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Research article

Reevaluating *Mycena* section *Amparoina* (Mycenaceae, Agaricales) in the northwestern Iberian Peninsula and Macaronesia, with descriptions of four new species and a new European record

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Abstract. *Mycena* section *Amparoina*, with 52 described taxa worldwide is the third largest section of the genus *Mycena* and it is characterized by the small basidiomata, the presence of acanthocysts and often cheroocytes that form the universal veil, and spinulose cheilocystidia and caulocystidia. In the present study we describe four new species namely *M. atlantica* sp. nov., *M. eucalypticola* sp. nov., *M. melanovelis* sp. nov. and *M. viridivelata* sp. nov., together with *M. corynephora*, collected in the northwestern of the Iberian Peninsula and some Macaronesian islands. Furthermore, *M. biornata* is a new record for the European mycobiota and has been recorded from different localities in Portugal and Spain. Sequences from the nuclear internal transcribed spacer (ITS) were generated to infer the relationships within *M. sect. Amparoina* using maximum likelihood and Bayesian inference. The phylogenetic evidence, along with the morphological features, supported the recognition of the four new species within the *M. sect. Amparoina*. In addition, the phylogenetic position of *M. sect. Amparoina* and its relationship with other sections of the genus *Mycena* are discussed. Detailed macro- and micromorphological descriptions, line-drawing illustrations, and photographs of the new species are provided.

Keywords. Agaricales, Mycenaceae, new taxa, phylogeny, taxonomy, systematics.

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Introduction

The genus *Mycena* (Pers.) Roussel belongs to the Mycenaceae Overeem and contains approximately 1312 species (Kalichman *et al.* 2020). It is a genus of saprotrophic, biotrophic, and mycorrhizal fungi (Guo *et al.* 1997; Grelet *et al.* 2017; Harder *et al.* 2021; Liu *et al.* 2024) that grow on the ground or on leaf litter, fruit remains, branches, bark, or trunks. It is characterized by medium-sized to tiny basidiomata. Species of *Mycena* are widely distributed around the world. Kühner (1938) published *M. sect. Sacchariferae* Kühner ex Sing. for the first time, including species with a granular or “sugar-coated” cap surface. Such ornamentation of the cap is due to remnants of the universal veil that is composed of specialised cells known as acanthocysts and cherocytes (Kühner 1938; Singer 1983; Desjardin 1993, 1995; Maas Geesteranus & de Meijer 1997, 1998; Bougher 2009; Aravindakshan & Manimohan 2015; Jagers *et al.* 2023). Acanthocysts and cherocytes can occur singly or in chains and form a powdery or mealy mass that is often arranged in spines or cones. Cherocytes are distinguished by their thick-walled cells and the presence or absence of vacuolar pigment. These cells are typically covered sparsely or densely with spinulae, and have one or multiple thick-walled spines, which can be more or less acute (Desjardin 1995). In contrast, acanthocysts are characterised by their thin-walled cells, hyaline or pigmented, covered sparsely or densely with minute obtuse warts or more frequently with spinulae (Desjardin 1995). Cherocytes, when present, confer substantial taxonomic value in the species identification.

Desjardin (1995) proposed a subdivision of *M. sect. Sacchariferae* into stirpes *Amparoina*, *Alphitophora*, and *Adscendens*, based on the presence or absence of basal disc, cherocytes, and caulocystidia ornamentation. Subsequently, Maas Geesteranus & de Meijer (1997) established the fourth stirps, *Fuscinea*, characterized by presenting acanthocysts with dark intracellular pigment, a character similar to that of some species of stirps *Amparoina*, where some species have yellowish pigments. In a recent publication, Na & Bau (2019b) cautioned that *M. sect. Sacchariferae* does not form a monophyletic group and proposed the new section *M. sect. Amparoina* T.Bau & Q.Na for species showing the presence of acanthocysts, occasional cherocytes, and spinulose cheilocystidia and caulocystidia.

The species of *M. sect. Amparoina* are typically found in tropical or subtropical environments. Following a thorough literature review, we identified a total of 52 species worldwide. In Europe, only two species are known to occur in the wild: the cosmopolitan *M. corynephora* Maas Geest. and the recently described *M. amoena* Jagers, Aronsen, Q.M.Holzappel & Nuytinck. Other species, such as *M. alphitophora* (Berk.) Sacc. and *M. chloroxantha* var. *appalachienensis* Desjardin, have been collected in tropical greenhouses (Bendiksen & Metsänheimo 1987; Brodegger *et al.* 2018). There is no research on the diversity of the group in Europe, and this is the first study to look at the issue. In recent years, several intriguing specimens of *Mycena* have been collected from the northwestern Iberian Peninsula and Macaronesia. As a result of these samplings, we provide the descriptions, molecular barcodes, and illustrations of six species of *M. sect. Amparoina* species from Spain and Portugal, including four species that are new to science. The aim of this study is to describe these new species providing morphological and molecular data to distinguish them from the closest described taxa.

Material and methods

Herbarium collections and morphological study

The samples were photographed macroscopically in situ and from moist chamber cultures of *Acacia*, *Laurus*, and *Salix* dead leaves with a Lumix TZ90 and an Olympus Tough TG6 digital cameras, using a tripod, natural light or led ring. The macroscopic descriptions are based on fresh material, which was subsequently dehydrated at 45°C for herbarium conservation in a Vidaxl food dehydrator or air dried. Once dried, the specimens were sealed in ziplock plastic bags and labeled. Voucher specimens have been deposited in the Herbarium of Alcalá University (AH), Instituto de Ecología, Mexico, Veracruz, Xalapa

(XAL), Couceiro's and Traba's personal herbaria with the acronyms (ACN) and (PR4) respectively. Images taken were processed with Adobe Photoshop®. Micromorphological data were obtained from fresh and dried fruitbodies. Free-handmade sections were made under a Motic SFL11C-2LBB dissecting microscope, rehydrated in water, and mounted on a slide in 2% Congo red to highlighting all tissues. Melzer's reagent was used to check amyloidity of the spores and dextrinoidity of the tissues. PIXIMÈTRE ver. 5.10 R 1541 was used for spore measurement. Spores were observed in water using an 100× oil immersion objective, choosing the "classique" format to present the results (<http://ach.log.free.fr/Piximetre/Piximetre5.htm>). For the microscopic study, the following equipment was used: an Olympus CX21 optical microscope with a Koppa microphotographic camera, an Olympus CX31 microscope with a CMOS 5MP camera, or an Olympus BX53 microscope with DIC Nomarski and Moticam 5000 cooler camera, connected to a personal computer. Terminology follows the glossary in Vellinga (1988).

DNA extraction, PCR and sequencing

Genomic DNA was extracted from fresh or recently dried material using the Omega Bio-tek E.Z.N.A.® HP Total RNA Kit, ref 6812-01. The entire internal transcribed spacer (ITS) region, comprising ITS1, 5.8S and ITS2, was amplified using primer pairs ITS1F/ITS4 (White *et al.* 1990; Gardes & Bruns 1993), and in some cases, where it was not possible to obtain the complete sequences, shorter fragments were amplified with the primer pairs ITS1/ITS2 and ITS3/ITS4 (White *et al.* 1990). The PCR thermocycling protocol was conducted as follows: initial denaturation at 95°C for 5 min; then 34 cycles of 30 s at 94°C, 30 s annealing at 55°C, 1 min elongation at 72°C and a final 10 min step at 72°C. PCR amplification products were separated by 1% agarose gel electrophoresis, stained with RedSafe Nucleic Acid Staining solution (iNtRON Biotechnology) and visualized with a Gel Doc XR+ Bio-Rad blue light for validation and then purified by ExoSAP-IT™ Express PCR Product Cleanup (Applied Biosystems) before the Sanger dideoxy sequencing. Amplicons were sequenced using the same primers as for amplification, at the Servicios de Apoio á Investigación (Vicerrectorado de Política Científica, Investigación y Transferencia, Universidade da Coruña, UDC). Sequencing was performed using the BigDye Terminator v3.1 Cycle Sequencing Kit and BigDye XTerminator™ Purification Kit (Applied Biosystems), followed by screening in an automatic 3500xL Genetic Analyzer (Applied Biosystems). In the tables and phylogenetic trees provided, sequences newly generated in this study are labelled in bold, and holotypes specimens are asterisked. The names of taxa retrieved from public databases are labelled as normal. Taxon name, GenBank accession no., and country of origin are given in Table 1.

Sequence alignment and phylogenetic analysis

To confirm the closest matches of the species, Basic Local Alignment Search Tool (BLAST) (Altschul *et al.* 1990) analysis was performed for each sequence against the National Center for Biotechnology Information (NCBI) (<https://www.ncbi.nlm.nih.gov/genbank/>) and The Barcode of Life Data (BOLD) (Ratnasingham *et al.* 2024) databases. The phylogenetic analysis based on nrITS sequence data is based on a dataset including the newly generated sequences, close relatives of the new taxa, available sequences of other species of the genus, relevant published phylogenies (Na & Bau 2019b; Jagers *et al.* 2023; Villarreal *et al.* 2023a, 2023b), and the outgroup species *Mycena pura* (Pers.) P.Kumm. Table 1 details the sequences used in the phylogenetic analysis.

A multiple sequence alignment was performed with the newly generated sequences and the selected species, using MAFFT ver. 7.475 (Katoh & Standley 2013), with the iterative refinement methods as G-INS-i strategy, and manually edited and trimmed afterwards in MEGA XI (Tamura *et al.* 2021). Phylogenetic relationships were estimated by using maximum likelihood (ML) and Bayesian inference (BI) approaches. ML analyses were performed in IQ-TREE ver. 2.2.0 (Nguyen *et al.* 2015). Best-fit substitution models for subsequent phylogenetic analyses were predicted with ModelFinder (Kalyaanamoorthy *et al.* 2017), implemented in IQ-TREE. To determine node support, 1000 thorough bootstrap replicates (BS, considered significant when $\geq 75\%$) were performed. The BI analysis was carried out in MrBayes ver. 3.2.7 (Ronquist *et al.* 2012). Substitution models were sampled within

Table 1 (continued on next 2 pages). Sequenced specimens used in phylogenetic analysis. Newly generated sequences are highlighted in bold and type specimens are marked with an asterisk (*).

Species name	GenBank accession no.	Voucher/strain no.	Country	Reference
<i>M. adscendens</i>	KT900140	Aronsen 120803	Norway	Aronsen & Larsson (2015)
<i>M. adscendens</i>	KT900142	Aronsen 061119	Norway	Aronsen & Larsson (2015)
<i>M. adscendens</i>	PP328931	PR4280722796	Spain	This study
<i>M. adscendens</i>	KT900141	Orstadius 329-05	Sweden	Aronsen & Larsson (2015)
<i>M. atlantica</i> sp. nov.	PV037609	AH59663*	Spain	This study
<i>M. atlantica</i> sp. nov.	PV037610	AH59666	La Palma-Spain	This study
<i>M. atlantica</i> sp. nov.	PV037611	AH60089	Madeira-Portugal	This study
<i>M. aff. discobasis</i>	MH414555	DED 8211	Sao Tomé	Cooper <i>et al.</i> (2018)
<i>M. alphitophora</i>	OP470587	iNAT129866340	USA	GenBank
<i>M. alphitophora</i>	MZ158564	iNAT13072966	USA	GenBank
<i>M. alphitophora</i>	MH136830	HMJAU43498	China	Na & Bau (2019a)
<i>M. alphitophora</i>	MH136831	HMJAU43686	China	Na & Bau (2019a)
<i>M. amoena</i>	OL772667	L0607542*	Netherlands	Jagers <i>et al.</i> (2023)
<i>M. amoena</i>	OL772666	L0607541	Netherlands	Jagers <i>et al.</i> (2023)
<i>M. antennae</i>	MH414552	BAP648*	Principe-Africa	Cooper <i>et al.</i> (2018)
<i>M. bicytidiata</i>	MK309773	HMJAU43648*	China	Na & Bau (2019b)
<i>M. bicytidiata</i>	MK309774	HMJAU43589	China	Na & Bau (2019b)
<i>M. biornata</i>	MZ393491	AH56003	Spain	This study
<i>M. biornata</i>	MZ393492	ACP2091	Mexico	This study
<i>M. bulbosa</i>	NOBAS2628-16	O-DFL-4305	Norway	Bold Systems
<i>M. bulbosa</i>	MW762808	AH20891	Spain	Plaza <i>et al.</i> (2021)
<i>M. capillata</i>	OL772669	L0063217*	Brazil	Jagers <i>et al.</i> (2023)
<i>M. castaneicola</i>	MH136826	HMJAU43578*	China	Na & Bau (2019a)
<i>M. castaneicola</i>	MH136827	HAMJAU43581	China	Na & Bau (2019a)
<i>M. chlorophos</i>	KJ206973	ACL142	Malaysia	Chew <i>et al.</i> (2013)
<i>M. chlorophos</i>	AB512312	305759	Japan	GenBank
<i>M. chloroxantha</i> var. <i>chloroxantha</i>	OQ427378	ACP2099	Mexico	This study
<i>M. chloroxantha</i> var. <i>chloroxantha</i>	OL772668	LO063621	Brazil	Jagers <i>et al.</i> (2023)
<i>M. chloroxantha</i> var. <i>appalachieniensis</i>	MK795669	KL-BK 59708	Austria	Brodegger <i>et al.</i> (2018)
<i>M. corynephora</i>	JF908368	MCVE 30n	Italy	Osmundson <i>et al.</i> (2013)
<i>M. corynephora</i>	JF908366	MCVE 30i	Italy	Osmundson <i>et al.</i> (2013)
<i>M. corynephora</i>	JF908367	MCVE 30l	Sweeden	Osmundson <i>et al.</i> (2013)
<i>M. corynephora</i>	JF908369	MCVE 30q	Italy	Osmundson <i>et al.</i> (2013)
<i>M. corynephora</i>	OQ427379	PR4061019661	Spain	This study
<i>M. corynephora</i>	PP267933	AH57612	Spain	This study
<i>M. corynephora</i>	MH136833	NX0569	China	Na & Bau (2019a)
<i>M. corynephora</i>	MH136832	NX0567	China	Na & Bau (2019a)
<i>M. corynephora</i>	MH136834	NX0573	China	Na & Bau (2019a)
<i>M. corynephora</i>	OP604434	SJiao	China	GenBank
<i>M. corynephora</i>	OP604433	Jiao	China	GenBank

Table 1 (continued). Sequenced specimens used in phylogenetic analysis. Newly generated sequences are highlighted in bold and type specimens are marked with an asterisk (*).

Species name	GenBank accession no.	Voucher/strain no.	Country	Reference
<i>M. deeptha</i>	JX481737	DM3334g	India	Aravindakshan <i>et al.</i> (2012)
<i>M. discobasis</i>	MW762807	AH56001	Spain	Plaza <i>et al.</i> (2021)
<i>M. discobasis</i>	MW881031	AH56002	Spain	Plaza <i>et al.</i> (2021)
<i>M. discogena</i>	MH414556	BAP 649	Principe	Cooper <i>et al.</i> (2018)
<i>M. eucalypticola</i> sp. nov.	PP865076	AH60108	Madeira-Potugal	This study
<i>M. eucalypticola</i> sp. nov.	OQ427383	PR4020422783	Spain	This study
<i>M. eucalypticola</i> sp. nov.	OQ427382	AH56005*	Spain	This study
<i>M. griseotincta</i>	MK309783	HMJAU43800*	China	Na & Bau (2019b)
<i>M. griseotincta</i>	MK309784	HMJAU43819	China	Na & Bau (2019b)
<i>M. griseotincta</i>	MK309782	HMJAU43805	China	Na & Bau (2019b)
<i>M. heteracantha</i>	MK309785	HMJAU43709	China	Na & Bau (2019b)
<i>M. heteracantha</i>	MK309786	HMJAU43711	China	Na & Bau (2019b)
<i>M. heteracantha</i>	MK309787	HMJAU43716	China	Na & Bau (2019b)
<i>M. hyalinostipata</i>	MH136828	HMJAU43693*	China	Na & Bau (2019a)
<i>M. hyalinostipata</i>	MH136829	HMJAU43701	China	Na & Bau (2019a)
<i>M. hygrophoroides</i>	MK309780	HMJAU43417*	China	Na & Bau (2019b)
<i>M. hygrophoroides</i>	MK309781	HMJAU43421	China	Na & Bau (2019b)
<i>M. illuminans</i>	KJ206980	ACL212	Malaysia	Chew <i>et al.</i> (2013)
<i>M. illuminans</i>	KJ206976	ACL175	Malaysia	Chew <i>et al.</i> (2013)
<i>M. illuminans</i>	KJ206975	ACL161	Malaysia	Chew <i>et al.</i> (2013)
<i>M. indigotica</i>	MH063433	WEI16-475 ex-type (TNM)*	Taiwan	Wei & Kirschner (2019)
<i>M. indigotica</i>	MF993026	WEI 16-475 (TNM)*	Taiwan	Wei & Kirschner (2019)
<i>M. interrupta</i>	MK733301	HMJAU43849	China	GenBank
<i>M. interrupta</i>	MK733300	HMJAU43791	China	GenBank
<i>M. lasiopus</i>	MH414557	BAP635	Sao Tomé-Africa	Cooper <i>et al.</i> (2018)
<i>M. lasiopus</i>	MH414558	BAP603	Sao Tomé-Africa	Cooper <i>et al.</i> (2018)
<i>M. longinqua</i>	MH414552	BAP648*	Sao Tomé-Africa	Cooper <i>et al.</i> (2018)
<i>M. melanovelis</i> sp. nov.	MZ393493	AH56004*	Spain	This study
<i>M. melanovelis</i> sp. nov.	OQ427381	ACN202241700	Spain	This study
<i>M. miscanthi</i>	MK309778	HMJAU43582	China	Na & Bau (2019b)
<i>M. miscanthi</i>	MK309779	HMJAU43584	China	Na & Bau (2019b)
<i>M. mucor</i>	KU861565	AAronsen 5-540914	Norway	GenBank
<i>M. mucor</i>	MW540678	H6036830	Finland	GenBank
<i>M. mucoroides</i>	KU861561	AAronsen 9-060913	Finland	GenBank
<i>M. mucoroides</i>	KU861560	AAronsen 1-300912	Norway	Aronsen & Læssøe (2016)
<i>M. oboensis</i>	MH414559	BAP669	Sao Tomé-Africa	Cooper <i>et al.</i> (2018)
<i>M. perlae</i>	MG926690	ACP1353	Mexico	Cortés-Pérez <i>et al.</i> (2019)
<i>M. perlae</i>	MG926691	ACP1669	Mexico	Cortés-Pérez <i>et al.</i> (2019)
<i>M. pseudoseta</i>	OR042680	AH56042	Spain	Villarreal <i>et al.</i> (2023a)

Table 1 (continued). Sequenced specimens used in phylogenetic analysis. Newly generated sequences are highlighted in bold and type specimens are marked with an asterisk (*).

Species name	GenBank accession no.	Voucher/strain no.	Country	Reference
<i>M. pseudoseta</i>	OR042679	AH56043	Spain	Villarreal <i>et al.</i> (2023a)
<i>M. pura</i>	PV365263	AH60089	Spain	This study
<i>M. rhenana</i>	OQ427377	PR4290820714	Spain	This study
<i>M. sp. sect. Amparoina</i>	MT571522	DH-2020	Honduras	Haelewaters <i>et al.</i> (2015)
<i>M. spinosissima</i>	MZ393495	ACP2022	Mexico	This study
<i>M. stylobates</i>	MW540728	F073091	Finland	GenBank
<i>M. stylobates</i>	MK234184	RA7L9-17	USA	GenBank
<i>M. stylobates</i>	OQ427376	PR4280820716	Spain	This study
<i>M. stylobates</i>	OR042678	AH57220	Spain	Villarreal <i>et al.</i> (2023a)
<i>M. substylobates</i>	MH216189	HMJAU43418*	China	Na & Bau (2019a)
<i>M. substylobates</i>	MH216190	HMJAU43444	China	Na & Bau (2019a)
<i>M. tenerrima</i>	MK309796	HMJAU43816	China	Na & Bau (2019b)
<i>M. tenerrima</i>	MK309795	HMJAU43646	China	Na & Bau (2019b)
<i>M. tenuispinosa</i>	MK478466	LE321750	Russia	GenBank
<i>M. tenerrima</i>	MW540675	H6036818	Finland	GenBank
<i>M. viridivellata</i> sp. nov.	PV037614	AH59694*	Spain	This study
<i>M. viridivellata</i> sp. nov.	PV037612	AH59669	Spain	This study
<i>M. viridivellata</i> sp. nov.	PV037613	AH59670	Spain	This study
<i>M. yalensis</i>	OQ427380	ACP2097	Mexico	This study

the GTR space (nst = mixed) allowing a gamma-distributed rate heterogeneity across sites and a proportion of invariant sites (rates = invgamma) to be estimated. The branch length prior was set as the unconstrained gamma Dirichlet prior (1,1,1,1). We ran four parallel analyses of four MCMC chains, preset for a maximum of 10 million generations, starting with a random tree and sampling one tree every 1000 generations. The runs were automatically stopped when the value of the average standard deviation of split frequencies was < 0.01 (calculated with a burn-in of 50% of the runs). The parameter files were inspected in Tracer ver. 1.7 (Rambaut *et al.* 2018) to confirm that the effective sample size (ESS) for each parameter was > 200. The parameters and trees were summarised after discarding the first 50% of the runs as burn-in, and branch support (posterior probability values, BPP, considered significant when ≥ 0.95) was calculated by computing a 50% majority rule consensus tree from the post-burn-in trees. The phylogram obtained was visualised and edited with FigTree ver. 1.4.4 (Rambaut 2019) and Inkscape vector graphics editor (Fig. 1). The final alignment and the resultant topologies were deposited in Figshare (<https://doi.org/10.6084/m9.figshare.28692605>).

Results

Molecular phylogeny

In this study, a total of 23 ITS sequences of *Mycena* spp. were generated and deposited in GenBank (Table 1), of which 22 were used in the phylogenetic analyses. The final aligned matrix comprises 97 sequences with 926 characters (including gaps), of which 514 are parsimony-informative, 360 constant, and 663 singleton sites. For ML analysis, the best substitution model is TPM2u+F+I+G4. The topologies of the phylogenetic trees obtained from the ML and BI analyses were very similar. The ML tree was

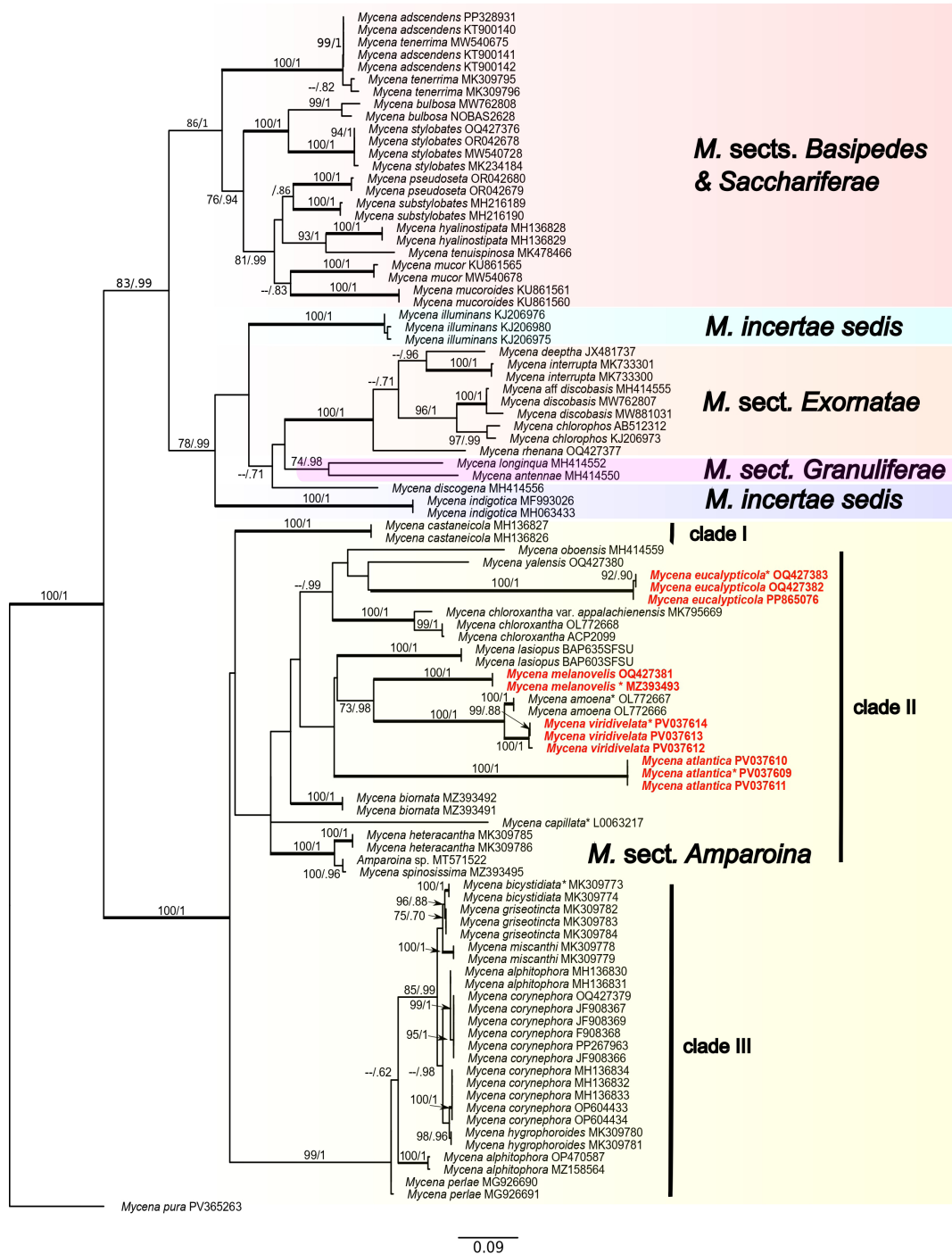


Fig. 1. Phylogram derived from maximum likelihood analysis based on ITS sequence data for *M. atlantica* M.Villarreal & Couceiro sp. nov., *M. biornata* Singer, *M. eucalypticola* Traba, Couceiro & M.Villarreal sp. nov., *M. melanovelis* Traba, Couceiro & M.Villarreal sp. nov., *M. viridivolata* M.Villarreal & Couceiro sp. nov. and allied species. Maximum likelihood bootstrap support values (BS) $\geq 70\%$ and Bayesian posterior probabilities (BPP) ≥ 0.80 values are indicated above branches. Thicker lines represent branches with maximum bootstrap values and posterior probabilities (BS = 100%, BPP = 1.0). The new species are highlighted in red. * indicates holotype. Bar = number of estimated changes/nucleotide.

chosen for presentation, with statistical support indicated through maximum likelihood bootstrap (BS) and Bayesian posterior probabilities (BPP) values (Fig. 1). The phylogenetic analyses showed that the sequences of the new *Mycena* species cluster in four distinct phylogenetic lineages that do not correspond to other species represented by data in our analysis. The first lineage, with high statistical support (BS = 100%, BPP = 1.0), consists of two sequences from Spain and one from Madeira island of the new species *M. eucalypticola* sp. nov. (OQ427383, PP865076 and OQ427382), which is recovered in an unsupported clade, together with a specimen determined as *M. yalensis* Singer (OQ427380) from Mexico and *M. oboensis* A.C.Cooper, Desjardin & B.A.Perry (MH414559) from Sao Tomé. The second lineage is formed by sequences of the new species *M. melanovelis* sp. nov. (MZ393493, OQ427381) from Spain (BS = 100%, BPP = 1.0), which is phylogenetically sister to a clade formed by *M. amoena* (LO607541, LO607542) from the Netherlands and *M. viridivelata* sp. nov. (PV037612, PV037613, PV037614) from Spain, which is the third lineage of the new species recovered with moderate statistical support (BS = 73%, BPP = 0.98). Moreover, the newly generated sequences of *M. biornata* from Spain and Mexico grouped in a branch with high statistical support (BS = 100%, BPP = 1.0); this species was positioned as a sister clade of an unsupported clade II that includes the four new species from Spain and Madeira island together with *M. oboensis*, *M. yalensis*, *M. chloroxantha* var. *appalachienensis* from the USA, *M. chloroxantha* Singer from Mexico, *M. lasiopus* Maas Geest. & de Meijer, and *M. amoena*. The new sequences of the Spanish *M. corynephora* samples group with several *M. corynephora* collections from Italy and two Chinese sequences, probably misidentified as *M. alphitophora* (MH136830, MH136831) with high statistical support (BS = 99%, BPP = 1.0). The newly generated sequences of *M. atlantica* sp. nov., *M. eucalypticola* sp. nov., *M. melanovelis* sp. nov. and *M. viridivelata* sp. nov. are distinct from all sequences of the ITS region available for other species of *M. sect. Amparoina*. Since the specimens from which the sequences were obtained are also morphologically distinct from all other known species of *M. sect. Amparoina*, we propose these species here as new to science.

Taxonomic treatment

Phylum Basidiomycota R.T.Moore
Class Agaricomycetes Doweld
Order Agaricales Underw.
Suborder Mycenineae R.L.Zhao, Vizzini & M.Q.He
Family Mycenaceae Overeem
Genus *Mycena* (Pers.) Roussel

Mycena atlantica M.Villarreal & Couceiro sp. nov.

Mycobank: MB [857443](#)

Figs 2–4, 19

Diagnosis

Mycena atlantica sp. nov. is macromorphologically similar to *M. alphitophora*, but differs in having a bigger size. Micromorphologically, it differs in having slightly smaller basidiospores $6.1\text{--}7.8 \times 4\text{--}5.5 \mu\text{m}$ (vs $8.1\text{--}9.7 \times 4.5\text{--}5.5 \mu\text{m}$ for *M. alphitophora*) and by the presence of cheroocytes in the pileipellis as well as a different nrITS molecular sequence.

Etymology

From Latin “Atlantĭcus”, from Greek “Ἀτλαντικός=Atlantikos”, the name has been extended since ca 1600 to the ocean between Europe and Africa, on one side, and America on the other.



Fig. 2. *Mycena atlantica* M. Villarreal & Couceiro sp. nov. A–B. AH59663 (holotype). C. AH59665. D. AH59668, detail of the lamellae and pileus surface. E. AH59664. F. AH59666. G. ACN2022040200.

Type material

Holotype

SPAIN • Coruña, Paio, Oza de los Ríos; 43°13'43" N, 8°10'05" W; 105 m a.s.l.; 17 Jun. 2022; *A. Couceiro s.n.*; bark of *Salix atrocinerea*; GenBank no.: [PV037609](#) (ITS); AH [AH59663].

Additional material examined

SPAIN • A Coruña, Paio, Oza de los Ríos; 43°13'43" N, 8°10'05" W; 105 m a.s.l.; 9 Jun. 2019; *A. Couceiro s.n.*; bark of *Salix atrocinerea*; AH [AH59664] • A Coruña, Ortigueira, Sta. Marta de Ortigueira, Playa de Morouzos; 43°41'51.9" N, 7°50'47.5" W; 9 m a.s.l.; 6 Nov. 2024; *A. Cortés-Pérez, A. Couceiro & M. Villarreal s.n.*; bark of *Salix atrocinerea*; AH [AH60332] • same locality as for preceding; 26 Dec. 2024; *A. Couceiro s.n.*; bark of a living trunk of *Salix atrocinerea*; ACN [ACN2024122600] • A Coruña, Cerdido, San Xoan dos Casás, Fraga de os Casás; 43°35'33" N, 7°54'11" W; 125 m a.s.l.; 2 Apr. 2022; *A. Couceiro s.n.*; bark of *Salix atrocinerea*; ACN [ACN2022040200] • Pontevedra, Cangas do Morrazo, Santo Andre do Hío, Playa de Barra; 42°16'10" N, 8°51'02" W; 34 m a.s.l.; 20 Dec. 2024; *A. Couceiro s.n.*; bark of a living trunk of *Salix atrocinerea*; ACN [ACN2024122000] • La Palma, Los Tilos Biosphere Reserve; 28°47'38" N, 17°47'48" W; 680 m a.s.l.; 4 Feb. 2022; *A. Jurado & M. Villarreal s.n.*; bark of *Ocotea foetens*; AH [AH59665] • La Palma, Cubo de la Galga; 28°46'10" N, 17°45'55" W; 240 m a.s.l.; 7 Feb. 2022; *A. Jurado & M. Villarreal s.n.*; AH [AH59667] • same locality as for preceding; 6 Feb. 2022; Genbank no.: [PV037610](#) (ITS); AH [AH59666] • same locality as for preceding; 7 Feb. 2022; *M. Villarreal s.n.*; on bark of *Ocotea foetens*; wetted 8 Feb. 2022, harvested from batch moist chambers on 20 Mar. 2022; AH [AH59668].

PORTUGAL • Madeira, Ribeira do Seixal; 32°48'16" N, 17°07'03" W; 570 m a.s.l.; 16 Feb. 2024; *A. Couceiro, C. Sos & M. Villarreal s.n.*; decaying wood of *Laurus novocanariensis*; GenBank no.: [PV037611](#) (ITS); AH [AH60089] • Sao Miguel, Ponta Delgada, 37°50'09" N, 25°47'12" W; 570 m a.s.l.; 6 Feb. 2025; *A. Couceiro, C. Sos & M. Villarreal s.n.*; trunk of *Laurus azorica*; AH [AH60346].

Description

Pileus 2–4(–5.5) mm diam., initially hemispherical to paraboloid, expanding to obtusely conic or broadly convex when ageing; margin translucent striated, crenulate, old very thin-fleshed; surface in young covered all over with groups of purely white ‘sugar-like’ granules or flakes, initially forming a closed layer, soon breaking up to a non-contiguous layer upon a white or a very pale grey surface, when mature still bearing small amounts of granules especially in the disc, white. Lamellae adnexed to narrowly adnate, subventricose to ventricose, (8–)10–13 reaching the stipe, with 1–3 series of lamellulae of variable length, white. Stipe 8–32 × 0.1–0.2(–0.4) mm, central, cylindrical, slightly widened at the base; initially longitudinally striated, surface entirely hirsute, watery white to watery grey; devoid of basal disc. Basidiomata greyish when dried. Odour and taste absent.

Basidiospores (6.1–)6.4–7.2(–7.8) × (4–)4.2–4.9(–5.5) µm; Q = (1.3–)1.4–1.6(–1.7); n = 100; Me = 6.8 × 4.5 µm; Qe = 1.5, ellipsoid or broadly ellipsoid to oblong, smooth, hyaline, amyloid, thin-walled, with one or two guttules. Basidia 13–21 × 4.8–7.3 µm, short clavate to obpyriform, 4-spored, rarely 2-spored, sterigmata 1.5–3 µm long, hyaline. Cheilocystidia forming a sterile band, (11–)12.6–18.8(–20) × (5.9–)7–11.4(–13) µm, clavate to broadly clavate, spinulose in the upper part, hyaline, thin-walled; spinulae 0.5–0.95 × 0.3–0.5 µm, cylindrical to subconical. Pleurocystidia absent. Pileipellis a cutis with acanthocysts and cherocytes; hyphae 1.5–13 µm diam., spinulose or smooth, dextrinoid. Acanthocysts (10.5–)12.4–30.5(–34) × 8.9–26(–32) µm, globose, subglobose, densely spinulose, hyaline, inamyloid, thin-walled; spinulae 0.6–3 × 0.5–1.5 µm, cylindrical or subconical; sometimes seen originating from septate, thin-walled, spinulose hyphae of about 2–6 µm diam. Cherocytes 8–30 × 7–23.5 µm (disregarding lobes), roundish to obtuse angular, with 2–6 conical to obtusely conical lobes, lobes extending up to 6 µm, hyaline, slightly dextrinoid, thick-walled up to 4 µm; covered with spinulae and warts hemispherical; spinulae and warts 0.45–1.5 × 0.2–0.75 µm; often seen originating from septate,

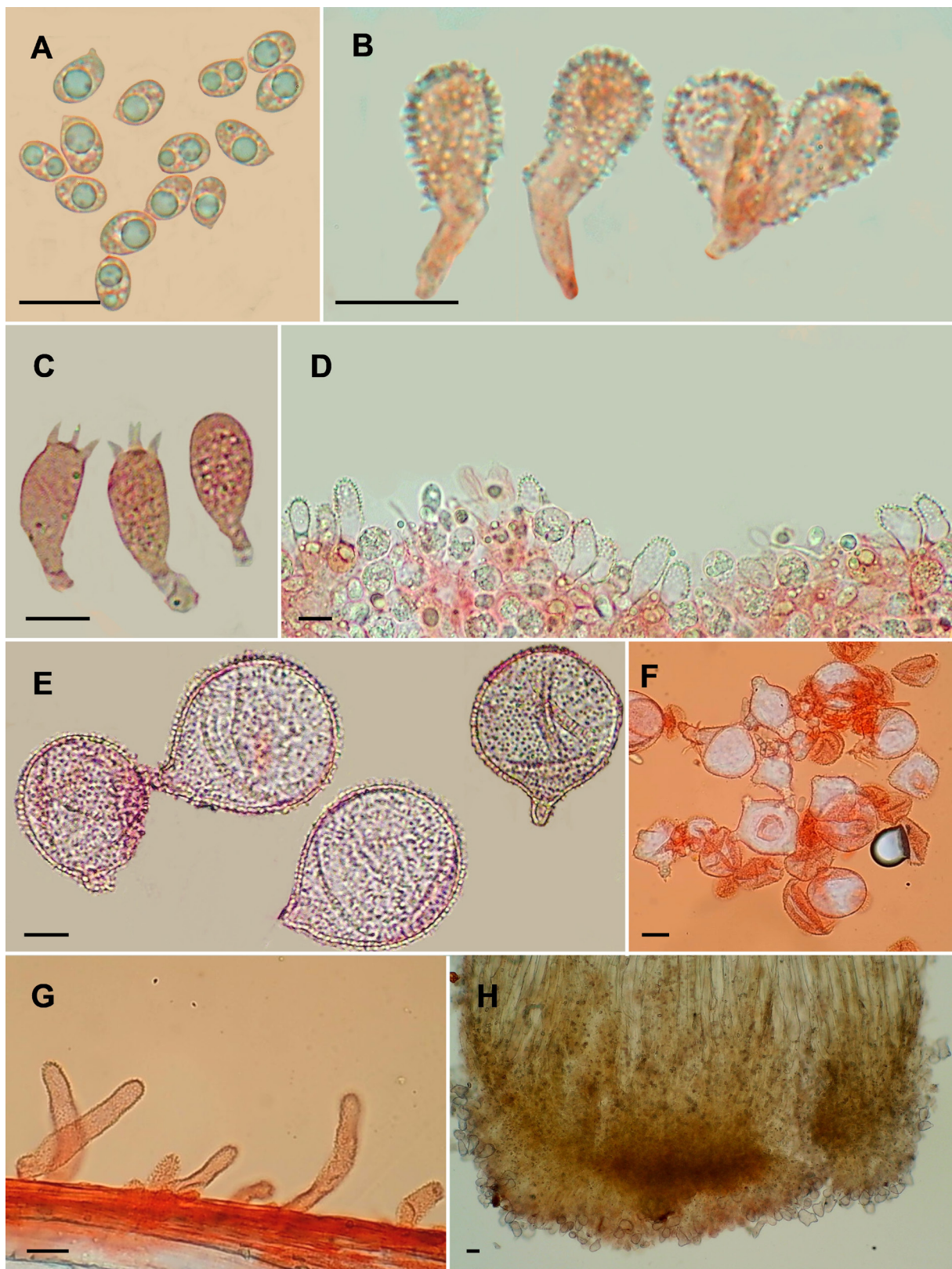


Fig. 3. Microscopic features of *Mycena atlantica* M.Villarreal & Couceiro sp. nov. (AH59663, holotype). A. Basidiospores. B. Cheilocystidia. C. Basidia and basidiole. D. Lamellar edge. E. Acanthocysts. F. Acanthocysts and cherocytes. G. Caulocystidia. H. Detail of the base of the stipe. Scale bars = 10 μ m.

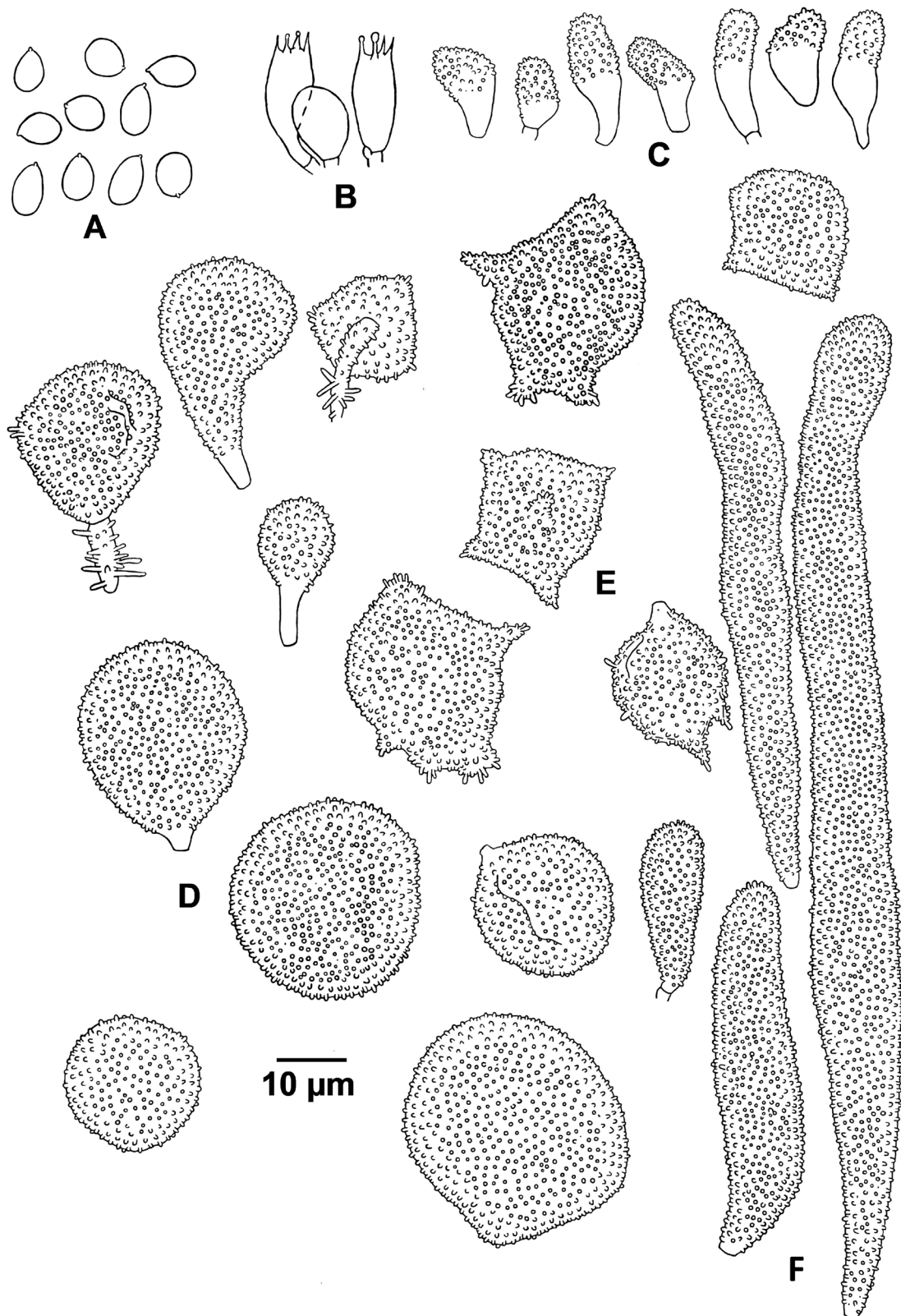


Fig. 4. Line drawings of *Mycena atlantica* M.Villarreal & Couceiro sp. nov. (AH59663, holotype). **A.** Basidiospores. **B.** Basidia and basidiole. **C.** Cheilocystidia. **D.** Acanthocysts. **E.** Cherocytes. **F.** Caulocystidia. Drawing by Manuel Villarreal.

slightly thick-walled spinulose hyphae of about 4 µm diam. Hypodermium composed of inflated hyphae up to 14 µm diam., hyaline, dextrinoid. Lamellar trama regular, hyphae up to 18 µm, inflated, hyaline, dextrinoid. Cortical and medullary hyphae of the stipe 2.5–16 µm diam., parallel, smooth, dextrinoid. Caulocystidia 14.8–88 × (3.6–)9.08–12.5 µm, ranging from short and broadly clavate or subcylindrical to long and cylindrical, apex even or somewhat wider, obtuse, densely and evenly spinulose overall, hyaline, inamyloid, thin-walled; spinulae 0.8–1.1(–1.8) × 0.3–0.7 µm, cylindrical or subconical. Clamp connections present.

Habitat and distribution

Scattered or gregarious on mossy trunks of *Salix atrocinerea*, *Laurus novocanariensis*, *Laurus azorica* and *Ocotea foetens*, during all seasons. Known from Galicia, La Palma (Canary Islands) in Spain, and from Sao Miguel (Azores) and Madeira in Portugal (Fig. 19).

Remarks

Mycena atlantica is characterized by its slightly robust basidiomata for a species of *M. sect. Amparoina*, its pure white basidiomata and its habitat, which is generally corticolous. Microscopically it shares many characteristics in common with *M. alphitophora*, a species originally described from Bermuda islands, which possess larger spores 7.5–10 × 4.5–5.5 µm (Desjardin 1995) and lack cherocytes. Following the keys of Desjardin (1995), *M. heteracantha* (Singer) Desjardin, a species known from South America and Asia, seems to be the closest species. However, primordia and immature pilei of *M. heteracantha* are covered with a universal veil in the form of conic spines, which is absent in *M. atlantica*. Besides, it has slightly larger basidiospores (8–10.5 × 4.8–6.7 µm) and cherocytes with longer spines like projections (8–32 µm long). Based on available sequences in public databases, it appears that *M. atlantica* has no known sibling species in the section, being phylogenetically very distant from both *M. alphitophora* and *M. heteracantha*.

Mycena biornata Singer

Mycobank: MB 317965

Figs 5–7, 19

Material examined

SPAIN • A Coruña, Pontedeume, Parroquia Santa María de Ombre, Fragas do Eume; 43°40'99" N, 8°8'44" W; 19 m a.s.l.; 16 Mar. 2021; *A. Couceiro* & *J.M. Traba s.n.*; dead leaves of *Laurus nobilis*; GenBank no.: [MZ393491](#) (ITS); AH [AH56003] • same data as for preceding; 20 May 2021; *M. Villarreal s.n.*; *Laurus* dead leaves in moist chamber; AH [AH56006] • same data as for preceding; 25 May 2021; AH [AH56024] • A Coruña, Pontedeume, Fragas do Eume; 43°42'52" N, 8°11'98" W; 9 m a.s.l.; 6 Dec. 2021; *A. Couceiro*, *M. Saavedra*, *J.M. Traba* & *M. Villarreal s.n.*; on dead leaves of *Laurus nobilis*; AH [AH56025].

MEXICO • Veracruz, Acatlán, Acatlán Volcano; 19°40'46" N, 96°51'14" W; 1930 m a.s.l.; 22 Sep. 2020; *A. Cortés-Pérez 2091*; tropical mountain cloud forest on leaf litter of *Fagus mexicana* and *Quercus* spp.; GenBank no.: [MZ393492](#) (ITS); XAL [ACP2091].

PORTUGAL • Azores, Sao Miguel, Ponta Delgada; 37°50'09" N, 25°47'12" W; 580 m a.s.l.; 6 Feb. 2025; *A. Couceiro*, *C. Sos* & *M. Villarreal s.n.*; on dead leaves of *Laurus azorica*; AH [AH60365].

Description

Primordia 0.3–3 mm diam., subglobose to paraboloid, sessile, covered with a universal veil formed by white granules and flocons. Pileus 3–12 mm diam., initially hemispherical to subglobose, expanding to campanulate, flattening with age; margin sulcate-striate; surface dry, granulose, from midway to the white pruinose or smooth margin, opaque, pure white or with very pale yellowish tinges; mature pilei often leaving granules only on the disc. Context white, thin, membranous. Lamellae ascending narrowly

adnate to subfree, tender, ventricose, ca 25 reaching the stipe, with 1–2 lamellulae, 0.5–0.7 mm broad, thin, white, with subhorizontal to convex undulated concolorous edge. Stipe 14–36 × 0.7–1 mm, central, cylindrical, equal to subequal, sometimes with a subbulbous base, hollow; surface dry, entirely hirsute elsewhere, opaque, white; arising from a small and white granulose basal disc. Odour and taste absent.

Basidiospores (6.8–)7.8–9.6(–11.5) × (3.9–)4.3–5.2(–5.7) μm; Q = (1.3–)1.6–2(–2.2); n = 100; Me = 8.8 × 4.8 μm; Qe = 1.8, ellipsoid to broadly ellipsoid, elongate or cylindric, smooth, hyaline, amyloid, thin-walled, with refractive guttules. Basidia 10–20 × 8.5–12.5 μm, broadly clavate, four-spored, with sterigmata up to 3.5 μm long, hyaline. Cheilocystidia forming a sterile band, 10–20 × 5–12 μm, clavate to broadly clavate, short-stalked, densely spinulose covered over much of the surface,

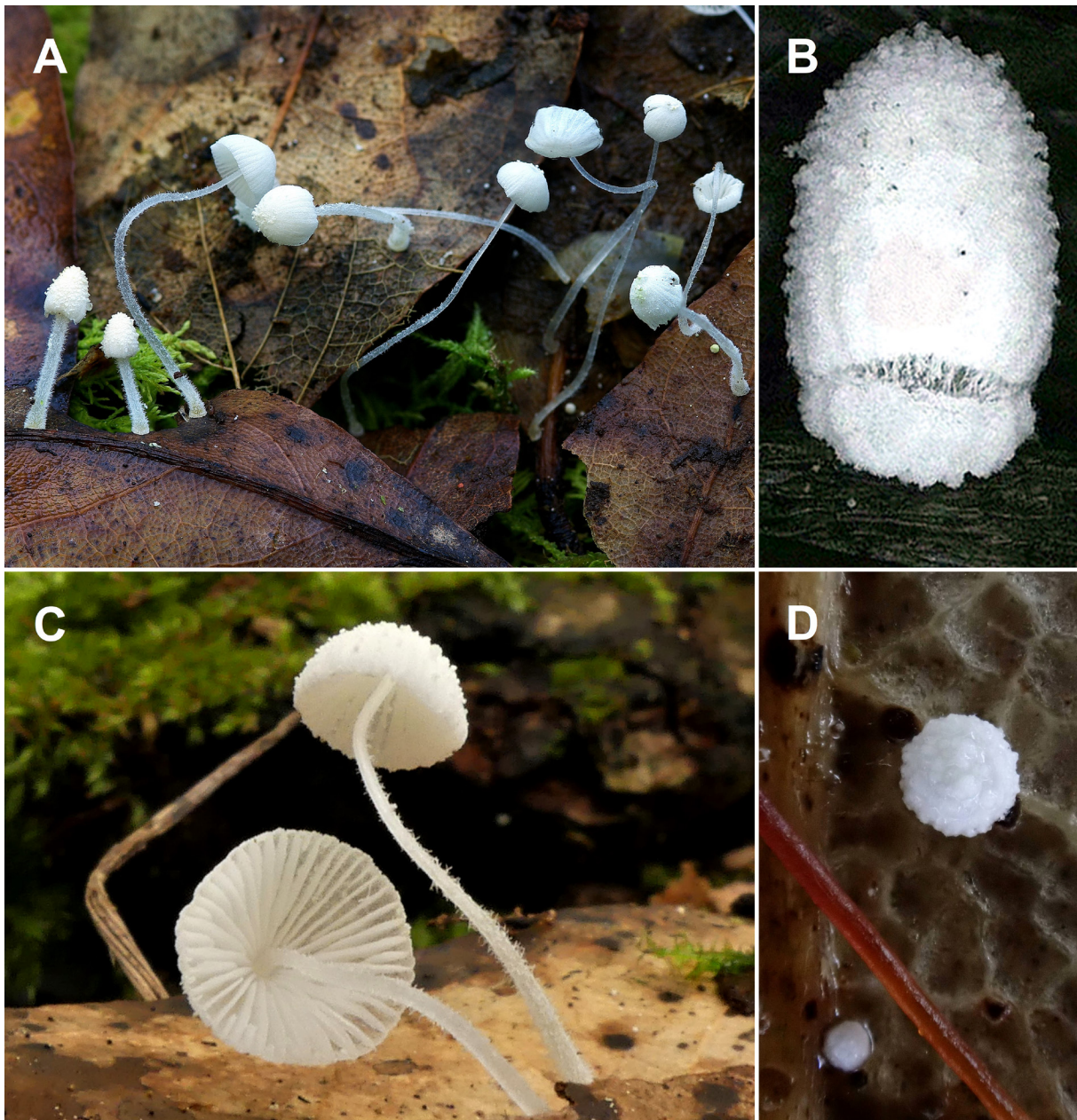


Fig. 5. *Mycena biornata* Singer. **A.** AH56003. **B.** AH56006, detail of a primordium breaking the basal disc. **C.** AH56025, fresh basidiomata fruiting on *Laurus nobilis* dead leaves. **D.** AH56006, primordia.

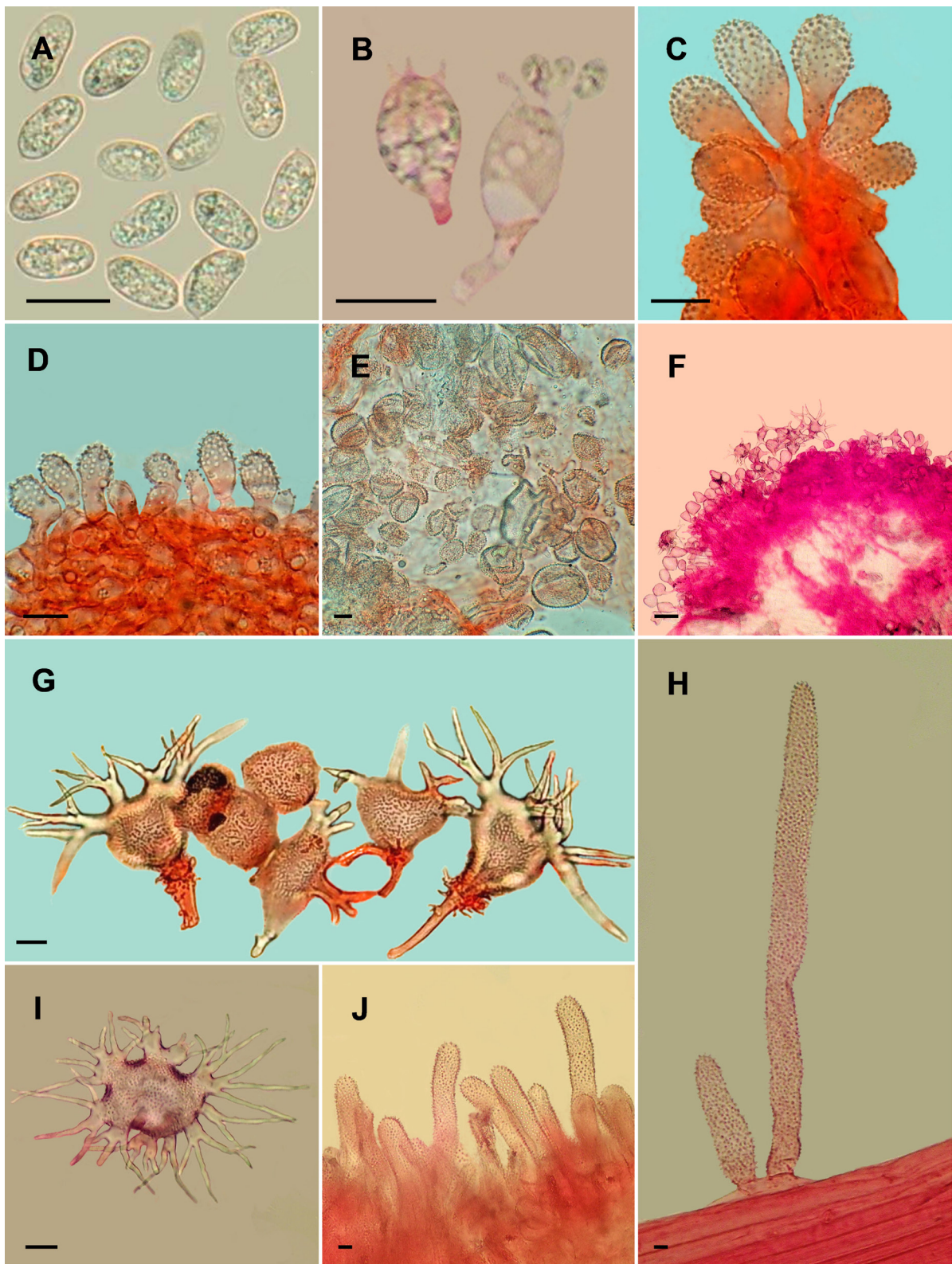


Fig. 6. Microscopic features of *Mycena biornata* Singer (AH56003). **A.** Basidiospores. **B.** Basidia. **C.** Acanthocysts of the pileus margin. **D.** Cheilocystidia. **E.** Pileipellis showing acanthocysts and cheilocytes. **F.** Detail of the basal disc. **G.** Cherocytes. **H, J.** Caulocystidia. **I.** Cherocyte. Scale bars = 10 μ m.

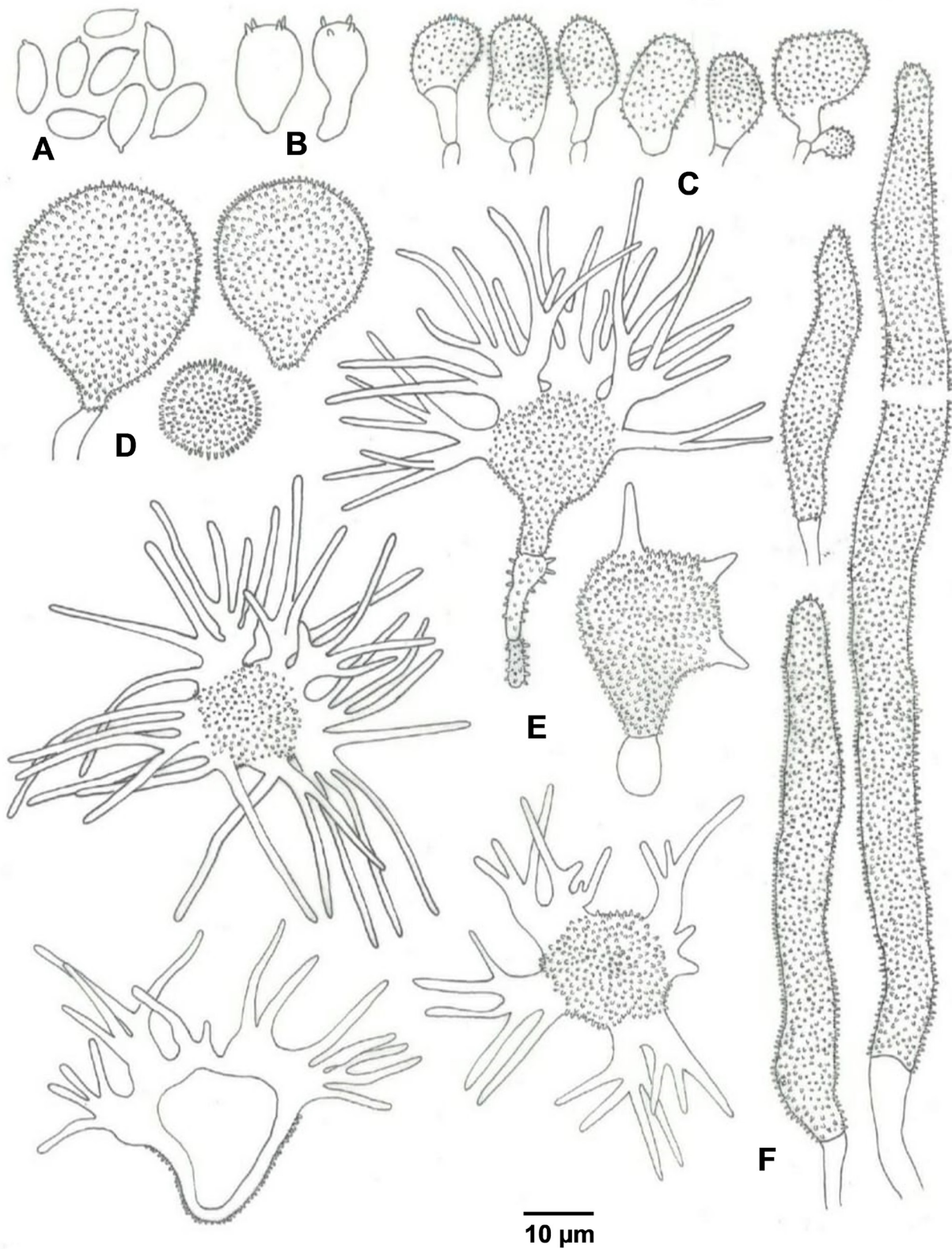


Fig. 7. Line drawings of *Mycena biornata* Singer (ACP2091). **A.** Spores. **B.** Basidia. **C.** Cheilocystidia. **D.** Acanthocysts. **E.** Cherocytes. **F.** Caulocystidia. Scale bar = 10 µm. Drawing by Alonso Cortés-Pérez.

hyaline, thin-walled; spinulae $0.9\text{--}1.3 \times 0.5 \mu\text{m}$, cylindrical or obtusely conical. Pleurocystidia absent. Pileipellis a cutis composed of hyphae radially aligned up to $10 \mu\text{m}$ diam., clamped, smooth to densely ornamented with minute excrescences, and terminating in acanthocysts that overlap in such a way as to give a subhymenoderm appearance. Acanthocysts $10\text{--}50 \mu\text{m}$ diam., globose, subglobose to heart-shaped, densely spinulose, hyaline, inamyloid, thin-walled; spinulae $0.6\text{--}2.5 \times 0.5\text{--}1.5 \mu\text{m}$, cylindrical or subconical. Granules of the universal veil formed by neuron-shaped cherocytes $9.3\text{--}36 \times 8\text{--}25 \mu\text{m}$, globose, subglobose to subangular or irregular in outline, densely ornamented, provided of 5–10 erect simple or ramified thick walled ($0.6\text{--}7.2 \mu\text{m}$) acute projections $2\text{--}37 \mu\text{m}$ long, hyaline or with fulvous contents, generally thickened at the base. Hypodermium composed of inflated and short-celled up to $20 \mu\text{m}$ diam., smooth, hyaline, inamyloid or strongly dextrinoid, thin-walled. Lamellar trama regular to subregular, hyphae up to $15 \mu\text{m}$ diam., inflated, short-celled, smooth, hyaline, strongly dextrinoid, thin-walled. Cortical and medullary hyphae of the stipe $5\text{--}15 \mu\text{m}$ diam., cylindrical, short-celled smooth, hyaline, dextrinoid, thin-walled, not gelatinized. Caulocystidia $50\text{--}420 \times 8\text{--}15 \mu\text{m}$, cylindrical to subclavate with rounded apex, densely and evenly spinulose overall, hyaline, thin-walled or slightly thick walled up to $0.7 \mu\text{m}$, numerous all over the stipe. Clamp connections are hard to find and only observed on the hyphae of the pileipellis.

Habitat and distribution

Scattered to gregarious on fallen leaves of several hardwoods, especially *Laurus nobilis* or *Fagus mexicana*. Known from Brazil, Mexico, Spain, and Portugal (Fig. 19).

Remarks

Mycena biornata is characterized by its white basidiomata, striking neuron-shaped cherocytes, and fruiting on fallen leaves of hardwoods, specially *Laurus* spp. in Spain and the Azores or *Fagus mexicana* in Mexico. The two sequences obtained for this species, one European and one American, are resolved as monophyletic, with maximum support (BS = 100%, BPP = 1), within the clade II of species belonging to the stirps *Amparoina* and *Fuscinea*, but without a close phylogenetic relationship with either of them. *Mycena biornata* was described by Singer (1973) with two varieties, *M. biornata* var. *biornata* and var. *manausensis* (Singer 1983), both from Brazil, the last differing from the type in having a greyish pileus and smaller spores. Both varieties of *M. biornata* were described with smooth cheilocystidia, which is an aberrant character for *M. sect. Amparoina* (Desjardin 1995), and was not described in any species of *M. sect. Amparoina*. Previously, Traba *et al.* (unpublished) proposed this species as *M. lourensis* nom. prov. although, considering that Singer erred in the interpretation of the cheilocystidia, given the macro- and microscopic similarities, we must accept that the species treated here is *Mycena biornata*. The holotype of *M. biornata* var. *biornata* does not exist and the material from *M. biornata* var. *manausensis* is extremely fragmentary and its study does not describe or illustrate the cheilocystidia, but the very typical morphology of the cherocytes and the illustrations by Singer (1983) leave no doubt as to the correct identification of this very rare species, which we rediscover a half-century later.

Mycena corynephora Maas Geest.

Mycobank: MB [108244](#)

Figs 8–9

Material examined

SPAIN • Gerona, Abadía Marti de Riells; $41^{\circ}46'37''$ N, $2^{\circ}30'46''$ W; 490 m a.s.l.; 25 Oct. 1994; G. Moreno, R. Pöder & C. Illana *s.n.*; on moss-covered bark of *Castanea sativa*; AH [AH18321] • same locality as for preceding; IB [IB94/906] • same locality as for preceding; MCVE [MCVE030b] • A Coruña, As Pontes, San Martiño de Goente, Teixedelos; $43^{\circ}28'34''$ N, $7^{\circ}50'58''$ W; 536 m a.s.l.; 19 Oct. 2019; A. Couceiro *s.n.*; bark of *Fagus sylvatica*; AH [AH57610] • A Coruña, Oza-Cesuras, San Pedro de Oza de los Ríos, Paio; $43^{\circ}13'45''$ N, $8^{\circ}10'15''$ W; 103 m a.s.l.; 4 Jan. 2019; A. Couceiro *s.n.*; bark of *Acacia melanoxylon*; AH [AH57609] • A Coruña, As Pontes, Teixedelo; $43^{\circ}25'38''$ N,

7°58'44" W; 500 m a.s.l.; 6 Oct. 2019; *A. Couceiro & J.M. Traba s.n.*; bark of *Betula* and *Fagus*; GenBank no.: [OQ427379](#); PR [PR4061019661] • A Coruña, Oza-Cesuras, San Pedro de Oza de los Ríos, Paio; 43°13'43" N, 8°10'12" W; 103 m a.s.l.; 20 Jun. 2022; *A. Couceiro s.n.*; bark of *Corylus avellana*; GenBank no.: [PP267933](#); AH [AH57612] • A Coruña, Oza-Cesuras, Nuestra Señora de Belén, Martín; 43°04'25" N, 8°04'25" W; 492 m a.s.l.; 6 Jan. 2025; *A. Couceiro s.n.*; bark of *Pseudotsuga menziesii*; ACN [ACN2025010600] • A Coruña, Oza-Cesuras, Dordaño, A Nabeira, 43°10'54" N, 8°13'44" W; 303 m a.s.l.; 7 Jan. 2025; *A. Couceiro s.n.*; bark of *Pseudotsuga menziesii*; ACN [ACN2025010700] • Asturias, El Pico; 43°18'46" N, 5°13'55" W; 440 m a.s.l.; 17 Aug. 2020; *A. Jurado & M. Villarreal s.n.*; bark of *Quercus pyrenaica*; AH [AH57611].

PORTUGAL • Azores, Sao Miguel, Vila Franca do Campo, Lagoa do Congro; 37°45'17" N, 25°24'26" W; 460 m a.s.l.; 3 Feb. 2025; *A. Couceiro, C. Sos & M. Villarreal s.n.*; bark of *Ocotea foetens*; AH [AH60366].

Description

Basidiomata small and delicate. Pileus 1–3(–6) mm diam., initially hemispherical expanding to broadly campanulate or convex; margin obscurely translucent-striate, crenate, covered with minute granules including some scattered projecting stalked granules, thin-fleshed; surface dry, persistently granulose, entirely and densely covered by minute white granules in continuous irregular floccose piles, granules less often forming collapsing, conic, pyramidal or tapering and curved piles of white granules up to 0.2 mm; white, unchanging with age or attaining a pale grey tinge near center. Lamellae broadly adnate, decurrent with a small tooth, subdistant, 7–14 reaching the stipe, with 0–1 lamellulae, ventricose, white at first then cream, edge white, fringed, glistening, also with granules near to the pileal margin of young specimens. Stipe 5–35 × 0.3–1.0 mm, central, cylindrical, equal to slightly tapering towards apex, solid, base without basal disc, base usually with some sparse short white hairs appressed on the substrate; surface dry, with abundant finger-like, round-topped, erect, white cystidia up to 0.1 mm tall, each separated from each other, these easily removed and therefore may be sparse or absent in some specimens particularly when very wet, white but dull cream when granules and cystidia are sparse revealing the background of the stipe, drying white; base of stipe with a short sleeve (0.5–1 mm) of piles of granules similar to those on the pileus. Odour not distinctive. Taste mild.

Basidiospores (6.2–)6.7–8.6(–9.5) × (5.6–)5.9–7(–7.6) μm; Q = 1–1.3(–1.5); n = 50; Me = 7.5 × 6.5 μm; Qe = 1.2, globose or subglobose to broadly ellipsoid, smooth, hyaline, weakly amyloid, thin-walled, with a guttule. Basidia 19–31 × 5–11 μm, clavate to broadly clavate, 4-spored, sterigmata to 6 μm long., clamped at base, hyaline. Cheilocystidia forming a sterile band, abundant, crowded, 18–32 × 9–19 μm, slender or broadly clavate, obpyriform, sphaeropedunculate, vesiculose, with narrow stalk 2.5–5.5 × 20 μm, densely spinulose except smooth in lower part, hyaline, thin-walled, clamped at base; spinulae 0.8 μm × 0.3 μm, subconical. Pleurocystidia absent. Pileipellis a hymeniderm when very young then a cutis of thin-walled, sometimes spinulose, dextrinoid, clamped elements 6–16 μm broad, giving rise to prostrate and erect acanthocysts. Acanthocysts abundant, sometimes detached, 15–32 × 9–19 μm, globose, obpyriform, vesiculose, sphaeropedunculate, thin-walled, hyaline to pale greyish in KOH or water, dextrinoid, entirely densely spinulose, spinulae bluntly conic, obtuse, up to 1.5 μm × 1 μm at the base. Cheroocytes single or catenulate in chains, variable in size and form: 9–32 × 9–19 μm, globose, obpyriform, vesiculose to irregular, thick-walled (up to 2.4 μm), with erect or curved thorn-like spines up to 17 μm × 6 μm present usually on only part of each element either densely so or scattered. Elements also are often spinulose at least in part with spinulae 1.5–3.5 μm × 1 μm. Others form a globose terminal 21–32 μm diameter arising from an erect, narrow (2–6 μm broad), smooth-walled, or ornamented stalk or chain of elements that project the terminal cell beyond the pileipellis. Hypodermium of thin-walled, smooth, dextrinoid hyphae, swollen up to 150 × 65 μm. Pileal trama a narrow layer of hyphae similar to hypodermium. Lamellar trama tightly packed, parallel, clamped hyphae 2.5–3.5 μm broad, strongly dextrinoid. Subhymenium hyphae similar to trama. Cortical and medullary hyphae of the stipe 3.5–

4.5 μm diam. near surface, wider in interior up to 15 μm diam., parallel, smooth, hyaline in KOH or water, dextrinoid, thin-walled. Caulocystidia 15–150 \times 8–20 μm , variable in shape: short forms clavate or vesiculose, longer forms cylindrical, sphaeropedunculate or contorted, with narrow smooth or spinulose stalk 3.5–4.5 μm curving outwards from the parallel hyphae of the stipe, densely and evenly spinulose overall, hyaline, amyloid, thin-walled; spinulae 1.5 \times 1 μm , conic to obtuse; abundant on majority of the stipe, some in loose fascicles. Clamp connections are present at all tissues.

Habitat and distribution

Growing solitary or gregarious on moss-covered bark of trees. Worldwide distributed.

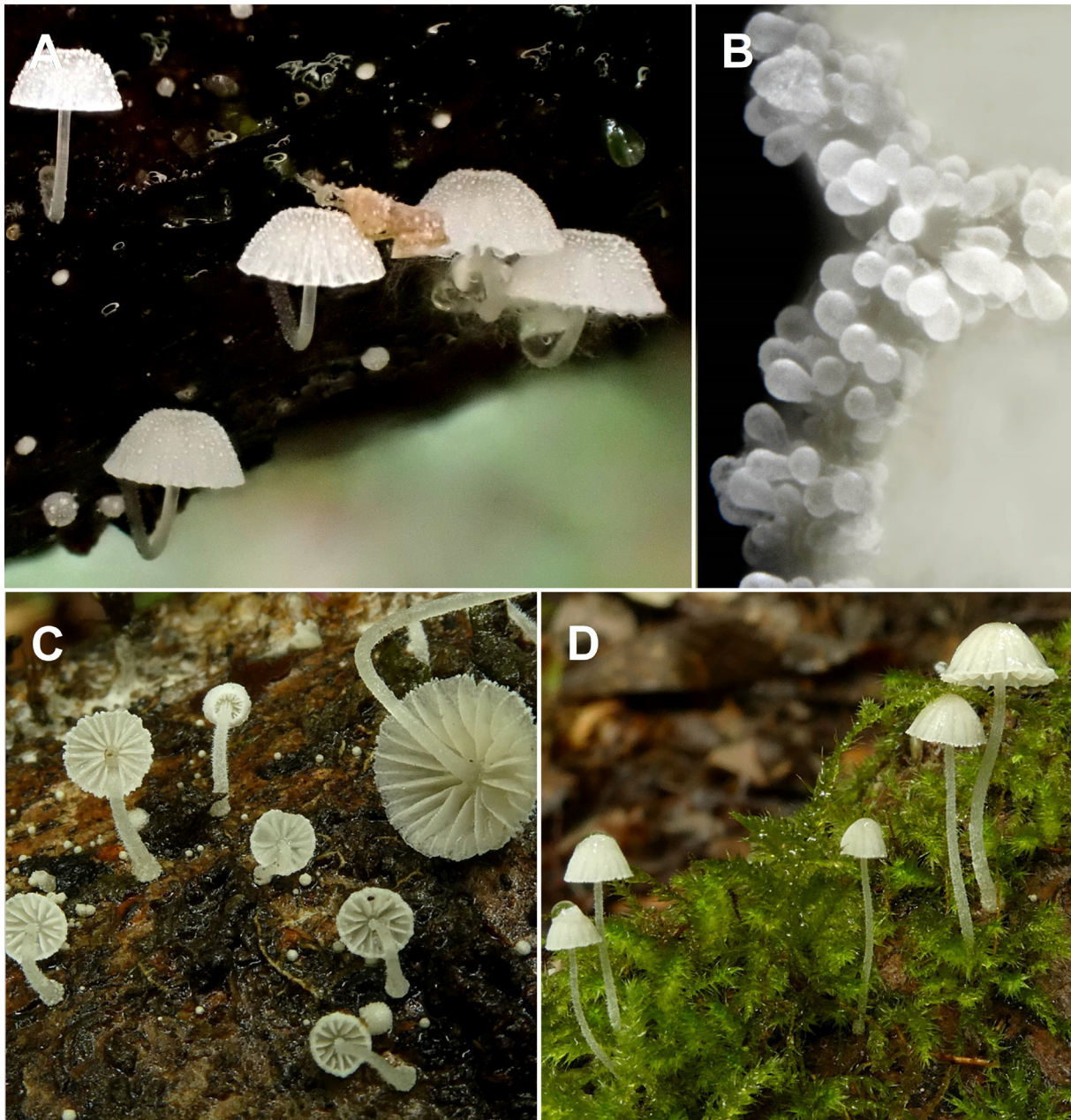


Fig. 8. *Mycena corynephora* Maas Geest. **A.** AH57612. **B.** AH576009, detail of the margin of the pileus showing acanthocysts and cheilocystidia. **C.** AH57612. **D.** ACN2025010700, fresh basidiomata fruiting on bark of deciduous trees.

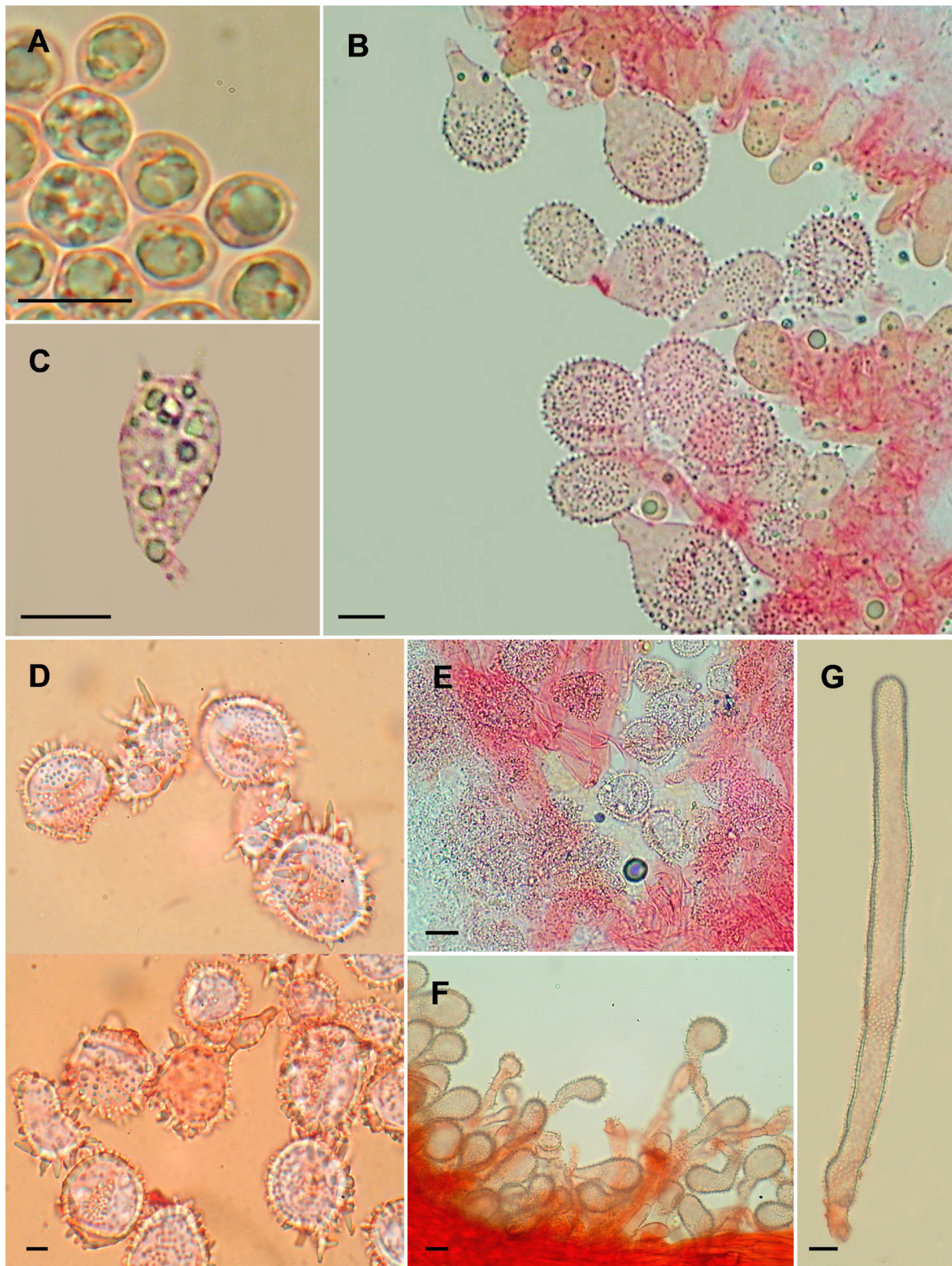


Fig. 9. *Mycena corynephora* Maas Geest. (AH57612). **A.** Basidiospores. **B.** Cheilocystidia. **C.** Basidium. **D.** Cherocytes. **E.** Pileipellis showing acanthocysts. **F.** Caulocystidia at the base of the stipe. **G.** Caulocystidia at the apex of the stipe. Scale bars = 10 μ m.

Remarks

Mycena corynephora is a well-known species in Europe described by Maas Geesteranus (1983a) and worldwide distributed, characterized by growing on moss-covered bark of hardwoods. Distinctive features of *M. corynephora* are a white furfuraceous to farinose pileus up to 6 mm wide, adnate white lamellae, furfuraceous stipe lacking basal disc, large globose to subglobose spores, 4-spored basidia, presence of clamp connections and densely spinulose caulocystidia. While in the literature, the species is always described as devoid of cherocytes, we have found that some young collections have this kind of cells. *Mycena judithiana* Bougher, described by Bougher (2009) from Australia, is characterised by subglobose spores and thick-walled elements with large projections that are interpreted as cherocytes. These projections are identical to those found in the primordia of some of our *M. corynephora* collections. Initially, this led us to interpret some of these collections as *M. judithiana*. However, the absence of sequences in the databases prevents us from determining whether they are the same or different species.

Two other species of *M. sect. Amparoina*, *M. yalensis* (of which we have sequenced a collection), and *M. globispora* (Manim. & Leelav.) Aravind. & Manim., also possess globose or subglobose basidiospores. Nevertheless, *M. yalensis* differs from *M. corynephora* in having smaller basidiospores ($6.4\text{--}6.8 \times 5.1\text{--}6.8 \mu\text{m}$), cystidia from the junction of the stipe base with the substrate with more densely arranged, shorter spines, and fructification on bark of *Alnus*. On the other side, *M. globispora* differs from *M. corynephora* in having predominantly bisporic basidia, cherocytes with broader excrescences towards the apex, and more narrow cylindrical caulocystidia with longest excrescences at the middle region. Unfortunately, it is not possible to compare the two species molecularly because no *M. globispora* sequences are available. Curiously, the European sequences of *M. corynephora* are clustered in a different clade from the Chinese sequences, so it seems to be a phylogenetically separated species that would need to be renamed. In addition, the Chinese collections labelled as *M. alphitophora* correspond well with *M. corynephora*.

Mycena eucalypticola Traba, Couceiro & M. Villarreal sp. nov.

MycoBank: MB [841234](#)

Figs 10–12, 19

Diagnosis

Mycena eucalypticola sp. nov. is distinguished from *M. globispora*, which has similar cherocytes, by its ellipsoid basidiospores and caulocystidia lacking long outgrowths in the middle.

Etymology

Referring to the substratum where the new species was first found.

Type material**Holotype**

SPAIN • A Coruña, Oza-Cesuras, Santiago de Reboredo; 43°13'46" N, 8°10'15" W; 122 m a.s.l.; 16 May 2021; *A. Couceiro s.n.*; on dead leaves of *Eucalyptus globulus*; GenBank no.: [MZ393494](#) (ITS, partial sequence, not used in the molecular analyses), [OQ427382](#) (ITS); AH [AH56005].

Additional material examined

SPAIN • A Coruña, Paderne, San Salvador de Velouzás, Condós; 43°18'46" N, 8°09'24" W; 122 m a.s.l.; 15 Jan. 2022; *A. Couceiro, J.M. Traba, A. Vila & M. Villarreal s.n.*; on dead leaves of *Eucalyptus globulus*; AH [AH56023] • A Coruña, Ortigueira, Playa de Morouzos; 43°41'55" N, 7°50'49" W; 7 m a.s.l.; 8 Dec. 2022; *A. Couceiro, A. Jurado, C. Sos & M. Villarreal s.n.*; on falling bark of *Laurus nobilis*; AH [AH57608] • Fragas do Eume, Pontedeume; 43°40'99" N, 8°8'44" W; 19 m a.s.l.; 3 Nov. 2024; *A. Cortés-Pérez, A. Couceiro & M. Villarreal s.n.*; on dead leaves of *Betula alba* and *Salix atrocinerea*; AH [AH60331] • A Coruña, Ortigueira, Playa de Morouzos; 43°41'54" N, 7°50'48" W; 7 m a.s.l.; 2

Mar. 2022; *J. Traba & A. Couceiro s.n.*; on leaves of *Salix atrocinerea*; GenBank no.: [OQ427383](#); PR [PR4020422783].

PORTUGAL • Madeira, Ribeira do Seixal; 32°48'16" N, 17°07'03" W; 570 m a.s.l.; 13 Feb. 2024; *A. Couceiro, C. Sos & M. Villarreal s.n.*; dead leaves of *Laurus novocanariensis*; AH [AH60107] • Madeira, Arco de São Jorge; 32°49'24" N, 16°57'13" W; 240 m a.s.l.; 14 Feb. 2024; *A. Couceiro, C. Sos & M. Villarreal s.n.*; dead leaves of *Laurus novocanariensis*; GenBank no.: [PP865076](#); AH [AH60108].

Description

Primordia 0.15–0.7 mm diam., hemispherical to paraboloid, covered with white granules, initially forming a closed layer, soon breaking up to a non-contiguous layer upon a white surface. Pileus 1–2 mm diam., initially conical or parabolic, expanding to hemispherical or convex to plano-convex with age; margin straight or slightly crenate, translucent-striated; surface delicately pruinose to granular throughout, almost furrowed, pure white. Context white, inconspicuous. Lamellae free, adnate or closely adnate, ascending, distant to subdistant, 5–8 reaching the stipe, with 0–1 lamellulae, up to 0.3 mm wide, white, with rectilinear or slightly convex edges, pruinose under lens and concolorous. Stipe 1–17 × 0.15–0.25 mm, central, filiform or very slightly enlarged towards the base, hollow; surface entirely covered by erect white hairs, insititious, white, watery white to almost translucent. Indistinct odour and taste.

Basidiospores (5.6–)6.4–8.3(–9.8) × (3.6–)3.9–5(–5.6) μm; Q = (1.4–)1.5–1.8(–2); n = 100; Me = 7.3 × 4.4 μm; Qe = 1.7, elongate to cylindrical, smooth, hyaline, amyloid, thin-walled, indistinctly guttulate. Basidia 9–17.5 × 7–9 μm, obovoid to broadly clavate, 2- or 4-spored, sterigmata up to 5 μm long., not clamped at the base. Cheilocystidia 15.5–22.6(–35.9) × 9.2–14.8 μm, ellipsoid, obovoid, clavate to fusoid or subcylindrical, covered densely with outgrowths, hyaline, thin-walled; outgrowths 0.5–1.6(–3) × 0.5–1 μm, cylindrical, mixed with the basidia. Pleurocystidia absent. Pileipellis a cutis covered by a universal veil composed of acanthocysts and cherocytes; hyphae 2–17 μm diam., smooth or covered by short outgrowths 0.5–2.5 × 0.5–1 μm, hyaline, with terminal acanthocysts 8.5–36(–47.5) × 8–25 μm, claviform or broadly claviform to subglobose or ovoid, covered densely with outgrowths, hyaline, thin-walled; outgrowths 0.5–2.5(–4.5) × 0.5–1 μm, cylindrical, apex obtuse. Acanthocysts abundant, sometimes detached, 15–32 × 9–19 μm, globose, obpyriform, vesiculose, sphaeropedunculate, entirely densely spinulose, hyaline to pale greyish in KOH or water, dextrinoid, thin-walled; spinulae up to 1.5 μm × 1 μm at base, bluntly conic, obtuse. Cherocytes 12.5–21.5 × 9–16 μm, ellipsoid, broadly clavate to obovoid, hyaline, thick-walled (up to 3 μm), covered with outgrowths, 0.5–4 × 0.5–3 μm, solid or thick-walled, crystalline-like rounded. Hypodermium, hyphae 3–25 μm diam., hyaline, dextrinoid. Lamellar trama regular to subregular; hyphae 2–21 μm diam., hyaline, dextrinoid. Cortical and medullary hyphae of the stipe 1–7.5 μm diam., with terminal or lateral caulocystidia. Caulocystidia 45–168 × 4–9(–11.5) μm, short to broadly clavate or subcylindrical to long and cylindrical, usually with subcapitate at apex, densely spinulose; hyaline, thin-walled; spinulae 0.5–5 × 0.5–1.25 μm, cylindrical or subconical. Clamp connections are present but hard to find.

Habitat and distribution

Growing gregarious on dead leaves of *Betula*, *Eucalyptus*, *Laurus*, and *Salix*. Known from Spain and Portugal (Fig. 19).

Remarks

M. eucalypticola sp. nov. is a predominantly foliicolous species that has been found fruiting on dead leaves of *Betula alba*, *Eucalyptus globulus*, *Salix atrocinerea*, and *Laurus novocanariensis* in four different localities of Galicia and Madeira. Only one collection has been found fruiting on decaying bark of *Laurus*. Macroscopically, it could be mistaken for a small species of *Hemimycena* Singer because of its absence of a basal disc and the diminutive white basidiomata featuring scant lamellae. However, it possesses amyloid spores and microcharacters that are very different from those of *Hemimycena* s. lat. Microscopically, it is characterised by its singular cherocytes provided with large globose

crystalline-like excrescences and ornamented caulocystidia frequently subcapitated. Only *M. globispora* (= *M. aliphitophora* var. *globispora* Manim. & Leelavathy) described from India (Aravindakshan & Manimohan 2015) shows a universal veil composed of similar cherocytes that are thick-walled and with broader excrescences towards the apex, and that are present both over the pileus and at the stipe base. However, this species differs from *M. eucalypticola* in having globose to subglobose basidiospores, and longer cylindrical caulocystidia with longest excrescences at the middle region. Unfortunately, there is no sequence for *M. globispora* to determine its phylogenetic proximity to *M. eucalypticola*.

M. eucalypticola sp. nov. should not be confused with *M. eucalypticola* Losa, which is a nomen nudum (Maas Geesteranus 1983b).

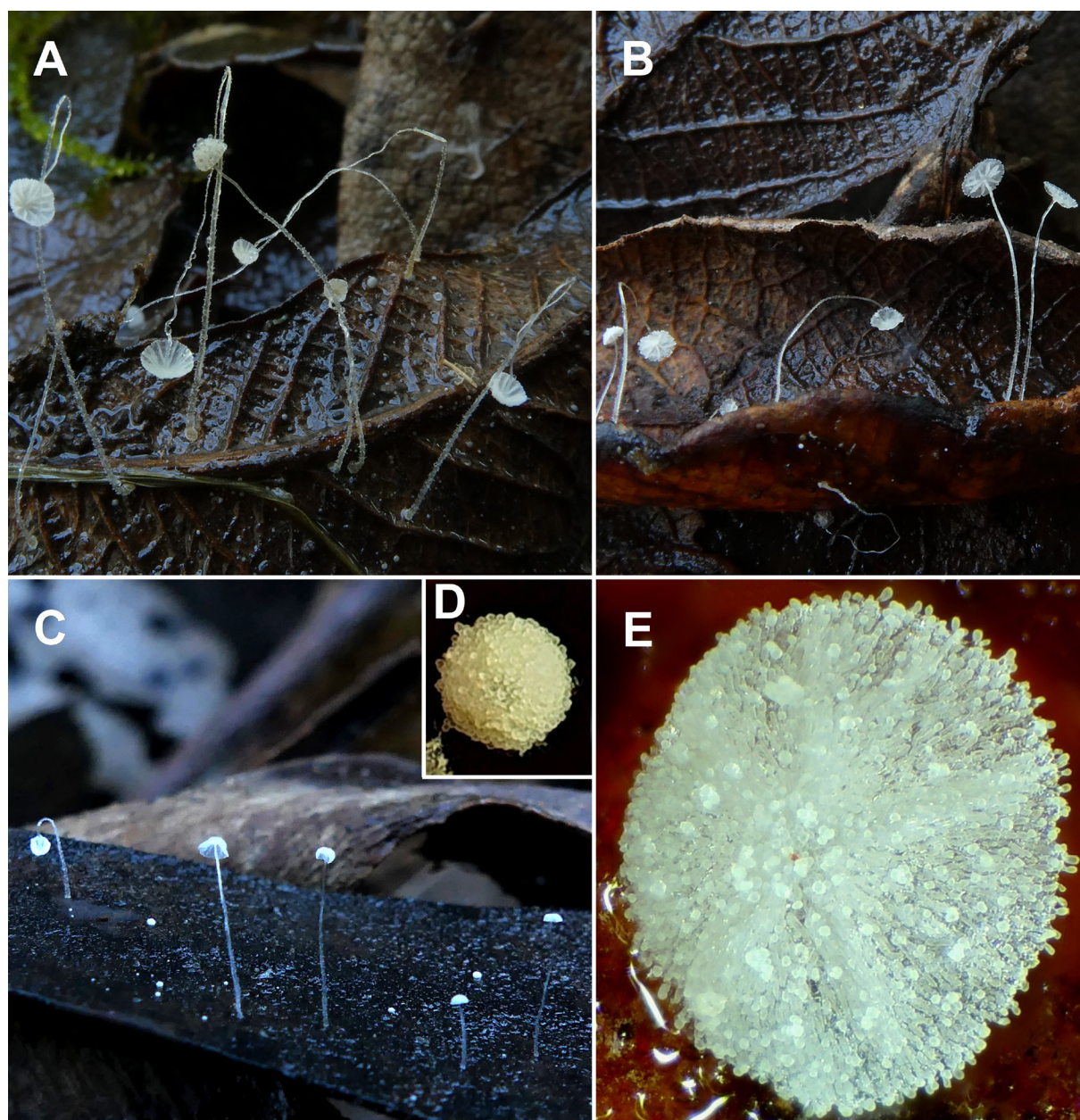


Fig. 10. *Mycena eucalypticola* Traba, Couceiro & M.Villarreal sp. nov. **A–B.** AH60331, fresh basidiomata fruiting on *Salix* and *Betula* dead leaves. **C.** AH56005 (holotype), fresh basidiomata fruiting on *Eucalyptus* dead leaves. **D–E.** AH57608, detail of the primordia.

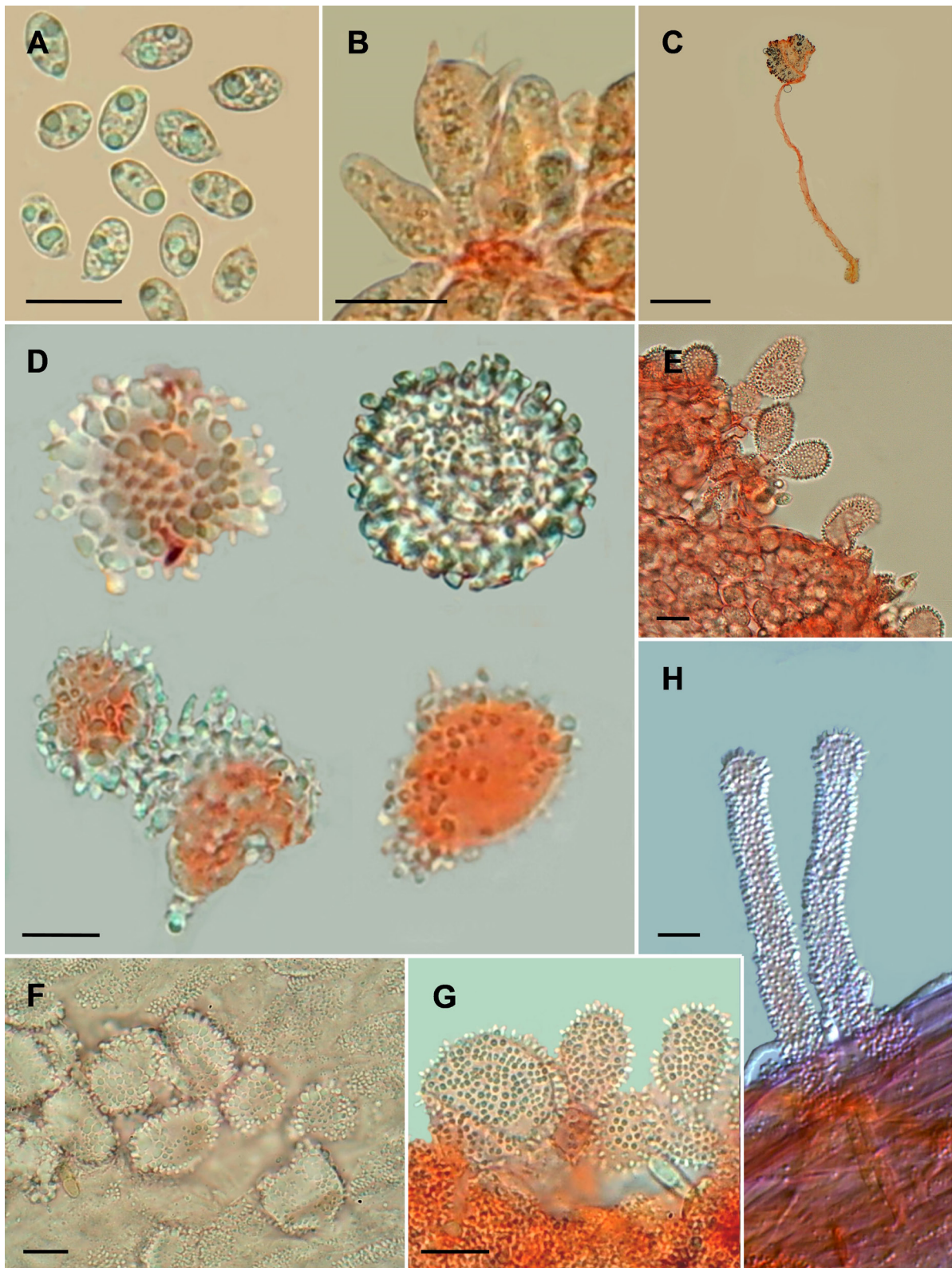


Fig. 11. Microscopic features of *Mycena eucalypticola* Traba, Couceiro & M.Villarreal sp. nov. (AH56005, holotype). **A.** Basidiospores. **B.** Basidia and basidioles. **C.** Basidiomata. **D.** Cherocytes. **E.** Cheilocystidia. **F.** Pileipellis. **G.** Terminal acanthocysts. **H.** Caulocystidia. Scale bars: A–B, D–H = 10 μ m; C = 1 mm.

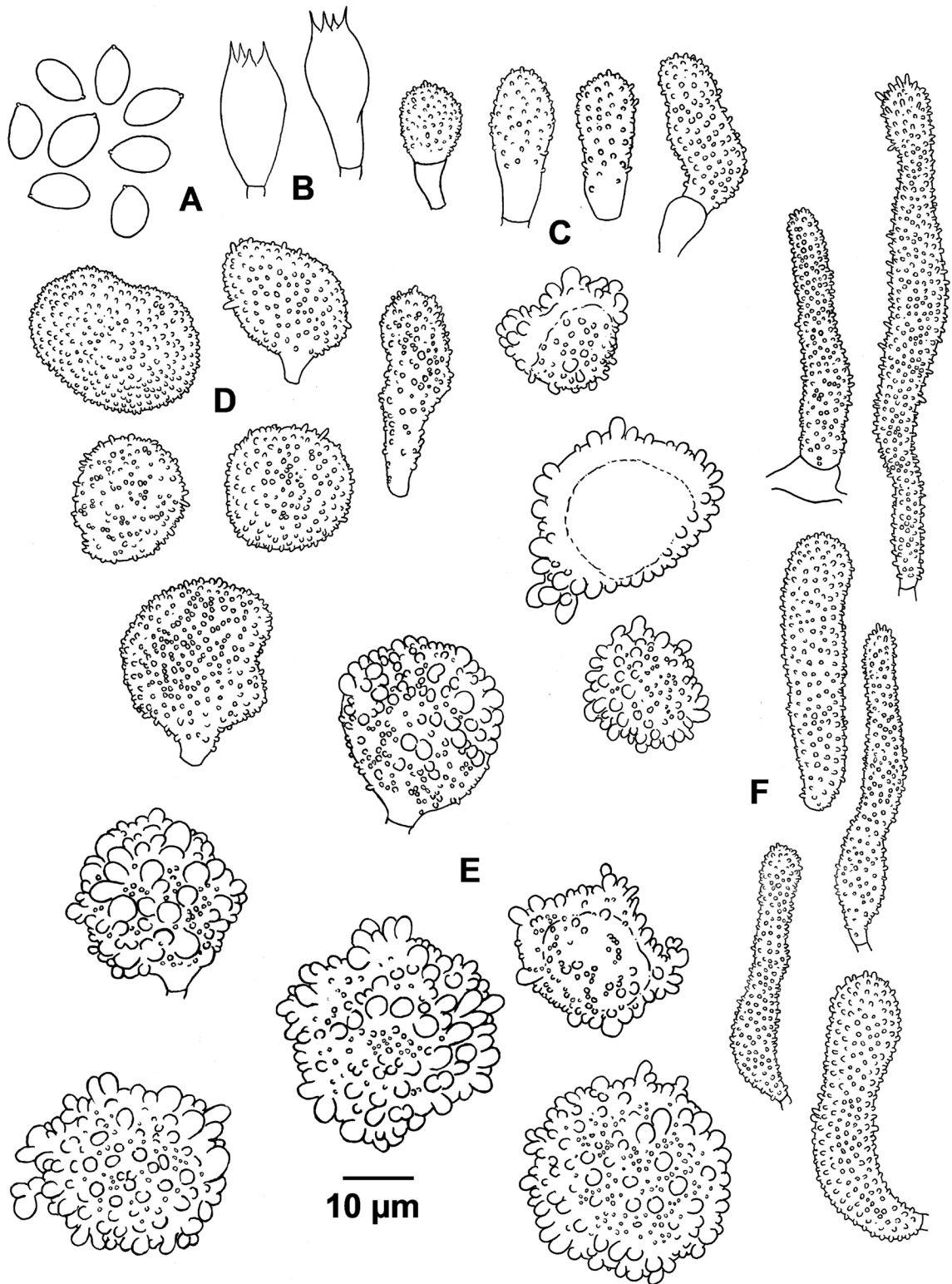


Fig. 12. Line drawings of *Mycena eucalypticola* Traba, Couceiro & M. Villarreal (AH56005, holotype). A. Spores. B. Basidia. C. Cheilocystidia. D. Acanthocysts. E. Cheroocytes F. Caulocystidia. Scale bar = 10 µm. Drawing by Manuel Villarreal.

Mycena melanovelis Traba, Couceiro & M. Villarreal, sp. nov.

Mycobank: MB [841233](#)

Figs 13–15, 19

Diagnosis

Mycena melanovelis sp. nov. differs from the very similar *M. lasiopus* Maas Geest. & de Meijer in having a smaller size, a white pileus, a small basal disc at the base of the stipe, more conspicuously lobed cheroocytes, completely spinulose caulocystidia, and absence of clamps.

Etymology

From the ancient Greek ‘μέλας’ (mélas: black), (genitive μέλανος mélanos) and from the Latin ‘velum’: covering, awning, curtain, sail, veil.

Type material

Holotype

SPAIN • A Coruña, San Benito de Mayal, Oza-Cesuras; 43°13'46" N, 8°10'15" W; 122 m a.s.l.; 16 May 2021; *A. Couceiro s.n.*; on dead leaves of *Acacia melanoxylon*; GenBank no.: [MZ393493](#) (ITS); AH [AH56004].

Additional material examined

SPAIN • A Coruña, San Benito de Mayal, Oza-Cesuras; 43°13'46" N, 8°10'15" W; 122 m a.s.l.; 6 Dec. 2021; *A. Couceiro, M. Saavedra & M. Villarreal s.n.*; on dead leaves of *Acacia melanoxylon*; AH [AH56026] • same locality as for preceding; 1 May 2021; *A. Couceiro s.n.*; AH [AH56027] • same locality as for preceding; 17 Apr. 2022; *A. Couceiro s.n.*; GenBank no.: [OQ427381](#) (ITS); ACN[ACN202241700].

PORTUGAL • Azores, Sao Miguel, Ribeira Grande; 37°47'42" N, 25°29'47" W; 220 m a.s.l.; 5 Feb. 2025; *A. Couceiro, C. Sos & M. Villarreal s.n.*; on dead leaves of *Acacia melanoxylon*; AH [AH60367] • Azores, Sao Miguel, Ponta Delgada, Canada da Areia; 37°44'57" N, 25°36'48" W; 11 m a.s.l.; 6 Feb. 2025; *A. Couceiro, C. Sos & M. Villarreal s.n.*; on dead leaves of *Acacia melanoxylon*; AH [AH60368].

Description

Primordia up to 0.7 mm diam., initially hemispherical to paraboloid, sessile, shining, covered with dark brown to blackish-brown granules, initially forming a closed layer, soon breaking up to a non-contiguous layer upon a whitish surface. Pileus up to 9 mm diam., at first campanulate, expanding to convex to plano-convex, flattening with age; margin striatulate to sulcate along the denticulate, translucent-striate, more pronouncedly sulcate when dried; surface dry, minutely granular, entirely white, retaining dark brown to blackish-brown granules of the veil at the disc. Context very thin and white. Lamellae, ascending-adnate, subdistant, 7–9 reaching the stipe, with 1 series of lamellulae, 0.3–0.5 mm broad, white, with convex to subhorizontal and concolorous lamellar edge, tender. Stipe 5–12 mm (up to 20 mm in culture) × 0.15–0.34 mm, filiform, central, equal, terete, bulbous at the base, hollow, fragile; surface dry, puberulous all over, watery white, arising from a small (up to 1 mm across), sulcate, floccose, white basal disc not always easily seen and sometimes apparently absent. Taste not recorded. Odour absent.

Basidiospores (6.6–)7.2–8.9(–9.8) × (2.9–)3.2–3.9(–4.5) μm; Q = (1.8–)2–2.5(–2.8); n = 100; Me = 8 × 3.6 μm; Qe = 2.3, elongated to cylindrical, smooth, hyaline, weakly amyloid, thin-walled, with refractive guttules. Basidia 10.71–12.67 × 7.89–9.46 μm, broadly clavate to obpyriform, 4-spored, with sterigmata up to 6.25 μm long., hyaline. Cheilocystidia forming a sterile band, 9.50–14.78 × 5.50–8.30 μm, clavate, subclavate to subcylindrical, hyaline, inamyloid, clampless, densely ornamented with warts 0.45–1.5 × 0.4–1.2 μm. Pleurocystidia absent. Pileipellis a cutis with terminal acanthocysts and cheroocytes conforming a subhymenoderm layer; repent hyphae 0.8–4.0 μm diam, cylindrical, smooth, hyaline, sometimes with brownish contents, dextrinoid, thin-walled, non-gelatinous. Acanthocysts

14.70–22.5 × 9.17–15.83 μm, subglobose, densely spinulose, hyaline to dark pigmented, inamyloid, thin-walled; spinulae 0.8–1.6 × < 0.8 μm. Cheroocytes more or less frequent, deterrent, 11.84–23.38 × 10.5–19.66 μm, predominantly globose, irregular in shape to heart-shaped, with (0–)2–6(–7) obtuse or obtusely conical lobes, with homogeneous dark brown contents, inamyloid, slightly thick-walled (up to 1.5 μm); densely warted, warts 0.8–1.6 × < 0.8 μm. Hypodermium composed of parallel hyphae up to 19 μm diam. Lamellar trama regular; hyphae 2–19 μm diam., hyaline, dextrinoid, thin-walled, non-gelatinous. Stipitipellis a cutis; cortical hyphae 1.5–4.6 μm diam., parallel, cylindrical, hyaline, dextrinoid, thin-walled; medullary hyphae 5–18 μm diam., smooth, hyaline, dextrinoid, thin-walled. Caulocystidia abundant, 23–230 × 5.6–10.4 μm, cylindrical to clavate, obtuse, densely spinulose overall,

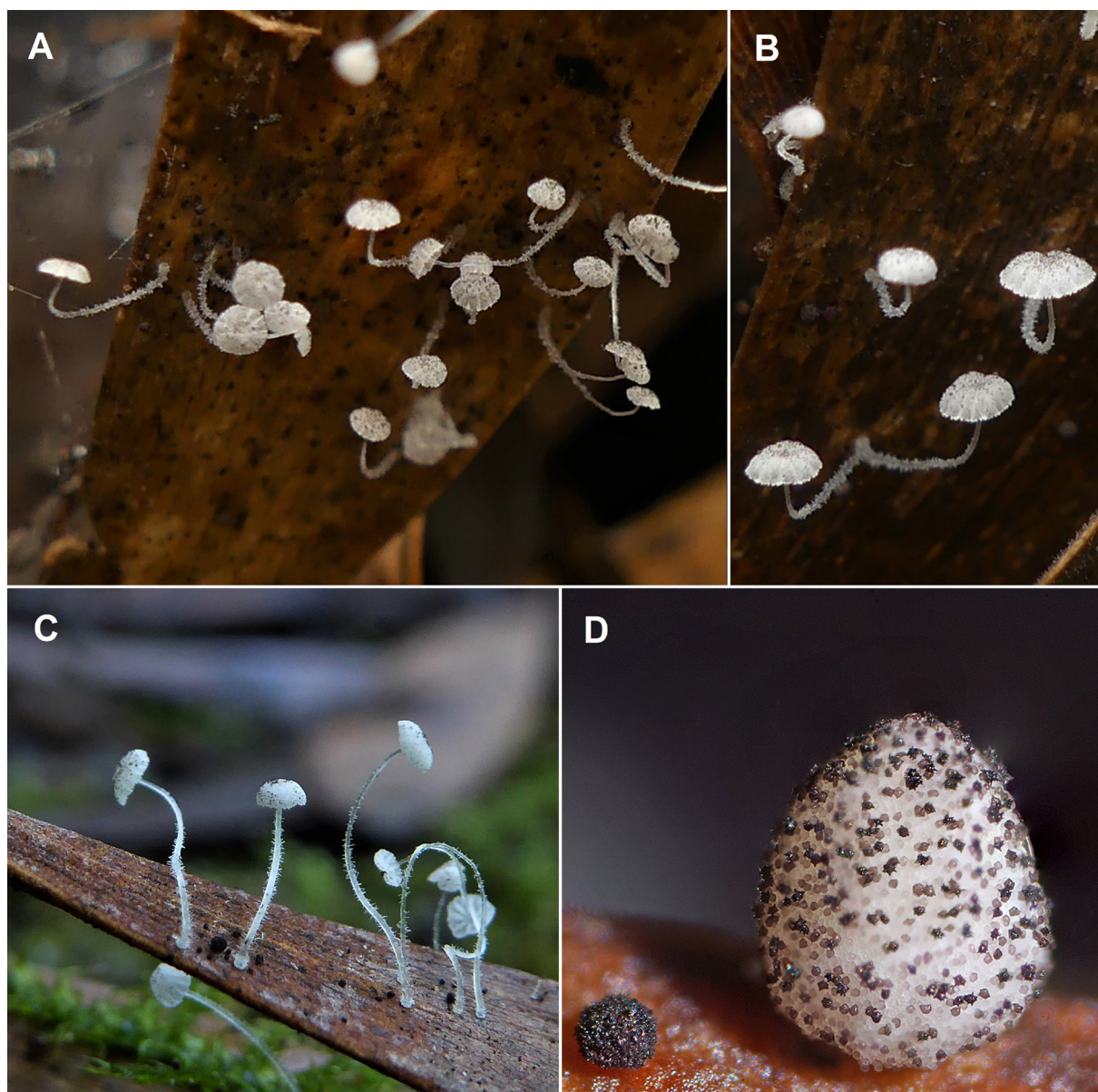


Fig. 13. *Mycena melanovelis* Traba, Couceiro & M.Villarreal sp. nov. **A–C.** AH56004 (holotype), fresh basidiomata growing on *Acacia melanoxylon* dead leaves. **D.** AH56027, detail of two primordia.

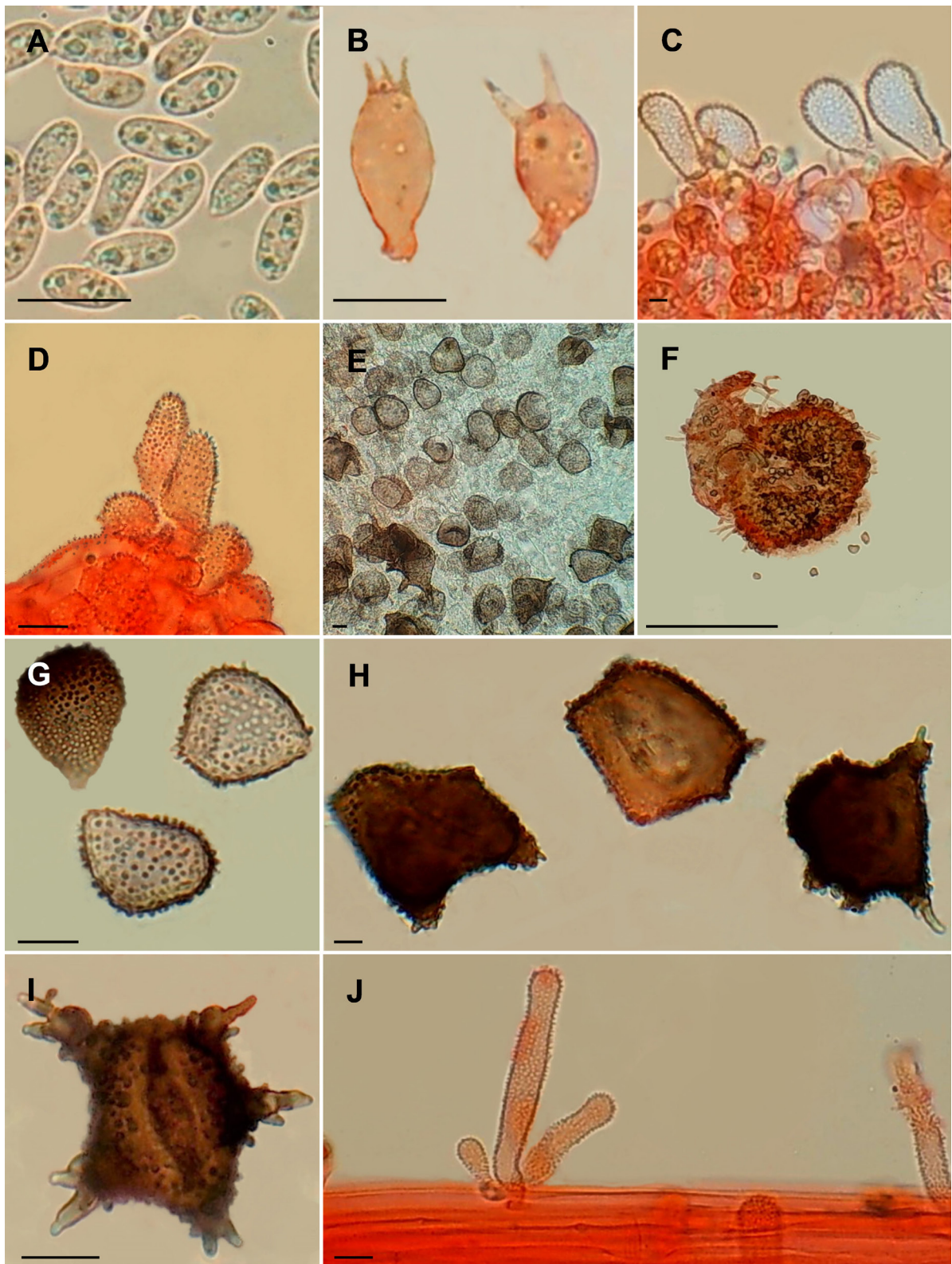


Fig. 14. Microscopic features of *Mycena melanovelis* Traba, Couceiro & M.Villarreal sp. nov. (AH56004, holotype). **A.** Basidiospores. **B.** Basidia. **C.** Cheilocystidia. **D.** Acanthocysts of the margin of the pileus. **E.** Pileipellis showing acanthocysts and cherocytes. **F.** Detail of the basal disc. **G.** Acanthocysts. **H.** Cherocytes. **I.** Cherocyte. **J.** Caulocystidia. Scale bars = 10 µm.

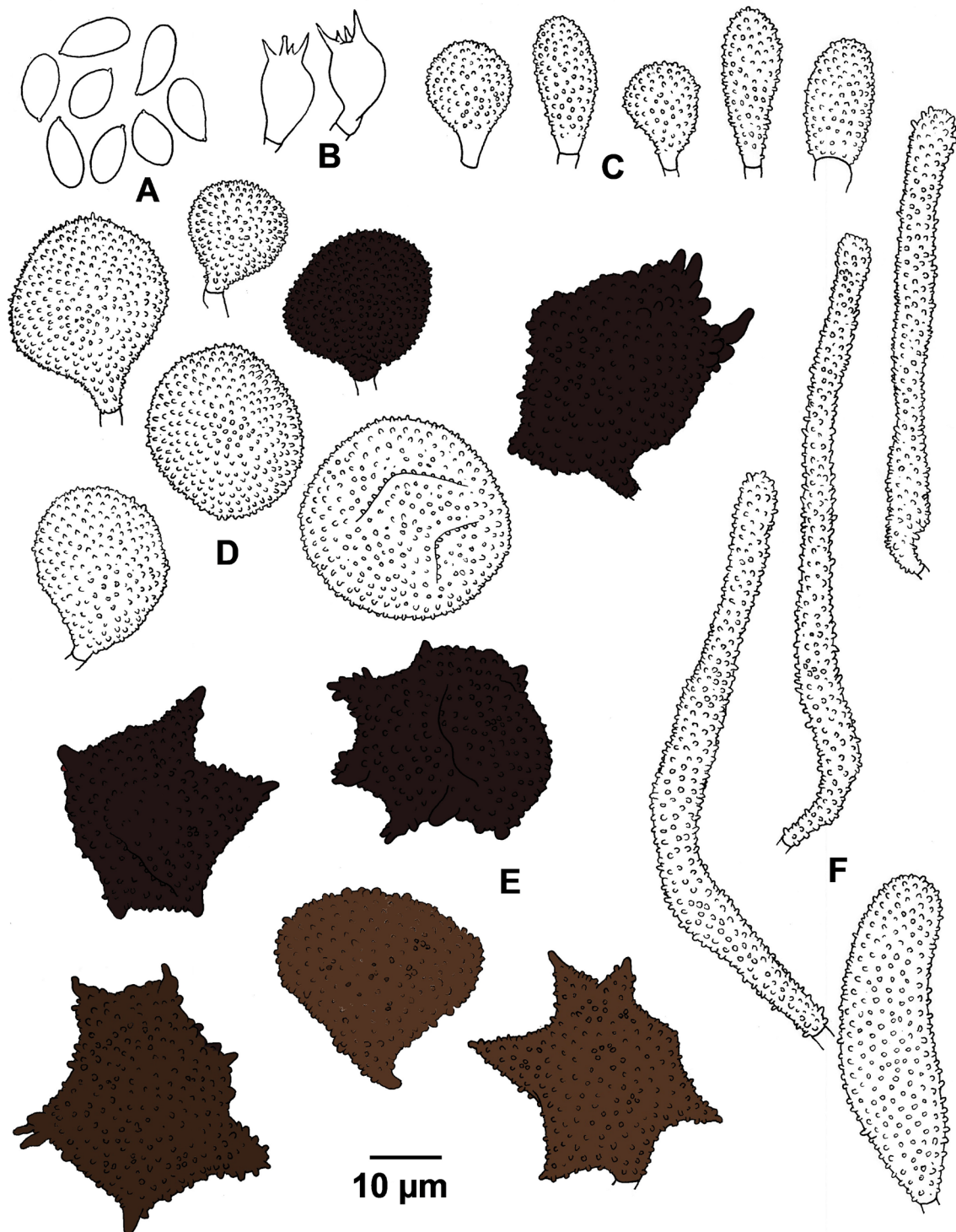


Fig. 15. Line drawings of *Mycena melanovelis* Traba, Couceiro & M. Villarreal sp. nov. (AH56004, holotype). A. Spores. B. Basidia. C. Cheilocystidia. D. Acanthocysts. E. Cheroocytes. F. Caulocystidia. Scale bar = 10 µm. Drawing by Manuel Villarreal.

hyaline, inamyloid, thin-walled; spinulae $0.8\text{--}2.4 \times < 0.8 \mu\text{m}$, cylindrical or subconic, obtuse. Clamp connections are absent in all tissues.

Habitat and distribution

Growing scattered to gregarious on dead leaves of *Acacia melanoxylon*. Known from Galicia (Spain) and Sao Miguel (Azores, Portugal), but probably introduced with its host *Acacia melanoxylon* from Australia (Fig. 19).

Remarks

Mycena melanovelis sp. nov. is another foliicolous species that fruits exclusively on dead leaves of *Acacia melanoxylon*. Macroscopically it is characterized by its delicate basidiocarps with white pileus covered with brownish granules and an entirely puberulous stipe arising from a small basal disc. Within the *M.* sect. *Amparoina*, species with coloured acanthocysts and cherocytes, the only species so far known with such dark brown pigmentation is *M. lasiopus*, originally described from Paraná (Maas Geesteranus & de Meijer 1998) and Sao Tomé (Cooper *et al.* 2018). The Afro-American species differs in that it has a slightly darker pileus, broader spores, numerous cheilocystidia, and irregularly shaped cherocytes without acute projections. The caulocystidia are almost smooth at the apex, and clamps are present in all tissues.

The fourth stirps *Fuscinea* suggested by Maas Geesteranus & de Meijer (1998) in their second work about *Mycena* from the state of Paraná, includes two Brazilian species: *M. fuscinea* Maas Geest. & de Meijer and *M. fuliginea* Maas Geest. & de Meijer. Both lack cherocytes, while being present in *M. melanovelis* sp. nov. Certainly, the fact that cherocytes tend to have an ephemeral nature as they are detersile structures could mean that the Brazilian species had these cells and they would not have been observed at the time of their description forcing us to compare our new species with them. *Mycena lasiopus* differs from *M. melanovelis* in having slightly darker pileus, broader spores, numerous cheilocystidia and less lobed cherocytes without acute projections, and the caulocystidia are almost smooth at the apex and clamps are present in all tissues. *Mycena fuscinea* differs in having a greyish brown pileus, bisporic basidia, and larger basidiospores ($8.1\text{--}9.8 \times 5.4\text{--}6.5 \mu\text{m}$ (Q = 1.6), whereas *M. fuliginea* is a corticolous-lignicolous species lacking a basal disc and having wider spores ($8.7\text{--}10.3 \times 4.7\text{--}5.4 \mu\text{m}$; Q = 2.0) than *M. melanovelis*.

Mycena viridivellata M. Villarreal & Couceiro sp. nov.

MycoBank: MB [857444](#)

Figs 16–19

Diagnosis

Mycena viridivellata sp. nov. differs from *M. amoena* in having dark green granules over the pileus, less conspicuously lobed cherocytes, slightly narrower spores and different habitat.

Etymology

The epithet derives from the Latin ‘viridis’, -e = green, and *velata* from the Latin ‘velum’ = veil, referring to the colour of the granules in the pileus surface.

Type material

Holotype

SPAIN • A Coruña, Santa Marta de Ortigueira, Playa de Morouzos; $43^{\circ}41'51.9''$ N, $7^{\circ}50'47.5''$ W; 9 m a.s.l.; 9 Dec. 2023; A. Couceiro, J. Mateos, C. Sos & M. Villarreal s.n.; bark of *Laurus nobilis*; GenBank no.: [PV037614](#) (ITS); AH [AH59694].

Additional material examined

SPAIN • A Coruña, Santa Marta de Ortigueira, Playa de Morouzos; 43°41'51.9" N, 7°50'47.5" W; 9 m a.s.l.; 15 Apr. 2022; *M. Villarreal s.n.*; with *Salix atrocinerea* dead leaves; wetted 18 Apr. 2022, harvested from batch moist chambers on 2 May 2022; GenBank no.: [PV037612](#) (ITS); AH [AH59669] • same locality as for preceding; harvested from batch moist chambers on 8 May 2022; AH [AH59671] • same locality as for preceding; 17 Dec. 2023; *A. Couceiro s.n.*; bark of *Laurus nobilis*; ACN [ACN2023120700] • same locality as for preceding; harvested from batch moist chambers on 3 May 2022; GenBank no.: [PV037613](#) (ITS); AH [AH59670].

Description

Primordia hemispherical to paraboloid, covered with dark green granules, initially forming a closed layer, soon breaking up to a non-contiguous layer upon a light grey surface, more whitish at the pileus margin; dried dark greyish green. Pileus 1.5–2.2 mm diam., initially paraboloid, expanding to obtusely conic or broadly convex in age; margin crenulate, translucent-striate, old very thin-fleshed, translucent; surface in young covered all over with groups of metallic green to dark green (sometimes nearly blackish green) ‘sugar-like’ granules on a whitish surface, mature white, still bearing small amounts of granules especially in the disc. Lamellae narrowly adnate, subventricose to ventricose, 8–12 reaching the stipe, with lamellulae of variable length, white. Stipe 8–22 × –1.2 mm, central, filiform, at the base slightly inflated; surface hirsute all over, watery grey to watery white; arising from a small spinulose basal disc. Odour and taste absent.

Basidiospores (7.8–)8.2–9.5(–10.1) × (3–)3.3–4(–4.3) µm; Q = (2–)2.2–2.7(–3); n = 100; Me = 8.8 × 3.6 µm; Qe = 2.4, cylindrical to bacilliform, smooth, hyaline, amyloid, thin-walled. Basidia 11–14.5 × 4.3–6.8 µm, obpyriform to clavate, 2 or 4-spored, sterigmata 2–4 µm long., hyaline. Cheilocystidia 10–25 × 6–13 µm, clavate to broadly clavate, sparsely spinulose in the upper part but more densely spinulose near the pileus margin, not forming a sterile band; spinulae 0.5–1 × 0.5 µm, cylindrical to subconical. Pleurocystidia absent. Pileipellis a cutis with acanthocysts and detersile cheroocytes; hyphae 2–13 µm diam., warty or smooth, dextrinoid. Acanthocysts 9–19 × 9.5–18.03 µm, globose to subglobose, densely warty, dark brownish green, dark green or hyaline, inamyloid, thin-walled; arising from a septated thin-walled, smooth or poorly warty hyphae of about 3 µm diam.; spinulae 0.5–1 × 0.5–1.5 µm, cylindrical or subconical. Marginal acanthocysts 13–27.6 × 6.6–11.4 µm, clavate, broadly clavate, ovoid or subglobose, densely spinulose, grey or hyaline, inamyloid, thin-walled; spinulae 0.5–1 × 0.5–1.5 µm, cylindrical or subconical. Cheroocytes 14–21 × 14–20 µm (bypassing lobes), roundish to obtuse angular, with 2–6 obtuse or obtusely conical lobes, lobes extending up to 6 µm, with a dark green vacuolar content, walls jade green or hyaline, thick-walled up to 4.5 µm; covered with short spinulae and warts; warts hemispherical, 0.4–2 × 0.4–2.5 µm; often seen originating from a septate slightly thick-walled, smooth hypha of about 1.5–3 µm diam. Hypodermium composed of inflated hyphae 11–26 µm diam., dextrinoid. Lamellar trama composed of inflated hyphae up to 25 µm diam., dextrinoid. Cortical and medullary hyphae of the stipe 6–26 µm diam., parallel, smooth, dextrinoid. Caulocystidia abundant throughout the stipe, 13–98 × 5–14 µm, ranging from short and broadly clavate or subcylindric to long and cylindric, sometimes constricted or bifurcated apex even or somewhat wider, obtuse, densely and evenly spinulose overall, hyaline, thin-walled, inamyloid; spinulae 0.5–1(–2) × 0.5–1 µm, cylindrical or subconical. Clamps not observed.

Habitat and distribution

Scattered or gregarious on dead leaves and bark of *Laurus nobilis* and *Salix atrocinerea* from April to the end of December. Known only from the type locality in Spain (Fig. 19).

Remarks

Mycena viridivellata sp. nov. has many macro- and microscopic similarities with the recently described *M. amoena* (Jagers *et al.* 2023), from which it differs in having cheroocytes with much thicker and more

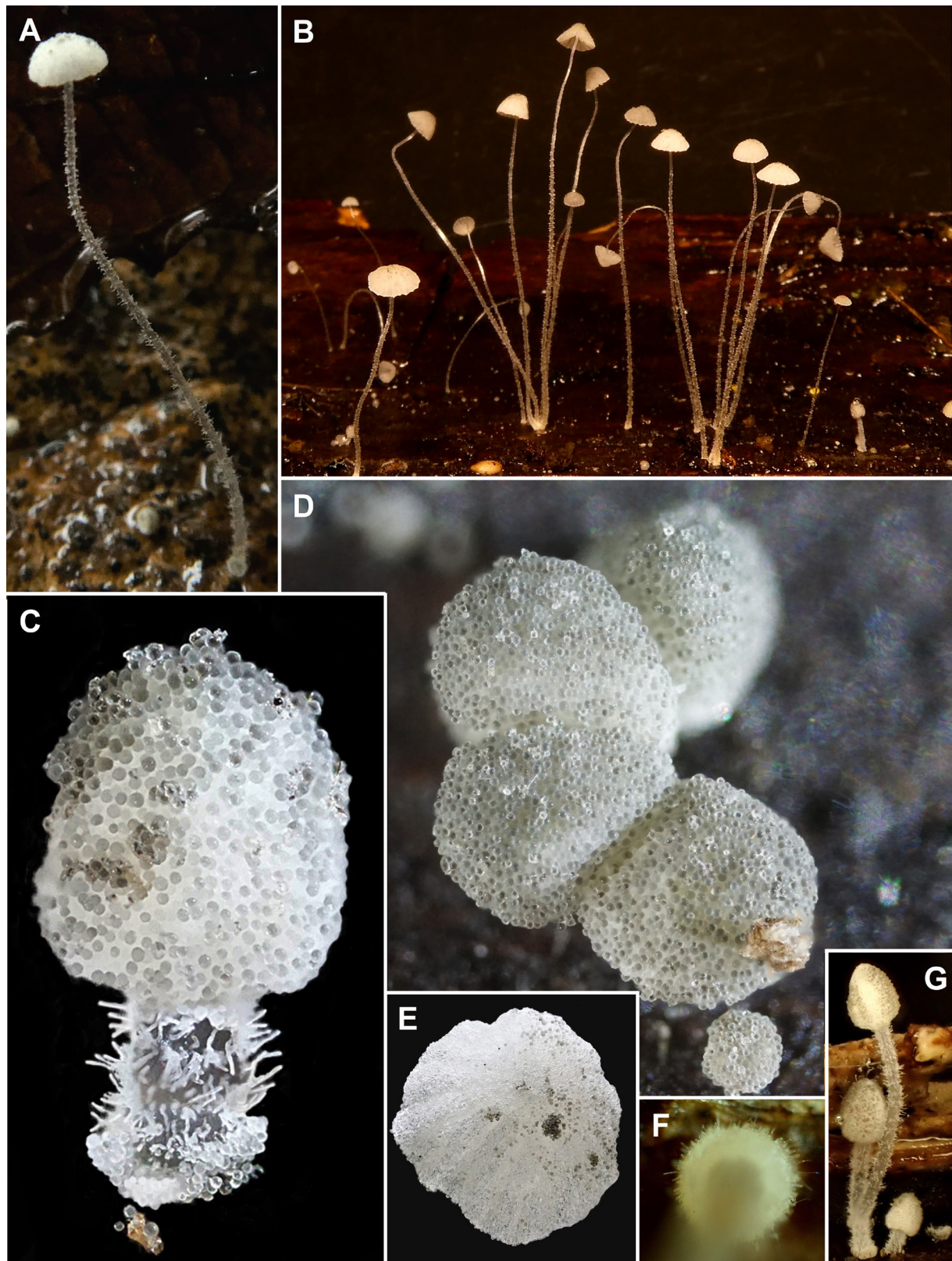


Fig. 16. *Mycena viridivellata* M.Villarreal & Couceiro sp. nov. **A.** AH59669. **B.** AH59694 (holotype). **C–D.** AH59694 (holotype), primordia. **E.** AH59669, detail of the pileus surface. **F.** AH59669, basal disc. **G.** AH59669, fresh basidiomata.

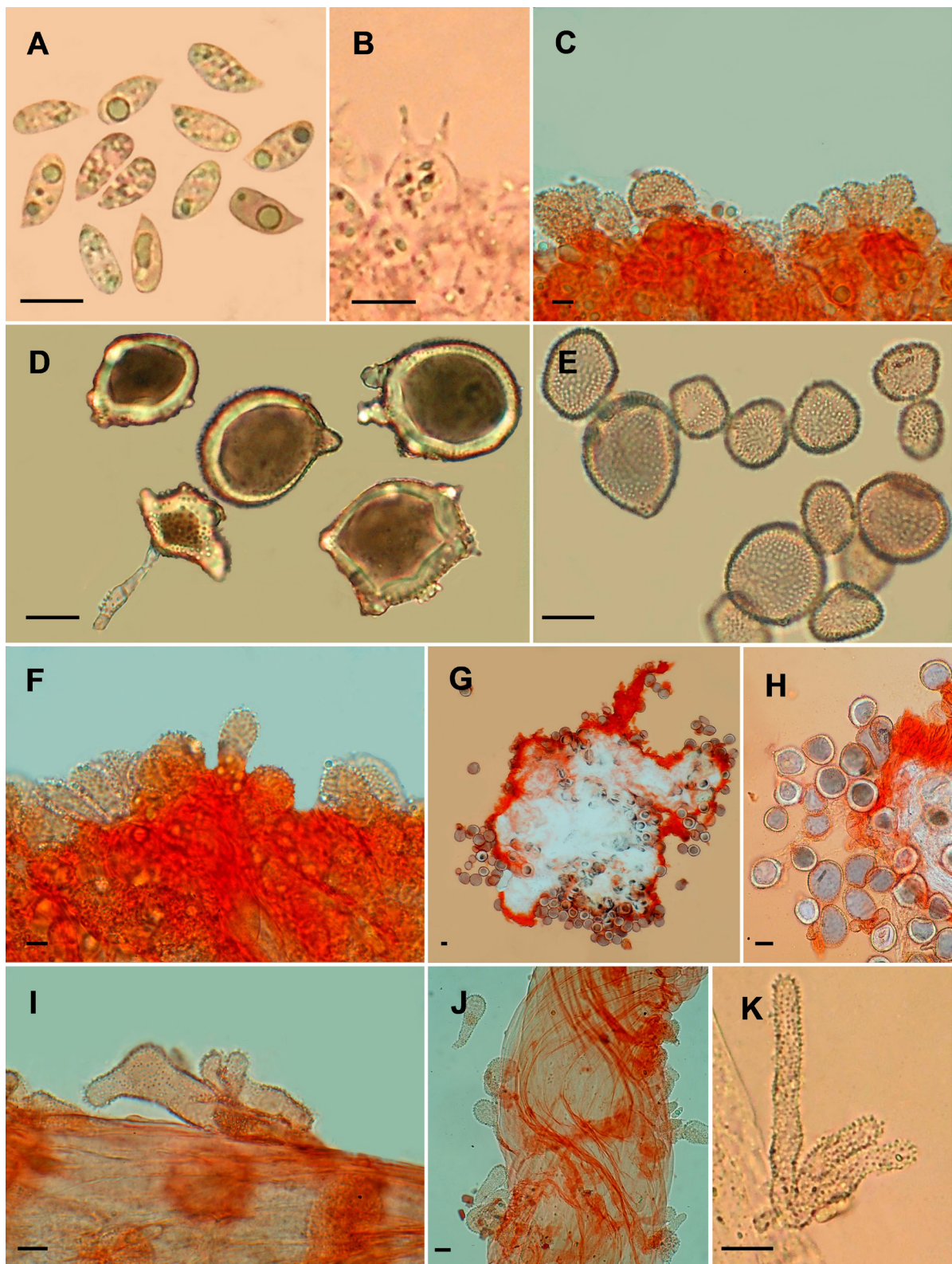


Fig. 17. Microscopic features of *Mycena viridivellata* M.Villarreal & Couceiro sp. nov. (AH59694, holotype). **A.** Basidiospores. **B.** Basidium. **C.** Cheilocystidia. **D.** Cherocytes. **E.** Acanthocysts. **F.** Terminal acanthocysts. **G.** Primordium. **H.** Cherocytes and acanthocysts of the basal disc. **I–K.** Caulocystidia. Scale bars = 10 μ m.

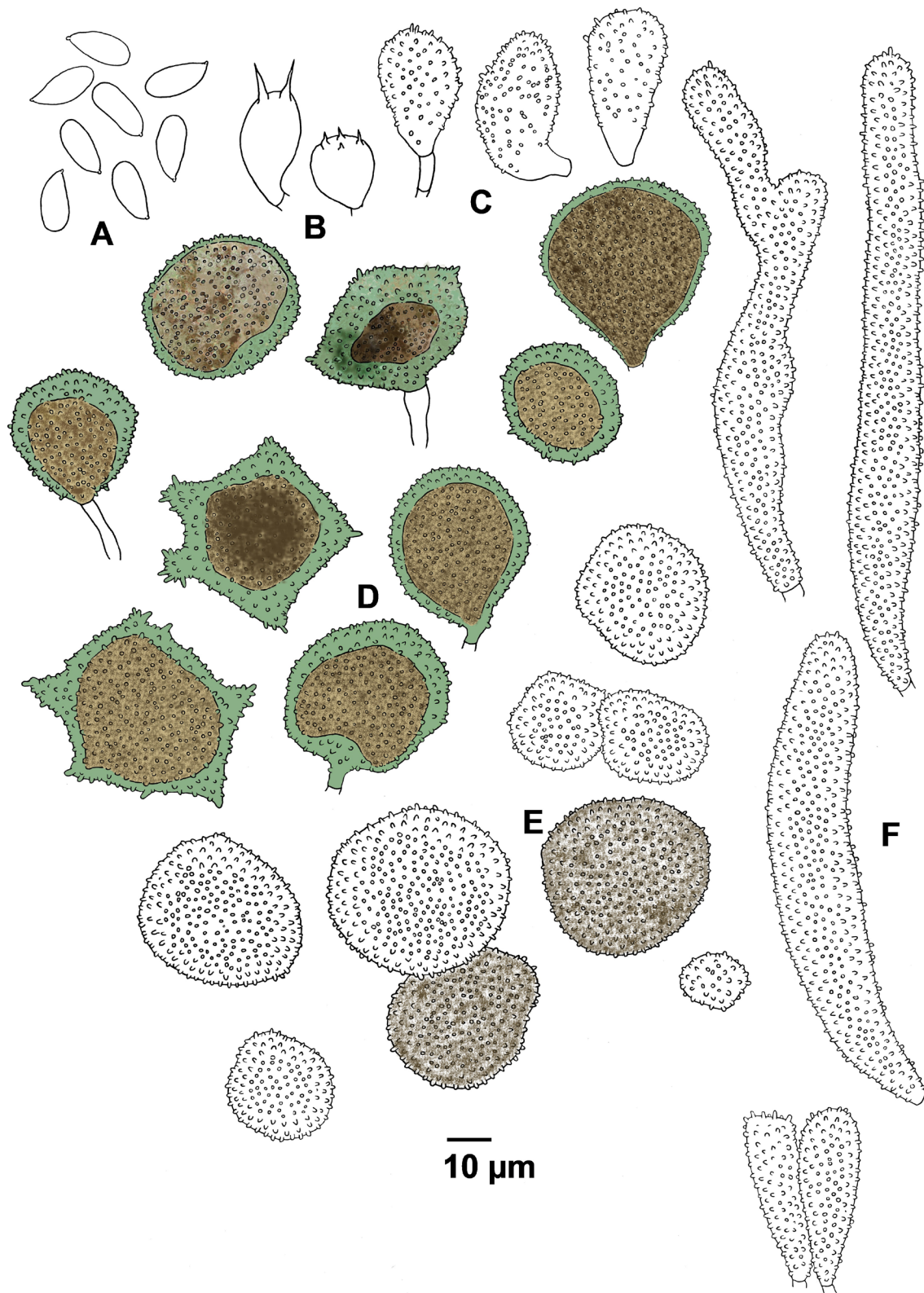


Fig. 18. Line drawings of *Mycena viridivelata* M.Villarreal & Couceiro sp. nov. (AH59694, holotype). A. Spores. B. Basidia. C. Cheilocystidia. D. Acanthocysts. E. Cheroocytes. F. Caulocystidia. Drawing by Manuel Villarreal.

refringent cell walls and darker intracellular pigment, which together give a dark green colour to the veil and somewhat more elongated basidiospores $Q_e = 2.4$ in *M. viridivelata* (vs $Q_e = 1.81\text{--}1.91$ in *M. amoena*). Besides, while *M. amoena* has been found fruiting on nuts and husks of *Corylus avellana*, *M. viridivelata* has been found on leaves and bark of *Laurus nobilis* and dead leaves of *Salix atrocinerea*. Molecularly, their ITS sequences are quite divergent, differing by at least 45 substitution and indel positions (93.84% similarity).

Discussion

Phylogenetic analyses revealed that *M. sect. Amparoina* forms a monophyletic group with the highest statistical support (BS = 100%, BPP = 1), distant from the clade containing species from the *M. sects. Basipedes* and *Sacchariferae* (BS = 100%, BPP = 1). This is consistent with Na & Bau (2019b) and Jagers *et al.* (2023). However, the phylogenetic position of *M. sect. Amparoina* appears to be quiet distant from the clade containing the type of the genus *M. galericulata* (Scop. ex Fr.) S.F.Gray (Bau *et al.* 2021; Traba *et al.* unpublished; Xiao *et al.* 2025). Furthermore, we confirm that the presence of acanthocysts, cheroocytes and caulocystidia densely covered with spines, are the main characters distinguishing this clade from other near-by clades such as *M. sect. Basipedes* (Fr.) Quél., *M. sect. Granuliferae* Maas Geest. & de Meijer, *M. sect. Exornatae* Maas Geest. or *M. sect. Sacchariferae*, in which acanthocysts can also be found, but always show smooth caulocystidia.

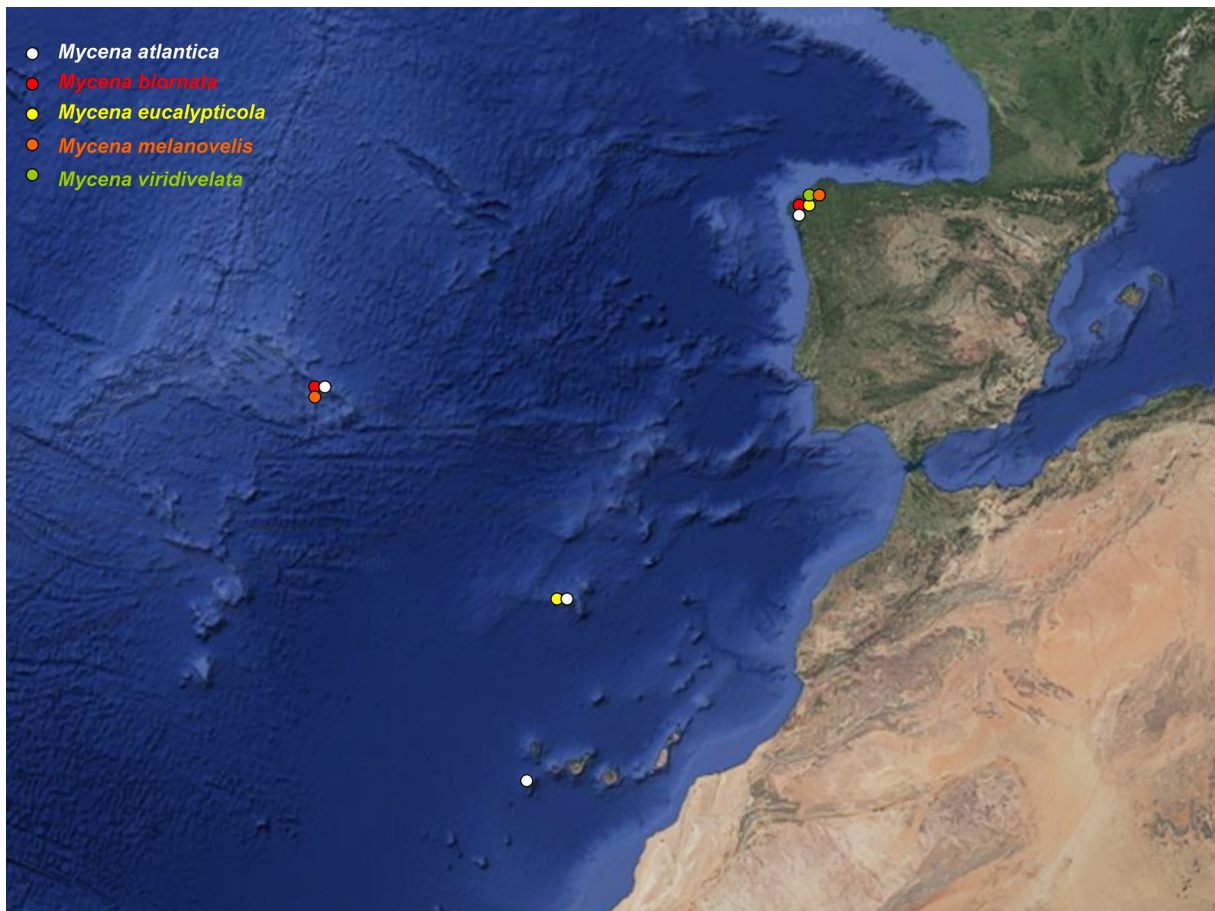


Fig. 19. Map showing the distribution of *M. biornata* and the new *Mycena* species described in this paper.

Na & Bau (2019b) and Jagers *et al.* (2023), in their phylogenetic studies, separated *M. sect. Amparoina* from *M. sect. Sacchariferae*, although they did not include the type of *M. sect. Basipedes*, *M. stylobates* (Fr.) Quél., in their analysis. Recently, Sandoval-Leiva *et al.* (2025) indicate that there are substantial issues with the phylogenetic classification of *M. sect. Sacchariferae*, demonstrating that this section is polyphyletic. This study addresses the presence of two clades with sequences designated as *M. tenerrima*/*M. adscendens*, for which there are no sequences of type material, complicating the precise phylogenetic placement of *M. tenerrima*. Deceuninck (2025) has recently clarified this situation, demonstrating that one of the clades actually belongs to *M. nucicola* Huijsman.

Soares *et al.* (2024) conducted a phylogenetic analysis using an extensive sampling strategy, focused on *Mycena* species for which ITS and 28S sequences were available in GenBank. This established a robust phylogenetic framework for *M. sect. Sacchariferae*. The sequences of *M. tenerrima* and *M. adscendens* were observed to cluster with those from species of *M. sect. Longisetae* Maas Geest. and *M. sect. Basipedes*, including *M. breviseta* Höhn. and *M. mucor* (Batsch) Quél. This is fully consistent with the hypothesis proposed by Desjardin & Horak (2002: 154: “Based on overall morphological similarities, we hypothesize that *Mycena sect. Longisetae* is a sister taxon to *Mycena sect. Sacchariferae*”). In Soares *et al.* (2024), they are forming a clade with robust statistical support (BS = 86%, BPP = 1) within a larger clade designated as “amicta”, which encompasses species belonging to *M. sections Exornatae, Granuliferae, Viscipelles* and other incertae sedis species. This finding is in line with the results of a phylogenetic study previously carried out in Traba *et al.* (unpublished).

There appears to be no direct correlation between clade *M. sections Basipedes/Sacchariferae* and any of the current morphological criteria. Nevertheless, there would be some correlation between this and the original concept of *M. sect. Basipedes* (Maas Geesteranus 1980: 73), which would comprise species currently classified in the *M. sections Basipedes, Bulbosae* Maas Geest., *Clavulares* Maas Geest., and *Longisetae* A.H.Sm. & Maas Geest. It could also perfectly include *M. sect. Sacchariferae*, as Singer (1983) noted in reference to the acanthocytes of *Amparoina* and *Mycena*, stating “...it in some species of *Mycena sections Sacchariferae* Kuhn. and *Basipedes* (Fr.) Kühner (probably to be united to form a single section—*Basipedes*...” (Singer 1983: 111). Traba *et al.* (unpublished) and Villarreal *et al.* (2023a, 2023b) have employed the same criteria. In the same way, Plaza *et al.* (2021) also synonymized the monotypic *M. sect. Bulbosae*, whose type species is *M. bulbosa* (Cejp) Kühner, with *M. sect. Basipedes*.

The ITS sequences of species within *M. sect. Amparoina*, as in other *Mycena* sections (e.g., *M. sect. Viscipelles* Kühner, see Villarreal *et al.* 2023b), are especially vulnerable to long-branch attraction phenomena due to a high number of gap-rich and nearly non-alignable regions, which may have resulted from frequent indel events. For this reason, phylogenetic relationships between the species in this section should be treated with caution.

Our phylogenetic analysis (Fig. 1) identified three distinct clades within *M. sect. Amparoina*, corroborating the findings of Jagers *et al.* (2023). The first clade (clade I) consists of two sequences of *Mycena castaneicola* T.Bau & Q.Na, described as a member of the stirps *Amparoina* (Na & Bau 2019a). This clade is situated on a comparatively long and early divergent branch, lacking statistical support for the clade II encompassing the other stirps containing species of *Amparoina* and *Fuscinea*. However, in the analysis of Jagers *et al.* (2023), it appears in a branch that is separate from the other species of *M. sect. Amparoina*. This is due to substantial sequence dissimilarity, which could suggest a distinct lineage within the section.

The stirps *Amparoina* (Desjardin 1995: 37) comprises species with or without basal disc and presence of cherocytes consisting of thin or thick-walled cells and spinulose caulocystidia. On the other hand, Maas Geesteranus & de Meijer (1998) suggested a fourth stirps *Fuscinea*, for members devoid of cherocytes and with acanthocysts with dark intracellular contents. Four species showing cherocytes and acanthocysts with coloured intracellular content (*M. amoena*, *M. lasiopus*, *M. melanovelis* sp. nov. and *M. viridivolata* sp. nov.) are grouped in a statistically unsupported clade far from *M. oboensis*, which also shows veil

cells with coloured content. This may indicate that the colouration of the veil cells should not be used to subdivide *M. sect. Amparoina*.

The stirps *Alphitophora* (Desjardin 1995: 37) contains species without a basal disc and cherocytes. As in Jagers *et al.* (2023), our phylogeny shows that most species of this stirps group in a well-supported monophyletic clade (Fig. 1, clade III, BS = 100%, BPP = 1), except for *M. yalensis*, a species described as lacking cherocytes, which in our analysis groups with species that possess them, such as *M. eucalypticola* sp. nov. and *M. oboensis*. This, together with the fact that *M. corynephora*, belonging to the stirps *Alphitophora*, has cherocytes, allows us to ensure that the presence or absence of this cell type is not a useful character for the subdivision of *M. sect. Amparoina*.

Most species of *M. sect. Amparoina* are known to inhabit tropical and subtropical regions. In this study, we rediscovered *M. biornata*, which was originally described in Brazil and is also present in Mexico. We also describe *M. melanovelis* sp. nov., which inhabits the fallen leaves of *Acacia melanoxylon*, a globally invasive plant of Australian origin. *Mycena amoena* and *M. corynephora* may be the only native taxa in Europe of *M. sect. Amparoina*, as *M. acanthophila* J.C.Zamora & Català, described in *M. sect. Sacchariferae* (Zamora & Català 2013), belongs to *M. sect. Polyadelphia* Singer ex Maas Geest. (Villarreal & Campos 2024; Villarreal *et al.* 2025). It is therefore unknown whether the new species are native or non-native. Thus, it seems plausible that the phenomenon of globalisation, together with global warming, favours the appearance of exotic species in more temperate latitudes.

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Data availability statement

The datasets generated during the current study are available on Figshare: <https://doi.org/10.6084/m9.figshare.28692605>

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