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***Fomitiporia* (Basidiomycota) revisited. Species concept,
phylogenetic structure and biogeographical patterns.**

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PUBLICATIONS

This thesis is based on the work presented in the following papers and manuscripts.

- I - Manuscript.....42**
Amalfi Mario, Yombiyeni Prudence, Decock Cony, 2010. *Fomitiporia* in sub-Saharan Africa: morphology and multigene phylogenetic analysis support three new species from the Guineo-Congolian rainforest. *Mycologia*, 102(6):1303–1317. DOI: 10.3852/09-083
- II - Manuscript.....85**
Amalfi Mario, [Tania Raymundo](#), Ricardo Valenzuela, Gabriel Castillo, Decock Cony. 2012. The *Fomitiporia robusta* complex in North America I. *Fomitiporia cupressicola* sp. nov., parasite on *Cupressus arizonica*, and additional unnamed clades in the southern USA and northern Mexico, evidenced by multilocus phylogenetic analyses. *Mycologia*, 104(4): 880–893. DOI: 10.3852/11-196.
- III - Manuscript.....122**
Mario Amalfi ,Cony Antonio Decock. 2013. *Fomitiporia castilloi* sp. nov., and multiples clades around *F. apiahyna* in Meso- and South America evidenced by multiloci phylogenetic inferences. *Mycologia*, 105(4):873-87. doi: 10.3852/11-423.
- IV - Manuscript.....166**
Mario Amalfi, Gerardo Robledo, Cony Decock. 2014. *Fomitiporia baccharidis* comb. nov., a little known species from high elevation Andean forests and its affinities within the neotropical *Fomitiporia* lineages. *Mycological Progress*; 13(4):1075-1087. DOI:10.1007/s11557-014-0995-x

V - Manuscript.....201

Marisa de Campos Santana, Mario Amalfi, Gerardo Robledo, Rosa Mara Borges da Silveira, Cony Decock. 2014. *Fomitiporia neotropica*, a new species from South America evidenced by multilocus phylogenetic analyses. *Mycological Progress*, 13(3):601-615. DOI:10.1007/s11557-013-0943-1

VI - Manuscript.....247

Mario Amalfi & Cony Decock. 2014. *Fomitiporia expansa*, an Undescribed Species from French Guiana. *Cryptogamie Mycologie*, 35(1):73-85. 2014. doi: <http://dx.doi.org/10.7872/crym.v35.iss1.2014.73>

VII - Manuscript.....370

[Tania Raymundo](#), [Cony Decock](#), [Ricardo Valenzuela](#), Mario Amalfi, [Joaquín Cifuentes](#), [Leticia Pacheco-Mota](#). 2012. Nuevos registros del género *Fomitiporia* (Hymenochaetales, Basidiomycota) en México New records of the genus *Fomitiporia* (Hymenochaetales, Basidiomycota) in Mexico. *Rev. Mex. Biodiv.* 05/2012; 83(2):313-328.

ABSTRACT

***Fomitiporia* (Basidiomycota) revisited. Species concept, phylogenetic structure and biogeographical patterns.**

Accurate species delimitations are important to understand factors driving diversification, and have implications for ecological and conservation studies. However, to give a definition of what is a “species”, which would be valid and applicable to all organisms, is challenging. Today the biologists tend to consider the species as a diversified " phenomenon " which can be characterized, morphologically, biologically, genetically, etc. rather than defined in its wholeness. Fungi raise particular problems in the determination of their "status" of species. Their range of intra-specific variations (both genetical and morphological) was poorly studied, what makes very difficult the determination of the significant characters for the establishment of diagnostic criteria. In this study we first tried to integrate the different species concept's approaches (morphological, phylogenetical, biological, ecological etc.) in order to improve the understanding of “the species” and create a “holistic” species concept. Moreover, the geographical distributions of most fungal species are also still poorly known; consequently, their origins and historical distributions remain largely understudied. High levels of cryptic diversity, scarce fossil records and poorly sampled regions can explain some of these shortcomings. Both issues were developed on an iconic group of wood decaying fungi, the genus *Fomitiporia* Murrill (Hymenochataceae), which includes parasitic and saprophytic species. *Fomitiporia*, constitutes one of the main genera of poroid Hymenochaetaceae, present in all the continents. It was extensively sampled worldwide in order to infer evolutionary patterns on a global scale. The particular interest in *Fomitiporia* also results from the importance of several species as primary etiological agents causing diseases of economically important perennial crops or trees. Taxonomy, phylogeny and biogeography of *Fomitiporia* were in “chaotic” state of flux. The application of an “holistic” species concept to this genus, allowed us to evidence and at least partially resolve its complex phylogenetic / biogeographic structure. Thanks to this integrative approach, seven new species and two new

combinations were described, two species proposed as new, three new combination proposed and ultimately fifteen unnamed taxa were evidenced and still need to be described and named in the Linnean system. Several morphological features, to date considered discriminating at species or genus level, such as the presence of hymenial setae or the dextrinoid basidiospores were demonstrated to be variable characters. Therefore the genus *Fomitiporia* was redefined on the basis of these findings. Furthermore, this study represent one of the firsts attempts to investigate fungal distributions in an evolutionary context. We used the “state of the art” phylogenetic techniques in order to investigate evolutionary relationships and historical biogeography. Molecular clock dating and ancestral area reconstruction analyses were carried out, as well as the most comprehensive phylogenetic analysis of the genus, based on the most complete taxon sampling to date. The results evidenced, for the first time, several phylogenetic lineages with a strong biogeographical structure, resulting from a complex evolutionary history. Our results suggest a probable Neotropical origin (Palaeocene–Eocene) followed by an early dispersal to the Andean cordillera (Eocene). From the ancestral Neotropical species, the Antarctic land bridge may have provided a corridor for migration between South America and Australia (early Miocene). Subsequently, our data strongly support the hypothesis of a boreotropical dispersal model, from South America to Africa via North America and Eurasia (passing through the North Atlantic land Bridge). From here, several dispersion events, back and forth to Asia, and ultimately an extreme long-range trans-Atlantic dispersal to the Neotropics, accompanied by a recent radiation were hypothesized.

INTRODUCTION

The modern biologists consider the hierarchical nature of the living systems as a consequence of an order based on the common relationships and the evolutionary affinities between the basic units of the "living": the species. However, to give a definition of the species, which would be valid and applicable to all organisms, is not an easy task. After all, today the biologists tend to consider the species as a diversified "phenomenon" which can be characterized, morphologically, biologically, genetically, etc. rather than defined in its wholeness. The speciation is generally seen as a dynamic process by which a genetically homogeneous and inter-crossable group of individuals divides in two or several groups of genetically different individuals isolated from the others from the reproductive point of view.

The reproductive isolation is indeed necessary in order to accumulate the genetic differences (by phenomena of mutation, selection, genetic drift etc.), which can lead to a unique and peculiar phenotypic expression.

Fungi raise particular problems in the determination of their "status" of species.

Indeed, we know very few about what constitutes an "individual"; for example, in the Malheur National Forest in Oregon, there is an enormous underground web: the mycelium of the mushroom *Armillaria solidipes* (previously known as *Armillaria ostoyae*), which extends over 9.6 km², weighs hundreds of tons, and presents uncountable fruit bodies (and was somewhere between 1.900 and 8.650 years old). The subterranean strands of this mycelium are all genetically homogeneous, it was thus defined as the biggest organism living on Earth. In these circumstances, the concept of what must be considered as organism or individual becomes blurred, what is rarely observed in the other reigns.

Furthermore, the range of intra-specific variations (both genetical and morphological) was poorly studied, what makes very difficult the determination of the significant characters for the establishment of a “diagnosis”.

Moreover mushrooms present complex life cycles of which the fruit body, the sexual stage commonly observed of the mushroom, constitute only a short-lived moment, and each of these stages (of the life cycle) can be subjected to different selective pressures, difficult to evaluate.

Nowadays, with the increasing interest in mushrooms, notably because of the products of their secondary metabolism, of fundamental importance in the field of biotechnologies (antibiotics, detoxications etc.), it became essential to have a precise and clear classification.

How could we study a product of the fungal metabolism if we do not even manage to identify exactly the species that produces it?

In this study, we tried to integrate the different species concept's approaches (morphological, phylogenetical, biological, ecological) in order to improve the understanding of “what is a species” and to define an “Holistic” species concept or a “consolidated species concept” (Quaedvlieg et al. 2014). In this way we could e.g. test the validity of the different diagnostic characters used until now to delimitate the “morphological species” and at the same time evaluate the genetic variation among individuals of the same “phylogenetic” species. Developing clear species concept will allow assessing accurately the level of endemism at species level and moreover will allow evaluating the biogeographical patterns and testing hypothesis about the origins and speciation processes within the genus that could explain the present distribution.

STATE OF THE ART

Fomitiporia Murrill (1907)

Fomitiporia (Hymenochaetaceae, Basidiomycota) has been the object of particular interest in the last decade; numerous species have been described worldwide (Amalfi and Decock 2013, 2014, Amalfi et al. 2010, 2012, 2014, de Campos Santana et al. 2014, Cloete et al. 2013, Coelho et al. 2009, Decock et al. 2005, 2007, Dai and Cui 2005, Dai et al. 2008, 2002, Fischer and Binder 2004, Fischer et al. 2005, Raymundo et al. 2012, Vlasák and Kout 2011, Zhou and Xue 2012). Additionally, a handful of taxa or phylogenetic species (PS) were shown using the principle of multiple gene genealogy concordance (Taylor et al. 2000, 2006) and remain to be described still (Amalfi and Decock 2013, 2014, de Campos Santana et al. 2014). For instance, as far as South America is concerned, Amalfi and Decock (2013, 2014) showed the occurrence of (at least) nine species / phylogenetic species sharing pileate basidiomata. They include *F. apiahyna*, *F. castilloi*, *F. baccharidis*, and 6 still unnamed species clades / phylogenetic species (Amalfi and Decock 2013, 2014).

The particular interest in *Fomitiporia* also results from the importance of several species as primary etiological agents or members of complexes of etiological agents, causing diseases of economically important perennial crops or trees. The best-documented cases concern *Fomitiporia* species as etiological agents of white rot symptoms associated with the complex, multifactorial Esca disease of *Vitis vinicola* worldwide. These species include *F. mediterranea* in the Mediterranean area of southern Europe (Fischer 2002), *F. australiensis* in Australia (Fischer et al. 2005), *F. capensis* in South Africa (Cloete et al. 2014), and *F. polymorpha* in North

America (Fischer and Binder 2004). Two species of *Fomitiporia* also are known causing white rot symptoms on branches or trunks of *Citrus* in orchards; they are *F. mediterranea* in southern Europe (Elena et al. 2006, González et al. 2006) and *F. maxonii* in the Caribbean (Cabrera et al. 2014). Other cultivated trees may also be affected by *Fomitiporia* species, including hazelnut (*Corylus avellana*) attacked by *F. mediterranea* in southern Europe (Pilotti et al. 2010). Sanbu-Sugi, an economically important cultivar of the Japanese cedar (*Cryptomeria japonica*), also is threatened in Japan by trunk rot caused by *F. torreyae* (Ota et al. 2014). Trunk rot and dieback of other coniferous and broadleaf trees in Japan (*Chamaecyparis pisifera*, *Sciadopitys verticillata*, or *Pyrus pyrifolia* var. *culta*) were also demonstrated to be caused by *F. torreyae* (Ota et al. 2014).

Fomitiporia was erected by Murrill (1907) and originally typified by *F. langloisii* (Decock et al. 2007, Murrill 1907). Nonetheless, for years, the genus was barely considered: it was mostly relegated as one of the numerous taxonomic synonyms of *Phellinus* (e.g. Bernicchia 1990, 2005, Bondartsev 1953, Corner 1991, Domański et al. 1967, Gilbertson 1979, Gilbertson and Ryvarden 1987, Larsen and Cobb-Poulsen 1990, Ryvarden 1978, 1991, Ryvarden and Gilbertson 1994, Ryvarden and Johansen 1980). *Fomitiporia langloisii* was also for years listed as one of the synonyms of *Phellinus punctatus*. *Phellinus punctatus* was associated with *P. robustus* and commonly recognized, informally, as the *P. punctatus* / *robustus* complex in which species concepts, as well as host range and species distribution were uncertain.

Fiasson (1983) was amongst the first to question the homogeneity of *Phellinus* as conceived by then (e.g. Bondartsev 1953, Domański et al. 1967, Gilbertson 1979, Ryvarden 1978, Ryvarden and Johansen 1980). Among others issues, he (Fiasson 1983) questioned the status of the *P. punctatus* / *P.*

robustus complex. On the basis of phenotypical characters, both morphological and non-morphological, including the chemical (triterpenoid) composition of the basidiomata, Fiasson (1983) delimited four alliances of species within *Phellinus*. These alliances were recognized at subgeneric level as four subgenera: the *Phellinus robustus* group (subgenus *Cyanovosporus*), the “less *Phellinus* of the *Phellinus*” as he stated, the *P. Ferrugineofuscus* and *Ochroporus* alliance (subgenus *Phellinidium*) defined by their pigment profile (hispidin and 3,14'-bishispidinyl without hypholomin B), the *P. ferreus* group (subgenus *Fuscoporia*) characterized by resupinate fruitbody, dikaryotic hyphae and allantoid basidiospores, and the *Phellinus* s.s., negatively defined as the residual groups and thus a paraphyletic pool of genus waiting to be assigned to an alliance. The *P. punctatus* / *robustus* complex surfaced then under *Phellinus* subgen. *Cyanovosporus* Fiasson.

Cyanovosporus comprised 6 species: *P. erectus*, *P. hartigii*, *P. hippophaeicola*, *P. punctatus*, *P. pseudopunctatus* and *P. robustus*, the latter being designated as type. Fiasson (1983) highlighted the main morphological features that would circumscribe this subgenus, of which, importantly, the cyanophilous and dextrinoid basidiospores. *Cyanovosporus* was poorly considered if at all; nevertheless, Rajchenberg (1988) noted that *Phellinus livescens*, a little known species from southern Andean forests, growing on *Nothofagus* (Fagaceae), could belong to this alliance, which he noted as *Phellinus* "cyanosporous" group of Fiasson and David (1984).

Soon after, however, Fiasson and Niemelä (1984) reached to the conclusions that *Cyanovosporus* corresponded to *Fomitiporia* as defined by Murrill (1907); they also considered worth reinstating the later name at genus level (Fiasson and Niemelä 1984). They redefined *Fomitiporia* with *F. punctata* as type, leaving *F. langloisii* in the limb of synonymies, and proposed the recombination *F. erecta*, *F. hartigii*, *F. hippophaeicola*, *F.*

pseudopunctata, and *F. robusta*. Fiasson and Niemelä (1984) confirmed the cyanophilous and dextrinoid basidiospores as the critical feature to circumscribe *Fomitiporia*, to which they added a brass-colored [copper brown] context, a little differentiated hyphal system with skeletal hyphae, variably present cystidioles, and variably present but often very rare, hymenial setae. Fischer (1996) confirmed the taxonomic conclusions of Fiasson and Niemelä (1984). Later on, extra-hymenial setae were reported also in several species (Gilbertson and Ryvarden 1987, Pieri and Rivoire 2000).

Early in the 21st century, genomic data (by that time the nuclear Large subunit LSU rDNA sequence data, Wagner and Fischer 2002) supported the monophyletic origin of four species of *Fomitiporia sensu* Fiasson & Niemelä (*F. hartigii*, *F. hippophaeicola*, *F. punctata*, and *F. robusta*). However until 2004 only 15 species were ascribed to the genus, and molecular data were available for only nine of them (Fig.1).

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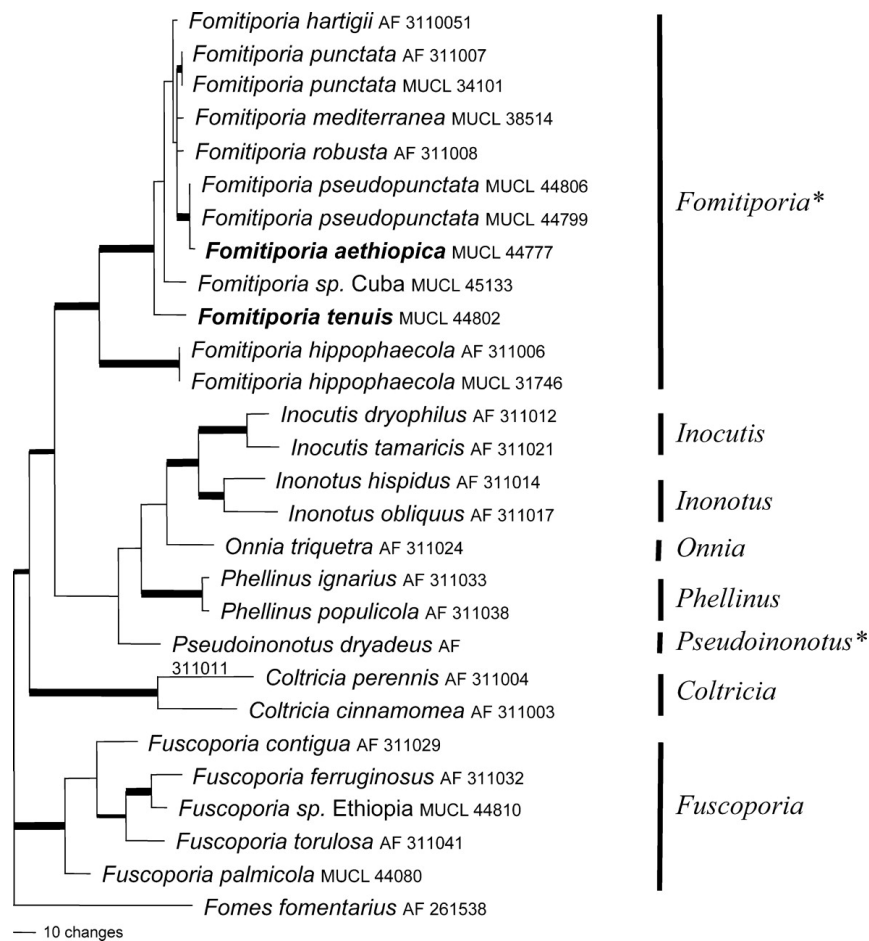


FIG 1. One of the three equally parsimonious trees obtained from a heuristic search. Branches in bold = bootstrapping >70% (Decock et al. 2005)

Furthermore efforts were fundamentally restricted to temperate geographic areas. Central Africa together with Southeast Asia and the Neotropical phytogeographic region remained still obscure in what regard the taxonomy of *Fomitiporia*, only the presumed cosmopolitans *F. punctata* and *F. robusta* were reported from these areas (Ryvarden and Johansen 1980, Ryvarden 2003).

Since Wagner and Fischer (2002), the monophily of the genus has been repeatedly confirmed based on single or multiple genomic loci and a continuously extending taxon sampling over a wide geographic range (Amalfi and Decock 2013, 2014, Amalfi et al. 2010, 2012, 2014, de Campos Santana et al. 2014, Dai et al. 2008, Decock et al. 2005, 2007, Zhou and Xue 2012). Thanks to these studies *Fomitiporia* is now widely accepted (e.g. Decock et al. 2005, 2007, Dai et al. 2008, Amalfi and Decock 2013, 2014, Zhou and Xue 2012) although Spirin et al. (2006) still considered it as a infrageneric entities of *Phellinus* viz. *Phellinus* sect. *Fomitiporia* (Murrill) Zmitr. et al. (2006).

The species concept within the *F. punctata* / *F. robusta* complex also remained uncertain. The common belief was that *P. punctatus* and *P. robustus* were cosmopolitan species (e.g. Cunningham 1965, Gilbertson and Ryvardeen 1987, Ryvardeen and Gilbertson 1994, Ryvardeen and Johansen 1980). As a collateral effect, both species had very plastic ecologies and wide distribution ranges. Nevertheless, Gilbertson and Ryvardeen (1987) stated that the “*Phellinus robustus* [*F. robusta*] complex is probably the most difficult taxonomic problem in the genus [*Phellinus*]”, with speciation resulting from “[physiological] adaptation to different substrata and vastly different environmental factors”. They realized that defining [morphological] species within the *P. punctatus* / *robustus* complex might reveal difficult. As one of the consequence, the status of the type species, *F. langloisii*, remained for a long time unquestioned. It is not before 2007, a century after its description (Murrill 1907), that Decock et al. (2005) showed that a *Fomitiporia* species spanning over the southeastern subtropical belts of the USA was morphologically and genetically distinct from *F. punctata* s.s. This species was then shown to correspond (morphologically) to *F. langloisii* that was reinstated as the correct type of *Fomitiporia* (Decock et al. 2007).

Nowadays, phylogenetic inferences based on both protein and non-protein coding DNA sequence data helped to circumvent the inherent difficulties in circumscribing species based on morphological features alone. The combination of phylogenetic signal from multiple DNA loci, morphological and ecological data such as host relationships or habitat (Amalfi et al. 2010, 2012, 2014, Amalfi and Decock 2013, 2014, de Campos Santana et al. 2013) and a consistent sampling efforts at a wide geographic scale helped to implement progressively a more integrate species concept (Puillandre et al. 2012) in *Fomitiporia*. Altogether, this improved significantly our understanding of the taxonomic / phylogenetic diversity of the genus, whatever the biogeographical areas considered (see for instance Amalfi and Decock, 2013, 2014, Amalfi et al. 2012, 2014).

This diversity is best evidenced nowadays using multigenic DNA sequence data or the Phylogenetic Species Recognition concept (PSR, Taylor et al 2000, see e.g. Amalfi et al 2010, Decock et al 2007, Fischer and Binder 2004, Vlasák and Kout 2011). *A posteriori*, evidencing diversity through PSR allow emphasizing the pertinence for species delimitation of morphological characters, though sometime subtle, or such features as the ecology (autecology), noteworthy the host relationships, often poorly considered (e.g. Tomšovský et al 2010a, b). It also allows defining the actual geographical distribution range of taxa that were, otherwise, considered as widely distributed (e.g. Decock et al 2007).

However, as previously stated, the homogeneity of classical morphological characters with frequent overlapping of form or size ranges, or the occurrence of subtle differences of, *a priori*, questionable taxonomic significances often render the standard phenotypical characterization of the taxonomic entities difficult.

Ecology (autecology), noteworthy the host relationships might provide clues to the characterization of the various species; however, ecology was, and still is, poorly considered in defining taxonomic entities within Hymenochaetales, and the importance of differential ecology (substrate, habitat) for defining taxonomic entities remains understudied in many cases. Molecular tools clearly help to distinguish cryptic species within *Fomitiporia* species (Decock et al 2005, 2007); *a posteriori*, it provides also clues to the understanding of the ecological (nutritional) specialization, such as host or niche specificity.

Amalfi and Decock (2013, 2014) and Amalfi et al. (2014) provided also the most comprehensive multilocus phylogenies of *Fomitiporia*. It allowed evidencing a marked phylogeographic structure within the genus with multiple lineages whose distributions at least partly overlap with the main biogeographical realms (Olson et al. 2001).

Within the bulk of Hymenochaetaceae, the *Fomitiporia* closest relative was first found to be *Phellinus uncisetus* (Decock et al. 2007); this was later on repeatedly confirmed (Amalfi and Decock 2013, 2014, Amalfi et al. 2010, 2012, 2014). *Phellinus uncisetus* is characterized by pileate basidiomata, subglobose, thick-walled, cyanophilous but undextrinoid basidiospores, and hymenial setae, which are apically hamate. This species is known so far from high elevation forests of the southern Andes, in Argentina where it occurs on *Polylepis* (Rosaceae) (Robledo et al 2003). In a phylogenetic perspective, *P. uncisetus* is so far an orphan species; it has no other closed relatives that the *Fomitiporia* lineage.

We present in this study the most comprehensive phylogenetic analysis of the genus, based on an extended taxon sampling. We also searched for the affinities of *Phellinus livescens* with other species of *Cyanovosporus*. As it is currently defined, the genus was found to be monophyletic. On the basis of

this work, the *Fomitiporia* lineage is expanded, *Fomitiporia* is defined and the affinities of undescribed isolates are considered, in order to include additional, unpublished materials originating from French Guiana, and *P. uncisetus*, *P. livescens* and an undescribed species from high elevation Andean forest in Ecuador. Several new lineages are defined within *Fomitiporia* and the definition of *Fomitiporia* is also emended. *Fomitiporia pulverulenta* sp. nov. nom prov, *Fomitiporia andina* sp. nov. nom prov, *Fomitiporia livescens* comb. nov. prov. , *Fomitiporia bambusina* comb. nov. prov. and *F. unciseta* comb. nov. prov. are proposed.

MATERIALS AND METHODS, AN OVERVIEW

Material.— Voucher specimens and sequences used in this study are listed in Table I and II (Annex I). Original herbarium specimens with a MUCL number are preserved at MUCL. A duplicate of type material of the species newly described is deposited at NY (herbarium acronyms are according to Thiers, continuously updated). Original MUCL living cultures are preserved at MUCL with a duplicate of the ex-type strain deposited at the CBS. Original strains used in this study were isolated during fieldwork (C. Decock and M. Amalfi) from fresh basidiome tissues or conidia, using malt extract agar supplemented by 2 ppm benomyl (benlate) and 50 ppm chloramphenicol (Untereiner et al. 1998), and later purified in the laboratory in case of persistent bacterial contamination. Additional living cultures were received from colleagues and culture collections, listed in Table I.

Specimens description.— Colors are described according to Korerup and Wanscher (1981). Specimens were examined in Melzer's reagent, lactic acid Cotton blue (Kirk et al 2001), and KOH 4%. All microscopic measurements were done in Melzer's reagent. In presenting the size range of the microscopic elements, 5% of the measurements were excluded from each end and are given in parentheses, when relevant. ave = arithmetic mean, R = the ratio of length / width of basidiospores, and ave_R = arithmetic mean of the ratio R, n = number of specimens examined. As a rule, 30 microscopic elements of the basidiomata (pores / basidiospores / chlamydospores / hyphae) were measured from each specimen.

DNA extraction.— DNA extraction is an essential step in all molecular approaches to characterize microbial diversity, but although extracting high quality DNA (in terms of DNA purity, yield, and PCR amplification success)

from pure cultures has shown to be a quite straight forward process using modern techniques such as silica binding methods, achieving the same results from herbarium collections, which are potentially an enormous resource for DNA studies (e.g. type specimen, rare species, different geographic localities), can be very difficult. The mains factors affecting the difficulty in obtaining amplifiable DNA from these collections are the drying methods used, the preservation history, and the specimen age.

Specimen's preparation: Several studies have demonstrated that most damage in herbarium DNA is caused by specimen preparation, with varying degrees of damage caused by different drying methods used, with only a marginal effect of subsequent preservation history (Pyle and Adams 1989, Harris 1993, Staats et al 2011), and no detectable effect of specimen age (Erkens et al 2008). In the past few years we have handled several collections dried by different methods, we have chosen 5 of these methods (air (room temperature), air (low heated at c.a. 55° C overnight), heat (high heat more than 60° C), silica gel, alcohol) and compared the results of 20 samples (of the same age) randomly chosen, dried by these techniques, in term of successful PCR amplifications (we tested the ITS, nucLSU, Tef1-alpha and RPB2 regions). The results (not shown) support the air-drying methods, both room temperature and low heat overnight, as the best performing drying methods (respectively 100% and 95% positive amplicons whatever the gene analyzes). The silica gel technique seems to perform very well for the taxa with monomitic hyphal system (such as *Coltricia*, some *Phylloporia* specimen, or *Cantharellus*) while the results for dimitic/pseudodimitic, or trimitic taxa (e.g. *Fomitiporia*, some *Phylloporia*, *Perenniporia* or *Ganoderma* taxa) were much lower than the air drying (67% of positive amplicons). The weakest results have been obtained with the high

heat drying, probably due to DNA denaturation/damages and heat induced formation of Maillard's bodies (DNA-protein complexes).

Pure cultures: The DNA was extracted from freshly collected mycelium from pure culture grown in liquid malt at 25°C in the dark. Extractions were carried out using the QIAGEN Dneasy plant Mini Kit (QIAGEN Inc.), and later purified with Geneclean® III kit (Q-Biogene), following the manufacturer's recommendations.

Herbarium specimens: several different techniques were used for extracting DNA from herbarium collections depending of their age. For freshly dried specimens (up to 2 years old) extractions were mainly carried out using the QIAGEN Dneasy plant Mini Kit (QIAGEN Inc.) according to manufacturer instruction; in some cases salting-out precipitation was performed following the CTAB 1 protocol (Amalfi and Baert unpublished) detailed in Annex II. The EDGF protocol (Annex II) as detailed in Dentinger et al. (2010) was also tested without significant increase in PCR amplicons. For older specimens we tested several methods and compared the results: silica binding (Dneasy plant Mini Kit) with standard protocol, silica binding (Dneasy plant Mini Kit) with prolonged incubation in Lysis Buffer and proteinase K, one to two weeks, two salting-out precipitations: CTAB 1 protocol and CTAB 2 (Annex II) protocol, this latter was optimized by a two weeks precipitation step (step 9 in CTAB 2 protocol Annex II) in ethanol at -20°C, Whatman FTA_PlantSaver cards DNA extraction protocol (Dentinger et al. 2010), direct PCR by Sigma Extract-N-Amp_Plant PCR Kit (Product Code XNAR), and some combination of these methods such as CTAB 1 extraction followed by Dneasy plant Mini Kit, or FTA cards and Sigma Extract-N-Amp processing. The best results in terms of DNA quality

(measured as the ratio of the absorbance at 260 and 280 nm (A₂₆₀/A₂₈₀)) and number of positive amplicons, were obtained by combining the CTAB 1 protocol (or protocol 2 for the most tough collections) followed by silica-binding, especially for the older samples. Nevertheless for most collections, aged between five and ten years old, the less time consuming (and expensive) Dneasy plant Mini Kit with a prolonged, two weeks incubation in Lysis Buffer and proteinase K seemed to be enough in order to obtain a PCR quality DNA.

PCR amplification — Several different strategies (in term of PCR master mix and protocols) and target loci have been deeply tested in order to improve amplification and sequencing succes, so that we could obtain the most robust phylogeny as possible (see table II for a full overview on PCR primers and programs used). PCR amplification was generally carried out in 50 µl reaction mix containing for each PCR tube 5 µl of 10X PCR buffer (100 mM Tris-HCl, pH 8.3, 500 mM potassium chloride, 2.5 mM magnesium chloride, 0.1% gelatin, 1.6 mg/mL bovine serum albumin), 3 µl of MgCl₂ (25mM), 1 µl of Deoxynucleotide Mix (dNTPs) (10mM), 1 µl of each primer (10 µM), 0,5 of *Taq* DNA polymerase, (0.05 units/µl), 10 ng template DNA and sterile (PCR grade, Nuclease-free) water to reach the final volume of 50 µl. We also successfully used the Sigma JumpStart *Taq* ReadyMix for PCR amplification, a component of the Plant DNA Extraction Kit, after increasing the MgCl₂ concentration in the ReadyMix to a final concentration of 2.5 mM and PROMEGA GoTaq® DNA Polymerase. For the most though PCR amplifications, whereas the DNA was degraded, or lesser than 10 ng, or in order to obtain blunt ends PCR products for cloning, the New Englan BoLabs inc. Phusion® High-Fidelity DNA Polymerase was successfully used. In these cases the reaction mix consisted in 4 µl of 5X

Phusion HF or GC, 0.4 µl of dNTPs (10mM), 1 µl of each primer (10 µM), 0.6 µl of dimethyl sulfoxide (DMSO)¹, a variable amount of DNA template (depending on concentration), 0.2 µl of Phusion® High-Fidelity DNA Polymerase (0.01 units/µl) and nuclease free sterile water to a final volume of 20 µl.

We have focalized our studies mainly on four regions/genes: two regions of the nuclear ribosomal DNA (rDNA), the internal transcribed spacer (ITS - 5.8S) which ranged c.a. 800 bps and the nuclear large subunit (nucLSU) ranging c.a. 1000 bps, which have been chosen as the official barcoding regions for fungi for their resolution at a species level, allowing easy and rapid comparison with the main DNA sequences repository such as GenBank or EBI; and two partial housekeeping genes: the translation elongation factor 1- α (*Tef1 alpha* c.a. 1200 bps) between exons 4 and 8 (Wendland and Kothe 1997) and *rpb2* (c.a. 800 bps), which encodes the second largest subunit of RNA polymerase II, between conserved domains 5 and 7 (Liu et al., 1999). Both of them have demonstrated multiple times to be of the most promising loci to contribute resolving the phylogeny of fungi (Liu et al. 1999, Liu and Hall 2004, Matheny 2005, Reeb et al. 2004, Wang et al. 2004, Zhang and Blackwell 2002, Baldauf and Palmer 1993, O'Donnell et al. 2001, Matheny et al. 2007, Rehner and Buckley 2005, Roger et al. 1999). Nevertheless several others loci were analyzed in order to improve the phylogenetic signal, refer to table II to a full synopsis. Generally speaking for each locus we sequenced at least strains (two per species) belonging to the main *Fomitiporia* lineages resolved from the ITS, nucLSU, *Tef1 alpha* and *RPB2* analyses, and tested the resulting sequences for phylogenetic signal, codon saturation and congruence with DAMBE, HyPhy

¹ The DMSO binds to the DNA at the Cytosine residue and changes its conformation which makes the DNA more labile for heat denaturation. In this way it lower of melting temperature (t_m) and increase the GC region. Since most of the primers are GC rich, DMSO indirectly facilitates the annealing of primers to the template and this enhances the amplification.

- Hypothesis testing using Phylogenies (Kosakovsky et al 2005), COMPAT.PY (Kauff and Lutzoni 2002) and visual screening.

Some of them such as the nuclear small subunit (nucSSU) or partial ATP6 gene, coding for the mitochondrial ATPase subunit 6, has shown to be highly conserved, e.g. for the ATP6 partial gene two to five bps differences appears to be discriminant at species level, making them of scarce utility in improving the phylogenetic signal. Otherwise the β -tubulin partial gene has shown to be excessively variable, being the intron present, which ranged from 200 to 2000 bps depending on the species, almost too variable for alignment. And even the exonic segment showed saturation at the 3rd position of the codons.

On the other hand the glyceraldehyde-3-phosphate dehydrogenase (*gpd*) genes (c.a. 1200 bps) and the largest subunit (RPB1) of RNA polymerase II resulted quite promising loci for phylogenetic applications. For what concerns RPB1, the nucleotide sequences of these gene fragments showed a moderate degree of similarity (72 to 76%) in the protein-encoding regions and only a low degree of similarity in the six introns presents in the 30 strains sequenced (56 to 66%).

The respective nucleotide sequences of these gene fragments showed a moderate degree of similarity (72 to 76%) in the protein-encoding regions and only a low degree of similarity in the introns (56 to 66%). Introns, where present, occurred at conserved positions, but the respective positions and numbers of introns in a given taxon varied. The length of the intron was found to vary between 55 and 98 nucleotides. It is reported that the positions of introns were strongly conserved in the *gpd* genes of the basidiomycota, although the numbers of them differs between taxa (genera or distant lineages). Likewise, the positions of the introns present in the *gpd* gene of the *Fomitiporia* strains studied were similar to those of the other

basidiomycota (e.g. *Ganoderma lucidum*), which may reflect the evolutionary divergence of these mushrooms. It has been remarked that the position of only one intron was conserved between basidiomycota and ascomycota (Harmsen *et al.*, 1992), suggesting the existence of a clear boundary between ascomycota and basidiomycota with respect to intron positioning with the *gpd* gene. These facts, joined to the good interspecific resolution power of *gpd* gene, make this locus a good candidate for a higher-level phylogenetic study of fungi. The main problem working with *gpd* gene was the frequent necessity of cloning (nested PCR) mainly due to the presence of multiple aplotypes (Kausrud *et al* 2007) or variation in introns length between strains. Thus the economic expenses exponentially increase with the price of cloning and the necessity of multiple sequencing per clones. A similar problem occurs with the very interesting RPB1 gene (c.a. 1400 bps), for which cloning or gel extraction were frequently needed. Also this latter presents two different levels of phylogenetic resolution, being the four introns present informative at species level while the exonic fragments resolved the main evolutionary lineages. Unfortunately these two promising markers were (for the moment) abandoned mainly for economic reasons but clearly they needed further studies.

DNA sequencing —. After visualization of positive PCR products on a 0.8% agarose gel, PCR amplicons were cleaned prior to sequencing using QIAquick® PCR purification kit (250) (QIAGEN Inc.), following the manufacturer's recommendations. Alternatively, in order to purify a larger number of samples at once we used a combination of exonuclease I and shrimp alkaline phosphatase. In this case to each sample was added 0.4 volumes of a master mix containing 1% exonuclease I (10 units / μ L), 10% shrimp alkaline phosphatase (1 unit / μ L) and water. The solutions were

mixed and incubated at 37°C for 15 min, then at 80°C for 15 min in a thermal cycler.

Some PCR (especially the ITS and *rpb2* loci) amplifications resulted in multiple amplicons; in this case the appropriate products were identified on 2% TAE gels in comparison to a 1 kb DNA ladder (ThermoFisher Scientific), excised, and purified with the GeneClean II Kit (MP BIOMEDICALS). When multiple PCR products could not be electrophoretically separated, the purified DNA amplicons were cloned into pJET1.2/blunt vector using a CloneJET PCR cloning kit (Fermentas), following the manufacturer's instructions. Ligated plasmids were transformed into DH5 α TM Chemically Competent *E. coli* cells (Invitrogen) by heat shock following the manufacturer's instructions. Three to five randomly chosen clones were re-amplified by direct colony PCR.

Sequencing reactions were performed using CEQ DTCS Quick Start Kit® (Beckman Coulter) according to the manufacturer's recommendations, with the primers LROR, LR3, LR3R, LR5 for the LSU; ITS1, ITS2, ITS3, ITS4 for the ITS (<http://biology.duke.edu/fungi/mycolab/primers.htm>); 2212R, 1953R, 983F, 2218R for *tefl* (Rehner and Buckley 2005, Matheny et al. 2007); and bRPB2-6F and bRPB2-7.1R (Matheny 2005) for *rpb2*.

Sequences were assembled and edited with the SequencherTM 4.8 software (Gene Codes Corporation, Ann Arbor, MI, U.S.A.).

Fig.2 PCR Programs and primers used in our studies

Fig.2 PCR Programs and primers used in our studies

nucLSU						
Name	Sequence 5'-3'	Position	Notes	PCR PROGRAM		
LROR	ACC CGC TGA ACT TAA GC	26-42	Vilgalys lab	1) 94°C 5 min	35 X	
LR3	CCG TGT TTC AAG ACG GG	651-635	Vilgalys lab	2) 94°C 1 min		
LR3R	GTC TTG AAA CAC GGA CC	638-654	Vilgalys lab	3) 50°C 1.30 min		
LR5	TCC TGA GGG AAA CTT CG	964-948	Vilgalys lab	4) 72°C 4 min		
LR6	CGC CAG TTC TGC TTA CC	1141-1125	Vilgalys lab	5) 72°C 10 min		
LR7	TAC TAC CAC CAA GAT CT	1418-1432	Vilgalys lab	6) 4°C INFINI		
nucLSU primers map (From Lutzoni Lab.)						
PCR: LROR-LR6 (LR5)						
Sequencing: LROR, LR3, LR3R, LR5						
ITS						
Name	Sequence 5'-3'	Position	Notes	PCR PROGRAM		
NS7	GAG GCA ATA ACA GGT CTG TGA TGC	1413-1436 (nucSSU)	White et al, 1990	1) 94°C 3 min	30 X	
ITS1	TCC GTA GGT GAA CCT GCG G	1773-1791 (nucSSU)	White et al, 1990	2) 94°C 1.30 min		
ITS2	GCT GCG TTC TTC ATC GAT GC	53-34	White et al, 1990	3) 55°C 1.30 min		
ITS3	GCA TCG ATG AAG AAC GCA GC	34-53	White et al, 1990	4) 72°C 2 min		
ITS4	TCC TCC GCT TAT TGA TAT GC	57-38 (nucLSU)	White et al, 1990	5) 72°C 10 min		
ITS5	GGA AGT AAA AGT CGT AAC AAG G	1749-1770 (nucSSU)	White et al, 1990	6) 4°C INFINI		
ITS-nucSSU primers map						
PCR: NS7-ITS4 (ITS5-ITS4)						
Sequencing: ITS1, ITS2, ITS3 and ITS4						
nucSSU						
Name	Sequence 5'-3'	Position	Notes	PCR PROGRAM		
NS1	GTA GTC ATA TGC TTG TCT C	20-38	White et al, 1990	1) 94°C 5 min	35 X	
NS2	GGC TGC TGG CAC CAG ACT TGC	573-553	White et al, 1990	2) 94°C 1 min		
NS3	GCA AGT CTG GTG CCA GCA GCC	553-573	White et al, 1990	3) 55°C 1.30 min		
NS4	CTT CCG TCA ATT CCT TTA AG	1150-1131	White et al, 1990	4) 72°C 4 min		
NS5	AAC TTA AAG GAA TTG ACG GAA G	1129-1150	White et al, 1990	5) 72°C 10 min		
NS6	GCA TCA CAG ACC TGT TAT TGC CTC	1436-1413	White et al, 1990	6) 4°C INFINI		
NS7	GAG GCA ATA ACA GGT CTG TGA TGC	1413-1436	White et al, 1990			
NS8	TCC GCA GGT TCA CCT ACG GA	1788-1769	White et al, 1990			
PCR: NS1-NS8						
Sequencing: NS1, NS2, NS3, NS4, NS5, NS6, NS7, NS8						

RPB1					
Name	Sequence 5'-3'	Position	Notes	PCR PROGRAM	
gRPB1-Af	GAR TGY CCD GGD CAY TTY GG		Matheny et al. 2002	1) 94°C 2 min	9 X
aRPB1-Br	TCC GCR CCY TCT TCY TTG G		Matheny et al. 2002	2) 94°C 40 sec	
gRPB1-Cr	CNG CDA TNT CRT TRT CCA TRT A		Matheny et al. 2002	3) 60°C 60 sec	
RPB1-Int2f	TTM BTC TRC TCG TTT YGC AC		Froslev et al 2005	4) 72°C 2 min	
RPB1-Int2.1f	GCT GAA CGA GSA GTG C		Froslev et al 2005	5) 94°C 45 sec	36 X
RPB1-Int2.2f	CGI TTT CGR TCG CTT GAT		Binder et al 2010		
RPB1-Int2.1r	GCA CTS CTC GYT CAG C		Froslev et al 2005		
			6) 53°C 1.30 min		
			7) 72°C 2 min		
			8) 72°C 10 min	9) 4°C INFINI	
RPB1 primers map (from Froslev et al 2005)					
PCR: gRPB1-Af/ gRPB1-Cr; (if multiple bands on gel) RPB1-Int2f/gRPB1-Cr (400bp shorter)					
Sequencing: RPB1-Af, RPB1-Int2.2f, RPB1-Int2.1r, RPB1-Cr and RPB1-Int2f, RPB1-Int2.1f RPB1-Int2.1r, RPB1-Cr					
Glyceraldehyde-3-Phosphate Dehydrogenase (GDP)					
Name	Sequence 5'-3'	Position	Notes	PCR PROGRAM	
CTK-052	CGG CCG TAT CGI CCT CCG TAA TGC		Kreuzinger et al 1996	1) 94°C 4 min	35 X
CTK-032rev	GAG TAA CCG CAT TCG TTA TCG TAC C		Kreuzinger et al 1996	2) 94°C 30 sec	
CTK-132	GTC TAC ATG TTC AAG TAC GAC TC		Kreuzinger et al 1996	3) 51°C 30 sec	
CTK-133rev	CCG ATG AAG TCA GIT GAC ACT AC		Kreuzinger et al 1996	4) 72°C 35 sec	
				5) 72°C 10 min	30 X
				6) 4°C INFINI	
				Nested PCR (CTK-132/133rev) 10 µl of PCR products diluted 1:200	
				1) 95°C 3 min	9 X
				2) 95°C 1.30 min	
				3) 55°C 30 sec	
				4) 52°C 30 sec	
				5) 72°C 1.30 min	30 X
				6) 95°C 45 sec	
				7) 54°C 1 min	
				8) 72°C 1 min	
				9) 95°C 1 min	
				10) 54°C 1 min	
				11) 72°C 10 min	
PCR: CTK-052-CTK-032rev, followed by cloning , nested PCR with CTK-132-133rev, or gel-excision, purification and reamplification					
Sequencing: CTK-052-CTK-032rev, or CTK-132-CTK-133rev					
Mitochondrial ATPase subunit 6 (ATP6)					
Name	Sequence 5'-3'	Position	Notes	PCR PROGRAM	
M13F-pUC+ ATP6-1	GIT TTC CCA GTC ACG AC + ATT AAT TSW CCW TTA GAW CAA TT		Olivier Raspé unpublished	94°C 3 min	5 X
M13F + ATP6-2	GTA AAA CGA CGG CCA GT + AAT TCT ANW GCA TCT TTA ATR TA		Olivier Raspé unpublished	94°C 30 sec	
				42°C 1 min	
				72°C 1 min	36 X
				94°C 30 sec	
				55°C 45 sc	
				72°C 1 min + 1 sec/cycle	
				72°C 7 min	
ATP6 primers map					
ATP 6 - 3 ATP 6 - 1 ATP 6 - 5f target area ATP 6 - 6r ATP 6 - 2 ATP 6 - 4 0.1 kb					
PCR: M13F-pUC + ATP6-1 AND M13F + ATP6-2					
Sequencing: M13F-pUC, M13F					

Phylogenetic analysis.— three hundred fifty eight specimens and cultures representing at least 67 species (or potential species clades) were included in the phylogenetic analysis (excluding the outgroups dataset). Our dataset included 92% of the taxa (based on Index Fungorum website: <http://www.indexfungorum.org>) currently accepted as belonging to the genus *Fomitiporia*. Materials and sequences used in this study are listed in Table I. Nucleotide sequences were automatically aligned with Clustal X (version 2.0.11) (Thompson et al. 1997), then manually adjusted as necessary with PhyDE® v0.9971 (Müller et al. 2010.). Potentially ambiguously aligned segments were also detected using the Gblocks v0.91b program (Castresana 2000; <http://molevol.cmima.csic.es/castresana/Gblocks.html>) with the settings "allow smaller final blocks", "allow gaps within blocks". The assignment of codon positions was confirmed by translating nucleotide sequences into predicted amino acid sequences using MacClade 4.0 (Maddison and Maddison 2000) and then compared with the annotated *F. mediterranea* sequence AFTOL ID 688. Some *rpb2* sequences (mainly from herbarium specimens) could not be obtained and were considered as missing data in the combined dataset. The indels present in our data sets, especially in the ITS1 region (Decock et al. 2007), were recoded as binary characters following the Simple Indel Coding method (SIC, Simmons and Ochoterena 2000) as implemented in the SeqState software (Müller 2005), in order to avoid long-branch attraction artifact.

Phylogenetic analyses were performed separately for each individual and concatenated loci using maximum parsimony (MP) as implemented in PAUP* version 4.0b10 (Swofford 2003), Bayesian inference (BI) as implemented in MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003) and Maximum likelihood (ML) as implemented in RAxML 7.0.4 (Stamatakis et al. 2008). *Onnia tomentosa* was chosen as outgroup following the results of

Larsson et al. (2006). In order to assess the generic status of *Fomitiporia*, strains of *Porodaedalea chrysoloma*, *Porodaedalea pini* and *Pseudoinonotus dryadeus* were also included in this study.

The most parsimonious trees (MPT) for each data set were identified using heuristic searches with 1,000 random addition sequences, further evaluated by bootstrap analysis, retaining clades compatible with the 50% majority-rule in the bootstrap consensus tree. Analysis conditions were tree bisection addition branch swapping (TBR), starting tree obtained via stepwise addition, steepest descent not in effect, MULTREES effective. Clades with a bootstrap support value (BS) above 85% were considered supported by the data.

Models of evolution for BI were estimated using the Akaike information criterion (AIC) as implemented in Modeltest 3.7 (Posada and Crandall 1998). In order to facilitate the data partitioning by codon position for the *tefl*, the three clade specific, confidently alignable introns, 51–63 bps long present (Amalfi et al. 2010) were excised and analyzed as a distinct partition. Therefore the dataset was subdivided into 12 data partitions: ITS1, 5.8S, ITS2, nucLSU, *tefl*-1st, -2nd, -3rd codon positions, *tefl* introns, *rpb2* 1st, -2nd, -3rd codon positions, and indels .

The best-fit models for each partition were implemented as partition-specific models within partitioned mixed-model analyses of the combined dataset (TABLE II). For analyzing the SIC data under BI, we used the Restriction Site Model (F81-like) of MrBayes 3.1.2 (Ronquist et al. 2005). All parameters were unlinked across partitions. Bayesian analyses were implemented with two independent runs, each with four simultaneous independent chains for ten million generations, starting from random trees, and keeping one tree every 1000th generation. The tree with the best

likelihood value (see below ML) was used as a starting tree for the Bayesian analyses. All trees sampled after convergence (ave. standard deviation of split frequencies <0.01 and confirmed using Tracer v1.4 [Rambaut and Drummond 2007]) were used to reconstruct a 50% majority-rule consensus tree (BC) and to calculate Bayesian posterior probabilities (BPP). BPP of each node was estimated based on the frequency at which the node was resolved among the sampled trees with the consensus option of 50% majority-rule (Simmons et al. 2004). Clades with BPP above 0.95 were considered significant.

Maximum likelihood (ML) searches conducted with RAxML involved 1000 replicates under the GTRGAMMAI model, with all model parameters estimated by the program. In addition 1000 bootstrap (ML BS) replicates were run with the same GTRGAMMAI model. We provided an additional alignment partition file to force RAxML software to search for a separate evolution model for each dataset including the recoded indels. Clades with Maximum likelihood bootstrap values of 85% or greater were considered supported by the data.

To detect the possible bias from substitution saturation, we tested the first, second and the third codon position of the coding region analyzed (*rpb2* and *tef1- α*) by using Xia's test (Xia and Lemey, 2009; Xia et al., 2003, as implemented in DAMBE (Xia and Xie, 2001)). Because the Iss.c is based on simulation results, there is a problem with more than 32 species. To circumvent this problem, DAMBE was used to randomly sample subsets of 4, 8, 16 and 32 OTUs multiple times and perform the test for each subset to see if substitution saturation exists for these subsets of sequences. In order to confirm the results of the Xia's method we also plotted transitions and transversions at the first, second, and third codon positions against Tamura-

Nei genetic distances with the aid of the DAMBE package, with an asymptotic relationship indicating the presence of saturation

To detect topological conflicts among data partitions, the nodes between the majority-rule consensus trees obtained in the MP analysis from the individual data sets were compared. Paired trees were examined for conflicts only involving nodes with BS > 70% (Lutzoni et al. 2004, Mason-Gamer and Kellogg 1996, 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. The software COMPAT.PY (Kauff and Lutzoni 2002) was also used in order to statistically confirm the combinability of datasets.

Ancestral range patterns have been inferred by a statistical dispersal-vicariance analysis (DIVA) based on Bayesian topology as implemented in the software RASP (Yu et al 2010), a set of sixteen discrete areas based on the known actual distributions of the *Fomitiporia* taxa were defined (Figs.3, 6): (A) North temperate, (B) Mediterranean, (C) Asian temperate, (D) Californian, (E) North American, (F) Sub-tropical USA, (G) Caribbean, (H) Mesoamerican, (I) Neotropical, (J) Andean, (K) Tropical Africa, (L) East African mountain, (M) Tropical Asia, (N) Australian, (O) West African Mountains, (P) South Africa.

The ancestral area analyses were conducted on a random sampling of 10000 dated trees estimated from BEAST (see below). The RASP analysis was based on a F81 model of evolution allowing for different rates of changes among ancestral areas. The Bayesian posterior probabilities were determined twice by running 10 chains fifty thousand generations, saving reconstructions every 100th generations.

Calibration strategies and divergence-time estimations — Two data matrices were used for molecular clock calibration. Dataset 1 was used for primary fossil calibration; dataset 2 covered only *Fomitiporia* and outgroup and was used for secondary calibration.

Since there are no known fossils of *Fomitiporia* for calibration, we used an extensive outgroup for which fossils are available. We included three Agaricomycetes fossils as primary calibration points: *Archaeomarasmius leggetti* (Hibbett et al., 1997) as the minimum age of the Agaricales; *Quatsinoporites cranhamii* (Smith et al., 2004) as the minimum age of the Hymenochaetales and a permineralized “sulloid” ECM associated with Pinus roots of at least 50 million years (LePage 2003). The first fossil is an agaricoid fruiting body that is comparable to the extant genera *Mycena*, *Marasmius*, *Marasmiellus*, *Collybia* and *Phaeomarasmius*, preserved in Dominican amber from the mid-Cretaceous (c. 90 My). In this calibration, we used the most recent common ancestor (MRCA) of the tricholomatoid, marasmioid and hygrophoroid clades, which included 186 species outside *Fomitiporia*. The second fossil is a poroid fruiting body from Apple Bay on Vancouver Island that dates to the Early Cretaceous (c. 113 My). This specimen can be assigned to the Hymenochaetales and compared to the extant genera *Phaeolus* in the Polyporales and *Cyclomyces* and *Inonotus* in the Hymenochaetales, granting a more precise estimation of time divergences. The third fossil dates of at least 50 MyBP and was used to calibrate the Boletales + Atheliales clade, which is in a sister position to Agaricales. Other clades included were *Pluteus* and *Volvopluteus* as sister taxa of the Amanitaceae in the pluteoid clade, and *Gautieria othii* as outgroup. The Hymenochaetales were not constrained as monophyletic, based on results from Matheny et al. (2007).

Divergence times were estimated with *beast* 1.8 (Drummond et al., 2012), using an uncorrelated log-normally distributed clock model. XML files were constructed with *BEAUti* 1.8 by importing separate NEXUS files of each gene partition. The gene partitions were unlinked for substitution and molecular-clock models and linked (concatenated) for gene trees. The substitution model GTR+ Γ +I was used for all genes in dataset 1 and for LSU in datasets 2;

SYM+ Γ +I was selected for *tefl*-alpha and *rpb2* in datasets 2. Orders and known clades within the Agaricales (Table 1; Annex I) were constrained to be monophyletic except for the Hymenochaetales. Two different tree-model priors were applied to the separate datasets: Yule for dataset 1, and constant coalescent for dataset 2.

The prior for the *ucld.mean* parameter was gamma distributed (shape = 1.0; scale = 0.001; offset = 0.0) for all genes. For fossil node calibrations, we used gamma-distributed priors (shape = 1.0; scale = 50.0; offset = 90.0 for *Agaricales*, 113.0 for Hymenochaetales or 50.0 for Boletales) with an arbitrarily 'long tail'. Subsequent analyses (datasets 2) were conducted using a normally distributed calibration of the *treeModel.rootHeight* parameter (mean, 58; SD, 1), according to the highest posterior density (HPD) of the time to the MRCA of the subgenus *Fomitiporia* obtained from Dataset 1. Four independent Markov chain Monte Carlo (MCMC) chains of 50,000,000 generations and sampling frequency of 5000 were conducted for each dataset. Convergence and mixing were assessed by comparing log files in *Tracer* 1.6 (Rambaut et al., 2013) and confirming that effective sample size (ESS) values were at least 200. An ultrametric maximum clade credibility (MCC) tree with mean and 95% HPD node ages and per-clade posterior probabilities was summarized using *TreeAnnotator* 1.8, with 10% burn-in

and a 0.8 posterior limit. XML, log and tree files are available on request to the author.

RESULTS

General results

The status of the *F. punctata-robusta* complex was partially assessed in our studies using a polyphasic approach combining both morphological and molecular data, and considering ecological / bio-geographical aspects. The collecting effort, mostly in tropical or subtropical areas, allow us to gather about 300 strains representing 98% of the species actually considered belonging to the genus. We tried to retrieve all the type/paratype of the known species from the various mycological collections, and whereas they were unavailable, lost or we couldn't obtain any DNA from the samples, we focused our effort in retrieving them by collecting in the type localities some fresh material morphologically congruous with the types.

All the strains have been identified on the base of the morphological species concept and sequenced for at least four independent genes. Furthermore, the phylogeny of most of the known species was inferred based on a combined data set of partial LSU, ITS-5.8 regions of the nuclear ribosomal DNA and partial *tef1- α* and RPB2 genes, under Maximum parsimony Bayesian inference, and Maximum likelihood, and the genetic data were linked with the bio-geographical/ecological/morphological ones to generate a “phylogeographic map” of the genotypes (Fig 3, in the external pocket).

Some other genes were tested to improve the phylogeny of the genus, e.g. B-tubulin or the SSU of the mitochondrial ribosomal DNA, both of them were excluded due to their lack of resolution (SSU) or excessive variability (B-tubulin was almost impossible to align even for closely related taxa).

We also tested some morphological character (e.g. spores volume) in relation with geographical information, evidencing a strong correlation between them.

From these studies, several new terminal clades emerged, some of them were described in the following chapters. Nevertheless, at least 18 terminal clades or phylogenetic species, some of them representing species new to science, are still to be described. For some of these unnamed species, names might exist in the "old" literature; especially, for instance, the types of Murrill should be carefully analyzed. However, the occurrence of cryptic species in *Fomitiporia* with no or poorly perceptible morphological change, evidenced only by molecular data (phylogenetic species concept / recognition) or ecological data (autecology), intrinsically, might place some doubts on the application of old, long forgotten names.

Furthermore, and although still undergoing changes, the combination of this data with the classical morphology allows us to improve the understanding of the species concepts within the genus, redefining the diagnostic characters to this latter (e.g. two strains from Ethiopian highlands previously identified as *F. pseudopunctata* (MUCL 44806 and MUCL 44799) because of the presence of hymenial setae, were proved to represent *F. aethiopica* (Amalfi et al 2010). It could be also the case with the sibling pair *F. mediterranea* / *F. pseudopunctata* that clusters together in a monophyletic group whatever the datasets analyzed (see below chapter 3 *F. neotropica*).

Our phylogenetic analysis also reveals a complex biogeographical structure of the genus, with several phylogenetic lineages corresponding to the main phytogeographic domains with a high level of endemism. In particular we were able to evidence so far.

One Andean / Patagonian endemic lineage, one relict clade (*F. calkinsii*), one Australian clade, and a core lineage comprising one Pan-temperate/ Holarctic clade, two African, one Asian and a large Neotropical endemic lineages. These latter contains two sister subclades one of them (chapter 2 Fig 1 clade A1) contains exclusively species having a resupinate basidiomes (though occasionally pseudopileate) such as *F. langloisii*, *F. maxonii*, *F. dryophila*, *F. sonora*, etc.; and the second one (Chapter 2 Fig 1 Clade A2) comprises exclusively species with pileate to pseudopileate basidiomes such as *F. tabaquilio*, *F. apiahyna*, *F. texana* etc.

Moreover our preliminary results show that the Neotropical collections with pileate basidiomes are distributed into 9 distinct terminal clades (sublineages). These clades pertain mainly to two lineages, the *F. apiahyna* and the *F. texana* lineages. *Fomitiporia castilloi* has an isolated position, basal to the *F. langloisii* lineage. Furthermore, a specimen from French Guiana (PS 19, MUCL 54415, Fig.3), identified as a *Fomitiporia* species on the basis of typical subglobose, thick-walled, dextrinoid and cyanophilous basidiospores, nested outside the *Fomitiporia* lineage as previously defined (Amalfi et al. 2010, 2012, 2014; Amalfi and Decock 2013, 2014; de Campos Santana et al. 2013), in a position basal to a lineage containing *Phellinus uncisetus*, *Phellinus livescens* and an unidentified *Phellinus* sp. PS 18 originating from Ecuadorian Andes.

PS 19 MUCL 54415 (Fig. 3) is distantly related from all other clades representing species with pileate basidiomes as yet reported from South, Meso-, and North America, or elsewhere (Amalfi et al. 2010, 2012; Dai et al. 2008; Decock et al. 2007; Fischer and Binder 2004; Vlasák and Kout 2011, Zhou and Xue 2012). It is also distantly related to all other clades representing potential species with pileate basidiomes, sympatric in the areas surveyed (PS 2, PS 3, PS 5, & PS 6, Fig. 3). In contrast, PS 19 is very basal

to the all *Fomitiporia* lineage, which contained to date only species with dextrinoid basidiospores.

The collection forming PS 19 shows a singular combination of morphological features, thereby defining one morphospecies. In addition to the dextrinoid basidiospores, it includes, noteworthy, a ptychogasteroid asexual form which development results in a pulverulent rusty brown layer (Fig. 4, B, C, Fig. 5, A, B) at the base of the basidiomata and neighbouring substrate. This layer is composed of thick-walled, mostly (sub)globose, yellowish to brownish conidia with a roughened external surface (Fig. 5). A roughly sulcate pileus, a broad margin, and basidiospores averaging 6.2 x 5.2 µm complete the characteristics of the species.

Search for a possible epithet for this species within *Fomitiporia* yielded no name that could apply to it. There are no other known *Fomitiporia* species with a ptychogasteroid asexual form. However, searching within the still vast *Phellinus sensu lato* (Larsen and Cobb-Pouille 1999), *Phellinus bambusinus* (Larsen and Cobb-Pouille 1999, Patouillard 1891, 1900) emerged.

Phellinus bambusinus (basionym: *Polyporus bambusinus* Pat., Patouillard 1891) is a little documented species. It was originally described on the basis of three specimens originating from Vietnam, growing on dead bamboo culms (Patouillard 1891). It was described also producing a chlamydosporic, ptychogasteroid asexual state, developing at the base of the basidiomata and forming a pulverulent, rusty brown layer of conidia [*les conidies forment une masse brune roussâtre qui s'attache très facilement aux doigts, fide* Patouillard 1891]. This conidial form was not "officially" named by then (Patouillard 1891) but informally referred to as "*Ptychogaster ferruginosus*" on the label of the type specimen (*fide* Stalpers 2000).

Two collections of *Phellinus bambusinus* (MUCL 51609, MUCL 51610), from Southern Yunnan, China, were examined but did not show the conidial layer as described by Patouillard (1891). However, in *in vitro* culture on artificial media (MA2), the strains obtained from the basidiomata of MUCL 51609, MUCL 51610 produced abundant conidia, which ontogeny and morphology are identical to those described by Patouillard (1891) and Stalpers (2000). They are also almost identical to those present in our specimens of PS 19, differing by their overall shape, more elongated, and their smooth surface.

Phellinus bambusinus was repeatedly described with adextrinoid basidiospores, a feature which is confirmed by the examinations of our own collections. Nevertheless, in our phylogenetic analysis, our two specimens of *P. bambusinus* nested within the core *Fomitiporia* lineage (Fig. 3, blue box); more specifically, *P. bambusinus* belongs to a well-supported lineage also comprising other bamboo specific species viz. *F. spinescens*, *F. bambusarum*, and an unnamed *Fomitiporia* species (MUCL 51593, Southern Yunnan, China, not included in the study for practical reasons).

These taxa form altogether a potential substrate specific lineage. The inclusion of *P. bambusinus* within *Fomitiporia* introduces consequently a species with non-dextrinoid basidiospores.

PS 19 and *P. bambusinus* are genetically well distinct (Fig. 3). They differ also in much of their morphological and ecological aspects, and geographical distribution. PS 19 has larger basidiomata than *P. bambusinus* (up to 10 cm wide, at least xx cm of growth in a year; ≤ 1.5 cm in *P. bambusinus*), dextrinoid basidiospores (adextrinoid in *P. bambusinus*), and a growth on angiosperm tree whereas *P. bambusinus* seems to be restricted to bamboo. PS 19 is also known so far only from the northeastern edge of the

Amazonian ecosystem, whereas *P. bambusinus* is known from Northern areas of Southeast Asia (southern China / northern Vietnam).

The unique collection forming PS 18 (MUCL EC-14-79) also shows a singular combination of morphological features, thereby also defining one morphospecies. The species is characterized by pileate basidiomata, a broad margin, hymenial setae subulate to mostly variably ventricose at the base, apically straight and acute, and globose, faintly dextrinoid (pinkish) basidiospores $ave = 6.2 \times 5.2 \mu m$. To date, only one species having the combination of pileate basidiomata and hymenial setae was known to occur in South America, *F. castilloi* (Amalfi and Decock 2013). *Fomitiporia castilloi* is to be found in lowland rainforest, and known to date from a single location in French Guiana, viz. the Nouragues Nature Reserve. However, PS18 is closely related to *Phellinus uncisetus* and *Phellinus livescens*. Both *P. uncisetus* and *P. livescens* also have hymenial setae, uncinated in the former, straight in the latter, and both have adextrinoid basidiospores (Robledo et al., 2003).

PS 18 and PS 19 are considered as representing distinct, undescribed species; they are therefore proposed as *F. pulverulenta* nom. Prov. and *F. andina* nom. Prov. (complete description pending). *Phellinus uncisetus*, *P. bambusinus* and *P. livescens* are considered to be members of *Fomitiporia*, and their combinations are proposed (*F. unciseta* comb. nov. prov., *F. bambusina* comb. nov. prov., *F. livescens* comb. nov. prov.)

As a consequence the circumscription of *Fomitiporia* is emended to include a ptychogasteroid, chlamydosporic asexual form and species with adextrinoid or only faintly dextrinoid (pinkish) basidiospores.

For coherence we have tried to focus our studies following the geographic structure evidenced, and therefore we will start our discussion from the African lineages (Chapter 1), then the Pan-temperate lineage

(chapter 2), and the Neotropical lineages (Chapter 3 to 6) which seems to encompass the largest species and lineage diversity. In the further discussion we will approach the Andeo-patagonian basal lineage, with emphasis on two newly discovered species and a redefinition of the whole genus. We will also present our preliminary results issued from our molecular clock and ancestral range analysis and discuss the phylogeographic structure of the genus clade by clade.

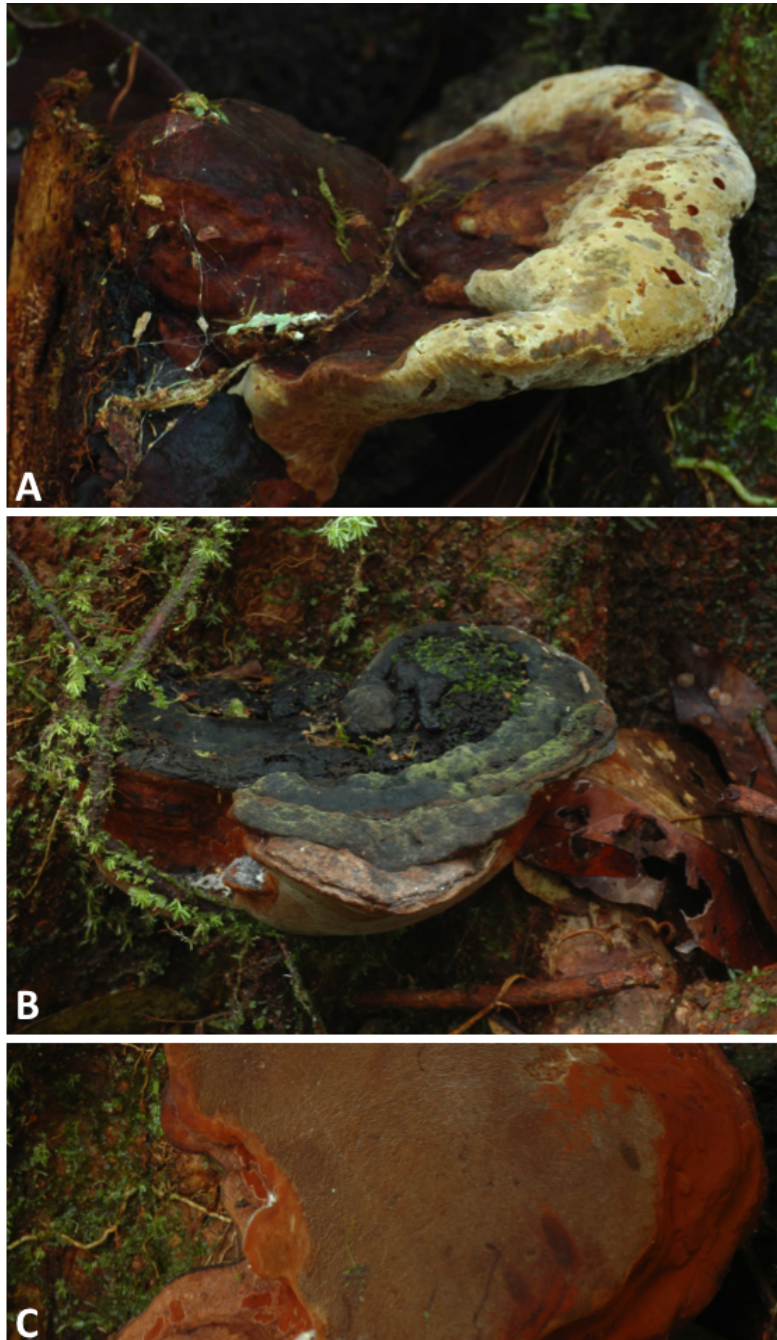


FIG. 4 Basidiomata of *F. pulverulenta* sp. nov. nom. prov. PS19 MUCL54415 *in situ*.

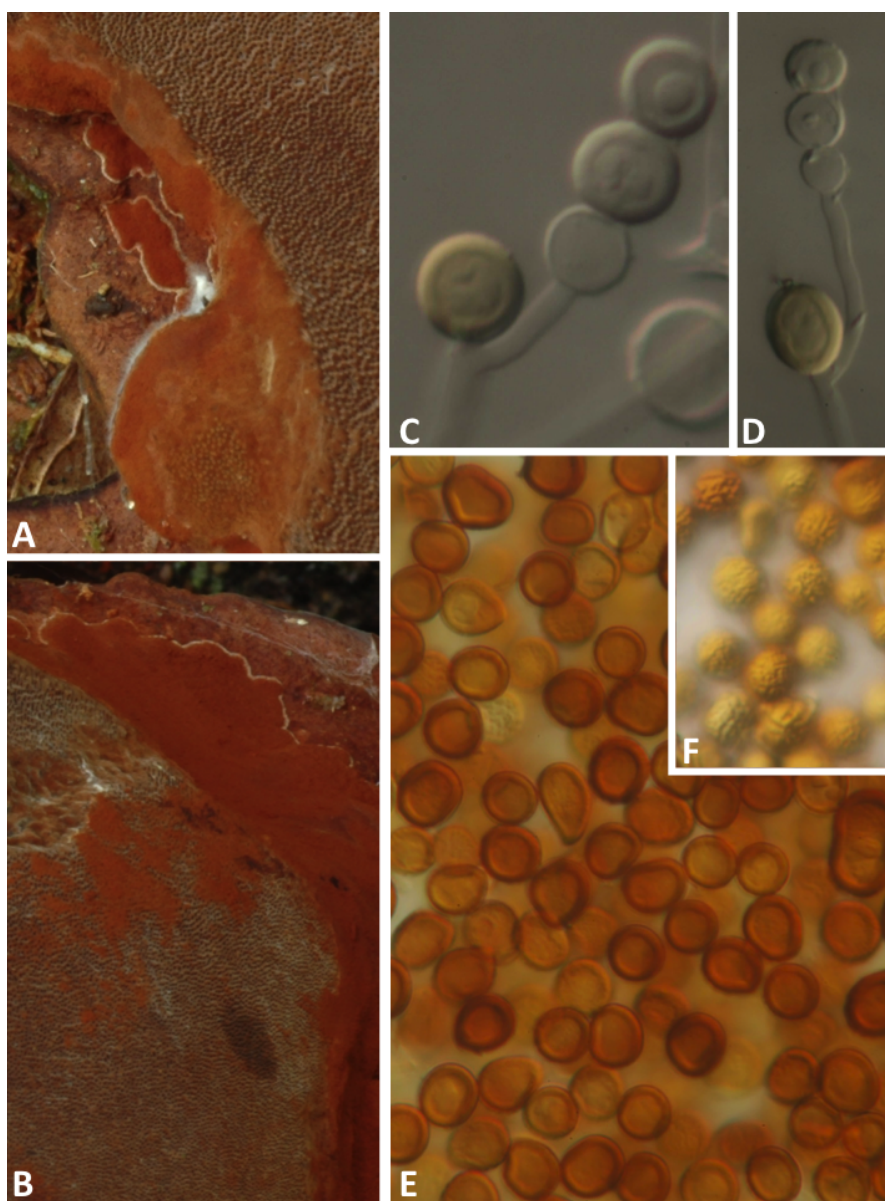


FIG. 5. Microscopical features of *F. pulverulenta* sp. nov. nom. prov. PS19 MUCL54415.

CHAPTER I

***Fomitiporia* (Hymenochaetales) in sub-Saharan Africa: Morphology and Multilocus phylogenetic analysis evidence three undescribed species from the Guineo-Congolian rainforest.**

In this paper for the first time the global phylogeographic structure of the genus *Fomitiporia* is evidenced by a multilocus phylogenetic analysis. We mainly discuss the Paleotropical (African) phylogenetic lineages of *Fomitiporia*. The occurrence of elements phylogenetically linked to the Mediterranean area in the East African mountains is also discussed.

Three new species from Guineo-Congolian phytogeographic region were described. (*Fomitiporia nobilissima* sp. nov., *F. gabonensis* sp. nov. and *F. ivindoensis* sp. nov.) . A new combination (*Fomitiporia apiahyna*) is proposed. The elongation factor 1 alpha (as well as the three introns present) was confirmed to be a remarkably useful marker for phylogenetic studies in *Fomitiporia*.

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***Fomitiporia* in sub-Saharan Africa: morphology and multigene phylogenetic analysis support three new species from the Guineo-Congolian rainforest.**

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Abstract: *Fomitiporia nobilissima* sp. nov., *F. gabonensis* sp. nov., and *F. ivindoensis* sp. nov., three species from the rainforest of the Guineo-Congolian phytogeographic region in Gabon, are described and illustrated by color pictures. These species share a pileate basidiome, small basidiospores,

and an absence of setae. The critical morphological features that differentiate them are the pileus habit or shape, pore surface color, pore diameter, and possibly their ecology. Each new species forms distinct but closely related clades in phylogenetic analysis of DNA sequences from nuclear ribosomal LSU, ITS, and translation elongation factor 1- α , considered either individually or concatenated. This, along with the occurrence of other species in sub-Saharan Africa and their phylogenetic relationships, are briefly discussed. A key to six species of *Fomitiporia* from sub-Saharan Africa is also provided. The new combination *Fomitiporia apiahyna* is also proposed.

INTRODUCTION

The taxonomy, phylogeny, and biogeography of *Fomitiporia* Murrill are in a state of flux. New species concepts or new taxa emerge continuously from what was considered as the *F. punctata*³ –*robusta* complex. Both names represent “collective” species that encompass a complexity greater than presumed (Dai and Cui 2005, Dai et al 2001, 2008, Decock et al 2005, 2007, Fischer 2002, Fischer and Binder 2004, Fischer et al 2005).

Efforts to understand the diversity within this complex have been particularly notable in Europe, especially in its southern and Mediterranean areas (Bernicchia 1990, David et al 1982, Fischer 2002, Pieri and Rivoire 2000), temperate and tropical America (Decock et al 2007, Fischer and Binder 2004, Urcelay et al 2000), and China (Cui and Dai 2008, Dai and Cui 2005, Dai and Zang 2002, Dai et al 2001, 2008). These areas have been continuously monitored revealing a certain local endemism.

Tropical Africa has been variably surveyed. Central Africa or, in biogeographical terms, the Guineo-Congolian phytogeographic region (or the Guineo-Congolian regional center of endemism, White 1979, 1983),

remains poorly investigated (Ryvarden 2000). Only *F. punctata* sensu lato is reported from this vast area of high biological diversity (Douanla-Meli 2007, Roberts and Ryvarden 2006, Ryvarden and Johansen 1980). Eastern Africa, mainly the Afromontane region (White 1979, 1983), has been better studied and, in addition to *F. punctata* s.l., six other species (either *Fomitiporia* or *Phellinus* of the *Fomitiporia* alliance) have been reported locally: *F. aethiopica*, *F. pseudopunctata*, *F. robusta*, *F. sublaevigata*, *F. tenuis*, and *P. apiahynus* (Decock et al 2005, Ipulet 2007, Niemelä in Härkönen et al 2003, Renvall and Niemelä 1993, Ryvarden and Gilbertson 1994, Ryvarden and Johansen 1980). In southern Africa, Fischer (2006) established that some isolates originating from esca diseased grapevine represent also a *Fomitiporia* species.

In the framework of taxonomic and phylogenetic studies of *Fomitiporia* (Decock et al 2005, 2007), specimens originating from the western edge of the Guineo-Congolian region in Gabon were critically studied. Morphological and multigenic phylogenetic studies proved to be concordant, and established the existence of three distinct species sharing pileate basidiomes, small basidiospores, and absence of setae. These three species could not be identified as any known taxa and are here described as new. Their phylogenetic affinities and reports of other *Fomitiporia* in Africa are critically discussed.

Materials and methods

Material.— Herbarium specimens are preserved at LBV, MUCL, and NY (herbarium acronyms are according to Thiers (continuously updated)). Living cultures are preserved at MUCL with the type strains of the new taxa deposited at the CBS. Original strains were isolated from basidiome tissue during fieldwork on malt extract agar with 2 ppm benomyl (benlate) and 50

ppm chloramphenicol and later purified in the laboratory in the case of persistent bacterial contamination.

Collection localities.— Materials were collected in the Northern and Northeastern areas of the Ipassa Makokou Biosphere Reserve (IM, 00°30' N – 012°46' E, elev 500 m), the areas surrounding the Kinguele hydroelectric station (about 00°26-27' N – 010°16' E, elev 80–220 m) at the Monts de Cristal National Park (MC), and La Mondah protected area (about 00°34' N – 009°20' E, elev 0–40 m). These forests belong to the Guineo-Congolian phytogeographic region, and more specifically to the lower Guinea sub-region (Vandeweghe 2005, 2006, White 1979, 1983), although the Northern and Northeastern areas of IM are influenced to some extent by the Congolian sub-region (Vandeweghe 2006). The La Mondah protected area is a hyper humid (precipitation > 3500 mm/year) littoral forest of the lower Guinea sub-region (Vandeweghe 2005).

Morphology and anatomy.— Basidiomes colors are described according to Kornerup and Wanscher (1981). Basidiome sections were examined in Melzer's reagent, lactic acid Cotton blue (Kirk et al 2001), and 4% KOH. All microscopic measurements were done in Melzer's reagent. In presenting the size range of the microscopic elements, 5% of the measurements were excluded from each end and are given in parentheses. ave = arithmetic mean, Q = ratio of length/width of basidiospores and ave-Q = arithmetic mean of the ratio Q. Thirty basidiospores were measured from each specimen.

Sequencing.— DNA extraction, amplification and sequencing of the nuclear ribosomal 5' end of the LSU and ITS regions (including 5.8S) are described in Decock et al (2007). For *tef1*, a fragment located between exons 4 and 8 (Wendland and Kothe 1997) was amplified using the primer pair 983F and 2218R (Rehner and Buckley 2005). A touchdown PCR was used

with an initial annealing temperature of 60 C following Rehner and Buckley (2005). Successful PCR reactions resulted in a single band observed on an 0.8% agarose gel, corresponding to approximately 1200 bp. Sequencing reactions were performed using CEQ DTCS Quick Start Kit® (Beckman Coulter), according to the manufacturer's recommendations, with the primers LROR, LR3, LR3R, LR5 for the LSU; ITS1, ITS2, ITS3, ITS4 for the ITS (<http://biology.duke.edu/fungi/mycolab/primers.htm>); and 2212R, 1953R, 983F, 2218R for *tef1* (Rehner and Buckley 2005, Matheny et al 2007).

TABLE I. List of species, collections, and sequences used in the phylogenetic analyses.

Genus / Species names number		GenBank accession		
Voucher specimens / cultures reference	Locality	nLSU	ITS	<i>tefl-α</i>
<i>Fomitiporia aethiopica</i> Decock, Bitew & G. Castillo				
MUCL 44777 (T)	Ethiopia	AY618204	GU478341	GU461893
MUCL 44806	Ethiopia	AY618202	GU461944	GU461892
<i>F. apiahyna</i> (Speg.) Amalfi, Robledo & Decock				
MUCL 51451	Ecuador	GU461997	GU461963	GU461896
MUCL 51485	Ecuador	GU461996	GU461962	GU461895
MUCL 51474	Ecuador	GU461995	GU461961	GU461894
<i>F. australiensis</i> Fischer, Edwards, Cunningt. & Pascoe				
VPRI 22859 = MUCL 49406 (PT)	Australia	GU462001	AY624997	GU461897
<i>F. bannaensis</i> Y.C. Dai				
MUCL 45926	Thailand	EF429217	GU461942	GU461898
MUCL 46950	China	EF429218	GU461943	GU461899
<i>F. dryophila</i> Murrill				

CFMR-TJV-93-234 = MUCL 46380	USA	EF429219 EF429238	GU461900
CFMR-TJV-93-259 = MUCL 46381	USA	EF429220 EF429239	GU461901
CFMR-TJV-92-232 = MUCL 46379	USA	EF429221 EF429240	GU461902
<i>F. erecta</i> (A. David, Dequatre & Fiasson) Fiasson			
MUCL 49871	France	GU461976GU461939	GU461903
<i>F. gabonensis</i> Amalfi & Decock			
MUCL 47576 (T)	Gabon	GU461990GU461971	GU461923
MUCL 51291	Gabon	GU461986 GU461967	GU461924
MUCL 51302	Gabon	GU461988 GU461969	GU461925
MUCL 51178	Gabon	GU461989 GU461970	GU461926
MUCL 51301	Gabon	GU461987 GU461968	GU461922
<i>F. hippophaeicola</i> (H. Jahn) Fiasson & Niemelä			
MUCL 31746	Belgium	AY618207 GU461945	GU461904
MUCL 31747	Belgium	GU461977 GU461946	GU461905
<i>F. ivindoensis</i> Decock, Amalfi & Yombiyeni			
MUCL 51311	Gabon	GU461979 GU461952	GU461907
MUCL 51312 (T)	Gabon	GU461978 GU461951	GU461906
<i>F. langloisii</i> Murrill			

CFMR-FP-94347-R = MUCL 46375	USA	EF429225	EF429242	GU461908
MUCL 46165 (= /01-77) (T of <i>F. hesleri</i>)	USA	EF429223	AY340026	GU461909
<i>F. maxonii</i> Murrill				
CRGF182 = MUCL 46017	Cuba	EF429230	EF433559	GU461910
CRGF183 = MUCL 46037	Cuba	EF429231	EF433560	GU461911
<i>F. mediterranea</i> M. Fisch.				
MUCL 38514	Italy	AY618201	GU461953	GU461912
MUCL 45670	France	GU461980	GU461954	GU461913
<i>F. nobilissima</i> Decock & Yombiyeni				
MUCL 51290	Gabon	GU461983	GU461964	GU461919
MUCL 51289 (T)	Gabon	GU461984	GU461965	GU461920
MUCL 47580	Gabon	GU461985	GU461966	GU461921
<i>F. polymorpha</i> M. Fisch.				
MUCL 46166 (= 91-42/3) (PT)	USA	DQ122393	GU461955	GU461914
MUCL 46167 (= 91-42/1) (PT)	USA	EF429233	GU461956	GU461915
<i>F. pseudopunctata</i> (A. David, Dequatre & Fiasson) Fiasson				
MUCL 51325	Czech	GU461981	GU461948	GU461916
<i>F. punctata</i> (Fr.) Murrill				

MUCL 34101	Germany	AY618200	GU461947	GU461917
MUCL 47629	Japan	GU461982	GU461950	GU461918
<i>F. punicata</i> Y.C. Dai, B.K. Cui & Decock				
Cui 23	China	GU461991	GU461974	GU461927
Cui 26	China	GU461992	GU461975	GU461928
<i>F. robusta</i> (P. Karst.) Fiasson & Niemelä				
MUCL 51327	Czech	GU461993	GU461949	GU461929
<i>Fomitiporia</i> “sp.”				
CBS 386.66 = MUCL 46181	Argentina	EF429234	EF433563	GU461930
<i>F. tabaquilio</i> (Urcelay, Robledo & Rajchenb.) Decock & Robledo				
MUCL 46230	Argentina	DQ122394	GU461940	GU461931
MUCL 47754	Argentina	GU461994	GU461941	GU461932
<i>F. tenuis</i> Decock, Bitew & G. Castillo				
MUCL 44802 (T)	Ethiopia	AY618206	GU461957	GU461934
MUCL 49971	Uganda	GU461999	GU461959	GU461933
MUCL 49948	Uganda	GU461998	GU461958	GU461935
<i>Phellinus linteus</i> (Berk. & M.A. Curtis) Teng				
MUCL 47139	Cuba	GU462002	GU461973	GU461936

P. uncisetus Robledo, Urcelay & Rajchenb.

MUCL 46231	Argentina	EF429235	GU461960	GU461937
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MUCL 47061	Argentina	GU462000	GU461972	GU461938
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T, PT = type, paratype.

Phylogenetic analysis.—Forty-seven specimens and cultures representing 23 taxa were included in the phylogenetic analysis. Materials and sequences used in this study are listed in Table I. Nucleotide sequences were automatically aligned with Clustal X (version 2.0.11) (Thompson et al 1997), then manually adjusted as necessary with the text editor in PAUP* (version 4.0b10). *Phellinus uncisetus* was designated as outgroup, following the conclusions reached by Decock et al (2007). Alignments are deposited at TreeBASE (<http://www.treebase.org/treebase/index.html>) under study accession number S2645 and matrix accession number M5074.

Phylogenetic analyzes were performed separately for each gene region and concatenated using maximum parsimony (MP) as implemented in PAUP* version 4.0b10 (Swofford 2003) and Bayesian inference (BI) as implemented in MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003).

For MP analyses gaps were treated as fifth base. The most parsimonious trees (MPT) for each data set were identified using heuristic searches with 1000 random addition sequences, further evaluated by bootstrap analysis, retaining clades compatible with the 50% majority-rule in the bootstrap consensus tree. Analysis conditions were tree bisection addition branch swapping (tbr), starting tree obtained via stepwise addition, steepest descent not in effect, MulTrees effective. A bootstrap support value (BS) above 75% was considered significant.

Models of evolution for Bayesian inference were estimated using the hLRT (hierarchical Likelihood Ratio Test) and AIC (Akaike Information Criterion) as implemented in Modeltest 3.7 (Posada and Crandall 1998). Bayesian analyzes were implemented with two independent runs, each with four simultaneous independent chains for twelve million generations, starting from random trees, and keeping one tree every 1000th generation. All trees sampled after convergence (ave. standard deviation of split frequencies

<0.01 and confirmed using Tracer v1.4 (Rambaut and Drummond 2007)) were used to reconstruct a 50% majority-rule consensus tree (BC) and to calculate posterior probabilities. The Bayesian posterior probability (BPP) of each node was estimated based on the frequency at which the node was resolved among the sampled trees with the consensus option of 50% majority-rule (Simmons et al 2004). A BPP above 0.95 was considered significant.

To detect topological conflicts among data partitions, the nodes between the majority-rule consensus trees obtained in the MP analysis from the individual data sets were compared. Paired trees were examined for conflicts only involving nodes with BS > 70% (Lutzoni et al 2004, Mason-Gamer and Kellogg 1996, 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 on the rival trees. Each locus in the combined data set was tested for all possible pairwise comparisons prior to inclusion.

RESULTS

Sequences data and analysis statistics are given in Table II.

DNA sequence comparisons.— The 5' region of the nLSU gene including the D1, D2 and D3 domains ranged between 872 and 875 bp. The overall length of the ITS-5.8S regions of our African collections ranged from 748–751 bps. This agrees with previously published data of the length of *Fomitiporia* ITS-5.8S regions, which ranges from 702 (*F. langloisii*, Decock et al 2007) to 749 nucleotide positions (*F. polymorpha*, Fischer and Binder 2004). Thirty characters judged too ambiguous to be aligned were excluded from further analysis. Amplicons ranging 1163–1172 bps were obtained from the partial *tef1* gene of our collections. This region appears to contain

three clade specific, confidently alignable introns; therefore no positions were excluded from the analysis.

The final DNA sequence alignments resulted in 903 characters including gaps for the LSU gene (47 positions being variable parsimony-uninformative, 89 parsimony-informative), 788 characters for the ITS dataset (105 positions being variable parsimony-uninformative, 322 parsimony-informative) and 1200 for the *tefl* region (100 being variable parsimony-uninformative, 290 parsimony-informative).

TABLE II. Summary of datasets of ITS rDNA, nLSU rDNA, and *tefl*

Properties	Dataset					
	ITS	nLSU	<i>tefl</i> 1st	<i>tefl</i> 2nd	<i>tefl</i> 3rd	<i>tefl</i> introns
Number of strains	47	47	47	47	47	47
Model selected	HKY + G	GTR + I + G	F81 + I + G	F81	GTR + G	HKY + I + G
Likelihood score	-3760.6226	-2403.2512	-651.4979	-520.4449	-2334.7529	-1446.7094
Base frequencies (A,C,G,T)	0.2630,	0.2559,	0.2863,	0.3144,	0.1189,	0.2504,
	0.2026,	0.2054,	0.1997,	0.2491,	0.3401,	0.2056,
	0.2073,	0.3046,	0.3627,	0.1606,	0.2514,	0.1628,
	0.3271	0.2341	0.1513	0.2759	0.2896	0.3812
Proportion of invariable sites	0	0.5703	0.8282	0	0	0.1461
Gamma shape	0.4204	0.5589	1.0190	0	1.1409	37.6521

Individual dataset comparisons.— Heuristic MP searches for nLSU, ITS, and *tefl* dataset considered individually yielded respectively four (202 steps long; CI = 0.767, RI = 0.868), three (962 steps long; CI = 0.873, RI = 0.873), and 16 (782 steps long; CI = 0.680, RI = 0.843) equally MPTs. All these MPTs, more specifically in the *tefl* and ITS analyses, exhibited very similar overall topology, at least for the clades with significant BS and BPP and differ essentially for some intra-species relationships. Moreover, for each dataset the strict consensus tree of the MPTs retains the same overall topology as the majority-rules consensus tree obtained in the corresponding BI. Sequences data and analysis statistics for each dataset and combined analysis are given in Table II. By comparing MP bootstrap tree topologies obtained for the ITS, nLSU, and *tefl* datasets, we did not found any conflicts involving significantly supported nodes, therefore the three datasets were combined.

Combined dataset analysis.— Thirty missing and ambiguous characters were excluded from the analysis of the combined dataset. Of the remaining 2861 characters, 251 variable characters were parsimony-uninformative and 574 characters were parsimony-informative.

The heuristic search produced 16 equally most parsimonious trees (1528 steps long; CI = 0.693, RI = 0.841), but one main topology that is highly concordant with the trees obtained by the individual data set and almost identical to the BC tree (Fig. 1).

The results of the phylogenetic inferences, independent of the three data sets analyzed individually (trees not shown) or combined (Fig. 1), are highly congruent, both under the parsimony hypothesis and the Bayesian inference. Several well-supported clades are resolved by the different analyses, although the relationships between these clades remain uncertain, the deeper internodes, in all topologies, being poorly supported whatever the analyses.

The clades include a neotropical clade, as evidenced by Decock et al (2007), to which the type of *Fomitiporia* (*F. langloisii*) belongs (Fig.1 clade A). A clade (Fig.1 clade B) with species originating from the temperate area of the northern hemisphere (*F. punctata* and *F. robusta*), the Mediterranean area (*F. erecta*, *F. pseudopunctata*, *F. mediterranea*), high elevation eastern Africa (*F. aethiopica*), western North America (*F. polymorpha*), and western Asia (*viz. F. punicata*) is also constantly retained although with variable support; it is very well supported in phylogenetic inferences based on *tef1* (tree not shown) and combined sequences data set (Fig. 1), and at a lower degree, in the LSU based inference (tree not shown).

Each of the inferences also resolved a moderately to well-supported clade (BS and BPP, depending on the data set used, ranging from 57 [nLSU dataset] to 100 % [ITS, *tef1*, and combined dataset]) comprising several

pileate collections from the Gabonese lowland rainforest (Fig.1 clade C). So far, this clade remains isolated but is notably distantly related to all other *Fomitiporia* species as yet reported from Africa (Decock et al 2005, Härkönen et al 2003, Ryvar den and Johansen 1980) or elsewhere, and for which sequences are known (Fig. 1). Considered individually or concatenated, all phylogenetic inferences also revealed an internal structure within this African clade, and concordantly and confidently resolved three well-supported, terminal sub-clades (Fig. 1).

Subsequent morphological examinations of the various collections pertaining to each of these three sub-clades showed combinations of morphological features unique to and characteristic of each, thereby defining three morphological types. The critical morphological features that differentiate them are the pileus habit and shape, pore surface color, and diameter of the pores (or number of pores per mm). These three species have no setae and share small basidiospores, which, on average, ranges between about $4.7\text{--}4.9 \times 4.1\text{--}4.3 \mu\text{m}$, among the smallest in the genus. We therefore concluded that these three morphotypes / clades represent three distinct species, described below as *F. nobilissima*, *F. gabonensis*, and *F. ivindoensis*.

key to *Fomitiporia* species in sub-Saharan Africa

- 1 Basidiospores $6.5\text{--}8 \mu\text{m}$ long, average $\geq 7 \mu\text{m}$2
 - 1' Basidiospores $4.0\text{--}6.0 \mu\text{m}$ long, average $\leq 5.5 \mu\text{m}$ long.....3
 - 2 Basidiome pileate, rounded to triquetrous.*F. robusta*
 - 2' Basidiome resupinate, cushion-shaped*F. aethiopica*
- Both species are known only from eastern dry mountain forest;

Fomitiporia pseudolaevigata (Niemelä in Härkönen et al 2003) is keyed out here as *F. aethiopica*.

- 3 Basidiome resupinate, thin, effused; hymenial setae always present; basidiospores 4.8–6.0 x 4.3–5.5 µm, ave = 5.3 x 4.9 µm; reported from humid forests of Central and East Africa..... ***F. tenuis***
- 3' Basidiome pileate or cushion-shaped; hymenial setae absent; known so far from lowland rainforest of the western edge of central Africa.....4
- 4 Basidiome cushion-shaped.....***F. ivindoensis***
- 4' Basidiome pileate.....5
- 5 Margin broadly rounded; pileus becoming large; reported so far only on *Gilbertiodendron dewevrei*.....***F. nobilissima***
- 5' Margin thin, acute; pileus applanate or obtriquetrous; hosts various.....6
- 6 Basidiome applanate, thin, up to 2 cm thick at the base; pores 8–9 (–10) per mm and honey to pale corky when fresh.....***F. ivindoensis***
F. apiahyna sensu Niemelä (Renvall and Niemelä 1993, Niemelä in Härkönen et al 2003) is keyed out here as *F. ivindoensis*.
- 6' Basidiome obtriquetrous, thick, 5–8 cm thick at the base; pores 6–7 (–8) per mm and brown to dark brown.....***F. gabonensis***

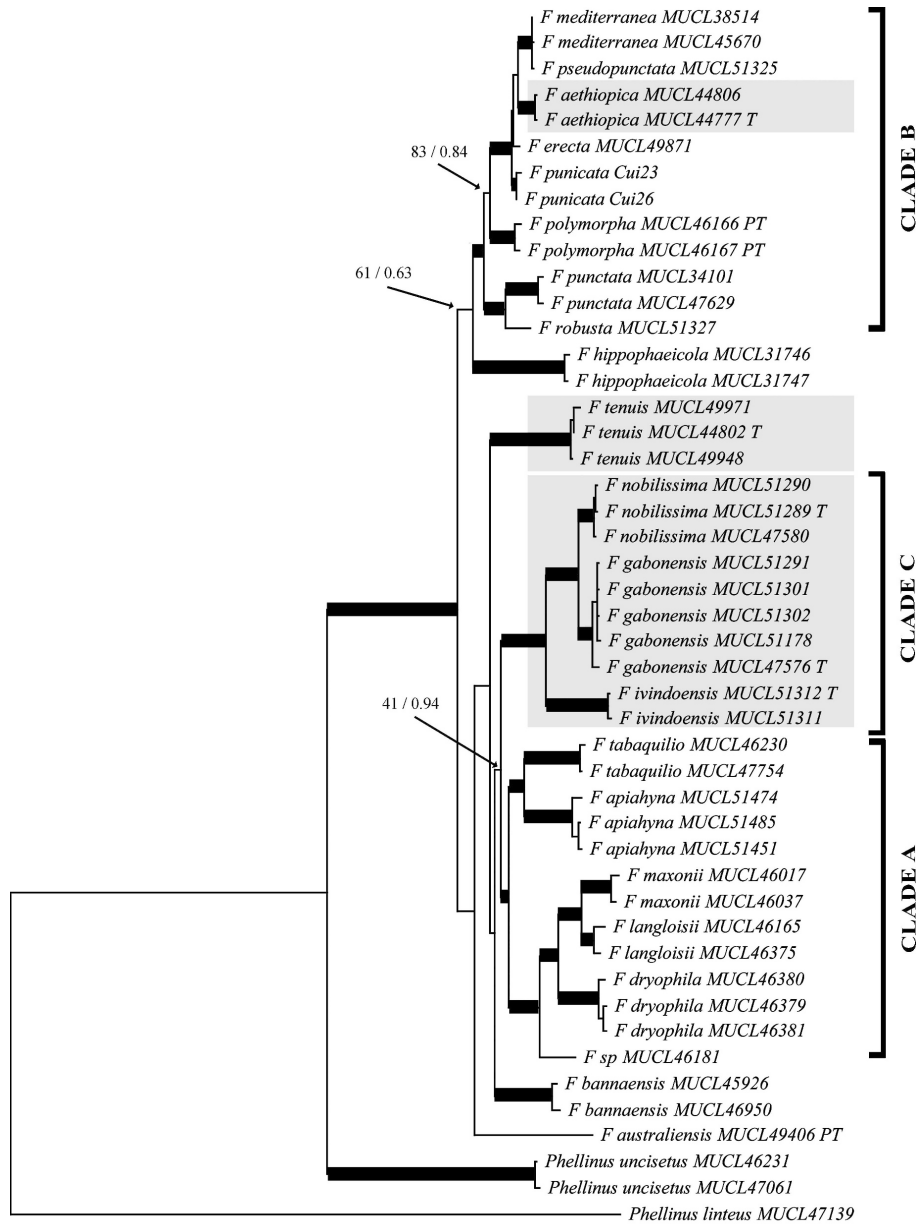


FIG. 1. The 50% majority rule consensus tree from Bayesian inference of the combined nuclear ITS, LSU and *tefl* sequences. Thickened branches in boldface indicate bootstrap support greater than 70% and Bayesian posterior probability greater than 0.95. African taxa are highlighted in shaded boxes (T, type; PT, paratype).

Taxonomy

Fomitiporia nobilissima Decock & Yombiyeni, sp. nov. Figs 2–3.

Mycobank: MB 515697

Basidiomata pileada, ampla, ad 250 mm longa, 300–400 mm lata et ad 110 mm basi crassa; pororum facies fumosa, pori rotundi, (6–) 7 (–8) per mm, (85–) 95–145 (–150) μ m (ave = 112 μ m diam); contextus 35 (–50) mm crassus, brunneus; tubi 35–70 mm crassi, brunnei; systema hypharum dimiticum, hyphae generatoriae hyalinae ad pallide luteae, afibulatae, hyphae skeletales flavo-brunneae, crassitunicatae, aseptatae; setae hymeniales carentes; basidiosporae subglobosae vel globosae, leviter crassitunicatae, hyalinae, adextrinoideae vel leviter dextrinoideae, cyanophileae, (4.0–) 4.3–5.5 (–6.0) $\times$ (3.5–) 3.7–5.0 (–5.0) μ m, (ave = 4.9 $\times$ 4.3 μ m).

HOLOTYPE hic designatus: Gabon, Prov Ogooué-Ivindo: Ipassa Makokou Biosphere Reserve, in a area of the forest dominated by *Gilbertiodendron dewevrei* (00°30,160'N - 012°46,781' E, elev 503 m), about 1.8 m high on a dead standing tree of *G. dewevrei*, about 0.9–1.0 m diam at the base, 2 Apr 2008, leg. C. Decock, P. Yombiyeni, and N. Yao, GA-08/384, MUCL 51289 (Isotype at NY) (culture ex-holotype MUCL 51289, CBS 125873).

Etymology: *nobilissima* refers to the large, remarkable basidiomes.

Basidiomes sessile, pileate, solitary, perennial; *pileus* nodulose at first, soon appanate then mostly thickly appanate (to slightly obtriquetrous in section, semi-circular to broadly attached in polar view, becoming large, projecting up to 250 mm long, 300–400 mm wide, and up to 110 mm thick at the base, heavy when fresh, with a hard, dense, woody consistency, becoming harder on drying, but then breaking easily into pieces; *pileus surface* irregularly tuberculate and concentrically sulcate, rimose with age

and on drying, grayish orange, cork-colored near the margin, soon turning light to dark brown, then almost black for most of the surface, dull and glabrous; *margin* regular, rather thick, obtuse, rounded, whitish to pale creamy when very fresh, pale corky to pale brown on drying; *pore surface* uniform, grayish brown (mainly 6D3–5–6 , café au lait, camel, sunburn, grayish cinnamon); *pores* small, round, regular, (6–) 7 (–8) per mm, (85–) 95–145 (–150) μm diam (ave = 112 μm diam); *dissepiments* thick, thin, agglutinated, (40–) 45–100 (–120) μm thick (ave = 64 μm thick).

Context up to 35 (–50) mm thick, with a densely fibrous texture and woody consistency, mainly brown (6D7-E7, autumn leaf, raw sienna, cognac to cocoa), or more grayish, streaked with white dots or small lines, the hyphae in dense fascicle bending toward, then perpendicular to the pileus surface; *tube layers* 35–70 mm thick, with up to at least 10 individual layers, 3–6 mm thick each, but generally poorly distinguishable, concolorous with the context or paler (6D6-E6, light brown, cinnamon, leather), with a dense fibrous texture and a hard woody consistency, easily broken along the tube layer line when dried.

Hyphal system dimitic in the context and the hymenophoral trama; hyphae sub-parallel in the hymenophoral trama; *generative hyphae* simple-septate, hyaline to pale yellowish, thin- to slightly thick-walled, sparingly branched 1.5–3 μm wide, difficult to find; *skeletal hyphae* identical in both the context and the hymenophoral trama, yellowish brown, unbranched, thick-walled, non-septate (or with occasional secondary septa), 2.0–3.0 μm wide, occasionally locally swellings.

Basidia mature not seen; cystidioles not seen; *basidiospores* globose to subglobose, up to obovoid, thick-walled, hyaline, cyanophilous, undextrinoid to moderately dextrinoid, the reaction more obvious on fresh, not dried basidiospores, with 0–1 guttules, (4.0–) 4.3–5.5 (–6.0) $\times$ (3.5–)

3.7–5.0 (–5.0) μm , (ave = $4.9 \times 4.3 \mu\text{m}$), $Q = 1.05\text{--}1.2$ (–1.3), (ave- $Q = 1.1$); *setae* absent; *chlamydospores* absent; *crystals* rare in the hymenium, rhomboid, of variable size.

Substrate: so far known from dead standing trunk of *Gilbertiodendron dewevrei* (Limballi, Fabaceae), associated with a white rot.

Habitat: Limballi dominated area within the lowland rainforest of the Guineo-Congolian center of endemism.

Additional specimens examined (paratypes): Gabon, Prov Ogooué-Ivindo: Ipassa Makokou Biosphere Reserve, in a *Gilbertiodendron dewevrei* dominating spot (00°30,160' N - 012°46,781' E, elev 503 m), at about 50 cm high on a dead standing tree of *G. dewevrei*, about 1,2 m diam at the base, 12 Apr 2006, C. Decock and N. Yao, GA/06-191 (MUCL 47580, culture ex. 47580); same locality, on a dead standing tree of *G. dewevrei*, about 1 m diam at the base, at about 20 cm above the soil level, 2 Apr 2008, C. Decock, P. Yombiyeni, and N. Yao, GA/08-385 (MUCL 51290, culture ex. 51290).

Fomitiporia gabonensis Amalfi & Decock, sp. nov. Figs 4–6.

Mycobank: MB 515698

Basidiomata pileada, obtriquetra, pilei facies plana vel leviter adscendens, pororum facies valde obliqua, umbrina, pori rotundi, 6–7 (–8) per mm, (85–) 95–125 (–145) μm diam (ave = 107 μm diam); contextus 3–5 mm crassus, brunneus; tubi stratosi, in series ad 10 singula strata, 2–8 mm crassa unaquidque; systema hypharum dimiticum, hyphae generatoriae hyalinae ad pallide luteae, afibulatae, hyphae skeletales flavo-brunneae, crassitunicatae, aseptatae; setae hymeniales carentes; basidiosporae subglobosae vel globosae, leviter crassitunicatae, hyalinae, adextrinoideae vel leviter dextrinoideae, cyanophileae, (4.0–) 4.2–5.3 (–6.0) $\times$ (3.5–) 3.5–4.5 (–4.8) μm , (ave = $4.7 \times 4.1 \mu\text{m}$). *HOLOTYPUS* hic designatus: Gabon, Prov Ogooué-Ivindo: Ipassa Makokou Biosphere Reserve, research plots

near the station, layon # 1, on the way to the bai of Mekadje (00°30,982' N - 012°47,644' E, elev 483 m), on a dead half-fallen trunk of unidentified angiosperm, 1–1.2 m diam., 1–3 m above soil, 11 Apr 2006, C. Decock and N. Yao, GA/06-179, MUCL 47576 (Isotype at NY) (culture ex-holotype MUCL 47576, CBS 125872).

Etymology: *gabonensis* refers to Gabon, the country of origin.

Basidiomes sessile, pileate, perennial, solitary, imbricate, or (sometimes) laterally fused, sometime in large number over the substrate; *pileus* small to medium sized, projecting 25–75 mm, 70–105 mm wide, and 50–80 mm thick at the base down to 1–2 mm thick at the very margin, sub-applanate when young, soon thickly obtriquetrous in section, with the pileus surface more or less plane or slightly ascending, and the pore surface strongly oblique (descending), semicircular to broadly attached in pole view, with a very hard and dense, woody consistency, the surface roughly concentrically sulcate, with a few rather broad folds and occasionally in between, some very narrow, sharper, and closed ones, light brown (6D6, cinnamon) near the very margin, soon homogeneously dark brown (6E7-F7), cognac, chestnut brown, 7F7), blackish brown (6F3-F4, chocolate brown, negro) up to black; *margin* regular, thin, acute, 1–2 mm thick, grayish orange (5B6, apricot) to light brown (6D6, cinnamon) when very fresh; *pores surface* in brown shade, light brown near the margin (6D6–7, cinnamon to raw sienna), to brown or dark brown (mainly 6E5–E7, 6F5, more grayish in older parts (6C6, caramel brown); *pores* small, round, regular, 6–7 (–8) per mm, (85–) 95–125 (–145) μm diam (ave = 107 μm diam); *dissepiments* thin to thick, agglutinated, (25–) 35–95 (–120) μm thick (ave = 58 μm thick).

Context reduced to a thin layer between the pileus surface and the tube layer, 3–5 mm thick, golden brown near the margin, soon dark brown (6E7,

cocoa brown), sometimes separated from the tube layer by an almost black line, consistency woody hard, texture densely fibrous; *tube layers* multiple, with up to 10 individual layers, 2–8 mm thick each, totaling up to 70 mm, often separated from each other by a thin layer of flesh or also by a thick dark, black line, grayish brown to light brown near the pore mouths (6D4–D7, camel, sunburn, cinnamon) discoloring progressively to dark brown (6D7, cocoa brown) towards the context, with a densely fibrous texture and a hard woody consistency; in the collections examined the context and older layers of tube are constantly eaten by the same, unidentified Coleoptera making large galleries.

Hyphal system dimitic in the context and the hymenophoral trama; hyphae sub-parallel in the hymenophoral trama; *generative hyphae* simple-septate, hyaline to pale yellowish, thin- to slightly thick-walled, sparingly branched 2.0–3 μm wide, difficult to find; *skeletal hyphae* identical in both the context and the hymenophoral trama, yellowish brown, unbranched, thick-walled, non-septate (1.8–) 2.1–3.0 μm wide; *setae* absent.

Basidia mature not seen; *cystidioles* not seen; *basidiospores* subglobose to globose, up to broadly obovoid, thick-walled, hyaline, cyanophilous, undextrinoid to moderately dextrinoid, the reaction more obvious on fresh, not dried basidiospores, (4.0–) 4.2–5.3 (–6.0) $\times$ (3.5–) 3.5–4.5 (–4.8) μm , (ave = 4.7 $\times$ 4.1 μm), Q = 1.0–1.3 (–1.3), (ave-Q = 1.15); *chlamydospores* absent; *crystals* commonly present in the hymenium, rhomboid, of variable size.

Substrate: so far known from dead, standing or fallen trunk of various angiosperm, associated with a white rot.

Habitat: lowland rainforest of the Guineo-Congolian center of endemism.

Additional specimens examined (paratypes): Gabon, Prov. Estuaire: La Mondah protected area, 00°34,713' N – 009°20,108' E, elev 40 m, on a dead standing trunk of an unidentified angiosperm, about 80 cm. diam, from the base up to 1.7 m high, 04 Apr 2009, *C. Decock*, *P. Yombiyeni*, and *J.-C. Moundza*, GA-09-503 (MUCL 52008); Monts de Cristal National Park, Kinguele hydroelectric central area, 00°26,849' N – 010°16,489' E, elev 151–223 m, on a dead stump of an unidentified angiosperm, about 1.5 m diam, 08 Apr 2009, *C. Decock*, *P. Yombiyeni*, and *J.-Y. Abaga Mekoulou*, GA-09-544 (MUCL); same locality, on a dead standing trunk of an unidentified angiosperm, from soil level up to 2 m high, 08 Apr 2009, *C. Decock*, *P. Yombiyeni*, and *J.-Y. Abaga Mekoulou*, GA/08-554 (MUCL 52017); PROV. Ogooué-Ivindo: Ipassa Makokou Biosphere Reserve, Kongou falls, near the Figet camp (00°17,469' N – 012°34,257' E, elev 487), on a standing living trunk of an unidentified angiosperm, at about 1–1.5 m above soil, 30 Mar 2008, *C. Decock*, *P. Yombiyeni*, and *N. Yao*, GA/08-347 (MUCL 51178, culture ex- MUCL 51178); research plots near the IRET station, layon # 1, starting from the station (00°31,136' N - 012°47,334' E, elev 506 m), on a dead rotten, still standing trunk of an unidentified angiosperm, at about 1 m above the soil, 27 Mar 2008, *C. Decock* and *P. Yombiyeni*, GA/08-312 (MUCL 51301, culture ex- MUCL 51301); GA/08-313 (MUCL 51302 culture ex- MUCL 51302); same data, (00°30,983' N - 012°47,680' E, elev 462 m) near a small tributary, on a dead rotten trunk of an unidentified angiosperm, 03 Apr 2008, *C. Decock* and *P. Yombiyeni*, GA/08-412 (MUCL 51291, culture ex- MUCL 51291).

Fomitiporia ivindoensis Decock, Amalfi et Yombiyeni, sp. nov.

Fig. 7.

Mycobank: MB 515699

Basidiomata pileada, applanada, tenua, ad 20 mm basi crassa, vel valde pulvinata; pororum facies favosa, pori rotundi, 8–9 (–10) per mm, (60–) 68–105 (–125) μm diam (ave = 85.1 μm diam); contextus 3–4 mm crassus, atrorubiginosus; tubi stratosi, in series ad 5–6 singula strata, 1.5–3 mm crassa unaquidque, favosa vel atrorubiginosa; systema hypharum dimiticum, hyphae generatoriae hyalinae ad pallide luteae, afibulatae, hyphae skeletales flavo-brunneae, crassitunicatae, aseptatae; setae hymeniales carentes; basidiosporae subglobosae vel globosae, leviter crassitunicatae, hyalinae, adextrinoideae vel leviter dextrinoideae, cyanophileae, (4.2–) 4.4–5.5 (–5.5) $\times$ (3.5–) 3.9–4.7 (–5.0) μm , (ave = 4.8 $\times$ 4.3 μm).

HOLOTYPUS hic designatus: Gabon, Prov. Ogooué-Ivindo: Ipassa Makokou Biosphere Reserve (00°30,207' N - 012°47,647' E, elev 486 m), on a dead fallen trunk, 1 m diam, still very hard, unidentified angiosperm, 01 Apr 2008, C. Decock and P. Yombiyeni, GA-08/366, MUCL 51312 (Isotype at NY) (culture ex-holotype MUCL 51312, CBS).

Etymology: *ivindoensis* refers to geographical origin, the Ivindo National Park.

Basidiomes sessile, cushion-shaped to strictly pileate, perennial; *cushion-shaped basidiome* projecting downward, ellipsoid to circular or irregular in outline when several individual basidiome are laterally fused, up to 200 mm in the longest size, 150 in the widest, 30 mm thick at the centre, the margin strongly indurate, densely and narrowly concentrically sulcate, brown near the pore surface (7E6–E7, rust brown, hazel), then dark brown (7F7) to almost black (7F4–F7); *pileate basidiome* solitary, applanate, thin, semi-circular (broadly attached), projecting up to 70 mm, 95 mm wide, up to 22 mm thick at the base, down to 1.5 mm at the very margin, with a hard woody and dense consistency, densely and narrowly concentrically sulcate

with numerous low but well delimited concentric rings, brown near the margin (7E6–E7, rust brown, hazel), soon dark brown (7F7) then almost black (dark grayish black (7F4–F7), the all pileus dull and glabrous; *margin* regular, thin, acute, pale, grayish orange (5B5) when fresh, drying brown (7E6–E7), brown, rust brown, hazel); *pore surface* honey-colored when fresh and actively growing (golden brown, 5B4-5 or 5C4-5), light brown on drying (6D6–D7), cinnamon to grayish cinnamon), slightly glancing with light; *pores* very small, round, regular, 8–9 (–10) per mm, (60–) 68–105 (–125) μm diam (ave = 85 μm diam); *dissepiments* thin to thick, agglutinated, (25–) 30–66 (–85) μm thick (ave = 47 μm thick).

Context reduced to a thin layer, 3–4 mm thick, dark reddish brown (7E6, dark copper brown), very hard, and densely fibrous, azonate; *tube layers* stratified, with 5 (–6) layers, each 1.5–3 (–4) mm thick, totaling up to 16 mm thick, (poorly) distinguishable, the younger layers concolorous with the pore surface, discoloring progressively toward the context to dark reddish brown, with a dense fibrous texture and a hard woody consistency.

Hyphal system dimitic in the context and the hymenophoral trama; hyphae sub-parallel in the hymenophoral trama; *generative hyphae* simple-septate, hyaline to pale yellowish, thin- to slightly thick-walled, sparingly branched 1.8–3 μm wide, difficult to find; *skeletal hyphae* identical in both the context and the hymenophoral trama, yellowish brown, unbranched, thick-walled, non-septate (or with occasional secondary septa), 2.3–3.2 μm . *Basidia* mature not seen; *cystidioles* not seen; *basidiospores* subglobose to globose, up to broadly obovoid, thick-walled, hyaline, cyanophilous, variably but distinctly dextrinoid, the reaction more obvious on fresh basidiospores, (4.2–) 4.4–5.5 (–5.5) $\times$ (3.5–) 3.9–4.7 (–5.0) μm , (ave = 4.8 $\times$ 4.3 μm), $Q = 1.0\text{--}1.2$ (–1.4), (ave- $Q = 1.13$); *setae* absent in all parts of the

basidiome; *cystidioles* not seen; *chlamydospores* absent; *crystals* rare in the hymenium, rhomboid, of variable size;

Substrate: so far known from dead, standing or fallen trunk of angiosperm, associated with a white rot.

Habitat: lowland rainforest of the Guineo-Congolian center of endemism.

Additional specimen examined (paratype): Gabon, Prov. Ogooué-Ivindo: Ipassa Makokou Biosphere Reserve (00°30,207' N - 012°47,647' E, alt. 486 m), on a dead fallen trunk, 1 m diam, still very hard, unidentified angiosperm, 01 Apr. 2008, C. Decock and P. Yombiyeni, GA-08/365 (MUCL 51311, culture ex- MUCL 51311, CBS 125871).



FIGS. 2–7. Basidiomata in situ. 2–3. *Fomitiporia nobilissima*; 3. Arrow indicates a white spore print. Bars = 20 cm. 4–6. *Fomitiporia gabonensis*. Bars = 5 cm. 7. *Fomitiporia ivindoensis*. Bar = 5 cm.

DISCUSSION

Fomitiporia nobilissima is remarkable for developing large basidiomes (FIGS. 2, 3) – probably the largest in the genus – with a very dense consistency that makes them heavy. Basidiospores are small (ave = 4.9 x 4.3 µm), slightly to moderately dextrinoid, the reaction being more marked when fresh, slower to develop or fainter on dried material. Setae have not been observed in the collections studied.

All the collected specimens of *F. nobilissima* were growing on dead limbali, *Gilbertiodendron dewevrei*, in an area of forest where this tree dominates. The species was not observed in similar limbali dominated areas in the Dja Biosphere Reserve (02°40'-03°23' N – 12°25'-13°35' E), located approximately 275 km to the north, in eastern Cameroon, during two surveys. It was neither found at IM nor MC, but nor did they harbor its potentially specific host. The possible host relationship (specificity / preference) of *F. nobilissima* / *G. dewevrei* needs to be evaluated; too few data are available for the time being in order to draw any conclusion in this respect. Host specificities / preferences are known in other species of the *Fomitiporia* alliance, e.g., *P. apiahynus* or *F. hippophaeicola* (H. Jahn) Fiasson & Niemelä (Gilbert et al 2002, Ryvarden and Gilbertson 1994) respectively.

The large specimens of *F. nobilissima* recall somewhat *Fulvifomes fastuosus* (Lév.) Bondartseva & S. Herrera or *F. nilgheriensis* (Mont.) Bondartseva & S. Herrera, both reported also from the western edge of Central Africa (Núñez and Daniels 1999, Roberts and Ryvarden 2006, Ryvarden and Johansen 1980, C. Decock, pers. obs.). However, the presence of globose, hyaline, and dextrinoid basidiospores immediately rules out the latter species and their relatives, which have brown basidiospores. When present, a white spore print below the basidiome (FIG. 3), which is

ferruginous brown in *F. fastuosus* and *F. nilgheriensis*, also helps to identify this species *in situ*.

Fomitiporia gabonensis and *F. ivindoensis* are similar. Both have pileate basidiomes, identical basidiospores, and lack setae. They differ in pileus shape: obtriquetrous and thick in *F. gabonensis* (FIGS. 4–6); typically applanate and thin, or cushion-shaped in *F. ivindoensis* (FIG. 7). The pores are (slightly) larger in *F. gabonensis*, 6–7 (–8) per mm (ave = 107 μ m diam) in contrast to 8–9 (–10) per mm (ave = 85 μ m diam) in *F. ivindoensis*. The collections of *F. ivindoensis*, collected actively growing and fertile, had a very pale pore surface when fresh, pale honey, pale corky (FIG. 7), slightly darkening on drying, and much paler than in *F. gabonensis*. These species might have different ecological requirements (different autecology): *F. gabonensis*, for the time being, has been found only on dead, rotten but still standing trees or stumps, from the base up to 2 m high; *F. ivindoensis* has been found on fallen and hard trunks, but not in contact with the soil, growing underside and laterally. More data are necessary to draw more definitive conclusions about their ecology. The collections of *F. gabonensis* studied are also consistently eaten by an unidentified beetle (Coleoptera), a feature not observed in the two collections of *F. ivindoensis*.

Fomitiporia gabonensis was found at the three localities surveyed in Gabon, while *F. ivindoensis* was collected so far only at IM. These forests belong, within the Guineo-Congolian phytogeographic region, to the lower Guinean sub-region although the northern and northeastern areas of IM have characteristics of the Congolian sub-region (Vandeweghe 2006). They are probably more widespread in the rainforest ecosystems of Gabon and neighboring regions but might be rare as is the case for many tropical species (Gilbert et al 2002). So far, we have not found them during two surveys in the Dja Biosphere Reserve (see above).

Among the other species with pileate basidiomes reported from Africa (Decock et al 2005, Härkönen et al 2003, Renvall and Niemelä 1993, Ryvarden and Johansen 1980), *F. gabonensis* and *F. ivindoensis* could be compared to *P. apiahynus sensu* Niemelä (Härkönen et al 2003, Renvall and Niemelä 1993), and, to a lesser degree, to *F. robusta*. *Fomitiporia robusta* differs in having larger basidiospores, reaching 8 µm in length (average length about 7–7.5 µm long, Decock et al 2005), occasional hymenial setae, and a pileus becoming rimose (Decock et al 2005, Ryvarden and Johansen 1980). It has been reported only in sub-Saharan Africa from the high elevation forests of the Gregorian rift (Decock et al 2005, Ryvarden and Johansen 1980). In a phylogenetic perspective (FIG. 1), it belongs to a different, distant clade, and has strong affinities with *F. punctata* and other taxa of the temperate Northern hemisphere (Decock et al 2007, Fischer and Binder 2004).

Fomitiporia ivindoensis is worth comparing to *P. apiahynus sensu* Niemelä (Härkönen et al 2003, Renvall and Niemelä 1993). The African (Tanzania) specimens of *P. apiahynus*, collected on *Ocotea usambarensis* (Lauraceae), were not examined. However, relying on the description provided (op. cit.), both species share a dark, sulcate pileus, absence of setae, and small basidiospores. *Fomitiporia ivindoensis* seemingly differs from *P. apiahynus sensu* Niemelä in having a much paler pore surface, but this could be difficult to evaluate, smaller pores, respectively 8–9 (–10) per mm and 5–7 per mm (fide Niemelä, op. cit.), and smaller basidiospores, respectively (4.2–) 4.4–5.5 (–5.5) × (3.5–) 3.9–4.7 (–5.0) µm and 5.2–6.7 (–7.0) × 4.7–6.1 (–6.2) µm (fide Niemelä, op. cit.). At present, *P. apiahynus sensu* Niemelä is known only from altitude forest of the eastern rift, while *F. ivindoensis* is known from lowland rainforest and also would differ by their ecology.

Additional comments on other species reported from sub-Saharan Africa

Fomitiporia punctata and *F. robusta*.— Both species are reported as cosmopolitan (Gilbertson and Ryvarde 1987, Núñez and Ryvarde 2001, Ryvarde 2004, Ryvarde and Gilbertson 1994, Ryvarde and Johansen 1980). However, literature reports on these species in tropical areas should be taken with caution; for instance, both taxa are in all probabilities absent from sub- to tropical America (Decock et al 2007) where they may be replaced by *F. dryophila* or *F. calkinsii*, for example.

In Africa, *F. punctata* and *F. robusta* are reported either from central regions (Douanla-Meli 2007, Roberts and Ryvarde 2006) and/or eastern areas (Decock et al 2005, Ryvarde and Johansen 1980). It can be reasonably assumed they do not occur in the Guineo-Congolian region. Whether they might occur locally in eastern Africa at higher elevations (Decock et al 2005, Ryvarde and Johansen 1980), as is the case for other fungi occurring otherwise northerly in temperate ecosystems (Degreef et al 2009) remains to be ascertained by molecular data. Collections of *F. punctata* from these areas should be carefully compared to *F. aethiopica* (see below).

F. pseudopunctata.— The species was originally described from southern France (David et al 1982) and is present in southern Europe and the Mediterranean area (Bernicchia 1990, Ryvarde and Gilbertson 1994). In Africa, Ryvarde and Gilbertson (1994) reported the species from Zimbabwe, and presumed it was widespread in eastern areas. Decock et al (2005) and Ipulet (2007) reported it from Ethiopia and Uganda, respectively. Decock et al (2005) also argued on the basis of biogeography that east Africa reports of *F. sublaevigata*, a taxon originally described from Australia

(Buchanan and Ryvarden 1993), might in fact be misidentifications of *F. pseudopunctata*.

Nevertheless, the Ethiopian (Decock et al 2005) and Ugandan (Ipulet 2007) specimens referred to as *F. pseudopunctata* were found to represent *F. aethiopica* (Fig. 1) and *F. tenuis* respectively [UGANDA, KABAROLE DIST: Kibale Nat. Park, Kanyawara K30 red, dead hanging branch, 26 Nov 2001, Ipulet F148 = MUCL 52681; dead trunk of *Milletia dura*, 20 Sep 2002, Ipulet F604; dead trunk, 13 May 2003, Ipulet F1531; Ngogo, 26 Nov 2002, Ipulet F712; KAMWENG DIST: Kanyanchu, 01 Dec 2002, Ipulet F1435]. The reports of *F. sublaevigata* might also represent *F. aethiopica*. Moreover, a collection [ZIMBABWE, EASTERN PROV: Mutare district, Vumba Mts, White Horse Inn, elev 1500 m, 20 Feb 1986, L. Ryvarden 23766] of *F. pseudopunctata* from Zimbabwe also represents *F. tenuis*.

Fomitiporia aethiopica.— The species was described and is so far only known in the dried mountainous forests of western and central Ethiopia at elevations ≥ 2500 m. The presence of setae is variable in the species, and setae-less specimens may be mistaken for *F. punctata*.

Fomitiporia aethiopica shares a clear phylogenetic background with several taxa having either a Mediterranean or eastern Asian distribution, especially the morphological complex *F. pseudopunctata*-*F. mediterranea*-*F. erecta*, and *F. punicata* (Dai et al 2008) respectively. These species form together a very well supported clade in *tefl*, ITS (data not shown), and combined sequences based phylogenetic inferences (Fig. 1). This clade is linked to *F. punctata* and *F. robusta*, as well as *F. polymorpha* known exclusively from western North America.

The occurrence in mountainous east Africa of taxa possibly identical or phylogenetically closely related to species known from Mediterranean or northern temperate areas is plausible. Connections between mountainous

eastern Africa and Mediterranean areas are well documented for plants. Several eastern Afrotropical species have their closest relatives in the Mediterranean or even in temperate areas of the northern hemisphere (Adams et al 1993, Assefa et al 2007, Hedberg 1970, Kerfoot 1975, Koch et al 2006, Smith and Cleef 1988). Biogeographical connections for fungi are less known at the present time (Degreef et al 2009).

Fomitiporia tenuis.— The species was originally described from humid mountainous forests of Ethiopia (Decock et al 2005). It is here reported for the first time in continental Africa from low land rainforests of Cameroon and Gabon, highland forest of Uganda (at about 1500 masl) and Zimbabwe, and in insular Africa from Madagascar.

Sequences from multiple accessions of this species form a clade but its relationship within the genus is unresolved (Fig. 1). Preliminary data also suggests the possible existence of two subclades within the present morphological concept of *F. tenuis*, thus separating collections originating from either lowland or highland forests (pers. obs.) and representing potentially distinct populations/taxa. More data are necessary to confirm these preliminary observations.

Phellinus apiahynus.— This species occurs widely in South America with reports from Brazil to Panama (Gilbert et al 2002, Ryvarden 2004). Both the morphology, especially the globose and dextrinoid basidiospores, and the DNA data (Fig. 1) clearly relate this species to *Fomitiporia* as currently circumscribed (Decock et al 2007, Wagner and Fischer 2001, 2002) [Specimens analyzed: ECUADOR, PROV. NAPO: Yasuni National Park, approx. 00°40' S - 076°23' W, elev. Approx. 190 m, on dead or living trunk or stump of *Ocotea* sp., 24 Jun- 5 Jul 2008, C. Decock and V. Luna, EC-08-01, EC-08-47, EC-08-68 (MUCL 51451, MUCL 51474, MUCL 51485)]; obviously it should be placed there, where it has affinities with

other taxa having pileate / pseudopileate basidiomes that are endemic in the New World, such as *F. tabaquilio* (Fig. 1). Consequently, the new combination *Fomitiporia apiahyna* (Speg.) Robledo, Decock & Rajchenberg comb. nov. (Mycobank: MB 516533) is proposed (basionym: *Fomes apiahynus* Speg., Fuegiani 11: 438, 1889).

Whether the east African collections (Härkönen et al 2003, Renvall and Niemelä 1993) represent *F. apiahyna* s.s. remains to be ascertained. Morphologically, *F. apiahyna sensu* Niemelä differ from *F. apiahyna* s.s. (neotropical collections) in having larger pores (5–7 per mm and 7–8 or 9 per mm, respectively) and (slightly) longer basidiospores (5.2–6.7 (–7.0) μm and 4.6–5.7 μm , respectively (Ryvarden 2004, Rajchenberg and Wright 1987, Wright and Blumenfeld 1984). Phylogenetic inferences (Fig. 1) has also shown that *F. apiahyna* s.s. is distantly related to any other species occurring in Africa for which DNA sequence data are available. No DNA sequence data are available from the Tanzanian specimens, and therefore, do not allow us to determine their phylogenetic relationships. However, phylogenetic inferences of a larger set of *Fomitiporia* species/specimens originating from all the tropical areas (data not shown) would favor the hypothesis of a strong bio-geographical structure within the genus with many local endemics at species or lineage level; so far, there is no species distribution range overlapping between the neotropics and the African paleotropics. From a biogeographical point of view, it would be also surprising to find the same species sharing an amphi-Atlantic distribution (Gilbert et al 2002, Ryvarden 2004)

If the African “*apiahyna*” can be equated to *F. apiahyna* s.s., notwithstanding the morphological differences (see above), it would constitute another lineage for the African *Fomitiporia*.

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LITERATURE CITED

- Adams RP, Demeke T, Abulfatih HA. 1993. RAPD DNA fingerprints and terpenoids: clues to past migrations of *Juniperus* in Arabia and east Africa. *Theor Appl Gen* 87:22–26.
- Assefa A, Ehrich D, Taberlet P, Nemomissa S, Brochmann C. 2007. Pleistocene colonization of afro-alpine ‘sky islands’ by the artic-alpine *Arabis alpina*. *Heredity* 99:133–142.
- Bernicchia A. 1990. Polyporaceae *s.l.* in Italia. Istituto di Patologia Vegetale, Bologna, Italy:1–808.
- Buchanan PK, Ryvarden L. 1993. Type studies in the Polyporaceae 24. Species described by Cleland, Rodway and Cheel. *Aust Syst Bot* 6:215–235.

- Cui BK, Dai YC. 2008. Wood-rotting in eastern China 2. A new species of *Fomitiporia* from Wanmulin Nature Reserve, Fujian Province. *Mycotaxon* 105:343–348.
- Dai YC, Zang M. 2002. *Fomitiporia tibetica*, a new species of Hymenochaetaceae. *Mycotaxon* 83:217–222.
- , Cui BK. 2005. Two new species of the *Hymenochaetaceae* from eastern China. *Mycotaxon* 94:341–347.
- , Zhang M, Zhou T-S. 2001. New and noteworthy species of Hymenochaetaceae from China. *Mycosystema* 20:16–21.
- , Cui BK, Decock C. 2008. A new species of *Fomitiporia* (Hymenochaetaceae, Basidiomycota) from China. *Mycol Res* 112:375–380.
- David A, Dequatre B, Fiasson JL. 1982. Two new *Phellinus* with globose, cyanophilous spores. *Mycotaxon* 14:160–174.
- Decock C, Bitew A, Castillo G. 2005. *Fomitiporia tenuis* and *Fomitiporia aethiopica* (Basidiomycetes, Hymenochaetales), two undescribed species from the Ethiopian Highlands: taxonomy and phylogeny. *Mycologia* 97:124–132.
- , Herrera Figueroa S, Robledo G, Castillo G. 2007. *Fomitiporia punctata* (Basidiomycota, Hymenochaetales) and its presumed taxonomic synonyms in America: taxonomy and phylogeny of some species from tropical / subtropical area. *Mycologia* 99:733–752.
- Degreef J, Fischer E, Sharp C, Raspé O. 2009. African *Morchella crassipes* revealed by analysis of nr DNA ITS. *Nov Hedw* 88:11–22.

Douanla-Meli C. 2007. Fungi of Cameroon. Ecological diversity with emphasis on the taxonomy of non-gilled Hymenomycetes from the Mbalmayo Forest Reserve. *Biblioth Mycol* 202:1–410.

Fischer M. 2002. A new wood-decaying Basidiomycetes species associated with Esca of grapevine: *Fomitiporia mediterranea* (Hymenochaetales). *Mycol Progress* 1:315–324.

———. 2006. Biodiversity and geographic distribution of Basidiomycetes causing esca-associates white rot in grapevine: a worldwide perspective. *Phytopath Mediterr* 45:S30–S42.

———, Binder M. 2004. Species recognition, geographic distribution, and host-pathogen relationships: a case study in a group of lignicolous Basidiomycetes, *Phellinus s.l.* *Mycologia* 96:799–811.

———, Edwards J, Cunnington JH, Pascoe IG. 2005. Basidiomycetous pathogens on grapevine: a new species from Australia – *Fomitiporia australiensis*. *Mycotaxon* 92:85–96.

Gilbert SG, Ferrer A, Carranza J. 2002. Polypore fungal diversity and host density in a moist tropical forest. *Biodivers Conserv* 11:947–957.

Gilbertson RL, Ryvarden L. 1987. North American Polypores. Part 2. *Megasporoporia – Wrightoporia*. *FungiFlora*, Oslo, Norway:433–885.

Härkönen M, Niemelä T, Mwasumbi L. 2003. Tanzanian mushroom – edible, harmful, and other fungi. Botanical Museum, Finnish Museum of Natural History, Helsinki, Finland:1–200.

Hedberg O. 1970. Evolution of the Afroalpine flora. *Biotropica* 2:16–23.

Ipuleet P. 2007. Ecology and Diversity of Pore Fungi (Aphyllophorales) in Bwindi Impenetrable and Kibale National Parks, Albertine Rift, Western Uganda [Doctoral dissertation]. Makerere University, Kampala, Uganda.

Kerfoot O. 1975. Origin and speciation of the Cupressaceae in Sub-Sahara Africa. *Boissiera* 24:145–150

Kirk PM, Cannon PF, David JC, Stalpers JA. 2001. Ainsworth & Bisby's Dictionary of the Fungi, 9th edition. CABI Publishing, Wallingford, UK:1–655.

Koch M, Kiefer C, Ehrich D, Vogel J, Brochmann C, Mummenhoff K. 2006. Three times out of Asia Minor: the phylogeography of *Arabis alpina* L (Brassicaceae). *Mol Ecol* 15:825–839.

Kornerup A, Wanscher JH. 1981. Methuen handbook of color, 3rd edition:1–282.

Lutzoni F, Kauff F, Cox CJ, McLaughlin D, Celio G, Dentinger B, Padamsee M, Hibbett D, James TY, Baloch E, Grube M, Reeb V, Hofstetter V, Schoch C, Arnold AE, Miadlikowska J, Spatafora J, Johnson D, Hambleton S, Crockett M, Shoemaker R, Sung G-H, Lücking R, Lumbsch T, O'Donnell K, Binder M, Diederich P, Ertz D, Gueidan C, Hansen K, Harris RC, Hosada K, Lim Y-W, Matheny B, Nishida H, Pfister D, Rogers J, Rossman A, Schmitt I, Sipman H, Stone J, Sugiyama J, Yahr R, Vilgalys R. 2004. Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. *Am J Bot* 91: 1446–1480.

Mason-Gamer RJ, Kellogg EA. 1996 Testing for phylogenetic conflict among molecular data sets in the tribe Triticeae (Gramineae). *Syst Biol* 45:524-545

Matheny PB, Wang Z, Binder M, Curtis JM, Lim YW, Nilsson RH, Hughes KW, Petersen RH, Hofstetter V, Ammirati JF, Schoch C, Langer GE, McLaughlin DJ, Wilson AW, Crane PE, Frøslev T, Ge ZW, Kerrigan RW, Slot JC, Vellinga EC, Liang ZL, Aime MC, Baroni TJ, Fischer M, Hosaka K, Matsuura K, Seidl MT, Vaura J, Hibbett DS. 2007. Contributions of *rpb2* and *tefl* to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Mol Phylogenet Evol* 43:430–451.

Núñez M, Daniëls PP. 1999. Fungi from the Dja Biosphere reserve (Cameroon) II. Polypores. *Mycotaxon* 73:235–246.

———, Ryvarden L. 2001. East Asian Polypores. Vol. 2. Polyporaceae *s. lato*. *Synopsis Fungorum* 14. FungiFlora, Oslo, Norway:166–522.

Pieri M, Rivoire B. 2000. Le genre *Phellinus*. Quelques espèces rares ou critiques en France, avec une clé des espèces du genre *Phellinus s.l.* signalées en Europe occidentale. *Bull Soc Mycol Fr.* 116: 305–331.

Posada D, Crandall KA. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.

Rajchenberg M, Wright JE. 1987. Type studies of Corticiaceae and Polyporaceae (Aphyllphorales) described by C. Spegazzini. *Mycologia* 79:246–264.

Rambaut A, Drummond AJ. 2007. Tracer v1.4, Available from <http://beast.bio.ed.ac.uk/Tracer>

Reeb V, Lutzoni F, Roux C. 2004. Contribution of RPB2 to multilocus phylogenetic studies of the euascomycetes (Pezizomycotina, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory. *Mol Phyl Evol* 32:1036–1060.

Rehner SA, Buckley E. 2005. A *Beauveria* phylogeny inferred from nuclear ITS and EF1-a sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97:84–98.

Renvall P, Niemelä T. 1993. *Ocotea usambarensis* and its fungal decayers in natural stands. *Bull Jard Bot Nat* 62:403–414.

Roberts P, Ryvarden L. 2006. Poroid fungi from Korup National Park, Cameroon. *Kew Bull* 61:55–78.

Ronquist F, Huelsenbeck JP. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.

Ryvarden L. 2000. A critical checklist of African Polypores. In: Associazione Micologica Bresadola (ed), *Micologia duemila*. Fondazione Centro Studi Micologici dell A.M.B., Vicenza, Italy:471–483.

———. 2004. Neotropical polypores 1. *Synopsis Fungorum* 19, FungiFlora, Oslo, Norway:1–229.

———, Johansen I, 1980. A preliminary polypores flora of East Africa. *FungiFlora*, Oslo, Norway:1–636.

———, Gilbertson RL. 1994. European Polypores 2. *Meripilus—Tyromyces*. *Synopsis Fungorum* 7 FungiFlora, Oslo, Norway:392–743.

Simmons MP, Pickett KM, Miya M. 2004. How meaningful are Bayesian support values? *Mol Biol Evol* 21:188–199.

Smith JMB, Cleef AM. 1988. Composition and origins of the world's tropicalpine floras. *J Biogeogr* 15:631–645.

Swofford, D. L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Thiers B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. (1997). The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Res* 25:4876-4882.

Urcelay C, Robledo G, Rajchenberg M. 2000. *Phellinus tabaquilio* sp. nov. from Córdoba mountains, Central Argentina. *Mycotaxon* 76:287–291.

Vandeweghe JP. 2005. Akanda et Pongara. Plages et mangroves. Wildlife Conservation Society, Libreville:1–207.

———. 2006. Ivindo et Mwagna: Eaux noires, forêts vierges et baïes. Wildlife Conservation Society, Libreville:1–272.

Wagner T, Fischer M. 2001. Natural groups and a revised system for the European poroid Hymenochaetales (Basidiomycota) supported by nLSU rDNA sequence data. *Mycol Res* 105:773–782.

———, Fischer M. 2002. Proceedings towards a natural classification of the worldwide taxa *Phellinus* and *Inonotus* s.l., and phylogenetic relationships of allied genera. *Mycologia* 94:998–1016.

Wendland J, Kothe E. 1997. Isolation of *tefl* encoding translation elongation factor EF1a from the homobasidiomycete *Schizophyllum commune*. *Mycol Res* 101:798–

802.

White F. 1979. The Guineo-Congolian region and its relationships to other Phytochoria. *Bull J Bot Nat Belgique* 49:1–384.

White, F. 1983. The vegetation of Africa, a descriptive memoir to accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa (3 Plates, Northwestern Africa, Northeastern Africa, and Southern Africa, 1:5,000,000). Unesco, Paris.

Wright JE, Blumenfeld SN. 1984. New South American species of *Phellinus* (Hymenochaetaceae). *Mycotaxon* 21:413–425.

Footnotes:

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³ Authorships of scientific name listed in TABLE I are not repeated in the text.

⁴ Specimens analyzed: ECUADOR, PROV. NAPO: Yasuni National Park, on dead or living trunk or stump of *Ocotea* sp., 24 Jun.- 05 Jul. 2008, C. Decock and V. Luna, EC-08-01, -47, -68 (MUCL 51451, MUCL 51474, MUCL 51485)

CHAPTER II

***Fomitiporia cupressicola* sp. nov., a parasite on *Cupressus arizonica*, and additional unnamed clades in the southern USA and northern Mexico, determined by multilocus phylogenetic analyses**

In this paper by using a multilocus phylogenetic approach and introducing for the first time our “holistic” species concept, we greatly improve our understanding of the genus. We discuss the Holarctic (North temperate) lineage of *Fomitiporia* as well as the status of the pileate specimens of *Fomitiporia* (*F. robusta* complex) in the USA. *Fomitiporia cupressicola* is described as new, and at least five unnamed terminal clades (phylogenetic species) were evidenced by our integrative approach. We improve the phylogenetic resolution by including partial *rpb2* gene in the analyses and for the first time we dealt with two large indels present in the ITS1 region shared by several species originating from the same phyto-geographic, by recoding them with as binary characters using the Simple Indel Coding method (SIC, Simmons and Ochoterena 2000) and thus avoiding long branch artifacts in the analysis. Furthermore the SIC methods allow us to integrate this evolutionary events in our analysis instead of excluding the ambiguous positions.

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***Fomitiporia cupressicola* sp. nov., parasite on *Cupressus arizonica*, and additional unnamed clades in the southern USA and northern Mexico, evidenced by multilocus phylogenetic analyses.**

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Abstract: *Fomitiporia cupressicola* is described on the basis of several collections originating from a forest at high altitude in the northern part of the western Mexican mountain range (*Sierra Madre Occidental*), found in living *Cupressus arizonica*. The species forms a monophyletic clade, basal

to a larger lineage comprising species originating mainly from temperate to Mediterranean areas of the northern hemisphere. The phylogenetic approach in *Fomitiporia* also revealed multiple unnamed clades within the *F. robusta* complex in the southern USA and northern Mexico, representing potential species. The status of the *F. robusta* complex in North America is briefly discussed.

Key words: *Phellinus sensu lato*, Hymenochaetaceae, polypores, North America, Biogeography.

Introduction

*Fomitiporia*⁴ (Hymenochaetaceae) was commonly segregated into two complexes or morphospecies: the *F. punctata* complex, representing species having resupinate basidiomata; the *F. robusta* complex, for species having pileate basidiomata.

In North America, Gilbertson and Ryvarden (1987) noted that the “*Phellinus robustus* [*F. robusta*] complex is probably the most difficult taxonomic problem in the genus”, with speciation resulting from “adaptation to different substrata and vastly different environmental factors”.

From then on and though still in a state of flux, understanding of the species concepts within the *F. robusta sensu* (American) *auctores* complex has improved; four species have been recognized locally: *F. bakeri*, *F. calkinsii*, *F. polymorpha*, and *F. texana* (Fischer and Binder 2004, Gilbertson and Ryvarden 1987, Larsen and Cobb-Poulsen 1990, Vlasák and Kout 2011). Furthermore, Vlasák and Kout (2011) raised the hypothesis that, *sensu stricto*, *F. robusta* is absent from NA.

However, given that the morphological background is intrinsically poor or poorly discriminative within this complex (Fischer and Binder 2004,

Gilbertson and Ryvarden 1987), delimiting species boundaries by using macro- and/or microscopical features only may prove critical. Other non-morphological descriptors should be integrated in order to circumscribe the species; these now invariably includes DNA sequence but could involve also ecological data such as host relationships or habitat. The importance of ecological features for characterizing taxonomic entities has been variously interpreted within the genus, and more broadly within the Hymenochaetaceae (e.g. Rizzo et al 2003, Tomšovský 2010a, b). Validation is almost case by case. For instance, presumed host specificities within *P. ignarius* or the *P. (Porodaedalea) pini* complexes (Fischer 1994, 1995, Fischer and Binder 1995, Niemelä 1975) were only partially confirmed (Tomšovský 2010a, b). Pieri and Rivoire (2000) also questioned the status and, as a consequence, the host specialization of *F. erecta* (David et al 1982) and *P. juniperinus* (Bernicchia 1990), two *Fomitiporia* (or *Phellinus* of the *Fomitiporia* alliance) species from Mediterranean areas, presumably having different hosts (*Quercus* versus *Juniperus*).

Application of the Phylogenetic Species (PS) concept using the principle of multiple gene genealogy concordance (GC, Taylor et al 2000, 2006) clearly helps to evidence the taxonomic diversity within *Fomitiporia* (e.g. Amalfi et al 2010, Decock et al 2007, Vlasák and Kout 2011). *A posteriori*, it may also validate the pertinence of *questionable* ecological descriptors and do more to circumscribe the (bio)geographical distribution range of the various entities (Tomšovský 2010a, b). Finally, integrating morphological, ecological, biogeographical, and DNA sequence data would yield a more complete (holistic) concept of the species.

During a revision of the taxonomy and analyzing the phylogenetic relationships within *Fomitiporia* in North America, the taxonomic status of several collections found growing on living *Cupressus arizonica*

(Cupressaceae) at high altitudes, in a humid forest of the western *Sierra Madre* range in Mexico was brought into question. These had most of the typical morphological features of *F. robusta* but, in addition to growing on gymnosperm, a multiloci phylogenetic analysis resolved these collections as a quite distinct, monophyletic clade; it was therefore interpreted as belonging to a distinct, undescribed species, proposed below as *Fomitiporia cupressicola*. The phylogenetic affinities of this new taxon and its host relationships (specialization) are discussed.

The phylogenetic approach in *Fomitiporia* also revealed multiple unnamed clades within the *F. robusta* complex in the southern USA and northern Mexico, representing potential species. This and the diversity within the *F. robusta* complex in North America are discussed.

Materials and methods

Material.— Herbarium specimens are preserved at MUCL, ENCB, and NY (herbarium acronyms are according to Thiers 2010). Living cultures are preserved at MUCL with the ex-type strain of the new taxon deposited at the CBS. Original strains were isolated during fieldwork, from basidiome tissues, on malt extract agar with 2 ppm benomyl (benlate) and 50 ppm chloramphenicol and later purified in the laboratory in the case of persistent bacterial contamination.

Collection localities.— Materials were collected in the western mountain range of Mexico (*Sierra Madre Occidental*), Durango State (ca. 23°27'32" N – 104°50'42" W, elev 2000–2900 m). These forests belong to the Mountain Mesoamerican phytogeographic region (Rzedowskii 2006) with *Cupressus arizonica*, *Juniperus deppeana* (Cupressaceae), *Abies duranguensis*, and *Pseudotsuga menziesii* (Pinaceae) as the dominant tree species.

Morphology and anatomy.— Basidiomes colors are described according to Kornerup and Wanscher (1981). Basidiome sections were examined in

Melzer's reagent, lactic acid Cotton blue (Kirk et al. 2001), and 4% KOH. All microscopic measurements were done in Melzer's reagent. In presenting the size range of the microscopic elements, 5% of the measurements were excluded from each end and given in parentheses. Ave = arithmetic mean, Q = ratio of length/width of basidiospores and ave_Q = arithmetic mean of the ratio Q. Thirty basidiospores were measured from each specimen.

Sequencing.— DNA extraction, amplification, and sequencing of the 5' end of the nuclear ribosomal LSU rRNA gene and ITS regions (including 5.8S) and of partial *tefl-α* gene are described in Decock et al (2007) and Amalfi et al (2010). The region located between domains 6 and 7 of the second largest subunit of the RNA polymerase II (*rpb2*) (Frøslev et al 2005, Matheny 2005) was amplified using the degenerate primers bRPB2-6F and bRPB2-7.1R (Matheny 2005). Successful PCR reactions resulted in a single band observed on a 0.8% agarose gel, corresponding to approximately 1200 bp.

TABLE I. List of species, collections, and sequences used in the phylogenetic analyses.

Genus / Species names Voucher specimens / cultures reference	GenBank accession number				
	Locality	nLSU	ITS	<i>tefl-α</i>	RPB2
<i>Fomitiporia aethiopica</i> Decock, Bitew & G. Castillo					
MUCL 44777 (T)	Ethiopia	AY618204	GU478341	GU461893	JQ087956
MUCL 44806	Ethiopia	AY618202	GU461944	GU461892	JQ087955
<i>F. apiahyna</i> (Speg.) Amalfi, Robledo & Decock					
MUCL 51451	Ecuador	GU461997	GU461963	GU461896	JQ087958
MUCL 51485	Ecuador	GU461996	GU461962	GU461895	JQ087957
<i>F. australiensis</i> Fischer, Edwards, Cunningt. & Pascoe					
VPRI 22859 = MUCL 49406 (PT)	Australia	GU462001	AY624997	GU461897	JQ087959
<i>Fomitiporia bakeri</i> (Murrill) Vlasák & Kout					
MUCL 51098	USA	JQ087901	JQ087874	JQ087928	JQ087960
<i>F. bannaensis</i> Y.C. Dai					
MUCL 45926	Thailand	EF429217	GU461942	GU461898	JQ087961
MUCL 46950	China	EF429218	GU461943	GU461899	JQ087962
<i>Fomitiporia calkinsii</i> (Murrill) Vlasák & Kout					

MUCL 51100	USA	JQ087902	JQ087875	JQ087929	JQ087963
MUCL 52346	Mexico	JQ087903	JQ087876	JQ087930	JQ087964
<i>F. cupressicola</i> (PS4) Amalfi, Raymundo, Valenzuela et Decock					
MUCL 52486 (T)	Mexico	JQ087904	JQ087877	JQ087931	JQ087965
MUCL 52488	Mexico	JQ087905	JQ087878	JQ087932	JQ087966
MUCL 52489	Mexico	JQ087906	JQ087879	JQ087933	JQ087967
MUCL 52490	Mexico	JQ087907	JQ087880	JQ087934	JQ087968
<i>F. dryophila</i> Murrill					
CFMR-TJV-92-232 = MUCL 46379	USA	EF429221	EF429240	GU461902	JQ087969
CFMR-TJV-93-234 = MUCL 46380	USA	EF429219	EF429238	GU461900	JQ087970
<i>F. erecta</i> (A. David, Dequatre & Fiasson) Fiasson					
MUCL 49871	France	GU461976	GU461939	GU461903	JQ087971
<i>F. gabonensis</i> Amalfi & Decock					
MUCL 47576 (T)	Gabon	GU461990	GU461971	GU461923	JQ087972
MUCL 51291	Gabon	GU461986	GU461967	GU461924	JQ087973
<i>Fomitiporia cf hartigii</i> (Allesch. & Schnabl) Fiasson & Niemelä					
MUCL 51295	USA	JQ087908	JQ087881	JQ087935	JQ087974
<i>Fomitiporia hartigii</i> (Allesch. & Schnabl) Fiasson & Niemelä					
MUCL 31400	Europe	JQ087909	JQ087882	JQ087936	JQ087975

F. hippophaeicola (H. Jahn) Fiasson & Niemelä

MUCL 31746	Belgium	AY618207	GU461945	GU461904	JQ087976
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MUCL 31747	Belgium	GU461977	GU461946	GU461905	JQ087977
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F. ivindoensis Decock, Amalfi & Yombiyeni

MUCL 51311	Gabon	GU461979	GU461952	GU461907	JQ087978
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MUCL 51312 (T)	Gabon	GU461978	GU461951	GU461906	JQ087979
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F. langloisii Murrill

CFMR-FP-94347-R = MUCL 46375	USA	EF429225	EF429242	GU461908	JQ087980
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MUCL 46165 (T of <i>F. hesleri</i>)	USA	EF429223	AY340026	GU461909	JQ087981
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F. maxonii Murrill

CRGF182 = MUCL 46017	Cuba	EF429230	EF433559	GU461910	JQ087983
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CRGF183 = MUCL 46037	Cuba	EF429231	EF433560	GU461911	JQ087982
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F. mediterranea M. Fisch.

AFTOL ID 688	ND	AY684157	AY854080	AY885149	AY803748
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MUCL 38514	Italy	AY618201	GU461953	GU461912	JQ087984
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MUCL 45670	France	GU461980	GU461954	GU461913	JQ087985
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F. nobilissima Decock & Yombiyeni

MUCL 47580	Gabon	GU461985	GU461966	GU461921	JQ087986
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MUCL 51289 (T)	Gabon	GU461984	GU461965	GU461920	JQ087987
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F. polymorpha M. Fisch.

MUCL 46166 (= 91-42/3) (PT)	USA	DQ122393	GU461955	GU461914	JQ087988
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MUCL 46167 (= 91-42/1) (PT)	USA	EF429233	GU461956	GU461915	JQ087989
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F. PS1

MUCL 51106	New Mexico	JQ087910	JQ087883	JQ087937	JQ087990
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F. PS2

MUCL 51105	Arizona	JQ087911	JQ087884	JQ087938	JQ087991
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F. PS3

MUCL 52350	Mexico	JQ087912	JQ087885	JQ087939	JQ087992
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F. PS5

MUCL 47756	Argentina	JQ087913	JQ087886	JQ087940	JQ087993
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MUCL 47757	Argentina	JQ087914	JQ087887	JQ087941	JQ087994
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MUCL 47758	Argentina	JQ087915	JQ087888	JQ087942	JQ087995
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F. PS6

MUCL FG10282	French Guyana	JQ087916	JQ087889	JQ087943	JQ087996
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F. PS7

MUCL 53009	South Africa	JQ087917	JQ087890	JQ087944	JQ087997
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F. pseudopunctata (A. David, Dequatre & Fiasson) Fiasson

MUCL 51325	Czech	GU461981	GU461948	GU461916	JQ087998
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MUCL 46168	France	JQ087918	JQ087891	JQ087945	JQ087999
<i>F. punctata</i> (Fr.) Murrill					
MUCL 34101	Germany	AY618200	GU461947	GU461917	JQ088000
MUCL 47629	Japan	GU461982	GU461950	GU461918	JQ088001
<i>F. punicata</i> Y.C. Dai, B.K. Cui & Decock					
Cui 23	China	GU461991	GU461974	GU461927	JQ088002
Cui 26	China	GU461992	GU461975	GU461928	JQ088003
<i>F. robusta</i> (P. Karst.) Fiasson & Niemelä					
MUCL 51297	Estonia	JQ087919	JQ087892	JQ087946	JQ088004
MUCL 51327	Czech	GU461993	GU461949	GU461929	JQ088005
<i>Fomitiporia sonora</i> (Gilb.) Y.C. Dai					
MUCL 47689 (T)	Arizona	JQ087920	JQ087893	JQ087947	JQ088006
<i>Fomitiporia</i> “sp.”					
CBS 386.66 = MUCL 46181	Argentina	EF429234	EF433563	GU461930	JQ088007
<i>F. tabaquilio</i> (Urcelay, Robledo & Rajchenb.) Decock & Robledo					
MUCL 46230	Argentina	DQ122394	GU461940	GU461931	JQ088008
MUCL 47754	Argentina	GU461994	GU461941	GU461932	JQ088009
<i>F. tenuis</i> Decock, Bitew & G. Castillo					
MUCL 44802 (T)	Ethiopia	AY618206	GU461957	GU461934	JQ088010

MUCL 49948	Gabon	GU461998	GU461958	GU461935	JQ088011
MUCL 49971	Uganda	GU461998	GU461958	GU461935	JQ088012
<i>Fomitiporia texana</i> (Murrill) Nuss					
MUCL 47690	Arizona	JQ087921	JQ087894	JQ087948	JQ088013
MUCL 51143	Arizona	JQ087922	JQ087895	JQ087949	JQ088014
<i>Fomitiporia torreyae</i> Y.C. Dai & B.K. Cui					
MUCL 47628	Japan	JQ087923	JQ087896	JQ087950	JQ088015
WC31	Chine	JQ087924	JQ087897	JQ087951	JQ088016
<i>Fomitiporia tsugina</i> Murrill					
MUCL 52702	USA	JQ087925	JQ087898	JQ087952	JQ088017
MUCL 52703	USA	JQ087926	JQ087899	JQ087953	JQ088018
<i>Phellinus juniperinus</i> Bernicchia & S. Curreli					
MUCL 51757	Tunisia	JQ087927	JQ087900	JQ087954	JQ088019
<i>P. uncisetus</i> Robledo, Urcelay & Rajchenb.					
MUCL 46231	Argentina	EF429235	GU461960	GU461937	JQ088020
MUCL 47061	Argentina	GU462000	GU461972	GU461938	JQ088021

T, PT = type, paratype.

Sequencing reactions were performed using CEQ DTCS Quick Start Kit® (Beckman Coulter), according to the manufacturer's recommendations, with primers LROR, LR3, LR3R, LR5 for the LSU; ITS1, ITS2, ITS3, ITS4 for the ITS (<http://biology.duke.edu/fungi/mycolab/primers.htm>); 2212R, 1953R, 983F, 2218R for *tefl* (Rehner and Buckley 2005, Matheny et al. 2007); and bRPB2-6F and bRPB2-7.1R (Matheny 2005) for *rpb2*.

Sequences were assembled and edited with Sequencher™ 4.8 software (Gene Codes Corporation, Ann Arbor, MI, U.S.A.).

Phylogenetic analysis.— sixty-eight specimens and cultures representing 36 species (or potential species clades) were included in the phylogenetic analysis. Materials and sequences used in this study are listed in Table I. Nucleotide sequences were automatically aligned with Clustal X (version 2.0.11) (Thompson et al. 1997), then manually adjusted as necessary with the text editor in PAUP* (version 4.0b10). Potentially ambiguously aligned segments were also detected using the Gblocks v0.91b program (Castresana 2000; <http://molevol.cmima.csic.es/castresana/Gblocks.html>) with the settings "allow smaller final blocks", "allow gaps within blocks". The alignment was then visually screened to detect additional ambiguously aligned regions. Alignments are deposited at TreeBASE (<http://www.treebase.org/treebase/index.html>).

Indels present within our data sets, especially in the ITS1 region (Decock et al 2007) were recoded as binary characters using the Simple Indel Coding method (SIC, Simmons and Ochoterena 2000) as implemented in SeqState software (Müller, 2005).

Phylogenetic analyzes were performed separately for each gene region and concatenated using maximum parsimony as implemented in PAUP* version 4.0b10 (Swofford 2003) and Bayesian inference as implemented in

MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003). *Phellinus uncisetus* was designated as outgroup (Decock et al 2007).

For parsimony analysis, gaps were treated as missing data. The most parsimonious trees for each data set were identified using heuristic searches with 1000 random addition sequences, further evaluated by bootstrap analysis, retaining clades compatible with the 50% majority-rule in the bootstrap consensus tree. Analysis conditions were tree bisection addition branch swapping (tbr), starting tree obtained via stepwise addition, steepest descent not in effect, MulTrees effective.

Models of evolution for Bayesian inference were estimated using the Akaike information criterion (AIC) as implemented in Modeltest 3.7 (Posada and Crandall 1998).. The dataset was subdivided into 10 data partitions: ITS1, 5.8S, ITS2, nucLSU, *tefl* 1st and 2nd codon position, *tefl* 3rd codon position, *tefl* introns, *rpb2* 1st and 2nd codon position, *rpb2* 3rd codon position, and indels (Table II).

The best-fit models for each partition were implemented as partition-specific models within partitioned mixed-model analyses of the combined dataset. Two optimal models of nucleotide substitution were selected for ITS regions, one for ITS1 and ITS2 (GTR+G) and the other for 5.8S (K80). The GTR+I+G model was used for nucLSU dataset. For the first and second codon position of the *tefl* region, was selected the HKY+G model while the GTR+I+G model was used for the third codon position and GTR+I for the *tefl* introns dataset. The HKY+G model and GTR+G were used for the *rpb2* region (respectively for the first and second codon and for the third codon position).

For analysis of SIC data under Bayesian inference, we used the MrBayes Restriction Site Model (F81-like) as recommended by Ronquist et al (2005). All parameters were unlinked across partitions. Bayesian analyses

were implemented with two independent runs, each with four simultaneous independent chains for six million generations, starting from random trees, and keeping one tree every 1000th generation.

To detect topological conflicts among data partitions, the nodes between the majority-rule consensus trees obtained in the parsimony analysis from the individual data sets were compared. Paired trees were examined for conflicts only involving nodes with bootstrap support value > 70% (Lutzoni et al. 2004, Mason-Gamer and Kellogg 1996, 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 on the rival trees.

RESULTS

Sequence data and statistical analysis are provided in Table II.

DNA sequence comparisons.— The 5' region of the nLSU gene including domains D1, D2, and D3 ranged from 871 (*F. langloisii*) to 877 bps (*F. cupressicola*). The ITS-5.8S region ranged from 662 (*Fomitiporia* sp. MUCL 47756, MUCL 47757 and MUCL 47758) to 753 bps (*Fomitiporia* sp. FG-10-282). This differs from previously published data regarding the length of *Fomitiporia* ITS-5.8S regions (702–704 [*F. hesleri*] to 746–749 bps [*F. polymorpha*], Decock et al 2007, Fischer and Binder 2004). A 70 bps long indel located near the 5' end of the ITS1 region of the strains MUCL 47756, MUCL 47757, and MUCL 47758 accounts for most of this variation. Decock et al (2007) already evidenced the absence of a 31 bps long fragment in the same region in *F. maxonii*, *F. dryophila*, *F. langloisii*, and *Fomitiporia* sp MUCL 46181. An identical 31 bps long deletion is present in the type strain of *F. sonorae* (CFMR RLG-10862-Sp / MUCL 47689). These two indels are located in the same region but given that they

Table II. Summary of ITS rDNA, LSU rDNA, *trf* and *rpb2* datasets

Properties	Datasets									
	ITS 1	5.8S	ITS 2	nLSU	<i>trf</i> 1st and 2nd	<i>trf</i> 3rd	<i>trf</i> 4th and 5th	<i>rpb2</i> 1st and 2nd	<i>rpb2</i> 3rd	Indels
Model selected	GTR + G	R80	GTR + G	GTR + I + G	GTR + I + G	GTR + I + G	HKY + G	SM + I + G	GTR + G	FSI like
Likelihood score	-1879.6792	-339.9105	-1873.1401	-2766.7249	-1185.0941	-2815.7737	-1612.9844	-1324.9868	-4347.7520	-
Base frequencies										
Freq. A =	0.2792	Equal	0.2503	0.2676	0.3075	0.1472	0.2616	Equal	0.2094	-
Freq. C =	0.1417	Equal	0.1703	0.2016	0.2197	0.3147	0.1970	Equal	0.1952	-
Freq. G =	0.1989	Equal	0.1971	0.2904	0.2629	0.2375	0.1559	Equal	0.3163	-
Freq. T =	0.3801	Equal	0.3823	0.2403	0.2099	0.3006	0.3855	Equal	0.2791	-
Proportion of invariable sites	-	-	-	0.6531	0.5860	0.1516	-	0.8146	-	-
Gamma shape	1.1153	-	0.4775	0.7819	1.0057	3.8859	2.7379	0.8951	1.4157	-

have different starting and ending positions, and given the results of the other datasets, they are best considered as two independent evolution events. Thirty characters judged too ambiguous to be aligned in the ITS-5.8S regions were excluded from further analysis.

Amplicons ranging from 1155 (*F. bakeri*) to 1172 bps (*F. australiensis*) were obtained from the partial *trf1*. This region contains three clade specific, confidently alignable introns; therefore no positions were excluded from the analysis.

The partial *rpb2* region ranged from 810 to 813 bps; *F. ivindoensis* presents an additional codon (GAG) in this region.

The final DNA sequence alignments resulted in 900 characters including gaps for the LSU gene (47 variable parsimony-uninformative and 98 parsimony-informative positions), 771 for the ITS dataset (78 variable parsimony-uninformative and 226 parsimony-informative positions), 1198 for the *trf1* region introns included (100 variable parsimony-uninformative and 322 parsimony-informative positions), 813 for the *rpb2* dataset (26 variable parsimony-uninformative and 253 parsimony-informative positions) and 332 for the recoded indels dataset (85 variable parsimony-uninformative and 245 parsimony-informative positions).

Individual dataset comparisons.— Sequence data and statistical analysis for each dataset and combined analysis are provided in Table II. Heuristic searches under maximum parsimony criterion for nLSU, ITS, *trf1*

and *rpb2* dataset (including the recoded indels) considered individually yielded respectively 590 (270 steps long; CI = 0.663, RI = 0.823), 10 (1246 steps long; CI = 0.576, RI = 0.825), 6 (944 steps long; CI = 0.632, RI = 0.846), and 294 (1018 steps long; CI = 0.377, RI = 0.777) equally parsimonious trees. All these most parsimonious trees, more specifically in the *tef1* and ITS analyses and, to a lesser degree, in the *rpb2* dataset exhibited very similar overall topology, at least for the clades with significant bootstrap support value and Bayesian posterior probability. They differ slightly in the relationships of terminal branches within the same lineage. Branch resolution and support was lowest for the nucLSU-based phylogeny. Moreover, for each dataset the strict consensus tree of the most parsimonious trees retains the same overall topology as the majority-rules consensus tree obtained in the corresponding Bayesian inference.

By comparing parsimony bootstrap consensus tree topologies obtained for the individual datasets, no conflict involving significantly supported nodes was found; the datasets were therefore combined.

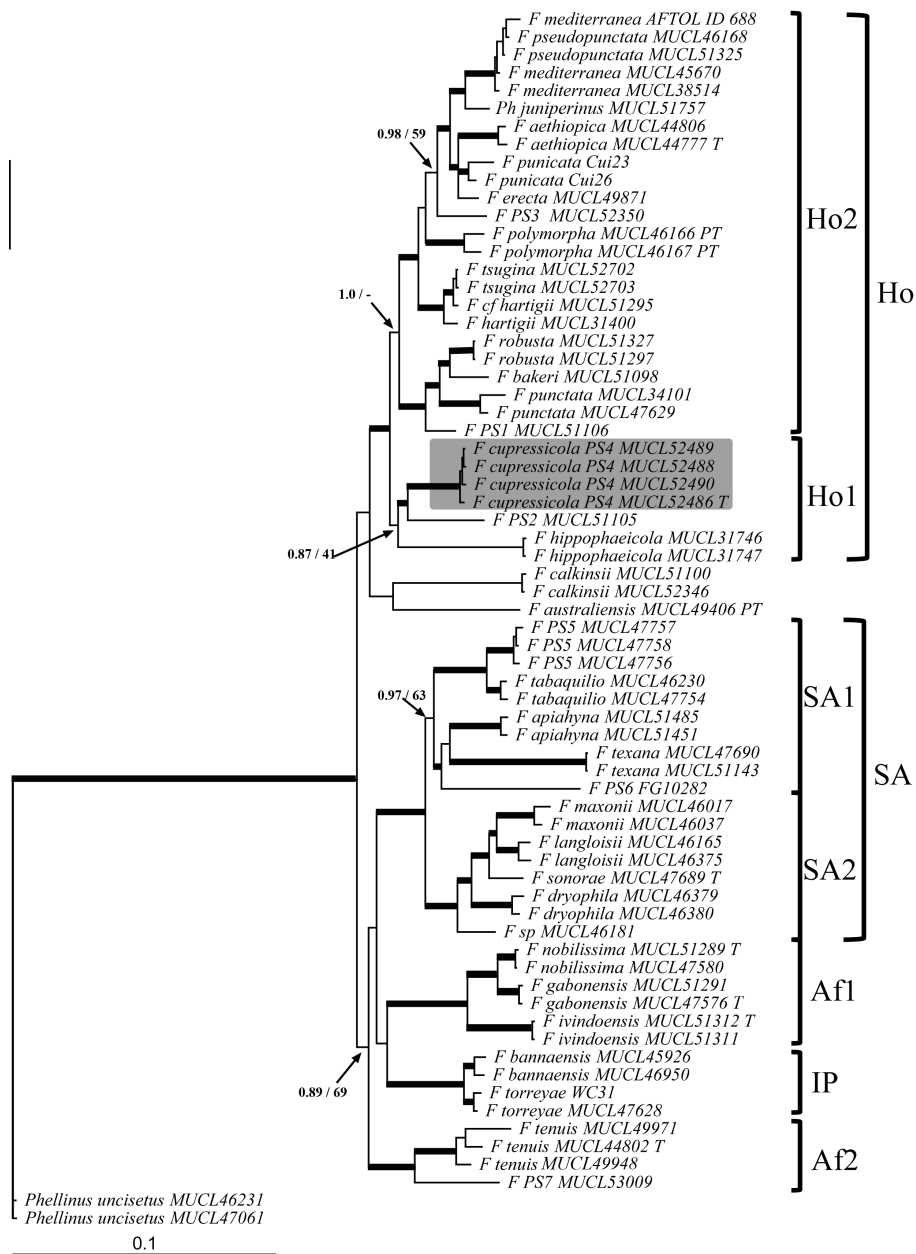


Fig. 1. The 50% majority-rule consensus tree from Bayesian inference of the combined nuclear ITS, LSU, *tef1* and *rpb2* sequences. Thickened branches in bold indicate bootstrap support greater than 70% and Bayesian posterior probability greater than 0.95. For selected nodes parsimony bootstrap support value and Bayesian posterior probabilities are respectively

indicated to the left and right of slashes (/). Ho: Holarctic clade; SA: South American clade; Af: African clade; IP: Indo-Pacific clade; T: type; PT: paratype.

Combined dataset analysis.— Thirty characters in the ITS-5.8S regions judged too ambiguous to be aligned. Of the remaining 4014 characters, 278 variable characters were parsimony-uninformative and 1144 characters were parsimony-informative.

The two Bayesian runs converged to stable likelihood values (-ln 22118.481, -ln 221385.301) after 1 479 000 generations and 4521 stationary trees from each analysis were used to compute a 50% majority rule consensus tree in PAUP* to calculate posterior probabilities.

The heuristic search produced 21 equally most parsimonious trees (3645 steps long; CI = 0.515, RI = 0.795, RC = 0.410), representing one main topology. This topology is coherent with previously published trees (Amalfi et al 2010), and is highly concordant with the topologies obtained analyzing the individual data set, and almost identical to the Bayesian consensus tree (Fig. 1). The main differences are the *F. tenuis* and *F. nobilissima* clades that are joined together in the parsimony analysis and the branching order within the *F. polymorpha* and *F. tsugina* clades that are switched in the parsimony topology.

Several large clades are resolved with strong supports by the different analyses (Fig. 1): these includes a “South American” (SA) clade with two subclades (SA1, SA2), two “African” (Af) clades (Af1, Af2), an “Indo-Pacific” (IP) clade, and a “Holarctic” (Ho) clade with two subclades (Ho1, Ho2).

These clades are identical to those recovered and discussed in Amalfi et al (2010). Their relationships remain uncertain, however, and the deeper internodes in all topologies are poorly supported, regardless of the analyses.

F. calkinsii clade shows uncertain relationships: it is either sister to the Holarctic clade (Bayesian inference) or basal to all *Fomitiporia* together with *F. australiensis* (maximum parsimony).

Within the presumed Holarctic lineage, four unnamed clades are evidenced (Fig. 1, Phylogenetic Species (PSs) 1, 2, 3, 4); these originate from the southern USA (PSs 1 & 2, respectively from New Mexico and Arizona) and northern Mexico (PS3, 4). PS 2 and PS3 are each represented by a single collection. PS1 is known from an additional collection but only its ITS sequence is available (see below). PS4 is represented by all specimens found growing on *C. arizonica* from forest at high altitude (> 2850 m) in the Mexican western *Sierra Madre* range. PS4 is closely related to PS2; they form a well-supported two species clade, with which *F. hippophaeicola* is associated, though with only moderate support. This three species clade (Fig.1 clade Ho2) is in a sister position to all other Holarctic taxa (Fig.1 clade Ho1), in all phylogenetic inferences, considered individually or concatenated.

The phylogenetic inferences also evidence various unnamed clades within the South American and African clades. *Fomitiporia* PS5, represented by three strains (Table I) and *Fomitiporia* PS6, so far represented by a single collection (Table I, FG-10-282), form isolated, distinct terminal branches/clades within the second South American clade (Fig. 1, SA2). *Fomitiporia* PS7, originating from South Africa, parasitic on grapevines and presumed to be involved in the local Esca disease, also forms a terminal clade within the second African clade (Fig. 1, Af2). This will be dealt with in different publications.

Morphological analysis.— Subsequent morphological examinations of the various collections of PS4 revealed no very conclusive combinations of morphological features unique to it and characteristic of it, which would

have defined a very unique morphological type. The main features that would differentiate it from other species occurring in North America are its ecology and possibly also its distribution. Morphological features (basidiome shape, pores size, skeletal hyphae, shape and size of basidiospores) overlap between the different species (with the remarkable exception of the basidiospores of *F. calkinsii*, distinctly smaller).

Ecological data.— PS4 is so far known only from living *C. arizonica* from high altitude (approx. 2850 m) humid conifer forest at the northern edge of the western *Sierra Madre* range in northern Mexico, experiencing mild summers and cold winters. The species was not found on the other local conifers (*Abies duranguensis*, *Pseudotsuga menziesii*, or *Juniperus deppeana*) nor on the few scattered angiosperms (mainly *Quercus*).

A search in the NY fungal database for *Fomitiporia* (*F. robusta* or *F. hartigii*, under *Fomitiporia* or *Phellinus*) associated with *Cupressus* spp. (*C. arizonica*) in the USA yielded no record (Ellen Bloch, pers. com.). Furthermore, DNA-based identification of a set of specimens identified as *F. robusta* morphospecies originating from the southern USA, from different hosts, did not reveal this species. This may suggest a narrow distribution range and a (local) species-specific host relationship.

Given the results of the phylogenetic inferences that identify PS4 as a Phylogenetic Species under the Phylogenetic Species Concept definition using the genealogical concordance principle (Taylor et al 2000), and the possible host specialization and restricted distribution, PS4 is described below as *F. cupressicola*.

Taxonomy

Fomitiporia cupressicola Amalfi, Raymundo, Valenzuela et Decock
sp. nov. Figs. 2–4, 11

MycoBank: MB 563786

Basidiomata perennis, pileada; pororum facies griseo-brunnea vel obscure brunnea; pori angulati, 5–6 per mm; tubi stratosi, in series, –15 mm longi; systema hypharum dimiticum; hyphae generatoriae, hyalinae ad pallidae luteae, simpliciter septatae; hyphae skeletales flavo-brunneae, crassitunicatae, aseptatae, 3.9–4.5 μ m diam; basidiosporae subglobosae vel obovoidae, leviter crassitunicatae, hyalinae, dextrinoideae, cyanophileae, (5.2–)6.5 x 7.0 (–7.8) μ m; hymenial setae ausente.

HOLOTYPE: MEXICO, DURANGO STATE: western *Sierra Madre* range, Municipality of Pueblo Nuevo, Ecological area "Predio Las Bayas", 23°27'32.5"N, 104°50'42.3"W, elev. approx. 2850 m, at the base of a living *Cupressus arizonica*, 03 Aug 2009, C. Decock, M. Amalfi, and T. Raymundo, MX-09-123 (MUCL 52486, Isotype at ENCB and NY; culture ex-holotype as MUCL 52486, CBS).

Etymology: “*cupressicola*”, growing on *Cupressus*.



FIGS. 2 A-F . *Fomitiporia cupressicola*; basidiomata in situ. A: General view of a young basidiome (MUCL 52487); B. Mature basidiome (MUCLMX09125), general view of the pileus surface. C. Pilear surface (MUCL52486). D. Details of the pore surface (MUCLMX-09-125). E. Young basidiome. F. Mature basidiome (MUCL 52535).

Basidioma perennial, pileate, sessile, single, semicircular to occasionally broadly attached, rounded, nodulose when young, soon thickly applanate to triquetrous, up to ungulate, projecting 35–80 mm, 60–120 mm wide, and 60–90 mm thick at the base, all basidiome with a corky to woody consistency; *pileus* velvety, azonate, yellowish brown (5D8) to brown (7D8) when young and in marginal areas of growing specimens, glabrous from the base and becoming zonate to concentrically sulcate in aging, finally slightly rimose when older, light brown (6D8), reddish brown (9D8), brownish red (10D8) to dark brown (6F5–6) and becoming black from the base; *margin* rounded, sterile, pale yellow to light yellow (4A3–5) in young specimens, grayish orange (5B6–7) to brownish yellow (5C7) or golden brown (5D7–8); *pore surface* yellowish brown (5F8) to light brown (6D4); *pores* rounded to oblong, (4–) 5–6 / mm, 160–180 μm in diam. (ave = 169 μm); *dissepiments* entire, 50–65 μm (ave = 53 μm) thick; tubes indistinctly stratified, longitude total up to 15 mm deep, grayish orange (5B4); *context* simple, zonated, up to 30 mm thick, fibrous, color golden brown (5D7).

Hyphal system dimitic in all part; *generative hyphae* simple septate, hyaline to golden brown, sparingly branched, 1.3–3.2 μm diam; *skeletal hyphae* golden brown to reddish brown, unbranched, thick-walled, in the *context* 3.9–4.5 μm in diam, the lumen 1.3–2.7 μm wide, in the *hymenophoral trama* 2.5–4.0 μm in diam, the lumen 0.7 – 1.5 μm wide, with a sub-parallel orientation.

Hymenium. basidioles subglobose, 12–15 $\times$ 11–11.5 μm ; *basidia* subglobose, hyaline, tetrasporic, 12–18 $\times$ 10–11.5 μm , sterigmata up to 3.5 μm long; *basidiospores* subglobose, globose to ovoid, hyaline, strongly dextrinoid, thick walled, smooth, (6.5–) 7.0–7.5 (–8.3) $\times$ (5.8–) 6.5–7.0 (–7.5) μm (ave = 7.0 $\times$ 6.6 μm) Q = (1.0–) 1.05–1.18 (–1.2) μm (ave_Q = 1.06

µm); *cystidioles* fusoid, hyaline, thin walled, 10.5–13.0 × 3.5–5.0 µm; *hymenial setae* absent; *chlamydospores* absent.

Type of rot: a white rot.

Ecology (host and habitat): Growing at the base of living trunks of *Cupressus arizonica*, among mosses, in high altitude, humid coniferous forests, characterized by *Abies duranguensis*, *Pseudotsuga menziesii*, *Cupressus arizonica*, and *Juniperus deppeana* as dominant species, with scattered *Quercus* spp. and *Pinus* spp.

Distribution: Known from a restricted area at the northern edge of the Mexican western *Sierra Madre* range, Durango State, Mexico.

Additional specimens examined: MEXICO, DURANGO STATE: western *Sierra Madre* Range, Municipality of Pueblo Nuevo, “Predio Las Bayas” ecological zone, 23°27’32.5” N, 104°50’42.3” W, elev approx 2850 m, at the base of a living *Cupressus arizonica*, 10 Aug 1995, *G. Salazar 174*; *ibid*, 20 Jul 1992, *R. Valenzuela 7162*; *ibid*, 19 Sep 2007, *T. Raymundo y R. Valenzuela 1731* (ENCB); *ibid*, 22 Aug 2008, *T. Raymundo y R. Valenzuela 2346* (ENCB); *ibid*, 03 Aug 2009, *C. Decock, M. Amalfi, and T. Raymundo, MX-09-124* (MUCL 52490 ; culture ex. as MUCL 52490); *ibid*, *MX-09-126* (MUCL 52487; culture ex. as MUCL 52487); *ibid*, *MX-09-127* (MUCL 52534; culture ex. as MUCL 52534); *ibid*, *MX-09-128* (MUCL 52535; culture ex. as MUCL 52535); *ibid*, *MX-09-129* (MUCL 52488; culture ex. as MUCL 52488); *ibid*, *MX-09-131* (MUCL 52489; culture ex. as MUCL 52489).

Remarks. — *Fomitiporia cupressicola* belongs to the *F. robusta* morphological complex; in that sense, it shares with other species of this complex a pileate basidiome, variably applanate to slightly ungulate, the upper surface slightly rimose with age, medium-sized pores (5–6 pores /mm), and subglobose, thick-walled, and dextrinoid basidiospores (Fischer

and Binder 2004, Gilbertson and Ryvarden 1987, Larsen and Cobb-Poulsen 1990, Ryvarden and Gilbertson 1994, Vlasák and Kout 2011). Hymenial setae are absent.

The species is best characterized by its ecological requirements, of which the host relationships and related habitats (see above), reflecting physiological adaptations toward host specialization. The species develops basidiomata near the trunk bases of *C. arizonica*, commonly among mosses. Its distribution range remains uncertain but our data may suggest a (very) restricted range. *Cupressus arizonica*, so far its only known host, has a very restricted, patchy distribution in North America, forming isolated small stands, extending from the southwestern United States to northern Mexico, remnants of an earlier (pre-pleistocene) widespread distribution; it is thought today to represent a near extinction relict in nature (Niering and Lowe 1984, Little and Elbert 1971, Brown 1982). *Fomitiporia cupressicola* has not been identified in a set of specimens of the *F. robusta* complex collected in the southern USA (see above). No *Fomitiporia* (or *Phellinus* of the *Fomitiporia* complex) with pileate basidiome have been reported on *Cupressus* in North America (Gilbertson and Ryvarden 1987), suggesting a narrow distribution range.

Presumed narrow geographic distribution and host range of poroid Hymenochaetaceae in North America are reported, e.g. *Phellinus coronadensis* Rizzo et al, apparently restricted to high elevation forests (> 2500 m) in Southern Arizona (USA) mountain range, preferentially (almost exclusively) on *Pinus strobiformis* (Rizzo et al 2003).

In USA and northern Mexico, *F. cupressicola* should be compared to *Fomitiporia* Phylogenetic Species (PS) 2, that is so far and from a phylogenetic perspective, its closest relative; they both form a two-species clade, basal within the Holarctic lineage (Fig. 1, Ho1). Though

phylogenetically more distantly related (Ho2), it should also be compared to *Fomitiporia* PS3 found in a neighboring area.

Both *Fomitiporia* PSs 2 and 3 are known from a single collection. The voucher specimen of PS2 is unavailable for the time being. It was collected in southern USA (Arizona), growing on *Purshia* (*Cowania*) *stansburiana* (Rosaceae), in a semi-dry ecosystem. PS3 was found in a locality nearby that of *F. cupressicola*, but at a lower elevation (about 2400 m), in a different, drier ecosystem characterized by a dominance of *Pinus* and *Quercus*, and growing on living oak. The morphology of this unique specimen does not differ consistently from other species of the *F. robusta* complex, including *F. cupressicola*. More collections are necessary to characterize these PSs.

Fomitiporia cupressicola could also be compared to other North America species growing on gymnosperms such as *F. hartigii* s.l. and *F. texana*, or to some species growing on angiosperms, notably *F. bakeri*, *F. calkinsii*, *F. polymorpha*, and *Fomitiporia* PS1. All these species form distinct terminal clades either within the same (Holarctic) (*F. bakeri*, *F. hartigii*, *F. robusta* s.l. Fig 1) or distant lineages (*F. texana* in clade SA2, *F. calkinsii* Fig 1). It is noteworthy that *F. texana* belongs to a very distant lineage within *Fomitiporia*, and is kin to some species with pileate basidiomes occurring in dry to semi-dry areas of South America (central Argentina) and the Andean Mountain range (Fig 1, SA2). *Fomitiporia calkinsii* forms a distinct, distant lineage, but whose affinities remain unresolved for the time being, however (Fig 1). All have also contrasting ecological requirements (host preference and related habitat) and their distributions apparently do not overlap.

In North America, *F. hartigii* (s.l., see Decock et al 2007, Fischer and Binder 2004) has a marked preference (possibly specificity) for hemlock (*Tsuga* sp., Gilbertson and Ryvarden 1987) (it preferably grows on *Abies* in

northern Europe, Ryvarden and Gilbertson 1994). The species distribution should follow the distribution of its host, in northern areas of USA. Morphologically, it differs from *F. cupressicola* in having resupinate to effused reflexed then with marginal pseudopilei (Gilbertson and Ryvarden 1987).

Fomitiporia texana is reported frequently in Cupressaceae, but only on *Juniperus* (Gilbertson and Ryvarden 1987, Lowe 1957). It occurs in southern, arid to semi-arid ecosystems of the USA (Gilbertson and Ryvarden 1987); it is also widely distributed in related environments in Mexico (pers. obs., table I). Morphologically, it has deeply rimose pilei with age and setoid hyphae (in the sense of Jahn 1976) in the hymenophoral trama, though variably abundant and sometimes absent (Gilbertson and Ryvarden 1987).

Fomitiporia calkinsii possibly has a narrow host range, growing exclusively on angiosperms, preferably (but not exclusively) including *Quercus* (Fagaceae) and *Carya* (Juglandaceae) (Amalfi et al 2010, Vlasák and Kout 2011). In the USA, it is found across the southeastern States or, in biogeographical terms, in the southern areas of the eastern deciduous (Piedmont oak-pine) and coastal plain mixed forests (Barbour and Billings 2000). It is also widely distributed in eastern Mexico on *Quercus* (pers. obs., Raymundo et al 2011). Morphologically, it has distinctly smaller pores (6–8 pores/mm) and smaller basidiospores (mainly $5.0\text{--}6.5 \times 5.0\text{--}6.0 \mu\text{m}$, Vlasák and Kout 2011, pers. obs.).

Fomitiporia bakeri apparently grows exclusively on *Betula* (Betulaceae) (Larsen and Cobb-Poulle 1990, Vlasák and Kout 2011, pers. obs.). It is known in the eastern deciduous forest of the USA (Vlasák and Kout 2011). Morphologically, it shares with *F. cupressicola* the pores size (5–6 / mm) Vlasák and Kout 2011). The basidiospores might be slightly

narrower in *F. bakeri* (5.5–6.5 μm wide, [Vlasák and Kout 2011] *versus* 6.5–7.0 (–7.5) μm wide in *F. cupressicola*).

Fomitiporia PS1 is known thus far from two collections originating in the southwestern USA, respectively New Mexico (Table 1) and California [specimen J.V.-0407-16G, USA, California, ITS sequence at GenBank GU136227, cited in Vlasák and Kout (2011)]; both were found growing on *Quercus* sp. Their voucher specimens are not available to us for the time being.

Diversity within the F. robusta complex in North America (USA and northern Mexico) —. *Fomitiporia robusta* s.l. has been widely reported in Mexico (e.g. Anell and Guzmán 1987, Ojeda-López et al 1986, Romero-Bautista et al 2010) and the southern USA (Gilbertson and Ryvar den 1987, Lowe 1957). As noted by Gilbertson and Ryvar den (1987), it forms a taxonomically difficult complex. Vlasák and Kout (2011) raised the hypothesis that, *sensu stricto*, the species is absent from North America, at least from the eastern temperate and southeastern subtropical areas, a hypothesis that our own data confirm (data not shown). *A fortiori*, all records from further south should be critically re-analyzed. The species may be restricted to Europe (extending to Eurasia).

In North America, *F. bakeri*, *F. calkinsii*, *F. texana*, and at a lesser degree, *F. polymorpha* have already been segregated from *F. robusta sensu* (American) *auctores* (Fischer and Binder 2004, Gilbertson and Ryvar den 1987, Larsen and Cobb-Poullé 1990, Vlasák and Kout 2011). Nevertheless, locally, the species concept in the *F. robusta* complex in America still needs to be more carefully assessed. Our phylogenetic studies show that other species will doubtlessly emerge from this complex; in addition to *F. cupressicola*, three additional unnamed clades (PSs 1, 2, & 3) representing potentially distinct species occur in southern USA or northern Mexico (Fig.

1), demonstrating a still wider diversity. However, few specimens are available and this impedes phenotypical and ecological characterization. More collections are necessary. Decock et al (2007) also described a wider than presumed species diversity in the *F. punctata* complex.

Within *Fomitiporia* (and more generally within the poroid Hymenochaetales), the apparent homogeneity of “standard” morphological characters, with overlaps of form or size range or the occurrence of subtle differences of *a priori* uncertain taxonomic significance often renders classical phenotypical identification difficult. Other non-morphological descriptors should be integrated to circumscribe many of these species.

Molecular tools clearly help to identify cryptic species within *Fomitiporia* (Amalfi et al 2010, Decock et al 2005, 2007, Fischer and Binder 2004); *a posteriori*, it could also provide clues to help in the understanding the importance of environmental factors (habitat, host, substrate, and niche), reflecting physiological adaptations, for characterizing taxonomic entities. Gilbertson and Ryvarden (1987) noted that within the *F. robusta* complex, speciation could have resulted from “[physiological] adaptation to different substrates and vastly different environmental factors”, as is probably the case in multiple fungal groups (e.g. Jargeat et al 2010). The multiplicity of phylogenetic species evidenced using single (Fischer and Binder 2004, Vlasák and Kout 2011) or multiple loci (Decock et al 2007, present study) and having potentially differential ecological requirements support this hypothesis in North America.

It is noteworthy that the taxonomic diversity within the *F. robusta* complex seems to be wider in North America than in Europe (*F. robusta* s.s., *F. hippophaeicola*, *F. hartigii* s.s. the complex *F. erecta* / *Ph. juniperinus* / *Ph. rosmarini*). However, an integrating approach has never been applied to

the European species, and would be necessary to tackle, *e.g.* the *F. erecta* / *Ph. juniperinus* / *Ph. rosmarini* complex.

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References

- Amalfi M, Yombiyeni P, Decock C 2010. *Fomitiporia* in sub-Saharan Africa: morphology and multigene phylogenetic analysis support three new species from the Guineo-Congolian rainforest. *Mycologia* 102: 1303–1317
- Anell JC., Guzmán G. 1987. Especies de Poliporáceos citadas del Estado de Veracruz. *Revista Mexicana de Micología* 3: 137–148.
- Barbour MG, Billings WD. 2000. North American terrestrial vegetation. 2^d edition. Cambridge University Press, USA: 1–708.

Bernicchia A. 1990. *Polyporaceae s.l.* in Italia. Istituto di Patologia Vegetale, Bologna, Italy:1–594.

Brown, DE. 1982. Relict conifer forests and woodlands. In: Brown, David E., ed. Biotic communities of the American Southwest--United States and Mexico. Desert Plants. 4(1-4): 70-71.

Castresana J, 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17: 540-552.

David A, Dequatre B, Fiasson JL. 1982. Two new *Phellinus* with globose, cyanophilous spores. *Mycotaxon* 14:160–174.

Decock C, Bitew A, Castillo G. 2005. *Fomitiporia tenuis* and *Fomitiporia aethiopica* (Basidiomycetes, Hymenochaetales), two undescribed species from the Ethiopian Highlands: taxonomy and phylogeny. *Mycologia* 97:124–132.

———, Herrera Figueroa S, Robledo G, Castillo G 2007. *Fomitiporia punctata* (Basidiomycota, Hymenochaetales) and its presumed taxonomic synonyms in America: taxonomy and phylogeny of some species from tropical/subtropical areas. *Mycologia* 99: 733-752.

Fischer M, 1994. Pairing tests in the *Phellinus pini* group. *Mycologia* 86:524–539.

———, 1995. *Phellinus igniarius* and its closest relatives in Europe. *Mycol Res* 99:735–744.

———, Binder M. 1995. *Phellinus* species on *Betula*. Mating tests, RFLP analysis of enzymatically amplified rDNA, and relations to *Phellinus alni*. *Karstenia* 35:67–84.

———, Binder M. 2004. Species recognition, geographic distribution, and host-pathogen relationships: a case study in a group of lignicolous Basidiomycetes, *Phellinus s.l.* *Mycologia* 96:799–811.

Frøslev TG, Matheny PB, Hibbett DS (2005). Lower level relationships in the mushroom genus *Cortinarius* (Basidiomycota, Agaricales): a comparison of RPB1, RPB2, and ITS phylogenies. *Molecular Phylogenetics and Evolution* 37: 602-618.

Gilbertson RL, Ryvarden L. 1987. North American Polypores. Part 2. *Megasporoporia – Wrightoporia*. Fungiflora, Oslo, Norway: 433–885.

Jahn HJ. 1976. *Phellinus hippophaecola* H. Jahn, a new species. *Mem NY Bot Gdn* 28:105–108.

Jargeat P, Martos F, Carriconde F, Gryta H, Moreau P-A, Gardes M. 2010. Phylogenetic species delimitation in ectomycorrhizal fungi and implications for barcoding: the case of the *Tricholoma scalpturatum* complex (Basidiomycota). *Mol Ecol* 19: 5216–5230.

Kirk PM, Cannon PF, David JC, Stalpers JA. 2001. Ainsworth & Bisby's Dictionary of the Fungi, 9th edition. CABI Publishing, Wallingford, UK:1–655.

Kornerup A, Wanscher JH. 1981. Methuen handbook of color, 3rd Edition:1–282.

Larsen MJ, Cobb-Poulsen LA. 1990. *Phellinus* (Hymenochaetaceae). *Synopsis Fungorum* 3, Oslo, Norway: Fungiflora:1–206.

Little, Elbert L., Jr. 1971. Atlas of United States trees. Volume 1: Conifers and important hardwoods. Misc. Publ. 1146. Washington, DC: U.S. Department of Agriculture. 9 p.

Lowe JL. 1957. Polyporaceae of North America. The genus *Fomes*. Syracuse, New York: State University College of Forestry, Syracuse University. 97 p.

Lutzoni F, Wagner P, Reeb V, Zoller S. 2000. Integrating ambiguously aligned regions of DNA sequences in phylogenetic analyses without violating positional homology, *Syst Biol* 49:628–651.

———, Kauff F, Cox CJ, McLaughlin D, Celio G, Dentinger B, Padamsee M, Hibbett D, James TY, Baloch E, Grube M, Reeb V, Hofstetter V, Schoch C, Arnold AE, Miadlikowska J, Spatafora J, Johnson D, Hambleton S, Crockett M, Shoemaker R, Sung G-H, Lücking R, Lumbsch T, O'Donnell K, Binder M, Diederich P, Ertz D, Gueidan C, Hansen K, Harris RC, Hosada K, Lim Y-W, Matheny B, Nishida H, Pfister D, Rogers J, Rossman A, Schmitt I, Sipman H, Stone J, Sugiyama J, Yahr R, Vilgalys R. 2004. Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. *Am J Bot* 91: 1446–1480.

Mason-Gamer RJ, Kellogg EA. 1996 Testing for phylogenetic conflict among molecular data sets in the tribe Triticeae (Gramineae). *Syst Biol* 45:524-545

Matheny PB (2005). Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*, Agaricales). *Molecular Phylogenetics and Evolution* 35: 1-20.

———, Wang Z, Binder M, Curtis JM, Lim YW, Nilsson RH, Hughes KW, Petersen RH, Hofstetter V, Ammirati JF, Schoch C, Langer GE, McLaughlin DJ, Wilson AW, Crane PE, Frøslev T, Ge ZW, Kerrigan RW, Slot JC, Vellinga EC, Liang ZL, Aime MC, Baroni TJ, Fischer M, Hosaka K, Matsuura K, Seidl MT, Vauria J, Hibbett DS. 2007. Contributions of *rpb2* and *tefl* to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Mol Phyl Evol* 43:430–451

Müller K. 2005. SeqState—primer design and sequence statistics for phylogenetic DNA data sets, *Applied Bioinformatics* 4:65–69.

Niemelä T. 1975. On Fennoscandian polypores. IV. *Phellinus igniarius*, *P. nigricans* and *P. populicola* n. sp. *Ann Bot Fenn* 12:93–122.

Niering, WA. Lowe, CH .1984. Vegetation of the Santa Catalina Mountains: community types and dynamics. *Vegetatio* 58, 30-58.

Ojeda-López S, de la Luz Sandoval M, Valenzuela R. 1986. Los poliporaceos de Mexico I. Descripción de algunas especies del noreste de Guanajuato. *Rev Mex Mic* 2 : 367–436.

Pieri M, Rivoire B. 2000. Le genre *Phellinus*. Quelques espèces rares ou critiques en France, avec une clé des espèces du genre *Phellinus s.l.* signalées en Europe occidentale. *Bull Soc Mycol Fr* 116:305–331.

Posada D, Crandall KA. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817–818

Raymundo T, Decock C, Valenzuela R, Amalfi M, Cifuentes J, Pacheco-Mota L. 2011. New records of the genus *Fomitiporia* (Hymenochaetales, Basidiomycota) in Mexico. *Rev Mex Biodiver* 83: in press.

Rambaut A, Drummond AJ. 2007. Tracer v1.4, [<http://beast.bio.ed.ac.uk/Tracer>]

Reeb V, Lutzoni F, Roux C. 2004. Contribution of RPB2 to multilocus phylogenetic studies of the euascomycetes (Pezizomycotina, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory. *Mol Phyl Evol* 32:1036–1060.

- Rehner SA, Buckley E. 2005. A *Beauveria* phylogeny inferred from nuclear ITS and EF1-a sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97:84–98
- Rizzo DM, Gieser PT, Burdsall HH. 2003. *Phellinus coronadensis*: a new species from southern Arizona, USA. *Mycologia* 95:74–79.
- Romero-Bautista L, Pulido-Flores G, Valenzuela R. 2010. Estudio micoflorístico de los hongos poliporoides del estado de Hidalgo, México. *Polibotánica* 29:1–28.
- Ronquist F, Huelsenbeck JP. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.
- , Huelsenbeck JP, Van der Mark P. 2005. MRBAYES 3.1 manual. In School of Computational Science, Florida State University 2005 Tallahassee, FL:School of Computational Science, Florida State University
- Ryvarden L, Gilbertson RL. 1994. European polypores 2. *Meripilus–Tyromyces*. *Synopsis Fungorum* 7, Oslo, Norway: Fungiflora: 392–743.
- Rzedowski J. 2006. Vegetation de México. 1st ed digital, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. http://www.conabio.gob.mx/institucion/centrodoc/doctos/vegetacion_de_mexico.html
- Simmons MP, Ochoterena H. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Syst Biol* 49:369–381.
- , Pickett KM, Miya M. 2004. How meaningful are Bayesian support values? *Mol Biol Evol* 21:188–199.

Swofford DL 2002. *PAUP: Phylogenetic Analysis Using Parsimony. Version 4.0b10*. Laboratory of Molecular Systematic, Smithsonian Institute, Washington DC.

Taylor JW, Geiser DM, Jacobson DJ, Kroken S, Kasuga T, Geiser DM, Hibbett DS, Fisher MC., 2000 Phylogenetic species recognition and species concepts in fungi. *Fungal Genet Biol* 31:21-32

———, Turner, E., Pringle, A., Dettman, J., Johannesson, H., 2006a. Fungal species: thoughts on their recognition, maintenance and selection. In: Gadd, G.M., Watkinson, S.C., Dyer, P.S. (Eds.), *Fungi in the Environment*. pp. 313–339.

Thiers, B. [continuously updated]. Index herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium, <http://sweetgum.nybg.org/ih/>.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. 1997. [The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools.](#) *Nucleic Acids Res* 25:4876–4882.

Tomšovský M, Sedlák P, Jankovský L. 2010a. Species recognition and phylogenetic relationships of European *Porodaedalea* (Basidiomycota, Hymenochaetales). *Mycol Progress* 9:225–233.

———, Vampola P, Sedlák P, Byrtusová Z, Jankovský L. 2010b. Delimitation of central and northern European species of the *Phellinus ignarius* group (Basidiomycota, Hymenochaetales) based on analysis of ITS and translation elongation factor 1 alpha DNA sequences. *Mycol Progress* 9:431–445.

Vlasák J, Kout J. 2011. Pileate *Fomitiporia* species in the USA. New combinations *Fomitiporia calkinsii* and *F. bakeri*. *Mycol Prog*: 10: 445–452

CHAPTER III

***Fomitiporia castilloi* sp. nov. and multiple clades around *F. apiahyna* and *F. texana* in Meso- and South America evidenced by multiloci phylogenetic inferences**

This paper is a continuation of our revision of the “*Fomitiporia robusta*” complex. The Neotropical *Fomitiporia* lineage is introduced. *Fomitiporia castilloi* from the lowland rainforest in French Guyana is described as new and its phylogenetic relationship discussed. The presence of *Fomitiporia robusta* in the Americas is questioned, as well as the distribution, ecology and “ definition ” of *Fomitiporia apiahyna* in the Neotropics. Six more unnamed terminal clades are resolved by our phylogenetic inferences. Strikingly four of them, clustering together in the *F. apiahyna* sublineage, and thus sharing a common ancestor, lived in sympatry in the same forest plot of c.a. 300 square meters in the Nouragues reserve (French Guyana). This presupposes a local sympatric speciation presumably driven by some sort of ecological segregation (hosts specificity, ecological niche adaptation etc.).

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***Fomitiporia castilloi* sp. nov., and multiple clades around *F. apiahyna* and *F. texana* in Meso- and South America evidenced by multiloci phylogenetic inferences.**

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Abstract: *Fomitiporia castilloi* sp. nov. from the lowland rainforest in French Guiana is described, illustrated and its phylogenetic affinities are commented. This species is characterized by pileate basidiomata, a plicate margin, abundant, variably shaped hymenial setae, and basidiospores averaging $\cong 6 \times 5 \mu\text{m}$. In phylogenetic inferences based on a DNA sequence data set of 4 loci (5' end of the LSU, ITS-5.8S, partial *Tef-1* and *rpb2*), *F. castilloi* has an isolated position, basal to a clade that is composed to date exclusively of neotropical species with resupinate basidiomata. The multiloci phylogenetic inferences also evidence an unreported complexity within the Neotropical area, with multiple clades in the vicinity of *F. apiahyna* and *F. texana*, representing additional potential species.

Key words: *Phellinus sensu lato*, Hymenochaetaceae, polypores, Neotropics, Biogeography.

Introduction

*Fomitiporia*³ is a genus of poroid Hymenochaetaceae, above all characterized by globose to subglobose, thick-walled, cyanophilous, and dextrinoid basidiospores, in addition to a dimitic (pseudodimitic) hyphal system. Hymenial setae and cystidioles are variably present (Fischer 1996). *Fomitiporia* was commonly segregated into two morphological complexes: the *F. punctata* complex, representing species having resupinate basidiomata [e.g. *F. langloisii* (type species), *F. punctata*, *F. pseudopunctata*, *F. aethiopica*, etc.]; the *F. robusta* complex, for species sharing pileate basidiomata (e.g. *F. bakeri*, *F. calkinsii*, *F. robusta*, etc.). Both complexes have been demonstrated to encompass a wider than presumed taxonomic diversity, whatever the biogeographical area considered (e.g. Amalfi et al. 2010, 2012, Decock et al. 2005, 2007, Dai et al. 2008, Fischer 2002, Fischer and Binder 2004, Vlasák and Kout 2011, Zhou and Xue 2012).

In the New World, the *F. punctata* complex has been dealt with, partly, by Fischer and Binder (2004) and Decock et al. (2007), whereas Fischer and Binder (2004), Vlasák and Kout (2011), and Amalfi et al. (2012) addressed the status of *F. robusta sensu* “North American” *auctores* (e.g. Gilbertson and Ryvarden 1987, Lowe 1957). As one of the consequences of these studies, the occurrence in North America of *F. robusta sensu stricto* (*s.s.*) was brought into question [in our opinion, *F. robusta s.s.* corresponds to *Phellinus robustus* var. *robustus sensu* Domański et al. (1967) or *Phellinus robustus sensu* Ryvarden (1978), both circumscriptions drawn on the basis of European specimens, and not polluted by data taken from materials of extra-European origins; in that sense, it corresponds to the *F. robusta* clade of Amalfi et al. (2010, 2012)]. Vlasák and Kout (2011) and Amalfi et al. (2012) raised the hypothesis that this species is absent from NA, where it is replaced by multiple taxa, morphologically comparable, but forming distinct phylogenetic units. These taxa also are characterized by

more discrete ecological requirements (ecological units) and narrower geographical distributions. Raymundo (2012) and Raymundo et al. (2012) failed also to identify *F. robusta* s.s. in Mexico, during a country wide survey of the genus, using both morphological and DNA-based identifications. In agreement with the above idea, all mentions of "*F. robusta*" from southern, tropical locations (e.g. Guyana, Woolley et al. 2008; Costa Rica, Ryvar den 2004) should be considered with caution, as *sensu lato* (s.l.), and critically analyzed.

In the Neotropics, *F. robusta* s.l. should be compared with *F. apiahyna*, which also has pileate basidiomes. *Fomitiporia apiahyna* is reported from southern Florida and southern Mexico (Vlasák et al. 2011, Raymundo et al. 2012) down to northeastern Argentina and southern Brazil (Amalfi et al. 2010, Gilbert et al. 2002, Loguercio Leite and Wright 1991, Rajchenberg and Wright 1987, Rajchenberg and de Meijer 1990, Ryvar den 2004, Wright and Blumenfeld 1984); it is more likely a Neotropical endemic (Amalfi et al. 2010).

As a continuation of the revision of the *Fomitiporia* species with pileate basidiomes in the New World (Amalfi et al. 2012, Raymundo et al. 2012), a set of specimens of Central and South American origin and tentatively identified as *F. robusta* (Woolley et al. 2008), *F. robusta sensu lato* (pers. obs.), and *F. apiahyna sensu* Ryvar den (2004) were gathered and analyzed. Among these collections, two specimens from the lowland rainforest of French Guiana drew our attention by a remarkable combination of morphological features. These collections are characterized by a blackish, roughly sulcate pileus, numerous, variably shaped hymenial setae, and basidiospores on average $\cong 6 \times 5 \mu\text{m}$. At first, the pileus habit and presence of hymenial setae call to mind *F. robusta*, one of the few *Fomitiporia* species with (occasional) hymenial setae (Domański et al. 1967, Ryvar den

1978, Ryvarden and Gilbertson 1994). Setae have never been reported in the Neotropical *F. apiahyna* (Rajchenberg and Wright 1987, Ryvarden 2004). Multiloci phylogenetic inferences, based on DNA sequence data of 4 loci (5' end of the LSU, ITS-5.8S, partial *tefl* and *rpb2*) resolved these two specimens as an isolated, monophyletic clade, that is kin to the *F. langloisii* lineage [*F. langloisii* (*Fomitiporia* type species) and related taxa, Decock et al. (2007), Amalfi et al. (2012)]. It is worth noting that the *F. langloisii* lineage contained to date only species having resupinate basidiomata. *Fomitiporia robusta* s.s. and, to a lesser degree, *F. apiahyna* are distantly related to *F. langloisii* (Amalfi et al. 2012).

These two specimens are interpreted as belonging to a distinct species, for which no name could be found (within the synonyms of *F. robusta* s.l., Murrill 1903, Robert et al. 2005, Ryvarden 1991) that could apply to it; hence it is described and illustrated below as *Fomitiporia castilloi* sp. nov.

The phylogenetic inferences also revealed multiple additional clades within our specimens, representing, in addition to *F. apiahyna* (Amalfi et al. 2010), 6 potentially undescribed phylogenetic species (PS), distributed over two Neotropical lineages: the *F. apiahyna* and the *F. texana* lineages. The complexity within the Neotropical *Fomitiporia* with pileate basidiomes is briefly discussed.

Materials and methods

Material.— Herbarium specimens are preserved at MUCL with a duplicate of type material deposited at NY (herbarium acronyms are according to Thiers, continuously updated). Living cultures are preserved at MUCL with a duplicate of the ex-type strain deposited at the CBS. Strains isolated by the authors (C. Decock) were obtained during fieldwork, from fresh basidiome tissues, using malt extract agar supplemented by 2 ppm

benomyl (benlate) and 50 ppm chloramphenicol (Untereiner et al. 1998), and later purified in the laboratory in case of persistent bacterial contamination. Voucher specimens and sequences (GenBank accession number) used in this study are listed in Table I.

Collection localities.— Most specimens used in this study were collected in the CNRS “inselberg” research plots, Nouragues Natural Reserve, French Guiana (approx 04°05.5' N, 52°40.6' W, <http://www.nouragues.cnrs.fr/F-inselberg.html>) and in the areas surrounding the Yasuni Biological Station, including the CTFS forest plot (<http://www.ctfs.si.edu/site/Yasuni>), Yasuni Biosphere Reserve, Ecuador (approximately 76°24'1.8''W, 0°40'16.7''S). These forests belong to the very humid rainforest of Guyana and western Amazonia, respectively (average precipitation is about 3000 mm/year in the Nouragues and Yasuni areas). Additional collections were gathered from Guyana (Woolley et al. 2008), the Lesser Antilles (Guadeloupe, Martinique), and Mesoamerica (eastern Mexico).

Morphology and anatomy.— Basidiome colors are described according to Kornerup and Wanscher (1981). Basidiome sections were examined in Melzer's reagent, lactic acid Cotton blue (Kirk et al. 2001), and KOH 4 %. All microscopic measurements were done in Melzer's reagent. In presenting the size range of the microscopic elements, 5% of the measurements were excluded from each end and are given in parentheses, ave = arithmetical mean, Q = ratio of length/width of basidiospores, and ave_Q = arithmetical mean of the ratio Q. Thirty basidiospores/setae were measured from each specimen.

Sequencing.— DNA extraction, amplification, and sequencing of the 5' end of the nuclear ribosomal LSU rRNA gene, ITS regions (including 5.8S), partial *tefl-α* gene, and the region located between domains 6 and 7 of

rpb2 (Frøslev et al. 2005, Matheny 2005) are described in Decock et al. (2007) and Amalfi et al (2010, 2012).

Sequencing reactions were performed using CEQ DTCS Quick Start Kit® (Beckman Coulter) according to the manufacturer's recommendations with the primers LROR, LR3, LR3R, LR5 for the LSU; ITS1, ITS2, ITS3, ITS4 for the ITS (<http://biology.duke.edu/fungi/mycolab/primers.htm>); 2212R, 1953R, 983F, 2218R for *tef1-α* (Rehner and Buckley 2005, Matheny et al. 2007); bRPB2-6F and bRPB2-7.1R for *rpb2* (Matheny 2005).

Sequences were assembled and edited with the Sequencher™ 4.8 software (Gene Codes Corporation, Ann Arbor, MI, USA).

Phylogenetic analysis.— One hundred and nine specimens or cultures representing 42 species or potential species/clades were included in the phylogenetic analysis. Nucleotide sequences were automatically aligned with Clustal X 2.0.11 (Thompson et al. 1997) with default settings. The alignment was further optimized and manually adjusted as necessary with the text editor in PAUP* 4.0b10. Potential ambiguously aligned segments were detected by Gblocks v0.91b (Castresana 2000; <http://molevol.cmima.csic.es/castresana/Gblocks.html>, settings "allow smaller final blocks", "allow gaps within blocks"). Sequences of protein-coding genes were manually aligned by direct examination with the software Se-Al v. 2.0a11 (University of Oxford). The assignment of codon positions was confirmed by translating nucleotide sequences into predicted amino acid sequences using MacClade 4.0 (Maddison and Maddison 2000) and then compared with the annotated *F. mediterranea* sequence AFTOL ID 688. The *rpb2* sequences from two *F. robusta* collections from Guyana (TH8903, TH8904) could not be obtained and were considered as missing data in the combined dataset.

The Alignment is deposited at TreeBASE (<http://www.treebase.org/treebase/index.html>) under study accession URL: <http://purl.org/phylo/treebase/phyloids/study/TB2:S12874>.

The indels present in our data sets, especially in the ITS1 region (Decock et al. 2007), were recoded as binary characters following the Simple Indel Coding method (SIC, Simmons and Ochoterena 2000) as implemented in the SeqState software (Müller 2005), in order to avoid long-branch attraction artifact.

The dataset was subdivided into 12 data partitions: ITS1, 5.8S, ITS2, nucLSU, *tefl*-1st, -2nd, -3rd codon positions, *tefl* introns, *rpb2* 1st, -2nd, -3rd codon positions, and indels (Table II).

Phylogenetic analyses were performed separately for each individual and concatenated loci using maximum parsimony (MP) as implemented in PAUP* version 4.0b10 (Swofford 2003), Bayesian inference (BI) as implemented in MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003) and Maximum likelihood (ML) as implemented in RAxML 7.0.4 (Stamatakis 2008). *Phellinus uncisetus* was used as outgroup (Decock et al. 2007).

The most parsimonious trees (MPT) for each data set were identified using heuristic searches with 1,000 random addition sequences, further evaluated by bootstrap analysis, retaining clades compatible with the 50% majority-rule in the bootstrap consensus tree. Analysis conditions were tree bisection and reconnection (tbr) branch swapping, starting tree obtained via stepwise addition, steepest descent not in effect, MulTrees effective. Clades with a bootstrap support value (BS) above 85% were considered confidently supported by the data.

Models of evolution for BI were estimated using the Akaike information criterion (AIC) as implemented in Modeltest 3.7 (Posada and Crandall 1998). In order to facilitate the data partitioning by codon position

for the *tefI*, the three introns present were excised and analyzed as a distinct partition.

The best-fit models for each partition were implemented as partition-specific models within partitioned mixed-model analyses of the combined dataset (Table II). For analysing the SIC data under BI, we used the Restriction Site Model (F81-like) of MrBayes 3.1.2 (Ronquist et al. 2005). All parameters were unlinked across partitions. Bayesian analyses were implemented with two independent runs, each with four simultaneous independent chains for ten million generations, starting from random trees, and keeping one tree every 1000th generation. The tree with the best likelihood value (see below ML) was used as a starting tree for the Bayesian analyses.

All trees sampled after convergence (ave. standard deviation of split frequencies <0.01 and confirmed using Tracer v1.4 [Rambaut and Drummond 2007]) were used to reconstruct a 50% majority-rule consensus tree (BC) and to calculate Bayesian posterior probabilities (BPP). BPP of each node was estimated based on the frequency at which the node was resolved among the sampled trees with the consensus option of 50% majority-rule (Simmons et al. 2004). A probability of 0.95 was considered significant.

Maximum likelihood (ML) searches conducted with RAxML involved 1000 replicates under the GTRGAMMAI model, with all model parameters estimated by the program. In addition 1000 bootstrap (ML BS) replicates were run with the same GTRGAMMAI model. We provided an additional alignment partition file to force RAxML software to search for a separate evolution model for each dataset including the recoded indels. Clades with Maximum likelihood bootstrap values of 85% or greater were considered supported by the data.

To detect topological conflicts among data partitions, the nodes between the majority-rule consensus trees obtained in the MP analysis from the individual data sets were compared. Paired trees were examined for conflicts only involving nodes with BS > 70% (Lutzoni et al. 2004, Mason-Gamer and Kellogg 1996, 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.

TABLE I. List of species, collections, and sequences used in the phylogenetic analyses.

Genus / Species names		GenBank accession number			
Voucher specimens / cultures reference					
	Locality	nLSU	ITS	<i>tefl-α</i>	RPB2
<i>Fomitiporia aethiopica</i> Decock, Bitew & G. Castillo					
MUCL 44777 (T)	Ethiopia	AY618204	GU478341	GU461893	JQ087956
MUCL 44806	Ethiopia	AY618202	GU461944	GU461892	JQ087955
<i>F. apiahyna</i> (Speg.) Amalfi, Robledo & Decock					
MUCL 51451	Ecuador	GU461997	GU461963	GU461896	JQ087958
MUCL 51454	Ecuador	JX093812	JX093769	JX093725	JX093856
MUCL 51456	Ecuador	JX093813	JX093770	JX093726	JX093857
MUCL 51474	Ecuador	JX093814	GU461961	JX093727	JX093858
MUCL 51485	Ecuador	GU461996	GU461962	GU461895	JQ087957
MUCL 53022	French Guiana	JX093815	JX093771	JX093728	JX093859
MUCL 53041	French Guiana	JX093816	JX093772	JX093729	JX093860
MUCL 53042	French Guiana	JX093817	JX093773	JX093730	JX093861
MUCL 53047	French Guiana	JX093818	JX093774	JX093731	JX093862
MUCL 53071	French Guiana	JX093819	JX093775	JX093732	JX093863

MUCL 53135	French Guiana	JX093820	JX093776	JX093733	JX093864
MUCL 53145	French Guiana	JX093821	JX093777	JX093734	JX093865
MUCL 53149	French Guiana	JX093822	JX093778	JX093735	JX093866
MUCL 53156	French Guiana	JX093823	JX093779	JX093736	JX093867
MUCL 53711	French Guiana	JX093824	JX093780	JX093737	JX093868
MUCL 53988	French Guiana	JX093825	JX093781	JX093738	JX093869
MUCL 53989	French Guiana	JX093826	JX093782	JX093739	JX093870
MUCL 53990	French Guiana	JX093827	JX093783	JX093740	JX093871
MUCL 53991	French Guiana	JX093828	JX093784	JX093741	JX093872
MUCL 53726	French Guiana	JX093829	JX093785	JX093742	JX093873
<i>F. australiensis</i> Fischer, Edwards, Cunningt. & Pascoe					
MUCL 49406 (PT)	Australia	GU462001	AY624997	GU461897	JQ087959
<i>Fomitiporia bakeri</i> (Murrill) Vlasák & Kout					
MUCL 51098	USA	JQ087901	JQ087874	JQ087928	JQ087960
<i>F. bannaensis</i> Y.C. Dai					
MUCL 45926	Thailand	EF429217	GU461942	GU461898	JQ087961
MUCL 46950	China	EF429218	GU461943	GU461899	JQ087962
<i>Fomitiporia calkinsii</i> (Murrill) Vlasák & Kout					
MUCL 51100	USA	JQ087902	JQ087875	JQ087929	JQ087963

MUCL 52346	Mexico	JQ087903	JQ087876	JQ087930	JQ087964
<i>F. castilloi</i> Amalfi & Decock					
MUCL 53481 (T)	French Guiana	JQ087916	JQ087889	JQ087943	JQ087996
MUCL 53980 (PT)	French Guiana	JX093830	JX093786	JX093743	JX093874
<i>F. cupressicola</i> (PS4) Amalfi, Raymundo, Valenzuela et Decock					
MUCL 52486 (T)	Mexico	JQ087904	JQ087877	JQ087931	JQ087965
MUCL 52488	Mexico	JQ087905	JQ087878	JQ087932	JQ087966
MUCL 52489	Mexico	JQ087906	JQ087879	JQ087933	JQ087967
MUCL 52490	Mexico	JQ087907	JQ087880	JQ087934	JQ087968
<i>F. dryophila</i> Murrill					
MUCL 46379	USA	EF429221	EF429240	GU461902	JQ087969
MUCL 46380	USA	EF429219	EF429238	GU461900	JQ087970
<i>F. erecta</i> (A. David, Dequatre & Fiasson) Fiasson					
MUCL 49871	France	GU461976	GU461939	GU461903	JQ087971
<i>F. gabonensis</i> Amalfi & Decock					
MUCL 47576 (T)	Gabon	GU461990	GU461971	GU461923	JQ087972
MUCL 51291	Gabon	GU461986	GU461967	GU461924	JQ087973
<i>Fomitiporia cf hartigii</i> (Allesch. & Schnabl) Fiasson & Niemelä					
MUCL 51295	USA	JQ087908	JQ087881	JQ087935	JQ087974

Fomitiporia hartigii (Allesch. & Schnabl) Fiasson & Niemelä

MUCL 31400	Europe	JQ087909	JQ087882	JQ087936	JQ087975
MUCL 53549	Europe	JX093831	JX093787	JX093744	JX093875
MUCL 53550	Europe	JX093832	JX093788	JX093745	JX093876
MUCL 53551	Europe	JX093833	JX093789	JX093746	JX093877

F. hippophaeicola (H. Jahn) Fiasson & Niemelä

MUCL 31746	Belgium	AY618207	GU461945	GU461904	JQ087976
MUCL 31747	Belgium	GU461977	GU461946	GU461905	JQ087977

F. ivindoensis Decock, Amalfi & Yombiyeni

MUCL 51311	Gabon	GU461979	GU461952	GU461907	JQ087978
MUCL 51312 (T)	Gabon	GU461978	GU461951	GU461906	JQ087979

F. langloisii Murrill

MUCL 46375	USA	EF429225	EF429242	GU461908	JQ087980
MUCL 46165 (T of <i>F. hesleri</i>)	USA	EF429223	AY340026	GU461909	JQ087981

F. maxonii Murrill

MUCL 46017	Cuba	EF429230	EF433559	GU461910	JQ087983
MUCL 46037	Cuba	EF429231	EF433560	GU461911	JQ087982

F. mediterranea M. Fisch.

AFTOL ID 688	ND	AY684157	AY854080	AY885149	AY803748
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MUCL 38514	Italy	AY618201	GU461953	GU461912	JQ087984
MUCL 45670	France	GU461980	GU461954	GU461913	JQ087985
<i>F. nobilissima</i> Decock & Yombiyeni					
MUCL 47580	Gabon	GU461985	GU461966	GU461921	JQ087986
MUCL 51289 (T)	Gabon	GU461984	GU461965	GU461920	JQ087987
<i>F. polymorpha</i> M. Fisch.					
MUCL 46166 (= 91-42/3) (PT)	USA	DQ122393	GU461955	GU461914	JQ087988
MUCL 46167 (= 91-42/1) (PT)	USA	EF429233	GU461956	GU461915	JQ087989
<i>F. pseudopunctata</i> (A. David, Dequatre & Fiasson) Fiasson					
MUCL 51325	Czech	GU461981	GU461948	GU461916	JQ087998
MUCL 46168	France	JQ087918	JQ087891	JQ087945	JQ087999
<i>F. punctata</i> (Fr.) Murrill					
MUCL 34101	Germany	AY618200	GU461947	GU461917	JQ088000
MUCL 47629	Japan	GU461982	GU461950	GU461918	JQ088001
MUCL 53548	Europe	JX093834	JX093790	JX093747	JX093878
<i>F. punicata</i> Y.C. Dai, B.K. Cui & Decock					
Cui 23	China	GU461991	GU461974	GU461927	JQ088002
Cui 26	China	GU461992	GU461975	GU461928	JQ088003
<i>F. robusta</i> (P. Karst.) Fiasson & Niemelä					

MUCL 51297	Estonia	JQ087919	JQ087892	JQ087946	JQ088004
MUCL 51327	Czech	GU461993	GU461949	GU461929	JQ088005
<i>Fomitiporia sonora</i> (Gilb.) Y.C. Dai					
MUCL 47689 (T)	Arizona	JQ087920	JQ087893	JQ087947	JQ088006
<i>Fomitiporia</i> “sp.”					
CBS 386.66 = MUCL 46181	Argentina	EF429234	EF433563	GU461930	JQ088007
MUCL 53675	French Guiana	JX093835	JX093791	JX093748	JX093879
<i>Fomitiporia</i> “sp.”					
MUCL 47756	Argentina	JQ087913	JQ087886	JQ087940	JQ087993
MUCL 47757	Argentina	JQ087914	JQ087887	JQ087941	JQ087994
MUCL 47758	Argentina	JQ087915	JQ087888	JQ087942	JQ087995
<i>Fomitiporia</i> “sp.”					
MUCL 53009	South Africa	JQ087917	JQ087890	JQ087944	JQ087997
<i>Fomitiporia</i> “sp.”					
MUCL 53114	French Guiana	JX093836	JX093792	JX093749	JX093880
<i>Fomitiporia</i> “sp.” PS1					
TH 8903	Guyana	JX093837	JX093793	JX093750	ND
TH 8904	Guyana	JX093838	JX093794	JX093751	ND
<i>Fomitiporia</i> “sp.” PS2					

MUCL 53108	French Guiana	JX093839	JX093795	JX093752	JX093881
MUCL 53705	French Guiana	JX093840	JX093796	JX093753	JX093882
MUCL 53992	Guadalupe	JX093841	JX093797	JX093754	JX093883
<i>Fomitiporia</i> “sp.” PS3 a					
MUCL 51464	Ecuador	JX093842	JX093798	JX093755	JX093884
MUCL 53034	French Guiana	JX093843	JX093799	JX093756	JX093885
MUCL 53106	French Guiana	JX093844	JX093800	JX093757	JX093886
MUCL 53111	French Guiana	JX093845	JX093801	JX093758	JX093887
MUCL 53785	French Guiana	JX093846	JX093802	JX093759	JX093888
MUCL 53793	French Guiana	JX093847	JX093803	JX093760	JX093889
MUCL 53800	French Guiana	JX093848	JX093804	JX093761	JX093890
MUCL 53985	French Guiana	JX093849	JX093805	JX093762	JX093891
<i>Fomitiporia</i> “sp.” PS3 b					
GC-FG-10-125	French Guiana	JX093850	JX093806	JX093763	JX093892
<i>Fomitiporia</i> “sp.” PS4					
MUCL 53993	Mexico	JX093851	JX093807	JX093764	JX093893
MUCL 53994	Mexico	JX093852	JX093808	JX093765	JX093894
<i>Fomitiporia</i> “sp.” PS5					
MUCL 51555	Martinica	JX093853	JX093809	JX093766	JX093895

MUCL 53797	French Guiana	JX093854	JX093810	JX093767	JX093896
<i>Fomitiporia</i> “sp.” PS6					
MUCL 53798	French Guiana	JX093855	JX093811	JX093768	JX093897
<i>F. tabaquilio</i> (Urcelay, Robledo & Rajchenb.) Decock & Robledo					
MUCL 46230	Argentina	DQ122394	GU461940	GU461931	JQ088008
MUCL 47754	Argentina	GU461994	GU461941	GU461932	JQ088009
<i>F. tenuis</i> Decock, Bitew & G. Castillo					
MUCL 44802 (T)	Ethiopia	AY618206	GU461957	GU461934	JQ088010
MUCL 49948	Gabon	GU461998	GU461958	GU461935	JQ088011
MUCL 49971	Uganda	GU461998	GU461958	GU461935	JQ088012
<i>Fomitiporia texana</i> (Murrill) Nuss					
MUCL 47690	Arizona	JQ087921	JQ087894	JQ087948	JQ088013
MUCL 51143	Arizona	JQ087922	JQ087895	JQ087949	JQ088014
<i>Fomitiporia torreyae</i> Y.C. Dai & B.K. Cui					
MUCL 47628	Japan	JQ087923	JQ087896	JQ087950	JQ088015
WC31	Chine	JQ087924	JQ087897	JQ087951	JQ088016
<i>Fomitiporia tsugina</i> Murrill					
MUCL 52702	USA	JQ087925	JQ087898	JQ087952	JQ088017
MUCL 52703	USA	JQ087926	JQ087899	JQ087953	JQ088018

Phellinus juniperinus Bernicchia & S. Curreli

MUCL 51757	Tunisia	JQ087927	JQ087900	JQ087954	JQ088019
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P. uncisetus Robledo, Urcelay & Rajchenb.

MUCL 46231	Argentina	EF429235	GU461960	GU461937	JQ088020
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MUCL 47061	Argentina	GU462000	GU461972	GU461938	JQ088021
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T, PT = type, paratype.

RESULTS

Sequence data and statistical analysis are provided in Table II.

DNA sequence comparisons.— The 5' region of the nLSU gene including domains D1, D2, and D3 ranged from 871 (*F. langloisii*) to 877 bps (*F. cupressicola*).

The ITS-5.8S region ranged from 662 (*Fomitiporia* sp. MUCL 47756, MUCL 47757, and MUCL 47758) to 780 bps (*Fomitiporia* sp. MUCL 53481 and MUCL 53980). This differs from previously published data (702–704 [*F. hesleri*] to 746–749 bps [*F. polymorpha*], Decock et al. 2007, Fischer and Binder 2004). The presence of indels of variable length near the 5' end of the ITS1 accounts for most of this variation. Decock et al. (2007) evidenced the absence of a 31 bps long fragment in *F. maxonii*, *F. dryophila*, *F. langloisii*, and *Fomitiporia* sp. MUCL 46181. An identical deletion is present in the type strain of *F. sonorae* (CFMR RLG-10862-Sp / MUCL 47689), *Fomitiporia* sp. MUCL 53675, and *Fomitiporia* sp. MUCL 53114. A 70 bps long indel is present in the strains *Fomitiporia* sp. MUCL 47756, MUCL 47757, and MUCL 47758. A nearly identical 76 bps long indel is present in the strains *Fomitiporia* spp. MUCL 53797, MUCL 53798, and MUCL 51555. Given that these indels have different starting and ending positions and considering the results obtained from the analysis of the other individual datasets (data not shown), they are best regarded as independent evolution events. Thirty characters judged too ambiguous to be aligned in the ITS-5.8S regions were excluded from all analyses.

Amplicons ranging from 1155 (*F. bakeri*) to 1172 bps (*F. australiensis*) were obtained from the partial *tefl*. This region contains three clade specific, confidently alignable introns.

The partial *rpb2* region ranged from 810 to 813 bps; *Fomitiporia ivindoensis* presents an additional codon (GAG) in this region.

The final DNA sequence alignments resulted in 897 characters, including gaps, for the LSU gene (28 variable parsimony-uninformative and 118 parsimony-informative positions), 797 for the ITS dataset (59 variable parsimony-uninformative and 264 parsimony-informative positions), 1202 for the *tef1* region, introns included (44 variable parsimony-uninformative and 363 parsimony-informative positions), and 813 for the *rpb2* dataset (19 variable parsimony-uninformative and 269 parsimony-informative positions) and 359 for the recoded indels dataset (93 variable parsimony-uninformative and 262 parsimony-informative positions).

Individual dataset comparisons.— Sequence data and statistical analysis for each dataset and combined analysis are provided in Table II.

By comparing MP bootstrap tree topologies obtained for the individual datasets, no conflict involving significantly supported nodes was found; the datasets were therefore combined.

Combined dataset analysis.— 4064 characters were included in the analysis of which 243 were variable but parsimony-uninformative and 1276 parsimony-informative.

The heuristic search produced 3657 equally most parsimonious trees (4247 steps long; CI = 0.482, RI = 0.841, RC = 0.406), representing one main topology.

The two Bayesian runs converged to stable likelihood values (-ln 25875.131, -ln 25889.657) after 5105000 generations and 4895 (about 50% of the sampled trees) stationary trees from each analysis were used to compute a 50% majority rule consensus tree in PAUP* to calculate posterior probabilities.

In the ML searches with RAxML the combined dataset alignment had 1800 distinct patterns with a proportion of gaps and undetermined characters of 9.03%.

The strict consensus of the 3657 equally most parsimonious trees was mostly identical to the BC tree (Fig. 1) and to the best scoring ML tree (tree score of $-\ln L = -25229.376611$). The topology of this tree is highly concordant with topologies obtained analyzing the individual datasets. It is also coherent with previously published trees (Amalfi et al. 2010, 2012).

The results show that our Neotropical collections with pileate basidiomes are distributed into 8 distinct clades (Fig. 1). One clade, named “*F. apiahyna s.s.*” on Fig. 1, encompasses 52 % and 83 % of our collections tentatively identified as *F. apiahyna sensu* Ryvardeen (2004), collected in French Guiana and Ecuador, respectively. This clade corresponds to the *F. apiahyna* clade of Amalfi et al. (2010, 2012). Four additional clades (PS 1, PS 2, PS 3, & PS 4 on Fig. 1) are resolved in the near vicinity of the “*F. apiahyna s.s.*” clade. Altogether, these five clades form the *F. apiahyna* lineage.

Two clades (PS 5 & PS 6, Fig. 1) are nested in the vicinity of *F. texana*; they form together the *F. texana* lineage. The remaining clade (PS 7, Fig. 1) is related to the *F. langloisii* lineage (Amalfi et al. 2012, Decock et al. 2007). The *F. apiahyna*, *F. texana*, and *F. langloisii* lineages form part of a larger, presumed South American lineage (Amalfi et al. 2012).

It is worth noting that PS 7 (Fig. 1) is distantly related to all other clades representing species with pileate basidiomes as yet reported from South, Meso-, and North America, or elsewhere (Amalfi et al. 2010, 2012; Dai et al. 2008; Decock et al. 2007; Fischer and Binder 2004; Vlasák and Kout 2011, Zhou and Xue 2012). It is also distantly related to all other clades representing potential species with pileate basidiomes, sympatric in the surveyed areas (*viz.* PS 2, PS 3, PS 5, & PS 6, Fig. 1). In contrast, basal to the *F. langloisii* lineage, PS 7 is more closely related to species with resupinate basidiomes *viz.* in addition to *F. langloisii*, *F. sonorae*, *F.*

maxonii, *F. dryophila* (the latter species occasionally with false pseudopilei, Decock et al. 2007, Raymundo et al. 2012). Three unnamed collections (*Fomitiporia* sp. MUCL 53675, *Fomitiporia* sp. MUCL 46181, and *Fomitiporia* sp. MUCL 53114) nested also within the *F. langloisii* lineage. They correspond to undescribed species, having also with resupinate basidiomes.

Morphological analysis.— The two collections forming PS 7 show a singular combination of morphological features, thereby defining one morphospecies. This includes a black, roughly sulcate pileus, a rounded, folded margin, abundant, variably shaped hymenial setae, and basidiospores averaging 6.2 x 5.2 µm. There are few *Fomitiporia* with pileate basidiomes and hymenial setae. This includes *F. robusta* s.s., *F. texana*, and *F. polymorpha*. They differ from our species in several morphological characters and perhaps more importantly their ecological requirements that would preclude their occurrence in the very humid, French Guiana rainforest.

Given the results of the phylogenetic inferences that identify PS 7 as a phylogenetic species, and the morphological data that define a unique morphotype, PS 7 is considered as representing a distinct, undescribed species. The search for a possible epithet within the synonyms of *F. robusta* s.l. (Ryvarden 1991, Robert et al. 2005) yielded no name that could apply to it. This species is therefore proposed below as *F. castilloi* sp. nov.

TABLE II. Summary of datasets of ITS rDNA, LSU rDNA, *tef1* and *rp62*

Properties	Datasets											
	ITS 1	5.8S	ITS 2	nLSU	<i>tef1</i> 1st	<i>tef1</i> 2nd	<i>tef1</i> 3rd	<i>tef1</i> introns	<i>rp62</i> 1st	<i>rp62</i> 2nd	<i>rp62</i> 3rd	Indels
Model selected	GTR+G	K80	GTR+I+G	GTR+I+G	GTR+I+G	F81+I	GTR+G	HKY+G	GTR+I+G	F81+I	GTR+G	F81-like
Likelihood score	-2182.2107	-337.426	-2069.1279	-9055.2548	-683.5805	-568.4256	-2813.7737	-1854.0367	-783.8632	-487.8718	-4977.1646	—
Base frequencies												
Freq. A =	0.2894	equal	0.2448	0.2618	0.2944	0.3080	0.1459	0.2737	0.2739	0.3072	0.2125	—
Freq. C =	0.1490	equal	0.1853	0.1995	0.1920	0.2538	0.3132	0.1899	0.2434	0.1833	0.1932	—
Freq. G =	0.1850	equal	0.1951	0.2931	0.3754	0.1571	0.2357	0.1535	0.3520	0.2073	0.3069	—
Freq. T =	0.3766	equal	0.3748	0.2456	0.1382	0.2811	0.3032	0.3830	0.1307	0.3022	0.2874	—
Proportion of invariable sites	—	—	0.0170	0.5700	0.8160	0.8870	—	—	0.5380	0.8570	—	—
Gamma shape	1.0360	—	0.400	0.4090	0.9480	—	1.3160	3.4510	0.4510	—	1.4670	—

Taxonomy

Fomitiporia castilloi Decock et Amalfi **sp. nov.** Fig. 2, A-E

Mycobank: MB 563792.

Basidiomata perennis, pileada, spathulata, subdimidiata, leviter obtriquetra; pilei facies plana vel leviter adscendens, obscura, nigricans;

margina crassa, plicata, griseo-aurantiaca; pororum facies griseo-brunnea; pori rotundi, 7–8 per mm, (75–) 80–100 μm diam; tubi stratosi, in series ad 8 singula strata, 1–3.5 mm crassa, -18 mm longi; systema hypharum dimiticum; hyphae generatoriae hyalinae ad pallide luteae, afibulatae; hyphae skeletales flavo-brunneae, crassitunicatae, aseptatae; setae hymeniales ferrugineo-fuscae, subulatae vel ventricosae, rectae vel sinuatae, apice acutae, saepe rectae vel interdum leviter curvatae, 22–35 $\times$ 6.0–10.0 μm ; basidiosporae subglobosae vel obovoidae, leviter crassitunicatae, hyalinae, dextrinoideae, cyanophileae, (5.5–) 5.8–6.5 (–6.8) $\times$ (4.5–) 5.0–5.5 (–5.5) μm .

HOLOTYPE: FRENCH GUIANA, MUNICIPALITY OF REGINA: Nouragues Natural Reserve, CNRS "inselberg" research plots, “Petit Plateau”, layon (track) 22, between F & G, approx 04°05.5' N, 52°40.6' W, elev. approx 120 m, on a dead standing trunk, broken at about 1.8 m high, deeply rotten and eaten by insects, hollowed, unidentified angiosperm, 06 Aug 2010, C. Decock, FG-10-282 (MUCL 53481; Isotype at NY, culture ex-holotype MUCL 53481, CBS).

Etymology: "castilloi", dedicated to Dr. Gabriel Castillo, University of Liège, Belgium, for his constant support and invaluable companionship in many collecting trips in French Guiana or elsewhere over the last 20 years.

Basidiomata pileate, perennial; *primordia* nodulose, thick, rounded, light grayish brown to light brown; *mature basidiomata* sessile, single; *pileus* slightly spathulate, subdimidiate to semi-circular, slightly ascending, applanate to slightly obtriquetrous in section, occasionally with a basal umbo, projecting 40–60 mm, 35–65 mm wide, up to 30 mm thick at the base (35–40 mm at the umbo); *consistency* overall hard corky to woody, texture dense; *pileus surface* roughly sulcate, with 3 to 4 large bands, faintly velvety when young, glabrous when mature, mainly dull blackish, dark grayish

black; *margin* thick, rounded, folded, plicate, pale grayish brown, cork colored when fresh (6[B–C]4, café au lait), light brown on drying (6[D–E]5, cinnamon), contrasting with the darker pileus surface, occasionally exuding golden droplets; *pore surface* oblique, ascending, light brown, light grayish brown when fresh (6[C– E] [3–4], brownish orange, café au lait, brownish beige), mostly identical on drying (6E[3–4]); *pores* round, 7–8 per mm, (75–) 80–100 μm diam. (ave = 91.5 μm); *dissepiments* entire, rounded (agglutinated), thick, 50–100 (–150) μm thick; *tubes* distinctly stratified, with up to 8 distinct layers, individual layers 1–3.5 mm height, totaling up to 18 mm, light brown (6D[4–6]) and contrasting with the context, but the youngest (active) layer darker brown (6E6, cocoa brown); *context* homogeneous, azonated, up to 20 mm thick at the base, with a dense texture and a (hard corky) to woody consistency, dark brown (6E[5–7], cocoa brown), discoloring to a thin black line at the surface.

Hyphal system dimitic; *generative hyphae* simple septate, hyaline to pale yellow, poorly branched, 1.3–3.2 μm diam; *skeletal hyphae* golden brown to reddish brown (in KOH), unbranched, straight, occasionally with local swelling or peltate apices, thick-walled but with an open lumen, especially in the hymenophoral trama, 3.5–6.0 μm diam (local swelling up to 8 μm) in the context; 3.5–5.5 μm diam in the hymenophoral trama (swelling up to 8 μm); *hyphae* in the dissepiments thick-walled and yellowish ending thin-walled, hyaline, and occasionally moniloid.

Hymenium: *hymenial setae* abundant, brown, thick-walled, mostly 22–35 (–37) $\times$ 6.0–10.0 μm , (ave = 30 $\times$ 7.9 μm), occasionally smaller, down to 12 $\times$ 6 μm , very variable in shape, sessile or shortly pedicellate (then with a hyphal-like base, first parallel to the tramal hyphae then abruptly bent into the hymenium), subulate or ventricose, variably straight to sinuous, occasionally curved (to strongly curved), the apex acute, straight,

occasionally slightly curved; *cystidioles* rare, fusoid, hyaline, thin-walled; *basidioles* pear-shaped to subglobose, $10\text{--}13.5 \times 9\text{--}10 \text{ }\mu\text{m}$; *basidia* subglobose, hyaline, $12\text{--}14.5 \times 10\text{--}11.5 \text{ }\mu\text{m}$, with four small sterigmata; *basidiospores* (globose), subglobose to obovoid, hyaline, dextrinoid, cyanophilous, distinctly thick-walled, smooth, $(5.5\text{--}) 5.8\text{--}6.5 \text{ (}\text{--}6.8) \times (4.5\text{--}) 5.0\text{--}5.5 \text{ (}\text{--}5.5) \text{ }\mu\text{m}$, (ave = $6.2 \times 5.2 \text{ }\mu\text{m}$), $Q = (1.05\text{--}) 1.1\text{--}1.25 \text{ (}\text{--}1.3) \text{ }\mu\text{m}$ (ave_Q = $1.19 \text{ }\mu\text{m}$); *basidiospores* print white; *chlamydospores* absent.

Type of rot: white rot.

Ecology (host and habitat): growing on a dead, decayed trunk of an unidentified angiosperm, in the lowland rainforest of French Guiana.

Distribution: known so far only from the type locality.

Additional specimen examined: FRENCH GUIANA, MUNICIPALITY OF REGINA: Nouragues Natural Reserve, CNRS "inselberg" research plots, "Petit Plateau", layon (track) 22, between F & G, approx $04^{\circ}05.5' \text{ N}$, $52^{\circ}40.6' \text{ W}$, elev. approx 120 m, on a dead standing trunk, broken at about 1.8 m high, deeply rotten and eaten by insects, hollowed, unidentified angiosperm, 28 Jun 2011, C. Decock, FG-11-375 (MUCL 53980).

Comments. — *Fomitiporia castilloi* is characterized by pileate basidiomes, applanate to slightly obtriquetrous, a mainly black, roughly sulcate pileus surface, a rounded and plicate margin, 7–8 pores / mm, 80–100 diam, with thick dissepiments, variable, straight to sinuous hymenial setae, and basidiospores averaging $6.2 \times 5.2 \text{ }\mu\text{m}$.

Mycelial growth is very slowly *in vitro* on the artificial culture media tested (MA2, CHA, DYPA, Untereiner et al. 1998): colonies on MA2 and CHA reached a diam of 5–7 mm after one month of incubation at 27°C , with the mycelium shortly velutinous. It grows slightly faster on media supplemented by yeast extract (DYPA).

Fomitiporia castilloi seems to be rare in the areas surveyed in French Guiana. It was collected from a single trunk, with the basidiomes distributed in two distinct zones: near the soil level and at about 1.0–1.2 m high. DNA was analyzed from one basidiome of each zone. The LSU and ITS sequences were identical but the *rpb2* and *tefl-α* sequences differed in 4 nucleotide positions; hence, these two basidiomes are considered as emerging from two genets. In comparison, the "*F. apiahyna s.s.*" clade is well represented in the same forest plots (Nourague, *Grand* and *Petit plateaux*), with 15 specimens collected by the same collector (CD).

Maj. 1881, LPS 24922 !]. *Fomitiporia apiahyna* has narrowly and sharply sulcate, black pilei, an acute, sharp margin (Fig 2f), and setae are absent. Setae are also absent from all other neotropical specimens of the *F. apiahyna* and *F. texana* lineages (forming clades PS 1, PS 2, PS 3 & PS 4 and PS 5 & PS 6).

Fomitiporia robusta s.s. differs by having, i.a., larger pores [4–6 / mm (Domański 1967), 5–6 pores /mm (Ryvarden 1978); 7–8 in *F. castilloi*] and basidiospores on average larger and with the upper range commonly ≥ 7.5 μm [e.g. $6.5\text{--}7.5 \times 6.0\text{--}7.0$ μm , ave = 7.1×6.7 μm (Decock et al. 2007); $6\text{--}8 \times 5.5\text{--}8$ μm (Domański 1967); $6.5\text{--}8.5 \times 5.5\text{--}7.5$ μm (Ryvarden 1978)]. Furthermore, this species occurs preferably on *Quercus* in Northern / Central Europe (Domański 1967, Jahn 1976, Ryvarden 1978).

Two other species occurring in America have occasional hymenial setae: *F. texana* (Gilbertson and Ryvarden 1987) and *F. polymorpha* (Fischer and Binder 2004). *Fomitiporia texana* differs from *F. castilloi* in having deeply rimose pilei and larger basidiospores ($7\text{--}9 \times 6.5\text{--}9$ μm , Gilbertson and Ryvarden 1987, Larsen and Cobb-Pouille 1990) whereas *F. polymorpha* forms resupinate to nodulose basidiomes and has also slightly larger basidiospores ($6.5\text{--}7.5 \times 5.5\text{--}6.5$ μm , Fischer and Binder 2004). These species also have very distinct habitats and ecologies. *Fomitiporia texana* occurs in dry, semi-desert ecosystems of southern USA and northern Mexico (Gilbertson and Ryvarden 1987, Raymundo et al. 2012). *Fomitiporia polymorpha* is known only from western USA, growing preferably on *Salix* (Fischer and Binder 2004).

Additional comments on *F. robusta* and *F. apiahyna* in South America.

Fomitiporia robusta. — *Fomitiporia robusta* s.l. was reported with a cosmopolitan distribution and multiple hosts (e.g. Dai 2010, Gilbertson and

Ryvarden 1987, Núñez and Ryvarden 2000, Ryvarden and Gilbertson 1994, Ryvarden and Johansen 1980). As noted by Gilbertson and Ryvarden (1987) and Amalfi et al. (2012), it forms a taxonomically difficult complex.

Data now available strongly suggest that *F. robusta* s.s. [*Phellinus robustus* var. *robustus sensu* Domański (1967) or *Phellinus robustus sensu* Ryvarden (1978), that, in our opinion, corresponds to the *F. robusta* clade (Fig 1, cf. also Amalfi et al. 2010, 2012)], is more likely to be restricted to Northern and Central Europe, perhaps extending over northern Eurasia.



FIGS. 2. Basidiomes of *Fomitiporia castilloi* (MUCL 53481) and *Fomitiporia apiahyna* (MUCL 53022) *in situ* (pictures Cony Decock): A, B, C, E., *F. castilloi*, mature basidiomata (A, B, E: scale bar = 40 mm; C: scale bar = 55 mm); D. *F. castilloi*, primordia, scale bar = 15 mm; E, *F. apiahyna* (scale bar = 50 mm).

It would be thus absent from the New World. *Fomitiporia robusta* *sensu* “North American” *auctores* (e.g. Gilbertson and Ryvarden 1987, Lowe 1957, Larsen and Cobb-Pouille 1999) was repeatedly demonstrated to

encompass various species but *F. robusta* s.s. These include *F. bakeri*, *F. calkinsii*, *F. dryophila*, *F. texana*, *F. polymorpha*, *F. cupressicola*, and several still unnamed taxa evidenced by molecular (DNA sequences) data (Amalfi et al. 2012, Decock et al. 2007, Vlasák and Kout 2011). Morphological and DNA-based identifications of a set of specimens identified as *F. robusta* s.l. originating from Mexico, from different hosts, also did not reveal this species (Raymundo 2012, Raymundo et al. 2012; pers. obs.).

The present data confirm that the neotropical collections previously identified as *F. robusta* in Woolley et al. (2008) or as *F. robusta sensu lato* growing on Fagaceae in Mexico (pers. data) are unrelated to *F. robusta* s.s. and to all other species of the *F. robusta* complex identified in North America (Amalfi et al. 2012, Vlasák and Kout 2011). These collections belong to two distinct species, within the *F. apiahyna* lineage (Fig 1). The entire basidiomata of these collections are not available for the time being, impeding any complete phenotypical characterization. Morphologically, they differ from *F. robusta* s.s. in having distinctly smaller basidiospores, of the size recorded in *F. castilloi*.

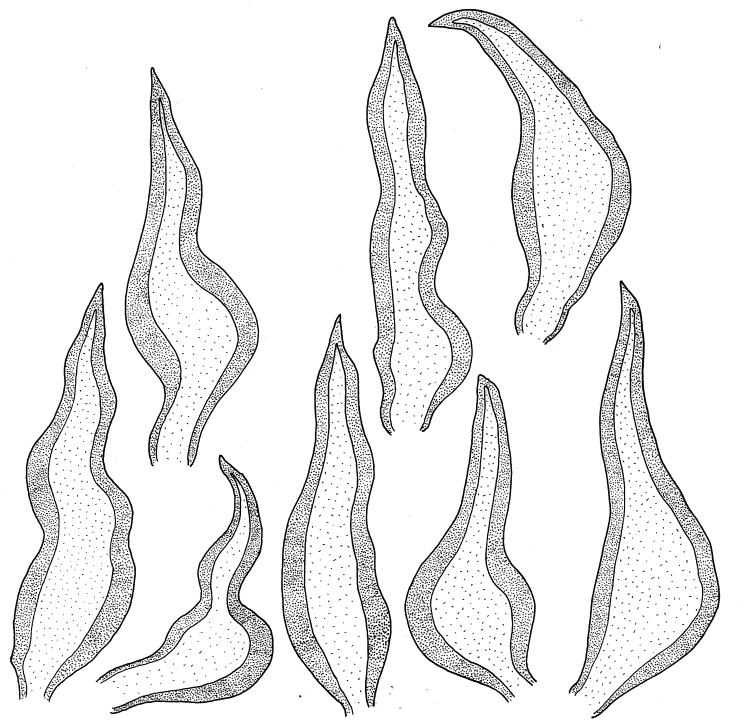


FIG. 3. Microscopical features of *Fomitiporia castilloi* (from the type): hymenial setae (scale bar = 15 μm).

Fomitiporia apiahyna.— *Fomitiporia apiahyna* was reported as widespread but rare in the Neotropics (Ryvarden 2004). It is cited from southern Brazil and northeastern Argentina (Loguercio Leite and Wright 1991, Rajchenberg and Wright 1987, Wright and Blumenfeld 1984), eastern Ecuador (Amalfi et al. 2010), Panama (Gilbert et al. 2002), and northerly from Costa Rica (Ryvarden 2004) to southern Mexico (Raymundo et al. 2012) and southern Florida (Vlasák et al. 2011).

Outside of the Neotropics, Renvall and Niemelä (1993) and Niemelä (in Härkönen et al. (2003) reported it from altitude forests of Tanzania, eastern Africa, growing on *Ocotea usambarensis* (Lauraceae). These African records have been strongly questioned, however (Amalfi et al. 2010).

From an ecological point of view, Gilbert et al. (2002) noted possible host specificity for members of *Ocotea* Aubl. (Lauraceae) in the Barro Colorado Islands, Panama. Ryvarden (2004) noted that the species was growing on various angiosperms, whereas Vlasák et al. (2011) recorded this species on *Sabal palmetto* (Walt.) Lodd. (Arecaceae).

The phylogenetic inferences segregated our Neotropical collections (Table 1, 27 specimens) of *F. apiahyna sensu* Ryvarden (2004) into 5 clades distributed over two lineages: the *F. apiahyna* lineage (clades *F. apiahyna*, PS1, PS 2, PS3 & PS4) and the *F. texana* lineage (clades PS 5 & PS 6). The "*F. apiahyna s.s.*" clade (Fig 1) is identified as *F. apiahyna s.s.* on the basis of morphological comparisons of the collections constitutive of this clade with the type specimen. It represents the most frequent species in the sampled plots [respectively 15 and 5 collections of *F. apiahyna s.s.* / 27 and 6 of *F. apiahyna s.l.* in the Nouragues (French Guiana) and Yasuni areas (Ecuador)]. The species may thus be locally common.

The hosts of our *F. apiahyna s.s.* specimens have been identified in a few cases only but encompass a higher than presumed botanical diversity

(Gilbert et al. 2002). It includes, in addition to *Ocotea* sp. (Lauraceae), *Licania alba*, *Licania* sp. (Chrysobalanaceae), and *Inga paraensis* (Fabaceae), and an unidentified Myrtaceae.

PS 3 was observed both in French Guiana (8/27) and Ecuador (1/6). PSs 2 & 5 are recorded from French Guiana and, respectively, the Lesser Antilles, Guadeloupe (PS 2) and Martinique (PS 5). The hosts of the specimens from PS 3 have been identified in one case only, viz. *Qualea rosea* (Vochysiaceae). The specimens on palm cited by Vlasák et al. (2011) were not available to us.

This study unveiled within the Neotropical *Fomitiporia* with pileate basidiomes a (phylo)genetic and, if once translated into the Linnean taxonomic scheme, a much wider than previously reported species diversity in Meso- and South America (Ryvarden 2004). It complements other data about the phylogenetic and taxonomic diversity within the *F. robusta* complex in America (Amalfi et al. 2012, Fischer and Binder 2004, Vlasák and Kout 2011). However, comparisons with various types are still necessary to tackle the *F. apiahyna* complex. This includes a revision of *Phellinus elegans* J.E. Wright & Blumenf., described from Argentina (Wright and Blumenfeld 1984), *Pyropolyporus crustosus* Murrill, and *P. haematoxyli* Murrill, both originating from Jamaica (Murrill 1903). These names might apply to some of the unnamed PSs (but see Decock et al. 2007 for the application of long forgotten names for "cryptic" species best evidenced by molecular data).

As a consequence, the reports of *F. apiahyna* in its presumed distribution range (from southern Florida to southern Brazil) should be better considered as *sensu auctores* or *sensu lato* and re-analyzed, considering a more integrated species concept, including molecular data.

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References

- Amalfi M, Yombiyeni P, Decock C. 2010. *Fomitiporia* in sub-Saharan Africa: morphology and multigene phylogenetic analysis support three new species from the Guineo-Congolian rainforest. *Mycologia* 102:1303–1317.
- , Raymundo T, Valenzuela R, Decock C 2012. Multilocus phylogenetic analyses (and host relationships) support the recognition of *Fomitiporia cupressicola* sp. nov., parasites on *Cupressus arizonica*, and evidence additional unnamed clades in southern USA and northern Mexico. *Mycologia* 104: 880–893

Castresana J, 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Mol Bio Evol* 17: 540–552.

Dai Y-C. 2010. Hymenochaetaceae (Basidiomycota) in China. *Fungal Diversity* 45:131–343.

———, Cui B-K, Decock C. 2008. A new species of *Fomitiporia* (Hymenochaetaceae, Basidiomycota) from China. *Mycol Res* 112: 375–380.

Decock C, Bitew A, Castillo G. 2005. *Fomitiporia tenuis* and *Fomitiporia aethiopica* (Basidiomycetes, Hymenochaetales), two undescribed species from the Ethiopian highlands: taxonomy and phylogeny. *Mycologia* 97:124–132.

———, Herrera Figueroa S, Robledo G, Castillo G. 2007. *Fomitiporia punctata* (Basidiomycota, Hymenochaetales) and its presumed taxonomic synonyms in America: taxonomy and phylogeny of some species from tropical/subtropical areas. *Mycologia* 99:733–752.

Domański S, Orlos SH, Skirgiello A. 1967. Grzyby (Zagwiowate II, Szczeciniakowate II). - Państwowe Wydawnictwo Naukowe, 395 pp. (1973 - Fungi: Polyporaceae II (pileatae), Mucronoporaceae II (pilaetae) - U.S. Dep. Commerce, Springfield, 332 pp.)

Fischer M. 1996. On the species complexes within *Phellinus*: *Fomitiporia* revisited. *Mycol Res* 100:1459–1467.

———. 2002. A new wood-decaying Basidiomycetes species associated with esca of grapevine: *Fomitiporia mediterranea* (Hymenochaetales). *Mycol Progress* 1: 315–324.

———, Binder M. 2004. Species recognition, geographic distribution, and host-pathogen relationships: a case study in a group of lignicolous Basidiomycetes, *Phellinus s.l.* Mycologia 96:799–811.

Frøslev TG, Matheny PB, Hibbett DS (2005). Lower level relationships in the mushroom genus *Cortinarius* (Basidiomycota, Agaricales): a comparison of RPB1, RPB2, and ITS phylogenies. *Molecular Phylogenetics and Evolution* 37: 602–618.

Gilbert SG, Ferrer A, Carranza J. 2002. Polypore fungal diversity and host density in a moist tropical forest. *Biodivers Conserv* 11:947–957.

Gilbertson RL, Ryvarden L. 1987. North American Polypores. Part 2. *Megasporoporia – Wrightoporia*. Fungiflora, Oslo, Norway: 433–885.

Härkönen M, Niemelä T, Mwasumbi L. 2003. Tanzanian mushroom – edible, harmful, and other fungi. Botanical Museum, Finnish Museum of Natural History, Helsinki, Finland:1–200.

Jahn H. 1976. Mitteleuropäische Porlinge (Polyporaceae s.l.) und ihr Vorkommen in Westfalen. *Bibl Mycol* 29: 1–143.

Kirk PM, Cannon PF, David JC, Stalpers JA. 2001. Ainsworth & Bisby's Dictionary of the Fungi, 9th edition. CABI Publishing, Wallingford, UK:1–655.

Kornerup A, Wanscher JH. 1981. Methuen handbook of color, 3rd Edition:1–282.

Larsen MJ, Cobb-Poulsen LA. 1990. *Phellinus* (Hymenochaetaceae). *Synopsis Fungorum* 3, Oslo, Norway: Fungiflora:1–206.

Loguercio Leite C, Wright JE 1991. Contribution to a biogeographical study of the austro-american xylophilous polypores (Aphyllphorales) from Santa Catarina, SC, Brazil. *Mycotaxon* 41:161–166.

Lowe JL. 1957. Polyporaceae of North America. The genus *Fomes*. Syracuse, New York: State University College of Forestry, Syracuse University. 97 p.

Lutzoni F, Kauff F, Cox CJ, McLaughlin D, Celio G, Dentinger B, Padamsee M, Hibbett D, James TY, Baloch E, Grube M, Reeb V, Hofstetter V, Schoch C, Arnold AE, Miadlikowska J, Spatafora J, Johnson D, Hambleton S, Crockett M, Shoemaker R, Sung G-H, Lücking R, Lumbsch T, O'Donnell K, Binder M, Diederich P, Ertz D, Gueidan C, Hansen K, Harris RC, Hosada K, Lim Y-W, Matheny B, Nishida H, Pfister D, Rogers J, Rossman A, Schmitt I, Sipman H, Stone J, Sugiyama J, Yahr R, Vilgalys R. 2004. Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. *Am J Bot* 91: 1446–1480.

Maddison D, Maddison W. 2000. MacClade 4.0. Analysis of phylogeny and character evolution. Sunderland, MA: Sinauer Associates.

Mason-Gamer RJ, Kellogg EA. 1996. Testing for phylogenetic conflict among molecular data sets in the tribe Triticeae (Gramineae). *Syst Biol* 45:524–545.

Matheny PB (2005). Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*, Agaricales). *Molecular Phylogenetics and Evolution* 35: 1–20.

———, Wang Z, Binder M, Curtis JM, Lim YW, Nilsson RH, Hughes KW, Petersen RH, Hofstetter V, Ammirati JF, Schoch C, Langer GE, McLaughlin DJ, Wilson AW, Crane PE, Frøslev T, Ge ZW, Kerrigan RW, Slot JC, Vellinga EC, Liang ZL, Aime MC, Baroni TJ, Fischer M, Hosaka K, Matsuura K, Seidl MT,

- Vaura J, Hibbett DS. 2007. Contributions of *rpb2* and *tefl* to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Mol Phyl Evol* 43:430–451.
- Müller K. 2005. SeqState—primer design and sequence statistics for phylogenetic DNA data sets, *Applied Bioinformatics* 4:65–69.
- Murrill WA. 1903. The Polyporaceae of North America II. The genus *Pyropolyporus*. *Bull Torrey Bot Club* 30: 109–120.
- Núñez M, Ryvarden L. 2000. East Asian Polypores. Vol. 1. Ganodermataceae and Hymenochaetaceae. *Fungiflora*, Oslo, Norway: 1–168.
- Posada D, Crandall KA. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817–818
- Rajchenberg M, De Meijer AR. 1990. New and noteworthy polypores from Paraná and São Paulo States, Brazil. *Mycotaxon* 38:173–185.
- , Wright JW. 1987. Type studies of Corticiaceae and Polyporaceae (Aphylliphorales) described by C. Spegazzini. *Mycologia* 79:246–264.
- Rambaut A, Drummond AJ. 2007. Tracer v1.4, [<http://beast.bio.ed.ac.uk/Tracer>]
- Raymundo T. 2012. Taxonomía y filogenia del género *Fomitiporia* Murrill (Hymenochaetales) en México. Universidad Autónoma Metropolitana, México, PhD dissertation thesis: 1–103.
- , Decock C., Amalfi M., Valenzuela R., Cifuentes J., Pecheco-Mota L. 2012. New records of the genus *Fomitiporia* (Hymenochaetales, Basidiomycota) in Mexico. *Rev Mex Biodiv*: 83:313–328

Reeb V, Lutzoni F, Roux C. 2004. Contribution of RPB2 to multilocus phylogenetic studies of the euascomycetes (Pezizomycotina, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory. *Mol Phyl Evol* 32:1036–1060.

Rehner SA, Buckley E. 2005. A *Beauveria* phylogeny inferred from nuclear ITS and EF1-a sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97:84–98

Renvall P, Niemelä T. 1993. *Ocotea usambarensis* and its fungal decayers in natural stands. *Bull Jard Bot Nat* 62:403–414.

Robert V, Stegehuis G, Stalpers J. 2005. The MycoBank engine and related databases. <http://www.mycobank.org>

Ronquist F, Huelsenbeck JP. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.

———, Huelsenbeck JP, Van der Mark P. 2005. MRBAYES 3.1 manual. In School of Computational Science, Florida State University 2005 Tallahassee, FL:School of Computational Science, Florida State University

Ryvarden L. 1978. The Polyporaceae of North Europe. Volume 2 (*Inonotus* – *Tyromyces*). Oslo, Norway: Fungiflora: 219–507.

———. 1991. Genera of Polypores: Nomenclature and taxonomy. *Synopsis Fungorum* 5:1–363.

———. 2004. Neotropical Polypores 1. *Synopsis Fungorum* 19:1–229.

———, Gilbertson RL. 1994. European polypores 2. *Meripilus–Tyromyces*. Synopsis Fungorum 7, Oslo, Norway: Fungiflora: 392–743.

———, Johansen I, 1980. A preliminary polypores flora of East Africa. Fungiflora, Oslo, Norway: 1–636.

Simmons MP, Ochoterena H. 2000. Gaps as characters in sequence-based phylogenetic analyses. Syst Biol 49:369–381.

———, Pickett KM, Miya M. 2004. How meaningful are Bayesian support values? Mol Biol Evol 21:188–199.

Stamatakis A, Hoover P, Rougemont J. 2008. A rapid bootstrap algorithm for the RAxML Web-Servers. Syst Biol 75:758–771.

Swofford, D. L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Thiers B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. 1997. [The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools.](#) Nucleic Acids Res 25:4876–4882.

Untereiner WA, Bonjean B, Decock C, Evrard P, de Frahan MH, Jamin N, Massart L, Nélissen L, Robert V, Bosschaerts M, Guissart F, De Brabandere J. 1998. MUCL Catalogue of strains (Fungi-Yeast). 3^e Ed. Published by the Belgian Office for Scientific, technical and Cultural Affairs, Brussels, Belgium.

Vlasák J, Kout J. 2011. Pileate *Fomitiporia* species in the USA. New combinations *Fomitiporia calkinsii* and *F. bakeri*. Mycol Progress 10: 445–452.

———, Kout J, Vlasák J Jr, Ryvarden L. 2011. New records of polypores from southern Florida. Mycotaxon 118:159–176.

Woolley LP, Henkell TW, Sillett SC. 2008. Reiteration in the monodominant tropical tree *Dicymbe corymbosa* (Caesalpiniaceae) and its potential adaptive significance. Biotropica 40: 32–43

Wright JE, Blumenfeld SN. 1984. New South American species of *Phellinus* (Hymenochaetaceae). Mycotaxon 21:413–425.

Zhou LW, Xue HJ. 2012. *Fomitiporia pentaphylacis* and *F. tenuitubus* spp. nov. (Hymenochaetales, Basidiomycota) from Guangxi, southern China. Mycol Progress 11: 907–913.

CHAPTER IV

***Fomitiporia baccharidis* comb. nov., a little known species from high elevation Andean forests and its affinities within the neotropical *Fomitiporia* lineages.**

This paper represents a continuation of our revision of the *Fomitiporia* species with pileate basidiomata in the New World. The new combination *Fomitiporia baccharidis*, originating from Andean high elevation forests, is proposed and the status of the pileate Neotropical subclade discussed. The American intracontinental phylogeographic structure seems to indicate complex biological / biogeographical histories.

***Fomitiporia baccharidis* comb. nov., a little known species from high elevation Andean forests and its affinities within the neotropical *Fomitiporia* lineages.**

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Abstract: in the frame of a revision of the *Fomitiporia* species with pileate basidiomata in the New World, several collections originating from Andean, high elevation forests of Argentina were found to represent a terminal clade in multilocus phylogenetic inferences (including nuclear ribosomal partial LSU and ITS-5.8S, partial *tef1-α* and RPB2 genes). These collections represent also a singular morphotype within *Fomitiporia*, characterized by mostly pileate basidiomata, with a soft corky consistency, roughly sulcate pilei, a “duplex” context with a thin black line, and

dextrinoid basidiospores, averaging $5.9 \times 5.3 \mu\text{m}$. It also has a well-marked autecology, occurring on shrubby trees in high elevation forest along the Andean range. A search in the literature for a name pointed toward *Phellinus baccharidis*, despite the fact that this species was repeatedly described with non-dextrinoid basidiospores. Examination of the type of *P. baccharidis* confirmed the main morphological features as previously described but for the reaction of basidiospores in Melzer's reagent, that was found to be strongly positive (dextrinoid), and an overall similarity with our own specimens; hence the new combination *Fomitiporia baccharidis* is proposed. The species is redescribed and illustrated. It is known so far from Argentina and Ecuador. Its phylogenetic relationships with the South American *Fomitiporia* are briefly discussed.

Key words: Andes, Basidiomycota, Biogeography, Neotropics, *Phellinus*, Phylogeny, Taxonomy.

Introduction

Fomitiporia (Hymenochaetales, Basidiomycota) has received much attention in the last 20 years. Many studies documented a larger than presumed phylogenetic and taxonomic diversity, whatever the areas considered (e.g. Amalfi et al. 2010, 2012, Amalfi and Decock 2013, de Campos Santana et al. 2014, Cloete et al. 2013, Coelho et al. 2009, Decock et al. 2005, 2007, Fischer et al. 2005, Vlasák and Kout 2011, Zhou and Xue 2012). Amalfi and Decock (2013) provided also the most comprehensive phylogenies of *Fomitiporia* to date, based on an extensive, worldwide in scope sampling. These studies allowed evidencing a marked phylogeographic structure within the genus with multiple lineages whose distributions mostly overlap with the main biogeographical realms (Olson et al. 2001).

As far as the Neotropics are concerned, Amalfi and Decock (2013) evidenced the occurrence of (at least) nine species / phylogenetic species sharing pileate basidiomata: they include *F. apiahyna*, *F. castilloi* and 7 unnamed species clades. Previously, only two species with pileate basidiomata were reported from the Neotropics, viz. *F. apiahyna* (e.g. Gilbert et al. 2002, Robledo et al. 2006, Ryvar den 2004) and *F. robusta* (Woolley et al. 2008). As one of the consequences, it was recommended that the mentions of *F. apiahyna* in its presumed distribution range in the Neotropics [from southern Florida (Vlasák et al. 2011), Mexico (Raymundo et al. 2012), Costa Rica (Ryvar den 2004), Panama (Gilbert et al. 2002), down to southern Brazil and Argentina (Loguercio Leite and Wright 1991, Rajchenberg and De Meijer 1990, Rajchenberg and Wright 1987, Robledo et al. 2006)] be considered as *sensu lato* or *sensu auctores*, and re-analyzed within the frame of an integrated species concept, including molecular data and whenever possible ecological data. *A fortiori*, the same applies for the mentions of *F. apiahyna* outside of the Neotropics (Renvall and Niemelä 1993).

In line with the above idea, as a continuation of the taxonomical revision and biogeographical survey of New World *Fomitiporia* species (Amalfi and Decock 2013, Amalfi et al. 2012, Campos Santana et al. 2014, Decock et al. 2007), we addressed the status of several specimens originating from high elevation forests of the Andean range in Argentina and Ecuador. These collections were previously identified as *F. apiahyna* (Robledo et al. 2006; Ryvar den, identification note on a herbarium label). Nevertheless, Amalfi and Decock (2013) showed that, in a phylogenetic perspective, the specimens from Argentina belong neither to the *F. apiahyna* species clade (*sensu* Amalfi and Decock 2013) nor to the *F. apiahyna* lineage (as defined by Amalfi and Decock 2013). These specimens were shown to pertain to a

distinct clade – hence representing a distinct phylogenetic species – in the vicinity of the *F. tabaquilio* species clade (Amalfi and Decock 2013). *Fomitiporia tabaquilio* is, in all probability, an Andean endemic species (Urcelay et al. 2000).

Search for a possible epithet for this species, within *Fomitiporia*, yielded no name that could apply to it. However, within the still vast *Phellinus sensu lato* (Larsen and Cobb-Poullé 1990, Ryvarden 2004), *Phellinus baccharidis* emerged as a possible candidate, although it was repeatedly described with non-dextrinoid basidiospores (Ryvarden & Johansen 1980, Larsen and Cobb-Poullé 1990, Ryvarden 2004); non-dextrinoid basidiospores would, *a priori*, exclude this species from *Fomitiporia* (Amalfi and Decock 2013, Campos Santana et al. 2014, Fischer 1996). Nevertheless, its macro-morphology (Larsen and Cobb-Poullé 1990, Ryvarden 2004) as well as its original ecological data (Patouillard and de Lagerheim 1893) pleaded for comparison with our specimens.

As a result of these studies, the new combination *Fomitiporia baccharidis* is proposed. The species is redescribed and illustrated and its ecology is also emphasized. Its phylogenetic affinities within the Neotropical *Fomitiporia* lineage are briefly discussed.

Materials and methods

Materials.— Herbarium specimens examined are preserved at CORD, MUCL, LPS and FH (herbarium acronyms are according to Thiers [continuously updated]). Living cultures examined are preserved at MUCL and at the CCC, Colección de Cultivos Córdoba, Instituto Multidisciplinario de Biología Vegetal, Córdoba, Argentina. Original strains were isolated from basidiome tissue during fieldwork on malt extract agar with 2 ppm benomyl (benlate) and 50 ppm chloramphenicol and later purified in the laboratory in the case of persistent bacterial contamination.

Morphology and anatomy.— Basidiomata colours are described according to Kornerup and Wanscher (1981). Basidiome sections were examined in Melzer's reagent, lactic acid Cotton blue (Kirk et al. 2001), and 4% KOH. All microscopic measurements were done in Melzer's reagent. In presenting the size range of the microscopic elements, 5% of the measurements were excluded from each end and are given in parentheses. ave = arithmetic mean, Q = ratio of length/width of basidiospores and ave-Q = arithmetic mean of the ratio Q. Thirty basidiospores were measured from each specimen, except when noted.

Sequencing.— DNA extraction, amplification, and sequencing of the 5' end of the nuclear ribosomal LSU rRNA gene, ITS regions (including 5.8S), partial *tefl-α* gene, and the region located between domains 6 and 7 of *rpb2* (Frøslev et al. 2005, Matheny 2005) are described in Decock et al. (2007), Amalfi et al. (2010, 2012) and Amalfi and Decock (2013).

Sequencing reactions were performed using CEQ DTCS Quick Start Kit® (Beckman Coulter) according to the manufacturer's recommendations with the primers LROR, LR3, LR3R, LR5 for the LSU; ITS1, ITS2, ITS3, ITS4 for the ITS (<http://biology.duke.edu/fungi/mycolab/primers.htm>); 2212R, 1953R, 983F, 2218R for *tefl-α* (Rehner and Buckley 2005, Matheny et al. 2007); and bRPB2-6F and bRPB2-7.1R for *rpb2* (Matheny 2005). Sequences were assembled and edited with the Sequencher™ 4.8 software (Gene Codes Corporation, Ann Arbor, MI, USA). The *rpb2* sequences from two *F. robusta* collections from Guyana (TH8903, TH8904) could not be obtained and were considered as missing data in the combined dataset.

Phylogenetic analysis.— One hundred and nine specimens / cultures representing 40 species or potential species/clades are included in the phylogenetic analysis. The dataset used in the present study to infer phylogenetic inferences is the same as used previously by Amalfi and

Decock (2013). The dataset is available at TreeBASE (<http://www.treebase.org/treebase/index.html>) under study accession URL: <http://purl.org/phylo/treebase/phyloids/study/TB2:S12874>. The methodologies and parameters for running phylogenetic analyses are described in details in Amalfi and Decock (2013) and not repeated here. Sequence data and statistical analysis are provided in Table II.

TABLE I. List of species, collections, and sequences used in the phylogenetic analyses.

Genus / Species names		GenBank accession number			
Voucher specimens / cultures reference					
	Locality	nLSU	ITS	<i>tefl-α</i>	RPB2
<i>F. aethiopica</i> Decock et al.					
MUCL 44777 (T) ^{c, h}	Ethiopia	AY618204	GU478341	GU461893	JQ087956
MUCL 44806 ^{c, h}	Ethiopia	AY618202	GU461944	GU461892	JQ087955
<i>F. apiahyna</i> (Speg.) Robledo et al.					
MUCL 51451 ^{c, h}	Ecuador	GU461997	GU461963	GU461896	JQ087958
MUCL 51454 ^{c, h}	Ecuador	JX093812	JX093769	JX093725	JX093856
MUCL 51456 ^{c, h}	Ecuador	JX093813	JX093770	JX093726	JX093857
MUCL 51474 ^{c, h}	Ecuador	X093814	GU461961	JX093727	JX093858
MUCL 51485 ^{c, h}	Ecuador	GU461996	GU461962	GU461895	JQ087957
MUCL 53022 ^{c, h}	French Guiana	JX093815	JX093771	JX093728	JX093859
MUCL 53041 ^{c, h}	French Guiana	JX093816	JX093772	JX093729	JX093860
MUCL 53042 ^{c, h}	French Guiana	JX093817	JX093773	JX093730	JX093861
MUCL 53047 ^{c, h}	French Guiana	JX093818	JX093774	JX093731	JX093862

MUCL 53071 ^{c, h}	French Guiana	JX093819	JX093775	JX093732	JX093863
MUCL 53135 ^{c, h}	French Guiana	JX093820	JX093776	JX093733	JX093864
MUCL 53145 ^{c, h}	French Guiana	JX093821	JX093777	JX093734	JX093865
MUCL 53149 ^{c, h}	French Guiana	JX093822	JX093778	JX093735	JX093866
MUCL 53156 ^{c, h}	French Guiana	JX093823	JX093779	JX093736	JX093867
MUCL 53711 ^{c, h}	French Guiana	JX093824	JX093780	JX093737	JX093868
MUCL 53988 ^{c, h}	French Guiana	JX093825	JX093781	JX093738	JX093869
MUCL 53989 ^{c, h}	French Guiana	JX093826	JX093782	JX093739	JX093870
MUCL 53990 ^{c, h}	French Guiana	JX093827	JX093783	JX093740	JX093871
MUCL 53991 ^{c, h}	French Guiana	JX093828	JX093784	JX093741	JX093872
MUCL 53726 ^{c, h}	French Guiana	JX093829	JX093785	JX093742	JX093873
<i>F. australiensis</i> Fischer et al.					
VPRI 22451a PT (MUCL 49406) ^{c, 5}	Australia	GU462001	AY624997	GU461897	JQ087959
<i>F. baccharidis</i> (Pat.) Decock et al.					
MUCL 47756 ^{c, h}	Argentina	JQ087913	JQ087886	JQ087940	JQ087993
MUCL 47757 ^{c, h}	Argentina	JQ087914	JQ087887	JQ087941	JQ087994
MUCL 47758 ^{c, h}	Argentina	JQ087915	JQ087888	JQ087942	JQ087995
<i>F. bakeri</i> (Murrill) Vlasák & Kout					
FP-134784-Sp (MUCL 51098) ^{c, 1}	USA	JQ087901	JQ087874	JQ087928	JQ087960

F. bannaensis Y.C. Dai

MUCL 45926 ^{c, h}	Thailand	EF429217	GU461942	GU461898	JQ087961
MUCL 46950 ^{c, h}	China	EF429218	GU461943	GU461899	JQ087962

F. calkinsii (Murrill) Vlasák & Kout

FP-71907-T (MUCL 51100) ^{c, 1}	USA	JQ087902	JQ087875	JQ087929	JQ087963
MUCL 52346 ^{c, h}	Mexico	JQ087903	JQ087876	JQ087930	JQ087964

Fomitiporia capensis M. Fisch. et al.

MUCL 53009 ^{c, 5}	South Africa	JQ087917	JQ087890	JQ087944	JQ087997
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F. castilloi Decock & Amalfi

MUCL 53481 (T) ^{c, h}	French Guiana	JQ087916	JQ087889	JQ087943	JQ087996
MUCL 53980 (PT) ^{c, h}	French Guiana	JX093830	JX093786	JX093743	JX093874

F. cupressicola Amalfi et al.

MUCL 52486 (T) ^{c, h}	Mexico	JQ087904	JQ087877	JQ087931	JQ087965
MUCL 52488 ^{c, h}	Mexico	JQ087905	JQ087878	JQ087932	JQ087966
MUCL 52489 ^{c, h}	Mexico	JQ087906	JQ087879	JQ087933	JQ087967
MUCL 52490 ^{c, h}	Mexico	JQ087907	JQ087880	JQ087934	JQ087968

F. dryophila Murrill

TJV-93-232 (MUCL 46379) ^{c, 1}	USA	EF429221	EF429240	GU461902	JQ087969
TJV-93-234 (MUCL 46380) ^{c, 1}	USA	EF429219	EF429238	GU461900	JQ087970

F. erecta (A. David et al.) Fiasson

MUCL 49871 ^{c, h}	France	GU461976	GU461939	GU461903	JQ087971
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F. gabonensis Amalfi & Decock

MUCL 47576 (T) ^{c, h}	Gabon	GU461990	GU461971	GU461923	JQ087972
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MUCL 51291 ^{c, h}	Gabon	GU461986	GU461967	GU461924	JQ087973
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F. hartigii (Allesch. & Schnabl) Fiasson & Niemelä

MAFF 11-20016 (MUCL 31400) ^c	Japan	JQ087909	JQ087882	JQ087936	JQ087975
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75-2 562 (MUCL 53549) ^{c, 4}	Estonia	JX093831	JX093787	JX093744	JX093875
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71-25 464 (MUCL 53550) ^{c, 4}	Estonia	JX093832	JX093788	JX093745	JX093876
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75-3 563 (MUCL 53551) ^{c, 4}	Estonia	JX093833	JX093789	JX093746	JX093877
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F. hippophaeicola (H. Jahn) Fiasson & Niemelä

MUCL 31746 ^{c, h}	Belgium	AY618207	GU461945	GU461904	JQ087976
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MUCL 31747 ^{c, h}	Belgium	GU461977	GU461946	GU461905	JQ087977
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F. ivindoensis Decock et al.

MUCL 51311 ^{c, h}	Gabon	GU461979	GU461952	GU461907	JQ087978
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MUCL 51312 (T) ^{c, h}	Gabon	GU461978	GU461951	GU461906	JQ087979
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F. langloisii Murrill

FP-94347-R (MUCL 46375) ^{c, 1}	USA	EF429225	EF429242	GU461908	JQ087980
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01-77/4 (MUCL 46165),

(T of <i>F. hesleri</i>) ^{c, 5}	USA	EF429223	AY340026	GU461909	JQ087981
<i>F. maxonii</i> Murrill					
MUCL 46017 ^{c, h} (= CRGF 182)	Cuba	EF429230	EF433559	GU461910	JQ087983
MUCL 46037 ^{c, h} (= CRGF 183)	Cuba	EF429231	EF433560	GU461911	JQ087982
<i>F. mediterranea</i> M. Fisch.					
AFTOL ID 688	ND	AY684157	AY854080	AY885149	AY803748
MUCL 38514 ^c	Italy	AY618201	GU461953	GU461912	JQ087984
MUCL 45670 ^{c, h}	France	GU461980	GU461954	GU461913	JQ087985
<i>Fomitiporia neotropica</i> Campos-Santana et al.					
MUCL 53114 ^{c, h}	French Guiana	JX093836	JX093792	JX093749	JX093880
<i>F. nobilissima</i> Decock & Yombiyeni					
MUCL 47580 ^{c, h}	Gabon	GU461985	GU461966	GU461921	JQ087986
MUCL 51289 (T) ^{c, h}	Gabon	GU461984	GU461965	GU461920	JQ087987
<i>F. polymorpha</i> M. Fisch.					
91-42/3 (MUCL 46166) (PT) ^{c, 5}	USA	DQ122393	GU461955	GU461914	JQ087988
91-42/1 (MUCL 46167) (PT) ^{c, 5}	USA	EF429233	GU461956	GU461915	JQ087989
<i>F. pseudopunctata</i> (A. David et al.) Fiasson					
MUCL 51325 ^{c, 2}	Czech	GU461981	GU461948	GU461916	JQ087998
MUCL 46168 ^{c, h}	France	JQ087918	JQ087891	JQ087945	JQ087999

F. punctata (Fr.) Murrill

MUCL 34101 ^{c, h}	Germany	AY618200	GU461947	GU461917	JQ088000
WD-2055 (MUCL 47629) ^{c, 3}	Japan	GU461982	GU461950	GU461918	JQ088001
71-8 298 (MUCL 53548) ^{c, 4}	Europe	JX093834	JX093790	JX093747	JX093878

F. punicata Y.C. Dai et al.

Cui 23 ^{h, 4}	China	GU461991	GU461974	GU461927	JQ088002
Cui 26 ^{h, 4}	China	GU461992	GU461975	GU461928	JQ088003

F. robusta (P. Karst.) Fiasson & Niemelä

CBS 389.72 (MUCL 51297) ^{c, 6}	Estonia	JQ087919	JQ087892	JQ087946	JQ088004
Tomsovský 1013 (MUCL 51327) ^{c, 2}	Czech	GU461993	GU461949	GU461929	JQ088005

F. sonorae (Gilb.) Y.C. Dai

RLG-10862-Sp (MUCL 47689, T) ^{c, 1}	USA	JQ087920	JQ087893	JQ087947	JQ088006
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Fomitiporia “sp.”

CBS 386.66 = MUCL 46181 ^{c, 6}	Argentina	EF429234	EF433563	GU461930	JQ088007
MUCL 53675 ^{c, h}	French Guiana	JX093835	JX093791	JX093748	JX093879

Fomitiporia “sp.” PS1

TH 8903 ^{h, 7}	Guyana	JX093837	JX093793	JX093750	ND
TH 8904 ^{h, 7}	Guyana	JX093838	JX093794	JX093751	ND

Fomitiporia “sp.” PS2

MUCL 53108 ^{c, h}	French Guiana	JX093839	JX093795	JX093752	JX093881
MUCL 53705 ^{c, h}	French Guiana	JX093840	JX093796	JX093753	JX093882
MUCL 53992 ^h	Guadelupe	JX093841	JX093797	JX093754	JX093883
<i>Fomitiporia</i> “sp.” PS3 a					
MUCL 51464 ^{c, h}	Ecuador	JX093842	JX093798	JX093755	JX093884
MUCL 53034 ^{c, h}	French Guiana	JX093843	JX093799	JX093756	JX093885
MUCL 53106 ^{c, h}	French Guiana	JX093844	JX093800	JX093757	JX093886
MUCL 53111 ^{c, h}	French Guiana	JX093845	JX093801	JX093758	JX093887
MUCL 53785 ^{c, h}	French Guiana	JX093846	JX093802	JX093759	JX093888
MUCL 53793 ^{c, h}	French Guiana	JX093847	JX093803	JX093760	JX093889
MUCL 53800 ^{c, h}	French Guiana	JX093848	JX093804	JX093761	JX093890
MUCL 53985 ^{c, h}	French Guiana	JX093849	JX093805	JX093762	JX093891
<i>Fomitiporia</i> “sp.” PS3 b					
GC-FG-10-125 ^{c, h}	French Guiana	JX093850	JX093806	JX093763	JX093892
<i>Fomitiporia</i> “sp.” PS4					
MUCL 53993 ^{c, h}	Mexico	JX093851	JX093807	JX093764	JX093893
MUCL 53994 ^{c, h}	Mexico	JX093852	JX093808	JX093765	JX093894
<i>Fomitiporia</i> “sp.” PS5					
MUCL 51555 ^{c, h}	Martinique	JX093853	JX093809	JX093766	JX093895

MUCL 53797 ^{c, h}	French Guiana	JX093854	JX093810	JX093767	JX093896
<i>Fomitiporia</i> “sp.” PS6					
MUCL 53798 ^{c, h}	French Guiana	JX093855	JX093811	JX093768	JX093897
<i>F. tabaquilio</i> (Urcelay et al.) Decock & Robledo					
MUCL 46230 ^{c, h}	Argentina	DQ122394	GU461940	GU461931	JQ088008
MUCL 47754 ^{c, h}	Argentina	GU461994	GU461941	GU461932	JQ088009
<i>F. tenuis</i> Decock et al.					
MUCL 44802 (T) ^{c, h}	Ethiopia	AY618206	GU461957	GU461934	JQ088010
MUCL 49948 ^{c, h}	Gabon	GU461998	GU461958	GU461935	JQ088011
MUCL 49971 ^{c, h}	Uganda	GU461998	GU461958	GU461935	JQ088012
<i>F. texana</i> (Murrill) Nuss					
RLG-7763-T (MUCL 47690) ^{c, 1}	USA	JQ087921	JQ087894	JQ087948	JQ088013
FP-89674-R (MUCL 51143) ^{c, 1}	USA	JQ087922	JQ087895	JQ087949	JQ088014
<i>F. torreyae</i> Y.C. Dai & B.K. Cui					
WD-199 (MUCL 47628) ^{c, 3}	Japan	JQ087923	JQ087896	JQ087950	JQ088015
WC31 ^h	Chine	JQ087924	JQ087897	JQ087951	JQ088016
<i>F. tsugina</i> Murrill					
Ft_San (MUCL 52702)	USA	JQ087925	JQ087898	JQ087952	JQ088017
Ft_T2-1 (MUCL 52703)	USA	JQ087926	JQ087899	JQ087953	JQ088018

MUCL 51295 ^c	USA	JQ087908	JQ087881	JQ087935	JQ087974
<i>Ph. juniperinus</i> Bernicchia & S. Curreli					
MUCL 51757 ^{c, h}	Tunisia	JQ087927	JQ087900	JQ087954	JQ088019
<i>Ph. uncisetus</i> Robledo et al.					
MUCL 46231 ^{c, h}	Argentina	EF429235	GU461960	GU461937	JQ088020
MUCL 47061 ^{c, h}	Argentina	GU462000	GU461972	GU461938	JQ088021

T, PT = type, paratype; ND*: available at MUCL

^c = culture available; ^h = voucher herbarium specimen corresponding to the culture available at the MUCL herbarium; ¹ cultures from CFMR, USDA, USA, courtesy of Dr. K. Nakasone); ² cultures from Faculty of Forestry and Wood Technology, Mendel University of Agriculture and Forestry in Brno, Czech Republic, courtesy of Dr. M. Tomšovský; ³ cultures from Microbial Ecology Lab Forestry and Forest Products Research Institute, courtesy of Prof. T. Hattori, Japan; ⁴ cultures from National History Museum, University of Tartu, Estonia, courtesy of K. Pöldmaa; ⁵ cultures from Regensburg University, Germany, courtesy of Dr. M. Fischer; ⁶ cultures from the CBS, The Netherlands, courtesy of Prof. P. Crous; ⁷ fragments of herbarium, courtesy of Prof. T. Henkel, USA; ⁸ fragments of herbarium, courtesy of Prof. Yu-Cheng Dai, China.

Results

DNA sequence comparisons.— The 5' region of the nLSU gene including domains D1, D2, and D3 ranged from 871 (*F. langloisii*) to 877 bps (*F. cupressicola*). The ITS-5.8S region ranged from 662 (*Fomitiporia* sp. MUCL 47756, MUCL 47757, and MUCL 47758) to 780 bps (*Fomitiporia* sp. MUCL 53481 and MUCL 53980). The presence of indels of variable length near the 5' end of the ITS1 accounts for most of this variation (cf. Amalfi and Decock 2013, Decock et al. 2007). Amplicons ranging from 1155 (*F. bakeri*) to 1172 bps (*F. australiensis*) were obtained from the partial *tef1*. This region contains three clade specific, confidently alignable introns. The partial *rpb2* region ranged from 810 to 813 bps; *Fomitiporia ivindoensis* presents an additional codon (GAG) in this region.

The final DNA sequence alignments resulted in 897 characters, including gaps, for the LSU gene (28 variable parsimony-uninformative and 118 parsimony-informative positions), 797 for the ITS dataset (59 variable parsimony-uninformative and 264 parsimony-informative positions), 1202 for the *tef1* region, introns included (44 variable parsimony-uninformative and 363 parsimony-informative positions), and 813 for the *rpb2* dataset (19 variable parsimony-uninformative and 269 parsimony-informative positions) and 359 for the recoded indels dataset (93 variable parsimony-uninformative and 262 parsimony-informative positions).

Individual dataset comparisons.— Sequence data and statistical analysis for each dataset and combined analysis are provided in Table II.

By comparing MP bootstrap tree topologies obtained for the individual datasets, no conflict involving significantly supported nodes was found; the datasets were therefore combined.

Combined dataset analysis.— 4064 characters were included in the analysis of which 243 were variable but parsimony-uninformative and 1276

Table 2. Summary of datasets of ITS1 DNA, LSU rDNA, *atf* and *rpb2*

Properties	Datasets													
	ITS 1	5.8S	ITS 2	atf LSU	<i>atf</i> Int	<i>atf</i> 2nd	<i>atf</i> 3rd	<i>rpb2</i> Int	<i>rpb2</i> 2nd	<i>rpb2</i> 3rd	Indels			
Model selected	GTR+G	K80	GTR+H+G	GTR+H+G	GTR+H+G	F81+I	GTR+G	GTR+H+G	F81+I	GTR+G	F81-like			
Likelihood score	-2,182.2107	-337.626	-2,069.1279	-3,055.2348	-683.5805	-568.4256	-2,815.7737	-1,854.0367	-783.8632	-487.8718	-4,977.1666			
Base frequencies														
Freq. A =	0.2894	Equal	0.2448	0.2618	0.2944	0.3080	0.1459	0.2737	0.2759	0.3072	0.2125			
Freq. C =	0.1490	Equal	0.1853	0.1995	0.1920	0.2538	0.3152	0.1899	0.2484	0.1833	0.1932			
Freq. G =	0.1850	Equal	0.1951	0.2931	0.2754	0.1571	0.2357	0.1535	0.3520	0.2073	0.3069			
Freq. T =	0.3766	Equal	0.3748	0.2456	0.1382	0.2811	0.3022	0.3830	0.1307	0.3022	0.2874			
Proportion of invariable sites	-	-	0.0170	0.5700	0.8160	0.8870	-	-	0.5380	0.8570	-			
Gamma shape	1.0160	-	0.400	0.4090	0.9480	-	1.3160	3.4510	0.4510	-	1.4670			

parsimony-informative. The heuristic search produced 3657 equally most parsimonious trees (4247 steps long; CI = 0.482, RI = 0.841, RC = 0.406), representing one main topology. The two Bayesian runs converged to stable likelihood values (-ln 25875.131, -ln 25889.657) after 5105000 generations and 4895 (about 50% of the sampled trees) stationary trees from each analysis were used to compute a 50% majority rule consensus tree in PAUP* to calculate posterior probabilities. In the ML searches with RAxML the combined dataset alignment had 1800 distinct patterns with a proportion of gaps and undetermined characters of 9.03%.

The strict consensus of the 3657 equally most parsimonious trees was mostly identical to the BC tree (Fig. 1) and to the best scoring ML tree (tree score of -lnL = -25229.376611). The topology of

this tree is highly concordant with topologies obtained analyzing the individual datasets. It is also coherent with previously published trees (Amalfi et al. 2010, 2012).

The results show that our Neotropical collections with pileate basidiomes are distributed into 9 distinct terminal clades and four lineages (Fig. 1; Amalfi and Decock 2013). The *F. apiahyna* lineage comprises *F. apiahyna* (*sensu* Amalfi and Decock 2013) and 4 additional clades / phylogenetic species (PS 1, PS 2, PS 3, & PS 4, Fig. 1). Two phylogenetic species (PS 5 & PS 6, Fig. 1) are nested in the vicinity of *F. texana*; they form together the *F. texana* lineage. The remaining clades correspond to *F.*

castilloi (Fig 1; PS 7 in Amalfi and Decock 2013), which nests in a position basal to the *F. langloisii* lineage, and to PS 8, that gathers our collections from high elevation forests of Argentina. PS 8 is closely related to *F. tabaquilio*. It is worth noting that the latter species is also an Andean species (Robledo et al. 2006, Urcelay et al. 2000). Altogether, *F. tabaquilio* and PS 8 form a small “Andean” lineage. These lineages (*F. apiahyna*, *F. texana*, *F. tabaquilio*, and the *F. castilloi* - *F. langloisii*) form altogether a large Neotropical lineage (Amalfi and Decock 2013).

Morphological analysis.— Subsequent morphological examinations of the various collections of PS 8 revealed a combination of unique morphological features, which define a unique morphotype. The main features that differentiate it from other species occurring in the Neotropics are the basidiome shape, the pileus surface organization and colour, and the context structure (duplex with a thin black line).

Ecological data.— PS 8 is so far is known only from Andean, high elevation (approx. 1900 to 3500 masl) forests in Argentina and Ecuador. It grows from living stems of shrubby trees from the understorey compartment.

Given the results of the phylogenetic inferences that identify PS 8 as a phylogenetic species that could be equated to a unique morphotype, and the specific autecology, it is considered to represent a distinct taxon. The search for a possible epithet within *Fomitiporia* (Murrill 1907) and the synonyms of *F. robusta* s.l. (Robert et al. 2005) yielded no name that could apply to it. Nevertheless, within the still vast *Phellinus sensu lato* (Ryvarden 2004, Larsen and Cobb-Poulsen 1990), *Phellinus baccharidis* emerged as a candidate.

Phellinus baccharidis [type specimen: Ecuador, Rio Machangara, Cotacollao (locality nowadays more likely in Quito suburb, Prov. Pichincha, at ca. 2800 masl), *commun sur troncs de* (common on trunks of) *Baccharis*

oblongifolia, Feb 1892, D. de Lagerheim, FH3059] shares with our collections the basidiomata habit, the pileus organization, a duplex context with a thin black line (Patouillard and de Lagerheim 1893, Ryvar den 2004, Larsen and Cobb-Pou l le 1990). It was collected in a similar environment. Although repeatedly described with non dextrinoid basidiospores (Larsen and Cobb-Pou l le 1990, Ryvar den 2004, Ryvar den and Johansen 1980), our type studies revealed strongly dextrinoid basidiospores. The new combination *Fomitiporia baccharidis* is proposed.

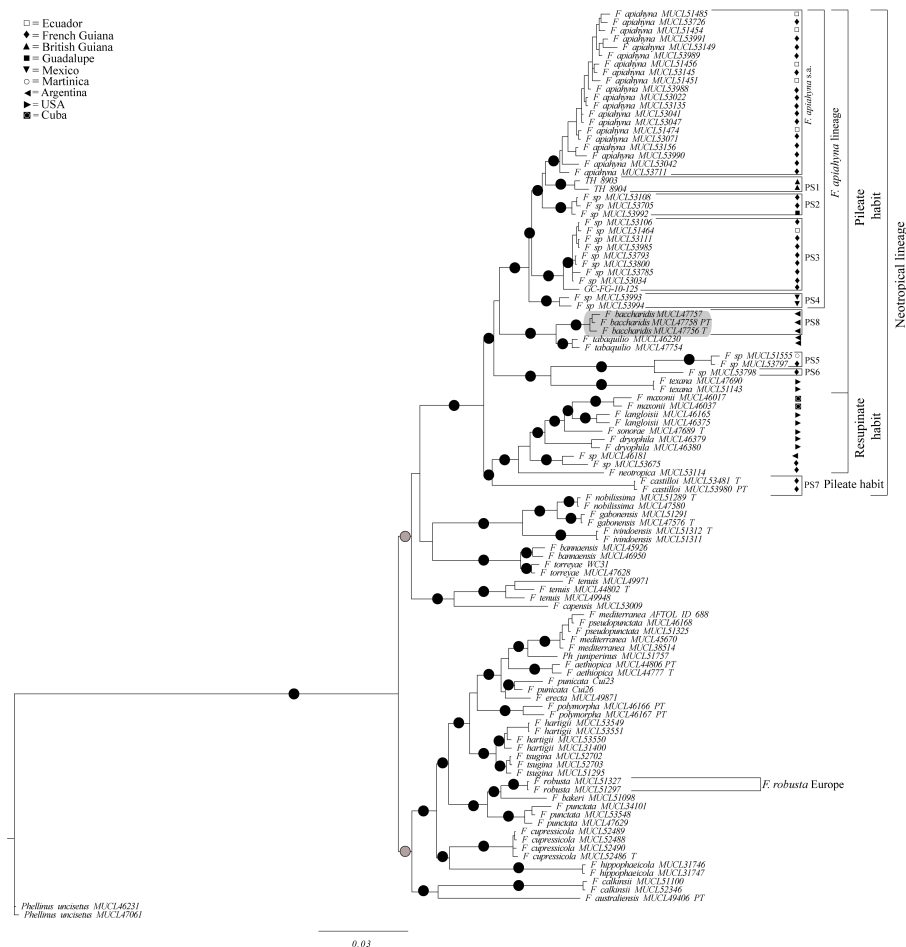


FIG. 1. The 50% majority-rule consensus tree from Bayesian inference of the combined ITS, LSU, *tef1* and *rpb2* sequences. Black dots on branches represent BPP, ML BS and BS of 99% or higher; grey dots on branches denote only BPP greater than 95% and ML BS greater than 85% but BS support lower than 50%.

Taxonomy

Fomitiporia baccharidis Decock, Robledo & Amalfi **comb. nov.**

Figs. 2–8, 11–12

Mycobank: MB 807284.

≡ *Polyporus baccharidis* Pat., Bull Soc Mycol Fr 9:129, 1893
[MB#180235], basionym.

≡ *Phellinus baccharidis* (Pat.) Pat., Essai Tax Hyménomyc: 97, 1900.
[MB#319737].

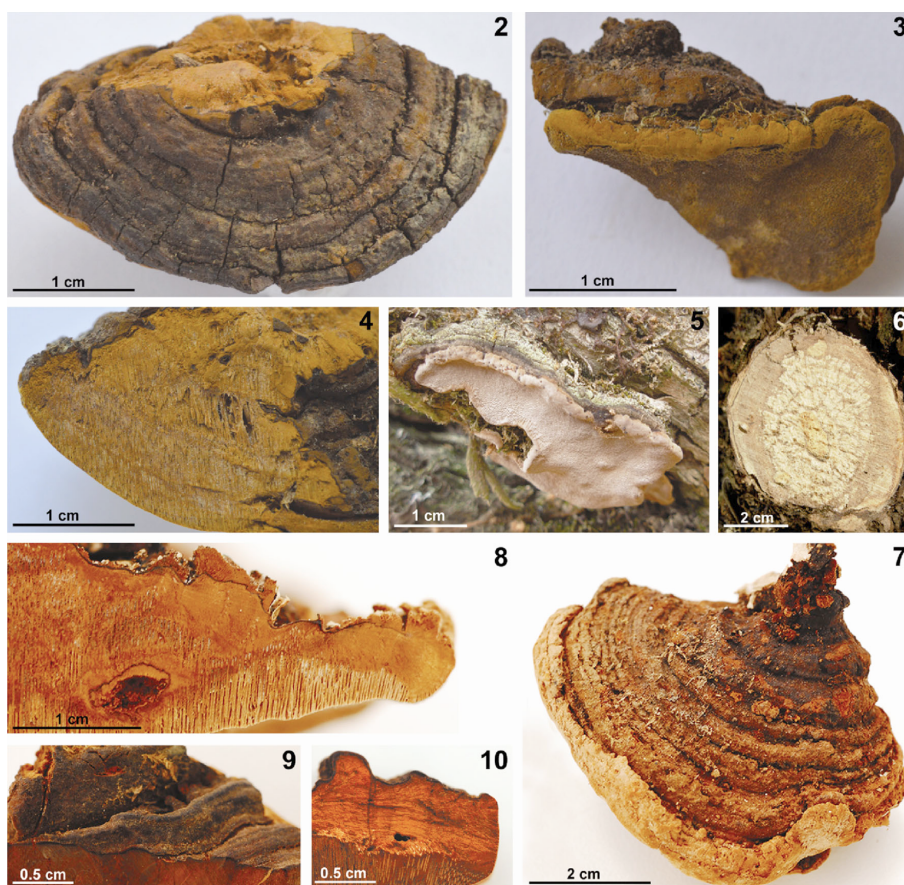
Basidiomata perennial, mostly pileate, occasionally effused reflexed, generally gregarious, emerging in groups; *pileus* dimidiate, triquetrous to bell shaped in section, attached and connected to the substrate at the base, up to $8 \times 6 \times 4$ cm, light in weight and of a corky consistence; *pilear* surface golden brown towards the margin, progressively darkening, dark brown to blackish toward the base, deeply and concentrically sulcate, the furrows delimiting lobes, glabrous, slightly irregular to finely scrupose, of soft corky consistency, indurating towards the base, with age covered by mosses and lichens; *margin* acute to rounded, dark golden brown; *pore surface* pale brown, with a pinkish tint, more commonly brown to copper brown, glancing with light and then turning golden; *pores* round, 8–10/mm, 75–110 μm diam (ave = 88 μm); *dissepiments* entire 20–50 (–60) μm (ave = 37 μm); *context* in brown shade, heterogeneous (duplex) with a lower dense and corky layer and a darker slightly compressible upper layer, both separated by a thin blackish line, wavy following the relief of the irregular pilear surface, thinning towards the base and disappearing with the hardened portion of the pilear surface; *tubes* distinctly layered, with up to 10 layers, each individual layer 2–3 mm thick, totaling up to 35 mm thick, in pale to greyish brown shade.

Hyphal system dimitic, identical in the context and hymenophoral trama; *generative hyphae* simple septate, hyaline and thin-walled to pale yellow and distinct-walled, 2–3 μm diam; *skeletal hyphae* golden to yellowish brown, thick-walled, 3–4 μm wide.

Hymenium: *basidia* subglobose to widely clavate, $10\text{--}12 \times 8\text{--}10\text{ }\mu\text{m}$, with 4 sterigmata; *basidiospores* subglobose to globose, slightly obovoid, smooth, hyaline, thick-walled, strongly cyanophilous, strongly dextrinoid, $(5.0\text{--}) 5.0\text{--}6.5\text{--}(7.0) \times (4.0\text{--}) 5.0\text{--}6.0\text{--}(6.0)\text{ }\mu\text{m}$ (ave = $5.9 \times 5.3\text{ }\mu\text{m}$) [in the type $(5.0\text{--}) 5.5\text{--}6.5\text{--}(6.5) \times (5.0\text{--}) 5.0\text{--}6.0\text{--}(6.0)\text{ }\mu\text{m}$, ave = $5.8 \times 5.1\text{ }\mu\text{m}$]; *setae* (hymenial / extrahymenial) absent.

type of rot: a white rot;

substrate, hosts, distribution: on living stems of shrubby trees; known hosts include *Baccharis oblongifolia* (Asteraceae [Patouillard and de Lagerheim 1893]), *Lepechinia* sp. (Lamiaceae), *Polylepis australis* (Rosaceae) and on an unidentified possible Melastomataceae; its known distribution ranges from NW Argentina, at ca. 1900 masl, to Central Ecuador, at elev. ca. 3500 masl.

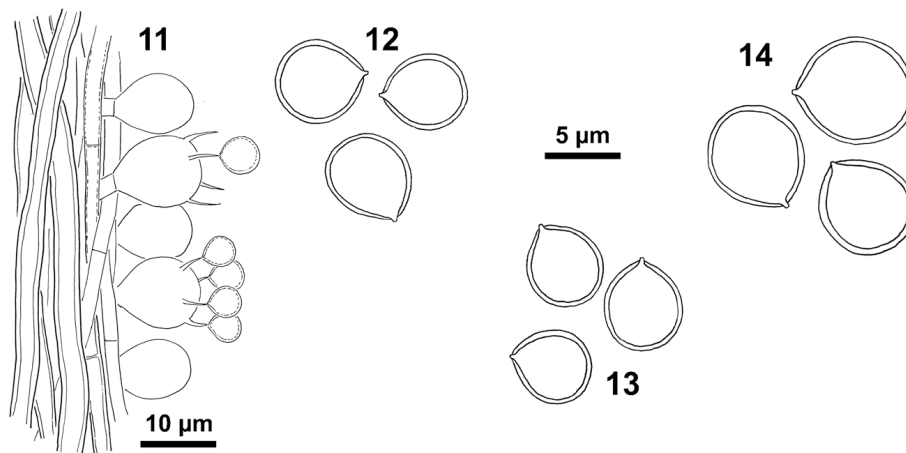


FIGS. 2–10. Macroscopic features of the basidiomes of *F. baccharidis* and *F. apiahyna*. 2–4. Holotype of *Fomitiporia baccharidis* (FH 3059). 2. General view and detail of the pileus surface (scale bar = 1 cm). 3. Section through basidiome showing context and blackish line (scale bar = 1 cm). 4. General view and detail of the margin (scale bar = 0.5 cm). 5–8. Collections from NW Argentina on *Lepechinia* sp. 5. general view of young pore surface (scale bar = 1 cm). 6. Section through stem of *Lepechinia* sp showing a white pocket rot (scale bar = 2 cm). 7. General view of basidiomes *in situ* (scale bar = 2 cm). 8. Section through basidiome showing context and blackish line (scale bar = 0.1 cm). 9–10. Holotype of *Fomitiporia apiahyna* (LPS). 9. View of the pileus surface (scale bar = 0.5 cm). 10. Section with the thick black line on the pileus (scale bar = 0.5 cm).

Specimens examined. Argentina, Prov. Tucumán, Dpt. Tañi del Valle, Quebrada del Portugués, alt. 1900 masl, on living stem of *Polylepis australis*, 19 Mar 2002, *Urcelay* 356 (CORD); *ibid.*, 26 May 2001, *Urcelay*

338 (CORD); *ibid.*, on dead laying stem of *Polylepis australis*, 26 May 2001, *Urcelay 358* (CORD); Dpto. Chicligasta, Parque Nacional Campo de los Alisos, arriba del puesto La Mesada, alt. 1900 masl, on living stem of *Lepechinia sp.*, 27 Jul 2006, *Robledo 745* (CORD); *ibid.*, *Robledo 743* (CORD); *ibid.*, *Robledo 744* (CORD). Ecuador, [current Prov. of Pichincha], Cotacollao, Rio Machangara, [at ca. 2800 masl], *commun sur troncs de Baccharis oblongifolia*, Feb 1892, de Lagerheim, FH3059 (HOLOTYPE); Prov. Pichincha, Yanacocha, Volcan Pichincha, Mountain forest with thick epiphyte covers and grassland, 78°34' W – 0°7'S, 3500 masl, on small tree, probably Melastomataceae, 5 Aug 1985, *T. Læssøe 59912*, O, MUCL.

Remarks. — *Fomitiporia baccharidis* is characterized by pileate (occasionally effused-reflexed) basidiomata, triquetrous in section, and mostly attached to the substrate by the upper part. The pileus surface is deeply, concentrically sulcate (Figs 2, 3, 5–7). The pores are small (8–10/mm). The context is heterogeneous (duplex) with two layers of difference consistency and colour, separated by a thin blackish line (Figs. 4, 8), a feature so far unique in *Fomitiporia*.



FIGS. 11–14. Microscopic features of *F. baccharidis*, *F. apiahyna* and *F. tabaquilio*. 11–12. Holotype of *Fomitiporia baccharidis* (FH 3059). 11. Hymenium with basidia and basidiospores, showing tramal skeletal hyphae and generative hyphae in the

subhymenium (scale bar = 10 μm). 12. Basidiospores. 13. Holotype Basidiospores of *Fomitiporia apiahyna* (LPS). Basidiospores (scale bar = 5 μm). Holotype of *Fomitiporia tabaquilio* (CORD). Basidiospores (scale bar = 5 μm).

Fomitiporia baccharidis is found on taxonomically diverse (cf. list of host plants above) shrubby plants of Andean mountainous forests, at elevation depending on the latitude, ranging between *ca.* 1900 masl in its southernmost (known) locality (NW Argentina) and up to *ca.* 3500 m in its northernmost (known) locality (Ecuador). The species may span along the Andean range at high elevation, following altitudinal forests; it should be searched for between Argentina and Ecuador, or even in northern areas, *i.e.* in Colombia and Venezuela. Ryvarden (2004) mentions the species (under *Ph. baccharidis*) for Venezuela, but without details about the local environment. Ryvarden (2004) also reports *F. baccharidis* from Brazil, but this report needs to be confirmed. Other Hymenochaetaceae have a similar distribution along the Andean range, e.g. *Inonotus venezuelicus* Ryvarden (Robledo et al. 2006).

Within its known (and potential) geographical distribution range, *F. baccharidis* should be compared to *F. tabaquilio*. Moreover, *F. tabaquilio* is *F. baccharidis*' closest phylogenetic kin (Fig. 1).

Fomitiporia tabaquilio was originally described from high elevation forests of Central Argentina (Urcelay et al. 2000), the botanical composition of which is dominated by *Polylepis spp.* (Robledo & Renison 2010). Since then, it has been recorded along the Andean range on various *Polylepis* species, including *P. australis* in Central Argentina, *P. australis* and *P. tomentella* in Northwestern Argentina (Robledo et al. 2006), and *P. sericea* and *Polylepis sp.* in high elevation (> 4000 masl) forests of Peru (cf. specimens examined below). Its distribution along the Andean mountainous forests might follow that of *Polylepis*. [*Specimens examined*: ARGENTINA, Prov. Córdoba: Dpto San Alberto, Los Gigantes, Valle de los Lisos, on

living stem of *Polylepis australis*, 31 Jan 2000, *Urcelay 194* (HOLOTYPE, CORD); *ibid.*, Dpto San Javier, El Hueco, 31°58'20"S, 64°56'42"O, alt. 2100 masl, on living stem of *Polylepis australis*, 30 May 2009, *Robledo 1996* (CORD); Prov. Jujuy: Dpto. Tumbaya, Quebraleña, on living stem of *Polylepis tomentella*, 19 Oct 2001, *Robledo 261* (CORD); Dpto. Capital, Tiraxi, nacientes del río Tiraxi, on living stem of *Polylepis australis*, 22 Jul 2006, *Robledo 741* (CORD); *ibid.*, Laguna de Yala, on living stem of *Polylepis australis*, 15 Jul 2006, *Robledo 739* (CORD); *Ibid.*, *Robledo 740* (CORD); Prov. Tucumán: Dpto. Tafi del Valle, Quebrada del Portugués, alt. 1900 masl, on living stem of *Polylepis australis*, 19 Mar 2002, *Urcelay 351* (CORD); Peru, Calca: Cusco, Quebrada de Yanacocha, 13°19'21" S, 72°03'06" O, alt. 4200 masl, on living stem of *Polylepis sp.*, (probably *P. subsericans* J.F. Macbride), 17 May 2006, G. Robledo, *Robledo 1911* CORD].

Fomitiporia tabaquilio differs from *F. baccharidis* in having dense, cushion-shaped to pseudopileate basidiomata, a dense homogeneous subiculum, and larger basidiospores ($6.0\text{--}7.5 \times 4.8\text{--}6.5 \mu\text{m}$ [Urcelay et al. 2000; Fig. 14] and $5.0\text{--}6.5 \times 5.0\text{--}6.0 \mu\text{m}$ [Fig. 12], respectively). Both species occur sympatrically, at least in NW Argentina, and their host range overlaps also. Nevertheless, they might be segregated micro-spatially by their host preference. Data currently available strongly suggest strict host specificity of *F. tabaquilio* toward *Polylepis spp.* whereas *F. baccharidis* is known from a broader host range (see above list of known hosts).

Fomitiporia baccharidis was previously reported as *F. apiahyna* (under *Phellinus apiahynus*) from Northwestern Argentina (Robledo et al. 2006) and Ecuador (Ryvarden, identification on the herbarium label, cf. specimen examined). *Fomitiporia baccharidis* and *F. apiahyna* have basidiospores of the same size range [$(5.0\text{--}) 5.0\text{--}6.5$ ($\text{--}7.0$) $\times$ ($4.5\text{--}) 5.0\text{--}6.0$

(–6.0), ave = 5.9 x 5.1 in the type of *F. apiahyna*, (Fig. 13), Brazil, Apiahy, J. Puiggari 1438, May 1881, LPS 24922 Holotype !]. However, *F. apiahyna* is a very distinct species in many aspects, including morphology, ecology, and phylogenetic affinities. *Fomitiporia apiahyna* forms much harder (woody) basidiomata, with a darker, almost black, pilear surface, flat to convex, narrowly concentrically sulcate with numerous thin and shallow furrows. In section, the pileus has a black crust of variable thickness depending on the age of the basidiomata, covering a homogeneously dense context (Figs. 9–10). *Fomitiporia apiahyna* (*sensu auctores*, cf. Amalfi and Decock 2013) is found growing on trunks of standing, living or dead trees in lowland humid forest, an ecosystem that is botanically highly diverse. It is known from Brazil, Costa Rica, Ecuador, French Guyana, Panama, and Venezuela (cf. e.g. Amalfi and Decock 2013, Gilbert et al. 2002, Loguercio-Leite and Wright 1991, Rajchenberg and De Meijer 1990).

Amalfi et al. (2012) and Amalfi and Decock (2013) provided the most comprehensive phylogenies of *Fomitiporia* to date, based on an extensive sampling worldwide in scope. They documented the existence of a notable worldwide phylogeographic structure within the genus with lineages having marked inter- and intra-continental disjunctions and distributions mostly overlapping with the main biogeographical realms (Olson et al. 2001). This reveals complex biological and biogeographical histories within the genus.

As far as the American continent is concerned, an intra-continental phylogeographic structure is present, indicating of complex biological / biogeographical histories. The species present in the American continent are distributed into two lineages, which distributions overlap with the “nearctic” (altogether the “nearctic” and “palearctic” species are mixed into a “holarctic” lineage; e.g. *F. bakeri*, *F. cupressicola*, *F. polymorpha*, *F. tsugina*) and the “neotropical” realms (Amalfi and Decock 2013, Amalfi et

al. 2012; e.g. *F. apialhyna sensu* Amalfi & Decock (2013), *F. maxonii*, *F. neotropica*, etc.). Both lineages are species rich in the American continent: current data suggest that the Neotropics are the area supporting the highest diversity of species with pileate basidiomata (Amalfi et al. 2012, Amalfi and Decock 2013).

Fomitiporia baccharidis and *F. tabaquilio* are both, more likely, Andean endemic. Our phylogenetic analyses support a single origin of these two species; they form altogether a well-supported, monophyletic, two-species lineage (Fig. 1). Sympatric speciation from a common ancestor, resulting from adaptation / specialization to different hosts and habitats, could be hypothesized in this case. The phylogenetic analyses also place this two-species clade within a much larger lineage, which is for the time being composed of (presumably) exclusively Neo-[tropical/subtropical] endemic species (Fig. 1, “Neotropical lineage”; Amalfi et al. 2012, Amalfi and Decock 2013).

Nevertheless, more samplings are necessary, both in lowland and highland of South America, but also in Central America low- and highlands and the Caribbean to draw possible evolutionary / biogeographical scenarios within the Neotropics. More globally, more samplings are still necessary worldwide; some areas are still very poorly surveyed, including e.g. Southeast Asia (Indo-Malay realms) and Australasia (Ota et al. 2014).

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References

- Amalfi M, Decock C. 2013. *Fomitiporia castilloi* sp. nov. and evidence for multiples clades around *F. apiahyna* in Meso- and South America, representing potential species. *Mycologia* 105: 873–887, doi:10.3852/11-423
- , Yombiyeni P, Decock C. 2010. *Fomitiporia* in sub-Saharan Africa: Morphology and multigene phylogenetic analysis support three new species from the Guineo-Congolian rainforest. *Mycologia* 102:1303–1317, doi:10.3852/09-083.
- , Raymundo T, Valenzuela R, Decock C. 2012. *Fomitiporia cupressicola* sp. nov., a parasite on *Cupressus arizonica*, and additional unnamed clades in the southern USA and northern Mexico, determined by multilocus phylogenetic analyses. *Mycologia* 104: 880–893, doi 10.3852/11-196.
- Campos-Santana M, Amalfi M, Robledo G, Borges da Silveira RM, Decock C. 2014 , *Fomitiporia neotropica*, a new species from South America evidenced by

multilocus phylogenetic analyses. Mycological Progress DOI10.1007/s11557-013-0943-1

Cloete M, Fischer M, Mostert L, Halleen F. 2013. A novel *Fomitiporia* species associated with esca on grapevine in South Africa. Mycol Prog: in press, doi 10.1007/s11557-013-0915-5

Coelho G, da Silveira RMB, Guerrero RT, Rajchenberg M. 2009. On poroid Hymenochaetales growing on bamboos in Southern Brazil and NE Argentina. Fungal Divers 36:1–8.

Decock C, Bitew A, Castillo G. 2005. *Fomitiporia tenuis* and *Fomitiporia aethiopica* (Basidiomycetes, Hymenochaetales), two undescribed species from the Ethiopian Highlands: taxonomy and phylogeny. Mycologia 97:124–132.

—, Herrera Figueroa S, Robledo G, Castillo G. 2007. *Fomitiporia punctata* (Basidiomycota, Hymenochaetales) and its presumed taxonomic synonyms in America: taxonomy and phylogeny of some species from tropical/subtropical areas. Mycologia 99: 733–752.

Fischer M. 1996. On the species complexes within *Phellinus*: *Fomitiporia* revisited. Mycol Res 100:1459–1467.

—, [Edwards J](#), [Cunnington JH](#), [Pascoe IG](#). 2005. Basidiomycetous pathogens on grapevine: a new species from Australia - *Fomitiporia australiensis*. Mycotaxon 92:85–96.

Frøslev TG, Matheny PB, Hibbett DS. 2005. Lower level relationships in the mushroom genus *Cortinarius* (Basidiomycota, Agaricales): a comparison of RPB1, RPB2 and ITS phylogenies. Mol Phylogenet Evol 37:602–618, doi:10.1016/j.ympev.2005.06.016.

Gilbert SG, Ferrer A, Carranza J. 2002. Polypore fungal diversity and host density in a moist tropical forest. *Biodivers Conserv* 11:947–957.

Kirk PM, Cannon PF, David JC, Stalpers JA. 2001. Ainsworth & Bisby's Dictionary of the Fungi, 9th edition. CABI Publishing, Wallingford, UK:1–655.

Kornerup A, Wanscher JH. 1981. Methuen handbook of color, 3rd Edition:1–282.

Larsen MJ, Cobb-Poulsen LA. 1990. *Phellinus* (Hymenochaetaceae). *Synopsis Fungorum* 3, Oslo, Norway: Fungiflora:1–206.

Loguercio-Leite C, Wright JE. 1991. Contribution to a biogeographical study of the Austro-American xylophilous polypores (Aphyllphorales) from the Santa Catarina Island, SC., Brazil. *Mycotaxon* 61:161–166.

Matheny PB. 2005. Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*, Agaricales). *Mol Phylogenet Evol* 35:1–20, doi:10.1016/j.ympev.2004.11.014

—, Wang Z, Binder M, Curtis JM, Lim YW, Nilsson RH, Hughes KW, Petersen RH, Hofstetter V, Ammirati JF, Schoch C, Langer GE, McLaughlin DJ, Wilson AW, Crane PE, Frøslev T, Ge ZW, Kerrigan RW, Slot JC, Vellinga EC, Liang ZL, Aime MC, Baroni TJ, Fischer M, Hosaka K, Matsuura K, Seidl MT, Vauria J, Hibbett DS. 2007. Contributions of *rpb2* and *tefl* to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Mol Phyl Evol* 43:430–451.

Murrill W. 1907. Polyporaceae. *North American Flora* 9:1–72.

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'amico JA, Itoua I, Strand H, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR. 2001.

Terrestrial Ecoregions of the World: A New Map of Life on Earth. BioScience, 51:933–938. doi: 10.1641/0006-3568(2001)051

Ota Y, Hattori T, Nakamura H, Terashima Y, Lee S-S, Miyuki Y, Sotome K. 2014. Taxonomy and phylogenetic position of *Fomitiporia torreyae*, a causal agent of trunk rot on Sanbu-sugi, a cultivar of Japanese cedar (*Cryptomeria japonica*) in Japan. Mycologia: **in press**, doi: 10.3852/13-045

Patouillard NT, de Lagerheim D. 1893. Champignons de l'Equateur. Bull Soc Mycol Fr 9:124–165.

Rajchenberg M, Wright JW. 1987. Type studies of Corticiaceae and Polyporaceae (Aphyllphorales) described by C. Spegazzini. Mycologia 79:246–264.

—, De Meijer AR. 1990. New and noteworthy polypores from Paraná and São Paulo States, Brazil. Mycotaxon 38:173–185.

Raymundo T, Decock C, Valenzuela R, Amalfi M, Cifuentes J, Pacheco-Mota L. 2012. New records of the genus *Fomitiporia* (Hymenochaetales, Basidiomycota) in Mexico. Rev Mex Biodivers 83:313–328.

Reeb V, Lutzoni F, Roux C. 2004. Contribution of RPB2 to multilocus phylogenetic studies of the euascomycetes (Pezizomycotina, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory. Mol Phyl Evol 32:1036–1060, doi:10.1016/j.ympev.2004.04.012

Rehner SA, Buckley E. 2005. A *Beauveria* phylogeny inferred from nuclear ITS and EF1-a sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. Mycologia 97:84–98

Renvall P, Niemelä T. 1993. *Ocotea usambarensis* and its fungal decayers in natural stands. Bull Jard Bot Nat 62:403–414.

Robert V, Stegehuis G, Stalpers J. 2005. The MycoBank engine and related databases. <http://www.mycobank.org>.

Robledo G, Renison D. 2010. Wood-decaying polypores in the mountains of Central Argentina in relation to *Polylepis* forest structure and altitude. Fung. Ecol. 3: 178-184.

—, Urcelay C, Domínguez L, Rajchenberg M. 2006. Taxonomy, ecology, and biogeography of polypores (Basidiomycetes) from Argentinean *Polylepis* woodlands. Can J Bot 84: 1561–1572.

Ryvarden L. 2004. Neotropical Polypores 1. Synopsis Fungorum 19:1–229.

—, Johansen I. 1980. A preliminary polypore flora of East Africa. Fungiflora, Oslo, Norway.

Thiers B. [continuously updated] Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>.

Urcelay C, Robledo GL, Rajchenberg M. 2000. *Phellinus tabaquilio* sp. nov. from Córdoba Mountains, central Argentina. Mycotaxon 76:287–291.

Vlasák J, Kout J. 2011. Pileate *Fomitiporia* species in the USA. New combinations *Fomitiporia calkinsii* and *F. bakeri*. Mycol Progress 10: 445–452.

—, Kout J, Vlasák J Jr, Ryvarden L. 2011. New records of polypores from southern Florida. Mycotaxon 118:159-176.

Woolley LP, Henkel TW, Sillett SC. 2008. Reiteration in the monodominant tropical tree *Dicymbe corymbosa* (Caesalpiniaceae) and its potential adaptive significance. *Biotropica* 40: 32–43

Zhou LW, Xue HJ. 2012. *Fomitiporia pentaphylacis* and *F. tenuitubus* spp. nov. (Hymenochaetales, Basidiomycota) from Guangxi, southern China. *Mycol Progress* 11: 907–913.

CHAPTER V

***Fomitiporia neotropica* , a new species from South America evidenced by multilocus phylogenetic analyses**

This paper results from an in-deep revision of Neotropical species of *Fomitiporia* with resupinate basidiomata. As previously evidenced, they are gathered in a sub-clade within a larger Neotropical lineage. *Fomitiporia neotropica* is described as new, and the resupinate Neotropical clade discussed. All the species from this lineage share an identical, apomorphic deletion of 31 bp near the 5' end of the ITS1 region of the ribosomal DNA. Our results also strongly suggest that *F. pseudopunctata* (setose) and as *F. mediterranea* (asetose) cover a single taxon (both phylogenetically and ecologically), for which the nomenclaturally correct name should be *F. pseudopunctata*.

The use of the presence/absence of hymenial setae as diagnostic character at species level is strongly questioned since several examples of variable presence inside a phylogenetic/ecologic species are presented (e.g. *F. aethiopica*, *F. neotropica*, *F. mediterranea/pseudopunctata* complex).

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***Fomitiporia neotropica*, a new species from South America
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Abstract During the revision of the Neotropical *Fomitiporia* species with resupinate basidiomata, several collections from southern Brazil, central Argentina, and French Guiana were found to represent an undescribed species, on the basis of molecular (DNA sequence) and additional morphological and distributional data. This taxon is described and illustrated as *Fomitiporia neotropica* sp. nov. The species belongs to the *Fomitiporia langloisii* lineage, the type lineage within *Fomitiporia*, which so far contains only species with resupinate basidiomata spanning exclusively over the Neotropics. *Fomitiporia neotropica* is morphologically variable regarding the presence / absence of hymenial setae and secondarily the pore size. It also inhabits distinct ecosystems characterised by variable moisture regimes. The range of divergent positions in the DNA sequences used in this study (ITS, 28S, partial *tefl-α*, and *rpb2*), between specimens from distant origins, are of the same magnitude as between specimens of other related species such as *F. langloisii*, *F. dryophila*, *F. maxonii*, or *F. mediterranea*. A key to the species from the *F. langloisii* lineage is given.

Key words Hymenochaetales, Neotropics, Phylogeny, Taxonomy.

Introduction

Fomitiporia (Hymenochaetales), typified by *F. langloisii* (Decock et al. 2007, Murrill 1907), is above all characterized by globose to subglobose, thick-walled, cyanophilous, and dextrinoid basidiospores, in addition to a dimitic (pseudodimitic) hyphal system. Basidiomata are resupinate to pileate. Cystidioles and hymenial setae are variably present (Fischer 1996). The genus has been segregated into two morphological complexes based on the pileus habit: species with pileate basidiomata have been referred to the *F. robusta* complex (e.g. *F. robusta*, *F. erecta*, *F. hippophaeicola*); species sharing resupinate basidiomata have been commonly referred to the *F.*

punctata complex (e.g. *F. langloisii*, *F. punctata*, *F. pseudopunctata*). The genus has received much attention in the last 10 years and the understanding of the phylogenetic structure of both morphological complexes has improved considerably. It is now evident that these two complexes have no phylogenetic grounds (Amalfi and Decock 2013, Amalfi et al. 2010, 2012) and the resupinate and pileate habits are spread throughout the genus.

The understanding of the taxonomic diversity and species distribution range, in all biogeographical areas, has also greatly improved (Amalfi and Decock 2013, Amalfi et al. 2010, 2012, Dai et al. 2008, Decock et al. 2005, 2007, Fischer and Binder 2004, Fischer et al. 2005, Raymundo et al. 2012, Vlasák and Kout 2011, Zhou and Xue 2012). As far as the New World is concerned, the *Fomitiporia robusta* complex has been addressed by Fischer and Binder (2004), Vlasák and Kout (2011), Amalfi et al. (2012), and Amalfi and Decock (2013). As one of the consequences of these studies, the occurrence of *F. robusta sensu stricto* (s.s.) in the Americas was brought into question [in our opinion, *F. robusta* s.s. corresponds to *Phellinus robustus* var. *robustus sensu* Domański et al. (1967) or *Phellinus robustus sensu* Ryvarden (1978), cf. Amalfi and Decock 2013)]; this species is more likely to be absent from the Americas where multiple species occur, however, named or still unnamed, and pertain to various lineages; recent data strongly suggest that the New World is the area supporting the highest diversity of species with pileate basidiomata (Amalfi et al. 2012, Amalfi and Decock 2013).

The *Fomitiporia punctata* complex in the New World has been comparatively less studied. *Fomitiporia punctata sensu* “North American auctores” (e.g. Gilbertson and Ryvarden 1987, Lowe 1966) has been reported from all over North America. However, the concepts used at that time encompassed, in addition to *F. punctata* s.s. [e.g. *sensu* Ryvarden

(1978) or Jahn (1967), both circumscriptions drawn on the basis of European specimens and not polluted by data taken from materials of extra-European origins; in that sense, it corresponds to the *F. punctata* clade of Amalfi et al. (2010, 2012) and Amalfi and Decock 2013)], at least three other taxa, as demonstrated by Fischer and Binder (2004) and Decock et al. (2007). In North America, *F. punctata* s.s. is more likely restricted to northern, north-eastern temperate areas (Boulet 2003, Brazee et al. 2012, Fischer and Binder 2004). Its southern limit of distribution is still uncertain (see Decock et al. 2007) but in all probability the species is absent from southern (southeastern, south-western) USA, and *a fortiori* southward (Decock et al. 2007, Raymundo et al. 2012). Two other species, morphologically distinct and phylogenetically distant from *F. punctata* s.s., span over the south-eastern subtropical belt of the USA or, in a biogeographical perspective, the south-eastern and coastal plain mixed forest provinces of the subtropical division (Decock et al. 2007). Two historical names were unearthed for these species, viz. *F. langloisii*, re-instated as the genus type, and *F. dryophila*. Beyond the United States, *F. langloisii* and *F. dryophila* were also spotted southerly in (north) eastern Mexico (Raymundo et al. 2012), which constitutes to date their known southern limit of distribution.

Ryvarden (2004) reported *F. punctata* as rare in tropical America. Still, however, the literature is rich in reports of *F. punctata* in the Neotropics (e.g. Carranza-Morse 1992, David and Rajchenberg 1985, Loguercio-Leite and Wright 1991, 1995, Ryvarden 2004, Ryvarden and Meijer 2002, Wright and Blumenfeld 1984). In the light of recent data (Decock et al. 2007, Amalfi and Decock 2013, Amalfi et al. 2012), in the Neotropics, *F. punctata* should be better considered as *sensu lato* or *sensu auctores*. More likely, the concepts used will prove to encompass other

species, of yet uncertain circumscriptions and perhaps belonging to distinct lineages, apart from *F. punctata* s.s.

Decock et al. (2007) also addressed the status of *F. maxonii*, a species poorly known at that time (Ryvarden 2004). This species is more distinctly "tropical" and is nowadays reported from southern Florida (Vlasák et al. 2011), the Greater Antilles, Mexico, Costa Rica and southerly, down to Argentina (Decock et al. 2007, Raymundo et al. 2012).

In line with the above idea, pursuing the revision of *Fomitiporia* in the New World (Amalfi et al. 2012, Amalfi and Decock 2013, Decock et al. 2007, Raymundo et al. 2012), we applied a multilocus phylogenetic approach (based on DNA sequence data of 5' end of the LSU, ITS-5.8S, partial *tefl* and *rpb2*) to a set of Neotropical specimens with resupinate basidiomata. These specimens were resolved as two distinct clades, representing two distinct phylogenetic species, both within the *F. langloisii* lineage. One of them, *F. neotropica* sp. nov., is described below. The second clade is represented by only two specimens and we refrain to name it for the time being.

Materials and methods

Collection localities of the new taxa.— Specimens from Argentina were collected in the provinces of Córdoba, Jujuy (*Parque Nacional Calilegua*) and Misiones. Specimens from Brazil were collected in Rio Grande do Sul, Morrinhos do Sul, Lajeado (approx. 29°21'54"S, 49°56'05"W), Itapuã, Parque Estadual de Itapuã (approx 30°21' – 30°26'S × 50°54'– 51°03'W), Porto Alegre, Refúgio da Vida Silvestre, UFRGS (approx. 30°03' S, 51°07'W), and Santa Catarina, Florianópolis, Unidade de Conservação Ambiental Desterro - UCAD (approx 27°31'50.8"S, 48°30'44.3"W). The specimen from French Guiana was collected in the

CNRS “inselberg” research plots, Nouragues Natural Reserve (approx. 04°05.5'N, 52°40.6'W, <http://www.nouragues.cnrs.fr/F-inselberg.html>). Voucher herbarium specimens of the new species are preserved at CORD, ICN and MUCL, with a duplicate of type material deposited at NY (herbarium acronyms are according to Thiers, continuously updated). The authors isolated the strains during fieldwork, from fresh basidiomata tissues, plated on malt extract agar supplemented by 2 ppm benomyl (benlate) and 50 ppm chloramphenicol (Untereiner et al. 1998). Cultures were later purified in the laboratory in case of persistent bacterial contamination. Living cultures of the new species are preserved at MUCL with a duplicate at ICN. A duplicate of the ex-type strain is preserved also at the CBS (The Netherlands) (culture collection acronym according to the World Federation for Culture Collections, http://www.wfcc.info/ccinfo/collection/by_country/b/).

Morphology and anatomy— Basidiomata colours are described according to Kornerup and Wanscher (1981). Basidiomata sections were examined in Melzer's reagent, lactic acid Cotton blue (Kirk et al. 2001), and KOH 4 %. All microscopic measurements were done in Melzer's reagent. In presenting the size range of the microscopic elements, 5% of the measurements were excluded from each end and are given in parentheses, ave = arithmetical mean, Q = ratio of length/width of basidiospores, and ave_Q = arithmetical mean of the ratio Q. Thirty pores, basidiospores, and setae were measured from each specimen.

Sequencing— One hundred and nine specimens and cultures representing 40 species (or potential species clades) were included in the phylogenetic analysis. Materials and sequences used in this study are listed in TABLE I. As a rule, DNA was extracted from pure culture, except when noted (TABLE I). DNA extraction, amplification and sequencing of the 5'

end of the nuclear ribosomal LSU rRNA gene, the ITS regions (including 5.8S), partial *tefl- α* gene, and the region between domains 6 and 7 of the second largest subunit of the *rpb2* (Frøslev et al. 2005, Matheny 2005) were as described in Decock et al. (2007) and Amalfi et al. (2010, 2012) and Amalfi and Decock (2013).

Phylogenetic analysis— The nucleotide alignment deposited at TreeBASE under study accession number "<http://purl.org/phylo/treebase/phylows/study/TB2:S12874>" (Amalfi and Decock 2013) was used as starting data set to align the additional sequences. Ambiguously aligned segments also were detected with the Gblocks 0.91b program (Castresana 2000; <http://molevol.cmima.csic.es/castresana/Gblocks.html>) with settings “ALLOW SMALLER FINAL BLOCKS”, “ALLOW GAPS WITHIN BLOCKS”. The alignment was screened visually to detect additional ambiguously aligned regions. Alignments are deposited at TreeBASE (<http://purl.org/phylo/treebase/phylows/study/TB2:S12298>). Indels present within our datasets, especially in the ITS1 region (Decock et al. 2007), were recoded as binary characters with the simple indel coding method (SIC, Simmons and Ochoterena 2000) as implemented in SeqState software (Müller 2005).

Phylogenetic analyses were performed separately for each locus and concatenated with maximum parsimony as implemented in PAUP* 4.0b10 (Swofford 2003), Bayesian inference as implemented in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003), and Maximum likelihood (ML) as implemented in RAxML 7.0.4 (Stamatakis et al. 2008). *Phellinus uncisetus* was designated as outgroup (Decock et al. 2007). The most parsimonious trees for each dataset were identified with heuristic searches with 1000 random addition sequences, further evaluated by bootstrap analysis, retaining clades compatible with the 50% majority rule in the bootstrap

consensus tree. Analysis conditions were tree bisection and reconnection and addition branch swapping (TBR), starting tree obtained via stepwise addition, steepest descent not in effect, MULTREES effective. Models of evolution for Bayesian inference were estimated with the Akaike information criterion (AIC) as implemented in Modeltest 3.7 (Posada and Crandall 1998). The dataset was subdivided into 10 data partitions: ITS1, 5.8S, ITS2, nucLSU, *tef1* 1st and 2nd codon position, *tef1* 3rd codon position, *tef1* introns, *rpb2* 1st and 2nd codon position, *rpb2* 3rd codon position and the recoded indels (TABLE II). The best-fit models for each partition were implemented as partition-specific models within partitioned mixed-model analyses of the combined dataset. Three optimal models of nucleotide substitution were selected for ITS regions, the GTR + G model was used for ITS1 and the HKY + G model for ITS2 while the K80 model was used for 5.8S. The GTR + I + G model was used for the nucLSU dataset, for the *rpb2* region (for the first and second codon and for the third codon position) and for the first and second codon position of the *tef1* region, while the GTR + G model was used for the third codon position and HKY + I for the *tef1* introns dataset. For analysis of SIC data under Bayesian inference, we used the MrBayes restriction site model (F81-like) as recommended by Ronquist et al. (2005). All parameters were unlinked across partitions. Bayesian analyses were implemented with two independent runs, each with four simultaneous independent chains for 8000000 generations, starting from random trees, and keeping one tree every 1000th generation. To detect topological conflicts among data partitions the nodes between the majority rule consensus trees obtained in the parsimony analysis from the individual datasets were compared. Paired trees were examined for conflicts only involving nodes with bootstrap support value (BS) $\geq 70\%$ (Lutzoni et al. 2004, Mason-Gamer and Kellogg 1996, Reeb et al. 2004). A

conflict was assumed to be significant if two relationships for the same set of taxa (one being monophyletic and the other non-monophyletic) were observed between trees. For Bayesian inference and ML analyses, congruence was tested by inspecting internodes with posterior probabilities $\geq 95\%$ resulting from the separate Bayesian and ML analyses (as outlined in Miadlikowska and Lutzoni 2004, Moncalvo et al. 2006).

Maximum likelihood (ML) searches conducted with RAxML involved 1000 replicates under the GTRGAMMAI model, with all model parameters estimated by the program. In addition 1000 bootstrap (ML BS) replicates were run with the same GTRGAMMAI model. We provided an additional alignment partition file to force RAxML software to search for a separate evolution model for each dataset including the recoded indels.

TABLE 1. List of species, collections, and sequences used in the phylogenetic analyses.

Genus / Species names		GenBank accession number			
Voucher specimens / cultures reference					
	Locality	nLSU	ITS	<i>tefl-α</i>	<i>rpb2</i>
<i>Fomitiporia aethiopica</i> Decock, Bitew & G. Castillo					
MUCL 44777 (T) ^{c, h}	Ethiopia	AY618204	GU478341	GU461893	JQ087956
MUCL 44806 ^{c, h}	Ethiopia	AY618202	GU461944	GU461892	JQ087955
<i>F. apiahyna</i> (Speg.) Robledo, Decock & Rajchenb.					
MUCL 51451 ^{c, h}	Ecuador	GU461997	GU461963	GU461896	JQ087958
MUCL 51485 ^{c, h}	Ecuador	GU461996	GU461962	GU461895	JQ087957
MUCL 53042 ^{c, h}	French Guiana	JX093817	JX093773	JX093730	JX093861
<i>F. australiensis</i> Fischer, Edwards, Cunningt. & Pascoe					
VPRI 22451a (MUCL 49406, PT ^c	Australia	GU462001	AY624997	GU461897	JQ087959
<i>Fomitiporia bakeri</i> (Murrill) Vlasák & Kout					
FP-134784-Sp (MUCL 51098) ^{c, 1}	USA	JQ087901	JQ087874	JQ087928	JQ087960
<i>F. bannaensis</i> Y.C. Dai					
MUCL 45926 ^{c, h}	Thailand	EF429217	GU461942	GU461898	JQ087961
MUCL 46926 ^{c, h}	China	KF444705	KF444682	KF444751	KF444728

MUCL 46930 ^{c, h}	China	KF444706	KF444683	KF444752	KF444729
MUCL 46948 ^{c, h}	China	KF444707	KF444684	KF444753	KF444730
MUCL 46950 ^{c, h}	China	EF429218	GU461943	GU461899	JQ087962
<i>Fomitiporia calkinsii</i> (Murrill) Vlasák & Kout					
FP-106252-Sp (MUCL 51095) ^{c, 1}	USA	KF444708	KF444685	KF444754	KF444731
FP-53385-T (MUCL 51099) ^{c, 1}	USA	KF444709	KF444686	KF444755	KF444732
FP-71907-T (MUCL 51100) ^{c, 1}	USA	JQ087902	JQ087875	JQ087929	JQ087963
CBS 175.34 (MUCL 51398) ^{c, 1}	USA	KF444710	KF444687	KF444756	KF444733
MUCL 52346 ^{c, h}	Mexico	JQ087903	JQ087876	JQ087930	JQ087964
MA-MX0945 ^{c, h}	Mexico	KF444711	KF444688	KF444757	KF444734
<i>F. castilloi</i> Amalfi & Decock					
MUCL 53481 (T) ^{c, h}	French Guiana	JQ087916	JQ087889	JQ087943	JQ087996
MUCL 53980 (PT) ^{c, h}	French Guiana	JX093830	JX093786	JX093743	JX093874
<i>F. cupressicola</i> Amalfi, Raymundo, Valenzuela et Decock					
MUCL 52486 (T) ^{c, h}	Mexico	JQ087904	JQ087877	JQ087931	JQ087965
MUCL 52488 ^{c, h}	Mexico	JQ087905	JQ087878	JQ087932	JQ087966
MUCL 52489 ^{c, h}	Mexico	JQ087906	JQ087879	JQ087933	JQ087967
MUCL 52490 ^{c, h}	Mexico	JQ087907	JQ087880	JQ087934	JQ087968
<i>F. dryophila</i> Murrill					

TJV-93-232 (MUCL 46379) ^{c, 1}	USA	EF429221	EF429240	GU461902	JQ087969
TJV-93-234 (MUCL 46380) ^{c, 1}	USA	EF429219	EF429238	GU461900	JQ087970
TJV-93-259 (MUCL 46381) ^{c, 1}	USA	EF429220	EF429239	GU461901	KF444735
FP-104030-T (MUCL 51144) ^{c, 1}	USA	KF444712	KF444689	KF444758	KF444736
<i>F. erecta</i> (A. David, Dequatre & Fiasson) Fiasson					
MUCL 49871 ^{c, h}	France	GU461976	GU461939	GU461903	JQ087971
MA-PA03 ^{c, h}	Italy	KF444713	KF444690	KF444759	ND
<i>F. gabonensis</i> Amalfi & Decock					
MUCL 47576 (T) ^{c, h}	Gabon	GU461990	GU461971	GU461923	JQ087972
MUCL 51291 ^{c, h}	Gabon	GU461986	GU461967	GU461924	JQ087973
<i>Fomitiporia hartigii</i> (Allesch. & Schnabl) Fiasson & Niemelä					
MAFF 11-20016 (MUCL 31400) ^c	Japan	JQ087909	JQ087882	JQ087936	JQ087975
75-2 562 (MUCL 53549) ^{c, 4}	Estonia	JX093831	JX093787	JX093744	JX093875
71-25 464 (MUCL 53550) ^{c, 4}	Estonia	JX093832	JX093788	JX093745	JX093876
75-3 563 (MUCL 53551) ^{c, 4}	Estonia	JX093833	JX093789	JX093746	JX093877
<i>F. hippophaeicola</i> (H. Jahn) Fiasson & Niemelä					
MUCL 31746 ^{c, h}	Belgium	AY618207	GU461945	GU461904	JQ087976
MUCL 31747 ^{c, h}	Belgium	GU461977	GU461946	GU461905	JQ087977
<i>F. ivindoensis</i> Decock, Amalfi & Yombiyeni					

MUCL 51311 ^{c, h}	Gabon	GU461979	GU461952	GU461907	JQ087978
MUCL 51312 (T) ^{c, h}	Gabon	GU461978	GU461951	GU461906	JQ087979
<i>F. langloisii</i> Murrill					
FP-94347-R (MUCL 46375) ^{c, 1}	USA	EF429225	EF429242	GU461908	JQ087980
01-77/4 (MUCL 46165), (T of <i>F. hesleri</i>) ^{c, 5}	USA	EF429223	AY340026	GU461909	JQ087981
FP-105-816-T (MUCL 46373) ^{c, 1}	USA	EF429226	EF429243	KF444760	ND
HHB-9868-Sp (MUCL 46377) ^{c, 1}	USA	EF429224	EF429241	KF444761	ND
01-712/2 (MUCL 46164) ^{c, 5}	USA	EF429222	AY340031	KF444762	ND
FP-105818-R (MUCL 46374) ^{c, 1}	USA	EF429227	EF429244	KF444763	ND
<i>F. maxonii</i> Murrill					
MUCL 46017 ^{c, h} (=CRGF 182)	Cuba	EF429230	EF433559	GU461910	JQ087983
MUCL 46037 ^{c, h} (=CRGF 183)	Cuba	EF429231	EF433560	GU461911	JQ087982
MUCL 51331 ^{c, h}	Argentina	KF444714	KF444691	KF444764	KF444737
MUCL 51540 ^{c, h}	Cuba	KF444715	KF444692	KF444765	KF444738
MUCL 51399 ^{c, h}	Cuba	KF444716	KF444693	KF444766	KF444739
MUCL 52340 ^{c, h}	Mexico	KF444717	KF444694	KF444767	KF444740
MUCL 53364 ^{c, h}	Mexico	KF444718	KF444695	KF444768	KF444741
<i>F. mediterranea</i> M. Fisch.					

AFTOL ID 688	ND	AY684157	AY854080	AY885149	AY803748
MUCL 38514	Italy	AY618201	GU461953	GU461912	JQ087984
MUCL 45670 ^{c, h}	France	GU461980	GU461954	GU461913	JQ087985
<i>Fomitiporia neotropica</i> sp. nov.					
MUCL 53114 ^{c, h}	French Guiana	JX093836	JX093792	JX093749	JX093880
MUCL 49549 ^{c, h}	Argentina	KF444719	KF444696	KF444769	KF444742
MUCL 54246 ^{c, h}	Brazil	KF444720	KF444697	KF444770	KF444743
MUCL 51335 (T) ^{c, h}	Argentina	KF444721	KF444698	KF444771	KF444744
MUCL 51336 ^{c, h}	Argentina	KF444722	KF444699	KF444772	KF444745
MUCL 54206 ^{c, h}	Brazil	KF444723	KF444700	KF444773	KF444746
MUCL 54196 ^{c, h}	Brazil	KF444724	KF444701	KF444774	KF444747
MUCL 54212 ^{c, h}	Brazil	KF444725	KF444702	KF444775	KF444748
<i>F. nobilissima</i> Decock & Yombiyeni					
MUCL 47580 ^{c, h}	Gabon	GU461985	GU461966	GU461921	JQ087986
MUCL 51289 (T) ^{c, h}	Gabon	GU461984	GU461965	GU461920	JQ087987
<i>F. polymorpha</i> M. Fisch.					
91-42/3 (MUCL 46166) (PT) ^{c, 5}	USA	DQ122393	GU461955	GU461914	JQ087988
91-42/1 (MUCL 46167) (PT) ^{c, 5}	USA	EF429233	GU461956	GU461915	JQ087989
<i>F. pseudopunctata</i> (A. David, Dequatre & Fiasson) Fiasson					

MUCL 51325 ^{c, 2}	Czech	GU461981	GU461948	GU461916	JQ087998
MUCL 46168 ^{c, h}	France	JQ087918	JQ087891	JQ087945	JQ087999
<i>F. punctata</i> (Fr.) Murrill					
MUCL 34101 ^{c, h}	Germany	AY618200	GU461947	GU461917	JQ088000
WD-2055 (MUCL 47629) ^{c, 3}	Japan	GU461982	GU461950	GU461918	JQ088001
71-8 298 (MUCL 53548) ^{c, 4}	Europe	JX093834	JX093790	JX093747	JX093878
<i>F. punicata</i> Y.C. Dai, B.K. Cui & Decock					
Cui 23	China	GU461991	GU461974	GU461927	JQ088002
Cui 26	China	GU461992	GU461975	GU461928	JQ088003
<i>F. robusta</i> (P. Karst.) Fiasson & Niemelä					
CBS 389.72 (MUCL 51297)	Estonia	JQ087919	JQ087892	JQ087946	JQ088004
Tomšovský 1013 (MUCL 51327) ^{c, 2}	Czech	GU461993	GU461949	GU461929	JQ088005
<i>Fomitiporia sonoriae</i> (Gilb.) Y.C. Dai					
RLG-10862-Sp (MUCL 47689) (T) ^{c1}	Arizona	JQ087920	JQ087893	JQ087947	JQ088006
<i>Fomitiporia</i> “spp.”					
CBS 386.66 = MUCL 46181 ^{c, 6}	Argentina	EF429234	EF433563	GU461930	JQ088007
MUCL 53675 ^{c, h}	French Guiana	JX093835	JX093791	JX093748	JX093879
MUCL 47756 ^{c, h}	Argentina	JQ087913	JQ087886	JQ087940	JQ087993
MUCL 47757 ^{c, h}	Argentina	JQ087914	JQ087887	JQ087941	JQ087994

MUCL 47758 ^{c, h}	Argentina	JQ087915	JQ087888	JQ087942	JQ087995
MUCL 53009	South Africa	JQ087917	JQ087890	JQ087944	JQ087997
FP-98505-T (MUCL 51105) ^{c, 1}	USA (Arizona)	JQ087911	JQ087884	JQ087938	JQ087991
RLG-10827 (MUCL 51106) ^{c, 1}	USA (New Mexico)	JQ087910	JQ087883	JQ087937	JQ087990
MUCL 52350	Mexico	JQ087912	JQ087885	JQ087939	JQ087992
MUCL 53993	Mexico	JX093851	JX093807	JX093764	JX093893
MUCL 53994	Mexico	JX093852	JX093808	JX093765	JX093894
MUCL 51555 ^{c, h}	Martinica	JX093853	JX093809	JX093766	JX093895
MUCL 53797 ^{c, h}	French Guiana	JX093854	JX093810	JX093767	JX093896
MUCL 53798 ^{c, h}	French Guiana	JX093855	JX093811	JX093768	JX093897
<i>F. tabaquilio</i> (Urcelay, Robledo & Rajchenb.) Decock & Robledo					
MUCL 46230 ^{c, h}	Argentina	DQ122394	GU461940	GU461931	JQ088008
MUCL 47754 ^{c, h}	Argentina	GU461994	GU461941	GU461932	JQ088009
<i>F. tenuis</i> Decock, Bitew & G. Castillo					
MUCL 44802 (T) ^{c, h}	Ethiopia	AY618206	GU461957	GU461934	JQ088010
MUCL 49948 ^{c, h}	Gabon	GU461998	GU461958	GU461935	JQ088011
MUCL 49971 ^{c, h}	Uganda	GU461998	GU461958	GU461935	JQ088012
<i>Fomitiporia texana</i> (Murrill) Nuss					
RLG-7763-T (MUCL 47690) ^{c, 1}	USA, Arizona	JQ087921	JQ087894	JQ087948	JQ088013

FP-89674-R (MUCL 51143) ^{c, 1}	USA, Arizona	JQ087922	JQ087895	JQ087949	JQ088014
<i>Fomitiporia torreyae</i> Y.C. Dai & B.K. Cui					
WD-199 (MUCL 47628) ^{c, 3}	Japan	JQ087923	JQ087896	JQ087950	JQ088015
WC31 ^h	Chine	JQ087924	JQ087897	JQ087951	JQ088016
<i>Fomitiporia tsugina</i> Murrill					
Ft_San (MUCL 52702)	USA	JQ087925	JQ087898	JQ087952	JQ088017
Ft_T2-1 (MUCL 52703)	USA	JQ087926	JQ087899	JQ087953	JQ088018
CBS125.40 (MUCL 51295)	USA	JQ087908	JQ087881	JQ087935	JQ087974
<i>Phellinus juniperinus</i> Bernicchia & S. Curreli					
MUCL 51757 ^{c, h}	Tunisia	JQ087927	JQ087900	JQ087954	JQ088019
MA-PA01 ^{c, h}	Italy	KF444726	KF444703	KF444776	KF444749
MA-PA02 ^{c, h}	Italy	KF444727	KF444704	KF444777	KF444750
<i>P. uncisetus</i> Robledo, Urcelay & Rajchenb.					
MUCL 46231 ^{c, h}	Argentina	EF429235	GU461960	GU461937	JQ088020
MUCL 47061 ^{c, h}	Argentina	GU462000	GU461972	GU461938	JQ088021

T, PT = type, paratype; ^c = culture available; ^h = voucher herbarium specimen corresponding to the culture available at the MUCL herbarium; ¹ cultures from CFMR, USDA, courtesy of Dr. K. Nakasone); ² cultures from Faculty of Forestry and Wood Technology, Mendel University of Agriculture and Forestry in Brno, Czech Republic, courtesy of Dr. M. Tomšovský; ³ cultures from Microbial Ecology Lab Forestry and Forest Products Research Institute, courtesy of Prof. T. Hattori, Japan; ⁴ cultures from National History Museum, University of Tartu, Estonia, courtesy of K. Põldmaa; ⁵ cultures from Regensburg University, Germany, courtesy of Dr. M. Fischer; ⁶ cultures from the CBS, The Netherlands, courtesy of Prof. P. Crous.

Results

DNA sequence comparisons— Sequence length and parsimony data for each dataset (length of aligned sequences, variable parsimony uninformative positions, parsimony informative positions, excluded characters) are summarized in Table II. As already evidenced by Decock et al. (2007) and confirmed by Amalfi et al. (2012), the species forming the *F. langloisii* lineage, namely *F. dryophila*, *F. langloisii*, *F. maxonii*, *F. sonora*, an unnamed *Fomitiporia* sp. MUCL 46181 and *Fomitiporia* sp. MUCL 53675 present a 31 bps long deletion near the 5' end of the ITS1 region. An identical deletion (in terms of length and position) is present in the ITS1 region of *Fomitiporia* sp. MUCL 53114, MUCL 51335, MUCL 51336, MUCL 54206, MUCL 54196, and MUCL 54212. This deletion seems to be a plesiomorphic character of the *F. langloisii* lineage.

Individual dataset comparisons — Sequence data and statistical analysis for each dataset and combined analysis are provided (Table II).

By comparing the tree topologies obtained for the individual datasets, no conflict involving significantly supported nodes was found using the reciprocal 70% BP and 95% PP and ML BS criterion; the datasets were therefore combined.

Table 2 Summary of datasets of ITS rDNA, LSU rDNA, *tef1*, and *rpb2*

Properties	Datasets									
	ITS 1	5.8S	ITS 2	nLSU	<i>tef1</i> 1st / 2nd	<i>tef1</i> 3rd	<i>tef1</i> introns	<i>rpb2</i> 1st / 2nd	<i>rpb2</i> 3rd	Indels
Alignment size	508	159	347	970	663	331	231	542	271	443
Variable parsimony										
uninformative positions	30	12	21	30	10	27	12	7	6	52
Parsimony informative positions	197	9	122	121	26	210	122	44	228	110
Excluded characters	36	–	–	–	–	–	–	–	–	–
Model selected	GTR+G	K80	HKY+G	GTR+I+G	GTR+I+G	GTR+G	HKY+I	GTR+I+G	GTR+I+G	F81-like
Likelihoodscore	–3,174.0623	–358.064	–2,129.7996	–865.2439	–1,300.0289	–3,378.2085	–1,910.0972	–1,359.6776	–5,219.0098	–
Base frequencies										
Freq. A =	0.2753	Equal	0.2493	0.2591	0.3070	0.1480	0.2771	0.2920	0.2284	–
Freq. C =	0.1794	Equal	0.1827	0.1980	0.2213	0.3142	0.1994	0.2143	0.1844	–
Freq. G =	0.1913	Equal	0.1959	0.2960	0.2627	0.2351	0.1564	0.2742	0.2970	–
Freq. T =	0.3541	Equal	0.3720	0.2469	0.2090	0.3028	0.3670	0.2194	0.2902	–
Proportion of invariable sites	–	–	–	0.6798	0.8443	–	0.1284	0.7884	0.0782	–
Gamma shape	0.6294	–	0.4957	0.7101	0.6896	1.5079	–	0.7969	2.1858	–

Combined dataset analysis—Thirty six characters in the ITS1 region were judged too ambiguous to be aligned. Of the remaining 4429 characters, 255 were variable but parsimony uninformative and 1352 were parsimony informative. The two Bayesian runs converged to stable likelihood values after 930000 generations and 7070 stationary trees from each analysis were used to compute a 50% majority rule consensus tree in PAUP* to calculate posterior probabilities (PP). In the ML searches with RAxML the combined dataset alignment had 1980 distinct patterns with a proportion of gaps and undetermined characters of 13.06%.

The heuristic search produced 1280 equally most parsimonious trees (4024 steps long; CI 0.495, RI 0.849, RC 0.420), representing one main topology. This topology is congruent with published trees (Amalfi et al. 2010, 2012, Amalfi and Decock 2013) and is highly concordant with the topologies obtained analysing the individual dataset and almost identical to the Bayesian consensus tree and to the optimal tree inferred under the Maximum likelihood criterion ($-\ln L = 26969.634$, FIG. 1). The results of the phylogenetic inferences, independently of analyzing the data sets individually or combined, were highly congruent and resolve the same clades and lineages as previously reported (Amalfi and Decock 2013, Amalfi et al. 2010, 2012).

Seven collections sharing resupinate basidiomata and originating from the Neotropics (*viz.* MUCL 53114, MUCL 51335, MUCL 51336, MUCL 54206, MUCL 54196, and MUCL 54212) clustered together in a new, well supported terminal clade (Fig. 1, PS1). Two additional collections from French Guiana and Argentina formed a second well supported terminal clade (FIG. 1, PS2). Both nest at the base of the *F. langloisii* lineage as defined by Decock et al. (2007) and confirmed by Amalfi et al. (2012) and Amalfi and Decock (2013).

Morphological analysis— Morphological examinations of our collections belonging to this new Neotropical clade PS1 revealed no absolute combination of morphological features thereby defining clearly one morphospecies. Some morphological parameters usually accounting as critical species descriptors are variable, or overlap with those of other species. These included the number of pores / mm (and the pores size), the basidiospores size, and the presence / absence of hymenial setae.

The number of pores / mm ranges mostly from 6–9, with the extremes of 5 and 12. The pore diameter ranges from (70–) 75–145 (–150) μm , and the individual (specimen) averages range from 86 μm to 120 μm . Only 12% of the pores are larger than 120 μm in diameter. The basidiospores are typical of *Fomitiporia*, subglobose to obovoid, slightly thick-walled, dextrinoid, and cyanophilous. Their size range is mainly 5.0–7.0 $\times$ 4.5–7.0 μm (ave = 5.9 $\times$ 5.7 μm). It overlaps much with the basidiospores size range of all other species of the *F. langloisii* lineage (Decock et al. 2007) but *F. dryophila* for which the basidiospores are larger (6.2–8.0 (–8.5) $\times$ 5.7–7.3 (–7.5) μm (ave = 7.0 $\times$ 6.5 μm , Decock et al. 2007).

Hymenial setae were observed in two specimens only, viz. MUCL 51335 and MUCL 51336 (cf. list of specimens examined below), both originating from Argentina. They are variably abundant, however: numerous in MUCL 51335 and scattered in MUCL 51336. In both specimens, they are mostly present in the dissepiment areas. They are also variable in shape, and often apically rounded (Fig. 3).

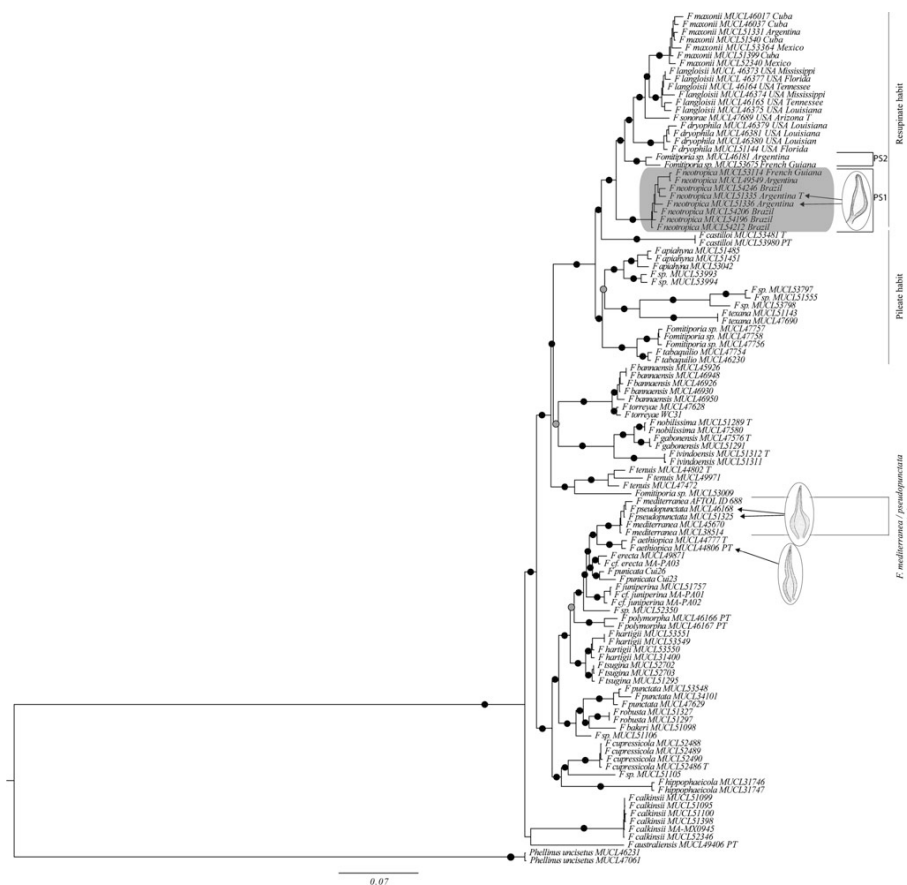


Fig. 1. The 50% majority-rule consensus tree from Bayesian inference of the combined ITS, LSU, *tef1* and *rpb2* sequences. Black dots on branches represent BPP, ML BS and BS of 99% or higher; grey dots on branches denote BPP greater than 95% and ML BS greater than 85% but BS support lower than 50%.

Discussion and taxonomic conclusions

Within the Hymenochaetaceae, the presence / absence, shape, and size of setae (hymenial or extra-hymenial) have been regarded as confident taxonomic features to delimit species boundaries (e.g. David et al. 1982). In *Fomitiporia*, however, this might not be always so absolute. The presence of hymenial setae seems to be a very constant character in several species such as *F. tenuis* (Decock et al. 2005, Cony Decock pers. obs.), *F. bannaensis*

(Dai et al. 2001, Cony Decock pers. obs.), or *F. spinescens* (Coelho and Wright 1996, Coelho et al. 2009, Ryvarden 2004, Cony Decock pers. obs.). However, in others, the presence of setae, hymenial or extra-hymenial, may be variable and should not be considered as a critical parameter defining morphospecies. Such cases exist in the *F. punctata* and *F. robusta* species complexes. It concerns, for instance, *F. aethiopica*, *F. pseudopunctata*, or *F. polymorpha*, and *F. robusta* or *F. erecta*.

Decock et al. (2005) first segregated collections from Ethiopian highlands into two species based on presence / absence of hymenial setae: *F. aethiopica*, for the asetose specimens, and *F. pseudopunctata* for the setose specimens. Nevertheless, a subsequent multilocus phylogenetic approach revealed that asetose and setose Ethiopian specimens together formed a monophyletic clade (Amalfi et al. 2010). Both asetose and setose specimens were, in fact, conspecific and belonged to *F. aethiopica* (Amalfi et al. 2010). Therefore, the species concept had to be redefined to include variably present and variably shaped hymenial setae (Amalfi et al. 2010).

The case of *F. pseudopunctata* / *F. mediterranea* is worth also discussing. *Fomitiporia pseudopunctata* was described and differentiated from *F. punctata* on the basis of presence / absence of hymenial setae, respectively (David et al. 1982). Molecular data confirmed that *F. pseudopunctata* and *F. punctata* represent two distinct taxa (Amalfi et al. 2010, 2012). They also have globally disjointed distribution ranges in Europe (though overlap is possible locally). *Fomitiporia mediterranea* was originally described based on specimens mainly originating from the Mediterranean areas, on *Vitis vinifera*, and related to Esca disease in Southern Europe (Fischer 2002). It has been shown later to be a widespread species in southern Europe on multiple, wild and cultivated hosts (e.g. *Citrus*, *Corylus*, *Platanus*, *Vitis*, Fischer 2002, Pilotti et al. 2005, 2010).

Fomitiporia mediterranea was distinguished also from *F. pseudopunctata* by the absence of setae (Fischer 2002).

However, phylogenetic inferences carried out from our multilocus dataset showed that specimens identified as *F. pseudopunctata* (setose) and as *F. mediterranea* (asetose) from Southern France and Italy merged together with the reference material of *F. mediterranea* AFTOL ID688 into a single, monophyletic clade. Furthermore, analysis of a large set of ITS sequences of *F. mediterranea* (mostly retrieved from GenBank), originating from its known distribution areas and multiple hosts, and of *F. pseudopunctata* gathered from wild hosts in southern Europe, resulted in a single, monophyletic clade. The *F. pseudopunctata* entries are dispersed within the “*F. mediterranea*” entries (data not shown). These results strongly suggest that these two binomials in fact cover a single taxon, for which the nomenclaturally correct name is *F. pseudopunctata*. The presence of hymenial setae is also a non-critical character to define morphologically this species.

Fomitiporia polymorpha was described based on combined morphological and molecular data (Fischer and Binder 2004). The occurrence of hymenial setae was emphasized also as variable among specimens, absent to scattered.

Several species with pileate basidiomata also present such variability as far as hymenial or extra-hymenial setae are concerned. They include in Europe *F. robusta* (David et al. 1982, Domański et al. 1967, Ryvar den 1978). Pieri and Rivoire (2000) also pointed out the presence / absence of both hymenial and extra-hymenial setae in *F. erecta* / *Phellinus juniperinus*. However, as stated by Amalfi et al. (2012), an integrating approach has never been applied to the European species, and would be necessary to tackle the *F. robusta* / *F. erecta* / *Ph. juniperinus* / *Ph. rosmarini* complex in

Europe. In North America, *F. texana* shows a similar variable presence of setae (Raymundo et al. 2012).

In our case, two setose (MUCL 51335 and MUCL 51336) and the five aetose specimens (MUCL 49549, MUCL 54206, MUCL 54196, MUCL 54212, and MUCL 54246) clustered within the same, monophyletic terminal clade (PS1, FIG. 1). The range of divergent positions in the DNA sequences used in this study (ITS, 28S, partial *tefl-a*, and *rpb2*), among specimens from distant origins (from French Guiana to Argentina), are of the same magnitude as among specimens of other species of this lineage, such as *F. langloisii*, *F. dryophila*, or still, *F. maxonii*. Furthermore, the two setose specimens did not form a two specimen subclade within this clade PS1; MUCL 51335 is genetically more closely related to MUCL 54246 than to MUCL 51336.

Given that our collections, setose or aetose, form a single clade, representing a phylogenetic unit, and notwithstanding the morphological variability, we interpret this as a single species. The search for a possible epithet within the synonyms of *F. punctata* (Decock et al. 2007, Ryvarden 1991, Robert et al. 2005) yielded no name that could apply to it. This species is therefore proposed below as *F. neotropica* sp. nov.

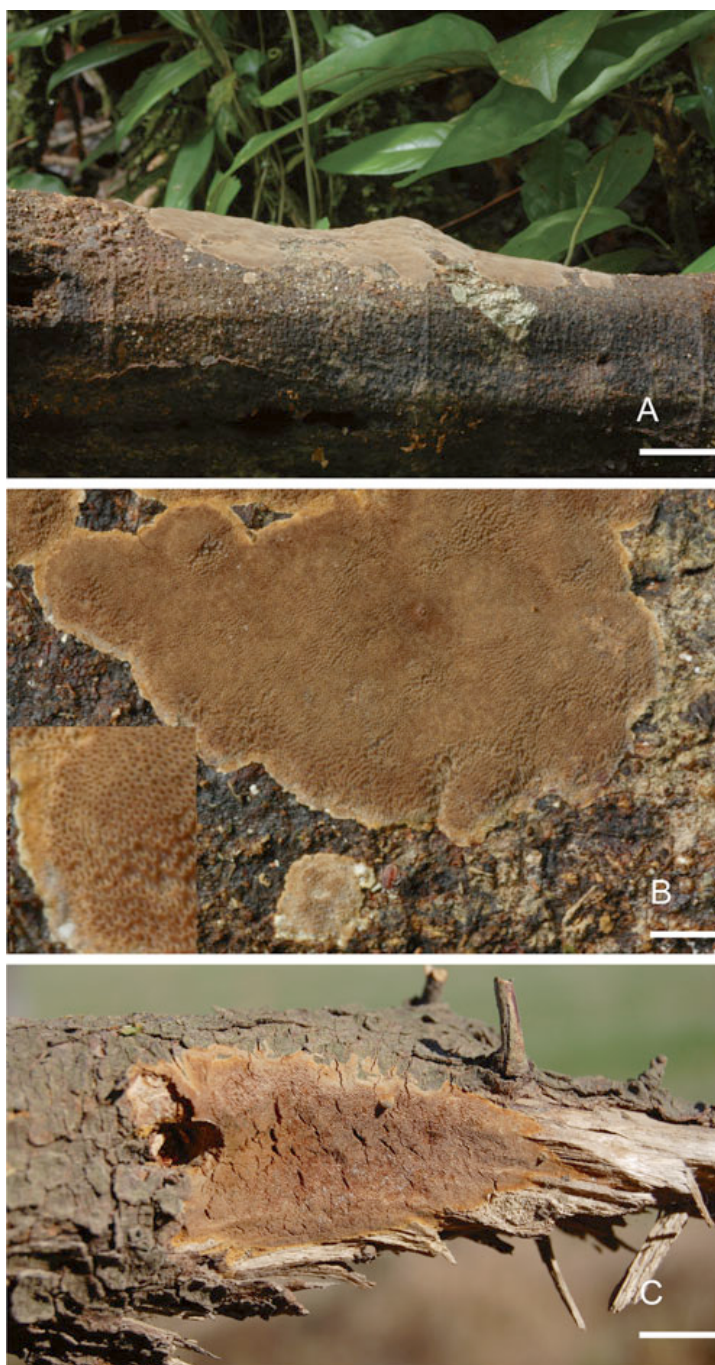


FIG. 2. *Fomitiporia neotropica*, Basidiomata *in situ*. A, B. Actively growing, single layered basidiomata in high moisture environment, French Guiana, MUCL 53114 (A, scale bar = 5

cm; B, scale bar = 2 cm). C. Argentina, older, drier basidiomata in environment with seasonal drought dry, MUCL 49549 (C, scale bar = .5 cm)

Taxonomy

Fomitiporia neotropica Campos-Santana, Amalfi, R.M. Silveira, Robledo et Decock, sp. nov. Figs. 2–4

Mycobank: MB X

Etymology: *neotropica*, from the distribution areas in the Neotropics.

Basidiomata resupinata, effusa; pororum facies griseo-brunnea vel brunnea; pori circulari, 6–9 per mm, (70–) 75–125 (–150) μm diam; tubi stratosi, ad 3.5 mm longi, in series ad min. 2 singula strata, 0.75–2.5 mm crassa; systema hypharum dimiticum; hyphae generatoriae afibulatae, hyalinae ad pallido-luteae; hyphae skeletales flavo-brunneae, crassitunicatae, aseptatae; setae hymeniales presentes ad ausentes, ferrugineo-fuscae, subulatae vel leviter ventricosae, rectae, apice acutae vel retundatae, 10.0–30.0 $\times$ 3.5–6.5 (–7.0) μm ; basidiosporae subglobosae vel globosae, leviter crassitunicatae, hyalinae, dextrinoideae, cyanophileae, 5.0–7.0 (–7.5) $\times$ 4.5–7.0 μm .

Holotypus hic designatus: Argentina, Provincia Jujuy, Calilegua Nationalis hortus, in mortuo stipite ignotae angiospermia, IV 2008, M. Amalfi, AR 7508, in herbarium MUCL 51335; isotypus in herbaria NY et CORD.

Basidiomata annual, resupinate, effused, following the substrate, adnate, extending up to 30 cm long, 14 cm wide, 1.5–5 mm in the thickest part, with a corky consistency when fresh, drying hard corky, with a densely fibrous texture; margin up to 0.5–2 mm wide, narrow, densely and very minutely velutinous, becoming slightly indurate on aging in multilayered specimens, from outside inside white, pale yellow (3A[3–4], greyish to brownish orange (5[B–C][4–6], (5C[6–7], yellow ochre, caramel), light to

dark brown on aging (6[D–E]6 cinnamon, 6F(7–8); *pore surface* in brown shade, commonly yellowish brown (5E[4–5], greyish brown, dark blonde, 5D[3–4]) to darker brown (6E[4–6], greyish chocolate brown, or 6F4, dark brown); *pores* small, round to ellipsoid at inclined parts, mostly 6–9 / mm (ranging from 5–12), (70–) 75–125 (–150) μm diam (ave = 119 μm); *dissepiments* entire, thin to thick, 20–110 μm diam (ave = 55 μm), commonly with free hyphal tips, sometimes with a greyish tint due to crystal deposit; *subiculum* 0.3–1.0 mm thick, densely fibrous, golden to light brown (5D[6–7], 5E8), homogeneous or with some denser, black, continuous or discontinuous thin lines; *tubes* uni- or bi-layered, indistinct or each one separated by a thin, slightly darker layer of sterile mycelium, 1.0–3.5 mm thick each, totalling up to 4 mm thick; *tube layer* concolorous with the pore surface.

Hyphal system dimitic, identical in the context and hymenophoral trama; *generative hyphae* hyaline to faintly yellow, thin-walled, sparsely branched 1.5–2.5 (–3) μm wide (ave = 2.0 μm), *skeletal hyphae* pale yellow brown to golden brown, thick-walled but with an open lumen, 2.5–4.0 μm wide (ave = 3.2 μm), with occasional local, intercalary or terminal swellings, tightly packed in the hymenophoral trama, with sub-parallel orientation.

Hymenium: *basidia* pyriform to subglobose, 7.5–9.5 $\times$ 7.0–9.5 μm , with four small sterigmata; *basidioles* identical in shape but slightly smaller; *hymenial setae* variably present, from absent to abundant, fusiform to slightly ventricose, slightly lageniform, apex pointed to rounded, 10.0–30.0 $\times$ 3.5–6.5 (–7.0) μm (ave = 16.8 $\times$ 4.6 μm), $Q = 2.08\text{--}5.71$ (ave_Q = 3.7); *basidiospores* subglobose to broadly obovoid, 5.0–7.0 (–7.5) $\times$ 4.5–7.0 μm (ave = 5.9 $\times$ 5.7 μm), $Q = 1\text{--}1.2$ (ave_Q = 1.05), thick-walled, the wall hyaline, cyanophilous, strongly dextrinoid; *chlamydospore* absent.

Type of rot: white rot;

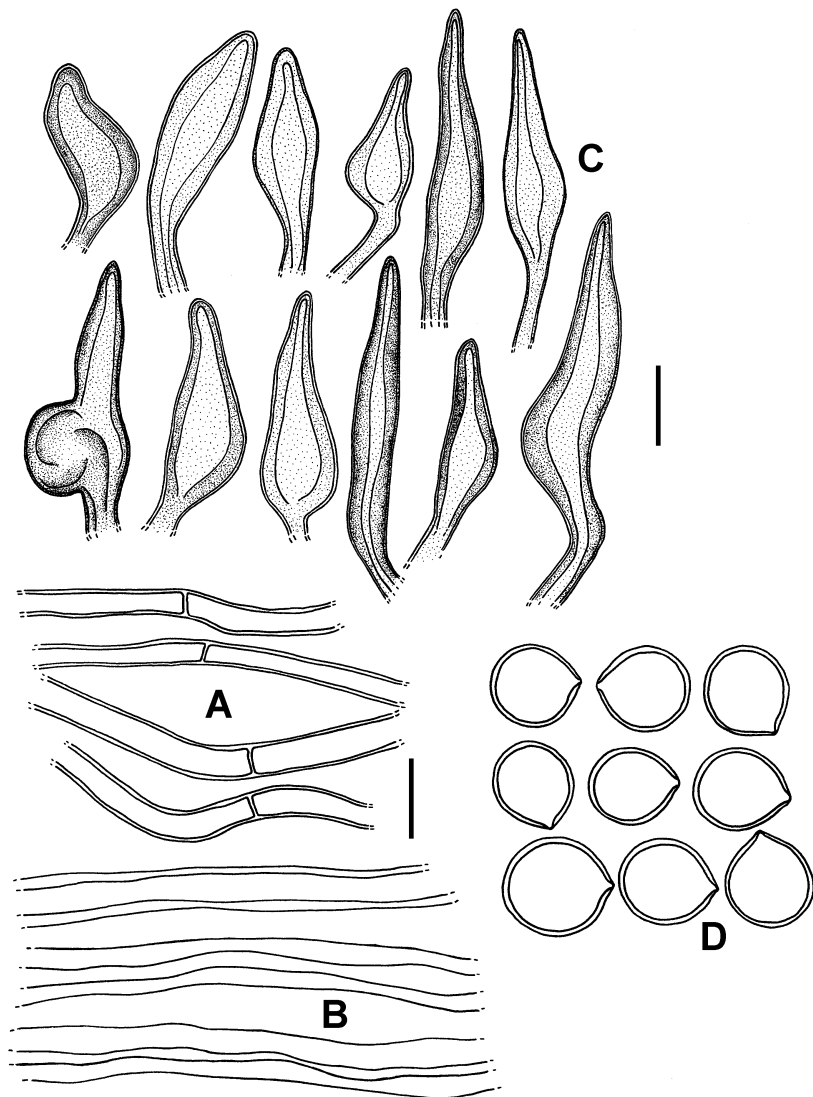
Substrate and hosts: dead fallen branches, occasionally still attached to the tree, dead trunk, or living branches; *Schinus sp.* (Anacardiaceae), unidentified angiosperms.

Specimens examined: ARGENTINA: Córdoba, San Justo, Miramar, Mar Chiquita, approx 30°55'59.1"S, 62°42'17.1"O, elev. approx. 76 m, on a stem and dead branches attached to the tree, *Schinus sp.*, Anacardiaceae, 29 Jul 2007, *Robledo 1713* (MUCL 49549; culture ex- MUCL 49549); Jujuy province, Parque Nacional Calilegua, sendero La Junta, on a dead standing trunk, unidentified angiosperm, Apr. 2008, *M. Amalfi*, *AR 7508* (**holotype**, MUCL 51335; **isotype** NY, culture ex-holotype MUCL 51335, CBS); sendero La Junta, Apr 2008, *M. Amalfi*, *AR 7608* (MUCL 51336, culture ex- MUCL 51336). BRAZIL: Rio Grande do Sul, Morrinhos do Sul, Lajeadoinho, approx 29°21'54"S, 49°56'05"W, elev. approx. 180 m, on a dicotyledonous dead wood, unidentified angiosperm, 13 Mar 2010, *Campos-Santana 030/10* (ICN 190598; culture ex-MUCL 54196); Santa Catarina, Florianópolis, Unidade de Conservação Ambiental Desterro-UCAD, approx 27°31'26.4"S, 48°30'31.7"W, elev. approx 198 m, on a dicotyledonous dead wood, unidentified angiosperm, 02 Oct 2010, *Campos-Santana 253/10* (ICN 190599; culture ex- MUCL 54206); Rio Grande do Sul, Itapuã, Parque Estadual de Itapuã, approx. 30°27'S – 30°20'S; 51°03'S – 50°50'W, elev. approx. 192 m, on a stem and dead branches attached to the tree, unidentified angiosperm, 16 Oct 2010, *Campos-Santana 319/10* (ICN 190600; culture ex- MUCL 54212); Rio Grande do Sul, Porto Alegre, Refúgio da Vida Silvestre da UFRGS, approx. 30°03' S, 51°07'W, elev. approx. 130 m, on a dead wood, unidentified angiosperm, 16 Aug 2011, *Campos-Santana 644/11* (ICN 190601; culture ex- MUCL 54246). FRENCH GUIANA, MUNICIPALITY OF REGINA: Nouragues Natural Reserve, CNRS "inselberg" research plots, "grand Plateau", approx.

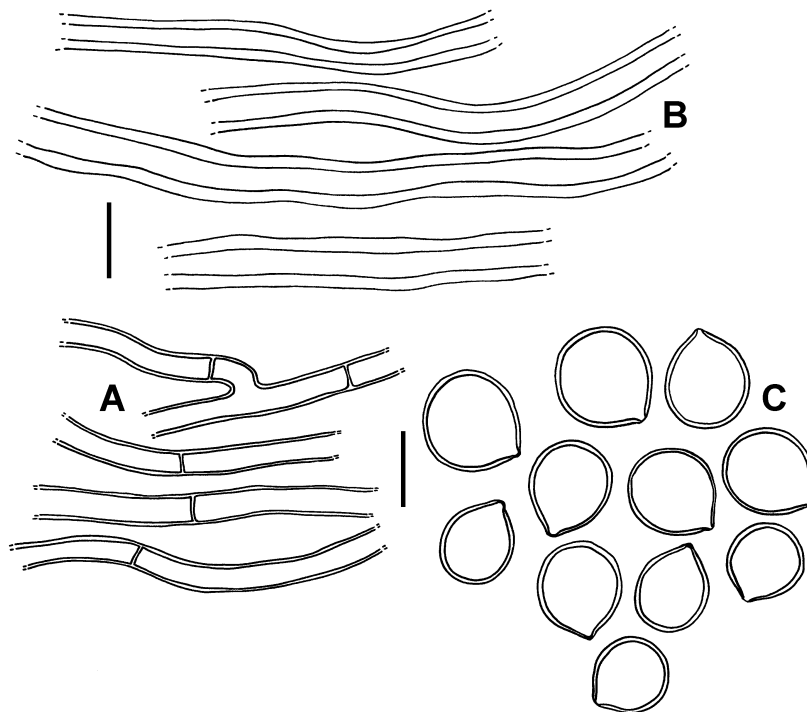
04°05.5' N, 52°40.6' W, elev. approx. 120 m, on a dead fallen branch, unidentified angiosperm, 04 Aug 2010, C. Decock, FG-10-263 (MUCL 53114, culture ex- MUCL 53114).

Comments. — *Fomitiporia neotropica* is characterized by the combination of a resupinate, effused, annual to biannual basidiomata, a white to yellow margin when fresh, a brown (light to dark brown) pore surface, small pores [mostly 6–9 / mm, (70–) 75–125 (–150) μm diam, ave = 119 μm], occasional presence of irregularly shaped setae, mostly located in the dissepiments, 10.0–30.0 $\times$ 3.5–6.5 (–7.0) μm , and basidiospores whose average size ranges from 5.4–6.3 $\times$ 5.0–6.1 μm (arithmetic mean of the individual averages = $5.9 \pm 0.25 \times 5.7 \pm 0.3 \mu\text{m}$, n = 7).

The most common phenotype within the specimens examined (6 specimens, from distinct geographic origins) is characterized by the lack of setae; the setose phenotype (2 specimens from the same forest spot in Argentina) seems to be the exception. We should not exclude, however, cases of extreme paucity of setae, which makes them difficult to observe. This unbalanced ratio seems also to be the case for other species with variable presence of setae such as e.g. *F. aethiopica* (Amalfi et al. 2010, Decock et al. 2005), *F. polymorpha* (Fischer and Binder 2004), or *F. robusta* (Ryvarden and Gilbertson 1994); the setose phenotype remains the exception for these taxa. It is unknown whether these phenotypes correspond to different genetic backgrounds, in which case it could not be evidenced by the genome loci examined, or if they represent differential expressions of a shared genotype, under different environmental circumstances. More data would be necessary to answer these questions.



Figs. 3. *Fomitiporia neotropica*, MUCL 51336. A. Generative hyphae. B. Skeletal hyphae. C. Hymenial setae. D. Basidiospores. Scale bar = 5 μ m



Figs. 4. *Fomitiporia neotropica*, MUCL 49549 A. Generative hyphae. B. Skeletal hyphae. C. Basidiospores. Scale bar = 5 μ m.

Fomitiporia neotropica has been recorded from living and dead (then attached or fallen) branches. In central Argentina, it has been found growing on living stems and dead branches of *Schinus sp.* Its distribution range encompasses various ecological zones and extends from the (very) humid rainforest in French Guiana to the semi-deciduous Atlantic Forest in southern Brazil, and the subtropical, seasonally drier forests of NE Argentina. This suggests wide ecological amplitude and perhaps a more widespread distribution in South America. French Guiana represents for the time being the northern extreme of its known distribution. The southernmost known localities are in subtropical areas of NE Argentina.

In a phylogenetic perspective, the species belongs to the *F. langloisii* lineage (Decock et al. 2007, Amalfi et al. 2012, Amalfi and Decock 2013). This lineage contains, in addition to *F. langloisii* and *F. neotropica*, the taxa *F. dryophila*, *F. maxonii*, *F. sonora*, and a still unnamed species that is known from two collections originating from Argentina and French Guiana. This lineage is more likely originating from and endemic in the Neotropics. It is distributed from the subtropical belt of south-eastern USA down to Argentina and Southern Brazil. All the species from this lineage share an identical, apomorphic deletion of 31 bp near the 5' end of the ITS1 region (Amalfi and Decock 2013, Amalfi et al. 2012, Decock et al. 2007), most likely inherited from a common ancestor.

Fomitiporia neotropica should be compared to the species of the *F. langloisii* lineage, and to a lesser degree to *F. punctata*. In a morphological and biogeographical perspective, *F. maxonii* should be compared to *F. neotropica*. Both species are very similar but for the presence of setae, that have never been reported in *F. maxonii* (Decock et al. 2007, Ryvar den 2004, Vlasák et al. 2011). However the distinction among aseptose specimens of *F. neotropica* and *F. maxonii* proved challenging; for the time being, we have been unable to detect any unequivocal, classical morphological characters that could be used confidently to differentiate the two species in the absence of setae. Subtle differences may include free hyphal tips in the dissepiments (non-agglutinated) covered with crystals in *F. neotropica*, while the hyphal tips are agglutinated in *F. maxonii*. This should be ascertained by examining more specimens in fresh conditions because the drying process may modify the aspect of the dissepiments. Both species also share some ecological parameters including the substrate (attached or fallen, dead branches, or living stems). Their distribution ranges overlap in South America; both species are known at least from Argentina [Argentinean specimen of *F.*

maxonii examined, the identity of which has been confirmed by sequence comparisons: ARGENTINA: Iguazú national park, 25°41.12' S – 54°26.8' W, on a dead branch attached to a living tree, approx. 2 m above ground, unidentified angiosperm, Apr 2008, *M. Amalfi Ar 3008*, MUCL 51331, culture ex.- MUCL51331]. *Fomitiporia maxonii* jumps to exotic, cultivated hosts such as *Citrus sp.* (Decock et al. 2007), a feature not yet registered for *F. neotropica*.

Fomitiporia sonora is a little known species with hymenial setae, recorded from southern USA and northern Mexico (Gilbertson and Ryvarden 1987, Raymundo et al. 2012). It is distinguished from *F. neotropica* by larger pores (5–6 / mm against 6–9 / mm) and longer setae (20–44 µm long against 10.0–30.0 µm, Gilbertson and Ryvarden 1987, Raymundo et al. 2012). *Fomitiporia sonora* and *F. neotropica* have also different ecological requirements and geographic distributions. *Fomitiporia sonora* is known from distinctly drier ecosystems of Arizona (southern USA) where it was collected on hop-bush (*Dodonaea viscosa*, Sapindaceae) (Gilbertson & Ryvarden 1987). It has been recorded from two localities in north-eastern Mexico (Raymundo et al. 2012) but this still needs molecular confirmation, however.

Fomitiporia dryophila differs from *F. neotropica* in having typically cushion-shaped to pseudopileate basidiomata and distinctly larger basidiospores (5.5–) 6.2–8.0 (–8.5) × (5.0–) 5.7–7.3(–7.5) µm (ave = 7.0 × 6.5 µm) (Decock et al. 2007). *Fomitiporia langloisii* shares with *F. neotropica* the basidiospore size, respectively mostly 5.3–6.7 × 4.8–6.0 µm (ave = 6.0 × 5.5 µm) and 5.0–7.0 × 4.5–7.0 µm (ave = 5.9 × 5.7 µm) (Decock et al. 2007). *Fomitiporia langloisii* has a much paler pore surface, greyish corky, honey-coloured, sometimes with a faint pinkish tint in young specimens (Decock et al. 2007, Raymundo et al. 2012), in which feature it

differs from *F. neotropica*. The distribution ranges of *F. langloisii*, *F. dryophila*, and *F. neotropica* are incompletely known. However, considering their current known distribution (Decock et al. 2007, Raymundo et al. 2012, Vlasák continuously updated <http://mykoweb.prf.jcu.cz/polypores/index.html>), habitats and related ecological parameters, it is unlikely that the distribution range of *F. langloisii* and *F. dryophila* would overlap with that of *F. neotropica*. *Fomitiporia langloisii* and *F. dryophila* are sympatric in the subtropical south-eastern belt of the USA (Decock et al. 2007) or in biogeographical term the south-eastern coastal plain mixed-forest provinces of the subtropical division. Both species were also recorded southerly, in north-eastern Mexico (Raymundo et al. 2012). *Fomitiporia dryophila* seems to grow preferably on *Quercus* sp. but other hosts are reported (Decock et al. 2007, Raymundo et al. 2012, Vlasák continuously updated <http://mykoweb.prf.jcu.cz/polypores/index.html>) whereas *F. langloisii* has a wider host range.

Fomitiporia punctata belongs to the Holarctic lineage (Amalfi and Decock 2013, Amalfi et al. 2012). It differs morphologically from *F. neotropica* in having distinctly larger basidiospores. The basidiospore size range of *F. punctata* as usually reported in northern-central Europe, North American, or temperate Asia, is 6.5–8.5 x 5.5–7.0 µm (Bernicchia 1990, 2005, Boulet 2003, Dai 1999, Domański 1972, Fischer and Binder 2004, Gilbertson and Ryvarden 1987, Núñez and Ryvarden 2000, Pieri and Rivoire 2000, Ryvarden and Gilbertson 1994). Ecologically, *F. punctata* inhabits distinct, temperate ecosystems of the northern hemisphere.

Tentative keys to the *Fomitiporia* species of the *F. langloisii* lineage, including *F. punctata*.

- 1a Basidiospores on average 6.9–7.2 μm long, upper range to 8.5 μm ; basidiomata cushion-shaped.....2
- 1b Basidiospores on average < 6.5 μm (5.0–6.2 μm , upper range < 7 μm); basidiomata effused..... 3
- 2a Pore surface brown; temperate areas of North America.....*F. punctata*
- 2b Pore surface pale coloured; margins indurate, blackish with age; subtropical, south-eastern USA, eastern Mexico..... *F. dryophila*
- 3a Hymenial setae present.....4
- 3b Hymenial setae absent..... 5
- 4a Pores 5–6 / mm; occurring in semi-desert area of southern USA / eastern Mexico..... *F. sonorae*
- 4b Pores 6–11 / mm; known from eastern South America, humid forest..... *F. neotropica*
- 5a Pore surface pale, cork coloured, honey; south-eastern USA, eastern Mexico..... *F. langloisii*
- 5b Pore surface darker, greyish brown to chocolate brown..... 6
- 6a Dissepiments agglutinated.....*F. maxonii*
- 6b Dissepiments with free hyphal tips, covered with crystals.....*F. neotropica*

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LITERATURE CITED

- Amalfi M, Yombiyeni P, Decock C. 2010. *Fomitiporia* in sub-Saharan Africa: Morphology and multigene phylogenetic analysis support three new species from the Guineo-Congolian rainforest. *Mycologia* 102:1303–1317, doi:10.3852/09-083.
- , Raymundo T, Valenzuela R, Decock C. 2012. *Fomitiporia cupressicola* sp. nov., a parasite on *Cupressus arizonica*, and additional unnamed clades in the southern USA and northern Mexico, determined by multilocus phylogenetic analyses. *Mycologia* 104: 880–893, doi 10.3852/11-196.
- , Decock C. 2013. *Fomitiporia castilloi* sp. nov. and evidence for multiples clades around *F. apiahyna* in Meso- and South America, representing potential species. *Mycologia* 105: 873–887, doi:10.3852/11-423
- Bernicchia A. 1990. *Polyporaceae s.l.* in Italia. Istituto di Patologia Vegetale, Bologna, Italy:1–594.
- . 2005. *Polyporaceae s.l.* in Italia. *Fungi Europaei*, ed. Candusso, Italy:1–808.

Boulet B. 2003. Les champignons des arbres de l'est de l'Amérique du Nord. Les publications du Québec, Québec, Canada: 1–727.

Brazee NJ, Lindner DL, Fraver S, D'Amato AW, Milo AM. 2012. Wood-inhabiting, polyporoid fungi in aspen-dominated forests managed for biomass in the U.S. Lake States. *Fung Ecol* 5:600–609, doi:10.1016/j.funeco.2012.03.002.

Carranza-Morse J. 1992. Pore fungi of Costa Rica. II. *Mycotaxon* 43:351–369.

Castresana J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analyses. *Mol Biol Evol* 17:540–552.

Coelho G, Wright JE. 1996. *Phellinus spinescens* sp. nov. on bamboo from South America. *Mycotaxon* 59:383–387.

—, da Silveira RMB, Guerrero RT, Rajchenberg M. 2009. On poroid Hymenochaetales growing on bamboos in Southern Brazil and NE Argentina. *Fungal Divers* 36:1–8.

Dai Y-C. 1999. *Phellinus sensu lato* (Aphylliphorales, Hymenochaetaceae) in East Asia. *Acta Bot Fennica* 166:1–115.

David A, Dequatre B, Fiasson J-L. 1982. Two new *Phellinus* with globose, cyanophilous spores. *Mycotaxon* 14:160–174.

—, Zhang X-Q, Zhou T-S. 2001. New and noteworthy species of Hymenochaetaceae from China. *Mycosystema* 20:16–21.

—, Cui BK, Decock C. 2008. A new species of *Fomitiporia* (Hymenochaetaceae, Basidiomycota) from China based on morphological and molecular characters. *Mycol Res* 112:375–380, doi:10.1016/j.mycres.2007.11.020.

David A, Rajchenberg M. 1985. Pore fungi from French Antilles and Guiana. *Mycotaxon* 22: 285–325.

—, Dequatre B, Fiasson JL. 1982. Two new *Phellinus* with globose, cyanophilous spores. *Mycotaxon* 14:160–174.

Decock C, Bitew A, Castillo G. 2005. *Fomitiporia tenuis* and *Fomitiporia aethiopica* (Basidiomycetes, Hymenochaetales), two undescribed species from the Ethiopian Highlands: taxonomy and phylogeny. *Mycologia* 97:124–132, doi:10.3852/mycologia.97.1.121.

—, Herrera Figueroa S, Robledo G, Castillo G. 2007. *Fomitiporia punctata* (Basidiomycota, Hymenochaetales) and its presumed taxonomic synonyms in America: taxonomy and phylogeny of some species from tropical/subtropical areas. *Mycologia* 99:733–752, doi:10.3852/mycologia.99.5.733.

Domański S. 1972. *Basidiomycetes: Aphyllophorales. Polyporaceae I. (resupinatae), Mucronoporaceae I (resupinatae)*. US Department of Agriculture Foreign Scientific Publication, Washington DC, USA.

—, Orlos SH, Skirgiello A. 1967. Grzyby (Zagwiowate II, Szczeciniakowate II). - Panstwowe Wydawnictwo Naukowe, 395 pp. (1973 - Fungi: Polyporaceae II (pileatae), Mucronoporaceae II (pilaetae) - U.S. Dep. Commerce, Springfield, 332 pp.)

Fischer M. 1996. On the species complexes within *Phellinus*: *Fomitiporia* revisited. Mycol Res 100:1459–1467.

—. 2002. A new wood-decaying Basidiomycete species associated with Esca of grapevine: *Fomitiporia mediterranea* (Hymenochaetales). Mycological Progress 1:315–324

—, Binder M. 2004. Species recognition, geographic distribution, and host-pathogen relationships: a case study in a group of lignicolous Basidiomycetes, *Phellinus* s.l. Mycologia 96:799–811.

—, [Edwards J](#), [Cunnington JH](#), [Pascoe IG](#). 2005. Basidiomycetous pathogens on grapevine: a new species from Australia - *Fomitiporia australiensis*. Mycotaxon 92:85–96.

Frøslev TG, Matheny PB, Hibbett DS. 2005. Lower level relationships in the mushroom genus *Cortinarius* (Basidiomycota, Agaricales): a comparison of RPB1, RPB2 and ITS phylogenies. Mol Phylogenet Evol 37:602–618, doi:10.1016/j.ympev.2005.06.016.

Gilbertson RL, Ryvarden L. 1987. North American Polypores. Part 2. *Megasporoporia* – *Wrightoporia*. Fungiflora, Oslo, Norway: 433–885.

Jahn H. 1967. Die resupinaten *Phellinus*-Arten in Mitteleuropa. Westf Pilzbr 6:37–124.

Kirk PM, Cannon PF, David JC, Stalpers JA. 2001. Ainsworth & Bisby's Dictionary of the Fungi, 9th edition. CABI Publishing, Wallingford, UK:1–655.

Kornerup A, Wanscher JH. 1981. Methuen handbook of color, 3rd Edition:1–282.

Loguercio-Leite C, Wright JE. 1991. Contribution to a biogeographical study of the Austro-American xylophilous polypores (Aphyllphorales) from the Santa Catarina Island, SC., Brazil. *Mycotaxon* 61:161–166.

—, —. 1995. The genus *Phellinus* (Hymenochaetaceae) on the island of Santa Catarina, Brazil. *Mycotaxon* 54:361–388.

Lowe JL. 1966. *Polyporaceae of North America. The Genus Poria*. State University College of Forestry, Syracuse University, Tech Pub 90:1–183.

Lutzoni F, Kauff F, Cox CJ, McLaughlin D, Celio G, Dentinger B, Padamsee M, Hibbett D, James TY, Baloch E, Grube M, Reeb V, Hofstetter V, Schoch C, Arnold AE, Miadlikowska J, Spatafora J, Johnson D, Hambleton S, Crockett M, Shoemaker R, Sung G-H, Lücking R, Lumbsch T, O'Donnell K, Binder M, Diederich P, Ertz D, Gueidan C, Hansen K, Harris RC, Hosada K, Lim Y-W, Matheny B, Nishida H, Pfister D, Rogers J, Rossman A, Schmitt I, Sipman H, Stone J, Sugiyama J, Yahr R, Vilgalys R. 2004. Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. *Am J Bot* 91: 1446–1480.

Mason-Gamer RJ, Kellogg EA. 1996. Testing for phylogenetic conflict among molecular data sets in the tribe Triticeae (Gramineae). *Syst Biol* 45:524–545, doi:10.1093/ sysbio/45.4.524

Matheny PB. 2005. Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*, Agaricales). *Mol Phylogenet Evol* 35:1–20, doi:10.1016/j.ympev.2004.11.014

Miadlikowska J, Lutzoni F. 2004. Phylogenetic classification of peltigeralean fungi (Peltigerales, Ascomycota) based on ribosomal RNA small and large subunits. *Am J Bot* 91:449–464, doi: 10.3732/ajb.91.3.449.

Moncalvo JM, Nilsson RH, Koster B, Dunham SM, Bernauer T, Matheny PB, Porter TM, Margaritescu S, Weiß M, Garnica S, Danell E, Langer G, Langer E, Larsson E, Larsson KH, Vilgalys R. 2006. The cantharelloid clade: dealing with incongruent gene trees and phylogenetic reconstruction methods. *Mycologia* 98: 937–948.

Murrill W. 1907. Polyporaceae. *North American Flora* 9:1–72.

Müller K. 2005. SeqState—primer design and sequence statistics for phylogenetic DNA data sets. *Appl Bioinform* 4:65–69, doi:10.2165/00822942-200504010-00008

Núñez M, Ryvarden L. 2000. East Asian Polypores. Volume I. *Synopsis Fungorum* 13; Fungiflora, Oslo, Norway: 1–168.

Pieri M, Rivoire B. 2000. Le genre *Phellinus*. Quelques espèces rares ou critiques en France, avec une clé des espèces du genre *Phellinus s.l.* signalées en Europe occidentale. *Bull Soc Mycol Fr.* 116:305–331.

Pilotti M, Gervasi F, Brunetti A. 2005. Molecular Identification of *Fomitiporia mediterranea* and *Eutypa lata/Libertella blepharis* in *Platanus × acerifolia*. *J Phytopath* 153:193–202.

—, Tizzani L, Brunetti A, Gervasi F, Di Lernia G, Lumia V. 2010. Molecular identification of *Fomitiporia mediterranea* on declining and decayed hazelnut. *J Pl Path* 92:115–129.

Posada D, Crandall KA. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817–818, doi:10.1093/bioinformatics/14.9.817

Raymundo T, Decock C, Valenzuela R, Amalfi M, Cifuentes J, Pacheco-Mota L. 2012. New records of the genus *Fomitiporia* (Hymenochaetales, Basidiomycota) in Mexico. *Rev Mex Biodivers* 83:313–328.

Reeb V, Lutzoni F, Roux C. 2004. Contribution of RPB2 to multilocus phylogenetic studies of the euascomycetes (Pezizomycotina, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory. *Mol Phyl Evol* 32:1036–1060, doi:10.1016/j.ympev.2004.04.012

Robert V, Stegehuis G, Stalpers J. 2005. The MycoBank engine and related databases. <http://www.mycobank.org>.

Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574, doi:10.1093/bioinformatics/btg180

—, —, van der Mark P. 2005. MrBayes 3.1 manual. Tallahassee, Florida: School of Computational Science, Florida State University.

Ryvarden L. 1978. The Polyporaceae of North Europe. Volume 2 (*Inonotus* – *Tyromyces*). Oslo, Norway: Fungiflora: 219–507.

—. 1991. Genera of Polypores. Nomenclature and taxonomy. *Synopsis Fungorum* 5, Oslo, Norway: Fungiflora: 1–363.

—. 2004. Neotropical polypores 1. *Synopsis Fungorum* 19, Oslo, Norway: Fungiflora: 1–229.

—, Gilbertson RL. 1994. European polypores 2. *Meripilus–Tyromyces*. *Synopsis Fungorum* 7, Oslo, Norway: Fungiflora: 392–743.

—, de Meijer AAR. 2002. Studies in Neotropical Polypores 14. New species from the State of Paraná, Brazil. *Synopsis Fungorum* 15, Oslo, Norway: Fungiflora: 34–69.

Simmons MP, Ochoterena H. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Syst Biol* 49:369–381, doi:10.1093/sysbio/49.2.369

Stamatakis A, Hoover P, Rougemont J. 2008. A rapid bootstrap algorithm for the RAxML Web-Servers. *Syst Biol* 75:758–771.

Swofford, D. L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. 1997. The Clustal X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Res* 25:4876–4882, doi:10.1093/nar/25.24.4876

Untereiner WA, Bonjean B, Decock C, Evrard P, de Frahan MH, Jamin N, Massart L, Nélissen L, Robert V, Bosschaerts M, Guissart F, De Brabandere J. 1998. MUCL Catalogue of strains (Fungi-Yeast). 3^e Ed. Published by the Belgian Office for Scientific, Technical and Cultural Affairs, Brussels, Belgium.

Vlasák J, Kout J. 2011. Pileate *Fomitiporia* species in the USA. New combinations *Fomitiporia calkinsii* and *F. bakeri*. *Mycol Prog* 10: 445–452.

—, Kout J, Vlasák J Jr, Ryvarden L. 2011. New records of polypores from southern Florida. *Mycotaxon* 118:159-176.

Wright JE, Blumenfeld SN. 1984. New South American species of *Phellinus* (Hymenochaetaceae). *Mycotaxon* 21:413–425.

Zhou LW, Xue HJ. 2012. *Fomitiporia pentaphylacis* and *F. tenuitubus* spp. nov. (Hymenochaetales, Basidiomycota) from Guangxi, southern China. Mycol Progress 11: 907–913.

CHAPTER VI

***Fomitiporia expansa*, an undescribed species from French Guiana**

Pursuing the revision of the Neotropical resupinate *Fomitiporia* species, a collection from French Guiana was found to represent a species new to science described and illustrated as *Fomitiporia expansa*. The species belongs to the *Fomitiporia langloisii* lineage, containing for the time being, exclusively species with resupinate basidiomata spanning over the Neotropics.

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***Fomitiporia expansa*, an undescribed species from French Guiana**

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Abstract – During the revision of the Neotropical *Fomitiporia* species, a collection from French Guiana was found to represent an undescribed species, on the basis of both morphological and molecular (DNA sequence) data. This taxon is described and illustrated as *Fomitiporia expansa* sp. nov. It is characterized by widely effused basidiomata, extending over 1 m long, with a variable greyish to light brownish grey pore surface, and microscopically in having basidiospores averaging 6.0×5.5 μm . It is known for the time being from a single specimen originating in the western edge of French Guiana, in rainforest. The species belongs to the *Fomitiporia langloisii* lineage. This lineage contains for the time being species with resupinate basidiomata spanning over the Neotropics.

Hymenochaetaceae / Neotropics / Phylogeny / Taxonomy.

INTRODUCTION

Fomitiporia Murrill (Hymenochaetales) is typified by *F. langloisii* (Decock *et al.* 2007, Murrill 1907). The genus is above all characterized by subglobose to globose, thick-walled, hyaline, cyanophilous, and dextrinoid basidiospores, in addition to a dimitic (pseudodimitic) hyphal system. Cystidioles, hymenial and extra-hymenial setae are variably present (Campos Santana *et al.* 2014, Fischer 1996, Pieri & Rivoire 2000). Basidiomata are resupinate to pileate.

Numerous studies have dealt with the genus in the last 20 years, evidencing a much larger than presumed taxonomic / phylogenetic diversity (*e.g.* Amalfi and Decock 2013, Amalfi *et al.* 2010, 2012, Campos Santana *et al.* 2014, Cloete *et al.* 2013, Decock *et al.* 2005, 2007, Fischer *et al.* 2005, Vlasák and Kout 2011, Zhou and Xue 2012).

Pursuing the revision of the New World *Fomitiporia* (Amalfi *et al.* 2012, Amalfi and Decock 2013, Campos Santana *et al.* 2014, Decock *et al.* 2007, Raymundo *et al.* 2012), a collection from the lowland rainforest of French Guiana drew the attention by a remarkable combination of morphological features of which resupinate, widely effused basidiomata, extending over 1 m long, with a bright greyish to greyish brown pore surface when fresh. Multilocus phylogenetic inferences, based on DNA sequence data of 4 loci (5' end of the LSU, ITS-5.8S, partial *tef1* and partial *rpb2*) resolved this specimen as an isolated branch, within the *F. langloisii*, type lineage.

It is interpreted as belonging to a distinct species, for which no name could be found that could apply to it (Decock *et al.* 2007); hence it is described and illustrated below as *Fomitiporia expansa* sp. nov.

Materials and methods

Collection localities of the new taxa. – The specimens from French Guiana were collected in the Marouini river valley, western French Guiana, approx. 02.73103° N – 054.01610° W, alt. approx. 130 masl and in the CNRS “inselberg” research plots, Nouragues Natural Reserve (approx. 04°05.5'N – 52°40.6'W, <http://www.nouragues.cnrs.fr/F-inselberg.html>). Voucher herbarium specimens of the collections from French Guiana are preserved at MUCL, CAY, and NY (herbarium acronyms are according to Thiers, continuously updated). The senior author isolated strains in pure culture during fieldwork, from fresh basidiomata tissues, plated on malt extract agar supplemented by 2 ppm benomyl (benlate) and 50 ppm chloramphenicol. The living strains are preserved at MUCL with a duplicate at the CBS (The Netherlands).

Morphology and anatomy. – Basidiomata colours are described according to Kornerup and Wanscher (1981). Basidiomata sections were examined in Melzer's reagent, lactic acid Cotton blue (Kirk et al. 2001), and KOH 4 %. All microscopic measurements were done in Melzer's reagent. In presenting the size range of the microscopic elements, 5% of the measurements were excluded from each end and are given in parentheses, ave = arithmetical mean, Q = ratio of length/width of basidiospores, and ave_Q = arithmetical mean of the ratio Q. As a rule, 30 elements (pores, hyphae, basidiospores) were measured, when sufficiently abundant.

Sequencing. – One hundred and nine specimens and cultures representing 40 species (or potential species clades) were included in the phylogenetic analysis. Materials and sequences used in this study are listed in Table I. As a rule, DNA was extracted from pure culture, except when noted (Table I). DNA extraction, amplification and sequencing of the 5' end

of the nuclear ribosomal LSU rRNA gene, the ITS regions (including 5.8S), partial *tefl-α* gene, and the region between domains 6 and 7 of the second largest subunit of the *rpb2* (Frøslev *et al.* 2005, Matheny 2005) were as described in Decock *et al.* (2007) and Amalfi *et al.* (2010, 2012) and Amalfi and Decock (2013).

Phylogenetic analysis. – The nucleotide alignment deposited at TreeBASE under study accession number "http://purl.org/phylo/treebase/phylows/study/TB2:S12874" (Campos Santana *et al.* 2014) was used as starting data set to align the additional sequence obtained from the strain MUCL55026. Ambiguously aligned segments were detected with the Gblocks 0.91b program (Castresana 2000; <http://molevol.cmima.csic.es/castresana/Gblocks.html>) with settings "ALLOW SMALLER FINAL BLOCKS", "ALLOW GAPS WITHIN BLOCKS". The alignment was screened visually to detect additional ambiguously aligned regions. Indels present within our datasets, especially in the ITS1 region (Decock *et al.* 2007), were recoded as binary characters with the simple indel coding method (SIC, Simmons and Ochoterena 2000) as implemented in SeqState software (Müller 2005).

Phylogenetic analyses were performed separately for each locus and concatenated with Bayesian inference as implemented in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003), and Maximum likelihood (ML) as implemented in RAxML 7.0.4 (Stamatakis *et al.* 2008). *Phellinus uncisetus* was designated as outgroup (Decock *et al.* 2007). Models of evolution for Bayesian inference were estimated with the Akaike information criterion (AIC) as implemented in Modeltest 3.7 (Posada and Crandall 1998). The dataset was subdivided into 10 data partitions: ITS1, 5.8S, ITS2, nucLSU, *tefl* 1st and 2nd codon position, *tefl* 3rd codon position, *tefl* introns, *rpb2* 1st and 2nd codon position, *rpb2* 3rd codon position, and the recoded indels

(Table II). The best-fit models for each partition were implemented as partition-specific models within partitioned mixed-model analyses of the combined dataset. Three optimal models of nucleotide substitution were selected for ITS regions, the GTR + G model was used for ITS1 and the HKY + G model for ITS2 while the K80 model was used for 5.8S. The GTR + I + G model was used for the nuLSU dataset, for the *rpb2* region (for the first and second codon and for the third codon position) and for the first and second codon position of the *tefl* region, while the GTR + G model was used for the third codon position and HKY + I for the *tefl* introns dataset. For analysis of SIC data under Bayesian inference, we used the MrBayes restriction site model (F81-like) as recommended by Ronquist *et al.* (2005). All parameters were unlinked across partitions. Bayesian analyses were implemented with two independent runs, each with four simultaneous independent chains for 6000000 generations, starting from random trees, and keeping one tree every 1000th generation. Before combining the data partitions, topological incongruence between the datasets was assessed using 1000 replicates of ML BS under the same models described above, on each locus separately. Paired trees were examined for conflicts only involving nodes with ML BS > 75% and Bayesian posterior probabilities (PP) > 95% (Lutzoni *et al.* 2004, Mason-Gamer and Kellogg 1996, 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.

Maximum likelihood (ML) searches conducted with RAxML involved 1000 replicates under the GTRGAMMAI model, with all model parameters estimated by the program. In addition 1000 bootstrap (ML BS) replicates were run with the same GTRGAMMAI model. We provided an additional

alignment partition file to force RAxML software to search for a separate evolution model for each dataset including the recoded indels.

TABLE 1. List of species, specimens/cultures, and sequences accession number (GenBank) included in the phylogenetic analyses.

Genus / species names		GenBank accession number			
Voucher specimens / cultures reference					
	Locality	nLSU	ITS	<i>tefl-a</i>	<i>rpb2</i>
<i>Fomitiporia aethiopica</i> Decock et al.					
MUCL 44777 (T) ^{c, h}	Ethiopia	AY618204	GU478341	GU461893	JQ087956
MUCL 44806 ^{c, h}	Ethiopia	AY618202	GU461944	GU461892	JQ087955
<i>F. apiahyna</i> (Speg.) Robledo et al.					
MUCL 51451 ^{c, h}	Ecuador	GU461997	GU461963	GU461896	JQ087958
MUCL 51485 ^{c, h}	Ecuador	GU461996	GU461962	GU461895	JQ087957
MUCL 53042 ^{c, h}	French Guiana	JX093817	JX093773	JX093730	JX093861
<i>F. australiensis</i> M. Fisch. et al.					
VPRI 22451a (MUCL 49406) PT ^{c, 8}	Australia	GU462001	AY624997	GU461897	JQ087959
<i>Fomitiporia bakeri</i> (Murrill) Vlasák & Kout					
FP-134784-Sp (MUCL 51098) ^{c, 1}	USA	JQ087901	JQ087874	JQ087928	JQ087960
<i>F. bannaensis</i> Y.C. Dai					
MUCL 45926 ^{c, h}	Thailand	EF429217	GU461942	GU461898	JQ087961
MUCL 46926 ^{c, h}	China	KF444705	KF444682	KF444751	KF444728
MUCL 46930 ^{c, h}	China	KF444706	KF444683	KF444752	KF444729
MUCL 46948 ^{c, h}	China	KF444707	KF444684	KF444753	KF444730
MUCL 46950 ^{c, h}	China	EF429218	GU461943	GU461899	JQ087962
<i>Fomitiporia calkinsii</i> (Murrill) Vlasák & Kout					
FP-106252-Sp (MUCL 51095) ^{c, 1}	USA	KF444708	KF444685	KF444754	KF444731
FP-53385-T (MUCL 51099) ^{c, 1}	USA	KF444709	KF444686	KF444755	KF444732

FP-71907-T (MUCL 51100) ^{c, 1}	USA	JQ087902	JQ087875	JQ087929	JQ087963
CBS 175.34 (MUCL 51398) ^{c, 1}	USA	KF444710	KF444687	KF444756	KF444733
MUCL 52346 ^{c, h}	Mexico	JQ087903	JQ087876	JQ087930	JQ087964
MA-MX0945 ^{c, h}	Mexico	KF444711	KF444688	KF444757	KF444734
<i>F. capenses</i> M. Fisch. et al.					
MUCL 53009 ^{c, 5}	South Africa	JQ087917	JQ087890	JQ087944	JQ087997
<i>F. castilloi</i> Amalfi & Decock					
MUCL 53481 (T) ^{c, h}	French Guiana	JQ087916	JQ087889	JQ087943	JQ087996
MUCL 53980 (PT) ^{c, h}	French Guiana	JX093830	JX093786	JX093743	JX093874
<i>F. cupressicola</i> Amalfi et al.					
MUCL 52486 (T) ^{c, h}	Mexico	JQ087904	JQ087877	JQ087931	JQ087965
MUCL 52488 ^{c, h}	Mexico	JQ087905	JQ087878	JQ087932	JQ087966
MUCL 52489 ^{c, h}	Mexico	JQ087906	JQ087879	JQ087933	JQ087967
MUCL 52490 ^{c, h}	Mexico	JQ087907	JQ087880	JQ087934	JQ087968
<i>F. dryophila</i> Murrill					
TJV-93-232 (MUCL 46379) ^{c, 1}	USA	EF429221	EF429240	GU461902	JQ087969
TJV-93-234 (MUCL 46380) ^{c, 1}	USA	EF429219	EF429238	GU461900	JQ087970
TJV-93-259 (MUCL 46381) ^{c, 1}	USA	EF429220	EF429239	GU461901	KF444735
FP-104030-T (MUCL 51144) ^{c, 1}	USA	KF444712	KF444689	KF444758	KF444736
<i>F. erecta</i> (A. David et al.) Fiasson					
MUCL 49871 ^{c, h}	France	GU461976	GU461939	GU461903	JQ087971
MA-PA03 ^{c, h}	Italy	KF444713	KF444690	KF444759	ND
<i>F. expansa</i> Decock & Amalfi sp. nov.					
MUCL 55026 (T) ^{c, h}	French Guiana	KJ401031	KJ401032	KJ401033	KJ401034
<i>F. gabonensis</i> Amalfi & Decock					
MUCL 47576 (T) ^{c, h}	Gabon	GU461990	GU461971	GU461923	JQ087972
MUCL 51291 ^{c, h}	Gabon	GU461986	GU461967	GU461924	JQ087973

<i>Fomitiporia hartigii</i> (Allesch. & Schnabl) Fiasson & Niemelä					
MAFF 11-20016 (MUCL 31400) ^c	Japan	JQ087909	JQ087882	JQ087936	JQ087975
75-2 562 (MUCL 53549) ^{c, 4}	Estonia	JX093831	JX093787	JX093744	JX093875
71-25 464 (MUCL 53550) ^{c, 4}	Estonia	JX093832	JX093788	JX093745	JX093876
75-3 563 (MUCL 53551) ^{c, 4}	Estonia	JX093833	JX093789	JX093746	JX093877
<i>F. hippophaeicola</i> (H. Jahn) Fiasson & Niemelä					
MUCL 31746 ^{c, h}	Belgium	AY618207	GU461945	GU461904	JQ087976
MUCL 31747 ^{c, h}	Belgium	GU461977	GU461946	GU461905	JQ087977
<i>F. ivindoensis</i> Decock et al.					
MUCL 51311 ^{c, h}	Gabon	GU461979	GU461952	GU461907	JQ087978
MUCL 51312 (T) ^{c, h}	Gabon	GU461978	GU461951	GU461906	JQ087979
<i>F. langloisii</i> Murrill					
FP-94347-R (MUCL 46375) ^{c, 1}	USA	EF429225	EF429242	GU461908	JQ087980
01-77/4 (MUCL 46165),					
(T of <i>F. hesleri</i>) ^{c, 5}	USA	EF429223	AY340026	GU461909	JQ087981
FP-105-816-T (MUCL 46373) ^{c, 1}	USA	EF429226	EF429243	KF444760	ND
HHB-9868-Sp (MUCL 46377) ^{c, 1}	USA	EF429224	EF429241	KF444761	ND
01-712/2 (MUCL 46164) ^{c, 5}	USA	EF429222	AY340031	KF444762	ND
FP-105818-R (MUCL 46374) ^{c, 1}	USA	EF429227	EF429244	KF444763	ND
<i>F. maxonii</i> Murrill					
MUCL 46017 ^{c, h} (= CRGF 182)	Cuba	EF429230	EF433559	GU461910	JQ087983
MUCL 46037 ^{c, h} (= CRGF 183)	Cuba	EF429231	EF433560	GU461911	JQ087982
MUCL 51331 ^{c, h}	Argentina	KF444714	KF444691	KF444764	KF444737
MUCL 51540 ^{c, h}	Cuba	KF444715	KF444692	KF444765	KF444738
MUCL 51399 ^{c, h}	Cuba	KF444716	KF444693	KF444766	KF444739
MUCL 52340 ^{c, h}	Mexico	KF444717	KF444694	KF444767	KF444740
MUCL 53364 ^{c, h}	Mexico	KF444718	KF444695	KF444768	KF444741

<i>F. mediterranea</i> M. Fisch.					
AFTOL ID 688	ND	AY684157	AY854080	AY885149	AY803748
MUCL 38514	Italy	AY618201	GU461953	GU461912	JQ087984
MUCL 45670 ^{c, h}	France	GU461980	GU461954	GU461913	JQ087985
<i>Fomitiporia neotropica</i> Campos Santana et al.					
MUCL 53114 ^{c, h}	French Guiana	JX093836	JX093792	JX093749	JX093880
MUCL 49549 ^{c, h, 7}	Argentina	KF444719	KF444696	KF444769	KF444742
MUCL 54246 ^{c, h}	Brazil	KF444720	KF444697	KF444770	KF444743
MUCL 51335 (T) ^{c, h}	Argentina	KF444721	KF444698	KF444771	KF444744
MUCL 51336 ^{c, h}	Argentina	KF444722	KF444699	KF444772	KF444745
MUCL 54206 ^{c, h}	Brazil	KF444723	KF444700	KF444773	KF444746
MUCL 54196 ^{c, h}	Brazil	KF444724	KF444701	KF444774	KF444747
MUCL 54212 ^{c, h}	Brazil	KF444725	KF444702	KF444775	KF444748
<i>F. nobilissima</i> Decock & Yombiyeni					
MUCL 47580 ^{c, h}	Gabon	GU461985	GU461966	GU461921	JQ087986
MUCL 51289 (T) ^{c, h}	Gabon	GU461984	GU461965	GU461920	JQ087987
<i>F. polymorpha</i> M. Fisch.					
91-42/3 (MUCL 46166) (PT) ^{c, 5}	USA	DQ122393	GU461955	GU461914	JQ087988
91-42/1 (MUCL 46167) (PT) ^{c, 5}	USA	EF429233	GU461956	GU461915	JQ087989
<i>F. pseudopunctata</i> (A. David et al.) Fiasson					
MUCL 51325 ^{c, 2}	Czech Rep.	GU461981	GU461948	GU461916	JQ087998
MUCL 46168 ^{c, h}	France	JQ087918	JQ087891	JQ087945	JQ087999
<i>Fomitiporia PS 4</i>					
MUCL 53993	Mexico	JX093851	JX093807	JX093764	JX093893
MUCL 53994	Mexico	JX093852	JX093808	JX093765	JX093894
<i>Fomitiporia PS 5</i>					
MUCL 51555 ^{c, h}	Martinique	JX093853	JX093809	JX093766	JX093895

MUCL 53797 ^{c, h}	French Guiana	JX093854	JX093810	JX093767	JX093896
<i>Fomitiporia PS 6</i>					
MUCL 53798 ^{c, h}	French Guiana	JX093855	JX093811	JX093768	JX093897
<i>Fomitiporia PS 8</i>					
MUCL 47756 ^{c, h, 7}	Argentina	JQ087913	JQ087886	JQ087940	JQ087993
MUCL 47757 ^{c, h, 7}	Argentina	JQ087914	JQ087887	JQ087941	JQ087994
MUCL 47758 ^{c, h, 7}	Argentina	JQ087915	JQ087888	JQ087942	JQ087995
<i>Fomitiporia PS 10</i>					
CBS 386.66 = MUCL 46181 ^{c, 6}	Argentina	EF429234	EF433563	GU461930	JQ088007
MUCL 53675 ^{c, h}	French Guiana	JX093835	JX093791	JX093748	JX093879
<i>F. punctata</i> (Fr.) Murrill					
MUCL 34101 ^{c, h}	Germany	AY618200	GU461947	GU461917	JQ088000
WD-2055 (MUCL 47629) ^{c, 3}	Japan	GU461982	GU461950	GU461918	JQ088001
71-8 298 (MUCL 53548) ^{c, 4}	Europe	JX093834	JX093790	JX093747	JX093878
<i>F. punicata</i> Y.C. Dai et al.					
Cui 23	China	GU461991	GU461974	GU461927	JQ088002
Cui 26	China	GU461992	GU461975	GU461928	JQ088003
<i>F. robusta</i> (P. Karst.) Fiasson & Niemelä					
CBS 389.72 (MUCL 51297) ^{c, 6}	Estonia	JQ087919	JQ087892	JQ087946	JQ088004
Tomšovský 1013 (MUCL 51327) ^{c, 2}	Czech Rep.	GU461993	GU461949	GU461929	JQ088005
<i>Fomitiporia sonoreae</i> (Gilb.) Y.C. Dai					
RLG-10862-Sp (MUCL 47689) (T) ^{c, 1}	USA	JQ087920	JQ087893	JQ087947	JQ088006
<i>Fomitiporia</i> “sp.”					
FP-98505-T (MUCL 51105) ^{c, 1}	USA	JQ087911	JQ087884	JQ087938	JQ087991
RLG-10827 (MUCL 51106) ^{c, 1}	USA	JQ087910	JQ087883	JQ087937	JQ087990
<i>F. tabaquilio</i> (Urcelay et al.) Decock & Robledo					

MUCL 46230 ^{c, h, 7}	Argentina	DQ122394	GU461940	GU461931	JQ088008
MUCL 47754 ^{c, h, 7}	Argentina	GU461994	GU461941	GU461932	JQ088009
<i>F. tenuis</i> Decock et al.					
MUCL 44802 (T) ^{c, h}	Ethiopia	AY618206	GU461957	GU461934	JQ088010
MUCL 49948 ^{c, h}	Gabon	GU461998	GU461958	GU461935	JQ088011
MUCL 49971 ^{c, h}	Uganda	GU461998	GU461958	GU461935	JQ088012
<i>Fomitiporia texana</i> (Murrill) Nuss					
RLG-7763-T (MUCL 47690) ^{c, 1}	USA	JQ087921	JQ087894	JQ087948	JQ088013
FP-89674-R (MUCL 51143) ^{c, 1}	USA	JQ087922	JQ087895	JQ087949	JQ088014
<i>Fomitiporia torreyae</i> Y.C. Dai & B.K. Cui					
WD-199 (MUCL 47628) ^{c, 3}	Japan	JQ087923	JQ087896	JQ087950	JQ088015
WC31 ^h	Chine	JQ087924	JQ087897	JQ087951	JQ088016
<i>Fomitiporia tsugina</i> Murrill					
Ft San (MUCL 52702)	USA	JQ087925	JQ087898	JQ087952	JQ088017
Ft T2-1 (MUCL 52703)	USA	JQ087926	JQ087899	JQ087953	JQ088018
CBS125.40 (MUCL 51295) ^{c, 6}	USA	JQ087908	JQ087881	JQ087935	JQ087974
<i>Phellinus juniperinus</i> Bernicchia & S. Curreli					
MUCL 51757 ^{c, h}	Tunisia	JQ087927	JQ087900	JQ087954	JQ088019
MA-PA01 ^{c, h}	Italy	KF444726	KF444703	KF444776	KF444749
MA-PA02 ^{c, h}	Italy	KF444727	KF444704	KF444777	KF444750
<i>P. uncisetus</i> Robledo et al.					
MUCL 46231 ^{c, h}	Argentina	EF429235	GU461960	GU461937	JQ088020
MUCL 47061 ^{c, h}	Argentina	GU462000	GU461972	GU461938	JQ088021
T, PT = type, paratype.					
^c = culture available; ^h = voucher herbarium specimen corresponding to the culture available at the MUCL herbarium; ¹ cultures from CFMR, USDA, USA, courtesy of Dr. K. Nakasone); ² cultures from Faculty of Forestry and Wood Technology, Mendel University of Agriculture and Forestry in Brno, Czech Republic, courtesy of Dr. M. Tomšovský; ³ cultures from Microbial Ecology Lab					

Forestry and Forest Products Research Institute, courtesy of Prof. T. Hattori, Japan; ⁴ cultures from National History Museum, University of Tartu, Estonia, courtesy of K. Põldmaa; ⁵ cultures courtesy of Dr. M. Fischer, Germany; ⁶ cultures from the CBS, The Netherlands, courtesy of Prof. P. Crous; ⁷ cultures from Colección de Cultivos Córdoba, Instituto Multidisciplinario de Biología Vegetal, Córdoba, Argentina, courtesy of Dr. G. Robledo; ⁸ cultures courtesy of Dr. I. Pascoe, Primary Industries Research Victoria, VPRI, Australia.

Results

DNA sequence comparisons. – Sequence length and parsimony data for each dataset (length of aligned sequences, variable parsimony uninformative positions, parsimony informative positions, excluded characters) are summarized in Table II. As already evidenced by Decock *et al.* (2007) and confirmed by Amalfi *et al.* (2012) and Campos Santana *et al.* (2014), the species forming the *F. langloisii* lineage, namely *F. dryophila*, *F. langloisii*, *F. maxonii*, *F. neotropica*, *F. sonora*, and an unnamed *Fomitiporia* sp. (MUCL 46181 and MUCL 53675) present a 31 bps long deletion near the 5' end of the ITS1 region. An identical deletion (in terms of length and position) is present in the ITS1 region of *Fomitiporia* sp. MUCL 55026. This deletion seems to be a plesiomorphic character inherited by all species of the *F. langloisii* lineage.

Individual dataset comparisons. – Sequence data and statistical analysis for each dataset and combined analysis are provided (Table II).

By comparing the tree topologies obtained for the individual datasets, no conflict involving significantly supported nodes was found using the reciprocal 75% ML BS and 95% PP criterion; the datasets were therefore combined.

Combined dataset analysis. – Thirty six characters in the ITS1 region were judged too ambiguous to be aligned. The two Bayesian runs converged to stable likelihood values after 645000 generations. 5355 stationary trees from each analysis were used to compute a 50% majority rule consensus tree in PAUP* 4.0b10 (Swofford 2003) and to calculate posterior probabilities (PP). In the ML searches with RAxML the combined dataset alignment had 2008 distinct patterns with a proportion of gaps and undetermined characters of 12.41%.

The topologies obtained analysing the individual dataset are highly congruent with published trees (Amalfi *et al.* 2010, 2012, Amalfi and Decock 2013, Campos Santana *et al.* 2014) and almost identical to the Bayesian consensus tree and to the optimal tree inferred under the Maximum likelihood criterion ($-\ln L = -27093.377$, Fig. 1). The results of the phylogenetic inferences, independently of analyzing the data sets individually or combined, were highly congruent and resolve the same clades and lineages as previously reported (Amalfi and Decock 2013, Amalfi *et al.* 2010, 2012, Campos Santana *et al.* 2013).

The collection MUCL 55026, originating from French Guiana, formed a new lineage within the *F. langloisii* clade (Fig. 1, PS 9).

Morphological analysis. – The collection MUCL 55026 shows a singular combination of morphological features, thereby defining also one morphospecies. This includes especially a widely effused basidiomata, extending over 1 m long and a bright greyish to pale brownish grey pore surface. There are no known *Fomitiporia* species developing such extended, effused basidiomata and a greyish pore surface when actively growing. The basidiospores are typical of *Fomitiporia*, subglobose to obovoid, slightly thick-walled, dextrinoid, and cyanophilous. Their size range is mainly $5.5\text{--}6.3 \times 5.0\text{--}5.7 \mu\text{m}$ (ave = $6.0 \times 5.5 \mu\text{m}$).

Given the results of the phylogenetic inferences that identify our collection as a phylogenetic species (Fig. 1, PS 9), and the morphological data that define a unique morphotype, PS 9 is considered as representing a distinct species. The search for a possible epithet within the synonyms of *F. punctata* (Decock *et al.* 2007, Robert *et al.* 2005) yielded no name that could apply to it. We therefore propose below this species as *Fomitiporia expansa* *sp. nov.*

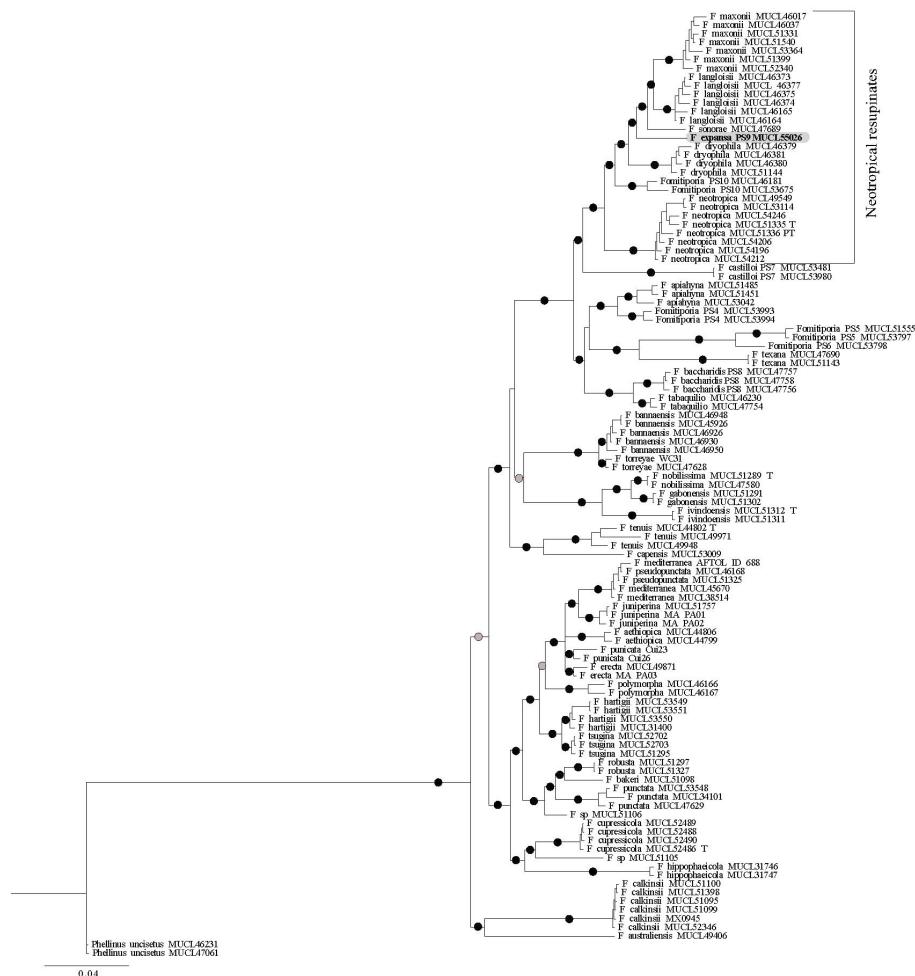


Fig. 1. The 50% majority-rule consensus tree from Bayesian inference of the combined ITS, LSU, *tef1* and *rpb2* sequences. Black dots on branches represent PP and ML BS of 99% or higher; grey dots on branches denote PP greater than 85% and ML BS greater than 75%.

Taxonomy

Fomitiporia expansa Decock & Amalfi, *sp. nov.* Figs. 2–4

Mycobank: MB 807669

Etymology: "*expansa*" refers to the extended, effused basidiomata.

Basidiomata perennial, resupinate, widely effused, following the substrate, adnate, extending up to > 100 cm long in the longest extension, 30 cm wide, 1.5–5 mm in the thickest part, with a corky consistency, fibrous, coriaceous texture when fresh, drying corky, light in weight; *margin* narrow, thin or slightly rounded in upper part, densely and very minutely velutinous, reddish to ferruginous brown (7D7, brick red, 8[D–E]6, reddish brown); *pore surface* bright greyish (4[B–C]1, greyish white to light grey), orange grey to brownish grey when actively growing (5B[2–4], 5C2, marble white, greyish orange, birch grey), drying cork to light brown, with sterile patches light reddish brown to ferruginous brown (7D7, brick red, 8[D–E]6, reddish brown); *pores* round to mostly ellipsoid, elongated, strongly stretched in most parts, mostly 5–6 / mm, (100–) 135–175 μm diam (ave = 148 μm); *dissepiments* entire, with free hyphal tips, occasionally pruinose due to crystal cover, thin to thick, 120–240 μm diam; *subiculum* indistinct fusing with the underneath decaying wood or when discernible 100–500 μm thick, homogeneous, densely fibrous, light brown (6D[6–7], cinnamon, autumn leaf); *tubes* up to 5 mm thick, probably multilayered but layers mostly indistinct, darker than the pore surface, greyish brown to brown, the oldest parts mottled with white stuff.

Hyphal system dimitic, identical in the context and hymenophoral trama; *generative hyphae* hyaline to faintly yellow, thin-walled, sparsely branched 1.5–2.5 (–3) μm wide (ave = 2.0 μm), *skeletal hyphae* pale yellow

brown to golden brown, thick-walled but with an open lumen, 2.5–4.0 μm wide (ave = 3.2 μm), tightly packed in the hymenophoral trama.

Hymenium: *basidia* pyriform to subglobose, 7.0–10 $\times$ 6.0–9.0 μm , with four small sterigmata; *basidioles* identical in shape but slightly smaller; *hymenial setae* absent; *basidiospores* subglobose to broadly obovoid, 5.5–6.3 (– 6.6) $\times$ 5.0–5.7 μm (ave = 6.0 $\times$ 5.5 μm) $Q = 1.0$ –1.2 (ave_Q = 1.1), thick-walled, the wall hyaline, cyanophilous, strongly dextrinoid; *basidiospores* print white; *chlamydospore* absent.

Type of rot: white rot.

Substrate and host: known from a dead standing trunk, unidentified angiosperm.

Specimen examined. FRENCH GUIANA, MUNICIPALITY OF MARIPASOULA: rainforest along the Marouini river valley, approx. 02,73103° N, 054.01610° W, elev. approx. 130 masl, on a dead standing trunk, approx. 70–80 cm diam. at 1 m high, broken at about 4 m high, unidentified angiosperm, 07 Jul. 2013, C. Decock, FG-13-658 (HOLOTYPE NY, Isotype MUCL 55026, CAY; culture ex-holotype MUCL 55026; CBS).

Remarks. The combination of a resupinate, effused, extended basidiomata, a greyish to light greyish brown pore surface, 5–6 pores / mm, absence of setae, and basidiospores averaging 6.0 $\times$ 5.5 μm characterized *F. expansa*.

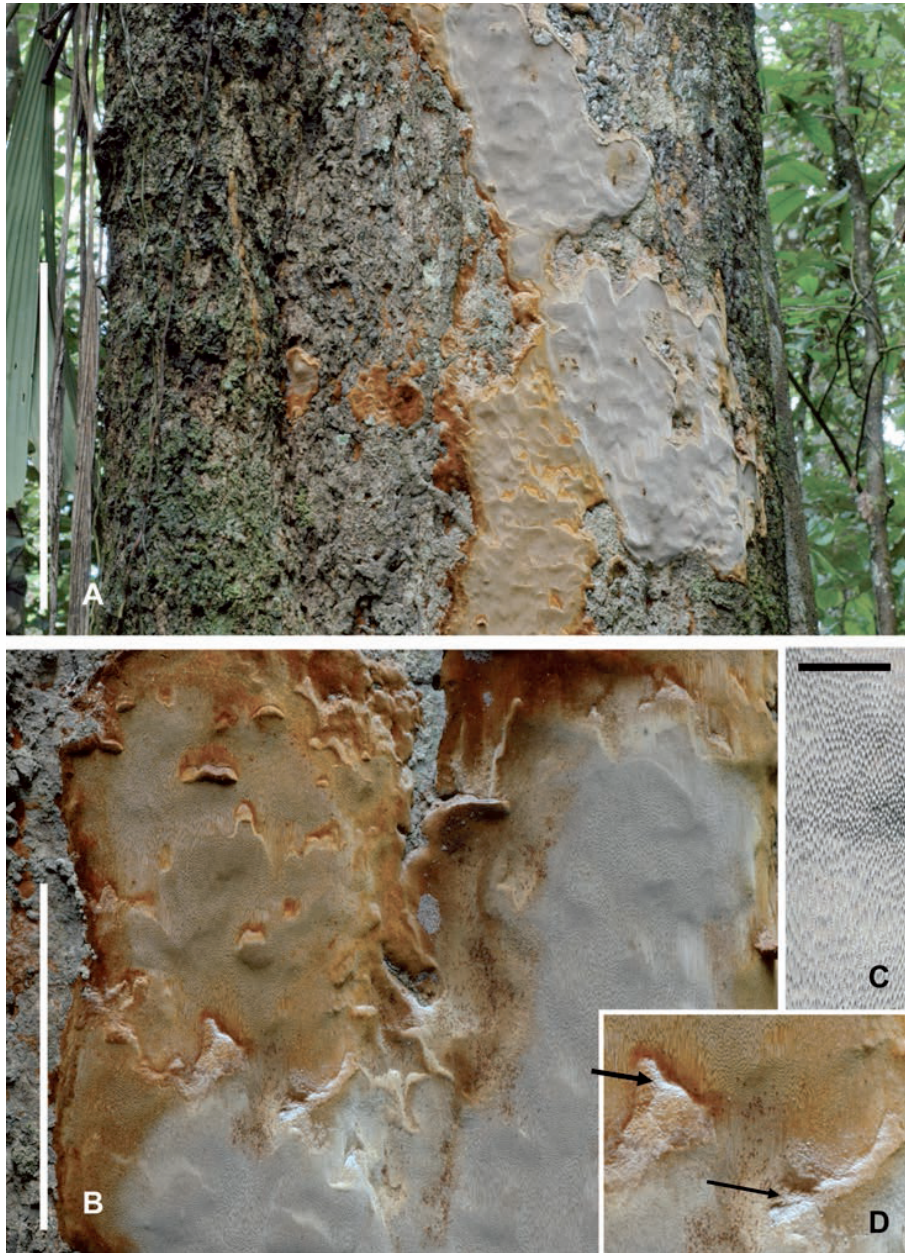


Fig. 2. *Fomitiporia expansa*, basidiomata *in situ* (MUCL 55026). A, B. Actively growing basidiomata (A, scale bar = 5 cm; B, scale bar = 2 cm). C. Detail of the pore surface (scale bar = 2 cm). D. White basidiospores print (arrow).

In a phylogenetic perspective, *F. expansa* nests within the *F. langloisii* lineage as defined first by Decock *et al.* (2007) and repeatedly confirmed (Amalfi *et al.* 2012, Amalfi and Decock 2013, Campos Santana *et al.* 2014). This lineage contains in addition to *F. langloisii* the species *F. dryophila*, *F. maxonii*, *F. neotropica*, *F. sonora*, and a still unnamed taxon (PS 10, Fig 1). The latter is known from two cultures, which voucher specimens originated from Argentina and French Guiana. The *F. langloisii* lineage is composed of species with resupinate basidiomata. This lineage is more likely endemic to the Neotropics; its distribution extends from the subtropical belt of south-eastern USA down to Argentina and Southern Brazil.

Morphologically and ecologically, *F. expansa* should be compared to *F. neotropica*; both species are likely to occur sympatrically in French Guiana. It could be also compared to *F. maxonii*, which has a wide distribution range in the Neotropics.

Campos Santana *et al.* (2014) described *F. neotropica* on the basis of a set of South American specimens, including collections from French Guiana. *Fomitiporia neotropica* differs from *F. expansa* in having much less extended basidiomata, with a distinctly brown pore surface and smaller pores, mostly 6–9 / mm (75–145 µm diam) (Campos Santana *et al.* 2014). *Fomitiporia neotropica* also presents, although very occasionally, hymenial setae (Campos Santana *et al.* 2014).

Fomitiporia neotropica and *F. expansa* both inhabit the same rainforest ecosystem in French Guiana but they might differ by some autecological features, or niche specialization. The specimen of *F. expansa* was found on a large (70–80 cm diam at 1 m high), dead but standing trunk (Fig. 2). In French Guiana, *F. neotropica* was found repeatedly on fallen, decayed branches or liana of a diam < to approximately 10 cm diam. It may

grow initially on branches (living or dead) still attached to the tree, somewhere in the intermediate canopy; basidiomata are found on the ground when the rotten branches (or liana) are fallen down, but should be looked for in the intermediate canopy.

Fomitiporia maxonii was originally described by Murrill (1907) and redescribed by Decock *et al.* (2007). In comparison to *F. expansa*, *F. maxonii* has a much darker, commonly brown to dark brown pore surface and small pores (7–9 (–10) / mm, (80–) 90–120 (–130) μm) (Decock *et al.* 2007). It has not been found so far in the rainforest of French Guiana.

For the time being, three species of *Fomitiporia* with resupinate basidiomata are known from French Guiana: in addition to *F. neotropica* (Campos Santana *et al.* 2014) and *F. expansa*, a third unnamed species (PS 10, Fig. 1) is known from two cultures (of which one, MUCL 53675, is originating from the Nouragues Nature Reserve, French Guiana). For the time being, the voucher herbarium specimens are not available for phenotypic characterization. These species occurs sympatrically, in the rainforest, but might have distinct habitat specialization.

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REFERENCES

- Amalfi M. & Decock C. 2013 – *Fomitiporia castilloi* sp. nov. and evidence for multiples clades around *F. apiahyna* in Meso- and South America, representing potential species. *Mycologia* 105: 873–887, doi:10.3852/11-423.
- Amalfi M., Yombiyeni P. & Decock C. 2010 – *Fomitiporia* in sub-Saharan Africa: Morphology and multigene phylogenetic analysis support three new species from the Guineo-Congolian rainforest. *Mycologia* 102:1303–1317, doi:10.3852/09-083.
- Amalfi M., Raymundo T., Valenzuela R. & Decock C. 2012 – *Fomitiporia cupressicola* sp. nov., a parasite on *Cupressus arizonica*, and additional unnamed clades in the southern USA and northern Mexico, determined by multilocus phylogenetic analyses. *Mycologia* 104: 880–893, doi 10.3852/11-196.
- Campos Santana M., Amalfi M., Robledo G., Borges da Silveira R.M., & Decock C. – 2014. *Fomitiporia neotropica*, an undescribed species from South America evidenced by multilocus phylogenetic analyses. *Mycological Progress*: in press, doi 10.1007/s11557-013-0943-1.
- Castresana J. 2000 – Selection of conserved blocks from multiple alignments for their use in phylogenetic analyses. *Molecular Biology and Evolution* 17:540–552.
- Cloete M., Fischer M., Mostert L. & Halleen F. 2013 – A novel *Fomitiporia* species associated with Esca on grapevine in South Africa. *Mycological Progress*: in press, doi 10.1007/s11557-013-0915-5.
- Decock C., Bitew A. & Castillo G. 2005 – *Fomitiporia tenuis* and *Fomitiporia aethiopica* (Basidiomycetes, Hymenochaetales), two undescribed species from the

Ethiopian Highlands: taxonomy and phylogeny. *Mycologia* 97:124–132, doi:10.3852/mycologia.97.1.121.

Decock C., Herrera Figueroa S, Robledo G, Castillo G. 2007 – *Fomitiporia punctata* (Basidiomycota, Hymenochaetales) and its presumed taxonomic synonyms in America: taxonomy and phylogeny of some species from tropical/subtropical areas. *Mycologia* 99:733–752, doi:10.3852/mycologia.99.5.733.

Fischer M. 1996 – On the species complexes within *Phellinus*: *Fomitiporia* revisited. *Mycological Research* 100:1459–1467.

Fischer M., [Edwards J.](#), [Cunnington J.H.](#) & [Pascoe I.G.](#) 2005 – Basidiomycetous pathogens on grapevine: a new species from Australia - *Fomitiporia australiensis*. *Mycotaxon* 92:85–96.

Frøslev T.G., Matheny P.B. & Hibbett D.S. 2005 – Lower level relationships in the mushroom genus *Cortinarius* (Basidiomycota, Agaricales): a comparison of RPB1, RPB2 and ITS phylogenies. *Molecular Phylogenetic and Evolution* 37:602–618, doi:10.1016/j.ympev.2005.06.016.

Kirk P.M., Cannon P.F., David J.C. & Stalpers J.A. 2001 – *Ainsworth & Bisby's Dictionary of the Fungi*, 9th edition. CABI Publishing, Wallingford, UK:1–655.
Kornerup A. & Wanscher J.H. 1981 – *Methuen handbook of color*, 3rd Edition:1–282.

Lutzoni F., Kauff F., Cox C.J., McLaughlin D., Celio G., Dentinger B., Padamsee M., Hibbett D., James T.Y., Baloch E., Grube M., Reeb V., Hofstetter V., Schoch C., Arnold A.E., Miadlikowska J., Spatafora J., Johnson D., Hambleton S., Crockett M., Shoemaker R., Sung G.-H., Lücking R., Lumbsch T., O'Donnell K., Binder M., Diederich P., Ertz D., Gueidan C., Hansen K., Harris R.C., Hosada K., Lim Y.-W., Matheny B., Nishida H., Pfister D., Rogers J., Rossman A., Schmitt I., Sipman H.,

Stone J., Sugiyama J., Yahr R. & Vilgalys R. 2004 – Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. *American Journal of Botany* 91: 1446–1480.

Mason-Gamer R.J., Kellogg E.A. 1996 – Testing for phylogenetic conflict among molecular data sets in the tribe Triticeae (Gramineae). *Systematic Biology* 45:524–545, doi:10.1093/sysbio/45.4.524.

Matheny P.B. 2005 – Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*, Agaricales). *Molecular Phylogenetics and Evolution* 35:1–20, doi:10.1016/j.ympev.2004.11.014.

Müller K. 2005 – SeqState-primer design and sequence statistics for phylogenetic DNA data sets. *Applied Bioinformatics* 4:65–69, doi:10.2165/00822942-200504010-00008.

Murrill W. 1907 – *Polyporaceae*. North American Flora 9:1–72.

Pieri M. & Rivoire B. 2000 – Le genre *Phellinus*. Quelques espèces rares ou critiques en France, avec une clé des espèces du genre *Phellinus* s.l. signalées en Europe occidentale. *Bulletin de la Société Mycologique de France* 116:305–331.

Posada D. & Crandall K.A. 1998 – Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817–818, doi:10.1093/bioinformatics/14.9.817.

Raymundo T., Decock C., Valenzuela R., Amalfi M., Cifuentes J. & Pacheco-Mota L. 2012 – New records of the genus *Fomitiporia* (Hymenochaetales, Basidiomycota) in Mexico. *Revista Mexicana de Biodiversidad* 83:313–328.

Reeb V., Lutzoni F. & Roux C. 2004 – Contribution of RPB2 to multilocus phylogenetic studies of the euascomycetes (Pezizomycotina, Fungi) with special

emphasis on the lichen-forming Acarosporaceae and evolution of polyspory. *Molecular Phylogenetics and Evolution* 32:1036–1060, doi:10.1016/j.ympev.2004.04.012.

Robert V., Stegehuis G. & Stalpers J. 2005 – The MycoBank engine and related databases. <http://www.mycobank.org>.

Ronquist F. & Huelsenbeck J.P. 2003 – MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574, doi:10.1093/bioinformatics/btg180.

Ronquist F., Huelsenbeck J.P. & van der Mark P. 2005 – MrBayes 3.1 manual. Tallahassee, Florida: School of Computational Science, Florida State University.
Simmons M.P. & Ochoterena H. 2000 – Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* 49:369–381, doi:10.1093/sysbio/49.2.369.

Stamatakis A., Hoover P. & Rougemont J. 2008 – A rapid bootstrap algorithm for the RAxML Web-Servers. *Systematic Biology* 57:758–771, doi:10.1080/10635150802429642.

Swofford D.L. 2003 – *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4*. Sinauer Associates, Sunderland, Massachusetts.

Vlasák J. & Kout J. 2011 – Pileate *Fomitiporia* species in the USA. New combinations *Fomitiporia calkinsii* and *F. bakeri*. *Mycological Progress* 10: 445–452, doi:10.1007/s11557-010-0715-0.

Zhou L.W. & Xue H.J. 2012 – *Fomitiporia pentaphylacis* and *F. tenuitubus* spp. nov. (Hymenochaetales, Basidiomycota) from Guangxi, southern China. *Mycological Progress* 11: 907–913, doi:10.1007/s11557-012-0806-1.

DISCUSSION

In the following, and a main result of the revision of the *Fomitiporia* species (Amalfi and Decock 2013, Amalfi et al. 2010, 2012, Campos Santana et al. 2013, Dai et al. 2008, Decock et al. 2005, 2007, Raymundo et al. 2012), we present here below the most comprehensive phylogenetic analysis of the genus, based on an extended taxon sampling. Several important conclusions result from this comprehensive phylogenetic analysis, of which the redefinition of the *Fomitiporia* lineage, and as a taxonomic consequence, the redefinition of the genus. Numerous phylogenetic species are also shown, waiting to be translated, in the Linnean taxonomic system, into “named species”. The phylogeographic structure of the genus is also highlighted, what is to our knowledge, the first case within the Hymenochaetales. The emergence of the *Fomitiporia* lineage and of its internal lineages / sublineages are tentatively dated. This study also demonstrates the very necessity to collect repeatedly, over and over, even in the same areas of tropical rainforest as in French Guiana, and a fortiori in virtually unknown areas, including e.g. Papua New Guinea, Borneo etc.

A specimen from the lowland rainforest of French Guiana drew our attention by presenting a thick, ferruginous brown powdery layer covering the lateral margins of the pileus, and made of thick-walled, brown chlamydospores. The basidiomata itself produce typical *Fomitiporia* basidiospores, viz. subglobose to slightly obovoid, dextrinoid, on average $\cong 6 \times 5 \mu\text{m}$ (Amalfi and Decock 2013); hence it was identified as a *Fomitiporia* species. Nevertheless, the origin of these chlamydospores was questioned, to know whether they are a part of the cycle of this species or whether they represent a contaminant (parasite). Pure cultures were obtained from the deep contextual tissue, in which no chlamydospores were observed, and

from the chlamydospores layer; both resulting cultures were identical and develop the same *Ptychogaster*-like anamorphic, chlamydosporic form.

Multiloci phylogenetic inferences, based on DNA sequence data of 4 loci (5' end of the LSU, ITS-5.8S, partial *tef1* and *rpb2*) resolved this specimen and the culture as an isolated, terminal branch, very basal to the *Fomitiporia* lineage as previously defined by Amalfi and Decock (2013, 2014), but also basal to *Phellinus uncisetus*. *Phellinus uncisetus* was so far considered as the *Fomitiporia* closest relative, and was so far an “orphan” species (Decock et al. 2007). This specimen is interpreted as belonging to a distinct species, of uncertain generic position, although the typical *Fomitiporia* basidiospores would argue for a placement in this genus. Nevertheless, this would include an asexual state in *Fomitiporia*, so far unknown. Hence it is described and illustrated below as *Fomitiporia pulverulenta* sp. nov (nom. prov.). Furthermore, if one considers this species as belonging to *Fomitiporia*, this would “automatically includes *Phellinus uncisetus* within *Fomitiporia* (Fig. 3). *Phellinus uncisetus* is a species occurring in high elevation southern Andes and characterized by globose, thick-walled, cyanophilous but non-dextrinoid basidiospores. It “looks” like a *Fomitiporia* but with adextrinoid basidiospores. It was phylogenetically basal to the *Fomitiporia* lineage, on a long orphan branch, and of uncertain generic affinities (Decock et al. 2007). Since then (Decock et al. 2007), two species were found closely related to *P. uncisetus*, viz . *P. livescens* (Rajchenberg et al. 2015) and *Phellinus* sp. PS18 (MUCL FG-14-79, Cony Decock). Both latter also have non-dextrinoid or very faintly pinkish basidiospores. Surprisingly *P. uncisetus*, *P. livescens* and this undescribed species from high elevation Andean forest in Ecuador (*Phellinus* sp. PS 18 MUCL EC-14-79, Cony Decock pers. coll.) clusters together in a well supported monophyletic, presumably “Andeo-Patagonian” lineage, which is

very basal to the bulk of the *Fomitiporia* species (Fig. 3, Clade 7). This would also expand the generic definition by including adextrinoid basidiospores.

This leads us to search within the *Fomitiporia* and more globally within *Phellinus* sensu lato (Larsen and Cobb-Poullé 1991) for other species sharing the same pattern or some features: perennial basidiomata, subglobose thick-walled, hyaline, cyanophilous, but non dextrinoid basidiospores, asexual, ptychogasterioid form. *Phellinus bambusinus* emerged!

Phellinus bambusinus is a poorly documented Southeast Asian species, growing on bamboo. It was originally described with an asexual form (Patouillard 1900) that is ontogenetically and morphologically related to the one observed in PS 19. On the basis of recent collections of this species, originating from subtropical Asia, its main features are confirmed, including non-dextrinoid basidiospores and presence of an asexual form *in vitro*. Non-dextrinoid basidiospores, *a priori*, also would exclude *P. bambusinus* from *Fomitiporia*. Nevertheless, phylogenetic inferences based on the 4 DNA loci data set showed this species to be closely affine to several *Fomitiporia* species of the core lineage and sharing the host (bamboo) specificity. They form within *Fomitiporia* a host specific bamboo lineage.

Phellinus sp. PS18 MUCL FG-14-79, shows a singular combination of morphological features, thereby defining one morphospecies. These features include especially a pileate basidiomata, a broad margin, hymenial setae, and globose, faintly dextrinoid (pinkish) basidiospores. Given the results of the phylogenetic inferences that identify our collection as a phylogenetic species (Fig. 3, PS18), and the morphological data that define a unique morphotype, PS 18 is considered as representing a distinct species. The search for a possible epithet within the synonyms of *F. robusta* yielded

no name that could apply to it, we therefore propose this species as *Fomitiporia andina* sp. nov (nom. prov.), and for practical reasons we will name it consequently from here on.

Moreover, our phylogenetic inferences, clearly related *Phellinus uncisetus*, *P. bambusinus* and *P. livescens*, to *Fomitiporia* as currently circumscribed, and their combinations are proposed (*F. unciseta* comb. nov. prov., *F. bambusina* comb. nov. prov., *F. livescens* comb. nov. prov., for facilitate the discussion we will use the new prov. names from here on).

The resulting *Fomitiporia* lineage is more clearly delimited from other generic entities within the Hymenochaetales. On the basis of this work, we also concluded that the *Fomitiporia* definition needed to be emended and its circumscription broadened in order to include species with non-dextrinoid basidiospores and/or producing *in natura* and/or in *in vitro* culture an asexual, ptychogasteroid reproductive form. Given their very basal position, and their long branches, both these two new lineages, the *F. pulverulenta* nom. prov. and the *F. unciseta* lineages, could be considered as phylogenetic relics.

***Fomitiporia* Murrill (1907) *emend* Decock et Amalfi.**

Basidiomata (annual) perennial, resupinate, widely effused, cushion-shaped, or pileate; *pileus* nodulose, obclavate, applanate, (ob)triquetrous to ungulate, small (from 2 cm wide) to large (up to 30 cm wide); *pileus* surface smooth to variably roughly or finely sulcate, up to rimose in aging, glabrous to variably shortly tomentose or with a crust; *context* homogeneous, rarely with a thin black line below a short tomentum.

Hyphal system (pseudo)dimitic; *generative hyphae* simple septate, hyaline to pale yellowish; *vegetative hyphae* as skeletal hyphae, moderately

thick-walled, with open lumen, yellowish, golden brown; *tramal setae* / *setal hyphae* in the hymenophoral trama absent or present, variably abundant within the same species, often irregularly shaped.

Hymenium: *basidia* barrel-shaped, with four sterigmata; *basidiospores* subglobose to obovoid, hyaline, thick-walled, cyanophilous, non- to strongly dextrinoid; *hymenial setae* absent or present, often variably abundant between specimens of the same species; *cystidioles* variably present, ventricose, lageniform.

Asexual form absent or present then ptychogasteroid; *conidiogenous* cells hyphal-like, unilocal, the conidiogenous locus apical: *conidiogenesis* holoblastic, basipetal; *conidia* solitary or in short chains, the older one at the apices, thick-walled, brown, the external surface smooth to faintly reticulate, accumulating in a powdery, ferruginous layer at the base of basidiomata and neighboring substrate.

Type of rot: a white rot.

Distribution: more likely cosmopolitan (Africa, America, Eurasia, South-East Asia, Australasia, Australia / New Zealand).

Type: *Fomitiporia langloisii* Murrill N. Amer. Fl. 9:7, 1907 (MB237612).

Comments. — *Fomitiporia* was above all characterized by its subglobose to globose, dextrinoid and cyanophilous basidiospores (Fiasson and Niemelä 1984, Fischer 1996). Other characters included a dimitic / pseudodimitic hyphal system with skeletal hyphae, variably present hymenial cystidioles and variably present hymenial setae. The present study extends the generic definition by incorporating species with adextrinoid or faintly (pinkish) dextrinoid basidiospores and presence of a macroscopic, ptychogasteroid, asexual form. An asexual form was not reported before in *Fomitiporia*. The conidiogenesis is holoblastic, basipetal, producing conidia

in short chains, which upon disintegration accumulate in a powdery ferruginous layer.

Species that produce an asexual form – if one except individual chlamydospores occasionally produced *in vitro* on artificial media – are few within the Hymenochaetaceae, and more globally, the Hymenochaetales. In addition to *F. bambusina* (comb nov. prov.) and *F. pulverulenta* sp. nov. nom. prov., a macroscopic asexual form is known in *Inonotus rickii*; this species produces both *in natura* and *in vitro* an asexual form referred to as *Ptychogaster cubensis* Pat. (Ryvarden 2003, Gilbertson and Ryvarden 1987, Stalpers 2000, Wright and Iaconis 1955). *Inonotus rickii* / *Ptychogaster cubensis* forms a macroscopic, nodulose structure, soft, spongy, and watery first, soon turning into a dry ferruginous powdery mass of thick-walled conidia (Gilbertson and Ryvarden 1987, Stalpers 2000, Wright and Iaconis 1955). Wright and Iaconis (1955) and Stalpers (2000) described its conidiogenesis, and the latter concluded that it is different from that occurring in *F. bambusina*.

Production of "chlamydospores" is also reported for *Hymenochaete rubiginosa* *in vitro*, on artificial culture media. It is so far unknown from the basidiomata in nature. It is also known in an *in vitro* culture of a species of *Inonotus* (*Inonotus cf. ochroporus*, MUCI 49987, C. Decock, pers. comm.), originating from Uganda.

More globally, within the Hymenochaetales, a morphologically and ontogenetically related (perhaps homologous) asexual form is known also in *Trichaptum sprucei* (Herrera and Decock 2007). *Oxyporus obducens* also produces a *Ptychogaster*-like asexual form. The ontogenesis (conidiogenesis) is uncertain, however; Stalpers (2000) noted that conidia are produced in apical chain, whereas they are basipetal in *T. sprucei* or

Fomitiporia spp., but the resulting chlamydospores are morphologically similar to those produce by *T. sprucei* or *Fomitiporia* spp.

As far as the dextrinoidity of the basidiospores are concerned, four species nesting within the *Fomitiporia* lineage as presently defined (Fig. 3), have undextrinoid basidiospores, viz. *F. unciseta*, *F. livescens*, and *F. andina* and *F. bambusina*.

The *Fomitiporia* lineages.

Amalfi et al. (2012) discussed the internal structure of the *Fomitiporia* lineage as by then defined. They recognized several major sublineages, each overlapping with a biogeographical domain. These sublineages included the residual stand-alone *F. calkinsii* sublineage, an Australasian sublineage, (Clade 6, Fig.3 and Fig. 6, in the external pocket) and the core sublineage. The core sublineage itself was formed of several clades: a large Neotropical clade (Clade 1), an African clade I (Clade 2), an indo-pacific clade (Clade 3), a Paleotropical /African clade II (Clade 4), and a Holarctic clade (Clade 5). The Neotropical clade could also be divided into several subclades, the *F. apiahyna* subclade, the *F. langloisii* subclade, the *F. texana* subclade, and a small “neo-Andean” clade (Amalfi and Decock 2014, Amalfi et al. 2012).

The discovery of *F. pulverulenta* and of *F. andina*, their relationships with *F. unciseta* and *Fomitiporia livescens* and their phylogenetic position in regards to the core *Fomitiporia* clade make the *Fomitiporia* lineage more clear-cut, with a clear discontinuity from other lineages within Hymenochaetaceae.

The phylogeny presented at Fig. 3 and Fig. 6 resulting from the different analyzes and representing the Maximum Likelihood tree, is based on the most exhaustive taxon sampling available to date, covering most of the known distribution range, including also basic characters such as the habits (pileate/resupinate), presence of hymenial setae, geographic origin, iki+/-, etc. It presents essentially the same topology as in previous studies (Amalfi and Decock 2013, 2014; Amalfi et al. 2012). The main and important difference between the present phylogenetic inferences and the previously published trees concern the position of *F. pulverulenta* nesting in a very basal position, with a long branch, and the relative position of *F.*

andina, *F. unciseta*, and *F. livescens* clade (Clade 7), the Australasian (Clade 6) lineage, and the residual *F. calkinsii* clade. Consequently, the limit of the *Fomitiporia* lineage could be questioned. *Fomitiporia andina*, which basidiospores are only faintly dextrinoid, is kin to *Fomitiporia unciseta* and *Fomitiporia livescens*, which basidiospores are described as non-dextrinoid. This would have excluded these species from the core *Fomitiporia* in which the species (but *F. bambusina*) have dextrinoid basidiospores. Nevertheless, they altogether form a lineage that is intermediate between the basal *F. pulverulenta* (which basidiospores are strongly dextrinoid) and the core *Fomitiporia* lineage. We concluded that this three species lineage, notwithstanding the non-dextrinoid basidiospores, is part of the *Fomitiporia* lineage. The new *Fomitiporia* lineage is therefore expanded and more clearcut.

The new *Fomitiporia* lineage could thus be divided into two residual relict, basal groups, *F. pulverulenta* on one side and *F. unciseta*, *F. andina*, *F. livescens* on the other side. Still, there is a stand-alone, orphan species, *F. calkinsii*, that forms also a relatively basal clade, that so far has not closest kins (at least supported by the analyses).

Basal, relict lineages:

--- The *Fomitiporia pulverulenta* (nom. prov.) lineage is known only from the South American rain forest in French Guiana. It is hypothesized to be a South American endemic. It has dextrinoid, subglobose basidiospores, and the notable ptychogasteroid anamorph. Its position on a long basal branch suggests the hypothesis of a relict species.

Clade 7 ---The *Fomitiporia andina* (nom. prov.), *F. unciseta* (comb. nov. prov.) and *F. livescens* (comb. nov. prov.) lineage. *Fomitiporia andina*, *F. unciseta* and *F. livescens* are known from high elevation Andean forest or the Patagonian Andes in Argentina. They form together a well-supported “Andeo-Patagonian” lineage (or paleo-andean), which is very basal to the bulk of the *Fomitiporia* species (Fig. 3 and Fig. 6) but of more recent origin than the *F. pulverulenta* lineage. Both *F. andina* and *F. unciseta* have pileate basidiomata. *Fomitiporia unciseta* is characterized by non-dextrinoid basidiospores and strongly apically curved hymenial setae. It is known only from high elevation Andes, at the timberline, growing on *Polylepis* (Rosaceae). *Polylepis* is an endemic small tree from the mid- and high-elevation regions of the tropical Andes. *Fomitiporia unciseta* was up to now an “orphan” species, standing alone basal to the *Fomitiporia* lineage.

Our molecular clock estimation combined with the RASP analysis support the hypothesis of a Neotropical origin of the most recent common ancestor about 38 MyBP. Our hypothesis is that the ancestral species colonized the Cordillera at the beginning of its uprising, and had originally a wider distribution. Speciation by vicariance occurred in more recent times, resulting from geographical isolation mainly due to the continuous Andean uplift. The radiation of this clade (c.a. 8 MyBP) seems to coincide with the uplift of northern Patagonian Andes in the late Miocene (c.a. 11 to 5 MyBP)

(Ramos et al. 2014). A similar pattern of speciation has been reported for several Andean plants species/genera (Marquínez et al. 2009, Berry et al. 2004, Filipowicz and Renner 2012).

Our studies have shown that the *Fomitiporia* species spanning over the Andean range belong to two distinct lineages with different (geographic and time) origins and affinities. Amalfi et al. (2014) already discussed the case of *F. baccharidis*, a species to be found also in high Andean cloud forest, so far known from Argentina and Ecuador, and sympatric with *F. andina* at the timberline in Ecuador, and *F. tabaquilio*, growing on *Polylepis* in high elevation Andean forest in Argentina and Peru (Amalfi et al. 2014). *Fomitiporia baccharidis* and *F. tabaquilio* form a well-supported clade that is included within a large “Neotropical” lineage gathering most species spanning over the new world south of Southern United States. Species from different historic background and affinities are thus sympatric in the Andean range, of which one –*F. andina*– seems to be relict and might represent an example of Andean paleo-endemism, whereas the *F. baccharidis*-*F. tabaquilio* clade, which pertains to the “modern” core *Fomitiporia* lineage, is of more recent origin, and represents an example of Andean neo-endemism..

Because of their long branches and basal position (deep phylogenetic lineage), *F. pulverulenta* and the *F. andina* / *F. unciseta* clade could be considered as two phylogenetic relicts. In a historical biogeographical perspective, these two deep endemic lineages could indicate paleo-endemism.

The lowland rainforest in French Guiana harbor several *Fomitiporia* species with pileate basidiomata. These species belong to four distinct lineages, the *F. apiahyna*, *F. texana*, *F. castilloi*, and *F. pulverulenta* lineages. The lowland rainforest in French Guiana thus hosts sympatrically both what could be hypothesized to represent a paleo-endemic on the one

side (presumed old species lying on a long branch, in this case, a deep, basal lineage, restricted to an area) and several neo-endemism species on the other side (or recently diverged species / lineages that are endemic). The same happens in the Andean elevation forests (the elevation varying according to the latitude), where also both paleo- and neo-endemism, at species and lineage level could be hypothesized, viz. respectively the *F. baccharidis*, *F. tabaquilio* lineage which would represent a neo-Andean lineage and the *F. andina*, *F. livescens*, and *F. unciseta*, which would represent a paleo-endemic lineage.

Both the Andean elevation forests and the Guiana rainforest might represent centers of mixed endemisms, although the extension ranges of these areas remain to be more accurately defined by intensive surveys in neighboring areas.

--- ***The F. calkinsii* lineage.**—

Fomitiporia calkinsii is still an orphan species. Its position is unclear, being weakly supported in a sister position to the “Australian” (Australasian / South pacific) lineage, which is also basal to the core *Fomitiporia* lineage. The species is so far only known from restricted geographic and ecological ranges. It spans over the Southeastern USA and northeastern Mexico, growing preferably on *Quercus*. It is a taxon of uncertain relationships and biogeographical history for the moment.

Clade 6 --- *The southern pacific [Australian – New Zealand] lineage.*—

This lineage comprises *F. australiensis* and two unnamed species originating from New Zealand (respectively *Fomitiporia* PS16 and PS17)

that were received as *P. robustus* (courtesy of the Fungal & Plant Disease Collection (PDD)).

It is uncertain still whether this lineage coincides with the Australasian ecoregion as defined by Olson et al. (2001). The Australasian ecoregion covers in addition to Australia and New Zealand, Papua New Guinea, the southern Indonesian islands and New Caledonia. Papua New Guinea and the southern Indonesian islands are mostly *terra incognita* as far as *Fomitiporia* is concerned. More samplings in these areas are necessary. Nevertheless it is noteworthy to remark that our RASP analysis support the hypothesis that the most recent common ancestor of those taxa originated from Southern South America c.a. 20 ± 6 MyBP. The abundance of fossils suggests that the Antarctic land bridge may have provided a corridor for migration between Australia and South America (Hill and Scriven, 1995; Ashworth and Cantrill, 2004; McGlone, 2006; Francis et al., 2008; Truswell and Macphail, 2009). The Antarctic land bridge remained in place from the late Cretaceous 65 million years ago (MyBP) through the Eocene epoch (34 MYBP), and until more recent times (20 MyBP), it may have included short island arcs joining Antarctica to Australia or Antarctica to South America (McLoughlin, 2001). This land bridge, associated with a tropical to temperate Antarctic climate (Francis et al. 2008), was thus available to support the dispersal of plant and animal species for about 75 to 95 million years after the separation of Africa (~130— 110 MyBP).

The final separation of Antarctica from Australia and South America opened the Tasmanian seaway and Drake Passage, giving rise to the cold Antarctic Circumpolar Current that isolated Antarctica from the other southern continents (Barker et al., 2006).

The core *Fomitiporia* lineages:

Clade 5 — The Holarctic / pan-temperate lineage—

As previously stated, Clade 5 contains collections from the Holarctic domain, including northern Mexico, North America, Europe and Temperate Asia (northern China, Korea, Japan), to which also pertain elements from the Afro-mountain domain.

Species that belong to this lineage have either resupinate basidiomata including *F. aethiopica*, *F. punctata*, *F. tsugina*, *F. pseudopunctata* / *F. mediterranea*, *Fomitiporia* *PS12* pileate basidiomata: *F. bakeri*, *F. cupressicola*, *F. hartigii*, *F. hippophaeicola*, *F. punicata*, *F. robusta*, *F. tenuitubus*, PS 13, 14, 15 (Amalfi et al. 2012); nodulose basidiomata such as *F. erecta*, *F. juniperina*, or both habits such as *F. polymorpha* (Fischer and Binder 2004).

Our results support the hypothesis that this clade originates in late Oligocene – early Miocene as a result of a boreotropical dispersal from South American ancestors to Africa passing through Mesoamerica, North America and ultimately, via the North Atlantic Land Bridge (NAB), Europe (including the Mediterranean area) and the temperate regions of Central Asia.

Most sub-clades have representatives from both continents (e.g. *F. robusta* and *F. bakeri*, *F. hartigii* and *F. tsugina*, see chapter II for a more detailed analysis) that show phylogenetic segregation, and most likely reproductive isolation. This pattern supports the hypothesis of allopatric speciation, which has been noted in other fungal biogeographical studies (e.g. Taylor et al. 2006, Geml et al. 2008, Giraud et al. 2008, Moncalvo and Buchanan 2008). It is noteworthy to remark that this lineage includes also two species from high elevation mountains of eastern (*F. aethiopica*) and

western (*Fomitiporia* PS12, Sao Tomé) Africa that will be discussed in the next paragraph.

Clade 4 - Clade 2 –The African lineages — Afromountain subclade —

The taxonomic and phylogenetic knowledge of *Fomitiporia* in sub-Saharan Africa have been apprehended by Decock et al. (2005), Amalfi et al. (2010), and Cloete et al. (2013).

Within the genus *Fomitiporia*, worldwide phylogenetic reconstruction showed the African species to cluster in three different, independent lineages, consequence of different evolutionary histories, spanning in different or similar biogeographical areas and perhaps co-existing at the transition areas.. African species are sorted into African endemic lineages, centered on either the Guineo-Congolian or the Zambesian endemism areas, and into non-endemic lineages. *F. tenuis*, a species widely distributed throughout tropical Africa, grouped together with *F. capensis*, originating from south Africa, in a first, African endemic lineage (Clade 4); *F.gabonensis*, *F.ivindoensis* and *F. nobilissima* (Clade 2), species from the Guineo-Congolian center of endemism, forms the second, distinct African-endemic lineage.

This first endemic lineage (Clade 4), is composed of two species, *F. tenuis* and *F. capensis*, both with resupinate basidiomes. *Fomitiporia tenuis* was originally described from Ethiopian medium elevation humid forest, and is widespread in central Africa, with records, from Ethiopia, Zimbabwe, Uganda, Congo (RDC), Cameroon, and Gabon (Amalfi et al. 2010). It is also reported from insular Africa in Madagascar (Amalfi et al. 2010). *Fomitiporia capensis* is known so far from South Africa only, associated with the Esca disease of *Vitis* in vineyard (its wild host remains so far

unknown). Our results support the hypothesis that this lineage represents the first colonization of Africa resulting of the boreotropical route taken by their Neotropical ancestors in early Miocene, and radiate probably as a result of ecological/geographical segregation in late Miocene (c.a. 15MyBP).

This second endemic lineage (Clade 2), comprises three species, *F. gabonensis*, *F. ivindoensis*, *F. nobilissima*, all three with pileate basidiomata, small basidiospores, and so far only known from the western edge of the Guineo-Congolian forest or the lower Guineo-Congolian regional center of endemism (White 1979, 1983), with the exception of *F. gabonensis*, also recorded once in eastern RDC. *Fomitiporia gabonensis* is the most common species in Gabon, found in all surveyed areas. However, surprisingly, it was not observed in the Dja Biosphere reserve in southern Cameroon. It occupies in the western Guineo-congolian rainforest the same niche as species of the *F. apiahyna* clade in the Amazonian forest. *Fomitiporia ivindoensis* is known from two collections. *Fomitiporia nobilissima* is known from several specimens, all collected in a Gilbertiodendron forest spot in Gabon. It was found only on *Gilbertiodendron dewevrei*, (Limballi, Fagaceae) and might be host specific. Our data support a tropical Asian origin for their mrca in early Miocene (c.a. 20 MyBP) and a recent sympatric radiation in the Guineo-congo center of endemism in late Miocene early Pliocene (8 MyBP) possibly by ecological adaptation (micro-segregation by host preferences/ecological niche). These three species and the clade 2 lineage are so far endemic to the Guineo-congo center of endemism. However, the taxonomic knowledge of poroid Hymenochaetaceae in sub-Saharan Africa remains still very fragmentary and critically understudied (Ryvarden 1998, 2000). *A fortiori*, even less is known about the phylogenetic relationships, origins, or biogeographical connections of the local species with other allopatric or sympatric species (Amalfi et al. 2010).

The “non-endemic” lineage comprises two species occurring in the Afromontane domains. *Fomitiporia PS12* originating from the western (Sao-Tome) and *F. aethiopica* from eastern edges (Ethiopia) of the Afromontane archipelago (Fig. 3, Fig. 6, pink box) nest within the “holarctic” clade (Amalfi et al. 2012). In a phylogenetic perspective they share a common ancestor with taxa originating from the Mediterranean and the temperate Asia (*F. erecta* and *F. punicata*).

The Ethiopian and Obô highlands belong to the so-called Afromontane archipelago regional centre of endemism (White 1979, 1983).

The Afromontane archipelago regional centre of endemism extends roughly from Ethiopia to South Africa in the east (the eastern rift) and from the Rwenzori mountains range to the southern volcanoes in RDC, in the Albertine Rift, in centre-east (White 1986). Additionally, some isolated mountains range of volcanic origin can be found to the west, at e.g. Mt Cameroon (Cameroon), and, in insular Africa, in Bioko (Equatorial Guinea) and Obô National Park (São Tome). These ecosystems are characterized by a fragmented pattern similar to archipelago and a high level of botanical endemism (4000 botanical taxa are reported from the Afromontane archipelago regional centre of endemism of which 3000 are endemic).

In a historical perspective, many of the plants species spanning over these ecosystems found their origin mostly through ancient and multiple taxa recruitments followed by local speciation / dispersion events. In addition to (local) tropical elements, its biota is composed of elements derived from (or phylogenetically connected to) the Cape Floristic region to the South and, more obviously, from Northern temperate or Mediterranean areas, up to Central Asia to the North (e.g. Gehrke & Linder 2009). Connections between mountainous eastern Africa and Mediterranean areas are well documented for plants (Adams et al. 1993, Assefa et al. 2007, Hedberg 1970,

Kerfoot 1975, Koch et al. 2006, Smith and Cleef 1988). It is still less known for Fungi at the present time (Amalfi et al. 2010, Degreef et al. 2009).

Dating estimation of divergence shows that they diverged from their Mediterranean relatives in the late Miocene about $7 \pm 2,5$ MyBP. On the other hand the RASP analyses to support that the most recent common ancestor of those taxa were widely distributed in the Mediterranean area.

During the late Miocene – early Pliocene's glaciation, the Ethiopian eco-region showed similarity with the Eurasian temperate ecosystems, whereas the tops of mountains were covered with glaciers. The climate changes in this period were likely to play an important role for dispersal among the mountain systems in East Africa (Moreau 1963; Hedberg 1969, 1970, 1986; Livingstone 1993); In this scenario the Red Sea (whom level had considerably fallen down) could have supplied a way for the north temperate species (plants and their possible parasites), in search of hotter zones to colonize, as exemplified for *Lepidium* and *Rorippa* by Mummenhoff et al. (2001) and Bleeker et al. (2002). The desertic zones of Kenya, as well as the flooded region near the Nile, would then have established significant obstacles to a larger immigration. When the climate began to get warmer (more “tropical”) during the Pliocene, Holarctics species would have taken refuge on the mountainous zones of Africa, drier and cooler, while the paleotropical species would have become established in the lower forests, thus providing a reasonable explanation of the combination of multiple origins of the African specimens (Kingdon, 1989).

These two Afromountain taxa (Sao tome and Ethiopia) diverged from each other approximately 6 to 4 MyBP and possibly represent two extremes of a complex of relict species forming an East-West gradient between the two (Albertin and Gregorian) rifts. The ancestral species could have been widely distributed in the lowland forest during the dryer period and remained

isolated on the cooler climate of the mountains when the temperatures increase, otherwise intermountain-hopping and isolation by distance could alternatively explain the speciation process that concerns these two species. This point needs to be clarified by gathering information about any possible intermediate species in the mountains that separate these extremes of the afro-mountain range. In this hypothetical scenario *F. pseudopunctata* / *mediterranea* would represent a more recent (4 to 2 MyBP) secondary migration “out of Africa” probably passing by the west coastal zones of Saharan Africa.

Clade 3 — The Indo-malaysian lineage—

This lineage contains so far exclusively taxa from south East Asia. Although several species (at least 12, *fide* Zhou and Xue 2011) of *Fomitiporia* have been reported from China, by extense field sampling and literature studies, we could retrieve only seven of them. Three species: *F. tenuitubus*, *F. punctata*, and *F. punicata*, are resolved as belonging to the Holarctic *Fomitiporia* lineage. Other species revised, such as *F. ellipsoidea* and *F. pusilla*, clusters in other taxonomic entities, in the specific in the genus *Phellinus*. Only four of them are well resolved as belonging to the Indo-Malaysian lineage. Almost all the taxa, with the exclusion of *F. pentaphylacis*, are characterized by resupinate basidiomes. *F. bannaensis*, *F. torreyae* and an unnamed collection from Malaysia (*Fomitiporia* sp TFMF 18103) are closely related species, morphologically and phylogenetically, of pathogenic wood-decaying fungi in forest ecosystems (Dai et al. 2007, Oto et al. 2014).

Our data suggest for this lineage an African origin followed by dispersal to south east asia (early Miocene) possibly via the almost dried Tethys sea. From here dispersal occurred backward towards tropical Africa

in late Miocene thus generating Clade 2 (Figs. 3, 6). Our boreotropical model supports the idea that dispersal between tropical Africa and south east Asia was possible during the Oligocene and early Miocene (Fig.3, Fig.6). This premise stems from geological evidence on the collision of the African and Eurasian plates during the Oligocene and the Miocene (Allen and Armstrong, 2008; Potter and Szatmari, 2009), creating land bridges between both continents. In addition, similar biogeographical patterns with coinciding dates have been recently observed and discussed in plants (Couvreur et al. 2011, Zhou et al. 2011, Bacon et al. 2012), mammals (Bibi, 2011), birds (Irestedt et al. 2011) and insects (Kodandaramaiah and Wahlberg, 2007), and ultimately mushrooms (Sánchez-Ramírez et al. 2014).

Clade 1 — The Neotropical lineage—

Our preliminary results indicate a late Oligocene - early Miocene origin of the Neotropical *Fomitiporia* sublineage, situated between 26 and 18 MyBP, from a tropical African ancestor, and a probable trans-Atlantic long range dispersal to the new world (see next paragraph below: evolutionary history of *Fomitiporia*).

Range expansion into South America, Meso-America reaching the subtropical belt of the USA some time during the Miocene (17 MyBP) followed this trans-Atlantic long range dispersal event. The observed dichotomy of the Neotropical lineage, divided into one “pileate” subclade and one mainly “resupinate” subclade, is estimated to have occurred in the same period.

The Neotropical lineage is, for the time being, the largest and the more diverse as far as species and sub-lineages are concerned. It contains multiple species, multiple clades and clades with a complex structure revealing multiple speciation processes, both sympatric / allopatric. The naming

“Neotropical” clade is kept to conform to previous publications. Nevertheless, a “bamboo-specific” clade nests within this Neotropical clade that comprises species spanning over both the Neotropics and Southeast Asia.

The Neotropics has been extensively well sampled during the last 5 years (Cony Decock) and at least 22 phylogenetic species have been shown. Comparatively, the same collecting efforts have been placed at the western edge of the Guineo-congolian rainforest, mostly in Gabon, but only 4 phylogenetic species have been found. For instance, 10 species with pileate basidiomata co-exist (are sympatric) in a small spot of rainforest in French Guiana (Nouragues Nature Reserve), whereas only 3 occurs in an analogous spot of rainforest in the western edge of the Guineo-Congolian endemism area in Gabon. In the same small forest plot of French Guiana, at least three different species with resupinate basidiomata occurs whereas only one (*F. tenuis*) was found so far in Gabon.

Moreover this clade contains the highest of the phylogenetic diversity, with species clustering in multiple, endemic sublineages. As previously stated, this clade contains two sister subclades: the first one contains exclusively species having a resupinate basidiomata (though occasionally pseudopileate) such as *F. langloisii*, *F. maxonii*, *F. expansa*, *F. dryophila*, *F. sonorae*, and *Fomitiporia* PS10 (Figs. 3, 6); the second one comprises species with pileate to pseudopileate basidiomata such as *F. tabaquilio*, *F. apiahyna*, *F. texana*, *F. baccharidis* and several unnamed species (PS 1 to PS6).

As previously discussed all the resupinate specimens belonging to this lineage, with the exclusion of the taxa growing on bamboos (see below), shares an identical plesiomorphic deletion of a 31 bps long fragment located near the 5' end of the ITS1 region of the ribosomal DNA.

The sublineage “*apiahyna*” comprises exclusively species with pileate basidiomata. It shows a species richness higher than everywhere else, with at least 5 species of which four (or five) represent undescribed taxa. *F. apiahyna*, *Fomitiporia* PS 1, PS 2, PS3a, PS3b, PS4 (Amalfi et al. 2013, Chapter III) all originate from a common ancestor, live in sympatry within the same forest plot of c.a. 1000 square meters in the “Nouragues reserve” (French Guyana). This presupposes a sympatric speciation presumably driven by some sort of ecological segregation (hosts specificity, ecological niche adaptation etc.).

The sublineage “*langloisii*” comprises almost exclusively species with resupinate basidiomata, in addition to *F. langloisii*, (Amalfi et al. 2013). It includes also *F. dryophila*, *F. expansa*, *F. maxonii*, *F. neotropica*, *F. sonora*, and *Fomitiporia* PS 10 (Amalfi and Decock 2014, de Campos Santana et al. 2014). Basal to this lineage, we could find two ancestral pileate species: *F. castilloi* and *Fomitiporia* PS11, both known so far only from French Guyana. In this sublineage several species occurs in sympatry; *F. langloisii* and *F. dryophila* occurs sympatrically at least in the subtropical belt of the Southeastern USA or, in a biogeographical perspective, in the southeastern and coastal plain mixed forest provinces of the subtropical division (Thorne 1994) (the Southern oak / pines forest, Duffield 1982, Decock et al. 2007); or *F. maxonii* and *F. neotropica* in North east Argentina (Iguazú national park, de Campos Santana et al. 2014).

The “Neo-Andean” sublineage. It comprises two species: *F. tabaquilo*, and *F. baccharidis* (Amalfi et al. 2014, chapter IV), distributed in the high elevation Andean forests of Argentina and Ecuador. These species reached the Andean plateau in late Miocene (12 MyBP), most likely from

Neotropical ancestors, and radiated sympatrically in early Pliocene (c.a. 4MyBP); hence they represent a neo-Andean clade that could be compared to Clade 7 (the *F. andina* / *F. unciseta*, *F. livescens* clade) which is paleo-Andean (Andino Patagonian).

Sublineage “*texana*” includes *F. texana* and *Fomitiporia* PS5 and PS6. This subclade has the apomorphic ecological feature of growing into semi-arid to arid ecosystem, what could request physiological / morphological adaptations.

The “bamusicolous” sublineage (Fig 3, Fig.6 blue box) contains species with resupinate to pileate basidiomata that share the apomorphic autecological feature of being specific to *Poaceae*. Our comprehensive phylogeny show so far four monophyletic taxa growing exclusively on wooden bamboos gathered in this lineage: *F. bambusarum* and *F. spinescens*, both recorded from North east Argentina and Southern Brazil; *F. Bambusina*, originally described from Vietnam and collected from Southern China (Yunnan province MUCL51609, MUCL51610, collected by Decock and Amalfi in 2010, and representing the first report of *F. bambusina* outside Vietnam) ; two additional taxa, not included in our study for practical reasons (lack of time), clusters in the very lineage by a preliminary ML analysis, viz. *F. sanctichampagnatii* from southern Brazil and an unnamed resupinate specie collected in Yunnan (China) on rotten bamboo. This latter was previously excluded from our dataset because of its non-dextrinoid basidiospores.

Our evolutionary analyses suggest a Neotropical origin for this lineage in the middle Miocene (c.a. 16MyBP) followed by a rapid radiation in late Miocene. Interestingly, our results coincide with the most recent hypothesis

on the origin and radiation of wooden Bamboos, both in time and distribution patterns (Hodkinson et al. 2010, Bouchenak-Khelladi et al. 2010). This would imply that the most recent common ancestor of the bambusicolous clade “colonized” the ancestral bamboo species before its radiation, and followed his host during its dispersion towards Africa and Asia. Moreover this pattern of host’s specificity and the dated phylogenies of both *Fomitiporia* and the *Poaceae*’s family, suggest coevolution as a basal factor of speciation in relation with the diversification of bamboos, possibly due to the very selective pressure of the host. Of course this hypothesis needs to be tested by including more species growing on bamboo from different locations, and more specimens in the analysis, and by focusing on this sublineage the dating and ancestral area inferences.

It is noteworthy that the taxa belonging to this clade showed consistently longer branches in the phylogenetic trees than taxa in other clades, which suggested an accelerated evolutionary rate in this group. It is known that environmental stress can accelerate the evolutionary rate of specific stress-response proteins and create new functions specialized for different environments, enhancing an organism’s fitness to stressful environments.

We used a phylogenetically based maximum likelihood procedure to identify shifts in rates of nucleotide substitutions as implemented in the software Brownie (O’Meara et al. 2006). Our preliminary results shown a statistically significant rate differences between the *Bambusicolous* subclade and the other five closest clades selected for the rates differences test ($P < 0.01$).

Host jumps or shifts by parasites or symbionts are often associated with bursts of species diversification driven by the exploitation of new adaptive zones (Schluter 2000; Fordyce 2010). To adapt to the new substrate

(or environment) an organism must repeatedly overcome new conditions and create a new set of unique metabolic reactions to a particular environmental stress.

This adaptive response to changing environmental conditions results in an acceleration of evolutionary rate of the lineage and the functional evolution of specific stress-response proteins, which favors organismic fitness to the new environment.

The potential links between rates of molecular evolution and ecological parameters should be further explored by comparing alternative Ornstein-Uhlenbeck models. These models would allow us to test the hypothesis that cladogenesis in the bambousicolous lineage is associated with shifts in host that might in turn explain changes in nucleotide substitution rate.

Moreover, assuming that all adaptive responses to a new environment (and a fortiori all evolution of phenotypes) results from minor increases in mutation rates of genes related to a particular stress, comparisons of the ratio of non-synonymous (K_a) / synonymous (K_s) substitutions ($\omega = K_a/K_s$), of targeted genes, such some ligninolytic enzyme (monooxygenase Lignin Peroxidases, Manganese Peroxidases, etc.), could provide a useful means for quantifying the impact of natural selection on molecular evolution (Kimura et al. 1983, Ohta 1992). Synonymous mutations are generally neutral in the course of evolution and do not result in changes to the amino acids in a protein, while non-synonymous mutations can occur under strong selective pressure and result in the altering of the amino acids in a protein. A value of $\omega = 1$ denotes a neutral mutation, ω less than 1 indicates purifying selection which describes selection against new variants, while ω greater than 1 denotes positive selection (adaptive molecular evolution), in that non-

synonymous mutations offer fitness advantages to the protein (Yang et al. 2000).

Evolutionary history of *Fomitiporia*: an overview:

Fungal distributions are mostly determined by genetic, ecological and morphological constraints (Pringle et al. 2009). For instance, ecological and phylogenetic studies have shown that some fungal species might be virtually free from dispersal barriers (Queloz et al. 2011), whereas others have strong biogeographical structures that may be related to host and habitat limitations (Geml et al. 2006, 2008; Matheny et al. 2009, Amalfi and Decock 2013, Amalfi et al. 2010, 2012, de Campos Santana et al. 2013 etc.).

Our molecular clock dating and ancestral area reconstruction results (Figs 3, 6), generated from a multilocus phylogeny of *Fomitiporia*, and based on the most extensive species / specimens sampling available for the time being, strongly suggest that *Fomitiporia* has a marked biogeographical structure, with a probable Neotropical origin (dating back to the Palaeocene–Eocene) followed by an early dispersal to the Andean cordillera (Eocene). From the ancestral Neotropical species, the Antarctic land bridge (ALB) may have provided a corridor for migration between South America and Australia (20 ± 6 MyBP). Subsequently, our data strongly support the hypothesis of a boreotropical dispersal model.

The boreotropical hypothesis refers to a warm phase in earth's climatic history during which megathermal (frost-intolerant) species extended much further north than they do today. A North Atlantic land Bridge (NAB) near the modern Greenland permitted overland dispersal of northern megathermal (boreotropical) species between Europe and North America during Eocene and Oligocene (Tiffney 1985, Morley 2000). Because some of the boreotropical flora was derived originally from Africa or South America, the NAB provided a circuitous dispersal path permitting exchanges between Africa and the Neotropics via North America and

Europe (Morley 2003). Fossil calibrated phylogenies suggest that several plant lineages in the Burseraceae (Weeks et al 2005), Meliaceae (Mueller et al 2006) Maraceae (Zerega et al 2005), Lauraceae (Chanderbali et al 2001), Sapotaceae (Smedmark and Andenberg 2007) and Melastomataceae (Renner et al 2001) arrived in South America via a north-south Boreotropical route; Inversely, the Malpighiaceae (Davis et al 2002) spread from south America to Africa and Asia through a south-north route. This latter path is rather consistent with our results. The ancestral species originating in the Neotropics may have spread through the boreotropical route, generating the pan-temperate/Holarctic lineage (Figs 3, 6 clade 5), before reaching Africa (*F. tenuis* lineage Clade 4) and Asia (*F. bannaensis* lineage Clade 3) in early Miocene. In this scheme, the *Fomitiporia nobilissima* lineage (Clade 2) might represent a secondary colonization “back to Africa” from southwest Asian ancestors.

More difficult to explain is the way back to South America to the Neotropical lineage (Clade 1). RASP analysis suggests an African ancestral distribution of the most recent common ancestor (mrca) of this lineage in early Miocene (c.a. 21 MyBP). Several recent studies have suggested that a substantial portion of today’s plant diversity in the Neotropics has resulted from the dispersal of taxa into that region rather than by vicariance. In general, three hypotheses should be considered in order to explain disjunct distribution of taxa between the Paleotropics and the Neotropics : (1) via the North Atlantic Land Bridge (NAB), (2) via the Bering Land Bridge (BLB), or (3) long range trans-oceanic dispersal from Africa directly onto the continent.

(1) North America and Europe being pretty well surveyed from a mycological point of view, the NAB scenario should imply several

extinctions events of North American and European stem lineages, in order to explain the lack of intermediate taxa (European and North American) belonging to the Neotropical lineage. Therefore, this scenario is highly improbable, and could be excluded.

(2) Even if the trans Beringian scenario could not be completely excluded, the molecular clock dating of the Paleotropical-Neotropical disjunction in *Fomitiporia* (c.a.21 MyBP), make this scenario unlikely. Tiffnay (1985) and Wolfe (1987) stated that at the Eocene–Oligocene transition (35 MyBP), there was a drastic climatic change; the climate became cooler and drier (the terminal Eocene event). This resulted in the demise of the boreotropical forest, subsequent trans-Beringian isolation and vicariance in the organisms living in the forest. The mixed mesophytic forest replaced the boreotropical forest. Although exchange of cold-temperate groups across Beringia probably continued in the Oligocene and Miocene, most dispersal of temperate groups across Beringia is considered to have stopped after the terminal Eocene event. Until late Miocene (14-10 MyBP) trans-Beringian dispersal was presumably dominated by boreal elements, while warm-temperate groups were restricted to widely disjoint southern refugia (Lafontaine and Wood, 1988). Nevertheless, the lack of data from the northeast temperate area (Far east Russia), as well as the partial data from Asia, prevent us from totally exclude this scenario.

(3) Although the Pacific and Atlantic islands are largely « *terra incognita* » as far as *Fomitiporia* is concerned (as well as for many other fungal groups), extreme long range dispersal from Africa to the Neotropics seems a scenario consistent with our results. A large number of subtropical and tropical plant families have disjunct distributions between the

Paleotropics and the Neotropics (Raven and Axelrod 1974), most commonly between tropical America and tropical Africa. Although such disjunct distributions have often been attributed to a presence on the Gondwana continent and subsequent vicariance events following the break up of this large landmass, in recent times, molecular dating analyses have shown that most plant families are too young to have originated before the break up of Gondwana. In several plants studies, long-distance dispersal by wind, water, rafting, or avian transport have been demonstrated to be the most likely scenario that could explain this kind of disjunct distribution (Renner et al. 2001; Dick et al. 2003, 2007; Givnish et al. 2004; Lavin et al. 2004; Pennington and Dick 2004; Schaefer et al. 2009).

Temporary island « bridges » between Africa and South America have also been considered to be important stepstones for dispersal (Morley 2003; Pennington and Dick 2004). Moreover in a recent study on *Cinchonoideae* subfamily (Rubiaceae) Manns et al (2012) showed that « the Neotropical and Paleotropical distributions of *Chiococceae* and *Guettardeae* are best explained by long-distance dispersals from the Neotropics to the Paleotropics during the Miocene ». This coincides with our dating estimation.

Tangled plant parts (“floating islands”) are constantly carried out into the tropical Atlantic from the deltas of the Congo, Senegal, and Amazon rivers, and some enter the conveyor belt like currents that transport debris (including plastic trash; Barnes 2002) in either direction across the Atlantic. Because of their speed, equatorial currents can transport larger floating objects with wind-exposed surfaces across the Atlantic in less than 2 weeks, and transport was probably faster across the narrower Atlantic of the late Oligocene. Indeed, if monkeys and rodents arrived to south America on a

uniquely successful floating island (Houle 1998, 1999), that same island would have carried lots of seeds, insects, and of course Fungi.

The gathering of new material (collections) originating from the Atlantic islands, including Ascencion, St. Helena, Trinidad, the Saint Peter and Saint Paul archipelago, which could constitute a relic step stone of this dispersion, could corroborate this hypothesis.

Notes on Sympatric speciation

Sympatric speciation, or the evolution of reproductive isolation without geographic barriers (Mayr 1963), remains a highly contentious topic, dating back to correspondence between Darwin and Wagner. It is currently understood as the evolution of reproductive isolation “within a single interbreeding unit” or between populations that initially use two distinct habitats but disperse freely between them (Futuyma & Mayer 1980). Geographic isolation occurs when the distance between populations exceeds individuals’ ability to disperse between them (‘cruising range’), or the intervening environments are inhospitable, precluding dispersal.

Mayr (1963) also argued that overlapping ranges are better explained by secondary contact between allopatrically derived species.

The key problem is that mating and recombination rapidly should break down linkage disequilibrium, preventing the formation of genetically distinct subgroups. However, it is not always easy to determine when isolation is geographic (extrinsic factors), as opposed to biological isolation arising from intrinsic differences (hosts preferences/specialization, ecological niche adaptation, etc.) among groups. Ambiguity arises because these factors may be difficult to distinguish empirically, and may interact if extrinsic barriers are conditional on individual’s biological traits.

Within *Fomitiporia*, we have encountered several examples of potential sympatric speciation cases (e.g. *F. langloisii* and *F. dryophila*, *F. maxonii* and *F. neotropica*, the *F. apiahyna* sublineage, *F. tabaquilio* and *F. baccharidis*, etc). Of course the relative frequency of sympatric speciation will be difficult to resolve, because biogeographic changes may have obscured the geographical patterns underlying many past speciation events.

In contrast, progress is being made on evaluating the empirical validity of key theoretical conditions for sympatric speciation.

Disruptive selection and direct selection on mating traits, which should facilitate sympatric speciation, are biologically well-supported factors. Nearly all models of sympatric speciation share a common framework. In an initially panmictic population, disruptive selection drives an evolutionary (rather than biogeographic) change in mating patterns. The result is reproductive isolation between subsets of the population's descendants, maintaining strong linkage or Hardy-Weinberg disequilibrium. The vast majority of models invoke disruptive selection arising from ecological interactions such as resource competition.

Generally speaking, hosts shift could directly confer reproductive isolation if mating occurs on the host. Clearly, evaluating host specificity for what concerns saprotrophic fungi can be quite difficult, especially in a tropical rain forest, where every fallen rotten branches found on ground could come from multiple trees.

Ecological divergence may also result in temporal reproductive isolation, since many species synchronize their breeding with peak resource availability. Very few are known about ecological succession of wood inhabiting Fungi. The main problem is that the “observed” mycological biodiversity – based on basidiomata observation –, might underestimate the “real” diversity, since several species, although present in the substrate, doesn't fructify, or produce sporocarps only under certain conditions (presence of specific hormones, humidity, temperature, inhibition by competitors, etc.).

The empirical evidence available to date is by no means sufficient to evaluate the importance of any factors, influencing sympatric speciation.

Nonetheless, it is clear that niche variation, frequency dependent competition, and resulting disruptive selection occur in a variety of systems.

On the other hand, geographic structure influences the mechanisms that might operate, and how strong these mechanisms should be to cause reproductive isolation. Furthermore, all speciation events occur in some geographic context, and the spatial distribution of biodiversity may depend on which speciation mechanisms are possible.

CONCLUSIONS AND PERSPECTIVES

Neither the morphological characterization nor the phylogenetic characterization, considered individually, demonstrated to be sufficient to describe the complex evolutionary history of this relatively young genus, presenting a rapid radiation often not followed by a morphological differentiation (cryptic species). Hence, the necessity to integrate other descriptors than the molecular and morphological ones, such as ecological, biological and biogeographical data in order to achieve a "global" or "holistic" species concept.

The application of an "holistic" species concept to a small genus such as *Fomitiporia*, allow us to evidence and at least partially resolve the complex phylogenetic/biogeographic structure of this latter.

Thanks to this integrative approach, seven new species and two new combinations were described (*F. nobilissima*, *F. gabonensis*, *F. ivindoensis*, *F. neotropica*, *F. expansa*, *F. castilloi*, *F. baccharidis*, *F. cupressicola*, *F. apiahyna*), two species proposed as new (*F. pulverulenta* nom. prov. and *F. andina* nom. prov.), three new combinations proposed (*F. unciseta* comb. nov. prov., *F. livescens* comb. nov. prov., *F. bambusina* comb. nov. prov.), and ultimately fifteen unnamed taxa were evidenced and still need to be described.

Several morphological features, to day considered discriminating at species or genus level, such as the presence of hymenial setae or the dextrinoid basidiospores were demonstrated to be variable characters. Therefore *Fomitiporia* was redefined on the basis of these findings.

In order to help understanding the current, "observed", distribution of the species molecular clock dating and ancestral area reconstruction analyses were carried out, as well as the most comprehensive phylogenetic analysis of

the genus, based on the most complete taxon sampling to date. The results evidenced, for the first time, several phylogenetic lineages within the genus, with a strong biogeographical structure, resulting from a complex evolutionary history. Our molecular clock dating and ancestral area reconstruction results suggest a probable Neotropical origin (Palaeocene–Eocene) followed by an early dispersal to the Andean cordillera (Eocene). From the ancestral Neotropical species, the Antarctic land bridge may have provided a corridor for migration between South America and Australia (early Miocene). Subsequently, our data strongly support the hypothesis of a boreotropical dispersal model, from South America to Africa via North America and Eurasia (passing through the North Atlantic land Bridge). From here, several dispersion events, back and forth to Asia, and ultimately an extreme long-range trans-Atlantic dispersal to the Neotropics, accompanied by a recent radiation were hypothesized.

Moreover, within *Fomitiporia*, we have encountered several examples of potential sympatric speciation cases (*F. langloisii* and *F. dryophila* in the subtropical belt of southern USA, *F. maxonii* and *F. neotropica* which distribution overlaps in South America, the *F. apiahyna* sublineage in French Guyana, *F. tabaquilio* and *F. baccharidis*, occurring sympatrically in the NW Argentina, etc).

Further investigations are clearly needed to fully understand the extant of *Fomitiporia* distribution. For example, how the peculiar physiology of a species could allow adaptation to a specific ecological niche (e.g. resistance to phenolic compounds or other molecules present in the woods, growth and fructification conditions, spore's penetration power in the host, host specificity, etc.) is still very poorly known. To evaluate host's specificity, a DNA extraction from the substrate could provide useful information (in the impossibility to obtain leaves or buds, wood bark including cambial tissues

or xylem coring seems to be a valid alternative for DNA extraction, Verbylaitė et al. 2010). Also wood coring and fungal DNA amplification could enlighten the hidden mycodiversity and provide element for evaluation the ecological succession.

Further analyses also are still needed to improve our understanding of the evolutionary history of *Fomitiporia*, and test our hypothesis. In order to explicitly assess the likelihoods of different geodispersal scenarios, the dispersal–extinction–cladogenesis model, as implemented in Lagrange (Ree and Smith, 2008), could provide useful information to reconstruct ancestral ranges by constraining dispersal in « ad hoc » biogeographical settings.

Our study also evidenced an acceleration of mutation rates in the « bambusicolous » sublineage, suggesting that ecological features might be contributory factors to global species diversity.

As previously stated, to explore the implications of ecologically or geographically determined variations in mutation rates more, deeper diversification rate tests should be performed.

Ultimately, several different geographic areas still remains *terra incognita* as far as *Fomitiporia* is concerned. The Russian federation, the Pacific islands, including New Guinea, New Caledonia, Fiji, Hawaii, and the smaller islands of Melanesia, Micronesia, and Polynesia, as well as the Atlantic islands (Ascension island, St. Helena, Trinidad, the Saint Peter and Saint Paul archipelago), are rather unexplored from a mycological point of view. The large equatorial rainforest of Asia, and perhaps more importantly the mountain range in Borneo, are also unexplored as far as *Fomitiporia* is concerned and molecular data that could place the specimens originating from these countries in a phylogenetic study are still few.

Furthermore, an integrating « holistic » approach has never been applied to the several complex of species spanning over both sides of the

Mediterranean areas, as for example the *F. erecta* / *F. juniperina* / *P. rosmarini* complex.

LITERATURE CITED

Allen MB and Armstrong H.A. 2008. Arabia–Eurasia collision and the forcing of mid-Cenozoic global cooling. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 26, 52–58.

Adams RP, Demeke T, Abulfatih HA. 1993. RAPD DNA fingerprints and terpenoids: clues to past migrations of *Juniperus* in Arabia and east Africa. *Theor Appl Gen* 87:22–26.

Amalfi M, Yombiyeni P, Decock C. 2010. *Fomitiporia* in sub-Saharan Africa: morphology and multigene phylogenetic analysis support three new species from the Guineo-Congolian rainforest. *Mycologia* 102:1303–1317.

———, Raymundo T, Valenzuela R, Decock C 2012. Multilocus phylogenetic analyses (and host relationships) support the recognition of *Fomitiporia cupressicola* sp. nov., parasites on *Cupressus arizonica*, and evidence additional unnamed clades in southern USA and northern Mexico. *Mycologia* 104: 880–893.

———, Decock C. 2013. *Fomitiporia castilloi* sp. nov., and multiples clades around *F. apiahyna* in Meso- and South America evidenced by multiloci phylogenetic inferences. *Mycologia* 2013 Jul-Aug;105(4):873-87. doi: 10.3852/11-423.

———, and Decock C. 2014. *Fomitiporia expansa*, an Undescribed Species from French Guiana. *Cryptogamie, Mycologie* 35(1):73-85. 2014. doi: <http://dx.doi.org/10.7872/crym.v35.iss1.2014.73>

———, Robledo G, Decock C. 2014. *Fomitiporia baccharidis* comb. nov., a little known species from high elevation Andean forests and its affinities within the

neotropical *Fomitiporia* lineages. *Mycological Progress* 06/2014; 13(4). DOI:10.1007/s11557-014-0995-x

Ashworth, AC and Cantrill DJ. 2004. Neogene vegetation of the Meyer Desert Formation (Sirius Group) Transantarctic Mountains, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 213, 65—82.

Assefa A, Ehrich D, Taberlet P, Nemomissa S , Brochmann C. 2007. Pleistocene colonization of afro-alpine 'sky islands' by the arctic-alpine *Arabis alpina*. *Heredity* 99: 133-142.

Baldauf S, Palmer J. 1993. Animals and fungi are each other's closest relatives—congruent evidence from multiple proteins. *Proc Natl Acad Sci USA* 90: 11558–11562, doi:10.1073/pnas.90.24.11558

Barker PF, Filippelli GM, Florindo F, Martin EE, Scher H D. 2007. Onset and Role of the Antarctic Circumpolar Current. *Deep Sea Research Part II: Topical Studies in Oceanography* 54 (21): 2388–2398. doi:10.1016/j.dsr2.2007.07.028.

Bacon CD, Baker WJ, Simmons M.P. 2012. Miocene dispersal drives island radiations in the palm tribe Trachycarpeae (Arecaceae). *Systematic Biology*, 61, 426–442.

Bernicchia A. 1990. Polyporaceae *s.l.* in Italia. Istituto di Patologia Vegetale, Bologna, Italy:1–808.

———. 2005. *Polyporaceae s.l.* in Italia. *Fungi Europaei*, ed. Candusso, Italy:1–808.

Berry PE, Hahn W J, Sytsma KJ, Hall JC, Mast A. 2004. Phylogenetic relationships and biogeography of *Fuchsia* (Onagraceae) based on non coding nuclear and chloroplast DNA data. *Am.J.Bot.* 91, 601–614.doi:

10.3732/ajb.91.4.601

Bibi F. 2011. Mio-Pliocene faunal exchanges and African biogeography: the record of fossil bovids. PLoS ONE, 6, e16688.

Binder, M., K. H. Larsson, P. B. Matheny, and D. S. Hibbett. 2010. Amylocorticiales ord. nov. and Jaapiiales ord. nov.: Early diverging clades of Agaricomycetidae dominated by corticioid forms. Mycologia, 102: 865-880

Bleeker W, Weber-Sporenberg C, Hurka H. 2002. Chloroplast DNA variation and Biogeography in the genus *Rorippa* Scop. (Brassicaceae). *Plant Biology*, 4:104–111.

Bouchenak-Khelladi Y, Verboom GA, Savolainen V, and Hodkinson T.R. 2010. Biogeography of the grasses (Poaceae): a phylogenetic approach to reveal evolutionary history in geographical space and geological time. *Botanical Journal of the Linnean Society* 162:543-557.

Bondartsev, A. 1953. The Polyporaceae of the European part of USSR and of Caucasia, Akad. Nauk. SSSR, Leningrad 1106 pp.

Brandley MC, Schmitz A, Reeder TW. 2005. Partitioned Bayesian analyses, partition choice, and the phylogenetic relationships of scincid lizards. *Syst Biol.* 54:373–390.

Brown JM, Lemmon AR. 2007. The importance of data partitioning and the utility of Bayes factors in Bayesian phylogenetics. *Syst Biol.* 56:643–655.

Buchanan PK, Ryvarden L. 1993. Type studies in the Polyporaceae 24. Species described by Cleland, Rodway and Cheel. *Aust Syst Bot* 6:215–235.

Cabrera R.I., Decock C., Herrera S., Ferrer J., Ortega I., Lopes S.A., Zamora V. 2014. First report of the fungus *Fomitiporia maxonii* Murrill causing Citrus wood rot in commercial orange and grapefruit groves in Cuba. *Crop Protection* 58: 67-72.

Castresana J, 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Mol Bio Evol* 17: 540–552.

Cloete M, Fischer M, Mostert L, Halleen F. 2013. A novel *Fomitiporia* species associated with esca on grapevine in South Africa. *Mycol Prog.* doi:10.1007/s11557-013-0915-5

Coelho G, Silveira RMB, Guerrero RT, Rajchenberg, M. 2009. On poroid Hymenochaetales growing on bamboos in southern Brazil and NE Argentina. *Fungal Diversity* 36: 1-8

Corner, E. J. H. 1991. Ad Polyporaceas. VII. Thexanthochroic polypores. *Beih Nova Hedwia*, Heft 101:1-175.

Couvreur T L P, Pirie M D, Chatrou L W, Saunders, R M K , Su Y C F , Richardson JE, Erkens R.H.J. 2011. Early evolutionary history of the flowering plant family Annonaceae: steady diversification and boreotropical geodispersal. *Journal of Biogeography*, 38, 664–680.

Cunningham GH. 1965. Polyporaceae of New Zealand. New Zealand Department of Science and Industrial Research Bulletin 164.

Cui BK, Dai YC. 2008. Wood-rotting in eastern China 2. A new species of *Fomitiporia* from Wanmulin Nature Reserve, Fujian Province. *Mycotaxon* 105:343–348.

de Campos Santana M, Amalfi M, Robledo G, Borges da Silveira RM, Decock C. 2013. *Fomitiporia neotropica*, a new species from South America evidenced by multilocus phylogenetic analyses. *Mycological Progress (Impact Factor: 1.61)*. 11/2013; DOI:10.1007/s11557-013-0943-1

Dai Y-C. 2010. Hymenochaetaceae (Basidiomycota) in China. *Fungal Diversity* 45:131–343.

———, Zhang M, Zhou T-S. 2001. New and noteworthy species of Hymenochaetaceae from China. *Mycosystema* 20:16–21

———, Cui BK. 2005. Two new species of the Hymenochaetaceae from eastern China. *Mycotaxon* 94:341–347.

———, Cui BK, Yuan HS, Li B.D. 2007. Pathogenic wood-decaying fungi in China. *For Pathol* 27:105–120

———, Cui B-K, Decock C. 2008. A new species of *Fomitiporia* (Hymenochaetaceae, Basidiomycota) from China. *Mycol Res* 112: 375–380.

———, Zang M. 2002. *Fomitiporia tibetica*, a new species of Hymenochaetaceae. *Mycotaxon* 83:217–222.

David A, Dequatre B, Fiasson JL. 1982. Two new *Phellinus* with globose, cyanophilous spores. *Mycotaxon* 14:160–174.

Decock C, Bitew A, Castillo G. 2005. *Fomitiporia tenuis* and *Fomitiporia aethiopica* (Basidiomycetes, Hymenochaetales), two undescribed species from the Ethiopian highlands:

taxonomy and phylogeny. *Mycologia* 97:121–129.

———, Herrera Figueroa S, Robledo G, Castillo G. 2007. *Fomitiporia punctata* (Basidiomycota, Hymenochaetales) and its presumed taxonomic synonyms in America: taxonomy and phylogeny of some species from tropical/subtropical areas. *Mycologia* 99:733–752.

Dentinger B T M, Margaritescu S, and Moncalvo J.-M. 2010. Rapid and reliable high-throughput methods of DNA extraction for use in barcoding and molecular systematics of mushrooms. *Molecular Ecology Resources* 10: 628–633.

Degreef J, Fischer E, Sharp C, Raspé O. 2009. African *Morchella crassipes* revealed by analysis of nrDNA ITS. *Nova Hedwigia* 88: 11-22

Dick CW, Abdul-Salim K, Bermingham E. 2003. Molecular systematics analysis reveals cryptic Tertiary diversification of a widespread tropical rain forest tree. *Am Nat* 162:691–703.

———, Bermingham E, MR Lemes, Gribel R. 2007. Extreme long-distance dispersal of the lowland tropical rainforest tree *Ceiba Pentandra* L. (Malvaceae) in Africa and the Neotropics. *Mol Ecol* 16:3039–3049.

Domański S, Orlos SH, Skirgiello A. 1967. Grzyby (Zagwiowate II, Szczeciniakowate II). - Państwowe Wydawnictwo Naukowe, 395 pp. (1973 - Fungi: Polyporaceae II (pileatae), Mucronoporaceae II (pilaetae) - U.S. Dep. Commerce, Springfield, 332 pp.)

Douanla-Meli C. 2007. Fungi of Cameroon. Ecological diversity with emphasis on the taxonomy of non-gilled Hymenomycetes from the Mbalmayo Forest Reserve. *Biblioth Mycol* 202:1–410.

Drummond AJ, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7, 214

Duffield J. 1982. Forest regions of North America. In: introduction to forest science, John Wiley & Sons.

Edgar RC, Batzoglou S. 2006. Multiple sequence alignment. *Curr Opin Struct Biol.* 16: 368–373.

Elena K., Fischer M., Dimou D., Dimou D.M., 2006. *Fomitiporia mediterranea* infecting citrus trees in Greece. *PhytopathologiaMediterranea* 45: 35–39. Canadian Journal of Botany, 1983, Vol. 61, N° 2 : pages 442-451.

Erkens RHJ, Cross H, Maas JW, Hoenselaar K, Chatrou LW. 2008. Assessment of age and greenness of herbarium specimens as predictors for successful extraction and amplification of DNA. *Blumea* 53: 407–428.

Farris JS. 1988. Hennig86, version 1.5. Program and documentation. Port Jefferson Station (NY): Distributed by the Author.

———, Kallersjö M, Kluge AG, Bult C. 1994. Testing the significance of incongruence. *Cladistics.* 10: 315–319.

Fiasson JL. 1983. Contribution synthétique à la taxinomie phylétique des Hyménochaetacées porées d'Europe, spécialement du genre *Phellinus*. Thèse 83, Université Claude Bernard Lyon I:1–73.

Fiasson J-L, David A. 1984. Approche taximétrique des hyménochétacées porées d'Europe (champignons, aphylophorales). *Can J Bot* 61: 442–451. (doi: 10.1139/b83-051)

———, Niemelä T. 1984. The Hymenochaetales: a revision of the European poroid taxa. *Karstenia* 24:14–28.

Fischer M. 2002. A new wood-decaying Basidiomycetes species associated with esca of grapevine: *Fomitiporia mediterranea* (Hymenochaetales). Mycol Progress 1: 315–324.

———. 2006. Biodiversity and geographic distribution of Basidiomycetes causing esca-associates white rot in grapevine: a worldwide perspective. Phytopath Mediterr 45:S30–S42.

———, Binder M. 2004. Species recognition, geographic distribution, and host-pathogen relationships: a case study in a group of lignicolous Basidiomycetes, *Phellinus s.l.* Mycologia 96:799–811.

———, Edwards J, Cunnington JH, Pascoe IG. 2005. Basidiomycetous pathogens on grapevine: a new species from Australia – *Fomitiporia australiensis*. Mycotaxon 92:85–96.

Filipowicz N, Renner SS. 2012. Brunfelsia (Solanaceae) : a genus evenly divided between South America and radiations on Cuba and other Antillean islands. Mol. Phylogenet. Evol. 64, 1–11.doi:10.1016/j.ympev.2012.02.026

Fordyce, J. A. 2010. Host shifts and evolutionary radiations of butterflies. Proc. R. Soc. B-Biol. Sci. 277:3735–3743.

Francis, J.E., Ashworth, A., Cantrill, D.J., Crame, J.A., Howe, J., Stephens, R., Tosolini, A-M. and Thorn, V. 2008a. 100 million years of Antarctic climate evolution: evidence from fossil plants. In: Cooper AK, Barrett PJ, Stagg H, Storey B, Stump E, Wise W (eds) Antarctica: A Keystone in a Changing World. Proceedings of the 10th International Symposium on Antarctic Earth Sciences. The National Academies Press, Washington, DC, 19-27.

Frøslev TG, Matheny PB, Hibbett DS (2005). Lower level relationships in the mushroom genus *Cortinarius* (Basidiomycota, Agaricales): a comparison of RPB1, RPB2, and ITS phylogenies. *Molecular Phylogenetics and Evolution* 37: 602–618.

Futuyma DJ, Mayer GC. 1980. Non-allopatric speciation in animals. *Syst. Zool.* 29: 254-71.

Gehrke B, Linder H.P. 2009. The scramble for Africa: pan-temperate elements on the African high mountains. *Proceedings of the Royal Society, B-Biological Sciences* 276: 2657-2665.

Geml J, Timling I, Robinson C H, Lennon N, Nusbaum HC, Brochman C, Noordeloos ME, Taylor D.L. 2012. An arctic community of symbiotic fungi assembled by long-distance dispersers: phylogenetic diversity of ectomycorrhizal basidiomycetes in Svalbard based on soil and sporocarp DNA. *Journal of Biogeography*, 39, 74–88.

Gilbert SG, Ferrer A, Carranza J. 2002. Polypore fungal diversity and host density in a moist tropical forest. *Biodivers Conserv* 11:947–957.

Gilbertson R. L. 1979. *Phellinus* (Aphylllophorales: Hymenochaetaceae) in western North America. *Mycotaxon* 9:51-89.

Gilbertson RL, Ryvarden L. 1987. North American Polypores. Part 2. *Megasporoporia – Wrightoporia*. Fungiflora, Oslo, Norway: 433–885.

Givnish TJ, KC Millam, TM Evans, JC Hall, JC Pires, PE Berry, Sytsma KJ . 2004. Ancient vicariance or recent long-distance dispersal? inferences about phylogeny and South American–African disjunctions in *Rapateaceae* and *Bromeliaceae* based on *ndhF* sequence data. *Int J Plant Sci* 165:S35–S54.

Glass, NL, Donaldson G. 1995. Development of primer sets designed for use with the PCR to amplify conserved genes from filamentous ascomycetes. *Applied & Environmental Microbiology* 61:1323-1330.

Goloboff PA. 1994. Nona: A Tree-searching program. Program and documentation [Internet]. Available from: <http://www.zmuc.dk/public/phylogeny/Nona-PeeWee>. Published by the author, Tucuman, Argentina.

———. 1999. Analyzing large datasets in reasonable times: solutions for composite optima. *Cladistics*. 15:415–428.

———, Farris J, Nixon K. 2003. T.N.T.: Tree Analysis Using New Technology. Program and documentation [Internet]. Available from: <http://www.zmuc.dk/public/phylogeny/tnt>.

———, Pol D. 2007. On divide-and-conquer strategies for parsimony analysis of large data sets: rec-I-dcm3 vs TNT. *Syst Biol*. 56:485–495.

———, Farris JS, Nixon KC. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*. 24:774–786. Golubchik T, Wise MJ, Eastal S, Jermin LS. 2007.

González, V., Tuset, J.J., Hinarejos, R., 2006. Hongos asociados a la podredumbre del leño (caries) de los cítricos. II. *Levante Agrícola* 45(379), 50-54.

Härkönen M, Niemelä T, Mwasumbi L. 2003. Tanzanian mushroom – edible, harmful, and other fungi. Botanical Museum, Finnish Museum of Natural History, Helsinki, Finland:1–200.

Harmsen, M.C., F.H. Schuren, S.M. Moukha, C.M. van Zuilen, P.J. Punt, and J.G. Wessels. 1992. Sequence analysis of the glyceraldehyde-3-phosphate dehydrogenase genes from the basidiomycetes *Schizophyllum commune*, *Phanerochaete chrysosporium* and *Agaricus bisporus*. *Curr. Genet.* 22, 447-454.

Harris SA. 1993. DNA analysis of tropical plant species: an assessment of different drying methods. *Plant Syst Evol* 188: 57–64.

Hedberg O. 1969. Evolution and speciation in a tropical high mountain flora. *Botanical Journal of the Linnean Society*, 1:135–148.

———. 1970. Evolution of the afroalpine flora. *Biotropica*, 2 :16–23.

———. 1986. Origins of the Afroalpine flora. In: *High Altitude Tropical Biogeography*. Oxford University Press, New York and Oxford : 443–468.

Hennebert G.L., Sutton B.C. 1994. Unitary parameters in conidiogenesis. In D.L. Hawksworth ed. *Ascomycetes Systematics: problems and perspectives in the nineties*. Plenum Press, New York. 65–76.

Hill RS, and Scriven, LJ. 1995. The angiosperm-dominated woody vegetation of Antarctica: a review. *Review of Palaeobotany and Palynology*, 86: 175-198.

Hodkinson TR, Chonghaile GN, Sungkaew S, Chase MW, Salamin N, Stapleton C.M.A. 2010. Phylogenetic analyses of plastid and nuclear DNA sequences indicate a rapid late Miocene radiation of the temperate bamboo tribe *Arundinarieae* (Poaceae, Bambusoideae), *Plant Ecology & Diversity*, 3:2, 109-120

Holmgren P, Holmgren NL, Barnett LC. 1990. *Index herbariorum*. Part I: The herbaria of the world. New York Botanical Garden, New York:1–693.

Houle A. 1998. Floating islands: a mode of long-distance dispersal for small and medium-sized terrestrial vertebrates. *Divers Distrib* 4: 201–216.

———. 1999. The origin of platyrrhines: an evaluation of the Antarctic scenario and the floating island model. *Am J Phys Anthropol* 109:541–559.

Ipulet P. 2007. Ecology and Diversity of Pore Fungi (Aphyllophorales) in Bwindi Impenetrable and Kibale National Parks, Albertine Rift, Western Uganda [Doctoral dissertation]. Makerere University, Kampala, Uganda.

Irestedt M, Gelang M, Sangster G, Olsson U, Ericson PGP, Alström P. 2011. Neumann's Warbler *Hemitesia neumanni* (Sylvioidea): the sole African member of a Palaeotropical Miocene avifauna. *Ibis*, 153, 78–86.

Jeffroy O, Brinkmann H, Delsuc F, Philippe H. 2006. Phylogenomics: the beginning of incongruence? *Trends Genet* 22:225-231

Katoh K, Kuma K, Toh H, Miyata T. 2005. MAFFT version 5: improvement in accuracy of multiple sequence alignment. *Nucleic Acids Res.* 33: 511–518.

———, Misawa K, Kuma K, Miyata T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Res.* 30: 3059–3066.

Kauff, F., Lutzoni, F. 2002. Phylogeny of the Gyalectales and Ostropales (Ascomycota, Fungi): among and within order relationships based on nuclear ribosomal RNA small and large subunits. *Mol. Phyl. Evol.* 25: 138-156

Kauserud H, Svegården IB, Saetre G-P, Knudsen H, Stensrud Ø, Schmidt O, Doi S, Sugiyama T, Högborg N. 2007. Asian origin and rapid global spread of the destructive dry rot fungus *Serpula lacrymans*. *Molecular Ecology*, **16**:3350-3360.

Kawakita A, Sota T, Ascher JS, Ito M, Tanaka H, Kato M. 2003. Evolution and phylogenetic utility of alignment gaps within intron sequences of three nuclear genes in bumble bees (*Bombus*). *Mol Biol Evol.* 20:87–92.

Kerfoot O. 1975. Origin and speciation of the Cupressaceae in Sub-Saharan Africa. *Boissiera* 24:145–614.

Kimura M. 1983. *The Neutral Theory of Molecular Evolution*. New York: Cambridge University Press: 367.

Kingdon J. 1989. *Island Africa: The evolution of Africa's rare animals and plants*. Princeton University Press. Princeton, NJ, USA.

Kirk PM, Cannon PF, David JC, Stalpers JA. 2001. *Ainsworth & Bisby's Dictionary of the Fungi*, 9th edition. CABI Publishing, Wallingford, UK:1–655.

Koch M, Kiefer C, Ehrich D, Vogel J, Brochmann C, Mummenhoff K. 2006. Three times out of Asia 620 Minor: the phylogeography of *Arabis alpina* L (Brassicaceae). *Mol Ecol* 15:825– 839.

Kodandaramaiah U, Wahlberg N. 2007. Out-of-Africa origin and dispersal-mediated diversification of the butterfly genus *Junonia* (Nymphalidae: Nymphalinae). *Journal of Evolutionary Biology*, 20, 2181–2191.

Kornerup A, Wanscher JH. 1981. *Methuen handbook of color*, 3rd Edition:1–282.

Kosakovsky Pond, S. L., S. D. Frost, and S. V. Muse. 2005. HyPhy: hypothesis testing using phylogenies. *Bioinformatics* 21:676–679.

Kreuzinger N, Podeu R, Gruber F, Göbl F, Kubicek CP., 1996. Identification of some ectomycorrhizal basidiomycetes by PCR amplification of their *gpd* (Glyceraldehyde-3-Phosphate Dehydrogenase) genes. *Appl Environ Microbiol* 62:3432-3438.

Lafontaine JD, Wood DM. 1988. A zoogeographic analysis of the Noctuidae (Lepidoptera) of Beringia, and some inferences about past Beringian habitat. *Memoirs of the Entomological Society of Canada* 144:109–123

Lanfear R, Calcott B, Ho SYW, Guindon S. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29 (6): 1695-1701.

Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, et al. 2007. Clustal W and Clustal X version 2.0. *Bioinformatics*. 23: 2947–2948.

Larsen MJ, Cobb-Poulsen LA. 1990. *Phellinus* (Hymenochaetaceae). *Synopsis Fungorum* 3, Oslo, Norway: Fungiflora:1–206.

Larsson K-H, Parmasto E, Fischer M, Langer E, Nakasone KK, Redhead SA. 2006. Hymenochaetales: a molecular phylogeny for the hymenochaetoid clade. *Mycologia* 98: 926–936

Lassmann T, Sonnhammer ELL. 2002. Quality assessment of multiple alignment programs. *FEBS Lett*. 529:126–130.

Lavin M, BP Schrire, G Lewis, RT Pennington, A Delgado-Salinas, MThulin, CE Hughes, AB Maros, Wojciechowski MF. 2004. Meta-community process rather than continental tectonic history better explains geographically structured phylogenies in legumes. *PhilosTrans R Soc B* 359:1509–1522.

Lewis PO. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Syst Biol.* 50: 913–925.

Liu YL, Whelen S, Hall BD. 1999. Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. *Molecular Biology and Evolution* 16: 1799-1808.

Liu YJ, Hall BD. 2004. Body plan evolution of ascomycetes, as inferred from an RNA polymerase II phylogeny. *Proc Natl Acad Sci USA* 101(13):4507–4512, doi:10.1073/pnas.0400938101

Livingstone D.A. 1993. Evolution of African climate. In: *Biological Relationships Between Africa and South America* (ed. Goldblatt P), Yale University Press, New Haven, Connecticut : 455–472.

Loguercio Leite C, Wright JE 1991. Contribution to a biogeographical study of the austro-american xylophilous polypores (Aphyllorphorales) from Santa Catarina, SC, Brazil. *Mycotaxon* 41:161–166.

Lowe JL. 1957. Polyporaceae of North America. The genus *Fomes*. Syracuse, New York: State University College of Forestry, Syracuse University. 97 p.

Lutzoni F, Kauff F, Cox CJ, McLaughlin D, Celio G, Dentinger B, Padamsee M, Hibbett D, James TY, Baloch E, Grube M, Reeb V, Hofstetter V, Schoch C, Arnold AE, Miadlikowska J, Spatafora J, Johnson D, Hambleton S, Crockett M,

Shoemaker R, Sung G-H, Lücking R, Lumbsch T, O'Donnell K, Binder M, Diederich P, Ertz D, Gueidan C, Hansen K, Harris RC, Hosada K, Lim Y-W, Matheny B, Nishida H, Pfister D, Rogers J, Rossman A, Schmitt I, Sipman H, Stone J, Sugiyama J, Yahr R, Vilgalys R. 2004. Assembling the fungal tree of life: progress, classification, and evolution of subcellular traits. *Am J Bot* 91: 1446–1480.

Maddison D, Maddison W 2000 *MacClade 4.0*. Analysis of phylogeny and character evolution. Sunderland, MA: Sinauer Associates.

Marquinez X, Lohmann L G, Salatino M L F , Salatino A, González F. 2009. Generic relationships and dating of lineages in Winteraceae based on nuclear (ITS) and plastid (rps16 and psbA-trnH) sequence data. *Mol. Phylogenet. Evol.* 53, 435–449. doi:10.1016/j.ympev.2009.07.001

Mason-Gamer RJ, Kellogg EA. 1996 Testing for phylogenetic conflict among molecular data sets in the tribe Triticeae (Gramineae). *Syst Biol* 45:524–545.

Matheny PB. 2005. Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*, Agaricales). *Molecular Phylogenetics and Evolution* 35: 1–20.

———, Wang Z, Binder M, Curtis JM, Lim YW, Nilsson RH, Hughes KW, Petersen RH, Hofstetter V, Ammirati JF, Schoch C, Langer GE, McLaughlin DJ, Wilson AW, Crane PE, Frøslev T, Ge ZW, Kerrigan RW, Slot JC, Vellinga EC, Liang ZL, Aime MC, Baroni TJ, Fischer M, Hosaka K, Matsuura K, Seidl MT, Vaura J, Hibbett DS. 2007. Contributions of *rpb2* and *tefl* to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Mol Phyl Evol* 43:430–451.

———, Aime MC, Bougler NL, Buyck B, Desjardin DE, Horak E, Kropp BR, Lodge DJ, Soyong

K, Trappe JM, Hibbett D.S. 2009. Out of the Palaeotropics? Historical biogeography and diversification of the cosmopolitan ectomycorrhizal mushroom family Inocybaceae. *Journal of Biogeography*, 36, 577–592.

Mayr E. 1963. *Animal Species and Evolution*. Cambridge, Mass.: Belknap Press. 811 pp.

McGlone, M. S. 2006: Becoming New Zealanders : immigration and the formation of the biota. In: Allen, R. B.; Lee, W. G. eds. *Biological invasions in New Zealand*. Ecological Studies 168. Berlin, Springer. Pp. 17-32.

McLoughlin S. The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany*. 2001;49:271–300.

Moncalvo JM, Buchanan P.K. 2008. Molecular evidence for long distance dispersal across the Southern Hemisphere in the *Ganoderma applanatum-australe* species complex (Basidiomycota). *Mycological Research* 112: 425-436.

Moreau R.E. 1963. Vicissitudes of the African biomes in the late Pleistocene. *Proceedings of the Zoological Society of London*, **141**, 395–421.

Morgenstern B. 2004. DIALIGN: multiple DNA and protein sequence alignment at BiBiServ. *Nucleic Acids Res.* 32: W33–W36.

Morley R. J. 2000. *Origin and evolution of tropical rain forests*. Chichester, UK: John Wiley & Sons.

———. 2003. Interplate dispersal paths for megathermal angiosperms. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 5–20.

Müller K. 2005. SeqState—primer design and sequence statistics for phylogenetic DNA data sets, *Applied Bioinformatics* 4:65–69.

Mummenhoff K, Franzke A. 2007. Gone with the bird: late Tertiary and Quaternary intercontinental long-distance dispersal and allopolyploidization in plants. *Systematics and Biodiversity* 5(03):255-260

Murrill WA. 1903. The Polyporaceae of North America II. The genus *Pyropolyporus*. *Bull Torrey Bot Club* 30: 109–120.

Murrill, W. A. 1907. Polyporaceae. *North American Flora* 9:1-72.

Murrill, W. A. 1912. The Polyporaceae of Mexico. *Bulletin. New York Botanical Garden* 8:137-153.

Notredame C, Higgins DG, Heringa J. 2000. T-Coffee: a novel method for fast and accurate multiple sequence alignment. *J Mol Biol.* 302: 205–217.

Nuin PAS, Wang Z, Tillier ERM. 2006. The accuracy of several multiple sequence alignment programs for proteins. *BMC Bioinformatics.* 7:471.

Núñez M, Daniëls PP. 1999. Fungi from the Dja Biosphere reserve (Cameroon) II. Polypores. *Mycotaxon* 73:235–246.

Núñez M, Ryvarden L. 2000. East Asian Polypores. Vol. 1. *Ganodermataceae and Hymenochaetaceae. Fungiflora, Oslo, Norway:* 1–168.

Nuss I. 1986. *Bibliotheca Mycol.* **105**: 108

Nylander JAA, Ronquist F, Huelsenbeck JP, Nieves-Aldrey J. 2004. Bayesian phylogenetic analysis of combined data. *Syst Biol.* 53:47–67.

O'Donnell K, Lutzoni FM, Ward TJ, Benny GL. 2001. Evolutionary relationships among mucoralean fungi (Zygomycota): evidence for family polyphyly on a large scale. *Mycologia* 93:286–296, doi:10.2307/3761650

Ogden TH, Rosenberg MS. 2007a. Alignment and topological accuracy of the direct optimization approach via POY and traditional phylogenetics via ClustalW + PAUP*. *Syst Biol*. 56: 182–193.

Ogden TH, Rosenberg MS. 2007b. How should gaps be treated in parsimony? A comparison of approaches using simulation. *Mol Phylogenet Evol*. 42: 817–826.

Ohta T. 1992. The nearly neutral theory of molecular evolution. *Annu Rev Ecol Syst*. 23:263–286.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., Kassem, K. R. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* 51(11):933-938.

Ota Y, Hattori T, Nakamura H, Terashima Y, Lee SS, Miyuki Y, Sotome K. 2014. Taxonomy and phylogenetic position of *Fomitiporia torreyae*, a causal agent of trunk rot on Sanbu-sugi, a cultivar of Japanese cedar (*Cryptomeria japonica*) in Japan. *Mycologia*.;106(1):66-76. doi: 10.3852/13-045.

Patouillard N. 1891. *Polyporus bambusinus*, nouveau polypore conidifère. *Bull Soc Mycol Fr* 7: 101–103.

Patouillard, N. 1900. Essai taxonomique sur les familles et les genres des Hyménomycètes. :1-184

Pennington RT, Dick CW. 2004. The role of immigrants in the assembly of the South American rainforest tree flora. *Philos TransR Soc B* 359:1611–1622.

Pyle MM, Adams RP. 1989. In situ preservation of DNA in plant specimens. *Taxon* 38: 576–581.

Pieri M, Rivoire B. 2000. Le genre *Phellinus*. Quelques espèces rares ou critiques en France, avec une clé des espèces du genre *Phellinus s.l.* signalées en Europe occidentale. *Bull Soc Mycol Fr.* 116:305–331.

Pilotti M., Tizzani L., Brunetti A., Gervasi F., Di Lernia G., Lumia V. 2010. Molecular identification of *Fomitiporia mediterranea* on declining and decayed hazelnut. *Journal of Plant Pathology.* 92 (1), 115–129.

Pitman NGA, Terborgh JW, Silman MR, Nunez P, Neill DA, Ceron CE, Palacios WA, Aulestia M. 2002. A comparison of tree species diversity in two upper Amazon forest. *Ecology* 83 :3210–3224.

Posada D, Crandall KA. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817–818.

Potter PE and Szatmari P. 2009. Global Miocene tectonics and the modern world. *Earth-Science Reviews*, 96, 279–295.

Pringle A, Bever J D, Gardes M, Parrent JL, Rillig MC and Klironomos, J.N. 2009. Mycorrhizal symbioses and plant invasions. *Annual Reviews in Ecology, Evolution, and Systematics*, 40, 699–715.

Puillandre N., Modica M. V., Zhang Y., Sirovich L., Boisselier M.C., Cruaud C., Holford M. & Samadi S. 2012. Large-scale species delimitation method for hyperdiverse groups. *Molecular Ecology* 21: 2671-2691. DOI: 10.1111/j.1365-294X.2012.05559.x

Quaedvlieg W, Binder M, Groenewald JZ, Summerell BA, Carnegie AJ, Burgess TI, Crous PW. 2014. Introducing the Consolidated Species Concept to resolve species in the Teratosphaeriaceae. *Persoonia* 33:1–40.

Queloz V, Sieber TN, Holdenrieder O, McDonald BA, Grunig, C.R. 2011. No biogeographical pattern for a root-associated fungal species complex. *Global Ecology and Biogeography*, 20, 160–169.

Rajchenberg M. 1988. Xylophilous Aphyllophorales (Basidiomycetes) from the southern Andean forests. Additions and corrections. II. *Sydowia* 40:235–249.

———, De Meijer AR. 1990. New and noteworthy polypores from Paraná and São Paulo States, Brazil. *Mycotaxon* 38:173–185.

———, Wright JW. 1987. Type studies of Corticiaceae and Polyporaceae (Aphyllophorales) described by C. Spegazzini. *Mycologia* 79:246–264.

Rambaut A, Drummond AJ. 2007. Tracer v1.4, [<http://beast.bio.ed.ac.uk/Tracer>]

Ramos ME, Folguera A, Fennell L, Giménez M, Litvak VD, Dzierma Y, Ramos V.A. 2014. Tectonic evolution of the North Patagonian Andes from field and gravity data (39-40°S). *Journal of South American Earth Sciences* 51: 59-75.

Raymundo T., Decock C., Amalfi M., Valenzuela R., Cifuentes J., Pecheco-Mota L. 2012. New records of the genus *Fomitiporia* (Hymenochaetales, Basidiomycota) in Mexico. *Rev Mex Biodiv*: 83:313–328

Raven PH, DI Axelrod 1974 Angiosperm biogeography and past continental movements. *Ann Mo Bot Gard* 61:539–673.

Ree RH, Smith SA. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, 57, 4–14.

Reeb V, Lutzoni F, Roux C. 2004. Contribution of RPB2 to multilocus phylogenetic studies of the euascomycetes (Pezizomycotina, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory. *Mol Phyl Evol* 32:1036–1060.

Rehner SA, Buckley E. 2005. A *Beauveria* phylogeny inferred from nuclear ITS and EF1- α sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97:84–98

Renner SS, G Clausen, K Meyer. 2001. Historical biogeography of Melastomataceae: the roles of Tertiary migration and long-distancedispersal. *Am J Bot* 88:1290–1300.

Renvall P, Niemelä T. 1993. *Ocotea usambarensis* and its fungal decayers in natural stands. *Bull Jard Bot Nat* 62:403–414.

Robert V, Stegehuis G, Stalpers J. 2005. The MycoBank engine and related databases. <http://www.mycobank.org>.

Roberts TE, Sargis EJ, Olson LE. 2009. Networks, trees, and treeshrews: assessing support and identifying conflict with multiple loci and a problematic root. *Syst Biol*. 58:257–270.

Robledo G, Urcelay C, Rajchenberg M. 2003. New species causing decay on living *Polylepis australis* in Cordoba, central Argentina. *Mycologia*. 95(2):347-53.

Roger AJ, Sandbloom O, Doolittle WF, Philippe H. 1999. An evaluation of elongation factor 1 α as a phylogenetic marker for eukaryotes. *Mol Biol Evol* 16:218–233

Ronquist F, Huelsenbeck JP. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.

———, Huelsenbeck JP, Van der Mark P. 2005. MRBAYES 3.1 manual. In School of Computational Science, Florida State University 2005 Tallahassee, FL:School of Computational Science, Florida State University

———, M. Teslenko, P. van der Mark, D. Ayres, A. Darling, S. H $\ddot{o}$ hna, B. Larget, L. Liu, M. A. Suchard, and J. P. Huelsenbeck. 2011. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst Biol* 61:539-42. doi:10.1093/sysbio/sys029).

Ryvarden L. 1991. Genera of Polypores: Nomenclature and taxonomy. *Synopsis Fungorum* 5:1–363.

Ryvarden L. 1978. The Polyporaceae of North Europe. Volume 2 (*Inonotus* – *Tyromyces*). Oslo, Norway: Fungiflora: 219–507.

———. 1991. Genera of Polypores. Nomenclature and taxonomy. *Synopsis Fungorum* 5, Oslo, Norway: Fungiflora:1–363.

———. 2000. A critical checklist of African Polypores. In: Associazione Micologica Bresadola (ed), *Micologia duemila*. Fondazione Centro Studi Micologici dell A.M.B., Vicenza, Italy:471–483.

———. 2004. Neotropical Polypores 1. *Synopsis Fungorum* 19:1–229.

———, de Meijer AAR. 2002. Studies in Neotropical polypores 14. New species from the State of Paraná, Brazil. *Synopsis Fungorum* 15:34–69.

———, Gilbertson RL. 1994. European polypores 2. *Meripilus–Tyromyces*. *Synopsis Fungorum* 7, Oslo, Norway: Fungiflora: 392–743.

———, Johansen I, 1980. A preliminary polypores flora of East Africa. *Fungiflora*, Oslo, Norway:1–636.

Simmons MP, Ochoterena H. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Syst Biol* 49:369–381.

———, Pickett KM, Miya M. 2004. How meaningful are Bayesian support values? *Mol Biol Evol* 21:188–199.

Sanchez-Ramirez S, Tulloss ER, Amalfi M, Moncalvo J.M. 2015. Palaeotropical origins, boreotropical distribution and increased rates of diversification in a clade of edible ectomycorrhizal mushrooms (*Amanita* section *Caesareae*). *Journal of Biogeography*; 42(2):351-363. DOI:10.1111/jbi.12402

Schaefer H, Heibl C, Renner SS .2009. Gourds afloat: a dated phylogeny reveals an Asian origin of the gourd family (Cucurbitaceae) and numerous oversea dispersal events. *Proc R Soc B* 276:843–851

Schluter, D. 2000. The ecology of adaptive radiation. Oxford Univ. Press, New York, NY.

Smith J M B, Cleef A.M. 1988. Composition and origin of the world's tropical alpine floras. *Journal of Biogeography* 15: 631-645.

Spirin W.A., Zmitrovich I.V, Malysheva V.F. 2006. To the systematics of *Phellinus* s.l. and *Inonotus* s.l. (Mucronoporaceae, Hymenochaetales). *Novosti Sistematiki Nizshikh Rastenii*. 40:153-188

Staats M, Cuenca A, Richardson JE, Vrielink-van Ginkel R, Petersen G, et al. 2011. DNA damage in plant herbarium tissue. *PLoS ONE* 6: e28448.

Stamatakis A, Hoover P, Rougemont J. 2008. A rapid bootstrap algorithm for the RAxML Web-Servers. *Syst Biol* 57:758–771.

Stalpers JA. 2000. The genus *Ptychogaster*. *Karstenia* 40:167-180.

Swofford, D. L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Talavera G, Castresana J. 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Syst Biol*. 56: 564–577.

Taylor JW, Geiser DM, Jacobson DJ, Kroken S, Kasuga T, Geiser DM, Hibbett DS, Fisher MC., 2000 Phylogenetic species recognition and species concepts in fungi. *Fungal Genet Biol* 31:21-32

———, Turner, E., Pringle, A., Dettman, J., Johannesson, H., 2006a. Fungal species: thoughts on their recognition, maintenance and selection. In: Gadd, G.M., Watkinson, S.C., Dyer, P.S. (Eds.), *Fungi in the Environment*. pp. 313–339.

Thiers B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>.

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG. 1997. The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Res* 25:4876–4882.

Thorne F. 1994. Phytogeography of North America North of Mexico: in *Flora of North America: North of Mexico Volume 1: Introduction*. Ed. ed. Flora of North America Editorial Committee, St Louis.

Tiffney, B. H. 1985. The Eocene North Atlantic Land Bridge: Its importance in Tertiary and modern phytogeography of the Northern Hemisphere. *Journal of the Arnold Arboretum*, 66, 243–273.

Truswell E, Macphail M. 2009. Polar forests on the edge of extinction: what does the fossil spore and pollen evidence from East Antarctica say?, *Australian Systematic Botany*, 22 (2): 57-106.

Untereiner WA, Bonjean B, Decock C, Evrard P, de Frahan MH, Jamin N, Massart L, Nélissen L, Robert V, Bosschaerts M, Guissart F, De Brabandere J. 1998. *MUCL Catalogue of strains (Fungi-Yeast)*. 3^e Ed. Published by the Belgian Office for Scientific, technical and Cultural Affairs, Brussels, Belgium.

Urcelay C, Robledo G, Rajchenberg M. 2000. *Phellinus tabaquilio* sp. nov. from Córdoba mountains, Central Argentina. *Mycotaxon* 76:287–291.

Vandeweghe JP. 2005. Akanda et Pongara. Plages et mangroves. Wildlife Conservation Society, Libreville:1–207.

———. 2006. Ivindo et Mwagna: Eaux noires, forêts vierges et baïes. Wildlife Conservation Society, Libreville:1–272.

Verbylaitė R, Beišys P, Rimas V, Kuusienė S. 2010. Comparison of Ten DNA Extraction. Protocols from Wood of European Aspen (*Populus tremula* L.). Baltic Forestry, 16 (1): 35-42.

Vlasák J, Kout J. 2011. Pileate *Fomitiporia* species in the USA. New combinations *Fomitiporia calkinsii* and *F. bakeri*. Mycol Progress 10: 445–452.

———, Kout J, Vlasák J Jr, Ryvarden L. 2011. New records of polypores from southern Florida. Mycotaxon 118:159–176.

Wagner T, Fischer M. 2001. Natural groups and a revised system for the European poroid Hymenochaetales (Basidiomycota) supported by nLSU rDNA sequence data. Mycol Res 105:773–782.

———, Fischer M. 2002. Proceedings towards a natural classification of the worldwide taxa *Phellinus* and *Inonotus s.l.*, and phylogenetic relationships of allied genera. Mycologia 94:998–1016.

Wallace IM, O'Sullivan O, Higgins DG, Notredame C. 2006. M-Coffee: combining multiple sequence alignment methods with T-Coffee. Nucleic Acids Res. 34: 1692–1699.

Wendland J, Kothe E. 1997. Isolation of *tefl* encoding translation elongation factor EF1a from the homobasidiomycete *Schizophyllum commune*. Mycol Res 101:798–802.

White F. 1979. The Guineo-Congolian region and its relationships to other Phytochoria. Bull J Bot Nat Belgique 49:1–384.

White, F. 1983. The vegetation of Africa, a descriptive memoir to accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa (3 Plates, Northwestern Africa, Northeastern Africa, and Southern Africa, 1:5,000,000). Unesco, Paris.

White T J, Bruns T, Lee S, Taylor JW 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR Protocols: A Guide to Methods and Applications* (M. A. Innis, D. H. Gelfand, J. J. Sninsky, & T. J. White, eds), Academic Press, New York: 315–322.

Wolfe JA. 1987. Late Cretaceous–Cenozoic history of deciduousness and the terminal Cretaceous event. Paleobiology 16: 215–226

Woolley LP, Henkel TW, Sillett SC. 2008. Reiteration in the monodominant tropical tree *Dicymbe corymbosa* (Caesalpinaceae) and its potential adaptive significance. Biotropica 40: 32–43

Wright JE, Blumenfeld SN. 1984. New South American species of *Phellinus* (Hymenochaetaceae). Mycotaxon 21:413–425.

———, Iaconis, CL. 1955. Estudios sobre Basidiomycetes. III. ‘*Polyporus rickii*’ f. sp. ‘*negundinis*’ sobre arces vivos. Rev. Invest. Agric. Buenos Aires 9 (2): 97-109

Yang ZH, Nielsen R, Goldman N, Pedersen A.M. 2000. Codon-substitution models for heterogeneous selection pressure at amino acid sites. *Genetics* 155:431–449.

Young ND, Healy J. 2003. GapCoder automates the use of indel characters in phylogenetic analysis. *BMC Bioinformatics*. 4:6.

Xia X, Xie Z. 2001. DAMBE: software package for data analysis in molecular biology and evolution. *J Hered* 92, 371–373.

———, Lemey, P., 2009. Assessing substitution saturation with DAMBE. In: Lemey, P. (Ed.), *The Phylogenetic Handbook*. Cambridge University Press, Cambridge, pp. 611–626.

———, Xie Z, Salemi M, Chen L, Wang,Y. 2003. An index of substitution saturation and its application. *Mol. Phylogenet. Evol.* 26, 1–7.

Zhang N, Blackwell M. 2002. Molecular phylogeny of *Melanospora* and similar pyrenomycetous fungi. *Mycol Res* 106:148–155, doi:10.1017/S0953756201005354

Zhou L-L, Su YCF, Thomas DC , Saunders R.M.K. 2011. ‘Out-of-Africa’ dispersal of tropical floras during the Miocene climatic optimum: evidence from *Uvaria* (Annonaceae). *Journal of Biogeography*, 39, 322–335.

Zhou LW, Xue HJ. 2012. *Fomitiporia pentaphylacis* and *F. tenuitubus* spp. nov. (Hymenochaetales, Basidiomycota) from Guangxi, southern China. *Mycol Progress*: DOI 10.1007/s11557-012-0806-1.

Zwickl DJ. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion (PhD dissertation). The University of Texas at Austin.

Annex I

Voucher specimens and sequences used in this study

Table 1. List of species, collections, and sequences used in the phylogenetic analyses.

Genus / Species names			GenBank accession number		
Voucher specimens / cultures reference					
Locality	nLSU	ITS	<i>tef1-α</i>	<i>rpb2</i>	
<i>Fomitiporia aethiopica</i> Decock, Bitew & G. Castillo					
MUCL 44777 (T) ^{c, h}	Ethiopia	AY618204	GU478341	GU461893	JQ087956
MUCL 44806 ^{c, h}	Ethiopia	AY618202	GU461944	GU461892	JQ087955
<i>F. apiahyna</i> (Speg.) Robledo, Decock & Rajchenb.					
MUCL 51451 ^{c, h}	Ecuador	GU461997	GU461963	GU461896	JQ087958
MUCL 51454 ^{c, h}	Ecuador	JX093812	JX093769	JX093725	JX093856
MUCL 51456 ^{c, h}	Ecuador	JX093813	JX093770	JX093726	JX093857
MUCL 51474 ^{c, h}	Ecuador	JX093814	GU461961	JX093727	JX093858
MUCL 51485 ^{c, h}	Ecuador	GU461996	GU461962	GU461895	JQ087957
MUCL 53022 ^{c, h}	French Guyana	JX093815	JX093771	JX093728	JX093859
MUCL 53041 ^{c, h}	French Guyana	JX093816	JX093772	JX093729	JX093860
MUCL 53042 ^{c, h}	French Guyana	JX093817	JX093773	JX093730	JX093861
MUCL 53047 ^{c, h}	French Guyana	JX093818	JX093774	JX093731	JX093862
MUCL 53071 ^{c, h}	French Guyana	JX093819	JX093775	JX093732	JX093863
MUCL 53135 ^{c, h}	French Guyana	JX093820	JX093776	JX093733	JX093864

MUCL 53145 ^{c, h}	French Guyana	JX093821	JX093777	JX093734	JX093865
MUCL 53149 ^{c, h}	French Guyana	JX093822	JX093778	JX093735	JX093866
MUCL 53156 ^{c, h}	French Guyana	JX093823	JX093779	JX093736	JX093867
MUCL 53711 ^{c, h}	French Guyana	JX093824	JX093780	JX093737	JX093868
MUCL 53988 ^{c, h}	French Guyana	JX093825	JX093781	JX093738	JX093869
MUCL 53989 ^{c, h}	French Guyana	JX093826	JX093782	JX093739	JX093870
MUCL 53990 ^{c, h}	French Guyana	JX093827	JX093783	JX093740	JX093871
MUCL 53991 ^{c, h}	French Guyana	JX093828	JX093784	JX093741	JX093872
MUCL 53726 ^{c, h}	French Guyana	JX093829	JX093785	JX093742	JX093873
MUCL 54407 ^{c, h}	French Guyana	This study	This study	This study	This study
MUCL 54408 ^{c, h}	French Guyana	This study	This study	This study	This study
MUCL FG-12-609	French Guyana	This study	This study	This study	This study
MUCL FG-12-537	French Guyana	This study	This study	This study	This study
<i>F. australiensis</i> Fischer, Edwards, Cunningt. & Pascoe					
VPRI 22451a PT (MUCL 49406) ^c	Australia	GU462001	AY624997	GU461897	JQ087959
VPRI22409b	Australia	This study	AY624995	This study	This study
<i>F. baccharidis</i> (Pat.) Decock et al.					
MUCL 47756 ^{c, h}	Argentina	JQ087913	JQ087886	JQ087940	JQ087993
MUCL 47757 ^{c, h}	Argentina	JQ087914	JQ087887	JQ087941	JQ087994

MUCL 47758 ^{c, h}	Argentina	JQ087915	JQ087888	JQ087942	JQ087995
<i>Fomitiporia bakeri</i> (Murrill) Vlasák & Kout					
FP-134784-Sp (MUCL 51098) ^{c, 1}	USA	JQ087901	JQ087874	JQ087928	JQ087960
<i>F. bannaensis</i> Y.C. Dai					
MUCL 45926 ^{c, h}	Thailand	EF429217	GU461942	GU461898	JQ087961
MUCL 46926 ^{c, h}	China	KF444705	KF444682	KF444751	KF444728
MUCL 46930 ^{c, h}	China	KF444706	KF444683	KF444752	KF444729
MUCL 46948 ^{c, h}	China	KF444707	KF444684	KF444753	KF444730
MUCL 46950 ^{c, h}	China	EF429218	GU461943	GU461899	JQ087962
<i>Fomitiporia calkinsii</i> (Murrill) Vlasák & Kout					
FP-106252-Sp (MUCL 51095) ^{c, 1}	USA	KF444708	KF444685	KF444754	KF444731
FP-53385-T (MUCL 51099) ^{c, 1}	USA	KF444709	KF444686	KF444755	KF444732
FP-71907-T (MUCL 51100) ^{c, 1}	USA	JQ087902	JQ087875	JQ087929	JQ087963
CBS 175.34 (MUCL 51398) ^{c, 1}	USA	KF444710	KF444687	KF444756	KF444733
MUCL 52346 ^{c, h}	Mexico	JQ087903	JQ087876	JQ087930	JQ087964
MA-MX0945 ^{c, h}	Mexico	KF444711	KF444688	KF444757	KF444734
<i>Fomitiporia capensis</i> M. Fisch. et al.					
MUCL 53009 ^{c, 5}	South Africa	JQ087917	JQ087890	JQ087944	JQ087997
<i>F. castilloi</i> Amalfi & Decock					

MUCL 53481 (T) ^{c, h}	French Guiana	JQ087916	JQ087889	JQ087943	JQ087996
MUCL 53980 (PT) ^{c, h}	French Guiana	JX093830	JX093786	JX093743	JX093874
MUCL FG-12-611	French Guyana	This study	This study	This study	This study
<i>F. cupressicola</i> Amalfi, Raymundo, Valenzuela et Decock					
MUCL 52486 (T) ^{c, h}	Mexico	JQ087904	JQ087877	JQ087931	JQ087965
MUCL 52488 ^{c, h}	Mexico	JQ087905	JQ087878	JQ087932	JQ087966
MUCL 52489 ^{c, h}	Mexico	JQ087906	JQ087879	JQ087933	JQ087967
MUCL 52490 ^{c, h}	Mexico	JQ087907	JQ087880	JQ087934	JQ087968
<i>F. dryophila</i> Murrill					
TJV-93-232 (MUCL 46379) ^{c, 1}	USA	EF429221	EF429240	GU461902	JQ087969
TJV-93-234 (MUCL 46380) ^{c, 1}	USA	EF429219	EF429238	GU461900	JQ087970
TJV-93-259 (MUCL 46381) ^{c, 1}	USA	EF429220	EF429239	GU461901	KF444735
FP-104030-T (MUCL 51144) ^{c, 1}	USA	KF444712	KF444689	KF444758	KF444736
<i>F. erecta</i> (A. David, Dequatre & Fiasson) Fiasson					
MUCL 49871 ^{c, h}	France	GU461976	GU461939	GU461903	JQ087971
MA-PA03 ^{c, h}	Italy	KF444713	KF444690	KF444759	-
<i>F. expansa</i> Decock & Amalfi					
MUCL 55026 (T) ^{c, h}	French Guiana	KJ401031	KJ401032	KJ401033	KJ401034
<i>F. gabonensis</i> Amalfi & Decock					

MUCL 47576 (T) ^{c, h}	Gabon	GU461990	GU461971	GU461923	JQ087972
MUCL 51291 ^{c, h}	Gabon	GU461986	GU461967	GU461924	JQ087973
MUCL 51302	Gabon	GU461988	GU461969	GU461925	this study
<i>Fomitiporia hartigii</i> (Allesch. & Schnabl) Fiasson & Niemelä					
MAFF 11-20016 (MUCL 31400) ^c	Japan	JQ087909	JQ087882	JQ087936	JQ087975
75-2 562 (MUCL 53549) ^{c, 4}	Estonia	JX093831	JX093787	JX093744	JX093875
71-25 464 (MUCL 53550) ^{c, 4}	Estonia	JX093832	JX093788	JX093745	JX093876
75-3 563 (MUCL 53551) ^{c, 4}	Estonia	JX093833	JX093789	JX093746	JX093877
CUI 9914	China	This study	This study	This study	This study
<i>F. hippophaeicola</i> (H. Jahn) Fiasson & Niemelä					
MUCL 31746 ^{c, h}	Belgium	AY618207	GU461945	GU461904	JQ087976
MUCL 31747 ^{c, h}	Belgium	GU461977	GU461946	GU461905	JQ087977
<i>F. ivindoensis</i> Decock, Amalfi & Yombiyeni					
MUCL 51311 ^{c, h}	Gabon	GU461979	GU461952	GU461907	JQ087978
MUCL 51312 (T) ^{c, h}	Gabon	GU461978	GU461951	GU461906	JQ087979
<i>Fomitiporia juniperina</i> Bernicchia & S. Curreli					
MUCL 51757 ^{c, h}	Tunisia	JQ087927	JQ087900	JQ087954	JQ088019
MA-PA01 ^{c, h}	Italy	KF444726	KF444703	KF444776	KF444749
MA-PA02 ^{c, h}	Italy	KF444727	KF444704	KF444777	KF444750

F. langloisii Murrill

FP-94347-R (MUCL 46375) ^{c, 1}	USA	EF429225	EF429242	GU461908	JQ087980
01-77/4 (MUCL 46165), (T of <i>F. hesleri</i>) ^{c, 5}	USA	EF429223	AY340026	GU461909	JQ087981
FP-105-816-T (MUCL 46373) ^{c, 1}	USA	EF429226	EF429243	KF444760	This study
HHB-9868-Sp (MUCL 46377) ^{c, 1}	USA	EF429224	EF429241	KF444761	This study
01-712/2 (MUCL 46164) ^{c, 5}	USA	EF429222	AY340031	KF444762	This study
FP-105818-R (MUCL 46374) ^{c, 1}	USA	EF429227	EF429244	KF444763	This study

F. maxonii Murrill

MUCL 46017 ^{c, h} (=CRGF 182)	Cuba	EF429230	EF433559	GU461910	JQ087983
MUCL 46037 ^{c, h} (=CRGF 183)	Cuba	EF429231	EF433560	GU461911	JQ087982
MUCL 51331 ^{c, h}	Argentina	KF444714	KF444691	KF444764	KF444737
MUCL 51540 ^{c, h}	Cuba	KF444715	KF444692	KF444765	KF444738
MUCL 51399 ^{c, h}	Cuba	KF444716	KF444693	KF444766	KF444739
MUCL 52340 ^{c, h}	Mexico	KF444717	KF444694	KF444767	KF444740
MUCL 53364 ^{c, h}	Mexico	KF444718	KF444695	KF444768	KF444741

F. mediterranea M. Fisch.

AFTOL ID 688	ND	AY684157	AY854080	AY885149	AY803748
MUCL 38514	Italy	AY618201	GU461953	GU461912	JQ087984

MUCL 45670 ^{c, h}	France	GU461980	GU461954	GU461913	JQ087985
<i>Fomitiporia neotropica</i> de Campos-Santana, Amalfi, R.M. Silveira, Robledo et Decock					
MUCL 53114 ^{c, h}	French Guiana	JX093836	JX093792	JX093749	JX093880
MUCL 49549 ^{c, h}	Argentina	KF444719	KF444696	KF444769	KF444742
MUCL 54246 ^{c, h}	Brazil	KF444720	KF444697	KF444770	KF444743
MUCL 51335 (T) ^{c, h}	Argentina	KF444721	KF444698	KF444771	KF444744
MUCL 51336 ^{c, h}	Argentina	KF444722	KF444699	KF444772	KF444745
MUCL 54206 ^{c, h}	Brazil	KF444723	KF444700	KF444773	KF444746
MUCL 54196 ^{c, h}	Brazil	KF444724	KF444701	KF444774	KF444747
MUCL 54212 ^{c, h}	Brazil	KF444725	KF444702	KF444775	KF444748
<i>F. nobilissima</i> Decock & Yombiyeni					
MUCL 47580 ^{c, h}	Gabon	GU461985	GU461966	GU461921	JQ087986
MUCL 51289 (T) ^{c, h}	Gabon	GU461984	GU461965	GU461920	JQ087987
<i>F. pentaphylacis</i> L.W. Zhou					
Yuan 6012 (T)	China	JQ003901	JQ003900	This study	This study
<i>F. polymorpha</i> M. Fisch.					
91-42/3 (MUCL 46166) (PT) ^{c, 5}	USA	DQ122393	GU461955	GU461914	JQ087988
91-42/1 (MUCL 46167) (PT) ^{c, 5}	USA	EF429233	GU461956	GU461915	JQ087989
<i>F. pseudopunctata</i> (A. David, Dequatre & Fiasson) Fiasson					

MUCL 51325 ^{c, 2}	Czech	GU461981	GU461948	GU461916	JQ087998
MUCL 46168 ^{c, h}	France	JQ087918	JQ087891	JQ087945	JQ087999
<i>F. punctata</i> (Fr.) Murrill					
MUCL 34101 ^{c, h}	Germany	AY618200	GU461947	GU461917	JQ088000
WD-2055 (MUCL 47629) ^{c, 3}	Japan	GU461982	GU461950	GU461918	JQ088001
71-8 298 (MUCL 53548) ^{c, 4}	Europe	JX093834	JX093790	JX093747	JX093878
CUI 9911	China	This study	This study	This study	This study
MUCL 53297	Korea	This study	This study	This study	This study
MUCL 53298	Korea	This study	This study	This study	This study
<i>F. punicata</i> Y.C. Dai, B.K. Cui & Decock					
Cui 23	China	GU461991	GU461974	GU461927	JQ088002
Cui 26	China	GU461992	GU461975	GU461928	JQ088003
<i>F. robusta</i> (P. Karst.) Fiasson & Niemelä					
CBS 389.72 (MUCL 51297)	Estonia	JQ087919	JQ087892	JQ087946	JQ088004
Tomšovský 1013 (MUCL 51327) ^{c, 2}	Czech	GU461993	GU461949	GU461929	JQ088005
MUCL 53300	Czech	This study	This study	This study	This study
MUCL 55089	France	This study	This study	This study	This study
<i>Fomitiporia sonorae</i> (Gilb.) Y.C. Dai					
RLG-10862-Sp (MUCL 47689) (T) ^{c1}					

	USA, Arizona	JQ087920	JQ087893	JQ087947	JQ088006
<i>Fomitiporia spinescens</i> (J.E. Wright & G. Coelho) G. Coelho, Guerrero & Rajchenb.					
MUCL 51329	Argentina	This study	This study	This study	This study
<i>F. tabaquilio</i> (Urcelay, Robledo & Rajchenb.) Decock & Robledo					
MUCL 46230 ^{c, h}	Argentina	DQ122394	GU461940	GU461931	JQ088008
MUCL 47754 ^{c, h}	Argentina	GU461994	GU461941	GU461932	JQ088009
<i>F. tenuis</i> Decock, Bitew & G. Castillo					
MUCL 44802 (T) ^{c, h}	Ethiopia	AY618206	GU461957	GU461934	JQ088010
MUCL 49948 ^{c, h}	Gabon	GU461998	GU461958	GU461935	JQ088011
MUCL 49971 ^{c, h}	Uganda	GU461998	GU461958	GU461935	JQ088012
MUCL MA-CA-07-106	Cameroon	This study	This study	This study	This study
MUCL 51309	Uganda	This study	This study	This study	This study
MUCL 47999	Madagascar	This study	This study	This study	This study
MUCL 51003	Gabon	This study	This study	This study	This study
MUCL KE-84	Kenya	This study	This study	This study	This study
<i>Fomitiporia tenuitubus</i> L.W. Zhou					
Yuan 5736 (T)	China	JQ003903	JQ003902	This study	This study
<i>Fomitiporia texana</i> (Murrill) Nuss					
RLG-7763-T (MUCL 47690) ^{c, 1}	USA, Arizona	JQ087921	JQ087894	JQ087948	JQ088013

MUCL 47691	USA, Arizona	This study	This study	This study	This study
FP-89674-R (MUCL 51143) ^{c, 1}	USA, Arizona	JQ087922	JQ087895	JQ087949	JQ088014
<i>Fomitiporia torreyae</i> Y.C. Dai & B.K. Cui					
WD-199 (MUCL 47628) ^{c, 3}	Japan	JQ087923	JQ087896	JQ087950	JQ088015
WC31 ^h	Chine	JQ087924	JQ087897	JQ087951	JQ088016
MUCL 49941	Chine	This study	This study	This study	This study
MUCL 49650	Chine	This study	This study	This study	This study
<i>Fomitiporia tsugina</i> Murrill					
Ft_San (MUCL 52702)	USA	JQ087925	JQ087898	JQ087952	JQ088017
Ft_T2-1 (MUCL 52703)	USA	JQ087926	JQ087899	JQ087953	JQ088018
CBS125.40 (MUCL 51295)	USA	JQ087908	JQ087881	JQ087935	JQ087974
<i>Fomitiporia</i> “spp.”					
<i>Fomitioria</i> sp. TFMF 18103	Malaysia	AB777980	AB777695	AB777950	AB778012
<i>Fomitiporia</i> “sp.” PS1					
TH 8903 ^{h, 7}	Guyana	JX093837	JX093793	JX093750	ND
TH 8904 ^{h, 7}	Guyana	JX093838	JX093794	JX093751	ND
<i>Fomitiporia</i> “sp.” PS2					
MUCL 53108 ^{c, h}	French Guiana	JX093839	JX093795	JX093752	JX093881

MUCL 53705 ^{c, h}	French Guiana	JX093840	JX093796	JX093753	JX093882
MUCL 53992 ^h	Guadalupe	JX093841	JX093797	JX093754	JX093883
<i>Fomitiporia</i> “sp.” PS3 a					
MUCL 51464 ^{c, h}	Ecuador	JX093842	JX093798	JX093755	JX093884
MUCL 53034 ^{c, h}	French Guiana	JX093843	JX093799	JX093756	JX093885
MUCL 53106 ^{c, h}	French Guiana	JX093844	JX093800	JX093757	JX093886
MUCL 53111 ^{c, h}	French Guiana	JX093845	JX093801	JX093758	JX093887
MUCL 53785 ^{c, h}	French Guiana	JX093846	JX093802	JX093759	JX093888
MUCL 53793 ^{c, h}	French Guiana	JX093847	JX093803	JX093760	JX093889
MUCL 53800 ^{c, h}	French Guiana	JX093848	JX093804	JX093761	JX093890
MUCL 53985 ^{c, h}	French Guiana	JX093849	JX093805	JX093762	JX093891
<i>Fomitiporia</i> “sp.” PS3 b					
GC-FG-10-125 ^{c, h}	French Guiana	JX093850	JX093806	JX093763	JX093892
<i>Fomitiporia</i> “sp.” PS4					
MUCL 53993 ^{c, h}	Mexico	JX093851	JX093807	JX093764	JX093893
MUCL 53994 ^{c, h}	Mexico	JX093852	JX093808	JX093765	JX093894
<i>Fomitiporia</i> “sp.” PS5					
MUCL 51555 ^{c, h}	Martinique	JX093853	JX093809	JX093766	JX093895
MUCL 53797 ^{c, h}	French Guiana	JX093854	JX093810	JX093767	JX093896

MUCL FG-14-881	French Guiana	This study	This study	This study	This study
<i>Fomitiporia</i> “sp.” PS6					
MUCL 53798 ^{c, h}	French Guiana	JX093855	JX093811	JX093768	JX093897
MUCL 54405	French Guiana	This study	This study	This study	This study
<i>Fomitiporia</i> “sp.” PS10					
CBS 386.66 = MUCL 46181 ^{c, 6}	Argentina	EF429234	EF433563	GU461930	JQ088007
MUCL 51333	Argentina	This study	This study	This study	This study
MUCL 49757	Argentina	This study	This study	This study	This study
MUCL 54244	French Guiana	This study	This study	This study	This study
MUCL 53675	French Guiana	JX093835	JX093791	JX093748	JX093879
MUCL FG-12-573	French Guiana	This study	This study	This study	This study
<i>Fomitiporia</i> “sp.” PS11					
MUCL FG-12-524	French Guiana	This study	This study	This study	This study
<i>Fomitiporia</i> “sp.” PS12					
MUCL ST-11-61	São Tome	This study	This study	This study	This study
MUCL 53560	São Tome	This study	This study	This study	This study
MUCL ST-11-58	São Tome	This study	This study	This study	This study
<i>Fomitiporia</i> “sp.” PS13					
MUCL 52350	Mexico	JQ087912	JQ087885	JQ087939	JQ087992

Fomitiporia “sp.” PS14

RLG-10827 (MUCL 51106) ^{c, 1}	USA	JQ087910	JQ087883	JQ087937	JQ087990
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Fomitiporia “sp.” PS15

FP-98505-T (MUCL 51105) ^{c, 1}	USA, Arizona	JQ087911	JQ087884	JQ087938	JQ087991
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Fomitiporia “sp.” PS16

MUCL 54022	New Zealand	This study	This study	This study	This study
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MUCL 54023	New Zealand	This study	This study	This study	This study
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Fomitiporia “sp.” PS17

MUCL 54021	New Zealand	This study	This study	This study	This study
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***Fomitiporia andina* sp. nov. nom. prov PS17**

MUCL EC-14-79	Ecuador	This study	This study	This study	This study
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***Fomitiporia pulverulenta* sp. nov. nom. prov PS18**

MUCL 54415	French Guiana	This study	This study	This study	This study
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MUCL FG-12-628	French Guiana	This study	This study	This study	This study
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Phellinus bambusarum (Rick) M.J. Larsen

MUCL 53437	Argentina	This study	This study	This study	This study
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P. bambusinus (Pat.)

MUCL 51609	China	This study	This study	This study	This study
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MUCL 51610	China	This study	This study	This study	This study
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P. livescens (Speg.) Rajchenb

MUCL 46885	Argentina	This study	This study	This study	This study
MUCL 49372	Argentina	This study	This study	This study	This study
MUCL 49371	Argentina	This study	This study	This study	This study

P. uncisetus Robledo, Urcelay & Rajchenb.

MUCL 46231 ^{c, h}	Argentina	EF429235	GU461960	GU461937	JQ088020
MUCL 47061 ^{c, h}	Argentina	GU462000	GU461972	GU461938	JQ088021

T, PT = type, paratype; ND*: available at MUCL

^c = culture available; ^h = voucher herbarium specimen corresponding to the culture available at the MUCL herbarium; ¹ cultures from CFMR, USDA, USA, courtesy of Dr. K. Nakasone); ² cultures from Faculty of Forestry and Wood Technology, Mendel University of Agriculture and Forestry in Brno, Czech Republic, courtesy of Dr. M. Tomšovský; ³ cultures from Microbial Ecology Lab Forestry and Forest Products Research Institute, courtesy of Prof. T. Hattori, Japan; ⁴ cultures from National History Museum, University of Tartu, Estonia, courtesy of K. Põldmaa; ⁵ cultures from Regensburg University, Germany, courtesy of Dr. M. Fischer; ⁶ cultures from the CBS, The Netherlands, courtesy of Prof. P. Crous.

Table 2. Species names/voucher and GenBank accession number used for the extended outgroup in the fossil-calibrated dating analysis.

Taxa (GenBank label)	Order / clade	LSU	<i>rpb2</i>	<i>tef1</i>
<i>Ampulloclitocybe clavipes</i>	Agaricales / hygrophoroid	AY639881	AY780937	AY881022
<i>Camarophyllum basidiosus</i>	Agaricales / hygrophoroid	DQ457651	DQ470828	-
<i>Cantharocybe gruberi</i>	Agaricales / hygrophoroid	DQ234540	DQ385879	DQ059045
<i>Chrysomphalina grossula</i>	Agaricales / hygrophoroid	EU652373	DQ470832	-
<i>Hygrocybe aff. conica</i>	Agaricales / hygrophoroid	AY684167	AY803747	AY883425
<i>Hygrocybe coccinea</i>	Agaricales / hygrophoroid	DQ457676	DQ472723	GU187705
<i>Hygrophorus auratocephalus</i>	Agaricales / hygrophoroid	DQ457672	DQ472720	-
<i>Hygrophorus pudorinus</i>	Agaricales / hygrophoroid	DQ457678	DQ472725	GU187710
<i>Mycena galericulata</i>	Agaricales / hygrophoroid	AY647216	DQ385888	-
<i>Mycena plumbea</i>	Agaricales / hygrophoroid	DQ470813	GU187729	-
<i>Phyllotopsis sp.</i>	Agaricales / hygrophoroid	AY684161	AY786061	DQ059047
<i>Pleurocybella porrigens</i>	Agaricales / hygrophoroid	EF537894	GU187740	-
<i>Pseudoarmillariella ectypoides</i>	Agaricales / hygrophoroid	DQ154111	DQ474127	GU187733
<i>Sarcomyxa serotina</i>	Agaricales / hygrophoroid	AY691887	DQ859892	GU187754
<i>Tricholomopsis decora</i>	Agaricales / hygrophoroid	AY691888	DQ408112	DQ029195
<i>Typhula phacorrhiza</i>	Agaricales / hygrophoroid	AY586724	AY218525	-
<i>Xeromphalina campanella</i>	Agaricales / hygrophoroid	DQ470826	GU187758	-
<i>Anthracoephyllum archeri</i>	Agaricales / marasmioid	AY745709	DQ385877	DQ028586
<i>Armillaria mellea</i>	Agaricales / marasmioid	AY700194	AY780938	AY881023
<i>Baeospora myosura</i>	Agaricales / marasmioid	DQ457648	DQ470827	GU187762
<i>Cheimonophyllum candidissimum</i>	Agaricales / marasmioid	DQ457654	DQ470831	GU187760
<i>Chondrostereum purpureum</i>	Agaricales / marasmioid	AY586644	AY218477	DQ457632

<i>Flammulina velutipes</i>	Agaricales / marasmiod	AY639883	AY786055	AY883423
<i>Gymnopus contrarius</i>	Agaricales / marasmiod	DQ457670	DQ472716	GU187700
<i>Gymnopus dryophilus</i>	Agaricales / marasmiod	AY640619	DQ472717	DQ408152
<i>Hemimycena gracilis</i>	Agaricales / marasmiod	DQ457671	DQ472719	GU187709
<i>Henningsomyces candidus</i>	Agaricales / marasmiod	AY571008	AY218513	AY883424
<i>Hydropus cf. scabripes</i>	Agaricales / marasmiod	DQ411536	DQ457634	-
<i>Marasmius rotula</i>	Agaricales / marasmiod	DQ457686	DQ474118	GU187723
<i>Megacollybia platyphylla</i>	Agaricales / marasmiod	AY702016	DQ385887	DQ435786
<i>Moniliophthora perniciosa</i>	Agaricales / marasmiod	AY916738	-	AY916741
<i>Mycena amabilissima</i>	Agaricales / marasmiod	DQ457691	DQ474121	GU187727
<i>Mycena aurantiidisca</i>	Agaricales / marasmiod	DQ470811	DQ474122	GU187728
<i>Mycetinis alliaceus</i>	Agaricales / marasmiod	AY635776	AY786060	AY883430
<i>Physalacria bambusae</i>	Agaricales / marasmiod	DQ097349	DQ474123	GU187732
<i>Porothelium fimbriatum</i>	Agaricales / marasmiod	DQ457673	DQ472721	-
<i>Xerula radicata</i>	Agaricales / marasmiod	AY645051	AY786067	DQ029194
<i>Amanita brunnescens</i>	Agaricales / pluteoid	AY631902	AY780936	AY881021
<i>Pleurotus ostreatus</i>	Agaricales / pluteoid	AY645052	AY786062	AY883432
<i>Pluteus romellii</i>	Agaricales / pluteoid	AY634279	AY786063	AY883433
<i>Volvariella gloiocephala</i>	Agaricales / pluteoid	DQ089020	-	-
<i>Asterophora agaricoides</i>	Agaricales / tricholomatoid	AF223190	DQ367431	DQ367424
<i>Callistosporum graminicolor</i>	Agaricales / tricholomatoid	GU187553	GU187815	GU187742
<i>Catathelasma ventricosum</i>	Agaricales / tricholomatoid	DQ089012	DQ470830	-
<i>Clitocybe candicans</i>	Agaricales / tricholomatoid	AY645055	DQ385881	DQ408149
<i>Clitocybe nebularis</i>	Agaricales / tricholomatoid	DQ457658	DQ470833	EF421081

<i>Clitocybe subditopoda</i>	Agaricales / tricholomatoid	AY691889	AY780942	DQ408151
<i>Clitopilus prunulus</i>	Agaricales / tricholomatoid	AY700181	GU384648	-
<i>Collybia tuberosa</i>	Agaricales / tricholomatoid	AY639884	AY787219	AY881025
<i>Entoloma prunuloides</i>	Agaricales / tricholomatoid	AY700180	DQ385883	DQ457633
<i>Infundibulicybe gibba</i>	Agaricales / tricholomatoid	DQ457682	DQ472727	GU187759
<i>Lepista irina</i>	Agaricales / tricholomatoid	DQ385885	DQ234538	DQ028591
<i>Lyophyllum boudieri</i>	Agaricales / tricholomatoid	DQ825430	DQ825411	EF421070
<i>Lyophyllum decastes</i>	Agaricales / tricholomatoid	AY207228	DQ367433	DQ367426
<i>Nolanea sericea</i>	Agaricales / tricholomatoid	AY207197	DQ367435	DQ367428
<i>Pseudoclitocybe cyathiformis</i>	Agaricales / tricholomatoid	EF551313	GU187815	GU187742
<i>Rhodocollybia maculata</i>	Agaricales / tricholomatoid	AY639880	AY787220	DQ061279
<i>Rhodocybe mundula</i>	Agaricales / tricholomatoid	AY700182	DQ474128	-
<i>Termitomyces sp.</i>	Agaricales / tricholomatoid	DQ110875	EF421010	EF421078
<i>Tricholoma myomyces</i>	Agaricales / tricholomatoid	TMU76459	DQ367436	DQ367429
<i>Tricholoma palustre</i>	Agaricales / tricholomatoid	AY700197	DQ484055	-
<i>Amylocorticium cebennense</i>	Amylocorticiales	GU187561	GU187770	GU187675
<i>Anomoloma albolutescens</i>	Amylocorticiales	GU187563	GU187768	GU187771
<i>Anomoloma myceliosum</i>	Amylocorticiales	GU187559	GU187766	GU187677
<i>Anomoporia bombycina</i>	Amylocorticiales	GU187564	GU187765	GU187674
<i>Podoserpula pusio</i>	Amylocorticiales	DQ470821	GU187804	-
<i>Serpulomyces borealis</i>	Amylocorticiales	GU187570	GU187782	GU187686
<i>Fibulorhizoctonia sp.</i>	Atheliales	AY635779	AY857985	AY879115
<i>Leptosporomyces raunkiaeri</i>	Atheliales	GU187588	GU187791	GU187719
<i>Aureoboletus thibetanus</i>	Boletales	DQ534577	DQ366279	DQ029199

<i>Austropaxillus boletinoides</i>	Boletales	HM135710	HM135765	HM135561
<i>Austropaxillus macnabbii</i>	Boletales	HM135706	-	HM135557
<i>Austropaxillus muelleri</i>	Boletales	HM135708	-	HM135559
<i>Austropaxillus squarrosus</i>	Boletales	HM135707	-	HM135558
<i>Austropaxillus statuum</i>	Boletales	HM135709	HM135764	HM135560
<i>Boletus edulis</i>	Boletales	HQ326927	GU187774	HQ326860
<i>Boletus projectellus</i>	Boletales	AY684158	AY787218	AY879116
<i>Bondarcevomyces taxi</i>	Boletales	DQ534672	-	GU187683
<i>Calostoma cinnabarinum</i>	Boletales	AY645054	AY780939	AY879117
<i>Chalciporus piperatus</i>	Boletales	DQ534648	-	GU187690
<i>Coniophora arida</i>	Boletales	GU187573	GU187775	GU187684
<i>Coniophora cerebella</i>	Boletales	GU187569	GU187776	GU187776
<i>Coniophora marmorata</i>	Boletales	GU187571	GU187780	GU187688
<i>Coniophora olivacea</i>	Boletales	GU187572	-	GU187689
<i>Coniophora puteana</i>	Boletales	GU187578	GU187778	-
<i>Gyrodon lividus</i>	Boletales	AF098378	GU187786	GU187701
<i>Hydnomerulius pinastri</i>	Boletales	GU187580	GU187787	GU187708
<i>Hygrophoropsis aurantiaca</i>	Boletales	AY684156	AY786059	AY883427
<i>Leucogyrophana arizonica</i>	Boletales	GU187582	GU187792	GU187714
<i>Leucogyrophana lichenicola</i>	Boletales	GU187583	GU187789	GU187715
<i>Leucogyrophana mollusca</i>	Boletales	GU187584	GU187795	-
<i>Leucogyrophana olivascens</i>	Boletales	GU187587	GU187790	GU187717
<i>Leucogyrophana romellii</i>	Boletales	GU187586	GU187794	GU187720
<i>Paxillus vernalis</i>	Boletales	AY645059	DQ457629	GU187693

<i>Pisolithus aurantioscabrosus</i>	Boletales	EU718146	FJ536648	FJ536681
<i>Pisolithus</i> sp. isolate ECV320	Boletales	EU718147	FJ536649	-
<i>Pisolithus tinctorius</i>	Boletales	EU718148	FJ536650	FJ536682
<i>Pseudomerulius curtisii</i>	Boletales	GU187589	GU187796	GU187725
AFTOL-ID1387	Boletales	AF518648	DQ366283	DQ059046
<i>Serpula himantoides</i> SH136	Boletales	GU187602	GU187811	GU187750
<i>Serpula incrassata</i> DAOM1705290	Boletales	GU187595	-	GU187751
<i>Serpula incrassata</i> MUCL30791	Boletales	AY491672	HM135757	HM135553
<i>Serpula lacrymans</i> REG-383	Boletales	GU187596	GU187809	GU187752
<i>Serpula lacrymans</i> SL198	Boletales	HM135656	HM135744	GU196454
<i>Serpula lacrymans</i> var. <i>shastensis</i>	Boletales	HM135656	HM135746	HM135544
<i>Serpula pulverulenta</i>	Boletales	GU187597	-	GU187753
<i>Serpula similis</i>	Boletales	GU187601	GU187812	GU187724
<i>Strobilomyces floccopus</i>	Boletales	AY612824	AY786065	AY883428
<i>Tapinella atrotomentosa</i>	Boletales	GU187603	GU187813	GU187757
<i>Tapinella panuoides</i>	Boletales	GU187604	-	This study
<i>Xerocomus impolitus</i>	Boletales	AF139715	-	JQ327034
<i>Xerocomus subtomentosus</i>	Boletales	AF139716	-	JQ327035
<i>Gomphidius roseus</i>	Boletales/Suillinae	DQ534669	GU187818	GU187702
<i>Rhizopogon nigrescens</i>	Boletales/Suillinae	GU187594	GU187806	GU187744
<i>Suillus bresadolae</i>	Boletales/Suillinae	GU187598	GU187810	GU187746
<i>Suillus pictus</i>	Boletales/Suillinae	AY684154	AY786066	AY883429
<i>Gautieria otthii</i>	Gomphales	This study	This study	This study
<i>Aurificaria luteombrina</i> MUCL43741	Hymenochaetales	This study	This study	This study

<i>Coltricia perennis</i>	Hymenochaetales	AJ406472	AY218526	AY885147
<i>Coltricia stuckertiana</i> Robledo219	Hymenochaetales	This study	This study	This study
<i>Cotylidia</i> sp.	Hymenochaetales	AY629317	AY883422	AY885148
<i>Fomitiporia mediterranea</i>	Hymenochaetales	AY684157	AY803748	AY885149
<i>Hydnochaete duportii</i>	Hymenochaetales	AY635770	-	DQ435793
<i>Hyphoderma praetermissum</i>	Hymenochaetales	AY700185	AY787221	AY885150
<i>Inocutis jamaicensis</i> MUCL53366	Hymenochaetales	This study	This study	This study
<i>Inonotus micantissimus</i> MUCL52413	Hymenochaetales	HM635664	This study	This study
<i>Onnia tomentosa</i> BUD-551-C-1	Hymenochaetales	JX110116	JX109986	JX110028
<i>Onnia tomentosa</i> MUCL54508	Hymenochaetales	This study	This study	This study
<i>Peniophorella praetermissa</i>	Hymenochaetales	AY707094	AY787221	AY885150
<i>Phaeolus schweinitzii</i>	Hymenochaetales	AY629319	DQ408119	DQ028602
<i>Phellinus amazonicus</i> MUCL51483	Hymenochaetales	This study	This study	This study
<i>P. amazonicus</i> MUCL53117	Hymenochaetales	This study	This study	This study
<i>P. amazonicus</i> MUCL53128	Hymenochaetales	This study	This study	This study
<i>P. caribaeo quercicolus</i> MUCL 46003	Hymenochaetales	DQ127279	This study	HM635725
<i>P. castanopsidis</i> CUI10153	Hymenochaetales	JQ837944	This study	This study
<i>P. castanopsidis</i> CUI10157	Hymenochaetales	JQ837945	This study	This study
<i>P. ellipsoideus</i> MUCL45929	Hymenochaetales	DQ127283	This study	This study
<i>P. ellipsoideus</i> MUCL47820	Hymenochaetales	This study	This study	This study
<i>P. ellipsoideus</i> MUCL47866	Hymenochaetales	This study	This study	This study
<i>P. gabonensis</i> MUCL52070	Hymenochaetales	HM635686	This study	HM635733
<i>Phellinus</i> sp MUC51487	Hymenochaetales	This study	This study	This study
<i>Phellinus</i> sp MUCL51334	Hymenochaetales	This study	This study	This study

<i>Phellinus</i> sp MUCL52001	Hymenochaetales	HM635696	This study	HM635737
<i>Phylloporia chrysa</i> MUCL52862	Hymenochaetales	HM635667	This study	This study
<i>Phylloporia fruticosa</i>	Hymenochaetales	HM635669	This study	This study
<i>Phylloporia minutispora</i> BA26	Hymenochaetales	HM635671	This study	This study
<i>Phylloporia nouraguensis</i> FG11409	Hymenochaetales	KC136224	This study	This study
<i>Phylloporia rzedowskii</i>	Hymenochaetales	HM635675	This study	This study
<i>Phylloporia</i> sp Rob526	Hymenochaetales	This study	This study	This study
<i>Phylloporia ulloai</i>	Hymenochaetales	HM635678	This study	This study
FP-135951	Hymenochaetales	JX110076	JX109946	JX109988
<i>Porodaedalea chrysoloma</i> MUCL54506	Hymenochaetales	This study	This study	This study
FP-102122-T	Hymenochaetales	JX110080	JX109950	JX109992
<i>Porodaedalea pini</i> MUCL54507	Hymenochaetales	This study	This study	This study
<i>Pseudoinonotus dryadeus</i> MUCL52401	Hymenochaetales	This study	This study	This study
<i>Pseudoinonotus dryadeus</i> MUCL54521	Hymenochaetales	This study	This study	This study
<i>Resinicium bicolor</i>	Hymenochaetales	AY700183	DQ457635	DQ061277

Annex II

DNA extraction protocols

ENZYMATIC/GLASS FILTER PLATE EXTRACTION FOR FUNGI

This protocol by Ivanova et al. (2006) is reproduced here slightly modified.
Modified by Simona Margaritescu and Bryn Dentinger Department of
Natural History, Royal Ontario Museum, Toronto, ON, Canada

Working solutions

Lysis Buffer (LB) contains 100 mM NaCl, 50 mM Tris-HCl at pH 8, 10mM EDTA at pH8 and 0.5% SDS. Buffer should be mixed using a magnetic stirrer and can be stored at room temperature.

Binding Buffer (BB) Used to make **Binding Mix** and **Protein Wash Buffer** (below).

Contains 6M guanidine thiocyanate (GuSCN), 20 mM EDTA (pH 8), 10mM Tris-HCl (pH6.4), and 4% Triton X-100. Mix buffer on a magnetic stirrer with heat. Buffer can be stored at room temperature, but a precipitate will most likely form. Warming the solution at 56 C for several minutes should help dissolve the precipitate before use, but making fresh buffer each time is recommended.

Binding Mix (BM) For each 100 mL, mix 50 mL **BB** and 50 mL ethanol (100%). Binding mix is stable at room temperature for a week.

Protein Wash Buffer (PWB) For each 100 mL mix 70 mL ethanol (100%), 26 mL **BB** and 4 mL sterile distilled water. Binding mix is stable at room temperature for a week.

Wash Buffer (WB) contains 60% ethanol (100%), 50 mM sodium chloride (NaCl), 10mM Tris-HCl (pH 7.4) and 0.5mM EDTA (pH 8). Should be stored at -200C.

Centifugation Protocol

Use the PALL glass fiber filtration 1.0 µM 350-µL well plates (no. 5031) for centrifugation.

1. Add a small amount of sample (~1-2 mm³) to each well of a 96-well PCR plate (we use the Sorenson 96-well ultraPlate; no. 21970). Instruments should be flamesterilized between samples to avoid cross contamination. Last well can be leftblank and used as a negative control.
2. Mix 5 mL of **Lysis Buffer (LB)** and 0.5 mL of Proteinase K (20 mg/mL) in a sterile container and dispense 100µl to each well. Cover each row with caps and incubate at 560C overnight (8 to 16 hours) to allow digestion.
3. Centrifuge at 1000 rcf for 1minute.

4. Add 100µl of **Binding Mix (BM)** to each sample. Mix by pipetting up and down few times.
5. Remove cap strips/cover and transfer the lysate (about 150µl) from the wells of microplate into the wells of the PALL glass fiber filtration (GF) plate placed on top of a square-well block. Seal the plate with adhesive cover.
6. Centrifuge at 1500 rcf for 10 min to bind DNA to the GF membrane.
7. Add 250µl of **Protein Wash Buffer (PWB)** to each well of the GF plate. Seal with a new adhesive cover and centrifuge at 1500rcf for 5 min. Discard the flowthrough.
8. Add 300µl of **Wash Buffer (WB)** to each well of the GF plate. Seal with a new cover and centrifuge at 1500rcf for 10 min.
9. To avoid incomplete **WB** removal, open the cover to relieve the vacuum that may have formed in the wells, seal the plate again and centrifuge the plates again at 1500rcf for 5 minutes. Discard the flow-through.
10. Repeat steps 8 and 9.
11. Remove the cover. Place the GF plate on a clean square-well block and incubate at 56°C for 30 min to evaporate residual ethanol.
12. Position a PALL collar (no. 5225) on a collection plate (Sorenson 96-well UltraAmp) and place plate and collar on top of a clean square-well block. Place GF PALL plate with DNA bound to the membrane on top of a PCR plate. Dispense 50µl of 0.1x TE buffer or water, pre-warmed at 56°C, directly onto the membrane of each well of GF plate and incubate at room temperature for few minutes and then seal plate.
13. Centrifuge at 1500rcf for 10 minutes to collect the eluted DNA. Remove the GF plate and discard it.
14. Cover DNA plate with aluminum foil. Keep at 40°C for temporary storage or at -20°C for long-term storage.

Optional Vacuum Manifold Protocol

Everything is carried out as above except that the liquids are slowly drawn through the GF membranes using a vacuum manifold (we use a Promega Vac-Man® Laboratory Vacuum Manifold). We have successfully used the PALL GF plates and Unifilter® Plates (Whatman Hydrophilic GF/C Filter, cat. No. 7700-2801) with the vacuum manifold. The final DNA elution step is then carried out in the centrifuge

References

Ivanova NV, Dewaard JR, Hebert PDN (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Molecular Ecology Notes* **6**, 998-1002.

CTAB 1 extraction of DNA from dry fungal specimens (Amalfi and Baert unpublished)

1. Add 0.3% (V/V) β -mercapto-ethanol (3 μ l / mL) to 2x CTAB buffer and keep at 60°C.
2. Powder the dry samples with a 5 mm bead in the Retsch Mill Mixer for 45 s at 25 mov/sec. Several rounds of grinding may be necessary (speed can be increased also).
3. Add 800 μ l pre-heated (60°C) extraction buffer.
4. Incubate samples at 60°C for 45 min. with periodic gentle mixing.
5. Remove samples from water bath and let them cool a little.
6. In the fume hood, add an equal volume (800 μ l) chloroform :isoamyl alcohol (24: 1). Mix gently but thoroughly.
7. Centrifuge at 13 000 g for 5 min (at room temp) . Label new 1.5 ml LowBind eppendorf tube.
8. Transfer the aqueous top phase (ca. 700 μ l) to the new labeled tube. Avoid interphase.
9. Repeat steps 6 to 8. Adjust volumes accordingly (700 μ l chloroform:isoamyl alcohol, ca. 600 μ l supernatant).
10. Add 0.8 volume (480 μ l) isopropanol at 4°C. Mix gently (c.a. 50 x) and incubate at 20°C for 10 min.
11. Centrifuge at 4°C and 16 000 g for 5 min.
12. Cautiously discard supernatant. Drain briefly on paper towel.
13. Add 600 μ l washing 70% EtOH. Swirl gently a few times. At this stage, samples can be stored overnight at -20°C.
14. Centrifuge at 4°C and 16 000 g for 5 min and pour off supernatant.
15. Invert tubes on a paper towel and allow the pellet to dry until the last traces of ethanol have evaporated (c.a. 1 hour).
16. Resuspend pellet in 50-100 μ l TE pH 8 10 minutes at 60°C (or until pellet has dissolved).
17. Add 2 μ l diluted (10 x) RNase A, mix and incubate 2 min at room temp. Keep the samples cool hereafter.

CTAB 2 DNA EXTRACTION PROTOCOL (Amalfi and Baert unpublished)

1. Sample 5 mg of leaf tissue into tubes; add a pinch of sterilised sand into each tube to ease grinding of the tissue.
2. Preheat 1 ml 2X CTAB buffer per sample in a 65°C water bath.
3. Grind samples using a Mixer Mill with metal beads. Perform short grinds (30 seconds to 1 minute) followed by cooling on ice to avoid heat damage to DNA. Alternatively, cool the grinding blocks in freezer prior to grinding. Stop once material is turned into a fine powder.
4. LYSIS: Add 1 ml of 2X CTAB buffer to each sample, and incubate at 65°C for 60 minutes.
5. CHLOROFORM EXTRACTION: Add an equal volume (750µl) of SEVAG, mixing gently but thoroughly. Extract for up to one hour for slimy or mucilaginous samples by rocking on an orbital shaker.
6. Spin at 13,000 rpm (8,000 rpm for tubes larger than eppendorfs) for 10 minutes.
7. Remove aqueous (top) phase containing DNA and transfer to a new Eppendorf tube. Dispose of SEVAG and plant debris in the SEVAG waste container.
8. Repeat the chloroform extraction (stage 5-7).
9. PRECIPITATION: Add 2/3 volume of -20°C isopropanol and mix gently to precipitate DNA. Leave in -20°C freezer for up to two weeks.
10. WASH-UP: Spin in a centrifuge at 13,000 rpm for 10 minutes to collect precipitate. Pour off liquid in the waste container in the fume cupboard. Add 750 µl of ice-cold 70% ethanol, shake well to dislodge pellet to facilitate “washing”, and wash for 60 minutes.
11. Spin down DNA at 13,000 rpm for 5 minutes. Pour off liquid and drain upside down for 5-10 minutes to allow alcohol to evaporate. If some ethanol is still left in tubes after 5-10 mins, do an extra spin in centrifuge and pipette the ethanol out carefully. Drying for too long can cause the DNA to be difficult to dissolve. You can also dry the samples in vacuum centrifuge for c. 5 mins.
12. Resuspend your DNA in 100 µl of TE buffer (pH 8).
13. RNA's REMOVAL: Add 1 µl (1 µl of RnaseA stock solution (Qiagen) per 100 µl DNA solution (100mg/ml)) per sample. Vortex, then incubate at 37°C for 20 min.
14. PRECIPITATION: Add 100 µl of cold ammonium acetate (7.5M) and 750 µl of 100% alcohol per sample, and incubate on ice/freezer for 30 mins.

15. WASH-UP: Spin in a centrifuge at 13,000 rpm for 10 minutes to collect precipitate. Pour off liquid in the waste container in the fume cupboard. Add 500 μ l of ice-cold 70% ethanol, shake well to dislodge pellets to facilitate “washing”, and wash for 30 minutes.
16. Spin down DNA at 13,000 rpm for 5 minutes. Pour off liquid and drain upside down for 5-10 minutes to allow alcohol to evaporate. If some ethanol is still left in tubes after 5-10 mins, do an extra spin in centrifuge and pipette the ethanol out carefully. Drying for too long can cause the DNA to be difficult to dissolve. You can also dry the samples in a vacuum centrifuge for c. 5 mins (low heat set).
17. Dissolve DNA in 75 μ l of dH₂O.

RECIPES FOR CTAB EXTRACTION

2X CTAB buffer (250 ml)

100mM Tris-HCl pH 8.0	25 ml (1M)
1.4M NaCl	70 ml (5M)
20mM EDTA	10 ml (0.5M)
CTAB (hexadecyltrimethylammonium bromide)	5 g (2%)
Water	until 250 ml
PVP-40	0.02g/1ml (polyvinylpyrrolidone)

SEVAG

24:1 chloroform : isoamyl alcohol

Wash Buffer

100% ETOH	75 ml (750 µl/sample)
7.5M NH ₄ Ac	10 ml (100 µl/sample)

TE buffer (100 ml at pH 8.0; 10mM Tris-HCl (pH 8) and 1mM EDTA) (1L/50ml)

Tris-HCL (1M)	1 ml (10ml/500µl)
EDTA (100mM)	1 ml (2ml/100µl)
H ₂ O	98 ml (1L/50ml)

Ammonium acetate (NH₄Ac) (50 ml) 7.5M (molecular weight = 77.08)

ammonium acetate	28.905 g
ddH ₂ O	50 ml

Annex III

Other published manuscript on *Fomitiporia*

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Nuevos registros del género *Fomitiporia* (Hymenochaetales, Basidiomycota) en México

New records of the genus *Fomitiporia* (Hymenochaetales, Basidiomycota) in Mexico

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Resumen. Se describen e ilustran por primera vez para México 6 especies del género *Fomitiporia*: *F. apiahyna*, *F. calkinsii*, *F. dryophila*, *F. langloisii*, *F. maxonii* y *F. texana*, y se amplía la distribución de *F. sonoreae* para el estado de Querétaro. Los ejemplares proceden de 18 estados de la República Mexicana, están depositados en los Herbarios CESUES, ENCB, FCME, IBUG, ITCV, MEXU, UJAT, UNL, UJED de México y en el MUCL de Bélgica. Se presenta un mapa de distribución de las especies estudiadas.

Palabras clave: *Phellinus*, Hymenochaetales, especies neotropicales, distribución.

Abstract. Six species of the genus *Fomitiporia* are described and illustrated for the first time from Mexico and they are *F. apiahyna*, *F. calkinsii*, *F. dryophila*, *F. langloisii*, *F. maxonii* y *F. texana*; *F. sonoreae* is reported from Querétaro State. The specimens are deposited in the Herbaria CESUES, ENCB, FCME, IBUG, ITCV, MEXU, UJAT, UNL, UJED from Mexico and MUCL and proceed from 18 states of the Mexican Republic. Besides, a distribution map of the species is presented.

Key words: *Phellinus*, Hymenochaetales, neotropical species, distribution.

Introducción

El género *Fomitiporia*, descrito por Murrill (1907), incluyó 17 especies que presentaban basidiomas perennes, resupinados con tubos y contexto de color marrón, y las esporas globosas e hialinas; se eligió *F. langloisii* Murrill como la especie tipo. El género fue considerado sinónimo de *Poria* por Saccardo (1912), Overholts (1953), Lowe (1966) y de *Phellinus* por Gilbertson (1979), Ryvarden y Johansen (1980), David et al., (1982), Gilbertson y Ryvarden (1987), Larsen y Cobb-Poulsen (1989), Corner (1991), Ryvarden (1991), Ryvarden y Gilbertson (1994), Núñez y Ryvarden (2000) y Bernicchia (2005). Sin embargo, Fiasson y Niemelä (1984), al realizar un análisis fenético utilizando caracteres morfológicos, genéticos y bioquímicos sobre diversos taxa europeos pertenecientes a los Hymenochaetales, reconocieron y enmendaron *Fomitiporia* y propusieron 5 nuevas combinaciones en el género, considerando *F. langloisii* como sinónimo de *F. punctata* (Fr.) Murrill. Recientemente, Fischer (1996, 2002), Wagner y Fischer (2001, 2002), Fischer y Binder (2004), Larsson et al. (2006) y Decock et al. (2005), al analizar secuencias de diversos genes del ADN, también reconocen *Fomitiporia* como válido. Decock et al. (2007) revisaron el estatus de las especies tropicales americanas del complejo *F. punctata* y encontraron que *F. langloisii* Murrill, *F. dryophila* Murrill y *F. maxonii* Murrill, consideradas como sinónimos de ésta, son especies válidas taxonómicamente, separándose de *F. punctata* por caracteres morfológicos, moleculares y ecológicos. El género *Fomitiporia* se caracteriza por presentar basidiomas resupinados, efuso-reflejados, pileados; himenóforo poroide; sistema hifal dimítico o pseudodimítico, setas himeniales y cistidiolos presentes o ausentes, esporas subglobosas a globosas, de paredes delgadas a gruesas, hialinas, dextrinoides y cianófilas (Decock et al., 2005, 2007). Las especies de este género crecen sobre madera de árboles vivos o muertos en gimnospermas y angiospermas, se distribuyen en regiones templadas y tropicales de todo el mundo y ocasionan una pudrición blanca. En México, diversos autores han citado en los géneros *Fomes* o *Phellinus* 4 especies de *Fomitiporia*. Murrill (1912) citó *Fomitiporia obliquiformis* Murrill para el estado de Morelos; sin embargo, esta especie fue sinonimizada con *Phellinus punctatus* (Fr.) Pilát (= *Fomitiporia punctata* [Fr.] Murrill) por Ryvarden (1985) al estudiar los ejemplares tipo de las especies descritas por Murrill. Posteriormente, *Fomes robustus* P. Karst. o *Phellinus robustus* (P. Karst.) Bourdot et Galzin (= *Fomitiporia robusta* [P. Karst.] Fiasson y Niemelä) han sido mencionadas por diversos autores en distintas regiones de México, como Welden y Lemke (1961) que la citan de Nuevo León y

Veracruz, Castillo et al. (1969) de Nuevo León, Galván-Villanueva y Guzmán (1977) de Morelos, Varela y Cifuentes (1979), Frutis y Guzmán (1983) y Romero-Bautista et al. (2010) de Hidalgo, Guzmán (1983) de Quintana Roo, Acosta y Guzmán (1984) de Zacatecas, Ayala y Guzmán (1984) de Baja California, Ojeda-López et al. (1986) de Guanajuato, Pérez-Silva y Aguirre-Acosta (1986) y Díaz-Moreno et al. (2009) de Chihuahua, Anell y Guzmán (1987) de Veracruz, Díaz-Barriga et al. (1988) de Michoacán, Nava-Mora y Valenzuela (1997) del Estado de México, Valenzuela et al. (2002) de Querétaro, Díaz-Moreno et al. (2005) de Durango y Montaña et al. (2006) de Sonora. Por otro lado, Valenzuela y Chacón-Jiménez (1992) citaron a *Phellinus sonoreae* Gilb. (= *Fomitiporia sonoreae* [Gilb.] Y. C. Dai) de la Reserva de la Biosfera El Cielo en Tamaulipas. Finalmente, Valenzuela et al. (2005) y Romero-Bautista et al. (2010) registraron *P. hartigii* (Allesch. et Schnabl) Pat. (= *F. hartigii* [Allesch. et Schnabl] Fiasson et Niemelä) para el estado de Hidalgo. Como parte de los trabajos que se han realizado sobre las especies poroides de Hymenochaetaceae (Raymundo y Valenzuela 2003; Raymundo et al., 2008, 2009; Valenzuela et al., 1996, 2005, 2007, 2010, 2011) en el presente trabajo se describen e ilustran 7 especies del género *Fomitiporia*; de esta manera, se pretende contribuir al conocimiento de la micoflora de México.

Materiales y métodos

En el presente estudio se realizaron 10 exploraciones de campo en los años 2009 y 2010, recolectándose 365 ejemplares de hongos poliporoides procedentes de los estados de Campeche, Durango, Guerrero, Hidalgo, Jalisco, Nuevo León, Querétaro, San Luis Potosí, Sonora y Tamaulipas, 20 de los cuales pertenecían al género *Fomitiporia*. Los ejemplares se fotografiaron in situ; posteriormente, fueron deshidratados, desinfectados, etiquetados y depositados en la Colección de Hongos del Herbario de la Escuela Nacional de Ciencias Biológicas, IPN (ENCB) con algunos duplicados en MUCL, UAMIZ y FCME. Se revisaron ejemplares depositados en las colecciones de hongos de los herbarios nacionales CESUES, ENCB, FCME, IBUG, ITCV, MEXU, UJAT, UJED y del extranjero MUCL y NY. Para determinar los colores se utilizó la tabla de Kornerup y Wanscher (1978). Los caracteres micromorfológicos se describieron siguiendo los lineamientos propuestos por Decock et al. (2007) y para los caracteres macroscópicos se siguió a Ryvarden (1991) y Cifuentes et al. (1986). Los dibujos están hechos a escala y para su elaboración se utilizó una cámara clara y un microscopio marca Zeiss modelo K-7; las

fotografías fueron tomadas con una cámara digital Nikon Coolpix 4300. El significado de algunos términos se basa en el “Diccionario ilustrado de micología” de Ulloa y Hanlin (2006)

Clave para las especies del género *Fomitiporia* en América.

1. Basidiomas pileado-sésiles 2
1. Basidioma resupinados, efuso-reflejados a pseudopileados 5
2. Setas himeniales presentes, basidioma de aplanado a unglado, poros de 4-6 por mm, basidiosporas de 7.0-9.0 X 6.5-9.0 μm *Fomitiporia texana*
2. Setas himeniales ausentes 3
3. Especie tropical, basidioma triangular a unglado, poros de 6-8 por mm, basidiosporas de (4.48) 4.7-5.12 (5.76) X 4.48-5.12 μm *F. apiahyna*
3. Especies templadas 4
4. Basidiomas en crecimiento sobre *Betula*, triangulares a unglados, poros de 5-6 por mm, basidiosporas de 6-8 X 5.5-6.5 μm *F. bakerii*
4. Basidiomas en crecimiento sobre *Quercus*, aplanados a unglados, poros de 5-6 (7) por mm, basidiosporas de (5.76)6.4-6.72 (7.04) X (5.12) 5.76-6.08 (6.72) μm *F. calkinsii*
5. Setas himeniales presentes 6
5. Setas himeniales ausentes 10
6. Especies en crecimiento sobre bambú..... 7
6. Especies en crecimiento sobre otros hospederos 9
7. Setas con espínulas apicales, basidiosporas de 5.5-7 X 5-6.5 μm *F. spinescens*
7. Setas sin espínulas apicales 8
8. Poros de 2-5 por mm, setas rectas, basidiosporas de 4.5-7 X 4.5-6.5 μm *F. sanctichampagnati*
8. Poros de 5-8 por mm, setas uncinadas, basidiosporas de 5-6.5 X 4.5-6 μm *F. uncinata*
9. Basidiomas que crecen sobre *Salix*, poros de 4-7 por mm, basidiosporas de (6.0)6.5-7.5(8.0) X (5.0)5.5-6.5(7.0) μm *F. Polymorpha*
9. Basidiomas que crecen sobre *Dodonea* o *Lysiloma*, poros de 5-6 por mm, basidiosporas de 5-6.0 (6.5) X 5-5.5 μm *F. sonoriae*
10. Basidiomas en crecimiento sobre coníferas (principalmente sobre *Tsuga* o *Abies*) *F. tsugina*
10. Basidiomas en crecimiento sobre angiospermas 11
11. Basidiomas en crecimiento sobre *Polylepis australis*, de resupinados a pseudopileados, poros de 4-6 por mm, basidiosporas de 6.0-7.5 X 4.8-6.5 μm *F. tabaquilio*
11. Basidiomas en crecimiento sobre otras angiospermas 12
12. Especie neotropical, basidiomas resupinados, poros de 7-9 por mm, basidiosporas de (4.5-)5.3-6.5(-7.0) X (4.0-) 4.8-6.0(-6.7) μm *F. maxonii*
12. Especies de zonas templadas de Norteamérica 13
13. Tamaño de la media de la basidiosporas de 7.0 μm , basidiomas pseudopileados, crece sobre *Quercus* o *Celtis* *F. dryophila*
13. Tamaño de la media de la basidiosporas menor de 6.0 μm , basidiomas resupinados, crece en *Carpinus*, *Cercis*, *Magnolia* y *Robinia*..... *F. langloisii*

Descripciones

Fomitiporia apiahyna (Speg.) Robledo, Decock et Rajchenberg (Figs. 1, 7A)

Mycologia 102 (6):2010. (DOI:10.3852/09-083) $\equiv$ *Fomes apiahynus* Speg.

Basidioma perenne de 60-120 X 22-50 X 22-40 mm, pileado-sésil, triangular a ungulado, ampliamente adherido, de consistencia leñosa. Píleo semicircular a conchado, marrón amarillento (5D8), marrón (7D8) en ejemplares jóvenes, amarillo claro (4A4) en los secos, glabro, zonado a surcado, rimoso en ejemplares viejos; margen entero, obtuso, estéril, de color marrón amarillento (5D8). Himenóforo de color marrón amarillento (5D8) a naranja grisáceo (5B4), con poros circulares a oblongos, de 7-8 por mm, de 130-142 μm de diámetro ($X=138 \mu\text{m}$); disepimiento entero, de 80-96 μm de grosor ($X=89 \mu\text{m}$); tubos de hasta 15 mm de longitud, concoloros con el himenóforo, estratificados. Contexto de hasta 30 mm de grosor, simple, color marrón dorado (5D7), fibroso, zonado concéntricamente. Sistema hifal dimitico, hifas generativas con septos simples, frecuentes, hialinas a marrón dorado, simples, no ramificadas, de 1.92-2.56 μm en diámetro; hifas esqueléticas marrón rojizo, simples, no ramificadas, de 3.2-3.84 μm en diámetro, de paredes gruesas (0.96-1.28 μm de grosor), lumen de 1.92-2.56 μm de ancho; el contexto con hifas generativas hialinas a amarillentas, de 2.24-3.2 μm en diámetro, hifas esqueléticas de color marrón rojizo, 3.2-3.84 μm de diámetro, paredes gruesas (1.28 μm de grosor), lumen 0.64 μm de ancho; trama himenoforal subparalela, de 48-64 μm de ancho, con hifas generativas de septos simples, hialinas, amarillentas a marrón dorado, de 2.4-3.2 μm de diámetro, paredes delgadas; hifas esqueléticas de color marrón amarillento, 3.84-4.48 μm in diámetro, de paredes gruesas (0.64-1.28 μm de grosor), lumen 1.92-2.56 μm de ancho; setas himeniales ausentes; cistidiolos ausentes; basidiolos 10.24-11.52 X 6-7.04 μm , subglobosos, hialinos; basidios de 12.8-14.4 X 7.68-8.32 μm , subglobosos, hialinos, tetraspóricos; basidiosporas (4.48) 4.7-5.12 (5.76) X 4.48-5.12 μm , ($X=4.91$ X 4.56 μm , $n=30$) $R=(0.8-1.04-1.1(-1.2))$, globosas, subglobosas a ovoides, hialinas, fuertemente dextrinoides, cianófilas, lisas, de paredes gruesas, clamidosporas ausentes. *Resumen taxonómico.* *Fomitiporia apiahyna* crece sobre madera de árboles vivos o muertos en bosque tropical caducifolio y bosque tropical perennifolio, ocasionando pudrición blanca; se encontró en altitudes de 60 a 245 m. *Ejemplares revisados.* TAMAULIPAS: municipio de Gómez Farías: 3 km al norte del Hotel Posada Campestre, sierra Madre Oriental, Reserva de la Biosfera El

Cielo. 23°05'05.7" N, 99°09'41.8" O, 28.VII.2009, *T. Raymundo* 2969, 2999, 3030 (ENCB, UAMIZ, MUCL). se puede quedar. CAMPECHE: municipio de Xpujil, Reserva de la Biosfera de Calakmul, alrededores de la zona arqueológica, 3.XII.2010, *T. Raymundo* 3585 (ENCB, MUCL). *Comentarios taxonómicos.* Esta especie se caracteriza por sus basidiomas pileados, de aplanados a unguados o triangulares en vista lateral, la superficie del píleo glabra, surcada a zonada concéntricamente, rimosa cuando viejos, himenóforo con poros pequeños de 7-8 (-9) por mm, la ausencia de setas himeniales y sus basidiosporas pequeñas ($< 6 \mu\text{m}$ en diámetro). La especie es afín a *F. texana*, la cual se diferencia porque presenta setas himeniales abundantes, y los poros y las basidiosporas son más grandes (de 4-6 por mm y $7.0\text{-}9.0 \times 6.5\text{-}9.0 \mu\text{m}$, respectivamente). *F. bakerii* y *F. calkinsii* carecen de setas himeniales, pero se separan por ser especies que crecen sobre *Betula* y *Quercus*, respectivamente, en zonas templadas y tienen los poros y basidiosporas más grandes que *F. apiahyna* (5-6 por mm vs. 7-9 por mm y $> 6 \mu\text{m}$ de diámetro vs. $< 6 \mu\text{m}$, respectivamente) y la especie europea *F. robusta* se separa por tener las basidiosporas más grandes (de $6\text{-}8 \mu\text{m}$ de diámetro). *Fomitiporia apiahyna* se menciona de Sudamérica y Costa Rica por Ryvarden (2004), como *Phellinus apiahynus* (Speg.) Rajchenb. et J. E. Wright, de Ecuador, por Amalfi et al. (2010). En el presente trabajo se cita por primera vez para México.



Figura 1. *Fomitiporia apiahyna*: A, basidioma; B, superficie del píleo. *T. Raymundo* 3030 (fotos R. Valenzuela). Escala 10 mm.

Fomitiporia calkinsii (Murrill) Vlasák et Kout (Figs. 2, 7B)

Mycological Progress 10 (4): 2011, DOI 10.1007/s11557.010.0715.0 $\equiv$ *Pyropolyporus calkinsii* Murrill, Bull. Torrey Bot. Club 30(2):109-120, 1908.

Basidiomas perennes, de 62-300 X 36-140 X 60-86 mm, pileado-sésiles, aplanados a unglados, ampliamente adheridos, de consistencia leñosa; píleo semicircular, de color marrón naranja a marrón amarillento (6C6-7, 6D6-7), marrón (6E6), marrón rojizo (7E7), marrón grisáceo (6D3-E3) a gris plata cuando maduro, gris obscuro (6F2) a negro cuando viejo, glabro, liso a zonado concéntricamente en ejemplares jóvenes, surcado cuando maduro o viejo, después agrietado con la edad, formando una costra negra de hasta 2 mm de grosor; margen estéril, redondeado, de pálido amarillento (4A2), amarillo claro (4A3) a café naranja (6C6-7, 6D6-7). Himenóforo de color naranja grisáceo (5B4), marrón grisáceo (6E3) a marrón rojizo obscuro (7E6), con poros circulares, de 5-6 (7) por mm, de 96-160 X 96-144 μm en diámetro ($X=128\mu\text{m}$); disepimiento entero, delgado a grueso 51.2-64 μm ($X=53.75\mu\text{m}$); tubos de 12-15 mm de longitud, estratificados, concoloros con los poros, con micelio blanquecino en las capas viejas. Contexto de 30-50 mm de grosor, amarillo (4A6), amarillo dorado a marrón (5D8), fibroso, zonado concéntricamente. Sistema hifal dimítico, hifas generativas de septos simples, hialinas a amarillento pálido, pared delgada, de 2.56-3.2 μm de diámetro, hifas esqueléticas marrón rojizo, paredes gruesas (0.96-1.28 μm), lumen (1.28-3.2 μm), 3.84-4.48 μm de diámetro; trama himenoforal subparalela, (48-) 80-96 (-115) μm de grosor, con hifas generativas de septos simples, hialinas, amarillentas a marrón rojizo, paredes delgadas, de 1.28-2.56 μm de diámetro, hifas esqueléticas marrón amarillento a marrón rojizo, de 2.56-3.84 μm de diámetro, paredes gruesas (0.96-1.28 μm), lumen (0.64-1.5 μm). Setas himeniales ausentes; cistidiolos de 10.4-12.8 X 3.2-4.8 μm , fusoides, hialinos, pared delgada. Basidiolos de 10.88-11.5 X 12.16-18 μm , subglobosos, hialinos. Basidios 12-14.4 X 10-11.4 μm , subglobosos, hialinos, tetraspóricos, esterigmas hasta 3.84 μm de largo. Basidiosporas de (5.76) 6.4-6.72 (7.04) X (5.12) 5.76-6.08 (6.72) μm ; ($X=6.49 \times 5.92\mu\text{m}$, $n=30$) $R=(1.0) 1.05-1.11 (1.2)$, subglobosas a ovoides, hialinas, dextrinoides, cianófilas, lisas, paredes gruesas. Clamidosporas ausentes. *Resumen taxonómico.* *Fomitiporia calkinsii* se encontró en la base, las partes medias y altas de los troncos de árboles vivos de *Quercus* spp. en bosques de encino, bosques mixtos de *Pinus*, *Quercus* y *Arbutus* y bosque mesófilo de montaña, en altitudes de 1 500 a 2 400 m; ocasiona una pudrición blanca en la madera. *Ejemplares revisados.* **México:** CHIHUAHUA: municipio de Urique, Cerocahui, sierra Tarahumara, 28.VII.2005, T. Raymundo y R. Valenzuela 467 (ENCB). GUANAJUATO: municipio de Victoria, San Agustín, 19.XII.1984, M. L. Sandoval 51, S. Ojeda 98 (ENCB). GUERRERO: municipio de Chilpancingo, aserradero Campo Morado, 17.V.1960, G.

Guzmán 2308 (ENCB); municipio de Taxco, Km. 8 de la carretera Taxco-Ixcateopan, cerca de Tetipac, 26.VII.1986, *López-Griego y Pérez-Ramírez 645* (FCME- 13745); cañada de Agua Fría, Omiltemi, 12.VIII.1984, *Romero-Palacios s.n.* (FCME-13134). HIDALGO: municipio de Tlanchinol, Km. 157 de la carretera Pachuca- Tampico, 2 km antes de llegar a Casetas, 11.V.1985, *S. Ojeda 109* (ENCB); Fosas de Tlanchinol, 15.V.1988, *R. Valenzuela 6075* (ENCB); municipio de Zacualtipán, Km.100 de la carretera Pachuca-Tampico, 2 km antes de llegar a Alumbres, 11.V.1985, *R. Valenzuela 4326* (ENCB). ESTADO DE MÉXICO: municipio de Tejupilco, Cañadas de Nanchititla, 22.III.1987, *R. Valenzuela 6113*; Km. 11 camino de terracería a Nanchititla, 8.VIII.1987, *R. Nava 414*; 30.VII.1988, *R. Valenzuela 6632*; 1 km al este del poblado de Nanchititla, 22, 1987, *A. González- Velázquez 696*; Km. 15 camino de terracería a Nanchititla, 8.X.1988, *A. Kong Luz 637*, *R. Nava 414*, 437; 8.VII.1990, *R. Valenzuela 7016* (todos en ENCB). NUEVO LEÓN: municipio de Santiago, La Chancaca, 12.XII.1967, *J. Castillo 213* (UANL, ENCB); Potrero Redondo, 2.VIII.1968, *R. S. Hector s/n* (UANL, ENCB); municipio de Monterrey, Las Huertas, 1.XI.1969, *C. Girón s.n.* (UANL, ENCB). OAXACA: municipio Santa Martha Latuví, 5.VIII.2007, *T. Raymundo y R. Valenzuela 1601* (ENCB). QUERÉTARO: Reserva de la Biosfera Sierra Gorda, municipio de Landa de Matamoros, Km. 230 carretera Jalpan-Xilitla, Parador Santa Martha, 21°16'23.1" N, 99°09'36.5" O, 16.VI.2009, *R. Fernández 4524* (ENCB); 24.VII.2009, *R. Valenzuela 13382*, *T. Raymundo 2903* (UAMIZ, MUCL). SAN LUIS POTOSÍ: Km. 64 de la carretera Río Verde-Cd. Valles, 11.XI.2007, *T. Raymundo y R. Valenzuela 1900* (ENCB); Huasteca potosina, municipio de Río Verde, Km. 81 de la carretera San Luis-Río Verde, 22°32'12" N, 100°27'31.2" O, 13.VI.2009, *A. Uribe y J. Vergara 10*, *R. Valenzuela 13343*, *T. Raymundo 2684* (ENCB). **Estados Unidos de América:** FLORIDA, enero de 1887, *W.W. Calkins s.n.* (NY 742982, 742984, ejemplares TIPO de *Pyropolyporus calkinsii* Murrill); marzo de 1923, *W. A. Murrill 215* (NY). *Comentarios taxonómicos.* Esta especie se caracteriza por presentar basidiomas pileados, de aplanados a ungulados, muy robustos, con la superficie del píleo concéntricamente zonada o surcada, agrietada en ejemplares viejos, el himenóforo con poros de 5-6 (7) por mm, setas himeniales ausentes y basidiosporas de tamaño medio (entre 6 y 7 µm de diámetro). Una especie afín es *F. robusta*; Lowe (1957) la menciona de Norteamérica, como *Fomes robustus*; Gilbertson (1979), Larsen y Cobb-Pouille (1989) y Gilbertson y Ryvarden (1987), como *Phellinus robustus*, y de México por los autores citados en la introducción.

No obstante, los ejemplares de América no corresponden con *F. robusta*, que es morfológicamente muy similar a *F. calkinsii*; sin embargo, el análisis filogenético recientemente realizado por Vlasák y Kout (2010) confirma la separación de ambas especies, aunado a que *F. robusta* se distribuye únicamente en Europa y norte de Asia, no así *F. calkinsii* que sólo se localiza en Norteamérica. Ambas utilizan *Quercus* como sustrato, lo que indica una especificidad por el hospedero. Finalmente, las características morfológicas de los ejemplares mexicanos corresponden con las de los ejemplares de *Pyropolyporus calkinsii* descrita por Murrill (1903); por tanto, esta especie se registra por primera vez para México.

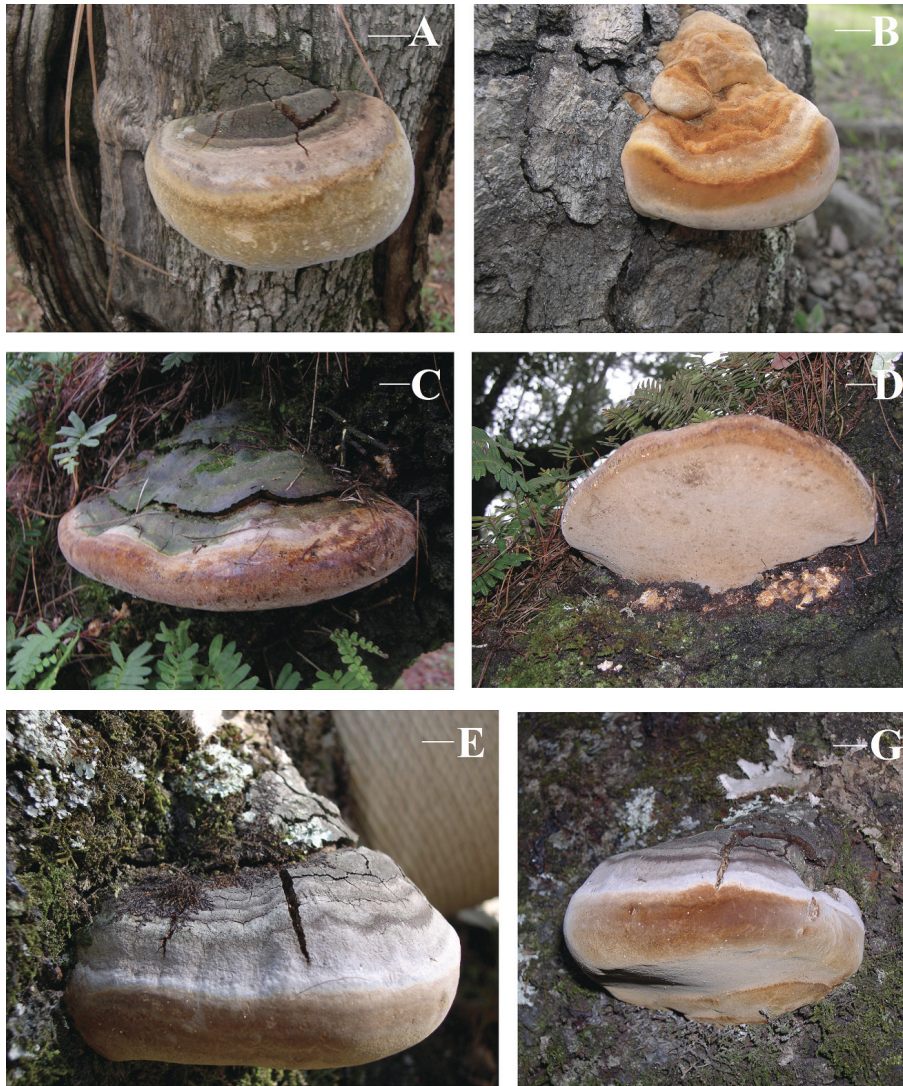


Figura 2. *Fomitiporia calkinsii*. A, basidioma, T. Raymundo y R. Valenzuela 467 (foto R. Valenzuela); B, basidioma, T. Raymundo y R. Valenzuela 1601 (foto R. Valenzuela); C, basidioma, D, himenoforo, R. Valenzuela 13382 (fotos R. Valenzuela); E-F, basidioma, T. Raymundo 2903 (fotos: T. Raymundo). Escala 10 mm.

Fomitiporia dryophila Murrill (Figs. 3, 7C).
North American Flora 9. Part I: 8, 1907.

Basidioma perenne, de 90-140 X 60-110 X 5-25 mm, resupinado a pseudopileado, de consistencia corchosa a leñosa. Pseudopíleo formándose por las capas de poros que se acumulan con la edad, de color gris oscuro a negro, agrietado a rimoso; margen estéril, hasta 2 mm de ancho, de color marrón dorado (5D8) a naranja grisáceo (5B4). Himenóforo de color miel, dorado a marrón dorado (6D6), opaco a ligeramente iridiscente con la edad, poros circulares, elongados en la parte con crecimiento oblicuo, de 6-8 por mm, 80-125 μm de diámetro ($X = 102.5 \mu\text{m}$). Tubos de 4 a 5 mm de longitud, concoloros con los poros, estratificados. Contexto de 10-20 mm de grosor, de color marrón claro (6D4) a marrón rojizo (6E8), leñoso, azonado. Sistema hifal dimítico, hifas generativas de septos simples, hialinas a pálido amarillento, de pared delgada, a veces bifurcadas, de 2-2.8 μm de diámetro; hifas esqueléticas marrón amarillento a marrón rojizo, de paredes gruesas (8-1.2 μm de grosor), de 2.4-3.2 μm de diámetro. Setas himeniales ausentes, cistidiolos no observados. Basidios de 14.8-16 X 9.6-12.6 μm , piriformes a globosos, hialinos, tetraspóricos, esterigmas de 2.4-3 μm de largo. Basidiosporas de (5.6) 6.4-8 (-8.4) X (5.0) 5.7-7.2 (-7.6) μm ($X = 7.2 \times 6.4 \mu\text{m}$, $n = 30$) $R = (1.0-) 1.05-1.2 (-1.3)$, subglobosas a globosas, hialinas, dextrinoides, cianófilas, lisas, de paredes gruesas; clamidosporas ausentes. *Resumen taxonómico.* *Fomitiporia dryophila* ocasiona pudrición blanca sobre *Byrsonima crassifolia* y *Psidium* en bosques tropicales de *Quercus oleoides* y *Byrsonima crassifolia* y de *Bumelia socorrensis* y *Psidium galapageium*, respectivamente, en altitudes de 200 a 850 m. *Ejemplares revisados.* **México:** COLIMA: isla Socorro, archipiélago Revillagigedo, 1.III.1967, R. Cruz 1605a (ENCB). JALISCO: municipio Guadalajara, barranca de Huentitán, 22.VII.1986, L. S. Vázquez 79 (IBUG, ENCB). NUEVO LEÓN: municipio Sabinas Hidalgo, Presa Sombreretillo, 4.IV.1985, R. Valenzuela 5196 (ENCB). QUERÉTARO: municipio Jalpan de Serra, Km.16 de la carretera Jalpan-Río Verde, 28.VI.1996, R. Valenzuela 8312 (ENCB). SONORA: municipio Álamos, Cañitas, 15.IX.2006, R. Valenzuela 13073, 13147 (CESUES, ENCB). TABASCO: municipio Jonuta, ejido Zapotero, 22.X.1991, Rodríguez-Bahena 1054 (UJAT, ENCB). **Estados Unidos de América:** FLORIDA, Duval County, Jacksonville, swamp forest, 28.XII.1953, A. S. Rhoads s/n. (Center Forest Mycology Research Fungi of Florida). *Comentarios taxonómicos.* Esta especie se caracteriza por presentar basidiomas resupinados a

pseudopileados, formándose estos últimos por las capas de poros que se acumulan con la edad; pseudopileo negro, agrietado a rimoso, ausencia de setas himeniales y las basidiosporas de 6.4 a 8 μm de diámetro. *F. dryophila* fue sinonimizada con *Fomes robustus* por Lowe (1957), con *Poria punctata* por Lowe (1966) y con *Phellinus punctatus* por Ryvarden (1985) y Gilbertson y Ryvarden (1987). Sin embargo, estudios filogenéticos realizados por Decock et al. (2007) reconocen *F. dryophila* como especie válida, separándola de *F. punctata* por tener la superficie de los poros más brillante y el margen formando un pseudopileo negro y rimoso. *Fomitiporia robusta* se separa por los basidiomas verdaderamente pileados y por la presencia de setas himeniales. Otra especie afín es *F. langloisii* que vive simpátricamente en el sur de los Estados Unidos de América (EUA) con *F. dryophila* y se traslapa parcialmente en los hospederos, pero se separa por sus basidiomas resupinados y las esporas más pequeñas, de 5.5-6.5 (-7) μm de diámetro (Decock et al., 2007). *Fomitiporia dryophila* se cita por primera vez para México de los estados de Colima, Jalisco, Nuevo León y Sonora.

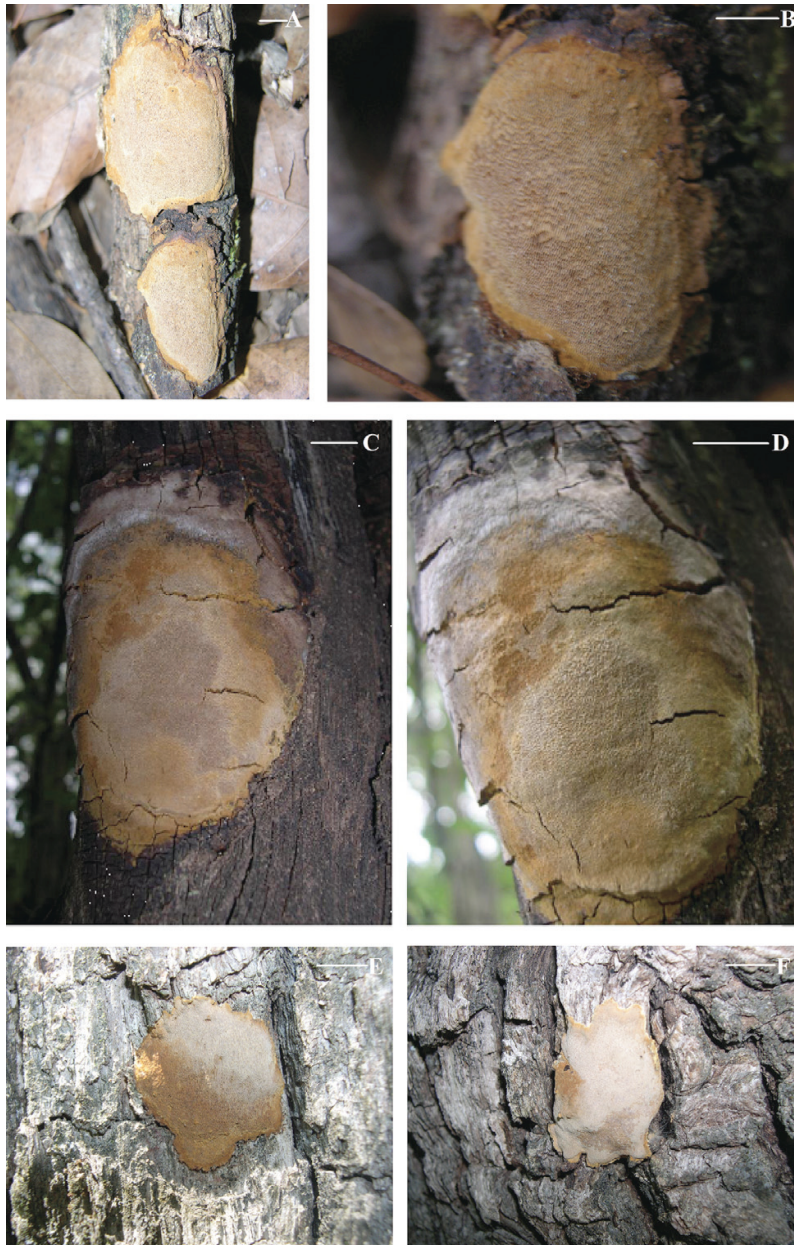


Figura 3. *Fomitiporia dryophila*. A-B, basidoma, *R. Valenzuela* 8312; C-D, basidioma, *R. Valenzuela* 13073; E-F, basidioma, *R. Valenzuela* 13147 (foto R. Valenzuela). Escala 10 mm.

***Fomitiporia langloisii* Murrill (Figs. 4, 7D)**

North American Flora 9.Part I: 9, 1907.

Basidioma perenne, de 50-90 X 20-50 X 2-18 mm, resupinado a efuso, ampliamente adherido, de consistencia leñosa a corchosa; margen velutinoso, pálido amarillento a dorado (5D8) a marrón (6D6)); superficie de los poros marrón grisáceo (6D5) a marrón dorado (5C4), en ejemplares jóvenes y en fresco con tintes rosados, ligeramente iridiscente en seco; poros circulares a elipsoides cuando el ejemplar crece oblicuo, (6-)7-8(-9)/mm, (95-)100-129(- 140) µm de diámetro. Disepimiento delgado, entero, de 25-50 µm de grosor; subiculum reducido a una delgada capa entre las capas de tubos de color canela a marrón naranja (6D6-7); tubos distinguiblemente estratificados de 12 (-15) mm de longitud, concoloros con los poros, con el tiempo van rellenándose de micelio blanquecino a amarillento. Sistema hifal dimítico, hifas generativas de septos simples, hialinas a amarillentas, de pared delgada 2-3 µm de diámetro. Hifas esqueléticas, subparalelas en la trama himenoforal, de color amarillento pálido a marrón dorado, de pared gruesa, de 2.5-3.7 µm de diámetro. Setas himeniales ausentes, basidiolos piriformes a subglobosos, 10-11.5 X 7.8-9.0 µm; basidios tetraspóricos, piriformes a subglobosos, cistidiolos hialinos, paredes delgadas, hifoides, fusiformes a lageniformes, base bulbosa, ápice elongado de 10-18 X 3.0-5.0 µm. Basidiosporas hialinas, globosas, subglobosas a ovoides, de paredes gruesas, cianófilas, dextrinoides, (4.7-)5.3-6.7 (-7.3)×(4.0-) 4.8-6.0 (-6.5) µm. *Resumen taxonómico.* Esta especie crece sobre madera muerta de diversas angiospermas, como *Cordia boiseieri* D. C., *Enrethia anacua* (T. et B.) I. M., en matorral xerófilo así como en *Quercus*, en altitudes de 700 m. *Ejemplares revisados.* COAHUILA: municipio de Múzquiz, 22.X.1999, R. Díaz 600, 616, 617, 619 (UJED, ENCB). MORELOS: municipio de Cuernavaca, frente a la cueva de los Amates, Km. 7 al este de Cuernavaca, 7.V.1977, J. Pérez-Ortiz 570 (ENCB). NUEVO LEÓN: municipio de Allende, Puente Raíces, 13.IV.1969, J. Castillo 629 (UANL, ENCB); municipio de Sabinas Hidalgo, Ojo de Agua, 5 km al NO de Sabinas Hidalgo, 7.VII.1988, R. Valenzuela 6539 (ENCB); Presa Sombreretillo, 4.IV.1985, R. Valenzuela 5194, 5196, 6903, 6904 (ENCB); 5 km al S de Sombreretillo, 28.XII.2007, R. Valenzuela 13192 (ENCB). SAN LUIS POTOSÍ: Km. 70 de la carretera Cd. Valles-Río Verde, 26.IX.2006, T. Raymundo y R. Valenzuela 1273; 13.VI.2009, T. Raymundo 2666, R. Valenzuela 13783 (ENCB). *Comentarios taxonómicos.* Esta especie se caracteriza por presentar basidiomas resupinados, ampliamente adheridos, por la ausencia de setas himeniales y las basidiosporas de menor tamaño, de

5.5-6.5 (-7) μm de diámetro. Una especie afín es *F. dryophila*, pero se separa por sus basidiomas pseudopileados y las esporas más grandes, de 6.4 a 8 μm de diámetro (Decock et al., 2007). *F. langloisii* se menciona por primera vez para México de los estados de Coahuila, Morelos, Nuevo León y San Luis Potosí. Véase comentarios taxonómicos de *F. dryophila* y *F. maxonii* para tener una mayor apreciación de las diferencias entre estas especies.

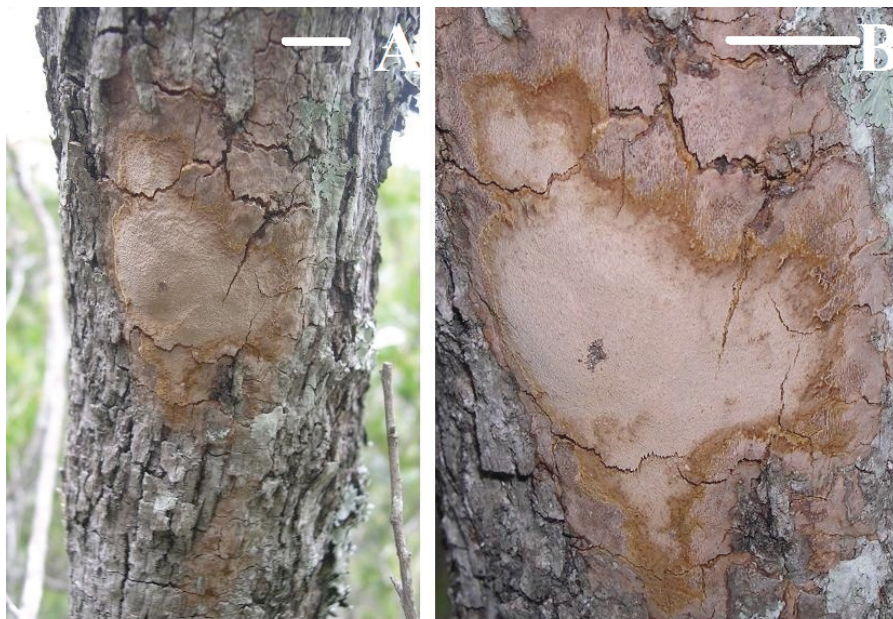


Figura 4. *Fomitiporia langloisii*. A-B, basidioma, T. Raymundo 2666 (fotos T. Raymundo). Escala 10 mm.

Fomitiporia maxonii Murrill (Figs. 5, 7E)
North American Flora 9. Part I: 11, 1907.

Basidioma perenne, de 200-1000 X 100-300 X 10-90 mm, resupinado, corchoso a leñoso, fácilmente separable del sustrato; margen estéril, de 4-10 mm de ancho, de blanquecino a amarillento pálido (3A4) cuando fresco, y marrón anaranjado (5C6), color caramelo a marrón oxidado cuando viejo o al secarse, densa y finamente aterciopelada, agudo. Himenóforo de color marrón a chocolate (6E5-6) cuando fresco, marrón grisáceo (6E4-5), marrón oscuro (6F5) cuando viejo o al secarse, iridiscente, entonces al moverse cambia a rubio dorado (6D4) o naranja grisáceo (5B4) o marrón grisáceo

ligero (6D5); poros circulares a elipsoides u oblicuos, 7-9 por mm, (80-) 90-120 (-30) μm ($X=104$); disepimiento entero, delgado, (20-) 20-52 (-65) μm , tubos hasta 9 mm de longitud, marrón grisáceo a marrón claro o color chocolate (6D7), estratificados, se van rellenando de micelio blanquecino a amarillento en las capas más viejas. Subículo de 0.3-1.5 mm de grosor, naranja pardusco (6D6- 7) a color canela (6E6), densamente fibroso, homogéneo o con una línea negra. Sistema hifal dimítico, hifas generativas de septos simples, hialinas a amarillentas, de paredes delgadas, 2-3 μm de diámetro; hifas esqueléticas, pálido amarillento a marrón dorado, paredes gruesas, 2.5-4.0 μm de diámetro. Setas himeniales ausentes; cistidiolos de 7.5-11.5 X 3.0 -5.5 μm , fusiformes, ventricosos a lageniformes, hialinos. Basidiolos de 7.5-9.0 X 6.0-8.5 μm , piriformes a subglobosos, hialinos. Basidios 7.5-10. 3 X 6.2-7.0 μm , piriformes a subglobosos, hialinos, tetraspóricos, esterigmas de 2.4-2.8 μm de largo. Basidiosporas (4.5-) 5.3-6.5 (-7.0) X (4.0-) 4.8-6.0 (-6.7) μm , ($X=6.0$ X 5.5 μm , $n=30$), $R=(1.0-1.1-1.2 (-1.3))$, subglobosas a globosas, ligeramente obovadas, hialinas, dextrinoides, cianófilas, lisas, de paredes gruesas; clamidosporas ausentes. Cristales romboidales hialinos, abundantes en el himenio. *Resumen taxonómico.* *Fomitiporia maxonii* es común sobre árboles vivos de *Citrus* en huertos o madera muerta de diversas angiospermas, como *Cordia*, en bosque tropical subcaducifolio en elevaciones de 600-1 500 m snm. Presenta amplia distribución en los bosques tropicales del continente americano, en Argentina, Belice (Ryvarden, 2004), Brasil (Ryvarden y De Meijer 2002), Argentina, Costa Rica, Cuba, Ecuador, Jamaica y Venezuela (Decock et al., 2007). *Ejemplares revisados.* HIDALGO: municipio de San Bartolo Tutotepec, 21.VIII.1969, *J. Gimete 175-A* (ENCB); municipio de Molango, plaza principal de Molango, 1.X.1992, *R. Valenzuela 6182* (ENCB). GUERRERO: municipio de Cocula, balneario Machito de las Flores, 11.III.2010, *T. Raymundo 3430* (ENCB); Km. 6 carretera Cocula-Cuetzala del Progreso, 17.IV.2010, *E. Salinas 421, 425, 427* (ENCB). JALISCO: municipio de La Huerta, Reserva de la Biosfera Chamela-Cuixmala, camino Ardilla, 23.X.2009, *T. Raymundo 3329*, *R. Valenzuela 13900* (ENCB); Eje Central, 27.IX.2010, *T. Raymundo 3479, 3501* (ENCB). MORELOS: 2 km al sur de la desviación a Ahuehuetzingo, sobre la carretera libre a Puente de Ixtla, 15.I.1995, *R. Valenzuela 7293* (ENCB). OAXACA: Río Salado, Km. 166 de la carretera Oaxaca a Puerto-Escondido, 14.IX.2003, *T. Raymundo y R. Valenzuela 268* (ENCB); Oaxaca de Juárez, instalaciones del CIIDIR, 7.VIII.2007, *T. Raymundo y R. Valenzuela 1566* (ENCB). QUERÉTARO: municipio de Pinal de Amoles, Km.160 de la carretera San Juan del Río-

Jalpan de Serra, 17.XI.1993, *R. Valenzuela* 7283 (ENCB). TAMAULIPAS: Km. 68 de la carretera Ciudad Victoria -Soto la Marina, 12.VI.1983, *R. Valenzuela* 1461 (ENCB); municipio de Hidalgo, huerta de naranjos con riego Hacienda Santa Engracia, 27.XI.2004, *F. C. Pérez-Sosa* 9 (ITCV, ENCB). VERACRUZ: municipio de Chiconquiaco, 2 km al norte de Chiconquiaco, 1.IX.1988. *R. Valenzuela* 6282 (ENCB). ARGENTINA: MUCL 51333. *Comentarios taxonómicos*. Se caracteriza por tener basidiomas resupinados, perennes con márgenes blanquecinos a amarillentos cuando frescos, el himenóforo es de color marrón a chocolate, iridiscente, dando tonalidades más brillantes, poros pequeños de 7-9 por mm, setas himeniales ausentes y basidiosporas de 5.3-6.5 (-7.0) μm . Fue sinonimizada con *P. punctatus* por Ryvar den (1985, 2004), pero se separan morfológicamente por el tamaño más grande de las esporas (de 6.5-8.0 μm) de esta especie y por el análisis filogenético que realizaron Decock et al. (2007) donde ambas especies se separan en clados distintos y dichos autores reconocen *F. maxonii* como especie válida. Especies afines son *F. langloisii* y *F. dryophila*; la primera, aunque con esporas de tamaño muy parecido, se separa por sus colores más brillantes en el himenóforo y poros ligeramente más grandes (de 6-8 por mm); se diferencia de la segunda por las basidiosporas más grandes (de 6.4-8 (-8.4) X (5.0) 5.7-7.2 (-7.6) μm) y por un pseudopíleo negro que desarrolla en el basidioma, aunado a que *F. maxonii* presenta una distribución amplia en el Neotrópico y en Sudamérica, sólo crece en ecosistemas tropicales y los requerimientos ecológicos de ambas especies, incluyendo hospederos, difieren. Decock et al. (2007) señalan que probablemente *F. maxonii* es endémica del Neotrópico. Este es el primer registro de la especie para México.

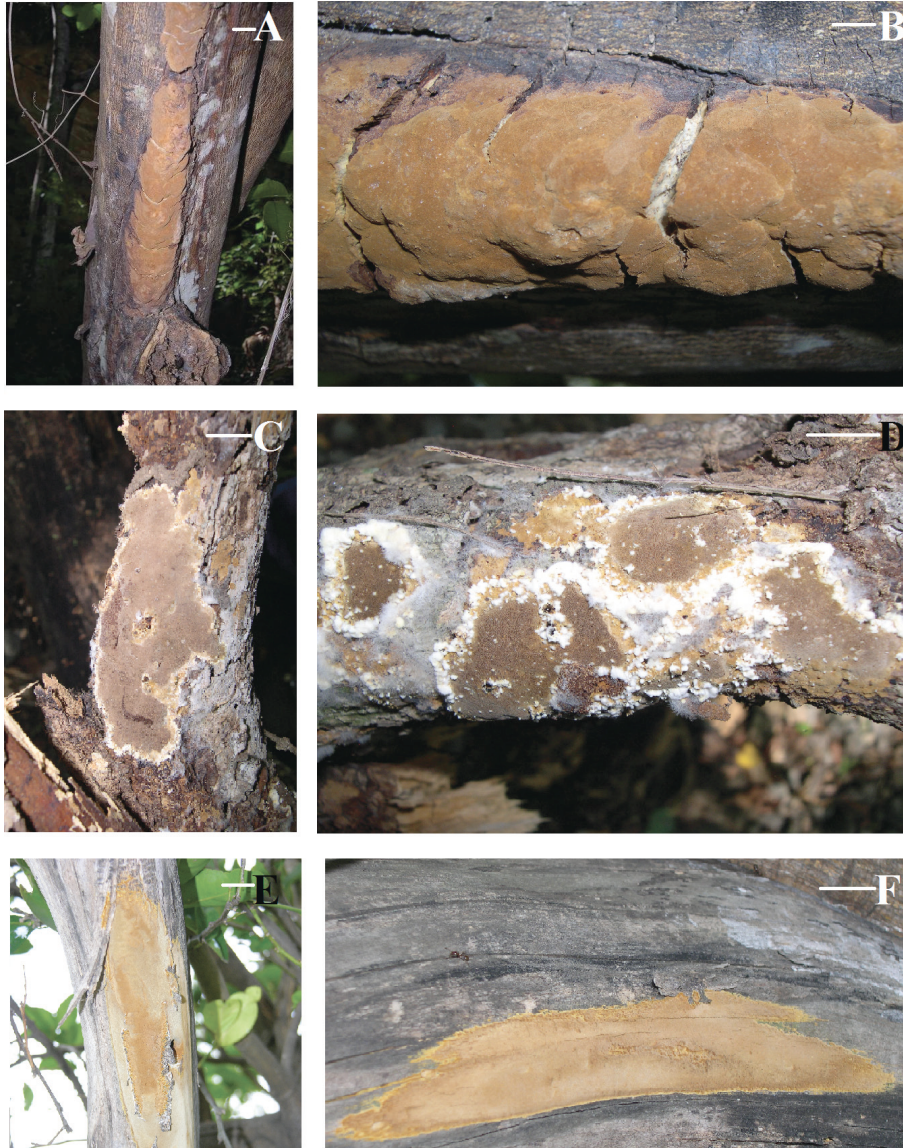


Figura 5. *Fomitiporia maxonii*. A-B, basidioma, *T. Raymundo* 3430 (foto T. Raymundo); C-D, basidioma, *T. Raymundo* 3329 (foto T. Raymundo); E-F, basidioma, *T. Raymundo* y *R. Valenzuela* 1566 (foto R. Valenzuela). Escala 10 mm.

Fomitiporia sonora (Gilb.) Y. C. Dai (Fig. 7F)
Mycotaxon 9: 77, 1979 $\equiv$ *Phellinus sonora* Gilb.

Basidioma perenne, de 50-70 X 25-30 X 10 mm, resupinado, completamente adherido, consistencia leñosa; margen estéril, de color café amarillento a pardo rojizo, velutinoso a glabro. Himenóforo de pardo amarillento a pardo rojizo, con poros circulares, de 5-6 por mm, disepimiento entero, tubos de hasta 7 mm de longitud, concoloros a los poros, estratificados, rellenos de micelio blanco y amarillo en los estratos más internos. Contexto hasta 3 mm de grosor, de color pardo amarillento, fibroso a corchoso, con una línea negra que lo separa del sustrato. Sistema hifal dimítico, con hifas generativas de septos simples, hialinas a amarillentas, de paredes delgadas, ramificadas, de 2.5-3 μ m de diámetro. Hifas esqueléticas, amarillentas a café rojizo, paredes subgruesas (1.2- 1.6 μ m), de 3.5-4 μ m de diámetro. Setas himeniales de 21-44 X 5-8 μ m, ventricosas, amarillentas a café rojizo, de paredes gruesas, escasas. Cistidiolos de 12-44 X 4-9.5 μ m, ventricoso-rostrados, con la porción apical alargada, hialinos, de paredes delgadas, abundantes. Basidios no observados. Basidiosporas de 5-6.0(-6.5) X 5-5.5 μ m, subglobosas a globosas, hialinas, dextrinoides, cianófilas, lisas, de paredes gruesas; clamidosporas ausentes. Cristales romboidales hialinos, de 9.5-17 X 5-10 μ m. *Resumen taxonómico.* Crece sobre *Lysiloma* en bosque tropical caducifolio, en altitudes de 240-350 m, conocida de Arizona, EUA (Gilbertson et Ryvardeen, 1987) y de Tamaulipas (Valenzuela y Chacón-Jiménez, 1991). *Ejemplares revisados.* TAMAULIPAS: municipio de Gómez Farías, Reserva de la Biosfera El Cielo, S. Chacón-Jiménez 82 (ITCV, ENCB). QUERÉTARO: municipio de Pinal de Amoles, La Cuesta, 13.XI.1993, R. Valenzuela 6252 (ENCB). *Comentarios taxonómicos.* *Fomitiporia sonora* se caracteriza por los basidiomas resupinados completamente adheridos al sustrato, poros de tamaño mediano (de 5-6 por mm), setas himeniales alargadas y por el tamaño de sus esporas, todo lo cual la separa de las especies del complejo *F. robusta* (*F. apiahyna*, *F. robusta*, *F. texana*, entre otras) por ser pileadas, y de las especies americanas del complejo *F. punctata* (*F. dryophila*, *F. maxonii* y *F. langloisii*) que carecen de setas himeniales. Fue citada por primera vez para México por Valenzuela y Chacón-Jiménez (1991); en el presente trabajo se amplía la distribución para el estado de Querétaro.

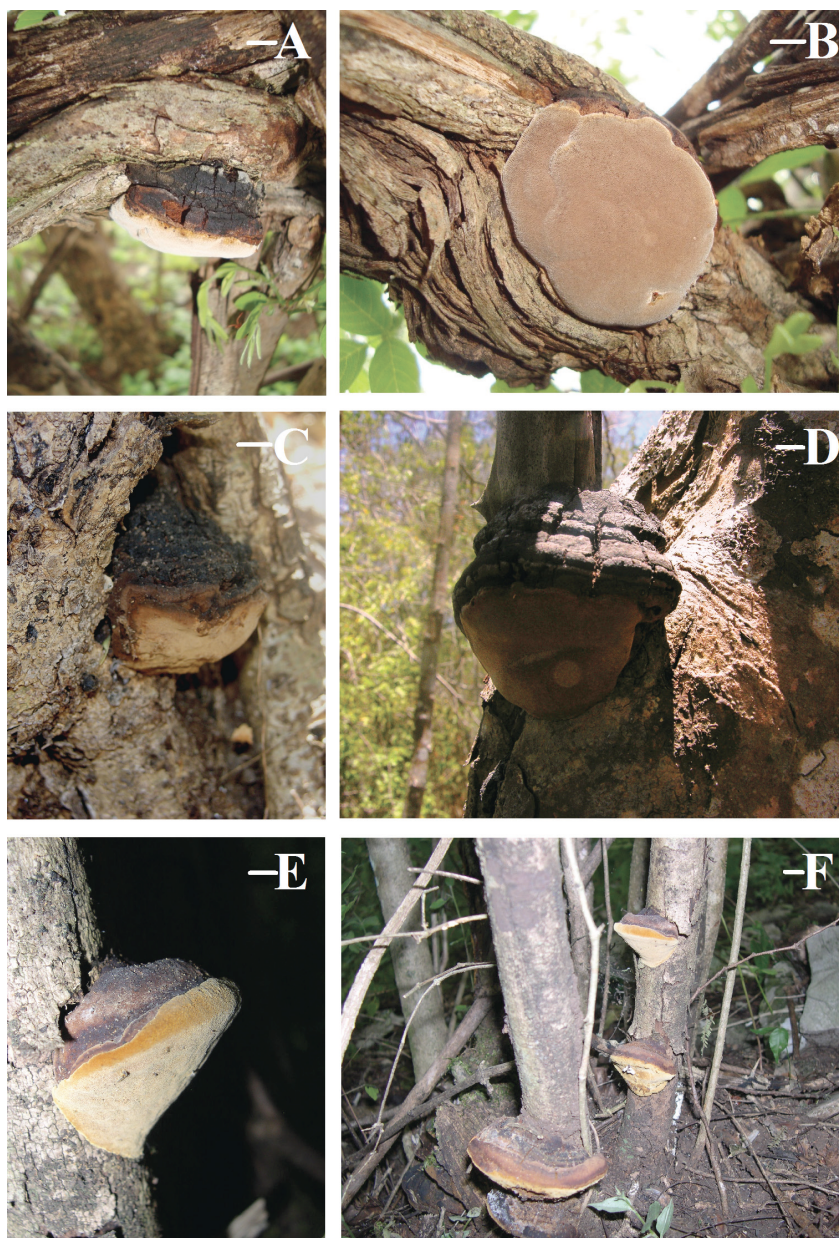


Figura 6. *Fomitiporia texana*: A-B, basidioma, *E. Salinas 08* (foto E. Salinas); C-D, basidioma, *R. Valenzuela 13924* (foto T. Raymundo); E-F, basidioma, *T. Raymundo* y *R. Valenzuela 1991* (foto T. Raymundo). Escala 10 mm.

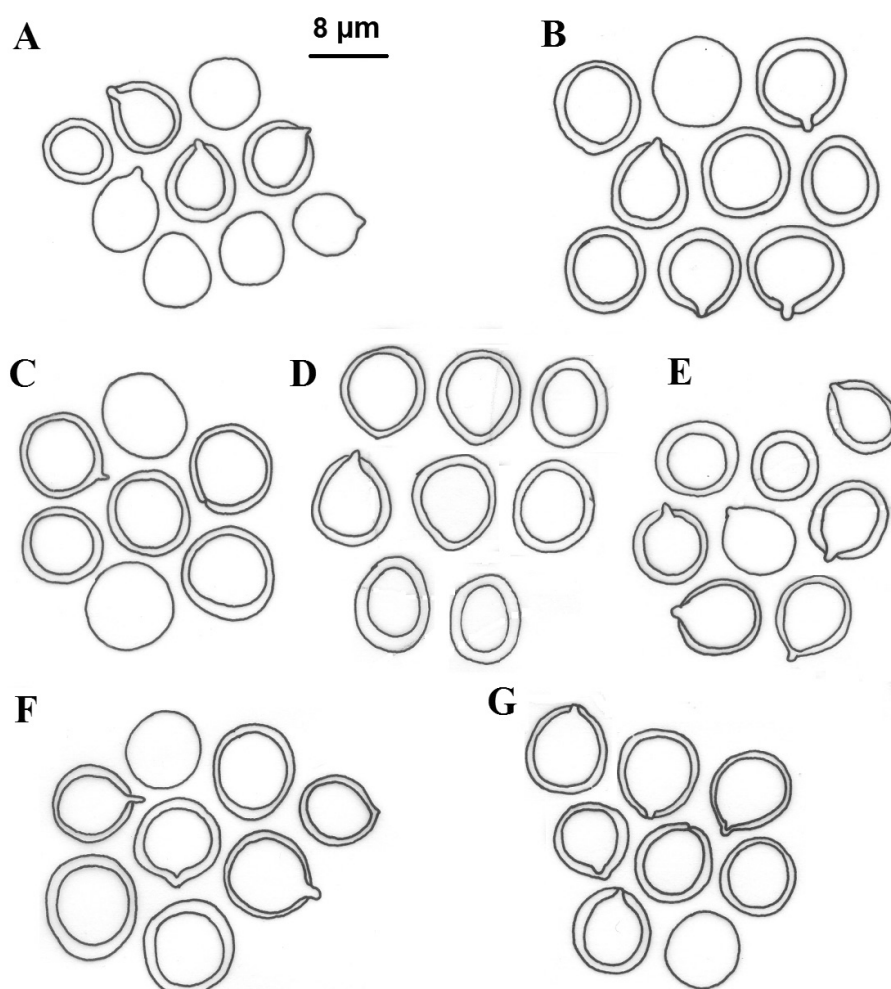


Figura 7. Basidiosporas de *Fomitiporia*: A, *F. apiatryna*; B, *F. calkinsii*; C, *F. dryophila*; D, *F. langloisii*; E, *F. maxonii*; F, *F. sonora*; G, *F. texana*.

Fomitiporia texana (Murrill) I. Nuss (Figs. 6, 7G)

Bibl. Mycol.105:108, 1986 $\equiv$ *Pyropolyporus texanus* Murrill

Basidioma perenne, de 60-70 X 40-60 mm, pileadosésil, triangular a unguulado, ampliamente adherido al sustrato, de consistencia leñosa. Píleo semicircular, de color marrón pálido a marrón amarillento cuando joven, de

marrón rojizo, marrón grisáceo a negro al madurar o cuando viejo; aterciopelado cuando joven, glabrescente al madurar, liso cuando joven, agrietado y rimoso al madurar, con una costra negra de hasta 2 mm de grosor. Margen estéril, obtuso y redondeado, aterciopelado cuando joven, glabrescente, de color marrón pálido, marrón amarillento a marrón rojizo. Himenóforo de color marrón pálido, a marrón amarillento, con poros circulares a oblongos, de 4-6 por mm, 204-288 X 196-224 μm de diámetro, ($X = 228 \mu\text{m}$), disepimiento entero, 144-176 μm de grosor. Tubos de 4-10 mm de longitud, concoloros a los poros, estratificados. Contexto de 20-36 (-50) mm de grosor, simple, azonado, fibroso, duro, de color marrón amarillento. Sistema hifal dimítico, hifas generativas con septos simples, hialinas a amarillentas, paredes delgadas, de 2.4- 3.2 μm de diámetro; hifas esqueléticas marrón rojizo, de paredes gruesas (0.8-2.0 μm), de 3.4-4.8 μm de diámetro. Trama himenoforal subparalela a ligeramente entrelazadas, de 60.8-80 μm de grosor, hifas generativas de septos simples, hialinas a pálido-amarillentas, de paredes delgadas, de 2.4-3.2 μm de diámetro; hifas esqueléticas de color marrón rojizo, de paredes gruesas (1.6-2 μm de grosor), de 3.4-4.8 μm de diámetro. Contexto con hifas esqueléticas dominantes, de color marrón rojizo, de paredes gruesas, de 4.0-4.8 μm de diámetro. Setas himeniales presentes o ausentes, de 13.6-21.6 X 5.6-8.8 μm , ventricosas, con el ápice recto y agudo, de paredes gruesas, de color marrón rojizo a marrón oscuro. Cistidiolos de 48-64 X 4.8-5.6 μm , hifoides, con la base bulbosa, hialinos, de paredes delgadas a gruesas. Basidios de 12-16 X 8.8-10.4 μm , subglobosos a ovoides, tetraspóricos, esterigmas delgados de 2.4-3 μm de largo. Basidiosporas (5.6-) 7-8.4 (-9) X (5.6) 6.5-8.0 μm , ($X = 7.4 \times 7.0 \mu\text{m}$, $n = 30$), $R = (1.0) 1.1-1.2 (-1.3)$, subglobosas, hialinas, fuertemente dextrinoides, cianófilas, lisas, de paredes gruesas. Clamidosporas ausentes.

Resumen taxonómico. *Fomitiporia texana* se encontró sobre una gran variedad de madera muerta o viva, entre la que se pudo identificar *Juniperus deppeana* (Cupressaceae), *Guaiaكومun officinale* (Zygophyllaceae), *Opuntia leptocaulis* (Cactaceae), *Cumbretum* (Cumbretaceae), *Citrus limonia* (Rutaceae); también sobre lianas. Los tipos de vegetación donde se desarrollan son matorral xerófilo, bosque tropical caducifolio, bosque tropical subcaducifolio y bosque de *Juniperus*. Esta especie se conocía de EUA, de los estados de Texas, Nuevo México y Arizona (Gilbertson y Ryvardeen, 1987). En el presente trabajo se cita y describe por primera vez para México. *Ejemplares revisados.* **México:** DURANGO: municipio de Peñón Blanco, La Concha, 6.VI.1992, R. Díaz-Moreno s/n (UJED); municipio de Pueblo Nuevo, Mexiquillo, 20.VII.1991, R. Valenzuela 7160

(ENCB). GUERRERO: municipio de Cocula, Xonacatla, 28.V.2010, *E. Salinas* 08, *J. Vera* 09 (ENCB); Machito de Las Flores, 18.IV.2010, *E. Salinas* 463, 509,529 (ENCB). JALISCO: municipio de Guadalajara, barranca de Huentitán, 25.XII.1975. *G. Guzmán* 12492 (ENCB, IBUG); municipio de La Huerta, Camino Ardilla, Reserva de la Biosfera Chamela-Cuixmala, 23.X.2009. *R. Valenzuela* 13869 (ENCB, MUCL), 28.IV.2010, *R. Valenzuela* 13924, 13926 (ENCB, MUCL); 28.IX.2010, *T. Raymundo* 3507, 3515 (ENCB, MEXU); Eje Central, 27.IX.2010, 28.IX.2010, *T. Raymundo* 3525. MICHOACÁN: municipio de Huetamo, Eréndira, 25 km al N de Huetamo, sobre la carretera a Tiquicheo, 5.XI.1977, *J. Tena* 7 (ENCB). NUEVO LEÓN: municipio de Sabinas Hidalgo, 5 km al NO de Sabinas Hidalgo, Ojo de Agua, 7.VII.1988, *R. Valenzuela* 6540 (ENCB). OAXACA: municipio de San Francisco Ixhuatán, bosque tropical, 7 m snm, 20.VIII.1980, *E. Teniente-Nivón* 11 (ENCB); Parque Nacional Lagunas de Chacahua, a 6 km de la Grúa, camino de terracería al este de Los Azufres, 15.IX.2003. *T. Raymundo* y *R. Valenzuela* 298 (ENCB). QUERÉTARO: municipio Jalpan de Serra, Km. 185 de la carretera Jalpan-Xilitla, 3.XI.2007. *T. Raymundo* y *R. Valenzuela* 1991 (ENCB). SAN LUIS POTOSÍ: Km. 70 de la carretera Río Verde-Cd. Valles, 1.XI.2007. *T. Raymundo* y *R. Valenzuela* 1966 (ENCB). SONORA: desierto central sonorense, municipio de Guaymas, “El Tigre”, ejido Francisco Villa, 11, 2009, *A. Sánchez* 146 (CESUES, ENCB); 22.VIII.2009. *T. Raymundo* 3234, 3235 (UAMIZ, MUCL). YUCATÁN: municipio de Santa Elena, Parque Estatal Kabah, 21.III.2007, *R. Sansores-Sánchez* 92 (UADY, ENCB). **Estados Unidos de América:** TEXAS, San Antonio, 31.X.1911, *G. G. Hedgcock*, sobre *Juniperus sabinoide*s (FP 9954). ARIZONA, Santa Cruz County, 10.XI.1967, *R. L. Gilbertson* 7763 (ARIZ, MUCL). *Comentarios taxonómicos.* Esta especie se caracteriza por presentar basidiomas pileados, de triangulares a ungulados, el píleo rimoso y con una costra negra, los poros son de tamaño mediano (de 4-6 por mm), setas himeniales se observaron únicamente en algunos ejemplares del estado de Jalisco, las esporas son grandes (de 7-8.4 (-9) X (5.6) 6.5- 8.0 µm). Especies afines son *F. robusta* y *F. calkinsii* pero sus esporas son más pequeñas (6-8 X 5.5-7 µm y 6-7 X 5.5-6 µm, respectivamente), la primera se distribuye en Europa y el Este de Asia y la segunda en Norteamérica; ambas crecen sobre *Quercus*, no así *F. texana*, que presenta gran variabilidad en cuanto a la selección de hospederos y crece tanto en gimnospermas (*Juniperus*) como en angiospermas (cactáceas, rutáceas, cumbretáceas, entre otras).

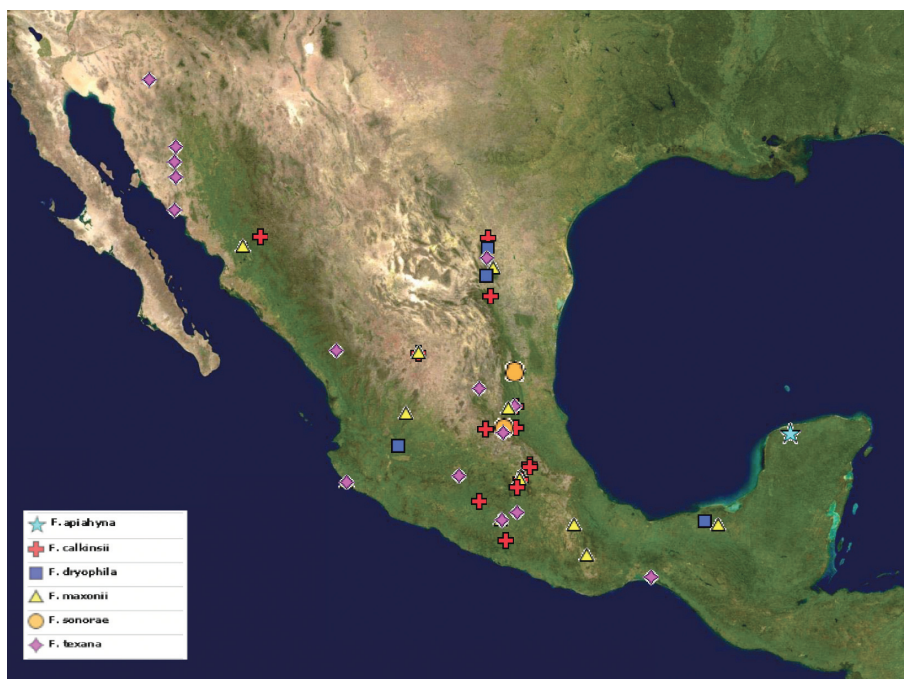


Figura 8. Distribución de las especies de *Fomitiporia* en México.

Discusión

La mayoría de los ejemplares de herbario revisados en el presente trabajo se encontraban determinados como *Phellinus punctatus* y *P. robustus*, debido a que se había seguido el criterio de Gilbertson et Ryvarden (1987) y Ryvarden (2004). Sin embargo, con las nuevas tendencias de la sistemática moderna, que incluye aspectos morfológicos, ecológicos, biogeográficos y filogenéticos, se reconoce que estas especies se distribuyen en Europa (Wagner y Fischer, 2001) y en el Este de Asia (Núñez y Ryvarden, 2000), y fue necesario, entonces, reclasificar los ejemplares de Norteamérica. Decock et al. (2007) y Vlasák y Kout (2010), al estudiar los tipos de las especies descritas por Murrill (1907), validaron *F. langloisii*, *F. dryophila*, *F. maxonii*, *F. calkinsii* y *F. bakeri* para sustituir en esta región los nombres de *P. punctatus* y *P. robustus*. Respecto a la distribución de las especies estudiadas, podemos señalar que *F. apiahyna*, *F. maxonii* y *F. sonoreae* se encontraron en zonas de vegetación tropical, no así *F. calkinsii* que se localizó únicamente en zonas de vegetación templada y *F. dryophila* y *F. langloisii* se ubicaron en zonas de vegetación árida. Por otro lado, *F. texana*

presentó una mayor distribución, encontrándose en zonas tropicales, templadas y áridas.

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Literatura citada

- Acosta, S. y G. Guzmán. 1984. Los hongos conocidos del estado de Zacatecas (México). Boletín de la Sociedad Mexicana de Micología 19:125-158.
- Amalfi, M., P. Yombiyeni y C. Decock. 2010. *Fomitiporia* in Sub-Saharan Africa: morphology and multigene phylogenetic analysis support three new species from the Guineo-Congolian rainforest. Mycologia 102:303-1317.
- Anell, J. C. y G. Guzmán. 1987. Especies de poliporáceos citadas del Estado de Veracruz. Revista Mexicana de Micología. 3:137-148.
- Ayala, N. y G. Guzmán. 1984. Los hongos de la península de Baja California. I. Las especies conocidas. Boletín de la Sociedad Mexicana de Micología. 19:73-91.
- Bernicchia, A. 2005. Polyporaceae s. l. Fungi Europaei 10, Candusso, Alassio. 808 p.
- Castillo, J., G. Guzmán y G. Sepúlveda. 1969. Estudios sobre los poliporáceos de Nuevo León. Ciencia 27:9-18.
- Cifuentes, J., M. Villegas y L. Pérez-Ramírez. 1986. Hongos. In Manual de Herbario, A. Lot y F. Chiang (eds.). Consejo Nacional de la Flora de México, A. C., México, D. F. p. 55-64.
- Corner, E. J. H. 1991. Ad Polyporaceas. VII. Thexanthochroic polypores. Beih

Nova Hedwia, Heft 101:1-175.

David, A., B. Dequatre y J. L. Fiasson. 1982. Two new *Phellinus* with globose, cyanophilous spores. Mycotaxon 14:160-174.

Decock, C., A. Bitew y G. Castillo. 2005. *Fomitiporia tenuis* and *Fomitiporia aethiopica* (Basidiomycota, Hymenochaetales): two undescribed species from the Ethiopian highlands: taxonomy and phylogeny. Mycologia 97:121-129.

Decock, C., S. Herrera Figueroa, G. Robledo y G. Castillo. 2007. *Fomitiporia punctata* (Basidiomycota, Hymenochaetales) and its presumed taxonomic synonyms in America: taxonomy and phylogeny of some species from tropical/subtropical area. Mycologia 99:733-752.

Díaz-Barriga, H., F. Guevara-Fefer y R. Valenzuela. 1988. Contribución al conocimiento de los macromicetos del estado de Michoacán. Acta Botanica Mexicana 2:21-44.

Díaz-Moreno, R., R. Valenzuela y J. G. Marmolejo. 2005. Flora micológica de bosques de pino y pino-encino, Durango, México. Ciencia UANL 8:362-369.

Díaz-Moreno, R., R. Valenzuela, J. G. Marmolejo y E. Aguirre-Acosta. 2009. Hongos degradadores de la madera en el estado de Chihuahua, México. Revista Mexicana de Biodiversidad 80:13-22.

Fiasson, J. L. y T. Niemalä. 1984. The Hymenochaetales: a revision of the European poroid taxa. Karstenia 24:14-28. Fischer, M. 1996. On the species complexes within *Phellinus*: *Fomitiporia* revisited. Mycological Research 100:459-467.

Fischer, M. 2002. A new wood-decaying Basidiomycetes species associated with yesca of grapevine: *Fomitiporia mediterranea* (Hymenochaetales). Mycological Progress 1:315-324.

Fischer, M. y M. Binder. 2004. Species recognition, geographic distribution and host-pathogen relationships: a case study in a group of lignicolous basidiomycetes, *Phellinus* s.l. Mycologia 96:799-811.

Frutis, I. y G. Guzmán. 1983. Contribución al conocimiento de los hongos del estado de Hidalgo. Boletín de la Sociedad Mexicana de Micología 18:219-265.

Galván-Villanueva, R. y G. Guzmán. 1977. Estudio florístico sobre los hongos destructores de la madera del grupo de los poliporáceos en el estado de Morelos. Boletín de la Sociedad Mexicana de Micología 11:35-98.

Gilbertson R. L. 1979. *Phellinus* (Aphylllophorales: Hymenochaetaceae) in western North America. *Mycotaxon* 9:51-89.

Gilbertson, R. L. y L. Ryvarde. 1987. North American polypores. *Megasporoporia-Wrightoporia*. vol. 2. Fungiflora, Oslo. 843 p.

Guzmán, G. 1983. Los hongos de la península de Yucatán. II. Nuevas exploraciones y adiciones micológicas. *Biotica* 6:71-100.

Kornerup, A. y J. H. Wanscher. 1978. *Methuen handbook of colour*, tercera edición. Eyre Methuen, London. 252 p.

Larsen, M. J. y L. A. Cobb-Poulsen. 1989. *Phellinus* (Hymenochaetaceae). A survey of the world taxa. *Synopsis Fungorum* 3. Fungiflora, Oslo. 206 p.

Larsson, K. H., Parmasto, M. Fischer, E. Langer, K. Nakasone y S. Redhead. 2006. Hymenochaetales: a molecular phylogeny for the hymenochaetoid clade. *Mycologia* 98:926-936.

Lowe, J. L. 1957. Polyporaceae of North America. The genus *Fomes*. Technical Publication 78. State University College of Forestry at Syracuse University, New York. 158 p.

Lowe, J. L. 1966. Polyporaceae of North America. The genus *Poria*. Technical Publication 90. State University College of Forestry at Syracuse University, New York. 83 p.

Murrill, W. A. 1903. The Polyporaceae of North America. II. The genus *Pyropolyporus*. *B. Torrey Botanical Club* 30:109-120.

Murrill, W. A. 1907. Polyporaceae. *North American Flora* 9:1-72.

Murrill, W. A. 1912. The Polyporaceae of Mexico. *Bulletin. New York Botanical Garden* 8:137-153.

Montaño, A., R. Valenzuela, A. Sánchez, M. Coronado y M. Esqueda. 2006. Aphylllophorales de Sonora, México. I. Algunas especies de la Reserva Forestal Nacional y Refugio de Fauna Silvestre Ajos-Bavispe. *Revista Mexicana de Micología* 23:7-26.

Nava-Mora, R. y R. Valenzuela. 1997. Los macromicetos de la sierra de Nanchititla, I. *Polibotánica* 5:21-36.

Núñez, M. y L. Ryvardeen, 2000. East Asian polypores, vol. 1, Ganodermataceae-Hymenochaetaceae. Synopsis Fungorum 13. Fungiflora, Oslo 168 p.

Ojeda-López, S., M. Sandoval y R. Valenzuela. 1986. Los poliporáceos de México, I. Descripción de algunas especies del noreste de Guanajuato. Revista Mexicana de Micología 2:367-436.

Overholts, L. D. 1953. The Polyporaceae of the United States, Alaska and Canada. University of Michigan Press, Ann Arbor. 466 p.

Pérez-Silva, E. y E. Aguirre-Acosta. 1986. Flora micológica del estado de Chihuahua, México. I. Anales del Instituto Biología Universidad Nacional Autónoma de México, Serie Botánica 57:17-32.

Raymundo, T. y R. Valenzuela. 2003. Los poliporáceos de México VI. Los hongos poliporoides del estado de Oaxaca. Polibotánica 16:79-112.

Raymundo, T., R. Valenzuela y J. Cifuentes. 2008. Dos nuevas especies del género *Phellinus* (Hymenochaetaceae, Basidiomycota) en México. Revista Mexicana de Biodiversidad 79:295-301.

Raymundo, T., R. Valenzuela y M. Esqueda. 2009. The family Hymenochaetaceae from México 4. New records from Sierra de Álamos-Río Cuchujaqui biosphere reserve. Mycotaxon 110:387-398.

Romero-Bautista, L. y R. Valenzuela. 2008. Los hongos poliporoides de las Áreas Naturales protegidas del estado de Hidalgo. In Estudios biológicos en las áreas naturales del estado de Hidalgo, México, G. Pulido-Flores, A. L. López-Escamilla y M. T. Pulido-Silva (eds.). Universidad Autónoma del Estado de Hidalgo, Pachuca. p. 29-39.

Romero-Bautista, L., G. Pulido-Flores y R. Valenzuela. 2010. Estudio micoflorístico de los hongos poliporoides del estado de Hidalgo, México. Polibotánica 29:1-28.

Ryvardeen, L. 1985. Type studies in the Polyporaceae. 17. Species described by W. A. Murrill. Mycotaxon 23:169- 198.

Ryvardeen, L. 1989. Type studies in the Polyporaceae. 21. Species described by C.G. Lloyd in *Cyclomyces*, *Daedalea*, *Favolus*, *Fomes*, and *Hexagonia*. Mycotaxon 35:229-236.

- Ryvarden, L. 1991. Genera of polypores, nomenclature and taxonomy. Synopsis Fungorum 5. Fungiflora, Oslo. 363 p.
- Ryvarden, L. 2004. Neotropical polypores I. Introduction, Ganodermataceae and Hymenochaetaceae. Synopsis Fungorum 19. Fungiflora, Oslo. 229 p.
- Ryvarden, L. e I. Johansen. 1980. A preliminar polypore flora of East Africa. Fungiflora, Oslo. 636 p.
- Ryvarden, L. y R. L. Gilbertson. 1994. European polypores. Part 2. *Meripilus-Tyromyces*. Synopsis Fungorum 7. Fungiflora, Oslo. p. 392-743.
- Ryvarden, L. y De Meijer. 2002. Studies in Neotropical Polypores 14. New species from the State of Paraná, Brazil. Synopsis Fungorum 15. Fungiflora, Oslo. p. 34-69.
- Saccardo, P. A. 1912. Sylloge fungorum omnium hucusque cognitorum, vol. XXI, Pars.VIII. Hymenomycetae- Phycomycetae (reprint, 1966). Johnson, New York. 928 p.
- Ulloa, M. y R. T. Hanlin. 2006. Nuevo diccionario ilustrado de micología. APS, St. Paul, Minnesota. 672 p.
- Valenzuela, R. y S. Chacón Jiménez. 1991. Los poliporáceos de México. III. Algunas especies de la Reserva de la Biosfera El Cielo, Tamaulipas. Revista Mexicana de Micología 7:39-70.
- Valenzuela, R., C. De la Huerta y R. Fernández. 2002. Los poliporáceos de México. V. Algunas especies del norte del estado de Querétaro. Polibotánica 14:85-122.
- Valenzuela, R., R. Nava y J. Cifuentes. 1996. La familia Hymenochaetaceae en México. I. El género *Hydnochaete* Bres. Polibotánica 1:7-15.
- Valenzuela, R., T. Raymundo y J. Cifuentes. 2005. La familia Hymenochaetaceae en México. II. Especies poco conocidas del género *Phellinus*. Revista Mexicana de Micología 20:13-19.
- Valenzuela, R., T. Raymundo y J. Cifuentes. 2007. La familia Hymenochaetaceae en México. III. El género *Aurificaria* D. A. Reid en México. Polibotánica 24:153-166.
- Valenzuela, R., T. Raymundo, J. Cifuentes, G. Castillo, M. Amalfi y C. Decock. 2010. Two undescribed species of *Phylloporia* from Mexico based on morphological and phylogenetic evidence. Mycological progress 10:341-349.

Valenzuela, R., T. Raymundo, J. Cifuentes, M. Esqueda, M. Amalfi y C. Decock. 2011. *Coltriciella sonorensis* sp. nov. (Basidiomycota, Hymenochaetales) from Mexico: evidence from morphology and DNA sequence data. Mycological Progress 11:181-189.

Varela, L. y J. Cifuentes. 1979. Distribución de algunos macromicetos en el norte del estado de Hidalgo. Boletín de la Sociedad Mexicana de Micología 13:75-88.

Vlasák, J. y J. Kout. 2010. Pileate *Fomitiporia* species in USA. New combinations *Fomitiporia calkinsii* and *F. bakeri*. Mycological Progress: DOI 10.1007/s11557-010-0715-0.

Wagner, T. y M. Fischer. 2001. Natural groups and a revised system for the European poroid Hymenochaetales (Basidiomycota) supported by nLSU rDNA sequence data. Mycological Research 105:773-782.

Wagner, T. y M. Fischer. 2002. Proceedings towards a natural classification of the worldwide taxa *Phellinus s.l.* and *Inonotus s.l.*, and phylogenetic relationships of allied genera. Mycologia 94:998-1016.

Welden, A. L. y P. A. Lemke. 1961. Notas sobre algunos hongos mexicanos. Boletín de la Sociedad Botánica de México 26:1-24.