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The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi (Homobasidiomycetes)

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Abstract Phylogenetic relationships of resupinate Homobasidiomycetes (Corticiaceae *s. lat.* and others) were studied using ribosomal DNA (rDNA) sequences from a broad sample of resupinate and nonresupinate taxa. Two datasets were analysed using parsimony, a 'core' dataset of 142 species, each of which is represented by four rDNA regions (mitochondrial and nuclear large and small subunits), and a 'full' dataset of 656 species, most of which were represented only by nuclear large subunit rDNA sequences. Both datasets were analysed using traditional heuristic methods with bootstrapping, and the full dataset was also analysed with the Parsimony Ratchet, using equal character weights and six-parameter weighted parsimony. Analyses of both datasets supported monophyly of the eight major clades of Homobasidiomycetes recognised by Hibbett and Thorn, as well as independent lineages corresponding to the *Gloeophyllum* clade, corticioid clade and *Jaapia argillacea*. Analyses of the full dataset resolved two additional groups, the athelioid clade and trechisporoid clade (the latter may be nested in the polyporoid clade). Thus, there are at least 12 independent clades of Homobasidiomycetes. Higher-level relationships among the major clades are not resolved with confidence. Nevertheless, the euagarics clade, bolete clade, athelioid clade and *Jaapia argillacea* are consistently resolved as a monophyletic group, whereas the cantharelloid clade, gomphoid-phalloid clade and hymenochaetoid clade are placed at the base of the Homobasidiomycetes, which is consistent with the preponderance of imperforate parenthesomes in those groups. Resupinate forms occur in each of the

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major clades of Homobasidiomycetes, some of which are composed mostly or exclusively of resupinate forms (athelioid clade, corticioid clade, trechisporoid clade, *Jaapia*). The largest concentrations of resupinate forms occur in the polyporoid clade, russuloid clade and hymenochaetoid clade. The cantharelloid clade also includes many resupinate forms, including some that have traditionally been regarded as heterobasidiomycetes (Sebacinaceae, Tulasnellales, Ceratobasidiales). The euagarics clade, which is by far the largest clade in the Homobasidiomycetes, has the smallest fraction of resupinate species. Results of the present study are compared with recent phylogenetic analyses, and a table summarising the phylogenetic distribution of resupinate taxa is presented, as well as notes on the ecology of resupinate forms and related Homobasidiomycetes.

Key words Corticiaceae, corticioid fungi, heterobasidiomycetes, Parsimony Ratchet, Polyporaceae, systematics, taxonomy, rDNA sequences

Introduction

The Homobasidiomycetes is a group of Fungi with approximately 16 000 described species (Kirk *et al*., 2001), including such familiar forms as gilled mushrooms, polypores, coral fungi and gasteromycetes. In addition to these, the Homobasidiomycetes includes relatively simple resupinate forms that have flattened, crust-like fruiting bodies. Resupinate Homobasidiomycetes resemble each other in gross morphology, but they are diverse in anatomical, ecological, physiological and genetic attributes, and they have long been regarded as polyphyletic. Untangling the relationships of this assemblage has proven to be one of the most difficult challenges of fungal systematics. The purpose of this study was to use molecular characters to provide an overview of the phylogenetic distribution of resupinate forms among the Homobasidiomycetes.

In the classical system of Fries (1821), resupinate forms were distributed among the Thelephoraceae, Meruliaceae, Hydnaceae and Polyporaceae, according to their hymenophore configurations. Later, with the application of anatomical characters, the diversity of resupinate forms and their relationships to non-resupinate taxa started to become apparent (Karsten, 1881; Patouillard, 1900). The early work in taxonomy of Aphyllophorales was summarised by Donk (1964) in his 'Conspectus of the families of Aphyllophorales'. Donk's work marked a major advance toward a phylogenetic classification of the non-gilled/non-gasteroid Homobasidiomycetes, which he divided into 21 families. In 1971, Donk admitted two more families to the Aphyllophorales.

Resupinate forms occur in 12 families of the Aphyllophorales *sensu* Donk (1971). Approximately 60 genera of resupinate forms were included in the Corticiaceae (Donk, 1964). Others were distributed among the Clavariaceae (e.g. *Clavulicium*), Coniophoraceae (*Coniophora*), Gomphaceae (*Ramaricium*), Hericiaceae (*Gloeocystidiellum*), Hymenochaetaceae (*Hymenochaete*), Lachnocladiaceae (*Scytinostroma*), Polyporaceae (*Poria*), Punctulariaceae (*Punctularia*), Stereaceae (*Xylobolus*), Thelephoraceae (*Tomentella*) and Tulasnellaceae (*Tulasnella*). Donk considered most of these latter families to be more or less natural (the Polyporaceae and Clavariaceae being exceptions), and they have remained largely intact in recent classifications. Donk was clearly unsatisfied with the status of the Corticiaceae, however, which he described as "chaotic", a "big Friesian conglomerate" and an "amorphous mass" (1964, p. 288; 1971, p. 5–6). The major problems in the systematics of resupinate Homobasidiomycetes still concern the relationships of the members of the Corticiaceae *sensu* Donk.

Some authors (Eriksson, 1958; Talbot, 1973; Hjortstam *et al*., 1988*a*) have employed a broad concept of the Corticiaceae that is based on Donk's circumscription of the family, while acknowledging that the group is unnatural. Parmasto (1986) adopted a narrower concept of the Corticiaceae than did Donk, and divided the group into 11 subfamilies. A radical approach to the taxonomy of resupinate forms, and basidiomycetes in general, was proposed by Jülich (1981), who distributed the genera of Corticiaceae *sensu* Donk among approximately 35 families in 16 orders. Jülich's classification was largely adopted by Ginns & Lefebvre (1993) in their compilation of lignicolous corticioid fungi of North America. Other major taxonomic treatments of resupinate Homobasidiomycetes include those of Jülich & Stalpers (1980), Hjortstam (1987), Hjortstam & K.-H. Larsson (1995), Hansen & Knudsen (1997), Hallenberg (1985) and Gilbertson & Ryvarden (1986, 1987, poroid forms).

The first major phylogenetic study of resupinate forms was that of Parmasto (1995), who used 86 morphological characters to study relationships of 156 genera, representing 1225 species of corticioid fungi. The strict consensus tree produced in that study was poorly resolved, indicating that morphology alone is not useful for estimating phylogenetic relationships in resupinate Homobasidiomycetes. A few resupinate forms started to appear in molecular phylogenetic studies in the 1990s, but the sampling was sparse (Gargas *et al*., 1995*a*; Hibbett & Donoghue, 1995; Nakasone, 1996; Hibbett *et al*., 1997; Bruns *et al*., 1998; Pine *et al*., 1999; Hallenberg & Parmasto, 1998). The first molecular study with a significant emphasis on resupinate forms was that of Boidin *et al*. (1998), who analysed nuclear ribosomal DNA (nuc rDNA) internal transcribed spacer (ITS) sequences in 360 species of Aphyllophorales and other basidiomycetes. The results of Boidin *et al*. should be viewed with caution because the ITS region is too divergent to be aligned across distantly related clades, and their analysis included no measures of branch support. Nevertheless, many of the terminal groupings in their trees are consistent with certain anatomical characters and have been supported in other studies (e.g. the Hericiales).

Hibbett & Thorn (2001) presented a "preliminary phylogenetic outline" of the Homobasidiomycetes that summarised

the results of diverse molecular phylogenetic studies. This "outline" divided the Homobasidiomycetes into eight major clades, which were given informal names (polyporoid clade, euagarics clade, etc.). Hibbett & Thorn indicated that resupinate forms occur in all of the major clades, but also noted that these forms had been undersampled in earlier studies. Recently, there have been several large phylogenetic studies focusing on the broad phylogenetic distribution of resupinate forms, including works by Hibbett & Binder (2002), E. Langer (2002), K.-H. Larsson *et al*. (2004) and Lim (2001; also Kim & Jung, 2000). There have also been several other studies with large numbers of resupinate forms that have focused on more restricted clades, including the russuloid clade (E. Larsson & K.-H. Larsson, 2003), hymenochaetoid clade (Wagner & Fischer, 2001, 2002*a*) and thelephoroid clade (Kõljalg *et al*., 2000, 2001, 2002).

The present study represents a continuation of the research reported by Hibbett & Binder (2002), who studied relationships among 481 species of Homobasidiomycetes, including 144 resupinate forms. The ataset of Hibbett & Binder (2002) included overlapping sets of sequences from nuclear and mitochondrial (nuc, mt) large and small subunit (lsu, ssu) rDNA regions, with a total aligned length of 3800 bp. One hundred and seventeen species in the dataset had all four regions, 78 species had three regions and 12 had two regions. All taxa were represented by the nuc-lsu rDNA, and 274 taxa had only this region. One hundred and seventy-four nuc-lsu rDNA sequences in Hibbett & Binder's (2002) study were published by E. Langer (2002) or Moncalvo *et al*. (2000). The intention of Hibbett & Binder's (2002) sampling regime was to allow the taxa with three or four regions to provide a backbone for the higher-level relationships (i.e. the major clades *sensu* Hibbett & Thorn, 2001), while using the taxa with only nuc-lsu rDNA to provide taxonomic breadth.

The eight major clades proposed by Hibbett & Thorn (2001) were recovered in the study of Hibbett & Binder (2002), although bootstrap support for these clades was generally weak (Hibbett, in press). Resupinate forms occurred in each clade, with the major concentrations in the polyporoid, russuloid and hymenochaetoid clades. Several additional small groups were also resolved: (1) a group of five resupinate species including *Vuilleminia comedens* and *Dendrocorticium roseocarneum*, which was labelled the "dendrocorticioid clade"; (2) a group of five species including *Sistotremastrum niveocremeum* (as *Paullicorticium niveocremeum)* and *Subulicystidium longisporum*, which was labelled the "*Paullicorticium* clade"; (3) a group of three pileate species, including *Gloeophyllum sepiarium, Neolentinus lepideus* and *Heliocybe sulcata*, which was labelled the "*Gloeophyllum* clade"; and (4) the resupinate species *Jaapia argillacea*, which was placed as the sister group of the bolete clade plus euagarics clade. Ancestral state reconstruction on several different trees using parsimony and maximum likelihood methods suggested that the common ancestor of the Homobasidiomycetes was resupinate, as suggested by Parmasto (1986, 1995) and others (Oberwinkler, 1985; Ryvarden, 1991). The plesiomorphic form of many of the major clades (polyporoid clade, russuloid clade, etc.) was ambiguous, however.

The studies by K.-H. Larsson *et al*. (2004), E. Langer (2002) and Lim (2001) are also major contributions to the systematics of resupinate Homobasidiomycetes. K.-H. Larsson *et al*. (2004) analysed nuc-lsu rDNA in 178 species, E. Langer (2002) analysed a combined dataset of nuc-lsu rDNA and several morphological characters in 220 species, and Lim (2001) used nuc-ssu rDNA to study relationships of 73 Homobasidiomycetes, including 48 resupinate species. Lim (2001) also performed analyses of ITS sequences in several clades of Homobasidiomycetes that include resupinate forms. The phylogenetic trees presented in these studies have many similarities with those of Hibbett & Binder (2002), but there are also some discrepancies, which are discussed later.

It is often difficult to reconcile the studies of Hibbett & Binder (2002), K.-H. Larsson *et al*. (2004), E. Langer (2002) and Lim (2001) because they employ overlapping but non-identical sampling regimes. Adding to the confusion, each of these studies employs different names for certain clades. For example, the *Paullicorticium* clade *sensu* Hibbett & Binder (2002) is called the trechisporoid clade by K.-H. Larsson *et al*. (2004) or the paullicorticioid and subulicystidioid clades by E. Langer (2002). Similarly, the *Dendrocorticium* clade *sensu* Hibbett & Binder is called the corticioid clade by K.-H. Larsson *et al*. (2004) or the laeticorticioid clade by Lim (2001).

The present study draws together a large body of data from recent phylogenetic analyses of resupinate Homobasidiomycetes and adds 158 new sequences from 76 species. The dataset contains 656 OTUs (operational taxonomic units), with multiple representatives of some species. Following the same general strategy as Hibbett & Binder (2002), some taxa are represented by four rDNA regions but the majority are represented only by nuc-lsu rDNA sequences, including almost all the relevant sequences that were available in GenBank (http://www.ncbi.nlm.nih.gov/Genbank/) as of June 2002. The occurrence of missing sequences in the dataset may be a source of error, and it certainly increases the computational burden. Even without missing data, a 656-OTU dataset would present an analytical challenge. This study employed the Parsimony Ratchet (Nixon, 1999), which has been shown to be an effective alternative to traditional heuristic search strategies for large datasets (e.g. Tehler *et al*., 2003).

Material and methods

Clade names

There is a great deal of inconsistency in the use of clade names in recent phylogenetic studies of Homobasidiomycetes (Kim & Jung, 2000; Hibbett & Thorn, 2001; Lim, 2001; Hibbett & Binder, 2002; E. Langer, 2002; K.-H. Larsson *et al*., 2004). The present study adopts the terms athelioid clade, trechisporoid clade, corticioid clade and phlebioid clade *sensu* K.-H. Larsson *et al*. (2004). Contrary to K.-H. Larsson *et al*. (2004), however, this study uses the term polyporoid clade in the broad sense of Hibbett & Thorn (2001) and Hibbett & Binder (2002). The restricted group that K.-H. Larsson *et al*. (2004) called the polyporoid clade appears to be equivalent to a clade that Hibbett & Donoghue (1995) called "group 1" in a study of

polypore phylogeny. This study refers to the group 1 clade as the "core polyporoid clade". Other clade names follow Hibbett & Thorn (2001).

Taxon sampling, molecular techniques and alignment

The full dataset includes nuc-ssu, nuc-lsu, mt-ssu and mt-lsu rDNA sequences from 656 isolates, including eight species of Auriculariales and ten Dacrymycetales, which were included for rooting purposes. One hundred and forty-two isolates have sequences of all four regions and form the core dataset; 102 isolates have three regions; 18 isolates have two regions; and 394 isolates have one region. All species are represented by nuc-lsu rDNA sequences. Many of the sequences used in this study are derived from earlier studies in our laboratory (Hibbett, 1996; Hibbett *et al*., 1997, 2000; Hibbett & Donoghue, 2001; Binder & Hibbett, 2002; Hibbett & Binder, 2002). The dataset also includes 167 nuc-lsu rDNA sequences from Moncalvo *et al*. (2002), 82 nuc-lsu rDNA sequences from E. Langer (2002), 46 nuc-lsu rDNA sequences from Wagner & Fischer (2001, 2002*a*, *b*) and 19 nuc-lsu rDNA sequences from K.-H. Larsson (2001). Six unpublished sequences of *Tomentella* and *Pseudotomentella* and three unpublished sequences of *Marchandiomyces* were generously provided by Urmas Kõljalg and Paula DePriest, respectively. One hundred and fifty-eight new sequences were generated for this study, including 44 nuc-ssu, 57 nuc-lsu, 29 mt-ssu and 28 mt-lsu rDNA sequences. Collection/isolate numbers and GenBank sequence accession numbers for all materials are available as supplementary data. This has been deposited as hard copy in the Biological Data Collection, General Library, The Natural History Museum, London (Email: genlib@nhm.ac.uk; Website:http://www.nhm.ac.uk/library). An electronic version is available on the *Cambridge Journals Online* website at http://uk.cambridge.org/journals/journal_catalogue.asp? mnemonic=sys.

The goal of the taxon sampling scheme was to include representatives of as many independent clades of resupinate forms as possible. Two hundred and fifty-nine resupinate species in 111 genera were included, which includes 87 genera that are recognised in Hjortstam's (1987) checklist of 218 corticioid genera. The potential for misidentifications is especially worrisome in this study because resupinate taxa are often difficult to identify. To provide a check for identification errors, 12 of the resupinate species in the dataset are represented by multiple isolates. Nineteen isolates are only identified to the generic level.

The dataset emphasises resupinate forms, so pileate and gasteroid forms are somewhat under-represented. For example, the euagarics clade contains approximately 63% of the described species in Homobasidiomycetes (Kirk *et al*., 2001) but is represented by only 35% of the species in the dataset. In contrast, the hymenochaetoid clade, russuloid clade, cantharelloid clade and the polyporoid clade are over-represented, owing to the concentrations of resupinate forms in these groups.

DNA was extracted from cultured mycelium or dried herbarium specimens using a SDS-NaCl extraction buffer, with phenol-chloroform extractions and ethanol precipitations (Lee & Taylor, 1990). PCR reactions were performed for two nuclear and two mitochondrial rDNA regions using the primer combinations LR0R-LR5 (nuc-lsu), PNS1-NS41 and NS19b-NS8 (nuc-ssu), ML5-ML6 (mt-lsu) and MS1-MS2 (mt-ssu). The PCR products were cleaned with the GeneClean Kit I (Bio101, La Jolla, California). Sequencing reactions using the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, Foster City, CA) were performed with primers LR0R, LR22, LR3, LR3R, LR5 (nuc-lsu), PNS1, NS19bc, NS19b, NS41, NS51, NS6, NS8 (nuc-ssu), ML5, ML6 (mt-lsu) and MS1, MS2 (mt-ssu) (Vilgalys & Hester, 1990; White *et al*., 1990; Hibbett, 1996; Moncalvo *et al*., 2000), and were run on an ABI 377 automated DNA sequencer (Applied Biosystems). Sequences were assembled using Sequencher 4.1 GeneCodes, Ann Arbor, MI) and were manually aligned in the editor of PAUP*4.0b510 (Swofford, 2003).

Phylogenetic analyses

Four sets of phylogenetic analyses were performed: (1) analyses of the core dataset including 142 OTUs (species) with all four rDNA regions; (2) a two-step heuristic parsimony analysis of the full dataset with all 656 OTUs and all sequences; (3) a Parsimony Ratchet (PR) analysis of the full dataset; and (4) a PR analysis of the full dataset using six-parameter weighted parsimony. Analyses 1–3 used equally weighted parsimony. All analyses were performed on Macintosh G4 computers with 477 or 500 MHz processors and 512 or 576 MB of RAM, running OS9.

Analyses of the core dataset

The goals of these analyses were to determine whether there is significant conflict between the nuclear and mitochondrial data partitions and to resolve the major groups and backbone phylogeny of the Homobasidiomycetes. Independent bootstrapped parsimony analyses were performed of the mt-rDNA (ssu + lsu) and nuc-rDNA (ssu + lsu) partitions (100 replicates, 1 random taxon addition sequence per replicate, MAXTREES = 10000, TBR branch swapping, keeping 1000 trees per replicate). Bootstrap consensus trees were created and taxa with positively conflicting positions in the two data partitions, each supported by bootstrap values >90%, were deemed to exhibit significant conflict. Subsequently, the nuc-rDNA and mt-rDNA partitions were combined and a heuristic search was performed with 1000 random addition sequences, MAXTREES = 10000, TBR branch swapping, saving 100 trees per replicate. A bootstrap analysis of the combined dataset was also performed (1000 replicates, 1 random taxon addition sequence per replicate, MAXTREES = 10000, TBR branch swapping, keeping all trees per replicate).

Two-step heuristic analyses of the full dataset

A two-step search protocol was employed. In the first step, a heuristic search was performed with 10 random taxon addition sequences (MAXTREES = 10000, TBR branch swapping,

keeping 10 trees per replicate) were performed. In the second step, TBR branch swapping was performed on the shortest trees found in the first step, keeping all trees up to the limit of MAXTREES. A bootstrap analysis was also performed, using 100 replicates (MAXTREES = 1000, 1 random taxon addition sequence per replicate, keeping 10 trees per replicate).

Equally weighted Parsimony Ratchet (PR) analyses of the full dataset

Traditional heuristic searches are hill-climbing procedures and are susceptible to being trapped in local optima. To improve the chance of finding the global optimum, heuristic searches typically use many replicate searches, each beginning with a unique starting tree. This approach can be effective, but it is time consuming, especially if each search attempts to recover all equally most parsimonious trees. PR analysis (Nixon, 1999) is a strategy for finding the most parsimonious tree(s) from large datasets that is designed to address some of the limitations of traditional heuristic searches. PR analysis is incorporated in NONA (Goloboff, 1998) and can also be implemented in PAUP* using the companion program PAUPRat (Sikes & Lewis, 2001). The analytical settings of the PR in PAUPRat and NONA differ slightly. This study used PAUPRat and PAUP* to perform PR analyses.

A PR analysis begins like a traditional heuristic search, with a single starting tree that is rearranged by branch swapping. Initially, all characters are subject to a uniform weighting regime. Periodically, a randomly selected subset of characters are reweighted (from two-fold to five-fold in PAUPRat), and branch swapping proceeds under this perturbed weighting regime (starting with the best tree obtained with the original weights). Following a period of branch swapping under the perturbed weights, the characters are returned to the original weights, which completes one iteration. The next iteration proceeds using the best tree found under the perturbed weights, which may be shorter, longer or equal in length to the best tree obtained before the data were reweighted.

The branch swapping routines that are performed under the original and perturbed character weights in each iteration are each susceptible to being trapped in local optima (tree 'islands'), just like standard heuristic analyses. The critical feature of PR analysis is that by periodically perturbing the character weights, the parsimony surface of treespace is distorted, which may make it possible (one hopes) to move away from a topology that was a local optimum under the original weighting regime. In this way, a PR search wanders through treespace, occasionally crossing 'valleys' that a traditional heuristic search cannot overcome. PR analyses are faster than traditional heuristic searches because they do not require that multiple starting trees be obtained by taxon addition (or another method) and subsequently refined through branch swapping. In addition, PR analysis does not attempt to find and swap through all the trees in any given island.

PR analyses of the full dataset were performed in batch mode using PAUP* and PAUPRat. Three sets of PR analyses were performed: (1) 20 runs with 200 iterations each (20×200) and 15% of the characters randomly reweighted in each iteration; (2) 20×200 iterations with 5% perturbation; and (3) 20×200 iterations with 25% perturbation.

Six-parameter weighted PR analyses of the full dataset

A set of PR analyses was performed under a six-parameter weighting regime (Stanger-Hall & Cunningham, 1998), which obtains weights for parsimony analyses based on rates of nucleotide substitutions estimated with maximum likelihood. Nucleotide transformation rates were estimated in PAUP* under a general time-reversible model, with equal rates of evolution for all sites and empirical base frequencies, using a tree and data matrix from Binder & Hibbett (2002) that includes 93 species, each with nuc-ssu, nuc-lsu, mt-ssu and mt-lsu rDNA. Rate matrices were converted to step-matrices for parsimony analysis using an Excel spreadsheet provided by Clifford Cunningham (http://www.biology.duke.edu/cunningham/), which takes the natural logarithm of the rates and converts them to proportions. Rates and weights for nuc-rDNA and mt-rDNA were estimated separately. For nuc-rDNA, the step-matrix values were A-C = 3, A-G = 2, A-T = 2, C-G = 2, C-T = 1, G-T = 3; for mt-rDNA, the step-matrix values were A-C = 2, A-G = 1, A-T = 2, C-G = 3, C-T = 1, G-T = 2. Six-parameter weighted PR analyses were performed with PAUP* and PAUPRat, with ten batches of 200 iterations each, with 15% of the characters reweighted in each iteration.

Results

Sequences and alignment

The nuc-ssu sequence of *Piriformospora indica* contained a 345 bp group I intron at position 1509 (Gargas *et al*., 1995*b*) that was removed prior to alignment. Nuc-ssu rDNA sequences of *Lentinellus* spp., *Artomyces (Clavicorona) pyxidata* and *Panellus stypticus* have also been shown to contain group I introns, but at a different position (Hibbett, 1996); sequences of these taxa in this dataset have had the intron sequences removed. Excluding the *P. indica* sequence, the nuc-ssu rDNA sequences ranged from 1059 bp (an incomplete sequence) in *Coniophora puteana* to 1790 bp in *Physalacria inflata*. The nuc-lsu rDNA sequences ranged from 870 bp in *Albatrellus ovinus* to 972 bp in *Scytinostroma renisporum*. The nuc-lsu rDNA of *Antrodia xantha* had a 65 bp insertion at position 830, which was also removed prior to alignment. No other major insertions or deletions were observed in the nuc-rDNA. The mt-ssu rDNA sequences ranged from 418 bp in *Cylindrobasidium laeve* to 613 bp in *Hydnochaete olivacea*. The mt-ssu rDNA sequences were divided into three blocks (blocks 3, 5, 7) to exclude hypervariable regions (Bruns & Szaro, 1992; Hibbett & Donoghue, 1995). The mt-lsu rDNA sequences ranged from 376 bp in *Dacryobolus sudans* to 680 bp in *Repetobasidium mirificium*. The 5′ end of the mt-lsu fragment is highly variable and was trimmed prior to alignment. The total aligned length of all four regions is 3807 bp, distributed as follows: nuc-ssu = 1859 bp, nuc-lsu = 1103 bp, mt-ssu = 485 bp (block 3 = 137 bp, block 5 = 262 bp, block 7 = 86 bp), and mt-lsu = 360 bp. One hundred and three positions were considered

Perturbation level	**5%**	**25%**	**15%**	**15%**
Weighting regime*	EP	EP	EP	WP
Runs × iterations	20 × 200	20 × 200	20 × 200	10 × 200
Best tree overall	29821	29820	29819	50092
No. times found	8	1	25	2
In n runs (run nos.)	1 (3[a])	1 (17[a])	3 (2[a], 3, 13)	2 (1, 6[a])
Runtime in h	270	396	322	2259
Trees < 29838 found in	17 h, 6 min	29 min	1 h, 8 min	n/a
Best tree found in	38 h, 21 min	325 h, 45 min	28 h, 11 min	197 h, 39 min
CI	0.149	0.149	0.149	0.146
RI	0.610	0.611	0.611	0.621

*EP = equally weighted parsimony, WP = six-parameter weighted parsimony; [a]Illustrated in Fig. 2.

Table 1 Performance of Parsimony Ratchet analyses of the full dataset with different levels of perturbation

ambiguously aligned and were excluded from analyses (nuc-lsu: 83 positions; mt-lsu: 20 positions). The same alignment was used for the analyses of the core dataset (142 OTUs) and full dataset (656 OTUs).

Analyses of the core dataset

With only the 142 core species included, the nuc-rDNA partition had 534 variable positions and 831 parsimony-informative positions, and the mt-rDNA partition had 120 variable positions and 501 parsimony-informative positions. There were no positively conflicting clades in the independent bootstrap analyses of the nuclear and mitochondrial regions that were supported with bootstrap values greater than 90% in both partitions, so the data were combined without pruning taxa or sequences. The most strongly supported conflict involved *Stephanospora caroticolor*, which was supported as a member of the euagarics clade (nuc-rDNA, bootstrap = 72%) or athelioid clade (mt-rDNA, bootstrap = 87%).

Parsimony analysis of the combined core dataset resulted in 97 equally most parsimonious trees (MPTs; 14 204 steps, CI = 0.234, RI = 0.498). The eight major clades of Homobasidiomycetes proposed by Hibbett & Thorn (2001), and the athelioid clade and the corticioid clade of K.-H. Larsson *et al.* (2004) were recovered as monophyletic groups in all MPTs, but the 'backbone' phylogeny was weakly supported (Fig. 1). The bolete clade, the russuloid clade, the cantharelloid clade, the gomphoid-phalloid clade and the thelephoroid clade received the highest bootstrap values (85–99%). The corticioid clade was moderately supported by 72%, while the hymenochaetoid clade (65%), the euagarics clade (59%), the athelioid clade (54%) and the polyporoid clade (54%) were weakly supported. The phlebioid clade and core polyporoid clade were supported at 91% and 95%, respectively. The placement of *Gloeophyllum sepiarium* (the only representative of the *Gloeophyllum* clade in this analysis) was unresolved. *Jaapia argillacea* was placed as the sister group to the bolete clade plus the athelioid clade and the euagarics clade (bootstrap = 62%). There were no representatives of the trechisporoid clade in the core dataset.

Two-step heuristic analyses of the full dataset

With all 656 OTUs included, the dataset had 2399 variable positions and 1732 parsimony-informative positions. The first step of the analysis produced 10 trees (29 864 steps, CI = 0.149, RI = 0.610), which were used as input trees for TBR branch-swapping in the second step. Ten thousand shorter trees (29 838 steps, CI = 0.148, RI = 0.611) were found in the second step of the analysis, which was aborted after 307 hours. Several of the major clades that were resolved in the core dataset analysis collapsed in the strict consensus of all trees, including the euagarics clade, the hymenochaetoid clade, the cantharelloid clade and the polyporoid clade. Bootstrap support > 50% was received for the bolete clade (93%), the gomphoid-phalloid clade (69%), the corticioid clade (81%), the *Gloeophyllum* clade (54%), the thelephoroid clade (97%) and the trechisporoid clade (69%). The trechisporoid clade was nested within the polyporoid clade in 86% of the trees. In the other 14% of the trees, however, it was placed as the sister group of the hymenochaetoid clade. The position of *Jaapia argillacea* was again resolved as the sister group to the bolete clade, the athelioid clade and the euagarics clade.

Equally weighted PR analyses of the full dataset

A series of PR analyses was performed with 5%, 15% and 25% of the characters perturbed (reweighted) (Table 1). PR analyses were characterised in terms of the minimum length of the trees; the number of minimum length trees; the number of individual runs that recovered minimum length trees; overall runtime; and the time required to find trees equal in length to the trees from the two-step heuristic search. In all PR analyses, the best tree(s) were found at relatively low frequency. The analysis with 15% of the characters perturbed had the best results, finding 25 shortest trees (29 819 steps, CI = 0.149, RI = 0.611; i.e. 19 steps shorter than the shortest trees found with the two-step heuristic search) that were recovered in three different runs (Fig. 2, Tables 1–2). In contrast, the analysis with 5% of the characters perturbed found eight trees of 29 821 steps in one run, and the analysis with 25% of the characters perturbed found one tree of 29 820 steps in one run. An increase in the

T2

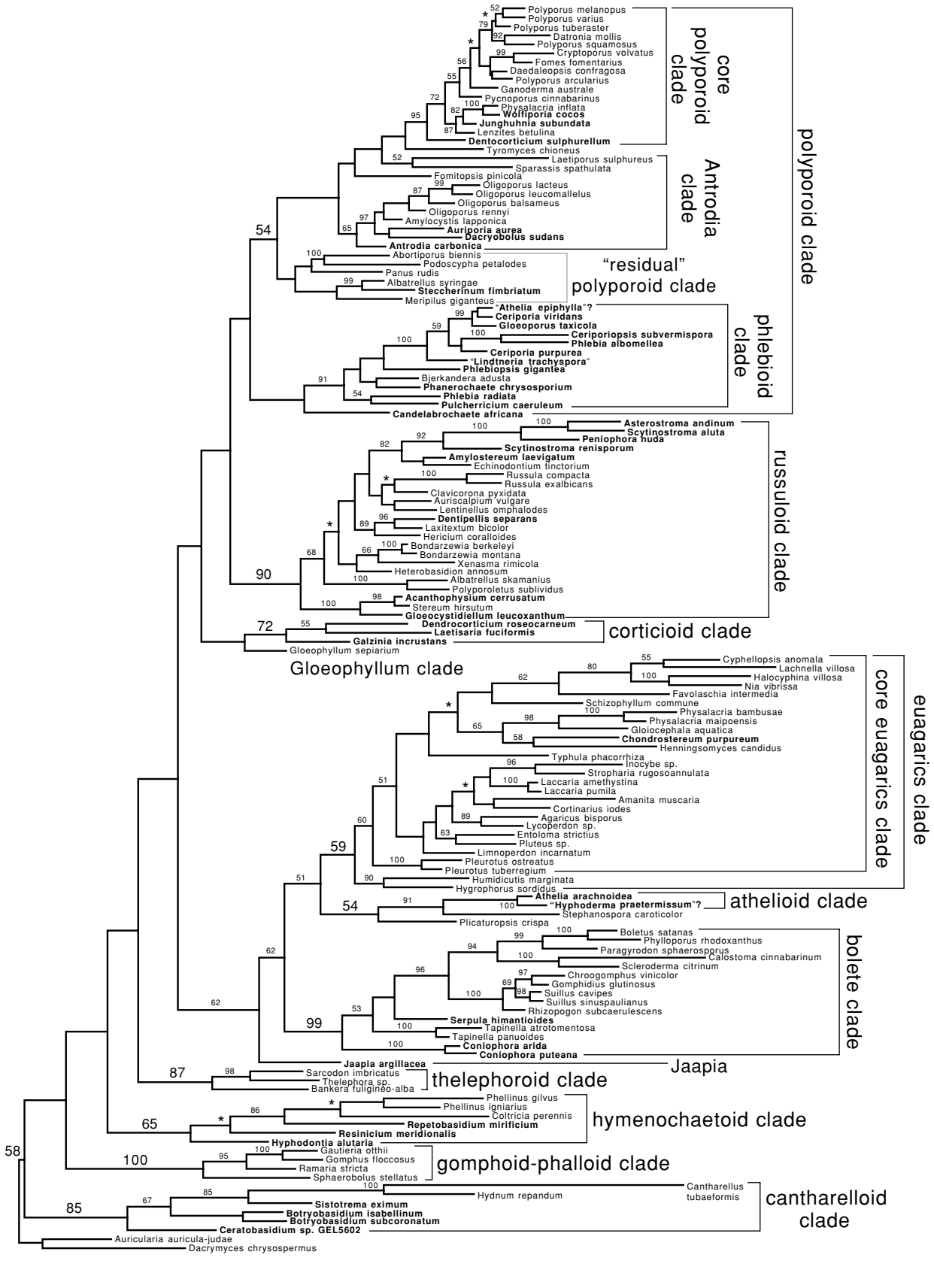

Figure 1 Phylogenetic relationships of Homobasidiomycetes based on parsimony analysis of the combined core data set with 142 species. One of 97 equally parsimonious trees. Bootstrap values greater than 50% are indicated above branches. Nodes marked with asterisks collapse in the strict consensus tree. Names of resupinate taxa are written in bold type. Species names in quotation marks followed by question marks indicate mislabelled isolates.

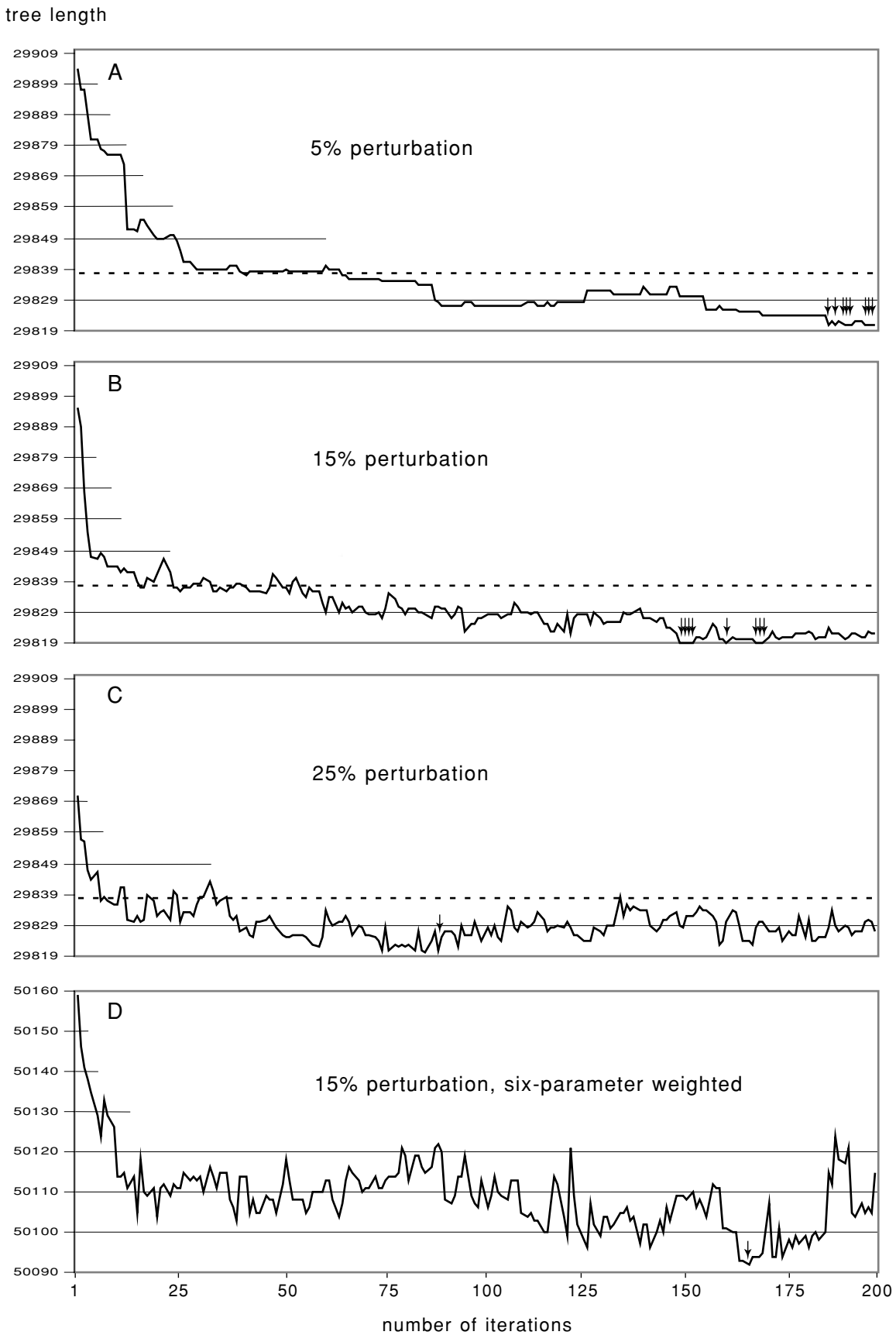

Figure 2 Performance graphs of equally weighted PR analyses with 5%, 15% and 25% perturbation levels (A–C), and one six-parameter weighted PR analysis with 15% perturbation (D). Each graph represents one run, with 200 iterations. Runs shown are those that found minimum length trees (for that perturbation level). Arrows indicate the number and the position of the shortest tree(s) found. The dotted line in A–C represents the length of the shortest trees (29 838 steps) obtained with the unperturbed two-step search approach.

Run no.	Topology	Iteration no.
2[a]	A	150
	B	151, 153
	C	152
	D	169, 170, 171
	E	162
3	B	170, 178, 186
	D	169, 172, 173, 174, 177
13	B	125, 126, 127
	D	69, 71, 73, 119, 120, 121

[a]Illustrated in Fig. 3.

Table 2 Distribution and topology classes of shortest trees recovered with the equally weighted PR analysis at 15% perturbation level

number of perturbed characters was correlated with increased runtimes, which were 270, 322 and 396 hours, with 5%, 15% and 25% of the characters perturbed, respectively.

The progress of the PR was strongly affected by the choice of perturbation levels (Fig. 2A-C). For example, the analysis with 5% of the characters perturbed (Table 1, Fig. 2A) advanced slowly, with long 'plateaus', up to 20–40 iterations in duration, in which no progress was made in tree lengths. While the 5% perturbation level yielded the most gradual progress, the 25% perturbation level yielded the most chaotic search profiles, with dramatic shifts in tree length between iterations (Fig. 2). The analysis with 25% perturbation found trees equal in length to the trees from the two-step heuristic search faster than the analyses with 5% and 15% perturbation levels (29 minutes, vs. 17 hours, 6 min. and 1 hour, 8 min., respectively), but never found trees as short as those recovered by the analysis with 15% perturbation level. The three runs with 15% perturbation that recovered the shortest trees found those trees between iterations 150–171 (run no. 2; eight trees), 169–186 (run no. 3; eight trees), and 69–127 (run no. 13; nine trees; Table 2).

In all of the shortest trees, the major clades of Homobasidiomycetes *sensu* Hibbett & Thorn (2001) and the athelioid, trechisporoid, corticioid and *Gloeophyllum* clades were resolved as monophyletic (Figs 3–4). Several other major topological features were shared by all trees (Figs 3–4): (1) the euagarics, bolete and athelioid clades formed a monophyletic group in all trees, with *Jaapia argillacea* as its sister group; (2) the trechisporoid clade (K.-H. Larsson *et al*., 2004) was nested within the polyporoid clade; (3) the cantharelloid, gomphoid-phalloid, and hymenochaetoid clades occupied a basal position; and (4) the *Gloeophyllum* and corticioid clades were sister groups (except in tree G, Fig. 3). None of these groupings received strong bootstrap support, however.

The minimum-length trees can be divided into five classes of topologies (A-E; Fig. 3), based on the variable aspects of the relationships among major clades. Topologies A, C and E were each found only once (i.e. one tree with each of these topologies was found), but trees with topology B were found eight times and trees with topology D were found 14 times (Table 2). Trees with topologies B and D were found in all three batches that recovered minimum-length trees (Table 2).

Six-parameter weighted PR analyses of the full dataset

Two shortest trees (50 092 steps, CI = 0.146, RI = 0.621) were found in two different runs (Table 1). Under equally weighted parsimony, these trees were 29 925 and 29 929 steps long (i.e. 106–110 steps longer than the shortest trees obtained in the equally weighted PR analyses). For comparison, the 25 shortest trees obtained in the equally-weighted PR analyses were 50 257–50 306 steps long under the six-parameter weighting regime (i.e. 165–214 steps longer than the shortest trees obtained in the six-parameter PR analysis).

The six-parameter PR analysis was very time consuming. Ten runs with 200 iterations each required 2259 hours of computer time. There are several differences in higher-level relationships implied by the two optimal trees. The most striking difference is that in one topology the trechisporoid clade is nested in the polyporoid clade (as in all shortest trees recovered with equally weighted PR analysis), whereas in the other topology the trechisporoid clade is placed as the sister group of the hymenochaetoid clade (Figs 3–4).

Discussion

Overall phylogenetic resolution

Bootstrap support for the major clades of Homobasidiomycetes was generally weak in the analysis of the full dataset. Missing sequences, or the presence of certain taxa whose positions are particularly labile (due to homoplasy), may have contributed to the low bootstrap values. One possible example of a 'destabilising' taxon is *Stephanospora caroticolor*, which was represented by all four rDNA regions, and was placed in either the euagarics clade or athelioid clade depending on whether the mt-rDNA or nuc-rDNA was analysed. As the number of taxa sampled increases, the chance of including species with aberrant sequences also increases. Therefore, it is not surprising that there is weak bootstrap support for many major clades in recent densely sampled phylogenetic studies of Homobasidiomycetes (e.g. Moncalvo *et al*., 2000; Hibbett & Binder, 2002; E. Langer, 2002; Moncalvo *et al*., 2002).

PR analysis was much more effective at finding minimum-length trees than the two-step heuristic search strategy. However, the success of the PR was sensitive to the choice of perturbation levels, and even with the optimal 15% perturbation level only 3 out of 20 runs found minimum-length trees, and no more than nine shortest trees were found in any single run. In contrast, Nixon (1999, p. 413) reported that "approximately three out of four" PR analyses of the 500-species *rbc*L dataset of Chase *et al*. (1993) recovered minimum-length trees. Apparently, the full dataset analysed in this study presents a more difficult parsimony landscape than the Chase *et al*. dataset. The results of this study highlight the importance of doing multiple PR runs with appropriate perturbation levels and an adequate number of iterations per run.

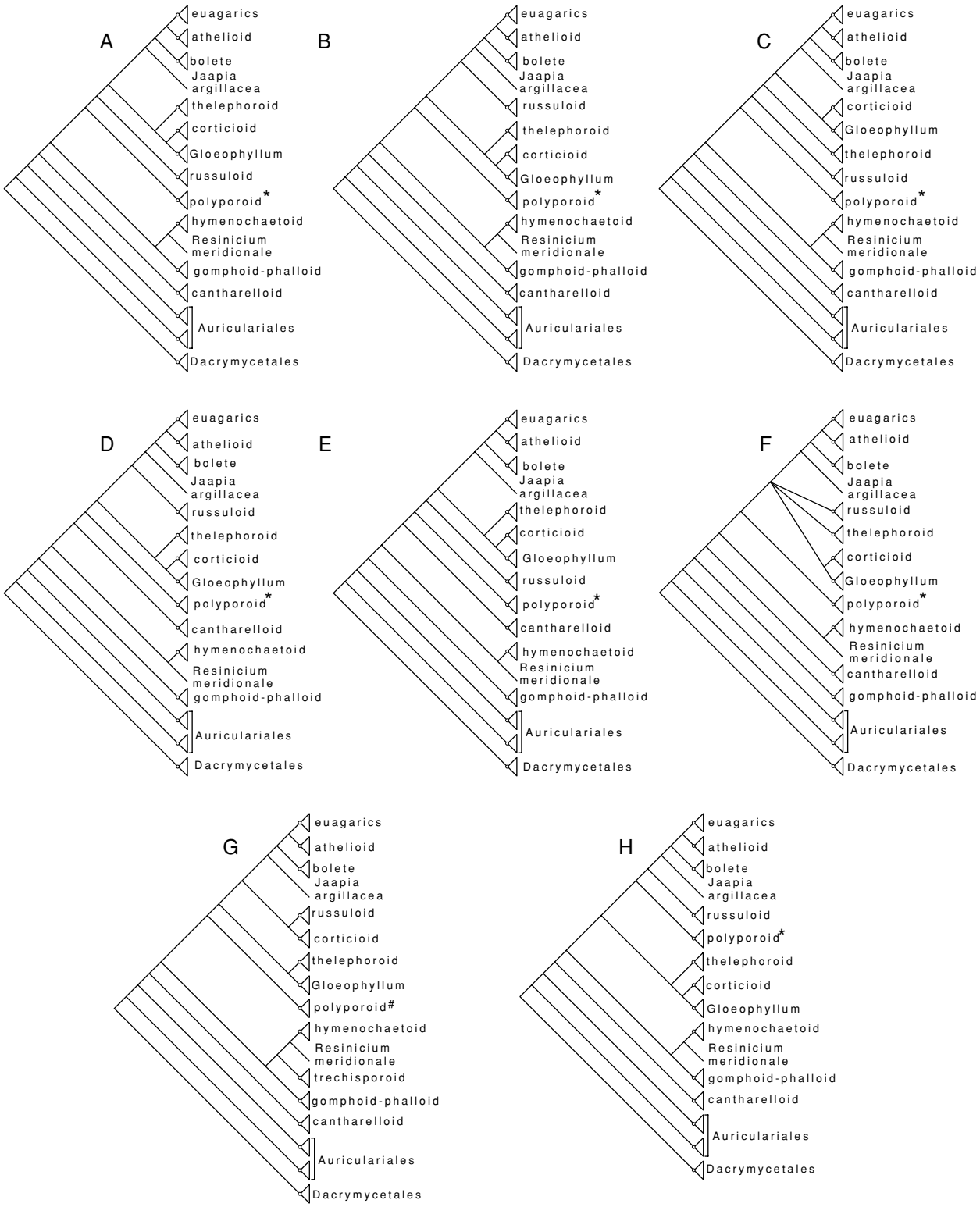

Figure 3 Simplified topologies of the shortest trees recovered using PR analysis with 15% perturbation. A–E = equally weighted analyses running 20 × 200 iterations. A = single tree obtained in one run. B = 8 trees obtained in three runs. C = single tree obtained in one run. D = 14 trees obtained in three runs. E = single tree obtained in one run. F = strict consensus of 25 trees A–E. G–H = six-parameter weighted analyses running 10 × 200 iterations. Alternative topologies G = tree one and H = tree two obtained in two different runs (see Fig. 4. for details). Polyporoid* = the polyporoid clade including the 'core' polyporoid clade, the trechisporoid clade, and the phlebioid clade. Polyporoid# = the polyporoid clade without the trechisporoid clade.

Six-parameter weighting increased the runtime of PR analysis approximately seven-fold relative to the equally weighted PR analysis with 15% perturbation. The increased runtime may be worthwhile, because character-state weighting based on realistic models of molecular evolution can improve the accuracy of parsimony analysis (Huelsenbeck, 1995; Cunningham, 1997). The six-parameter trees share many features of the equally weighted trees, but there are also some differences, perhaps the most notable of which is that in one of the six-parameter trees (topology G, Fig. 3) the trechisporoid clade is the sister group of the hymenochaetoid clade. The position of the trechisporoid clade was also quite labile in the analyses of Hibbett & Binder (2002), where it was placed in or near the polyporoid clade, hymenochaetoid clade, russuloid clade or Auriculariales.

The differences among the trees produced here and those obtained in earlier studies (Binder & Hibbett, 2002; Hibbett & Binder, 2002) indicate that there is considerable uncertainty about the higher-level phylogenetic relationships of Homobasidiomycetes (Fig. 3). Nevertheless, the trees recovered in PR analyses all support the monophyly of the eight major clades of Homobasidiomycetes *sensu* Hibbett & Thorn, as well as the corticioid clade, athelioid clade, *Gloeophyllum* clade and trechisporoid clade (which was nested within the polyporoid clade in most trees) (Hibbett & Thorn, 2001; K.-H. Larsson *et al*., 2004). In this regard, the results of the PR analyses of the full dataset are consistent with the results of the core dataset analysis. Other aspects of the higher-level topology shared by the core and full dataset analyses include the monophyly of the clade that contains the bolete, euagarics, and athelioid clades, and its sister group relationship with *Jaapia argillacea*, and the basal position of the cantharelloid, gomphoid-phalloid, and hymenochaetoid clades (see below). Thus, it appears that the species with multiple regions in the full dataset were able to provide a 'backbone' for the phylogeny, even though 60% of the OTUs were represented only by the nuc-lsu rDNA.

Relationships of Homobasidiomycetes to heterobasidiomycetes

This study sampled representatives of four of the five orders of 'heterobasidiomycetes' *sensu* Wells (1994; Wells & Bandoni, 2001), including the Auriculariales, Ceratobasidiales, Dacrymycetales and Tulasnellales but did not sample the Tremellales.

Auriculariales s. str.

PR analyses suggest that the Auriculariales *s. str*. (by which we mean Auriculariales excluding Sebacinaceae; see below) is a paraphyletic assemblage of lineages from which the Homobasidiomycetes have been derived (Figs 3–4). Several other studies have also concluded that the Auriculariales is closely related to the Homobasidiomycetes, whereas the Dacrymycetales and Tremellales have a more basal position in the Hymenomycetes (Swann & Taylor, 1993, 1995; Gargas *et al*., 1995*a*; Begerow *et al*., 1997; E. Langer, 2002; K.-H. Larsson *et al*., 2004). Analyses by E. Langer (2002) and Weiß & Oberwinkler (2001) suggest that the Auriculariales *s. str*. is monophyletic, but with weak bootstrap support, while Hibbett & Binder (2002) recovered trees that showed the group to be monophyletic or paraphyletic (as in the present study). Thus, it remains ambiguous whether the Auriculariales *s. str*. is monophyletic or paraphyletic. Six of the eight isolates of Auriculariales *s. str*. included in this study are resupinate (Fig. 4). The pileate forms include *Pseudohydnum gelatinosum*, which has a hydnoid hymenophore, and *Auricularia auricula-judae*, which has a smooth hymenophore. These two species are apparently not closely related (as was also shown by Weiß & Oberwinkler, 2001), which suggests that there have been multiple origins of pileate fruiting bodies within the Auriculariales *s. str*. (Fig. 4).

Dacrymycetales

The Dacrymycetales is strongly supported as monophyletic (bootstrap = 100%, Fig. 4). Nine of the Dacrymycetales in this study have erect fruiting bodies that are variously coralloid, spathulate, pendulous, or lobate, but one species, *Cerinomyces grandinioides*, has a resupinate fruiting body. The tree in Fig. 4 suggests that the resupinate fruiting body of *C. grandinioides* is the product of reduction, but bootstrap support for the internal topology of the Dacrymycetales is weak.

Tulasnellales, Ceratobasidiales and Sebacinaceae

The placements of Auriculariales *s. str*. and Dacrymycetales in this study are consistent with the traditional division between heterobasidiomycetes *sensu* Wells and Homobasidiomycetes (e.g. Stalpers, in Kirk *et al*., 2001). However, PR analyses place the Tulasnellales, Ceratobasidiales and Sebacinaceae (Auriculariales *s. lat*.) in the cantharelloid clade (Fig. 4). These taxa include forms with highly reduced resupinate to incrusting or coralloid fruiting bodies. Parenthesomes are imperforate in Tulasnellales (Moore, 1978; G. Langer, 1994; Wells, 1994) and Sebacinaceae (Khan & Kimbrough, 1980), and perforate with large pores in Ceratobasidiales (Müller *et al*., 1998; Wells & Bandoni, 2001). Basidial morphology is quite varied. The basidia of Ceratobasidiales are deeply divided by fingerlike sterigmata, but are not septate, whereas those of Tulasnellales have inflated epibasidia that develop adventitious septa, and those of Sebacinaceae are longitudinally septate. Spore repetition has been demonstrated in all three groups (Wells & Bandoni, 2001). Based on these characters, the Tulasnellales, Ceratobasidiales and Sebacinaceae have been classified as heterobasidiomycetes (Wells & Bandoni, 2001).

The relationships among heterobasidiomycetes and Homobasidiomycetes suggested by the present study conflict with the findings of a recent study by Weiß & Oberwinkler (2001), which suggested that: (1) the Auriculariales *s. lat*. is composed of three independent clades, including Auriculariales *s. str*. (43 species), Sebacinaceae (nine species), and a minor clade including *Ceratosebacina calospora* and *Exidiopsis gloeophora*; (2) the Sebacinaceae is the sister group of all other Hymenomycetes; (3) the Ceratobasidiales (represented by *Ceratobasidium pseudocornigerum*) and Dacrymycetales are sister taxa; and (4) the Ceratobasidiales-Dacrymycetales clade is the sister group of the Homobasidiomycetes. These results were based on a 600 bp region of nuc-lsu rDNA that was analysed with neighbour-joining. Taylor *et al*. (2003) obtained similar results, again based on analyses of up to 600 bp of nuc-lsu rDNA.

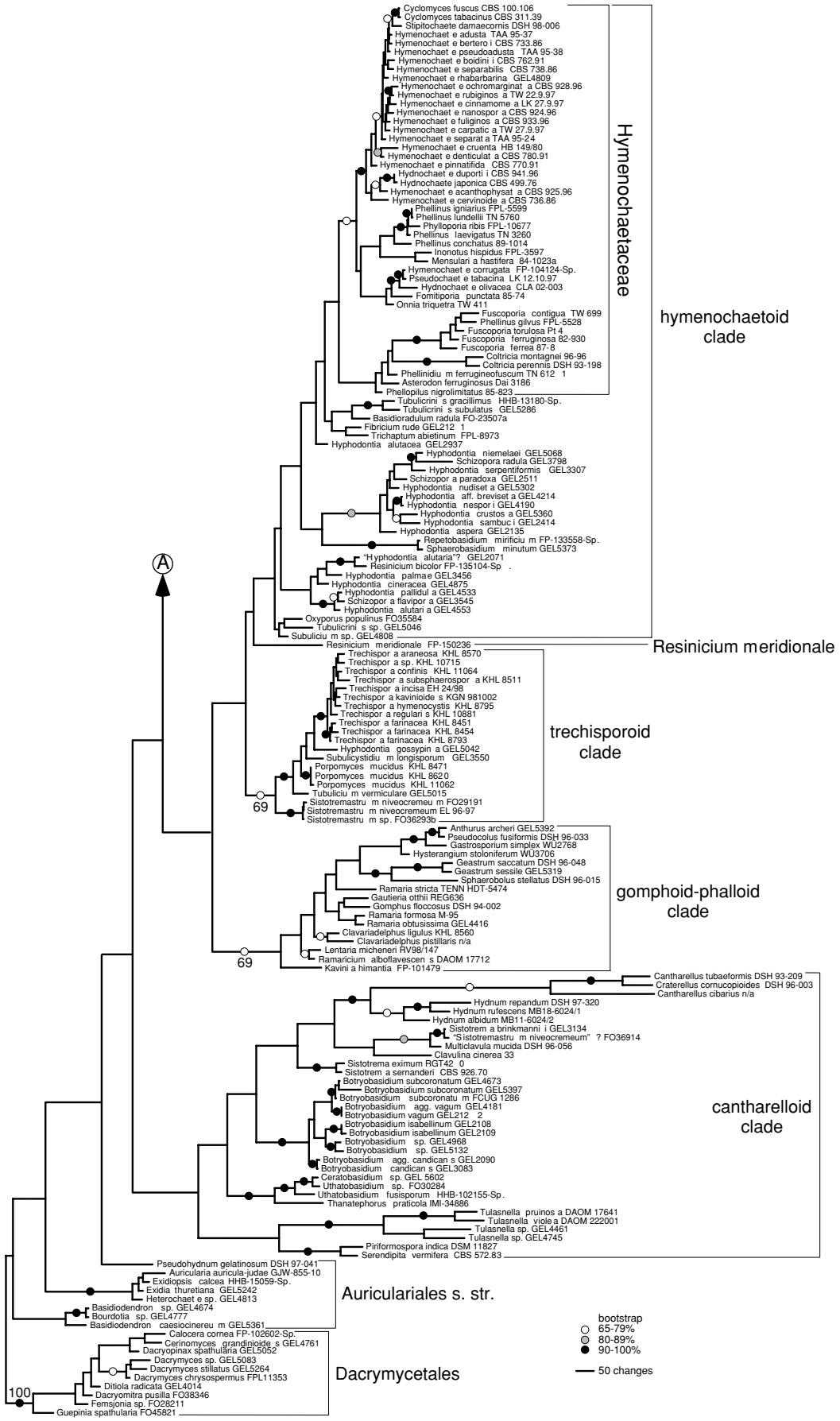

Figure 4 For Legend see facing page.

To compare results of the present study with those of Weiß & Oberwinkler (2001), the sequences of Sebacinaceae, *Ceratobasidium pseudocornigerum*, *Ceratosebacina calospora* and other taxa were downloaded, combined with a subset of sequences from the present study, and subjected to bootstrapped parsimony analyses (Hibbett, unpublished). The sequences of Sebacinaceae from the study of Weiß & Oberwinkler (2001) and *Serendipita vermifera* from the present study were moderately strongly supported as a clade (bootstrap = 89%), confirming that *S. vermifera* is an appropriate 'placeholder' for the Sebacinaceae, but *Ceratobasidium pseudocornigerum* and *Ceratosebacina calospora* could not be placed in any clade with confidence (bootstrap < 50 %, Hibbett, unpublished). These results suggest that the Ceratobasidiales as presently delimited could be polyphyletic. In addition, analyses of mt-lsu rDNA by Bruns *et al*. (1998) suggested that *Waitea circinata*, which is placed in the Ceratobasidiales (Tu *et al*., 1977; Roberts, 1999), is closely related to the resupinate homobasidiomycete *Piloderma croceum*, which is probably a member of the athelioid clade (see below). Conflicting results were obtained by DePriest and colleagues (unpublished), who performed analyses of ITS and partial nuc-lsu rDNA sequences that suggested that *Waitea circinata* is in the corticioid clade (see below). The placement of *Waitea* will remain unresolved until additional loci and isolates are examined. Nevertheless, neither of the analyses cited above suggest that it is closely related to the cantharelloid clade.

The isolates of *Ceratobasidium, Thanatephorus* and *Uthatobasidium* included in the present study are strongly supported as monophyletic and are placed in the cantharelloid clade in the PR analyses. Bootstrap support for the cantharelloid clade is weak in the full dataset analyses, but in the core dataset analysis, *Ceratobasidium* sp. is nested in the cantharelloid clade, with moderately strong bootstrap support (85%, Figs 1, 4). Taking the results of previous studies into account, the Ceratobasidiales as a whole may be polyphyletic, but *Ceratobasidium, Thanatephorus* and *Uthatobasidium* appear to form a monophyletic group within the cantharelloid clade.

Serendipita vermifera is strongly supported as the sister group of the root symbiont *Piriformospora indica* (Verma *et al*., 1998) and the *Serendipita–Piriformospora* clade is placed as the sister group of the Tulasnellales, in the cantharelloid clade (Fig. 4). Monophyly of the *Serendipita–Piriformospora*–Tulasnellales clade is weakly supported (Fig. 4). Nevertheless, these results are consistent with the results of mt-lsu rDNA analysis by Bruns *et al*. (1998), which resolved a clade that includes *Tulasnella irregularis* and "*Sebacina* sp." and placed it as the sister group of *Cantharellus* with strong (98%) bootstrap support (also see Kristiansen *et al*., 2001). Weiß & Oberwinkler (2001) did not include Tulasnellales in their analyses of nuc-lsu rDNA sequences, but they cited unpublished analyses of nuc-ssu rDNA sequences, which apparently placed the Tulasnellales near the Auriculariales. In contrast, E. Langer (1998) found strong support (bootstrap = 95%) for a clade including *Tulasnella eichleriana* and two species of *Botryobasidium*, which is a member of the cantharelloid clade (see below), based on mt-ssu rDNA sequences. In addition, Kottke *et al*. (2003) and Bidartondo *et al*. (2003) found moderately strong (bootstrap = 88–89%) support for a clade including three species of *Tulasnella*, several liverwort symbionts, and *Multiclavula mucida*, which is also a member of the cantharelloid clade, based on nuc-lsu rDNA sequences. Comparable results were obtained by Hibbett & Binder (2002) and Hibbett & Donoghue (2001). Tulasnellales have highly divergent nuclear rDNA sequences (Weiß & Oberwinkler, 2001; Hibbett, unpublished), so it is possible that the results described by Weiß and Oberwinkler are due to 'long branch attraction'.

Basal Homobasidiomycetes

The cantharelloid clade, gomphoid-phalloid clade and hymenochaetoid clade appear to be among the earliest-diverging groups in the Homobasidiomycetes (Figs 1, 3, 4). In addition, the trechisporoid clade is placed as the sister group of the hymenochaetoid clade in one of the topologies obtained with six-parameter weighted PR analysis (Figs 3, 4). Bootstrap support for the placements of these clades are weak (Figs 1, 4), but ultrastructural characters of septal pores are consistent with the view that they occupy basal positions.

Imperforate parenthesomes have been found in the cantharelloid clade (*Botryobasidium*, *Cantharellus*, *Piriformospora*, *Sebacina*, *Tulasnella*), gomphoid-phalloid clade (*Geastrum*, *Ramaria*), hymenochaetoid clade (*Basidioradulum*, *Coltricia*, *Hymenochaete*, *Hyphodontia*, *Schizopora*, *Trichaptum*, etc.), and trechisporoid clade (*Hyphodontia gossypina*, *Subulicystidium longisporum*), as well as the Auriculariales and Dacrymycetales (Traquair & McKeen, 1978; Moore, 1980; 1985; G. Langer, 1994; Verma *et al*., 1998; Müller *et al*., 2000; Hibbett & Thorn, 2001; Wells & Bandoni, 2001; E. Langer, 2002; K.-H. Larsson et al., 2004). Most other Homobasidiomycetes have perforate parenthesomes (examples are known in the euagarics, polyporoid, bolete, thelephoroid and russuloid clades), which probably represent a derived condition (E. Langer, 1998; Hibbett & Thorn, 2001; E. Langer, 2002). However, imperforate parenthesomes have been reported in the polyporoid clade (*Phanerochaete sordida*) and perforate parenthesomes have been reported in the gomphoid-phalloid clade (*Clathrus*), cantharelloid

Figure 4 Phylogenetic distribution of resupinate forms among the Homobasidiomycetes, based on six-parameter weighted PR analyses of the full 656-OTU dataset. This phylogram represents topology G (Fig. 3); see figure for branch length scale. Ranges of bootstrap values obtained using equally weighted parsimony greater than 65% are indicated with shaded dots on branches (white = 65–79%; grey = 80–89%; black = 90–100%). Exact bootstrap values for major clades are also written along branches, where they are above 50%. Species names are followed by strain numbers that were used to generate 25S sequences. Species names in quotation marks followed by question marks indicate mislabelled isolates. Names of resupinate taxa are written in bold type. Major clades of Homobasidiomycetes are indicated with brackets. This is part of the phylogenetic tree, including Dacrymycetales, Auriculariales and basal clades of Homobasidiomycetes.

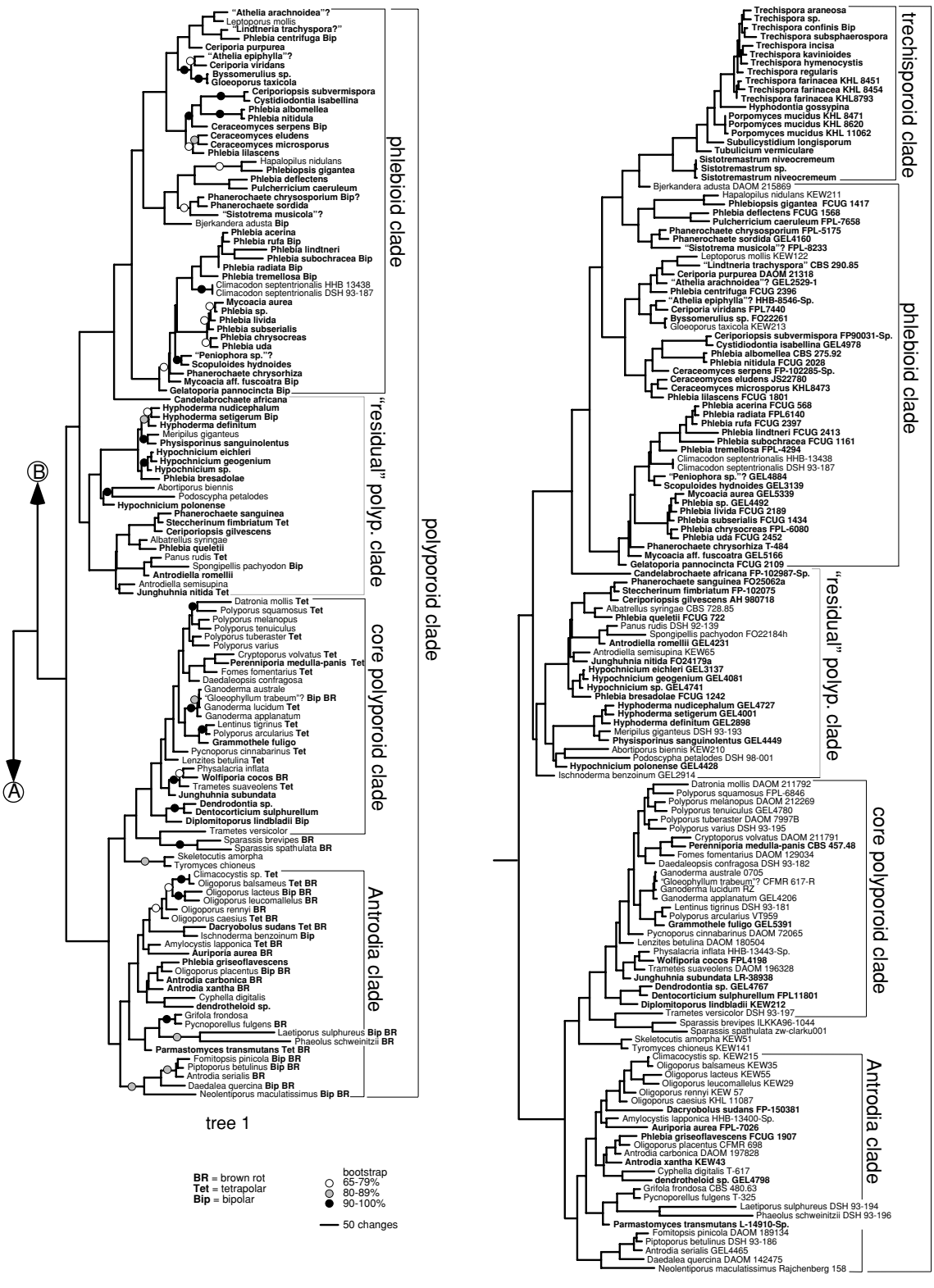

Figure 4 Continued Polyporoid clade. Tree 1 represents topology G, in which the trechisporoid clade is the sister group of the hymenochaetoid clade, and tree 2 represents topology H, in which the trechisporoid clade is nested within the polyporoid clade (Fig. 2). Mating systems for taxa where this is known are indicated in tree 1 (Tet = tetrapolar, Bip = bipolar). Species that produce a brown rot are also indicated (BR).

clade (Ceratobasidiales, *Sistotrema brinkmannii*), hymenochaetoid clade (*Hyphoderma praetermissum*) and trechisporoid clade (*Trechispora subsphaerospora*) (Eyme & Parriaud, 1970; E. Langer & Oberwinkler, 1993; G. Langer, 1994; Keller, 1997; Wells & Bandoni, 2001). These reports, which should be confirmed, suggest that there has been

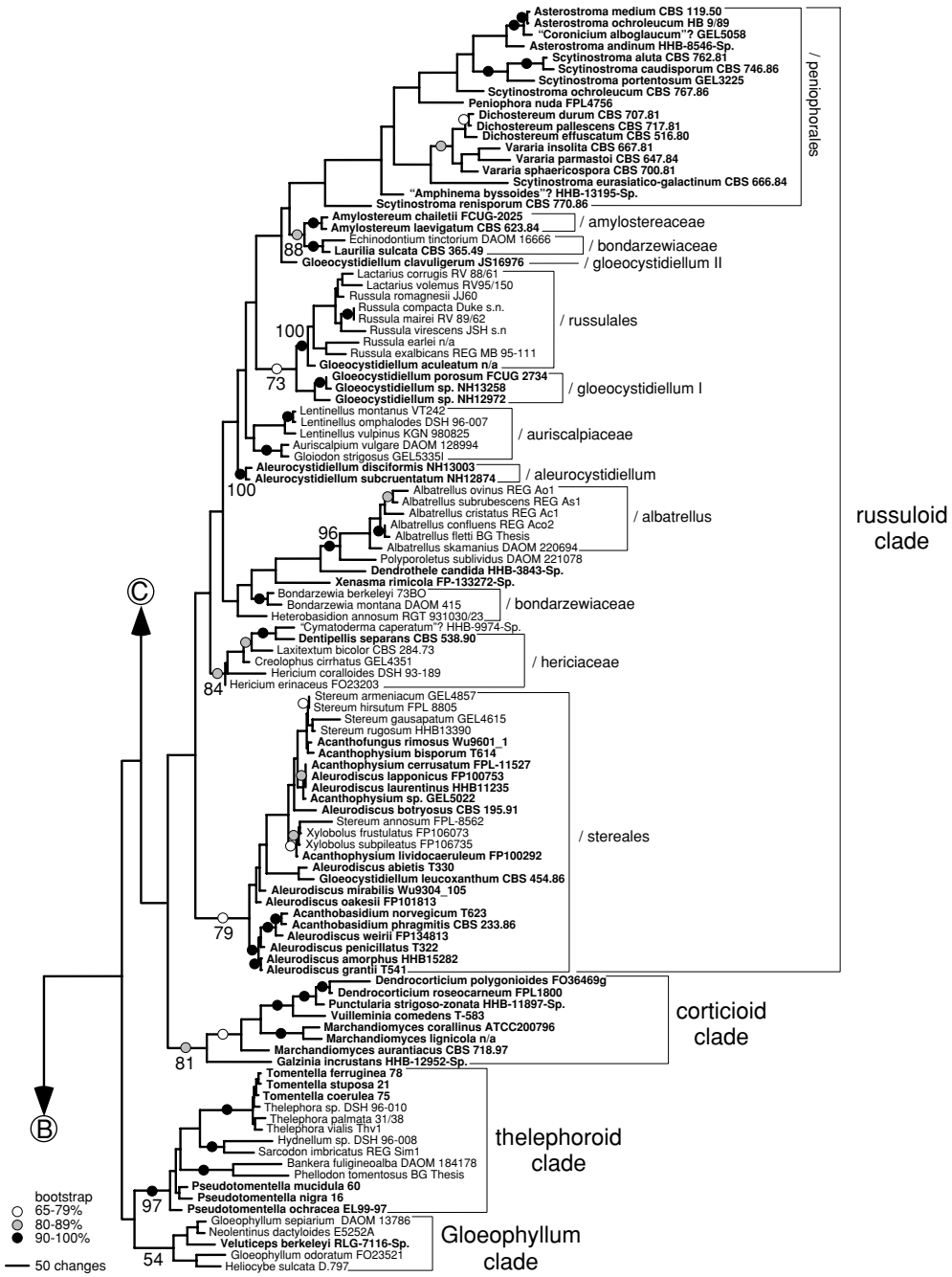

Figure 4 Continued *Gloeophyllum*, thelephoroid, corticioid, and russuloid clades. Groups within the russuloid clade correspond to groups recognised by E. Larsson and K.-H. Larsson.

extensive homoplasy in parenthesome evolution, possibly including reversals from perforate to imperforate parenthesomes (K.-H. Larsson *et al*., 2004). Nevertheless, the occurrence of imperforate parenthesomes in the Auriculariales *s. str.* and Dacrymycetales, and their preponderance in the cantharelloid, gomphoid-phalloid, hymenochaetoid, and trechisporoid clades suggests that this is the plesiomorphic condition in the Homobasidiomycetes, which is consistent with the topology inferred with rDNA sequences. The core dataset tree and five of the topologies obtained in PR analyses of the full dataset suggest that the cantharelloid clade is the sister group of the other Homobasidiomycetes, but bootstrap support is weak (Figs 1, 3, 4).

Phylogenetic distribution of resupinate forms within the Homobasidiomycetes

Resupinate forms occur in every major clade of Homobasidiomycetes (Hibbett & Binder, 2002; K.-H. Larsson *et al*., 2004). The following sections and Table 3 provide a clade-by-clade overview of the distribution of resupinate forms, based on this and other studies. Notes on ecology are also provided. More detailed commentary on the morphology and taxonomy of many of the resupinate forms in this study can be found in E. Larsson (2002), E. Langer (2002), and other works cited below. It is not the purpose of this study to infer the historical pattern of transformations between resupinate and

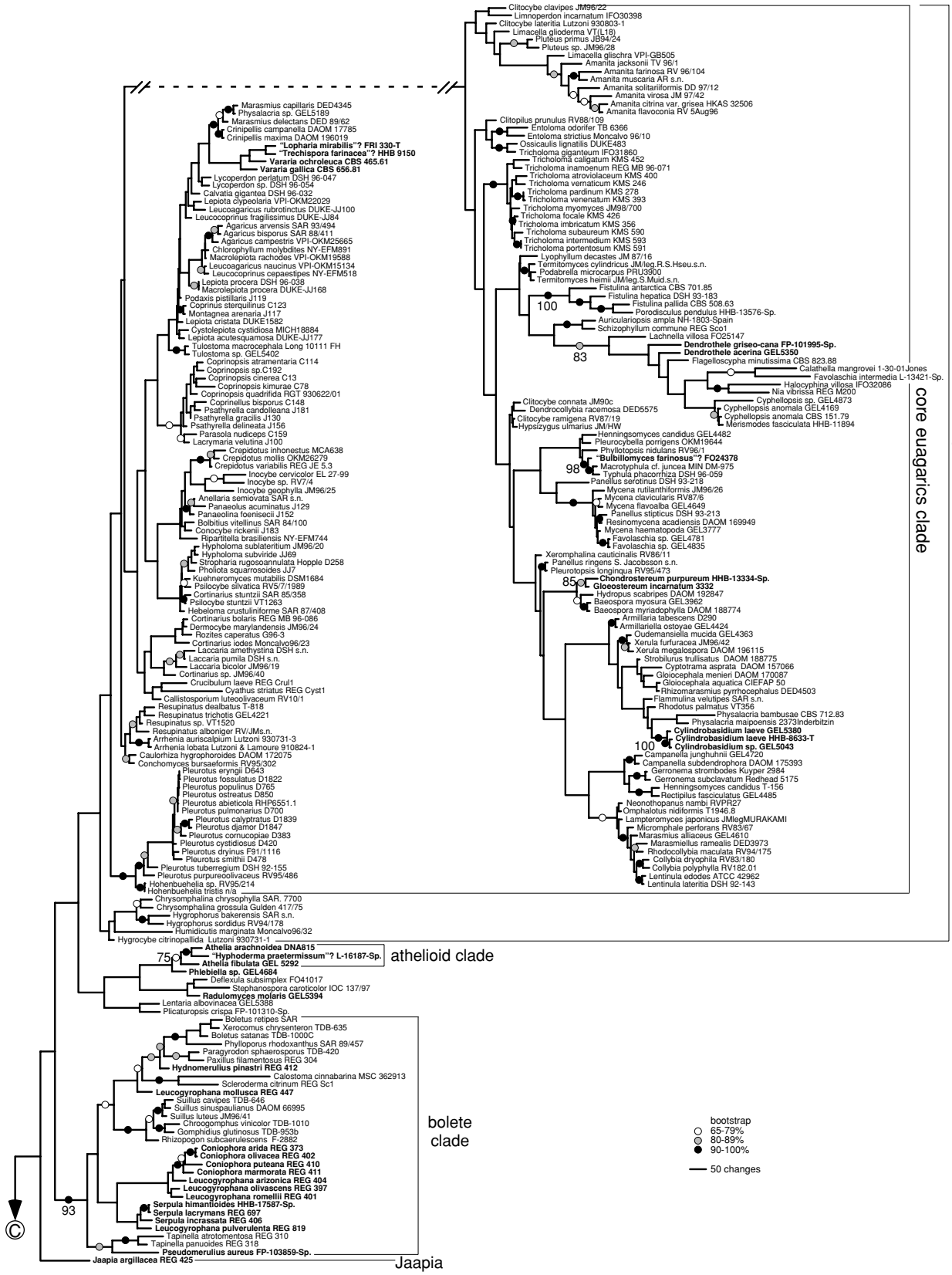

Figure 4 Continued *Jaapia argillacea*, bolete clade, athelioid clade, and euagarics clade.

Clade Subclade/species	Sequences[a]	Isolates[b] This study	 Other studies
Athelioid clade			
'Amphinema byssoides'	1,2	– HHB 13195-Sp.	A + EL 11-98
Athelia arachnoidea	1,2	+ 815	B – 'GEL 2529.1'
	2	– 'GEL 2529.1'	
Athelia decipiens			A + JS 4930
'Athelia epiphylla'	**1,2,3,4**	– HHB-8546-sp	A + EL 12-98
Athelia fibulata	2	+ GEL 5292	B – GEL 5292
Atheliopsis subinconspicua			A + KHL 8490
Byssocorticium pulchrum			A + KHL 11710
Piloderma byssinum			A + KHL 8456
Piloderma lanatum			A + JS 24861
Tylospora asterophora			A + KHL 8566
Bolete clade			
Coniophora arida	**1**,2,3,4	+ MB-1823-sp	A + KHL 8547 B + AF098375 C + SFC 990911-57
Coniophora marmorata	2	+ 411	
Coniophora olivacea	2	+ 402	
Coniophora puteana	**1**,2,3,4	+ FP-102430sp	
Hydnomerulius pinastri	2	+ 412	
Leucogyrophana arizonica	2	+ 404	
Leucogyrophana mollusca	2	+ 447	
Leucogyrophana olivascens	2	+ 397	
Leucogyrophana pulverulenta	2	+ 819	
Leucogyrophana romellii	2	+ 401	A + KHL 11066
Pseudomerulius aureus	**1,2,3**	+ FP-103859sp	A + B.Norden C + SFC 970927-4
Serpula himantioides	1,2,3,4	+ HHB-17587sp	B + GEL 5395
Serpula incrassata	2,4	+ 406	
Serpula lacrymans	2	+ 697	
Cantharelloid clade			
Botryobasidium agg. *candicans*	2	+ GEL 2090	B + GEL 2090
Botryobasidium agg. *vagum*	2	+ GEL 4181	B + GEL 4181
Botryobasidium botryosum			A + KHL 11081
Botryobasidium candicans	2	+ GEL 3083	B + GEL 3083
Botryobasidium isabellinum	2	+ GEL 2108	B + GEL 2108
	1,2,3,4	+ GEL 2109	C + GEL 2109
Botryobasidium sp.	2	+ GEL 4698	B + GEL 4698
	2	+ GEL 5132	B + GEL 5132
Botryobasidium subcoronatum	2	+ GEL 4673	B + GEL 4673
	2	+ GEL 5397	B + GEL 5397
	1,2,3,4	+ FCUG 1286	C + GEL 1286
Botryobasidium vagum	2	+ GEL 2122	
Ceratobasidium sp.	**1,2,3,4**	+ GEL 5602	
Haplotrichum conspersum			A + KHL 11063 C + SFC990123-15
Membranomyces delectabilis			A + KHL 11147
Multiclavula mucida[c]	1,2,3	+ DSH 93-056	C + DSH 93-056
Piriformospora indica[c]	**1,2,3**	+ DSM 11827	

Table 3 Phylogenetic distribution of resupinate and other selected reduced species among the major clades of Homobasidiomycetes and outgroups (Auriculariales and Dacrymycetales), as estimated by the present study, K.-H. Larsson *et al.* (2004), Langer (2002), Lim (2001; nuc-ssu rDNA analyses only), and Kim & Jung (2000)

Clade Subclade/species	Sequences[a]	Isolates[b] This study	 Other studies
Serendipita vermifera[d]	2	+ CBS 572.83	
Sistotrema alboluteum			A + UK 166
Sistotrema brinkmannii	2	+ GEL 3134	A + NH 11412/2206
			B + FO 31682
			B + GEL 3134
Sistotrema confluens[c]			A + PV 174
Sistotrema coronilla			A + NH 7598/785
Sistotrema diademiferum			C + SFC990521-13
Sistotrema eximum	1,2,3,4	+ RGT 420	
Sistotrema sernanderi	2,3	+ CBS 926.70	
'Sistotrema muscicola'	1,2,3	– FPL 8233	A + KHL 8794
Thanatephorus praticola	1,2,3	+ IMI-34886	
Tulasnella obscura			B + GEL 4624
Tulasnella pruinosa	2,3,4	+ DAOM 17641	
Tulasnella sp.	2	+ GEL 4461	B + GEL 4461
	2	+ GEL 4745	B + GEL 4745
Tulasnella violea	**2**,3	+ DAOM 222001	
Uthatobasidium fusisporum	1,2,3	+ HHB 102155sp	
Uthatobasidium sp.	2	+ FO 30284	B + FO 30284
Corticioid clade			
Corticium roseum			A + EL 13-98
			C + [e]SFC 991231-9
Dendrocorticium polygonioides	2	+ FO 36469g	B + FO 36469g
Dendrocorticium roseocarneum	1,2,3,4	+ FPL 1800	A + FPL 1800
Dendrothele maculata			A + HHB 10621
Erythricium laetum			A + GB/NH14530
Galzinia incrustans	1,2,3,4	+ HHB-12952sp	
Laetisaria fuciformis	**1,2,3,4**	+ NJ-2 Jackson	
Marchandiomyces aurantiacus	2	+ DePriest	
Marchandiomyces corallinus	2	+ DePriest	
Marchandiomyces lignicola	2	+ DePriest	
Punctularia strigoso-zonata	1,2	+ HHB-11897sp	A + LR 40885
Vuilleminia comedens	1,2,3	+ T-583	A + EL 1-99
			B + GEL 4110
			C + SFC 990326-21
Vuilleminia macrospora			A + EL 21-99
Euagarics clade			
Amylocorticium cebennense			A + JS 24813
Amylocorticium subincarnatum			A + ÅS-95
Anomoporia bombycina			A + GG u612
Anomoporia kamtschatica			A + KHL 11072
Athelia bombacina			C + no data
Auriculariopsis ampla[c]	**2,3,4**	+ NH 1803	
'Bulbillomyces farinosus'	2,	+ FO 24378	B + FO 24378
Calathella mangrovei[c]	1,2,3	+ 1-30-01Jones	
Calyptella campanula[c]			B +
Ceraceomyces tessulatus			?KHL 8474
Chondrostereum purpureum	1,2,3,4	+ HHB-13334sp	A + EL 59-97
			B + GEL 5348
			C + SFC 971001-13
			C + CBS 427.72

Table 3 Continued.

Clade Subclade/species	Sequences[a]	Isolates[b] This study	 Other studies
Coronicium alboglaucum	2	+ GEL 5058	A — NH 4208/377 B — GEL 5058
Cylindrobasidium laeve	1,2,**3**,4 2	+ HHB-8633-T + GEL 5380	A + Ulvesund B + GEL 5380 C + SFC990121-8
Cylindrobasidium sp.	2	+ GEL 5043	B + GEL 5043
Cyphellopsis anomala[c]	1,2,3,4 2	+ CBS 151.79 + GEL 4169	B + GEL 4169
Cyphellopsis sp.[c]		+ GEL 4873	B + GEL 4873
Cystostereum murraii			C + CBS 257.73
Dendrothele acerina	2	+ GEL 5350	B + GEL 5350
Dendrothele griseocana	**2**	+ FP 101995-sp	
'dendrotheloid' sp.			B + GEL 4798
Favolaschia intermedia[c]	1,2,3,4	+ L-13421-sp	
Flagelloscypha minutissima[c]	1,2,4	+ CBS 823.88	
Gloeostereum incarnatum[c]	2	+ NH 3332	
Halocyphina villosa[c]	1,2,3,4	+ IFO 32086	
Henningsomyces candidus[2]	1,2,3,4	+ GEL 4482	B + GEL 4482
Hypochniciellum subillaqueatum			A + KHL 8493
Lachnella villosa[c]	1,2,3,4	+ CBS 609.87	B + FO 25147
Merismodes fasciulatus[c]	1,2,3	+ HHB-11894	
Mucronella calva			B + GEL 4458
Mycoacia copelandii			C + SFC990710-6
Phlebiella pseudotsugae			A + NH 10396/1953
Plicaturopsis crispa[c]	**1,2,3,4**	?FP 101310-sp	B — GEL 4132 C — SFC 990320-8
Rectipilus fasciculatus			B + GEL 4485
Schizophyllum commune[c]	1,2,3,4	+ DSH 96-026	B + GEL 4623
***Gloeophyllum* clade**			
Boreostereum radiatum			C + CBS 417.61
Donkioporia expansa			C + CBS 299.93
Gloeophyllum sepiarium[c]	1,2,3,4	+ DAOM 137861	
Heliocybe sulcata[c]	1,2,3	+ D. 797	
Veluticeps berkeleyi	1,**2,4**	+ RLG-7116-sp	C + CBS 725.68
Gomphoid-phalloid clade			
Kavinia alboviridis			A + EL 16-98
Kavinia himantia	**1,2,3,4**	+ FP-101479sp	A + LL-98
Kavinia sp.			B — FO 25092
Ramaricium alboflavescens	**1**,2,4	+ DAOM-17712	
Hymenochaetoid clade			
Asterodon ferruginosum			A + KHL 11176
Basidioradulum radula	1,2,3	+ FO 23507a	A + NH 9453 B + GEL 4107 C + no data
Fibricium rude	2	+ GEL 2121	B + GEL 2121
Hyphoderma guttuliferum			A + NH 12012/2438
Hyphoderma praetermissum	1,2,3,4	— 'L-16187-sp.'	A + NH 9536/1708 B + GEL 4845
Hyphodontia aff. *breviseta*	2	+ GEL 4214	B + GEL 4214
Hyphodontia alienata			A + EL14-98
Hyphodontia agg. *alutaria*			B + GEL 2034

Table 3 Continued.

Clade Subclade/species	Sequences[a]	Isolates[b] This study	 Other studies
Hyphodontia alutaria	1,2,3,4	+ 'GEL 2071'	C + 'GEL 2071'
	2	+ GEL 4553	
Hyphodontia alutacea	2	+ GEL 2397	B + GEL 2937
Hyphodontia aspera	2	+ GEL 2135	A + KHL 8530
			B + GEL 2135
Hyphodontia barbajovis			B + GEL 3806
Hyphodontia borealis			A + JS 26064
Hyphodontia breviseta			A + JS 17863
Hyphodontia cineracea	2	+ GEL 4875	B + GEL 4875
Hyphodontia crustosa	2	+ GEL 5360	B + GEL 5360
Hyphodontia nespori	2	+ GEL 4190	B + GEL 4190
Hyphodontia niemelaei	2	+ GEL 5068	
Hyphodontia nudiseta	2	+ GEL 5302	B + GEL 5302
Hyphodontia pallidula	2	+ GEL 4533	B + GEL 4533
Hyphodontia palmae	2	+ GEL 4536	B + GEL 3456
Hyphodontia quercina			A + KHL 11076
Hyphodontia sambuci	2	+ FO 42008	B + GEL 2414
Hyphodontia serpentiformis	2	+ GEL 3307	B + GEL 3307
Oxyporus populinus[c]	2	+ FO 35584	B + FO 35584
Repetobasidium mirificium	**1,2,3,4**	+ FP-133558sp	
Resinicium bicolor	1,2,3	+ FP-135104sp	A + NH 11540/2228
			B — GEL 4664
			C + HHB 10103
			C + CBS 253.73
Schizopora flavipora	2	+ GEL 3545	B + GEL 3545
Schizopora paradoxa	1,2,3	+ GEL 2511	B + GEL 4188
			C — GEL 2511
Schizopora radula	2,3	+ GEL 3798	
Sphaerobasidium minutum	2	+ GEL 5373	B + GEL 5373
Subulicium sp.	2	+ GEL 4808	B + GEL 4808
Trichaptum abietinum[c]	1,2,3	+ FPL 8973	B + GEL 5237
Tubulicrinis gracillimus	1,2	+ HHB-13180sp	
Tubulicrinis subulatus	2	+ GEL 5286	A + KHL 11079
			B + GEL 5286
Tubulicrinus sp.	2	+ GEL 5046	B + GEL 5046
Hymenochaetaceae			
Fomitoporia punctata	2	+ 85-74	
Fuscoporia contigua	2	+ TW 699	
Fuscoporia ferrea	2	+ 87-8	
Fuscoporia ferruginosa	2	+ 82-930	
Hydnochaete olivacea	**1,2,3**	+ CLA 02-003	
Hymenochaete acanthophysata	2	+ CBS 925.96	
Hymenochaete adusta	2	+ TAA 95-37	
Hymenochaete berteroi	2	+ CBS 733.86	
Hymenochaete boidinii	2	+ CBS 726.91	
Hymenochaete carpatica	2	+ TW 27.9.97	
Hymenochaete cervinoidea	2	+ CBS 736.86	
Hymenochaete cinnamomea	2	+ LK 27.9.97	A + EL 6-99
Hymenochaete corrugata	1,2,3	+ FP-104124sp	
Hymenochaete cruenta	2	+ HB 149/80	
Hymenochaete denticulata	2	+ CBS 780.91	

Table 3 Continued.

Clade Subclade/species	Sequences[a]	Isolates[b] This study	 Other studies
Hymenochaete duportii	2	+ CBS 941.96	
Hymenochaete fuliginosa	2	+ CBS 933.96	
Hymenochaete japonica	2	+ CBS 499.76	
Hymenochaete nanospora	2	+ CBS 924.96	
Hymenochaete ochromarginata	2	+ CBS 928.96	
Hymenochaete pinnatifida	2	+ CBS 770.91	
Hymenochaete pseudoadusta	2	+ TAA 95-38	
Hymenochaete rhabarbarina	2	+ GEL 4809	B + GEL 4809
Hymenochaete rubiginosa	2	+ TW 22.9.97	
Hymenochaete separabilis	2	+ CBS 738.86	
Hymenochaete separata	2	+ TAA 95-24	
Hymenochaete sp.	2		A + KHL 11024
Mensularia hastifera	2	+ 84-1023a	
Phellinidium ferrugineofuscum	2	+ TN 6121	
Phellinus laevigatus	2	+ TN 3260	
Phellopilus nigrolimitatus[c]	2	+ 85-823	
Pseudochaete tabacina	2	+ FPL 3000	
Jaapia			
Jaapia argillacea	1,2,3,4	+ Reg 425	
Polyporoid clade			
core polyporoid clade			
Dendrodontia sp.	2	+ GEL 4767	B + GEL 4767
Dentocorticium sulphurellum	1,2,3,4	+ FPL 11801	C + FPL 11801
Diplomitoporus crustulinus			C – CBS 443.48
Diplomitoporus lindbladii	**1**,2	+ KEW 212	B + GEL 4653
Grammothele fuligo	2	+ GEL 5391	B + GEL 5391
Junghuhnia subundata	1,2,3,4	+ LR-38938	
Lopharia cinerascens			A + EL 63-97
			C + CBS 486.62
Lopharia mirabilis	**1,2,3**	– FRI 330-T	C + SFC 990623-11??
Perenniporia medulla-panis	1,2,3	+ CBS 45	
Wolfiporia cocos	1,2,3,4	+ FPL 4198	C + ATCC 13490
phlebioid clade			
Anomoporia albolutescens			C + CBS 337.63
Bjerkandera adusta[c]	1,2,3,4	+ DAOM 21586	C + DAOM 21586
Byssomerulis corium			A + KHL 8593
Byssomerulius sp.	2	+ FO 22261	B + FO 22261
Ceraceomyces eludens	2	+ JS22780	A + JS 22780
Ceraceomyces microsporus	2	+ KHL 8473	
Ceraceomyces serpens	1,2,3	+ FP-102285-sp	A + KHL 8478
Ceriporia purpurea	1,2,3,4	+ DAOM 21318	C + DAOM 21316
Ceriporia viridans	1,2,3,4	+ FPL 7440	A + KHL 8765
			B + FO 24398
Ceriporiopsis subvermispora	1,2,3,4	+ FP 90031-sp.	C – CBS 525.92
Climacodon septentrionale[c]	2,4	+ HHB 13438-sp	
	2	+ DSH 93-187	
Cystidiophora castanea			C + SFC 980119-2
Cystidiodontia isabellina	2	+ GEL 4978	B + GEL 4978
Gelatoporia pannocincta	2	+ FCUG 2109	
Gloeoporus taxicola[c]	1,2,3,4	+ KEW 213	A + 98
			C + SFC 000111-3
			C + SFC 950815-16

Table 3 Continued.

Clade Subclade/species	Sequences[a]	Isolates[b] This study	 Other studies
Irpex lacteus			C + ??SFC 951007-39
			C + IFO 5367
'Lindtneria trachyspora'	1,2,3,4	+ CBS 290.85	
Lopharia spadicea			C + CBS 474.48
Mycoacia aff. *fuscoatra*	2	+ GEL 5166	B + GEL 5166
Mycoacia aurea	2	+ GEL 5339	A + NH 14434
			B + GEL 5339
Mycoacia uda			B + GEL 3102
Mycoaciella bispora			A + EL 13-99
Oxyporus latemarginatus			C + ATCC 9408
Phanerochaete chrysorhiza	2	+ T-484	
Phanerochaete chrysosporium	1,2,3,4	+ FPL 5175	C + FPL 5175
Phanerochaete sordida	2	+ GEL 4160	B + GEL 4160
			C + SFC 980201-11
Phlebia acerina	2	+ FCUG 568	
Phlebia albomellea	**1,2,3,4**	+ CBS 275.92	
Phlebia centrifuga	2	+ FCUG 2396	B + AF 141618
Phlebia chrysocreas	**1,2,3**	+ FPL6080	A + KHL 10216
Phlebia deflectens	2	+ FCUG 1568	
Phlebia lilascens	2	+ FCUG 1801	
Phlebia lindtneri	2	+ FCUG 2413	A + NH 12239/2413
Phlebia livida	2	+ FCUG 2189	
Phlebia nitidula	2	+ FCUG 2028	
Phlebia radiata	1,2,3,4	+ FPL 6140	A + NH 12118/2423
			B + AF 141627
			B + GEL 5258
			C + FPL 6140
			C + ??KCTC 6759
Phlebia rufa	2	+ FCUG 2397	A + NH 12094/2397
Phleba sp.	2	+ GEL 4492	B + GEL 4492
Phlebia subochracea	2	+ FCUG 1161	
Phlebia subserialis	2	+ FCUG 1434	
Phlebia tremellosa	**2**,3	+ FPL 4294	A + NH 10162/1813
Phlebia uda	2	+ FCUG 2452	
Phlebiopsis gigantea	1,2,3,4	+ FP-101815-sp	B + GEL 2500
Pulcherricium caeruleum	1,2,3,4	+ FPL 7658	C + ??IFO 4974
			C + FPL 7658
Rigidoporus vinctus			C + ATCC 32575
Scopuloides hydnoides	2	+ GEL 3139	B + GEL 3139
			B + GEL 3859
Antrodia clade			
Antrodia carbonica[c]	1,2,3,4	+ DAOM 197828	C + DAOM 197828
Antrodia serialis[c]	2	+ GEL 4465	B + GEL 4465
Antrodia xantha	1,2,3	+ KEW 43	
Auriporia aurea	1,2,3,4	+ FPL 7026	
Dacryobolus karstenii			C + SFC 971006-13
Dacryobolus sudans	**1,2,3,4**	+ FP-150381	
Parmastomyces transmutans	**1**,2	+ L-14910-sp	
Melanoporia nigra			C + CBS 341.63
residual polypores (*incertae sedis*)			
Antrodiella americana			– CBS 386.51
Antrodiella romellii	2	+ GEL 4231	B + GEL 4231

Table 3 Continued.

Clade Subclade/species	Sequences[a]	Isolates[b] This study	 Other studies
Antrodiella semisupina[c]	**2**	+ KEW 65	B + GEL 4513
Candelabrochaete africana	1,2,3,4	+ FP-102987-sp	
Ceriporiopsis gilvescens	2	+ KEW 16	
Columnocystis abietina			C + HHB 12622-sp
Columnocystis ambigua			C + CBS 136.63
Cyphella digitalis[c]	**2,3**	+ Thorn-617	
'dendrotheloid' sp.	2	+ GEL 4798	
Hyphoderma definitum	2	+ GEL 2898	B + GEL 2898
Hyphoderma incrustatum			A + KHL 6685/2029
Hyphoderma nemorale			A + EM 2793/2324
Hyphoderma nudicephalum	2	+ GEL 4727	B + GEL 4727
Hyphoderma obtusum			A + JS 17804
Hyphoderma occidentale			A + KHL 8469G
Hyphoderma roseocremeum			A + NH 10545/1945
Hyphoderma setigerum	2	+ GEL 4001	A + KHL 8544/1264 B + GEL 4001
Hypochnicium eichleri	2	+ GEL 3137	B + GEL 3137
Hypochnicium geogenium	2	+ GEL 4081	B + GEL 4081
Hypochnicium polonense	2	+ GEL 4428	B + GEL 4428
Hypochnicium sp.	2	+ GEL 4741	B + GEL 4741
Junghuhnia nitida	2	+ FO 24179a	B + FO 24179a C – SFC 940903-7
Phanerochaete sanguinea	2	+ FO 25062a	B + FO 25062a
Phlebia bresadolae	2	+ FCUG 1242	
Phlebia griseoflavescens	2	?FCUG 1907	
Phlebia queletii	2	+ FCUG 722	
Physisporinus sanguinolentus	2	+ GEL 4449	B + GEL 4449
Skeletocutis amorpha[c]	**2**	+ KEW 51	
Skeletocutis subincarnata[c]			B + GEL 3129
Steccherinum fimbriatum	1,2,3,**4**	+ FP-102075	
Resinicium meridionale			
Resinicium meridionale	**1,2,3,4**	+ FP-150236	
Russuloid clade			
Acanthobasidium norvegicum	2	+ T-623	
Acanthobasidium phragmitis	2	+ CBS 233.86	
Acanthofungus rimosus	2	+ Wu 9601-1	
Acanthophysium bisporum	2	+ T614	
Acanthophysium cerrusatum	1,2,3,4	+ FPL11572	A + NH 11910/2350[f]
Acanthophysium lividocaeruleum	2	+ FP 100292	
Acanthophysium sp.	2	+ GEL 5022	B + GEL 5022
Aleurocystidiellum disciformis	2	+ T529	
Aleurocystidiellum subcruentatum	2	+ GEL 5288	
Aleurodiscus abietis	2	+ T-330	
Aleurodiscus amorphus	2	+ HHB 15282	C + no data
Aleurodiscus botryosus	1,2,3	+ CBS 195.91	C + CBS 195.91
Aleurodiscus grantii	2	+ T541	
Aleurodiscus lapponicus	2	+ FP-100753-Sp	
Aleurodiscus laurentianus	2	+ HHB 11235	
Aleurodiscus mirabilis	2	+ Wu 9304	
Aleurodiscus oakesii	2	+ FP 101813	
Aleurodiscus penicillatus	2	+ T-322	

Table 3 Continued.

Clade Subclade/species	Sequences[a]	Isolates[b] This study	 Other studies
Aleurodiscus weirii	2	+ FP 134813	
Amylostereum areolatum[c]			A + NH 8041/1080
			B – GEL 5265
			C + CBS 334.66
Amylostereum chailettii	1,2,3	+ FCUG 2025	C + CBS 480.83
Amylostereum laevigatum	1,2,3,4	+ CBS 623.8	
Asterostroma andinum	1,2,3,4	+ HHB-9023-sp	
Asterostroma laxum			A + EL 33-99
Asterostroma medium	2	+ CBS 119.50	
Asterostroma musicola			A + GB/KHL9573
Asterostroma ochroleuca	2	+ HB 9/89	
Dendrothele candida	**2**	+ HHB 3843-sp	
Dentipellis separans	1,2,3,4	+ CBS 538.90	
Dichostereum durum	2	+ CBS 707.81	
Dichostereum effuscatum	2	+ CBS 516.80	A + GG 930915
Dichostereum pallescens	1,2,3	+ CBS 717.8	
Gloeocystidiellum aculeatum	2	+ AF265546	
Gloeocystidiellum clavigerum	2	+ JS 16976	
Gloeocystidiellum leucoxanthum	1,2,3,4	+ CBS 454.86	C + CBS 454.86
Gloeocystidiellum porosum	2,3	+ CBS 510.85	
Gloeocystidiellum sp.	2	+ NH 13258	
Gloeocystidiellum sp.	2	+ NH 12972	
Gloeocystidiellum subaerisporum			A + KHL 8695
Gloeodontia discolor			A + KHL 10099
Gloeohypochnicium analogum			A + NH 12140
Gloeopeniophorella convolvens			A + KHL 10103
Gloiothele lactescens			A + EL 8-98
Lachnocladium sp.[c]			A + KHL 10556
Laurilia sulcata	1,2,4	+ CBS 365.49	
Laxitextum bicolor[2]	1,2,3,4	+ CBS 284.73	A + NH 5166/1350
			C + CBS 284.73
Peniophora cinerea			A + NH 9808/1788
Peniophora incarnata			A + NH 10271/1909
Peniophora nuda	1,2,3,4	+ FPL 4756	C + FPL 4756
'*Peniophora* sp.'	2	– GEL 4884	B – GEL 4884
Scytinostroma aluta	1,2,3,4	+ CBS 762.81	C + no data
Scytinostroma caudisporum	**1,2,4**	+ CBS 746.86	
Scytinostroma euarasiatico-galactinum	**1,2,3**	+ CBS 666.84	
Scytinostroma ochroleucum	**2**	+ CBS 767.86	
Scytinostroma odoratum			A + KHL 8546
Scytinostroma portentosum	2,3,4	+ CBS 503.48	B – GEL 3225
Scytinostroma renisporum	**1,2,3,4**	+ CBS 770.86	
Stereum armeniacum[c]			B + GEL 4857
Stereum gausapatum[c]			B + GEL 4615
			C + CBS 348.39
Stereum hirsutum[c]	1,2,3,4	+ FPL 8805	A + NH 7960/1022
			B + GEL 4599
			C + FPL 8805
Stereum ostrea[c]			C + SFC 960921-8
Stereum rugosum[c]	2	+ HHB 13390-sp	A + NH 11952/2353
Stereum subtomentosum[c]			C + ??SFC 990709-12

Table 3 Continued.

Clade Subclade/species	Sequences[a]	Isolates[b] This study	 Other studies
'Vararia gallica'	–	?CBS 656.81	
Vararia insolita	1,2,3	+ CBS 667.81	
Vararia investiens			A + 164122
'Vararia ochroleucum'	2	– CBS 683.81	
Vararia parmastoi	**2,3**	+ CBS 647.84	
Vararia sphaericospora	**2,3**	+ CBS 700.81	
Vesiculomyces citrinus			A + EL 53-97
Xenasma rimicola	**1,2,3,4**	+ FP-133272-sp	
Xylobolus annosum[c]			C + ??CBS 490.76
Xylobolus frustulatus	2	+ FP 106073	
Xylobolus subpileatus	2	+ FP 106735	
Thelephoroid clade			
Amaurodon viridis			A + 149664
Pseudotomentella mucidula	2	+ Koljalg 60	
Pseudotomentella nigra	2	+ Koljalg 16	
Pseudotomentella ochracea	2	+ GB, EL99-97	B + AF092847
Pseudotomentella tristis			A + 159485
Tomentella botryoides			A + KHL 8453
Tomentella caerulea	2	+ Koljalg 75	
Tomentella ferruginea	2	+ Koljalg 78	
Tomentella stuposa	2	+ Koljalg 21	
Tomentella terrestris			A + 159557
Tomentellopsis echinospora			A + KHL 8459
Trechisporoid clade			
Hyphodontia gossypina	2	?GEL 5042	B + GEL 5042
Porpomyces mucidus	2	+ KHL 8471	
	2	+ KHL 8620	
	2	+ KHL 11062	
Sistotremastrum niveocremeum	2	+ EL 96-97	A + EL 96-97
	2	+ FO 29191[g]	B + FO 36914
			B + FO 29191
'Sistotremastrum niveocremeum'	2	– FO 36914	
Sistotremastrum sp.	2	+ FO 36293b	B + FO 36293b
Sublicystidium longisporum	2	+ GEL 3550	B + GEL 5217a
Sublicystidium sp.			A + KHL 10780
Trechispora araneosa	2	+ KHL 8570	A + KHL 8570
Trechispora confinis	2	+ KHL 11064	A + KHL 11064
			A + KHL 11197
Trechispora farinacea	2	+ KHL 8451	A + KHL 8793
	2	+ KHL 8454	
	2	+ KHL 8793	
'Trechispora farinacea'	2	– HHB 9150	
Trechispora hymenocystis	2	+ KHL 8795	A + KHL 8795
Trechispora incisa	2	+ EH 24/98	
Trechispora kavinioides	2	+ KGN 981002	A + PN 1824
Trechispora nivea			A + G.Kristiansen
Trechispora regularis	2	+ KHL 10881	A + KHL 10881
Trechispora sp.	2	+ KHL 10715	
Trechispora subsphaerospora	2	+ KHL 8511	A + KHL 8511
Tubulicium vermiculare	2	+ GEL 5015	B + GEL 5015
Tubulicium vermiferum			A + KHL 8714

Table 3 Continued.

Clade Subclade/species	Sequences[a]	Isolates[b] This study	 Other studies
Auriculariales			
Basidiodendron caesiocinereum	2	+ GEL 5361	B + GEL 5361
Basidiodendron sp.	2	+ GEL 4674	B + GEL 4674
Bourdotia sp.	2	+ GEL 4777	B + GEL 4777
Exidia thuretiana	2	+ GEL 5242	B + GEL 5242
Exidiopsis calcea	**1,2**	+ HHB-15059-sp	A + KHL 11075
Heterochaete sp.	2	+ GEL 4813	B + GEL 4813
Dacrymycetales			
Cerinomyces crustulinus			A + KHL 8688
Cerinomyces grandinioides	2	+ GEL 4761	B + GEL 4761
Paullicorticium ansatum			A + KHL 8553
Incertae sedis			
Deflexula subsimplex[c]	2	?FO 41017	B – FO 41017
Phlebiella sp.	2	?GEL 4684	B – GEL 4684
Radulomyces confluens			A + KHL 8792
Radulomyces molaris	2	– GEL 5394	A + ML 0499
			B + GEL 5394
Radulomyces rickii			A + JK 951007

[a] Key to sequences: 1 = nuc-ssu, 2 = nuc-lsu, 3 = mt-ssu, 4 = mt-lsu; numbers in bold type indicate sequences newly reported in this study.

[b] Symbols preceding isolate numbers: + indicates that species is placed in this clade; – indicates that species was placed in a different clade; the placement in this table reflects hypothesised correct placement; ? indicates that species is placed in this clade, but there is uncertainty about the placement or the identification of the isolate; ?? indicates that it is not certain if this isolate was the source of the sequence; names and strain numbers in quotation marks indicate that isolate may be misidentified. Other studies referenced: A = K.-H. Larsson *et al.* (2004); B = Langer (2002); C = Lim (2001) and Kim & Jung (2000).

[c] Non-resupinate species.

[d] As *Sebacina vermifera*.

[e] As *Laeticorticium roseocarneum*.

[f] As *Aleurodiscus cerrusatus*.

[g] As *Paullicorticium niveocremeum*.

erect forms. Readers interested in this subject should refer to Hibbett & Binder (2002) and K.-H. Larsson *et al.* (2004).

This study included 39 genera of resupinate Homobasidiomycetes that are represented by more than one species (Table 3). Of these, 27 are not resolved as monophyletic (not considering certain taxa where misidentifications are likely; i.e. '*Sistotrema muscicola*' and '*Trechispora farinacea*', see below), which indicates how much work there is to be done in the taxonomy of resupinate Homobasidiomycetes (Fig. 4). There are also many individual isolates whose placements conflicted with their expected positions based on morphology or molecular data from other isolates. Some of these results are probably due to misidentifications, which underscores the importance of studying multiple accessions of individual species when working with taxonomically challenging organisms. Other problematical results may be due to the usual vagaries of molecular systematics, including PCR contamination and clerical error. Because we cannot positively identify the sources of error in most cases, the problematical sequences are designated as 'mislabelled'.

1. Cantharelloid clade

Support for the monophyly of the cantharelloid clade was discussed previously. The cantharelloid clade includes a seemingly heterogeneous assortment of taxa that have been regarded as Homobasidiomycetes or heterobasidiomycetes. Basidial morphology is remarkably diverse, including not only the various 'heterobasidioid' forms, but also clavate or urniform holobasidia with six or eight sterigmata (e.g., *Botryobasidium subcoronatum, Sistotrema brinkmannii*), and elongate cylindric holobasidia with two to four sterigmata (e.g., *Clavulina cinerea, Cantharellus cibarius*). The topology in Fig. 4 implies that holobasidia may be derived within the cantharelloid clade, and therefore may not be homologous with holobasidia in the rest of the Homobasidiomycetes. Admittedly, this hypothesis is based on a weakly supported topology within the cantharelloid clade (Fig. 4). Nevertheless, it is consistent with observations that holobasidia in the cantharelloid clade are stichic (meaning that the axis of the first meiotic division is oriented parallel to the length of the basidium) whereas holobasidia in the remaining clades of Homobasidiomycetes are

chiastic (first meiotic spindle is oriented transversely) (Pine *et al*., 1999; Hibbett & Thorn, 2001).

The cantharelloid clade includes a mixture of resupinate and non-resupinate forms. Non-resupinate forms include *Cantharellus* spp., *Craterellus cornucopoides*, *Hydnum* spp., *Clavulina cinerea* and *Multiclavula mucida*. Resupinate forms occur in six well-supported clades: (1) Tulasnellales; (2) *Piriformospora-Serendipita*; (3) Ceratobasidiales; (4) *Botryobasidium*; (5) *Sistotrema eximum* and *S. sernanderi*; and (6) *Sistotrema brinkmannii* and *'Sistotremastrum niveocremeum'* (Fig. 4). The first three groups have already been discussed.

Botryobasidium is represented by eleven sequences from at least four species, most of which were included in the analysis of E. Langer (2002). Basidia and basisidiospores are highly variable in *Botryobasidium* (G. Langer, 1994; G. Langer *et al*., 2000). For example, *B. subcoronatum* has six sterigmata per basidium and smooth navicular spores, whereas *B. isabellinum* has four sterigmata and spiny globose spores (G. Langer, 1994). Other *Botryobasidium* species have as few as two or as many as eight sterigmata (and in this way resemble *Sistotrema*) and spores that are elliptic, cylindrical, ovoid or 'bananiform' (G. Langer *et al*., 2000). Nevertheless, many *Botryobasidium* species share anatomical characters, including a unique rectangular hyphal branching and production of a *Haplotrichum* anamorph (G. Langer, 1994). *Botryobasidium* is strongly supported as monophyletic (Fig. 4).

The two groups that contain *Sistotrema* isolates are not resolved as sister taxa. Comparable results were obtained by K.-H. Larsson *et al*. (2004), who suggested that the basidia with 6–8 sterigmata have been overemphasised as a generic character. The *Sistotrema brinkmannii*-*'Sistotremastrum niveocremeum'* clade is placed as the sister group of *Multiclavula mucida*, which suggests the occurrence of a transformation between clavarioid and resupinate fruiting body forms. Two potentially mislabelled sequences involve these groups (Fig. 4, Table 3). The first is the isolate labelled '*Sistotremastrum niveocremeum*' (FO36914), which is placed as the sister group of *Sistotrema brinkmannii* (Fig. 4). Two other isolates of *S. niveocremeum* are included in this analysis, as well as one isolate labelled *Sistotremastrum* sp., and all three are tightly clustered in the trechisporoid clade. The second problem is an isolate labelled '*Sistotrema muscicola*' (FPL8233) that is placed in the phlebioid clade. K.-H. Larsson *et al*. (2004) examined a different isolate of *S. muscicola* and found that it is placed in the cantharelloid clade, as are the three other species of *Sistotrema* included here.

The composition of the cantharelloid clade in this study agrees with the findings of K.-H. Larsson *et al*. (2004) and E. Langer (2002), who sampled many of the same groups that were included in this study. Resupinate taxa that K.-H. Larsson *et al*. (2004) sampled that were not represented in the present study include *Haplotrichum conspersum*, which is an anamorph of *Botryobasidium*, and *Membranomyces delectabilis*, which was originally classified as a species of *Clavulicium*. Basidia in *Clavulicium* and *Membranomyces* have two to four sterigmata, which (when two-spored) resemble basidia of the coral fungus *Clavulina* (Eriksson & Ryvarden, 1973; K.-H. Larsson *et al*., 2004). *Clavulicium* has been placed in the Clavulinaceae (Donk, 1964; Parmasto, 1968), but Eriksson & Ryvarden (1973) retained it in the Corticiaceae. The analysis of K.-H. Larsson *et al*. (2004) placed *M. delectabilis* as the sister group of *Clavulina cristata*, which provides another example of a resupinate-clavarioid transformation in the cantharelloid clade. Another noteworthy taxon that was included in the analysis of K.-H. Larsson *et al*. (2004) but not the present study is *Sistotrema confluens*, which produces pileate-stipitate fruiting bodies with a poroid to hydnoid hymenophore. The analysis of K.-H. Larsson *et al*. (2004) placed *S. confluens* as the sister group of a clade containing *Sistotrema muscicola* and *Hydnum repandum*. Taken together, the results of K.-H. Larsson *et al*. (2004) and the present study suggest that there have been numerous transformations between resupinate and non-resupinate forms in the clade containing *Sistotrema, Clavulicium, Multiclavula, Clavulina, Hydnum* and Cantharellaceae (Fig. 4).

Species in the cantharelloid clade have diverse nutritional modes. *Botryobasidium* is reportedly saprotrophic (G. Langer *et al*., 2000). The Ceratobasidiales and Tulasnellales include saprotrophs, orchid symbionts, liverwort symbionts and economically important plant pathogens (Stalpers & Andersen, 1996; Roberts, 1999; Hietala *et al*., 2001; Kristiansen *et al*., 2001; Wells & Bandoni, 2001; Bidartondo *et al*., 2003; Kottke *et al*., 2003). Sikaroodi *et al*. (2001) showed that a lichenicolous (lichen-inhabiting) asexual fungus, which they called "marchandiomyces-like", is closely related to *Thanatephorus praticola* and "*Rhizoctonia* sp.", and may therefore be a member of the Ceratobasidiales (other *Marchandiomyces* species are in the corticioid clade; see below). The Cantharellaceae, *Clavulina* and *Hydnum* are well known as ectomycorrhizal, and recently it has been demonstrated that Sebacinaceae also form ectomycorrhizae, orchid mycorrhizae, ericoid mycorrhizae and associations with liverworts (Warcup, 1988; Kristiansen *et al*., 2001; Berch *et al*., 2002; Selosse *et al*., 2002; Bidartondo *et al*., 2003; Kottke *et al*., 2003; Urban *et al*., 2003). *Piriformospora indica* is a recently discovered root symbiont with no known fruiting body that has been shown to promote the growth of some plant hosts (Varma *et al*., 1999). It is strongly supported as the sister group of *Serendipita vermifera*, but it does not form the mantle or hartig net associated with typical ectomycorrhizae. Finally, *Multiclavula mucida* is a basidiolichen (Gargas *et al*., 1995*a*; Lutzoni, 1997). Thus, the cantharelloid clade provides an excellent opportunity to study the evolution of symbioses in Homobasidiomycetes, including switches between diverse hosts and apparent shifts between parasitism and mutualism.

2. Gomphoid-phalloid clade

Monophyly of the gomphoid-phalloid clade is strongly supported in the core dataset analysis (bootstrap = 100%) but only weakly supported in the analysis of the full dataset (bootstrap = 69%). Nevertheless, the gomphoid-phalloid clade is strongly supported in other phylogenetic studies (Bruns *et al*., 1998; Hibbett *et al*., 2000; Humpert *et al*., 2001;

Binder & Hibbett, 2002; K.-H. Larsson *et al*., 2004). This relatively small clade contains an amazing diversity of gasteroid and hymenomycetous fruiting body forms, which have been discussed previously (Hibbett *et al*., 1997; Pine *et al*., 1999; Humpert *et al*., 2001). Resupinate taxa in the gomphoid-phalloid clade in the present study include *Kavinia himantia* and *Ramaricium alboflavescens* (Fig. 4). These results agree with those of Bruns *et al*. (1998), Humpert *et al*. (2001) and K.-H. Larsson *et al*. (2004), who found strong support for the inclusion of *Kavinia alboviridis* in the gomphoid-phalloid clade. In contrast, the analysis of E. Langer (2002) did not resolve the gomphoid-phalloid clade as monophyletic and placed an isolate of '*Kavinia* sp.' as the sister group of a clade including *Coronicium alboglaucum* and *Scytinostroma portentosum*, with strong support (bootstrap = 96%). Results of the present study suggest that these taxa are actually members of the russuloid clade (see below), suggesting either that *Kavinia* is polyphyletic (with one part in the russuloid clade) or the isolate of *Kavinia* studied by E. Langer (2002) was mislabelled.

Ramaricium has a smooth, corticioid fruiting body, whereas the fruiting body of *Kavinia* is composed of spines arising from a loose subiculum (Eriksson & Ryvarden, 1976; Eriksson *et al*., 1981). Spores are variable in these genera, being either smooth or warted, and cyanophilous or not. The occurrence of warted cyanophilous spores as well as green staining reactions to iron salts suggest a relationship to Gomphaceae (Eriksson, 1954; Donk, 1964; Ginns, 1979). The basal position of *Kavinia* in Fig. 4 is consistent with the view that resupinate forms are plesiomorphic in the gomphoid-phalloid clade, but the internal topology of the group is weakly supported in this study, as was also the case in the analyses of Bruns *et al*. (1998), Humpert *et al*. (2001) and K.-H. Larsson *et al*. (2004).

Ginns (1979) and Ginns & Lefebvre (1993) reported that *K. alboviridis* and *Ramaricium* spp. are saprotrophs that are associated with a white rot and often occur on wood that is dry and suspended off the ground. In contrast, Eriksson & Ryvarden (1976, p. 757) reported that the fruiting bodies of *K. himantia* occur on well decayed wood and are "often spreading over loose debris and soil", and Eriksson *et al*. (1981, p. 1246) reported that in North Europe *R. alboochraceum* has been collected "only in the basal parts of moss carpets". These observations suggest that *Ramaricium* and *Kavinia* have diverse ecologies. The fruiting behaviour reported by Eriksson and colleagues is consistent with a mycorrhizal habit (e.g. as in *Tomentella*), although there has been no demonstration (that we are aware of) that either *Kavinia* or *Ramaricium* forms mycorrhizae.

3. Trechisporoid clade

The trechisporoid clade was discovered after the 'overview' of Homobasidiomycetes by Hibbett & Thorn (2001). The trechisporoid clade is here represented by 20 nuc-lsu rDNA sequences, which originate from the studies of K.-H. Larsson (2001) and E. Langer (2002). In the present study and that of E. Langer (2002), the group received only moderate support (bootstrap = 69% and 76%, respectively), but in analyses by K.-H. Larsson (2001) and K.-H. Larsson *et al*. (2004) the group was strongly supported (bootstrap > 95%). E. Langer (2002) found 100% bootstrap support for two subclades, which he called the paullicorticioid and subulicystidioid clades, and K.-H. Larsson (2001) found strong support for the separation of *Trechispora* and *Porpomyces mucidus* (bootstrap = 100%). In the present study, the groups identified by K.-H. Larsson (2001) and E. Langer (2002) are interdigitated, with the paullicorticioid clade *sensu* E. Langer (which includes only *S. niveocremeum* and '*Sistotremastrum* sp.') placed as the sister group of the rest of the trechisporoid clade, with strong support (Fig. 4).

The higher-level placement of the trechisporoid clade is very unstable. Depending on the analysis, the trechisporoid clade is placed in or near the polyporoid clade, russuloid clade, hymenochaetoid clade or Auriculariales (K.-H. Larsson, 2001; Hibbett & Binder, 2002; E. Langer, 2002; K.-H. Larsson *et al*., 2004; Fig. 3). Two species in the trechisporoid clade, *Sistotremastrum niveocremeum* and *Trechispora confinis*, have been reported to have bipolar mating systems, which is a relatively rare condition in Homobasidiomycetes (Boidin & Lanquetin, 1984; Nakasone, 1990*a*). The occurrence of bipolar mating systems in these species is consistent with the placement of the trechisporoid clade in the phlebioid clade (a subgroup of the polyporoid clade; see below), as suggested by some analyses (Fig. 4, tree 2). Unfortunately, only nuc-lsu rDNA sequences are available for the trechisporoid clade. Obtaining sequences of additional genes from this group, as well as more data on septal pore ultrastructure and mating systems, should be a priority.

The trechisporoid clade is composed primarily of resupinate species with smooth, poroid or odontioid hymenophores, although some taxa in *Trechispora* become flabelliform or stipitate (K.-H. Larsson, 2001). Diverse anatomical characters occur in this clade, including hyphal cords and ampullate septa (*Trechispora, Porpomyces*), ampullate septa (*Trechispora*), rooted lyocystidia (*Tubulicium*), cystidia or subicular hyphae with various forms of crystalline ornamentation (*Subulicystidium, Hyphodontia gossypina, Trechispora* spp.) and basidia with six sterigmata (*Sistotremastrum*) (Keller, 1985; G. Langer, 1994; K.-H. Larsson, 1994, 2001; E. Langer, 2002; K.-H. Larsson *et al*., 2004). K.-H. Larsson *et al*. (2004) stated that there are no obvious anatomical, physiological or ecological characters that unite this group. The occurrence of *Hyphodontia gossypina* in the trechisporoid clade is surprising because most species of *Hyphodontia* occur in the hymenochaetoid clade (see below). Based on cystidial morphology, E. Langer (2002) predicted that several other species of *Hyphodontia* will eventually be placed in the trechisporoid clade. One isolate in this study labelled '*Trechispora farinacea*' (HHB 9150) is placed in the euagarics clade (Fig. 4, Table 3). There are three other isolates of *T. farinacea* clustered in the trechisporoid clade, indicating that the isolate in the euagarics clade is mislabelled.

4. Hymenochaetoid clade

The hymenochaetoid clade includes the Hymenochaetaceae, several groups of resupinate and poroid fungi that have traditionally been classified in the Corticiaceae and

Polyporaceae *sensu* Donk (1964), and possibly certain pileate-stipitate forms that have been classified in the Tricholomataceae (*Cantharellopsis*, *Omphalina, Rickenella*) and Podoscyphaceae or Corticiacae (*Cotylidia*) (Reid, 1965; Talbot, 1973; Eriksson & Ryvarden, 1975; Singer, 1986; Hibbett & Thorn, 2001; Moncalvo *et al*., 2002; Redhead *et al*., 2002). The hymenochaetoid clade is weakly supported in both the core dataset analysis (bootstrap = 65%) and the analysis of the full dataset (bootstrap < 50%, Figs 1, 4), and a previous analysis of nuc-ssu rDNA alone failed to support monophyly of the group (Kim & Jung, 2000). Nevertheless, it received moderate support in the analysis of K.-H. Larsson *et al*. (2004, bootstrap = 77–86%), and strong support in the four-region analyses of Binder & Hibbett (2002, bootstrap = 95–98%), albeit with a much reduced sample of taxa.

The Hymenochaetaceae has long been regarded as a natural group with several unifying features (Oberwinkler, 1977), including the xanthochroic reaction (blackening in KOH), absence of clamp connections, production of a white rot and presence of setae in many species. The close relationship between the Hymenochaetaceae and taxa that lack this combination of features is surprising. Nevertheless, almost all the species of the hymenochaetoid clade investigated have imperforate parenthesomes, which is consistent with their grouping based on rDNA sequences (Traquair & McKeen, 1978; Moore, 1980, 1985; E. Langer & Oberwinkler, 1993; Müller *et al*., 2000; Hibbett & Thorn, 2001). One other species of the hymenochaetoid clade, *Coltricia perennis*, was reported to have perforate parenthesomes (Moore, 1980) but was later shown to have imperforate parenthesomes (Müller *et al*., 2000).

The one member of the hymenochaetoid clade that has been demonstrated to have perforate parenthesomes is *Hyphoderma praetermissum* (Hallenberg, 1990; E. Langer & Oberwinkler, 1993). K.-H. Larsson *et al*. (2004) showed that *H. praetermissum* and *H. guttuliferum* are in the hymenochaetoid clade (however, their analysis also showed that other *Hyphoderma* spp. are in the polyporoid clade, see below). In contrast, the analysis of E. Langer (2002) suggested that *H. praetermissum* is outside of the hymenochaetoid clade and is the sister group of *Resinicium bicolor*. These results may be a consequence of the high weight given to parenthesome type in the combined analysis of molecular and morphological characters by E. Langer (2002). The analysis of K.-H. Larsson *et al*. (2004) and the present study suggest that *Resinicium* is in the hymenochaetoid clade (Fig. 4, Table 3). This study included one isolate labelled '*H. praetermissum*' (L-16187) that was placed in the athelioid clade; this is almost certainly a mislabelled isolate (Fig. 4, Table 3).

There are numerous resupinate forms within the Hymenochaetaceae. Most are in *Hymenochaete*, which is traditionally limited to taxa with a smooth hymenophore. Wagner & Fischer (2002*a*) showed that *Hymenochaete* is paraphyletic, and they suggested that *Hydnochaete duportii* and *H. japonica* (resupinate forms with hydnoid hymenophores) should be transferred to *Hymenochaete*, along with *Stipitochaete damaecornis* (pileate-stipitate with a smooth hymenophore), *Cyclomyces fuscus*, and *C. tabacinus* (pileate with a concentrically lamellate hymenophore). They also demonstrated that *Hymenochaete tabacina* is distantly related to other species of *Hymenochaete*, and they erected the segregate genus *Pseudochaete* to accommodate it. Results of the present study suggest that the resupinate species *Hymenochaete corrugata* and *Hydnochaete olivacea* are closely related to *P. tabacina*, and are therefore candidates for transfer to *Pseudochaete* (Fig. 4). Resupinate fruiting bodies also occur in other genera of Hymenochaetaceae (e.g. *Phellinus*, *Fuscoporia* and *Asterodon*), which indicates there have been numerous transformations between pileate and resupinate fruiting body forms in the Hymenochaetaceae, as described by Wagner & Fischer (2002*a*, *b*).

The paraphyletic assemblage of 'non-Hymenochaetaceae' in the hymenochaetoid clade is dominated by resupinate forms, including *Hyphodontia* (by far the largest genus, with approximately 64 species; Kirk *et al*., 2001), *Basidioradulum*, *Fibricium*, *Hyphoderma* pro parte, *Repetobasidium*, *Schizopora*, *Sphaerobasidium*, *Subulicium* and *Tubulicrinis* (Fig. 4, Table 3). *Hyphodontia* and related taxa have been studied in detail using molecular and morphological approaches by E. Langer (1994, 1998, 2002) and E. Langer & Oberwinkler (1993). Most of the sequences of these taxa in this analysis were published by E. Langer (1998, 2002). Two sequences of *Hyphodontia alutaria* are included in this analysis. One isolate (GEL4553) is nested in a clade with *H. pallidula* and *Schizopora flavipora*, whereas the other (GEL2071) is grouped with *Resinicium bicolor* (FP-135104-Sp.). Both clades receive strong support (Fig. 4). *Hyphodontia alutaria* and *H. pallidula* are morphologically very similar (Eriksson & Ryvarden, 1976), suggesting that isolate GEL2071 is mislabelled.

There is considerable variation in cystidia in these groups, including variation in position (tramal vs. hymenial), shape (tubular, capitate, rooted, etc.), and presence or absence of crystalline incrustation (E. Langer, 1994). Cladistic analyses of morphological and molecular characters (E. Langer, 1994, 1998, 2002) suggested that *Hyphodontia* is not monophyletic and that cystidial morphology can provide clues to relationships. The groups recognised by E. Langer (2002) are not resolved as monophyletic in this analysis (Fig. 4), suggesting that there may be more homoplasy in the evolution of anatomical features than previously realised.

One noteworthy group in the hymenochaetoid clade is that containing *Repetobasidium mirificum* and *Sphaerobasidium minutum* (the latter represented by a sequence from E. Langer, 2002). *Repetobasidium* is distinguished by the production of 'repeating' basidia, which arise from inside the base of pre-existing spent basidia (Eriksson *et al*., 1981). The results of the present study support suggestions by Eriksson *et al*. (1981, 1984) that *Sphaerobasidium* and *Repetobasidium* are closely related, which were based on the shape of the basidia and the shared presence of capitate cystidia that are encrusted by oily exudates.

Non-resupinate forms in the basal part of the hymenochaetoid clade in this study include *Trichaptum* and *Oxyporus*, which have been included in several studies using different isolates and molecular regions (Hibbett & Donoghue, 1995; E. Langer, 2002; K.-H. Larsson *et al*., 2004; Wagner & Fischer, 2002*b*). The giant polypore of the Pacific Northwest

of the USA, *Bridgeoporus nobilissimus*, has also been shown to be a member of this group based on mt-ssu rDNA sequences (Redberg *et al*., 2003). Perhaps the most surprising taxa to be placed in the hymenochaetoid clade are certain minute agarics (*Omphalina* pro parte, *Rickenella*, *Cantharellopsis*) and stipitate stereoid forms (*Cotylidia*). Analyses by Moncalvo *et al*. (2002) and Redhead *et al*. (2002) group these taxa with representatives of the hymenochaetoid clade, but with weak bootstrap support (60–68%). Nevertheless, K.-H. Larsson *et al*. (2004) included a sequence of *Rickenella fibula*, which was also placed in the hymenochaetoid clade, with moderate support (bootstrap = 77–86%).

Many members of the hymenochaetoid clade fruit on substantial woody substrates, produce a vigorous white rot, and act as saprotrophs or parasites of woody plants, including timber pathogens (e.g. *Phellinus weirii*, which causes laminated root rot) and the causal agent of the 'black measles' grapevine disease (*Fomitoporia punctata*; Larignon & Dubos, 1997). The pileate-stipitate polypore *Coltricia perennis* fruits on soil and has been reported to form ectomycorrhizae (Danielson, 1984). We can only guess at the nutritional mode of many of the resupinate forms, however, especially those that produce ephemeral fruiting bodies on well-decayed wood (e.g. *Repetobasidium mirificum*) (Eriksson *et al*., 1981). Another ecologically enigmatic member of the hymenochaetoid clade is *Bridgeoporus nobilissimus*, which is associated with a brown rot but cannot be cultivated from spores (Burdsall *et al*., 1996; Redberg *et al*., 2003). The agaricoid and stipitate stereoid forms are associated with mosses and liverworts, indicating yet another nutritional mode in this clade (Redhead *et al*., 2002). Finally, the resupinate forms *Hyphoderma praetermissum* and *H. guttuliferum* are reported to trap and kill nematodes by means of adhesive stephanocysts (Tzean & Liou, 1993).

5. Polyporoid clade

The polyporoid clade contains one of the major concentrations of resupinate Homobasidiomycetes, including true corticioid forms (those with smooth hymenophores), as well as resupinate polypores that have previously been classified in *Poria s. lat*. Other taxa in the polyporoid clade include pileate polypores, agarics (*Lentinus*, *Panus*), stipitate stereoid forms (*Podoscypha*) and the 'cauliflower fungus' *Sparassis*. Members of the group are ecologically important as wood decayers and timber pathogens. There are no documented mycorrhizal species.

The monophyly of the polyporoid clade is controversial. Several single-gene analyses have suggested that the group is polyphyletic or paraphyletic, including studies based on nuc-lsu rDNA (Hibbett & Vilgalys, 1993; E. Langer, 2002; K.-H. Larsson *et al*., 2004), nuc-ssu rDNA (Kim & Jung, 2000) and mt-ssu rDNA (Hibbett & Donoghue, 1995). Nevertheless, in the four-region analyses of Binder & Hibbett (2002) and the present study (Fig. 1) the group has consistently been resolved as monophyletic. In analyses of the full dataset in the present study, the polyporoid clade is either monophyletic or paraphyletic. In the latter case, the trechisporoid clade is nested within the polyporoid clade (Figs 3, 4).

Numerous subgroups have been resolved within the polyporoid clade and have been given informal and Linnaean names (Hibbett & Donoghue, 1995; Boidin *et al*., 1998; Kim & Jung, 2000; Hibbett & Donoghue, 2001; Lim, 2001; E. Langer, 2002; K.-H. Larsson *et al*., 2004; de Koker *et al*., 2003). The polyporoid clade is here divided into three main groups, the core polyporoid clade, *Antrodia* clade and phlebioid clade. Relationships among these groups are not well resolved, and some 'residual' taxa are not assigned to any group. The following discussion emphasises three suites of characters that have been important in polypore taxonomy: decay mode (white rot vs. brown rot), mating system (bipolar vs. tetrapolar), and hyphal system (mono-, di- or trimitic construction).

The core polyporoid clade is equivalent to a clade that Hibbett & Donoghue (1995) recognised based on mt-ssu rDNA sequences, which they called "group 1" (also see Hibbett & Donoghue, 2001; Binder & Hibbett, 2002). It is also equivalent to the "polyporoid clade" *sensu* K.-H. Larsson *et al*. (2004), the Polyporaceae *sensu* Kim & Jung (2000) and the "*Trametes* group" of Lim (2001). The clades "polyporoid 14" and "poroid-dendrotheloid 24" of E. Langer (2002) are also in this group, as are the Perenniporiales and Trametales *sensu* Boidin *et al*. (1998). The core polyporoid clade is strongly supported in the analysis of the core dataset (bootstrap = 95%, Fig. 1), where it is represented by 16 species, but it is weakly supported in the analysis of the full dataset, where it is represented by 29 species (Fig. 4).

Most taxa in the core polyporoid clade produce a white rot, are dimitic or trimitic, and have a tetrapolar mating system (Gilbertson & Ryvarden, 1986, 1987; Hibbett & Donoghue, 1995, 2001; Fig. 4). Apparent exceptions include *Diplomitoporus lindbladii*, which is bipolar, and *Wolfiporia cocos*, which produces a brown rot (Gilbertson & Ryvarden, 1986, 1987). However, the analysis of Kim & Jung (2000) suggested that *Wolfiporia cocos* is not in the core polyporoid clade, but rather is closely related to *Laetiporus sulphureus* and *Phaeolus schweinitzii* (*Cantharellus tubaeformis* is also in this group in their analysis, which is surely an artefact). *Wolfiporia cocos*, *L. sulphureus* and *P. schweinitzii* are united by the production of a brown rot and the habit of growing as saprotrophs or pathogens on the roots and bases of living trees (Gilbertson & Ryvarden, 1986, 1987), which suggests that they may be closely related. The isolate of '*W. cocos*' in this analysis is strongly supported as a member of the polyporoid clade (Fig. 1), however, and it might be mislabelled. Thus, the placement of *Wolfiporia cocos* needs to be tested with additional isolates.

In the analysis of the full dataset, *Sparassis spathulata* and *S. brevipes* are nested within the core polyporoid clade (Fig. 4). This result contradicts the results of the analysis of the core dataset (Fig. 1), which groups *Sparassis* and *Laetiporus* (Fig. 1), as well as a multi-gene analysis (mt-rDNA, nuc-rDNA and RNA polymerase II; Wang *et al*., 2004), which groups *Sparassis*, *Phaeolus* and *Laetiporus*. *Sparassis* spp. produce a brown rot and form fruiting bodies at the bases of living trees, as do *Phaeolus* and *Laetiporus* (and *Wolfiporia*). Therefore, the placement of *Sparassis* in the analysis of the core dataset (Fig. 1) is probably correct. Another problematical result in the core polyporoid clade concerns the isolate labelled '*Gloeophyllum trabeum*', which is nested with three isolates of *Ganoderma* spp. (Fig. 4). *Gloeophyllum trabeum* has a bipolar mating system, dimitic construction, brown context, and

produces a brown rot, all of which justify its placement in *Gloeophyllum* (Gilbertson & Ryvarden, 1986). It is likely that the '*G. trabeum*' isolate included here is actually a *Ganoderma* that has been mislabelled. Another incongruous taxon in this clade is *Physalacria inflata*, which produces minute, capitate, monomitic fruiting bodies (Singer, 1986). There are no obvious characters that would support its strongly supported placement here as the sister group of *Wolfiporia cocos* (Figs 1, 4), which should be confirmed with additional isolates and genes.

Resupinate forms in the core polyporoid clade include polypores (*Diplomitoporus lindbladii*, *Grammothele fuligo*, *Junghuhnia subundata*, *Perenniporia medulla-panis* and *Wolfiporia cocos*) and corticioid forms (*Dendrodontia* sp. and *Dentocorticium sulphurellum*). *Dendrodontia* sp. and *Dentocorticium sulphurellum* are strongly supported as sister taxa (Fig. 4), which is consistent with suggestions that *Dendrodontia* and *Dentocorticium* are closely related (Boidin & Gilles, 1998; Fig. 4). *Dentocorticium sulphurellum* is dimitic with skeletal hyphae and has dendrohyphidia (Larsen & Gilbertson, 1974). Hjortstam & Ryvarden (1980*a*, *b*) suggested that it resembles *Scytinostroma*, but that is in the russuloid clade (see below).

Non-resupinate forms in the core polyporoid clade include Polyporaceae (e.g. *Polyporus* spp., *Pycnoporus cinnabarinus, Lenzites betulina*, *Fomes fomentarius*), Ganodermataceae, and *Lentinus s. str*. A clade containing the polypores *Tyromyces chioneus* (pileate) and *Skeletocutis amorpha* (resupinate to effused-reflexed) is resolved as the sister group of the core polyporoid clade (Fig. 4). This placement is weakly supported, but it is consistent with the possession of dimitic hyphal construction, tetrapolar mating system, and white rot in both *T. chioneus* and *S. amorpha* (Gilbertson & Ryvarden, 1987).

The term "*Antrodia* clade" was introduced by Hibbett & Donoghue (2001) for a group of 14 species that produce a brown rot (except *Grifola frondosa*, which produces a white rot) and have bipolar mating systems (as far as is known). The *Antrodia* clade contains several groups that have been recognised previously, including "group 6" of Hibbett & Donoghue (1995), the Fomitopsidaceae and Laetiporaceae *sensu* Kim & Jung (2000), the Fomitopsidales and Phaeolales *sensu* Boidin *et al*. (1998), the clade "polyporoid 15" of E. Langer (2002), and the "Brown rot group" of Lim (2001). In the present study, the *Antrodia* clade contains 26 species with support in the analysis of the full dataset. In the analysis of the core dataset, the entire *Antrodia* clade is again weakly supported (bootstrap = 65%), but the node above *Antrodia carbonica* (the sister group to the rest of the clade) is strongly supported (bootstrap = 97%; Fig. 1).

At least two species in the *Antrodia* clade produce a white rot including *Climacocystis* sp. and *Grifola frondosa* (Gilbertson & Ryvarden, 1986). The apparent reversals to white rot in these taxa suggests that their brown rot precursors may have retained the genes for lignin-degrading enzymes (Hibbett & Donoghue, 2001). The white rot polypore *Ischnoderma benzoinum* is placed in the *Antrodia* clade in some topologies, but in others it is placed among other white rot species in the 'residual' polypores (Fig. 4; see below). The latter placement suggests a more parsimonious scenario for the evolution of decay modes.

Six species in the *Antrodia* clade are reported to be tetrapolar, including *Amylocystis lapponica*, *Climacocystis* sp., *Dacryobolus sudans*, *Parmastomyces transmutans*, *Oligoporus balsameus* and *O. caesius* (Gilbertson & Ryvarden, 1986, 1987; Nakasone, 1990*a*). The mingled distribution of bipolar and tetrapolar mating systems in the *Antrodia* clade (Fig. 4) suggests that mating loci in this group are subject to rearrangements or 'self-compatible' mutations that can interconvert bipolar and tetrapolar systems (Hibbett & Thorn, 2001).

Resupinate forms in the *Antrodia* clade include the polypores *Antrodia carbonica, A. xantha, Auriporia aurea, Parmastomyces transmutans*, and the corticioid forms *Dacryobolus sudans*, *Phlebia griseoflavescens* and an isolate labelled 'dendrotheloid *sp*.' from the work of E. Langer (2002). The placement of *P. griseoflavescens* away from other species of *Phlebia* in the phlebioid clade is striking, but Eriksson *et al*. (1981, p. 1122) indicated that it is "not a very typical member of the genus". Data on decay type would be useful to evaluate its placement, because other species of *Phlebia* are associated with a white rot (Nakasone, 1990*a*; Ginns & Lefebvre, 1993). Another potentially problematical taxon in the *Antrodia* clade is *Cyphella digitalis* (type species of the Cyphellaceae). There are no obvious characters that support this placement, which should be tested. Finally, the analysis of K.-H. Larsson *et al*. (2004) suggested that the stereoid fungus *Lopharia cinerescens* is in the core polyporoid clade, whereas the analysis of Kim & Jung (2000) suggested that *L. spadicea* is in the phlebioid clade. If both results are correct, then *Lopharia* is polyphyletic.

The delimitation of the phlebioid clade adopted here deviates slightly from that of K.-H. Larsson *et al*. (2004), who introduced the term. Here, it is based on the results of the analysis of the core dataset, which recovered a strongly supported clade (bootstrap = 91%) that contains 12 species, including taxa that Hibbett & Donoghue (1995, 2001) identified as "group 5" or the "*Phlebia* clade". In the analysis of the full dataset, the phlebioid clade is a weakly supported group of 44 isolates, which is the least inclusive clade that contains all 12 species of the phlebioid clade resolved in the analysis of the core dataset (Figs 1, 4). The phlebioid clade overlaps with the Phanerochaetaceae and Steccherinaceae *sensu* Kim & Jung (2000), the Phanerochaetales and Phlebiales *sensu* Boidin *et al*. (1998), clades "phanerochaetoid 19.1" and "phlebioid 19.2" of E. Langer (2002), the "*Irpex* group", "*Phanerochaete* group", and "*Phlebia* group" of Lim (2001), and clades A-D (clade A was called the "Phanerochaete core group") of de Koker *et al*. (2003).

Members of the phlebioid clade are distinguished by the combination (in most taxa) of a monomitic construction, bipolar mating system and production of a white rot (Hibbett & Donoghue, 2001; K.-H. Larsson *et al*., 2004). Taxa that have been demonstrated to have bipolar mating systems include *Bjerkandera adusta, Ceraceomyces serpens, Gelatoporia pannocincta, Lopharia spadicea, Phlebia centrifuga, P. radiata, P. rufa, P. subochracea, P. subserialis* and *P. tremellosa* (Domanski, 1972; Gilbertson & Ryvarden, 1986; Nakasone,

1990*a*; Ginns & Lefebvre, 1993). However, *Phlebia chrysocreas* has been listed as "possibly tetrapolar", and *Irpex lacteus, Phanerochaete chrysosporium* and *P. sordida* have been suggested to be homothallic (Nakasone, 1990*a*: 252). Hyphal anatomy is also variable in the phlebioid clade; *Lopharia spadicea* and *Rigidoporus vinctus*, which Kim & Jung (2000) showed to be in the phlebioid clade, are both dimitic with skeletal hyphae (Eriksson & Ryvarden, 1976; Gilbertson & Ryvarden, 1987).

The phlebioid clade contains many resupinate taxa, including the large corticioid genera *Phanerochaete* (63 spp.) and *Phlebia* (50 spp., Kirk *et al*., 2001), neither of which is resolved as monophyletic (Fig. 4). Other corticioid taxa include *Byssomerulius* sp., *Ceraceomyces* spp., *Gloeoporus taxicola*, *Mycoacia* spp., *Phlebiopsis gigantea*, *Pulcherricium caeruleum* and *Scopuloides hydnoides* (Fig. 4, Table 3). Eriksson and colleagues (Eriksson & Ryvarden, 1973, 1976; Eriksson *et al*., 1978, 1981, 1984) commented on similarities among many of these genera and *Phlebia* and *Phanerochaete*, particularly with regard to hymenial anatomy (with basidia forming a dense palisade).

One potentially problematic isolate in the phlebioid clade is that of *Lindtneria trachyspora*, which is a resupinate form. *Lindtneria trachyspora* was expected to cluster with the false truffle *Stephanospora caroticolor*, but in this analysis *S. caroticolor* is placed in the athelioid clade (see below; Fig. 4). *Lindtneria trachyspora* and *S. caroticolor* share a characteristic coarse ornamentation of the spores (Oberwinkler & Horak, 1979; Jülich, 1981) and an uncommon chemical compound in fungi, 2-chlor-4-nitrophenol (Hellwig: 1999: 110). Moreover, analyses with additional *L. trachyspora* isolates and the *S. caroticolor* sequence from the present study (K.-H. Larsson, unpublished) suggest that *L. trachyspora* is closely related to *S. caroticolor*, as well as two species of the resupinate genus *Cristinia*. All three genera have a cyanophilous granulation in immature basidia and strongly cyanophilous spore walls. Based on these characters, Eriksson & Ryvarden (1975) suggested that *Cristinia* and *Lindtneria* might be related. Thus, it is likely that the isolate of '*L. trachyspora*' used in this study is mislabelled.

Other problematical results in the phlebioid clade concern the isolates labelled *Athelia arachnoidea, A. epiphylla, Sistotrema muscicola* and *Peniophora* sp., which were expected to be placed in the athelioid, cantharelloid and russuloid clades (see those sections). It is likely that all four are mislabelled.

Resupinate polypores in the phlebioid clade include *Ceriporia* spp., *Ceriporiopsis subvermispora* and *Gelatoporia pannocincta* (Fig. 4). Pileate polypores include *Bjerkandera adusta*, *Climacodon septentrionale*, *Hapalopilus nidulans* and *Rigidoporus vinctus* (Fig. 4). In addition, Kim & Jung (2000) showed that *Oxyporus latemarginatus* is in the phlebioid clade and is closely related to *Rigidoporus vinctus*. Other studies have suggested that *Oxyporus populinus* is in the hymenochaetoid clade and is closely related to *Bridgeoporus nobilissimus*, which was formerly placed in *Rigidoporus* (Fig. 4; Hibbett & Donoghue, 1995; Burdsall *et al*., 1996; Wagner & Fischer, 2002*b*; Redberg *et al*., 2003). Collectively, these results suggest that *Oxyporus* and *Rigidoporus s. lat*. are polyphyletic, with some species in the polyporoid clade and others in the hymenochaetoid clade.

Twenty-three 'residual' species in the polyporoid clade could not be placed in the core polyporoid clade, *Antrodia* clade or phlebioid clade (Fig. 4). Resupinate forms among these taxa include the corticioid forms *Hyphoderma* spp., *Hypochnicium* spp., *Candelabrochaete africana*, *Phanerochaete sanguinea*, *Phlebia bresadolae*, and *P. queletii*, the hydnoid fungus *Spongipellis pachyodon*, and the polypores *Antrodiella romellii*, *Ceriporiopsis gilvescens*, *Junghuhnia nitida* and *Physisporinus sanguinolentus* (Fig. 4). Pileate taxa include polypores (*Abortiporus biennis, Albatrellus syringae, Meripilus giganteus*), agarics (*Panus rudis*) and stipitate stereoid forms (*Podoscypha petalodes*). These taxa overlap with the Steccherinaceae and Podoscyphaceae *sensu* Kim & Jung (2000), the Hyphodermatales and Podoscyphales *sensu* Boidin *et al*. (1998), and clades "hyphodermoid 20–23", which formed a paraphyletic assemblage in the analysis of E. Langer (2002). In the present analysis, the residual taxa and phlebioid clade form a weakly supported monophyletic group (Fig. 4) that corresponds to the phlebioid clade *sensu* K.-H. Larsson *et al*. (2004).

The Podoscyphaceae of Kim & Jung (2000) is a weakly supported group (bootstrap = 56%) that includes *Cymatoderma caperatum* (a stipitate stereoid form), along with *Podoscypha petalodes* and *Panus rudis*. Boidin *et al*. (1998) also found a close relationship between *Podoscypha* and *Cymatoderma*, as well as *Hypochnicium cystidiatum*. An isolate identified as *C. caperatum* is included in the present analysis, but it is placed in the russuloid clade (Fig. 4). Based on the results of Kim & Jung (2000) and Boidin *et al*. (1998), it is likely that the isolate of '*C. caperatum*' in this study is mislabelled.

With additional data, it is possible that some of the residual taxa will be placed in the phlebioid or core polyporoid clades, but probably not the *Antrodia* clade, which includes mostly brown rot taxa. For example, *Hyphoderma* spp., which are monomitic corticioid forms that have bipolar mating systems, may be correctly placed in the phlebioid clade, as suggested by K.-H. Larsson *et al*. (2004). The same could be said for *Spongipellis pachyodon*, which is also monomitic and bipolar (Gilbertson & Ryvarden, 1987). In contrast, *Junghuhnia nitida* and *Panus rudis* are dimitic and have tetrapolar mating systems (Gilbertson & Ryvarden, 1986; Johnson & Methven, 1994, for *P. conchatus*), and *Hypochncium* spp. are monomitic with tetrapolar mating systems (Nakasone, 1990*a*, data on mating systems for *Hypochnicium* spp. were not taken from the same species sampled in the present study). The heterogeneity in anatomical and genetic characters in the residual polypores and the low bootstrap support for the node uniting them with the phlebioid clade (Figs 1, 4) are the reasons why these species are not classified in the phlebioid clade in this study.

6. *Gloeophyllum* clade

Gloeophyllum sepiarium was placed as an isolated species in analyses of homobasidiomycete phylogeny by Hibbett & Donoghue (1995), Hibbett *et al*. (1997) and Binder & Hibbett (2002), and the recent *Dictionary of the Fungi 9th edn*. lists *Gloeophyllum* as the sole genus in the Gloeophyllaceae (Kirk

et al., 2001). Several recent studies have identified close relatives of *Gloeophyllum*, however. Thorn *et al*. (2000) performed analyses of nuc-lsu rDNA sequences, which showed that *G. sepiarium* is in a clade with *Heliocybe sulcata*, *Neolentinus lepideus*, *N. kauffmanii* and *N. dactyloides* (bootstrap = 71%). Monophyly of these taxa was confirmed in a combined analysis of nuc-ssu and mt-ssu rDNA sequences by Hibbett & Donoghue (2001; *G. sepiarium, N. lepideus, H. sulcata*; bootstrap = 97%). Analyses of nuc-ssu rDNA sequences by Kim & Jung (2000) suggested that *G. sepiarium* is closely related to *Donkioporia expansa*, *Boreostereum radiatum* and *Veluticeps berkeleyi*, but with weak (52%) bootstrap support. In addition, the analysis of Kim & Jung (2000) placed *Columnocystis abietina* in the polyporoid clade, which contradicts the suggestion that *Columnocystis* and *Veluticeps* are synonyms (Hjortstam & Tellería, 1990; Nakasone, 1990*b*). Lim (2001) performed an analysis of nuc-ssu rDNA sequences that provided stronger support (bootstrap = 86%) for the monophyly of *G. sepiarium*, *V. berkeleyi* and *B. radiatum* (using the same sequences as in Kim & Jung, 2001), but the analysis did not include *D. expansa*. In the present study, the *Gloeophyllum* clade includes *G. sepiarium, G. odoratum, N. dactyloides* and *V. berkeleyi* (Fig. 4). Bootstrap support is weak (54%) but the resolution of this clade is consistent with the results of the studies cited previously.

Members of the *Gloeophyllum* clade have diverse fruiting bodies, including pileate-sessile poroid to lamellate forms (*Gloeophyllum*), pileate-stipitate lentinoid agarics (*Heliocybe*, *Neolentinus*), resupinate polypores (*Donkioporia*) and resupinate to effused-reflexed stereoid forms (*Boreostereum radiatum, Veluticeps berkeleyi*). The unifying features of the group are ecological and anatomical. All members of the clade are wood decayers and are either dimitic with skeletal hyphae, or trimitic (Redhead & Ginns, 1985; Gilbertson & Ryvarden, 1986; Chamuris, 1988; Nakasone, 1990*b*). Gilbertson & Ryvarden (1986) commented on the anatomical similarity between *Gloeophyllum* and *Donkioporia*.

Decay chemistries are variable in the *Gloeophyllum* clade. Most members of this group have been shown to produce a brown rot, including *Gloeophyllum* spp., *Heliocybe sulcata, Neolentinus* spp. and *Veluticeps berkeleyi* (Martin & Gilbertson, 1973; Redhead & Ginns, 1985; Gilbertson & Ryvarden, 1986; Nakasone, 1990*a*, *b*). The exceptions are *Donkioporia expansa* and *Boreostereum radiatum*, which are reported to produce a white rot (Gilbertson & Ryvarden, 1986; Nakasone, 1990*a*). The mode of decay in *Boreostereum radiatum* is somewhat ambiguous, however. Substrates associated with fruiting bodies have been found to show either brown rot or white rot, and cultural studies for the presence of extracellular oxidases have yielded conflicting results (Chamuris, 1988; Nakasone, 1990*a*).

Mating systems are also variable in the *Gloeophyllum* clade. *Neolentinus* and *Gloeophyllum* are reported to have bipolar mating systems (Redhead & Ginns, 1985; Gilbertson & Ryvarden, 1986), whereas *Veluticeps* has a tetrapolar mating system (Martin & Gilbertson, 1973), which is very unusual for a brown-rot fungus (Ryvarden, 1991), and *Boreostereum* has been presumed to be homothallic (Chamuris, 1988; Nakasone, 1990*a*). Thus, the *Gloeophyllum* clade provides an excellent system in which to study transformations between different mating systems and decay modes (as well as fruiting body forms) in closely related taxa.

7. Thelephoroid clade

This clade is equivalent to the order Thelephorales, which contains two families: Thelephoraceae, with angular and pigmented spores, and Bankeraceae, with hyaline ornamented spores (Stalpers, 1993). Donk (1964) suggested that the Bankeraceae and Thelephoraceae are not closely related, but later authors have united them (Jülich, 1981; Stalpers, 1993; Kirk *et al*., 2001). Analyses by K.-H. Larsson *et al*. (2004) and Binder & Hibbett (2002) found moderately strong support for the monophyly of the Thelephoraceae plus Bankeraceae. The present study includes two species of Bankeraceae (*Bankera fuligineoalba* and *Phellodon tomentosus*) and ten species of Thelephoraceae, which are strongly supported as a clade (bootstrap = 97%, Fig. 4). The Bankeraceae appears to be nested within the Thelephoraceae, but the basal nodes in the thelephoroid clade are not strongly resolved (Fig. 4). These results corroborate those of K.-H. Larsson *et al*. (2004), who also studied multiple exemplars of Bankeraceae and Thelephoraceae.

The thelephoroid clade contains resupinate, clavarioid and pileate forms, with smooth, hydnoid or poroid hymenophores. Taxonomy of the resupinate forms has been studied by Kõljalg and colleagues (Larsen, 1968, 1974; Kõljalg, 1996; Kõljalg *et al*., 2000, 2001, 2002), using morphological and molecular approaches. Resupinate taxa in this analysis include *Tomentella* and *Pseudotomentella*. The pattern of relationships in Fig. 4 suggests that there have been multiple transformations between resupinate and erect forms in the thelephoroid clade. K.-H. Larsson *et al*. (2004) sampled several resupinate Thelephoraceae that were not included in this study, including *Tomentellopsis echinospora* and *Amaurodon viridis*.

Non-resupinate Thelephorales fruit on soil and have been regarded as ectomycorrhizal, whereas resupinate Thelephorales typically fruit on wood and have been interpreted as saprotrophic (e.g. Stalpers, 1993). However, molecular studies (Bruns *et al*., 1998; Taylor & Bruns, 1999; Kõljalg *et al*., 2000, 2001, 2002) have demonstrated that many (perhaps all?) resupinate Thelephorales are ectomycorrhizal, often forming a dominant component of the mycorrhizal community.

8. Corticioid clade

This is a recently discovered clade (Boidin *et al*., 1998; K.-H. Larsson *et al*., 2004) that was not included in the overview of Homobasidiomycetes by Hibbett & Thorn (2001). One species in this group, *Dendrocorticium roseocarneum*, was included in the analysis of Binder & Hibbett (2002; also see Hibbett & Donoghue, 2001), where it was placed (without bootstrap support) as the sister group of the rest of the Homobasidiomycetes. Other taxa that are probably placed in the corticioid clade based on this and other studies include *Corticium roseum, Cytidia salcina, Dendrocorticium polygonioides, Dendrothele maculata*, *Duportella tristicula*, *Erythricium laetum, Galzinia incrustans*, *Laetisaria fuciformis,*

Limonomyces roseipellis, Marchandiomyces aurantiacus (teleomorph *Marchandiobasidium aurantiacum*; Diederich *et al*., 2003), *M. corallinus*, *Punctularia strigoso-zonata*, *Vuilleminia comedens* and *V. macrospora* (Boidin *et al*., 1998; Hallenberg & Parmasto, 1998; Lim, 2001; Sikaroodi *et al*., 2001; Hibbett & Binder, 2002; E. Langer, 2002; K.-H. Larsson *et al*., 2004; V. Andjic, unpublished; P. DePriest *et al*., unpublished; Table 3). Members of the corticioid clade have been classified as the Vuilleminiales (Boidin *et al*., 1998; E. Langer, 2002). K.-H. Larsson *et al*. (2004) showed that *Dendrothele maculata* is a member of the corticioid clade, but they also cited unpublished analyses that suggest that *Dendrothele* is highly polyphyletic. In the present study, *D. acerina* and *D. griseocana* are placed in the euagarics clade, *D. candida* is placed in the russuloid clade, and an isolate labelled "dendrothelioid" from the study of E. Langer (2002) was placed in the polyporoid clade (Fig. 4).

The delimitation of the corticioid clade proposed here (Table 3) conflicts somewhat with the results of Boidin *et al*. (1998) and P. DePriest *et al*. (unpublished). The ITS analysis of Boidin *et al*. (1998) suggested that (1) *Erythricium laetum* is closely related to *Athelia decipiens* (athelioid clade, contra K.-H. Larsson *et al*., 2004) and (2) *Duportella tristicula* and other *Duportella* species are nested in *Peniophora* (russuloid clade, contra Hallenberg & Parmasto, 1998). However, the analysis of Boidin *et al*. (1998) did support monophyly of a clade containing *Corticium, Dendrocorticium, Punctularia* and *Vuilleminia*, which is consistent with the present analysis and other studies cited above. Analyses by P. DePriest *et al*. (unpublished) based on nuclear rDNA sequences suggested that *Rhizoctonia zeae* and its teleomorph *Waitea circinata* (Ceratobasidiales) and *Tretopileus sphaerophorus* (mitosporic fungi) are in the corticioid clade. *Waitea circinata* is reported to have pinkish white basidiocarps and a probasidial stage (Roberts, 2003), which are also found in other taxa in the corticioid clade (see below). However, a study by Bruns *et al*. (1998) suggests that *Waitea circinata* is in the athelioid clade (see below), and evidence from multiple studies that were discussed previously suggests that other taxa of the Ceratobasidiales are in the cantharelloid clade. At this time, the placements of *Waitea circinata* and *Tretopileus sphaerophorus* must be regarded as unresolved.

The sample of taxa in the corticioid clade in this study largely overlaps with that in the study of K.-H. Larsson *et al*. (2004). In both analyses, the group is moderately to strongly supported (bootstrap = 81% in this study, 93–96% in K.-H. Larsson *et al*., 2004). The higher-level position of the corticioid clade differs in this study and that of K.-H. Larsson *et al*. (2004), but in neither analysis is it placed as the sister group of the Homobasidiomycetes (as in the analysis of Binder & Hibbett, 2002). Diederich *et al*. (2003) showed that *Marchandiobasidium* has perforate parenthesomes, which is consistent with the view that the corticioid clade is not one of the basal clades of Homobasidiomycetes (contra Binder & Hibbett, 2002). In additon, *Corticium roseum* (as *Laeticorticium roseum*) and *C. boreoroseum* (as *Laeticorticium lundellii*) were also reported to have perforate parenthesomes (Keller, 1997).

There is no obvious synapomorphy for the corticioid clade. Most members of the group are resupinate, but *Punctularia strigoso-zonata* forms effused-reflexed fruiting bodies, *Cytidia salicina* forms fruiting bodies that are almost cupulate, and *Marchandiomyces* spp. are lichen-inhabiting asexual forms that produce sclerotia. Several taxa produce dendrohyphidia (branched hymenial hairs), including *Corticium roseum*, *Cytidia salicina*, *Dendrocorticium polygonioides*, *D. roseocarneum*, *Dendrothele maculata*, *Punctularia strigoso-zonata* and *Vuilleminia comedens*. In this analysis, the members of the corticioid clade that produce dendrohyphidia are strongly supported as a monophyletic group (Fig. 4), although that is not the case in the study of K.-H. Larsson *et al*. (2004). Another feature shared by some taxa in this group is the production of pink, red or orange pigments in the fruiting bodies, which occurs in *Corticium roseum*, *Cytidia salicina*, *Erythricium laetum*, *Galzinia incrustans* and *Marchandiomyces* spp. In addition, *Laetisaria fuciformis* and *Limonomyces roseipellis* produce characteristic pink-red hyphal masses on infected grasses, and *Punctularia strigoso-zonata* is reported to produce pink mycelial mats in culture (Nakasone, 1990*a*). The chemical nature of the pigments is not known.

The corticioid clade is ecologically diverse. Most species are apparently saprotrophic and are associated with a white rot, primarily of angiospermous wood (Eriksson & Ryvarden, 1975; Eriksson *et al*., 1981; Chamuris, 1988; Hjortstam *et al*., 1988*b*; Nakasone, 1990*a*; Ginns & Lefebrve, 1993; Wu & Chen, 1993). Several taxa produce fruiting bodies on attached branches and standing trunks (e.g. *Corticium roseum, Cytidia salicina, Dendrocorticium roseocarneum, Dendrothele maculata, Vuilleminia comedens*) and have anatomical features that have been interpreted as adaptations for xeric habitats, including the production of a catahymenium and delayed basidial maturation (Eriksson & Ryvarden; 1975, 1976; Eriksson *et al*., 1981; Chamuris, 1988; Hjortstam *et al*., 1988*b*). These features may allow the fruiting body to remain viable during periods of drought and rapidly produce basidiospores during brief intervals when moisture is available (Hallenberg & Parmasto, 1998). Other taxa in the corticioid clade do not inhabit exposed substrates. For example, Eriksson & Ryvarden (1975) reported that *Erythricium laetum* (which was sampled by K.-H. Larsson *et al*., 2004) occurs under moist conditions on decayed wood and branches of deciduous trees, dead leaves and wet soil. Similarly, *Galzinia incrustans* occurs on decayed wood in moist environments (Eriksson & Ryvarden, 1975).

Biotrophic nutrition also occurs in the corticioid clade. *Laetisaria fuciformis* (which was included in the core dataset analysis, but inadvertently excluded from the other analyses; Fig. 1) is a plant pathogen that causes 'red thread' disease of turfgrasses (Stalpers & Loerakker, 1982). Analyses by V. Andjic (unpublished) based on ITS sequences suggest that *L. fuciformis* is closely related to *Limonomyces roseipellis*, which causes a similar 'pink patch' disease of turfgrasses. An unusual ecological habit is found in *Marchandiomyces aurantiacus* and *M. corallinus*, which are parasites of corticolous or saxicolous (rock-inhabiting) lichens (Etayo & Diederich, 1996; Sikaroodi *et al*., 2001; Diederich *et al*., 2003). Finally, Burt (1926) reported that *Erythricium laetum* occurs on living

mosses (as well as wood), which suggests that it may also have the capacity for biotrophic nutrition.

9. Russuloid clade

The russuloid clade includes agaricoid forms, polypores, coral fungi, hydnoid fungi and many resupinate taxa. Most members of this group are saprotrophic, but there are also ectomycorrhizal species (Russulaceae, *Albatrellus* pro parte) and timber pathogens (*Heterobasidion, Echinodontium*). Some lignicolous species in the russuloid clade form symbiotic associations with insects, including woodwasps (associated with *Amylostereum*; Slippers *et al*., 2001) and bark beetles (associated with *Entomocorticium*; Hsiau, 1996; Klepzig *et al*., 2001). Many members of the russuloid clade have spores with amyloid walls or ornamentations and gloeoplerous hyphae and cystidia. Based on these characters, Donk (1964, 1971) suggested that there are relationships among many of the species now placed in this clade, and Oberwinkler (1977) grouped many of them in the order Russulales (also see Stalpers, 1996).

In the present study, the russuloid clade is represented by 85 isolates (82 species). The clade is weakly supported in the analysis of the full dataset, but strongly supported in the analysis of the core dataset (bootstrap = 90%, 23 species; Figs 1, 4). Groups within (or equivalent to) the russuloid clade that have been resolved in other molecular phylogenetic studies with a broad taxonomic focus include the Russulales, Hericiales, Lachnocladiales and Peniophorales *sensu* Boidin *et al*. (1998), the Stereaceae, Hericiaceae, and Amylostereaceae *sensu* Kim & Jung (2000), the clade "russuloid 12" of E. Langer (2002) and the "russuloid clade" and "peniophoroid clade" *sensu* Lim (2001). Several phylogenetic studies have focused on groups within the russuloid clade, including *Aleurodiscus s. lat*. and related taxa (Wu *et al*., 2001), *Stereum* and *Xylobolus* (Lim, 2001), *Peniophora* (Hallenberg & Parmasto, 1998), the *Gloeocystidiellum porosum-clavuligerum* complex (Larsson & Hallenberg, 2001), and the Russulaceae (S. L. Miller *et al*., 2001, 2002). Many mt-lsu rDNA, nuc-lsu rDNA, and ITS sequences of ectomycorrhizal Russulaceae have been analysed in ecological studies (e.g., Taylor & Bruns, 1997; Bruns *et al*., 1998; Bergemann & Miller, 2002).

By far the most thorough phylogenetic study of the russuloid clade as a whole is that of E. Larsson & K.-H. Larsson (2003), who studied relationships among 127 isolates that represent *c*. 120 species. The dataset emphasised resupinate taxa, many of which have been traditionally classified in *Gloeocystidiellum s. lat*. Based on analyses of nuc-lsu rDNA, 5.8S rDNA, and ITS sequences, E. Larsson & K.-H. Larsson (2003) divided the russuloid clade into 13 major clades, which were labelled using the notation convention adopted by Moncalvo *et al*. (2002; e.g. '/russulales'). The following discussion is organised according to the classification of E. Larsson & K.-H. Larsson (2003), which should be consulted for detailed information about relevant characters and prior taxonomy.

/stereales. This group contains lignicolous resupinate, discoid and effused-reflexed to pileate taxa that have been classified in the Stereaceae *s. str*. (*Stereum, Xylobolus*), *Aleurodiscus s. lat*. and its segregates (e.g. *Acanthophysium*), and *Gloeocystidiellum s. lat*. The latter is represented in this study only by *Gloeocystidiellum leucoxanthum*, but many other *Gloeocystidiellum* segregates were included in this group by E. Larsson & K.-H. Larsson (2003; e.g. *Boidinia*). The /stereales is moderately to strongly supported in this analysis (core dataset bootstrap = 100%, full dataset bootstrap = 79%), and was strongly supported by E. Larsson & K.-H. Larsson (2003; bootstrap = 97%), as well as Kim & Jung (2000; bootstrap = 93%).

/hericiaceae. This clade includes resupinate (*Dentipellis separans*), effused-reflexed (*Laxitextum bicolor*) and pileate (*Hericium* spp.) forms, all with spores that have amyloid echinulae (Stalpers, 1996). An isolate labelled as '*Cymatoderma caperatum*' appears in this clade in the present study, but that is most likely an artefact, as discussed previously (see above). In other respects, the results of the present study (Figs 1, 4) agree with those of E. Larsson & K.-H. Larsson (2003) for this clade.

/bondarzewiaceae and /amylostereaceae. There are minor differences between the results of the present study and that of E. Larsson & K.-H. Larsson (2003) with respect to these groups. The present study recovered a moderately supported (bootstrap = 88%) clade that includes the stereoid, effused-reflexed species *Amylostereum chailettii, A. laevigatum* and *Laurilia sulcata*, and the pileate, hydnoid form *Echinodontium tinctorium* (Fig. 4). These taxa all have incrusted cystidia, which is consistent with the view that they are closely related (Eriksson & Ryvarden, 1973; Gilbertson & Ryvarden, 1986; Chamuris, 1988). However, the study of E. Larsson & K.-H. Larsson (2003) grouped *Amylostereum* spp. with the coral fungus *Artomyces* (= *Clavicorona*) *pyxidatus* in the /amylostereaceae (bootstrap = 73%), and placed *L. sulcata* and *E. tinctorium* with the polypores *B. berkeleyi* and *H. annosum* in the /bondarzewiaceae (bootstrap = 78%). Here, *Bondarzewia* spp. and *H. annosum* form a paraphyletic group from which /albatrellus is derived (Fig. 4). In contrast, *Bondarzewia* and *Heterobasidion* were strongly supported (bootstrap = 91%) as monophyletic in the analysis of Bruns *et al*. (1998). Both cause white rot in the heartwood, roots, and bases of living trees, and *H. annosum* is a serious timber pathogen (Gilbertson & Ryvarden, 1986).

/albatrellus. The analysis of the full dataset recovered a strongly supported clade (bootstrap = 96%) that includes the pileate-stipitate polypores *Albatrellus* pro parte and *Polyporoletus sublividus* (*A. syringae* is in the polyporoid clade, however; Fig. 4). Some species of *Albatrellus* have amyloid spores and gloeoplerous hyphae (the latter are also found in *P. sublividus*), which is consistent with their placement in the russuloid clade, as suggested by Stalpers (1992).

The corticioid forms *Dendrothele candida* and *Xenasma rimicola* form a paraphyletic group at the base of the /albatrellus clade in this study (Fig. 4), but this placement is weakly supported and is not suggested by any obvious morphological characters. E. Larsson & K.-H. Larsson (2003) found that a similar species, *Pseudoxenasma verrucisporum* (which shares similarly ornamented spores and pleurobasidia), is in the russuloid clade, but could not identify its closest relatives (Eriksson *et al*., 1981; Hjortstam *et al*., 1988*b*; Stalpers, 1996). It is possible that *X. rimicola* and *P. verrucisporum* are closely related,

and it would be desirable to include them in the same analysis. There are no obvious characters that support the placement of *D. candida* as a close relative of *Albatrellus* and *Polyporoletus* (Fig. 4), although it also has amyloid spores (Lemke, 1964*b*, as *Aleurocorticium candidum*).

Another resupinate form that may be related to /albatrellus is *Byssoporia terrestris*, which was sampled by Bruns *et al.* (1998). *Byssoporia terrestris* has smooth inamyloid spores and no gloeoplerous system (Eriksson & Ryvarden, 1973, as *Byssocorticium terrestre*), which is unusual for a member of the russuloid clade. Nevertheless, it is reported to be ectomycorrhizal, as are *Albatrellus ovinus* and *A. fletti* (Kropp & Trappe, 1982; Gilbertson & Ryvarden, 1986; Agerer *et al.*, 1996). Other russuloid species of *Albatrellus* and *P. sublividus* may also be ectomycorrhizal, but this is controversial (Gilbertson & Ryvarden, 1986; Ginns, 1997; *Albatrellus syringae* in the polyporoid clade is thought to be lignicolous). Neither the present analysis or that of E. Larsson & K.-H. Larsson (2003) suggest that the russuloid species of *Albatrellus* are closely related to the Russulaceae (Figs 1, 4). Therefore, the *Albatrellus* group, including *B. terrestre* and *P. sublividus*, probably represents an independent origin of the ectomycorrhizal habit in the russuloid clade.

/aleurocystidiellum. The present study finds strong support (bootstrap = 100%) for the monophyly of *Aleurocystidiellum disciformis* and *A. subcruentatum*, which were segregated from *Aleurodiscus sensu lato* (Lemke, 1964*a*), but do not resolve their closest relatives with confidence (Fig. 4). These results mirror those of E. Larsson & K.-H. Larsson (2003).

/auriscalpiaceae. This weakly suported clade includes agaricoid (*Lentinellus* spp.) and hydnoid taxa (*Auriscalpium*, *Gloiodon*; Fig. 4). E. Larsson & K.-H. Larsson (2003) recovered a moderately supported clade (bootstrap = 86%) with the same genera represented by more species and isolates than in the present study, plus *Dentipratulum bialoviesense*. *Gloiodon* and *Dentipratulum* are resupinate or effused-reflexed, whereas the others are pileate. O. K. Miller (1971) found that *Lentinellus cochleatus* produces a coralloid fruiting body when cultured at low temperatures, which suggests that developmental programs in this clade may be quite labile.

/gloeocystidiellum I and /russulales. One of the most striking findings of E. Larsson & K.-H. Larsson (2003) is that the Russulaceae is nested within a clade of resupinate taxa traditionally classified in *Gloeocystidiellum s. lat*. The same result is obtained in the present study. Here, a clade equivalent to /gloeocystidiellum I (*G. porosum* and two unidentified isolates) is moderately supported as the sister group of /russulales (Fig. 4). The latter is strongly supported (bootstrap = 100%) and includes *Gloeocystidiellum aculeatum*, which agrees with the findings of E. Larsson & K.-H. Larsson (2003), who sampled additional resupinate taxa (*Gloeopeniophorella* spp., *Boidinia* spp.) that form a paraphyletic group in /russulales. It is remarkable that the Russulaceae, with its agaricoid, gasteroid and pleurotoid forms, is derived from simple corticioid forms. It remains an open question whether the switch to an ectomycorrhizal nutritional mode in Russulaceae (including pleurotoid forms, Henkel *et al.*, 2000) is either a cause or consequence of the shift from corticioid to pileate forms.

/gloeocystidiellum II. The clade /gloeocystidiellum II is here represented only by a single isolate of *G. clavuligerum*, whereas E. Larsson & K.-H. Larsson (2003) included five isolates representing *G. clavuligerum*, *G. bisporum* and *G. purpureum*. In both studies the closest relatives of /gloeocystidiellum II are not resolved with confidence (Fig. 4).

/peniophorales. In the present analysis, the /peniophorales clade includes resupinate taxa that have been classified in the Lachnocladiaceae (*Asterostroma*, *Dichostereum, Scytinostroma, Vararia*; Reid, 1965; Hallenberg, 1985) and Corticiaceae *s. lat*. (*Peniophora nuda*, *Amphinema byssoides* and *Coronicium alboglaucum*; Fig. 4). However, in the analysis of K.-H. Larsson *et al.* (2004), *Amphinema byssoides* is placed in the athelioid clade and *C. alboglaucum* is placed in the euagarics clade, suggesting that the positions of these taxa here could be artefacts.

Monophyly of the /peniophorales is weakly supported in the present study, but it was strongly supported in the analysis of E. Larsson & K.-H. Larsson (2003, bootstrap = 95%). The latter study included the same groups that were sampled here (excluding *A. byssoides* and *C. alboglaucum*) as well as several corticioid taxa representing *Gloeocystidiellum s. lat*. (*Gloeocystidiellum irpiscescens, Gloiothele* spp. *Vesiculomyces citrinus*), *Confertobasidium* spp. and *Metulodontia nivea*. Also included in their study was an unidentified isolate of *Lachnocladium*, which is a group of tropical coralloid fungi that may be related to the tropical cantharelloid genera *Dichantharellus* and *Dichopleuropus* (Reid, 1965; Corner, 1966, 1970). Except for these last three genera, the /peniophorales contains only resupinate or effused-reflexed forms. Nevertheless, the /peniophorales is very diverse in anatomical characters, including species with smooth or ornamented, amyloid or inamyloid spores, with or without a gloeoplerous system, and with or without dextrinoid dichohyphidia or asterohyphidia (Hallenberg, 1985; Stalpers, 1996; E. Larsson & K.-H. Larsson, 2003). The latter have been regarded as diagnostic for the Lachnocladiaceae, which is not resolved as monophyletic in this study or that of E. Larsson & K.-H. Larsson (2003).

The higher-level relationships of the Lachnocladiaceae have been controversial. Donk (1964) classified the genera of the Lachnocladiaceae in two subfamilies of the Hymenochaetaceae, the Vararioideae (*Vararia* and *Lachnocladium*) and Asterostromatoideae (*Asterostroma*), but placed *Scytinostroma* in the Corticiaceae. He suggested that the Asterostromatoideae could be a link between the Vararioideae and Hymenochaetoideae (Hymenochaetaceae in the present sense). This idea may have been based in part on the presence in *Asterodon ferruginosum* of 'asterosetae', which are stellate structures that resemble the asterohyphidia of *Asterostroma* (Corner, 1948). Müller *et al.* (2000) showed that *A. ferruginosum* has imperforate parenthesomes, which is consistent with its placement in the Hymenochaetaceae. Later, Wagner & Fischer (2001) used nuc-lsu rDNA sequences to study relationships of *A. ferruginosum* and *Asterostroma* spp., which they found to be nested in the Hymenochaetaceae and Lachnocladiaceae, respectively. This result severed the last possible link between the Lachnocladiaceae and Hymenochaetaceae, and

supported Oberwinkler's (1977) suggestion that the Lachnocladiaceae is related to the Russulales.

10. Bolete clade and Jaapia

The bolete clade (= Boletales) is a major contingent of ectomycorrhizal fungi in the Homobasidiomycetes that includes a considerable diversity of fruiting body morphologies. Resupinate forms among the Boletales are brown-rotting saprotrophs and parasites with preference for coniferous woods – deciduous trees are less frequently attacked. Some species like the dry rot fungi *Serpula lacrymans* and *S. himantioides* decay timber and cause significant structural damage in buildings (Jennings & Bravery, 1991). *Coniophora puteana* and other *Coniophora* spp. are commonly called 'cellar fungi' and require higher humidity levels (hence the name wet rot) to colonise and decay wooden structures in basements (see Ginns, 1982, for details). Nilsson & Ginns (1979) demonstrated that the brown-rotters among the Boletales, including stipitate-pileate forms, show a particular degrading mode by breaking down pure cellulose *in vitro*, despite the lack of cellulolytic activity which is a typical reaction of brown-rotting fungi when pure cellulose is offered as substrate. Exceptions in Nilsson & Ginns' study were *Pseudomerulius aureus* and *Tapinella atrotomentosa*, which retrieved negative test results for cellulase. The nutritional mode of *T. atrotomentosa* is still somewhat ambiguous. Kropp & Trappe (1982) found that rotten logs on which *T. atrotomentosa* fruits contain abundant conifer roots. They traced the mycelium of a *T. atrotomentosa* fruiting body to nearby western hemlock roots, which were covered with the same mycelium. A pure culture synthesis of hemlock seedlings and *T. atrotomentosa* mycelium was not successful. Kämmerer *et al*. (1985), however, used a different system testing *T. atrotomentosa* and *Jaapia argillacea* positive for cellulase, suggesting that both fungi are brown-rotters (so-called 'Coniophoraceae rot').

The bolete clade is monophyletic, as shown in various nuc-lsu rDNA analyses (Jarosch, 2001; Binder & Bresinsky, 2002; K.-H. Larsson *et al*., 2004), and it receives 93–99% bootstrap support in the present study (Figs 1, 4). It is supported in other studies using different loci, for example, *atp6* amino acid sequences provided bootstrap support of 99% (Kretzer & Bruns, 1999) and mitochondrial large subunit sequences moderately supported the bolete clade by 70% (Bruns *et al*., 1998). The euagarics clade was strongly supported (94%) as the sister group of the bolete clade (bootstrap = 100%) using a four region dataset (nuc-ssu, nuc-lsu, mt-ssu, mt-lsu rDNA) including a 82 species sampling of Homobasidiomycetes (Binder & Hibbett, 2002). The present study sampled 30 Boletales species including 14 resupinate species mostly drawn from Bresinsky *et al*. (1999), which are distributed in the genera *Coniophora*, *Leucogyrophana*, *Pseudomerulius*, *Serpula* (Coniophorineae) and *Hydnomerulius* (Paxillineae).

The *Jaapia* clade, consisting of a single species, *J. argillacea*, was discovered in the study of Hibbett & Binder (2002) and it is placed as the sister group of the euagarics clade, bolete clade and athelioid clade (Figs 1, 4). *Jaapia* has been listed in the Coniophoraceae (e.g. Jülich, 1981) based on resupinate, cream coloured fruiting bodies having a farinous texture, light yellow and smooth, fusiform, thick-walled, cyanophilous spores. Hallenberg (1985), however, found the combination of morphological characters not convincing enough to place *Jaapia* in the Coniophoraceae and left the genus among the corticioid fungi. Chemical findings that could assist placing *Jaapia* are lacking as yet, since Besl *et al*. (1986) did not detect any pigments in a *Jaapia* culture including pulvinic acids and derivatives, which are the major pigments of the Boletales. If the placement of *Jaapia argillacea* in the present study using the same isolate as Kämmerer *et al*. (1985) and Besl *et al*. (1986) is correct, then this might suggest that resupinate fruiting bodies, lack of pigments, and saprotrophy with a Coniophoraceae-type rot (or some combination) are plesiomorphic conditions for the euagarics clade, bolete clade and athelioid clade.

The most comprehensive study on resupinate Boletales is the study of Jarosch (2001) using multiple isolates of 15 species in five genera. Jarosch (2001) received 96% (neighbour-joining) bootstrap support for the Coniophorineae, conflicting with the results of the present study and the studies of Bresinsky *et al*. (1999) and Binder & Bresinsky (2002), in which the Coniophorineae was not resolved as monophyletic (bootstrap < 50%). The studies of Bruns *et al*. (1998) and Kretzer & Bruns (1999) also suggest that the Coniophorineae is polyphyletic, but neither study included *Leucogyrophana* spp. Besl *et al*. (1986) analysed the occurrence of pulvinic acids and their derivatives and additional compounds in the Coniophoraceae and noticed that the distribution of pigments is not only complex, but some unique chemical patterns correspond to the pigments found in stipitate-pileate members of the Boletales. These findings suggested several morphological transformations from resupinate to stipitate-pileate fruiting bodies and that *Leucogyrophana sensu* Ginns (1978) is polyphyletic. Based on secondary metabolites, Besl *et al*. (1986) predicted relationships between *Serpula lacrymans* and *Austropaxillus statuum* (syn. *Paxillus statuum*), *Hydnomerulius pinastri* (syn. *Leucogyrophana pinastri*) and *Paxillus involutus*, *L. mollusca* and *Hygrophoropsis aurantiaca*, and *L. olivascens* and *Tapinella panuoides*. Except for the latter hypothesis, all the other relationships assumed by Besl *et al*. (1986) received strong support in several phylogenetic studies (Bresinsky *et al*., 1999; Jarosch, 2001; Jarosch & Besl, 2001). Recently, Jarosch (2001) showed another remarkable morphological transformation between *Coniophora* spp. and two southern hemisphere species, '*Paxillus*' *chalybaeus* from New Caledonia and '*Paxillus*' *gymnopus* from Colombia, with paxilloid habit (stipitate-pileate, lamellate hymenophore and involute margin), nested within the *Coniophora* clade (bootstrap = 100%).

The present study supports in addition a close relationship of *Pseudomerulius aureus* and *Tapinella* spp. with 86%, which is controversial to the placement of *Tapinella* in Jarosch (2001), where it is nested between *Coniophora* and *Leucogyrophana* (bootstrap = 81%). Little is known about the pigments of *P. aureus* (Gill & Steglich, 1987) and microscopical characters, except for the identical rhizomorph type of *P. aureus* and *T. panuoides* (Agerer, 1999, p. 33), do not indicate its relationship to *Tapinella*. K.-H. Larsson *et al*. (2004) found

support > 80% for *P. aureus* and *Bondarcevomyces taxi* as a basal clade in the Boletales, not including *Tapinella* spp. *Bondarcevomyces taxi* is a brown-rot fungus with a bright orange pileus and a poroid hymenophore that has been separated from *Hapalopilus* (polyporoid clade) by Parmasto & Parmasto (1999) and it was provisionally placed in the Sparassidaceae. Additional phylogenetic analyses support a *Pseudomerulius–Bondarcevomyces–Tapinella* clade (= Tapinellaceae) with values > 90% (Binder, unpublished).

11. Athelioid clade

This group, which is exclusively composed of resupinate forms, was identified by K.-H. Larsson *et al*. (2004). In their analysis, the athelioid clade is moderately to strongly supported (bootstrap = 77–97%) and includes *Athelia epiphylla, A. decipiens*, *Piloderma byssinum, P. lanatum*, *Tylospora asterophora, Byssocorticium pulchrum, Athelopsis subinconspicua* and *Amphinema byssoides*. This is probably the same clade that Boidin *et al*. (1998) identified based on ITS sequences, which they called the Atheliales. The Atheliales *sensu* Boidin *et al*. (1998) included *Amyloathelia amylacea, Leptosporomyces roseus* and *Fibulomyces septentrionalis*, which are resupinate taxa with an athelioid form (Eriksson & Ryvarden, 1975, 1976; Hjortstam & Ryvarden, 1979), as well as *Athelia epiphylla* and *A. arachnoidea*. However, the analysis of Boidin *et al*. (1998) placed *A. decipiens* as a close relative of *Erythricium laetum*, which K.-H. Larsson *et al*. (2004) found to be in the corticioid clade (see above). In the present analysis, the athelioid clade receives moderate support (bootstrap = 75%) and is represented only by *Athelia arachnoidea*, *A. fibulata* and an isolate labelled '*Hyphoderma praetermissum*' (Fig. 4), which is probably mislabelled, as noted previously. In addition, two isolates in the present study labelled '*Athelia epiphylla*' and '*A. arachnoidea*' were placed in the phlebioid clade, and one isolate labelled '*Amphinema byssoides*' was placed in the russuloid clade (Fig. 4). Based on the results of K.-H. Larsson *et al*. (2004), these three isolates are also probably mislabelled (see Table 3 for sources).

Both the present analysis and that of K.-H. Larsson *et al*. (2004) resolved a monophyletic group that includes the athelioid clade, bolete clade and euagarics clade, albeit with weak bootstrap support. The analysis of K.-H. Larsson *et al*. (2004) placed the athelioid clade as the sister group of the bolete clade, but all analyses in the present study placed it as the sister group of the euagarics clade (Figs 1, 3, 4). Similarly, the analysis of Bruns *et al*. (1998) placed a clade containing *Piloderma croceum* and *Waitea circinata* as the sister group of a clade containing most of the euagarics clade (except the Hygrophoraceae), although again bootstrap support was weak. Taken together, the results of these studies suggest that the athelioid clade is closely related to the euagarics clade, and may be its sister group.

The athelioid clade clusters with a paraphyletic assemblage that includes an odd mixture of resupinate (*Radulomyces molaris, Phlebiella* sp.), coralloid-clavarioid (*Lentaria albovinacea, Deflexula subsimplex*), pileate (*Plicaturopsis crispa*) and hypogeous gasteroid (*Stephanospora caroticolor*) forms (Fig. 4). Bootstrap support for this group is weak in the analysis of the full dataset (Fig. 4), but in the core dataset analysis the clade containing *S. caroticolor*, *Athelia arachnoidea* and '*H. praetermissium*' receives moderately strong support (bootstrap = 91%; Fig. 1). Results from K.-H. Larsson *et al*. (2004) and additional analyses with an extended dataset (K.-H. Larsson, unpublished) indicate that the species that cluster here with the athelioid clade may represent several independent clades, including one clade that contains *S. caroticolor* and the resupinate forms *Lindtneria trachyspora* and *Cristinia* spp. (see above, under phlebioid clade). In the present analyses these clades are too sparsely sampled to be resolved, however. Additional data are needed to determine if this heterogeneous assemblage is an artefact.

Members of the athelioid clade share a resupinate habit with a typically 'loose' monomitic hyphal construction, often with rhizomorphs (Eriksson & Ryvarden, 1973; Eriksson *et al*., 1981; Hjortstam *et al*., 1988*b*). Spores in the group are generally smooth and ellipsoid to globose, but *Tylospora* has angular spores that are smooth or warted, for which reason it has been placed in the Thelephorales (Stalpers, 1993).

In contrast to its morphological simplicity, the athelioid clade displays great diversity in ecological strategies. Species of *Amphinema, Byssocorticium, Piloderma* and *Tylospora* enter into ectomycorrhizal symbioses, and often form a major component of mycorrhizal communities (Danielson & Pruden, 1989; Ginns & Lefebvre, 1993; Erland, 1996; Bradbury *et al*., 1998; Eberhardt *et al*., 1999; Kernaghan *et al*., 2003; Lilleskov *et al*., 2002; Shi *et al*., 2002). *Athelia* spp. are not known to form mycorrhizae, but they enter into other kinds of biotrophic associations. *Athelia arachnoidea* (and its *Rhizoctonia* anamorph) acts as a lichen parasite or a pathogen of carrots in cold storage, and also functions as a saprotroph on leaf litter (Arvidsson, 1976; Gilbert, 1988; Adams & Kropp, 1996). *Athelia epiphylla* has been suggested to form lichens with cyanobacteria, and it also acts as a primary decayer of leaf and needle litter and is associated with white rot of *Populus tremuloides* (Jülich, 1978; Lindsey & Gilbertson, 1978; Larsen *et al*., 1981). Finally, Matsuura *et al*. (2000) described a symbiosis involving *Athelia* sp. (as *Fibularhizoctonia* sp.) and termites, in which the fungus forms sclerotia that mimic termite eggs. Worker termites handle the sclerotia as if they were eggs, and the presence of sclerotia in termite nests appears to enhance egg viability. The benefit to the fungus (if any) is not clear, but might include dispersal to new substrates (Matsuura *et al*., 2000). Reconstructing the pattern of shifts in ecological strategies in *Athelia* is hampered by the difficulty of species identification in this group (Adams & Kropp, 1996). Indeed, the results of the present analysis and others cited previously indicate that isolates of *Athelia* spp. are often mislabelled.

12. Euagarics clade

With over 8400 species, the euagarics clade is by far the largest of the eight major clades recognised by Hibbett & Thorn (2001). The majority of taxa are agaricoid and correspond (in large part) to the suborder Agaricineae of Singer (1986)

and its many gasteroid derivatives. It is now recognised that there are also scattered clavarioid forms in the group (Hibbett *et al*., 1997; Pine *et al*., 1999; Hibbett & Thorn, 2001; K.-H. Larsson *et al*., 2004; Moncalvo *et al*., 2002). The most comprehensive phylogenetic study of the euagarics clade so far is that of Moncalvo *et al*. (2002), which included 877 isolates represented by nuc-lsu rDNA sequences. The only species that approaches a 'resupinate' form in that study is *Gloeostereum incarnatum*, which produces sessile conchate fruiting bodies that may be resupinate at the point of attachment (Petersen & Parmasto, 1993). Several other studies have shown that certain resupinate forms are in the euagarics clade (Kim & Jung, 2000; Lim, 2001; E. Langer, 2002; K.-H. Larsson *et al*., 2004), but the sampling of agaricoid taxa has generally been too limited to address the placements of the resupinate forms on a fine scale (but see Langer, 2002, which included 54 species from the euagarics clade). The present study included a large sample (206 sequences) of non-resupinate forms in the euagarics clade, most of which are from the studies of Moncalvo *et al*. (2000, 2002).

The euagarics clade receives weak bootstrap support in the analyses of both the core and full datasets (Figs 1, 4). Nevertheless, the general topology, with the Hygrophoraceae as the sister group of the 'core euagarics clade', is consistent with the strongly supported results of Binder & Hibbett (2002). One problematical aspect of the results here concerns the placements of the unclassified taxa that form a paraphyletic group at the base of the athelioid clade, including the corticioid forms *Phlebiella* sp. and *Radulomyces molaris*, both represented by sequences from the work of E. Langer (2002; also see Hibbett & Binder, 2002; Fig. 4). In the analysis of E. Langer (2002) these taxa were nested in the euagarics clade, although their closest relatives were not identified with confidence. Similar results were obtained by K.-H. Larsson *et al*. (2004), who found a well supported (bootstrap > 80%) clade containing three species of *Radulomyces, Phlebiella pseudotsugae* and *Coronicium alboglaucum*, which was weakly supported as the sister group of the clavarioid forms *Typhula phacorrhiza* and *Macrotyphula juncea*. Taken together, the results of these analyses suggest that *Radulomyces, Phlebiella* and *Coronicium* are nested within or closely related to the euagarics clade. It would be valuable to obtain additional sequences of these taxa, which at present are represented only by nuc-lsu rDNA sequences. Other than their corticioid habit, there are no obvious characters that suggest a close relationship among *Radulomyces, Phlebiella* and *Coronicium* (K.-H. Larsson *et al*., 2004).

At least four groups of resupinate forms are nested in the core euagarics clade (Fig. 4). One of these groups is an odd assemblage including two Lachnocladiaceae (*Vararia ochroleucum, V. gallica*), *Lopharia mirabilis* and *Trechsipora farinacea* (Fig. 4). In this and other studies (Lim, 2001; K.-H. Larsson *et al*., 2004), sequences of these genera are placed in the russuloid clade, polyporoid clade and trechisporoid clade (respectively), suggesting that their placement in the euagarics clade is erroneous, possibly reflecting misidentifications.

Dendrothele. Two isolates of the polyphyletic corticioid genus *Dendrothele* (*D. griseocana, D. acerina*) are nested in a moderately supported (bootstrap = 83%) clade that also includes cyphelloid and aquatic Homobasidiomycetes (Fig. 4). This result is consistent with the results of the study of E. Langer (2002), which was the source of the sequence of *D. acerina* and several of the cyphelloid forms. In that analysis, these taxa were grouped in clade "cyphelloid 35". A clade including *Schizophyllum commune* and the cupulate *Auriculariopsis ampla* is weakly supported as the sister group of the *Dendrothele*-cyphelloid clade (Fig. 4), which is consistent with the results of Binder *et al*. (2001) and Nakasone (1996).

Chondrostereum, *Gloeostereum* and *Cystostereum*. The effused-reflexed, stereoid fungus *Chondrostereum purpureum* and *Gloeostereum incarnatum* are moderately supported (bootstrap = 85%) as a monophyletic group. These results are consistent with those of Moncalvo *et al*. (2002) who showed that *G. incarnatum* is in the euagarics clade, and Kim & Jung (2000), E. Langer (2002), K.-H. Larsson *et al*. (2004), and Lim (2001), who showed that *C. purpureum* is in the euagarics clade. The studies of Kim & Jung (2000) and Lim (2001) also suggested that the resupinate to effused-reflexed stereoid fungus *Cystostereum murraii* is in this group.

In contrast to Kim & Jung (2000) and Lim (2001), the analysis of Boidin *et al*. (1998) suggested that *Cystostereum murraii* is in the phlebioid clade (Phanerochaetales). *Cystostereum murraii* is dimitic, whereas *C. purpureum* is monomitic, which might seem to support the results of Boidin *et al*. (1998). Nevertheless, both taxa have hyphae in the context with swollen, bladderlike ends. The arrangement of these cells in the two species is strikingly similar in the illustrations of Eriksson & Ryvarden (1973, 1975), which supports the conclusions of Kim & Jung (2000) that *C. purpureum* and *C. murraii* are closely related. In *C. murraii* the vesicles contain oil droplets. The "embedded gloeocystidia" described in *G. incarnatum* (Petersen & Parmasto, 1993, p. 1214) might be homologous.

Moncalvo *et al*. (2002) showed that *Cheimonophyllum candidissum*, which is a minute pleurotoid agaric, is the sister group of *G. incarnatum*, and named the resulting clade the /gloeostereae. The sister group of the /gloeostereae included the pileate-stipitate agarics *Hydropus scabripes*, *Baeospora myosura* and *B. myriadophylla* (Tricholomataceae *s. lat*.), which were classified as the /baeosporoid clade. The sister group relationship of /gloeostereae and /baeosporoid is weakly supported in this analysis, which includes many of the same sequences as in Moncalvo *et al*. (2002). Nevertheless, if this topology is correct, then it suggests a transformation series from pileate-stipitate agarics (*Baeospora* spp., *H. scabripes*), to pleurotoid agarics (*C. candidissimum*), conchate-partly resupinate forms with a reduced hymenophore (*G. incarnatum*), and finally effused-reflexed or fully resupinate stereoid forms (*C. purpureum, C. murraii*).

Cylindrobasidium. Three isolates of the corticioid genus *Cylindrobasidium*, including two from the study of E. Langer (2002) are strongly supported (bootstrap = 100%) as a monophyletic group (Fig. 4). As in the analysis of E. Langer (2002), *Cylindrobasidium* is nested in a clade that includes the agaric genera *Armillaria* and *Oudesmansiella* (many others are included in the present study; Fig. 4). The analysis of K.-H.

Larsson *et al*. (2004) weakly supported monophyly of *Cylindrobasidium laeve* and *Chondrostereum purpureum*. If the taxa that were not sampled by K.-H. Larsson *et al*. (2004) were pruned from the trees produced in the present study, then *C. laeve* and *C. purpureum* would again be resolved as sister taxa (Fig. 4).

One problematical result concerns a sequence of the corticioid fungus *Bulbillomyces farinosus*, which is placed in a clade with the clavarioid forms *Typhula phacorrhiza* and *Macrotyphula juncea*, the pleurotoid agarics *Phyllotopis nidulans* and *Pleurocybella porrigens*, and the cyphelloid *Henningsomyces candidus* (Fig. 4). This group is equivalent to the clade "collybioid, clavarioid 28" that was resolved in the study of E. Langer (2002). The monophyly of *Bulbillomyces, Typhula* and *Macrotyphula* is strongly supported (bootstrap = 98%), but there are no characters that would support this placement. *Bulbillomyces farinosus* produces a sclerotial anamorph (*Aegerita candida*), and in this regard it superficially resembles *Typhula phacorrhiza*, which also produces sclerotia, but the sclerotia differ in size, colour and anatomical features (Remsberg, 1940; Jülich, 1974). Analyses with alternative sequences of *Bulbillomyces farinosus* derived from two different cultures and one *Aegerita candida* isolate suggest that *Bulbillomyces farinosus* is closely related to *Hypochnicium* spp. in the residual polypore clade, which is a more explicable position (K.-H. Larsson unpublished, M. Binder & D. Hibbett, unpublished).

Finally, K.-H. Larsson *et al*. (2004) resolved a weakly supported clade containing two resupinate polypores (*Anomoporia bombycina* and *A. kamtschatica*) and four corticioid fungi (*Amylocorticium* spp., *Ceraceomyces tessulatus*, *Hypochniciellum subillaqueatum*), which was placed as the sister group of the rest of the euagarics clade. None of these species were sampled here, although three different species of *Ceraceomyces* were included in both the present study and that of K.-H. Larsson *et al*. (2004) and found to be in the phlebioid clade (see above). Analyses with additional sequences of *Ceraceomyces tessulatus* and *Anomoporia* spp., including *A. albolutescens*, have upheld the phylogenetic position suggested in Larsson *et al*. (2002) (K.-H. Larsson, unpublished). In contrast, the analysis of Kim & Jung (2000) placed *A. albolutescens* in the *Antrodia* clade. This placement would be consistent with the reported production of a brown rot by *A. albolutescens* (Gilbertson & Ryvarden, 1986), but it is inconsistent with the results of K.-H. Larsson *et al*. (2004) which are based on multiple isolates. It is likely that the '*A. albolutescens*' isolate studied by Kim & Jung (2000) is mislabelled. Bootstrap support for the basal nodes of the euagarics clade was weak in the study of K.-H. Larsson *et al*. (2004), so it remains unclear whether these last resupinate taxa are actually members of the euagarics clade. Even if they are, the fraction of species that are resupinate in the euagarics clade is much lower than in other major groups of Homobasidiomycetes (*c*. 4% in this dataset). One possible explanation for this pattern is that the abundance of resupinate forms in groups such as the hymenochaetoid clade, russuloid clade and cantharelloid clade reflects a plesiomorphic condition in these more basal groups (Hibbett & Binder, 2002). Alternatively, the rate of reversals to resupinate forms (or the rate of speciation of resupinate forms) may be lower in the euagarics clade than in other clades of Homobasidiomycetes.

Conclusions and future directions

Resupinate forms are scattered throughout all of the major clades of Homobasidiomycetes, as well as heterobasidiomycetes. Some of the recently recognised groups of Homobasidiomycetes, such as the athelioid clade, corticioid clade and trechisporoid clade (K.-H. Larsson *et al*., 2004), and the lone taxon *Jaapia argillacea*, are composed entirely, or almost entirely, of resupinate forms (Fig. 4). The present study analysed one of the larger phylogenetic datasets in fungi to date (but see Moncalvo *et al*., 2002; Tehler *et al*., 2003), but it still included less than half of the genera of corticioid fungi recognised by Hjortstam (1987). As sampling of resupinate taxa continues, it is possible that new major clades will be discovered. Such discoveries could aid analyses of higher-level phylogenetic relationships of Homobasidiomycetes by identifying taxa that break up internodes deep in the tree (including those that determine the boundary between the Homobasidiomycetes and heterobasidiomycetes), many of which have proven difficult to resolve (Binder & Hibbett, 2002).

Designing a sampling scheme for the remaining resupinate taxa will be challenging. For many groups, there are few anatomical characters to provide clues to higher-level relationships, and the monophyly of individual genera is often questionable. For example, *Hyphoderma* is now understood to include species in the hymenochaetoid clade and polyporoid clade. Similarly, species of *Veluticeps* and *Columnocystis*, which were once proposed as generic synonyms, occur in the *Gloeophyllum* clade and polyporoid clade. These examples are particularly dramatic, but numerous other genera of resupinate fungi have been found to be polyphyletic in this and other studies cited previously (e.g. *Sistotrema*, *Hyphodontia, Schizopora, Phlebia, Phanerochaete, Aleurodiscus, Gloeocystidiellum*, etc.). Many of the older genera have been split into smaller, putatively natural groups, but even some of these have been found to be polyphyletic (e.g. *Boidinia*; E. Larsson & K.-H. Larsson, 2003). Thus, an exemplar-based approach to sampling could lead to significant underestimates of the phylogenetic diversity of resupinate Homobasidiomycetes.

Ultimately, it will be necessary to construct phylogeny-based classifications that include all the species of resupinate and non-resupinate Homobasidiomycetes. Moreover, it will be necessary to include multiple accessions of individual species, because they can reveal misidentifications (which the present study shows are common), as well as provide insight into biogeography and intraspecific variation.

To develop comprehensive phylogenetic classifications will require either simultaneous analyses of very large datasets, or analytical approaches that reconcile overlapping datasets, such as supertree methods (Sanderson *et al*., 1998). Simultaneous analyses have certain advantages, not the least of which is that they permit the estimation of branch lengths, which are necessary for molecular clock studies and maximum-likelihood analyses of character evolution. However, simultaneous

analyses of large datasets are computationally challenging, especially if model-based methods are employed. Using the Parsimony Ratchet, the present study succeeded in analysing a 656-OTU dataset with six-parameter weighted parsimony, but even this large dataset included only about one fifth of the 3130 nuc-lsu rDNA sequences of Homobasidiomycetes that are available in GenBank as of this writing.

Given the limitations of current computer hardware and algorithms, a rigorous simultaneous analysis of all the available homobasidiomycete sequences would be very difficult. To develop detailed phylogenetic hypotheses within individual clades will require more focused efforts, as exemplified by the studies of E. Larsson & K.-H. Larsson (2003) in the russuloid clade and Moncalvo *et al*. (2002) in the euagarics clade. At the same time, analyses of multigene datasets of exemplars from the major groups will be needed to estimate higher-level relationships. In the present study and that of Binder & Hibbett (2002), a dataset with four mitochondrial and nuclear rDNA regions was used for this purpose. It should be a priority to sequence these same regions in exemplars of the major clades that have so far been studied only with single genes, such as the athelioid clade and trechisporoid clade. Of course, not all nodes will be resolved with rDNA alone (e.g. the polyporoid clade; Binder & Hibbett, 2002), so exploration of protein-coding loci will also be necessary to resolve the phylogenetic relationships of resupinate Homobasidiomycetes.

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