis*,). The final dataset with introduced gaps comprised 2048 nucleotide positions, but 1005 of them, above all the whole ITS2 region, were excluded from analyses because of alignment difficulties. *Exidia recisa* was selected as outgroup. Data on specimens sequenced for this study are listed in Table 1. Corresponding vouchers are deposited in Herbarium GB, Göteborg University, Sweden. Sequences downloaded from GenBank are listed in Table 2.

Heuristic MP analysis was performed using PAUP 4.0 (200 random taxon addition replicates, keeping, at most, 100 trees per replicate, MAXTREES = 20K). The analysis used 1043 characters of which 483 were constant, 149 variable but parsimony uninformative, and 411 (39 %) parsimony informative. Gaps were treated as unknowns. Branch support was estimated with the BS option in PAUP (100 replicates, five random addition sequences per replicate, keeping 50 trees per replicate, MAXTREES = 15K).

A heterogeneous Bayesian inference run was set up in MrBayes 3.1 (Ronquist & Huelsenbeck 2003) with model parameters estimated separately for 5.8S and LSU using MrModeltest 2.2 (Nylander 2004). Eight Metropolis-Coupled MCMC (MCMCMC) chains with a temperature of 0.2 were initiated; these were run for 10M generations with tree and parameter sampling every 5K generations (2K trees). The burn-in was set to 50 % (1K trees).

Results

The parsimony analysis returned 64 equally shortest trees (length 4502, CI = 0.2035, RI = 6182). The ingroup represents 12 of the orders in *Agaricomycetes* (Hibbett *et al.* 2007). *Agaricales* and *Polyporales* were not recovered as monophyletic, whereas the rest of the orders appeared monophyletic and moderately to strongly supported by BS (77–100 %; Fig 1).

Table 1 – Specimens sequenced for this study. All vouchers are kept at herbarium GB, Göteborg University, Sweden

Species	Herbarium no	Origin	GenBank no
Amylocystis lapponica (Romell) Singer	KHL 11755	Finland	EU118603
Arrhenia retiruga (Bull.:Fr.) Redhead	EL 76/03	Sweden	EU118604
Athelia pyriformis (M. P Christ.) Jülich	Hjm 18581	Sweden	EU118605
Athelidium aurantiacum Oberw.	KHL 11068	Sweden	EU118606
Botryobasidium subcoronatum (Höhn. & Litsch.) Donk	KHL s.n.	Sweden	EU118607
Byssoporia terrestris (DC.:Fr.) M. J. Larsen & Zak	Hjm 18172	Sweden	EU118608
Candelabrochaete septocystidia (Burt) Burds.	ÅS-95	Sweden	EU118609
Ceraceomyces borealis (Romell) J. Erikss. & Ryvarden	KHL 8432	Sweden	EU118610
Ceraceomyces violascens (Fr.:Fr.) Jülich	KHL 11169	Norway	EU118611/EU118612
Ceriporia reticulata (Nees:Fr.) Domanski	KHL 11981	Norway	EU118613/EU118614
Chaetodermella luna (D.P. Rogers & H. S. Jacks.) Rauschert	NH 8482	Norway	EU118615
Clavulina cinerea (Bull.:Fr.) J. Schröt.	KHL 11694	Finland	EU118616
Clavulinopsis helvola (Pers.:Fr.) Corner	EL 111/04	Sweden	EU118617
Clavulinopsis laeticolor (Berk. & M. A. Curtis) R. H. Petersen	EL 8/00	Finland	EU118618
Columnocystis abietina (Fr.:Fr.) Pouzar	KHL 12474	Sweden	EU118619
Cristinia helvetica (Pers.) Parmasto	Kristiansen s.n.	Norway	EU118620
Cyphellostereum laeve (Fr.) D. A. Reid	JJ 020909	Sweden	EU118621
Cystidiodontia laminifera (Berk. & M. A. Curtis) Hjortstam	KHL 13057	Costa Rica	EU118622
Cystostereum murrayi (Berk. & M. A. Curtis) Parmasto	KHL 12496	Sweden	EU118623
Dacryobolus karstenii (Bres.) Parmasto	KHL 11162	Norway	EU118624

Table 1 – (*continued*)

Species	Herbarium no	Origin	GenBank no
Dentipellis leptodon (Mont.) Maas Geest.	GB 011123	Uganda	EU118625
Globulicium hiemale (Laurila) Hjortstam	KHL 961221	Sweden	EU118626
Gloeoporus dichrous (Fr.:Fr.) Bres.	KHL 11173	Norway	EU118627
Gomphus clavatus (Pers.:Fr.) Gray	EL 64/03	Sweden	EU118628
Haplotrichum curtisii (Berk.) Hol.-Jech.	KHL 12950	Costa Rica	EU118629
Hyphodermella corrugata (Fr.) J. Erikss. & Ryvarden	KHL 3663	Norway	EU118630
Hyphodontia alutaria (Burt) J. Erikss.	KHL 11978	Norway	EU118631
Hyphodontia arguta (Fr.) J. Erikss.	KHL 11938	Sweden	EU118632/EU118633
Hyphodontiella multiseptata Å. Strid	Ryberg 021022	Sweden	EU118634
Hypochnicium polonense (Bres.) Å. Strid	NH 12117	Russia	EU118635
Jaapia argillacea Bres.	KHL 11734	Finland	EU118636
Jaapia ochroleuca (Bres.) Nannf. & J. Erikss.	KHL 8433	Sweden	EU118637
Junghuhnia nitida (Pers.:Fr.) Ryvarden	KHL 11903	Sweden	EU118638
Laetisaria fuciformis (McAlpine) Burds.	Hjm 18391	Sweden	EU118639
Lentaria dendroidea (O.R. Fr.) J. H. Petersen	SJ 98012	Sweden	EU118640/EU118641
Leptosporomyces galzinii (Bourdot) Jülich	KHL 11079	Sweden	EU118642
Leucogyrophana mollusca (Fr.) Pouzar	KHL 11160	Norway	EU118643
Leucogyrophana romellii Ginns	KHL 8413	Sweden	EU118644
Lichenomphalia umbellifera (L:Fr.) Redhead *et al.*	JR 2501	Sweden	EU118645
Lindtneria trachyspora (Bourdot & Galzin) Pilát	KGN 390/00	Sweden	EU118646
Merulicium fusisporum (Romell) J. Erikss. & Ryvarden	Hjm s.n.	Sweden	EU118647
Meruliopsis taxicola (Pers.:Fr.) Bondartsev	Kuljok 00/75	Sweden	EU118648
Mycoacia kurilensis Parmasto	KHL 12224	USA	EU118649
Oligoporus guttulatus (Peck) Gilb. & Ryvarden	KHL 11739	Finland	EU118650
Peniophora pini (Schleich.:Fr.) Boidin	Hjm 18143	Sweden	EU118651
Phanerochaete affinis (Burt) Parmasto	KHL 11839	Sweden	EU118652
Phanerochaete sordida (P. Karst.) J. Erikss. & Ryvarden	KHL 12054	Norway	EU118653
Phlebia firma J. Erikss. & Hjortstam	Edman K268	Sweden	EU118654
Phlebia nitidula (P. Karst.) Ryvarden	Nyström 020830	Sweden	EU118655
Phlebia subochracea (Bres.) J. Erikss. & Ryvarden	KGN 162/95	Sweden	EU118656
Phlebia unica (H. S. Jacks. & Dearden) Ginns	KHL 11786	Sweden	EU118657
Phlebiella aff. *ardosiaca*	KHL 12928	Costa Rica	EU118658
Phlebiella christiansenii (Parmasto) K. H. Larss. & Hjortstam	KHL 11689	Finland	EU118659
Phlebiella vaga (Fr.) P. Karst.	KHL 11065	Sweden	EU118660/EU118661
Phlebiopsis flavidoalba (Cooke) Hjortstam	KHL 13055	Costa Rica	EU118662
Podoscypha multizonata (Berk. & Broome) Pat.	Jahn 751012	Germany	EU118663
Radulomyces notabilis (H. S. Jacks.) Parmasto	EL 5/97	Canary Islands	EU118664
Scopuloides hydnoides (Cooke & Massee) Hjortstam & Ryvarden	KHL 11916	Sweden	EU118665
Sistotremastrum suecicum J. Erikss.	KHL 11849	Sweden	EU118666/EU118667
Steccherinum fimbriatum (Pers.:Fr.) J. Erikss.	KHL 11905	Sweden	EU118668
Steccherinum ochraceum (Pers.:Fr.) Gray	Ryberg s.n.	Sweden	EU118669/EU118670
Steccherinum robustius (J. Erikss. & S. Lundell) J. Erikss	Nordén s.n.	Sweden	EU118671
Stypella papillata A. Möller	KHL 11751	Finland	EU118672
Tapinella atrotomentosa (Batsch) Šutara	EL 3/03	Sweden	EU118673
Tomentellopsis bresadoliana (Sacc. & Trotter) Jülich & Stalpers	JEH 031011	Sweden	EU118674

Three groups did not fall within any of the orders recognized by Hibbett *et al.* (2007). *Amylocorticiaceae* seemed firmly established in the vicinity of *Agaricales*, whereas the *Phlebiella* family and the *Jaapia* family did not show affinities in any direction. The hypothesis often forwarded that *Jaapia* is related to boletes (e.g. Nannfeldt & Eriksson 1953; Jülich 1982) was not supported.

The Bayesian consensus tree has very much the same topology as the parsimony trees (Fig 1). A notable exception on order level was that *Agaricales* was recovered as monophyletic (PP value 0.99). Forty-four clades were recognized as potentially corresponding to families and only three of them, *Hygrophoraceae*, *Polyporaceae*, and the *Rickenella* family, lacked acceptable support. The remaining 41 clades received PP values of 0.97–1.00.

In the parsimony analysis, the majority of family clades received moderate to strong BS support, and only eight of them were unsupported or receive low support (Fig 1). In *Agaricales, Hygrophoraceae* was weakly supported; in *Polyporales,* the *Byssomerulius* family, *Meruliaceae*, and *Polyporaceae* were unsupported; in *Russulales, Hericiaceae* received a surprisingly low 54 % support; and in *Hymenochaetales,* the *Rickenella* family was unsupported and *Tubulicrinaceae* waekly supported. Of the three unplaced family clades *Amylocorticiaceae* was unsupported.

Almost all terminal taxa found a place in one of the family clades. *Radulomyces notabilis* was selected as a representative for *Polyporaceae*, but in the analyses family placement was unclear. Two *Serpula* species and *Leucogyrophana romellii* did not cluster within any of the groups

Table 2 – Sequences downloaded from GenBank

Species	GenBank no.
Albatrellus ovinus	AF506393
A. subrubescens	AF506395
Aleurocystidiellum disciforme	AF506402
A. subcruentatum	AF506403
Aleurodiscus amorphus	AF506397
Amaurodon viridis	AY463374/AY586625
Amphinema byssoides	AY463375/AY586626
Amylocorticium subincarnatum	AY463377/AY586628
Amylostereum areolatum	AF506405
A. laevigatum	AF506407
Aphanobasidium pseudotsugae	AY463450/AY586696
Athelia epiphylla	AY463382/AY586633
Atheloderma mirabile	DQ873692
Athelopsis subinconspicua	AY463383/AY586634
Auriscalpium vulgare	AF506375
Boidinia aculeata	AF506433
B. granulata	AF048880
Bondarcevomyces taxi	AY463386/AY586637
Byssomerulius corium	AY463389/AY586640
Ceraceomyces serpens	AY463390/AY586641
C. tessulatus	AY463391/AY586642
Ceriporia viridans	AF347109
Chondrostereum purpureum	AY463393/AY586644
Clavaria fumosa	AY463396/AY586646
Clavulina cristata	AY463398/AY586648
Coniophora olivacea	AF098376
C. puteana	AJ583426
Coronicium alboglaucum	AY463400/AY586650
Dendrothele acerina	AJ406581
D. griseo-cana	AY293178
Dentipellis fragilis	AF506387
Dentipratulum bialovicense	AF506389
Echinodontium sulcatum	AF506414
E. tinctorium	AF506430
Erythricium laetum	AY463407/AY586655
Exidia recisa	AF347112
Exidiopsis calcea	AY463406/AY586654
Gloeocystidiellum porosum	AF310094
Gloeocystidiellum sp.	AF310089
Gloeocystidiopsis cryptacanthus	AF506442
Gloeodontia columbiensis	AF506444
G. discolor	AF506445
G. pyramidata	AF506446
G. subasperispora	AF506404
Gloeopeniophorella convolvens	AF506445
Gloeostereum incarnatum	AF141637
Gloiodon strigosus	AF506449
Gloiothele lactescens	AF506453
Haplotrichum conspersum	AY463409/AY586657
Hericium abietis	AF506456
H. erinaceus	AF506460
Hydnocristella himantia	AY463435/AY586682
Hydnomerulius pinastri	AJ419917/AF352044
Hydnum repandum	AF347095
Hygrophoropsis aurantiaca	AY463411/AY586659
Hymenochaete cinnamomea	AY463416/AY586664
H. rubiginosa	AY463417/AY586665
Hyphoderma obtusum	AY463422/AY586670
H. setigerum	AY463425/AY586673
Hyphodontia aspera	AY463427/AY586675
Hyphodontia detritica	DQ677507
Hyphodontia nespori	DQ873622
H. quercina	AY463430/AY586678
Hypochniciellum subillaqueatum	AY463431/AY586679
Inonotus radiatus	AF311018
Kavinia alboviridis	AY463434
Lactarius volemus	AF506411
Laxitextum bicolor	AF310102
Lenzites betulinus	AY463436/AY586683
Megalocystidium luridum	AF596421
Membranomyces delectabilis	AY463442/AY586688
Mycoacia aurea	AY463445/AY586691
Mycoaciella bispora	AY463446/AY586692
Paxillus involutus	AF098385
Phellinus chrysoloma	AF311026
Phlebia georgica	DQ873645
Phlebia tremellosa	AF141632
Polyporoletus sublividus	DQ389663
Polyporus brumalis	AF347108
Porpomyces mucidus	AF347091
Pseudomerulius aureus	AY463455/AY586701
Pseudotomentella tristis	AF274771
Punctularia strigosozonata	AY463456/AY586702
Resinicium furfuraceum	DQ873648
Rickenella fibula	AY463464/AY586710
Russula violacea	AF506465
Scytinostroma ochroleucum	AF506468
S. odoratum	AF506469
Serpula himantioides	AM076555
S. incrassata	AY491673
Sistotrema alboluteum	AY463467/AY586713
Sistotrema biggsii	AM259217
S. brinkmannii	AF506473
S. eximum	AF393076
S. muscicola	AF506474
Sistotrema sernanderi	AF506476
Sistotremastrum niveocremeum	AF347094
Skvortzovia furfurella	DQ873649
Sphaerobasidium minutum	DQ873652
Stereum hirsutum	AF506479
Subulicystidium sp.	AY463468/AY586714
Tomentellopsis echinospora	AY463472/AY586718
Trametes versicolor	AF347107
Trechispora farinacea	AF347089
T. hymenocystis	AF347090
Tubulicrinis globisporus	DQ873655
Tubulicrinis inornatus	DQ873659
Tubulicrinis subulatus	AY463478/AY586722
Vararia ochroleuca	AF506485
Veluticeps berkeleyi	AY293219
Wrightoporia lenta	AF506489
Vuilleminia comedens	AY463482/AY586725
Xerocomus chrysenteron	AF347103

within *Boletales* and family assignment for them remains unresolved.

Agaricales, *Boletales*, *Atheliales*, and *Amylocorticiaceae* formed a monophyletic group in the Bayesian analysis (pp 1.00), which indicates that the recent circumscription of *Agaricomycetidae* to include the former three orders only, may have to be emended (Hibbett *et al.* 2007). In the parsimony tree, the *Phlebiella* family formed an unsupported sister-clade relationship with *Amylocorticiaceae*, whereas the Bayesian analysis recovered *Phlebiella* in a polytomy with *Trechisporales* and *Polyporaceae*.

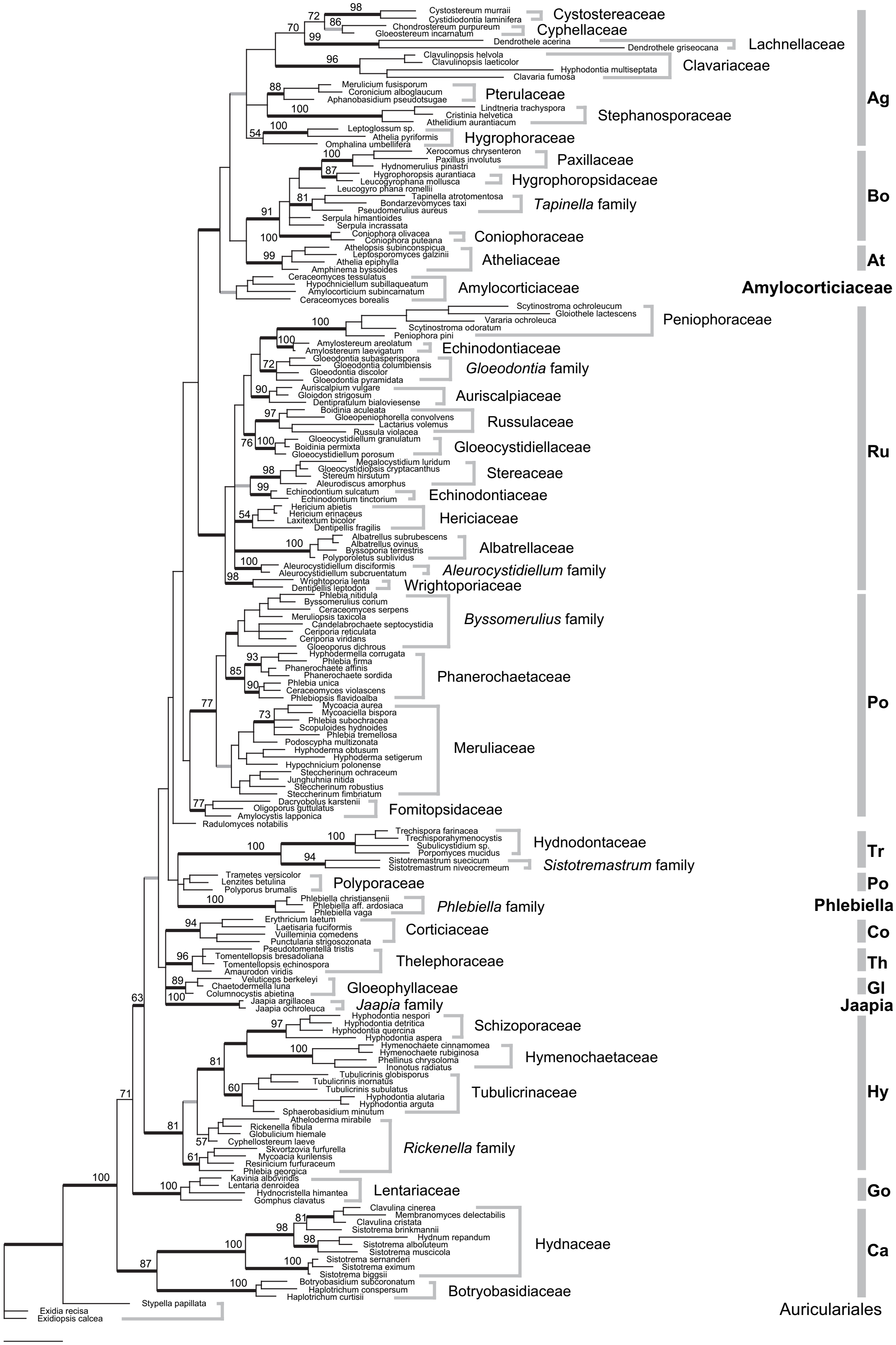

Fig 1 – Phylogenetic relationships inferred from 5.8S and nuLSU rDNA sequences using Bayesian analysis. A 50 % majority-rule consensus cladogram; branch lengths reflect estimated number of changes per site. BS values from a parsimony analysis are indicated for all deeper nodes. PP values of 0.97–0.99 are shown as thicker branches in grey and PP values of 1.00 are shown as thicker branches in black. Ag, *Agaricales*; At, *Atheliales*; Bo, *Boletales*; Ca, *Cantharellales*; Co, *Corticiales*; Gl, *Gloeophyllales*; Go, *Gomphales*; Hy, *Hymenochaetales*; Po, *Polyporales*; Ru, *Russulales*; Th, *Thelephorales*; Tr, *Trechisporales*.

Taxonomy

A tentative family classification for corticioid fungi

I have deliberately chosen to express an opinion on relationships for most corticioid genera also when there are only weak or doubtful arguments to rely on. In each case I have considered published information, our own unpublished data, and my knowledge of corticioid fungi morphology. It is not unusual to find conflicting information concerning the relationships among species and clades. In such cases I have tried either to select the solution with support from most studies, or to restudy the case with the addition of unpublished data. However, it is not possible here to account for all the temporary phylogenetic analyses that lie behind the classification. The system of families should be viewed as a preliminary hypothesis that must be subject to much testing and revision before it becomes stable.

The family concept rests on two assumptions. One is the ambition to recognize strongly supported, monophyletic clades only. The other is the strict adherence to the classification by Hibbett *et al.* (2007). In most cases I have chosen as families the most inclusive of the supported clades within each order. Deviations from this strategy usually depend on information received from published phylogenies with a denser sampling. One example is the *Rickenella* family in *Hymenochaetales,* which is not recognized as monophyletic in the present analyses but was recovered as a supported clade by Larsson *et al.* (2006). A more resolved classification that takes into account additional hierarchical levels between family and genus is beyond the scope of the present study and must be founded on analyses with a much more elaborate sampling.

Only families that are known to include corticioid fungi are considered. This means that *Agaricales, Boletales*, and *Gomphales* are treated only fragmentily and that the definition of families within these orders is particularly uncertain. For each family all corticioid genera that are considered to be members are listed but no others. It is far beyond the scope of the present paper to attempt to place non-corticioid genera as well.

A question mark attached to the genus name indicates an uncertainty that may stem from a lack of molecular data, either because no representative of the genus has yet been sequenced or beacuse the type of an admittedly polyphyletic genus was not sequenced. Another reason to express doubt can be conflicting information in published phylogenies.

When families are named, the priority rules in the *Code* have to be applied, meaning that the oldest legitimate name is the correct one unless a conserved name exists. The latter exception applies to *Corticiaceae*, which is conserved against the older *Vuilleminiaceae*. The families discussed here have been sifted out through consideration of the sequenced fraction of all *Agaricomycotina*. We do not yet know the limits of all these families, and therefore, do not know whether additional names will come into play. I have tried to make an educated guess but I do not claim to have exhausted all possibilities. When no family name was found I have refrained from suggesting a new one and instead provisionally labelled such families with a genus name. Orders are listed alphabetically as are families within each order. The unplaced families *Amylocorticiaceae*, *Jaapia* family, and *Phlebiella* family are listed as *incertae sedis* after all orders.

Table 3 presents a list of corticioid genera and their place in the classification, if known. For most genera placed to family, one of seven selected major publications with an emphasis on corticioid species (including the present paper) are quoted as the prime source of information. For some genera the reference is given as ‘Larsson unpubl.’ because sequences were not included in a published analysis. Further references are listed under remarks. All genera that have the type species sequenced are indicated in the table.

Agaricales Underw. 1899

It certainly was a great surprise when phylogenetic trees inferred from molecular data placed corticioid, clavarioid, and gastroid species deeply embedded among the true agarics (Hibbett *et al.* 1997; Moncalvo *et al.* 2002; Larsson *et al.* 2004, Matheny *et al.* 2007a). A close relationship among *Agaricales*, *Boletales*, and *Atheliales* was detected in several studies (Larsson *et al.* 2004; Binder *et al.* 2005; Matheny *et al.* 2007b), but the limits for *Agaricales* have remained obscure. The sampling for this study is focused on corticioid taxa and such a biased selection was not supposed to reveal any new truths about the delimitation of *Agaricales*.

Cystostereaceae Jülich 1982

?Crustomyces, Cystidiodontia, Cystostereum, ?Parvobasidium, ?Parvodontia

The family is typified by *Cystostereum murrayi*, a wood-decaying species, causing white rot in both hardwood and softwood, with a worldwide distribution. A characteristic feature of the basidiomata is numerous bladder-like gloeocystidia the contents of which often become yellowish. Similar gloeocystidia occur also in *Cystidiodontia* and *Crustomyces,* and both genera possibly belong here.

Clavariaceae Chev. 1826

Hyphodontiella, ?Mucronella

Clavaria and *Clavulinopsis* seem to form a distinct clade worthy of recognition as a family (Pine *et al.* 1999). Along with the clavarioid element we find *Hyphodontiella* with its thin and strictly resupinate basidiomata. No obvious morphological details connect *Hyphodontiella* and the clavarioid taxa. The genus *Mucronella* may also belong here but data are not consistent. *Mucronella* species have minute, unbranched, downward-growing clavarioid basidiomata but differ from the other species in its weakly ornamented, amyloid spores.

Cyphellaceae Lotsy 1907

Chondrostereum, Cunninghammyces, Gloeostereum, Granulobasidium

Chondrostereum and *Gloeostereum* are genera that have enclosed, vesicular gloeocystidia that in *Gloeostereum* are often yellowish. It is more difficult to find morphological similarities among the aforementioned genera and *Cunninghammyces* and *Granulobasidium* that are referred here by the molecular analyses. *Cunninghammyces* has pleurobasidia and globose, distinctly ornamented spores, whereas *Granulobasidium* has long, terminal basidia, globose, weakly ornamented spores,

Table 3 – Genera of corticioid fungi with type species epithet and possible place in the classification

Genus[a]	Order[b]	Family	Ref[c]	nLSU[d]	Remarks
Acanthobasidium Oberwinkler 1965 (*delicatum*)	Ru	*Stereaceae*	B	X	*A. phragmitis* sequenced, a synonym of *A. delicatus*
Acanthofungus Sheng H. Wu 2000 (*rimosus*)	Ru	*Stereaceae*	B	X	
Acanthophysellum Parmasto 1967 (*lividocoeruleum*)	Ru	*Stereaceae*	B	X	Close to *Xylobolus*. Genus limits unclear
Acanthophysium G. Cunn. 1963 (*apricans*)	Ru	*Stereaceae*			According to Wu *et al.* (2000) a syn. of *Xylobolus*
Adustomyces Jülich 1979 (*lusitanicus*)	Ag	?	*	X	Affinities to *Pterulaceae* ?
Aleurobotrys Boidin 1985 (*botryosus*)	Ru	*Stereaceae*	B	X	According to Wu *et al.* (2001) close to *Acanthophysellum*
Aleurocystidiellum P.A. Lemke 1964 (*subcruentatum*)	Ru	*Aleurocystidiellum* fam.	D	X	
Aleurocystis G. Cunn. 1956 (= *habgallae*)	?				Maybe related to *Cytidia* (*Corticiales*)
Aleurodiscus J. Schröt. 1888 (*amorphous*)	Ru	*Stereaceae*	B	X	Most species in *Aleurodiscus* s. l. not sequenced
Aleuromyces Boidin & Gilles 2001 (*gabonicus*)	Ru	*Stereaceae ?*			Syn. *Aleurodiscus ?*
Alutaceodontia Hjortstam 2002 (*alutacea*)	Hy	?		X	Syn. Kneiffiella ? See Larsson et al. 2006
Amaurodon J. Schröt. in Cohn 1888 (*viride*)	Th	*Thelephoraceae*		X	Incl. *Hypochnopsis, Lazulinospora, Tomentellago*
Amaurohydnum Jülich 1978 (*flavum*)	?				
Amauromyces Jülich 1978 (*pallidus*)	?				Two species, probably not congeneric
Amethicium Hjortstam 1983 (*rimosum*)	?				
Amphinema P. Karst. 1892 (=*byssoides*)	At	*Atheliaceae*	E	X	
Amyloathelia Hjortstam & Ryvarden 1979 (*amylacea*)	Am ?				Compare Boidin *et al.* (1998)
Amylobasidium Ginns 1988 (*tsugae*)	?				With affinities to *Dendrothele* s. l.
Amylocorticiellum Spirin & Zmitr. 2002 (*subillaqueatum*)	Am	*Amylocorticiaceae*	E	X	Segregated from *Hypochniciellum*
Amylocorticium Pouzar 1959 (*subsulphureum*)	Am	*Amylocorticiaceae*	E	X	
Amylodontia Nikol. 1967 (*parmastoi*)	Ru ?	*Hericiaceae ?*			Syn. *Dentipellis ?*
Amylofungus Sheng H. Wu 1995 (*corrosus*)	Ru ?	*Peniophoraceae ?*			Seems to be close to *Vesiculomyces*
Amylohyphus Ryvarden 1978	Gl ?				
Amylostereum Boidin 1958 (*chailletii*)	Ru	*Echinodontiaceae*	C	X	Compare Kim & Jung (2000)
Amyloxenasma Hjortstam & Ryvarden 2005 (*grisella*)	Am	*Amylocorticiaceae*	*		*A. allantospora* sequenced
Aphanobasidium Jülich 1979 (*subnitens*)	Ag	*Pterulaceae*	D		*A. pseudotsugae* sequenced
Asterodon Pat. 1894 (*ferruginosus*)	Hy	*Hymenochaetaceae*		X	Compare Larsson *et al.* 2007
Asterostroma Massee 1889 (*apalum*)	Ru	*Peniophoraceae*	D		Several species sequenced
Athelia Pers. 1822 (*epiphylla*)	At	*Atheliaceae*	E	X	Polyphyletic genus
Athelicium K.H. Larss & Hjortstam 1986 (*stridii*)	Ag	*Hygrophoraceae*	*	X	With affinities to omphalinoid taxa
Athelidium Oberwinkler 1965 (*aurantiacum*)	Ag	*Stephanosporaceae*	!	X	
Atheloderma Parmasto 1968 (*mirabile*)	Hy	*Rickenella* family	!	X	
Athelopsis Parmasto 1968 (*glaucina*)	At	*Atheliaceae*	D	X	Polyphyletic genus
Auriculariopsis Maire 1902 (*ampla*)	Ag	*Schizophyllaceae*		X	
Australicium Hjortstam & Ryvarden 2002 (*singulare*)	Po ?	*Phanerochaetaceae ?*			
Australohydnum Jülich 1978 (=*dregeanum*)	Po ?	*Phanerochaetaceae ?*	A		Only ITS sequenced
Basidioradulum Nobles 1967 (*radula*)	Hy	?	E	X	
Boidinia Stalpers & Hjortstam 1982 (*furfuracea*)	Ru	*Russulaceae*	D	X	Polyphyletic genus
Boreostereum Parmasto 1968 (*radiatum*)	Gl	*Gloeophyllaceae*	A	X	
Botryobasidium Donk 1931 (*subcoronatum*)	Ca	*Botryobasidiaceae*	F	X	
Botryodontia Hjortstam 1987 (*cirrata*)	Hy ?		*		*B. semispathulata* sequenced
Botryohypochnus Donk 1931 (*isabellinus*)	Ca	*Botryobasidiaceae*		X	Syn. Botryobasidium. See Langer (2002)
Brevicellicium K.H. Larss. & Hjortstam 1978 (*exile*)	Tr	*Hydnodontaceae*	*	X	
Bulbillomyces Jülich 1974 (*farinosus*)	Po	*Meruliaceae*		X	Close to *Hypochnicium*. See Larsson (2007)
Byssocorticium Bondartsev & Singer 1944 (*atrovirens*)	At	*Atheliaceae*	E		*B. pulchrum* sequenced
Byssomerulius Parmasto 1967 (*corium*)	Po	*Byssomerulius* family	E	X	
Byssoporia M.J. Larsen & Zak 1978 (*terrestris*)	Ru	*Albatrellaceae*	!	X	
Cabalodontia Piatek 2004 (*queletii*)	Po	*Meruliaceae*	*	X	
Caerulicium Jülich 1981 (*neomexicanum*)	At ?				With affinities to *Byssocorticium*
Campylomyces Nakasone 2004 (*tabacinus*)	Gl ?				Close to *Veluticeps ?*
Candelabrochaete Boidin 1970 (*africana*)	Po	*Meruliaceae ?*	*	X	Polyphyletic genus

(*continued on next page*)

Table 3 – (*continued*)

Genus[a]	Order[b]	Family	Ref[c]	nLSU[d]	Remarks
Cejpomyces Pouzar 1970 (*terrigenus*)	?				With affinities to *Ceratobasidiaceae* ?
Ceraceohydnum Jülich 1978 (*brunneum*)	Po	*Meruliaceae*			Syn. *Mycoaciella*
Ceraceomyces Jülich 1972 (*tessulatus*)	Am	*Amylocorticiaceae*	E	X	Polyphyletic genus
Ceratobasidium D.P. Rogers 1935 (*calosporum*)	Ca	*Ceratobasidiaceae*			
Cericium Hjortstam 1995 (*luteoincrustatum*)	Ag ?				May have affinities to *Cystostereaceae*
Cerinomyces Martin 1949 (*pallidus*)	Da		E	X	
Cerocorticium Henn. 1899 (=*molle*)	?				
Chaetodermella Rauschert 1988 (*luna*)	Gl		!	X	
Chaetoporellus Bondartsev & Singer 1944 (*latitans*)	Hy	?			Syn. *Kneiffiella* ? *C. curvisporus* sequenced. See Larsson et al. (2006)
Chondrostereum Pouzar 1959 (*purpureum*)	Ag	*Cyphellaceae*	E	X	
Clavulicium Boidin 1957 (=*macounii*)	?		*	X	
Climacodon P. Karst. 1881 (*septentrionalis*)	Po	*Phanerochaetaceae*	F	X	
Columnocystis Pouzar 1959 (*abietina*)	Gl	*Gloeophyllaceae*	!	X	Syn. *Veluticeps*
Conferticium Hallenb. 1980 (*insidiosum*)	Ru	*Stereaceae*	D		*C. ochraceum* sequenced. Paraphyletic genus
Confertobasidium Jülich 1972 (*olivaceoalbum*)	Ru	*Peniophoraceae*	D	X	
Coniophora DC 1815 (=*puteana*)	Bo	*Coniophoraceae*		X	
Coniophorafomes Rick 1934 (*stereoides*)	Ru	?	*	X	Syn. *Scytinostromella cerina*
Coniophoropsis Hjortstam & Ryvarden 1986 (*obscura*)	Bo ?				
Conohypha Jülich 1975 (*albo-cremea*)	?		*	X	
Coralloderma D.A. Reid 1965 (*acroleucum*)	?				
Corneromyces Ginns 1976 (*kinabalui*)	Bo ?				
Coronicium J. Erikss. & Hjortstam 1975 (*gemmiferum*)	Ag	*Pterulaceae*	E		*C. alboglaucum* sequenced
Corticium Pers. 1794 (*roseum*)	Co	*Corticiaceae*	E	X	
Cotylidia P. Karst. 1881 (*undulata*)	Hy	*Rickenella* family	*	X	
Cristinia Parmasto 1968 (*helvetica*)	Ag	*Stephanosporaceae*	!	X	
Crustoderma Parmasto 1968 (*dryinum*)	?		*	X	
Crustodontia Hjortstam & Ryvarden 2005 (*chrysocreas*)	Po	*Meruliaceae*	F	X	
Crustomyces Jülich 1978 (*subabruptus*)	Ag ?	*Cystostereaceae* ?			With affinities to *Cystostereum*
Cunninghammyces Stalpers 1985 (*umbonatus*)	Ag	*Cyphellaceae*	*	X	
Cyanobasidium Jülich 1979 (*chordulatum*)	Ag ?	*Stephanosporaceae* ?			With affinities to *Lindtneria* ?
Cyanodontia Hjortstam 1987 (*spathulata*)	?				
Cylindrobasidium Jülich 1974 (=*laeve*)	Ag	*Physalacriaceae*	E	X	
Cymatoderma Jungh. 1840 (*elegans*)	Po	*Meruliaceae*	*		*C. caperatum* sequenced. See Yoon *et al.* (2003)
Cyphellostereum D.A. Reid 1965 (*pusiolum*)	Hy	*Rickenella* family		X	*C. leave* sequenced. See Larsson *et al.* (2007)
Cystidiodontia Hjortstam 1983 (=*laminifera*)	Ag	*Cystostereaceae*	!	X	*Polyporaceae* according to Binder *et al.* (2005)
Cystostereum Pouzar 1959 (*murrayi*)	Ag	*Cystostereaceae*	!	X	*Polyporaceae* according to Lim (2001)
Cytidia Quél. 1888 (=*salicina*)	Co	*Corticiaceae*	A	X	See also Hallenberg & Parmasto (1998)
Cytidiella Pouzar 1954 (=albomellea)	Po	*Byssomerulius* family	F	X	
Dacryobasidium Jülich 1981 (*coprophilum*)	Ag ?	*Stephanosporaceae* ?			Syn. *Cristina* ?
Dacryobolus Fr. 1849 (*sudans*)	Po	*Fomitopsidaceae*	F	X	
Dendrocorticium M.J. Larsen & Gilb. 1974 (*polygonioides*)	Co	*Corticiaceae*	F	X	See also Hallenberg & Parmasto (1998)
Dendrodontia Hjortstam & Ryvarden 1980 (*bicolor*)	Po ?	*Polyporaceae* ?			Syn. *Dentocorticium* ? See Binder *et al.* (2005)
Dendrophora Chamuris 1987 (*versiforme*)	Ru	*Peniophoraceae*			See Hsiau & Harrington (2003)
Dendrophysellum Parmasto 1968 (*amurense*)	?				
Dendrothele Höhn. & Litsch. 1907 (=*griseo-cana*)	Ag	*Lachnellaceae*	F	X	Polyphyletic genus
Dentipellis Donk 1962 (*fragilis*)	Ru	*Hericiaceae*	D	X	Polyphyletic genus
Dentipratulum Domanski 1965 (*bialoviesense*)	Ru	*Auriscalpiaceae*	D	X	
Dentocorticium M.J. Larsen & Zak 1974 (*ussuricum*)	Po	*Polyporaceae*	F		*D. sulphurellum* sequenced
Dextrinocystidium Sheng H. Wu 1995 (*sacratum*)	Ru ?	*Stereaceae* ?			
Dextrinocystis Gilb. & M. Blackw. 1988 (*capitata*)	Tr ?	*Trechisporaceae* ?			With affinities to *Tubulicium*
Dextrinodontia Hjortstam & Ryvarden 1980 (*molliuscula*)	Tr ?	*Trechisporaceae* ?			Syn. *Trechispora* ?
Dichostereum Pilát 1926 (*durum*)	Ru	*Peniophoraceae*	D	X	
Dichopleuropus D.A. Reid 1965 (*spathulatus*)	?				

Table 3 – (*continued*)

Genus[a]	Order[b]	Family	Ref[c]	nLSU[d]	Remarks
Donkia Pilát 1936 (*pulcherrima*)	Po	*Phanerochaetaceae*	*	X	See Lim (2001)
Duportella Pat. 1915 (=*tristicula*)	Ru	*Peniophoraceae*			See Boidin *et al.* (1998)
Echinodontium Ellis & Everh. 1900 (*tinctorium*)	Ru	*Echinodontiaceae*	C	X	
Efibula Sheng H. Wu 1990 (*tropica*)	Po	*Phanerochaetaceae ?*	A		*E. pallido-virens* sequenced
Elaphocephala Pouzar 1983 (*iocularis*)	?				
Entomocorticium H.S. Whitney *et al.* 1987 (*dendroctoni*)	Ru	*Peniophoraceae*			See Hsiau & Harrington (2003)
Epithele Pat. 1900 (*typhae*)	Po	*Polyporaceae*	*	X	See also Boidin *et al.* (1998)
Epithelopsis Jülich 1976 (*fulva*)	?				
Erythricium J. Erikss. & Hjortstam 1970 (*laetum*)	Co	*Corticiaceae*	E	X	
Erythromyces Hjortstam & Ryvarden 1990 (*crocicreas*)	?				
Exobasidiellum Donk 1931 (*graminicolum*)	?				
Fibriciellum J. Erikss. & Ryvarden 1975 (*silvae-ryae*)	Tr	*Trechisporaceae*			
Fibricium J. Erikss. 1958 (*rude*)	Hy	?	F	X	Polyphyletic genus
Fibrodontia Parmasto 1968 (*gossypina*)	Tr	*Hydnodontaceae*	F	X	
Fibulomyces Jülich 1972 (*mutabilis*)	At	*Atheliaceae*	*	X	Polyphyletic genus
Flavodon Ryvarden 1973 (*flavus*)	Po ?	*Polyporaceae ?*			
Flavophlebia K.H. Larss. & Hjortstam 1977 (*sulfureoisabellina*)	?				
Galzinia Bourdot 1922 (*pedicellata*)	Co	*Corticiaceae*	F		*G. incrustans* sequenced
Globuliciopsis Hjortstam & Ryvarden 2004 (*fuegiana*)	?				
Globulicium Hjortstam 1973 (*hiemale*)	Hy	*Rickenella* family		X	See Larsson et al. (2006)
Gloeocorticium Hjortstam & Ryvarden 1986 (*cinerascens*)	?				
Gloeocystidiellum Donk 1931 (*porosum*)	Ru	*Gloeocystidiellaceae*	D	X	Genus probably polyphyletic
Gloeocystidiopsis Jülich 1982 (*flammea*)	Ru	*Stereaceae*	D	X	
Gloeodontia Boidin 1966 (*discolor*)	Ru	*Gloeodontia* family	D	X	
Gloeohypochnicium Hjortstam 1987 (*analogum*)	Ru	?	D	X	
Gloeomyces Sheng H. Wu 1996 (*graminicola*)	Ru	*Stereaceae*	D	X	See comments in Larsson & Larsson (2003)
Gloeopeniophorella Rick 1934 (*rubro-flava*)	Ru	*Russulaceae*	D		*G. convolvens* sequenced
Gloeosoma Bres. 1920 (*vitellina*)	Ru	*Stereaceae ?*			See Wu *et al.* (2001)
Gloeostereum S. Ito & Imai 1933 (*incarnatum*)	Ag	*Cyphellaceae*	F	X	
Gloiodon P. Karst. 1879 (*strigosus*)	Ru	*Auriscalpiaceae*	D	X	
Gloiothele Bres. 1920 (*lamellosa*)	Ru	*Peniophoraceae*	D	X	
Grammothele Berk. & M.A. Curtis 1868 (*lineata*)	Po	*Polyporaceae*	F		*G. fuligo* sequenced
Grammothelopsis Jülich 1981 (*macrospora*)	Po ?				
Granulobasidium Jülich 1979 (*vellereum*)	Ag	*Cyphellaceae*	E	X	
Gyrodontium Pat. 1900 (=*sacchari*)	Bo	*Coniophoraceae*		X	See Carlier *et al.* (2004)
Hemmesomyces Gilb. & Nakasone 2003 (*puauluensis*)	?				
Heteroacanthella Oberw. *et al.* 1990 (*variabile*)	?				See Roberts (1998)
Hjortstamia Boidin & Gilles 2002 (*friesii*)	Po	*Phanerochaetaceae ?*			Close to *Porostereum*
Hydnocristella R.H. Petersen 1971 (*himantia*)	Go	*Lentariaceae*	F	X	Distinct from *Kavinia*
Hydnodon Banker 1913 (*thelephora*)	Tr	*Hydnodontaceae*	*	X	Syn. Trechispora. See Ryvarden (2002)
Hydnomerulius Jarosch & Besl 2001 (*pinastri*)	Bo	*Paxillaceae*	F	X	See Jarosch & Besl (2001)
Hydnophlebia Parmasto 1967 (*chrysorhiza*)	Po	*Meruliaceae*	F	X	See also De Koker *et al.* (2003)
Hyphoderma Wallr. 1883 (=*setigerum*)	Po	*Meruliaceae*	E	X	Polyphyletic genus
Hyphodermella J. Erikss. & Ryvarden (*corrugata*)	Po	*Phanerochaetaceae*	*	X	
Hyphodermopsis Jülich 1982 (*polonensis*)	Po	*Meruliaceae*		X	Syn. *Hypochnicium ?* See Langer (2002)
Hyphodontia J. Erikss. 1958 (*pallidula*)	Hy	*Tubulicrinaceae*	F	X	See also Larsson *et al.* (2007)
Hyphodontiastra Hjortstam 1999 (*virgaecola*)	?				
Hyphodontiella Å. Strid 1975 (*multiseptata*)	Ag	*Clavariaceae*	!	X	
Hyphoradulum Pouzar 1987 (*conspicuum*)	Po ?				
Hypochnella J. Schröt 1888 (*violacea*)	?				
Hypochniciellum Hjortstam & Ryvarden 1980 (*ovoideum*)	Am ?		E		Type not sequenced
Hypochnicium J. Erikss. 1958 (*bombycinum*)	Po	*Meruliaceae*	F	X	See also Nilsson & Hallenberg (2003)
Inflatostereum D.A. Reid 1965 (*glabrum*)	?				
Intextomyces J. Erikss. & Ryvarden 1976 (*contiguus*)	?				
Irpex Fr. 1828 (*lacteus*)	Po	*Byssomerulius* family	A	X	Resequenced by Larsson (unpubl.)
Irpicodon Pouzar 1966 (*pendulus*)	Am	*Amylocorticiaceae*		X	See Niemelä *et al.* (2007)
Jaapia Bres. 1911 (*argillacea*)	Ja	*Jaapia* family	F	X	Maybe a distinct order
Jacksonomyces Jülich 1979 (*phlebioides*)	Po	*Meruliaceae*			
Kavinia Pilát 1938 (=*alboviridis*)	Go	*Lentariaceae*	E	X	
Kneiffiella P. Karst. 1889 (*barba-jovis*)	Hy	?	*	X	

(*continued on next page*)

Table 3 – (*continued*)

Genus[a]	Order[b]	Family	Ref[c]	nLSU[d]	Remarks
Korupella Hjortstam & P. Roberts 2000 (*denticulata*)	?				
Laetisaria Burds. 1979 (*fuciformis*)	Co	*Corticiaceae*	F	X	
Lagarobasidium Jülich 1974 (=*detriticum*)	Hy	*Schizoporaceae*		X	Syn. *Xylodon* ? See Larsson (2007)
Laurilia Pouzar 1959 (*sulcata*)	Ru	*Echinodontiaceae*	D	X	Syn. *Echinodontium* ?
Laxitextum Lentz 1955 (*bicolor*)	Ru	*Hericiaceae*	D	X	
Lazulinospora Burds. & M.J. Larsen (*wakefieldiae*)	Th	*Thelephoraceae*	*		Syn. Amaurodon. *L. cyaneus* sequenced
Leifia Ginns 1998 (*flabelliradiata*)	Hy	*Rickenella* family	*	X	Syn. *Odonticium* ?
Lepidomyces Jülich 1979 (*subcalceus*)	Ag ?	*Pterulaceae* ?			With affinities to *Aphanobasidium* ?
Leptocorticium Hjortstam & Ryvarden 2002 (*cyatheae*)	Co ?				
Leptosporomyces Jülich 1972 (*galzinii*)	At	*Atheliaceae*	*	X	Probably a polyphyletic genus
Leucogyrophana Pouzar 1958 (*mollusca*)	Bo	*Hygrophoropsidaceae*	F	X	Polyphyletic genus. See Jarosch & Besl (2001)
Lilaceophlebia Spirin & Zmitr. 2004 (*livida*)	Po	*Meruliaceae*	F	X	Introduced with 16 widely different species
Licrostroma P.A. Lemke 1964 (*subgiganteum*)	Ru	*Stereaceae* ?			With sulpho-positive gloeocystidia
Limonomyces Stalpers & Loer. 1982 (*roseipellis*)	Co ?				
Lindtneria Pilát 1938 (*trachyspora*)	Ag	*Stephanosporaceae*	!	X	
Litschauerella Oberw. 1965 (*abietis*)	Tr ?	*Hydnodontaceae* ?			With morphological affinities to *Tubulicium*
Lobulicium K.H. Larss. & Hjortstam 1982 (*occultum*)	At	*Atheliaceae*	*	X	
Lopharia Kalchbr. & MacOwan 1881 (=*mirabilis*)	Po	*Polyporaceae*	E	X	
Luellia K.H. Larss. & Hjortstam 1974 (*recondita*)	Tr	*Hydnodontaceae*	*	X	
Lyoathelia Hjortstam & Ryvarden 2004 (*laxa*)	At ?				
Marchandiobasidium Diederich & Schultheis 2003 (*aurantiacum*)	Co	*Corticiaceae*		X	See Lawrey *et al.* (2007)
Megalocystidium Jülich 1978 (*leucoxanthum*)	Ru	*Stereaceae*	D	X	
Melzericium Hauerslev 1975 (*udicola*)	?				
Melzerodontia Hjortstam & Ryvarden 1980 (*aculeata*)	Hy ?				
Membranomyces Jülich 1975 (*spurius*)	Ca	*Hydnaceae*	*	X	See also Larsson *et al.* (2004)
Merulicium J. Erikss. & Ryvarden 1976 (*fusisporum*)	Ag	*Pterulaceae*	!	X	
Meruliopsis Parmasto 1954 (*taxicola*)	Po	*Byssomerulius* family	E	X	The genus differs from the type of *Gloeoporus*
Metulodontia Parmasto 1968 (*nivea*)	Ru	*Peniophoraceae*	D	X	
Minostroscyta Hjortstam & Ryvarden 2001 (*discoidalis*)	?				
Mucronella Fr. 1874 (*calva*)	Ag	*Clavariaceae* ?	E	X	
Mycoacia Donk 1931 (*fuscoatra*)	Po	*Meruliaceae*	F	X	The genus is polyphyletic
Mycoaciella J. Erikss. & Ryvarden 1978 (*bispora*)	Po	*Meruliaceae*	E	X	
Mycobonia Pat. 1894 (*flava*)	?				
Mycoleptodonoides Nikol. 1952 (*vassiljevae*)	Po	*Meruliaceae* ?			
Mycorrhaphium Maas Geest. 1962 (*adustum*)	Po	*Meruliaceae* ?			
Mycothele Jülich 1976 (*disciformis*)	?				
Nodotia Hjortstam 1987 (=*lyndoniae*)	Po	*Meruliaceae*	*	X	Syn. Hypochnicium ?
Nothocorticium Greslebin & Rajchenb. 1999 (*patagonicum*)	?				
Odonticium Parmasto 1968 (*romellii*)	Hy	*Rickenella* family	*	X	The genus is probably polyphyletic
Odontiopsis Hjortstam & Ryvarden 1980 (*hyphodontina*)	Hy ?	?			
Oliveonia Donk 1958 (*fibrillosa*)	Ca ?	*Ceratobasidiaceae* ?			Roberts (1998) refers *Oliveonia* to *Exidiales*
Oncobasidium P.H.B. Talbot & Keane 1971 (*theobromae*)	Ca ?	*Ceratobasidiaceae* ?			Syn. *Thanatephorus* according to Roberts (1999)
Palifer Stalpers & P.K. Buchanan 1991 (*verecunda*)	Hy	*Schizoporaceae*	*	X	Syn. *Xylodon* ?
Papyrodiscus D.A. Reid 1979 (*ferrugineus*)	?				
Parastereopsis Corner 1976 (*borneensis*)	?				
Parvobasidium Jülich 1975 (*cretatum*)	Ag ?	*Cystostereaceae* ?			
Parvodontia Hjortstam & Ryvarden 2004 (*luteocystidia*)	Ag ?	*Cystostereaceae* ?			
Paullicorticium J. Erikss. 1958 (*pearsonii*)	?		*	X	Seems most related to *Dacrymycetales*
Peniophora Cooke 1879 (*quercina*)	Ru	*Peniophoraceae*	F	X	
Peniophorella P. Karst. 1889 (*pubera*)	Hy	*Rickenella* family	E	X	See Larsson (2007)
Phaeoradulum Pat. 1900 (*guadelupense*)	Bo	?			
Phanerochaete P. Karst. 1889 (=*velutina*)	Po	*Phanerochaetaceae*		X	Polyphyletic genus. See de Koker *et al.* (2003)
Phlebia Fr. 1821 (*radiata*)	Po	*Meruliaceae*	F	X	Polyphyletic genus. See Parmasto & Hallenberg (2000)
Phlebiella P. Karst. 1890 (*vaga*)	Ph	*Phlebiella* family	!	X	
Phlebiopsis Jülich 1978 (*gigantea*)	Po	*Phanerochaetaceae*		X	See Langer (2002)

Table 3 – (*continued*)

Genus[a]	Order[b]	Family	Ref[c]	nLSU[d]	Remarks
Phlyctibasidium Jülich 1974 (*polyporoideum*)	?		*	X	
Physodontia Ryvarden & H. Solheim 1977 (*lundellii*)	Hy	?	*	X	
Pileodon P. Roberts & Hjortstam 1998 (*megaspora*)	Gl ?				Close to *Veluticeps* ? See also Nakasone (2004)
Piloderma Jülich 1969 (=*fallax*)	At	*Atheliaceae*	E	X	
Pirex Hjortstam & Ryvarden 1985 (*concentricus*)	Po	?			Syn. *Pseudolagarobasidium* ? See de Koker *et al.* (2003)
Plicatura Peck 1872 (*nivea*)	Am ?				
Plicaturopsis D.A. Reid 1964 (*crispa*)	Am	*Amylocorticiaceae*	F	X	See also Niemelä *et al.* (2007)
Podoscypha Pat. 1900 (=*nitidula*)	Po	*Meruliaceae*	C		In its original sense probably not monophyletic
Podoserpula D.A. Reid 1963 (*pusio*)	Am ?			X	See Matheny *et al.* (2006)
Porogramme Pat. 1900 (=*albocincta*)	?				
Porostereum Pilát 1937 (=*spadiceum*)	Po	*Phanerochaetaceae*		X	See Yoon *et al.* (2003)
Pseudolagarobasidium J.C. Jang & T. Chen 1985 (*subvinosum*)	Po	*Phanerochaetaceae* ?			
Pseudomerulius Jülich 1979 (*aureus*)	Bo	*Tapinella* family	F	X	
Pseudoxenasma K.H. Larss. & Hjortstam 1976 (*verrucisporum*)	Ru	*Russulaceae* ?	D	X	
Pteridomyces Jülich 1979 (*galzinii*)	At ?				With affinities to *Athelopsis*
Punctularia Pat. 1895 (=*subhepatica*)	Co	*Corticiaceae*	F	X	
Radulodon Ryvarden 1972 (*americanus*)	Po	*Meruliaceae*	*		*R. erikssonii* sequenced
Radulomyces M.P. Christ 1960 (*confluens*)	Ag	*Pterulaceae*	E	X	
Ramaricium J. Erikss. 1954 (*occultum*)	Go ?	*Lentariaceae* ?	F		Type not sequenced. Compare *Phlyctibasidium*
Repetobasidiellum J. Erikss. & Hjortstam 1981 (*fusisporum*)	?				
Repetobasidium J. Erikss. 1958 (*vile*)	Hy	*Rickenella* family	F		Type not sequenced
Resinicium Parmasto 1968 (*bicolor*)	Hy	*Rickenella* family	F	X	Polyphyletic genus
Rhizochaete Greslebin *et al.* 2004 (*brunnea*)	Po	*Phanerochaetaceae*		X	See Greslebin *et al.* (2004)
Ripexicium Hjortstam 1995 (*spinuliferum*)	?				
Rogersella Liberta & Navas 1978 (=*griselinae*)	Hy	*Schizoporaceae*	*	X	Syn. *Xylodon* ?
Roseograndinia Hjortstam & Ryvarden 2005 (*rosea*)	Po ?	*Phanerochaetaceae* ?			
Sarcodontia Schulz.1866 (=*crocea*)	Po	*Meruliaceae*		X	Unpublished sequence in GenBank
Schizopora Velen. 1922 (=*paradoxa*)	Hy	*Schizoporaceae*	F	X	Syn. *Xylodon* ?
Scopulodontia Hjortstam 2007a (=*latemarginata*)	?				
Scopuloides Hjortstam & Ryvarden 1979 (*hydnoides*)	Po	*Meruliaceae*	F	X	
Scotoderma Jülich 1974 (*viride*)	?				
Scotomyces Jülich 1978 (=*subviolaceus*)	?		*	X	
Scytinostroma Donk 1956 (*portentosum*)	Ru	*Peniophoraceae*	D	X	Polyphyletic genus
Scytinostromella Parmasto 1968 (*heterogenea*)	Ru	?	D	X	Polyphyletic genus
Sebacinella Hauerslev 1977 (*nodosa*)	Ca ?	*Ceratobasidiaceae* ?			Syn. *Oliveonia* according to Roberts (1998)
Serpula Gray 1821 (=*lacrymans*)	Bo	?	F	X	See also Carlier *et al.* (2004)
Serpulomyces Zmitr. 2001 (*borealis*)	Am	*Amylocorticiaceae*	!	X	
Sistotrema Fr. 1821 (*confluens*)	Ca	*Hydnaceae*	E	X	Paraphyletic genus
Sistotremastrum J. Erikss. 1958 (*suecicum*)	Tr	*Sistotremastrum* fam.	!	X	
Sistotremella Hjortstam 1984 (*perpusilla*)	?				
Skeletohydnum Jülich 1979 (*nikau*)	Po ?				
Skvortzovia Bononi & Hjortstam 1987 (*furfurella*)	Hy	*Rickenella* family	!	X	See also Larsson et al. (2006)
Sphaerobasidium Oberw. 1965 (*minutum*)	Hy	*Tubulicrinaceae* ?	F	X	
Stecchericium D.A. Reid 1963 (=*seriatum*)	Ru	*Wrightoporiaceae* ?			Perhaps related to *Scytinostromella* or *Wrigthoporia*
Steccherinum S.F. Gray 1821 (*ochraceum*)	Po	*Meruliaceae*	!	X	Polyphyletic genus
Stereofomes Rick 1828 (*nodulosus*)	Ru	*Peniophoraceae*			Syn. *Scytinostroma* ?
Stereopsis D.A. Reid 1965 (*radicans*)	?		*	X	
Stereum Pers. 1794 (*hirsutum*)	Ru	*Stereaceae*	D	4	
Subulicium Hjortstam & Ryvarden 1979 (*lautum*)	Hy ?				
Subulicystidium Parmasto 1968 (*longisporum*)	Tr	*Hydnodontaceae*	F	X	
Suillosporium Pouzar 1958 (*cystidiatum*)	?				
Thanatephorus Donk 1956 (=*cucumeris*)	Ca	*Ceratobasidiaceae*	F	2	See Roberts (1998)
Thujacorticium Ginns 1988 (*mirabile*)	?		*	X	
Tofispora Langer 1994 (*repetospora*)	Ca	*Ceratobasidiaceae* ?			
Tomentellopsis Hjortstam 1970 (*echinospora*)	Th	*Thelephoraceae*	E	X	
Trechinotus E.C. Martini & Trichies 2004 (*smardae*)	?		*	X	
Trechispora P. Karst. 1890 (=*hymenocystis*)	Tr	*Hydnodontaceae*	E	X	

(*continued on next page*)

Table 3 – (continued)

Genus[a]	Order[b]	Family	Ref[c]	nLSU[d]	Remarks
Tubulicium Oberw. 1965 (*vermiferum*)	Tr	*Hydnodontaceae*	E	X	
Tubulicrinis Donk 1956 (*glebulosus*)	Hy	*Tubulicrinaceae*	F	X	Polyphyletic genus
Tylospora Donk 1960 (=*asterophora*)	At	*Atheliaceae*	E	X	
Uncobasidium Hjortstam & Ryvarden 1978 (*luteolum*)	?				
Uthatobasidium Donk 1956 (*fusisporum*)	Ca	*Ceratobasidiaceae*	F	X	
Vararia P. Karst. 1898 (=*investiens*)	Ru	*Peniophoraceae*	D	X	See also Boidin *et al.* (1998)
Veluticeps Pat. 1894 (*berkeleyi*)	Gl	*Gloeophyllaceae*	F	X	
Vesiculomyces Hagström 1977 (*citrinus*)	Ru	*Peniophoraceae*	D	X	
Vuilleminia Maire 1902 (*comedens*)	Co	*Corticiaceae*	C	X	
Waitea Warcup & P.H.B. Talbot 1962 (*circinata*)	Co	*Corticiaceae*		X	DePriest *et al.*(2005)
Xenasma Donk 1957 (*rimicola*)	?				Binder *et al.* (2005) refer *Xenasma* to *Russulales*
Xenosperma Oberw. 1965 (*ludibundum*)	?				
Xylobolus P. Karst. 1881 (*frustulatus*)	Ru	*Stereaceae*	D	X	See also Wu *et al.* (2001)
Xylodon Gray 1821 (*quercinum*)	Hy	*Schizoporaceae*		X	See Larsson *et al.* (2006)
Ypsilonidium Donk 1972 (*sterigmaticum*)	Ca ?	*Ceratobasidiaceae ?*			Syn. *Thanatephorus ?*

a Type species epithets are given in parenthesis. When preceded by = the original epithet is synonymized with the current epithet given here.
b Order names are abbreviated as follows: Ag, *Agaricales*; At, *Atheliales*; Bo, *Boletales*; Ca, *Cantharellales*; Co, *Corticiales*; Da, *Dacrymycetales*; Gl, *Gloeophyllales*; Go, *Gomphales*; Hy, *Hymenochaetales*; Po, *Polyporales*; Ru, *Russulales*; Th, *Thelephorales*; Tr, *Trechisporales*. Families without order affiliation are Am, *Amylocorticiaceae*, Ja, *Jaapia* family; Ph, *Phlebiella* family.
c This column lists some important papers that had an emphasis on corticioid species. A, Lim (2001); B, Wu *et al.* (2001); C, Hibbett & Binder (2002); D, Larsson & Larsson (2003); E, Larsson *et al.* (2004); F, Binder *et al.* (2005); !, this study; *, Larsson unpublished.
d X = a nuLSU sequence of the type species is available in GenBank or as unpublished data.

and chlamydospores. Neither of them have any kind of cystidia. Both genera have thick-walled basidiospores and were once placed in *Hypochnicium* (Boidin *et al.* 1986, as *H. pleurobasidiatum*; Eriksson & Ryvarden 1976).

Hygrophoraceae Lotsy 1907

Athelicium, Athelia p.p.

Athelicium is a genus combining unusually small basidiomata with larger than average basidia and spores. Species grow on wood exposed to drought. In phylogenetic analyses *Athelicium* associates with *Lichenomphalia* and *Arrhenia* species and with *Athelia pyriformis*. The last species was first described as a *Xenasma* (Christiansen 1960), then moved to *Athelidium* (Oberwinkler 1965), and finally referred to *Athelia* (Jülich 1972). None of these arrangements is appropriate, nor is it feasable to put it in *Athelicium*. A separate genus for *Athelia pyri-formis* is probably the best solution.

Lachnellaceae Boud. 1907

Dendrothele

A recent paper on the phylogeny of cyphelloid basidiomycetes has contributed much new information to take into consideration when agaric phylogeny is discussed (Bodensteiner *et al.* 2004). One distinct clade recovered by Bodensteiner *et al.* (2004), and named by them as the *Nia* clade, is composed of several cyphelloid genera, the marine species *Nia vibrissa*, and two species of *Dendrothele*, one being the generic type *D. griseo-cana*. *Dendrothele* is a highly polyphyletic genus and representatives occur in i. a. *Corticiales*, *Russulales*, and possibly *Polyporales*. *Dendrothele* species grow on the bark of living trees and have convergently developed similar properties for survival in an exposed environment. These adaptations include dendrohyphidia and a strong incrustation as protection against desiccation, and a catahymenium as an adaptation to intermittent sporulation. The oldest family name available seems to be *Lachnellaceae* (Matheny *et al.* 2007a).

Physalacriaceae Corner 1970

Cylindrobasidium

The corticioid genus *Cylindrobasidium* is firmly established as a member of *Agaricales* through several investigations (Hibbett & Binder 2002; Langer 2002; Larsson *et al.* 2004). Moncalvo *et al.* (2002) recovered a clade with representatives for among others *Rhodotus, Flammulina, Strobilurus, Gloiocephala, Xerula*, and *Armillaria*. They called this clade /physalacriaceae. Binder *et al.* (2005) found the same clade, but with a slightly different sampling, that also included *Cylindrobasidium laeve* and two species of *Physalacria*. If *Armillaria* in future phylogenetic analyses remains a member of the clade, as indicated by Matheny *et al.* (2007a), then *Armillariaceae* is available as an older name. *Cylindrobasidium* and *Physalacria* are sister taxa. The mainly tropical genus *Physalacria* consists of small stalked species with a more or less globose and hollow head. Species have fusiform or ventricose cystidia, narrowly clavate basidia, and mostly pip-shaped to fusiform spores. The same micro-characters are found in *Cylindrobasidium*.

Pterulaceae Corner 1970

Aphanobasidium, Coronicium, ?Lepidomyces, Merulicium, Radulomyces

Pterula is typified by *Pterula subulata* Fr. and this species is not yet among those sequenced. Therefore, the adoption of the name *Pterulaceae* for this group must be taken with some caution. Pteruloid fungi have recently come into focus when it was shown that leaf-cutting ants in the genus *Apterostigma* cultivate a *Pterula*-related fungus (Munkacsi *et al.* 2004). Larsson *et al.* (2004) found that a seemingly odd set of corticioid species with *Radulomyces, Coronicium*, and *Phlebiella* *pseudotsugae* was recovered inside the euagarics clade. To this group we can now add *Merulicium fusisporum*. After the recent publication of *Pterula* sequences it is possible to establish a connection with the corticioid species mentioned. *Pterula* species are dimitic and often have elliptical to navicular spores. The same spore morphology characterizes *Coronicium*, *Merulicium*, and *Phlebiella pseudotsugae* whereas the spores in *Radulomyces* are different. *Pterula* and *Merulicium* are dimitic but the other genera are monomitic. *Phlebiella pseudotsugae* is apparently not congeneric with the type species *P. vaga*, which here is referred to a separate family. For *P. pseudotsugae,* the genus *Aphanobasidium* is available, and it now seems appropriate to use *Phlebiella* in a more restricted sense as advocated by Jülich (1979) and Boidin & Gilles (1989).

Schizophyllaceae Roze 1876

Auriculariopsis

With its cupulate basidiomata *Auriculariopsis* will not be perceived as corticioid but was treated in *The Corticiaceae of North Europe* (Eriksson & Ryvarden 1975) and is, therefore, also discussed here. It is well known that the type of *Auriculariopsis* is closely related to *Schizophyllum*. It has also been suggested that *Cytidiella albomellea* should be placed together with *Auriculariopsis* but such an arrangement receives no support in molecular phylogenies (Nakasone 1996; Binder *et al.* 2005). It is likely that *Meruliaceae* (Polyporales) is the correct place for *Cytidiella*. Nakasone (1996) synonymized *Cytidiella* with *Phlebia* but taking recent data into account *Cytidiella* seems best placed in the *Byssomerulius* family and not close to *Phlebia* s.s.

Stephanosporaceae Oberw. & Horak 1979

Athelidium, Cristinia, ?Cyanobasidium, ?Dacryobasidium, Lindtneria

This family was introduced for *Lindtneria* and the gastroid *Stephanospora*. Both genera have highly characteristic thick-walled, strongly ornamented, cyanophilous spores, and in both genera, species have orange yellow to reddish basidiomata. *Lindtneria* also has a cyanophilous granulation in immature basidia and the same phenomenon can be observed in the smooth-spored genus *Cristinia*. A connection between *Lindtneria* and *Cristinia* was predicted by Eriksson & Ryvarden (1975) and is now confirmed by molecular data. *Athelidium aurantiacum*, the only species in the genus, is a quite rare species with simple-septate hyphae, thin-walled smooth spores, and basidia without cyanophilous granulation. The only character pointing to the other species in the family is the bright yellow–orange basidioma colour.

Incertae sedis

Adustomyces

Atheliales Jülich 1982

This small order is composed entirely of corticioid species. Its position close to *Agaricales* and *Boletales* was earlier indicated (Larsson *et al.* 2004, Binder *et al.* 2005) and again confirmed here (Fig 1).

Atheliaceae Jülich 1982

Amphinema, Athelia, Athelopsis, Byssocorticium, ?Caerulicium, Fibulomyces, Leptosporomyces, Lobulicium, ?Lyoathelia, Piloderma, ?Pteridomyces, Tylospora

All species have pellicular basidiomata of a simple construction with thin-walled hyphae in a monomitic hyphal system. Cystidia are rare and, if present, are little differentiated. Most species were once included in a broadly defined *Athelia* but later distributed over several smaller genera (Jülich 1972). The validity of some of these genera, e.g. *Fibulomyces* and *Confertobasidium* has been questioned (Eriksson & Ryvarden 1975). However, molecular data seem to support a narrow genus concept close to the one advocated by Jülich (1972). Molecular data also indicate that both *Athelia* and *Athelopsis* are polyphyletic. *Byssoporia terrestris* was originally included in *Byssocorticium* but segregated because of the non-blue basidioma, thin-walled spores, and unclamped basidial bases (Larsen & Zak 1978). Bruns *et al.* (1998) recovered *Byssoporia* close to *Russulaceae* when studying mtSSU data and this surprising position is confirmed here (*Albatrellaceae*; Fig 1).

Boletales E.-J. Gilbert 1931

Boletales emerges as a monophyletic taxon with good support in several molecular phylogenetic analyses (Binder & Hibbett 2002; Larsson *et al.* 2004; Binder *et al.* 2005; Matheny *et al.* 2007b). All corticioid fungi in *Boletales* are wood-inhabiting and associated with a brown rot, some of them causing significant damage in timber constructions. The subdivision of *Boletales* with regard to corticioid taxa was not resolved in the present phylogeny and other published trees of the *Boletales* either did not consider the corticioid element (e.g. Grubisha *et al.* 2001; Binder & Bresinsky 2002) or demonstrate conflicting evidence (e.g. Jarosch & Besl 2001; Carlier *et al.* 2004; Binder *et al.* 2005; Binder & Hibbett 2007).

Coniophoraceae Ulbr. 1928

Coniophora, Gyrodontium, ?Leucogyrophana p.p.

The circumscription of *Coniophoraceae* can not be settled with available data and published phylogenies do not give support for the inclusion of *Leucogyrophana* and *Serpula*. According to Jarosch & Besl (2001), *Leucogyrophana* is polyphyletic and could be reduced to just the type and included in *Hygrophoropsidaceae,* whereas the rest of *Leucogyrophana* would stay with *Coniophora*. The latter solution gains support from both secondary metabolite investigations (Jarosch 2001) and published data (Binder *et al.* 2005) but is rejected by our own analyses. Binder & Hibbett (2007) suggest that *Serpula* is referred to *Serpulaceae* and our own data does not contradict that arrangement. However, until a more inclusive dataset is analysed we prefer to list *Serpula* among *Incertae sedis*.

Hygrophoropsidaceae Kühner 1980

Leucogyrophana

See discussion under *Coniophoraceae*.

Paxillaceae Maire 1902

Hydnomerulius

The only corticioid genus that possibly could be placed here is *Hydnomerulius*, recently created for *Hydnum pinastri* (Jarosch & Besl 2001). The arrangement is supported by molecular data, as well as seconday metabolite composition (Jarosch 2001), but rejected by the analyses by Binder & Hibbett (2006). *Paxillus* is generally regarded as mycorrhizal but the nutritional strategy for *Hydnomerulius* is not known. However, fruit bodies of *H.*

pinastri are sometimes found in connection with dead wood and roots deeply buried in the soil, which would be the expected place if the fungus is parasitic or mycorrhizal.

Tapinella family

Pseudomerulius, Leucogyrophana p.p.

Binder *et al.* (2005) recovered a well-supported group including *Tapinella* and *Pseudomerulius aureus*. Larsson *et al.* (2004) showed that *Pseudomerulius* was separated from other corticioid taxa in *Boletales* and accompanied by *Bondarzevomyces taxi*. We have recently found that also *Leucogyrophana montana* has its place here. There is no family name available for this constellation. *Pseudomerulius aureus* forms effused to effused-reflexed basidiomata and *Leucogyrophana montana* is strictly effused.

Incertae sedis

Coniophoropsis, ?Corneromyces, Phaeoradulum, Serpula

Cantharellales Gäum. 1926

The circumscription of *Cantharellales* has been controversial. In several phylogenetic analyses (e.g. Hibbett & Binder 2002; Binder *et al.* 2005; Lawrey *et al.* 2007) *Tulasnellaceae* and *Ceratobasidiaceae* are included in *Cantharellales* but support for that arrangement has sometimes been weak. A recent multi-gene study of *Basidiomycota* shows better resolution (Matheny *et al.* 2007b) and implies that *Tulasnellaceae* and *Ceratobasidiaceae* really belong to *Cantharellales*. This is also the arrangment accepted by Hibbett *et al.* (2007). Both families include species with holobasidia and spore-repetition. The latter character is usually associated with heterobasidiomycetes. However, it has been customary to include *Ceratobasidiaceae* among the corticioid fungi but to exclude *Tulasnellaceae* because of its strongly deviating basidium morphology. That convention is followed here.

Botryobasidiaceae Jülich 1982

Botryobasidium, Botryohypochnus

Presently two genera are included in this well-supported family, *Botryobasidium* with smooth spores and usually 6–8 sterigmata and *Botryophypochnus* with spiny spores and 4-sterigmate basidia. According to molecular data recognition of *Botryohypochnus* makes *Botryobasidium* paraphyletic, which supports the synonymization suggested by Langer (1994). All species produce thin, delicate basidiomata with characteristic wide hyphae and many species are associated with anamorphs from the form-genus *Haplotrichum*. Little is known about their ecology.

Ceratobasidiaceae G. W. Martin 1948

Ceratobasidium, ?Oliveonia, ?Oncobasidium, ?Sebacinella, Thanatephorus, Tofispora, Uthatobasidium, ?Ypsilonidium

Ceratobasidium, *Thanatephorus*, and *Uthatobasidium* all develop thin, delicate basidiomata with wide hyphae and short basidia with 2–4 sterigmata. Genus limits are unclear. Roberts (1999) preferred a wide concept for *Thanatephorus* and included also *Uthatobasidium*, *Ypsilonidium*, and *Tofispora*, the last with asperulate spores. Molecular phylogenetic analyses have presented conflicting information regarding the homogeneity of *Ceratobasidium* (Kottke *et al.* 2003; Taylor *et al.* 2003), which suggests that more species but also alternative genes should be sampled.

Hydnaceae Chev. 1826

Membranomyces, Sistotrema

This family displays stipitate, clavarioid and resupinate basidioma types and smooth, hydnoid, and poroid hymenophore configurations. The clavarioid *Clavulina* has characteristic 2-sterigmate basidia and rounded, slightly thick-walled spores with strongly light-refracting contents. The same basidium and spore morphology is seen in the corticioid *Membranomyces* (Larsson *et al.* 2004). *Sistotrema* is typified by the stipitate-hydnoid *S. confluens*, whereas the rest of the genus consists of resupinate species. The genus is clearly non-monophyletic (Nilsson *et al.* 2006a; Moncalvo *et al.* 2007). The type and a few other species with poroid basdiomata form together with *Hydnum* and possibly also *Cantharellus* a well-supported subclade where ectomycorrhiza seems to be the nutritional strategy (Nilsson *et al.* 2006a). Remaining species have to be distributed over several genera.

Corticiales K.H. Larss. 2007

Corticiaceae Herter 1910

Corticium, Cytidia, Dendrocorticium, Dendrothele p.p., Erythricium, Galzinia, Laetisaria, ?Leptocorticium, ?Limonomyces, Marchandiobasidium, Marchandiomyces, Punctularia, Vuilleminia, Waitea

Also in a strict sense *Corticiaceae* remains a family for corticioid species only. The family is characterized by spores with a pink colour of the spore-wall, which is evident in a spore print. Most species are saprotrophic wood fungi, but some are parasitic on grasses or lichens. Many species develop a catahymenium with probasidia deeply sunken in a dense layer of dendrohyphidia. This seems to be an adaptation to desiccation.

Marchandiomyces is an anamorph genus with species developing orange to red sclerotia on lichens (DePriest *et al.* 2005). Also the recently described lichenicolous genus *Marchandiobasidium* belongs here (Diederich *et al.* 2003; Lawrey *et al.* 2007). *Waitea* has earlier been placed in *Ceratobasidiaceae* because it is associated with the anamorph *Rhizoctonia zeae*, but is now shown to have its place in *Corticiaceae* (DePriest *et al.* 2005). *Waitea* has basidia with the same morphology as other members of *Corticiaceae* and quite different from those occurring in *Ceratobasidiaceae*. Besides, basidiomata are pinkish, another feature not seen among members of *Ceratobasidiaceae*.

Gloeophyllales Thorn 2007

Gloeophyllaceae Jülich 1982

?Amylohyphus, Boreostereum, ?Campylomyces, Chaetodermella, ?Pileodon, Veluticeps

Species within this family are saprotrophs and all are associated with a brown rot. All the corticioid genera have a hymenium composed of basidia and numerous incrusted but otherwise undifferentiated cystidioles of a size similar to the basidia. Hyphae and cystidioles in *Boreostereum* have a characteristic brown incrustation that turns greenish in potassium hydroxide (KOH). When collected *Boreostereum* basidiomata are often sterile and cystidioles are dominating the hymenium. Several species have long, projecting cystidia and spores are usually fairly large and narrowly ellipsoid.

Columnocystis was originally kept separate from *Veluticeps* but the morphological similarities were independently pointed out by Hjortstam & Tellería (1990) and Nakasone (1990a). In nuSSU phylogenetic analyses by Kim & Jung

(2000) and Yoon *et al.* (2003) *Columnocystis abietina* and *C. ambigua* group with *Meripilus giganteus* whereas *Veluticeps berkeleyi*, *Gloeophyllum sepiarium*, and *Boreostereum radicatum* occur together on a different branch. In our own analyses using nuLSU the connection between *Columnocystis abietina* and *Veluticeps berkeleyi* is strong, thus supporting the synonymy suggested by Hjortstam & Tellería (1990).

Pileodon and *Campylomyces* may belong here (Hjortstam *et al.* 1998; Nakasone 2004). *Campylomyces* is segregated from *Veluticeps*, and according to Nakasone (2004), the three genera have striking similarities.

Gomphales Jülich 1982

Gomphales is one of four orders constituting the subclass *Phallomycetidae* (Hosaka *et al.* 2007). The other three orders, *Geastrales*, *Hysterangiales*, and *Phallales*, are composed entirely of various gasteromycetes and are not of interest for the present study.

Lentariaceae Jülich 1982

Hydnocristella, Kavinia, ?Ramaricium

Kavinia and *Hydnocristella* are usually listed among the corticioid fungi but they could equally well be regarded as clavarioid. Their downward-facing hydnoid basidiomata are composed of numerous fertile spines developing from a common sterile mycelial mat. Molecular data support that Kavinia is restricted to species with ornamented spores, whereas smooth-spored species are referred to *Hydnocristella*.

The only truly corticioid genus that has been associated with *Gomphales* is *Ramaricium*. The type species, *R. occultum*, has ornamented spores whereas the single species sequenced, *R. alboflavescens*, has smooth spores. In phylogenetic analyses (Binder *et al.* 2005), as well as micromorphological characters, *R. alboflavescens* shows affinities to the clavarioid genus *Lentaria*. However, the position of the verrucose-spored *Ramaricium occultum* may well be elsewhere in *Gomphales*. *Ramaricium polyporoideum* is not at all related and its position within *Agaricomycotina* is not settled. For this species the genus name *Phlyctibasidium* should be used (Jülich 1974).

Hymenochaetales Oberw. 1977

The original definition of *Hymenochaetales* covered approximately the same taxa as those forming *Hymenochaetaceae* in the present study. When Donk (1948) introduced *Hymenochaetaceae* he also added *Asterostroma*, *Vararia*, and *Scytinostroma*. They are now all placed in *Peniophoraceae* within *Russulales* (Larsson & Larsson 2004). From molecular phylogenetic inference we have learned that *Hymenochaetales* also covers a number of corticioid genera with quite different traits from those characterizing *Hymenochaetaceae* (Langer 1998; Binder *et al.* 2005; Larsson *et al.* 2007). *Hymenochaetales* has changed from a morphologically and physiologically well-defined group to a jumble of basidioma types, life strategies, and microcharacters. The family structure suggested here includes a great deal of uncertainty and many genera are left without a family assignment. A recent comprehensive analysis of *Hymenochaetales* (Larsson *et al.* 2007) recovered a partly different clade structure. For this reason I have chosen to give the *Rickenella* family a delimitation that makes it paraphyletic in relation to the present analyses (Fig 1).

Hymenochaetaceae Donk 1948

Asterodon, Hymenochaete, Pseudochaete

Asterodon, *Hymenochaete*, and the recently segregated *Pseudochaete*, are usually not treated among the corticioid fungi but included here as they have the typical effused, resupinate basidioma construction and a non-poroid hymenophore.

Hymenochaetaceae is a well-defined group with wood-decaying species causing white rot. All species have simple-septate hyphae, a darkening reaction when treated with KOH (xanthocroic reaction), and special thick-walled, golden brown cystidia called setae (not in all species!). In some analyses the corticioid genera *Basidioradulum* and *Fibricium* occur nested in *Hymenochaetaceae* but this position is not consistent (Wagner & Fischer 2002b). Neither genera have the characters typical for *Hymenochaetaceae*, except association with white rot, and a recent anlysis places them outside *Hymenochaetaceae* (Larsson *et al.* 2007). *Fibricium* is polyphyletic and it is probably only the type (*F. rude*) that is a member of *Hymenochaetales*.

The systematics of *Hymenochaetaceae* is well studied by molecular methods, which has resulted in considerable generic rearrangements, especially among the poroid species formerly treated as *Phellinus* and *Inonotus* (Wagner & Fischer 2002a,b).

Rickenella family

Atheloderma, Cotylidia, Cyphellostereum, Globulicium, Hyphoderma p.p., Leifia, Mycoacia p.p., Odonticium, Peniophorella, Phlebia p.p., Repetobasidium, Resinicium, Skvortzovia

This group probably deserves recognition at family level as already pointed out by Redhead *et al.* (2002) but its delimitation is unclear. It includes a perplexing mixture of fruiting body morphologies: omphalinoid agarics, stipitate stereoid species, and resupinate species, and a variety of nutritional strategies. Several of the species with erect basidiomata live in association with bryophytes and for at least one corticioid species, *Resinicium bicolor*, interactions with green algae has been reported (Poelt & Jülich 1969). *Globulicium* grows on thin, attached or newly fallen branches of *Picea abies*. The basal basidioma layer often contains green algae but a direct interaction with these has not been observed. *Peniophorella* species, recently segregated from *Hyphoderma* (Larsson 2007), have echino- or stephanocysts, organs that are designed to catch nematodes.

Molecular data indicate that *Resinicium* is polyphyletic and should be restricted to species with asterocystidia and large halocystidia. In phylogenetic analyses the genus takes various positions (Larsson *et al.* 2004, Binder *et al.* 2005) and Langer (2002) claims that it is not a member of *Hymenochaetales*. *Resinicium furfuraceum*, *R. meridionalis*, *R. pinicola*, *Mycoacia kurilensis*, *Skvortzovia furfurella*, and *Phlebia georgica* emerge as a possible distinct taxon for which *Skvortzovia* is available as a genus name. Species in the group are characterized by a smooth to hydnoid hymenophore, a dense hyphal structure, and small often subcapitate hymenial cystidia with a more or less distinct halo.

Odonticium romellii has many morphological similarities to *Hyphodontia* and *Tubulicrinis*, e.g. an odontioid hymenium, thick-walled hyphae in aculei, basally thickened basidia walls, and allantoid spores. Sequence data place *Leifia flabelliradiata* as a sister taxon, supporting the transfer of *L. flabelliradiata* to *Odonticium* recently made by Zmitrovich (2001). The connection is not obvious when only morphological information is considered.

Schizoporaceae Jülich 1982

Lagarobasidium, Palifer, Rogersella, Schizopora, Xylodon

Hyphodontia is a large genus with almost 100 species described. Molecular phylogenies show that *Hyphodontia* is polyphyletic (Langer 2002; Binder *et al.* 2005; Larsson *et al.* 2007). *Hyphodontia* is typified with *Gonatobotrys pallidula* and the species centred around the type form a small and well-delimited group characterized by lagenocystidia and septate hymenial cystidia (see *Tubulicrinaceae*). Jülich & Stalpers (1980) adopted *Kneiffiella* as a replacement for *Hyphodontia* but this initiative was later made obsolete by conservation. However, *Kneiffiella* is a valid genus name for *Hyphodontia* species with tubular cystidia of tramal origin. Larsson *et al.* (2007) recovered *Kneiffiella* as a distinct clade well separated from *Hyphdontia s.s.* but here we have choosen to list *Kneiffiella* among *incertae sedis*. The largest part of a split *Hyphodontia* includes species with a variety of hymenial cystidia. For this group the oldest available name is *Xylodon*, typified with *X. quercinum*. It may include also the types of *Lagarobasidium*, *Lyomyces*, *Palifer*, *Rogersella*, and *Schizopora*, but a final delimitation of *Xylodon* will require a detailed analysis of the whole family.

Tubulicrinaceae Jülich 1982

Hyphoderma p. p., Hyphodontia, ?Sphaerobasidium, Tubulicrinis

This family is centred around *Tubulicrinis*, which is a distinct and easily recognized group of species characterized by often strongly amyloid lyocystidia. *Sphaerobasidium minutum* and the very rare *Hyphoderma involutum* probably should be included. They belong to a group of corticioid species with an affinity for brown-rotted wood decayed by *Fomitopsis pinicola* and are frequently found together with *Tubulicrinis* spp.

Sphaerobasidium has been compared with *Repetobasidium* (Eriksson *et al.* 1984) and they were also recovered as sister taxa by Binder *et al.* (2005). However, in our analyses a single *Sphaerobasidium* sequence finds its place in the vicinity of *Tubulicrinis*, whereas *Repetobasidium* shows affinites to the *Rickenella* clade (Larsson *et al.* 2007). Another sequence of *Sphaerobasidium* is needed to reveal which position is the correct one.

Incertae sedis

Alutaceodontia, Basidioradulum, ?Botryodontia, Chaetoporellus, Fibricium, Kneiffiella, ?Melzerodontia, ?Odontiopsis, Physodontia, ?Subulicium

Polyporales Gäum. 1926

The circumscription of this order is controversial. Larsson *et al.* (2004) preferred to recognize a separate phlebioid clade that would encompass the majority of the corticoid species from *Polyporales*. The phlebioid clade emerges as a well-supported group also in the present analysis combining the *Byssomerulius* family, *Phanerochaetaceae*, and *Meruliaceae* (Fig 1). Binder *et al.* (2005) identified four subclades in Polyporales, *viz.* the phlebioid clade, the residual polypore clade, the core polypore clade, and the *Antrodia* clade. The first two would correspond to the phlebioid clade in Larsson *et al.* (2004). The multi-gene basidiomycete phylogeny by Matheny *et al.* (2007b) is the first comprehensive study that has generated statistical support for the polyporoid clade *sensu* Binder *et al.* (2005). Still, *Polyporales* stands out as the least resolved clade in *Agaricomycotina* and the classification adopted here must be regarded as highly provisional.

As far as known, all species in *Polyporales* are saprobes, although some species may also occur as parasites and attack living trees. All species in the phlebioid subclade cause white rot, whereas the remaining portions of *Polyporales* include both brown-rot and white-rot groups.

Byssomerulius family

Byssomerulius, Candelabrochaete p.p., *Ceraceomyces* p.p., *Cytidiella, ?Deflexula, Hydnopolyporus, Irpex, Meruliopsis, Phanerochaete* p.p., *Phlebia* p.p.

Corticioid species in this family have a monomitic hyphal system with or without clamps. Most species have a membranaceous basidioma construction with a loose subiculum and a dense, thickening hymenium that often is merulioid when fresh. Cystidia are rare and, when present, are little differentiated. It is possible that the stipitate stereoid/poroid genus *Hydnopolyporus* and the clavarioid genus *Deflexula* belong here. The latter genus has negatively geotropical basidiomata and is probably not monophyletic. Some *Deflexula* species are reported to cluster with *Pterula* in *Pterulaceae* (*Agaricales*) (Munkacsi *et al.* 2004). Parmasto (1968) described the subgenus *Phanericium* for *Phanerochaete* species lacking cystidia. Molecular data support the recognition of *Phanericium* as an independent genus (Lim 2001; de Koker *et al.* 2003). Wu (1990) introduced *Efibula* for species with non-clamped hyphae and a dense, almost *Phlebia*-like consistency. Among the species placed in *Efibula* were *Phanerochaete avellanea*, which is considered close to *Phanerochaete tuberculata* (Burdsall 1985), and *Phlebia pallidovirens*. In phylogenetic analyses *Phanerochaete avellanea* and *P. tuberculata* are sister taxa (De Koker *et al.* 2003) and would both fit in the *Byssomerulius* family, whereas *Phlebia pallidovirens* shows affinities with *Phanerochaetaceae* (Lim 2001).

According to Lim (2001) *Irpex lacteus* is related to *Bjerkandera* that seems to belong in *Phanerochaetaceae*. Conversely, Ko *et al.* (2001) recovered *Irpex lacteus* in a clade together with *Oxyporus latemarginatus* and *Hexagonia hydnoides*. Our own sequence of *I. lacteus* appears related to *Hydnopolyporus* and *Deflexula*.

At least one species of *Candelabrochaete* is included. *Candelabrochaete* species have characteristic short-celled, wide, simple-septate hyphae and multiseptate cystidia. Most species are tropical but *C. septocystidia* and *C. verruculosa* are found in temperate regions. *Candelabrochaete* is typified by *C. africana*, which takes an isolated position within the phlebioid clade in Binder *et al.* (2005). This indicates that *Candelabrochaete* is polyphyletic and it is here suggested that *Candelabrochaete s.s.* belongs in *Meruliaceae*.

Fomitopsidaceae Jülich 1982

Dacryobolus, Phlebia p.p.

This family corresponds to the *Antrodia* clade of Binder *et al.* (2005). Brown-rot decay is the dominating life strategy and most species are polypores. In phylogenetic analyses support for the family is weak at best and it is questionable whether it can be kept together as one family. In phylogenetic trees there is a tendency for a separation of species with robust basidiomata and a trimitic hyphal system (e.g. *Fomitopsis, Piptoporus,* and *Daedalea*) from those with more soft basidiomata and a mono- or dimitic hyphal system (e.g. *Oligoporus, Amylocystis,* and *Dacryobolus*).

Corticioid species are probably few. *Dacryobolus*, a genus with characteristic, narrow basidia and also narrow, allantoid spores, belongs here. *Phlebia griseoflavescens*, certainly not a typical *Phlebia*, is another corticioid species with its place in *Fomitopsidaceae*.

Meruliaceae Rea 1922

Bulbillomyces, Cabalodontia, ?Candelabrochaete, Ceraceohydnum, Crustodontia, Cymatoderma, Hydnophlebia, Hyphoderma, Hyphodermopsis, Hypochnicium, Jacksonomyces, Lilaceophlebia, Mycoacia, Mycoaciella, ?Mycoleptodonoides, ?Mycorrhaphium, Nodotia, Phlebia, Podoscypha, Radulodon, Sarcodontia, Scopuloides, Steccherinum

The wide circumscription for *Meruliaceae* adopted here is certainly provisional. This large family is dominated by corticioid genera but also includes some polypores e.g. *Antrodiella*, *Ceriporiopsis s.s.*, *Junghuhnia*, and *Physisporinus*, and the stipitate stereoid genera *Podoscypha* and *Cymatoderma* (Boidin *et al.* 1998). The family includes a well-supported subclade covering the majority of species placed in *Phlebia s.s.* and some related genera with a similar basidioma construction (Fig 1). *Phlebia* species have a dense, often gelatinous consistency and narrow basidia in a dense palisade. All species tested to date have a bipolar mating system and an astatocoenocytic nuclear behaviour is common (Boidin & Lanquetin 1984). However, *Phlebia* is still a polyphyletic genus also after the segregation of many atypical species.

The remaining corticioid elements are morphologically rather heterogeneous. *Hyphoderma* and *Hypochnicium* have soft basidiomata, nodose-septate hyphae, usually more or less tubular cystidia, and large basidia and spores. *Hyphoderma* has a bipolar mating system, whereas *Hypochnicium* is tetrapolar. *Steccherinum* includes species with corticioid and effused-reflexed basidiomata and a hydnoid hymenophore. All species have a dimitic hyphal system, although in some species skeletal hyphae are so reduced as to look more like long, thick-walled cystidia. As pointed out many times *Junghuhnia* species are very similar to *Steccherinum*. Molecular data support a close relationship but a redisposition of species should be postponed until more sequences are available, including the type of *Junghuhnia*.

Abortiporus is a soil-dwelling polypore that is closely related to *Podoscypha*, especially *P. multizonata* (Binder *et al.* 2005). It is also worth mentioning that non-mycorrhizal species of *Albatrellus*, e.g. *A. syringae*, are included in this family (Binder *et al.* 2005), whereas *Albatrellus s.s.* has its place in *Russulales*.

Phanerochaetaceae Jülich 1982

?Australicium, ?Australohydnum, Climacodon, Donkia, ?Efibula, ?Hjortstamia, Hyphodermella, Phanerochaete, Phlebia p.p., Phlebiopsis, Porostereum, Rhizochaete, ?Roseograndinia

This family is also primarily composed of corticioid species. *Phanerochaete* is a large but polyphyletic genus in need of revision. All species in *Phanerochaete s.s.* (type *P. velutina*) have encrusted cystidia and multiclamped septa at basal hyphae (De Koker *et al.* 2003). Non-cystidiate *Phanerochaete* species belong in the *Byssomerulius* family and species with cystidia in combination with entirely clamp-free hyphae have recently been combined into *Rhizochaete* (Greslebin *et al.* 2004). *Porostereum* may be a member of *Phanerochaetaceae*. According to Lim (2001) and Ko *et al.* (2001) *Porostereum spadiceum* is a sister taxon to *Bjerkandera adusta* and *Phanerochaete chrysosporium*. In Binder *et al.* (2005) *Bjerkandera* is recovered together with *Phanerochaete s s.*

Greslebin *et al.* (2004) introduced *Rhizochaete* for cystidiate, rhizomorphic, clamped and non-clamped species earlier placed in *Ceraceomyces* and *Phanerochaete*. For the analyses in this paper, two species not included in *Rhizochaete* by Greselebin *et al.* (2004) were sampled, *viz. Ceraceomyces violascens* and *Phlebia unica*. *Phlebiopsis gigantea* and *P. flavidoalba* seem to be members of the family. *Phlebiopsis* includes non-clamped species with a dense consistency throughout their basidiomata and with numerous encrusted, thick-walled cystidia, so-called metuloids. Many tropical species display this set of characters but it is doubtful whether all of them will find a place in *Phlebiopsis*.

Polyporaceae Corda 1839

?Dendrodontia, ?Dentocorticium, Epithele, ?Flavodon, Grammothele, Lopharia

Polyporaceae is dominated by polypores most of which have a trimitic hyphal system and cause white rot. The corticioid species have in general robust basdiomata and often a hydnoid or epitheloid hymenophore. Many *Lopharia* species have been moved to *Porostereum* (Hjortstam & Ryvarden 1990) and this arrangement receives support from molecular data (Yoon *et al.* 2003). An interesting find concerns *Epithele typhae* that seems firmly connected with *Polyporaceae* (compare Boidin *et al.* 1998). This monomitic species, which grows on living stems of various marsh plants (*Carex, Scirpus, Typha*), has its hymenium covered with sterile hyphal pegs (epitheloid). The same hymenial construction can be found in *Grammothele* and some related genera that are usually treated as polypores. *Grammothele fuligo* is sequenced and recovered in *Polyporaceae* (Binder *et al.* 2005). Another corticioid species occurring in *Polyporaceae* is *Dentocorticium sulphurellum* with dendrophydia and a dimitic hyphal system. The type species, *D. ussuricum*, has a monomitic hyphal system, which prompted Boidin & Gilles (1989) to move *D. sulphurellum* to the dimitic genus *Dendrodontia*.

Incertae sedis

Grammothelopsis, Hymenogramme, Hyphoradulum, Pirex, Pseudolagarobasidium, Skeletohydnum, Terana

Russulales Kreisel ex P.M. Kirk, P.F. Cannon & J.C. David (2001)

Larsson & Larsson (2003) performed a rather detailed molecular study of *Russulales* and recovered 13 subclades. Eleven of them are here, with minor changes, accepted as families. The detailed discussions regarding this order in Larsson & Larsson (2003) and Binder *et al.* (2005) are not repeated here and each family is only briefly described. Gloeocystidia and/or gloeoplerous hyphae with aldehyde-rich contents seem to be the derived character that identifies this order.

Albatrellaceae Nuss 1980

Byssoporia

This family is composed of the stipitate polypore genera *Albatrellus* and *Polyporoletus*, some gasteroid taxa, and the corticioid genus *Byssoporia* (Bruns *et al.* 1998; Miller *et al.* 2006). *Byssoporia* is reportedly mycorrhizal. The type species, *B. terrestris*, was formerly included in *Byssocorticium* in *Atheliales* but was segregated on account of different basidioma colour, universally non-clamped hyphae, and presence of rhizomorphs (Larsen & Zak 1978).

Aleurocystidiellum family

Aleurocystidiellum

Aleurocystidiellum with two species is the only genus in this family. Both species form disc-like basidiomata on the bark of living trees and because they also have amyloid spores they were formerly placed in *Aleurodiscus*. However, several morphological and cultural characters distinguish them from *Aleurodiscus* and the two genera do not seem to be closely related.

Auriscalpiaceae Maas Geest. 1963

Dentipratulum, Gloiodon

Auriscalpiaceae includes hydnoid species that are stipitate (*Auriscalpium*), effused-reflexed (*Gloiodon*), or resupinate (*Dentipratulum*). The lamellate and sessile *Lentinellus* also seems to belong here but could also constitute a family of its own. *Dentipratulum* has basidiomata similar to *Mucronella* but differs in the presence of gloeocystidia.

Echinodontiaceae Donk 1961

Amylostereum, Laurilia

Larsson & Larsson (2003) recovered a clade with *Echinodontium* and *Laurilia* together with *Bondarzewia* and *Heterobasidion* and called that clade *Bondarzewiaceae*. Other investigators (e.g. Binder & Hibbett 2002; Hibbett & Binder 2002; Binder *et al.* 2005) have identified *Echinodontium* and *Amylostereum* as sister taxa. As the latter studies were based on a more comprehensive set of characters drawn from several genes, these results are here viewed as more credible. In the present phylogeny (Fig 1), *Echinodontaceae* is polyphyletic, with *Amylostereum* and *Echinodontium* recovered in separate subclades.

Gloeocystidiellaceae Jülich 1982

Gloeocystidiellum

Gloeocystidiellum was introduced as a repository for all monomitic corticioid species with amyloid spores and gloeocystidia (Donk 1931). Larsson & Larsson (2003) showed that *Gloeocystidiellum* must be restricted to a few species with ornamented spores around the type, *G. porosum*. Surprisingly even this small group of species split in two clades that are not sister groups despite extremely small differences in morphology (Larsson & Larsson 2003). Here only the clade including *G. porosum* is accounted for, whereas the position of the *G. clavigerum* group remains an unsolved problem in the classification.

Gloeodontia family

Gloeodontia

The single genus comprises corticioid species with hydnoid or smooth hymenophores and a mono- or dimitic hyphal system.

Hericiaceae Donk 1964

?Amylodontia, Dentipellis, Laxitextum

The family was primarily outlined for monomitic aphyllophoralean species having much branched hydnoid or clavarioid basidiomata, amyloid spores, and a gloeoplerous hyphal system. The family originally also included *Artomyces pyxidatus*. The two corticioid genera in this family are *Dentipellis* and *Laxitextum*, both covering species with soft basidiomata, a tendency to develop a reflexed margin, and with either hydnoid or smooth hymenophore.

Peniophoraceae Lotsy 1907

?Amylofungus, Asterostroma, Confertobasidium, Dendrophora, Dichostereum, Duportella, Entomocorticium, Gloiothele, Metulodontia, Peniophora, Scytinostroma, Stereofomes, Vararia, Vesiculomyces

This is a large and rather heterogeneous family, although it appears monophyletic in most analyses. It is almost totally dominated by corticioid species and the prime exception is the clavarioid genus *Lachnocladium*. The family includes *Lachnocladiaceae*, which was introduced for genera with a combination of russuloid characters and dextrinoid dendro-, dicho-, and asterohyphidia (*Asterostroma, Dichostereum, Scytinostroma*, and *Vararia*). Phylogenetic analyses show that dextrinoid hyphidia do not define a monophyletic group. Recently we have also discovered several undescribed species as sister taxa to *Vararia* and *Scytinostroma* but totally devoid of any dextrinoid hyphidia.

Russulaceae Roze 1876

Boidinia, Gloeopeniophorella, ?Pseudoxenasma

The analyses in Larsson & Larsson (2003) showed that the ancestor of the mycorrhizal agarics *Russula* and *Lactarius* probably had corticioid characteristics. The corticioid genera *Boidinia* and *Gloeopeniophorella* clearly belong to *Russulaceae*, whereas the position of *Pseudoxenasma* is less resolved. The latter species grows on still attached or newly fallen branches of *Picea abies* and the basidiomata often develop over mats of green algae. None of the corticioid species in the family shows any sign of mycorrhizal activity.

Stereaceae Pilát 1930

Acanthobasidium, Acanthofungus, Acanthophysellum, Acanthophysium, Aleurobotrys, Aleurodiscus, Conferticium, ?Dextrinocystidium, Gloeocystidiopsis, Gloeomyces, ?Gloeosoma, ?Licrostroma, Megalocystidium, Stereum, Xylobolus

The family is composed of corticioid and effused-reflexed species. Many species have acanthohyphidia, cystidia-like hymenial organs with a more or less prominent apical part closely beset with prongs, like a bottle brush. *Stereum* and *Aleurodiscus* are the largest genera. Both are dominated by species growing in exposed positions, for example dead branches still attached to trees. The acanthohyphidia are probably a protection against desiccation. *Aleurodiscus* has been divided into many smaller genera and some of them are closely related to

Stereum and *Xylobolus*. Several corticioid species were formerly placed in *Gloeocystidiellum* but are now segregated as *Conferticium*, *Gloeocystidiellopsis*, and *Megalocystidium*.

Wrightoporiaceae Jülich 1982

Dentipellis p.p., *?Steccherium*

Wrightoporia is a rather large genus of mainly tropical polypores, all characterized by a dimitic hyphal system, ornamented amyloid spores, and presence of gloeoplerous hyphae or cystidia. The same characteristics are present in the corticioid genus *Scytinostromella*. Interestingly both genera are highly polyphyletic and none of the *Scytinostromella* species can with certainty be assigned to any of the families described here. So far *Wrightoporiaceae* includes the type species of *Wrightoporia*, *Dentipellis leptodon*, and possibly also the type of *Steccherium*.

Incertae sedis

Coniophorafomes, Gloeohypochnicium, Scytinostromella

Thelephorales Corner ex Oberw. 1976

The thelephoroid fungi have long been regarded as a natural group, and even if many species have effused, resupinate basidiomata they have usually been kept separate from *Corticiaceae* in a wide sense. Some uncertainty regarding the disposition of species with hyaline or weakly ornamented spores has prevailed, e.g. for *Amaurodon*, *Lazulinospora* (synonymized under *Amaurodon*), and *Tomentellopsis*. Recent molecular investigations have clearly shown that these genera also belong in *Thelephorales*. The internal structure of the order is currently under study (Urmas Kõljalg, pers. comm.) and here only one family is listed without further comments.

Thelephoraceae Chev. 1826

Amaurodon, Pseudotomentella, Tomentella, Tomentellopsis

Trechisporales K.H. Larss. 2007

This small order comprises mostly corticioid fungi some of which have a poroid hymenophore. The clavarioid genus *Scytinopogon* should possibly be included. All species are monomitic and have nodose-septate hyphae and many species have rhizomorphs. The nutritional mode is not known but species often occur on strongly decayed wood or other debris on the ground and there is the possibility that at least some species are soil-dwelling saprotrophs or involved in interactions with plants (Dunham *et al.* 2007).

Hydnodontaceae Jülich 1982

Brevicellicium, ?Dextrinocystis, ?Dextrinodontia, Fibriciellum, Fibrodontia, ?Litschauerella, Luellia, Porpomyces, Subulicystidium, Trechispora, Tubulicium

Hydnodon thelephorum is a tropical stipitate species that recently was transferred to *Trechispora* (Ryvarden 2002). Except for basidioma type, it has all the characteristics of a *Trechispora*, *viz.* soft consistency, ampullate septa on subicular hyphae, short cylindrical basidia, and hyaline ornamented spores. The same characters are also present in the clavarioid genus *Scytinopogon*, which Jülich (1982) placed in the same order (*Hydnodontales* syn. *Trechisporales*) as *Trechispora* but in a separate family. Jülich (1982) clearly understood the affinities within this family and included both *Brevicellicium* and *Trechispora* in *Hydnodontaceae*, and that arrangement is now confirmed by molecular data. Larsson (2001) showed that *Porpomyces mucidus*, a resupinate polypore, also has a place near *Trechispora*. *Dextrinodontia* and *Fibriciellum* are other candidates for inclusion in *Hydnodontaceae*.

Luellia, Subulicystidium, and *Tubulicium* are assigned here solely as a result of molecular phylogenetic analyses. These species have no morphological traits in common with *Trechispora* and are also quite different when mutually compared. That *Fibrodontia gossypina* belongs to *Hydnodontaceae* comes as a surprise (but see Binder *et al.* 2005). *Fibrodontia* looks very much like a *Hyphodontia* (*Hymenochaetales*) with its odontoid hymenophore, skeletal-like hyphae that terminate in the aculei, and small subglobose spores (Eriksson *et al.* 1981).

Sistotremastrum family

Sistotremastrum

This family is strongly supported as a sister group to *Hydnodontaceae* (Larsson *et al.* 2004). Its single genus *Sistotremastrum* has species with mostly 6-sterigmate basidia. There are no obvious characters to link it with *Hydnodontaceae*.

Familia incertae sedis

Amylocorticiaceae Jülich 1982

?Amyloathelia, Amylocorticiellum, Amylocorticium, Amyloxenasma, Ceraceomyces, Fibulomyces p.p., *?Hypochniciellum, Irpicodon, ?Plicatura, Plicaturopsis, ?Podoserpula, Serpulomyces*

Most corticioid species in *Amylocorticiaceae* have amyloid spore walls, as does the polypore genus *Anomoporia*, which also belongs here. *Irpicodon* and *Plicaturopsis* have effused-reflexed basidiomata but most species have strictly effused basidiomata. A majority of species are associated with brown rot decay, but in *Anomoporia* at least some species seem to cause white rot (Niemelä *et al.* 2007). *Amyloxenasma* may be a member of this family. The genus is segregated from *Phlebiella* and is thus characterized by pleurobasidia and dense, gelatinous basidiomata. In that sense, it diverges from the other species in *Amylocorticiaceae* but the amyloid spore wall is indicative of *Amylocorticiaceae*. *Hypochniciellum* is a polyphyletic genus that is here represented by *H. subillaqueatum*. The morphologically similar *H. cremeoisabellinum* does not belong to the family and the type species, *H. ovoideum*, awaits sequencing.

Jaapia family

Jaapia

Jaapia is a genus with just two species, both developing very thin and delicate basidiomata and always growing on wood in wet places. Both species have large spindle-shaped and somewhat thick-walled spores where the inner spore-wall gets deeply stained by cotton blue. The same reaction can be observed in *Coniophora* and *Serpula*. The spore shape and staining reaction were the main arguments for putting *Jaapia* in or close to *Coniophoraceae* (Nannfeldt & Eriksson 1953). Recent phylogenetic analyses sometimes recover *Jaapia* close to *Boletales* but always in a sister-group position. On classification it is more consistent to let *Jaapia* form a separate order.

Phlebiella family

Phlebiella

Phlebiella is typified by *P. vaga*, a very common species in northern nemoral and boreal forests. Pleurobasidia are the main diagnostic character for the genus. Recently we have encountered several instances when molecular data unanimously place non-pleurobasidiate specimens in the *Phlebiella* clade. However, such specimens have other attributes typical of *Phlebiella*, e.g. a soft but dense hyphal structure, traces of brown staining of subicular hyphae, presence of rhizomorph-like structures, and ellipsoid ornamented spores. Thus it seems clear that the pleurobasidium is of little use for the definition of genera and families.

Genera incertae sedis

Adustomyces, Aleurocystis, Amaurohydnum, Amauromyces, Amethicium, Amylobasidium, Cejpomyces, Cericium, Cerocorticium, Clavulicium, Conohypha, Coralloderma, Crustoderma, Cyanodontia, Dendrophysellum, Dichopleuropus, Elaphocephala, Epithelopsis, Erythromyces, Exobasidiellum, Flavophlebia, Globuliciopsis, Gloeocorticium, Hemmesomyces, Heteroacanthella, Hyphodontiastra, Hypochnella, Inflatostereum, Intextomyces, Korupella, Licrostroma, Melzericium, Minostroscyta, Mycobonia, Mycothele, Nothocorticium, Oliveonia, Oncobasidium, Papyrodiscus, Parastereopsis, Paullicorticium, Phlyctibasidium, Porogramme, Repetobasidiellum, Ripexicium, Scopulodontia, Scotoderma, Scotomyces, Sistotremella, Stereopsis, Suillosporium, Thujacorticium, Trechinotus, Uncobasidium, Xenasma, Xenosperma

There are nine genera for which the type species is sequenced but that still could not be assigned to any of the orders accepted here: *Clavulicium, Conohypha, Crustoderma, Paullicorticium, Phlyctibasidium, Scotomyces, Stereopsis, Thujacorticium*, and *Trechinotus*. When included in nuLSU phylogenetic analyses these taxa always occur on long branches, several of them close to the base of the tree. To this group of oddballs should also be added *Hyphoderma argillaceum* and presumably also other *Hyphoderma* species with morphological similarities to *H. argillaceum*.

Discussion

The classification of the corticioid fungi in Agaricomycetes has posed a particularly difficult problem to solve (Donk 1964). With the help of molecular data a first attempt to place the genera of corticioid fungi in monophyletic groups tentatively corresponding to families is presented. To do this it is necessary first to identify the phylogenetic position for the type species. For 162 genera of the 282 listed in Table 3 there is now a sequence of the type species available. This leaves 120 genera for which the position of the type species is not known, and for almost 50 of them an appropriate position can not be suggested, even at order level.

Even if an impressive number of genera are now positioned according to the type, the total number of species that it has been possible to classify is still low. This is because most larger genera presently have a morphology-based circumscription that apparently makes them polyphyletic. One example is *Hyphoderma* with currently *ca* 100 species. It is typified by *H. setigerum*, which in itself is a species complex (Nilsson *et al.* 2003). *H. setigerum* is here placed in *Meruliaceae* within *Polyporales*. Judging from molecular data and morphology about 25 *Hyphoderma* species belong to the same family. Another 20 species are segregated as *Peniophorella* and moved to *Hymenochaetales* (Larsson *et al.* 2006). The same order also houses several other *Hyphoderma* species but in different families than *Peniophorella*. The rest of *Hyphoderma*, about half of the species, can not be properly placed until they become molecularly characterized.

From molecular phylogenies we learn that corticioid fungi are phylogenetically diverse and present in all major evolutionary lineages among Agaricomycetes (Larsson *et al.* 2004, Binder *et al.* 2005). A similar pattern emerges when a cladistic classification at the family level is constructed. Many families are composed of mixtures of the fruiting body types that made up the basis for the Friesian classification. However, at genus level it seems that macromorphology is an important taxonomic marker also in a cladistic classification. We still see few examples of genera that mix corticioid species with other fruiting body types and when it happens it concerns effused monomitic species with a poroid hymenophore as in *Sistotrema* and *Trechispora*. The evolutionary interpretation of this pattern is not clear and attempts to reconstruct the evolution of fruiting body types have yielded conflicting results (Hibbett & Binder 2002; Hibbett 2004). One reason could be that the dataset used for ancestral character state analysis did not reflect the phylogenetic diversity displayed by the most ancestral groups.

Higher-order relationships for fungi are now sufficiently well known to allow for the establishment of a Linnean hierarchy down to order including only monophyletic groups (Hibbett *et al.* 2007). The present paper is an attempt to construct a phylogenetic family classification for a diverse group, and the result is at least partly promising. The best-studied order within *Agaricomycotina* is undoubtedly the *Russulales* (Larsson & Larsson 2003) and phylogenetic analyses yield good statistical support for most of its families. *Polyporales* presently stands out as the least resolved group, which is all the more annoying as it also is the most speciose one when only corticioid fungi are counted. *Hymenochaetales* also lacks resolution and some distinct genera did not show any clear affinities with the families suggested. In such cases a solution could be to erect more families. However, that would presently not communicate any additional infomation on relationships, which is one of the purposes behind a classification.

The obvious way forward from here is to add both more taxa and more characters for phylogenetic analyses. Ignorance of tropical diversity is certainly one of the main obstacles and can only be remedied by expanded collecting. It is also genera with a tropical distribution that dominate among those 120 for which the type is not yet sequenced. In addition to ribosomal genes we need to explore characters from protein-coding genes, if possible genes that are involved in functional traits like decay or symbiosis.

Ideally a classification should be intuitively understandable once the key characters for each taxon are known. Even if many of the results presented here seem bewildering morphology is still important. Still far too many species have not been adequately described and illustrated. With new molecular-based hypothesis on relationships at hand we also need to reinterpret existing descriptions. In addition we must look for other neglected information connected to variations in life strategy. The division of decay characteristics in white rot and brown rot appears useful also in the molecular era and thus provides an encouraging example. Mating type, nuclear behaviour, ultrastructure, and secondary metabolites are other examples of information that must be explored further and integrated with molecular data.

Non-overlapping datasets and non-standard selection of genes obstruct the comparison of published phylogenies. It would be of great help if at least one standard gene was included in all analyses. The obvious choice for fungi is the nu-rLSU gene for higher order relationships and the ITS region for the study of single genera or species complexes. The protocol used by the Göteborg mycology group involves sequencing of the full ITS region and *ca* 1200 bp of LSU for all species not earlier sequenced. For higher-order phylogenetic analyses we can then also incorporate the small and conservative 5.8 gene from the ITS region, which has proved quite helpful (Larsson *et al.* 2004).

Misidentified sequences are another problem that sometimes makes it difficult to interpret and discuss results from molecular data that are in conflict with morphology (Nilsson *et al.* 2006b). It must be underlined that sequencing results that are difficult to explain should be confirmed by resequencing, preferably by using a different DNA source. This is especially important when cultured mycelium is used as acquiring a culture in itself involves risks of contamination or other sources of error.

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