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In this 8th contribution to the Fungal Systematics and Evolution series published by Sydowia, the authors formally describe 11 species: *Cortinarius caryae*, *C. flavolilacinus*, *C. lilaceolamellatus*, *C. malodorus*, *C. olivaceolamellatus*, *C. quercophilus*, *C. violaceoflavescens*, *C. viridicarneus*, *Entoloma meridionale* (Agaricales), *Hortiboletus rupicapreus* (Boletales), and *Paraglomus peruvianum* (Paraglomerales). The following new country records are reported: *Bolbitius callistus* (Agaricales) from Russia and *Hymenoscyphus equiseti* (Helotiales) from Sweden. *Hymenoscyphus equiseti* is proposed as a new combination for *Lanzia equiseti*, based on ITS and LSU sequence data in combination with morphological study.

Keywords: 11 new species, 2 new records, 1 new combination, Agaricomycetes, Bolbitiaceae, Boletales, Cortinariaceae, Entolomataceae, Glomeromycetes, Helotiales, integrative taxonomy, Leotiomycetes.

Materials and methods

Sample collection, isolation, and specimen examination

Basidiomata of *Cortinarius* (Pers.) Gray were collected in the province of Quebec, Canada, photographed *in situ* or in the laboratory, then dried at 40 °C. The habitat, altitude, soil characteristics, and nearby trees were noted. Macro-anatomical characters were described from fresh basidiomata and from photographs, with the color codes of Kornerup & Wanscher (1978). Macrochemical reactions were noted on fresh basidiomata. Micro-anatomical studies were conducted on exsiccatae with a Nikon Labophot microscope (Nelville, NY) and a Moticam 2500 digital camera. Tissues were rehydrated in isopropanol 70 %, hand-sectioned, and observed in Melzer's reagent; KOH 3% and sodium dodecyl sulphate (SDS) Congo Red were also used for better visualization and pigment observation. Microstructures were measured with the aid of an optical micrometer, and descriptions follow Brandrud et al. (1990–2014) concepts. A minimum of 30 basidiospores per basidioma, obtained from spore print or natural deposit on cortina or veil, were randomly selected and measured using the following notation: [a/b/c] (d–)e–f(–g), where 'a/b/c' represent respectively the total number of spores, basidiomata, and collections, 'e' and 'f' the 5th and 95th centile of the measured values, and 'd' and 'g' the extreme values. Q (minimum and maximum length/width ratio) and Q_{av} (average length/width ratio) were calculated. Collections are kept in fungaria (sensu Thiers continuously updated), or in the private fungarium of Renée Lebeuf (R.L., collections labeled as HRL).

For the *Entoloma* study, morphological methods, as well as molecular protocols and phylogenetic analyses, followed those by Dima et al. (2021).

Collections of *Hortiboletus* Simonini, Vizzini & Gelardi were made in Vietnam in tropical mountain polydominant forests with tree species of Anacardiaceae, Fagaceae, Meliaceae, Myrtaceae, and Theaceae, and in pine plantations of *Pinus kesiya* with some Fagaceae. Fresh basidiomata were photographed in the field and their macromorphological features were studied. Color codes in the description follow Kornerup & Wanscher (1978). Microscopical characters were studied with a light Zeiss Axioscope A1 microscope with AxioCam 1Cc 3 camera and program tools AxioVisionRel.4.6. (Carl Zeiss, Jena, Germany). Basidiospores, basidia, and hymenial cystidia were observed in squash preparations of small parts of the tubes in 5 % KOH. The pileipellis was examined on a radial section of the pileus, the stipitipellis on longitudinal slice in 5 % KOH. Basidiospore and pileipellis end cell dimensions are based on 31 measurements, whereas cystidia and basidia dimensions are based on the measurements of at least 10 structures per collection. Basidia were measured without sterigmata, and the spores without hilum. Spore length to width ratios are reported as Q (Pham et al. 2020, 2021). Specimens are kept in LE (sensu Thiers continuously updated).

For the *Paraglomus* J.B. Morton & D. Redecker study, soil samples were repeatedly taken at 0–30 cm depth between January 2018 and December 2019, in agricultural fields in Peru. Sites were located in Requena (6°31'30"S, 76°45'38.38"W, 468 m a.s.l.) with *Coffea arabica* (coffee) and in Barranquita (6°44'19.64"S, 76°35'41.32"W, 321 m a.s.l.) with *Plukenetia volubilis* (inka nut). Both sites are located in the El Dorado Province of the San Martín State in the transition zone of Peruvian Amazonia lowlands and adjacent Andean low mountain ranges. These sites are traditional agroforestry sites, where the inka nut is grown in mixed cultures together with maize, beans, and other field crops, while coffee is grown with *Inga edulis*, which is a neotropical nitrogen-fixing and shadow-providing tree, also called joaquiniquil, cuaniquil, guama, or guaba. Both inka nut and coffee have been grown without addition of chemical fertilizers and pesticides. Mean annual temperatures are about 28–32 °C, with variation between 22 and 36 °C throughout the year. Mean annual precipitation is approximately 1,250 mm. In the greenhouse of the Facultad de Ciencias Agrarias, Universidad Nacional de San Martín, bait cultures were established under ambient temperature conditions, in cylindrical 3 l pots with 3 kg of substrate. The substrate consisted of a 2:1:1 mixture of field-collected soil samples, vermiculite, and coarse river sand. The substrate mixtures were autoclaved at 121 °C for 60 min, three weeks before establishment of bait cultures. At inoculation and bait culture establishment, pots were first filled to 75 % with the autoclaved substrate. Next, 100 g of rhizospheric soils were added to the substrate surface. Five seeds of either *Medicago sativa* (alfalfa), *Sorghum vulgaris*, or *Urochloa brizantha* were surface-sterilized using 0.5 % sodium hypochlorite and then seeded in order to establish arbuscular mycorrhizal fungal (AMF) associations. Finally, the seeds were covered with the remaining 25 % of the autoclaved substrate. The cultures were maintained in the greenhouse for eight months, with 21.4 ± 2.0 °C, 29.0 ± 3.0 °C, and 36.0 ± 2.0 °C as minimum, mean, and maximum temperatures, respectively. Relative humidity ranged from 46 % to 72 % between January and December 2020. The pots were irrigated every other day and fertilized with Long Ashton Nutrient Solution every two weeks, with reduced P contents (60 % reduction = 20 µg P/ml, Hewitt 1966). Thus far, establishment of living cultures has failed. Single spores of *Paraglomus peruvianum* sp. nov. were separated from the bait culture samples by a wet sieving process as described by Sieverding (1991). The described morphological spore characteristics and their subcellular structures are based on observations of specimens mounted in polyvinyl alcohol-lactic acid-glycerol (PVLG, Koske & Tessier 1983), Melzer's reagent, a 1:1 mixture of PVLG and Melzer's reagent (Brundrett et al. 1994), a 1:1 mixture of lactic acid to water, and tap water (Spain 1990). Terminology of spore structures follows Błaszkowski (2012) and Oehl et al. (2016) for species with glomoid spore formation. Photographs were taken with a digital camera (Leika DFC 295) on a Leitz Laborlux S compound microscope (Stuttgart, Germany), using Leica Application Suite Version version 4.1 software. Specimens mounted in PVLG and a 1:1 mixture of PVLG and Melzer's reagent were deposited at Z and ZT (Zürich, Switzerland). Staining of the mycorrhizal root structures was carried out according to Vierheilig et al. (1998).

Macroscopic description was based on fresh *Bolbitius* Fr. basidiomata, with color codes following the RAL K7 Classic color range system (https://www.ralcolor.com/). For a general description of the species, literature data were also used. The collections were examined according to standard techniques used in fungal taxonomy (Clémençon 2009, Ivoilov et al. 2017). Microscopic observations were made from dried material mounted in 5 % KOH and 10% Congo Red in NH_4OH using a Zeiss Axio Scope. A1 and Axio Imager.A1 light microscope with differential interference contrast (DIC). To observe the spore surface under a scanning electron microscope (SEM), spore material was prepared following Pegler & Young (1972). Images were captured using a JEOL JSM-6390LA Analytical Scanning Electron Microscope (Peabody, MA). Drawings of microstructures were made using InkScape from microphotographs taken with AxioCam MRc5 and AxioVision Microscopy software. Basidiospore dimensions were based on at least 30 basidiospores from each basidioma; n indicates this number. Spore dimensions are provided as (a–)b–c(–d), with b–c containing at least 90% of all values and a and d representing extreme values. Q indicates the basidiospore length/width ratio, Q_{av} represents the mean length/width quotient of the total basidiospores measured. All examined specimens are deposited in LE (sensu Thiers continuously updated).

For the *Hymenoscyphus* Gray study, the morphology of apothecia was examined in fresh and dried material. The freehand sections of fruitbodies were studied in tap water, 3 % potassium hydroxide (KOH), ammoniacal Congo Red, Lugol's (IKI = 1 % I_2, 3 % KI), and Melzer's reagent. The following symbols and abbreviations were used in the morphological description: *, living cells studied; †, dead cells studied; {}, the number of studied specimens; {T}, from type; bb, blue at low and high iodine concentration; LBs, lipid bodies; OCI, relative lipid content (oil content index, 0=no lipid, 5=maximum possible content); VBs, vacuolar bodies. The studied specimens are kept in the following fungaria: H, TAAM, UPS (sensu Thiers continuously updated), and the private collections of Ilkka Kytövuori (I.K.) and Marja Pennanen (M.P.).

DNA extraction, PCR amplification, and sequencing

Sequences of the internal transcribed spacer (ITS) region of the ribosomal RNA gene (rDNA), consisting of spacers ITS1 and ITS2 and the conserved 5.8S component, were obtained for the newly described *Cortinarius* species as part of a recent study aiming at sequencing major *Cortinarius* collections from public (CMMF and QFB) and private fungaria in the province of Quebec, Canada (Landry et al. 2021).

DNA was extracted from herbarium material of *Hortiboletus rupicapreus* sp. nov. using the NucleoSpin Plant II kit (Macherey-Nagel, Düren, Germany). The ITS region was amplified with primers ITS1f and ITS4B (Gardes & Bruns 1993), and elongation translation factor 1-α (*tef1*) with Boletaceae-specific primers EF1-B-F1 and EF1-B-R (Wu et al. 2014). PCR conditions were as follows: For ITS: initial denaturing at 95 °C for 4 min; then 35 cycles of denaturing at 94 °C for 1 min, annealing at 52 °C for 1 min, and extension at 72 °C for 1 min; and a final extension step of 72 °C for 3 min. For *tef1*: initial denaturing at 95 °C for 3 min; then 8 cycles of denaturing at 98 °C for 20 s, annealing at 60 °C for 40 s, and extension at 72 °C for 2 min; then 36 cycles of denaturing at 98 °C for 20 s, annealing at 53 °C for 90 s, and extension at 72 °C for 2 min; and a final extension step of 72 °C for 10 min. PCR products were purified with the Fermentas Genomic DNA Purification Kit (Thermo Fisher Scientific, Waltham, MA) and sequenced on an ABI 3130 Genetic Analyzer (Applied Biosystems, Foster City, CA). Raw data were edited and assembled in MEGA X (Kumar et al. 2018). Newly generated sequences were deposited in NCBI GenBank, https://www.ncbi.nlm.nih.gov/genbank/ (Tab. 1).

Intact, healthy spores of *Paraglomus peruvianum* sp. nov. were isolated from one bait culture pot initially inoculated with soil from the site in Requena, and cleaned by friction on fine filter paper (Corazon-Guivin et al. 2019). Spores were surface-sterilized (Mosse 1962) for 20 min using a solution of 2 % chloramine T, 0.02 % streptomycin, and Tween 20 (2–5 drops in 25 ml final volume), and rinsed five times in milli-Q H_2O. Fifteen spores were selected under a laminar flow hood and individually transferred into Eppendorf PCR tubes. Crude extract was obtained by crushing the 15 spores together with a sterile disposable fine-tipped pilon in 3 µl milli-Q H_2O using a stereoscope (Carl Zeiss) at 5× magnification. Direct PCR of these crude extracts was performed in an Eppendorf Mastercycler nexus (Hamburg, Germany) with the Platinum Taq DNA Polymerase High Fidelity enzyme (Invitrogen, Carlsbad, CA) following the manufacturer's instructions, with 0.4 µM of each primer. A two-step PCR was conducted to amplify the ribosomal fragment consisting of partial SSU, ITS, and partial LSU rDNA using primers SSUmAf/LSUmAr and SSUmCf/LSUmBr, consecutively, according to Krüger et al. (2009). PCR products from the second round of amplifications (~1,500 bp in length) were separated by electrophoresis on 1.2 % agarose gels stained with Diamond Nucleic Acid Dye (Promega, Madison, WI) and viewed by UV illumination. Bands of the expected size were excised with a scalpel. The amplified DNA was gel extracted with the GFX PCR DNA and Gel Band Purification Kit (Sigma-Aldrich, St. Louis, MO) following the manufacturer's instructions, cloned into the pCR2.1 TOPO TA cloning vector (Invitrogen), and transformed into One Shot TOP10 chemically competent *Escherichia coli* (Invitrogen). Nine recombinant colonies were selected by blue/white screening and the presence of inserts detected by PCR amplification with KOD DNA Polymerase (Sigma-Aldrich) using universal forward and reverse M13 vector primers. After isolation from transformed cells, plasmids were sequenced on both strands with M13F/M13R primers and the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). Sequences were read using a 3730xl DNA Analyzer (Applied Biosystems).

For the *Bolbitius* study, PCR was performed directly from small fragments of dried basidiomata without prior DNA purification using the Phire Plant Direct PCR Kit (Thermo Scientific, Pittsburg, PA) following the manufacturer's instructions. Amplification of the ITS region was done using primers ITS1f and ITS4B (White et al. 1990, Gardes & Bruns 1993). The PCR products were purified with the GeneJET Gel Extraction Kit (Thermo Scientific). Sequencing was performed using the same primers on an ABI model 3500 Genetic Analyzer (Applied Biosystems). Raw sequence data were edited and assembled using Molecular Evolutionary Genetics Analysis Version 7.0 (MEGA7) software (Kumar et al. 2016); newly generated sequences were uploaded to NCBI GenBank (Tab. 1).

For *Hymenoscyphus* collections deposited at TAAM, DNA was extracted from dried specimens using the High Pure PCR Template Preparation Kit (Roche, Basel, Switzerland). The ITS region was amplified using the primers ITSOF (5'–ACTTGGTCATTTAGAGGAAGT–3') (Tedersoo et al. 2008) and ITS4 (White et al. 1990). PCR was performed using PuRe Taq Ready-To-Go PCR beads (Amersham Pharmacia Biotech, Piscataway, NJ) following Pärtel et al. (2017). Cycling conditions included initial denaturation at 95 °C for 15 min; followed by 35 cycles of denaturation at 95 °C for 30 s, annealing at 55 °C for 30 s, and extension at 72 °C for 1 min; and a final extension step at 72 °C for 10 min. PCR products were purified using Exo-Sap enzymes (Sigma, St. Louis, MO). Sequencing was performed by Macrogen. Molecular procedures were different for the Swedish material; DNA extractions were done with the QIAamp DNA Micro Kit (Qiagen, Valencia, CA) using 1–3 apothecia as starting material, following the manufacturer's protocol. PCR amplifications were done with the following primer pairs: NS1/NS6 for SSU (White et al. 1990), ITS1f/ITS4 for ITS (White et al. 1990, Gardes & Bruns 1993), and LR0R/LR5 and LR0R/LR7 for LSU (Vilgalys & Hester 1990, Hopple 1994). Cycling conditions followed Gómez-Zapata et al. (2021). Purification and sequencing was outsourced to Genewiz (Plainfield, NJ). Forward and reverse sequence reads were assembled and edited in Sequencher version 5.2.3 (Gene Codes Corporation, Ann Arbor, MI).

Phylogenetic analyses

Newly generated *Cortinarius* sequences (Landry et al. 2021) were supplemented with sequences of closely related species as found by BLAST searches in NCBI GenBank and UNITE (Abarenkov et al. 2010) and of species belonging to closely related sections as delimited in recent infrageneric classifi-

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

Species	ID (isolate, strain[1], status[2], voucher)	Country, host	ITS	LSU	rDNA	*tef1*	Reference(s)
"Cenangium" acuum	TAAM:198449	Czech Repulic, *Pinus sylvestris*	LT158445	KX090828			Pärtel et al. (2017)
"Lanzia" berggrenii	ICMP:19614	Australia, *Nothofagus cunninghamii*	KC164645	KC164640			Johnston & Park (2013)
"Lanzia" ovispora	PDD:70881	New Zealand, *Elaeocarpus dentatus*	MH578500	MH587172			P.R. Johnston & D. Park, unpubl.
"Rutstroemia" luteovirescens	TU:104450	Estonia, *Acer platanoides*	LT158431	KX090814			Pärtel et al. (2017)
Archaeospora trappei	Att178-3	UK			FR750036		Krüger et al. (2012)
Archaeospora trappei	Att178-3	UK			FR750038		Krüger et al. (2012)
Bicornispora seditiosa	WU:32446, T	Spain, *Acer monspessulanum*	KF499360	KF499360			Galán et al. (2015)
Bolbitius aleuriatus	voucher 3029	Italy	JF907770				Osmundson et al. (2013)
Bolbitius bisporus	LE 303558	Russia	KR425534				Malysheva et al. (2015)
Bolbitius callisteus	PBM 2638	USA	EU477860				K.W. Hughes & P.B. Matheny, unpubl.
Bolbitius callistus	ALV9432		MF093747				P. Bjorck & A. Tudzarovski, unpubl.
Bolbitius callistus	LE F 331684	Russia	MW763060				This study
Bolbitius callistus	LE F 331685	Russia	MW763061				This study
Bolbitius callistus	LE 313564	Russia	MW763062				This study
Bolbitius coprophilus	LE 11317	Russia	KR425527				Malysheva et al. (2015)
Bolbitius coprophilus	LE 18905	Russia	KR425525				Malysheva et al. (2015)
Bolbitius coprophilus	LE 18599	Russia	KR425526				Malysheva et al. (2015)
Bolbitius coprophilus	LE 287244	Russia	KR425524				Malysheva et al. (2015)
Bolbitius demangei	voucher 4030	Italy	JF907771				Osmundson et al. (2013)
Bolbitius excoriatus	WU16355, T	Spain	KC456418				Örstadius & Larsson (2013)
Bolbitius excoriatus	LO23-10	Sweden	KC456419				Örstadius & Larsson (2013)
Bolbitius lacteus	LE 303559	Russia	KR425523				Malysheva et al. (2015)
Bolbitius lacteus	MSC 378485	USA	AY194520				Hallen et al. (2003)
Bolbitius muscicola	PDD: 87721	New Zealand	JQ694118				J.A. Cooper, D. Park & P.R. Johnston, unpubl.
Bolbitius pallidus	LE 234343, T	Russia	KR425533				Malysheva et al. (2015)
Bolbitius pallidus	LE 303557	Russia	KR425535				Malysheva et al. (2015)
Bolbitius psittacinus	BRNM 705079, T	Czech Republic	EF648217				Hausknecht et al. (2007)
Bolbitius reticulatus	WU30001	Hungary	JX968249				Tóth et al. (2013)
Bolbitius reticulatus	LE 227536	Russia	KR425531				Malysheva et al. (2015)
Bolbitius reticulatus	LE 253961	Russia	KR425529				Malysheva et al. (2015)
Bolbitius reticulatus	LE 303560	Russia	KR425533				Malysheva et al. (2015)
Bolbitius reticulatus var. *plutaoides*	LE 234342	Russia	KR425532				Malysheva et al. (2015)
Bolbitius subvolvatus	strain WU28379	Italy	JX968248				Tóth et al. (2013)
Bolbitius titubans	LE 303556	Russia	KR425522				Malysheva et al. (2015)
Bolbitius titubans	LE 214359	Russia	KR425521				Malysheva et al. (2015)
Bolbitius titubans	LE 289428	Russia	KR425519				Malysheva et al. (2015)
Bolbitius titubans	LE 287256	Russia	KR425518				Malysheva et al. (2015)
Bolbitius titubans	LE 265066	Russia	KR425511				Malysheva et al. (2015)
Bolbitius titubans	LE 202345	Russia	KR425512				Malysheva et al. (2015)
Bolbitius titubans	LE 303562	Russia	KR425513				Malysheva et al. (2015)
Bolbitius titubans	LE 258041	Russia	KR425514				Malysheva et al. (2015)
Bolbitius titubans	LE 235346	Russia	KR425509				Malysheva et al. (2015)
Bolbitius variicolor	MSC 378488	USA	AY194535				Hallen et al. (2003)
Bolbitius variicolor	voucher 2303	Italy	JF907768				Osmundson et al. (2013)
Bolbitius viscosus	TENN:PBM3032	USA	HQ840656				Matheny et al. (2015)
Bolbitius vitellinus	MSC 378484	USA	AY194519				Hallen et al. (2003)
Bolbitius vitellinus	WTU:MTS5020	USA	DQ200920				Matheny et al. (2007)
Botrytis cinerea	CBS:179.71	The Netherlands, *Cichorium endivia*	MH860054	MH871836			Vu et al. (2019)
Bulgariella pulla	DHP-06-607	USA	KJ704848	KJ704849			Iturriaga et al. (2017)

Tab. 1 (continued).

Species	ID (isolate, strain[1], status[2], voucher)	Country, host	ITS	LSU	rDNA	*tef1*	Reference(s)
Cenangiopsis quercicola	TAAM:178677	Denmark, *Quercus robur*	LT158425	KX090811			Pärtel et al. (2017)
Chlorencoelia torta	H.B. 8415	Taiwan, *unknown deciduous wood*	LT158424	KX090810			Pärtel et al. (2017)
Chlorencoelia versiformis	DAOM:C251598	Canada, unknown hardwood	MH457140	MH455361			McCullin et al. (2019)
Ciboria amentacea	CBS:130.31	England, *Alnus glutinosa*	MH855156	MH866604			Vu et al. (2019)
Ciborinia erythronii	CBS:300.31, T	USA, *Erythronium albidum*	NR_159764	NG_063974			Vu et al. (2019)
Ciborinia gentianae	JCM:13253, T	Japan, *Gentiana triflora* var. *japonica*	NR_153945	NG_059038			G. Okada, T. Iida & M. Ohkuma, unpubl.
Clitopilopsis hirneola	CBS:126.46	France	MH856141				Vu et al. (2019)
Clitopilus prunulus	CBS:129.42	United Kingdom	FJ770389				Hartley et al. (2009)
Connersia rilstonii	CBS:537.74	Canada, *Populus* sp.	KJ755499	AF096189			Suh & Blackwell (1999), Malloch et al. (2016)
Cordierites frondosus	HKAS41508		AY789355	AY789354			Wang et al. (2005)
Cortinarius aff. *meinhardii*	YL4384	Canada	MN750883				Landry et al. (2021)
Cortinarius aff. *meinhardii*	HRL1789	Canada	MN750884				Landry et al. (2021)
Cortinarius aff. *pallidifolius*	YL3953	Canada	MN751084				Landry et al. (2021)
Cortinarius aff. *pallidifolius*	YL3896	Canada	MN751416				Landry et al. (2021)
Cortinarius aff. *scaurotraganoides*	HRL0578	Canada	MN751514				Landry et al. (2021)
Cortinarius aff. *serratissimus*	HL1422	Canada	MN751521				Landry et al. (2021)
Cortinarius alnobetulae	G:00126512/R. Kühner:Sa-53-6 T	France	NR130188				Liimatainen et al. (2014)
Cortinarius amnicola	MICH 10315, T	USA	NR130190				Liimatainen et al. (2014)
Cortinarius amnicola	HRL1302	Canada	MN750961				Landry et al. (2021)
Cortinarius anomalo-ochrascens	PC:R. Henry 2805, T	France	MH846269				Brandrud et al. (2018)
Cortinarius aptecohaerens	YL2018	Canada	MT607418				Landry et al. (2021)
Cortinarius aptecohaerens	PC:R. Henry 71359, T	France	MT934880				Liimatainen et al. (2020)
Cortinarius arenicola	MICH 10317, T	USA	NR130191				Liimatainen et al. (2014)
Cortinarius aureofulvus	IB19870221		GU363496				Garnica et al. (2011)
Cortinarius aureofulvus	HRL2486	Canada	MN751002				Landry et al. (2021)
Cortinarius bivelosimilis	H:T. Niskanen 10-014, T	Canada	MF379636				Liimatainen et al. (2017)
Cortinarius bivelosimilis	HRL1795	Canada	MN751025				Landry et al. (2021)
Cortinarius bivelus	MQ17108	Canada	MN751027				Landry et al. (2021)
Cortinarius bivelus	S:F44841, T	Sweden	KP866159				Liimatainen et al. (2020)
Cortinarius boulderensis	MICH 10323, T	USA	NR121207				Niskanen et al. (2006)
Cortinarius boulderensis	MQ17128	Canada	MN751033				Landry et al. (2021)
Cortinarius bulbopodius	PC:R. Henry 70671, T	France	KY315438				Frøslev et al. (2017)
Cortinarius calojanthinus	IB 19970220	USA	NR130200				Liimatainen et al. (2014)
Cortinarius calojanthinus	HRL2840	Canada	MN751049				Landry et al. (2021)
Cortinarius caryae	YL2054	Canada	MN750898				Landry et al. (2021)
Cortinarius caryae	YL0816	Canada	MN750895				Landry et al. (2021)
Cortinarius caryae	YL3385	Canada	MN750897				Landry et al. (2021)
Cortinarius caryae	HRL1300	Canada	MN750894				Landry et al. (2021)
Cortinarius caryae	HRL0878	Canada	MN750893				Landry et al. (2021)
Cortinarius caryae	HRL3013, T	Canada	MT607407				Landry et al. (2021)
Cortinarius caryae	YL4401	Canada	MN750896				Landry et al. (2021)
Cortinarius caryae [as *C. aurilicis*]	HRL1297	Canada	KJ705135				J.A. Bérubé et al., unpubl.
Cortinarius caryae [as *C. aurilicis*]	MycoMap # 1281	USA	MK575227				S.D. Russell, unpubl.
Cortinarius castaneicolor	MICH 10331, T	USA	NR130203				Liimatainen et al. (2014)
Cortinarius chrysolitus	MICH 10332, T	USA	NR120302				Niskanen et al. (2013)
Cortinarius cisqhale	UC 1860822, T	USA	NR157867				Bojantchev (2013)

Tab. 1 (continued).

Species	ID (isolate, strain[1], status[2], voucher)	Country, host	ITS	LSU	rDNA	*tef1*	Reference(s)
Cortinarius cisqhale	H:T. Niskanen 12-065	USA	MT934971				Liimatainen et al. (2020)
Cortinarius citrinifolius	MICH 10334, T	USA	NR130206				Liimatainen et al. (2014)
Cortinarius coelopus	HO 990504A3		AY669640				Garnica et al. (2005)
Cortinarius croceus	H 6031266, T	Finland	NR131863				Niskanen (2014)
Cortinarius cupreorufus	S:F47383, T	Sweden	NR130213				Liimatainen et al. (2014)
Cortinarius delaportei	PC:R. Henry 8673, T	France	NR130215				Liimatainen et al. (2014)
Cortinarius delaportei	TUB 011853	Germany	AY669534				Garnica et al. (2005)
Cortinarius elotoides	IB 19870060, T	USA	NR137120				Liimatainen et al. (2014)
Cortinarius elotoides	HRL2478	Canada	MN751194				Landry et al. (2021)
Cortinarius flavolilacinus	HRL3320, T	Canada	MW845277				Landry et al. (2021)
Cortinarius fulgens	CBH56- TENN: 073113	USA	MH615054				P.B. Matheny & R.A. Swenie, unpubl.
Cortinarius fuligineofolius	IB 19910682, T	USA	NR130219				Liimatainen et al. (2014)
Cortinarius fulvo-ochrascens	PC:R. Henry 314, T	France	MH846266				Brandrud et al. (2018)
Cortinarius glaucocephalus	IB 19950679, T	USA	NR130221				Liimatainen et al. (2014)
Cortinarius glaucocyanopus	GK5034, T	France	MH846274				Brandrud et al. (2018)
Cortinarius herpeticus	S F44759 T-CFP936	Sweden	NR130224				Liimatainen et al. (2014)
Cortinarius herpeticus f. *altaicus*	MQ18R351	Canada	MN751285				Landry et al. (2021)
Cortinarius herpeticus f. *altaicus*	IB20010094, T		AF478584				Moser & Peintner (2002)
Cortinarius herpeticus f. *altaicus*	YL3817	Canada	MN751282				Landry et al. (2021)
Cortinarius koldingensis	C:F-100309, T	Denmark	KT222911				Frøslev et al. (2015)
Cortinarius lilaceolamellatus	HRL0945	Canada	MN751540				Landry et al. (2021)
Cortinarius lilaceolamellatus	YL3513	Canada	MN751542				Landry et al. (2021)
Cortinarius lilaceolamellatus	HRL2206, T	Canada	MN751543				Landry et al. (2021)
Cortinarius lilaceolamellatus	YL4042	Canada	MN751541				Landry et al. (2021)
Cortinarius luteicolor	MICH 10389, T	USA	NR153016				Liimatainen et al. (2014)
Cortinarius luteobrunnescens	MICH 10371, T	USA	NR130227				Liimatainen et al. (2014)
Cortinarius majoranae	KS CO1392		KJ421071				Garnica et al. (2016)
Cortinarius malachioides	H:7000977, T	Canada	MH846281				Brandrud et al. (2018)
Cortinarius malodorus	YL1730	Canada	MN751643				Landry et al. (2021)
Cortinarius malodorus	HRL1489, T	Canada	MN751642				Landry et al. (2021)
Cortinarius malodorus	YL2480	Canada	MN751641				Landry et al. (2021)
Cortinarius meinhardii	TUB 011443		AY174840				Garnica et al. (2003)
Cortinarius metarius	MICH 10374, T	USA	NR130229				Liimatainen et al. (2014)
Cortinarius mikedavisii	UC 1860820, T	USA	NR120313				Schoch et al. (2014)
Cortinarius montanus	MICH 10377, T	USA	NR130231				Liimatainen et al. (2014)
Cortinarius mussivus	O-F-260372	Norway	UDB036360*				K. Abarenkov, unpubl.
Cortinarius nanceiensis	O:TEB278-10	Norway	KY315435				Frøslev et al. (2017)
Cortinarius ochraceobrunneus	G 00126800, T	France	NR130235				Liimatainen et al. (2014)
Cortinarius odorifer	TUB 011383		AY174817				Garnica et al. (2003)
Cortinarius odorifer var. *luteolus*	CFP1105		DQ663336				Frøslev et al. (2007)
Cortinarius olearioides	AB00-10-191		DQ663364				Frøslev et al. (2007)
Cortinarius olearioides	CFP862	France	DQ663365				Frøslev et al. (2007)
Cortinarius olivaceolamellatus	HRL2819, T	Canada	MN751569				Landry et al. (2021)
Cortinarius olivaceolamellatus	HRL2820	Canada	MN751568				Landry et al. (2021)
Cortinarius oliveopetasatus	IB 1995360, T	USA	NR130237				Liimatainen et al. (2014)
Cortinarius olympianus	MICH 10386, T	USA	NR130238				Liimatainen et al. (2014)
Cortinarius orichalceus var. *olympianus*	MICH 10390, T	USA	NR153015				Liimatainen et al. (2014)
Cortinarius pallidifolius	MICH 10392, T	USA	NR130240				Liimatainen et al. (2014)
Cortinarius parasuaveolens (= *C. pseudogracilior*)	PC:P. Moënne-Loccoz 4858, T	France	NR130248				Liimatainen et al. (2014)

Tab. 1 (continued).

Species	ID (isolate, strain[1], status[2], voucher)	Country, host	ITS	LSU	rDNA	*tef1*	Reference(s)
Cortinarius percomis	H K. Liimatainen & T. Niskanen 08-041, T	Finland	NR130242				Liimatainen et al. (2014)
Cortinarius pseudobovinus	IB 19890300, T	USA	NR131791				Niskanen et al. (2006)
Cortinarius pseudocephalixus	G:293291/1, T	France	KF732392				Liimatainen et al. (2014)
Cortinarius pseudocephalixus [as *C. cephalixus*]	TUB 011444	Germany	AY174784				Garnica et al. (2003)
Cortinarius quercophilus	HRL0494	Canada	MN751644				Landry et al. (2021)
Cortinarius quercophilus	YL1672, T	Canada	MN751645				Landry et al. (2021)
Cortinarius quercophilus	clone man7_soil_C11	USA, soil	GU328626				I.P. Edwards & D.R. Zak, unpubl.
Cortinarius quercophilus [as *Cortinarius* sp.]	BHS2009-56	USA	GU289650				D.S. Hibbett, B.H. Seitzman & M.L. Sandoval, unpubl.
Cortinarius quercophilus [as *Cortinarius* sp.]	APBP088	USA	MK982182				A.T. Hudon & T.R. Horton, unpubl.
Cortinarius riederi	H:I. Kytövuori 98-1171, T	Finland	MH846263				Brandrud et al. (2018)
Cortinarius sanguineus	SL22091940 (UPS), T	Sweden	JN114099				Niskanen et al. (2012)
Cortinarius scaurotraganoides	PC:R. Henry 70538, T	France	MT935417				Liimatainen et al. (2020)
Cortinarius scaurus	YL3532	Canada	MN751518				Landry et al. (2021)
Cortinarius scaurus	S F44777, T	Switzerland	NR130262				Liimatainen et al. (2014)
Cortinarius scaurus	YL1265	Canada	MN751519				Landry et al. (2021)
Cortinarius scaurus var. *sphagnophilus*	TUF109660	Estonia	UDB031145*				I. Saar, unpubl.
Cortinarius sejunctifolius	H:T. Niskanen 04-880	Finland	MT935425				Liimatainen et al. (2020)
Cortinarius serarius	S:F44754, T	Sweden	NR130263				Liimatainen et al. (2014)
Cortinarius serratissimus	IB:M. Moser 1960-0004, T	Switzerland	MT935433				Liimatainen et al. (2020)
Cortinarius sp.	NVE 485	Colombia	KF937324				Vasco-Palacios et al. (2014)
Cortinarius sp. *IUMQ3586*	HRL0355	Canada	MN751539				Landry et al. (2021)
Cortinarius sp. *IUMQ3775*	YL2052	Canada	MN751607				Landry et al. (2021)
Cortinarius sp. *IUMQ416*	YL3292	Canada	MN751635				Landry et al. (2021)
Cortinarius sp. *IUMQ436*	CMMF003506	Canada	MT607412				Landry et al. (2021)
Cortinarius sphagnophilus	MQ17017	Canada	MN751532				Landry et al. (2021)
Cortinarius sphagnophilus	HL0840	Canada	MN751533				Landry et al. (2021)
Cortinarius sphagnophilus sensu Garnica et al. 2016	F16399	Canada	FJ039620				Harrower et al. (2011)
Cortinarius sphagnophilus sensu Garnica et al. 2016	JFA13111	USA	FJ717592				Harrower et al. (2011)
Cortinarius sphagnophilus-2 sensu Garnica et al. 2016	UBC F17134 OC62		GQ159877				Harrower et al. (2011)
Cortinarius subpurpureophyllus	MICH 10421, T	USA	KF732450				Liimatainen et al. (2014)
Cortinarius subrimosus	MICH 10424, T	USA	MT935525				Liimatainen et al. (2020)
Cortinarius subrimosus	YL4221	Canada	MN751511				Landry et al. (2021)
Cortinarius subserratissimus	H I. Kytövuori 11-017, T	Sweden	NR131881				Liimatainen et al. (2020)
Cortinarius subsolitarius	YL1758	Canada	MN751671				Landry et al. (2021)
Cortinarius subsolitarius	MICH 10426, T	USA	NR130272				Liimatainen et al. (2014)
Cortinarius subsolitarius	HRL0898	Canada	MN751670				Landry et al. (2021)
Cortinarius subsolitarius	YL1825	Canada	MN751669				Landry et al. (2021)
Cortinarius subsulfurinus	H:T. Niskanen 11-093, T	USA	NR153051				Dima (2015)
Cortinarius superbus	MICH 10430, T	USA	NR130274				Liimatainen et al. (2014)
Cortinarius traganus	CFP763, T	Sweden	MT935361				Liimatainen et al. (2020)
Cortinarius traganus	ANT146	Canada	MN992365				Landry et al. (2021)
Cortinarius triangulus	PC:R. Henry 80869, T	France	NR171373				Liimatainen et al. (2014)

Tab. 1 (continued).

Species	**ID (isolate, strain[1], status[2], voucher)**	**Country, host**	**ITS**	**LSU**	**rDNA**	***tef1***	**Reference(s)**
Cortinarius venustissimus	PC:5371, T	Sweden	MT935580				Liimatainen et al. (2020)
Cortinarius violaceoflavescens	HRL1825	Canada	MN751571				Landry et al. (2021)
Cortinarius violaceoflavescens	HRL1826, T	Canada	MN751572				Landry et al. (2021)
Cortinarius violaceoflavescens	YL4402	Canada	MN751573				Landry et al. (2021)
Cortinarius violaceonitens	TUB 019776		KJ421028				Garnica et al. (2016)
Cortinarius violaceonitens	YL3531	Canada	MN751769				Landry et al. (2021)
Cortinarius violaceonitens	PC:R. Henry 2190, T	France	KF732425				Liimatainen et al. (2014)
Cortinarius virentophyllus	MICH 10439, T	USA	NR130284				Liimatainen et al. (2014)
Cortinarius viridicarneus	HRL1325, T	Canada	KJ705136				J.A. Bérubé et al., unpubl.
Cortinarius viridicarneus	HRL0315	Canada	MN750891				Landry et al. (2021)
Cortinarius viridirubescens	IB 19950688, T	USA	NR130285				Liimatainen et al. (2014)
Cortinarius xanthochlorus	S:F44373		EU057047				Garnica et al. (2009)
Cortinarius xanthosuavis	TUB 019746		KJ420986				Garnica et al. (2016)
Dicephalospora huangshanica	KUS-F52405	South Korea, *Castanopsis cuspidata*	JN033408	JN086711			Han et al. (2014)
Diplolaeviopsis ranula	NBM:FL-14388	Canada, *Lecanora strobilina*	KP984782	KP984785			Etayo et al. (2015)
Encoelia furfuracea	TAAM:137509	Estonia, *Corylus avellana*	LT158482	KX090796			Pärtel et al. (2017)
Entoloma azureosquamulosum	HKAS53408	China	JQ410334				He et al. (2012)
Entoloma caeruleopolitum	K(M)128161	United Kingdom	MF977965				J.J. Elsey, unpubl.
Entoloma callipygmaeum	LE 253784, T	Russia	MZ145207				Dima et al. (2021)
Entoloma kauffmanii	KA13-1202	South Korea	KR673675				Kim et al. (2015)
Entoloma meridionale	ACAM 2018-0151	Greece	OL679697				This study
Entoloma meridionale	L0607587	Spain	OL679701				This study
Entoloma meridionale	CNF1-2117	Croatia	OL679702				This study
Entoloma meridionale	ACAM 2018-0153, T	Greece	OL679700				This study
Entoloma meridionale	ACAM 2018-0152	Greece	OL679699				This study
Entoloma meridionale	ACAM 2014-0127	Greece	OL679698				This study
Entoloma minutigranulosum	LE 302096, T	Russia	MZ145214				Dima et al. (2021)
Entoloma mougeotii	LE254352	Russia	KC898446				Morozova et al. (2014)
Entoloma poliopus	G4742	Estonia	UDB0332859*				R. Pau, unpubl.
Entoloma pudens	L 0608054	The Netherlands	MW934594				Crous et al. (2021)
Entoloma septentrionale	O-F-254295, T	Norway	MW340904				Noordeloos et al. (2021)
Entoloma sp.	TUF120259	Estonia	UDB024650*				I. Saar, unpubl.
Entoloma sp.	soil sample	USA	KP889939				S.H.A. Guichon & S.W. Simard, unpubl.
Entoloma sp.	MEL2382758	Australia	KP012941				G. Bonito, M. Barrett, F. Udovicic & T. Lebel, unpubl.
Entoloma subcorvinum	TENN070435	USA	KY744169				P.B. Matheny, S.A. Trudell & M.G. Wood, unpubl.
Galeropsis desertorum	PR 154181	Czech Republic	AY194534				Hallen et al. (2003)
Grovesinia moricola	KUS-F26901	Korea, *Humulus japonicus*	KC460209	KX098504			Cho et al. (2013)
Grovesinia pyramidalis	CBS:737.68	The Netherlands, *Acer pseudoplatanus*		MH878399			Vu et al. (2019)
Grovesinia pyramidalis	1836.K	USA, *Juglans nigra*	Z81433	AJ226081			Holst-Jensen et al. (1998, 1999)
Gyroporus castaneus	JMP0028	USA	EU819468				Palmer et al. (2008)
Gyroporus cyanescens	NAMA190	USA	EU819495				Palmer et al. (2008)
Heyderia abietis	HMAS:71954		AY789297	AY789296			Wang et al. (2005)
Hortiboletus amygdalinus	NIBR-FG0000502792	South Korea	MW578955				Kim et al. (2021)
Hortiboletus bubalinus [as *Hortiboletus* sp.]	KR-M-0044351	Germany	MT005978				M. Scholler, unpubl.
Hortiboletus indorubellus	CAL: DC 14-002, T	India	NR_154076				Das et al. (2016)
Hortiboletus kohistanensis	LAH35327, T	Pakistan	MG988192				Naseer et al. (2019)
Hortiboletus napaeus	FHMU3325	China	MT646445				Xie et al. (2020)
Hortiboletus rubellus	JV00-357	Denmark	UDB001406*				L. Tedersoo, unpubl.

Tab. 1 (continued).

Species	**ID (isolate, strain[1], status[2], voucher)**	**Country, host**	**ITS**	**LSU**	**rDNA**	***tef1***	**Reference(s)**
Hortiboletus rubellus	FLAS-F-61506	USA	MH211937				B.S. Kaminsky, M.E. Smith, R. Healy & B. Spakes Richter, unpubl.
Hortiboletus rubellus [as *Hortiboletus* sp.]	KR-M-0044799	Germany	MT006029				M. Scholler, unpubl.
Hortiboletus rupicapreus	LE 312677, T	Vietnam	MW784161	MW760391		MZ424894	This study
Hortiboletus rupicapreus	LE 312678	Vietnam	MW784162	MW760392		MZ424893	This study
Hymenoscyphus aff. *scutula*	CBS:101:66	The Netherlands, *Solidago canadensis*	MH858736	MH870369			Vu et al. (2019)
Hymenoscyphus albidoides	HMAS:264140, T	China, *Picrasma quassioides*	KF188722	NG_059508			Zheng & Zhuang (2014)
Hymenoscyphus as "cf. *menthae*"	HMAS:75934	China, dead wood	AY348588				Zhang & Zhuang (2004)
Hymenoscyphus as *"menthae"*	NBRC:109865	Japan, *Hydrangea* sp.	AB926063	AB926132			Zhao et al. (2016)
Hymenoscyphus aurantiacus	HMAS:264144	China	KJ472288	KJ472229			Zheng & Zhuang (2015)
Hymenoscyphus aurantiacus	HMAS:264143, T	China, unidentified deciduous tree	KJ472289	KJ472228			Zheng & Zhuang (2015)
Hymenoscyphus berggrenii	ICMP:19614	Australia, *Nothofagus cunninghamii*	KC164645	KC164640			Johnston & Park (2013)
Hymenoscyphus calyculus	HMAS:264146	China	KJ472291	KJ472233			Zheng & Zhuang (2015)
Hymenoscyphus caudatus	EST2588	China, *Fraxinus* sp.	KU569309				Drenkham et al. (2017)
Hymenoscyphus caudatus	HMAS:82060	China	AY348577	KJ472235			Zhang & Zhuang (2004); Zheng & Zhuang (2015)
Hymenoscyphus caudatus	HMAS:82057	China	AY348576	KJ472234			Zhang & Zhuang (2004); Zheng & Zhuang (2015)
Hymenoscyphus caudatus	HMAS:264150	China	KF188730				Zheng & Zhuang (2014)
Hymenoscyphus caudatus	HMAS:82063	China	AY348578				Zhang & Zhuang (2004)
Hymenoscyphus caudatus	HMAS:82073	China	AY348579				Zhang & Zhuang (2004)
Hymenoscyphus caudatus	NBRC:109867	Japan, *Alnus* sp.	AB926065	AB926134			Zhao et al. (2016)
Hymenoscyphus caudatus	CBS:137.92	Germany, *Alnus* sp.	KC481687				Hamelin et al. (2013)
Hymenoscyphus caudatus	H.B. 7588c	Germany, *Fagus sylvatica*	KM114539				Gross et al. (2015)
Hymenoscyphus equiseti	D. Haelew. F-1493b	Sweden, *Equisetum fluviatile*	OL679971	OL679906			This study
Hymenoscyphus equiseti	D. Haelew. F-1493c	Sweden, Equisetum fluviatile	OL679972	OL679907			This study
Hymenoscyphus equiseti	D. Haelew. F-1493d	Sweden, *Equisetum fluviatile*	OL679973	OL679908			This study
Hymenoscyphus equiseti	TAAM:194261, T	Russia, *Equisetum fluviatile*	UDB038358*				This study
Hymenoscyphus equiseti	TAAM:198531	Finland, *Equisetum fluviatile*	UDB0778487*				This study
Hymenoscyphus fraxineus [as *H. pseudoalbidus*]	ZT:Myc 2022, T	Switzerland, *Fraxinus excelsior*	GU586904				Queloz et al. (2011)
Hymenoscyphus fructigenus	TNS:F-44644	Japan, *Quercus* sp.	AB926057	AB926144			T. Hosoya et al., unpubl.
Hymenoscyphus haasticus	ICMP:19598, T	New Zealand, *Nothofagus menziesii*	NR_137108				Johnston & Park (2013)
Hymenoscyphus haasticus	ICMP:19603	New Zealand, *Nothofagus menziesii*	KC164644	KC164639			Johnston & Park (2013)
Hymenoscyphus koreanus	KUS F52847_01, T	South Korea, *Fraxinus chinensis* subsp. *rhynchophylla*	NR_152904				Gross & Han (2015)
Hymenoscyphus linearis	Chic01	Japan, *Fraxinus platypoda*	KM114521				Gross et al. (2015)
Hymenoscyphus macrodiscus	HMAS:264158, T	China, unidentified deciduous tree	KJ472296				Zheng & Zhuang (2015)
Hymenoscyphus macroguttatus	H.B. 7034	Spain, *Crataegus monogyna*	DQ431179				Baral et al. (2007)
Hymenoscyphus menthae	H.B. 5846	Liechtenstein, *Solidago canadensis*	KM114537				Gross et al. (2015)

Tab. 1 (continued).

Species	ID (isolate, strain[1], status[2], voucher)	Country, host	ITS	LSU	rDNA	*tef1*	Reference(s)
Hymenoscyphus occultus	CBS:139469, T	South Korea, *Fraxinus chinensis* subsp. *rhynchophylla*	NR_147434				Gross & Han (2015)
Hymenoscyphus ohakune	ICMP:19601, T	New Zealand, *Fuscospora cliffortioides*	NR_137109	NG_066420			Johnston & Park (2013); P.R. Johnston & D. Park, unpubl.
Hymenoscyphus phalaridis [as *Hymenoscyphus* sp.]	H.B. 8393	Germany, *?Phalaris arundinacea*	KM114544				Gross et al. (2015)
Hymenoscyphus pusillus	HMC 21525, T	Poland, *Fraxinus pennsylvanica*	MH476516				Kowalski & Bilański (2019)
Hymenoscyphus qinghaiensis	HMAS:264175, T	China, *Populus* sp.	KJ472297				Zheng & Zhuang (2015)
Hymenoscyphus repandus	H.B. 9057	Germany, *Fallopia sachalinensis*	KT876975	KT876975			H.-O. Baral & G. Marson, unpubl.
Hymenoscyphus reynoutriae	G.M. 2015-10-06.1	Luxembourg, *Fallopia sachalinensis*	MH221038	MH221038			Baral (2019)
Hymenoscyphus scutula	G.M. 2014-12-25.2	Luxembourg, unknown herbaceous plant	MK674606	MK674606			G. Marson, unpubl.
Hymenoscyphus scutula	CBS:480.97	USA, unknown herbaceous plant	KC481695				Hamelin et al. (2013)
Hymenoscyphus sp.	PDD:105205	New Zealand, *Phormium tenax*	MH921852				P.R. Johnston & D. Park, unpubl.
Hymenoscyphus subferrugineus [as *H. calyculus*]	F267859	Spain, Genista *hispanica* subsp. *occidentalis*	KF588380				Johnston et al. (2014)
Hymenoscyphus subferrugineus [as *H. sinicus*]	HMAS:264193	China	KJ472299	KJ472253			Zheng & Zhuang (2015)
Hymenoscyphus tetrasporus	HMAS:266592, T	China, unidentified monocot	KJ472302				Zheng & Zhuang (2015)
Hymenoscyphus virgultorum	TU:104736	Germany, *Betula* sp.	UDB034372*				H. Tamm, unpubl.
Hymenoscyphus waikaia	ICMP:19599	New Zealand, *Nothofagus menziesii*	KC164646	KC164641			Johnston & Park (2013)
Hymenoscyphus waikaia	PDD:102886, T	New Zealand, *Nothofagus menziesii*	KC164667				Johnston & Park (2013)
Hymenoscyphus yui	HMAS:266595, T	China, unidentified deciduous tree	KJ472303	KJ472258			Zheng & Zhuang (2015)
Hymenotorrendiella eucalypti	CPC 11050	Indonesia, *Eucalyptus* sp.	DQ195788	DQ195800			Crous et al. (2006)
Hymenotorrendiella madsenii	PRJ D672	New Zealand, *Nothofagus* sp.	AY755336	KJ606676			Johnston & Park (2005); Johnston et al. (2014)
Innospora majewskii	isolate 1	unknown, soil			KY630229		Błaszkowski et al. (2017)
Innospora majewskii	isolate 7	unknown, soil			KY630232		Błaszkowski et al. (2017)
Innospora majewskii	isolate 9	unknown, soil			KY630234		Błaszkowski et al. (2017)
Ionomidotis fulvotingens	G.M. 2013-06-19	Luxembourg, *Cornus sanguinea*	KY462807	KY462807			H.-O. Baral & G. Marson, unpubl.
Lambertella corni-maris	CLX4075	USA, *Malus domestica*	KC958562	KC964858			Wiseman et al. (2015)
Lambertella subrenispora	CBS 811.85, T	Japan, *Aster ageratoides* var. *ovata*	MH861915	MH873604			Vu et al. (2019)
Lanzia allantospora	CBS:124334	New Zealand, *Agathus australis*	AB926154				T. Hosoya et al., unpubl.
Lanzia echinophila	F132998	Spain, *Quercus ilex*	KF588371				Johnston et al. (2014)
Lanzia sp.	TNS:F-40081	Japan, *Fagus crenata*	AB926068	AB926138			T. Hosoya et al., unpubl.
Lanzia sp.	TNS:F-40096	Japan, *Castanea crenata*	AB926072	AB926141			T. Hosoya et al., unpubl.
Lanzia sp.	TNS:F-40038	Japan	AB926060	AB926129			T. Hosoya et al., unpubl.
Lanzia sp.	TNS:F-40120	Japan	AB926084	AB926165			T. Hosoya et al., unpubl.
Llimoniella gregorellae	CBFS:JV9954	Czech Repulic, *Gregorella humida*	KJ559531	KJ559553			Suija et al. (2015)
Macroskyttea parmotrematis	UGDA:Kukwa 11316, T	Bolivia, *Parmotrema aberrans*	KP984784	KP984788			Etayo et al. (2015)
Moellerodiscus iodotingens	F119677	Spain, *?Prunus lusitanica*	KJ941080	KJ941054			Galán et al. (2015)
Moellerodiscus lentus	H.B. 7050	France, *Malus domestica*	KJ941083	KJ941056			Galán et al. (2015)
Monilinia fructicola	CBS:127259	Australia, *Prunus persica* var. *persica*	MH864497	MH875934			Vu et al. (2019)

Tab. 1 (continued).

Species	ID (isolate, strain[1], status[2], voucher)	Country, host	ITS	LSU	rDNA	*tef1*	Reference(s)
Monilinia laxa	CBS:489.50	The Netherlands, *Prunus domestica*	MH856718	MH868237			Vu et al. (2019)
Paraglomus bolivianum		Bolivia, soil			JX122775		Mello et al. (2013)
Paraglomus bolivianum		Bolivia, soil			JX122776		Mello et al. (2013)
Paraglomus bolivianum		Bolivia, soil			JX122777		Mello et al. (2013)
Paraglomus brasilianum	Att260-8	Brazil, soil			FR750052		Krüger et al. (2012)
Paraglomus brasilianum	Att260-8	Brazil, soil			FR750053		Krüger et al. (2012)
Paraglomus brasilianum	Att260-8	Brazil, soil			FR750054		Krüger et al. (2012)
Paraglomus laccatum	Att960-3	UK, soil			FR750083		Krüger et al. (2012)
Paraglomus laccatum	isolate 25	unknown, soil			KY630227		Błaszkowski et al. (2017)
Paraglomus laccatum	isolate 26	unknown, soil			KY630228		Błaszkowski et al. (2017)
Paraglomus occidentale		Peru, soil			MN081578		Corazon-Guivin et al. (2020)
Paraglomus occidentale		Peru, soil			MN081579		Corazon-Guivin et al. (2020)
Paraglomus occidentale		Peru, soil			MN081580		Corazon-Guivin et al. (2020)
Paraglomus occultum	CL700A clone 866b	Colombia, soil			KT250828		Bills (2015)
Paraglomus occultum	FL703 clone 875a	USA, soil			KT250829		Bills (2015)
Paraglomus occultum	FL703 clone 876a	USA, soil			KT250835		Bills (2015)
Paraglomus pernambucanum	isolate G19	Brazil, soil			JX122770		Mello et al. (2013)
Paraglomus pernambucanum	isolate G20	Brazil, soil			JX122771		Mello et al. (2013)
Paraglomus pernambucanum	isolate G21	Brazil, soil			JX122772		Mello et al. (2013)
Paraglomus peruvianum	clone 1, T	Peru, soil			MW794283		This study
Paraglomus peruvianum	clone 2, T	Peru, soil			MW794284		This study
Paraglomus peruvianum	clone 3, T	Peru, soil			MW794285		This study
Paraglomus peruvianum	clone 4, T	Peru, soil			MW794286		This study
Paraglomus peruvianum	clone 5, T	Peru, soil			MW794287		This study
Paraglomus peruvianum	clone 6, T	Peru, soil			MW794288		This study
Paraglomus peruvianum	clone 7, T	Peru, soil			MW794289		This study
Paraglomus peruvianum	clone 8, T	Peru, soil			MW794290		This study
Paraglomus peruvianum	clone 9, T	Peru, soil			MW794291		This study
Pervetustus simplex	isolate a3	unknown, soil			KY630249		Błaszkowski et al. (2017)
Pervetustus simplex	isolate B4	unknown, soil			KY630250		Błaszkowski et al. (2017)
Pervetustus simplex	isolate 91	unknown, soil			KY630251		Błaszkowski et al. (2017)
Phaeohelotium aff. *epiphyllum* [as *Hymenoscyphus imberbis*]	TU:104386	Estonia, *Pinus sylvestris*		KX090813			Pärtel et al. (2017)
Phaeohelotium cf. *imberbe*	D. Haelew. F-262	Germany, *Alnus* sp.	OL679974	OL679909			This study
Phaeohelotium monticola (type species)	H.B. 8612	Germany, *Fagus sylvatica*	KC411991				Baral et al. (2013)
Piceomphale bulgarioides	TAAM:198322	Estonia, *Picea abies*	LT158469	KX090836			Pärtel et al. (2017)
Pseudolanzia piceetorum	H.B. 10139	Germany, *Picea abies*	MK679683	MK679683			This study
Pycnopeziza sejournei	C:JHP 11.054	France, *Hedera helix*	LT158443	KX090827			Pärtel et al. (2017)
Pycnopeziza sympodialis	CBS:332.39	USA, *Alnus rugosa*	MH856037	MH867534			Vu et al. (2019)
Rutstroemia firma	TU:104481	Estonia, *Alnus incana*	LT158450	KX090832			Pärtel et al. (2017)
Sarcotrochila longispora	CBS:273.74, T	Canada, *Pinus contorta*	NR_138393	NG_066161			Crous et al. (2014)
Sclerencoelia fraxinicola	H.B. 9358, T	Germany, *Fraxinus excelsior*	KT876983	KT876983			Pärtel et al. (2017)
Sclerotinia sclerotiorum	KR1121_1	Switzerland, air	KC311494	KC311494			Gorfer et al. 2014
Seaverinia geranii	CBS:168.24	USA, *Pelargonium* sp.	MH854790	MH866294			Vu et al. (2019)
Stamnaria austriaca	D. Haelew. F-940b	Austria, *Equisetum variegatum*	KT972708	KT972709			Baral & Haelewaters (2015)
Stamnaria yugrana	D. Haelew. F-603a, T	Russa, *Equisetum sylvaticum*	NR_169670	OL679910			Haelewaters et al. (2018), this study
Torrendiella ciliata	F132996	Spain, *Quercus ilex*	KC412008	KJ627220			Johnston et al. (2014)
Uncultured fungus clone 1_58		Finland, *Picea abies*	KF274115				Terhonen et al. (2013)
Uncultured fungus clone WJ95			KU931364				Mao et al. (2018)
Uncultured Helotiales clone 10JWuC10	MOTU151	Germany, *Zea mays*	HG937022				Moll et al. (2016)
Uncultured Helotiales clone 10JWuC54	MOTU151	Germany, *Zea mays*	HG937023				Moll et al. (2016)
Unguiculariopsis lettaui	TU64867	Estonia, *Evernia prunastri*	KJ559543	KJ559566			Suija et al. (2015)

Tab. 1 (continued).

Species	ID (isolate, strain[1], status[2], voucher)	Country, host	ITS	LSU	rDNA	*tef1*	Reference(s)
Xerocomellus chrysenteron	MTB26	Germany	MN947363				A.M. Khokon & A. Polle, unpubl.
Xerocomellus chrysenteron	AH38968	Spain	KU355473				Crous et al. (2016)
Xerocomellus poederi	AH45803, T	Spain	NR_155971				Crous et al. (2016)
Xerocomellus sarnarii	MCVE 28577, T	Italy	NR_138006				Ariyawansa et al. (2015)
Xerocomus ferrugineus	SAT-16-237-02	USA	MT955157				S. Trudell & M. Gordon, unpubl.
Xerocomus subparvus	LE 315595	Vietnam	MT893600				Pham & Morozova (2020)
Xerocomus subtomentosus	ANT013-QFB28575	Canada	MN992545				J. Landry & J. Berube, unpubl.

[1] Herbarium abbreviations follow Index Herbariorum (Thiers continuously updated).
[2] T: ex-type strain. * from UNITE database (https://unite.ut.ee).

cation studies (Liimatainen et al. 2014, 2020; Soop et al. 2019). Sequences from species belonging to section *Dermocybe* were selected as outgroup. Sequences were aligned using MUSCLE version 3.7 (Edgar 2004) and corrected manually as needed. Phylogenetic trees were constructed with the help of MEGA7 (Kumar et al. 2016) with default settings. Maximum likelihood was inferred based on the Tamura-Nei model (Tamura & Nei 1993). ML bootstrap (MLBS) analysis was performed with 100 replicates. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Joining and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value.

Previously generated ITS sequences of *Hortiboletus* were downloaded from NCBI GenBank and supplemented with the newly generated ones from our Vietnamese material. Sequences were aligned with MAFFT version 7 (https://mafft.cbrc.jp/alignment/server/) using the Q-INS-i option (Katoh et al. 2019). Phylogenetic reconstructions were performed with Bayesian inference (BI) using MrBayes version 3.2.1 (Ronquist et al. 2012) with the following parameters: GTR+I evolutionary model of nucleotide substitution, two independent runs, each with 3,000,000 generations, and four chains with sampling frequency of 100. To check for convergence of Markov chain Monte Carlo (MCMC) analyses and to get estimates of the posterior distribution of parameter values, Tracer version 1.7.1 was used (Rambaut et al. 2018). The final tree was edited in Adobe Illustrator CS4 (San Jose, CA).

Newly generated SSU–ITS–LSU rDNA sequences of *Paraglomus peruvianum* sp. nov. were supplemented with other related glomeromycotan sequences downloaded from NCBI GenBank. Sequences were aligned in ClustalX (Larkin et al. 2007). *Archaeospora trappei* (R.N. Ames & Linderman) J.B. Morton & D. Redecker was included as outgroup. Prior to phylogenetic analysis, the model of nucleotide substitution was estimated using Topali 2.5 (Milne et al. 2004), resulting in GTR+G. Bayesian inference was performed in MrBayes version 3.1.2 (Ronquist & Huelsenbeck 2003), with two runs over 2×10^6 generations, sampling frequency of 200, and burn-in value of 25 %. Maximum Likelihood analysis was done in PhyML (Guindon & Gascuel 2003), with the GTR+G model of nucleotide substitution and bootstrapping with 1,000 replicates.

For the *Bolbitius* study, 3 new ITS sequences were generated. In addition, 38 ITS sequences, including the outgroup, were downloaded from NCBI GenBank based on BLAST searches and taxonomic relatedness. Sequences were aligned with the MUSCLE tool incorporated into MEGA7 (Kumar et al. 2016). Phylogenetic reconstructions were performed with Maximum Likelihood (ML) and Bayesian inference (BI) analyses. The best-fit substitution model was estimated under the Akaike Information Criterion (AIC) using the FindModel tool, available at http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html, resulting in the GTR+G model. ML was inferred using the online RAxML BlackBox tool available at https://raxml-ng.vital-it.ch/#/ (Kozlov et al. 2019), with 100 bootstrap replicates. BI analyses were performed with MrBayes version3.2.5 (Ronquist et al. 2012), for two independent runs, each with 5 million generations, under the GTR+G model, and four chains with sampling frequency of 100. Convergence was assessed in Tracer version 1.7.1 (Rambaut et al. 2018). We accepted the result where the Effective Sample Size (ESS) was ≥200 and the Potential Scale Reduction Factor (PSRF) was close to 1.

For the *Hymenoscyphus* study, ITS and LSU sequences were aligned separately on the CIPRES Science Gateway (Miller et al. 2010) using the default settings of MUSCLE version 3.7 (Edgar 2004). Alignments were trimmed in TrimAl version 1.2 (Capella-Gutiérrez et al. 2009) with a minimum 50 % of positions conserved, a gap threshold of 0.6, and other parameters at default. The best model of molecular evolution at each locus was selected under AIC using jModelTest2 version 2.1.6 (Darriba et al. 2012). Alignments were then concatenated in Mesquite version 3.61 (Maddison & Maddison 2019). The maximum likelihood (ML) tree was inferred using IQ-TREE version 1.6.12 (Nguyen et al. 2015) with 1,000 bootstrap replicates and two partitions (ITS, LSU) to accommodate different models of molecular evolution (Chernomor et al. 2016). The Bayesian tree was inferred using BEAST version 1.10.4 (Suchard et al. 2018) on CIPRES and other programs that are part of the BEAST package: BEAUTi, LogCombiner, and TreeAnnotater. Beast was run in four iterations from a random starting tree with a lognormal relaxed clock, Birth-Death Incomplete Sampling speciation tree prior (Stadler 2009) and MCMC chain of 80 million with sampling frequency of 8,000. Results of individual and combined runs were viewed in Tracer v 1.7.1 (Rambaut et al. 2018) to verify effective sample sizes (ESS) ≥200 for run statistics, and LogCombiner was used to combine runs. A burn-in of 10 % was specified at each run to increase ESS, and TreeAnnotator was used to generate a consensus Maximum Clade Credibility (MCC) tree without additional burn-in. For an improved placement of *H. equiseti* comb. nov. among most closely related species, a second, smaller ITS-only dataset was constructed with 24 isolates of *Hymenoscyphus*. ITS sequences were aligned using MUSCLE (Edgar 2004) and then trimmed at the conserved motifs 5'–CATTA–3' (3' end of SSU) and 5'–GACCT–3' (5' end of LSU); the alignment portion between these motifs was included in the ML analysis (Dentinger et al. 2011). ML was inferred using IQ-TREE (Nguyen et al. 2015) with the appropriate model of nucleotide substitution as selected by ModelFinder under AICc (Chernomor et al. 2016, Kalyaanamoorthy et al. 2017). Final trees with support values were visualized in FigTree version 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/) and edited in Inkscape version 0.92.4. Intra- and interspecific divergence in the ITS region was calculated using the Compute Pairwise Distances (p-distances) function in MEGA7 with gaps/missing data treatment set at 'pairwise deletion' and default settings for other parameters.

Taxonomy

Basidiomycota, Agaricomycetes, Agaricales, Cortinariaceae

***Cortinarius* section** *Calochroi*

Cortinarius caryae Lebeuf, A. Paul, J. Landry & Y. Lamoureux, **sp. nov.** – Figs. 1, 2
MycoBank no.: MB 839556

Diagnosis. – Differs from the similar *Cortinarius olearioides* Rob. Henry by its pale yellow, olive yellow to pale yellow-brown lamellae, white cortina, light yellow universal veil, and geographic distribution. Basidiospores 9.5–11.5 × 5.0–7.0 µm, on average 10.3 × 5.8 µm. Pileipellis simplex.

Holotypus. – CANADA. Quebec, Sainte-Anne-de-Bellevue, Arboretum Morgan, 45°25'56.25"N, 73°56'44.40"W, 58 m above sea level (a.s.l.), in a deciduous forest of *Carya ovata*, *Quercus rubra*, and *Acer* sp., 3 September 2019, *leg.* R. Lebeuf & A. Paul, HRL3013 (DAOM 984903; holotype).

Description. – Pileus 50–120 mm in diam., hemispherical, becoming convex then applanate and depressed at center, viscid to glutinous, deep yellow, light to deep orange yellow, light to dark orange, greyish orange (4A8, 4½A4, 4½A8, 5AB8, 5B5), brownish orange (6C7) when bruised; margin involute, inflexed, then straight, with age uplifting at the very edge and undulating, concolorous. – Lamellae adnexed to emarginate, close, pale yellow, olive yellow to pale yellow-brown when young, developing rusty brown stains with age, concave, somewhat eroded, 5–10 mm broad. – Cortina white. – Stipe 34–70 mm long, 15–26 mm at apex, fibrillose, light yellow (4A5) to yellowish white (4A2), with a marginate and most often turbinate bulb 18–30 mm across, sometimes flattened at base, orangish brown when bruised; universal veil light yellow. – Context thick, pale yellow (4A3), sometimes whitish, slightly darker yellow near stipe periphery, stained orange-brown in larva perforations. – Odor pleasant, of honey or pastry. – Taste mild. – Mycelium white, sometimes with a lilac hue. – Exsiccatae between brownish yellow and brownish orange (5½C8), older basidiomata between light and greyish orange (5AB6). (Microscopic exam in Melzer's reagent) – Basidiospores [181/6/4] 9.5–11.0(–11.5) × (5.0–)5.5–6.0(–7.0) µm, on average (av.) 10.3 × 5.8 µm, Q=1.50–2.10, Q_{av}=1.76, limoniform, less frequently amygdaliform, in some collections strongly papillate, coarsely verrucose, moderately dextrinoid. – Basidia 26–44 × 8–9.5 µm, 4-spored, clavate, colorless at first but developing a brownish yellow agranular pigment; in

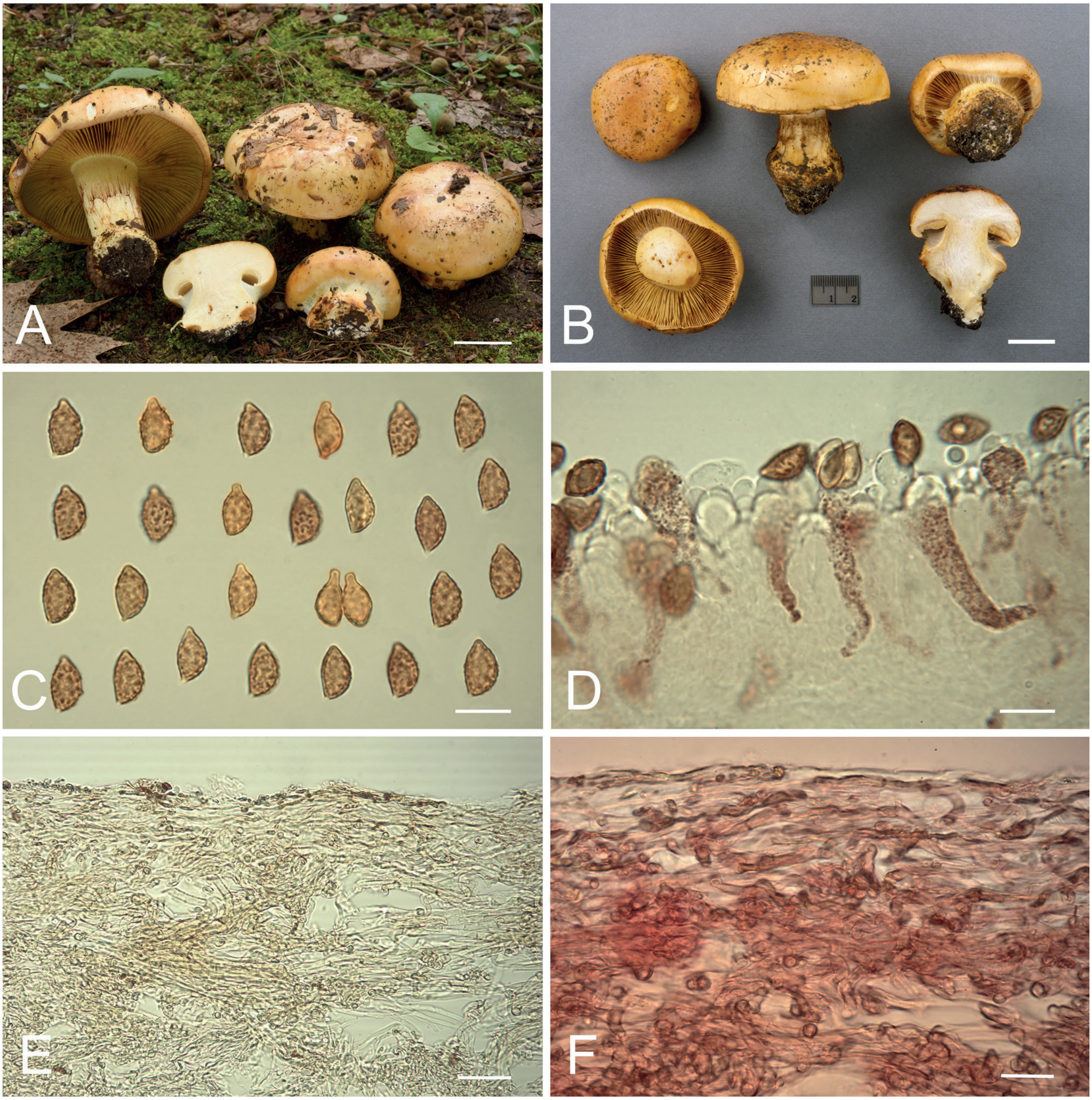

Fig. 1. *Cortinarius caryae*. **A.** Basidiomata *in situ*, collection DAOM 984903 (holotype). **B.** Basidiomata, collection CMMF003385. **C.** Basidiospores. **D.** Pigmented basidia in KOH. **E.** Pileipellis section in Melzer's reagent. **F.** Pileipellis section in SDS Congo Red. Scale bars A–B 20 mm, C–D 10 µm, E–F 25 µm.

3 % KOH colorless at first, becoming reddish brown with numerous small dark brown granules. – Lamellar trama hyphae pale yellow, smooth, aguttulate. – Stipe apex hyphae pale yellow, smooth, aguttulate. – Cortina pale yellow, smooth, aguttulate. – Hymenial cystidia absent. – Pileipellis simplex: epicutis with a moderately developed gelatinous matrix, outermost hyphae (veil) 1.5–2 µm wide, with an intracellular golden yellow pigment; hyphae in matrix 1.5–5 µm wide, slightly to moderately interwoven, mostly smooth, some finely incrusted, occasionally more coarsely spirally incrusted, a few with intraparietal or intracellular darker yellow pigment; basal layer

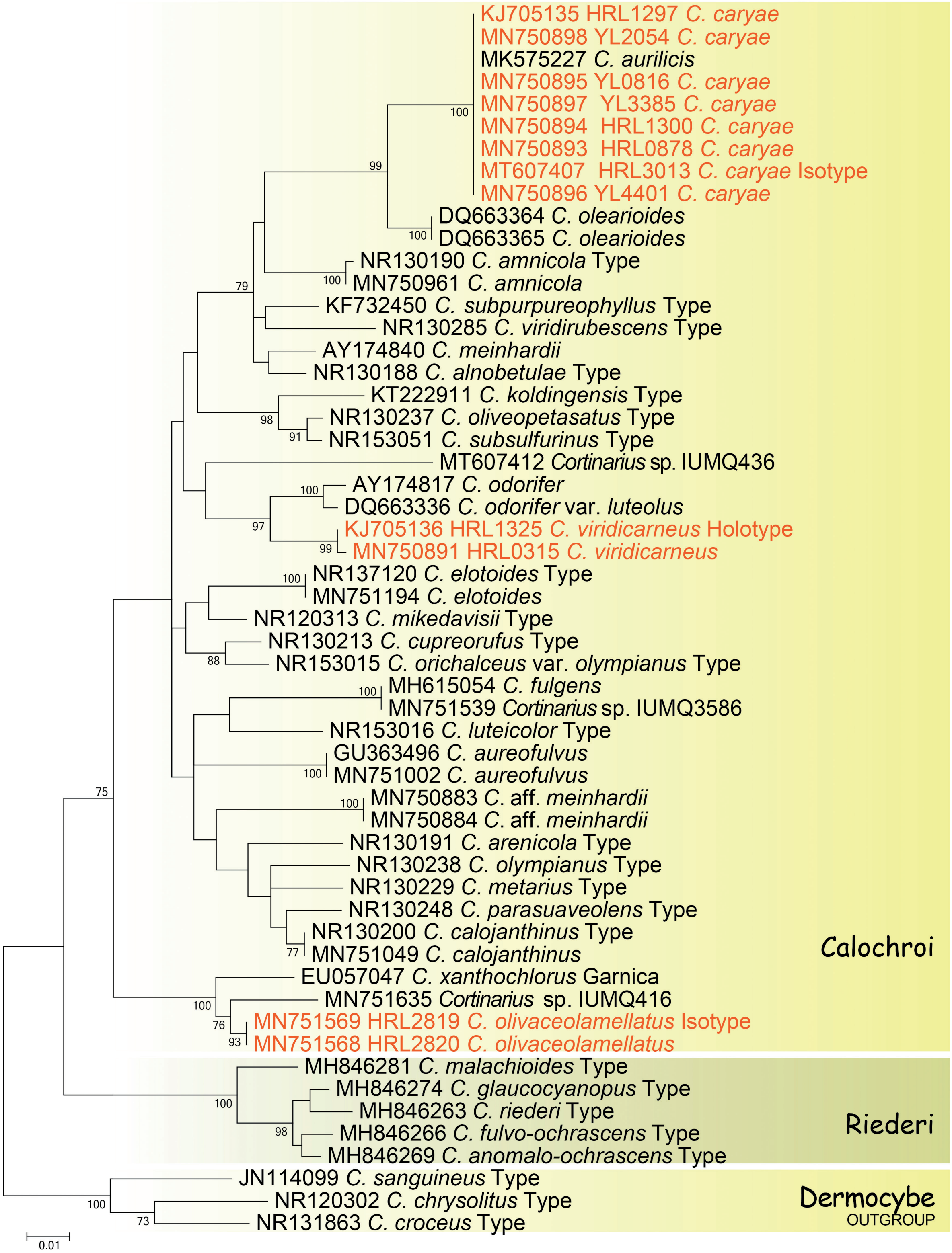

Fig. 2. Phylogeny of selected *Cortinarius* species in Euphlegmacia sections *Calochroi* and *Riederi* reconstructed from an ITS dataset. The tree topology with the highest log likelihood (-lnL=4045,3280) is shown, resulting from ML inference performed in MEGA7. For each node, the ML bootstrap (MLBS) if >70 is presented. Section designations following Soop et al. (2019), new species highlighted in red, bar indicating the expected number of substitutions per site.

of 3–10 µm wide hyphae, subparallel, interwoven or in bundles, mostly smooth, rarely spirally incrusted, a few with intraparietal or intracellular darker yellow pigment; hypoderm absent. – Clamp connections present in all tissues. – Macrochemical reaction: vinaceous red with 10 % KOH on pileus, bulb, and veil, pinkish on stipe base; negative on pileus context.

Etymology. – Referring to the host tree of the species, *Carya* spp.

Habitat and distribution. – Gregarious or more rarely caespitose in association with *Carya* in hardwood forests (*Carya ovata*, *C. cordiformis*, *Fagus grandifolia*, *Quercus rubra*, *Tilia americana*), in September, in calcareous and argillaceous soil. Known from Canada (Quebec) and the USA (Indiana).

Additional material examined. – *Ibid.* (QFB32677; isotype). Sequences ex-isotype: MT607407 (ITS). – CANADA. Quebec, Sainte-Anne-de-Bellevue, Arboretum Morgan, in a deciduous forest of *Carya ovata* and *Quercus rubra*, 13 September 2011, *leg.* R. Lebeuf & A. Paul, HRL0878 (QFB29921); Hitchinbrooke, Réserve écologique du Boisé-des-Muir, in a mixed forest of *Carya ovata*, *Fagus grandifolia*, and *Tsuga canadensis*, 23 September 2012, *leg.* R. Lebeuf, HRL1300 (QFB29948); *ibid.*, HRL1297 (in R.L.); Longueuil, under *Quercus rubra* with *Carya ovata* nearby, in argillaceous soil, 16 September 1993, *leg.* Y. Lamoureux, YL2054 (CMMF002054); Laval, under *Carya cordiformis*, in argillaceous soil, 28 September 1999, *leg.* Y. Lamoureux, YL3385 (CMMF003385); Repentigny, under *Carya cordiformis* and *C. ovata*, with *Fagus grandifolia* and *Tilia americana* nearby, on low ground, in damp argillaceous and calcareous soil, 24 September 2018, *leg.* Y. Lamoureux, YL4401 (CMMF020758).

Notes. – The ITS sequence of the isotype is distinct from other members of section *Calochroi*, deviating from *Cortinarius olearioides* (GenBank acc. no. DQ663364) by 24 substitutions and indels. With its marginate bulb, vividly-colored yellow to orange viscid pileus, coarsely-ornamented limoniform to amygdaliform spores, absence of hypoderm, and the vinaceous red KOH reaction of the pileus, bulb, and veil, *C. caryae* possesses morphological characters consistent with section *Calochroi* as defined by Frøslev et al. (2007). This newly described species used to be referred to as *C. olearioides* in Quebec but, as demonstrated previously (Landry et al. 2021), our phylogenetic analysis of ITS sequences from *Calochroi* species show that *C. caryae* and *C. olearioides* are sister species, the latter being absent from the North American continent (Fig. 2). *Cortinarius olearioides* differs by its yellow to orange-yellow lamellae, pale yellow cortina, orange to orange-brown veil (Soop 2018), and its geographic distribution. *Cortinarius viridicarneus* sp. nov., described below, differs by its yellow-green context, odor of anise, larger basidiospores measuring (10.5–) 11.0–12.5(–13.0) × (6.5–)7.0–8.0 µm, and an association with *Tsuga*.

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Basidiomycota, Agaricomycetes, Agaricales, Cortinariaceae

Cortinarius section *Calochroi*

Cortinarius viridicarneus Lebeuf, A. Paul & J. Landry, **sp. nov.** – Figs. 2, 3
MycoBank no.: MB 839557

Diagnosis. – Differs from the European *Cortinarius odorifer* Britzelm. by its genetic distance at the ITS locus, geographic distribution in North America, and slightly larger basidiospores, measuring 10.5–13.0 × 6.5–8.0 µm, on average 11.9 × 7.3 µm. Pileipellis simplex.

Holotypus. – CANADA. Quebec, Hitchinbrooke, Réserve écologique du Boisé-des-Muir, 45°5'8.26"N, 74°6'49.35"W, 64 m a.s.l., under *Tsuga canadensis* in a mixed forest including also at a distance *Fagus grandifolia*, *Betula* sp., and *Acer* sp., 7 October 2012, *leg.* R. Lebeuf, HRL1325 (DAOM 984901; holotype). Sequences ex-holotype: KJ705136 (ITS).

Description. – Pileus 40–95 mm in diam., convex then applanate and depressed at center, glutinous, golden yellow, orange to brownish orange (5B7, 5½B7, 7C8) at center; margin inflexed then straight, undulating with age, pale greenish yellow to light orange ((4–5)A(3–4)). – Lamellae adnexed to emarginate, close, olivaceous yellow when young. – Cortina yellow. – Stipe 30–80 mm long, 8–15 mm at apex, fibrillose, concolorous with pileus margin, with a marginate bulb 17–30 mm across often stained reddish brown; universal veil greenish yellow. – Context vividly colored, either entirely yellow-green (3A4(–3B4)), or mostly yellow (3A(6–7)) and with a yellow-green color at least over the lamellae. – Odor strong of anise. – Taste mild. – Mycelium white. – Exsiccatae reddish brown (8F7). (Microscopic exam in Melzer's reagent) – Basidiospores [180/6/2] (10.5–)11.0–12.5(–13.0) × (6.5–)7.0–8.0 µm, av. 11.9 × 7.3 µm, Q=1.44–2.00, Q_{av}=1.63, limoniform to amygdaliform, weakly dextrinoid, coarsely verrucose. – Basidia 39–54(–60) × 10–12.5(–14) µm, 4-spored, clavate, when young colorless, with age developing reddish brown granules; in 3 % KOH when young colorless, with age becoming purple with numerous small dark brown granules. – Lamellar trama hyphae pale yellow, smooth, aguttulate; in KOH purple with blackish granules. – Stipe apex hyphae: outer hyphae pale yellow, smooth; inner hyphae pale yellow with some small to minute brown granules. – Cortina hyphae pale yellow,

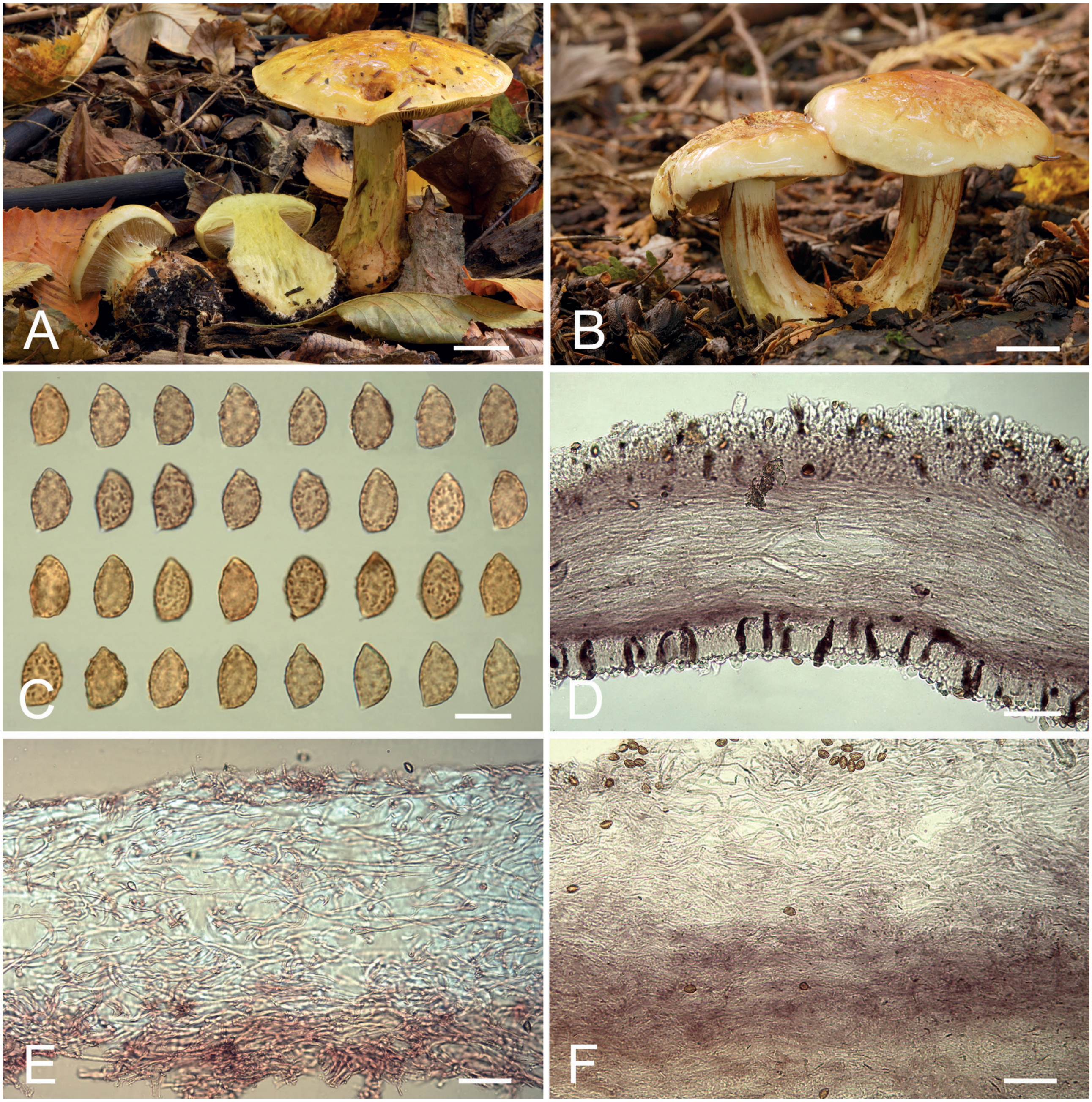

Fig. 3. *Cortinarius viridicarneus*. **A.** Basidiomata *in situ*, collection DAOM 984901 (holotype). **B.** Basidiomata *in situ*, collection QFB29899. **C.** Basidiospores. **D.** Lamellar section in KOH. **E.** Pileipellis section in SDS Congo Red. **F.** Pileipellis section in KOH. Scale bars A–B 20 mm, C 10 µm, D–F 50 µm.

smooth. – Hymenial cystidia absent. – Pileipellis simplex: epicutis with a well-developed gelatinous matrix, hyphae in matrix 1–4 µm wide, ascending-interwoven, sand brown, smooth, in KOH purplish grey; basal layer of 3–5 µm wide hyphae, subparallel above, in bundles below, pale yellow, smooth, in KOH purplish to purplish red with extra- and intracellular small dark granules; hypoderm absent. – Clamp connections present in all tissues. – Macrochemical reactions: vivid red with 10 % KOH on pileus and context.

Etymology. – Referring to the vivid green-yellow color of the context.

Habitat and distribution. – Gregarious under conifers, probably associated with *Tsuga*, in early October. Thus far confirmed from two sites in Quebec, Canada.

Additional material examined. – CANADA. Quebec, Sainte-Sophie, in an old coniferous forest of *Tsuga canadensis* and *Thuja occidentalis* in damp soil, 1 October 2009, *leg.* J. Nuzzolese, HRL0315 (QFB29899).

Notes. – The ITS sequence of the holotype is distinct from other members of section *Calochroi*. *Cortinarius viridicarneus* has a sister relationship with the group formed by two European varieties of *Cortinarius odorifer*, i.e., var. *luteolus* (M.M. Moser) Nespiak (= *Cortinarius regis-romae* Rob. Henry sensu Garnica et al. 2016) (GenBank acc. no. DQ663336) and var. *odorifer* Britzelm. (GenBank acc. no. AY174817), deviating from them by 21 substitutions and indels (Fig. 2). Morphologically, its marginate bulb, vividly-colored viscid pileus, coarsely-ornamented limoniform to amygdaliform spores, absence of hypoderm, and vivid-red KOH reaction of the pileus and context are consistent with section *Calochroi* as defined by Frøslev et al. (2007). *Cortinarius viridicarneus* shows two characters that, combined, make it unique among the North American *Calochroi*: its strong anise odor and its yellow-green context, at least in some parts. Besides its geographic distribution, no clear macroscopic, microscopic, or ecological character can clearly separate it from the two sister varieties of *C. odorifer*, even though var. *luteolus* produces slightly narrower spores (6.5–7.5 µm in Brandrud 1990–2014).

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

Basidiomycota, Agaricomycetes, Agaricales, Cortinariaceae

Cortinarius* section *Calochroi

Cortinarius olivaceolamellatus Lebeuf, A. Paul & J. Landry, **sp. nov.** – Figs. 2, 4
MycoBank no.: MB 839558

Diagnosis. – Characterized by its strongly innately-fibrillose, greyish orange then dark brownish orange pileus, oli-

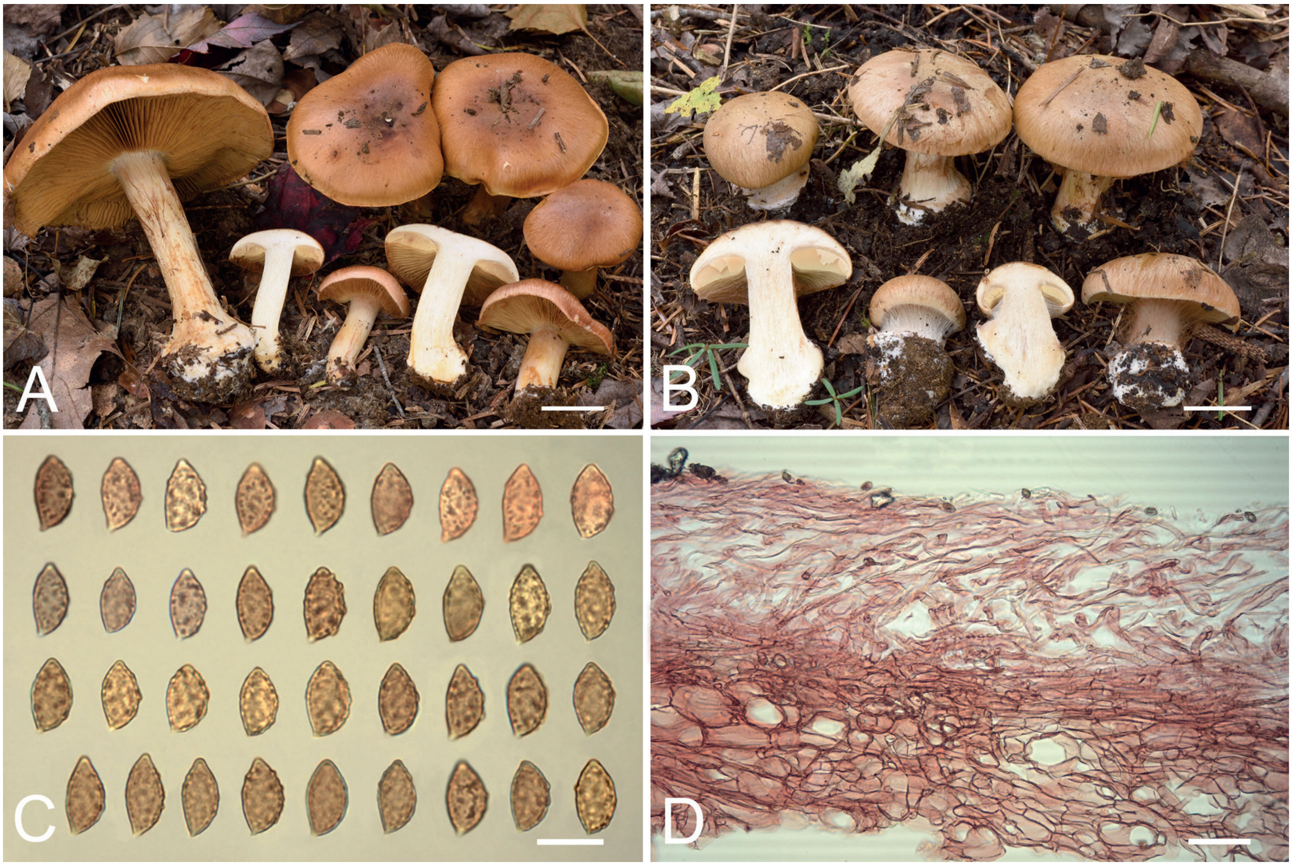

Fig. 4. *Cortinarius olivaceolamellatus*. **A.** Basidiomata *in situ*, collection DAOM 984904 (holotype). **B.** Younger basidiomata *in situ*, collection QFB31059. **C.** Basidiospores. **D.** Pileipellis section in SDS Congo Red. Scale bars A–B 20 mm, C 10 µm, D 50 µm.

vaceous yellow young lamellae, marginate bulb, pale yellow context, and fruity odor. Basidiospores 10–12.5 × 5.5–7.5 µm, on average 11.4 × 6.3 µm. Pileipellis simplex.

Holotypus. – CANADA. Quebec, Saint-Stanislas, Parc de la rivière Batiscan, trail Le Buis, 46°34'47.0"N, 72°24'45.4"W, 82 m a.s.l., in a mixed forest of *Fagus grandifolia*, *Abies balsamea*, and *Acer* sp., 8 October 2018, *leg.* R. Lebeuf & A. Paul, HRL2819 (DAOM 984904; holotype).

Description. – Pileus 26–94 mm in diam., convex then plano-convex to pulvinate, viscid, greyish orange (5B3½) at first, becoming brownish orange (5½C8), with abundant darker brown innate fibrils on the whole surface; margin inflexed to deflexed, concolorous. – Lamellae adnate to adnexed, close, olive yellow then rusty brown, eroded, 5–9 mm broad. – Cortina white, copious. – Stipe 37–64 mm long, 9–18 mm at apex, whitish at apex, with orangish brown fibrils on a pale-yellow background, with a marginate bulb 7–26 mm across; basal mycelium white. – Context thick, in young basidiomata pale yellow at stipe base, white elsewhere, becoming pale yellow in all parts with age, unchanging when cut or bruised. – Odor pleasant, fruity. – Taste mild. – Exsiccatae around raw sienna (6D7). (Microscopic exam in Melzer's reagent) – Basidiospores [180/6/2] (10.0–)10.5–12.5 × (5.5–)6.0–7.0(–7.5) µm, av. 11.4 × 6.3 µm, Q=1.53–2.08, Q_{av}=1.82, limoniform to amygdaliform, with a narrow apex, about half with a small beak, moderately dextrinoid, moderately to coarsely verrucose, warts isolated or confluent, unevenly distributed. – Basidia 29–50 × 8–12 µm, 4-spored, clavate, yellow in KOH. – Lamellar trama hyphae yellow, smooth, with a few small to minute concolorous guttules. – Stipe apex hyphae smooth, yellow, with a few small concolorous guttules, some outermost hyphae with sand-brown intracellular pigment. – Hymenial cystidia absent. – Pileipellis simplex: epicutis with a well-developed gelatinous matrix, hyphae in matrix 1.5–11 µm wide, repent, ascending or interwoven, smooth or spirally incrusted, yellow, aguttulate and agranular, some with intracellular brownish yellow pigment or parietal amber-like pigment; basal hyphae somewhat wider in general, 7–15 µm, subparallel to interwoven, spirally incrusted, brownish yellow, rarely with darker intracellular pigment; hypoderm absent. – Clamp connections present in all tissues. – Macrochemical reaction: reddish brown with 10 % KOH on the pileus and the bulb rim, pale brown on the basal mycelium and the pileus context.

Etymology. – Referring to the olivaceous yellow color of the young lamellae.

Habitat and distribution. – In large groups in a mixed forest of *Fagus grandifolia*, *Abies balsamea*, and *Acer* sp. by the river, in argillaceous soil, found in early October. Thus far known from a single location in Quebec, Canada.

Additional material examined. – *Ibid.* (QFB31058; isotype). Sequences ex-isotype: MN751569 (ITS). – CANADA. Quebec, Saint-Stanislas, Parc de la rivière Batiscan, trail Le Buis, 46°34'47.0"N, 72°24'45.4"W, 82 m a.s.l., in a mixed forest of *Fagus grandifolia*, *Abies balsamea*, and *Acer* sp., by the river, in argillaceous soil, 8 October 2018, *leg.* R. Lebeuf & A. Paul, HRL2820 (QFB31059).

Notes. – The ITS sequence of the isotype is distinct from other members of section *Calochroi*, deviating from *Cortinarius xanthochlorus* Rob. Henry (GenBank acc. no. EU57047) by 15 substitutions and indels. With its marginate bulb, viscid pileus vividly colored in mature specimens, moderately to coarsely ornamented limoniform to amygdaliform spores, absence of hypoderm, and the reddish brown KOH reaction of the pileus and bulb rim, *C. olivaceolamellatus* possesses morphological characters consistent with section *Calochroi* as defined by Frøslev et al. (2007). Interestingly, the innately fibrillose pileus, considered by these authors to be an exceptional character for the section, is also observed in the subclade formed in our phylogeny by *C. olivaceolamellatus*, *C. xanthochlorus*, and *Cortinarius* sp. IUMQ416 (Landry et al. 2021), the latter being an undescribed species collected in a deciduous forest in Quebec, Canada (Fig. 2). Distinguishing characters of *C. olivaceolamellatus* include the color change from young (greyish orange) to old specimens (dark brownish orange), strongly innately-fibrillose pileus, olivaceous yellow lamellae, pale yellow context, and fruity odor. *Cortinarius xanthochlorus*, thus far not reported from North America, shows greenish- or olivaceous yellow tinges in its pileus, lamellae, stipe, and context, and produces larger basidiospores, measuring 12–14 × 7–8 µm (Jeppesen et al. 2012). *Cortinarius* sp. IUMQ416, with a similarly colored pileus, differs by its lilac-pink stipe.

The description of some of our new taxa is based on collections made in a single location but we feel that the advantages for their formal description far outweigh the disadvantages given the large number of *Cortinarius* spp. in North America, the difficulty to interpret descriptions by older authors, the frequent discovery of cryptic species and new taxa, and the difficulty or impossibility to sequence old type material. Even though many old type specimens were already sequenced, and neo- or epitypes were selected for some species (e.g., Liimatainen et al. 2014, 2020), not all types have been dealt with,

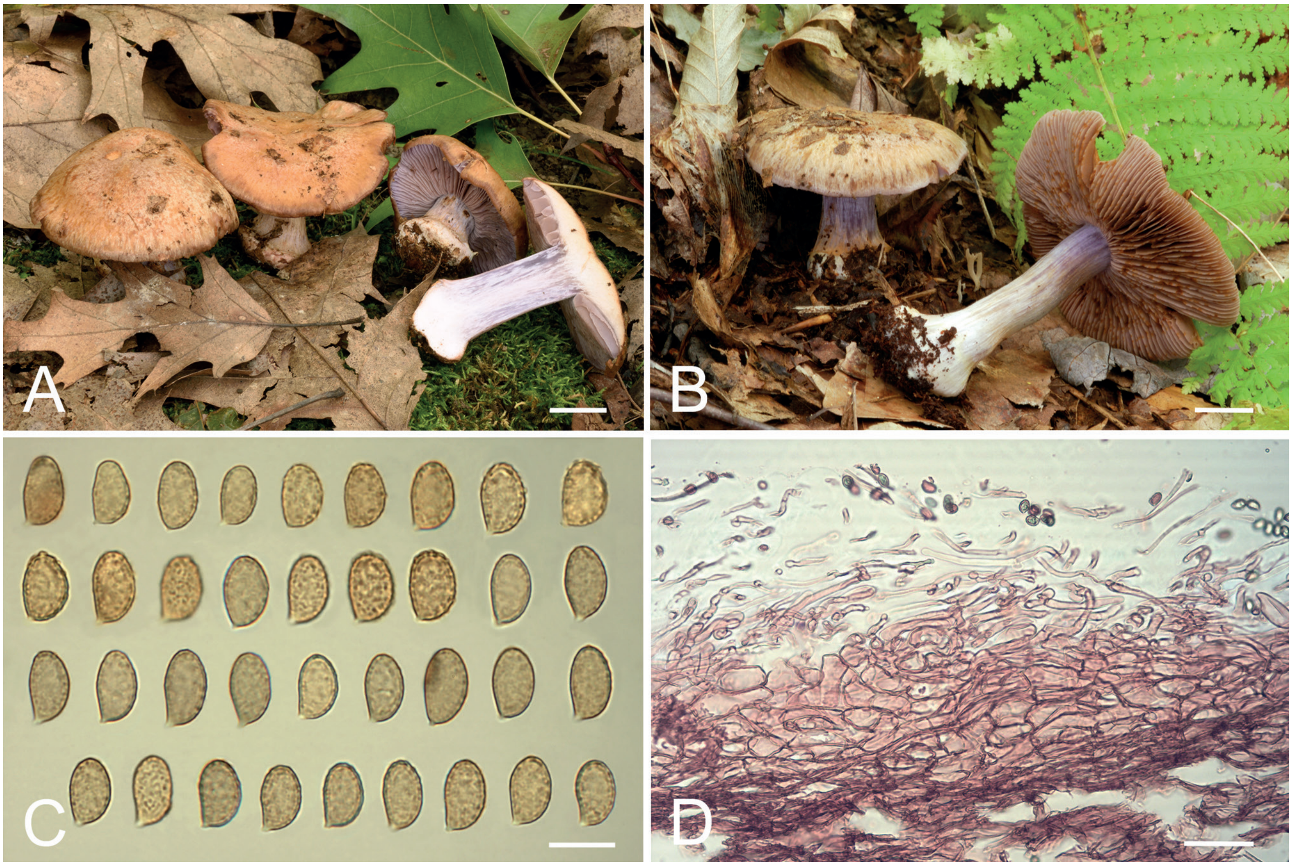

Fig. 5. *Cortinarius lilaceolamellatus*. **A.** Basidiomata *in situ*, collection DAOM 984905 (holotype). **B.** Basidiomata *in situ*, collection QFB29937. **C.** Basidiospores. **D.** Pileipellis section in SDS Congo Red. Scale bars A–B 20 mm, C 10 µm, D 50 µm.

and it is always possible that earlier names will turn up for species more recently described. However, the attribution of a barcode to new species allows us to better understand the diversity, distribution, and combination of species in different habitats and their importance in the structure of forest ecosystems.

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

Basidiomycota, Agaricomycetes, Agaricales, Cortinariaceae

Cortinarius section *Scauri*

Cortinarius lilaceolamellatus Lebeuf, A. Paul, J. Landry & Y. Lamoureux, **sp. nov.** – Figs. 5, 6
MycoBank no.: MB 839559

Diagnosis. – Characterized by its greyish orange pileus with watery marks, pale violet lamellae, marginate bulb shallowly rounded or flattened at base, odor of honey, ellipsoid basidiospores measuring 9.0–13.0 × 5.5–8.0 µm, on average 10.7 × 6.7 µm, and lack of green pigment in the epicutis. Pileipellis duplex.

Holotypus. – CANADA. Quebec, Sainte-Anne-de-Bellevue, Arboretum Morgan, 45°25’42.8”N, 73°57’22.9”W, 61 m a.s.l, in a mixed forest of *Fagus grandifolia*, *Tsuga canadensis*, and *Quercus rubra*, 10 October 2015, *leg.* R. Lebeuf & A. Paul, HRL2206 (DAOM 984905; holotype).

Description. – Pileus 50–80 mm in diam., convex then applanate, viscid, light orange with a greyish tone (4½A3, 4½A4, 5A2½, 5A3½ (–5B3½), 5A4(–5B4)), with numerous pale to dark brown watery streaks and blotches, particularly at margin; margin inflexed then straight, with age uplifting and undulating, concolorous, on young specimens sometimes whitish. – Lamellae adnexed, close, pale violet when young, developing orange-brown spots with age, somewhat eroded, 5–6 mm broad. – Stipe 40–80 mm long, 10–18 mm at apex, fibrillose, striate, violet-white (18A2) to light violet (18A4), with a marginate bulb 22–32 mm across, shallowly rounded or flattened at base, whitish, slowly turning orange-brown when bruised; universal veil pale yellow (4A3). – Context firm, orange-white (5A2) in the pileus, whitish in the bulb, pale to light violet (18A3–

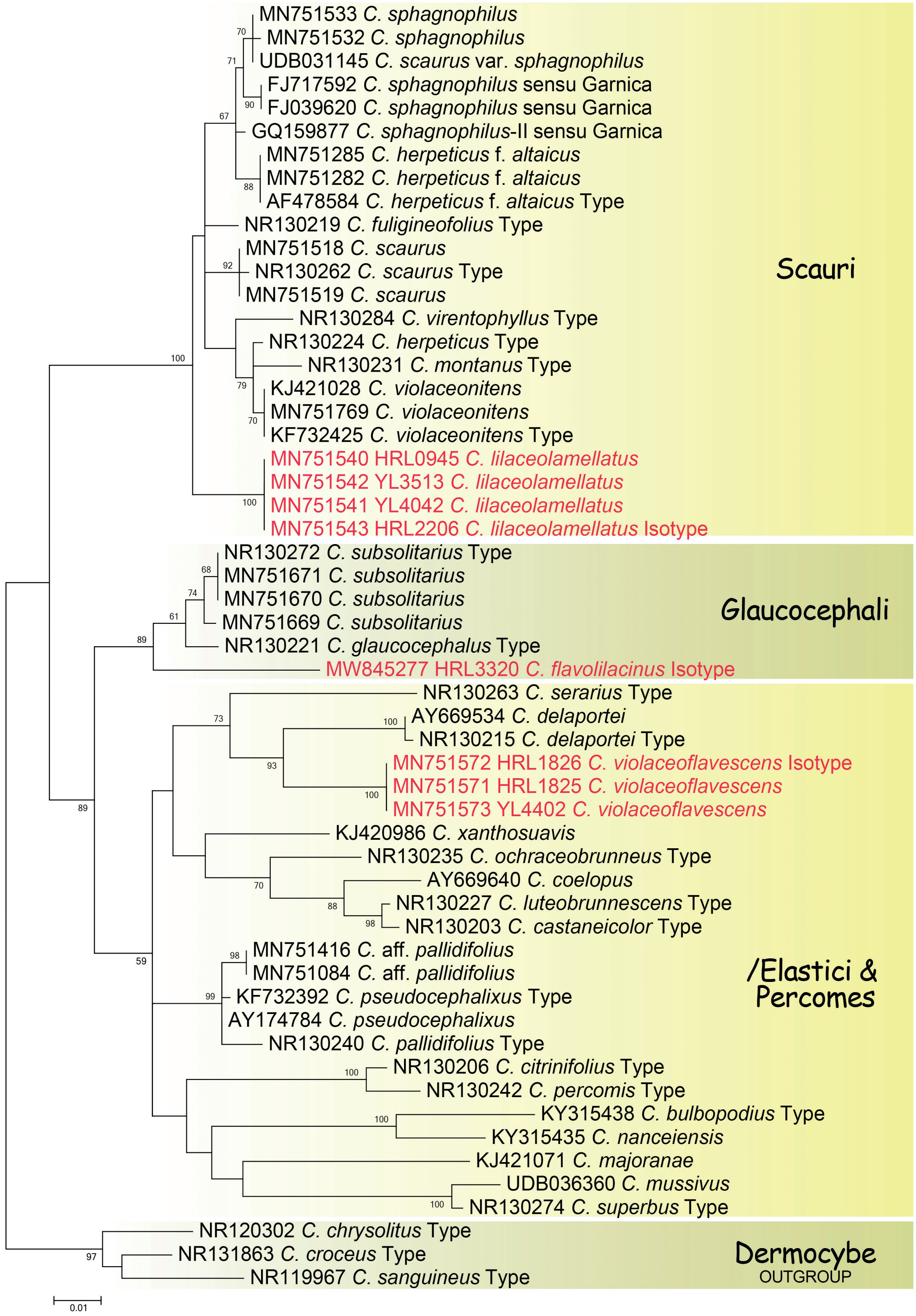

Fig. 6. Phylogeny of selected *Cortinarius* species in sections *Scauri*, *Glaucocephali*, *Elastici*, and *Percomes* reconstructed from an ITS dataset. The tree topology with the highest log likelihood (-lnL=3680,2444) is shown, resulting from ML inference performed in MEGA7. For each node, the ML bootstrap (MLBS) if >70 is presented. Section designations following Liimatainen et al. (2014) and Soop et al. (2019), new species highlighted in red, bar indicating the expected number of substitutions per site.

4) in the stipe. – Odor either absent or pleasant, of honey or fruity. – Taste mild. – Mycelium white. – Exsiccatae greyish brown (6EF4). (Microscopic exam in Melzer's reagent) – Basidiospores [240/8/4] (9.0–)10.0–11.5(–13.0) × (5.5–)6.0–7.5(–8.0) µm, av. 10.7 × 6.7 µm, Q=1.31–1.86, Q_{av}=1.59, ellipsoid, rarely oblong to subamygdaliform, moderately verrucose, often more coarsely at apex, a small proportion with suprahilar depression, not dextrinoid. – Basidia 30–41 × 10–12 µm, 4-spored, clavate to subventricose, colorless at first, but developing a brownish yellow intracellular pigment with age; in 3 % KOH colorless at first, becoming pale brown with small dark brown granules. – Lamellar trama hyphae pale yellow, smooth, aguttulate. – Stipe apex hyphae pale yellow, smooth, aguttulate. – Hymenial cystidia absent. – Pileipellis duplex: epicutis with a well-developed gelatinous matrix, uppermost hyphae (veil) 1.5–2 µm wide, with an intracellular olive yellow pigment; hyphae in matrix 3–6 µm wide, pale yellow, mostly smooth, some finely spirally incrusted close to the hypoderm; hypoderm well developed, hyphae 7–25 µm wide, smooth, yellow; transition layer with the cortex brownish yellow, hyphae 3–12 µm. – Clamp connections present in all tissues. – Macrochemical reaction: brown on pileus with 10 % KOH.

Etymology. – Referring to the pale violet lamellae.

Habitat and distribution. – Gregarious in mixed forests, probably associated with conifers, in the fall. Thus far only known from Quebec, Canada.

Additional material examined. – *Ibid.* (QFB29980; isotype). Sequences ex-isotype: MN751543 (ITS). – CANADA. Quebec, Pointe-au-Chêne, in a mixed forest of *Quercus rubra*, *Fagus grandifolia*, and various conifers, 20 September 2011, *leg.* R. Lebeuf & A. Paul, HRL0945 (QFB29937); Chertsey, in conifer needles, under *Abies balsamea* and *Betula* sp., 18 September 2000, *leg.* Y. Lamoureux, YL3513 (CMMF003513); Rawdon, under various conifers (*Picea* sp., *Abies balsamea*, *Pinus* sp.) in sphagnum, 16 September 2006, *leg.* Y. Lamoureux, YL4042 (CMMF004042).

Notes. – The ITS sequence of the isotype is distinct from other members of section *Scauri* by at least 16 substitutions and indels (Fig. 6). With its watery marks on the pileus, ellipsoid spores, duplex pileipellis, and odor of honey, *C. lilaceolamellatus* possesses morphological characters consistent with section *Scauri* as defined by Saar et al. (2015). The green pigment present in the epicutis hyphae of most *Scauri* spp. is absent in our species, a character also observed by Liimatainen et al. (2014) for *Cortinarius herpeticus* Fr., also placed in section *Scauri*. Other distinguishing characters of *C. lilaceolamellatus* are its greyish orange pileus, pale violet lamellae, marginate bulb shallowly rounded or flattened at base, lack of greenish tints in the basidiomata, and large basidiospores for the section. *Cortinarius sphagnophilus* Peck has a darker pileus, brown to dark brown, and smaller basidiospores, measuring 9–10.5 × 6–7 µm (Brandrud et al. 1990–2014). *Cortinarius violaceonitens* (Rob. Henry) Moënne-Locc. has smaller amygdaliform–fusoid spores, measuring 9.3–10.7 × 5.4–6.3 µm (Liimatainen et al. 2014). *Cortinarius herpeticus* also has smaller spores (9–10.5 × 6–7 µm) and its lamellae are bluish green to olivaceous green (Brandrud et al. 1990–2014). *Cortinarius herpeticus* f. *altaicus* M.M. Moser & Peintner, genetically distinct from f. *herpeticus* according to our ITS phylogeny (Fig. 6), also has a darker pileus and produces shorter basidiospores, 8.8–9.8–11.2 × 5.9–6.5–7.6 µm (Moser & Peintner 2002).

Authors: R. Lebeuf, J. Landry, Y. Lamoureux & A. Paul

Basidiomycota, Agaricomycetes, Agaricales, Cortinariaceae

Cortinarius clade /*Glaucocephali*

Cortinarius flavolilacinus Lebeuf, A. Paul & J. Landry, **sp. nov.** – Figs. 6, 7
MycoBank no: MB 839560

Diagnosis. – Small- to medium-sized *Cortinarius* with a pale violet-grey pileus showing darker violet streaks, a pale yellow cast and light yellow to orange spots; lamellae pale violet grey; stipe bulbous to submarginate, dull violet above the pale orange base; context white to yellowish white in the pileus, gradually darker yellow towards the stipe base; and cortina violet white. Basidiospores 7–8.5 × 4.0–4.5 µm, on average 8.1 × 4.4 µm. Pileipellis duplex.

Holotypus. – CANADA. Quebec, Saint-Narcisse, Parc de la rivière Batiscan, trail Le Buis, 46°33'31.38"N, 72°24'53.07"W, 70 m a.s.l., in a predominantly deciduous forest of *Quercus rubra*, *Acer* sp., *Populus tremuloides*, with a few *Abies* trees, 23 September 2020, *leg.* R. Lebeuf & A. Paul, HRL3320 (DAOM 984906).

Description. – Pileus 21–52 mm in diam., convex to pulvinate, plano-convex, sometimes with a low and wide umbo, viscid, violet grey (18(B–D)2½) with darker innate fibrils, showing a pale yellow cast ((3–4)A3) at the center and also along the margin, with prominent small to large light yellow to orange spots ((4–5)A(4–6)), also bearing numerous pale or darker lilac grey to dull violet (15BC2, 15E4, 17E5) radial watery streaks especially at the margin; margin inflexed then straight, with the very edge becoming reflexed with age, when young greyish violet (18½B5) from the universal veil. – Lamellae

Fig. 7. *Cortinarius flavolilacinus*, collection DAOM 984906 (holotype). **A.** Basidiomata *in situ*. **B.** Basidiospores. **C.** Pileipellis section in SDS Congo Red. Scale bars A 20 mm, B 10 µm, C 25 µm.

emarginate, close, 2.5–4 mm broad, eroded at edge, pale violet grey (18B2) when young. – Cortina violet-white (17A2). – Universal veil greyish violet (18½B5), leaving an evanescent thin membrane on the bulb rim. – Stipe 26–30 × 5–10 mm, equal above the bulbous to submarginate base 9–13 mm across, solid, fibrillose-striate, dull violet (18D(3–4)) becoming violet grey (18B2) with age, base light orange (5A4, 5A5) on a whitish background. – Context white to yellowish white (4A2) in the pileus, gradually passing into pale yellow (4A3) in the stipe base, violaceous grey in stipe periphery, firm. No color changes noted in any part of basidiomata. – Odor none. – Taste mild. (Microscopic exam in Melzer's reagent) – Basidiospores [120/4/1] (7.0–)7.5–8.5 × (4.0–)4.2–4.5 µm, av. 8.1 × 4.4 µm, Q=1.60–2.13, Q_{av}=1.82, amygdaliform, less frequently limoniform, with a small suprahilar depression, moderately verrucose, weakly dextrinoid. – Basidia 31–37 × 8–9 µm, 4-spored, clavate; older basidia developing a yellow intracellular pigment in Melzer's reagent and 3 % KOH, and blackish granules in KOH. – Lamellar trama hyphae smooth, yellow. – Stipe apex hyphae smooth, yellow. – Hymenial cystidia absent. – Pileipellis duplex: epicutis with a moderately-developed gelatinous matrix, hyphae 1.5–7 µm wide, repent to interwoven, yellow, spirally incrusted, some with intracellular brownish yellow pigment; hypoderm present, hyphae 8–23 µm wide, smooth, darker yellow. – Clamp connections present in all tissues. – Macrochemical reaction: brownish orange with 10 % KOH on the pileus, the bulb rim, and the pileus and stipe context.

Etymology. – Referring to the yellow and lilac color of the pileus.

Habitat and distribution. – In tight group but not caespitose in a predominantly deciduous forest of *Quercus rubra*, *Acer* sp., *Populus tremuloides*, with a few *Abies* trees, close to a large *Quercus rubra*. Thus far known from a single location in Quebec, Canada.

Additional material examined: *Ibid.* (QFB32945; isotype). Sequences ex-isotype: MW845277 (ITS).

Notes. – The ITS sequence of the isotype is unique in the Euphlegmacia (Soop et al. 2019), differing by more than 25 substitutions-indels from its closest relative (Fig. 6). This species, in a basal position relative to clade /*Glaucocephali* as defined by Soop et al. (2019), is unique on account of its small to medium size, pale violet pileus with a yellow cast developing prominent yellow to orange spots with age, violet stipe above the light orange base, and duplex pileipellis. Two other species in clade /*Glaucocephali* differ by the following characters: *Cortinarius subsolitarius* A.H. Sm. produces more robust basidiomata with a 40–100-mm pileus and a stipe at apex 10–15 mm broad, a dark dull bluish violet color in pileus, lamellae, stipe, and stipe context, and a greenish then yellowish cast in the pileus with age (Smith 1942); *Cortinarius glaucocephalus* M.M. Moser, Ammirati & Halling differs by its more robust basidiomata, with a 40–100-mm pileus and a stipe at apex 12–19 mm broad, its variable and much darker colors, dark bluish green, nearly black to blue-green when young, yellowish brown to red-brown on disc with age, its (sub)limoniform basidiospores measuring 8.2–9.4 × 4.1–5.0 µm, and its growth in coniferous forests.

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

Basidiomycota, Agaricomycetes, Agaricales, Cortinariaceae

Cortinarius sections *Elastici/Percomes*

Cortinarius violaceoflavescens Lebeuf, A. Paul, J. Landry & Y. Lamoureux, **sp. nov.** – Figs. 6, 8
MycoBank no.: MB 839561

Diagnosis. – Characterized by its robust basidiomata, violet-grey pileus quickly turning yellow then greyish orange, prominent marginal bulb rounded or flattened at the base, pale yellow to greyish orange universal veil, large amygdaloid basidiospores measuring 10–13.5 × 5.5–7.5 µm, on average 11.9 × 6.5 µm, and abundant extracellular and/or incrusting granular pigment present in the pileipellis, lamellar trama, and upper stipe hyphae in Melzer's reagent. Pileipellis simplex.

Holotypus. – CANADA. Quebec, Laval, Boisé Sainte-Dorothée, 45°32'22.4"N, 73°49'14.5"W, 32 m a.s.l., in a mixed forest of *Quercus rubra*, *Carya ovata*, *Tsuga canadensis*, *Tilia americana*, and *Populus* sp., 17 September 2014, *leg.* R. Lebeuf & A. Paul, HRL1826 (DAOM 984907; holotype).

Description. – Pileus 62–110 mm in diam., hemispherical truncate, becoming plano-convex then applanate and depressed at center, viscid, glabrous or at times innately fibrillose, greyish lilac to violet grey (15B2, 15C2, 17B2, 18B2, 18B3) at first, quickly taking a pale yellow then greyish orange color (4A3, 4½A3, 5B5); margin incurved then straight, undulating with age, naked or adorned with veil remnants. – Lamellae adnate, close to crowded, rather broad, violet grey (18B2). – Cortina white. – Stipe 25–75 mm long, 18–30 mm at apex, fibrillose, between violet white and bluish white (18½A2), with a marginate bulb 35–50 mm across, pale to light violet (18A3½) under the veil in button stage, rounded or flattened at base, bearing white rhizomorphs and remnants of the pale yellow to greyish orange universal veil. – Context compact, firm, white in the pileus, violet-white (18A2) in the stipe. – Odor pleasant. – Taste mild. – Exsiccatae pale yellow orange (4½A3) to greyish orange (5AB4). (Microscopic exam in Melzer's reagent) – Basidiospores [180/6/3] (10.0–)11.0–13.0(–13.5) × (5.5–)6.0–7.0(–7.5) µm, av. 11.9 × 6.5 µm, Q=1.40–2.17, Q_{av}=1.82, amygdaliform with a suprahilar depression, moderately to strongly dextrinoid, moderately to strongly verrucose, warts high and isolated. – Basidia 34–45 × 8.5–12 µm, 4-spored, clavate. Older basidia developing a pale olivaceous to brownish yellow pigment in 3 % KOH. – Lamellar trama hyphae yellow, covered with abundant round or elongate brown granules. – Cortina incrusted with small sand-brown granules. – Veil hyphae granular-incrusted or smooth. – Stipe apex hyphae: outer hyphae yellow, smooth or covered with round or elongate sand-brown granules; inner hyphae covered with abundant round or elongate sand-brown granules. – Hymenial cystidia absent. – Pileipellis simplex: epicutis with a well-developed gelatinous layer filled with numerous extracellular round or elongate sand-brown refractive granules, uppermost hyphae (veil) pale yellow, smooth or granular-

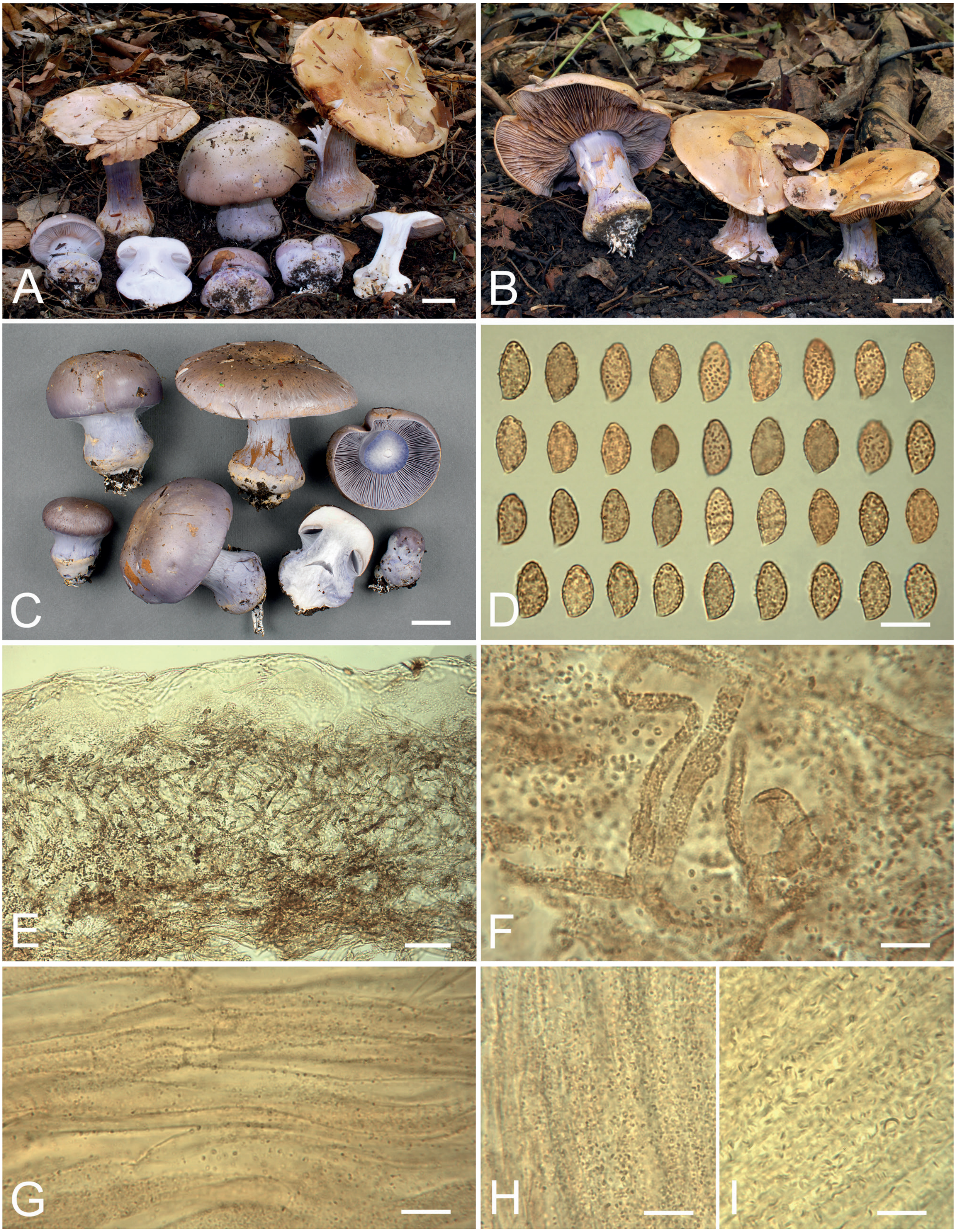

Fig. 8. *Cortinarius violaceoflavescens*. **A.** Basidiomata *in situ*, collection DAOM 984907 (holotype). **B.** Basidiomata *in situ*, collection QFB30983. **C.** Basidiomata, collection CMMF020759. **D.** Basidiospores. **E.** Pileipellis section. **F.** Epicutis details. **G.** Lamellar trama hyphae. **H.** Upper stipe hyphae (collection DAOM 984907). **I.** Upper stipe hyphae (collection CMMF020759). E–I In Melzer's reagent. Scale bars A–C 20 mm, D and F–I 10 µm, E 50 µm.

incrusted, 1.5–3 µm wide; hyphae in matrix 2–6 µm wide, mostly ascending, interwoven, heavily incrusted with refractive, round or elongate, sand-brown granules; basal hyphae 4–10 µm diam., interwoven to intertwined in bundles, yellowish brown, granule-incrusted, in places less so than the superior ones, some spirally incrusted; hypoderm absent. Granules seen in the different parts of the basidiomata in Melzer's absent in 3 % KOH. – Clamp connections present in all tissues. – Macrochemical reaction: pale yellow with 10 % KOH on context, brownish or yellowish on pileus, pinkish on veil; no reaction with NH_4OH.

Etymology. – Referring to the rapidly yellowing violet pileus.

Habitat and distribution. – Gregarious to caespitose in deciduous or mixed forests of *Carya ovata*, *Carya cordiformis*, *Quercus rubra*, *Tsuga canadensis*, *Populus* sp., *Tilia* sp., and *Fagus grandifolia*, in calcareous and argillaceous soil, in the fall. Probably associated with *Carya* spp. Thus far only known from two locations in Quebec, Canada.

Additional material examined. – *Ibid.* (QFB30984; isotype). Sequences ex-isotype: MN751572 (ITS). – *Ibid.* (WTU-F-073586; isotype). – CANADA. Quebec, Laval, Boisé Sainte-Dorothée, in a mixed forest of *Quercus rubra*, *Carya ovata*, *Tsuga canadensis*, and *Populus* sp., 17 September 2014, *leg.* R. Lebeuf & A. Paul, HRL1825 (QFB30983, WTU-F-073585); Repentigny, in a deciduous forest of *Tilia* sp., *Fagus grandifolia*, *Carya ovata*, and *C. cordiformis*, in calcareous and argillaceous soil, 24 September 2018, *leg.* Y. Lamoureux, YL4402 (CMMF020759).

Notes. – The ITS sequence of one of the isotypes is distinct from other members of the Euphlegmacia, deviating from *Cortinarius delaportei* Rob. Henry (GenBank acc. no. NR_130215) by 30 substitutions and indels. *Cortinarius violaceoflavescens* is well characterized by its robust basidiomata, violet-grey pileus quickly turning yellow to greyish orange, prominent marginal bulb rounded or flattened at base, large amygdaloid basidiospores, and abundant extracellular and/or incrusting granular pigment present in the pileipellis, lamellar trama, and stipe hyphae in Melzer's reagent. The granules were not observed in 3 % KOH. In our phyloge-

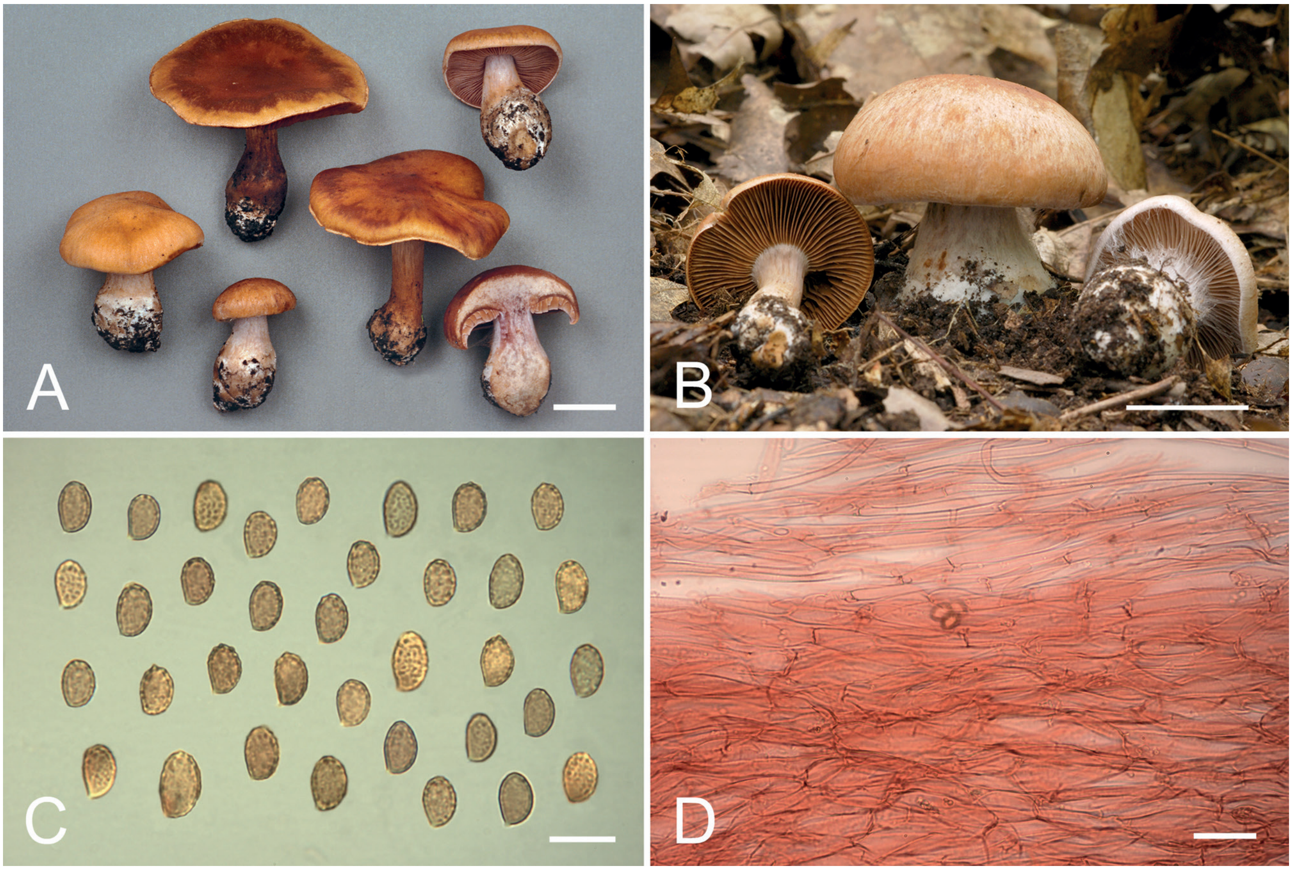

Fig. 9. *Cortinarius quercophilus*. **A.** Basidiomata, collection CMMF001672 (holotype). **B.** Basidiomata *in situ*, collection QFB29849. **C.** Basidiospores. **D.** Pileipellis section in SDS Congo Red. Scale bars A–B 20 mm, C 10 µm, D 25 µm.

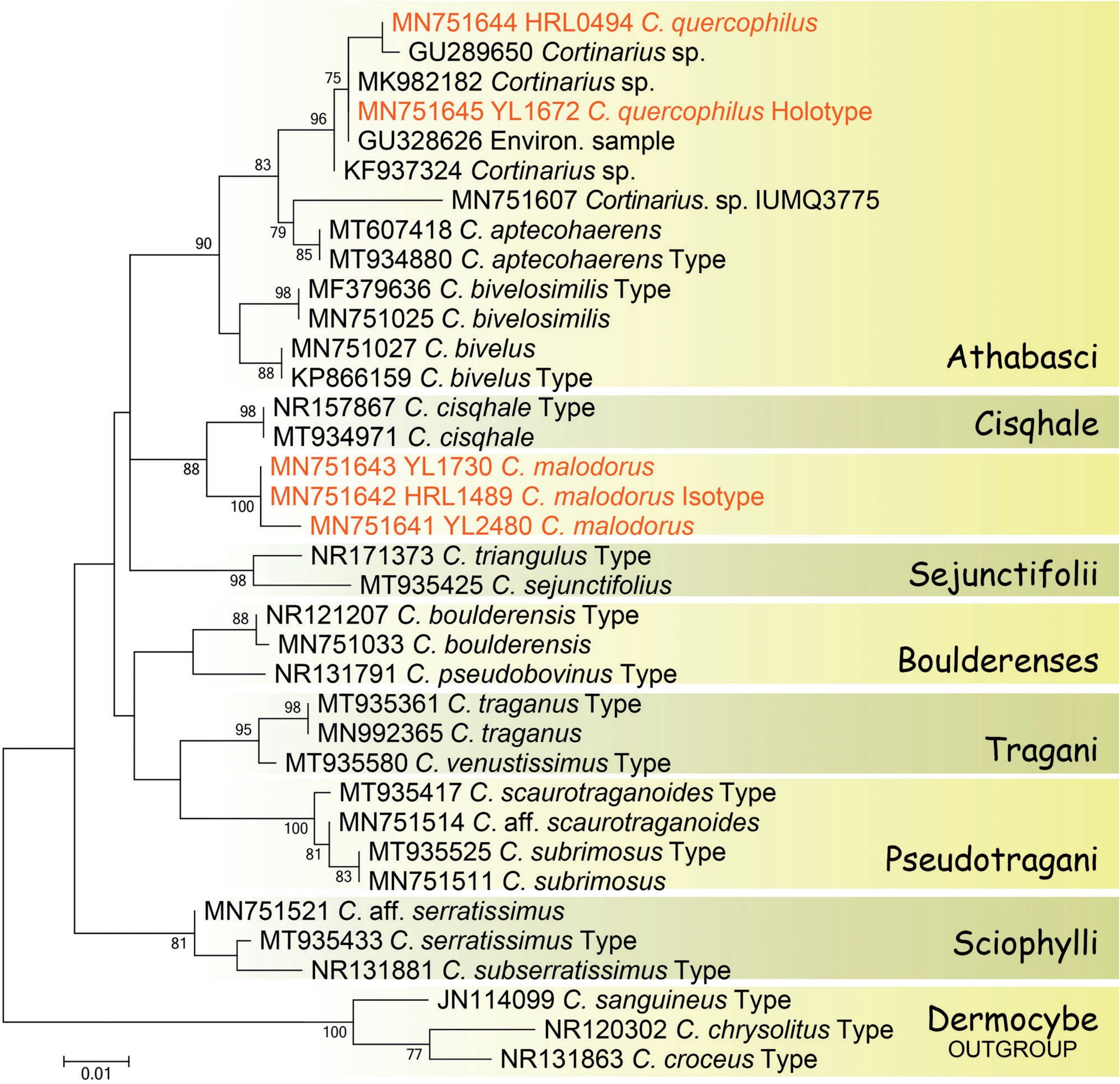

Fig. 10. Phylogeny of selected *Cortinarius* species and sections in subgenus *Telamonia*. The tree with the highest log likelihood (-lnL=-2214,7868) is shown, resulting from ML inference performed in MEGA7. For each node, the ML bootstrap (MLBS) if >70 is presented. Section designations following Liimatainen et al. (2020), new species highlighted in red, bar indicating the expected number of substitutions per site.

netic tree, *C. violaceoflavescens* forms with *Cortinarius serarius* Fr. and its sister species *C. delaportei* a small subclade within the combined sections *Elastici/Percomes* as interpreted by Liimatainen et al. (2014) (Fig. 6). Whereas species in these sections usually display yellowish or yellowish-brownish colors, except for some fugacious lilac or violaceous tints in lamellae or stipe apex in some species, the three species in this subclade show, at least in young age, distinct violet tints in the stipe, lamellae, and context for *C. delaportei*, in the pileus, stipe, and context for *C. serarius*, and in all parts for the here described *C. violaceoflavescens*.

In section *Caerulescentes*, *Cortinarius caerulescens* (Schaeff.) Fr. produces smaller and less coarsely ornamented basidiospores measuring 8–10 × 4.5–

5.5 µm, and *C. caesiocanescens* M.M. Moser also produces smaller spores (8.5–10.5 × 5–6 µm) and is found in coniferous forests of *Pinus* or *Picea*. *Cortinarius glaucocyanopus* Rob. Henry, in section *Riederi*, has a somewhat similar habit, but it is less robust, its pileus is pale ochraceous to cream yellow from the beginning, and its basidiospores are ellipsoid to subamygdaliform and wider, measuring on average 11.2–12.0 × 7.2–7.3 µm. All these similar species lack the granular pigment seen in *C. violaceoflavescens*.

Authors: R. Lebeuf, J. Landry, Y. Lamoureux & A. Paul

Basidiomycota, Agaricomycetes, Agaricales, Cortinariaceae

Cortinarius section *Athabasci*

Cortinarius quercophilus Y. Lamoureux, Lebeuf, A. Paul & J. Landry, **sp. nov.** – Figs. 9, 10
MycoBank no.: MB 839426

Diagnosis. – Pileus slightly viscid but soon dry, pale light orange, greyish orange to brownish orange, reddish brown at maturity when water-soaked, stipe clavate to bulbous, at times submarginate, growth in the summer, in July and August with *Quercus rubra*. Basidiospores 7.0–11.0 × 5.0–6.5 µm, on average 7.9 × 5.2 µm. Pileipellis duplex.

Holotypus. – CANADA. Quebec, Longueuil, in a deciduous forest of *Quercus rubra* with a few *Fagus grandifolia* and *Acer saccharum*, 16 July 1992, *leg.* Y. Lamoureux, YL1672 (CMMF001672; holotype). Sequences ex-holotype: MN751645 (ITS).

Description. – Pileus 30–90 mm in diam., hemispherical, convex then applanate, slightly viscid but soon dry, slightly hygrophanous, light orange, greyish orange to brownish orange (4½A4, 5½A5, 5½B4, 6C7, 6C8), reddish brown (around 8D7) at maturity when water-soaked, with brown (7D7, 7F7) innate fibrils and watery marks; margin inflexed to deflexed, then applanate and undulating, adorned with white fibrillose veil remnants. – Lamellae sinuate to emarginate, close to subdistant, 5–8 mm broad, light brown to violaceous brown with a whitish margin, then rusty brown from spores. – Cortina white. – Stipe 37–85(–110) mm long, 6–18 mm at apex, 12–30 mm at base, clavate to bulbous, at times submarginate, fibrillose, apex greyish, sometimes violaceous in young specimens, below pale brownish yellow to greyish orange, with age darkening to brownish orange, adorned with white mycelium at base. – Universal veil white, mostly persistent at bulb rim. – Context thick, marbled, orange-white to pale brownish orange in pileus, greyish to violaceous in upper stipe, pale brownish orange below. – Odor earthy. – Taste earthy. – Exsiccatae dark brown (7F7, 8F5). (Microscopic exam in Melzer's reagent) – Basidiospores [121/4/2] 7.0–8.5(–11.0) × 5.0–5.5(–6.5) µm, av. 7.9 × 5.2 µm, Q=1.27–1.80, Q_{av}=1.50, ellipsoid, finely to moderately verrucose, moderately dextrinoid. – Basidia 27–34 × 8–9 µm, 4-spored, clavate; developing a brownish yellow pigment with age in Melzer's and 3 % KOH. – Lamellar trama hyphae pale yellow, smooth. – Stipe apex hyphae yellow, smooth. – Hymenial cystidia absent. – Pileipellis duplex: epicutis moderately thick to thick, of repent weakly gelatinized hyphae 3–8 µm wide, smooth, pale yellow; hypoderm present, well differentiated or not, hyphae 4–18 µm wide, subparallel, smooth, darker yellow, very pale brown in KOH. – Clamp connections present in all tissues. – Macrochemical reaction: grey-brown with 10 % KOH on context, blackish on pileus.

Etymology. – Referring to the ectomycorrhizal association with *Quercus*.

Habitat and distribution. – Solitary or in groups of a few basidiomata under *Quercus rubra*, in various types of soil, in summer (July, August). Relatively frequent, following the distribution of its host tree in southeastern Canada and northeastern USA. Known from Quebec, Canada. Also known from the States of Massachusetts, Michigan, and New York in the USA, based on ITS sequence data. One ITS sequence from Colombia, in South America, is also a close match to *C. quercophilus* and might represent this species, but details about the collection are lacking.

Additional material examined. – CANADA. Quebec, Notre-Dame-de-l'Île-Perrot, in a deciduous forest of *Quercus rubra* and *Fagus grandifolia*, in argillaceous soil, 8 August 2010, *leg.* R. Lebeuf & A. Paul, HRL0494 (QFB29849); Saint-Narcisse, Parc de la rivière Batiscan, trail Le Buis, in a deciduous forest of *Fagus grandifolia* and *Quercus rubra*, 26 July 2021, *leg.* R. Lebeuf & A. Paul, HRL3376 (R.L.); Saint-Stanislas, Parc de la rivière Batiscan, trail La Gélinotte, in a deciduous forest of *Quercus rubra* and *Fagus grandifolia*, 30 July 2021, *leg.* R. Lebeuf & A. Paul, HRL3382 (R.L.); *ibid.*, HRL3383 (R.L.).

Notes. – The ITS sequence of the holotype is distinct from other members of subgenus *Telamonia*, section *Athabasci*, deviating from *Cortinarius aptecohaerens* Rob. Henry (GenBank acc. no. MT934880) by 14 substitutions and indels (Fig. 10). *Cortinarius quercophilus* displays three unusual characters for a member of subgenus *Telamonia*: it grows in the summer, in July and August; the bulbous to submarginate stipe and slightly viscid pileus are characters that are associated with phlegmacioid fungi, whereas the hygrophaneity, dull reaction to KOH and ellipsoid basidiospores are rather

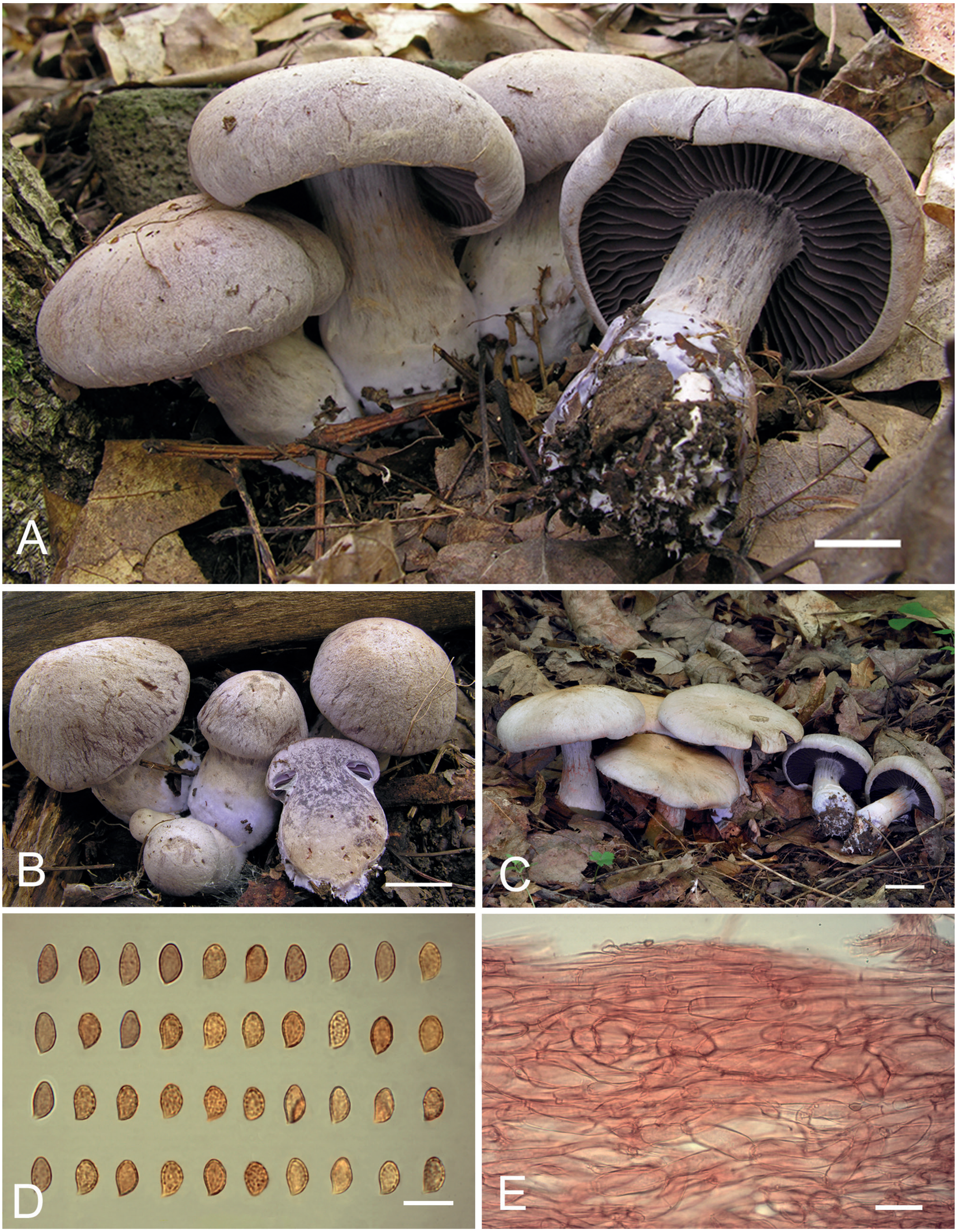

Fig. 11. *Cortinarius malodorus*. A–B. Basidiomata *in situ* from same site as holotype (collection not conserved). **C.** Basidiomata *in situ*, collection CMMF024763 (holotype). **D.** Basidiospores. **E.** Pileipellis section in SDS Congo Red. Scale bars A–C 20 mm, D 10 µm, C 25 µm.

characteristic of subgenus *Telamonia*; and it usually grows solitary or in small groups of a few individuals, rarely more. Morphologically, it shows characters consistent with section *Athabasci* as defined by Niskanen et al. (2015) (i.e., subhygrophanous pileus, clavate to bulbous stipe), whereas other characters are disparate (i.e., greyish orange pileus).

Authors: R. Lebeuf, J. Landry, Y. Lamoureux & A. Paul

Basidiomycota, Agaricomycetes, Agaricales, Cortinariaceae

Cortinarius* subgenus *Telamonia

Cortinarius malodorus Y. Lamoureux, Lebeuf, A. Paul & J. Landry, **sp. nov.** – Figs. 10, 11
MycoBank no.: MB 839425

Diagnosis. – Characterized by its pale violet to purple pileus and stipe when young, dark purple to dark violaceus distant and broad lamellae, abundant pale yellow universal veil, pale violet mycelium, unpleasant odor of rancid peanuts, and early growth in deciduous forests of *Quercus* and *Carya* in argillaceous soil. Basidiospores measuring 6.5–9 × 4.2–5.0 µm, on average 7.8–4.6 µm. Pileipellis duplex. Different from *C. camphoratus* (Fr.) Fr., which also has an unpleasant odor, but is associated with conifers, produces smaller basidiospores, and has a poorly differentiated hypoderm.

Holotypus. – CANADA. Quebec, Boucherville, 45°36’15.5”N, 73°23’49.0”W, 46 m a.s.l., in a deciduous forest of *Quercus rubra* and *Carya ovata*, 14 July 2013, *leg.* R. Lebeuf & A. Paul, HRL1489 (CMMF024763; holotype).

Description. – Pileus 70–120(–150) mm in diam., convex then plano-convex, dry, matted-fibrillose by pale yellow fibrils (4A3) on a pale violet to violet-grey background (17B2, 17½A2, 18A2), when very fresh sometimes with purple watery streaks, with age smoother, orange-grey (5AB2), concolorous at margin; margin involute to incurved, remaining so for a long time, undulating with age, adorned with veil remnants. – Lamellae sinuate to emarginate, distant, broad (6–9 mm), dark purple to dark violet (14F5, 17F5, 18A6) and remaining so for a long time. – Cortina white. – Stipe 40–70 mm long, 11–15 mm at apex, 18–22 mm at base, bulbous, fibrillose, greyish violet (18B2½) with darker violet streaks, below apex covered with the fibrillose pale yellow (4A3) universal veil, at base covered with pale violet mycelium turning dark violet when bruised. – Context thick, dark violet-marbled in the pileus and upper stipe, pale yellow (4A3) at stipe base. – Odor unpleasant, of rancid peanuts, stronger in lamellae at maturity. – Taste unpleasant. – Exsiccatae greyish brown (6E3½). (Microscopic exam in Melzer’s reagent) – Basidiospores [120/4/2] (6.5–)7.0–8.5(–9.0) × 4.2–5.0 µm, av. 7.8 × 4.6 µm, Q=1.44–2.00, Q_{av}=1.69, ellipsoid–amygdaliform, ellipsoid, with a suprahilar depression, finely to moderately verrucose, weakly or not dextrinoid. – Basidia 30–45 × 7–8 µm, 4-spored, narrowly clavate; in Melzer’s reagent and 3 % KOH often brownish yellow or olive yellow, with or without blackish granules. – Lamellar trama hyphae pale yellow, agranular. – Stipe apex hyphae pale yellow, agranular, aguttulate. – Hymenial cystidia absent. – Pileipellis duplex: epicutis thin to moderately thick, made of 3–10 rows of repent hyphae 3–8 µm wide, smooth, pale yellow to pale olive yellow; hypoderm present, hyphae 8–25 µm wide, smooth, pale olive yellow. – Clamp connections present in all tissues. – Macrochemical reaction: greyish with 5 % KOH on context and pileus.

Etymology. – Referring to the unpleasant odor.

Habitat and distribution. – In small to large groups in forests of *Quercus rubra*, *Q. macrocarpa*, and *Carya ovata* in low ground, in argillaceous soil, in summer (July, August). Known only from the south shore of the island of Montreal, in Quebec, Canada.

Additional material examined. – *Ibid.* (QFB29870; isotype). Sequences ex-isotype: MN751642 (ITS). – CANADA. Quebec, Longueuil, in a deciduous forest of *Quercus rubra* and *Carya* sp., in argillaceous soil close to a dried pond, 8 August 1992, *leg.* Y. Lamoureux, YL1730 (CMMF001730); *ibid.* 14 August 1995, leg. YL2480 (CMMF002480).

Notes. – The ITS sequence of the isotype is distinct from other members of subgenus *Telamonia*, deviating from its closest relative *Cortinarius cisqhale* Bojantchev (GenBank acc. no. NR_157867) by 14 substitutions and indels (Fig. 10). *Cortinarius malodorus* is easily recognized in the field by its overall violet to purple colors, distant and broad dark purple to dark violet lamellae, pale yellow universal veil, early growth in deciduous forests of *Quercus* and *Carya* in argillaceous soil, small basidiospores and, above all, its unpleasant odor of rancid peanuts. It has been observed regularly for almost thirty years in its restricted location. It is genetically close to *C. cisqhale*, described from the west coast of North America by Bojantchev (2013) and type species of the recently created section *Cisqhale* (Niskanen et al. 2020). The phylogenetic placement of *C. malodorus* in section *Cisqhale* is unlikely because its macromorphological characters (violet matted-fibrillose pileus, dark violet to dark purple lamellae, bulbous stipe, violet to pale

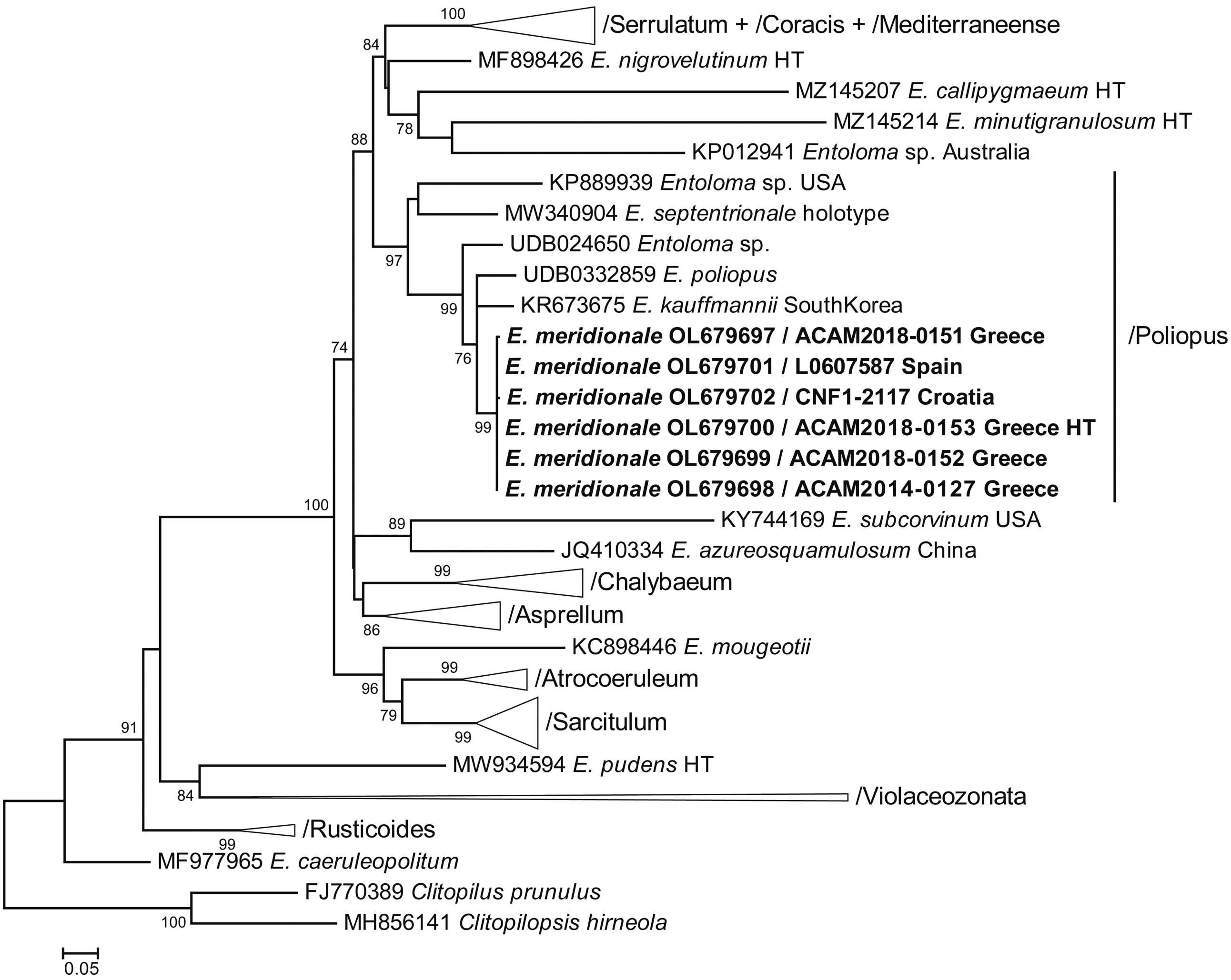

Fig. 12. Phylogeny of *Entoloma* subgenus *Cyanula*, depicting the relationship of *E. meridionale* within clade */Poliopus*, reconstructed from an ITS dataset. The topology is the result of ML inference performed with PhyM 3.1 with the following settings: GTR+I+G model of nucleotide substitution, gamma distribution of 10 rate categories, and tree topology search as SPR (subtree pruning and regrafting). Branch support was tested using the non-parametric, Shimodaira-Hasegawa version of the approximate likelihood-ratio test (SH-aLRT). For each node, the PhyML SH-aLRT support value, if >50, is presented. Main clades within the subgenus are collapsed. Bar indicating expected number of changes per site; HT = holotype.

yellow context, pale yellow universal veil, unpleasant odor) are not consistent with those defining that section, and it also lacks an olivaceous pigment in the lamellae. A few other species of *Telamonia*, all with larger basidiospores, have similar colors: *Cortinarius alboviolaceus* (Pers.) Fr. and *Cortinarius acutispissipes* Rob. Henry have an earthy odor and grow under *Betula* and *Populus*; *Cortinarius odoritraganus* Niskanen, Liimat. & Ammirati, much similar and associated with *Quercus*, has a pleasant odor of pear and a thick universal veil forming a membranous sheath on the stipe base; *Cortinarius traganus* (Fr.) Fr., with an odor of pear, has a yellow-brown to orange-brown context and grows with conifers; *Cortinarius camphoratus* (Fr.) Fr., with an unpleasant odor like *C. malodorus*, is restricted to coniferous forests; and *Cortinarius torvus* (Fr.) Fr. and a yet-to-be-described North American (NAm) vicariant (Landry et al. 2021) are mostly found under *Fagus* and also possess distant purplish lamellae when young, but they have a pleasant odor, a thick membranous whitish universal veil forming a pseudo-annulus on the stipe, and larger basidiospores: 9–11 × 5–7 µm for *C. torvus* (Brandrud et al. 1990–2014), 8–10.5 × 5–6.5 µm for the NAm vicariant (R. Lebeuf, unpubl. data).

Authors: R. Lebeuf, J. Landry, Y. Lamoureux & A. Paul

Fig. 13. *Entoloma meridionale*. **a.** Habit, blue form. **b.** Habit, pink form. **c.** Basidiospores. **d.** Cheilocystidia. a, c, d, collection ACAM 2018-0151; b, collection CNF 1/2117. Scale bars 10 µm.

Basidiomycota, Agaricomycetes, Agaricales, Entolomataceae

Entoloma meridionale Mešić, Vila, Polemis, Noordel. & Dima, **sp. nov.** – Figs. 12, 13

= *Entoloma reinwaldii* sensu Mešić & Tkalčec *in* Mycotaxon 105: 296 (2008).
Mycobank No.: MB 840119

Holotypus. – GREECE. Peloponnese, Korinthos, Onnia Mountains, 37°52'21"N, 22°55'27"E, 337 m a.s.l., 29 December 2018, *leg.* M. Gkilas MG 1640 (ACAM 2018-0153; holotype). Sequences ex-holotype: OL679700 (ITS).

Description. – Basidiomata medium-sized, collybioid. – Pileus 13–40 mm in diam., truncately conical or hemispherical, expanding to convex or plano-convex, with flattened and sometimes weakly umbilicate, rarely subumbonate center, greyish black, grey-blue or blue, or pink, lilac pink, orangish pink or brownish especially at center, not distinctly hygrophanous, not translucently striate in the blue variant, or at most in old specimens which then develop a translucent and sulcate margin, but distinctly so, up to 3/4 of radius in pink population, minutely, densely squamulose in central part, towards margin radially fibrillose. – Lamellae unequal with numerous lamellulae, adnate to adnexed, emarginate, moderately distant to fairly crowded, sometimes relatively thick, whitish or with bluish or lilac reflections, then pure pink, with entire or irregular, concolorous or in part tinged blue edge, which sometimes develops with age; in pink specimens the lamella edge may have a pinkish tinge. – Stipe 35–60 × 1.5–3 mm, central, (sub)cylindrical, straight to curved, sometimes slightly broadened towards base blue, concolorous with pileus, or dirty pink in pink variants; smooth or minutely pruinose (lens!), particularly at apex, polished or with scattered appressed fibrils, white tomentose at base. –

Context thin. – Odor weak, pleasant, indistinct. – Taste mild, somewhat fruity. – Basidiospores (9.5–)10.0–12.5 × (6.5–) 7.0–9.0 µm, av. 10.1–11.3 × 7.1–7.9 µm, Q=1.2–1.7, Q_{av}=1.4–1.5, heterodiametrical, (5–)6–8(–9)-angled in side-view. – Basidia 25–40 × 9–15 µm, 4-spored, subcylindrical to clavate. – Lamellar edge usually sterile, in few cases fertile in the same collection, concolorous or getting a blue tinge with age. – Cheilocystidia in dense clusters, born on septate hyphae, terminal elements 14–70 × 6–18 µm, narrowly clavate to subcylindrical, non-pigmented or with faint blue intracellular pigment. – Pileipellis a cutis of cylindrical hyphae, up to 18 µm wide at margin, at center a trichoderm to almost hymenidermal, made up of inflated elements, 23–50 × 12–28 µm. Pigment intracellular, blue or pink. – Stipitipellis a cutis of thin-walled, cylindrical hyphae, with (especially at apex) bundles of patent cylindrical terminal endings ("caulocystidia"). – Clamp connections absent from all tissues.

Etymology. – From "meridionalis" (Latin), referring to the southern distribution of the species.

Habitat and distribution. – Terrestrial in Mediterranean shrub vegetation or thermophilous pine forests; with species like *Arbutus unedo*, *Pinus halepensis*, *Cistus monspeliensis*, *C. salviifolius*, *C. incanus*, *C. creticus*, *Erica arborea*, *Juniperus oxycedrus* subsp. *macrocarpa*, *Pistacia lentiscus*, and *Phillyrea* sp. Widespread in the Mediterranean area—known from Croatia, Greece, and Spain.

Additional material examined. – CROATIA. Istria, Premantura peninsula, near the town of Pula, 25 m a.s.l., 2 December 2000, *leg.* Z. Tkalčec & A. Mešić (CNF 1/2111, 1/2117) (pink variants). –GREECE. Peloponnese, Korinthos, Onnia Mountains, 337 m a.s.l., 5 December 2014, *leg.* M. Gkilas, MG122 (ACAM 2014-0127); *ibid.*, 23 December 2018, *leg.* M. Gkilas MG1621 (ACAM 2018-0151); *ibid.*, 23 December 2018, *leg.* M. Gkilas, MG1623 (pink variant) (ACAM 2018-0152). – SPAIN. Sierra Morena, Jaén, 370 m a.s.l., under *Arbutus unedo*, among mosses and grasses, 7 March 2014, *leg.* J. Gómez (L-0607587).

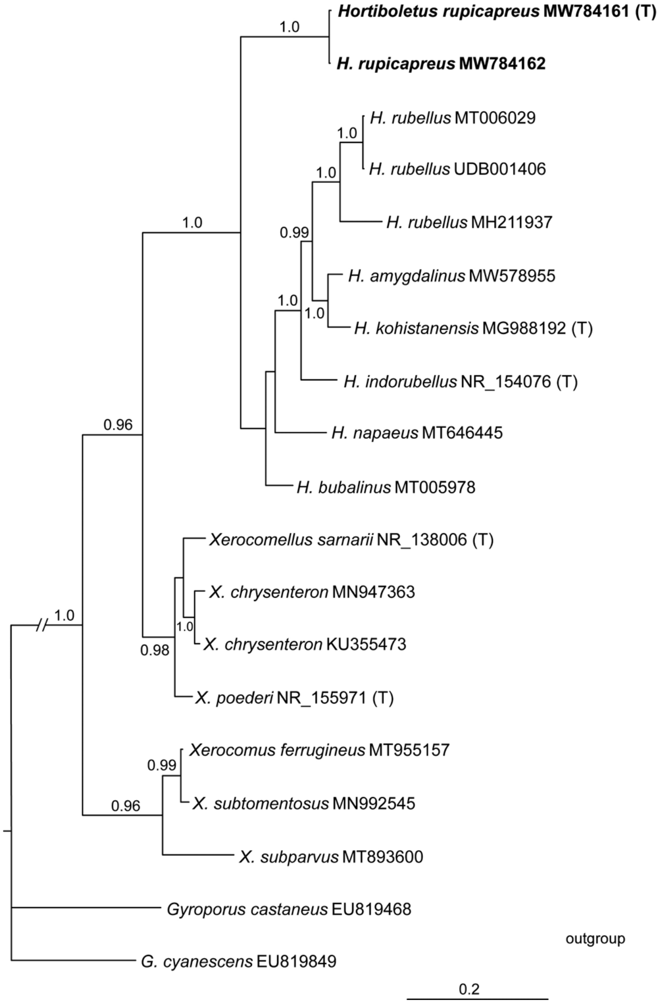

Fig. 14. Phylogeny of *Hortiboletus* reconstructed from an ITS dataset. The topology is the result of Bayesian inference (BI) performed with MrBayes. For each node, the BI posterior probability (BIPP) if >0.95 is presented above/below the branch leading to that node. Bar indicating the expected number of nucleotide changes per site.

Notes. – *Entoloma meridionale* is a rather striking blue species with pink variants. It is further characterized by having a polished or at most innately fibrillose stipe, and medium-sized basidiospores, on average well over 10 µm long, which enables differentiation from similar species such as *E. erhardii* Noordel., Dima, Svetash., Læssøe & Kehlet (with smaller basidiospores) and *E. corvinum* (Kühner) Noordel. lookalikes with a non-polished stipe with dark blue fibrils. Interestingly, the lamellar edge is either concolorous or developing a blue pigment in the cheilocystidia, a phenomenon this species shares with for example *E. violaceoserrulatum* Noordel., Brandrud, Morozova & Dima. *Entoloma meridionale* was first found in its pink variant, and was reported as *E. reinwaldii* from Croatia by Mešić & Tkalčec (2008) based on morphological analysis of two collections made on the Istrian peninsula. Later, it was also discovered in Greece. However, molecular evidence based on ITS showed that the Croatian material was not conspecific with *E. reinwaldii*, but belonged in a very distant clade, close to *E. poliopus* (Romagn.) Noordel. (Fig. 12). The ITS sequences appeared to be identical with collections from Spain and Greece of a so far unpublished, blue colored species within subgenus *Cyanula*. The earlier reported Croatian specimens

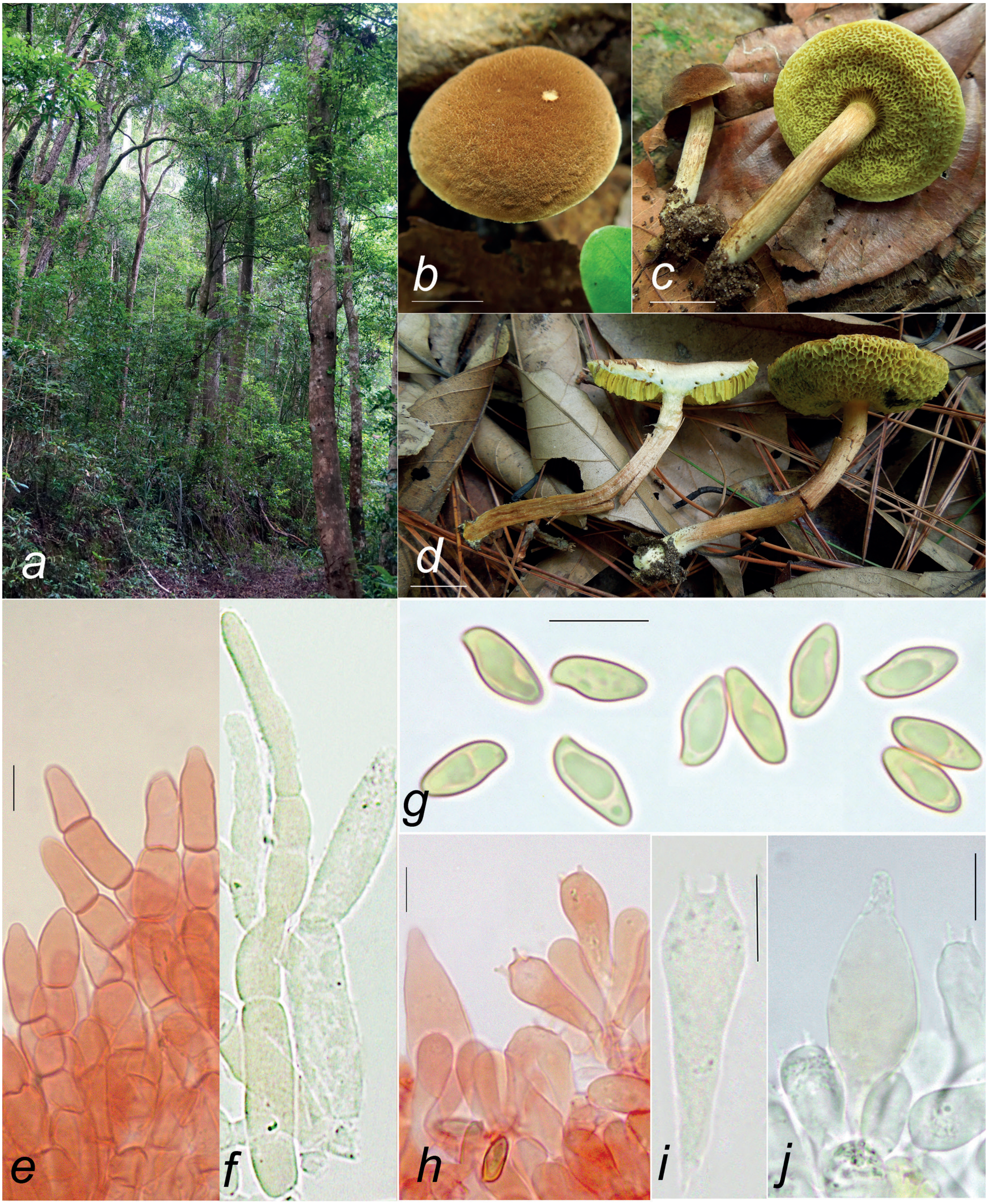

Fig. 15. *Hortiboletus rupicapreus*, collections LE 312677 (holotype), LE 312678 (paratype). **a.** Type locality in Kon Ka Kinh National Park, Vietnam. **b–d.** Basidiomata *in situ*. **e.** Pileipellis of young specimen. **f.** Pipeipellis of mature specimen. **g.** Basidiospores. **h.** Caulobasidia and caulocystidia. **i.** Basidium. **j.** Cheilocystidia. Scale bars b–d 1 cm, e–i 10 µm.

(Mešić & Tkalčec 2008) apparently were just a pink variant of this species. Pink variants occur frequently and are widespread all over the ITS–LSU tree of *Entoloma* subgenus *Cyanula*, and thus far at least a dozen species have shown to have a pink variant besides a variant with either blue, violaceous, or brown colored basidiomata (B. Dima et al., unpubl. data). *Entoloma meridionale* belongs to a rather diverse /Poliopus clade (Dima et al. 2021) with several closely related blue species, in gross morphology similar to either *E. cyanulum* (Lasch) Noordel. or *E. poliopus*. This clade includes more undescribed species, which will be formally published in due course.

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Basidiomycota, Agaricomycetes, Boletales, Boletaceae

Hortiboletus rupicapreus Svetash., A.V. Alexandrova, O.V. Morozova & T.H.G. Pham, **sp. nov.** – Figs. 14, 15
MycoBank no.: MB 839620

Holotypus. – VIETNAM. Gia Lai Province, Mang Yang District, Kon Ka Kinh National Park, A Yun, 14°13'11.70"N, 108°19'32.40"E, 1200 m a.s.l., on soil in tropical mountain forests dominated by trees of Anacardiaceae, Fagaceae, Meliaceae, Myrtaceae, Theaceae, ridges on slopes, 18 May 2016, *leg.* A.V. Alexandrova (LE 312677; holotype). Sequences ex-holotype: MW784161 (ITS), MW760391 (LSU), MZ424894 (*tef1*).

Description. – Basidiomata small to medium-sized, xerocomoid. – Pileus 15–40 mm in diam, first hemispherical, then convex, flattened with age, sometimes slightly depressed in the center; fleshy; margin initially curved downwards, then straight, not or only slightly extending beyond the tubes; surface dry, finely suede to velvety or felted, cracking into tiny squamules; color varying from buff, beige, and pale ochraceous brown to yellow brown and brown (4B6–8, 5A3–5, 5B4–6, 5–5–7, 6A3–4); context 3–7 mm thick in the pileus center, yellowish (1A2–3), slightly changing to light bluish near the tubes when bruised. – Hymenophore slightly depressed around the stipe apex, tubes 2–5 mm in length, intense lemon yellow (2A5–8) to dark yellow (3A6–8, 3B5–8) with a greenish tint, turning bluish when bruised; pores angular, 1–1.5(–2) mm in diam., with age becoming radially elongated up to 2–2.5 mm in length. – Stipe 30–70 × 4–7 mm, almost cylindrical, sometimes curved, solid; surface dry, minutely pruinose especially at the apex, longitudinally fibrillose, brownish, concolorous with the pileus or slightly lighter, whitish at the base; context firm, fibrous, brownish with reddish tinge, darker than the pileus context, unchanging or slowly turning light bluish in the stem apex, without red dots at the base. – Odor weak. – Taste not reported. – Basidiospores (8.5–)9.4–10(–11.2) × (3.7–)4.1–4.3(–4.7) µm, Q=(2.1–)2.3(–2.6), ellipsoid–subfusoid, tapering towards the apex, inequilateral in side view, with a weak suprahilar depression, olivaceous-yellow-brown in KOH, smooth. – Basidia 24–38 × 8–11.5 µm, 4-spored, clavate. – Hymenial cystidia various in shape and size, from lageniform to fusoid, ventricose or almost clavate, 30–60 × 11–15 µm, thin-walled, colorless or yellowish in KOH. – Hymenophoral trama boletoid. – Pileipellis a physalo-palisadoderm, 90–120 µm thick, composed of chains of thin-walled (< 0.5 µm) hyphae 6–15 µm wide, almost colorless or slightly yellowish in KOH; pileipellis elements almost smooth to finely incrusted (in Congo Red dissolved in NH_4OH); pileipellis hyphae of young specimens consising of chains with rather short almost smooth cells 12–16 × 7.5–9.5 µm with subfusiform, lageniform, or clavate terminal cells 12–27 × 6–12 µm, whereas the cells of pileipellis hyphae of mature and old specimens seemingly becoming thinner, longer, more or less incrusted, and tending to form tufts, terminal cells 17–50 × 5.5–10.5 µm, subfusiform, narrow clavate or subcylindrical with obtuse apex. – Stipitipellis of the stipe apex a caulohymenium of basidiolae-like cells with scattered caulobasidia 23–30 × 7–10 µm, and caulocystidia 23–56 × 10–19 µm, lageniform, fusoid, or subcylindrical. – Clamp connections absent in all tissues.

Etymology. – "*rupicapreus*" (Latin), equivalent of the English word "chamois", referring to the yellowish-brown color of chamois leather and the characteristic suede surface.

Habitat and distribution. – Solitary and in small groups on soil in tropical mountain evergreen forests. Thus far only known from Vietnam.

Additional material examined. – VIETNAM. Gia Lai Province, Mang Yang District, Kon Ka Kinh National Park, A Yun, 14°12'18.68"N, 108°18'58.72"E, 1,000 m a.s.l., on soil in pine plantations of *Pinus kesiya* with some Fagaceae, 15 March 2016, *leg.* A.V. Alexandrova (LE 312678).

Notes. – *Hortiboletus rupicapreus* is characterized by the light brownish basidiomata, velutinous cap surface finely cracking on tiny squamules, rather large radially elongated pores, and small basidiospores. Basidiomata of *H. rupicapreus* look quite similar to other tropical species, such as *H. amygdalinus* Xue T. Zhu & Zhu L. Yang, *H. indorubellus* K. Das, D. Chakr., Baghela, S.K. Singh &

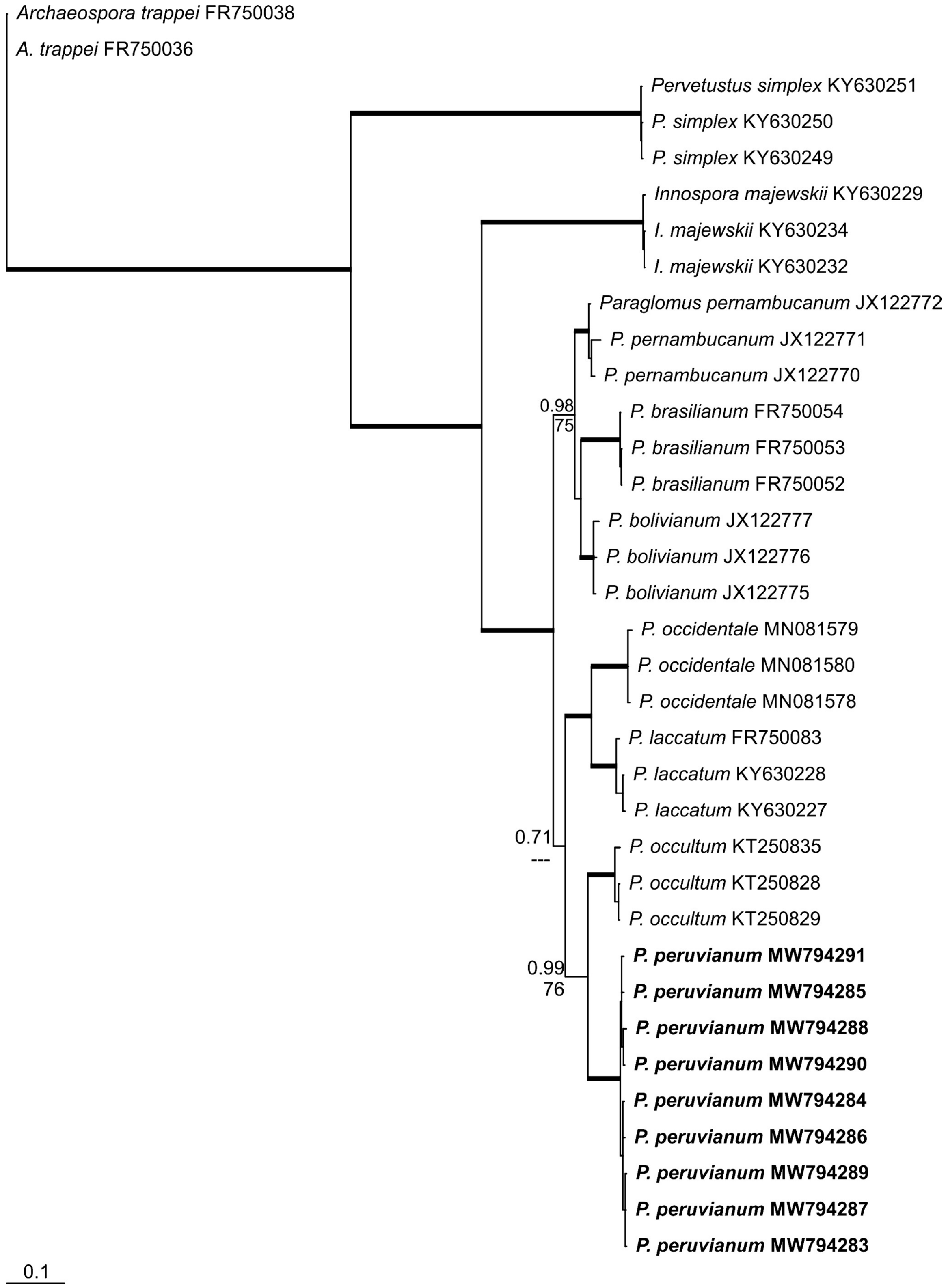

Fig. 16. Phylogeny of Paraglomeromycetes reconstructed from an SSU–ITS–LSU rDNA dataset. For each node, BI posterior probability (BIPP) and ML bootstrap (MLBS) values if >70 are presented, as BIPP/MLBS. Thick branched represent clades with BIPP and MLBS >95. Sequences labeled with their GenBank accession numbers, newly generated sequences in boldface.

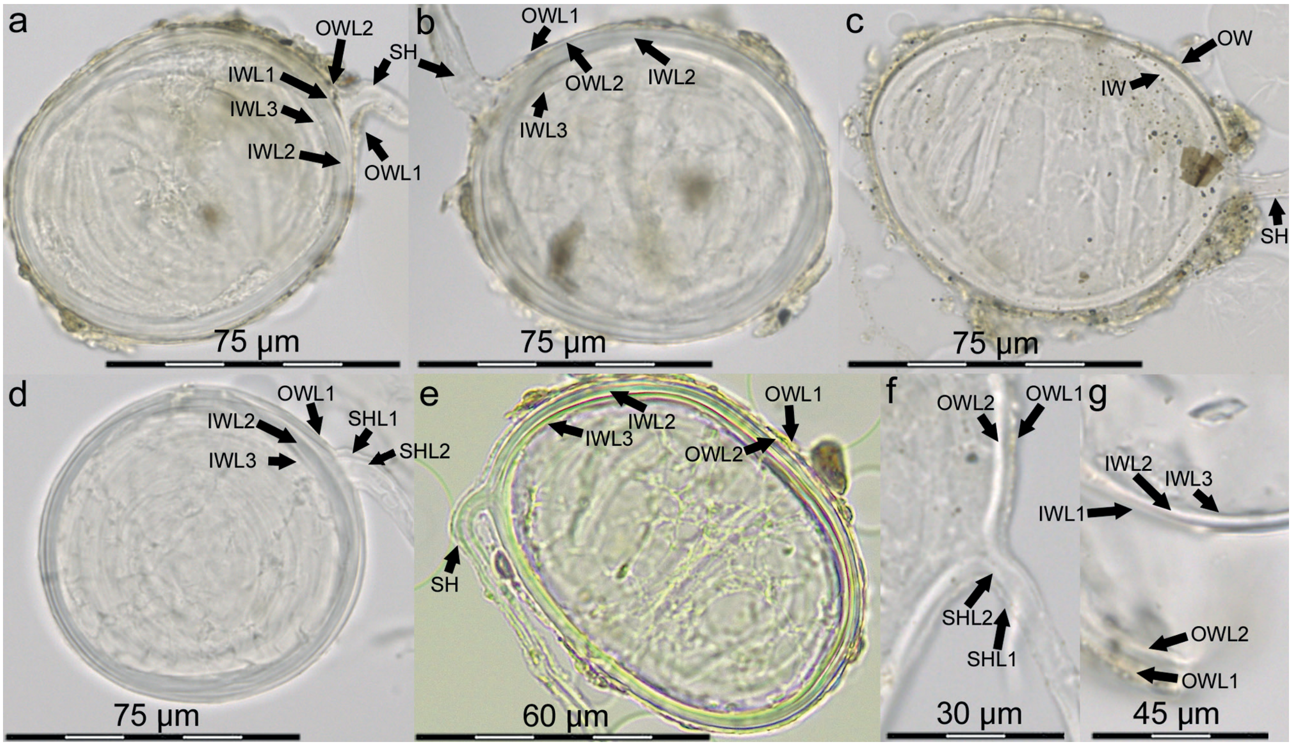

Fig. 17. *Paraglomus peruvianum*. **a–c.** Spores in PVLG with two walls, the outer wall (OW) and inner wall (IW), and their multiple layers (OWL1–3 and IWL1–3), often showing debris on the outer spore surface, adherent to degrading OWL1; subtending hyphae (SH) straight to usually recurved, formed by the continuation of OW towards the mycelia hyphae; spore pore at the spore base, generally closed by IW. **d.** OWL1 already completely degraded from OW, without any debris left on the spore surface; IWL3 flexible, visible inside the spore due to several circular folds. **e.** IWL3 staining yellowish to light yellow in 1:1 mixture of PVLG and Melzer's reagent. **f.** OW of a young, developing spore; OWL1 already degrading, showing a rough surface (also observable in Fig. 1a); OWL2 smooth, unit. **g.** Spore wall of a mature spore; IWL2 is thickest, whereas IWL1 and IWL3 are thin, flexible, and difficult to observe.

Dentinger, *H. kohistanensis* A. Naseer, S. Sarwar & A.N. Khalid, *H. napaeus* N.K. Zeng, H.J. Xie, S. Jiang & Zhi Q. Liang, and *H. subpaludosus* (W.F. Chiu) Xue T. Zhu & Zhu L. Yang. However, all of them have some reddish parts in basidiomata or at least a reddish-pinkish tint of the pileus/stipe surface. *Hortiboletus amygdalinus* (Wu et al. 2016), *H. indorubellus* (Das et al. 2016), *H. kohistanensis* (Naseer et al. 2019), and *H. subpaludosus* (Wu et al. 2016) are characterized by larger and/or wider basidiospores and often wider terminal cells of the pileipellis. Both *H. kohistanensis* and *H. subpaludosus* have basidiomata that are larger than those of *H. rupicapreus*. Compared to *H. rupicapreus*, *H. napaeus* (Xie et al. 2020) has basidiomata that are similar in size, but its pileus is pinkish, basidiospores are somewhat larger, measuring (8–)9–11(–13) × 4–5 μm, and pleurocystidia are wider (up to 19 μm). The species was previously reported "ad interim" by Pham et al. (2021), in a paper on the diversity of the boletoid fungi of the of protected areas of Kon Tum Plateau in Vietnam.

Authors: T.Yu. Svetasheva, A.V. Alexandrova, O.V. Morozova & T.H.G. Pham

Glomeromycota, Paraglomeromycetes, Paraglomerales, Paraglomeraceae

Paraglomus peruvianum Corazon-Guivin, G.A. Silva & Oehl, **sp. nov.** – Figs. 16, 17
MycoBank: MB 839204

Diagnosis. – Spores hyaline, measuring (60–)70–91(–102) × (60–)70–89(–95) μm in diam., with a bi- to triple-layered outer wall and a triple-layered inner wall. Differing from spores of *P. occultum* (C. Walker) J.B. Morton & D. Redecker by a significantly thicker inner wall.

Holotype. – PERU. San Martín State, El Dorado Province, Requena, 6°31'30"S, 76°45'38.38"W, 468 m a.s.l., coffee plantation, 22 October 2018, *leg.* M.A. Corzaon-Guivin (ZT Myc 64708; holotype). Sequences ex-holotype: MW794283–MW794291 (ITS).

Description. – Spores globose to subglobose, hyaline, oval to ovoid, bi-walled, (60–)70–91(–102) × (60–)70–89(–95) µm in diam., terminally or intercalary on cylindrical to slightly funnel-shaped subtending hyphae, singly in soils or rarely in roots. – Outer wall (OW) 2.3–3.9 µm thick, hyaline, bi- to triple-layered (OWL1–3); outer layer OWL1 short-lived, evanescent, 0.4–0.9 µm thick, often incorporating a large quantity of debris in degradation stages; OWL2 persistent, 1.5–2.2 µm thick; OWL3 flexible to semi-flexible, 0.4–0.8 µm thick, generally tightly adherent to OWL2, difficult to detect. – Inner wall (IW) 3.5–6.0 µm thick, composed of three tightly adherent layers (IWL1–3), but often only IWL2 is clearly observable; IWL1 0.5–1.0 µm thick, unit; IWL2 2.5–4.0 µm thick, often finely laminate; IWL3 0.5–1.0 µm thick, flexible, showing several folds in crushed and uncrushed spores, often staining yellowish to light yellow in Melzer's reagent. – Subtending hyphae of spores sometimes straight to often recurved or double recurved (C- to S-shaped), generally cylindrical to slightly funnel-shaped, to rarely flared or inflated, (12–)25–80 µm long, 6.5–11.5 µm broad at the spore base, usually tapering to 3.0–6.0 µm within a short distance to the spore base towards the mycelia hyphae; outer spore wall continuing in the subtending hyphae, while the inner wall seemingly forming *de novo* within the spore and closing the pore at the spore base. – Subtending hyphal wall 1.8–3.1 µm thick at the spore base tapering to 1.1–2.2 µm towards the mycelia. – Pore approximately 3.0–6.5 µm wide at the spore base, generally separated from the spore by the IW, or rarely, , when IWL1 and IWL2 reach into the subtending hyphae for a few µm, closed only by a septum arising from IWL3.

Etymology: Referring to Peru, the country from which the fungus was first reported.

Habitat and distribution. Thus far found in two agroforestry sites, a coffee plantation in Requena and an inka nut plantation in Barranquita, both located in the El Dorado Province, San Martín State, in the Peruvian Amazonia lowlands and adjacent low mountain ranges—up to 468 m a.s.l.

Additional material examined. – *Ibid.* (ZT Myc 64708; isotype). PERU. San Martín State, El Dorado Province, Barranguito, 6°44'19.64"S, 76°35'41.32"W, 321 m a.s.l., inka nut plantation, 22 October 2018, *leg.* M.A. Corzaon-Guivin (ZT Myc 66295).

Notes. – *Paraglomus peruvianum*, based on spore morphology and molecular phylogenetic data (Fig. 16), clearly belongs to the order Paraglomerales of the class Paraglomeromycetes (Wijayawardene et al. 2020). The new species can be distinguished from all other species in Paraglomerales by its spore wall structure. The most similar species are *P. laccatum* (Błaszk.) Renker, Błaszk. & Buscot, *P. occidentale* Corazon-Guivin, G.A. Silva & Oehl, and *P. occultum* (Mello et al. 2013, Corazon-Guivin et al. 2020). *Paraglomus peruvianum* and *P. occidentale* both have a substantially thicker inner wall, more precisely a thicker and finely laminate IWL2 (2.4–4.0 µm thick), compared to *P. occultum*, in which IWL2 is unit, and its total IW generally is <2.5 µm thick (1.2–2.0 µm, Morton & Redecker 2001, Corazon-Guivin et al. 2020). *Paraglomus peruvianum* and *P. occidentale* can be distinguished by the color reaction in Melzer's reagent: IWL3 stains yellowish to light yellow in *P. peruvianum*, whereas OWL1 stains yellow-grayish to grayish and OWL2 stains yellow to generally dark yellow in *P. occidentale* (Corazon-Guivin et al. 2020). The thickness and lamination of OWL2 is generally much more pronounced in *P. laccatum* (5.9–7.9 µm) than in *P. occidentale*, *P. occultum*, and *P. peruvianum*, and in any other *Paraglomus* sp. described so far (Błaszkowski 1988, Renker et al. 2007, Corazon-Guivin ez al. 2020). All other *Paraglomus* species might have at least one ornamented spore wall layer (Spain & Miranda 1996, Mello et al. 2013), or larger spores (Rose & Trappe 1980, Walker & Rhodes 1981, Oehl et al. 2011, Corazon-Guivin et al. 2020).

Nucleotide BLAST searches of generated rDNA sequences in NCBI GenBank resulted in *P. occultum* as closest match, with 91.3 % shared identity. Unidentified *Paraglomus* sequences related to *P. peruvianum* (>97 % shared identity) were found in rhizosphere soils and roots from maize cultivated in China (Zeng et al. 2014), roots and soil from paddy fields cultivated in China (Wang et al. 2015), and soil from switchgrass (*Panicum virgatum*) in Wisconsin, USA (Dirks & Jackson 2020). Our phylogenetic reconstruction of a partial SSU, ITS, and partial LSU rDNA dataset placed *P. peruvianum* in a clade sister to *P. occultum* (MLBS=76, BIPP=0.99). This clade (*P. occultum*, *P. peruvianum*) was retrieved as sister to (*P. laccatum*, *P. occidentale*) with moderate support from BI (BIPP=0.71) (Fig. 16).

Paraglomus peruvianum is known from San Martín State in Peru, isolated from the rhizosphere of coffee and the inka nut. However, sequences closely related to *P. peruvianum* (>97 % shared identity) were identified from maize and rice fields in China and from switchgrass fields in the USA, that is, in different continents and under different soil and climate conditions (Zeng et al. 2014, Wang

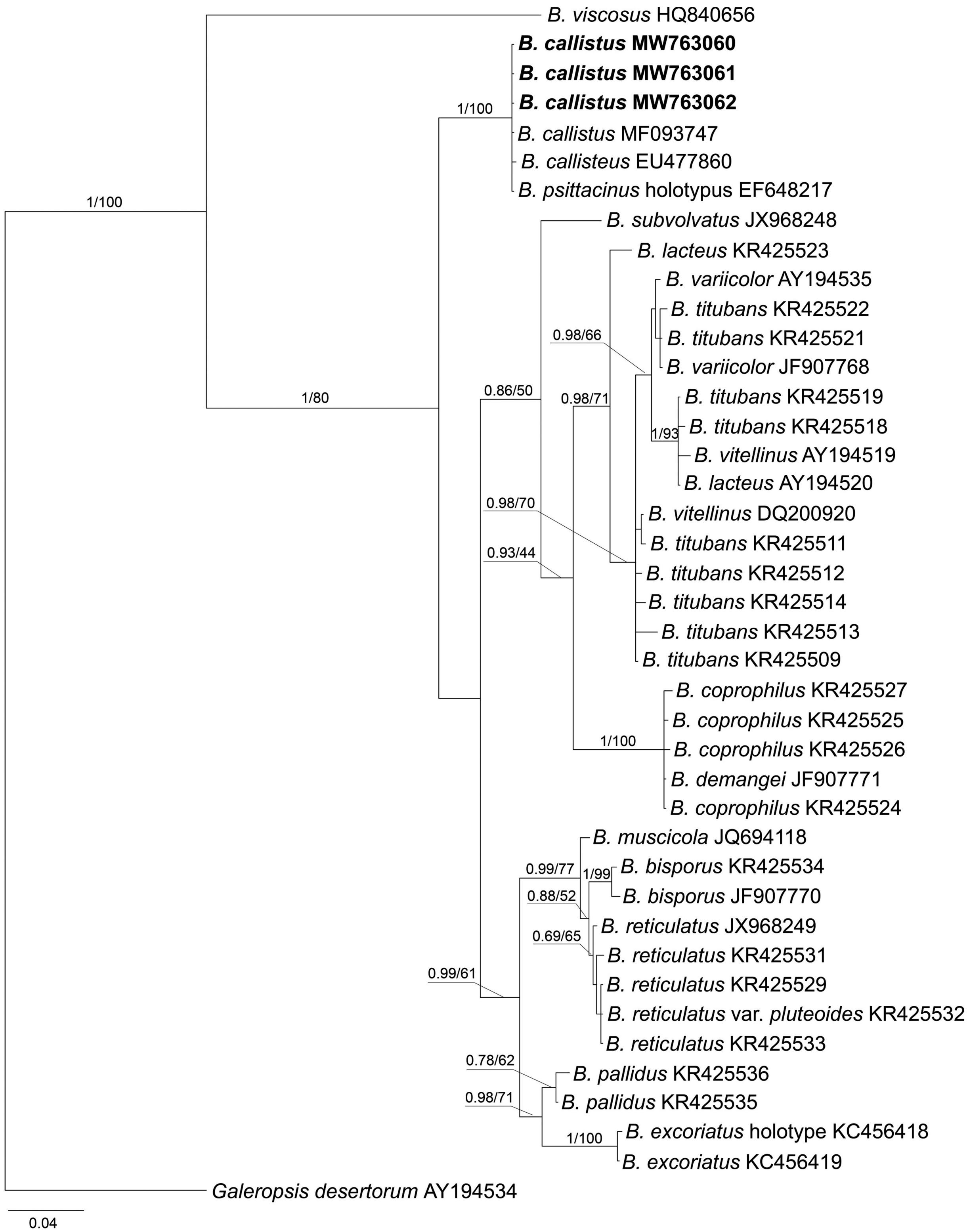

Fig 18. Phylogeny of *Bolbitius* reconstructed from an ITS dataset. The topology is the result of Bayesian inference (BI) performed with MrBayes. For each node, BI posterior probability (BIPP) and ML bootstrap (MLBS) values are presented above the branch leading to that node, as BIPP/MLBS. All tips labeled with taxon name and GenBank accession number, newly generated sequences in bold.

Fig. 19. *Bolbitius callistus*. **a–b.** Basidiomata *in situ*, collection LE 313564. **c–d.** Young basidiomata, collection LE F-331684. **e.** Mature basidioma, collection LE F-331684. **f.** Old basidioma and two very young ones with dark-colored pileus and distinctly bluish stipe, collection LE F-331684. **g.** Basidiomata *in situ*, collection LE F-331685. Scale bar 1 cm.

et al. 2015, Dirks & Jackson 2020). Species of Paraglomerales often have a worldwide distribution, from the cold and moist to hot and (semi-)arid regions around the globe (e.g., Mello et al. 2013, Oehl & Körner 2014, Al-Yahya'ei et al. 2017). More detailed studies are needed to show whether *P. peruvianum* also has a wide geographic distribution, in many agricultural and natural habitats around the world.

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Interesting taxonomical notes, new hosts, and geographical records

Basidiomycota, Agaricomycetes, Agaricales, Bolbitiaceae

Bolbitius callistus (Peck) Watling [as "*callisteus*"], Kew Bulletin 31(3): 592 (1977). – Figs. 18–21

Basionym. – *Agaricus callistus* Peck, Bulletin of the Buffalo Society of Natural Sciences 1: 52 (1873).

Synonyms. – *Galera callista* (Peck) Sacc., Sylloge Fungorum 5: 865 (1887).

Pluteolus callistus (Peck) Peck, Annual Report on the New York State Museum of Natural History 46: 140 (1894).

Bolbitius gloiocyaneus Atk., Annales Mycologici 6: 54 (1908).

Bolbitius psittacinus Hauskn., Antonín & Polčák, Czech Mycology 59(1): 2 (2007).

Material examined. – RUSSIA. Novgorod Region, vicinity of Krasnofarforny settlement, floodplain oak forest with *Tilia*, *Ulmus*, *Populus tremula*, on fallen decayed branches of *Quercus*, 15 July 2019, *leg.* L. Kalinina (LE F-331684); *ibid.*, on debarked *Populus tremula* trunk, 15 July 2019, *leg.* L. Kalinina (LE F-331685); Khanty-Mansi Autonomous Okrug, Surgut district, vicinity of Ugut village, mixed floodplain forest in the Bolshoy Yugan river basin with *Picea obovata*, *Pinus sibirica*, *Abies sibirica*, *Populus tremula*, and *Betula pubescens*, on well-rotted trunk of *Populus tremula*, 9 September 2019, *leg.* T. Bulyonkova (LE 313564).

Description. – Basidiomata small- to medium-sized. – Pileus 8–25 mm in diam.; parabolical, hemispherical, or convex when young; becoming convex, umbonate, plano-convex, with striate margin, surface glabrous, viscid, with age wrinkled at center; usually very variable in color, with deep colors when very young, ocean blue (5020) or blue green (6004), with age gradually changing from yellow orange (2000) to coral red (1005), including numerous shades [i.e., red orange (2001), orange brown (8023), copper brown (8004), honey yellow (1005), ochre yellow (1024), curry (1027)] to greenish-ochre [pine green (6028), olive green (6003), reseda green (6011)]. – Lamellae adnate, then free, crowded, with lamellulae, slightly ventricose, grey white (9002) when young, changing to sand yellow (1002), brown beige (1011) with slightly serrulate somewhat paler edge. – Stipe 25–60 × 2–4 mm, cylindrical, broadened at the base, with basal mycelium, fragile, hollow, yellowish to green beige (1000), ivory (1014) with distinct pastel blue (5024) tint at the base, entirely pruinose. – Context thin, whitish. – Odor not distinctive. – Taste not distinctive. – Basidiospores 8.0–10.7 × 5.0–6.0(–6.4) µm [n=90], $Q=1.40–2.10$, $Q_{av}=1.70$, ellipsoid to oblong, never lentiform, orange-brown in KOH, slightly thick-walled, with clearly visible central germ-pore; smooth at ×40 using compound microscopy, very indistinctly ornamented at ×100 using DIC optics, and clearly ornamented under SEM; entirely covered with numerous isolated rounded hemispherical papillae (surface with goose bumps). – Basidia predominantly 4-spored, 19–27 × 8–11 µm, clavate or broadly clavate. – Cheilocystidia numerous, 27.6–64.5(–82.0) × 4.0–8.6 (–10.4) µm, subcylindrical, often narrowly fusiform in lower part, with prolonged obtuse apex 3.0–4.9 µm width, hyaline, thin-walled, with one to three septa at the base. – Pleurocystidia absent. – Pileipellis hymeniform; composed of 24–53(–55) × 11–20 µm, broadly clavate, obovoid, subglobose pedunculate elements, in chains, thin-walled, from hyaline to very pale yellowish (in water preparation); covered with gelatinous matrix. – Pileocystidia absent. – Stipitipellis a cutis, containing fascicles of caulocystidia, 37–96 (–120) × 5.7–9.2 µm, subcylindrical or irregularly cylindrical, sometimes septate, mixed with slightly ventricose elements with small projections and somewhat broadened apex, hyaline, slightly thick-walled. – Clamp connections present and numerous in all parts of basidioma.

Habitat and distribution. – On rotten wood and debris of hardwood in damp places, also on wooden chips and sawdust. Repeatedly found in Canada and the USA, with additional records from the Czech Republic (Hausknecht et al. 2007, Björk & Tudzarovsky 2017), Slovenia (Watling 1987), and Sweden (Björk & Tudzarovsky 2017).

Notes. – The genus *Bolbitius* Fr. was erected by Fries (1838) to accommodate *Bolbitius vitellinus* (Pers.) Fr., which is presently considered a synonym of *Bolbitius titubans* (Bull.) Fr. According to Index Fungorum (2021), more than 70 species of *Bolbitius*

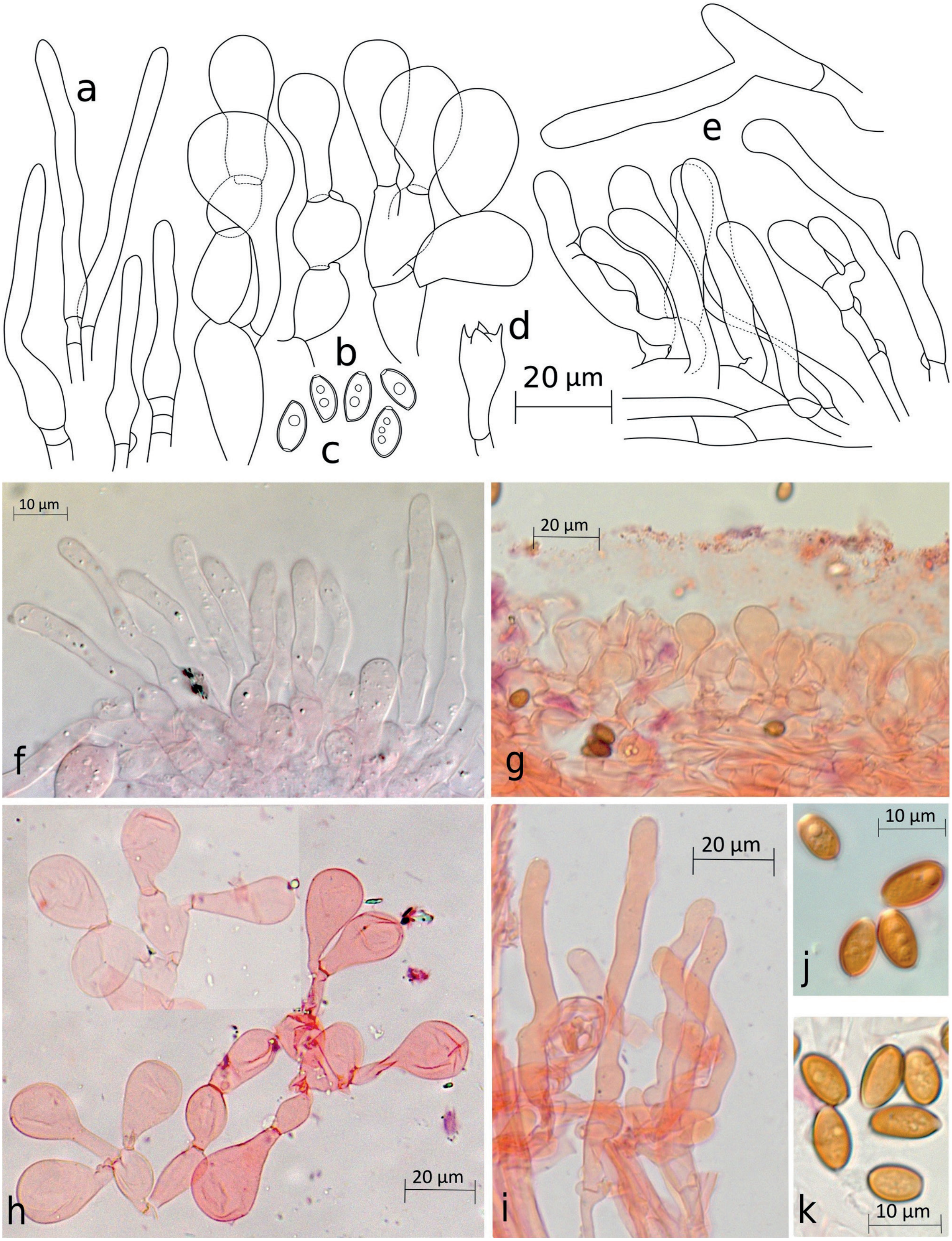

Fig. 20. Microstructures of *Bolbitius callistus*, drawn (a–d) and photographed (f–k). **a.** Cheilocystidia. **b.** Pileipellis elements. **c.** Basidiospores. **d.** Basidia. **e.** Caulocystidia. **f.** Cheilocystidia. **g.** Pileipellis with gelatinous matrix. **h.** Pileipellis elements. **i.** Caulocystidia. **j.** Basidiospores, view with DIC, slightly and unclear ornamentation can be observed. **k.** Basidiospores, view under light microscope, no ornamentation can be observed.

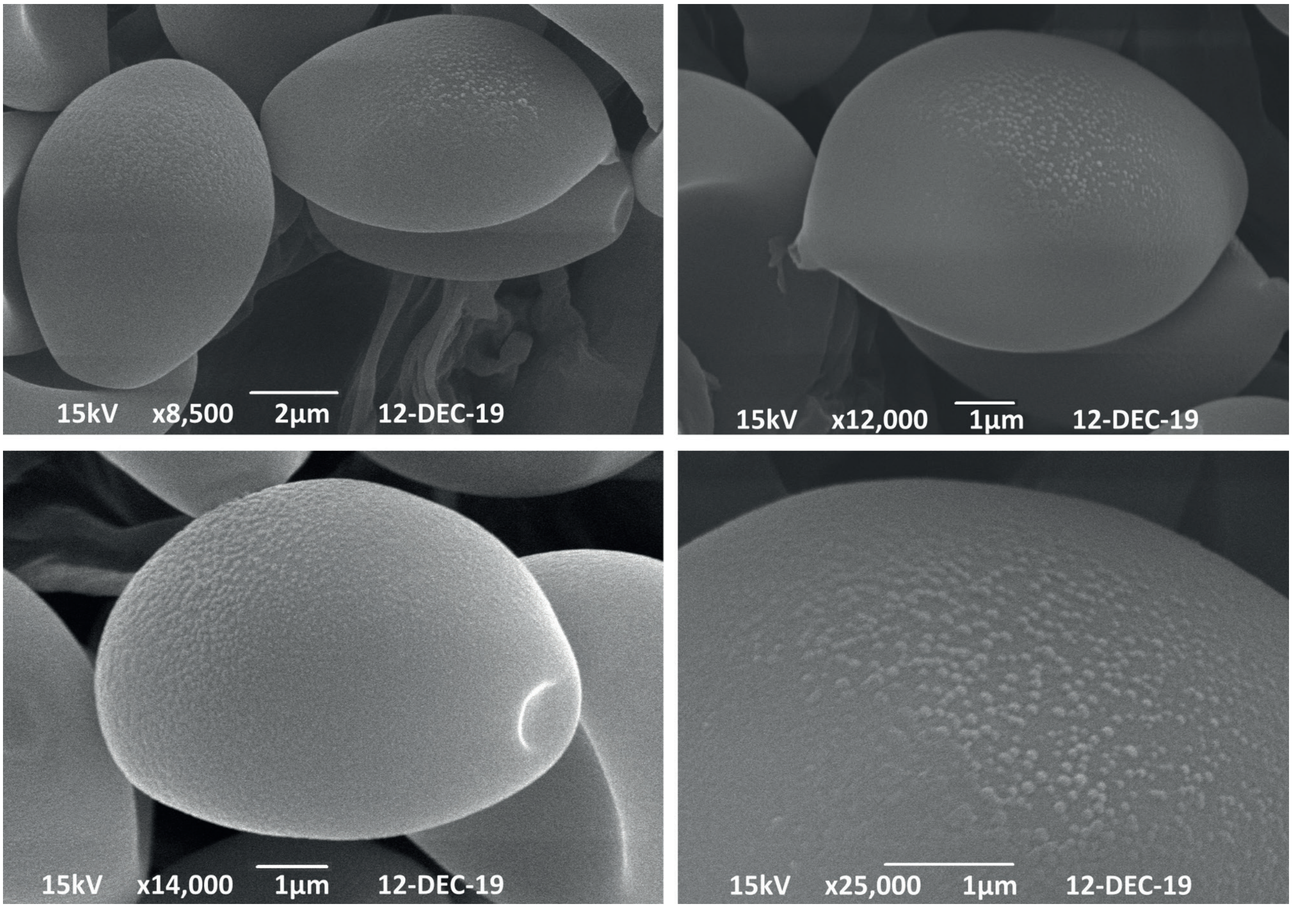

Fig. 21. SEM micrographs of *Bolbitius callistus* basidiospores with clearly visible ornamentation.

are known. Members of the genus are easily recognized by fragile, often deliquescent, and brightly colored basidiomata, viscid to glutinous pileus with striate-plicate margin, free or narrowly adnate ochraceous to rusty brown lamellae, mainly lageniform or utriform cystidia, the presence of pseudoparaphyses in the hymenium, and a hymeniform pileipellis. Among all species of the genus, *B. callistus* is noticeable for its peculiar basidioma coloration, which prompted the author of the species to recognize it as "one of the prettiest Agarics" (Peck 1873). The pigmentation of its basidiomata can gradually change from green, olivaceous, and blue in young and immature specimens to a rich orange, tawny rust, purple, or red in later stages of basidioma development (Watling 1987). *Bolbitius callistus* was described by Peck (1873) from North America as *Agaricus callistus*. Later, the taxon was considered as a member of the genera *Galera* and *Pluteolus*. It was Watling (1977) who transferred it to the genus *Bolbitius* (as *B.* "*callisteus*"). This fungus, although rare, is quite widespread in North America. There are also records of the species from Slovenia (Watling 1987) and Sweden (Björk & Tudzarovsky 2017). Based on an ITS phylogeny, Björk & Tudzarovsky (2017) demonstrated that the Czech species *B. psittacinus* Hauskn., Antonín & Polčák (Hausknecht et al. 2007) was conspecific with American and European collections of *B. callistus*. As a result, *B. callistus* is also known from the Czech Republic.

During our survey of the funga of northwestern Russia and Siberia, some collections of this fungus were collected and fully illustrated both macro- and microscopically. The phylogenetic reconstruction of an ITS sequence dataset (Fig. 18) demonstrated that the Russian material is conspecific with the studied American and European collections of *B. callistus*. These collections represent the first report of *B. callistus* in Russia and in the Asian territory of Eurasia. The examination of the basidiospores under SEM revealed for the first time the presence of a distinct pattern of ornamentation on their surface.

Our Russian collections correspond well not only with the original description of *B. callistus* (Peck 1873), but also with the descriptions of North American and European specimens studied by Watling (1987). Only two features were not observed in our material: pileocystidia, which were registered as “scattered fusoid-ventricose, pyriform or ventricose-rostrate” elements in the pileipellis of North American collections (actually, these elements could be not pileocystidia, but elements of the pileipellis proper), and hyphae with a brownish olive vacuolar pigment in the gelatinized matrix covering the pileipellis. Based on our observations, we regard these characters as fairly variable, with a possibility of quantitative change in different specimens.

Ecological preferences of the species are quite interesting. According to the protologue, the type habitat represents “exsiccated water holes in swampy woods” although six years later Peck noted that it grew on wood in damp places (Watling, 1987). Having analyzed numerous collections of the species, Watling came to the conclusion that the natural habitat of *B. callistus* includes twigs and smaller woody debris in damp places. Both Russian finds were made on middle-sized fallen branches and fallen decayed trunks of deciduous trees (presumably *Populus tremula* and *Quercus robur*) in vernal ponds, meaning that the substrate was submerged in water for several months. Based on this observation, we assume that that the most suitable natural habitat of this species are vernal ponds with sufficient amounts of wood debris.

In our opinion, the localities of the Czech and Swedish material highlight the ability of *B. callistus* species to take advantage of human activities that result in abundant and strongly degraded substrates, such as sawdust and wood chips. Taking into account the proximity of the Czech locality to the Juhyn River, it is highly likely that *B. callistus* “jumped” from its natural habitat to an artificial man-made substratum. This substratum shift can explain the observed differences in basidioma size in Czech and Sweden specimens compared with Russian collections. Also Watling (1987) came to the conclusion that the size of basidiomata generally correlates with the type of substratum; larger basidiomata of *B. callistus* are characteristic of collections found growing on wood chips or sawdust, whereas collections found on more natural substrata such as twigs or fallen trunk, have a smaller pileus and stipe.

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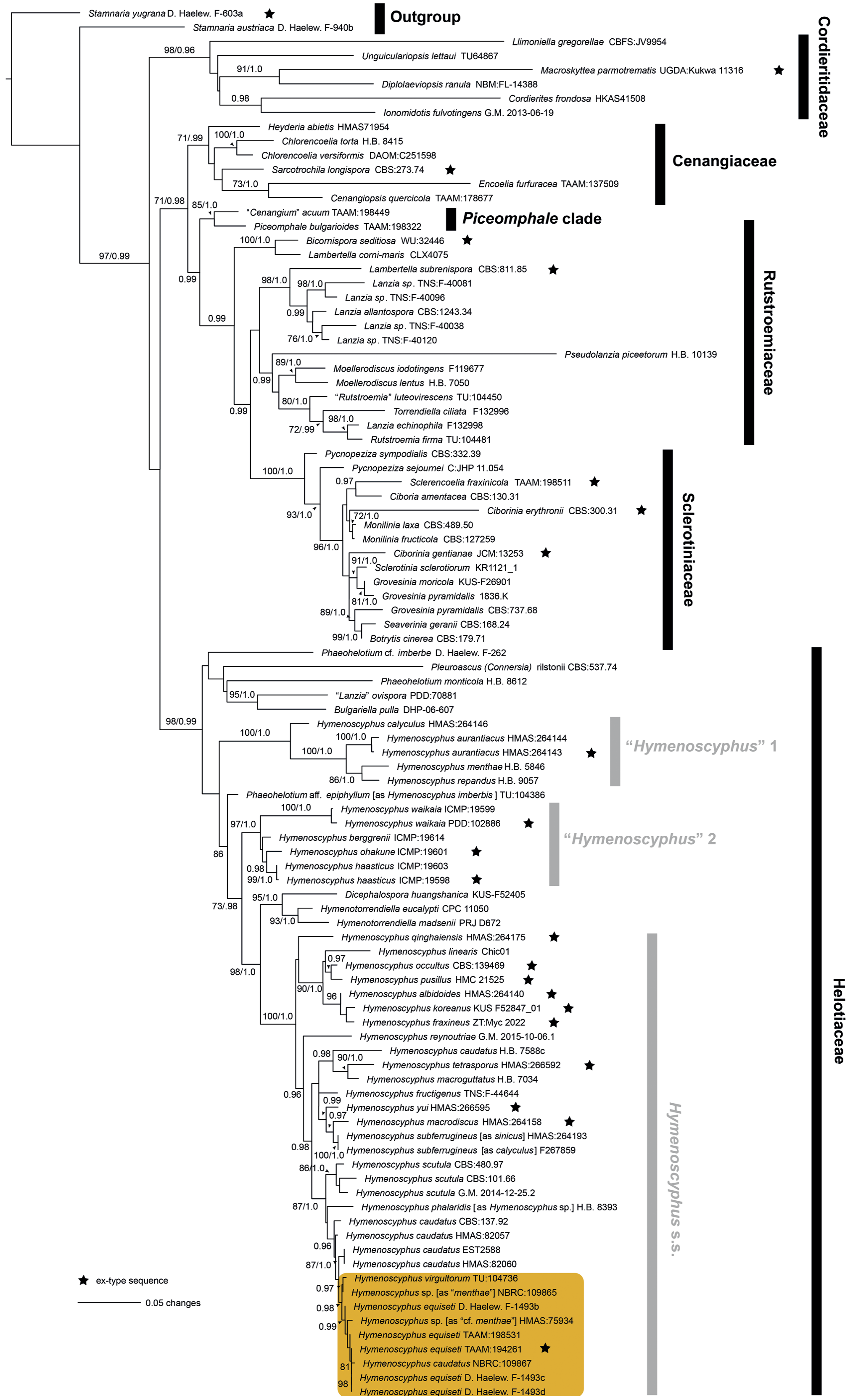
Ascomycota, Leotiomycetes, Helotiales, Helotiaceae

Hymenoscyphus equiseti (Raitv.) Baral, Pärtel, Haelew., Myhrer & Pennanen, **comb. nov**. – Figs. 22–26
MycoBank no.: MB 842026

Basionym. – *Lanzia equiseti* Raitv., Nov. Sist. Niz. Rast. 21: 116 (1984).

Material examined. – SWEDEN. Hälsingland, Gävleborg län, Nordanstig, 2.2 km WNW of Bergsjö, NW of Bjåsta, 61°59’24.6”N, 17°01’10.1”E, 54 m a.s.l., on stems of *Equisetum fluviatile* (Equisetales, Equisetaceae) standing or lying on bank of a river connecting two lakes, also on dead stems standing in shallow water, 21 August 2018, *leg.* J. Myhrer (UPS:BOT:F-923028, isolates D. Haelew. F-1493b,c,d). – FINLAND. North Karelia, Ilomantsi, Mutalahti village, 62°26’49”N, 31°7’14”E, 149 m a.s.l., on shore of a lake, old stems of *E. fluviatile*, 20 August 2010, *leg.* M. Pennanen (M.P. 100807E); Pirkanmaa, Ylä-Pirkanmaa, 11 km S of Virrat, 7 km SW of Hauhuu, Sikosaari Island, between boathouse and bridge to Järviniemi, 62°8’38.7”N, 23°47’54.6”E, 96 m a.s.l., stems of *E. fluviatile*, 27 September 1995, *leg.* I. Kytövuori (H 6057148, TAAM:198531, I.K. 95-1600, isolate KL533). – RUSSIA. Karelia, Ladoga Lake, Valamo Island, ~61°22’N, 30°56’E, ~5 m a.s.l., stems of *E. fluviatile*, 2 October 1980, *leg.* V.A. Melnik (TAAM:194261; isotype, isolate KL214).

Description. – Apothecia rehydrated (0.5–)0.8–1.5(–1.8) mm in diam., receptacle 0.28–0.35 mm thick (0.2–0.3 mm at margin), round, non-gelatinous, scattered to subgregarious; disc whitish to pale yellowish, slightly concave to flat, margin thin, smooth, exterior whitish; short- to long-stipitate, stipe 0.3–1.7 × 0.2–0.35 mm, white, near base often light ochre-brown, smooth, erumpent from beneath epidermis, without an obvious stroma. – Asci *135–160 × 15–18.5 µm {1}, †135–165 {1} × (10.5–)12–15 µm {2}, †111–153 × 12–15 µm {T} (protologue †120–130 × 11.5–13.5 µm), 8-spored, spores *obliquely biseriate, *pars sporifera* *77–80 µm long (†90–130 µm); apex (†) conical, apical dome †1.8–2.3 µm thick, amyloid ring occupying lower 2/3 up to total height of dome, †1.5–2 µm high, 1.4–1.9 µm wide, IKI medium to strongly blue (bb) {3}, *Hymenoscyphus*-type, without apical chamber; base with short stalk arising from simple septa {4}. – Ascospores *(25–)27–31(–32) × (6–)6.7–7.5(–8) µm {2}, †24.3–32 × (5.7–)6.5–7(–8.3) µm {1}, †23–33 × 5.5–7 µm {T} (protologue †27–30 × 5.5–6.5 µm), slightly scutuloid, cylindrical to slightly clavate, straight to slightly inequilateral, often distinctly constricted in the middle, non-septate, apex obtuse to subacute, symmetrical to slightly asymmetrical, base shortly conical; both ends with one very short (0.5–1 µm) bristle (setula), with a faint non-gelatinous sheath detaching from the base of ejected spores; multiguttulate, lipid content high (OCI 5), large LBs (1.5–)2.5–5 µm in diam. {1}, interspersed with many small


Stamnaria yugrana D. Haelew. F-603a ★
Stamnaria austriaca D. Haelew. F-940b
Outgroup
98/0.96
Limoniella gregorellae CBFS:JV9954
Unguiculariopsis lettaui TU64867
91/1.0
Macroskyttea parmotrematis UGDA:Kukwa 11316 ★
Diplolaeviopsis ranula NBM:FL-14388
0.98
Cordierites frondosa HKAS41508
Ionomidotis fulvotingens G.M. 2013-06-19
Cordieritidaceae
Heyderia abietis HMAS71954
71/.99
100/1.0
Chlorencoelia torta H.B. 8415
Chlorencoelia versiformis DAOM:C251598
Sarcotrochila longispora CBS:273.74 ★
73/1.0
Encoelia furfuracea TAAM:137509
Cenangiopsis quercicola TAAM:178677
Cenangiaceae
71/0.98
85/1.0
"Cenangium" acuum TAAM:198449
Piceomphale bulgarioides TAAM:198322
Piceomphale clade
100/1.0
Bicornispora seditiosa WU:32446 ★
Lambertella corni-maris CLX4075
97/0.99
0.99
Lambertella subrenispora CBS:811.85 ★
98/1.0
98/1.0
Lanzia sp. TNS:F-40081
Lanzia sp. TNS:F-40096
0.99
Lanzia allantospora CBS:1243.34
Lanzia sp. TNS:F-40038
0.99
76/1.0
Lanzia sp. TNS:F-40120
Pseudolanzia piceetorum H.B. 10139
89/1.0
Moellerodiscus iodotingens F119677
0.99
Moellerodiscus lentus H.B. 7050
"Rutstroemia" luteovirescens TU:104450
80/1.0
0.99
Torrendiella ciliata F132996
98/1.0
Lanzia echinophila F132998
72/.99
Rutstroemia firma TU:104481
Rutstroemiaceae
Pycnopeziza sympodialis CBS:332.39
100/1.0
Pycnopeziza sejournei C:JHP 11.054
0.97
Sclerencoelia fraxinicola TAAM:198511 ★
Ciboria amentacea CBS:130.31
93/1.0
Ciborinia erythronii CBS:300.31 ★
72/1.0
Monilinia laxa CBS:489.50
96/1.0
Monilinia fructicola CBS:127259
Ciborinia gentianae JCM:13253 ★
91/1.0
Sclerotinia sclerotiorum KR1121_1
Grovesinia moricola KUS-F26901
Grovesinia pyramidalis 1836.K
81/1.0
89/1.0
Grovesinia pyramidalis CBS:737.68
Seaverinia geranii CBS:168.24
99/1.0
Botrytis cinerea CBS:179.71
Sclerotiniaceae
Phaeohelotium cf. imberbe D. Haelew. F-262
Pleuroascus (Connersia) rilstonii CBS:537.74
Phaeohelotium monticola H.B. 8612
95/1.0
"Lanzia" ovispora PDD:70881
Bulgariella pulla DHP-06-607
98/0.99
Hymenoscyphus calyculus HMAS:264146
100/1.0
100/1.0
Hymenoscyphus aurantiacus HMAS:264144
100/1.0
Hymenoscyphus aurantiacus HMAS:264143 ★
Hymenoscyphus menthae H.B. 5846
86/1.0
Hymenoscyphus repandus H.B. 9057
"Hymenoscyphus" 1
Phaeohelotium aff. epiphyllum [as Hymenoscyphus imberbis] TU:104386
100/1.0
Hymenoscyphus waikaia ICMP:19599
97/1.0
Hymenoscyphus waikaia PDD:102886 ★
Hymenoscyphus berggrenii ICMP:19614
86
Hymenoscyphus ohakune ICMP:19601 ★
0.98
Hymenoscyphus haasticus ICMP:19603
99/1.0
Hymenoscyphus haasticus ICMP:19598 ★
"Hymenoscyphus" 2
95/1.0
Dicephalospora huangshanica KUS-F52405
73/.98
Hymenotorrendiella eucalypti CPC 11050
93/1.0
Hymenotorrendiella madsenii PRJ D672
Hymenoscyphus qinghaiensis HMAS:264175 ★
Hymenoscyphus linearis Chic01
0.97
Hymenoscyphus occultus CBS:139469 ★
98/1.0
Hymenoscyphus pusillus HMC 21525 ★
90/1.0
96
Hymenoscyphus albidoides HMAS:264140 ★
Hymenoscyphus koreanus KUS F52847_01 ★
100/1.0
Hymenoscyphus fraxineus ZT:Myc 2022 ★
Hymenoscyphus reynoutriae G.M. 2015-10-06.1
0.98
Hymenoscyphus caudatus H.B. 7588c
90/1.0
Hymenoscyphus tetrasporus HMAS:266592 ★
Hymenoscyphus macroguttatus H.B. 7034
0.96
Hymenoscyphus fructigenus TNS:F-44644
0.99
Hymenoscyphus yui HMAS:266595 ★
0.97
Hymenoscyphus macrodiscus HMAS:264158 ★
Hymenoscyphus subferrugineus [as sinicus] HMAS:264193
0.98
Hymenoscyphus subferrugineus [as calyculus] F267859
100/1.0
86/1.0
Hymenoscyphus scutula CBS:480.97
Hymenoscyphus scutula CBS:101.66
Hymenoscyphus scutula G.M. 2014-12-25.2
87/1.0
Hymenoscyphus phalaridis [as Hymenoscyphus sp.] H.B. 8393
Hymenoscyphus caudatus CBS:137.92
Hymenoscyphus caudatus HMAS:82057
0.96
Hymenoscyphus caudatus EST2588
87/1.0
Hymenoscyphus caudatus HMAS:82060
★ ex-type sequence
Hymenoscyphus virgultorum TU:104736
0.97
Hymenoscyphus sp. [as "menthae"] NBRC:109865
0.05 changes
0.98
Hymenoscyphus equiseti D. Haelew. F-1493b
0.99
Hymenoscyphus sp. [as "cf. menthae"] HMAS:75934
Hymenoscyphus equiseti TAAM:198531
Hymenoscyphus equiseti TAAM:194261 ★
81
Hymenoscyphus caudatus NBRC:109867
98
Hymenoscyphus equiseti D. Haelew. F-1493c
Hymenoscyphus equiseti D. Haelew. F-1493d
Hymenoscyphus s.s.
Helotiaceae

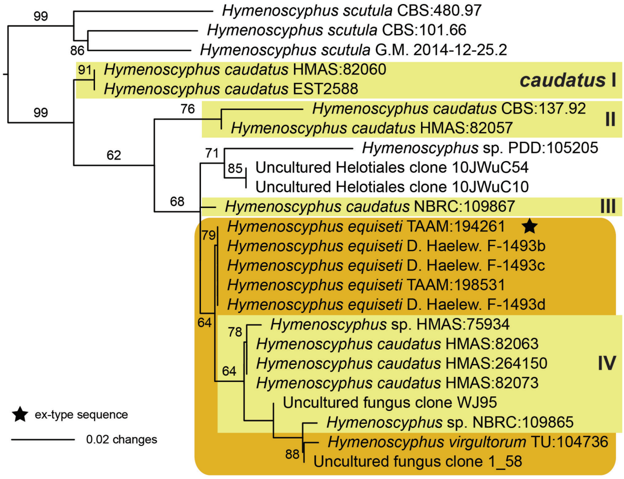


Fig. 23. Phylogeny of *Hymenoscyphus* species reconstructed from an ITS dataset. The topology is the result of ML inference performed with IQ-TREE. For each node, MLBS ≥60 is presented above or below the branch leading to that node. Stars (★) indicating ex-type sequences, annotations *caudatus* I through IV indicating the four clades in which samples identified as *H. caudatus* are included.

LBs, LBs in dead spores aggregated in irregular lumps; overmature spores not observed. – Paraphyses apically cylindrical, terminal cell *40–50 × (2–)3–3.2(–4) µm {1}, †(32–)40–50 × (2–)2.5–4(–4.8) µm {2}; containing strongly refractive, hyaline, globose to subangular VBs 1–2.7 µm diam. in upper 25–37 µm {1}. – Medullary excipulum hyaline, ~50 µm thick in receptacle, of loose *textura intricata*. – Ectal excipulum hyaline to pale yellowish-ochraceous, of thin-walled, horizontally oriented *textura prismatica* from base to margin, cells at lower flanks *13–33 × 8–13 µm {1}, †8.5–12.5 × 4.5–7.5 µm {T} (protologue †8–12 × 5–7 µm); exterior without cortical hyphae or hair-like protrusions, complete tissue without crystals. – Anamorph unknown.

Hosts and distribution. – Thus far only found on previous year's stems of *Equisetum fluviatile* {4}. Mature apothecia observed from August through October on shores of freshwater bodies. Thus far reported from Russia (Republic of Karelia), Finland, and Sweden (Raitviir 1984, this study).

Notes. – *Hymenoscyphus equiseti* was previously only known from a single collection from Valamo Island, in the Republic of Karelia in northwestern Russia (Raitviir 1984). The holotype is located at LE, and multiple isotypes are present at BPI, CUP, FH, K, NY, S, TAAM (TAAM:194261, examined in this study), and UPS. Based on morphology and molecular phylogenetic data, the here examined isotype collection (Fig. 26) concurs with the other three collections reported in this study. *Hymenoscyphus equiseti* is a morphologically well-defined species when compared with other *Hymenoscyphus*-like species known on *Equisetum*: *Roseodiscus equisetinus* (Velen.) Baral and *R. rhodoleucus* (Fr.) Baral are easily distinguished by their rosaceous disc, *Calycina*-type of apical ring, and smaller, oblong-ciborioid ascospores lacking setulae and with a low lipid content (Baral & Krieglsteiner 2006). Other species growing on *Equisetum* and earlier placed in *Hymenoscyphus* or *Helotium* Pers. are *Hymenoscyphus calamarius* (Velen.) P. Sharma and *Helotium telmateiae* Velen. According to Svrček's (1985) revision of their holotypes, *H. calamarius* (ascospores †9.5–15 × 4–5 µm) is a synonym of the wood-inhabiting *Phaeohelotium imberbe* (Bull.) Svrček, and *H. telmateiae* (ascospores †6–8 × 1.5–2.0 µm) is a synonym of *Psilachnum inquilinum* (P. Karst.) Dennis.

Raitviir (1984) placed *Hymenoscyphus equiseti* in *Lanzia* Sacc. because he saw a thin stroma from which the apothecia emerge. No evident stroma could be observed in the specimens studied by us, although the stems looked externally sometimes entirely dark. A black stroma was earlier considered an indication for a relationship with sclerotiniaceous fungi, in particular Rutstroemiaceae. Yet, morphological characteristics (shape of ascus apical ring, scutuloid ascospores) of some species earlier placed in *Lanzia* pointed to the genus *Hymenoscyphus*, and molecular data supported this view (Baral & Bemmann 2014). Within the genus *Lanzia*, Raitviir (1984) characterized *L. equiseti* by short setulae at the spore ends. Actually, such setulae are completely unknown in members of Rutstroemiaceae in the present circumscription of the family, but they are typical of many species of *Hymenoscyphus*. Also scutuloid spores are not observed in sclerotiniaceous fungi but typical of *Hymenoscyphus*.

The aligned, trimmed, and concatenated ITS–LSU dataset included 98 isolates and 1,383 characters (ITS: 95 sequences, 517 characters; LSU: 74 sequences, 866 characters). Of these 1,383 total char-

Fig. 22. Phylogeny of Helotiaceae and related families reconstructed from a concatenated ITS–LSU dataset. The topology is the result of ML inference performed with IQ-TREE. For each node, MLBS ≥70 and BIPP ≥0.95 are presented above or below the branch leading to that node. Stars (★) indicating ex-type sequences.

Fig. 24. *Hymenoscyphus equiseti* apothecia on stems of *Equisetum fluviatile*. **1a, 1b.** Finland, North Karelia (M.P. 100807E); fresh apothecia. **2a–e.** Sweden, Hälsingland (UPS:BOT:F-923028); fresh apothecia. **3a–c.** Russia, Karelia, (TAAM:198531); more or less rehydrated apothecia. Photos M. Pennanen (1a, 1b), J. Myhrer (2a–e), K. Pärtel (3a–c).

acters, 714 were constant, 171 singleton, and 498 parsimony-informative. The selected models were GTR+I+G (ITS, -lnL=10642.87) and TIM3+I+G (LSU, -lnL=7605.97). The topology of our Bayesian and ML trees were identical among supported (MLBS ≥70 and BIPP ≥0.95) nodes (Fig. 22). The relationships among higher clades are consistent with prior phylogenies in these groups when considering depth of sampling in certain families, including those in Zhao et al. (2016) (ITS, LSU, *rpb2*; focus on Rutstroemiaceae), Zhang & Zhuang (2004) (ITS; focus on *Hymenoscyphus*), and Zheng & Zhuang (2015) (ITS, LSU, β-tubulin; focus on *Hymenoscyphus*).

The clade with *H. equiseti* is only supported in our Bayesian analysis of the two-locus dataset (BIPP=0.99), and includes *H.* "*caudatus*" (P. Karst.) Dennis from Japan (NBRC:109867, on *Alnus* sp.) and *H.* "cf. *menthae*" (W. Phillips) Baral from China (HMAS:75934, on dead wood). The broader clade supported by BIPP=0.96 (highlighted in yellow in Fig. 22) contains little structure in a cluster of species including *H. caudatus* (HMAS:82057 and HMAS:82060, substrate unknown; EST2588, on leaves of *Fraxinus* sp.; CBS:137.92, on leaves of *Alnus* sp.), *H.* "cf. *menthae*" (NBRC:109865, on ?stems of *Hydrangea* sp.), and *H. virgultorum* (Fr.) W. Phillips (TU:104736, on wood of *Betula* sp.). Unfortunately, several of these isolates lack associated morphological information to compare with *H. equiseti*. Based on the names assigned to these isolates, all

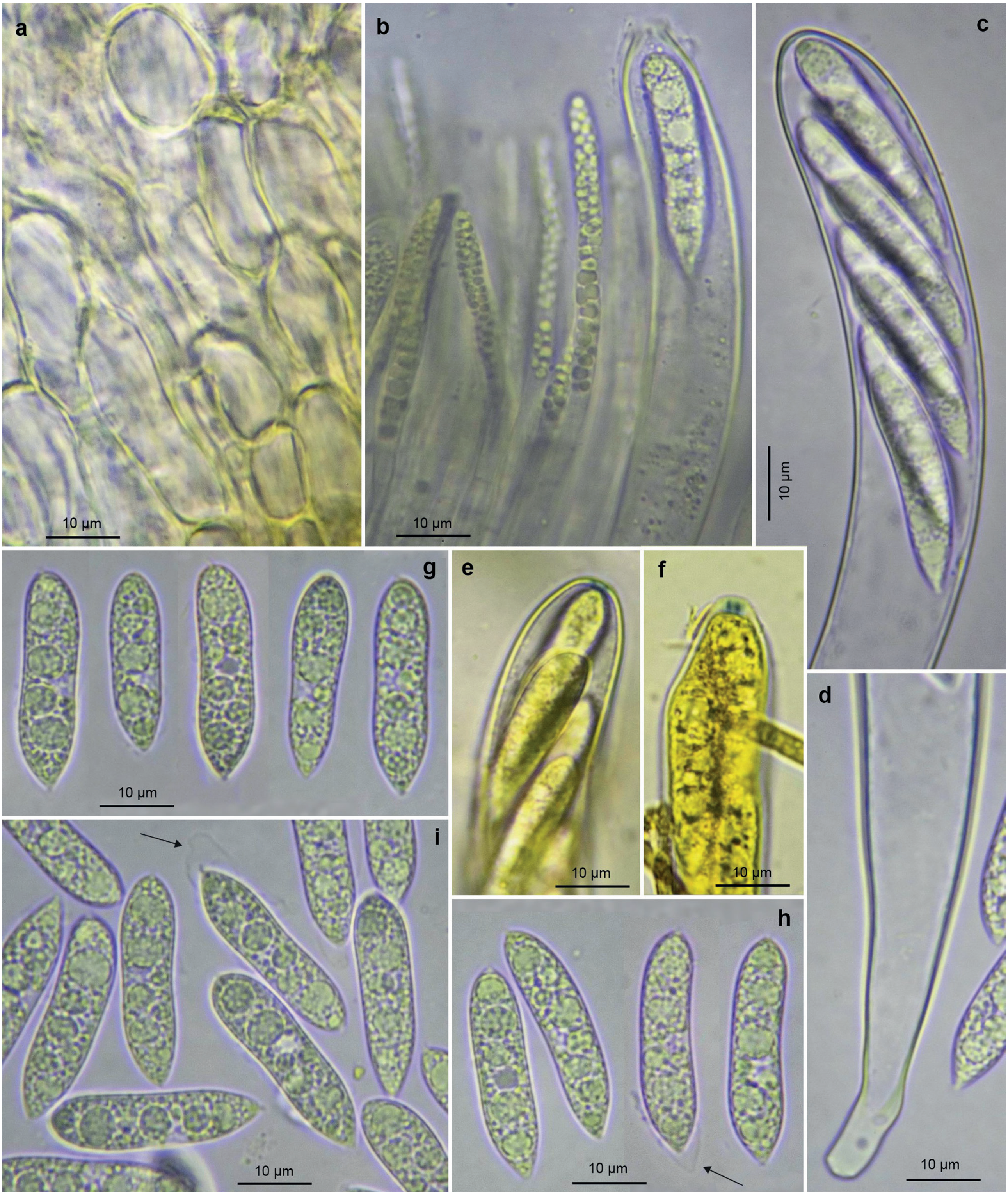


Fig. 25. *Hymenoscyphus equiseti*, collection UPS:BOT:F-923028. **a.** Ectal excipulum in surface view (squash mount). **b.** Paraphyses with multiguttulate refractive vacuoles (VBs) and partially emptied ascus. **c, d.** Mature, fully turgescent ascus (upper and lower part), base truncate (simple-septate). **e.** Upper part of living mature ascus. **f.** Upper part of dead mature ascus. **g–i.** Freshly ejected ascospores, arrows pointing at detaching sheaths. All in living state, except for f; a–d, g–i in water; e–f in Lugol's solution (IKI). Photos J. Myhrer.

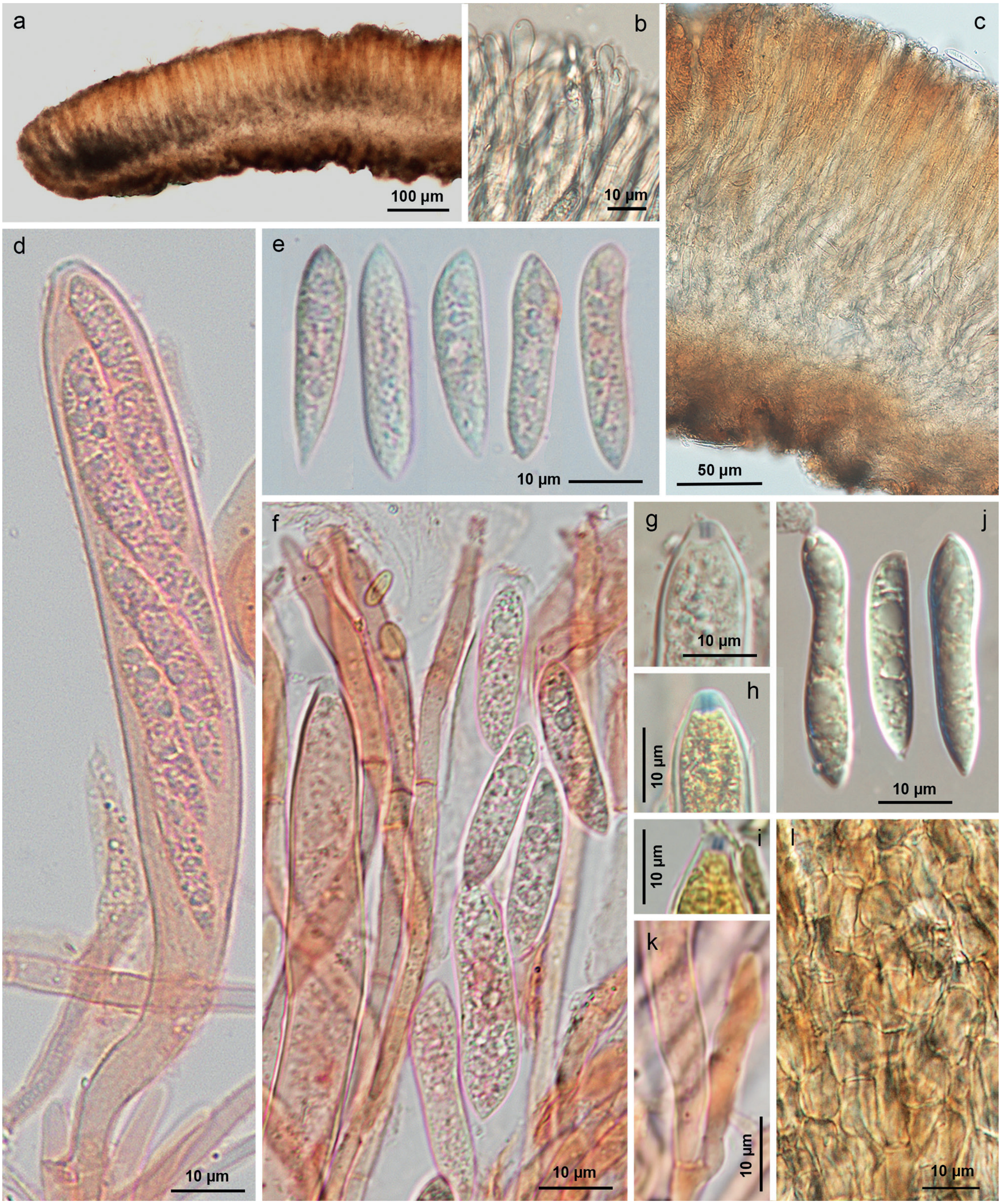


Fig. 26. *Hymenoscyphus equiseti*, collection TAAM:194261 (isotype). **a, c.** Cross-section of apothecium. **b.** Cells in marginal part of apothecium (squash mount). **d.** Mature ascus. **e, j.** Ejected ascospores. **f.** Paraphyses and ascospores. **g–i.** Apices of juvenile to submature asci. **k.** Basal part of ascus with a simple septum. **l.** Ectal excipulum (squash mount). All in dead state; a, c in water; b, l in KOH; d–e, k in Congo Red; g in Melzer's reagent; h–j in Lugol's solution (IKI). Photos K. Pärtel.

should be differentiated from *H. equiseti* by their smaller ascospores (among other features).

Hymenoscyphus virgultorum, typically collected on woody substrates, has ascospores measuring 14–23 × 3–5 µm in Phillips (1893), *18–24 × 3.5–4.0 µm in Baral & Krieglsteiner (1985), *(16–)19–22(–28) × 3.8–4.3(–5.2) µm in H.B. 9845 (TU:104736), and †13.5–16.3 × 4.0–5.0 µm in Delivorias et al. (2010). *Hymenoscyphus menthae*, known to occur on herbaceous stems of monocots and dicots, has ascospores measuring *(15–)17–22(–26) × 3.5–4.2(–4.5) µm (Baral 2015), whereas the wood-inhabiting *H.* "cf. *menthae*" has ascospores measuring †12–18 × 4–5(–6) µm [Zhang & Zhuang 2002, as *H.* cf. *consobrinus* (Boud.) Hengstm.]. The identity of *H. menthae* was clarified by Baral (2015) from an isolectotype, and its placement in our phylogenetic tree is based on confirmed material (H.B. 5846, Fig. 22). *Hymenoscyphus caudatus* is likely a species complex (Zhang & Zhuang 2004) that has been reported from many geographic locations and substrates (leaves of different angiosperm trees) with both morphological and molecular variation. Arendholz (1979) examined numerous collections of this species, including an isotype, for which no separate description was provided. Compared to *H. equiseti*, smaller ascospores are reported for *H. caudatus*: *16–20 × 4–5 µm in Kimbrough & Atkinson (1972), 16–21 × 4–5 µm in Arendholz (1979), (14–)16–23(–26) × 4–5(–6) µm in Dumont & Carpenter (1982), *15–18 × 4.5–5.5 µm in Baral & Krieglsteiner (1985), and *17–20 × (4.7–)5–6 µm in H.B. 7588c.

The aligned and trimmed ITS dataset included 24 isolates and 464 characters, of which 426 were constant and 24 characters were parsimony-informative. The selected model was TNe+R2 (-lnL= 1023.596). *Hymenoscyphus equiseti* isolates are all retrieved in a single, well-supported (MLBS=79) clade in our ITS-based phylogeny (Fig. 23). The low p-distances (0.4–1.5 %) within the orange-colored clade (MLBS=64) and particularly between *H. equiseti* and *H.* "*caudatus*" NBRC 109867 (0.4 % = 2 nt) question our concept of *H. equiseti* being strictly confined to *Equisetum* (Tab. 2). On the other hand, the full ITS and LSU identity within *H. equiseti* from three remote collection sites supports our narrow species concept, and the report of much smaller ascospores in *H.* "cf. *menthae*" from China suggests that its p-distance of 0.7 % (= 3 nt) to *H. equiseti* (Tab. 2) is sufficient to speak of two different species.

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Tab. 2. Intra- and interspecific p-distances between closely related *Hymenoscyphus* species. Roman numbers I–IV refer to *caudatus* clades I through IV as highlighted in Fig. 23.

	H. equiseti	*H. caudatus* III–IV	*H. virgultorum*	*H. caudatus* I–II	*H. scutula*
H. equiseti	0 %				
H. caudatus III–IV	0.4–0.7 %	0–1.1 %			
H. virgultorum	1.1 %	0.4–1.5 %	–		
H. caudatus I–II	1.8–2.9 %	1.5–3.6 %	2.4–3.1 %	0–2.2 %	
H. scutula	4.1–4.3 %	3.8–5.0 %	3.8–4.0 %	3.6–5.0 %	2.4–3.3 %

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References

Abarenkov K., Nilsson R.H., Larsson K.-H., Alexander I., Eberhardt U., Erland S., et al. (2010) The UNITE database for molecular identification of fungi – recent updates and future perspectives. *New Phytologist* **186**(2): 281–285.

Al-Yahya'ei M.N., Mullath S.K., AlDhaheri L.A., Kozłowska A., Błaszkowski J. (2017) *Dominikia emiratia* and *Rhizoglomus dunense*, two new species in the Glomeromycota. *Botany* **95**: 629–639.

Ammirati J., Niskanen T., Liimatainen K., Bojantchev D., Peintner U., Kuhnert-Finkernagele R., Cripps C. (2017) Spring and early summer species of *Cortinarius*, subgenus *Telamonia*, section *Colymbadini* and */Flavobasilis*, in the mountains of western North America. *Mycologia* **109**(3): 443–458.

Arendholz W.R. (1979) *Morphologisch-taxonomische Untersuchungen an blattbewohnenden Ascomyceten aus der Ordnung der Helotiales*. PhD thesis, Universität Hamburg, Hamburg, Germany.

Ariyawansa H.A., Hyde K.D., Jayasiri S.C., Buyck B., Thilini Chethana K.W., Dai D.Q., et al. (2015) Fungal diversity notes 111–252—taxonomic and phylogenetic contributions to fungal taxa. *Fungal Diversity* **75**: 27–274.

Baral H.-O. (2015) *Hymenoscyphus menthae*, *H. macroguttatus* and *H. scutula*, a comparative taxonomic study emphasizing the value of spore guttulation and croziers. *Ascomycete.org* **7**(6): 255–287.

Baral H.-O. (2019) *Hymenoscyphus reynoutriae* sp. nov. (= *H. dearnessii* s. auct.), a neomycete in Europe, and *H. phalaridis* sp. nov., specific to monocots (Helotiaceae, Helotiales). *Mycologia Montenegrina* **20**: 11–40.

Baral H.-O., Bemmann M. (2014) *Hymenoscyphus fraxineus* vs. *H. albidus* – A comparative light-microscopical study on the causal agent of European ash dieback and related foliicolous, stroma-forming species. *Mycology* **5**: 228–290.

Baral H.-O., Galan R., Lopez J., Arenal F., Villareal M., Rubio V., et al. (2007) *Hymenoscyphus crataegi* (Helotiales), a new species from Spain and its phylogenetic position within the genus *Hymenoscyphus*. *Sydowia* **58**(2): 145–162.

Baral H.-O., Galán R., Platas G., Tena R. (2013) *Phaeohelotium undulatum* comb. nov. and *Phaeoh. succineoguttulatum* sp. nov., two segregates of the *Discinella terrestris* aggregate found under *Eucalyptus* in Spain: taxonomy, molecular biology, ecology and distribution. *Mycosystema* **32**(3): 386–428.

Baral H.-O., Haelewaters D. (2015) *Rommelaarsia flavovirens* gen. et sp. nov. (Helotiales), a new discomycete on *Equisetum* with a peculiar asexual state. *Ascomycete.org* **7**: 321–330.

Baral H.-O., Krieglsteiner G.J. (1985) Bausteine zu einer Askomyzeten–Flora der Bundesrepublik Deutschland: In Süddeutschland gefundene Inoperculate Discomyzeten – mit taxonomischen, ökologischen und chorologischen Hinweisen und einer Farbtafel. *Beihefte zur Zeitschrift für Mykologie* **6**: 1–160.

Baral H.-O., Krieglsteiner L. (2006) *Hymenoscyphus subcarneus*, a little known bryicolous discomycete found in the Bialowieza National Park. *Acta Mycologica* **41**(1): 11–20.

Bills R.J. (2015) *Phylogenetic relationships among arbuscular mycorrhizal fungal species in the deeply rooted Archaeosporales (Glomeromycota)*. Doctoral dissertation, West Virginia University, Morgantown.

Björk P., Tudzarovsky A. (2017) *Bolbitius callistus*, papegojskivinling, funnen i Sverige. *Svensk Mycologisk Tidskrift* **38**(2): 2–6.

Błaszkowski J. (1988) Three new vesicular–arbuscular mycorrhizal fungi (Endogonaceae) from Poland. *Bulletin of the Polish Acadamy of Sciences. Biological Sciences* **36**: 271–275.

Błaszkowski J. (2012) *Glomeromycota*. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.

Błaszkowski J., Kozłowska A., Crossay T., Symanczik S., Al-Yahya'ei M.N. (2017) A new family, Pervetustaceae with a new genus, *Pervetustus*, and *P. simplex* sp. nov. (Paraglomerales), and a new genus, *Innospora* with *I. majewskii* comb. nov. (Paraglomeraceae) in the Glomeromycotina. *Nova Hedwigia* **105**(3–4): 397–410.

Bojantchev D. (2013) *Cortinarius* of California: eight new species in subg. *Telamonia*. *Mycotaxon* **123**: 375–402.

Brandrud T.E., Lindström H., Marklund H., Melot J., Muskos S. (1990–2014) Cortinarius *Flora Photographica*. Cortinarius HB, Östansjö, Sweden.

Brandrud T.E., Schmidt-Stohn G., Liimatainen K., Niskanen T., Frøslev T.G., Soop K., et al. (2018) *Cortinarius* sect. *Riederi*: taxonomy and phylogeny of the new section with European and North American distribution. *Mycological Progress* **17**(12): 1323–1354.

Brundrett M., Melville L., Peterson L. (1994) *Practical Methods in Mycorrhizal Research*. Mycologue Publications, University of Guelph, Guelph, Ontario.

Capella-Gutiérrez S., Silla-Martínez J.M., Gabaldón T. (2009) TrimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. *Bioinformatics* **25**(15): 1972–1973.

Chernomor O., von Haeseler A., Minh B.Q. (2016) Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology* **65**(6): 997–1008.

Cho S.E., Park J.H., Choi Y.J., Lee S.H., Lee C.K., Shin H.D. (2017) Occurrence of leaf spot caused by *Cristulariella depraedans* on *Acer ginnala*. *Forest Pathology* **47**(1): e12302.

Clémençon H. (2009) *Methods for working with macrofungi. Laboratory cultivation and preparation of large fungi for light microscopy*. IHW-Verlag, Eching, Germany.

Corazon-Guivin M.A., Mendoza A.C., Guerrero-Abad J.C., Vallejos-Tapullima A., Carballar-Hernández S., da Silva G.A., Oehl F. (2019) *Funneliglomus*, gen. nov., and *Funneliglomus sanmartinensis*, a new arbuscular mycorrhizal fungus from the Amazonia region in Peru. *Sydowia* **71**: 17–24.

Corazon-Guivin M.A., Mendoza, A.C., Guerrero-Abad, J.C., Vallejos-Tapullima, A., Rios-Ramirez, O., Vallejos-Torres, G., et al. (2020) *Paraglomus occidentale*, a new arbuscular mycorrhizal fungus from the sources of the Amazon river in Peru, with a key to the Paraglomeromycetes species. *Sydowia* **72**: 85–94.

Crous P.W., Cowan D.A., Maggs-Kölling G., Yilmaz N., Thangavel R., Wingfield M.J., et al. (2021) Fungal Planet description sheets: 1182–1283. *Persoonia* **46**: 313–528.

Crous P.W., Verkley G.J., Groenewald J.Z. (2006) Eucalyptus microfungi known from culture. 1. *Cladoriella* and *Fulvoflamma* genera nova, with notes on some other poorly known taxa. *Studies in Mycology* **55**: 53–63.

Crous P.W., Wingfield M.J., Richardson D.M., Le Roux J.J., Strasberg D., Edwards J., et al. (2016) Fungal Planet description sheets: 400–468. *Persoonia* **36**: 316–458.

Darriba D., Taboada G.L., Doallo R., Posada D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* **9**(8): 772–772.

Das K., Chakraborty D., Baghela A., Singh S.K., Dentinger B.T.M. (2016) New species of xerocomoid boletes (Boletaceae) from Himalayan India based on morphological and molecular evidence. *Mycologia* **108**(4): 753–764.

Delivorias P., Dimitriadis I., Gonou-Zagou Z., Kapsanaki-Gotsi E. (2010) Some interesting species of *Hymenoscyphus* from Greece. *Mycologia Balcanica* **7**: 87–92.

Dentinger B.T., Didukh M.Y., Moncalvo J.M. (2011) Comparing COI and ITS as DNA barcode markers for mushrooms and allies (Agaricomycotina). *Plos One* **6**(9): e25081.

Dima, B. (2015) Nomenclatural novelties. *Index Fungorum* **252**: 1.

Dima B., Brandrud T.E., Corriol G., Jansen G.M., Jordal J.B., Khalid A.N., et al. (2021) Fungal Systematics and Evolution: FUSE 7. *Sydowia* **73**: 271–340.

Dirks A.C., Jackson R.D. (2020) Community structure of arbuscular mycorrhizal fungi in soils of switchgrass harvested for bioenergy. *Applied and Environmental Microbiolology* **86**: e00880–20.

Drenkhan R., Solheim H., Bogacheva A., Riit T., Adamson K., Drenkhan T., et al. (2017) *Hymenoscyphus fraxineus* is a leaf pathogen of local *Fraxinus* species in the Russian Far East. *Plant Pathology* **66**(3): 490–500.

Dumont K.P., Carpenter S.E. (1982) Los hongos de Colombia—VII: Leotiaceae—IV: *Hymenoscyphus caudatus* and related species from Colombia and adjacent regions. *Caldasia* **13**(64): 567–602.

Edgar R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32**(5): 1792–1797.

Etayo J., Flakus A., Suija A., Kukwa M. (2015) *Macroskyttea parmotrematis* gen. et sp. nov. Helotiales, Leotiomycetes, Ascomycota, a new lichenicolous fungus from Bolivia. *Phytotaxa* **224**(3): 247–257.

Fries E.M. (1838) *Epicrisis Systematis Mycologici, seu Synopsis Hymenomycetum*. Typographia Academica, Uppsala.

Frøslev T.G, Brandrud T.E., Dima B. (2017) *Cortinarius stjernegaardii* and *C. kristinae* (Basidiomycota, Agaricales), two new European species with a mainly northern distribution. *Mycological Progress* **16**: 145–153.

Frøslev T.G., Jeppesen T.S., Dima, B. (2015) *Cortinarius koldingensis*—a new species of *Cortinarius*, subgenus *Phlegmacium* related to *Cortinarius sulfurinus*. *Mycological Progress* **14**: 73.

Frøslev T.G., Jeppesen T.S., Laessøe T., Kjøller R. (2007) Molecular phylogenetics and delimitation of species in *Cortinarius* section *Calochroi* (Basidiomycota, Agaricales) in Europe. *Molecular Phylogenetics and Evolution* **44**: 217–227.

Galán R., Checa J., Blanco M.N., Platas G., Tena R., Tello S., et al. (2015) Taxonomic position of the genus *Bicornispora* and the appearance of a new species *Bicornispora seditiosa*. *Mycologia* **107**(4): 793–807.

Gardes M., Bruns T.D. (1993) ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**(2): 113–118.

Garnica S., Schön M.E., Abarenkov K., Riess K., Liimatainen K., Niskanen T., et al. (2016) Determining threshold values for barcoding fungi: lessons from *Cortinarius* (Basidiomycota), a highly diverse and widespread ectomycorrhizal genus. *FEMS Microbiology Ecology* **92**(4): fiw045.

Garnica S., Spahn P., Oertel B., Ammirati J., Oberwinkler F. (2011) Tracking the evolutionary history of *Cortinarius* species in section *Calochroi*, with transoceanic disjunct distributions. *BMC Evolutionary Biology* **11**: 213.

Garnica S., Weiß M., Oertel B., Ammirati J., Oberwinkler F. (2009) Phylogenetic relationships in *Cortinarius*, section *Calochroi*, inferred from nuclear DNA sequences. *BMC Evolutionary Biology* **9**: 1.

Garnica S., Weiß M., Oertel B., Oberwinkler F. (2003) Phylogenetic relationships of European *Phlegmacium* species (*Cortinarius*, Agaricales). *Mycologia* **95**(6): 1155–1170.

Garnica S., Weiß M., Oertel B., Oberwinkler F. (2005) A framework for a phylogenetic classification in the genus *Cortinarius* (Basidiomycota, Agaricales) derived from morphological and molecular data. *Canadian Journal of Botany* **83**: 1457–1477.

Gómez-Zapata P.A., Haelewaters D., Quijada L., Pfster D.H., Aime M.C. (2021) Notes on *Trochila* (Ascomycota, Leotiomycetes), with new species and combinations. *MycoKeys* **78**: 21–47.

Gorfer M., Klaubauf S., Berger H., Strauss J. (2014) The fungal contribution to the nitrogen cycle in agricultural soils. In: *Metagenomics of the Microbial Nitrogen Cycle: Theory, Methods and Applications* (ed. Marco D.) Caister Academic Press, Norfolk: 209–225.

Gross A., Han J.G. (2015) *Hymenoscyphus fraxineus* and two new *Hymenoscyphus* species identified in Korea. *Mycological Progress* **14**(4): 1–13.

Gross A., Hosoya T., Zhao Y.J., Baral H.-O. (2015) *Hymenoscyphus linearis* sp. nov: another close relative of the ash dieback pathogen *H. fraxineus*. *Mycological Progress* **14**(4): 20.

Guindon S., Gascuel O. (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *System Biology* **52**(5): 696–704.

Haelewaters D., Filippova N.V., Baral H.-O. (2018) A new species of *Stamnaria* (Leotiomycetes, Helotiales) from Western Siberia. *MycoKeys* **32**: 49–63.

Hallen H.E., Watling R., Adams G.C. (2003) Taxonomy and toxicity of *Conocybe lactea* and related species. *Mycological Research* **107**(8): 969–979.

Hamelin R.C., Tanguay P., Uzunovic A.A. (2013) *Molecular detection assays of forest pathogens*. Canadian Forest Service, Natural Resources Canada, Quebec, Canada

Han J.G., Hosoya T., Sung G.H., Shin H.D. (2014) Phylogenetic reassessment of Hyaloscyphaceae sensu lato (Helotiales, Leotiomycetes) based on multigene analyses. *Fungal Biology* **118**(2): 150–167.

Hartley A.J., de Mattos-Shipley K., Collins C.M., Kilaru S., Foster G.D., Bailey A.M. (2009) Investigating pleuromutilin-producing *Clitopilus* species and related basidiomycetes. *FEMS Microbiology Letters* **297**(1): 24–30.

Harrower E., Ammirati J., Cappuccino A., Ceska O., Kranabetter J.M., Kroeger P., et al. (2011) *Cortinarius* species diversity in British Columbia and molecular phylogenetic comparison with European specimen sequences. *Botany* **89**(11): 799–810.

Hausknecht A., Antonín V., Polčák J. (2007) A new, conspicuously coloured *Bolbitius* species from the Czech Republic. *Czech Mycology* **59**(1): 1–9.

He X. L., Li T.H., Jiang Z.D., Shen Y.H. (2012) Four new species of *Entoloma* s.l. (Agaricales) from southern China. *Mycological Progress* **11**: 915–925.

Hewitt E.J. (1966) *Sand and water culture methods used in the study of plant nutrition*. Farnhan Royal, Commonwealth Agricultural Bureau, Farnham, England.

Hoist-Jensen A., Vaage M., Schumacher T. (1998) An approximation to the phylogeny of *Sclerotinia* and related genera. *Nordic Journal of Botany* **18**(6): 705–719.

Holst-Jensen A., Vaage M., Schumacher T., Johansen S. (1999) Structural characteristics and possible horizontal transfer of group I introns between closely related plant pathogenic fungi. *Molecular Biology and Evolution* **16**(1): 114–126.

Hopple J.S. Jr. (1994) *Phylogenetic investigations in the genus* Coprinus *based on morphological and molecular characters*. PhD thesis, Duke University, Durham, NC.

Index Fungorum (2021) http://www.indexfungorum.org/names/Names.asp (accessed 5 December 2021).

Iturriaga, T., LoBuglio, K.F., Pfister, D.H. (2017) *Bulgariella pulla*, a Leotiomycete of uncertain placement, with an uncommon type of ascus opening. *Mycologia* **109**(6): 900–911.

Ivoilov A.V., Bolshakov S.Yu., Silaeva T.B. (2017) *The study of species diversity of macromycetes: a manual*. Publisher of the Mordovia State University, Saransk.

Jeppesen T.S., Frøslev T.G., Brandrud T.E. (2012) Subgen. *Phlegmacium* (Fr.) Trog. In: Knudsen H., Vesterholt J. (eds) *Funga Nordica: agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera. 2nd revised edition*. Nordsvamp, Copenhagen: 782–826.

Johnston P.R., Park D. (2005) *Chlorociboria* (Fungi, Helotiales) in New Zealand. *New Zealand Journal of Botany* **43**(3): 679–719.

Johnston P.R., Park D. (2013) The phylogenetic position of *Lanzia berggrenii* and its sister species. *Mycosystema* **32**(3): 366–385.

Johnston P., Park D., Baral H.-O., Galan R., Platas G., Tena R. (2014) The phylogenetic relationships of *Torrendiella* and *Hymenotorrendiella* gen. nov. within the Leotiomycetes. *Phytotaxa* **177**(1): 1–25.

Kalyaanamoorthy S., Minh B.Q., Wong T.K., von Haeseler A., Jermiin L.S. (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* **14**(6): 587–589.

Katoh K., Rozewicki J., Yamada K.D. (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* **20**: 1160–1166.

Kim M., Lee J.S., Park J.Y., Kim C. (2021) First report of six macrofungi from Daecheongdo and Socheongdo Islands, Korea. *Mycobiology* **49**(5): 454–460.

Kimbrough J.W., Atkinson M. (1972) Cultural features and imperfect stage of *Hymenoscyphus caudatus*. *American Journal of Botany* **59**(2): 165–171.

Kornerup A., Wanscher J.H. (1978) *Methuen Handbook of Colour. 3rd edition*. Methuen Publishing, London.

Koske R.E., Tessier B. (1983) A convenient, permanent slide mounting medium. *Mycological Society of America Newsletter* **34**: 59.

Kowalski T., Bilański P. (2019) *Hymenoscyphus pusillus*, a new species on leaves of *Fraxinus pennsylvanica* in Poland. *Forest Pathology* **49**(1): e12481.

Kozlov A.M., Darriba D., Flouri T., Morel B., Stamatakis A. (2019) RAxML-NG: A fast, scalable, and user-friendly tool for maximum likelihood phylogenetic inference. *Bioinformatics* **35**(21): 4453–4455.

Krüger M., Kruger C., Walker C., Stockinger H., Schussler A. (2012) Phylogenetic reference data for systematics and phylotaxonomy of arbuscular mycorrhizal fungi from phylum to species level. *New Phytologist* **193**(4): 970–984.

Krüger M., Stockinger H., Krüger C., Schüßler A. (2009) DNA-based species level detection of Glomeromycota: one PCR primer set for all arbuscular mycorrhizal fungi. *New Phytologist* **183**(1): 212–223.

Kumar S., Stecher G., Li M., Knyaz C., Tamura K. (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* **35**(6): 1547–1549.

Kumar S., Stecher G., Tamura K. (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* **33**: 1870–1874.

Landry J., Lamoureux Y., Lebeuf R., Paul A., Lambert H., Labbé R. (2021) Répertoire des cortinaires du Québec, 1re édition. Mycoquébec. Québec.

Larkin M.A., Blackshields G., Brown N.P., Chenna R., McGettigan P.A., McWilliam H., et al. (2007) Clustal W and Clustal X version 2.0. *Bioinformatics* **23**(21): 2947–2948.

Liimatainen K., Niskanen T., Dima B., Ammirati J.F., Kirk P.M., Kytövuori I. (2020) Mission impossible completed: unlocking the nomenclature of the largest and most complicated subgenus of *Cortinarius*, *Telamonia*. *Fungal Diversity* **104**: 291–331.

Liimatainen K., Niskanen T., Dima B., Kytövuori I., Ammirati J.F., Frøslev T.G. (2014) The largest type study of Agaricales species to date: bringing identification and nomenclature of *Phlegmacium* (*Cortinarius*) into the DNA era. *Persoonia* **33**: 98–140.

Liimatainen K., Niskanen T., Kytövuori I. (2017) Nomenclatural novelties. *Index Fungorum* **339**: 1–5.

Maddison W.P., Maddison, D.R. (2019) Mesquite: a modular system for evolutionary analysis. Version 3.61. http://www.mesquiteproject.org (accessed 19 April 2021).

Malloch D., Sigler L., Hambleton S., Vanderwolf K.J., Gibas C.F.C., McAlpine D.F. (2016) Fungi associated with hibernating bats in New Brunswick caves: the genus *Leuconeurospora*. *Botany* **94**(12): 1171–1181.

Malysheva E.F., Malysheva V.F., Svetasheva T.Y. (2015) Molecular phylogeny and taxonomic revision of the genus *Bolbitius* (Bolbitiaceae, Agaricales) in Russia. *Mycological Progress* **14**(8): 64.

Mao J., Xiao M., Chen X., Liang C., Dong M., Su Y., et al. (2018) Effect of fertilization mode on chemical components in tobacco leaves and their relationships with microbial characteristics in organic tobacco of karst region. *Southwest China Journal of Agricultural Sciences* **31**(1): 111–117.

Matheny P.B., Moreau P.A., Vizzini A., Harrower E., de Haan A., Contu M., Curti M. (2015) *Crassisporium* and *Romagnesiella*: two new genera of dark-spored Agaricales. *Systematics and Biodiversity* **13**(1): 28–41.

Matheny P.B., Wang Z., Binder M., Curtis J.M., Lim Y.W., Henrik Nilsson R., et al. (2007) Contributions of rpb2 and tef1 to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Molecular Phylogenetics and Evolution* **43**(2): 430–451.

McMullin D.R., Tanney J.B., McDonald K.P., Miller J.D. (2019) Phthalides produced by *Coccomyces strobi* (Rhytismataceae, Rhytismatales) isolated from needles of *Pinus strobus*. *Phytochemistry Letters* **29**: 17–24.

Mello C.M.A., da Silva G.A., Assis D.M.A., Pontes J.S., Ferreira A.C.A., Leão M.P.C., et al. (2013) *Paraglomus pernambucanum* sp. nov. and *Paraglomus bolivianum* comb. nov., and biogeographic distribution of *Paraglomus* and *Pacispora*. *Journal of Applied Botany and Food Quality* **86**: 113–125.

Mešić A., Tkalčec Z. (2008) *Entoloma reinwaldii*, a rare species new to Croatia. *Mycotaxon* **105**: 295–300.

Miller M.A., Pfeiffer W., Schwartz T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *2010 Proceedings of the Gateway Computing Environments Workshop* (GCE), New Orleans, LA: 1–8.

Milne I., Wright F., Rowe G., Marshal D.F., Husmeier D., McGuire G. (2004) TOPALi: Software for automatic identification of recombinant sequences within DNA multiple alignments. *Bioinformatics* **20**(11): 1806–1807.

Moll J., Hoppe B., König S., Wubet T., Buscot F., Krüger D. (2016) Spatial distribution of fungal communities in an arable soil. *Plos One* **11**(2): e0148130.

Morozova O.V., Noordeloos M.E., Vila J. (2014) *Entoloma* subgenus *Leptonia* in boreal-temperate Eurasia: towards a phylogenetic species concept. *Persoonia* **32**: 141–169.

Morton J.B., Redecker D. (2001) Two new families of Glomales, Archaeosporaceae and Paraglomaceae, with two new genera *Archaeospora* and *Paraglomus*, based on concordant molecular and morphological characters. *Mycologia* **93**(1): 181–195.

Moser M., Peintner U. (2002) The species complex *Cortinarius scaurus–C. herpeticus* based on morphological and molecular data. *Micologia e vegetazione mediterranea* **17**(1): 3–17.

Mosse B. (1962) Establishment of vesicular-arbuscular mycorrhiza under aseptic conditions. *Journal of Genetic Microbiology* **27**: 509–520.

Naseer A., Sarwar S., Khalid A.N., Healy R., Smith M.E. (2019) Hortiboletus kohistanensis (Boletaceae), a new bolete species from temperate and subalpine oak forests of Pakistan. *Phytotaxa* **388**(3): 239–246.

Nguyen L., Schmidt H.A., von Haeseler A., Minh B.Q. (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. *Molecular Biology and Evolution* **32**(1): 268–274.

Niskanen T. (2014) Nomenclatural novelties. *Index Fungorum* **197**: 1–4.

Niskanen T., Laine S., Liimatainen K., Kytövuori I. (2012) *Cortinarius sanguineus* and equally red species in Europe with an emphasis on northern European material. *Mycologia* **104**(1): 242–253.

Niskanen T., Liimatainen K., Ammirati J.F., Hughes K.W. (2013) *Cortinarius* section *Sanguinei* in North America. *Mycologia* **105**(2): 344–356.

Niskanen T., Liimatainen K., Ammirati J., Kytövuori I. (2020) Nomenclatural novelties. *Index Fungorum* **439**: 1–12.

Niskanen T., Liimatainen K., Kytövuori I. (2006) Taxonomy, ecology and distribution of *Cortinarius rubrovioleipes* E. Bendiksen & K. Bendiksen and *C. hinnuleoarmillatus* Reumaux (Basidiomycota, Agaricales) in Fennoscandia. *Karstenia* **46**(1): 1–12.

Niskanen T., Liimatainen K., Kytövuori I., Ammirati J. (2015) Nomenclatural novelties. *Index Fungorum* **256**: 1–2.

Noordeloos M.E., Lorås J., Eidissen S.E., Brandrud T.E., Bendiksen E., Morozova O., et al. (2021) Three new *Entoloma* species of the Cyanula clade (Entolomataceae, Agaricales) from (sub)alpine habitats in Northern Norway and Sweden. *Sydowia* **73**: 185–196.

Oehl F., Körner C. (2014) Multiple mycorrhization at the coldest place known for Angiosperm plant life. *Alpine Botany* **124**: 193–198.

Oehl F., Santos V.M., Palenzuela J. (2016) *Paraglomus turpe*, a new arbuscular mycorrhizal fungal species from Central European agricultural soils. *Nova Hedwigia* **103**(3–4): 491–499.

Örstadius L., Larsson E. (2013) *Bolbitius excoriatus*, flagnande guldskivling, funnen på spillning i Sverige. *Svensk Mykologisk Tidskrift* **34**(2): 2–6.

Osmundson T.W., Robert V.A., Schoch C.L., Baker L.J., Smith A., Robich G., et al. (2013) Filling gaps in biodiversity knowledge for macrofungi: contributions and assessment of an herbarium collection DNA barcode sequencing project. *PLoS ONE* **8**(4): e62419.

Palmer J.M., Lindner D.L., Volk T.J. (2008) Ectomycorrhizal characterization of an American chestnut (*Castanea dentata*) dominated community in Western Wisconsin. *Mycorrhiza* **19**(1): 27–36.

Pärtel K., Baral, H.-O., Tamm H., Põldmaa K. (2017) Evidence for the polyphyly of *Encoelia* and Encoelioideae with reconsideration of respective families in Leotiomycetes. *Fungal Diversity* **82**(1): 183–219.

Peck, C.H. (1893) Descriptions of new species of fungi. *Bulletin of the Buffalo Society of Natural Sciences* **1**: 41–72.

Pegler D.N., Young T.W.K. (1972) Basidiospore form in the British species of *Inocybe*. *Kew Bulletin* **26**(3): 499–537.

Pham T.H.G., Morozova O.V. (2020) Boletoid fungi (Boletaceae, Basidiomycota) of the Bidoup – Nui Ba National Park (Vietnam). *Turczaninowia* **23**(4): 88–98.

Pham T.H.G., Morozova O.V., Alexandrova A.V. (2021) Boletoid fungi (Boletaceae, Basidiomycota) of protected areas of Kon Tum Plateau (Central Highlands of Vietnam). *Turczaninowia* **24**(3): 65–76.

Phillips W. (1893) *A manual of the British discomycetes, with descriptions of all the species of fungi hitherto found in Britain, included in the family and illustrations of the genera*. Kegan Paul, Trench, Trübner & Co., London.

Queloz V., Grünig C.R., Berndt R., Kowalski T., Sieber T.N., Holdenrieder O. (2011) Cryptic speciation in *Hymenoscyphus albidus*. *Forest Pathology* **41**(2): 133–142.

Raitviir A. (1984) *Lanzia equiseti* Raitv. species nova. *Novitates Systematicae Plantarum non Vascularium* (*Новости систематики низших растений*) **21**: 116–118.

Rambaut A., Drummond A.J., Xie D., Baele G., Suchard M.A. (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* **67**(5): 901–904.

Renker C., Błaszkowski J., Buscot F. (2007) *Paraglomus laccatum* comb. nov. - a new member of Paraglomeraceae (Glomeromycota). *Nova Hedwigia* **84**(3–4): 395–407.

Rambaut A., Drummond A.J., Xie D., Baele G., Suchard M.A. (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* **67**(5): 901–904.

Ronquist F., Huelsenbeck J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**(12): 1572–1574.

Ronquist F., Teslenko M., van der Mark P., Ayres D.L., Darling A., Höhna S., et al. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**(3): 539–542.

Rose S.L., Trappe J.M. (1980) Three new endomycorrhizal *Glomus* spp. associated with actinorrhizal shrubs. *Mycotaxon* **10**: 413–420.

Saar G., Dima B., Schmidt-Stohn G., Brandrud T.E., Bellù F., Frøslev T.G., et al. (2015) *Cortinarius* sous-genre *Phlegmacium* section *Purpurascentes* en Europe. *Journal des J.E.C.* **17**: 135–148.

Schoch C.L., Robbertse B., Robert V., Vu D., Cardinali G., Irinyi L. et al. (2014) Finding needles in haystacks: linking scientific names, reference specimens and molecular data for Fungi. *Database* **2014**: bau061.

Sieverding E. (1991) *Vesicular–arbuscular mycorrhiza management in tropical agrosystems*. Sonderpublikation der GTZ, Eschborn, Germany.

Smith A.H. (1942) New and unusual Cortinarii from Michigan, with a key to the North American species of subgenus *Bulbopodium*. *Bulletin of the Torrey Botanical Club* **69**(1): 44–64.

Soop K. (2018) Cortinarius in Sweden, 16th revised edition. Éditions Scientrix, Mora, Sweden.

Soop K., Dima B., Cooper J.A., Park D., Oertel B. (2019) A phylogenetic approach to a global supraspecific taxonomy of *Cortinarius* (Agaricales) with an emphasis on the southern mycota. *Persoonia* **42**: 261–290.

Spain J.L. (1990) Arguments for diagnoses based on unaltered wall structures. *Mycotaxon* **38**: 71–76.

Spain J.L., Miranda, J.C. (1996) *Glomus brasilianum*: an ornamented species in the Glomaceae. *Mycotaxon* **60**: 137–142.

Stadler T. (2009) On incomplete sampling under birth–death models and connections to the sampling-based coalescent. *Journal of Theoretical Biology* **261**(1): 58–66.

Suchard M.A., Lemey P., Baele G., Ayres D.L., Drummond A.J., Rambaut A. (2018) Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evolution* **4**(1): vey016.

Suh S.O., Blackwell M. (1999) Molecular phylogeny of the cleistothecial fungi placed in Cephalothecaceae and Pseudeurotiaceae. *Mycologia* **91**(5): 836–848.

Suija A., Ertz D., Lawrey J.D., Diederich P. (2015) Multiple origin of the lichenicolous life habit in Helotiales, based on nuclear ribosomal sequences. *Fungal Diversity* **70**(1): 55–72.

Svrček M. 1985 [1984]. A taxonomic revision of inoperculate discomycetes described by J. Velenovský in the genus *Helotium*, preserved in National Museum, Prague. *Sborník Národního Musea v Praze (B)* **40**(3–4): 129–215.

Tamura K., Nei M. (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution* **10**: 512–526.

Tedersoo L., Jairus T., Horton B.M., Abarenkov K., Suvi T., Saar I., Kõljalg U. (2008) Strong host preference of ectomycorrhizal fungi in a Tasmanian wet sclerophyll forest as revealed by DNA barcoding and taxon-specific primers. *New Phytologist* **180**: 479–490.

Terhonen E., Sun H., Buee M., Kasanen R., Paulin L., Asiegbu F.O. (2013) Effects of the use of biocontrol agent (*Phlebiopsis gigantea*) on fungal communities on the surface of *Picea abies* stumps. *Forest Ecology and Management* **310**: 428–433.

Thiers B. (continuously updated) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanic Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih/ (accessed 3 December 2021).

Tóth A., Hausknecht A., Krisai-Greilhuber I., Papp T., Vágvölgyi C., Nagy L.G. (2013) Iteratively refined guide trees help improving alignment and phylogenetic inference in the mushroom family Bolbitiaceae. *PLoS ONE* **8**(2): e56143.

Vasco-Palacios A.M., López-Quintero C., Esperanza Franco-Molano A. Boekhout T. (2014) *Austroboletus amazonicus* sp. nov. and *Fistulinella campinaranae* var. *scrobiculata*, two commonly occurring boletes from a forest dominated by *Pseudomonotes tropenbosii* (Dipterocarpaceae) in Colombian Amazonia. *Mycologia* **106**(5): 1004–1014.

Vierheilig H., Coughlan A.P., Wyss U., Piché Y. (1998) Ink and vinegar, a simple staining technique for arbuscular-mycorrhizal fungi. *Applied and Environmental Microbiology* **64**(12): 5004–5007.

Vilgalys R., Hester M. (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* **172**: 4238–4246.

Vu D., Groenewald M., De Vries M., Gehrmann T., Stielow B., Eberhardt U., et al. (2019) Large-scale generation and analysis of filamentous fungal DNA barcodes boosts coverage for kingdom fungi and reveals thresholds for fungal species and higher taxon delimitation. *Studies in Mycology* **92**: 135–154.

Walker C., Rhodes L.H. (1981) *Glomus albidus*: A new species in the Endogonaceae. *Mycotaxon* **12**: 509–514.

Wang Y., Li T., Li Y., Björn L.O., Rosendahl S., Olsson P.A., et al. (2015) Community dynamics of arbuscular mycorrhizal fungi in high-input and intensively irrigated rice cultivation systems. *Applied and Environmental Microbiology* **81**: 2958–2965.

Wang Z., Binder M., Hibbett D.S. (2005) Life history and systematics of the aquatic discomycete *Mitrula* (Helotiales, Ascomycota) based on cultural, morphological, and molecular studies. *American Journal of Botany* **92**(9): 1565–1574.

Watling R. (1977) Observations on the Bolbitiaceae, 13 & 14. *Kew Bulletin* **31**(3): 587–594.

Watling R. (1987) Observations on the Bolbitiaceae – 30 *Agaricus callistus* Peck. *Mycologia* **79**(2): 310–313.

White T.J., Bruns T., Lee S., Taylor J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR protocols: a guide to methods and applications* (eds. Innis M.A., Gelfand D.H., Sninsky J.J., White T.J.), Academic Press, New York, NY: 315–322.

Wijayawardene N.N., Hyde K.D., Al-Ani L.K.T., Tedersoo L., Haelewaters D., Rajeshkumar K.C., et al. (2020) Outline of fungi and fungi-like taxa. *Mycosphere* **11**(1): 1060–1456.

Wiseman M.S., Dugan F.M., Kim Y.K., Xiao C.L. (2015) A postharvest fruit rot of apple caused by *Lambertella corni-maris* in Washington State. *Plant Disease* **99**(2): 201–206.

Wu G., Feng B., Xu J., Zhu X.T., Li Y.C., Zeng N.K., et al. (2014) Molecular phylogenetic analyses redefine seven major clades and reveal 25 new generic lineages in the fungal family Boletaceae. *Fungal Diversity* **69**: 93–115.

Wu G., Li Y.C., Zhu X.T., Zhao K., Han L.H., Cui Y.Y., et al. (2016). One hundred noteworthy boletes from China. *Fungal Diversity* **81**: 25–188.

Xie H.J., Lin W.F., Jiang S., Xue R., Wu L.L., Zhang Y.Z., et al. (2020). Two new species of *Hortiboletus* (Boletaceae, Boletales) from China. *Mycological Progress* **19**(11): 1377–1386.

Zeng H., Tan F., Zhang Y., Feng Y., Shu Y., Wang J. (2014) Effects of cultivation and return of *Bacillus thuringiensis* (Bt) maize on the diversity of the arbuscular mycorrhizal community in soils and roots of subsequently cultivated conventional maize. *Soil Biology & Biochemistry* **75**: 254–263.

Zhang Y.H., Zhuang W.Y. (2002) Re-examinations of *Helotium* and *Hymenoscyphus* (Helotiales, Helotiaceae): specimens on deposit in HMAS. *Mycotaxon* **81**: 35–43.

Zhang Y.H., Zhuang W.Y. (2004) Phylogenetic relationships of some members in the genus *Hymenoscyphus* (Ascomycetes, Helotiales). *Nova Hedwigia* **78**(3–4): 475–484.

Zhao Y.J., Hosaka K., Hosoya T. (2016) Taxonomic re-evaluation of the genus *Lambertella* (Rutstroemiaceae, Helotiales) and allied stroma-forming fungi. *Mycological Progress* **15**(12): 1215–1228.

Zheng H.D., Zhuang W.Y. (2014) *Hymenoscyphus albidoides* sp. nov. and *H. pseudoalbidus* from China. *Mycological Progress* **13**(3): 625–638.

Zheng H.D., Zhuang W.Y. (2015) Five new species of *Hymenoscyphus* (Helotiaceae, Ascomycota) with notes on the phylogeny of the genus. *Mycotaxon* **130**(4): 1017–1038.

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