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Clitocybula azurea in Argentina: redescription and phylogenetic position

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Abstract—*Clitocybula azurea,* which was described by Singer in 1973 from Brazil and Venezuela, is characterized by its bluish to grayish blue tinges, narrow lamellae, cespitose and lignicolous habit, and small, amyloid, subglobose basidiospores. However, despite its striking coloration, the species is not described or illustrated in recent literature. The species is here redescribed and illustrated, its distribution extended to Argentina, and its phylogenetic position analysed.

Key words—*Agaricales*, Atlantic forest, ITS, *Marasmiaceae*, mushroom, taxonomy

Introduction

Clitocybula Métrod is a phylogenetically well-defined genus, related to other genera of the hydropoid clade (Matheny & al. 2006), also including *Megacollybia* Kotl. & Pouzar, *Hydropus* Kühner ex Singer, *Trogia* Fr., *Gerronema* Singer, *Porotheleum* Fr., *Leucoinocybe* Singer ex Antonín & al., and *Lignomphalia* Antonín & al. (Antonín & al. 2019). It is a small genus, with c. 15 species (Antonín & al. 2019), with a wide morphological diversity and exhibiting small clitocyboid, omphalioid, collybioid, mycenoid or pleurotoid habits (Singer 1962, Bigelow 1973, Antonín & al. 2019). Barrasa & al. (2006)

defined *Clitocybula* based on five main characteristics: the radially fibrillose to squamulose pileus surface; the absence of a cellular hypoderm and pleurocystidia [except for their occasional presence as in *C. azurea* (Singer 1962)]; the presence of cheilocystidia and dermatocystidia; amyloid smooth basidiospores; and lignicolous habit. *Clitocybula* is restricted to the temperate regions of both hemispheres (Singer 1986, Latha & al. 2015), plus several tropical-subtropical species, e.g., *C. azurea* and *C. cyanocephala* (Pat.) Singer from the neotropics (Singer 1973), *C. omphaliiformis* Pegler from Africa (Pegler 1977), *C. canariensis* Barrasa & al. from Canary Islands (Barrasa & al. 2006), and *C. sulcata* K.N.A. Raj & Manim. from India (Latha & al. 2015).

Because of the absence of the recent description and illustration in the literature, the aim of this work is to re-describe and illustrate *Clitocybula azurea* based on new collections, expand its distribution area, and analyze its phylogenetic position.

Materials & methods

Morphological studies

The specimens were collected in Misiones province, Argentina, and they were photographed and described macroscopically in situ, and then analyzed morphologically and identified following the criteria and terminology proposed by Vellinga (1988) and Lodge & al. (2004). The color terminology follows Kornerup & Wanscher (1978). Tissues were cut by hand and mounted in a solution of 5% KOH (v/w) with 1% floxin aqueous solution for microscopical examination. Melzer's reagent (Wright & Albertó 2002) was used to verify amyloid reaction. The microscopic structures were measured directly with 1000× immersion objective or through photographs taken with a Leica EC3 built-in camera using ImageJ software (Schneider & al. 2012). The notation L = refers to the number of true lamellae (ranging from the stipe insertion to the margin of pileus) counted at the pileus margin. The minimum-maximum intervals were provided for the different microscopic structures. For basidiospores, n = indicates the number of basidiospores measured, x = the average value, Q = length:width ratio, and Qx = mean value of Q. Nomenclatural authorities follow Index Fungorum (2020); herbarium acronyms follow Thiers (2020). The collected specimens were dried, frozen for a week, and conserved in the Herbarium, Instituto de Botánica del Nordeste, Corrientes, Argentina (CTES).

DNA extraction, amplification, and sequencing

DNA isolation from small parts of fungal tissue, polymerase chain reaction (PCR) amplification, and sequencing of PCR products were performed through the Barcode of life Project following protocols in Ivanova & al. (2008) and Ivanova & Grainger (2006). The nuclear ribosomal internal transcribed spacer region (ITS) was amplified using the basidiomycete specific primer set: ITS1-F (CTTGGTCATTTAGAGGAAGTAA)

Table 1: Sequences of species of *Clitocybula* and related genera, with *Baeospora myosura* as outgroup, used in the phylogenetic analyses. Sequences obtained in this study are in **bold.**

Species	Specimen voucher	Origin	ITS	Reference
Baeospora myosura	AFTOL-ID 1799	USA	DQ484063	Matheny & al. 2006
*C. atrialb*a	AFTOL-ID 1529	USA	DQ192179	Curtis & al. unpubl.
C. azurea	**Alberti ADA015-17**	**Argentina**	**MT009482**	**This work**
	Niveiro 3173	**Argentina**	**MT009483**	**This work**
C. familia	BRNM 736053	Czechia	JF730328	Antonín & al. 2011
	X21	Czechia	LN714532	Větrovský & al. 2016
C. aff. *lacerata*	GRSM77072	USA	FJ596916	Hughes & al. 2009
C. lacerata	PRM:951559 (Neotype)	Czechia	MK713541	Antonín & al. 2019
	LE6639	Russia	HM191746	Malysheva & al. 2011
	LE262744	Russia	HM191747	Malysheva & al. 2011
	16837	USA	JF908760	Garbelotto & al. unpubl.
C. oculus	PRM 934963	USA	LT854020	Antonín & al. 2019
	BIOUG24046-E05	Canada	KT695404	Telfer & al. 2015
	3512	Canada	KM406971	Berube & al. unpubl.
	BIOUG24046-B03	Canada	KT695321	Telfer & al. 2015
	LIP (Moreau CAN 13-50)	Canada	LT854017	Antonín & al. 2019
	PBM 1156 (WTU)	USA	DQ192178	Curtis & al. unpubl.
Clitocybula sp.	TENN60306/TFB12058	USA	EU623637	Hughes & al. 2007
Lignomphalia lignicola (as *C. lignicola*)	LE262727	Russia	HM191731	Malysheva & al. 2011, Antonín & al. 2019
	LE6625	Russia	HM191732	Malysheva & al. 2011, Antonín & al. 2019
Leucoinocybe taniae (as *C. flavoaurantia*)	D	Italy	HM191743	Malysheva & al. 2011, Antonín & al. 2019
	GDOR (Type)	Italy	HM191744	Malysheva & al. 2011, Antonín & al. 2019
Megacollybia marginata	LE 202274	Russia	EU623688	Hughes & al. 2007
	HR 90203	Czechia	LT854047	Antonín & al. 2019
M. clitocyboidea	TENN062231 (Type)	Japan	NR119690	Hughes & al. 2007
	HMJAU4024/TENN62230	China	EU623670	Hughes & al. 2007
Trogia infundibuliformis	KUN HKAS56709	China	JQ031776	Yang & al. 2012
	KUN HKAS63661	China	JQ031775	Yang & al. 2012
T. venenata	KUN HKAS54710	China	JQ031772	Yang & al. 2012
	KUN HKAS56679	China	JQ031773	Yang & al. 2012

and ITS4-B (CAGGAGACTTGTACACGGTCCAG) (Gardes & Bruns 1993). The PCR products were sequenced in the Canadian Centre for DNA Barcoding (CCDB), Canada.

Molecular phylogeny

The dataset was compiled using our data (MT009482, MT009483) and 28 sequences selected from GenBank based on BLAST results and previous works (Malysheva & al. 2011, Antonín & al. 2019); *Baeospora myosura* (Fr.) Singer was selected as outgroup (Table 1). Sequence editing was done in BioEdit 7.2.5 (Hall 1999). Sequences were aligned by MAFFT 7 (Katoh & Standley 2013) under the Q-INS-i criteria. When necessary, the alignment was manually adjusted with MEGA 5 (Tamura & al. 2011). Potential ambiguously aligned segments of ITS1-ITS2 were detected by Gblocks 0.91b (Castresana 2000).

Phylogenetic reconstruction was inferred using Maximum Likelihood (ML) and Bayesian Inference (BI) separately. Maximum Likelihood was carried out in RaxML-HPC v.8 (Stamatakis 2014), searching for the best scored trees with GTRGAMMA model for the entire dataset with all the default parameters estimated by the software. The analysis first involved 100 ML searches, each starting from one randomized stepwise addition parsimonious tree. Only the best scored ML tree was kept, and the confidence of nodes was accessed through Rapid bootstrapping (BS).

Bayesian Inference (BI) was performed in MrBayes 3.2.6 (Ronquist & al. 2012). The evolutionary models for BI were estimated using the Akaike Information Criterion (AIC), as implemented in jModelTest2 v.1.6. (Guindon & Gascuel 2003, Darriba & al. 2012), and implemented with two independent runs, each beginning from random trees with four simultaneous independent chains. A total of 2×10^7 generations were carried out, sampling one tree every 1×10^3 generations.

Only the BI tree is shown, indicating support values (BPP/BS) at each node. A node was considered to be strongly supported if it showed a BPP ≥0.95 and/or BS ≥90%, while moderate support was considered BPP ≥0.70 and/or BS ≥70%.

Results

Phylogenetic analysis

The original dataset comprised 30 taxa and 1562 positions. The Gblocks curated dataset comprised 540 positions, of which 320 were constant, 220 variable, and 183 parsimony informative. The best substitution model was estimated as: TPM3uf+G. The resulting BI tree agreed with the ML analysis. Five well-defined clades were recovered from all analyses: *Leucoinocybe* (1/100), *Lignomphalia* (1/100), *Megacollybia* (1/100), *Trogia* (0.77/–), and *Clitocybula* (0.98/70). *Baeospora myosura* was used as outgroup. *Clitocybula azurea* sequences grouped closely with *C. familia* (0.78/–). The *Clitocybula* clade includes a second subclade formed by *C. lacerata* and *C. oculus* (Fig. 1).

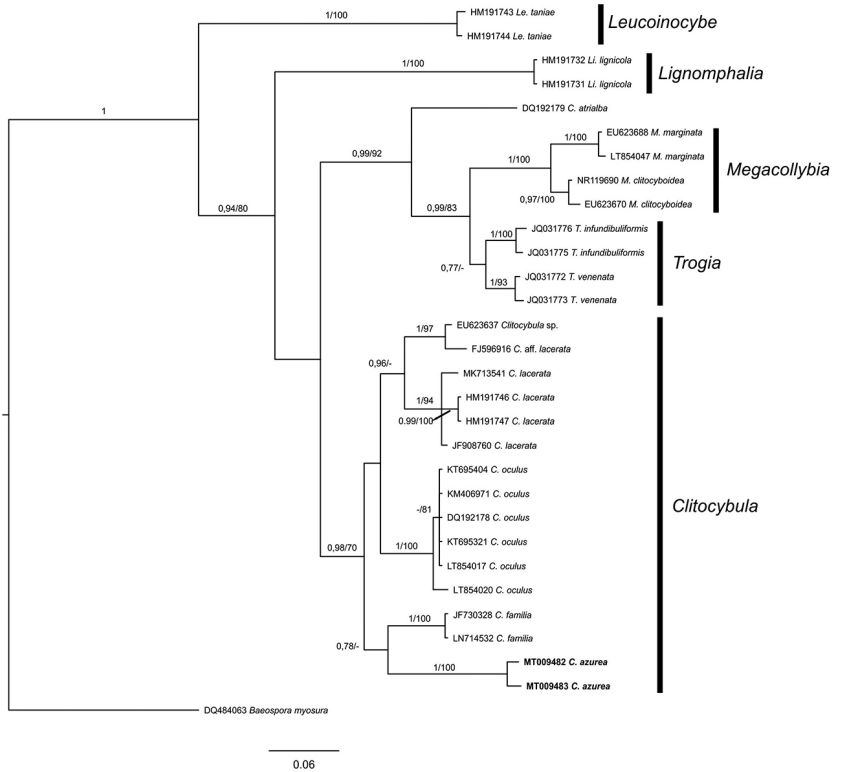

Fig. 1: Molecular phylogeny of species of *Clitocybula* and related genera, with *Baeospora myosura* as outgroup, carried out by Bayesian Inference based on dataset of ITS sequences. Bayesian posterior probabilities BPP ≥0.7, and Bootstrap values BS ≥70% are shown.

Taxonomy

Clitocybula azurea Singer, Beihefte zur Sydowia 7: 18 (1973). Figs 2–4

Basidiomata gregarious, in small clusters or densely cespitose, xylophagous. Pileus ≤20 mm broad, plano-convex to convex with undulate margin when young, then broadly conical, finally convex with acute papilla; thin and delicate, distinctly hygrophanous, dark blue (22F5-8) when young, then dark turquoise (24F6-8) to dark green (26F5-8), striate with greyish (23A2 "bluish white", to 26A2 "greenish white") lines radiating from the pileus center, finally white with a slight greenish hue, greyish turquoise (24D5) to greyish green (26D5) on the disc to completely white (1A1) to greenish-white (25A2) towards margin, dry, innately fibrillose; margin

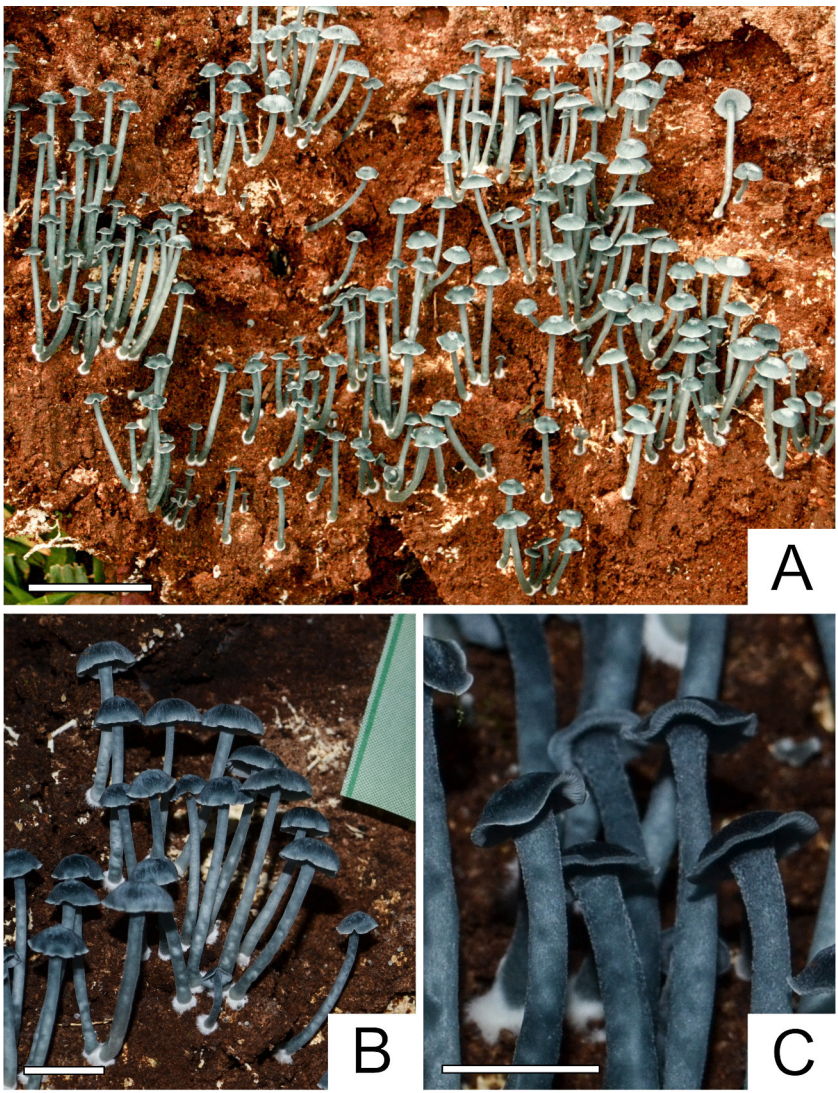

Fig. 2: *Clitocybula azurea* (Alberti ADA015-17), young specimens. A. General aspect; B. Habit and basidioma detail; C. Pileus and stipe surface detail. Scale bars: A = 10 cm; B, C = 1 cm.

straight to wavy. Context thin, concolorous with the pileus surface, odor and taste indistinct. Lamellae subfree to adnate, very narrow (<0.5 mm), crowded to close (2–3 L/mm), dark blue when young, turning whitish,

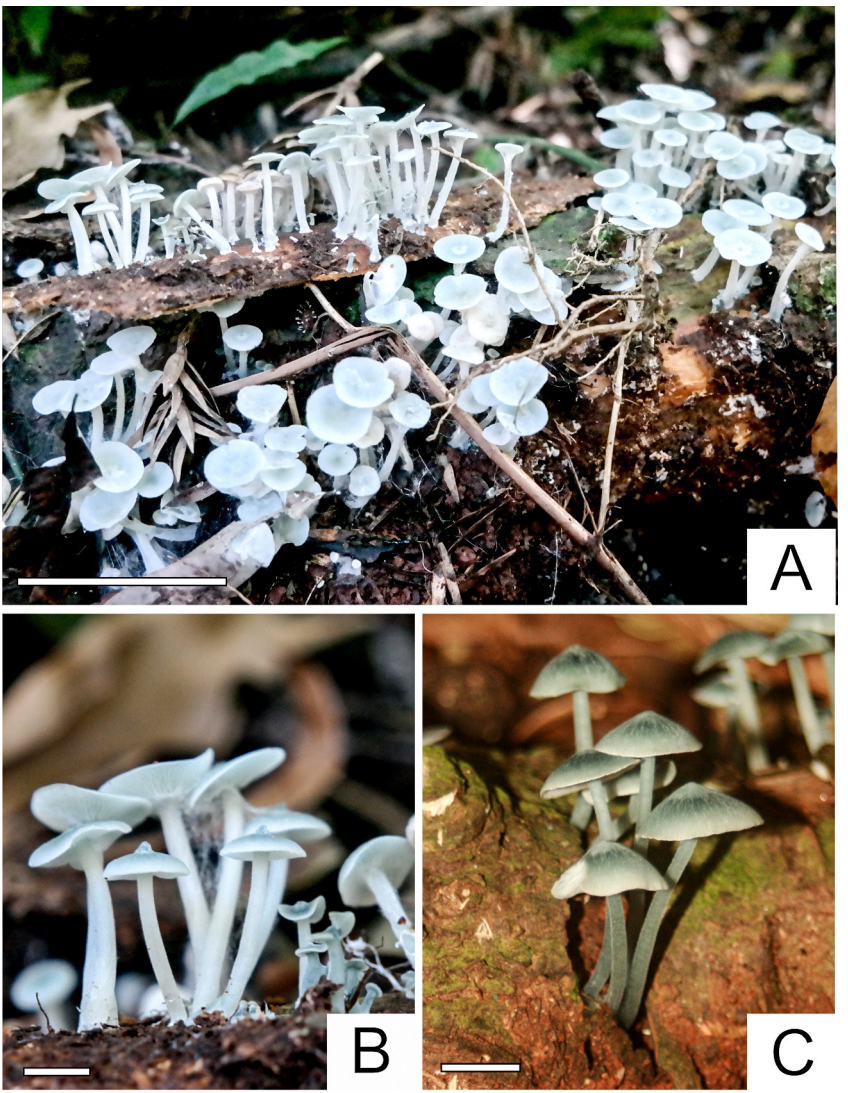

Fig. 3: *Clitocybula azurea*, mature specimens. A, B. General aspect, habit, and detail of whitish basidioma (Niveiro 3165); C. Basidioma detail of an intermediate state (Niveiro 3134). Scale bars: A = 10 cm; B, C = 1 cm.

with even concolorous edge; with two ranks of lamellulae. Stipe central, 10–40(–60) × 3–8 mm, cylindrical, equal or slightly narrowing towards the apex, hollow, surface concolorous with the pileus surface, fibrillose, dry,

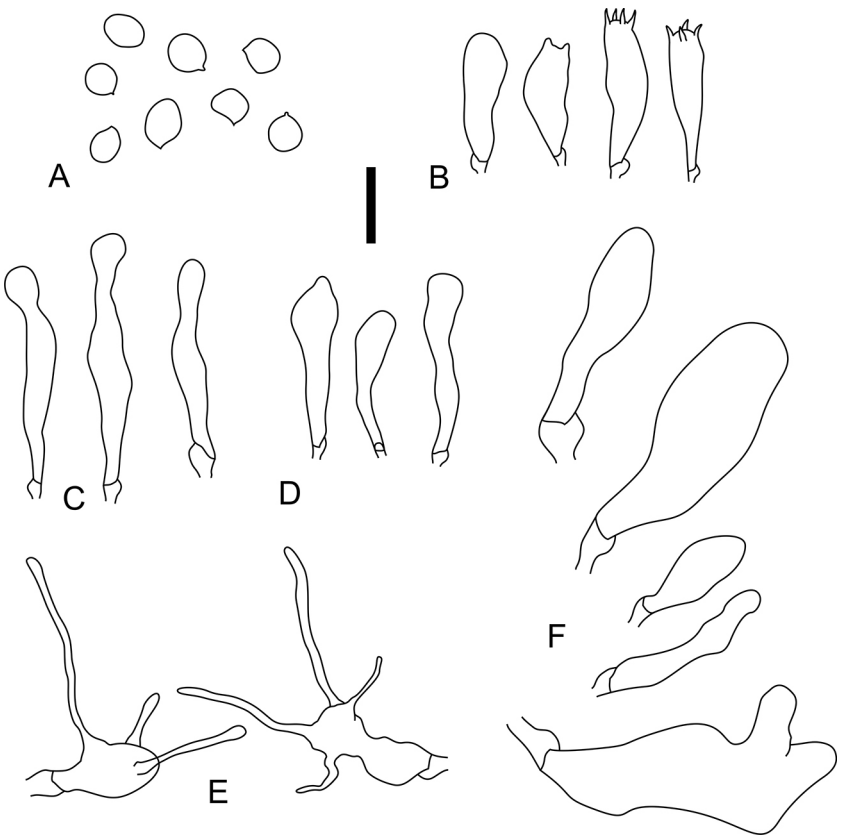

Fig. 4: *Clitocybula azurea* (Niveiro 3165). A. Basidiospores; B. Basidia and basidioles; C. Cheilocystidia; D. Pleurocystidia; E. Pileocystidia; F. Caulocystidia. Scale bar = 10 µm.

with a white (1A1) basal mycelial patch. Annulus absent. Spore-print not observed, presumably white.

Basidiospores 4–6.5 × 3–5 µm, x = 5.2 × 4.2 µm, Q = 1.04–1.44, Qx = 1.23, n = 25; subglobose in frontal view, broadly ellipsoid in side-view, with ventral side plane, without a suprahilar depression, amyloid, hyaline, smooth, thin-walled. Basidia 16–23(–28) × 4–6 µm, clavate, 4-spored, hyaline, thin-walled. Basidioles 15–20 × 4–8 µm, clavate, thin-walled. Cheilocystidia and pleurocystidia 18–30 × 3.5–8 µm, versiform, cylindrical, clavate, utriform, with apical papilla or subcapitate, scattered and inconspicuous in young specimens, more visible in mature specimens. Hymenophoral trama subregular; hyphae 2.5–6 µm diam, thin-walled, inamyloid. Pileipellis

a cutis made up of prostrate, more or less parallel hyphae; hyphae 2.5–7 µm diam, smooth, inamyloid, thin-walled, with pileocystidia as terminal elements. Pileocystidia broadly clavate to subglobose, 7–10 × 5–8 µm, with 3-5 filamentous excrescences of 12–22 × 1.5–2.5 µm. Stipitipellis a cutis made up of smooth, 3–6 µm diam hyphae. Caulocystidia 27–39.5(–47) × 6.5–14 µm, cylindrical to clavate, occasionally with 2–3 lobes at the apex, either concentrated in scattered fascicles or scattered and solitary, the latter in general cylindrical and smaller (27–33 × 6.5–9 µm) than those grouped in fascicles. Clamp connections present.

Ecology—Growing on decaying wood, logs, and stumps of gymnosperms and angiosperms. Caespitose, forming groups of numerous (c. 10) to very abundant (60–90) basidiomes.

Distribution—Known from Brazil (São Paulo State, type locality) and Venezuela (Bolivar State) (Singer 1973); Jamaica and Costa Rica (GBIF 2020); and Argentina (Misiones Province).

Specimens examined—**ARGENTINA**, **Misiones**: **Gral. Belgrano**, San Antonio, Campo Anexo Manuel Belgrano (CAMB-INTA) 26°02′12″S 53°47′23″W, 822 m a.s.l., in forestation of *Araucaria angustifolia* (Bertol.) Kuntze, with understory of *Alsophila setosa* Kaulf., 23/03/2017, leg. Niveiro 3159 (CTES); leg. Niveiro 3165 (CTES); leg. Niveiro 3173 (CTES: GenBank MT009483); leg. Alberti ADA015-17 (CTES; GenBank MT009482); in forestation of *Araucaria angustifolia* behind CAMB, 26°03′08″S 53°46′14″W, 23/03/2017, leg. N. Niveiro 3134 (CTES).

Comments—*Clitocybula azurea* is characterized by its bluish to grayish blue tinges, the narrow lamellae, the cespitose and lignicolous habit, and the small, amyloid, subglobose basidiospores. Only two *Clitocybula* species with bluish coloration are known: *C. cyanocephala* and *C. azurea*, both known from the neotropics (Singer 1979). *Clitocybula cyanocephala* differs by its broad lamellae and larger basidiospores (5.5–6.5 × 4.5–5 µm) (Singer 1979). The Argentinean *C. azurea* specimens have slightly larger basidiospores (4–6.5 × 3–5 µm) than those described by Singer (1979) (3–4.5 µm broad), making the delimitation between both species more difficult due to the partial overlapping spore ranges. However, the character of the lamellae (narrow and crowded to close in *C. azurea* vs. broad and subclose to medium distant in *C. cyanocephala*) is enough to distinguish the two species.

Pegler (1983), recombined *Clitocybula cyanocephala* as *Calocybe cyanocephala* (Pat.) Pegler, because he did not observe amyloid basidiospores in either the type material or new specimens from the Lesser Antilles.

Another *Clitocybula* species that resembles *C. azurea* in its caespitose and mycenoid habit is *C. familia* (Peck) Singer, which differs by its beige-brown

pileus with an olivaceous grey tinge (and lacking grayish blue tinges) when fresh (Antonín & al. 2011).

Microscopically similar species are *C. abundans* (Peck) Singer and *C. oculus* (Peck) Singer, with morphologically similar basidiospores, cheilocystidia, and caulocystidia (Bigelow 1973, Antonín & al. 2011, 2019). However, these species are easily separated by their macroscopic characters: *C. abundans* has a whitish pileus, often with a darker to fuscous center (Bigelow 1973, Antonín & al. 2019), and in addition to a similar coloration to *C. abundans, C. oculus* has a squamulose stipe (Bigelow 1973).

Mycena interrupta (Berk.) Sacc. [= *M. cyanocephala* Singer] is a bluish species know from the temperate region of southern hemisphere (Singer 1969, Horak 1983, Gates & Ratkowsky 2014) that macroscopically resembles *C. azurea* differs in its larger basidiospores (9–12 × 6–8 µm), diverticulate cheilocystidia, and pseudoamyloid trama (Horak 1980).

Discussion

Clitocybula is a small genus with a wide morphological diversity and is phylogenetically well-defined. Our study, as well as those by Malysheva & al. (2011) and Antonín & al. (2019), indicates that *Clitocybula* s.l. should be divided into more genera such as *Lignomphalia* and *Leucoinocybe*. The addition of the Argentinean *C. azurea* specimens reinforces *Clitocybula* as a well-defined genus.

Within *Clitocybula*, Antonín & al. (2019) showed that *C. familia* is related to *C. oculus* and *C. lacerata* (Scop.) Métrod as another related clade. However, adding *C. azurea* to the analysis divides these four species into two main clades: *Clitocybula azurea* with *C. familia*, moderately supported (BPP = 0.78); and *C. oculus* with *C. lacerata*, unsupported (Fig. 1). Further analyses are necessary (including species not yet sequenced), to fully resolve the relationships among these species. Unfortunately, there are no available sequences of the other bluish, morphologically similar species, *C. cyanocephala* to confirm whether these are related to each other or even to all other mycenoid *Clitocybula* species.

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