

# New insights on *Bjerkandera* (Phanerochaetaceae, Polyporales) in the Neotropics with description of *Bjerkandera albocinerea* based on morphological and molecular evidence

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**Background and aims** – *Bjerkandera* is one of the few poroid genera in the Phanerochaetaceae family known to date. The genus has a worldwide distribution and is characterized by effused-reflexed, pileate basidiomata with a pale cream to smoky or mouse grey hymenophore that becomes darker when dried, and a monomitic hyphal structure with clamped generative hyphae. Morphological and phylogenetic studies have traditionally accepted only two species in the genus, *B. adusta* (generic type) and *B. fumosa*, both described from temperate Europe. Recently, three additional species, *B. atroalba*, *B. centroamericana* and *B. mikrofumosa* were described from the Neotropics. While studying polypores in the Yungas forests of northwest Argentina and the Atlantic Forest of southeast Brazil, several specimens of *Bjerkandera* were gathered. A comparative morphological study revealed that some of these specimens do not correspond to any of the known species in the genus. This study aimed to propose a broad species-level phylogenetic hypothesis for *Bjerkandera* in the Neotropics and worldwide and to discuss the taxonomic status and diversity of the species in this genus.

**Methods** – This study is based on a morphological examination of specimens collected between 2012 and 2017, and on a revision of original collections, including the type specimens. A total of eleven ITS and seven nLSU sequences were generated and phylogenetic analyses based on Bayesian Inference (BI) and Maximum Likelihood (ML) were performed.

**Key results** – An extensive documentation of the species diversity within *Bjerkandera* in the Neotropics is presented. Genetic data of *B. mikrofumosa* were obtained for the first time and its phylogenetic position was tested. Additionally, its geographic distribution was extended in the Neotropics to Argentina and Brazil. Finally, molecular and morphological evidence was used to propose a new species for the genus, *Bjerkandera albocinerea* sp. nov.

**Conclusion** – This study provides an update of the known diversity of the genus in the Neotropics and worldwide. In addition, our results indicate that the number of taxa in *Bjerkandera* has been underestimated by morphological evidence, and may actually be greater than traditionally accepted.

**Keywords** – Cryptic species; Neotropical polypores; phylogeny; taxonomy.

## INTRODUCTION

The genus *Bjerkandera* (Polyporales, Basidiomycota) was described by Karsten (1879) and typified with *Bjerkandera adusta* (Willd.) P.Karst. The genus has been traditionally established based on morphological characters and mating system characteristics, differing from other polyporoid genera by the combination of the pale cream to smoky or mouse grey hymenophore becoming greyish to blackish when bruised or dried; two-layered context with a white, fibrous upper layer and a brown to black ceraceous layer at the base of the tubes; a monomitic hyphal system, generative hyphae with abundant clamps, thin- to thick-walled, subglobose to ellipsoid basidiospores; heterocytic nuclear behaviour, and bipolar mating system (biological data from *B. adusta*, Rajchenberg 2011). These features were used by some authors to include *B. adusta* (and, therefore, the genus as a whole) within *Gloeoporus* Mont. (Pilát 1937; Corner 1989). However, phylogenetic analyses have shown that these two genera belong to independent lineages with *Bjerkandera* species grouped within the family Phanerochaetaceae Jülich and *Gloeoporus* species grouped within the family Ipicaceae Spirin & Zmitr. (Binder et al. 2013; Miettinen et al. 2016; Justo et al. 2017).

According to MycoBank (<http://www.mycobank.org/>), there are several names associated with *Bjerkandera*. Nonetheless, morphological and phylogenetic studies have traditionally accepted only two species in the genus, *B. adusta* and *B. fumosa* (Pers.) P.Karst. Both species have been originally described from temperate Europe, growing mainly on dead hardwood logs and rarely on conifers (Bondartseva et al. 2014; Ryvarden & Melo 2017). In addition, both species have been widely recorded in different biomes of the world (Gilbertson & Ryvarden 1986; Ryvarden & Gilbertson 1993; Núñez & Ryvarden 2001; Bernicchia 2005; Robledo et al. 2006; Dai et al. 2007; Rajchenberg & Robledo 2013; Zmitrovich et al. 2016). Morphologically, *B. adusta* and *B. fumosa* are rather similar, differing by the size of their pores (6–7 per mm in the former and (1–)2–4(–5) per mm in the latter) and the presence of paler tubes separated from the context by a greyish dark line in *B. fumosa*. Zmitrovich et al. (2016) provided a morphological revision of *B. adusta* and *B. fumosa* specimens in Eastern Europe and Northern Asia, highlighting their high intraspecific morphological variability, substrate specialization and recognizing several morphotypes that have not been phylogenetically tested.

The genus *Bjerkandera* was first reported from the Neotropics by Spegazzini (1919), with *B. fumosa* recorded from Northwest (NW) Argentina. However, the record was considered uncertain by Robledo & Rajchenberg (2007) because there was no reference herbarium material. From then on, *B. fumosa* and other species in the genus have been extensively recorded in Brazil, Chile, Costa Rica, Cuba, Jamaica, and Venezuela (Rick 1960; Ryvarden 2000; Ryvarden & Iturriaga 2001; Baltazar & Gibertoni 2009; Tura et al. 2010; Westphalen & Silveira 2013). Currently, based on morphological examination of type specimens and phylogenetic analyses, Westphalen et al. (2015) proposed the combination of the Brazilian species *Tyromyces atroalbus* (Rick) Rajchenb. in *Bjerkandera* and described a new species from Mexico, *B.*

*centroamericana* Kout, Westphalen & Tomšovský, expanding the knowledge of the genetic and morphological diversity of the genus. Additionally, *B. mikrofumosa* Ryvarden was recently described from Venezuela (Ryvarden 2016) based on morphological data without evidence of its phylogenetic relationships. It is known so far from the type specimen.

While studying polypores from the Yungas forests of NW Argentina and the Atlantic Forest of Southeast (SE) Brazil, we made several collections of specimens identified as *Bjerkandera* spp. A comparative morphological study between the collected specimens and examination of molecular evidence revealed that some of our collections represent a new species of *Bjerkandera*, here described.

Also, a species-level phylogenetic hypothesis for the genus based on the internal transcribed spacer (ITS) and the large subunit of ribosomal RNA genes (nLSU), morphological descriptions, comments, illustrations, and an identification key are presented.

## MATERIALS AND METHODS

### Morphological analysis

This study was based on morphological examination of specimens collected from 2012 to 2017 in the Yungas of NW Argentina and the Atlantic Forest of SE Brazil (Morone 2014). Specimens from the herbaria CORD, ICN, LIL, NY, O, PACA and SP were studied. Herbarium names are abbreviated according to Thiers (continuously updated). For microscopic analysis, free-hand sections of basidiomata prepared in cotton blue with lactic acid, indicator of cyanophilic (CB+) or acyanophilic (CB–) reactions, were mounted on microscope slides and observed using phase-contrast objectives and immersion oil. Melzer's reagent was used to determine the presence of amyloid or dextrinoid reaction or negative reaction (IKI–). Additionally, 3% of KOH was used for microscopy. In KOH and to a lesser extent also in Melzer's reagent, the hyphal walls swell inward, and our measurements of hyphal wall thickness and width, and size of basidiospores are not valid for these reagents (Miettinen et al. 2018). All microscopic structures were measured using an eyepiece micrometre and 30 measurements were taken from each structure. When presenting spore size, 5% of the measurements at each end of the range are given in parentheses. Drawings of microstructures were made using a camera lucida with the exception of spores, which were drawn free-hand. Statistics were calculated with R v.3.2.2 (R Core Team 2013). Abbreviations and codes used for the measurements are as follows: L = mean length, W = mean width, Q = L/W (average length divided by average width), Q' = length/width ratio of individual spores, n = number of spores measured for a given number of specimens. Fresh spore prints were obtained and used for preparation of polysporic cultures. Cultures were grown in malt extract agar (MEA) or potato dextrose agar (PDA) at 25°C and described following Nobles (1965).

**Table 1 – Data for ITS and nLSU sequences used in the phylogenetic analyses.**

Origin: ISO code (country).

Species	Collector/Herbarium number(Herbarium)	Origin	ITS Genbank	nLSU Genbank	Source
<i>Bjerkandera adusta</i>	BRNM771948		KT305935	KT305935	Westphalen et al. 2015
<i>B. adusta</i>	BRNM771946		KT305936	KT305936	Westphalen et al. 2015
<i>B. adusta</i>	olrim918	LI	AY787666	–	Lygis et al. 2005
<i>B. adusta</i>	CCBAS930	PL	FJ608590	–	Homolka et al. 2010
<i>B. adusta</i>	BAFC3301	AR	FJ850965	–	Robles et al. 2011
<i>B. adusta</i>	M59	LV	JF340266	–	Arhipova et al. 2012
<i>B. albocinerea</i>	MV346 (SP)	BR	MH025421	MH025421	this study
<i>B. albocinerea</i>	RP317 (SP)	BR	MH025420	–	this study
<i>B. albocinerea</i>	MW559/17 (SP)	BR	MH025419	MH025419	this study
<i>B. atroalba</i>	MW425	BR	KT305930	KT305930	Westphalen et al. 2015
<i>B. atroalba</i>	MV158	BR	KT305932	KT305932	Westphalen et al. 2015
<i>B. atroalba</i>	MV266	BR	KT305931	KT305931	Westphalen et al. 2015
<i>B. centroamericana</i>	JK0610A13	MX	KT305934	KT305934	Westphalen et al. 2015
<i>B. centroamericana</i>	JK0610A14	MX	KT305933	KT305933	Westphalen et al. 2015
<i>B. fumosa</i>	BRNM771947		KT305937	KT305937	Westphalen et al. 2015
<i>B. fumosa</i>	DAOM215869	CA	DQ060097	–	unpublished
<i>B. fumosa</i>	N37	LV	FJ903376	–	Arhipova et al. 2012
<i>B. fumosa</i>	SFC201210094		KJ704824	KJ704839	Jung et al. 2014
<i>B. mikrofumosa</i>	MV353 (SP)	BR	MH025416	MH025416	this study
<i>B. mikrofumosa</i>	MV363 (SP)	BR	MH023526	MH023526	this study
<i>B. mikrofumosa</i>	MV398 (SP)	BR	MH023527	MH023527	this study
<i>B. mikrofumosa</i>	MV420 (SP)	BR	MH023525	MH023525	this study
<i>B. mikrofumosa</i>	MV433 (SP)	BR	MH025418	–	this study
<i>B. mikrofumosa</i>	MV435 (SP)	BR	MH025417	MH025417	this study
<i>B. mikrofumosa</i>	Catania 3269 (CORD)	AR	MH025414	–	this study
<i>B. mikrofumosa</i>	Robledo 1170 (CORD)	AR	MH025415	–	this study
<i>B. mikrofumosa</i>	P9	CO	JN861758	–	unpublished
<i>Bjerkandera</i> sp.	YHHM2		KF578081	–	unpublished
<i>Bjerkandera</i> sp.	ATCC90940	NL	DQ060096	–	unpublished
<i>Byssomerulius corium</i>	KHL8593		AY463389	AY586640	Larsson et al. 2004
<i>Ceriporiopsis carnegieae</i>	RLG7277T	US	KY948792	KY948854	Justo et al. 2017
<i>C. carnegieae</i>	JV120945	CN	KX081134	–	unpublished
<i>Gloeoporus dichrous</i>	BRNM709971	SL	EU546097	FJ496709	Tomšovský & Ryvarden 2008
<i>Irpex lacteus</i>	DO421951208	SW	JX109852	JX109852	Binder et al. 2013
<i>Mycoacia fuscoatra</i>	KHL13275	ES	JN649352	JN649352	Sjökvis et al. 2012
<i>M. nothofagi</i>	KHL13750	FR	GU480000	GU480000	Moreno et al. 2011
<i>Phlebia radiata</i>	AFTOL484		AY854087	AF287885	Floudas & Hibbett 2015
<i>P. nitidula</i>	GB020830	SW	EU118655	EU118655	Larsson 2007
<i>Porostereum spadiceum</i>	KUC2013051	KR	KJ668473	KJ668325	Jang et al. 2016
<i>P. spadiceum</i>	Wu9708-104	CN	–	DQ679918	Wu et al. 2007
<i>Terana caerulea</i>	FP10473	US	KP134980	KP135276	Floudas & Hibbett 2015
<i>Trametopsis cervina</i>	TJV93216T	US	JN165020	JN164796	Justo et al. 2017

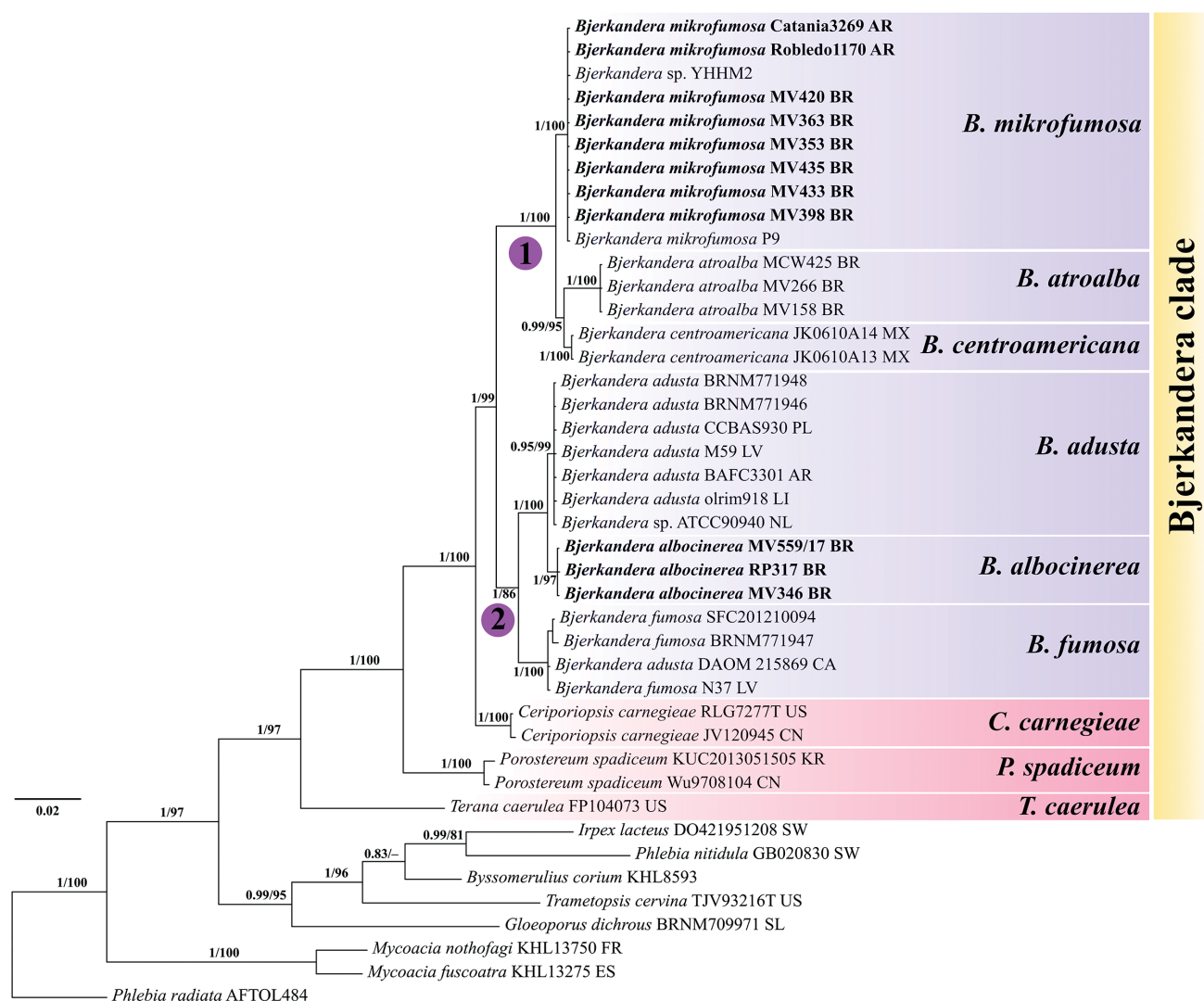
## DNA extraction, PCR amplification and sequencing

Total DNA was extracted from small pieces of dried basidiomata ground with a pestle in a porcelain mortar containing liquid nitrogen. The powder was transferred to centrifuge microtubes and mixed with lysis buffer consisting of 2% CTAB, 1.4 M NaCl, 0.10 M Tris-HCl, 0.1% mercaptoethanol, 20 mM EDTA, and incubated at 65°C for at least 2 h. After one round of chloroform extraction, DNA was precipitated with isopropyl alcohol (Doyle 1987). The following primers were used for both PCR amplification and sequencing: ITS1–ITS4 (including ITS1, 5.8S, and ITS2) for the ITS region and LR0R–LR7 for the nLSU region (White et al. 1990; Gardes & Bruns 1993; Hopple & Vilgalys 1999). PCR reactions for ITS and nLSU genes were performed in a 25 µL volume reaction and conducted on a thermal cycler (C1000 Touch™ Thermal Cycler Bio-Rad) following the cycling parameters described by Oghenekaro et al. (2014).

PCR products were visualized with 1.5% agarose gel electrophoresis. Amplified products were purified and sequenced in both directions on an Applied Biosystem 3730xl DNA analyzer (MacroGen Ltd., South Korea).

## Taxon sampling and phylogenetic inference

Sequencing chromatograms were visualized, assembled and edited using the Consed/PhredPhrap package (Ewing & Green 1998; Ewing et al. 1998; Gordon et al. 1998; Gordon & Green 2013). Once assembled, consensus sequences were queried against the GenBank database using BLAST (<http://blast.ncbi.nlm.nih.gov/>) and their pairwise identity was recorded. All newly generated consensus sequences were deposited in GenBank. For this study, eleven ITS and seven nLSU sequences were generated. The additional 30 ITS and 21 nLSU sequences were retrieved from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>). *Phlebia radiata* Fr. was



**Figure 1** – Phylogenetic relationships of *Bjerkandera* species inferred from a combined dataset of ITS and nLSU sequences. The topology is recovered from the BI analysis with PP/BS support values given at the nodes. All sequences obtained in this study are in bold. The bar indicates the number of expected substitutions per position.



**Table 2 – Basidiospores measurements (µm) of six *Bjerkandera* species.**

For L' and W', the 5% extreme tails are given in parentheses. When literature is indicated the number of measurements and Q' values are unknown.

Species/specimen	L' (length variation)	L	W' (width variation)	W	Q' (L'/W' ratio)	Q (L/W ratio)	n
<b><i>B. adusta</i></b>	<b>(4.13–)4.30–5.75(–6.13)</b>	<b>4.93</b>	<b>(2.43–)2.50–3.35(–3.50)</b>	<b>2.98</b>	<b>(1.35–)1.42–1.80(–1.90)</b>	<b>1.66</b>	–
<i>Motato-Vásquez</i> 973	(4.00–)4.21–5.80(–6.00)	4.80	2.50–3.00(–3.50)	3.00	(1.30–)1.35–1.75(–1.80)	1.60	30
<i>Motato-Vásquez</i> 993	(4.01–)4.20–5.70(–6.0)	4.77	2.51–3.40(–3.50)	2.90	(1.40–)1.48–1.85(–2.00)	1.67	30
Zmitrovich et al. (2016)	(4.00–)4.32–5.50(–6.50)	4.90	(2.23–)2.50–3.50	3.00	–	1.63	–
Ryvarden & Melo (2017)	4.50–6.00	5.25	2.50–3.50	3.00	–	1.75	–
<b><i>B. albocinerea</i></b>	<b>(3.43–)3.50–4.47(–4.57)</b>	<b>3.91</b>	<b>(2.00–)2.03–2.57(–2.63)</b>	<b>2.37</b>	<b>(1.43–)1.47–1.85(–1.95)</b>	<b>1.65</b>	<b>90</b>
holotype	(3.40–)3.50–4.53(–4.60)	3.85	2.00–2.56(–2.60)	2.35	(1.46–)1.48–1.89(–2.00)	1.65	30
<i>Motato-Vásquez</i> 346	3.51–4.50(–4.68)	4.00	(2.00–)2.10–2.56(–2.6)	2.43	(1.42–)1.45–1.84(–2.00)	1.65	30
<i>Pires</i> 317	(3.42–)3.50–4.43(–4.50)	3.87	2.05–2.60(–2.70)	2.34	(1.41–)1.48–1.83(–1.85)	1.65	30
<b><i>B. atroalba</i></b>	<b>(3.50–)3.74–5.33(–5.50)</b>	<b>4.50</b>	<b>(2.77–)2.83–3.75(–3.90)</b>	<b>3.31</b>	<b>(1.18–)1.19–1.68(–1.83)</b>	<b>1.44</b>	<b>90</b>
<i>Rick</i> s.n. (Lectotype)	4.00–5.00	4.50	(2.91–)3.00–3.80(–4.00)	3.34	(1.22–)1.24–1.62(–1.67)	1.40	30
<i>Motato-Vásquez</i> 158	(3.5–)3.72–5.5	4.61	(2.90–)3.00–3.95(–4.00)	3.38	(1.16–)1.18–1.66(–1.83)	1.42	30
<i>Motato-Vásquez</i> 266	(3.00–)3.54–5.50(–6.02)	4.51	2.50–3.56(–3.71)	3.21	1.16–1.75(–2.00)	1.50	30
<b><i>B. centroamericana</i></b>	<b>(3.60–)3.80–4.40(–5.00)</b>	<b>4.47</b>	<b>3.02–4.44(–4.50)</b>	<b>3.74</b>	<b>(1.09–)1.10–1.32(–1.43)</b>	<b>1.20</b>	<b>40</b>
Kout, J. 0610/A7 (holotype)							
<b><i>B. fumosa</i></b>	<b>5.25–6.76(–6.93)</b>	<b>6.06</b>	<b>(2.50–)2.53–3.58(–3.73)</b>	<b>3.05</b>	<b>(1.56–)1.68–2.24(–2.38)</b>	<b>1.90</b>	–
Zmitrovich et al. (2016)	5.50–7.20	6.35	2.50–3.70	3.10	–	2.04	–
Ryvarden & Melo (2017)	5.50–7.00	6.25	2.50–3.50	3.00	–	2.08	–
NY333864	5.02–6.00(–6.54)	5.71	(2.53–)2.61–3.58(–3.70)	3.10	(1.54–)1.71–2.07(–2.16)	1.90	30
<i>Motato-Vásquez</i> 974	5.00–6.85(–7.02)	5.91	2.50–3.63(–4.02)	3.01	(1.57–)1.64–2.41(–2.60)	2.00	30
<b><i>B. mikrofumosa</i></b>	<b>(3.38–)3.48–4.75(–4.80)</b>	<b>4.04</b>	<b>(2.23–)2.34–3.00(–3.10)</b>	<b>2.60</b>	<b>(1.29–)1.33–1.79(–1.84)</b>	<b>1.55</b>	<b>190</b>
Ryvarden 417468 (holotype)	(3.50–)3.78–4.52	4.10	(2.32–)2.50–3.01	2.65	(1.25–)1.33–1.61(–1.70)	1.50	40
<i>Motato-Vásquez</i> 353	(3.24–)3.35–4.50(–4.62)	3.90	2.30–2.81(–3.10)	2.51	(1.28–)1.34–1.69(–1.84)	1.54	30
<i>Motato-Vásquez</i> 398	3.50–5.00	4.20	2.30–3.00	2.61	(1.26–)1.33–1.88(–1.91)	1.60	30
<i>Motato-Vásquez</i> 420	(3.44–)3.51–4.52(–4.60)	4.00	(2.33–)2.48–3.26(–3.34)	2.65	1.27–1.70(–1.72)	1.51	30
<i>Motato-Vásquez</i> 433	(3.20–)3.30–5.02	3.92	(2.05–)2.25–3.07	2.56	1.32–2.00	1.54	30
<i>Motato-Vásquez</i> 435	3.50–5.00	4.14	(2.23–)2.30–3.00	2.55	(1.34–)1.40–1.84(–1.88)	1.60	30

defined as root. The final ITS and nLSU datasets were subsequently aligned using MAFFT v.7 under E-INS-i strategy with no cost for opening gaps and equal cost for transformations (command line: *mafft –genafpair –maxiterate 1000*) (Kato & Standley 2013) and visualized in BioEdit (Hall

1999). All sequences used in this analysis are listed in table 1.

Phylogenetic analyses were conducted in MrBayes v.3.2.6 (Ronquist et al. 2012). The nucleotide substitution models for each marker were determined with jModeltest

v.2.1.4 (Darriba et al. 2012) based on the corrected Akaike Information Criterion (AICc). The best-fit models for ITS and nLSU were TPM3uf+I+G and TIM3+I+G respectively. For the analysis, the substitution models were set as unlinked. Bayesian inference (BI) was implemented by four Markov chain Monte Carlo (MCMC) independent runs, each starting from random trees and with four simultaneous independent chains, performing 20 million generations, and sampling every 1000<sup>th</sup> generations until the average standard deviation of the split frequencies dropped below 0.01. The programme Tracer v.1.6 (Rambaut et al. 2014) was used to check if the Markov chains had reached stationarity by examining the effective sample size values and to determine the correct number of generations to discard as burn-in for the analyses. The first 20% of the sampled trees was discarded whereas the remaining ones were used to reconstruct a 50% majority-rule consensus tree. Clade robustness was expressed as posterior probabilities.

We also analysed the previous dataset using maximum likelihood (ML) within the context of static homology to evaluate whether our results were sensitive to different optimality criteria. Tree searches were performed using the parallel implementation of GARLI (v.2.0; Zwickl 2006–2011). For each partition model and selected substitution model, we conducted a total of 1000 independent search replicates and remaining default parameters from the GARLI configuration file. Bootstrap frequencies were calculated from 1000 pseudo-replicate analyses using default search parameters. Bootstrap results were compiled using SUMTREES (v.3.1.0; Sukumaran & Holder 2010). All phylogenetic analyses were run remotely at the CIPRES Science Gateway (Miller et al. 2010).

## RESULTS

### Phylogenetic analysis

The combined dataset included 41 ITS sequences with 630 characters and 28 nLSU sequences with 941 characters including gaps. The dataset resulted in an aligned length of 1571 characters, of which 1177 characters were constant, 89 were uninformative variable, and 305 were parsimony-informative characters. We show the topology recovered from BI analysis with PP and BS support values given in the nodes (fig. 1).

The average standard deviation of split frequencies in the four independent BI runs was 0.005982, and the posterior inspection of the runs' log files in Tracer showed that the 20% of trees discarded as burn-in to construct the consensus tree was a suitable value.

The topology recovered in our phylogenetic analyses (fig. 1) was overall consistent with previous results reported by Westphalen et al. (2015) and Justo et al. (2017). The genus *Bjerkandera* was recovered as a monophyletic clade (PP = 1.0, BS = 100), forming a sister clade with *Ceriporiopsis carnegieae* (D.V.Baxter) Gilb. & Ryvarden (PP = 1.0, BS = 100). Our analyses recovered six species within *Bjerkandera* grouped into two different clades, named 1 and 2 in figure 1. The clade 1 (PP = 1.0, BS = 100) groups *B. mikrofumosa* (*B.*

*atroalba*, *B. centroamericana*), and the clade 2 (PP = 1.0, BS = 86) groups *B. fumosa* (*B. adusta*, *B. albocinerea*).

A full description of *B. albocinerea* and a more detailed description of *B. mikrofumosa* based on a larger number of recent collections are presented below. Morphological comparisons of the species currently accepted in the genus are presented in tables 2 and 3. The morphological characters of *B. adusta* and *B. fumosa*, for the construction of the comparative morphological tables mentioned above, followed data collected in this study and data published by Ryvarden & Gilbertson (1993), Zmitrovich et al. (2016), and Ryvarden & Melo (2017).

### Taxonomy

*Bjerkandera albocinerea* Motato-Vásq., Robledo & Gugliotta, **sp. nov.**

Mycobank No.: MB 824562

Figs 2–3

**Diagnosis** – Differs from other species of *Bjerkandera* by the combination of sordid white pilear surface and brown-greyish to black pore surface.

**Types** – Brazil: São Paulo, São Luiz do Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virginia, 6 Jun. 2017, *Westphalen 559/17* (holotype: SP, SP466870; isotype: H); São Paulo, São Luiz do Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virginia, 7 May 2015, *Motato-Vásquez MV346* (paratype: SP, SP466871); São Paulo, São Luiz do Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virginia, 20 Aug. 2014, *Pires 317* (paratype: SP, SP466241).

**Etymology** – “*albocinerea*” – *albo* (Latin) white; *cinerea* (Latin) grey; refers to the colour combination of the basidiomata.

**Description** – Basidiomata annual, sessile, adnate, pileated to effused-reflexed, effused up to 8 cm long × 3 cm wide × 0.5 cm thick at base; pileus 0.5–2.5 cm long × 0.8–2.0 cm wide, waxy and juicy when fresh to leathery when dry, often fused together; pilear surface sordid white when fresh to pale cream when dry, azonate, finely velvety; pileus margin entire, thin to slightly blunt, sterile, velutinous, white, mostly narrow up to 0.1 cm broad, constricting upon drying and tending to roll inwards. Context divided into two layers, the upper layer slightly fibrous, white when fresh to ochraceous yellow when dry, 90–100 µm thick, lower layer clearly contrasting at the base of the tubes, waxy and dark grey, 45–55 µm thick. Pore surface shallow, dark brownish grey, changing to a darker colour, almost black, in bruised parts or when dried, pores round, 8–11 per mm; dissepiments slightly lacerated, up to 14–18.2 µm thick; tube layer not stratified, up to 0.4 cm deep. No change observed in KOH. Odour faintly fungoid or absent.

Hyphal system monomitic; generative hyphae with clamp connections, CB+, KOH–, IKI–; context hyphae mostly running horizontally; in the upper layer hyaline, thick-walled to solid, loose, (4.0–)4.5–6.3(–6.5) µm diam.; in the lower layer hyaline to yellowish, thin to slightly thick-walled, strongly agglutinated, (2.5–)2.8–4.0(–4.1) µm diam. Tramal hyphae

**Table 3 – Morphological comparison of the currently accepted species in *Bjerkandera*.**  
Only significant macromorphological characteristics are presented. For comparison of culture characteristics see the reference.

	<i>B. adusta</i>	<i>B. albocinerea</i>	<i>B. atroalba</i>	<i>B. centroamericana</i>	<i>B. fumosa</i>	<i>B. mikrofumosa</i>
<b>Pilear surface</b>	subtomentose to matt or rugulose, with subochraceous zones	finely velvety, azonate	glabrous to velutinate, often with concentric zones	slightly tomentose, azonate	tomentose to matt, often with cinnamomeous zones	velvety to finely tomentose and superficially grooved towards the margin
<b>Pilei colour</b>	cream to isabelline, then greyish to greyish-blue	sordid white to pale cream	white to cream, then pale brownish-grey to dark grey	white to brownish	pale-cream to isabelline or tan	pale golden brown
<b>Context</b>	light cream to greyish, with a greyish-black line at the base of the tubes	white to ochraceous with a dark grey line at the base of the tubes	white to cream, homogeneous or with interwoven black lines	pale buff, with interwoven black lines	tan to buff with a brownish-cinnamon layer above the tubes	cream to pale brown with a dark grey line at the base of the tubes
<b>Pores shape and number of pores per mm</b>	round to angular, 6–7/mm	round, 8–11/mm	angular, 2–5/mm	angular, 7–11/mm	round to angular (1–)2–4(–5)/mm	angular, (6–)7–9(–10)/mm
<b>Poroid surface</b>	initially cream then smoky-grey to blackish mouse-grey	dark brown grey to almost black when bruised	initially white to cream becoming straw coloured when dry or darker when touched	sordid white, becoming dark brown or grey when wounded	whitish cream to yellowish, becoming grey when bruised	pale brown to smoky, becoming dark grey when bruised
<b>Hyphae</b>	thin to thick-walled, often inflated in upper layer	thick-walled to solid and inflated in upper layer, thin-walled in the trama	thin to slightly thick-walled	thin to slightly thick-walled	thin to thick-walled, in some parts swelling	thin to thick-walled, narrow
<b>Hyphal consistency</b>	rather loose, lower layer agglutinated and interwoven	rather loose and parallel in the upper layer; agglutinated and interwoven in lower layer and trama	rather dense	rather dense, interwoven in the trama	rather loose, lower layer agglutinated and interwoven	rather dense, interwoven in trama and context; strongly agglutinated in the lower layer
<b>Basidiospores shape</b>	subellipsoid	oblong-ellipsoid to ellipsoid	broadly ellipsoid	subglobose to broadly ellipsoid	ellipsoid to cylindric	ellipsoid
<b>Species code</b>	Nobles (1964)	this study	Motato-Vásquez et al. 2016	–	Nobles (1964)	this study

hyaline to yellowish, thin to slightly thick-walled, tightly interwoven, (2.0–)2.2–3.1(–3.2)  $\mu\text{m}$  in diam. Cystidia and cystidioles absent. Basidia clavate, sometimes with an intermediate constriction,  $L' \times W' = (9.4\text{--})10\text{--}12.7(\text{--}12.8) \times 3.7\text{--}5.6(\text{--}6.0)$   $\mu\text{m}$ , with four sterigmata up to 2.5–2.8  $\mu\text{m}$  long. Basidiospores oblong-ellipsoid to ellipsoid (3.43–)3.50–4.47(–4.57)  $\times$  (2.0–)2.03–2.57(–2.63)  $\mu\text{m}$ ,  $L = 3.91$   $\mu\text{m}$ ,  $W = 2.37$   $\mu\text{m}$ ,  $Q' = (1.43\text{--})1.47\text{--}1.85(\text{--}1.95)$   $\mu\text{m}$ ,  $Q = 1.65$   $\mu\text{m}$  ( $n = 90/3$ ), hyaline, thin-walled, smooth, often with one or a few droplets, weakly CB+, IKI–.

**Ecology** – Growing on rotten logs of unidentified angiosperms, in areas of Atlantic Forest from Southeast Brazil.

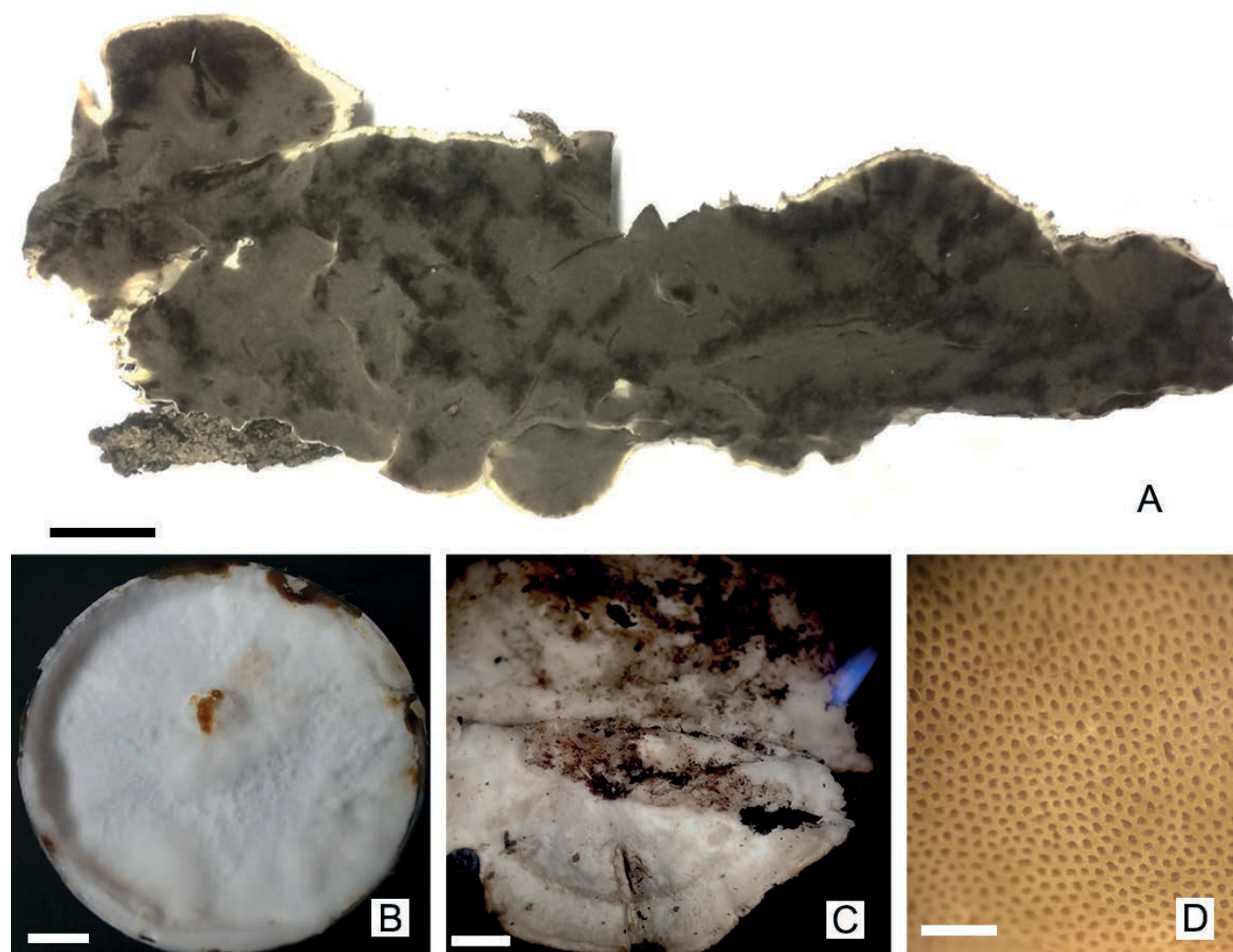
**Culture characteristics** – Growth rapid, plates covered in one week. Macromorphologically, the growing zone is characterized by regular, appressed, finely cottony, white mat and the aerial zone is characterized by pale brown mycelium; submerged zone presents white to cream mycelium. Reverse agar becoming pale brown. Odour faintly fungoid to absent. Micromorphologically, the growing zone presents simple-septate, frequently branched, thin-walled, (2.2–)2.5–3.4  $\mu\text{m}$  diam. generative hyphae; aerial mycelium formed by much

branched, thick-walled, 5.2–6.5  $\mu\text{m}$  diam., clamped generative hyphae. Some hyphae incrustated with polyhedral crystals, sparsely distributed on the hyphae; chlamydospores not observed.

Species code: 2.4.7.32.36.39.41.50.54.

**Remarks** – *Bjerkandera albocinerea* is characterized by a sordid white pilear surface, that becomes pale cream upon drying, contrasting strongly with the dark brownish grey to almost black poroid surface (fig. 2A, C). *Bjerkandera atroalba* and *B. centroamericana* have an almost white pilear surface and also occur in the Neotropics. However, both differ from *B. albocinerea* by the whitish hymenophore surface when fresh, becoming darker only in bruised parts when dried. In addition, *B. atroalba* has bigger pores (2–5 per mm) and *B. centroamericana* has slightly wider basidiospores, (3.60–)3.80–4.40(–5.00)  $\times$  3.02–4.44(–4.50), see tables 2 and 3.

**Strains examined (polysporic cultures)** – **Brazil:** São Paulo, São Luiz do Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virginia, 6 Jun. 2017, *Westphalen* 559/17



**Figure 2** – *Bjerkandera albocinerea* (SP466870 – holotype). **A.** Basidiomata. **B.** Mycelial growth after six weeks in MEA (MV346, CCIBt). **C.** Pilear surface detail. **D.** Poroid surface detail. Photographs by V. Motato-Vásquez. Scale bars: A, B, C = 1 cm; D = 0.5 mm.



(holotype: SP, CCIBt4365); São Paulo, São Luiz do Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virginia, 7 Jun. 2017, *Motato-Vásquez MV346* (paratype: SP, CCIBt4636).

*Bjerkandera mikrofumosa* Ryvarden (Ryvarden 2016: 44).

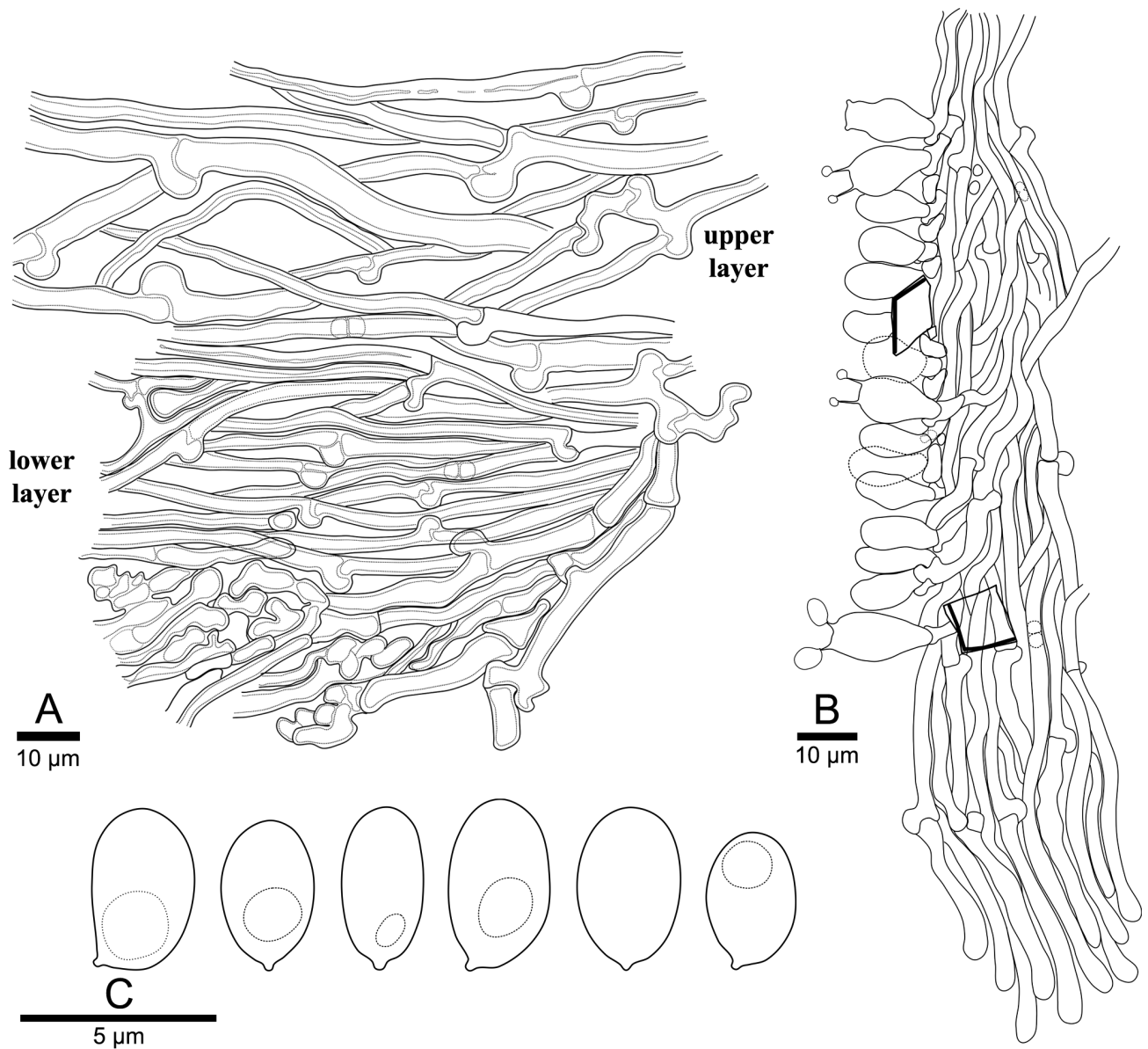
MycoBank No.: MB 552297

Figs 3–4

**Type** – Venezuela: Aragua state, Choroni, 400 m a.s.l., 5 Feb. 2006, on dead hardwood log, *L. Ryvarden 417468* (holotype: O!).

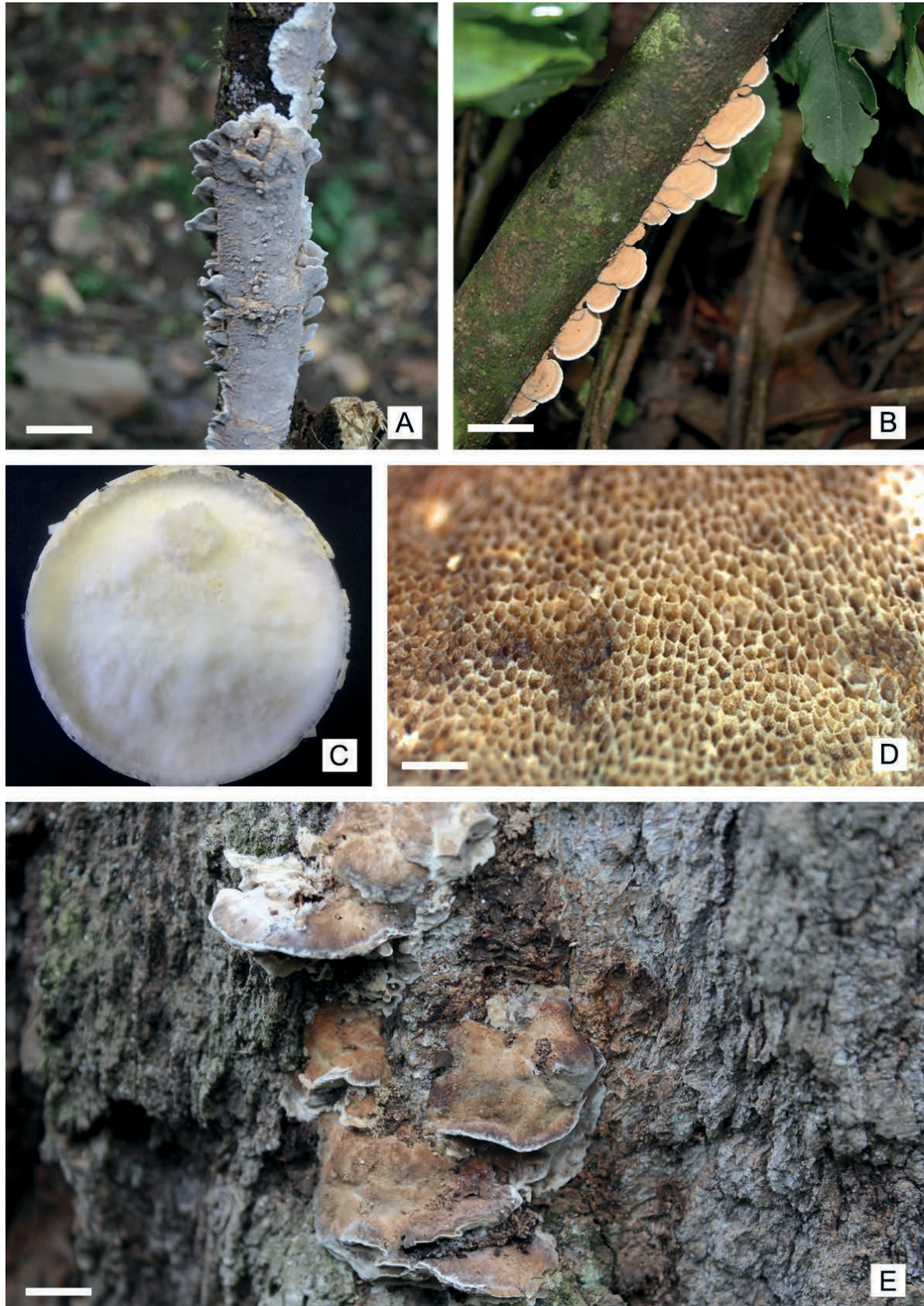
**Description** – Basidiomata annual, sessile, effused-reflexed, with an extended resupinate portion up to 15–18 cm long  $\times$  2.5–3.0 cm wide  $\times$  0.1–0.3 cm thick; pilei minute, imbricated

in vertical substrates or laterally fused on horizontal substrates, up to 0.4–2.5 cm long  $\times$  1.0–4.0 cm wide, coriaceous, flattened, dimidiated to flabelliform; upper surface velvety to finely tomentose and superficially grooved towards the margin, pale golden-brown, unchanged on drying specimens; pileus margin entire, white when fresh to dark brown when dry, sterile, thin, up to 1 mm wide. Context divided into two layers, the upper layer slightly fibrous, cream to pale brown, up to 70–80  $\mu$ m thick, lower layer clearly contrasting at the base of the tubes, waxy and dark grey, up to 40  $\mu$ m thick. Pore surface pale to smoky brown changing to dark grey only in bruised parts; pores shallow, angular, (6–)7–9(–10) per mm; dissepiments slightly lacerated, up to 10–13.4  $\mu$ m thick; tube layer not stratified, up to 0.2 cm deep. No change observed in KOH. Odour absent.



**Figure 3** – Microscopic structure of *Bjerkandera albocinerea*. **A.** Two-layered context. **B.** Hymenium and tramal hyphae with rhomboid crystals. **C.** Basidiospores. Illustrations by V. Motato-Vásquez.





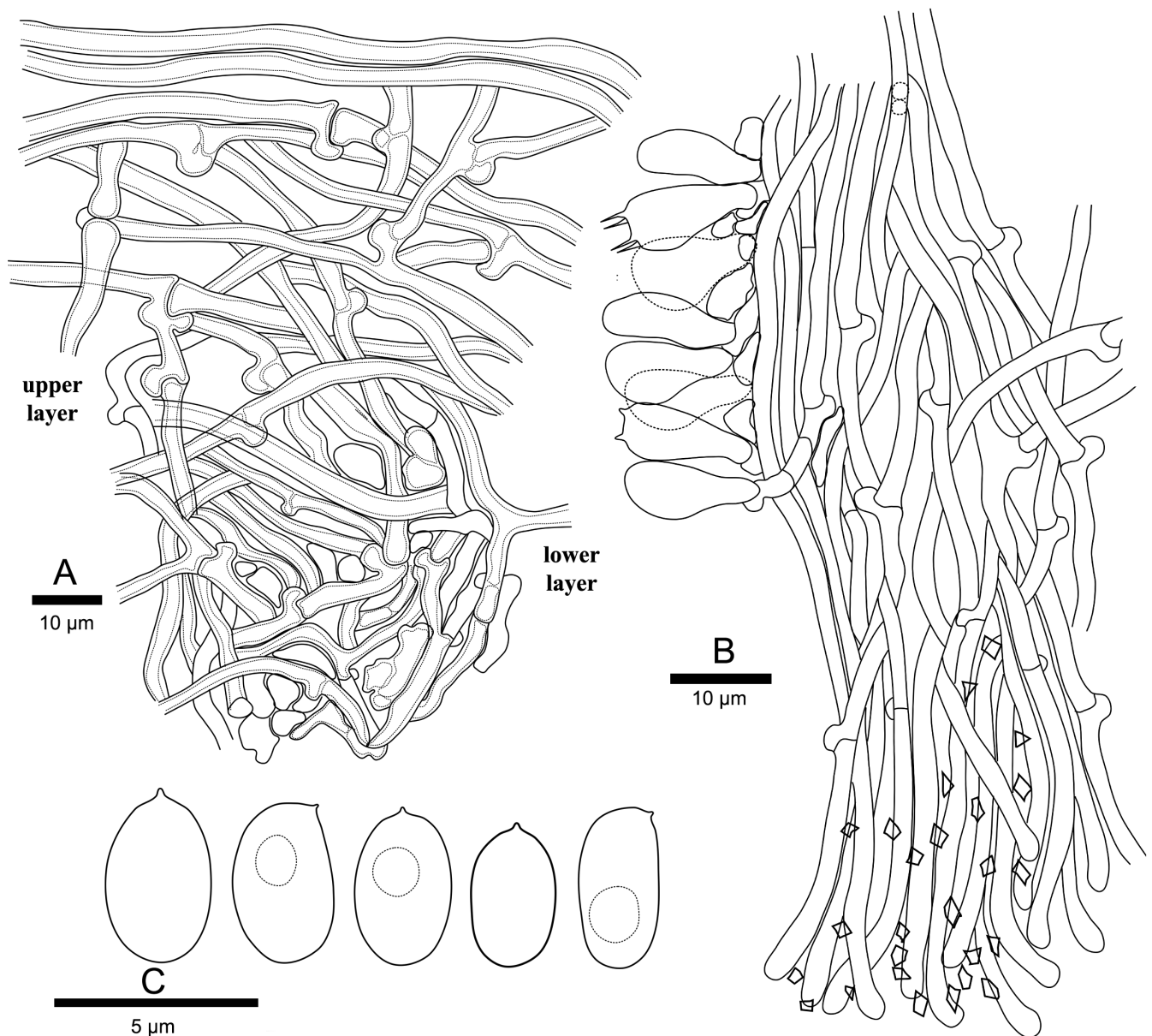
**Figure 4** – Macroscopic features of *Bjerkandera* species. **A–D.** *Bjerkandera mikrofumosa* (SP466878). **A.** Hymenophoral surface. **B.** Pilear surface. **C.** Mycelial growth after six weeks in MEA (MV435, CCIBt). **D.** Poroid surface detail. **E.** Basidiomata of *Bjerkandera fumosa* (SP498907). Photographs by V. Motato-Vásquez. Scale bars: A, B, E = 1 cm; D = 0.5 mm.

Hyphal system monomitic; generative hyphae with clamp connections, CB+, KOH–, IKI–; context hyphae mostly running horizontally but often with a less clear orientation; hyphae in the upper layer hyaline to yellowish, thin- to thick-walled but with a wide lumen, (3.1–)3.7–4.2(–5.0)  $\mu\text{m}$  diam.; in the lower layer hyphae are similar to those in the upper layer but strongly agglutinated. Tramal hyphae hyaline to yellowish, thin to slightly thick-walled, tightly interwoven, 2.2–3.1  $\mu\text{m}$  diam. Cystidia and cystidioles absent. Basidia mostly clavate, 8.4–10.4  $\times$  5–6  $\mu\text{m}$ , with four sterigmata. Basidiospores ellipsoid,  $L' \times W' = (3.38\text{--})3.48\text{--}4.75(4.80) \times (2.23\text{--})2.34\text{--}3.00(3.10)$   $\mu\text{m}$ ,  $L = 4.04$   $\mu\text{m}$ ,  $W = 2.60$   $\mu\text{m}$ ,  $Q' = (1.29\text{--})1.33\text{--}1.79(1.84)$   $\mu\text{m}$ ,  $Q = 1.55$   $\mu\text{m}$  ( $n = 190/6$ ),

hyaline, thin-walled, smooth, often with one or a few droplets, weakly CB+, IKI–.

**Ecology** – Growing on dead hardwood logs and branches in the north of Venezuela, Yungas forests of NW Argentina and the SE part of the Brazilian Atlantic Forest. Based on the high number of collected specimens and those deposited in national collections, we assume it would be a relatively common species to find in those biomes, and it should have a wide distribution along the Amazonian domain.

**Culture characteristics** – Growth rapid, plates covered in one week. Macromorphologically, growing zone very cottony, regular to irregular, white to yellowish; aerial zone characterized by flocculent and villous mycelium, forming



**Figure 5** – Microscopic structure of *Bjerkandera mikrofumosa*. **A.** Two-layered context. **B.** Hymenium and tramal hyphae with rhomboid crystals. **C.** Basidiospores. Illustrations by V. Motato-Vásquez.



Key to accepted species of *Bjerkandera* worldwide

1. Pores 2–5 per mm ..... 2
- 1'. Pores smaller, 6–11 per mm ..... 3
2. Pilear surface white to cream, basidiospores broadly ellipsoid,  $(3.50\text{--})3.74\text{--}5.33\text{--}(5.50) \times (2.77\text{--})2.83\text{--}3.75\text{--}(3.90) \mu\text{m}$  ..... *Bjerkandera atroalba*
- 2'. Pilear surface pale golden brownish, basidiospores ellipsoid to cylindric,  $5.25\text{--}6.76\text{--}(6.93) \times (2.50\text{--})2.53\text{--}3.58\text{--}(3.73) \mu\text{m}$  ..... *Bjerkandera fumosa*
3. Basidiospores subglobose to broadly ellipsoid,  $Q = 1.2$ ,  $(3.60\text{--})3.80\text{--}4.40\text{--}(5.00) \times 3.02\text{--}4.44\text{--}(4.50) \mu\text{m}$ ,  $L = 4.47 \mu\text{m}$ ,  $W = 3.74 \mu\text{m}$  ..... *Bjerkandera centroamericana*
- 3'. Basidiospores oblong-ellipsoid to ellipsoid,  $Q = >1.4$  ..... 4
4. Pores 6–7 per mm, basidiospores subellipsoid,  $L = 4.93 \mu\text{m}$ ,  $W = 2.98 \mu\text{m}$  ..... *Bjerkandera adusta*
- 4'. Pores 7–11 per mm, basidiospores oblong-ellipsoid to ellipsoid ..... 5
5. Pores angular, poroid surface brown to smoky, pilear surface pale golden brown, basidiospores ellipsoid ..... *Bjerkandera mikrofumosa*
- 5'. Pores round, poroid surface dark brownish grey to almost black, pilear surface sordid white to pale cream, basidiospores oblong-ellipsoid to ellipsoid ..... *Bjerkandera albocinerea*

a coriaceous superior layer, submerged zone with white to cream mycelium. Reverse agar whitening. Odour undetermined. Micromorphologically, the growing zone formed by thin-walled simple-septate hyphae and clamped hyphae,  $2.0\text{--}3.0 \mu\text{m}$  diam., the older part of the mat being composed of clamped hyphae; aerial zone formed by clamped, thin to thick-walled and branched generative hyphae,  $3.2\text{--}5.5 \mu\text{m}$  diam. Fibre hyphae not observed. Chlamydospores present in different colonies but un abundant, intercalary and terminal, solitary or several growing together, with slightly thickened walls, usually ellipsoid,  $8.9\text{--}14.5 \times 5.5\text{--}7.5 \mu\text{m}$ .

Species code: 2.4.7.34.36.38.(40).41.53.54.

**Remarks** – *Bjerkandera mikrofumosa* has a very similar morphology to *B. fumosa* and can be distinguished by the fairly smaller basidiomata and small pores (table 3). Microscopically, its basidiospores are ellipsoid ( $Q = 1.55$ ) and small (table 2), whereas in *B. fumosa* they are ellipsoid to almost cylindrical ( $Q = 1.90$ ). Even though specimens of *B. mikrofumosa* have been found in herbaria erroneously identified as *B. fumosa*, both morphological and molecular data support the hypothesis that these species form independent, not closely related lineages within *Bjerkandera*.

**Strains examined (polysporic cultures)** – **Brazil:** São Paulo, São Paulo, Parque Estadual da Cantareira, 8 May 2012, *Motato-Vásquez* 202 (SP, CCIBt4360); São Paulo, São Paulo, Parque Estadual das Fontes do Ipiranga, 21 May 2015, *Motato-Vásquez* 435 (SP, CCIBt4361); São Paulo, São Paulo, Parque Estadual das Fontes do Ipiranga, 30 Nov. 2015, *Motato-Vásquez* 605 (SP, CCIBt4559).

**Additional specimens examined** – **Argentina:** Jujuy, Ledesma, Parque Nacional Calilegua, Mesada de las Colmenas, road to La Lagunita,  $23^{\circ}45'18''\text{S}$ ,  $64^{\circ}51'13''\text{W}$ , 717 m a.s.l., 6 Mar. 2005, *Robledo* 561 (CORD); Jujuy, Ledesma, Parque Nacional Calilegua, road to La Junta,

$23^{\circ}44'12''\text{S}$ ,  $64^{\circ}50'60''\text{W}$ , 800 m a.s.l., 7 Mar. 2005, *Robledo* 436 (CORD); Jujuy, Ledesma, Parque Nacional Calilegua, Abra de Cañas,  $23^{\circ}40'54.8''\text{S}$ ,  $64^{\circ}54'2.4''\text{W}$ , 1702 m a.s.l., 27 Mar. 2007, *Robledo* 1097 (CORD); Jujuy, Ledesma, Parque Nacional Calilegua, road to La Cascada,  $23^{\circ}42'1.5''\text{S}$ ,  $64^{\circ}51'56.8''\text{W}$ , 1082 m a.s.l., 22 May 2007, *Robledo* 1577 & *Robledo* 1644 (CORD); Jujuy, Ledesma, Parque Nacional Calilegua, road to Tataupá,  $23^{\circ}44'12''\text{S}$ ,  $64^{\circ}50'60''\text{W}$ , 800 m a.s.l., 28 Mar. 2007, *Robledo* 1148 (CORD); Jujuy, Ledesma, Parque Nacional Calilegua, road to Tataupá,  $23^{\circ}44'33.3''\text{S}$ ,  $64^{\circ}51'8''\text{W}$ , 745 m a.s.l., 2 Apr. 2008, *Robledo* 1898 (CORD); Salta, Anta, Parque Nacional El Rey, road to Cascada Los Lobitos,  $24^{\circ}41'42''\text{S}$ ,  $64^{\circ}36'43''\text{W}$ , 895 m a.s.l., 9 Mar. 2005, *Robledo* 616 & *Robledo* 1062 (CORD); Salta, Anta, Parque Nacional El Rey, road to Las Chuñas,  $24^{\circ}43'1.5''\text{S}$ ,  $64^{\circ}38'51.5''\text{W}$ , 886 m a.s.l., 24 Mar. 2007, *Robledo* 1012 (CORD); Salta, Sta. Victoria Oeste, Parque Nacional Baritú, Lipeo, road to Las Termas,  $22^{\circ}25'36.9''\text{S}$ ,  $64^{\circ}44'23.1''\text{W}$ , 1155 m a.s.l., 5 May 2007, *Robledo* 1208 (CORD); Salta, Sta. Victoria Oeste, Parque Nacional Baritú, Lipeo, road to Baritú,  $22^{\circ}26'21.6''\text{S}$ ,  $64^{\circ}44'7.8''\text{W}$ , 1222 m a.s.l., 5 May 2007, *Robledo* 1242 (CORD); Salta, Sta. Victoria Oeste, Parque Nacional Baritú, forest of Nogales between Lipeo and Baritú,  $22^{\circ}27'20.8''\text{S}$ ,  $64^{\circ}44'34.5''\text{W}$ , 1653 m a.s.l., *Robledo* 1378 & *Robledo* 1379 (CORD); Tucumán, Trancas, Dique el Cadillal,  $26^{\circ}37'24.5''\text{S}$ ,  $65^{\circ}11'55.6''\text{W}$ , 623 m a.s.l., 18 Feb. 2007, *Robledo* 780 & *Robledo* 796 (CORD); Salta, Sta. Victoria Oeste, Parque Nacional Baritú, road to Las Termas,  $22^{\circ}25'36.9''\text{S}$ ,  $64^{\circ}44'23.1''\text{W}$ , 1155 m a.s.l., 5 May 2007, *Robledo* 1170 (CORD); Salta, Sta. Victoria Oeste, Parque Nacional Baritú, road to Las Termas,  $22^{\circ}25'36.9''\text{S}$ ,  $64^{\circ}44'23.1''\text{W}$ , 1155 m a.s.l., 5 May 2007, *Catania* 3269 (CORD); Tucumán, Trancas, Las Tacanas,  $26^{\circ}17'2.1''\text{S}$ ,  $65^{\circ}31'13.4''\text{W}$ , 1229 m a.s.l., 22 Mar. 2007, *Robledo* 928, *Robledo* 930 & *Robledo* 932 (CORD).



**Brazil:** Rio de Janeiro, along Estrada Dona Castorina, 27 Nov. 1928, *Smith, L.B. s.n.* (LIL); São Paulo, São Paulo, Serra da Cantareira, *Puttemans A. 933* (SP, SP141794); São Paulo, São Paulo, Parque Estadual da Cantareira, 8 May 2012, *Motato-Vásquez MV202* (SP, SP445611); São Paulo, São Paulo, Parque Estadual da Cantareira, 27 Jun. 2012, *Motato-Vásquez, Westphalen & Bolaños MV232* (SP, SP445612), *Motato-Vásquez, Westphalen & Bolaños MV239* (SP, SP445613) & *Motato-Vásquez, Westphalen & Bolaños MV241* (SP, SP445614); São Paulo, São Paulo, Parque Estadual das Fontes do Ipiranga, 21 May 2015, *Motato-Vásquez MV435* (SP, SP466876); São Paulo, São Paulo, Parque Estadual das Fontes do Ipiranga, 30 Nov. 2015, *Motato-Vásquez MV605* (SP, SP466879); São Paulo, São Paulo, Parque Estadual das Fontes do Ipiranga, 9 May 2017, *Gugliotta 1614* (SP, SP466868); São Paulo, São Luiz do Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virginia, 7 May 2015, *Motato-Vásquez MV353* (SP, SP466872) & *Motato-Vásquez MV363* (SP, SP466873), São Paulo, Ribeirão Grande, Parque Estadual Intervales, 5 Feb. 2013, *Motato-Vásquez & Westphalen MV302* (SP, SP445615); São Paulo, Ribeirão Grande, Parque Estadual Intervales, 7 Jun. 2015, *Motato-Vásquez MV433* (SP, SP466875); Rio de Janeiro, Parque Nacional Itatiaia, 26 Nov. 2015, *Motato-Vásquez MV589* (SP, SP466880); Rio Grande do Sul, Nova Roma do sul, Ponta Velha, *Westphalen 527/17* (SP, SP466869); Rio Grande do Sul, Dom Pedro de Alcântara Mato da Cova Funda, 9 Mar. 2008, *Reck 030/08* (ICN, ICN154014); Rio Grande do Sul, Dom Pedro de Alcântara Mato da Cova Funda, 29 Mar. 2008, *Reck 037/08* (ICN, ICN154029).

#### Additional revised taxa

*Bjerkandera adusta* (Willd.) P.Karst. (Karsten 1879). – *Boletus adustus* Willd. (Willdenow 1787).

**Specimens examined – Finland:** Helsinki, Biological Stattio Lemmi, University of Helsinki, 18 Sep. 2017, *Motato-Vásquez, V., Miettinen, O., Niemelä T. MV973* (SP, SP498906); Helsinki, Kaisaniemi, Botanical Garden Helsinki, *Motato-Vásquez, V. MV993* (SP, SP498909) & *MV997* (SP, SP498910).

*Bjerkandera atroalba* (Rick) Westph. & Tomšovský (Westphalen et al. 2015). – *Polyporus atroalbus* Rick (Rick 1935). – *Tyromyces atroalbus* (Rick) Rajchenb. (Rajchenberg 1987).

**Type** – Brazil: Rio Grande do Sul, Pouso Novo, 1932, *J. Rick s.n.* (lectotype (of *P. atroalbus*!): PACA, PACA18397).

**Additional specimens examined – Brazil:** São Paulo, São Paulo, Parque Estadual da Cantareira, 6 Dec. 2011, *Motato-Vásquez MV59* (SP, SP445629); São Paulo, São Paulo, Parque Estadual da Cantareira, 7 Mar. 2012, *Motato-Vásquez 158* (SP, SP445629); São Paulo, São Paulo, Parque Estadual da Cantareira, 30 Jul. 2012, *Motato-Vásquez 266* (SP, SP445672).

*Bjerkandera centroamericana* Kout, Westphalen & Tomšovský (Westphalen et al. 2015).

**Type** – Mexico: Veracruz, San Andrés Tuxtla municipality, near Montepío, dead hardwood, 18.575000°N, 095.040833°W; 14 Oct. 2006, *Jiří Kout 0610/A7* (holotype: SP, SP466336!).

*Bjerkandera fumosa* (Pers.) P.Karst. (Karsten 1879). – *Boletus fumosus* Pers. (Persoon 1801).

**Specimens examined – Czechia [“Czechoslovakia”]:** Pruhonice pr. Praha, Bohemia centr., in horto publico castelli, ad codicem cf. *Ulmus laevis*, 13 Nov. 1970, *F. Kotlaba s.n.* (CORD).

**Finland:** Helsinki, Biological Stattio Lemmi, University of Helsinki, 18 Sep. 2017, *Motato-Vásquez, V., Miettinen, O., Niemelä T. MV974* (SP, SP498907).

**United States:** Kansas, Topeka, 24 Nov. 1983, *s. coll. s.n.* (NY, 1752889); Bartholomew, Nov. 1892, *s. coll. s.n.* (NY, 1752888); Massachusetts, Norwood, Oct. 1936, *D.H. Linder & D. Darker s.n.* (NY); Massachusetts, Rockport, on elm stump, 18 Nov. 1887, *s. coll. s.n.* (NY, 333864, NY, 333921).

#### DISCUSSION

In our phylogenetic analysis, we focus on the evolutionary relationships of the genus *Bjerkandera*, one of the few polyporoid genera of the Phanerochaetaceae family. The overall topology recovered of the *Bjerkandera* clade was widely consistent with previous studies (fig. 1) (Floudas & Hibbett 2015; Westphalen et al. 2015; Miettinen et al. 2016; Justo et al. 2017). The relationship between *Bjerkandera* and *Ceriporiopsis carnegieae* as sister taxa was recovered with strong support (PP = 1.0, BS = 100) in accordance with results shown by Justo et al. (2017).

*Ceriporiopsis carnegieae* was originally described as *Poria carnegieae* by Baxter (1941) from southern Arizona, as an important agent of decay on the saguaro cactus [*Carnegiea gigantea* (Engelm.) Britton & Rose]. Macromorphologically, *C. carnegieae* is characterized by the resupinate and effused basidiomata, poroid surface, deeply cracked in older specimens, margin finely fimbriate or fibrillose with very delicate mycelial strands, and subiculum less than 1 mm thick. Micromorphologically, it is characterized by the monomitic hyphal system, thin-walled clamped generative hyphae and oblong to short-cylindric basidiospores. In studies of pure cultures, Gilbertson & Canfield (1972) found that the decay caused by this species typically corresponds to white rot fungi but gives no oxidase reaction on gallic and tannic acid media or with gum guaiac solution; additionally, mating tests revealed a heterothallic nuclear behaviour and bipolar type of mating system. The authors discussed that the key code based on Nobles (1965) places the species in the same group of *B. adusta*; however, they suggested that due to morphological differences between them, these species should be placed in different genera. Our analysis showed that *C. carnegieae* is phylogenetically closer to *Bjerkandera* species than to *C. gilvescens* (Bres.) Domański (the type species of *Ceriporiopsis* Domański), which is nested in the family Meruliaceae. Although these data support the hypothesis

that *Ceriporiopsis* is not a suitable genus for the species, we prefer to keep *C. carnegieae* separate from *Bjerkandera* until a more detailed study can be made including a larger taxon sampling and additional morphological and molecular evidence.

In this study, we recognized *Bjerkandera* as a monophyletic genus (PP = 1.0, BS = 99) based on the phylogenetic analysis of sequences from the ribosomal ITS and nLSU regions. *Bjerkandera atroalba* is recovered within clade 1 (fig. 1) as sister taxon of *B. centroamericana* (PP = 0.99, BS = 95), in accordance to the topology reported by Westphalen et al. (2015). Both species are very similar morphologically. They are distinguished by the size of the pores (2–5 per mm in the former and 7–11 per mm in the latter) and, microscopically, by the basidiospore shape (slightly wider spores in *B. centroamericana*, table 2).

*Bjerkandera mikrofumosa*, the third member of clade 1, was recovered as a monophyletic lineage (PP = 1.0, BS = 100). This is the first time that the species has been included in a phylogenetic analysis. Although the type specimen of *B. mikrofumosa* was not sequenced, comparative morphological analyses of the type and the sequenced specimens from Argentina and Brazil showed no differences. Additionally, we studied several Neotropical specimens from different herbaria, mainly collected in the Atlantic Forest of SE Brazil and of NW Argentine Yungas, that were identified as *B. fumosa*. We came to address all these examined specimens as *B. mikrofumosa*. *Bjerkandera fumosa* has been reported with a high intraspecific morphological variability, which is probably the cause of erroneous identifications. In our study we use different lines of evidence (morphological, molecular and cultural) and we find that both species form independent, not closely related lineages within *Bjerkandera*. Through rigorous examination and comparison, both species can be morphologically differentiated by the basidiomata, pores and basidiospores size and shape, which are bigger in *B. fumosa* (tables 2, 3). *Bjerkandera mikrofumosa* can be differentiated from *B. centroamericana* by the pilear and poroid surface colour (table 3). Microscopically, the basidiospores of *B. centroamericana* are slightly wider, subglobose to broadly ellipsoid ( $Q' = 1.20$ ), whereas in *B. mikrofumosa* are mainly ellipsoid ( $Q' = 1.55$ , table 2).

All species in clade 1 have a Neotropical distribution. Some specimens of *B. atroalba* have been recorded in the SE of the United States (Westphalen et al. 2015); however, more molecular data on these specimens is necessary to clarify if *B. atroalba* has a wider distribution on the American continent or if the North American specimens represent a different lineage.

In clade 2 (fig. 1), the conventionally accepted evolutionary relationship of *B. adusta* and *B. fumosa* as sister taxa has changed due to the inclusion of *Bjerkandera albocinerea*, the new Neotropical species described here. The new species forms a highly supported lineage as the sister taxon of *B. adusta* (PP = 1.0, BS = 100). Both species can be easily differentiated by the slightly bigger pores (6–7 per mm, table 2) and basidiospores of *B. adusta* (table 3).

*Bjerkandera adusta*, originally described from temperate Europe, has been extensively recorded in the Neotrop-

ics (Ryvarden 2000; Ryvarden & Iturriaga 2001; Robledo et al. 2003; Baltazar & Gibertoni 2009). Westphalen et al. (2015) included in their phylogenetic analysis sequences of *B. adusta* from temperate Argentina and from different specimens of an endophytic fungus isolated from *Hevea brasiliensis* leaves in Peru (Martin et al. 2015; Yuan et al. 2010). The authors reported that these sequences are almost identical to those of European specimens and form a strongly supported clade with *B. adusta*. So far, it seems that *B. adusta* is the only species of the genus with a worldwide distribution. However, it is still necessary to obtain additional molecular data from Neotropical specimens identified as *B. adusta* to properly assess their identity.

*Bjerkandera fumosa* was recovered at the base of clade 2 with full support (PP = 1.0, BS = 100). Superficially, the species is similar and easily confused with *B. adusta*, especially when basidiomata are immature. Nevertheless, experts have already documented several useful morphological characters to differentiate both species (see tables 2 and 3). Recent studies have shown that the morphological diversity across the whole distributional area of both species may be high and worth studying in detail. Jung et al. (2014) studied the intraspecific variation between ITS sequences from Korean specimens of *B. adusta* and *B. fumosa*. The authors reported that both species show little intraspecific variation (0.0–0.55% in the former and 0.0% in the latter), whereas interspecific variation is high (5.15–5.89%), indicating that DNA data are useful to distinguish *B. adusta* from *B. fumosa*. This information is also useful for accurate identification, especially when morphological characters are not suitable for analysis (e.g., cultures or fragments from dried specimens).

As documented above, *B. fumosa* and some of its synonyms have been widely recorded from Neotropical biomes. Recently, Zmitrovich et al. (2016) listed two forms of *B. fumosa* from Cuba recorded by Murrill (1907). The authors suggested that *B. terebrans* (Berk. & M.A.Curtis) Murrill is probably a form of *B. fumosa* with a stipe-like base whereas *B. subsimulans* Murrill may actually be an *Abortiporus* Murrill species. Unfortunately, sequences of *B. fumosa* available at GenBank are mostly from temperate regions; and although the data shown in our study do not allow to define the specific limits for *B. fumosa*, there is a strong evidence, at least in the Neotropics, pointing out that this species may encompass a species complex, as clearly exemplified by *B. mikrofumosa*. Future studies should invest efforts to re-evaluate the diagnostic characters of *B. fumosa*, to examine and recollect Neotropical specimens in type localities, to compare type specimens, to obtain new molecular data and to test the evidence under the light of phylogenetic inference.

This study provided the most extensive documentation of the species diversity within *Bjerkandera* to date. Also, it contributes to the expansion of the species-level phylogeny of the genus in the Neotropics and worldwide with morphological and molecular evidence, providing a phylogenetic backbone for the interspecific relationships within the genus. In addition, our results indicate that the number of taxa in *Bjerkandera* has been underestimated by morphological evidence, and may actually be greater than traditionally accepted.

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