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A phylogenetic overview of the antrodia clade (Basidiomycota, Polyporales)

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Abstract: Phylogenetic relationships among members of the antrodia clade were investigated with molecular data from two nuclear ribosomal DNA regions, LSU and ITS. A total of 123 species representing 26 genera producing a brown rot were included in the present study. Three DNA datasets (combined LSU-ITS dataset, LSU dataset, ITS dataset) comprising sequences of 449 isolates were evaluated with three different phylogenetic analyses (maximum likelihood, maximum parsimony, Bayesian inference). We present a phylogenetic overview of the five main groups recovered: the fibroporia, laetiporus, postia, laricifomes and core antrodia groups. Not all of the main groups received strong support in the analyses, requiring further research. We were able to identify a number of well supported clades within the main groups.

Key words: brown rot, molecular phylogeny

Introduction

The antrodia clade was first identified by Hibbett and Donoghue (2001) as a subgroup within the larger polyporoid clade (Hibbett and Thorn 2001) in which 11 genera that produce a brown rot were included (*Antrodia*, *Auriporia*, *Daedalea*, *Fomitopsis*, *Laetiporus*, *Oligoporus*, *Postia*, *Neolentiporus*, *Phaeolus*, *Piptoporus*, *Sparassis*). The apparent evolutionary relationships among some of these genera also were observed in Hibbett and Donoghue (1995) and Boidin et al. (1998). Since then members of the antrodia clade have been the focus of several molecular studies investigating phylogenetic relationships among these species and other wood-decay fungi. Higher level phylogenetic studies also have recognized the genera *Amylocystis*, *Dacryobolus*, *Melanoporia*, *Pycnoporellus*, *Sarcoporia* and *Wolfiporia* as part of the antrodia clade (SY Kim and Jung 2000, 2001; Binder and Hibbett 2002; Hibbett and Binder 2002; SY Kim et al. 2003; Binder et al. 2005), while the genera *Antrodia*, *Daedalea*, *Fomitopsis*, *Laetiporus* and *Sparassis* have received attention in regard to species delimitation (SY Kim et al. 2001, 2003; KM Kim et al. 2005, 2007; Desjardin et al. 2004; Wang et al. 2004; Wu et al. 2004; Dai et al. 2006; Blanco-Dios et al. 2006; Chiu 2007; Lindner and Banik 2008; Yu et al. 2010; Banik et al. 2010, 2012; Garcia-Sandoval et al. 2011; Lindner et al. 2011; Rajchenberg et al. 2011; Zhou and Wei 2012; Bernicchia et al. 2012; Spirin et al. 2012, 2013). These studies also established that some of the genera are not monophyletic and several modifications have been proposed: the segregation of *Antrodia* s.l. into three genera (*Antrodia* s.s., *Amyloporia*, *Fibroporia*); the segregation of *Fomitopsis* s.l. into *Fomitopsis* s.s., *Pilatoporus*, *Rhodofomes* and *Laricifomes*; and the creation of *Taiwanofungus* to place two species from Taiwan formerly classified in *Antrodia*. Other studies on brown-rot fungi have proposed the independent use of the generic concepts of *Oligoporus*, *Postia*, *Rhodonia*, *Ryvardenia* and *Spongiporus* to place several species treated under the genus *Postia* s.l. (Rajchenberg 1994, 1995, 2006; Niemelä et al. 2005; Schigel et al. 2006; Spirin et al. 2006; Pildain and Rajchenberg 2012); and the genus *Gilbertsonia* has been proposed to accommodate *Fibroporia angulopora* (Parmasto 2001).

Although research has focused on subsets of species in the clade, no synthesis has been presented that includes a broad phylogenetic overview of the antrodia clade with a complete sampling of relevant genera. According to the studies mentioned above, at least 25 different genera could be part of the antrodia clade. Therefore, in the present study we used nuclear rDNA sequence data to evaluate the clade from a broad phylogenetic perspective. We also included genus *Crustoderma*, not compared in previous studies, considering a total of 26 brown-rot genera. The genus *Grifola* Gray is not included here because it appeared as a sister group of the core polyporoid clade in Justo and Hibbett (2011), not related to members of the antrodia clade as suggested by Wu et al. (2004), Binder et al. (2005), Dai et al. (2006), Yu et al. (2010) and Garcia-Sandoval et al. (2011). The questions surrounding the phylogenetic position of *Grifola* are addressed in more detail by Binder et al. (2013).

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For a better understanding of the genera involved in this study we provide a review of their main characteristics: type species, geographic distribution and references for taxa description (TABLE I), and morphological, ecological and biological characters (TABLE II). Morphological and ecological data are from references herein (TABLE I), while information on mating systems and nuclear behavior are from Boidin and Lanquetin (1984, 1997) and Rajchenberg (2011).

The antrodia clade is of ecological and evolutionary importance because the vast majority of brown-rot species belong to this clade and this group also contain important forest pathogens (e.g. *Fomitopsis*, *Laetiporus*, *Phaeolus* spp.; Gilbertson and Ryvarden 1986, Dai et al. 2007, Holmquist et al. 2009). Although the ability to produce brown rot has evolved independently at least five times, approximately 70% of known brown-rot species are in the antrodia clade, making this by far the largest clade of brown-rot fungi (Hibbett and Donoghue 2001, Garcia-Sandoval et al. 2011). Brown-rot fungi degrade cellulose and hemicellulose in wood using enzymatic processes relative to white-rot species (Highley and Illman 1991, Baldrian and Valášková 2008 and references therein, Tomšovský et al. 2009, Floudas et al. 2012) and help create habitat for animals, insects, other fungi and tree seedlings (Lonsdale et al. 2008, Olsson et al. 2011). In addition, some species directly influence forest structure and succession (Toljander et al. 2006, Lonsdale et al. 2008, Rajala et al. 2012). Fungal species that produce brown rot also play an important role in carbon sequestration (Fukami et al. 2010); the highly recalcitrant residues produced by brown rot have the potential to remain locked in soil for hundreds to thousands of years, while white-rot species may return the majority of carbon directly to the atmosphere (Gilbertson 1980, 1981).

In addition to their ecological contribution, several members of the antrodia clade play an economically important role as indoor wood-decay fungi and as a good source of food and pharmaceutical or biotechnological product (Overholts 1953, Bagley and Richter 2001, Vaidya and Singh 2012). Species of *Antrodia*, *Fomitopsis* and *Rhodonia* contribute in economic losses in both timber production and damage of structural wood in buildings in North America and Europe (Schmidt and Moreth 2003, Schmidt 2007). *Wolfiporia cocos*, distinguished by the production of large sclerotia, has been used as food in North America, in traditional medicine in Asia and in certain pharmacological studies (Wang et al. 2012). Biotechnological studies also have demonstrated the potential use of *W. cocos* in the bioprocessing of copper containing wood and the ability of this species to produce compounds with metal chelating capability, especially iron-reducing compounds (de Groot and Woodward 1998, Woodward and de Groot 1999, Machuca et al. 2001, Arantes and Milagres 2006). Species of *Laetiporus* and *Sparassis* also are considered edible (Gilbertson and Ryvarden 1986, Light and Woehrel 2009), while some *Crustoderma* and *Laetiporus* species have been tested in bioremediation including the degradation of treated wood and wastewater (Mtui and Masalu 2008, Choi et al. 2009). Certain brown-rot species (e.g. *Daedalea quercina*, *Fomitopsis pinicola*, *Laetiporus sulphureus*, *Rhodonia placenta*, *Wolfiporia cocos*) are used to understand the mechanisms involved in wood degradation, and to facilitate these analyses their whole genome has been sequenced (Martinez et al. 2009, Vanden-Wymelenberg et al. 2011, Floudas et al. 2012, http://www.jgi.doe.gov/). *Taiwanofungus camphoratus* is considered one of the most valued medicinal fungi in Taiwan, where it has been used for the prevention and treatment of several ailments including liver diseases, cancer and hypertension; therefore, this species has received attention in biochemical studies (Wu et al. 1997, 2004; Hseu et al. 2007; Juan et al. 2010; Geethangili and Tzeng 2011). *Laricifomes officinalis* fruiting bodies contain biologically active compounds (Zjawiony 2004) and have been used for medicinal purposes since ancient times (Gilbertson 1980, Wasser 2010).

The main objectives of this study are to incorporate sequence data from the nuclear large subunit (LSU) and internal transcribed spacer (ITS) regions to: (i) present a phylogenetic overview of groups within the antrodia clade and (ii) identify unique terminal clades that may delimit genera. The information gained from this study will help with understanding the evolution, prevalence and distribution of brown-rot fungi in forest ecosystems while assessing the monophyly of genera and determining species limits. The present study employs broad taxonomic sampling using only two genetic loci; results may be used to identify appropriate exemplars for studies using multiple loci or whole genomes.

MATERIALS AND METHODS

Taxon sampling.—DNA sequences of the ITS (ITS1, 5.8, ITS2) and 5′ end of the LSU regions of nuclear rDNA representing about 123 species of 26 brown-rot genera were used in the present study. Of these, 240 ITS and 261 LSU were newly generated from herbarium specimens and cultures obtained from the Center for Forest Mycology Research (US Forest Service, Northern Research Station, Madison, Wisconsin) and the University of Helsinki Herbarium, Finland; 128 ITS and 106 LSU were retrieved from GenBank (Benson et al. 2011), and 21 ITS and 22 LSU

unpublished sequences were provided by K.-H. Larsson et al. (Göteborg University, Sweden). Most LSU sequences were 915–955 bp long, while those of ITS were 650–705 bp. Novel sequences correspond primarily to species of *Antrodia*, *Amylocystis*, *Amyloporia*, *Auriporia*, *Crustoderma*, *Dacryobolus*, *Fibroporia*, *Oligoporus*, *Sarcoporia*, *Phaeolus*, *Piptoporus*, *Postia*, *Pycnoporellus*, *Rhodonia* and *Spongiporus* from specimens collected in North America (USA, Canada), Europe (Finland, Russia) and Asia (China, Indonesia, Japan, Taiwan) associated mainly with conifers. GenBank sequences come from molecular studies on decay fungi; these represent mostly species of *Daedalea*, *Fomitopsis*, *Laetiporus*, *Laricifomes*, *Ryvardenia*, *Sparassis*, *Taiwanofungus* and *Wolfiporia* collected mainly from USA, Japan, Taiwan, Thailand and Argentina and associated mostly with hardwoods. The sequences of K.-H. Larsson et al. represent species of *Antrodia*, *Oligoporus*, *Postia* and *Rhodonia* from Europe. Two taxa, *Boletopsis leucomelaena* (Pers.) Fayod and *Hydnellum geogenium* (Fr.) Banker (order Thelephorales), were used as outgroup in the phylogenetic analyses. The information for all these sequences and GenBank accession numbers are provided (SUPPLEMENTARY TABLE I).

DNA isolation, PCR and sequencing.—DNA extraction, amplification and sequencing from dried specimens followed Palmer et al. (2008); whereas those from cultures followed a modified version with eight-well 0.2 mL PCR strip tubes (Lorch et al. 2012). The ITS region was amplified with primers ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990) while the 5′ end of the LSU region was amplified with primers LROR and LR5 (Vilgalys and Hester 1990). Thermo-cycler conditions were: initial denaturation at 94 C (2 min), followed by 30 cycles of denaturation at 94 C (40 s), primer annealing at 53 C (40 s) and elongation at 72 C (130 s); and a final extension step of 72 C (5 min). Sequences provided by K.-H. Larsson et al. were generated following Larsson et al. (2004). Sequences were edited with Sequencher 4.8 (Gene Codes Corp., Ann Arbor, Michigan). Sequences generated in the present study were deposited in GenBank, (accession numbers KC585059–KC585405, KC595889–KC595955) and the alignments were deposited in TreeBASE (SN14283).

Phylogenetic analyses.—DNA sequences were aligned with MAFFT 6 (Katoh and Toh 2008); the Q-INS-I algorithm, especially suited for highly diverged sequences, was used for the alignment of ITS; the G-INS-I algorithm, better suited for sequences with global homology, was used for LSU sequences. The alignments were manually adjusted with MacClade 4.08 (Maddison and Maddison 2002). Visual inspection was especially important in the ITS dataset that includes divergent sequences. Regions with no discernible alignment pattern across the dataset were excluded from the analyses. The nLSU and ITS were analyzed separately with maximum likelihood, maximum parsimony and Bayesian methods. We searched for strongly supported positive conflict between the LSU and ITS datasets by comparing the phylogenetic trees from both datasets. We considered a node to be well supported if it received bootstrap values equal to or greater than 70% and or posterior probabilities equal to or greater than 0.95 in at least two of the three analyses. We identified those nodes in the LSU trees and looked for a strongly supported conflicting topology in the ITS tree and repeated the process identifying well supported nodes in the ITS tree and comparing them to the LSU trees. No strongly supported conflicts were detected and therefore a combined LSU+ITS dataset was constructed by concatenating both alignment files in MacClade.

The GTR model of nucleotide substitution was determined to be the best by jModelTest (Darriba et al. 2012). The parameters for phylogenetic analyses were: (i) maximum likelihood analyses (ML) run in the RAxML server 7.2.8. (Stamatakis et al. 2008) with 100 rapid bootstrap replicates, (ii) equally weighted parsimony analyses (MP) performed with PAUP* 4.0.b10 (Swofford 2002) with 1000 heuristic search replicates performed with starting trees generated by stepwise addition with random additions sequences followed by tree bisection reconnection branch swapping and up to two trees kept in each replicate, with bootstrap analysis estimated from 1000 replicates with 10 random taxon addition sequences and branch swapping set to subtree pruning and regrafting, and (iii) Bayesian analyses (BY) run with MrBayes 3.1 (Ronquist and Huelsenbeck 2003) for 10 000 000 generations with four chains and trees sampled every 100 generations with the a priori burn-in set to 2 500 000 generations. Convergence was assessed by examining effective sample sizes (ESS values) of the log likelihoods for each run and confirming that they were over 200 and also by visually inspecting the likelihood plots through time in TRACER (Rambaut and Drummond 2007). The ESS values for each analysis were: LSU (531.841, 528.838), ITS (598.034, 760.687) and combined (946.452, 1245.380).

RESULTS

The phylogenetic relationships among members of the antrodia clade were evaluated with three DNA sequence datasets (LSU+ITS, LSU, ITS) and three phylogenetic analyses (ML, MP, BY). The trees generated from those analyses were largely congruent, but the ML trees topologies only are illustrated here. The results are based primarily on the topology of the best tree from the ML analysis of the combined LSU+ITS (FIG. 1A–E); the separate best trees from ML analyses of the LSU and ITS datasets are provided (SUPPLEMENTARY FIGS. 1, 2). The combined LSU+ITS dataset included 324 ingroup sequences and 1434 characters, of which 571 (40%) were parsimony informative and 801 were constant; the LSU dataset included 387 ingroup sequences with 931 characters of which 321 (34%) were parsimony informative and 569 were constant; and the ITS dataset included 389 ingroup sequences and 509 characters, of which 276 (54%) were parsimony informative and 201 were constant; areas in the ITS1 and ITS2 regions (approx. 150 bp) that could not be confidently aligned were excluded. Strong support = >90 in ML and MP and

TABLE I. Antrodia clade genera, type species, number of described and sampled taxa, distribution and references to described taxa

Genera	Type species	Described taxa	Sampled taxa	Distribution	References (taxon descriptions)[a]
Amylocystis Bondartsev & Singer	*Amylocystis lapponica* (Romell) Bondartsev & Singer ex Singer	2	1	North America, Europe, Asia	26, 38, 68
Amyloporia Singer	*Amyloporia xantha* (Fr.) Bondartsev & Singer ex Bondartsev	~10	7	North and South America, Europe, Africa, Australia	1, 2, 10, 18, 26, 35, 37, 38, 39, 49, 78, 99
Antrodia P. Karst.	*Antrodia serpens* (Fr.) P. Karst.	~60	28	North, Central and South America, Europe, Asia, Africa, Australia	3, 6, 18, 26, 36, 38, 47, 51, 55, 57, 60, 62, 66, 75, 84, 86, 88, 89, 90, 97, 104, 106
Auriporia Ryvarden	*Auriporia aurea* (Peck) Ryvarden	4	2	North and South America, Europe, Asia	9, 26, 38, 42, 64, 72
Crustoderma Parm.	*Crustoderma dryinum* (Berk. & M.A. Curtis) Parmasto	17	7	North America, Europe, Asia	11, 13, 21, 22, 32, 34, 61, 67, 77, 93
Dacryobolus Fr.	*Dacryobolus sudans* (Alb. & Schw.: Fr.) Fr.	5	2	North and South America, Europe, Asia, Africa	5, 16, 19, 56, 93
Daedalea Pers.	*Daedalea quercina* Fr.	~60	5	North and South America, Europe, Asia, Africa	10, 17, 26, 27, 38, 4, 98, 103, 105
Fibroporia Parmasto	*Fibroporia vaillantii* (DC.) Parmasto	~7	7	North and South America, Europe, Africa, Australia	2, 3, 26, 38, 63, 78, 84, 102
Fomitopsis P. Karst.	*Fomitopsis pinicola* (Sw.) P. Karst.	~40	12	North and South America, Europe, Asia, Africa, Australia	10, 23, 24, 26, 38, 48, 54, 78, 81, 83, 100
Gilbertsonia Parmasto	*Gilbertsonia angulopora* (M.J. Larsen & Lombard) Parmasto	1	1	North America	15, 65
Laetiporus Murr.	*Laetiporus speciosus* Battarra ex Murrill [= *Laetiporus sulphureus* (Bull.) Murrill]	12	9	North and South America, Europe, Asia, Australia	10, 26, 38, 44, 59, 78, 85, 92, 101
Laricifomes Kot. & Pouzar	*Laricifomes officinalis* (Vill.) Kotl. & Pouzar	1	1	North America, Europe, Asia	26, 38, 54
Melanoporia Murr.	*Melanoporia nigra* (Berk.) Murrill	2	2	North America, Asia	3, 29, 40, 58
Neolentiporus Rajchenb.	*Neolentiporus maculatissimus* (Lloyd) Rajchenb.	1	1	S South America, Australia	44, 78, 50
Oligoporus Bref.	*Oligoporus farinosus* Bref., [= *Oligoporus rennyi* (Berk. & Broome) Donk]	~10	6	North and South America, Europe, Asia	2, 3, 10, 16, 29, 25, 41, 46, 63, 73, 79
Phaeolus (Pat.) Pat.	*Phaeolus schweinitzii* (Fr.) Pat.	2	1	North and South America, Europe	29, 41, 94
Piptoporus P. Karst.	*Piptoporus betulinus* (Bull.) P. Karst.	3	2	North America, Europe, Asia	29, 41, 29, 87
Postia Fr.	*Polyporus lacteus* Fr. [= *Postia lactea* (Fr.) P. Karst.]	~30	12	North and South America, Europe, Asia, Australia	3, 4, 10, 12, 16, 29, 41, 45, 78, 63, 75, 80, 82, 95
Pycnoporellus Murrill	*Pycnoporellus fulgens* (Fr.) Donk	2	2	North America, Europe	3, 8, 29, 41

TABLE I. Continued

Genera	Type species	Described taxa	Sampled taxa	Distribution	References (taxon descriptions)[a]
Rhodonia Niemelä	*Rhodonia placenta* (Fr.) Niemelä, K.H. Larss. & Schigel	1	1	North America, Europe	3, 29, 41, 79
Ryvardenia Rajchenb.	*Ryvardenia cretacea* (Lloyd) Rajchenb.	2	1	S South America, Australia, New Zealand	30, 43, 78
Sarcoporia P. Karst.	*Sarcoporia polyspora* P. Karst. [= *Parmastomyces transmutans* (Overh.) Ryvarden & Gilb.]	~6	1	North America, Europe, Asia	29, 20, 41, 53, 73, 96
Sparassis Fr.	*Sparassis crispa* (Wulfen) Fr.	8	5	North America, Europe, Asia	7, 31, 69, 70, 74, 76, 91
Spongiporus Murr.	*Spongiporus leucospongia* (Cooke & Harkn.) Murrill	~15	2	North America, Europe, Africa	3, 10, 16, 41, 79
Taiwanofungus Sheng H. Wu, Z.H. Yu, Y.C. Dai & C.H. Su	*Taiwanofungus camphoratus* (M. Zang & C.H. Su) Sheng H. Wu, Z.H. Yu, Y.C. Dai	2	2	Asia	33, 71
Wolfiporia Ryvarden & Gilb.	*Wolfiporia cocos* (F.A. Wolf) Ryvarden & Gilb.	5	3	North America, Asia, Africa	3, 10, 14, 29, 28, 41, 52

[a] References for brown-rot species descriptions. (1) Lowe 1946, (2) Lombard and Gilbertson 1965, (3) Lowe 1966, (4) Lowe and Lombard 1973, (5) Eriksson and Ryvarden 1975, (6) Niemelä and Ryvarden 1975, (7) Martin and Gilbertson 1976, (8) Niemelä 1980, (9) Parmasto 1980, (10) Ryvarden and Johansen 1980, (11) Gilbertson 1981, (12) Jülich 1982, (13) Nakasone and Gilbertson 1982, (14) Ginns and Lowe 1983, (15) Larsen and Lombard 1983, (16) Lindsey and Gilbertson 1983, (17) Roy and Mitra 1983, (18) David and Tortič 1984, (19) Manjón et al. 1984, (20) Ryvarden and Gilbertson 1984 (21) Nakasone 1984, (22) Nakasone1985, (23) Niemelä 1985, (24) Carranza-Morse and Gilbertson 1986, (25) Erkkilä and Niemelä 1986, (26) Gilbertson and Ryvarden 1986, (27) Rajchenberg 1986, (28) Ryvarden et al. 1986, (29) Gilbertson and Ryvarden 1987, (30) Rajchenberg 1987, (31) Burdsall and Miller 1988, (32) Gilbertson and Blackwell 1988, (33) Zang and Su 1990, (34) Boidin and Gilles 1991, (35) Niemelä et al. 1992, (36) Renvall and Niemelä 1992, (37) Gilbertson and Adaskaveg 1993, (38) Ryvarden and Gilbertson 1993, (39) Vampola and Pouzar 1993, (40) Hattori and Ryvarden 1994, (41) Ryvarden and Gilbertson 1994, (42) Salcedo-Larralde 1994, (43) Rajchenberg 1994, (44) Rajchenberg 1995, (45) Rajchenberg and Buchanan 1996, (46) Gilbertson and Ristich 1997, (47) Henrici and Ryvarden 1997, (48) Mossebo and Ryvarden 1997, (49) Roy and De 1997, (50) Bernicchia and Ryvarden 1998, (51) Chang and Chou 1998, (52) Dai 1998, (53) Kotiranta 1998, (54) Kotlaba and Pouzar 1998, (55) Chang and Chou 1999, (56) Boidin and Gilles 2000, (57) Buchanan and Ryvarden 2000, (58) Parmasto and Kollom 2000, (59) Burdsall and Banik 2001, (60) Bernicchia and Ryvarden 2001, (61) Gilbertson 2001, (62) Lodge et al. 2001, (63) Niemelä et al. 2001, (64) Núñez and Ryvarden 2001, (65) Parmasto 2001, (66) Dai and Niemelä 2002, (67) Gilbertson and Nakasone 2003, (68) Hattori 2003, (69) Desjardin et al. 2004, (70) Wang et al. 2004, (71) Wu et al. 2004, (72) Coelho 2005, (73) Niemelä et al. 2005, (74) Blanco-Dios et al. 2006, (75) Dai and Penttilä 2006, (76) Dai et al. 2006, (77) Kotiranta and Saarenoksa 2006, (78) Rajchenberg 2006, (79) Spirin et al. 2006, (80) Wei and Dai 2006, (81) Aime et al. 2007, (82) Dai and Hattori 2007, (83) Kim et al. 2007, (84) Spirin 2007, (85) Tomšovský and Jankovský 2008, (86) Valenzuela et al. 2008, (87) Choeyklin et al. 2009, (88) Du et al. 2009, (89) Gorjón and Bernicchia 2009, (90) Kout and Vlasák 2009, (91) Light and Woehrel 2009, (92) Ota et al. 2009, (93) Bernicchia and Gorjón 2010, (94) de Jesus and Ryvarden 2010, (95) Hattori et al. 2010, (96) Vlasák and Kout 2010, (97) Cui et al. 2011, (98) Lindner et al. 2011, (99) Rajchenberg et al. 2011, (100) Zhou and Wei 2012, (101) Banik et al. 2012, (102) Bernicchia et al. 2012, (103) Drechsler-Santos et al. 2012, (104) Spirin et al. 2012, (105) Li and Cui 2013, (106) Spirin et al. 2013.

PP > 0.95 in BY; while moderate support = >70 in ML, >50 in MP and PP > 0.90 in BY.

Most of the 123 species of brown-rot fungi in this study were represented in the three datasets with the exception of *Crustoderma longicystidiatum*, *Daedalea dickinsii*, *Neolentiporus maculatissimus*, *Piptoporus soloniensis*, *Postia japonica*, *Wolfiporia cartilaginea* and *W. cocos*, which were included only in the LSU dataset. *Amyloporia nothofaginea*, *A. stratosa*, *Antrodia serialiformis*, *Daedalea dickinsii*, *D. neotropica*, *D. pseudodochmia*, *D. stereoides*, *Fibroporia bohemica*, *F. citrina* and *Laetiporus portentosus* were included only

TABLE II. Antrodia clade genera, synoptic table of the dominant (•) and less dominant (+) characters among species

	Basidiocarp						Hymenophore			Hymenophore color						
Genera	Annual	Perennial	Pileate	Stipitate	Resupinate	Effused reflexed	Poroid (pores circular or angular)	Smooth (tuberculate – odontoid)	Daedaloid	White (-Cream -Brown)	Cream (-Brown)	Pinkish (-Purplish -Brown)	Yellow (-Brown)	Orange	Gray (Brown)	Brown (-Black)
Amylocystis	•		+			•	•			•						
Amyloporia	+	•			•	+	•			•	•		•			
Antrodia	•				•	+	•		+	•	+			+		
Auriporia	•		+		•		•		+		+		•			
Crustoderma	•				•	+		•			•		•		•	
Dacryobolus	•				•	•		•			•					
Daedalea	•	•	•			+	•		•		•	•	•			
Fibroporia	•				•	+	•			•	•		•	•		
Fomitopsis	•	•	•			+	•				•	•				
Gilbertsonia	•				•	+	•				•					
Laetiporus	•		•	•			•			•	•		•			
Laricifomes		•	•				•			•						
Melanoporia		•			•		•									•
Neolentiporus	•		•				•			•	•					
Oligoporus	•		•		•	+	•			•						
Phaeolus	•		•	•		+	+		•				•	•		
Piptoporus	•		•				•			•						
Postia	•		•		•	+	•			•	•					
Pycnoporellus	•				•	+	•							•		
Rhodonia	•				•	+	•					•				
Ryvardenia	•		•				•			•			•			
Sarcoporia	•		•		•	+	•				•					
Sparassis	•		•	•			•	•		•	•		•			
Spongiporus	•				•	+	•				•					
Taiwanofungus	•		•		•	+	•					•	•	•		
Wolfiporia	•				•	•	•			•	•		•			

TABLE II. Continued

Genera	Spores					Habitat-Substrate		Cystidia		Hyphal system			Gen. hyphae		Mating system			Nuclear behavior			
	Cylindric	Ellipsoid	Allantoid	Ovoid	Amyloid	Conifers	Hardwoods	Present	Absent	Monomitic	Dimitic	Trimitic	Clamped	Amyloid	Homothallic	Bipolar	Tetrapolar	Normal	Heterocytic	Astatocoenocytic	Holocoenocytic
Amylocystis	•		•		•	•	+	•		•			•	•			•	•			
Amyloporia	•		•			•	+		•		•	+					•		•		
Antrodia	•	•				•	•		•		•		•		•	•		•			
Auriporia	•	•	+			•	+	•		•	+		•			•				•	
Crustoderma	+	•				•	•	•		•			•			•				•	
Dacryobolus			•			•		•		•	•		•				•	•			
Daedalea	•	•					•		•			•	•			•		•			
Fibroporia		•				•	+		•		•		•				•	•			
Fomitopsis	•	•				•	•		•			•	•			•		•			
Gilbertsonia		•				•			•		•		•			•					
Laetiporus		+		•		+	•		•		•					•					•
Laricifomes	•	•				•			•		•	+	•								
Melanoporia		•		•			•		•		•		•								
Neolentiporus	•	•					•	•			•		•			•				•	
Oligoporus	•	•				•	+		•	•			•								
Phaeolus		•		•		•	+	•		•	+										•
Piptoporus	•	•					•		•		•	•	•			•		•			
Postia	•		•			•	+	•	•	•	•		•				•	•			
Pycnoporellus	•	•				•		•		•					•						•
Rhodonia		•				•			•	•			•	•			•		•		
Ryvardenia		•		+			•		•	•	+		•			•				•	
Sarcoporia	•					•	•		•	•			•				•		•		
Sparassis		•		•		•	+	+	•	•			+								
Spongiporus	•		•			•			•	•			•				•	•			
Taiwanofungus	•	+		•			•		•		•	+	•								
Wolfiporia	•	•		•		•	+		•		•										

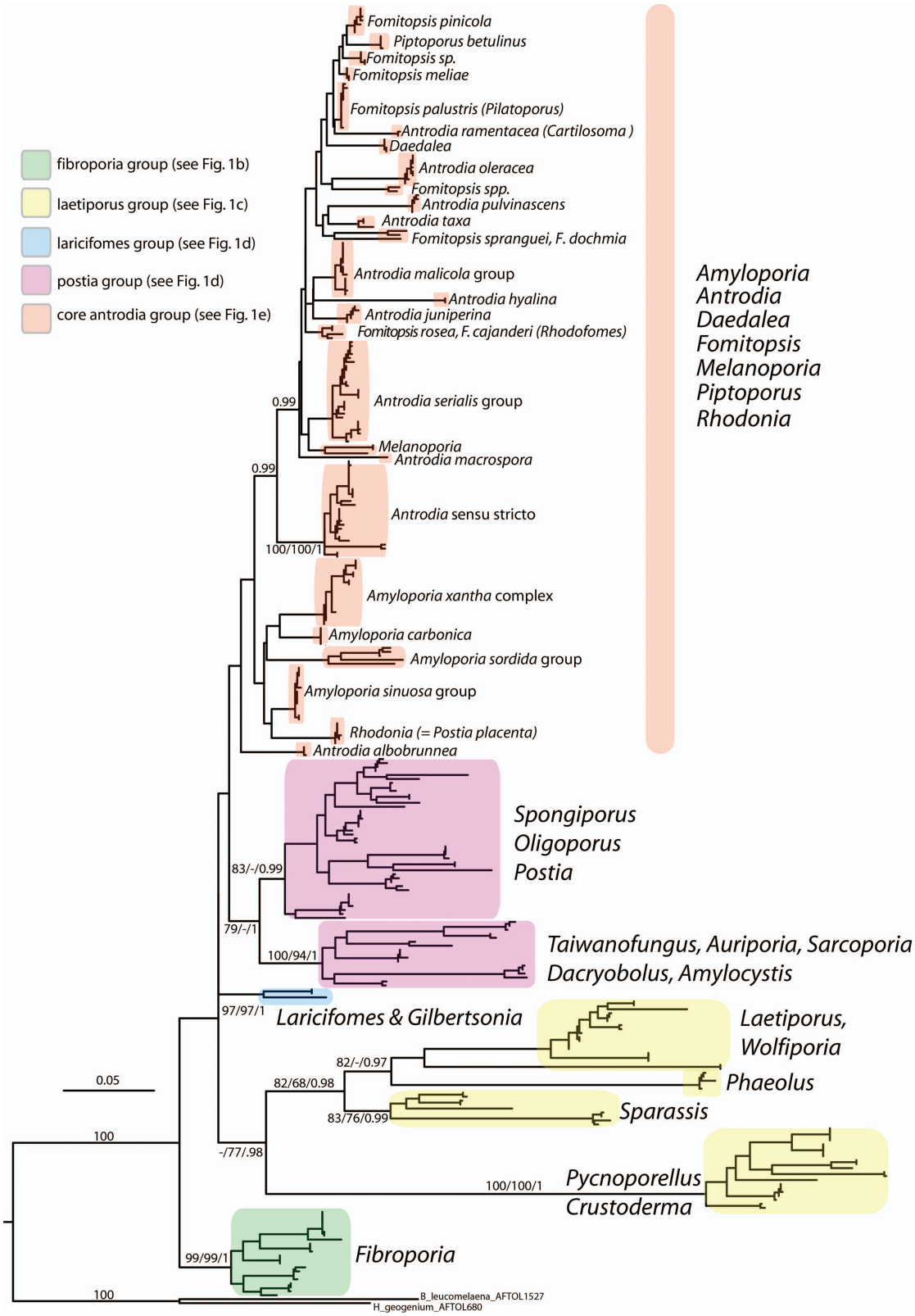

FIG. 1. A. Phylogenetic relationships of members of the antrodia clade inferred from the analyses of the combined dataset (nuclear LSU and ITS rDNA sequences). Topology from maximum likelihood analysis. Support values along branches are from maximum likelihood bootstrap (≥70), maximum parsimony bootstrap (≥50) and Bayesian analyses (PP ≥0.95) respectively. Generic types are indicated by ★. B. Phylogeny of the fibroporia group. C. Phylogeny of the laetiporus group. D. Phylogeny of postia and laricifomes groups. E. Phylogeny of the core antrodia group.

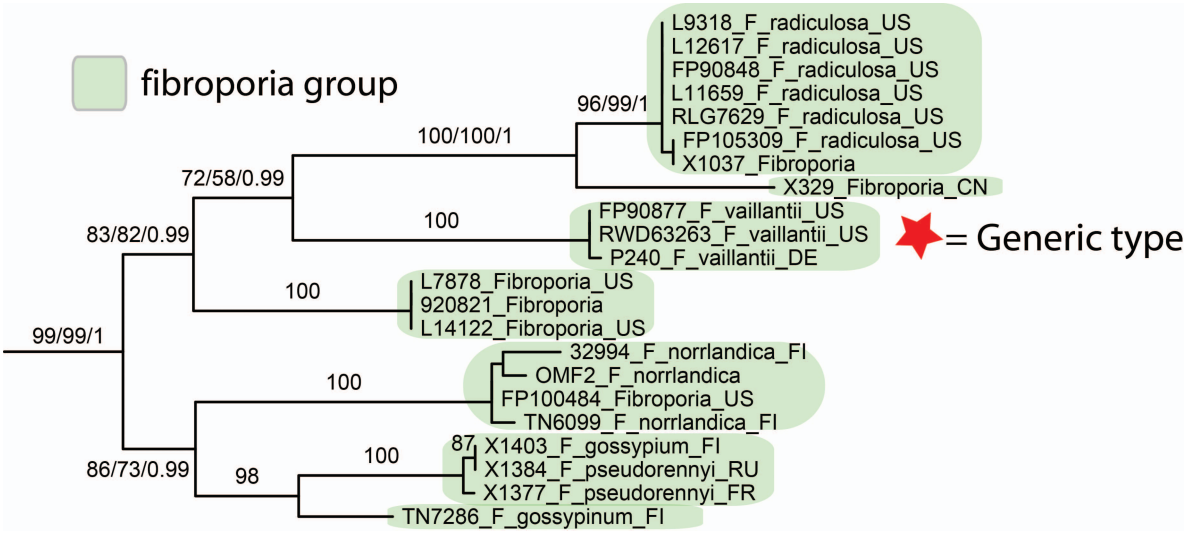

FIG. 1. Continued.

in the ITS dataset, and sequences of different isolates of *Ryvardenia campyla* were included in the ITS and LSU datasets; therefore 19 species were not represented in the combined dataset.

Overall, members of the antrodia clade were grouped into five moderately to strongly supported main groups in the analyses of the combined dataset (FIG. 1A–E): the fibroporia, laetiporus, laricifomes, postia and the core antrodia groups.

The fibroporia group.—The genus *Fibroporia* was recovered as a monophyletic, well supported inde-

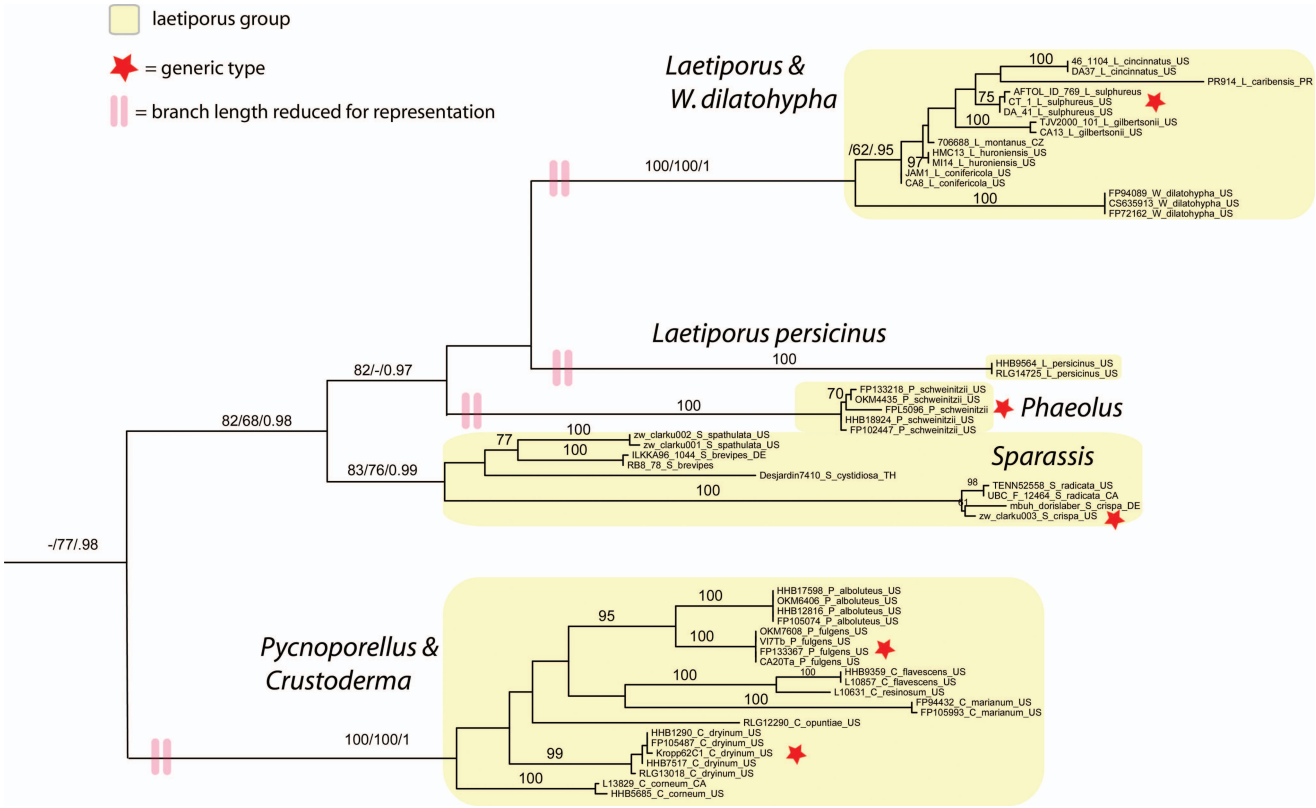

FIG. 1. Continued.

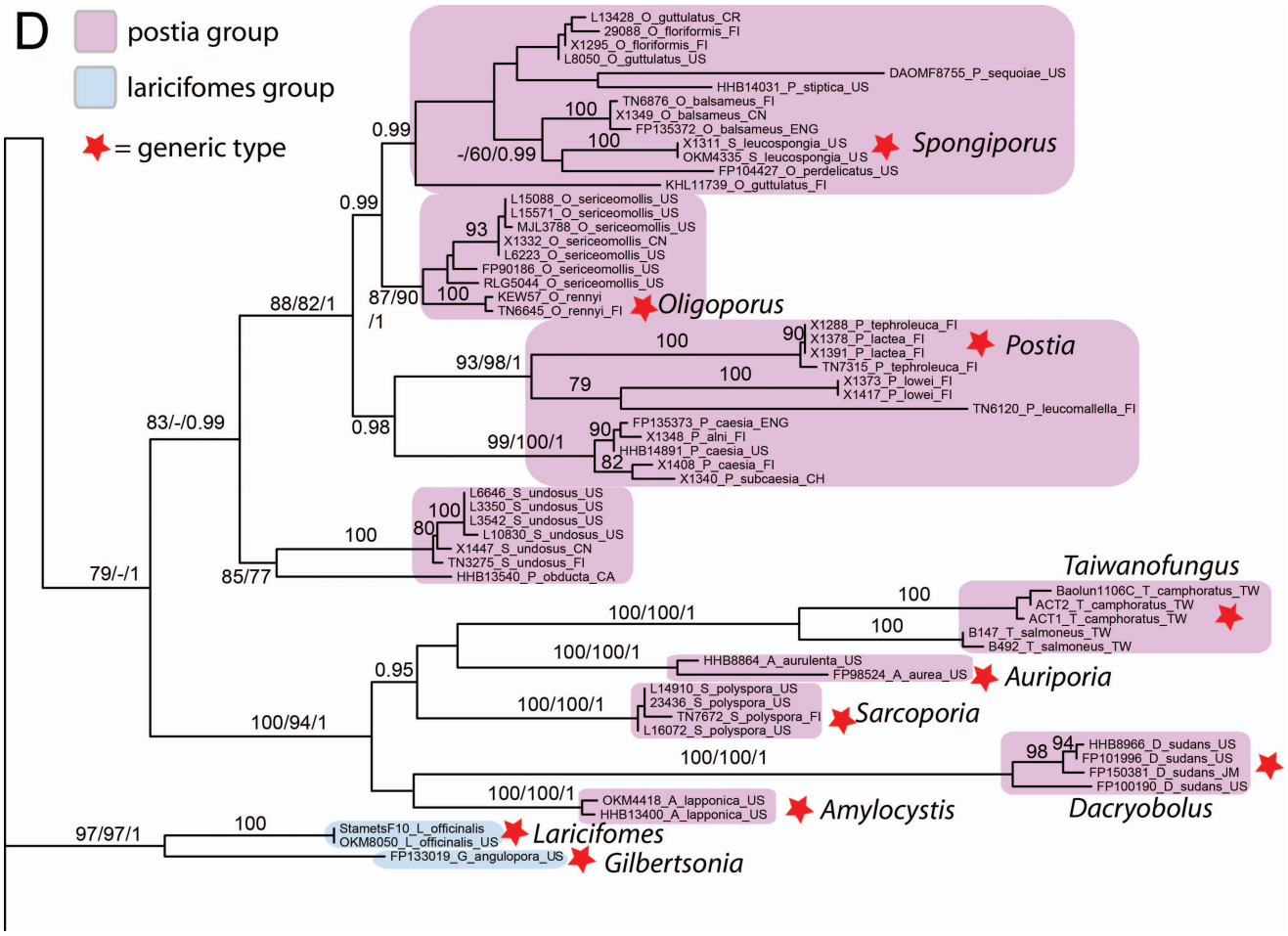

FIG. 1. Continued.

pendent clade, separate from other members of the antrodia clade and from other *Antrodia* and *Amyloporia* species. This group was well supported in all analyses of the combined and LSU datasets but not in the analyses of the ITS dataset (FIG. 1B; SUPPLEMENTARY FIGS. 1, 2). Two moderate to well supported subclades were found among *Fibroporia* species in the combined dataset. A subclade containing sequences of *F. vaillantii*, *F. radiculosa* and *Fibroporia* sp. (L7878, 920821, L14122) and the other containing sequences of *F. norrlandica*, *F. gossypium* and *F. pseudorennyi*.

The laetiporus group.—The laetiporus group contains species of *Laetiporus*, *Wolfiporia*, *Phaeolus*, *Sparassis*, *Crustoderma* and *Pycnoporellus* and received moderate to strong support in the MP and BY analyses of the LSU-ITS dataset (FIG. 1A, C). This assemblage not only contains morphologically diverse genera, but also the sequences in this clade were highly divergent compared to the rest of the antrodia clade, forming long branches in all the analyses and topologies. Within this group two well supported clades were obtained: the core laetiporus clade, containing species of *Laetiporus*, *W. dilatohypha*, *Phaeolus* and *Sparassis*, and the pycnoporellus clade, including species of *Crustoderma*, *Pycnoporellus* and *W. cocos* (the latter included only in the LSU dataset). The core laetiporus clade also received strong bootstrap support in the analyses of the ITS dataset (SUPPLEMENTARY FIG. 2), but not in the LSU dataset (SUPPLEMENTARY FIG. 1), while the pycnoporellus clade received strong support in all analyses of the ITS and LSU datasets as well.

Within the core laetiporus clade (FIG. 1C), molecular phylogenetic analyses indicated that *Laetiporus* and *Wolfiporia* as currently defined are not monophyletic, whereas the monophyly of *Sparassis* was supported. The relationships among *Laetiporus* species is unclear; we found similar results to those reported by Lindner and Banik (2008), in which sequences of *Laetiporus* sensu stricto (*L. cincinnatus*, *L. caribensis*, *L. sulphureus*, *L. gilbertsonii*, *L. huroniensis*, *L. montanus*, *L. conifericola*) appeared more closely related to *W. dilatohypha* than to *L. persicinus*

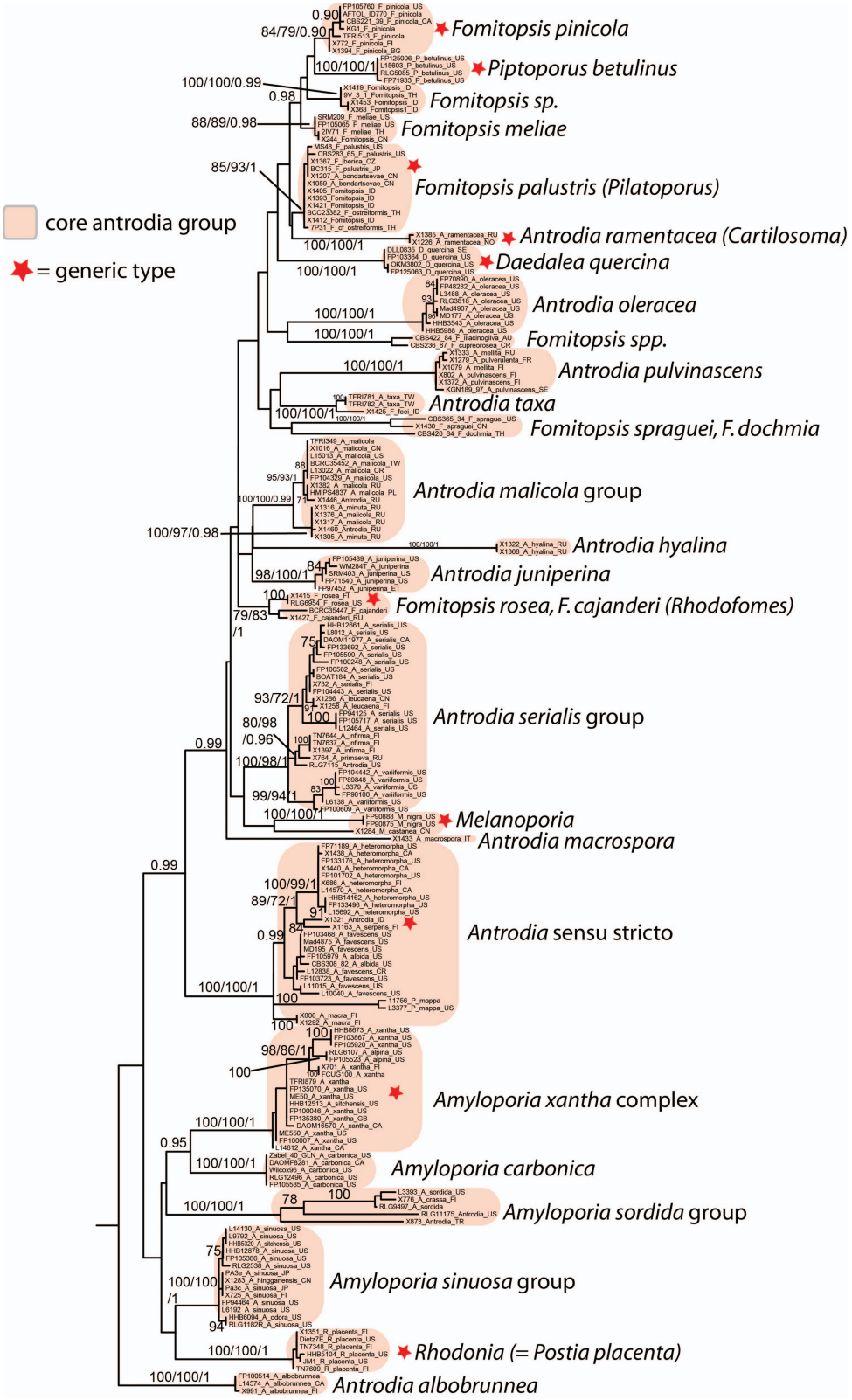

FIG. 1. Continued.

or *L. portentosus*. The placement of *L. persicinus* and *L. portentosus* was not resolved although they clustered with *Sparassis* and *Phaeolus* in some topologies. The sequence of *W. cartilaginea* was nested within the *W. dilatohypha* clade in the analyses of the LSU dataset, indicating that these species are not closely related to *W. cocos* (SUPPLEMENTARY FIG. 1).

Within the pycnoporellus clade (FIG. 1C), *Pycnoporellus* resolved as a monophyletic genus with *P. alboluteus* and *P. fulgens* being closely related; however *Crustoderma* was not monophyletic and the phylogenetic relationships among the seven species included in the analyses were not resolved. In all analyses of the LSU dataset (SUPPLEMENTARY FIG. 1), which is the only dataset that includes *W. cocos*, *Pycnoporellus* and *Crustoderma* formed a clade with *L. persicinus* and *W. cocos*. Sequences of *W. cocos* from USA, Japan and the Dominican Republic formed a monophyletic clade.

The laricifomes group.—Phylogenetic analyses demonstrated that the genus *Laricifomes* is not related to *Fomitopsis*, the genus in which it previously was placed (Kim et al. 2005, Zhou and Wei 2012) but instead forms a small but distinct lineage within the antrodia clade (FIG. 1A, D). Here *L. officinalis* appeared closely related to the genera *Ryvardenia* and *Gilbertsonia* in the analyses of the ITS and LSU datasets in which sequences of the three genera were represented; that association was moderately to strongly supported in all analyses (SUPPLEMENTARY FIGS. 1, 2).

The postia group.—This group received moderate support in the ML and BY analyses of the combined dataset (FIG. 1A, D) and in the MP analyses of the LSU dataset (SUPPLEMENTARY FIG. 1). This group contains two main clades: the core postia clade and sarcoporia. The core postia clade was recovered as a monophyletic group in all analyses of the three datasets, while the sarcoporia clade was recovered as monophyletic in the combined and ITS datasets. Within the core postia clade four subclades were resolved: the spongiporus clade, containing sequences of *S. leucospongia*, *Oligoporus balsameus*, *O. floriformis*, *O. guttulatus*, *O. perdelicatus*, *Postia sequoiae* and *P. stiptica*; the oligoporus clade including sequences of *O. rennyi* and *O. sericeomollis*; the *Postia* sensu stricto clade containing *P. lactea*, *P. alni*, *P. caesia*, *P. leucomallella*, *P. lowei*, *P. subcaesia* and *P. tephroleuca*; and the spongiporus undosus clade composed of *Spongiporus undosus* and *Postia obducta*.

The *core antrodia group.*—This group was recovered in the analyses of the combined (FIG. 1A, E) and ITS (SUPPLEMENTARY FIG. 2) datasets and included species in seven genera of the antrodia clade: *Amyloporia*, *Antrodia*, *Daedalea*, *Fomitopsis*, *Melanoporia*, *Piptoporus* and *Rhodonia*. The genus *Neolentiporus*, present in the LSU analyses (SUPPLEMENTARY FIG. 1), also seems to belong to this group. The core antrodia group lacks bootstrap support, and the relationships among these genera were not resolved; however several well supported lineages were obtained within it. In addition, the apparent association of six of these genera (excluding *Amyloporia*, *Neolentiporus*) was supported in the BY analysis of the combined dataset (FIG. 1A).

Amyloporia was not statistically supported as a monophyletic group in the present study, but most of the species believed to belong to this genus formed an independent group with the genus *Rhodonia* separated from other *Antrodia* species. Several strongly supported groups of species were recovered among *Amyloporia* species: the *Amyloporia xantha* complex (containing *A. xantha* and *A. alpina*) related to *Amyloporia carbonica*; the *Amyloporia sordida* group including *A. sordida* and *A. crassa* (closely related to a clade containing *A. stratosa* sequences in the ITS dataset); and the *Amyloporia sinuosa* group including *A. sinuosa*, *A. hingganensis*, *A. odora* and *A. sitchensis* (the isolate HHB-12513 [AY966451, AY333830] previously identified as *A. sitchensis* fell within the *Antrodia xantha* complex).

Sequences of *Rhodonia* from North America and Europe formed a well supported monophyletic clade in all analyses, separated from *Postia* species, and supporting the suggestions of Niemelä et al. (2005). As reported in molecular studies of Kim et al. (2001), Binder et al. (2005) and Garcia-Sandoval et al. (2011), *Rhodonia* grouped with *Amyloporia* species in all the topologies but the association was not always statistically supported. However sequences of *Amyloporia nothofaginea* formed a strongly supported monophyletic group with *Rhodonia placenta* in the analyses of the ITS dataset (SUPPLEMENTARY FIG. 2). The LSU sequence AY515355 (CBS336.49) corresponding to an isolate from Argentina (used in studies such as *R. placenta*) does not fall within the rhodonia clade but instead grouped with *A. juniperina* (SUPPLEMENTARY FIG. 1), while the LSU sequence AY333829 (HHB-5298), previously identified as *A. sitchensis*, fell within the rhodonia clade (SUPPLEMENTARY FIG. 1).

Several *Antrodia* species were segregated into moderately to strongly supported groups (*Antrodia* sensu stricto clade, *Antrodia serialis* group, *Antrodia malicola* group, *Antrodia pulvinascens* clade), while others appear as orphan lineages distributed in the clade (*Antrodia albobrunnea*, *A. hyalina*, *A. juniperina*, *A. macrospora*, *A. oleracea*, *A. taxa*, *A. ramentacea*).

The *Antrodia* sensu stricto clade includes *A. serpens*, *A. favescens* and *A. heteromorpha* closely related to *A.*

macra and *Postia mappa*. The *Antrodia malicola* group comprises *A. malicola* and *A. minuta*. Within this group a close relationship between *A. malicola* and *A. minuta* was shown and three subclades were observed: one including American and Asian isolates of *A. malicola* (conspecific isolates), a second including only European isolates of *A. malicola* and a third containing *A. malicola* and *A. minuta* isolates from Russia. The *Antrodia pulvinascens* clade includes Eurasian isolates of *A. pulvinascens*, *A. mellita* and *A. pulverulenta*. This clade grouped with *A. taxa*, *F. feei* and *F. spraguei* in some topologies (FIG. 1E, SUPPLEMENTARY FIG. 1) but without bootstrap support.

The relationships and placement of *A. albobrunnea* (isolates from Canada, Finland), *A. hyalina* (recently described from Russia), *A. juniperina* (described from USA but apparently with a worldwide distribution), *A. macrospora* (= *A. albidioides* from the Mediterranean, see Spirin et al. 2013), *A. oleracea* (originally described from USA but also present in Asia and Africa), *A. taxa* (originally described from Taiwan) and *A. ramentacea* (originally described from Scotland but reported also from Argentina) among other brown-rot fungi was not resolved. *Antrodia albobrunnea* occurred in a clade distant from other *Antrodia* species in all topologies. Sequences of *A. juniperina* from North America formed a monophyletic group with those from Ethiopia and Macedonia in the analyses of the ITS dataset. Sequences of *A. ramentacea* from Norway and Russia appeared identical in the ITS dataset and closely related to another sequence of *A. ramentacea* from Argentina. Sequences of *Antrodia taxa* were grouped with those of *F. feei* (described from Brazil) from Indonesia and Australia in the LSU analyses.

Daedalea species formed a monophyletic group (daedalea clade) within which sequences of *D. quercina* were grouped with *D. dickinsii* and *D. pseudodochmia*, and sequences of *D. neotropica* grouped with one *D. quercina* sequence (SUPPLEMENTARY FIG. 1). *Daedalea stereoides* appeared as a sister group of the daedalea clade (supported in the BY analysis of the ITS dataset [SUPPLEMENTARY FIG. 1]; in this analysis the daedalea clade belonged to the same lineage as sequences of *Antrodia taxa*, while in the combined dataset [FIG. 1E] sequences of *D. quercina* grouped with *Fomitopsis* species).

The phylogenetic analyses suggest that at least nine of the 12 *Fomitopsis* species included in this study represent phylogenetic species. Five well supported groups were found among *Fomitopsis* species: the *Fomitopsis* sensu stricto clade (well supported in the BY analysis of LSU-ITS dataset) containing sequences of *F. pinicola*, *P. betulinus*, *F. meliae* and *Fomitopsis* sp. (unidentified specimens from Indonesia and Thailand); the *Fomitopsis palustris* clade (well supported in all the analyses of the combined and ITS datasets) including sequences of *F. palustris*, *F. iberica*, *F. ostreiformis*, *A. bondartsevae* and *Fomitopsis* sp. (specimens from Indonesia); the *Fomitopsis spraguei* clade (strongly supported) containing sequences of *F. spraguei* from North America and Asia; the *Fomitopsis rosea* clade (supported in all the analyses of the combined dataset) containing sequences of *F. rosea* and *F. cajanderi*; and the *Fomitopsis* spp. clade containing sequences of *F. lilacinogilva*, *F. cupreorosea* and a sequence of *F. feei* (from Mexico, SUPPLEMENTARY FIG. 2). Another sequences of *F. feei* (from Finland) grouped with *Antrodia taxa* in the LSU dataset analyses (SUPPLEMENTARY FIG. 1). The association of *F. dochmia* with other *Fomitopsis* species was not statistically supported; therefore its placement remains unclear. The LSU sequence of *Piptoporus soloniensis* fell within the *Antrodia serialis* group in analyses based on the LSU dataset (SUPPLEMENTARY FIG. 1); therefore that sequence is not related to *P. betulinus*.

With respect to the genus *Melanoporia*, sequences of *M. nigra* and *M. castanea* grouped together in all the ML analyses of the combined and ITS datasets (FIG. 1E, SUPPLEMENTARY FIG. 2) but not in the LSU dataset (SUPPLEMENTARY FIG. 1), indicating that this genus may not be monophyletic. Although this genus fell within the core Antrodia clade, its relationship with other genera or species remains unresolved. The sequence of *Neolentiporus maculatissimus* grouped with the daedalea clade in the analyses based on the LSU dataset (SUPPLEMENTARY FIG. 1), but this association was not statistically supported.

DISCUSSION

The present study provides a phylogenetic outline of the antrodia clade and identifies numerous terminal groups that could form the basis of an eventual generic reclassification of this group of brown-rot fungi. Our results support the segregation of the genus *Antrodia* s.l. into *Antrodia* and *Fibroporia* because the monophyly of *Amyloporia* was not supported. Several *Fomitopsis* species can be grouped within *Fomitopsis* s.s., while others should be placed under *Rhodofomes*. The placement of *Piptoporus betulinus* within *Fomitopsis* s.s. requires nomenclatural revision. *Postia* species can be classified under the genera *Postia* and *Oligoporus*, and *Spongiporus undosus* probably should be placed in a different genus. We also agree that the genera *Gilbertsonia*, *Rhodonia*, *Ryvardenia* and *Taiwanofungus* represent independent taxa. Overall, further work is needed including additional taxon sampling and multilocus and genomic analyses to refine evolutionary relationships among the diverse members of antrodia clade.

The fibroporia group.—Our results agree with findings from other studies (Kim et al. 2001, Yu et al. 2010, Rajchenberg et al. 2011, Bernicchia et al. 2012, Pildain and Rajchenberg 2012), where *Fibroporia* species formed a distinct phylogenetic group separated from *Antrodia* sensu lato, suggesting that these species are not closely related to the other *Antrodia* species. *Fibroporia* species also differ from other *Antrodia* species in the development of a fimbriate to rhizomorphic margin; middle-sized, slightly cyanophilous and slightly thick-walled spores; and some display a tetrapolar rather than bipolar mating system. Most of the species that fall within genus *Fibroporia*, except *F. radiculosa* (from USA) and *F. gossypium* (from Argentina), originally were described from Europe. The monophyly of the genus *Fibroporia* was not supported in the analyses of the ITS dataset (SUPPLEMENTARY FIG. 2), which included sequences of *F. bohemica* (from Czech Republic) and *F. citrina* (from Italy). The subclade of *F. norrlandica*, *F. gossypium* and *O. pseudorennyi* was the only statistically supported clade in the analyses of this group. *Fibroporia citrina*, although within the fibroporia clade, did not appear closely related to other *Fibroporia* species, while sequences of *F. bohemica* grouped with *Fibroporia* sp. (L7878, 920821, L14122), suggesting the presence of *F. bohemica* in North America. In addition sequences of *F. norrlandica* grouped with *Fibroporia* sp. (FP100484), suggesting the presence of *F. norrlandica* in North America.

The laetiporus group.—The close relationships among members of the core laetiporus clade also was observed in Kim and Jung (2000), Lindner and Banik (2008), Yu et al. (2010) and Garcia-Sandoval et al. (2011), while the apparent relationship between the core laetiporus clade and *Pycnoporellus* also was suggested by Wang et al. (2004), Lindner and Banik (2008) and Garcia-Sandoval et al. (2011). Although members of these genera differ in the shape of their basidiocarps, they share certain micro characters: most of their hyphal systems are monomitic without clamp connections (*Laetiporus* and *Wolfiporia* are dimitic, *Sparassis* may have clamps) and form ellipsoid to ovoid spores; in addition species of *Laetiporus*, *Phaeolus* and *Pycnoporellus* display a holocoenocytic nuclear behavior (TABLE II).

Within *Sparassis* we obtained results similar to Desjardin et al. (2004) and Wang et al. (2004), in that *S. spathulata* and *S. brevipes* formed a clade with *S. cystidiosa* as their sister group while *S. crispa* formed a clade with *S. radicata*. Sequences of *Phaeolus schweinitzii* formed a monophyletic group that clustered with *Laetiporus* species in the analyses of the combined dataset; this result also was observed in Hibbett and Donoghue (1995), Boidin et al. (1998), Kim and Jung (2001), Hibbett and Binder (2002) and Dai et al. (2006). This study also demonstrates a close evolutionary relationship between *Crustoderma* and *Pycnoporellus* and their association with *W. cocos*, which has not been demonstrated in studies. Some *Crustoderma* and *Pycnoporellus* species form resupinate basidiocarps, produce a monomitic hyphal system and ellipsoid spores but differ in the form of the hymenophore (TABLE II).

The laricifomes group.—Although further study is required to strength the association among *Laricifomes*, *Ryvardenia* and *Gilbertsonia*, our results suggest that these genera can be considered as independent taxa. Pildain and Rajchenberg (2012) also supported the use of the genus *Ryvardenia*. These three genera differ in their distributions (*L. officinalis* is circumglobal, *Ryvardenia* is from the southern hemisphere and *Gilbertsonia* is from North America) as well as in several morphological characters; *Laricifomes* forms perennial pileate basidiocarps, *Ryvardenia* produces annual pileate basidiocarps and *Gilbertsonia* has annual resupinate basidiocarps (TABLE II). Many of the species in these genera produce ellipsoid spores, lack hymenial cystidia, produce a dimitic hyphal system and display a bipolar mating system.

The postia group.—Although not all species formerly treated under *Oligoporus*, *Postia* and *Spongiporus* are represented in this study, and recognizing that further studies are necessary to clarify the species groupings within these genera, our results support the independent use of at least two genera: the genus *Oligoporus* to place species that grouped within the spongiporus and oligoporus clades and genus *Postia* for species that grouped within the postia sensu stricto clade. Erkkilä and Niemelä (1986) sought to differentiate the two genera on the basis of spore shape and spore-wall thickness, but their division is not supported in our analyses. Our results also suggest that *Spongiporus undosus* and *Postia obducta* do not belong in *Postia* or *Oligoporus*. Some of the associations observed here also were obtained in the preliminary study by Schigel et al. (unpubl). Species under these genera share similar morphological characters, including annual basidiocarps that are mostly pileate, a hyphal system that is monomitic with clamps, cystidia in some species and the production of mostly cylindrical to allantoid basidiospores. Well known species in these groups have shown tetrapolarity and normal nuclear behavior with uninucleate basidiospores (TABLE II).

Within the sarcoporia clade we obtained two groups (not statistically supported), one including species of *Auriporia*, *Sarcoporia* and *Taiwanofungus*

and the other one containing sequences of *Amylocystis lapponica* and *Dacryobolus sudans*. A close relationship between these genera has not been suggested before, and although the species within this clade are morphologically different they share some characters: most species have resupinate basidiocarps with monomitic hyphal systems with clamp connections and they produce cylindrical to allantoid spores. In addition, *Amylocystis*, *Dacryobolus* and *Sarcoporia* display a tetrapolar mating system and most of them have a north temperate to worldwide distribution (TABLES I, II).

The core antrodia group.—Some *Amyloporia* species included in this study originally were described from Europe (e.g. *A. alpina*, *A. crassa*, *A. sinuosa*, *A. xantha*), while others were described from North America (e.g. *A. carbonica*, *A. odora*, *A. sitchensis*). One species in this group was described from China (*A. hingganensis*) and one from Argentina (*A. stratosa*). The phylogenetic relationships among some of these species also was demonstrated by Rajchenberg et al. (2011) and Pildain and Rajchenberg (2012). The relationships among *A. alpina*, *A. crassa*, *A. sordida* and *A. xantha* were demonstrated by David and Tortič (1984) on morphological and biological grounds; they placed these species under the genus *Amyloporiella*. Several *Amyloporia* species possess a tetrapolar mating system, displaying heterocytic nuclear behavior with uninucleate spores. We found that both *A. xantha* and *A. sinuosa* may represent species complexes and that the identities of *A. odora* and *A. sitchensis* are not clear. To define the final placement of these species more isolates and sequences of additional gene regions are needed in that some of these species are poorly represented in this study. The phylogenetic relationship between *Amyloporia nothofaginea* and *Rhodonia placenta* also was observed in the study by Pildain and Rajchenberg (2012). *Rhodonia placenta*, originally described from Sweden, is also known from North America, while *A. nothofaginea* was described from Argentina. These species differ in several morphological characters, distribution and host association although they display a similar mating system and nuclear behavior.

Within *Antrodia* sensu stricto clade, *Antrodia serpens* is a European species, *A. favescens* is a North American species and *A. heteromorpha* is distributed in Eurasia and North America. *Antrodia macra* was described from Norway but has a wide distribution in Europe and has been reported also from Asia, while *P. mappa* has been found in North America and Eurasia; these species share some morphological characters including somewhat larger cylindrical spores. These results indicate that *P. mappa* belongs to the genus *Antrodia* and that the isolates FCUG-1100 and FCUG-1396, previously identified as *A. albida*, correspond to *A. heteromorpha*. Similar results were reported by Spirin et al. (2013), in which a more detailed study and sampling of members of *Antrodia* sensu stricto was conducted; among other findings, they reported that isolates previously identified as *A. albida* from North America correspond to *A. favescens* and that *A. serpens* has not been found in North America.

The antrodia serialis group contains *A. serialis*, *A. serialiformis*, *A. leucaena*, *A. infirma*, *A. primaeva* and *A. variiformis*; these species differ in their distribution and in some morphological characters such as the color of the basidiocarp and basidiospore size. *Antrodia serialis*, *A. serialiformis* and *A. variiformis* originally were described from North America, *A. infirma* and *A. primaeva* from Finland and *A. leucaena* from China. *Antrodia serialis*, *A. variiformis*, *A. infirma* and *A. primaeva* are associated with gymnosperms, while *A. serialiformis* and *A. leucaena* are associated with angiosperms. The associations among several of these species also were reported in Yu et al. (2010), Rajchenberg (2011) and Spirin et al. (2012). In this study sequences of *A. serialis* nested in at least three subclades in the analyses of the ITS dataset: One clade includes representatives from western North America (NA); the second contains specimens from eastern NA and the sequence of *A. serialiformis*; and the third includes American and European species. These results suggest that *A. serialis* might represent a species complex and also support the comments of Kout and Vlasák (2009) about the possible misidentification of isolates of *A. serialis* and *A. serialiformis*. Within the *Antrodia malicola* group, *Antrodia malicola* is a North American species also present in Japan and Africa, whereas *A. minuta* has been reported only from Russia; these species differ in their distributions and *A. minuta* is distinguished by its tiny pileate basidiocarps, although they have similar basidiospores.

The close relationship between *A. pulvinascens* and *A. pulverulenta* was shown in Spirin et al. (2012); based on morphological characters *A. pulvinascens* was thought to be related to *A. crassa*, *A. pulverulenta* to *A. hyalina* and *A. mellita* to *A. heteromorpha*, although these relationships were not supported by molecular data. The sequence of *A. macrospora* appears in different places in the topologies of the three datasets. The association of *A. bondartsevae* with *F. ostreiformis* also was demonstrated by Spirin et al. (2012). *Antrodia hyalina* and *A. oleracea* clustered together in the analyses of the ITS dataset, and these species share some morphological characters including cylindrical spores of similar size and an associa-

tion with angiosperms. With respect to *Antrodia ramentacea*, Spirin (2007) suggested that this species should be excluded from the genus *Antrodia* based on its soft and fleshy fruiting bodies and gelatinous hymenophore and proposed it be placed in the genus *Cartilosoma* Kotlába & Pouzar.

Fomitopsis species were not grouped within the same clade, demonstrating the polyphyly of this genus, as indicated in phylogenetic studies by Kim et al. (2005, 2007), Yu et al. (2010) and Zhou and Wei (2012). Most of the *Fomitopsis* species included in the analyses have a worldwide distribution, however not all species are well represented in this study. More sequences, including ex-type sequences, need to be examined to determine the species delimitation in the genus. However based on our results we suggest that the genus *Rhodofomes* should be used to group members of the *F. rosea* clade while the use of the genus *Pilatoporus* needs further study. Our results also support the placement of *Piptoporus betulinus* within the *Fomitopsis* sensu stricto clade as has been reported in other molecular studies (Hibbett and Donoghue 1995, Boidin et al. 1998, Hibbett and Binder 2002, Kim et al. 2003, Binder et al. 2005, Dai et al. 2006, Garcia-Sandoval et al. 2011, Zhou and Wei 2012). This result creates a nomenclatural conundrum, involving two well known genera, both described by Karsten (1881), neither of which therefore has priority over the other. Both species produce brown rot and share the same mating system and nuclear behavior, but they differ in the structure of their basidiocarp and host specificity: *P. betulinus* is restricted to birch while *F. pinicola* is associated mainly with coniferous wood.

Although the relationships among *Daedalea* species agreed with the findings of Lindner et al. (2011) the relationship between this genus and other members of the antrodia clade remains unresolved. Sequences of *D. quercina* also grouped with *Antrodia*, *Fomitopsis*, *Piptoporus* and *Neolentiporus* in previous studies (e.g. Hibbett and Donoghue 1995, Kim and Jung 2001, Yu et al. 2010, Bernicchia et al. 2012); although these genera share some morphological characters they differ in the form of the hymenophore (TABLE II). The genus *Neolentiporus* also appeared as part of the core antrodia clade, as shown in Garcia-Sandoval et al. 2011, but its placement remains unresolved.

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SUPPLEMENTARY TABLE I. Species and isolates included in the study, their vouchers, locality and GenBank accession

Species	Isolate number	Locality	ITS GenBank accession no.	LSU GenBank accession no.
Amylocystis lapponica (Romell) Bondartsev & Singer ex Singer	HHB-13400-Sp	USA, Alaska	KC585237	KC585059
	OKM-4418-Sp	USA, Montana	KC585238	KC585060
	KHL-11755		–	EU118603
Amyloporia carbonica (Overh.) Vampola & Pouzar	DAOM-F-8281-T	Canada, British Columbia	KC585239	KC585061
	FP-105585-Sp	USA, Oregon	KC585240	KC585062
	RLG-12496-Sp	USA, Nevada	KC585241	KC585063
	Wilcox-96	USA, California	KC585242	KC585064
	Zabel-40-GLN	USA, New York	KC585243	KC585065
Amyloporia nothofaginea Rajchenb. & Gorjón	BAFC519794 (=MMBP-2011)	Argentina	JF713078	–
	BAFC519796 (=MBP-2011a)	Argentina	JF713079	–
Amyloporia sinuosa (Fr.) Rajchenb., Gorjón & Pildain	FP-105386-Sp	USA, New Hampshire	KC585244	KC585066
	FP-94464-Sp	USA, Idaho	KC585245	KC585067
	HHB-12878-Sp	USA, Alaska	KC585246	KC585068
	L-14130-Sp	USA, New York	KC585247	KC585069
	L-6192-Sp	USA, Colorado	KC585248	KC585070
	L-9792-Sp	USA, Arizona	KC585249	KC585071
	Pa-3C	JapanYamagata Prefecture	KC585250	KC585072
	Pa-3e	JapanShizuoka Prefecture	KC585251	KC585073
	RLG-2538	USA, New York	EU232196	EU232288
	X725 (=Miettinen-12407)	Finland	JQ700270	JQ700270
	P-115 (=RLG-2538)	USA	AJ416068	–
	P-211 (G-214)	Germany, Karlsrube	AJ345011	–
	RLG-1182R	USA, Arizona	AY966450	AY333831
Amyloporia sitchensis (D.V. Baxter) Vampola & Pouzar	HHB-5320-Sp	USA, Montana	KC585252	KC585074
	HHB-5298	USA, Montana	–	AY333829
	HHB-12513	USA, Alaska	AY966451	AY333830
Amyloporia sordida (Ryvarden & Gilb.) Vampola & Pouzar	L-3393-R	USA, New York	KC585253	KC585075
	RLG-9497		EU232193	EU232289
Amyloporia stratosa (J.E. Wright & J.R. Deschamps) Rajchenb., Gorjón & Pildain	MR-10679	Argentina	JF713081	–
	Gates-FF259	Australia, Tasmania	JF713080	–
Amyloporia xantha (Fr.) Bondartsev & Singer	DAOM-16570	Canada, British Columbia	KC585254	KC585076
	Denmark-Myc	Norway, Porsgrunn	–	KC585077
	FP-100007-R	USA, California	KC585255	KC585078
	FP-100046-R	USA, New York	KC585256	KC585079
	FP-103867-Sp	USA, Maryland	KC585257	KC585080
	FP-105920-Sp	USA, South Dakota	KC585258	KC585081
	FP-135070-Sp	USA, Montana	KC585259	KC585082
	FP-135380-Sp	England, Crewkerne	KC585260	KC585083
	HHB-8673	USA, Arizona	KC585261	KC585084
	L-14612-Sp	Canada, Alberta	KC585262	KC585085
	ME-50	USA, Wisconsin	KC585263	KC585086

numbers.

Species	Isolate number	Locality	ITS GenBank accession no.	LSU GenBank accession no.
Amyloporia xantha (Fr.) Bondartsev & Singer	ME-550-R	USA, Washington	KC585264	KC585087
	FCUG-100		–	EU232283
	TFRI-879		EU232210	EU232284
	isolate P209 (G185)	Turkey	AJ415569	–
	Sample 43		AJ006681	–
	CBS 155.79	Germany, Teutoburger Wald	DQ491424	–
	X701 (=Miettinen-12400)	Finland	JQ700269	JQ700269
Antrodia albida (Fr.) Donk	CBS 308.82	USA, Wisconsin	DQ491414	AY515348
	FP-105979	USA, Maryland	EU232189	EU232272
	sample 31		AJ006680	–
	FCUG-1100		–	AY333846
	FCUG-1396		–	AY333845
Antrodia albobrunnea (Romell) Ryvarden	FP-100514		EU232215	EU232299
	L-14574-Sp	Canada, Alberta	KC585265	KC585088
	X991 (=Miettinen-13277.2)	Finland	KC595889	KC595889
Antrodia alpina (Litsch.) Gilb. & Ryvarden	FP-105523-Sp	USA, Oregon	KC585266	KC585089
	RLG-6107-Sp	USA, Montana	KC585267	KC585090
Antrodia bondartsevae Spirin (=*Antrodia wangii*)	X1059 (=Dai-7172)	China	JQ700275	JQ700275
	X1207 (Dai-6613)	China	JQ700277	JQ700277
	Cui5525		FJ617303	–
Antrodia crassa (P. Karst.) Ryvarden	X776 (=Helo-60707009)	Finland	KC595890	KC595890
Antrodia favescens (Schwein.) Vlasák & Spirin, comb. nov.	FP-103468-Sp	USA, Maryland	KC585268	KC585091
	FP-103723-Sp	USA, Virginia	KC585269	KC585092
	L-10040-Sp	USA, Arizona	KC585270	KC585093
	L-11015-Sp	USA, North Carolina	KC585271	KC585094
	L-12838-Sp	Costa Rica, San José	KC585272	KC585095
	Mad-4875-R	USA, Wisconsin	KC585273	KC585096
	MD-195	USA, Wisconsin	KC585274	KC585097
Antrodia heteromorpha (Fr.) Donk	FP-101702-Sp	USA, New York	KC585275	KC585098
	FP-133176-Sp	USA, Wisconsin	KC585276	KC585099
	FP-133496-Sp	USA, Oregon	KC585277	KC585100
	FP-71189-R	USA, Pennsylvania	KC585278	KC585101
	HHB-14162-T	USA, Alaska	KC585279	KC585102
	L-14570-Sp	Canada, Alberta	KC585280	KC585103
	L-15692-Sp	USA, New York	KC585281	KC585104
	X1438 (=Niemelä-2589)	Canada	KC543147	KC543147
	X1440 (=Niemelä-2621)	Canada	KC543148	KC543148
	X686 (=Niemelä-6348)	Finland	JQ700268	JQ700268
	CBS 200.91	Canada, Nova Scotia	DQ491415	–
Antrodia hingganensis Y.C. Dai & Pentillä	X1283 (=Dai-3748)	China	KC595893	KC595893
Antrodia hyalina Spirin, Miettinen & Kotir.	X1322 (=Spirin-2772)	Russia	JQ700283	JQ700283
	X1368 (=Kotiranta-19668)	Russia	JQ700284	JQ700284

Species	Isolate number	Locality	ITS GenBank accession no.	LSU GenBank accession no.
Antrodia infirma Renvall & Niemelä	TN-7637 (=4236)	Finland	KC595894	KC595894
	TN-7644 (=4238)	Finland	KC595895	KC595895
	X1397 (=Miettinen-13262.2)	Finland	JQ700287	JQ700287
Antrodia juniperina (Murrill) Niemelä & Ryvarden	FP-105489-Sp	USA, Maryland	KC585282	KC585105
	FP-71540-R	USA, Maryland	KC585283	KC585106
	FP-71586-R	USA, Virginia	–	KC585107
	FP-97452-T	Ethiopia	KC585284	KC585108
	SRM-403-T	USA, Nebraska	KC585285	KC585109
	WM-284T		EU232212	EU232295
	CBS 639.75	Tanzania, Mount Kilimanjaro	–	AY515347
	CBS 117.40	USA, Maryland	DQ491416	–
	Macedonici 07/8020	Macedonia	FM872462	–
	Macedonici 01/2095	Macedonia	FM872461	–
Antrodia leucaena Y.C. Dai & Niemelä	X1258 (=Pennanen-927)	Finland	JQ700278	JQ700278
	X1286 (=Dai-2910a)	China	JQ700281	JQ700281
Antrodia macra (Sommerf.) Niemelä	X806 (=Hottola-2729)	Finland	KC543134	KC543134
	X1292 (=Niemelä-7865)	Finland	KC543138	KC543138
	MUAF 887	Czech Republic	EU340898	–
Antrodia macrospora Bernicchia & De Dominci (=*A. albidoides*)	X1433 (=Bernicchia-5672)	Italy	KC543146	KC543146
Antrodia malicola (Berk. & M.A. Curtis) Donk	FP-104329-Sp	USA, Maryland	KC585286	KC585110
	HMIPS-4837	Poland?, Ustrzyki Dolne	KC585287	KC585111
	L-13022-Sp	Costa Rica, Alajuela	KC585288	KC585112
	L-15013-Sp	USA, Indiana	KC585289	KC585113
	TFRI-349		EU232213	EU232296
	MJL-1167-Sp	USA, New York	–	AY333835
	BCRC-35452	Taiwan	DQ013299	AY333837
	X1016 (=Miettinen-10595.1)	China	KC595896	KC595896
	X1382 (=Spirin)	Russia	JQ700282	JQ700282
	X1317 (=Spirin-30.V.2000)	Russia	KC595900	KC595900
	X1376 (=Spirin-3447)	Russia	KC595901	KC595901
Antrodia mellita Niemelä & Penttillä	X1079 (=Miettinen-2645)	Finland	KC595897	KC595897
	X1333 (=Spirin-3315)	Russia	KC543139	KC543139
Antrodia minuta Spirin	X1305 (=Spirin-2680)	Russia	KC595898	KC595898
	X1316 (=Spirin-2785)	Russia	KC595899	KC595899
Antrodia odora (Peck ex Sacc.) Gilb. & Ryvarden	HHB-6094R	USA, Arizona	EU232194	EU232286
Antrodia oleracea (R.W. Davidson & Lombard) Ryvarden	FP-48282-R	USA, Michigan	KC585290	KC585114
	FP-70890-Sp	USA, Georgia	KC585291	KC585115
	HHB-3543-Sp	USA, Michigan	KC585292	KC585116
	HHB-5988-Sp	USA, Arizona	KC585293	KC585117
	L-3488-R	USA, New York	KC585294	KC585118
	Mad-4907	USA, Texas	KC585295	KC585119

Species	Isolate number	Locality	ITS GenBank accession no.	LSU GenBank accession no.
Antrodia oleracea (R.W. Davidson & Lombard) Ryvarden	MD-177	USA, Wisconsin	KC585296	KC585120
	RLG-3818	USA, North Carolina	EU232198	EU232291
Antrodia primaeva Renvall & Niemelä	X764 (=Miettinen-117)	Russia	JQ700272	JQ700272
Antrodia pulverulenta B. Rivoire	X1279 (=Rivoire-3450)	France	JQ700280	JQ700280
Antrodia pulvinascens (Pilát) Niemelä	X802 (=Miettinen-7488.1)	Finland	JQ700274	JQ700274
	X1372 (=Pennanen-1532)	Finland	JQ700286	JQ700286
	KGN189-97	Sweden	JQ700291	JQ700291
Antrodia ramentacea (Berk. & Broome) Donk	X1226 (=Marstad-274.09)	Norway	KC543137	KC543137
	X1385 (=Spirin-2540)	Russia	KC595903	KC595903
	MR-11937	Argentina, Neuquén	JF713082	–
Antrodia serialis (Fr.) Donk	Boat-184	USA, Massachusetts	KC585297	KC585121
	DAOM-11977	Canada, British Columbia	KC585298	KC585122
	FP-100248-T	USA, Colorado	KC585299	KC585123
	FP-100562-T	USA, New Hampshire	KC585300	KC585124
	FP-104443-Sp	USA, Colorado	KC585301	KC585125
	FP-105717-Sp	USA, Maryland	KC585302	KC585126
	FP-105599	USA, Wyoming	EU232199	EU232293
	FP-133692-Sp	USA, Oregon	KC585303	KC585127
	FP-134828-Sp	USA, Idaho	–	KC585128
	FP-94125	USA, North Carolina	KC585304	KC585129
	HHB-12661-Sp	USA, Alaska	KC585305	KC585130
	L-12464-Sp	USA, North Carolina	KC585306	KC585131
	L-8012-Sp	USA, Washington	KC585307	KC585132
	X732 (=Miettinen-12401)	Finland	JQ700271	JQ700271
	Macedonici 91/2181	Macedonia	FM872469	–
	Macedonici 06/7170	Macedonia	FM872468	–
	CBS 306.82	Germany, Reinhausen	DQ491417	–
	P213 (G102)	Germany	AJ344139	–
Antrodia serialiformis Kout & Vlasák	JK-2009a	USA	FJ788412	–
Antrodia serpens (Fr.) P. Karst.	X1163 (=Niemelä-8555)	Finland	KC543136	KC543136
Antrodia taxa T.T. Chang & W.N. Chou	TFRI-781	Taiwan?	EU232191	EU232275
	TFRI-782	Taiwan?	EU232192	EU232276
Antrodia variiformis (Peck) Donk	FP-100609-Sp	USA, Minnesota	KC585308	KC585133
	FP-104442-Sp	USA, Colorado	KC585309	KC585134
	FP-89848-R	USA, Utah	KC585310	KC585135
	FP-90100-Sp	USA, New York	KC585311	KC585136
	L-3379-R	USA, New York	KC585312	KC585137
	L-6138-SP	USA, Colorado	KC585313	KC585138
	CBS 309.82	USA, New York	DQ491418	AY515344
	CBS 375.82	USA, New York	–	AY515345
Antrodia sp.	RLG-11175-R	USA, Arizona	KC585314	KC585139
	RLG-7115-Sp	USA, Arizona	KC585315	KC585140
	X873 (=Klepsland-277)	Turkey	KC595891	KC595891
	X1321 (=Miettinen-11605)	Indonesia	KC595892	KC595892

Species	Isolate number	Locality	ITS GenBank accession no.	LSU GenBank accession no.
Antrodia sp.	X1460 (=Spirin-1460)	Russia	KC595902	KC595902
Auriporia aurea (Peck) Ryvarden	FP-98524	USA, New Mexico	KC585316	KC585141
	FPL-7026		–	AF287846
Auriporia aurulenta A. David, Tortič & Jelić	HHB-8864	USA, Mississippi	KC585317	KC585142
	PRM-915967	Czech Republic	GU594153	–
Crustoderma corneum (Bourdot & Galzin) Nakasone	HHB-5685-Sp	USA, Montana	KC585318	KC585143
	L-13829-Sp	Canada, Ontario	KC585319	KC585144
Crustoderma dryinum (Berk. & M.A. Curtis) Parmasto	FP-105487-Sp	USA, Maryland	KC585320	KC585145
	HHB-1290-Sp	USA, New Mexico	KC585321	KC585146
	HHB-7517-Sp	USA, Michigan	KC585322	KC585147
	Kropp62ClEugene	USA, Oregon	KC585323	KC585148
	RLG-13018-Sp	USA, Arizona	KC585324	KC585149
Crustoderma flavescens Nakasone & Gilb.	HHB-9359-Sp	USA, Wisconsin	KC585325	KC585150
	L-10857-Sp	USA, North Carolina	KC585326	KC585151
Crustoderma longicystidiatum (Litsch.) Nakasone	FCUG-502	Norway	–	AY219388
Crustoderma marianum Nakasone	FP-105993-Sp	USA, Maryland	KC585327	KC585152
	FP-94432-Sp	USA, Maryland	KC585328	KC585153
Crustoderma opuntiae Nakasone & Gilb.	RLG-12290-Sp	USA, Arizona	KC585329	KC585154
Crustoderma resinosum (H.S. Jacks. & Dearden) Gilb.	L-10631-Sp	USA, Washington	KC585330	KC585155
Dacryobolus sudans (Alb. & Schwein.) Fr.	FP-100190-Sp	USA, Colorado	KC585331	KC585156
	FP-101996-Sp	USA, Wisconsin	KC585332	KC585157
	FP-150381	Jamaica	KC585333	KC585158
	HHB-8966-Sp	USA, Mississippi	KC585334	KC585159
Dacryobolus karstenii (Bres.) Oberw. ex Parmasto	KHL-11162		–	EU118624
Daedalea quercina (L.) Pers.	FP-103364-T	USA, Georgia	KC585335	KC585160
	FP-125063-T	USA, New Hampshire	KC585336	KC585161
	OKM-3802-Sp	USA, Maryland	KC585337	KC585162
	DLL08-35	Sweden	KC585338	KC585163
	IHD-H-D4		EU787455	–
	P-320		EU768810	–
	47786	Norway	FJ403212	–
	18198	Belize	FJ403211	–
Daedalea dickinsii Yasuda	027	China	EU661878	–
	KUC9199		–	JF416685
	KUC8811		–	EU024963
Daedalea neotropica D.L. Lindner, Ryvarden & T.J. Baroni	DLC04-80	Belize	FJ403217	–
	DLC04-100	Belize	FJ403218	–
Daedalea pseudodochmia (Corner) T. Hatt.	10533	China	FJ403210	–
Daedalea stereoides Fr.	10551	Ethiopia	FJ403215	–
Fibroporia bohemica Bernicchia, Vampola & Prodi	Vampola 3/04	Czech Republic, Bohemia	HM590889	–

Species	Isolate number	Locality	ITS GenBank accession no.	LSU GenBank accession no.
Fibroporia bohemica Bernicchia, Vampola & Prodi	PRM-859138	Czech Republic, Bohemia	HM590890	–
Fibroporia citrina (Bernicchia & Ryvarden) Bernicchia & Ryvarden	HUBO-7715	Italy, Emilia-Romagna	GU991573	–
	HUBO-7887	Italy, Emilia-Romagna	HM542005	–
Fibroporia gossypium (Speg.) Parmasto	X1403 (=Miettinen-13991)	Finland	KC595905	KC595905
	HUBO-7724	Italy, Sardinia	HM590880	–
	MR-10569	Argentina, Chubut	JF713075	–
	TN-7286 (=4243)	Finland	KC595906	KC595906
Fibroporia norrlandica (Berglund & Ryvarden) Niemelä	32994 (=4151)	Finland	KC595909	KC595909
	TN-6099 (=4115)	Finland	KC595907	KC595907
	OFM2			
Fibroporia pseudorennyi (Spirin) Spirin	X1377 (=Rivoire-3914)	France	KC595927	KC595927
	X1384 (holotype)	Russia	KC595928	KC595928
Fibroporia radiculosa (Peck) Parmasto	FP-105309-R	USA, Florida	KC585339	KC585164
	FP-90848-T	USA, Maryland	KC585340	KC585165
	L-11659-Sp	USA, New York	KC585341	KC585166
	L-12617	USA, South Carolina	KC585342	KC585167
	L-9318	USA, Arizona	KC585343	KC585168
	RLG-7629-Sp	USA, Arizona	KC585344	KC585169
	Cui-2797	China	FJ644284	–
Fibroporia vaillantii (DC.) Parmasto	FP-90877-R	USA, New Jersey	KC585345	KC585170
	FP-97397	USA, Pennsylvania	–	KC585171
	RWD-63-263	USA, Colorado	KC585346	KC585172
	P240	Germany	AJ421068	AJ583429
	25794		–	
	P107 (FPRL 14)	United Kingdom	AJ249266	–
	HUBO-8158	Italy, Sardinia	HM590886	–
	240	Germany	AM286436	–
	P113 (DFPG-6911)	New Zealand	AJ344140	–
	MR-11938	Argentina, Neuquén	JF713077	–
Fibroporia sp.	FP-100484-Sp	USA, Virginia	KC585347	KC585173
	920821			
	L-7878-Sp	USA, Washington	KC585348	KC585174
	L-14122-Sp	USA, New York	KC585349	KC585175
	X329 (=Miettinen-9992)	China	KC595904	KC595904
Fomitopsis cajanderi (P. Karst.) Kotl. & Pouzar	BCRC-35447		EU232200	EU232294
	CBS 225.39	USA, Oregon	–	AY515324
	X1427 (=Spirin-28.V.2000)	Russia	KC595915	KC595915
Fomitopsis cupreorosea (Berk.) J. Carranza & Gilb.	CBS 236.87	Costa Rica	DQ491373	AY515325
Fomitopsis dochmia (Berk. & Broome) Ryvarden	CBS 426.84	Thailand, Doi Inthanon	DQ491401	AY515326
Fomitopsis feei (Fr.) Kreisel	X1425 (=Miettinen-13120)	Indonesia	KC595916	KC595916
	X1439 (=Schigel-5234)	Australia	–	KC595917
	CBS 424.84	Mexico, Michoacan	DQ491402	–

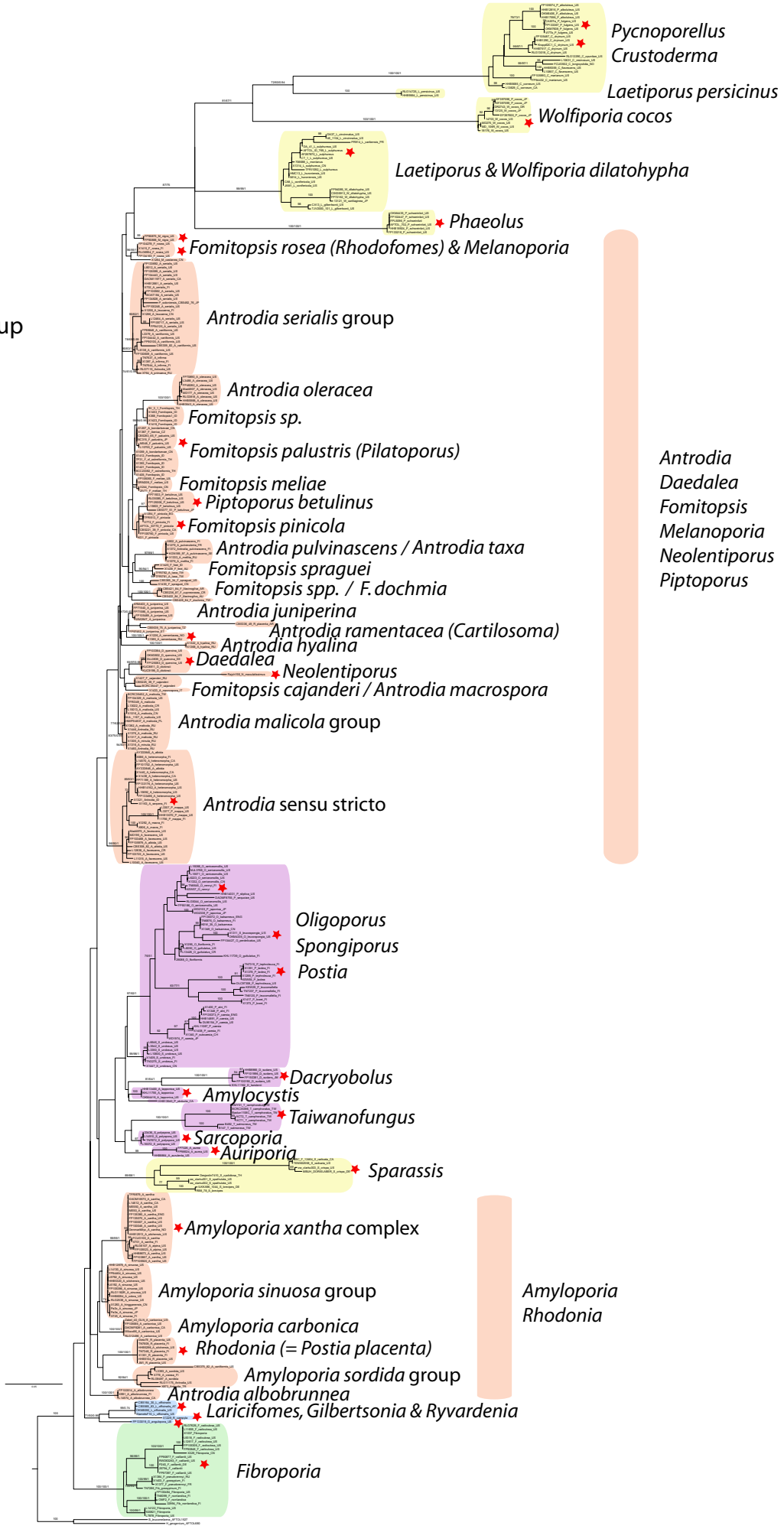
Species	Isolate number	Locality	ITS GenBank accession no.	LSU GenBank accession no.
Fomitopsis iberica Melo & Ryvarden	X1367 (=Vampola 19.VI.1995)	Czech Republic	KC595930	KC595930
Fomitopsis lilacinogilva (Berk.) J.E. Wright & J.R. Deschamps	CBS 422.84	Australia, New South Wales	DQ491403	AY515329
	CBS 421.84	Argentina	–	AY515328
Fomitopsis meliae (Underw.) Gilb.	FP-105065	USA, Mississippi	KC585350	KC585176
	SRM-209	USA, Nebraska	KC585351	KC585177
	2IV-7-1	Thailand?	FJ372674	FJ372696
	X244 (=Miettinen-10071)	China	KC595914	KC595914
Fomitopsis ostreiformis (Berk.) T. Hatt.	BCC-23382	Thailand	FJ372684	FJ372706
	7P-3-1	Thailand	FJ372678	EJ372700
Fomitopsis palustris (Berk. & M.A. Curtis) Gilb. & Ryvarden	MS-48	USA, Wisconsin	KC585352	KC585178
	L-15755	USA, Maryland	–	KC585179
	CBS 283.65	USA, Georgia	DQ491404	AY515333
	BC315	Japan	AB604156	AB604155
	TYP0507		EU024965	–
Fomitopsis pinicola (Sw.) P. Karst.	AFTOL-ID-770		AY854083	AY684164
	CBS 221.39	Canada, British Columbia	DQ491405	AY515334
	FP-105760	USA, Idaho	–	AY333811
	TFRI-513		EU232197	EU232290
	X772 (=Miettinen-12391)	Finland	JQ700273	JQ700273
	X1394 (=Miettinen-12439.1)	Bulgaria	KC595922	KC595922
	KG1			
	UBC-F16252	Canada	EF530947	–
	CIRM-BRFM 971		GU731552	–
	KMJ-812		FJ418162	–
Fomitopsis rosea (Alb. & Schwein.) P. Karst.	FP-134163	USA, Montana	–	KC585180
	FP-104278	USA, Maine	–	AY333809
	RLG-6954	USA, Arizona	KC585353	KC585181
	X1415 (=Niemi-118)	Finland	KC595923	KC595923
	HOU-17408		DQ491412	–
	FrRo47.1	Finland	AJ415551	–
	FrKu36.4	Finland	AJ415553	–
Fomitopsis spraguei (Berk. & M.A. Curtis) Gilb. & Ryvarden	X1430 (=Dai-5983)	China	KC595924	KC595924
	CBS 365.34	USA	DQ491406	AY515335
Fomitopsis sp.	X368 (=Miettinen-8737.1)	Indonesia	KC595910	KC595910
	X1393 (=Miettinen-11573)	Indonesia	KC595918	KC595918
	X1421 (=Miettinen-13162)	Indonesia	KC595921	KC595921
	X1412 (=Miettinen-14311)	Indonesia	KC595920	KC595920
	X1405 (=Miettinen-14417)	Indonesia	KC595919	KC595919
	X1419 (=Miettinen-13019)	Indonesia	KC595911	KC595911
	X1423 (=Miettinen-13076)	Indonesia	–	KC595912

Species	Isolate number	Locality	ITS GenBank accession no.	LSU GenBank accession no.
Fomitopsis sp.	X1453 (=Miettinen-5486)	Indonesia	KC595913	KC595913
	9V-3-1	Thailand	FJ372677	FJ372699
	X56	Italy?	HM126460	–
Gilbertsonia angulopora (M.J. Larsen & Lombard) Parmasto	FP-133019	USA, Oregon	KC585354	KC585182
Laetiporus caribensis Banik & D. L. Lindner	PR-914	Puerto Rico	EU402548	EU402526
Laetiporus cincinnatus (Morgan) Burds., Banik & T.J. Volk	DA-37(Ta)	USA, Wisconsin	EU402557	EU402521
	46-1104	USA, Louisiana	EU402560	EU402522
Laetiporus conifericola Burds. & Banik	CA-8(Ta)	USA, California	EU402575	EU402523
	JAM-1	USA, Alaska	EU402577	EU402524
Laetiporus gilbertsonii Burds.	CA-13	USA, California	EU402549	EU402527
	TJV2000-101	USA, Florida	EU402553	EU402528
Laetiporus huroniensis Burds. & Banik	HMC-3	USA, Michigan	EU402571	EU402540
	MI-14	USA, Michigan	EU402573	EU402539
Laetiporus montanus Černý ex Tomšovský & Jankovský	L12-706688	Czech Republic	EU840558	EUF884419
Laetiporus persicinus (Berk. & M.A. Curtis) Gilb.	HHB-9564-Sp	USA, Florida	EU402579	EU402513
	RLG-14725-Sp	USA, Louisiana	EU402581	EU402512
Laetiporus portentosus (Berk.) Rajchenb.	CBS 307.39	Australia	HQ332384	–
Laetiporus sulphureus (Bull.) Murrill	DA-41(Ta)	USA, Wisconsin	–	KC585183
	CT-1	USA, Connecticut	EU402565	EU402532
	X1314 (=Miettinen-10558)	China	–	KC595925
	AFTOL-ID-769		DQ221108	AY684162
	TFRI-1092		–	EU232302
	DSH93-194		–	AF287870
Laricifomes officinalis (Batsch) Kotl. & Pouzar	OKM-8050	USA, Idaho	KC585355	KC585184
	CBS 565.83	Austria	–	AY515332
	CBS 164.30	Siberia	–	AY515331
	Stamets-F10	USA	EU854442	EU854448
Melanoporia castanea (Imazeki) T. Hatt. & Ryvarden	X1284 (=Miettinen-10517.1)	China	KC595926	KC595926
Melanoporia nigra (Berk.) Murrill	FP-90875	USA, Washington, D.C.	KC585356	KC585185
	FP-90888	USA, Maryland	KC585357	KC585186
Neolentiporus maculatissimus (Lloyd) Rajchenb.	Rajchenberg-158	Argentina	–	AF518632
Oligoporus balsameus (Peck) Gilb. & Ryvarden	FP-135372-Sp	England	KC585358	KC585187
	KEW-35		–	AF518640
	X1349 (=Miettinen-10468)	China	KC595933	KC595933
	TN-6876 (=4118)	Finland	KC595934	KC595934
Oligoporus floriformis (Quél.) Gilb. & Ryvarden	X1295 (=Murdoch-224)	Finland	KC595936	KC595936
	29088 (=4120)	Finland	KC595937	KC595937

Species	Isolate number	Locality	ITS GenBank accession no.	LSU GenBank accession no.
Oligoporus guttulatus (Peck ex Sacc.) Gilb. & Ryvarden	L-13428-Sp	Costa Rica, San José	KC585359	KC585188
	L-8050	USA, Washington	KC585360	KC585189
	KHL-11739	Finland	EU118650	EU118650
Oligoporus perdelicatus (Murrill) Gilb. & Ryvarden	FP-104427-Sp	USA, Colorado	KC585361	KC585190
Oligoporus rennyi (Berk. & Broome) Donk	KEW-57		AY218416	AF287876
	TN-6645 (=4148)	Finland	KC595929	KC595929
Oligoporus sericeomollis (Romell) Bondartseva	FP-90186-R	USA, Georgia	KC585362	KC585191
	L-15571-Sp	USA, New York	KC585363	KC585192
	L-6223-Sp	USA, Colorado	KC585364	KC585193
	L-15088-Sp	USA, New York	KC585365	KC585194
	MJL-3788-Sp	USA, Michigan	KC585366	KC585195
	RLG-5044-Sp	USA, New York	KC585367	KC585196
	X1332 (=Miettinen-10474)	China	KF112878	KF112878
Phaeolus schweinitzii (Fr.) Pat.	FP-102447-Sp	USA, Michigan	KC585368	KC585197
	FP-133218-Sp	USA, Oregon	KC585369	KC585198
	FPL-5096		AY218422	AF287882
	OKM-4435-T	USA, Montana	KC585370	KC585199
	AFTOL-702	USA, New York?	–	AY629319
	HHB-18924	USA	EU402515	EU402515
Piptoporus betulinus (Bull.) P. Karst.	FP-125006-T	USA, New Hampshire	KC585371	KC585200
	FP-71933-T	USA, Massachusetts	KC585372	KC585201
	L-15603-Sp	USA, New York	KC585373	KC585202
	RLG-5085-Sp	USA, Pennsylvania	KC585374	KC585203
	CBS 378.51	Austria	DQ491423	–
	CBS 377.51	Japan	–	AY515352
Piptoporus soloniensis (Dubois) Pilát	CBS 492.76	Japan	–	AY515354
Postia alni Niemelä & Vampola	X1348 (=Miettinen-14211)	Finland	KC595931	KC595931
	X1400 (Niemi)	Finland	–	KC595932
Postia caesia (Schrad.) P. Karst.	DL96-154	USA, Michigan	–	KC585204
	FP-135373-Sp	England, Madehurst	KC585375	KC585205
	HHB-14891	USA, Washington	KC585376	KC585206
	KHL-11087		–	AF347111
	X1408 (=Miettinen-13610)	Finland	KC595935	KC595935
	WD-1974	Japan	–	AB569119
Postia japonica Y.C. Dai & T. Hatt.	WD-2103	Japan	–	AB569122
	WD-2338	Japan	–	AB569121
Postia lactea (Fr.) P. Karst.	X1378 (=Niemelä-7742)	Finland	KC595938	KC595938
	X1391 (=Kotiranta-20058)	Finland	KC595939	KC595939
	KEW-55		–	AY293205
Postia leucomallella (Murrill)	KEW-29		–	AF393072
	TN-6120 (=4010)	Finland	KC595940	KC595940
	TN-7237 (=4011)	Finland	KC595943	KC595943
Postia lowei (Pilát ex Pilát) Jülich	X1373 (=Pennanen-1254)	Finland	KC595941	KC595941
	X1417 (Onni Miettinen)	Finland	KC595942	KC595942

Species	Isolate number	Locality	ITS GenBank accession no.	LSU GenBank accession no.
Postia mappa (Overh. & J. Lowe) M.J. Larsen & Lombard	HHB-13070	USA, Alaska	–	KC585207
	L-3307-R	USA, New York	–	KC585208
	L-3377	USA, New York	KC585377	KC585209
	Penttila-11756 (=4239)	Finland	KC543113	KC543113
Postia obducta (Berk.) Lombard & Larsen	HHB-13540-Sp	Canada, British Columbia	KC585378	KC585210
Postia sequoiae (Bonar) M.J. Larsen & Lombard	DAOM-F-8755-T	USA, California	KC585379	KC585211
Postia stiptica (Pers.) Jülich	HHB-14031	USA, Alaska	KC585380	KC585212
Postia subcaesia (A. David) Jülich	X1340 (=Miettinen-10637)	China	KC595944	KC595944
Postia tephroleuca (Fr.) Jülich	DLC97-308	USA, Michigan	–	KC585213
	X1288 (=Miettinen-13613)	Finland	KC595946	KC595946
	TN-7315 (=4138)	Finland	KC595945	KC595945
Pycnoporellus alboluteus (Ellis & Everh.) Kotl. & Pouzar	FP-105074-Sp	USA, Colorado	KC585381	KC585214
	HHB-12816-Sp	USA, Alaska	KC585382	KC585215
	HHB-17598-Sp	USA, Alaska	KC585383	KC585216
	OKM-6406-Sp	USA, Montana	KC585384	KC585217
Pycnoporellus fulgens (Fr.) Donk	CA-20(Ta)	USA, California	KC585385	KC585218
	FP-133367-Sp	USA, Oregon	KC585386	KC585219
	OKM-7608-T	USA, Alaska	KC585387	KC585220
	VI-7(Tb)	USA, Wisconsin	KC585388	KC585221
Rhodonia placenta (Fr.) Niemelä, K.H. Larss. & Schigel	JM1	USA, Alaska	KC585389	KC585222
	Dietz7E	USA, California	KC585390	KC585223
	HHB-5104-Sp	USA, Montana	KC585391	KC585224
	X1351	Finland	KC595950	KC595950
	CBS 336.49	Argentina	–	AY515355
	Niemelä-7609 (=3007)	Finland	KC595951	KC595951
	Niemelä-7348 (=4004)	Finland	JQ700293	JQ700293
	P100	Germany	AJ416069	–
	P120 (FPRL 280)	Germany, Berlin	AJ249267	–
	MAD-698	USA, Maryland	AY089735	–
Ryvardenia campyla (Berk.) Rajchenb.	X1229 (=Hallenberg-15265)	New Zealand	–	KC595952
	NZFS2826	New Zealand	JQ390051	–
	NZFS2828	New Zealand	JQ390052	–
Sarcoporia polyspora P. Karst.	234-36	USA, Pennsylvania	KC585392	KC585225
	L-14910-Sp	USA, New York	KC585393	KC585226
	L-16072-Sp	USA, New York	KC585394	KC585227
	TN-7672 (=4227)	Finland	KC595953	KC595953
Sparassis brevipes Krombh.	RB8/78/ss22		AY218439	AY218401
	ILKKA-96-1044	Germany	AY218441	AY218403
Sparassis crispa (Wulfen) Fr.	MBUH-DORISLABER	Germany	AY218442	AY218404
	zw-clarku003	USA, Massachusetts	AY218430	AY218393
	X950 (=Nummelin 23.IX.2006)	Finland	KC595954	KC595954
Sparassis cystidiosa Desjardin & Zheng Wang	DEDesjardin-7410	Thailand	AY256891	AY256890

Species	Isolate number	Locality	ITS GenBank accession no.	LSU GenBank accession no.
Sparassis radicata Weir	TENN-52558	USA, Washington	AY218450	AY218411
	UBC-F12464	Canada	AY218443	AY218405
Sparassis spathulata (Schwein.) Fr.	zw-clarku001	USA, Massachusetts	AY218428	AY218391
	zw-clarku002	USA, New Hampshire	AY218429	AY218392
Spongiporus leucospongia (Cooke & Harkn.) Murrill	OKM-4335	USA, Idaho	KC585395	KC585228
	X1311 (=Ahonen-37)	USA	KC595955	KC595955
Spongiporus undosus (Peck) A. David	L-10830-Sp	USA, North Carolina	KC585396	KC585229
	L-3350	USA, New York	KC585397	KC585230
	L-3542	USA, New York	KC585398	KC585231
	L-6646	USA, Colorado	KC585399	KC585232
	X1409 (=Miettinen-OMC701)	Finland	–	KC595947
	X1447 (=Dai-2055)	China	KC595948	KC595948
	TN-3275 (=4247)	Finland	KC595949	KC595949
Taiwanofungus camphoratus (M. Zang & C.H. Su) Sheng H. Wu, Z.H. Yu, Y.C. Dai & C.H. Su	ACT1	Taiwan	EU232205	EU232281
	ACT2	Taiwan	EU232204	EU233380
	BCRC-35396	Taiwan	AY378094	AY333844
	Baulon-1106C	Taiwan	JN165025	JN165027
	CMY-01	Taiwan	–	AY333842
Taiwanofungus salmoneus (T.T. Chang & W.N. Chou) Sheng H. Wu, Z.H. Yu, Y.C. Dai & C.H. Su	B147	Taiwan	EU232202	EU232278
	B492	Taiwan	EU232203	EU232279
Wolfiporia cocos (F.A. Wolf) Ryvarden & Gilb.	MD-106-R	USA, Oregon	–	EU402519
	MD-275	USA, Oregon	–	EU402520
	18176	USA, North Carolina	–	KC585233
	14703	USA, Iowa	–	KC585402
	DR-2743	Dominican Republic	–	KC585403
	13125	Japan, Tsukuba	–	KC585404
	K1	Japan	–	EF397598
	KANP. No. 7067	Japan	–	EF397599
	KANP. No. 7233	Japan	–	EF397600
Wolfiporia cartilaginea Ryvarden	13121	Japan, Kyushu	–	KC585405
Wolfiporia dilatohypha Ryvarden & Gilb.	CS-63-59-13-A-R	USA, Kentucky	KC585400	KC585234
	FP-72162-R	USA, Tennessee	EU402556	KC585235
	FP-94089-R	USA, West Virginia	KC585401	KC585236
Boletopsis leucomelaena (Pers.) Fayod	AFTOL-1527		DQ484064	DQ154112
Hydnellum geogenium (Fr.) Banker	AFTOL-680		DQ218304	AY631900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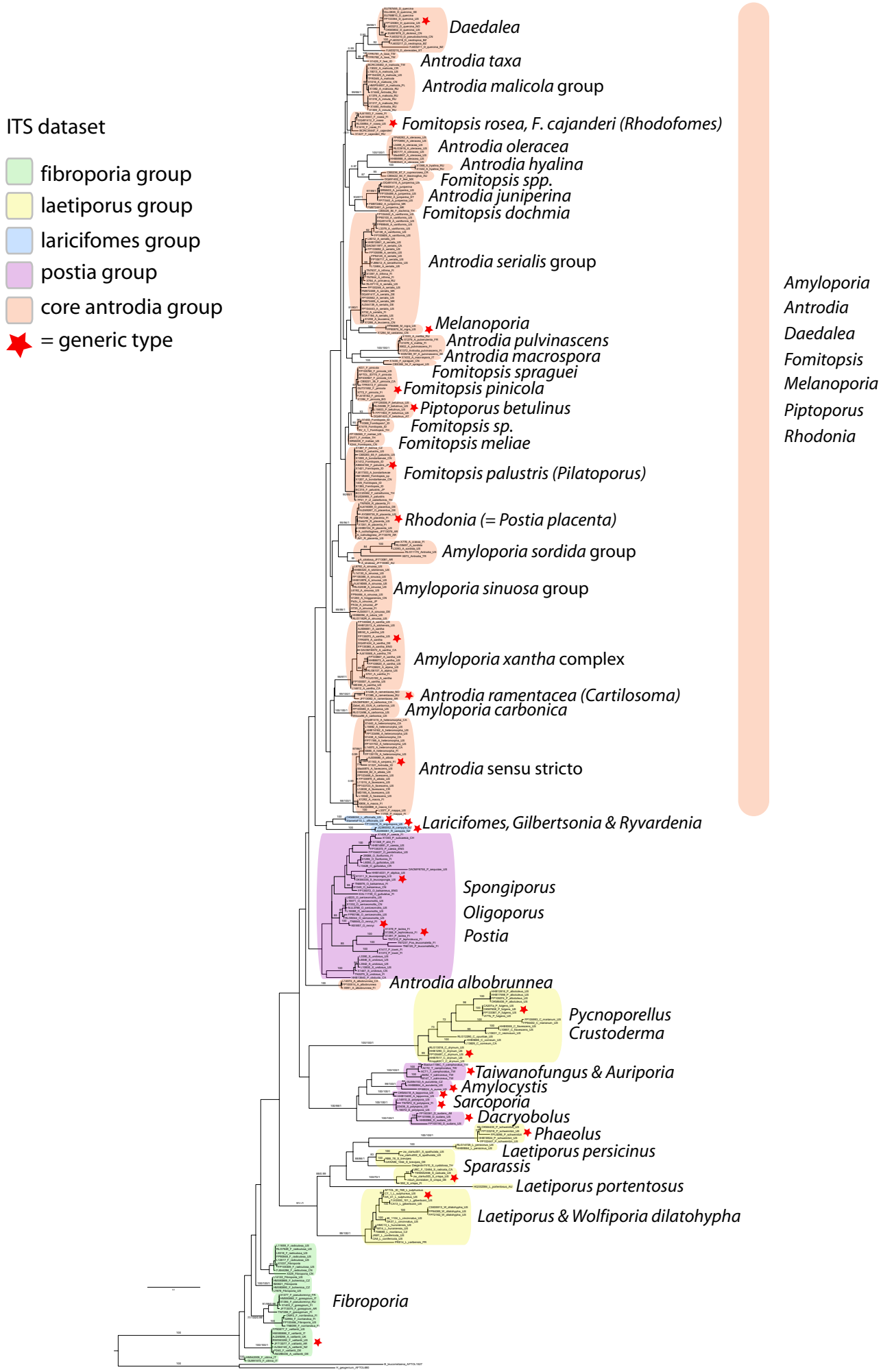
fibroporia group
laetiporus group
laricifomes group
postia group
core antrodia group
= generic type
Pycnoporellus
Crustoderma
Laetiporus persicinus
Wolfiporia cocos
Laetiporus & Wolfiporia dilatohypha
Phaeolus
Fomitopsis rosea (Rhodofomes) & Melanoporia
Antrodia serialis group
Antrodia oleracea
Fomitopsis sp.
Fomitopsis palustris (Pilatoporus)
Fomitopsis meliae
Piptoporus betulinus
Fomitopsis pinicola
Antrodia pulvinascens / Antrodia taxa
Fomitopsis spraguei
Fomitopsis spp. / F. dochmia
Antrodia juniperina
Antrodia ramentacea (Cartilosoma)
Antrodia hyalina
Daedalea
Neolentiporus
Fomitopsis cajanderi / Antrodia macrospora
Antrodia malicola group
Antrodia sensu stricto
Antrodia
Daedalea
Fomitopsis
Melanoporia
Neolentiporus
Piptoporus
Oligoporus
Spongiporus
Postia
Dacryobolus
Amylocystis
Taiwanofungus
Sarcoporia
Auriporia
Sparassis
Amyloporia xantha complex
Amyloporia sinuosa group
Amyloporia carbonica
Rhodonia (= Postia placenta)
Amyloporia sordida group
Antrodia albobrunnea
Laricifomes, Gilbertsonia & Ryvardenia
Amyloporia
Rhodonia
Fibroporia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laetiporus group
laricifomes group
postia group
core antrodia group
= generic type
Daedalea
Antrodia taxa
Antrodia malicola group
Fomitopsis rosea, F. cajanderi (Rhodofomes)
Antrodia oleracea
Antrodia hyalina
Fomitopsis spp.
Antrodia juniperina
Fomitopsis dochmia
Antrodia serialis group
Melanoporia
Antrodia pulvinascens
Antrodia macrospora
Fomitopsis spraguei
Fomitopsis pinicola
Piptoporus betulinus
Fomitopsis sp.
Fomitopsis meliae
Fomitopsis palustris (Pilatoporus)
Rhodonia (= Postia placenta)
Amyloporia sordida group
Amyloporia sinuosa group
Amyloporia xantha complex
Antrodia ramentacea (Cartilosoma)
Amyloporia carbonica
Antrodia sensu stricto
Laricifomes, Gilbertsonia & Ryvardenia
Spongiporus
Oligoporus
Postia
Antrodia albobrunnea
Pycnoporellus
Crustoderma
Taiwanofungus & Auriporia
Amylocystis
Sarcoporia
Dacryobolus
Phaeolus
Laetiporus persicinus
Sparassis
Laetiporus portentosus
Laetiporus & Wolfiporia dilatohypha
Fibroporia
Amyloporia
Antrodia
Daedalea
Fomitopsis
Melanoporia
Piptoporus
Rhodonia

SUPPLEMENTARY FIG. 1. Phylogenetic relationships of members of the antrodia clade inferred from the analyses of the nLSU dataset (rDNA sequences). Topology from maximum likelihood analysis. Support values along branches are from maximum likelihood bootstrap (≥70), maximum parsimony bootstrap (≥50) and Bayesian analyses (PP ≥0.95) respectively. Red star indicates generic types.

SUPPLEMENTARY FIG. 2 . Phylogenetic relationships of members of the antrodia clade inferred from the analyses of the nuclear ITS dataset (rDNA sequences). Topology from maximum likelihood analysis. Support values along branches are from maximum likelihood bootstrap (≥70), maximum parsimony bootstrap (≥50) and Bayesian analyses (PP ≥0.95) respectively. Red star indicates generic types.