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

Beatriz Ortiz-Santana[1]
Daniel L. Lindner
US Forest Service, Northern Research Station, Center for Forest Mycology Research, One Gifford Pinchot Drive, Madison, Wisconsin 53726

Otto Miettinen
Botanical Museum, University of Helsinki, PO Box 7, 00014, Helsinki, Finland

Alfredo Justo
David S. Hibbett
Clark University, Biology Department, 950 Main Street, Worcester, Massachusetts 01610

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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[1] Corresponding author. E-mail: bortizana@fs.fed.us

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	•	•		•		•	+		•		•										

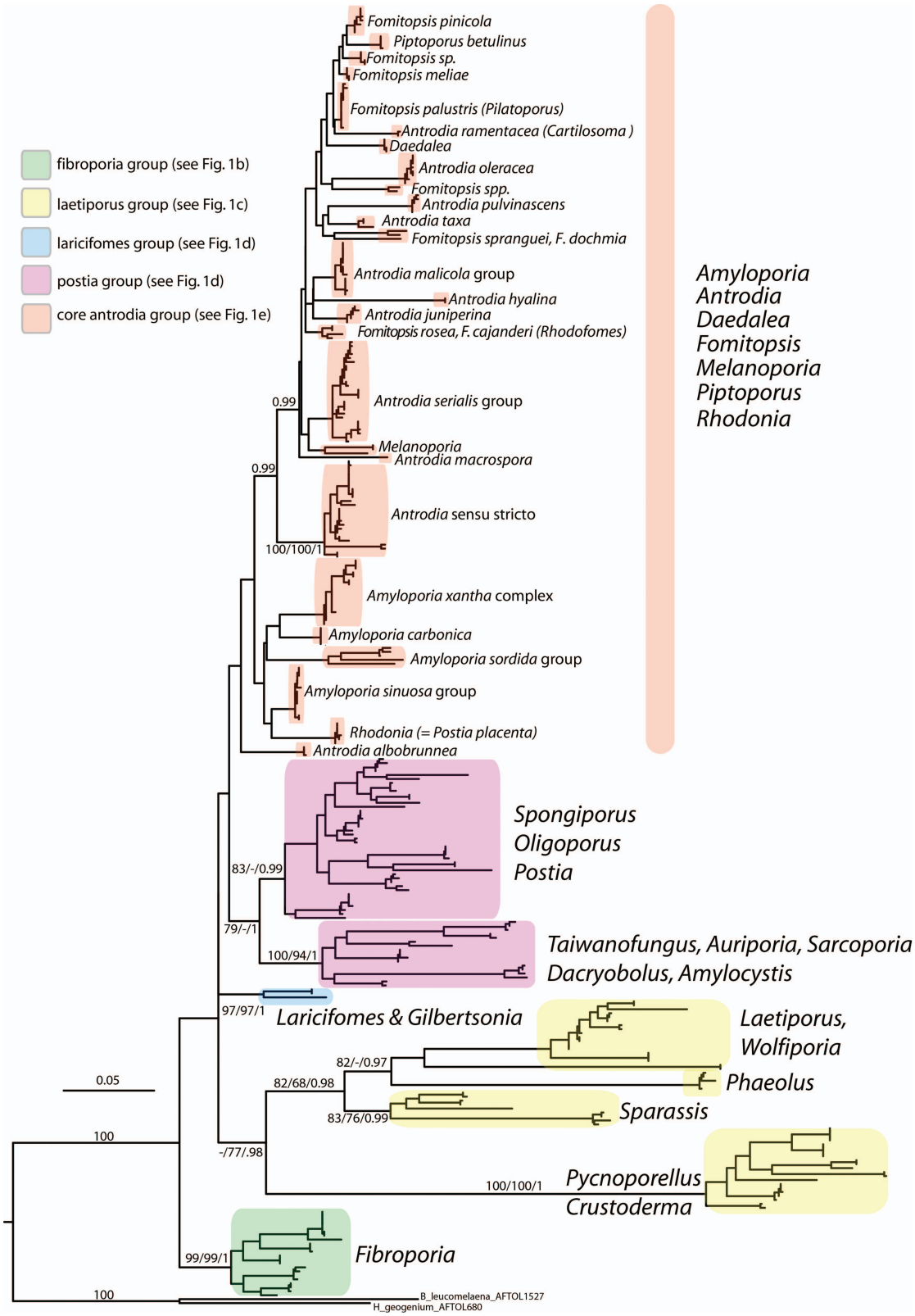

FIG. 1. A. Phylogenetic relationships of members of the antrodia clade inferred from the analyses of the combined dataset (nuclear LSU and ITS rDNA sequences). Topology from maximum likelihood analysis. Support values along branches are from maximum likelihood bootstrap (≥70), maximum parsimony bootstrap (≥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.

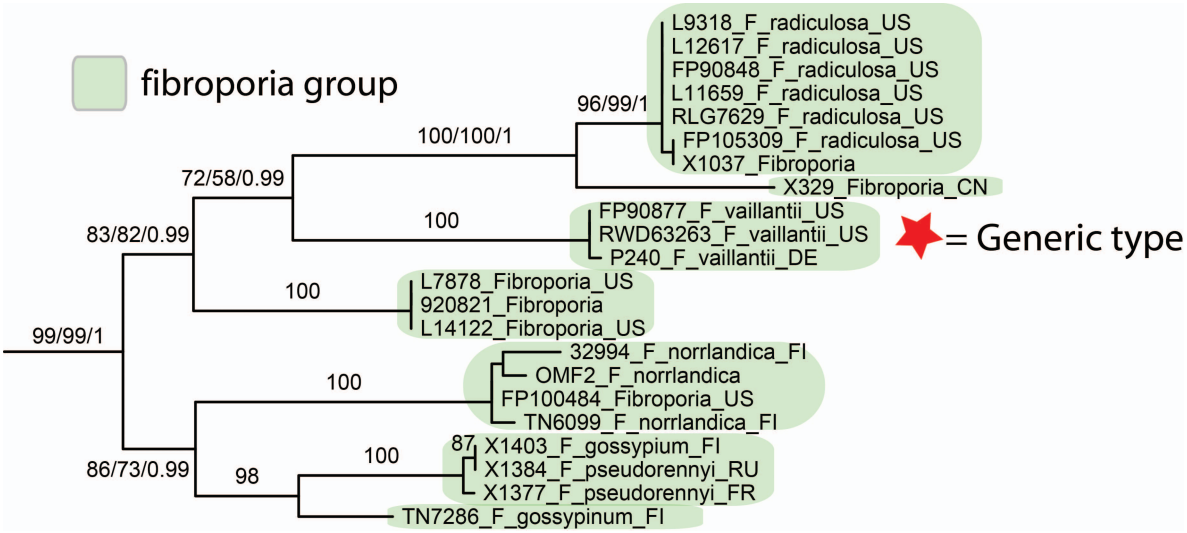

FIG. 1. Continued.

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-

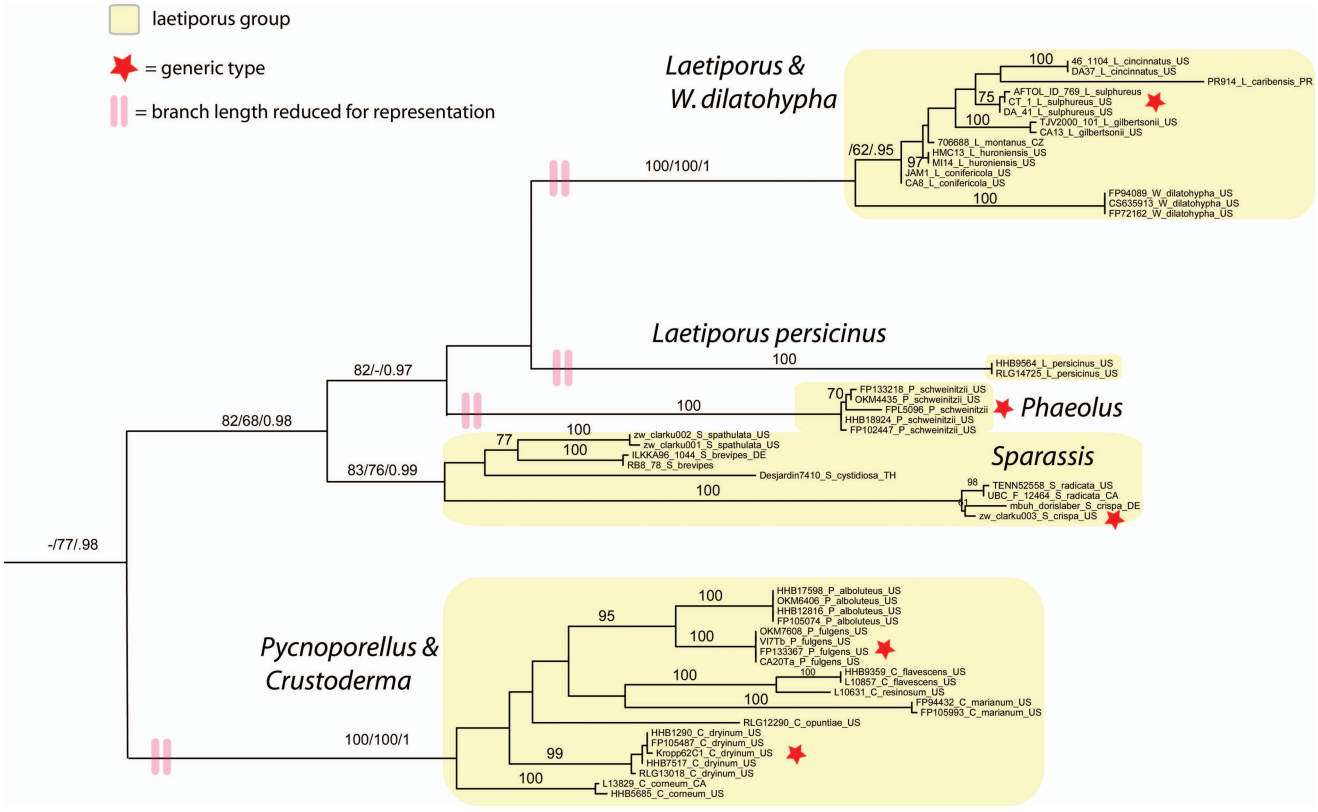

FIG. 1. Continued.

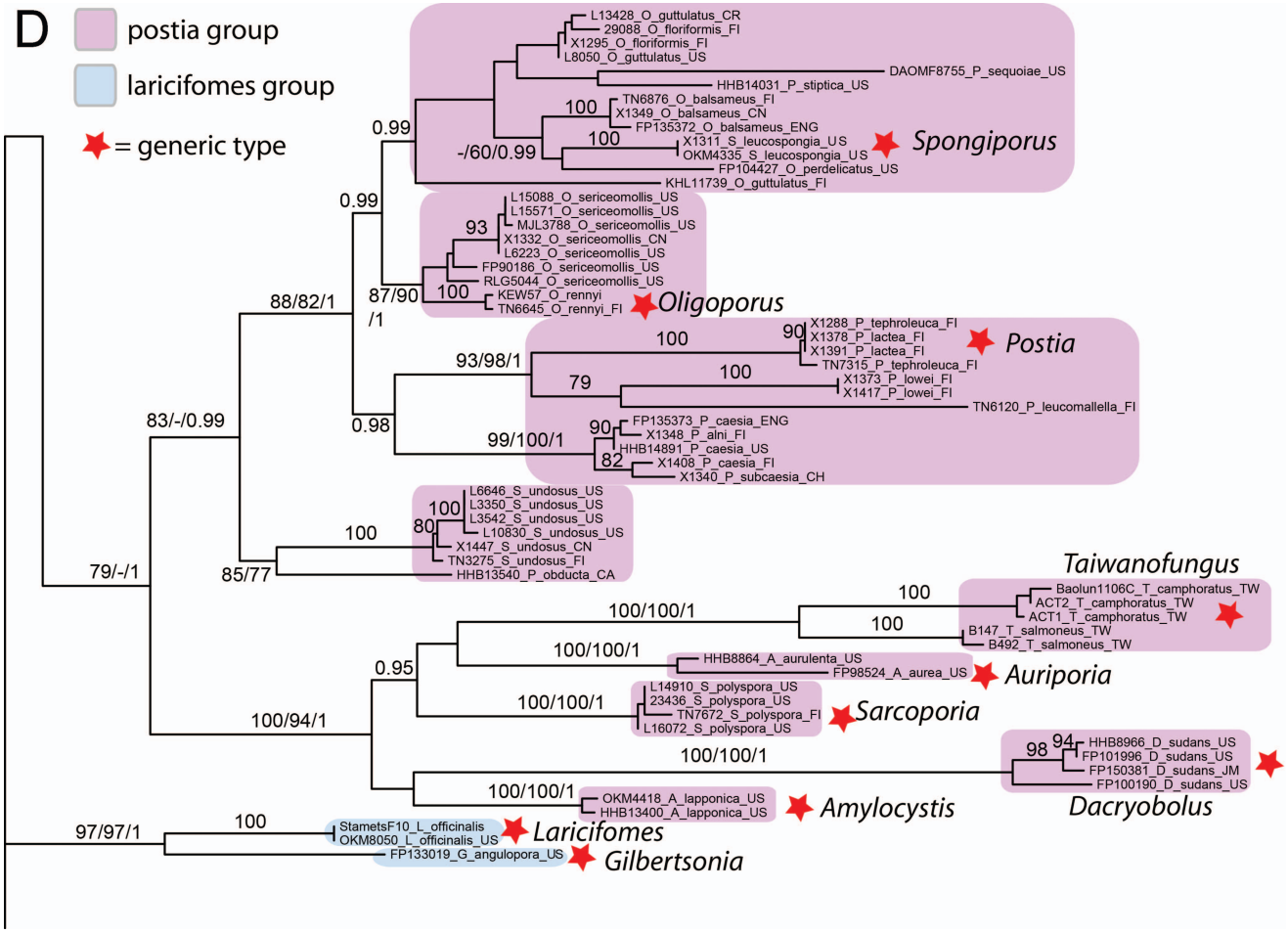

FIG. 1. Continued.

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*

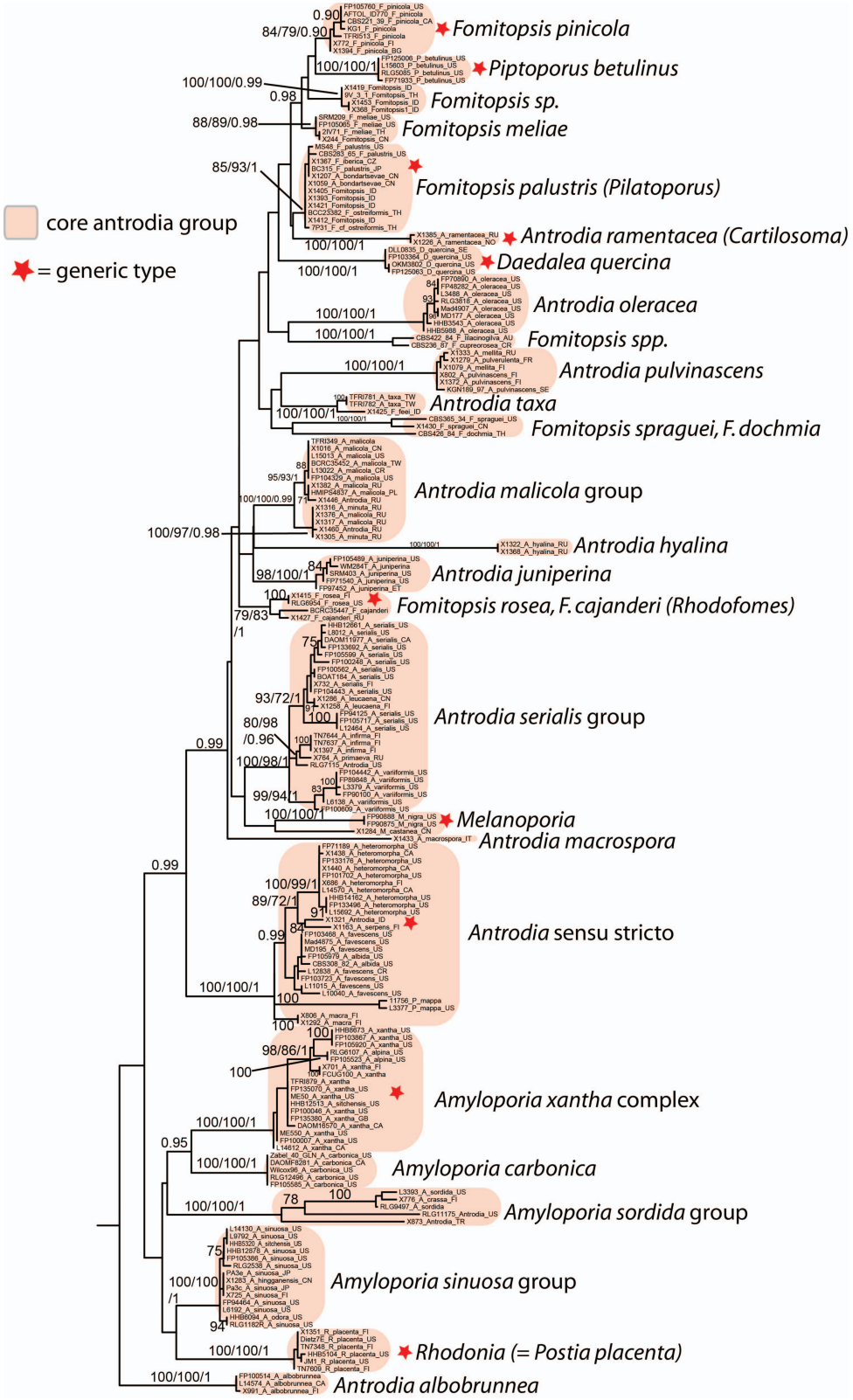

FIG. 1. Continued.

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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