

## Fungal Systematics and Evolution: FUSE 8

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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 *Paraglomerus 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 vulgare*, or *Urochloa briantha* 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  $21.4 \pm 2.0$  °C,  $29.0 \pm 3.0$  °C, and  $36.0 \pm 2.0$  °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 *Paraglomerum 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 Błaszowski (2012) and Oehl et al. (2016) for species with glomoid spore formation. Photographs were taken with a digital camera (Leica 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 (Cléménçon 2009, Ivoilov et al. 2017). Microscopic observations were made from dried material mounted in 5 % KOH and 10 % Congo Red in NH<sub>4</sub>OH 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<sub>2</sub>, 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 (Lan-dry 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- $\alpha$  (*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<sub>2</sub>O. 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 pylon in 3 µl milli-Q H<sub>2</sub>O 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'-ACTTGGT-CATTTAGAGGAAGT-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 *Cortinari* 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 <sup>1</sup> , status <sup>2</sup> , voucher) | Country, host                             | ITS      | LSU      | rDNA     | <i>tef1</i> | Reference(s)                                  |
|---|---|---|----------|----------|----------|-------------|---|
| <i>“Cenangium” acuum</i>                            | TAAM:198449   | Czech Republic, <i>Pinus sylvestris</i>   | LT158445 | KX090828 |          |             | Pärtel et al. (2017)                          |
| <i>“Lanzia” berggrenii</i>                          | ICMP:19614  | Australia, <i>Nothofagus cunninghamii</i> | KC164645 | KC164640 |          |             | Johnston & Park (2013)                        |
| <i>“Lanzia” ovispora</i>                            | PDD:70881   | New Zealand, <i>Elaeocarpus dentatus</i>  | MH578500 | MH587172 |          |             | P.R. Johnston & D. Park, unpubl.              |
| <i>“Rutstroemia” luteovirescens</i>                 | TU:104450   | Estonia, <i>Acer platanoides</i>          | LT158431 | KX090814 |          |             | Pärtel et al. (2017)                          |
| <i>Archaeospora trappei</i>                         | Att178-3  | UK  |          |          | FR750036 |             | Krüger et al. (2012)                          |
| <i>Archaeospora trappei</i>                         | Att178-3  | UK  |          |          | FR750038 |             | Krüger et al. (2012)                          |
| <i>Bicornispora seditiosa</i>                       | WU:32446, T   | Spain, <i>Acer monspessulanum</i>         | KF499360 | KF499360 |          |             | Galán et al. (2015)                           |
| <i>Bolbitius aleuriatus</i>                         | voucher 3029  | Italy                                     | JF907770 |          |          |             | Osmundson et al. (2013)                       |
| <i>Bolbitius bisporus</i>                           | LE 303558   | Russia                                    | KR425534 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius callisteus</i>                         | PBM 2638  | USA                                       | EU477860 |          |          |             | K.W. Hughes & P.B. Matheny, unpubl.           |
| <i>Bolbitius callistus</i>                          | ALV9432   |   | MF093747 |          |          |             | P. Björck & A. Tudzarovski, unpubl.           |
| <i>Bolbitius callistus</i>                          | LE F 331684   | Russia                                    | MW763060 |          |          |             | This study                                    |
| <i>Bolbitius callistus</i>                          | LE F 331685   | Russia                                    | MW763061 |          |          |             | This study                                    |
| <i>Bolbitius callistus</i>                          | LE 313564   | Russia                                    | MW763062 |          |          |             | This study                                    |
| <i>Bolbitius coprophilus</i>                        | LE 11317  | Russia                                    | KR425527 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius coprophilus</i>                        | LE 18905  | Russia                                    | KR425525 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius coprophilus</i>                        | LE 18599  | Russia                                    | KR425526 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius coprophilus</i>                        | LE 287244   | Russia                                    | KR425524 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius demangei</i>                           | voucher 4030  | Italy                                     | JF907771 |          |          |             | Osmundson et al. (2013)                       |
| <i>Bolbitius excoriatus</i>                         | WU16355, T  | Spain                                     | KC456418 |          |          |             | Örstadius & Larsson (2013)                    |
| <i>Bolbitius excoriatus</i>                         | LO23-10   | Sweden                                    | KC456419 |          |          |             | Örstadius & Larsson (2013)                    |
| <i>Bolbitius lacteus</i>                            | LE 303559   | Russia                                    | KR425523 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius lacteus</i>                            | MSC 378485  | USA                                       | AY194520 |          |          |             | Hallen et al. (2003)                          |
| <i>Bolbitius muscicola</i>                          | PDD: 87721  | New Zealand                               | JQ694118 |          |          |             | J.A. Cooper, D. Park & P.R. Johnston, unpubl. |
| <i>Bolbitius pallidus</i>                           | LE 234343, T  | Russia                                    | KR425533 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius pallidus</i>                           | LE 303557   | Russia                                    | KR425535 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius psittacinus</i>                        | BRNM 705079, T  | Czech Republic                            | EF648217 |          |          |             | Hausknecht et al. (2007)                      |
| <i>Bolbitius reticulatus</i>                        | WU30001   | Hungary                                   | JX968249 |          |          |             | Tóth et al. (2013)                            |
| <i>Bolbitius reticulatus</i>                        | LE 227536   | Russia                                    | KR425531 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius reticulatus</i>                        | LE 253961   | Russia                                    | KR425529 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius reticulatus</i>                        | LE 303560   | Russia                                    | KR425533 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius reticulatus</i> var. <i>plutaoides</i> | LE 234342   | Russia                                    | KR425532 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius subvolvatus</i>                        | strain WU28379  | Italy                                     | JX968248 |          |          |             | Tóth et al. (2013)                            |
| <i>Bolbitius titubans</i>                           | LE 303556   | Russia                                    | KR425522 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius titubans</i>                           | LE 214359   | Russia                                    | KR425521 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius titubans</i>                           | LE 289428   | Russia                                    | KR425519 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius titubans</i>                           | LE 287256   | Russia                                    | KR425518 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius titubans</i>                           | LE 265066   | Russia                                    | KR425511 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius titubans</i>                           | LE 202345   | Russia                                    | KR425512 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius titubans</i>                           | LE 303562   | Russia                                    | KR425513 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius titubans</i>                           | LE 258041   | Russia                                    | KR425514 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius titubans</i>                           | LE 235346   | Russia                                    | KR425509 |          |          |             | Malysheva et al. (2015)                       |
| <i>Bolbitius variicolor</i>                         | MSC 378488  | USA                                       | AY194535 |          |          |             | Hallen et al. (2003)                          |
| <i>Bolbitius variicolor</i>                         | voucher 2303  | Italy                                     | JF907768 |          |          |             | Osmundson et al. (2013)                       |
| <i>Bolbitius viscosus</i>                           | TENN:PBM3032  | USA                                       | HQ840656 |          |          |             | Matheny et al. (2015)                         |
| <i>Bolbitius vitellinus</i>                         | MSC 378484  | USA                                       | AY194519 |          |          |             | Hallen et al. (2003)                          |
| <i>Bolbitius vitellinus</i>                         | WTU:MTS5020   | USA                                       | DQ200920 |          |          |             | Matheny et al. (2007)                         |
| <i>Botrytis cinerea</i>                             | CBS:179.71  | The Netherlands, <i>Cichorium endivia</i> | MH860054 | MH871836 |          |             | Vu et al. (2019)                              |
| <i>Bulgariella pulla</i>                            | DHP-06-607  | USA                                       | KJ704848 | KJ704849 |          |             | Iturriaga et al. (2017)                       |

Tab. 1 (continued).

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



Tab. 1 (continued).

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

Tab. 1 (continued).

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

Tab. 1 (continued).

| Species  | ID (isolate, strain <sup>1</sup> , status <sup>2</sup> , voucher) | Country, host                               | ITS        | LSU      | rDNA | <i>tef1</i> | Reference(s)   |
|--|---|---|------------|----------|------|-------------|--|
| <i>Cortinarius venustissimus</i>                           | PC:5371, T  | Sweden                                      | MT935580   |          |      |             | Liimatainen et al. (2020)                              |
| <i>Cortinarius violaceoflavescens</i>                      | HRL1825   | Canada                                      | MN751571   |          |      |             | Landry et al. (2021)                                   |
| <i>Cortinarius violaceoflavescens</i>                      | HRL1826, T  | Canada                                      | MN751572   |          |      |             | Landry et al. (2021)                                   |
| <i>Cortinarius violaceoflavescens</i>                      | YL4402  | Canada                                      | MN751573   |          |      |             | Landry et al. (2021)                                   |
| <i>Cortinarius violaceonitens</i>                          | TUB 019776  |   | KJ421028   |          |      |             | Garnica et al. (2016)                                  |
| <i>Cortinarius violaceonitens</i>                          | YL3531  | Canada                                      | MN751769   |          |      |             | Landry et al. (2021)                                   |
| <i>Cortinarius violaceonitens</i>                          | PC:R.Henry 2190, T  | France                                      | KF732425   |          |      |             | Liimatainen et al. (2014)                              |
| <i>Cortinarius virentophyllus</i>                          | MICH 10439, T   | USA   | NR130284   |          |      |             | Liimatainen et al. (2014)                              |
| <i>Cortinarius viridicarneus</i>                           | HRL1325, T  | Canada                                      | KJ705136   |          |      |             | J.A. Bérubé et al., unpubl.                            |
| <i>Cortinarius viridicarneus</i>                           | HRL0315   | Canada                                      | MN750891   |          |      |             | Landry et al. (2021)                                   |
| <i>Cortinarius viridirubescens</i>                         | IB 19950688, T  | USA   | NR130285   |          |      |             | Liimatainen et al. (2014)                              |
| <i>Cortinarius xanthochlorus</i>                           | S:F44373  |   | EU057047   |          |      |             | Garnica et al. (2009)                                  |
| <i>Cortinarius xanthosuavis</i>                            | TUB 019746  |   | KJ420986   |          |      |             | Garnica et al. (2016)                                  |
| <i>Dicephalospora huangshanica</i>                         | KUS-F52405  | South Korea, <i>Castanopsis cuspidata</i>   | JN033408   | JN086711 |      |             | Han et al. (2014)                                      |
| <i>Diplolaevioopsis ranula</i>                             | NBM:FL-14388  | Canada, <i>Lecanora strobilina</i>          | KP984782   | KP984785 |      |             | Etayo et al. (2015)                                    |
| <i>Encoelia furfuracea</i>                                 | TAAM:137509   | Estonia, <i>Corylus avellana</i>            | LT158482   | KX090796 |      |             | Pärtel et al. (2017)                                   |
| <i>Entoloma azureosquamulosum</i>                          | HKAS53408   | China                                       | JQ410334   |          |      |             | He et al. (2012)                                       |
| <i>Entoloma caeruleopolitum</i>                            | K(M)128161  | United Kingdom                              | MF977965   |          |      |             | J.J. Elsey, unpubl.                                    |
| <i>Entoloma callipygmaeum</i>                              | LE 253784, T  | Russia                                      | MZ145207   |          |      |             | Dima et al. (2021)                                     |
| <i>Entoloma kauffmannii</i>                                | KA13-1202   | South Korea                                 | KR673675   |          |      |             | Kim et al. (2015)                                      |
| <i>Entoloma meridionale</i>                                | ACAM 2018-0151  | Greece                                      | OL679697   |          |      |             | This study   |
| <i>Entoloma meridionale</i>                                | L0607587  | Spain                                       | OL679701   |          |      |             | This study   |
| <i>Entoloma meridionale</i>                                | CNF1-2117   | Croatia                                     | OL679702   |          |      |             | This study   |
| <i>Entoloma meridionale</i>                                | ACAM 2018-0153, T   | Greece                                      | OL679700   |          |      |             | This study   |
| <i>Entoloma meridionale</i>                                | ACAM 2018-0152  | Greece                                      | OL679699   |          |      |             | This study   |
| <i>Entoloma meridionale</i>                                | ACAM 2014-0127  | Greece                                      | OL679698   |          |      |             | This study   |
| <i>Entoloma minutigranulosum</i>                           | LE 302096, T  | Russia                                      | MZ145214   |          |      |             | Dima et al. (2021)                                     |
| <i>Entoloma mougeotii</i>                                  | LE254352  | Russia                                      | KC898446   |          |      |             | Morozova et al. (2014)                                 |
| <i>Entoloma poliopus</i>                                   | G4742   | Estonia                                     | UDB032859* |          |      |             | R. Pau, unpubl.  |
| <i>Entoloma pudens</i>                                     | L 0608054   | The Netherlands                             | MW934594   |          |      |             | Crous et al. (2021)                                    |
| <i>Entoloma septentrionale</i>                             | O-F-254295, T   | Norway                                      | MW340904   |          |      |             | Noordeloos et al. (2021)                               |
| <i>Entoloma</i> sp.  | TUF120259   | Estonia                                     | UDB024650* |          |      |             | I. Saar, unpubl.                                       |
| <i>Entoloma</i> sp.  | soil sample   | USA   | KP889939   |          |      |             | S.H.A. Guichon & S.W. Simard, unpubl.                  |
| <i>Entoloma</i> sp.  | MEL2382758  | Australia                                   | KP012941   |          |      |             | G. Bonito, M. Barrett, F. Udovicic & T. Lebel, unpubl. |
| <i>Entoloma subcorvinum</i>                                | TENN070435  | USA   | KY744169   |          |      |             | P.B. Matheny, S.A. Trudell & M.G. Wood, unpubl.        |
| <i>Galeropsis desertorum</i>                               | PR 154181   | Czech Republic                              | AY194534   |          |      |             | Hallen et al. (2003)                                   |
| <i>Grovesinia moricola</i>                                 | KUS-F26901  | Korea, <i>Humulus japonicus</i>             | KC460209   | KX098504 |      |             | Cho et al. (2013)                                      |
| <i>Grovesinia pyramidalis</i>                              | CBS:737.68  | The Netherlands, <i>Acer pseudoplatanus</i> |            | MH878399 |      |             | Vu et al. (2019)                                       |
| <i>Grovesinia pyramidalis</i>                              | 1836.K  | USA, <i>Juglans nigra</i>                   | Z81433     | AJ226081 |      |             | Holst-Jensen et al. (1998, 1999)                       |
| <i>Gyroporus castaneus</i>                                 | JMP0028   | USA   | EU819468   |          |      |             | Palmer et al. (2008)                                   |
| <i>Gyroporus cyanescens</i>                                | NAMA190   | USA   | EU819495   |          |      |             | Palmer et al. (2008)                                   |
| <i>Heyderia abietis</i>                                    | HMAS:71954  |   | AY789297   | AY789296 |      |             | Wang et al. (2005)                                     |
| <i>Hortiboletus amygdalinus</i>                            | NIBR-FG0000502792   | South Korea                                 | MW578955   |          |      |             | Kim et al. (2021)                                      |
| <i>Hortiboletus bubalinus</i> [as <i>Hortiboletus</i> sp.] | KR-M-0044351  | Germany                                     | MT005978   |          |      |             | M. Scholler, unpubl.                                   |
| <i>Hortiboletus indorubellus</i>                           | CAL: DC 14-002, T   | India                                       | NR_154076  |          |      |             | Das et al. (2016)                                      |
| <i>Hortiboletus kohistanensis</i>                          | LAH35327, T   | Pakistan                                    | MG988192   |          |      |             | Naseer et al. (2019)                                   |
| <i>Hortiboletus napaeus</i>                                | FHMU3325  | China                                       | MT646445   |          |      |             | Xie et al. (2020)                                      |
| <i>Hortiboletus rubellus</i>                               | JV00-357  | Denmark                                     | UDB001406* |          |      |             | L. Tedersoo, unpubl.                                   |

Tab. 1 (continued).

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



Tab. 1 (continued).

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

Tab. 1 (continued).

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

Tab. 1 (continued).

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

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

<sup>2</sup> 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 *Hortibolletus* 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 *Paraglomerus peruvianum* sp. nov. were supplemented with other related glomeromycotan se-

quences 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  $2 \times 10^6$  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 Black-Box tool available at <https://raxml-ng.vital-it.ch/#/> (Kozlov et al. 2019), with 100 bootstrap replicates. BI analyses were performed with MrBayes version 3.2.5 (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  $\geq 200$  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 TreeAnnotator. 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)  $\geq 200$  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'-CATT-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***

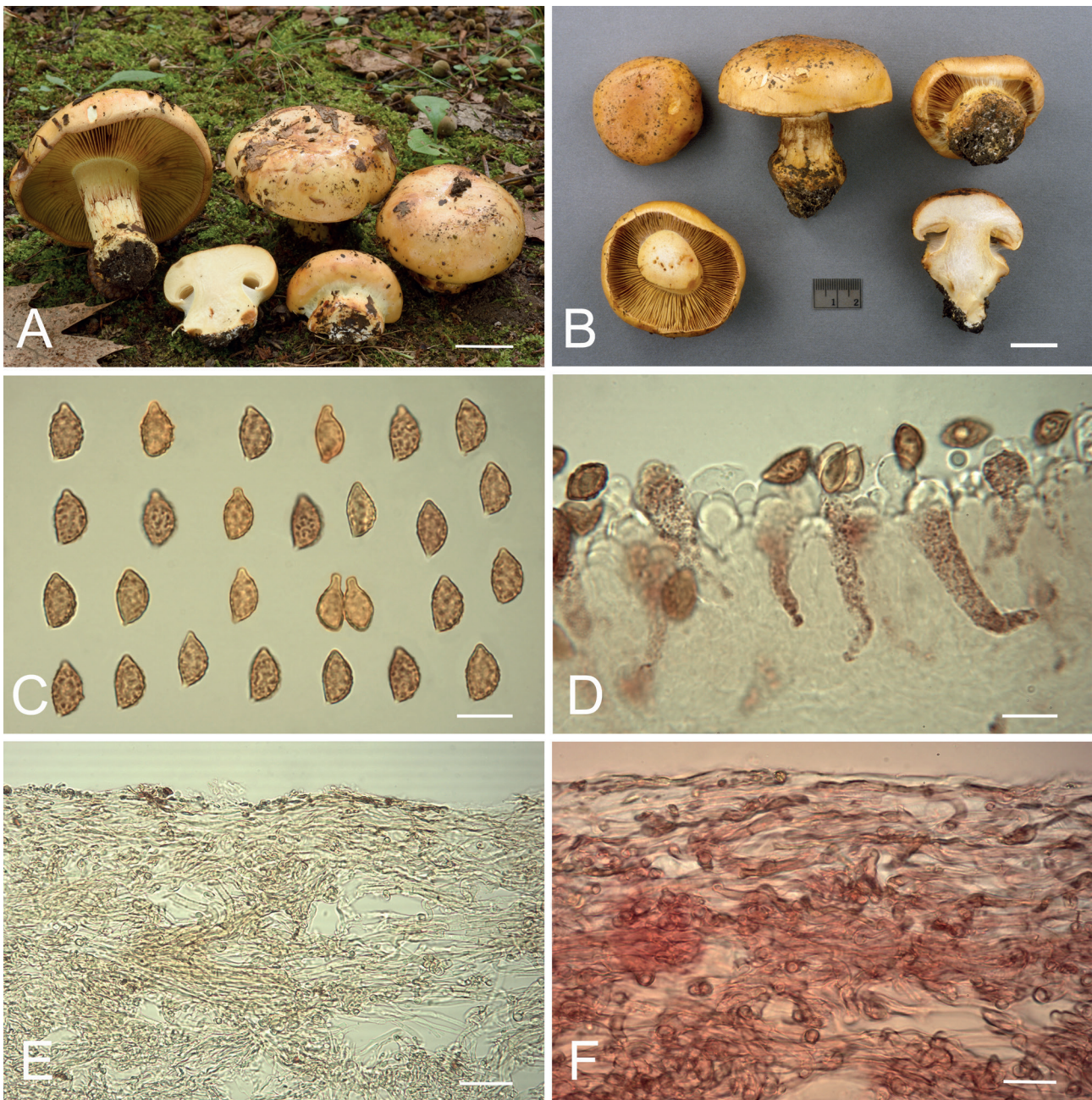
***Cortinarius caryae* Lebeuf, A. Paul, J. Landry & Y. Lamoureux, sp. nov.** – Figs. 1, 2  
Mycobank no.: MB 839556

**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  $9.5\text{--}11.5 \times 5.0\text{--}7.0 \mu\text{m}$ , on average  $10.3 \times 5.8 \mu\text{m}$ . Pileipellis simplex.

**Holotypus.** – CANADA. Quebec, Sainte-Anne-de-Bellevue, Arboretum Morgan,  $45^{\circ}25'56.25''\text{N}$ ,  $73^{\circ}56'44.40''\text{W}$ , 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 appanate 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 [ $181/6/4$ ]  $9.5\text{--}11.0\text{--}(11.5) \times (5.0\text{--})5.5\text{--}6.0\text{--}(7.0) \mu\text{m}$ , on average (av.)  $10.3 \times 5.8 \mu\text{m}$ ,  $Q=1.50\text{--}2.10$ ,  $Q_{av}=1.76$ , limoniform, less frequently amygdaliform, in some collections strongly papillate, coarsely verrucose, moderately dextrinoid. – Basidia  $26\text{--}44 \times 8\text{--}9.5 \mu\text{m}$ , 4-spored, clavate, colorless at first but developing a brownish yellow agranular pigment; in

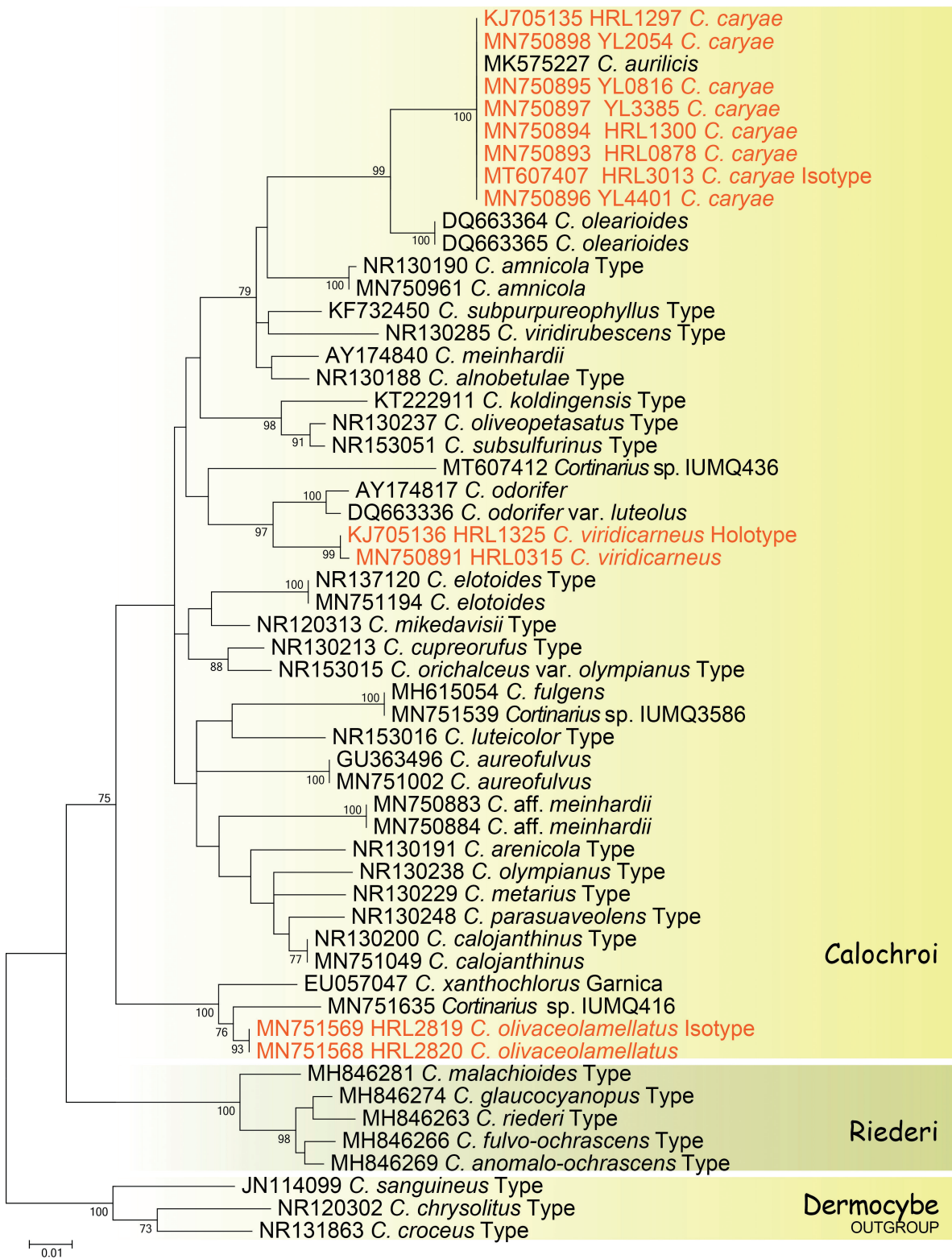




**Fig. 1.** *Cortinarius caryae*. **A.** Basidiomata *in situ*, collection DAOM 984903 (holotype). **B.** Basidiomata, collection CMMF003385. **C.** Basidiospores. **D.** Pigmented basidia in KOH. **E.** Pileipellis section in Melzer's reagent. **F.** Pileipellis section in SDS Congo Red. Scale bars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

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  $\mu$ m wide, with an intracellular golden yellow pigment; hyphae in matrix 1.5–5  $\mu$ m wide, slightly to moderately interwoven, mostly smooth, some finely incrustated, occasionally more coarsely spirally incrustated, 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 ( $-\ln L=4045,3280$ ) 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 incrustated, 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 Bois-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*.

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

**Basidiomycota, Agaricomycetes, Agaricales, Cortinariaceae**

***Cortinarius* section *Calochroi***

***Cortinarius viridicarneus* Lebeuf, A. Paul & J. Landry, sp. nov.** – Figs. 2, 3

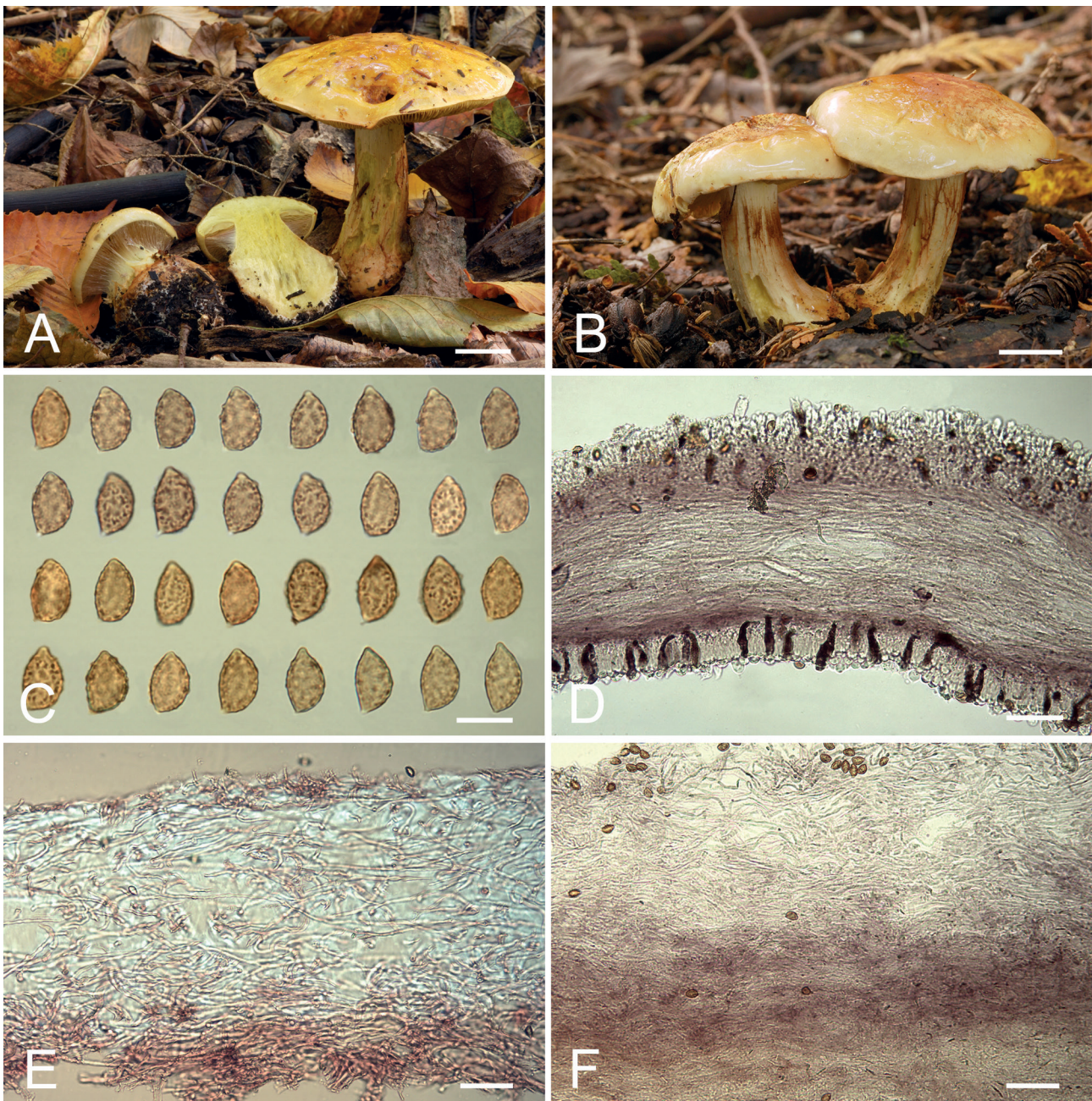
MycoBank no.: MB 839557

**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 Bois-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<sub>av</sub>=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  $\mu$ m, D–F 50  $\mu$ m.

smooth. – Hymenial cystidia absent. – Pileipellis simplex: epicutis with a well-developed gelatinous matrix, hyphae in matrix 1–4  $\mu$ m wide, ascending-interwoven, sand brown, smooth, in KOH purplish grey; basal layer of 3–5  $\mu$ m wide hyphae, subparallel above, in bundles below, pale yellow, smooth, in KOH purplish to pur-

plish 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  $\mu\text{m}$  in Brandrud 1990–2014).

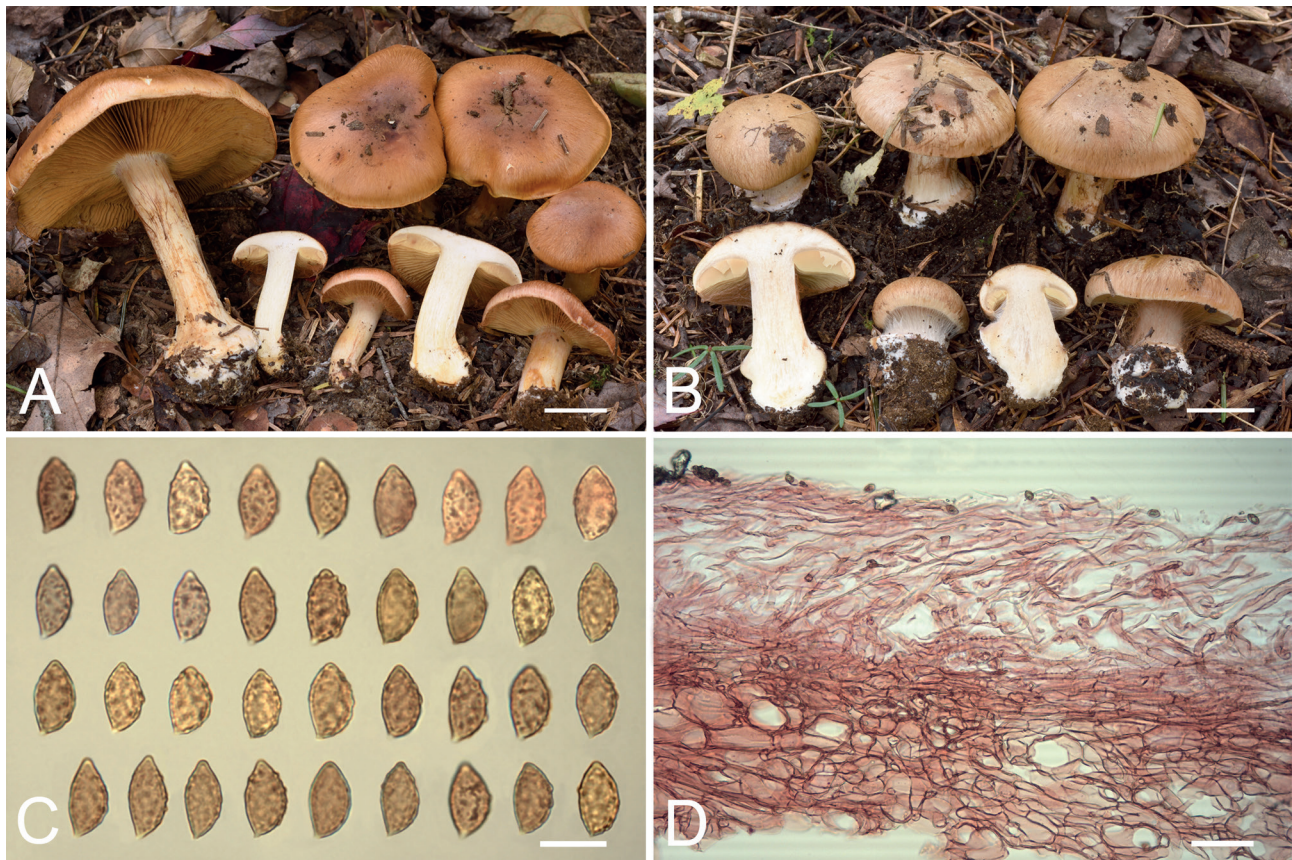
**Authors:** R. Lebeuf, J. Landry & A. Paul

**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  $\mu\text{m}$ , D 50  $\mu\text{m}$ .

vaceous yellow young lamellae, marginate bulb, pale yellow context, and fruity odor. Basidiospores  $10\text{--}12.5 \times 5.5\text{--}7.5 \mu\text{m}$ , on average  $11.4 \times 6.3 \mu\text{m}$ . Pileipellis simplex.

**Holotypus.** – CANADA. Quebec, Saint-Stanislas, Parc de la rivière Batiscan, trail Le Buis,  $46^{\circ}34'47.0''\text{N}$ ,  $72^{\circ}24'45.4''\text{W}$ , 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] ( $10.0\text{--}10.5\text{--}12.5 \times (5.5\text{--}6.0\text{--}7.0\text{--}7.5) \mu\text{m}$ , av.  $11.4 \times 6.3 \mu\text{m}$ ,  $Q=1.53\text{--}2.08$ ,  $Q_{av}=1.82$ , 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  $\times$  8–12  $\mu\text{m}$ , 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  $\mu\text{m}$  wide, repent, ascending or interwoven, smooth or spirally incrustated, yellow, aguttulate and agranular, some with intracellular brownish yellow pigment or parietal amber-like pigment; basal hyphae somewhat wider in general, 7–15  $\mu\text{m}$ , subparallel to interwoven, spirally incrustated, 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.

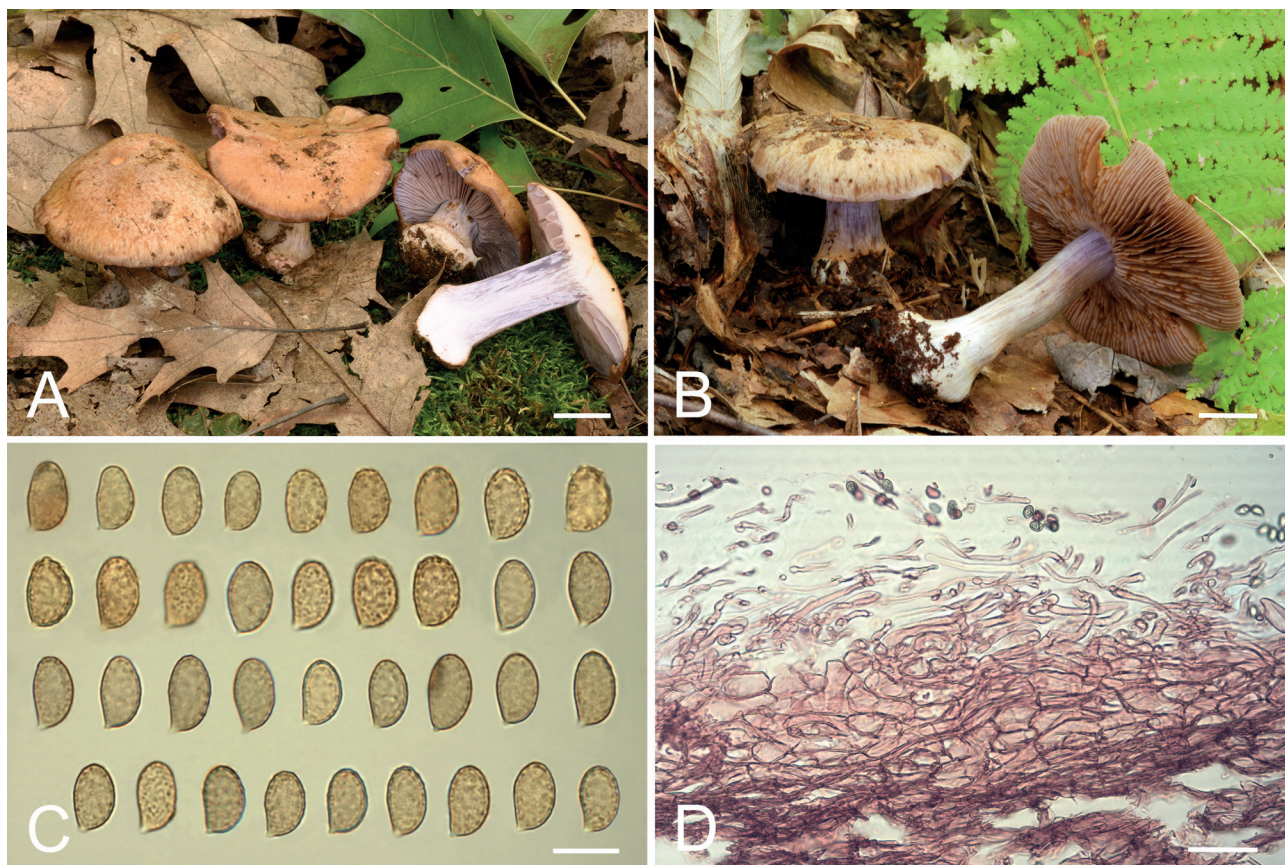
**Habitat and distribution.** – In large groups in a mixed forest of *Fagus grandifolia*, *Abies balsamea*, and *Acer* sp. by the river, in argillaceous soil, found in early October. Thus far known from a single location in Quebec, Canada.

**Additional material examined.** – *Ibid.* (QFB31058; isotype). Sequences ex-isotype: MN751569 (ITS). – CANADA. Quebec, Saint-Stanislas, Parc de la rivière Batiscan, trail Le Buis,  $46^{\circ}34'47.0''\text{N}$ ,  $72^{\circ}24'45.4''\text{W}$ , 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  $12\text{--}14 \times 7\text{--}8 \mu\text{m}$  (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  $\mu$ m, D 50  $\mu$ m.

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**

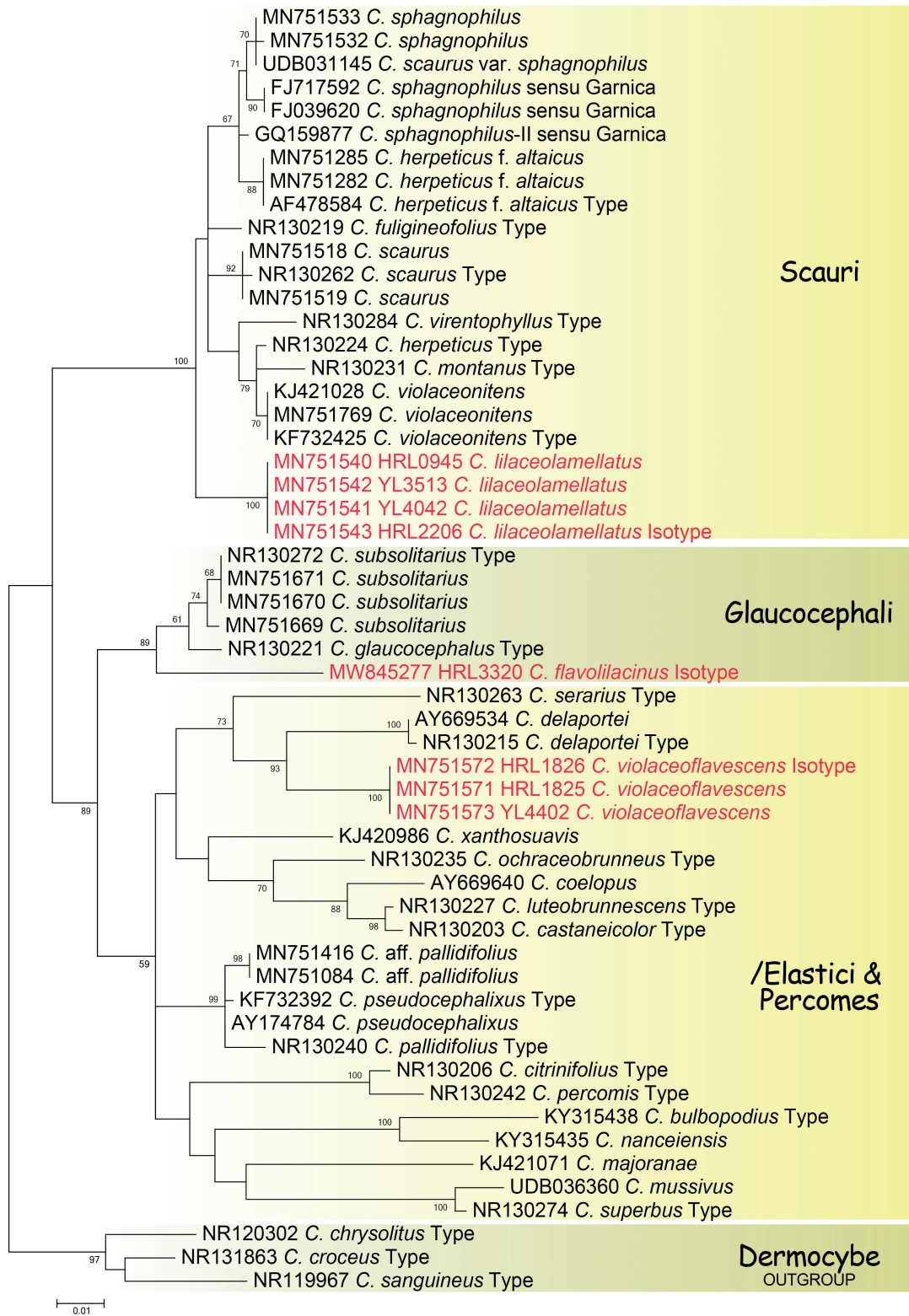
***Cortinarius* section *Scauri***

***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  $\times$  5.5–8.0  $\mu$ m, on average 10.7  $\times$  6.7  $\mu$ m, 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 *Cortinari* 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. – O d o r either absent or pleasant, of honey or fruity. – T a s t e mild. – M y c e l i u m white. – E x s i c c a t a e greyish brown (6EF4). (Microscopic exam in Melzer's reagent) – B a s i d i o s p o r e s [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<sub>av</sub>=1.59, ellipsoid, rarely oblong to subamygdaliform, moderately verrucose, often more coarsely at apex, a small proportion with suprahilar depression, not dextrinoid. – B a s i d i a 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. – L a m e l l a r t r a m a hyphae pale yellow, smooth, aguttulate. – S t i p e apex hyphae pale yellow, smooth, aguttulate. – H y m e n i a l c y s t i d i a absent. – P i l e i p e l l i s 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 incrustated 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. – C l a m p c o n n e c t i o n s present in all tissues. – M a c r o c h e m i c a l r e a c t i o n : brown on pileus with 10 % KOH.

E t y m o l o g y. – Referring to the pale violet lamellae.

H a b i t a t a n d d i s t r i b u t i o n. – Gregarious in mixed forests, probably associated with conifers, in the fall. Thus far only known from Quebec, Canada.

A d d i t i o n a l m a t e r i a l e x a m i n e d. – *Ibid.* (QFB29980; isotype). Sequences ex-isotype: MN751543 (ITS). – C A N A D A. 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).

N o t e s. – 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) Moëgne-Loec. 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).

A u t h o r s : R. Lebeuf, J. Landry, Y. Lamoureux & A. Paul

## Basidiomycota, Agaricomycetes, Agaricales, Cortinariaceae

### *Cortinarius* clade / *Glaucocephali*

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

D i a g n o s i s. – 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.

H o l o t y p u s. – C A N A D A. 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).

D e s c r i p t i o n. – P i l e u s 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. – L a m e l l a e



**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  $\mu$ m, C 25  $\mu$ m.

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. – *C o n t e x t* white to yellowish white (4A2) in the pileus, gradually passing into pale yellow (4A3) in the stipe base, violaceous grey in stipe pe-

riphery, firm. No color changes noted in any part of basidiomata. – *O d o r* none. – *T a s t e* mild. (Microscopic exam in Melzer's reagent) – *B a s i d i o s p o r e s* [120/4/1] (7.0–)7.5–8.5 × (4.0–)4.2–4.5  $\mu$ m, av. 8.1 × 4.4  $\mu$ m,  $Q=1.60$ –2.13,  $Q_{av}=1.82$ , amygdaliiform, less frequently limoniform, with a small suprahilar depression, moderately verrucose, weakly dextrinoid. – *B a s i d i a* 31–37 × 8–9  $\mu$ m, 4-spored, clavate; older basidia developing a yellow intracellular pigment in Melzer's reagent and 3% KOH, and blackish granules in KOH. – *L a m e l l a r t r a m a* hyphae smooth, yellow. – *S t i p e* apex hy-



phae 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 incrustated, 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.

**Etyymology.** – 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 subsolarius* 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***

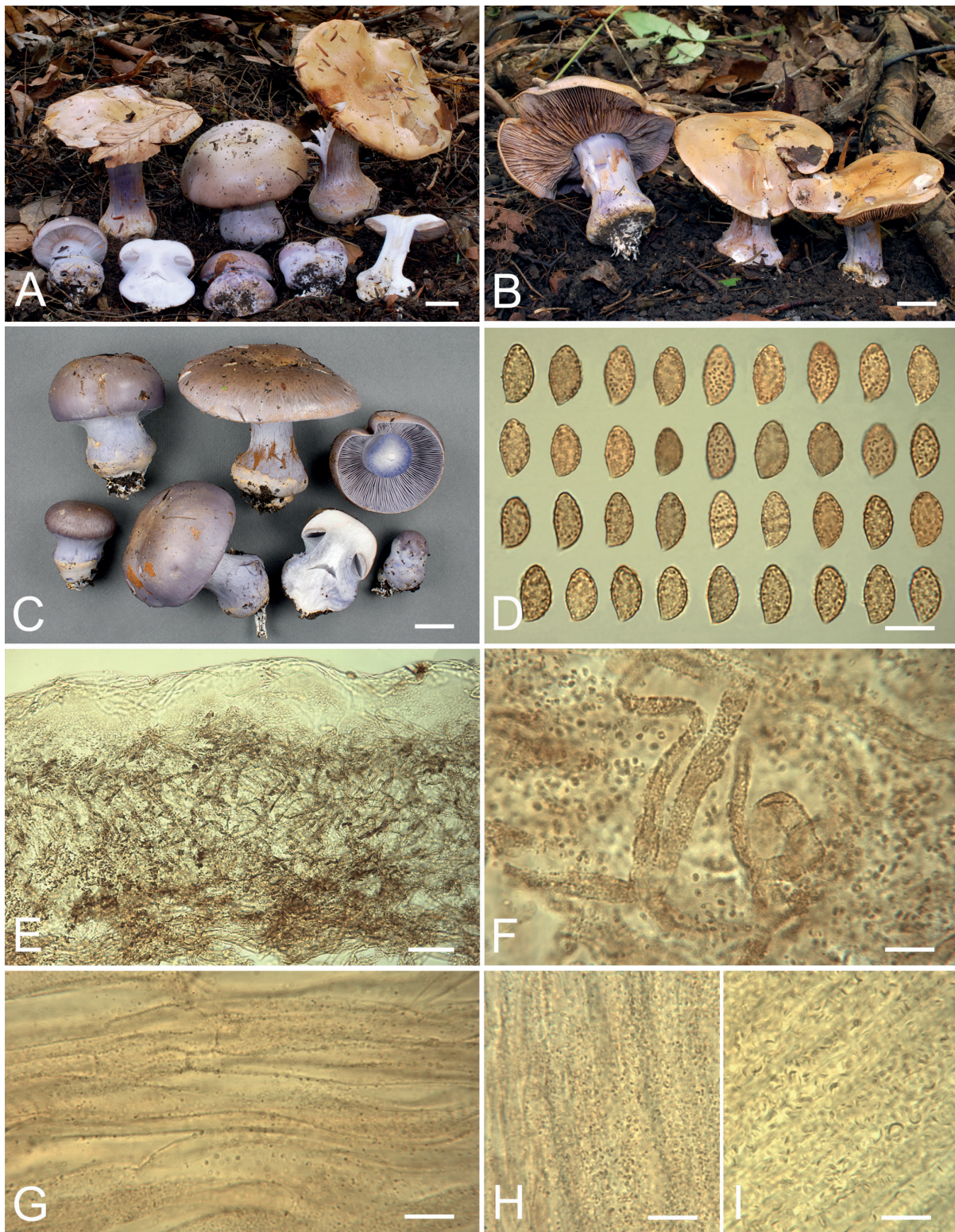
***Cortinarius violaceoflavescens*** Lebeuf, A. Paul, J. Landry & Y. Lamoureux, **sp. nov.** – Figs. 6, 8  
Mycobank no.: MB 839561

**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 planoconvex 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<sub>av</sub>=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 incrustated with small sand-brown granules. – Veil hyphae granular-incrustated 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.



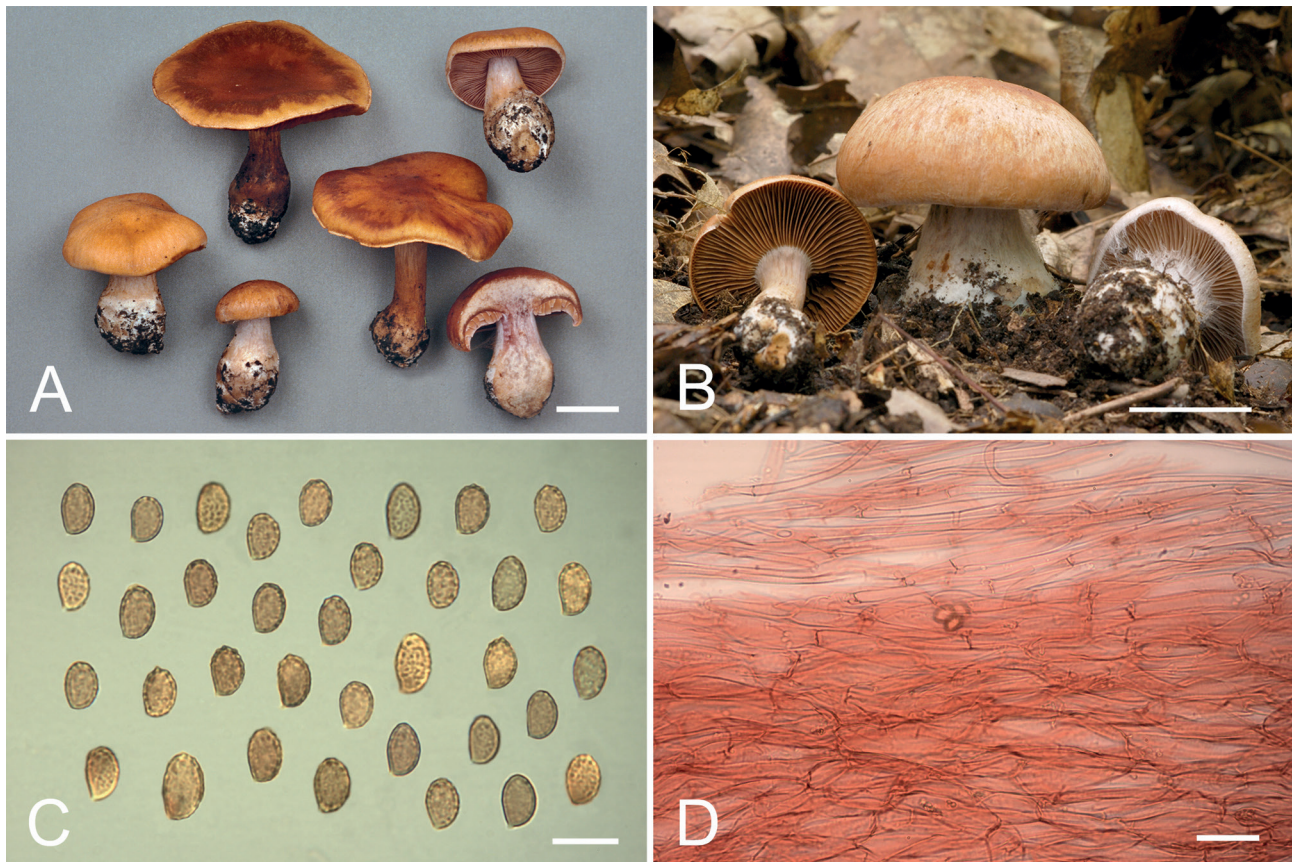
incrusted, 1.5–3  $\mu\text{m}$  wide; hyphae in matrix 2–6  $\mu\text{m}$  wide, mostly ascending, interwoven, heavily incrusted with refractive, round or elongate, sand-brown granules; basal hyphae 4–10  $\mu\text{m}$  diam., interwoven to intertwined in bundles, yellowish brown, granule-incrusted, 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  $\text{NH}_4\text{OH}$ .

**Etyymology.** – Referring to the rapidly yellowing violet pileus.

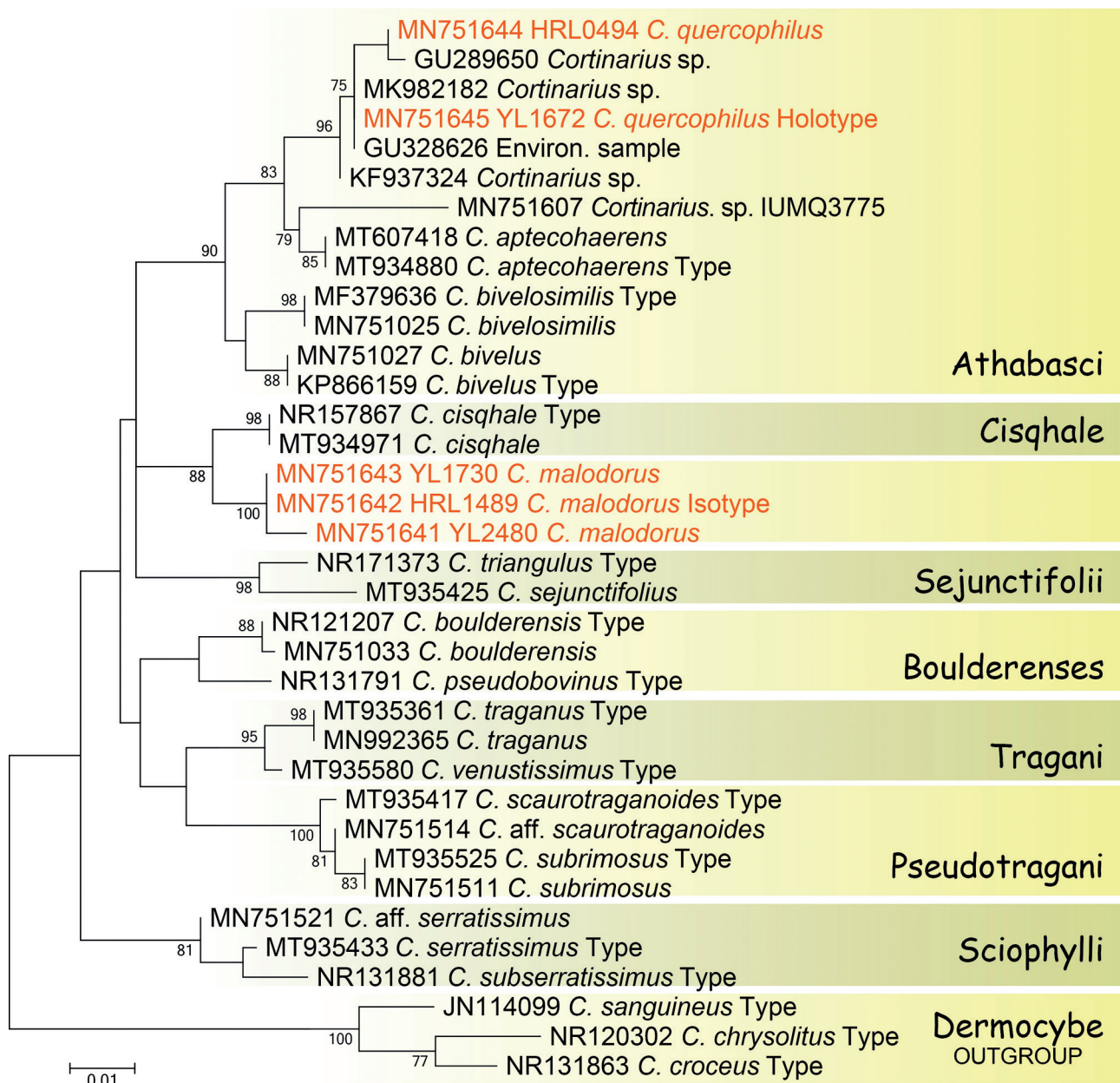
**Habitat and distribution.** – Gregarious to caespitose in deciduous or mixed forests of *Carya ovata*, *Carya cordiformis*, *Quercus rubra*, *Tsuga canadensis*, *Populus* sp., *Tilia* sp., and *Fagus grandifolia*, in calcareous and argillaceous soil, in the fall. Probably associated with *Carya* spp. 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 incrusted 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  $\mu\text{m}$ , D 25  $\mu\text{m}$ .



**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  $\mu\text{m}$ , and *C. caesiocanescens* M.M. Moser also produces smaller spores (8.5–10.5  $\times$  5–6  $\mu\text{m}$ ) and is found in coniferous forests of *Pinus* or *Picea*. *Cortinarius glaucocyanopus* Rob. Henry, in section *Riedereri*, 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  $\times$  7.2–7.3  $\mu\text{m}$ . 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  $\times$  5.0–6.5  $\mu\text{m}$ , on average 7.9  $\times$  5.2  $\mu\text{m}$ . 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. – *Cortinaria* 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. – Ex-

siccatae dark brown (7F7, 8F5). (Microscopic exam in Melzer's reagent) – Basidiospores [121/4/2] 7.0–8.5(–11.0)  $\times$  5.0–5.5(–6.5)  $\mu\text{m}$ , av. 7.9  $\times$  5.2  $\mu\text{m}$ , Q=1.27–1.80, Q<sub>av</sub>=1.50, ellipsoid, finely to moderately verrucose, moderately dextrinoid. – Basidia 27–34  $\times$  8–9  $\mu\text{m}$ , 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  $\mu\text{m}$  wide, smooth, pale yellow; hypoderm present, well differentiated or not, hyphae 4–18  $\mu\text{m}$  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.

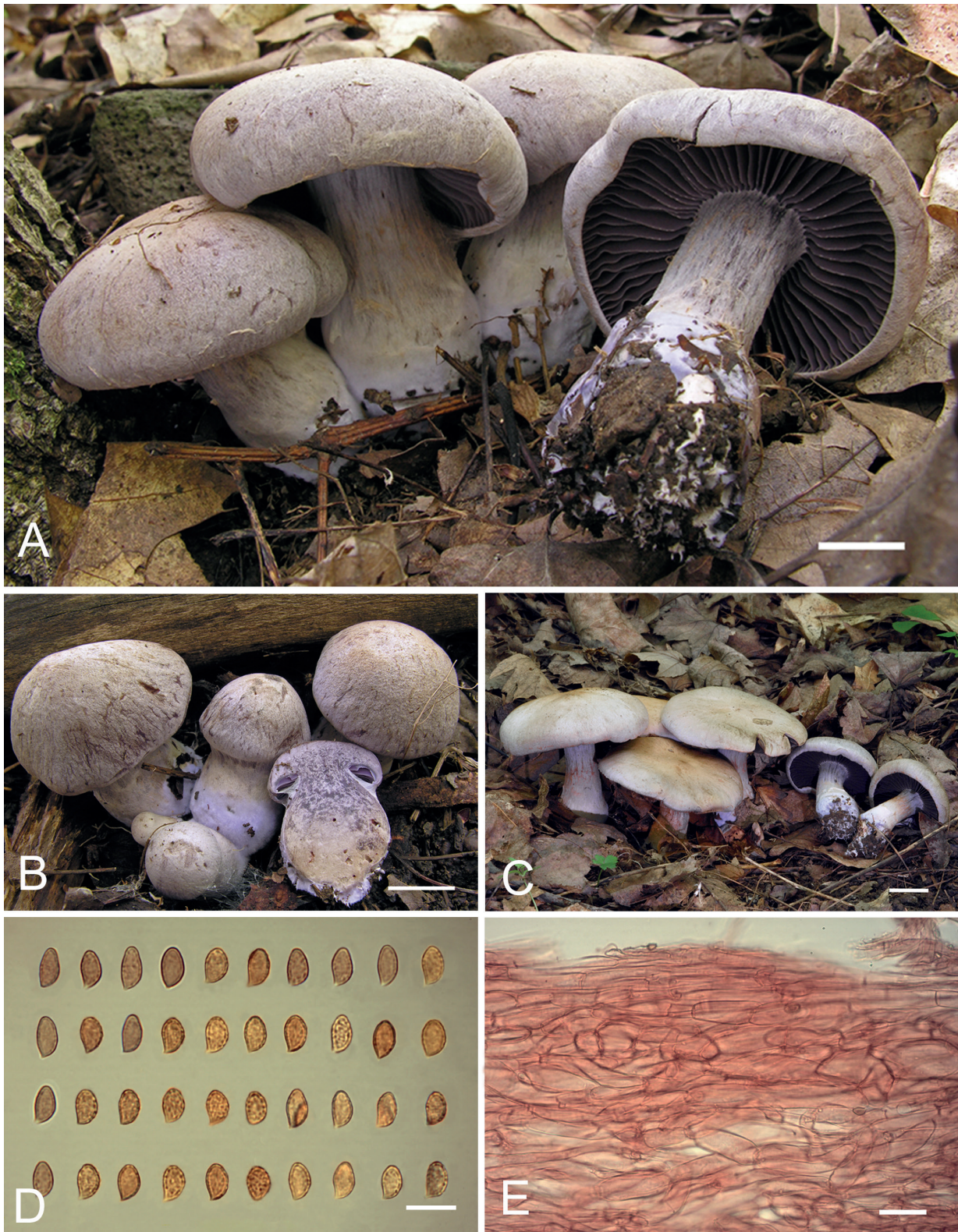
*Etymology.* – Referring to the ectomycorrhizal association with *Quercus*.

*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 Gélinothe, 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 hygrophanicity, dull reaction to KOH and ellipsoid basidiospores are rather





**Fig. 11.** *Cortinarius malodoros*. 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  $\mu$ m, E 25  $\mu$ m.



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 violaceous 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  $6.5\text{--}9 \times 4.2\text{--}5.0 \mu\text{m}$ , on average  $7.8\text{--}4.6 \mu\text{m}$ . 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,  $45^{\circ}36'15.5''\text{N}$ ,  $73^{\circ}23'49.0''\text{W}$ , 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) – Basidi-

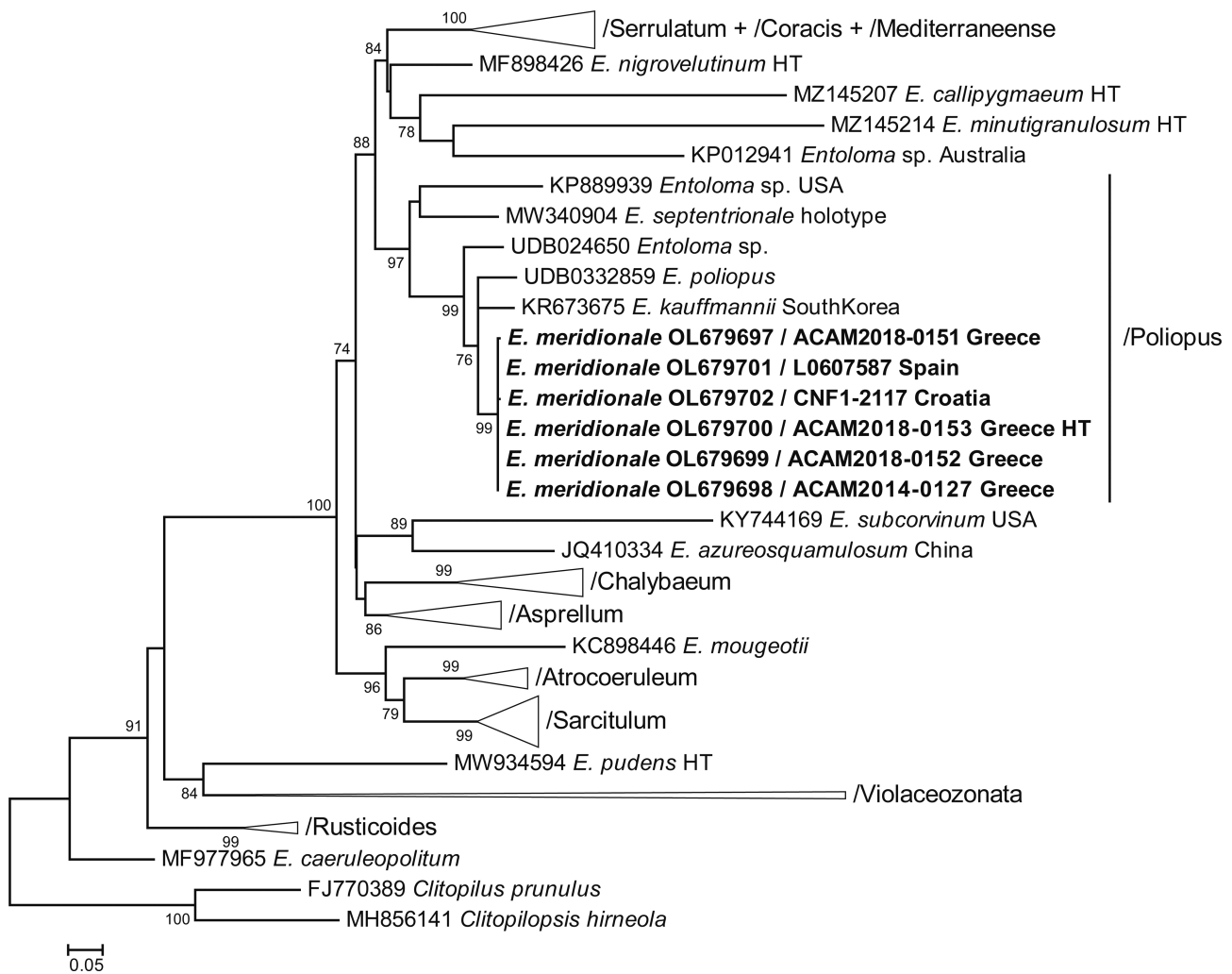
ospores [120/4/2] ( $6.5\text{--}7.0\text{--}8.5\text{--}9.0 \times 4.2\text{--}5.0 \mu\text{m}$ , av.  $7.8 \times 4.6 \mu\text{m}$ ,  $Q=1.44\text{--}2.00$ ,  $Q_{av}=1.69$ , ellipsoid-amygdaliform, ellipsoid, with a suprahilar depression, finely to moderately verrucose, weakly or not dextrinoid. – Basidia  $30\text{--}45 \times 7\text{--}8 \mu\text{m}$ , 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  $3\text{--}8 \mu\text{m}$  wide, smooth, pale yellow to pale olive yellow; hypoderm present, hyphae  $8\text{--}25 \mu\text{m}$  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 co-

nifers; *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  $\mu\text{m}$ .

**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  $\times$  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. –

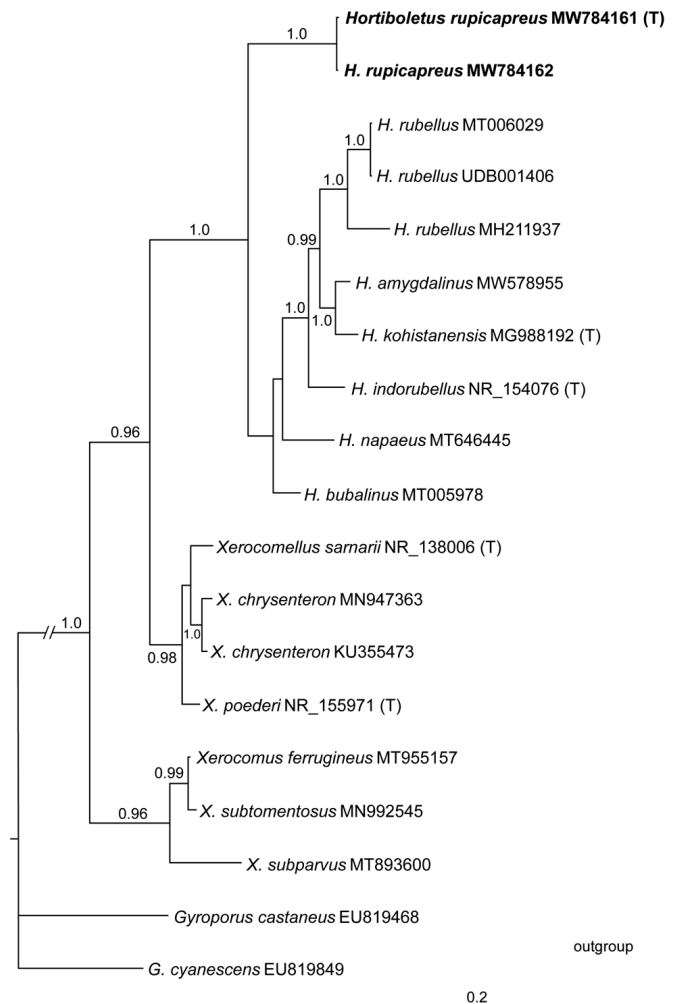
Context thin. – Odor weak, pleasant, indistinct. – Taste mild, somewhat fruity. – Basidiospores (9.5–)10.0–12.5 × (6.5–) 7.0–9.0 μm, av. 10.1–11.3 × 7.1–7.9 μm, Q=1.2–1.7, Q<sub>av</sub>=1.4–1.5, heterodiametrical, (5–)6–8(–9)-angled in side-view. – Basidia 25–40 × 9–15 μm, 4-spored, subcylindrical to 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. salvifolius*, *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).

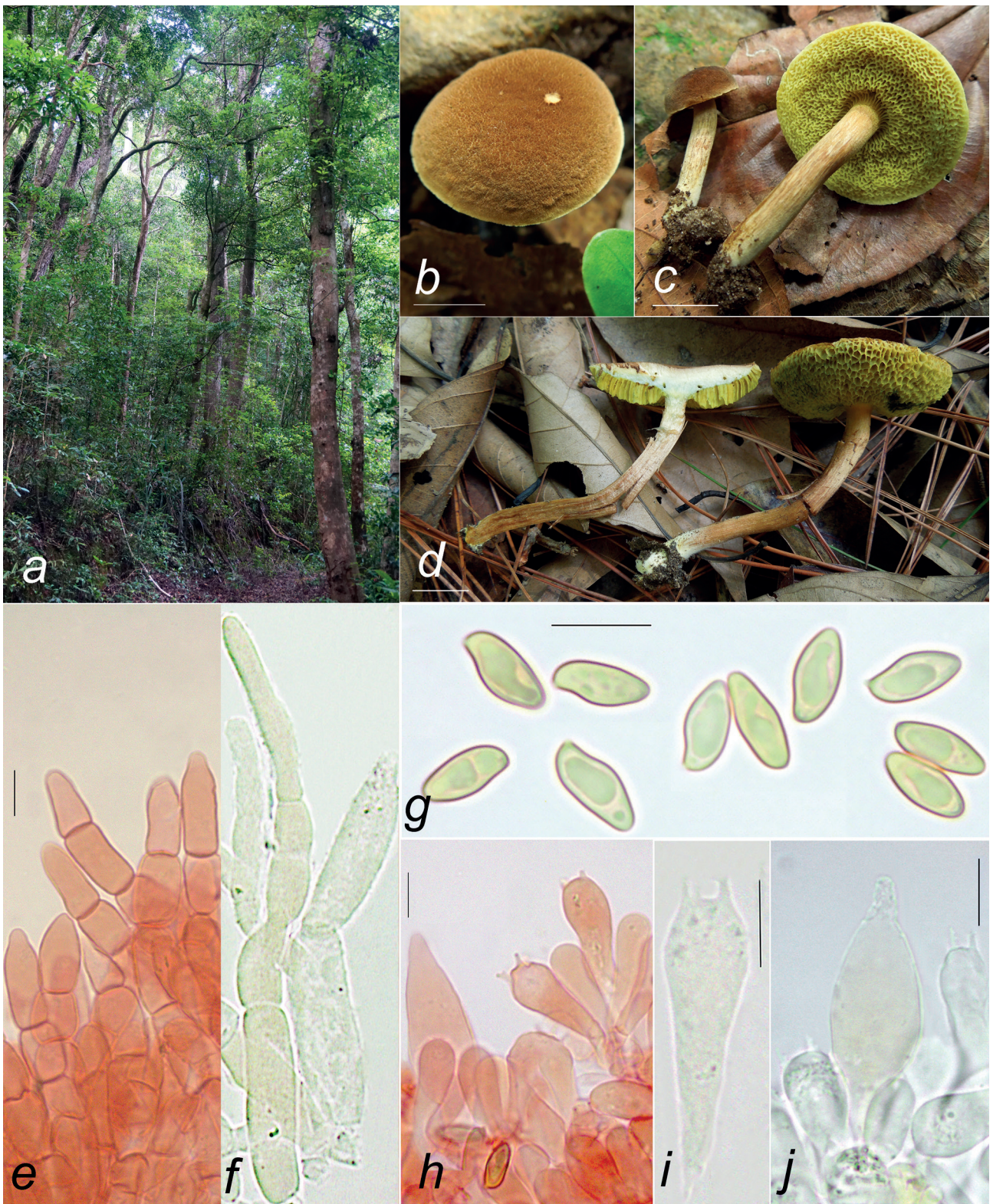
**Notes.** – *Entoloma meridionale* is a rather striking blue species with pink variants. It is further characterized by having a polished or at most innately fibrillose stipe, and medium-sized basidiospores, on average well over 10 μm long, which enables differentiation from similar species such as *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



**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.

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.** Pileipellis of mature specimen. **g.** Basidiospores. **h.** Caulobasidia and caulocystidia. **i.** Basidium. **j.** Cheilocystidia. Scale bars b–d 1 cm, e–i 10  $\mu$ m.



(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; con-

text 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 incrustated (in Congo Red dissolved in NH<sub>4</sub>OH); pileipellis hyphae of young specimens consisting 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 incrustated, 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.

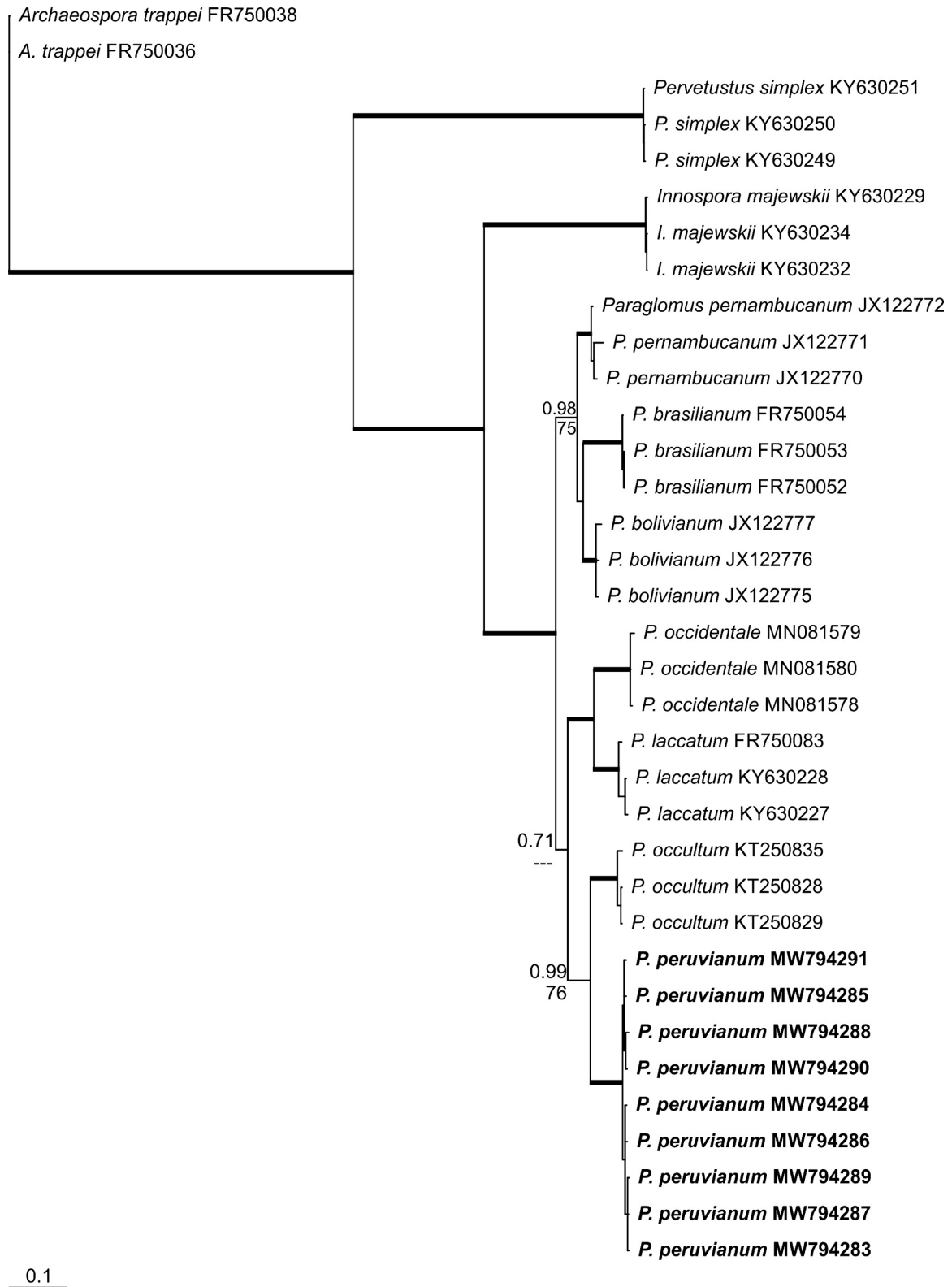
*Etymology.* – “*rupicapreus*” (Latin), equivalent of the English word “chamois”, referring to the yellowish-brown color of chamois leather and the characteristic suede surface.

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

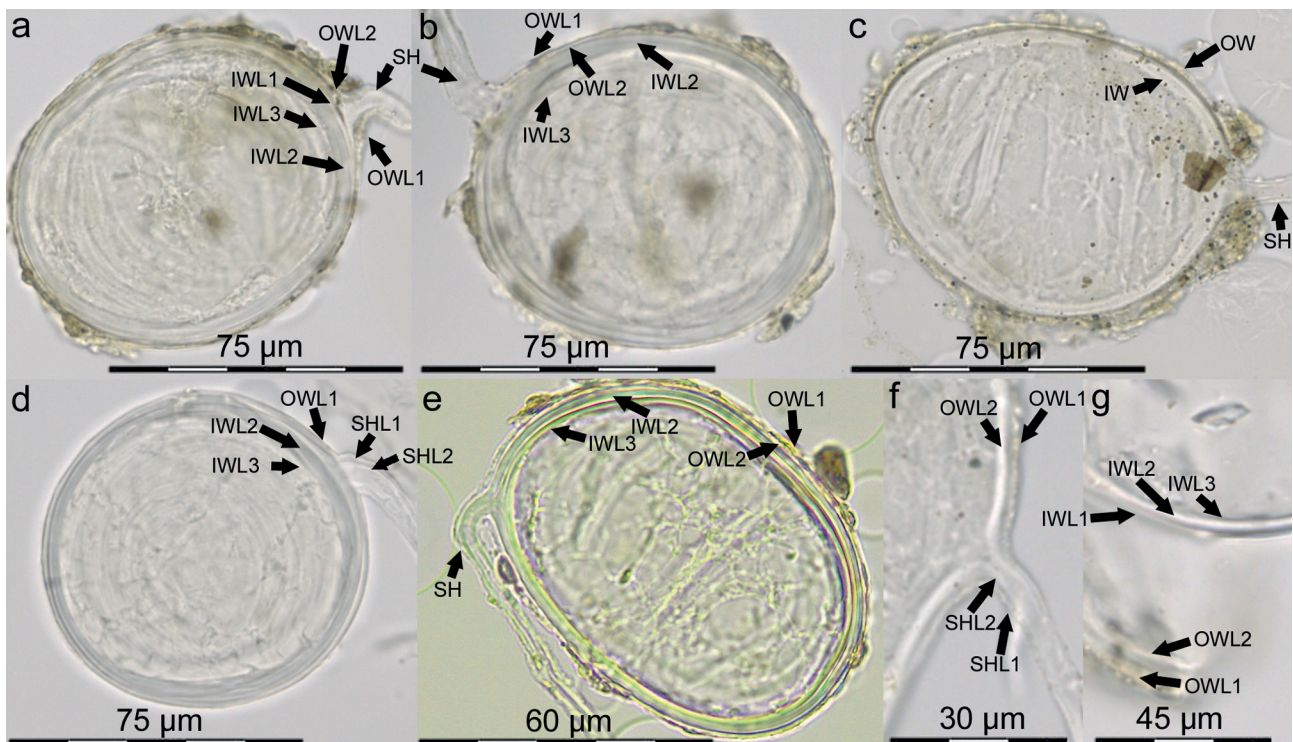
*Additional material examined.* – VIETNAM. Gia Lai Province, Mang Yang District, Kon Ka Kinh National Park, A Yun, 14°12'18.68"N, 108°18'58.72"E, 1,000 m a.s.l., on soil in pine plantations of *Pinus kesiya* with some Fagaceae, 15 March 2016, *leg.* A.V. Alexandrova (LE 312678).

*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.** *Paraglomeromycetes 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 di-

versity of the boletoid fungi of the of protected areas of Kon Tum Plateau in Vietnam.

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### Glomeromycota, Paraglomeromycetes, Paraglomerales, Paraglomeraceae

***Paraglomeromycetes 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.

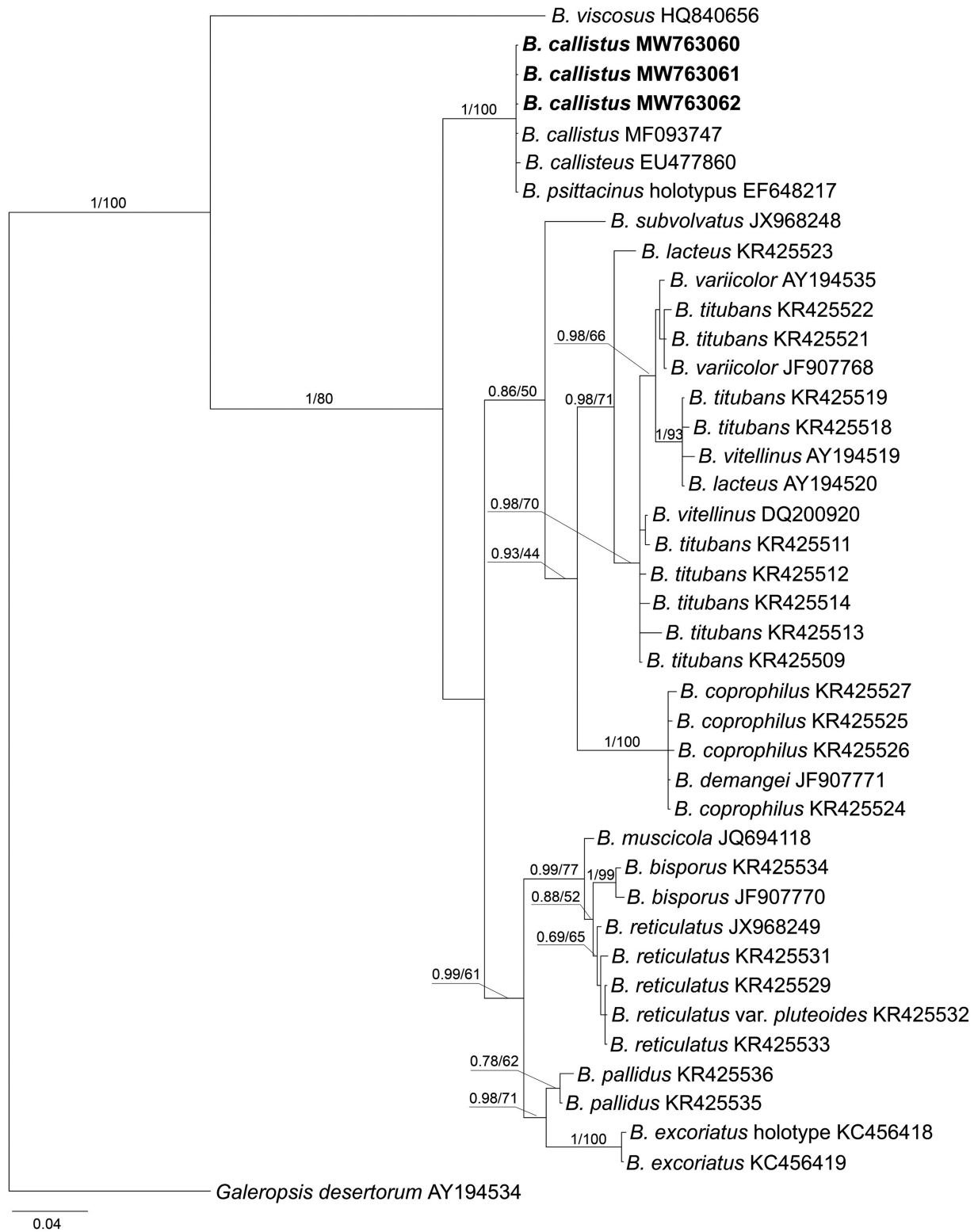
**Additional material examined.**—*Ibid.* (ZT Myc 64709; isotype). PERU. San Martín State, El Dorado Province, Barranguito, 6°44′19.64″S, 76°35′41.32″W, 321 m a.s.l., inka nut plantation, 22 October 2018, *leg.* M.A. Corzaon-Guivin (ZT Myc 66295).

**Notes.** – *Paraglomus peruvianum*, based on spore morphology and molecular phylogenetic data (Fig. 16), clearly belongs to the order Paraglom-

erales 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* (Błaszcz.) Renker, Błaszcz. & 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 (Błaszczowski 1988, Renker et al. 2007, Corazon-Guivin et 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 Krasnofarfony 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).

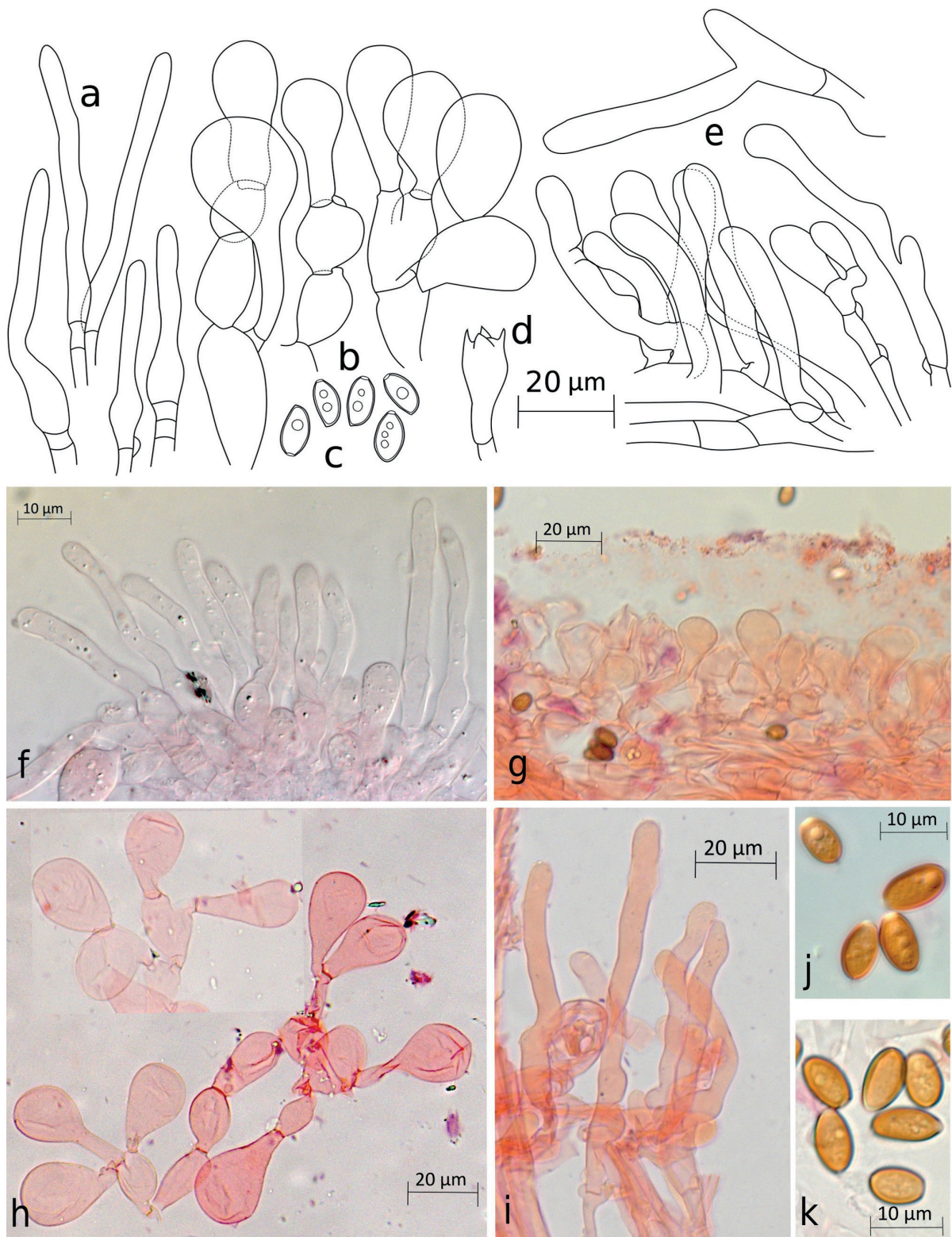
*Description.* – Basidiomata small- to medium-sized. – Pileus 8–25 mm in diam.; parabolical, hemispherical, or convex when young; becoming convex, umbonate, plano-convex, with striate margin, surface glabrous, viscid, with age wrinkled at center; usually very variable in color, with deep colors when 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<sub>av</sub>=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 acutis, 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.



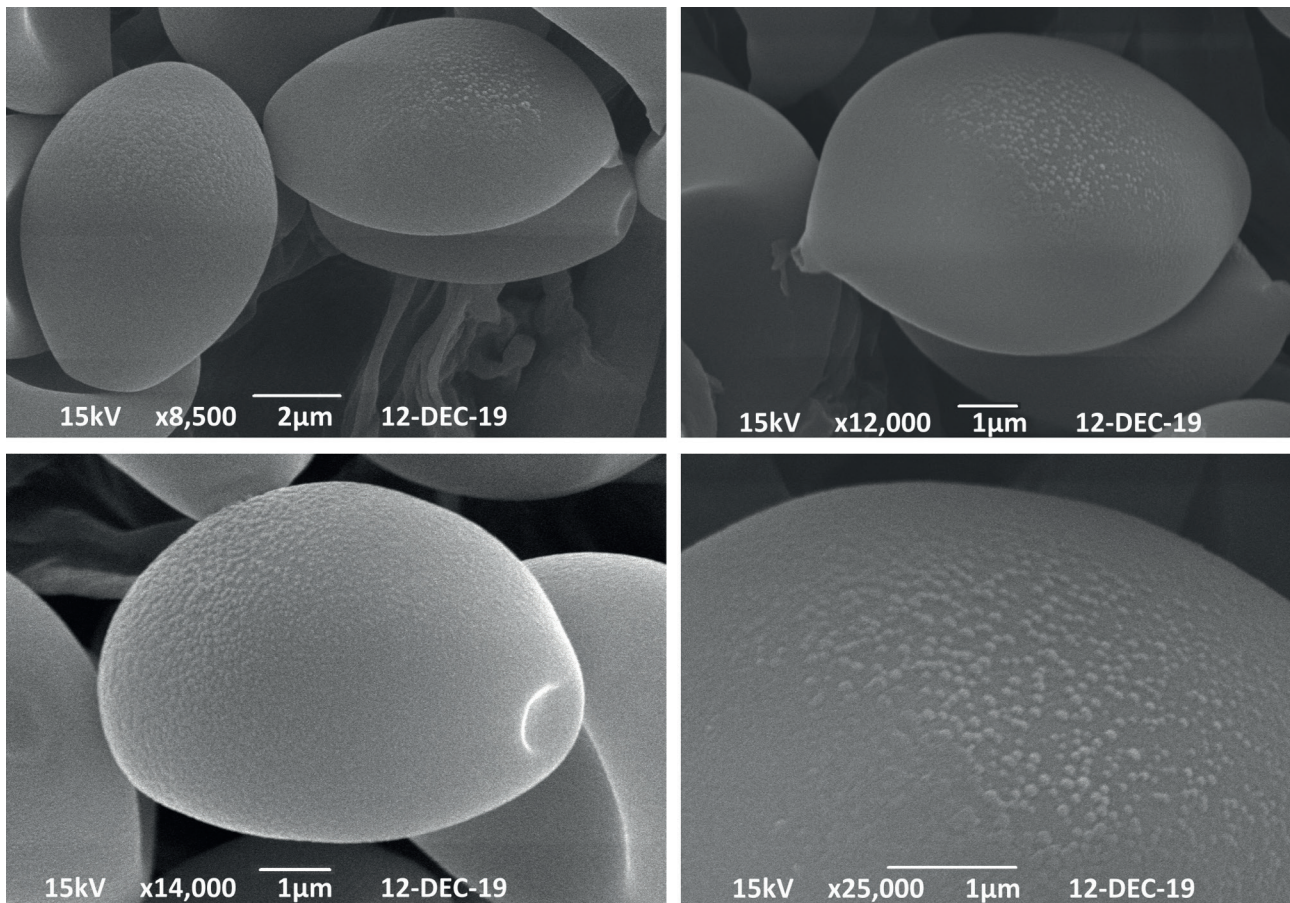


Fig. 21. SEM micrographs of *Bolbitius callistus* basidiospores with clearly visible ornamentation.

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 pseudo-paraphyses 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 Ameri-

ca. 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 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

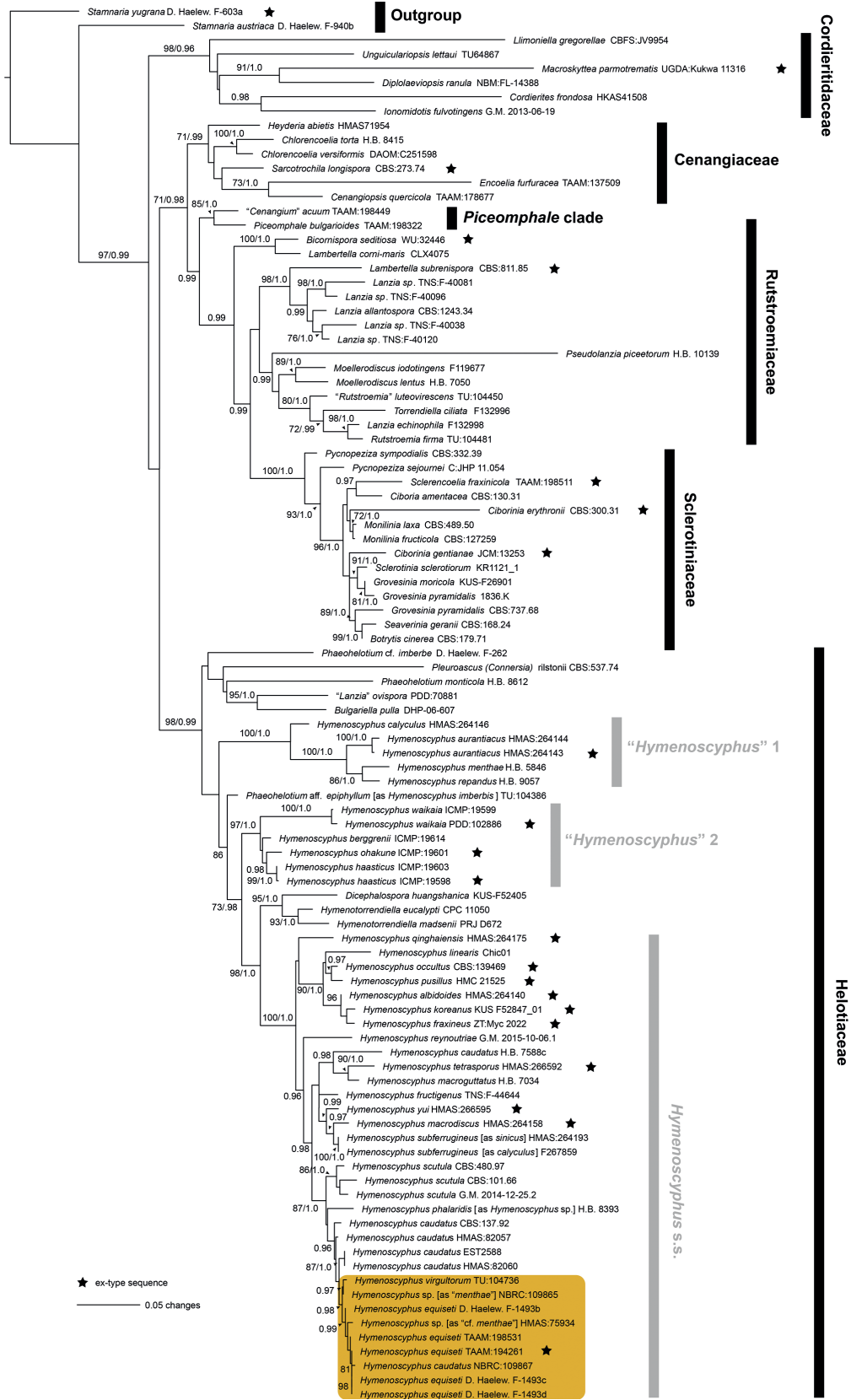
*Hymenoscyphus equiseti* (Raitv.) Baral, Pärtel, Haelew., Myhrer & Pennanen, **comb. nov.** – Figs. 22–26

Mycobank no.: MB 842026

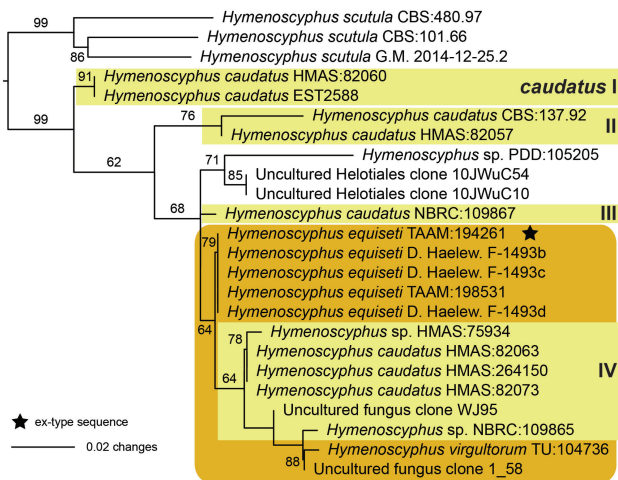
*Basionym.* – *Lanzia equiseti* Raitv., Nov. Sist. Niz. Rast. 21: 116 (1984).

*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 Järvinemi, 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







**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  $\geq 60$  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. – P a r a p h y s e s apically cylindrical, terminal cell  $*40\text{--}50 \times (2\text{--})3\text{--}3.2(4) \mu\text{m}$  {1},  $\dagger(32\text{--})40\text{--}50 \times (2\text{--})2.5\text{--}4(4.8) \mu\text{m}$  {2}; containing strongly refractive, hyaline, globose to subangular VBs  $1\text{--}2.7 \mu\text{m}$  diam. in upper  $25\text{--}37 \mu\text{m}$  {1}. – M e d u l l a r y excipulum hyaline,  $\sim 50 \mu\text{m}$  thick in receptacle, of loose *textura intricata*. – E c t a l excipulum hyaline to pale yellowish-ochraceous, of thin-walled, horizontally oriented *textura prismatica* from base to margin, cells at lower flanks  $*13\text{--}33 \times 8\text{--}13 \mu\text{m}$  {1},  $\dagger 8.5\text{--}12.5 \times 4.5\text{--}7.5 \mu\text{m}$  {T} (protologue  $\dagger 8\text{--}12 \times 5\text{--}7 \mu\text{m}$ ); exterior without cortical hyphae or hair-like protrusions, complete tissue without crystals. – A n a m o r p h unknown.

H o s t s a n d d i s t r i b u t i o n. – 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).

N o t e s. – *Hymenoscyphus equiseti* was previously only known from a single collection from Valamo Island, in the Republic of Karelia in north-

western 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  $\dagger 9.5\text{--}15 \times 4\text{--}5 \mu\text{m}$ ) is a synonym of the wood-inhabiting *Phaeohelotium imberbe* (Bull.) Svrček, and *H. telmateiae* (ascospores  $\dagger 6\text{--}8 \times 1.5\text{--}2.0 \mu\text{m}$ ) 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 & Bemmam 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  $\geq 70$  and BIPP  $\geq 0.95$  are presented above or below the branch leading to that node. Stars (★) indicating ex-type sequences.



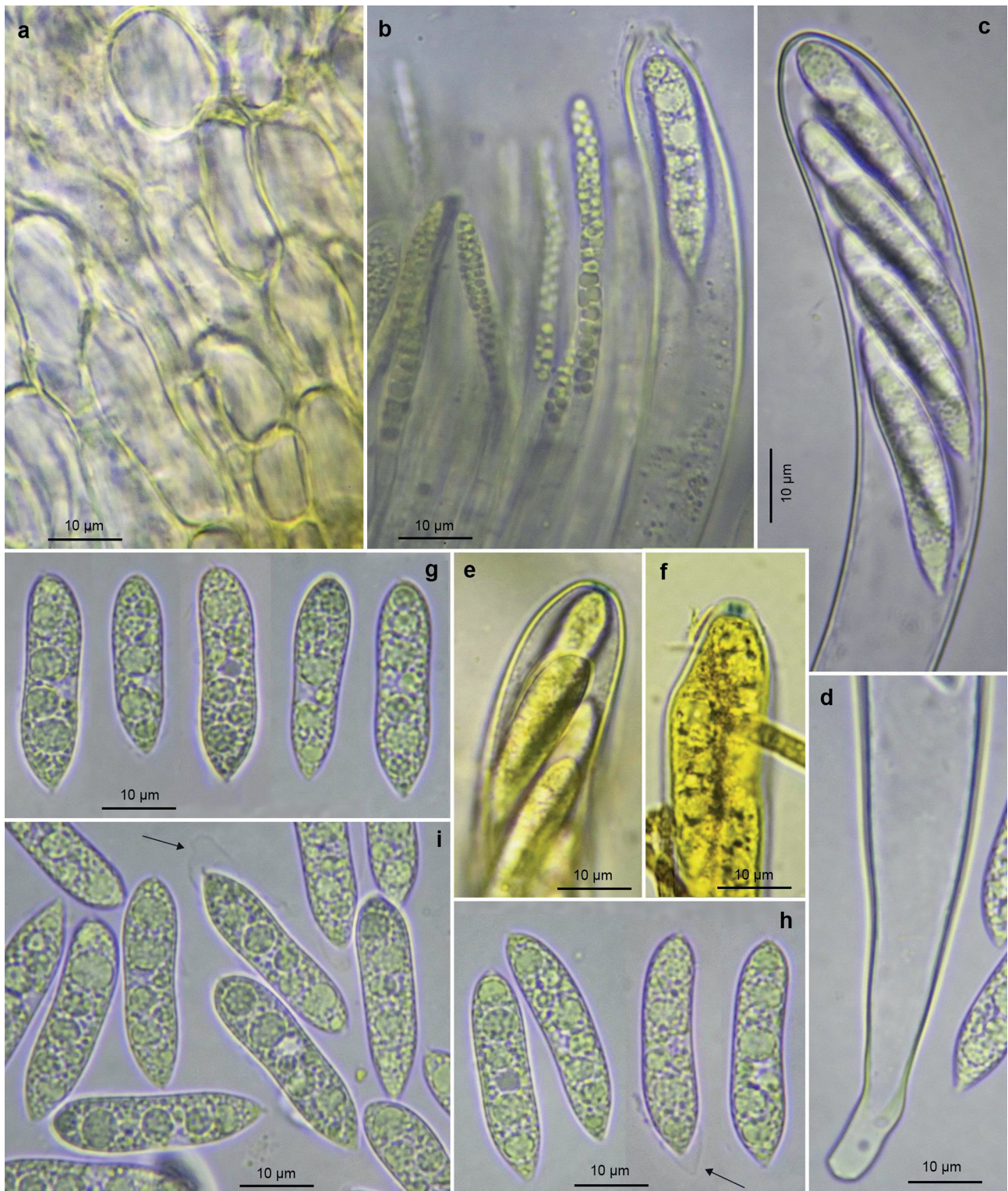
**Fig. 24.** *Hymenoscyphus equiseti* apothecia on stems of *Equisetum fluviatile*. **1a, 1b.** Finland, North Karelia (M.P. 100807E); fresh apothecia. **2a–e.** Sweden, Hälsingland (UPS:BOT:F-923028); fresh apothecia. **3a–c.** Russia, Karelia, (TAAM:198531); more or less rehydrated apothecia. Photos 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,  $-\ln L=10642.87$ ) and TIM3+I+G (LSU,  $-\ln L=7605.97$ ). The topology of our Bayesian and ML trees were identical among supported (MLBS  $\geq 70$  and BIPP  $\geq 0.95$ ) 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,  $\beta$ -tubulin; focus on *Hymenoscyphus*).

The clade with *H. equiseti* is only supported in our Bayesian analysis of the two-locus dataset

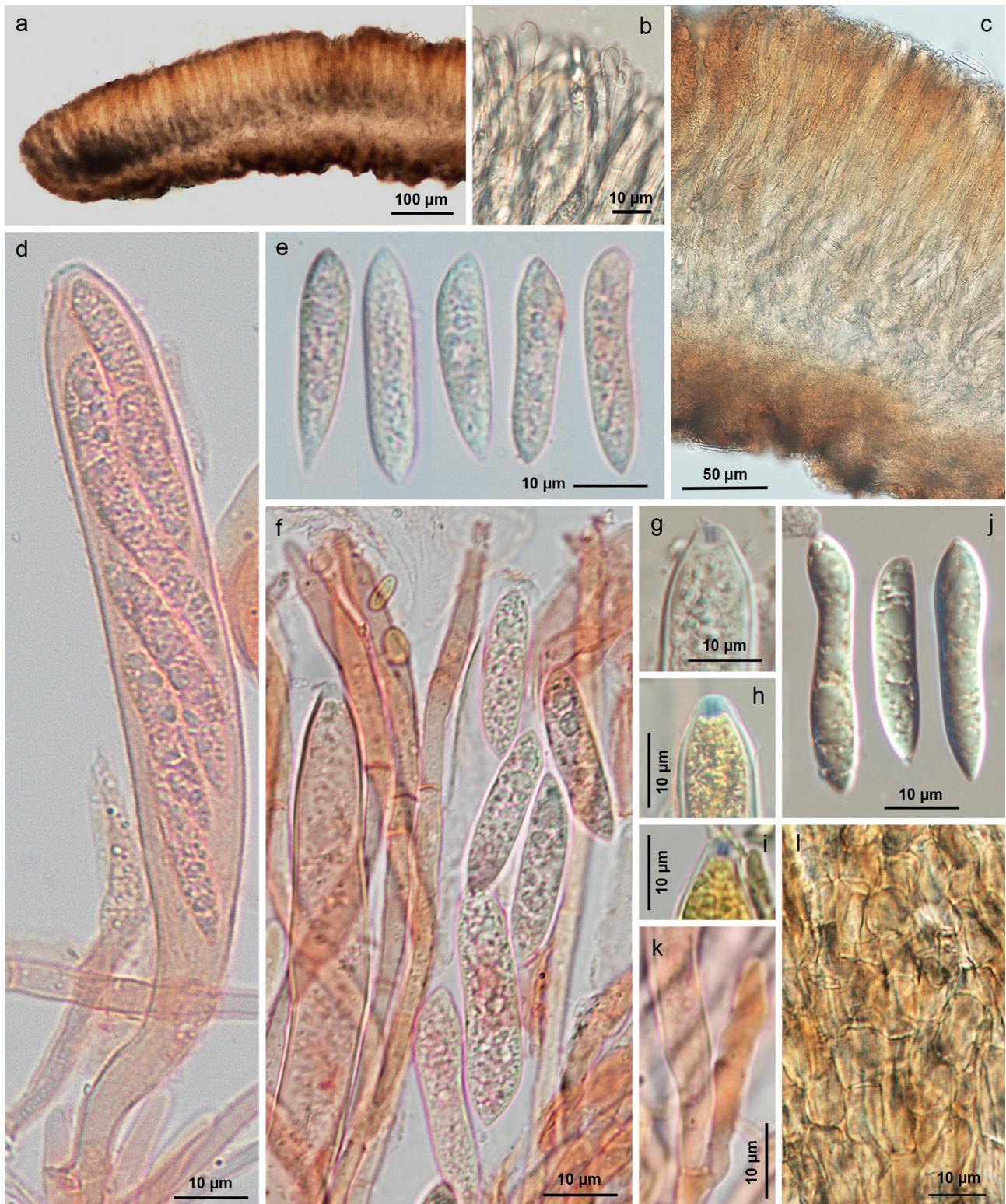
(BIPP=0.99), and includes *H. "caudatus"* (P. Karst.) Dennis from Japan (NBRC:109867, on *Alnus* sp.) and *H. "cf. menthae"* (W. Phillips) Baral from China (HMAS:75934, on dead wood). The broader clade supported by BIPP=0.96 (highlighted in yellow in Fig. 22) contains little structure in a cluster of 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 turgent 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  $14\text{--}23 \times 3\text{--}5 \mu\text{m}$  in Phillips (1893),  $*18\text{--}24 \times 3.5\text{--}4.0 \mu\text{m}$  in Baral & Krieglsteiner (1985),  $*(16\text{--})19\text{--}22\text{--}(28) \times 3.8\text{--}4.3\text{--}(5.2) \mu\text{m}$  in H.B. 9845 (TU:104736), and  $\dagger 13.5\text{--}16.3 \times 4.0\text{--}5.0 \mu\text{m}$  in Delivorias et al. (2010). *Hymenoscyphus menthae*, known to occur on herbaceous stems of monocots and dicots, has ascospores measuring  $*(15\text{--})17\text{--}22\text{--}(26) \times 3.5\text{--}4.2\text{--}(4.5) \mu\text{m}$  (Baral 2015), whereas the wood-inhabiting *H. "cf. menthae"* has ascospores measuring  $\dagger 12\text{--}18 \times 4\text{--}5\text{--}(6) \mu\text{m}$  [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*:  $*16\text{--}20 \times 4\text{--}5 \mu\text{m}$  in Kimbrough & Atkinson (1972),  $16\text{--}21 \times 4\text{--}5 \mu\text{m}$  in Arendholz (1979),  $(14\text{--})16\text{--}23\text{--}(26) \times 4\text{--}5\text{--}(6) \mu\text{m}$  in Dumont & Carpenter (1982),  $*15\text{--}18 \times 4.5\text{--}5.5 \mu\text{m}$  in Baral & Krieglsteiner (1985), and  $*17\text{--}20 \times (4.7\text{--})5\text{--}6 \mu\text{m}$  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.

|                           | <i>H. equiseti</i> | <i>H. caudatus</i><br>III–IV | <i>H. virgultorum</i> | <i>H. caudatus</i> I–II | <i>H. scutula</i> |
|---------------------------|--------------------|------------------------------|-----------------------|-------------------------|-------------------|
| <i>H. equiseti</i>        | 0 %                |                              |                       |                         |                   |
| <i>H. caudatus</i> III–IV | 0.4–0.7 %          | 0–1.1 %                      |                       |                         |                   |
| <i>H. virgultorum</i>     | 1.1 %              | 0.4–1.5 %                    | –                     |                         |                   |
| <i>H. caudatus</i> I–II   | 1.8–2.9 %          | 1.5–3.6 %                    | 2.4–3.1 %             | 0–2.2 %                 |                   |
| <i>H. scutula</i>         | 4.1–4.3 %          | 3.8–5.0 %                    | 3.8–4.0 %             | 3.6–5.0 %               | 2.4–3.3 %         |

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