In Press at Mycologia, preliminary version published on April 24, 2015 as doi:10.3852/14-170

Short title: Phylogeny of Hymenochaetaceae

The phylogenetic position of poroid Hymenochaetaceae (Hymenochaetales, Basidiomycota) from Patagonia, Argentina

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Abstract: Six poroid Hymenochaetaceae from Patagonia, Argentina, were studied phylogenetically with nuc rDNA internal transcribed spacer (ITS) and partial 28S rDNA sequences, together with morphological data. Two new genera and a new species are introduced as well as two new combinations proposed. *Arambarria destruens* gen. et sp. nov. is proposed for a taxon fruiting on fallen or standing, dead *Diostea juncea* and *Lomatia hirsuta* and previously recorded erroneously as *Inocutis jamaicensis*; it is distinguished by annual, effused to effused-reflexed basidiomes forming pilei, a monomitic hyphal system, thick-walled and yellowish basidiospores (brownish chestnut in potassium hydroxide solution), lack of a granular core in the context and lack of setoid elements. *Nothophellinus* gen. nov. is proposed to accommodate *Phellinus andinopatagonicus*, the main white wood-rotting polypore of standing *Nothofagus pumilio* and also an important wood-decayer of other *Nothofagus* species from southern Argentina and Chile. It is morphologically similar to *Phellopilus*

(type species *P. nigrolimitatus*) but differs by lacking setae. The new combinations *Pseudoinonotus crustosus* and *Phellinopsis andina* are proposed for *Inonotus crustosus* and *Phellinus andinus* respectively. *Phellinus livescens*, which decays the sapwood of several standing *Nothofagus* species, is closely related to *Phellinus uncisetus*, a Neotropical species related to *Fomitiporia*; for the time being *P. livescens* is retained in *Phellinus* sensu lato. An unidentified taxon responsible for a white heart-rot in living *Austrocedrus chilensis* grouped with *Phellinus caryophyllii* and *Fulvifomes inermis*, but its generic affinities remain ambiguous. Transmission electron microscopy studies confirm this unidentified taxon has an imperforate parenthesome, which is typical of the Hymenochaetaceae.

Key words: imperforate parenthesome, molecular phylogeny, polypores, taxonomy

INTRODUCTION

The poroid Hymenochaetaceae Donk (Hymenochaetales) is a group of Agaricomycotina (Basidiomycota) that contains many important pathogenic species in forests worldwide. Some species in this group produce white heart-rots and/or canker-rots of many tree species, while others are actively involved in the degradation of fallen wood. In addition, some species have potential medicinal value (Dai et al. 2009, Wu et al. 2012). For these reasons many taxa of this group have been intensively studied and characterized, with most placed in *Phellinus* Quél. and *Inonotus* P. Karst. Donk (1960, 1964) presented nomenclatural and taxonomic definitions for these and other related genera, while Ryvarden (1991) characterized them morphologically. General morphological, taxonomic and biogeographic treatments of *Phellinus* and *Inonotus* can be found in Gilbertson and Ryvarden (1986, 1987), Larsen and Cobb-Poulle (1990), Ryvarden (2004, 2005), Dai (2010), and Ryvarden and Melo (2014).

Genera of poroid Hymenochaetaceae traditionally were characterized by morphological features, mainly annual vs. perennial basidiomes, hyphal systems, spore shape, spore wall features (thickness and reaction to iodine-potassium iodide and cotton blue solutions) and presence/absence of setae and granular core in the context (see references above). Despite the shortcomings of morphology, efforts to define more robust generic concepts by including non-morphological features are rare. Cultural features in the group are generally distinct in the family but homogeneous at genus or species rank (Nobles 1965, Stalpers 1978). Therefore identification of cultured strains is difficult unless specific knowledge of habitat and host is available. This is different from other aphyllophoraceous fungi, as shown by Nobles (1965), Stalpers (1978) and Nakasone (1990). Mating types in poroid Hymenochaetaceae have rarely been established because the lack of clamp formation complicates the determination of mating compatibility in this entire group. Nuclear behavior of the mycelium (Boidin 1971), a character that has been useful in the delimitation of aphyllophoroid genera, especially when coupled with mating type (Boidin and Lanquetin 1984, Rajchenberg 2011 and references therein), is rarely studied. Exceptions include the works of Kühner (1950) and Fiasson and Niemelä (1984) who reported the secondary mycelium as binucleate, oligonucleate or coenocytic for several species and genera. For a summary of results, coupled with other biological and morphological features in the poroid Hymenochaetaceae, see Rajchenberg (2011). Fiasson and Bernillon (1977), Fiasson (1982) and Fiasson and Niemelä (1984) showed that different combinations of pigments within the poroid Hymenochaetaceae were useful taxonomic markers for genera. Later Fischer (1987, 1996) showed that ploidy in *Fomitiporia* Murrill was a valid taxonomic feature. Based on differences in morphology, kinds of pigment production, cultural features and cytology, species in *Phellinus* sensu lato (s.l.) and *Inonotus* s.l. were placed in smaller, more homogeneous genera by Fiasson and Niemelä (1984). Their generic concepts are supported by molecular phylogenetic studies (Wagner and Fischer 2002, Larsson et al. 2006). DNA sequence

comparisons and phylogenetic analyses are presently widely used to define genera and species in the Hymenochaetaceae (Decock et al. 2006, Dai 2010, Brazee and Lindner 2013, Tian et al. 2013, Zhou and Qin 2013, Parmasto et al. 2014). Current classifications of the family include 19 genera based almost exclusively on phylogenetic analysis of the D1, D2 and D3 domains of the nuc 28S RNA gene. The 28S sequences provide suitable resolution for identifying the major lineages, with good support for many terminal clades and internal branches (Wagner and Fischer 2002, Larsson et al. 2006, Dai 2010, Zhou and Qin 2013, Parmasto et al. 2014). Sequence analysis of the nuc rDNA internal transcribed spacer regions (ITS) is rarely used because this region is too divergent to align across the Hymenochaetales (Larsson et al. 2006).

Rajchenberg (2006) summarized knowledge on the poroid, aphyllophoroid fungi found in Patagonia, Argentina. Recent research analyzed the phylogenetic position of several genera and/or species in *Antrodia* P. Karst., *Neolentiporus* Rajchenb., *Polyporus* P. Micheli ex Adans., *Postia* Fr. and *Ryvardenia* Rajchenb. recorded from Patagonia (Rajchenberg et al. 2011, Rajchenberg and Pildain 2012, Pildain and Rajchenberg 2013, Dai et al. 2014). Nine poroid Hymenochaetaceae are recorded from that region, namely *Hymenochaete porioides*, *Inocutis jamaicensis*, *Inonotus crustosus*, *Phellinus andina*, *P. andinopatagonicus*, *P. inermis*, *P. livescens*, *P. senex* and an undetermined Hymenochaetaceae sp.; their distribution and hosts are provided (TABLE I) and basidiomes are illustrated (FIG. 1). Hymenochaetaceae sp. originally was isolated from living *Austrocedrus chilensis* exhibiting a white heart-rot (Barroetaveña and Rajchenberg 1996); because basidiomes of this taxon have never been found, its identity remains unknown.

Poroid Hymenochaetaceae from the austral landmasses with origins in Gondwana are not included in most phylogenetic studies published over the past decade. The aim of our work was to investigate the taxonomy of the endemic taxa of poroid Hymenochaetaceae known from Patagonia using a molecular phylogenetic approach.

MATERIALS AND METHODS

Strains and herbarium specimens.—Strains studied, with their voucher specimens, are deposited at the author's institutional culture collection (CIEFAPcc) and phytopathological herbarium (CIEFAP). Some duplicates are deposited at BAFC culture collection as indicated in the text. Herbarium designations follow Thiers (2014), and culture collection designations follow that of the World Federation for Culture Collection website (www.wfcc.info). Strains included in this study are provided (SUPPLEMENTARY TABLE I).

Morphology.—Description of basidiomes and terms used follow Ryvarden and Melo (2014). Spores measurements of the described new taxon are expressed as L × W (L = mean spore length as the arithmetic average of all spores ± SD, W = mean spore width as the arithmetic average of all spores ± SD), Q as the variation in the L/W ratios between the specimens studied, and n/s = number of spores measured from a given number of specimens.

DNA extraction and PCR conditions.—For DNA extraction, poroid Hymenochaetaceae species from Patagonia collections were cultured in malt peptone broth with 10% (v/v) of malt extract (Merck) and 0.1% (w/v) Bacto peptone (Difco), 2 mL medium in 15 mL tubes. The cultures were incubated at 25 C for 15 d in darkness. Total DNA was extracted with the UltraClean™ Microbial DNA Isolation Kit (MO BIO Laboratories Inc., Solana Beach, California), according to the manufacturer's instructions. Fifty milligrams tissue from herbarium specimens were ground with a mortar and pestle, extracted at 65 C for 10 min in 300 µL bead solution (UltraClean™ Microbial DNA Isolation Kit, MO BIO laboratories Inc., Solana Beach, California) with the addition of 10 µL proteinase K solution (20 mg/mL) following the manufacturer's instructions. DNA quantification was performed by ultraviolet spectroscopy. Primers LR0R and LR5 (Vilgalys and Hester 1990) were used to amplify the partial 28S, including the D1/D2 domains and primers ITS5 and ITS4 (White et al. 1990), for the amplification of the full ITS region (i.e. ITS1, ITS2 and the intervening 5.8S RNA gene). PCR reaction mixtures for amplification of both regions included dNTPs (0.25 mM of each), 2.5 mM $MgCl_2$, 1× PCR buffer supplied with the polymerase enzyme; 0.1 mM each of primer; 100–500 ng DNA; 6% bovine serum albumin (BSA, Promega Corp.) and 1.25 U GoTaq polymerase (Promega, Madison, Wisconsin). The final reaction volume was 25 µL. The PCR reactions were performed in a thermal cycler (MyCycler™, BioRad) as follows:95 C for 2 min, 30 cycles of 94 C for 30 s, 52 C for 30 s, 72 C for 1 min, followed by 72 C for 8 min (Larsson and Larson 2003). PCR products were separated on a 1% (w/v) agarose gel stained with GelRed™ Nucleic Acid Stain (Biotium Inc., Hayward, California), and the bands were visualized under UV illumination. The amplified fragments were purified and sequenced with an ABI 3700 automated sequencer (Perkin-Elmer, Foster City, California) at the DNA

Synthesis and Sequencing Facility, Macrogen (Seoul, Korea). Sequences generated in this study were submitted to GenBank (SUPPLEMENTARY TABLE I).

Data set selection.—As a framework for taxon selection, we used sequences of representative species of the genera defined by Larsson et al. (2006), Parmasto et al. (2013) and Zhou et al. (2012, 2014) on morphological and molecular evidence and so far accepted in the Hymenochaetaceae. Whenever possible, sequences of the generic type species were included. More taxa and sequences in the *Fomitiporella-Fulvifomes-Inocutis* subclade were incorporated to enhance phylogenetic resolution.

Sequence and phylogenetic analyses.—Sequence data generated in this study were manually edited with BioEdit 7.0.9.0 (Hall 1999), and additional sequences were retrieved from GenBank. Two datasets were analyzed for this study:one for the 28S gene (84 ingroup sequences) and one for ITS region (25 ingroup sequences). The ITS dataset was used to strengthen the proposed new genus *Arambarria* and ascertain its phylogenetic relationships with related genera. Alignment of 28S and ITS sequence datasets were performed automatically with MAFFT (Katoh and Standley 2013) and were visually inspected and manually adjusted with MEGA 6 (Tamura et al. 2013). Ambiguously aligned nucleotide positions with no discernible alignment pattern across the dataset were identified and and removed from subsequent phylogenetic analyses with GBLOCK 0.91b (Castresana 2000). Alignments were submitted to TreeBASE (Study ID 16018).

Phylogenetic relationships were inferred with maximum likelihood (ML) and Bayesian (BA) optimality criteria for both datasets. The best-fit models of evolution were determined with AIC (Akaike 1974) implemented in jModelTest (Posada 2008; darwin.uvigo.es), and these were used for both the ML and BA analyses. Branch support was determined with nonparametric bootstrapping implemented in RAxML 7.2.8 (Stamatakis et al. 2014), using the default parameters, executed on the CIPRES (cyberinfrastructure for phylogenetic research) Science Gateway 3.1 (Miller et al. 2010; www.phylo.org/sub_sections/portal) with bootstrap statistics calculated from 1000 bootstrap replicates. Bayesian phylogenetic analyses were performed with Mr Bayes. 3.2.2 (Ronquist and Huelsenbeck 2003) for 10 000 000 generations, with four chains and trees sampled every 100 generations. Log files for each run were viewed in Tracer 1.6.0 (evolve.zoo.ox.ac.uk/software.html/tracer) to determine convergence. Branch support was assessed using posterior probabilities calculated from the posterior set of trees after stationarity was reached. Trees generated before stationarity were discarded and the rest of the trees were summarized in a majority-rule consensus tree from the four independent runs. Trees inferred from the 28S dataset were rooted with *Antrodia carbonica* (Overh.) Ryvarden & Gilb.

(GenBank:AF287844) and *Fomes fomentarius* (L.) Fr. (AF261538), following Wagner and Fisher (2002) and Dai (2010). Trees inferred from the ITS dataset were rooted with *Fomitiporia punctata* (P. Karst.) Murrill (AF515563).

Electron microscopy.—Hymenochaetaceae sp. culture CIEFAPcc 85 (Argentina, Chubut, Futaleufú, Los Cipreses, "La 106" Ranch), isolated from white fibrous heart rot of *Austrocedrus chilensis*, 21 Aug 1991, was used for transmission electron microscopy. Mycelium taken from liquid 1.25% malt extract (ME) cultures was chemically fixed overnight at 4C in 4% glutaraldehyde buffered with sodium cacodylate 0.1M, rinsed with fresh sterilized ME and post-fixated for 2 h in 1% osmium tetroxide buffered with a 50:50 cacodylate-ME solution. After several rinses (5 min each) with fresh ME, mycelium was stained with uranyl acetate 0.5% for 2 h, then washed with distilled water and dehydrated in a graded acetone series (every 10% 10–90%, 95% and finally three times in 100%) to be infiltrated in a graded series (25%, 50%, 75%, 100%) and flat embedded in Spurr's low viscosity resin and polymerized at 70 C for 2 d. Thin sections were cut with a diamond knife (Diatome Ltd., Bienne, Switzerland) in a Riechert-Jung Ultracut ultramicrotome (C. Reichert Optische Werke, Wien, Austria). Sections of 60–90 nm thickness were mounted on Formvar-coated grids and post-stained with 1% aqueous uranyl acetate (120 min) and lead citrate (30 min). Sections were observed with a Jeol 100 CX-II electron microscope (Jeol Ltd., Akishima, Tokyo, Japan) at the CCT-Bahía Blanca center (Centro Científico y Tecnológico CONICET-Bahía Blanca).

RESULTS

Phylogenetic analysis.—The 28S dataset included 84 ingroup sequences with 880 characters. The ITS dataset included 25 ingroup sequences with 429 characters. The best fitting models of evolution for the 28S and ITS data sets as determined using jModelTest were GTR+I+G and JC models respectively. Convergence of the Bayesian analyses after removal of the first 10% (10 000) trees was determined by observing that the standard deviation of split frequencies reached <0 .01, effective sample size (ESS) values for all parameters were > 200 and that parameters had reached a stationary stage after a 10% burn-in. The phylogenetic analysis of 28S sequences of poroid Hymenochaetaceae, which includes collections from Patagonia, Argentina, is presented (FIG. 2). The trees generated from ML and BA analyses were congruent. We present only the ML tree topology here (FIG. 2).

Within the *Inocutis-Fomitiporella* clade, specimens from Patagonia previously identified as *I. jamaicensis* grouped together in a distinct new clade in both 28S (ML = 100%, BA = 100%) and ITS (ML = 93%, BA = 100) analyses, proposed below as the new genus *Arambarria*. The internal topology of *Inocutis-Fomitiporella* clade is not fully resolved despite using both 28S and ITS sequences (FIGS. 2, 3). Species of *Fomitiporella* are placed together in all analyses. *Phellinus caryophylli* (Racib.) G. Cunn., formerly placed under *Fomitiporella* by Wagner and Fischer (2002), grouped with *Fulvifomes inermis* (Ellis & Everh.) Y.C. Dai. in both 28S and ITS analyses. Strains CIEFAPcc88 and CIEFAPcc107 grouped with the former species in a highly supported clade for both sequence datasets (28S:ML = 96%, BA = 100%; ITS:ML = 70%, BA = 97%) (FIGS. 2, 3).

Pseudoinonotus crustosus belongs to the *Pseudoinonotus* clade, a group that has weak support in the ML (51%) and BA (65%) but is nonetheless a distinct group within the Hymenochaetaceae (Wagner and Fischer 2001, 2002; Parmasto el al. 2014). *Phellinopsis andina* grouped within the *Phellinopsis* clade with high support in both analyses (28S:ML = 100%, BA = 100%). *Phellinus livescens*, a taxon that decays sapwood of several standing *Nothofagus* species, is sister to *Phellinus uncisetus* (28S:ML = 100%, BA = 100%); both taxa are closely related to the *Fomitiporia* clade (28S:ML = 99%, BA = 100%).

Partial 28S sequences of the three *Phellinus andinopatagonicus* strains are very similar and form a distinct clade clearly delimited (28S = 100%, BA = 100%) from other genera of Hymenochaetales (FIG. 2). We propose a new genus, *Nothophellinus*, for this taxon. The position of *Nothophellinus* was within the *Asterodon-Fuscoporia-Phellinidium-Pyrrhoderma-Phellopilus-Inonotopsis-Coltricia* clade but with low support (FIG. 2).

Transmission electron microscopy.—The trilaminate septa showed two electronically dense layers separated by a clear central stratum. Inside dolipores (i.e. septal pore swelling) an electron translucent area surrounded the internal fibrous reticulated material (FIG. 4A, black arrowhead). The

plasmalemma was continuous from cell to cell but cytoplasmatic continuity was interrupted by granular occlusions that appeared as non-perforate, dark bands (FIG. 4B, o), over which the imperforate, rigid and partially membranous parenthesomes (i.e. septal pore caps, ca. 500 × 40 nm) appeared. The parenthesome external layers were continuous with the endoplasmic reticulum (FIG. 4B, er) and within parenthesomes a narrow dark line was observed (FIG. 4B, ml). In a few median sections, a discontinuity in the electronic density of parenthesomes was observed, but the dark median line was always continuous. Between dolipores and parenthesomes, cytoplasm was less dense and filaments longitudinally disposed could be observed radiating from dolipores to parenthesomes (FIG. 4A, white arrow). This septal pore structure corresponds well with the O1-P2 type of dolipore-parenthesome complex sensu Moore (1985). The reticulated material inside dolipores looks similar to what was described by Setliff et al. (1972) in *Onnia tomentosa* (Fr.) P. Karst. Granular banded occlusions over pores are characteristics of this type of pore complex; in our material they extend into the dolipore channel. According to Traquair and McKeen (1978) these non-perforate bands are characteristic of actively growing hyphae like ours. This type of parenthesome is characteristic of the Hymenochaetaceae (Larsson et al. 2006).

TAXONOMY

Arambarria Rajchenb. & Pildain, gen. nov.

MycoBank MB809349

Basidiomes poroid, annual to reviving, effused to effused-reflexed, context homogeneous, not developing a granular core, hyphal system monomitic, generative hyphae simple-septate, walls thickened and brown, setae none, basidiospores ellipsoid to broadly ellipsoidal, thick-walled, walls yellow in water, reddish chestnut in KOH, IKI−, acyanophilous.

Typification:Arambarria destruens Rajchenb. & Pildain (type).

*Etymology:*Named after Dr María Angélica Arambarri, former Director of LPS Herbarium, in honor of her contributions on taxonomy of microfungi of southern Argentina.

*Notes:*This new, monotypic genus differs morphologically from other poroid, monomitic Hymenochaetaceae by the combination of yellow (reddish chestnut in KOH), thick-walled basidiospores, lack of a granular core and no setoid elements. The proposal of this genus is supported by molecular phylogenetic analysis (FIGS. 2, 3). It belongs to a larger clade together with *Inocutis* Fiasson & Niemelä and *Fomitiporella* Murrill. *Inocutis* is most similar because of its monomitic hyphal system and yellow basidiospores that become reddish chestnut in KOH but differs morphologically by the formation of a granular core in the context. *Fomitiporella* differs by developing perennial basidiomes and a dimitic hyphal system (Wagner and Fischer 2002). *Arambarria* presents characters similar to *Inonotus* sensu stricto (s.s.) as defined by Wagner and Fischer (2002), but the latter differs by the presence of setoid elements (hymenial and/or trama setae), by a dimitic hyphal system in certain species and/or by thin-walled basidiospores.

Arambarria destruens Rajchenb. & Pildain, sp. nov. FIGS. 1A, 5

MycoBank MB809350

*Typification:*ARGENTINA, CHUBUT, Lago Puelo National Park, W arm of Lago Puelo, oriental slope of Valle de las Lágrimas, Los Tineos stream, on stem and branches of a dead *D. juncea* in *Austrocedrus chilensis* forest, 10 May 1996, *M. Rajchenberg 11172* (**holotype** BAFC 34575). Ex-type strains BAFCcc 1500, CIEFAPcc192. GenBank accessions:ITS AY072033, 28S KP347520.

Etymology:destruens (*L.*), destroying, referring to the destructive capacity of this species producing a white heart-rot.

*Diagnosis:*Basidiome annual to reviving, effused to effused-reflexed, forming small pilei, context devoid of a granular core, hyphal system monomitic, setae absent, basidiospores broadly

ellipsoidal to ovoid, thick-walled, yellow but turning chestnut in KOH solution. Producing a white rot in the substrate.

Basidiome annual to reviving, resupinate to effused-reflexed, small or covering up to 30 × 7 cm surface in a continuous body, generally forming reflexed pilei in the upper and lateral margins and, when formed, pilei appearing first as if nodular but developing into broadly attached and semicircular bodies, 2.5–4 cm wide, 1.2–1.8 cm radius and up to 1.5 cm thick at the base, or pilei elongated; the margins blunt and up to 2–3 mm thick. Pilea surface pubescent to strigose at the base, but loosing the hairs with age and then surface indurated, lacking a crust, cracked or not, hairy portions light tobacco, glabrous portions dark brown with black striae. Pores generally roundish to irregular, subgyrose, 3–3.5(–4.5)/mm, light tobacco brown to yellowish brown when newly developed, turning dark chestnut brown upon maturity, with pore mouths ashy gray. Context thin in resupinate portions, but up to 8 mm thick in pileate specimens, without a granular core, milk chocolate brown to dark reddish brown, sometimes developing a black line under the pilea surface restricted to reflexed portions. Tubes up to 12 mm long. Hyphal system monomitic. Generative hyphae simple-septate, 2–3(–4) µm diam, slightly thick-walled, hyaline to light brown, to (3–)4–6 µm diam, with up to 1(–1.5) µm thick, chestnut walls, always with a wide lumen. Basidia clavate to barrel shaped, 13–16 × 7–8 µm, with four sterigmata up to 2 µm long. Setoid elements absent. Basidiospores broadly ellipsoidal, ellipsoidal to ovoid, with a straight lateral side, thick-walled, first hyaline, soon becoming yellowish in water but reddish chestnut in 3% KOH, L × W = 6.07 ± 0.32 × 4.43 ± 0.37 µm (range = 5.5–6.5 × 4.0–5.0 µm), Q = 1.37, n/s = 90/3, IKI−, acyanophilous.

*Associated wood-rot:*white.

*Ecology and hosts:*On dead branches and stems of *Lomatia hirsuta* (Proteaceae) and *Diostea juncea* (Verbenaceae). Also producing a rot in cultivated *Vitis vinifera* in central Chile.

*Distribution:*Endemic to the southern South American forests of Argentina, possibly also in southern Chile on the same hosts.

*Culture description:*Rajchenberg and Wright (1998), based on strains from Patagonia under the name *Inocutis jamaicensis* (Murrill) A.M. Gottlieb, J.E. Wright & Moncalvo.

*Species code:*2.6.8.11.32.37.39.40.44.54. (Rajchenberg and Wright 1998).

*Sexuality and nuclear behavior of the mycelium:*Unknown.

Other specimens examined:ARGENTINA, CHUBUT, Lago Puelo National Park, W arm of Lago Puelo, Valle de las Lágrimas, Los Tineos stream, 4 May 1998, *A. Greslebin AG159*1. CHUBUT, Los Alerces National Park, Lago Verde, track to Lago Menéndez, ca. 50 m from the bridge on Arrayanes river, on fallen trunk of *L. hirsuta*, 9 May 1996, *M. Rajchenberg 11116* (BAFC 34592, isolate BAFCcc 1508, CIEFAPcc 194). Ibid., Lago Futalaufquen, Cerro Dedal, beginning of the track towards the mountain's top, on fallen branch of *Diostea juncea*, 9 May 1997, *M. Rajchenberg 11230*, (BAFC 34591). Ibid., Lago Futalaufquen, 'head' of the lake, on dead branches of living *Diostea juncea* at the lake shore, 12 Dec 2012, *M. Rajchenberg 12504* and *12505*. Ibid., 25 May 2011, M. *Rajchenberg 12478* (isolate CIEFAPcc 347).

Notes:Arambarria destruens is based on specimens previously described as *Inocutis jamaicensis* from Patagonia (Rajchenberg 2006, cf. also Rajchenberg and Wright 1988). It is characterized by a monomitic hyphal system, ellipsoidal, yellow thick-walled basidiospores and effused to effused-reflexed basidiomes. Although microscopically it looks very similar to the type of *Inonotus jamaicensis* Murrill (NY!), the latter differs in developing pileate basidiomes with a duplex context that develops a granular core and a distinct black layer between the upper and lower parts (Reid 1955, Gilbertson and Ryvarden 1987, Ryvarden 2005). The importance of a duplex context with a black layer and no granular core as significant distinguishing features of *Arambarria destruens* were not recognized when the specimens were identified as *I. jamaicensis*.

Strain Fv.Ch-7 of *Fomitiporella* sp. (GenBank accession:DQ459301) from Chile and isolated from *Vitis vinifera* grouped with 100% support with *Arambarria destruens* and might be the same species.

Nothophellinus Rajchenb. & Pildain, gen. nov.

MycoBank MB809351

Basidiome perennial, pileate, poroid, cuticle present, context xanthochroic, hyphal system ditrimitic with simple-septate generative hyphae, skeletal hyphae and few binding hyphae. Basidiospores cylindrical to obclavate, thin-walled, IKI−, acyanophilous. Hymenial setae or setal hyphae absent. Associated with white wood-rot.

Typification:Nothophellinus andinopatagonicus (J.E. Wright & J.R. Deschamps) Rajchenb. & Pildain, comb. nov. (FIG. 1B)

MycoBank MB809355

≡ *Pyrrhoderma andinopatagonicum* J.E. Wright & J.R. Deschamps, Rev. Invest. Agropecu. INTA, ser. 5 Pat. Veg. 9:154, 1972 (basionym) (BAFC!).

≡*Phellinus andinopatagonicus* (J.E. Wright & J.R. Deschamps) Ryvarden, Mycotaxon 22:164, 1985.

Etymology:notho- (*Gr.*), similar to or false), *phellinus,* being similar to species of *Phellinus*.

*Notes:*This new, monotypic genus from southern South America is well defined by phylogenetic analyses of the 28S. Morphologically this taxon is characterized by perennial, pileate basidiomes with a thick cuticle on the pileus, a thick context that may present white hyphal cords or crossed by cuticle bands, a ditrimitic hyphal system with simple-septate generative hyphae, skeletal hyphae and few to frequent binding hyphae that are found in the lower context area near the tubes and/or near the contextual hyphal cords, cylindrical to obclavate, thin-walled, IKI− and acyanophilous basidiospores, lageniform, fusiform or mammiform cystidioles, and by lack of setoid elements.

The type species is an important and frequent wood-, heart-rotting taxon of several *Nothofagus* species in southern Argentina and Chile and an important pathogen of *N. pumilio* (Cwielong and Rajchenberg 1995). For a full account of its morphology see Wright and Deschamps (1972, 1975) and Rajchenberg (2006). Cultural features and nuclear behavior of the secondary mycelium (i.e. coenocytic) were provided by Rajchenberg and Greslebin (1995). *Nothophellinus andinopatagonicus* was believed to be related to *Phellopilus* Niemelä, T. Wagner & M. Fisch. (Niemelä et al. 2001) because they share similar macro- and microscopic features (Rajchenberg 2006), except *Phellopilus* develops hymenial setae and a secondary mycelium with oligonucleate hyphal segments (cf. Fiasson and Niemelä 1984). Our results showed that *Phellopilus* and *Nothophellinus* are distantly related based on the 28S analyses (FIG. 2), suggesting that the presence or absence of setoid elements in the basidiome may be a valuable indicator of phylogenetic relatedness among poroid Hymenochaetaceae (Wagner and Fischer 2002, Dai 2010).

Nothophellinus andinopatagonicus and *Pyrrhoderma* Imazeki were considered closely related because they both form a thick, pilea crust (Wright and Deschamps 1972). Our analyses showed that *N. andinopatagonicus* and *Pyrrhoderma adamantinum* (Berk.) Imazeki are not related. *Pyrrhoderma* differs from *Nothophellinus* by producing a monomitic hyphal system and globose to subglobose basidiospores.

Phellinopsis andina (Plank & Ryvarden) Rajchenb. & Pildain, comb. nov. FIGS. 1C, 1D

MycoBank MB809356

≡ *Phellinus andinus* Plank & Ryvarden, Mycotaxon 16:114, 1982 (basionym)(O!, BAFC!).

For a full description see Plank and Ryvarden (1982) and Rajchenberg (2006). The species is characterized by an annual to reviving, resupinate habit, pores 5.5–6 per mm, trama setae of variable length, 30–50(–80) µm long, and large basidiospores, 7–8(–9) × 5–6(–6.5) µm.

*Notes:*Our results clearly indicate the placement of *Ph. andinus* in *Phellinopsis* Y.C. Dai (Dai 2010, Zhou and Qin 2013). *Phellinopsis* is a poroid genus in the Hymenochaetaceae characterized by a dimitic hyphal system, setae that arise from trama hyphae (vs. hymenial setae in *Phellinus* s.s.), and basidiospores with thickened, IKI−, acyanophilous walls that are hyaline but turn yellow with age. Zhou and Qin (2013) offered supporting molecular and phylogenetic evidence for this genus following works by Wagner and Fischer (2002), Jeong et al. (2005), Larsson et al. (2006) and Dai (2010). Both Plank and Ryvarden (1982) and Rajchenberg (2006) described the setae of *Ph. andinus* as trama setae because they are embedded in the dissepiments but, because basidiomes of this species are strictly resupinate and annual, they may be confused with hymenial setae. Spore walls in *Phellinopsis* are yellow when old (Plank and Ryvarden 1982, Dai 2010), but this was not confirmed by Rajchenberg (2006). *Phellinopsis andina* differs from other species in the genus (Zhou and Qin 2013) by having the largest basidiospores so far known and by growing on Myrtaceae. It also forms annual basidiomes, a feature shared with *Ph. junipericola* Zhou (Zhou and Qin 2013).

Pseudoinonotus crustosus (Speg.) Rajchenb. & Pildain, comb. nov. FIG. 1F

MycoBank MB809354

≡ *Polyporus* (*Resupinatus*) *crustosus* Speg., Bol. Acad. Nac. Cs. Córdoba 11:64, 1887 (basionym)(LPS!).

≡ *Inonotus crustosus* (Speg.) J.E. Wright & J.R. Deschamps, Fl. Criptog. Tierra del Fuego 11(3):22, 1975.

≡*Phellinus crustosus* (Speg.) A.M. Gottlieb, J.E. Wright & Moncalvo, Mycol. Progress 1:309, 2002.

*Notes:*Phylogenetic results here show that *P. crustosus* is congeneric with *Pseudoinonotus* Wagner and Fischer (2001). Earlier, Gottlieb et al. (2002) transferred this species to *Phellinus* s.s. but at that time a proper comparison with *Pseudoinonotus* was not possible. *Pseudoinonotus* is characterized by annual, pileate basidiomes, a monomitic hyphal system, subglobose basidiospores that are hyaline, thick-walled, dextrinoid and cyanophilous and hymenial setae that when present are usually curved and/or hooked. *Pseudoinonotus crustosus* displays these features but is distinguished by a

resupinate growth habit, with loose margins that quickly incurve upon drying, ellipsoidal to obovoid, IKI−, acyanophilous basidiospores, and abundant, curved hymenial setae that may be apically incrusted (Rajchenberg 2006).

Phellinus livescens (Speg.) Rajchenb., Sydowia 40:246,1987. FIG. 1E

≡ *Fomes livescens* Speg., Bol. Acad. Cienc. Córdoba 27:342, 1924 (LPS!).

≡*Phellinus igniarius* (L.) Quél. var. *resupinatus* Bres. *sensu* Wright & Deschamps (1972)

*Notes:*This species decays the sapwood of several standing *Nothofagus* species, producing a white fibrous canker-rot. It is similar to *Phellinus igniarius* because of its globose, thick-walled, hyaline, IKI− basidiospores and the subulate to subventricose hymenial setae but distinguished by producing a resupinate basidiome with indurate margins that may sometimes resemble a pileus and by cyanophilous spore walls (Wright and Deschamps 1972, Rajchenberg 2006). Our 28S analyses (FIG. 2) revealed it to be closely related to *Phellinus uncisetus* Robledo, Urcelay & Rajchenb. (2003). *Phellinus uncisetus* is a Neotropical species described from NW Argentina that is sister to *Fomitiporia* (Decock et al. 2006). Both *P. uncisetus* and *P. livescens* differ from *Fomitiporia* by lacking dextrinoid basidiospores, although they are cyanophilic. They are kept in *Phellinus* s.l. pending further analyses. ITS data from *P. uncisetus* were unavailable, but our ITS analysis showed a relationship of *P. livescens* with the *Fomitiporia* clade, supporting the 28S analysis (data not shown).

Hymenochaetaceae sp.

This unidentified fungus is the causal agent of an important white heart-rot of standing *Austrocedrus chilensis* in Patagonia, Argentina. Barroetaveña and Rajchenberg (1996) characterized this heart-rot decay as well as the cultural features of isolated strains, but basidiomes (including sterile conks) were never found despite persistent searches for many years. Our results support it is a distinct taxon within the poroid, dimitic Hymenochaetaceae with globose, thick-walled basidiospores with

yellowish walls (chestnut in KOH) and devoid of setoid structures. It groups with *Fulvifomes inermis* and *Phellinus caryophylli* with high support. *Fulvifomes inermis* is a widespread species in the northern and southern hemispheres originally described from USA (Cunningham 1965, Gilbertson and Ryvarden 1987, Sharma 1995, Rajchenberg 2006, Dai 2010 among others), while *P. caryophylli* is known from eastern Asia and Australia (Cunningham 1965, Ryvarden and Johansen 1980, Sharma 1995). The three form a clade unrelated to either *Fulvifomes* s.s. or *Fomitiporella* s.s., but further research is needed to find a more stable taxonomy for these species.

DISCUSSION

The general topological relationships among the different groups of poroid Hymenochaetaceae obtained from for the 28S dataset agree with those reported by Dai et al. (2010) and Parmasto et al. (2014). Our analyses show quite clearly that two Patagonian members of the poroid Hymenochaetaceae were included within previously described genera (*Phellinopsis andina*, *Pseudoinonotus crustosus*), two resulted in new, distinct clades, proposed as new genera here (*Arambarria* and *Nothophellinus*) and two (*Phellinus livescens* and Hymenochaetaceae sp.) clustered in two different, unresolved groups of taxa (FIG. 2).

It was surprising that *A. destruens* consistently and repeatedly grouped with *Fomitiporella* in our phylogenetic analyses. Nevertheless the latter consistently appeared as the sister group of *Inocutis* in previous phylogenetic studies (Wagner and Fischer 2002, Parmasto et al. 2014). Gottlieb et al. (2002) identified specimens of the new taxon in *Inocutis* as *I. jamaicensis*; they based their study on specimens determined and provided by the senior author (BAFCcc 1500 GenBank AY072033, BAFCcc 1508 AY072029); their placement in *Inocutis* is justified because at that time the phylogenetic distinction between *Inocutis* and *Fomitiporella* was unknown. Wagner's and Fischer's (2002) study of *I. jamaicensis* is based on a North American specimen and is likely to be *I. jamaicensis* s.s.

This study provides the first estimation of phylogenetic relationship of poroid Hymenochaetaceae from southern South America. Our phylogenetic analyses recovered the same topologies and primary phylogenetic relationships shown by Wagner and Fischer (2002), Dai (2010) and Parmasto et al. (2014). The Hymenochaetaceae phylogeny is currently based mainly upon 28S partial sequences, as in other phylogenetic studies within Basidiomycota (e.g. Garcia-Sandoval 2011, Birkebak et al. 2013); the branching pattern remains poorly resolved. Lower-level phylogenic groups, as in *Fomitiporella-Inocutis-Arambarria*, also are not resolved in ITS-based trees. For a complete understanding of the taxonomy and diversity of the family, future phylogenetic studies must include representative taxa from all continents and forest biomes. Molecular phylogenetic studies offer a useful tool for investigating evolutionary relationships, although they do not fully identify the key morphological or biological characters needed for taxonomic distinction.

ACKNOWLEDGMENTS

Shaun Pennycook (Auckland, New Zealand) provided advice on nomenclatural problems. Li-Wei Zhou (Chinese Academy of Science, China) kindly provided information on sequences not yet available from international databases. Daniel L. Lindner (USDA Forest Service, Madison, Wisconsin) kindly reviewed a preliminary version of this manuscript. Thanks are also due to editors and anonymous reviewers for their suggestions to improve the text. Pablo Sandoval (Universidad de Chile in Santiago) provided Fig. 1F and authorized its publication. Authors are members of the Research Career of CONICET. This work was financially by grant PIP-CONICET 80101000 (to MR). We acknowledge the continued support of Administración de Parques Nacionales for permits to collect specimens.

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LEGENDS

FIG. 1, A□F. Basidiomes of the endemic poroid Hymenochaetaceae from Patagonia. A. *Arambarria destruens*. B. *Nothophellinus andinopatagonicus*. C,D. *Phellinopsis andina*. C. young basidiome. D. mature revived basidiome. E. *Phellinus livescens*. D. *Pseudoinonotus crustosus* (photograph by P. Sandoval). Bars = 2 cm

FIG. 2. Maximum likelihood tree from partial 28S dataset reveals the placement of Hymenochaetaceae from Patagonia. Thick vertical black bars identify root branch for the taxonomic lineage indicated by the adjacent label. Numbers in node branches identify the statistics bootstrap percentages and Bayesian posterior probabilities for that branch. Maximum likelihood bootstraps from 1000 iterations. Bayesian posterior probabilities from 1000 iterations (10 000 000 runs sampling every 100th iteration). Bootstrap values ≥ 50% followed by the Bayesian posterior probability (≥ 95%) are indicated in the node branches; □ = support values lower than 50/95%. Boldface = Patagonian specimens. T = sequences obtained from the genic type species.

FIG. 3. Phylogram of *Inocutis-Fomiporella-Arambarria* generated from ITS sequence data with maximum likelihood and Bayesian analysis. Thick vertical black bars identify root branch for the taxonomic lineage indicated by the adjacent label. Numbers in node branches identify the statistics bootstrap percentages and Bayesian posterior probabilities in percentage for that branch. Maximum likelihood bootstraps from 1000 iterations. Bayesian posterior probabilities from 1000 iterations (10 000 000 runs sampling every 100th iteration). Boldface identifies Patagonian specimens. Bootstrap values ≥ 50% followed by the Bayesian posterior probability (≥ 95%) are indicated in the node branches; □ I = support values lower than 50/95%. Boldface = sequences from Patagonian forests.

FIG. 4. A, B. Hymenochaetaceae sp. Dolipore apparatus. A. Dolipore section showing fibrous reticulated material (black arrow) and longitudinally arranged filaments (white arrow). B. Section showing features associated with the dolipore-parenthesome apparatus: P = parenthesome; D = dolipore; er = endoplasmatic reticulum; o = granular occlusions; ml = narrow dark line.

FIG. 5. *Arambarria destruens*, microscopic features. a. basidiospores. b. basidia. c. generative hyphae. Bars: 4a = 10 µm, 4b, c = 20 µm.

FOOTNOTES

Submitted 27 Jun 2014; accepted for publication 10 Mar 2015.

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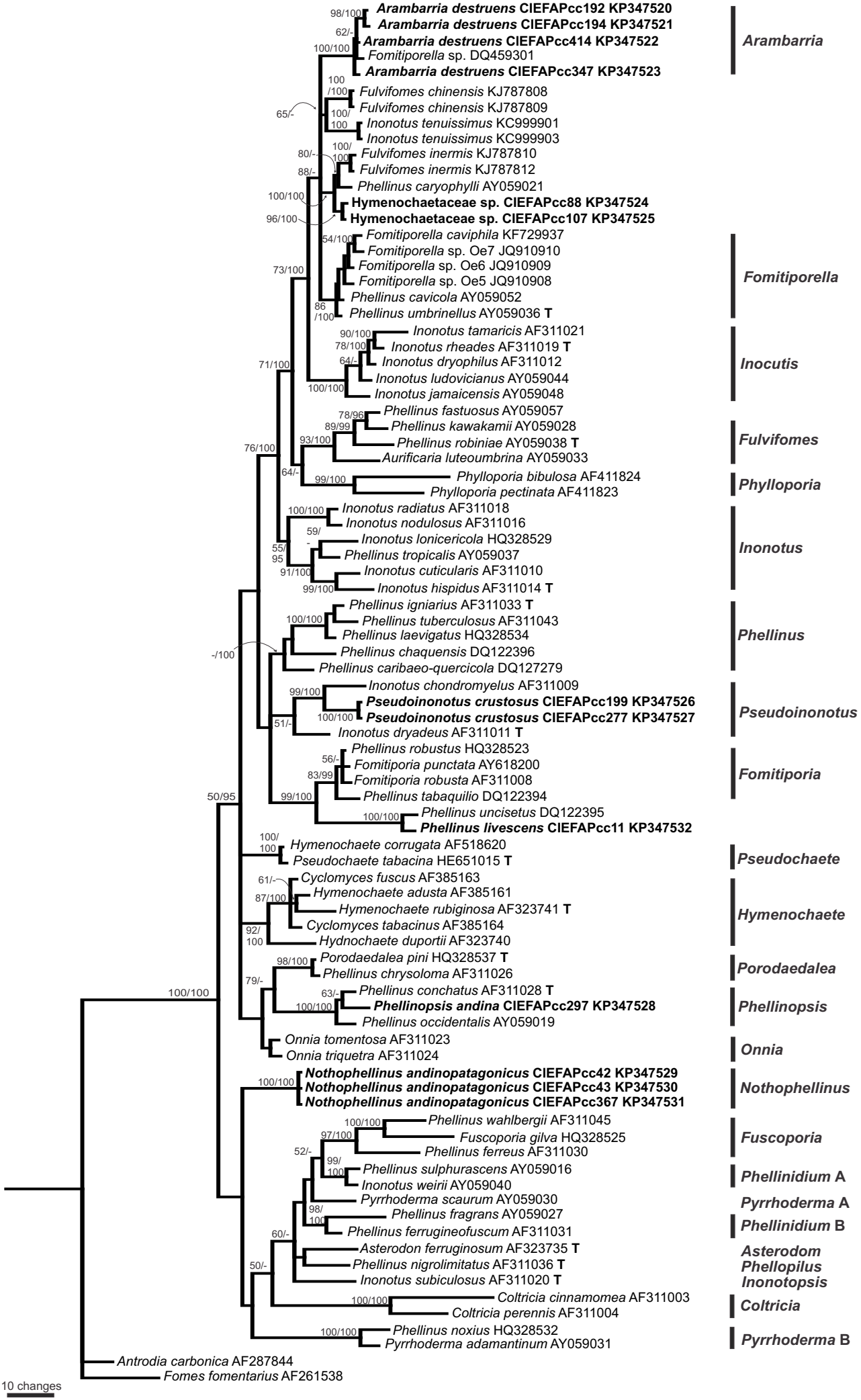
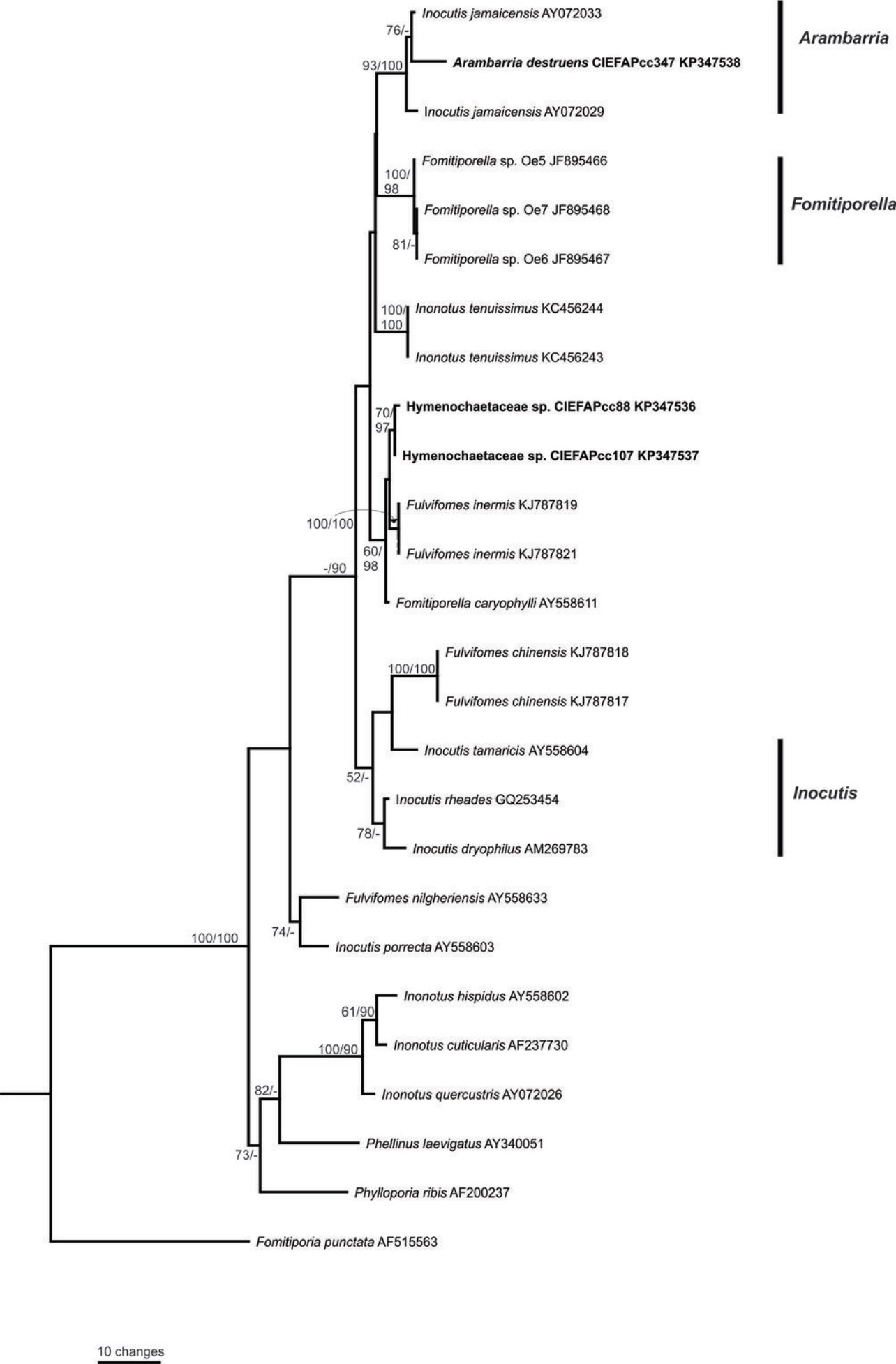
TABLE I. Poroid Hymenochaetaceae from Patagonia, Argentina and their current names

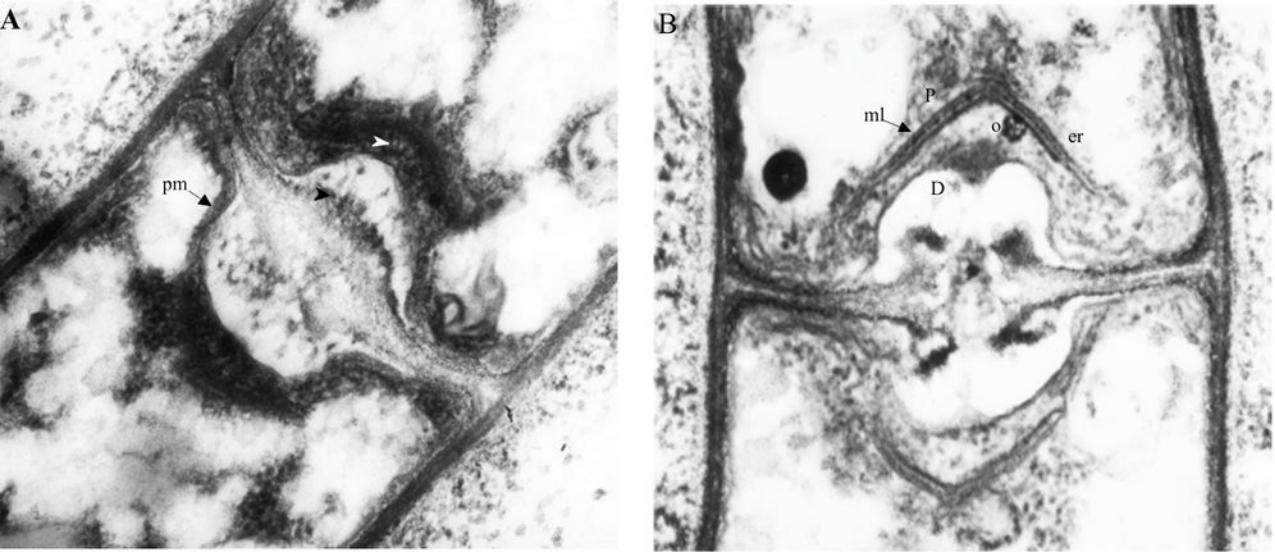
Species	Current names proposed herein	Geographic distribution	Host(s)
Hymenochaetaceae sp.[a]	Hymenochaetaceae sp.	Endemic (Patagonia)	*Austrocedrus chilensis*
Hymenochaete porioides[b] T. Wagner & M. Fischer (=*Cyclomyces tabacinus* [Mont.] Pat.)	Not treated	Pantropical	*Nothofagus dombeyi* and other undetermined angiosperms
Inocutis jamaicensis[b] (Murrill) Gottlieb, J.E. Wright & Moncalvo	*Arambarria destruens* Rajchenb. & Pildain	Neotropical	*Diostea juncea*, *Lomatia hirsuta*
Inonotus crustosus[b] (Speg.) J.E. Wright & J.R. Deschamps	*Pseudoinonotus crustosus* (Speg.) Rajchenb. & Pildain	Endemic (Patagonia)	*Nothofagus betuloides*, *N. dombeyi*, *N. pumilio*
Phellinus andina[b] Plank & Ryvarden	*Phellinopsis andina* (Plank & Ryvarden) Rajchenb. & Pildain	Endemic (Patagonia)	*Luma apiculata*, *Myrceugenia exsucca*
Phellinus andinopatagonicus[b] (J.E. Wright & J.R. Deschamps) Ryvarden	*Nothophellinus andinopatagonicus* (J.E. Wright & J.R. Deschamps) Rajchenb. & Pildain	Endemic (Patagonia)	*Nothofagus antarctica*, *N. betuloides*, *N. dombeyi*, *N. nervosa*, *N. pumilio*
Phellinus inermis[b] (Ellis & Everh.) G. Cunn.	Not treated	Amphitropical	*Diostea juncea*, *Escalonia* sp., *Nothofagus dombeyi*, *Maytenus boaria*, *Weinmannia trichosperma*. Also on *Eucryphia cordifolia* and *Tepualia stipularis* in southern Chile
Phellinus livescens[b] (Speg.) Rajchenb.	*Phellinus livescens* (Speg.) Rajchenb.	Endemic (Patagonia)	*Nothofagus antarctica*, *N. betuloides*, *N. dombeyi*, *N. pumilio*
Phellinus senex[b] (Nees & Mont.) Imaz.	Not treated	Pantropical and temperate areas	*Dascyphyllum diachantoides*, *Luma apiculata*, *Myrceugenia exsucca*, *Weinmannia trichosperma*. In southern Chile also recorded on *Tepualia stipularis*.

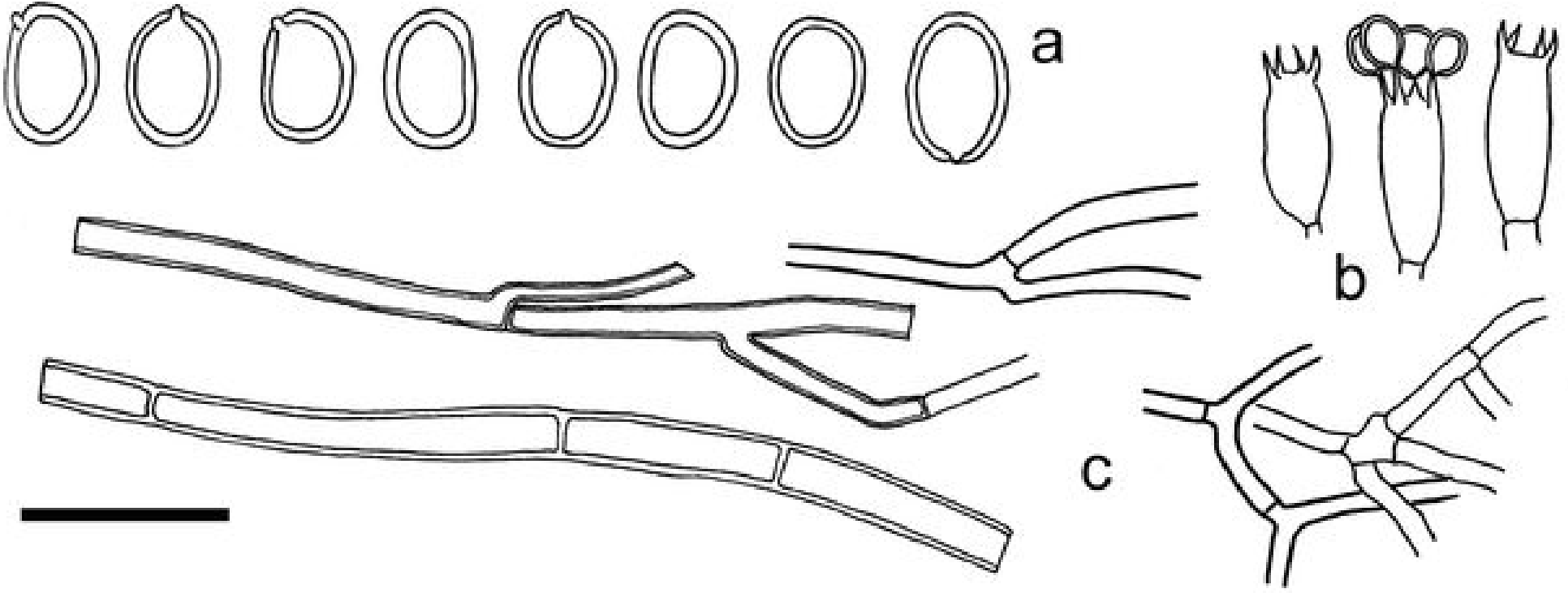
[a] Barroetaveña and Rajchenberg (1996).
[b] Rajchenberg (2006).


A
B
C
D
E
F


Arambarria destruens CIEFAPcc192 KP347520
Arambarria destruens CIEFAPcc194 KP347521
Arambarria destruens CIEFAPcc414 KP347522
Fomitiporella sp. DQ459301
Arambarria destruens CIEFAPcc347 KP347523
Fulvifomes chinensis KJ787808
Fulvifomes chinensis KJ787809
Inonotus tenuissimus KC999901
Inonotus tenuissimus KC999903
Fulvifomes inermis KJ787810
Fulvifomes inermis KJ787812
Phellinus caryophylli AY059021
Hymenochaetaceae sp. CIEFAPcc88 KP347524
Hymenochaetaceae sp. CIEFAPcc107 KP347525
Fomitiporella caviphila KF729937
Fomitiporella sp. Oe7 JQ910910
Fomitiporella sp. Oe6 JQ910909
Fomitiporella sp. Oe5 JQ910908
Phellinus cavicola AY059052
Phellinus umbrinellus AY059036 T
Inonotus tamaricis AF311021
Inonotus rheades AF311019 T
Inonotus dryophilus AF311012
Inonotus ludovicianus AY059044
Inonotus jamaicensis AY059048
Phellinus fastuosus AY059057
Phellinus kawakamii AY059028
Phellinus robiniae AY059038 T
Aurificaria luteoumbrina AY059033
Phylloporia bibulosa AF411824
Phylloporia pectinata AF411823
Inonotus radiatus AF311018
Inonotus nodulosus AF311016
Inonotus lonicericola HQ328529
Phellinus tropicalis AY059037
Inonotus cuticularis AF311010
Inonotus hispidus AF311014 T
Phellinus igniarius AF311033 T
Phellinus tuberculosus AF311043
Phellinus laevigatus HQ328534
Phellinus chaquensis DQ122396
Phellinus caribaeo-quercicola DQ127279
Inonotus chondromyelus AF311009
Pseudoinonotus crustosus CIEFAPcc199 KP347526
Pseudoinonotus crustosus CIEFAPcc277 KP347527
Inonotus dryadeus AF311011 T
Phellinus robustus HQ328523
Fomitiporia punctata AY618200
Fomitiporia robusta AF311008
Phellinus tabaquilio DQ122394
Phellinus uncisetus DQ122395
Phellinus livescens CIEFAPcc11 KP347532
Hymenochaete corrugata AF518620
Pseudochaete tabacina HE651015 T
Cyclomyces fuscus AF385163
Hymenochaete adusta AF385161
Hymenochaete rubiginosa AF323741 T
Cyclomyces tabacinus AF385164
Hydnochaete duportii AF323740
Porodaedalea pini HQ328537 T
Phellinus chrysoloma AF311026
Phellinus conchatus AF311028 T
Phellinopsis andina CIEFAPcc297 KP347528
Phellinus occidentalis AY059019
Onnia tomentosa AF311023
Onnia triquetra AF311024
Nothophellinus andinopatagonicus CIEFAPcc42 KP347529
Nothophellinus andinopatagonicus CIEFAPcc43 KP347530
Nothophellinus andinopatagonicus CIEFAPcc367 KP347531
Phellinus wahlbergii AF311045
Fuscoporia gilva HQ328525
Phellinus ferreus AF311030
Phellinus sulphurascens AY059016
Inonotus weirii AY059040
Pyrrhoderma scaurum AY059030
Phellinus fragrans AY059027
Phellinus ferrugineofuscum AF311031
Asterodon ferruginosum AF323735 T
Phellinus nigrolimitatus AF311036 T
Inonotus subiculosus AF311020 T
Coltricia cinnamomea AF311003
Coltricia perennis AF311004
Phellinus noxius HQ328532
Pyrrhoderma adamantinum AY059031
Antrodia carbonica AF287844
Fomes fomentarius AF261538
10 changes
Arambarria
Fomitiporella
Inocutis
Fulvifomes
Phylloporia
Inonotus
Phellinus
Pseudoinonotus
Fomitiporia
Pseudochaete
Hymenochaete
Porodaedalea
Phellinopsis
Onnia
Nothophellinus
Fuscoporia
Phellinidium A
Pyrrhoderma A
Phellinidium B
Asterodom
Phellopilus
Inonotopsis
Coltricia
Pyrrhoderma B


Inocutis jamaicensis AY072033
76/-
Arambarria destruens CIEFAPcc347 KP347538
93/100
Inocutis jamaicensis AY072029
Arambarria
Fomitiporella sp. Oe5 JF895466
100/
98
Fomitiporella sp. Oe7 JF895468
81/-
Fomitiporella sp. Oe6 JF895467
Fomitiporella
100/
100
Inonotus tenuissimus KC456244
Inonotus tenuissimus KC456243
70/
97
Hymenochaetaceae sp. CIEFAPcc88 KP347536
Hymenochaetaceae sp. CIEFAPcc107 KP347537
Fulvifomes inermis KJ787819
100/100
Fulvifomes inermis KJ787821
60/
98
-/90
Fomitiporella caryophylli AY558611
Fulvifomes chinensis KJ787818
100/100
Fulvifomes chinensis KJ787817
Inocutis tamaricis AY558604
52/-
Inocutis rheades GQ253454
78/-
Inocutis dryophilus AM269783
Inocutis
Fulvifomes nilgheriensis AY558633
74/-
100/100
Inocutis porrecta AY558603
Inonotus hispidus AY558602
61/90
Inonotus cuticularis AF237730
100/90
82/-
Inonotus quercustris AY072026
Phellinus laevigatus AY340051
73/-
Phylloporia ribis AF200237
Fomitiporia punctata AF515563
10 changes


A
pm
B
ml
P
o
er
D


a
b
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