Phytotaxa 494 (1): 042–058
https://www.mapress.com/j/pt/

Article

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

https://doi.org/10.11646/phytotaxa.494.1.2

Taxonomic and nomenclatural novelties in *Leucoagaricus* (Agaricaceae) from Brazil

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Abstract

Leucoagaricus nzumbae sp. nov. (Agaricaceae) is described based on morphological and molecular data from Teresópolis, Rio de Janeiro, Brazil. This species is characterized by the delicate small basidiomes that turn completely lilac when dried, brownish color of the pileus surface, and trichodermal elements with intracellular and parietal brown pigments of the pileus covering. A lectotype and an epitype are designated for *Leucoagaricus gongylophorus*, a symbiotic fungus of leaf-cutting ants. Full description, nomenclatural notes, and illustrations of fresh basidiomes *in situ* and of the main macro-and micromorphological features of both species are provided.

Keywords: Agaricales, *Lepiota s.l.,* Tropics

Introduction

Leucoagaricus Locq. *ex* Singer (1948) includes widely distributed saprotrophic mushrooms that colonize soil, with greater number of species in the tropics than in the temperate zone (Vellinga 2004a). Around 135 species are known (He *et al.* 2019), which are characterized by the white to cream spore print, entire or slightly striate but not plicate pileus margin, free lamellae, metachromatic basidiospores in Cresyl blue, and absence of clamp connections and pseudoparaphyses (Singer 1948, 1986).

Leucoagaricus is placed in Agaricaceae based on its agaricoid habit and basidiospore morphology (Singer 1948, 1986). Molecular studies show that the genus may not be monophyletic and is within *Leucocoprinus* Patouillard (1888) (Johnson & Vilgalys 1998, Johnson 1999, Vellinga 2004b, Vellinga *et al.* 2011). However, taxonomic, and phylogenetic relationships among some species of *Leucoagaricus* and *Leucocoprinus* remain unclear due to the large number of species in the clade and low representation in molecular studies (Vellinga 2004b, Vellinga *et al.* 2011).

During fieldwork in the evergreen Atlantic Forest in Teresópolis, Rio de Janeiro, Brazil, two remarkable species of *Leucoagaricus* were found. *Leucoagaricus nzumbae* is proposed as a new species based on morphological and molecular data. *Leucoagaricus gongylophorus* (Möller 1893: 70) Singer (1986: 477) is a rarely fruiting and noteworthy species that is cultivated by attine ants (Attini, Formicidae, Hymenoptera) and is recorded for the first time for Rio de Janeiro State. In this paper, we provide taxonomic comments, georeferenced data for the collection locations and illustrations of both species. The typification of *Leucoagaricus gongylophorus* is discussed and proposed, and a sequence from a basidiome is provided for the first time for this species.

Accepted by Else Vellinga: 27 Jan. 2021; published: 31 Mar. 2021

Material and methods

Sampling and morphological studies

The collections included in this work were made in the Brazilian Atlantic Forest according to the methods laid out by Lodge *et al.* (2004). Macroscopic characters noted from fresh specimens follow Lodge *et al.* (2004) and the color annotations follow Kornerup & Wanscher (1978; e.g., 6C4). The specimens were dried using an electric dryer at 40°C for approximately 8h (Lodge *et al.* 2004). Microscopic studies were based on freehand sections of dry material, mounted on slides with water, 3% KOH, or 3% KOH plus Congo red, Cresyl blue or Melzer's reagent (Largent 1977, Singer 1986). Photomicrographs were obteined using a Zeiss Axioskope equipped with AxioCam MRm digital camera and analyzed with the AxioVision Rel.4.6 software. At least 20 measurements of each microstructure were made for each specimen. Terminology follows Vellinga (1988) and Vellinga & Noordeloos (2001). The abbreviation *L.* is used for *Lepiota* (Pers.: Fr.) Gray (1821) and *La.* for *Leucoagaricus*. Q indicates the range of the quotient of length and width of the basidiospores (Largent *et al.* 1977, Vellinga 1988). The collections were deposited in the RB herbarium at the Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil, or otherwise noted. Herbarium abbreviations follow Thiers (continuously updated).

DNA extraction, primers, PCR and sequencing

A small piece of the fresh basidiomes was preserved in silica gel for DNA extraction, which was done using the CTAB method (Dentinger *et al.* 2010). Optimal dilutions of the DNA were used to amplify the internal transcribed spacer (ITS). PCR amplifications were made with the previously described primers ITS1F and ITS4 (White *et al.* 1990, Gardes & Bruns 1993) in an Eppendorf MasterCycler thermal cycler. The PCR products were cleaned and sequenced by Macrogen Inc. Sequence chromatograms were corrected using the software Geneious v.6.1.8 (http://www.geneious.com, Kearse *et al.* 2012) and the sequences were deposited in GenBank (accession numbers MT605380–MT605383).

Phylogenetic analyses

Our analysis included four newly generated ITS sequences and 77 were retrieved from GenBank (Table 1). The ingroup includes representatives of the Leucoagaricus/Leucocoprinus clade. The sequences chosen for comparison were based on results of BLAST search for the newly generated ITS sequences with zero e-value. In addition, were included sequences of *Leucoagaricus* species which exhibit a color change when damaged and dried (Liang *et al.* 2010; Vellinga 2010, Vellinga *et al.* 2010, Vizzini *et al*. 2017, Sysouphanthong *et al.* 2018, Latha *et al.* 2020), those related to *La. gongylophorus* and a number of attine ant cultivars from previous phylogenetic studies (Mueller *et al.* 1998, Vellinga 2004, Vellinga & Davis 2006, Ortiz *et al.* 2008, Vo *et al.* 2009, Muñoz *et al*. 2015), and some representative species of *Leucoagaricus* sect. *Rubrotincti* Singer (Ge *et al*. 2015, Hussain *et al.* 2018, Ullah *et al.* 2020). Also four ITS sequences from fungus ants' gardens of *Acromyrmex coronatus* (Genbank accession number MN473881), *Acromyrmex heyeri* Forel (Genbank accession number KJ531208), *Acromyrmex laticeps* Emery (Genbank accession number AY642807), and *Acromyrmex striatus* Roger (Genbank accession number MK685751), each from a different Brazilian biome (Cerrado, Pampa, Amazonian, and Atlantic Forest, respectively) were incorporated. Four ITS sequences of *Lepiota* species were included in the ingroup because they are in the *Leucoagaricus/Leucocoprinus* clade even though the new combinations into *Leucoagaricus* have not yet been made (see Table I). Three sequences of *Agaricus* Linnaeus (1753) were selected as the outgroup.

The alignments were made using MAFFT v. 7, with the E-INS-i strategy (Katoh & Standley 2013), and then manually adjusted with AliView (Larsson 2014). The dataset was divided into three data partitions: ITS1, 5.8S, ITS2. Maximum likelihood (ML) analyses were conducted using Standard RAxML version 8.2.11 (Stamatakis 2014). The ML analyses involved 100 ML searches, each one starting from one randomized step-wise addition parsimony tree, under a GTRGAMMA model, with all other parameters estimated by the software. Individual alpha-shape parameters, GTR rates, and empirical base frequencies will be estimated and optimized for each partition through the-q option. To verify the reliability of the nodes, multi-parametric bootstrapping replicates under the same model were computed, allowing the program to halt bootstrapping automatically using the autoMRE option (-f a-m GTRGAMMA-p-x-q-#autoMRE). A branch was considered strongly supported if it had bootstrap support (BS) ≥ 90% and moderately supported if it had BS ≥ 70%.

TABLE 1. Specimens and sequences used for the molecular analyses. The sequences generated in this work are in bold.

Taxon	Voucher	Country	Genebank accession number
Agaricus rufoaurantiacus	JBSD126476	Dominican Republic	MF511127
Agaricus rufoaurantiacus	JBSD126479	Dominican Republic	MF511135
Agaricus **sp.**	**CHC281**	**Brazil**	**MT605383**
Lepiota **cf.** ***abruptibulba***	PA156	Panama	AF079732
Lepiota decorata	L.L. Norvell 2051224	U.S.A.	GU136197
Lepiota flammeotincta	ecv3315	U.S.A.	GU136165
Lepiota flammeotincta	DUKE-JJ97	Costa Rica	U85331
Lepiota fuliginescens	ecv3219	U.S.A.	GU136186
Lepiota oculata	ecv3100	U.S.A.	EU141947
Lepiota roseolivida	ecv2990	U.S.A.	EF121816
Lepiotaceae sp.	BR006	Brazil	EF527287
Lepiotaceae sp.	PA341	Panama	AF079747
Lepiotaceae sp.	BR032	Brazil	EF527311
Leucoagaricus adelphicus	ecv2584 Holotype	U.S.A.	AY243623
Leucoagaricus adelphicus	ecv2772 Paratype	U.S.A.	AY243624
Leucoagaricus amanitoides	R.M. Davis Paratype	U.S.A.	EF080871
Leucoagaricus amazonicus	A. Ortiz 162841 Holotype	Colombia	EU940371
Leucoagaricus asiaticus	LAH10012012 Holotype	Pakistan	KP164971
Leucoagaricus atroazureus	HKAS42670 Holotype	China	EU416301
Leucoagaricus badius	SH148 Holotype	Pakistan	KU647736
Leucoagaricus barssii	ecv2342	Netherlands	AF295931
Leucoagaricus brunneus	Z. Ullah LS4 Holotype	Pakistan	MH990662
Leucoagaricus callainitinctus	CAL 1799 Holotype	India	MT108797
Leucoagaricus **cf.** ***coerulescens***	Mushroom Observer 115977	Mexico	MF629828
Leucoagaricus croceobasis	AH-40434 Holotype	Spain	KF853414
Leucoagaricus cupresseus	J.&A. Guinberteau 99121300	Greece	AY243632
Leucoagaricus dacrytus	R.B. Balsley 1084 Holotype	U.S.A.	GU903309
Leucoagaricus dyscritus	ecv3956 Holotype	U.S.A.	GU136180
Leucoagaricus erythrophaeus	ecv3243 Holotype	U.S.A.	GQ258469
Leucoagaricus flammeotinctoides	ecv3729 Holotype	U.S.A.	GU136173
Leucoagaricus flammeotinctoides	ecv3247 Paratype	U.S.A.	GU136174
Leucoagaricus flavovirens	HKAS29580 Holotype	China	EU416293
Leucoagaricus gaillardii	MCVE16517	Italy	GQ329064
Leucoagaricus georginae	ecv2238	Netherlands	AY176413
Leucoagaricus gongylophorus	Isolate O	Brazil	AY642807
Leucoagaricus gongylophorus	Isolate LABIMIC LG014	Brazil	KJ531208
Leucoagaricus gongylophorus	Isolate SES090303	Brazil	MK685751
Leucoagaricus gongylophorus	Isolate RB02	Brazil	MN473881
Leucoagaricus gongylophorus	**FTF192 Epitype**	**Brazil**	**MT605382**
Leucoagaricus hesperius	ecv3515 Holotype	U.S.A.	GU139788
Leucoagaricus hesperius	ecv3431 Paratype	U.S.A.	GU139790
Leucoagaricus houaynhangensis	PS2014-1448 Holotype	Lao	KX640915
Leucoagaricus idae-fragum	MCVE29362	Italy	MF768439
Leucoagaricus idae-fragum	LIP97113001 Holotype	France	MF768441
Leucoagaricus infuscatus	ecv3506 Holotype	U.S.A.	EU141944
Leucoagaricus ionidicolor	ecv2280	Netherlands	AY176415

......*continued on the next page*

TABLE 1 (Continued)

Taxon	Voucher	Country	Genebank accession number
Leucoagaricus jubilaei	J.&A. Guinberteau 99101101	France	AY243635
Leucoagaricus lateritiopurpureus	LE289361 Epitype	Russia	JX133173
Leucoagaricus leucothites	ecv2050	Netherlands	AF482865
Leucoagaricus melanotrichus	ecv2262	Netherlands	AY176417
Leucoagaricus nympharum	C. Bas 9269	Germany	AF482868
Leucoagaricus nzumbae	**CHC348 Holotype**	**Brazil**	**MT605380**
Leucoagaricus nzumbae	**CHC349 Paratype**	**Brazil**	**MT605381**
Leucoagaricus ophthalmus	ecv2536 Holotype	U.S.A.	EU141953
Leucoagaricus orientiflavus	HKAS54260 Holotype	China	GU084262
Leucoagaricus pakistaniensis	SJF13 Holotype	Pakistan	KU647727
Leucoagaricus pardalotus	ecv3313 Holotype	U.S.A.	GQ258479
Leucoagaricus pilatianus	J.&A. Guinberteau 99101608	France	AY243626
Leucoagaricus proximus	LE262861 Holotype	Russia	JX133172
Leucoagaricus pyrrhophaeus	ecv3268 Holotype	U.S.A.	GU136199
Leucoagaricus pyrrhulus	ecv3306 Holotype	U.S.A.	GQ258474
Leucoagaricus sabinae	ANGE305 Paratype	Dominican Republic	KM983666
Leucoagaricus sabinae	ANGE306 Holotype	Dominican Republic	KM983667
Leucoagaricus subcrystallifer	Z.W. Ge 878 Holotype	China	KP096236
Leucoagaricus subpurpureolilacinus	Z.W. Ge 406 Holotype	China	KP096233
Leucoagaricus tangerinus	HKAS50036 Holotype	China	KF501437
Leucoagaricus tener	ecv2261	Netherlands	AY176444
Leucoagaricus truncatus	Z.W. Ge 793 Holotype	China	KP096235
Leucoagaricus umbonatus	LAH-SHL1 Holotype	Pakistan	KU647737
Leucoagaricus variicolor	AH40328 Holotype	Spain	JX880030
Leucoagaricus viridariorum	AH46526 Holotype	Spain	KU041689
Leucoagaricus viridiflavus	AK80a Neotype	India	GU574745
Leucoagaricus viridiflavus	TNS Kasuya B620	Japan	KF963609
Leucoagaricus viriditinctus	R.P.J. de Kok F61	Indonesia	AF482873
Leucoagaricus viriditinctus	HKAS 50033	China	EU419375
Leucoagaricus wychanskyi	H.A. Huijser	Netherlands	AF482874
***Leucoagaricus* sp.**	ecv2484	U.S.A.	GU136182
***Leucoagaricus* sp.**	ecv3723	U.S.A.	GU136200
***Leucoagaricus* sp.**	ecv3757	U.S.A. (Hawaii)	MN582746
***Leucoagaricus* sp.**	ecv3754	U.S.A. (Hawaii)	MN582747
***Leucoagaricus* sp.**	ecv3634	Thailand	MN582750
Leucocoprinus* cf. *zamurensis	PA415	Panama	AF079753
Leucocoprinus* cf. *zamurensis	PA408	Panama	EU561487

Bayesian inference (BI) analyses were made using the software MrBayes 3.2.6 (Ronquist & Huelsenbeck 2003). These analyses were implemented by four independent runs, each one starting from random trees, with four simultaneous independent chains, and 5,000,000 generations were performed, keeping one tree every 1,000th generation. Four rate categories were used to approximate the gamma distribution, and the nucleotide substitution rates were fixed to the estimated values. All the parameters were estimated separately for the individual partitions. Of all trees sampled, 25% were discarded as burn-in and checked by the convergence criterion (frequencies of average standard deviation of split <0.01) in Tracer v.1.7.1 (Rambaut & Drummond 2018). The remaining trees were used to reconstruct a 50% majority-rule consensus tree and to estimate Bayesian posterior probabilities (hereafter BPP) of the branches. A branch was considered strongly supported if it had a BPP ≥ 0.95 and moderately supported if it had a BPP ≥ 0.8. The trees produced were adjusted with FigTree v1.4 (Rambaut 2012).

Results

Phylogenetic analyses

The ITS data set consisted of 81 sequences and 997 characters, 510 from ITS1, 158 from 5.8S and 329 from ITS2. There was no incongruence between the ML and the BI analyses, and only the ML tree with both BS and BPP values is shown in Figure 1. *Leucoagaricus nzumbae* were retrieved in a well-supported clade (BS= 96 %, BPP= 1). *Leucoagaricus gongylophorus* appears in a long branch into a clade moderately supported only by the posterior probability (BS= 23 %, BPP= 0.81).

Taxonomy

***Leucoagaricus gongylophorus* (Möller) Singer** (1986: 477) (Figs 2, 3A–B, 4A–D, 5A–B) ≡*Rozites gongylophorus* Möller ≡*Rozites gongylophora* Möller *orth. var.* ≡*Pholiota gongylophora* (Möller) Saccardo (1895: 152) ≡*Leucocoprinus gongylophora* (Möller) Heim (1957: 293) ≡*Pholiota gongylophora* (Möller) Rick (1961: 391), *nom. superfl. et illeg.*

Type Lectotype [designated here]:—BRAZIL [Icon]: Tab. V, Fig 1–12, *in* Möller 1893.

Type Epitype [designated here]:—BRAZIL, Rio de Janeiro: Teresópolis, Parque Nacional da Serra dos Órgãos, left side of the entrance gate to Mozart Catão trail, on an active nest of an undetermined species of *Acromyrmex* Mayr, 22°27'06.7"S, 42°59'29.1"W, 08 November 2017, *Heisecke et al., C.H.C. 463* (RB!, duplicate FLOR!).

Basidiome pluteoid. Pileus easily detachable from stipe, 80–160 mm diameter, convex to plano-convex; surface dry, smooth, dull red to greyish red (10C3, 10C4), entire at the center then splitting radially and forming fibrillose appressed to uplifted scales (10C5) on pinkish white background; margin minutely sulcate to appendiculate, straight, exceeding the lamellae; context 3 mm thick, white, reddish brown when damaged. Lamellae 3–4 mm, free, ventricose, white to pinkish white, yellowish when old; edge entire, concolorous with the sides. Stipe 95–250 × 9.5–35 mm, more than 2/3 buried in the substrate, central, cylindrical, fistulose; surface punctate-fibrillose, with appressed scales bellow the annulus, white to pinkish white, changing to yellowish to dark brown when damaged; base attached to a compact mycelial mass underground in an active leaf-cutting ant garden. Annulus superior, membranous, well-developed, mobile, easily detachable, descending, white with brown edge. Odor sweet, slightly pungent, pleasant, like ripe fruit or flowers when fresh, bread-like when dry.

Basidiospores of two types: 5.5–8 × 4.2–5.9 µm (Q = 1.1–1.7), subglobose to oblong, ovoid to amygdaliform in side view and ellipsoid in front view; less frequently larger, 9.5–15.2 × 4.6–6.8 µm (Q = 1.8–2.4), oblong to subcylindric; both types guttulate, yellowish to hyaline in water and KOH, dextrinoid, metachromatic, thick-walled, with an inconspicuous germ pore. Basidia 26.6–37.3 × 8.2–12 µm, clavate, frequently 4-spored, but some 1-or 2-spored. Cheilocystidia 27.9–53.7 × 9.2–16.9 µm, ventricose-rostrate to clavate, thin-walled. Pleurocystidia absent. Pseudoparaphyses absent. Hymenophoral trama subregular; subhymenium cellular. Pileus covering made up of interwoven, cylindrical to slightly articulate, repent hyphae, with reddish to pinkish intracellular content. Abundant oleiferous hyphae present in all parts of the basidiomes. Clamp connections absent.

Additional specimens examined:—BRAZIL. Santa Catarina: Florianópolis, Parque Municipal do Córrego Grande, pau-jacaré trail, on an active nest of an undetermined species of *Acromyrmex* Mayr, 27°35'55.0"S, 48°30'36.0"W, 20 m, 15 March 2016, *Linhares et al., F.T.F. 192* (FLOR, duplicate RB).

Distribution and Habitat:—Caribbean, South and Central America (Möller 1893, Saccardo 1895, Bailey 1920, Heim 1957, Weber 1958, 1966, 1972, Kreisel 1972, Pagnocca *et al.* 2001, Schultz & Brady 2008, Solomon *et al.* 2019). Always in association with leaf-cutting ants of the genera *Acromyrmex* and *Atta* Fabricius (Higher-Attini), so the occurrence of *La. gongylophorus* is limited to the distribution of the ant partner. Usually only registered as the anamorphic phase, especially in active nests. Basidiomes caespitose, in inactive and active nests.

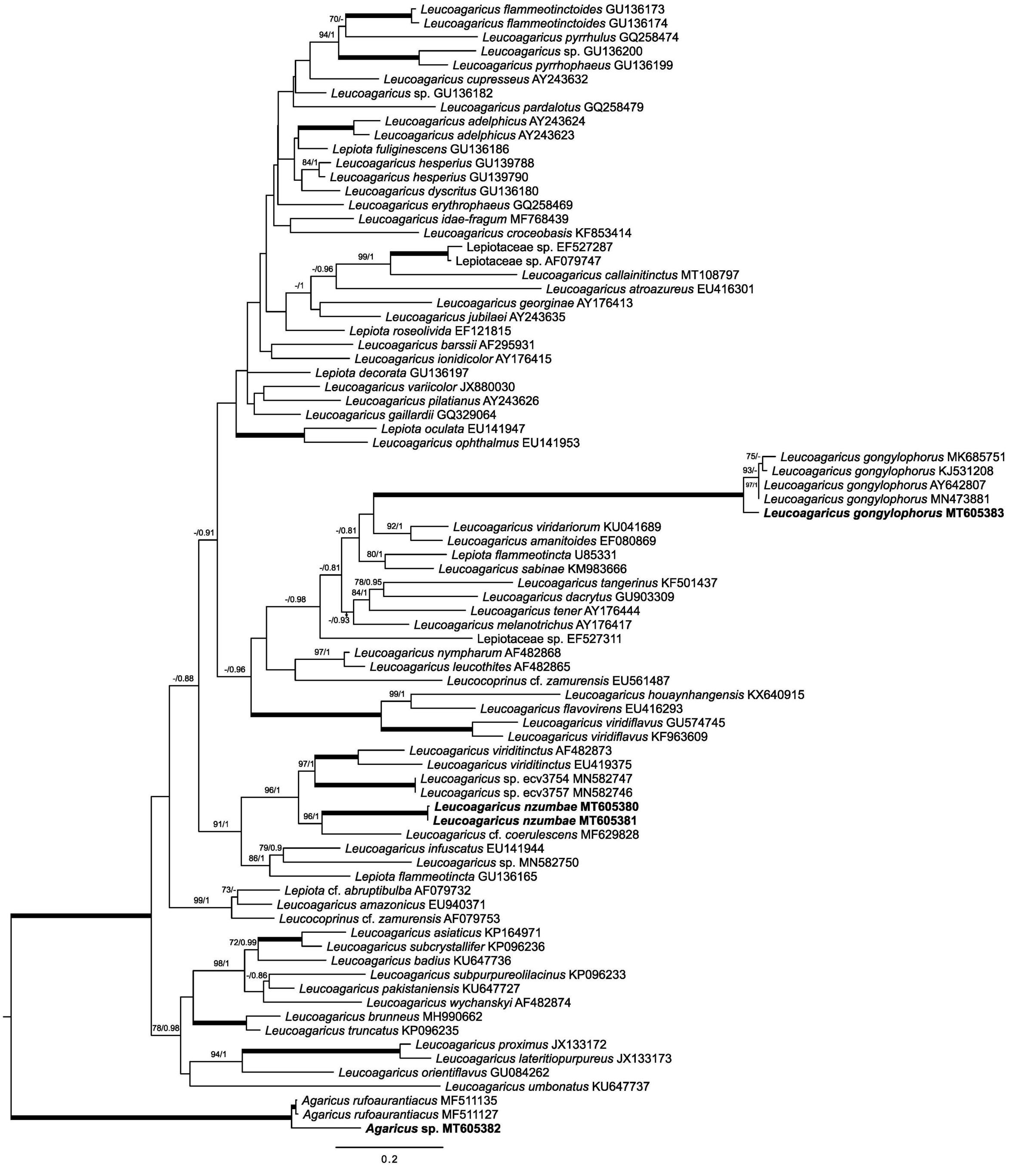
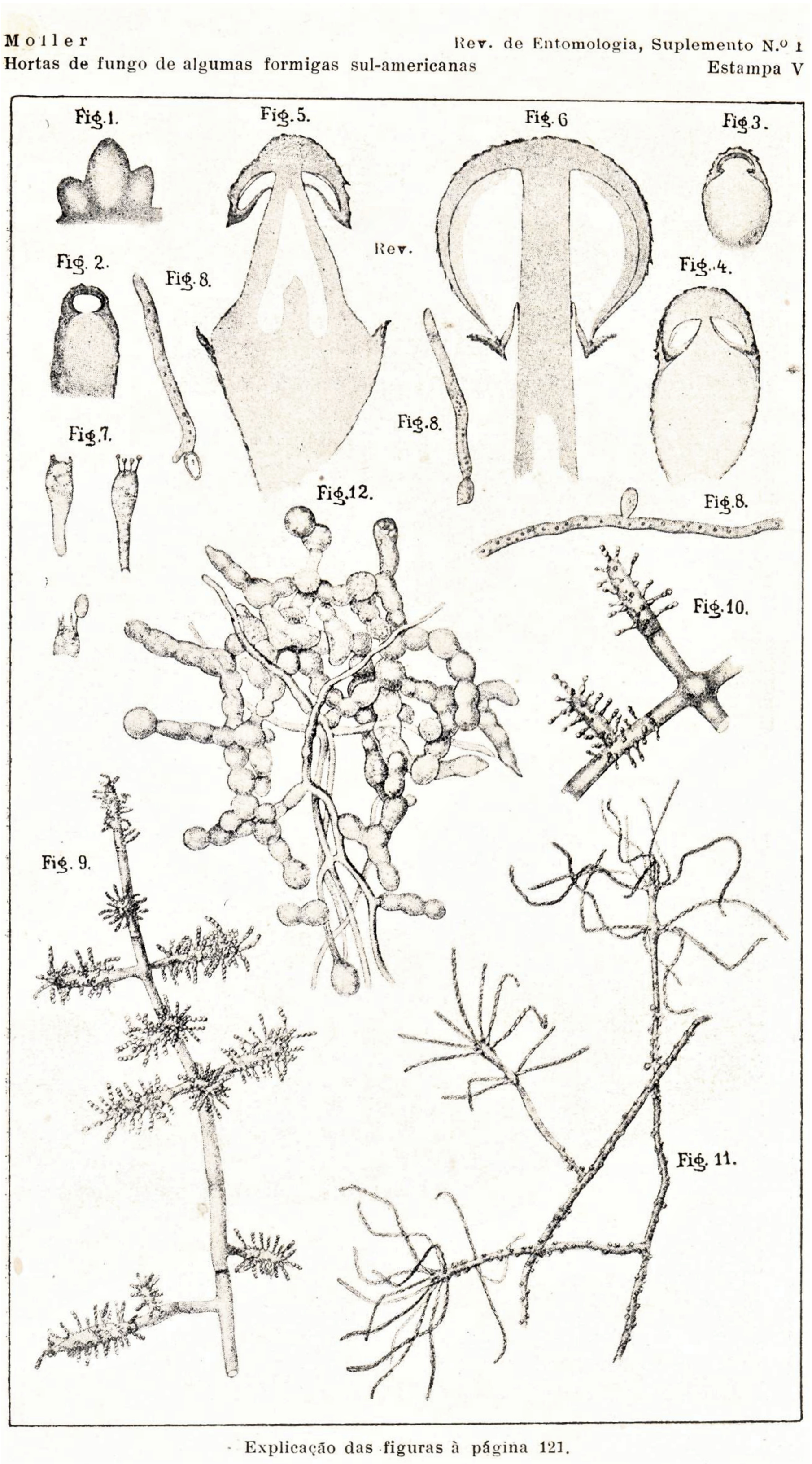


FIGURE 1. Phylogenetic tree based on Maximum Likelihood analysis of ITS sequences showing relationship among *La. nzumbae*, *La. gongylophorus* and related species. Bootstrap (BS) (above 70%) and posterior probability (BPP) (above 0.8) support values are shown above the branches (BS/BPP). The branches with BS= 100 % and BPP= 1 are in bold. The sequences generated in this work are in bold. Genebank accession number are given for each terminal. *Agaricus* sp. (MT605382), and *A. rufoaurantiacus* were used as the outgroup.



Moller

Hortas de fungo de algumas formigas sul-americanas

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Estampa V

· Explicação das figuras à página 121.

FIGURE 2. Lectotype of *Leucoagaricus gongylophorus.* Tab. V, from Möller 1893. Fig. 1–6. Cross-sections through various old fruiting bodies of the agaricines cultivated by the *Atta* species (*Rozites gongylophorus*). 1–5 natural size.; 6 slightly reduced in size. Fig. 7. Basidia of the same fungus, with fallen, just laid and a ripe spore still attached. Magnification 1: 500. Fig. 8. Three germinated spores of the same fungus. Magnification 1: 500. Fig. 9. Those on the mushroom garden of the *Atta* species after removal of the "Strong" conidia form appearing in ants. Magnification 1: 220. Fig. 10. Smaller piece of mycelium with the same not yet fully developed Conidia carriers. Magnification 1: 300. Fig. 11. Those in the mushroom garden of the *Atta* species, after removal of the "weak" conidia form with the "Pearl threads". Magnification 1: 220. Fig. 12. The "strand swellings" occurring there. Magnification 1: 220.

FIGURE 3. Photographs of fresh basidiomes *in situ*. A–B. *Leucoagaricus gongylophorus* C.H.C. 463 (Epitype). B. Detail of the base of the stipe attached to the fungal garden of leaf-cutting ants. C. *Leucoagaricus nzumbae* C.H.C.349 (Holotype). Scale bars are 50 mm for A and B and 10 mm for C. Photos by C. Heisecke.

Nomenclature:—Alfred Möller was a German mycologist who studied fungal species growing on nests of leaf-cutting ants in Blumenau, Santa Catarina State, Brazil (Möller 1893). Möller described *Rozites gongylophorus* and collected several other specimens while he was working in Blumenau (Möller 1893, Friederichsen 1977). Most of these collections were deposited in the Berlin (B) and Hamburg (HBG) herbaria (Friederichsen 1977). However, it seems that many specimens collected by Möller were destroyed during World War II; although, a few are still at B and HBG (Friederichsen 1977). Möller (1893) did not designate a type but mentioned four different collections of the fungus growing on ant nests (November 1891, *Gärtner*; 50 steps of the first location, 19 February 1892; near the Parque Municipal de Blumenau, 17 March 1892; 12 km up river, 30 March 1892, *A. Müller*). None of those collections of *R. gongylophorus* were found and they appear to have been destroyed (Dr. Matthias Schultz, *pers. comm.*). Therefore, we selected a plate from the protologue of *R. gongylophorus* (Fig 2) as the lectotype in accordance with art. 9.3 of the International Code of Nomenclature for algae, fungi, and plants (Turland *et al.* 2018).

Möller's originally orthography was *Rozites gongylophora* (Möller 1893), but the correct spelling is *Rozites gongylophorus* since generic names ending in -*ites* are treated as masculine to comply with art. 62.4 of the Code (Turland *et al.* 2018).

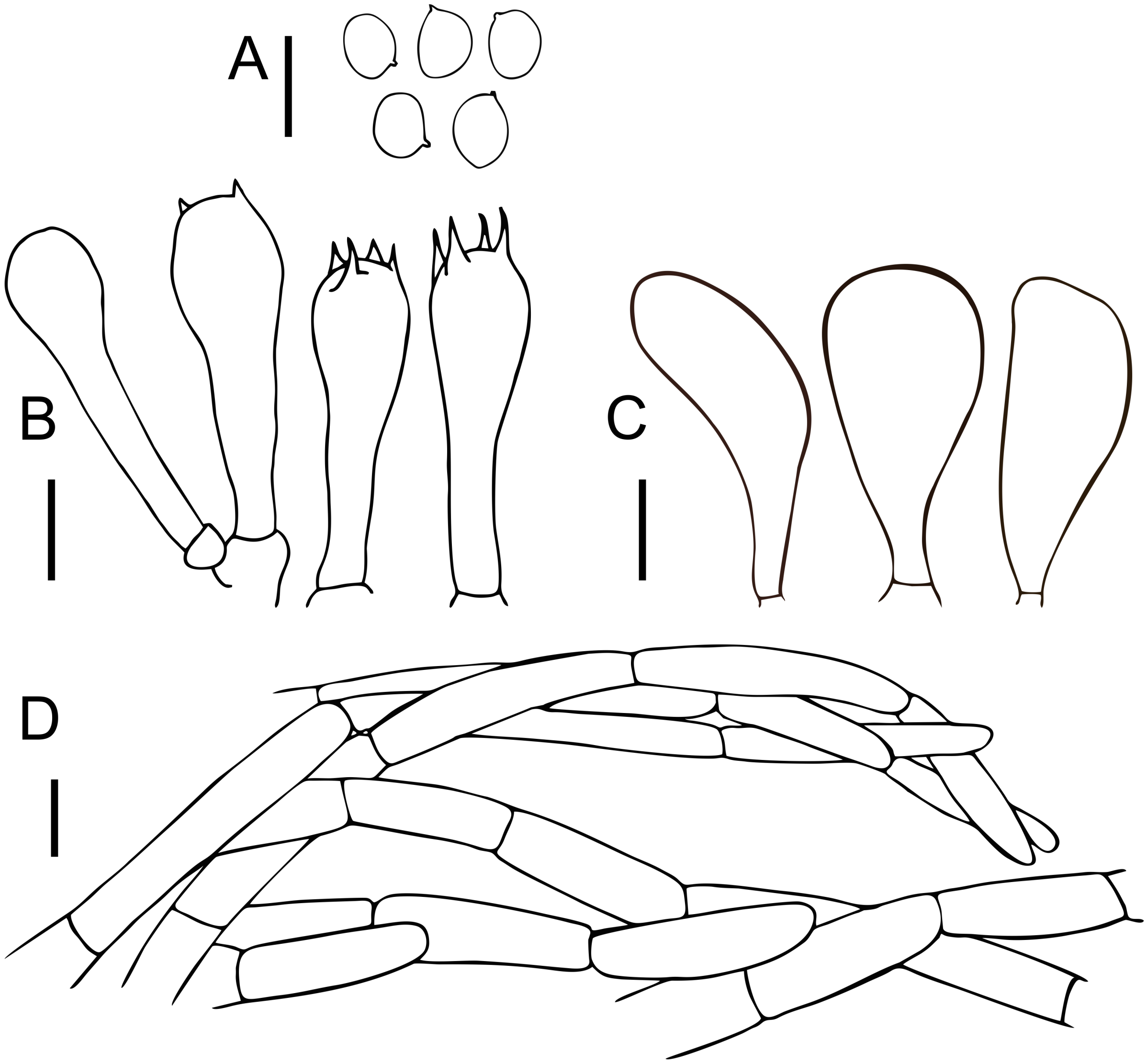

FIGURE 4. *Leucoagaricus gongylophorus* C.H.C. 463 (Epitype). A. Basidiospores. B. Basidia. C. Cheilocystidia. D. Pileus covering. Scale bars are 10 µm for A–C and 20 µm for D. Illustration by C. Heisecke.

Möller (1893) extensively described both the anamorph and basidiome development. However, characters used to identify the teleomorph were poorly detailed and ambiguous. Thus, we are proposing an epitype (according to the Code art. 9.9) (Turland *et al.* 2018). We selected the collection *C.H.C. 463* as the epitype because of the large number of basidiomes and because both the anamorph and teleomorph phases (holomorph) are well represented.

Based on the ochraceous color of the basidiospores, this species was placed in *Rozites* Karsten (1879: XX) by Möller (1893), and then *Pholiota* Kummer (1871: 22) by Saccardo (1895). Later, Rick (1961) also combined the species into *Pholiota*, but the name was superfluous and therefore, illegitimate (art. 52.1 of the Code) (Turland *et al.* 2018). Singer (1951) also suggested that the species belong to *Agaricus*, but a valid combination was not made. Heim (1957) noted that basidiospores in *Lepiota s.l.* are "polychromatic", showing a variety of colors, and based on the robust basidiomes, well-developed ring and basidiospore morphology, placed it in *Leucocoprinus*. The description in Heim (1957) is consistent with the concept of *Leucoagaricus*, so Singer (1986) transferred the species to *Leucoagaricus*.

Kreisel (1972) doubted the identity and generic position of *Rozites gongylophorus* proposed by Möller (1893) and described a new genus and species, *Attamyces bromatificus*, based on a fungus garden of *Atta insularis* Guérin-Méneville collected in Cuba. Singer (1986) suggested that these could be conspecific, however, formal synonymizing was not done. Here, we consider it a single species, *La. gongylophorus*. Also, Kreisel (1972) did not indicate a type, therefore, the name was not validly published (art. 40.1 and art. 40.2 of the Code) (Turland *et al.* 2018) and does not have nomenclatural status.

Taxonomy:—Möller (1893) described *La. gongylophorus* in the protologue as a curious fungus growing on the top of an ant nest as if it was a pedestal. The basidiomes were big and fleshy and had the following features: pileus reaching 16 cm with dense violaceus to black scales on the surface; lamellae free; stipe fistulose, bulbous, up to 24 cm tall, 2 cm wide at the top and 4 cm wide at the base, with some remnants of the universal veil at the base, surface white along the upper portion and with violaceus scales under the annulus; and annulus well-developed, placed at 3/4 of the height of the stipe, pendant, with scales similar to the pileus surface. However, the description of the microstructures only mentioned the clavate, 30 µm tall basidia and nearly hyaline, 8 µm basidiospores (Möller 1893). Later, Fisher *et al.* (1994) and Spielmann & Putzke (1998) expanded the description for *La. gongylophorus* based on their collections.

The characteristics of the studied specimens in this work largely match the descriptions in the protologue (Möller 1893), and those by Saccardo (1895), Heim (1957), Fisher *et al.* (1994), and Spielmann & Putzke (1998). Spielmann & Putzke (1998) found subglobose or sometimes subcylindric basidiospores that were 8–16 × 4–8 µm. The specimen C.H.C. 463 has subglobose basidiospores that are 5.5–8 × 4.2–5.9 µm (Fig 4A). The specimen F.T.F. 192 has two types of basidiospores (Fig 5A): most spores are subglobose and match the ones observed in specimen C.H.C. 463; the second type is rare, subcylindric and larger (9.5–15.2 × 4.6–6.8 µm). The collection F.T.F. 192 also has a few 1-spored basidia, which are absent in the other collections studied (Fig 5B).

Leucoagaricus gongylophorus is the most studied species in the genus due to its mutualistic association with leaf-cutting ants of the genera *Acromyrmex* and *Atta* Fabricius, which are the dominant herbivores in several Neotropical ecosystems and major pests of human agriculture (Möller 1893, Schultz & Brady 2008, Solomon *et al.* 2019). Most of these studies are based on the cultivars and only a few focus on fungal taxonomy and systematics (Möller 1893, Saccardo 1895, Heim 1957, Fisher *et al.* 1994, Mueller *et al.* 1998, Spielmann & Putzke 1998). This may be because basidiomes are rarely produced and their formation seems to be suppressed by the ants (Möller 1941, Heim 1957, Fisher *et al.* 1994, Mueller 2002). Also, differently of the fungi cultivated by the primitive Attini ants (so called lower-Attini) (Vo *et al.* 2009), free living basidiomes of *La. gongylophorus* separate from their ant hosts have yet to be found (Schultz & Brady 2008).

Two other *Leucoagaricus* species associated with leaf-cutting ants were described in South America. *Leucoagaricus weberi* J.J. Muchovej, Della Lucia & R.M.C. Muchovej (1991:1309) was described based on a single basidiome from a fungus garden of a live nest reared *in vitro* (Muchovej *et al.* 1991). *Leucoagaricus amazonicus* A. Ortiz & Franco-Mol. *in* Ortiz *et al.* (2008: 373) was found growing solitary on dump piles produced by Attini ants outside their nest (Ortiz *et al.* 2008). *Leucoagaricus weberi* and *La. gongylophorus* share some characteristics, such as the presence of oleiferous hyphae and basidiospores with a germ pore, but they differ by the dark brown to black squamules on the pileus surface and the white stipe that turns brown to reddish brown when dried in *La. weberi*, while *La. gongylophorus* has vinaceus squamules and the stipe turns brownish when damaged(Möller 1893, Saccardo 1895, Muchovej *et al.* 1991, Spielmann & Putzke 1998), although this color does not remain when the basidiome is dried. *Leucoagaricus amazonicus* basidiomes are smaller than those of *La. gongylophorus*. *Leucoagaricus amazonicus* has dark brown fibrils and squamules on the pileus, a trichodermal pileus covering and capitate cheilocystidia filled with brown content, while *La. gongylophorus* has vinaceus scales on the pileus, a repent pileus covering and clavate cheilocystidia without brown content. They are not closely related and appear in separate clades within *Leucoagaricus* and *Leucocoprinus*, based on the analyses of ITS sequences (Fig 1, Ortiz *et al.* 2008).

A few big and fleshy species of *Leucoagaricus* have been recorded in Brazil (Rick 1937, 1961, Batista 1957, Grandi *et al.* 1984, Sobestiansky 2005, De Meijer 2006, Albuquerque *et al.* 2007, Rother & Silveira 2008, 2009, Rosa & Capelari 2009, Ferreira & Cortez 2012, Magnago *et al.* 2013), and *Leucoagaricus lilaceus* Singer *in* Singer

& Digilio (1952: 274) from Argentina is macromorphologically the most similar. Besides the size of the basidiomes, both species also share the violaceus hue in the pileus surface, but *La. lilaceus* grows solitary, the pileus surface is velutinous with punctate apressed scales, the stipe has an abruptly bulbous base with rhizomorphs, and the white lamellae change to pinkish when dried and brownish in herbaria collections (Singer & Digilio 1952, Rother & Silveira 2009); while *La. gongylophorus* is ceaspitose, emerging from a mycelial mass inside the leaf-cutting ant garden, the pileus surface has uplifted scales, and has a yellowish to reddish brown staining reaction throughout the basidiome. Micromorphologically, *La. lilaceus* could be distinguished by the trichodermal palisadic pileus covering (Singer & Digilio 1952, Rother & Silveira 2009), while *La. gongylophorus* has an interwoven pileus covering. Unfortunately, there are no available sequences from the Brazilian specimens.

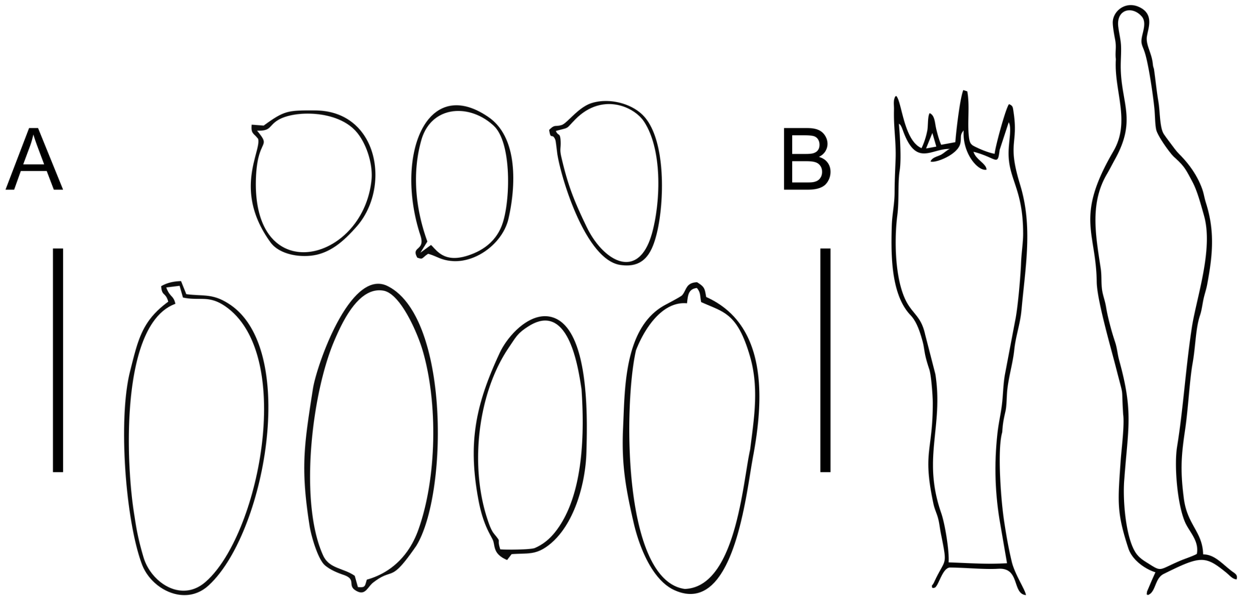

FIGURE 5. *Leucoagaricus gongylophorus* F.T.F. 192. A. Basidiospores. B. Basidia. Scale bars are 10 µm. Illustration by C. Heisecke.

Leucoagaricus leucothites (Vittadini 1835: 310) Wasser (1977: 308) and *Leucoagaricus nympharum* (Kalchbrenner 1873: 10) Bon (1977: 19) were also been reported in Brazil (Rick 1937, 1961 Grandi *et al.* 1984, De Meijer 2006, Albuquerque *et al.* 2007) and sequences from European and North American specimens were included in our phylogenetic analyses (Fig 1). *Leucoagaricus leucothites* has white basidiomes that could turn yellowish when exposed and brownish when dried, basidiospores with a germ pore, and the cheilocystidia are cylindrical to narrowly clavate with acuminated or subcapitate apex (Vellinga 2001); and the specimen determined as *La. nympharum* from Brazil probably belongs to a different species.

Our phylogenetic analyses (Fig 1) confirm the identity of the ant fungus on molecular basis. The sequence from the basidiome of *La. gongylophorus* was compared with sequences from the ant garden of four different species of *Acromyrmex* in different Brazilian biomes where the occurrence of *La. gongylophorus* was determined based on the distribution of the leaf-cutting ants (Möller 1893, Solomon *et al.* 2019). Although, the phylogenetical position of *La. gongylophorus* is not completely solved within the Leucoagaricus/Leucocoprinus clade, since the species appear forming a long branch in a group with low to moderate support (Fig. 1, Johnson & Vilgalys 1998, Mueller *et al.* 1998, 2001, Vellinga 2004b, Vellinga *et al.* 2011).

Leucoagaricus nzumbae **C. Heisecke, A.A. Carvalho & M.A. Neves** ***sp. nov.*** (Figs 3C, 6A–C)
MycoBank:—MB 835923

Type:—BRAZIL. Rio de Janeiro: Teresópolis, Parque Nacional da Serra dos Órgãos, first part of the Pedra do Sino trail, 22°27’02.7”S, 43°00’06.3”W, 09 December 2016, *Heisecke & Duque, C.H.C. 348* (holotype RB).

Pileus 10–13 mm diameter, hemispherical, planeo-convex or applanate, sometimes umbonate; surface dry, smooth and brown at the center (6E8), then splitting radially and forming brownish orange fibrillose scales (6C5) on a white to yellowish-white background (1A1, 1A2); margin entire, straight, exceeding the lamellae; context less than 1 mm broad, white, not changing when damaged. Lamellae free, ventricose, 1–3 mm wide, white to yellowish; edge entire, concolorous with the sides. Stipe 20–30 × 2–3 mm, central, cylindrical, fistulose; surface fibrillose, white. Annulus superior to central, membranous, fragile, easily detachable, ascending, white. The entire basidiome turns lilac when dried (15B4, 15C4).

Basidiospores 5.2–6.9 × 3.3–4.8 µm (Q = 1.29–1.91), broadly ellipsoid to oblong, ovoid in side view, uniguttulate, yellowish in water, paler or hyaline in KOH, dextrinoid, metachromatic, thin-walled, without a germ pore. Basidia 17.5–30 × 6.6–9.3 µm, clavate, 4-spored. Cheilocystidia absent. Pleurocystidia absent. Pseudoparaphyses absent. Hymenophoral trama subregular, subhymenium cellular. Pileus covering made up of upright trichodermal elements, 19.8–67.9 × 4.7–9.8 µm, cylindrical to irregular, often tapering upwards with obtuse apex, thick-walled, with brown intracellular and parietal pigments, often encrusted, brown in water and paler in KOH. Scattered oleiferous hyphae present in the pileus context. Clamp connections absent.

Paratypes:—BRAZIL. Rio de Janeiro: Teresópolis, Parque Nacional da Serra dos Órgãos, first part of the Pedra do Sino trail, 22°27’02.7”S, 43°00’06.3”W, 09 December 2016, *Heisecke & Duque, C.H.C. 349* (RB, FLOR); *idem*, 11 December 2016, *Heisecke & Duque, C.H.C. 365* (RB); *idem*, 19 December 2017, *Heisecke & Duque, C.H.C. 498* (RB); *idem*, 16 March 2019, *Heisecke & Duque, C.H.C. 525* (RB).

Etymology:—In honor of Nzumba, a deity from the Afro-Brazilian religion Candomblé Bantu, who dresses in purple and has mud as his representative element. This name was chosen because the type was collected alongside an imperial trail, probably built by slaves, the muddy habitat of the species and the purplish color of the basidiomes when dry.

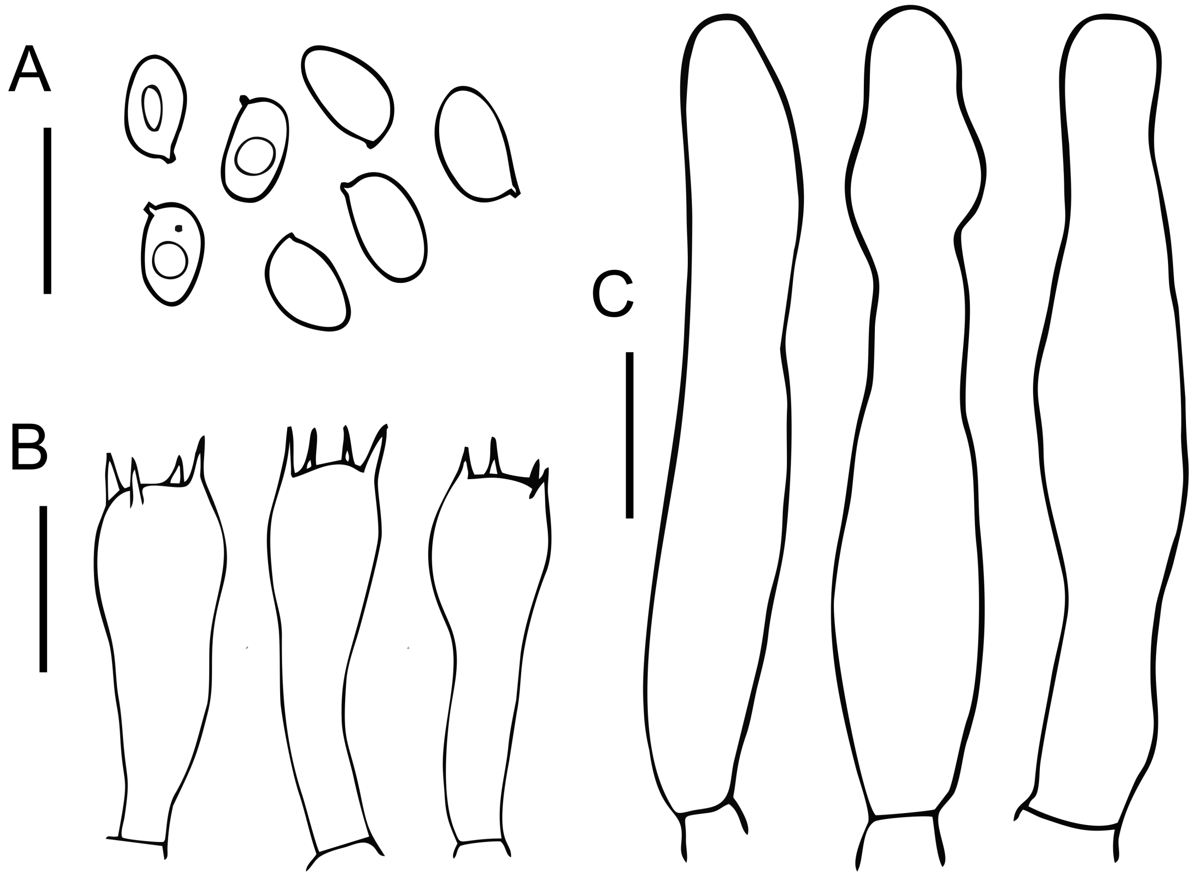

FIGURE 6. *Leucoagaricus nzumbae* C.H.C.349 (Holotype). A. Basidiospores. B. Basidia. C. Elements of the pileus covering. Scale bars are 10 µm. Illustration by C. Heisecke.

Distribution and habitat:—Solitary in small groups, in the shade on moist ground among litter and clay, in tropical cloud forest in the Atlantic Forest in Rio de Janeiro State.

Taxonomy:—This species can be recognized by the small basidiomes that turn completely lilac when dried, the brownish color of the pileus surface, and the trichodermal elements with intracellular and parietal brown pigments in the pileus covering. The lack of cheilocystidia is unusual for *Leucoagaricus* species. However, after exhaustive analyses of all basidiomes collected, not a single cystidium was found, and the lamella edge is formed only by basidioles and basidia.

Due to the small size of the basidiomes (Fig 3C, pileus 10–13 mm wide and stipe 20–30 mm long), *La. nzumbae* resembles specimens of *Lepiota*, but the basidiospores are metachromatic and clamp connections are absent in the entire basidiome (Fig 6A–C).

Based on molecular data, *La. nzumbae* was retrieved in a strongly supported clade along with other species that also change color on drying. The clade is formed by a Mexican specimen labeled as *Leucoagaricus* cf. *coerulescens* (Peck 1899:63) J. F. Liang, Zhu L. Yang & Xu (2010: 1147), an undescribed species from Hawaii (ecv3754 and ecv3757), and the Asian species *Leucoagaricus viriditinctus* (Berkeley & Broome 1871: 503) J.F. Liang, Zhu L. Yang & J. Xu *in* Liang *et al.* (2010: 1146), characterized by their basidiomes that turn bluish green when dehydrated, which is quite different from *La. nzumbae* which turns lilac.

The color changes of the basidiomes in response to bruising or drying are important characteristics for the taxonomy of *Lepiota s.l.* (Reid 1990, Liang *et al.* 2010, Vellinga 2006, 2010, Vellinga *et al.* 2010). The lilac tint of *La. nzumbae* when dry is like that found in other representatives of *Leucoagaricus. Leucoagaricus lilaceus*, originally reported for Argentina and then Brazil (Sobestiansky 2005, De Meijer 2006, Rother & Silveira 2008, 2009, Ferreira & Cortez 2012), has a robust fleshy basidiome with whitish lamellae that turn pinkish with age and when dried, and the stipe base is abruptly bulbous with rhizomorphs (Singer & Digilio 1952, Rother & Silveira 2009). *Leucoagaricus variicolor*, from Spain, has yellowish to ochraceus-cream, volvate, fleshy basidiomes that turn pinkish when dried and has spheropedunculate cheilocystia (Muñoz *et al.* 2012). *Lepiota roseolivida* Murrill (1912: 234) from the U.S.A. also has delicate basidiomes that turn lilac when dried, but the pileus surface is livid to dull rose-lilac when fresh, which is different from the brownish color on a whitish background present in *La. nzumbae*. *Lepiota roseolivida* also has larger amygdaliform basidiospores (6.7–9.8 × 3.8–5.7 µm) and clavate cheilocystidia (Murrill 1912, Vellinga 2006).

Some species of *Leucoagaricus* described from Brazil show morphological affinities to *La. nzumbae*: *Leucoagaricus confusus* (Rick 1937: 341) Singer (1951: 422), *Leucoagaricus imperialis* (Spegazzini 1889: 382) Pegler (1997: 33) and *Leucoagaricus tricolor* Singer (1989: 98). Both *La. confusus* and *La. tricolor* have small basidiomes as in *La. nzumbae* (pileus diameter <20 mm,) (Rick 1937, Singer 1951, 1989). However, *La. confusus* could be differentiated by a yellowish pileus surface, absence of reaction when damaged or dried, and bigger basidiospores (10 × 5 µm) (Rick 1937, Singer 1951); and *La. tricolor*, by the reddish-brown pileus surface, lamella color that changes from grey to brownish grey on drying and the fasciculate pileus covering (Singer 1989). Meanwhile, *Leucoagaricus imperialis* (Spegazzini 1889: 382) Pegler (1997: 33) has a brownish pileus surface as in *La. nzumbae*, but differs from it by the bigger basidiomes (pileus 40−50 mm diameter, stipe 100 × 4−5 mm) that are mostly whitish and change to brownish when dried, and the larger basidiospores (8−12 × 5.5−6.5 µm) (Spegazzini 1889, Pegler 1997).

Another *Leucoagaricus* species reported from Brazil and morphologically related to *La. nzumbae* is *Leucoagaricus sulphurellus* (Pegler 1983: 420) B.P. Akers *in* Akers, Angels & Kimbrough (2000: 48), described from the Caribbean islands (Pegler 1983, 1997, Wartchow *et al.* 2008, Rosa & Capelari 2009). This species shares the small basidiome (pileus 8−21 mm diameter) and the brownish pileus surface with *La. nzumbae*, but it differs by its sulphur yellow basidiome, that changes color to pinkish brown and then blue-green when damaged, basidiospores with a germ pore, and the appressed pileus covering (Pegler 1983, Akers *et al*. 2000).

Acknowledgments

The first author thanks CAPES for the PhD fellowship. The authors thank Fernanda Linhares for collecting and sequencing one of the specimens, Nathan Smith for the English revision and PARNASO for the collecting permits and support during fieldwork. Comments by Marcus Felippe Oliveira da Silva, Nelson Menolli Jr., Tiara Souza Cabral, an anonymous reviewer and the editor greatly improved the manuscript.

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