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***Phellinotus*, a new neotropical genus in the Hymenochaetaceae (Basidiomycota, Hymenochaetales)**

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Abstract

A new poroid genus with two conspicuous and common species growing on living Fabaceae trees is described from the Seasonally Dry Tropical Forests biome of Brazil. Both taxa in this forest pathogen genus resemble *Phellinus rimosus* macroscopically, but are distinguished by a dimitic hyphal system with skeletal hyphae present only in the trama of the tube layer while the context remains monomitic, and by the ellipsoid, thick-walled, adaxially flattened, yellow basidiospores that turn chestnut brown in KOH solution. Molecular and morphological studies of Brazilian specimens macroscopically similar to the *Phellinus rimosus* species complex were carried out to solve their phylogenetic relationships among the Hymenochaetaceae. *Phellinotus gen. nov.* with *P. neoaridus sp. nov.* as the genus type and *P. piptadeniae comb. nov.* are presented and described. Phylogenetically, *Phellinotus* is closely related to *Arambarria*, *Inocutis*, *Fomitiporella* and other taxonomically unresolved terminal clades, and unrelated to *Fulvifomes* and *Phylloporia*. *Phellinotus* and other genera of poroid Hymenochaetaceae that lack setae or setal hyphae and produce thick-walled, colored (pale yellow to rusty brown) basidiospores form a phylogenetic group here named the ‘phellinotus clade’. Our results indicate the need to include taxa from unexplored areas in order to get a thorough understanding of the phylogeny of the Hymenochaetaceae.

Key words: forest pathogen, *Fulvifomes*, molecular phylogeny, mycodiversity, *Phellinus rimosus* complex, polypores, taxonomy

Introduction

Hymenochaetaceae Donk (Hymenochaetales Oberw., Agaricomycetes Doweld) comprises about 400 species and, as originally circumscribed (Donk 1964), is not a monophyletic family (Larsson *et al.* 2006). Traditionally, the family has been characterized by wood-decaying fungi with styrylpyrone contents that are responsible for a positive xanthochroic reaction on the basidiomata (e.g., a black coloration of the surface and tissues in 5% KOH solution), simple-septate hyphae and setal elements (Cannon & Kirk 2007). Most poroid Hymenochaetaceae were placed in *Phellinus* Qué. (1886:172) and *Inonotus* P. Karst. (1879:39), except for species of *Coltricia* Gray (1821:644), *Phylloporia* Murrill (1904:141) and *Cyclomyces* Kunze ex Fr. (1830:512), which have macro- and micro-morphological characters that allow for their ready identification (Ryvarden 1991). Species of *Phellinus* and *Inonotus* are defined primarily by the type of hyphal system, either monomitic or dimitic (with skeletal hyphae) hyphal systems, and the annual or perennial habit of the basidiomata (Pilát 1936–42, Cunningham 1947). Species with a dimitic hyphal system and perennial basidioma were placed in *Phellinus* whereas species with a monomitic hyphal system and annual basidioma were identified as *Inonotus* (Fiasson & Niemelä 1984, Corner 1991, Wagner & Fischer 2001). In this context, several smaller genera proposed by Murrill at the beginning of the 20th century were considered as synonyms of *Phellinus* and

Inonotus (Pilát 1936–42, Cunningham 1947). Among the perennial species (*Phellinus s.l.*) those with pileate basidioma, *Pyropolyporus* Murrill (1903:109) and *Porodaedalea* Murrill (1905:367) were proposed on account of their poroid and daedaloid hymenophores, respectively and those with resupinate basidioma, *Fomitiporia* Murrill (1907:7) and *Fomitiporella* Murrill (1907:12) were proposed on account of their hyaline and brown spores, respectively. *Fulvifomes* Murrill (1914:49) was proposed to accommodate *Pyropolyporus* species with brown spores. Among the annual species (*Inonotus s.l.*), *Fuscoporia* Murrill (1907:3) and *Fuscoporella* Murrill (1907:6) were distinguished by their hyaline and brown spores, respectively (Murrill 1903, 1904, 1905, 1907, 1914).

Nevertheless, before the advent of molecular phylogenetics, authors neglected those names and accepted *Phellinus* and *Inonotus* in a wide sense (Lowe 1957, Reid 1963, Pegler 1964, Gilbertson & Ryvarden 1986 and 1987, Wright & Blumenfeld 1984, Larsen & Cobb-Pouille 1990, Ryvarden 2004, 2005). However, *Phellinus* and *Inonotus* were shown to be polyphyletic by molecular phylogenetics and reinforced the observation that the type of hyphal system and basidioma persistence are not valid generic traits in the Hymenochaetaceae (Wagner & Fischer 2002).

A revision of the European taxa of *Phellinus* and *Inonotus* was proposed by Fiasson & Niemelä (1984). They identified smaller species groups that they recognized as morphologically distinct genera, including *Inocutis* Fiasson & Niemelä (1984:24), a new genus based on morphological, cultural, chemical, and nuclear behavioural data. Since then, Fiasson & Niemelä's (1984) results were corroborated by Niemelä *et al.* (2001) and Wagner & Fischer (2001, 2002) through molecular and morphological methods. These studies and others (e.g. Zhou & Qin 2013) supported the genera *Aurificaria* D.A. Reid (1963:278), *Fomitiporella*, *Fomitiporia*, *Fuscoporia*, *Inocutis*, *Inonotus s.s.*, *Mensularia* Lázaro Ibiza (1916:736), *Phellinidium* (Kotl.) Fiasson & Niemelä (1984:25), *Phellinopsis* Y.C. Dai (2010:309), *Phellinus s.s.*, *Phellopilus* Niemelä T., Wagner & M. Fischer (2001:53), *Phylloporia* Murrill, *Porodaedalea* and *Pseudoinonotus* T. Wagner & M. Fischer (2001:781).

Larsson *et al.* (2006) presented a molecular phylogenetic analysis of the Hymenochaetales which supported several different genera of poroid Hymenochaetaceae. Other studies have contributed to the phylogenetic relationships among the Hymenochaetaceae, such as those by Decock *et al.* (2005, 2006, 2007), Jeong *et al.* (2005), Dai *et al.* (2008), Dai (2010), Tura *et al.* (2012), Tian *et al.* (2013), Zhou & Qin (2013), Parmasto *et al.* (2014), Zhou (2014a), Rajchenberg *et al.* (2015), Zhou (2015) and Zhou *et al.* (2015). However, the classification of this group is incomplete because, as with other regions, neotropical taxa were often absent in the phylogenetic studies.

Research on poroid Hymenochaetaceae in the Caatinga dry woodlands, a northeastern Brazilian part of the Seasonally Dry Tropical Forests biome - SDTFs (Särkinen *et al.* 2011), recovered several specimens that macroscopically resemble the *Phellinus rimosus* species complex (Ryvarden 2004). Specimens were identified as *Phellinus piptadeniae* Teixeira (1950:118), repeatedly recorded on *Piptadenia* Benth. (1840:135), and *P. rimosus* (Berk.) Pilát (1940:80) *s.l.* on *Caesalpinia* L. (1753:380) (Drechsler-Santos *et al.* 2010). Species in the *P. rimosus* species complex are characterized by having woody, pileate basidiomata with a cracked (rimose) pileus, a dimittic hyphal system throughout the basidioma, a lack of setae, and ellipsoid, thick-walled, chestnut to rusty brown basidiospores (Fiasson & Niemelä 1984). These morphological features indicate that *P. rimosus* and similar species belong in *Fulvifomes*, as proposed by Fiasson & Niemelä (1984) and confirmed by Dai (2010). The aim of this study was to investigate the identity of *P. rimosus s.l.* and *P. piptadeniae* from Caatinga, Brazil, and to investigate the phylogenetic relationship of these species to *Fulvifomes* and other Hymenochaetaceae.

Materials and methods

Collections

Collecting was carried out in the Caatinga dry woodlands in the states of Alagoas, Ceará, Paraíba, Pernambuco, Rio Grande do Norte and Sergipe (Brazil) and specimens were deposited in the herbaria at CORD, FLOR, HTSA, O, URM, and Centro Forestal CIEFAP (Esquel, Argentina). Herbarium codes follow Thiers (2015).

Morphological studies

Basidiomata were macro- and micro-morphologically analyzed. Microscopic observations were carried out on basidioma sections stained with 3–5% KOH and 1% phloxine, neutral lactophenol, cotton blue, or Melzer's reagent (Largent *et al.* 1977, Ryvarden 1991). Measurements were taken from 3% KOH preparations, following a sampling of 40 (n = 40) structures such as pores/mm, basidiospores, and diameter of hyphae. The size of microscopic elements is given as values (or an interval) followed by 5% variation in parentheses. Abbreviation and symbols are KOH+ =

changing color (reacting) in KOH; IKI- = not reacting in Melzer's reagent; CB± = weakly cyanophilous; (!) = type studied; (≡) = homotypic synonym; (=) = heterotypic synonym; and Q = quotient of basidiospores length (L) / width (W), L = mean of length (arithmetic mean of all basidiospores), and W = mean of width; ave. = arithmetic average; ave.Q = Q arithmetic average. To access and determine the hyphal system under microscopy, sections from the trama of tube layer and context of basidiomata under the pilear surface and between the tube layers were carefully dissected under a stereomicroscope after incubation in 3–5% NaOH for 48h at 40°C (Decock *et al.* 2010). Reference material of *Phellinus piptadeniae* [BRAZIL. São Paulo: Campinas, Bosque dos Jequitibás, on living *Piptadenia communis* Beth. (1841:337–338), 12 September 1943, A.R. Teixeira and P.R. Santos sine numerus (*sn*) (paratype IAC 4365)], *Pyropolyporus robiniae* Murrill (1903:114) [USA. Ohio: January 1957, Lloyd 223 (lectotype NY 743007)], *Phylloporia parasitica* Murrill (1904:141) [COLOMBIA. Santa Marta: near Bonda, 16 December 1898, C. F. Baker *sn* (lectotype K-M 00705227)], *Arambarria destruens* Rajchenb. & Pildain (2015:759) [ARGENTINA. Chubut: Lago Puelo National Park, W arm of lago Puelo, oriental slope of Valle de las Lágrimas, Los Tineos stream, 10 May 1996, M. Rajchenberg III72 (holotype BAFC 34575)], and *Fomitiporella umbrinella* (Bres.) Murrill (1907:13) [BRAZIL. Santa Catarina: Blumenau, Parque Nacional da Serra do Itajaí, 27°02'20" S, 49°03'24" W, 12 June 2012, MAB Silva & al. 271 (FLOR 49263)] were used for morphological comparisons.

DNA extraction

Fragments of basidioma (30 mg) were ground with a pestle in a porcelain mortar containing liquid nitrogen. The resulting powder was transferred to a 1.5 mL pre-warmed (65°C) microcentrifuge tube containing 700 µL of extraction buffer [CTAB 2%, 100 mM Tris-HCl pH 8, 1.4 M NaCl, 20 mM EDTA, 1% PVP (Rogers & Bendich 1985)] and incubated at 65°C for at least 30 minutes. DNA was extracted once with chloroform-isoamyl alcohol (24:1), precipitated with isopropanol, washed with 70% ethanol, and re-suspended in 50 µL ultrapure water (Góes-Neto *et al.* 2005).

Polymerase chain reaction and sequencing

Reaction mix and parameters for PCR amplification of the full ITS (Internal transcribed spacer of nuclear ribosomal RNA gene) regions followed Kaliyaperumal & Kalaichelvan (2008) using the primers ITS1 and ITS4 (White *et al.* 1990). For the nLSU (Large sub-unit of nuclear ribosomal RNA gene), amplification was carried out with parameters and reagent concentrations given by Góes-Neto *et al.* (2005) using the primers LR0R and LR7 (Moncalvo *et al.* 2000). The amplicons were purified using the PureLink PCR Purification Kit (Invitrogen) and the purified products were sequenced at the Human Genome Research Center of the Universidade de São Paulo (USP, Brazil) in an ABI-310 Capillary Sequencer (PerkinElmer, Wellesley Massachusetts, USA). Primers LR0R/LR5 and ITS1/ITS4 were used for sequencing the nLSU and ITS, respectively. The sequences were deposited in the GenBank (Benson *et al.* 2009).

Phylogenetic analysis

Seven ITS and seven nLSU sequences obtained in this study were used to search for sequences of the closest related taxa, using BLASTn searches in the GenBank (see Appendix 1). Most of the sequences and species in this study represent the currently accepted genera of Hymenochaetaceae based on phylogenetic concepts (Wagner & Fischer 2002, Larsson *et al.* 2006, Rajchenberg *et al.* 2015). ITS and nLSU sequences obtained in this study and those retrieved from GenBank are added to the final matrix. *Trichaptum sector* (Ehrenb.) Kreisel (1971:84) was defined as the outgroup, based on previous papers that showed this genus as related to Hymenochaetaceae within Hymenochaetales (Larsson *et al.* 2006). All specimens and sequences used in this study are listed in the Appendix 1.

The final ITS and nLSU datasets were then automatically aligned with Mafft v.7 (Katoh & Standley 2013) under the E-INS-I and G-INS-I strategies, respectively. The first strategy is suitable for regions with multiple conserved domains and long gaps, while the second is for regions with global homology. Both of the alignments were manually adjusted as necessary with MEGA v.6.0 (Tamura *et al.* 2013). Unreliably aligned positions in the ITS alignment were detected using GBLOCKS v.0.91b (Castresana 2000), using the following parameters: minimum number of sequences for a conserved position and for a flank position, both set to 43; maximum number of contiguous nonconserved positions set to 6; minimum length of a block set to 3; and allowed gap positions set to with half. The final alignment was then divided in four partitions: ITS 1, 5.8S, ITS 2 and nLSU. The best nucleotide substitutions model for each partition was estimated using the AIC (Akaike Information Criterion), as implemented in jModelTest2 v.2.1.6 (Darriba *et al.* 2012, Guindon & Gascuel 2003).

Two phylogenetic routines were used to reconstruct the relationships hypothesis, using the concatenated dataset with the four partitions: Maximum Likelihood (ML) and Bayesian Inference (BI). ML analysis was carried out as implemented in RAxML v.8.1.24 (Stamatakis 2014), available in the CIPRES science gateway (Miller *et al.* 2010).

The analysis first involved 100 ML hill-climbing searches, each one starting from one randomized stepwise addition parsimony tree, under a GTRGAMMAI model, with all parameters estimated by the software. Only the best-scored likelihood tree from all searches was kept. To access the reliability of the nodes, multiparametric bootstrapping replicates under the same model were computed, allowing the program to halt bootstrapping automatically by the autoMRE option. The bootstrap values were then annotated to the best likelihood tree find. An additional file with the partitions was informed to force the software to estimate the parameters for each partition independently, through all steps of the analyses.

To check for incongruences among the partitions, each partition was analyzed under ML separated under the same parameters described above, comparing the resulting topologies and looking for conflicts only involving branches with $BS \geq 70\%$ (Reeb *et al.* 2004). A conflict was assumed to be significant if two different relationships for the same set of taxa (one being monophyletic and the other non-monophyletic) were observed in rival trees.

BI was performed in the program Mr. Bayes v.3.2.6 (Ronquist *et al.* 2012). The analysis was implemented by two MCMC independent runs, each one starting from random trees and with four simultaneous independent chains, performing 15,000,000 generations, keeping one tree every 1000th generation. Four rate categories were used to approximate the gamma distribution, and the nucleotide substitutions rates were fixed to the estimated values. The first 20% of the sampled trees was discarded as burn-in, checked by the convergence criterion (frequencies of average standard deviation of split < 0.01) in Tracer v.1.6 (Rambaut *et al.* 2014), while the remaining ones were used to reconstruct a 50% majority-rule consensus tree and to estimate Bayesian Posterior Probabilities (BPP) of the branches.

A node was considered to be strongly supported if it showed a $BPP \geq 0.95$ and/or $BS \geq 90\%$, while moderate support was considered when $BPP \geq 0.9$ and/or $BS \geq 70\%$. The alignment was deposited in TreeBASE (<http://www.treebase.org/treebase/index.html>), under accession ID: 18406.

Results

Molecular analyses

The aligned matrix of the ITS 1 dataset was 160 bp, for the 5.8s was 155 bp, for the ITS 2 was 195 bp, while for nLSU dataset it was 853 bp, resulting in a final gapped matrix of 1363 bp.

The concatenated dataset included sequences from 82 fungal specimens representing the main genera of Hymenochaetaceae, and one representing the outgroup. According to the preceding analyses, GTR +I+G (ITS1), JC (5.8s), K80+G (ITS2) and GTR+I+G (nLSU) were chosen as the best-fit substitution models for each dataset. During the BI analyses, the independent Markov chains reach stability after 921,000 generations, which confirmed that the used 20% burn-in value was appropriate. The bootstopping criteria of the ML algorithm found that 252 pseudoreplicates were sufficient for the dataset.

The phylogenetic reconstructions based on ML and BI analyses for the combined ITS+nLSU datasets did not show major conflicts in the tree topology and were mostly congruent, which allowed us to combine them (Fig. 1). Overall, most of the current genera were recognized in the analyses. The studied specimens from Caatinga, previously determined as *P. rimosus s.l.* and *P. piptadeniae* (Drechsler-Santos *et al.* 2010), clustered in the same generic clade with high support ($BS=99$, $BPP=1$), however separated from the currently known genera. This clade is here recognized as a new genus *Phellinotus*. It is nested in a more inclusive clade composed of poroid members of the Hymenochaetaceae in which setal elements are absent and possess colored and thick-walled basidiospores, e.g., *Arambarria* Rajchenb. & Pildain (2015: 759), *Fomitiporella*, *Fulvifomes*, *Inocutis*, and *Phylloporia*, among other taxonomically unresolved lineages. This more inclusive clade, with significant support in both analyses, moderate in ML ($BS=87$) and strong in BI ($BPP=1$), is here named the ‘phellinotus clade’. Despite some lower support values in some basal branches, the overall topology from both ML and BI analyses is quite similar within this clade. *Phellinotus* appears to be the sister group of specimens identified as *Inocutis dryophila* (Berk.) Fiasson & Niemelä (1984:25), but this relationship was not significantly supported by the data analyzed. The relationship with other genera of the ‘phellinotus clade’ remains unresolved, but species of *Arambarria* and *Fomitiporella* and specimens determined as *Fulvifomes chinensis* (Pilát) Y.C. Dai, *F. inermis* (Ellis & Everh.) Y.C. Dai (2010:187), *Inonotus tenuissimus* H.Y. Yu, C.L. Zhao & Y.C. Dai (2013:64), and unidentified isolates CIEFAPcc88 and 107 (Rajchenberg *et al.* 2015) appear to be closely related to *Phellinotus* (Fig. 1). Also, the genera *Fulvifomes s.s.* and *Phylloporia* were recovered within the ‘phellinotus clade’. The data also showed that the two species under study are closely related but can be considered as two distinct species. *Phellinus rimosus s.l.* specimens from Caatinga, Brazil were unrelated to *Fulvifomes s.s.* (*P. rimosus*). Therefore, they were assigned to a new species *Phellinotus neoaridus*.

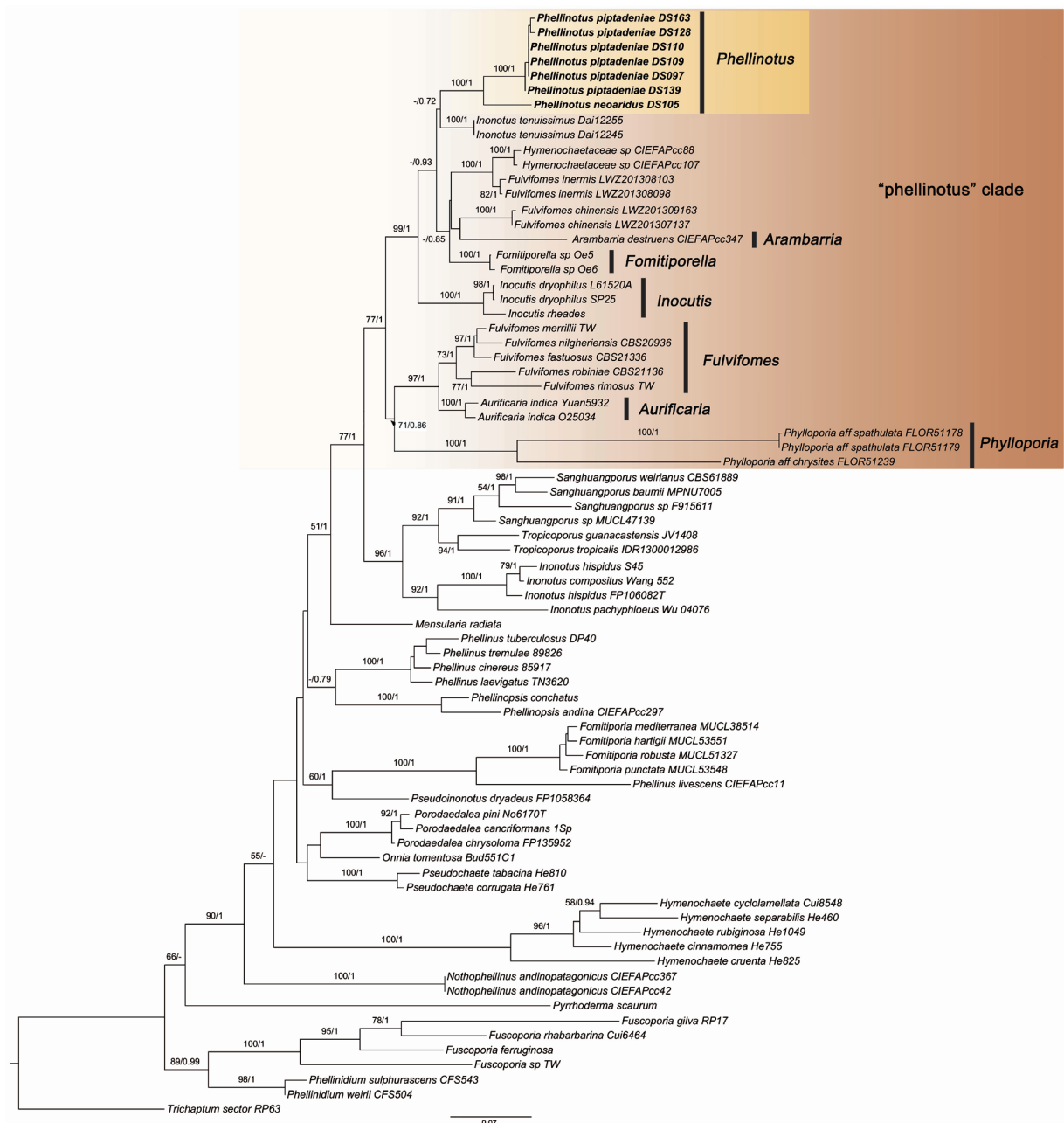


FIGURE 1. Phylogram of Hymenochaetaceae recovered from ITS (ITS1, 5.8S, ITS2) and nuLSU regions, inferred by Maximum likelihood analysis (log likelihood -16996.695988). Support values along branches are bootstrap from ML (≥ 50 , before slash) and Bayesian posterior probability (≥ 0.7 , after slash). *Trichaptum sector* was used to root the tree.

Taxonomy

Phellinotus Drechsler-Santos, Robledo & Rajchenb. *gen. nov.*

Typus generis:—*Phellinotus neoaridus* Drechsler-Santos & Robledo.

Mycobank no:—MB804717

Etymology:—“*Phelli*” from *Phellinus* + “*notus*” (ear) from *Inonotus*, in reference to *Phellinus s.l.* and *Inonotus s.l.*, which traditionally were considered dimitic and monotic, respectively. *Phellinotus* combines both dimitic and monomitic hyphal systems in different parts of basidiomata.

Diagnosis:—Basidioma pileate, annual to perennial; hymenophore poroid. Hyphal system dimitic with skeletal hyphae found only in trama of tube layer; generative hyphae with simple septa, skeletal hyphae aseptate. Basidiospores ellipsoid, adaxially flattened, thick-walled, pale yellow, becoming chestnut brown in KOH solution. Setae and cystidioles absent.

Description:—*Basidioma* annual to perennial, pileate, appanate to ungluate, fulvous brown to dark brown. *Pileus* brown to blackened, rugose to rimose. *Context* with a black line near/below the upper surface, distinct or indistinct. *Tubes* stratified, with or without contextual tissue layer between them. *Hymenophore* poroid, pores irregularly rounded, fulvous brown to deep brown. *Hyphal system* dimitic with skeletal hyphae restricted to the trama of tube layer; contextual generative hyphae in different stages of development, thin- to thick-walled, first regularly septate, branched, becoming sclerified and some portions of thick-walled hyphae sparsely simple-septate; tramal hyphae with simple-septate generative and skeletal hyphae. *Setae* and other sterile elements absent. *Basidia* not observed. *Basidiospores* broadly ellipsoid to ellipsoid, adaxially flattened, smooth, thick-walled, yellow in lactophenol, becoming chestnut brown in KOH solution, weakly cyanophilous, IKI-

Habitat and distribution:—Found on living members of the family Fabaceae, with host specialization (Teixeira 1950, Drechsler-Santos *et al.* 2010, as *Phellinus rimosus* and *P. piptadeniae*). So far known from the South American Seasonally Dry Tropical Forest (SDTF) biome, from the seasonally dry forests of the Atlantic Forest (states of Santa Catarina and São Paulo) and Caatinga (states of Alagoas, Bahia, Ceará, Paraíba, Pernambuco, Rio Grande do Norte and Sergipe) domains of Brazil, and from lowland SDTF of northwestern Peru (Drechsler-Santos *et al.* 2010, 2013, Salvador-Montoya *et al.* 2015).

TABLE 1. Morphological features of poroid Hymenochaetaceae genera.

Genera	Substrate	Basidioma		Hyphal System	Setae	Basidiospores		
		Shape	Tube layers			Shape	Colour	Wall/Dextrinoid/KOH reaction
<i>Arambarria</i>	DW	RES/EFR	AN	MO	Lacking	EBE; FLT	Yellow	Thick / - / +
<i>Asterodon</i>	CW	RES/EFR	AN	DI	Hymenial; simple/branched	EBE	Hyaline	Thin / - / -
<i>Aurificaria</i>	DW	PIL	AN	MO	Lacking	EBE; FLT	Yellow	Thick / - / +
<i>Cylindrosporus</i>	DW	PIL	AN	MO	Hymenial	CYL	Hyaline	Thin / - / -
<i>Fomitiporella</i>	DW	RES/EFR	P	MO/DI	Lacking	EBE; FLT	Brown	Thick / - / +
<i>Fomitiporia</i>	DW/CW	RES/EFR/ PIL	P	MO/DI	Lacking or rare; hymenial	GLB	Hyaline	Thick / + / -
<i>Fulvifomes</i>	DW	RES/EFR/ PIL	P	DI	Lacking	GLB/ EBE; FLT	Yellow	Thick / - / +
<i>Fuscoporia</i>	DW/CW	RES/EFR/ PIL	AN/P	MO/DI	Hymenial	EBE/ALL/ CYL	Hyaline	Thin / - / -
<i>Inocutis</i>	DW	PIL	AN	MO	Lacking	EBE; FLT	Yellow/ brown	Thick / - / -
<i>Inonotopsis</i>	CW	RES	AN	MO	Lacking	EBE	Hyaline	Thin / - / -
<i>Inonotus s.s.</i>	DW	RES/EFR/ PIL	AN/P	MO/DI	Mostly presente; hymenial/Setal hyphae	EBE/GLB	Yellow/ brown	Thin-thick / - / -
<i>Mensularia</i>	DW	RES/EFR/ PIL	AN	MO	Hymenial/ tramal	EBE	Hyaline	Thick / + / -
<i>Nothophellinus</i>	DW	PIL	P	DI-TRI	Lacking	CYL/OBC	Hyaline	Thin / - / -
<i>Onnia</i>	CW	SST	AN	MO	Tramal to hymenial	EBE/GLB	Hyaline	Thin / - / -
<i>Phellinidium</i>	CW	RES/EFR/ PIL	AN/P	MO	Setal hyphae	EBE/ALL/ CYL	Hyaline	Thin / - / -

...Continued on next page

TABLE 1. (Continued)

Genera	Substrate	Basidioma		Hyphal System	Setae	Basidiospores		
		Shape	Tube layers			Shape	Colour	Wall/Dextrinoid/KOH reaction
<i>Phellinus s.s.</i>	DW	RES/EFR/ PIL	P	DI	Hymenial	EBE/GLB	Hyaline	Thin-thick / - / -
<i>Phellinopsis</i>	DW	RES/EFR/ PIL	P	DI	Arising from trama	EBE	Hyaline/ Yellow	Thick / - / -
<i>Phellinotus</i>	DW	PIL	P	DI	Lacking	EBE; FLT	Yellow	Thick / - / +
<i>Phellopilus</i>	CW	RES/EFR/ PIL	P	DI-TRI	Hymenial	OBC/CYL	Hyaline	Thin / - / -
<i>Phylloporia</i>	DW	RES/EFR/ PIL	AN/P	MO/DI	Lacking	EBE/ CYL; FLT	Pale yellow	Thick / - / -
<i>Porodaedalea</i>	CW	RES/EFR/ PIL	P	DI	Hymenial	EBE/GLB	Hyaline	Thin-thick / - / -
<i>Pseudoinonotus</i>	DW/CW	PIL	AN	MO/DI	Hymenial	GLB	Hyaline	Thick / + / -
<i>Pyrrhoderma</i>	DW	PIL/SST	AN/P	MO	Lacking	GLB	Hyaline	Thin / - / -
<i>Sanghuangporus</i>	DW	EFR/PIL	P	DI	Hymenial	EBE/GLB	Pale yellow	Thick / - / -
<i>Tropicoporus</i>	DW	RES/EFR/ PIL	AN/P	DI	Hymenial	EBE/GLB	Pale yellow	Thick / - / -

DW = deciduous wood, **CW** = coniferous wood; **DI** = dimitic, **MO** = monomitic, **TRI** = trimitic, **P** = perennial, **AN** = annual-biannual, **RES** = resupinate, **EFR** = effused-reflexed, **PIL** = pileate, **SST** = substipitate to stipitate, **EBE** = ellipsoid-broadly ellipsoid, **FLT** = flattened, **GLB** = globose-subglobose, ellipsoid, **ALL** = allantoid, **CYL** = cylindrical-subcylindrical, **OBC** = obclavate, (+) or (-) = positive or negative reaction in the basidiospores wall. Genera of the ‘phellinotus clade’ are presented in bold type.

Remarks:—*Phellinotus* is characterized by a pileate basidioma often with a rimose pileus, a dimitic hyphal system with skeletal hyphae only present in the trama of the tube layer, and adaxially flattened, ellipsoid, thick-walled, pale yellow basidiospores that turn chestnut brown in KOH solution. The absence of setae and setal hyphae and the presence of colored (pale yellow to brown) and thick-walled basidiospores indicate that *Phellinotus* is morphologically similar to *Arambarria*, *Aurificaria*, *Fomitiporella*, *Fulvifomes*, *Inocutis*, and *Phylloporia* (Larsson *et al.* 2006, Rajchenberg *et al.* 2015). *Fomitiporella* and *Fulvifomes* have a dimitic hyphal system throughout the basidioma, while species of *Arambarria*, *Aurificaria* and *Inocutis* are monomitic. Additionally, some species of *Fulvifomes* have mainly globose to subglobose, yellowish basidiospores (Wagner & Fischer 2002), that become ferruginous to fulvous in KOH (5.5–6 × 4.5–5.5 µm, as observed in the lectotype of *Pyropolyporus robiniae* Murrill), while *Phylloporia* produces smaller, light yellow basidiospores (Ryvarden 2004), as observed in the lectotype of *P. parasitica* Murrill. *Fomitiporella* also produces basidiospores that turn darker in KOH, as verified in reference material of *F. umbrinella*, the genus type, collected in the type locality (FLOR49263); however, species in this genus develop resupinate basidiomata and are saprobes (Murrill 1907, Teixeira 1994, Zhou 2014b) (Table 1). This morphologically and molecularly related (Fig. 1) group of genera, e.g., *Arambarria*, *Fomitiporella*, *Fulvifomes*, *Inocutis*, *Phylloporia*, and other taxonomically unresolved lineages, is named here as the ‘phellinotus clade’. *Inonotopsis* Parmasto (1973:12) and *Pyrrhoderma* Imazeki (1966:4) are poroid members of the Hymenochaetaceae that also lack setae and setal hyphae; however, they are phylogenetically unrelated and morphologically differ from members of the ‘phellinotus clade’ by producing thin-walled basidiospores.

Phellinotus neoaridus Drechsler-Santos & Robledo *sp. nov.* (Figs 2A–G, 3A, C, E, Table 2)

Typus:—BRAZIL. Pernambuco: Serra Talhada, Estação Experimental do IPA, on living caatingueira tree (*Caesalpinia sp.*), 7°53'29" S, 38°18'17" W–490m alt., 09 December 2008, *Drechsler-Santos DSI05PE* (holotype URM 80362, isotype FLOR 53152).

Mycobank no:—MB805901

Etymology:—*neoaridus*, in reference to the neotropical semiarid region of Brazil covered by Caatinga, a seasonally dry forest of the SDTFs biome (Särkinen *et al.* 2011), where the species was first encountered.

Diagnosis:—Basidioma pileate, annual to perennial, distinctly rimose; black lines near the upper surface of the pileus present; tubes distinctly stratified, hymenophore poroid (3–6/mm). Hyphal system dimitic with skeletal hyphae restricted to trama of tube layer. Basidiospores ellipsoid (5–7 × 4–5.5 µm), adaxially flattened, thick-walled, yellow, chestnut brown in KOH. Pathogenic on *Caesalpinia* spp.

Description:—*Basidioma* mostly perennial, more rarely annual to bi-annual, pileate, projecting up to 150 mm, 100 mm wide and 80 mm thick at base, first appanate, triquetrous to strongly unguulate with age, sometimes with a basal umbo; hard; usually solitary or in groups of several basidiomata widespread along the substrate; margin appanate to convex, always distinct from older parts, cream to ochre orange at first, then turning brown with age. *Pileus* variable in color, first cream to reddish yellow or olive to black, dull when rimose, azonate then sulcate, and finally strongly rimose. *Context* 11–21 mm thick in young, 3–5 mm thick in unguulate specimens, weakly zonate near the base to azonate towards the margin, with black lines near the upper surface of the pilei, granular core variably present, pale to dark brown, becoming black with KOH, a thick gray to black crust present above *context*. *Tubes* stratified, dark reddish brown, without distinct tissue development between layers.

TABLE 2. Detailed morphology (n=40) of *Phellinotus* species and their hosts.

<i>Phellinotus</i> species/specimens	Basidioma		Context dark line	Pore surface	Basidiospores		Skeletal hypha (µm long)	Hosts
	P	AU		Pores/mm	ave. size (µm)	Shape		
<i>Phellinotus neoaridus</i>	P	AU	Indistinct	3–6	5.6–6 × 4.2–5	BE-E	110–560	on <i>Caesalpinia</i> spp.
URM 80494	P	AU	Indistinct	3–4 (–5)	5.6 × 4.2	BE-E	150–300	<i>C. pyramidalis</i>
Robledo 1974	P	AU	Indistinct	3–4 (–5)	5.7 × 4.4	BE-E	110–250	<i>Caesalpinia</i> sp.
URM 80299	P	U	Indistinct	(3–) 4–6	5.9 × 4.5	BE-E	205–554	<i>Caesalpinia</i> sp.
URM 80411	P	AU	Indistinct	(4–) 5–6	5.8 × 4.8	BE-E	237–560	<i>Caesalpinia</i> sp.
URM 80419	P	U	Indistinct	4–6	5.7 × 4.5	BE-E	189–339	<i>Caesalpinia</i> sp.
URM 80422	P	AU	Indistinct	4–5 (–6)	5.9 × 4.9	BE-E	209–489	<i>Caesalpinia</i> sp.
URM 80536	P	T	Indistinct	(4–) 5–6	5.9 × 4.9	BE-E	220–524	<i>Caesalpinia</i> sp.
URM 80577	P	U	Indistinct	4–5 (–6)	5.6 × 4.6	BE	175–372	<i>Caesalpinia</i> sp.
URM 80579	P	AU	Indistinct	(4–) 5–6	6.0 × 5.0	BE-E	264–446	<i>Caesalpinia</i> sp.
URM 80769	P	U	Indistinct	(4–) 5–6	6.0 × 4.8	BE	245–426	<i>Caesalpinia</i> sp.
URM 80362 (holotype)	P	U	Indistinct	(3–) 4–5 (–6)	5.9 × 4.3	BE	198–277	<i>Caesalpinia</i> sp.
<i>Phellinotus piptadeniae</i>	P	AU	Distinct	3–6	5–5.3 × 3.6–4.2	BE-E	230–754	mostly on <i>Piptadenia</i> spp.
IAC 4365 (paratype)	P	AU	Distinct	3–5	5.3 × 4.2	BE-E	280–520	<i>P. gonoachanta</i>
Robledo 1982	P	AU	Distinct	(4–) 5–6	5.1 × 4.0	E	250–500	<i>Piptadenia</i> sp.
URM 80322	AN	A	Distinct	4–5 (–6)	5.1 × 4.1	BE-E	230–615	<i>Mimosa</i> sp.
URM 80345	P	T	Distinct	(4–) 5–6	5.0 × 3.6	E	300–754	<i>Senegalia</i> sp.
URM 80768	P	T	Distinct	(4–) 5–6	5.2 × 3.7	E	268–504	<i>P. stipulacea</i>

A = appanate, AU = appanate to unguulate, BE = broadly ellipsoid, E = ellipsoid, P = perennial, AN = annual-biannual, U = unguulate, T = triquetrous. Compilation of variation data about species is presented in bold type.

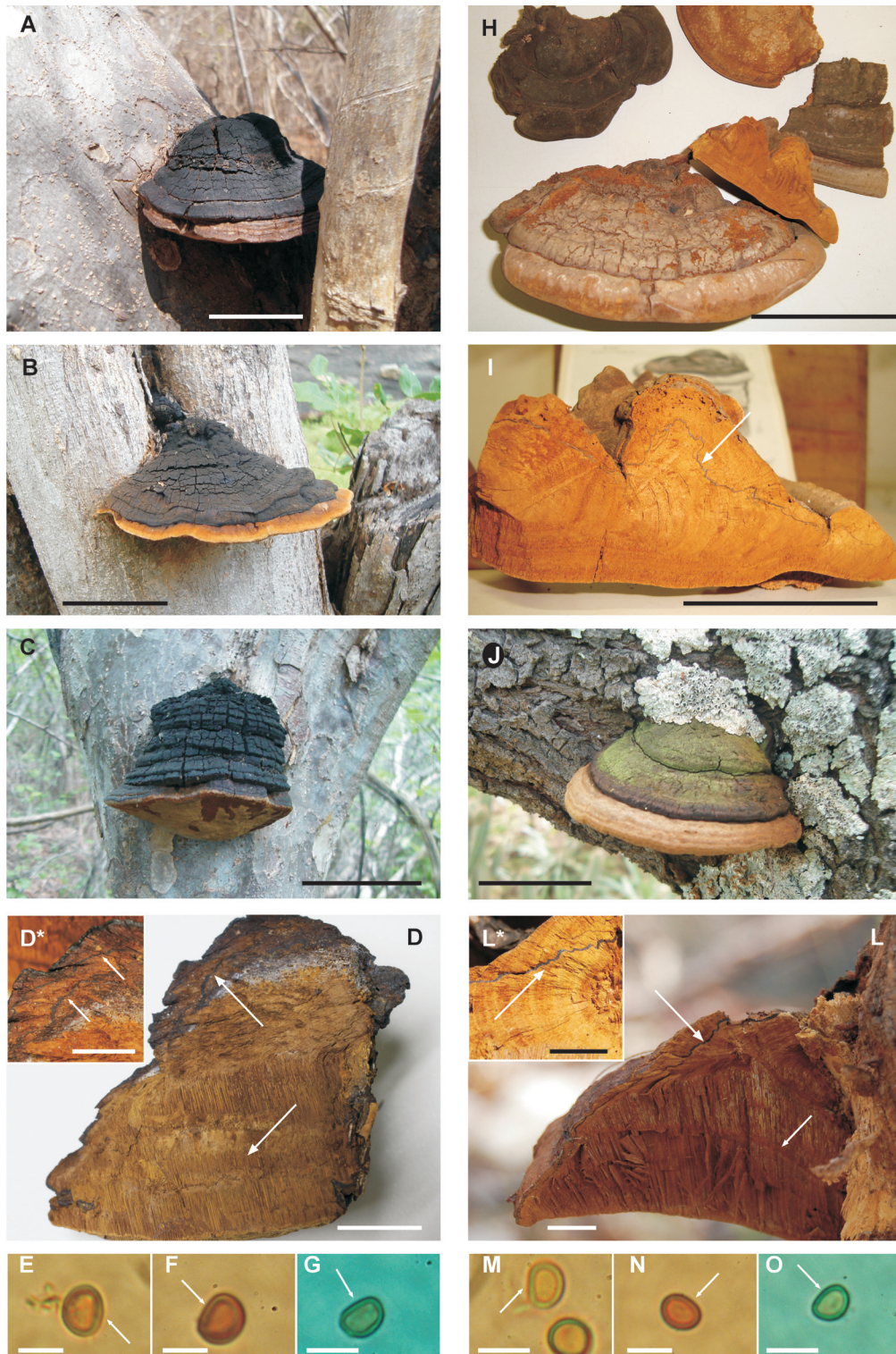


FIGURE 2. *Phellinotus* species. *P. neoaridus*. (A) holotype on specific host (lenticels of *Caesalpinia* sp. in detail); (B) applanate to triquetrous basidioma with a distinct ochre-orange margin (URM80410); (C) ungulate with strongly rimose upper surface and brownish margin (URM80641) (Bars = 5 cm); (D): isotype context and tubes lacking tissue layer between the tubes, in detail (D*) the black line near the upper surface (Bars = 1 cm); (E–G) basidiospores, white arrows are indicating the adaxially flattened surface [(E) lactophenol, (F) KOH+, (G) CB±; Bars = 5 µm]; *P. piptadeniae*. (H) paratype (IAC4365); (I) context in detail showing the distinct black line in the paratype; (J) mature triquetrous, developing applanate basidiomata on *Piptadenia* spp. (URM 80768) (Bars = 5 cm); (L) black line and tissue layer between the tubes are showing in detail in L and L* (Bars = 1 cm); (M–O) basidiospores, white arrows are indicating the adaxially flattened surface [(M): lactophenol, (N) KOH+, (O) CB±; Bars = 10 µm]. Photos of basidiomata (A, B, C, D, H, I, J) by Elisandro Ricardo Drechsler-Santos except for ‘L’ which is by Gerardo Lucio Robledo; photos of spores (E, F, G, M, N, O) by Carlos Salvador-Montoya.

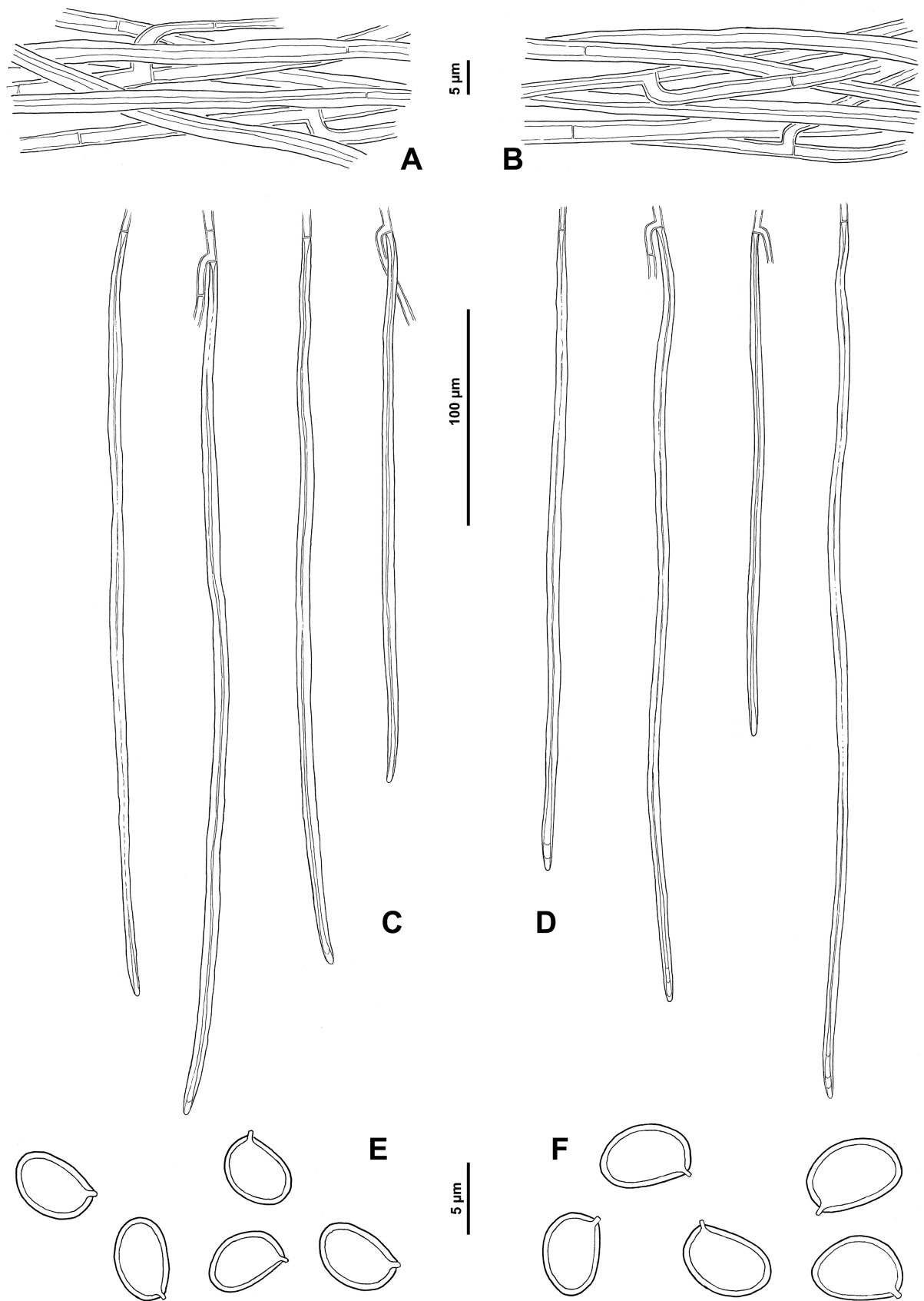


FIGURE 3. Microscopic elements of *Phellinotus* species in line drawings. (A, C, E) *P. piptadeniae* (IAC 4365). (A) hyphal system of context; (C) skeletal hyphae from trama of tube layer; (E) basidiospores. (B, D, F) *P. neoaridus* (URM 80362). (B) hyphal system of context; (D) skeletal hyphae from trama of tube layer; (F) basidiospores. Drawings by Gerardo Lucio Robledo.

Hymenophore poroid, pores round, some elongated, 3–6/mm, (90–)150–280(–350) μm wide, reddish yellow to dark brown; dissepiments entire, (20–)40–150(–300) μm wide. *Hyphal system* dimitic with skeletal hyphae restricted to the trama of the tube layer; contextual generative hyphae pale yellow to dark reddish brown, thin to thick-walled, lumen (3–)4–6(–7) μm wide, regularly simple-septate with ramifications, then becoming sclerified and septa in some portions of thick-walled hyphae destroyed, sometimes forming secondary septa; trama of tube layer composed of generative simple-septate and skeletal hyphae; generative hyphae hyaline, pale yellow to fulvous, thin to thick-walled, (0.5–)1–2(–3) μm wide, forming terminal, dark reddish brown skeletal hyphae, (110–)232–533(–560) \times (3–)4–6(–7) μm , lumen absent to 1–1.5 μm wide, with 1–4 adventitious septa at the narrow to obtuse apex; granular core with few to many sclereoid hyphae. *Basidia* not observed. *Basidiospores* broadly ellipsoid to ellipsoid, 5–6.5(–7) \times 4–5(–5.5) μm (ave. = 5.8 \times 4.7 μm), Q = 1.2–1.3 (ave. Q = 1.2), adaxially flattened, smooth, thick-walled, yellow, chestnut brown in KOH, weakly cyanophilous, IKI–.

Habitat and distribution:—Commonly found on living *Caesalpinia* spp. (Fabaceae) (Drechsler-Santos *et al.* 2010, 2013, as *P. rimosus*). Some basidiomata, mostly those that are annual or bi-annual, are found fallen on the ground near the tree where they presumably developed. Usually, unguulate specimens with many tube layers were found on the tree trunk as well. This species is widely distributed in the Brazilian semiarid region (Caatinga dry woodlands), from the states of Alagoas, Bahia, Ceará, Paraíba, Pernambuco, Rio Grande do Norte and Sergipe.

Remarks:—The typical triquetrous to unguulate basidiomata with a black rimose pileus and reddish brown hymenophore are useful in distinguishing this species. When present, the context of *P. neoaridus* is weakly zonate developing one or more dark lines below the rimose upper surface of the pileus and some basidiomata present a very distinct granular core. *Phellinotus piptadeniae* is similar, but develops a less rimose pilear surface, a distinct black line in the context, and smaller basidiospores. Additionally, it grows repeatedly on *Piptadenia* spp. (Drechsler-Santos *et al.* 2010, 2013, as *Phellinus rimosus*).

Material examined:—BRAZIL. Alagoas: São José da Tapera, Fazenda do Sr. Rudá, on living *Caesalpinia* sp., 9°32'47" S, 37°33'11" W–227m alt., 17 June 2008, Drechsler-Santos & al. DS017AL (URM 80411, O); *ibid*, on living *Caesalpinia* sp., 9°32'49" S, 37°33'27" W–224m alt., 17 June 2008, Drechsler-Santos & al. DS009AL (URM 80579); *ibid*, on living *Caesalpinia* sp., 9°32'49" S, 37°33'29" W–230m alt., 17 June 2008, Drechsler-Santos DS007AL (URM 80410). Ceará: Reriutaba, Serrote de Boqueirão on living *Caesalpinia* sp., 4°01'13" S, 40°38'43" W–290m alt., 15 June 2007, Drechsler-Santos DS034CE (URM 80847); *ibid*, on living *Caesalpinia* sp., 4°01'15" S, 40°38'41" W–280m alt., 15 June 2007, Drechsler-Santos DS033CE (URM 80536). Paraíba: Sumé, Fazenda Almas, on living *Caesalpinia pyramidalis* Tul., 7°28'21" S, 36°53'28" W–686m alt., 10 August 2008, Drechsler-Santos & Rajchenberg DS044PE (URM 80494). Pernambuco: Cabrobó, Fazenda Mosquito, on living *Caesalpinia* sp., 08°23'06" S, 39°25'30" W–75m alt., 21 November 2009, Robledo 1974 (CORD); Serra Talhada, Estação Experimental do IPA, on living *Caesalpinia* sp. 7°53'49" S, 38°18'12" W–501m alt., 5 March 2009, Drechsler-Santos & al. DS143PE (URM 80769); *ibid*, on living *Caesalpinia* sp., 7°53'50" S, 38°18'11" W–560m alt., 5 March 2009, Drechsler-Santos DS151PE (URM 80764); *ibid*, on living *Caesalpinia* sp., 7°53'20" S, 38°18'25" W–486m alt., 11 March 2008, Drechsler-Santos DS056PE (URM 80641); *ibid*, on living *Caesalpinia* sp., 7°53'47" S, 38°8'12" W–502m alt., 5 March 2009, Drechsler-Santos DS140PE (URM 80741); *ibid*, 7°55'78" S, 38°17'39" W–504m alt., 12 September 2007, Drechsler-Santos DS22PE (URM 80299, O). Sergipe: Niterói on living *Caesalpinia* sp., 9°45'23" S, 37°27'56" W–57m alt., 16 June 2008, Drechsler-Santos & al. DS042SE (URM 80422); Poço Redondo, Trilha de Angicos, on living *Caesalpinia* sp., 9°38'08" S, 37°40'42" W–30m alt., 14 June 2008, Drechsler-Santos DS001SE (URM 80419); *ibid*, on living *Caesalpinia* sp., 9°39'08" S, 37°40'42" W–30m alt., 14 June 2008, Drechsler-Santos & al. DS009SE (URM 80568); Porto da Folha, on living *Caesalpinia* sp., 9°54'40" S, 37°16'16" W–10m alt., 15 June 2008, Drechsler-Santos & al. DS026SE (URM 80577).

Phellinotus piptadeniae (Teixeira) Drechsler-Santos & Robledo *comb. nov.* (Figs 2H–O, 3B, D, F, Table 2)

≡ *Phellinus piptadeniae* Teixeira, Bragantia 10: 118, 1950 (IAC, paratype !).

≡ *Fomitiporella piptadeniae* (Teixeira) Teixeira, Revista Brasileira de Botânica 15(2): 126, 1992.

Mycobank no:—MB805902

Description:—*Basidioma* annual to bi-annual or perennial, pileate, projecting up to 250 mm, 300 mm wide and 150 mm thick at base, applanate to triquetrous; hard; usually solitary, but also gregarious or many basidiomata widespread along the substrate; margin applanate, usually distinct from older parts of basidioma, pale brown to brown. *Pileus* variable in color, first cream to reddish yellow, becoming olive to black grayish, first azonate, afterwards with sulcate

zones and finally cracked to rimose. *Context* 20–60 mm thick, zonate, with a distinct black line separating it in two parts, pale, fulvous to reddish brown, becoming black with KOH, a thin to slightly thick dark brown crust present above context. *Tubes* distinctly stratified, reddish to dark brown, with context layers among the strata of tubes. *Hymenophore* poroid, pores round, 3–6/mm, (100–)130–200(–230) μm wide, reddish yellow to dark brown; dissepiment entire, (40–)60–160(–200) μm . *Hyphal system* dimitic with skeletal hyphae restricted to trama of tube layer; contextual generative hyphae in different stages of development, pale yellow to reddish dark brown, thin to thick-walled, (4–)5–8(–10) μm wide, always with wide lumen (2–)2.5–5(–8) μm wide, first regularly septate, branched, becoming sclerified and some portions of thick-walled hyphae sparsely simple-septate; tramal hyphae formed by generative and skeletal hyphae; generative hyphae simple-septate, hyaline, pale yellow to fulvous, thin to thick-walled in different stages of development, (1–)2–2.5(–3) μm wide; skeletal hyphae terminal, reddish dark brown, (230–)280–470(–760) μm long, (3.5–)5–8(–10) μm wide, lumen 1–2(–3) μm to solid, some with small aborted ramifications and geniculate portions at the base or apex, with one to four adventitious septa at the apex, which is narrow to obtuse. *Basidia* not found. *Basidiospores* broadly ellipsoid to ellipsoid, (4.5–)5–5.5(–6) \times 3.5–4.5(–5) μm (ave.= 5.1 \times 3.9 μm), Q = 1.2–1.4 (ave.Q = 1.3), adaxially flattened, smooth, thick-walled, yellowish, becoming chestnut brown in KOH, weakly cyanophilous, IKI-.

Habitat and distribution:—*Phellinotus piptadeniae* is a very common pathogen of living *Piptadenia* spp. (Fabaceae), also found on *Eugenia* L. (1753:470) (Myrtaceae) and on other genera of Fabaceae such as *Libidibia* (DC.) Schldl. (1830: 192), *Mimosa* L. (1753:516), *Pithecolobium* Mart. (1837:114), and *Senegalia* Raf. (1838:119) (Drechsler-Santos *et al.* 2010, 2013, Salvador-Montoya *et al.* 2015, as *Phellinus piptadeniae*). Most specimens from Caatinga are annual or bi-annual. Occasionally, basidiomata are large and perennial with many tube layers, such as the paratype (IAC 4365!) from the SDTFs of Atlantic Forest in Santa Catarina and São Paulo states (Teixeira 1950, Salvador-Montoya *et al.* 2015). Additionally, this species is widely distributed in the Brazilian Caatinga dry woodlands of Alagoas, Bahia, Ceará, Paraíba, Pernambuco, Rio Grande do Norte and Sergipe states and was recently recorded for lowland SDTF of northwestern Peru (Salvador-Montoya *et al.* 2015).

Remarks:—This species is morphologically variable, but the slightly rimose pileus, fulvous to reddish brown context and a longitudinal dark line in the middle of the basidioma context are diagnostic (Drechsler-Santos *et al.* 2010, Salvador-Montoya *et al.* 2015). *Phellinotus piptadeniae* presents slightly smaller basidiospores (ave.= 5.1 \times 3.9 μm versus 5.8 \times 4.7 μm) than those of *P. neoaridus*. Additionally, it is repeatedly found on living *Piptadenia* spp. (Drechsler-Santos *et al.* 2010), not yet recorded on *Caesalpinia* spp.

Material examined:—BRAZIL. Alagoas: São José da Tapera, Fazenda do Sr. Rudá, on living *Mimosa* sp., 9°32'45" S, 37°33'12" W–231m alt., 17 June 2008, Drechsler-Santos DS16AL (URM 80414). Bahia: Senhor do Bonfim, Serra do Santana, Fazenda Passaginha, Vasconcellos-Neto J.R.T. 195 (HUEFS 133884, O). Ceará: Reriutaba, Boqueirão, on living *Piptadenia stipulacea* (Benth.) Ducke (1930:126), 4°01'30" S, 40°38'21" W–197m alt., 14 June 2007, Drechsler-Santos DS23CE (URM 80466, O). Paraíba: Sumé, Fazenda Almas, on living *Mimosa ophthalmocentra* Mart. ex Benth. (1875:415), 7°28'21" S, 36°53'28" W–686m alt., 11 August 2008, Drechsler-Santos & Rajchenberg DS52PB (URM 80498). Pernambuco: Cabrobó, Fazenda Mosquito, on living *Mimosa* sp., 21 September 2009, Robledo 1982 (CORD); Caruaru, Estação Experimental do IPA, on living *Mimosa* sp., 8°13'50" S, 35°55'14" W–569m alt., 6 August 2006, Drechsler-Santos DS163PE (URM 80766, O); *ibid*, on living *Senegalia* sp., 8°13'51" S, 35°55'13" W–558m alt., 10 December 2008, Drechsler-Santos & al. DS128PE (URM 80361); *ibid*, on living *Mimosa* sp., 8°13'53" S, 35°55'12" W–562m alt., 10 December 2008, Drechsler-Santos & al. DS109PE (URM 80322); *ibid*, on living *Senegalia* sp. (CB01), 10 December 2008, Drechsler-Santos & al. DS110PE (URM 80345); Parque Nacional do Catimbau, Barro Branco, on living *Piptadenia moniliformis* Benth. (1841:339–340), 8°30'0" S, 37°18'57" W–818m alt., 9 February 2007, Drechsler-Santos & al. DS158 (URM 80884); *ibid*, Breu, on living *P. stipulacea*, 8°30'29" S, 37°16'58" W–964m alt., 22 June 2007, Drechsler-Santos DS240 (URM 80854, O); *ibid*, Casa da Farinha, on living *P. stipulacea*, 8°33'38" S, 37°13'89" W–839m alt., 31 October 2007, Drechsler-Santos & al. DS280 (URM 80602); *ibid*, Cerca de Pedra, on living *P. moniliformis*, 8°29'04" S, 37°19'24" W–723m alt., 9 February 2007, Drechsler-Santos & al. DS152 (URM 80694); *ibid*, Dor de Dente, on living *P. stipulacea*, 8°30'33" S, 37°16'59" W–958m alt., 23 July 2007, Drechsler-Santos & al. DS253 (URM 80737); *ibid*, Morro do Cachorro, on living *Pithecolobium polycephallum* Benth. (1844:219), 8°34'28" S, 37°14'47" W–751m alt., 5 August 2006, Drechsler-Santos DS64 (URM 80667, O); *ibid*, Muquém, on living *P. moniliformis*, 8°29'42" S, 37°19'03" W–795m alt., 29 September 2006, Drechsler-Santos DS85 (URM 80713); *ibid*, on living *P. stipulacea*, 8°30'10" S, 37°17'76" W–921m alt., 25 January 2008, Drechsler-Santos & al. DS300 (URM 80595); *ibid*, Pedra Solteira, on living *P. moniliformis*, 8°29'42" S, 37°19'03" W–795m alt., 27 May 2006, Drechsler-Santos DS003 (URM 80825); *ibid*, on living *P. stipulacea*, 8°32'52" S, 37°14'38" W–922m alt., 15 April 2007, Drechsler-Santos & al. DS207 (URM 80697); *ibid*, Trilha da Batinga, on living *P. stipulacea*,

8°30'47" S, 37°16'57" W–957m alt., 28 September 2006, *Drechsler-Santos & al. DS76* (URM 80730); *ibid*, Trilha das Torres, on living *P. stipulacea*, 8°34'20" S, 37°14'44" W–764m alt., 8 July 2006, *Drechsler-Santos DS101* (URM 80662, O); *ibid*, Trilha do Pereira, on dead *Eugenia rostrifolia* D. Legrand (1957:2), 8°30'37" S, 37°14'39" W–943m alt., 10 July 2006, *Drechsler-Santos & al. DS133* (URM 80890); Petrolina, Embrapa Semi-árido, on living *Mimosa arenosa* (Willd.) Poir. (1810:66), 9°04'22" S, 40°01'91" W–386m alt., 17 April 2008, *Drechsler-Santos DS6PETRO* (URM 80436, HTSA, O); Serra Talhada, Estação Experimental do IPA, on living *P. stipulacea*, 7°53'27" S, 38°18'22" W–503m alt., 11 March 2008, *Drechsler-Santos DS72PE* (URM 80631); *ibid*, on living *Mimosa sp.*, 11 March 2008, *Drechsler-Santos & al. DS74PE* (URM 80317); *ibid*, on living *Piptadenia sp.*, 7°54'01" S, 38°18'05" W–513m alt., 5 March 2009, *Drechsler-Santos DS139PE* (URM 80768, O); *ibid*, on living *Mimosa sp.*, 7°53'29" S, 38°18'17" W–490m alt., 9 July 2008, *Drechsler-Santos & al. DS97PE* (URM 80360, O). Rio Grande do Norte: Estação Ecológica do Seridó-ESEC, 19 February 2007, *Silva & al. Sn* (URM 80883). Sergipe: Niterói, 9°45'20" S, 37°27'55" W–65m alt., 16 June 2008, *Drechsler-Santos & al. DS40SE* (URM 80567).

Discussion

Phellinotus and its phylogenetic affinities

Phellinotus is considered a pathogenic polypore, common on living members of the family Fabaceae, and so far endemic to the Neotropics. Within the ‘*phellinotus* clade’, *Phellinotus* is closely related, both phylogenetically and morphologically, to *Arambarria*, *Inocutis*, *Fomitiporella* and some other taxonomically unresolved lineages (Fig. 1, Table 1). *Phellinotus* develops skeletal hyphae in the trama of the tube layer whereas *Arambarria* and *Inocutis* lack skeletal hyphae entirely. *Fomitiporella* differs from *Phellinotus* by its saprotrophic habit, resupinate basidiomata and skeletal hyphae that occur throughout the basidioma (Murrill 1907, Teixeira 1994, Zhou 2014b). *Inocutis dryophila*, the closest lineage in our phylogeny, is distributed in the Holarctic region, has ellipsoid to ovoid, thick-walled and brownish basidiospores, as well as a monomitic hyphal system throughout the basidioma; it also grows on living oaks (Ryvarden 2005). *Fulvifomes chinensis* and *F. inermis* also present broadly ellipsoid, fairly thick-walled, yellowish and cyanophilous basidiospores (Dai 2010); on the other hand, they have effused-reflexed and resupinate basidiomata, respectively, besides a dimittic hyphal system both in the context and trama of the tubes. Their phylogenetic position is still unresolved (Zhou 2014a). *Inonotus tenuissimus* was described from China as having ellipsoid, thick-walled and yellowish basidiospores and a monomitic to dimittic hyphal system with “skeletal-like” hyphae in the trama of tube layer (Yu *et al.* 2013), which could be interpreted as a similar hyphal system to *Phellinotus*. However, the resupinate and adnate annual basidiomata and absence of cyanophilous reaction in the basidiospores of *I. tenuissimus* are quite different from the new genus. Isolates CIEFAPcc107 and cc88 from Patagonia (named as *Hymenochaetaceae sp.*) are known only from mycelium isolates of wood and their basidiomata have not been recorded; they form a distinct phylogenetic species (Rajchenberg *et al.* 2015).

Phellinotus is also phylogenetically close to *Fulvifomes s.s.* and *Phylloporia*. This group of related genera, previously noted by Wagner & Fischer (2002), Larsson *et al.* (2006), Zhou (2014a), Rajchenberg *et al.* (2015) and Zhou *et al.* (2015), named here as the ‘*phellinotus* clade’, deserves special taxonomic recognition. This is a group of poroid *Hymenochaetaceae* taxa with thick-walled and colored basidiospores and without setae or setal hyphae. Additionally, the adaxially flattened basidiospores seems to be an important taxonomic feature and probably phylogenetically significant for the ‘*phellinotus* clade’. Actually, despite *Phellinotus*, in our morphological analysis of types of *Arambarria* (*A. destruens*), *Fomitiporella* (*F. umbrinella*), *Fulvifomes* (*Pyropolyporus robiniae*), and *Phylloporia* (*P. parasitica*) we were able to observe adaxially flattened basidiospores. Type specimens of *Fulvifomes chinensis*, *F. inermis* and *Inonotus tenuissimus* should be revised to confirm this character. This is a feature usually not checked and not found in the literature, except by Kotlaba & Pouzar (1978, 1979), who mentioned it in the description of *Phellinus robiniae* (Murrill) A. Ames (1913:246), *P. rimosus s.s.*, *P. coffeatorporus* Kotl. & Pouzar (1979: 259), and *P. resinaceus* Kotl. & Pouzar (1979: 261).

Fulvifomes s.s. (*F. rimosus* group excluding *F. chinensis* and *F. inermis*) is macro- and micro- morphologically similar to *Phellinotus*, but distinguishable mainly by the shape of its basidiospores and hyphal system (Table 1). The shape of the basidiospore is an important feature, as recognized by Murrill (1914), who segregated *Fulvifomes* from *Pyropolyporus* Murrill (1903:109) based on *Pyropolyporus robiniae* [= *Fulvifomes robiniae* (Murrill) Murrill (1914:49)] as genus type. The lectotype of *Phellinus robiniae* presents subglobose, 5.5–6 × 4.5–5(–5.5) µm basidiospores. *Aurificaria* is characterized by basidiospores that turn dark olivaceous green in KOH and by a monomitic hyphal

system (Ryvarden 2004). Phylogenetic studies by Larsson *et al.* (2006) and Zhou (2014c), based on ITS and nLSU, show that *Aurificaria* is a basal sister clade of *Fulvifomes s.s.* Zhou (2014c) proposed its synonymy with *Fulvifomes*, which would expand the concept of *Fulvifomes* by including monomitic and dimitic species with annual or perennial basidiomata and basidiospores that can turn brown or green in KOH.

Phylloporia species are mostly parasitic on lianas and roots of shrubs and trees, which are difficult to identify in the Neotropics (Ryvarden 2004). As a result, the extent of host specialization of *Phylloporia* species is unknown. *Phylloporia* and *Phellinotus* share the black line in the context; however, the former is distinguished by its smaller, yellow basidiospores that remain slightly yellowish in KOH (Ryvarden 2004).

The occurrence of different types of hyphal systems in the same basidioma is well documented and has been used to distinguish taxa (Niemelä *et al.* 2001, Tian *et al.* 2013). The *Inonotus linteus* (Berk. & M.A. Curtis) Teixeira (1992:126) species-complex, like *Phellinotus* species, develops perennial basidiomata with skeletal hyphae restricted to the trama of the tube layer (Tian *et al.* 2013, Vlasák *et al.* 2013). However, it differs from *Phellinotus* by the presence of hymenial setae and is not phylogenetically related. Phylogenetic studies confirmed its relationship with *Inonotus* (Wagner & Fischer 2002), and the closely related recently described genera *Sanghuangporus* Sheng H. Wu, L.W. Zhou (2015:6) & Y.C. Dai and *Tropicoporus* L.W. Zhou, Y.C. Dai & Sheng H. Wu (2015:7) (Zhou *et al.* 2015), are also positioned outside of the ‘*phellinotus* clade’. Indeed, the sequences available in GenBank, identified as *Inonotus linteus* (*Tropicoporus*) should be taxonomically re-evaluated, as some vouchers are actually placed in the *Sanghuangporus* clade (e.g., vouchers F915611 and MUCL74139) (Fig. 1).

The current phylogenetic scenario shows that the diversity of the group is higher than expected and the incorporation of specimens and taxa from other unexplored regions of the world into phylogenetic studies is necessary to attain a better understanding of the diversity and natural classification of Hymenochaetaceae.

Phellinotus and its species

Phellinus piptadeniae was proposed by Teixeira (1950) and described as host specific on living *Piptadenia communis* Benth. [= *Piptadenia gonoacantha* (Mart.) J.F. Macbr. (1919:17)]. He described it as having a large basidioma with a smooth pilear surface that becomes rimose at maturity, a golden brown and lustrous context with a distinct black line, and stratified tubes forming 4–5 pores/mm on the hymenophore. Regarding particular microscopic characters, the hyphal construction of the basidioma deserves special attention. Teixeira (1950) described two types of hyphae in the context, branched or not, with walls not much thickened and simple-septa present in the unbranched hyphae. He did not mention the specific type of hyphal system present. Later, he transferred this species to *Fomitiporella* as *F. piptadeniae* (Teixeira) Teixeira (1992:126) (Teixeira 1992), again without describing the hyphal system. Later, he described *Fomitiporella* as dimitic and closely related to *Phellinus* and *Phylloporia* (Teixeira 1994).

According to Ryvarden (2004), *Phellinus piptadeniae* is closely related to *Phellinus rimosus*; moreover, he suggested that molecular work would be necessary to determine if *P. piptadeniae* was an immature stage of *P. rimosus* or not. *Phellinus piptadeniae* is morphologically and ecologically a well-delimited species (Teixeira 1950, Drechsler-Santos *et al.* 2010), whereas *Phellinus rimosus* is considered to be a taxonomic complex of three or more cryptic species, namely, *P. badius* (Berk. ex Cooke) G. Cunn. (1965:273), *P. rimosus s.s.* and *P. robiniae* (Kotlaba & Pouzar 1978). Interestingly, most of these species seem to be host-specific and geographically restricted (Kotlaba & Pouzar 1978, 1979). Species in the *P. rimosus* complex are characterized by having woody, pileate basidiomata with a cracked to strongly rimose pileus, a lack of setae, and ellipsoid, thick-walled, chestnut to rusty brown basidiospores (Fiasson & Niemelä 1984). *Fulvifomes* has a dimitic hyphal system and globose to subglobose basidiospores (Table 1).

Key to *Phellinus s.l.* and *Inonotus s.l.* and related poroid/hydroid genera of Hymenochaetaceae

1.	Basidiospores hyaline and slightly to strongly dextrinoid	2
1.	Basidiospores hyaline to chestnut brown and not dextrinoid	4
2.	Basidiospores ellipsoid, hyphal system monomitic, setae (hymenial or tramal) present	<i>Mensularia</i>
2.	Basidiospores globose, hyphal system monomitic or dimitic, if present, setae only hymenial	3
3.	Basidiomata perennial, resupinate to pileate, setae absent, occasionally present	<i>Fomitiporia</i>
3.	Basidiomata annual, pileate, hymenial setae present	<i>Pseudoinonotus</i>
4.	Setae (any type) present	5
4.	Setae (any type) absent	17
5.	Asterosetae present	<i>Asterodon</i> Pat.
5.	Asterosetae absent, hymenial setae and/or setal hyphae present	6
6.	Hyphal system monomitic throughout	7
6.	Hyphal system dimitic, at least in the trama of tube layer, or trimitic	11

7.	Setal hyphae present	8
7.	Setal hyphae absent	9
8.	Basidiospores hyaline, thin-walled, hymenial setae absent	<i>Phellinidium</i>
8.	Basidiospores yellow to brown, thick-walled, hymenial setae absent or present	<i>Inonotus s.s.</i>
9.	Basidiomata sessile pileate to substipitate, basidiospores thin-walled.....	<i>Inonotus s.l.</i>
9.	Basidiomata sessile resupinate/pileate, basidiospores thick-walled.....	10
10.	Basidiomata stipitate, sub-stipitate or centrally sessile, basidiospores ellipsoid to globose, tramal to hymenial setae present	<i>Onnia</i> P. Karst
10.	Basidiomata sessile, basidiospores cylindrical, hymenial setae present	<i>Cylindrospor</i> L.W. Zhou & Y.C. Dai
11.	Basidiospores obclavate to cylindric, hyphal system dimitic-trimitic.....	<i>Phellopilus</i>
11.	Basidiospores ellipsoid, broadly ellipsoid to globose-subglobose, hyphal system dimitic	12
12.	Basidiospores thin-walled, basidiospores ellipsoid/allantoid/cylindrical, generative hyphae with crystals	<i>Fuscoporia</i>
12.	Basidiospores slightly thick- to thick- walled, basidiospores ellipsoid/to subglobose-globose, generative hyphae without crystals	13
13.	Hyphal system mono-dimitic, contex monomitic, trama of tube layer dimitic.....	14
13.	Hyphal system dimitic throughout	15
14.	Basidiomata annual to perennial, resupinate to pileate, basidiospores when ellipsoid mostly < 3.5 µm wide, exclusively in tropical zone.....	<i>Tropicoporus</i>
14.	Basidiomata perennial, resupinate, effused-reflexed to pileate, basidiospores when ellipsoid mostly > 3.5 µm wide, in boreal, temperate, subtropical to tropical zones	<i>Sanguangporus</i>
15.	Tramal setae penetrating into hymenium	<i>Phellinopsis</i>
15.	Tramal setae absent	16
16.	On coniferous wood	<i>Porodaedalea</i>
16.	On hardwood	<i>Phellinus s.s.</i>
17.	Basidiospores thin-walled	18
17.	Basidiospores thick-walled	20
18.	Basidiospores cylindrical to obclavate	<i>Nothophellinus</i>
18.	Basidiospores subglobose to ellipsoid	19
19.	Basidiomata resupinate, basidiospores ellipsoid, on coniferous wood	<i>Inonotopsis</i>
19.	Basidiomata pileate/substipitate, basidiospores subglobose, on deciduous wood	<i>Pyrrhoderma</i>
20.	Hyphal system monomitic.....	21
20.	Hyphal system dimitic, at least in the trama of tube layer	25
21.	Basidiospores ellipsoid smaller than 5 µm, hyaline in KOH	<i>Phylloporia</i>
21.	Basidiospores usually larger than 5 µm	22
22.	Basidiospores yellowish, becoming dark olivaceous green in KOH	<i>Aurificaria</i>
22.	Basidiospores do not become dark olivaceous green in KOH	23
23.	Basidiospores yellowish to yellowish brown, becoming chestnut brown in KOH, thick-walled and adaxially flattened	24
23.	Basidiospores without this combination of characters	<i>Inonotus s.l.</i>
24.	Granular core present at the base of the context	<i>Inocutis</i>
24.	Granular core absent at the base of the context	<i>Arambarria</i>
25.	Basidiospores usually shorter than 5 µm, hyaline in KOH	<i>Phylloporia</i>
25.	Basidiospores usually larger than 5 µm, becoming chestnut brown in KOH	26
26.	Basidiospores globose to subglobose	<i>Fulvifomes</i>
26.	Basidiospores ellipsoid to broadly ellipsoid	27
27.	Skeletal hyphae restricted to the trama of tube layer	<i>Phellinotus</i>
27.	Skeletal hyphae found throughout the basidiomata	28
28.	Basidiomata resupinate.....	<i>Fomitiporella</i>
28.	Basidiomata pileate	<i>Phellinus s.l.</i>

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Taxon; Geographic origin; Collection reference; Substrate;
GenBank accession.

nLSU sequences

- Arambarria destruens* Rajchenb. & Pildain; Argentina/Chubut; CIEFAPcc 347; *Diostea juncea*; KP347523.
- Cylindrosporopus flavidus* L.W. Zhou; China, Da 13213; on fallen angiosperm wood; KP875561.
- Fomitiporella sp.*; Ethiopia; Oe5; JQ910908. *Fomitiporella sp.*; Ethiopia; Oe6; JQ910909.
- Fomitiporia hartigii* (Allesch. & Schnabl) Fiasson & Niemel; Europe/Estonia; MUCL 53551; JX093833. *F. mediterránea* M. Fischer; Europe/Italy; MUCL 38514; living branch; AY618201. *F. punctata* (Fr.) Murrill; Europe/Estonia; MUCL 53548; JX093834. *F. robusta* (P. Karsten) Fiasson & Niemel; Europe/Czech Republic; MUCL 51327; GU461993.
- Fulvifomes chinensis* (Pilát) Y.C. Dai; China/ Zhashui; LWZ 20130916-3; on dead standing angiosperm; KJ787809. *F. chinensis*; China/ Weishan; LWZ 20130713-7; on fallen angiosperm trunk; KJ787808. *F. fastuosus* (Lév.) Bondartseva & S. Herrera; Philippines; CBS 213.36; *Gliricidia sepium*; AY059057. *F. indicus* (Masse) L.W. Zhou; Zimbabwe/Midlands; O 25034; KC879259. *F. indicus* (Masse) L.W. Zhou; China/Ningming; Yuan 5932; on living tree of *Bombax ceiba*; JX866777. *F. inermis* (Ellis & Everh.) Y.C. Dai; China/Qimen; LWZ 20130810-3; on fallen angiosperm branch; KJ787812. *F. inermis*; China/Qimen; LWZ 20130809-8; on living angiosperm tree; KJ787811. *F. merrillii* (Murrill) Baltazar & Gibertoni; Taiwan; JX484002. *F. nilgheriensis* (Mont.) Bondartseva & S. Herrera; USA; CBS 209.36; on dead deciduous wood; AY059023. *F. rimosus* (Berk.) Fiasson & Niemel; Taiwan; JX484003. *F. robiniae* (Murrill) Murrill; USA; CBS 211.36; *Robinia pseudo-acacia*; AY059038.
- Fuscoporia atlantica* Motato-Vásquez, Pires & Gugliotta; Brazil; MV230; KP058517. *F. gilva* (Schwein.) T. Wagner & M. Fisch.; Brazil; RP 17; KP859305. *F. senex* (Nees & Mont.) Ghob.-Nejh.; KUC20110922-13; JX463652. *F. torulosa* (Pers.) T. Wagner & M. Fisch.; Csezh Republic; 759; AM269865.
- Hymenochaetaceae sp.*; Argentina/Chubut; CIEFAPcc88; *Austrocedrus chilensis*; KP347524. *Hymenochaetaceae*

ITS sequences

- Arambarria destruens* Rajchenb. & Pildain; Argentina/Chubut; CIEFAPcc 347; *Diostea juncea*; KP347538.
- Cylindrosporopus flavidus* L.W. Zhou; China, Da 13213; on fallen angiosperm wood; KP875564.
- Fomitiporella sp.*; Ethiopia; Oe5; JF895466. *Fomitiporella sp.*; Ethiopia; Oe6; JF895467.
- Fomitiporia hartigii* (Allesch. & Schnabl) Fiasson & Niemel; Europe/Estonia; MUCL 53551; JX093789. *F. mediterránea* M. Fischer; Europe/Italy; MUCL 38514; living branch; GU461953. *F. punctata* (Fr.) Murrill; Europe/Estonia; MUCL 53548; JX093790. *F. robusta* (P. Karsten) Fiasson & Niemel; Europe/Czech Republic; MUCL 51327; GU461949.
- Fulvifomes chinensis* (Pilát) Y.C. Dai; China/ Zhashui; LWZ 20130916-3; on dead standing angiosperm; KJ787818. *F. chinensis*; China/ Weishan; LWZ 20130713-7; on fallen angiosperm trunk; KJ787817. *F. fastuosus* (Lév.) Bondartseva & S. Herrera; Philippines; CBS 213.36; *Gliricidia sepium*; AY558615. *F. inermis* (Ellis & Everh.) Y.C. Dai; China/Qimen; LWZ 20130810-3; on fallen angiosperm branch; KJ787821. *F. inermis*; China/ Qimen; LWZ 20130810-8; on living angiosperm tree; KJ787820. *F. indicus* (Masse) L.W. Zhou; Zimbabwe/ Midlands; O 25034; KC879262. *F. indicus* (Masse) L.W. Zhou; China/Ningming; Yuan 5932; on living tree of *Bombax ceiba*; KC879261. *F. merrillii* (Murrill) Baltazar & Gibertoni; Taiwan; JX484013. *F. nilgheriensis* (Mont.) Bondartseva & S. Herrera; USA; CBS 209.36; on dead deciduous wood; AY558633. *F. rimosus* (Berk.) Fiasson & Niemel; Taiwan; JX484016. *F. robiniae* (Murrill) Murrill; USA; CBS 211.36; *Robinia pseudo-acacia*; AY558646.
- Fuscoporia atlantica* Motato-Vásquez, Pires & Gugliotta; Brazil; MV230; KP058515. *F. gilva* (Schwein.) T. Wagner & M. Fisch.; Brazil; RP 17; KP859295. *F. senex* (Nees & Mont.) Ghob.-Nejh.; KUC20110922-13; JX463658. *F. torulosa* (Pers.) T. Wagner & M. Fisch.; Csezh Republic; 759; AM269803.
- Hymenochaetaceae sp.*; Argentina/Chubut; CIEFAPcc 88; *Austrocedrus chilensis*; KP347536. *Hymenochaetaceae*