

# Fungal Systematics and Evolution: FUSE 10

Herman Lambert<sup>1</sup>, İsmail Acar<sup>2</sup>, Ayten Dizkirici Tekpınar<sup>3</sup>, Guy Fortin<sup>1</sup>, Nataliya Ivanushkina<sup>4</sup>, Karin Jacobs<sup>5</sup>, Yves Lamoureux<sup>1</sup>, Jacques Landry<sup>1</sup>, Renée Lebeuf<sup>1</sup>, Aleksey Kachalkin<sup>4,6</sup>, Aysenur Kalmer<sup>3</sup>, Jean-Marc Moncalvo<sup>7</sup>, André Paul<sup>1</sup>, Breyten Van der Merwe<sup>5</sup>, Justin Williams<sup>8</sup>, Georgios I. Zervakis<sup>9</sup>, Galina Kochkina<sup>4</sup>, Mikhail Vainshtein<sup>4</sup>, Bálint Dima<sup>10</sup>, Francesco Dovana<sup>11</sup>, Giuliano Ferisin<sup>12</sup>, Ekaterina Malysheva<sup>13</sup>, Viktor Papp<sup>14</sup>, Hana Ševčíková<sup>15</sup>, Irmgard Krisai-Greilhuber<sup>16</sup> & Danny Haelewaters<sup>17,18</sup>

<sup>1</sup> MycoQuébec, 1313 rue Louis-Francoeur, Québec, QC G1Y 1N7, Canada

<sup>2</sup> Department of Organic Agriculture, Başkale Vocational High School, Van Yüzüncü Yıl University, 65080 Van, Türkiye

<sup>3</sup> Department of Molecular Biology and Genetics, Faculty of Science, Van Yüzüncü Yıl University, 65080 Van, Türkiye

<sup>4</sup> All-Russian Collection of Microorganisms, G.K. Skryabin Institute of Biochemistry and Physiology of Microorganisms, Pushchino Center for Biological Research of the Russian Academy of Sciences, 142290 Pushchino, Russia

<sup>5</sup> Department of Microbiology, Stellenbosch University, 7602 Stellenbosch, South Africa

<sup>6</sup> M.V. Lomonosov Moscow State University, 119234 Moscow, Russia

<sup>7</sup> Department of Natural History, Royal Ontario Museum & Department of Ecology and Evolutionary Biology, University of Toronto, Ontario M5S 2C6, Canada

<sup>8</sup> 8001 Cape Town, South Africa

<sup>9</sup> Laboratory of General and Agricultural Microbiology, Agricultural University of Athens, 11855 Athens, Greece

<sup>10</sup> Department of Plant Anatomy, Institute of Biology, Eötvös Loránd University, 1117 Budapest, Hungary

<sup>11</sup> Dipartimento di Bioscienze, Biotecnologie e Ambiente, Campus Universitario “Ernesto Quagliariello”, Università degli Studi di Bari Aldo Moro, 70125 Bari, Italy

<sup>12</sup> Associazione Micologica Bassa Friulana, 33052 Cervignano del Friuli, Italy

<sup>13</sup> Komarov Botanical Institute of the Russian Academy of Sciences, 197022 Saint-Petersburg, Russia

<sup>14</sup> Institute of Horticultural Plant Biology, Szent István University, 1118 Budapest, Hungary

<sup>15</sup> Department of Botany, Moravian Museum, 659 37 Brno, Czechia

<sup>16</sup> Department of Botany and Biodiversity Research, Vienna University, 1030 Wien, Austria

<sup>17</sup> Research Group Mycology, Department of Biology, Ghent University, 9000 Ghent, Belgium

<sup>18</sup> Faculty of Science, University of South Bohemia, 370 05 České Budějovice, Czechia

\* e-mail: danny.haelewaters@gmail.com

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In this 10<sup>th</sup> contribution to the Fungal Systematics and Evolution series published by *Sydowia*, 14 species are formally described: *Amanita cingulatoides* from Canada, *A. confundens*, *A. elongatior*, *A. fusca*, *A. fuscozonata*, *A. leptorhacopus*, *A. magna*, *A. olivaceodisca*, *A. piceina*, *A. pulla*, and *A. quercifulva* from Canada and the USA, *Hebeloma uzunii* from Türkiye, *Pleurotus overstrandensis* from South Africa, and *Saksenaea ozerskayae* from Russia. *Pluteus keselakii* is reported for the first time from Czechia and Slovenia. Three invalidly published names are validated with corrected typification: *Cortinarius balteatoindicus*, *C. indopurpurascens*, and *C. ulkhagarhiensis*. Finally, *Thaxterogaster shoreae* is combined into *Cortinarius*.

Keywords: Agaricomycetes, Amanitaceae, Cortinariaceae, Hymenogastraceae, Mucoromycetes, Pleurotaceae, Pluteaceae. – 14 new species, 1 new record, 3 validations, 1 new combination.

## Materials and methods

Sample collection, isolation, and specimen examination

*Amanita* Pers. collections were photographed in situ and/or in the lab, and their macromorphological features were derived from both field notes and pictures. Color codes used are those of Kornerup & Wanscher (1978). Microscopic studies were per-

formed on exsiccatae rehydrated in 3 % ammonia and examined as is, in water or in SDS Congo Red. Melzer’s reagent was used to check amyloidity. Lactophenol Cotton Blue was used to assess cyanophily. Microscopic elements were studied using a Leitz Ortholux II, an Olympus CH-2 or a Nikon Labophot equipped with digital camera and were measured with a calibrated micrometric reticule or from pictures using Piximetre version 5.10 (ACH logiciel),

France). Dimensions of basidiospores are given as: [a/b/c] (min )D1 D9(max), where a = number of measured spores, b = number of studied basidiomata, and c = number of studied collections; min and max are the extreme values of the distribution; and D1 and D9 are the first and ninth decile. Q denotes the length/width ratio of basidiospores in side view, and Qm refers to the arithmetical mean. Lamellar trama dimensions were measured according to Hanss & Moreau (2017). Universal veil was studied on the volval part free from the stipe except when indicated. Collections are deposited in public fungaria (CMMF and QFB) or are kept in the private fungaria of Herman Lambert (collections labelled as HL) or Renée Lebeuf (collections labelled as HRL) when not otherwise indicated.

Fresh basidiomata of *Hebeloma* (Fr.) P. Kumm. were collected during the Apri-May rainy seasons of 2020 and 2021 in Genç forest, Murat River Basin, Bingöl district. Collected samples were dried and deposited in the Fungarium of Van Yüzüncü Yıl University (VANF). The specimens were characterized morphologically using the terminology of Vesterholt (2005) and Beker et al. (2016). Macroscopic descriptions of basidiomata were made based on field notes and color photographs made with a Canon (EOS 60D) camera equipped with Tokina 100 mm macro lens. For each specimen at least 45 spores were measured in Melzer's reagent. The length and width of each spore was measured and its Q value (ratio of length to width) calculated. Average length, width and Q value were calculated and recorded. The assessment of spore characters follows Vesterholt (2005): spore ornamentation on a scale from O0 (smooth) to O4 (ornamentation fairly strong, and always visible without immersion), the loosening of the perispore P0 (not loosening) to P3 (strongly and constantly loosening) and the dextrinoidity of the spores in Melzer's reagent from D0 (indextrinoid) to D4 (strongly dextrinoid, immediately becoming dark brick to dark reddish brown). Microscopic features were examined using a Leica DM500 research microscope and measured with the Leica Application Suite (version 3.4.0) programme. Scanning electron microscope (SEM) microphotographs of basidiospores were taken using a ZEISS GeminiSEM.

*Pleurotus* (Fr.) P. Kumm. basidiomata were collected from several sites near the town of Gansbaai in the Overberg region of South Africa in April 2023. Specimens were photographed *in situ* and their macromorphological features were described. Specimens were collected and preserved for further study by maintaining them at 37 °C until they were entirely dehydrated. The micromorphology was exam-

ined by rehydrating the collected specimens in 3 % KOH and fixing them to slides using Shears mounting fluid. Some structures were enhanced using Congo Red. The basidiospores, cheilocystidia, basidia, and sterigmata were measured using a Nikon Eclipse E800 microscope, with a CFI plain Apochromat VC 100× lens. No fewer than 20 examples of each feature were examined and measured at 1000× magnification. Basidiospores were selected at random and measured in length (L) and width (W); their measurements are presented as La–Lb–Lc × Wa–Wb–Wc, with Xa = the lowest value, Xb = average of the measurements, and Xc = the highest value. The spore mean quotient (Q) is given as Lb over Wb. Cheilocystidia and basidia were measured in length and width.

The *Saksena* S.B. Saksena strain was obtained from an ascoma of the commercial product “Piedmont white truffle” (*Tuber magnatum* Picco) purchased from a trading company. For surface sterilization, the ascoma was immersed in 96 % ethanol for 2 min and then rinsed with sterile distilled water. The outer layers of the truffle were cut with sterile scalpels. Next, fragments of the inner part of the ascoma were sterilely excised and transferred to the surface of malt extract agar (MEA) supplemented with lactic acid (0.4 vol %) for elimination of bacteria and grown at 28 °C. A series of passages were carried out to check the purity. The absence of bacterial contamination was checked on rich medium – Plate Count Agar (Difco, Waltham, Massachusetts). The following nutrient media were used during morphological studies: MEA, Potato dextrose agar (PDA), Czapek's agar (CZA), and oatmeal agar (OA).

The macroscopic description of *Pluteus keselakii* Ševčíková, P.-A. Moreau & Borovička is based on observations of fresh specimens. The micro-morphological characteristics are based on the study of fresh and dried material. Dry specimens were rehydrated in distilled water or 10 % KOH before observation and mounted in aqueous Congo Red. Colors of microscopic characteristics were studied in water. Q indicates the quotient of length and width of the spores in sideview. In the basidiospore dimension notation, (a)b–c–d(e), b–d is the range including 95 % of the measured values, c is the average value, and (a) and (e) represent the extreme values. Q represents the range of the length/width ratio for all measured spores. For all microscopic structures, 30 elements were measured. Voucher specimens are deposited at GDOR (Museo Civico di Storia Naturale Giacomo Doria, Genova, Italy) and BRNM (Moravian Museum, Brno, Czechia). The drawings in Fig. 33 were edited in GNU Image Manipulation Program (GIMP) version 2.10.2.

DNA extraction, PCR amplification, and sequencing

For the *Amanita* study, all DNA extractions, PCR amplifications, and Sanger sequencing of newly generated nuclear ribosomal internal transcribed spacer (ITS) sequences were conducted in the Mycology Laboratory at the Royal Ontario Museum following the protocol established by Dentinger et al. (2010) or were outsourced to the Canadian Centre for DNA Barcoding (<https://ccdb.ca>). The generated chromatograms were visually examined and edited with 4Peaks software (<https://nucleobytes.com/4peaks/index.html>), as necessary. The finalized sequences were deposited in the National Center for Biotechnology Information (NCBI) GenBank database (<https://www.ncbi.nlm.nih.gov/genbank/>).

For the *Hebeloma* study, DNA was extracted from dried specimens following the procedure Doyle and Doyle (1987). Primer pairs N-nc18S10(F)/C26A(R) (Wen & Zimmer 1996), and EF1-983F/EF1-1567R (Rehner & Buckley 2005) were used to amplify the ITS and translation elongation factor 1- $\alpha$  gene (*tef1*), respectively. PCR was performed in 25  $\mu$ l volume per reaction. Cycling conditions were as follows: initial denaturation at 95 °C for 4 min; followed by 30 cycles of denaturation at 94 °C for 1 min, annealing at 55 °C (ITS) or 54 °C (*tef1*) for 1 min, and extension at 72 °C for 1 min; and final extension at 72 °C for 5 min. Amplification success was confirmed by agarose (1 %) gel electrophoresis. Sequencing of the amplified products was outsourced, using an ABI 3730XL automated sequencer (BM Labosis, Ankara, Türkiye).

For the *Pleurotus* study, total genomic DNA was extracted from four dried basidiomata, using the ZR Quick-DNA Fungal/Bacterial Miniprep Kit (Zymo Research, Irvine, California), following manufacturer's instructions. About 10 mg of the dried basidioma was used per extraction. Successful DNA extractions were visualized on a 1 % agarose gel stained with ethidium bromide. The extracted DNA was kept at -20 °C until PCR was performed. The ITS and the large subunit (LSU) ribosomal RNA gene were targeted using the universal primers ITS1/ITS4 (White et al. 1990) and LR0R/LR5 (Vilgalys & Hester 1990, Hopple 1994), respectively. PCR amplification and sequence reactions were run in accordance with Van der Merwe et al. (2023). Successful sequence reactions were sent for analysis at the Central Analytical Facilities (CAF) and analyzed using an ABI3730xl sequencer (CAF, Stellenbosch University). The ends of the generated sequences were trimmed for quality control using

Chromas 2.6.6 (Technelysium, South Brisbane, Australia). The ITS and LSU sequences were deposited in GenBank (Tab. 1).

Genomic DNA was isolated from the monosporic culture of the *Saksenaea* strain following the protocol from Glushakova et al. (2016). The ITS region and D1/D2 domains of the LSU rDNA were amplified using the primer pair ITS1f/LR5 (White et al. 1990, Gardes & Bruns 1993), and sequenced using the same primers and internal primer ITS4. Amplification and sequencing of the *tef1* gene was performed with the primer pair EF1-983F/EF1-1567R (Rehner & Buckley 2005). The polymorphic PCR products of ITS and *tef1* were cloned into the pAL2-T vector and sequenced. Sequencing of amplified (LSU) and amplified and cloned (ITS and *tef1*) regions was outsourced to Evrogen JSC (Moscow, Russia). The obtained sequence reads were assembled with DNA Baser Sequence Assembler 4 (Heracle BioSoft S.R.L., Pitești, Romania). The newly generated sequences were deposited in GenBank (Tab. 1).

DNA was extracted from dried *Pluteus keselakii* basidiomata with a CTAB protocol (Doyle & Doyle 1987) and the Phytosorb Kit (ZAO Syntol, Moscow, Russia), following the manufacturer's instructions. The ITS region was amplified with primer pair ITS1F/ITS4 (White et al. 1990, Gardes & Bruns 1993). Raw sequence reads were assembled and edited in Geneious version 11.1.5 (Kearse et al. 2012) and then submitted to GenBank (Tab. 1).

#### Phylogenetic analyses

Newly generated ITS sequences from *Amanita* sect. *Vaginatae* were supplemented with closely related sequences as retrieved from BLAST searches in NCBI GenBank and UNITE, and with sequences of selected species in respective clades of section *Vaginatae* as circumscribed by Varga et al. (2024), Hanns & Moreau (2017) and Codjia et al. (2023). Sequence alignments were performed using MUSCLE (Edgar 2004) and manually adjusted using MEGA version 11 software (Tamura et al. 2021). MEGA11 with default settings was used to infer sequences' relatedness, following the Maximum Likelihood (ML) method and the Tamura-Nei model (Tamura & Nei 1993). ML bootstrap (MLBS) analyses were performed with 100 replicates.

Eight new sequences were generated for the *Hebeloma* study (Tab. 1). ITS and *tef1* sequences were aligned separately using MAFFT version 7.221 (Kato & Standley 2013) and subsequently processed with CLUSTALW (Larkin et al. 2007). Ambiguous

**Tab. 1.** Details of sequences and isolates included in the BLAST searches and phylogenetic analyses for the new species and interesting reports.

Species name	ID (status, strain, isolate, voucher)	Country, isolation source	ITS	LSU	TEFI	Reference(s)
<i>Amanita</i> aff. <i>fulva</i>	HL144-QFB33056	Canada	PP762869			This study
<i>Amanita</i> aff. <i>fulvoides</i>	McN3389-CMMF005521	Canada	PP762920			This study
<i>Amanita</i> aff. <i>lignitincta</i>	LE 296457	Russia	KM658292			Malysheva & Kovalenko (2015)
<i>Amanita</i> aff. <i>lignitincta</i>	LE 296454	Russia	KM658297			Malysheva & Kovalenko (2015)
<i>Amanita</i> <i>albidostipes</i>	HKAS95189	China	MH508501			Cui (2023)
<i>Amanita</i> <i>albidostipes</i>	HKAS 57358, T	China	NR_159585			Cui (2023)
<i>Amanita</i> <i>albogriseascens</i> f. <i>subglobispora</i>	JMH2015020, T	France	MIN490648			Hanss & Moreau (2017)
<i>Amanita</i> <i>alseides</i>	JMH2015021, T	France	MIN490649			Hanss & Moreau (2017)
<i>Amanita</i> <i>annulata</i>	MHKMU L.P.Tang 1671	China	MZ005574			Zhang (2021)
<i>Amanita</i> <i>annulata</i>	MHKMU L.P.Tang 1730	China	MZ005573			Zhang (2021)
<i>Amanita</i> <i>argentea</i>	JMH2014015	France	MIN490675			Hanss & Moreau (2017)
<i>Amanita</i> <i>basiana</i>	RET 308-4	Italy	KP258986			R.E. Tulloss et al., unpubl.
<i>Amanita</i> <i>beckeri</i>	JMH2015027	France	MIN490686			Hanss & Moreau (2017)
<i>Amanita</i> <i>beckeri</i>	SOMF30422	Bulgaria	ON287053			Assyov (2022)
<i>Amanita</i> <i>betulae</i>	G:P Neville 02091911a, T	France	MIN490668			Hanss & Moreau (2017)
<i>Amanita</i> <i>betulae</i>	HL203A	Canada	PP464307			This study
<i>Amanita</i> <i>brunneofuliginea</i> f. <i>ochraceomaculata</i>	G:P Neville 97071327a, T	Italy	MIN490673			Hanss & Moreau (2017)
<i>Amanita</i> <i>brunneofuliginea</i> f. <i>ochraceomaculata</i>	JMH2018005	France	MIN490660			Hanss & Moreau (2017)
<i>Amanita</i> <i>brunneofuliginea</i> f. <i>ochraceomaculata</i>	PAMI6082703	France	MIN490688			Hanss & Moreau (2017)
<i>Amanita</i> <i>brunneoumbonata</i>	BZ2015_67	Thailand	MF461579			Thongbai (2018)
<i>Amanita</i> <i>calida</i>	JA-CUSSTA 9325	Spain	OK316926			Illescas & Plaza (2022)
<i>Amanita</i> <i>calida</i>	JA-CUSSTA 9324, T	Spain	OK316924			Illescas & Plaza (2022)
<i>Amanita</i> <i>ceciliae</i>	JV05-394	Denmark	UDB002315*			Varga et al. (2024)
<i>Amanita</i> <i>ceciliae</i>	JMM20180914	France	MIN490692			Hanss & Moreau (2017)
<i>Amanita</i> cf. <i>vaginata</i>	TRTC157298	USA	ON392631			J.M. Moncalvo & S. Margaritescu, unpubl.
<i>Amanita</i> <i>cingulata</i>	HKAS 75600, T	China	NR_159585			Liu (2017)
<i>Amanita</i> <i>cingulata</i>	HKAS:100640	China	MF952721			Liu (2017)
<i>Amanita</i> <i>cingulatoides</i>	HL075a	Canada	PP762812			This study
<i>Amanita</i> <i>cingulatoides</i>	HL081a, T	Canada	PP762934			This study
<i>Amanita</i> <i>cingulatoides</i>	HL139	Canada	PP762902			This study
<i>Amanita</i> <i>cingulatoides</i>	HL170A	Canada	PP762707			This study
<i>Amanita</i> <i>cingulatoides</i>	HL171A	Canada	PP762844			This study

Species name	ID (status, strain, isolate, voucher)	Country, isolation source	ITS	LSU	TEFI	Reference(s)
<i>Amanita cingulatooides</i>	HL215	Canada	PP762708			This study
<i>Amanita cingulatooides</i>	HL216	Canada	PP762853			This study
<i>Amanita cingulatooides</i>	HL219	Canada	PP762900			This study
<i>Amanita cingulatooides</i>	HL220	Canada	PP762836			This study
<i>Amanita cingulatooides</i>	HL246	Canada	PP762886			This study
<i>Amanita confundens</i>	HL105a-QFB32921, T	Canada	PP762937			This study
<i>Amanita confundens</i>	HL157A	Canada	PP762799			This study
<i>Amanita confundens</i>	YL4307	Canada	PP762746			This study
<i>Amanita confundens</i>	HL114a-QFB32930	Canada	PP762723			This study
<i>Amanita confundens</i>	HL178A	Canada	PP762742			This study
<i>Amanita confundens</i>	HL113a-QFB32929	Canada	PP762713			This study
<i>Amanita coryli</i>	G:P Neville 02091903, T	France	MN490667			Hanss & Moreau (2017)
<i>Amanita coryli</i>	HL120-QFB33031	Canada	PP762935			This study
<i>Amanita crocea</i>	AF-D56	United Kingdom	UDB002438*			I. Saar, unpubl.
<i>Amanita crocea</i>	O-F-254049	Norway	UDB037446*			I. Saar, unpubl.
<i>Amanita electra</i>	DL140901a	France	MN490646			Hanss & Moreau (2017)
<i>Amanita elongator</i>	RET 521-9 CMMF001956	Canada	MK471234			R.E. Tulloss et al., unpubl.
<i>Amanita elongator</i>	RET 621-10	USA IL	MK377373			R.E. Tulloss et al., unpubl.
<i>Amanita elongator</i>	RET 642-9	USA PA	MK377374			R.E. Tulloss et al., unpubl.
<i>Amanita elongator</i>	RET 524-10	USA PA	KY952153			R.E. Tulloss et al., unpubl.
<i>Amanita elongator</i>	HL060a	Canada	PP762775			This study
<i>Amanita elongator</i>	HRL0093, T	Canada	PP796051			This study
<i>Amanita elongator</i>	Q3651	Canada	PP796090			This study
<i>Amanita flavidocerea</i>	BZ2015_60	Thailand	MF461578			Thongbai (2018)
<i>Amanita fulva</i>	JMH2018006	France	MN490693			Hanss & Moreau (2017)
<i>Amanita fulva</i>	HL206A	Canada	PP464308			This study
<i>Amanita fulva</i>	RET 078-8	Switzerland	MK141039			R.E. Tulloss et al., unpubl.
<i>Amanita fulva</i>	RET 714-10	USA	MK522019			R.E. Tulloss et al., unpubl.
<i>Amanita fulva</i>	iNaturalist # 136274675	USA	OP749630			S.D. Russell, unpubl.
<i>Amanita fulva</i>	RET 706-7	USA	MK522008			R.E. Tulloss et al., unpubl.
<i>Amanita fulvooides</i>	G:P Neville 05101805, T	France	MN490672			Hanss & Moreau (2017)
<i>Amanita fulvooides</i>	HL077a-QFB32893	Canada	PP762876			This study
<i>Amanita fulvooides</i>	G:P Neville 05101805	France	MN490672			Hanss & Moreau (2017)
<i>Amanita fusca</i>	HL097a-QFB32913, T	Canada	PP762926			This study
<i>Amanita fusca</i>	HL228	Canada	PP762730			This study
<i>Amanita fusca</i>	HL189A	Canada	PP762845			This study
<i>Amanita fusca</i>	HL149	Canada	PP762757			This study

Species name	ID (status, strain, isolate, voucher)	Country, isolation source	ITS	LSU	TEFI	Reference(s)
<i>Amanita fusca</i>	HRL3393	Canada	PP762827			This study
<i>Amanita fusca</i>	HL187A	Canada	PP762737			This study
<i>Amanita fusca</i>	HL194A	Canada	PP762807			This study
<i>Amanita fuscozonata</i>	HL143-QFB33055	Canada	PP762726			This study
<i>Amanita fuscozonata</i>	HL177A	Canada	PP762880			This study
<i>Amanita fuscozonata</i>	HL104a-QFB32920	Canada	PP762794			This study
<i>Amanita fuscozonata</i>	HL096a-QFB32912, T	Canada	PP762736			This study
<i>Amanita fuscozonata</i>	HL057a-QFB32876	Canada	PP762804			This study
<i>Amanita fuscozonata</i>	HRL3323-QFB32869	Canada	PP762753			This study
<i>Amanita fuscozonata</i>	HRL3173-QFB32862	Canada	PP762773			This study
<i>Amanita fuscozonata</i>	HRL3197-QFB32866	Canada	PP762763			This study
<i>Amanita fuscozonata</i>	HL175A	Canada	PP762837			This study
<i>Amanita fuscozonata</i>	HL185A	Canada	PP762833			This study
<i>Amanita fuscozonata</i>	HL134	Canada	PP762942			This study
<i>Amanita fuscozonata</i>	HL100a	Canada	PP762735			This study
<i>Amanita fuscozonata</i>	HL133	Canada	PP762871			This study
<i>Amanita griseocarrulea</i>	MV 21.5369, T	Italy	ON818545			Migliozzi & Donato (2022)
<i>Amanita griseocarrulea</i>	MV 20.86431	Italy	ON994667			Migliozzi & Donato (2022)
<i>Amanita griseocarrulea</i>	MV 21.5369	Italy	ON818545			Migliozzi & Donato (2022)
<i>Amanita griseofolia</i>	HKAS 38159, T	China	NR_119498			Zhang (2004)
<i>Amanita griseofolia</i>	HKAS:71016	China	KU714556			Tang (2017)
<i>Amanita herculis</i>	JA-Cussta 9355, T	Spain	OR427365			Crous (2023)
<i>Amanita herculis</i>	JA-Cussta 9353	Spain	OR427363			Crous (2023)
<i>Amanita huijsmanii</i>	LIP:Massart 89A1	France	MN490684			Hanss & Moreau (2017)
<i>Amanita leptorhacopus</i>	RPL30063	Canada	PP796088			This study
<i>Amanita leptorhacopus</i>	HL225	Canada	PP762950			This study
<i>Amanita leptorhacopus</i>	HRL1487	Canada	PP796086			This study
<i>Amanita leptorhacopus</i>	HRL1583, T	Canada	PP796087			This study
<i>Amanita leptorhacopus</i>	HRL3724	Canada	PP762949			This study
<i>Amanita leptorhacopus</i>	HRL3726	Canada	PP762819			This study
<i>Amanita leptorhacopus</i>	HL137	Canada	PP762776			This study
<i>Amanita leptorhacopus</i>	HRL0844	Canada	PP796085			This study
<i>Amanita liquii</i>	HKAS 36611, T	China	AY436462			Zhang (2004)
<i>Amanita magna</i>	HL1067, T	Canada	PP796114			This study
<i>Amanita magna</i>	HL061a	Canada	PP762873			This study
<i>Amanita magna</i>	HL094a	Canada	PP762872			This study
<i>Amanita magna</i>	HL224	Canada	PP762770			This study

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<i>Amanita magna</i>	HRL3234	Canada	PP762704			This study
<i>Amanita magna</i>	YL2877	Canada	PP762930			This study
<i>Amanita magnivolvata</i>	H:M. Aalto 1600 (H), T	Finland	MN490645			Hanss & Moreau (2017)
<i>Amanita mortenii</i>	TB.85.133	Greenland	UDB002335*			Varga et al. (2024)
<i>Amanita mortenii</i>	RET 294-8	Greenland	KT317713			R.E. Tulloss et al., unpubl.
<i>Amanita olivaceodisca</i>	HRL2284-QFB32690	Canada	PP762899			This study
<i>Amanita olivaceodisca</i>	HRL2285-QFB32691, T	Canada	PP762779			This study
<i>Amanita olivaceogrisea</i>	TAAMI17580	Estonia	MN490663			Hanss & Moreau (2017)
<i>Amanita olivaceogrisea</i>	TAAMI18350	Estonia	MN490664			Hanss & Moreau (2017)
<i>Amanita opaca</i> f. <i>cettoi</i> [as <i>supravolvata</i> ]	JMH2016027, T	France	MN493559			Varga et al. (2024)
<i>Amanita orientalis</i> [as sp. QC-2023c]	HKAS127638	China	OR042760			Cui (2023)
<i>Amanita orientalis</i> [as sp. QC-2023c]	EFHAAU1367, T	China	OR042759			Cui (2023)
<i>Amanita pachyvolvata</i>	AB11-08-56	France	MN490652			Hanss & Moreau (2017)
<i>Amanita pekeoides</i>	JAC13244	New Zealand	MT863761			J.A. Cooper, unpubl.
<i>Amanita piceina</i>	HL240	Canada	PP762818			This study
<i>Amanita piceina</i>	HL239, T	Canada	PP762883			This study
<i>Amanita piceina</i>	HL234	Canada	PP762755			This study
<i>Amanita piceina</i>	HL233	Canada	PP762797			This study
<i>Amanita piceina</i>	HL232	Canada	PP762781			This study
<i>Amanita piceina</i>	HL231	Canada	PP762766			This study
<i>Amanita piceina</i>	HL210A	Canada	PP762761			This study
<i>Amanita populiphila</i>	RET 103-4, T	USA	NR_154689			R.E. Tulloss et al., unpubl.
<i>Amanita populiphila</i>	RET 506-5	USA	KX270317			R.E. Tulloss et al., unpubl.
<i>Amanita protecta</i>	NY00066692, T	USA	KP224324			R.E. Tulloss et al., unpubl.
<i>Amanita prudens</i>	MP220407, T	Spain	OP279587			Plaza (2022)
<i>Amanita prudens</i>	RET 847-2	Italy	MW526944			R.E. Tulloss et al., unpubl.
<i>Amanita prudens</i>	MP220123	Spain	OP279588			Plaza (2022)
<i>Amanita pulla</i>	HRL1534A-1, T	Canada	PP796083			This study
<i>Amanita pulla</i>	HRL1488	Canada	PP796082			This study
<i>Amanita pulla</i>	HL012	Canada	PP796081			This study
<i>Amanita pulla</i>	RPL30455	Canada	PP796084			This study
<i>Amanita pulla</i>	HL218	Canada	PP762724			This study
<i>Amanita pulla</i>	HL078a	Canada	PP762849			This study
<i>Amanita pulla</i>	HL079a	Canada	PP762858			This study
<i>Amanita pulla</i>	HL080a	Canada	PP762705			This study

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<i>Amanita pulla</i>	HL084a	Canada	PP762783			This study
<i>Amanita pulla</i>	HL095a	Canada	PP762817			This study
<i>Amanita pulla</i>	HL106a	Canada	PP762884			This study
<i>Amanita pulla</i>	HL138	Canada	PP762744			This study
<i>Amanita pulla</i>	HL140	Canada	PP762916			This study
<i>Amanita pulla</i>	HL159A	Canada	PP762739			This study
<i>Amanita pulla</i>	HL182A	Canada	PP762706			This study
<i>Amanita pulla</i>	RPL30455	Canada	PP762800			This study
<i>Amanita pulla</i>	HL214	Canada	PP762788			This study
<i>Amanita quercifulva</i>	HL264	Canada	PP762717			This study
<i>Amanita quercifulva</i>	HL131-QFB33043	Canada	PP762914			This study
<i>Amanita quercifulva</i>	HL132-QFB33044	Canada	PP762782			This study
<i>Amanita quercifulva</i>	HRL1466, T	Canada	PP796116			This study
<i>Amanita quercifulva</i>	HRL1475	Canada	PP796117			This study
<i>Amanita rhacopus</i>	CMMF 002171, T	Canada	NR_173776			Lambert et al. (2018)
<i>Amanita rhacopus</i>	HL180A	Canada	PP762865			This study
<i>Amanita shennongjiana</i>	HKAS 75553, T	China	NR_159595			Cui (2018)
<i>Amanita shennongjiana</i>	HKAS 75554	China	MH508591			Cui (2018)
<i>Amanita simulans</i>	TO AM161112, T	Italy	KX834255			Vizzini (2017)
<i>Amanita sinicoflana</i>	HL153	Canada	PP762768			This study
<i>Amanita</i> sp.	iNaturalist # 29472325	USA	MZ2226687			G.M. Taylor, unpubl.
<i>Amanita</i> sp.	iNaturalist # 29957786	Canada	MZ227239			G.M. Taylor, unpubl.
<i>Amanita</i> sp.	DAVFP:29751	Canada	OQ225653			S. Berch & A. Bazzicalupo, unpubl.
<i>Amanita</i> sp.	YSU-F-13949	Russia	PP277328			I.A. Gorbunova, unpubl.
<i>Amanita</i> sp.	iNaturalist # 16442327	USA	MZ197981			G.M. Taylor, unpubl.
<i>Amanita</i> sp. (uncultured, root)	clone d1_1Ama	China	JQ347155			Q. Gao & Z.L. Yang, unpubl.
<i>Amanita</i> sp. 'lividella'	HL204A	Canada	PP464498			This study
<i>Amanita</i> sp. '58'	RET 317-4 haplotype h2	USA	KX185615			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. '58'	iNaturalist # 136441226	USA	OP749627			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'A06'	iNaturalist # 56282418	USA	ON059203			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'A06'	RET 236-2	USA	KX354362			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'adventicometa'	RET 703-8	USA	KY549357			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'albemarlenensis'	RET 690-3	USA	MK085521			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'albemarlenensis'	RET 867-6	USA	OR295561			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'albemarlenensis'	RET 845-1	USA	MZ313269			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'albemarlenensis'	RET 868-2	USA	MZ377300			R.E. Tulloss et al., unpubl.



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<i>Amanita</i> sp. 'albemarlandensis'	RET 421-2	USA	MT468567			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'albiceps'	RET 845-2	USA	MN963577			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'albiceps'	RET 845-9	USA	MN963576			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'aurorae'	RET 629-2	USA	MK569760			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'barrowsii'	Mushroom Observer # 468028	USA	OK491620			T.A. Clements, unpubl.
<i>Amanita</i> sp. 'bleakwoodensis'	RET 416-3	USA	OK044795			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'cattaraugana'	RET 694-9A	USA	KX261521			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'cattaraugana'	iNaturalist # 17017713	USA	MZ6667923			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'chiricahuana'	RET 676-10	USA	KY435391			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'chiricahuana'	CMP 1818	USA	KX219636			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'clarionensis'	RET 478-8	USA	MZ271864			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'DEUT02'	RET 307-9	Germany	MW526941			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'DEUT03'	RET 305-1	Germany	MW526943			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'georgiensis'	RET 675-4D	USA	MZ539434			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'georgiensis'	RET 858-8	USA	MZ318066			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'glenosomma'	iNaturalist # 29206074	USA	MZ668210			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'glenosomma'	RET 302-2	USA	MT445429			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'GSM05'	gsm05	USA	MK580724			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'IN02'	iNaturalist # 8538933	USA	MZ6667973			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'IN12'	iNaturalist # 181672136	USA	PP436563			S. Ostuni et al., unpubl.
<i>Amanita</i> sp. 'IN12'	iNaturalist # 130311226	USA	OP749509			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'IN29'	Mycomap # 6775	USA	MZ6667996			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'IN44'	iNaturalist # 130409549	USA	OP643044			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'IN44'	iNaturalist # 130409549	USA	OP549077			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'IN63'	iNaturalist # 130235318	USA	OP749579			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'insinuans'	RET 685-8	USA	KY435394			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'insinuans'	RET 843-9	USA	MN755839			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'jakeslandingensis'	RET 849-6	USA	MN963593			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'justicei'	RET 444-8	USA	KY614228			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'LA02'	RET 802-9	USA	MK351808			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'labliannulus'	RET 518-7	USA	OR297556			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'longicuneus'	RET 699-3B	USA	KY580766			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'longicuneus'	RET 374-9	USA	KX018799			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'longicuneus'	RET 509-6	Canada	MW579513			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'longicuneus'	RET 379-9	USA	MN650859			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'longicuneus'	iNaturalist # 129772546	USA	OP470576			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'longicuneus'	RET 446-7	USA	ON500640			R.E. Tulloss et al., unpubl.

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<i>Amanita</i> sp. 'longicuneus'	RET 492-8	USA	ON500642			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'longicuneus'	iNaturalist # 137710109	USA	OP749498			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'M15'	RET 252-3	Mexico	MK377375			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'M15'	RET 256-4	Mexico	MK377376			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'MO06'	RET 690-10	USA	KY614233			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'MO06'	RET 875-5	USA	ON637057			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'N46'	RET 319-5	USA	MN820545			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'N49'	RET 438-4	USA	MT122208			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'N51'	782	USA	MK580805			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'N63'	RET 686-3	USA	KY952151			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'N63'	RET 373-8	Canada	MN650852			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'N63'	RET 075-3	USA	KY924838			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'N68'	Mushroom Observer # 375602	USA	ON705318			I.G. Safonov & L. V. Kudzma, unpubl.
<i>Amanita</i> sp. 'N68'	RET 697-2	USA	MH939272			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'OR01'	3840	USA	PP542044			J. Matanzas, unpubl.
<i>Amanita</i> sp. 'OR01'	RET 417-10	USA	KY655774			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'pascagoula'	RET 724-9	USA	MN963586			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'penetratrix'	RET 769-1	USA	MH836563			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'penetratrix'	RET 437-4	USA	KX219639			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'petroleum'	RET 858-6	USA	MZ265204			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'QUE04'	iNaturalist # 58346873	USA	ON059239			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'QUE04'	RET 536-8	USA	MG252699			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'SI4'	iNaturalist # 13936523	USA	OP541698			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'SI4'	RET 845-6	USA	MZ158290			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'SI4'	RET 783-3	USA	MZ158289			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'salmonriverensis'	RET 479-3	USA	MK569746			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'salmonriverensis'	Mushroom Observer # 471821	USA	ON554823			I.G. Safonov & M. Gordon, unpubl.
<i>Amanita</i> sp. 'saraha'	RET 268-9	USA	MW538975			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'semiobruta'	RET 691-1	USA	KY435402			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'semiobruta'	RET 691-6	USA	KY435403			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'sharkriverensis'	RET 300-6	USA	KY549350			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'sharkriverensis'	iNaturalist # 137710135	USA	OP749648			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'sharkriverensis'	Mushroom Observer # 431493	USA	ON950147			I.G. Safonov & L. V. Kudzma, unpubl.
<i>Amanita</i> sp. 'sharkriverensis'	RET 810-3	USA	OQ916432			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'sharkriverensis'	RET 881-10	USA	OK042092			R.E. Tulloss et al., unpubl.

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<i>Amanita</i> sp. 'sp-44'	RET 180-10	USA	KY549349			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'sp-44'	MycMap # 7378	USA	MZ668168			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'sp-44'	MycMap # 7427	USA	MZ668170			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'sp-44'	iNaturalist # 56813625	USA	ON059222			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'sp-44'	MycMap # 8085	USA	MZ667978			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'sp-61'	iNaturalist # 185829777	USA	PP574116			S. Ostuni et al., unpubl.
<i>Amanita</i> sp. 'sp-S14'	MycMap # 6468	USA	MN906207			S.D. Russell, unpubl.
<i>Amanita</i> sp. 'sp-S14'	RET 854-4	USA	OR030811			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'sp-W103'	RET 714-6	USA	MT013989			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'subnigra'	RET 155-9	USA	KP711843			R.E. Tulloss et al., unpubl.
<i>Amanita</i> sp. 'subnigra'	HRL3274-QFB32868	Canada	PP762927			This study
<i>Amanita</i> sp. TAC14	Mushroom Observer # 396912	USA	MT232417			T.A. Clements, unpubl.
<i>Amanita</i> sp. TAC14	Mushroom Observer # 428476	USA	MW989515			T.A. Clements, unpubl.
<i>Amanita</i> sp. 'W103'	RET 667-9	USA	MK085519			R.E. Tulloss et al., unpubl.
<i>Amanita spadicea</i>	DL170917a	France	MN490685			Hanss & Moreau (2017)
<i>Amanita spadicea</i>	DL170917a	France	MN490685			Hanss & Moreau (2017)
<i>Amanita spadicea</i>	RET 306-4	Germany	MT036490			R.E. Tulloss et al., unpubl.
<i>Amanita spadicea</i>	RET 594-8	Turkey	MW426549			R.E. Tulloss et al., unpubl.
<i>Amanita sponosa</i>	LIP0401747, PAM18110303	Spain	OQ357629			Hanss & Moreau (2022)
<i>Amanita sponosa</i>	LIP0401746, PAM18102001	Spain	OQ357630			Hanss & Moreau (2022)
<i>Amanita submembranacea</i>	HKAS96167	Austria	MH508625			Hanss & Moreau (2022)
<i>Amanita submembranacea</i>	MB-001174	Germany	MH508626			Cui (2023)
<i>Amanita umbrinolutea</i>	LIP:LIP 0401238	France	MN490658			Hanss & Moreau (2017)
<i>Amanita umbrinolutea</i>	G:Neville 97-07-13-20, T	France	MN490681			Hanss & Moreau (2017)
<i>Amanita umbrinolutea</i>	G:Neville 97-07-13-20	France	MN490681			Hanss & Moreau (2017)
<i>Amanita variicolor</i>	CMMF 003787, T	Canada	NR_159564			Lambert et al. (2018)
<i>Amanita variicolor</i>	HL0257	Canada	MG734657			Lambert et al. (2018)
<i>Amanita variicolor</i>	HL122	Canada	PP762743			This study
<i>Amanita variicolor</i>	CMMF003787, T	Canada	NR_159564			Lambert et al. (2018)
<i>Amanita velosa</i>	7004	USA	GQ250409			K.A. Harper & R.M. Davis, unpubl.
<i>Amanita vladimiri</i>	BRNM825828, T	Czechia	MW208927			Šev íková et al. (2021)
<i>Amanita vladimiri</i>	BRNM825828	Czechia	MW208927			Šev íková et al. (2021)
<i>Amanita vladimiri</i>	BRNM825829	Czechia	MW208926			Šev íková et al. (2021)
<i>Amanitaceae</i> sp.	iNaturalist # 89927041	USA	OP681769			P. Palmer, S. Jakob, H. Singer & M. Kuzmina, unpubl.
<i>Apophysomyces elegans</i>	CBS 476.78, NRRL 22325	India, soil	FN556440	FN554249		Alvarez et al. (2010b)
<i>Hebeloma alpinicola</i>	HJB15611	Georgia	ON202499		ON167789	Eberhardt et al. (2022b)

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<i>Hebeloma alpinicola</i>	HJB11019	Iceland	ON202500		ON167790	Eberhardt et al. (2022b)
<i>Hebeloma bingolense</i>	VANF7896A	Türkiye	MW617997			Acar et al. (2022)
<i>Hebeloma bingolense</i>	VANF7896B	Türkiye	MW617998			Acar et al. (2022)
<i>Hebeloma bingolense</i>	VANF7949A	Türkiye	MW617999			Acar et al. (2022)
<i>Hebeloma bingolense</i>	VANF7949B	Türkiye	MW618000			Acar et al. (2022)
<i>Hebeloma clavulipes</i>	HJB13093	France	KY271856			Beker et al. (2017)
<i>Hebeloma colvinii</i>	C-F-107346	Greenland	MW445749		ON167786	Eberhardt et al. (2021)
<i>Hebeloma colvinii</i>	C-F-104035	Greenland	MW445748		ON167785	Eberhardt et al. (2021-2022a)
<i>Hebeloma dunense</i>	KRAM:F53052	Poland	KT071018		KT071084	Eberhardt et al. (2015)
<i>Hebeloma dunense</i>	KRAM:F57434	Poland	KT071022		KT071088	Eberhardt et al. (2015)
<i>Hebeloma erebium</i>	LOD:IK-H0182	Poland	KT218463		KT217682	Grilli et al. (2016)
<i>Hebeloma excedens</i>	HJB16817	Mexico	ON202527		ON167805	Eberhardt et al. (2022a)
<i>Hebeloma excedens</i>	ZT:ZT9830	USA	MK281121			Cripps et al. (2019)
<i>Hebeloma excedens</i>	ZT:ZT7475	USA	MK281122			Cripps et al. (2019)
<i>Hebeloma excedens</i>	HJB16980	USA	ON202529		ON167807	Eberhardt et al. (2022b)
<i>Hebeloma fuscatum</i>	IB19880082	Norway	MW445825			Beker et al. (2017)
<i>Hebeloma fuscatum</i>	HJB12046	Norway	KY271851			Beker et al. (2017)
<i>Hebeloma grandisporum</i>	KRAM:F47189	Romania	KT071023		KT071089	Eberhardt et al. (2015)
<i>Hebeloma hygrophilum</i>	C-F-112528	Greenland	MW445818			Eberhardt et al. (2021)
<i>Hebeloma hygrophilum</i>	C-F-137115	Greenland	MW445821			Eberhardt et al. (2021)
<i>Hebeloma marginatulum</i>	KRAM:F46901	Poland	KT071028		KT071090	Eberhardt et al. (2015)
<i>Hebeloma marginatulum</i>	HJB11151	Switzerland	KT071029		KT071091	Eberhardt et al. (2015)
<i>Hebeloma mesophaeum</i>	KRAM:F57417	Slovakia	KT071036		KT071098	Eberhardt et al. (2015)
<i>Hebeloma mesophaeum</i>	KRAM:F47178	Slovakia	KT071034		KT071096	Eberhardt et al. (2015)
<i>Hebeloma mesophaeum</i>	HJB10166	Belgium	KT218250		KT217611	Grilli et al. (2016)
<i>Hebeloma mesophaeum</i>	KRAM:F47191	Slovakia	KT071033		KT071095	Eberhardt et al. (2015)
<i>Hebeloma mesophaeum</i>	KRAM:F57431	Romania	KT071038		KT071100	Eberhardt et al. (2015)
<i>Hebeloma monticola</i>	C:JV-97-250	Sweden	MZ019456			Eberhardt et al. (2022a)
<i>Hebeloma nigellum</i>	C:JV02_722	Denmark	KT071043		KT071102	Eberhardt et al. (2015)
<i>Hebeloma nigellum</i>	TUR:KK04_02	Finland	KT071044		KT071103	Eberhardt et al. (2015)
<i>Hebeloma oreophilum</i>	KRAM:F57428	Slovakia	KT071049		KT071107	Eberhardt et al. (2015)
<i>Hebeloma psammophilum</i>	HJB13337	France	ON202552		ON167818	Eberhardt et al. (2022a)
<i>Hebeloma psammophilum</i>	HJB12970	France	ON202553		ON167819	Eberhardt et al. (2022a)
<i>Hebeloma pubescens</i>	HJB16886	Canada	ON202554		ON167820	Eberhardt et al. (2022a)
<i>Hebeloma pubescens</i>	HJB12057	Norway	KY271837		ON167771	Beker et al. (2017), Eberhardt et al. (2022a)
<i>Hebeloma spetsbergense</i>	C-F-119733	Greenland	MW445822			Eberhardt et al. (2021)

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<i>Hebeloma subtortum</i>	VANF1242	Türkiye	MG914656			Dizkirci et al. (2019)
<i>Hebeloma subtortum</i>	HJB13784	Spain	ON202564		ON167824	Eberhardt et al. (2022b)
<i>Hebeloma subtortum</i>	TNS-F-61666	Japan	MZ782131		ON167788	Eberhardt et al. (2022b)
<i>Hebeloma subtortum</i>	IB19800904	Spain	KX765789			Beker et al. (2016)
<i>Hebeloma subtortum</i>	BP78500	Hungary	KX765790			Beker et al. (2016)
<i>Hebeloma subtortum</i>	H:H4006	Finland	KX765791			Beker et al. (2016)
<i>Hebeloma subtortum</i>	PC0022089	France	KX765788			Beker et al. (2016)
<i>Hebeloma subtortum</i>	HJB12925	Italy	ON202563		ON167823	Eberhardt et al. (2022a)
<i>Hebeloma subtortum</i>	HJB10698	United Kingdom	ON202565		ON167825	Eberhardt et al. (2022a)
<i>Hebeloma uzunii</i>	VANF1121, T	Türkiye	ON505062		ON512567	This study
<i>Hebeloma uzunii</i>	VANF1121T2	Türkiye	ON505063		ON512568	This study
<i>Hebeloma uzunii</i>	VANF1154	Türkiye	ON505064		ON512565	This study
<i>Hebeloma uzunii</i>	VANF1154IA2	Türkiye	ON505065		ON512566	This study
<i>Hebeloma velutipes</i>	HJB11623/ HJB11315	Belgium	KT218357		KT217649	Grilli et al. (2016)
<i>Hohenbuehelia mastrucata</i>	TRTC 152314, T		NR_154082	NG060671		G. Consiglio & L. Setti, unpubl.
<i>Hohenbuehelia valesiaca</i>	Roux 2975	France	KU355340	KU355399		G. Consiglio & L. Setti, unpubl.
<i>Pleurotus abieticola</i>	HKAS46100	China (Tibet)	KP771695	KP867909		Z.L. Yang, X.B. Liu & J.W. Liu, unpubl.
<i>Pleurotus australis</i>	ICMP 21585	New Zealand	MH395977	MH396002		B.S. Weir, D. Park, J.A. Cooper & P.K. Buchanan, unpubl.
<i>Pleurotus australis</i>	ICMP 18149	New Zealand	MH395972	MH395996		B.S. Weir, D. Park, J.A. Cooper & P.K. Buchanan, unpubl.
<i>Pleurotus australis</i>	RY95/568	New Zealand (ITS)	AY315762	AF261432		Zervakis et al. (2004); J.M. Moncalvo, J.E. Johnson, R. Vilgalys & S. Redhead, unpubl.
<i>Pleurotus calypttratus</i>	CBS 325.85	China	EU424283	EU365640		S. Gao, J.X. Zhang, & Y.B. Bian, unpubl.
<i>Pleurotus cornucopiae</i>	CBS 283.37		MH855911	MH867415		Vu et al. (2019)
<i>Pleurotus cystidiosus</i>	CBS 615.80		EU424279	EU365636		S. Gao, J.X. Zhang, & Y.B. Bian, unpubl.
<i>Pleurotus cystidiosus</i>	ACCC51280		EU424280	EU365637		S. Gao, J.X. Zhang, & Y.B. Bian, unpubl.
<i>Pleurotus cystidiosus</i> var. <i>formosensis</i>	CBS 100129, T		NR_103594	NG_057793		S. Gao, J.X. Zhang, & Y.B. Bian, unpubl.
<i>Pleurotus djamar</i>	CBS 100134		EU424287	EU365644		S. Gao, J.X. Zhang, & Y.B. Bian, unpubl.
<i>Pleurotus dryinus</i>	CBS 481.72	Germany	EU424292	MH872241		S. Gao, J.X. Zhang, & Y.B. Bian, unpubl.; Vu et al. (2019)
<i>Pleurotus dryinus</i>	CBS 449.77		EU424291	EU365648		S. Gao, J.X. Zhang, & Y.B. Bian, unpubl.

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<i>Pleurotus eryngii</i> var. <i>tuoliensis</i>	CCMSSC01433	China	KP867912	KP867900		Z.L. Yang, X.B. Liu & J.W. Liu, unpubl.
<i>Pleurotus giganteus</i>	CMU54-1	Thailand	JQ724360	JQ724361		J. Kumla, N. Suwannarach & S. Lumyong, unpubl.
<i>Pleurotus opuntiae</i>	SAF 251	Italy	MH620771	MK182780		Zervakis et al. (2019)
<i>Pleurotus opuntiae</i>	SAF 252	Italy	MH620772	MK182781		Zervakis et al. (2019)
<i>Pleurotus ostreatus</i>	TENN 53662, T		NR_163515	NG_027634		P.B. Matheny, K.W. Hughes, R.H. Petersen & D.S. Hibbett, unpubl.
<i>Pleurotus ostreatus</i>	HKAS84903	Germany	KP867913	KP867901		Z.L. Yang, X.B. Liu & J.W. Liu, unpubl.
<i>Pleurotus overstrandensis</i>	PO2, T	South Africa	OR101946	OR101950		This study
<i>Pleurotus overstrandensis</i>	PO1	South Africa	OR101947	OR101951		This study
<i>Pleurotus overstrandensis</i>	PO3	South Africa	OR101948	OR101952		This study
<i>Pleurotus overstrandensis</i>	PO4	South Africa	OR101949	OR101953		This study
<i>Pleurotus parsoniae</i>	ICMP 18169	New Zealand	MH395975	MH396000		B.S. Weir, D. Park, J.A. Cooper & P.K. Buchanan, unpubl.
<i>Pleurotus placentodes</i>	HKAS51745	China	KR827693	KR827695		Z.L. Yang & X.B. Liu, unpubl.
<i>Pleurotus placentodes</i>	HKAS57781	China	KR827694	KR827696		Z.L. Yang & X.B. Liu, unpubl.
<i>Pleurotus pulmonarius</i>	Dai 19968	China	OL437264	OL434413		Y.C. Dai, unpubl.
<i>Pleurotus pulmonarius</i>	HKAS86009	China	KP867918	KP867906		Z.L. Yang, X.B. Liu & J.W. Liu, unpubl.
<i>Pleurotus tuber-regium</i>	CBS 850.95	Nigeria	MH862563	MH874190		Vu et al. (2019)
<i>Pleurotus tuber-regium</i>	BORHF0648	Malaysia	MH178086	MH178091		S.F. Foo & J.S. Sathya Seelan, unpubl.
<i>Pluteus aesoniensis</i>	MCVE30112, T	Italy	MZ412508			Dovana et al. (2022)
<i>Pluteus</i> aff. <i>cinereofuscus</i>	TNSF12400	Japan	HM562115			Justo et al. (2011b)
<i>Pluteus</i> aff. <i>cinereofuscus</i>	AJ216	Spain	HM562046			Justo et al. (2011b)
<i>Pluteus</i> aff. <i>cinereofuscus</i>	LE 303665	Russia	KX216324			Malysheva et al. (2016)
<i>Pluteus anatolicus</i>	Holotype	Turkey	MT523034			Kaygusuz et al. 2021
<i>Pluteus beniensis</i>	RSPF 0299	Brazil	JQ065029			A. Justo, N. Menolli Jr. & A.M. Mirnis, unpubl.
<i>Pluteus bizioi</i>	Holotype	Italy	MG946813			Ferisin et al. (2019)
<i>Pluteus</i> cf. <i>jamaicensis</i>	SP416738	Brazil	KM983709			Menolli et al. (2015)
<i>Pluteus cinereofuscus</i>	AJ229	Portugal	HM562108			Justo et al. (2011b)
<i>Pluteus cinereofuscus</i>	AJ324	Spain	HM562124			Justo et al. (2011b)
<i>Pluteus cludens</i>	50497, T	Portugal	HM562118			Justo et al. (2011b)
<i>Pluteus extremiorientalis</i>	LE262872, T	Russia	NR_153249			Crous et al. (2014)
<i>Pluteus floccipes</i>	BRNM766737, T	Czech Republic	LN794642			Ševčíková & Borovička (2015)

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<i>Pluteus fluminensis</i>	SF393711	Brazil	FJ816664			Menolli et al. (2010)
<i>Pluteus fuliginovenosus</i>	SF393705	Brazil	FJ816662			Menolli et al. (2010)
<i>Pluteus hubetensis</i>	HMJAU45200	China	MH167353			W. Fengjian & L. Yu, unpubl.
<i>Pluteus jamaicensis</i>	SP393706	Brazil	FJ816657			Menolli et al. (2010)
<i>Pluteus karstedtia</i>	FK1700, T	Brazil	KM983682			Menolli et al. (2015)
<i>Pluteus kesselkii</i>	BRNM817402, T	Slovakia	MN250223			Ševčíková et al. (2020)
<i>Pluteus kesselkii</i>	LIP0401385	France	MN250224			Ševčíková et al. (2020)
<i>Pluteus kesselkii</i>	BRNM825841	Czech Republic	ON090362			This study
<i>Pluteus kesselkii</i>	GDOR5094	Slovenia	ON090363			This study
<i>Pluteus ludwigii</i>	MCVE30136, T	Slovenia	MK834525			Crous et al. (2019)
<i>Pluteus multiformis</i>	AH40107, T	Spain	NR_119877			Justo et al. (2011a)
<i>Pluteus nanus</i>	BRNM761723	Czech Republic	LN866290			Ševčíková & Borovička (2015)
<i>Pluteus nanus</i>	UC1859980	USA	KF306030			N.H. Nguyen, E.C. Vellinga, G.M. Cobian, A.J. Fernandez & T.D. Bruns, unpubl.
<i>Pluteus nanus</i> f. <i>griseopus</i>	888	Italy	JF908611			Osmundson et al. (2013)
<i>Pluteus pallescens</i>	AJ214	Spain	HM562056			Justo et al. (2011b)
<i>Pluteus rimosoaffinis</i>	SP416740	Brazil	KM983706			Menolli et al. (2015)
<i>Pluteus sapicola</i>	SP394382	Brazil	HM562148			Justo et al. (2011b)
<i>Pluteus</i> sp.	PDD 110518	New Zealand	MN738674			J.A. Cooper, unpubl.
<i>Pluteus</i> sp.	JLF1767	USA	MK634597			J.L. Frank, unpubl.
<i>Pluteus tenebromarginatus</i>	GC17102401, T	France	MT079860			Corriol et al. (2020)
<i>Pluteus terricola</i>	PDD105916	New Zealand	MN738648			J.A. Cooper, unpubl.
<i>Pluteus terricola</i>	PDD106511	New Zealand	MN738653			J.A. Cooper, unpubl.
<i>Saksenaea boninensis</i>	Sak3	Japan, litter	MK757862			Takashima et al. (2023)
<i>Saksenaea boninensis</i>	CBS 147591 (sak-4), T	Japan, litter	MK757863	MK757859	LC474957	Takashima et al. (2023)
<i>Saksenaea boninensis</i>	Sak5	Japan, litter	MK757864			Takashima et al. (2023)
<i>Saksenaea boninensis</i>	Sak6	Japan, litter	MK757865			Takashima et al. (2023)
<i>Saksenaea doristiae</i>	BiMM-F232	Serbia, water from private well	MK559697	MK570305	MK569515	Labuda et al. (2019)
<i>Saksenaea erythrospora</i>	CBS 138279	India, human	KM102733			Tendolkar et al. (2015)
<i>Saksenaea erythrospora</i>	CIMCE001	Venezuela, human skin	KU951560			S.E. Morales, J.Y. Rodriguez, G. Rodriguez & C. Cantillo, unpubl.
<i>Saksenaea erythrospora</i>	FMR 13392	India, human	KR527481			Chander et al. (2017)
<i>Saksenaea erythrospora</i>	FMR 13516	India, human	KR527482			Chander et al. (2017)
<i>Saksenaea erythrospora</i>	FMR 13580	India, human	KR527483			Chander et al. (2017)

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<i>Saksenaea erythrospora</i>	RTCC239110910	Thailand, human	JF433911			P. Chongtrakro & P. Onpaew, unpubl.
<i>Saksenaea erythrospora</i>	UTHSC 06-576	“Middle East”, blood	FR687331			Alvarez et al. (2010a)
<i>Saksenaea erythrospora</i>	UTHSC 08-3606, T	USA, bovine fetus	NR_149333	NG_059935	HM776691	Alvarez et al. (2010a)
<i>Saksenaea erythrospora</i>	UZ1908 15	Malaysia, human	KU321692			R. Mohd Tap & S.J. Ginsapu, unpubl.
<i>Saksenaea erythrospora</i>	CNM-CM8808	India, human	MN598586			A. Alastruey-Izquierdo & J. Chander, unpubl.
<i>Saksenaea loutrophoriformis</i>	M-1012/15	India, palate necrotic tissue	LT796164			Crous et al. (2017)
<i>Saksenaea loutrophoriformis</i>	UTHSC 08-379, T	USA, eye	FR687330	HM776682	HM776693	Crous et al. (2017)
<i>Saksenaea longicolla</i>	C17	South Korea, soil sediment in a reservoir	MW393835			Nam et al. (2021)
<i>Saksenaea longicolla</i>	Sak-06	South Korea, soil sediment in a reservoir	MW393836			Nam et al. (2021)
<i>Saksenaea longicolla</i>	NNIBRFG21789, T	South Korea, soil sediment in a reservoir	MW393837*	MW391840	MW401668	Nam et al. (2021)
<i>Saksenaea longicolla</i>	Sak-19	South Korea, soil sediment in a reservoir	MW393838			Nam et al. (2021)
<i>Saksenaea longicolla</i>	Sak-21, KACC48577	South Korea, soil sediment in a reservoir	MK430970			Nam et al. (2021)
<i>Saksenaea oblongispora</i>	CBS 133.90, T	Brazil, forest soil	NR_137569	NG_057868	HM776687	Alvarez et al. (2010a)
<i>Saksenaea ozerskayae</i>	VKM F-5019, T	Russia, Tuber magnatum	PP280821-PP280826	PP600326	PP439981-PP439983	This study
<i>Saksenaea trapezispora</i>	UTHSC DI 15-1, T	USA, knee wound of a soldier	NR_147690	LT607407	LT607408	Crous et al. (2016)
<i>Saksenaea trapezispora</i>	1855	Iran, Human skin	MK321959			S. Khodavaisy, K. Ahmadi, A. Vaezi & H. Badali, unpubl.
<i>Saksenaea vasiformis</i>	AJ1-1	China, Isaria cicadae	MH059541			Q. Qu, unpubl.
<i>Saksenaea vasiformis</i>	ATCC 28740	USA, craniofacial tissue and brain	FR687322			Alvarez et al. (2010a)
<i>Saksenaea vasiformis</i>	ATCC 60625	USA, human wrist lesion at arterial catheter site	FR687323			Alvarez et al. (2010a)
<i>Saksenaea vasiformis</i>	CNRMA 05.1337	French Guiana, human tissue	EU182902			Blanchet et al. (2008)



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<i>Saksenaea vasiformis</i>	CNRMA 07.577	France, human skin	EU644757			Lechevalier et al. (2008)
<i>Saksenaea vasiformis</i>	CNRMA 08.1143	France, human	KP132600			Irinyi et al. (2015)
<i>Saksenaea vasiformis</i>	CNRMA F/9-83	France, human skin lesions	FR687325			Alvarez et al. (2010a)
<i>Saksenaea vasiformis</i>	F5	India, human	MF187627			P. Das, R. C. Boro & M. Barooah, unpubl.
<i>Saksenaea vasiformis</i>	FMR 10131	Spain, cutaneous lesion	FR687326			Alvarez et al. (2010a)
<i>Saksenaea vasiformis</i>	NRRL 2443, T	India, soil	FR687327	HM776679	AF157291	Alvarez et al. (2010a)
<i>Saksenaea vasiformis</i>	PHF-MC2	Iran, human	MK346253			Badiee et al. (2020)
<i>Saksenaea vasiformis</i>	PHF-MC200	Iran, human	MK501620			Badiee et al. (2020)
<i>Saksenaea vasiformis</i>	PHF-MC201	Iran, human	MK499472			Badiee et al. (2020)
<i>Saksenaea vasiformis</i>	CNRMA 05.1337	French Guiana, human tissue	EU182902			Blanchet et al. (2008)
<i>Saksenaea vasiformis</i>	PWQ2338	Australia, human	KP132601			Irinyi et al. (2015)
<i>Saksenaea vasiformis</i>	TN254AU15	Tunisia, human	KU314816			H. Trabelsi, S. Neji, F. Cheikhrouhou, H. Sellami, F. Makni, A. Ghorbel & A. Ayadi, unpubl.
<i>Saksenaea vasiformis</i>	UTHSC 09-528	USA, human tissue	FR687329			Alvarez et al. (2010a)
<i>Saksenaea vasiformis</i>	UTHSC R-2974	USA, human tissue	FR687332			Alvarez et al. (2010a)
<i>Saksenaea vasiformis</i>	MG754348	Greece, human	MG754348			A. Velegraki & M. Arabatzis, unpubl.
<i>Saksenaea vasiformis</i>	F-375	India, human	OQ299499			P. Nimmy, P. Sreekumay, C.N. Chitra, S. Sreejith, V. Hallur & S. Supriya, unpubl.
<i>Saksenaea vasiformis</i>	NCCPF:111021	India, human	MZ619078			S. Singh & S.M. Rudramurthy, unpubl.
<i>Saksenaea vasiformis</i>	NCCPF:111022	India, soil	OP648298			S. Singh & S.M. Rudramurthy, unpubl.
<i>Saksenaea vasiformis</i>	ZESA8	Iraq, plant root	MW340912			S.A. Alghammi & Z.A. Alteneh, unpubl.
<i>Saksenaea</i> sp.	Cesf-21	China, rhizosphere soil	MK775965			T. Shan, unpubl.
<i>Saksenaea</i> sp.	F2Sc	China	OL981347			C. Uwaremwe, unpubl.
<i>Saksenaea</i> sp.	MF11	Mexico, Acalypha gaumeri (Euphorbiaceae)	MT606215			M. Gamboa-Angulo, G. Heredia, H. Lumberras-Martinez, M. Gomez-Krupko, R.R. Magana-Gallegos, J. Aviles-Gomez & F. Moo Koh, unpubl.
<i>Uncultured Basidiomycota</i>	A2	Australia	DQ672275			Midgley et al. (2007)
<i>Uncultured Basidiomycota</i>		North Carolina	AY969369			O'Brien et al. (2005)

<sup>1</sup> Herbarium abbreviations follow Index Herbariorum (Thiers continuously updated).

<sup>2</sup> T: type. \* from UNITE database (<https://unite.ut.ee>).

regions at the beginning and end parts of the alignments were manually trimmed. Alignments were then concatenated in Mesquite version 3.61 (Maddison & Maddison 2019). *Hebeloma erebium* (Huijsman) Beker & U. Eberh. and *H. velutipes* Bruchet (*H. sect. Velutipes*) were chosen as outgroup. Phylogenetic reconstructions were performed with both Maximum likelihood (ML) and Bayesian Inference (BI) methods. The appropriate model of nucleotide evolution was determined using Modeltest-NG v.0.2.0 (Darriba et al. 2020) based on the corrected Akaike information criterion (AICc). The concatenated data set included 50 taxa with a total of 1199 characters, and TIM2+I+G4 model was determined as the most suitable model for ML analysis. GTR+I+G was determined as the most suitable model for BI analysis. The ML analyses were performed in RAxML-NG (Kozlov et al. 2018) via the CIPRES Science Gateway using automatic MRE bootstopping set to a maximum of 1000 bootstraps, with a 0.01 cutoff value. MrBayes version 3.2.6 (Ronquist et al. 2003) was employed to conduct BI analyses. Markov Chain Monte Carlo (MCMC) method was used with all the remaining settings set to default (incremental heating scheme of chains, unconstrained branch length, and uninformative topology priors). Two runs with four chains of MCMC iterations were performed for 5 million generations when the average standard deviations of split frequencies were <0.01 (the first 20 % of generations were treated as burn-in). A majority rule consensus tree of the remaining trees was calculated. Trees were visualized using Figtree version 1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>).

The newly generated *Pleutorus* sequences were subjected to a BLAST search against NCBI GenBank's standard *nr/nt* nucleotide database (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>). ITS and LSU sequences of closely related species of *Pleurotus* and outgroup taxa *Hohenbuehelia mastrucata* (Fr.) Singer and *H. valesiaca* (Ces. ex Sacc.) Singer were downloaded in FASTA format (Tab. 1). Alignments were performed on the ITS and LSU sequences using the MUSCLE Alignment function (Edgar 2004) on Geneious Prime version 2023.1.2. The aligned ITS and LSU datasets were manually trimmed at the ends, and concatenated. The 1018-bp concatenated alignment was uploaded to TreeBase (TreeBase submission ID: 30825) and Figshare (<https://doi.org/10.6084/m9.figshare.25603860>). The concatenated ITS–LSU dataset was used to perform BI and ML analyses. Bayesian analyses were run on MrBayes 3.2.6 using Geneious Prime (Ronquist et al. 2012). The alignment was analyzed using the

HKY85 substitution model, with four parallel runs of 5,000,000 generations. The sampling frequency was set at every 1,000 generations, and the posterior probability values were calculated after the first 25 % of trees were discarded as burn-in. Further, an ML analysis was run using RAxML on Geneious Prime, with 1,000 rapid bootstrap replicates and the GTRGAMMA model. The best-scoring tree was kept (Stamatakis et al. 2008, Polemis et al. 2023).

Obtained sequences of *Saksenaea*, as well as closely related sequences of type strains and yet undescribed species from GenBank were aligned using the online version of the MAFFT algorithm (Katoh et al. 2019). Two datasets were constructed: an ITS dataset with 56 sequences and a concatenated ITS–LSU–*tef1* dataset with 27 sequences, both including *Apophysomyces elegans* P.C. Misra, K.J. Srivast. & Lata as outgroup. Phylogenetic trees were reconstructed in MEGA 6 (Tamura et al. 2013) by using ML with the GTR substitution model with gamma-distributed rate heterogeneity and 1,000 bootstrap replicates.

Based on the BLAST results and according to the outcomes of recent phylogenetic studies on *Pluteus* sect. *Celluloderma*, representative sequences belonging to the /cinereofuscus clade were selected for the phylogenetic analysis. *Pluteus bizioi* Ferisin, Dovana & Justo and *P. karstedtia* Menolli, Justo & Capelari were used as outgroup. Sequences were aligned using MAFFT version 7.450 (Katoh & Toh 2008) with default parameters in Geneious version 11.1.5. ML was inferred with IQ-TREE 2 (Minh et al. 2020). The HKY+F+G4, K2P, and K3P+G4 models were selected for ITS1, 5.8S, and ITS2, respectively using ModelFinder (Kalyaanamoorthy et al. 2016). A total of 1000 ultrafast bootstrap (UFBS) replicates were used (Hoang et al. 2018).

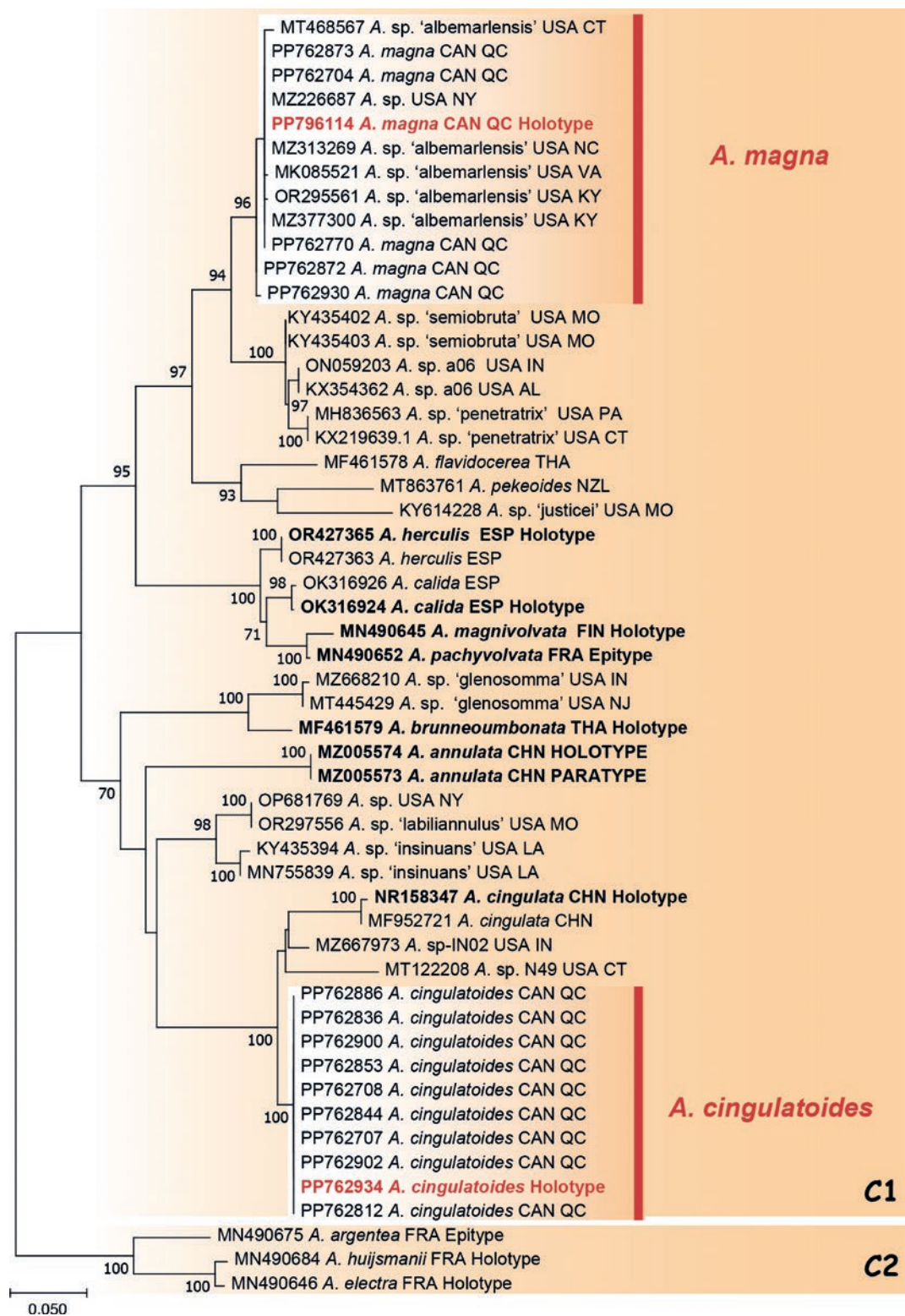
## Taxonomy

### Basidiomycota, Agaricomycetes, Agaricales, Amanitaceae

#### *Amanita* section *Vaginatae*

*Amanita magna* H. Lambert, Y. Lamoureux & J. Landry, **sp. nov.** – Fig. 1, 2  
Mycobank no.: MB 854395

**Diagnosis.** – Differs from other species of *Amanita* section *Vaginatae* with grey-brown pileus by the combination of large basidiomata (pileus diameter up to 140 mm, stipe length up to 330 mm), greyish brown naked pileus often with a paler zone between umbo and marginal striations, white stipe with greyish brown fibrils arranged in a zebroid pattern, membranous universal veil leaving a white volva, and growth with *Fagus*.



**Fig. 1.** Phylogeny of selected *Amanita* species in section *Vaginatae* Clade 1 reconstructed from an ITS dataset using species from Clade 2 as outgroup. The tree topology with the highest log likelihood ( $-\ln L = 4155.51$ ) is shown, resulting from ML inference performed in MEGA11. For each node, the ML bootstrap (MLBS) if  $>70\%$  is presented. Clade designations follow Hanns & Moreau (2017) and Codjia et al. (2023). New species highlighted in red, bar indicating the expected number of substitutions per site.



**Fig. 2.** *Amanita magna*. **A–C.** Basidiomata. **A.** HL1067 (holotype). **B.** HL094A. **C.** HRL3234. **D.** Details of lamellar trama in SDS Congo Red. **E.** Basidiospores in water. **F.** Hymenium in SDS Congo Red. Scale bars D, F 10 µm; E 5 µm.

**Holotypus.** – CANADA, Québec, Québec City, boisé Neilson, 46° 45' 24.2" N, 71° 19' 20.6" W, under *Fagus grandifolia*, *Quercus rubra*, and *Abies balsamea*, 28 August 2011, *leg.* H. Lambert, HL1067 (QFB35506; holotype). Sequences ex-holotype: PP796114 (ITS).

**Description.** – Pileus 80–140 mm in diameter, rounded conical then appanate, slightly depressed with a prominent umbo, smooth, dark brown to greyish brown at umbo (6EF6, 6F5, 6F3), progressively paler down to the marginal striations (6CD3), brown (6D3, 6D4, 6DE6) at margin, striate

on 30–40 % of the pileus radius. – Lamellae free, close, whitish to brownish, up to 10 mm broad, with truncate lamellulae of various length. – Stipe 200–330 × 10–20 mm, cylindrical to slightly tapering upward, covered entirely or partially with dense greyish brown fibrils (6DE3½) arranged in a zebroid pattern with age, stuffed then hollow. – Annulus absent. – Universal veil membranous, white, forming a saccate volva 30–60 mm long almost completely buried in soil. – Context white, unchanging when cut or bruised. – Odor and taste

not distinctive. – Spore deposit white. – Basidiospores [1040/10/7] (7.7)9.0–11.0(13.2) × (7.3)8.3–10.2(12.0) μm, on average 10.0 × 9.3 μm, Q = (1.00)1.03–1.13(1.22), Qm = 1.08, globose to subglobose, smooth, thin-walled, hyaline, inamyloid, cyanophilic. – Lamellar trama 60–120 μm thick, made of branching filamentous hyphae 2–7.5 μm wide connected with ellipsoid to subfusiform inflated cells measuring 20–45(70) × 7–20(25) μm. – Subhymenium ramose to inflated-ramose, 18–32 μm thick, in 3–4 layers, made of cylindrical, inflated to irregularly-shaped cells measuring 7.5–20 × 5.5–13(18) μm. – Basidia 47–60 × 12–18 μm, clavate, 4-spored. – Volva almost homogenous, 550–1200 μm thick; external layer composed of parallel filamentous hyphae 3–7.5(11) μm wide arranged vertically; central and internal layer mostly composed of ± interwoven filamentous hyphae 3–7(9) μm wide, of rare globose (a- or shortly pedunculate), subglobose to pyriform inflated cells measuring 40–100 × (20)40–80(100) μm, and of very rare cylindrical, fusoid, sometimes branched, and inflated cells in chains measuring 55–120 × 11–28(48) μm. – Clamp connections absent.

**Etyymology.** – From the Latin *magna*, large, referring to the large size of the basidiomata.

**Habitat and distribution.** – Solitary to gregarious, under *F. grandifolia* and *Q. rubra*, from July to September in Canada. Known from Québec, in Canada, and according to the ITS sequences available in public databases (labelled as *Amanita* sp. '*albemarlandensis*'), from the states of Connecticut, Kentucky, New York, North Carolina, and Virginia in the USA.

**Additional material examined.** – CANADA. Québec, Saint-Jean-Chrysostome, under *F. grandifolia*, *Betula alleghaniensis*, and *Acer* sp., 16 August 1996, leg. Y. Lamoureux, YL2877 (CMMF002877); *ibid.*, in deciduous forest, 12 August 2017, leg. J. Landry, HL061A (QFB32879); Québec City, boisé Neilson, in deciduous forest of *F. grandifolia* and *Q. rubra*, 12 August 2020, leg. H. Lambert, HL094A (QFB32910); *ibid.*, 28 July 2021, leg. H. Lambert, HL141; *ibid.*, 21 August 2022, leg. H. Lambert, HL197; *ibid.*, 20 August 2020, leg. R. Lebeuf, HRL3234 (QFB32867); Réserve Nationale de faune du Cap Tourmente, in mixed forest of *F. grandifolia*, *T. canadensis*, and *Populus tremuloides*, 28 July 2023, leg. H. Lambert, HL224 (QFB32867).

**Notes.** – The ITS sequence of the holotype is distinct from other species of section *Vaginatae* clade 1, deviating from its closest relative, an undescribed species labelled *Amanita* sp. '*semiobruta*', by more than 25 substitutions and indels (93 % identity) (Fig. 1). The zonate dark brown to grey-brown pileus and the long stipe developing a zebroid pattern with age are stable characters of *A.*

*magna*. *Amanita elongatior*, described below, differs by the presence of yellow tones in the pileus and the azonate pileus. Both are large but rare species associated with deciduous trees. *Amanita piceina*, described below, is similar in size but grows under *Picea*. Small basidiomata of *A. magna* could also be confused with *A. fuscozonata* and *A. fusca*, described below, which have a paler stipe, white to light grey, not deeply buried in the soil. Found in the coastal forests of western North America, from southwestern Canada to central California, *Amanita pachycolea* D.E. Stuntz is similar, but grows under *Pinus* (Thiers & Ammirati 1982, Siegel & Schwarz 2016).

**Authors:** H. Lambert, Y. Lamoureux, J. Landry & R. Lebeuf

## Basidiomycota, Agaricomycetes, Agaricales, Amanitaceae

### *Amanita* Section *Vaginatae*

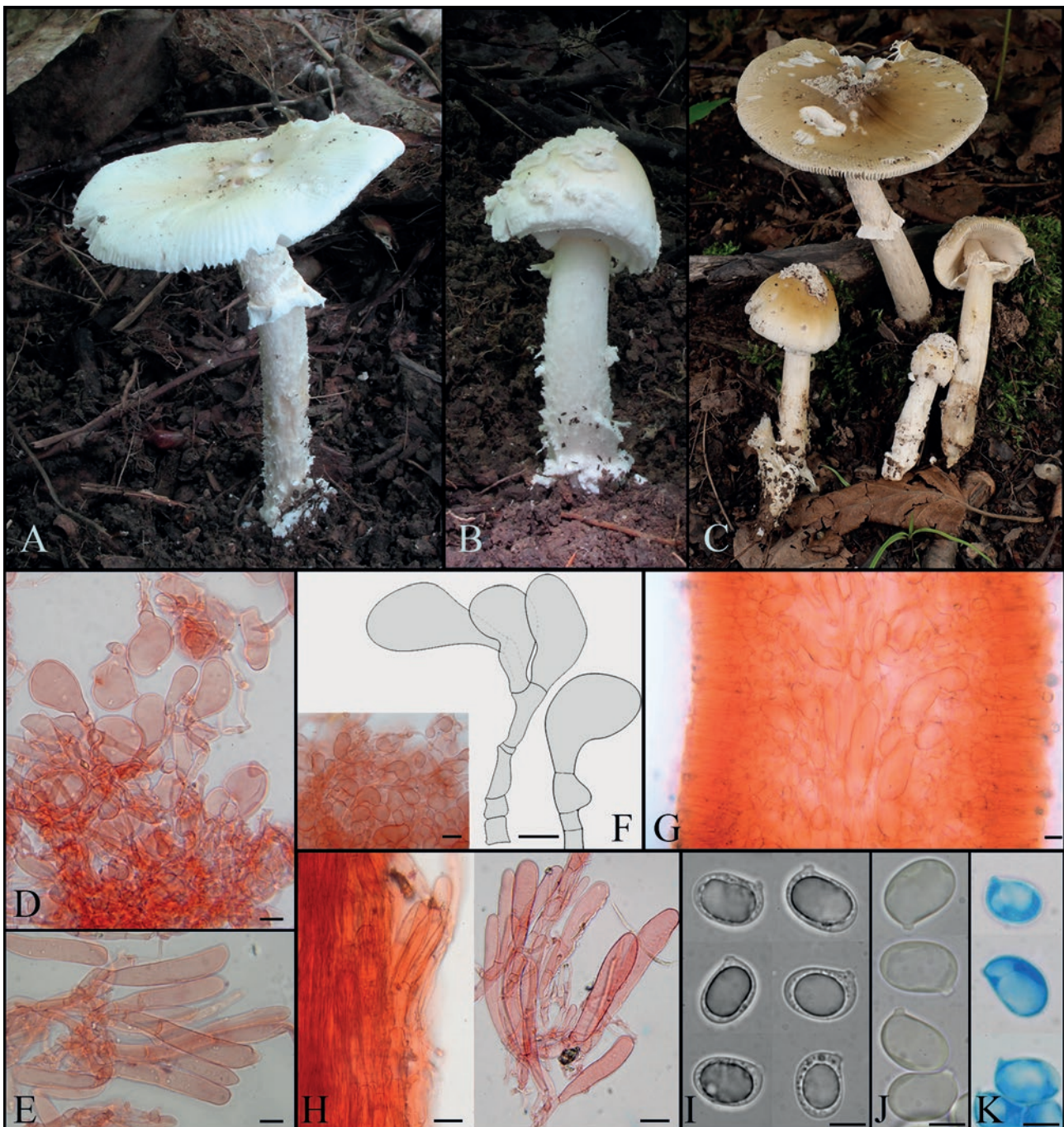
*Amanita cingulatoides* H. Lambert & J. Landry, sp. nov. – Figs. 1, 3

MycoBank no.: MB 854396

**Diagnosis.** – Differs from its sister annulate species *Amanita cingulata* by the cream pileus which becomes yellowish brown with age, white friable universal veil browning with age, broader spores (9.1–11.1 × 6.6–7.8 μm vs. 9–11.5 × 5.5–7 μm in *A. cingulata*), and geographic location (Canada vs. China).

**Holotypus.** – CANADA. Québec, Québec City, 46° 47' 33.7" N, 71° 21' 50.3" W, in mixed forest of *Populus tremuloides*, *Betula papyrifera*, and young *Abies balsamea*, 13 July 2023, leg. H. Lambert, HL081A (QFB32897; holotype). Sequences ex-holotype: PP762934 (ITS).

**Description.** – Pileus 44–120 mm in diameter, convex then applanate, with or without a low umbo, at first pale cream (5A2) with white margin, with age becoming golden to greyish orange (5AB4½), yellowish brown (5EF6½) on disk, adorned with warts or small to medium patches from the universal veil; margin paler, striate on 20–33 % of the pileus radius. – Lamellae free, close, thin, whitish, flocculose at the edge, 4–9 mm broad, with a few truncate lamellae. – Stipe 60–140 × 5–12 mm, subcylindrical or slightly narrowing upward, fibrillose to floccose, often with a zebroid pattern better seen between the annulus and apex, whitish, turning brown when bruised at least at the base, stuffed then hollow. – Partial veil membranous, thin, fugacious, leaving an annulus on the stipe or remnants at the pileus margin, upper side flocculose, underside smooth, whitish. – Universal veil friable, woolly, leaving patches or warts on the pileus and ringlike remnants at stipe base,



**Fig. 3.** *Amanita cingulatoides*. **A–C.** Basidiomata. **A, B.** HL081A (holotype). **C.** HL217. **D–H.** Microscopic details in SDS Congo Red. **D.** Inflated hyphae at the upper side of partial veil. **E.** Elongated hyphae at the underside of partial veil. **F.** Inflated cells from lamellar edge. **G.** Lamellar trama. **H.** Stipitipellis (left) and acrophysalids from stipitipellis (right). **I–H.** Basidiospores in water (I) in Melzer's reagent (J), and in Cotton Blue (K). Scale bars D, E, G 10  $\mu\text{m}$ ; F, H 20  $\mu\text{m}$ ; I–K 5  $\mu\text{m}$ .

whitish then brownish (6C4). – Context thin, white, becoming slightly brownish when cut or bruised. – Odor indistinct. – Spore deposit white. – Basidiospores [953/12/8] (8.0)9.1–11.1(13.5)  $\times$  (5.7)6.6–7.8(9.2)  $\mu\text{m}$ , av. 10.1  $\times$  7.2  $\mu\text{m}$ , Q

= (1.17)1.27–1.57(1.82),  $Q_m$  = 1.41, ellipsoid to broadly ellipsoid, smooth, thin-walled, hyaline, inamyloid, cyanophilic. – Lamellar trama 60–130  $\mu\text{m}$  thick, made of branching filamentous hyphae 3–8  $\mu\text{m}$  wide connected with abundant cylindrical,

ellipsoid to subfusiform inflated cells 15–60 × 8–30 µm. – Subhymenium ramose to inflated-ramose, 16–32 µm thick, in 2–3 layers, made of cylindrical, inflated to irregularly-shaped cells measuring 8–17 × 4–11 µm. – Basidia 38–52 × 11–16 µm, clavate, 1-, 2- or 4-spored. – Volva 1000–1200 µm thick in young specimens before fragmentation, without clear layers, composed of filamentous hyphae 2.5–7(10) µm wide, of globose, subglobose or sometimes pyriform cells up to 60(90) × 60 µm, very abundant inside the volva context, and of infrequent cylindrical, ellipsoid or fusoid inflated cells in chains measuring 25–50(85) × 10–25(40) µm, the proportion of filamentous hyphae increasing from the inside to the outside of the volva. – Velar remnants on pileus more than 600 µm thick, composed homogeneously of globose to subglobose cells measuring 20–50(60) × 18–45 µm, of much less frequent filamentous hyphae 3–7 µm wide, and of inflated cells in chains measuring 30–70 × 9–20(30) µm. – Partial veil 200–260 µm thick, composed of interwoven, branching and thin-walled filamentous hyphae 2.5–6.5 µm wide, ending on the upper side with subglobose, pyriform to spheropedunculate inflated cells measuring (12)19–36(45) × 9–29 µm, and on the underside with abundant cylindrical or pyriform-elongate inflated cells sometimes 1–2 septate measuring 44–100 × (7)10–14(17) µm and arranged in a cutis. – Stipitipellis a cutis made of thin-walled colorless filamentous hyphae 3–6(7) µm wide; subpellis containing clavate acrophysalids measuring 55–160 × 10–22 µm, some in clusters erected as a trichoderm. – Clamp connections absent.

**Etymology.** – From the Latin *cingulatus*, cingulate, and *oides*, similar to, referring to the similarity with its sister annulate species *A. cingulata*.

**Habitat and distribution.** – Solitary, in subhydric clay soils in mixed forests of *P. tremuloides*, *B. papyrifera*, and *Abies balsamea*, in July. Thus far found only in the Québec City area, in Canada.

**Additional material examined.** – CANADA. Québec, Québec City, in mixed forest of *P. tremuloides*, *B. papyrifera*, *Picea* sp., and *Abies balsamea*, 9 July 2020, leg. H. Lambert, HL075A (QFB32891); *ibid.*, 28 July 2021, HL139 (QFB33051); *ibid.*, 22 July 2022, HL170A (QFB35512), HL171A (QFB35513); *ibid.*, 13 July 2023, HL215 (QFB35524), HL216 (QFB35525), HL219 (QFB35527), HL220 (QFB35528).

**Notes.** *Amanita cingulatooides* differs from all other *Amanita* section *Vaginatae* in northeastern North America by the presence of an annulus, the small velar remnants left on the pileus, and its ellipsoid basidiospores. Confusion is possible with

pale forms of *A. russuloides* Peck growing in the same habitat, but that species has a smooth subbulbous stipe, usually with a distinct collar above the small bulb (Bunyard & Justice 2020). *Amanita farinosa* Schwein., another small and pale *Amanita*, has a grey to brownish grey universal veil leaving powdery material on the whitish pileus, lacks an annulus, produces smaller spores, and is associated with *Quercus* and *Fagus* (Tulloss & Yang 2024). The ITS sequence of the holotype is unique in section *Vaginatae* clade 1, differing by more than 12 substitutions-indels from its closest relative, an undescribed annulate species from Indiana, USA, labelled *Amanita* sp. IN02 (Tulloss & Yang 2024), and by more than 25 substitutions and indels from *A. cingulata* J.W. Liu & Zhu L. Yang, an annulate species from China (Fig. 1). The former differs from *A. cingulatooides* by its orange-tan pileus and growth close to *Quercus*, while the latter is almost white and is associated with Fagaceae and Pinaceae (Liu 2017). Most others annulate *Vaginatae* were described from Africa (Tang 2015), except for *A. basiana* Tulloss & M. Traverso, from Italy (Tulloss & Traverso 2001).

Most *Amanita* in section *Vaginatae* have a sterile lamellar edge composed of undifferentiated hyphae ending with one or more globose, subglobose or spheropedunculate inflated cells better seen on young specimen. In *A. cingulatooides*, the upper side of the annulus is made of the same elements than the lamellar edge. This supports the hypothesis that elements of the lamellar edge in section *Vaginatae* originate from the aborted partial veil after cleavage of lamellae from adjacent tissue during development of the hymenophore (Bas 1969, Reijnders 1963, Neville & Poumarat 2004). It should also be noted that the elements on the underside of *A. cingulatooides* annulus are similar to the acrophysalids from the stipe.

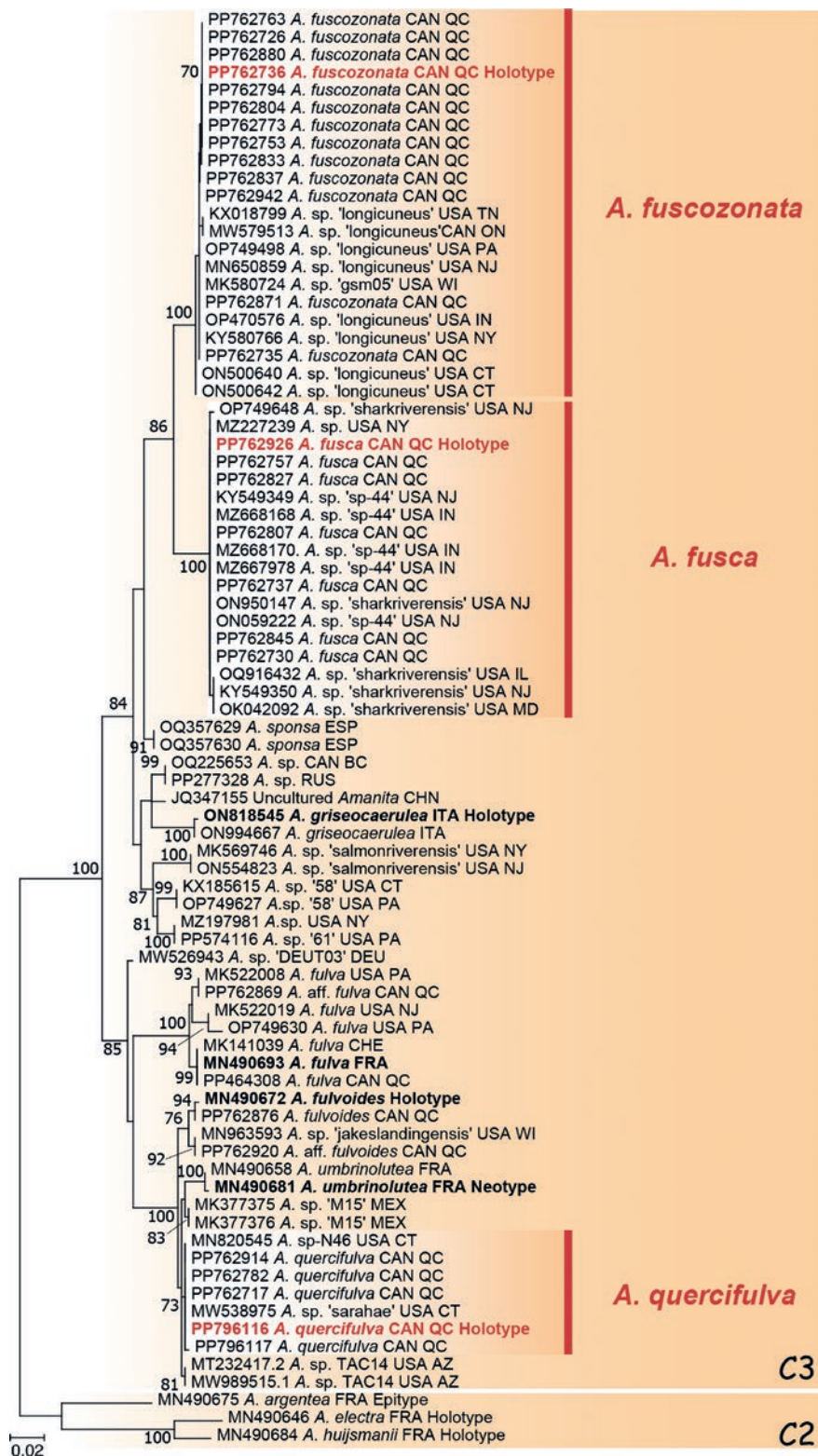
**Authors:** H. Lambert, G. Fortin, R. Lebeuf & J. Landry

## Basidiomycota, Agaricomycetes, Agaricales, Amanitaceae

### *Amanita* section *Vaginatae*

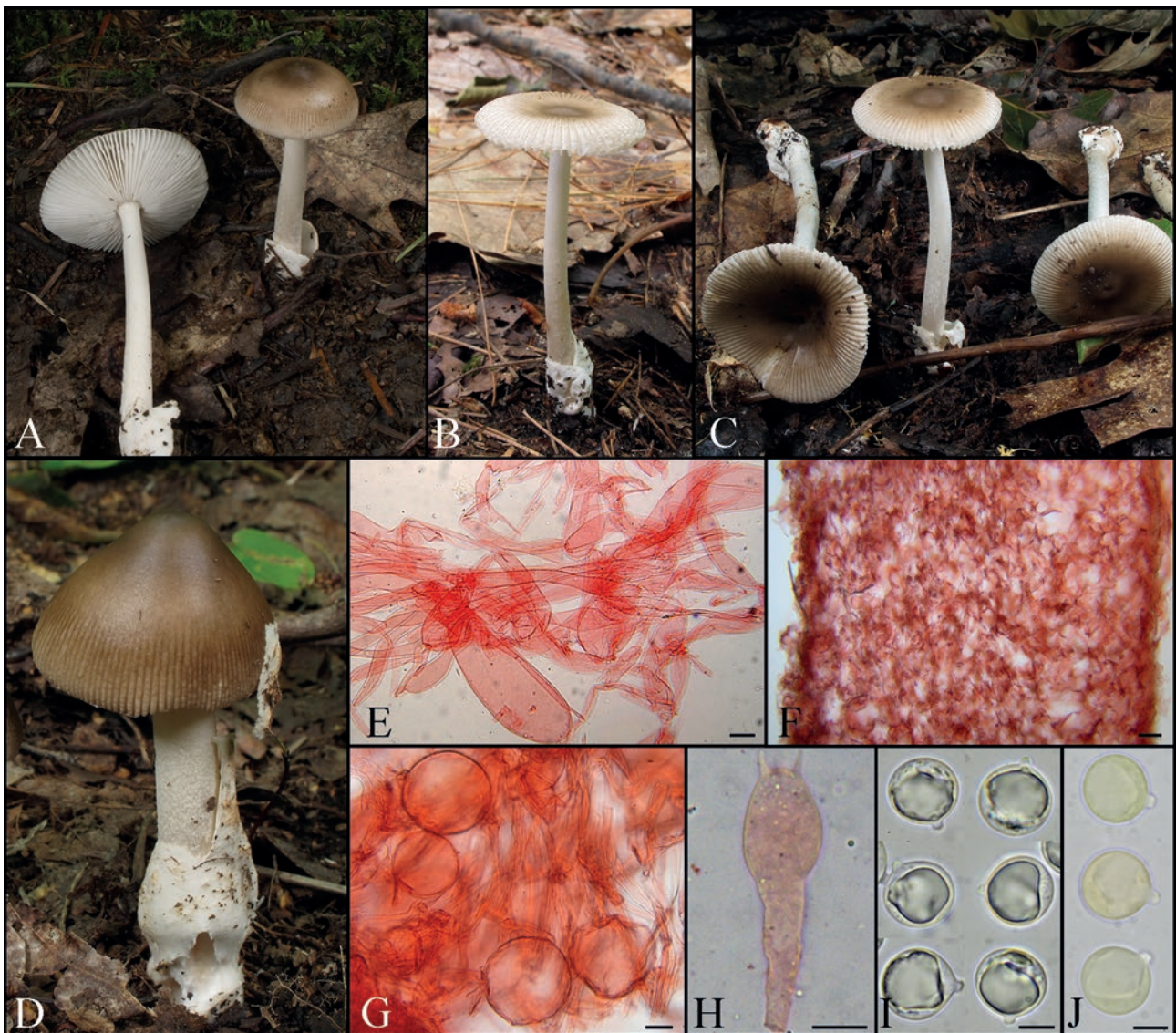
*Amanita fuscozonata* H. Lambert, Lebeuf, Y. Lamoureux & J. Landry, **sp. nov.** – Figs. 4, 5  
Mycobank no.: MB 854397

**Diagnosis.** – Differs from other grey-brown species of *Amanita* section *Vaginatae* by the combination of medium-size, zonate, greyish brown pileus, white to very light brown stipe, membranous universal veil leaving a white volva, and growth with deciduous trees.



**Fig. 4.** Phylogeny of selected *Amanita* species in section *Vaginatae* Clade 3 reconstructed from an ITS dataset using species from Clade 2 as outgroup. The tree topology with the highest log likelihood ( $-\ln L = 2488.97$ ) is shown, resulting from ML inference performed in MEGA11. For each node, the ML bootstrap (MLBS) if  $>70\%$  is presented. Clade designations follow Hanns & Moreau (2017) and Codjia et al. (2023). New species highlighted in red, bar indicating the expected number of substitutions per site.





**Fig. 5.** *Amanita fuscozonata*. **A–D.** Basidiomata. **A.** HL096A (holotype). **B.** HL057A. **C.** HL100A. **D.** HL143A. **E–H.** Microscopic details in SDS Congo Red. **E.** Lamellar trama hyphae. **F.** Volva. **G.** Central layer of volva. **H.** Basidia. **I, J.** Basidiospores in water (I) and in Melzer's reagent (J). Scale bars E, G, H 10  $\mu\text{m}$ ; F 50  $\mu\text{m}$ ; I, J 5  $\mu\text{m}$ .

**Holotypus.** – CANADA. Québec, Québec City, boisé Neilson, 46° 45' 24.8" N, 71° 19' 25.3" W, in mixed forest of *Abies balsamea*, *Quercus rubra*, and *Fagus grandifolia*, 12 August 2020, leg. H. Lambert, HL096A (QFB32912; holotype); Sequences ex-holotype: PP762736 (ITS)

**Description.** – Pileus 30–70 mm in diameter, convex to rounded-conical when young, soon becoming campanulate then applanate, slightly to strongly depressed with age, with a small to prominent umbo, smooth, greyish brown, brownish orange to brown (5B3, 5CD4, 5C5, 5E6, 6DE4), darker at disk (5F5, 7F7), with a paler zone at mid-radius; margin striate on 30–50 % of the pileus radius, some-

times tuberculate. – Lamellae free, subdistant to close, 3–8 mm broad, with truncate lamellulae, whitish to cream (4A2½). – Stipe 60–150(200)  $\times$  3–12 mm, tapering upward, stuffed then hollow, finely covered with thin white fibrils becoming light brown (5½B2) with age and forming or not a zebroid pattern. – Annulus absent. – Universal veil membranous, white, thin, fragile, leaving a saccate volva 20–40 mm high, adnate at base, flaring above. – Context white, unchanging when cut or bruised. – Odor not distinctive. – Spore deposit white. – Basidiospores [1026/14/9] (8.8)9.8–11.2(12.7)  $\times$  (8.1)9.2–10.6(11.7)  $\mu\text{m}$ , on average 10.2  $\times$  9.5  $\mu\text{m}$ , Q

= (1.00)1.02–1.10(1.15), Qm = 1.06, globose to subglobose, smooth, thin-walled, hyaline, inamyloid, cyanophilic. – Lamellar trama 50–100 µm thick, made of relatively abundant branching filamentous hyphae 3–7.5(11) µm wide connected with ellipsoid to subfusiform inflated cells up to 110 × 30 µm. – Subhymenium ramose to inflated-ramose, 15–30 µm thick, in 3–4 layers, made of cylindrical, inflated to irregularly-shaped cells measuring 7–20 × 6–16 µm. – Basidia 45–65 × 14–17 µm, clavate, 4-spored. – Volva 3-layered: external layer 35–80 µm thick, central layer 200–900 µm thick, internal layer 25–55 µm thick; external and internal layers composed exclusively of filamentous hyphae 4–6(7) µm wide; central later composed of filamentous hyphae (3)4–10 µm wide regularly distributed, less frequent globose cells 30–60 µm wide and rare inflated cells in chains measuring up to 120 × 30 µm. – Clamp connections absent.

**Etymology.** – Referring to the dark grey-brown zonations of the pileus.

**Habitat and distribution.** – Solitary or in small groups under various deciduous trees (*Betula*, *Quercus*, *Fagus*), from July to September in Québec and Ontario, Canada. Collections of *Amanita* sharing the same ITS sequence in public databases were made in almost all the eastern states of the USA, from Indiana to the Atlantic coast and from the Canadian border down to North Carolina.

**Additional material examined.** – CANADA. Québec, Longueuil, 9 July 1992, leg. Y. Lamoureux, YL1645 (CMMF001645); Sainte-Catherine-de-la-Jacques-Cartier, in mixed forest of *B. alleghaniensis*, *Abies balsamea*, and *P. tremuloides*, 7 July 2012, leg. H. Lambert, HL003 (QFB 35496); Québec City, boisé Neilson, in mixed forest of *Abies balsamea* and *Quercus* sp., 25 August 2013, leg. H. Lambert, HL029 (QFB 35503); *ibid.*, 12 August 2020, HL100 (QFB32916); *ibid.*, 23 July 2022, HL175A; Longueuil, in forest of *Q. rubra*, 6 July 1992, leg. Y. Lamoureux, YL1633 (CMMF001633); Québec City, under *F. grandifolia*, 3 August 2022, leg. H. Lambert, HL185A; Sainte-Croix-de-Lotbinière, in deciduous forest of *F. grandifolia* and *Quercus* sp., 17 July 2016, leg. H. Lambert, HL057A (QFB32876); Québec City, Parc de la Plage-Jacques-Cartier, in deciduous forest of *Quercus* sp. and *F. grandifolia*, 13 August 2020, leg. H. Lambert, HL104A (QFB32920); *ibid.*, 27 July 2021, HL133 (QFB33045), HL134 (QFB33046); Sainte-Pétronille, in mixed forest of *F. grandifolia*, *Quercus* sp., *P. tremuloides*, *B. alleghaniensis*, and *Tsuga canadensis*, 29 July 2021, leg. H. Lambert, HL143 (QFB33055); Saint-Casimir, rang Saint-Charles, in mixed forest of *B. alleghaniensis* and *T. canadensis*, 1 August 2020, leg. R. Lebeuf & A. Paul, HRL3173 (QFB32862); Saint-Stanislas, Parc de la rivière Batiscan, Murphy sector, in deciduous forest of *F. grandifolia*, *P. tremuloides*, and *B. alleghaniensis*, 7 August 2020, leg. R. Lebeuf & A. Paul, HRL3197 (QFB32866); Saint-Stanislas, Parc de la rivière Batiscan, Barrage sector, in mixed forest of *Fraxinus* sp., *P. tremuloides*, and *Abies balsamea*, 24 September 2020, leg. R. Lebeuf & A. Paul, HRL3323 (QFB32869); Champlain, rang Saint-Pierre, in deciduous forest of *Acer* sp. and *F. grandifolia*, 26

July 2022, leg. R. Lebeuf & A. Paul, HRL3741; Saint-Ubalde, Parc naturel régional de Portneuf, Lac Carillon, in mixed forest of *B. alleghaniensis*, *A. balsamea*, and *T. canadensis*, 16 August 2022, leg. R. Lebeuf & A. Paul, HRL3830, HRL3831.

**Notes.** – *Amanita fuscozonata* has an ITS distinct from other members of section *Vaginatae* clade 3, differing by 18 substitutions and indels from its closest relative, the newly described *Amanita fusca* (Fig. 4). The pileus is typically greyish brown to brown, darker at disk, and shows a paler band above the striations; the margin may appear paler when the pileus is expanded. The stipe is variable in size and can reach 200 mm in length. *Amanita fusca*, described below, is very similar, but its pileus is more uniformly colored, and it has slightly larger spores on average (10.9 × 10.4 µm) than *A. fuscozonata* (10.2 × 9.5 µm), with a similar average Q = 1.05 vs. 1.06. *Amanita pulla*, described below, also associated with deciduous trees, has a pileus more uniformly colored dark grey to dark brownish grey, without brownish orange tint, and spores with a larger average Q of 1.25. *Amanita brunneofulginea* Zhu L. Yang, a highly variable cosmopolitan species described from China and reported from northeastern North America (as *Amanita subnigra* Y. Lamoureux nom. prov. in Lamoureux 2006), has a darker pileus, its volva is often covered with orange-brown patches in the North American form, and it is associated with Pinaceae (Hanss & Moreau 2017). In *Amanita sinicoflava* Tulloss, the pileus is sometimes zonate but it is olive yellow, and the white volva becomes greyish with age (Tulloss 1988). *Amanita pachycolea* D.E. Stuntz, a common species in western North America, also has a zonate dark brown pileus, but it is more robust, and its long and thick white saccate volva develops ochraceous spots with age (Thiers & Ammirati 1982, Siegel & Schwarz 2016).

**Authors:** H. Lambert, Y. Lamoureux, R. Lebeuf & J. Landry

## Basidiomycota, Agaricomycetes, Agaricales, Amanitaceae

### *Amanita* section *Vaginatae*

*Amanita fusca* H. Lambert, Lebeuf & J. Landry, **sp. nov.** – Figs. 4, 6

MycoBank no.: MB 854398

**Diagnosis.** – Differs from other grey-brown species of *Amanita* section *Vaginatae* by the combination of medium-size pileus with dominant brown colors, white to brownish stipe, membranous universal veil leaving a white volva, and growth with deciduous trees.

**Holotypus.** – CANADA. Québec, Québec city, boisé Neilson, 46° 45' 23.1" N, 71° 19' 19.2" W, under *Quercus rubra*



**Fig. 6.** *Amanita fusca*. **A–C.** Basidiomata. **A.** HL097A (holotype). **B.** HL189A. **C.** HRL3393. **D–F.** Basidiospores in water (D), in Melzer's reagent (E), and in Cotton Blue (F). **G.** Pileipellis (top) and pileus context (bottom) in water. Scale bars D–F 5 µm, G 20 µm.

and *Fagus grandifolia*, on clay soil, 12 August 2020, *leg.* H. Lambert, HL097A (QFB32913; holotype). Sequences ex-holotype: PP762926 (ITS)

**Description.** – Pileus 30–70 mm in diameter, rounded-conical, becoming campanulate then appanate, slightly to strongly depressed with age, with a small to prominent umbo, smooth, brownish orange, brown to greyish brown (5C5, 5E6, 6½C3, 6C3½, 6E4), darker at disk (5E4, 5EF7); margin paler, striate and often tuberculate on 20–50 % of the pileus radius. – Lamellae free, subdistant to close, 3–6 mm broad, with 0–1 tier of truncate lamellulae of varying length, whitish to cream (4A2). – Stipe 80–120 × 5–12 mm, tapering upward, whitish, pruinose at the apex, covered below with fine white then light brown (6B4) fibrils, stuffed then hollow. – Annulus absent. – Universal veil membranous, white, thick, leaving a

saccate volva 20–40 mm high, adnate at base, flaring above. – Context white, unchanging when cut or bruised. – Odor not distinctive. – Spore deposit white. – Basidiospores [522/6/5] (8.9)10.0–11.6(13.1) × (7.8)9.4–11.1(12.4) µm, on average 10.9 × 10.4 µm, Q = (1.00)1.01–1.10(1.17), Qm = 1.05, globose to subglobose, smooth, thin-walled, hyaline, inamyloid, cyanophilic. – Lamellar trama 100–130 µm broad, made of abundant branching filamentous hyphae 2.5–6 µm wide connected with ellipsoid to subfusiform inflated cells measuring 20–55 × 8–18 µm. – Subhymenium ramose to inflated-ramose, 15–25 µm thick, in 3–4 layers, made of cylindrical to irregularly-shaped cells measuring 7–20 × 3–7 µm. – Basidia 47–60 × 13–19 µm, clavate, 4-spored. – Volva 3-layered: external layer 150–280 µm thick, central layer 300–700 µm thick, internal layer 180–320 µm thick; external and inter-

nal layers predominantly made of filamentous hyphae (1.5)2.5–5  $\mu\text{m}$  wide, with few globose cells; central layer made of regularly distributed filamentous hyphae 2.5–5  $\mu\text{m}$  wide, of less frequent globose cells 10–40  $\mu\text{m}$  wide, and of rare inflated hyphae in chains measuring up to 60  $\times$  20  $\mu\text{m}$ . – *Pileipellis* 2-layered; upper layer gelatinized, 40–70  $\mu\text{m}$  thick, composed of scattered, repent hyphae 2.5–4.5  $\mu\text{m}$  wide; lower layer 40–100  $\mu\text{m}$  thick, made of interwoven filamentous hyphae 3–9  $\mu\text{m}$  wide and of brown-pigmented cylindrical, ellipsoid or pyriform inflated cells 35–40  $\times$  10–20  $\mu\text{m}$  in chain or terminal. – **Clamp connections** absent.

**E t y m o l o g y.** – From the Latin *fuscus*, dark, referring to the dark brown pileus.

**Habitat and distribution.** – Solitary or in small groups under deciduous trees, from July to September in Québec, Canada, and in the states of Maryland, New Jersey, Pennsylvania and Wisconsin in the USA based on ITS sequences available in public databases.

**Additional material examined.** – CANADA. Québec, Lévis, parc Valéro, in mixed forest of *Quercus rubra* and *Fagus grandifolia*, 4 September 2021, leg. H. Lambert, HL149 (QFB33061); Québec City, boisé Marly, in mixed forest of *Q. rubra* and *F. grandifolia*, 3 August 2022, leg. H. Lambert, HL187A (QFB35515); Québec City, in forest of *Q. rubra*, *F. grandifolia*, and *P. tremuloides*, 12 August 2022, leg. H. Lambert, HL189A (QFB35516); Québec City, close to Jean-Lesage airport, in deciduous forest of *Populus* sp. and *B. papyrifera*, 16 August 2022, leg. H. Lambert, HL194A (QFB35518); Saint-Ubalde, in mixed forest of *Abies balsamea* and *B. papyrifera*, 10 August 2021, leg. R. Lebeuf & G. René, HRL3393 (QFB33072).

**Notes.** – *Amanita fusca* formed a highly supported sister group with *A. fuscozonata*, but their ITS sequence similarity is less than 94 % (18 substitutions and indels) (Fig. 4). These two species are very similar and could be very difficult to separate based on the morphological characters and habitat. The pileus of *A. fusca* is more uniformly colored, whereas it is more distinctly zonate and may appear paler at the margin in *A. fuscozonata*. *Amanita fusca* has slightly larger spores on average (10.9  $\times$  10.4  $\mu\text{m}$ ) than *A. fuscozonata* (10.2  $\times$  9.5  $\mu\text{m}$ ), but with a similar average Q of 1.05 vs. 1.06. *Amanita pulla*, described below, is also associated with deciduous trees but has a uniformly-colored dark grey pileus, in some collections dark grey only at disk and much paler grey elsewhere. *Amanita brunneofulginea* Zhu L. Yang has a darker pileus, its volva is often covered with orange-brown patches in the North American form, and it is associated with Pinaceae (Hanss & Moreau 2017). In *Amanita sinicoftava* Tulloss, the pileus is olive yellow, sometimes

zonate and the white volva becomes greyish with age (Tulloss 1988).

**Authors:** H. Lambert, R. Lebeuf & J. Landry

## Basidiomycota, Agaricomycetes, Agaricales, Amanitaceae

### *Amanita* section *Vaginatae*

*Amanita quercifulva* Lebeuf, H. Lambert, A. Paul & J. Landry, **sp. nov.** – Figs. 4, 7

MycoBank no.: MB 854399

**Diagnosis.** – Differs from other species of section *Vaginatae* by the combination of yellow-orange pileus, darker in the center and often paler at mid-radius, white membranous volva developing brownish orange stains with age, and growth in deciduous forests including *Quercus*.

**Holotypus.** – CANADA. Québec, Boucherville, 45° 35' 48.9" N, 73° 23' 44.4" W in deciduous forest of *Quercus rubra*, *Carpinus caroliniana*, and *Carya ovata*, 6 July 2013, leg. R. Lebeuf & A. Paul, HRL1466 (DAOM 984973; holotype). Sequences ex-holotype: PP796116 (ITS).

**Description.** – **Pileus** 27–65 mm in diameter, paraboloid to campanulate, then applanate-umbonate, when young yellow-orange (4½A6), then paler yellow-orange (4½A4) with a yellowish-brown disk (5E7½), often paler at mid-radius, without veil remnants; margin straight becoming reflexed in age, striate on 35–40 % of the pileus radius. – **Lamellae** free, close, white, 4–5 mm broad, with 0–1 tier of lamellulae. – **Stipe** 95–135  $\times$  5–8 mm, tapering toward the apex, white-flocculose at apex, below covered with short white fibrils often forming a zebroid pattern on a yellow-orange background. – **Annulus** absent. – **Universal veil** 30–50 mm high, membranous, white, leaving at stipe base a saccate volva which is adnate in the lower third and flaring above, and which discolors brownish orange with age. – **Context** white, unchanging when cut or bruised. – **Odor** not distinctive. – **Taste** mild. – **Spore deposit** white. – **Basidiospores** [397/7/4] (9.3)10.2–12.6(14.5)  $\times$  (8.4)9.7–12.2(13.9)  $\mu\text{m}$ , on average 11.3  $\times$  11.0  $\mu\text{m}$ , Q = (1.00)1.01–1.08(1.16), Qm = 1.03, globose to subglobose, smooth, thin-walled, hyaline, inamyloid, cyanophilic. – **Lamellar trama** 60–120  $\mu\text{m}$  thick, made of branching filamentous hyphae 3–11  $\mu\text{m}$  wide connected with ellipsoid to subfusiform inflated cells measuring 15–60  $\times$  8–25  $\mu\text{m}$ . – **Subhymenium** ramoso to inflated-ramoso, 18–30  $\mu\text{m}$  thick, in 2–4 layers, made of cylindrical, inflated to irregularly-shaped cells measuring 8–17  $\times$  6–13  $\mu\text{m}$ . – **Basidia** 45–60  $\times$  13–20  $\mu\text{m}$ , clavate, 4-spored. – **Volva** 3-layered: external layer 30–200  $\mu\text{m}$  thick, central layer 300–600  $\mu\text{m}$  thick, internal layer 35–100  $\mu\text{m}$  thick; external and internal layers composed exclusively of filamentous



**Fig. 7.** *Amanita quercifulva*. **A–C.** Basidiomata. **A.** HRL1466 (holotype). **B.** HRL1475. **C.** HL131. **D.** Lamellar trama in SDS Congo Red. **E, F.** Basidiospores in water (**E**) and in Melzer's reagent (**F**). Scale bars **D** 20  $\mu\text{m}$ ; **E, F** 5  $\mu\text{m}$ .

hyphae 3.5–9  $\mu\text{m}$  wide; central layer composed of regularly distributed filamentous hyphae 3–7(10)  $\mu\text{m}$  wide, of less frequent globose cells, up to 55  $\mu\text{m}$  wide, and of rare inflated cells in chains measuring up to 120  $\times$  20  $\mu\text{m}$ . – Clamp connections absent.

**Etymology.** – Referring to the similarity with *Amanita fulva* Fr. and the distinctive association with *Quercus*.

**Habitat and distribution.** – Solitary or in small groups in argillaceous soils of deciduous

forests of *Quercus*, *Carya*, *Carpinus*, and *Betula*, in July and August. Probably associated with *Quercus*. Thus far known from Québec, in Canada, and from the states of Arizona, Connecticut, and Pennsylvania in the USA, based on the ITS sequences available in public databases.

**Additional material examined.** – CANADA. Québec, Sainte-Anne-de-Bellevue, in deciduous forest of *Q. rubra* and *B. papyrifera*, 7 July 2013, leg. R. Lebeuf & A. Paul, HRL1475; Québec City, in deciduous forest of *Q. rubra* and *F.*

*grandifolia*, 27 July 2021, leg. H. Lambert HL131 (QFB33043), HL132 (QFB33044).

**Notes.** – *Amanita quercifulva* has a clearly distinct ITS among other members of *Amanita* section *Vaginatae* clade 3. The sequence differs by 7 and 11 substitutions and indels from its closest relatives *A. fulvoldes* Neville & Poumarat and *A. umbrinolutea* (Secr. ex Gillet) Bataille, respectively (Fig. 4). *Amanita fulvoldes* differs by its pileus color that quickly changes from rusty brown in young age to grey-brown, and by the usually brown lamellar edge in mature basidiomata (Neville & Poumarat 2009). *Amanita umbrinolutea*, known from Europe, differs by its grey-brown pileus with a narrow darker zone (almost black) right above the striations, the usually brown lamellar edge in mature basidiomata, and its association with conifers (Roux 2006). *Amanita quercifulva* is mainly distinguished from *Amanita fulva* Fr. by its more orange tint and probable association with *Quercus*, the latter being usually found under conifers (*Abies*, *Picea*, *Tsuga*) and *Betula*, often in damp soils. Species of the *Amanita crocea* complex display a more vivid yellow-orange to orange pileus. *Amanita olivaceodisca*, described below, is similar, but its pileus usually has an olive tint at disk and its volva does not discolor brownish orange with age. *Amanita sinicoflava* Tulloss has an olivaceous yellow pileus and a volva which turns grey with age (Tulloss 1988). Our ITS sequences are a 100 % match with collections from Connecticut given the provisional name *Amanita sarahae* in Tulloss & Yang (2024) and most likely represent the same species. More studies will be needed to establish whether two undescribed species (sp. ‘*nishidae*’ and sp. M15) are conspecific with *A. quercifulva*, their ITS being only at 2 and 3 substitutions-indels from *A. quercifulva*, respectively.

**Authors:** R. Lebeuf, A. Paul, H. Lambert & J. Landry.

## Basidiomycota, Agaricomycetes, Agaricales, Amanitaceae

### *Amanita* section *Vaginatae*

*Amanita leptorhacopus* Lebeuf, H. Lambert & J. Landry, **sp. nov.** – Figs. 8, 9  
Mycobank no.: MB 854401

**Diagnosis.** – Differs from *Amanita rhacopus* by a slenderer habit, paler grey pileus, stipe with a small round bulb, narrower spores (8.7–10.2  $\mu\text{m}$  vs. 9.0–11.1  $\mu\text{m}$  in *A. rhacopus*), and growth with hardwoods.

**Holotypus.** – CANADA. Québec, Sainte-Anne-de-Bellevue, Arboretum Morgan, 45° 25' 36.7" N, 73° 56' 13.6" W, in deciduous forest of *Quercus rubra* and *Carpinus caroliniana*,

30 August 2013, leg. R. Lebeuf & A. Paul, HRL1583 (DAOM 984975; holotype). Sequences ex-holotype: PP796087 (ITS).

**Description.** – Pileus 28–68 mm in diameter, convex then applanate with a small low umbo, brownish grey to brownish orange (5C2, 5C3, 5C4, 6C2, 6C3½), sometimes darker at disk, covered with small to medium patches from the universal veil; margin lighter colored, striate on 30–40 % of the pileus radius. – Lamellae free, subdistant to close, whitish, flocculose at the edge, 3–9 mm broad, with 0–1 tier of truncate lamellulae of varying length. – Stipe 60–125  $\times$  3–8 mm, tapering toward the apex, usually bearing a small roundish bulb, 7–11 mm wide at base, pulverulent above, becoming progressively fibrillose, flocculose then floccose towards the base, sometimes forming a zebroid pattern, at first whitish then concolorous with the pileus on a white background, stuffed then hollow. – Universal veil friable, breaking into loose small to medium patches on the pileus surface and at the stipe base, at first whitish then grey to brownish grey, becoming browner on the pileus surface with age. – Annulus absent. – Context fragile, thin, white, unchanging when cut or bruised. – Odor none. – Taste mild. – Spore deposit white. – Basidiospores [1191/16/13] (8.2)9.4–11.1(12.9)  $\times$  (7.6)8.7–10.2(11.8)  $\mu\text{m}$ , on average 9.8  $\times$  9.3  $\mu\text{m}$ , Q = (1.00)1.03–1.13(1.35), Qm = 1.06, predominantly subglobose, also globose, smooth, thin-walled, hyaline, inamyloid, cyanophilic. – Lamellar trama 70–150  $\mu\text{m}$  thick, made of branching filamentous hyphae 3–9  $\mu\text{m}$  wide connected with abundant ellipsoid to subfusiform inflated cells measuring up to 60  $\times$  20  $\mu\text{m}$ . – Subhymenium ramose to inflated-ramose, 25–40  $\mu\text{m}$  thick, in 3–4 layers, made of cylindrical, inflated to irregularly-shaped cells measuring 7–16  $\times$  4–10  $\mu\text{m}$ . – Basidia 50–70  $\times$  12–16  $\mu\text{m}$ , clavate, 4-spored. – Volva with poorly-delimited layers: external layer 50–100  $\mu\text{m}$  thick, composed of filamentous hyphae and spherocytes in a gelatinous matrix; central layer 300–900  $\mu\text{m}$  thick, composed of filamentous hyphae 2.5–9  $\mu\text{m}$  wide, of much more abundant globose (a- or shortly pedunculate) to subglobose cells measuring 20–45(60)  $\times$  18–45  $\mu\text{m}$ , and of less frequent inflated cells in chains measuring 20–70(100)  $\times$  10–30  $\mu\text{m}$ . – Velar remnants on pileus without layer, composed of very abundant globose to subglobose cells measuring (20)30–55(80)  $\times$  20–50(65)  $\mu\text{m}$ , borne on branched and frequently septate filamentous hyphae 3.5–9(11)  $\mu\text{m}$  wide or on cylindrical, ellipsoid, subglobose or globose inflated cells (single or in chains of 2 cells) measuring 20–50(65)  $\times$  11–25(30)  $\mu\text{m}$ . – Clamp connections absent.



**Fig. 8.** Phylogeny of selected *Amanita* species in section *Vaginatae* Clade 4 reconstructed from an ITS dataset using species from Clade 3 as outgroup. The tree topology with the highest log likelihood ( $-\ln L = 3227.00$ ) is shown, resulting from ML inference performed in MEGA11. For each node, the ML bootstrap (MLBS) if  $>70\%$  is presented. Clade designations follow Hanns & Moreau (2017) and Codjia et al. (2023). New species highlighted in red, bar indicating the expected number of substitutions per site.



**Fig. 9.** *Amanita leptorhacopus*. **A–F.** Basidiomata. **A, B.** HRL1583 (holotype). **C.** HL074. **D.** HL082. **E, F.** HRL1487 (white form). **G–H.** Basidiospores in water (G) and in Melzer's reagent (H). Scale bars G, H 5  $\mu$ m.

**Etymology.** – From the Greek *leptos*, meaning slender, and the specific epithet *rhacopus*, for its resemblance to the more robust *Amanita rhacopus*.

**Habitat and distribution.** – In small groups, in rich subhydric soils of deciduous or mixed forests, in July and August; seemingly associated with various hardwoods. So far confirmed from southern Québec, in the St. Lawrence River valley. Also present in the states of Maine and New York in the USA, according to ITS sequences available in public databases.

**Additional material examined.** – CANADA. Québec, Notre-Dame-de-l'Île-Perrot, Blvd. Saint-Joseph, in deciduous forest of *Q. rubra* and other hardwoods, 26 August 2011, *leg.* R. Lebeuf & A. Paul, HRL0844; Boucherville, chemin d'Anjou, in a deciduous forest of *Q. rubra* and *Carya ovata*, 14 July 2013 (white form), *leg.* R. Lebeuf & A. Paul, HRL1487; Saint-Narcisse, Parc de la rivière Batiscan, in mixed forest of *Fraxinus* sp., *T. canadensis*, *Q. rubra*, *B. papyrifera*, and *B. al-ghamiensis*, 3 August 2020, *leg.* R. Lebeuf & A. Paul, HRL3178 (QFB32863); Québec City, close to Jean-Lesage Airport, in

mixed forest of *B. papyrifera*, *P. tremuloides*, and *Picea glauca*, 2 July 2020, *leg.* H. Lambert, HL074 (QFB32890); *ibid.*, 9 July 2020, HL076 (QFB32892); *ibid.*, 11 July 2020, HL082 (QFB32898), HL083 (QFB32899); *ibid.*, 28 July 2021, HL137 (QFB33049); *ibid.*, 22 July 2022, HL168; *ibid.*, 31 July 2022, HL181; *ibid.*, 16 August 2022, HL192.

**Notes.** – *Amanita leptorhacopus* has a unique ITS among section *Vaginatae* clade 4 with as closest relative the European *A. ceciliae* (Berkeley & Broome) Bas and the Chinese *A. griseofolia* Zhu L. Yang, both with less than 89 % identity (Fig. 8). It is rather easy to recognize in the field on account of its relatively small size, grey to brownish grey universal veil leaving patches on the pileus and at the stipe base, white then pale grey to pale brownish grey stipe bearing a small, rounded bulb, and growth under hardwoods, possibly of the family Fagaceae. It is rarely encountered in its habitat. A white form (HRL1487), found only once, has an ITS sequence that differs from the holotype at only one



position, a position which shows heterogeneity in other collections of the species. Except for the white color overall, no difference in macroscopic characters, spore size and shape or habitat could be detected. *Amanita leptorhacopus* could be confused with *A. rhacopus* Y. Lamoureux, but the latter is more robust, has a darker pileus, a bulbless stipe, broader spores (9.0–11.1 µm) and usually grows with conifers (Lambert et al. 2018). *Amanita ceciliae* differs by a larger habit, browner pileus and larger spores (Tulloss & Yang 2024). One of our collections (HRL0844) was previously studied by R.E. Tulloss and given the provisional code *Amanita* sp-QUE03 on the website Amanitaceae.org (Tulloss & Yang 2024).

Authors: R. Lebeuf, A. Paul, H. Lambert & J. Landry

### Basidiomycota, Agaricomycetes, Agaricales, Amanitaceae

#### *Amanita* section *Vaginatae*

*Amanita pulla* Lebeuf, H. Lambert & J. Landry, sp. nov. – Figs. 8, 10

Mycobank no.: MB 854400

Diagnosis. – Differs from other species of *Amanita* section *Vaginatae* by the combination of dark grey, brownish grey to light grey pileus with a dark center, white stipe turning brown at least at the base with age or when bruised, membranous universal veil white-colored with pale orange-brown parts leaving a saccate volva at stipe base, broadly ellipsoid spores (on average 10.0 × 8.0 µm), and growth under hardwoods.

Holotypus. – CANADA. Québec, Sainte-Anne-de-Bellevue, Arboretum Morgan, 45° 25' 36.7" N, 73° 56' 13.6" W, in deciduous forest of *Quercus rubra* and *Carpinus caroliniana*, 12 August 2013, leg. R. Lebeuf & A. Paul, HRL1534 (DAOM 984974; holotype). Sequences ex-holotype: PP796083 (ITS).

Description. – Pileus 35–90 mm in diameter, parabolic, becoming convex then applanate with a small low umbo, viscid then dry, at first dark brownish grey (6EF3, 7EF3) with a dark grey disk (7F1), becoming somewhat paler with age, rarely light grey at the margin with a medium grey center (6E1) from the beginning and remaining so, naked or with a few small to large patches from the universal veil; margin concolorous, striate on 25–40 % of the pileus radius. – Lamellae free, close, whitish, flocculose at the edge, 4–7 mm broad, with 0–1 tier of truncate, mostly short, lamellulae. – Stipe 45–160 × 5–12 mm, tapering toward the apex, fibrillose, sometimes showing a zigzag pattern, sometimes pruinose at apex, whitish, turning brown with age or when bruised at least at the base, stuffed then hollow. – Universal veil membranous, forming a saccate volva 25–45 mm high, which

sometimes breaks into small to large patches on the pileus surface, whitish with pale orange-brown parts, at times brownish orange to golden yellow at stipe base. – Annulus absent. – Context thin, white, unchanging when cut or bruised. – Odor indistinct or unpleasant. – Taste mild. – Spore deposit white. – Basidiospores [1262/17/11] (7.5)9.1–10.9(13.0) × (6.5)7.3–8.8(11.0) µm, on average 10.0 × 8.0 µm, Q = (1.03)1.14–1.36(1.63), Qm = 1.25, subglobose to broadly ellipsoid, more rarely ellipsoid, smooth, thin-walled, hyaline, inamyloid, cyanophilic. – Lamellar trama 70–125 µm thick, made of relatively abundant branching filamentous hyphae (3)4–9 µm wide connected with ellipsoid to subfusiform inflated cells measuring up to 50 × 20 µm. – Subhymenium ramose to inflated-ramose, 15–30 µm thick, in 3–4 layers, made of cylindrical, inflated to irregularly-shaped cells measuring 6–15 × 5–10 µm. – Basidia 42–56 × 11–14 µm, clavate, 4-spored. – Volva 3-layered: external layer 90–220 µm thick, central layer 460–800 µm thick, internal layer 80–160 µm thick; external layer composed exclusively of filamentous hyphae 3.5–9(10) µm wide; central layer composed of regularly distributed filamentous hyphae 3.5–9.5 µm wide, of less frequent globose to subglobose cells measuring 30–60 × 20–50 µm, and of infrequent cylindrical to pyriform-elongate inflated cells in chains measuring up to 140 × 30 µm; internal layer composed mostly of filamentous hyphae 3–9 µm wide and cylindrical to ellipsoid inflated cells measuring 55–130(160) × 13–25 µm. – Clamp connections absent.

Etymology. – From the Latin *pullus*, dark grey, referring to the dark grey pileus.

Habitat and distribution. – Isolated or in small groups, in rich subhydric soils of deciduous forests, in July and August; seemingly associated with various hardwoods. So far confirmed from southern Québec, in the St. Lawrence River valley, and from Indiana, New York, and Pennsylvania in the USA, based on ITS sequences available in public databases.

Additional material examined. – CANADA. Québec, Boucherville, chemin d'Anjou, in deciduous forest of *Q. rubra* and *Carya ovata*, 14 July 2013, leg. R. Lebeuf & A. Paul, HRL1488; Saint-Augustin-de-Desmaures, Boisé-Saint-Félix, in deciduous forest of *B. papyrifera*, *Tilia americana*, and *Fraxinus* sp., 22 August 2012, leg. H. Lambert, HL012 (QFB35499); Québec City, close to Jean-Lesage airport, in deciduous forest of *Populus grandidentata* and *B. papyrifera*, 11 July 2020, leg. H. Lambert, HL078A (QFB32894); *ibid.*, in deciduous forest of *P. tremuloides*, *B. papyrifera*, and *F. grandifolia*, 11 July 2020, leg. H. Lambert, HL079A (QFB32895), HL080A (QFB32896), HL084A (QFB32900); *ibid.*, 13 August 2020, HL106A (QFB32922); *ibid.*, 28 July 2021, HL138



**Fig. 10.** *Amanita pulla*. **A–C.** Basidiomata. **A.** HRL1534 (holotype). **B.** HL084A. **C.** HL159A. **D, E.** Basidiospores in water (**D**) and in Melzer's reagent (**E**). Scale bars **D, E** 5 µm.

(QFB33050), HL140 (QFB33052); *ibid.*, 18 July 2022, HL159A; *ibid.*, 31 July 2022, HL182A; Québec City, boisé Neilson, in deciduous forest of *Q. rubra*, *B. papyrifera*, and *F. grandifolia*, 12 August 2020, *leg.* H. Lambert, HL095A (QFB32911).

**Notes.** – *Amanita pulla* has a unique ITS among other members of section *Vaginatae* clade 4. The sequence is only 96 % similar to its closest relatives, which are as yet undescribed (Fig. 8). It is recognized by its usually dark grey to brownish grey

pileus, rarely with a dark grey center and light grey elsewhere, its medium size, its white stipe and saccate volva and its growth under hardwoods; it seems to favour rich subhydryc soils. Its broadly ellipsoid spores (average  $Q = 1.25$ ) distinguish it from almost all other formally described exannulate *Vaginatae*. Light-colored basidiomata could be confused with *A. fuscozonata*, described above, but the latter produces globose to subglobose basidiospores ( $Q_m =$

1.06) and its pileus shows a paler zone in mid-radius. *Amanita brunneofuliginea* Zhu L. Yang has a darker pileus, often zonate, its volva is often beset with orange-brown patches in the North American form, and it grows with Pinaceae (Hanss & Moreau 2017).

*Authors:* R. Lebeuf, H. Lambert & J. Landry

## Basidiomycota, Agaricomycetes, Agaricales, Amanitaceae

### *Amanita* section *Vaginatae*

*Amanita confundens* H. Lambert, Y. Lamoureux & J. Landry, **sp. nov.** – Figs. 11, 12  
Mycobank no.: MB 854402

*Diagnosis.* – Differs from other species of *Amanita* section *Vaginatae* by the combination of variably-colored pileus, in tones of white, grey to brownish grey; lamellae with a light salmon tint; white cylindrical stipe; white membranous universal veil leaving a volva at stipe base; and growth with deciduous trees.

*Holotypus.* – CANADA. Québec, Québec City, 46° 45' 01.4" N, 71° 18' 20.2" W, in forested area with *Quercus* and *Fagus* in clay soil, 13 August 2020, *leg.* H. Lambert, HL105 (QFB32921; holotype). Sequences ex-holotype: PP762937 (ITS).

*Description.* – Pileus 30–100 mm in diameter, rounded-conical to convex, then applanate with a low umbo, smooth, grey to brownish grey (5B1, 5BC2½, 6BC2½), darker at disk, or white with a pale yellowish tint (4A2) at disk, naked or with a few small to large patches from the universal veil; margin striate on 33–60 % of the pileus radius. – Lamellae free, close, whitish to salmon tinted (6A3). – Stipe 60–180 × 5–15 mm, cylindrical to slightly tapering upward, smooth to slightly fibrillose, white, stuffed then hollow. – Annulus absent. – Universal veil membranous, white, fragile, leaving a saccate volva up to 40 mm high, adnate on 5–15 mm at stipe base and flaring above, and sometimes a large velar remnant on the pileus. – Context white, unchanging when cut or bruised. – Odor and taste not distinctive. – Spore deposit white. – Basidiospores [706/8/6] (7.3)8.6–10.6(12.3) × (6.7)7.8–9.6(11.9) µm, on average 10.2 × 9.2 µm, Q = (1.00)1.04–1.15(1.28), Qm = 1.11, subglobose, rarely broadly ellipsoid, smooth, thin-walled, hyaline, inamyloid, cyanophilic. – Lamellar trama 60–100 µm thick, made of branching filamentous hyphae 2.5–9.5 µm wide connected with abundant ellipsoid to subfusiform inflated cells, terminal or in chains, measuring up to 135 × 50 µm – Subhymenium ramose to inflated-ramose, 24–34 µm thick, in 3–4 layers, made of cylindrical, inflated to irregularly-shaped cells

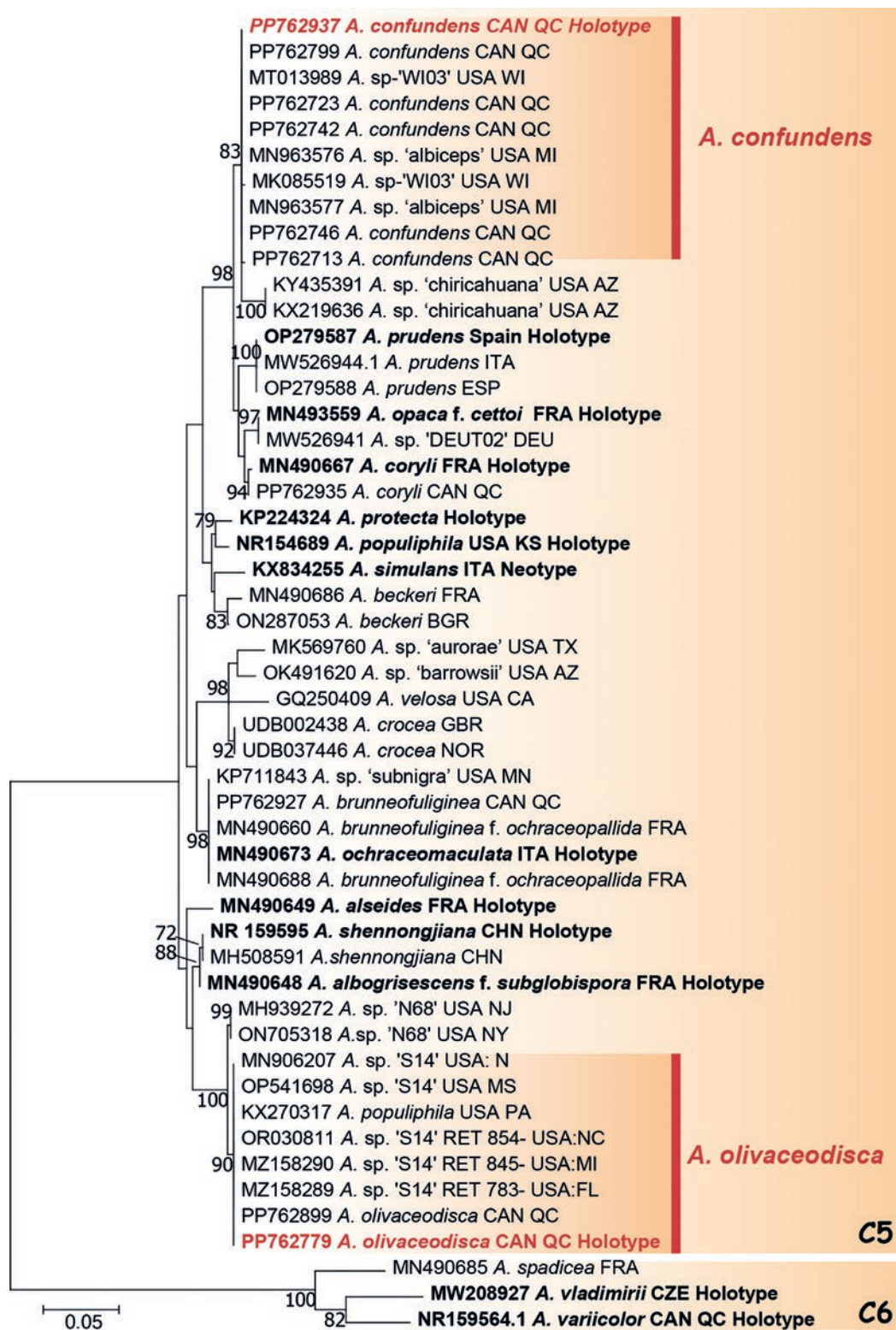
measuring 8–21 × 6–17 µm. – Basidia 35–55 × 10–17 µm, clavate, 4-spored. – Volva 3-layered: external layer 40–130 µm thick, central layer 200–350 µm thick, internal layer 30–50 µm thick; external and internal layers composed exclusively of filamentous hyphae 3.5–8 µm wide; central layer made of filamentous hyphae (3.5)4.5–8 µm wide uniformly distributed and of much more abundant inflated cells in chains measuring up to 130 × 35 µm, with subglobose terminal cells measuring 27–50 × 24–40 µm. – Clamp connections absent.

*Etymology.* – From the Latin *confundo*, confusing, for the variously-colored pileus.

*Habitat and distribution.* – Solitary or scattered under *Quercus*, *Fagus*, *Populus*, and other deciduous trees, from July to September. Reported from Québec and Ontario in Canada, and from Michigan and Wisconsin in the USA.

*Additional material examined.* – CANADA. Québec, Longueuil, under *Populus* sp. close to a *Quercus* and *Carya* forest, in clay soil, 19 August 1998, *leg.* Y. Lamoureux YL3225 (CMMF003225); Rawdon, in deciduous forest of *Q. rubra*, *F. grandifolia*, and *B. papyrifera*, 23 August 2015, *leg.* Y. Lamoureux YL4307; Boucherville, in deciduous forest of *Q. rubra*, *F. grandifolia*, *Carya ovata*, *Carpinus caroliniana*, *Ostrya virginiana*, and *Tilia americana*, 6 July 2013, *leg.* R. Lebeuf & A. Paul, HRL1464; *ibid.*, 8 August 2020, *leg.* M. Ledecq, H. Aubin & J. Dussault, HL113A (QFB32929), HL114A (QFB32930); Québec City, in deciduous forest of *Q. rubra* and *F. grandifolia*, 13 July 2022, *leg.* H. Lambert, HL157A; *ibid.*, 26 July 2022, HL178A.

*Notes.* – *Amanita confundens* has a distinct ITS among other members of *Amanita* section *Vaginatae* clade 5. The sequence suggests a sister group relationship with *A. coryli* Neville & Poumarat, *A. opaca* Dima, Bidaud & D. Varga, *A. prudens* Manuel Plaza, and two undescribed species, from which it differs by at least 7 substitutions and indels (Fig. 11). The original concept was of a species with a white pileus, sometimes with yellowish to brownish tints at center, provisionally called *A. albiceps* by Lamoureux (2006), which is now shown to represent a white form of a markedly colored species. It is distinguished by its variably-colored pileus, white to brownish grey and paling with age, a light salmon tint in the lamellae more visible in young stage, and growth with *Quercus*, *Fagus*, *Populus*, and other hardwoods. *Amanita fuscozonata* and *A. fusca*, both described above, share the same habitat but have browner pileus and stipe. *Amanita coryli*, which develops pale to darker pinkish tints in the lamellae when drying, has a greyish beige pileus, predominantly globose spores and is associated with *Corylus* in Europe (Neville & Poumarat 2009); it is genetically confirmed from Québec and has been



**Fig. 11.** Phylogeny of selected *Amanita* species in section *Vaginatae* Clade 5 reconstructed from an ITS dataset using species from Clade 6 as outgroup. The tree topology with the highest log likelihood ( $-\ln L = 2534.43$ ) is shown, resulting from ML inference performed in MEGA11. For each node, the ML bootstrap (MLBS) if  $>70\%$  is presented. Clade designations following Hanns & Moreau (2017) and Codjia et al. (2023). New species highlighted in red, bar indicating the expected number of substitutions per site.



**Fig. 12.** *Amanita confundens*. **A–C.** Basidiomata. **A.** HL105A (holotype). **B.** YL3225 (white form). **C.** HL178A. **D.** Central layer of volva in SDS Congo Red. **E, F.** Basidiospores in water (E) and in Melzer's reagent (F). Scale bars D 10 µm; E, F 5 µm.

found in forested areas including various trees, i.e., *Populus*, *Betula*, *Fagus*, *Acer*, *Abies*, *Alnus*, *Picea*, and *Tsuga*. An as-yet undescribed species provisionally called *A. lividella* Y. Lamoureux (Lamoureux 2015) differs from the white form of *A. confundens* by its pale beige pileus especially in dry weather, never pure white neither darker at disk, its more friable universal veil leaving a fragile volva at stipe base and sometimes a few patches on the pi-

leus, and its probable association with *Betula*. *Amanita ristichii* Tulloss, also with pinkish lamellae, bears an annulus and produces larger ellipsoid spores measuring  $(9.2)10.2\text{--}13.9(17.0) \times (6.6)7.0\text{--}9.0(12.8) \mu\text{m}$ , predominantly on two-spored basidia (Tulloss 1989). *Amanita murrilliana* Singer displays beige or pale yellow colors in the pileus, bears a small annulus and produces ellipsoid spores measuring  $(8.5)9.6\text{--}12.7(14.2) \times (5.6)6.5\text{--}9.0(10.5) \mu\text{m}$

(Tulloss & Yang 2024). The well-known *A. amerivivosa* Tulloss, Kudzma & M. A. Tulloss, in section *Phalloideae*, is a more robust species with a thick volva, a bulbous stipe with an annulus, a non-striate pileus margin and amyloid spores (Tulloss et al. 2021). *Amanita populiphila* Tulloss & E. Moses is a less slender species with a white, off-white, pale tan or pale cream pileus often adorned at first with more numerous velar remnants, and with a short cupuliform volva (Tulloss & Moses 1995). *Amanita nivalis* Grev., a white species found in Northern Europe, is smaller, its pileus margin is less striate, it produces larger spores measuring  $(8.2)10.0\text{--}13.5(21) \times (7.1)8.8\text{--}12.0(19.5) \mu\text{m}$ , and it is associated with *Salix* and *Betula* (Tulloss & Yang 2024).

*Authors:* H. Lambert, Y. Lamoureux, G. Fortin, R. Lebeuf & J. Landry

### Basidiomycota, Agaricomycetes, Agaricales, Amanitaceae

#### *Amanita* section *Vaginatae*

*Amanita olivaceodisca* Lebeuf, A. Paul & J. Landry, **sp. nov.** – Figs. 11, 13

MycoBank no.: MB 854403

*Diagnosis.* – Differs from other species of *Amanita* section *Vaginatae* by the combination of variously-colored pileus in tones of greyish orange, brownish orange, pale yellowish grey, very pale grey to almost white, very often with an olive hue at disk, striate on 25–35 % of the radius; white universal veil forming a submembranous volva at the base of the stipe, adnate below, flaring upward, and at times leaving medium to large patches on the pileus; white-floccose stipe developing a greyish orange hue with age; and growth in predominantly deciduous forests of *Fagus grandifolia*, *Tsuga canadensis*, and *Populus grandidentata* in clay soil.

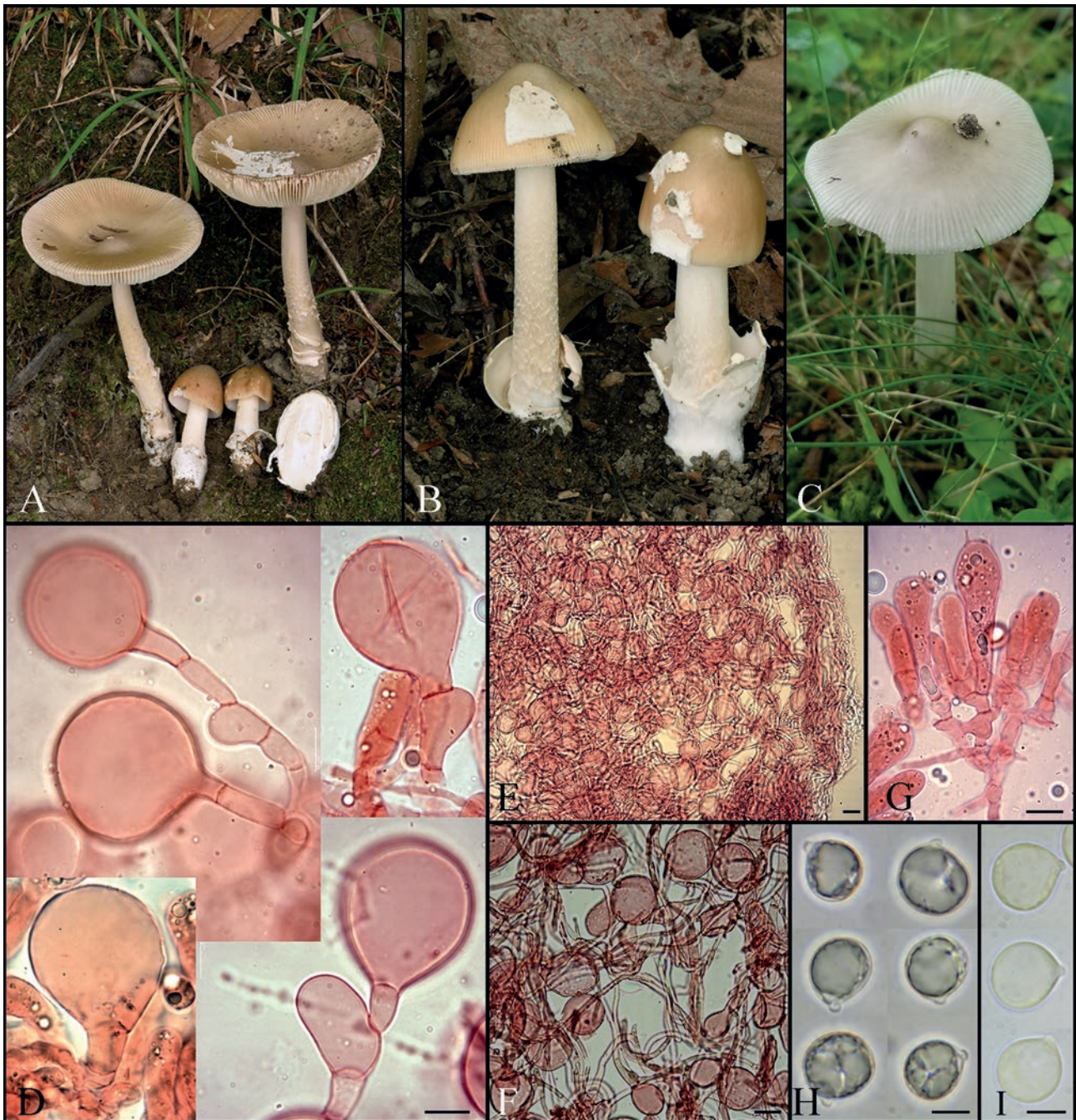
*Holotypus.* – CANADA. Québec, Notre-Dame-du-Mont-Carmel, Parc nature La Gabelle, 46° 26' 50.0" N, 72° 44' 01.9" W, in mixed forest of *F. grandifolia*, *T. canadensis*, *P. grandidentata*, and *Q. rubra*, in clay soil, 28 August 2016, *leg.* R. Lebeuf & A. Paul, HRL2285 (DAOM 984976; holotype), Sequences ex-holotype: PP762779 (ITS).

*Description.* – Pileus 44–76 mm in diameter, at first paraboloid, expanding via campanulate or plano-convex to applanate and most often umbonate, slightly viscid, naked or sometimes bearing medium to large patches from the universal veil; color variable, greyish orange, brownish orange, pale yellowish grey, very pale grey to almost white (2AB2, 4AB2, 5B3, 5B3½, 5B5, 5C3), very often with an olivaceous hue at disk (4B3); margin straight becoming reflexed with age, striate 25–35 % of the pileus radius. – Lamellae free, close, white, flocculose at the edge, 4–9 mm broad, with 0–1 tier of attenuated lamellulae of variable length, a good proportion of which are attached by their base to

the next lamella. – Stipe 56–116 long, 4–9 mm at apex, tapering toward the apex, subclavate in young basidiomata (11–13 mm broad at base), white-flocculose at apex, below white-floccose over a light greyish orange background, darker greyish orange with age, stuffed then hollow. – Annulus absent. – Universal veil 20–28 mm high, submembranous, white, leaving at stipe base a saccate volva which is adnate in the lower half and flaring in the upper half, and at times medium to large patches on the pileus surface. – Context fragile, thin, white, unchanging when cut or bruised. – Odor unpleasant at stipe base or none. – Taste mild. – Spore deposit white. – Basidiospores  $[60/2/2] (7.5)8\text{--}10(11) \times (7)7.5\text{--}9.5(10) \mu\text{m}$ , on average  $8.9 \times 8.3 \mu\text{m}$ ,  $Q = 1.00\text{--}1.18$ ,  $Q_m = 1.07$ , globose to subglobose, inamyloid, cyanophilic, smooth, hyaline, with a cylindrical apiculus. – Pileipellis 2-layered: suprapellis an ixocutis 40–100  $\mu\text{m}$  thick, made of repent narrow hyphae 1–3  $\mu\text{m}$  wide in a gelatinous matrix; subpellis 50–100  $\mu\text{m}$  thick, dense, made of filamentous subparallel to interwoven hyphae 2–8  $\mu\text{m}$  broad, the wider hyphae constricted at septa, with scattered branched, sinuous vascular hyphae 4–10  $\mu\text{m}$  wide. – Lamellar trama 70–130  $\mu\text{m}$  thick made of filamentous hyphae 2–4  $\mu\text{m}$  wide and non-terminal physaloid elements 20–70  $\times$  10–22  $\mu\text{m}$ . – Subhymenium ramose to inflated-ramose, 15–30  $\mu\text{m}$  thick, made of cylindrical or inflated hyphae 7–15  $\mu\text{m}$  long. – Basidia 35–59  $\times$  12–15  $\mu\text{m}$ , 4-spored, clavate; sterigmata 3–5  $\mu\text{m}$  long. – Universal veil material on stipe 3-layered: external layer 100–150  $\mu\text{m}$  thick, of mostly straight, branched, interwoven filamentous hyphae 4–9  $\mu\text{m}$  wide with rare inflated terminal cells; central layer 300–350  $\mu\text{m}$  thick, a mixture of filamentous interwoven hyphae 3–8  $\mu\text{m}$  wide and of abundant pyriform, ellipsoid, clavate, hourglass-shaped, subglobose and globose terminal cells 24–67  $\times$  13–50  $\mu\text{m}$ ; internal layer thin, about 40  $\mu\text{m}$  thick, of curved and densely entangled branched filamentous hyphae 3–4  $\mu\text{m}$  wide with occasional inflated terminal cells, this layer covered in part by a gelatinous matrix up to 40  $\mu\text{m}$  thick from the pileipellis. – Clamp connections absent.

*Etymology.* – Referring to the frequent olivaceous color of the pileus center.

*Habitat and distribution.* – In small groups, in clay soils of predominantly deciduous forests of *F. grandifolia*, *T. canadensis*, *P. grandidentata*, and *Q. rubra* (the latter absent from one of the two sites), in August. Thus far confirmed from southern Québec, in Canada. Also confirmed in the states of Florida, Indiana, Michigan, North Caroli-



**Fig. 13.** *Amanita olivaceodisca*. **A–C.** Basidiomata. **A.** HRL2285 (holotype). **B.** HRL2284. **C.** Mycomap 6468, photo S. Russell. **D–I.** Microscopic details in SDS Congo Red. **D.** Inflated hyphae at lamellar edge. **E.** Volva central (left) and external (right) layer. **F.** Volva central layer. **G.** Hymenium. **H–I.** Basidiospores in water (H) and in Melzer's reagent (I). Scale bars D, G 10  $\mu$ m; E 50  $\mu$ m; F 20  $\mu$ m; H, I 5  $\mu$ m.

na, and Pennsylvania in the USA based on identical sequences in public databases.

**Additional material examined.** – *Ibid.* (QFB32691; isotype). Sequences ex-isotype: PP762779 (ITS). – CANADA. Québec, Notre-Dame-du-Mont-Carmel, Parc na-

ture La Gabelle, in mixed forest of *F. grandifolia*, *T. canadensis*, and *P. grandidentata*, 28 August 2016, leg. R. Lebeuf & André Paul, HRL2284 (QFB32690).

**Notes.** – *Amanita olivaceodisca* has an ITS distinct from other members of section *Vaginatae*

clade 5, with only 97 % identity to the closest described species, *A. shennongjiana* from China (Fig. 11). It differs by 4 substitutions and indels from an undescribed species labeled *Amanita* sp. N68 (Tulloss & Yang 2024). The main distinguishing character of *A. olivaceodisca* is the frequent olive tint at disk on the variously colored pileus in tones of greyish orange, brownish orange, yellowish grey to very pale grey. *Amanita populiphila* shows a paler pileus without olive hue, its universal veil frequently leaves warts or patches on the pileus, it is strictly associated with *Populus*, and it produces larger spores,  $10.9 \times 9.8 \mu\text{m}$  on average (Tulloss & Moses 1995). *Amanita quercifulva*, described above, and *Amanita fulva* Fr. do not show olive hue on the pileus, and their volva develops brownish orange stains with age. *Amanita sinicoflava* Tulloss has an olivaceous yellow pileus, and its volva is white at first but turns grey with age (Tulloss 1988).

*Authors:* R. Lebeuf, A. Paul & J. Landry

### Basidiomycota, Agaricomycetes, Agaricales, Amanitaceae

#### *Amanita* section *Vaginatae*

*Amanita piceina* H. Lambert & J. Landry, **sp. nov.** – Figs. 14, 15

MycoBank no.: MB 854404

*Diagnosis.* – Differs from other species of *Amanita* section *Vaginatae* by the combination of large basidiomata (pileus diameter up to 120 mm, stipe length up to 250 mm), yellowish brown to dull brown, naked and sometimes zonate pileus, stipe with fibrils concolorous with the pileus and arranged in a zebroid pattern, deeply buried in the soil, long white volva, and growth with *Picea*.

*Holotypus.* – CANADA. Québec, Lévis, 46° 46' 09.9" N, 71° 12' 10.4" W, in *Picea* plantation, 12 September 2023, *leg.* H. Lambert, HL239 (QFB35533; holotype). Sequences ex-holotype: PP762883 (ITS).

*Description.* – Pileus 80–120 mm wide, rounded-conical, campanulate, then applanate with a large umbo, naked, dark brown (5½F8) to yellowish brown (5EF7), then dull brown (5D4½), dark brown (5½F8) at disk; margin striate on 10–40 % of the pileus radius, reflexed with age. – Lamellae close, with truncate lamellulae of varying length, 6–10 mm broad, whitish to pale orange (5A2½). – Stipe 180–250 × 8–12 mm, tapering toward the apex, deeply buried in the soil (on 60–100 mm), with fibrils concolorous with the pileus, arranged in a zebroid pattern, longitudinally fibrillose-striate at apex. – Annulus absent. – Universal veil membranous, thick, tough, white, forming a long (up to 60 mm) and thick saccate volva. – Context white, unchanging when cut or bruised. – Odor not distinctive. – Spore deposit white. – Basidi-

ospores [367/4/3] (9.3)10.0–11.3(12.1) × (7.9)8.6–9.8(10.4)  $\mu\text{m}$ , on average  $10.6 \times 9.1 \mu\text{m}$ ,  $Q = (1.04)1.09–1.24(1.33)$ ,  $Q_m = 1.16$ , subglobose to broadly ellipsoid, smooth, thin-walled, hyaline, inamyloid, cyanophilic. – Lamellar trama 100–200  $\mu\text{m}$  thick, made of branching filamentous hyphae 3–8  $\mu\text{m}$  wide connected with abundant ellipsoid to subfusiform inflated cells measuring up to  $70 \times 25 \mu\text{m}$ , often in chain. – Subhymenium ramose to inflated-ramose, 25–45  $\mu\text{m}$  thick, in 3 layers, made of cylindrical, inflated to irregularly-shaped cells measuring  $7–21 \times 4–13 \mu\text{m}$ . – Basidia  $40–56 \times 12–15 \mu\text{m}$ , clavate, mostly 4-spored. – Volva 3-layered: external layer 150–200  $\mu\text{m}$  thick, central layer 500–1000  $\mu\text{m}$  thick, internal layer 175–350  $\mu\text{m}$  thick; external and internal layers a cutis composed exclusively of filamentous, branched, interwoven hyphae (2.5)4–8  $\mu\text{m}$  wide; central layer composed of branched filamentous hyphae (3)4–8(10)  $\mu\text{m}$  wide regularly in cluster, of infrequent globose to subglobose terminal inflated cells measuring up to  $95 \times 65 \mu\text{m}$  and of rare inflated cells measuring up to  $120 \times 30 \mu\text{m}$ . – Pileipellis 2-layered: suprapellis an ixocutis 10–100  $\mu\text{m}$  thick, made of repent narrow hyphae 1–3  $\mu\text{m}$  wide in a gelatinous matrix; subpellis a cutis 70–130  $\mu\text{m}$  thick, dense, made of branched, filamentous, subparallel to interwoven hyphae 4–8(10)  $\mu\text{m}$  wide. – Clamp connections absent.

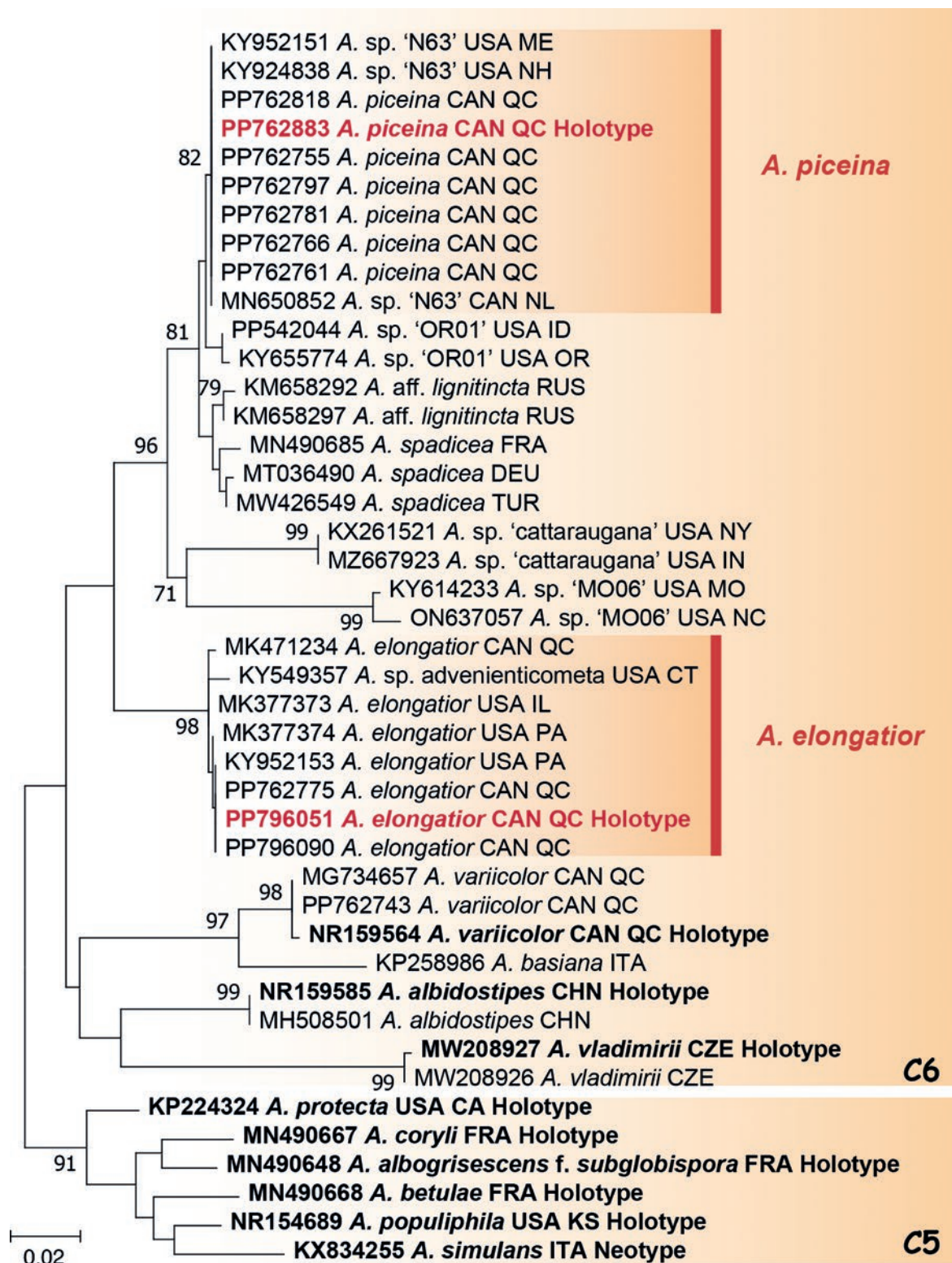
*Etymology.* – From the Greek *picea*, spruce, for the association with *Picea*.

*Habitat and distribution.* – Solitary or in small groups in acidic soils, under *Picea*, from July to September. Known from Québec and Newfoundland and Labrador in Canada, and from the states of Maine and New Hampshire in the USA, based on publicly available ITS sequences.

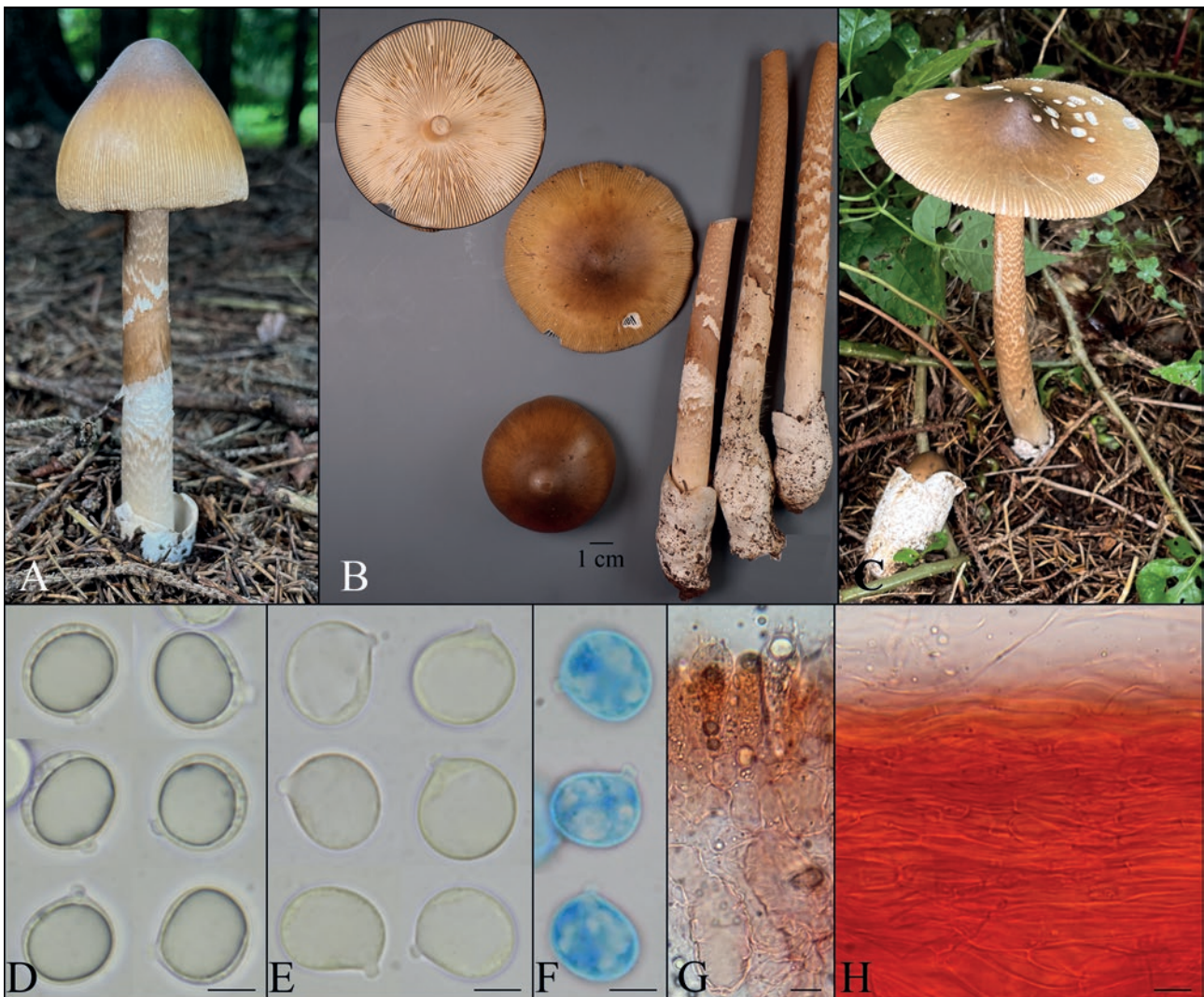
*Additional material examined.* – CANADA. Québec, Sutton, under *Picea* sp., 26 September 2020, *leg.* L. Fortin, HL116 (QFB32932); Sainte-Hélène-de-Chester, in *Picea* plantation with *Betula* sp., 7 August 2022, *leg.* P. Organ, HL208 (QFB32878); *ibid.*, 8 August 2022, HL209, HL210; *ibid.*, 31 August 2023, HL231 (QFB35529), HL232 (QFB35530), HL233 (QFB35531); Lévis, in *Picea* plantation, 11 September 2023, *leg.* A. Bégin, HL234 (QFB35532); *ibid.*, 12 September 2023, *leg.* H. Lambert, HL240 (QFB35534).

*Notes.* – The ITS sequence of the holotype is distinct from other members of *Amanita* sect. *Vaginatae* clade 6. *Amanita piceina* has a sister group relationship with the European *A. spadicea* Persoon, deviating from it by 7 substitutions and indels. It is also closely related to two putative species labelled “OR01” and *A. aff. lignitincta*, differing from them by 5 and 7 substitutions-indels, respectively (Fig. 14). *Amanita piceina* is well characterized by its robustness, its dark brown to yellowish





**Fig. 14.** Phylogeny of selected *Amanita* species in section *Vaginatae* Clade 6 reconstructed from an ITS dataset using species from Clade 5 as outgroup. The tree topology with the highest log likelihood ( $-\ln L = 2604.79$ ) is shown, resulting from ML inference performed in MEGA11. For each node, the ML bootstrap (MLBS) if  $>70\%$  is presented. Clade designations following Hanns & Moreau (2017) and Codjia et al. (2023). New species highlighted in red, bar indicating the expected number of substitutions per site.



**Fig. 15.** *Amanita piceina*. **A–C.** Basidiomata. **A, B.** HL239 (holotype). **C.** HL240. **D–F.** Basidiospores in water (D), in Melzer's reagent (E), and in Cotton Blue (F). **G–H.** Microscopic details in SDS Congo Red. **G.** Part of lamellar trama. **H.** Pileipellis. Scale bars D–F 5 µm; G, H 10 µm.

brown pileus, its long stipe deeply buried in the soil and covered with fibrils concolorous with the pileus and forming a zebroid pattern with age, and its association with *Picea*. *Amanita spadicea* is much similar but is associated with *Fagus* (Moreau et al. 2023) and is not reported from North America. *Amanita elongatior* grows with *Quercus* and *Fagus*, its stipe fibrils are paler than the pileus, and it produces shorter spores with an average Q of 1.07. *Amanita magna* has a more orange-brown pileus, without yellow tint. *Amanita fuscozonata* is less robust, does not show yellow tints in the pileus, and its stipe is not deeply buried in the soil. *Amanita brunneofuliginea* Zhu L. Yang is also less robust, its volva is often covered with orange-brown patches

in the North American form, and it grows with Pinaceae (Hanss & Moreau 2017).

*Authors:* H. Lambert, J. Landry & R. Lebeuf

**Basidiomycota, Agaricomycetes, Agaricales, Amanitaceae**

***Amanita* section *Vaginatae***

***Amanita elongatior*** Y. Lamoureux, H. Lambert, Lebeuf & J. Landry, **sp. nov.** – Figs. 14, 16  
Mycobank no.: MB 854405

**Diagnosis.** – Differs from other species of *Amanita* section *Vaginatae* by the combination of large basidiomata (pileus diameter up to 130 mm, stipe length up to 200–300 mm), dark brown to yellowish brown, naked pileus, stipe with

fibrils paler than the pileus and arranged in a zebroid pattern, deeply buried in the soil, long white volva, and growth with *Quercus* and *Fagus*.

**Holotypus.** – CANADA. Québec, Boucherville, 45° 35' 57.4" N, 73° 25' 19.5" W under *Quercus rubra*, 12 July 2008, leg. R. Lebeuf & A. Paul, HRL0093 (CMMF027666; holotype). Sequences ex-holotype: PP796051 (ITS).

**Description.** – Pileus 80–130 mm in diameter, paraboloid then applanate with a broad umbo, naked, viscid to moist, sometimes pruinose at disk, dark brown (5F8, 5½F8) to yellowish brown (5D4½, 5EF7), dark brown at disk (5½F8, 6EF8); margin striate on 15–45 % of the pileus radius, reflexed with age. – Lamellae close to crowded, white or with a salmon tint, with 0–1 tier or lamellulae. – Stipe 150–200(300) × 10–20 mm, cylindrical to tapering upward, whitish to pale brown, less frequently medium brown, developing a zebroid pattern with age, deeply buried in the soil, stuffed then hollow. – Annulus absent. – Universal veil membranous, thick, tough, white, forming a long (up to 60 mm) and thick saccate volva. – Context white, unchanging when cut or bruised. – Odor not distinctive. – Spore deposit white. – Basidiospores [187/3/2] (8.1)8.8–10.6(12.3) × (7.7)8.2–9.9(11.3) µm, on average 9.6 × 9.0 µm, Q = (1.00)1.02–1.11(1.18), Qm = 1.07, globose to subglobose, smooth, thin-walled, hyaline, inamyloid, cyanophilic. – Lamellar trama 80–200 µm thick, made of relatively abundant branched filamentous hyphae 4–8.5 µm wide connected with ellipsoid to subfusiform inflated cells up to 90 × 35 µm. – Subhymenium inflated-ramose, 30–42 µm thick, in 3–4 layers, made of cylindrical, inflated to irregularly-shaped cells measuring 8–20 × 5–13(20) µm. – Basidia 45–65 × 12–16 µm, clavate, mostly 4-spored, occasionally 1- or 2-spored. – Volva 3-layered: external layer 130–300 µm thick, central layer 500–800 µm thick, internal layer 35–75 µm thick; external and internal layers composed exclusively of filamentous hyphae 4–9(13) µm wide; central layer composed of filamentous hyphae (3)4–10 µm wide regularly in clusters, of infrequent globose to subglobose inflated cells measuring up to 95 × 70 µm, and of inflated cells in chains measuring up to 120 × 40 µm. – Clamp connections absent.

**Etymology.** – From the Greek *elongatus*, elongate, and *ior*, longer, referring to the long stipe of the species.

**Habitat and distribution.** – Solitary or in small groups in rich soils, under *Quercus* and *Fagus*, from July to September. Known from Québec in Canada, and from the states of Connecticut, Illinois, and Pennsylvania in the USA based on ITS sequences available in public databases.

**Additional material examined.** – CANADA. Québec, Mont-Saint-Hilaire, under *Q. rubra* in old-growth forest of *Quercus* and *F. grandifolia*, 9 July 1993, leg. Y. Lamoureux, YL1956 (CMMF001956); Saint-Nicolas, in deciduous forest of *Q. rubra* and *F. grandifolia*, 3 September 2011 leg. M. Roussel (QFB3651); Québec City, in deciduous forest of *Q. rubra* and *F. grandifolia*, 14 July 2017, leg. J. Landry, HL060A (QFB32878).

**Notes.** – *Amanita elongatior* has a unique ITS among other members of section *Vaginatae* clade 6. The sequence is only 96 % similar to its closest relative (Fig. 14). The species is remarkable by its robustness, its yellowish brown pileus with a broad umbo and its stipe which is always deeply buried in the soil. *Amanita piceina* is very similar, but its stipe fibrils are darker, concolorous with the pileus, and it grows under *Picea*. The European *A. spadicea* differs by its ITS sequence and habitat under *Fagus sylvatica* (Moreau et al. 2023). According to the original description by Persoon, *A. spadicea* grows under *Quercus* (Neville & Poumarat 2009). *Amanita magna* is also associated with *Fagus* and *Quercus* but has no yellow tint in the pileus. *Amanita piceina* has longer spores and is associated with *Picea*. *Amanita fuscozonata*, *A. fusca*, and *A. pulla* share the same habitat but they are less robust, they do not show yellow tints in the pileus, and their stipe is not deeply buried in the soil. *Amanita brunneofuliginea* Zhu L. Yang is also less robust, its volva is often decorated with orange-brown patches in the North American form, and it grows with Pinaceae (Hanss & Moreau 2017). *Amanita penetratrix* Tulloss nom. prov., another robust species with a deeply buried stipe, has a brown to grey-brown pileus without yellow tints (Tulloss & Yang 2024). *Amanita penetrans* Tulloss nom. prov. also possesses a long stipe deeply buried in the substrate, but its pileus, similarly colored as *A. elongatior*, is smaller (Tulloss & Yang 2024). *Amanita albidostipes* Y.Y. Cui, Q. Cai & Zhu L. Yang, described from China, is a smaller species with a white stipe and is associated with *Pinus* (Cui et al. 2018).

**Authors:** H. Lambert, Y. Lamoureux, R. Lebeuf & J. Landry

## Basidiomycota, Agaricomycetes, Agaricales, Hymenogastraceae

### *Hebeloma* section *Hebeloma*

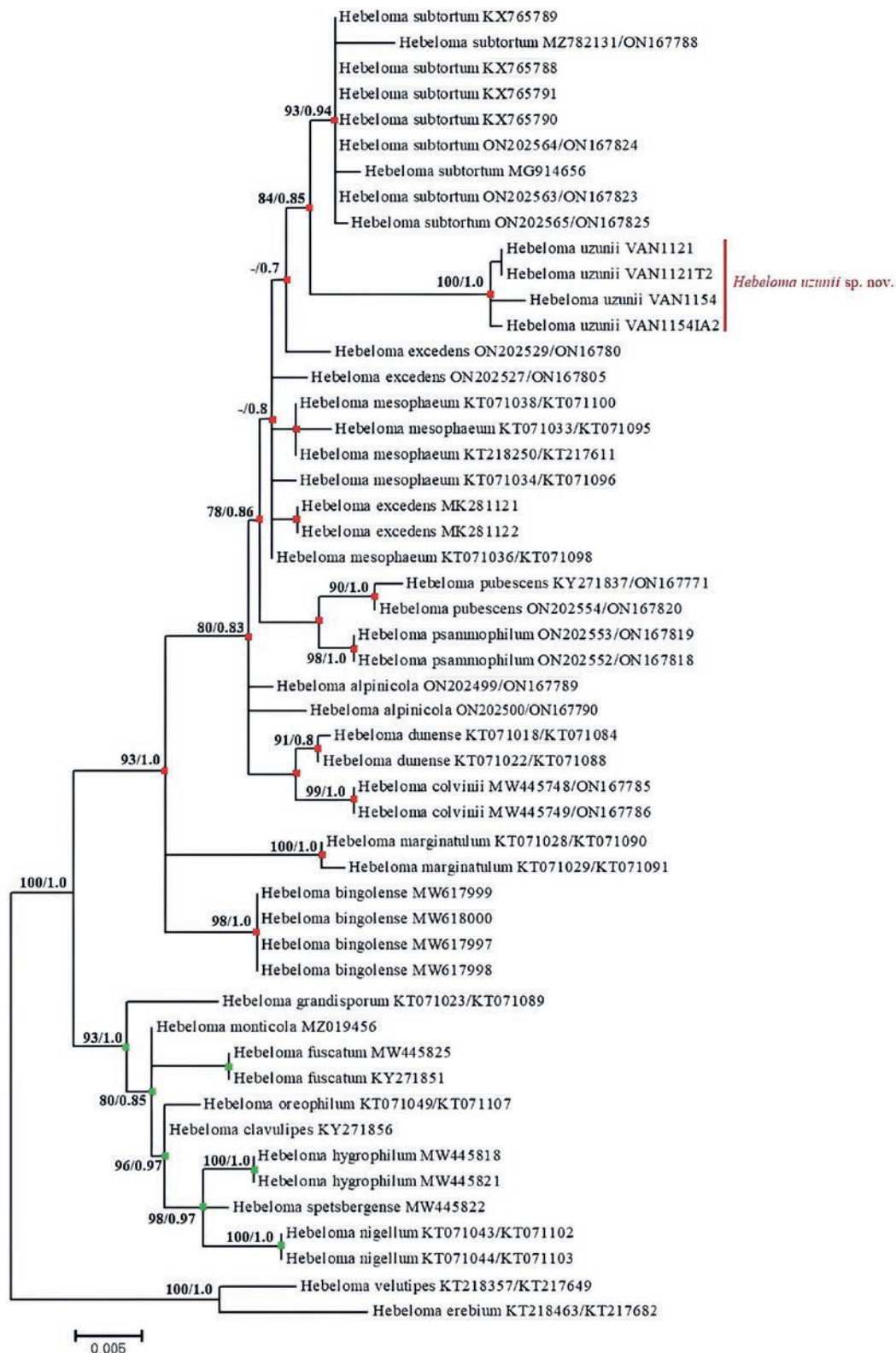
*Hebeloma uzunii* I. Acar, Kalmer & Dizkirici, **sp. nov.** – Figs. 17–21

MycoBank no.: MB 843697

**Diagnosis.** – Differs from *Hebeloma subtortum* by its shorter basidioma and the consistently ellipsoid spores. Unique molecular autapomorphies in the ITS at positions 2



**Fig. 16.** *Amanita elongatior*. **A–C.** Basidiomata. **A, B.** HRL0093 (holotype). **C.** HL060A. **D, E.** Basidiospores in water (**D**) and in Melzer's reagent (**E**). **F.** External layer of volva in ammonia. **G.** Central layer of volva in SDS Congo Red. **I.** Internal layer of volva in ammonia. Scale bars **D, E** 5 µm; **F, H** 20 µm; **G** 50 µm.



**Fig. 17.** Phylogeny of *Hebeloma* sect. *Hebeloma*, reconstructed from a combined ITS-*tef1* dataset. For each node, the ML bootstrap (MLBS) if  $\geq 50$  and BI posterior probabilities (BIPP) if  $\geq 0.5$  are presented. *Hebeloma mesophaeum* species complex marked with red nodes, *H. nigellum* species complex marked with green nodes, bar indicating the expected number of substitutions per site.



Fig. 18. Basidiomata of *Hebeloma uzunii*. A. VANF1121 (holotype). B. VANF1154. Photos İ. Acar.

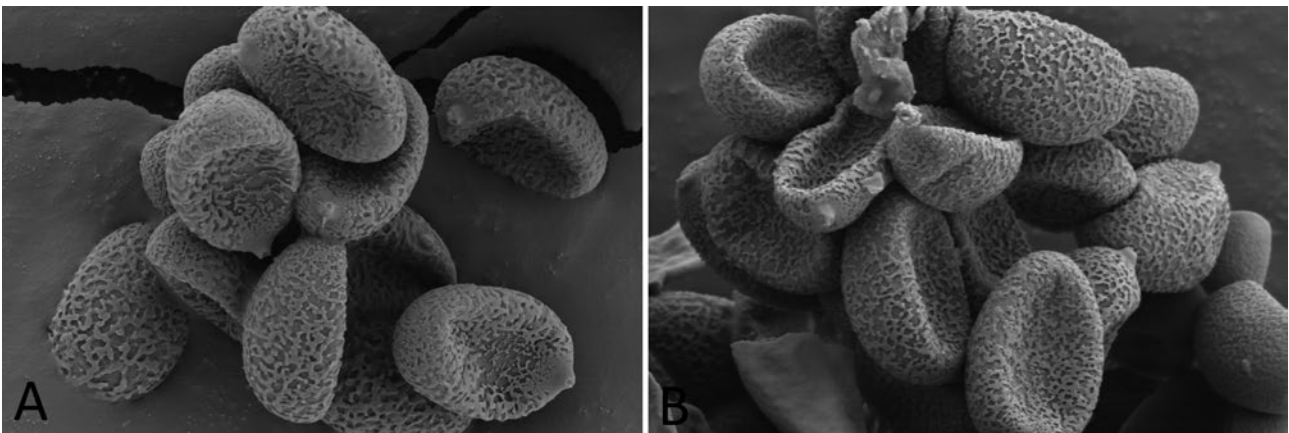


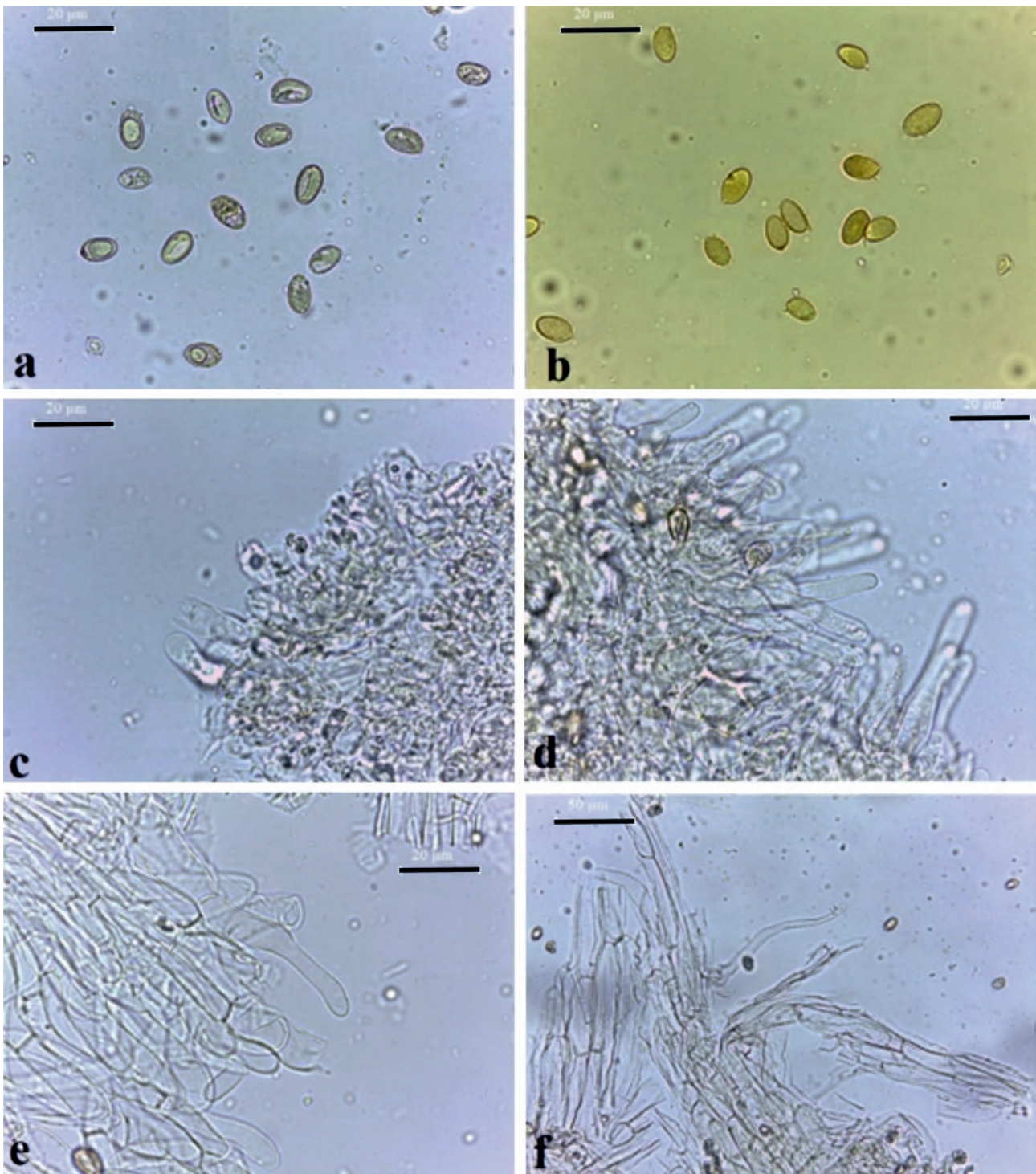
Fig. 19. Scanning electron micrographs of basidiospores of *Hebeloma uzunii* (VANF1121, holotype).

(C), 9 (G), 15 (A), 24 (G), 139 (G, insertion), 143 (C), 147 (C), 173 (A), and 603 (C), and in the *tef1* at positions 163 (T), 382 (T to G), 375 (C, insertion), 379 (T), 383 (A), 472 (C), and 538 (C).

**Holotypus.** – Türkiye, Bingöl, Genç Coniferous Forest, 38° 44' 51.9" N, 40° 33' 42.4" E, 1059 m a.s.l., under *Pinus sylvestris*, 18 May 2020, leg. I. Acar (VANF1121; holotype). Sequences ex-holotype: ON505062 (ITS), ON512567 (*tef1*)

**Description.** – Pileus 30–80 mm diam; hemispherical when young, then convex to planoconvex, incurved at margin, margin smooth, scalloped, wavy, viscid usually bicolored but sometimes unicolored, at center usually brown tones from clay-buff to isabella or milky coffee, lighter at the margin but not clearly two-toned, covered with veil tissue or not. – Lamellae L = 40–70, frequent lamellulae, subdecurrent or emarginate to sinuate, up to 3–4 mm wide, subdistant to close, pale white at first, later cream-brown following spore maturity, isabella to milky coffee, buff. – Context thick

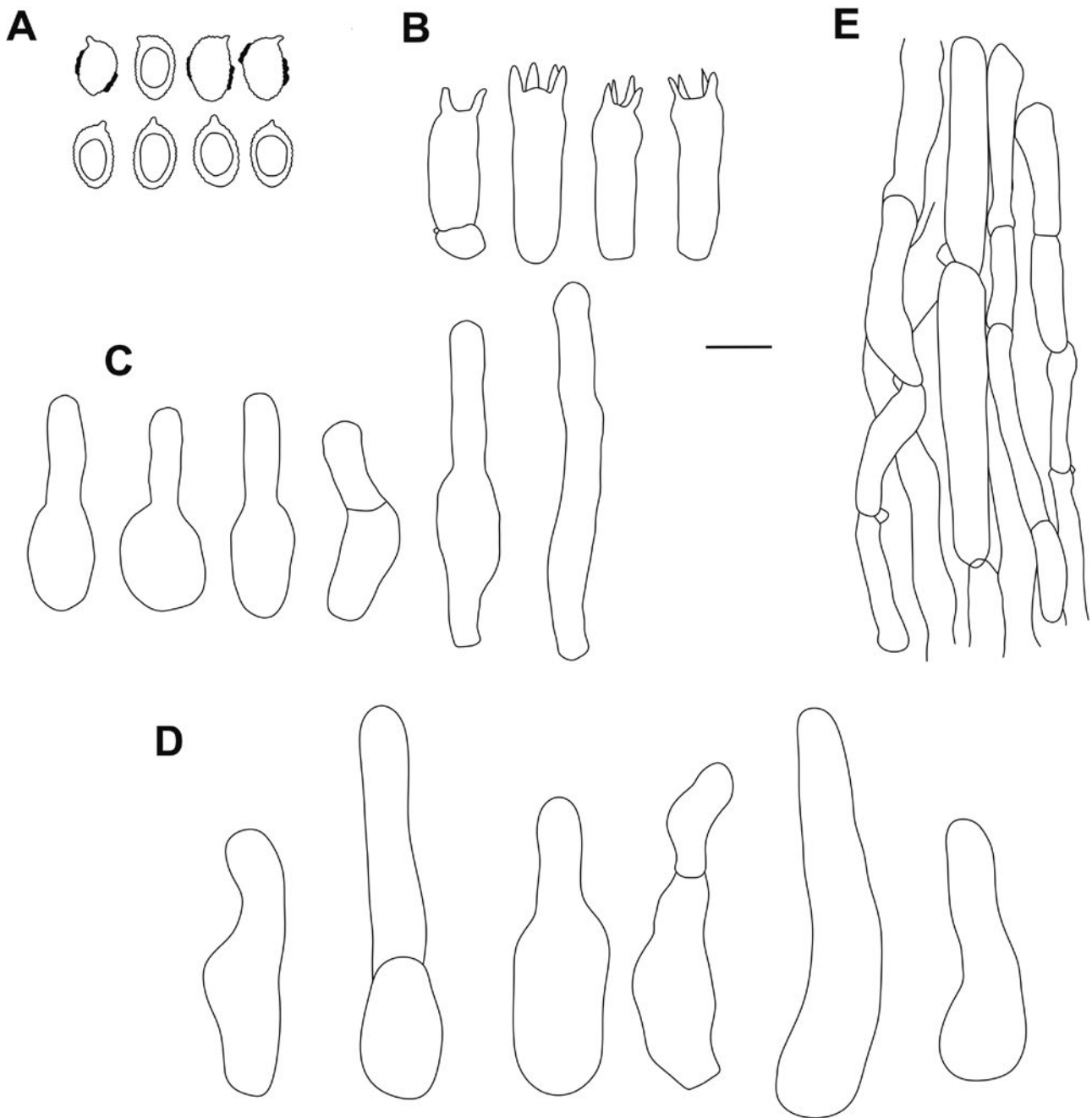
in the center of the pileus, whitish in pileus and stipe apex and yellowish brown in lower stipe down to blackish at base, taste not distinctive, odor not determined. – Stipe 40–70 × 6–15 × 5–9 (median) × 10–20 (base) mm, central, slightly curved, narrowing at the base, pruinose particularly at the apex, white to yellow, brownish towards the base; fibrillose; rooting no. – Basidiospores 8.2–10 × 5–6.7(–7) μm, (n = 45), avQ = 1.57, avl = 9.5 μm, avw = 6.1 μm, mainly ellipsoid, ellipsoid-cylindrical, slightly dextrinoid (D0–D1); weakly verrucose (O1–O2), not calyptrate (P0), light yellow to light green, thin walled, smooth apiculus. – Basidia 15.5–30.7 × 5.5–7.8(–8.5) μm (n = 30), subcylindrical to subclavate; 2 or 4 sterigmata, with a basal clamp. – Cheilocystidia 30–55 × 4.4–6.5(–7.3), at the base 6–13 μm, (n = 20); cylindrical in the upper part and slightly swollen to more swollen at the base,



**Fig. 20.** Micromorphology of *Hebeloma uzunii* (VANF1121, holotype). **a, b.** Basidiospores in water (**a**) and in Melzer's reagent (**b**). **c–f.** Microscopic characteristics in water. **c.** Basidia. **d.** Cheilocystidia. **e.** Caulocystidia. **f.** Ixocutis. Bars 20 µm.

rarely septate, main shape lageniform-ventricose, occasionally geniculate, sometimes cylindrical with capitate or clavate apex. – Caulocystidia 40–70 ×

5.2–8(–8.7), at the base 7(–7.5)–14 µm, (n = 20); similar to cheilocystidia, sometimes uniseptate. – Pleurocystidia not found. – Pileipellis an ixocu-



**Fig. 21.** Micromorphology of *Hebeloma uzunii* (VANF1121, holotype). **a.** Basidiospores. **b.** Basidia. **c.** Cheilocystidia. **d.** Caulocystidia. **e.** Ixocutis. Bar 10  $\mu\text{m}$ . Drawing İ. Acar.

tis up to 20  $\mu\text{m}$  wide; hyphae cylindrical, usually hyphal ends clavate, hyaline; septa with clamps. – Exsiccate pileus yellowish brown to honey brown; lamellae milky brown; stipe yellowish brown, darker at base.

**E t y m o l o g y.** – Honoring Prof. Dr. Yusuf Uzun, who has made significant contributions to mycology in Türkiye.

**Habitat and distribution.** – In small groups in a predominantly conifer forest associated with *Pinus sylvestris*. Thus far only known from two locations in Bingöl, Türkiye.

**Additional material examined.** – *Ibid.*, 17 April 2021, *leg.* İ. Acar (VANF1154).

**Notes.** – *Hebeloma uzunii* is characterized by its cream to milky brown pileus with white margin,



cream-brown lamellae, pruinose buff stipe, weakly dextrinoid, and ellipsoid to ellipsoid-cylindrical basidiospores. The section *Hebeloma* is one of the largest sections of the genus and consists of 20 species including *H. bingolense* I. Acar, Dizkirici, Kalmer & Y. Uzun, which was recently described from Türkiye (Acar et al. 2022). The phylogeny presented here supports that *H. uzunii* forms a clearly distinct position in the *H. mesophaeum* (Pers.) Quél. species complex of section *Hebeloma* and is most closely related to *H. subtortum* P. Karst. (Fig. 17).

The new species may be confused with *H. subtortum* in morphology because they both produce a white to brownish pileus. Comparing their macroscopic and microscopic characteristics in detail, *H. subtortum* differs from the new species by its slenderer basidiomata (pileus 20–100 mm in diameter, stipe 70–90 mm in length), stipe width greater than 4 mm, large number of lamellae (at least 50), mostly ovoid basidiospores, and longer caulocystidia (up to 90 µm vs. 70 µm in *H. uzunii*) with limited shape (Beker et al. 2016, Dizkirici et al. 2019). *Hebeloma mesophaeum*, another closely related species, is distinct from *H. uzunii* based on a more umbonate and distinctly bicolored pileus with a more intensely reddish-brown center, more than 50 full-length lamellae, and longer caulocystidia (up to 130 µm vs. 70 µm in *H. uzunii*). Micromorphologically, *H. mesophaeum* has relatively small ellipsoid basidiospores that are smooth to slightly rough and not dextrinoid (Beker et al. 2016, Cripps et al. 2019).

*Authors*: İ. Acar, A. Kalmer & A. Dizkirici Tekpinar

#### Basidiomycota, Agaricomycetes, Agaricales, Pleurotaceae

*Pleurotus overstrandensis* B. Van der Merwe, G. Zervakis, J. Williams & K. Jacobs, **sp. nov.** – Figs. 22–25

Mycobank number: MB 849271

*Holotypus*. – SOUTH AFRICA. Western Cape province, Overstrand Local Municipality, 34° 33' 04.9" S, 19° 25' 14.6" E, 40 m a.s.l., on sandy soil, 3 April 2023, *leg.* J. Williams, PO2 (PREM 63388; holotype). Sequences ex-holotype: OR101946 (ITS), OR101950 (LSU).

*Description*. – Pileus fleshy, initially convex with large scales, growing to concave, often cracked in appearance, 100–250 mm, up to 450 mm in diameter, tomentose grey-white, pale cream, aging to tan, margin becoming irregularly wavy with age. – Lamellae decurrent, extending halfway down the stipe in shallow ridges; crowded under pileus, pale tan in color. – Stipe filled, central to subcentral, pale with olive tint with age, 30–80 mm, broad above-ground (up to 40 mm); presence of ro-

bust, long (more than twice the length of the stipe) pseudorhiza running underground; flesh firm and elastic, solid, white to cream. – Odor cucumber to farinaceous. – Spore print pale white. – Basidiospores 11.2–13.1–15.5 × 3.3–4.2–4.9 µm, Q = 3.1, mostly with granular content, cylindrical with minute suprahilar depression. – Basidia 35–45 × 6–8 µm, subclavate to cylindrical, granular; 4-spored, sterigmata large, up to 3 µm long; basidiales abundant. – Cheilocystidia 25–35 × 4–7 µm, abundant on lamellar edge, mostly clavate to elongated subclavate, hyaline, typically swelling to a rostrum at the apex. – Pleurocystidia not observed. – Colony characteristics pale cream, cottony-tomentose on potato dextrose agar, slightly granular throughout with raised protrusions becoming smooth towards margins, reverse unchanged; under microscope hyphae granular, clamp connections present, microdroplets visible on short pegs borne on aerial hyphae.

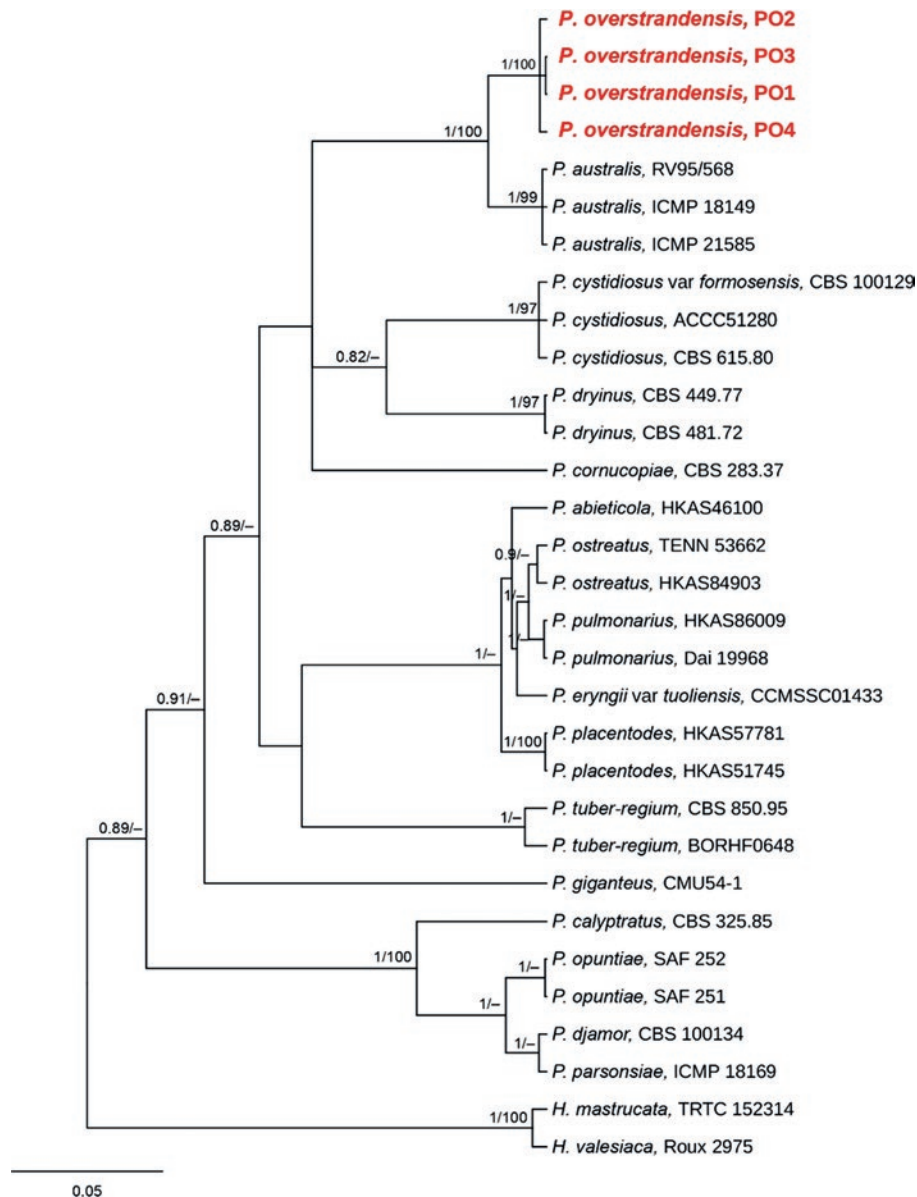
*Etymology*. – Named after the Overstrand region of South Africa, where the type specimen was found.

*Habitat and distribution*. – Thus far only known from South Africa, from the Overstrand Local Municipality of the Western Cape, and east to the Agulhas plain. Isolated populations have been recorded on the Cape Peninsula. From April (autumn) through September (mid-spring) on sandy coastal soil, consisting of ancient coastal limestone deposits, where roots and stems of grasses and other herbaceous plants are present.

*Additional material examined*. – *Ibid.*, 50-km radius around 34° 34' 21.9" S, 19° 21' 26.0" E, 3 April 2023, *leg.* J. Williams, PO1, PO3, PO4.

*Notes*. – *Pleurotus* comprises mostly of saprotrophic fungi, with some species referred to as “oyster mushrooms”. The genus consists of ca. 40 species distributed in temperate to tropical regions. Several *Pleurotus* species are of great commercial significance; they are cultivated on a wide range of lignocellulosic substrates and produce large yields of edible fruiting bodies (Guzmán 2000, Royse et al. 2017, Zervakis & Koutrotsios 2017). *Pleurotus* mushrooms are an important source of food in Africa; several species, including *P. citrinopileatus* Singer, *P. djamor* (Rumph. ex Fr.) Boedijn, and *P. ostreatus* (Jacq.) P. Kumm., are widely cultivated on the continent (Musieba et al. 2012, Otieno et al. 2015, Kinge et al. 2020, Ndifon 2022).

In April 2023, the authors visited the Overstrand region of South Africa (near the town of Gansbaai) after reports of large, edible, white-gilled mushrooms came to light. Impressive basidiomata were



**Fig. 22.** Phylogeny of *Pleurotus* reconstructed from a concatenated ITS–LSU dataset, inferred from BI analyses. BI posterior probabilities (BIPP)  $\geq 0.75$  and ML bootstrap (MLBS)  $\geq 90$  are presented as BIPP/MLBS. Sequences generated in this study in red and boldface, scale bar indicates 0.05 nucleotide substitutions per site.

found fruiting on ancient seashell-rich coastal dune soil among herbaceous plants at sea level. They often appear in large numbers after the first heavy autumn rains. The unique habitat, ecology, and morphology of the specimens sampled, coupled with the lack of studies on African macrofungi led to the hypothesis that this might represent a new species. The examination of morphoanatomical features of basidiomata combined with molecular phylogenetic analyses demonstrated that this fungus is a new species of *Pleurotus*.

The basidiomata were so unusual that their identification – even to genus level – was not easy based on their macromorphological features alone. However, when the biological material was microscopically examined and phylogenetically analyzed, the fungus was placed in the genus *Pleurotus*, and to a previously unknown species described here as *Pleurotus overstrandensis*. The ITS and LSU sequences from the four basidiomata shared 93.6–94.7 % and 99.1–99.2 % identity with *Pleurotus australis* Sacc., respectively. In addition, the topolo-



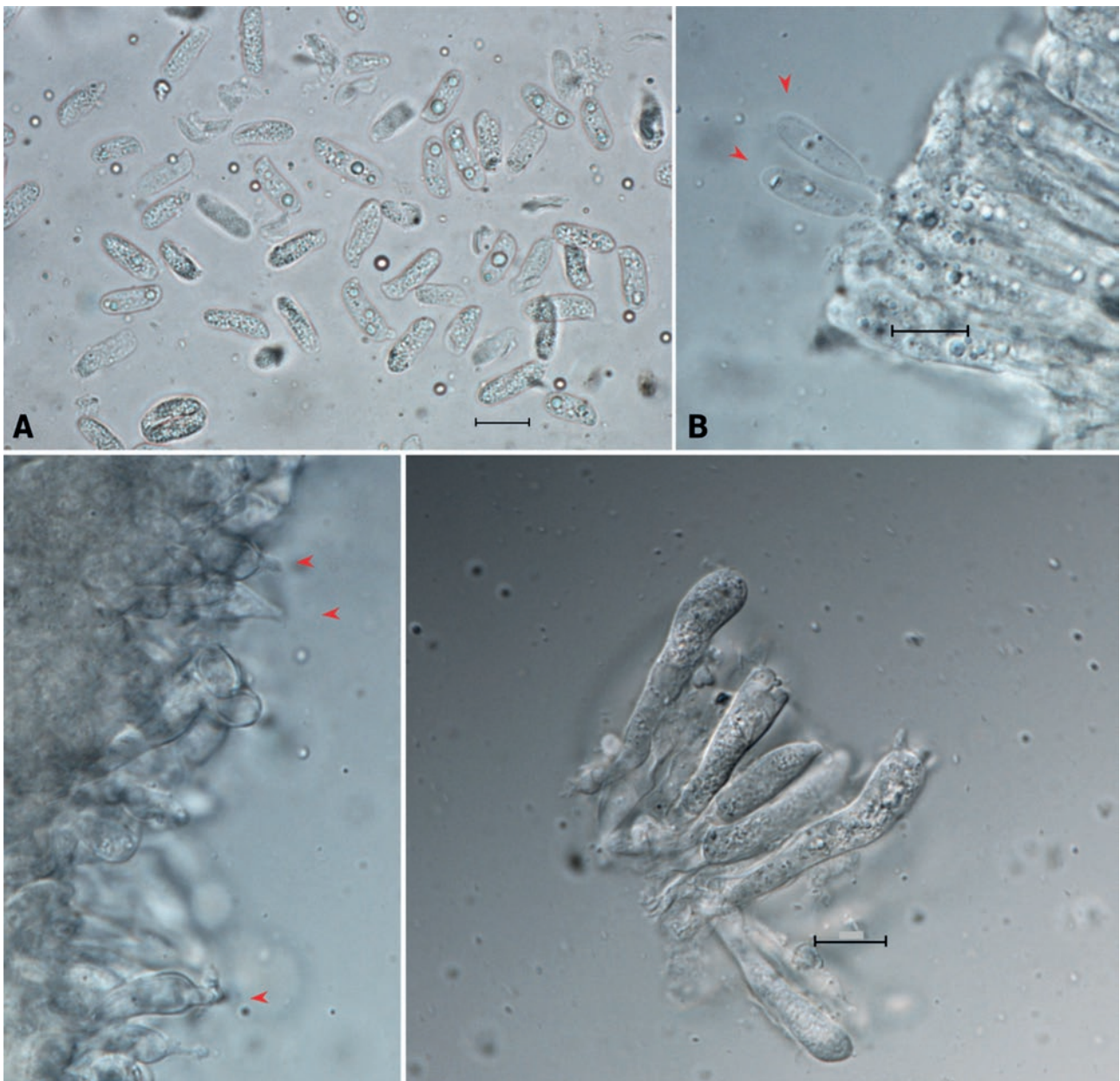
Fig. 23. *Pleurotus overstrandensis* basidiomata in the field at varying stages of development. Photos J. Williams.

gies in the respective phylogenetic trees generated from BI and ML analyses were almost identical. On the Bayesian tree selected to illustrate relationships within the genus *Pleurotus* (Fig. 22), the specimens under study were grouped in a maximally supported clade placed sister to *P. australis*.

The ecology of *P. overstrandensis* remains largely unknown. Although most likely saprotrophic, characteristic nematotoxic droplets are visible on aerial hyphae (Fig. 25), so *P. overstrandensis* is possibly predatory in nature as well. The production of

nematotoxic microdroplets noted on secretory appendages scattered throughout the mycelium of *P. overstrandensis* is a common feature among several *Pleurotus* species, and of diagnostic value for members of the respective family (Thorn & Barron 1984, Thorn et al. 2000).

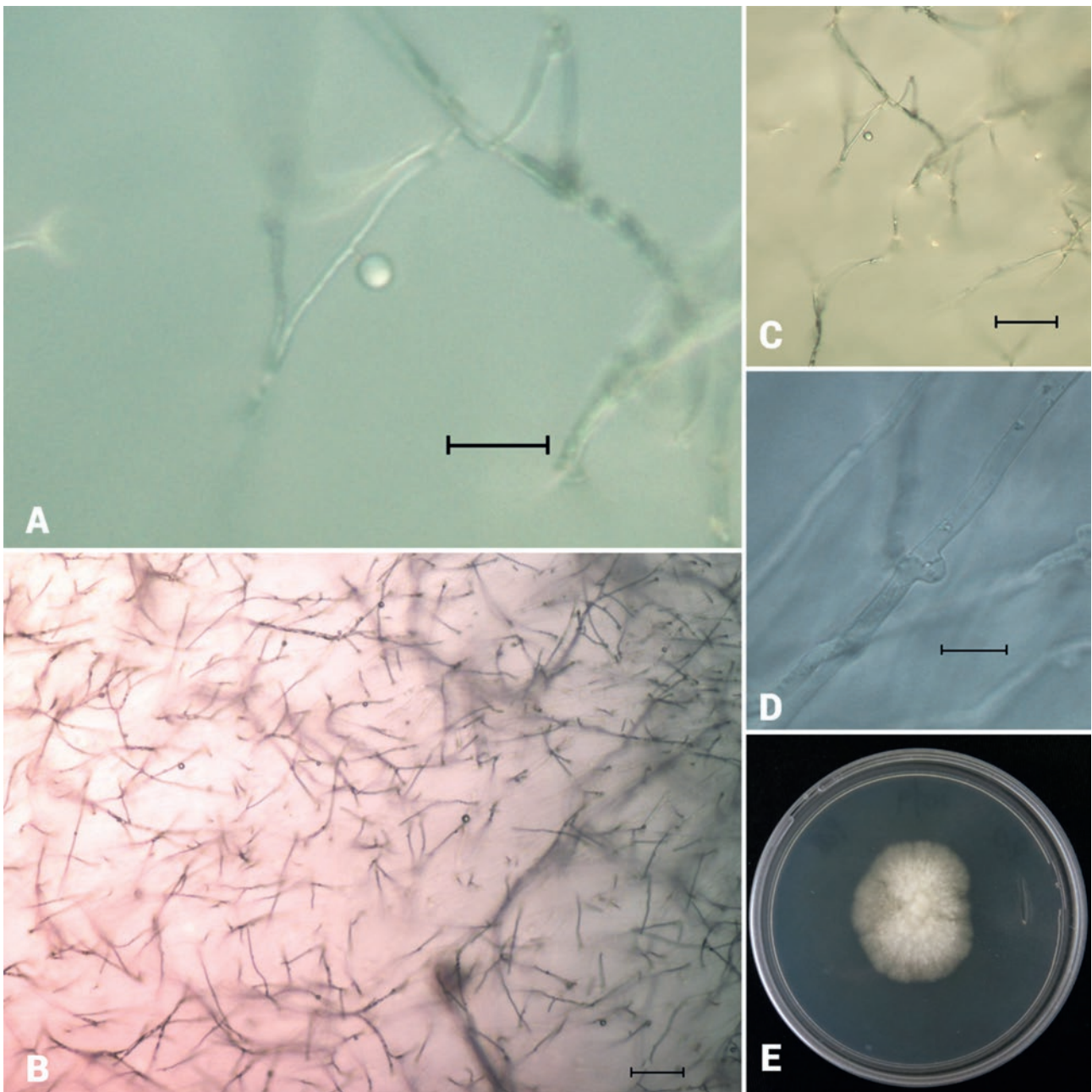
When *P. overstrandensis* is compared with the phylogenetically closest relative, *P. australis*, it differs by the significantly larger size of basidiomata, the coarse-scaly pileus surface (vs. smooth in *P. australis*), the presence of pseudorhiza, absence of



**Fig. 24.** Micromorphological characteristics of *Pleurotus overstrandensis*, collection PO2 (holotype). **A.** Basidiospores. **B.** Basidia and basidiospores (indicated with arrowheads). **C.** Cheilocystidia (indicated with arrowheads). **D.** Basidia and basidioles. Bars 10 µm. Photos B. Van der Merwe.

pleurocystidia, and basidiospores with granular appearance (vs. hyaline in *P. australis*) (Segedin et al. 1995). In addition, *P. australis* occurs in Australia and New Zealand, growing on wood and roots of *Leptospermum* and other native trees and shrubs. *Pleurotus overstrandensis* has thus far only been recorded in the Western Cape province of South Africa, always fruiting on the ground, often in sandy soil, in between the stems and roots of herbaceous

plants. Our phylogenetic analyses shows clear separation between the two species, which are grouped in sister clades with high to maximum support, both originating from the Southern Hemisphere. This is also the case for other mushroom species reported from the southern part of Africa and Australia (and/or New Zealand), e.g., *Hericium opheliae* vs. *H. novae-zealandiae* (Van der Merwe et al., 2023), and an undescribed *Morchella* species from



**Fig. 25.** Culture characteristics of *Pleurotus overstrandensis*. **A–C.** Microdroplets present on short pegs throughout aerial hyphae. **D.** Clamp connections. **E.** Mycelium colony on potato dextrose agar (PDA) after 2 weeks of growth. Bars A, B 20  $\mu\text{m}$ ; C 50  $\mu\text{m}$ ; D 10  $\mu\text{m}$ . Photos B. Van der Merwe.

the Western Cape and *M. australiana* (B. Van der Merwe et al. unpublished).

*Pleurotus* species are of great importance as important food sources due to their rapid growth, non-fastidious nature, adaptability to a large range of lignocellulosic substrates, and nutritional value (Pakela 1997, Khan & Tania 2012, Masevhe et al. 2015). Therefore, the description of this new, possi-

bly indigenous oyster mushroom not only improves our knowledge of local biodiversity but could also have far-reaching effects regarding its commercial exploitation. However, further studies are needed to determine the feasibility of its cultivation, dietetic properties, and future prospects.

*Authors:* B. Van der Merwe, G.I. Zervakis, J. Williams & K. Jacobs

## Mucoromycota, Mucoromycetes, Mucorales, Saksenaaceae

***Saksenaea ozerskayae*** Kochkina, Kachalkin, Ivanushkina & Vainshtein, **sp. nov.** – Figs. 26–28  
MycoBank no.: MB 856841

**Diagnosis.** – Differs from *S. vasiformis* in its spores that are 1.5× larger in size. Differs from all species in the genus *Saksenaea* in its inability to grow at 37 °C.

**Holotypus.** – RUSSIAN FEDERATION. Moscow, isolated from ascoma of *Tuber magnatum* (Ascomycota, Pezizomycetes, Pezizales, Tuberales), 14 September 2023, leg. M.B. Vainshtein, TB-1 (VKM H-0004; holotype). Ex-type culture: VKM F-5019. Ex-holotype sequences: PP280821–PP280826 (ITS), PP600326 (LSU), PP439981–PP439983 (*tef1*).

**Description.** – Hyphae hyaline, branched, sparsely septate, 5–12 µm wide. – Sporangio-phores erect, arising singly, dark-brown, unbranched, roughened, 70–90 × 5–10 µm. – Rhizoids well developed, dichotomously branched. – Sporangia terminal, multi-spored, flask-shaped, echinulate, 85–140 µm in length; spherical venter-like basal part, 35–50 × 30–40 µm; long neck, 50–100 µm, with apical mucilaginous plug; obovate spheroid columella, 30–33 × 20–22 µm. – Sporangiospores cylindrical, smooth-walled, 7–13 × 3–5 µm. – Zygospores not observed.

**Culture characteristics.** – Colonies on CZA at 25 °C whitish or pale yellow, floccose, with small lumps of aerial mycelium, reaching 75–80 mm after 5 days of incubation, reverse colourless. On MEA, PDA, and OA showing similar features as on CZA, but more whitish, no sporulation. Optimal temperature of growth between 20 °C and 25 °C. No growth was observed at 37 °C and above. On CZA after 5 days colonies reaching 37–42 mm in diameter at 15 °C, 60–64 mm diameter at 20 °C, 75–80 mm diameter at 25 °C, 13–17 mm diameter at 30 °C, and no growth at 0 °C, 37 °C, and 42 °C.

**Etymology.** – Named in honor of Dr. Svetlana Ozerskaya (1953–2022), the permanent leader of the VKM mycological group for nearly 40 years, for her contributions to the study of fungal diversity.

**Habitat and distribution.** – Russia, isolated from ascoma of white truffle, *Tuber magnatum*.

**Notes.** – The presence of extrinsic mycelium in the ascomata of fungi in the genus *Tuber* P. Micheli ex F.H. Wigg. was discovered over a hundred years ago. Pacioni & Leonardi (2016) reviewed the literature on this subject and proposed “truffle-inhabiting fungi” (TIF) to refer to the truffle-specific mycobio- biome. Here we report a species in the genus *Saksenaea* as a TIF for the first time.

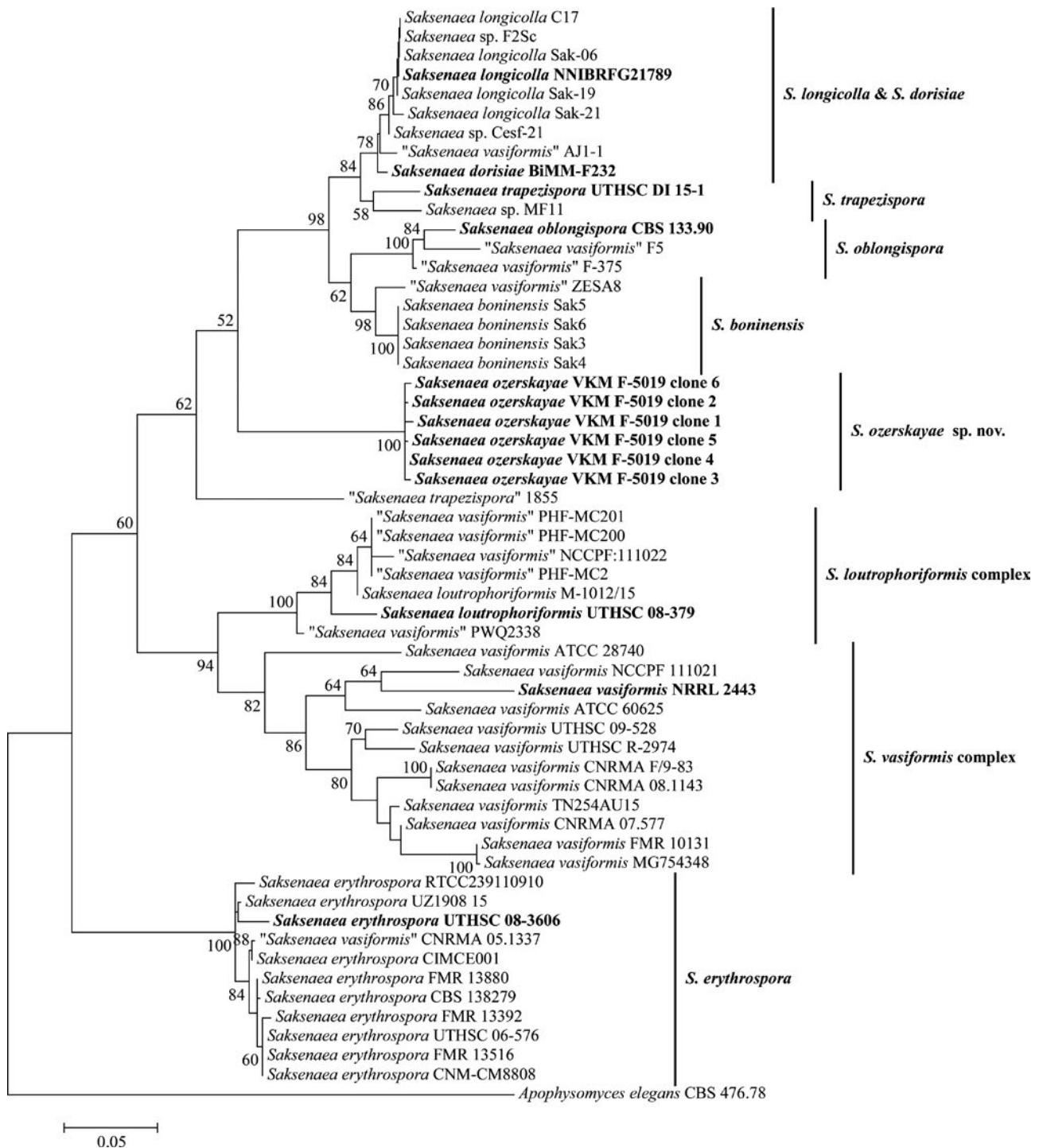
The heterogeneity of the ITS region posed difficulties for direct sequencing of the PCR product for

accurate identification of the isolated strain as multiple nucleotide peaks were present in the sequence traces. ITS sequence heterogeneity has been reported early for different fungal phyla (Wang & Yao 2005, Woo et al. 2010, Solieri et al. 2013, Lebeuf et al. 2023), and cloning followed by sequencing of clones were traditionally used to solve this. Six clones with different sequences of the ITS region were obtained for the studied strain, VKM F-5019. The differences between the ITS sequences of the obtained clones are 0.31–1.01 %, representing 1–4 nucleotide substitutions and 0–4 deletions.

BLAST searches reveal that the obtained ITS sequences for strain VKM F-5019 shares highest similarity (87 %) with *Saksenaea* sp. strain Cesf-21 (GenBank accession no. MK775965) and *S. vasiformis* S.B. Saksena isolate AJ1-1 (MH059541). Limiting BLAST searches to sequences from type material results in the following closest hits: *S. trapezispota* D.A. Sutton, Stchigel, Wiederhold, Guarro & Cano UTHSC DI 15-1 (GenBank accession no. NR\_147690), *S. oblongispota* Álvarez, Stchigel, Cano & Guarro CBS 133.90 (NR\_137569), *S. dorisiae* R. Labuda, A. Bernreiter, C. Schüller, J. Strauss & M. Wagner BiMM-F232 (MK559697), and *S. boninensis* Y. Takash. & K. Narisawa Sak4 (MK757863), with 88–89 % similarity. These results indicate that the strain VKM F-5019 represents a new species in the genus *Saksenaea*, which is also observed in the ITS tree (Fig. 26).

*Saksenaea ozerskayae* is placed sister to the clade with *S. boninensis*, *S. dorisiae*, *S. longicolla* D.J. Lee, B. Nam & Y.J. Choi, *S. oblongispota*, and *S. trapezispota*. The results of our phylogenetic analysis confirm previous findings (Takashima et al. 2023) that some sequences deposited in GenBank as “*Saksenaea vasiformis*” do not cluster with the ex-type strain of *S. vasiformis* NRRL 2443. In our opinion, the clades in the phylogenetic tree reconstructed from the ITS dataset (Fig. 26) labelled as *S. vasiformis* complex and *S. loutrophoriformis* Deanna A. Sutton, Stchigel, Chander, Guarro & Cano complex, should be studied in detail due to the high variety of the strains.

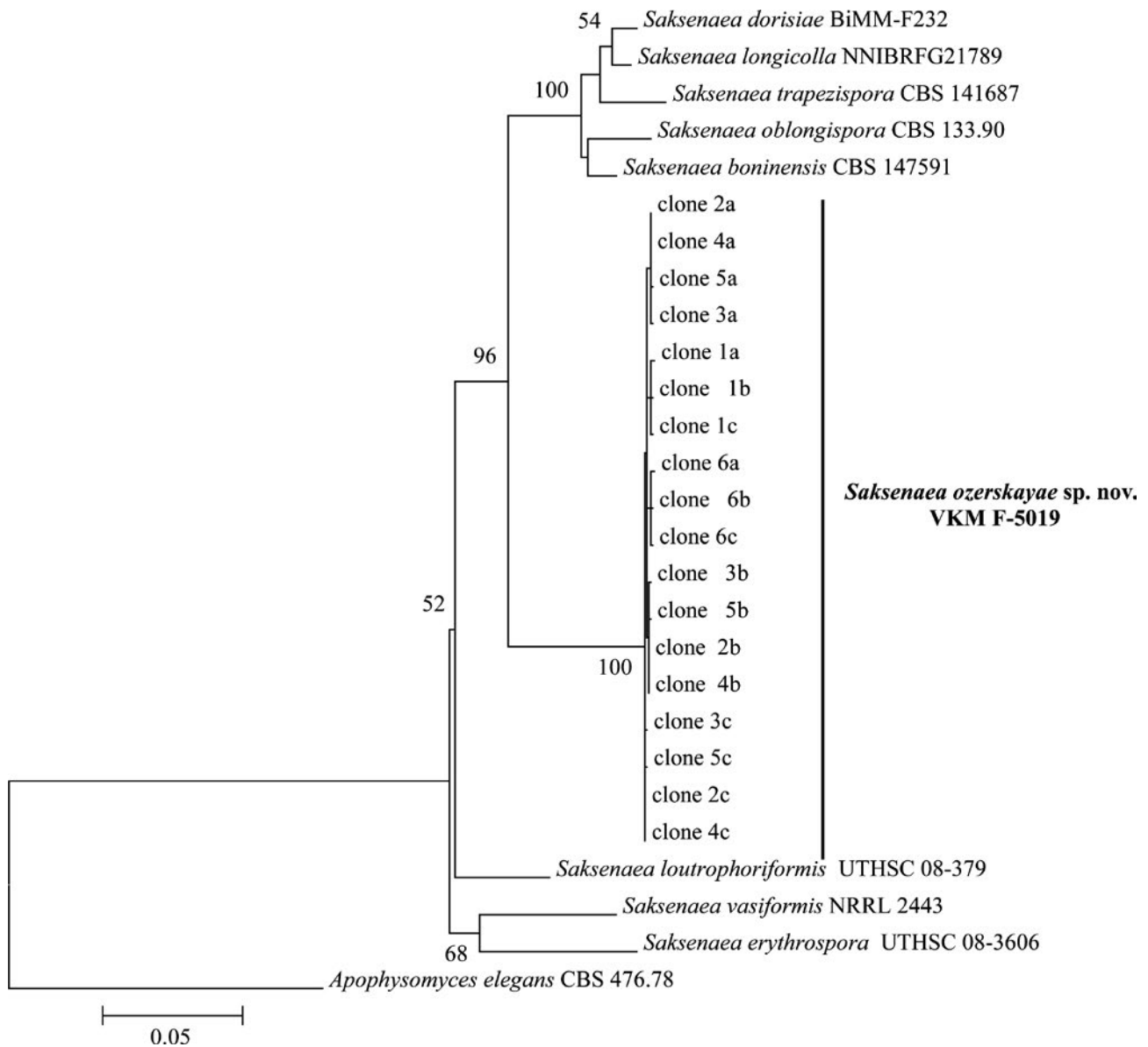
The newly generated partial LSU sequence of *S. ozerskayae* shares highest similarity (96 %) with *S. boninensis* Sak4 (GenBank accession no. MK757859): 35 nucleotide substitutions and 3 deletions. The *tef1* region of *S. ozerskayae* is heterogeneous, as is also the case for the ITS. Three clones with different sequences for the *tef1* gene were obtained for strain VKM F-5019. The differences between the *tef1* sequences of the obtained clones are 0.90–1.25 %, representing 5–7 nucleotide substitu-



**Fig. 26.** Phylogeny of *Saksenaea* reconstructed from an ITS dataset with *Apophysomyces elegans* as outgroup. The topology is the result of ML inference performed with MEGA 6. ML bootstrap (MLBS) values  $\geq 50$  are shown above the nodes. Scale bar indicates 0.05 substitutions per site. The new species and ex-type strains are highlighted in bold.

tions. The *tef1* sequences of *S. ozerskayae* share highest similarity (~95 %) with *S. boninensis* Sak4 (GenBank accession no. LC474957) and *S. loutro-*

*phoriformis* M-1012/15 (LT796166). The phylogeny reconstructed from the concatenated ITS–LSU–*tef1* dataset shows that the different clones (ITS and



**Fig. 27.** Phylogeny of *Saksenaea* species and clones of *S. ozerskayae* reconstructed from a concatenated ITS–LSU–*tef1* dataset with *Apophysomyces elegans* as outgroup. The topology is the result of ML inference performed with MEGA 6. ML bootstrap (MLBS) values  $\geq 50$  are shown above the nodes. Scale bar indicates 0.05 substitutions per site. The clone numbers denote different ITS sequences, and letters denote different *tef1* sequences.

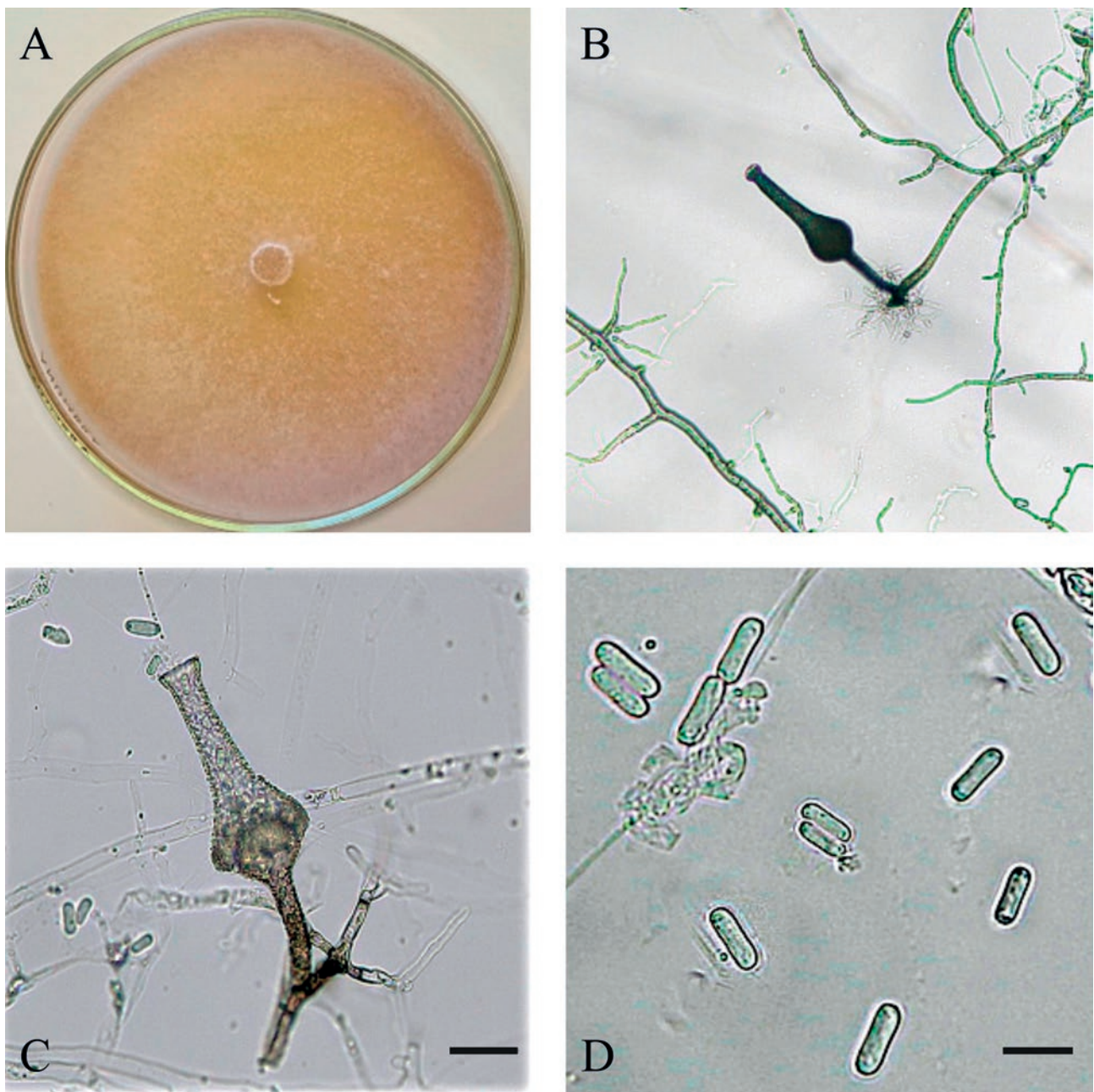
*tef1*) combinations of strain VKM F-5019 represent a distinct lineage in the genus (Fig. 27).

The size of the sporangium (mean 120.1  $\mu\text{m}$ ) and length of the neck of the sporangium (mean 83.3  $\mu\text{m}$ ) is similar to the majority of species in the genus. Morphologically, differences are best observed when comparing sporangiospores among different species of *Saksenaea*.

According to the shape of spores, all species can be divided into two groups. *Saksenaea boninensis*,

*S. dorisiae*, *S. longicolla*, *S. oblongisporea*, and *S. vasiformis* have spores mostly bacilliform, oblong, cylindrical. On the other hand, *S. erythrospora*, *S. loutrophoriformis*, and *S. trapezisporea* produce spores that are trapezoid-shaped; bacilliform, bilaterally compressed and rounded at both ends; ellipsoid, biconcave in a lateral view. The new species belongs to the first group of species with cylindrical spores that, however, are longer compared to other species (7–14  $\times$  3–5  $\mu\text{m}$ ). Characteristically,





**Fig. 28.** Morphology of *Saksenaea ozerskayae*. **A.** Colony growth on MEA after 7 days at 25 °C. **B.** Sporangium with rhizoid. **C.** Detail of the sporangium: flask-shaped basal part, oblate spheroid-shaped columella, and long neck with open apical mucilaginous plug. **D.** Sporangiospores. Bars C 25  $\mu$ m, D 10  $\mu$ m.

the ratio of average spore width and length in *S. ozerskayae* is 0.40, whereas in other species it varies from 0.50 to 0.65. *Saksenaea vasiformis* is the exception, with a ratio of about 0.42, but its spores are considerably smaller ( $5\text{--}7 \times 2\text{--}3 \mu\text{m}$ ) than those of *S. ozerskayae*.

Fungi in the genus *Saksenaea* are often causative agents of mycoses (about 3 % of all infections caused by fungi of Mucorales) (Jeong et al. 2019), but they are still not fully understood as causative agents. The strain of the new species is radically different from all other members of the genus *Sakse-*

*naea* by its inability to grow at temperature of 37 °C. It is the first non-thermotolerant strain in the genus *Saksenaea*. It gives serious grounds to believe that this species cannot be a causative agent in warm-blooded animals and humans.

*Authors:* G. Kochkina, A. Kachalkin, N. Ivanushkina & M. Vainshtein

### Interesting taxonomical notes, new hosts, and geographical records

#### Basidiomycota, Agaricomycetes, Agaricales, Cortinariaceae

*Cortinarius balteatoindicus* Dima, Semwal, V. Papp, Brandrud & V.K. Bhatt, **sp. nov.**  
Mycobank number: MB 854959

*Cortinarius balteatoindicus* Dima, Semwal, V. Papp, Brandrud & V.K. Bhatt, *Persoonia* 44: 375 (2020), *nom. inval.*, Art. 40.7 (Shenzhen) [Mycobank number: MB 834802]; see here for validating description

*Synonym.* – *Phlegmacium balteatoindicum* (Dima, Semwal, V. Papp, Brandrud & V.K. Bhatt) Niskanen & Liimat., in Niskanen & Liimat., *Index Fungorum* 528: 9 (2022), *nom. inval.*, Art. 35.1 (Shenzhen) [Mycobank number: MB 559968]

*Holotypus.* – INDIA. Uttarakhand, Pauri Garhwal, Teka, 30° 6' 21" N, 78° 45' 12" E, 1965 m a.s.l., 4 September 2015, *leg.* K.C. Semwal, KCS 2509 (WU-Myc53457; holotype). Ex-holotype sequences: MT137516 (ITS), MT241837 (LSU).

*Notes.* – As a result of the study of Kamal C. Semwal's collections originating from Uttarakhand, North India, six species of *Cortinarius* (Pers.) Gray were described across several studies (Song et al. 2019; Crous et al. 2020a, b; Yuan et al. 2020). The holotypes of *Cortinarius lilacinoarmillatus* Semwal & Dima (Song et al. 2019), *C. indorusseus* Dima, Semwal, V.K. Bhatt & Brandrud, and *C. paurigarhwalensis* Semwal, Dima & Soop (Yuan et al. 2020) were deposited in the Central National Herbarium (CAL). However, in the descriptions of *C. balteatoindicus* Dima, Semwal, V. Papp, Brandrud & V.K. Bhatt, *C. indopurpurascens* Dima, Semwal, Brandrud, V. Papp & V.K. Bhatt (Crous et al. 2020b), and *C. ulkhagarhiensis* Dima, Semwal, V. Papp, Brandrud & V.K. Bhatt (Crous et al. 2020a), the authors neglected to specify the appropriate herbarium code when designating the type specimens. They referenced the type specimen voucher numbers solely as “KCS 2509”, “KCS 2442”, and “KCS 2490”, respectively. Consequently, the mentioned three names are not validly published according to Art. 40.7 of the International Code of Nomenclature (Turland et al. 2018).

The genus *Cortinarius* was subsequently divided into ten different genera by Liimatainen et al. (2022b), resulting in the reclassification of *C. balteatoindicus* into the genus *Phlegmacium* (Fr.) Wünsche (Liimatainen et al. 2022a). However, the name *Phlegmacium balteatoindicum* (Dima, Semwal, V. Papp, Brandrud & V.K. Bhatt) Niskanen & Liimat. is also invalid, because the new name of a species to which the taxon is assigned must be validly published either previously or at the same time (Art. 35.1, Turland et al. 2018). A similar situation exists for the species *C. indopurpurascens*. Following the systematic concept proposed by Liimatainen et al. (2022b), Ghosh et al. (2023) described *Thaxterogaster shoreae* A. Ghosh, D. Chakr., K. Das & Vizzini from India, which, based on phylogenetic analyses, is the sister species of *C. indopurpurascens*. Therefore, they proposed transferring the species to the genus *Thaxterogaster* Singer and introduced the name *T. indopurpurascens* (Dima, Semwal, Brandrud, V. Papp & V.K. Bhatt) A. Ghosh, D. Chakr., K. Das & Vizzini (Ghosh et al. 2023).

However, in a recent study, Gallone et al. (2024) re-examined the phylogenomic dataset provided by Liimatainen et al. (2020b) using both concatenation and multispecies coalescent approaches and identified extensive gene-tree/species-tree conflicts. Gallone et al. (2024) confirmed the monophyly of only four out of the ten proposed genera, concluding that current evidence does not support splitting the genus *Cortinarius* at this time. Based on this, we continue to support the retention of the genus *Cortinarius* as a single entity and intend to discuss the invalidly described species (i.e., *C. balteatoindicus*, *C. indopurpurascens*, and *C. ulkhagarhiensis*) within this genus. To validate the names, we present the corrected type citations along with references to the original descriptions in this work. The type specimens were deposited at the Herbarium of the University of Vienna (WU). In accordance with Article F.5.7 (May et al. 2019), new identifiers for the names have been secured from MycoBank. In addition, following the broader interpretation of the genus *Cortinarius* according to Gallone et al. (2024), we do not recognize *Thaxterogaster* as an independent genus and thus combine *Thaxterogaster shoreae* into the genus *Cortinarius*.

*Authors:* B. Dima & V. Papp

#### Basidiomycota, Agaricomycetes, Agaricales, Cortinariaceae

*Cortinarius indopurpurascens* Dima, Semwal, Brandrud, V. Papp & V.K. Bhatt, **sp. nov.**  
Mycobank number: MB 854960

*Cortinarius indopurpurascens* Dima, Semwal, Brandrud, V. Papp & V.K. Bhatt, *Persoonia* 45: 403 (2020), *nom. inval.*, Art. 40.7 (Shenzhen) [Mycobank number: MB 837766]; see here for validating description.

**Synonym.** – *Thaxterogaster indopurpurascens* (Dima, Semwal, Brandrud, V. Papp & V.K. Bhatt) A. Ghosh, D. Chakr., K. Das & Vizzini, *Taiwania* 68(1): 29 (2023), *nom. inval.*, Art. 35.1 (Shenzhen) [Mycobank number: MB 837766]

**Holotypus.** – INDIA. Uttarakhand, Pauri Garhwal, Mundneshwar, 29° 01' 05" N, 78° 44' 32" E, 1820 m a.s.l., 12 August 2015, *leg.* K.C. Semwal, KCS 2442 (WU-Myc53458; holotype). Ex-holotype sequences: MW135432 (ITS).

*Authors:* B. Dima & V. Papp

### Basidiomycota, Agaricomycetes, Agaricales, Cortinariaceae

*Cortinarius shoreae* (A. Ghosh, D. Chakr., K. Das & Vizzini) Dima & V. Papp, **comb. nov.**  
Mycobank number: MB 854962

**Basionym.** – *Thaxterogaster shoreae* A. Ghosh, D. Chakr., K. Das & Vizzini, *Taiwania* 68(1): 27 (2023)

*Authors:* B. Dima & V. Papp

### Basidiomycota, Agaricomycetes, Agaricales, Cortinariaceae

*Cortinarius ulkhagarhiensis* Dima, Semwal, V. Papp, Brandrud & V.K. Bhatt, **sp. nov.**  
Mycobank number: MB 854961

*Cortinarius ulkhagarhiensis* Dima, Semwal, V. Papp, Brandrud & V.K. Bhatt, *Persoonia* 44: 377 (2020), *nom. inval.*, Art. 40.7 (Shenzhen) [Mycobank number: MB 834804]; see here for validating description

**Holotypus.** – INDIA. Uttarakhand, Pauri Garhwal, Ulkhagarhi, 30° 09' 36" N, 78° 50' 53" E, 2025 m a.s.l., 31 August 2015, *leg.* K.C. Semwal, KCS 2490 (WU-Myc53459; holotype). Ex-holotype sequences: MT137517 (ITS), MT241838 (LSU).

*Authors:* B. Dima & V. Papp

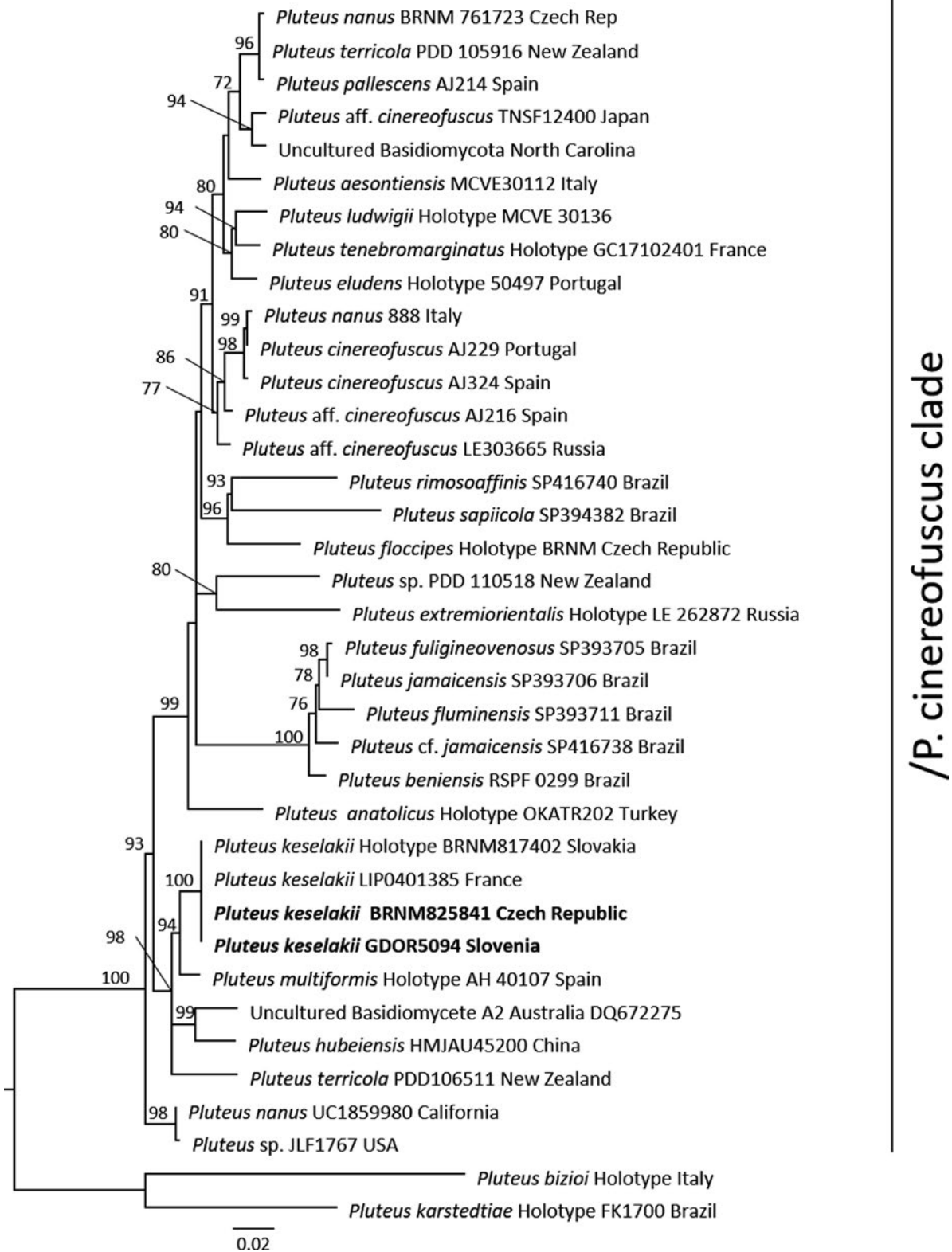
### Basidiomycota, Agaricomycetes, Agaricales, Pluteaceae

*Pluteus keselakii* Ševčíková, P.-A. Moreau & Borovička, *Phytotaxa* 432(2): 184 (2020). – Figs. 29–33

**Material examined.** – CZECHIA. South Moravian Region, Brno, Mariánské údolí valley, near pond on soil under *Alnus glutinosa* with *Urtica dioica*, 27 August 2019, *leg.* H. Ševčíková (BRNM 825841). SLOVENIA. Gorizia Region, Nova

Goricâ, Panoveč Park, on a gravel road on small buried woody shrubs in mixed deciduous forest with *Fagus sylvatica* and *Carpinus betulus*, 25 July 2020, *leg.* G. Ferisin (GDOR5094).

**Description.** – Pileus 10–31 mm in diameter (up to 17 mm in Slovenian collection) broad, initially campanulate later applanate to plano-concave, not umbonate, margin crenulate, eroded to slightly rimose in older specimens; surface velvety, opaque, smooth in the center (in the Czech collection) or rugose-venose from the center towards the margin in young specimens (in the Slovenian collection), margin sulcate up to half of the radius, radially cracked when old, not hygrophanous; light brown to dark brown, darker at the center, dark brown when drying. – Lamellae moderately distant, L = 30–46, l = 1–2, free, slightly ventricose, up to 5 mm broad, when young whitish, later pinkish, lamellar edge flocculose-eroded, concolorous in the Czech collection and concolor to light brown in the old specimens in the Slovenian collection. – Stipe 21–47 × 2–3 mm, cylindrical, sometimes with slightly enlarged base, curved or straight, longitudinally fibrillose or striate-twisted, white, in some basidiomata very pale brownish at the base, finely pruinose to weakly squamulose, sometimes with light brown or white floccules. – Context white to whitish. – Smell indistinct. – Taste not recorded. – Basidiospores (6.1–)6.2–6.8–7.4(–7.6) × (4.9–)5.4–5.7–6(–6.2) µm in the Slovenian collection and (5.0–)5.5–7.4–8(–8.8) × (5.0–)5.5–6.1–7.2(–8.0) µm in the Czech collection, Q = 1.00–1.40, Qm = 1.20, globose, subglobose to (broadly) ellipsoid. – Basidia 24–28 × 8–9 µm, clavate, 4-spored, hyaline or light brown. – Pleurocystidia 39–69 × 13–18 µm in the Czech collection and 49–106 × 14–35 µm in the Slovenian collection, scarce to moderately abundant, narrowly utriform to utriform, fusiform with obtuse apex or spatulate, clavate, without or with 6–10(–13) µm long pedicel, thin-walled, hyaline. – Cheilocystidia 53–102 × 24–34 µm in the Slovenian collection, 23–46(–57) × 10–17(–23) µm in the Czech collection, narrowly clavate to broadly clavate, subutriform, composed of elements with obtuse apex, thin-walled, hyaline or with light brown intracellular pigment (in 10 % KOH). – Lamellar edge partially fertile, with basidia and cheilocystidia or sterile. – Pileipellis an euhymeniderm composed of sphaeropedunculate, ovoid, obovoid to broadly clavate terminal elements with short neck, very rarely mucronate, subutriform or irregular, 21–65 × 8–36 µm, with brown to blackish-brown intracellular pigment (in water), thin-walled. – Caulocystidia scattered and scarce in some basidiomata, numerous in others, in tufts or not, present on



**Fig. 29.** Phylogeny of the *Pluteus cinereofuscus* clade reconstructed from an ITS dataset. The topology is the result of ML inference performed with RAxML. For each node, ultrafast bootstrap (UFBS) if  $\geq 70$  is presented above the branch leading to that node. Newly generated sequences are in bold.



Fig. 30. Basidiomata of *Pluteus keselakii* in the field, collection GDOR5094 (Slovenia).

the whole stipe and densely covered in the upper part,  $25\text{--}72(92) \times 8\text{--}19 \mu\text{m}$ , subcylindrical, narrowly clavate to clavate, fusiform or utriform with obtuse apex, thin-walled, mostly colorless, in some basidiomata also with brown intracellular pigment (in 10 % KOH) in the Czech collection; caulocystidia in the Slovenian collection present only at apex of stipe, similar to cheilocystidia in shape and size. – Clamp connections absent in all tissues.

**Habitat and distribution.** – On soil or on small buried woody shrubs. Thus far reported from Czechia, France, Slovakia and Slovenia.

**Notes.** – *Pluteus keselakii* is a recently described species by Ševčíková et al. (2020) based on two collections from France and Slovakia. It was originally characterized by a brown pileipellis composed of sphaeropedunculate to broadly clavate elements, a whitish stipe covered by distinct brown floccules over its whole length consisting of caulo-

cystidia in tufts, mostly narrowly utriform to utriform or fusiform pleurocystidia with obtuse apex, brown lamellar edge, at least near the pileus margin and growth on rich soil without visible connection to wood. In this study, two collections of *P. keselakii* from Czechia and Slovenia are described and compared with the protologue. These two collections showed some differences compared to what was reported in the original description. Both collections showed the absence or the presence only in some basidiomata of the brown pigmentation of the lamellar edge and the relative scarce presence or absence of brown pigmented cheilocystidia. Ševčíková & Borovička (2015) considered the brown lamellar edges as variable feature within species in *Pluteus* section *Celluloderma*, Ševčíková et al. (2020) expected it exactly for their new species *P. keselakii*, moreover, some lamellae in the holotype collection were colored only near the pileus margin, while oth-

Tab. 2. Description of the main characteristics observed in the studied collections of *Pluteus keselakii*.

Collections Herbarium no. GenBank acc. no.	Pileipellis	Lamellar edge	Stipe	Basidiospores			Caulocyst- idia	Cheilocystidia	Pleurocystidia
				av1	avw	avQ			
Slovakia BRNM 817402 (holotype) GenBank MN250223	Brown, reddish brown to dark brown, dark brown to almost blackish when young	Brown, in some lamellae brownish only near pileus margin	White, densely covered with brown floccules	7.48	6.76	1.10	Present throughout the stipe length, in tufts, brown	22–55(65) × 10–15(25) µm, narrowly clavate to clavate, rarely subutri- form, thin-walled, hyaline or with brown intracellular pigment; <i>lamellar edge</i> sterile	42–74 × 17–30 µm, narrowly utriform to utriform, some with median constriction, fusiform with obtuse apex or spathulate, rarely clavate
France LIP 0401385 PAM99052202 GenBank MN250224	Light chestnut brown	Brown to grey brown	White, densely covered with brown floccules	7.52	6.83	1.11	Present throughout the stipe length, in tufts, brown	22–60(65) × 10–19(26), narrowly clavate to clavate, rarely subutri- form, thin-walled, hyaline or with brown intracellular pigment; <i>lamellar edge</i> sterile	42.5–80 × (17)18–30(35) µm, narrowly utriform to utriform, some with median constriction, rarely fusiform with obtuse apex or spathu- late, clavate
Czechia BRNM 825841	Brown to dark brown, blackish when young	Whitish to light brown	White, light brown- grey at the base, covered with whitish or light brown floccules	7.4	6.1	1.21	Present throughout the stipe length, in some basidiomata scarce, brown; in some hyaline in tufts or not	23–46(57) × 10–17(23) µm, clavate to broadly clavate, rarely subutriform or fusiform, hyaline or with light brown intracellular pigment; <i>lamellar edge</i> sterile	39–69 × 13–18 µm, narrowly utriform to utriform, fusiform with obtuse apex or spathu- late, clavate
Slovenia GDOR 5094	Brown to dark brown, blackish when young	Whitish to light brown	White, covered with whitish floccules, brown- greyish at the base	6.9	5.7	1.20	Present only in the upper part of the stipe	53–102 × 24–34 µm, narrowly clavate to broadly clavate, subutriform, thin- walled, hyaline or with light brown intracellu- lar pigment; <i>lamellar edge</i> not sterile	49–106 × 14–35 µm, utriform to narrowly utriform, broadly clavate, rarely narrowly fusiform



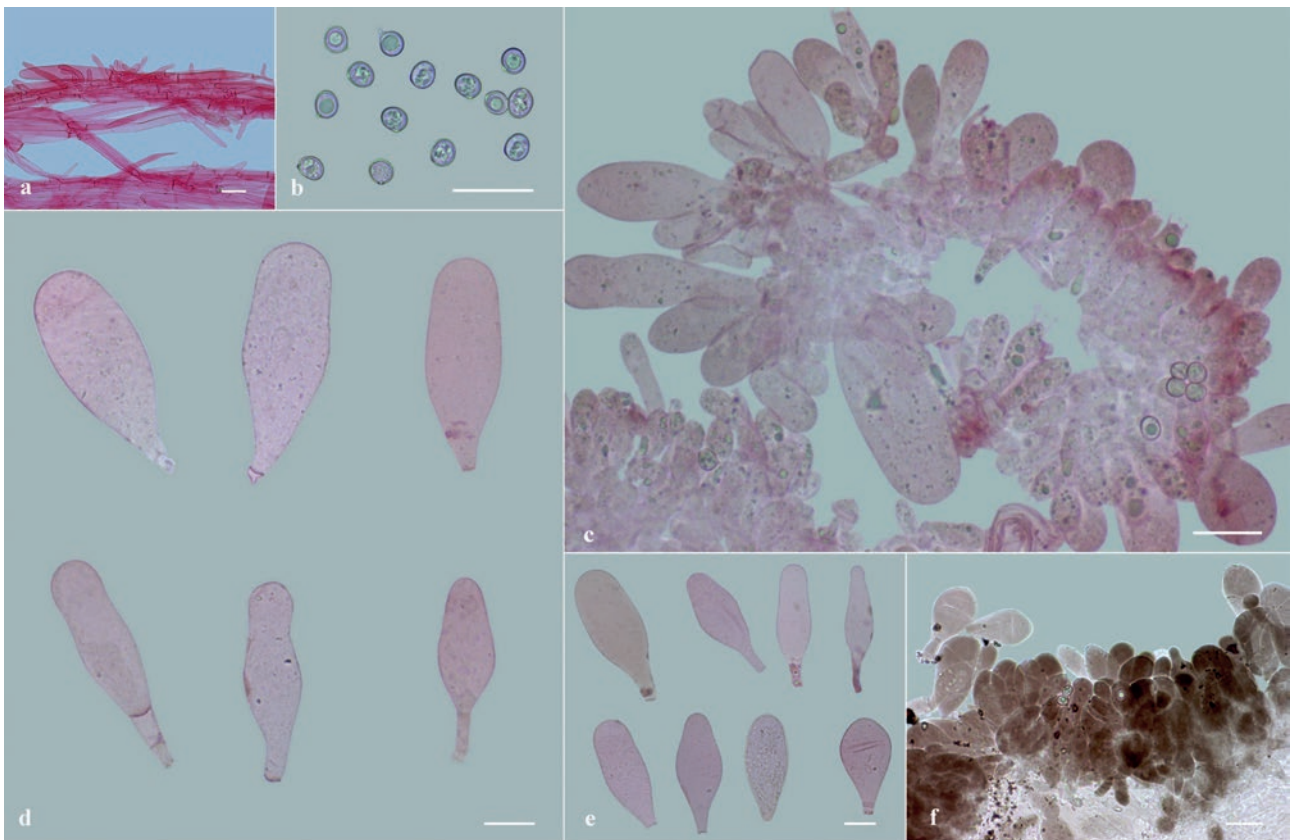
Fig. 31. *Pluteus keselakii*, collection BRNM825841 (Czechia).

er lamellae of the same basidioma were colored along the entire length.

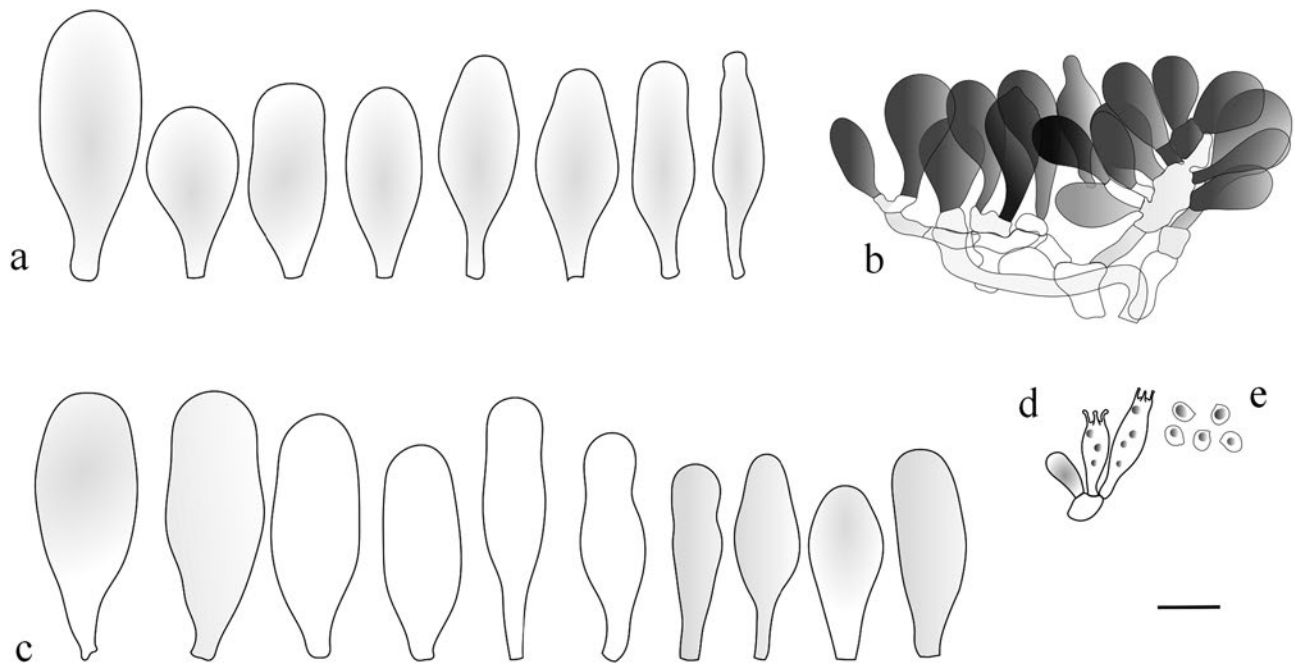
However, stipes with distinct, abundant brown floccules, and the presence of copious brown caulocystidia in tufts over the entire surface of the stipe, reported in the Slovak and French collections, have not been observed in these new collections from Czechia and Slovenia. The Czech collection showed stipes with hyaline caulocystidia in tufts but also with single scarce hyaline caulocystidia or scarce caulocystidia with a brown intracellular pigment. Otherwise, the Slovenian collection shows only rarely hyaline caulocystidia at the stipe apex. Although several specimens grew on soil, as was reported in the original description, some basidiomata from the Slovenian collection (Fig. 30) grew on decaying twigs. In light of the new collections, *P. keselakii* seems to present great morphological variability: (i) the brown pileus can be completely smooth to radially rugose-venose at the center, (ii) the color of the lamellar edge can be entirely dark

brown, brownish only near the pileus margin, or completely white, (iii) the lamellar edge is sterile to fertile, (iv) the stipe is covered by distinct brown or white floccules, (v) caulocystidia are present in tufts or scattered, on the entire surface of the stem or only on the upper part, and (vi) cheilocystidia have variable sizes in different collections.

Molecular phylogenetic analysis confirmed the morphological identification, all four sequences of *P. keselakii* grouped in the same clade with maximum support (UFBS = 100, Fig. 29). The features of the collections studied are shown in Tab. 2. In our phylogenetic analysis, *P. keselakii* is placed sister to *P. multififormis* Justo, A. Caball. & G. Muñoz (UFBS = 94), and it is also morphologically similar to *P. keselakii* but differs in having highly variable morphology of the pileipellis cells (from the original description: “clavate, spheropedunculate, utriform, narrowly lageniform, ovoid, conical, fusiform, flexuose, some mucronate or rostrate, some irregularly shaped”) and scarce pleurocystidia (Justo et al.



**Fig. 32.** Microscopic characteristics of *Pluteus keselakii*, collection GDOR5094. a. Stipitipellis. b. Spores. c–d. Cheilocystidia. e. Pleurocystidia. f. Pileipellis. Bar 20  $\mu\text{m}$ .



**Fig. 33.** Microscopic characteristics of *Pluteus keselakii*, collection GDOR5094. a. Pleurocystidia. b. Pileipellis. c. Cheilocystidia. d. Basidia. e. Basidiospores. Bar 20  $\mu\text{m}$ .



2011a). Ševčíková et al. (2020) considered the entire stipe surface covered with distinct dark floccules on a pale background and wider pleurocystidia up to 30 µm of *P. keselakii*, as two characteristic elements to separate it from *P. multiformis*, but these features are not constant in all basidiomata of *P. keselakii*. In conclusion, *P. keselakii* is a highly variable species from the morphological point of view that shares many features with the other species belonging to the /cinereofuscus clade, and in its various forms, only the genetic analysis allows for correct identification.

*Authors:* G. Ferisin, H. Ševčíková, E. Malysheva & F. Dovana

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