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Mycena luxaustralis, a new bioluminescent species in section *Sacchariferae* from southern Chile

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Abstract. Bioluminescent fungi emit light through chemical luminescence of fungal tissues. More than 100 species of bioluminescent fungi have been described in five distinct groups of *Agaricales*: *Omphalotus*, *Armillaria*, the *Lucentipes* lineage within *Marasmiineae*, the *Eoscyphella* lineage, and the mycenoid lineage. The mycenoid lineage includes the largest number of described bioluminescent taxa. Recent efforts to document and describe fungal biodiversity in Chile documented several collections of a bioluminescent *Mycena* species found exclusively on the dead rachises of *Parablechnum chilense*, a fern species endemic to temperate forests of Chile and Argentina. This species is related to *Mycena tenerrima* (= *M. adscendens*) from the Northern Hemisphere, but is both morphologically and phylogenetically distinct. Here, we describe this species as *Mycena luxaustralis* sp. nov., including morphological descriptions and analysis of ITS and 28S sequences.

Key words: *Basidiomycota*, Chile, internal transcribed spacer (ITS), mycenoid lineage, new taxon, Patagonia

Introduction

Bioluminescent fungi, fungi that emit light through chemical luminescence of fungal tissues, have long drawn the attention of mycologists, naturalists, and casual observers (Desjardin et al. 2008). Their ability to emit light is notable from an ecological and evolutionary perspective. The ecological role of bioluminescence in fungi is still unclear (Stevani et al. 2013), although there are several hypotheses about its function. For instance, bioluminescence may attract spore dispersers, or it may repel negatively phototrophic fungivores (Sivinski 1981; Desjardin et al. 2008; Stevani et al. 2013; Oliveira et al. 2015). According to estimates by Haddock et al. (2009) bioluminescence has originated independently in different types of organisms at least 40 times. Despite the multiple origins of bioluminescence, light production is always based on the oxidation of the luciferin protein by the enzyme luciferase (Oliveira et al. 2012; Ke & Tsai 2022). In the case of *Agaricales*, the results of Oliveira et al. (2012) suggest that there was a single evolutionary origin of bioluminescence. Currently, there are more than 100 known species of bioluminescent fungi (Ke & Tsai 2022; Lu et al. 2024), a very small proportion of the 17,291 *Agaricales* species (He et al. 2019). These bioluminescent species are distributed in five lineages (Desjardin et al. 2010; Chew et al. 2015; Kotlobay et al. 2018; Ke & Tsai 2022; Silva-Filho et al. 2023): *Omphalotus* (12 spp.), *Armillaria* (10 spp.), the *Lucentipes* lineage within *Marasmiineae* (2 spp.), the *Eoscyphella* lineage (1 sp.) and the mycenoid lineage (85 spp.).

The mycenoid lineage contains most of the known bioluminescent species and most of them belong to the diverse genus *Mycena* which comprises about 600 species worldwide (Kirk et al. 2008; He et al. 2019). South American species of *Mycena* were studied by Spegazzini (1887, 1899), Rick (1938), Dennis (1961), Singer (1950, 1969, 1973, 1989), Singer & Digilio 1952, Raithelhuber (1984a, b, 1985a–e, 1996a, b, 2004), Maas Geesteranus & de Meijer (1997, 1998), and more recently by Desjardin et al. (2007, 2010), Alvez & Nascimento (2014), Niveiro et al. (2010, 2011, 2012, 2015) and Martinez et al. (2020). In Chile, approximately 70 taxa of *Mycena* are recorded (Singer 1959, 1969; Mujica & Vergara 1980; Garrido 1985; Valenzuela & Moreno 1995; Lazo 2001; Minter & Peredo López 2006). However, the knowledge of the genus *Mycena* is still scarce and new studies are needed to understand and clarify the species diversity in this group. Their relatively small and fragile basidiomata make collecting specimens of *Mycena* difficult,

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and in many cases the collections are not well-preserved or carefully studied, leaving many uncertainties about diversity within the genus.

Recent efforts to document and describe fungal biodiversity in Chile have resulted in collections of several bioluminescent *Mycena* specimens from forests in southern Chile. In addition to being bioluminescent, these basidiomes were produced exclusively on the dead rachises of *Parablechnum chilense*. This species of fern is endemic to temperate forests of Chile and Argentina, an important and widespread forest type across large areas of southern South America. The aim of this study is to characterize the microscopic and macroscopic morphology and provide information about the phylogenetic position of our bioluminescent *Mycena* specimens, which we describe here as *Mycena luxaustralis* sp. nov.

Materials and methods

Taxon sampling. Basidiomes were collected on several collecting campaigns between May to Oct 2022 during the fall and spring seasons in forests in southern Chile. Collections were obtained from four sites in the Los Lagos and Aysén regions. The basidiomes of the fungus developed exclusively on dead rachises of *Parablechnum chilense*. Photographs of luminescent basidiomes were taken in complete darkness with a Nikon Z6 camera (Tokyo, Japan) with a 60 mm macro lens (1–3 min exposure), and fresh tissues of some specimens were preserved in CTAB (details below). Specimens were dried in a food dehydrator at 40°C and stored in plastic bags with silica gel. Voucher specimens were deposited in the Herbarium of the Museo Regional de Aysén (MURAY) and the Florida Museum of Natural History at the University of Florida (FLAS).

Morphology and microscopy. Macromorphological descriptions are based on fresh material, according to Largent (1986) and Lodge et al. (2004). Micromorphological features were obtained from dried specimens rehydrated with 70% (v/v) ethanol and distilled water, then mounted in Melzer's reagent, 3% (w/v) potassium hydroxide (KOH) or 1% (w/v) Congo red. The following notations are used: L = number of lamellae reaching the stipe; x = arithmetic mean of the spore length and width; Q = quotient of length and width indicated as a range of variation; Qm = mean of Q values; n = number of spores measured. Basidiospore statistics include xm, the arithmetic mean of the spore length by spore width (± SD) for n basidiospores measured; Q, the ratio of spore length to spore width, expressed as a range for all basidiospores measured; Qm, the mean of all Q values (± SD). Microscopic measurements were presented as format of (min–) 5^{th}–95^{th} percentile (–max).

Molecular protocols. DNA was extracted from fresh specimens using an alkaline extraction buffer following the methods of Vandepol et al. (2020). We also used a modified CTAB extraction protocol (Gardes & Bruns 1993) to extract DNA of some specimens. The nuclear rDNA internal transcribed spacer (ITS) region ITS1-5.8S-ITS2 and nuclear large subunit (28S) rDNA were PCR-amplified using the primer pairs ITS1F/ITS4 (White et al. 1990; Gardes & Bruns 1993) and LR0R/LR5 (Hopple & Vilgalys 1994) following the protocols of Gardes & Bruns (1993). PCR products were visualized on 1.5% agarose gels and Sanger sequenced bidirectionally with the same primers by Eurofins Genomics (Louisville, KY, USA).

Phylogenetic analysis. Initial BLAST searches of ITS and 28S sequences indicated a phylogenetic affinity (95–98% ITS similarity, 99–99.6% 28S similarity) to sequences identified as *M. adscendens* or *M. tenerrima*. We therefore selected sequences from the /amicta phylogenetic lineage identified by Soares et al. (2024), which includes *M. tenerrima* (= *adscendens*) (Sect. *Sacchariferae* sensu Na & Bau 2019b) and other species that traditionally belong to the following sections: *Amictae*, *Brunneisetosa*, *Extornatae*, *Granuliferae*, *Longisetae*, *Polyadelpha*, and some (e.g., *M. illuminans*) that are incertae sedis (Chew et al. 2013). Morphologically, the members of this clade /amicta are diverse and have a variety of morphological features (see Discussion). In addition to sequences used by Soares et al. (2024), we used BLAST similarity to identify other ITS and 28S sequences nested within the /amicta lineage outlined in Soares et al. (2024). We focused on this study because their analysis included samples with both ITS and 28S sequences, while many samples in GenBank are only represented by ITS sequences. The ITS analysis excluded *M. illuminans*, *M. indigotica*, and *M. lazulina* due to unalignable indels present in the ITS1 region that reduced overall alignment quality. However, these three species are represented in the 28S analysis and concatenated ITS+28S analysis.

Sequences were aligned with the MUSCLE (3.8.425) algorithm (Edgar 2004) using default settings in the software program GENEIOUS (2020.2.4) (Auckland, NZ) and checked manually. Ambiguously aligned regions were removed from all alignments with GBLOCKS software (Talavera & Castresana 2007) using the least stringent settings for all alignments. Sequences of *M. hygrophoroides* were selected as an outgroup based on the position of this species in the /alphitophora lineage in Soares et al. (2024) and Na & Bau (2019b). Maximum Likelihood phylogenetic analysis was conducted for all alignments using the RAXML-NG program with GTR+G model of nucleotide substitution and 1,000 bootstrap replicates to evaluate support for nodes. Nodes were considered supported when ML bootstrap values were ≥70%. All analyses were performed on the University of Florida HiPerGator supercomputing cluster.

Results

Taxonomy

Mycena luxaustralis Sandoval-Leiva & Calle, sp. nov. (Figs 1, 2)

MycoBank MB 853542

Diagnosis: Pileus whitish, powdery to granulose; lamellae nearly free, sometimes forming a pseudocollarium, white; stipe hyaline, glabrescent at the apex, hirsute downward, with a hirsute to

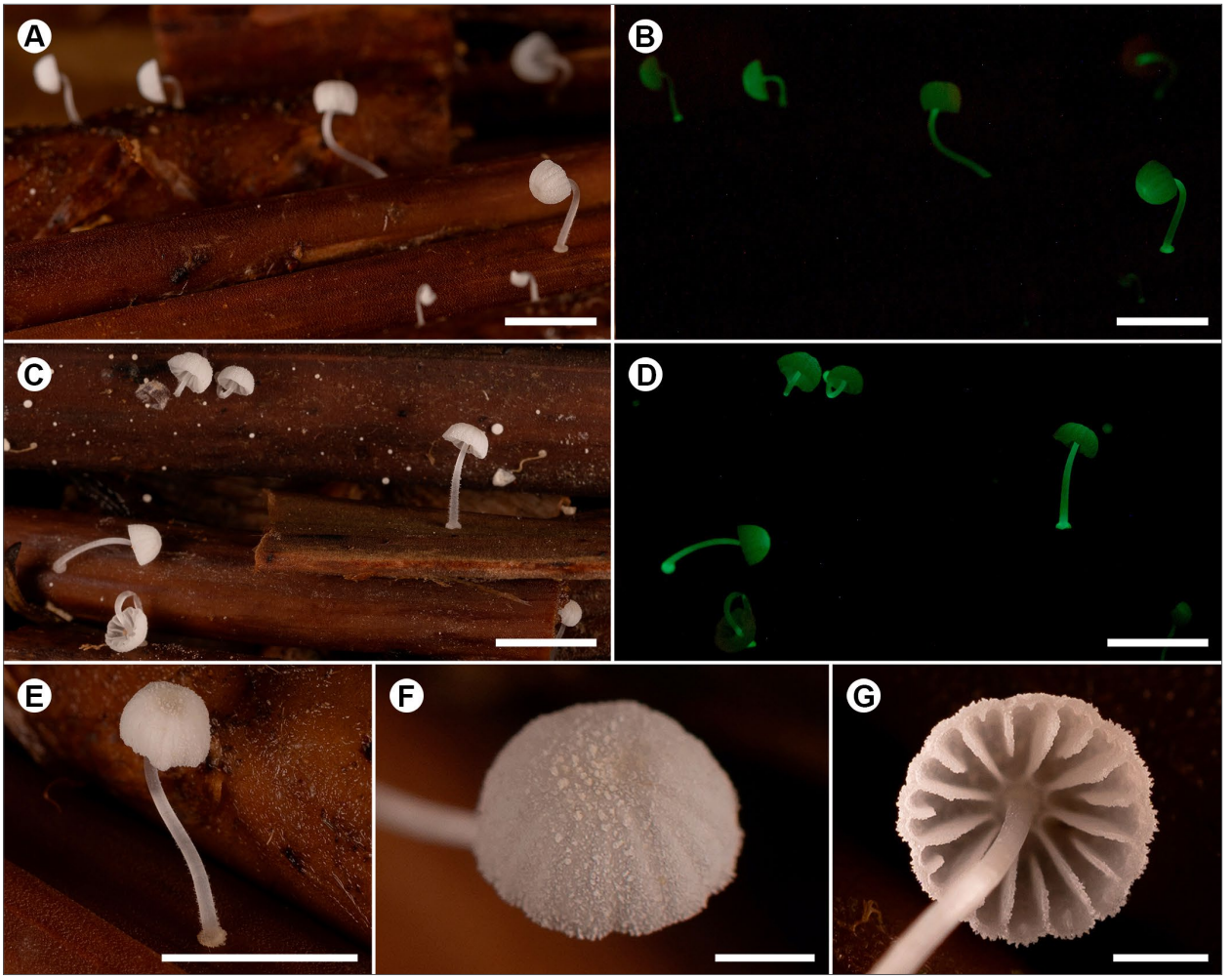

Figure 1. Fresh basidiomes of *Mycena luxaustralis*. Photographs in daylight (A, C) and in darkness (B, D). A–D – group of basidiomes on dead rachises and pinna rachises of *Parablechnum chilense*; E – detail of basidiome; F – detail of pileus granulose surface; G – detail of lamellae. Scales: A–E = 5 mm; F, G = 1 mm.

glabrous basal disc; entire basidiome bioluminescent; basidiospores globose to subglobose; cherocytes absent; obovoid (pyriform) acanthocysts; caulocystidia smooth, awl-shaped or lanceolate, smooth, with one to three appendages sometimes branched. Occurring on dead stipes, rachises and pinna rachises of *Parablechnum chilense*.

Holotype: Chile, Los Lagos, Municipality Hualaihué, Reserva Vodudahue, next to the Troliguan river, 42°29′26″S, 72°21′13″W, elev. 23 m, on dead stipes, rachis and pinna rachis of *Parablechnum chilense*, 27 May 2022, P. Sandoval-Leiva, A. Calle & J. Hepp PSL-4210 (MURAY-BF 0001 – holotype; FLAS-F-72737 – isotype). GenBank: ITS = PP725273; 28S = PP725279.

Etymology. From *lux* = light (L.) and *australis* = south (L.), referring to the light emitted by the basidiomes and by its distribution in southern Chile.

Description. Pileus 1–3 mm diameter, hemispherical to paraboloid, then convex to plano-convex, sulcate, translucently striate; margin irregularly crenulate, translucent striate; surface dry, pulverulent or granulose, disc light grayish to gray and white to pale grayish toward the margin; context white, thin, fragile (Fig. 1A–G). Lamellae nearly free, sometimes forming a pseudocollarium, white, edges concolorous with the faces (Fig. 1G). Stipe (1.5–)2–6.5(–10.5) × 0.3–0.5 mm, fragile, hyaline, glabrescent at the apex, hirsute downward, arising from a hirsute to glabrous basal disc up to 0.7 mm (Fig. 1A–E). Odor and taste indistinct. Entire basidiome bioluminescent, emitting bright green light. Mycelium bioluminescence undetermined.

Basidiospores (5.6–)6.6–7.9(–9.0) × (5.5–)6.4–7.6 (–8.0) µm [xm = 7.32 ± 0.51 × 6.96 ± 0.45 µm, Q = (1.00–)1.0–1.1 (–1.13), Qm = 1.05 ± 0.03, n = 50], globose to subglobose, hyaline, usually with one big guttule, thin-walled, weakly amyloid (Fig. 2E). Basidia 20–32 × 7–14 µm, 4-spored, clavate to cylindro-clavate (Fig. 2D). Cheilocystidia (11.7–)21.4–40.1 × (5.1–)11.9–21.4 µm, numerous, clavate, cylindro-clavate, obpyriform or spherical, hyaline, densely spinulose, mainly over upper half, hyaline, inamyloid, thin-walled; spinulae cylindrical to subconic, obtuse, 0.5–2.0 × 0.5–1.0 µm, some spinulae longer, up 8 µm (Fig. 2F). Pleurocystidia absent. Cherocytes absent. Pileipellis a cutis of inflated hyphae with acanthocyst terminal cells; hyphae 1–7 µm wide, spinulose, hyaline, non-gelatinous, inamyloid or weakly dextrinoid; acanthocysts 15–44 × 13–24 µm, clavate, obpyriform, oval or sphaeropedunculate, densely spinulose, hyaline, inamyloid (Fig. 2A–C). Hypodermium of strongly dextrinoid hyphae up to 25 µm diam, hyaline,

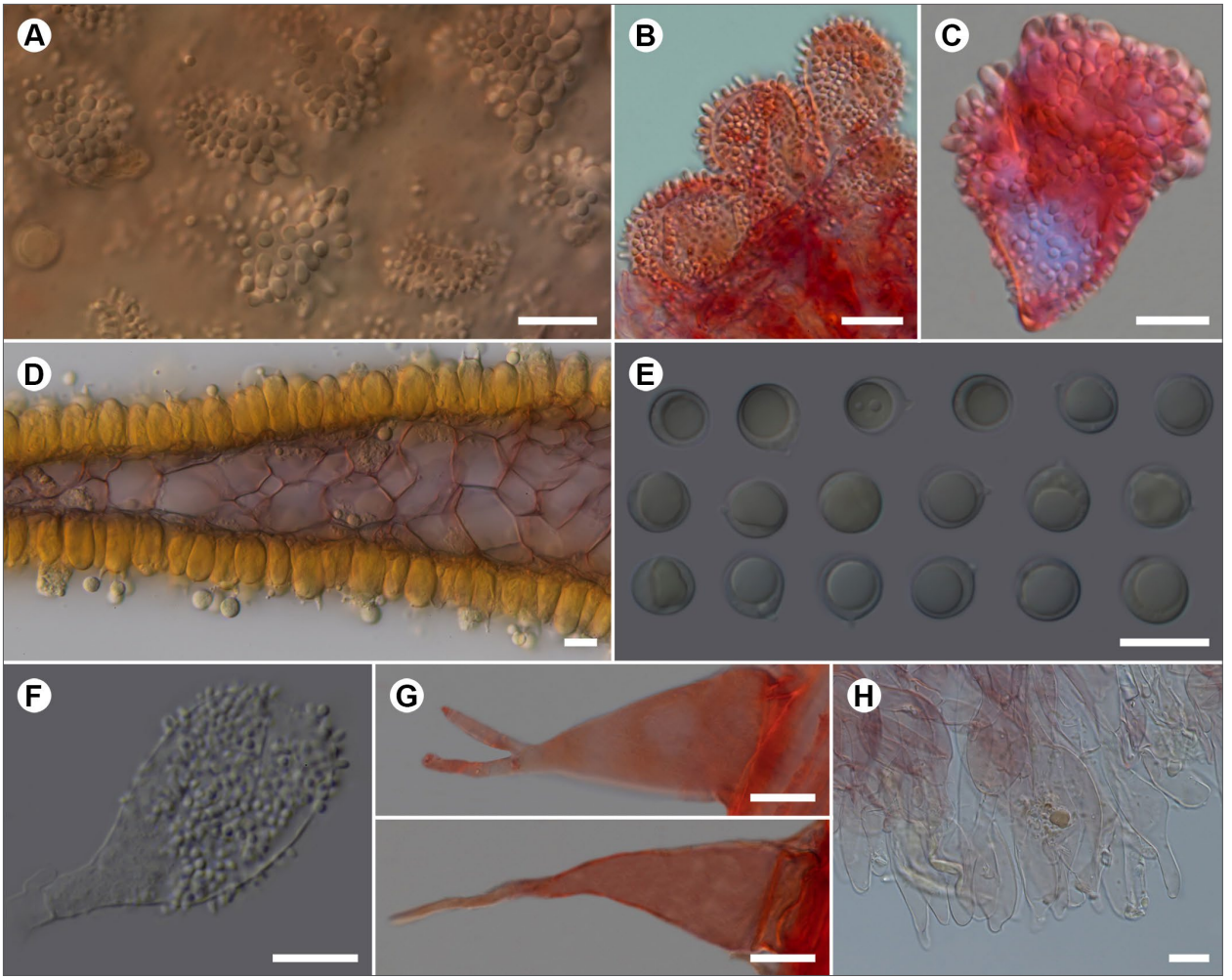

Figure 2. Micromorphological features of *Mycena luxaustralis*. A – top view of pileus with abundant acanthocysts; B–C – detail of acanthocysts; D – gill cross section; E – spores; F – detail of cheilocystidium; G – detail of caulocystidia; H – detail of basal disc cystidia. Scales: A–G = 10 µm. Reagents: A, F = KOH (3%); B, C, G – KOH (3%) with Congo red; D, E, H – Melzer's reagent.

thin-walled, non-gelatinous. Tramal hyphae similar, but narrower (Fig. 2D). Stipe tissue monomitic; cortical and medullary hyphae parallel, 3–25 µm wide, cylindric, smooth, non-gelatinous, non-incrusted, hyaline, strongly dextrinoid, thin-walled. Caulocystidia 25–90 × 9–25 µm, awl-shaped or lanceolate, smooth, with one to three appendages sometimes branched, smooth, hyaline, inamyloid, thin-walled (Fig. 2H). Basal disc cystidia 28.5–82.5(–118.7) × 7.8–19.3 µm, mostly fusiform or clavate, usually rostrate, sometimes lanceolate, lageniform or irregularly shaped, smooth or rarely some develop sparse apical spinulae, hyaline, inamyloid or weakly dextrinoid, thin-walled (Fig. 2G). Clamp connections scarce and difficult to discern.

Ecology and distribution. Occurring on dead stipes, rachises and pinna rachises of the fern *Parablechnum chilense*, with a known distribution in coastal forest environments between Los Lagos and Aysen regions of southern Chile, but can probably be found with the host fern species across its range in southern South America.

Other specimens examined. CHILE. Los Lagos: Municipality Llanquihue, dense native forest with *Myrtaceae*, 41°14′58.74″S, 73°15′20.76″W, elev. 179 m, on dead rachis of *Parablechnum chilense*, 22 Oct. 2022, A. Calle PSL-4729 (MURAY-BF 0002). GenBank: ITS = PP725275; 28S = PP725281. *Ibid*. Municipality Chonchi, native forest with *Drimys winteri* J.R. Forst. & G. Forst. and other native trees, 42°47′37.84″S, 73°46′23.11″W, elev. 127 m, on dead rachis of *Parablechnum chilense*, 23 Sept. 2022, A. Calle & C. Miranda PSL-4568 (MURAY-BF 0003). GenBank: ITS = PP725274; 28S = PP725280. *Ibid*. Municipality Hualaihué, Reserva Vodudahue, Vivero trail way, 42°29′34″S, 72°21′16″W, elev. 4 m, on dead stipes, rachis and pinna rachis of *Parablechnum chilense*, 25 May 2022, P. Sandoval-Leiva & A. Calle PSL-4160 (MURAY-BF 0004; FLAS-F-72738). GenBank: ITS = PP725271; 28S = PP725277. *Ibid*. trail way to waterfall, 42°28′18.05″S, 72°22′19.14″W, elev. 357 m, on dead stipes, rachis and pinna rachis of *Parablechnum chilense*, 26 May 2022, P. Sandoval-Leiva & A. Calle PSL-4183 (MURAY-BF 0005; FLAS-F-72739). GenBank: ITS = PP725272; 28S = PP725278. *Ibid*. Placeta, 42°29′00″S, 72°23′07″W, elev. 12 m, on dead stipes, rachises and pinna rachises of *Parablechnum chilense*, 26 May 2022, P. Sandoval-Leiva & A. Calle PSL-4212 (MURAY-BF 0006). Aysén: Municipality Aysén, Road to Puerto Aysén in *Nothofagus dombeyi* forest margins with scrub of *Fuchsia magellanica* with *Chusquea culeou*, 45°29′34.04″S, 72°14′5.26″W, elev. 91 m, on dead rachis of *Parablechnum chilense*, 11 June 2022, P. Saldivia 3791 (MURAY). GenBank: ITS = PP725270; 28S = PP725276.

Phylogenetic analysis. The resulting ITS alignment included 92 sequences with 452 characters, and the

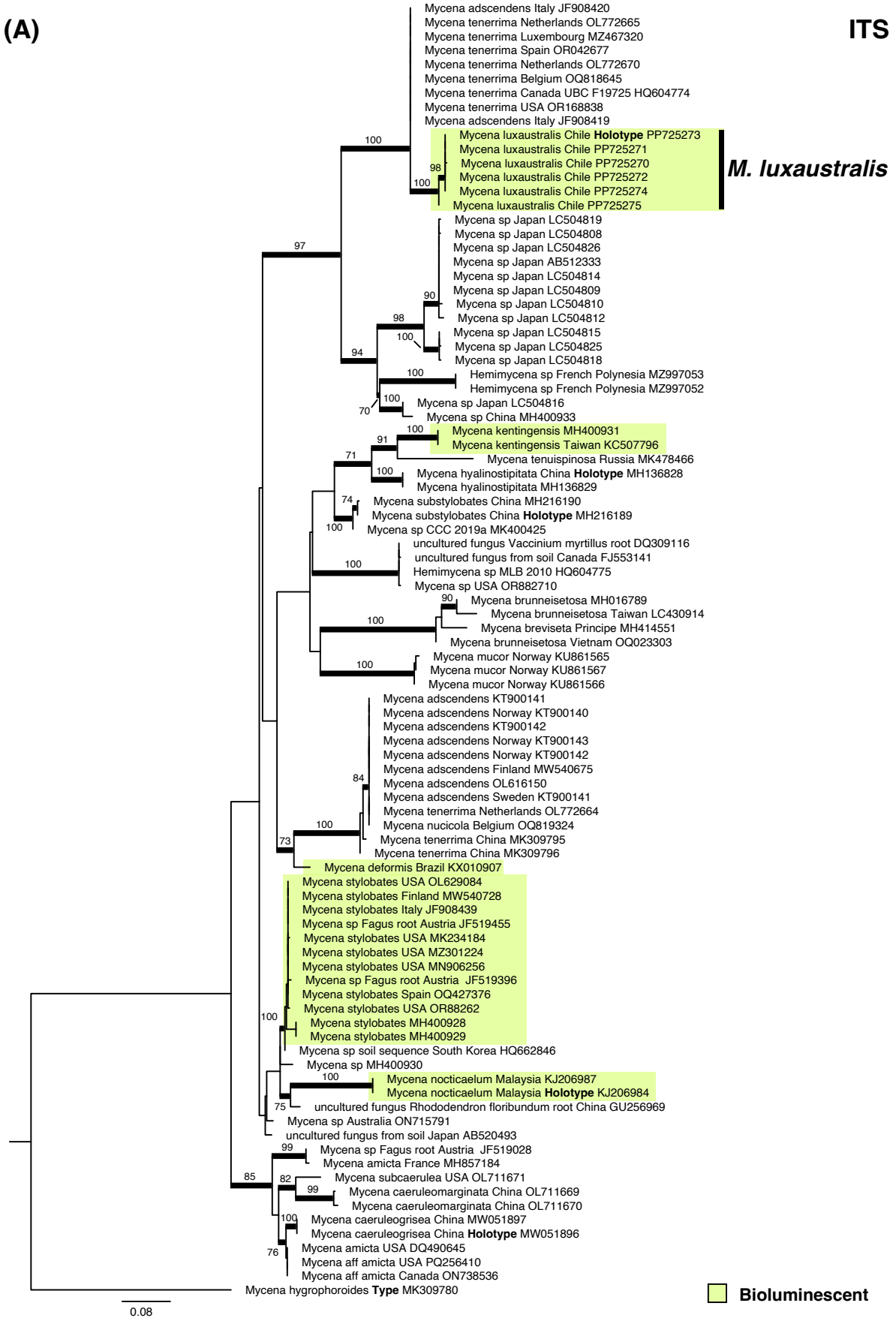

Figure 3. Maximum Likelihood phylogenetic analysis of ITS (A), 28S (B), and concatenated ITS+28S (C) sequences of *Mycena luxaustralis* and related species. Support for branches in each analysis was assessed with 1,000 bootstrap replicates. Branches were considered supported by bootstrap values ≥70 and are indicated by thickened lines. Species with known bioluminescent properties in basidiomes and/or mycelium are indicated with colored blocks.

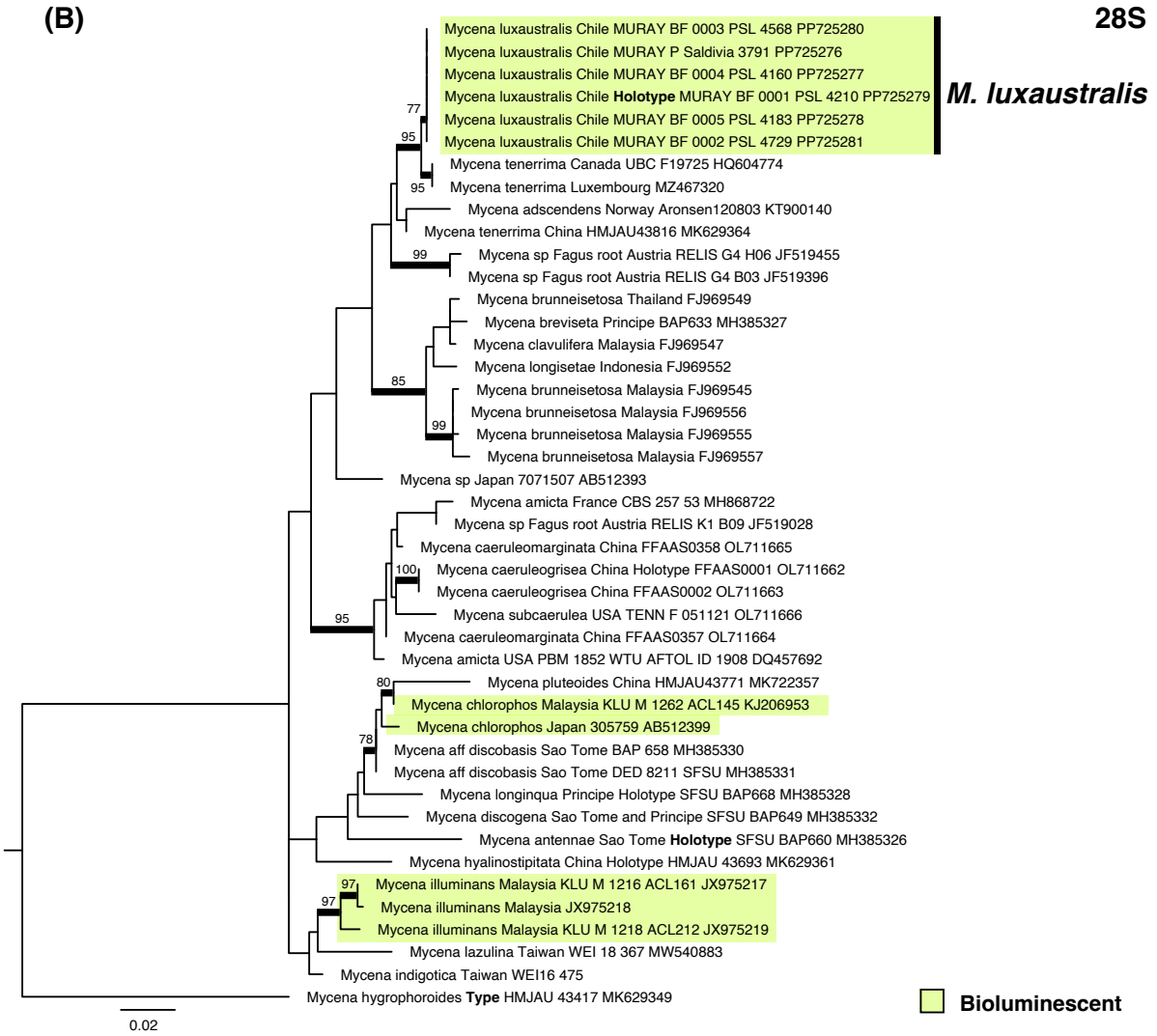

Figure 3. Continued.

resulting 28S alignment included 36 sequences with 582 characters, and the concatenated ITS+28S alignment included 36 sequences with 1,002 characters. Maximum Likelihood analysis showed that *M. luxaustralis* is distinct from other *Mycena* sequences included in our analysis (Fig. 3). ITS and 28S sequences generated from our samples formed well-supported clades in all phylogenetic analyses (ITS, 28S, ITS+28S), and in each analysis, a well-supported sister clade was formed by specimens from North America and Europe identified as *M. adscendens* or *M. tenerrima*, which are synonyms. Sequences from specimens identified as *M. adscendens* or *M. tenerrima* formed more than one clade, however, suggesting that the phylogenetic concept of *M. tenerrima* (= *adscendens*) needs further clarification.

Discussion

The species in the genus *Mycena* sect. *Sacchariferae* Kühner ex Singer are characterized by having a granulose, floccose or pulverulent pileus surface and a basal disc at the base of the stipe (although this feature is occasionally absent from some taxa in this group). The uneven pileus surface in this group of fungi is mainly due to the presence of numerous acanthocysts, which are the remains of the universal veil. Desjardin (1995) subdivided this section into three stirps, *Amparoina*, *Adscendens* and *Alphitophora*, then Maas Geesteranus & de Meijer (1997) added stirps *Fuscinea*. However, Na & Bau (2019b) elevated stirps *Amparoina* to section *Amparoina*, including members of stirps *Amparoina* and stirps *Alphitophora*, based on phylogenetic evidence. Their phylogenetic concept of sect. *Sacchariferae* was therefore limited to stirps *Adscendens* in their analysis, including only *M. adscendens* (= *tenerrima*), *M. hyalinostipitata*, and *M. substylobates*. Further investigation of questions of the monophyly of section *Sacchariferae* and the correspondence of morphological features with phylogenetic clades remain hindered by a lack of DNA sequence data for many *Mycena* species in this section. For instance, no sequence data are available for any species in stirps *Fuscinea*.

The morphological features of *M. luxaustralis* support its placement in the morphologically defined section *Sacchariferae* and stirps *Adscendens* (see below), but our phylogenetic analysis revealed that there are major

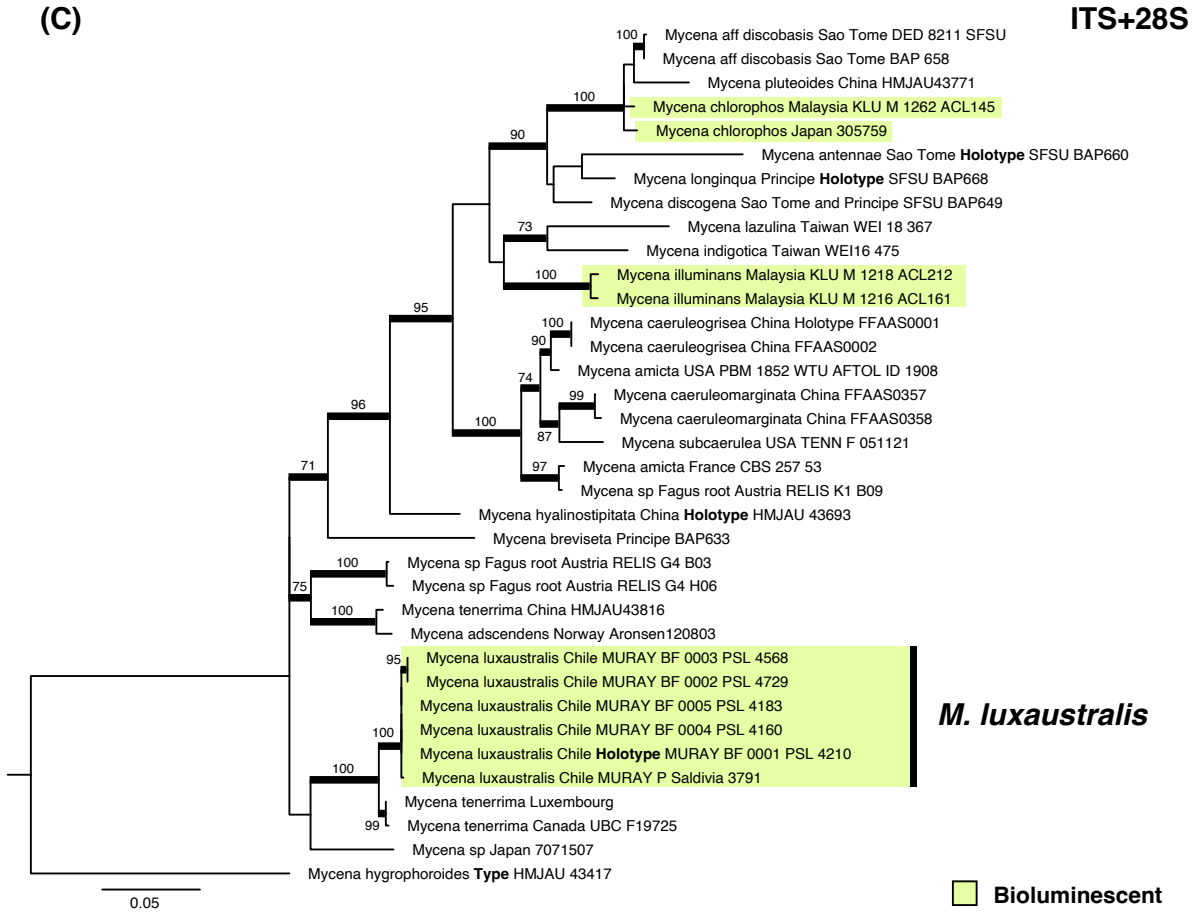

Figure 3. Continued.

issues with the phylogenetic concepts of *Mycena* section *Sacchariferae* and stirps *Adscendens* that cannot be immediately resolved with the data currently available for species in this section and stirps. Our ITS, 28S and concatenated ITS+28S analyses all support the monophyly of *M. luxaustralis* and its relationship as a sister clade to a group of specimens identified as *M. tenerrima* (= *adscendens*) (Fig. 3). However, since no sequences of type material from *M. tenerrima* or *M. adscendens* exist, and there are two clades with sequences identified as this species, the exact phylogenetic position of *M. tenerrima* remains unclear. Furthermore, other species that have been proposed as members of stirps *Adscendens* (*M. hyalinostipitata*, *M. substylobates*, and *M. kentingensis*) are not monophyletic with either clade identified as *M. tenerrima* (Fig. 3). This suggests that stirps *Adscendens sensu* Na & Bau (2019b) is polyphyletic, but the phylogenetic boundaries of stirps *Adscendens* cannot be established without further clarity on which phylogenetic clade corresponds to the *M. tenerrima* or *M. adscendens* type specimens. Furthermore, our ITS+28S analysis shows that *M. lazulina*, which was placed by morphology within sect. *Sacchariferae* by Na et al. (2022), does not show a clear phylogenetic association with any other species placed in stirps *Adscendens* included in our analysis (*M. hyalinostipitata*, *M. kentingensis*, *M. luxaustralis*, *M. substylobates*, or *M. tenerrima*). Instead, *M. lazulina* is resolved as a sister clade to another blue-colored species, *M. indigotica*, which was not placed in any morphological section of *Mycena* due to its *Favolaschia*-like poroid hymenophore (Na et al. 2022). Na et al. (2022) placed *M. lazulina* in sect. *Sacchariferae* based in part on the presence of acanthocysts, but our analysis suggests that presence or absence of acanthocysts is not a phylogenetically consistent character for sect. *Sacchariferae*. Finally, a specimen identified as *M. discogena* from Saõ Tomé and Príncipe was included in our ITS+28S analysis and placed in a clade with *M. longinqua* (sect. *Polyadelphia*), *M. antennae* (sect. *Granuliferae*), and others. If the identification of this specimen as *M. discogena* is correct, it suggests this species is not closely affiliated with other members of stirps *Adscendens*. However, there are no other sequences of specimens (including types) identified as *M. discogena*.

Clearly, there are major problems with correspondence between morphological sections and stirps of *Mycena* and phylogenetic analyses. In this work, we refer to the /amicta clade, which is a phylogenetic clade delimited by Soares et al. (2024) and has no direct correspondence to any morphological concept of sections. This clade includes members of sections *Basidipes*, *Extornatae*, *Sacchariferae*, but also includes sequences from unidentified specimens and environmental sequences. While Soares et al. (2024) did not attempt to establish phylogenetic boundaries for any *Mycena* section or stirps, their broad sampling strategy targeting all *Mycena* specimens with

ITS and 28S sequences available in GenBank provided a more robust phylogenetic context for section *Sacchariferae* than other works (e.g., Na & Bau 2019a, b) that used a more limited selection of sequences. Merging phylogenetic and morphological concepts of *Mycena* sections and stirps is a task that will require generating sequence data for many species that are not currently represented in public sequence databases, particularly type specimens, and is beyond the scope of this work.

Mycena luxaustralis has a unique combination of characteristic macroscopic and microscopic features. Macroscopically, this species is characterized by a granulose pileus and basally hirsute stipe that emerges from a well-developed basal disc, as well as the fact that it is bioluminescent. Microscopically, *M. luxaustralis* is characterized by its globose and amyloid spores, numerous densely spinulose cheilocystidia and acanthocysts, smooth caulocystidia, as well as the lack of cherocytes. Taken together, these morphological features indicate that *M. luxaustralis* belongs to the section *Sacchariferae* and stirps *Adscendens* as they are currently understood through morphological characters (Desjardin 1995; Aravindakshan & Manimohan 2015; Na & Bau 2019a).

The most closely related species to *M. luxaustralis*, both morphologically and phylogenetically, is *M. tenerrima* [syn. *M. adscendens*]. *Mycena tenerrima* also belongs to sect. *Sacchariferae* and has been considered a cosmopolitan species with a wide distribution (Na & Bau 2019a). *Mycena tenerrima* can be differentiated from *M. luxaustralis* by its pip-shape spores (8–9.5 × 5–5.8 µm), 2-spored basidia, lageniform to cylindrical caulocystidia (20–65 × 3.5–13.5 µm) and lageniform to fusiform cheilocystidia with slender necks which may be smooth or covered by warts in the middle section (Maas Geesteranus 1981; Desjardin 1995; Maas Geesteranus & de Meijer 1997). Singer (1959, 1969) reported *M. tenerrima* from Chile, but he mentioned in the description the presence of ellipsoid spores and basidia that were either 2-, 3- or 4-spored basidia.

Some similar species of *Mycena* have also been reported from Chile. Desjardin (1995) recognized four species of *Mycena* sect. *Sacchariferae* in Chile: *M. discogena*, *M. dryopteridis*, *M. triplotricha* and *M. mostnyae*. Like *M. luxaustralis*, these four species also belong to stirps *Adscendens*, but they have several important morphological differences from *M. luxaustralis*. *Mycena mostnyae* differs by its basidiomata that are dark bluish grey when young, its subdistant to distant lamellae (up to 17 true lamellae vs. 9 true lamellae in *M. luxaustralis*), its ellipsoid spores (7.5–8.5 × 3.7–5 µm) and its caulocystidia that are ampullaceous or ventricose, but not acute (Desjardin 1995). *Mycena triplotricha* is easily differentiated by its long caulocystidia, which may be up to 200 µm long. *Mycena discogena*, described from Juan Fernandez Island (Chile), is characterized by its greyish brown, flocculose-pruinose pileus, subdistant lamellae that are often pseudocollariate, a white, pruinose to pubescent stipe that arises from a well-developed basal disc and smooth awl-shaped caulocystidia. This species differs notably from *M. luxaustralis* in its broadly ellipsoid spores (7–9.5 × 5–6 µm) with a Q value between 1.4–1.7 and the fact that it has two types of cystidia in the basal disc (Desjardin 1995). *Mycena dryopteridis* is perhaps the most similar Chilean species to *M. luxaustralis*. Both species are found on the petioles and rachises of pteridophytes and have macromorphologically similar basidiomata that share the small, white, pulverulent pileus. However, *M. dryopteridis* has a rudimentary basal disc, broadly ellipsoidal spores (7.4–9.2 × 5–6 µm) and larger caulocystidia, 30–100 × 6.5–20 µm, that are subcylindrical to broadly lanceolate and have an obtuse apex (Desjardin 1995).

There are two additional Chilean *Mycena* species that Singer (1962, 1975, 1986) considered affiliated with sect. *Sacchariferae*. The first of these is *M. copriniformis*, which was redescribed by Singer (1969) and whose macroscopic characteristics coincide with the section *Sacchariferae*. However, Desjardin (1995) maintained this species as *incertae sedis* because he considered Singer's microscopic description to be unclear. According to Singer's description, *M. copriniformis* also has ellipsoid spores. The other species, *M. nothomyrciae*, was considered by Singer (1959) to belong to sect. *Sacchariferae*, but was excluded from that section by Desjardin (1995) due to its microscopic characteristics, including the ellipsoid to cylindrical-ellipsoid spores that clearly differentiate it from *M. luxaustralis*.

Worldwide, there are other species that share many similarities with *M. luxaustralis*, such as the delicate basidiomes, the stipe with a basal disk that is covered by smooth caulocystidia, and the lack of cherocytes. These include *M. nucicola*, *M. discopus* (Maas Geesteranus 1981), *M. dissimilis* (Maas Geesteranus & de Meijer 1997), *M. hyalinostipitata* (Na & Bau 2019b), *M. apala* and *M. furfuracea* Aravind. & Manim (Aravindakshan & Manimohan 2015). *Mycena nucicola*, known only from Europe, differs by its pip- shaped spores (7–9 × 4–5 µm) and subglobose, densely diverticulated caulocystidia that are scattered in the stipe and abundant on the basal disc (Maas Geesteranus 1981). Although there is no modern detailed microscopic analysis of *M. discopus*, it is described as having broadly adnate lamellae (Maas Geesteranus 1981) and Desjardin (1995) considered it as a possible synonym of *M. nucicola*. *Mycena dissimilis*, described from Brazil, differs from *M. luxaustralis* by its pip-shaped spores (8–9.8 × 4.5–6.3 µm) and its caulocystidia that are clavate and long stalked or subcylindrical with a slightly inflated apex that is densely spinulose (Maas Geesteranus & de Meijer 1997). *Mycena hyalinostipitata* Na & Bau, known only from China, shares with *M. luxaustralis* the awl-shaped to fusiform caulocystidia, but it differs in the narrow elliptical to cylindrical spores and bisporic basidia (Na & Bau 2019a). *Mycena substylobates* Na & Bau, also described from China, is clearly differentiated by its irregularly shaped and smooth caulocystidia (Na & Bau 2019b). *Mycena apala* and *M. furfuracea*, both species described from India, are differentiated by their oblong to ellipsoid spores (Aravindakshan & Manimohan 2015).

Considering that globose spores are one of the diagnostic characters that differentiate *M. luxaustralis* from

the previously treated species, it is important to mention that there are several species in section *Sacchariferae* that also have globose to subglobose spores. These include *M. corynephora*, *M. yalensis*, and *M. pulvinibasis*. *Mycena corynephora* and *M. yalensis* differ from *M. luxaustralis* in that they lack a basal disc and they were included in stirps *Alphitophora* by Desjardin (1995), a stirps now included in section *Amparoina* by Na & Bau (2019b), based on the phylogenetic reconstructions of sect. *Sacchariferae*. In the case of *M. pulvinibasis*, a species originally described from Madagascar, it differs from *M. luxaustralis* by its 2-spored basidia and also by its glabrous stipe which apparently lacks caulocystidia (Desjardin 1995).

Another unusual feature of *M. luxaustralis* is that it has only been found in forest environments in southern Chile on the decaying stipes and rachises of *Parablechnum chilense*. This growth habit may confuse it with *M. blechnophila*, which grows specifically on dead fronds of *Blechnum* sp. (Singer et al. 1965). However, the morphological characteristics of *M. blechnophila* differ significantly from *M. luxaustralis*, including the larger size of its basidiomata (pileus up to 12 mm in diameter) which are grayish and finely pubescent and a stipe without a basal disc. *Mycena blechnophila* is also differentiated microscopically by its ellipsoid spores (7.3–10 × 4.5–5.5 µm) and ventricose and smooth pleurocystidia and cheilocystidia.

Finally, documenting new species in native Patagonian forests in Chile is not only fundamental for generating baseline information of biodiversity, but also crucial to reiterate the importance of these highly unique ecosystems that are vulnerable to human disturbance. These ecosystems face multiple threats due to land-use change, primarily in the form of large-scale deforestation to make way for industrial pine and eucalypt plantations, which are highly prone to forest fires that threaten native fire-intolerant forests (Gonzales et al. 2023). This paper documents a new species *Mycena luxaustralis*, just one small example that highlights the high biodiversity of these underexplored forest environments. This species is just one of many new and interesting taxa that require these native forests for their growth and survival.

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References

Alvez, M. H. & Nascimento, C. C. 2014. *Mycena margarita* (Murrill) Murrill, 1916 (*Basidiomycota*: *Agaricales*: *Mycenaceae*): A bioluminiscent agaric first recorded in Brazil. *Check List* 10(1): 239–243. https://doi.org/10.15560/10.1.239

Aravindakshan, D. M. & Manimohan, P. 2015. *Mycenas of Kerala*. SporePrint Books, Calicut, India.

Chew, A. L., Tan, Y., Desjardin, D. E., Musa, M. Y. & Sabaratnam, V. 2013. Taxonomic and phylogenetic re-evaluation of *Mycena illuminans*. *Mycologia* 105(5): 1325–1335. https://doi.org/10.3852/13-009

Chew, A. L. C., Desjardin, D. E., Tan, Y. S., Musa, M. Y. & Sabaratnam,V. 2015. Bioluminescent fungi from Peninsular Malaysia – a taxonomic and phylogenetic overview. *Fungal Diversity* 70: 149–187. https://doi.org/10.1007/s13225-014-0302-9

Dennis, R. W. G. 1961. Fungi venezuelani: IV. *Kew Bulletin* 15(1): 67–156. https://doi.org/10.2307/4115784

Desjardin, D. E. 1995. A preliminary accounting of the worldwide members of *Mycena* sect. *Sacchariferae*. *Bibliotheca Mycologica* 159: 1–89.

Desjardin, D. E., Capelari, M. & Stevani, C. 2007. Bioluminescent *Mycena* species from Sao Paulo, Brazil. *Mycologia* 99: 317–331. https://doi.org/10.3852/mycologia.99.2.317

Desjardin, D. E., Oliveira, A. G. & Stevani, C. V. 2008. Fungi bioluminescence revisited. *Photochemical and Photobiological Science* 7: 170–182. https://doi.org/10.1039/b713328f

Desjardin, D. E., Perry, B. A., Lodge, D. J., Stevani, C. V. & Nagasawa, E. 2010. Luminescent *Mycena*: new and noteworthy species. *Mycologia* 102: 459–477. https://doi.org/10.1080/15572536.2007.11832592

Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797. https://doi.org/10.1093/nar/gkh340

Gardes, M. & Bruns, T. D. 1993. ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2: 113–118. https://doi.org/10.1111/j.1365-294x.1993.tb00005.x

Garrido, N. 1985. *Index Agaricalium Chilensium*. Bibliotheca Mycologica 99, J. Cramer, Vaduz, 399 pp.

González, M. E., Galleguillos, M., Lopatin, J., Leal, C., Becerra-Rodas, C., Lara, A. & San Martín, J. 2023. Surviving in a hostile landscape: *Nothofagus alessandrii* remnant forests threatened by mega-fires and exotic pine invasion in the coastal range of central Chile. *Oryx* 57(2): 228–238. https://doi.org/10.1017/S0030605322000102

Haddock, S. H., Moline, M. A. & Case, J. F. 2009. Bioluminescence in the sea. *Annual Review of Marine Science* 2(1), 443–493. https://doi.org/10.1146/annurev-marine-120308-081028

He, M. Q., Zhao, R. L., Hyde, K., Begerow, D., Kemler, M., Yurkov, A., Mckenzie, E., Raspé, O., Kakishima, M., Sanchez-Ramirez, S., Vellinga, E., Halling, R., Papp, V., Zmitrovich, I., Buyck, B., Ertz, D., Wijayawardene, N., Cui, B. K., Schoutteten, N. & Kirk, P. 2019. Notes, outline and divergence times of *Basidiomycota*. *Fungal Diversity* 99: 105–367. https://doi.org/10.1007/s13225-019-00435-4

Hopple, J. S., Jr. & Vilgalys, R. 1994. Phylogenetic relationship among coprinoid taxa and allies based on data from restriction site mapping of nuclear rDNA. *Mycologia* 86: 96–107. https://doi.org/10.1080/00275514.1994.12026378

Ke, H-M. & Tsai, I. J. 2022. Understanding and using fungal bioluminescence – recent progress and future perspectives. *Current Opinion in Green and Sustainable Chemistry* 33: 100570. https://doi.org/10.1016/j.cogsc.2021.100570

Kirk, P. M., Cannon, P., Minter, D. W. & Stalpers, J. A. 2008. *Dictionary of the Fungi* (10th Ed.). CAB International, Wallingford, United Kingdom. 784 pp.

Kotlobay, A. A., Sarkisyan, K., Mokrushina, Y. A., Marcet-Houben, M., Serebrovskaya, E. O., Markina, N. M., Gonzalez Somermeyer, L., Gorokhovatsky, A. Y., Vvedensky, A., Purtov, K. V., Petushkov, V. N., Rodionova, N. S., Chepurnyh, T. V., Fakhranurova, L., Guglya, E. B., Ziganshin, R., Tsarkova, A. S., Kaskova, Z. M., Shender, V., Abakumov, M., Abakumova, T. O., Povolotskaya, I. S., Eroshkin, F. M., Zaraisky, A. G., Mishin, A. S., Dolgov, S. V., Mitiouchkina, T. Y., Kopantzev, E. P., Waldenmaier, H. E., Oliveira, A. G., Oba, Y., Barsova, E., Bogdanova, E. A., Gabaldón, T., Stevani, C. V., Lukyanov, S., Smirnov, I. V., Gitelson, J. I., Kondrashov, F. & Yampolsky, I. V. 2018. Genetically encodable bioluminescent system from fungi. *Proceedings of the National Academy of Sciences of the United States of America* 115(50): 12728–12732. https://doi.org/10.1073/pnas.1803615115

Largent, D. L.1986. *How to Identify Mushrooms to Genus I: Macroscopic Features*. Eureka, Mad River Press, USA. 166 pp.

Lazo, W. 2001. *Hongos de Chile. Atlas Micológico*. Facultad de Ciencias de la Universidad de Chile, Santiago.

Lodge, D. J., Ammirat, J. F., O'Dell, T. E., Mueller, G. M., Huhndorf, S. M., Wang, C., Stokland, J., Schmit, J. P., Ryvarden, L., Leacock, P., Mata, M., Umaña, L., Wu, Q. & Czederpiltz, D. L. 2004. Terrestrial and lignicolous macrofungi. In: *Biodiversity of Fungi: Inventory and Monitoring Methods*, pp. 127–158. Elsevier Inc. https://doi.org/10.1016/B978-012509551-8/50011-8

Lu, W., Priyashantha, A. K. H., Galappaththi, M. C. A., Tibpromma, S., Dai, D., Patabendige, N. M., Premarathne, B. M., Kulasuriya, D. M., Ediriweera, A. N., Nimalrathna, T. S., Suwannarach, N., Lumyong, S., Tang, A., Shao, S. & Karunarathna, S. C. 2024. Fungal bioluminescence: past, present, and future. *Diversity* 16(9): 539. https://doi.org/10.3390/d16090539

Maas Geesteranus, R. A. 1981. Studies in Mycenas 16–25. *Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen Section C*. 84(2): 211–220.

Maas Geesteranus, R. A. & de Meijer, A. A. 1997. Mycenae paranaenses. *Verhandelingen der Koninklijke Nederlandsche Akademie van Wetenschappen. Afdeeling Natuurkunde*, *Tweede Reeks* 97: 1–164.

Maas Geesteranus, R. A. & de Meijer, A. A. 1998. Further Mycenas from the state of Paraná, Brazil. *Persoonia* 17(1): 29–46.

Martínez, A. P., Suarez, J. M. & Lechner, B. E. 2020. Tres nuevos registros de *Agaricomycetes* para la Argentina: *Cortinarius casimiri* var. *hoffmannii*, *Lactarius hepaticus* y *Mycena margarita*. *Darwiniana, Nueva Serie* 8(2): 438–448. https://doi.org/10.14522/darwiniana.2020.82.888

Minter, D. W. & Peredo López, H. 2006. *Hongos de Chile*. [Online]. Accessed June 2024. http://www.cybertruffle.org.uk/chilfung

Mujica, R. F. & Vergara, C. C. 1980. *Flora Fungosa Chilena*. Revisada y Actualizada por Edgard Oehrens. 2ª Edición. Universidad de Chile, Fac. de Agronomía, Cs. Agrícolas. Santiago de Chile. 124 pp.

Na, Q. & Bau, T. 2019a. *Mycena* section *Sacchariferae*: three new species with basal discs from China. *Mycological Progress* 18: 483–493. https://doi.org/10.1007/s11557-018-1456-8

Na, Q. & Bau, T. 2019b. Recognition of *Mycena* sect. *Amparoina* sect. nov. (*Mycenaceae*, *Agaricales*), including four new species and revision of the limits of sect. *Sacchariferae*. *MycoKeys* 52: 103–124. https://doi.org/10.3897/mycokeys.52.34647

Na, Q., Liu, Z., Zeng, H., Ke, B., Song, Z., Cheng, X. & Ge, Y. 2022. Taxonomic studies of bluish *Mycena* (*Mycenaceae*, *Agaricales*) with two new species from northern China. *MycoKeys* 90: 119–145. https://doi.org/10.3897/mycokeys.90.78880

Niveiro, N., Popoff, O. F. & Albertó, E. O. 2010. Contribución al conocimiento de los *Agaricales* s.l. de la Selva Paranaense Argentina. *Boletín de la Sociedad Argentina de Botánica* 45(1–2): 17–27.

Niveiro, N., Popoff, O. F. & Albertó, E. O. 2011. *Mycena holoporphyra* (*Mycenaceae*, *Agaricomycetes*), primer registro para la Argentina. *Darwiniana* 49(2): 252–256.

Niveiro, N., Popoff, O. F., Desjardin, D. & Albertó, E. O. 2012. *Mycena moconensis*, a new species of section *Polyadelphia* from Argentina. *Mycotaxon* 119: 167–173.

Niveiro, N., Popoff, O. F. & Albertó, E. O. 2015. Presencia de *Mycena paranaensis* para la micobiota Argentina y reconsideración de *Mycena leaiana*. *Darwiniana, Nueva Serie* 3(1): 89–95. https://doi.org/10.14522/darwiniana.2015.31.635

Oliveira, A. G., Desjardin, D. E., Perry, B. A. & Stevani, C. V. 2012. Evidence that a single bioluminescent system is shared by all known bioluminescent fungal lineages. *Photochemical & Photobiological Sciences* 11(5): 848–852. https://doi.org/10.1039/c2pp25032b

Oliveira, A., Stevani, C., Waldenmaier, H., Viviani, V., Emerson, J., Loros, J. & Dunlap, J. 2015. Circadian Control Sheds Light on Fungal Bioluminescence. *Current Biology* 25(7): 964–968. https://doi.org/10.1016/j.cub.2015.02.021

Raithelhuber, J. 1984a. Die Gattung *Mycena* in Südamerika (1). *Metrodiana* 10(1): 5–21.

Raithelhuber, J. 1984b. Die Gattung *Mycena* in Südamerika (2). *Metrodiana* 10(2): 23–46.

Raithelhuber, J. 1985a. Die Gattung *Mycena* in Südamerika (3). *Metrodiana* 11(1): 2–25.

Raithelhuber, J. 1985b. Die Gattung *Mycena* in Südamerika (4). *Metrodiana* 11(2): 31–50.

Raithelhuber, J. 1985c. Die Gattung *Mycena* in Südamerika (5). *Metrodiana* 12(1): 3–9.

Raithelhuber, J. 1985d. Llave para determinar las Micenas sudamericanas. *Metrodiana* 12(1): 12–20.

Raithelhuber, J. 1985e. Key to the species of *Mycena* in South America. *Metrodiana* 12(2): 25–32.

Raithelhuber, J. 1996a. Agaric flora of South America (11). *Metrodiana* 23(1): 10–52.

Raithelhuber, J. 1996b. Agaric flora of South America (12). *Metrodiana* 23(3): 124–152.

Raithelhuber, J. 2004. *Nueva Flora Micológica Argentina*. Stuttgart, Mycosur. 576 p.

Rick, J. 1938. Agarici Riograndenses. *Lilloa* 2: 3–311.

Silva-Filho, A., Mombert, A., Nascimento, C., Nóbrega, B., Soares, D., Martins, A., Domingos, A., Santos, I., Della-Torre, O., Perry, B., Desjardin, D., Stevani, C. & Menolli, N. 2023. *Eoscyphella luciurceolata* gen. and sp. nov. (*Agaricomycetes*) Shed Light on *Cyphellopsidaceae* with a New Lineage of Bioluminescent Fungi. *Journal of Fungi* 9(10): 1004. https://doi.org/10.3390/jof9101004

Singer, R. 1950. Type studies on *Basidiomycetes* IV. *Lilloa* 23: 147–246.

Singer, R. 1959. *Basidiomycetes* from Masatierra (Juan Fernandez Islands, Chile). *Arkiv för Botanik* (2) 4: 371–400.

Singer, R. 1962. *Agaricales in modern taxonomy*. 2nd Ed. pp. 915. J. Cramer, Weinheim.

Singer, R. 1969. Mycoflora Australis. *Beihefte zur Nova Hedwigia* 29: 1–405.

Singer, R. 1973. Diagnoses Fungorum novorum Agaricalium III. *Beihefte Sydowia* 7: 1–106.

Singer, R. 1975. *The Agaricales in modem taxonomy*. 3rd Ed. pp. 912. J. Cramer, Vaduz.

Singer, R. 1986. *The Agaricales in modern taxonomy*. 4th Ed. pp. 981. Koeltz Scientific Books, Koenigstein Germany.

Singer, R. 1989. New taxa and new combinations of *Agaricales* (Diagnoses Fungorum Novorum Agaricalium IV). *Fieldiana Botany* 21: 1–133.

Singer, R. & Digilio, A. P. L. 1952. Pródromo de la Flora Agaricina Argentina. *Lilloa* 25: 6–461.

Singer, R., Moser, M., Gamundí, I. J., De La Sota, E. R. & Sarmiento, G. 1965. Forest mycology and forest communities in South America. *Mycopathologia* 26: 129–191. https://doi.org/10.1007/bf02049773

Sivinski, J. 1981. Arthropods attracted to luminous fungi. *Psyche* 88: 383–390. https://doi.org/10.1155/1981/79890

Soares, C. C. B., Cabral, T. S., Vargad-Isla, R., Cardoso, J. S., Rodrigues, D. P., Ishikawa, N. K. & Oliveira, J. J. S. 2024. *Mycena lamprocephala*, a new luminescent species from the Brazilian

Amazon. *Phytotaxa* 634(3): 187–203. https://doi.org/10.11646/phytotaxa.634.3.1

Spegazzini, C. 1887. Fungi patagonici. *Boletin de la Academia Nacional de Ciencias de la República Argentina* 11: 5–64. http://dx.doi.org/10.5962/bhl.title.4071

Spegazzini, C. 1899. Fungi argentini novi v. critici. *Anales del Museo Nacional de Historia Natural "Bernardino Rivadavia"* 6: 6–365.

Stevani, C. V., Oliveira, A. G., Mendes, L. F., Ventura, F. F., Waldenmaier, H. E., Carvalho, R. P. & Pereira, T. A. 2013. Current status of research on fungal bioluminescence: Biochemistry and prospects for ecotoxicological application. *Photochemistry and Photobiology* 89(6): 1318–1326. https://doi.org/10.1111/php.12135

Talavera, G. & Castresana, J. 2007. Improvement of Phylogenies after Removing Divergent and Ambiguously Aligned Blocks from Protein Sequence Alignments. *Systematic Biology* 56: 564–577. https://doi.org/10.1080/10635150701472164

Valenzuela E. & Moreno, G. 1995. Contribución al estudio del género *Mycena* (*Agaricales*, *Basidiomycotina*) en la X Región de Chile. *Boletín de la Sociedad Micológica de Madrid* 20: 179–194

Vandepol, N., Liber, J., Desirò, A., Na, H., Kennedy, M., Barry, K., Grigoriev, I. V., Miller, A. N., O'Donnell, K., Stajich, J. E. & Bonito, G. 2020. Resolving the *Mortierellaceae* phylogeny through synthesis of multi-gene phylogenetics and phylogenomics. *Fungal Diversity* 104: 267–89. https://doi.org/10.1007/s13225-020-00455-5

White, T. J., Bruns, T. D., Lee, S. B. & Taylor, J. W. 1990. Amplification and Direct Sequencing of Fungal Ribosomal RNA Genes for Phylogenetics. In: Innis, M. A., Gelfand, D. H., Sninsky, J. J. & White, T. J. (eds), *PCR Protocols: A Guide to Methods and Applications*, pp. 315–322. Academic Press, New York. http://dx.doi.org/10.1016/B978-0-12-372180-8.50042-1