Short communication

The Amazonian luminescent *Mycena cristinae* sp. nov. from Brazil

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ABSTRACT

A new luminescent lignicolous fungal species, *Mycena cristinae* sp. nov., is proposed from the Central Amazon forest. This is unique and supported by morphological evaluation along with LSU- and ITS-based phylogenetic analyses. The basidiomata have mostly fuscous olivaceous brown pileus, adnate to subdecurrent and distant lamellae, and stipe with slightly bulbous base (basal mycelium absent). It also has inamyloid and/or weakly amyloid basidiospores, ramose cheilocystidia and a pileipellis composed of an aerated tangle of slender, diverticulate hyphae forming a coraloid pellicle overlaying the hypodermium. The luminescence is evident in the basidiomata (especially the stipe) and in the mycelium on the substrate. The LSU phylogenetic trees reveal that *M. cristinae* is sister to *M. coralliformis* within the *Mycenaceae* clade. In the ITS trees, it forms a unique lineage grouping with undetermined *Mycena* taxa. Morphological data support *M. cristinae* as a different species compared to previously described taxa.

Keywords: Agaricales, Amazon forest, *Mycenaceae*, phylogeny, taxonomy

Article history: Received 11 May 2020, Revised 14 May 2021, Accepted 17 May 2021, Available online 20 November 2021.

Bioluminescence is one of the oldest reported natural phenomena, dating back to the earliest records of the ancient Greeks (Virk, 2015). In his classic book on luminescence, Havey (1957) mentions that Georg Everard Rumph (1637–1706) reported in “Herbarium Ambroiense” that Indonesian natives carry luminescent fungus in their hands like a lantern to keep them from wandering off a path at night. In “Lights in the Forest” (Ishikawa, Ikeda, Baniwa, & Bruno, 2019), Aldevan Baniwa (of the Baniwa indigenous people with mother of the Tukano indigenous people) reported that in north-western Amazonia it is common for the native people to say that they can be guided at night by “glowing” fallen leaves and branches on the ground, especially on moonless nights in the fully dark forest. These fallen leaves and branches colonized by luminescent fungi help them to find the trail back when there is no torch or flashlight.

The first mushroom-forming species described as luminescent from Brazil was *Gerronema viridilucens* Desjardin, Capelari & Stevani, in the Atlantic Rainforest of São Paulo State (Desjardin, Capelari, & Stevani, 2005). *Mycena lacrimans* Singer, originally de-

scribed from the Brazilian Amazon (Singer, 1989), was reported to be luminescent by Desjardin and Braga-Neto (2007). Similarly, *M. discobasis* Métrod, *M. fera* Maas Geest. & de Meijer and *M. singeri* Lodge were reported as luminescent only in Desjardin, Capelari, and Stevani (2007). Since then, nineteen species of luminescent fungi have been reported in Brazil (Table 1). To date, the total number of known luminescent fungi worldwide is 102 species (91 + six in Cortés-Pérez et al., 2019; + four in Terashima, Takahashi, & Taneyama, 2016; + one in Karunarathna et al., 2020). Overviews and discussion of many aspects of fungal luminescence (taxonomy, evolution, ecology, physiology, etc.) are provided by Desjardin, Oliveira, and Stevani (2008), Waldenmaier, Oliveira, and Stevani (2012) and Oliveira, Carvalho, Waldenmaier, and Stevani (2013).

Mycena discobasis, *M. lacrimans*, *M. fera* and *M. singeri* (and others in Table 1) are cases that point to a possible daylight sampling bias mentioned by Desjardin et al. (2007), which suggests that luminescence is more frequent in *Mycena* than we now think. As most mycological forays are conducted during the day (mostly in the morning), many *Mycena* species do not show luminescence. In evolutionary terms, *Mycenaceae* may include numerous species sharing this ecologically and adaptively important trait, since similar secondary metabolites often follow systematic relations (Gottli-

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Table 1 Luminescent mushrooms reported in Brazil, with geographical locations and citations

Species (year of publication)	Luminescent tissue (tested or putative)	Brazilian State	Ref. of the luminescence
<i>Gerronema viridilucens</i> Desjardin, Capelari & Stevani (2005)	Whole basidiome and mycelium culture ^a	São Paulo	Desjardin et al. 2005
<i>Mycena</i> aff. <i>abieticola</i> Singer, Beih.	Whole basidiome ^b	São Paulo	Desjardin et al. 2010
<i>M. albororida</i> Maas Geest. & de Meijer (1997)	Basidiome ^d	Paraná	Desjardin et al. 2016
<i>M. aspratilis</i> Maas Geest. & de Meijer (1997)	Lamellae ^b	Paraná	Desjardin et al. 2010
<i>M. asterina</i> Desjardin, Capelari & Stevani (2007)	Lamellae and pileus ^a	Paraná, São Paulo	Desjardin et al. 2007
<i>M. deformis</i> Maas Geest. & de Meijer (1997)	Mycelium on substrate ^b	Paraná, São Paulo	Desjardin et al. 2016
<i>M. deusta</i> Maas Geest. & de Meijer (1997)	Basidiome ^d	Paraná	Desjardin et al. 2016
<i>M. discobasis</i> Métrod (1949)	Lamellae edges and stipe's apex and base ^b	São Paulo	Desjardin et al. 2007
<i>M. fera</i> Maas Geest. & de Meijer (1997)	Whole basidiome ^b	Paraná, São Paulo	Desjardin et al. 2007
<i>M. globulispota</i> Maas Geest. & de Meijer (1997)	Lamellae and stipe ^b	Paraná, São Paulo	Desjardin et al. 2016
<i>M. lacrimans</i> Singer (1989)	Stipe ^b	Amazonas	Desjardin & Braga-Neto 2007
<i>M. lucentipes</i> Desjardin, Capelari & Stevani (2007)	Stipe and mycelium ^a	São Paulo, Mato Grosso do Sul	Desjardin et al. 2007
<i>M. luxaeterna</i> Desjardin, B.A. Perry & Stevani (2010)	Stipe and mycelium culture ^a	São Paulo	Desjardin et al. 2010
<i>M. luxarboricola</i> Desjardin, B.A. Perry & Stevani (2010)	Whole basidiome ^a	Paraná	Desjardin et al. 2010
<i>M. margarita</i> (Murrill) Murrill (1916)	Whole basidiome ^c	Ceará	Alves & do Nascimento 2014
<i>M. oculisymphae</i> Desjardin, B.A. Perry & Stevani (2016)	Whole basidiome ^a	São Paulo	Desjardin et al. 2016
<i>M. singeri</i> Lodge (1988)	Stipe and lamellae ^b	São Paulo	Desjardin et al. 2007
<i>Neonothopanus gardneri</i> (Berk. ex Gardner) Capelari, Desjardin, B.A. Perry, T. Asai & Stevani (2011)	Whole basidiome and mycelium culture ^a	Piauí, Tocantins ^e	Capelari et al. 2011
<i>Resinomycena petarensis</i> Desjardin, B.A. Perry & Stevani (2016)	Mycelium on substrate ^a	São Paulo	Desjardin et al. 2016

^a Description of new luminescent species.^b Description of luminescence for the species.^c First record of luminescent species for the region.^d The authors cited A. A. R. de Meijer's personal communication about occurrence and luminescence of species.^e Holotype from Vila de Natividade collected in 1839, at the time in the state of Goiás, but currently in the state of Tocantins.

eb, 1982). There is also luminescence that can only be perceived through a photometer and goes undetected by the human eye, even in the dark (Desjardin et al., 2007). Thus, it is possible that many of the already described or yet to be discovered *Mycena* species are luminescent, but are not regarded as such because specimens were collected during the day and no test was done in the dark or with a photometer. For example, *M. discobasis* tested positive in Brazilian specimens (Desjardin et al., 2007), but *Mycena* aff. *discobasis* (from São Tomé and Príncipe) tested negative (Cooper, Desjardin, & Perry, 2018), so luminescence may not be universal within *Mycena* even for closely related species. Nonetheless, luminescence occurs in *Mycena* s. l. spread over 16 sections, leading Desjardin et al. (2007) to suspect “that the metabolic pathway leading to bioluminescence in mycenoid fungi serves an important biological role and that it evolved once early in the evolutionary history of the lineage and that the final light-emitting step(s) was lost numerous times.”

Based on Moncalvo et al. (2002) and Matheny et al. (2006), Desjardin et al. (2008) observed that the known luminescent fungal species are all basidiomycetes in three well-defined families (*Omphalotaceae*, *Physalaciaceae* and *Mycenaceae*) and an undefined fourth group that includes *Gerronema viridilucens* and *M. lucentipes* Desjardin, Capelari & Stevani. Following Dentinger et al. (2016), all these taxa belong to the order *Agaricales*, suborder *Marasmiineae*. Within *Mycenaceae*, phylogenetic analysis is still in progress to elucidate the monophyletic groups that will define *Mycena* s. str. and closely related genera.

Mycena galericulata (Scop.) Gray is the type species of *Mycena* (Pers.) Roussel, the type genus of *Mycenaceae*. The species of this genus are mushroom-forming fungi, mostly saprotrophic, functioning as decomposers of leafy or woody debris of fallen plant litter or on humus in humid tropical and temperate forests (Singer, 1986; Aronsen & Læssøe, 2016). The basidiomata may present a wide variety of macro- and micromorphological characteristics and habit varying from mycenoid, omphalioid to less frequently collybioid (Singer, 1986; Maas Geesteranus & de Meijer, 1997; Aronsen & Læssøe, 2016). Based on the Index Fungorum database (accessed on Mar 10th, 2020), 2,317 records/names are currently associated

with *Mycena*, from which 219 were segregated or combined into other genera, and the remaining 2,098 names (including synonyms and infraspecific taxa) are distributed in 49 sections, 10 subsections and six stirpes. Taxonomy of *Mycena* s. l. is overly complex and infrageneric classification generally relies on morphology, but the patterns found in species, particularly from tropical forests, are not always congruent with the concepts of the numerous sections.

To date, *Mycena* has not been conclusively circumscribed based on phylogenetic analyses. Moncalvo et al. (2002) and Matheny et al. (2006) were the first to show *Mycena* as a polyphyletic group, with a part within *Mycenaceae* and another part closer to *Marasmiaceae*. Chew, Desjardin, Tan, Musa, and Sabaratnam (2015) evaluated luminescent species of *Mycena* s. l. (*Mycenaceae*) in a comprehensive LSU-based phylogenetic analysis, which also included luminescent species of *Omphalotaceae* and *Physalaciaceae*. Their LSU-based tree showed species groups of *Favolaschia* (Pat.) Pat., *Filoboletus* Henn., *Panellus* P. Karst., *Poromycena* Overeem and *Roridomyces* Rexer embedded in multiple positions within the large *Mycena* clade (Mycenoid lineage clade). In that context, *Mycena* also did not form a monophyletic group within *Mycenaceae*. A smaller ITS-based phylogenetic tree in Terashima et al. (2016) only evaluated the phylogenetic placement of three luminescent *Mycena* species from Japan among close *Mycena* taxa, neither testing the monophyly of *Mycena* nor of its sections. Cooper et al. (2018) provided LSU- and ITS-based phylogenetic trees including *Mycena* species from São Tomé and Príncipe. Their ITS tree was useful more to verify the phylogenetic placement of 1 *Filoboletus* and 13 *Mycena* species, while the LSU tree of a broad sample (ingroup: subclass *Agaricomycetidae*) presented the *Mycenaceae* clade, where *Mycena* was not monophyletic, and included species of *Cruentomyces* R.H. Petersen, Kovalenko & O.V. Morozova, *Filoboletus*, *Panellus* and *Roridomyces*. Thus, *Mycena* is still polyphyletic within *Mycenaceae*, and a monophyletic genus concept is still to be proposed.

In Jul 2018, during a nocturnal foray conducted during the Natural History field meeting at the upper Cuieiras River Base, Manaus (Field Museum Project JST/JICA, SATREPS, 2015), specimens of a luminescent mushroom-forming fungal species were

found. An additional collection was made in May 2019. The primary goal of this study was to combine morphological and LSU- and ITS-based phylogenetic analyses to evaluate whether this luminescent species is a new or an already described *Mycena* species, perhaps one without mention of its luminescence. The phylogenetic trees and the unique species-level morphology by comparison to the literature led us to conclude that this represents a new species, *Mycena cristinae*.

The Cuieiras River Biological Reserve (reference point: 2°35.37 S, 60°06.92 W) covers 22,735 ha in the lower Negro River basin, and is located 60 km northwest of Manaus, Amazonas State, Brazil (Marques Filho, Dallarosa, & Pacheco, 2005). The regional vegetation is typically primary forest with trees reaching 30–40 m in height (Jardim & Hosokawa, 1986/87). The Reserve consists of a mosaic of terra-firme (upland) (Prance, 1978), campinarana (white sand) (Adeney, Christensen, Vicentini, & Cohn-Haft, 2016) and igapó (seasonally flooded black water swamp) (Junk et al., 2011) forests. The climate is “Am” in the Köppen classification (Radam, 1978), with mean temperature of 26.7 °C and high rainfall, with monthly precipitation around 150 mm on average during the rainy season (between Oct and Jun) and lower rainfall from Jul to Sep (less than 99 mm/mo), typical of the Central Amazon (Marques Filho et al., 2005). The soils on the terra-firme are principally Alic Yellow Oxisols (Chauvel, 1982; Oliveira et al., 2008), with high acidity and poor in nutrients (Ranzani, 1980). The station was established by the “Museu da Floresta” Project (INPA/MCTIC) in cooperation with Kyoto University (Japan) for research activities, scientific tourism and field training about Amazonian biodiversity.

Three fresh specimens (set of basidiomata) were collected. The main collection was photographed in the field at night, both in the full dark and with camera flash, along with photographs in the laboratory. Macroscopic description was based on fresh materials. Lamellae spacing was derived according to *L*, number of lamellae that reach from the pileus edge to the stipe apex, and *l*, number of series of lamellulae. Color-coding was according to Online Auction Color Chart (Kramer, 2004). Collections were dried at 40 °C in a food dehydrator or in silica gel. For microscopic description, thin sections of dried basidiomata were rehydrated in 70% ethanol and mounted in 5% KOH or in Melzer’s reagent. Basidiospore dimensions were measured as the min.–max. range of length × the range of width, followed by: x_{mm} , the min.–max. range of the arithmetic means of length × of width; x_{mm} , the mean of the arithmetic means of length (± standard deviation – SD) × of width (± SD); Q_{mm} , the min.–max. range of the means of length/width; Q_{mm} , the mean of the means of length/width (± SD); *n*, the number of spores measured; and *s*, the number of collections examined. Microstructures were described using a DM 2500 optical microscope (Leica, Wetzlar), with line drawings of the structures made with a drawing tube coupled with the light microscope. The collections were deposited at INPA Herbarium.

For the DNA sequencing, this study was registered in SisGen (Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado) under the number ACEEA19. DNA extraction, PCR amplification of the nuc rITS (ITS1–5.8S–ITS2) and nuc rLSU (28S) and sequencing procedures followed Oliveira, Vargas-Isla, Cabral, Rodrigues, and Ishikawa (2019). The primers used were ITS5/ITS4 and LR0R/LR5, respectively (White, Bruns, Lee, & Taylor, 1990). The ITS region was successfully sequenced from two of three collections, while sequencing of the LSU region only succeeded for LR0R from the holotype. Forward and reverse reads were assembled to obtain consensus sequences of the new species in Geneious R7. The sequences generated from the specimens were deposited in the GenBank database (NCBI).

LSU-based phylogenetic analyses were conducted in two steps:

1) the new LSU sequence and the mycenoid or *Mycenaceae* lineage (Chew et al., 2015; Cooper et al., 2018) + some representatives of a hydropoid lineage (Moncalvo et al., 2002; Matheny et al., 2006; Cooper et al., 2018) + some representatives of *Omphalotus* (*Omphalotaceae*) lineage (Moncalvo et al., 2002; Matheny et al., 2006; Chew et al., 2015); 2) close (first hundred) sequences from a BLAST search with the new LSU sequence as the query + all LSU sequences in GenBank determined as *Cruetomyces*, *Favolaschia*, *Filobolus*, *Mycena*, *Mycenoporella*, *Pannellus*, *Poromyces*, *Roridomyces* and *Resinomyces* (*Mycenaceae* clade). The first step aimed to verify the phylogenetic placement of the new species whether within the *Mycenaceae* lineage or within the hydropoid lineage, having the *Omphalotus* lineage as the outgroup. The second aimed to zoom-in on the *Mycenaceae* lineage to observe the clades formed by the nine listed genera and the affiliation of the new species.

ITS-based phylogenetic analyses were performed in two steps: 1) the first hundred sequences retrieved from a BLAST search in GenBank using the newly generated ITS sequences as the query + all ITS data named as *Mycena* (vouchered and non-vouchered) in GenBank; 2) species-level determined sequences of *Mycena* in the region of the tree from the previous analysis depicted with a blue dashed circumscription + representatives of *M. galericulata* (light blue highlight) (Supplementary Fig. S3). In the first step, the BLAST search with the newly generated ITS sequences recovered data deemed to be the closest taxa to *M. cristinae* (84.29–91.65% identity, 53–100% query cover), many undetermined fungal strains or as *Mycena* sp. In the second, the criterion of selecting species-level determined data was only not followed for the strains that grouped with the new species with strong support.

The alignments were produced via MUSCLE v3.8.31 (Edgar, 2004) and edited in Geneious R7 (Kearse et al., 2012). Poor quality sequences or distant taxa (not close to the targeted ingroup core through observation of the alignment) were removed from the datasets. The nucleotide substitution model selected was GTR+I+G via MrModeltest 2.3. (Nylander, 2004) for all alignments. The alignments and tree files can be found at TreeBASE 26922. All sequences from GenBank used in the analyses are identified by their accession number in the trees.

Excepting for the first step of the ITS-based analyses, we conducted MC³ Bayesian analyses (BA) with MrBayes 3.2.1 (Ronquist et al., 2012), using default settings from the model (Nst = 6). The BA consisted of two independent runs of: a) 5,000,000 generations, sampled every 500 generations, six independent chains and two swaps for the second step of the ITS-based analyses; b) 10,000,000 generations, sampled every 1,000 generations, six independent chains and two swaps for both steps of the LSU-based analyses. Burn-in was set at 10%. Final trees followed the 50% majority-rule consensus method. Branch lengths were summarized based on the 95% highest posterior density credible interval. Maximum Likelihood analysis (ML) was performed for all four steps. The trees were constructed using the GTR+Γ+I model in RaxML 7.0.4 (Stamatakis, 2006) with fast-bootstrapping implementing CAT approximations for 1,000 pseudoreplicates and a full ML optimization for the final tree. The exception was for the second step of the ITS-based analyses where GTRGAMMAI was implemented with GAMMA+P-Invar Model parameters estimated up to an accuracy of 0.001 Log Likelihood units. The phylogenetic trees were visualized in FigTree 1.3.1 and edited in CorelDraw X7.

Taxonomy

Mycena cristinae J.S. Oliveira, sp. nov. Figs. 1–3.
 MycoBank no.: MB 836834.

Etymology: *In memoriam* of Dr. Cristina Sayuri Maki (professor at UFAM – Federal University of Amazonas), beloved friend who recently passed away.

Diagnosis: Pileus 7–22 mm diam, striate-sulcate, grayish brown or fuscous olivaceous brown. Lamellae adnate to subdecurrent, 10–14. Stipe pale olivaceous, with slightly bulbous base without mycelium. Basidiomata and mycelium luminescent, with a green-yellow light. Basidiospores $6.7\text{--}8.7 \times 4.7\text{--}6 \mu\text{m}$, inamyloid or weakly amyloid. Cheilocystidia ramose. Pileus trama dextrinoid: 1) the hypodermium, upper layer of inflated, pale brown hyphae; 2) lower layer similar to the lamellar trama. Pileipellis is a coralloid pellicle of slender hyphae overlaying the hypodermium. Lignicolous.

Type: BRAZIL, Amazonas State, Manaus, upper Cuieiras River, along trail on the terra firme near the Upper Cuieiras River Station - INPA, 3 Jul 2018, J.S. Cardoso & F. Andriolli JS347 (**holotypus**, INPA 287129).

Gene sequences ex-holotype: MT921381 (ITS) and MT921384 (LSU).

Pileus 7–22 mm diam (Fig. 1A, D, H), campanulate, convex to plano-convex, or plane, umbilicate or shallowly depressed, rugulose, margin pellucid-striate to somewhat irregular, but distinctly striate-sulcate (shallow sulci), slightly scrobiculate due to venular hymenophore between lamellae, margin decurved to straight, edge entire to crenate; surface glabrous, dull at the disc, somewhat translucent at the margin, overall moist (not slimy), wax-like bright when fresh, non-hygrophanous, grayish brown (OAC639) or mainly fuscous olivaceous brown (OAC640), darker at the center and in the sulci; membranous, delicate, context thin (< 1 mm), whitish. Lamellae (Fig. 1A, E, H) adnate to subdecurrent, distant, straight (horizontal) to slightly arched (concave), $L = 10\text{--}14$, mostly intervenose, $l = 2$, pale grayish brown (OAC723) fading to pale cream (around OAC809) near the edge, opaque, sometimes pruinose, edge even, non-marginate. Stipe (Fig. 1A, E–H) $13\text{--}26 \times 1\text{--}2$ mm, central, cylindrical, equal, with a slightly bulbous base without basal mycelium, sometimes slightly compressed, delicate cartilaginous, hollow, flexuous, glabrous, smooth or slightly fibrillose, humid with waxy bright, grayish beige (OAC802) to pale brown (OAC730) or pale olivaceous (OAC722), sometimes whitish olive-green (around OAC830) at the apex. Odor not verified. Luminescent (Fig. 1B, C), glowing with a distinct green-yellow light in the dark, more intense on the stipe toward the base, along with the mycelium (invisible in daylight) covering the substrate; pileus and hymenophore emitting a faint light as though covered by soot, but with slightly brighter lamellae or sulci.

Basidiospores (Fig. 2A) $6.5\text{--}9\text{--}(10) \times 4\text{--}6\text{--}(8) \mu\text{m}$ [$x_{\text{m}} = 7.1\text{--}7.7 \times 4.4\text{--}5.1 \mu\text{m}$, $x_{\text{mm}} = 7.4 (\pm 0.3) \times 4.8 (\pm 0.4) \mu\text{m}$; $Q_{\text{m}} = 1.4\text{--}1.6$; $Q_{\text{mm}} = 1.5 (\pm 0.1)$; $n = 30$; $s = 3$], obovoid, ellipsoid to subellipsoid, some lacrymoid, smooth, hyaline, thin-walled, very weakly amyloid (especially the small droplets), sometimes seemingly inamyloid. Basidia (Fig. 2B) $20\text{--}27\text{--}(31) \times 5.5\text{--}8 \mu\text{m}$, clavate, smooth, hyaline, thin-walled, 4-sterigmate, inamyloid. Basidioles (Fig. 2C) $20\text{--}27 \times 5.5\text{--}8 \mu\text{m}$, clavate to cylindrical, smooth, hyaline, thin-walled, inamyloid. Pleurocystidia absent. Cheilocystidia (Fig. 2D) forming a sterile lamellar edge, but not present on all parts along the margin, hyphoid and branched, or cystidioid and ramose, then similar to Rameales-type structures, or coralloid, main body $12.5\text{--}55 \times 3.5\text{--}$

$10.5 \mu\text{m}$, cylindrical, contorted clavate, turbinate, or irregular in outline, some apically branched, hyaline, inamyloid; diverticula apical, some along the sides, short to elongate, $2\text{--}20.5 \times 1\text{--}3 \mu\text{m}$, filamentous or cylindrical, digitiform, verruciform, to knob-like, with constrictions, or irregular in outline, simple or branched, solid, hyaline, apex obtuse to rounded. Lamellar trama dextrinoid, subregular to irregular, interwoven, $1.5\text{--}8.5 \mu\text{m}$ diam, cylindrical or catenulate (some slightly inflated), smooth, hyaline, thin-walled. Pileus trama dextrinoid, irregular, interwoven, non-gelatinous, composed of two distinct layers: 1) upper (Fig. 3B), forming the hypodermium of the interface with the pileipellis, a somewhat slender stratum composed of cylindrical, inflated hyphae, distinctly broader than those of the lower layer, $5\text{--}47.5 \mu\text{m}$ diam, conspicuous, pale brown in KOH, dark brownish red in Melzer, thin-walled to slightly thick-walled, smooth, packed; 2) lower (Fig. 3C), between the hypodermium and the hymenium, often wider than the upper layer, irregular, looser, composed of interwoven, slender, cylindrical hyphae, $1.5\text{--}8.5\text{--}(14) \mu\text{m}$ diam, similar to those of the lamellar trama, hyaline, smooth, thin-walled. Pileipellis (Fig. 3A) consists of a very thin, very loose-aerated and short tangle of abundantly branched, slender hyphae, forming a distinctly coralloid pellicle overlaying or entangled with the outmost broad hyphae of the hypodermium, non-gelatinous, the slender hyphae similar to those of the stipitipellis, hyphae $0.7\text{--}2.5\text{--}(3) \mu\text{m}$ diam, branched, smooth, hyaline, inamyloid, moderately diverticulate, diverticula short, $0.7\text{--}2.5 \times 0.7\text{--}1.5 \mu\text{m}$, verruciform to digitiform, apex rounded. Stipe trama strongly dextrinoid, cortical hyphae parallel, hyphae cylindrical to inflated, slightly catenulate, $1.5\text{--}18 \mu\text{m}$ diam, those of the stipe apex hyaline, those below hyaline to pale brown, bleaching in KOH solution, smooth, moderately thick-walled; scarce solid hyphae, pale yellow, conspicuous, fuscous or translucent instead of hyaline, seemingly oleiferous in sarcomitic tissue, vermiform or irregular in outline, some nodose, $3\text{--}6 \mu\text{m}$ diam; internal hyphae undistinguished. Stipitipellis (Fig. 2E) composed of very slender hyphae, $1.5\text{--}4 \mu\text{m}$ diam, externally incrustated with pale brown granules (more on the base), and/or diverticulate, forming a loose layer similar to the pileipellis, diverticula verruciform, digitiform to setulae-like, hyaline, branched; caulocystidia absent. Clamp connections present in all tissues.

Habit and habitat: Solitary to gregarious, some in clusters or caespitose, on rotten wood (stumps or trunk) of dicotyledonous trees (some of *Oleaceae*), the dead wood sometimes also covered by bryophytes.

Additional material examined: BRAZIL, Amazonas State, Manaus, upper Cuieiras River, Cantarelos trail on terra-firme, 4 Sep 2018, J.S. Cardoso & F. Andriolli JS351 (INPA 287130); along trail on the terra-firme near the upper Cuieiras River Station - INPA, 25 May 2019, J.S. Cardoso & F. Andriolli JS767 (INPA 287131), same site as the holotype.

Mycena cristinae is characterized by growing on dead trunks or stumps where its mycelium is only visible in the dark due to the bright green-yellow luminescence. The basidiomata are also luminescent, with stipe brighter than the hymenophore and pileus. There is uncertainty whether the basidiospores are inamyloid or faintly amyloid in all three collections, similar to *M. castaneomarginata* Singer, *M. castaneostipitata* Singer, *M. depilata* Singer, *M. hemitrichialis* Singer, *M. lacrimans* Singer, *M. microstena* Singer, and *M. subtenerrima* Singer (Singer, 1989). The cheilocystidia are singular in shape, hyphoid and branching elements, or cystidioid similar to Rameales-type structures. The pileus trama has an upper layer composed of distinctly inflated, pale brown hyphae evident in KOH solution. Both pileipellis and stipitipellis are coralloid, consisting of a pellicular layer of very slender, branching and divertic-

Fig. 1 – Macroscopic view of *Mycena cristinae* (J.S. Cardoso & F. Andriolli JS347, holotype – INPA 287129). A: basidiomata *in situ*, at night, using camera flash. B: basidiomata *in situ*, at night, without camera flash. C: basidiomata and mycelium on the substrate *in situ*, at night, without camera flash. D: pileus surface. E: hymenophore. F: stipe base. G: stipe base accompanied by fragment of the substrate with bryophytes. H: whole set of basidiomata. D–H photographed in lab using camera flash and room light. Bars: 10 mm. Photos: Francisco Farroñay (A–C); Julia S. Cardoso (D–H).

ulate hyphae entangled with the broader hyphae of the hypodermium just below. This pellis texture helps to keep the surfaces moist, but they are not slimy (gelatinous matrix absent). Cystidioid caulocystidia and pleurocystidia are absent. The stipe is insititious with a slightly bulbous base, non-viscid and not exuding drops. The lamellae are non-marginate, adnate to subdecurrent, distant, straight to slightly arched. The combination of morphological characteristics of *M. cristinae* prevent its unambiguous placement in

one of the several traditional sections of *Mycena*. Assuming the spores are typically amyloid, the species may fit as a non-marginate lamellae member of sect. *Rubromarginatae* (Maas Geesteranus, 1980; Maas Geesteranus & de Meijer, 1997; Robich, 2016).

The coralloid pellicle forming both pileipellis and stipitipellis, the hypodermium of the pileus with more inflated hyphae, the cheilocystidia bearing apical projections, the absence of pleurocystidia, the faintly amyloid (small droplets of the protoplasm) basid-

Fig. 2 – Microscopic features (100×) of *Mycena cristinae* (J.S. Cardoso & F. Andriolli JS347, holotype – INPA 287129). A: basidiospores. B: basidia. C: basidioles. D: cheilocystidia. E: hyphae of the stipitipellis. Bar: 10 µm. Illustration by: J. J. S. Oliveira & J. S. Cardoso.

iospores, the stipe having a slightly bulbous base without basal mycelium, some subdecurrent lamellae with series of lamellulae and the striate-sulcate pileus in basidiomata of *M. cristinae* are

strong morphological affinities to the lignicolous and luminescent *M. coralliformis* A.L.C. Chew & Desjardin placed in sect. *Rubro-marginatae* (Chew et al., 2015). The luminescence (emitting yel-

Fig. 3 – Profile section of the pileus (20×) of *Mycena cristinae* (J.S. Cardoso & F. Andriolli JS347, holotype – INPA 287129). A: pileipellis. B: pileus trama upper stratum. C: pileus trama lower stratum. D: hymenial layer. Bar: 10 µm. Illustration by: J. J. S. Oliveira.

lowish green light) in *M. coralliformis*, a lignicolous species described from Peninsular Malaysia, is only observed from its mycelium on the substrate and in culture media. The basidiomata of *M. coralliformis* also differs by having marginate lamellae (edge bicolorous with coffee brown) that are less numerous ($L = 9\text{--}11$) with 2–3 series of lamellulae; by the complete absence of gray or olivaceous pigments in the pileus and stipe (with more bulbous base), by having smaller (less variable in size) basidiospores [$6.4\text{--}7.2 \times 4.4\text{--}4.8$ (-5.2) µm]; by having simpler, dark brown and stag-horn cheilocystidia; by having a hypodermium and pileus trama hyaline to yellowish; and by having broader ($2\text{--}4.8$ µm diam) hyphae of the coralloid hyphae of the pileipellis.

Mycena cristinae is not similar to any other described luminescent *Mycena* species, except for a very vague morphological resemblance to *M. fulgoris* Cortés-Pérez & Desjardin (Cortés-Pérez et al., 2019) and *M. noctilucens* Corner *sensu* Chew et al. (2015). *Mycena fulgoris* differs by having paler pileus (mostly beige or pale brown with a white margin), by being luminescent only on the stipe, which has strigose basal mycelium, by having more regularly shaped cheilocystidia (narrowly to broadly clavate or fusiform, rostrate or furcate with 1–4 apical projections), and by having a pileipellis in the form of a cutis of repent, narrow, diverticulate hyphae and a similar hypodermium but hyaline. *Mycena noctilucens* differs by having smoother and non-olivaceous pileus, by the less numerous lamellae (8–10), by the dark brown to yellowish brown stipe, which has a downy pad of basal mycelium, by having broader and more ellipsoid basidiospores ($5.6\text{--}7.2$ µm), by having

smaller ($2.5\text{--}10 \times 2\text{--}5$ µm) more regularly shaped cheilocystidia (clavate to ventricose, usually with mucronate or furcate to digitate apical protuberance), and by having a more regular pileipellis (a cutis of smooth, sometimes diverticulate hyphae). Even more vaguely similar, the luminescent *M. lucentipes* (Desjardin et al., 2007), described from the Atlantic Rainforest (São Paulo, Brazil), whose phylogenetic placement is outside *Mycenaceae* and closer to *G. viridilucens* (the hydropoid clade in Matheny et al., 2006), and *M. silvaelucens* B.A. Perry & Desjardin (Desjardin, Perry, Lodge, Stevani, & Nagasawa, 2010), especially the pattern of the luminescence of the basidiomata.

There are three other lignicolous species worthy of comparison: *M. paraboliciformis* Singer (Singer, 1969; Pegler, 1983), *M. parabolica* (Fr.) Quél. and *M. trinitatis* Dennis (Dennis, 1951). They are morphologically and ecologically very similar to *M. cristinae*, all described from South America, but their luminescent properties are unknown. *Mycena paraboliciformis* differs mainly by producing distinctly amyloid, somewhat larger basidiospores ($8\text{--}10 \times 5\text{--}7$ µm), shorter basidia ($15\text{--}20$ µm), and smaller ($15\text{--}30 \times 7\text{--}17$ µm), more regular cheilocystidia (Singer, 1969; Pegler, 1983). *Mycena parabolica*, as described in Dennis (1951), differs mainly by forming larger pileus ($20\text{--}30$ mm diam), which are more sepia-colored, and by the larger basidiospores ($8\text{--}10 \times 6\text{--}7$ µm). Pegler (1983) considered *M. paraboliciformis* to be a synonym of *M. parabolica*, but this was not formalized. *Mycena trinitatis* differs from *M. cristinae* mainly by having smaller basidiomata (pileus up to 5 mm diam, stipe less than 1 mm thick), and by forming non-diverticu-

Fig. 5 – Best-scored Maximum Likelihood (ML) tree (TL: 3.675817) and 50% majority-rule consensus tree (TL: 9.930820) via Bayesian analysis (BA) of the second step of the ITS-based phylogenetic analyses. Strongly supported nodes are represented by thick black stems while moderately to weakly supported nodes are in gray. Significant statistical support values of Bootstrap ML ($\geq 70\%$)/Posterior Probability BA (≥ 0.95) are provided.

late, cylindric-ventricose cheilocystidia (Dennis, 1951).

Mycena cristinae was found with its glowing mycelium dominating a trunk in an advanced stage of decay and the paratypes were also found on woody substrates. Singer (1989) described 43 new *Mycena* species whose luminescence properties are unknown, but *M. lacrimans* was later reported to be luminescent by Desjardin and Braga-Neto (2007). This species presents an intense, yellowish green luminescence at the stipe apex that fades away towards the base. The intense luminescence of the stipe apex causes the pileus

disc and proximal extremity of the lamellae (adnate to subdecurrent) to glow, but with weaker intensity. Basidiomata of *M. lacrimans* grow on fallen dicotyledonous leaves and small twigs (terra-firme, Amazon forest, Brazil) and is very distinct in morphology from *M. cristinae*. Among the other 42 *Mycena* species, 10 are lignicolous: *M. castaneostipitata*, *M. depilata*, *M. fuscocystidiata* Singer, *M. griseoradiata* Singer, *M. icterinoides* Singer, *M. intervenosa* Singer (Nom. illegit., Art. 53.1, Index Fungorum), *M. lecythidacearum* Singer, *M. microstena*, *M. microtephra* Singer, and *M.*

pluvialis Singer. Among these species, *M. cristinae* is similar only to *M. castaneostipitata* and *M. lecythidacearum*. *Mycena castaneostipitata* differs mainly by having a violaceous brown, smaller pileus (8–9 mm diam), which is papillate in young stages, by having lamellae presenting brown micro dots under hand lens that are caused by the melleus, incrustated pleurocystidia coated by straminous or melleus resin, by the stipe with basal mycelium, and by presenting part of the pileipellis with gelatinous stratum (Singer, 1989). *Mycena lecythidacearum* differs mainly by the stipe with basal mycelium, by the distinctly amyloid basidiospores, and by the pileipellis originally gelatinous (Singer, 1989). *Mycena lecythidacearum* has the hypodermium of fuscidulous, inflated hyphae with intracellular pigment, which is comparable to the hypodermium in *M. cristinae*. Other somewhat similar, but foliicolous species in Singer (1989) are *M. delica* Singer and *M. pantopolia* Singer. *Mycena delica* is similar in the macroscopic features, but the stipe has a basal mycelium, and it is quite dissimilar in the micromorphology. *Mycena pantopolia* produces entirely grayish and thinner/tender basidiomata (pileus $\pm$ 5 mm diam; stipe 28–33 $\times$ 0.5 mm), more crowded lamellae, stipe with a white basal mycelium, distinctly amyloid, smaller and narrower basidiospores (3.3–4.8 μ m), and cheilocystidia with different shapes.

As result of the LSU-based phylogenetic analyses, the ML tree of the first step is presented in Fig. 4. This analysis consisted of 109 strains with the final number of 894 characters (nucleotides) in the trimmed alignment. The BA tree of the corresponding step is provided in Supplementary Fig. S1, along with ML and BA trees of the second step (Supplementary Fig. S2) and detailed data about all analyses. The broad LSU tree of Fig. 4 shows a major, strongly supported clade determined as *Mycenaceae* (in the olive-green dashed rectangle), sister to a smaller, strongly supported clade named /hydropoid, and an *Omphalotaceae* minor clade as the outgroup. The LSU phylogeny reveals that *M. cristinae* is sister (BS 88/ PP 1.0) to *M. coralliformis* (no ITS available) within the *Mycenaceae* clade rather than in /hydropoid (Fig. 4) like some *Mycena* species. These two species grouped along with an uncultured *Mycenoid* sp. (FJ179469) in the second step analysis (Supplementary Fig. S2). This close relationship between *M. coralliformis* and *M. cristinae* is expressed in meaningful shared morphological characteristics of the basidiomata that reflect close evolutionary history. Since *Mycena* sect. *Rubromarginatae* seems polyphyletic (Chew et al., 2015; and Fig. 4 in this paper), these two may form their own section. Meanwhile, the LSU tree including genera of *Mycenaceae* sampled in the second step was poorly resolved (Supplementary Fig. S2), except for some small clades. A cladistic delimitation to *Mycena* and close genera in *Mycenaceae* is still pending.

From the ITS-based phylogenetic analyses, the ML tree of the first step (Supplementary Fig. S3) had mostly unsupported resolution as expected, but served to identify the closest *Mycena* species relative to the newly proposed one in GenBank. The strains determined at species-level within the blue-dashed circumscription were selected along with *M. galericulata* strains for the second step. Exceptionally, only three undetermined *Mycena* strains (those forming a strongly supported clade with *M. cristinae*) were brought to this dataset. This consisted of 86 strains with the final number of 562 characters in the trimmed alignment. Both ML and BA trees (rooted at midpoint) present *M. cristinae* in the basal clade along with *M. albiceps* (Peck) Gilliam, *M. citricolor* (Berk. & M.A. Curtis) Sacc., *M. galericulata* and *M. noctilucens*, even though quite distant from them (Fig. 5). The new species is rather close to three undetermined strains 'FJ179469 Uncultured *Agaricales* clone GSM5', 'KP191964 *Mycena* sp. TL2529' and 'MN492639 *Mycena* sp. NW949', forming a strongly supported clade (see Supplementary

Fig. S3).

In conclusion, *M. cristinae* is the second morphologically described *Mycena* species in the central Amazon forest to be verified *in situ* as luminescent and the first to be evaluated in phylogenetic analyses (including LSU and ITS data). Future studies may discover more luminescent fungal species in the great Amazonian biodiversity.

Disclosure

The authors declare no conflicts of interest. All the activities undertaken in this study comply with current Brazilian laws. The accession number of the Brazilian National System of Management of Genetic Heritage and Associated Traditional Knowledge (SisGen) is ACEEA19.

Acknowledgements

This study was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) with a scholarship from the Programa Nacional de Pós-doutorado (PNPD) granted to J.J.S. de Oliveira, post-doctoral fellow DIBOT, INPA. R. Vargas-Isla thanks the Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) for a DTI fellowships (proc. no. 062.00219/2020), and T.S. Cabral thanks PNPD/CAPES for post-doctoral fellowships in the PPG-GCBEV, INPA. C.R. Clement thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a research fellowship (proc. no. 303477/2018-0). We thank Francisco Farroñay for the photographs of the new species in the field. The authors thank the INPA Herbarium and the anonymous peer-reviewers. This study was supported by FAPEAM, Centro de Estudos Integrados da Biodiversidade Amazônica (CENBAM), CNPq, Biodiversity Research Program (PPBio), Japan Science and Technology Agency/Japan International Cooperation Agency-Science and Technology Research Partnership for Sustainable Development (JST/JICA-SATREPS) and Japan Society for the Promotion of Science/ Fostering Joint International Research (19KK0189) and JSPS Core-to-Core Program (JPJSCCA20170005).

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