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# Phlebiodontia rajchenbergii gen. et sp. nov. (Polyporales, Meruliaceae) from the Brazilian Atlantic Forest based on morphological and molecular evidence

*Phlebiodontia rajchenbergii gen. et sp. nov.* (Polyporales, Meruliaceae) del Bosque Atlántico Brasileño con base en evidencia morfológica y molecular

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## ABSTRACT

*Phlebiodontia* is proposed as a new genus in the Meruliaceae based on morphological and molecular data. The genus is typified by *Phlebiodontia rajchenbergii*, a new species proposed for Brazil, and also includes *P. acanthocystis* (Hawaii) and *P. subochracea* (Germany), which are new combinations proposed in this study. The species of *Phlebiodontia* are morphologically characterized by yellowish ceraceous basidiomes, with slightly warted to hydnoid hymenophore, monomitic hyphal system, clamped generative hyphae, presence of smooth thin-walled cystidia and broadly ellipsoid to allantoid basidiospores. The phylogenetic relationships of *Phlebiodontia* and the related taxa in Meruliaceae were inferred from a 4-locus dataset including nuc rDNA ITS1-5.8S-ITS2 (ITS), the D1-D2 domains of 28S rDNA (28S), RNA polymerase II

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largest subunit (*rpb1*) and translation elongation factor 1- (*tef1*). This work presents complete descriptions, comments and discussion about morphology and distribution of *Phlebiodontia* species.

Keywords — Corticioid fungi; neotropical forest; phlebioid clade; phylogeny; taxonomy.

#### RESUMEN

*Phlebiodontia* es propuesto como un género nuevo en la familia Meruliaceae con base en datos morfológicos y moleculares. El género es tipificado por *Phlebiodontia rajchenbergii*, una especie nueva propuesta de Brasil, y también incluye *P. acanthocystis* (Hawaii) y *P. subochracea* (Alemania), las cuales son nuevas combinaciones propuestas en este estudio. Las especies en *Phlebiodontia* se caracterizan morfológicamente por los basidiomas amarillos, ceráceos, con himenóforo levemente verrugoso a hidnoide, estructura hifal monomítica, hifas generativas con fíbula, presencia de cistidios de pared fina y lisa y basidiosporas ampliamente elipsoides a alantoides. Las relaciones filogenéticas de *Phlebiodontia* y taxones relacionados en Meruliaceae fueron inferidos a partir de un conjunto de datos con 4 locus incluyendo nuc rDNA ITS1-5.8S-ITS2 (ITS), los dominios D1-D2 del 28S rADN (28S), la subunidad mayor de la ARN polimerasa II (*rpb1*) y el factor de elongación de translación 1- (*tef1*). Se presentan descripciones completas, comentarios y discusión acerca de la morfología y la distribución geográfica de las especies de *Phlebiodontia*.

Palabras clave — Bosques neotropicales; clado phlebioide; filogenia; hongos corticioides; taxonomía.

#### INTRODUCTION

The phlebioid clade within Polyporales includes three lineages at family level, Irpicaceae, Meruliaceae and Phanerochaetaceae (Binder *et al.*, 2005; Justo *et al.*, 2017). The taxonomy of many genera belonging to these families is not currently settled, and a good example is the genus *Phlebia*, belonging to the family Meruliaceae (Justo *et al.*, 2017), described by Fries (1821) and typified by *P. radiata* Fr.

Originally, *Phlebia* included species with resupinate basidiomes, hymenophore with veins (merulioid), monomitic hyphal system, clamped generative hyphae and thin-walled cystidia (Donk, 1957). However, several species with hydnoid to odontioid hymenophore have also been included in the genus throughout the years, as well as a few dimitic species and others with simple septa, largely expanding its circumscription (Nakasone 1991, 1996, 1997, 2002; Nakasone & Burdsall, 1984). Generally, all species included in *Phlebia* are characterized by the gelatinized and agglutinated nature of the hyphae, often becoming hard to observe and discern in dried specimens. Cystidia can be present or absent in the genus and the basidiospores are allantoid to ellipsoid, smooth, thin-walled, IKI- and CB- (Eriksson *et al.*, 1981; Bernicchia & Gorjón, 2010; Gorjón, 2020). This wider morphological concept

for *Phlebia* has repeatedly been shown to be polyphyletic (Larsson *et al.*, 2004; Binder *et al.*, 2013; Floudas & Hibbett, 2015; Justo *et al.*, 2017).

With the addition of molecular data to taxonomic and systematic studies, many new genera have been introduced or resurrected to accommodate some species from *Phlebia s.l.* (i.e., *Allophlebia, Cabalodontia, Crustodontia, Geesterania, Hermanssonia, Lilaceophlebia, Mycoacia, Mycoaciella, Phlebiopsis, Scopuloides* and *Resinicium*) (Floudas & Hibbett, 2015; Papp & Dima, 2017; Westphalen *et al.*, 2018, 2021; Huang & Zhao, 2020; Huang *et al.* 2020; Lira *et al.*, 2022; Liu *et al.*, 2022; among others). Recently, Chen *et al.* (2021) provided a wide overview of the Phlebioid clade and the Meruliaceae, and showed that *Phlebia s.l.* is still polyphyletic, with members addressed in all families of the phlebioid clade. The authors (op. cit.) suggested that description of other new genera may be necessary to provide a natural classification with monophyletic groups.

During our investigations of corticioid fungi from Southeastern Brazilian Atlantic Forest, specimens of *Phlebia s.l.* were collected. Morphological and phylogenetic studies showed that these represent a new species, which forms a monophyletic clade with *P. acanthocystis* Gilb. & Nakasone and *P. subochracea* (Bres.) J. Erikss. & Ryvarden. This new lineage is genetically distant from *Phlebia s.s.* Therefore, in this study we aim to describe a new genus for this clade. Additionally, we provide full descriptions, and illustrations of the new species and comments on the new combinations proposed.

### MATERIAL AND METHODS

#### Morphological analysis

Specimens were collected during field trips in the Southeastern Brazilian Atlantic Forest in São Paulo State. All descriptions are based on well-developed (mature) specimens. Macromorphological characteristics (texture, consistency, shape and color) are based on fresh and dried specimens and measurements were made under a stereo microscope. For micromorphological analysis, free-hand sections of the basidiomes were prepared on microscope slides with cotton blue (Merck 1275) in lactic acid solution prepared following Miettinen et al. (2006), indicator of cyanophilic (CB+) or acyanophilic (CB") reactions. Melzer's reagent (IKI) was used to determine the presence or absence of amyloid and dextrinoid reactions. Abbreviations IKI- means neither amyloid nor dextrinoid reactions are present. All microscopical structures were measured with the aid of an eyepiece micrometer with a subjective accuracy of 0.1  $\mu$ m, using x1000 magnification. At least 20 hyphae from the subiculum and hymenophoral trama, 10 basidia and 30 basidiospores were measured per each specimen. When presenting variation of hyphal width and basidiospore size, the 20% and 5% extreme tails are given in parentheses, respectively (hyphal width variation is larger than spore size variation, Miettinen et al., 2018). In microscopic descriptions, the following abbreviations are used: L – average of basidiospore length; W – average of basidiospore width; Q' - Length/Width ratio of individual spores; Q - L/W, i.e. average length divided by average width; n - number of basidiospores measured /

number of specimens examined. Statistical measures were calculated with R version 3.2.2 (R Core Team, 2013). Illustrations were made using a drawing tube and then imported and redrawn to vector graphics on Inkscape (v. 0.91).

Fresh spore prints were obtained and used for preparation of polysporic cultures. Cultures were grown in malt extract agar (MEA) or potato dextrose agar at 25 °C. The species codes describing the cultures follow the Species Code of Nobles (1965) with the modifications summarized by Nakasone (1965). The isolates were preserved in sterile distilled water (Castellani, 1967; Burdsall & Dorworth, 1994) and deposited in the Coleção de Culturas de Algas, Cianobactérias e Fungos (CCIBt) of the Instituto de Pesquisas Ambientais, São Paulo, Brazil.

## DNA extraction, PCR amplification and sequencing

Mycelial cultures were grown for seven days on potato dextrose agar (PDA) at 25°C and used for DNA extraction. The samples were transferred to centrifuge microtubes and then homogenized with glass beads (Sigma Aldrich) and pestle in a 1.5 ml centrifuge tube. Further steps were performed according to the kit manufacturer's protocol of the E.Z.N.A. Forensic DNA kit (Omega Bio-tek).

The following primers were used for both PCR amplification and sequencing: ITS1/ITS5 (including ITS1, 5.8S, and ITS2) for the ITS region (White et al., 1990), CTB6/LR7 for the 28S region (Vilgalys & Hester, 1990; Haynes et al., 1995), 983F/1567R for tef1-á (Matheny et al., 2007). Attempts at sequencing the rpb1 region were made, but unsuccessful. Polymerase chain reactions (PCR) were carried out using the BlastTaq<sup>TM</sup> 2X Master Mix (abm) in a 25  $\mu$ L volume reaction and conducted on a thermal cycler (C1000 Touch<sup>™</sup> Thermal Cycler Bio-Rad). For ITS and 28S regions the cycling parameters described by Oghenekaro et al. (2014) were followed, while for tef1, the Miettinen et al. (2018) protocol was followed. PCR products were visualized in 1.5% agarose gel by electrophoresis. Amplified products were purified and sequenced in both directions with the same primers at Macrogen Ltd. (South Korea). The electropherograms of forward and reverse sequences were assembled and visualized using the Consed/PhredPhrap package (Ewing & Green, 1998; Ewing et al., 1998; Gordon et al., 1998; Gordon & Green, 2013). The electropherograms were visually inspected to ensure good sequence quality and ambiguous sequence reads were discarded. Double peaks were interpreted as true base ambiguities when they were detected in both forward and reverse sequencing electropherograms. Once assembled, consensus sequences were queried against the entire GenBank database using BLAST (http://blast.ncbi.nlm.nih.gov/) and their pairwise identity was recorded. All newly generated consensus sequences were deposited at GenBank.

### Taxon sampling and phylogenetic analysis

The consensus sequences generated in this study and the related sequences chosen based on Justo *et al.* (2017) and Chen *et al.* (2021) downloaded from GenBank (www. ncbi.nlm.nih.gov/genbank/, Table 1) were aligned using MAFFT v.7.299 (Katoh &

**Table 1** (part 1 of 8). Taxa sampled and used for the phylogenetic analyses of this study . For each collection, the species name, voucher and GenBank accession number are provided. Missing information is indicated with an n-dash (–). Newly deposited sequences are indicated in bold.

**Tabla 1 (parte 1 de 8).** Taxones muestreados en este estudio y utilizados en los análisis filogenéticos. Para cada colección, se proporciona el nombre de la especie, el voucher y el número de acceso de GenBank. La información faltante se indica con un guión (–). Las secuencias recién depositadas se indican en negrita.

Species	Geographi	Collection		GenBank acce	ession numbe	ər	Reference
	(ISO code)	reterence	ITS	28S	tef1	Rpb1	
Allophlebia C.R.S	. de Lira, Giberto	oni & K.H. Larss.					
<i>A. ludoviciana</i> (Burt.) C.R.S. de Lira, Gibertoni & K.H. Larss.	BR	URM 93251	MN04465 9	MN044661	-	-	Lira <i>et al.</i> (2022)
A. ludoviciana	BR	URM 93329	MN04465 8	MN044660	-	-	Lira <i>et al.</i> (2022)
A. ludoviciana	BR	RP 134	KP859299	KP859308	-	-	Unpublishe d
A. ludoviciana	EC	O-F-110340	MT974604	MT982121	-	-	Lira <i>et al.</i> (2022)
A. ludoviciana	US	HHB-8715-Sp	KY948770	KY948846	MZ91366 2	KY948913	Justo <i>et al.</i> (2017); Chen <i>et al.</i> (2021)
A. ludoviciana	US	HHB-6564-SP	MZ637036	MZ637240	MZ91366 1	MZ748461	Chen <i>et al.</i> (2021)
Allophlebia sp.	TW	Wu 1703-54	MZ637038	MZ637241	MZ91366 3	MZ748462	Chen <i>et al.</i> (2021)
<b>Aurantiopileus</b> Gi	nns, D.L. Lindne	r & T.J. Baroni					
<i>A. mayanensis</i> Ginns, D.L. Lindner & T.J. Baroni <b>(T)</b>	BZ	TJB10228	HM77214 0	HM772139	-	-	Ginns <i>et al.</i> (2010)
A. mayanensis	CR	JV 1504/128	KT156706	-	-	-	Vlasák et al. (2016)
Aurantiporus Mur	rill						
<i>A. albidus</i> Rajchenb. & Cwielong	AR	CIEFAP-117	KY948739	KY948848	-	KY948925	Justo <i>et al.</i> (2017)
A. croceus (Pers.) Murrill	CZ	BRNM 737561	JQ821320	JQ821317	-	-	Dvořák et al. (2014)
A. aff. croceus	MY	Miettinen-16483	KY948745	KY948901	-	KY948927	Justo <i>et al.</i> (2017)
Ceriporiopsis Dor	nanski						
C. gilvescens (Bres.) Domanski	CZ	BRNM 710166	FJ496684	FJ496720	-	-	Tomšovský et al. (2010)
C. gilvescens	US	L3519Sp	KY948761	_	-	-	Justo <i>et al.</i> (2017)
C. gilvescens	TW	Chen 3340	MZ636936	MZ637099	MZ91365 1	MZ748446	Chen <i>et al.</i> (2021)
Ceriporiopsis s.l.							
C. alboaurantia C.L. Zhao, B.K.	CN	Cui 4136	KF845955	KF845948	-	-	Zhao & Cui (2014)

**Table 1** (part 2 of 8). Taxa sampled and used for the phylogenetic analyses of this study . For each collection, the species name, voucher and GenBank accession number are provided. Missing information is indicated with an n-dash (–). Newly deposited sequences are indicated in bold.

**Tabla 1 (parte 2 de 8).** Taxones muestreados en este estudio y utilizados en los análisis filogenéticos. Para cada colección, se proporciona el nombre de la especie, el voucher y el número de acceso de GenBank. La información faltante se indica con un guión (–). Las secuencias recién depositadas se indican en negrita.

C. alboaurantia	CN	Cui2877	KF845954	KF845947	_	_	Zhao & Cu (2014)
<i>C. fimbriata</i> C.L. Zhao & Y.C. Dai (T)	CN	Dai 11672	KJ698633	KJ698637	_	-	Zhao <i>et al.</i> (2015)
C. fimbriata	CN	Cui 1671	KJ698634	KJ698638	-	-	Zhao <i>et al.</i> (2015)
<i>C. guidella</i> (Bernicchia & Ryvarden	IT	HUBO 7659	FJ496687	FJ496722	_	-	Tomšovsky et al. (2010
C. <i>kunmingensis</i> C.L. Zhao <b>(T)</b>	CN	CLZhao 153	KX081073	KX081075	-	-	Zhao & Wu (2017)
C. kunmingensis	CN	CLZhao 152	KX081072	KX081074	-	-	Zhao & Wu (2017)
C. lagerheimii Laessoe & Ryvarden	CN	Dai 12304	KX161647	KX161651	_	-	Zhao <i>et al.</i> (2017)
C. lagerheimii	CN	58240	KX008365	KX081077	-	-	Zhao <i>et al.</i> (2017)
C. pseudoplacenta Vlasák & Ryvarden <b>(T)</b>	US	PRM 899297	JN592497	JN592504	_	_	Vlasák et al. (2012)
C. pseudoplacenta	US	Miettinen 18997	KY948744	KY948902	_	KY948902	Justo et al (2017)
C. pseudoplacenta	US	JV050952	JN592499	JN592506	-	-	Vlasák et al. (2012)
C. rosea C.L. Zhao & Y. C. Dai (T)	CN	Dai 13573	KJ698635	KJ698639	_	-	Zhao & Da (2014)
C. rosea	CN	Dai 13584	KJ698636	KJ698640	-	-	Zhao & Da (2014)
Climacodon P. Karst	t.		1				1
C. septentrionalis (Fr.) P. Karst. <b>(T)</b>	US	AFTOL ID 767	AY854082	AY684165	AY86487 2	-	Lutzoni et al. (2004)
C. septentrionalis	US	FP 72067	KP135345	-	_	-	Floudas & Hibbett (2015)
<i>C. sanguineus</i> (Beeli) Maas Geest.	GA	BR502018072879 7	KX810931	KX810932	KX81093 4	-	Moreno el al. (2017)
Crustodontia Hjortst	am & Ryvar	den	1	<u> </u>	<u> </u>	<u> </u>	
<i>C. chrysocreas</i> (Berk. & M.A. Curtis) Hjortstam & Ryvarden	US	HHB-6333-Sp	KP135358	KP135263	_	KP134861	Floudas & Hibbett (2015)
C. chrysocreas	US	FP102161sp	AY219367	-	_	-	De Koker e al. (2003)
<i>C. nigrodontea</i> (C.L. Zhao & R.X.	CN	CLZhao 2758	MT896824	-	-	-	Huang <i>et a</i> (2020)

**Table 1** (part 3 of 8). Taxa sampled and used for the phylogenetic analyses of this study . For each collection, the species name, voucher and GenBank accession number are provided. Missing information is indicated with an n-dash (–). Newly deposited sequences are indicated in bold.

**Tabla 1 (parte 3 de 8).** Taxones muestreados en este estudio y utilizados en los análisis filogenéticos. Para cada colección, se proporciona el nombre de la especie, el voucher y el número de acceso de GenBank. La información faltante se indica con un guión (–). Las secuencias recién depositadas se indican en negrita.

Chen & Sheng H. Wu <b>(T)</b>							
C. nigrodontea	CN	CLZhao 2729	MT896823	MT896819	-		Huang <i>et al.</i> (2020)
<i>C. taiwanensis</i> C.C. Chen & Sheng H. Wu <b>(T)</b>	TW	TNM: F31196	MZ636944	MZ637106	-	MZ748466	Chen <i>et al.</i> (2021)
C. tongxiniana (C.L. Zhao) C.C. Chen & Sheng H. Wu <b>(T)</b>	CN	CLZhao 2255	MT020773	MT020751	_	_	Huang & Zhao (2020)
Crustodontia sp.	NZ	CBS 125889	MH86408 7	MH875546	-	-	Vu <i>et al.</i> (2019)
Crustodontia sp.	NZ	HHB 17984	KP135359	KP135261	-	KP134860	Floudas & Hibbett (2015)
Crustodontia sp.	KR	KUC 2012112324	KJ668482	KJ668335	-	-	Jang <i>et al.</i> (2016)
Geesterania Westph	nalen, Tomso	vsky & Rajchenberg					
G. carneola (Bres.) Westphalen & Rajchenberg <b>(T)</b>	BR	MW388/12	KY174999	KY174999	KY17501 3	-	Westphalen et al. (2018)
<i>G. davidii</i> Westphalen & Rajchenberg <b>(T)</b>	BR	MW396/12	KY174998	KY174998	KY17501 6	_	Westphalen et al. (2018)
Hermanssonia Zmit	r.						
<i>H. centrifuga</i> (P. Karst.) Zmitr.	US	HHB-9239-Sp	KP135380	KP135262	MZ91372 1	KP134844	Floudas & Hibbett (2015)
H. centrifuga	US	L15541	KP135381	-			Floudas & Hibbett (2015)
H. centrifuga	SE	CBS 125890	MH86408 8	MH875547	-	-	Vu <i>et al.</i> (2019)
Hydnophanerochae	te Sheng H.	Wu & C.C. Chen					
<i>H. odontoidea</i> (Sheng H. Wu) Sheng H. Wu & C.C. Chen <b>(T)</b>	TW	CWN 00776	LC363487	GQ470663	LC387376	LC363498	Wu <i>et al.</i> (2010); Chen <i>et al.</i> (2018)
H. odontoidea	TW	Wu 010635	LC379000	LC379154	LC387374	LC379154	Chen <i>et al.</i> (2018)
Hydnophlebia Parm	nasto						
<i>H. alachuana</i> (Murrill) C.C Chen & Sheng H. Wu	US	FP-103881-Sp	KP135341	KP135201	_	KP134845	Floudas & Hibbett (2015)
<i>H. aurantia</i> C.C. Chen & Sheng H. Wu <b>(T)</b>	TW	WEI 18-623	MZ636982	MZ637143	MZ91371 9	MZ748459	Chen <i>et al.</i> (2021)

**Table 1** (part 4 of 8). Taxa sampled and used for the phylogenetic analyses of this study . For each collection, the species name, voucher and GenBank accession number are provided. Missing information is indicated with an n-dash (–). Newly deposited sequences are indicated in bold.

**Tabla 1 (parte 4 de 8).** Taxones muestreados en este estudio y utilizados en los análisis filogenéticos. Para cada colección, se proporciona el nombre de la especie, el voucher y el número de acceso de GenBank. La información faltante se indica con un guión (–). Las secuencias recién depositadas se indican en negrita.

<i>H. canariensis</i> Telleira, M. Dueñas & M.P. Martin <b>(T)</b>	ES	MA-Fungi 86622	KF483012	KF528103	_	_	Tellería et al. (2017)
H. canariensis	CV	MA-Fungi 86623	KF480313	KF528104	-	-	Tellería et al. (2017)
<i>H. chrysorhiza</i> (Eaton) Parmasto	US	FD-282	KP135338	KP135217	-	KP134848	Floudas & Hibbett (2015)
<i>H. gorgonea</i> Telleira, M. Dueñas & M.P. Martin <b>(T)</b>	CV	MA-Fungi 86659	KF483049	KF528140	-	-	Tellería <i>et</i> al. (2017)
H. gorgonea	CV	MA-Fungi 86658	KF483048	KF528139	-	-	Tellería et al. (2017)
<i>H. meloi</i> Telleira, M. Dueñas & M.P. Martin (T)	CV	MA-Fungi 86654	KF483044	KF528135	-	_	Tellería et al. (2017)
<i>H. omnivora</i> (Shear) Hjortstam & Ryvarden	US	KKN-112-Sp	KP135334	KP135216	-	KP134846	Floudas & Hibbett (2015)
H. omnivora	US	ME-497	KP135332	KP135218	-	KP134847	Floudas & Hibbett (2015)
Lilaceophlebia (Par	masto) Spirin	& Zmitr.					
<i>L. livida</i> (Pers.) Spirin & Zmitr. <b>(T)</b>	FI	FBCC 937	LN611122	LN611122	-	-	Kuuskeri et al. (2015)
Lilaceophlebia sp.	US	FP-135046-Sp	KY948758	KY948850	MZ91365 8	KY948850	Justo <i>et al.</i> (2017); Chen <i>et al.</i> (2021)
Luteochaete C.C. C	hen & Sheng	H. Wu.					
<i>L. subglobosa</i> (Sheng H. Wu) C.C. Chen & Sheng H. Wu	CN	CLZhao 3475	MK88189 7	MK881787	-	_	Huang <i>et al.</i> (2020)
L. subglobosa	TW	GC 1605-4	MZ636995	MZ637156	MZ91364 5	MZ748455	Chen <i>et al.</i> (2021)
L. subglobosa <b>(T)</b>	TW	Wu 870918	MZ636996	GQ470662	MZ91364 6	MZ748456	Wu <i>et al.</i> (2010); Chen <i>et al.</i> (2021)
Luteoporia F.Wu, Ji	a J. Chen & S	S.H. He	1	1	1	1	1
L. albomarginata F.Wu, Jia J. Chen & S.H. He <b>(T)</b>	CN	Dai 15229	KU598873	KU598878	_	_	Wu <i>et al.</i> (2016)
L. albomarginata	TW	GC17021-1	MF496147	LC379155	LC387377	LC379160	Chen <i>et al.</i> (2018)
<i>L. citriniporia</i> Z.B. Liu & Yuan Yuan	LK	Dai 19507	MT872218	MT872216	-	-	Liu & Yuan (2020)

**Table 1** (part 5 of 8). Taxa sampled and used for the phylogenetic analyses of this study . For each collection, the species name, voucher and GenBank accession number are provided. Missing information is indicated with an n-dash (–). Newly deposited sequences are indicated in bold.

**Tabla 1 (parte 5 de 8).** Taxones muestreados en este estudio y utilizados en los análisis filogenéticos. Para cada colección, se proporciona el nombre de la especie, el voucher y el número de acceso de GenBank. La información faltante se indica con un guión (–). Las secuencias recién depositadas se indican en negrita.

<i>L. lutea</i> (G. Cunn.) C.C. Chen & Sheng H. Wu	TW	GC1409-1	MZ636998	MZ637158	MZ91365 6	MZ637158	Chen <i>et a</i> (2021)
Merulius clade							
P. fuscotuberculata C.L. Zhao <b>(T)</b>	CN	CLZhao 10239	MT020760	MT020738	-	-	Huang & Zhao (2020)
P. hydnoidea Schwein.	US	HHB-1993-Sp	KY948778	KY948853	-	KY948921	Justo <i>et al</i> (2017)
P. leptospermi (G. Cunn.) Stalpers	NZ	TTT1607	HQ15341 3	-	_	-	Ghobad- Nejhad & Hallenberg (2012)
P. nantahaliensis Nakasone & Burds. <b>(T)</b>	US	HHB-2816-Sp	KY948777	KY948852	MZ91370 1	KY948920	Justo <i>et al</i> (2017)
<i>P. serialis</i> (Fr.) Donk	US	FCUG2868	HQ15342 9	-	-	-	Ghobad- Nejhad & Hallenberg (2012)
<i>P. tomentopileata</i> C.L. Zhao <b>(T)</b>	CN	CLZhao 9563	MT020765	MT020743	-	_	Huang & Zhao (2020)
P. tomentopileata	TW	GC 1602-67	MZ637040	MZ637244	MZ91370 2	MZ748457	Chen <i>et al</i> (2021)
P. tremellosa (Schrad.) Nakasone & Burds.	CN	Wu 1109-73	MZ637041	MZ637245	MZ91370 3	MZ748458	Chen <i>et a</i> (2021)
P. tremellosa	FR	CBS 21756	MH85758 9	MH869138	_	-	Vu <i>et al.</i> (2019)
Mycoacia Donk							
<i>M. fuscoatra</i> (Fr.) Donk	EE	KHL 13275	JN649352	JN649352	-	-	Sjökvist e al. (2012)
M. fuscoatra	US	HHB10782Sp	KP135365	KP135265	-	KP134857	Floudas 8 Hibbett (2015)
<i>M. nothofagi</i> (G. Cunn.) Ryvarden	US	HHB4273Sp	KP135369	KP135266	-	KP134858	Floudas 8 Hibbett (2015)
<i>M. subfascicularis</i> (Wakef.) Hjortstam	TW	Wu 1004-11	MZ637008	_	MZ91365 3	MZ748448	Chen <i>et a</i> . (2021)
Mycoaciella J. Erikss	. & Ryvarde	n	1	I	1	1	
<i>M. bispora</i> (Stalpers) J. Erikss. & Ryvarden	EE	El 13_99	-	AY586692	_	_	Larsson e al. (2004)
<i>M. efibulata</i> C.C. Chen & Sheng H. Wu	TW	Wei 16-167	MZ637010	MZ637170	MZ91365 7	MZ748468	Chen <i>et a</i> (2021)

**Table 1** (part 6 of 8). Taxa sampled and used for the phylogenetic analyses of this study . For each collection, the species name, voucher and GenBank accession number are provided. Missing information is indicated with an n-dash (–). Newly deposited sequences are indicated in bold.

**Tabla 1 (parte 6 de 8).** Taxones muestreados en este estudio y utilizados en los análisis filogenéticos. Para cada colección, se proporciona el nombre de la especie, el voucher y el número de acceso de GenBank. La información faltante se indica con un guión (–). Las secuencias recién depositadas se indican en negrita.

<b>a</b> <i>ii i</i>							
O. alborubescens (Bourdot & Galzin) V. Papp & Dima	CN	912941	KU509501	_	_	_	Unpublishe d
O. alborubescens	CZ	BRNU 627479	JQ821319	JQ821318	-	-	Dvořak <i>et</i> al. (2014)
O alborubescens	HU	BP106943	MG09786	MG097867	_	MG21372	Papp &
(T)			4			4	Dima (2017)
O. alborubescens	-	46	AJ006683	-	-	-	Yao et al. (1999)
Pappia Zmitr.							
<i>P. fissilis</i> (Berk. & M.A Curtis) Zmitr.	CZ	BRNM 699803	HQ72829 2	HQ729002	-	-	Tomšovský (2012)
P. fissilis	US	CBS 67770	MH85989 7	MH871687	-	-	Vu <i>et al.</i> (2019)
Phlebia Fr.							
P. acerina Peck	CN	GC 1708-40	MZ637030	MZ637234	MZ91369	MZ748454	Chen et al.
					8		(2021)
P. acerina	US	FD301	KP135378	KP135260	-	KP134862	Floudas & Hibbett (2015)
<i>P. floridensis</i> Nakasone & Burds.	US	HHB 9905Sp	KP135383	KP135264	-	KP135264	Floudas & Hibbett (2015)
<i>P. lindtneri</i> (Pilát) Parmasto	NO	GB 501	KY948772	KY948847	-	KY948923	Justo <i>et al.</i> (2017)
<i>P. radiata</i> Fr.	FR	CBS 297.53	MH85721 2	MH868751	-	-	Vu <i>et al.</i> , (2019)
P. radiata	US	AFTOL 484	AY854087	AF287885	AY88515 6	AY864881	Lutzoni et al. (2004)
<i>P. rufa</i> (Pers.) M.P. Christ.	SE	FBCC297	LN611092	LN611092	-	-	Kuuskeri <i>et</i> al. (2015)
P. rufa	NZ	CBS 126034	MH86389 6	MH875357	-	-	Vu <i>et al.</i> (2019)
<i>P. setulosa</i> (Berk. & M.A. Curtis) Nakasone	US	HHB-6891-Sp	KP135382	KP135267	MZ91365 0	KP134864	Floudas & Hibbett (2015)
Phlebia s.l.			1	1			
<i>P. ailaoshanensis</i> C.L. Chao	CN	CLZhao 3996	MH78492 6	MH784936	-	-	Shen <i>et al.</i> (2018)
<i>P. albida</i> H. Post	ES	GB1833	AY219368	_	MZ91367 5	-	De Koker ei al. (2003)
P. albomellea (Bondartsev)	US	FP-101843	AY219369	-	-	-	De Koker ei al. (2003)

**Table 1** (part 7 of 8). Taxa sampled and used for the phylogenetic analyses of this study . For each collection, the species name, voucher and GenBank accession number are provided. Missing information is indicated with an n-dash (–). Newly deposited sequences are indicated in bold.

**Tabla 1 (parte 7 de 8).** Taxones muestreados en este estudio y utilizados en los análisis filogenéticos. Para cada colección, se proporciona el nombre de la especie, el voucher y el número de acceso de GenBank. La información faltante se indica con un guión (–). Las secuencias recién depositadas se indican en negrita.

<i>P. aurea</i> (Fr.) Nakasone	US	RLG-5075-Sp	KY948759	MZ637161	MZ91372 0	KY948918	Justo <i>et al.</i> (2017)
P. brevispora Nakasone	US	HHB-7024-Sp	MZ637032	MZ637236	MZ91366 7	MZ748452	Chen <i>et al.</i> (2021)
P. coccineofulva Schwein.	US	HHB 11466sp	KY948766	KY948851	MZ91371 9	KY948915	Justo <i>et al.</i> (2017); Chen <i>et al.</i> (2021)
<i>P. formosana</i> Sheng H. Wu	TW	GC 1604-42	MZ637033	MZ637237	MZ91364 8	MZ748460	Chen <i>et al.</i> (2021)
P. leptospermi (G. Cunn.) Stalpers	NZ	CBS 126031	MH86389 4	MH875355	-	-	Vu <i>et al.</i> (2019)
Phlebia lividina Hjortstam	US	HHB 4160Sp	KY948755	KY948849	MZ91365 9	KY948916	Justo <i>et al.</i> (2017); Chen <i>et al.</i> (2021)
<i>P. nitidula</i> (P. Karst.) Ryvarden	CA	T 407	KY948747	-	-	KY948961	Justo <i>et al.</i> (2017)
P. aff. subochracea	US	HHB-8494-Sp	KY948768	KY948845	-	KY948912	Justo <i>et al.</i> (2017)
P. subserialis (Bourdot & Galzin) Donk	FR	CBS 211.54	MH85729 6	MH868828	-	-	Vu <i>et al.</i> (2019)
Phlebiodontia Mota	to-Vásq. & V	Vestphalen					
P. acanthocystis (Gilb. & Nakasone) Motato-Vásq. & Westphalen	CN	CLZhao 21794	ON24814 5	_	_	_	Unpublishe d
P. acanthocystis	KR	KUC 2013100133	KJ668484	KJ668337	-	-	Jang et al. (2016)
P. acanthocystis	TW	GC 170330	LC387338	LC387343	LC387384	-	Chen <i>et al.</i> (2018)
P. acanthocystis	TW	GC 1809-21	MZ637029	MZ637233	-	-	Chen <i>et al.</i> (2021)
P. acanthocystis	US	FP150571	KY948767	KY948884 4	-	KY948844	Justo <i>et al.</i> (2017)
P. aff. acanthocystis	NZ	CBS 125861	MH86381 6	-	-	-	Vu <i>et al.</i> (2019)
P. aff. acanthocystis	US	JP1C-5X	MG64929 0	-	-	-	Unpublishe d
<i>P. rachenbergii</i> Westphalen & Motato-Vásq. <b>(T)</b>	BR	MCW626	OP265191	OP265189	OP27182 9	-	Present study
P. rachenbergii	BR	MCW636	OP265192	OP265190	OP27183 0	-	Present study
P. subochracea (J. Erikss. &	DK	FCUG 1161	AF141630		-	-	Parmasto & Hallenberg

**Table 1** (part 8 of 8). Taxa sampled and used for the phylogenetic analyses of this study . For each collection, the species name, voucher and GenBank accession number are provided. Missing information is indicated with an n-dash (–). Newly deposited sequences are indicated in bold.

**Tabla 1 (parte 8 de 8).** Taxones muestreados en este estudio y utilizados en los análisis filogenéticos. Para cada colección, se proporciona el nombre de la especie, el voucher y el número de acceso de GenBank. La información faltante se indica con un guión (–). Las secuencias recién depositadas se indican en negrita.

Motato-Vásq. &							
Gugliotta							
P. subochracea	SE	KGN 162/95	EU118656	EU118656	_	_	Larsson
	02		20110000	20110000			(2007)
Phlebiporia Jia J. Ch	en, B.K. Cui	& Y.C. Dai					
P. bubalina Jia J.	CN	Dai 13168	KC782526	KC782528	_	_	Chen & Cu
Chen, B.K. Cui & Y.C. Dai <b>(T)</b>							(2014)
Phlebiporia sp.	TW	Wu 1210-7	MZ637061	-	MZ91364 7	MZ748390	Chen <i>et al.</i> (2021)
Sarcodontia Schulze	r						
S. crocea	US	OMC1488	KY948798	KY948903	-	KY948928	Justo et al.
(Schwein.) Kotl. (T)							(2017)
S. uda (Fr.) Nikol.	US	FP101544-Sp	KP135361	KP135232	MZ91364 9	KP134859	Floudas & Hibbett (2015); Chen <i>et al.</i> (2021)
Scopuloides (Masse	e) Höhn. & l	litsch.					
S. allantoidea	TW	GC 1602-11	MZ637080	MZ637278	-	-	Chen et al.
C.C. Chen & Sheng H. Wu <b>(T)</b>							(2021)
S. allantoidea	TW	Wei 16-060	MZ637081	MZ637279	MZ91366 4	MZ748463	Chen <i>et al.</i> (2021)
S. <i>dimorpha</i> (Sang H. Lin & Z.C. Chen) C.C. Chen & Sheng H. Wu	US	FP-102935-Sp	KP135353	KP135285	-	KP134855	Floudas & Hibbett (2015)
S. hydnoides (Cooke & Massee) Hjortstam & Ryvarden <b>(T)</b>	US	FP-150473	KP135355	KP135284	_	KP134854	Floudas & Hibbett (2015)
S. rimosa (Cooke) Jülich	US	HHB-15484-Sp	KP135352	KP135281	MZ91366 5	KP134851	Floudas & Hibbett (2015)
Stereophlebia Zmitr.							
S. tuberculata	CN	Wu 1708-107	MZ637089	MZ637286	MZ91366	MZ748450	Chen et al.
(Berk. & M.A. Curtis) Zmitr.					0		(2021)
S. tuberculata (T)	TW	Chen 3242	MZ637988	MZ637285	-	-	Chen <i>et al.</i> (2021)
ROOT			1	<u> </u>		1	
Candelabrochaete africana Boidin	PR	FP-102987-Sp	KP135294	KP135199	-	KP134872	Floudas & Hibbett

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Standley, 2013). The ITS and 28S regions were aligned using the L-INS-I strategy (command line: mafft—localpair-maxiterate 1000). The coding regions were aligned using the E-INS-I strategy with no cost for opening gaps and equal cost for transformations (command line: mafft—genafpair—maxiterate 1000). After alignment, sequences were translated and checked for stop codons using Aliview v.1.18 (Larsson, 2014). The combined dataset includes 131 sequences of ITS, 114 of 28S, 39 of *tef1*, and 55 of *rpb1*. Phylogenetic relationships were inferred in a maximum likelihood framework as implemented in IQTREE v.2.0 (Nguyen *et al.*, 2015). *Candelabrochaete africana* Boidin (Polyporales, Basidiomycota) was used as the root (Chen *et al.*, 2021). ModelFinder (Kalyaanamoorthy *et al.*, 2017) was used to select the optimal partition scheme and substitution models (Table 2). Ten independent runs, including the calculation of the ultrafast Bootstrap (Hoang *et al.*, 2018) and the Shimodaira-Hasegawa approximate likelihood-ratio test (SH aLRT) (Guindon *et al.*, 2010), were conducted with the following command line: iqtree -s concat.nex -spp partition.nex. best scheme.nex -B 1000 -alrt 1000 -pers 0.2 -nstop 1000.

Subset	Partition names	Model
1	ITS	GTR+F+R6
2	28S	GTR+F+R4
3	TEF Codon 1	F81+F+R3
4	TEF Codon 2	GTPM3+F+I+G4
5	TEF Codon 3	TIM2+F+R4
6	Intron	TN+F+R3
7	RPB1 Codon 1	GTR+F+R6
8	RPB1 Codon 2	GTR+F+I+G4
9	RPB1 Codon 3	TIM2e+R4

Table 2. Best partition scheme and best-fit models selected by ModelFinder for the IQ-TREE analysis.Table 2. Mejor esquema de partición y modelos de mejor ajuste seleccionados por ModelFinderpara el análisis IQ-TREE.

## RESULTS

## **Phylogenetic inference**

For this study, we generated two consensus sequences of ITS, two of 28S and two of *tef1* (Table 1). In total, the ITS+28S+*rpb1*+*tef1* dataset had an aligned length of 4301 characters for 132 terminals of 88 taxa, of which 1656 are parsimony-informative, 446 singleton sites and 2199 are constant sites. The best tree inferred in a maximum likelihood framework from ten independent runs has a log likelihood = -57683.5350. The molecular data obtained show that the specimens studied nest in

a monophyletic clade with *Phlebia acanthocystis* and *P. subochracea* with high support (Fig. 1). The species in this clade are morphologically similar in presenting smooth elongated leptocystidia, sometimes with small knobs or projections at the apical part (acanthocystidia) and yellowish ceraceous basidiomes with agglutinated hyphae. Additionally, these are genetically and morphologically separated from *Phlebia s.s.* (core *Phlebia* clade *sensu* Chen *et al.*, 2021). These data support the proposition of a new genus to accommodate the three species (Fig. 1). Below, comments and descriptions of the newly proposed taxa are presented.

# Phlebiodontia Motato-Vásq. & Westphalen gen. nov. Mycobank: 845081 Type species: Phlebiodontia rajchenbergii Westphalen & Motato-Vásq.

**Etymology**.— *Phlebiodontia* (Gk) = "phlebia–" referring to genus *Phlebia*, "–dontia" tooth.

**Basidiome** annual, resupinate, slightly warted to hydnoid, ceraceous, bright to pale yellow when fresh becoming cinnamon buff to light brown when dried. Margin abrupt to fibrillose. When present, aculei regular to irregular, cylindrical to conical, sometimes flattened and agglutinated when dried. Subiculum with thick crystalline layer near substrate. Hyphal system monomitic, generative hyphae clamped. Leptocystidia smooth, thin-walled, obclavate, fusiform to ventricose, tapering towards the apex, sometimes with small knobs or projections at the apical part (acanthocystidia). Basidia clavate, with four sterigmata. Basidiospores broadly ellipsoid to allantoid, thin-walled, smooth, IKI–, CB–.

**Comments.**—*Phlebiodontia* is characterized by ceraceous yellowish basidiomes, with slightly warted to hydnoid hymenophore, monomitic hyphal system, clamped generative hyphae and presence of thin-walled leptocystidia. The cystidia are sometimes sparse and hard to find (Nakasone & Gilbertson, 1998). The genus currently includes three species, P. acanthocystis, described from United States (Hawaii), the new species P. rajchenbergii, from Brazil and P. subochracea, from Germany. These species are very similar and can be distinguished mostly by difference in the hymenophore configuration and by the shape and size of the basidiospores. Phlebiodontia is included in the Hydnophlebia clade (as defined by Chen et al., 2021) and forms a sister group with Allophlebia C.R.S. de Lira, Gibertoni & K.H. Larss. and Ceriporiopsis fimbriata C.L. Zhao & Y.C. Dai. Allophlebia, typified by A. ludoviciana (Burt) C.R.S. de Lira & K.H. Larss., differs from Phlebiodontia species by the presence of heavily encrusted cylindrical metuloid cystidia immersed in the hymenium (Lira et al., 2022). Another genus included in this clade is Hydnophlebia Parmasto, typified by H. chrysorhiza (Torr.) Parmasto. However, species in this genus can be easily distinguished from *Phlebiodontia* by the bright reddish orange to yellow hymenophore, margins with mycelial cords formed by encrusted hyphae, cylindrical cystidia and cylindrical to subglobose basidiospores (Tellería et al., 2017).

Fig. 1. Phylogenetic relationships in Meruliaceae inferred from a combined dataset of ITS+28S+rpb1+tef1 conducted by IQ-TREE optimal tree (log likelihood = -57683.5350). All sequences generated in this study are indicated in bold. Values at nodes indicate ultrafast bootstrap (left) and the Shimodaira-Hasegawa approximate likelihood-ratio test (right); minus (-) indicates support values lower than 70% bootstrap. Type specimens are indicated with a (T) and generic types with a star. Two codes after voucher specimens indicate the country of origin (ISO 3166 - Alpha 2, for United States ISO 3166-2). The bar indicates the number of expected substitutions per position.

Fig. 1. Relaciones filogenéticas en Meruliaceae inferidas de un conjunto de datos combinados de ITS+28S+rpb1+tef1 realizado por el árbol óptimo IQ-TREE (verosimilitud logarítmica = -57683,5350). Todas las secuencias generadas en este estudio se indican en negrita. Los valores en los nodos indican ultrafast bootstrap (izquierda) y la prueba de verosimilitud aproximada de Shimodaira-Hasegawa (derecha); menos (-) indica valores de soporte inferiores al 70 % de bootstrap. Los especímenes tipo se indican con una (T) y los tipos genéricos con una estrella. Dos códigos después de los especímenes indican el país de origen (ISO 3166 - Alpha 2, para Estados Unidos ISO 3166-2). La barra indica el número de sustituciones esperadas por posición.



0.2

# Phlebiodontia acanthocystis (Gilb. & Nakasone) Motato-Vásq. & Westphalen comb. nov. Phlebia acanthocystis Gilb. & Nakasone, Folia cryptog. Estonica 33: 85 (1998). Mycobank: 845084 Description in: Nakasone & Gilbertson (1998).

**Geographical distribution and ecology.**— the species was reported growing on wood and bark of numerous angiosperms branches (Martini, 2016). It was originally described from Hawaii, but there are records of the species worldwide (Maekawa *et al.*, 2003; Duhem, 2008; Gorjón *et al.*, 2012; Jang *et al.*, 2016; Zíbarová, 2017).

**Comments.**— *Phlebiodontia acanthocystis* is characterized by ceraceous and pale yellowish resupinate basidiomes, odontoid hymenophore, absence of reaction in 3% KOH, a monomitic hyphal system with clamped hyphae, obclavate cystidia gradually tapering toward the apex (leptocystidia), sometimes with several small knobs at the apical part, and small, ellipsoid to short cylindrical basidiospores  $[3.0-4.5(-5.0) \times (1.8-)2.0-2.5 \mu m$ , Nakasone & Gilbertson, 1998; Maekawa *et al.*, 2003]. The species differs from *P. rajchenbergii* by wider and larger ellipsoid basidiospores and from *P. subochracea* by the configuration of the hymenophore, being smooth to irregularly warted in the latter.

## Phlebiodontia rajchenbergii sp. nov. Westphalen & Motato-Vásq. (Fig. 2). Mycobank: 845083

**Diagnosis.**— *Phlebiodontia rajchenbergii* can be recognized within the genus by the combination of yellow hydnoid (4–7 aculei per mm) hymenophore, cylindrical to allantoid basidiospores  $(3.8-)3.9-4.5(-4.6) \times 1.7-1.9 \,\mu\text{m}$  and presence of thin-walled acanthocystidia, obclavate, fusiform to ventricose, tapering towards the apex.

**Type**.— BRAZIL, São Paulo, Ribeirão Grande, Parque Estadual Intervales, - 24,265419, -48,412661, 27.II.2018, *M.C. Westphalen 626/19* (holotype, SP; isotype CUVC).

**Etymology.**— Rajchenbergii (Lat., masculine): in honor of Prof. Dr. Mario Rajchenberg (Argentina) in recognition for his devotion and important contributions to the knowledge of mycology and forest pathology.

**Basidiomes** resupinate, adnate, forming patches up to 10 cm on the substratum, ceraceous, becoming very fragile and brittle upon drying. Sterile margins whitish, very thin to absent, less than 1 mm wide. Hymenophore hydnoid, teeth cylindrical, often flattened and fused, with acute apices, pale yellow when fresh, becoming beige to pale brown upon drying, 0.5–1 mm long and 4–7 per mm. Subiculum very thin, formed by a faint layer of hyphae, white to cream, approximately 0.1 mm thick.

*Hyphal structure* monomitic; generative hyphae clamped, thin- to slightly thickwalled, nodose-septate, somewhat agglutinated in dried specimens, 2–4  $\mu$ m wide; gloeopleurous-like hyphae strongly staining with cotton blue present in the trama, but sometimes difficult to observe, 3.5–5  $\mu$ m wide.



**Fig. 2.** A-B) Basidiome of *Phlebiodontia rajchenbergii* (MCW626, holotype). C) Culture of *P. rajchenbergii* in Potato Dextrose Agar (PDA, MCW626, holotype), seven days of growth. D) Basidiospores. E) Acanthocystidia. Scale bars A-B = 1 cm; D = 2  $\mu$ m, E = 10  $\mu$ m. Petri dish = 9 cm diam. Photos by: A-B. M.C. Westphalen and C. V. Motato-Vásquez. Drawings by V. Motato-Vásquez.

**Fig. 2.** A-B) Basidioma de *Phlebiodontia rajchenbergii* (MCW626, holotipo). C) Cultivo de *P. rajchenbergii* en Agar Papa Dextrosa (PDA, MCW626, holotipo), siete días de crecimiento. D) Basidiosporas. E) Acantocistidios. Barras A-B = 1 cm; D = 2  $\mu$ m, E = 10  $\mu$ m. Placa de petri = 9 cm diam. Fotos por: A-B: M.C. Westphalen y C: V. Motato-Vásquez. Dibujos de V. Motato-Vásquez.

**Leptocystidia** thin-walled, obclavate, fusiform to ventricose, tapering towards the apex, sometimes with small knobs or projections at the apical part (acanthocystidia), imbedded in the hymenium and projecting above it,  $22-30 \times 3.5-5.5 \ \mu\text{m}$ . Basidia clavate, 4-sterigmate,  $13-16 \times 4-4.5 \ \mu\text{m}$ .

**Basidiospores** cylindrical to allantoid, often flattened at one side, hyaline, thinwalled, CB-, IKI-,  $(3.8-)3.9-4.5(-4.6) \times 1.7-1.9 \mu \text{m}$ , Lm  $\times$  Wm = 4.2  $\times 1.8$  im, Q' = (2.1-)2.2-2.4, Qm = 2.3 (n = 45/2).

**Culture characters.**— plates covered in three weeks. Advancing zone regular, appressed, subfelty, becoming finely cottony, white to yellowish. Margin even, appressed. Sweet odor. Reverse whitening. Generative hyphae of advancing zone 5–7  $\mu$ m wide, thin walled, simple-septate and some with clamps, hyphae in the submerged mycelium clamped, thin to thick-walled, very branched, 3–5  $\mu$ m diam.

Chlamydospores terminal or intercalary, thin walled, globose, 9–14.7  $\mu$ m diam., rare to abundant after the second week.

Species code: 2.4.7.(14).34.35.36.38.40.41.42.54.

**Geographical distribution and ecology**.— Growing on dead logs of unidentified angiosperms. Known only from southeastern Brazil Atlantic forest in São Paulo State.

**Comments.**— *Phlebiodontia rajchenbergii* is characterized by ceraceous hydnoid basidiomes, cylindrical to allantoid basidiospores and presence of thin-walled cystidia with a tapering apex (smooth leptocystidia or acanthocystidia with knobs at the apex). Phylogenetically, it nests close to *P. acanthocystis s. s.* in a strongly supported clade (BS= 97%, SH=100%, Fig. 1). These species share a similar morphology, but *P. acanthocystis* can be distinguished by wider and larger ellipsoid basidiospores [ $3.5-4.5(-5) \times 2-2.5 \mu m$ , Nakasone & Gilbertson, 1998]. *Allophlebia ludoviciana* was described from USA (Louisiana) an also reported from Brazil, but is easily distinguished by the presence of heavily encrusted cylindrical metuloid cystidia immersed in the hymenium (Lira et al., 2022). *Phlebiodontia rajchenbergii* forms a sister clade with a specimen sequenced from New Zealand (CBS 125861) misidentified as *P. acanthocystis*. Further studies may clarify if this specimen could represent another undescribed species in the genus.

Additional studied material.— BRAZIL, São Paulo, Ribeirão Grande, Parque Estadual Intervales, -24,265419, -48,412661, 28.II.2018, *M.C. Westphalen 636/18* (paratype, SP).

Phlebiodontia subochracea (Bres.) Motato-Vásq. & Gugliotta comb. nov. Grandinia subochracea Bres., Hedwigia 33: 206 (1894).
Phlebia subochracea (Bres.) J. Erikss. & Ryvarden, Cortic, N. Eur., 4 (Oslo): 873 (1976).
= Peniophora danica M.P. Christ., Friesia 5: 207 (1956). Mycobank: 845085
Description in: Eriksson et al. (1981), Nakasone et al. (1982).

**Geographical distribution and ecology.**— recorded growing on *Carpinus sp., Salix sp.* and *Quercus sp.*, widespread in Europe (Bernicchia & Gorjón, 2010). Also cited from North America (Eriksson *et al.*, 1981; Nakasone *et al.*, 1982)

**Comments.**— *Phlebiodontia subochracea* is characterized by a membranous basidiome with smooth to warted hymenophore when young, becoming strongly warted when mature, thin-walled subulate leptocystidia and cylindrical to ellipsoid basidiospores [6–8 × 2.5–3.5  $\mu$ m, Eriksson & Ryvarden, 1976]. The characteristic warted hymenophore and the larger basidiospores differentiates it from the other two species in *Phlebiodontia*. *Phlebia ochraceofulva* (Donk & Galzin) Donk has been compared with *P. subochacea*. The former presents broader basidiospores, about 3–4  $\mu$ m wide, and a more agglutinated hyphal texture (Bernicchia & Gorjón, 2010). Additionally, *P. subochracea* has been compared with *A. ludoviciana*. Both species are bright yellow-olive when fresh but tan or light brown when dry. Microscopically,

*P. subochracea* has broader basidiospores and lacks the encrusted cystidia found in *A. ludoviciana*. In addition, Nakasone *et al.* (1982) carried out fertility tests showing that the species are not conspecific.

#### Identification Key to Phlebiodontia species

1	Hymenophore smooth to warted	P. subochracea
1'	Hymenophore hydnoid	
2	Basidiospores ellipsoid, 2–2.5 $\mu$ m wide	P. acanthocystis
2'	Basidiospores cylindrical to allantoid, up to 1.9 $\mu$ m wide	P. rajchenbergii

## DISCUSSION

Based on a multigene phylogenetic analysis, Chen *et al.* (2021) divided the taxa of Meruliaceae into four clades: (I) The core *Phlebia* clade, (II) the *Mycoacia* clade, (III) the *Sarcodontia* clade, and (IV) the *Hydnophlebia* clade. Currently, the *Hydnophlebia* clade includes *Hydnophlebia*, some species of *Ceriporiopsis s. l.* and the recently described monotypic genus *Allophlebia*. In this study, we expand the knowledge of the *Hydnophlebia* clade with the addition of the new genus *Phlebiodontia*, including the new species *P. rajchenbergii*, and two new combinations (*i. e., Phlebiodontia acanthocystis* and *Phlebiodontia subochracea*). Phylogenetically, based on ITS+28S+*rpb1*+*tef1* sequence dataset (Fig. 1), *Phlebiodontia* forms a strongly supported sister clade to *Allophlebia plus Ceriporiopsis fimbriata* (BS= 95%, HS= 92%).

Morphologically, *Phlebiodontia* presents warted to hydnoid basidiomes and cystidia with tapering apices, frequently with coralloid knobs and protuberances (acanthocystidia), which is a unique characteristic among hydnoid *Phlebia* species (Zíbarová, 2017). These features differ from the generic concept of *Phlebia s.s. sensu* Chen *et al.* (2021), which is characterized by merulioid hymenophore, usually with cystidia and allantoid to ellipsoid basidiospores. *Hydnophlebia* also includes hydnoid species with monomitic hyphal system (with simple septate or clamped hyphae). However, it differs from *Phlebiodontia* by brightly colored and soft basidiomes, margins with mycelial cords and usually the presence of tubular to ventricose leptocystidia that are tubular to ventricose. Species in *Phlebiodontia* differ also from *A. ludoviciana* by the absence of heavily encrusted metuloid cystidia.

*Phlebiodontia acanthocystis* was described from Hawaii (Nakasone & Gilbertson, 1998) but since then, the species has been recorded in different regions of the globe. However, morphological descriptions have shown important variations, mainly in the size of the cystidia and basidiospores, which could indicate a species complex (Duhem, 2008; Gorjón *et al.*, 2012; Jang *et al.*, 2016; Zíbarová, 2017). Phylogenetically, the sequenced specimen from Hawaii (type locality, FP150571), available from GenBank, groups with several specimens from Asia in a strongly supported clade (BS= 100%; HS= 100%, Fig. 1), representing in this study *P. acanthocystis s. s.* Other two specimens sequenced identified as '*Phlebia acanthocystis*' available in GenBank come from: i) an endophytic fungus from the United States (JP1C5X), and ii) a

specimen from New Zealand (CBS125861). Both taxa represent different lineages inside *Phlebiodontia* for which there is not yet a taxonomic study available. These phylogenetic data, together with the distribution pattern and morphological data also support the hypothesis that *P. acanthocystis*, as currently defined, is a species complex. Unfortunately, we could not examine the type specimen of *P. acanthocystis* since when we requested the loan it could not be located in the BPI herbarium, where it was originally deposited. According to the collection database at CFMR they have an isotype. However, due to the pandemic situation caused by SARS-CoV-2 in which the herbarium collections were closed, this information could not be verified in this study. If no type is available, it would be a priority to propose a new type specimen. A good candidate would be the specimen sequenced from Hawaii (FP150571), if it is in good condition.

Phlebiodontia subochracea was originally described as Grandinia subochracea Bres. (Bresadola, 1894), from Germany. The species is widely distributed in Europe (Bernicchia & Gorjón, 2010), causing white rot in different plant families (Martini, 2016). Nakasone et al. (1982) studied the types of G. subochracea and Corticium granulatum Burt., a species described from the United States (Idaho; Burt, 1926). The authors (op. cit.) conclude that the species are synonyms with priority for G. subochracea. In the original description Burt (1926) indicates that the incrustation of the hyphae is an important character for the recognition of C. granulatum. Nevertheless, this characteristic is not reported in any description of the European specimens of P. subochracea. Additionally, the size of the spores reported by Burt (op. cit.,  $4-5 \times 2-3$  $\mu$ m) are considerably different from those reported for European specimens [6–8  $\times$  2.5–3.5  $\mu$ m, Eriksson & Ryvarden, 1976]. In terms of molecular data, there are sequences available in GenBank of specimens identified as P. subochracea from the United States (HHB 8494Sp) and from Europe (KGN 162-95, FCUG 1161). The specimen from the United States forms a sister clade with A. ludoviciana. However, the European specimens nested in the new genus Phlebiodontia. We suggest that the North American specimens identified as 'P. subochracea' should be directly compared with the holotype of C. granulatum and the sequenced specimen should be revised to verify if there are any misidentifications.

The data and discussions provided in this study allow the circumscription of species previously placed in *Phlebia s.l.*, contributing to the rearrangement of the relationships in a traditional group of corticioid fungi. Additionally, the new species proposed in this study, *Phlebiodontia rajchenbergii*, shows the importance of continuing to study the native *Funga* of the Brazilian Atlantic Forest, a hotspot of biodiversity of which very little is still known.

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