Hymenochaetales: a molecular phylogeny for the hymenochaetoid clade

Karl-Henrik Larsson[1]

> *Department of Plant and Molecular Sciences, Göteborg University, Box 461, SE 405 30 Göteborg, Sweden*

Erast Parmasto

> *Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, 181 Riia Street, 51014 Tartu, Estonia*

Michael Fischer

> *Staatliches Weinbauinstitut, Merzhauser Straße 119, D-79100 Freiburg, Germany*

Ewald Langer

> *Universität Kassel, FB 18 Naturwissenschaft, FG Ökologie, Heinrich-Plett-Straße 40, D-34132 Kassel, Germany*

Karen K. Nakasone

> *USDA Forest Service, Forest Products Laboratory, 1 Gifford Pinchot Drive, Madison, Wisconsin 53726*

Scott A. Redhead

> *ECORC, Agriculture & Agri-Food Canada, CEF, Neatby Building, Ottawa, Ontario, K1A 0C6 Canada*

Abstract: The hymenochaetoid clade is dominated by wood-decaying species previously classified in the artificial families Corticiaceae, Polyporaceae and Stereaceae. The majority of these species cause a white rot. The polypore *Bridgeoporus* and several corticioid species with inconspicuous basidiomata live in association with brown-rotted wood, but their nutritional strategy is not known. Mycorrhizal habit is reported for *Coltricia perennis* but needs confirmation. A surprising element in the hymenochaetoid clade is a group of small white to brightly pigmented agarics earlier classified in *Omphalina*. They form a subclade together with some similarly colored stipitate stereoid and corticioid species. Several are associated with living mosses or one-celled green algae. *Hyphoderma pratermissum* and some related corticioid species have specialized organs for trapping and killing nematodes as a source of nitrogen. There are no unequivocal morphological synapomorphies known for the hymenochaetoid clade. However almost all species examined ultrastructurally have dolipore septa with continuous parenthesomes while perforate parenthesomes is the normal condition for other homobasidiomycete clades. The agaricoid Hymenochaetales have not been examined. Within Hymenochaetales

the Hymenochaetaceae forms a distinct clade but unfortunately all morphological characters supporting Hymenochaetaceae also are found in species outside the clade. Other subclades recovered by the molecular phylogenetic analyses are less uniform, and the overall resolution within the nuclear LSU tree presented here is still unsatisfactory.

Key words: Basidiomycetes, Bayesian inference, *Blasiphalia*, corticioid fungi, *Hyphodontia*, molecular systematics, phylogeny, *Rickenella*

INTRODUCTION

Morphology.—The hymenochaetoid clade, herein also called the Hymenochaetales, as we currently know it includes many variations of the fruit body types known among homobasidiomycetes (Agaricomycetidae). Most species have an effused or effused-reflexed basidioma but a few form stipitate mushroom-like (agaricoid), coral-like (clavarioid) and spathulate to rosette-like basidiomata (FIG. 1). The hymenia also are variable, ranging from smooth, to poroid, lamellate or somewhat spinose (FIG. 1). Such fruit body forms and hymenial types at one time formed the basis for the classification of fungi. Thus the hymenochaetoid clade, as it is defined here, draws its members from several families as circumscribed in premolecular classifications: Agaricaceae, Polyporaceae, Corticiaceae, Stereaceae and Hymenochaetaceae but includes only the type genus for the last family name.

Micromorphological characters are exceedingly variable. Three basic kinds of hyphae involved in construction of basidiomycete basidiomata (viz. generative hyphae, skeletal hyphae and binding hyphae) are present although most species have only the generative type. Spores are mainly smooth but vary in shape from the large globose ones found in *Globulicium hiemale* to the extremely narrow and strongly bent spores in *Hyphodontia* (*Chaetoporellus*) *latitans*. A few species have finely ornamented spores (viz. *Coltriciella* spp. and *Hyphodontia* (*Rogersella*) *griseliniae*).

Most species have some kind of vegetative (sterile) cells in the fruit body tissue, often sharing the space with the basidia in the hymenium (SUPPLEMENTARY FIG. 1). They collectively could be called cystidia but because some of them have a distinctive form, unique terms have been introduced for them. The majority of species in Hymenochaetaceae have a characteristic kind of cystidia called setae (FIG. 1J). These thick-
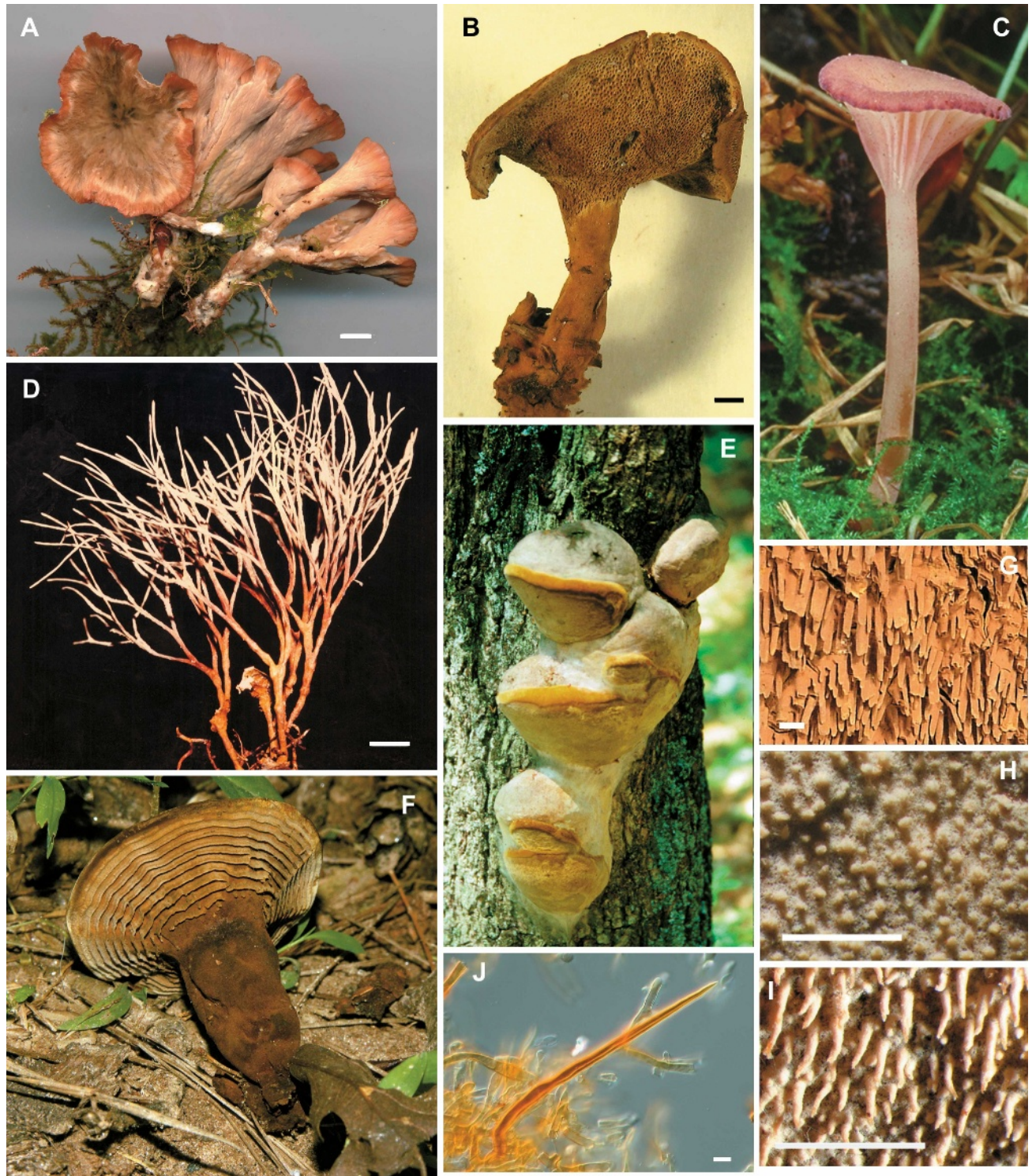
FIG. 1. Macro and micro characters in Hymenochaetales. A–I. Basidiome and hymenophore types. A, *Cotylidia pannosa*, stipitate with smooth hymenophore (photo David Mitchel, www.nifg.org.uk/photos.htm). B. *Coltricia perennis*, stipitate with poroid hymenophore. C. *Contumyces rosella*, stipitate with lamella. D. *Clavariachaete rubiginosa* (photo Roy Halling) E. *Phellinus robustus*, sessile to effuse-reflexed with poroid hymenophore (photo Andrej Kunca, Forest Research Institute, Slovakia, www.forestryimages.org). F. *Coltricia montagnei*, stiptate with contrical lamella (photo Dianna Smith, www.mushroomexpert.com). G. *Hydnochaete olivacea*, resupinate to effuse-reflexed with coarse, compressed aculei. H. *Resinicium bicolor*, resupinate with small, rounded aculei. I. *Hyphodontia arguta*, resupinate with acute aculei. J, setal cystidium in *Hymenochaete cinnamomea*. Bars: A, D = 10 mm, B = 2 mm; G–I = 1 mm, J = 10 μm.

walled, dark, brown and usually acutely pointed cells can be observed with a hand lens and give the species a beard-stubble look. Their function is possibly to protect the hymenium from insects. Thin-walled and hyaline cystidia characterize the hymenium in all species of *Hyphodontia*, many other small genera of corticioid fungi and some of the agaricoid and stereoid genera. Often these cystidia are pestle-shaped with a globular apex. The exact function is not known but a general idea is that leptocystidia emerging beyond the basidial layer function as excretory organs because in living specimens the apex of such cystidia often are covered by a droplet that disappears or dissolves when material is mounted for observation microscopically. In some cases the apical droplet seems encased in a vesicle and resists dissolution. The most well developed vesicle-bearing cystidia, called halocystidia, are found in *Resinicium bicolor* and related species. Crystal-covered cystidia are other indications of excretion capacity. In *Hyphodontia* and *Resinicium* some species have lagenocystidia that are hypha-like but with a needle-like termination. At the apex these cystidia carry a rosette of crystals, presumably composed of calcium-oxalate. Thin- to thick-walled cystidia with an apical crystal cap characterize species in the polypore genera *Trichaptum* and *Oxyporus* and thick-walled, strongly encrusted cystidia (metuloids, lamprocystidia) can be seen in *Hyphoderma puberum* and a few other species. In *Tubulicrinis* all species have lyocystidia, a hallmark of the genus. These cystidia have a thick-walled ''stem'' and a thin-walled variously shaped apex. The thick-walled part is usually more or less amyloid and dissolves easily in 5% KOH. Gloeocystidia (enclosed cystidia with more or less refractive contents) are not common but occur in *Hyphoderma praetermissum* and related species and in *Physodontia*. *Hyphoderma praetermissum* also is known for its stephanocysts. These are one- or two-celled hemispherical or globose structures that occur on hyphae in the substrate, and they are not always detectable in the basidiomata (for excellent illustrations see Hallenberg 1990). Hallenberg (1990) showed that stephanocysts can develop on germinating spores, at least when they are dispersed on an artificial medium such as malt agar. Hallenberg concluded that stephanocysts were essential for adsorption. On the other hand Tzean and Liou (1993) suggested that stephanocysts were nematode-catching organs and that the fungus uses nematodes as a nitrogen source. Related species have morphologically similar but one-celled structures called echinocysts.

Basidium shape can be a useful taxonomical character. The corticioid genus *Repetobasidium* owes its name to the ability for repeated formation of new basidia from the same apical cell and not, as usual, through hyphal branching (SUPPLEMENTARY FIG. 1). Each new basidium bursts through the old, empty basidium leaving a progressively longer row of sheathing basidia walls along the subtending hypha. Basidial repetition is not unique for *Repetobasidium*, although this is the genus where it first was observed and described (Eriksson 1958).

Ultrastructural characteristics as observed with a scanning or transmission electron microscope are of limited importance for the taxonomy and classification of higher fungi. The prime exception is the septal pore apparatus that differs markedly among various groups, and these anatomical differences correlate well with basidiomycete higher order classifications. Agaricomycetidae is characterized by a septal pore apparatus called a dolipore. In a dolipore the septal pore is surrounded on each side of the septum by a half-dome-shaped membrane called parenthesomes because in a TEM picture it looks like the septum is placed within parentheses. Most homobasidiomycetes have parenthesomes that are perforated by a number of small openings and appear as dashed marks in the TEM; however a small number of species instead have nonperforate parenthesomes. Because species in Auriculariales and Tulasnellales have the nonperforate type, this is regarded as the ancestral condition from which the perforated developed. In Hymenochaetales as well as in Cantharellales both types occur, which indicate that the evolution of parenthesome type is more complicated than initially understood.

Ecology.—Saprotrophy is the dominating life strategy in Hymenochaetales. Most species live in deadwood and satisfy their energy needs by decaying the polysaccharides cellulose, hemicellulose and lignin. When all these molecules are degraded at roughly equal rates the resulting decay is called white-rot as opposed to brown-rot, which leaves most of the lignin intact (Rayner and Boddy 1988). The capacity to cause brown-rot is a derived condition that has developed repeatedly from white-rot ancestors on several occasions during evolution (Gilbertson 1980, Hibbett and Donoghue 2001). In Hymenochaetales only one case of suspected brown-rot is reported (viz. the gigantic polypore *Bridgeoporus nobilissimus* [Redberg et al 2003]) but experimental data is lacking.

Many corticioid species with thin and inconspicuous basidiomata occur on strongly brown-rotted wood where most cellulose already is removed by a brown-rot fungus such as *Fomitopsis pinicola* (polyporoid clade). Examples from Hymenochaetales include *Sphaerobasidium minutum, Tubulicrinis* spp. *Repetobasidium* spp. and *Hyphoderma involutum.* The life

strategy of such secondary rot fungi is not known, and although they live in close connection to brown-rotted wood it is too simplistic to classify them as actively performing brown-rot.

Several polyporoid Hymenochaetales genera, such as *Phellinus, Inonotus, Fomitiporia, Porodaedalea* and *Trichaptum,* are strong primary decayers. Some colonize living trees, thus blurring the distinction between saprotrophic and parasitic strategies. Most species invading living trees attack the dead tissue in the center of stems (i.e. the heartwood) and therefore may not directly harm the host, except to weaken the trunks making them vulnerable to strong winds. Some heart-rot fungi (e.g. *Inonotus obliquus* on *Betula* spp.) can break through the sapwood and form black cankers on stems.

Few species actually kill their host but these can become serious pathogens for forestry or urban landscaping (*Inonotus ulmicola*). *Phellinidium weirii* (≡ *Phellinus weirii*) causes laminated root rot in Douglas-fir and other conifers of western North America. In infected stands there is a long-term impact on stand structure and the fungus is one of the most important disturbance agents in Pacific conifer forests (Hansen and Goheen 2000). Another example is *Phellinus tremulae* that occurs almost everywhere aspen species grow and is reported to be able to spread through the sapwood. Among the Hymenochaetales, species causing the greatest losses to forestry are *Porodaedalea pini* (≡ *Phellinus pini*) growing on pines and *Phellinus igniarius* growing on various hardwoods. Both species destroy the heart-wood.

A distinct group of brightly colored to whitish Hymenochaetales fruit directly on or in association with bryophytes. Basidiomata are either mushroom-like, with lamellae and central stipes (e.g. *Rickenella* and *Cantharellopsis*) or more stereoid, with smooth to wrinkled hymenia (e.g. *Cyphellostereum* and *Cotylidia*). Colonized bryophytes appear healthy, but it has been shown that living rhizoids of mosses can be penetrated by *Rickenella fibula* (Redhead 1981) and that another species, *R. pseudogrisellum,* forms clasping digitate appresoria on the rhizoids of the liverwort *Blasia* (Redhead 1980, 1981), sometimes being dispersed by infecting gemmae of *Blasia* (Redhead 1980) together with a symbiotic *Nostoc* (Redhead unpubl). In general it is not known whether these Hymenochaetales parasitize their host or whether the connection is of a more mutualistic nature. Separation of the *Rickenella* subclade from the Agaricales in general where *Omphalina* and *Gerronema* are placed, and interspersion of other taxa, led to the recognition of several small agaric genera (*Cantharellopsis, Contumyces, Loreleia* and *Sphagnomphalia,* which more

correctly is named *Gyroflexus*) for agaricoid species (Redhead et al 2002).

Several species forming corticioid basidiomata frequently contain one-celled green algae in the basal basidioma layer. Examples from Hymenochaetales include *Resinicium bicolor* and *Globulicium hiemale.* The algal connection in *Resinicium* was studied by Poelt and Jülich (1969) but they were unable to establish any direct hyphal invasion of algal cells. However they noted a more proliferous hyphal branching close to the algae. Similar connections with algae are known also in other homobasidiomy-cete orders but a direct parasitism of algae is known only with certainty in the corticioid genus *Athelia* (Poelt and Jülich 1969). At least one Hymenochae-tales species is lichenized (Palice et al 2005). It bears the curious name *Omphalina foliacea* and was de-scribed based on sterile thalli only. Although lacking basidiomes it was placed in *Omphalina* with other lichenized omphalinoid agarics currently classified as *Lichenomphalia* in the Agaricales. The lichenized fungus, which is not necessarily agaricoid, lacks a unique generic name.

Two more life strategies should be mentioned briefly. Danielson (1983) studied the ectomycorrhiza formed by *Pinus banksiana* (jack pine) both in vivo and in vitro. One of the supposed symbionts was the stipitate poroid *Coltricia perennis,* which forms basi-diomata on dry sandy forest soils. Danielson was able to synthesize a mycorrhizal association with pine seedlings in the laboratory and even managed to get basidiomata. However living mycorrhizal root tips formed with *Coltricia* have not been detected in nature. Umata (1995) studied the ability of aphyllo-phoralean fungi to induce germination in seeds of the achlorophyllous orchid *Galeola altissima.* He found that several wood-decaying fungi, including *Phellinus* sp., induced germination in the laboratory, but for only one of these fungi, *Erythromyces crocicreas,* has a connection to orchids been demonstrated in the wild.

The nematode-capturing ability established for stephanocyst and echinocyst producing *Hyphoderma* species is yet another nutritional mode shown by species in Hymenochaetales (Tzean and Liou 1993). Stephanocysts and echinocysts are covered by an adhesive mucilage and attach easily to the nematode cuticle. Captured nematodes are killed and the bodies penetrated by hyphae. Tzean and Liou (1993) tested a number of corticioid fungi for nematode-destroying capacity. All species with stephanocysts and echino-cysts could kill nematodes but a number of other *Hyphoderma* species lacking these structures also seemed to kill nematodes by being toxic. Nematodes feeding on hyphae from the latter group of

Hyphoderma species died within 2 h. The fungus then produced hyphae that coiled around the nematode and penetrated the body. Toxic *Hyphoderma* species are not related to those carrying the specialized nematode-catching organs. Only the latter group belongs to Hymenochaetales while the toxic species belong to the polyporoid clade (Hibbett and Thorn 2001). A nematode-killing feeding behavior also has developed independently among *Pleurotus* and *Hohenbuehelia* species in Agaricales (Thorn et al 2000).

Economic importance.—The enzymes and secondary metabolites produced by fungi have received considerable interest for their potential use as drugs or for biotechnological applications. Several species of *Phellinus* and *Inonotus* are used in Asian folk medicine and the products are commercially available. One example is *Phellinus baumii* (often erroneously called *Phellinus linteus*) that is known for its use in traditional Chinese medicine (Ying et al 1987) and in several countries marketed as a drug against cancer, diabetes and toxicity (Shon et al 2003). *Phellinus rimosus* is reported as a drug used by tribes in Kerala in India (Ajith and Janardhanan 2003). Indigenous people in Siberia use chaga as a cleansing and disinfecting substance but the same substance also has been used against liver and heart ailments and in cancer therapy. Chaga is produced from *Inonotus obliquus* and commercially available. There is a rich scientific literature reporting the identification of substances and the effects they may have.

The cellulolytic and ligninolytic enzymes produced by wood-decaying fungi have been studied intensively with the aim of bringing them into practical use in the pulp and paper industry or for cleaning industrial waste products. One of the best studied model organism is *Phanerochaete chrysosporium* that belongs in the polyporoid clade (Hibbett and Thorn 2001), but some interest also has been devoted to species of Hymenochaetaceae (Wesenberg et al 2003).

History and classification.—Hymenochaetales was introduced by Oberwinkler 1977. His circumscription was more or less the same as for Hymenochaetaceae by Donk (1964) and Patouillard (1900) who recognized what he called Série des Igniaires. The characters emphasized by Patouillard and his successors were the uniformly brown hyphae and basidiomata, the simple-septate hyphae, the setae, the blackening of tissue when mounted in KOH (xanthochroic reaction) and the association with white rot. Donk included, with some hesitation, the corticioid genera *Vararia* and *Asterostroma* and the clavarioid *Lachnocladium* because he regarded the dicho- and asterohyphidia occurring in these taxa as modified setae. However Oberwinkler (1977) noted that other

characters (spore amyloidity, gloeocystidia) pointed these latter three genera in the direction of Russulales and molecular phylogenetic studies have confirmed that conclusion (Larsson and Larsson 2003). Donk (1964) also included *Phaeolus schweinitzii* in Hymenochaetaceae although it has no setae and is associated with a brown rot. Parmasto and Parmasto (1979) indicated that its brown pigment is different from the hymenochaetoid fungi and that a xanthochroic reaction is not specific for Hymenochaetaceae. Molecular data confirm that *Phaeolus* does not belong to Hymenochaetales but rather has its place in the vicinity of *Laetiporus* in Polyporales (Binder et al 2005).

Already the first comprehensive molecular study of the homobasidiomycetes indicated that Hymenochaetales *sensu* Oberwinkler should be interpreted more broadly (Hibbett and Donoghue 1995). The sampling of 62 mainly polyporoid taxa showed that *Oxyporus* and *Trichaptum* were closely related to Hymenochaetales despite lacking setae, xanthocroic reaction, brownish hyphae and, in the case of *Trichaptum*, having nodose-septate hyphae. However *Trichaptum* was known to have imperforate parenthesomes, which pointed to a relationship with Hymenochaetales and also set the dolipore morphology in focus for further study. Langer and Oberwinkler (1993) already had ascertained that several corticioid species (viz. *Hyphodontia* spp., *Basidioradulum radula* and *Schizopora paradoxa*) have imperforate parenthesomes. In a subsequent molecular investigation (Hibbett et al 1997) these three genera were included and found to cluster with Hymenochaetales, *Oxyporus* and *Trichaptum*. However the strain of "*Hyphodontia alutaria*" (GEL 2071) used as a DNA source actually represents *Resinicium bicolor* (cf. Binder et al 2005).

Hibbett and Thorn (2001) provided the first description of what here is called Hymenochaetales (as hymenochaetoid clade) taking into account all the new results received from molecular phylogenetic studies. Moncalvo et al (2002) showed that species from the stipitate stereoid genus *Cotylidia* and the agaricoid genera *Cantharellopsis*, *Omphalina* and *Rickenella* also had their place in or close to Hymenochaetales. Redhead et al (2002) reclassified these agarics in the Hymenochaetales. Larsson et al (2004) provided a second overview of the group and a third was published recently (Binder et al 2005), both with an emphasis on corticioid taxa.

The Hymenochaetales in its original sense (i.e. *Phellinus*, *Inonotus*, *Hymenochaete* and related genera, with setae, xanthochroic reaction, simple-septate hyphae etc.) here will be referred to as Hymenochaetaceae. The family includes close to 400 species. They are found in all parts of the world, and because all

species form quite conspicuous basidiomata they have been extensively collected and studied. Recent morphological descriptions and keys to the poroid taxa can be found in Gilbertson and Ryvarden (1986, 1987), Larsen and Cobb-Poulle (1990), Núñez and Ryvarden (2000) and Ryvarden (2004). *Hymenochaete* and related genera with a nonporoid hymenophore are treated by Léger (1998) and Parmasto (2001, 2005).

Species in Hymenochaetaceae contain a group of organic compounds called styrylpyrones. Similar compounds also are known from various plant families and they probably form part of a defense against infections and browsing. The distribution of styrylpyrones within Hymenochaetaceae has been used in the classification of the group (Fiasson 1982, Fiasson and Bernillon 1983). Chemical characters together with detailed morphological studies prompted Fiasson and Niemelä (1984) to accept 10 genera for the poroid species in Europe as a replacement for the prevailing classification with only two genera: *Inonotus* for monomitic and annual species and *Phellinus* for species with dimitic and perennial basidiomata.

Hymenochaete originally was introduced for species with effused to effused-reflexed basidiomata and a smooth hymenophore. For similar taxa with a hydnoid hymenophore the artificial genus *Hydnochaete* is available. Two neotropical species with stipitate basidiomata and a smooth hymenophore were placed in *Stipitochaete* and those with a clavarioid basidioma in *Clavariachaete*. There are several other genera within Hymenochaetaceae that are morphologically distinct and therefore kept separate by most authors. The laterally stipitate genus *Cyclomyces* carries its name because the type species has a concentrically lamellate hymenophore. The same hymenophore configuration sometimes can be found also in specimens of *Coltricia montagnei* while neighboring fruit bodies may be strictly poroid. *Onnia* and *Coltricia* species have stipitate basidiomata and a poroid hymenophore, but the latter genus is regarded as distinct because setae are lacking. This is also true for *Aurificaria* that differs by an olivaceous discoloring of the basidiospores in KOH. Setae also are lacking in *Coltriciella* but its spores are finely ornamented, quite unique within Hymenochaetaceae. Finally *Pyrrhoderma* has laterally stipitate basidiomata with the cap covered by a shiny crust.

The phylogeny of Hymenochaetaceae has been thoroughly studied by molecular methods (e.g. Wagner and Fischer 2001, 2002a, b). These studies indicated that Hymenochaetaceae, as it formerly was circumscribed, was not a monophyletic group. Some corticoid species (viz. *Basidioradulum radula* and *Hyphodontia quercina*) and two polypore genera, *Schizopora* and *Trichaptum*, were intermixed among typical hymenochaetoid species. On the other hand the molecular data gave support to the work of Fiasson and Niemelä (1984) who divided the poroid genera *Inonotus* and *Phellinus* in several smaller groups based on morphology and chemical characters. The new classification for the poroid species is in general well supported by morphological, physiological and ecological characters but does not support a division between monomitic annual taxa and dimitic perennial ones.

The situation within *Hymenochaete* and other genera with a smooth or hydnoid hymenophore appears less resolved when molecular data are analyzed. Wagner and Fischer (2002b) found that all species they sampled belonged to one clade except *Hymenochaete tabacina* that clustered among some of the poroid species. Consequently a new genus, *Pseudochaete*, was introduced (Wagner and Fischer 2002b).

The mushroom-forming species in Hymenochaetales are all of the omphalinoid type (viz. small fruit bodies with rather thick, shallow and strongly decurrent lamellae). The first hint that not all omphalinoid agarics belonged to the same clade came in a paper on the phylogeny of agaric fungi (Moncalvo et al 2000) and a subsequent paper with a broader sampling, which established that some species are members of the hymenochaetoid clade (Moncalvo et al 2002). In a companion paper Redhead et al (2002) studied the phylogeny and classification of these hymenochaetoid agarics and showed that they all are associated with bryophytes. The last two studies also were the first to expose that the stipitate stereoid genus *Cotylidia* seemed related to the omphalinoid species in Hymenochaetales. *Cotylidia* formerly was classified together with other stipitate stereoid species in Podoscyphaceae. Now it has been shown that *Podoscypha* has its place in the clade called polyporoid by Hibbett and Thorn (2001) and far removed from *Cotylidia* (Kim and Jung 2000).

Hymenochaetales includes a number of species with thin, effused basidiomata and with a smooth to hydnoid hymenophore. Such fungi traditionally have been placed in a single family Corticiaceae, widely acknowledged as an artifical family (Donk 1964, Jülich 1982). Jülich (1982) published a comprehensive classification for corticioid fungi using morphology only. The corticioid taxa included in Hymenochaetales are drawn from four of the orders in Jülich's classification, which further emphasizes the difficulties that have plagued all attempts to fit corticioid fungi into a morphology-based classification. It was not until DNA characters became available that the

phylogeny of corticioid fungi could be investigated reliably. Now we know that corticoid fungi occur in every major homobasidiomycete clade (Larsson et al 2004, Binder et al 2005).

Hyphodontia is the largest genus of corticioid fungi in Hymenochaetales with ca. 90 species. Descriptions and keys to most *Hyphodontia* species are found in Langer (1994).

MATERIALS AND METHODS

ITS and nLSU sequences available at GenBank were compiled and complemented with sequences generated for this study. The GenBank sequences originate from a number of studies, not all of them published. In many cases one lab has deposited a sequence from one of the regions in question while another lab has contributed another, both being labeled with the same species name but generated from different specimens. We have combined sequences from different sources when they are identified as conspecific. We took a calculated risk that a compilation trusting the names attached to sequences might introduce ambiguities as to sequence homogeneity. We consider that risk to be outweighed by the advantages of a denser sampling and a data matrix with fewer missing data. The dataset was trimmed to remove duplicates, unidentified specimens and some sequences that were deemed too short to give a reliable signal. After preliminary analyses (not shown) a number of sequences from densely sampled subclades within Hymenochaetaceae (e.g. *Inonotus* and *Phellinus*) were removed to receive a more manageable dataset without sacrificing resolution at and above the genus level. Thirty-five sequences, mainly of corticioid species, have not been published before. Two species from Cantharellales (*Sistotrema*) and two species from Auriculariales (*Exidiopsis, Protodontia*) are included as outgroup. All information on specimens made use of in this study along with GenBank accession numbers is available in SUPPLEMENTARY TABLE I.

The dataset included 174 ingroup sequences and 1552 nucleotide positions including introduced gaps. However ITS1 and ITS2 were deemed too variable and were excluded from analyses together with several variable regions within LSU. Protocols for DNA extraction, PCR and sequencing followed Larsson and Larsson (2003) and Larsson et al (2004).

Heuristic maximum parsimony analyses were performed with PAUP*4.0 (200 random taxon addition replicates, keeping 50 trees per replicate, MAXTREES = 15 000). The analysis used 1025 characters of which 529 were constant, 135 variable but parsimony uninformative and 361 parsimony informative. Branch support was estimated with nonparametric bootstrapping as implemented in PAUP*4.0 (100 replicates, 10 random addition sequences per replicate, keeping 50 trees per replicate, MAXTREES = 15 000).

Bayesian inference of phylogeny was performed with MrBayes 3.0B4 (Ronquist and Huelsenbeck 2003). MrModelTest 2.2 (Nylander 2004) was used to estimate separate best-fit models of evolution for 5.8S and LSU. A heterogeneous Bayesian inference was set up with model parameters estimated separately for each partition. Eight Metropolis-coupled Markov chain Monte Carlo (MCMCMC) chains with a temperature of 0.2 C were initiated; these were run 3 000 000 generations with tree and parameter sampling every 1500 generations (2000 trees). The initial burn-in was set to 50% (1000 trees). A 50% majority-rule consensus cladogram was computed from the remaining trees; the proportions of this tree correspond to Bayesian posterior probabilities (BPP).

RESULTS AND DISCUSSION

MP analysis of the nLSU+5.8S dataset resulted in 200 equally parsimonious trees with little support for deeper nodes. The MP tree file with all shortest trees and the bootstrap tree file are available as supplementary material. The models GTR+I+G (LSU) and SYM+G (5.8S) were supported as the best fit models for the two data partitions and employed in MrBayes analyses. Chain convergence was attained well ahead of the initial burn-in threshold and chain mixing was found to be satisfactory. A 50% majority-rule consensus cladogram with Bayesian posterior probabilities (FIG. 2); branch lengths reflect estimated number of changes per site.

Bayesian inference produced a fairly well resolved tree with high posterior probability values for several clades. Major monophyletic clades are discussed briefly below in alphabetical order as indicated on the tree.

(A) Oxyporus *clade.*—*Oxyporus* is a genus of white-rotting polypores that often attack living trees of both hardwoods and conifers. Mostly it is only the heartwood that is decayed but at least one species also can invade the sapwood, which of course is detrimental for the tree. *Bridgeoporus nobilissimus* previously was classified in *Oxyporus* but recently segregated because it is suggested to be a brown rot agent (Burdsall et al 1996). The phylogenetic position of *Bridgeoporus* within Hymenochaetales was not investigated here.

(B) Rickenella *clade.*—This group is a mixture of species with effused, stipitate stereoid and stipitate lamellate basdiomata. No morphological characters are diagnostic of the group together, but it is interesting to note that nutritional modes include various interactions with other living organisms (association with bryophytes, association with green algae and predation on nematodes, all of which could serve as nitrogen sources). Within the larger clade are some well defined groups and at least three of them can be recognized by morphology. *Resinicium* in a restricted sense emerges as a well supported genus characterized by large halocystidia. *Hyphoderma praetermissum* together with related nematode-catch-
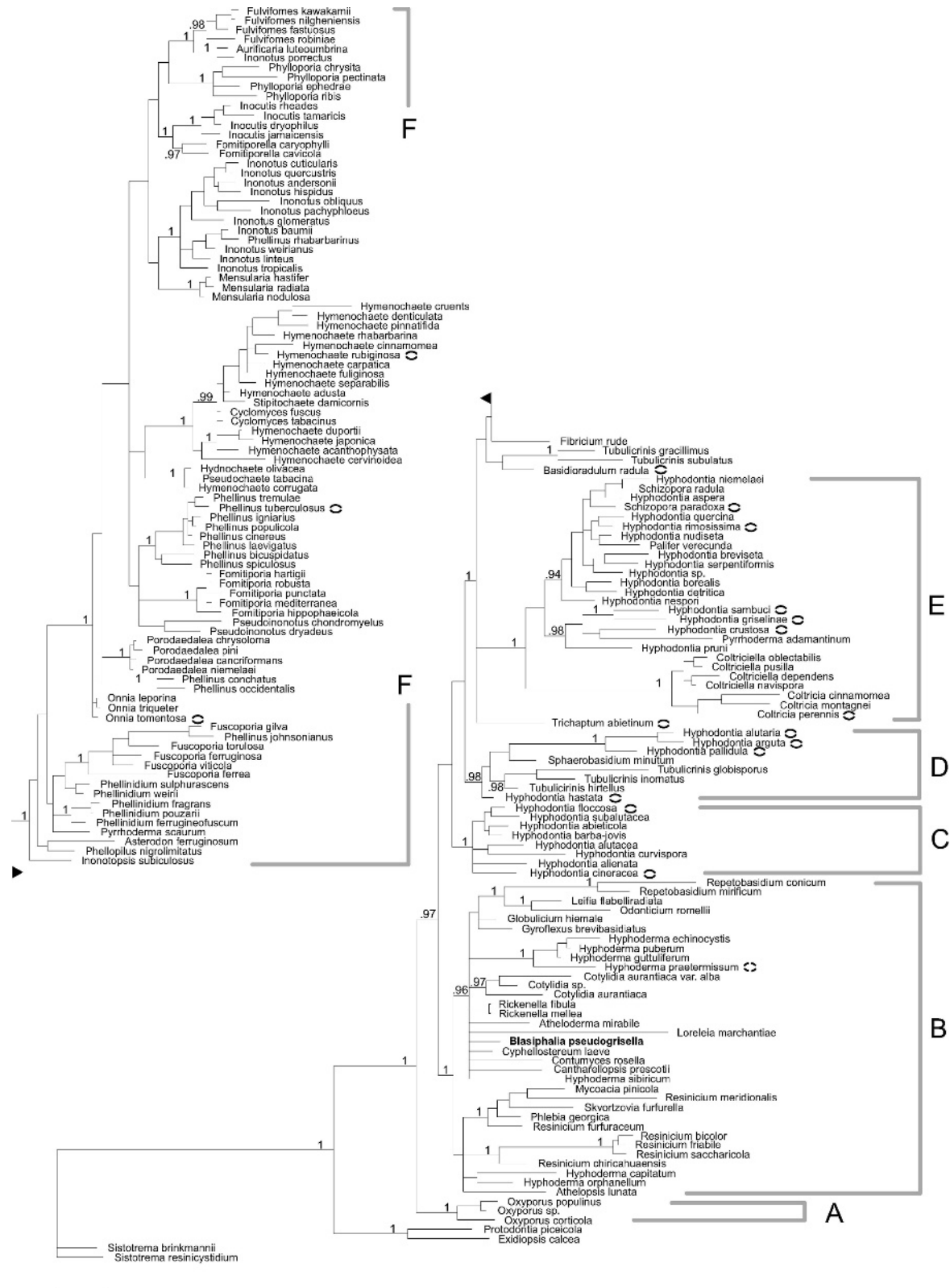
FIG. 2. Phylogenetic relationships of Hymenochaetales inferred from 5.8S and nucLSU rDNA sequences with Bayesian analysis. A 50% majority rule consensus cladogram Bayesian posterior probabilities ≥ 0.94 are shown above internodes; branch lengths reflect estimated number of changes per site. Closed horizontal parentheses indicate that the species has dolipores with continuous parenthesomes. Broken horizontal parentheses indicate presence of the perforated parenthesome type. A. *Oxyporus* clade. B. *Rickenella* clade. C. *Kneiffiella* clade. D. *Hyphodontia* clade. E. *Coltricia* clade. F. Hymenochaetaceae clade.

ing species are also supported as monophyletic. For this group the name *Peniophorella* is available (Larsson in press). The *Skvortzovia* subclade unites several corticioid species that until now have been placed in different genera. Burdsall and Nakasone (1981) pointed out the similarities exhibited by cultures of *Mycoacia meridionalis* and *Odontia furfurella*, and Nakasone (1990) placed the two together in *Resinicium*. Hjortstam and Bononi (1987) erected *Skvortzovia* to encompass *Odontia furfurella*. It seems appropriate to refer also the other species to the same genus. All have small hymenial cystidia with an apical cap of exudated material. *Leifia*, *Odonticium* and *Repetobasidium* are three corticioid genera that morphologically do not seem to have anything in common, and the possibility that the group is an artifact caused by the analysis must be considered. *Odonticium romellii* (type species) has an odontioid hymenium, thick-walled simple-septate hyphae and narrowly allantoid spores. Zmitrovich (2001) recently suggested a connection with *Leifia flabelliradiata* and also made a combination to *Odonticium*. Although the agaricoid taxa now placed in the Hymenochaetales appeared to be congeneric in an early analysis (Lutzoni 1997) and only later were suggested to represent several genera (Redhead et al 2002), it is only after combining data on additional taxa (*Rickenella fibula* and *Cyphellostereum laeve*, Larsson et al 2004) and other corticioid taxa in the current analysis that the diversity is revealed further. Each of the genera stands alone save for *Rickenella*, and there the appresoria-forming *Blasia* parasite, *R. pseudogrisella*, appears to be separable from other *Rickenella* that penetrate rhizoids directly and therefore should be reclassified as is here proposed:

Blasiphalia Redhead, gen. nov., *a Rickenello appressoriis praesentibus differt*. Differs from *Rickenella* by presence of appresoria. Etymology: Latinized nonsense word from fragments of *Blasia* and *Omphalia* (f.). Type: *Blasiphalia pseudogrisella* (AH Sm) Redhead.

Blasiphalia pseudogrisella (AH Sm) Redhead, comb. nov.; basionym: *Mycena pseudogrisella* AH Sm, North American Species of *Mycena*, p 124, 1947.

(C) Kneiffiella *clade.*—Most species in this clade either have long, tubular cystidia originating in the subiculum (pseudocystidia; SUPPLEMENTARY FIG. 1E) or thin-walled, tubular hymenial cystidia. The group seems quite natural and was recovered also in the MP strict consensus tree but generated no significant bootstrap support. *Kneiffiella* is an old genus name available for this group and most combinations are already in place (Jülich and Stalpers 1980).

(D) Hyphodontia *clade.*—The *Hyphodontia* species in this clade includes the type species, *H. pallidula*. *Hyphodontia sensu stricto* apparently will become a quite small genus with 5–6 closely related species only. They all are characterized by septate cystidia in combination with lagenocystidia (SUPPLEMENTARY FIG. 1I). With its spectacular lyocystidia, *Tubulicrinis* is morphologically well defined but in this analysis the genus is split in two groups. The phylogeny presented here is certainly not the final word on the composition of the *Hyphodontia* clade.

(E) Coltricia *clade.*—This clade holds a mixture of corticioid species and two genera that earlier were classified with Hymenochaetaceae. A sample of *Hyphodontia* species form two clades, a weakly supported one centered on *Hyphodontia aspera* and a moderately supported clade that includes *H. crustosa*, *H. sambuci* and *H. pruni*. The latter group also includes *Pyrrhoderma adamantinum*. This is a stipitate poroid species that usually is placed in Hymenochaetaceae, and the phylogenetic position shown here needs confirmation. All *Hyphodontia* species have various types of hymenial, little differentiated and often capitate cystidia. *Coltricia* and *Coltriciella* form a strongly supported clade. These genera of stipitate polypores show most of the traits that characterize Hymenochaetaceae but they mostly lack setae. However among Asian and South American species of *Coltricia* there are species with setae or setal hyphae (viz. *C. hamata*, *C. duostratosa*, *C. tomentosa* and *C. vallata*). *Coltriciella* differs clearly from *Coltricia* by finely ornamented spores but the phylogenetic analysis gave no support for a separation in two genera.

(F) Hymenochaetaceae *clade.*—The Hymenochaetaceae in its traditional sense is not supported as monophyletic in our analysis. This is in accordance with the results received by Wagner and Fischer (2002b). However the Bayesian inference supports a monophyletic Hymenochaetaceae that excludes only *Coltricia* and *Coltriciella*. The subdivision of *Phellinus* and *Inonotus* into smaller genera in general is supported strongly here. Exceptions include *Onnia*, *Phellinidium* and *Pseudoinonotus* and these genera might have to be revised. The segregation of *Pseudochaete* from *Hymenochaete* also is supported while genera erected on account of a specific fruit body type or hymenium configuration (*Stipitochaete*, *Hydnochaete*) are not.

In molecular analyses with a homobasidiomycetewide sampling the hymenochaetoid clade has received mainly low or moderate support values (e.g. Hibbett et al 1997, Larsson et al 2004, Binder et al 2005). Binder and Hibbett (2002) managed to raise bootstrap values to 95% when four gene regions and

three representatives for the clade were included. The four genes studied (nuclear SSU and LSU, mitochondrial SSU and LSU) also were analyzed separately and in combinations of two and three genes. The data shows that most phylogenetic signal seems to emanate from the mitochondrial genes and especially the SSU region. Future phylogenetic investigations in Hymenochaetales should take advantage of that result.

No unequivocal morphological synapomorphies support Hymenochaetales, and the order presently can be defined only in terms of molecular data. The occurrence of dolipores with continuous parenthesomes and the possibility that this structure is a synapomorphy for Hymenochaetales have gained considerable interest. However *Hyphoderma praetermissum* has perforate parenthesomes (Langer and Oberwinkler 1993, Keller 1997). The tree topology (FIG. 2) still indicates that continuous parenthesomes might define a monophyletic group consisting of clades C–F. Further exploration of septal ultrastructure for species here referred to clades A and B is desirable.

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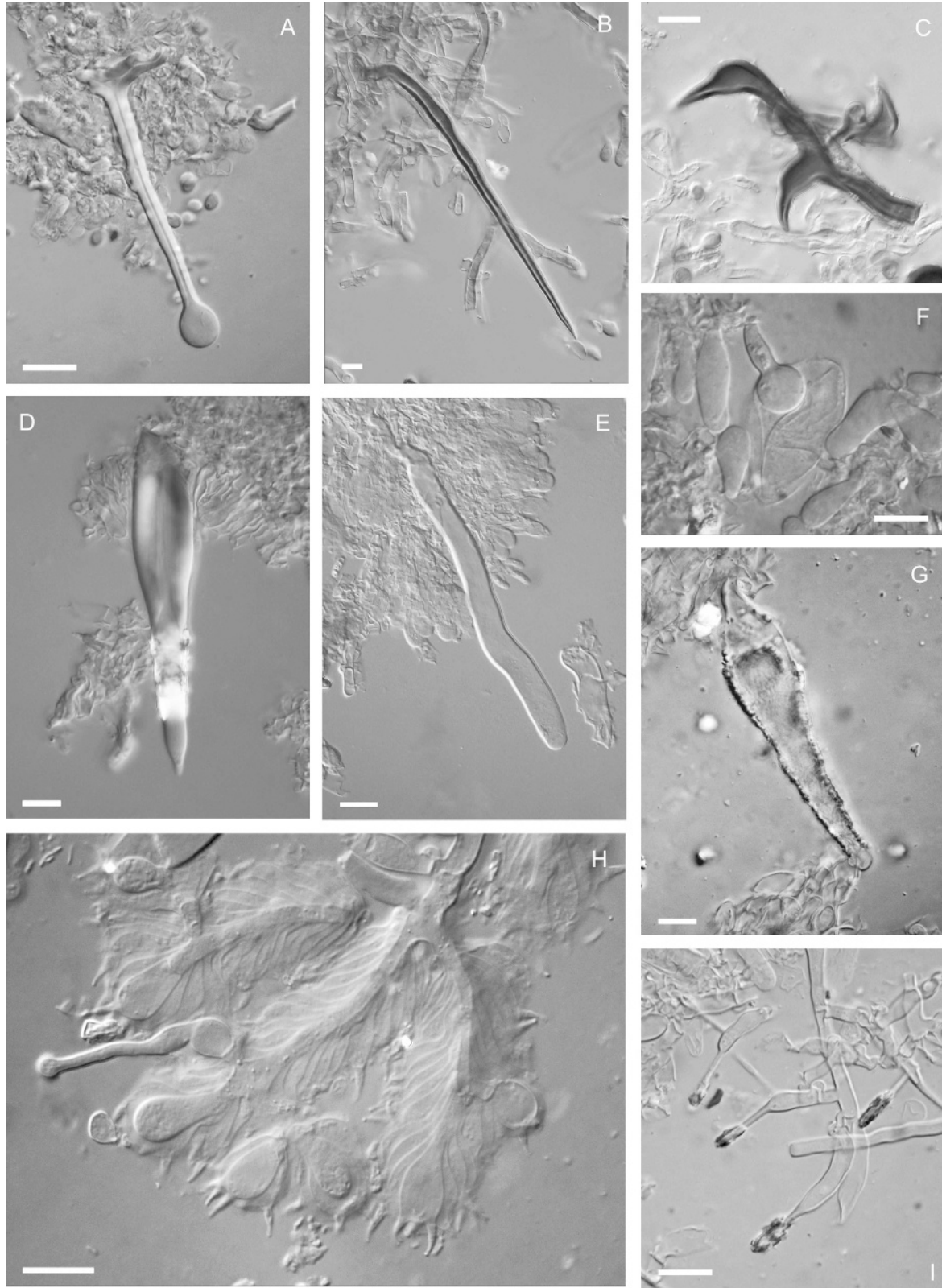
SUPPLEMENTARY FIG. 1. Microscopic characters in Hymenochaetales. A, *Tubulicrinis accedens*, lyocystidium. B, *Hymenochaete cinnamomea*, hymenial seta. C, *Inonotus cuticularis*, branched and hooked seta from the upper pileus surface. D, *Tubulicrinis subulatus*, lyocystidium. E, *Hyphodontia subalutacea*, pseudocystidium originating in the subiculum. F, *Resinicium granulare*, halocystidium with partly collapsed halo. G, *Hyphoderma puberum*, thickwalled, encrusted cystidium (metuloid). H, *Repetobasidium vestitum*, basidia with rows of remnants of old basidia walls anda capitate hymenial cystidium. I, *Hyphodontia arguta*, lagenocystidia with apical incrustation. Scale bar = 10 μm.
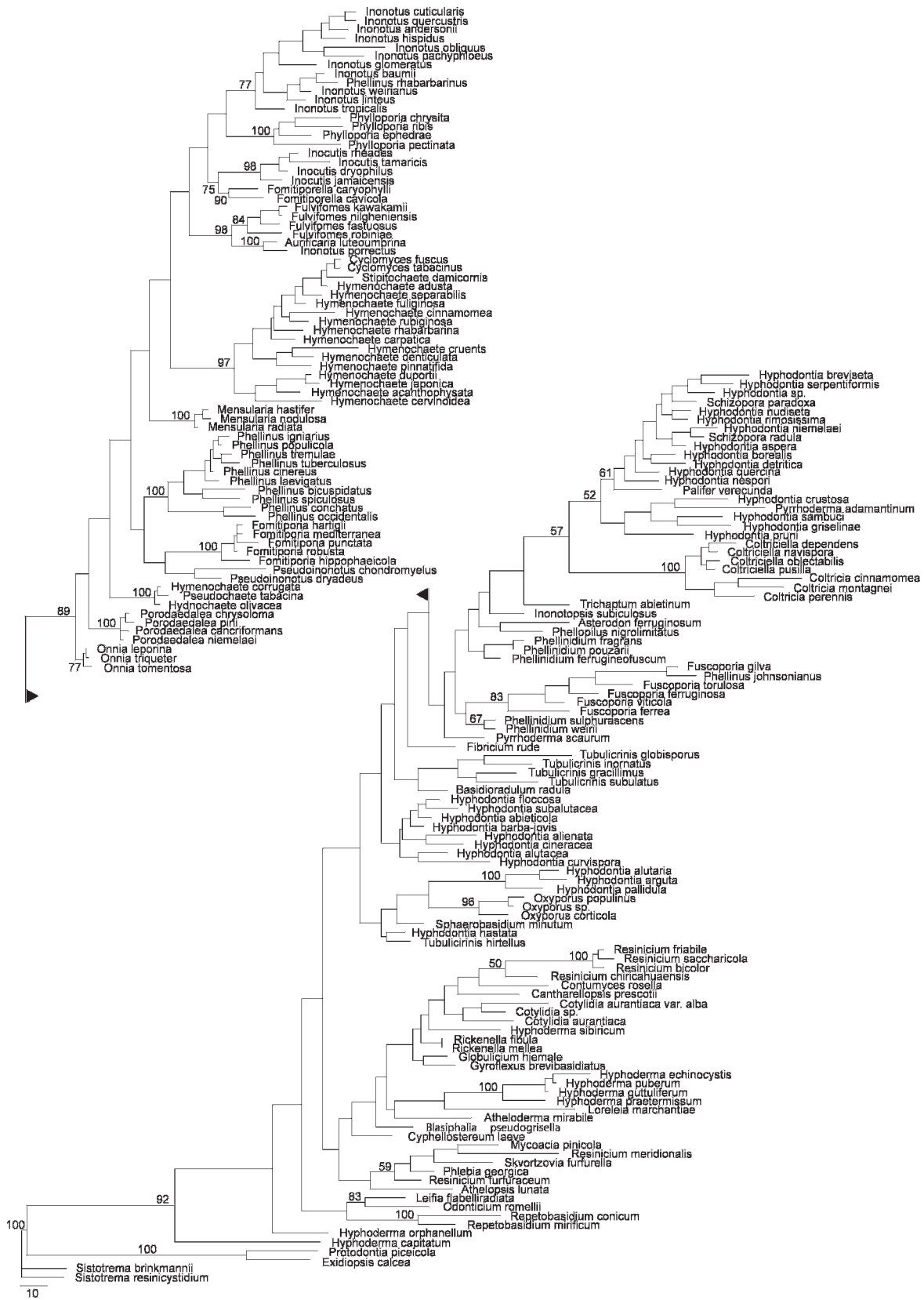
SUPPLEMENTARY FIG 2.   Maximum parsimony tree for Hymenochaetales with bootstrap values indicated.

SUPPLEMENTARY TABLE I.   GenBank numbers for all sequences used in analyses

Species	ITS1	5.8S	ITS2	Nuc LSU
Asterodon ferruginosum		AY463380		AY586631
Aurificaria luteoumbrina				AY059033
Coltricia cinnamomea				AF311003
Coltricia montagnei				AY039683
Coltricia perennis	DQ234559	DQ234559	DQ234559	AF287854
Coltriciella dependens				AY059059
Coltriciella navispora				AY059062
Coltriciella oblectabilis				AY059061
Coltriciella pusilla				AY059060
Cyclomyces fuscus				AF385163
Cyclomyces tabacinus				AF385164
Fomitiporella caryophylli	AY558611	AY558611	AY558611	AY059021
Fomitiporella cavicola				AY059052
Fomitiporia hartigii	AY558621	AY558621	AY558621	AF311005
Fomitiporia hippophaëicola	AY558622	AY558622	AY558622	AF311006
Fomitiporia mediterranea	AY854080	AY854080	AY854080	AY684157
Fomitiporia punctata	AF515563	AF515563	AF515563	AF311007
Fomitiporia robusta	AY558645	AY558645	AY558645	AF311008
Fulvifomes fastuosus	AY558615	AY558615	AY558615	AY059057
Fulvifomes kawakamii				AY059028
Fulvifomes nilgheniensis	AY558633	AY558633	AY558633	AY059023
Fulvifomes robiniae				AF411825
Fuscoporia ferrea	AY558617	AY558617	AY558617	AF311030
Fuscoporia ferruginosa	AYl89700	AYl89700	AYl89700	AF311032
Fuscoporia gilva	AF250932	AF250932	AF250932	AF518636
Fuscoporia torulosa	AY558649	AY558649	AY558649	AF311041
Fuscoporia viticola	AY558653	AY558653	AY558653	AY885166
Hydnochaete duportii				AY635770
Hydnochaete japonica	AY558596	AY558596	AY558596	AF385153
Hydnochaete olivacea				AY293185
Hymenochaete acanthophysata				AF385144
Hymenochaete adusta	AY558594	AY558594	AY558594	AF385161
Hymenochaete carpatica				AF385158
Hymenochaete cervinoidea				AF385157
Hymenochaete cinnamomea		AY463416		AY586664
Hymenochaete corrugata				AF518620
Hymenochaete cruenta				AF385152
Hymenochaete denticulata	AY558595	AY558595	AY558595	AF385155
Hymenochaete fuliginosa				AF385154
Hymenochaete pinnatifida				AF385149
Hymenochaete rhabarbarina				AJ406468
Hymenochaete rubiginosa		AY463417		AY586665
Hymenochaete separabilis				AF385146
Inocutis dryophilus				AF311012
Inocutis jamaicensis	AY072029	AY072029	AY072029	AY059048
Inocutis rheades	AF237731	AF237731	AF237731	AF311019
Inocutis tamaricis	AY558604	AY558604	AY558604	AF311021
Inonotopsis subiculosus				AF311020
Inonotus anderssonii	AY558599	AY558599	AY558599	AY059041
Inonotus baumii	AF200230	AF200230	AF200230	AY059058
Inonotus cuticularis	AF237730	AF237730	AF237730	AF311010
Inonotus glomeratus	AF247968	AF247968	AF247968	AY059032
Inonotus hispidus	AY558602	AY558602	AY558602	AF518623
Inonotus linteus	AF153010	AF153010	AF153010	AF458461
Inonotus obliquus	AY251310	AY251310	AY251310	AY279001

Species	ITS1	5.8S	ITS2	Nuc LSU
Inonotus pachyphloeus	AY558635	AY558635	AY558635	AY059020
Inonotus porrectus	AY558603	AY558603	AY558603	AY059051
Inonotus quercustris	AY072026	AY072026	AY072026	AY059050
Inonotus tropicalis	AY641432	AY641432	AY641432	AY598826
Inonotus weirianus	AY558654	AY558654	AY558654	AY059035
Mensularia hastifer				AF311013
Mensularia nodulosa				AF311016
Mensularia radiata	AF237732	AF237732	AF237732	AF311018
Onnia leporina				AF311022
Onnia tomentosa	AY558607	AY558607	AY558607	AF311023
Onnia triqueter				AF311024
Phellinidium ferrugineofuscum				AF311031
Phellinidium fragrans	AY558619	AY558619	AY558619	AY059027
Phellinidium pouzarii				AF311039
Phellinidium sulphurascens	AY829344	AY829344	AY829344	AY059016
Phellinidium weirii	AY829342	AY829342	AY829342	AY829346
Phellinus bicuspidatus	AY189699	AY189699	AY189699	AY059022
Phellinus cinereus	AY340048	AY340048	AY340048	AF311027
Phellinus conchatus	AY558614	AY558614	AY558614	AF311028
Phellinus ingniarius	AF110991	AF110991	AF110991	AY839834
Phellinus (Fuscoporia) johnsonianus	AF250931	AF250931	AF250931	AF458458
Phellinus laevigatus	AF053226	AF053226	AF053226	AF311034
Phellinus occidentalis	AY558634	AY558634	AY558634	AY059019
Phellinus populicola	AY558638	AY558638	AY558638	AF311038
Phellinus (Inonotus) rhabarbarinus	AY558642	AY558642	AY558642	AF458466
Phellinus spiculosus	AY189702	AY189702	AY189702	AY059055
Phellinus tremulae	AY340064	AY340064	AY340064	AF311042
Phellinus tuberculosus	AY558652	AY558652	AY558652	AF311043
Phellopilus nigrolimitatus	AY558632	AY558632	AY558632	AF311036
Phylloporia chrysita				AF411821
Phylloporia ephedrae				AF411826
Phylloporia pectinata				AF411823
Phylloporia ribis	AY558643	AY558643	AY558643	AF311040
Porodaedalea canchriformans	AF200242	AF200242	AF200242	AY059029
Porodaedalea chrysoloma	AY189706	AY189706	AY189706	AF311026
Porodaedalea niemelaei				AY059054
Porodaedalea pini	AY558636	AY558636	AY558636	AF311037
Pseudochaete tabacina	AY558598	AY558598	AY558598	AF385145
Pseudoinonotus chondromyelus				AF311009
Pseudoinonotus dryadeus	AY558601	AY558601	AY558601	AF311011
Pyrrhoderma adamantinum				AY059031
Pyrrhoderma scaurum				AY059030
Stipitochaete damicornis				AF385162
Blasiphalia pseudogrisella	U66437	U66437	U66437	U66437
Cantharellopsis prescotii				AF261461
Contumyces rosella	U66452	U66452	U66452	U66452
Cotylidia aurantiaca				AF261460
Cotylidia aurantiaca var alba				AF261458
Cotylidia diaphana				AF261459
Cotylidia sp.	AY854079	AY854079	AY854079	AY629317
Cyphellostereum laeve				AY745705
Gyroflexus brevibasidiatus	U66441	U66441	U66441	U66441
Loreleia marchantiae	U66432	U66432	U66432	U66432
Rickenella fibula	DQ241782	DQ241782	DQ241782	AY700195
Rickenella mellea	U66438	U66438	U66438	U66438
Atheloderma mirabile		DQ873592	DQ873592	DQ873592

Species	ITS1	5.8S	ITS2	Nuc LSU
Athelopsis lunata	DQ873593	DQ873593	DQ873593	DQ873593
Basidioradulum radula	DQ234537	DQ234537	DQ234537	AY700184
Fibricium rude				AY700202
Globulicium hiemale	DQ873595	DQ873595	DQ873595	DQ873595
Hyphoderma echinocystis		DQ677494		DQ681200
Hyphoderma guttuliferum		AY463419		AY586667
Hyphoderma praetermissum	DQ873597	DQ873597	DQ873597	DQ873597
Hyphoderma puberum	DQ873599	DQ873599	DQ873599	DQ873599
Hyphoderma capitatum		DQ677491	DQ677491	DQ677491
Hyphoderma orphanellum		DQ677500	DQ677500	DQ677500
Hyphoderma sibiricum		DQ677503	DQ677503	DQ677503
Hyphodontia abieticola	DQ873601	DQ873601	DQ873601	DQ873601
Hyphodontia alienata		AY466401	AY466401	AY586727
Hyphodontia alutacea				AJ406453
Hyphodontia alutaria	DQ873603	DQ873603	DQ873603	DQ873603
Hyphodontia arguta		DQ873605	DQ873605	DQ873605
Hyphodontia aspera	DQ873606	DQ873606	DQ873606	DQ873607
Hyphodontia barbajovis	DQ873608	DQ873608	DQ873608	DQ873609
Hyphodontia borealis		AY463429		AY586677
Hyphodontia breviseta	DQ873612	DQ873612	DQ873612	DQ873612
Hyphodontia cineracea				AJ406450
Hyphodontia crustosa	DQ873614	DQ873614	DQ873614	DQ873614
Hyphodontia curvispora		DQ873615	DQ873615	DQ873616
Hyphodontia detritica		DQ677507	DQ677507	DQ677507
Hyphodontia floccosa	DQ873618	DQ873618	DQ873618	DQ873618
Hyphodontia hastata		DQ873619		DQ873620
Hyphodontia nespori	DQ873622	DQ873622	DQ873622	DQ873622
Hyphodontia niemelaei				AJ406462
Hyphodontia nudiseta				AJ406460
Hyphodontia pallidula				AJ406594
Hyphodontia paradoxa	AF145571	AF145571	AF145571	AY059067
Hyphodontia pruni	DQ873624	DQ873624	DQ873624	DQ873625
Hyphodontia quercina		AY463430		AY586678
Hyphodontia radula	AF145570	AF145570	AF145570	AJ406466
Hyphodontia rimosissima	DQ873627	DQ873627	DQ873627	DQ873628
Hyphodontia sambuci				AJ406461
Hyphodontia serpentiformis				AJ406465
Hyphodontia subalutacea	DQ873633	DQ873633		DQ873634
Hyphodontia sp.	DQ873633	DQ873633	DQ873633	DQ873634
Leifia flabelliradiata		DQ873635	DQ873635	DQ873635
Mycoacia pinicola	DQ873637	DQ873637	DQ873637	DQ873637
Odonticium romellii		DQ873639	DQ873639	DQ873639
Oxyporus corticola	DQ873641	DQ873641	DQ873641	DQ873641
Oxyporus latemarginatus	AF163047	AF163047	AF163047	
Oxyporus populinus				AJ406467
Palifer verecunda	DQ873642	DQ873642	DQ873642	DQ873643
Phlebia georgica	DQ873645	DQ873645	DQ873645	DQ873645
Repetobasidium conicum	DQ873647	DQ873647	DQ873647	DQ873647
Repetobasidium mirificum				AY293208
Resinicium bicolor		AY463463		AF518645
Resinicium chiricahuaensis				DQ863692
Resinicium friabile				DQ863690
Resinicium furfuraceum	DQ873648	DQ873648	DQ873648	DQ873648
Resinicium meridionalis				DQ863693
Resinicium saccharicola				DQ863691
Rogersella griselinae	DQ873651	DQ873651	DQ873651	DQ873651

Species	ITS1	5.8S	ITS2	Nuc LSU
Skvortzovia furfurella		DQ873649	DQ873649	DQ873649
Sphaerobasidium minutum		DQ873652	DQ873652	DQ873653
Trichaptum abietinum		AF347104	AF347104	AF347104
Tubulicrinis globisporus	DQ873655	DQ873655	DQ873655	DQ873655
Tubulicrinis gracillimus				AF518661
Tubulicrinis hirtellus	DQ873657	DQ873657	DQ873657	DQ873657
Tubulicrinis inornatus		DQ873659	DQ873659	DQ873659
Tubulicrinis subulatus		AY463478		AY586722
Sistotrema brinkmannii	X	X	X	X
Sistotrema resinicystidium	X	X	X	X
Exidiopsis calcea		AY463406		AY586654
Protodontia piceicola	DQ873660	DQ873660	DQ873660	DQ873660