Phytotaxa 321 (3): 277–286
http://www.mapress.com/j/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.321.3.5

South American *Fomitiporia* (Hymenochaetaceae, Basidiomycota) 'jump on' exotic living trees revealed by multi-gene phylogenetic analysis

GUILLERMO MORERA[1], GERARDO ROBLEDO[1], VALERIA FERREIRA-LOPES[1] & CARLOS URCELAY[1,2,3]
[1] *Laboratorio de Micología, Instituto Multidisciplinario de Biología Vegetal (CONICET UNC), Casilla de Correo 495, Córdoba 5000, Argentina. Tel: +54-0351-5353800*
[2] *Facultad de Ciencias Exactas, Físicas y Naturales. Universidad Nacional de Córdoba*
[3] *curcelay@imbiv.unc.edu.ar*

Abstract

Morphological and molecular analyses of *Fomitiporia neotropica* specimens occurring in different native and exotic tree hosts were performed. For molecular analyses we used three markers (LSU, ITS and *tef*1-α). The molecular analyses revealed the existence of two morphologically similar species. One of them, *Fomitiporia impercepta sp. nov.*, is described here. The phylogenetic position of these species reveals a South American origin and their occurrence on exotic living tree species hints at their capabilities of new host jump events in evolution. These species do not share same hosts suggesting they are not completely generalist wood-decay fungi.

Key words: host specificity, LSU, ITS and *tef*1-α markers, mycogeography, poroid hymenochaetales

Introduction

Polypore fungi (Basidiomycota, Agaricomycetes) are primarily responsible for the decay of wood in forests (Overwinkler 1994). Although polypores are usually considered as a single functional entity (i.e. wood decaying fungi), the species decaying wood in living trunks (heart-rot parasites *sensu* Rajchenberg & Robledo 2013) have been regarded as ecologically different from those decaying wood from dead trunks and branches (Urcelay & Robledo 2004).

Widespread wood decay fungi like *Schizophyllum commune* and *Trametes versicolor* are usually generalists which are able to grow on dead wood of several tree species (UNITE database: Abarenkov *et al*. 2010). Inversely, those decaying wood in living trunks are possibly more selective in terms of host and geographic distribution (e.g. Robledo *et al*. 2006).

In a recent study done in central Argentina, we observed that some specimens of *Fomitiporia* with resupinate basidiocarp (previously identified as *F. punctata sensu lato*, Hymenochaetales, Basidiomycota) were growing on different tree species, either native from South America or exotic introduced from North America and Asia (Heredia *et al.* 2014). These specimens were, *a priori*, identified as *F. neotropica* (Campos Santana *et al.* 2014). However, some widely distributed species of polypores may correspond to 'species complexes' difficult to distinguish by the morphology of their sporocarps, each with either narrower host or distribution ranges (Fisher & Binder 2004, Taylor *et al*. 2006, Decock *et al*. 2007). The *Fomitiporia* specimens occurring in Argentina on living tree species of different origins could correspond to different cryptic species, each colonizing a specific host.

Determination of the geographic origin of a fungal species occurs on native and exotic hosts is not a simple task (Deprez-Lousteau *et al*. 2010). However, when the phylogenetic distribution of taxa is related to their geographic origins (Moncalvo & Buchanan 2008), the native or exotic status of a fungal species in a defined area could be inferred. This is the case of *Fomitiporia* Murrill for which, based on multi-gene phylogenetic reconstructions, major lineages with Holarctic, Indo-Pacific, African and Neotropical origins have been recognized (Amalfi *et al*. 2012, Ota *et al*. 2014). If the specimens of *Fomitiporia* found in central Argentina nest within one of the Neotropical clades (Amalfi *et al*. 2012), their occurrence on exotic trees introduced from North America and Asia might be attributed to a capacity

Accepted by Dhanushka Udayanga: 17 Aug. 2017; published: 19 Sept. 2017

for 'jumping on' novel exotic hosts, as seen in other species in the genus (Cabrera *et al*. 2014, Cloete *et al*. 2015). Alternatively, if they belong to non-Neotropical clades, their occurrence on exotic trees might be attributed to either long dispersal capacity or co-introduction with their original hosts such as that observed for other parasites (Lymbery *et al*. 2014).

The objectives of this study were to determine the species diversity of morphologically defined specimens of *Fomitiporia* decaying wood of native and exotic trees in central Argentina and their geographical origin. We performed a multigene phylogenetic analyses (LSU, ITS and *tef*1-α) of specimens occurring in different native and exotic tree hosts. In addition, we measured and statistically analyzed several morphological features. As a result of the analyses presented below, a new species of resupinate *Fomitiporia* is described here.

Materials and methods

Specimens analyzed: *Fomitiporia* specimens with a resupinate habit were collected from native and exotic trees of central Argentina, between 2010 and 2013. Ten of them were selected for phylogenetic analysis. For each specimen we recorded the identity and geographical origin of the host assigned according to Zuloaga *et al*. (2008) and Giorgis & Tecco (2014) (Table 1). The same information was taken for all specimens of the *Fomitiporia langloisii* clade *sensu* Amalfi & Decock (2014).

Morphological studies: basidiomata were macro- and micro-morphologically analyzed. Basidiomata colors are described according to Ridgeway (1912). Microscopic observations were carried out on basidioma sections mounted on 3–5% KOH plus 1% phloxine and on Melzer's reagent. All measurements were conducted on Melzer´s reagent preparations and forty measurements (n=40) were taken in each specimen for the followings structures: basidiospores size (length and width), pores diameter, dissepiments thickness and hyphae diameter. In presenting the size range of these structures, 5% of the measurements were excluded from each end and are given in parentheses when relevant. Abbreviation and symbols are: ave = arithmetic average, Q = quotient of basidiospores length / width.

Extraction, amplification and DNA sequencing: fragments of basidioma (*ca.*30 mg) were ground mechanically in 2 ml tubes with 3 sterile stainless steel balls of 3mm diam. shaken at 3000 oscillations *per* minute for 1–2 minutes in Mjolnir 1.0 Tissue Lyser (Mjolnir1.0 Tissue Lyser, developed by Gerardo Robledo & Daniel Franchi at Laboratorio de Micologia, IMBIV-CONICET, works with oscillations of 3 cm and adjustable speed of 0–3000 revolutions *per* minute). The resulting powder was transferred to a 1.5 mL pre-warmed (65ºC) tubes containing 800 µL of extraction buffer [CTAB 2%, 100 mM Tris-HCl pH 8, 1.4 M NaCl, 20 mM EDTA, 1% PVP , β-Mercaptoetanol (0.2 %)] and incubated at 65ºC for 60 minutes. DNA was extracted twice with chloroform-isoamyl alcohol (24:1), precipitated with isopropanol and sodium acetate during 30–40 minutes at -80°C, washed with 70% ethanol, and finally re-suspended in 50 µL ultrapure water.

PCR amplifications were performed with the GoTaq® Green Master Mix (Promega Corporation, Madison, Wisconsin, USA), following the manufacturer protocol and amplification conditions in accordance to the authors of the used primer pairs. Primer pairs LR0R and LR5 (Cubeta *et al*. 1991, Vilgalys & Hester 1990), ITS-6R and ITS-8F (Dentinger *et al*. 2010) and 2218-R and 983-F (Rehner & Buckley 2005) were used to the amplification of the nuclear ribosomal ITS regions (Internal Transcribed Spacer, including 5.8S), nLSU rRNA gene (28S) and partial *tef*1-α gene (Translation Elongation Factor 1-α), respectively. The amplification products were purified and sequenced trough the Sanger dideoxy method in Macrogen Incorporation© (Seoul, Republic of Korea). We obtained a total of 6, 8 and 3 sequences of nLSU, ITS and *tef*1-α, respectively. They were manually inspected and assembled by BioEdit v. 7.0.0 (Hall 1999). Finally we uploaded the sequences in GenBank ® (http://www.ncbi.nlm.nih.gov/genbank). Both newly and previously published sequences used in the phylogenetic reconstruction are listed in Table 1.

Phylogenetic analyses: nucleotide sequences were aligned and manually inspected using MUSCLE (Edgar 2004) as implemented in MEGA v 6 (Tamura *et al*. 2013), with default settings. Each genetic marker (LSU, ITS and *tef*1-α) was individually aligned and the estimation of the best-fit nucleotide evolutionary model was also applied to each individual dataset, according to Bayesian Information Criterion as implemented in jModelTest v 2.0 (Santorum *et al*. 2014). Indels present within our ITS dataset were recoded as binary characters with the simple indel coding method, SIC (Simmons & Ochoterena 2000) as implemented in FastGap V1.2 software (Borchsenius 2009). The individual datasets, including the indels matrix, were combined in a Nexus file comprising 41 specimens representing 8 putative species. *Fomitiporia castilloi* was designated as outgroup (Amalfi & Decock 2013, Amalfi *et al*. 2014). The final alignment was deposited in TreeBASE (http://www.treebase.org/treebase/index.html), under accession ID 21428.

TABLE 1. List of *Fomitiporia* species, specimens/cultures, host´s identity and origin, locality and sequences accession number (GenBank) included in the phylogenetic analyses. Accessions in boldface are new sequences generated in this study. T= type; E=exotic, N= native, n/d = no data.

Species Voucher/ Culture references	Host Species	Origin	Country	GenBank Accession numbers ITS	LSU	*tef*1-α
Fomitiporia impercepta Morera, Robledo & Urcelay						
Urcelay 543, CORDC00005285	*Ligustrum lucidum* W.T. Aiton	E	ARG	MF615299	-	MF624763
Robledo 2594, CORDC00005289 (**T**)	*Lithraea molleoides* (Vell.) Engl.	N	ARG	MF615298	MF615266	-
Robledo 2024, CORDC00005287	*Ligustrum lucidum*	E	ARG	MF615296	MF615264	-
Robledo 2028, CORDC00005288	*Ligustrum lucidum*	E	ARG	MF615297	MF615265	-
Urcelay 509, CORDC00005284	*Robinia pseudoacacia* L.	E	ARG	MF615295	MF615267	MF624762
Urcelay 584, CORDC00005286	*Cupressus* sp.	E	ARG	-	MF615268	MF624764
MUCL 53675	n/d		GUF	JX093791	JX093835	JX093748
MUCL 46181, (CBS 386.66)	*Pouteria salicifolia* (Spreng.) Radlk.	N	ARG	EF433563	EF429234	GU461930
Fomitiporia castilloi Amalfi & Decock						
MUCL 53481 (**T**)	Unidentified angiosperm	-	GUF	JQ087889	JQ087916	JQ087943
MUCL 53980	Unidentified angiosperm	-	GUF	JX093786	JX093830	JX093743
Fomitiporia dryophila Murrill						
MUCL 46380	*Celtis occidentalis* L.		USA	EF429238	EF429219	GU461900
MUCL 46381	*Quercus virginiana Mill*.		USA	EF429239	EF429220	GU461901
MUCL 46379	*Quercus nigra* L.		USA	EF429240	EF429221	GU461902
MUCL 51144	*Quercus* sp.		USA	KF444689	KF444712	KF444758
Fomitiporia expansa Decock & Amalfi						
MUCL 55026 (**T**)	Unidentified angiosperm		GUF	KJ401032	KJ401031	KJ401033
Fomitiporia langloisii Murrill						
MUCL 46164	Unidentified angiosperm		USA	AY340031	EF429222	KF444762
MUCL 46373	*Magnolia acuminata* (L.) L.		USA	EF429243	EF429226	KF444760
MUCL 46377	*Quercus nigra*		USA	EF429241	EF429224	KF444761
MUCL 46375	*Cercis canadensis* L.		USA	EF429242	EF429225	GU461908
MUCL 46374	*Magnolia* sp.		USA	EF429244	EF429226	KF444763
MUCL 46165	n/d		USA	AY340026	EF429227	GU461909
Fomitiporia maxonii Murrill						
MUCL 51331	Unidentified angiosperm		ARG	KF444691	KF444714	KF444764
MUCL 46037	*Citrus paradisi* Macfad		CUB	EF433560	EF429231	GU461911
MUCL 51540	n/d		CUB	KF444692	KF444715	KF444765
MUCL 51399	n/d		CUB	KF444693	-	KF444766
MUCL 52340	n/d		MEX	KF444694	KF444717	KF444767
MUCL 53364	n/d		MEX	KF444695	KF444718	KF444768
MUCL 46017	*Citrus* sp.		CUB	EF433559	EF429230	GU461910
Fomitiporia neotropica Campos Santana *et al.*						
Urcelay 544, CORDC00005290	*Fraxinus americana* L.	E	ARG	MF615300	-	-
Urcelay 576, CORDC00005291	*Geoffroea decorticans* (Gillies ex Hook. & Arn.) Burkart	N	ARG	MF615301	-	-
Urcelay 594, CORDC00005292	Undetermined	N	ARG	MF615302	-	-
Robledo 2184 CORDC00005293	*Campsis grandiflora* (Thunb.) K.Schum.	E	ARG	-	MF615269	-
MUCL 54212	Unidentified angiosperm	n/d	BRA	KF444702	KF444725	KF444775
MUCL 54196	Unidentified angiosperm	n/d	BRA	KF444701	KF444724	KF444774
MUCL 54206	Unidentified angiosperm	n/d	BRA	KF444700	KF444723	KF444773
MUCL 51336	n/d		ARG	KF444699	KF444722	KF444772
MUCL 51335 (**T**)	Unidentified angiosperm	n/d	ARG	KF444698	KF444721	KF444771
MUCL 54246	Unidentified angiosperm	n/d	BRA	KF444697	KF444720	KF444770
MUCL 53114	Unidentified angiosperm	n/d	GUF	JX093792	JX093836	JX093749
MUCL 49549	*Schinus* sp.	n/d	ARG	KF444696	KF444719	KF444769
Fomitiporia sonorae (Gilb.) Y.C. Dai						
MUCL 47689 (**T**)	n/d		USA	JQ087893	JQ087920	JQ087947

Bayesian Inference (BI) was applied to the combined dataset, which was performed by MrBayes v 3.2.6 (Ronquist & Huelsenbeck 2003), with base frequencies, rates of nucleotide substitution, gamma shape and proportion of invariant sites estimated by the software. BI was implemented by 5 independent runs starting from random trees with four simultaneous chains, 5 million MCMC generations keeping one tree every 1000th generation. Four rate categories were used to approximate the gamma distribution and 40% of the sampled trees were discarded as burn-in. Because of the computational cost of the analysis, the 5 runs were done separately and the trees generated for each one were combined afterwards with the software LogCombiner as implemented in the BEAST package v1.8.0 (Drummond *et al*. 2012). The remaining trees from each run were used to reconstruct a 50% majority-rule consensus tree and to estimate Bayesian posterior probabilities (BPP) of the branches. Those nodes receiving BPP ≥ 0.95 were considered strongly supported, while nodes with 0.94 ≥ BPP ≥ 0.7 were considered moderately supported. Convergence diagnostics statistics were analyzed in Tracer v.1.6 (Rambaut *et al.* 2014).

Statistical analysis of morphological data: once studied specimens were assigned to phylogenetic clades after molecular analyses, we statistically searched for differences in basidiospores size (length and width), Q = ratio of length/ width of basidiospores, pore diameter and dissepiments thickness between species. Since data were not normally distributed we used Mann Whitney test non-parametric test. Data were analyzed with the statistical software *Infostat* (Di Rienzo *et al*. 2008).

Results

Phylogenetic analyses: the final alignment of LSU resulted of 36 sequences resulted in 811 bp length, including gaps. The estimated best-fit nucleotide evolutionary model was TIM1 + I, with likelihood score of 14.907.09, and base frequencies as following: A = 0.2635, C = 0.2052, G = 0.2956, T = 0.2357 and proportion of invariable sites = 0.8470. The final alignment of ITS resulted in 39 sequences with 795 bp length including gaps. The estimated best-fit nucleotide evolutionary model was TrN + G, with likelihood score of 2100.8110, and base frequencies as following: A = 0.2563, C = 0.2056, G = 0.2021, T = 0.3360 and gamma shape = 0.2390. The final alignment of *tef*1-α resulted in 37 sequences with 1169 bp length, including gaps. Its estimated best-fit evolutionary model was TIM3ef + G, with likelihood score of 2969.7236, frequency of 0.25 equal for all bases, and gamma shape = 0.2610. The combined datasets for MrBayes resulted in a Nexus file with 41 specimens and 2832 characters length, with 4 partitions, as mixed data (DNA and standard). 'HKY substitution rate' (nst = 2) was applied to all partitions, 'gamma rate' was applied to indels, ITS and *tef*1-α datasets and 'proportion of invariable sites rate' was applied to the 28S dataset with no gamma distribution.

The combined log files in Tracer presented Effective Sample Size (ESS) above 11165 for all the parameters. The mean Logarithm of Likelihood (LnL) was -7096.2779 (ESS = 11463), with standard deviation of 7.9033 and variance of 62.462. The marginal probability distribution overlapped. The Joint-Marginal Probability Distribution Graphic showed no tendencies and the trace files showed that all the parameters reached stationary frequencies. We generated five 50% majority-rule consensus trees with identical topology and slightly different support values. One of them with the highest support values is shown in Fig. 1.

The studied *Fomitiporia* specimens with resupinate basidiomata were distributed in two strongly supported clades (BPP = 1.0). One clade represents *F. neotropica* as defined by Campos Santana *et al.* (2014). The second clade represents the undescribed '*Fomitiporia* PS10' as defined by Amalfi & Decock (2014); this clade constitutes a phylogenetic species that we describe here as *Fomitiporia impercepta sp. nov.* Both species, *F. neotropica* and *F. impercepta,* form a moderately supported clade (BPP = 0.77). This later clade is the sister clade (BPP = 1) to all other neotropical species with resupinate habit, *i.e. Fomitiporia dryophila*, *F. expansa*, *F. langloisii F. maxonii* and *F. sonorae*, which in turn grouped together with the highest support value. *Fomitiporia castilloi* presents a pileate habit.

Morphological analysis: the morphological characters of the specimens of each clade were measured and analyzed to evaluate the existence of statistical differences between the two species. Despite the existence of some differences in average values, no statistical differences were observed for any of the analized variables: basidiospores length (p=0,2785), basidiospores width (p=0,1436), Q (p=0,2049), pores diameter (p= 0,2187) and dissepiments thickness (p=0,1951).

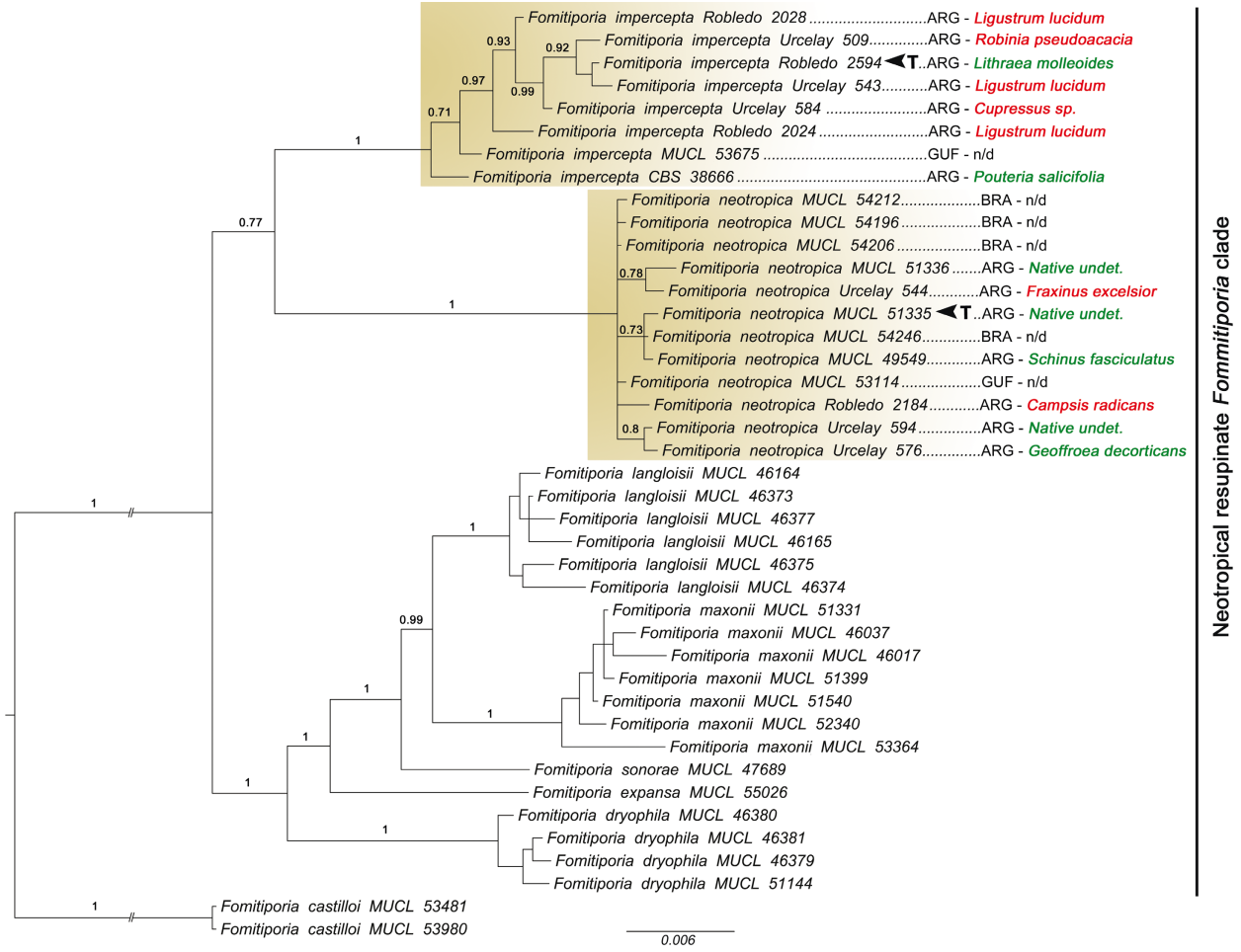

FIGURE 1. One of the five 50% majority-rule consensus trees from Bayesian inference of combined ITS, nLSU and *tef*1-α sequences. BPP is shown above branches. Brown boxes shows two sister clades: *Fomitiporia neotropica* and *Fomitiporia impercepta*, clustered together (BPP=0.77). Exotic trees are noted in red and native trees in green. T=type, ARG=Argentina, GUF=French Guiana, BRA=Brasil.

Taxonomy

Fomitiporia impercepta Morera, Robledo and Urcelay *sp. nov*. (Fig. 2 a–b)

Mycobank: MB 817799.

Type:—ARGENTINA. Córdoba: San Javier, Loma Bola, Cruce de Arroyos, 749 meters above sea level (m asl), 32°13'31.06" S, 65° 0'25,23" W., 24 April 2013, On living trunk of *Lithraea molleoides* (Vell.) Engl. Leg. Gerardo Robledo. *CORDC00005289* (CORD).

Etimology: from the latin '*impercepta*', unnoted, imperceptible, in reference to cryptic species.

Basidiomata perennial, resupinate, cushion-shaped, extending up to 6 cm long, 3 cm wide, 0.2–1 cm in the thickest part, with a corky consistency with fresh to hard corky consistency when it dries; *margin* narrow, up to 0.2–2 mm wide, densely velutinous, buckthorn brown (plate XV, color or hue number 17′, tone i) to Dresden brown (XV,17′, k) becoming light orange-yellow (III, 17′, d) to apricot yellow (IV, 19, b) to the edge. In old specimens margin becoming mouse gray (LI, 15′′′′′) to deep mouse gray (LI, 15′′′′, i), *pore surface,* buffy brown (XL, 17′′, i) to Isabella (XXX, 19′′, i), becoming pallid mouse grey (LI, 15′′′′′, f) to pale smoke gray (XLVI, 21′′′′, f) on aging; *pores*, round to ellipsoid at inclined parts, 5–7/mm, (77.5) 90–142.6 (167.5) µm diam., ave= 113.07 µm; *dissepiments* entire, thin to thick, 20–82.5 µm thick, ave= 43.67 µm; *context* densely fibrous, buckthorn brown (XV, 17′, i) to Dresden brown (XV, 17′, k), homogeneous in its extension, very thin 0.2–1 mm thick; *tubes* uni- or multi-layered, light dresden brown (XV,17′, k) to light orange-yellow (III, 17′, d), 0.2–4 mm thick each, totaling up to 10 mm thick, separated by a thin, slightly darker layer of sterile mycelium (Fig. 2b).

Hyphal system dimitic, identical in the context and hymenophoral trama; *generative hyphae* hyaline to faintly yellow, thin-walled, occasionally thickened and golden brown, sparsely branched (1.5–) 2.0–3 µm diam, ave= 2.17 µm, *skeletal hyphae* pale yellow brown to golden brown, thick-walled, but with an open lumen, 2–3.0 (4.0) µm diam, ave= 2.6 µm, with occasional wall constrictions where lumen becomes capillary.

Hymenium: *basidia* subglobose, 9–10 × 8–9 µm, with four small sterigmata; *basidioles* identical in shape but slightly smaller; *hymenial setae* absent*; basidiospores* globose to subglobose, (4.0) 5.0–6.0 (7.0) × 4.0–6.0 (7.0) µm, ave= 5.6 × 5.1 µm, Q= 1–1.37, ave= 1.11, thick walled, hyaline and strongly dextrinoid; *Chlamydospores* absent.

Type of rot: white rot.

Substrate and hosts: living trunks and dead branches attached to living trunk of *Lithraea molleoides* (native Anacardiaceae), *Pouteria salicifolia* (native Sapotaceae), *Ligustrum lucidum* (exotic Oleaceae), *Robinia pseudoacacia* (exotic Fabaceae), and *Cupressus* sp. (exotic Cupressaceae).

Distribution: so far known from South America (central Argentina and French Guiana).

Examined specimens:—ARGENTINA, Córdoba: Calamuchita, Intiyaco, 31°57’30.75” S, 64°42’44.20” W, 1154 m asl., living trunk of *Robinia pseudoacacia* L., Carlos Urcelay, 6 May 2012. *CORDC00005284* (CORD) .—ARGENTINA, Córdoba: Capital, Ciudad Universitaria, 31°26’7.75” S, 64°11’8.05” W, 444 m asl., base of living trunk of *Ligustrum lucidum* W.T. Aiton, Guillermo Morera, 15 May 2012. *CORDC00005285* (CORD).—ARGENTINA, Córdoba: Capital, Ciudad Universitaria, 31°26’7.75” S, 64°11’8.05” W, 444 m asl., living trunk of *Cupressus* sp., Carlos Urcelay, 16 August 2012. *CORDC00005286* (CORD).—ARGENTINA, Córdoba: Capital, Ciudad Universitaria, Facultad de Artes, 31°26’7.6” S, 64°11’26” W, 439 m asl., dead branch attached to living trunk of *Ligustrum lucidum* W.T. Aiton, Gerardo Robledo and Carlos Urcelay, 22 March 2010. *CORDC00005287* (CORD).—ARGENTINA, Córdoba: Capital, Ciudad Universitaria, Facultad de Artes, 31°26’7.6” S, 64°11’26” W, 439 m asl., base of living trunk of *Ligustrum lucidum* W.T. Aiton, Gerardo Robledo, 22 March 2010. *CORDC00005288* (CORD).

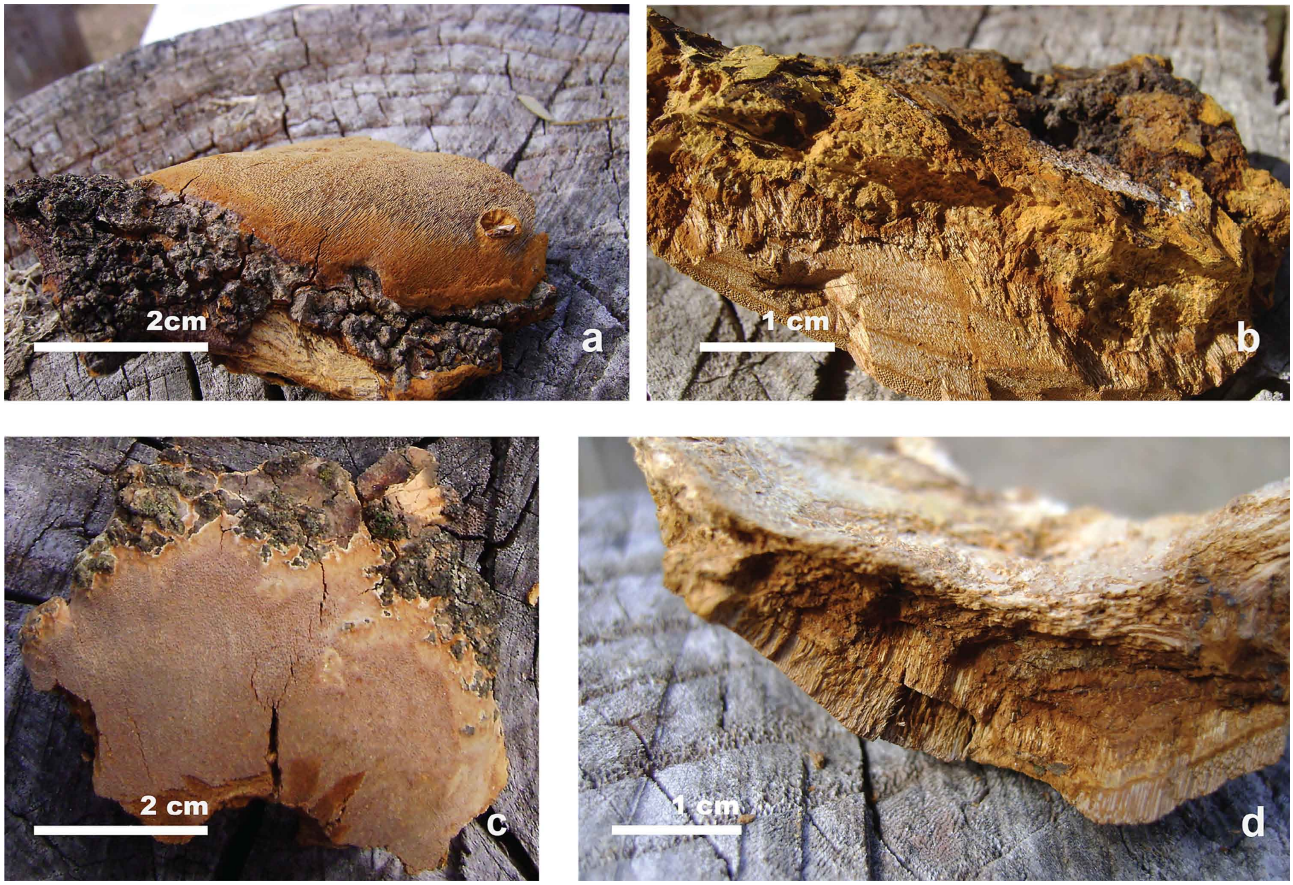

FIGURE 2. *Fomitiporia impercepta* (CORDC00005289): a. pore surface; b. tube layers. *Fomitiporia neotropica* (CORDC00005290): c. pore surface; d. tube layers.

Discussion

Among the specimens of *Fomitiporia* found on native and exotic trees in the studied region, four corresponded to *F. neotropica* and six corresponded to a previously undescribed species here named as *F. impercepta*. We did not find measurable morphological features that allow differentiating *F. impercepta* from *F. neotropica* (*cfr.* morphological analyses in results section, Fig. 2). However, some specimens of *F. impercepta* have more than two tube layers (up to four) and a whitish color pattern in old tubes filled by generative hyphae, suggesting a perennial habit against the annual to biennial habit of *F. neotropica*.

Fomitiporia impercepta and *F. neotropica* are similar species belonging to the "Neotropical resupinate" clade within *Fomitiporia* (Decock *et al*. 2007, Amalfi *et al*. 2012, Campos Santana *et al.* 2014). This clade is represented by Neotropical species with resupinate basidiome and extends from southeastern USA to southeastern of Brazil and central Argentina (Decock *et al*. 2007, Amalfi & Decock 2014, Campos Santana *et al.* 2014). The phylogenetic reconstruction showed that *F. impercepta* is a sister clade to *F. neotropica*; These two species clade is distant from the others neotropical species, *i.e. Fomitiporia dryophila*, *F. maxonii*, *F. langloisii*, *F. sonorae* and *F. expansa* (Fig. 1). The topology of the neotropical resupinate *Fomitiporia* species clade recovered in our analysis, i.e. *F. neotropica* and *F. impercepta* as a sister clades, differs from those previously shown (Campos Santana *et al*. 2014, Amalfi *et al*. 2014).

Fomitiporia impercepta occurs simpatrically with *F. neotropica*, *F. expansa* and *F. maxonii* at a regional scale. *Fomitiporia expansa* differs in forming effused and extended basidiomata up to 1 meter long in the longest extension, 30 cm wide and 1.5–5 mm in the thickest part (Amalfi & Decock 2014), whereas *F. impercepta* shows smaller basidiomata up to 6 cm long and 10 mm thick. *Fomitiporia maxonii* can be distinguished by the smaller pores, 7–10/mm (Decock *et al*. 2007).

Among native trees, the studied specimens of *F. neotropica* occured on *Geoffroea decorticans* (Fabaceae), *Schinus fasciculata* (Anacardiaceae) from Chaquean region and other unidentified trees from pristine tropical forest in northwest and northeast Argentina and Southeast Brazil. In central Argentina, it was also found on exotics *Fraxinus excelsior* (Oleaceae) and *Campsis grandiflora* (Bignonaceae) introduced from North America and Asia (China), respectively. In turn, *F. impercepta* occured on the native tress *Lithraea molleoides* (Anacardiaceae) and *Pouteria salicifolia* (Sapotaceae), ans on the exotic *Cupressus* sp. (Holartic Gymnosperm), the North American *Robinia pseudoacacia* (Fabaceae), and *Ligustrum lucidum* (Oleaceae) from China. It is remarkable, that despite their sympatric distribution, until now *F. neotropica* and *F. impercepta* have not been found in the same host species, either native or exotic, suggesting some degree of host selectivity.

These findings reveal that the two *Fomitiporia* studied here are capable of 'jump on' exotic trees. This phenomenon has been observed in other species in the genus such *F. maxonii* causing wood rot in living Asian *Citrus* planted in Cuba (Cabrera *et al.* 2014) and the Holartic *F. polymorpha* causing esca-disease in living Asian *Vitis vinifera* in West North America (Cloete *et al*. 2015). In these cases, they constitute a treat to the perennial crops. Instead, the exotic trees *Ligustrum lucidum* and *Robinia pseudoacacia*, decayed by *F. neotropica* and *F. impercepta*, are major invaders in natural ecosystems from central Argentina (Giorgis & Tecco 2014). Therefore, these fungal species are good candidates for long-term biological control over invasive trees in the studied region.

Conclusion

The multigene analysis revealed the existence of two morphologically similar species in the studied resupinate *Fomitiporia* specimens. One of these species is described as new and the other species was identified as *F. neotropica*. The phylogenetic position of these species revealed a South American origin and their occurrence on exotic living trees suggest their capabilities to jump on new hosts.

Acknowledgments

Authors wish to acknowledge the assistance of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and the Universidad Nacional de Córdoba, both of which support facilities used in this project. Financial support was provided by FONCYT (PICT 1676) and Fondo IBOL Conicet. C. Frontera and N. Sapag are kindly acknowledged for language revision.

References

Abarenkov, K., Henrik, N.R., Larsson, K-H., Alexander, I.J., Eberhardt, U., Erland, S., Høiland, K., Kjøller, R., Larsson, E., Pennanen, T., Sen, R., Taylor, A.F.S., Tedersoo, L., Ursing, B.M., Vrålstad, T., Liimatainen, K., Peintner, U. & Kõljalg, U. (2010) The UNITE database for molecular identification of fungi–recent updates and future perspectives. *New Phytologist* 186 (2): 281–285. https://doi.org/10.1111/j.1469-8137.2009.03160.x

Amalfi, M. & Decock, C. (2013) *Fomitiporia castilloi sp. nov.* and multiple clades around *F. apiahyna* and *F. texana* in Meso- and South America evidenced by multiloci phylogenetic inferences. *Mycologia* 105 (4): 873–887. https://doi.org/10.3852/11-423

Amalfi, M. & Decock, C. (2014) *Fomitiporia expansa*, an undescribed species from French Guiana. *Cryptogamie Mycologie* 35 (1): 72–86. https://doi.org/10.7872/crym.v35.iss1.2014.73

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 (6): 1303–1317. https://doi.org/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 (4): 880–893. https://doi.org/10.3852/11-196

Borchsenius, F. (2009) *FastGap 1.2*. Department of Biosciences, Aarhus University, Denmark. http://www.aubot.dk/FastGap_home.htm (accessed 20 June 2016)

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. https://doi.org/10.1016/j.cropro.2014.01.006

Campos Santana, M., Amalfi, M., Robledo, G., Borges da Silveira, R.M. & Decock, C. (2014) *Fomitiporia neotropica*, a new species from South America evidenced by multilocus phylogenetic analyses. *Mycological Progress* 13 (3): 601–615. https://doi.org/10.1007/s11557-013-0943-1

Cloete, M., Fischer, M., Mostert, L. & Halleen, F. (2015) Hymenochaetales associated with esca-related wood rots on grapevine with a special emphasis on the status of esca in South African vineyards. *Phytopatholia Mediterranea* 54 (2): 299.

Crous, P.W., Gams, W., Stalpers, J.A., Robert, V. & Stegehuis, G. (2004) MycoBank: an online initiative to launch mycology into the 21st century. *Studies in Mycology* 50 (1): 19–22.

Cubeta, M.A., Echandi, E., Abernethy, T. & Vilgalys, R. (1991) Characterization of anastomosis groups of Binucleate Rhizoctonia species Using Restriction Analysis of an Amplified Ribosomal RNA Gene. *Phytopathology* 81 (11): 1395–1400. https://doi.org/10.1094/Phyto-81-1395

Decock, C., Figueroa, S.H., 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 (5): 733–752. https://doi.org/10.1080/15572536.2007.11832537

Dentinger, B.T.M., Margaritescu, S. & 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 (4): 628–633. https://doi.org/10.1111/j.1755-0998.2009.02825.x

Desprez-Loustau, M.L., Courtecuisse, R., Robin, C., Husson, C., Moreau, P.a., Blancard, D., Selosse, M.a., Lung-Escarmant, B., Piou, D. & Sache, I. (2010) Species diversity and drivers of spread of alien fungi (*sensu lato*) in Europe with a particular focus on France. *Biological Invasions* 12 (1): 157–172. https://doi.org/10.1007/s10530-009-9439-y

Dereeper, A., Guignon, V., Blanc, G., Audic, S., Buffet, S., Chevenet, F., Dufayard, J.F., Guindon, S., Lefort, V., Lescot, M., Claverie, J.M. & Gascuel, O. (2008) Phylogeny.fr: robust phylogenetic analysis for the non-specialist. *Nucleic Acids Research* 36 (2): W465–W469. https://doi.org/10.1093/nar/gkn180

Di Rienzo, J.A., Casanoves, F., Balzarini, M.G., Gonzalez, L., Tablada, M. & Robledo, C.W. (2008) InfoStat, versión 2008, Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.

Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7 *Molecular Biology And Evolution* 29 (8): 1969–1973.

https://doi.org/10.1093/molbev/mss075

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32 (5): 1792–1797.
https://doi.org/10.1093/nar/gkh340

Finlay, B.J. (2002) Global dispersal of free-living microbial eukaryote species. *Science* 296 (5570): 1061–1063.
https://doi.org/10.1126/science.1070710

Fischer, M. & Binder, M. (2004) Species recognition, geographic distribution and host-pathogen relationships: a case study in a group of lignicolous basidiomycetes, Phellinus sl. *Mycologia* 96 (4): 799–811.
https://doi.org/10.1080/15572536.2005.11832927

Giorgis, M. & Tecco, P. (2014) Árboles y arbustos invasores de la Provincia de Córdoba (Argentina): una contribución a la sistematización de bases de datos globales. *Boletín de la Sociedad Argentina de Botánica* 49 (4): 581–603.

Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic acids symposium series* 41: 95–98.

Heredia, F., Morera, G., Robledo, G., Cagnolo, L. & Urcelay, C. (2014) Interacciones entre hongos de la madera (Agarycomycetes) y árboles nativos y exóticos de un ecosistema urbano (Córdoba, Argentina). *Bosque Valdivia* 35: 391–398.
https://doi.org/10.4067/S0717-92002014000300013

Lymbery, A.J., Morine, M., Kanani, H.G., Beatty, S.J. & Morgan, D.L. (2014) Co-invaders: The effects of alien parasites on native hosts. *International Journal for Parasitology: Parasites and Wildlife* 3 (2): 171–177.
https://doi.org/10.1016/j.ijppaw.2014.04.002

Matheny, P.B., Wang, Z., Binder, M., Curtis, J.M., Lim, Y.W., Nilsson, R.H., Hughes, K.W., Hofstetter, V., Ammirati, J.F., Schoch, C.L. & Langer, E. (2007) Contributions of rpb2 and tef1 to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Molecular phylogenetics and evolution* 43 (2): 430–451.
https://doi.org/10.1016/j.ympev.2006.08.024

Moncalvo, J.M. & 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 (4): 425–436.
https://doi.org/10.1016/j.mycres.2007.12.001

Oberwinkler, F. (1994) Evolution of functional groups in Basidiomycetes (Fungi). *In:* Schulze, E.-D. & Mooney, H.A. (Eds.) *Biodiversity and Ecosystem Function.* Springer-Verlag, Berlin, pp. 143–63.
https://doi.org/10.1007/978-3-642-58001-7_7

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* 106 (1): 66–76.
https://doi.org/10.3852/13-045

Rajchenberg, M. & Robledo, G. (2013) Pathogenic polypores in Argentina. *Forest Pathology* 43: 171–184.
https://doi.org/10.1111/efp.12032

Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. (2014) *Tracer v1.6.* Available from: http://beast.bio.ed.ac.uk/Tracer (accessed 1 September 2017)

Rehner, S.A. & 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 (1): 84–98.

Ridgway R. (1912) *Color standards and color nomenclature*. The author Washington, D.C.
https://doi.org/10.5962/bhl.title.62375

Robert, V., Stegehuis, G. & Stalpers, J. (2005) The MycoBank engine and related databases. Available from: http://www.mycobank.org. (accessed 1 September 2017)

Robert, V., Vu, D., Amor, A.B.H., Wiele, N., Brouwer, C., Jabas, B., Szoke, S., Dridi, A., Triki, M., Daoud, S.B., Chouchen, O., Vaas, L., de Cock, A., Stalpers, J.A., Stalpers, D., Verkley, G.J.M., Groenewald, M., dos Santos, F.B., Stegehuis, G., Li, W., Wu, L., Zhang, R., Ma, J., Zhou, M., Gorjón, S.P., Eurwilaichitrv, L., Ingsriswang, S., Hansen, K., Schoch, C., Robbertse, B., Irinyi, L., Meyer, W., Cardinali, G., Hawksworth, D.L., Taylor, J.W. & Crous, P.W. (2013) MycoBank gearing up for new horizons. *IMA fungus* 4 (2): 371–379.
https://doi.org/10.5598/imafungus.2013.04.02.16

Robledo, G., Urcelay, C., Dominguez, L. & Rajchenberg, M. (2006) Taxonomy, ecology, and biogeography of polypores (Basidiomycetes) from Argentinian Polylepis woodlands. *Botany* 84 (10): 1561–1572.
https://doi.org/10.1139/b06-109

Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19 (12): 1572–1574.

https://doi.org/10.1093/bioinformatics/btg180

Santorum, J.M., Darriba, D., Taboada, G.L. & Posada, D. (2014) jmodeltest.org: selection of nucleotide substitution models on the cloud. *Bioinformatics* 30 (9): 1310–1311.
https://doi.org/10.1093/bioinformatics/btu032

Simmons, M.P. & Ochoterena, H. (2000) Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* 49 (2): 369–381.
https://doi.org/10.1093/sysbio/49.2.369

Simmons, M.P., Pickett, K.M. & Miya, M. (2004) How meaningful are Bayesian support values? *Molecular Biology and Evolution* 21 (1): 188–199.
https://doi.org/10.1093/molbev/msh014

Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA 6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution* 30 (12): 2725–2729.
https://doi.org/10.1093/molbev/mst197

Taylor, J.W., Turner, E., Townsend, J.P., Dettman, J.R. & Jacobson, D. (2006) Eukaryotic microbes, species recognition and the geographic limits of species: examples from the kingdom Fungi. *Philosophical Transactions of the Royal Society B: Biological Sciences* 361 (1475): 1947–1963.
https://doi.org/10.1098/rstb.2006.1923

Urcelay, C. & Robledo, G. (2004) Community structure of polypores (*Basidiomycota*) in Andean Alder wood in Argentina: functional groups among wood-decay fungi? *Austral Ecology* 29 (4): 471–476.
https://doi.org/10.1111/j.1442-9993.2004.01387.x

Vilgalys, R. & Hester, M. (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptoccocus species. *Journal of Bacteriology* 172 (8): 4238–4246.
https://doi.org/10.1128/jb.172.8.4238-4246.1990

Zuloaga, F.O., Morrone, O. & Belgrano, M.J. (2008) *Catalogue of the Vascular Plants of the Southern Cone (Argentina, Southern Brazil, Chile, Paraguay and Uruguay). Volume 2: Dicotyledoneae: Acanthaceae-Fabaceae (Abarema-Schizolobium).* Missouri Botanical Garden Press.