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Mycena lamprocephala, a new luminescent species from the Brazilian Amazon

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Abstract

A luminescent fungus growing on decaying leaves and sticks was collected in terra-firme forest at the upper Cuieiras river, Amazonas, Brazil. Morphological study and phylogenetic analysis (based on ITS+LSU data) confirmed it as a new species of *Mycena*. *Mycena lamprocephala sp. nov*. is characterized macroscopically by small, thin, basidiomata with an olivaceous brown pileus and glutinous stipe, and microscopically by diverticulate pleurocystidia, ramose cheilocystidia, and thin, diverticulate and branching pileipellis hyphae. The luminescence of the pileus and of the mycelium in the substrate is typically green and sometimes pulsating. This is the third luminescent species of Mycenaceae described from the Amazon Forest.

Key words: Agaricales, bioluminescence, Mycenaceae, Neotropical mycodiversity, taxonomy

Introduction

Bioluminescence is a natural phenomenon in which organisms are able to emit light, being recognized as 'living lights' (Mahish *et al.* 2021). Having independently evolved dozens of times, the ability of living organisms to emit light has been observed in about 10,000 species from 800 genera, although these numbers may be an underestimate of the actual number of luminescent species (Haddock *et al.* 2010). Among the luminescent species, 125 species of mushroom-forming fungi have been recorded to date (Mihail 2015, Terashima *et al.* 2016, Chang *et al.* 2020, Oliveira *et al.* 2021, Cortés-Pérez *et al.* 2023, Oba & Hosaka 2023, Silva-Filho *et al.* 2023). These fungi represent five distinct lineages belonging to the clades named Omphalotus, Armillaria, Mycenoid, Lucentipes and Eoscyphella (Desjardin *et al.* 2008, 2010, Chew *et al.* 2015, Silva-Filho *et al.* 2023). Oliveira *et al.* (2021) listed 19 species of luminescent

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fungi already described for Brazil, plus a new species, *Mycena cristinae* J.S. Oliveira (2021: 398). More recently, Silva-Filho *et al.* (2023) described a new genus and a new species of luminescent fungi, *Eoscyphella luciurceolata* Silva-Filho, Stevani & Desjardin (2023: 15), bringing the total to 21. Of these, 17 species belong to the genus *Mycena* (Pers.) Roussel (1986: 64). Although the origin, evolution, physiological-adaptive advantage, and ecological function of bioluminescence in fungi have not yet been fully elucidated (Desjardin *et al.* 2008, Oliveira *et al.* 2013), some studies have glimpsed some aspects such as the origin, dynamics and light emission mechanism of fungal luciferase (Oliveira *et al.* 2012, 2015, Ke *et al.* 2020).

Mycena is the type genus of the Mycenaceae family and the most species-rich of the family in Brazil, with 160 records *(*Spegazzini 1889, Rick 1919, 1938, 1961, Singer 1953, 1973, 1983, 1989, Bononi *et al.* 1981, 1984, 2008, Raithelhuber 1984a, 1984b, 1985a, 1985b, 1991, Capelari & Maziero 1988, Putzke 1994, Maas Geesteranus & de Meijer 1997, 1998, Desjardin *et al.* 2007, 2010, 2016, Alves & Nascimento 2014, Mendoza *et al.* 2018, Oliveira *et al.* 2021, Patrício *et al.* 2023). Species in the genus are mushroom-forming and mostly saprophytic, playing a vital function in litter decomposition in tropical and humid temperate forests (Singer 1986, Aronsen & Læssøe 2016). The basidiomata can be very small and thin to large and slightly robust, with mycenoid, omphalinoid or, more rarely, collybioid habit (Singer, 1986). An enormous diversity of macro- and micromorphological characteristics are observed across species, leading to taxonomic complexity that makes it difficult to define the stable limits at genus, infragenus and species level (Niveiro *et al.* 2012).

Early molecular work by Moncalvo *et al.* (2002), revealed *Mycena* to be a polyphyletic group in the Agaricales. In Matheny *et al.* (2006), *Mycena* species form three independent lineages: Mycenaceae *s. str*., including the type species *M. galericulata* (Scop.) Gray (1821: 619), within the Tricholomatoid clade and at least two separate lineages within the Marasmioid clade. In Dentinger *et al.* (2016), Mycenaceae *s. str.* branched within the suborder Marasmiineae (clade Marasmioid in Matheny *et al.* 2006) rather than in the suborder Tricholomatinae (clade Tricholomatoid in Matheny *et al.* 2006). Chew *et al.* (2015) evaluated luminescent species from *Mycena* and other closely related taxa in a broad phylogenetic reconstruction in the context of luminescent fungi. Their mycenoid clade is the largest, containing members of *Mycena*, *Filoboletus* Hennings (1900: 146), *Favolaschia* (Pat) Patouillard (1892: 116), *Roridomyces* Rexer (1994: 132) and *Panellus* P. Karsten (1879: 14), but *Mycena* does not form a monophyletic group in the LSU tree. In Cooper *et al.* (2018) and Oliveira *et al.* (2021), the phylogeny based on the LSU places the analyzed species in two different clades, Mycenaceae and hydropoid. Despite the advances in molecular phylogenetic studies, *Mycena* remains without clear cladistic definition as well as other genera within Mycenaceae *s. str*.

The hydropoid clade (Moncalvo *et al.* 2002, Bodensteiner *et al.* 2004, Matheny *et al.* 2006) includes species of *Atheniella* Redhead, Moncalvo, Vilgalys, Desjardin & B.A. Perry (2012: 1), which correspond to the adonis clade in Moncalvo *et al.* (2002) and other species of *Mycena* sect. *Adonideae* (Fr.) Quél. (Redhead 2012, 2013, 2016a, b). *Phloeomana* Redhead (2013: 2), composed by species of *Mycena* section *Hiemales* Konrad & Maubl. (Holec & Kolařík, 2017), was also included in the clade as well as *Leucoinocybe* Singer (1943: 143) ex Antonín, Borovička, Holec & Kolařík (2019: 441) and *Lignomphalia* Antonín, Borovička, Holec & Kolařík (2019: 443) (segregated from *Clitocybula* (Singer) Singer ex Métrod (1952: 74)) (Antonin *et al.* 2019). *Mycena auricoma* Har. Takahashi. (1999: 73), present in Matheny *et al.* (2006), was recombined in *Leucoinocybe* (Matheny *et al.* 2020) and *Mycena lapalmaensis* Dähncke & Robich (2010: 99) is currently a synonym of *Porotheleum omphaliiforme* (Kühner) Vizzini, Consiglio & M. Marchetti (2022: 110) (Consiglio *et al.* 2022). The hydropoid clade is currently recognized as the *Porotheleaceae* Murrill (Antonín *et al.* 2019; Vizzini *et al.* 2019, 2022, Kalichman *et al.* 2020; Matheny *et al.* 2020; Consiglio *et al.* 2021).

Mycena lacrimans Singer (1989: 78) was described from the Reserva Florestal Adolpho Ducke, Manaus, Amazonas State, Brazil and was only attested as luminescent by a new collection from km 83 (Manaus-Careiro districts) of the Federal Road BR-319 close to the Paraná do Castanho-Mirim River (Singer 1989, Desjardin & Braga-Neto 2007). Oliveira *et al.* (2021) described *M. cristinae* from the upper Cuieiras river region, in the same municipality and state in Brazil and it is the second luminescent fungal species described from the Amazon Forest. The present study addresses the taxonomy and the phylogenetic placement of a luminescent *Mycena* species, different to that described by Oliveira *et al.* (2021) and also found in the upper Cuieiras river, municipality of Manaus, Amazonas. Combined ITS and LSU phylogenetic analyzes were implemented to verify the uniqueness of *M. lamprocephala sp. nov.* and to resolve the relationship with other mycenoid species within and between Mycenaceae s. str. (for the first time in analysis concatenating the two markers) and Porotheleaceae (hydropoid clade). After morphological and molecular phylogenetic analyses, we concluded that it was a new luminescent species.

Material and methods

Sampled area

The Upper Cuieiras River Biological Reserve (Reserva Biológica do Alto Cuieiras) is located in the Environmental Preservation Area ME Rio Negro—South Sector (geographic coordinates: 2°35'37''S 60°06'92'' W). It comprises about 22,735 ha, approximately 60 km north from Manaus, Amazonas State, Brazil (Marques Filho *et al.* 2005). This is an undisturbed area, with primary lowland vegetation, which includes the Igarapé Asu Basin, combining upland forest (terra-firme) and flooded igapó forests, with several plateaus intercalated by valleys, forming many "igarapés" (streams) (LBA 2015). The soil is of the Alic Yellow Latosol type, with a clay-like texture and good drainage (Chauvel 1982). The climate is typical of the Central Amazon with high temperatures (25.2°C to 33.2°C); abundant rainfall throughout the year (monthly average >150 mm between October and June) and a short dry season (monthly average < 150 mm between July and September); and average monthly relative humidity greater than 80 % (Marques *et al.* 2005).

Morphological analyses

The three collections each contained a single basidiome. The basidiome in the best condition was photographed *in situ* at night both in the dark and with camera flash, and also in the laboratory. The macromorphological observations were based on the fresh basidiome. Color codes are according to Kornerup & Wanscher (1978). Terminology of macroscopic characteristics follows Largent (1973) and for microscopic features Largent *et al.* (1977) and Vellinga (1988). The specimens were dried at 40 °C.

Microstructures were examined from hand-made sections of dried basidiome, treated with 70 % ethyl alcohol, rehydrated with 3 % aqueous KOH and stained with 1 % Congo Red. Melzer's reagent was used to test the amyloidy/dextrinoidy/inamyloidy of basidiospores, hyphae and cystidia (Singer, 1986). For the microscopic measurements of basidiospores and cystidia, the values of the min.-max. length × width interval were annotated as well as the diameter of various hyphae, with 30 measurements made for basidiospores, 15 for cystidia and 10 for hyphae following Oliveira (2014). Basidiospore dimensions were used in simple statistical metrics where the arithmetic mean (x_m) of length (± standard deviation, SD) × width (± SD) was calculated; the variation X_{min}–X_{max} of the length × X_{min}–X_{max} of the width; mean variation of the length/width quotient values (± SD) (Q_m); and the number of measured spores (*n*). For the additional collections, in addition to the variation X_{min}–X_{max} of length × X_{min}–X_{max} of width, the following measurements were obtained: the min.–max. of the means (x_{mv}) of length × min.–max. width means; the mean of the length means (x_{mm}) (± SD) × the mean of the width means (± SD); min.-max. the values of Q_m (Q_{mv}); the mean of the Q_m values (± SD) (Q_{mm}); number of spores measured per collection (*n*/*c*); and *c*, number of analyzed collections. The spacing of the lamellae was determined by the number of full-length lamellae (*L*) and the number of series of lamellulae (*l*). The collections were deposited in the herbarium INPA.

Sequencing

This study is registered with SisGen (Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado) under the number A40241E. DNA extraction, PCR amplification and sequencing of the ITS and LSU were carried out following Oliveira *et al.* (2019). According to White *et al.* (1990), the primers pairs used in the procedures were ITS5 and ITS4 (for the ITS) and LR0R and LR5 (for the LSU). Reads were assembled and sequences were edited in Geneious R7 (Kearse *et al.* 2012) and deposited in GenBank (NCBI).

Phylogenetic analyses

Objective searches for sequences in the GenBank database were made to cover species of genera in Mycenaceae (Matheny *et al.* 2006, Chew *et al.* 2015, Oliveira *et al.* 2021) with specimens having both ITS and LSU available. All sequences of these two types assigned to *Mycena* were downloaded. The same was done for some representatives of Porotheleaceae members, and a few allied Omphalotaceae members used to form the outgroup (Chew *et al*. 2015, Antonín *et al*. 2019, Vizzini *et al*. 2019, 2022, Matheny *et al*. 2020, Kalichman *et al*. 2020, Consiglio *et al.* 2021). Using the newly generated sequences, BLAST searches were also performed in order to retrieve the closest lineages.

Data were respectively gathered into ITS or LSU datasets. The two datasets were aligned in MUSCLE v3.8.31 (Edgar 2004) and edited in Geneious R7. Poor quality sequences were removed from the datasets and badly or ambiguously aligned sites were trimmed from the alignments. Edited ITS and LSU alignments were assessed in MrModeltest 2.3. (Nylander 2004) for the selection of the best scored nucleotide substitution model. Then, the ITS and LSU alignments were concatenated using the JAVA application concat.jar.

With the GTR+G+I nucleotide substitution model selected for both partitions, Maximum Likelihood (ML) analysis was performed in RaxML 7.0.4 (Stamatakis, 2006) using the GTR+Γ+I model implementing CAT approximations with 1,000 fast-bootstrapping pseudoreplicates and a full ML optimization for the best-scored tree. The Bayesian Analysis (BA) implementing MC^3 chains in two independent runs was conducted in MrBayes 3.2.1 (Ronquist *et al.* 2012), using default settings from the model (Nst = 6) partitioned per marker. The runs consisted of 10,000,000 generations, sampled every 1,000 generations, four independent chains and two swaps. Burn-in was set at 10 %. Final trees followed the 50 % majority-rule consensus method and branch lengths were summarized based on the 95 % highest posterior density credible interval. The phylogenetic trees were visualized in FigTree 1.3.1 and edited in CorelDraw X7. The newly generated sequences and all others included in the analyses are presented in the Supplementary Material, Table S1.

Results

Taxonomy

Mycena lamprocephala C. B. Soares & J. S. Oliveira, *sp. nov.* Figs. 1–4.
MycoBank MB 850761

Holotype:—BRAZIL. AMAZONAS State: Municipality of Manaus, upper Cuieiras River Reserve—INPA, access trail to the base, 2°42'44.6"S 60°23'17.5"W, solitary, in dried eudicotyledonous leaves and sticks in the litter, terra-firme forest, 30 May 2019, *J.S. Cardoso; T. Morbach & F. S. Andriolli JS801* (INPA 292235). GenBank: ITS = OR727532.

Etymology:—From the Greek: λαμπρόσ (lamprós) = brighting, and κεφάλι (kefáli) = head; refers to the luminescent pileus.

Diagnosis: Pileus (5–6 mm diam.) olivaceous brown, luminescent; stipe glutinous; pileus and lamellae trama with brown, cystidioid hyphae segments; pleurocystidia clavate to subfusiform, densely spinulose; cheilocystidia branched, ramose; pileipellis composed of diverticulate-coralloid hyphae immersed in a gelatinous matrix. The combination of these characters differentiate it from any similar species.

Description:—*Basidiome* omphalinoid, thin, small. *Pileus* 5–6 mm diam., hemispherical to convex-truncate, becoming convex, orbicular, sulcato-striate, with shallow vein-like grooves between sulci, center depressed, margin decurved, edge crenate to crenulate, slightly wavy, surface glabrous at the center or when moist, finely furfuraceous to pruinose at the margin when dry, slightly rugose, waxy; light brown (7D6) to brown (7E7) with a slight olive tinge, center and sulci dark brown (7F6); context gray-brown (7E3), very thin (< 1 mm). *Lamellae* subdecurrent to decurrent, arcuate to curved, or slightly sinuate, distant, *L* = 11, lamellulae ventricose, *l* = 1, faces pruinose, whitish brown with a slight olive tinge (5B3), edges paler, white to cream (5A2), hymenium between the lamellae concolorous with the context. *Stipe* 33–39 × 0.8 mm, centrally attached, cylindrical, thin, equal, smooth, hollow, fragile, longitudinally ridged, covered with a thick hyaline gelatinous layer, gray-brown (7E3) mixed with olive brown tinge, or concolorous with the pileus, subinsitititious with a small basal disc formed by rigid gelatinous material, orange-brown (5C4), without basal mycelium. *Luminescence* of the basidiome restricted to the pileus, glow is a green sheen, sometimes intermittent, flashing at a slow frequency; scanty mycelial luminescence on the substrate also noticed.

Basidiospores 5.4–8.3 (9) × (2.4) 3–5.2 µm [x_{rm} = 6.9–8.1 × 4–4.5 µm, x_{mm} = 7.5 (± 0.8) × 4.2 (± 0.5) µm, Q_{rm} = 1.8–1.9, Q_{mm} = 1.8 (± 0.3), n/s = 30, s = 3], ellipsoid to subellipsoid, some lacrymoid, hyaline, smooth, thin-walled, amyloid. *Basidia* 17.4–25 × 6.1–7.9 µm, clavate, smooth, hyaline or with fuscous content, 2–4 sterigmate, thin-walled, inamyloid, with or without clamp connection at the base. *Basidioles* 12.8–21.3 × 4.9–7 µm, cylindrical to clavate, smooth, hyaline, thin-walled, inamyloid, with clamp connection at base. *Pleurocystidia* 19.3–35.1(56.2) × 6.2–15.4(23.1) µm, clavate to subfusiform, cylindrical-clavate, sometimes pyriform, thin-walled, hyaline, densely spinulose at the apex, base smooth or almost so, spinulae 1.3–5.7 × 0.4–1.6 µm, cylindrical to verruciform, dense, longer at apex of the main body, scarce and smaller towards the base, clamp connections not observed. *Cheilocystidia* abundant, hyaline, composing the sterile lamellar edge, 16.5–44.3 × 2.9–7.2 µm, clavate, coralloid, irregular in shape, bilobed to branched, ramose,

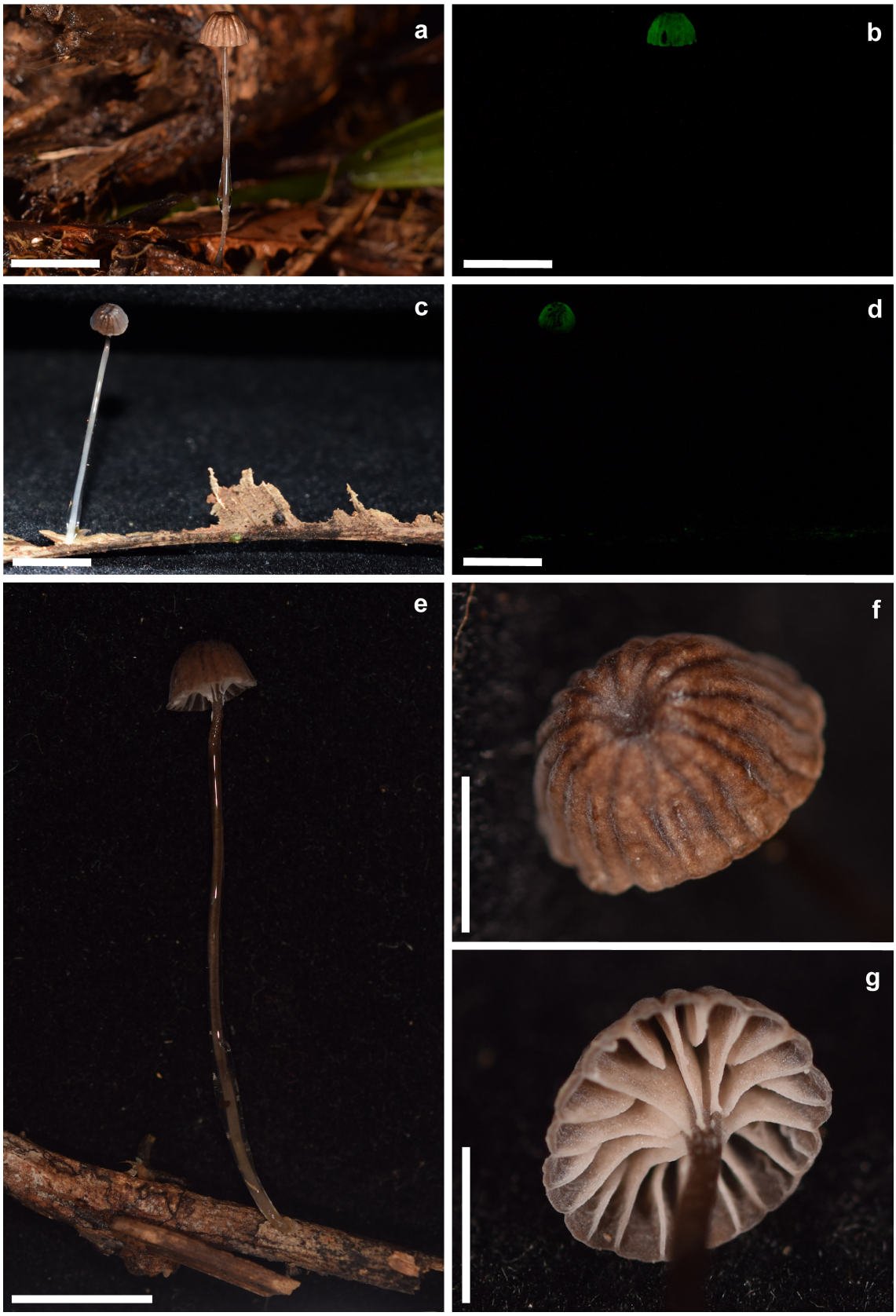

FIGURE 1. Macroscopic basidiomata of *Mycena lamprocephala*. **a.** solitary basidiome, at night, with camera flash (J.S. Cardoso; T. Morbach & F.S. Andriolli JS800); **b.** the same frame of letter "a" without camera flash showing the luminescent pileus; **c.** solitary basidiome, at night, with camera flash (D.L. Komura; T. Morbach; S.S. Vieira; A. Santos de Paula & E.S. Amorim DLK2704); **d.** the same frame of letter "b" without camera flash showing the luminescent pileus and the mycelium in the leaf petiole; **e.** solitary basidiome, at night, with camera flash (J.S. Cardoso; T. Morbach & F. S. Andriolli JS801); **f.** pileus surface of JS801 with camera flash; **g.** hymenophore of JS801 with camera flash. Scale bars **(a–e)** 10 mm; **(f–g)** 3 mm. Photos **a–b**, **e–g** J. S. Cardoso; **c–d** by D.L. Komura.

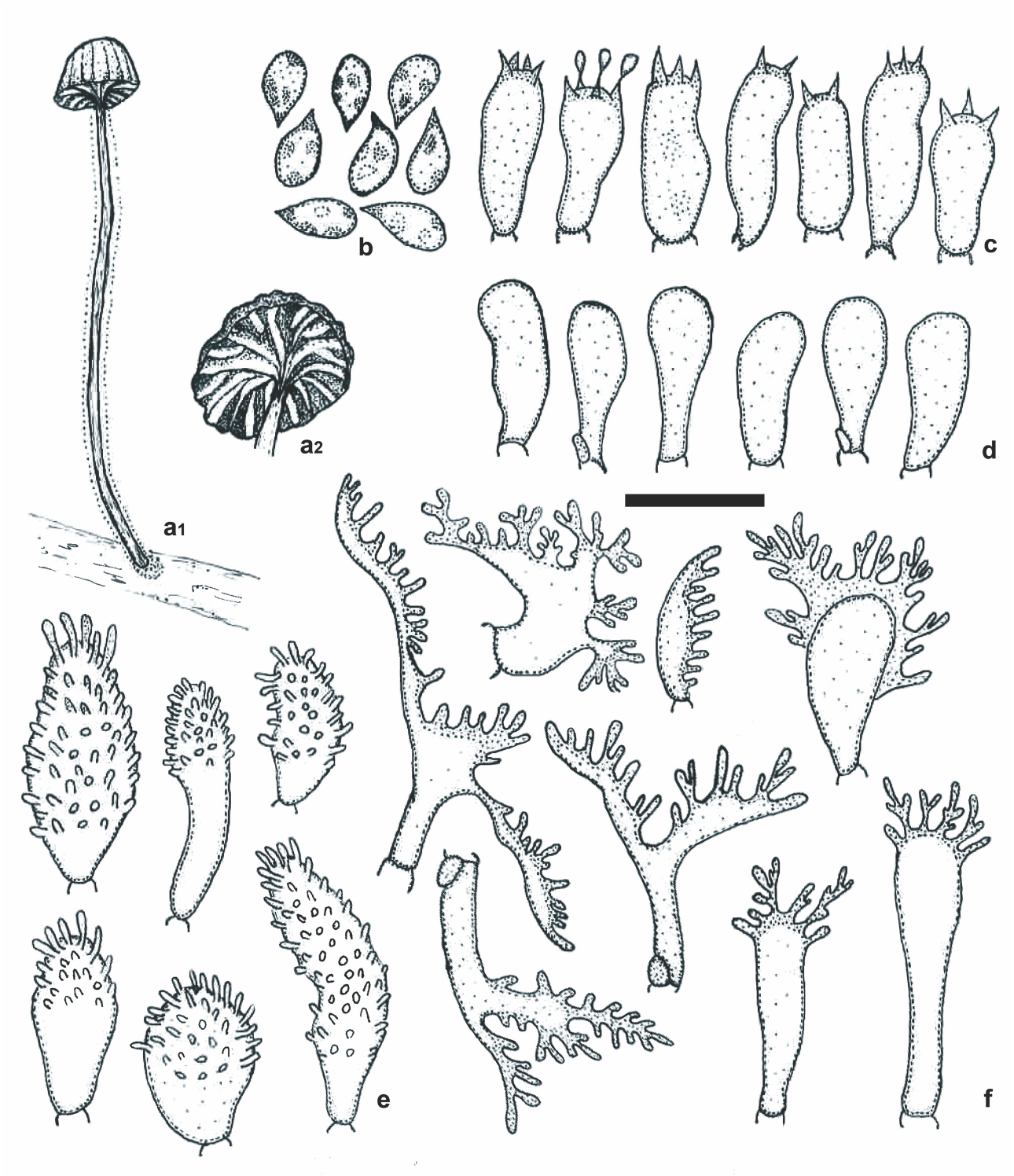

FIGURE 2. Microscopy of *Mycena lamprocephala* (JS801). **a1–a2.** basidiome; **b.** basidiospores; **c.** basidia; **d.** basidioles; **e.** pleurocystidia; **f.** cheilocystidia. *Scale bars* **(a1)** 10 mm; **(a2)** 5 mm; **(b–f)** 15 µm. Drawings by: Célia C.B. Soares.

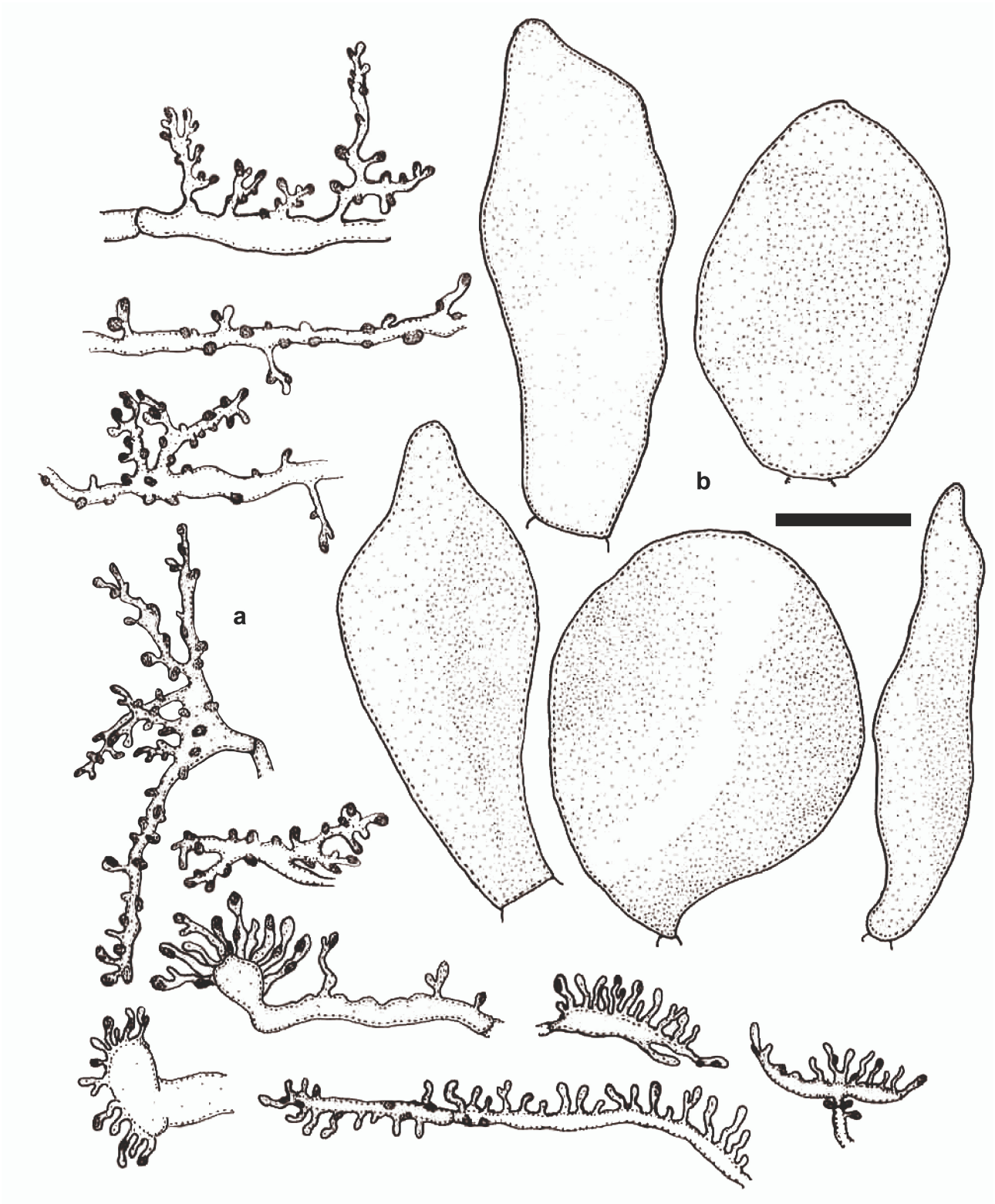

FIGURE 3. Microscopy of *Mycena lamprocephala* (JS801). **a.** hyphae of the pileipellis; **b.** tramal cystidioid hyphae segments. *Scale bars* **(a–b)** 15 µm. Drawings by: Célia C.B. Soares.

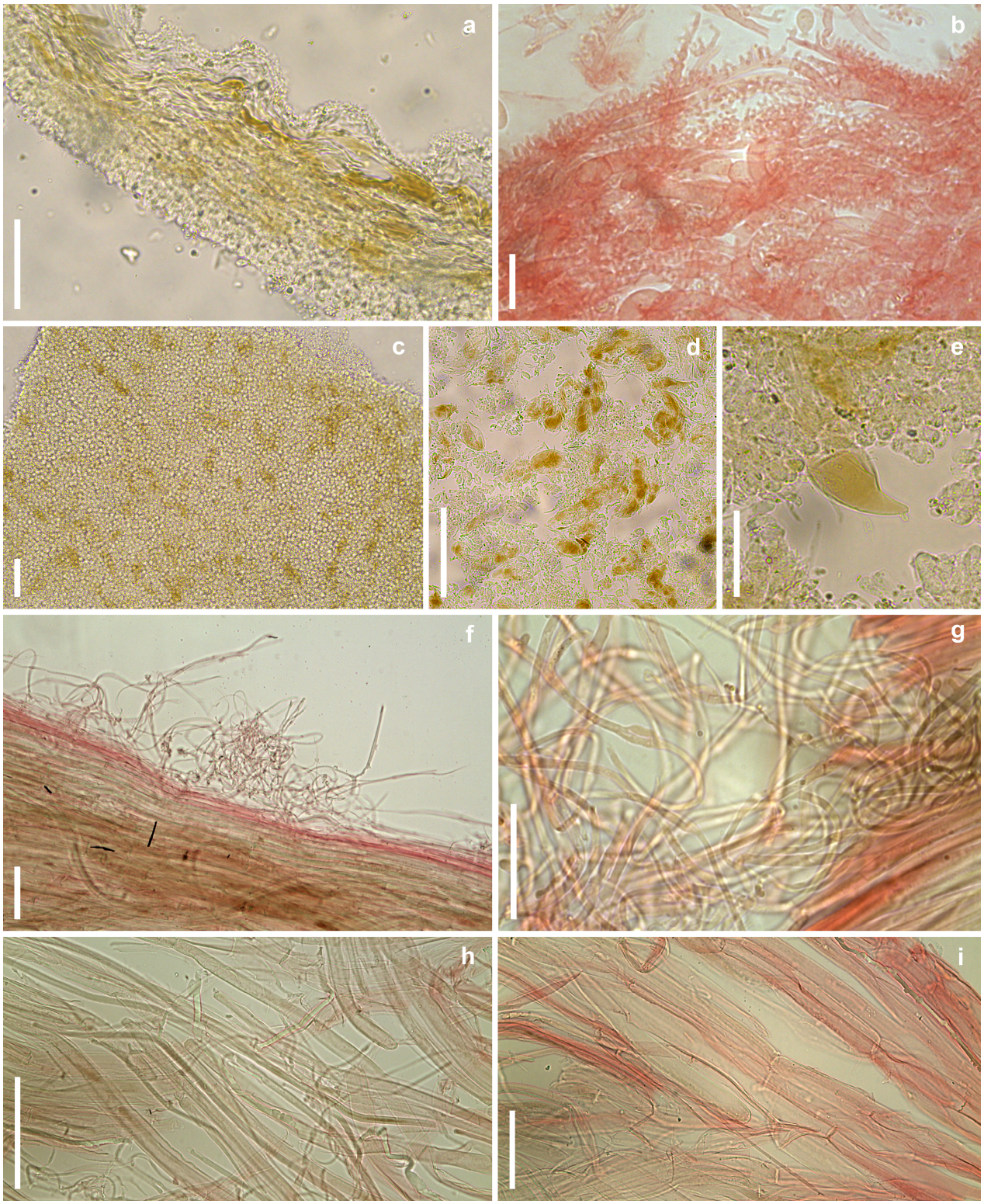

FIGURE 4. Microscopy of *Mycena lamprocephala* (JS801). **a.** profile section of the pileus showing the pileipellis and the pileus trama; **b.** diverticulate hyphae of pileipellis; **c.** mottled lamellar face; **d–e.** tramal cystidioid hyphae segments; **f.** longitudinal section of the stipe showing the stipetipellis and the hyphae of the cortex; **g.** filiform hyphae of stipetipellis; **h**. complexity of hyphae of the stipe trama; **i.** catenulated hyphae of the stipe trama. *Scale bars* **(a, c, d, f–i)** 50 µm; **(b,e)** 15 µm.

thin-walled, inamyloid, clamp connection present at base; diverticula, cylindrical, digitiform, 2.3–4.6 × 0.1–1.7 µm, simple to furcate, hyaline, thin-walled. *Lamellar trama* dextrinoid, irregular, interwoven hyphae, cylindrical, 3–4.8 µm diam., regular in outline, smooth, thin-walled, clamp connections present. *Pileus trama* dextrinoid, subregular, composed of cylindrical hyphae, 1.5–6.6 µm diam., smooth, thin-walled, hyaline, clamp connections absent. *Lamellae and pileus trama* mottled with brown, cystidioid hyphal segments imbedded in the regular hyphal trama; cystidioid segments 22.5–82.7 × 10.9–26.1 µm, clavate, obclavate, lageniform to fusiform, inflated, with brown pigmentation (6E6), irregular in outline, smooth, thin-walled. *Pileipellis* an ixocutis of repent, interwoven, cylindrical to irregular in outline, branched, diverticulate hyphae, 1.9–2.7 µm diam., hyaline, thin-walled, inamyloid, imbedded in a gelatinous matrix; diverticula verruciform to irregularly cylindrical, 0.6–1.9 × 0.4–0.9 µm, simple or furcate, hyaline, thin-walled. *Stipe trama* strongly dextrinoid, cortical hyphae subregular, cylindrical, 6,4–17 µm diam., regular in outline, smooth, thin-walled, clamp connections not observed; internal hyphae with a complex arrangement, parallel, regular in outline and in the arrangement, with diverse shapes, narrow and filamentous, and cylindrical to catenulated, inflated, 6.1–20.6 µm diam., hyaline, smooth, thin-walled, clamp connections absent; cystidioid segments also present. *Stipetipellis* composed of slender hyphae, 1.5–4.3 µm diam., filiform, smooth, cylindrical, occasionally forming tufts or tangles in some points on the surface of the stipe, absent in other places, thin-walled, clamp connections not observed; no gelatinous layer or matrix after treatment in KOH solution. Basal disc formed by interwoven hyphae similar to those on the cortex of the stipe, some inflated hyphae with dense cellular content, 6.6–15.7 µm diam., thick-walled, 1.4–4.2 µm diam., smooth, without clamp connections.

Growth habit:—Solitary, growing on dry leaves of eudicotyledonous plant, on the midrib, leaf blade and on decomposing branches in the litter, in the Amazon rainforest, in terra-firme forest type, between May and June.

Additional material examined:—BRAZIL. Amazonas, Municipality of Manaus, upper Cuieiras River Reserve—INPA, access trail to the base, 2°42’44.6”S 60°23’17.5’’W, 29 May 2019, *J.S. Cardoso; T. Morbach & F. S. Andriolli JS800* (INPA 292234, GenBank: ITS = OR727531, LSU = OR762048); Pajurá trail, 2°42’43.1”S 60°23’18.9’’W, 04 June 2019, *D.L. Komura; T. Morbach; S.S. Vieira; A. Santos de Paula & E.S. Amorim DLK2704* (INPA 292236, GenBank: ITS = OR727533, LSU = OR762049).

Notes:—*Mycena lamprocephala* is typically characterized by a brownish basidiome, thick glutinous stipe, pleurocystidia and cheilocystidia of dissimilar shape, and a pileipellis composed of diverticulate-coralloid hyphal layer immersed in a gelatinous matrix.

The great diversity of morphological structures combined, especially microscopic, strongly distinguish *M. lamprocephala* from any other known mycenoid species and the set of characteristics is not clearly congruent with any section currently recognized in the genus. *Mycena aspratilis* Maas Geesteranus & de Meijer (1997: 44) (*Mycena* sect. *Aspratiles* Maas Geesteranus & de Meijer (1997: 44*)*), in which luminescence was not verified, seems to be the most similar species in morphology. It differs by having a stipe with a white pubescent basal disc due to the presence of thick-walled, cylindrical caulocystidia, cylindrical, thick-walled cheilocystidia, densely covered by digitiform diverticula, and reduced pleurocystidia similar to the cheilocystidia (Maas Geesteranus & de Meijer 1997). Another somewhat similar species, *M. lacrimans* Singer (suggestively akin to *Mycena* sect. *Aspratiles*,) although luminescent, diverges in having a whitish pileus, dry stipe, lack of pleurocystidia, differently shaped cheilocystidia with broad, knob-like, apical appendages, and distinct pileipellis elements (Singer 1989, Desjardin & Braga-Neto 2007). Luminescence was reported in the pileus, lamellae and the stipe of *M. lacrimans* (Desjardin & Braga-Neto 2007) but not from the mycelium in the substrate as in *M. lamprocephala* (Fig. 1d).

Mycena lamprocephala may be comparable to species of *Mycena* sect. *Euspeireae*, but species of that section differ by having a gelatinous separable pellicle forming the pileipellis and by the more or less smooth hymenial cystidia (Maas Geesteranus & de Meijer 1997). Also, in species of sect. *Euspeireae*, the cortical hyphae of the stipe can be observed immersed in a gelatinous matter in KOH solution while this was not seen in *M. lamprocephala* because, although probably an ixocutis when fresh, the gelatinous matter dissolves completely in KOH solution.

Phylogenetic analysis

The resulting ML tree is displayed in two parts in Figs. 5 and 6, with quite similar topology to the BA tree. Three major clades are represented: /omphalotaceae as the outgroup which also has luminescent species, /porotheleaceae having genera segregated from *Mycena* along with some luminescent species, and /mycenaceae which is the largest and more well-represented clade in this analysis. Clade /mycenaceae is strongly supported (BS 97; PP 1.0) while /porotheleaceae is unsupported. Within /mycenaceae, *M. lamprocephala*, depicted in green-yellow, is placed in the upper part of the

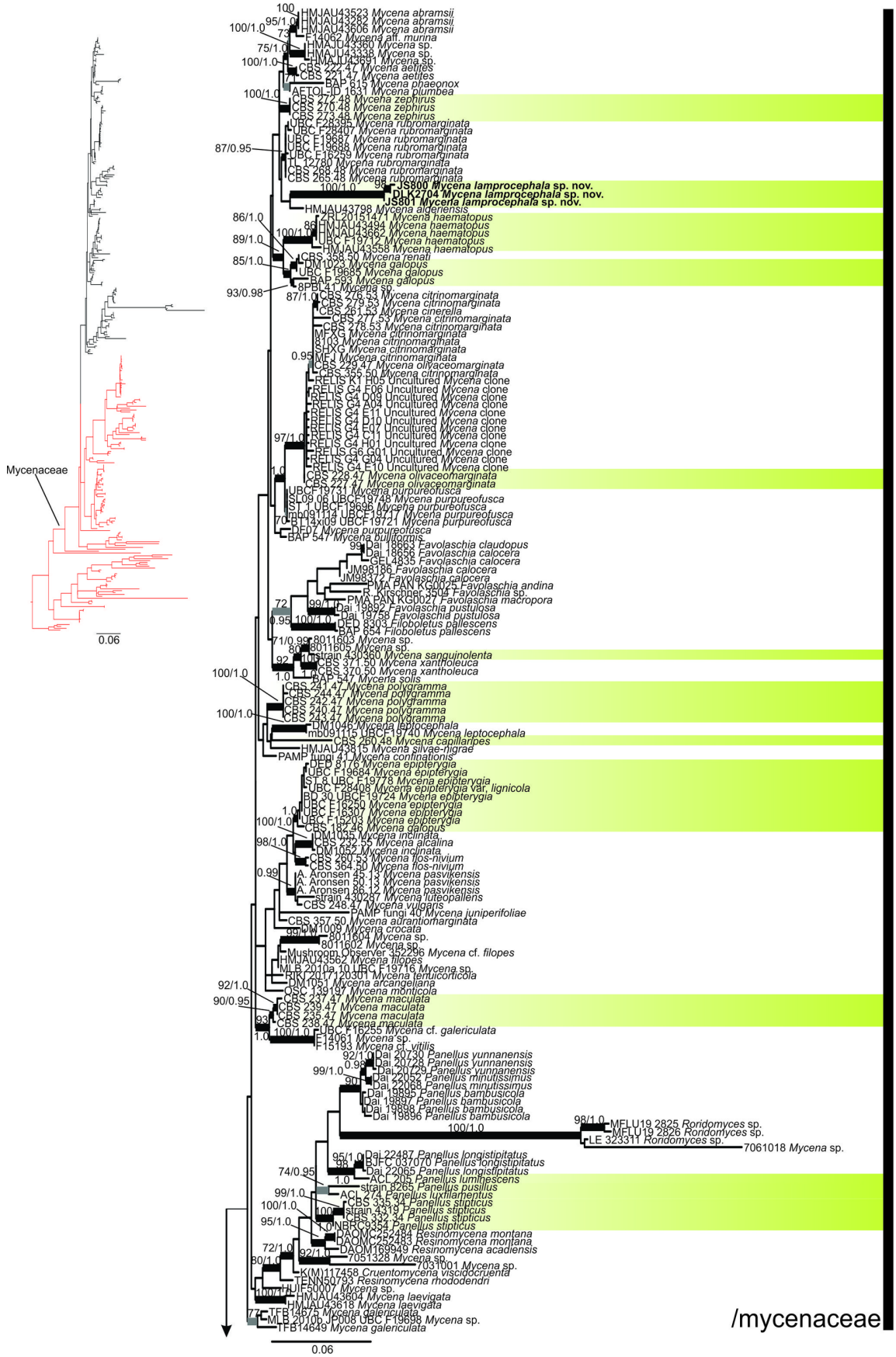

FIGURE 5. Maximum likelihood best-scored tree of combined ITS and LSU aligned dataset—Part 1, showing the upper part of /mycenaceae. Bootstrap (BS) support values are provided at the nodes along with posterior probability (PP) support values are from the Bayesian analysis of the same dataset. The supported stems are bold black for strongly supported (BS ≥ 80 % or PP ≥ 0.98) and gray bold for moderately supported (BS ≥ 70 % or PP ≥ 0.95). Taxa depicted in green-yellow are known to be luminescent.

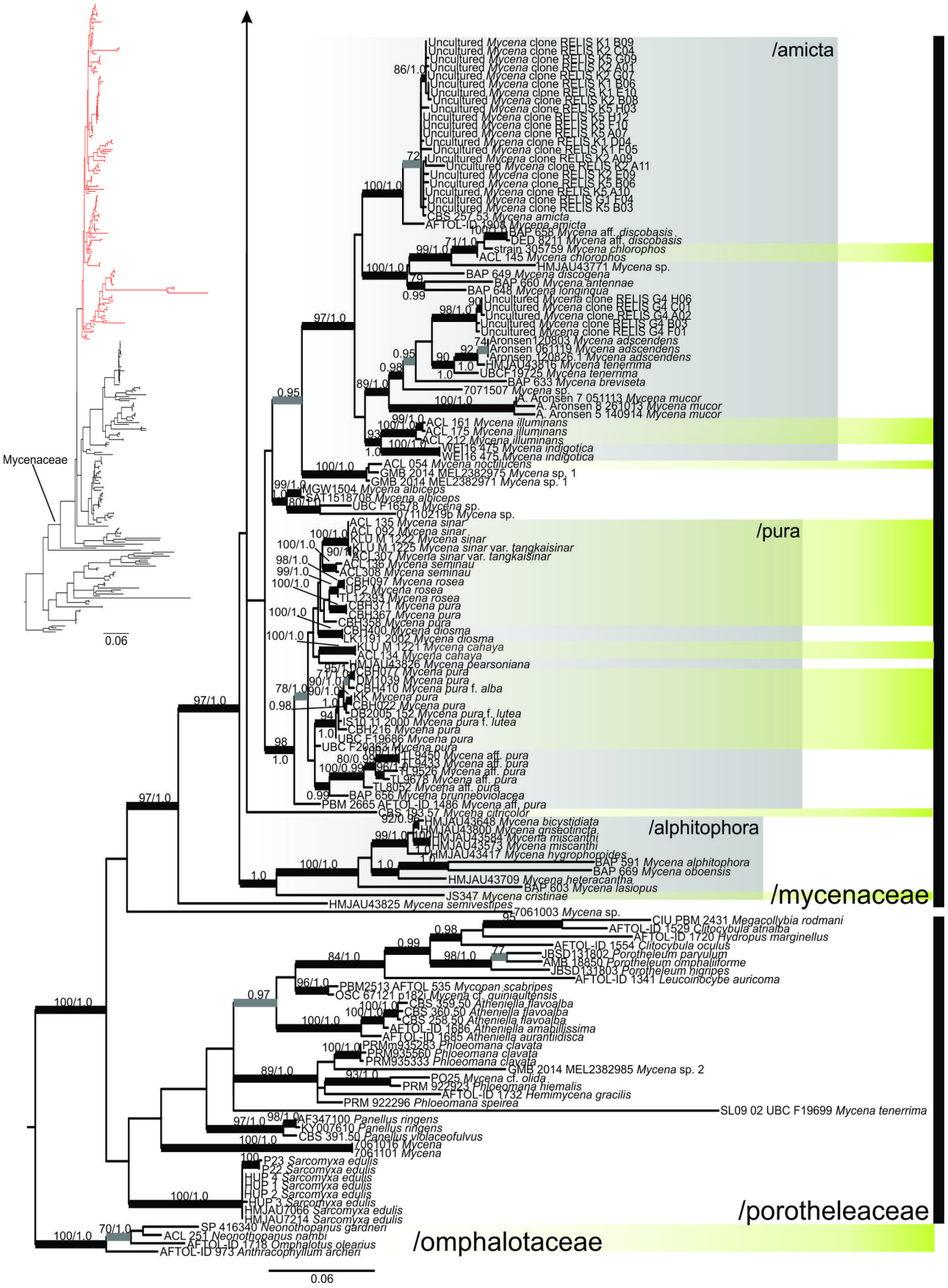

FIGURE 6. Continue.

clade (Fig. 5). This part is more unresolved with multiple branches into polytomy, having members of *Cruentomycena* R.H. Petersen, Kovalenko & O.V. Morozova (2008: 123) *Panellus*, *Resinomycena* Redhead & Singer (1981: 151) and *Roridomyces* forming a more distinctive cluster, *Favolaschia* and *Filoboletus* in another cluster, and several *Mycena* lineages scattered in many branches without intermediate to deep resolution. *Mycena lamprocephala* seems to be sister to *M. algeriensis* Maire (Kühner 1938: 490) but without support, and these two are sister to *M. rubromarginata* (Fr.) P. Kummer (1871: 109) without support. The second part of /mycenaceae (Fig. 6) is more resolved than the first part, harboring at least three strongly supported clades and two small species branches. Strongly supported small clades or branches in /porotheleaceae represent the genera *Atheniella*, *Clitocybula*, *Hemimycena* Singer (1938: 194), *Hydropus* Kühner ex Singer (1948: 127), *Leucoinocybe*, *Megacollybia* Kotlába & Pouzar (1972: 220) *Mycopan* Redhead, Moncalvo & Vilgalys (2013: 1), *Phloeomana*, *Porotheleum* Fries (1818: 272) and *Sarcomyxa* P. Karsten (1891: 62) while some named *Mycena* and *Panellus* are just embedded. Relationships among these lineages are partly unsupported.

The BLAST searches (Jul. 2023) with the ITS and the LSU sequences of *M. lamprocephala* did not yield significant results as the species is genetically very distant from all species represented in GenBank.

Discussion

Combining all described morphological characteristics, *M. lamprocephala* is unique as there are no close nor comparable species in *Mycena s.l.* except *M. aspratilis* and *M. lacrimans*. The combination of characteristics of the new species may fit most in *Mycena* sect. *Aspratiles* Maas Geest. & de Meijer (44:1997) and *Mycena* sect. *Euspeireae* Maas Geest. (Maas Geesteranus 1989), but the classification between these sections seems uncertain. This uniqueness is also reflected in the genetic information (ITS and LSU). Such degree of morphological and genetic distinction led us to evaluate the species in a broad phylogeny including /mycenaceae and /porotheleaceae (and allies) clades to verify its family level placement. The placement of *M. lamprocephala* in the phylogenetic tree (Fig. 5) confirms it in Mycenaceae (Fig. 4). Although /mycenaceae is a strongly supported clade that well represents the Mycenaceae family, genus-level clades allowing genera delimitation within the family are still inconclusive when combining ITS and LSU, especially for *Mycena*. The much more numerous taxa in the phylogenetic tree assigned to *Mycena s. str*. do not form a monophyletic group. They are segregated into two parts: 1) upper part (Fig. 5) which is more unresolved; 2) lower part (Fig. 6) which is more resolved into well-defined and strongly supported subclades.

The upper part includes two lineages that seem to be misplaced by long-branch attraction effect: i) specimens of *Roridomyces*; and ii) *M. lamprocephala*. Although this latter branched as sister to *M. algeriensis*, such a relationship seems artificial. The *Roridomyces* lineage seems falsely nested in a monophyletic and strongly supported group including *Panellus*, *Resinomycena* and *Cruentomycena*. The type species of *Mycena* is included in this upper part too (Fig. 5) where species branches are mostly in polytomy. Although some similarity can be found to *Roridomyces*, especially the glutinous stipe, there is no evidence that *M. lamprocephala* is a member of that genus. The lower part of /mycenaceae (Fig. 6) includes three more expressive monophyletic groups of *Mycena* spp.: /amicta, /pura and /alphitophora. Also, four independent *Mycena* species lineages are present in this part. Overall, the tree topology seems congruent with the LSU trees in Chew *et al*. (2014) and Oliveira *et al.* (2021), and also with the ITS+LSU tree in Liu e*t al.* (2022). A clade-based *Mycena* definition is still needed to elucidate genera in Mycenaceae and which of the *Mycena* species will remain in the genus.

The luminescent species present in the tree belong to the lineages /mycenaceae and /omphalotaceae (Fig. 5; 6), but none forms a monophyletic group with *M. lamprocephala* and most are in polytomy. In the upper part of /mycenaceae (Fig. 5), we found the luminescent *M. zephirus* (Fr.) P. Kummer (1871: 110), *M. haematopus* (Pers.) P. Kummer (1871: 108) and *M. galopus* (Pers.) P. Kummer (1871: 108), *M. sanguinolenta* (Alb. & Schwein.) P. Kummer (1871: 108), *M. polygramma* (Bull.) Gray (1821: 619), *M. epipterygia* (Scop.) Gray (1821: 619), *M. inclinata* (Fr.) Quélet (1872: 105) *M. maculata* P. Karsten (1889: 89), and four species of *Panellus*, *P. luminescens* (Corner) Corner (1986: 132), *P. pusillus* (Pers. ex Lév.) Burdsall & O.K. Miller (1975: 85), *P. luxfilamentus* A.L.C. Chew & Desjardin (2015: 183) and *P. stipticus* (Bull.) P. Karsten (1879: 96) (Chew *et al.*, 2014, Desjardin *et al*., 2007). In the lower part of /mycenaceae, we found luminescent members in three groups: *Mycena chlorophos* (Berk. & M.A. Curtis) Saccardo (1887: 301) and *M. illuminans* Hennings (1903: 309) in the /amicta group; *M. cahaya* A.L.C. Chew & Desjardin (2014: 979), *M. pura* (Pers.) P. Kummer (1871: 107) (and forms), *M. rosea* Gramberg (1912: 36), *M. seminau* A.L.C. Chew & Desjardin (2014: 985) and *M. sinar* A.L.C. Chew & Desjardin (2014: 983) (and varieties) in the /pura group;

and *M. cristinae* in the /alphitophora group (Chew *et al.*, 2014, Desjardin *et al*., 2007, Oliveira *et al.*, 2021). In the outgroup /omphalotaceae, three other luminescent species are *Neonothopanus gardneri* (Berk.) Capelari, Desjardin, B.A. Perry, T. Asai & Stevani (2011: 1435), *N. nambi* (Speg.) R.H. Petersen & Krisai (1999: 210) and *Omphalotus olearius* (DC.) Singer (1948: 133) (Chew *et al.*, 2014). Although some luminescent species are known as being related to Porotheleaceae, no representatives were included in this analysis.

Conclusion

Combining genetic and morphological data with the literature on all *Mycena* species, *M. lamprocephala* is a new species and the third luminescent fungi known from the Amazon Forest. It is recognized in the field by the basidiomata with glutinous stipe and dark olivaceous brown pileus, with a waxy surface. The luminescence is perceived on the pileus and scanty mycelial traces in the substrate. Due to its unique morphology, its classification in *Mycena* is uncertain between sect. *Aspratiles* and sect. *Euspeireae*. The ITS+LSU phylogenetic analyses confirmed that *M.* is a member of Mycenaceae. However, a clade-based delimitation for *Mycena* and other genera as monophyletic groups in the family remains an issue to be resolved in future studies, with the use of more markers in multilocus analyses.

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