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Amanita arroasiana Hanss, Polesel, Zupan & Dima, sp. nov., a new European species from sect. Vaginatae, stirps *Nivalis* (Amanitaceae; Agaricales)

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Amanita arroasiana Hanss, Polesel, Zupan & Dima, sp. nov., a new European species from sect. *Vaginatae*, stirps *Nivalis* (Amanitaceae; Agaricales)

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ABSTRACT
Amanita arroasiana Hanss, Polesel, Zupan & Dima, sp. nov. is introduced as a new species, based on five collections from Austria, Hungary, France and Slovenia and one additional soil sequence data from Estonia. This new species likely forms ectomycorrhizal associations with *Quercus* L. and *Carpinus* L., although *Betula* L. cannot be excluded as a potential host. Detailed description and illustrations of its morphological features are presented. Phylogenetic analysis of nrITS and combined nrLSU sequences placed it in the stirps *Nivalis* sect. *Vaginatae*. Variation in the colour of the pileus during growth, going from dark to light, a rather thick but relatively fragile volva of type II, coloured in its upper half and a unique microscopy of the pileus, the lamellar trama, the subhymenium and the volva are the main morphological characteristics of this species.

KEY WORDS
Agaricomycetes, Basidiomycota, ectomycorrhizal fungi, phylogenetic analysis, new species.

RÉSUMÉ
*Description d'*Amanita arroasiana*, Hanss, Polesel, Zupan & Dima, sp. nov., une espèce européenne nouvelle, de la section* Vaginatae*, stirpe* Nivalis *(Amanitaceae; Agaricales).*
Amanita arroasiana Hanss, Polesel, Zupan & Dima, sp. nov. est décrite comme une espèce nouvelle sur la base de cinq collections provenant d'Autriche, de Hongrie, de France et de Slovénie, ainsi que de la séquence d'un échantillon de sol d'Estonie. Elle est probablement ectomycorhizienne avec *Quercus* L., *Carpinus* L., bien que *Betula* L. ne puisse être exclu en tant qu'hôte potentiel. L'analyse phylogénétique des séquences nrITS et nrLSU combinées la situe dans la stirpe *Nivalis* de la section *Vaginatae*. Les principaux caractères distinctifs sont la variabilité chromatique du chapeau, du jaune au brun foncé, d'une collection à l'autre, une volve de type II épaisse mais se cassant facilement sur le bord, ochracée dans sa moitié supérieure, ainsi que de nombreuses particularités microscopiques du chapeau, de la trame des lames, du sous-hyménium et de la volve.

MOTS CLÉS
Agaricomycetes, Basidiomycota, champignons ectomycorhiziens, analyse phylogénétique, espèce nouvelle.

INTRODUCTION

The globally distributed genus *Amanita* Pers. is one of the most iconic and taxonomically complex groups of basidiomycetous macrofungi in Agaricales. Predominantly ectomycorrhizal (EcM) *Amanita* species are ecologically significant and functionally important across diverse terrestrial ecosystems, from xerophilic tropical lowland forests to arctic-alpine microhabitats (Gilbert 1941; Bas 1969; Singer 1986). A basal saprotrophic lineage with a squarrose universal veil has been segregated into the genus *Saproamanita* Redhead, Vizzini, Drehmel & Contu (Redhead *et al.* 2016), but this concept did not achieve broad recognition among mycologist (Tulloss *et al.* 2016). The vast majority of species in genus *Amanita*, however, form mutualistic symbioses with trees.

Molecular phylogenetic research over the past few decades has significantly reshaped our understanding of the genus (Weiss *et al.* 1998; Drehmel *et al.* 1999; Oda *et al.* 1999; Zhang *et al.* 2004; Redhead *et al.* 2016; Tulloss *et al.* 2016; Cui *et al.* 2018). According to the current, widely accepted classification (Cui *et al.* 2018) *Amanita* is divided into three subgenera of which *Amanita* includes, among others, sect. *Vaginatae* (Fr.) Quél, to which the fungi discussed in this study belong. The estimated total number of species in the genus *Amanita* is around 1000 (Yang *et al.* 2018), of which approximately 700 are currently accepted globally (Codjia *et al.* 2023). Over 220 taxa have been described in the last two decades, highlighting the rapid pace of discovery driven by molecular tools and improved sampling of previously underexplored regions. This surge in new taxa has revealed the limitations of morphology-based taxonomy, as many previously morphologically identified species are now understood to be parts of cryptic complexes (Zhang *et al.* 2015; Thongbai *et al.* 2018).

Amanita sect. *Vaginatae*, commonly known as the "ringless "Amanitas", is a diverse and taxonomically challenging groups within the genus (Ševčíková *et al.* 2021). Species in this section are typically characterized by their non-amyloid, white spores, absence of an annulus on the stipe, grey, often brownish-grey pileus, but being able to have almost all colours except pure blue, a striate to sulcate pileus margin, an elongated stipe lacking a basal bulb, well-developed volva of all types at the stipe base, and clampless basidia (Yang 1997). Similarly to other macrofungi, many species in the sect. *Vaginatae* have a white form. Recent molecular phylogenetic studies employing integrated morphological assessments and multi-locus phylogenetic analyses (commonly using (nr)ITS, (nr)LSU, RPB1/RPB2, and TEF1-α) have revealed a remarkably high level of cryptic diversity within the section (e.g., Kim *et al.* 2013; Malysheva & Kovalenko 2015; Tang *et al.* 2015; Vizzini *et al.* 2016; Liu *et al.* 2017; Cui *et al.* 2018; Thongbai *et al.* 2018; Lambert *et al.* 2018; Ullah *et al.* 2019). In Europe, Hanss & Moreau (2020) initiated the first large-scale revision of grey-coloured species within sect. *Vaginatae*, identifying and stabilizing 28 phylogenetic species based on nrDNA ITS sequences and morphology. This foundational work has since been expanded through numerous additional studies (Ševčíková *et al.* 2021; Migliozzi & Donato 2022a, b; Illescas & Plaza 2022; Plaza 2022; Hanss & Moreau 2022; Crous *et al.* 2023; Illescas 2023). Varga *et al.* (2024), studying a compilation of collections from Hungary, Norway and France described three new species of sect. *Vaginatae* on the

basis of molecular phylogenetic analysis with four loci (nrDNA ITS, nrDNA LSU, RPB1 and TEF1-α) and macroscopic as well as microscopic features. Many in this study recognized new stirps have been added to the one defined in Hanss & Moreau (2020) to form a total number of 22 stirps for sect. *Vaginatae*. In 2024, further new publications increased the number of *Vaginatae* species from Europe, describing *Amanita ampelivelata* (Hanss *et al.* 2024), *A. cerris*, *A. pseudoargentea*, *A. sublividopallescens* (Migliozzi & Di Palma 2024), and *A. corylophila* (Crous *et al.* 2024). One species in stirps *Nivalis* was included in the phylogenetic analysis by Varga *et al.* (2024) as *Amanita* sp. without further taxonomic conclusion due to lack of sufficient material. The aim of this study is to formally describe a new *Vaginatae* species from strips *Nivalis* since during the last two years, new records of this species have appeared from Austria, Hungary and Slovenia making us possible to study this species in more details.

MATERIAL AND METHODS

Macromorphological studies

Macroscopic observations were conducted using fresh collections. All samples were photographed either in situ or in laboratory on plates to document the key morphological features of the basidiomata. Colours were identified using the colour code of the Royal Botanic Garden Edinburgh (1969). Terminology and description of volva are taken from Fraiture (1993). To ensure clarity, macroscopic descriptions in this study avoid superfluous details and emphasize the distinct, unique features of the new species described herein. In the descriptions, we focused on highlighting the particularities of the new species introduced in this study.

Microscopy

Bas (1969) was followed for microscopic examination methods and the terminology used for describing microscopical structures and basidiospore characteristics. Bas (1969) was also followed for the types of subhymenium and they were reproduced and numbered from one to five in Hanss & Moreau (2020). Observations were conducted using a Nikon Eclipse 220 microscope at magnifications of 100×, 400× and 1000×. On the microscope, a camera Tucsen Mycstack-20 Mpx, special model of Microscopie & Services, recording photos is connected to the computer. The software IC Capture 2.3 is calculating imaging and enables images processing.

Microscopic preparations were obtained from dried material. Sections were cut using a Ranvier microtome, and the extracted fragments were reinflated in "ramollisseur GDS" and mounted in SDS Congo red, following Clémençon (1999). Alternatively, some fragments were reinflated and mounted in ammoniacal Congo red with ¼ to ⅕ of phloxin.

Basidiospore length, width and Q-value (length/width ratio of a basidiospore in sideview) were manually determined for 30 spores per specimen. Sections of volva were made on their upper part, where remains of partial veil on their internal face are usually absent.

Molecular analyses

Genomic DNA was extracted from 4-5 mm pieces of dried herbarium specimens using i) the NucleoSpin Plant II Mini Kit (Macherey-Nagel, Düren, Germany) following the manufacturer's instructions or ii) based on the protocol communicated by the MycoSeq project of the Société Mycologique de France/CEFE Montpellier (see also Hanss & Moreau 2020) using the REDExtract-N-Amp Plant PCR Kit (Sigma-Aldrich, Saint Louis, MO, United States), also following the manufacturer's instructions, or by employing the method described in Gruhn *et al.* (2017). Nuclear ribosomal internal transcribed spacer (nrDNA ITS) amplifications were performed with ITS1F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990) primers and nuclear ribosomal large subunit (LSU) was amplified with primers LR0R and LR5 (Vilgalys & Hester 1990) using polymerase chain reaction (PCR) followed as described by Varga *et al.* (2024). Success of the reactions were checked in 1.5% agarose gel stained with EcoSafe, and illuminated by UV-transilluminator (NuGenius, Syngene). Sanger sequencing was performed at LGC Genomics (Berlin, Germany) or at Eurofins Genomics (Ebersberg, Germany). For sequence assembly and editing CodonCode Aligner package (CodonCode Corp., Centerville, Massachusetts, United States) were used. The sequences were compared to those available in GenBank (https://www.ncbi.nlm.nih.gov/genbank/) and UNITE (https://unite.ut.ee/) databases (Table 1) using the BLASTn algorithm (Altschul *et al.* 1990). ITS and LSU sequences were separately aligned with MAFFT online v7 (http://mafft.cbrc.jp/alignment/server) using E-INS-i setting for ITS, G-INS-i for LSU (Katoh & Standley 2013). Nucleotide alignments were edited and concatenated in SeaView 5 (Gouy *et al.* 2021). For maximum likelihood phylogenetic analysis, PhyML 3.0 (Guindon *et al.* 2010) was applied, using the GTR model of evolution. Branch support was assessed using the non-parametric, Shimodaira-Hasegawa, version of the approximate likelihood-ratio test (SH-aLRT), implemented in the latest release of PhyML. The resulting phylogenetic tree was edited in MEGA 7 (Kumar *et al.* 2016) and Microsoft PowerPoint.

RESULTS

Phylogeny

The final alignment for *Amanita* sect. *Vaginatae* stirps *Nivalis* is composed of 55 nrDNA ITS and 19 LSU sequences, and 1659 characters (ITS: 619, LSU: 1040) including gaps. The concatenated two-locus alignment is included in the Appendix 1. The resulting topology of the ML analysis is well resolved and include several distinct, strongly supported clades (SH-aLRT >90%) showing in Figure 1. The five newly generated ITS and one LSU sequences were deposited in GenBank (Table 1). The sequences of the specimens belonging to *Amanita* sp. in Varga *et al.* (2024) form a strongly supported monophyletic group (SH-aLRT = 100%) comprising specimens from multiple European countries including Slovenia (holotype), Austria, France, Hungary, and Estonia. This clade is phylogenetically distinct and reresents a well-defined species level lineage within *Amanita* sect. *Vaginatae*

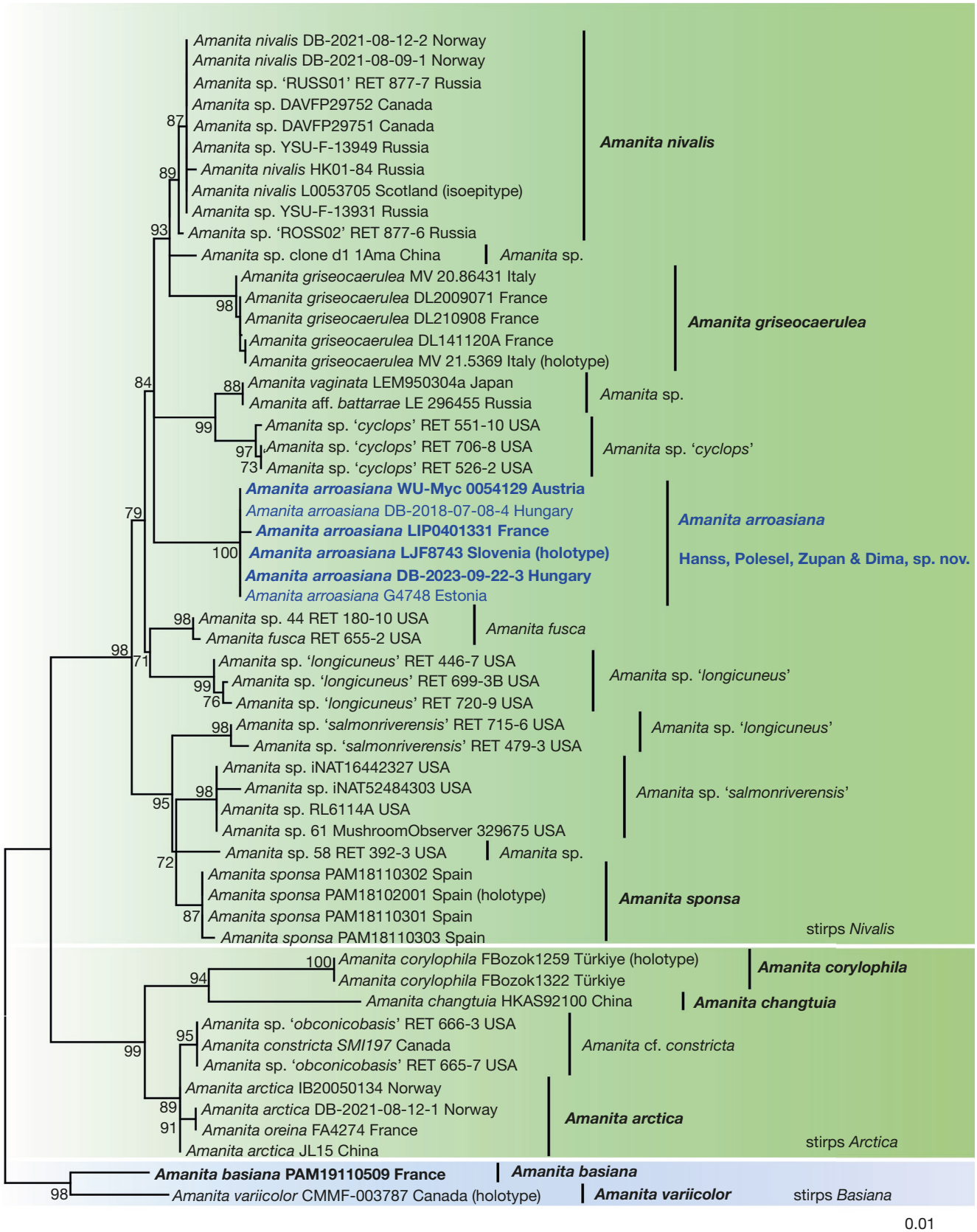

Fig. 1. — Maximum likelihood (PhyML) phylogenetic tree showing the relationship of *Amanita* sect. Vaginatae stirps *Nivalis*. The new species *A. arroasiana* Hanss, Polesel, Zupan & Dima, sp. nov., highlighted in **blue**. Newly generated sequences are marked in **boldface**. SH-aLRT ≥70% are indicated at the branches. The scale bar representing 0.01 expected change per site per branch.

strips *Nivalis*. The phylogenetic placement of this distinct clade justifies its description as a new species, well differentiated from all described species in sect. *Vaginatae*. The closest phylogenetic relatives of the lineage include *A. nivalis*, *A. griseocaerulea* and *A. sponsa*, as well as several unnamed or informally designated North American taxa (e.g., *Amanita* sp. "cyclops", *A.* sp. "longicuneus", *A.* sp. "sharkriverensis", *A.* sp. "salmonriverensis"). The presence of undescribed or informally named "cryptic" taxa from North America highlights the continued need for taxonomic revision within this morphologically and genetically diverse group, particularly in under-sampled geographical regions.

Taxonomy

Family Amanitaceae E.-J. Gilbert

Genus *Amanita* Pers.

Amanita arroasiana Hanss, Polesel, Zupan & Dima, sp. nov. (Figs 2; 3; 4)

Diagnosis. — *Amanita arroasiana* Hanss, Polesel, Zupan & Dima, sp. nov. is remarkable for its buff to dark brown pileus, its type II volva, which is white in colour with an ochraceus upper outer surface. It differs from the other species in *Amanita* sect. *Vaginatae* by its ITS nucleotide composition and several unique microscopic features, e.g., a very thin pileus context (approximately 50 µm), a 400 µm thick pileipellis surmounted by a gelatinized layer of free hyphae, a budding subhymenial tree that can form several branches, a strictly filamentous lamellar trama, and a rather fragile volva comprising three well-differentiated strata.

Type material. — **Slovenia** • Ljutomer, Ljutomerski park, under *Quercus robur* L., *Carpinus betulus* L. on acidic, sandy, clay soil; 46°31'15.1"N, 16°11'30.4"E; 25.X.2024; *E. Zupan*; holotype: LJF8743; GenBank: PZ631850 (ITS).

Additional collections examined. — **Austria** • Burgenland, Oberpullendorf, Unterfrauenhaid, Herrschaftswald, under *Quercus*; 28.X.2024; *G. Koller*; WU-Myc 0054129; GenBank: PZ631847 (ITS).

Hungary • Borsod-Abaúj-Zemplén County, Zubogy, under *Quercus* and *Carpinus*; 5.VII.2018; *B. Dima & L. Albert*; DB-2018-07-08-4 (ELTE); GenBank: PP375688 (ITS) • Heves County, Mátra Mts, Pásztó-Mátrakeresztes, under *Quercus* and *Carpinus*; 22.IX.2023; *B. Dima*; DB-2023-09-22-3 (ELTE); GenBank: PZ631849 (ITS) **France** • Forêt domaniale d'Andigny, GenBank: PZ631848 (ITS).

Etymology. — The epithet *arroasiana* means from Arroasia, the latin name of Arrouaise forest, an ancient and immense French forest dating back to prehistoric times, of which the forest of Andigny (department Aisne) is a vestige. The first finding of *Amanita arroasiana* Hanss, Polesel, Zupan & Dima, sp. nov. was discovered there (Polesel 2020).

MycoBank. — MB 864457.

Habitat and distribution. — The species has been found five times, twice in Hungary and once each in Austria, France and Slovenia, under *Quercus*, *Carpinus* and possibly with *Betula*. ITS sequence data from environmental samples show that *A. arroasiana* occurs also in Estonia (Fig. 1). A recent study in *Quercus rubra* plantations in Hungary also yielded a root sequence belonging to *A. arroasiana* (pers. com. Péter Balázs, Eötvös Loránd University, Budapest).

Phylogenetic relationship. — *Amanita arroasiana* Hanss, Polesel, Zupan & Dima, sp. nov. belongs to stirps *Nivalis* and is related to *Amanita nivalis*, *A. griseocaerulea* and *A. sponsa* as well as several undescribed species from North America and Asia (Fig. 1).

Description

Pileus

4-7 cm diameter, at first obtuse then flattening until it becomes clearly depressed, with a deeply ridged margin. Colour varying from cigar-brown (16) to buff (52), sometimes tarnished by grey, for example clay buff (32) to drab (33), darker in the centre, with a somewhat silky sheen, sometimes covered with relatively thick beige partial veil remains. Colour seems to vary little over the life of an individual.

Lamellae

Moderately crowded, 4 mm high, of uniformly whitish colour.

Stipe

5 cm long, straight or curved, white or beige, 0.5-1 cm, medium thick to relatively thin, with a thin partial veil at first very discreet and then clearly visible but with a relatively, discrete grain.

Volva

Up to 2.5 cm high, relatively thick, distinctly of type II, with several lobes. The white lower half, positioned against the stipe, seemingly buried; the upper half, ochraceous, open in lobes forming a corolla. On the mature specimen, fragile lobes of the volva eventually falling off.

Basidiospores

Almost globose, small and very regular for a species of sect. *Vaginatae*, 9.3-11.5 × 8.9-10.9 µm, Av = 10.12 × 9.85 µm, Qav = 1.03.

Basidia

Of medium size, relatively slender and regular, 63-68 × 13-15 µm, rarely stockier, e.g., 51 × 17 µm.

Lamellar trama

110 µm thick in its middle, composed exclusively of hyphae, without the presence of physaloid cells. In the middle of the trama some thick hyphae of 5-6 µm present, blackening to SDS Congo red. Trama itself consisting of 1.5-4 µm thick entangled hyphae.

Subhymenium

Unique by its subhymenial cells with one or two lateral projections, type 1b, of rounded shape.

Subhymenial cell

Cylindrical, 4-6 µm thick (excluding projections) and of variable height, 7-14 µm. The resulting subhymenial tree usually forming several branches, suggesting budding (of basidia or branches) of lateral projections on the subhymenial cell.

TABLE 1. — Sequences used for the phylogenetic study. Abbreviations: **ITS**, internal transcribed spacer; **LSU**, large subunit of the nrDNA.

Taxon name	Voucher/strain/isolate	GenBank/UNITE accession no. ITS	LSU	Country	References
Amanita arctica Bas, Knudsen & T.Borgen	JL15	ON059325	–	China	Gao, pers. com.
	FA4274 (as *A. oreina*)	OR419842	–	France	Armada *et al.* (2023)
	IB20050134	KX834234	–	Norway	Vizzini *et al.* (2016)
	DB-2021-08-12-1	PP375771	PP375266	Norway	Varga *et al.* (2024)
Amanita arroasiana Hanss, Polesel, Zupan & Dima, sp. nov.	WU-Myc 0054129	PZ631847	–	Austria	this study
	G4748	UDB0374610	–	Estonia	unpublished
	LIP0401331	PZ631848	–	France	this study
	DB-2018-07-08-4 (as *A.* sp. 3)	PP375688	PP375225	Hungary	Varga *et al.* (2024)
	DB-2023-09-22-3	PZ631849	–	Hungary	this study
	LJF8743 (holotype)	PZ631850	–	Slovenia	this study
Amanita basiana Tulloss & M.Traverso	PAM19110509	PZ631851	PZ625999	France	this study
A. changtuia Zhu L.Yang, Y.Y.Cui & Q.Cai	HKAS92100	MH508299	MH486442	China	Cui *et al.* (2018)
Amanita cf. *constricta*	SMI197 (as *A. constricta*)	HQ650724	–	Canada	Kranabetter *et al.* (2009)
	RET 666-3 (as *A.* sp. "*obconicobasis*")	MT073015	in ITS	United States	Tulloss *et al.*, pers. com.
	RET 665-7 (as *A.* sp. "*obconicobasis*")	OK076901	in ITS	United States	Tulloss *et al.*, pers. com.
Amanita corylophila Bozok, Taşkın, İsm. Şen & Assyov	FBozok1259 (holotype)	PP430369	–	Türkiye	Crous *et al.* (2024)
	FBozok1322	PP430370	PP434580	Türkiye	Crous *et al.* (2024)
Amanita fusca H. Lamb., Lebeuf & J. Landry	RET 180-10 (as *A.* sp. 44)	KY549349	–	United States	Tulloss *et al.*, pers. com.
	RET 655-2	OK299168	in ITS	United States	Tulloss *et al.*, pers. com.
Amanita griseocaerulea Migl. & Donato	DL2009071	PP375692	–	France	Varga *et al.* (2024)
	DL210908	PP375693		France	Varga *et al.* (2024)
	DL141120A	PP375691	PP375228	France	Varga *et al.* (2024)
	MV 20.86431	ON994667	–	Italy	Migliozzi & Donato (2022a)
	MV 21.5369 (holotype)	ON818545	–	Italy	Migliozzi & Donato (2022a)
Amanita nivalis Grev.	DAVFP29752 (as *A.* sp.)	OQ225654	OQ256222	Canada	Berch & Bazzicalupo, pers. com.
	DAVFP29751 (as *A.* sp.)	OQ225654	OQ256221	Canada	Berch & Bazzicalupo, pers. com.
	DB-2021-08-12-2	PP375690	PP375227	Norway	Varga *et al.* (2024)
	DB-2021-08-09-1	PP375689	PP375226	Norway	Varga *et al.* (2024)
	RET 877-7 (as *A.* sp.)	MW526933	–	Russia	Tulloss *et al.*, pers. com.
	YSU-F-13949 (as *A.* sp.)	PP277328	–	Russia	Gorbunova, pers. com.
	HK01.84	UDB002338	–	Russia	unpublished
	YSU-F-13931 (as *A.* sp.)	PP277307	–	Russia	Gorbunova, pers. com.
	RET 877-6	MW526934	in ITS	Russia	Tulloss *et al.*, pers. com.
	L0053705 (isoepitype)	–	AF024466	Scotland	Weiß *et al.* (1998)
Amanita sp.	clone d1 1Ama	JQ347155	–	China	Gao & Yang (2016)
	LEM950304a (as *A. vaginata*)	AB015691	–	Japan	Oda *et al.* (1999)
	LE 296455 (as *A.* aff. *battarrae*)	KM658300	KM658307	Russia	Malysheva & Kovalenko (2015)
	iNAT16442327	MZ197981	–	United States	Taylor, pers. com.
	iNAT52484303	OM004001	–	United States	Jakob, unublished
	RL6114A	GQ166890	–	United States	Avis *et al.*, pers. com.
	Mushr.Obs.329675 (as *A.* sp. 61)	MT357079	in ITS	United States	Clements, pers. com.
	RET 392-3 (as *A.* sp. 58)	MN650858	in ITS	United States	Tulloss *et al.*, pers. com.
Amanita sp. "*cyclops*"	RET 551-10	MT445428	in ITS	United States	Tulloss *et al.*, pers. com.
	RET 706-8	MG252695	MG252694	United States	Tulloss *et al.*, pers. com.
	RET 526-2	MW013158	in ITS	United States	Tulloss *et al.*, pers. com.
Amanita sp. "*longicuneus*"	RET 446-7	ON500640	in ITS	United States	Tulloss *et al.*, pers. com.
	RET 699-3B	KY580766	KY580764	United States	Tulloss *et al.*, pers. com.
	RET 720-9	MW538979	in ITS	United States	Tulloss *et al.*, pers. com.
Amanita sp. "*salmonriverensis*"	RET 715-6	MK569747	MK569741	United States	Tulloss *et al.*, pers. com.
	RET 479-3	MK569746	–	United States	Tulloss *et al.*, pers. com.
Amanita sponsa Hanss, Gasch & P.-A. Moreau	PAM18110302	OQ357631	–	Spain	Hanss & Moreau (2020)
	PAM18102001 (holotype)	OQ357630	–	Spain	Hanss & Moreau (2020)
	PAM18110301	PP375694	–	Spain	Varga *et al.* (2024)
	PAM18110303	OQ357629	–	Spain	Hanss & Moreau (2020)
Amanita variicolor Y.Lamoureux	CMMF-003787 (holotype)	MG734656	–	Canada	Lambert *et al.* (2018)



FIG. 2. — Representative specimens of *Amanita arroasiana* Hanss, Polesel, Zupan & Dima, sp. nov.: **A**, **B**, LJF8743, Slovenia, holotype; **C**, DB-2018-07-08-4 (Hungary); **D**, **H**, **I**, WU-Myc 00054129 (Austria); **E**, LIP0401331 (France); **F**, **G**, DB-2023-09-22-3 (Hungary). Photos credits: A, B, E. Zupan; C, F, G, B. Dima; D, H, I, G. Koller; E, P.-A. Moreau.

Lamellar edge
Not appearing to have any marginal cells but the upper row of basidia caught in a gelation.

Pileipellis
Ixocutis, remarkable for the 300-400 µm thick gelified part containing many free hyphae of 2-4 µm width, and cutis width only 40-50 µm; cutis only thickened up to 120 µm near the lamellae, and composed of 4-5 µm thick hyphae, parallel to each other, at first alone and then mixed with a few rare physaloid cells.

Context
Remarkably thin, of thickness proportional to the thickness of the cutis, only increased near the lamellae, varying from 50-200 µm, composed of often ovoid-physaloid cells, for example 33 × 60 µm or 20 × 35 µm, or elongated especially when acrophysalids, e.g., 30 × 110 µm or 13 × 100 µm. Physaloid cells fixed by hyphae 5-6 µm thick, rarely thinner.

Stipe wall
850 µm thick with an outer layer 100-200 µm thick, denser. The whole made up of an interlocking of more or less cylindrical, elongated acrophysalids of variable length, 60-300 µm, and width varying slightly 28-48 µm, terminating in hyphae (2)3-4 µm thick. On the outer stratum, a slight helical arrangement. The resulting material perfectly rigid.

Volva
900-1100 µm thick, with three strata. The middle stratum or main stratum, much wider than the others, having a structure similar to a crocea-type structure, i.e. with relatively distant from each other clusters, formed by physaloid cells, ovoid to subglobose (45-80 × 30-40 µm) towards which numerous hyphae (4-10 µm thick) and some cylindrical acrophysalids (25 × 80-90 µm). converging. Close to outer and inner layers, the clusters being tighter against each other. Outer stratum an ixocutis about 200 µm thick formed by thinner hyphae (2-4(5) µm thick) very weakly helicoidally arranged, in mixture with numerous ovoid or subglobose physaloid cells, weakly or not attached to the hyphae. The upper gelled, congophobic part, 40-80 µm thick and mainly composed of very thin hyphae (2-3 µm). The inner stratum about 100 µm thick composed of hyphae and physaloid cells of the same type as the main stratum but wrapped in a layer of hyphae, arranged in a spiral.

Remarks
The taxonomic status of *A. arroasiana* Hanss, Polesel, Zupan & Dima, sp. nov. on species level is unequivocally supported by nrITS-LSU sequence analysis of this study and the multilocus phylogeny of the nrITS, nrLSU, *RPB1* and TEF-1α DNA regions published by Varga *et al.* (2024, as *Amanita* sp. 3 in Fig. 3). The species is ecologically linked to the oak-hornbeam forests, as evidenced by our collections. Macroscopically, the colour of the pileus varies from cigar brown to beige, while the type II white volva is remarkable for its large beige lobes which tend to break easily at the base once the basidiomata are mature. Several more collections will help us to get a more complete understanding of the macroscopic variations of *Amanita arroasiana* Hanss, Polesel, Zupan & Dima, sp. nov. The species has a unique microscopic characteristics that allows it to be easily distinguished from all the other species of the sect. *Vaginatae*, a very thin pileus whose context thickness between the lamellae does not exceed 50 µm, a pileipellis, an almost dry ixocutis in the desiccated material, remarkable for the 300 to 400 µm thick layer of free, gelified hyphae, a stipe wall with two layers, a lamellar trama composed exclusively of hyphae, without physaloid cells, a unique subhymenium by its subhymenial cells with one or two lateral projections, type 1b, the resulting subhymenial tree usually forming several branches, suggesting that lateral projections on the subhymenial cell are budding (of basidia or branches). The volva has three distinct strata, the main or central stratum having a structure composed clusters of relatively distant from each other, a structure that we call a crocea-type structure which is also found for example in *A. amplivelata* (Hanss *et al.* 2024). To the best of our knowledge, we are unaware of any older formally described taxon identical or to highly similar to *A. arroasiana*. However, species whose pileus colour and habitat may match those of *A. arroasiana* include *A. lividopallescens*, *A. sublividopallescens*, *A. albogrisescens*, *A. alseides*, *A. fulvoides*, *A. griseocaerulea*, *A. opaca*, *A. spadicea*, and *A. suberis*. Excluding those with an incompatible volva type narrows the list to *A. albogrisescens*, *A. fulvoides*, *A. opaca*, *A. griseocaerulea*, and *A. suberis*. *Amanita fulvoides* typically presents rust-colored spots on the volva, while *A. opaca*, *A. griseocaerulea*, and *A. suberis* lack ochre coloration on the upper parts of the volva, effectively ruling them out. Furthermore, the microscopic features of *A. arroasiana* differ from these remaining species in three key parameters: volva structure, subhymenium, and lamellar trama.

DISCUSSION

Taxonomic notes on stirps *Nivalis*

The type species of stirps *Nivalis*, where *A. arroasiana* belongs to, is *A. nivalis* Grev. This species was originally found on the alpine grasslands of the Grampian Mountains in northern Scotland that is snow-covered for a hundred days a year. *Amanita nivalis* is usually considered as a white species with a pale ochraceous pileus centre according to Greville's text, and the illustration given in Greville's protologue shows a whitish *Amanita* with a wide, opened volva in its upper part (Greville 1823). On the website Amanitaceae.org (Tulloss & Yang 2025), the same plate is shown in a "foxed" version of the entire mushroom, including the volva. We have collections with bright ochraceous stained volvas but the colouring of the Tulloss plate is very strong. Greville's type material was lost, so another Scottish mycologist, Roy Watling proposed a neotype (Watling 1985) which was later considered as "not Code compliant", because original material (Greville's illustration, plate 18 in Greville 1823) has been available for

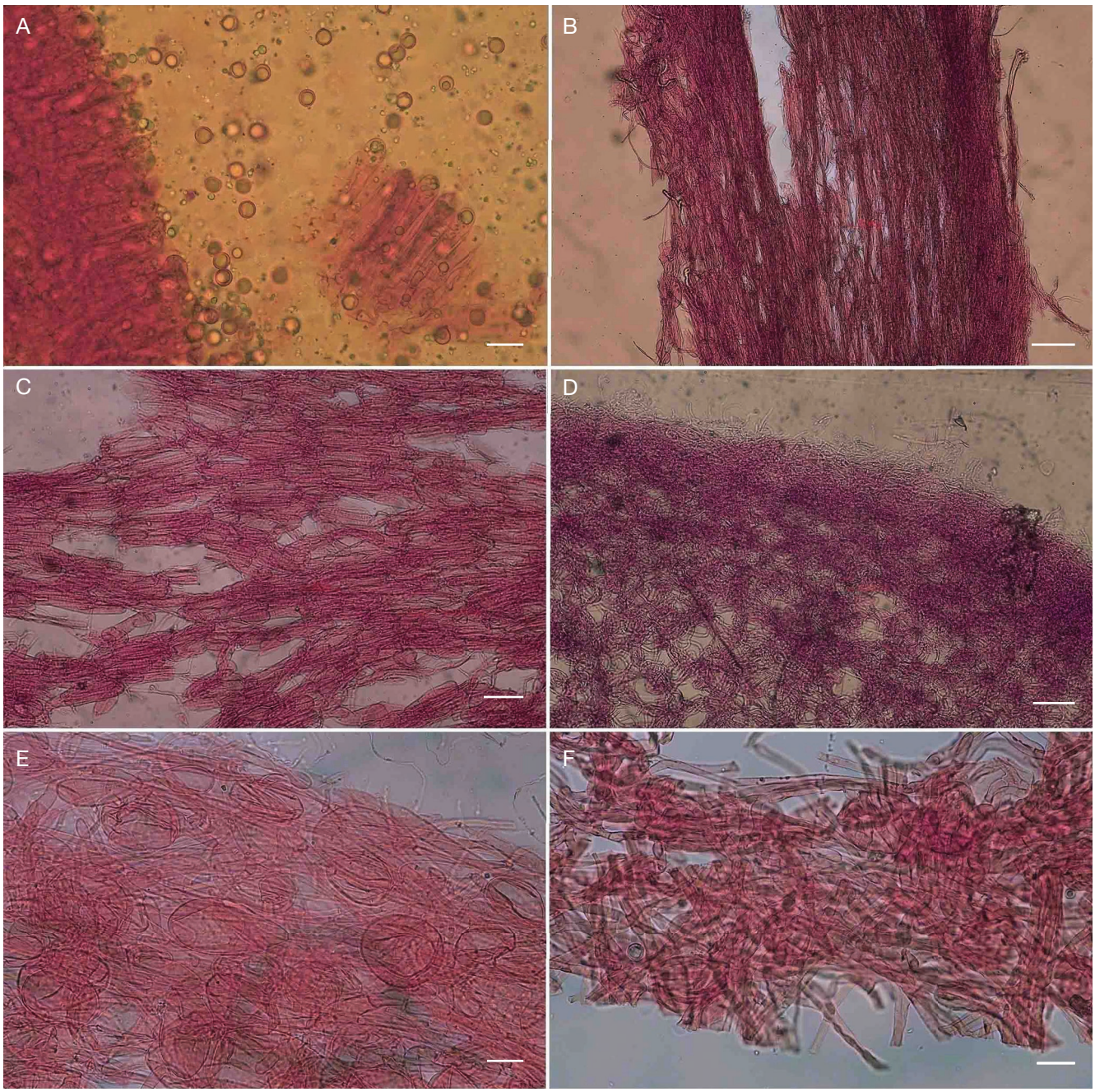

Fig. 3. — Characteristic microstructures of the newly described *Amanita arroasiana* Hanss, Polesel, Zupan & Dima, sp. nov. (collections DB 2018-07-08-4 and DB 2023-09-22-3): **A**, basidiospores; **B**, wall of stipe, general view; **C**, wall of stipe, detail of tissue; **D**, structure of volva, general view; **E**, structure of volva, external stratum; **F**, structure of volva internal stratum. Scale bars: A, C, E, F, 20 µm; B, D, 100 µm. Photos credits: J.-M. Hanss.

lectotypification (Shenzhen art. 9.12). Watling (1987) characterised *A. nivalis* as a *Vaginatae* species "relatively small, whitish to pale greyish buff with a prominent membranous sulcate volva". Recently, Tulloss *et al.* (2015) has lectotypified *A. nivalis* based on Greville's original illustration, and they proposed Watling's ineffective neotype as epitype. The morphology and phylogeny of this classical species need to be studied in more details in the future. The other European species of stirps *Nivalis* are *A. griseocaerulea* Migliozzi & Donato and *A. sponsa* Hanss, Gasch & P.-A. Moreau. *Amanita griseocaerulea* is an oak related species which has been found so far in the Lazio region of Italy, in the Normandy region of France, in Bulgaria (B. Assyov, pers. comm.) and in Spain. The pileus varies in colour, intense mauve, bluish, sepia brown or light brown, the white stem is often impregnated with blue, grey-blue or light grey, from the base. It is the microscopy of the volva that allows us to be recognized for sure: the filamentous side of the volva, with the very long hyphae forming numerous laces in the manner of a spaghetti dish, is to our knowledge unique among the *Vaginatae*. *Amanita sponsa*, found to date only in Andalusia, under holm oaks (*Quercus ilex*) and chestnut trees (*Castanea sativa*), is a

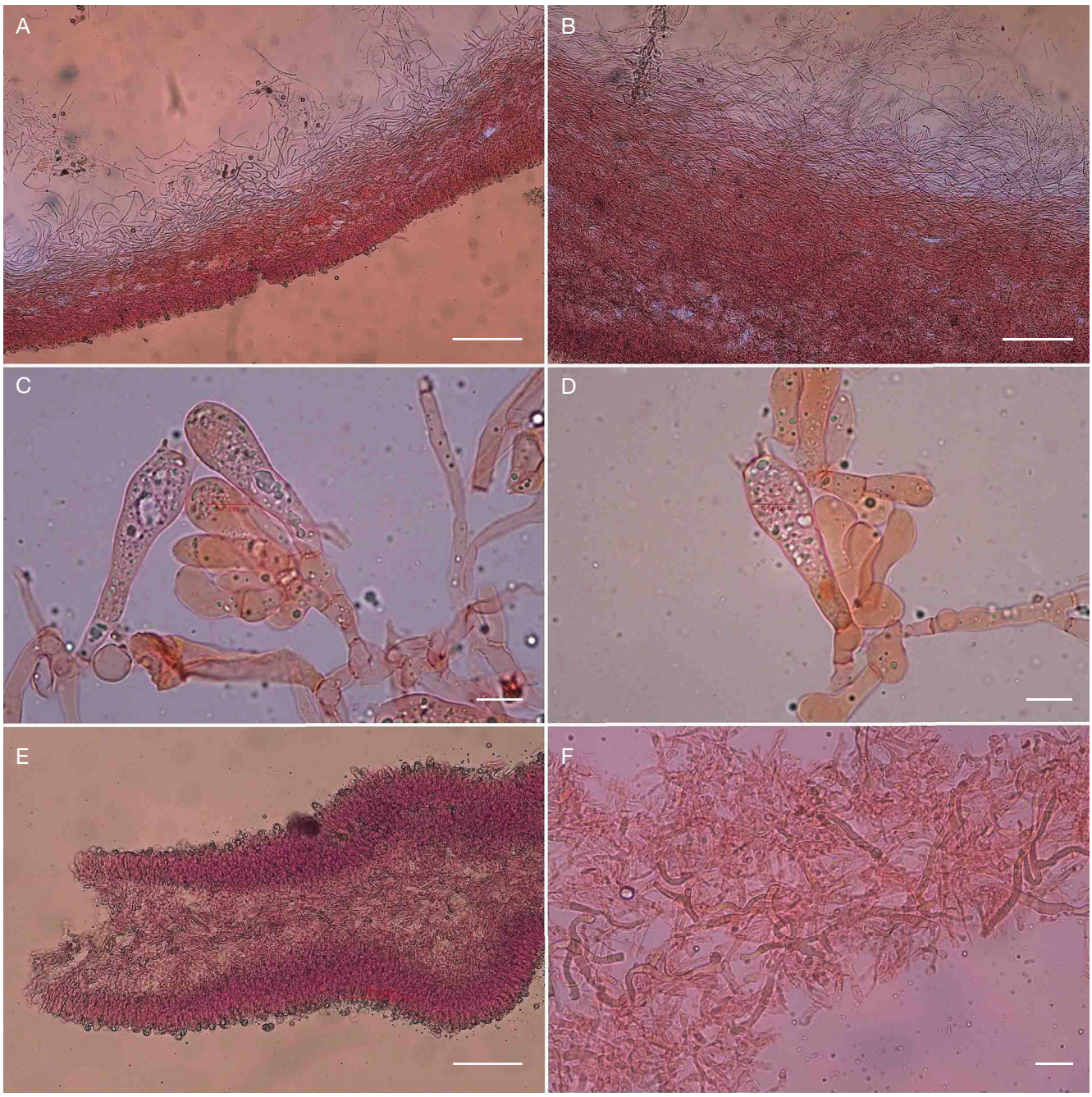

Fig. 4. — Characteristic microstructures of the newly described *Amanita arroasiana* Hanss, Polesel, Zupan & Dima, sp. nov. (collections DB 2018-07-08-4 and DB 2023-09-22-3): **A**, pileus, structure between two lamellae; **B**, pileus, above a lamella; **C**, subhymenial tree; **D**, subhymenial cells; **E**, lamellar trama, general structure; **F**, lamellar trama détail of the elements. Scale bars: A, B, E, 100 µm; C, D, 10 µm; F, 20 µm. Photos credits: J.-M. Hanss.

grey species in its youth that can be reminiscent of a non-silvery *A. argentea* that would turn brown with age. Here too, the microscopy of the volva allows it to be identified with certainty. The volva is covered by a gelled stratum 400 to 500 µm thick, the ungelified part has a banal structure of in all directions entangled hyphae and physaloid cells. The three species of the stirps *Nivalis* we studied (*Amanita arroasiana* Hanss, Polesel, Zupan & Dima, sp. nov., *A. griseocaerulea* and *Amanita sponsa*), have unique microscopic characterstics that make them identifiable in a reliable way.

Additions to microscopical observations

The microscopic methods applied in this study follow those described by Bas (1969), which are widely adopted by the current taxonomists of the genus. Thin sections reveal a striking histological variability of certain tissues which, combined with the observations of the basidiospores, subhymenium, edge of the lamellae, and macroscopic features, enables the development of identification keys for the European *Vaginatae* species. Such a key, focusing on species with silvery-grey pileus, can be found in Hanss & Moreau (2020).

In most cases, detailed microscopy is essential for resolving species identification in *Amanita* sect. *Vaginatae*. However, executing this properly, requires a good understanding of *Amanita* morphology, precise technique, and appropriate equipment for preparing adequate sections. During our study of numerous species, we observed that the angle of divergence of the physaloid elements in the lamellar trama decreases, sometimes to zero, during drying. Upon rehydration, it does not return to its initial value and may, in some cases, remain at zero. The hyphae in *Amanita* are generally hyaline, although they can exhibit a yellowish tint when grouped into large clusters. The pigment in *Amanita* is of vacuolar type (Kühner 1934; Kühner & Romagnesi 1951; Bas 1969). In living cells, the colour of the vacuoles is recommended to examine by plasmolysis. With age, the pigment precipitates, generally forming amorphous granules, more rarely crystals. For dried specimens, Kühner & Romagnesi (1951) recommended a two-step method to visualize the pigment. Additionally, in the universal and partial veils of certain species (e.g., those in Clade 4 in Hanss & Moreau 2020; Varga *et al.* 2024), the number of brown sphaerocysts increases with age. This accumulation causes blackening which may be due to a necropigment or colour changes resulting from the degeneration of hyphal contents. The volva of *Amanita* has highly variable microscopic structure (Yang & Oberwinkler 1999); it serves a crucial component of the universal veil, providing protection during the early development stages of the fungus. During the development of basidiomata in *Amanita* sect. *Vaginatae*, an annulus does not form; instead, the partial veil is distributed across the surface of the stipe and the inner surface of the middle and lower volva. Although the partial veil is structurally distinct from the universal veil, its presence can complicate the morphological interpretation of the universal veil. For this reason, we primarily study the structure of the upper part of the volva. At the base of the volva lies the limbus internus, the examination of which can also be informative. By preparing thin sections rather than squash mounts, we can observe the true composition of the volval elements, including their spatial arrangement, orientation, and degree of entanglement. This sectioning method yields significantly more information than crushing the tissue, a process that destroys the structural integrity and makes the original tissue arrangement impossible to recognize.

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REFERENCES

Altschul S. F., Gish W., Miller W., Myers E. W. & Lipman D. J. 1990. — Basic local alignment search tool. *Journal of Molecular Biology* 215 (3): 403-410. https://doi.org/10.1016/S0022-2836(05)80360-2

Armada F., Bellanger J.-M. & Moreau P.-A. 2023. — *Champignons de la zone alpine*. Federation mycologique et botanique Dauphine-Savoie, Annemasse, 376 p.

Bas C. 1969. — Morphology and subdivision of *Amanita* and a monograph of its section *Lepidella*. *Persoonia* 5 (4): 285-573.

Clémençon H. 1999. — Du (bon) usage du (bon) rouge congo. *Schweizerische Zeitschrift für Pilzkunde* 77 (5): 247-252.

Codjia J. E. I., Sánchez-Ramírez S., Ndolo Ebika S. T., Wu G., Margaritescu S., Komura D. L., Oliveira J. J. S., Ryberg M., Tulloss R. E., Yorou N. S., Moncalvo J.-M. & Yang Z.-L. 2023. — Historical biogeography and diversification of ringless *Amanita* (section *Vaginatae*) support an African origin and suggest niche conservatism in the Americas. *Molecular Phylogenetics and Evolution* 178: 107644. https://doi.org/10.1016/j.ympev.2022.107644

Crous P. W., Costa M. M., Kandemir H., Vermaas M., Vu D., Zhao L., [...] & Groenewald J. Z. 2023. — Fungal Planet description sheets: 1550-1613. *Persoonia* 51: 280-417. https://doi.org/10.3767/persoonia.2023.51.08

Crous P. W., Jurjević Z., Balashov S., De La Peña-Lastra S., Mateos A., Pinruan U., [...] & Groenewald J. Z. 2024. — Fungal Planet description sheets: 1614-1696. *Fungal Systematics and Evolution* 13: 183-440. https://doi.org/10.3114/fuse.2024.13.11

Cui Y.-Y., Cai Q., Tang L.-P., Liu J.-W. & Yang Z.-L. 2018. — The family *Amanitaceae*: molecular phylogeny, higher-rank taxonomy and the species in China. *Fungal Diversity* 91 (1): 5-230. https://doi.org/10.1007/s13225-018-0405-9

Drehmel D., Moncalvo J.-M. & Vilgalys R. 1999. — Molecular phylogeny of *Amanita* based on large-subunit ribosomal DNA sequences: implications for taxonomy and character evolution. *Mycologia* 91 (4): 610-618. https://doi.org/10.1080/00275514.1999.12061059

Fraiture A. 1993. — Les Amanitopsis d'Europe (genre *Amanita*, Agaricales, Fungi) – Synthèse critique de la littérature. *Opera Botanica Belgica* 5: 1-128.

Gao Q. & Yang Z. L. 2016 — Diversity and distribution patterns of root-associated fungi on herbaceous plants in alpine meadows of southwestern China. *Mycologia* 108 (2): 281-291.

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

Gilbert E.-J. 1941. — Amanitaceae. *Iconographia Mycologica* 27 (suppl. 1-3): 1-427, 73 pl.

Gouy M., Tannier E., Comte N. & Parsons D. P. 2021. — Seaview version 5: a multiplatform software for multiple sequence alignment, molecular phylogenetic analyses, and tree reconciliation, *in* Katoh K. (ed). *Multiple Sequence Alignment. Methods in Molecular Biology.* Vol. 2231. Humana, New York: 241-260. https://doi.org/10.1007/978-1-0716-1036-7_15

Greville R. K. 1823. — *Scottish cryptogamic Flora*. MacLachlan & Stewart, Edinburgh, Baldwin, Cradock & Joy, London, 1 (1-6): pl. 18.

Gruhn G., Dumez S., Moreau P.-A., Roy M., Morreale O., Schimann H. & Courtecuisse R. 2017. — The genus *Resinicium* in French Guiana and the West Indies: a morphological and molecular survey, revealing *Resinicium grandisporum* sp. nov. *Cryptogamie Mycologie* 38 (4): 469-483. https://doi/10.7872/crym/v38.iss4.2017.1

Guindon S., Lethiec F., Duroux P. & Gascuel O. 2010. — PHYML Online – a web server for fast maximum likelihood-based phylogenetic inference. *Nucleic Acids Research* 33 (issue suppl_2): W557-W559. https://doi.org/10.1093/nar/gki352

Hanss J.-M. & Moreau P.-A. 2020. — Une révision des Amanites "vaginées" (*Amanita* sect. *Vaginatae*) en Europe. 1ère partie: quelques amanites argentées. *Bulletin de la Société Mycologique de France* 133 (1-2): 67-141.

Hanss J.-M. & Moreau P.-A. 2022. — Une révision des Amanites "vaginées" (*Amanita* sect. *Vaginatae*) en Europe. 2e partie: validations et typifications. *Bulletin de la Société Mycologique de France* 138 (3-4): 249-250.

Hanss J.-M., Bozok F., Assov B., Yarar M., Borovička J., Ševčíková H., Corriol G., Moreau P.-A. & Taşkin H. 2024. — *Amanita amplivelata* (*Amanitaceae*, *Agaricales*), a remarkable new Eurasian species of the section V*aginatae*. *Phytotaxa* 660 (1): 1-21. https://doi: 10.11646/phytotaxa.660.1.1

Illescas T. 2023. — *Amanita meridioceciliae* sp. nov., un nuevo taxón mediterráneo perteneciente a *Amanita* series Ceciliae. *Revista Catalana de Micologia* 43: 111-123.

Illescas T. & Plaza M. 2022. — *Amanita calida* sp. nov., una nueva especie europea de *Amanita* sect. *Vaginatae*. *Fungi Iberici* 2: 41-54.

Katoh K. & Standley D. M. 2013. — MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30 (4): 772-780. https://doi: 10.1093/molbev/mst010

Kim C. S., Jo J. W., Kwag Y. N., Oh J., Shrestha B., Sung G. H. & Han S. K. 2013. — Four newly recorded *Amanita* species in Korea: *Amanita* sect. *Amanita* and sect. *Vaginatae*. *Mycobiology* 41 (3): 131-138. https://doi.org/10.5941/MYCO.2013.41.3.131

Kranabetter J. M., Friesen J., Gamiet S. & Kroeger P. 2009. — Epigeous fruiting bodies of ectomycorrhizal fungi as indicators of soil fertility and associated nitrogen status of boreal forests. *Mycorrhiza* 19 (8): 535-548.

Kumar S., Stecher G. & Tamura K. 2016. — MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. *Molecular Biology and Evolution* 33 (7): 1870-1874. https://doi.org/10.1093/molbev/msw054

Kühner R. 1934. — Observations sur la localisation cytologique des substances colorées chez les agarics et les bolets. *Le Botaniste* 26: 347-369.

Kühner R. & Romagnesi H. 1951. — *Flore analytique des Champignons supérieurs*. Masson et Cie éditeurs, Paris: 176-177.

Lambert H., Fortin G., Labbé R., Labrecque J., Bérubé J. A., Landry J., Ilyukhin E., Margaritescu S., Moncalvo J.-M. & Lamoureux Y. 2018. — Validation of two *Amanita* species from eastern North America: *A. rhacopus* sp. nov. and *A. variicolor* sp. nov. *MycoKeys* 38: 47-57. https://doi.org/10.3897/mycokeys.38.27041

Liu J.-W., Cai Q., Cui Y.-Y. & Yang Z.-L. 2017. — *Amanita cingulata*, a new annulate species of *Amanita* sect. *Vaginatae* from subtropical China. *Phytotaxa* 326 (1): 41-53. https://doi.org/10.11646/phytotaxa.326.1.3

Malysheva E. F. & Kovalenko A. E. 2015. — Fungi of the Russian Far East. 4. Contribution to the study of *Amanita* sect. *Vaginatae* in the central Sikhote-Alin. *Mikologiya i Fitopatologiya* 149: 151-163.

Migliozzi V. & Donato G. 2022a. — *Amanita* section *Vaginatae* in Lazio. First contribution. Institution of *Amanita griseocaerulea* sp. nov., description of *Amanita fulvoides* and *Amanita huijsmanii*. *Mycological Observations* 5: 11-38.

Migliozzi V. & Donato G. 2022b. — Nomenclatural novelties. *Index Fungorum* 527: 1.

Migliozzi V. & Di Palma F. 2024. — Cinque nuove entità di *Amanita* Sezione V*aginatae*, rinvenute in Italia centrale. *Bollettino del Circolo Micologico "G. Carini"* 87: 3-14.

Oda T., Tanaka C. & Tsuda M. 1999. — Molecular phylogeny of Japanese *Amanita* species based on nucleotide sequences of the internal transcribed spacer region of nuclear ribosomal DNA. *Mycoscience* 40 (1): 57-64. https://doi.org/10.1007/BF02465674

Plaza M. 2022. — Nueva aportación europea al estudio de Amanita sect. Vaginatae: *Amanita prudens* sp. nov. *Boletín Informativo Sociedad Micológica Extremeña* 22: 3-12.

Polesel G. 2020. — *Contribution à l'inventaire mycologique de la Forêt Domaniale d'Andigny (Aisne). Analyse fonctionnelle et patrimoniale.* Thèse pour le Diplôme d'Etat de Docteur en Pharmacie. Université de Lille, 466 p.

Redhead S. A., Vizzini A., Drehmel D. C. & Contu M. 2016. — *Saproamanita*, a new name for both *Lepidella* E.-J. Gilbert and *Aspidella* E.-J. Gilbert (*Amaniteae*, *Amanitaceae*). — *IMA Fungus* 7 (1): 119-129. https://doi.org/10.5598/imafungus.2016.07.01.07

Royal Botanic Garden Edinburgh 1969. — *Flora of the British fungi: colour identification chart*. HMSO, Edinburgh, 4 p.

Ševčíková H., Hanss J.-M. & Moreau P.-A. 2021. — *Amanita vladimirii* (*Amanitaceae, Agaricales*), a new European species in section *Vaginatae*. *Phytotaxa* 482 (2): 159-172. https://doi.org/10.11646/phytotaxa.482.2.4

Singer R. 1986. — The *Agaricales* in modern taxonomy, 4th edn. Koeltz Scientific Books, Koenigstein, 981 p.

Tang L. P., Cai Q., Lee S., Buyck B., Zhang P. & Yang Z.-L. 2015. — Taxonomy and phylogenetic position of species of *Amanita* sect. *Vaginatae* s. l. from tropical Africa. *Mycological Progress* 14 (39): 1-15. https://doi.org/10.1007/s11557-015-1061-z

Thongbai B., Hyde K. D., Lumyong S. & Raspé O. 2018. — High undescribed diversity of *Amanita* section *Vaginatae* in northern Thailand. *Mycosphere* 9 (3): 462-494. https://doi.org/10.5943/mycosphere/9/3/3

Tulloss R. E., Rodríguez-Caycedo C., Hughes K. W., Geml J., Kudzma L. V., Wolfe B. E. & Arora D. 2015. — Nomenclatural changes in *Amanita*. II. *Amanitaceae* 1 (2): 1-6.

Tulloss R. E., Kuyper T., Vellinga E. C., Yang Z.-L., Halling R. E., Geml J., Sanchez-Ramírez S., Goncalves S. C., Hess J. & Pringle A. 2016. — The genus *Amanita* should not be split. *Amanitaceae* 1 (3): 1-16.

Tulloss R. E. & Yang Z.-L. (eds). 2025. — Studies in the *Amanitaceae*. https://amanitaceae.mushroomobserver.org [Accessed 2 July 2026].

Ullah S., Wilson A. W., Tulloss R. E., Fiaz M., Mueller G. M. & Khalid A. N. 2019. — *Amanita cinis* and *A. olivovaginata* (Basidiomycota, Amanitaceae), two new species, and the first record of *A. emodotrygon*, from Northwestern Pakistan. *Turkish Journal of Botany* 43: 1-19. https://doi.org/10.3906/bot-1903-21

Varga D., Hanss J.-M., Moreau P.-A., Kovács G. M. & Dima B. 2024. — Phylogenetic and morphological studies reveal large diversity and three new species in *Amanita* sect. *Vaginatae* (Agaricales, Basidiomycota) from Europe. *Mycological Progress* 23: 38. https://doi.org/10.1007/s11557-024-01974-0

Vilgalys R. & Hester M. 1990 — Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* 172 (8): 4238-4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

VIZZINI A., ZOTTI M., TRAVERSO M., ERCOLE E., MOREAU P.-A., KIBBY G., CONSIGLIO G., CULLINGTON P., ARDRON P., MOINGEON J.-M. & PEINTNER U. 2016. — Variability, host range, delimitation and neotypification of *Amanita simulans* (*Amanita* section *Vaginatae*): collections associated with *Helianthemum* grasslands, and epitypification of *A. lividopallescens*. *Phytotaxa* 280 (1): 1-22. https://doi.org/10.11646/phytotaxa.280.1.1

WATLING R. 1985. — Observations of *Amanita nivalis* Greville. *Agarica* 6 (12): 327-335.

WATLING R. 1987. — Larger arctic-alpine fungi in Scotland, *in* LAURSEN G. A., AMMIRATI J. A. & REDHEAD S. A. (eds), *Arctic and Alpine Mycology* II, Springer Science and Business Media, New York, 364 p.

WEISS M., YANG Z.-L. & OBERWINKLER F. 1998. — Molecular phylogenetic studies in the genus *Amanita*. *Canadian Journal of Botany* 76 (7): 1170-1179. https://doi.org/10.1139/cjb-76-7-1170

WHITE T. J., BRUNS T., LEE S. & TAYLOR J. 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*. Academic Press, New York: 315-322.

YANG Z.-L. 1997. — Die *Amanita*-Arten von Südwestchina. *Bibliotheca Mycologia* 170: 1-240.

YANG Z.-L. & OBERWINKLER F. 1999. — Die Fruchtkörperentwicklung von *Amanita muscaria* (Basidiomycetes). *Nova Hedwigia* 68 (3-4): 441-468.

YANG Z.-L., CAI Q. & CUI Y. Y. 2018. — Phylogeny, diversity and morphological evolution of *Amanitaceae*. *Biosystematics and Ecology Series* 34: 359-380.

ZHANG L. F., YANG J. B. & YANG Z.-L. 2004. — Molecular phylogeny of eastern Asian species of *Amanita* (Agaricales, Basidiomycota): taxonomic and biogeographic implications. *Fungal Diversity* 17: 219-238.

ZHANG P., TANG L. P., CAI Q. & XU J. P. 2015. — A review on the diversity, phylogeography and population genetics of *Amanita* mushrooms. *Mycology* 6 (2): 86-93. https://doi.org/10.1080/21501203.2015.1042536

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APPENDIX

APPENDIX 1. — See detailed ITS-LSU alignment here: https://sciencepress.mnhn.fr/sites/default/files/documents/en/mycologie2026v47a9_s1.pdf; https://doi.org/10.5252/cryptogamie-mycologie2026v47a9_s1.