

# *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- $\alpha$*  and RPB2 genes). These collections also represent 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 forests 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, which 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 so far known from Argentina and Ecuador. Its phylogenetic relationships with the South American *Fomitiporia* are briefly discussed.

Mario Amalfi and Gerardo Robledo contributed equally to the research and should be considered co-first authors.

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## 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; 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) have also provided the most comprehensive phylogenies of *Fomitiporia* to date, based on an extensive, worldwide sampling. These studies allowed the evidencing of 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 seven unnamed species clades. Previously, only two species with pileate basidiomata have been reported from the Neotropics, i.e. *F. apiahyna* (e.g. Gilbert et al. 2002; Robledo et al. 2006; Ryvarden 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, Ryvarden 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; Ryvardeen, 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-Pouille 1990; Ryvardeen 2004), *Phellinus baccharidis* emerged as a possible candidate, although it was repeatedly described with non-dextrinoid basidiospores (Ryvardeen and Johansen 1980; Larsen and Cobb-Pouille 1990; Ryvardeen 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-Pouille 1990; Ryvardeen 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 (2014)). 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 (1978). 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 *tef1-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<sup>®</sup> (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); and bRPB2-6F and bRPB2-7.1R for *rpb2* (Matheny 2005; Reeb et al. 2004). Sequences were assembled and edited with the Sequencher<sup>™</sup> 4.8 software (Gene Codes, 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 (Table 1). 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 2.

**Table 1** List of species, collections, and sequences used in the phylogenetic analyses

Genus/species names		GenBank accession number			
		nLSU	ITS	<i>tef1-<math>\alpha</math></i>	RPB2
Voucher specimens / cultures reference	Locality				
<i>F. aethiopica</i> Decock et al.					
MUCL 44777 (T) <sup>a,b</sup>	Ethiopia	AY618204	GU478341	GU461893	JQ087956
MUCL 44806 <sup>a,b</sup>	Ethiopia	AY618202	GU461944	GU461892	JQ087955
<i>F. apiahyna</i> (Speg.) Robledo et al.					
MUCL 51451 <sup>a,b</sup>	Ecuador	GU461997	GU461963	GU461896	JQ087958
MUCL 51454 <sup>a,b</sup>	Ecuador	JX093812	JX093769	JX093725	JX093856
MUCL 51456 <sup>a,b</sup>	Ecuador	JX093813	JX093770	JX093726	JX093857
MUCL 51474 <sup>a,b</sup>	Ecuador	X093814	GU461961	JX093727	JX093858
MUCL 51485 <sup>a,b</sup>	Ecuador	GU461996	GU461962	GU461895	JQ087957
MUCL 53022 <sup>a,b</sup>	French Guiana	JX093815	JX093771	JX093728	JX093859
MUCL 53041 <sup>a,b</sup>	French Guiana	JX093816	JX093772	JX093729	JX093860
MUCL 53042 <sup>a,b</sup>	French Guiana	JX093817	JX093773	JX093730	JX093861
MUCL 53047 <sup>a,b</sup>	French Guiana	JX093818	JX093774	JX093731	JX093862
MUCL 53071 <sup>a,b</sup>	French Guiana	JX093819	JX093775	JX093732	JX093863
MUCL 53135 <sup>a,b</sup>	French Guiana	JX093820	JX093776	JX093733	JX093864
MUCL 53145 <sup>a,b</sup>	French Guiana	JX093821	JX093777	JX093734	JX093865
MUCL 53149 <sup>a,b</sup>	French Guiana	JX093822	JX093778	JX093735	JX093866
MUCL 53156 <sup>a,b</sup>	French Guiana	JX093823	JX093779	JX093736	JX093867
MUCL 53711 <sup>a,b</sup>	French Guiana	JX093824	JX093780	JX093737	JX093868
MUCL 53988 <sup>a,b</sup>	French Guiana	JX093825	JX093781	JX093738	JX093869
MUCL 53989 <sup>a,b</sup>	French Guiana	JX093826	JX093782	JX093739	JX093870
MUCL 53990 <sup>a,b</sup>	French Guiana	JX093827	JX093783	JX093740	JX093871
MUCL 53991 <sup>a,b</sup>	French Guiana	JX093828	JX093784	JX093741	JX093872
MUCL 53726 <sup>a,b</sup>	French Guiana	JX093829	JX093785	JX093742	JX093873
<i>F. australiensis</i> Fischer et al.					
VPRI 22451a PT (MUCL 49406) <sup>a,c</sup>	Australia	GU462001	AY624997	GU461897	JQ087959
<i>F. baccharidis</i> (Pat.) Decock et al.					
MUCL 47756 <sup>a,b</sup>	Argentina	JQ087913	JQ087886	JQ087940	JQ087993
MUCL 47757 <sup>a,b</sup>	Argentina	JQ087914	JQ087887	JQ087941	JQ087994
MUCL 47758 <sup>a,b</sup>	Argentina	JQ087915	JQ087888	JQ087942	JQ087995
<i>F. bakeri</i> (Murrill) Vlasák & Kout					
FP-134784-Sp (MUCL 51098) <sup>a,d</sup>	USA	JQ087901	JQ087874	JQ087928	JQ087960
<i>F. bannaensis</i> Y.C. Dai					
MUCL 45926 <sup>a,b</sup>	Thailand	EF429217	GU461942	GU461898	JQ087961
MUCL 46950 <sup>a,b</sup>	China	EF429218	GU461943	GU461899	JQ087962
<i>F. calkinsii</i> (Murrill) Vlasák & Kout					
FP-71907-T (MUCL 51100) <sup>a,d</sup>	USA	JQ087902	JQ087875	JQ087929	JQ087963
MUCL 52346 <sup>a,b</sup>	Mexico	JQ087903	JQ087876	JQ087930	JQ087964
<i>Fomitiporia capensis</i> M. Fisch. et al.					
MUCL 53009 <sup>a,c</sup>	South Africa	JQ087917	JQ087890	JQ087944	JQ087997
<i>F. castilloi</i> Decock & Amalfi					
MUCL 53481 (T) <sup>a,c</sup>	French Guiana	JQ087916	JQ087889	JQ087943	JQ087996
MUCL 53980 (PT) <sup>a,b</sup>	French Guiana	JX093830	JX093786	JX093743	JX093874
<i>F. cupressicola</i> Amalfi et al.					
MUCL 52486 (T) <sup>a,b</sup>	Mexico	JQ087904	JQ087877	JQ087931	JQ087965
MUCL 52488 <sup>a,b</sup>	Mexico	JQ087905	JQ087878	JQ087932	JQ087966

Table 1 (continued)

Genus/species names		GenBank accession number			
		nLSU	ITS	<i>tef1-<math>\alpha</math></i>	RPB2
Voucher specimens / cultures reference	Locality				
MUCL 52489 <sup>a,b</sup>	Mexico	JQ087906	JQ087879	JQ087933	JQ087967
MUCL 52490 <sup>a,b</sup>	Mexico	JQ087907	JQ087880	JQ087934	JQ087968
<i>F. dryophila</i> Murrill					
TJV-93-232 (MUCL 46379) <sup>a,d</sup>	USA	EF429221	EF429240	GU461902	JQ087969
TJV-93-234 (MUCL 46380) <sup>a,d</sup>	USA	EF429219	EF429238	GU461900	JQ087970
<i>F. erecta</i> (A. David et al.) Fiasson					
MUCL 49871 <sup>a,b</sup>	France	GU461976	GU461939	GU461903	JQ087971
<i>F. gabonensis</i> Amalfi & Decock					
MUCL 47576 (T) <sup>a,b</sup>	Gabon	GU461990	GU461971	GU461923	JQ087972
MUCL 51291 <sup>a,b</sup>	Gabon	GU461986	GU461967	GU461924	JQ087973
<i>F. hartigii</i> (Allesch. & Schnabl) Fiasson & Niemelä					
MAFF 11-20016 (MUCL 31400) <sup>a</sup>	Japan	JQ087909	JQ087882	JQ087936	JQ087975
75-2 562 (MUCL 53549) <sup>a,c</sup>	Estonia	JX093831	JX093787	JX093744	JX093875
71-25 464 (MUCL 53550) <sup>a,c</sup>	Estonia	JX093832	JX093788	JX093745	JX093876
75-3 563 (MUCL 53551) <sup>a,c</sup>	Estonia	JX093833	JX093789	JX093746	JX093877
<i>F. hippophaeicola</i> (H. Jahn) Fiasson & Niemelä					
MUCL 31746 <sup>a,b</sup>	Belgium	AY618207	GU461945	GU461904	JQ087976
MUCL 31747 <sup>a,b</sup>	Belgium	GU461977	GU461946	GU461905	JQ087977
<i>F. ivindoensis</i> Decock et al.					
MUCL 51311 <sup>a,b</sup>	Gabon	GU461979	GU461952	GU461907	JQ087978
MUCL 51312 (T) <sup>a,b</sup>	Gabon	GU461978	GU461951	GU461906	JQ087979
<i>F. langloisii</i> Murrill					
FP-94347-R (MUCL 46375) <sup>a,d</sup>	USA	EF429225	EF429242	GU461908	JQ087980
01-77/4 (MUCL 46165), (T of <i>F. hesleri</i> ) <sup>a,c</sup>	USA	EF429223	AY340026	GU461909	JQ087981
<i>F. maxonii</i> Murrill					
MUCL 46017 <sup>a,b</sup> (=CRGF 182)	Cuba	EF429230	EF433559	GU461910	JQ087983
MUCL 46037 <sup>a,b</sup> (=CRGF 183)	Cuba	EF429231	EF433560	GU461911	JQ087982
<i>F. mediterranea</i> M. Fisch.					
AFTOL ID 688	ND	AY684157	AY854080	AY885149	AY803748
MUCL 38514 <sup>a</sup>	Italy	AY618201	GU461953	GU461912	JQ087984
MUCL 45670 <sup>a,b</sup>	France	GU461980	GU461954	GU461913	JQ087985
<i>Fomitiporia neotropica</i> Campos-Santana et al.					
MUCL 53114 <sup>a,b</sup>	French Guiana	JX093836	JX093792	JX093749	JX093880
<i>F. nobilissima</i> Decock & Yombiyeni					
MUCL 47580 <sup>a,b</sup>	Gabon	GU461985	GU461966	GU461921	JQ087986
MUCL 51289 (T) <sup>a,b</sup>	Gabon	GU461984	GU461965	GU461920	JQ087987
<i>F. polymorpha</i> M. Fisch.					
91-42/3 (MUCL 46166) (PT) <sup>a,c</sup>	USA	DQ122393	GU461955	GU461914	JQ087988
91-42/1 (MUCL 46167) (PT) <sup>a,c</sup>	USA	EF429233	GU461956	GU461915	JQ087989
<i>F. pseudopunctata</i> (A. David et al.) Fiasson					
MUCL 51325 <sup>a,f</sup>	Czech	GU461981	GU461948	GU461916	JQ087998
MUCL 46168 <sup>a,b</sup>	France	JQ087918	JQ087891	JQ087945	JQ087999
<i>F. punctata</i> (Fr.) Murrill					
MUCL 34101 <sup>a,b</sup>	Germany	AY618200	GU461947	GU461917	JQ088000
WD-2055 (MUCL 47629) <sup>a,g</sup>	Japan	GU461982	GU461950	GU461918	JQ088001
71-8 298 (MUCL 53548) <sup>a,c</sup>	Europe	JX093834	JX093790	JX093747	JX093878

**Table 1** (continued)

Genus/species names	Locality	GenBank accession number			
		nLSU	ITS	<i>tef1-<math>\alpha</math></i>	RPB2
<i>F. punicata</i> Y.C. Dai et al.					
Cui 23 <sup>b,j</sup>	China	GU461991	GU461974	GU461927	JQ088002
Cui 26 <sup>b,j</sup>	China	GU461992	GU461975	GU461928	JQ088003
<i>F. robusta</i> (P. Karst.) Fiasson & Niemelä					
CBS 389.72 (MUCL 51297) <sup>a,h</sup>	Estonia	JQ087919	JQ087892	JQ087946	JQ088004
Tomsovský 1013 (MUCL 51327) <sup>a,f</sup>	Czech	GU461993	GU461949	GU461929	JQ088005
<i>F. sonora</i> (Gilb.) Y.C. Dai					
RLG-10862-Sp (MUCL 47689, T) <sup>a,d</sup>	USA	JQ087920	JQ087893	JQ087947	JQ088006
<i>Fomitiporia</i> "sp."					
CBS 386.66=MUCL 46181 <sup>a,h</sup>	Argentina	EF429234	EF433563	GU461930	JQ088007
MUCL 53675 <sup>a,b</sup>	French Guiana	JX093835	JX093791	JX093748	JX093879
<i>Fomitiporia</i> "sp." PS1					
TH 8903 <sup>b,i</sup>	Guyana	JX093837	JX093793	JX093750	ND
TH 8904 <sup>b,i</sup>	Guyana	JX093838	JX093794	JX093751	ND
<i>Fomitiporia</i> "sp." PS2					
MUCL 53108 <sup>a,b</sup>	French Guiana	JX093839	JX093795	JX093752	JX093881
MUCL 53705 <sup>a,b</sup>	French Guiana	JX093840	JX093796	JX093753	JX093882
MUCL 53992 <sup>b</sup>	Guadalupe	JX093841	JX093797	JX093754	JX093883
<i>Fomitiporia</i> "sp." PS3 a					
MUCL 51464 <sup>a,b</sup>	Ecuador	JX093842	JX093798	JX093755	JX093884
MUCL 53034 <sup>a,b</sup>	French Guiana	JX093843	JX093799	JX093756	JX093885
MUCL 53106 <sup>a,b</sup>	French Guiana	JX093844	JX093800	JX093757	JX093886
MUCL 53111 <sup>a,b</sup>	French Guiana	JX093845	JX093801	JX093758	JX093887
MUCL 53785 <sup>a,b</sup>	French Guiana	JX093846	JX093802	JX093759	JX093888
MUCL 53793 <sup>a,b</sup>	French Guiana	JX093847	JX093803	JX093760	JX093889
MUCL 53800 <sup>a,b</sup>	French Guiana	JX093848	JX093804	JX093761	JX093890
MUCL 53985 <sup>a,b</sup>	French Guiana	JX093849	JX093805	JX093762	JX093891
<i>Fomitiporia</i> "sp." PS3 b					
GC-FG-10-125 <sup>a,b</sup>	French Guiana	JX093850	JX093806	JX093763	JX093892
<i>Fomitiporia</i> "sp." PS4					
MUCL 53993 <sup>a,b</sup>	Mexico	JX093851	JX093807	JX093764	JX093893
MUCL 53994 <sup>a,b</sup>	Mexico	JX093852	JX093808	JX093765	JX093894
<i>Fomitiporia</i> "sp." PS5					
MUCL 51555 <sup>a,b</sup>	Martinique	JX093853	JX093809	JX093766	JX093895
MUCL 53797 <sup>a,b</sup>	French Guiana	JX093854	JX093810	JX093767	JX093896
<i>Fomitiporia</i> "sp." PS6					
MUCL 53798 <sup>a,b</sup>	French Guiana	JX093855	JX093811	JX093768	JX093897
<i>F. tabaquilio</i> (Urcelay et al.) Decock & Robledo					
MUCL 46230 <sup>a,b</sup>	Argentina	DQ122394	GU461940	GU461931	JQ088008
MUCL 47754 <sup>a,b</sup>	Argentina	GU461994	GU461941	GU461932	JQ088009
<i>F. tenuis</i> Decock et al.					
MUCL 44802 (T) <sup>a,b</sup>	Ethiopia	AY618206	GU461957	GU461934	JQ088010
MUCL 49948 <sup>a,b</sup>	Gabon	GU461998	GU461958	GU461935	JQ088011
MUCL 49971 <sup>a,b</sup>	Uganda	GU461998	GU461958	GU461935	JQ088012
<i>F. texana</i> (Murrill) Nuss					
RLG-7763-T (MUCL 47690) <sup>a,d</sup>	USA	JQ087921	JQ087894	JQ087948	JQ088013
FP-89674-R (MUCL 51143) <sup>a,d</sup>	USA	JQ087922	JQ087895	JQ087949	JQ088014

**Table 1** (continued)

Genus/species names		GenBank accession number			
		nLSU	ITS	<i>tef1-<math>\alpha</math></i>	RPB2
Voucher specimens / cultures reference	Locality				
<i>F. torreyae</i> Y.C. Dai & B.K. Cui					
WD-199 (MUCL 47628) <sup>a,g</sup>	Japan	JQ087923	JQ087896	JQ087950	JQ088015
WC31 <sup>j</sup>	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 <sup>a</sup>	USA	JQ087908	JQ087881	JQ087935	JQ087974
<i>Ph. juniperinus</i> Bernicchia & S. Curreli					
MUCL 51757 <sup>a,b</sup>	Tunisia	JQ087927	JQ087900	JQ087954	JQ088019
<i>Ph. uncisetus</i> Robledo et al.					
MUCL 46231 <sup>a,b</sup>	Argentina	EF429235	GU461960	GU461937	JQ088020
MUCL 47061 <sup>a,b</sup>	Argentina	GU462000	GU461972	GU461938	JQ088021

*T*, *PT* type, paratype; *ND*\* available at MUCL

<sup>a</sup> Culture available

<sup>b</sup> Voucher herbarium specimen corresponding to the culture available at the MUCL herbarium

<sup>c</sup> Cultures from Regensburg University, Germany, courtesy of Dr. M. Fischer

<sup>d</sup> Cultures from CFMR, USDA, USA, courtesy of Dr. K. Nakasone

<sup>e</sup> Cultures from National History Museum, University of Tartu, Estonia, courtesy of K. Põldmaa

<sup>f</sup> Cultures from Faculty of Forestry and Wood Technology, Mendel University of Agriculture and Forestry in Brno, Czech Republic, courtesy of Dr. M. Tomšovská

<sup>g</sup> Cultures from Microbial Ecology Lab Forestry and Forest Products Research Institute, courtesy of Prof. T. Hattori, Japan

<sup>h</sup> Cultures from the CBS, The Netherlands, courtesy of Prof. P. Crous

<sup>i</sup> Fragments of herbarium, courtesy of Prof. T. Henkel, USA

<sup>j</sup> 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 bp (*F. cupressicola*). The ITS-5.8S region ranged from 662 (*Fomitiporia* sp. MUCL 47756, MUCL 47757, and MUCL 47758) to 780 bp (*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 1,155 (*F. bakeri*) to 1,172 bp (*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 bp; *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),

1,202 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 2.

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

A total of 4,064 characters were included in the analysis of which 243 were variable but parsimony-uninformative and 1,276 parsimony-informative. The heuristic search produced 3,657 equally most parsimonious trees (4,247 steps long; CI=

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

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>rpb2</i> 1st	<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	HKY+G	GTR+H+G	F81+I	GTR+G	F81-like
Likelihood score	-2,182.2107	-337.426	-2,069.1279	-3,055.2348	-683.5805	-568.4256	-2,815.7737	-1,854.0367	-783.8632	-487.8718	-4,977.1646	-
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	0.3152	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	-

0.482, RI=0.841, RC=0.406), representing one main topology. The two Bayesian runs converged to stable likelihood values ( $-\ln 25,875.131$ ,  $-\ln 25,889.657$ ) after 5,105,000 generations and 4,895 (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 1,800 distinct patterns with a proportion of gaps and undetermined characters of 9.03 %.

The strict consensus of the 3,657 equally most parsimonious trees was mostly identical to the BC tree (Fig. 1) and to the best scoring ML tree (tree score of  $-\ln L = -25,229.376611$ ). 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 nine 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 four additional clades / phylogenetic species (PS 1, PS 2, PS 3, and PS 4; Fig. 1). Two phylogenetic species (PS 5 and 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).

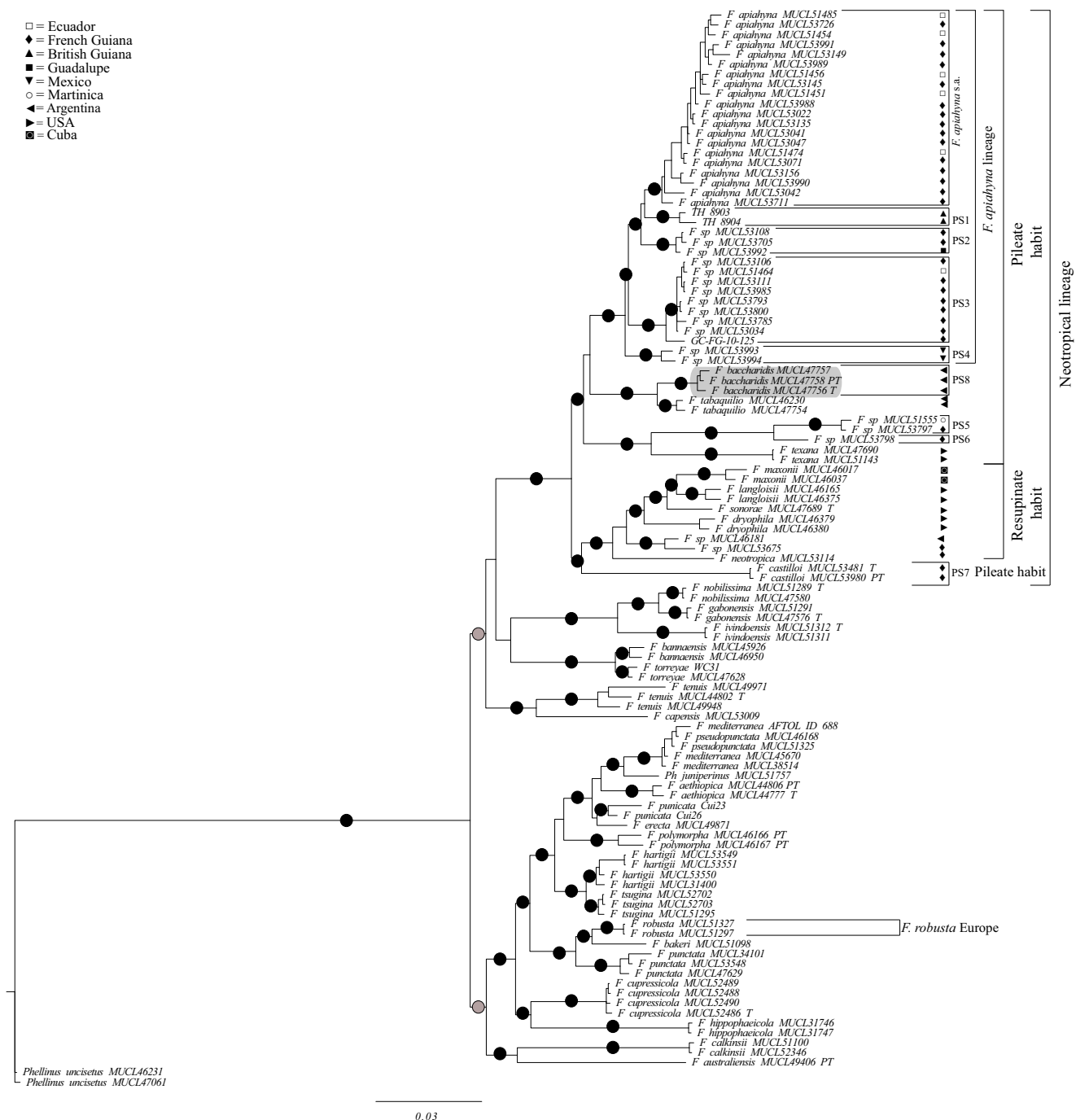
#### Morphological analysis

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 known only from Andean, high elevation (approx. 1,900–3,500 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



**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 %

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-Pouille 1990), *Phellinus baccharidis* emerged as a candidate.

*Phellinus baccharidis* [type specimen: ECUADOR, Rio Machangara, Cotocollao (locality nowadays more likely in Quito suburb, Prov. Pichincha, at ca. 2,800 m asl), *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; Ryvarden 2004; Larsen and Cobb-Pouille 1990). It was collected in a similar environment. Although repeatedly described with non-dextrinoid basidiospores (Larsen and Cobb-Pouille 1990; Ryvarden 2004; Ryvarden and Johansen 1980), our type studies revealed strongly dextrinoid basidiospores. The new combination *Fomitiporia baccharidis* is proposed.

## Taxonomy

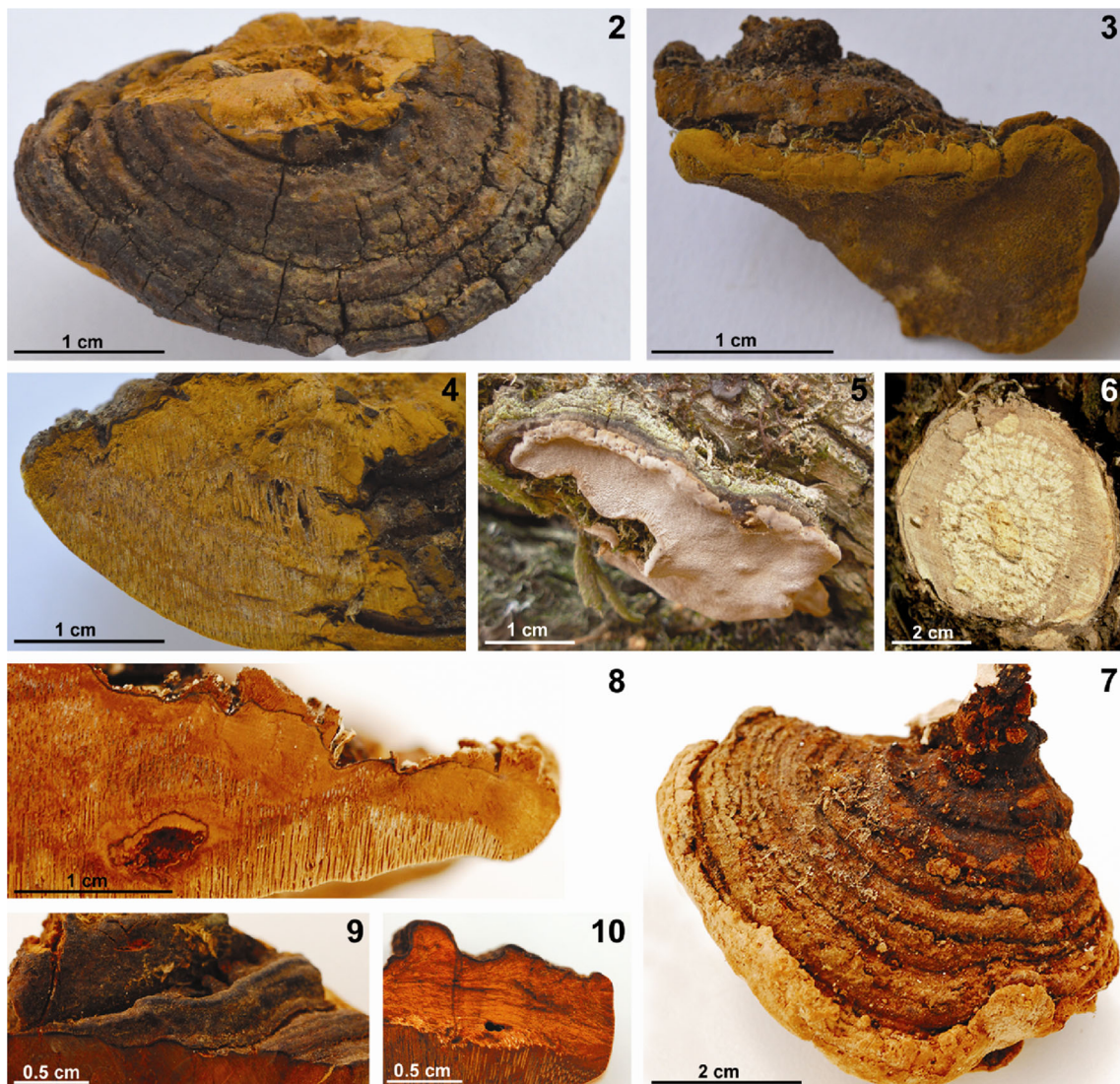
*Fomitiporia baccharidis* Decock, Robledo & Amalfi **comb. nov.** Figs. 2–8, 11–12

Mycobank: MB 807284.

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

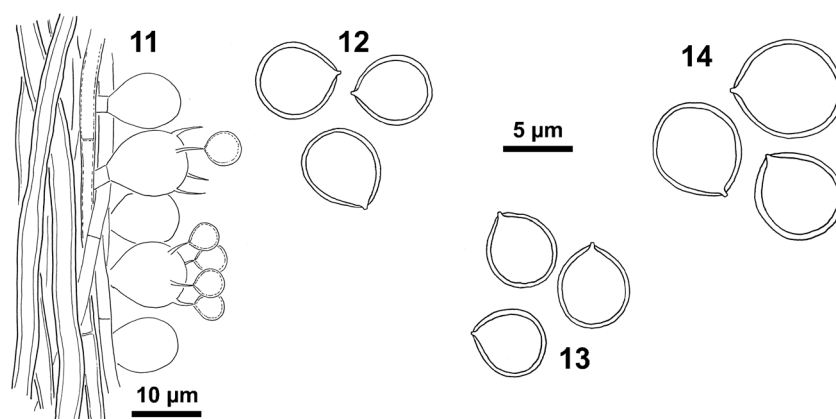
≡ *Phellinus baccharidis* (Pat.) Pat., Essai Tax Hyménomyc: 97, 1900. [MB#319737].

*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 8×6×4 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



**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 pilear surface (scale bar 1 cm). 3 Section trough 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 trough 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 trough basidiome showing context and blackish line (scale bar 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)



**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)

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, 10–12 × 8–10 µm, with 4 sterigmata; *basidiospores* subglobose to globose, slightly obovoid, smooth, hyaline, thick-walled, strongly cyanophilous, strongly dextrinoid, (5.0–) 5.0–6.5 (–7.0) × (4.0–) 5.0–6.0 (–6.0) µm (ave=5.9 × 5.3 µm) [in the type (5.0–) 5.5–6.5 (–6.5) × (5.0–) 5.0–6.0 (–6.0) µm, ave=5.8 × 5.1 µm]; *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. 1,900 masl, to Central Ecuador, at elev. ca. 3,500 masl.

*Specimens examined.* ARGENTINA, Prov. Tucumán, Dpt. Tafi del Valle, Quebrada del Portugués, alt. 1,900 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. 1,900 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], Cotocollao, Rio Machangara, [at ca. 2,800 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, 3,500 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, 6, 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*.

*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. 1,900 masl in its southernmost (known) locality (NW Argentina) and up to ca. 3,500 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 and 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 (>4,000 m asl) 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"W, alt. 2,100 m asl, 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. Tafí del Valle, Quebrada del Portugués, alt. 1,900 m asl, 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"W, alt. 4,200 m asl, 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 [6.0–7.5 × 4.8–6.5 µm (Urcelay et al. 2000; Fig. 14) and 5.0–6.5 × 5.0–6.0 µm (Fig. 12), respectively]. Both species occur sympatrically, at least in NW Argentina, and their host range also overlaps. Nevertheless, they might be segregated microspatially 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–) 5.0–6.5 (–7.0) × (4.5–) 5.0–6.0 (–6.0), ave=5.9 × 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 “palaearctic” 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. apiahyna sensu* Amalfi and 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 endemics. Our phylogenetic analyses support a single origin of these two species; they form together 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 lowlands 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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