



What are the *Laetiporus* species present in southern South America?

¿Cuáles son las especies de *Laetiporus* presentes en el sur de América del Sur?

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ABSTRACT

The identity and phylogenetic relationships of *Laetiporaceae* taxa (Polyporales, Basidiomycota) remain poorly studied. In this work we carry out a multigene phylogenetic analysis to identify the *Laetiporus* species that grow in South America and move forward the understanding of the phylogenetic relationships among the poroid genera of *Laetiporaceae* within the antrodia clade. Based on the morphology and molecular phylogenetic data, two new genera are proposed, *Berckurtia* to accommodate *Berckurtia persicina* comb. nov. and *Atlantiporus* to accommodate *Atlantiporus squalidus* comb. nov., and 2 other new combinations *Kusaghiporia talpae* and *Laetiporus*

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dilatohyphus. A key to the poroid genera of the Laetiporaceae is also provided and the taxonomic implications for these species and related taxa are discussed.

Keywords — Antrodia clade; brown-rot polypores; Neotropical polypores; taxonomy.

RESUMEN

La identidad de los taxones, así como las relaciones entre géneros y especies de Laetiporaceae presentes en América del Sur, siguen siendo poco estudiadas. En este trabajo llevamos a cabo un análisis filogenético multigen para identificar las especies de *Laetiporus* que crecen en América del Sur y avanzar en la comprensión de las relaciones filogenéticas entre los géneros poroides de Laetiporaceae dentro del clado antrodia. Con base en la morfología y la evidencia filogenética molecular, se proponen dos nuevos géneros, *Berkcurtia* para acomodar a *Berkcurtia persicina* y *Atlantiporus* para acomodar a *Atlantiporus squalidus*, y 2 nuevas combinaciones *Kusaghiporia talpae* y *Laetiporus dilatohyphus*. También se proporciona una clave para los géneros poroides de Laetiporaceae y se discuten las implicaciones taxonómicas para estas especies y taxones relacionados.

Palabras clave — Clado antrodia; políporos de pudrición castaña; políporos neotropicales; taxonomía.

INTRODUCTION

The genus *Laetiporus* Murrill is widely distributed in the world causing brown rot on living hardwoods and conifers. *Laetiporus* belongs Laetiporaceae within the antrodia clade, a subgroup within the larger polyporoid clade in which at least 11 genera that produce a brown rot were included (*Antrodia* P. Karst., *Auriporia* Ryvar den, *Daedalea* Pers., *Fomitopsis* P. Karst., *Laetiporus* Murrill, *Oligoporus* Bref., *Postia* Fr., *Neolentiporus* Rajchenb., *Phaeolus* (Pat.) Pat., *Piptoporus* P. Karst. and *Sparassis* Fr.) (Ortiz Santana et al., 2013). *Laetiporus* species are in general easily recognized macroscopically by a pileate basidiomata, often imbricated, with a variable coloration from pale yellow to sulfur yellow, salmon to orange on the upper part of the pileus and a concolorous poroid hymenophore (Banik et al., 2012). Microscopically *Laetiporus* is characterized by ellipsoid to ovoid hyaline, smooth basidiospores and particular thick-walled binding hyphae in the context (Lindner & Banik, 2008). For a long time, all specimens with this general morphology were attributed to *Laetiporus sulphureus* and the species was reported as “cosmopolitan”. In the last 20 years this concept changed and more than 20 species are now recognized under the broad concept of *L. sulphureus*, each one circumscribed to a particular geographical region or substrate or combination of both (Banik et al., 1998; Burdsall & Banik, 2001; Ota et al., 2009; Lindner & Banik, 2011; Banik et al., 2012; Song et al., 2014; Pires et al., 2016; Song & Cui, 2017; Kout et al., 2019). Asia and North America have the greatest number of *Laetiporus* species cited in the world (Tomšovský & Jankovský, 2008; Ota et al., 2009; Banik et al., 2012; Song et al., 2014; Song & Cui, 2017; Song et al., 2018) while for Central and South

America few species have been recorded. *Laetiporus caribensis* Banik & D.L. Lindner was described from Puerto Rico (Banik *et al.*, 2012), *Laetiporus lobatus* J. Vlasák, J. Kout & D.L. Lindner from Costa Rica (Kout *et al.*, 2019), *Laetiporus squalidus* R.M. Pires, Motato-Vásq. & Gugliotta from the Atlantic rain forest of Brazil (Pires *et al.*, 2016) and *Laetiporus gilbertsonii* Burds. originally described for southern North America (Burdall & Banik, 2001) was recorded in North Argentina (Banik *et al.*, 2012). In South America there are numerous records of *Laetiporus* as *Laetiporus sulphureus* whose identity must be reassessed in the current phylogenetic scenario. In addition, studies in the Southern Hemisphere are few (Vasaitis *et al.*, 2009; Pires *et al.*, 2016; Song & Cui, 2017) and the relationships amongst *Laetiporus* species and related taxa within Laetiporaceae and the antrodia clade remain unresolved.

The aim of this work is to recognize the *Laetiporus* species growing in South America, specifically Argentina, Brazil, Paraguay and Uruguay and to move forward with understanding the phylogenetic relationships among poroid genera of *Laetiporaceae* within the antrodia clade.

MATERIALS AND METHODS

Specimens and Morphological analyses

Specimens were collected from native and exotic trees of Argentina, Brazil, Paraguay and Uruguay. Collected specimens, type and reference materials studied are kept in CORD, FLOR, FACEN and SP Herbaria. Herbarium acronyms follow Thiers (2022).

Basidiomata were analyzed macroscopically under binocular stereoscope. For microscopical analysis, freehand sections were mounted on Melzer's reagent, sodium hydroxide (3%), potassium hydroxide (3%), phloxine and congo red, and observed under optical microscope. All measurements, forty *per* character (n=40), were conducted on Melzer's reagent.

Extraction, amplification and DNA sequencing

DNA extraction was carried out from dry basidiomata with CTAB method of Doyle (1991) modified by Robledo *et al.* (2015); samples were pulverized and put into thermostatic bath with 800 μ l of CTAB and β -Mercaptoethanol (0.2 %). After 60 minutes, samples were centrifuged for 15 minutes at 14000 rpm. Then, 800 μ l of isoamyl-chloroform were added and centrifuged; 500 μ l of the supernatant were recovered and the last step was repeated. Then, 400 μ l were recovered and put into the freezer (-80°C) adding 700 μ l of isopropanol and 50 μ l of sodium acetate. An hour later, samples were centrifuged and washed with ethanol 70%; and finally, ethanol was evaporated, and samples were resuspended with 100 μ l of 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. The gene regions ITS of the nuclear ribosomal (Internal Transcribed Spacer, including 5.8S), LSU rRNA gene (28S) and partial *tef-1 α* gene (Translation Elongation

Factor 1- α) were amplified with the primer pairs ITS-6R and ITS-8F (Dentinger *et al.*, 2010), LR0R and LR5 (Cubeta *et al.*, 1991; Vilgalys & Hester, 1990) and 2218-R and 983-F (Rehner & Buckley, 2005) respectively. The amplification products were purified and sequenced through the Sanger dideoxy method in MacroGen Inc. © (Seoul, Republic of Korea). We obtained a total of eight, six and three sequences of ITS, LSU and *tef-1 α* , respectively; that 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>) (Table 1).

Phylogenetic analyses

The sequences generated in this study were combined with sequences retrieved from GenBank (NCBI) to compose two datasets. The first dataset (1) was constructed with ITS, LSU, and *tef-1 α* sequences from species of *Laetiporus s.l.* in order to clarify phylogenetic relationships and generic delimitation within Laetiporaceae. The second dataset (2) was constructed with ITS sequences of *L. gilbertsonii* from the south, central and North America, in order to test the current concept of the species. The newly generated sequences and additional sequences downloaded from GenBank are listed in Table 1. For both datasets, each sequence matrix (ITS, LSU, and *tef-1 α*) was individually aligned using MAFFT v.7 (Kato *et al.*, 2019), under the G-INS-i criteria. Then, they were manually inspected and edited using MEGA v.6 (Tamura *et al.*, 2013). Both ITS matrices were subdivided into three data partitions, ITS1, 5.8S and ITS2, while *tef-1 α* was subdivided into introns, and 1st, 2nd, and 3rd codon positions. The best-fit model of nucleotide evolution to each partition of the datasets was selected by AIC (Akaike Information Criterion) using jModel-Test2 v. 1.6 (Guindon & Gascuel, 2003, Darriba *et al.*, 2012). Bayesian Inference (BI) and Maximum Likelihood (ML) phylogenetic analyses were applied to both datasets. BI was performed using MrBayes 3.2 (Ronquist *et al.*, 2012) with two independent runs, each one beginning from random trees with four simultaneous independent chains, performing 10 million replications, and sampling one tree every 1000 generations. The first 2.5 million sampled trees were discarded as burn-in, while the remaining ones were used to reconstruct a 50 % majority-rule consensus tree and calculate Bayesian posterior probabilities (BPP) of the clades. ML searches were conducted with RAxML-HPC v. 8.2.3 (Stamatakis, 2014). The analysis first involved 100 ML searches, each one starting from one randomized stepwise addition parsimony tree, under a GTRGAMMA model, with all other parameters estimated by the software. Only the best-scored likelihood tree from all the searches was kept to assess the reliability of the nodes. Multiparametric bootstrapping replicates under the same model are computed, allowing the program to halt bootstrapping automatically by the autoMRE option. An additional alignment partition file to force RAxML software to search for a separate evolution model for each partition was used. jModel-Test2 v. 1.6, MrBayes 3.1.2, and RAxML-HPC 8.2.3 were performed in the CIPRES science gateway (Miller *et al.*, 2010; <http://www.phylo.org/>). A node was considered strongly supported if it showed BS (bootstrap) $\geq 80\%$ and / or BPP ≥ 0.95 (Hyde *et al.*, 2013). Hereafter, support values are presented as BPP/BS in the text.

Table 1 (part 1 of 3). Taxon sampling, specimen-voucher, geographic location substrata and GenBank accession numbers. New sequences generated in this study are in boldface.**Tabla 1 (parte 1 de 3).** Muestreo de taxones, especimen-voucher, ubicación geográfica, sustratos y números de acceso de GenBank. Las nuevas secuencias generadas en este estudio están en negrita.

Species voucher/cultures	Locality	Substrate	GenBank Accession Number		
			ITS	LSU	tef 1- α
<i>Piptoporellus soloniensis</i>					
Cui11386	China		KR605802	KR605741	KR610732
Cui11390	China		KR605803	KR605742	KR610733
Dai 11872	China		KR605804	KR605743	KR610731
<i>Piptoporellus triqueter</i>					
Dai13121	China		KR605807	KR605746	KR610738
<i>Pycnoporellus fulgens</i>					
Cui 10033	China		KX354458	KX354512	KX354687
<i>Sparassis crispa</i>					
AFTOL-ID 703			DQ250597	AY629321	DQ056289
<i>Rhodonía placenta</i>					
Wei 1406	China		KF699129	KT893750	KT893748
<i>Amyloporia carbonica</i>					
Cui 12212	China		KR605816	KR605755	KR610745
<i>Amyloporia xantha</i>					
Cui11544	China		KR605817	KR605756	KR610746
<i>Kusaghiporia talpae</i>					
M. Campi 80, G305	Paraguay	<i>Tipuana tipu</i>	—	OP526817	OP485085
C. Mancuello 002, G309	Paraguay	<i>Handroanthus sp.</i>	—	OP526818	—
PR-2	Puerto Rico		—	EU402543	—
<i>Kusaghiporia usambarensis</i>					
JMH-01 (Type)	Tanzania		—	MH010044	MH048871
JMH-02	Tanzania		—	MH010045	MH048869
IJV40-2	Tanzania		—	KM593894	—
IJV40-2	Tanzania		—	KM593895	—
<i>Laetiporus persicinus</i>					
HBB9564	USA, Florida	<i>Pinus taeda</i>	EU402579	EU402513	—
RLG14725	USA, Louisiana	<i>Quercus virginiana</i>	EU402581	EU402512	—
RLG14739	USA, Louisiana		EU402582	—	—
CBS 274-92	USA, Louisiana	<i>Quercus virginiana</i>	JQ686188	—	—
HBB9668	USA, Florida	<i>Quercus virginiana</i>	EU402580	—	—
<i>Phaeolus schweinitzii</i>					
FP-133218	USA: Oregon	<i>Tsuga</i>	KC585369	KC585198	—
FP-102447	USA: Michigan	<i>Pinus sp.</i>	KC585368	KC585197	—
OKM-4435-T	USA: Montana	<i>Abies grandis</i>	KC585370	KC585199	—
FPL5096			AY218422	AF287882	—
AFTOL 702			—	AY629319	DQ028602
DA-38	USA	<i>Prunus serotina</i>	EU402585	EU402514	—
Dai 8025	CHINA		KX354457	KX354511	KX354686
<i>Wolfiporia cocos</i>					
CBK 1, BJFC	China		KX354453	KX354689	KX354688
MD-106	USA	<i>Alnus sp.</i>	EU402594	EU402519	—
MD-275	USA	<i>Pinus contorta</i>	EU402595	EU402520	—
<i>Wolfiporia dilatohypha</i>					
CS-63-59-13-A-R	USA: Kentucky	<i>Quercus velutina</i>	KC585400	KC585234	—
FP-94089-R	USA: West Virginia	<i>Quercus rubra</i>	KC585401	KC585236	—
<i>Laetiporus ailaoshanensis</i>					
Dai 15629	China		KY886714	KY886740	KY886781
Dai 15655	China		KY886715	KY886741	KY886782
Dai 13567	China		KX354470	KX354498	KX354623
Dai 13256, BJFC016516	Yunnan, China	<i>Lithocarpus sp.</i>	KF951289	KF951317	KX354625
<i>Laetiporus caribensis</i>					
PR6583 TYPE	Puerto Rico	<i>Guarea guidonia</i>	NR119999	—	—
PR914	Puerto Rico	angiosperm	JN684762	—	—
PR6521	Puerto Rico	angiosperm	JN684771	—	—
<i>Laetiporus cincinnatus</i>					
DA-37	Wisconsin, USA	<i>Quercus velutina</i>	EU402557	EU402521	AB472661
Dai12811, BJFC013116	Connecticut, USA	<i>Quercus sp.</i>	KF951291	KF951304	KX354605
WS-1-6 (monosporic)	USA: Wisconsin		AB472627	—	AB472662

RESULTS

Phylogenetic analyses

Dataset 1 included sequences from 90 fungal specimens, with 2403 characters, of which 1238 were constant, 904 parsimony informative and 153 singletons. Dataset 2 included sequences from 43 specimens, with 517 characters, of which 460

Table 1 (part 2 of 3). Taxon sampling, specimen-voucher, geographic location substrata and GenBank accession numbers. New sequences generated in this study are in boldface.**Tabla 1 (parte 2 de 3).** Muestreo de taxones, especimen-voucher, ubicación geográfica, sustratos y números de acceso de GenBank. Las nuevas secuencias generadas en este estudio están en negrita.

JV0709/168-J	Virginia, USA	<i>Quercus sp.</i>	KF951290	KF951305	—
<i>Laetiporus conifericola</i>					
CA-8	California, USA	<i>Sequoia sempervirens</i>	EU402575	EU402523	AB472663
JAM-1	Alaska, USA	<i>Tsuga heterophylla</i>	EU402577	EU402524	AB472664
JV0709/81-J	California, USA	<i>Picea sp.</i>	KF951292	KF951327	—
<i>Laetiporus cremeiporus</i>					
Cui10586	Sichuan, China	<i>Lagerstroemia indica</i>	KF951277	KF951297	KX354602
Cui10991	Hubei, China	<i>Quercus sp.</i>	KF951279	KF951298	KX354641
Cui10988	Hubei, China	<i>Quercus sp.</i>	KF951278	KF951299	—
Dai10045	Jilin, China	<i>Quercus sp.</i>	KF951280	KF951300	—
Dai10107	Jilin, China	<i>Quercus sp.</i>	KF951281	KF951301	KX354604
Li 140927, BJFC			KX354459	KX354485	KX354603
F-19719 (monosporic)	Japan, Miyagi	<i>Quercus sp.</i>	AB308177	—	AB308252
F-19727 (monosporic)	Japan, Kumamoto	hardwood	AB308178	—	AB308253
F-21720 (monosporic)	Japan, Ibaraki	<i>Quercus mongolica</i>	AB308182	—	AB308256
FH1387	Japan, Hokkaido	<i>Taxus cuspidate</i>	AB308175	—	AB308250
<i>Laetiporus gilbertsonii</i>					
Urcelay 496, G14	Argentina	<i>Gleditsia amorphoides</i>	OP526823	OP526820	—
Robledo 2552, G54	Argentina	<i>Schinus fasciculatus</i>	OP526824	OP526821	—
Robledo 3296, G57	Argentina	<i>Schinus fasciculatus</i>	OP526825	OP526819	—
MCampi32-G304	Paraguay	<i>Eucalyptus sp.</i>	OP526826	—	—
MCampi30, G308	Paraguay		OP526827	OP526822	—
RP234, SP466046	Brazil	<i>Eucalyptus sp.</i>	KP765240	—	—
RP152, SP466044	Brazil	<i>Eucalyptus sp.</i>	KP765237	—	—
SP307821	Brazil	<i>Eucalyptus sp.</i>	KP765241	—	—
Robledo 47	Argentina, Yungas	<i>Schinus sp.</i>	JN684769	—	—
CFMR:OR-2	USA: Oregon	<i>Quercus sp.</i>	KU668967	—	—
Lowe12954	Costa Rica		JN684767	—	—
BZ544	Belize		JN684768	—	—
SP35	USA: California		AM269785	—	—
TJV2000-101 (<i>v. pallidus</i>)	Florida, USA	<i>Quercus sp.</i>	EU402553	EU402528	AB472668
L-12954 (<i>v. pallidus</i>)	Costa Rica	unknown hardwood	EU402551	—	—
FP150268 (<i>v. pallidus</i>)	Jamaica	<i>Eucalyptus sp.</i>	EU402552	—	—
TJV95-106-6	USA		AB472640	—	AB472669
6676	Uruguay	<i>Eucalyptus sp.</i>	EU840673	—	—
5032	Uruguay	<i>Eucalyptus sp.</i>	EU840668	—	—
6695	Uruguay	<i>Eucalyptus sp.</i>	EU840680	—	—
5055	Uruguay	<i>Eucalyptus sp.</i>	EU840669	—	—
5564	Uruguay	<i>Eucalyptus sp.</i>	EU840671	—	—
6688	Uruguay	<i>Eucalyptus sp.</i>	EU840675	—	—
6694	Uruguay	<i>Eucalyptus sp.</i>	EU840679	—	—
6677	Uruguay	<i>Eucalyptus sp.</i>	EU840674	—	—
5067	Uruguay	<i>Eucalyptus sp.</i>	EU840670	—	—
6689	Uruguay	<i>Eucalyptus sp.</i>	EU840676	—	—
CA-7 (monosporic)	USA		AB472636	—	AB472665
OR-2 (monosporic)	USA: Oregon	<i>Quercus sp.</i>	AB472638	—	AB472667
CA-13	USA, Florida	<i>Quercus sp.</i>	EU402549	EU402527	AB472666
JV 1109/31	USA	<i>Quercus sp.</i>	KF951293	KF951306	KX354630
CFMR:2695	USA: California		KX065950	KX065984	—
HW339500			HW339500	—	—
<i>Laetiporus huroniensis</i>					
HMC-3	USA, Michigan	<i>Tsuga canadensis</i>	EU402571	EU402540	—
HMC-1	USA, Michigan	<i>Tsuga canadensis</i>	EU402569	KX065985	AB472670
MI-7-1	USA, Michigan		AB472642	—	AB472671
MI-14	USA, Michigan	<i>Tsuga canadensis</i>	EU402573	EU402539	AB472672
<i>Laetiporus montanus</i>					
Cui10011	Jilin, China	gymnosperm	KF951274	KF951315	KX354617
Cui10015	Jilin, China	gymnosperm	KF951273	KF951311	KX354618
Cui1710	Inner Mongolia, China	<i>Larix sp.</i>	KF951275	KF951314	—
Dai11203	Inner Mongolia, China	<i>Larix sp.</i>	KF951276	KF951313	—
Dai 15888			KX354466	KX354494	KX354619
WD2303	Japan, Yamanashi	Conifer	AB308194	—	AB308265
WD2304	Japan, Yamanashi		AB308195	—	AB308266
WD2305	Japan, Yamanashi		AB308196	—	AB308267
94081417M11	Switzerland, Muntertal	<i>Larix decidua</i>	AB472619	—	AB472656
9407102M1Q	Switzerland, Zernez	<i>Larix decidua</i>	AB472620	—	AB472657
JV0407/27	Czech Republic	<i>Abies sp.</i>	KF951294	KF951312	—
<i>Laetiporus squalidus</i>					

were constant, 30 parsimony informative and 22 singletons. For dataset 1 the evolutionary models selected were TrNef+I+G (ITS1), TIM1ef+G (5.8S), HKY+I+G (ITS2), TrN+G (LSU), TVM+I (tef-1 α 1st codon pos.), TrN+I (2nd codon pos.) and TIM2+G (3rd codon pos.) and HKY+I+G (tef-1 α introns), with 510 charac-

Table 1 (part 3 of 3). Taxon sampling, specimen-voucher, geographic location substrata and GenBank accession numbers. New sequences generated in this study are in boldface.**Tabla 1 (parte 3 de 3).** Muestreo de taxones, especimen-voucher, ubicación geográfica, sustratos y números de acceso de GenBank. Las nuevas secuencias generadas en este estudio están en negrita.

<i>Laetiporus squalidus</i>						
RP 232, SP466047 TYPE	Brazil, São Paulo	<i>Eucalyptus</i> sp.	KP765238	KP765242	—	—
<i>Laetiporus sulphureus</i> (Europe-Asia)						
Dai12154, BJFC012671	Czech Republic	<i>Quercus</i> sp.	KF951295	KF951302	—	—
JV1106/15, BJFC015826	Czech Republic	<i>Picea</i> sp.	KF951296	KF951303	—	—
L13-706696	Czech Republic	<i>Sorbus aucuparia</i>	EU840565	EU884420	—	—
MUCL 8890	Belgium: Heverlee	<i>Taxus baccata</i>	AB472605	—	AB472644	—
MUCL 34165	Germany, Bayern		AB472608	—	AB472645	—
MUCL 39390	Belgium		AB472609	—	AB472646	—
9405292MH	Switzerland, Zurich	<i>Fraxinus excelsior</i>	AB472612	—	AB472649	—
Dai 12826	China		KR605819	KR605762	KR610753	—
<i>Laetiporus sulphureus</i> (North America)						
TJV99-150	Wisconsin, USA	<i>Fraxinus pensylvanica</i>	EU402567	EU402530	—	—
MAS-2	Massachusetts, USA	<i>Quercus rubra</i>	EU402568	EU402531	—	—
GR-12	Wisconsin, USA	angiosperm	EU402561	EU402534	AB472658	—
CT-1	Connecticut, USA	<i>Acer</i> sp.	EU402565	EU402532	AB472659	—
DA-41	Wisconsin, USA	<i>Salix</i> sp.	EU402566	EU402533	AB472660	—
<i>Laetiporus versisporus</i>						
Dai13160, BJFC013371	Yunnan, China	angiosperm	KF951266	KF951320	—	—
Dai7268, BJFC001160	Fujian, China	angiosperm	KF951267	KF951326	—	—
Cui5488, BJFC003529	Hainan, China	angiosperm	KF951268	KF951321	—	—
Cui7882, BJFC006371	Jiangxi, China	angiosperm	KF951269	KF951323	—	—
Cui9154, BJFC008092	Beijing, China	<i>Robinia</i> sp.	KF951270	KF951322	—	—
Dai13052, BJFC013275	Yunnan, China	<i>Castanea</i> sp.	KF951271	KF951324	—	—
Cui10992, BJFC013914	Yunnan, China	<i>Quercus</i> sp.	KF951272	KF951325	—	—
WD153, F-14748	Japan, Chiba	<i>Castaneopsis cuspidata</i>	AB308157	—	AB308238	—
WD820, F-15910	Japan, Ogasawara	hardwood	AB308135	—	AB308219	—
WD2437, F-19732	Japan, Miyazaki	hardwood	AB308141	—	AB308226	—
WD2320, F-19733	Japan, Miyazaki		AB308142	—	AB308227	—
WD2442, F-21721	Japan, Miyama		AB308149	—	AB308230	—
WD2444, F-19740	Japan, Kagoshima		AB308151	—	AB308232	—
<i>Laetiporus zonatus</i>						
Cui10403, BJFC011298	Yunnan, China	<i>Quercus</i> sp.	KF951282	KF951307	—	—
Cui10404, BJFC011299	Yunnan, China	<i>Quercus</i> sp.	KF951283	KF951308	—	—
HKAS54701	Yunnan, China	angiosperm	KF951285	KF951309	—	—
HKAS71806	Yunnan, China	angiosperm	KF951284	KF951310	—	—
<i>Laetiporus</i> sp.						
EUC-1	Hawaii, USA	<i>Eucalyptus saligna</i>	EU402545	EU402541	—	—
KOA-1	Hawaii, USA	<i>Acacia koa</i>	EU402546	EU402542	—	—
Munez 207	Costa Rica	Unknown	JN684764	—	—	—
Robledo 1122	Argentina	<i>Schinus</i> sp.	JN684765	—	—	—
RV4A	South Africa	<i>Eucalyptus</i> sp.	EU840662	—	—	—
RV5A	South Africa	<i>Eucalyptus</i> sp.	EU840663	—	—	—

ters, of which 460 were constant and 30 parsimony informative. Dataset 2 included sequences from 43 fungal specimens, with 517 characters, of which 460 were constant and 30 parsimony informative. Evolutionary models for dataset 2 were TPM2+G (ITS1) and JC (5.8S and ITS2).

The topology recovered in our phylogenetic analysis (Fig. 1) was overall consistent with previous results (Ortiz-Santana *et al.*, 2013; Justo *et al.*, 2017; Chen & Cui, 2016; Hussein *et al.*, 2018; Donatha *et al.*, 2020). Eight main lineages were recovered in the topology, corresponding to *Laetiporaceae* genera of *Sparassis*, *Pycnoporellus*, *Wolfiporia*, *Phaeolus*, *Kusaghiporia* and three independent lineages of taxa usually classified within *Laetiporus* namely: *Laetiporus squalidus*, *Laetiporus persicinus* and the main clade of *Laetiporus* species here defined as *Laetiporus* s.s. The specimens from Paraguay that purportedly constitute *Laetiporus persicinus* grouped with a specimen named *Polyporus* cf. *talpae* Cooke from Puerto Rico (Lindner & Banik, 2008) and with a species recently described from Africa for which the new genus *Kusaghiporia* J. Hussein, S. Tibell & Tibuhwa, was proposed (Hussein *et al.*, 2018). Specimens of *Laetiporus persicinus* from areas relatively close to the type locality, *i.e.* South Caro-

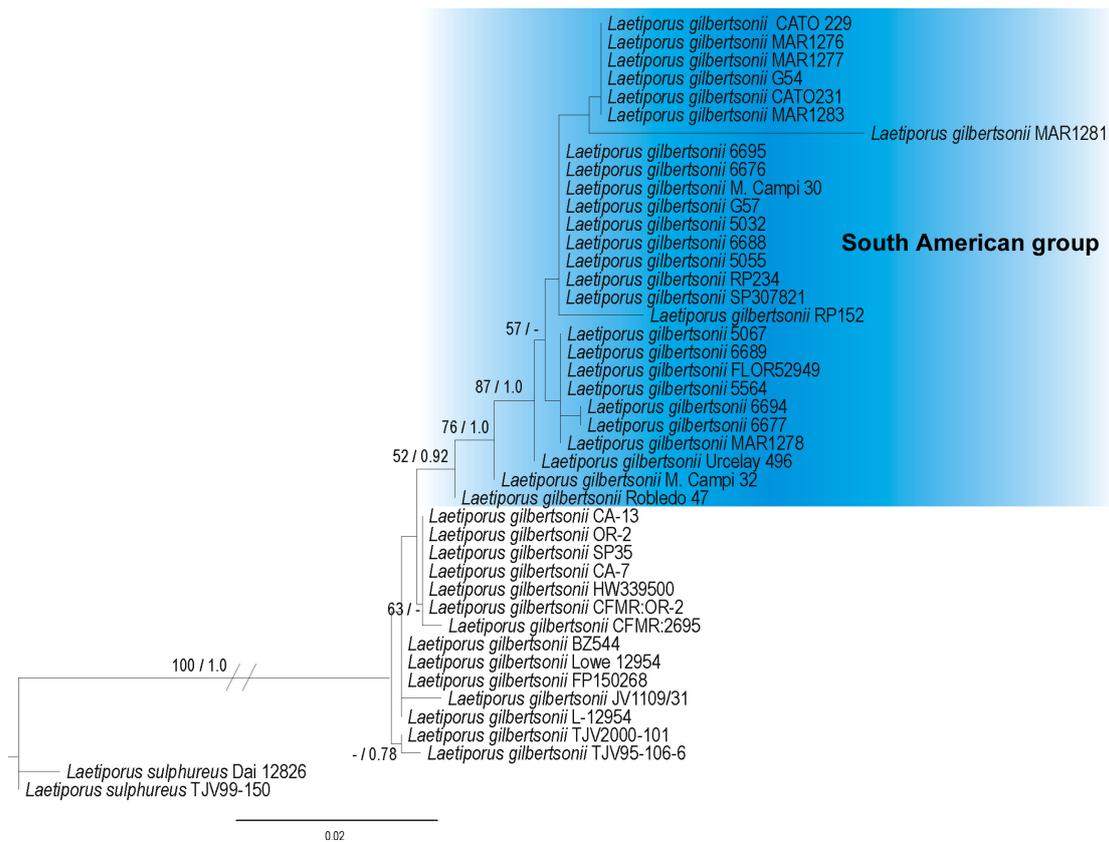


Fig. 2. Maximum likelihood (ML) tree positioning the South American specimens of the *Laetiporus gilbertsonii* complex, based on ITS sequence data. Bayesian posterior probability above 0.7 and Bootstrap values above 50 % are shown.

Fig. 2. Árbol de Máxima verosimilitud posicionando especímenes sudamericanos del complejo *Laetiporus gilbertsonii*, basados en secuencias ITS. Se muestran la probabilidad posterior por encima de 0.7 y valores de Bootstrap por encima del 50%.

Taxonomy

Atlantiporus Drechsler-Santos & Robledo gen. nov.

Mycobank: MB844421

Type species: Atlantiporus squalidus (R.M. Pires, Motato-Vásquez & Gugliotta)
Azevedo-Oliveira, Drechsler-Santos & Robledo

Etymology: in reference to Atlantic Forest, where the genus was found and so far, is endemic.

Basidiomata anual, resupinate forming narrow and small imbricated pilei, soft when fresh to hard when dry. Pileus amorphous, broadly attached, upper surface glabrous, azonate, slightly rugose, cream to pale brown when fresh and light ochraceous when dried. Margin irregular. Context homogeneous, azonate, concolorous. Pore surface present only under parts of resupinate and/or pileate basidiomata, cream when fresh to brown when dry, pores rounded and decurrent, tubes concolorous with pore surface, dissepiments entire, thin to slightly thick. Hyphal system dimitic; tubes composed by generative hyphae simple-septate, thin to thick-walled and skeletal-binding hyphae hyaline, thick-walled, branched with not so short branches, and

tortuous, not dissolving in KOH; context composed by gloeohyphae simple-septate, straight and unbranched, unusually branched and binding hyphae richly branched, sometimes with many thick-walled short branches, not dissolving in KOH. Basidia clavate, hyaline, with 4 sterigmata. Basidiospores ellipsoid to broadly ellipsoid, hyaline, smooth, slightly thick-walled, IKI-.

Remarks.— *Atlantiporus* is recognized macroscopically by the pale color of the resupinate basidiomata, with small imbricate, whitish and amorphous pilei. Microscopically it presents a dimitic hyphal system with skeleto-binding hyphae not dissolving in KOH and gloeohyphae restricted to the context. *Laetiporus* differs by having a trimitic hyphal system with binding hyphae restricted to the context and dissolving in KOH and straight and unbranched skeletal hyphae restricted to the trama of the tubes. The genus is so far known from one species, *A. squalidus*, and the phylogenetic relationships within Laetiporaceae are not clear.

Atlantiporus squalidus (R.M. Pires, Motato-Vásquez & Gugliotta) Azevedo-Oliveira, Drechsler-Santos & Robledo **comb. nov.** Figs 3-4
Mycobank: MB 844422

Basionym: *Laetiporus squalidus* R.M. Pires, Motato-Vásquez & A.M. Gugliotta, Nova Hedwigia 102 (3–4): 482 (2016) [MB#811581]

Remarks.— The morphological analysis of the type specimen reveals some particularities not observed in the original description. In the context we observed abundantly gloeohyphae (120–350 x 10–25 μm), thin to thick-walled, rarely branched and with simple septa, more than one can be observed in long gloeohyphae. Probably, those hyphae could correspond to the inflated generative hyphae described in the original description (Pires *et al.*, 2016). In the trama, skeleto-binding hyphae are parallelly arranged. True skeletal hyphae were not observed. Some branches of skeleto-binding hyphae were observed projecting into the hymenium (30–70 x 5–7 μm) like skeleto cystidia. Apart from these observations all the morphology agrees with the original description (Pires *et al.*, 2016). Additionally, the specimen FLOR 67251 presents a translucent margin that was not described in the fresh type specimen (cf. FIG 7 in Pires *et al.*, 2016). The size and shape of basidiospores are almost the same between specimens (Holotype: 6–7 x 4–5.5 μm , n=40, Q=1.3; FLOR 67251 5–6 x 4–5 μm , n=40, Q=1.2).

Ecology and Distribution.— Growing on dead or dead parts of living angiosperms. The host of the type specimen was not identified. The specimen from Parque Nacional de São Joaquim (Southern Brazil) was growing on *Schinus engleri* F.A. Barkley. The genus is so far known from Brazilian Atlantic Forest, recorded for the Tropical Upper Hills Broadleaved Forest of type locality (above 700m a.s.l.) at São Paulo and Subtropical Upper Highlands Cloud Broadleaved Dwarf-Forest of Santa Catarina state (above 1600m a.s.l.).



Fig. 3. Macroscopic features of *Atlantiporus squalidus*. A) Basidiome holotype (SP466047, photo by R.M. Pires in Pires *et al.*, 2016) B) Basidiome C) Pore surface and longitudinal section showing tubes and context (FLOR67251, photos by C. Azevedo-Oliveira). Scale bar = 1 cm.

Fig. 3. Características macroscópicas de *Atlantiporus squalidus*. A) Basidioma del holotipo (SP466047, fotografía R.M. Pires en Pires *et al.*, 2016); B) Basidioma. C) Superficie del poro y corte transversal mostrando tubo y contexto (FLOR67251, fotografía de C. Azevedo-Oliveira). Barra = 1 cm.

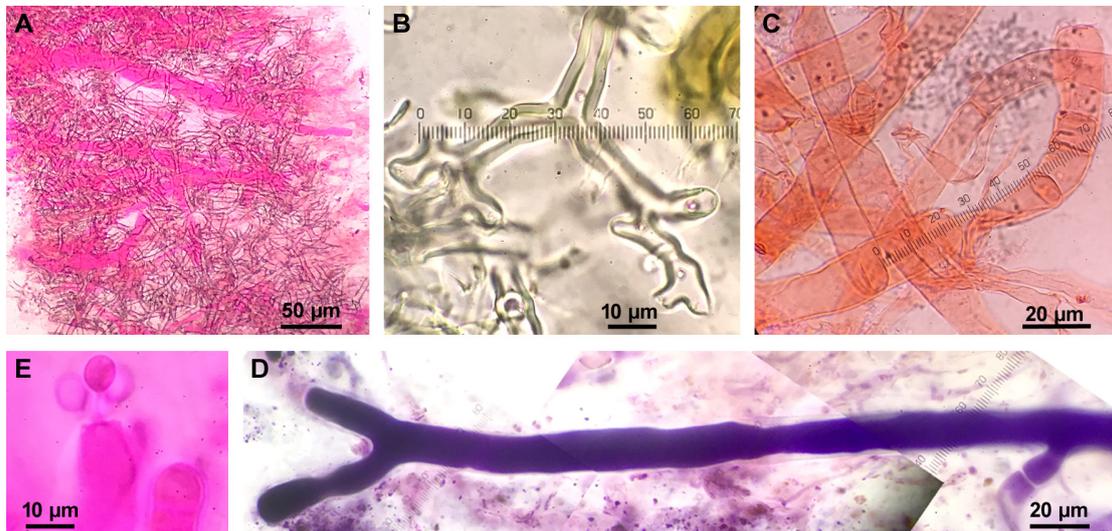


Fig. 4. Microscopic features of *Atlantiporus squalidus*. A) Context (holotype). B) Skeleton-binding hyphae from context (holotype). C) Gloeohyphae from context (holotype). D) Entire gloeohyphae from context in Cresyl Blue (FLOR67251, composed image). E) Basidium and basidiospores (FLOR67251).

Fig. 4. Características microscópicas de *Atlantiporus squalidus*. A) Contexto (holotipo). B) Hifas esqueleto-ligadoras del contexto (holotipo). C) Gloeohifas del contexto (holotipo). D) Gloeohifas del contexto en Azul de Cresilo (FLOR67251, imagen compuesta). E) Basidio y basidiosporas (FLOR67251).

Conservation status.— This species is listed in the IUCN Red List as Vulnerable, according to criterium C2a(ii) (Drechsler-Santos *et al.*, 2020, as *Laetiporus squalidus*).

Examined material.— BRAZIL. São Paulo State: São Luiz do Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, 23°26'23" S, 45°14'18" W, 11-II-2014, Col. Pires RP232, C.M. Ishida (SP466047); Santa Catarina State, Urubici, Parque Nacional de São Joaquim, Núcleo Santa Bárbara, 28°09'13,9" S, 49°38'24,5" W, 27-II-2019, Col. Oliveira, C.A.T.: CATO267, Funez, L.A., Costa-Rezende, D.H., Ribeiro-Nardes, W. (FLOR 67251). Growing on: *Schinus engleri* F.A. Barkley.

***Berkcurtia* Robledo & Campi gen. nov.**

Mycobank: MB 844423

Etymology: honoring the mycologists M. J. Berkeley and M.A. Curtis.

Type species: Berkcurtia persicina (Berk & M.A. Curtis) Robledo & Campi.

Basidiomata seasonal, central to eccentrically stipitate. Pileus single or several arising from a central stipe and then rosette-like, up to 50 cm diam; pilear surface light to dark brown, sometimes with a pink tint. Context homogeneous, azonate, pale tan to pinkish. Pore surface pinkish tan to creamy tan, staining blackish-brown when bruised, pores round, dissepiments entire, thin. Hyphal system trimitic; generative hyphae with simple septa, thick-walled; skeletal hyphae restricted to the trama of the tubes and dichotomously branched; binding hyphae restricted to the context, both vegetative hyphae dissolving nearly completely in 2–5% KOH, gloeopleurous hyphae present in the context. Cystidia lacking. Basidia clavate, 4-sterigmate. Basidiospores broadly ovoid, hyaline, thin-walled, smooth, IKI-.

Remarks.— *Berkcurtia* is recognized by the huge central to eccentrically stipitate brown to dark brown basidiomata arising from the ground with the pore surface staining blackish-brown when bruised. Microscopically it is characterized the trimitic hyphal system with skeletal hyphae restricted to the trama of the tubes and the binding hyphae restricted to the context. Macroscopically is very reminiscent of *Kusaghiporia*, however *Kusaghiporia* species have a whitish pore surface that turns reddish when bruised and have a dimitic hyphal system with skeletal hyphae mostly restricted to the context. Morphological differences with other poroid genera of *Laetiporaceae* are summarized in Table 2. The genus is so far known from one species, *B. persicina*, and the phylogenetic relationships within *Laetiporaceae* are not clear.

***Berkcurtia persicina* (Berk & M.A. Curtis) Robledo & Campi comb. nov.**

Mycobank: MB 844424

Basionym: *Polyporus persicinus* Berk. & M.A. Curtis, *Annals and Magazine of Natural History* 12: 430 (1853).

Remarks.— *Berkcurtia persicina* is so far the only species in the genus and the specimens included in the phylogenetic analysis suggest that the species is restricted to southern USA in North America. The species has been treated for a long time under *Laetiporus* in spite of the obvious morphological differences and the known phylogenetic relationships with other genera (Gilbertson & Ryvardeen, 1986; Burdsall & Banik, 2001; Lindner & Banik, 2008; Ortiz Santana *et al.*, 2013). Macroscopically *Berkcurtia persicina* differs from *Laetiporus* species by shape, size and coloration of basidiomata, and microscopically the binding hyphae are different from *Laetiporus* (Table 2).

Table 2. Synoptic comparison among poroid genera of Laetiporaceae. GH= generative hyphae, BH= biding hyphae, SH= skeletal hyphae, SB= sekeleto-binding hyphae).

Tabla 2. Comparación sinoptica entre géneros poroides de Laetiporaceae. GH= hifas generativas, BH= hifas ligadoras, SH= hifas esqueléticas, SB= hifas esquelétoligadoras).

	Hyphal system	Basidiospores	Basidiomata	Ecology & Distribution
	All taxa with simple septa.	All taxa with smooth, thin walled, hyaline, IKI-	Annual in all species	
Laetiporus	Trimitic GH hyaline, thin to distinct walled BH thick-walled, profusely branched, only in the context. Dissolving in KOH SH thick walled, straight restricted to the tubes. Gloepleurous hyphae -, Cystida -	Ovoid to broadly ellipsoid	Sessile to stipitate; upper surface orange at first, becoming brown, strigose to fibrillose; pore surface orange to greenish brown, pores daedaleoid to circular, up to 2 mm in diam; context orange to brown	Worldwide <i>Laetiporus sulphureus</i> occurs as a brown heart-rot of hardwood species (especially <i>Quercus</i> spp.) throughout the eastern USA and Mexico
Atlantiporus	Dimitic GH hyaline, thin to thick-walled, frequently branched. BH richly branched, hyaline, thick-walled, restricted to context, not dissolving in KOH SH straight absent Gloepleurous hyphae +(context), Skeletocystida present SB present in the trama of the tubes.	Ellipsoid to broadly ellipsoid	Resupinate, upper surface glabrous, azonate, slightly rugose, cream to pale brown. Pore surface cream when fresh to brown when dried, pores 3–5 /mm. Context concolorous with the pileus.	South America Atlantic Forest, Brazil.
Kusaghiporia	Dimitic GH hyaline, thin to distinct walled SH thick walled, straight hyaline, thick-walled, often branching dichotomously, mostly restricted to the context Gloepleurous hyphae + (context), Cystida -	Globose to subglobose	Centrally to eccentrically stipitate, several pileus arising from a central stipe, upper surface grayish to chestnut color, with dark pillars zoned from the center towards the margin, velvety. Pore surface whitish in fresh, turning brown, pores up to 3/mm. Context whitish or grayish, rusts when cutting, with dark pink tones that then darken to graphite color.	Found growing at the base of the trees <i>Maesopsis eminii</i> and <i>Ficus natalensis</i> . Tanzania, Central Africa. Colonizing roots of native species of <i>Handrohantus</i> , <i>Inga marginata</i> and exotic species of <i>Delonix regia</i> , <i>Tipuana tipu</i> , <i>Bauhinia</i> sp. Paraguay, South America
Phaeolus	Monomitic GH, thin walled, brown, sparsely to freely branched Gloepleurous hyphae -, Cystida + frequent, yellowish, cylindrical	Broadly ellipsoid to ovoid	Sessile or stipitate, spatulate to orbicular, single or imbricate, upper surface strigose, tomentose to velutinate, zonate, deep reddish brown to ochre. Pore surface yellow to olive when young, bruising dark brown, 1–3/mm. Context yellowish brown, oxidizing dark brown	Circumglobal species in boreal and north temperate regions, coniferous forests in Europe.
Berkcurtia	Trimitic GH hyaline, thin-walled BH dendritically branched, hyaline, occasionally septate, thick-walled Dissolving in KOH , restricted to the context. SH sinuous and undulating, occasionally septate, thick-walled Gloepleurous hyphae + (context), Cystida absent	Broadly ovoid	Centrally or eccentrically stipitate with a single pileus or several arising from a central stipe, upper surface of pileus light to dark, finely tomentose to hispid. Pore surface pinkish tan to creamy tan, 3–4/mm. Context pale tan to pinkish tan.	Roots of hard hardwoods especially <i>Quercus</i> spp. and <i>Pinus</i> spp. Southeast of the United States and Puerto Rico
Pycnoporellus	Monomitic GH, thin-walled to thick-walled, mostly encrusted Gloepleurous hyphae -, Cystida + not encrusted, mostly thin-walled, tubular and projecting	cylindric to oblong- ellipsoid	Pileate or resupinate, when pileate, broadly attached and semicircular or somewhat elongated; pileus tomentose and zonate, bright orange to rust coloured; pore surface orange, pores medium to large, angular; tubes concolorous with pore surface; context orange to orange-buff, soft and fibrous; all tissues deep red in KOH;	Small boreal genus with two species, both occurring in Europe on dead conifers, but also on hardwoods in North America.

Kusaghiporia talpae (Cooke) Campi, Drechsler-Santos

& Robledo **comb. nov.** Figs. 5-6

Mycobank: MB 844420

Basionym: *Polyporus talpae* Cooke, Grevillea 16 (77): 15, 1887.

Basidiomata annual, centrally to eccentrically stipitate and forming a huge rosette, solitary or often 2-3 basidiomata confluent. Pileus up to 80cm diam, margin entire, wavy, 10–15 mm thick, fleshy when fresh, hard and light when dry. Pilear surface irregular, velvety when developing becoming glabrous with time, opaque, color variable, during young stages of development greyish to chestnut, whitish to creamy towards the margins where the growth is active, darkening with age forming a thin crust, with some dark and hard zones. Context fibrous, creamy, turning to grayish or blackish when cut, showing black lines result of the growing pulse of the pileus (Fig. 5 A-G). Margin sterile, blunt thick, lobulated, undulated and whitish in active growing. Pore surface whitish turning dark pinkish when bruised (Fig. 5 K) and light brown when dry. Tube layer very thin, up to 5 mm; pores 5–10/mm, circular, dissepiments sterile, entire, thin to thick.

Hyphal system dimitic. Tube layer monomitic with simple-septate generative hyphae, 4–5 μm diam., thin-walled, and with lateral branches. Context dimitic with scarce thick-walled, straight, skeletal hyphae, hyaline, often branching dichotomously. Basidiospores subglobose, 6–7 \times 4–5 μm , thin-walled, smooth, hyaline, with cytoplasmic refracting droplets, IKI-. Basidia clavate, 18–24 \times 7–9 μm , with 4 sterigmata, simple septate at the base and abundant cytoplasm content.

Culture characteristics.— Macroscopic characteristics: growth moderate in Potato Dextrose Agar (PDA), covering the dish in 20 days. Mats felty, covering the dish homogeneously, surface mycelium not abundant, adhered to the surface of the agar, later cottony towards the margins, whitish cream. After 25 days the mycelium started to increase in density, turning cottony, color remained whitish cream. Microscopic characteristics: submerged mycelium composed of generative hyphae with simple septa, thin- to irregularly thick-walled, 17–29 μm in diam., occasionally branched, clamp connections absent. Aerial mycelium 3.6–5.6 μm in diam., thin-walled, simple septa regular, hyaline, occasionally branched, with terminal and intercalary chlamydospores. Chlamydospores globose, 12.5–26.5 μm in diam., thick-walled with walls up to 3 μm , hyaline, with greenish droplets, abundant throughout the mycelium.

Remarks.— The species is characterized by its particular development and the large pilei merging into a huge basidiome above 50 cm in diameter. Microscopically, it presents a dimitic hyphal system with skeletal hyphae restricted to the context. *Kusaghiporia usambarensis* J. Hussein, S. Tibell & Tibuhwa morphologically resembles *K. talpae*, the difference between both species relies mainly in the phylogenetic evidence and distribution. *Kusaghiporia usambarensis* is so far known from Usambara Mountains, Tanzania, Africa (Hussein et al., 2018), whereas *K. talpae* is known from the Neotropical region. Differences with other poroid Laetiporaceae genera are summarized in the Table 2.

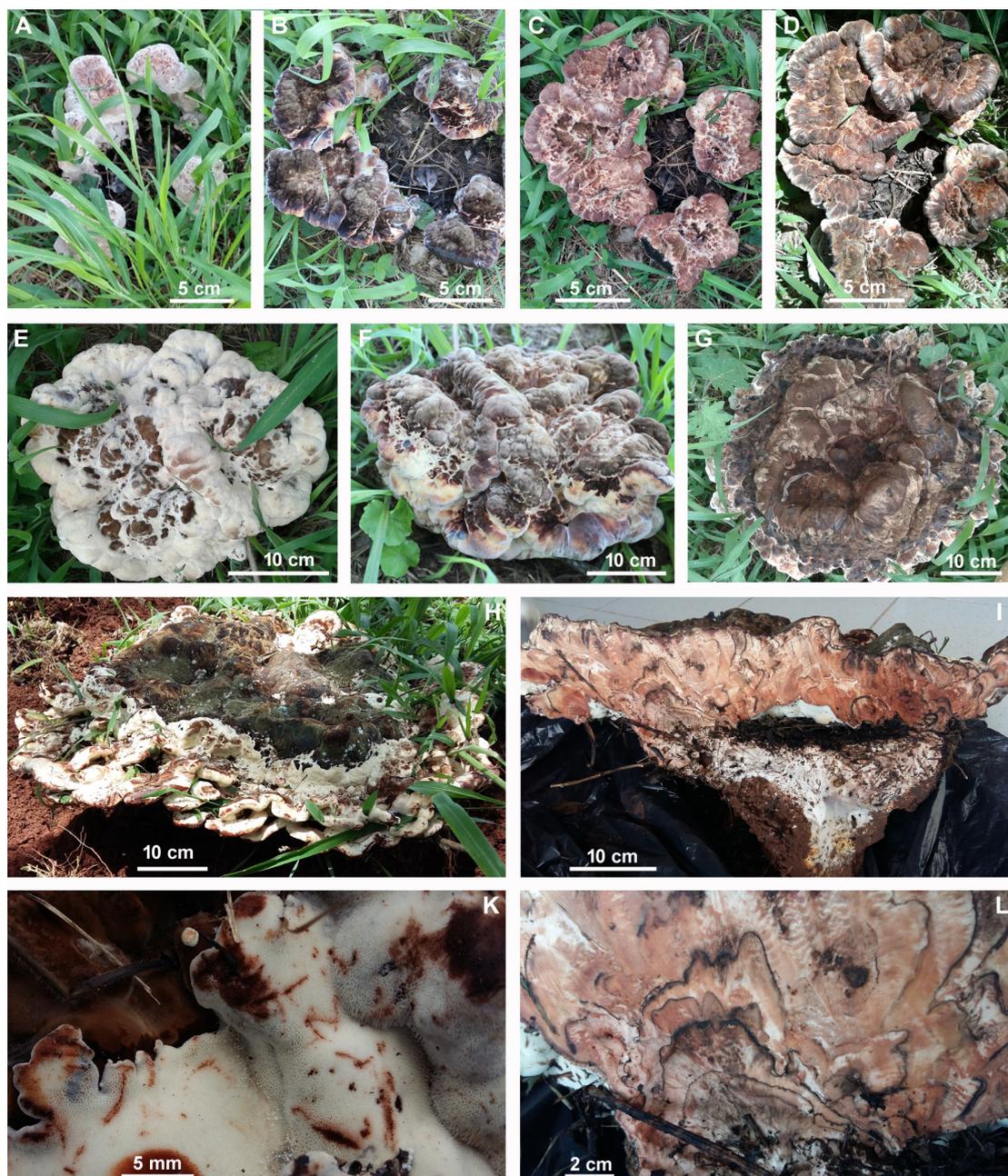


Fig. 5. Macroscopic features of *Kusaghiporia talpae* (CM002, FACEN 4973). A-H) General view during a time lapse of 22 days. I, L) Longitudinal section of basidiome showing context and the whitish core of the stipe. K) Close up of the pore surface showing reddish spots where touched (photos by M. Campi).

Fig. 5. Características macroscópicas de *Kusaghiporia talpae* (CM002, FACEN 4973). A-H) Vista general del basidioma durante un lapso de 22 días. I, L) Corte longitudinal mostrando contexto y el centro blanquecino del estípite. K) Detalle de los poros mostrando coloración rosácea al tacto (fotografía de M. Campi).

Due to the huge basidiomata, *K. talpae* has not been ignored by mycologist, but the taxonomic position of the species was never tested by phylogenetic analysis. Fidalgo & Fidalgo (1967) described a similar morphology and peculiar development for samples of Trinidad, Brazil and Puerto Rico under the name *Meripilus talpae*



Fig. 6. Microscopic features of *Kusaghiporia talpae* (CM002, FACEN 4973). A-B) Skeletal hyphae from context. C-D) Gloeohyphae from context. E) Generative hyphae from tube trama. F) Basidium and basidioles, G) Basidiospores. H) Culture general view. I-J) Chlamydispores and generative hyphae from culture (photos by M. Campi).

Fig. 6. Características microscópicas de *Kusaghiporia talpae* (CM002, FACEN 4973). A-B) Hifas esqueléticas del contexto. C-D) Gloeohifas del contexto. E) Hifas generativas de la trama de los tubos. F) Basidios y basidiolas. G) Basidiosporas. H) Vista general del cultivo. I-J) Clamidosporas e hifas generativas del cultivo (fotografía de M. Campi).

(Cooke) D.A. Reid, albeit with a monomitic hyphal system. The presence of skeletal hyphae may have gone unnoticed due to their scarcity in the context. Lindner & Banik (2008) analyzed two specimens from Puerto Rico (PR-2 and PR6326) under the name *Laetiporus persicinus* and concluded that it was likely to be *Polyporus talpae* Cooke, described from Brazil, however suggested further studies to determine the correct taxonomic position. In our phylogenetic analyses Puerto Rico's specimen PR-2 grouped with *Kusaghiporia talpae* from South America. The placement of this species in *Meripilus* P. Karst is not correct since the type species of *Meripilus*, *Meripilus gigentus* (Pers.) P. Karst., is located in a phylogenetically distant family Meripilaceae, in the residual clade of Polyporales (Justo et al., 2017). *Meripilus tropicalis* Guzmán & Pérez-Silva present a similar macro-and micromorphology than *K. talpae*, however differs by its larger pores, (1-3/mm) and basidiospores ($6-8.5 \times 5.2-6 \mu\text{m}$) (Guzmán

& Perez Silva, 1975). Whether or not *M. tropicalis* is another *Kusaghiporia* species would be resolved by including the species in molecular phylogenetic analyses.

Material examined.— PARAGUAY. Central Department., San Lorenzo City, Universidad Nacional de Asunción, 25°23'21.55" S 57°10'56.1" W, 20-XI-2015, C. Mancuello 002 (FACEN 4973); Central Department, San Lorenzo City, Universidad Nacional de Asunción, 25°23'21.55" S 57°10'56.1" W, 04-IV-2016, M. Campi 080 (FACEN 4974); Central Department, Aregua City, Kokue Guasu, S 25°20'50.7" W, 57°22'16.59", 14-III-2022, M. Campi 850 (FACEN 4975).

Laetiporus dilatohyphus (Ryvarden & Gilb.) Robledo & Campi **comb. nov.**

Basionym: *Wolfiporia dilatohypha* Ryvarden & Gilb., Mycotaxon 19: 141 (1984)

Mycobank: MB 844425

Remarks.— Our results show *Wolfiporia dilatohypha* Ryvarden & Gilb. groups inside *Laetiporus s.s.* (Ortiz Santana *et al.*, 2013) related to the east Asian taxon *Laetiporus cremeiporus* Y. Ota & T. Hatt. (63/1.0). The species is characterized by the resupinate basidiomata with a monomitic hyphal system.

Laetiporus gilbertsonii Burds. Figs 7-8

Specimens from South America integrating the 'South American group' (Fig. 2) are characterized as follow:

Basidiomata annual, sessile, pileus semicircular, broadly attached to the substrate, imbricated, up to 300 mm wide × 90–160 mm long and 15 to 30 mm thick, fleshy and soft when fresh, light and brittle with chalk consistency when dry. Pilear surface velutinose when young, glabrous when mature, creamy with yellowish shades when fresh that lightens and turn whitish when mature and/or dry, usually with stretch marks and radial undulations when it is developing, concentrically zonate with grayish wrinkles when fresh. Margin rounded, entire, sterile, wavy, salmon in fresh samples, turning ferruginous where it has been touched when it dries. Context white, 150–200 mm thick at the base. Tube layer of 1.5 mm thick, whitish to cream, darker than the context, darkening light brown when dry, pores circular, 3–4 / per mm, dissepiments entire to occasionally lacerated. Context dimitic, composed of generative and binding hyphae; generative hyphae simple septate, 9–11 μm diam., 1 μm thick wall, hyaline. Binding hyphae 5–12 μm , highly branched and intertwined, hyaline, which dissolve completely in 5% KOH. Tube layer dimitic, composed of generative and skeletal hyphae; generative hyphae simple septate 4–6 μm , thin-walled; skeletal hyphae 5–7 μm diam, straight to somewhat wavy, with a wall of 1 μm thickness that dissolve completely in 5% KOH. Subhymenium formed by a compact tissue of 4–5 μm diam., generative hyphae interwoven which give rise to hymenium elements (basidioles). Basidia clavate, 20 × 5–6 μm , with 4 sterigmata. Basidiospores ellipsoidal, 5–6.6 × 3.6–5.1 μm , thin-walled, smooth, IKI-

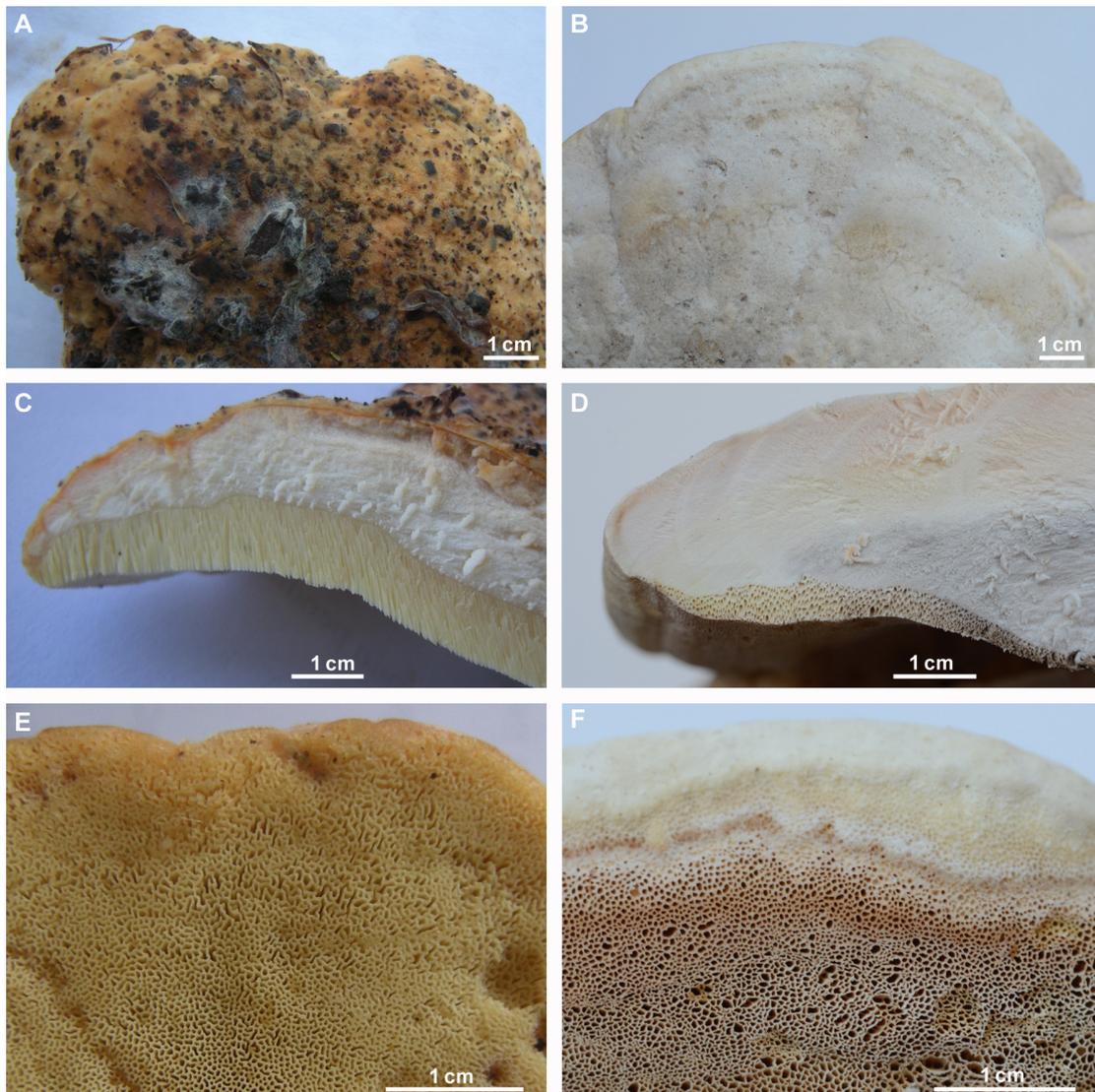


Fig. 7 Morphological features of *Laetiporus gilbertsonii*, 'South American group'. A-C) Robledo2552 on *Schinus fasciculatus* and D-F) Robledo 3295 on *Eucalyptus sp.*: A-B) Detail of the pilear surface. C-D) Longitudinal section showing context and tube layer. E-F) Detail of the pore surface.

Fig. 7. Características macroscópicas de *Laetiporus gilbertsonii*, 'grupo Sudamericano'. A-C) Robledo2552 on *Schinus fasciculatus* and D-F) Robledo 3295 en *Eucalyptus sp.* A) Detalle de la superficie del pileo. C) Corte longitudinal mostrando el contexto y la capa de tubos. E-F) Detalle de la superficie de los poros.

Culture characteristics.— Cultures growing rather fast, covering the dish in 7 days (Fig. 8 A-C). Mats whitish-cream, at first lax, covering homogeneously the surface of the agar, later increasing the density and cottony towards the margins. After 14 days, the mycelium started to reach the dish walls and lid (Fig. 8 A-C). Submerged mycelium composed of generative hyphae with simple septa, with thin- to slightly thickened walls, 7–9.2 μm in diam. Aerial mycelium thin-walled, simple septa regular, hyaline, branched, 4–6.6 μm in diam., with terminal tree like branching (Fig. 8 F), where terminal chlamydospores are produced. Chlamydospores abundant, globose to pyriform, 6–9 \times 5–8 μm , hyaline, with greenish guttules, thin to slightly thick-walled, smooth, IKI- (Fig. 8 D-F).

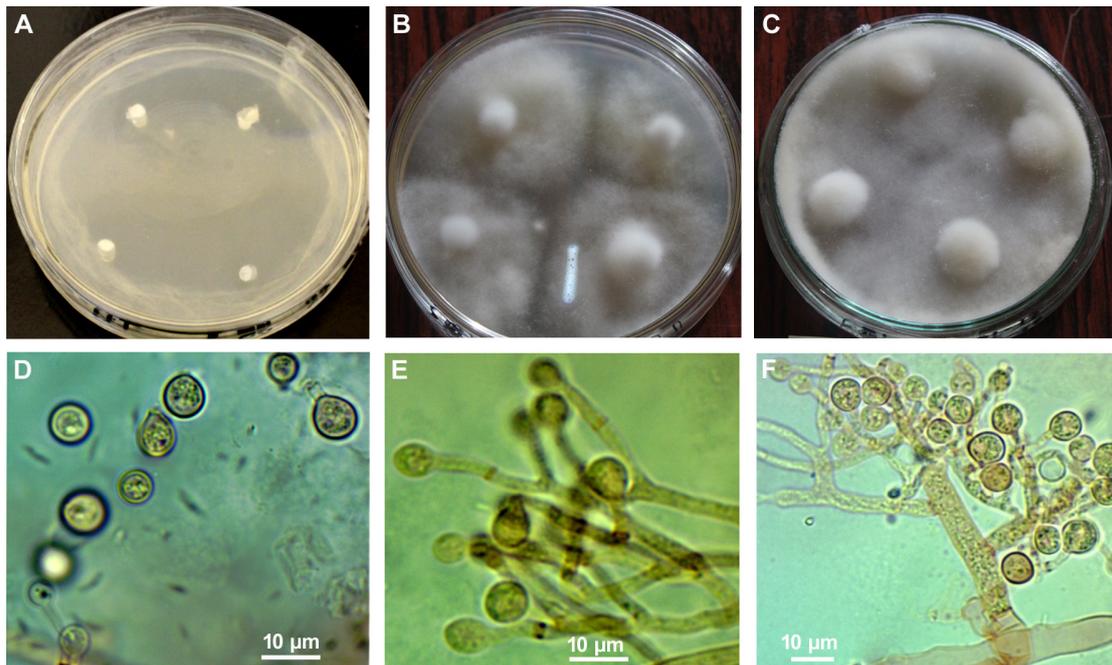


Fig. 8. *Laetiporus gilbertsonii*, 'South American group', cultural features. A-C) 14 days sequence general view. D-F) Chlamydospores and generative hyphae (photos by M. Campi). Aerial mycelium with terminal tree like branching and chlamydospores.

Fig. 8. Características de cultivo de *Laetiporus gilbertsonii*, 'grupo Sudamericano'. A-C) vista general de una secuencia de 14 días. D-F) Chlamidosporas e hifas generativas (photos by M. Campi).

Remarks.— Phylogenetic analysis of the 'gilbertsonii' complex based on the ITS showed that the samples from South America, here recognized as the 'South American group', grouped together, however without support to recognize them as a different species (Fig. 2). Specimens of the 'South American group' fit the general morphological circumscription of *L. gilbertsonii*, differing only in that they have a darker or more intense cream color of the pileus and pore surface than *L. gilbertsonii* specimens from North America. Regarding the ecology, *L. gilbertsonii* from North America has been collected in *Quercus* and *Eucalyptus* (Burdson & Banik, 2001) whilst the 'South American group' occurs on native host species of *Gleditsia* and *Schinus*, although is recurrently observed jump on *Eucalyptus* spp in plantations and urban areas (Table 1).

The taxonomical status of the 'South American group' in relation to *L. gilbertsonii* complex needs to be examined further. Previous evidence suggest that ITS-based data are useful to establish species groups within *Laetiporus* (Banik *et al.*, 2012). This seems not applicable to the *L. gilbertsonii* complex. Interestingly, the ITS alignment showed a 9 bases indel shared by all specimens of the 'South American group' (Fig. 9). An additional marker should help to resolve the phylogenetical relationships within the *L. gilbertsonii* complex, unfortunately we were unsuccessful in obtaining *tef-1 α* sequences from the specimens studied.

Material examined.— PARAGUAY. Cordillera Department, Piribebuy City, 25°30'47,08"S, 57°04'17,5"W, 08-VII-2015, M. Campi 074 (FACEN 4978); Cordillera

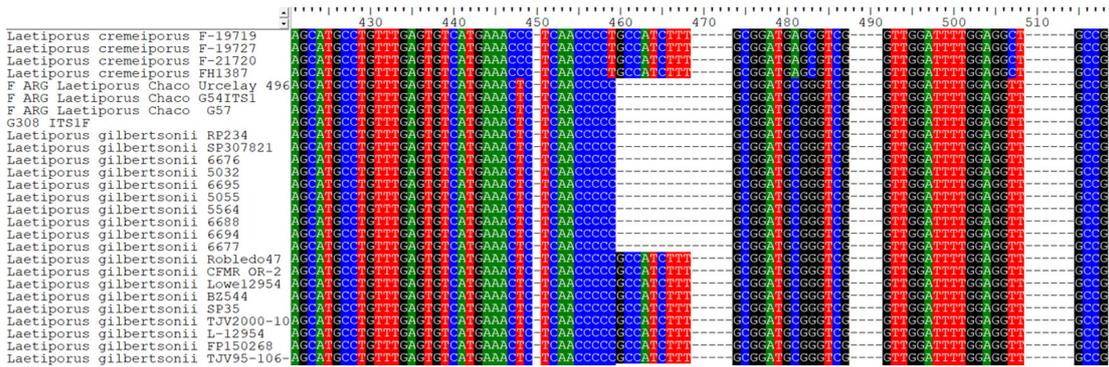


Fig. 9 ITS alignment showing a 9 bases indel shared by all specimens of *Laetiporus gilbertsonii* 'South American group'.

Fig. 9 Alineamiento ITS mostrando un indel de 9 bases compartido por los especímenes *Laetiporus gilbertsonii* 'grupo Sudamericano'.

Department, Caacupé City, 25°22'53.2"S, 57°12'21.9"W, 03-IV-2016, M. Campi 030 (FACEN 4976); Cordillera Department, Caacupé City, 25°22'53.2"S, 57°12'21.9"W, 03-IV-2016, M. Campi 032 (FACEN 4977).

Key to the poroid genera of *Laetiporaceae*

- 1 Basidiomata whitish, cream to orange, typically pileate and spatulate, to occasionally effused reflexed or resupinate, arising from wood 2
- 1' Basidiomata brownish, stipitate, arising from the ground 4
- 2 Basidiomata resupinate, hyphal system monomitic *Laetiporus dilatohyphus*
- 2' Basidiomata resupinate to pileate, hyphal system di to trimitic 3
- 3 Basidiomata pileate; hyphal system trimitic; binding hyphae thick-walled, much branched and interlocked restricted to the context dissolving in KOH, gloeohyphae absent in the context, skeletal hyphae thick-walled, straight restricted to the tubes; skeletal cystidia absent *Laetiporus*
- 3' Basidiomata resupinate with small imbricate pileus; hyphal system dimitic; binding hyphae thick-walled, much branched not restrict to the context and not dissolving in KOH, gloeohyphae present and restrict to the context; skeletal hyphae straight absent in the trama of tubes, skeleton-binding hyphae present in the trama of the tubes not dissolving in KOH; skeletal cystidia present *Atlantiporus*
- 4 Hyphal system monomitic 5
- 4' Hyphal system dimitic 6
- 5 Basidiomata stipitate on the ground from roots or occasionally sessile on the base of living trees, upper surface orange at first darkening to yellowish brown to dark reddish brown at maturity; gloeocystidia present *Phaeolus*

- 5' Basidiomata resupinate to effused reflexed on dead wood, bright orange turning to rust colored fulvous when dry, all tissues deep red in KOH, gloeocystidia absent *Pycnoporellus*
- 6 Basidiomata with a whitish context changing to dark greyish, pore surface whitish turning dark reddish when bruised *Kusaghiporia*
- 6' Basidiomata brownish; pores surface pinkish tan to creamy tan, turning blackish-brown when bruised *Berkcurtia*

DISCUSSION

From the cosmopolitan *Laetiporus sulphureus* to tens of species of restricted distribution

In the last 20 years several species of *Laetiporus* have been described based on phylogenetic evidence. The wide and cosmopolitan concept of *Laetiporus sulphureus* shifted to a *sensu stricto* concept referred to a phylogenetic clade that includes specimens from areas near the type locality. There are still records of *Laetiporus sulphureus* from different areas of the world that need to be revised under the light of phylogenetic data. So far, based on phylogenetic data, *Laetiporus* s.s. species are native species that seem to jump on *Eucalyptus* spp in different parts of the world (Table 1, cf. substrata and origins), such as Africa, South America, North America (Van Der Westhuizen, 1959; Burdsall & Banik, 2001; Dai *et al.*, 2007, Silveira *et al.*, 2008). Strikingly, to the best of our knowledge, there are no published reports of *Laetiporus* species on *Eucalyptus* in the natural distribution of *Eucalyptus*. Traditionally, the presence of *Laetiporus* in southern South America was recorded mostly exclusively on urban and non-urban *Eucalyptus* spp plantations even when other exotic plant species were available. These records were attributed to *Laetiporus sulphureus* (e.g.; Wright & Deschamps, 1975; Vizcarra Sanchez & Deschamps, 1982; Meijer, 2008; Holmquist *et al.*, 2009; Radic & Injac, 2009; Rajchenberg & Robledo, 2013). Currently, based on phylogenetic analyses we know that *Laetiporus gilbertsonii* is the correct name for the species growing in native substrates in Southern South America and most of those growing on *Eucalyptus* spp. The presence of specimens phylogenetically related to *Laetiporus sulphureus* from Europe has been reported in Uruguay growing on *Eucalyptus* spp (Vasaitis *et al.*, 2009), however they have not been found in our sampling.

Berkcurtia and *Kusaghiporia*

In South America big brownish polypores arising from soil have been attributed to *Laetiporus persicinus*, as it could be interpreted from the proposed synonymies, *Polyporus talpae* Cooke and *Polyporus glaziovii* Henn. from Brazil. Under the light of our results the facultative heterotypic synonyms of *L. persicinus* should be investigated in order to clarify their taxonomic status and to define natural distributions of this species. So far, the two known *Kusaghiporia* species are present at tropical and subtropical regions in South America and Africa. *Polyporus subcolossus* Berk,

described from Congo could represent a *Kusaghiporia* species or *K. usambarensis* in which case *Polyporus subcolossus* has priority. Another polypore species that share a similar distribution is *Phaeotrametes decipiens* (Berk.) J.E. Wright. The species is present in central Argentina, South Africa, but also Australia and is considered a gondwanic taxon (Ryvarden, 1991). *Dendrochaete vallata* G. Cunn. is also considered heterotypic synonym of *Laetiporus persicinus*. Whether or not *Kusaghiporia* is another example of a gondwanic taxon could be unveiled through morphological analyses of specimens of Oceania and their inclusion in phylogenetic analyses.

The taxonomic position of *Berkcurtia persicina* has been widely discussed being placed in several genera throughout the years since its original description (Berkeley, 1872), *i.e.* *Scutigera* Paulet (Murril, 1903), *Meripilus* P. Karst. (Ryvarden, 1972), *Buglossoporus* Kotl. & Pouzar (Corner, 1984) and *Cladoporus* Pers. (Teixeria, 1992). Its position in *Laetiporus* (Gilbertson, 1981) was questioned and its placement in other genera was suggested (Burdall & Banik, 2001). This was later confirmed by Lindner & Banik (2008) who sought for similar sequences in the GenBank (NCBI) databases using ITS, LSU and mtSSU regions with no significant similarity to any known genus, suggesting that its placement in a new genus was warranted. *Berkcurtia persicina* was described from South Carolina (USA) as *Laetiporus persicinus* and it is well represented in the phylogenetic analysis. Tropical, in particular Caribbean records of facultative heterotypic synonyms of *Berkcurtia persicina*, *v.g.* *Amauroderma brittonii* Murrill from Jamaica, should be revised since the specimen from Puerto Rico represent a *Kusaghiporia* species (Fig. 1). The same is suggested for the European records of *Laetiporus persicinus* (Ryvarden & de Melo, 2014).

Similar to what was observed for *L. sulphureus* at species level, the generic diversity within this remarkable group of polypores is greater than previous expected. According to our results, characteristics of the hyphal system, *i.e.* structure and chemical reactions, and finally the phylogenetic evidence are crucial for delimiting genera in the group. Further phylogenetic studies including additional coding markers are needed to resolve the phylogenetic relationships between the genera.

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