

## Fungal Systematics and Evolution: FUSE 6

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Fungal Systematics and Evolution (FUSE) is one of the journal series to address the “fusion” between morphological data and molecular phylogenetic data and to describe new fungal taxa and interesting observations. This paper is the 6th contribution in the FUSE series—presenting one new genus, twelve new species, twelve new country records, and three new combinations. The new genus is: *Pseudozeugandromyces* (Laboulbeniomyces, Laboulbeniales). The new species are: *Albatrellopsis flettioides* from Pakistan, *Aureoboletus garciae* from Mexico, *Entomophila canadense* from Canada, *E. frigidum* from Sweden, *E. porphyroleucum* from Vietnam, *Erythrophylloporus flammans* from Vietnam, *Marasmiellus boreoorientalis* from Kamchatka Peninsula in the Russian Far East, *Marasmiellus longistipes* from Pakistan, *Pseudozeugandromyces tachypori* on *Tachyporus pusillus* (Coleoptera, Staphylinidae) from Belgium, *Robillarda sohagensis* from Egypt, *Trechispora hondurensis* from Honduras, and *Tricholoma kenanii* from Turkey. The new records are: *Arthrorhynchus eucampsipodae* on *Eucampsipoda africanum* (Diptera, Nycteribiidae) from Rwanda and South Africa, and on *Nycteribia vexata* (Diptera, Nycteribiidae) from Bulgaria; *A. nycteribiae* on *Eucampsipoda africanum* from South Africa, on *Penicillidia conspiciua* (Diptera, Nycteribiidae) from Bulgaria (the first undoubted country record), and on *Penicillidia pachymela* from Tanzania; *Calvatia lilacina* from Pakistan; *Entoloma shangdongense* from Pakistan; *Erysiphe quercicola* on *Ziziphus jujuba* (Rosales, Rhamnaceae) and *E. urticae* on *Urtica dioica* (Rosales, Urticaceae) from Pakistan; *Fanniomyces ceratophorus* on *Fannia canicularis* (Diptera, Faniidae) from the Netherlands; *Marasmiellus biformis* and *M. subnuda* from Pakistan; *Morchella anatolica* from Turkey; *Ophiocordyceps ditmarii* on *Vespula vulgaris* (Hymenoptera, Vespidae) from Austria; and *Parvacoccum pini* on *Pinus cembra* (Pinales, Pinaceae) from Austria. The new combinations are: *Appendiculina gregaria*, *A. scaptomyzae*, and *Marasmiellus rodhallii*. Analysis of an LSU dataset of *Arthrorhynchus* including isolates of *A. eucampsipodae* from *Eucampsipoda africanum* and *Nycteribia* spp. hosts, revealed that this taxon is a complex of multiple species segregated by host genus. Analysis of an SSU–LSU dataset of Laboulbeniomyces sequences revealed support for the recognition of four monophyletic genera within *Stigmatomyces* sensu lato: *Appendiculina*, *Fanniomyces*, *Gloandromyces*, and *Stigmatomyces* sensu stricto. Finally, phylogenetic analyses of Rhytismataceae based on ITS–LSU ribosomal DNA resulted in a close relationship of *Parvacoccum pini* with *Coccomyces strobili*.

Keywords: 1 new genus, 12 new species, 12 new records, 3 new combinations, Agaricomycetes, integrative taxonomy, Laboulbeniomyces, Leotiomycetes, Pezizomycetes, Rhytismataceae, Sordariomycetes, *Stigmatomyces*.

With only 138,000 formally described fungal species (Kirk 2019) out of an estimated 2.2–3.8 million (Hawksworth & Lücking 2017) to 6 million (Taylor et al. 2014), between 97.7 and 93.7% of fungal species are left to be characterized. These may be discovered in poorly studied habitats and geographic areas (e.g., tropical rainforests), as molecular novelties, *within* cryptic taxa, in fungal collections (e.g., new species hidden under current names and in unidentified material), and during studies of plant and insect collections (Hawksworth & Lücking 2017, Wijayawardene et al. 2020). This large discrepancy between described and undescribed species needs to be addressed and recent work has

shown that mycologists are nowhere near levelling off the curve in describing new species (Hyde et al. 2020b). Together with other series—Fungal Biodiversity Profiles (Rossi et al. 2020), Fungal Diversity Notes (Hyde et al. 2020a), Fungal Planet (Crous et al. 2020a), Mycosphere Notes (Pem et al. 2019), New and Interesting Fungi (Crous et al. 2020b)—the Fungal Systematics and Evolution series published by *Sydowia* contributes to a much-needed acceleration of discovery and description of fungal diversity. The present paper is the sixth contribution in the FUSE series published by *Sydowia*, after Crous et al. (2015), Hernández-Restrepo et al. (2016), Krisai-Greilhuber et al. (2017), Liu et al. (2018), and Song

et al. (2019). Altogether, one family, six genera, 67 species, and 22 combinations have been introduced in the FUSE series.

Authors who wish to contribute to the next part in this series, FUSE 7, can e-mail submissions to Danny Haelewaters (danny.haelewaters@gmail.com) or Irmgard Krisai-Greilhuber (irmgard.greilhuber@univie.ac.at). Specific Author's Guidelines for FUSE submissions are available on the website of Sydowia (<http://www.sydowia.at/instructions/instructions.htm>).

## Materials and Methods

### Sample collection, isolation, and specimen examination

For the *Albatrellopsis* study, basidiomata were collected in coniferous forests in the Miandam valley of Swat District, Pakistan. Basidiomata were dug out at their base using a knife and photographed in their natural habitat using a Canon Power shot A470 camera (Tokyo, Japan). Macro-morphological characters from fresh basidiomata were noted in the field. Color codes follow Munsell Color Company (1954). Specimens were dried by placing them in front of a hot air fan set at 40–45 °C. Dried specimens were kept at -20 °C for two weeks as a pest-control measure and then deposited at SWAT (herbarium acronyms sensu Thiers continuously updated). Microscopic characters of herbarium specimens were observed using a BM 120 light microscope (BOECO, Hamburg, Germany) with an MVV 3000 camera (Byomic). Tissues were rehydrated using distilled water and mounted in 5 % KOH. Congo red (1 % aqueous solution) was used for staining hyaline structures, whereas Melzer's reagent was used for checking amyloidity of basidiospores and hyphae. Twenty randomly selected basidiospores, basidia, and hyphae from each available collection were measured using Piximètre computer software (Henriot & Cheypne 2020). Measurements are presented as (a-)b-c(-d) with 'b-c' representing the 90 % confidence interval, 'a' and 'd' extreme values. 'Q' stands for the range of length/width ratio of basidiospores.

Basidiomata of *Aureoboletus* were collected in the state of Oaxaca, Mexico in forests dominated by oaks (*Quercus* spp.). Protocols for sampling macrofungi as described by Lodge et al. (2004) were followed. The color descriptions were according to Kornerup & Wanscher (1978). Microscopic features from tubes, pileus, and stipe of dried basidiomata were measured at 100× magnification in 5 % KOH,

Melzer's reagent, and Congo red. The following abbreviations are used: 'Q' for length/width ratio, 'L<sub>av</sub>' for average length, 'W<sub>av</sub>' for average width, and 'n' for the number of basidiospores measured. At least 30 cystidia, basidia, and basidiospores were measured. Basidiospores were observed using a DSM 950 scanning electron microscope (Zeiss, White Plains, NY). All specimens are deposited at ITCV and MEXU.

For the *Entoloma* spp. nov. study, collections were photographed in the field. Macroscopic characters were noted immediately after collecting. Color codes follow Munsell Soil Color Company (1954) for *E. canadense* sp. nov. and Kornerup & Wanscher (1978) for *E. porphyroleucum* sp. nov. Microscopic characters were studied with a Leica DMLS microscope with a drawing tube and a Touptek Photonics camera (Zhejiang, China); a Zeiss Axioscope A1 microscope with AxioCam 1Cc 3; and a Zeiss Axiophot microscope with DC controlled Cree XP-G3 R3 CRI 90+ LED illumination, Plan Neofluar objectives 40×/1.30 Oil, 100×/1.30 Oil (Zeiss), DIC optics, a 12MP Touptek video camera with SONY Exmor IMX226 CMOS sensor (Tokyo, Japan), and ToupView video & image processing software (Touptek Photonics). Spores, basidia, and cystidia were observed in squash preparations of small parts of the lamellae in 5 % KOH or 1 % Congo Red in concentrated NH<sub>4</sub>OH. *Pileipellis* was examined on a radial section of the pileus in 5 % KOH. *Stipitipellis* was examined in 10% Ammonia. Size dimensions are based on measurements of 20 basidiospores, basidia, and cystidia, of which at least 10 structures per collection. Basidiospores were measured without apiculus, and basidia without sterigmata. Basidiospore length × width ratios are reported as Q. Other abbreviations used in *Entoloma* descriptions are 'Q<sub>av</sub>' for the average Q value, 'L' for the number of entire lamellae, and 'l' for number of lamellulae between each pair of entire lamellae. Collections are deposited at the following herbaria: GB, L, and LE.

Collections of *Erythrophyllporus* were made in semi-evergreen tropical forests with Fagaceae (*Lithocarpus* spp.) and Dipterocarpaceae in Vietnam. Macro-morphological features were studied based on fresh collections as well as by the analysis of the photos made in the field. Color codes in the description follow Kornerup & Wanscher (1978). Microscopic characters were studied with a light Zeiss Axioscope A1 microscope with an AxioCam ICc 3 camera and AxioVisionRel.4.6 software (Carl Zeiss, Oberkochen, Germany). Basidiospores, basidia, and hymenial cystidia were observed in

squash preparations of small parts of the lamellae in 5 % KOH. The pileipellis was examined on a radial section of the pileus, the stiptipellis on longitudinal slice of the stipe in 5 % KOH. Basidiospore dimensions are based on 20 measurements, whereas cystidia and basidia dimensions are based on observing at least 10 structures per collection. Basidia were measured without sterigmata, and the spores without hilum. Basidiospore length  $\times$  width ratios are reported as 'Q'. Specimens are deposited at LE.

Russian *Marasmiellus* basidiomata were sampled at the western foothills (ca. 906 m a.s.l.) of the volcano Avachinskaya Sopka at the eastern Kamchatka Peninsula. Description of basidiomata is based both on notes and photos taken *in situ* and observations of dried specimens. Color designations follow Kornerup & Wanscher (1978). Microscopic observations were made from dried material mounted in 5 % KOH, Congo Red, or Melzer reagent using an Axio Imager A1 light microscope (Carl Zeiss) equipped with differential interference contrast (DIC) optics and a Zeiss AxioCam MRc5 digital camera with AxioVision SE64 version 4.9.1 software. Basidiospore size was estimated from measurements of 60 basidiospores from three basidiomata; main values represented at least 90 % of the measurements and extreme values are enclosed in parentheses. 'Q' is the length/width ratio of basidiospores and 'Q<sub>av</sub>' stands for the average Q value. Statistics of hymenial elements and hyphae of pileipellis and caulocystidia are based on measurements of at least 10 structures from each of three basidiomata. Drawings were prepared with Inkscape version 0.91 software (<https://inkscape.org/r/>). Ex-type culture LE-BIN 4081 was obtained from spore print of a mature basidioma. After spore germination, the young mycelium was transferred in new Petri plates with beer-wort agar (BWA; beer-wort from brewery "Severnye pivovarni" in Russia, concentration 4 %, agar 20 g/l; Difco, Thermo Fisher Scientific, Waltham, MA). Culture characteristics were described by standard methods and terminology (Stalpers 1978). Inoculum plugs (7 mm diam.) were placed mycelium side down in the center of Petri plates (90 mm diam.) containing malt extract agar (MEA; malt extract 15 g/l, Condalab, Madrid, Spain; agar 20 g/l, Difco) and potato dextrose agar (PDA; potato dextrose broth 19.5 g/l, Panreac, Darmstadt, Germany; agar 20 g/l, Difco). Three replicates on each medium were incubated for eight weeks in a growth chamber (TS 1/80, Russia) at 25 °C in dark. Linear mycelium extension was recorded every other day until the plate was covered. Colony radius was measured in four mutually per-

pendicular directions (n=12); standard deviation (SD) was estimated in Excel (Microsoft, Redmond, WA). Extracellular oxidase reactions were tested according to Pointing (1999). The advancing zone and activity of oxidoreductases were studied after 10 days, colony morphology at weeks 4 and 8. Micromorphology was studied under transmitted light using a Zeiss Axio Imager A1 and Axio Scope A1 at week eight. *Gymnopus dichrous* (Berk. & M.A. Curtis) Halling, strain LE-BIN 1134 (USA, North Carolina, Jackson County, Highlands, Whiteside Cove Road, on dry tree, 12 July 1999) was used for comparative study. The holotype is deposited at LE. Ex-type strain LE-BIN 4081 is preserved in the Basidiomycete Culture Collection of the Komarov Botanical Institute of the Russian Academy of Sciences (Saint Petersburg, Russia) as stock cultures in glass tubes on BWA slants, in 2-ml vials under distilled water at 4 °C, and in cryovials on 10 % glycerol at -80 °C (freezing rate 1 °C/min).

Pakistani *Marasmiellus* basidiomata were collected in Ayubia National Park (Khyber Pakhtunkhwa Province) during the monsoon season in 2016–2017. This area represent one of the moist temperate forests in Pakistan, mostly dominated by conifers including *Abies pindraw*, *Cedrus deodara*, and *Pinus wallichiana* (Pinales Pinaceae), and *Taxus wallichiana* (Pinales, Taxaceae), along with broad-leaved oaks (Fagales, Fagaceae, *Quercus* spp.) (Saima et al. 2009, Raja et al. 2014, Razzaq et al. 2014). Collections were photographed *in situ*, morphologically characterized in the field, vouchered, and dried using a fan heater. Color codes were assigned following Munsell Color Company (1954). Microscopic characters including basidiospores, basidia, cystidia, pileipellis, and stiptipellis were observed from material mounted in 5 % KOH, Congo red, and Melzer's reagent under a CH30 light microscope (Olympus). Line drawings were made free-handed. Specimens are deposited at LAH.

For the *Pseudozeugandromyces* study, insect hosts were collected with a mouth-operated aspirator and immediately stored in 96 % denaturated ethanol. Screening and removal of Laboulbeniales thalli was done at 50 $\times$  magnification using an Olympus SZ61 stereomicroscope (Tokyo, Japan). Thalli were mounted in Amann medium (Benjamin 1971) and slides were sealed with transparent nail varnish. Insect hosts and microscope slides are deposited at BR. Drawings and measurements were made using an Olympus BX51 light microscope with drawing tube, digital camera, and AnalySIS software (Soft Imaging System GmbH, Münster, Germany).

For the *Robillarda* study, senescent and dried leaf litter baits of different plant species—including *Eucalyptus rostrata* (Myrtales, Myrtaceae), *Ficus nitida* (Rosales, Moraceae), *Phoenix dactylifera* (Arecales, Areaceae), and *Phragmites australis* (Poales, Poaceae)—were submerged in the Nile river and irrigation canals in Sohag Governorate, Egypt from December 2015 to December 2016. Leaves were baited in plastic mesh bags and collected randomly monthly. Collected decaying leaves were placed in clean plastic bags and returned to the laboratory, where they were rinsed first under tap water and then under sterile distilled water. Samples were incubated in Petri plates lined with sterile, wet filter paper at room temperature and sprayed with sterile distilled water periodically to avoid drying. Samples were periodically examined using an SZ62 stereomicroscope (Olympus) over 3 months of incubation for the presence of fungal sporulating structures. Fungi were mounted in freshwater and examined under a BX51 compound microscope (Olympus) equipped with DIC optics. Permanent slides were prepared using the double cover-glass method by Volkmann-Kohlmeyer & Kohlmeyer (1996). A herbarium collection of the new *Robillarda* species was prepared by drying decaying leaves with fungus material at 60 °C for 24 h and then deposited at CBS. Single-spore cultures were obtained by cutting open pycnidia with a sterile razor blade. The centrum tissue containing conidia was removed with sterile forceps and placed in sterile freshwater. Small drops of the spore suspension were placed on PDA (Oxoid, Basingstoke, England) and CMA (Oxoid) media and incubated at 22 °C in dark. Germinated spores were transferred to new plates. Colony characteristics and sporulation were noted after 2–3 weeks of growth. Conidiomata were measured both on leaves collected from the field and in pure culture. Measurements of 30 pycnidia were made under an SZ62 stereomicroscope (Olympus) from vertical sections that were prepared using a Leica CM1100 cryostat (Leica Biosystems, Nussloch, Germany). Sizes of conidia and conidial appendages were based on 50 measurements in freshwater.

The *Trechispora* specimen was collected during an exploratory fungal survey in Cusuco National Park, a Mesoamerican cloud forest in Honduras, between 22 June and 13 July 2019 (details in Haelewaters et al. 2020b, Martin et al. 2020). Fresh material was photographed *in situ*. The specimen was assigned a HONDURAS19-F collection number and metadata were recorded on site, including data, specific locality, geographic coordinates, substratum, and surrounding habitat notes.

Back at Base Camp (located at 1572 m a.s.l.), a rice-sized piece of tissue was removed from the specimen and stored in a 1.5 ml Eppendorf tube with 600 µl of Nuclei Lysis Solution (Promega, Madison, WI) and stored until DNA extraction could be performed. After processing, the specimen was dried with silica gel. Examination of microscopic characters was done in Congo Red and Melzer's reagent using an Olympus CX21 light microscope and a Nikon Eclipse Ni-E fluorescence microscope (Melville, NY). Measurements of microscopic structures were performed at 100× magnification. At least thirty basidiospores, 20 basidia, and 20 hyphae were measured. Sizes of basidia and basidiospores (excluding ornaments) are presented as follows: (a–)b–c(–d), with 'b–c' indicating the 90 % confidence interval, and 'a' and 'd' representing extreme values. Drawings were made using a drawing tube at 6000× magnification for basidiospores and at 1500× magnification for other elements. Scanning electron microscope (SEM) images were taken with a JEOL 5800 LV SEM (Peabody, MA).

*Tricholoma basidiomata* were collected at coniferous forests in Genç (Bingöl Province, Turkey) in 2018 and photographed with a Canon EOS 60D camera (Tokyo, Japan) equipped with Tokina 100 mm macro lens (New Delhi, India). Specimens were dried, kept in Ziploc bags, and deposited at VPH. Micromorphology of the basidiomata was analyzed using a Leica DM500 microscope. Sections of lamellae were mounted in tap water and Melzer's reagent. Size values reported for basidiospores were based on at least 40 measurements and include the mean length × mean width ± standard deviation and 'Q', representing the length-width ratio of basidiospores. Photographs of basidiospores were taken by field-emission SEM (Zeiss Sigma 300; White Plains, NY) using an accelerating voltage of 10 kV. Other abbreviations used in the description are 'L' for the number of entire lamellae, and 'l' for number of lamellulae between each pair of entire lamellae.

For the *Arthrorhynchus* study, bats were captured and screened for ectoparasites in Bulgaria (2017; Sándor et al. 2019), Rwanda (2008), and South Africa (2010–2017). Ectoparasites were stored in 98 % ethanol at –80 °C. Bat flies were screened for the presence of *Arthrorhynchus* thalli (Ascomycota, Laboulbeniomycetes, Laboulbeniales) under 40–50× magnification. Bat fly identification was based on several keys (Theodor 1957, 1967, 1968, 1973) and bat fly taxonomy follows Dick & Graciolli (2013) and Graciolli & Dick (2018). In addition, African bat flies stored in 70 % ethanol at

the entomology collection of the California Academy of Sciences (San Francisco, CA) were screened for Laboulbeniales: *Basilia blainvillii blainvillii* (Leach, 1817) from Uganda (n=8), *Dipseliopoda biannulata* (Oldroyd, 1953) from Uganda (n=10), *Nycteribia schmidlii* Schiner, 1853 from Uganda (n=1), *Penicillidia fulvida* (Bigot, 1885) from Kenya (n=2), *P. pachymela* Speiser 1900 from Tanzania (n=26), and *Phthiridium hoogstraali* (Theodor, 1957) from Kenya (n=8). Thalli were removed from their bat fly host at the point of attachment using a micropin and mounted in Heinz PVA mounting medium. Voucher slides are deposited at PUL. Mounted specimens were viewed at 200–1000× magnification. Light microscopy photographs of slide-mounted thalli were taken using an Olympus BD40 microscope equipped with a 40× phase-contrast lens and Olympus DP71 digital camera and viewed using the Olympus DP Controller software. Line and stipple drawings of thalli were made using photographs as reference material with PITT artist pens (Faber–Castell, Nürnberg, Germany). Drawings were scanned using an HP Scanjet G5040 scanner (Palo Alto, CA) and edited with Photopea (<https://www.photopea.com/>).

During the exploration of gasteroid fungal diversity in Pakistan, two collections of *Calvatia lilacina* were collected at two different localities. These were Mansehra (975 m a.s.l.) and Deosai Plains (4114 m a.s.l.). Specimens were labelled and morphological features were noted in the field. Collections were dried overnight using a fan heater and brought to the laboratory for further analysis. Microscopic study was done by making slides of gleba and peridium. Glebal material was examined mounted in lactophenol, trypan blue, and 5 % KOH. Illustrations of microscopic features were made with the help of a DM750 binocular microscope (Leica Microsystems) with camera lucida attached. Specimens are deposited at LAH.

Basidiomata of *Entoloma* were collected over several years at the Quaid-i-Azam Campus of the University of the Punjab in Pakistan during the rainy season. Morphological characters were noted from fresh material and photographs; colors follow Munsell Color Company (1954). Specimens were vouchered and dried using fan heater. Microscopic characters were examined based on dried material (lamellae, pileus, stipe) mounted in 2 % KOH, Congo red, and Melzer's reagent under an MX4300H light microscope (Meiji Techno). For basidiospores, the notation 'n/m/p' indicates that 'n' basidiospores were measured from 'm' basidiomata of 'p' collections. Dimensions of basidiospores are given as

length × width, each as (a–)b–c(–d) with 'b–c' indicating the 90 % confidence interval, and 'a' and 'd' representing extreme values; 'Q' stands for length/width ratio and 'Q<sub>av</sub>' stands for the average Q value (Liang & Yang 2011). All collections are deposited at LAH.

For the *Erysiphe* study, phytopathogenic surveys were conducted in Himalayan moist temperate forests in Khyber Pakhtunkhwa Province, Pakistan. Plants of *Urtica dioica* (Urticaceae) and *Ziziphus jujuba* (Rhamnaceae) infected with powdery mildew fungi were collected and photographed in the field. Samples were brought to the lab and photographed under an EMZ-5TR stereomicroscope (Meiji Techno, Saitama, Japan). Scratch mounts of infected portions were prepared in lactophenol. Microscopic examinations were done under a LABOMED (Labo America Inc., Fremont, CA) light microscope and anatomical dimensions of conidia, conidiophores, appressoria (anamorph); chasmothecia, asci, and ascospores (teleomorph) were measured using Scope Image 9.0 (X5) image-processing software (Bioimager, Maple, Ontario, Canada). A JEOL JSM-5910 scanning electron microscope (Peabody, MA) was used for more accurate identification. Pathogenicity was assessed by pressing a diseased leaf onto young leaves of three asymptomatic, potted plants of *Urtica dioica* and *Ziziphus jujuba*. Three non-inoculated plants (for each pathogen) were used as controls. Plants were maintained at 23 °C and 80 % relative humidity (RH) in a greenhouse at the Botanical Garden of the University of the Punjab (Lahore, Pakistan). The fungus on the inoculated leaves was morphologically identical to the fungus on the original infected leaves.

For the *Fanniomyces* study, fly specimens were collected in pitfall traps of dead crayfish (described in De Kesel & Haelewaters 2019) or by hand and screened for the presence of Laboulbeniales thalli (Ascomycota, Laboulbeniomycetes) under 40–50× magnification. Thalli were removed from their host using Minuten Pins (BioQuip, Rancho Dominguez, CA) inserted onto wooden rods. Thalli or groups of thalli were embedded in Amann solution (Benjamin 1971) with the help of a droplet of Hoyer's medium as described by Haelewaters et al. (2015b). Slides are deposited at FH. Mounted thalli were viewed at 200–1000× magnification using an Olympus BX40 light microscope with Olympus XC50 digital camera and MicroSuite Special Edition software 3.1 (Soft Imaging Solutions GmbH). Line and stipple drawings were made using photographs as reference material, with PITT artist pens (Faber–Castell). Drawings were scanned using an HP Scanjet

G5040 scanner and then edited with Photopea (<https://www.photopea.com/>).

Two specimens of *Morchella* Dill. ex Pers. were collected in 2015 in the Province of Antalya, Turkey. The morphological features and ecological notes were recorded from young to mature fruiting bodies and ascomata. Ascomata were photographed in their natural habitat. The macro-morphological descriptions and images of ascomata were based on fresh material. For micro-morphological structures, the dried ascomata were rehydrated in distilled water or 3 % KOH, and subsequently stained with Congo Red (to stain cell components) and cotton blue (to check ascospore ornamentation). The following abbreviations are used in the description: 'L<sub>av</sub>' for the average length of all the measured ascospores, 'W<sub>av</sub>' for the average width of all the measured ascospores, 'Q' for the quotient of length and width of all the measured ascospores, and 'Q<sub>av</sub>' for the average of all calculated Q values for all ascospores measured. At least thirty mature ascospores were measured. The collections are deposited at the personal fungarium of O. Kaygusuz at Isparta University of Applied Sciences, Turkey.

For the *Ophiocordyceps* study, macromorphological features were studied on fresh collection as well as by the analysis of photos taken in the field. Micromorphological structures were studied on dried material under a Zeiss Axio Imager.A2 light microscope, equipped with AxioVision Release 4.8.2. software. Measurements were done with a 100× oil immersion objective (1000× magnification). Drawings were produced with the aid of a drawing tube. Observations of microscopic features as well as measurements, and drawings were made from slide preparations stained with 5 % KOH. The specimen is deposited at WU.

Fresh material of *Parvacoccum pini* was collected during a students' course on management and forest protection in high-altitude afforestations and protective forests, taking place at the Sticklerhütte, Hintermuhr (Salzburg, Austria) in a subalpine stand of *Pinus cembra* (Pinales, Pinaceae) at ca. 1800 m a.s.l. Dead, corticated branches of *Pi. cembra* still attached to the trees were collected, brought to the laboratory, and checked for the presence of fungi. Study of macromorphology of *Parvacoccum pini* was done by using a Nikon SMZ 1500 stereomicroscope (Nelville, NY) equipped with a Nikon DS-U2 digital camera. For light microscopy, a Zeiss Axio Imager.A1 compound microscope (Oberkochen, Germany), equipped with DIC optics and a Zeiss AxioCam 506 colour digital camera was used. Microscopic observations of *Parvacoccum pini* were

made in 3 % KOH except where noted. Images and data were gathered using the following software packages: NIS-Elements D version 3.22.15 (Nikon) or Zeiss ZEN Blue Edition. For certain images of ascomata and conidiomata, stacking software Zerene Stacker version 1.04 (Zerene Systems LLC, Richland, WA) was used. Measurements are reported as maxima and minima in parentheses and the range representing the mean plus and minus the standard deviation of a number of measurements given in parentheses. *Parvacoccum pini* was isolated in pure culture from ascospores as described in Jaklitsch (2009) and grown on 2 % corn meal agar plus 2 % w/v dextrose (CMD). The herbarium specimen was deposited at WU, and the living culture is maintained in the personal collection of the author.

DNA extraction, PCR amplification, and sequencing

For the *Albatrellopsis* study, genomic DNA was extracted using the CTAB method of Allen et al. (2006). For molecular phylogenetic analysis, the internal transcribed spacer (ITS) region including was amplified using primers ITS1F (Gardes & Bruns 1993) and ITS4 (White et al. 1990). PCR amplification followed Khan et al. (2017), with initial denaturation at 94 °C for 4 min; followed by 40 cycles of denaturation at 94 °C for 1 min, annealing at 55 °C for 1 min, extension at 72 °C for 1 min; and final extension at 72 °C for 10 min. Purification and sequencing of PCR products was outsourced to the BGI Genomics (Hong Kong). Generated forward and reverse reads were assembled using BioEdit version 7.2.5 (Hall 1999).

For the *Aureoboletus* study, genomic DNA was extracted from 2–3 mg of tissue using a CTAB method (Doyle & Doyle 1987). DNA was quantified with a NanoDrop ND-1000 spectrophotometer (Thermo Fisher Scientific). Dilutions for each isolate were prepared resulting in DNA concentration of 20 ng/μl as a basis for PCR amplification. Sequences were obtained of the nuclear large subunit (LSU) of the ribosomal RNA gene (rDNA) as well as the genes for the RNA polymerase II largest and second largest subunits (*rpb1*, *rpb2*). The primer sets used for amplifying these fragments were: LR0R/LR5 for LSU (Vilgalys & Hester 1990, Hopple 1994), RPB1-Af/fRPB1-Cr for *rpb1*, and bRPB2-6F/bRPB2-7.1R (sensu Wu et al. 2014). The reaction mixture for PCR was prepared in a final volume of 15 μl containing 1× enzyme buffer, 0.8 μm of 0.2 μm dNTPs, 100 ng of DNA extract, 20 pmol of each primer, and 2 units of *Taq* DNA polymerase (Pro-

mega). Cycling conditions were as follows: for LSU; initial denaturation at 96 °C for 2 min; followed by 35 cycles of denaturation at 94 °C for 1 min, annealing at 48 °C for 30 s, extension at 72 °C for 1 min; and final extension at 72 °C for 5 min. For *rpb1* and *rpb2*: same conditions, except for annealing at 52 °C for 30 s. All PCR reactions were carried out in an MJ Research PTC-200 Thermal Cycler (BIO-RAD, Ciudad de México, Mexico). The amplifications were verified by electrophoresis in a 1.5 % agarose gel prepared with 1× TAE buffer (Tris Acetate-EDTA), run at 95 V for 1 h. The gel was dyed with GelRed (Biotium, Hayward, CA) and bands were visualized using an INFINITY 3000 transilluminator (Vilber Lourmat, Eberhardzell, Germany). PCR products were purified with the ExoSAP kit (Affymetrix, Santa Clara, CA) and prepared for the sequencing reaction using the BigDye Terminator version 3.1 kit (Applied Biosystems, Foster City, CA). Sequencing was done with a 3730xl DNA Analyzer (Applied Biosystems) at the Instituto de Biología, Universidad Nacional Autónoma de México. Forward and reverse sequence reads were assembled and edited using BioEdit version 7.0.5 (Hall 1999). Consensus sequences were submitted to NCBI GenBank (accession nos. MH337251, MT228976–MT228986).

DNA of *Entoloma* spp. nov. was extracted from dried herbarium material using the NucleoSpin® Plant II kit (Macherey-Nagel, Düren, Germany). The ITS region was amplified with primer sets ITS1F/ITS4, ITS1F/ITS4B, and ITS1F/ITS2 (White et al. 1990, Gardes & Bruns 1993), whereas LSU was amplified with primers LR0R and LR5 (Vilgalys & Hester 1990, Hopple 1994). PCR products were purified with the Fermentas Genomic DNA Purification Kit (Thermo Fisher Scientific). Purified PCR products were sequenced using the same primers on an ABI model 3130 Genetic Analyzer (Applied Biosystems) or commercially at LGC Genomics (Berlin, Germany). Alternatively, DNA extraction, PCR amplification, and Sanger sequencing were performed as part of the Norwegian Barcode of Life project (NorBOL) and followed Larsson et al. (2004, 2018). Chromatograms were checked and edited with the CodonCode Aligner package (CodonCode Corporation, Centerville, MA) and MEGA X (Kumar et al. 2018). Sequence comparison with public and personal databases followed Noordeloos et al. (2017). Newly generated sequences were submitted to GenBank (Tab. 1).

*Erythrophyllporus* DNA was extracted from herbarium material using NucleoSpin® Plant II kit (Macherey-Nagel, Düren, Germany). The ITS region was amplified with primers ITS1F and ITS4B

(Gardes & Bruns 1993), and translation 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 denaturation at 95 °C for 4 min; then 35 cycles of denaturation at 94 °C for 1 min, annealing at 52 °C for 1 min, extension at 72 °C for 1 min; and a final extension step of 72 °C for 3 min. For *tef1*: initial denaturation at 95 °C for 3 min; then 8 cycles of denaturation at 98 °C for 20 s, annealing at 60 °C for 40 s, 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, 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) and sequenced on an Applied Biosystems 3130 Genetic Analyzer. Raw data were edited and assembled in MEGA X (Kumar et al. 2018). Newly generated sequences were deposited in NCBI GenBank (Tab. 1).

Total DNA was extracted from small fragments of dried basidiomata as well as from culture mycelium of *Marasmiellus boreoorientalis* sp. nov., using the GeneJET Plant Genomic DNA Purification Mini Kit (Thermo Fisher Scientific) according to the manufacturer's instructions. PCR amplifications were performed with primer sets ITS1F/ITS4B (Gardes & Bruns 1993) for ITS and LR0R/LR5 (Vilgalys & Hester 1990, Hopple 1994) for LSU. Successful PCR products were purified with the GeneJET PCR Purification Kit (Thermo Fisher Scientific) following the manufacturer's protocol. Sanger sequencing was performed with an ABI model 3130 Genetic Analyzer (Applied Biosystems). Forward and reverse sequence reads were assembled to obtain consensus sequences and ambiguous edges were trimmed. Chromatograms were checked with Chromas version 2.6.6 (<https://www.technelysium.com.au>). The sequence from the basidioma was aligned with that obtained from the culture to confirm identity.

For the Pakistani *Marasmiellus* study, genomic DNA was extracted from lamellae of dried basidiomata following a modified CTAB method (Lee et al. 1988). The ITS region was amplified using universal primers ITS1F and ITS4 (White et al. 1990, Gardes & Bruns 1993). For PCR, the following cycling conditions were used (Saba et al. 2020): initial denaturation at 94 °C for 1 min; 35 cycles of denaturation at 94 °C for 1 min, annealing at 53 °C for 1 min, and extension at 72 °C for 1 min; followed by final extension at 72 °C for 8 min. Amplified PCR products were purified and sequenced by Tsing Ke Biotech. Forward and reverse sequence reads were



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

Species name	ID (isolate, strain, status, voucher)	Country, isolation source	SSU	ITS	LSU	<i>rpb1</i>	<i>rpb2</i>	<i>tef1</i>	Reference(s)
<i>Albatrellopsis confluens</i>	PV 101-93 GB	Czech Republic		AF506393					Larsson & Larsson (2003)
<i>Albatrellopsis fletti</i>	DAVFP-27659	Canada		JF899544					Miller & Buyck (2002)
<i>Albatrellopsis fletti</i>	398IF62	USA		AY061738					Miller & Buyck (2002)
<i>Albatrellopsis fletti</i>	MICH AHS82164			AY621802					Albee-Scott (2007)
<i>Albatrellopsis flettioides</i>	MM72	Pakistan		MT040747					This study
<i>Albatrellopsis flettioides</i>	MM76	Pakistan		MT040748					This study
<i>Albatrelus anellaneus</i>	p816i	USA		EU669392					Gordon M. & Zych P., unpubl.
<i>Albatrelus anellaneus</i>	p817i	USA		EU669393					Gordon M. & Zych P., unpubl.
<i>Albatrelus citrinus</i>	Muskos 850928 (S)	Sweden		AY198190					Ryman et al. (2003)
<i>Albatrelus citrinus</i>	Ryman 6061 (UPS F-007387)	Sweden		AY198192					Ryman et al. (2003)
<i>Albatrelus ovinus</i>	Fransson 2 (UPS F-015551)	Sweden		AY198203					Ryman et al. (2003)
<i>Albatrelus ovinus</i>	Daneil 11/8 00 (UPS F-015554)	Sweden		AY198198					Ryman et al. (2003)
<i>Albatrelus piceiphilus</i>	Cui2220	China		DQ789396					Cui et al. (2008)
<i>Albatrelus piceiphilus</i>	Cui2220	China		DQ789397					Cui et al. (2008)
<i>Albatrelus roseus</i>	SWAT000135	Pakistan		MF110285					Khan et al. (2018)
<i>Albatrelus roseus</i>	LAH35288	Pakistan		MF110297					Khan et al. (2018)
<i>Albatrelus similis</i>		USA		AY963566					Cui et al. (2008)
<i>Albatrelus subrubescens</i>	Jaederfeldt 11/10 1995	Sweden		AY198204					Ryman et al. (2003)
<i>Albatrelus subrubescens</i>	Ryman 6085 (UPS F-007381)	Sweden		AY198208					Ryman et al. (2003)
<i>Albatrelus subrubescens</i>	OR996	Belgium		KT947121					Vadhanarat S., Lumyong S. & Raspé O., unpubl.
<i>Appendiculina entomophila</i> [as <i>Stigmatomyces entomophilus</i> ]	D. Haelew. 1062c	Netherlands, <i>Drosophila funebris</i>	MG958014						This study
<i>Appendiculina entomophila</i> [as <i>Stigmatomyces entomophilus</i> ]	D. Haelew. 1063a	Netherlands, <i>Drosophila funebris</i>	MH040561						Haelewaters et al. (2018b)
<i>Appendiculina gregaria</i> [as <i>Stigmatomyces gregarius</i> ]	D. Haelew. 1008a	Sierra Leone, Diopsidae sp.	MG438348						Haelewaters et al. (2019c)
<i>Appendiculina gregaria</i> [as <i>Stigmatomyces gregarius</i> ]	D. Haelew. 1008b	Sierra Leone, Diopsidae sp.	MH040562						Haelewaters et al. (2018b)
<i>Appendiculina gregaria</i> [as <i>Stigmatomyces gregarius</i> ]	LG642	Sierra Leone, Diopsidae sp.	MG674225						Goldmann & Weir (2018)
<i>Appendiculina scaptomyzae</i> [as <i>Stigmatomyces</i> ]			AF431758						Weir & Hughes (2002)
<i>Arthrorynchus eucampsipodae</i>	D. Haelew. 1491a	Bulgaria, <i>Nycteribia vacata</i>			MT241715				This study
<i>Arthrorynchus eucampsipodae</i>	D. Haelew. 1498a	Rwanda, <i>Eucampsipoda africanaum</i>	MT235694		MT235717				This study
<i>Arthrorynchus eucampsipodae</i>	D. Haelew. 1498b	Rwanda, <i>Eucampsipoda africanaum</i>	MT235695		MT235718				This study
<i>Arthrorynchus eucampsipodae</i>	D. Haelew. 1499a	Slovakia, <i>Nycteribia schmidti</i>	MT235696		MT235719				This study

Species name	ID (isolate, strain, status, voucher)	Country, isolation source	SSU	ITS	LSU	<i>rpb1</i>	<i>rpb2</i>	<i>tef1</i>	Reference(s)
<i>Arthrorhynchus nycteribiae</i>	D. Haelew. 1484b	Bulgaria, <i>Penicillidia conspicua</i>			MT235715				This study
<i>Arthrorhynchus nycteribiae</i>	D. Haelew. 1484c	Bulgaria, <i>Penicillidia conspicua</i>			MT235716				This study
<i>Arthrorhynchus nycteribiae</i>	D. Haelew. 1505a	Bulgaria, <i>Penicillidia conspicua</i>	MT235697		MT235720				This study
<i>Arthrorhynchus nycteribiae</i>	D. Haelew. 1015d	Hungary, <i>Penicillidia conspicua</i>	MG438336		MG438363				Haelewaters et al. (2019c)
<i>Arthrorhynchus nycteribiae</i>	Edeleny_13.xi.2014	Hungary, <i>Penicillidia conspicua</i>	KY094496		KY094497				Haelewaters et al. (2017)
<i>Aureoboletus auriflammeus</i>	DD973	USA			AY612818				Wu et al. (2016)
<i>Aureoboletus auriporus</i>	BDCR0431	Costa Rica			AY612818	HQ161871			Dentinger et al. (2010)
<i>Aureoboletus catenarius</i>	HKAS 54463	China			NG057093	KT990348			Wu et al. (2016)
<i>Aureoboletus duplicatoporus</i>	HKAS 50498	China			KF112361	KF112754			Wu et al. (2014)
<i>Aureoboletus formosus</i>	GDGM44441	China			NG057082	KT291751			Zhang et al. (2015a)
<i>Aureoboletus garciae</i>	MEXU 29006, T	Mexico			MH337251	MT228979	MT228983		This study
<i>Aureoboletus garciae</i>	MEXU 30133	Mexico			MT228976	MT228980	MT228984		This study
<i>Aureoboletus garciae</i>	MEXU 30134	Mexico			MT228977	MT228981	MT228985		This study
<i>Aureoboletus garciae</i>	MEXU 30135	Mexico			MT228978	MT228982	MT228986		This study
<i>Aureoboletus gentilis</i>	MG372a	Italy			KF112344	KF112557	KF112741		Wu et al. (2014)
<i>Aureoboletus imitrus</i>	MB03104	USA			KF030239	KF030239			Nuhn et al. (2013)
<i>Aureoboletus longicollis</i>	HKAS 53398	China			KF112376	KF112625	KF112755		Wu et al. (2014)
<i>Aureoboletus marroninus</i>	GDGM43288	China			NG057040	KT291753			Zhang et al. (2015b)
<i>Aureoboletus mirabilis</i>	HKAS 57776	China			KF112360	KF112624	KF112743		Wu et al. (2014)
<i>Aureoboletus moravicus</i>	MG374a	Italy			KF112421	KF112559	KF112745		Wu et al. (2014)
<i>Aureoboletus nephrosporus</i>	HKAS 74929	China			NG057094	KT990896	KT990358		Wu et al. (2016)
<i>Aureoboletus projectellus</i>	AFTOLID713	USA			AY684158	AY788850	AY787218		Binder & Hibbett (2007)
<i>Aureoboletus quercus-spinosae</i>	GDGM 43755	China			NG057121	KY039963	KY039958		Zhang et al. (2017)
<i>Aureoboletus roxanae</i>	DS626-07	USA			KF030311	KF030381			Nuhn et al. (2013)
<i>Aureoboletus tenuis</i>	HKAS 75104	China			KT990518	KT990897	KT990359		Wu et al. (2016)
<i>Aureoboletus thibetanus</i>	HKAS 57692	China			KT990524	KT990901	KT990365		Wu et al. (2016)
<i>Aureoboletus tomentosus</i>	HKAS 80485	China			KT990894	KT990353			Wu et al. (2016)
<i>Aureoboletus viscidipes</i>	HKAS 77103	China			KT990519	KT990360			Wu et al. (2016)
<i>Aureoboletus viscosus</i>	HKAS 53398	China				KF112755			Wu et al. (2014)
<i>Aureoboletus yunnanensis</i>	HKAS 75050	China			KT990520	KT990898	KT990361		Wu et al. (2016)
<i>Aureoboletus zangii</i>	HKAS 74751	China			KT990521	KT990899	KT990362		Wu et al. (2016)
<i>Autoicomycetes falcatus</i>		USA, Hydrophiliidae sp.	MG687407						Goldmann & Weir (2018)
<i>Autoicomycetes recurvatus</i>	AW911B	USA, Hydrophiliidae sp.	MG687409						Goldmann & Weir (2018)
<i>Bordea</i> sp.	LG483	Namibia, Staphylinidae sp.	MG687403						Goldmann & Weir (2018)
<i>Calbatia brasiliensis</i>	UFRN-Fungos 3039	Brazil		MK660493					Crous et al. (2019)

Species name	ID (isolate, strain, status, voucher)	Country, isolation source	SSU	ITS	LSU	<i>rpb1</i>	<i>rpb2</i>	<i>tef1</i>	Reference(s)
<i>Cabatia caatinguensis</i>	UFRN Fungos 2945	Brazil		MG871364					Crous et al. (2018)
<i>Cabatia candida</i>	MJ3514	Hungary		DQ112624					Larsson & Jeppson (2008)
<i>Cabatia chilensis</i>	AH 19509	Chile		AJ486965					Crous et al. (2018)
<i>Cabatia chilensis</i>	BAFC 26765	Argentina		AJ486966					Crous et al. (2018)
<i>Cabatia craniiformis</i>	420526MF0033	China		MH141988					Crous et al. (2019)
<i>Cabatia craniiformis</i>	420526MF0084	China		MG719618					Crous et al. (2019)
<i>Cabatia craniiformis</i>	610723MF0044	China		KY950480					Crous et al. (2019)
<i>Cabatia cretacea</i>	MJ4302	Norway		DQ112598					Larsson & Jeppson (2008)
<i>Cabatia cretacea</i>	MJ4105	Iceland		DQ112597					Larsson & Jeppson (2008)
<i>Cabatia cyathiformis</i>	JTT10	USA		MF686508					Crous et al. (2018)
<i>Cabatia cyathiformis</i>	AH 25232	France		AJ486864					Crous et al. (2018)
<i>Cabatia cyathiformis</i>	LPS 7785b	Paraguay		AJ486865					Crous et al. (2018)
<i>Cabatia cyathiformis</i>	AH 25225	USA		AJ486866					Crous et al. (2018)
<i>Cabatia cyathiformis</i>	Lloyd 36803	USA		AJ486867					Crous et al. (2018)
<i>Cabatia cyathiformis</i>	ISC 369507	USA		AJ486868					Crous et al. (2018)
<i>Cabatia cyathiformis</i>	HAMB 2811	Cuba		AJ486869					Crous et al. (2018)
<i>Cabatia cyathiformis</i>	1831-1833	Brazil		AJ486872					Crous et al. (2018)
<i>Cabatia cyathiformis</i>	9-VI-1890	Vietnam		AJ486873					Crous et al. (2018)
<i>Cabatia cyathiformis</i>	GFW (Kreisel) leg. Lopez Nov. 1990	France		AJ617493					Crous et al. (2018)
<i>Cabatia fragilis</i>	Cragin 523 (NY)	USA		AJ486957					Crous et al. (2018)
<i>Cabatia fragilis</i>	AH 25227	Pakistan		AJ486958					Crous et al. (2018)
<i>Cabatia fragilis</i>	AH 24114	Argentina		AJ486959					Crous et al. (2018)
<i>Cabatia fragilis</i>	K 56043	Australia		AJ486960					Crous et al. (2018)
<i>Cabatia fragilis</i>	AH 21915	Spain		AJ486961					Crous et al. (2018)
<i>Cabatia fragilis</i>	PAD 3309	Italy		AJ486962					Crous et al. (2018)
<i>Cabatia fragilis</i>	AH 25228	Mongolia		AJ486963					Crous et al. (2018)
<i>Cabatia fragilis</i>	AAH 25226	Ghana		AJ486964					Crous et al. (2018)
<i>Cabatia fragilis</i>	Sydow 941 (M)	USA		AJ486871					Crous et al. (2018)
<i>Cabatia fragilis</i>	AH 18553	Mexico		AJ486870					Crous et al. (2018)
<i>Cabatia gigantea</i>	CFRM FP-98552	Germany		AJ617492					Gargas A. & Krueger D., unpubl.
<i>Cabatia holothurioides</i>	LE 287408	Vietnam		JQ734547					Rebriev (2013)
<i>Cabatia leiospora</i>	AN014671 (ARIZ)	USA		EU833652					Crous et al. (2018)
<i>Cabatia lilacina</i>	CPK1	Pakistan		MN544913					This study
<i>Cabatia lilacina</i>	NYG207	Pakistan		MN544914					This study
<i>Cabatia rubroflava</i>	TENN:059078	Argentina		KY559335					Crous et al. (2018)
<i>Cabatia</i> sp.	CPK4	Pakistan		MT940849					This study
<i>Cabatia turneri</i>	MJ5251	Norway		DQ112594					Larsson & Jeppson (2008)
<i>Cabatia turneri</i>	Lange 08-95	Greenland		DQ112596					Larsson & Jeppson (2008)
<i>Camptomyces</i> sp.	D. Haelew. 1222b	Tanzania, <i>Astermus</i> sp.	MF314140						Haelewaters et al. (2018b)
			MF314141						

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<i>Ceratomyces mirabilis</i>		USA, Hydrophilidae sp.	MG679452						Goldmann & Weir (2018)
<i>Chantransiopsis</i> sp.	LG589	Costa Rica, Cucujidae sp.	MG687411						Goldmann & Weir (2018)
<i>Chitonomyces affinis</i>		USA, Dytiscidae sp.	MG679288						Goldmann & Weir (2018)
<i>Chitonomyces simplex</i>		USA, <i>Laccophilus maculosus</i>	JN127389						Goldmann & Weir (2012)
<i>Chitonomyces spiniger</i>		USA, <i>Laccophilus maculosus</i>	JN127397						Goldmann & Weir (2012)
<i>Chlorenchoclia versiformis</i>	DAOMC 251598	Canada, hardwood log		MH457140	MH455361				McMullin et al. (2019)
<i>Coccomyces guizhouensis</i>	439A	China, <i>Pinus armandii</i>		JX317677					Lei et al. (2013)
<i>Coccomyces guizhouensis</i>	439B	China, <i>Pinus armandii</i>		JX317678					Lei et al. (2013)
<i>Coccomyces mucronatus</i>	R73	China, <i>Castanopsis eyrei</i>		GU138732					Lin Y.R., Wang S.J., Gao X.M., Gu T.T., Chen J.L. & Zheng Q., unpubl.
<i>Coccomyces piniicola</i>	HOU 486A	China, <i>Pinus armandii</i>		JX317676	MH457155				Lei et al. (2013)
<i>Coccomyces strobil</i>	DAOMC 251575	Canada, <i>Pinus strobus</i>		MH457129	MH457155				McMullin et al. (2019)
<i>Coccomyces strobil</i>	DAOMC 251589	Canada, <i>Pinus strobus</i>		MH457130	MH457157				McMullin et al. (2019)
<i>Coccomyces strobil</i>	DAOMC 251937	Canada, <i>Pinus strobus</i>		MH457131	MH457156				McMullin et al. (2019)
<i>Coccomyces strobil</i>	NB-641A	Canada, <i>Pinus strobus</i>		MH457133					McMullin et al. (2019)
<i>Coccomyces strobil</i>	NB-645C	Canada, <i>Pinus strobus</i>		MH457134					McMullin et al. (2019)
<i>Colpoma quercinum</i>	COL	Austria, <i>Quercus robur</i>		MT707243	MT707243				This study
<i>Coreomyces</i> sp.	H73-1	Sweden, <i>Sigara lateralis</i>	KY523236		KY350525				Sundberg et al. (2018)
<i>Coreomyces</i> sp.	H81-1	Denmark, <i>Sigara striata</i>	KY523242		KY350533				Sundberg et al. (2018)
<i>Coreomyces</i> sp.	H82-1	Sweden, <i>Sigara lateralis</i>	KY523243		KY350534				Sundberg et al. (2018)
<i>Crocinoletus rufaureus</i>	HKAS 53424	China		AF343320				KF112206	Wu et al. (2016)
<i>Diplomitoporus crustulinus</i>		South Korea							Kim et al. (2001)
<i>Drechmeria gunthii</i>	OSC76404	Lepidoptera (pupa)		AF339522					Sung et al. (2001)
<i>Drechmeria sinense</i>	CBS 567.95	Nematoda		AJ292417	AF339545				Sung et al. (2001)
<i>Entoloma abortitum</i>	GDGM27313	China		JQ291565					He et al. (2012)
<i>Entoloma abortitum</i>	HMJAU1955	China		JQ281483					He et al. (2012)
<i>Entoloma albogriseum</i>	4475	Canada		KJ705171					Berube J.A., Gadomski J., Labbe R., Leboeuf R., Gagne P., Dube J., et al., unpubl.
<i>Entoloma albotomentosum</i>	CUH:AM253	India		KX904354					Acharya et al. (2017)
<i>Entoloma alpinum</i>	SAAS774 Type	China		KJ658969					He et al. (2014)
<i>Entoloma uter</i>	HMLD1051	China		KC257439					Wang & Bau (2013)
<i>Entoloma byssisedum</i>	RBG Kew K(M)39744	England		EU784209					Brock et al. (2009)
<i>Entoloma byssisedum</i> var. <i>byssisedum</i>	JVG 1080907-1	Spain		KJ001413					Vila et al. (2014)
<i>Entoloma byssisedum</i> var. <i>microsporium</i>	SAAS1828	China		KU312120					He X.-L., unpubl.

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<i>Entoloma byssisedum</i> var. <i>microsporium</i>	SAAS1160	China		KU312118					He X.-L., unpubl.
<i>Entoloma byssisedum</i> var. <i>microsporium</i>	JVG 1061028-3	Spain		KJ001409					Vila et al. (2014)
<i>Entoloma canadense</i>	L0608150	Canada		MT940868					This study
<i>Entoloma canadense</i>	L0608149, T	Canada		MT940867	MK277990				This study
<i>Entoloma canadense</i> [as <i>E. porphyrophaeum</i> ]	iNaturalist 8606743	USA		MN906139					S.D. Russell, unpubl.
<i>Entoloma canadense</i> [as <i>E. sp.</i> ]	TRTC156878	Canada		JN021014					Dentinger et al. (2011)
<i>Entoloma canadense</i> [as <i>Trichopilus porphyrophaeus</i> ]	VHAs09/02	USA		EF421111					Hofstetter et al. (2014)
<i>Entoloma cetratum</i>	LE235480	Russia		KC898450					Morozova et al. (2014)
<i>Entoloma cettii</i>	WU 11500, T	Italy		NR_138020					Kokkonen (2015)
<i>Entoloma conchatum</i>	SAAS28817	China		KU312103					He X.-L., unpubl.
<i>Entoloma conchatum</i>	SAAS1378	China		KU312108					He X.-L., unpubl.
<i>Entoloma conchatum</i>	SAAS1712	China		KU312111					He X.-L., unpubl.
<i>Entoloma cremealbum</i>	O:300037, T	Finland		NR_152933					Kokkonen (2015)
<i>Entoloma flabellatum</i>	SAAS1080	China		KU312115					He X.-L., unpubl.
<i>Entoloma flabellatum</i>	SAAS1501	China		KU312116					He X.-L., unpubl.
<i>Entoloma frigidum</i>	0266-07-24-2016	Sweden		MT940872					This study
<i>Entoloma frigidum</i>	0271-07-25-2016	Sweden		MT940873					This study
<i>Entoloma frigidum</i>	GB-0202302 (EL46-07), T	Sweden		MT585817	MT585817				This study
<i>Entoloma frigidum</i>	GB-0202314	Sweden		MT940871					This study
<i>Entoloma frigidum</i>	GB-0202303	Sweden		MT940870					This study
<i>Entoloma frigidum</i>	GB-0202316	Sweden		MT940874					This study
<i>Entoloma frigidum</i>	GB-0202315	Sweden		MT940875					This study
<i>Entoloma frigidum</i>	O-F-252043	Norway		MT940869					This study
<i>Entoloma fuscomarginatum</i>	K(M)109022, T	United Kingdom		MT940864					This study
<i>Entoloma fuscomarginatum</i>	O-F-252055 (KB-EB 67/09)	Norway		MT940861					This study
<i>Entoloma fuscotomentosum</i>	JHP348-C6258	Greenland		LN850605					Kokkonen (2015)
<i>Entoloma fuscotomentosum</i> [as <i>E. sp.</i> ]	FA17766	Iceland		UDE000927*					Tedersoo L., unpubl.
<i>Entoloma graphitipes</i>	O-F-76067	Norway		KU127249					Weholt et al. (2015)
<i>Entoloma gregarium</i>	SAAS1493	China		KU312125					He X.-L., unpubl.
<i>Entoloma inutile</i>	Arnolds 3644 (L)	The Netherlands		MT940863					This study
<i>Entoloma jubatum</i>	K(M)160719	United Kingdom		MF979793					Elsley J.J., unpubl.
<i>Entoloma jubatum</i>	O-F-249209 / TEB352-13	Norway		MT878367					This study
<i>Entoloma lilacinroseum</i>	Bon8110012 (L), T	France		MT940860					This study
<i>Entoloma neglectum</i>	158/05	Finland		LN850557					Kokkonen (2015)
<i>Entoloma neglectum</i>	JV20020	Finland		LN850558					Kokkonen (2015)
<i>Entoloma pefense</i>	FK0759, T	Brazil		KU686890					Karstedt & Capelari (2017)

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<i>Entoloma phaeocyathus</i>	LIP JVG 960203, T	Spain		KJ001418					Vila et al. (2014)
<i>Entoloma pleurotoides</i>	SAAS1215	China		KU312112					He X.-L., unpubl.
<i>Entoloma pleurotoides</i>	SAAS1252	China		KU312113					He X.-L., unpubl.
<i>Entoloma pleurotoides</i>	SAAS1354	China		KU312114					He X.-L., unpubl.
<i>Entoloma porphyrescens</i>	NLN988012119 (L)	Tasmania		MT878366					This study
<i>Entoloma porphyroleucum</i>	LE312490, T	Vietnam		MT940862	MT950278				This study
<i>Entoloma porphyrophaeum</i>	O-F-287910	Norway		MT940866					This study
<i>Entoloma porphyrophaeum</i>	Winkel 864 (L)	The Netherlands		MT940865					This study
<i>Entoloma porphyrophaeum</i>	TUI20672	Estonia		UD8034969*					Saar I., unpubl.
<i>Entoloma ravinense</i>	PSC3331	Australia		KX387622					Catcheside et al. (2016)
<i>Entoloma reductum</i>	SAAS1019	China		KU312117					He X.-L., unpubl.
<i>Entoloma reductum</i>	SAAS1019	China		KU312123					He X.-L., unpubl.
<i>Entoloma scabiosum</i>	O-F-288007	Norway		MT878365					Saar I., unpubl.
<i>Entoloma sericeomitidum</i>	TB7144	USA		EF421108					Hofstetter et al. (2014)
<i>Entoloma</i> aff. <i>sericomitidum</i>	MUSH143-07	Canada		JN021018					Dentinger et al. (2011)
<i>Entoloma shandongense</i>	HMLD1796, T	China		KC257440					Wang & Bau (2013)
<i>Entoloma shandongense</i>	CUH: AM109	India		KP241852					Acharya et al. (2015)
<i>Entoloma shandongense</i>	LAH 36554	Pakistan		MT255022					This study
<i>Entoloma shandongense</i>	LAH 36555	Pakistan		MT252944					This study
<i>Entoloma shandongense</i>	LAH 36556	Pakistan		MT252945					This study
<i>Entoloma shandongense</i>	LAH 36650	Pakistan		MT255041					This study
<i>Entoloma</i> sp.	src741	USA		DQ974695					Smith et al. (2007)
<i>Entoloma</i> sp.	SAAS8064	China		KU312119					He X.-L., unpubl.
<i>Entoloma</i> sp.	SAAS083001	China		KU312121					He X.-L., unpubl.
<i>Entoloma</i> sp.	SAAS369	China		KU312104					He X.-L., unpubl.
<i>Entoloma</i> sp.	SAAS1220	China		KU312122					He X.-L., unpubl.
<i>Entoloma</i> sp.	CM13 219	New Caledonia		KY774199					Carricorde et al. (2019)
<i>Entoloma</i> sp. [as <i>Richoniella</i> sp.]	MEL2321963	Australia		KP191922					Lebel T. & Cooper J., unpubl.
<i>Entoloma</i> sp. [as <i>uncultured Entolomataceae</i> ]	BH2104F	Tasmania		JF960762					Horton (2011)
<i>Entoloma undatum</i>	LE312417	Russia		MF476910					Morozova et al. (2018)
<i>Entoloma undatum</i>	JVG11111118-5	Spain		KJ001410					Vila et al. (2014)
<i>Entoloma undatum</i>	JVG11111118-5	Spain		KJ001412					Vila et al. (2014)
<i>Erysiphe akebiae</i>	MUMH<JPN>-4649	Japan, <i>Akebia trifoliata</i>		LC010075					Takamatsu et al. (2015)
<i>Erysiphe alphitoides</i>	OE2015PM1CS	United Kingdom, <i>Wisteria brachybotrys</i>		KY660832					Ellingham (2017)
<i>Erysiphe alphitoides</i>	OE2015PMCS278	United Kingdom, <i>Quercus robur</i>		KY660890					Ellingham (2017)
<i>Erysiphe alphitoides</i>	MUMH 3169	Argentina, <i>Quercus robur</i>		AB292702					Takamatsu et al. (2007)

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<i>Erysiphe alphitoides</i>		United Kingdom, <i>Wisteria sinensis</i>		EF183498					Henricot & Cook (2007)
<i>Erysiphe alphitoides</i>	MUMH 2619	Japan, <i>Quercus dentata</i>		AB292700					Takamatsu et al. (2007)
<i>Erysiphe alphitoides</i>		United Kingdom, <i>Sorbaria sorbifolia</i>		KC489094					Denton et al. (2013)
<i>Erysiphe alphitoides</i>	MUMH 1443	Switzerland, <i>Quercus robur</i>		AB257431					Takamatsu et al. (2006)
<i>Erysiphe alphitoides</i>	MUMH 773	Lithuania, <i>Quercus robur</i>		AB292710					Takamatsu et al. (2007)
<i>Erysiphe alphitoides</i>	MUMH 631	Switzerland, <i>Quercus robur</i>		AB292708					Takamatsu et al. (2007)
<i>Erysiphe aquilegiae</i>	OE2013PM37	United Kingdom, <i>Aquilegia</i> sp.		KY653187					Ellingham (2017)
<i>Erysiphe aquilegiae</i>	OE2014PM139CS	United Kingdom, <i>Aquilegia vulgaris</i>		KY653190					Ellingham (2017)
<i>Erysiphe aucubae</i>	KUS:F29313	South Korea, <i>Aucuba japonica</i>		KY406744					Cho et al. (2017)
<i>Erysiphe buhrii</i>	OE2015PM196CS	United Kingdom, <i>Silene dioica</i>		KY660922					Ellingham (2017)
<i>Erysiphe buhrii</i>	OE2015PM194CS	United Kingdom, <i>Silene dioica</i>		KY660881					Ellingham (2017)
<i>Erysiphe "caricae"</i>	KW:58355	Ukraine, <i>Carica papaya</i>		LC009901					Takamatsu et al. (2015)
<i>Erysiphe castaneigena</i>	KUS:F28761	South Korea, <i>Castanea crenata</i>		KY926846					Cho et al. (2017)
<i>Erysiphe castaneigena</i>	KUS:F28837	South Korea, <i>Castanea crenata</i>		KY926847					Cho et al. (2017)
<i>Erysiphe circaeae</i>	OE2015PMCS214	United Kingdom, <i>Circaea lutetiana</i>		KY660882					Ellingham (2017)
<i>Erysiphe euonymicola</i>	OE2015PMCS277	United Kingdom, <i>Euonymus</i> sp.		KY660889					Ellingham (2017)
<i>Erysiphe euonymicola</i>	OE2015PM191CS	United Kingdom, <i>Euonymus</i> sp.		KY660925					Ellingham (2017)
<i>Erysiphe glycines</i>	MUMH<JPN>-396	Japan, <i>Desmodium lacinum</i>		LC028953					Takamatsu et al. (2015)
<i>Erysiphe glycines</i>	MUMH<JPN>-0396	Japan, <i>Desmodium lacinum</i>		LC009948					Takamatsu et al. (2015)
<i>Erysiphe glycines</i>	MUMH<JPN>-396	Japan, <i>Desmodium lacinum</i>		LC028953					Takamatsu et al. (2015)
<i>Erysiphe glycines</i>	MUMH<JPN>-0396	Japan, <i>Desmodium lacinum</i>		LC009948					Takamatsu et al. (2015)
<i>Erysiphe hedwigii</i>	OE2015PMCS206	United Kingdom, <i>Viburnum opulus</i>		KY660921					Ellingham (2017)
<i>Erysiphe hedwigii</i>	OE2015PM8CS	United Kingdom, <i>Viburnum tinus</i>		KY660869					Ellingham (2017)
<i>Erysiphe heraclei</i>	OE2013PM27	United Kingdom, <i>Heracleum sphondylium</i>		KY660749					Ellingham (2017)
<i>Erysiphe heraclei</i>	OE2016PMCS5	United Kingdom, <i>Anthriscus sylvestris</i>		KY661135					Ellingham (2017)
<i>Erysiphe hypophylla</i>	MUMH 2361	Japan, <i>Quercus crispula</i>		AB292711					Takamatsu et al. (2007)

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<i>Erysiphe hypophylla</i>	MUMH 294	Japan, <i>Quercus cuspidata</i>		AB292712					Takamatsu et al. (2007)
<i>Erysiphe loniceræ</i>	OE2015PM141CS	United Kingdom, <i>Lonicera</i> sp.		KY653175					Ellingham (2017)
<i>Erysiphe loniceræ</i>	OE2015PMCS202	United Kingdom, <i>Lonicera japonica</i>		KY660868					Ellingham (2017)
<i>Erysiphe loniceræ</i>	OE2015PM30CS	United Kingdom, <i>Lonicera periclymenum</i>		KY660891					Ellingham (2017)
<i>Erysiphe maclaayæ</i>	MUMH54s	Japan		AB016048					Takamatsu et al. (1999)
<i>Erysiphe miranda</i>	KUSF31068	South Korea, <i>Viburnum opulus</i> var. <i>sargentii</i>		MN431616					Bradshaw et al. (2020)
<i>Erysiphe miranda</i>	KUSF31014	South Korea, <i>Viburnum opulus</i> var. <i>sargentii</i>		MN431612					Bradshaw et al. (2020)
<i>Erysiphe penicillata</i>	MUMH<JPN>:1432	Germany, <i>Alnus incana</i>		LC009987					Takamatsu et al. (2015)
<i>Erysiphe penicillata</i>	KR:M36341	Germany, <i>Alnus glutinosa</i>		MN759661					Pastircakova K., Adamcikova K., Mikusova P. & Adamcik S., unpubl.
<i>Erysiphe pseudoloniceræ</i>	MUMH86	<i>Cocculus trilobus</i>		AB015915					Takamatsu et al. (1999)
<i>Erysiphe pseudoloniceræ</i>	MUMH<JPN>:2107	Japan, <i>Cocculus trilobus</i>		LC010010					Takamatsu et al. (2015)
<i>Erysiphe quercicola</i>	MUMH3230	Thailand, <i>Biza orellana</i>		AB237789					Limkaisang et al. (2006)
<i>Erysiphe quercicola</i>	MUMH3231	Thailand, <i>Biza orellana</i>		AB237790					Limkaisang et al. (2006)
<i>Erysiphe quercicola</i>	MUMH2606	Thailand, <i>Biza orellana</i>		AB237788					Limkaisang et al. (2006)
<i>Erysiphe quercicola</i>	MUMH3210	Malaysia, <i>Citrus sinensis</i>		AB237793					Limkaisang et al. (2006)
<i>Erysiphe quercicola</i>	VPRI30172	East Timor, <i>Citrus limon</i>		AB237791					Limkaisang et al. (2006)
<i>Erysiphe quercicola</i>	VPRI30173	East Timor, <i>Citrus reticulata</i>		MK559490					Fonseca (2020)
<i>Erysiphe quercicola</i>	M2	Vietnam, <i>Mangifera indica</i>		KM260686					Thanh Tam L. T., Minh Thanh H., Xuan Hoat T., Ngoc Dung P., Liem N. V., Minh Khue N., Tri M. V. & Viet Cuong H., unpubl.
<i>Erysiphe quercicola</i>	M3	Vietnam, <i>Mangifera indica</i>		KM260687					Thanh Tam L. T., Minh Thanh H., Xuan Hoat T., Ngoc Dung P., Liem N. V., Minh Khue N., Tri M. V. & Viet Cuong H., unpubl.
<i>Erysiphe quercicola</i>	JF5	Pakistan, <i>Ziziphus sjujuba</i>		MN394113					This study
<i>Erysiphe quercicola</i>	M1	Vietnam, <i>Mangifera indica</i>		KM260685					Thanh Tam L. T., Minh Thanh H., Xuan Hoat T., Ngoc Dung P., Liem N. V., Minh Khue N., Tri M. V. & Viet Cuong H., unpubl.
<i>Erysiphe quercicola</i>	M4	Vietnam, <i>Mangifera indica</i>		KM260688					Thanh Tam L. T., Minh Thanh H., Xuan Hoat T., Ngoc Dung P., Liem N. V., Minh Khue N., Tri M. V. & Viet Cuong H., unpubl.
<i>Erysiphe quercicola</i>	MUMH3267	Australia, <i>Mangifera indica</i>		AB237800					Limkaisang et al. (2006)



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<i>Erysiphe quercicola</i>	HAL 1975 F	Thailand, <i>Quercus</i> sp.		AB292692					Takamatsu et al. (2007)
<i>Erysiphe quercicola</i>	MUMH3227	Indonesia, <i>Acacia</i> sp.		AB237810					Limkaisang et al. (2006)
<i>Erysiphe quercicola</i>	MUMH3268	Thailand, <i>Mangifera indica</i>		AB237801					Limkaisang et al. (2006)
<i>Erysiphe quercicola</i>	MUMH 1952	Japan, <i>Quercus crispula</i>		AB292688					Takamatsu et al. (2007)
<i>Erysiphe schizandrae</i>	MUMH<JPN>-2582	Russia, <i>Schisandra chinensis</i>		LC010049					Takamatsu et al. (2015)
<i>Erysiphe symphoricarpi</i>	OE2015PM186CS	United Kingdom, <i>Symphoricarpos albus</i>		KY660867					Ellingham (2017)
<i>Erysiphe syringae-japonicae</i>	MUMH 1736	Switzerland, <i>Syringa vulgaris</i>		AB295458					Seko et al. (2008, 2011)
<i>Erysiphe syringae-japonicae</i>	MUMH<JPN>-7020	Azerbaijan, <i>Syringa vulgaris</i>		LC270849					Abasova et al. (2018)
<i>Erysiphe tortilis</i>	OE2014PM83CS	United Kingdom, <i>Cornus sericea</i>		KY660755					Ellingham (2017)
<i>Erysiphe urticae</i>	T-XJUF	China, <i>Urtica fissa</i>		KF582797					Zhang F.L. & Li C.W., unpubl.
<i>Erysiphe urticae</i>	OE2015PMC550	United Kingdom, <i>Urtica dioica</i>		KY660866					Ellingham (2017)
<i>Erysiphe urticae</i>	LAH36173	Pakistan, <i>Urtica dioica</i>		MN922834					This study
<i>Erysiphe urticae</i>	LAH36156	Pakistan, <i>Urtica dioica</i>		MN636273					This study
<i>Erysiphe urticae</i>	QHU2017009	Iran, <i>Urtica dioica</i>		AB104524					Khodaparast et al. (2004)
<i>Erysiphe urticae</i>	HMNWAFU-CF2000016	China		MT309705					Bai L., unpubl.
<i>Erysiphe wallrothii</i>	TPU-1729	China, <i>Boehmeria gracilis</i>		KR048078					Bai L., unpubl.
<i>Erythrophylloporus flammans</i>	LE 312491, T	<i>Vaccinium hirtum</i>		LC010088					Takamatsu et al. (2015)
<i>Erythrophylloporus flammans</i>	LE 312521	Vietnam		MT298114					This study
<i>Erythrophylloporus fagicola</i>	Garay 215	Vietnam		MT881670					This study
<i>Erythrophylloporus aurantiacus</i>	REH 7271 (USJ), T	Mexico							Vadthananarat et al. (2019)
<i>Erythrophylloporus paucicarpus</i>	OR 1151 (CMUB), T	Costa Rica							Vadthananarat et al. (2019)
<i>Erythrophylloporus paucicarpus</i>	OR 0689	Thailand							Vadthananarat et al. (2019)
<i>Erythrophylloporus paucicarpus</i>	OR 1135	Thailand							Vadthananarat et al. (2019)
<i>Erythrophylloporus cinnabarinus</i>	GDGM 70536, T	Thailand							Vadthananarat et al. (2019)
<i>Erythrophylloporus cinnabarinus</i>	GDGM 46541	China		MH374036					Zhang & Li (2018)
<i>Erythrophylloporus cinnabarinus</i>	GDGM 44440	China		MH374038					Zhang & Li (2018)
<i>Erythrophylloporus suthepensis</i>	SV0236 (CMUB), T	China		MH374037					Zhang & Li (2018)
<i>Erythrophylloporus suthepensis</i>	OR0615B	Thailand							Vadthananarat et al. (2019)
<i>Euzodiomyces lathrobbii</i>	LG260B	Thailand							Vadthananarat et al. (2019)
<i>Fanniomyces burdigalensis</i>	LG6798	Greece, Staphylinidae sp.	MG687402						Goldmann & Weir (2018)
<i>Fanniomyces ceratophorus</i>	D. Haelew. 1136h	Portugal, Sphaeroceridae sp.	MG696299						Goldmann & Weir (2018)
<i>Fibrodontia alba</i>	TNM F24944, T	USA, <i>Fammia canicularis</i>	MG958013						Haelewaters et al. (2018b), this study
<i>Fibrodontia gossypina</i>	AFTOL-ID 599	Taiwan							Yurchenko & Wu (2014)
		La Réunion							Matherly P.B. & Hibbett D.S., unpubl.

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<i>Fungal sp. 16</i>	GM 17-33	USA		KF359654					Baird et al. (2014)
<i>Gliocephalis hyalina</i>	DAOM 229465	Canada, <i>Glycine max</i> (soybean)	AH012810						Jacobs et al. (2005)
<i>Gloeandromyces dickii</i>	D. Haelew. 1323b, T	Panama, <i>Trichobius joblingi</i>	MG958011	MH040582					Haelewaters et al. (2018b)
<i>Gloeandromyces nycteribitidarum</i>	D. Haelew. 1334c	Panama, <i>Megistopoda aranea</i>	MH040534	MH040567					Haelewaters et al. (2018b)
<i>Gloeandromyces pageanus f. alarum</i>	D. Haelew. 1306b, T	Panama, <i>Trichobius joblingi</i>	MH040541		MH040574				Haelewaters et al. (2018b)
<i>Gloeandromyces pageanus f. alarum</i>	D. Haelew. 1322a	Panama, <i>Trichobius joblingi</i>	MH040543		MH040577				Haelewaters et al. (2018b)
<i>Gloeandromyces pageanus f. alarum</i>	D. Haelew. 1327a	Panama, <i>Trichobius joblingi</i>	MH040544		MH040578				Haelewaters et al. (2018b)
<i>Gloeandromyces pageanus f. pageanus</i>	D. Haelew. 1425a	Panama, <i>Trichobius dugesioides</i>	MH040536	MH040569					Haelewaters et al. (2018b)
<i>Gloeandromyces pageanus f. polymorphus</i>	D. Haelew. 619a	Trinidad, <i>Trichobius joblingi</i>	MH040537		KT800008				Haelewaters et al. (2015a, 2018b)
<i>Gloeandromyces pageanus f. polymorphus</i>	D. Haelew. 1272a, T	Panama, <i>Trichobius dugesioides</i>	MH040540		MH040573				Haelewaters et al. (2018b)
<i>Gloeandromyces pageanus f. polymorphus</i>	D. Haelew. 1315b	Panama, <i>Trichobius joblingi</i>	MH040542		MH040576				Haelewaters et al. (2018b)
<i>Gloeandromyces streblae f. sigmomorphus</i>	D. Haelew. 1320b, T	Panama, <i>Trichobius joblingi</i>	MH040545		MH040579				Haelewaters et al. (2018b)
<i>Gymnopus alpinus</i>	TENN:F-55834	UK		DQ480114					Mata et al. (2007)
<i>Gymnopus androsaceus</i>	TFB5037	Canada		KY026749					Petersen & Hughes (2016)
<i>Gymnopus androsaceus</i>	CBS 333.50	France		MH856650					Vu et al. (2019)
<i>Gymnopus aquosus</i>	TFB10996	USA		DQ449971					Mata et al. (2007)
<i>Gymnopus aquosus</i>	BRNM 710027	Czech Republic		JX536170					Antonin et al. (2013)
<i>Gymnopus bicolor</i>	AWW116, T	Indonesia (Bali)		AY263423					Wilson et al. (2004)
<i>Gymnopus confluens</i>	TENN:F-65131	USA		KP710288					Hughes & Petersen (2015)
<i>Gymnopus confluens</i>	TENN:F-55879	United Kingdom (Scotland)		KP710302					Hughes & Petersen (2015)
<i>Gymnopus dichrous</i>	TENN:F-56726	USA		AY256702					Mata et al. (2004b)
<i>Gymnopus dichrous</i>	TFB7920	USA		DQ450007					Mata et al. (2007)
<i>Gymnopus dichrous</i>	TENN:F-61624, clone c10b	USA		JF313683					Hughes K.W., Petersen R.H. & Lodge D.J., unpubl.
<i>Gymnopus dichrous</i>	TENN:F-56727	USA		KY026655					Petersen & Hughes (2016)
<i>Gymnopus dichrous</i>	65068-13714	USA		KY242493					Petersen & Hughes (2016)
<i>Gymnopus dichrous</i>	65069-13715-1	USA		KY242494					Petersen & Hughes (2016)
<i>Gymnopus dichrous</i>	65069-13715-2	USA		KY242495					Petersen & Hughes (2016)
<i>Gymnopus dichrous</i>	65070-13716-7	USA		KY242496					Petersen & Hughes (2016)
<i>Gymnopus dichrous</i>	65070-13716-10	USA		KY242497					Petersen & Hughes (2016)
<i>Gymnopus dichrous</i>	65070-13716-11	USA		KY242498					Petersen & Hughes (2016)
<i>Gymnopus dichrous</i>	65071-13717	USA		KY242499					Petersen & Hughes (2016)
<i>Gymnopus dichrous</i>	65071-13717	USA		KY242500					Petersen & Hughes (2016)

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<i>Gymnopus aff. dichrous</i> I	TENN:F-67859	USA		KY026696					Petersen & Hughes (2016)
<i>Gymnopus dryophilus</i>	DUKE 193401	Sweden		JX536159					Antonin et al. (2013)
<i>Gymnopus dryophilus</i>	KAI2-0395	South Korea		KR673450					Kim et al. (2015)
<i>Gymnopus dryophilus</i>	MushroomObserver: 268012	Mexico		KY655332					Rockefeller A., unpubl.
<i>Gymnopus dysodes</i>	KAI2-1237	South Korea		KR673491					Kim et al. (2015)
<i>Gymnopus dysodes</i>	TENN:F-61125	USA		KY026666					Petersen & Hughes (2016)
<i>Gymnopus erythropus</i>	WTU JFA12910	USA		DQ449998					Mata et al. (2007)
<i>Gymnopus erythropus</i>	610723MF0024	China		KY950460					Zhu M., unpubl.
<i>Gymnopus foetidus</i>	TENN:F-65806	USA		KY026682					Petersen & Hughes (2016)
<i>Gymnopus foetidus</i>	TENN:F-69280	Slovakia		KY026731					Petersen & Hughes (2016)
<i>Gymnopus foliophilus</i>	TENN:F-50013	USA		KY026620					Petersen & Hughes (2016)
<i>Gymnopus foliophilus</i>	TENN:F-51221	USA		KY026631					Petersen & Hughes (2016)
<i>Gymnopus fusipes</i>	TENN:F-69254	Slovakia		KY026727					Petersen & Hughes (2016)
<i>Gymnopus fusipes</i>	TENN:F-11439	Austria		AF505777					Mata et al. (2004b)
<i>Gymnopus hybridus</i>	TFB11454	Austria		DQ449980					Mata et al. (2007)
<i>Gymnopus indoctoides</i>	AWW125	Indonesia		AY263424					Wilson et al. (2004)
<i>Gymnopus luxurians</i>	FB10350	USA		AF505765					Mata et al. (2004a)
<i>Gymnopus luxurians</i>	TENN:F-50619	Switzerland		DQ450022					Mata et al. (2007)
<i>Gymnopus luxurians</i>	KUC20080725-28	South Korea		KW496469					Jang S., Jang Y., Lee H.B. & Kim J.-J., unpubl.
<i>Gymnopus micromphaloides</i>	TENN:68165,T	USA		NR_137864					Petersen & Hughes (2014)
<i>Gymnopus octor</i>	TFB9015	USA		DQ449959					Mata et al. (2007)
<i>Gymnopus octor</i>	BRNM 728539	Czech Republic		JX536167					Antonin et al. (2013)
<i>Gymnopus octor</i>	TFB6981	United Kingdom		DQ449968					Mata et al. (2007)
<i>Gymnopus perforans</i>	TENN:F-50319	Sweden		KY026625					Petersen & Hughes (2016)
<i>Gymnopus perforans</i> subsp. <i>transatlanticus</i>	AV100918	Canada		KY026743					Petersen & Hughes (2016)
<i>Gymnopus peronatus</i>	TENN:F-50540	Sweden		DQ450017					Mata et al. (2007)
<i>Gymnopus peronatus</i>	UBC F28402	Canada		KP454027					Berbee M., Bazzicalupo A. & Le Renard L., unpubl.
<i>Gymnopus pinophilus</i>	TENN:F-67846	USA		KY026695					Petersen & Hughes (2016)
<i>Gymnopus pinophilus</i>	TENN:F-69212	USA		KY026726					Petersen & Hughes (2016)
<i>Gymnopus ramulicola</i>	GDGM:43884,T	China		NR_158481					Deng et al. (2016)
<i>Gymnopus sequoiae</i>	TENN:F-69325	USA		KY026740					Petersen & Hughes (2016)
<i>Gymnopus spongiosus</i>	TENN:F-59640	USA		DQ480113					Mata et al. (2007)
<i>Gymnopus subnudus</i>	WRW 08-462	USA		KY026765					Petersen & Hughes (2016)
<i>Herpomyces chaetophilus</i>	D. Haelew. 483b	USA, <i>Periplaneta americana</i>	MG438319		MG438350				Haelewaters et al. (2019c)
<i>Herpomyces chaetophilus</i>	D. Haelew. 483e	USA, <i>Periplaneta americana</i>	MG438320		MG438351				Haelewaters et al. (2019c)
<i>Herpomyces chaetophilus</i>	D. Haelew. 602b	USA, <i>Periplaneta americana</i>	KT800023		KT800009				Haelewaters et al. (2015a)

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<i>Herpomycetes chaetophilus</i>	D. Haelew. 1097b	Panama, <i>Periplaneta americana</i>	MG438321		MG438352				Haelewaters et al. (2019c)
<i>Herpomycetes chaetophilus</i>	D. Haelew. 1097c	Panama, <i>Periplaneta americana</i>	MG438322		MG438353				Haelewaters et al. (2019c)
<i>Herpomycetes leurolestis</i>	Debr_Ppal	Hungary, <i>Phoetalia pallida</i>	MG438323		MG438354				Haelewaters et al. (2019c)
<i>Herpomycetes periplanetae</i>	D. Haelew. 602c	USA, <i>Periplaneta americana</i>	KT800025		KT800010				Haelewaters et al. (2015a)
<i>Herpomycetes periplanetae</i>	D. Haelew. 602d	USA, <i>Periplaneta americana</i>	MG438327		MG438357				Haelewaters et al. (2019c)
<i>Herpomycetes periplanetae</i>	D. Haelew. 1187d	USA, <i>Periplaneta americana</i>	MG438331		MG438359				Haelewaters et al. (2019c)
<i>Herpomycetes periplanetae</i>	TW437c	USA, <i>Periplaneta americana</i>	MG438324		MG438355				Haelewaters et al. (2019c)
<i>Herpomycetes periplanetae</i>	TW448b	USA, <i>Periplaneta americana</i>	MG438325		MG438356				Haelewaters et al. (2019c)
<i>Herpomycetes shelfordellae</i>	Bud_Slat	Hungary, <i>Shelfordella lateralis</i>	MG438333		MG438361				Haelewaters et al. (2019c)
<i>Herpomycetes shelfordellae</i>	DE_HerpBL1	Hungary, <i>Shelfordella lateralis</i>	KT800026		KT800011				Haelewaters et al. (2015a)
<i>Herpomycetes</i> sp.	H77-1	USA, <i>Parcoblatta cf. lata</i>	KY523239		KY350529				Sundberg et al. (2018)
<i>Herpomycetes stylopygae</i>	Bud_Bori	Hungary, <i>Blatta orientalis</i>	MG438332		MG438360				Haelewaters et al. (2019c)
<i>Hesperomycetes virescens</i>	D. Haelew. 316a	USA, <i>Harmonia axyridis</i>	MG438339		KJ842339				Haelewaters et al. (2018b, 2019c)
<i>Hesperomycetes virescens</i>	D. Haelew. 334b	Netherlands, <i>Harmonia axyridis</i>	MG438340		MG438364				Haelewaters et al. (2019c)
<i>Hesperomycetes virescens</i>	D. Haelew. 486c	USA, <i>Harmonia axyridis</i>	KT800029		KT800014				Haelewaters et al. (2015a)
<i>Hesperomycetes virescens</i>	D. Haelew. 655c	South Africa, <i>Cheilomenes propinqua</i>	KU574866		KU574867				Haelewaters et al. (2016)
<i>Hesperomycetes virescens</i>	D. Haelew. 659b	South Africa, <i>Cheilomenes propinqua</i>	MG760590 (659a)		MG745342				Haelewaters et al. (2018a)
<i>Hesperomycetes virescens</i>	D. Haelew. 1174a	Netherlands, <i>Harmonia axyridis</i>	MG760598		MG745345				Haelewaters et al. (2018a)
<i>Hesperomycetes virescens</i>	D. Haelew. 1188g	USA, <i>Harmonia axyridis</i>	MG438341		MG438365				Haelewaters et al. (2019c)
<i>Hesperomycetes virescens</i>	D. Haelew. 1231a	Italy, <i>Adalia bipunctata</i>	MG760603		MG745350				Haelewaters et al. (2018a)
<i>Hesperomycetes virescens</i>	D. Haelew. 1248b	Italy, <i>Adalia decempunctata</i>	MG760606		MG745353				Haelewaters et al. (2018a)
<i>Hesperomycetes virescens</i>	D. Haelew. 1268b	Japan, <i>Harmonia axyridis</i>	MG760610		MG745357				Haelewaters et al. (2018a)
<i>Hesperomycetes virescens</i>	D. Haelew. 1268d	Japan, <i>Harmonia axyridis</i>	MG760611		MG745358				Haelewaters et al. (2018a)
<i>Heyderia abietis</i>	OSC60392			AY769290	AY769289				Wang et al. (2005)
<i>Houarungia cheoi</i>	HKAS 62269	China			KF112385				Wu et al. (2014)
<i>Ilyomyces</i> sp.	LTI179	USA, Staphylinidae sp.	MG687397						Goldmann & Weir (2018)
<i>Laboulbenia bruchii</i>	D. Haelew. 1346b	Panama, <i>Neolema adunata</i>	MIN530040		MIN394843				Haelewaters et al. (2019b), Blackwell et al. (2020)
<i>Laboulbenia calathi</i>	D. Haelew. 1007a	Netherlands, <i>Calathus melanocephalus</i>	MG438342						Haelewaters et al. (2019c)
<i>Laboulbenia cristata</i>	LG613	Taiwan, Staphylinidae sp.	MG696296						Goldmann & Weir (2018)

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<i>Laboulbenia pedicellata</i>	H84-1	Sweden, <i>Dyschirius globosus</i>	KY523244		KY350537				Sundberg et al. (2018)
<i>Laboulbenia</i> sp.	D. Haelew. 971a	Panama, <i>Systenia</i> sp.	MG438345						Haelewaters et al. (2019c)
<i>Laboulbeniopsis termitarius</i>	DAH 18	USA, <i>Reticulitermes flavipes</i>	AY212810						Henk et al. (2003)
<i>Laboulbeniopsis termitarius</i>	LtersP02	Japan, <i>Reticulitermes speratus</i>	MF785100						Guswenrivo et al. (2018)
<i>Laanmaoa asiatica</i>	HKAS 63592	China		GU138714				KM605152	Wu et al. (2015)
<i>Lophodermium jiangnanense</i>	R44	China							Lin Y.R., Wang S.J., Gao X.M., Gu T.T., Chen J.L. & Zheng Q., unpubl.
<i>Lophodermium nitens</i>	NB-283-2K	Canada, <i>Pinus strobus</i>		MH457132					McMullin et al. (2019)
<i>Lophodermium nitens</i>	PMM2-5-7	USA, <i>Pinus monticola</i>		MG877520	MG877520				Salas-Lizana & Oono (2018)
<i>Lophodermium piceae</i>	Hou et al. 55			HQ902160	HQ902153				Fan et al. (2012)
<i>Lophodermium piceae</i>	ZK53/08	Czech Republic, <i>Picea abies</i>		FR837918					Koukol et al. (2012)
<i>Lulworthia grandispora</i>	AFTOL-ID 424		DQ522855		DQ522856				Schoch et al. (2009)
<i>Lulworthia lignoarenaria</i>	PP915		FJ176848		FJ176903				Schoch et al. (2009)
<i>Lyophyllum decastes</i>	Ldec4Q106	New Zealand		JN983978					Visnovsky et al. (2011)
<i>Lyophyllum decastes</i>	Ldec2Q106	New Zealand		JN983980					Visnovsky et al. (2011)
<i>Lyophyllum decastes</i>	Ldec7Q106	New Zealand		JN983981					Visnovsky et al. (2011)
<i>Lyophyllum decastes</i>	Ldec3Q106	New Zealand		JN983983					Visnovsky et al. (2011)
<i>Marasmiellus biformis</i>	LAH 36408	Pakistan		MT162680					This study
<i>Marasmiellus biformis</i>	LAH 36409	Pakistan		MT162681					This study
<i>Marasmiellus biformis</i>	TENN:F-65586	USA		KJ416248					Petersen & Hughes (2014)
<i>Marasmiellus biformis</i>	TENN:F-65189	USA		KJ416249					Petersen & Hughes (2014)
<i>Marasmiellus biformis</i>	TENN:F-68108	USA		KJ416246					Petersen & Hughes (2014)
<i>Marasmiellus "biformis"</i>	10146(1)	China		KM083047					Tian H., unpubl.
<i>Marasmiellus "biformis"</i>	10146(2)	China		KM083048					Tian H., unpubl.
<i>Marasmiellus "biformis"</i>	JS160901-64	South Korea		MG407676					Lee J.S., Kim C., Choi S.Y. & Lee H.B., unpubl.
<i>Marasmiellus boreorientalis</i>	LE 323323, T	Russia		MN597452					This study
<i>Micromphale brassicolens</i>	TENN:F-55550	Russia		DQ449889					Mata et al. (2007)
<i>Micromphale brassicolens</i>	TENN:F-59293	Austria		DQ449990					Mata et al. (2007)
<i>Marasmiellus brunneigracilis</i>	AWW01	Indonesia		AY263434					Wilson et al. (2004)
<i>Marasmiellus collybioides</i>	FB10080	Costa Rica		AF505772					Mata et al. (2007)
<i>Marasmiellus confluens</i>	KUC20140820A-21	South Korea		KX513743					Jang et al. (2016)
<i>Marasmiellus confluens</i>	TENN:F-60736	Russia		KP710289					Hughes & Petersen (2015)
<i>Marasmiellus confluens</i>	CUH AM083	India		KJ817065					Dutta et al. (2015)
<i>Marasmiellus cylindricus</i> (as <i>Gymnopus</i> )	TENN:F-58097, T	Costa Rica		NR_119464					Schoch et al. (2014)
<i>Marasmiellus dichrous</i> = <i>Gymnopus dichrous</i>	TENN:F-60029	USA		KY026665					Petersen & Hughes (2016)

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<i>Marasmiellus dichrous</i>	TENN:F-56727	USA		KY026656					Petersen & Hughes (2016)
<i>Marasmiellus disjunctus</i>	TENN:F-69172, T	USA		KJ416252					Petersen & Hughes (2014)
<i>Marasmiellus encficola</i>	TENN:F-69123, T	Canada		NR_137613					Petersen et al. (2016)
<i>Marasmiellus gibbosus</i>	TFB11586	USA		DQ450020					Mata et al. (2007)
<i>Marasmiellus istanbulensis</i>	KATO_fungi_3596, T	Turkey		KX184795					Seshi et al. (2018)
<i>Marasmiellus juniperinus</i> = <i>Gymnopus juniperinus</i>	TFB10782	Argentina		KY026661					Petersen & Hugher (2016)
<i>Marasmiellus juniperinus</i>	TENN:F-59540	USA		AY256708					Mata et al. (2004b)
<i>Marasmiellus longistipes</i>	LAH 35979, T	Pakistan		MK957247					This study
<i>Marasmiellus longistipes</i>	LAH 35980	Pakistan		MK957248					This study
<i>Marasmiellus longistipes</i>	LAH 36411	Pakistan		MK957249					This study
<i>Marasmiellus melanopus</i>	AWW54	Indonesia		AY263425					Wilson et al. (2004)
<i>Marasmiellus menchune</i>	DED5866	Indonesia		AY263426					Wilson et al. (2004)
<i>Marasmiellus menchune</i>	TFB11587	USA		DQ450043					Mata et al. (2007)
<i>Marasmiellus mesoamericanus</i>	TFB10411	Costa Rica		DQ450036					Mata et al. (2007)
<i>Marasmiellus mesoamericanus</i>	TFB11005, T	Costa Rica		NR_119583					Mata et al. (2007)
<i>Marasmiellus micromphaleoides</i>	TENN:F-68165, T	USA		NR_137864					Petersen & Hughes (2014)
<i>Marasmiellus neotropicus</i> [as <i>Gymnopus</i> ]	TFB10416	Costa Rica		AF505769					Mata et al. (2007)
<i>Marasmiellus nonnullus</i> = <i>Gymnopus nonnullus</i>	TFB14278	USA		KY026701					Petersen & Hughes (2016)
<i>Marasmiellus nonnullus</i>	AWW55	Indonesia		AY263446					Wilson et al. (2004)
<i>Marasmiellus parvulus</i>	TENN:F-58113, T	Costa Rica		NR_119584					Mata et al. (2007)
<i>Marasmiellus peronatus</i>	LE-BIN1364	Russia		KY026755					Petersen & Hughes (2016)
<i>Marasmiellus peronatus</i>	LE-BIN1898	Russia		KY026756					Petersen & Hughes (2016)
<i>Marasmiellus polygrammus</i> [as <i>Gymnopus</i> ]	URM 90016	Brazil		KY074641					Coimbra et al. (2016)
<i>Marasmiellus polygrammus</i> [as <i>Gymnopus</i> ]	URM 90017	Brazil		KY074642					Coimbra et al. (2016)
<i>Marasmiellus pseudoluxurians</i>	TFB11711	Dominican Republic		DQ450024					Mata et al. (2007)
<i>Marasmiellus pseudoluxurians</i>	TENN:F-68144, T	USA		NR_137863					Petersen & Hughes (2014)
<i>Marasmiellus ramealis</i>	TENN:F-62867	Sweden		JF313670					Hughes K.W., Petersen R.H. & Lodge D.J., unpubl.
<i>Marasmiellus ramealis</i>	TENN:F-65132	Belgium		KJ416235					Petersen & Hughes (2014)
<i>Marasmiellus stevensoniae</i> [as <i>Gymnopus</i> ]	PDD-95844	New Zealand		HQ533036					Johnston P.R. & Park D., unpubl.
<i>Marasmiellus stevensoniae</i> [as <i>Gymnopus</i> ]	TFB7571	New Zealand		DQ450034					Mata et al. (2007)
<i>Marasmiellus stevensoniae</i> [as <i>Gymnopus</i> ]	TENN:F-61061	New Zealand		KJ416244					Petersen & Hughes (2014)

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<i>Marasmiellus rodhali</i> [as <i>Gymnopus</i> ]	SFSU:BAP 630	São Tomé and Príncipe		MF100981					Desjardin & Perry (2017)
<i>Marasmiellus rodhali</i> [as <i>Gymnopus</i> ]	SFSU:BAP 627, T	São Tomé and Príncipe		MF100982					Desjardin & Perry (2017)
<i>Marasmiellus subcyathiformis</i> [as <i>Gymnopus</i> ]	URM 90023	Brazil		KY404982					Coimbra et al. (2016)
<i>Marasmiellus subcyathiformis</i> [as <i>Gymnopus</i> ]	URM 90022	Brazil		KY404983					Coimbra et al. (2016)
<i>Marasmiellus subnudus</i>	LAH 36410	Pakistan		MT162682					This study
<i>Marasmiellus subnudus</i>	KUC20150814-11	Korea		KX513747					Jang et al. (2016)
<i>Marasmiellus subnudus</i>	KUC20150814-19	Korea		KX513748					Jang et al. (2016)
<i>Marasmiellus subnudus</i>	TFB10331	USA		DQ450018					Mata et al. (2007)
<i>Marasmiellus subnudus</i>	TENN:F-61138	USA		KY026667					Petersen & Hughes (2016)
<i>Marasmiellus tambinganensis</i>	AWW39	Indonesia		AY263450					Wilson et al. (2004)
<i>Marasmiellus trogioides</i> [as <i>Gymnopus</i> ]	SFSU:AWW51, T	Indonesia		NR_152884					Wilson et al. (2004)
<i>Marasmiellus trogioides</i> [as <i>Gymnopus</i> ]	AWW51	Indonesia		AY263428					Wilson et al. (2004)
<i>Morchella americana</i>	LIP:PhC73, T	USA		KM588004					Richard et al. (2015)
<i>Morchella anatolica</i>	LIP:PhC233	Spain		KM587974					Richard et al. (2015)
<i>Morchella anatolica</i>	JA-Cussta 1485	Spain		KJ802105					Loizides et al. (2015)
<i>Morchella anatolica</i>	OKA-1B	Turkey		MF228801					This study
<i>Morchella anatolica</i>	OKA-2B	Turkey		MF228802					This study
<i>Morchella angusticeps</i>	M304	USA		JQ723055					Du et al. (2012b)
<i>Morchella danalii</i>	HT436	Turkey		JN085117					Taşkın et al. (2012)
<i>Morchella danensis</i>	AH18336	Spain		KU865007					Loizides et al. (2016)
<i>Morchella elata</i>	MR 4	India		GQ228469					Kanwal et al. (2011)
<i>Morchella esculenta</i>	YAAS1426	China		KM485935					Chen L.-J., Zhao Y.-C. & Chai H.-M., unpubl.
<i>Morchella eximia</i>	LIP:PhC70, T	France		KM588002					Richard et al. (2015)
<i>Morchella eximoides</i>	F130641	Sweden		KM587917					Richard et al. (2015)
<i>Morchella exuberans</i>	M.Loizides ALV3210	Cyprus		KU865013					Loizides et al. (2016)
<i>Morchella galilaea</i>	HT485	Turkey		JQ723082					Du et al. (2012b)
<i>Morchella importuna</i>	MS879	Israel		MF170632					Tietel & Masaphy (2018)
<i>Morchella kakticolor</i>	M288	Canary Island		JQ723065					Du et al. (2012b)
<i>Morchella punctipes</i>	M837	USA		JQ723030					Du et al. (2012b)
<i>Morchella rufobrunnea</i>	ALV00156	Cyprus		JX292973					Loizides et al. (2015)
<i>Morchella rufobrunnea</i>	ALV00159	Cyprus		JX292974					Loizides et al. (2015)
<i>Morchella sceptrififormis</i>	LIP:PhC76, T	USA		KM588005					Richard et al. (2015)
<i>Morchella semitibera</i>	LIP:PhC 99	France		KJ174320					Moreau et al. (2014)

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<i>Morchella septentrionalis</i>	M9	USA		JQ723064					Du et al. (2012a)
<i>Morchella sextelata</i>	HL1	China		KX809732					Chai et al. (2017)
<i>Morchella snijderi</i>	JLF3802	USA		MH198768					Frank J.L., unpubl.
<i>Morchella tomentosa</i>	M105	USA		JQ723016					Du et al. (2012b)
<i>Morchella tridentina</i>	OKA-TR-T1	Turkey		MK734141					Kaygusuz et al. (2019)
<i>Morchella ulmaria</i>	LIP-PhC124,T	Canada		KM587943					Richard et al. (2015)
<i>Mycenastrum corium</i>	MJ5467	Sweden		DQ112628					Larsson & Jeppson (2008)
<i>Neolibatrellus caeruleoporus</i>	OSC 66097	Canada		KC985126					Audet & Luther (2015)
<i>Neolibatrellus caeruleoporus</i>	DAVFP 28304	Canada		KC862265					Audet & Luther (2015)
<i>Neoboletus obscureumbrinus</i>	HKAS 89014	China						KT990793	Wu et al. (2016)
<i>Nycteromyces streblidinus</i>	D. Haelew. 1324b	Panama, <i>Trichobius joblingi</i>	MH040554		MH040590				Haelewaters et al. (2018b)
<i>Omphalotus illudens</i>	TENN:F-54507	USA		AY313271					Mata et al. (2004b)
<i>Omphalotus olearius</i>	Culture 9061b	France		AY313277					Mata et al. (2004b)
<i>Omphalotus olearius</i>	CBS 164.51	Austria		MH856796					Vu et al. (2019)
<i>Omphalotus olivascens</i>	TENN:F-55337	USA		AY313281					Mata et al. (2004b)
<i>Ophiocordyceps dipterigena</i>	Ophdip1899	Colombia, Diptera (adult fly)			KJ917368				Sanjuan et al. (2015)
<i>Ophiocordyceps ditmarii</i>	A1481	Austria, Hymenoptera ( <i>Vespula vulgaris</i> )		MT878364	MT937097				This study
<i>Ophiocordyceps formicarum</i>	TNS F18565	Hymenoptera ( <i>Camponotus</i> sp.)			KJ878888				Quandt et al. (2014)
<i>Ophiocordyceps forquignonii</i>	OSC 151908	Diptera (adult fly)			KJ878889				Quandt et al. (2014)
<i>Ophiocordyceps forquignonii</i>	OSC 151902	Diptera (adult fly)			KJ878876				Quandt et al. (2014)
<i>Ophiocordyceps forquignonii</i>	4H4-2010	dead fly in forest		HQ662164					O'Hanlon R. & Harrington T.J., unpubl.
<i>Ophiocordyceps forquignonii</i>	UoC-17.06.84			AJ786562					Stensrud et al. (2005)
<i>Ophiocordyceps globiceps</i>	MFLUCC 18-0495 (T)	Thailand, Diptera		MH725816	MH725830				Xiao et al. (2019)
<i>Ophiocordyceps globiceps</i>	MFLU 18-0661	Thailand, Diptera		MH725816	MH725830				Xiao et al. (2019)
<i>Ophiocordyceps granospora</i>	BBH43209 (T)	Thailand, Hymenoptera ( <i>Polyrhachis</i> sp.)		MH028143	MH028156				Khonsanit et al. (2018)
<i>Ophiocordyceps irangiensis</i>	NBRC 101401	Thailand, Hymenoptera (ant)		JN943336	JN941427				Schoch et al. (2012)
<i>Ophiocordyceps irangiensis</i>	NBRC 101399	Thailand, Hymenoptera (ant)		JN943334	JN941425				Schoch et al. (2012)
<i>Ophiocordyceps khaoyaiensis</i>	BBH43205 (T)	Thailand, Hymenoptera ( <i>Polyrhachis armata</i> )		MH028150	MH028153				Khonsanit et al. (2018)
<i>Ophiocordyceps megacuculla</i>	BBH43217 (T)	Thailand, Hymenoptera ( <i>Polyrhachis</i> sp.)		MH028148	MH028162				Khonsanit et al. (2018)
<i>Ophiocordyceps myrmecophila</i>	TNS 27120	Hymenoptera (ant)			KJ878895				Quandt et al. (2014)
<i>Ophiocordyceps pseudolloydii</i>	MFLUCC 15-0889	Hymenoptera (adult ant)		MF351725					Xiao et al. (2017)
<i>Ophiocordyceps sphecocephala</i>	NBRC 101416	Thailand, Hymenoptera (wasp)		JN943348	JN941443				Schoch et al. (2012)



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<i>Ophiocordyceps sphecocephala</i>	4169	unknown, Hymenoptera (wasp)			AF327390				Artjariyasripong et al. (2001)
<i>Ophiocordyceps thanathonenensis</i>	MFU16-2909	Thailand, Hymenoptera (ant)		MF850376	MF850377				Xiao et al. (2017)
<i>Ophiocordyceps tricenstri</i>	NBRC:106968	Japan, Hemiptera		AB968410	AB968423				Ban et al. (2015)
<i>Ophiocordyceps tricentri</i>	94214	Hemiptera		AB027376	AB027376				Nikoh & Fukatsu (2000)
<i>Parvacoecium pini</i>	ATCC 66185, T	Canada, <i>Pinus monticola</i>		UDB035391*					Saar I., unpubl.
<i>Parvacoecium pini</i>	TRY	Austria, <i>Pinus cembra</i>		MT707244	MT707244				This study
<i>Peyritsihiella angolensis</i>	LG479	Namibia, Staphylinidae sp.	MG687385						Goldmann & Weir (2018)
<i>Phylloporus bellus</i>	HKAS 56763	China			JQ967196				Zeng et al. (2013)
<i>Phylloporus luziensis</i>	HKAS 75077	China						KF112298	Wu et al., 2016
<i>Polyandromyces coptosomalis</i>	D. Haelew. 313f	Ecuador, <i>Phoecia</i> sp.	KT800035		KT800020				Haelewaters et al. (2015a)
<i>Polyandromyces coptosomalis</i>	HM499a	Canary Islands, <i>Acrosternum</i> sp.	MG438347						Haelewaters et al. (2019c)
<i>Polypus dispansus</i>	NY 7979	Canada		FJ439516					Audet (2010)
<i>Polypus dispansus</i>	OSC 61288	USA		EU852810					Gordon M., unpubl.
<i>Prolixandromyces triandrus</i>	Nagyvisnyo1	Hungary, <i>Velia saulii</i>	LT158294		LT158295				Pflegler et al. (2016)
<i>Pseudotracheloma metapoditum</i>	MB-002938 / GB 0066422	China / Sweden		MF034220	NG_060122				Sánchez-García et al. (2014), Reschke et al. (2018)
<i>Pulveroboletus macrosporus</i>	HKAS 57628, T	China						KT990812	Wu et al. (2016)
<i>Pyxidiphora arvernensis</i>		Netherlands, <i>Rhizoctonia solani</i>	FJ176839		FJ176894				Schoch et al. (2009)
<i>Pyxidiphora microspora</i>	MG200	Poland	MG438334		MG438362				Haelewaters et al. (2019c)
<i>Pyxidiphora</i> sp.			AY212811						Henk et al. (2003)
<i>Pyxidiphora</i> sp.	IMI-1989	Canada, dung of <i>Alces alces</i>	AF313769						Weir & Blackwell (2001b)
<i>Rhytisma acerinum</i>	Hou 203			GQ253100	FJ495190				Wang et al. (2009), Hou et al. (2010)
<i>Rickia laboulbenioides</i>	SR4s	Denmark, <i>Cylindroiulus punctatus</i>	MH040558		MH040593				Haelewaters et al. (2018b)
<i>Rickia laboulbenioides</i>	SR5s	Denmark, <i>Cylindroiulus punctatus</i>	MN530041		MK500060				Haelewaters et al. (2019a), Blackwell et al. (2020)
<i>Rickia pachyiuli</i>	SR1s	Serbia, <i>Pachyiulus hungaricus</i>	MH040559		MH040594				Haelewaters et al. (2018b)
<i>Rickia pachyiuli</i>	SR8s	Serbia, <i>Pachyiulus hungaricus</i>	MT604592		MK500058				Haelewaters et al. (2019a), this study
<i>Rickia pachyiuli</i>	SR13s	Serbia, <i>Pachyiulus hungaricus</i>	MN530042		MK500059				Haelewaters et al. (2019a), Blackwell et al. (2020)
<i>Rickia wasmannii</i>	ADK6272a	Belgium, <i>Myrmica sabuleti</i>	MN530043		MK500050				Haelewaters et al. (2019a), Blackwell et al. (2020)
<i>Rickia wasmannii</i>	DE_Rak4	Hungary, <i>Myrmica scabrinodis</i>	KT800037		KT800021				Haelewaters et al. (2015a)
<i>Rugiboletus brunneiporus</i>	HKAS 68586	China						KT990812	Wu et al. (2016)

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<i>Rugibolletus extremorientalis</i>	HKAS 63635	China						KF112198	Wu et al. (2016)
<i>Scutiger ellisii</i>	States J. WYEF	USA		KJ411956					Albee-Scott (2007)
<i>Scutiger ellisii</i>	JLF1838	USA		JX415333					Frank J.L., unpubl.
<i>Scutiger pes-caprae</i>	QFB7993			FJ439514					Audet (2010)
<i>Scutiger pes-caprae</i>	PV 153-95			AF506394					Larsson & Larsson (2003)
<i>Stigmatomyces borealis</i>	AW979	USA, <i>Parydra breviceps</i>	JN635186						Weir A., unpubl.
<i>Stigmatomyces chamaenijiae</i>	D. Haelew. 1137a	Portugal, cf. <i>Chamaenijia</i> sp.	MH040564						Haelewaters et al. (2018b)
<i>Stigmatomyces chamaenijiae</i>	D. Haelew. 1137c	Portugal, cf. <i>Chamaenijia</i> sp.	MH040565						Haelewaters et al. (2018b)
<i>Stigmatomyces limnophorae</i>	D. Haelew. 1802c	Malaysia, <i>Sarcophaga javanica</i>	MT341792		MT341789				Nur Aliah N.A., Liu J., Azmiera N. & Chin C., unpubl.
<i>Stigmatomyces limnophorae</i>	D. Haelew. 1802d	Malaysia, <i>Sarcophaga javanica</i>	MT341793		MT341790				Nur Aliah N.A., Liu J., Azmiera N. & Chin C., unpubl.
<i>Stigmatomyces limnophorae</i>	D. Haelew. 1802e	Malaysia, <i>Sarcophaga javanica</i>	MT341794		MT341791				Nur Aliah N.A., Liu J., Azmiera N. & Chin C., unpubl.
<i>Stigmatomyces limnophorae</i>	AW785	USA, Muscidae sp.	AF407576						Weir & Blackwell (2001b)
<i>Stigmatomyces protrudens</i>			AF298232		AF298234				Weir & Blackwell (2001a)
<i>Stigmatomyces rugosus</i>	D. Haelew. 1138a	Portugal, <i>Psilopa</i> sp.	MH040563						Haelewaters et al. (2018b)
<i>Stigmatomyces rugosus</i>			AF431759						Weir & Hughes (2002)
<i>Subbaromyces splendens</i>	CBS 357.53 (isolate AA1)	USA, trickling filter beds	MN526931		MN526934				Blackwell et al. (2020)
<i>Subbaromyces splendens</i>	CBS 357.53 (isolate B)	USA, trickling filter beds	MN526932		MN526935				Blackwell et al. (2020)
<i>Tetrameronychia</i> sp.	LG653	Costa Rica, Carabidae sp.	MG687412						Goldmann & Weir (2018)
<i>Tetrigomyces africanus</i>	LG652	Sierra Leone, <i>Gyllotalpa</i> sp.	MG687405						Goldmann & Weir (2018)
<i>Therrya abiericola</i>	HOU 447A	China, <i>Abies</i> sp.		KP322574	KP322580				Li Z.-J., Liu W.-T., Ma H.-Y. & Hou C.-L., unpubl.
<i>Therrya fuckelii</i>	2003-16/3	Norway, <i>Pinus sylvestris</i>		JF793669					Solheim et al. (2013)
<i>Therrya fuckelii</i>	2004-9/2	Norway, <i>Pinus sylvestris</i>		JF793670					Solheim et al. (2013)
<i>Therrya pini</i>	2004-9/13	Norway, <i>Pinus sylvestris</i>		JF793676					Solheim et al. (2013)
<i>Therrya pini</i>	CBS 177.56	Netherlands, <i>Pinus</i> sp.		MH857568	KC312684				Tian et al. (2013), Vu et al. (2019)
<i>Trechispora alnicola</i>	CBS 577.83	USA		DQ411529	AY635768				Matherly P.B. & Hibbett D.S., unpubl.
<i>Trechispora araneosa</i>	GB KHL8570	Sweden		AF347084	AF347084				Larsson et al. (2004)
<i>Trechispora coltaerens</i>	TU 110332	Estonia		UDE008249*					Ortynets et al. (2015)
<i>Trechispora coltaerens</i>	TU 115568	Estonia		UDE016421*					Ortynets et al. (2015)
<i>Trechispora confinis</i>	GB KHL11064	Sweden		AF347081	AF347081				Larsson et al. (2004)
<i>Trechispora cyatheae</i>	FR 0219442	La Réunion		UDE024014*	UDE024015*				Ortynets et al. (2015)
<i>Trechispora cyatheae</i>	FR 0219443, T	La Réunion		UDE024016*	UDE024017*				Ortynets et al. (2015)
<i>Trechispora cyatheae</i>	FR 0219446	La Réunion		UDE024020*	UDE024021*				Ortynets et al. (2015)
<i>Trechispora echinoeristalina</i>	TU 110414	Papua New Guinea		UDE013050*	UDE013050*				Ortynets et al. (2015)
<i>Trechispora echinoeristalina</i>	FR 0219445, T	La Réunion		UDE024018*	UDE024019*				Ortynets et al. (2015)

Species name	ID (isolate, strain, status, voucher)	Country, isolation source	SSU	ITS	LSU	<i>rpb1</i>	<i>rpb2</i>	<i>tef1</i>	Reference(s)
<i>Trechispora echinoecristallina</i>	FR 0219448	La Réunion		UDB024022*					Ordynets et al. (2015)
<i>Trechispora echinoecristallina</i>	FR 0219449	La Réunion		UDB024023*					Ordynets et al. (2015)
<i>Trechispora echinospora</i>	MA-Fungi 82485, T	Brazil		JX392845	JX392846				Telleria et al. (2013)
<i>Trechispora farinacea</i>	GB KHL8454	Sweden		AF347083	AF347083				Larsson et al. (2004)
<i>Trechispora farinacea</i>	TUB 011825	Germany		EU909231	EU909231				Krause et al. (2011)
<i>Trechispora farinacea</i>	MA-Fungi 79474	France		JX392855					Telleria et al. (2013)
<i>Trechispora hondurensis</i>	HONDURAS19-F016a, T	Honduras		MT571523	MT636540				This study
<i>Trechispora hondurensis</i>	HONDURAS19-F016b, T	Honduras			MT636541				This study
<i>Trechispora hymenocystis</i>	TL11112	Denmark		UDB000778*					Ordynets et al. (2015)
<i>Trechispora hymenocystis</i>	GB KHL8795	Sweden		AF347090	AF347090				Larsson et al. (2004)
<i>Trechispora incisa</i>	GB EH24/98	Sweden		AF347085	AF347085				Larsson et al. (2004)
<i>Trechispora karvinoides</i>	GB KGN981002	Norway		AF347086	AF347086				Larsson et al. (2004)
<i>Trechispora laevis</i>	TU 115551	Estonia		UDB016406*	UDB016406*				Ordynets et al. (2015)
<i>Trechispora mollusca</i>	CFMR DLL2010-077	USA		JQ673209					Brazee et al. (2012)
<i>Trechispora mollusca</i>	CFMR DLL2011-186	USA		KJ140681					Brazee et al. (2012)
<i>Trechispora nitea</i>	GB G. Kristiansen	Norway		AY463474	AY586720				Telleria M.T., Duenas M. & Martin M.P., unpubl.
<i>Trechispora nitea</i>	GB 0102694	Sweden		KU747096	KU747089				Telleria M.T., Duenas M. & Martin M.P., unpubl.
<i>Trechispora regularis</i>	GB KHL10881	Jamaica		AF347087	AF347087				Larsson et al. (2004)
<i>Trechispora sp.</i>	KHL146968	Brazil		MH290763	MH290763				Chikowski R.S., Larsson K.-H. & Gibertoni T.B., unpubl.
<i>Trechispora sp.</i>	URM 85884	Brazil		MK514945	MH280003				Chikowski R.S., Larsson K.-H. & Gibertoni T.B., unpubl.
<i>Trechispora stevensonii</i>	TU 115499	Estonia		UDB016467*					Ordynets et al. (2015)
<i>Trechispora stevensonii</i>	KHL14654	Norway			MH290762				Chikowski R.S., Larsson K.-H. & Gibertoni T.B., unpubl.
<i>Trechispora stevensonii</i>	MA-Fungi 70669			JX392841	JX392842				Telleria et al. (2013)
<i>Trechispora stevensonii</i>	MA-Fungi 70645			JX392843	JX392844				Telleria et al. (2013)
<i>Trechispora subsphaerospora</i>	GB KHL8511	Sweden		AF347080	AF347080				Larsson et al. (2004)
<i>Tricholoma acerbum</i>	MC00-204 / G0188	Slovenia / Hungary		LT000134	MK278598				Heilmann-Clausen et al. (2017), Varga et al. (2019)
<i>Tricholoma aestuans</i>	MC94-008	Denmark		LT000007					Heilmann-Clausen et al. (2017)
<i>Tricholoma aestuans</i>	AL-ECM6	Canada		MH809950					LeFait et al. (2019)
<i>Tricholoma album</i>	MB-003025 / TFB1.3753	China / USA		MF034297	KU058544				Sánchez-García & Matheny (2017), Reschke et al. (2018)
<i>Tricholoma anatolicum</i>	HD1058	Turkey		MF612194					Intini et al. (2003)

Species name	ID (isolate, strain, status, voucher)	Country, isolation source	SSU	ITS	LSU	rpb1	rpb2	tef1	Reference(s)
<i>Tricholoma argyraceum</i>	MC03-251 / AF00.07	Slovakia / France		LT000127	MF344961				Heilmann-Clausen et al. (2017), Corriol & Jargeat (2018)
<i>Tricholoma argyraceum</i>	224464	North American		MK607504					Russell S.D. & Grootmyers D., unpubl.
<i>Tricholoma atrodisicum</i>	4660-HRL 1225 / MSG132	Canada / USA		KJ705254	KU058546				Sánchez-García & Matheny (2017); Benube J.A., Gadomski J., Labbe R., Leboeuf R., Gagne P., Dube J., et al., unpubl.
<i>Tricholoma aurantium</i>	102121 / G0756	China / Hungary		MF034300	MK278600				Reschke et al. (2018), Varga et al. (2019)
<i>Tricholoma bakamatsutake</i>	51221	Japan		AF204807					Kikuchi et al. (2000)
<i>Tricholoma bonii</i>	790	Turkey		KY121105					Şen et al. (2018)
<i>Tricholoma bonii</i>	MB-301516	China		MF034240					Reschke et al. (2018)
<i>Tricholoma bonii</i>	MB-305154	China		MF034321					Reschke et al. (2018)
<i>Tricholoma boudieri</i>	MB-002507	China		MF034286					Reschke et al. (2018)
<i>Tricholoma bufonium</i>	C19 AQUI / P62 AQUI	Germany		AY462030	AY462031				Comandini et al. (2004)
<i>Tricholoma caligatum</i>	NAMA 2015-018 / PBM3899	USA		MH910606	KU058548				Sánchez-García & Matheny (2017); Russell S.D., Rojas J.A. & Vilgalys R., unpubl.
<i>Tricholoma cingulatum</i>	MB-302066 / Rim03	China / France		MF034310	MF344963				Corriol & Jargeat (2018), Reschke et al. (2018)
<i>Tricholoma filamentosum</i>	MB-000950 / MB-002942	China		MF034280	MF034222				Reschke et al. (2018)
<i>Tricholoma filamentosum</i>	C-F35924	Sweden		LT000165					Heilmann-Clausen et al. (2017)
<i>Tricholoma flavovirens</i>	SMI317 / TFB13553	Canada / USA		HQ650740	KU058551				Kranabetter et al. (2009), Sánchez-García & Matheny (2017)
<i>Tricholoma frondosae</i>	MC96-235 / TAA146369a	Denmark / Estonia		LT000023	AM946472				Saar et al. (2009), Heilmann-Clausen et al. (2017)
<i>Tricholoma frondosae</i>	MB-301979	China		MF034245					Reschke et al. (2018)
<i>Tricholoma fulvum</i>	MB-001087 / GLM 46034	China / Germany		MF034281	AY207309				Walther et al. (2005), Reschke et al. (2018)
<i>Tricholoma huronense</i>	KMS248	USA		AF377229					Bidartondo & Bruns (2002)
<i>Tricholoma ilkkiae</i>	S_F513823	Sweden		NR159051					Heilmann-Clausen et al. (2017)
<i>Tricholoma imbricatum</i>	KGP24	USA		DQ822836					Reschke et al. (2018)
<i>Tricholoma inocybeoides</i>	MB-003215 / Ville06	China / France		MF034299	MF344962				Corriol & Jargeat (2018), Reschke et al. (2018)
<i>Tricholoma japonicum</i>	MR27	Japan		AB036900					Murata H. (2000)
<i>Tricholoma kenanii</i>	Acar 1114A, T	Turkey		MN541841	MN541829				This study

Species name	ID (isolate, strain, status, voucher)	Country, isolation source	SSU	ITS	LSU	rpb1	rpb2	tef1	Reference(s)
<i>Tricholoma kenanii</i>	Acar 1114B, T	Turkey		MN541842	MN541830				This study
<i>Tricholoma kenanii</i>	Acar 1114C, T	Turkey		MN541843	MN541831				This study
<i>Tricholoma kenanii</i>	Acar 1114D, T	Turkey		MN541844	MN541832				This study
<i>Tricholoma kenanii</i>	Acar 1114E, T	Turkey		MN541845	MN541833				This study
<i>Tricholoma kenanii</i>	Acar 1114F, T	Turkey		MN541846	MN541834				This study
<i>Tricholoma lascivum</i>	MB-303096	China		MF034316					Reschke et al. (2018)
<i>Tricholoma moseri</i>	KMS447 / G1986	USA		AF377211	MK278609				Bidartondo & Bruns (2002), Varga et al. (2019)
<i>Tricholoma moseri</i>	PP46 G11	USA		EU726334					Hynes (2009)
<i>Tricholoma myomyces</i>	SMI323 / F146374	Canada / China		FJ845443	JN389376				Kranabetter et al. (2009); Yu X.-D., Deng H. & Yao Y.-J., unpubl.
<i>Tricholoma myomyces</i>	MICH53128	USA		JN389291					Yu X.-D., Deng H. & Yao Y.-J., unpubl.
<i>Tricholoma myomyces</i>	54-349	USA		MH038082					Hart et al. (2018)
<i>Tricholoma orribens</i>	MC03-243	Slovakia		LT000132					Heilmann-Clausen et al. (2017)
<i>Tricholoma pardinum</i>	DBG:25191 / KMS 278	China / USA		MF034205	U76462				Reschke et al. (2018); Shanks K. & Vilgalys R., unpubl.
<i>Tricholoma pessundatum</i>	JV04-482	Denmark		LT000032					Heilmann-Clausen et al. (2017)
<i>Tricholoma platyphyllum</i>	SMI309	Canada		FJ845445					Kranabetter et al. (2009)
<i>Tricholoma portentosum</i>	615 / KMS 591	Japan / USA		AB036896	U76464				Murata H., unpubl.; Shanks K. & Vilgalys R., unpubl.
<i>Tricholoma roseoacereum</i>	IK881120	Finland		LT000072					Heilmann-Clausen et al. (2017)
<i>Tricholoma saponaceum</i>	TF98-098 / TFB12328	France / USA		LT000087	KU058555				Heilmann-Clausen et al. (2017), Sánchez-García & Matherly (2017)
<i>Tricholoma sculpturatum</i>	ID PAN 758 / AF00.53	Poland / France		KM085371	MF344960				Corriol & Jargeat (2018); Trocha L.K. & Rudy E.M., unpubl.
<i>Tricholoma squarulosum</i>	CBS 705.84	Belgium		MH861819					Yu et al. (2019)
<i>Tricholoma stiparophyllum</i>	MC95-117	Sweden		LT000190					Heilmann-Clausen et al. (2017)
<i>Tricholoma sulphureum</i>	JMP0092	USA		EU819448					Palmer et al. (2008)
<i>Tricholoma terreum</i>	MICH53128 / C 59416	China		JN389295	EU653305				Yu X.-D., Deng H. & Yao Y.-J., unpubl.
<i>Tricholoma terreum</i>	MICH53431 / C 35153	China		JN389302	EU653302				Yu X.-D., Deng H. & Yao Y.-J., unpubl.
<i>Tricholoma terreum</i>	K(M)124681	China		EU439315					Yu X.-D., Deng H. & Yao Y.-J., unpubl.

Species name	ID (isolate, strain, status, voucher)	Country, isolation source	SSU	ITS	LSU	<i>rpb1</i>	<i>rpb2</i>	<i>tef1</i>	Reference(s)
<i>Tricholoma terreum</i>	1504	China		KY121102					Sen et al. (2018)
<i>Tricholoma transmutanans</i>	4499	Canada		KJ705236					Berube J.A., Gadomski J., Labbe R., Leboeuf R., Gagne P., Dube J., et al., unpubl.
<i>Tricholoma triste</i>	JuV5271F	Estonia		LT000066					Heilmann-Clausen et al. (2017)
<i>Tricholoma triste</i>	JHC97-169	Sweden		LT000194					Heilmann-Clausen et al. (2017)
<i>Tricholoma triste</i>	DBG:22631	China		MF034270					Heilmann-Clausen et al. (2017)
<i>Tricholoma umbonatum</i>	TRgmb00651	Italy		LT000114					Heilmann-Clausen et al. (2017)
<i>Tricholoma ustale</i>	MB-303111 / GLM 46036	China / Germany		MF094317	AY207306				Walther et al. (2005), Reschke et al. (2018)
<i>Tricholoma ustaloides</i>	68K	Poland		KX034212					Halama et al. (2016)
<i>Tricholoma venenatum</i>	OUC99352 / KMS 393	Canada / USA		DQ367922	U76463				Durall et al. (2006), Shanks K. & Vilgalys R., unpubl.
<i>Tricholoma viridiivaceum</i>	OTA:61887 / PBM3093	New Zealand		JX178633	JF706317				Baroni & Matheny (2011), Teasdale et al. (2013)
<i>Trybliidiopsis magnesi</i>	DAOMC 252096	Canada, <i>Picea glauca</i>		MK748209	MK748168				Tanney & Seifert (2019)
<i>Trybliidiopsis pinastri</i>	CBS 445.71	Slovakia, <i>Picea abies</i>		JF793678					Solheim et al. (2013)
<i>Trybliidiopsis pinastri</i>	G.M. 2018-06-09.5	Luxembourg, <i>Picea abies</i>		MN007233					Marson G., unpubl.
<i>Trybliidiopsis pinastri</i>	HOU 198	Germany, <i>Picea</i> sp.		KC312678	KC312680				Wang et al. (2014)
<i>Trybliidiopsis sichuanensis</i>	HOU 300	China, <i>Picea retroflexa</i>		KC312677	KC312679				Wang et al. (2014)
<i>Trybliidiopsis sichuanensis</i>	HOU 306	China, <i>Picea brachytyla</i>		KC312676	KC312683				Wang et al. (2014)
<i>Trybliidiopsis sinensis</i>	HOU 814	China, <i>Picea asperata</i>		KC312674	KC312681				Wang et al. (2014)
Uncultured <i>Gymnopus</i>	3_M367	Japan		LC013344					Kinoshita et al. (2016)
<i>Xanthoporus peckianus</i>	QFB 7987	Canada		FJ439513					Audet (2010)
<i>Xanthoporus syringae</i>	Ryman 6388 (UPS F-015633)	Sweden		AY198209					Ryman et al. (2003)
<i>Xanthoporus syringae</i>				AY621804					Cui et al. (2008)
<i>Xeroceps stamianus</i>	WTU 9750	USA		EU697276					Gordon M., unpubl.
<i>Xeroceps stamianus</i>	p870i	USA		EU697275					Gordon M., unpubl.
<i>Xeroceps rugosellus</i>	HKAS 68292	China		KT990686	KT991019				Wu et al. (2016)
<i>Xeroceps subtomentosus</i>	VDKO 0987	Belgium							Vadthananat et al. (2018)
<i>Zodiomyces vorticellarius</i>	MG003	Poland, <i>Helochares obscurus</i>	KT800038		KT800022				Haelewaters et al. (2015a)
<i>Zodiomyces vorticellarius</i>	AW819	USA, Hydrophilidae sp.	AF407577						Weir & Blackwell (2001b)

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

assembled and edited using BioEdit version 7.0.9 (Hall 1999). All sequences generated in this study were submitted to GenBank (Tab. 1).

A culture of *Robillarda sohagensis* sp. nov. was grown in yeast and malt extract with glucose (YMG) broth (4 g yeast extract, 10 g glucose, 10 g malt extract in 1 l H<sub>2</sub>O) for DNA extraction, using the UltraClean Microbial DNA Kit (MoBio Laboratories, Carlsbad, CA). Partial LSU was amplified using primers LR0R and LR7 (Vilgalys & Hester 1990, Hopple 1994). PCR reactions were done in 25- $\mu$ l reactions with 20 ng of template DNA, 2.5  $\mu$ l of 10 $\times$  Fast buffer, 2.5 mM dNTPs, 0.25  $\mu$ M of each primer, and 0.125  $\mu$ l of 5 units/ $\mu$ l SpeedSTAR HS Taq polymerase (TaKaRa Bio, Shiga, Japan). Cycling parameters included an initial denaturation step at 98 °C for 2 min; 30 cycles of denaturation at 98 °C for 5 s, annealing at 52 °C for 15 s, and extension at 72 °C for 20 s; and final extension at 72 °C for 1 min. Purification and sequencing were done following Abdel-Wahab et al. (2009).

DNA extraction of the *Trechispora hondurensis* sp. nov. specimen was done from a rice-sized piece of tissue that was isolated in the field, using the Wizard Genomic DNA Purification Kit (Promega) following the manufacturers' instructions. PCR amplification targeted the internal transcribed spacer (ITS) of the ribosomal RNA (rRNA) gene using primers ITS1F and ITS4 (White et al. 1990, Gardes & Bruns 1993), and the nuclear large subunit of the rRNA gene (LSU) using primers LR0R and LR7 (Vilgalys & Hester 1990, Hopple 1994). PCR conditions followed Haelewaters et al. (2020c). Purification and sequencing using the same primers were outsourced to Genewiz (Plainfield, NJ).

DNA was extracted from six basidiomata of *Tricholoma kenanii* sp. nov. following Doyle & Doyle (1987) with minor modifications. The ITS and LSU regions were amplified using primer sets Nnc18S10/C26A (Wen et al. 1996) and LR0R/LR5 (Vilgalys & Hester 1990, Hopple 1994), respectively. Amplifications were carried out in 50- $\mu$ l reactions containing about 30 ng of fungal DNA, 3  $\mu$ l (ITS)/5  $\mu$ l (LSU) of each 10 mM primer, 3  $\mu$ l of 10 mM dNTPs, 5  $\mu$ l of 10 $\times$  buffer, 5  $\mu$ l of 25 mM MgCl<sub>2</sub>, and 0.3  $\mu$ l of 5u/ $\mu$ l Taq DNA polymerase (Thermo Fisher Scientific). Reactions were performed in a thermocycler using the following conditions: initial denaturation at 95 °C for 3 min; followed by 35 cycles of denaturation at 94 °C for 40 s, annealing at 50 °C for 45 s, and elongation at 72 °C for 2 min; and final extension at 72 °C for 5 min. PCR success was checked in 1 % TAE agarose gel stained with Gelred dye at 90 V for 30 min; positive

PCR products were sequenced with the same primers, using an ABI 3730XL automated sequencer (Applied Biosystems). All newly generated sequences were submitted to NCBI GenBank under the following accession nos.: MN541841–MN541846 (ITS), MN541829–MN541834 (LSU).

DNA was isolated from *Arthrorhynchus* thalli using the REPLI-g Single Cell Kit (Qiagen, Valencia, CA) with modifications (Haelewaters et al. 2019c). DNA extracts were stored at -20 °C until PCR amplification. Amplification of SSU and LSU was done using primers NSL1 (5'-GTAGTGTCTCCTCRATGCTTTTGAC-3') and NSL2 (5'-AATCYAAGAATTCACCTCTGAC-3') for SSU (Haelewaters et al. 2015a), and LR0R (5'-ACCCGCTGAACCTTAA-GC-3') and LR5 (5'-ATCCTGAGGGAACTTC-3') for LSU (Vilgalys & Hester 1990, Hopple 1994). In one case, we were only able to generate a good LSU sequence using two primers combinations: LR0R and LR5, and LIC24R (5'-GAAACCAACAGG-GATTG-3') and LR3 (5'-GGTCCGTGTTTCAA-GAC-3') (Vilgalys & Hester 1990, Miadlikowska & Lutzoni 2000). PCR reactions consisted of 12.3  $\mu$ l of Taq polymerase (Top-Bio, Prague, Czech Republic), 2.5  $\mu$ l of each 10  $\mu$ M primer, 6.7  $\mu$ l of H<sub>2</sub>O, and 1  $\mu$ l of template DNA. Amplification reactions were run under the following thermocycler conditions: initial denaturation at 94 °C for 3 min; then 35 cycles of denaturation at 94 °C for 30 sec, annealing at 50 °C for 30 sec, extension at 72 °C for 1 min/1 kb and final extension at 72 °C for 10 min. Purification of successful PCR products and sequencing were outsourced to SeqMe (Dobříš, Czech Republic). Generated forward and reverse sequence reads were assembled, trimmed, and edited in Sequencher version 4.10.1 (Gene Codes Corporation, Ann Arbor, MI).

For molecular analysis of *Calvatia* specimens, genomic DNA was extracted from gleba material using the DNeasy Plant Mini Kit (Qiagen) following the manufacturer's protocol. The ITS and LSU regions were amplified using primer pairs ITS1F/ITS4 and LR0R/LR5, respectively (White et al. 1990, Vilgalys & Hester 1990, Gardes & Bruns 1993, Hopple 1994). Successfully amplified PCR products were sequenced with the ABI BigDye Terminator Sequencing Kit version 3.1 using the PCR primers. Sequences were read using an AB113730xl capillary sequencer (Applied Biosystems) at the Harvard University Bauer Core Facility in Cambridge, MA. Forward and reverse sequence reads were assembled and edited using Sequencher version 3.0 (Gene Codes Corporation). Sequences generated during this study were submitted to NCBI GenBank (Tab. 1).

During the *Entoloma* study, Genomic DNA was extracted from fresh specimens following a modified CTAB protocol (Lee et al. 1988). The ITS region was amplified using primers ITS1F and ITS4 (White et al. 1990, Gardes & Bruns 1993). Amplifications were done in 25- $\mu$ l reactions containing 0.125  $\mu$ l of 5 units/ $\mu$ l EconoTaq DNA Polymerase (Lucigen, Middleton, WI), 2.5  $\mu$ l 10 $\times$  Reaction Buffer (Lucigen), 0.5  $\mu$ l dNTPs, 1.25  $\mu$ l of each 10  $\mu$ M primer, 14.375  $\mu$ l of ddH<sub>2</sub>O, and 5  $\mu$ l of template DNA. PCR conditions were as follows (sensu Saba et al. 2020): initial denaturation at 94 °C for 1 min; followed by 35 cycles of denaturation at 94 °C for 1 min, annealing at 53 °C for 1 min, and extension at 72 °C for 1 min; and a final extension step at 72 °C for 8 min. PCR products were checked on 1 % agarose gel. Purification of successful PCR products and Sanger sequencing using the same primers were outsourced to Tsing Ke Biotech. Forward and reverse sequence reads were assembled and edited using BioEdit version 7.0.9 (Hall 1999). All sequences generated in this study were submitted to GenBank (accession numbers MT2529444–MT252945, MT255022, MT255041).

Mycelia and chasmothecia of *Erysiphe* were used for DNA extraction with the Gene Jet Plant Genomic DNA Purification Mini Kit (Thermo Fisher Scientific, Waltham, MA) (Andersson et al. 2017). PCR amplification of the ITS region was done using primers PMITS1 (5'-TCGGACTGGCCyAGGGA-GA-3') and PMITS2 (5'-TCACTCGCCGTTACT-GAGGT-3') (Cunnington et al. 2003). Purification and sequencing were outsourced to BGI (Shenzhen, China) and Tsing Ke Biotech (Beijing, China). Raw sequence reads were assembled and edited in BioEdit version 7.2.5 (Hall 1999).

During the *Fanniomyces* study, DNA was isolated from 2–8 thalli from a single host using the Extract-N-Amp Plant PCR Kit (Sigma-Aldrich, St. Louis, MO) or the REPLI-g Single Cell Kit (Qiagen), both with modifications. For the Extract-N-Amp Plant PCR Kit, thalli were placed in a 1.5 ml Eppendorf tube with 20  $\mu$ l of Extraction Solution, followed by an incubation at 56 °C for up to 1 hour in a Shake 'N Bake Hybridization Oven (Boekel Scientific, Feasterville, PA) as in Haelewaters et al. (2018b). Thalli were manually crushed using a sterile micropestle and then incubated at 95 °C for 10 min. After incubation, 60  $\mu$ l of Dilution Solution was added, bringing the total volume to 80  $\mu$ l (Haelewaters et al. 2015a). For the REPLI-g Single Cell Kit, thalli were cut in half through the perithecium using a #10 surgical blade on disposable Bard-Parker handle (Aspen Surgical, Caledonia, MI),

picked up, and placed in a 0.2 ml PCR tube with 2  $\mu$ l of PBS solution. After adding 1.5  $\mu$ l of D2 buffer, the PCR tube was incubated at 65 °C for 30 min. Subsequent steps were according manufacturer's instructions, except that only half the amounts of listed reagents were used (Haelewaters et al. 2019c). Amplification of the nuclear ribosomal RNA small and large subunits (SSU and LSU) was done using the following primer sets: NSL1/R, NSL1/NSL2, and SL122/NSL2 for SSU (Landvik et al. 1997, Wrzosek 2000, Haelewaters et al. 2015a); LR0R/LR5 and LIC24R/LR3 for LSU (Vilgalys & Hester 1990, Hopple 1994, Miadlikowska & Lutzoni 2000). PCR reactions consisted of 12.3  $\mu$ l of 2 $\times$  PPP Master Mix (Top-Bio), 2.5  $\mu$ l of both 10  $\mu$ M primers, 5.7–6.7  $\mu$ l of H<sub>2</sub>O, and 1–2  $\mu$ l of DNA. Amplification reactions were run under the following thermocycler conditions: initial denaturation at 94 °C for 3 min; then 35 cycles of denaturation at 94 °C for 30 sec, annealing at 50 °C for 30 sec, extension at 72 °C for 1 min/1 kb; and final extension at 72 °C for 10 min. Purification and Sanger sequencing were outsourced to SeqMe. Raw sequence reads were assembled, trimmed, and edited in Sequencher version 4.10.1 (Gene Codes Corporation).

Total genomic DNA of *Morchella* was extracted from fresh or dried materials using the ZR Fungal/Bacterial DNA MiniPrep kit (Zymo research, Irvine, CA). PCR of the ITS region was performed using primers ITS1F and ITS4 (White et al. 1990, Gardes & Bruns 1993). Amplifications were done in 25- $\mu$ l volumes with 12.5  $\mu$ l of OneTaq Quick-Load 2 $\times$  Master Mix with Standard Buffer (New England Biolabs, Ipswich, MA), 1  $\mu$ l of each 10  $\mu$ M primer, 9.5  $\mu$ l of ddH<sub>2</sub>O, and 1  $\mu$ l of DNA template. Thermal conditions were as follows: initial denaturation at 95 °C for 5 min; 35 cycles of denaturation at 94 °C for 45 s, annealing at 54 °C for 35 s, and extension at 72 °C for 1 min; and final extension at 72 °C for 10 min (Kaygusuz et al. 2019). Sanger sequencing of successful PCR products, with the same primers used in the PCR reactions, was outsourced to Source Bioscience (Berlin, Germany). Raw sequence files were edited with Chromas Lite version 2.1.1 (<http://technelysium.com.au/wp/chromas/>) and assembled in BioEdit version 7.2.5 (Hall 1999). The edited sequences were then used for BLAST searches in NCBI GenBank. Newly generated sequences were deposited in GenBank (accession nos. MF228801 and MF228802).

DNA of *Ophiocordyceps* was amplified directly from samples with the Phire Plant Direct PCR Master Mix Kit (Thermo Scientific, USA). Amplification of the regions ITS and LSU was done using primer



sets ITS1F/ITS4 (White et al. 1990, Gardes & Bruns 1993) and LR0R/LR5 (Vilgalys & Hester 1990, Hople 1994), respectively. PCRs were performed in 20- $\mu$ l volume containing 7  $\mu$ l ddH<sub>2</sub>O, 1  $\mu$ l of sample (from dilution protocol), 0.5  $\mu$ M of each primer, and 10  $\mu$ l of 2 $\times$  Phire Plant Mastermix PCR Buffer, including the Phire Hot Start II DNA polymerase. The PCR reactions were performed under the following conditions: initial denaturation at 98 °C for 5 min; followed by 40 cycles of denaturation at 98 °C for 5 s, annealing at 55 °C for 5 s, and extension at 72 °C for 20 s; followed by a final extension at 72 °C for 1 min. PCR products were visualized by gel electrophoresis in 1.5 % agarose gel stained with ethidium bromide. Sequencing of the amplicons was carried out with the primers used for amplification by Eurofins Genomics (Ebersberg, Germany). Chromatograms were checked and edited with CodonCode Aligner version 4.2.5 (CodonCode Corporation). Newly generated sequences were deposited in GenBank (Tab. 1).

Extraction of genomic DNA from liquid cultures of *Parvacoccum pini* was performed following Voglmayr & Jaklitsch (2011) using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany). The ITS region and an approximately 1.2-kb fragment of the LSU gene were amplified as a single fragment, with the primers V9G (de Hoog & Gerrits van den Ende 1998) and LR5 (Vilgalys & Hester 1990). DNA was cycle sequenced with the ABI PRISM Big Dye Terminator Cycle Sequencing Ready Reaction Kit version 3.1 (Applied Biosystems), using the same PCR primers in addition to primers ITS4 (White et al. 1990), LR3 (Vilgalys & Hester 1990), and LR2R-A (Voglmayr et al. 2012). Sanger sequencing was performed on an automated DNA sequencer (ABI 3730xl Genetic Analyzer, Applied Biosystems).

#### Phylogenetic analyses

Generated ITS sequences of *Albatrellopsis* were subjected to BLAST search in NCBI GenBank and all available sequences of *Albatrellopsis* and related albatrelloid taxa were downloaded for subsequent phylogenetic analysis (Tab. 1). *Diplomitoporus crustulinus* (Bres.) Domański (GenBank accession no. AF343320) was included as outgroup taxon. ModelFinder (Kalyaanamoorthy et al. 2017) was used to select the best-fitting model of nucleotide substitution under the Bayesian information criterion (Posada & Buckley 2004), resulting in TIME+G4 (-lnL=4815.6358). A maximum likelihood (ML) inference analysis was performed using IQ-TREE

(Nguyen et al. 2015) and ultrafast bootstrap was done with 10000 replicates (Hoang et al. 2017).

For the *Aureoboletus* study, newly generated sequences and closely related sequences downloaded from NCBI GenBank (Tab. 1) were used for molecular phylogenetic analyses. *Hourangia cheoi* (W.F. Chiu) Xue T. Zhu & Zhu L. Yang, *Phylloporus bellus* (Masse) Corner, and *Xerocomus rugosellus* (W.F. Chiu) F.L. Tai were selected as outgroups, following Wu et al. (2016) and Fang et al. (2019). Each locus (LSU, *rpb1*, *rpb2*) was aligned using the online version of MAFFT version 7 (Katoh et al. 2002, 2017; Katoh & Standley 2013). Small manual adjustments to maximize similarity between characters were made in PhyDE (Müller et al. 2005). The aligned datasets were concatenated into a single matrix of 29 taxa and 2286 characters using Mesquite version 3.2 (Maddison & Maddison 2017). The best evolutionary model for nucleotide substitution was selected using PartitionFinder (Lanfear et al. 2014, 2016; Frandsen et al. 2015). Bayesian inference (BI) was performed using MrBayes version 3.2.6 (Ronquist et al. 2012). All parameters were unlinked across partitions. The convergence of the different chains was visualized in Tracer version 1.6 (Rambaut et al. 2014). After removal of 25 % burn-in, TreeAnnotator 1.8.4 (Drummond et al. 2012) was used to infer the maximum clade credibility (MCC) tree with highest product of individual clade posterior probabilities (BIPP).

For the *Entoloma* spp. nov. study, closely related ITS sequences were downloaded from NCBI GenBank and the UNITE database (Abarenkov et al. 2010) and then aligned with MAFFT online version 7, using the E-INS-i option (Katoh & Standley 2013). The alignment was checked and edited in SeaView 4 (Gouy et al. 2010). Phylogenetic analysis was performed in PhyML version 3.0 (Guindon et al. 2010) using the non-parametric Shimodaira-Hasegawa version of the approximate likelihood-ratio test (SH-aLRT) and the GTR+I+ $\Gamma$  evolutionary model of nucleotide substitution. The best-scoring tree was edited in MEGA 7 (Kumar et al. 2016) and Adobe Illustrator CS4.

Previously generated *tef1* sequences of *Erythro-phyllporus* (Zhang & Li 2018, Vadthanarat et al. 2019) were downloaded from NCBI GenBank and supplemented with the newly generated sequence from our Vietnam material. Sequences were aligned with MAFFT online version 7 using the Q-INS-i option (Katoh & Standley 2013). Bayesian inference was performed using MrBayes version 3.2.1 (Ronquist et al. 2012) under the GTR+I evolutionary model of nucleotide substitution—for two inde-

pendent runs, each with 3,000,000 generations. Four chains were run starting from a random starting tree, with a 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).

The BLAST algorithm (Altschul et al. 1990) was used to search for homologous sequences of *Marasmiellus boreoorientalis* sp. nov. in the NCBI GenBank nr/nt database. Closely related sequences were downloaded and phylogenetic relationships were evaluated based on ITS sequences. Oliveira et al. (2019) observed congruence between the topologies of their ITS and concatenated ITS–LSU trees in Omphalotaceae. Our phylogenetic analysis included ITS sequences belonging to various sections of *Marasmiellus* and *Gymnopus* sensu lato (s.l.); *Omphalotus olearius* (GenBank accession no. MH856796) was selected as outgroup (Tab. 1). ITS sequences were aligned using MUSCLE (Edgar 2004) and corrected manually if necessary. The GTR+I+G nucleotide substitution model was inferred via the FindModel web implementation of ModelTest (<http://hiv.lanl.gov/content/sequence/findmodel/findmodel.html>). For maximum likelihood (ML) analysis, the aligned sequences were loaded in PhyML 3.0 (Guindon et al. 2010) with default settings and 100 rapid bootstrap replicates. An MCMC Bayesian inference (BI) analysis was performed with MrBayes version 3.2.5 (Ronquist & Huelsenbeck 2003) with 10,000,000 generations (sampling frequency every 100 generations, four chains, two independent runs). To check for convergence of MCMC analyses and to assess estimates of the posterior distribution of parameter values, Tracer version 1.7.1 was used (Rambaut et al. 2018). We accepted the result, with the effective sample size (ESS) > 200 and the potential scale reduction factor (PSRF) ~ 1. Phylogenetic trees were visualized with the Interactive Tree Of Life (iTOL) tool version 4.0 (Letunic & Bork 2019).

Generated ITS sequences of the Pakistani *Marasmiellus* collections were subjected to a BLAST search. Closely related sequences were downloaded from NCBI GenBank (Saba & Khalid 2014, Desjardin & Perry 2017, Oliveira et al. 2019). Sequences were aligned using MAFFT online version 7 software (Kato & Standley 2013). Manual editing was done in BioEdit software version 7.0.9 (Hall 1999). All positions containing gaps were treated as missing data for phylogenetic analysis. Maximum likelihood (ML) analysis was performed on the Cipres

Science Gateway (Miller et al. 2010) using RAxML–HPC2 on XSEDE 8.2.10 (Stamatakis 2014) by selecting the GTRCAT substitution model. ML bootstrapping was performed with 1000 replicates. The resulting phylogenetic tree was visualized in FigTree1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>) and then exported to Inkscape (Free Software Foundation, Boston, MA) for editing.

For the *Robillarda* study, sequences similar to our newly generated LSU sequence were downloaded from NCBI GenBank and aligned using ClustalX (Thompson et al. 1997). Our final LSU dataset consisted of 27 isolates—including 10 *Robillarda*, 15 representatives of other genera in Sporocadaceae, and 2 taxa in Phlogicylindriaceae as outgroup (Tab. 1). We performed maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) analyses. MP was performed in PAUP\* 4.0 (Swofford 2002) using heuristic searches with random stepwise-addition trees and tree bisection-reconnection branch swapping; bootstrap analysis was done with 1000 replicates. ML was performed in PAUP\* 4.0 using TIMeF as the evolutionary model of nucleotide substitution, as determined in Modeltest 3.7 (Posada & Crandall 1998) under the Akaike Information Criterion. Posterior probabilities (BIPP) were obtained in MrBayes version 3.1.2 (Ronquist & Huelsenbeck 2003), under the best-fit model (SYM+G) as selected by Hierarchical Likelihood Ratio Tests (hLRT) in MrModeltest version 2.2 (Nylander 2004).

For the *Trechispora* study, two datasets were prepared, a concatenated ITS–LSU dataset and a single-locus dataset with LSU sequences. Sequences of *Trechispora* were downloaded from NCBI GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) and the UNITE database (Abarenkov et al. 2010), mostly from the studies by Larsson et al. (2004) and Ordynets et al. (2015) and supplemented with a few other more recent sequences (Tab. 1). Sequences of both loci were aligned using MUSCLE (Edgar 2004) on the Cipres Science Gateway (Miller et al. 2010), and then trimmed using TrimAl version 1.3 (Capella-Gutiérrez et al. 2009) with gap threshold (–gt) of 0.6 and minimal coverage (–cons) of 0.5. This resulted in a final ITS alignment with 36 isolates and 587 characters of which 289 were constant and 252 were parsimony-informative, and a final LSU alignment with 28 isolates and 860 characters of which 703 were constant and 91 were parsimony-informative. For both datasets, the appropriate model of nucleotide substitution was selected by considering the Akaike Information Criterion (AIC) using ModelFinder (Kalyaanamoorthy et al. 2017).

Selected models were GTR+F+R3 (ITS,  $-\ln L=5246.977$ ) and GTR+F+R2 (LSU,  $-\ln L=2884.018$ ). Maximum likelihood (ML) inference was conducted using IQ-TREE (Nguyen et al. 2015) under partitioned models (Chernomor et al. 2016). We ran two analyses, for the concatenated ITS–LSU dataset and for LSU alone. Ultrafast bootstrapping was done with 1000 replicates (Hoang et al. 2018). Final trees with ML bootstrap support (MLBS) were visualized in FigTree version 1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>) and edited in Adobe Illustrator 24.1.1.

For the *Tricholoma* study, we compared newly generated ITS sequences with the NCBI GenBank nr/nt nucleotide database using the BLAST tool. To evaluate the phylogenetic placement of our Turkish specimens, closely related sequences of ITS and LSU were downloaded from GenBank. Phylogenetic analyses were performed for the concatenated ITS–LSU dataset using Bayesian Inference (BI) in MrBayes version 3.2 (Ronquist et al. 2012). MCMC analyses were run for 1,000,000 generations, saving trees every 1000 generations, under the GTR+I+ $\Gamma$  evolutionary model of nucleotide substitution. A conservative burn-in of 25 % was applied after checking for convergence of the log-likelihood curves. A majority rule consensus tree of the remaining trees was calculated. Branch support was determined by BI Posterior Probabilities (BIPP).

Recent studies have proven the usefulness of the LSU region as a secondary barcode for Laboulbeniomyces fungi (Haelewaters et al. 2018a, Sundberg et al. 2018, Walker et al. 2018). As a result, for the *Arthrorhynchus* study, phylogenetic relationships at species-level were inferred by analyzing the LSU dataset by maximum likelihood (ML). The LSU dataset comprised eight LSU sequences, of which seven were newly generated (Tab. 1). Sequences were aligned using MUSCLE version 3.7 (Edgar 2004) on the Cipres Science Gateway (Miller et al. 2010). We then used IQ-TREE version 1.6.7 on the command line, treating the dataset as a single partition (Nguyen et al. 2015, Chernomor et al. 2016). We used the built-in ModelFinder (Kalyaanamoorthy et al. 2017) to select an appropriate model of nucleotide substitution under Akaike Information Criterion correct for small sample size (AICc). The selected model was TPM2u+F ( $-\ln L=1387.689$ ). Ultrafast bootstrapping was done with 1000 replicates (Hoang et al. 2018). The final tree with ML bootstrap support values was visualized in FigTree version 1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>) and edited in Photopea (<https://www.photopea.com/>).

Nucleotide BLAST searches of newly generated *Calvatia* ITS sequences against the NCBI GenBank nr/nt database were performed for comparison with closely related sequences. Similar sequences were downloaded from GenBank. *Mycenastrum corium* (Guers.) Desv. (Agaricales, Agaricaceae) was chosen as an outgroup (GenBank accession no. DQ112628). Multiple alignment of the in total forty ITS sequences was performed using MUSCLE (Edgar 2004) available on the Cipres Science Gateway (Miller et al. 2010). Molecular phylogenetic analysis of the aligned ITS dataset was conducted using MEGA X (Kumar et al. 2018). ML MODELTEST in MEGA X was used to select the best model of nucleotide substitution; the selected model was T92+G (Tamura 1992). Rapid bootstrap analysis was performed with 1000 replicates.

Newly generated ITS sequences of *Entoloma* were compared with the NCBI GenBank nr/nt nucleotide database using the BLAST tool. Sequences that shared 100% identity with our query sequences and closely related ones from Wang & Bau (2013) and Acharya et al. (2015) were downloaded from GenBank. *Lyophyllum decastes* (Fr.) Singer was selected as outgroup (sensu He et al. 2012). Sequences were aligned using MAFFT (Katoh et al. 2002) under default settings. Phylogenetic relationships were inferred from the aligned ITS dataset by maximum likelihood (ML), maximum parsimony (MP), and Bayesian inference (BI) analyses. ML was done using RAXML–HPC2 version 8.2.10 (Stamatakis 2014) under the GTRCAT substitution model. A bootstrap (MLBS) analysis was performed with 1000 replicates. MP analysis in PAUP 4.0a167 (Swofford 2002) consisted of 500 stepwise-addition trees using random sequence addition replicates followed by tree bisection-reconnection (TBR) branch swapping; all equally most parsimonious trees were saved. Robustness of branches was estimated using 1000 bootstrap replicates with TBR branch swapping, a rearrangement limit of 1000, and MaxTrees of 100. BI was performed using BEAST on XSEDE 1.8.0 (Drummond et al. 2012), with four MCMC chains run for 10 million generations under the GTR+T evolutionary model and a strict clock to allow for uniform evolutionary rates across branches. Tracer 1.6 (Rambaut et al. 2014) was used to check trace plots and effective sample sizes (ESS). After removal of 25 % burn-in for all runs, trees files were combined in LogCombiner 1.8.4 (Drummond et al. 2012). TreeAnnotator 1.8.4 was used to generate consensus trees with 0 % burn-in and to infer the maximum clade credibility (MCC) tree with the highest clade posterior probabilities (BIPP).

For the *Erysiphe* study, generated ITS sequences were compared to the NCBI GenBank nr/nt nucleotide database with BLAST. Similar sequences were downloaded (Tab. 1). Two ITS datasets were created, one for *E. quercicola* and one for *E. urticae*. Sequences were aligned using MUSCLE version 3.8 (Edgar 2004), which is available on the Cipres Science Gateway portal (Miller et al. 2010). After alignment, manual editing was done in BioEdit version 7.2.5 (Hall 1999). Phylogenetic analyses were performed through Cipres (Miller et al. 2010). Maximum likelihood inference was done for both datasets using RAxML-HPC2 version 8.1.11 (Stamatakis 2014) under the GTRCAT substitution model. A bootstrap (MLBS) analysis was performed with 1000 replicates.

Two FASTA files with newly generated SSU and LSU sequences of *Fanniomyces* and *Stigmatomyces* were uploaded to T-BAS version 2.1 (Carbone et al. 2019). We used the “Place Unknowns” tool to place these sequences onto the Laboulbeniomycetes reference tree v2 (Blackwell et al. 2020). We selected the “de novo” option for the RAxML placement, with 500 bootstrap replicates and *Rhizopus oryzae* (Mucoromycota) as outgroup. The resulting files were downloaded and the aligned SSU and LSU datasets were trimmed to 102 and 62 isolates, respectively. We used the command-line version of IQ-TREE to perform a robust maximum likelihood (ML) analysis of the concatenated SSU–LSU dataset, under multiple partitions (Nguyen et al. 2015, Chernomor et al. 2016). We used the IQ-TREE built-in ModelFinder (Kalyaanamoorthy et al. 2017) to select appropriate models of nucleotide substitution under the Akaike Information Criterion (AIC). Models were GTR+F+R3 (SSU,  $-\ln L = 11835.524$ ) and GTR+F+R4 (LSU,  $-\ln L = 10923.759$ ). Ultrafast bootstrapping was done with 1000 replicates (Hoang et al. 2018). The final tree with ML bootstrap support values was visualized in FigTree version 1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>) and edited in Adobe Illustrator version 24.1.1.

For the *Morchella* study, two sequences of ITS were generated. Twenty-seven related sequences were downloaded from NCBI GenBank for phylogenetic analyses (Tab. 1). All sequences were aligned by MAFFT version 7.110 (Katoh & Standley 2013). *Gyromitra gigas* (Krombh.) Cooke (GenBank accession no. MH938669) and *Gyromitra ticiniana* Littini (MH938674) were selected as outgroup taxa. Phylogenetic analyses were performed for the ITS dataset by both maximum likelihood (ML) and Bayesian inference (BI) methods. The ML analysis was per-

formed through the Cipres Science Gateway web-portal (Miller et al. 2010) using RAxML version 8.2.10 (Stamatakis 2014), employing the GTRGAMMA model with 1000 bootstrap (MLBS) replicates and default settings for other parameters. Bayesian inference was carried out using an MCMC approach in MrBayes version 3.2.2 (Ronquist et al. 2012). Two Markov chains were run for 10 million generations, with a tree sampling frequency of 1000. The initial 25 % of trees were excluded as burn-in, and a 50 % majority consensus tree of the remaining trees was then used to calculate posterior probabilities (BIPP). Branch lengths were estimated as mean values over the sampled trees. Topologies of both analyses were displayed with FigTree version 1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>); the BI topology was further edited in Adobe Illustrator CS7. Clade names follow Richard et al. (2015), Clowez & Moreau (2018), and Du et al. (2019).

Sequences of *Ophiocordyceps* spp., and of *Drechleria gunnii* (Berk.) Spatafora, Kepler & C.A. Quandt and *D. sinensi* (K.Q. Zhang, L. Cao & Z.Q. Liang) Spatafora & Kepler as outgroup, were aligned with MAFFT online version 7 using the E-INS-i option (Katoh & Standley 2013). The ITS–LSU alignment was checked and edited in SeaView 4 (Gouy et al. 2010). Phylogenetic analysis was performed in raxmlGUI 1.5 (Silvestro & Michalak 2012) using the GTRGAMMA nucleotide substitution model and a MLBS analysis with 2000 replicates to test the branch support. An additional Bayesian analysis was performed with MrBayes version 3.1.2 (Ronquist & Huelsenbeck 2003) using the GTR+G nucleotide substitution model. Four Markov chains were run for 5,000,000 generations with sampling every 1,000 generations and a 30 % burn-in. The best scoring tree from the ML analysis was edited with MEGA6 (Tamura et al. 2013).

For the *Parvacoccum pini* study, newly generated ITS–LSU sequences were aligned with selected NCBI GenBank sequences of Rhytismataceae; *Chlorenchocelia versiformis* and *Heyderia abietis* (Cenangiaceae) were used as outgroup taxa (Tab. 1). Sequence alignments were produced with the server version of MAFFT (<http://mafft.cbrc.jp/alignment/server/>) and checked and refined using BioEdit version 7.2.6 (Hall 1999). Maximum parsimony (MP) analysis was performed with PAUP version 4.0a167 (Swofford 2002). All molecular characters were unordered and given equal weight, gaps were treated as missing data, and the COLLAPSE command was set to MINBRLEN. MP analysis was done using 1000 replicates of heuristic search with random addition of sequences and subsequent tree bi-

section-reconnection (TBR) branch swapping (MULTREES option in effect, steepest descent option not in effect). Bootstrap analyses with 1000 replicates were performed in the same way but using five rounds of random sequence addition and subsequent branch swapping during each bootstrap replicate. Maximum likelihood (ML) inference was performed with RAxML (Stamatakis 2006) as implemented in raxmlGUI 1.3 (Silvestro & Michalak 2012), using the ML + rapid bootstrap setting and the GTRGAMMA substitution model with 1000 bootstrap replicates.

### Taxonomy

**Basidiomycota, Agaricomycetes, Russulales, Albatrellaceae**

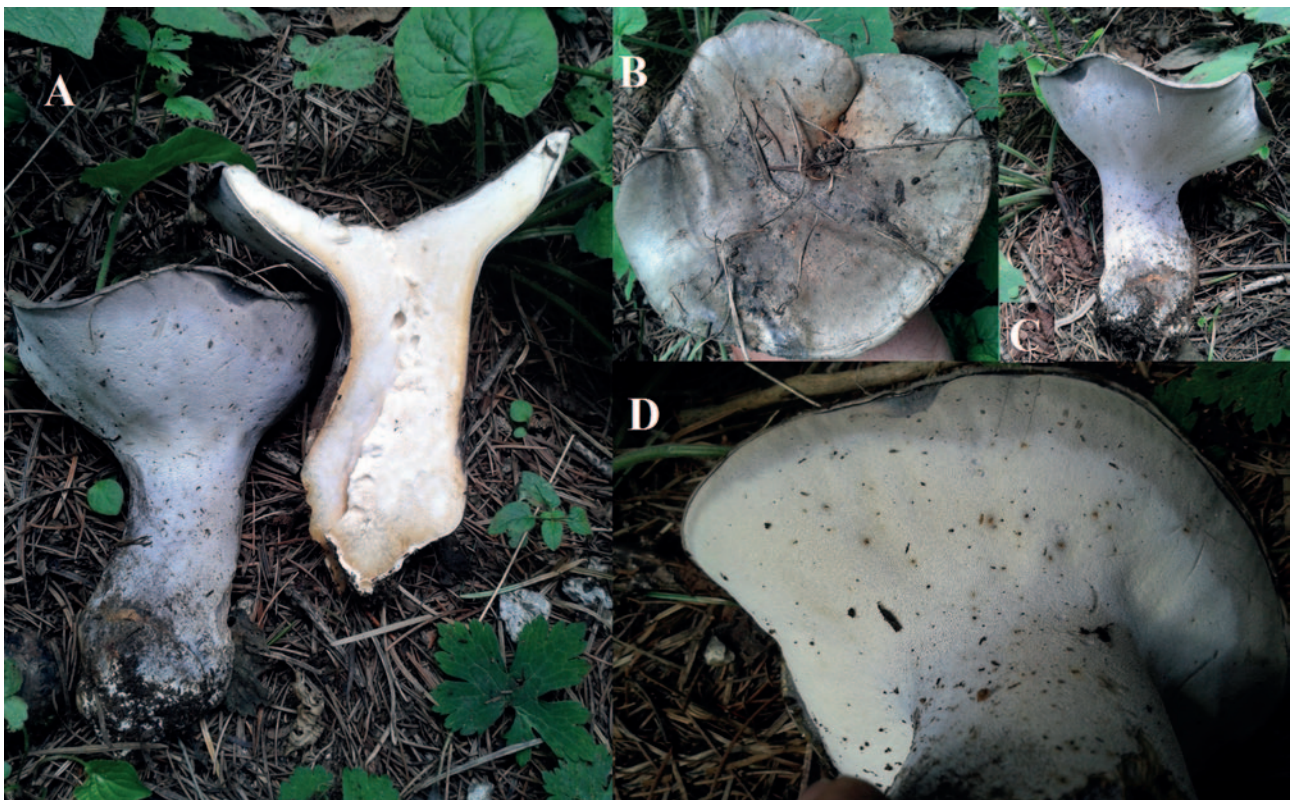
*Albatrellopsis flettioides* J. Khan, sp. nov. – Figs. 1–2  
MycoBank no.: MB 834512

**Diagnosis.** – Different from other *Albatrellopsis* species by its grey to pale bluish-grey pileus, greyish white hymenium, the pileus margin exceeding the hymenium, and reticulate to lacerate grey stipe.

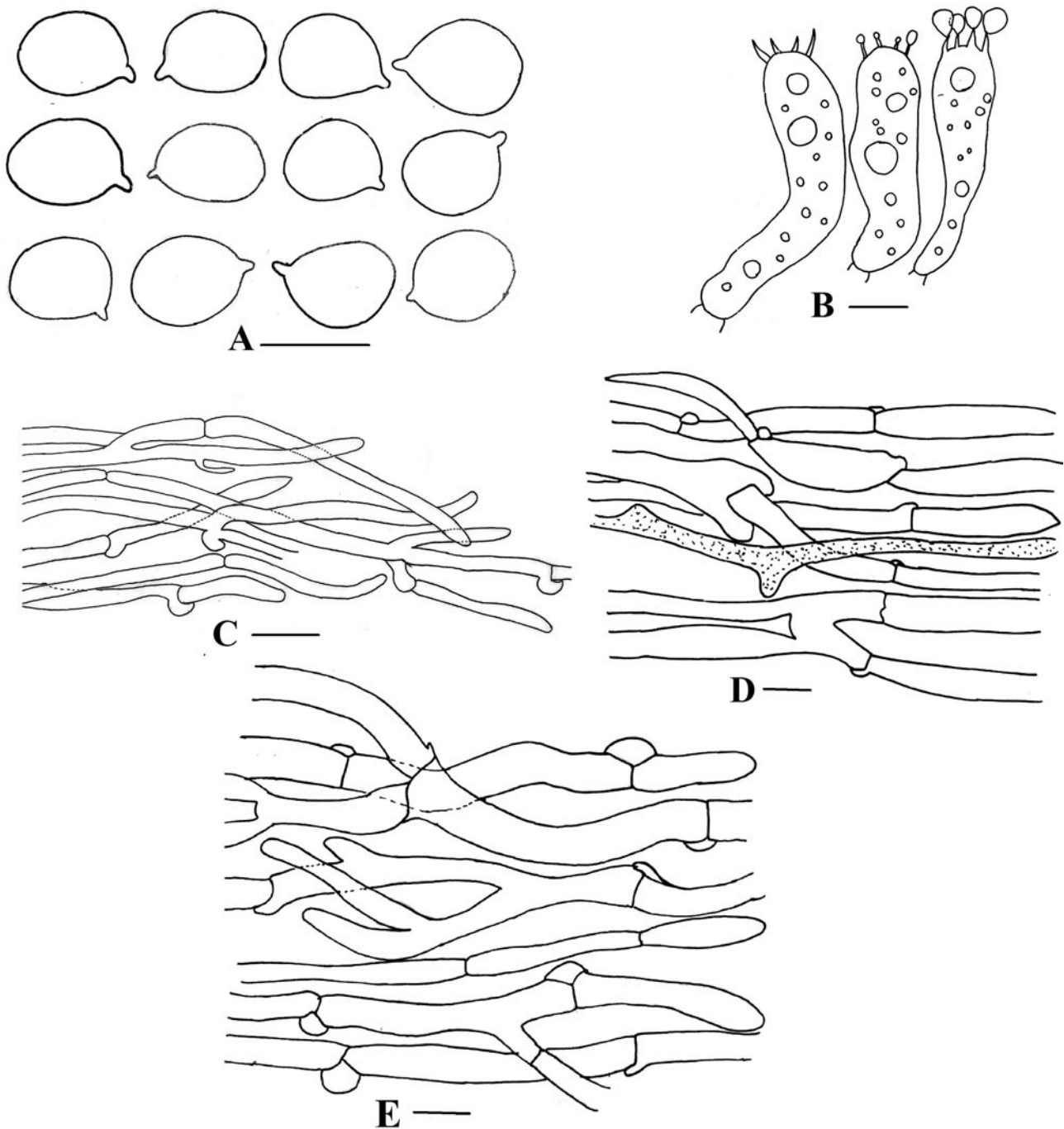
**Holotypus.** – PAKISTAN. Khyber Pakhtunkhwa Province, Swat District, Miandam valley, 35°04'07.8"N, 72°35'43.0"E,

2000 m a.s.l., on soil under *Pinus wallichiana* (Pinales, Pinaceae), 23 August 2014, leg. J. Khan, MM72 (SWAT-MM72; holotype). Sequences ex-holotype: MT040747 (ITS).

**Description.** – Basidiomata terrestrial, solitary. – Pileus up to 100 mm in diam., plano-convex to concave, more or less circular in outline; surface smooth, sticky when wet, shiny, grey (10Y6/2) to pale bluish-grey (5B6/2) when young, developing rusty brown (7.5YR7/6) stains with age, not bluing upon handling or bruising; margin arched, exceeding the hymenium, more or less finely velutinous. – Context dry, firm, 5–7 mm at mid-radius, continuous with the stipe, under the pileipellis greyish white to cream, elsewhere white with light orange to yellowish tinge (7.5YR6/8). – Hymenium greyish white (7.5GY7/2) with a darker (7.5GY4/2) marginal area, unchanging or slightly turning greyish (7.5GY5/2) when bruised, decurrent ending in reticulation on the stipe, pores angular to irregular, very small, up to 7 per mm; tube layer thin,  $\leq 1$ mm, separable from the context. – Stipe 50–70  $\times$  30–35 mm, central, terete, unequal with a more or less napiform base, reticulate to lacerate, grey (7.5GY4/2); context solid, fleshy, yellowish red to rusty brown (7.5YR6/8) just beneath the stipiti-



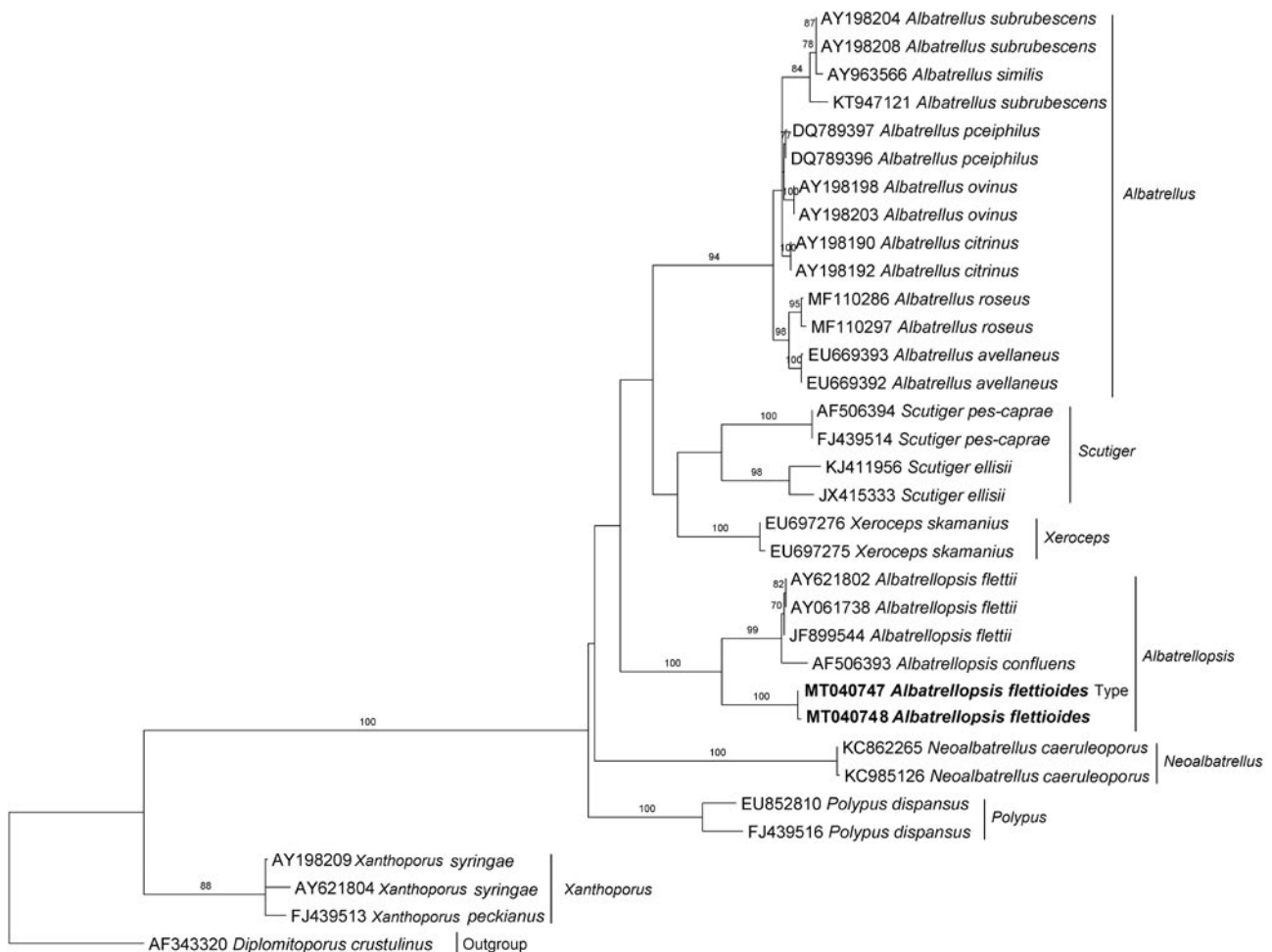
**Fig. 1.** *Albatrellopsis flettioides*, collection SWAT-MM72 (holotype). **A.** Color photo showing context and pore surface. **B.** Pileus surface showing grey and rusty brown coloration. **C.** Complete basidioma in natural habitat. **D.** View of hymenium.



**Fig. 2.** Microscopic features of *Albatrellopsis flettioides*. **A.** Basidiospores. **B.** Basidia. **C.** Hymenophoral trama. **D.** Context. **E.** Pileipellis. Scale bars A–C 4  $\mu$ m, D–E 7  $\mu$ m, del. J. Khan.

pellis, cream yellowish red (2.5YR9/2) towards the center. – Smell and taste not recorded. – Basidiospores (4.2–)4.6–5(–5.4)  $\times$  (3.4–)3.8–4(–4.4)  $\mu$ m, Q=1.2–1.4, broadly ellipsoid in side view, ovoid in face view, thin-walled, hyaline to very lightly staining in KOH, weakly amyloid. – Basidia

22–25  $\times$  5–7  $\mu$ m, club shaped to irregular, 4-spored, guttulate. – Trametal hyphae thin, 2–3  $\mu$ m wide, hyaline to slightly brownish in KOH, parallel to slightly woven, branched, thin-walled, the hyaline hyphae less congophilous than the darker hyphae. – Contextual hyphae  $\leq$  7  $\mu$ m wide, hyaline in



**Fig. 3.** Phylogeny of *Albatrellopsis* and related genera reconstructed from an ITS dataset. The topology is the result of ML inference performed with IQ-TREE. For each node, the MLBS (if  $\geq 70$ ) is presented above the branch leading to that node. The new species *A. flettioides* is highlighted in boldface.

KOH, hyphae randomly woven, branched, gloeopleurous hyphae present, rare, scattered,  $\leq 7 \mu\text{m}$  in diameter, contents oily, golden brown in KOH. – *Pileipellis* a trichoderm, hyphae frequently branched, woven, septate,  $\leq 6 \mu\text{m}$  wide, terminal elements narrowly clavate to cylindrical,  $20\text{--}40 \times 5\text{--}6 \mu\text{m}$ . – *Stipitipellis* an interrupted hymeniderm, hyphae  $5\text{--}7 \mu\text{m}$  in diameter. – *Clamp connections* present in all types of tissues. – *Hyphal system* monomitic.

**Etymology.** – *flettioides*, referring to the close resemblance between the new species and *Albatrellopsis flettii*.

**Habitat and distribution.** – On soil under *Pinus wallichiana* in coniferous forests. Thus far only recorded in Pakistan.

**Additional material examined.** – PAKISTAN. Khyber Pakhtunkhwa Province, Swat District, Miandam val-

ley,  $35^{\circ}04'11.2''\text{N}$ ,  $72^{\circ}35'45.8''\text{E}$ , 2100 m a.s.l., on soil under *Pinus wallichiana*, 23 August 2014, leg. Junaid Khan, MM-76 (SWAT000702).

**Notes.** – *Albatrellopsis* Teixeira is a small genus with only two described species including *A. confluens* (Alb. & Schwein.) Teixeira and *A. flettii* (Morse ex Pouzar) Audet. Species of *Albatrellopsis* have convex and sometimes confluent, overlapping pilei, white pores, common clamp connections, rare gloeopleurous hyphae in the trama, hyphal acantho-appendages at the base of the stipe, a monomitic hyphal system, and mostly weakly amyloid basidiospores (Pouzar 1972, Audet 2010). During our macrofungal surveys in the Miandam valley of Swat District, we encountered two collections of *Albatrellopsis*. Morphological comparison with the two accepted species in the genus led us to conclude that our collections might represent new species.

Our molecular phylogenetic analysis of the ITS dataset supported this conclusion. This dataset consisted of 34 sequences, two of which were newly generated (Tab. 1), and 782 characters with 337 parsimony-informative ones. In the resulting ITS tree (Fig. 3), our *A. flettioides* sequences were placed sister to a clade comprising *A. confluens* and *A. flettii* with maximum support.

Morphologically, the species is most similar to *A. flettii*, which has a grayish to hoary pileus and a matching hyphal anatomy. However, it can be separated based on its white hymenium that turns apricot to salmon upon maturation, and its drying, white, and smooth stipe (Gilbertson & Ryvarden 1986)—contrasting to the whitish grey hymenium, and concolorous, reticulate to lacerate stipe of *A. flettioides*. *Albatrellopsis flettioides* is also different in its pileus margin that exceeds the hymenium and the basidiospores that are larger compared to *A. flettii* ( $4.2\text{--}5.4 \times 3.4\text{--}4.4 \mu\text{m}$  vs.  $3.5\text{--}4 \times 2.5\text{--}3 \mu\text{m}$ ; Morse 1941). The hyphal anatomy (clamped context and tramal hyphae of same size and shape) and basidiospore shape of *A. confluens* are similar to those of *A. flettioides*. *Albatrellopsis confluens*, however, can be distinguished by its pale orange to pinkish buff pileus surface (Zheng et al. 2004).

This report does not only present a new species for science; with no previous records of *Albatrellopsis* in Pakistan, it also adds a previously unreported genus to the country's Funga (sensu Kuhar et al. 2018).

*Authors:* J. Khan, H. Sher, S. Hussain & A.N. Khalid

### Basidiomycota, Agaricomycetes, Boletales, Boletaceae

*Aureoboletus garciae* Ayala-Vásquez & Aguirre-Acosta, **sp. nov.** – Figs. 4–5  
MycoBank no.: MB 835042

*Holotypus.* – MEXICO. Estado de Oaxaca, Mixistlán de la Reforma municipality, Santa María Mixistlán town, 2211 m a.s.l.,  $17^{\circ}08'41''\text{N}$ ,  $96^{\circ}05'21''\text{W}$ , in *Quercus scytophylla* (Fagales, Fagaceae) forest, 23 August 2016, *leg.* R. Castro-Rivera (MEXU 29006; holotype). Sequences ex-holotype: MH337251 (LSU), MT228979 (*rpb1*), MT228983 (*rpb2*).

*Description.* – Basidiomata pileate-stipitate, small. – Pileus 8–23 mm in diam., convex, with furfuraceous surface, dry, vivid blue (20A8–20A6), violet blue (19A6), to light blue (19A5), with some reddish (11A5) tones, margin sterile. – Hymenophore adnate, with rounded pores 0.2–0.3 mm in diam., bright yellow (4A8) unchanging when cut; tubes 5–7 mm long, concolorous to the

pores. – Stipe 30–35 × 5–6 mm, cylindrical, with furfuraceous to rimose surface, whitish to pale red (11A4) near the apex, deep red to reddish brown (9D8–9E8) in mature specimens. – Context 5 mm thick, whitish, bruising pink (11A4) to pale red (11A3) when young, yellow when mature, context of the stipe whitish with some pale yellow tones in the middle and base. – Smell and taste indistinct. – Basidiospores  $9\text{--}14 \times 4\text{--}5\text{--}(6) \mu\text{m}$  ( $L_{av}=10$ ,  $W_{av}=5$ ,  $Q=1.7$ ,  $n=35$ ), ellipsoid to fusiform, smooth with or without conspicuous suprahilar depression, hyaline in KOH, yellowish brown in Melzer's reagent, thin-walled. – Basidia  $25\text{--}49 \times 8\text{--}9 \mu\text{m}$ , clavate, 4-spored, sterigmata  $3\text{--}5 \times 0.5\text{--}1.0 \mu\text{m}$ , hyaline, thin-walled. – Pleurocystidia  $28\text{--}50 \times 7\text{--}13 \mu\text{m}$ , clavate, fusoid or mucronated, hyaline in KOH, pale brown in Melzer's reagent, thin-walled. – Cheilocystidia  $50\text{--}65 \times 7\text{--}10 \mu\text{m}$ , clavate-ventricose to fusoid, hyaline in KOH, brownish yellow in Melzer's reagent, thin-walled. – Hymenophoral trama bilateral, composed of a central stratum with tubulose hyphae, 4–10  $\mu\text{m}$  diameter, with gelatinized walls, hyaline, thin-walled; lateral stratum composed of tubulose hyphae, 5–14  $\mu\text{m}$  diameter, hyaline, thin-walled. – Pileipellis composed of a trichodermium of tubulose, loosely interwoven hyphae, 12–67 × 7.4–15  $\mu\text{m}$ , with cylindrical, mammillate, clavate or subglobose terminal cells, hyaline in KOH, with cellular content in Melzer's reagent, thin-walled. – Stipitipellis 70–81  $\mu\text{m}$  thick, composed of turbinate, mammillate or pedunculate caulocystidia, 35–67 × 14–19  $\mu\text{m}$ , hyaline in KOH, thick-walled (1.0–1.6  $\mu\text{m}$ ).

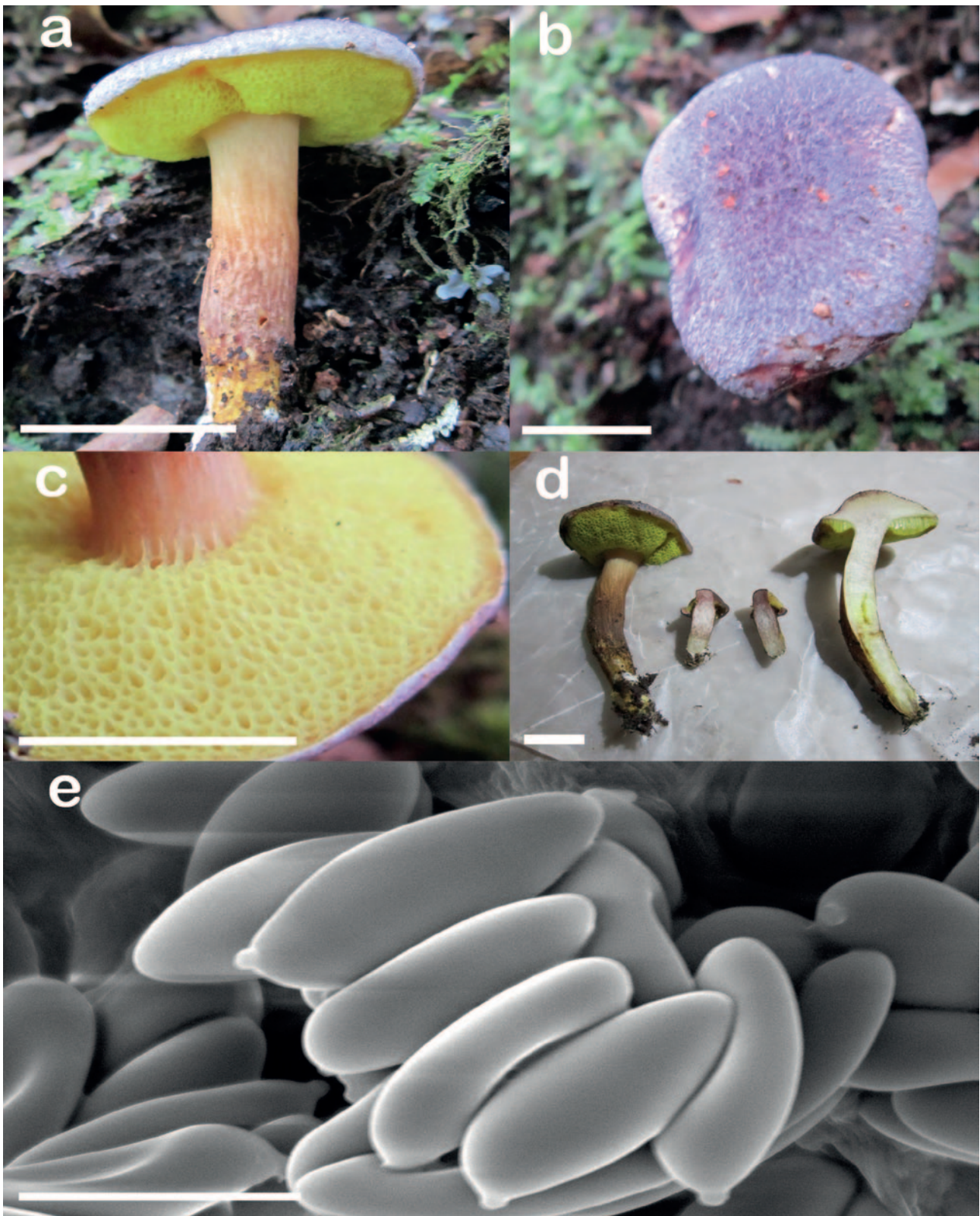
*Etymology.* – In honor of Dr. Jesús García Jiménez, eminent Mexican mycologist and pioneer in the study of the Mexican boletes.

*Habitat and distribution.* – Solitary under *Quercus laurina* and *Q. scytophylla* in oak and montane cloud forests, currently known from Oaxaca, Mexico.

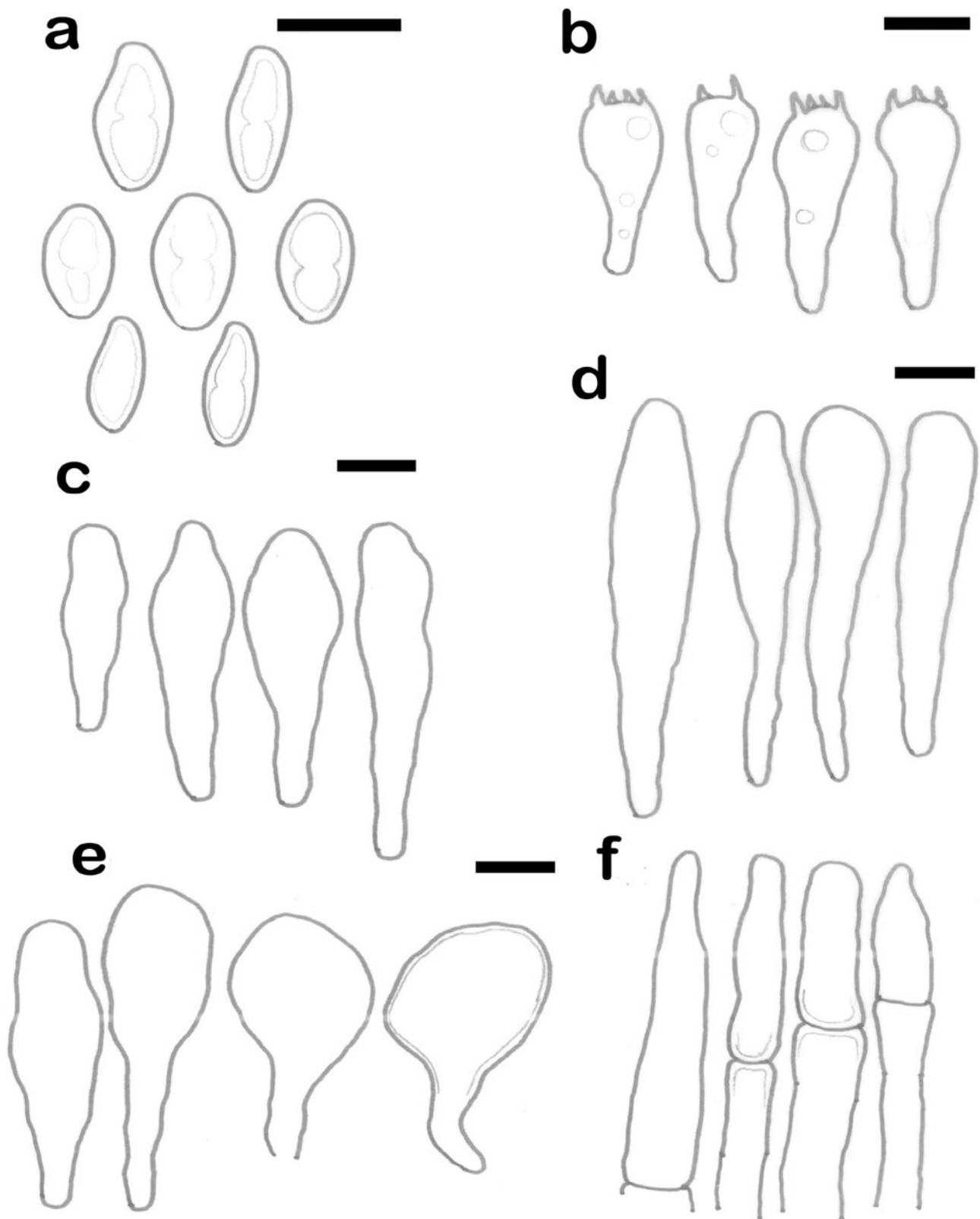
*Additional material examined.* – MEXICO. Estado de Oaxaca, Mixistlán de la Reforma municipality, Santa María Mixistlán town, 2465 m a.s.l.,  $17^{\circ}09'30''\text{N}$ ,  $96^{\circ}04'27''\text{W}$ , 4 September 2016, *leg.* O. Ayala-Vásquez (MEXU-30133, ITCV-873); *Ibid.*, 2211 m a.s.l.,  $17^{\circ}08'41''\text{N}$ ,  $96^{\circ}05'21''\text{W}$ , 5 September 2017, *leg.* O. Ayala-Vásquez (MEXU-30134, ITCV-983); *Ibid.*, 2211 m a.s.l.,  $17^{\circ}08'41''\text{N}$ ,  $96^{\circ}05'21''\text{W}$ , 12 September 2017, *leg.* O. Ayala-Vásquez (ITCV-1022); *Ibid.*, 2230 m a.s.l.,  $17^{\circ}08'44.79''\text{N}$ ,  $96^{\circ}05'19.38''\text{W}$ , 12 October 2017, *leg.* O. Ayala-Vásquez (ITCV-1028); *Ibid.*, 2211 m a.s.l.,  $17^{\circ}08'41''\text{N}$ ,  $96^{\circ}05'21''\text{W}$ , 5 August 2017, *leg.* O. Ayala-Vásquez (MEXU-29426, ITCV-848); *Ibid.*, 2465 m a.s.l.,  $17^{\circ}09'30''\text{N}$ ,  $96^{\circ}04'27''\text{W}$ , 24 July 2017, *leg.* O. Ayala-Vásquez (MEXU-30135, ITCV-886).

*Notes.* – The genus *Aureoboletus* Pouzar was proposed by Pouzar (1957), with *A. gentilis* (Qué.)

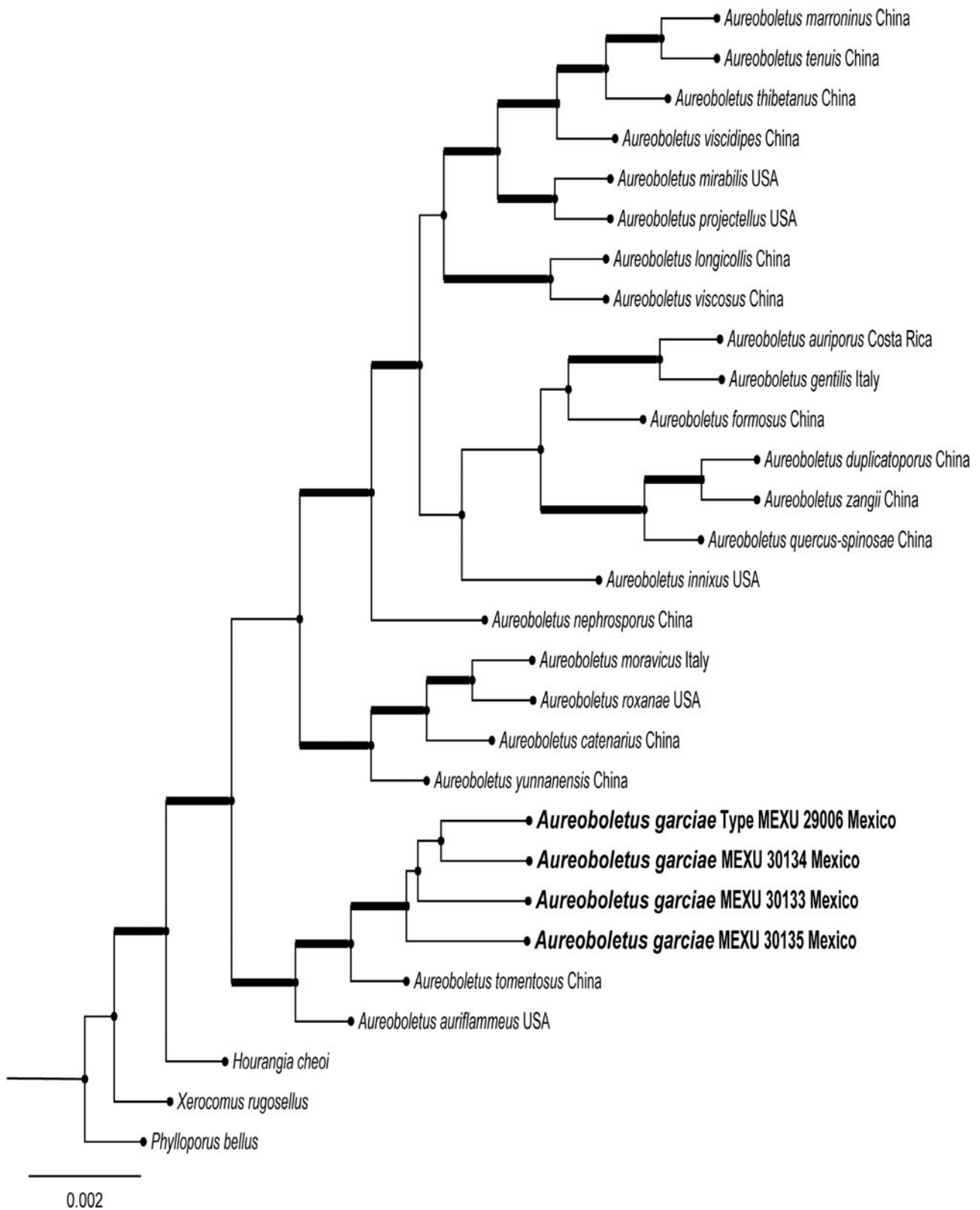




**Fig. 4.** *Aureoboletus garciae*, collection MEXU 29006 (holotype). **a.** Basidiomata. **b.** Detail of the pileus. **c.** Detail of the hymenophore. **d.** Detail of the context. **e.** SEM micrograph of basidiospores. Scale bars a–d 10 mm, e 10  $\mu$ m.



**Fig. 5.** Microscopic features of *Aureoboletus garciae*. **a.** Basidiospores. **b.** Basidia. **c.** Pleurocystidia. **d.** Cheilocystidia. **e.** Caulocystidia. **f.** Elements of pileipellis. Scale bars 10  $\mu\text{m}$ .



**Fig. 6.** Phylogeny of *Aureoboletus* reconstructed from a concatenated LSU-*rpb1-rpb2* dataset. The MCC topology is the result of Bayesian inference performed with MrBayes. Thick lines represent BIPP  $\geq 0.95$ . The new species *A. garciae* is highlighted in boldface.

Pouzar as type species. The genus can be found in temperate and subtropical forests (Pouzar 1957; Klofac 2010; Zhang et al. 2014, 2015b). At present, between 33 and 42 species are recognized, depending on the source (Zhang et al. 2019, Species Fungorum 2020, Wijayawardene et al. 2020). The genus is distinguished by pileate-stipitate basidiomata; a viscid or sometimes tomentose pileus surface; an adnate hymenium; yellow tubes, with rounded to angular golden pores never bruising when touched; and a central or fusoid stipe that is inflated to acute at the base, with a glabrous to pruinose surface (Klofac 2010, Wu et al. 2016, Bessette et al. 2017). Microscopically, species of *Aureoboletus* are characterized by usually smooth, rarely longitudinally striate, subfusiform basidiospores; light yellow to yellow, bilateral hymenophoral trama with tubulose hyphae; and a pileipellis composed of ixotrichoderm or sometimes a trichoderm (Wu et al. 2016).

The Mexican oak forest possesses a wide diversity of boletes (García-Jiménez & Garza-Ocañas 2001), which has been investigated in recent years (García-Jiménez & Garza-Ocañas 2001, Ayala-Vásquez et al. 2018, García-Jiménez et al. 2019). Nevertheless, some areas such as the mountains of south Mexico remain unexplored, with some of the sampled fungi being undescribed.

Features of *A. garciae* are consistent with those of the genus. The bluish colour of the pileus is the main characteristic that distinguishes *A. garciae* from other *Aureoboletus* species. *Aureoboletus garciae* is associated with Fagaceae—potentially forming ectomycorrhizal associations with *Quercus laurina* (a Central American-endemic species) and *Q. scytophylla* (a Mexican-endemic species). The new species shares its habitat with other *Aureoboletus* species such as *A. innixus* (Frost) Halling, A.R. Bessette & Bessette, *A. roxanae* (Frost) Klofac, and *A. russellii* (Frost) G. Wu & Zhu L. Yang (Ayala-Vásquez et al. 2018, García-Jiménez et al. 2019). Bayesian inference recovered *A. garciae* as sister to *A. tomentosus* G. Wu & Zhu L. Yang with high support (Fig. 6). Morphologically, this species is characterized by bright orange-yellow basidiomata, a tomentose pileus surface, context without colour change when bruised, and ovoid basidiospores that are shorter compared to *A. garciae* (Wu et al. 2016, Zhang et al. 2019). These combined morphological and molecular results confirm the status of *A. garciae* as a new species.

**Authors:** O. Ayala-Vásquez, J.I. de la Fuente, C.R. Martínez-González, R. Castro-Rivera & E. Aguirre-Acosta

## Basidiomycota, Agaricomycetes, Agaricales, Entolomataceae

***Entoloma canadense*** Noordel., G.M. Jansen & Dima, **sp. nov.** – Fig. 7

Mycobank no.: MB 836840

**Holotypus.** – Canada. Newfoundland and Labrador Province, Point Armour Historic Site, 51°27'38.16"N, 56°51'34.06"W, 7 September 2005, leg. M.E. Noordeloos, 2005127a (L0608149; holotype). Sequences ex-holotype: MT940867 (ITS), MK277990 (LSU).

**Description.** – Basidiomata medium-sized, tricholomatoid. – Pileus 30–40 mm in diam., conico-convex, expanding to plano-convex with low umbo, with deflexed margin, not hygrophanous, not translucently striate, moderately dark brown with a slight violaceous-purple or plum-colored tinge when very fresh (7.5YR6–5/2–4; 10YR 2–5/3–4) or 2.5R 5/4. 5YR 4–3/3), entirely very finely squamulose. – Lamellae moderately crowded (L=25–50, l=5–7–9), adnate-emarginate, ventricose, pale cream-colored white then sordid grey-pink with an entire or eroded, concolorous edge. – Stipe 25–50 × 4–10 mm, cylindrical, entirely fibrillose-striate with pale vinaceous-brown fibrils and flocks, white and smooth at base. – Context pale pinkish grey. – Smell and taste indistinct. – Basidiospores (6.0–)6.9–9.2 × 4.6–6.9 µm, average 7.6–8.1 × 5.4–5.8 µm, Q=1.2–1.7, Q<sub>av</sub>=1.41, heterodiametrical 6–8 angled in side-view, thin-walled with rather weak angles. – Basidia 30–37 × 9.5–10.5 µm, clavate, 4-spored, clamped. – Lamella edge heterogeneous with scattered cheilocystidia. – Cheilocystidia 32–55 × 8–20 × 5–10 µm, rather variable, the majority lecithiform, sometimes vesiculose, up to 50 µm wide. – Hymenophoral trama regular, made up of cylindrical to inflated elements, 100–250 × 5–20 µm wide, also very wide hyphae up to 50 µm present. – Pileipellis cutis to trichoderm, cylindrical hyphae 6–20 µm wide, with pale brown intracellular pigment. – Clamp connections present in hymenium, rare to absent in other tissues.

**Etymology.** – Referring to Canada, where the holotype of the new species was collected.

**Habitat and distribution.** – In a semi-natural grassland, grazed by wildlife, near *Abies balsamica* (Pinales, Pinaceae) and in a coastal arctic heathland with *Empetrum* (Ericales, Ericaceae) and dwarf *Salix* (Malpighiales, Salicaceae). Thus far only known from eastern Canada and the eastern USA.

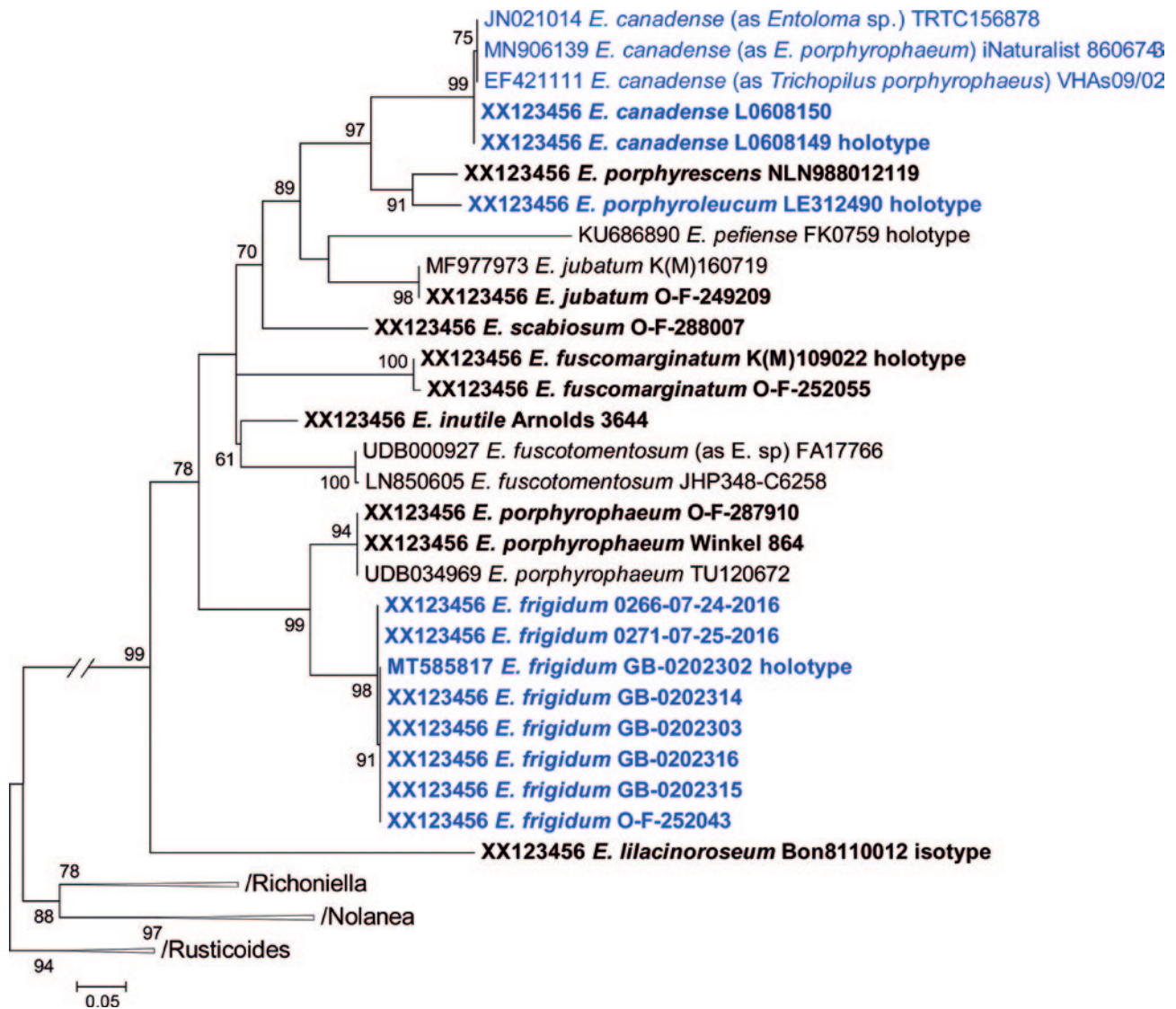
**Additional material examined.** – CANADA. Newfoundland and Labrador Province, Gros Morne National Park, Killdevil Camp, 49°27'10.01"N, 57°45'13.86"W, 4 September 2005, leg. M.E. Noordeloos, 2005121 (L0608150).



**Fig. 7.** *Entoloma canadense*, collection L0608149 (holotype) **a.** Basidiomata *in situ*. **b.** Basidiospores. **c.** Cheilocystidia, **d.** Pileipellis. Scale bars a–d 10  $\mu$ m.

**Notes.** – *Entoloma canadense* belongs to the *Trichopilus* clade of *Entoloma* P. Kumm. The phylogenetic placement in this clade (Fig. 8) is morphologically supported by the presence of lecythiform cheilocystidia and trichodermal pileipellis. We generated 19 new ITS sequences representing ten spe-

cies in the *Trichopilus* clade—thereby greatly expanding the coverage of this clade in public databases. Within *Trichopilus*, *E. canadense* is distinct from other described species and placed sister to a clade with *E. porphyrescens* E. Horak from Tasmania and *E. porphyroleucum* sp. nov. from Vietnam



**Fig. 8.** Phylogeny of *Entoloma* reconstructed from an ITS dataset. The topology is the result of ML inference performed in PhyML. MLBS values (>60) are shown at the nodes. Sequences newly generated for this study are highlighted in boldface; newly described species are highlighted in blue.

(Fig. 8). Morphologically it is distinct from these species because of the minutely squamulose, moderately dark to dark brown pileus with violaceous to violaceous-red (plum) tinges when fresh, its small basidiospores, and scattered, in majority lecithiform cheilocystidia (Fig. 7). *Entoloma fuscomarginatum* P.D. Orton [= *E. elodes* (Fr.) P. Kumm.] has a smoother, micaceous pileus without violaceous tinges, and larger basidiospores. The new species may be misidentified as *E. porphyrophaeum* (Fr.) P. Karst. [= *Trichopilus porphyrophaeus* (Fr.) P.D. Orton], which is a European species with a similarly colored pileus but differs in a stouter habitus, much larger basidiospores, and cheilocystidia often with

a long, moniliform apex. *Entoloma frigidum* from northern Sweden is macroscopically similar to *E. canadense* but has much larger basidiospores. *Entoloma scabinellum* Peck, a poorly known species described from eastern USA, has similar microscopic characters, but there is reasonable doubt that it represents the same species, since it was described as a small *Nolanea* (Fr.) P. Kumm. (pileus of 12–20 mm in diam., minutely scabrous). Sequences are lacking and the type is unavailable for sequencing, but *E. scabinellum* may belong to *Trichopilus* on account of the lecithiform cystidia.

*Authors:* M.E. Noordeloos, G.M. Jansen & B. Dima

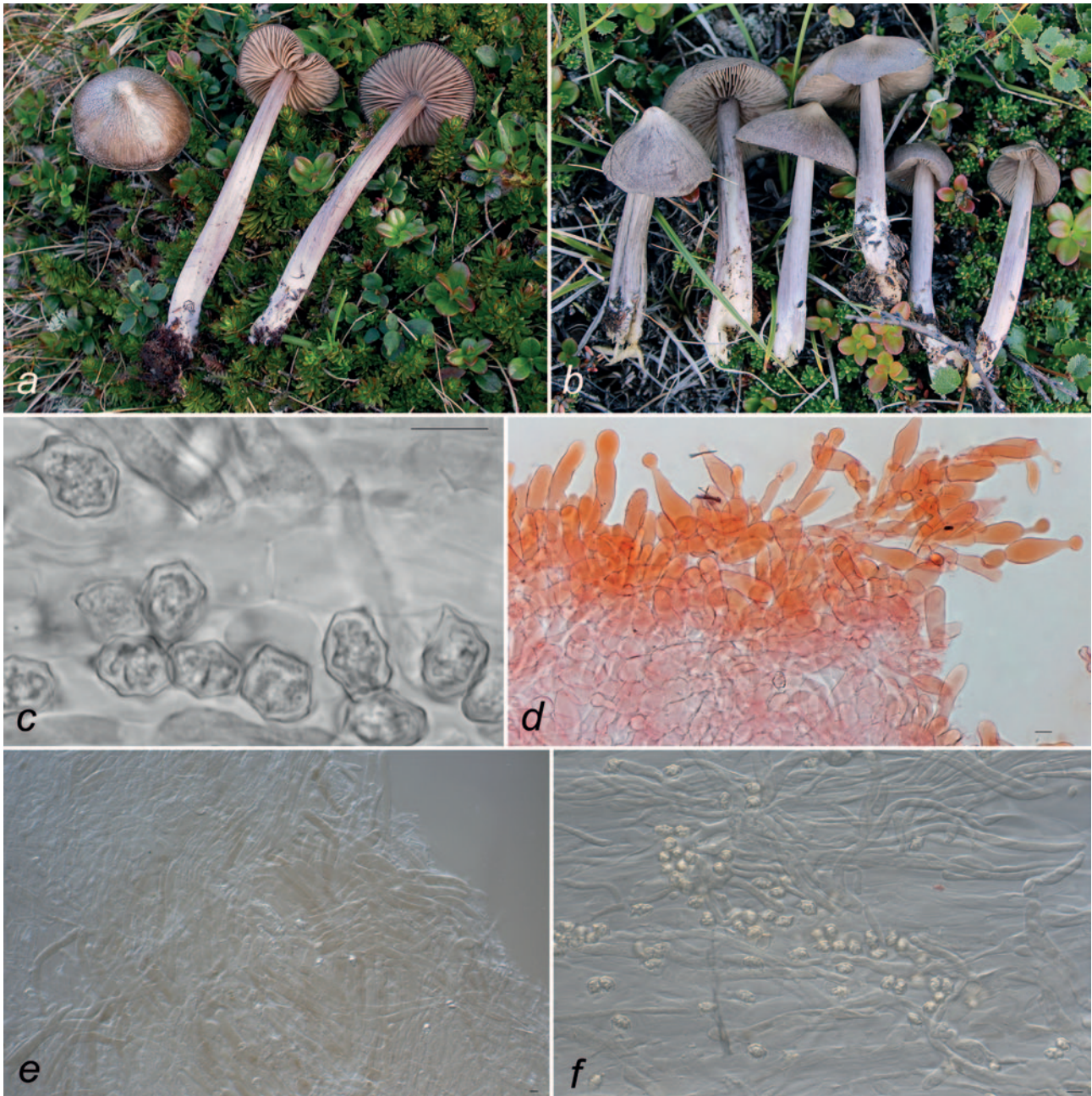
**Basidiomycota, Agaricomycetes, Agaricales, Entolomataceae**

*Entoloma frigidum* Noordel., E. Larss., Bendiksen, G.M. Jansen & Dima, **sp. nov.** – Fig. 9  
Mycobank no.: MB 836841

**Holotypus.** – SWEDEN. Torne Lappmark, Jukkasjärvi, Latnajavagge, 8 August 2007, *leg.* E. Larsson, EL46-07 (GB-

0202302; holotype). Sequences ex-holotype: MT585817 (ITS+LSU).

**Description.** – Basidiomata small to medium-sized, tricholomatoid. – Pileus 30–50 mm in diam., conical only slightly expanding to conico-convex or convex with umbo, with straight or slightly deflexed margin, not hygrophanous, not translucently striate, uniformly mouse grey or with



**Fig. 9.** *Entoloma frigidum*. **a.** Basidiomata *in situ*, collection GB-0202302 (holotype). **b.** Basidiomata *in situ*, collection EL189-16. **c–f.** Microstructures, from collection GB-0202302 (holotype). **c.** Basidiospores. **d.** Cheilocystidia. **e.** Pileipellis. **f.** Stipitipellis. Scale bars 10 µm.

a slight porphyry-purple sheen, very finely tomentose-radially fibrillose all over, often with a glaucous impression in parts, not squamulose. – Lamellae normally distant, deeply adnate-emarginate, ventricose, pale then pink with slight grey tinge, with more or less concolorous, slightly eroded edge. – Stipe 60–90 × 3–7 mm, gradually but slightly broadening towards base, more or less concolorous with pileus, base paler, almost white, innately fibrillose lengthwise. – Context firm, pale in inner part, else greyish. – Smell and taste indistinct. – Basidiospores (10–)11.0–15 × 6.0–9.5 µm, average 13.0 × 8.3 µm, Q=1.3–1.9, Q<sub>av</sub>=1.48–1.57, with a bumpy-nodulose outline, many of them with a star-formed content. – Basidia 38–68 × 12–15 µm, 4-spored, clavate, clamped. – Lamella edge heterogeneous. – Cheilocystidia 36–70 × 6–20 × 5.5–13.5 µm, lageniform to tibiiform, usually with broad basal part, short to long neck, and rounded capitulum, frequently septate, clamped. – Pleurocystidia absent. – Hymenophoral trama regular, made up of cylindrical hyphae, 4–25 µm wide, no clamps seen. – Pileipellis a cutis of long, terminal elements, 90–350 × 5–23 µm, with brown intracellular pigment, no clamps seen. – Stipitipellis a cutis of cylindrical hyphae, 4.5–23 µm wide with pale brown intracellular pigment. – Vascular hyphae present in trama and in stipitipellis. – Caulocystidia present at apex of stipe, 38–72 × 11–17 µm, clavate, lageniform, sometimes tibiiform. – Clamp connections present in hymenium at base of basidia, elsewhere rare or absent.

**Etymology.** – *frigidum* = cold, referring to the climate in which this species thrives.

**Habitat and distribution.** – In oligotrophic alpine heath with and *Arctostaphylos*, *Empetrum* (Ericales, Ericaceae), *Betula nana* (Fagales, Betulaceae), and *Salix* spp. (Malpighiales, Salicaceae), and in sandy pine forest with *Betula nana*, dominated by *Empetrum* and *Vaccinium vitis-idaea* (Ericales, Ericaceae). Currently only known from the northernmost parts of Sweden and Norway.

**Additional specimens examined.** – *Ibid.* (L0607966, isotype). – SWEDEN. Lule Lappmark, Jokkmokk, Padjelanta, Ajajure, 16 August 2016, leg. E. Larsson, EL189-16 (GB-0202303); *Ibid.*, Padjelanta, Ajajure, 16 August 2016, leg. J. Olsson (GB-0202316); *Ibid.*, Padjelanta, Vielggsbakte, 12 August 2016, leg. S. Kuoljok (GB-0202315); Torne Lappmark, Jukkasjärvi, Abisko, Latnja, 16 August 2013, leg. P.-A. Moreau, PAM13-23 (GB-0202314). – NORWAY. Finnmark, Karasjok, Basevuovdi N by River Øvre Anarjohka, 20 August 2013, leg. A.-M. Bendiksen, EB 201/13 (O-F-252043).

**Notes.** – *Entoloma frigidum*, according to our molecular phylogenetic results, belongs to the

*Trichopilus* clade where it forms the sister species of *E. porphyrophaeum* (Fig. 8) to which it has a superficial resemblance, particularly with regard to the size and shape of the basidiomats, but with a mouse-grey color, sometimes with slightly purplish tinge. In the ITS region, *E. frigidum* and *E. porphyrophaeum* differ by more than 60 substitution and indel positions. Microscopically, *E. frigidum* can be distinguished by the somewhat larger basidiospores and shape of its cheilocystidia (Fig. 9). As far as we know, this species has a northern boreal-alpine distribution in northernmost Scandinavia. *Entoloma fuscotomentosum* F.H. Møller, another species with a nordic distribution, seems to prefer coastal habitat, and differs by the small basidiospores and grey-brown, fibrillose-subsquamulose pileus. To our knowledge, there are no other morphologically similar species occurring in the same habitat with which *E. frigidum* can be confused.

**Authors:** M.E. Noordeloos, E. Larsson, E. Bendiksen, G.M. Jansen & B. Dima

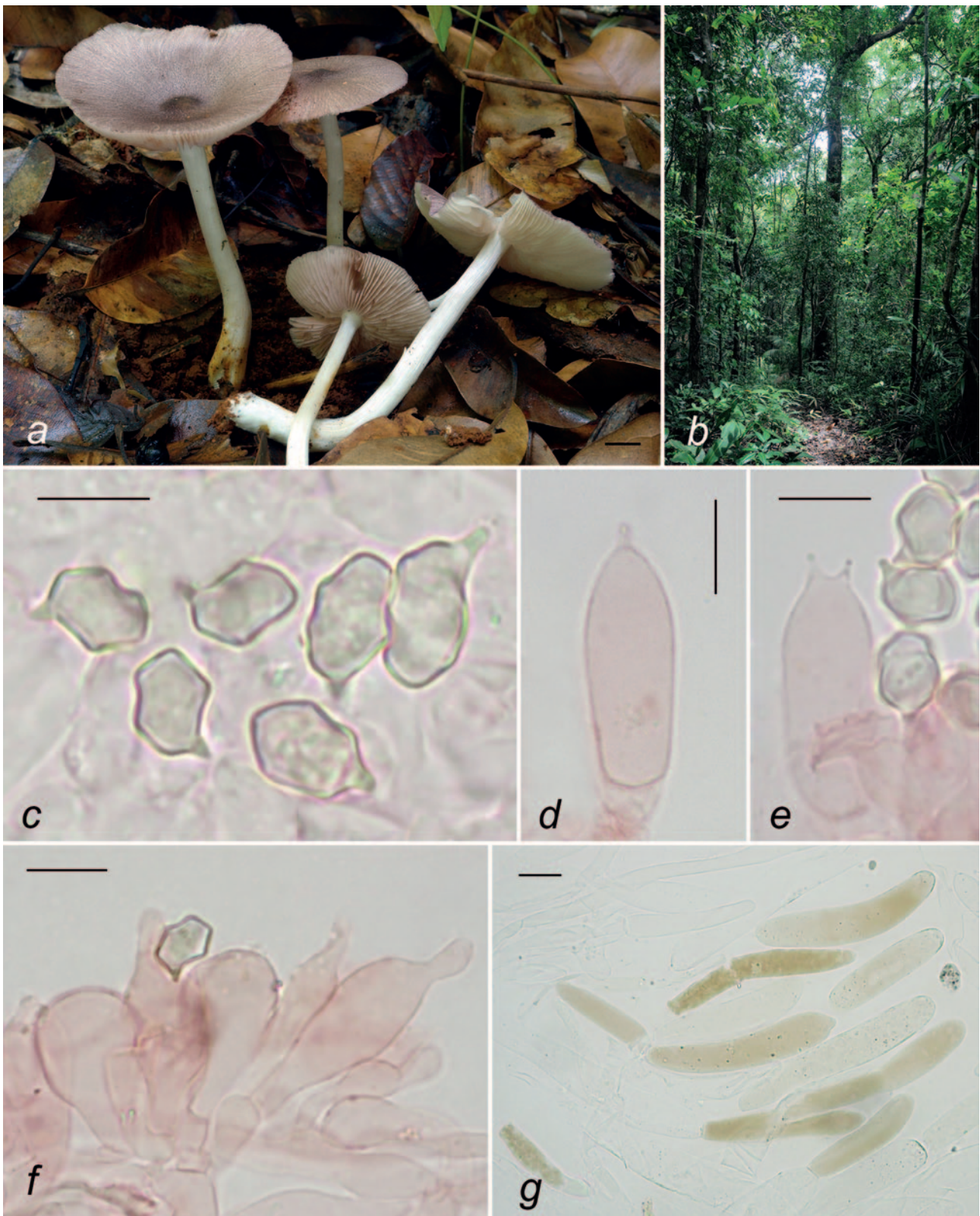
#### Basidiomycota, Agaricomycetes, Agaricales, Entolomataceae

***Entoloma porphyroleucum*** O.V. Morozova, Noordel. & Dima, **sp. nov.** – Fig. 10  
MycoBank no.: MB 835245

**Holotypus.** – VIETNAM. Binh Phuoc Province, Bu Gia Map District, Bu Gia Map National Park, right bank of Dak Ca River, 12°12'15.41"N, 107°12'13.25"E, 370 m a.s.l., on soil, 19 May 2011, leg. O. Morozova (LE 312490; holotype). Sequences ex-holotype: MT940862 (ITS), MT950278 (LSU).

**Description.** – Basidiomata medium-sized, collybioid to tricholomatoid. – Pileus 30–60 mm in diam., conico-convex expanding to plano-convex, with small conical umbo, depressed when old with small acute umbo in the depression, with more or less straight margin, not hygrophanous, not translucently striate, light purplish-brown (8C3, 8D3–4, 9C3, up to 13D4), darker in the center (8E3, 9E4, 10E4–5), densely radially fibrillose in the center, fibrils more spread towards the margin, showing white background. – Lamellae moderately distant, adnexed, adnate-emarginate, ventricose, whitish or cream at first, becoming pink and brownish-pink, with white dentate edge. – Stipe 50–100 × 4–10 mm, cylindrical, distinctly broadened towards the base, white, longitudinally striate, white tomentose at base. – Context white, unchanging. – Smell faint. – Taste not reported. – Basidiospores of two types, (i) from 4-spored basidia, small, 7.5–9.5 × 5.5–7 µm, average 8.5 × 6 µm, Q=1.3–1.5, Q<sub>av</sub>=1.4, heterodiametrical, with 5–6 angles in





**Fig. 10.** *Entoloma porphyroleucum*, collection LE 312490 (holotype). **a.** Basidiomata *in situ*. **b.** Type locality. **c.** Basidiospores. **d–e.** Basidia. **f.** Cheilocystidia. **g.** Pileipellis. Scale bars a 1 cm, c–g 10  $\mu$ m.

side-view; and (ii) from 1–2-spored basidia, large, 10–12 × 5.5–8 µm, average 11 × 6.5 µm, Q=1.4–1.9, Q<sub>av</sub>=1.7, irregular, with poorly defined angles. – Basidia 22–27 × 8.5–9 µm, 1–4-spored, clavate to cylindrical, clampless. – Cheilocystidia 17–31 × 8–17 µm, forming a sterile edge, of intermixed two types: vesiculose to spheropedunculate or lageniform. – Pileipellis a cutis with the transition to a trichoderm of cylindrical to slightly inflated or fusiform hyphae 10–20 µm wide with swollen terminal elements with slightly thickened apex and brownish intracellular pigment. – Caulocystidia absent. – Clamp connections absent.

**Etymology.** – From Greek ‘πορφυρεός’ (purpureus) and ‘λευκός’ (white, light), referring to the light purple tint of the pileus surface and white stipe.

**Habitat and distribution.** – In small groups on soil in tropical evergreen mixed forests. Known from Vietnam.

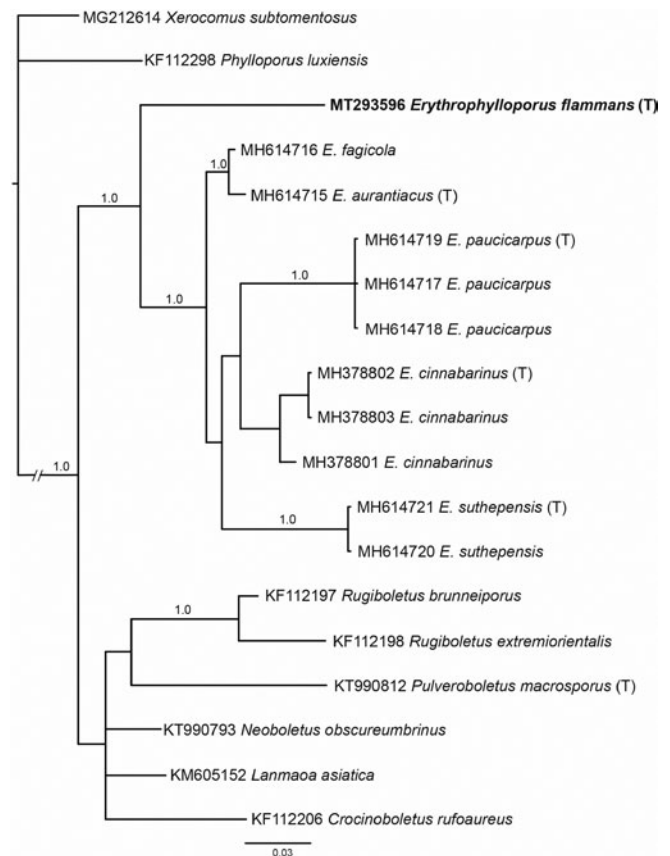
**Notes.** – *Entoloma porphyroleucum* is a remarkable species with purplish-brown, radially fibrillose pileus and white stipe. In spite of the absence of typical lecithiform cheilocystidia, it is placed in the *Trichopilus* clade based on molecular phylogenetic data (Fig. 8). *Entoloma porphyroleucum* resembles *E. porphyrescens* based on its pileus color, the presence of small basidiospores, and the two types of cheilocystidia (Horak 1973). However, *E. porphyrescens* can be differentiated from the new species by the colored stem the predominantly lecithiform cheilocystidia. In addition, the geographical distribution and habitat of these two species are completely different. *Entoloma porphyrescens* was described from New Zealand from *Nothofagus–Dacrydium–Podocarpus* forests; it also frequently occurs in Tasmania in wet *Eucalyptus* and *Nothofagus* forests (Noordeloos & Gates 2012). Finally, the new species distinctly differs from the European *E. porphyrophaeum* (Fr.) P. Karst. by its white stipe, small basidiospores, and the absence of lecithiform cheilocystidia (Noordeloos 1992).

**Authors:** O.V. Morozova, M.E. Noordeloos & B. Dima

### Basidiomycota, Agaricomycetes, Boletales, Boletaceae

***Erythrophyllporus flammans*** O.V. Morozova, T.H.G. Pham & E.S. Popov, **sp. nov.** – Fig. 11  
Mycobank no.: MB 835244

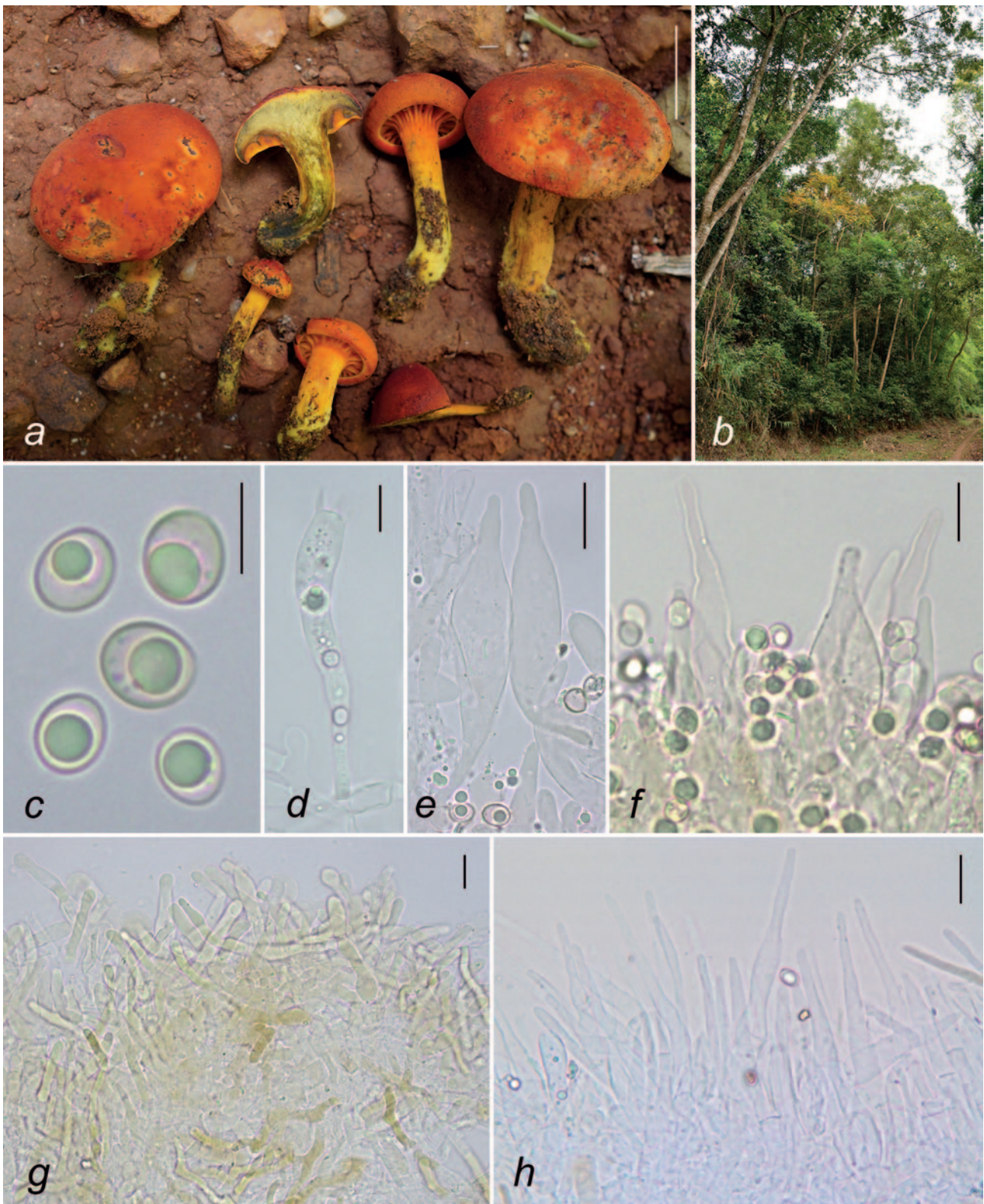
**Holotypus.** – VIETNAM. Binh Phuoc Province, Bu Gia Map District, Bu Gia Map National Park, environs of ranger station 2, along road to Bu Gia Map, 12°11'31.3"N,



**Fig. 11.** *Erythrophyllporus flammans*, collection LE 312491 (holotype). **a.** Basidiomata *in situ*. **b.** Type locality: Vietnam, Bu Gia Map National Park, the road in a tropical evergreen mixed forest. **c.** Basidiospores. **d.** Basidium. **e.** Pleurocystidia. **f.** Cheilocystidia. **g.** Pileipellis. **h.** Caulocystidia. Scale bars a 1 cm, c–h 10 µm.

107°12'16.2"E, 540 m a.s.l., on soil in semi-evergreen tropical forests with Fagaceae (*Lithocarpus* spp.) and Dipterocarpaceae, 30 November 2018, leg. O. Morozova & E. Popov (LE 312491; holotype). Sequences ex-holotype: MT298114 (ITS), MT293596 (tef1).

**Description.** – Basidiomata small to medium sized, fleshy. – Pileus 15–35 mm diam, initially hemispherical, becoming convex to applanate, with incurved margin at first, reddish orange, flame red (7A7–8, 7B8, 8A7–8, 8B8), surface dry, velutinose, tomentose or felted, minutely scaled. – Lamellae decurrent, subdistant, thick, up to 4 mm broad, salmon, deep orange, pastel red, reddish orange (6A4–8, 7A5–7, 8A5–7). – Stipe 15–30 × 6–8 mm, almost cylindrical, sometimes curved, solid; reddish orange to yellowish red (6A7, 8A7) at apex, orange to vivid yellow at base (up to 3A6–8), punctated with orange, reddish orange to orange red dots; with yellow (2A5–7) basal mycelium. – Context light to vivid yellow (3A7–8, 4A7–8),



**Fig. 12.** Phylogeny of *Erythrophylloporus* isolates reconstructed from a *tef1* dataset. The topology is the result of Bayesian inference performed with MrBayes. For each node, the BI PP (if >0.95) is presented above the branch leading to that node. The scale bar represents the number of nucleotide changes per site.

reddish orange under the surface, turning dark blue to blackish blue. Smell weak, taste mild. – **B a s i d i o s p o r e s**  $6.2\text{--}8.2 \times 5\text{--}6.5 \mu\text{m}$ , average  $7 \times 5.7$ ,  $Q=1.1\text{--}1.3$ ,  $Q_{av}=1.2$ , broadly ellipsoid, to ovoid, smooth, thin walled, yellowish to yellowish brown in KOH, with a large oil drop, inamyloid. – **B a s i d i a**  $41\text{--}58 \times 7.8\text{--}10.4 \mu\text{m}$ , 2–4-spored, subcylindrical to narrowly clavate, clampless. – **L a m e l l a** edge heterogeneous with scattered cheilocystidia. – **C h e i l o c y s t i d i a**  $50\text{--}105 \times 8\text{--}18 \mu\text{m}$ , fusiform or lageniform, thin walled, colorless. – **P l e u r o c y s t i d i a**  $50\text{--}115 \times 7.5\text{--}15 \mu\text{m}$ , originating in subhymenium and hymenophoral trama, broadly fusiform or lageniform, sometimes septate, thin walled, colorless or containing yellowish-brown to brown in KOH pigments. – **H y m e n o p h o r a l t r a m a** subparallel, slightly divergent. – **P i l e i p e l l i s** a trichoderm made up of palisade of interwoven cylindrical cells  $4\text{--}8 \mu\text{m}$  broad, with terminal cells  $33\text{--}66 \times 5\text{--}11 \mu\text{m}$ , cylindrical to narrowly lageniform or capitate with slightly thickened walls and brownish yellow in KOH intracellular pigment. – **S t i p i t i p e l l i s** a caulohymenium in upper part, then trichoderm with abundant caulocystidia, up to  $100 \mu\text{m}$  thick. – **C a u l o c y s t i d i a**  $55\text{--}100 \times 6\text{--}11 \mu\text{m}$ , narrowly conical, narrowly fusiform or lageniform, with slightly thickened walls and brownish yellow in KOH intracellular pigment, or hyaline. – **C l a m p c o n n e c t i o n s** absent.

**E t y m o l o g y.** – Referring to the bright reddish orange color of the basidiomata, like a flame, ‘*flam-mans*’ (Latin) – flaming.

**H a b i t a t a n d d i s t r i b u t i o n.** – Solitary or in groups on naked soil in semi-evergreen tropical forests with Fagaceae (*Lithocarpus* spp.) and Dipterocarpaceae of Vietnam.

**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.** – VIETNAM. Binh Phuoc Province, Bu Gia Map District, Bu Gia Map National Park, environs of ranger station 2, path to Dak Ca River,  $12^{\circ}12'3.9''\text{N}$ ,  $107^{\circ}12'15.6''\text{E}$ , 420 m a.s.l., 22 May 2011, *leg.* O. Morozova (LE 312521); *Ibid.*, along road to Bu Gia Map,  $12^{\circ}11'31.3''\text{N}$ ,  $107^{\circ}12'16.2''\text{E}$ , 540 m a.s.l., 25 November 2017, *leg.* E. Popov (LE 312492).

**N o t e s.** – Genus *Erythrophyllporus* Ming Zhang & T.H. Li, the lamellate representative of Boletaceae, was recently described from China with *E. cinnabarinus* Ming Zhang & T.H. Li as the type species (Zhang & Li 2018). *Erythrophyllporus* is nested within the *Pulveroboletus*-group-clade and is very distant from the morphologically similar *Phylloporus* (subfamily Xerocomoideae), although both possess lamellae. *Erythrophyllporus flammans* is a typical representative of the genus, characterized by the lamellate hymenophore, the intense reddish

orange color of the pileus and lamellae, bright yellow basal mycelium, ovoid, ellipsoid to broadly ellipsoid basidiospores with non-bacillate surface, and pleurocystidia originating from the subhymenium or from hymenophoral trama (Zhang & Li 2018, Vadthanarat et al. 2019). Since the vast majority of sequence data available for *Erythrophyllporus* are *tef1*, we performed a phylogenetic analysis based on this single gene. According to our *tef1* sequence data, our species is rather distant from other representatives of the genus (p-distance 12–17 %), but it forms a monophyletic clade with them with maximum support (Fig. 12). Morphologically it differs from *E. paucicarpus* Raspé, Vadthanarat & Lumyong by bluing context (vs. reddening), from *E. suthepensis* Vadthanarat, Raspé & Lumyong by its larger basidiospores ( $6\text{--}8 \times 5\text{--}6.5 \mu\text{m}$  vs.  $4.5\text{--}6 \times 3.5\text{--}4.5 \mu\text{m}$ ), and from *E. cinnabarinus* Ming Zhang & T.H. Li by the absence of yellowish brown pigments in cheilocystidia, and slightly larger ( $6\text{--}8 \times 5\text{--}6.5 \mu\text{m}$  vs.  $5.5\text{--}7 \times 4.5\text{--}5.5 \mu\text{m}$ ) and more ovoid basidiospores ( $Q_{av}=1.2$  vs. 1.3). The description of *Phylloporus coccineus* Corner from Singapore (Corner 1970) also corresponds to an *Erythrophyllporus* species as evidenced by the crimson to scarlet lamellate basidiomata with orange to orange-red lamellae and yellow basal mycelium, and broadly ellipsoid to subglobose smooth basidiospores, which are larger ( $7.5\text{--}10 \times 6.5\text{--}8 \mu\text{m}$ ) compared to *E. flammans*.

**A u t h o r s:** O.V. Morozova, P.T.H. Giang & E.S. Popov

## Basidiomycota, Agaricomycetes, Agaricales, Omphalotaceae

***Marasmiellus boreoorientalis* Kiyashko, sp. nov.** – Figs. 13–16

Mycobank no.: MB 833087

**H o l o t y p u s.** – RUSSIAN FEDERATION. Kamchatka Territory, Yelizovo District, Nature Park “Volcanoes of Kamchatka”, special protected area “Nalychevo Nature Park”, W-foothills of Avachinskaya Sopka volcano, thicket of *Alnus alnobetula* subsp. *fruticosa* (Fagales, Betulaceae), on alder litter,  $53^{\circ}15'39.5''\text{N}$ ,  $158^{\circ}44'35.7''\text{E}$ , 906 m a.s.l., 24 August 2017, *leg.* N.V. Psurtseva (LE 323323; holotype). Sequences ex-holotype: MN597452 (ITS), MN597444 (LSU).

**D e s c r i p t i o n.** – Basidiomata small, marasmioid or micromphaloid. – Pileus up to 20 mm, applanate with straight, deflexed or reflexed margin, sometimes with shallow central depression, radially grooved, occasionally slightly rugulose at center, finely innately fibrillose to subsquamulose, hygrophanous, sudan brown (6D8) to burnt sienna (7D8) or henna (7E8) at central disc, not fading with

age, brighten to brownish yellow (5C8) or greyish orange (5B4) towards the margin especially along grooves, margin whitish, becoming wavy and crenulate with age. – Lamellae narrowly adnate, rather distant, L=16–19, with numerous lamellulae, ventricose, slightly thickened, whitish, light brown (7D4–5) spotted when old, edge concolourous, sometimes slightly eroded. – Stipe 18–26 × 1–1.5 mm, usually cylindrical but sometimes flattened and with longitudinal groove, tapering towards the base, flexible when moist, tough when dry, brown (7E8) or reddish brown (8E8), more or less evenly coloured or darkening to very dark brown (8F5–3) towards the base, with distinct velutinous hyaline vestiture sometimes weakly developed in the middle part, hairy-tomentose at the base, hairs dark brown. – Context very thin, concolourous with surface, odour and taste not observed. – Basidiospores (6.6–)7.1–9.0(–12.7) × 3.4–4.8(–7.3) μm, average 8.6±1.2 × 4.3±0.7 μm, Q=1.6–2.4, Q<sub>av</sub>=2.0±0.6, varying in shape and size, ellipsoid to lacrymoid or subfusoid in face view, sometimes with broad apiculus, with several drops, thin-walled, smooth, inamyloid. – Basidia 19.8–33.3 × 4.9–6.9 μm, clamped, narrowly clavate to subcapitate, (2)4-spored, occasionally with very large sterigmata (up to 10 μm), with drops, which are sometimes yellowish. – Basidioles 15.3–30.4 × 3.0–6.2 μm, cylindrical, subclavate or with slightly restricted apex. – Cheilocystidia abundant, 14.8–50.5 × 8.2–20.5 μm, broadly clavate to pyriform or spheropedunculate, sometimes with small constrictions or septate, frequently with thickened up to 1 μm brownish walls. – Pleurocystidia absent or inconspicuous. – Pileipellis composed of radially oriented, rarely branched, cylindrical or inflated hyphae lacking diverticulate branchlets, (2.8–)4.8–15.8(–18.1) μm diam., often with thickened walls, pigmented, roughly encrusted, encrustation brownish, spiral, zebroid to irregular, sometimes with solid calluses in profile, terminal cells clavate or broadly fusiform, more rarely tapering, (12.6–)30.5–94.7 × (6.0–)8.3–18.2(–21.2) μm. – Stipitipellis a cutis composed of cylindrical, thick-walled, pigmented cells (1.9–)2.5–7.6(–8.5) μm in diam., hyphae smooth or encrusted as in pileipellis, sometimes producing roughly encrusted clavate terminal cells. – Caulocystidia abundant, (18.8–)37.2–87.7 × 7.6–13.7 μm, arising as side branches of surface hypha or as differentiated terminal cells, thick-walled (up to 1.5 μm), brownish pigmented, more or less cylindrical, flexuous or utriform on long thin stalk. – Clamp connections present in all tissues.



Fig. 13. Basidiomata of *Marasmiellus boreoorientalis* in the field, collection LE 323323 (holotype). Scale bar 10 mm.

Culture characteristics. – Mean growth rate 2.7 mm/day on BWA and MEA, 2.3 mm/day on PDA, plates covered in 16 days in BWA and MEA, in 18 days on PDA. – Macromorphology of colonies depending on cultural media, but outlines even and marginal hyphae appressed on all media. – Colony mat thick woolly-cottony on BWA, thin appressed woolly-filamentous with radially ordered hyphae on MEA and PDA, vaguely zonate with tendency to develop brownish-ochraceous pigmentation, on BWA with concentric bands of

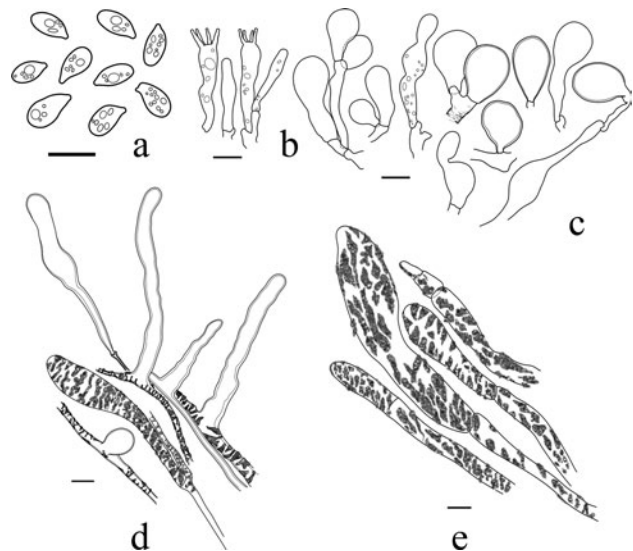


Fig. 14. Microstructures of *Marasmiellus boreoorientalis*. a. Basidiospores. b. Basidia and basidioles. c. Cheilocystidia. d. Caulocystidia and encrusted hyphae with terminal stipitipellis cells. e. Hyphae of pileipellis. Scale bars 10 μm.

thick dense mycelium with pigmented parts, on MEA and PDA with dense center and very thin, transparent mycelial mat at the colony periphery, on MEA with whitish woolly-powdery zone ca. 35 mm around inoculum and small brownish-ochraceous spots at the periphery, on PDA also with pigmented crust ca. 10 mm around inoculum, reverse bleached on all media, on MEA and PDA with brown spots (especially on PDA). – Smell weak, undefinable. – Oxidoreductases test negative. – Micromorphology not so strongly depending on cultural media as micromorphology; clamps on all hyphae, simple, slightly compressed, sometimes sprouting, on BWA aerial hyphae 2.0–2.5 µm

Notes. – The generic limits and relationships of the two largest genera of Omphalotaceae, *Marasmiellus* Murrill and *Gymnopus* (Pers.) Roussel, along with *Micromphale* Gray, have been discussed for a long time (Mata et al. 2004b, Wilson & Desjardin 2005, Mešić et al. 2011, Petersen & Hughes 2016, Sesli et al. 2018, Oliveira et al. 2019). Most studies recognized the polyphyletic nature of *Gymnopus* s.l. as well as the unstable concept of both *Marasmiellus* and *Micromphale*. Oliveira et al. (2019) carried out a taxonomical revision of *Gymnopus*, *Marasmiellus*, and *Micromphale* on the basis of ITS and combined ITS–LSU phylogenetic analyses. The authors transferred species of *Gymnopus* sect. *Vesti-*

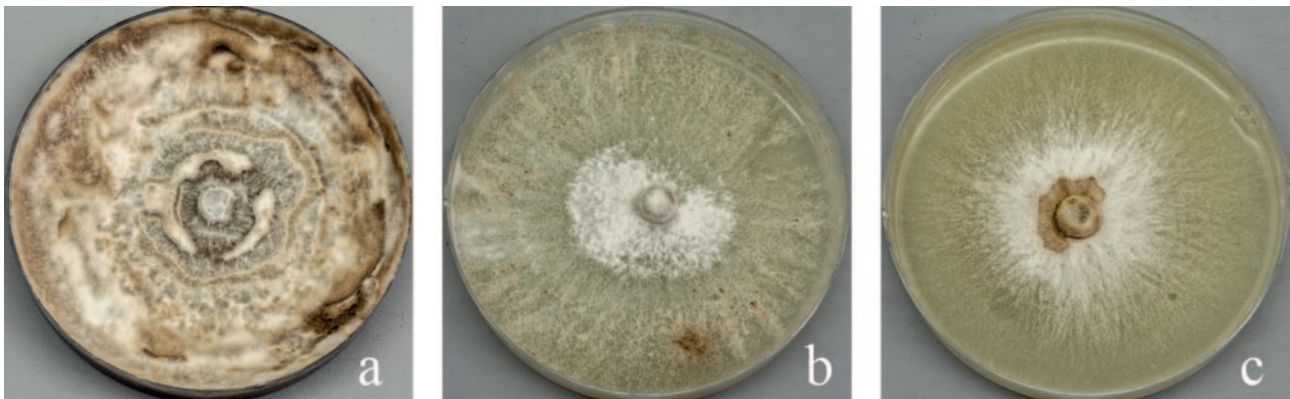


Fig. 15. Pure cultures of *Marasmiellus boreoorientalis* in 90-mm Petri dishes, after 8 weeks of growth. **a.** Culture on BWA. **b.** Culture on MEA. **c.** Culture on PDA.

diam., usually rarely septate and branched, sometimes with slightly thickened walls, substrate hyphae 2.0–5.0 µm diam., more often septate and brush-like branched with short irregular branches, on MEA and PDA aerial and substrate mycelia do not clearly separate from each other and look like substrate mycelia on BWA, but on PDA hyphae more vacuolated; crust is formed from hyphae 2.0–2.5 µm in diam. with slightly thickened and pigmented walls, short-celled and abundantly branched; everywhere on all media hyphae form round to irregular shaped swellings up to 12 µm in diam. with short cylindrical outgrowths, usually intercalary, rarely in terminal position; also on all media clusters of brownish crystals are found.

**Etymology.** – *boreoorientalis*—meaning “north-eastern”—indicating the geographical location of the holotype, northeastern Russia.

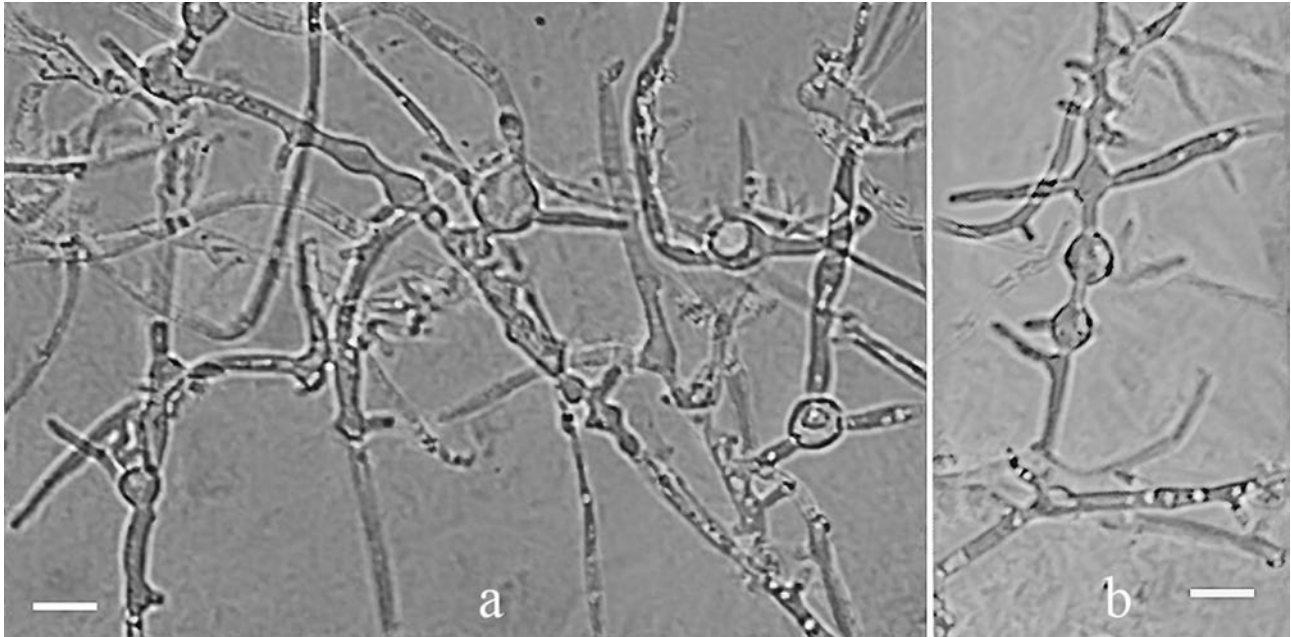
**Habitat and distribution.**—On alder litter (*Alnus alnobetula* subsp. *fruticosa*). Only known from the type locality in the foothills of Avachinskaya Sopka volcano, eastern Kamchatka, Russia.

*pedes* to *Marasmiellus* and described a new genus *Paragymnopus* J.S. Oliveira to accommodate members of *Micromphale* sect. *Perforantia*. To clarify the phylogenetic position of the new species *Marasmiellus boreoorientalis*, we conducted BI and ML analyses of ITS sequences, resulting in two trees with the same topology (Fig. 17). Our phylogenetic analyses revealed two strongly supported major clades that correspond well to *Gymnopus* sensu stricto (s.s.) and *Marasmiellus*, and a third sister clade corresponds to *Paragymnopus* (sensu Oliveira et al. 2019). The *Marasmiellus* clade consists of several lineages; *M. boreoorientalis* is nested in a strongly supported subclade with *M. dichrous* (Berk. & M.A. Curtis) J.S. Oliveira, *M. istanbulensis* E. Sesli, Antonín & E. Aytaç, *M. micromphaloides* (R.H. Petersen & K.W. Hughes) J.S. Oliveira, and one uncultured specimen that may represent an undescribed taxon. Our new species is clearly distant from the rest of members of the subclade. The ITS sequence of *M. boreoorientalis* shares 89.53–91.97 % identity (query cover 95–100 %) with sequences of *M. di-*

chrous, 91.51 % (query cover 78 %) with *M. istanbulensis*, and 89.3 % (query cover 85 %) with *M. micromphaloides*.

In the field, *M. boreoorientalis* may resemble *Paragymnopus foliophilus* (R.H. Petersen) J.S. Oliveira and *P. perforans* (Hoffm.) J.S. Oliveira, both occurring on litter, because of their rather small fruitbodies with appanate radially grooved pileus and vested dark brown stipes. The new species

base with a tuberculate knob, somewhat larger basidiospores, and diverticulate branchlets on pileipellis hyphae. *Marasmiellus dichrous* also grows more slowly (mean growth rate on BWA 1.9 mm/day, on MEA 1.5 mm/day, on PDA 1.4 mm/day) and possesses clear differences in colony morphology on all media (an appressed to submerged uneven advancing zone, thinner and more pigmented mat with a stronger developed crust, unbleached



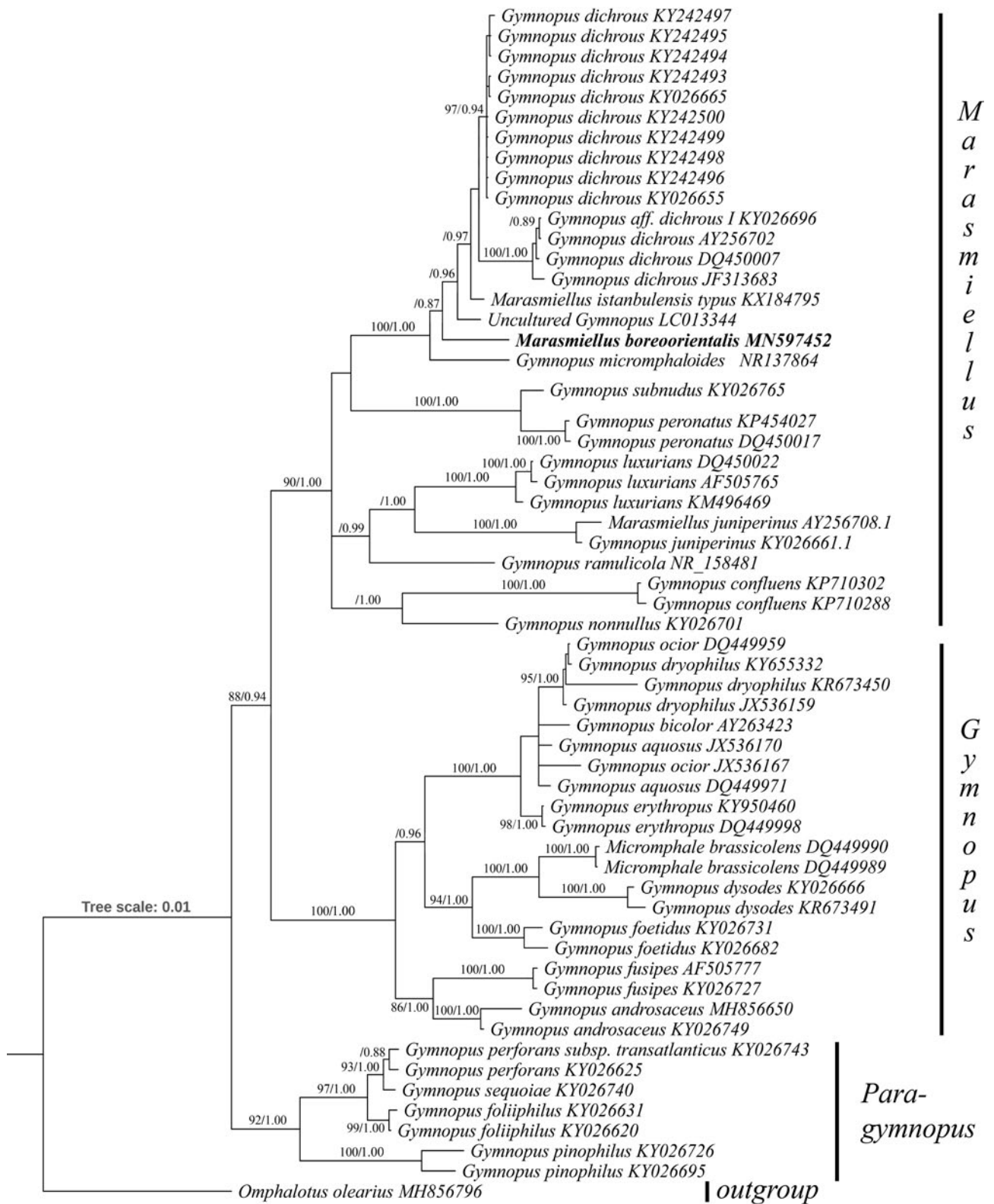
**Fig. 16.** *Marasmiellus boreoorientalis* on PDA, after 8 weeks of growth. **a–b.** Characteristic swellings of vegetative hyphae of *Marasmiellus boreoorientalis*. Scale bars 10  $\mu$ m.

can be distinguished from those species by the absence of a mucoid matrix in its pileipellis. In addition, *M. boreoorientalis* combines a number of other characteristic features: a brighter and contrastingly colored pileus lacking pinkish tints, slightly larger basidiospores compared to *P. foliophilus* and *P. perforans*, numerous well-developed cheilocystidia often with thickened brownish walls, roughly encrusted hyphae of pileipellis sometimes having ventricose terminal cells, absence of pileal hairs, its habitat on alder litter. Finally, *M. boreoorientalis* is phylogenetically very distantly related to both *P. foliophilus* and *P. perforans* (Fig. 17).

Among phylogenetically close species, *M. dichrous* is more robust and inhabits dead wood of broadleaved trees, mainly *Fagus*. Further, it differs from *M. boreoorientalis* in having a dark brown to reddish brown pileus eventually fading to light reddish-brown or clay overall, an olive brown stipe

cultural media, and the absence of swellings with outgrowths). The new species is distinguished from *M. micromphaloides* by its contrastingly colored cap with orange-brown center and whitish margin; distinctly larger basidiospores; broader cheilocystidia; the absence of pileocystidia; and straight, non-branched caulocystidia. *Marasmiellus istanbulensis* differs from *M. boreoorientalis* by paler colored basidiomata, shorter basidiospores with  $Q_{av}=1.7$ , smooth stipitipellis hyphae, and caespitose growth on bark of dead *Quercus petraea* wood (Fagales, Fagaceae).

The type locality is situated at the western foothills of Avachinskaya Sopka, an active stratovolcano. The last large eruption occurred in 1945, at which time volcanic ashes fell on a distance of 400 km from the crater. The total volume of andesite–basalt explosion material was about 0.3 km<sup>3</sup> (Melekescev et al. 1994). The vegetation was de-



**Fig. 17.** Phylogeny placement of *Marasmiellus boreoorientalis* inferred from an ITS dataset. The topology is the result of Bayesian inference performed in MrBayes. For each node, support values (MLBS<sup>3</sup>85/BIPP $\geq$ 0.85) are presented above the branch leading to that node. The new species is highlighted in boldface.



stroyed over an area of ca. 200 km<sup>2</sup> (Grishin 2003). As a result, the contemporary landscapes of this territory are relatively young. The eastern volcanic region of Kamchatka is characterized by a rather poor and uniform vegetation. The upper limit of the forest belt (600–900 m a.s.l.) is composed of monodominant thickets of *Alnus alnobetula* subsp. *fruticosa* and *Pinus pumila* (Pinales, Pinaceae), which do not form intermixed forest stands. This allows us to presume a wider distribution of *M. boreorientalis*, at least in Kamchatka. It can be also expected that this species will be found in the continental part of the Russian Far East and, perhaps, in the mountains of Japan.

*Authors:* A.A. Kiyashko & N.V. Psurtseva

### Basidiomycota, Agaricomycetes, Agaricales, Omphalotaceae

*Marasmiellus longistipes* Muh. Ali, Niazi & Khalid, **sp. nov.** – Figs. 18–19

MycoBank no.: MB 831702

*Holotypus.* – PAKISTAN. Khyber Pakhtunkhwa Province, Abbottabad District, Ayubia National Park, 33°51'54.83"N, 73°8'19.57"E, 2400 m a.s.l., 15 July 2016, leg. M. Ali & A.R. Niazi, KH 55 (LAH 35979; holotype). Sequences ex-holotype: MK957247 (ITS).

*Description.* – *Pileus* 18–30 mm in diam., convex or plano-convex, membranous, slightly umbonate, striated, glabrous, creamy (10YR/9) in center with grayish tinge becoming light (2.5Y9/2) towards margin, delicate; margin slightly wavy, uplifted, entire becomes ruptured at maturity; context thin, creamy, 0.5–1.0 mm thick. – *Lamellae* adnexed, entire, thorough, white (2.5R9/2) at early stage, while pale white (2.5YR8/4) when mature. – *Stipe* 70–105 × 3–5 mm, central, equal to sub-equal towards base, non-striated, light brown (10R4/4) towards apex to dark brown (2.5YR3/4) towards base, and entirely pubescent. – *Basidiospores* (6.0–)6.5–9.0(–9.5) × (2.0–)3.0–3.5(–4.0) μm, Q=2.0–3.5, Q<sub>av</sub>=2.6, oblong or narrowly fusiform apiculate, guttulate, smooth, thin-walled, inamyloid, hyaline in 5 % KOH. – *Basidia* 15–21.5 × 5.6–7.2 μm, narrowly clavate, bisporic to tetrasporic, thin-walled, hyaline in 5 % KOH. – *Pleurocystidia* absent. – *Cheilocystidia* 21–28 × 5.5–7.0 μm, hyaline and thin-walled, variously shaped, forked, contorted, fusoid or flexuose. – *Basidioles* 15–22 × 3–6 μm, subclavate to clavate, abundant, thin-walled, hyaline in 5 % KOH. – *Pileipellis* a cutis of hyphae 4–7.5 μm in diam., cylindrical, branched, frequently septate, some slightly constricted at septa, broader hyphae more

constricted at septa, hyaline, terminal elements with rounded ends, clamp connections present. – *Stipitipellis* hyphae 3.5–5.0 μm in diam., cylindrical, parallel, thin-walled and hyaline, septate, clamp connections present, terminal elements narrowly rounded. – *Caulocystidia* 3.0–5.5 μm in diam., sub-cylindrical, slightly contorted, hyaline.

*Etymology.* – A combination of two Latin words, 'longus' (= long) and 'stipes' (= stipe), referring to the long stipe.

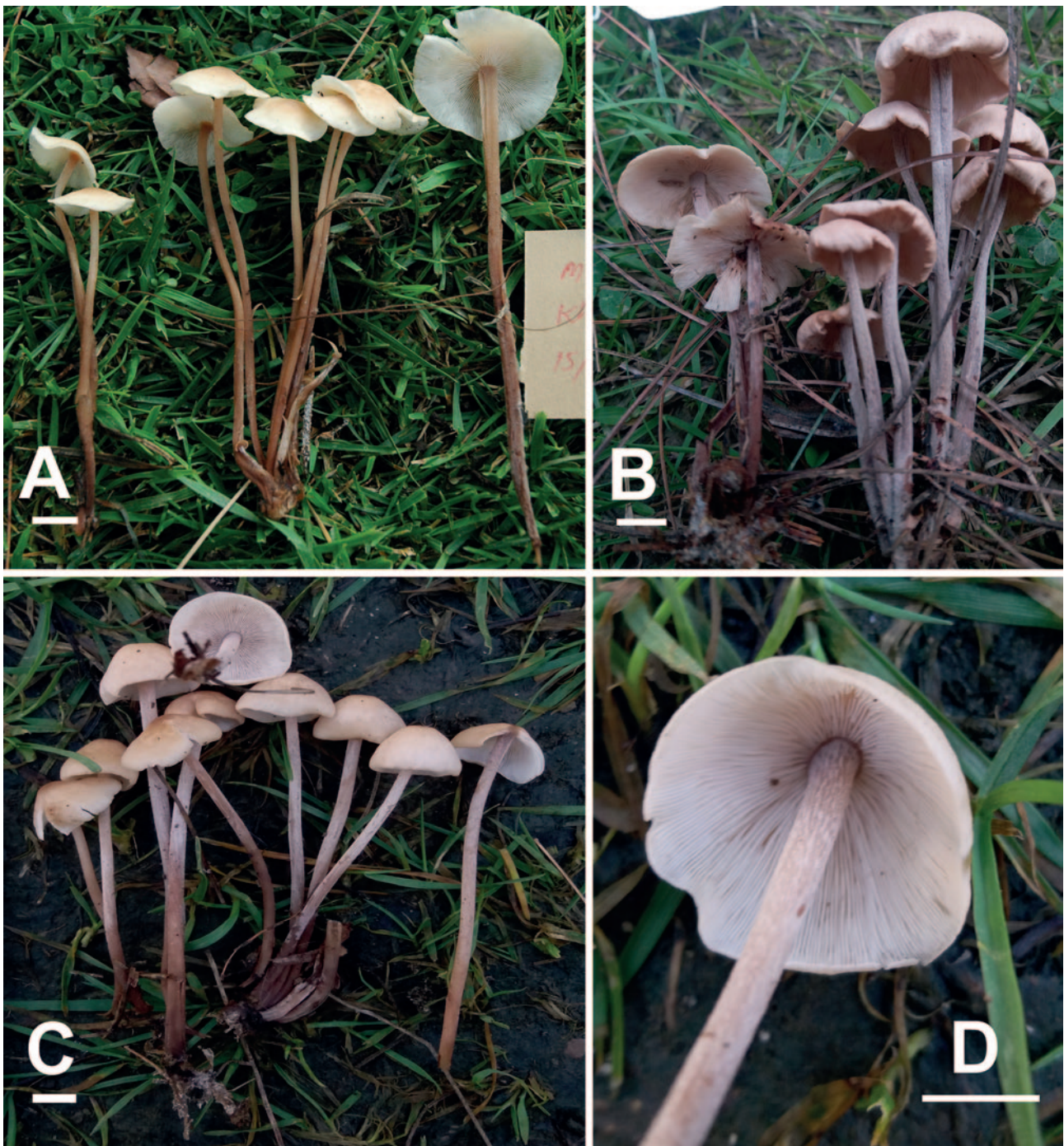
*Habitat and distribution.* – Growing in small bunches on woody litter in pine-dominated moist temperate forests of Pakistan.

*Additional material examined.* – *Ibid.*, 16 July 2017, leg. M. Ali & A.R. Niazi, KH 24A (LAH 35980); *Ibid.*, 12 August 2017, leg. M. Ali & A.R. Niazi, KH 369 (LAH 36411).

*Notes.* – Studies by Wilson & Desjardin (2005), Dutta et al. (2015), and Oliveira et al. (2019) focused on the phylogenetic placement of various “gymnoid”, “marasmoid”, and “marasmielloid” taxa (Agaricales). They considered *Marasmiellus* to represent a large group including type species of at least two genera (*Collybiopsis* Earle and *Marasmiellus*) and taxa belonging to *Gymnopus* sect. *Vestipedes*. In their phylogenetic reconstruction of a combined ITS–LSU dataset, Oliveira et al. (2019) retrieved support for several monophyletic genera: *Marasmiellus* s.s., *Pusillomyces* J.S. Oliveira, *Connopus* R.H. Petersen, “*Pallidocephalus*”, *Rhodocollybia* Singer, *Lentinula* Earle, *Gymnopus* s.s., *Paragymnopus*, *Gymnopanella* Sand.-Leiva, J.V. McDonald & Thorn, *Mycetinis* Earle, and *Omphalotus* Fayod.

The ITS sequences of our *Marasmiellus* collections KH55, KH24A, and KH369 shared 94 % identity with *Marasmiellus confluens* (Pers.) J.S. Oliveira (GenBank accession nos. KJ817065, KP710289, KX513743) and *Marasmiellus stevensoniae* (E. Horak) J.S. Oliveira (DQ450034, HQ533036, KJ416244). The aligned ITS dataset consisted of 68 sequences (Tab. 1), including 57 ingroup taxa representing 30 species of *Marasmiellus*, in addition to eight species of *Gymnopus* and three species of *Omphalotus* as outgroup (Moncalvo et al. 2002, Mata et al. 2004b, Saba & Khalid 2014). The resulting ITS tree (Fig. 20) shows that collections KH55, KH24A, and KH369 are retrieved in /Clade A sensu Oliveira et al. (2019). This clade contains the type species, *M. juniperinus* Murrill, and thus corresponds to *Marasmiellus* s.s. Our Pakistani collections form a separate monophyletic branch with maximum support, close to *M. confluens* and *M. stevensoniae*.

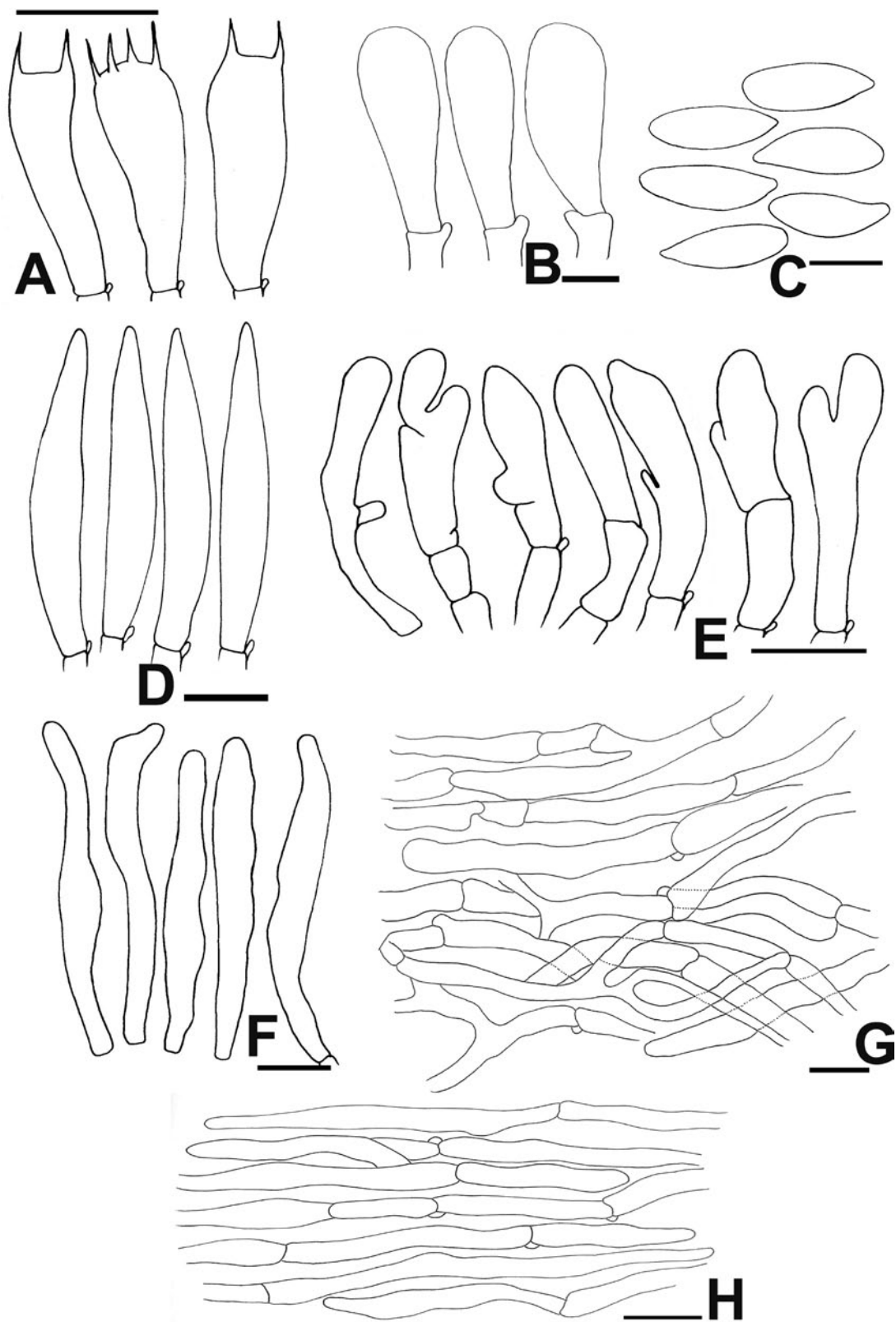
Our new species *M. longistipes* can be differentiated from these two species by several morphological characters. *Marasmiellus confluens* (Hughes &



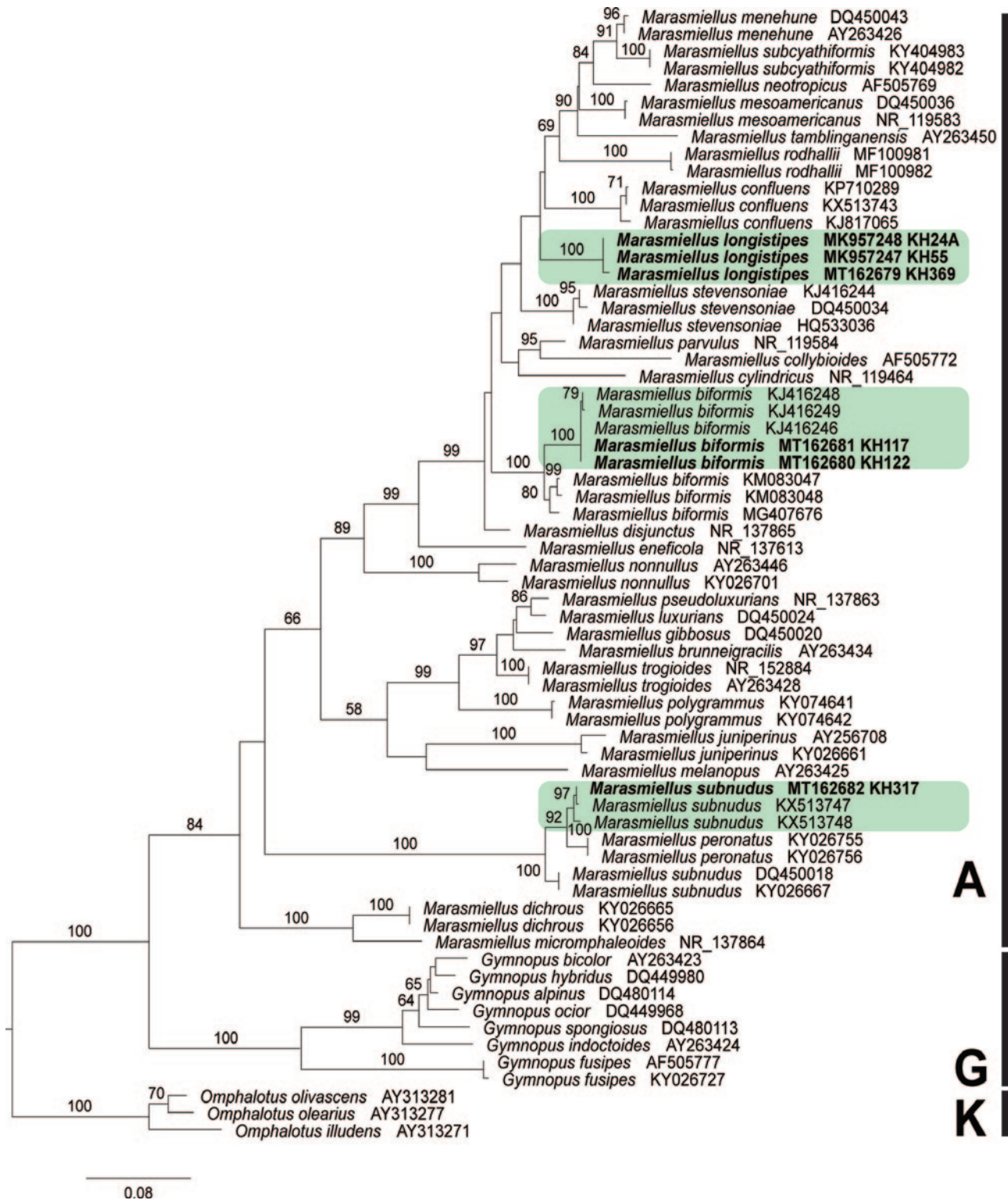
**Fig. 18.** *Marasmiellus longistipes*, basidiomata *in situ*. **A.** Collection LAH 35979 (holotype). **B.** Collection LAH 35980. **C–D.** Collection LAH 36411. Scale bars A–D 1 cm.

Peterson 2015) is different from *M. longistipes* in having a red-brown to dark red-brown pileus; a stipe that is pale or brown, orange-brown, sometimes even with a purplish tinge; slightly lacrymoid to ellipsoid or subfusoid basidiospores; and more

elongate cheilocystidia ( $27.5\text{--}70 \times 2.8\text{--}5.6 \mu\text{m}$  vs.  $21\text{--}28 \times 5.5\text{--}7.0 \mu\text{m}$  in *M. longistipes*) with different shapes, including irregularly clavate, cylindrical, and strangulated (Halling 1983, Antonín & Noordeloos 1997, Kerekes & Desjardin 2009, Deng



**Fig. 19.** Microstructures of *Marasmiellus longistipes*. **A.** Basidia. **B.** Basidiospores. **C.** Basidioles. **D, E.** Cheilocystidia. **F.** Caulocystidia. **G.** Pileipellis. **H.** Stipitipellis. Scale bars A, D–H 10  $\mu$ m; B–C 5  $\mu$ m; *del.* M. Ali.



**Fig. 20.** Phylogeny of *Marasmiellus* species reconstructed from a ITS dataset of 57 sequences. The topology is the result of ML inference performed in RAxML. For each node, the MLBS  $\geq 50$  is shown above the branch leading to that node. Species collected in this study are highlighted in green; newly generated sequences are highlighted in boldface; ex-type sequences are denoted with "T". Clade designations are sensu Oliveira et al. (2019): /Clade A, *Marasmiellus* sensu stricto; /Clade G, *Gymnopus* sensu stricto; /Clade K, *Omphalotus*.

et al. 2016). *Marasmiellus stevensoniae* is separated by its reddish-brown pileus; light to dark brown stipe; ellipsoid basidiospores; and longer and broader cheilocystidia (22–40 × 6.5–10 µm) that are also variable in shape from clavate to lageniform or ventricose (Kerekes & Desjardin 2009). In terms of sequence divergence, there are 30 nucleotide polymorphisms in the ITS among sequences of *M. confluens* and *M. longistipes*; similarly, there are 27 nucleotide polymorphisms among ITS sequences of *M. longistipes* and *M. stevensoniae*.

During our phylogenetic study of *Marasmiellus*, we came across one species of *Gymnopus* that is part of /Clade A as per Oliveira et al. (2019) and thus needs to be combined in *Marasmiellus*:

***Marasmiellus rodhallii*** (Desjardin & B.A. Perry) Muh. Ali, Niazi & Khalid, **comb. nov.** MycoBank no.: MB 837377.

**Basionym.** – *Gymnopus rodhallii* Desjardin & B.A. Perry, *Mycosphere* 8(9): 1372 (2017).

**Authors:** M. Ali, H. Bashir, A.R. Niazi & A.N. Khalid

#### Ascomycota, Laboulbeniomyces, Laboulbeniales, Laboulbeniaceae

***Pseudozeugandromyces*** De Kesel & Haelew., **gen nov.**

MycoBank no.: MB 835916

**Etymology.** – *Pseudo-* from Greek, referring to the morphological similarities to *Zeugandromyces*.

**Description.** – Receptacle axis composed of three superposed cells (I, II, III); cell II higher than broad, pentagonal, apically supporting cells III and VI. – Primary appendage composed of a basal cell carrying two simple antheridial branches of superposed cells, each with a single intercalary antheridium. – Perithecium one per thallus, asymmetrical, gradually tapering upwards, with a broad and rounded apex.

**Type species.** – *Pseudozeugandromyces tachypori* De Kesel & Haelew.

***Pseudozeugandromyces tachypori*** De Kesel & Haelew., **sp. nov.** – Fig. 21  
MycoBank no.: MB 835915

**Holotypus.** – BELGIUM. West Flanders Province, Knokke-Heist, Nature reserve Het Zwin, on *Tachyporus pusillus* Gravenhorst, 1806 (Coleoptera, Staphylinidae, Tachyporinae, Tachyporini), ADK658 [host label], 17 July 1992, leg. G. Haeghebaert, slide BR5020212154341V (2 thalli from abdomen; holotype).

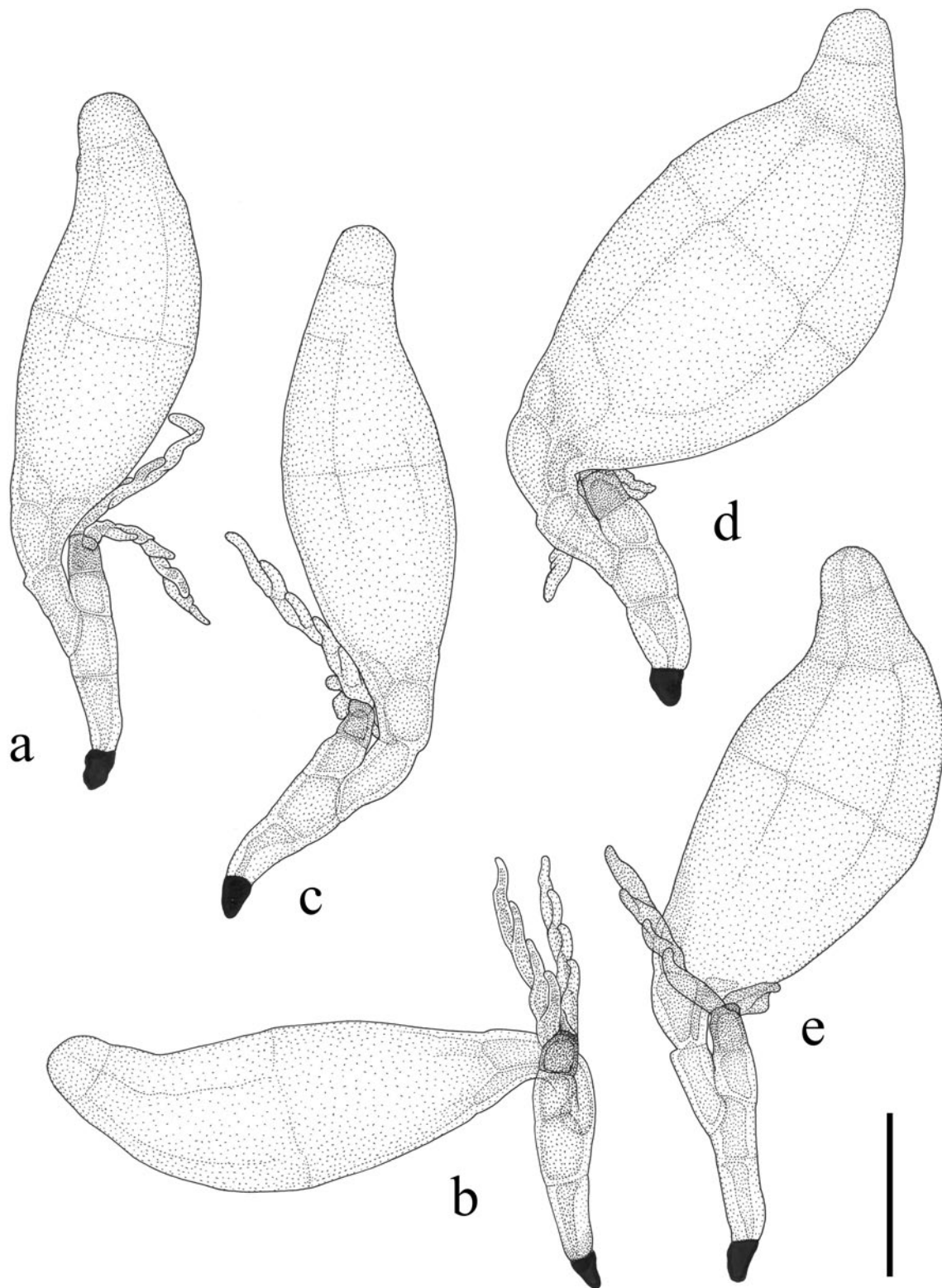
**Description.** – Thallus 229–290 µm, amber in color. – Receptacle 70–83 µm high, its axis composed of superposed cells I, II, and III. – Cell I 25–35 µm high, 2–3× higher than broad, widest above. – Cell II 25–35 µm high, up to 2× higher than broad, pentagonal, apically supporting cells III and VI. – Cell III 12–18 µm high, isodiametrical, apically carrying the primary appendage. – Primary appendage up to 80 µm long; composed of a single, dark basal cell of 9–10 × 8–10 µm, carrying two simple antheridial branches at the apex. – Antheridial branches simple, very thin, hyaline to amber, composed of a series of 4–6 single, intercalary antheridia with bent and laterally extending necks. – Cell VI 30–40 µm high, 2× higher than broad, free, apically supporting cells VII and m. – Cells VII and VI together measuring 50–80 µm high. – Cells VII and m of similar height, both higher than broad, laterally connected and frequently kinked in dorsal (posterior) direction. – Perithecium 135–173 × 55–88 µm, asymmetrical, with venter, widest in the middle, gradually tapering upwards, apex slightly curved in anterior direction, wall cells of unequal height; apex relatively broad and round, with very similar and poorly differentiated ostiolar lips. – Ascospores 42 × 5.0 µm.

**Etymology.** – Named after the host on which the fungus was found.

**Hosts and distribution.** – Thus far only known on *Tachyporus pusillus* in Belgium.

**Additional material examined.** – BELGIUM. West Flanders Province, Knokke-Heist, Nature reserve Het Zwin, on *Tachyporus pusillus*, ADK656 [host label], 19 June 1992, leg. G. Haeghebaert, slides BR5020212153313V (4 thalli from left protochanter) and BR5020212152286V (1 thallus from left procoxa); *Ibid.*, on *T. pusillus*, ADK1682 [host label], 12 April 1992, leg. G. Haeghebaert, slides BR5020212151258V (3 thalli from metathorax) and BR5020212150220V (3 thalli from metathorax).

**Notes.** – Since 2010, three new genera of Laboulbeniales have been described (Rossi & Santamaría 2012, Santamaría et al. 2017, Reboleira et al. 2018). These are *Opilionomyces* Santam., Enghoff, Gruber & Reboleira from harvestmen (Opiliones, Dicranolasmatidae), *Rodaucea* W. Rossi & Santam. from cholevine beetles (Coleoptera, Leiodidae), and *Thaxterimyces* Santam., Reboleira & Enghoff from millipedes (Chordeumatida, Metopidiotrichidae). Elsewhere in this paper, we reinstate *Appendiculina* Berl. and *Fanniomyces* T. Majewski, bringing the number of accepted genera in the order to 144. Here, we introduce another new genus, *Pseudozeugandromyces*, to accommodate a species



**Fig. 21.** *Pseudozeugandromyces tachypori* from *Tachyporus pusillus*. **a.** Mature thallus from abdomen, slide BR5020212154341V (holotype). **b.** Mature thallus from abdomen, slide BR5020212154341V (holotype). **c.** Mature thallus from left prothorax, slide BR5020212153313V. **d.** Mature thallus from left prothorax, slide BR5020212152286V. **e.** Mature thallus from metathorax, slide BR5020212151258V. Scale bar 50  $\mu\text{m}$ , del. A. De Kesel.

that we long thought of as a member of *Zeugandromyces* Thaxt. (De Kesel 1997).

Even though *P. tachypori* is morphologically very similar to *Zeugandromyces*, it is different in the following characteristics: cell II is higher than broad, the appendage is composed of two antheridial branches, and antheridia are not borne in pairs as typically in *Zeugandromyces*. In addition, the five species of *Zeugandromyces* have only been reported from hosts in the subfamily Paederinae (Coleoptera, Staphylinidae) (Tavares 1985, Rossi & Bernardi 2018). *Pseudozeugandromyces tachypori* is described from *Tachyporus pusillus*, a member of Tachyporinae (Staphylinidae). Interestingly, this subfamily is known to host a wide variety of Laboulbeniales with representatives from eight genera, including *Clonophoromyces* Thaxt., *Corethromyces* Thaxt., *Dimeromyces* Thaxt., *Dimorphomyces* Thaxt., *Misgomyces* Thaxt., *Rickia* Cavara, *Smeringomyces* Thaxt., *Stichomyces* Thaxt. (Frank 1982), and now also *Pseudozeugandromyces*. Of these, *Clonophoromyces*, *Smeringomyces*, and *Stichomyces* are known only from tachyporine hosts.

The morphologically closely related genus *Zeugandromyces* includes five described species. Species of *Zeugandromyces* are recognized by the following characteristics: cells I, II, and III are superposed; cell II is broader than high; cell III is much shorter than cell VI; cell VII and the perithecial basal cells are short; and sessile antheridia are borne in pairs on an unbranched primary appendage (Thaxter 1912, Tavares 1985). Currently, no sequences are available. *Zeugandromyces* species are found in North America, South America, southeastern and eastern Asia (Thaxter 1931, Sugiyama & Majewski 1985, Try et al. 2017, Rossi & Bernardi 2018).

The new species differs from taxa in *Zeugandromyces* (Thaxter 1931, Rossi & Bernardi 2018) by its two slender antheridial branches, non-flattened basal cells of the perithecium, and the conspicuously rounded perithecial apex (Fig. 21). Moreover, *P. tachypori* lacks deep black pigmentations and as a result can be easily separated from both *Z. pseudomedalis* (which has a pigmented cell II) and *Z. stilici* (Thaxt.) I.I. Tav. (which has a blackish basal cell of the receptaculum). The remaining species – *Z. assingii* W. Rossi & M. Bernardi, *Z. australis* Thaxt., and *Z. orientalis* (Thaxt.) I.I. Tav. – have more robust appendages and tapering perithecial necks with almost pointed apices.

The host of *P. tachypori*, *Tachyporus pusillus*, is a widely distributed species throughout Europe and

Asia, with a preference for managed habitats (Bohác et al. 2005, Sushko 2016). Although *T. pusillus* is eurytopic (Lohse 1964) and fairly common in Belgium (Segers 1986), infected specimens were obtained only in the transition zone between coastal sand dunes and saltmarshes. Thalli of *P. tachypori* were found on the procoxa and protrochanter, as well as on the abdomen and meso- and metathorax. Thalli on the abdomen of the insect usually have the receptacle closely appressed to the integument. However, due to a dorsal kink in cells VI, VII, and m, the perithecium is positioned perpendicularly with respect to the integument. In many cases, the antheridial branches are also perpendicular to the insect's integumental surface.

The new genus *Pseudozeugandromyces* is related to not only *Zeugandromyces* but also *Stigmatomyces* Thaxt. Tavares (1985) hypothesized that *Zeugandromyces* may be ancestral to *Stigmatomyces*. Molecular phylogenetic analyses are needed to determine the evolutionary relationships among these three closely related genera. Of those, only sequences have been generated for species of *Stigmatomyces* s.l. (Weir & Blackwell 2001a, 2001b; Weir & Hughes 2002; Goldmann & Weir 2018; Haelewaters et al. 2018b, 2019c). After a shelf life (*vide* Fontaine et al. 2012) of 28 years, we opted to formally describe the new taxon based on morphological data to make the data available to other researchers. In doing so, our hope is that fresh collections may be made to support future molecular work.

*Authors:* A. De Kesel & D. Haelewaters

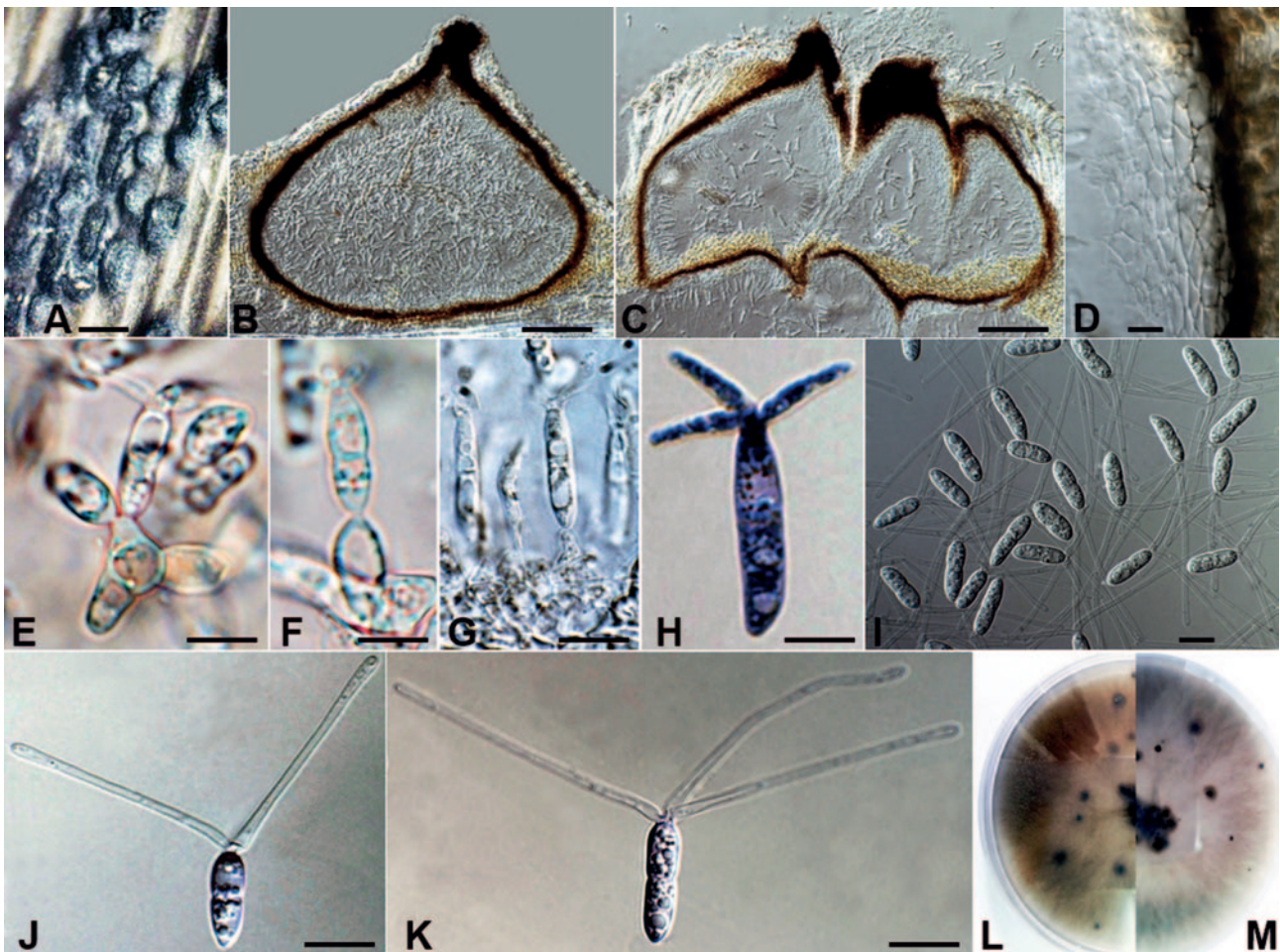
## Ascomycota, Sordariomycetes, Amphisphaeriales, Sporocadaceae

***Robillarda sohagensis*** Abdel-Wahab, Abul-Ezz & Bakhit, *sp. nov.* – Fig. 22  
Mycobank no.: MB 835007

*Diagnosis.* – Different from other species of *Robillarda* by its larger conidiomata (765–2025 × 270–495 µm), conidia (13–21 × 3–4 µm), and conidial appendages (26–41 µm).

*Holotypus.* – EGYPT. Sohag Governorate, Nile river, 26°33'53"N, 31°42'19"E, on decaying submerged leaves of *Phoenix dactylifera* (Arecales, Arecaceae), 28 January 2015, *leg.* S.R. Abul-Ezz (CBS H-23861; holotype). Sequences ex-holotype: MT160349 (ITS). Culture ex-holotype: deposited at the microbial culture collection of Sohag University, Egypt (SUMCC 2063).

*Description.* – Follicolous. – Sexual morph undetermined. – Asexual morph coelomycetous; conidiomatastromatic to pycnidoid, scattered to gregarious, occasionally confluent, erumpent to superficial, uni- or plurilocular with as many as three locules, ovoid, subglobose, elongated,



**Fig. 22.** *Robillarda sohagensis*, collection CBS H-23861 (holotype). **A.** Pycnidia on leaflet of *Phoenix dactylifera* (date palm). **B–C.** Vertical sections through pycnidia. **D.** Magnified part of the peridium. **E–G.** Conidiogenous cells attached to conidia. **H.** Young conidium, in toluidine blue. **I–K.** Conidia. **L–M.** Colony on CMA (front and reverse). **E–K.** Photos from culture. Scale bars A–C 100  $\mu\text{m}$ , D–K 10  $\mu\text{m}$ .

765–2025  $\times$  270–495  $\mu\text{m}$ , average 1194  $\times$  402  $\mu\text{m}$  (n=30), dark brown to black; dehiscing by split in the apical wall. – **Peridium** 21–60  $\mu\text{m}$  thick, generally thicker at the upper part of the pycnidia than the lower part, forming *textura angularis*, two-layered; outer layer 5–28  $\mu\text{m}$  thick, consisting of thick-walled, brown to dark-brown cells; inner layer 12–32  $\mu\text{m}$  thick, consisting of thin-walled, hyaline, polygonal to flattened cells. – **Conidiophores** reduced to conidiogenous cells lining the cavity of the conidioma. – **Conidiogenous cells** ampulliform, hyaline, aseptate, smooth, thin-walled, 3.1–3.9  $\times$  1.7–2.7  $\mu\text{m}$ , proliferating sympodially at the apex. – **Conidia** 13–21  $\times$  3–4  $\mu\text{m}$ , average 17.4  $\times$  3.5  $\mu\text{m}$  (n=50), composed of a 1-septate conidium body and a separate apical cell modified into a branched appendage; conidium body fusiform-ellipsoid with rounded ends, straight or slightly curved, wall

smooth, slightly constricted at the middle septum, hyaline, guttulate; apical cell 0.8–1.3  $\times$  1.6–1.9  $\mu\text{m}$ , ampulliform to irregular, dividing into 2–3 divergent appendages. – **Appendages** devoid of cell contents, attenuated toward the apex, flexuous, slightly swollen at the tip, 26–41  $\mu\text{m}$  in length, average 31.3  $\mu\text{m}$  (n=50), 1.0–1.5  $\mu\text{m}$  wide at the broadest point; mean conidium body length/width ratio 4.8.

**Culture characteristics.** – **Colonies** on PDA reaching 83–85 mm diam. after 3 weeks at 22  $^{\circ}\text{C}$ , dense growth, spreading, circular with entire edge, rough with dense white-grey tufts of hyphae, from above white-grey in the center, olivaceous grey in outer region, from below dark grey, conidiomata dark-brown to black, scattered, immersed to erumpent, stromatic, covered by mycelia. – **Colonies** on CMA reaching 75–80 mm diam. after 3 weeks at 22  $^{\circ}\text{C}$ , sparse mycelium, flat,

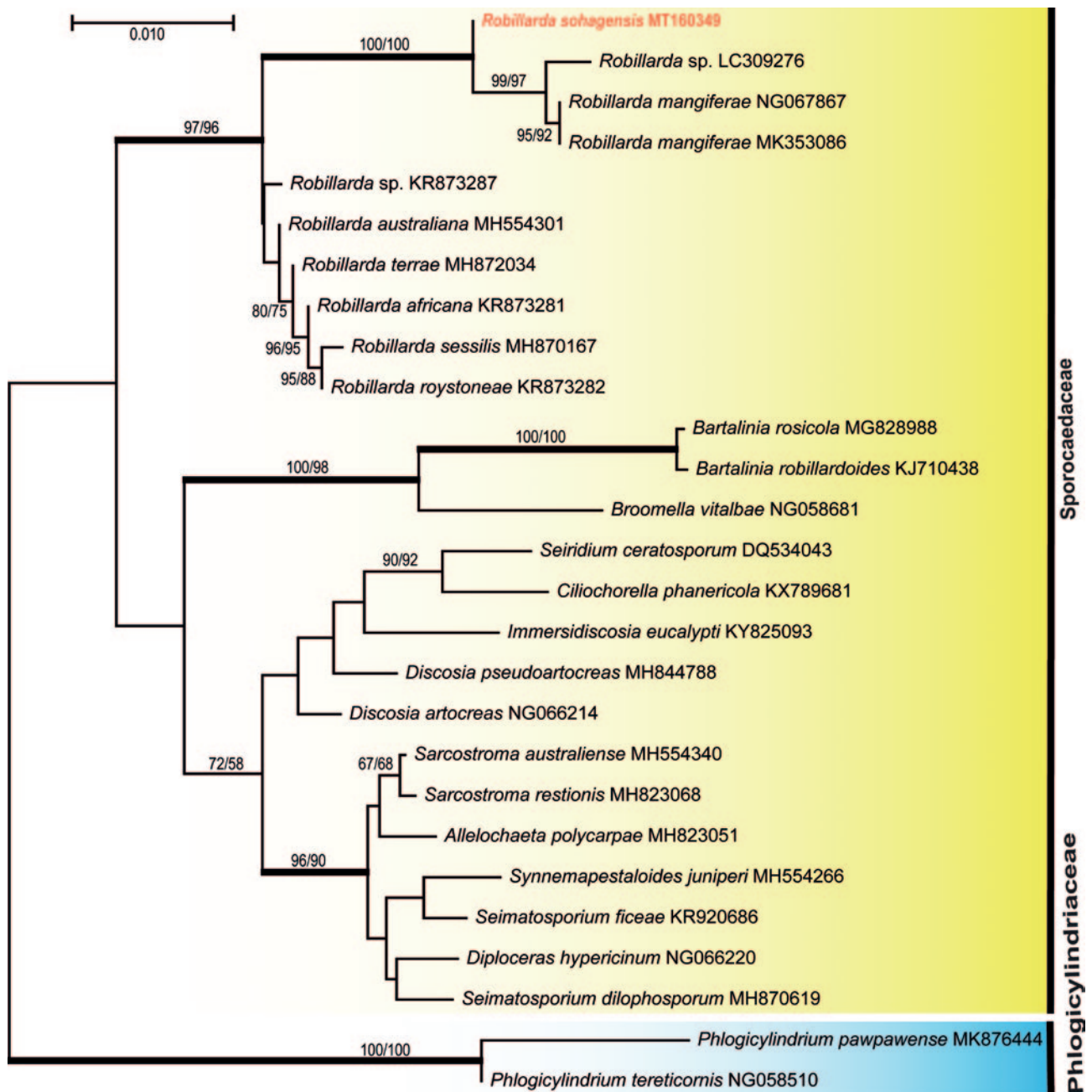


spreading, circular with entire edge, from above olivaceous brown, from below dull olivaceous brown, conidiomata drak-brown to black, scattered, immersed to erumpent. – Conidiomata formed on sterilized *Phragmites* leaves incubated with pure culture of the fungus, 855–1935 × 405–810 µm, average 1390 × 610 µm (n=35). – Conidia 14–21 × 4–5 µm, average 17.35 × 4.95 µm (n=50).

Appendages branches 40–53 × 1.0–1.5 µm, average 47 × 1.2 µm (n=50).

**Etymology.** – *sohagensis*, after Sohag Governorate in Egypt, where the holotype was collected.

**Hosts and distribution.** – On decaying submerged leaves of *Phoenix dactylifera* in the Nile river and irrigation canals. Thus far only known from the type locality in Sohag Governorate, Egypt.



**Fig. 23.** Phylogeny of *Robillarda* and representatives of Sporocadaceae reconstructed from an LSU dataset. Two *Phlogicylindrium* spp. served as outgroup taxa. The topology is the result of a neighbor-joining analysis performed in MEGA X. For each node, MLBS and MPBS (if  $\geq 50$ ) are presented. Thick lines represent BIPP  $\geq 0.95$ . The new species *R. sohagensis* is highlighted in red.

Notes. – Nag Raj (1993) revised the 28 species placed in *Robillarda* and accepted four species: *R. citricola* Nag Raj, *R. gossypii* Erem., *R. rhizophorae* Kohlm., and *R. sessilis* Sacc. (type species). He transferred twelve species (five to *Pseudorobillarda* M. Morelet, one to each of the following genera: *Chaetoconis* Clem., *Ciliochorella* Syd., *Dilophospora* Desm., *Hyalotiella* Papendorf, *Neottiospora* Desm., *Pestalotiopsis* Steyaert, and *Pseudoneottiospora* Faurel & Schotter) and rejected the twelve other species. Crous et al. (2015) described three new species in the genus: *Robillarda africana* Crous & Giraldo from South Africa, *R. roystoneae* Crous & Giraldo from Hong Kong, and *R. terrae* Crous & Giraldo from India. More recently, *R. australiana* F. Liu, L. Cai & Crous from Australia (Liu et al. 2019a) and *R. mangiferae* Thiyag., Wanas., Phookamsak & K.D. Hyde from China (Phookamsak et al. 2019) were described. In total, the number of currently accepted *Robillarda* species is nine. Only one of these are is marine species (Kohlmeyer 1969).

Our LSU dataset included 515 characters of which 429 were constant and 72 were parsimony-informative. Molecular phylogenetic analyses of this LSU dataset placed *R. sohagensis* within *Robillarda* but distinct from previously described species (Fig. 23). *Robillarda sohagensis* was retrieved as sister to a clade with *R. mangiferae* and *Robillarda* sp. strain MS9788 with maximum support. Our new species is characterized by larger conidiomata, larger conidial dimensions, and longer appendage arms compared to those reported for the nine previously described species in the genus. *Robillarda sohagensis* differs from its close relative *R. mangiferae* by having multiloculate conidiomata that are much larger (765–2025 × 270–495 µm vs. 250–310 × 300–340 µm in *R. mangiferae*) (Phookamsak et al. 2019). *Robillarda mangiferae* is associated with leaf blight on *Mangifera* sp. (Sapindales, Anacardiaceae), whereas *R. sohagensis* is a freshwater species. Shimoyama et al. (2018) isolated *Robillarda* sp. strain MS9788 from submerged decaying stems of *Phragmites* sp. near swamps at Kaw in French Guiana, and studied its ability to produce natural products. However, no morphological details of the fruiting structure of the fungus were provided. As a result, morphological comparison between *Robillarda* sp. from French Guiana and our newly described *R. sohagensis* is not possible.

#### Key to *Robillarda* species

1. Unilocular conidiomata .....2
- 1\*. Uni- to plurilocular conidiomata .....3
2. Conidiomata dehiscence by ostiole .....4

- 2\*. Conidiomata dehiscence by a longitudinal split .....5
3. Conidiomata dehiscence by ostiole .....6
- 3\*. Conidiomata dehiscence by a longitudinal split, conidia hyaline, 13–21 × 3–4 µm ...*R. sohagensis*
4. On leaves of *Mangifera*, conidia hyaline, 7.5–12 × 2.5–4.5 µm ..... *R. mangiferae*
- 4\*. On other hosts, conidia hyaline to pale brown .7
5. Conidia hyaline, 9.5–13.5 × 3–3.5 µm, marine .....*R. rhizophorae*
- 5\*. Conidia hyaline to pale brown or pale olivaceous .....9
6. Apical appendage with up to 3 branches .....8
- 6\*. Apical appendage with up to 4 branches, conidia hyaline to pale brown, 11.5–19 × 2.4–3.5 µm .....*R. terrae*
7. Text Conidial wall smooth, 10–13 × 2.5–3.5 µm .....*R. africana*
- 7\*. Conidial wall verruculose, 9–14 × 3–3.5 µm, on *Gossypium hirsutum*..... *R. gossypii*
8. Conidial length shorter than 13 µm, 9–13 × 2.5–3.5 µm ..... *R. sessilis*
- 8\*. Conidial length longer than 13 µm, 13–16 × 2.5–3.5 µm .....*R. roystoneae*
9. Conidia hyaline to pale brown, 8.5–13.5 × 1.5–2 µm .....*R. australiana*
- 9\*. Conidia pale olivaceous, 12–15 × 3–4 µm ..... *R. citricola*

Authors: S.R. Abul-Ezz, M.S. Bakhit, A.I.I. Abdel-Hafiz & M.A. Abdel-Wahab

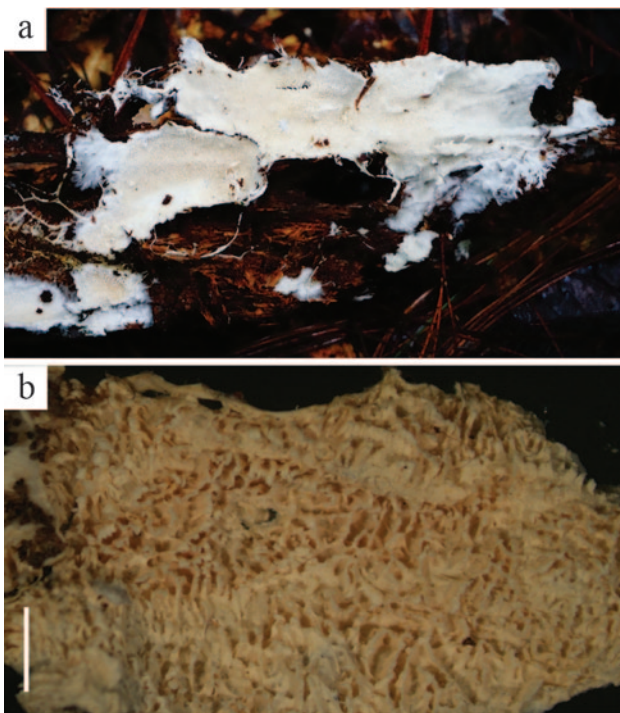
#### Basidiomycota, Agaricomycetes, Trechisporales, Hydnodontaceae

*Trechispora hondurensis* Schoutteten & Haelew., sp. nov. – Figs. 24–26  
Mycobank no.: MB 835787

Diagnosis. – Different from *T. echinospora*, *T. farinae*, and *T. regularis* by its poroid to hydroid hymenophore with coalescing spines; the presence of hyphal cords; ellipsoid, aculeate basidiospores measuring (3.2–)3.67–3.84(–4.0) × (2.5–)2.76–2.89(–3.0) µm; and the absence of large, encrusted cystidia.

Holotypus. – HONDURAS. Departments of Cortés and Santa Bárbara, Cusuco National Park, Base Camp Transect 1, at 120 m, very decomposed log, 22 June 2019, leg. D. Haelewaters & P. Medina-van Berkum, HONDURAS-F016 (GENT; holotype).

Description. – Basidioma resupinate, effuse, loosely adnate, margin arachnoid to fibrillose, with formation of distinct white cords. – Hymenophore first fibrillose to subporoid, later becoming hydroid to partly irpicoid; individual spines fragile, reaching up to 0.8 mm, locally coalescing; whitish to cream colored when fresh, pale



**Fig. 24.** *Trechispora hondurensis*. **a.** *In-situ* photograph of basidioma. **b.** Detail of hymenophore showing a poroid area. Scale bar 2 mm.

ochraceous when dried; young parts of the hymenophore may be covered with a very thin, arachnoid, white mycelial veil; subiculum very thin (0.1 mm), not separable from the hymenophore. – Hyphal system monomitic, clamped at all septa, with ampullate septa, straight, sometimes anastomosing. – Hyphal cords soft, composed of generative hyphae of 1.5–4.5  $\mu\text{m}$  in diam., with ampullaceous swellings up to 8.0  $\mu\text{m}$  in diam., sometimes covered by crystals of various shapes and sizes; often intertwined and anastomosing; some parts very dense, consisting of agglutinated hyphae. – Subicular hyphae thin-walled, 4.5–6.0  $\mu\text{m}$  diam.; ampullate swellings up to 14  $\mu\text{m}$ . – Subhymenial hyphae thin-walled, 1.5–4.5  $\mu\text{m}$  diam.; ampullate swellings up to 8  $\mu\text{m}$ . – Hyphae regularly encrusted with crystals; at the apex of individual spines, differentiated hyphal ends may be present, exhibiting variable shapes and often regularly encrusted with fine crystals. – Cystidia absent. – Basidia cylindrical to suburniform, often with a modest median constriction, with four sterigmata and a basal clamp, (8.0–)12.0–15.7(–20.0)  $\times$  (4.0–)4.4–6.5  $\mu\text{m}$ ; in general, basidia have a terminal appearance but some pleural basidia have been observed. Basidiospores (sub)urniform. – Basidiospores aculeate,

with obtuse spines  $\leq 0.5 \mu\text{m}$ , thin-walled (sometimes slightly thick-walled), apiculate, ellipsoid, adaxial side slightly concave to straight, (3.2–)3.67–3.84 (–4.0)  $\times$  (2.5–)2.76–2.89(–3.0)  $\mu\text{m}$  (measured without ornamentation), inamyloid. – Anamorph not observed.

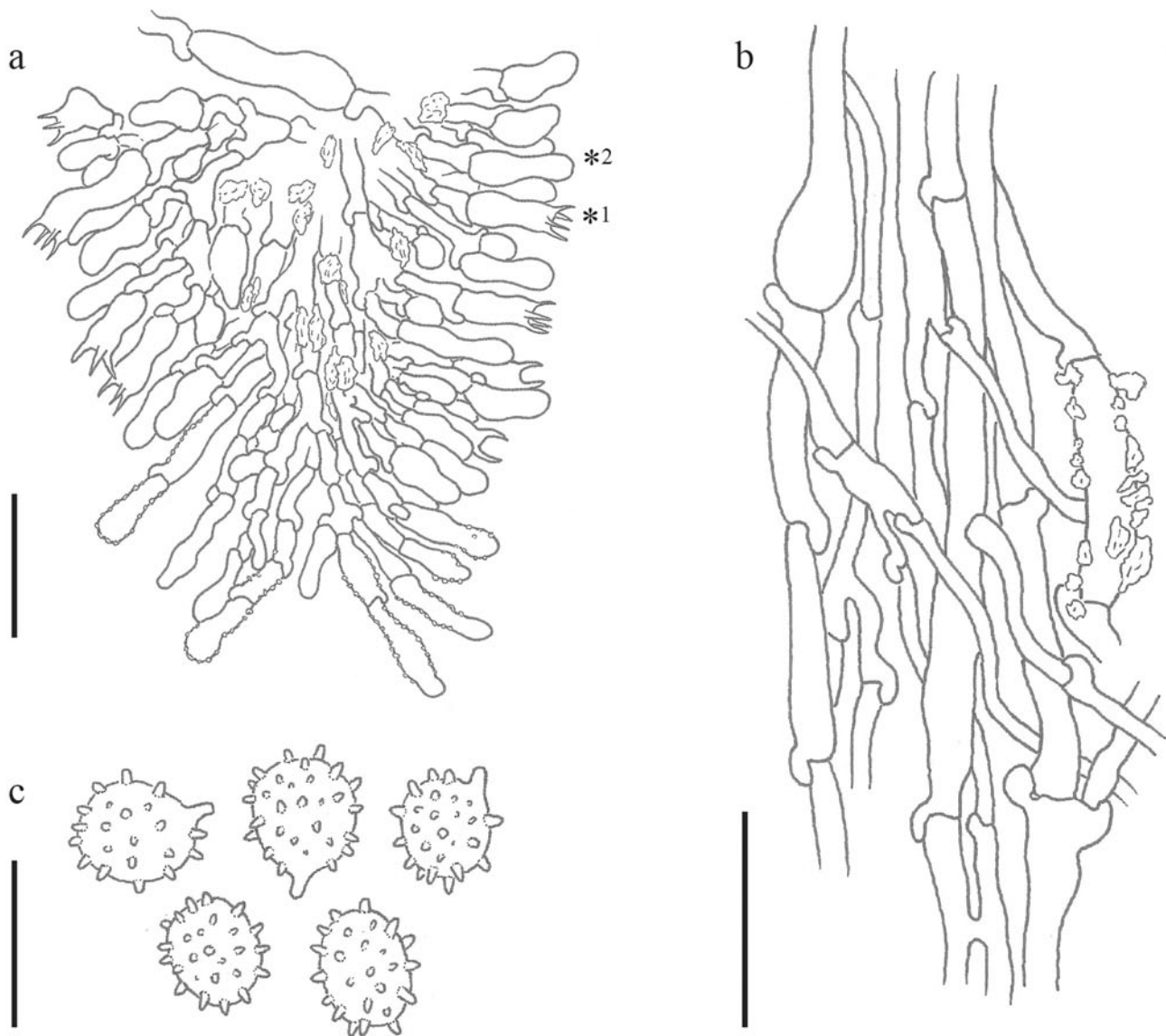
**Etymology.** – Referring to the country where the holotype was collected, Honduras.

**Habitat and distribution.** – Only known from Cusuco National Park, a broadleaved montane rain forest in Honduras. It was collected near the Base Camp site at ~1,572 m a.s.l., growing on decaying plant remnants (small twig fragments, leaf litter, and nut shells).

**Additional material examined.** – *Ibid.* (PUL F26163; isotype). Sequences ex-isotype: MT571523 (ITS), MT636540, MT636541 (LSU).

**Notes.** – *Trechispora* P. Karst. is a basidiomycete genus of crust-like fungi, currently including (48–)54 species (He et al. 2019, Species Fungorum 2020). All species are presumed saprotrophs, decaying a wide range of plant remnants. Only a few species have been described from other substrates such as termite nests or soil. The genus was erected to accommodate *Trechispora onusta* P. Karst., a poroid species from Finland (Karsten 1890). Most of the known species have been described from northern temperate areas in Europe and North America – which may merely be a reflection of the activities of mycologists working with corticioid fungi. So far, only 15 species of *Trechispora* have been described from (sub)tropical areas, of which only four from Central and South America. Phookamsak et al. (2019) stated that 27 *Trechispora* species have been reported from (sub)tropical areas. This may indicate a predominantly temperate and boreal distribution of the genus, although some authors suggest that these species are not rare in (sub)tropical regions (Larsson 1992, 1995; Ordynets et al. 2015). In general, much diversity remains to be uncovered in the genus.

*Trechispora* species have a wide variety in macro- and micromorphological characters. Basidiomata are light-colored, fragile, and mostly resupinate, although exceptions exist, including four pileate-stipitate species – *Trechispora gillesii* (Maas Geest.) Libert, *T. thelephora* (Lév.) Ryvarden (Albee-Scott & Kropp 2010), and two undescribed species from Guyana (Haelewaters et al. 2020b). Some species are characterized by hyphal cords or rhizomorphs at the margins. The configuration of hymenophores ranges from smooth to poroid, grandinoid, odontoid, and even hydroid in some species; all of these are likely adaptations towards an en-



**Fig. 25.** *Trechispora hondurensis*, micromorphological features drawn from the holotype (GENT). **a.** Structure of an individual spine of the basidioma, with basidia (\*1), basidioles (\*2), and hyphal ends at the apex encrusted with fine crystals. **b.** Hyphal cord, non-agglutinated part. **c.** Basidiospores. Scale bars a–b 20  $\mu\text{m}$ , c 5  $\mu\text{m}$ , *del.* N. Schoutteten & A. Verbeke.

larged surface promoting spore production (Liu et al. 2019b). The hyphal system is either monomitic, consisting of clamped generative hyphae only (most species), or dimitic, consisting of generative and skeletal hyphae. A typical feature for *Trechispora* species are the ampullate septa in some of the generative hyphae, visible under the light microscope as swollen hyphae near the septa, although their abundance varies between species. Many *Trechispora* species are characterized by calcium oxalate crystals, often with specific shapes and found attached to hyphae in the subiculum and hyphal

ords. Due to their specific shapes and organization in the basidiomata, these crystals are taxonomically informative (Larsson 1994). Basidia (meiosporocysts) are four-sterigmate, short, and generally cylindrical to clavate. Basidiospores are either thin- or thick-walled, smooth or ornamented, with a variety in shape and length of the spines in the latter type. For some species, conidial stages have been described.

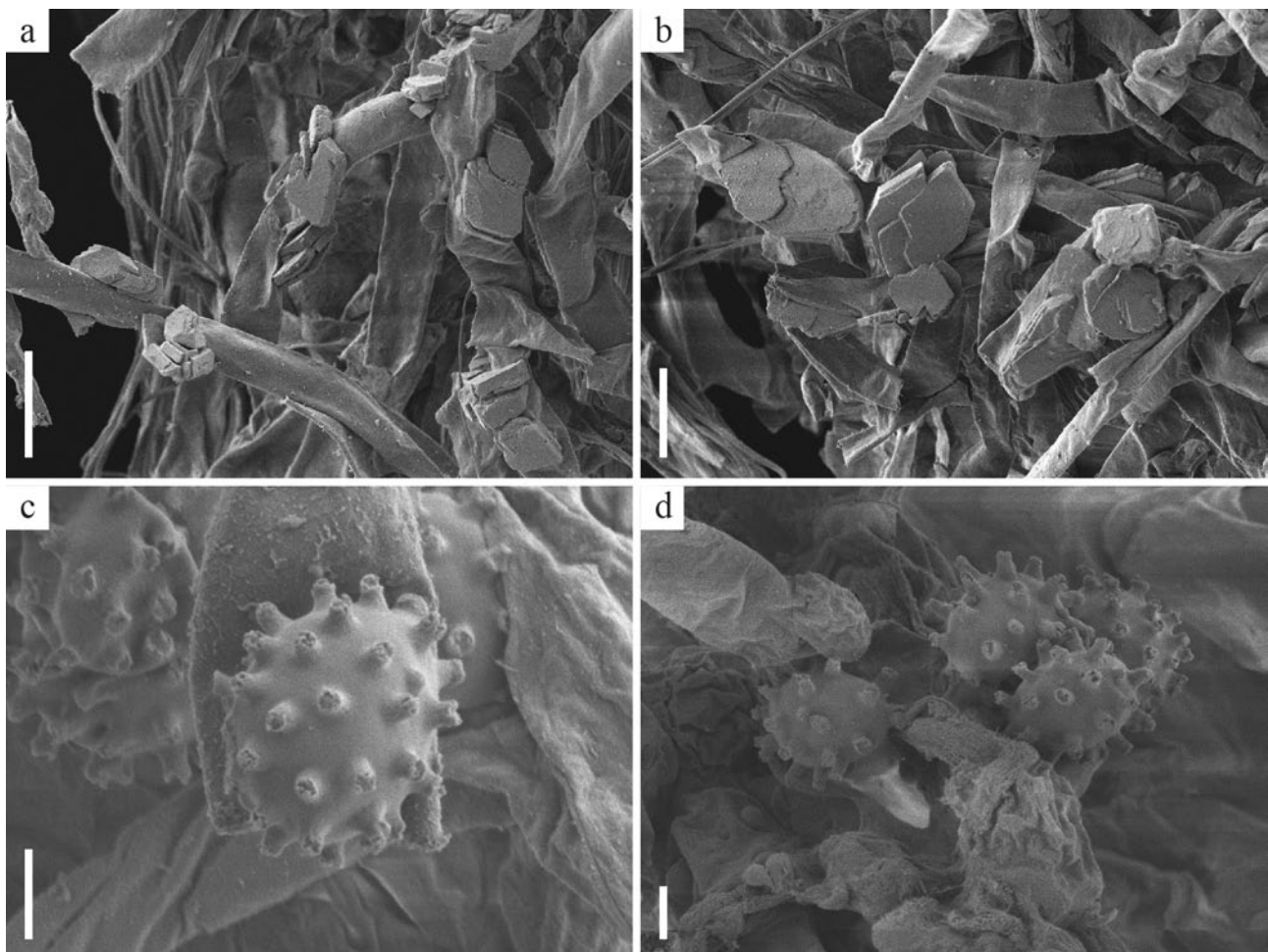
The Honduran collection agrees well with typical microscopic characteristics for *Trechispora* (e.g., the fragile basidioma and ampullaceous septa).

However, based on combined morphological and molecular evidence, it cannot be assigned to any of the currently described species in the genus. *Trechispora hondurensis* clearly shows a light colored basidioma and peripheral hyphal cords. The hymenophore is variably organized; young regions are poroid (sometimes covered by a mycelial veil) while mature regions are hydroid, with locally coalescing spines. Unlike most species in the genus, this specimen has more or less differentiated hyphal ends of variable shape in the hymenium positioned at the spinal tips in the basidioma (Fig. 25). These cells are slightly projecting above the basidia and covered with very small roundish calcium oxalate crystals, more or less regularly organized.

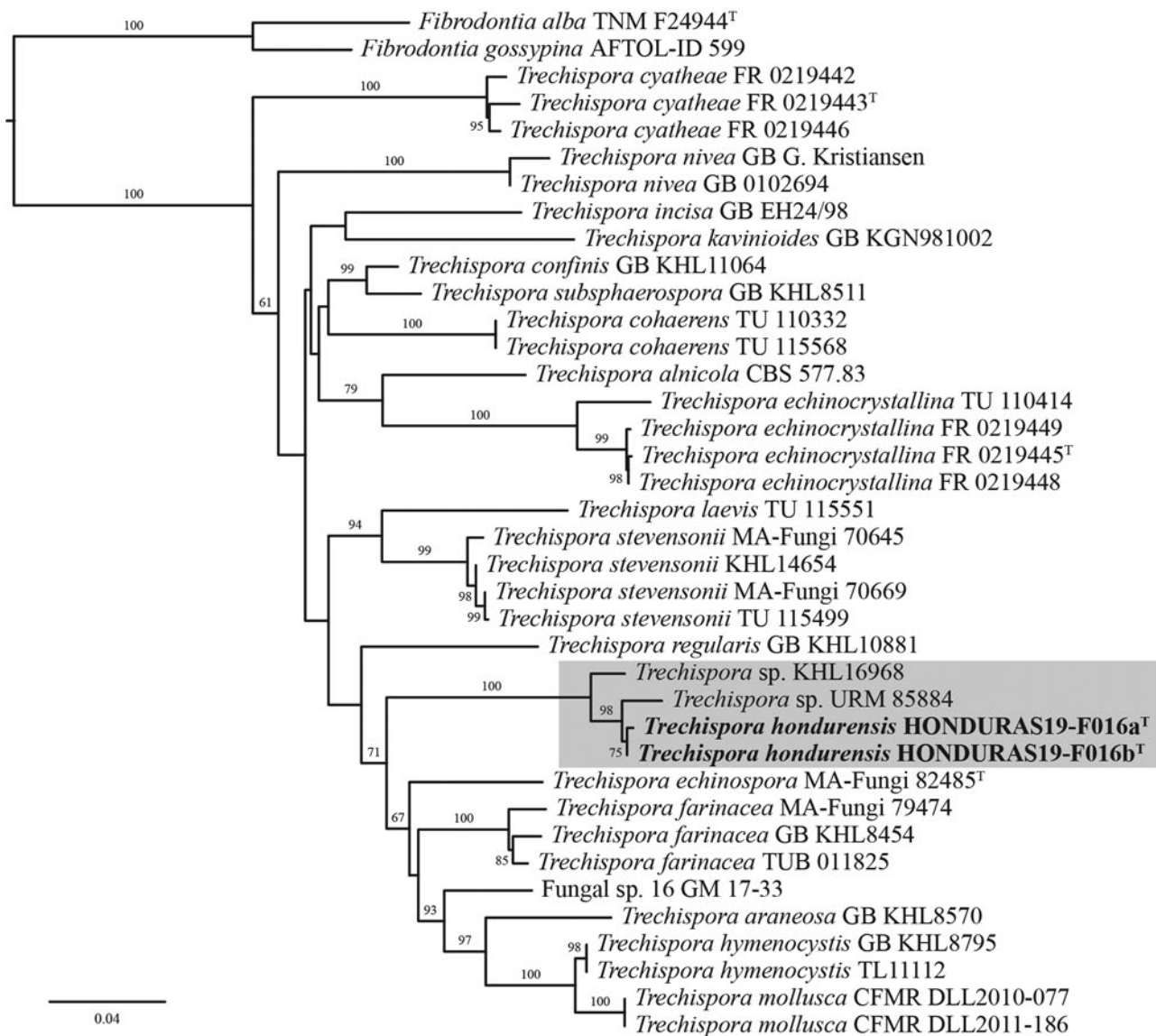
Both phylogenetic analyses (ITS–LSU and LSU alone) retrieved *Trechispora hondurensis* in a maximum-supported clade with two *Trechispora* isolates from Brazil (KHL16968, URM 85884) (Figs. 27–

28). Micromorphological work on this Brazilian material is unavailable. Given the evolutionary distances among isolates of *Trechispora cyatheae* Ordynets, Langer & K.H. Larss., *T. echinocrystallina* Ordynets, Langer & K.H. Larss., and *T. farinacea* (Pers.) Liberta, the Brazilian isolates in our trees may represent *T. hondurensis*—possibly extending the distributional range of this species to South America. The closest phylogenetic relatives of *T. hondurensis* are *T. echinospora* Telleria, M. Dueñas, I. Melo & M.P. Martín, *T. farinacea*, and *T. regularis* (Murrill) Liberta. In the phylogenetic reconstruction of the LSU dataset (Fig. 28), high support was found for a sister relationship between *T. farinacea* and *T. hondurensis* (including Brazilian isolates KHL16968 and URM 85884).

Remarkably, both *T. echinospora* and *T. regularis* are described from tropical areas—*T. echinospora* from Equatorial Guinea in tropical sub-Saharan



**Fig. 26.** *Trechispora hondurensis*, scanning electron micrographs. **a–b.** Encrustations on hyphae. **c–d.** Basidiospores, which are ellipsoid and aculeate. Scale bars a–b 5 µm, c–d 1 µm.

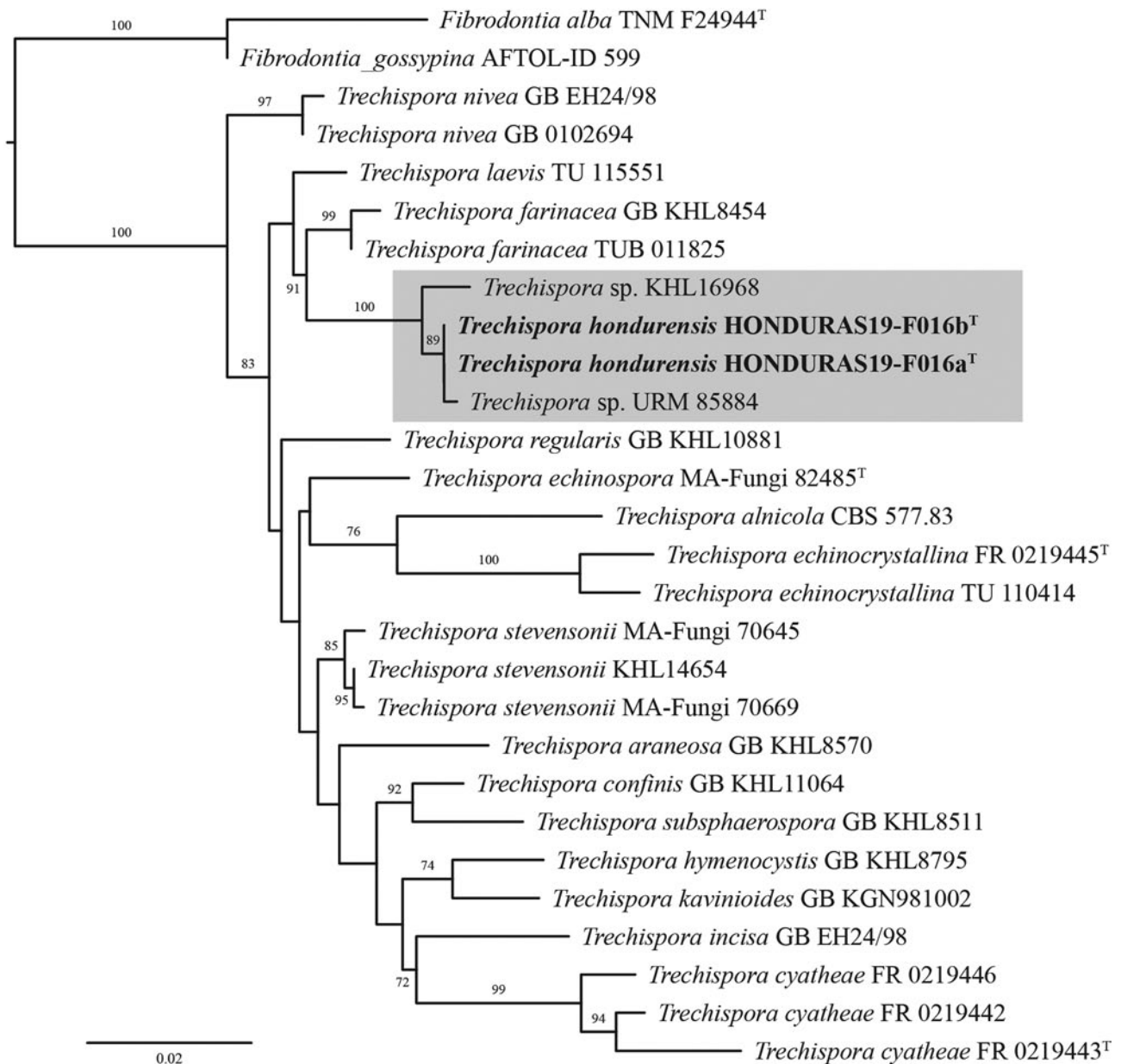


**Fig. 27.** Phylogeny of *Trechispora* isolates reconstructed from a combined ITS–LSU dataset. The topology is the result of ML inference performed with IQ-TREE. For each node, the MLBS (if >60) is presented above/below the branch leading to that node. The new species *T. hondurensis* is highlighted in grayscale.

Africa and *T. regularis* from Jamaica in the Caribbean (Liberta 1973, Phokaamsak et al. 2019). *Trechispora echinospora* can be distinguished from *T. hondurensis* based on its farinaceous to grandinoid basidioma; its larger and globose basidiospores (4–5 µm excluding ornamentation) with long, sharp and evenly distributed spines of up to 1 µm in length; the presence of sphaerocytes [often referred to as sphaerocysts in *Trechispora* literature]; and the absence of hyphal cords and crystals. *Trechispora regularis* is characterized by a poroid hymenophore but is easily distinguished from *T. honduren-*

*sis* by the presence of many large (up to 60 µm), encrusted cystidia. In addition to Jamaica where the type was collected, *T. regularis* has also been reported from the USA, Costa Rica, Brazil, and Paraguay (Liberta 1973).

*Trechispora farinacea* was based on material from Scandinavia [as *Hydnum farinaceum* Pers. ex Fr.] and is a common species in northern temperate areas around the world. Note that it has also been reported from the Caribbean, South America, and southern Australia (sensu Liberta 1973), although it remains to be proven that these specimens are truly



**Fig. 28.** Phylogeny of *Trechispora* isolates reconstructed from a single-locus dataset including LSU sequences only. The topology is the result of ML inference performed with IQ-TREE. For each node, the MLBS (if >60) is presented above/below the branch leading to that node. The new species *T. hondurensis* is highlighted in grayscale.

representative of *T. farinacea* (Larsson 1995). Much variation has been described in the macromorphology of *T. farinacea*, although basidiomata are mostly smooth to grandinoid or odontoid, often soft and cushion-like, whereas the basidioma of *T. hondurensis* is poroid to hydroid. Micromorphologically, *T. farinacea* has larger basidiospores, measuring 4.0–4.5(–5.0) × 3.3–3.7 μm, and the short spines of its basidioma consist of rather short-celled hy-

phae (Hjortstam et al. 1988). In *T. hondurensis*, these spines are composed of long-celled hyphae.

Morphologically, the here described *T. hondurensis* is somewhat reminiscent of the temperate species *T. verruculosa* (G. Cunn.) K.H. Larss. in having an effused hydroid basidioma consisting of coalescing spines. However, basidiospores of *T. verruculosa* are slightly cyanophilous and larger, measuring (4.5–)4.7–5.2(–5.5) × (3.5–)4.0–4.5 μm (Larsson

1996). *Trechispora verruculosa* is described from Auckland, New Zealand [as *Odontia verruculosa* G. H. Cunn.] and has been reported from several countries in Europe and from China. No sequences are currently available for this taxon.

*Authors:* D. Haelewaters, N. Schoutteten, A. Verbeke & M.C. Aime

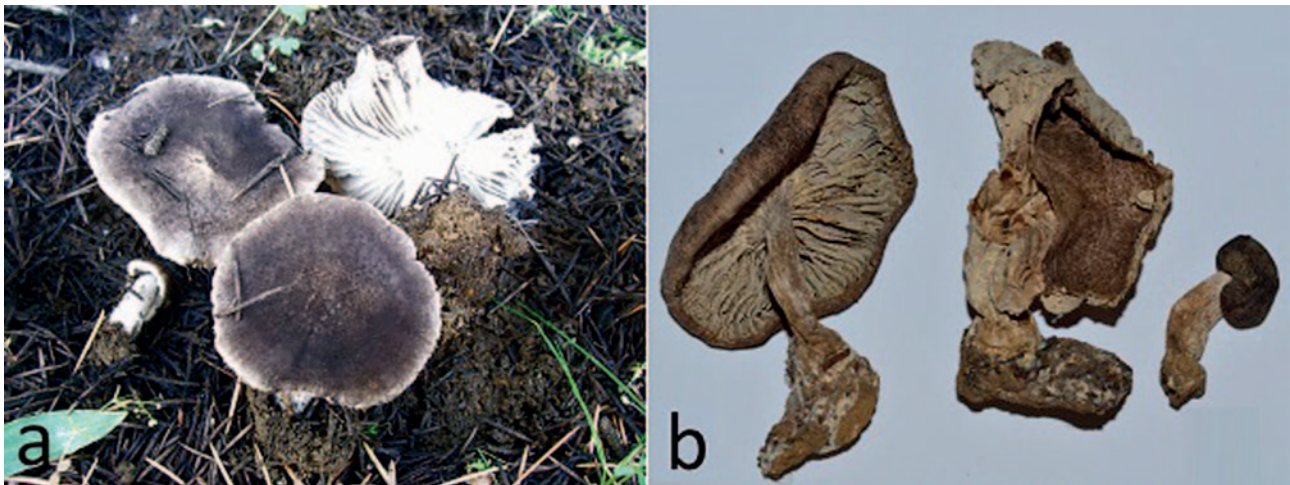
**Basidiomycota, Agaricomycetes, Agaricales, Tricholomataceae**

***Tricholoma kenanii*** I. Acar, S. Aldemir & A. Dizkirici, **sp. nov.** – Figs. 29–31

MycoBank no.: MB831905

*Holotypus.* – TURKEY. Bingöl Province, Genç, 38°44'54.05"N, 40°33'41.92"E, 1049 m a.s.l., coniferous forest, near *Pinus* spp., 18 October 2018, *leg.* I. Acar, VANF 7600 (VPF; holotype). Sequences ex-holotype: MN541841–MN541846 (ITS), MN541829–MN541834 (LSU).

grey-white, smooth, context white, fragile. – *Basidiospores* (6.1–)7.0–9.1 × 4.0–5.5 μm, (n=40 and Q=1.5–1.65), on average 7.44 × 4.72, ellipsoid, thin-walled, smooth, hyaline, guttulate, inamyloid. – *Basidia* 26.5–36.5 × 6–9 μm, cylindrical-clavate, with 2 or 4 sterigmata, without basal clamp connection. – *Cheilocystidia* 16.7–28.5 × 5.2–8.0 μm, clavate, irregular, abundant, hyaline, twisted, sometimes polymorph. – *Pleurocystidia* not seen. – *Pileipellis* up to 44 μm, made up of irregular to slightly parallel hyphae, dark brown-pigmented, without clamp connections. – *Pileus* tramal hyphae 7–16 μm wide, hyaline to yellow brown. – *Lamellar trama* parallel, guttulate, hyphae mostly 8–20 μm in diam., thin-walled, hyaline. – *Stipitipellis* with longitudinally arranged, appressed, parallel hyphae, 8–14 μm in diam., without



**Fig. 29.** *Tricholoma kenanii*. a. Basidiomata in natural habitat b. Preserved (dried) basidiomata from the VPF fungarium.

*Description.* – *Pileus* 15–55 mm in diam., conical when young, then plane, slightly umbo-nate, outward curved when old, surface radially fibrillose towards margin, scaly, a white zone at the margin, darker to the center, greyish, dark-greyish, blackish brown, whitish towards margin, with white velar remnants on the edges, a cortina when young. – *Context* whitish, thick in the pileus center, thinner to the edges. – *Edibility* unknown. – *Lamellae* whitish, grey-white, broad, L=60–90, l=1–3, emarginate, shortly with tooth decurrent, edges crenate, with lamellulae. – *Stipe* 25–40 × 7–10 mm, surface longitudinally fibrillose, cylindrical, sometimes curved when mature, basally distinctly clavate, or occasionally bulbous, somewhat rooting, whitish,

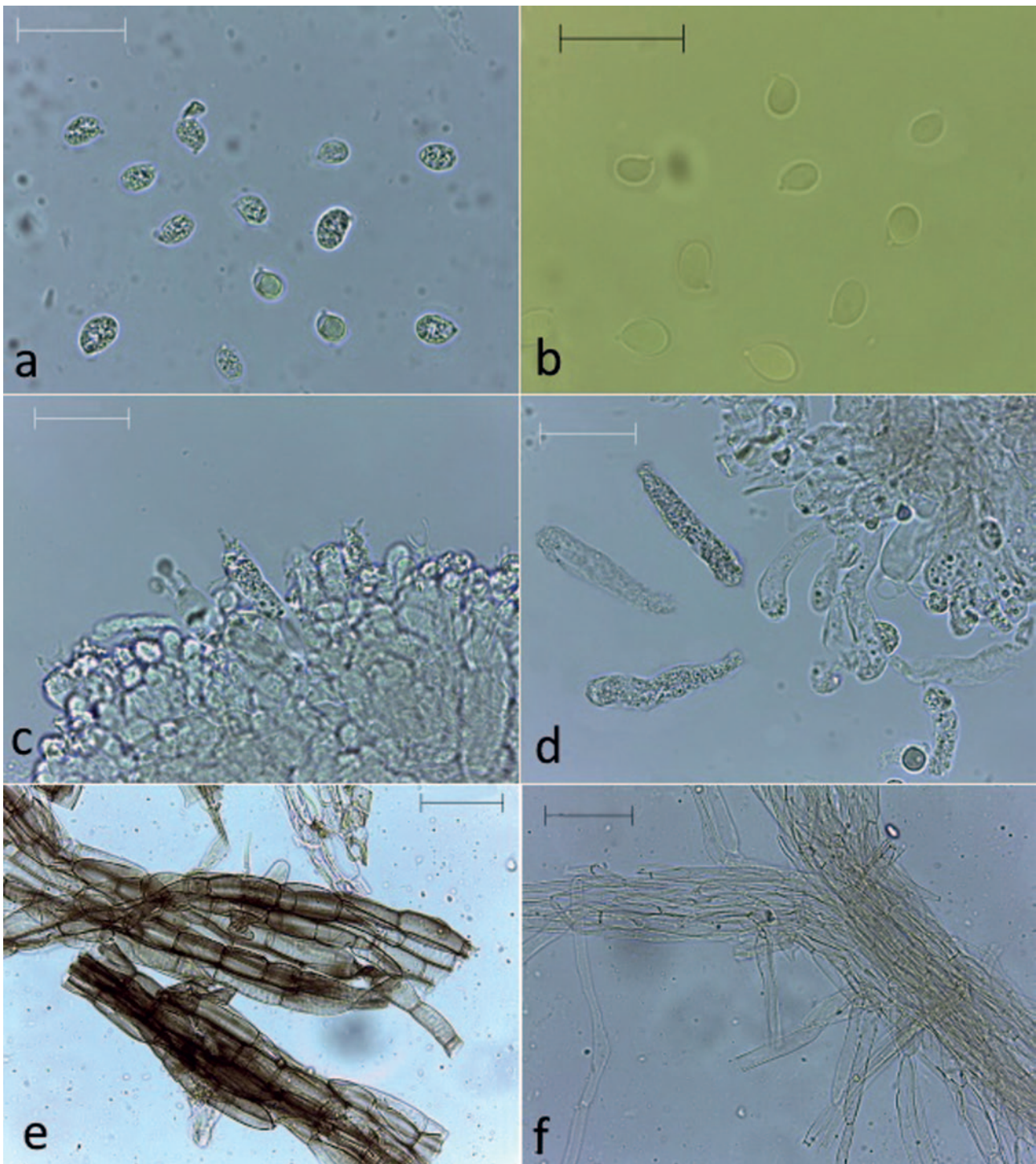
clamp connections, thin-walled, hyaline to light yellowish. – *Caulocystidia* not seen.

*Etymology.* – *kenanii*, in honor of Prof. Dr. Kenan Demirel†, who made significant contributions to mycology in Turkey and died in 2019.

*Habitat and distribution.* – In subalpine areas in coniferous forests with *Pinus* sp. of the Eastern Anatolia Region, Turkey.

*Notes.* – The agaric genus *Tricholoma* (Fr.) Staude was introduced as a section by Fries (1821) and subsequently proposed as a genus by Staude (1857). The genus is mainly characterized by fleshy basidiomata; white, cream to yellowish emarginate lamellae; white spore print; and hyaline, smooth, inamyloid spores (Christensen & Heilmann-Claus-





**Fig. 30.** *Tricholoma kenanii*, collection VPF Fungi 7600 (holotype). **a–b.** Basidiospores in distilled water (a) and in Melzer's reagent (b). **c.** Basidia. **d.** Cheilocystidia. **e.** Pileipellis. **f.** Pileus tramal hyphae. Scale bars a–d 20  $\mu\text{m}$ , e–f 50  $\mu\text{m}$ .

en 2013, Reschke et al. 2018). The pileal surface, the cellular structure of the pileipellis, the color of the pileus, and the presence vs. absence of clamps are

important characters for species delimitation in the genus (Bon 1984, Singer 1986, Heilmann–Clausen et al. 2017, Reschke et al. 2018). *Tricholoma* species

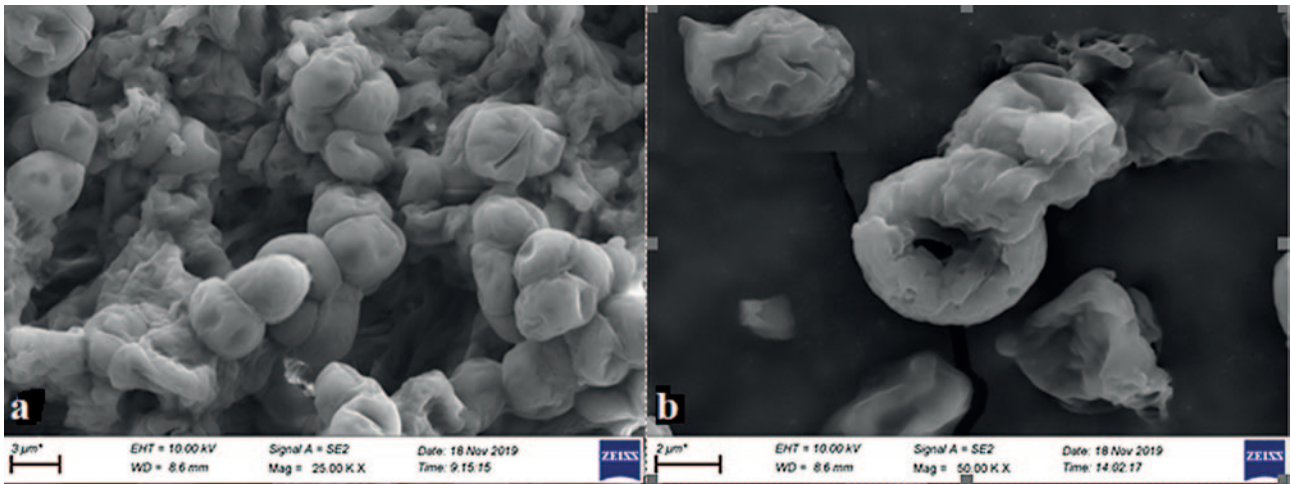


Fig. 31. *Tricholoma kenanii*. Field-emission scanning electron micrographs of basidiospores. a. At 25,000Kx. b. At 50,000Kx.

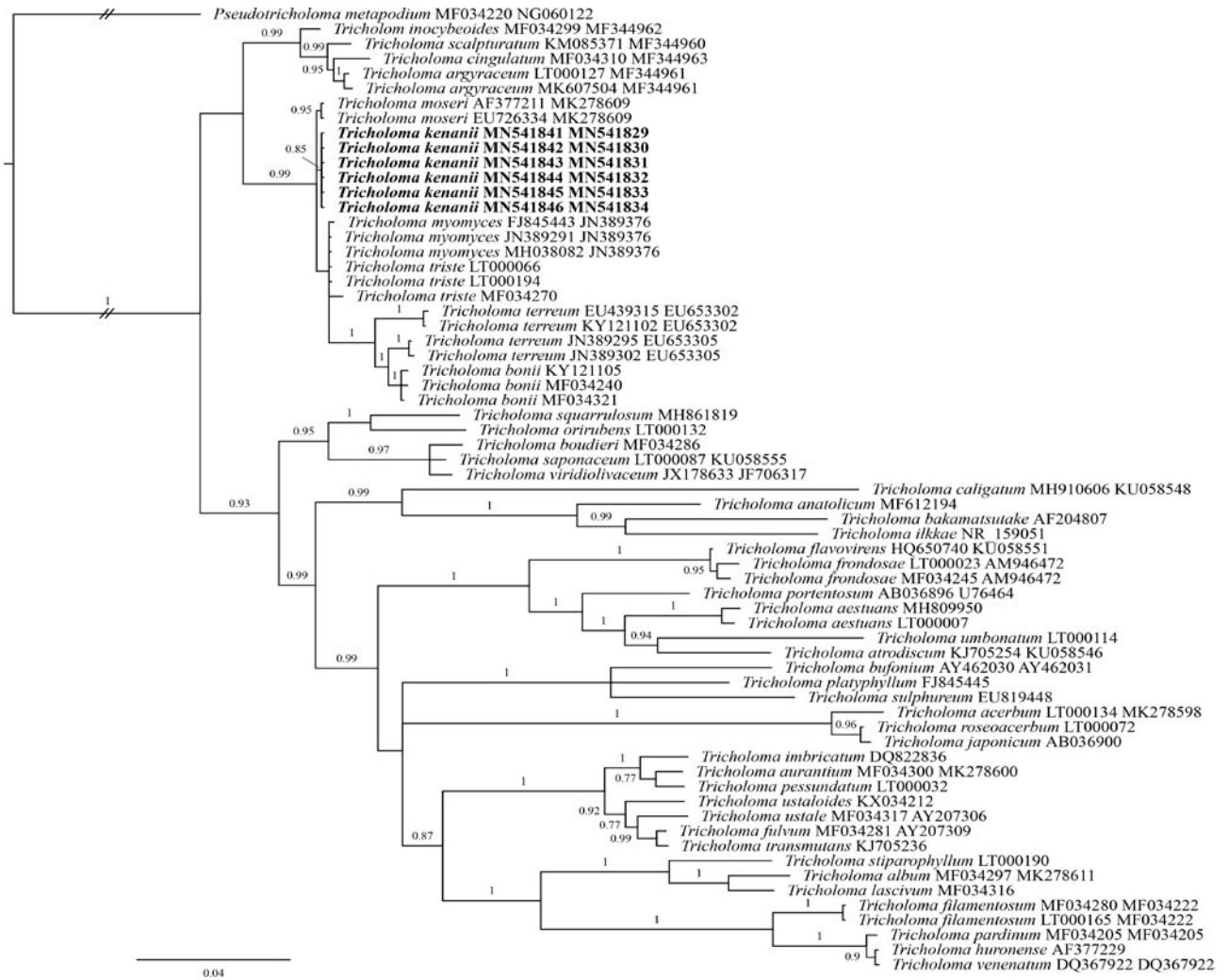


Fig. 32. Phylogeny of *Tricholoma* species showing the placement of *T. kenanii*, reconstructed from a concatenated ITS–LSU data-set. The topology is the result on Bayesian inference performed with MrBayes. Sequences of the newly described species are highlighted in boldface. Only BIPP >0.75 are shown.

exhibit very similar microscopic features, and are characterized by hyaline, subglobose to oblong spores; simple pileipellis structures; and a lack of well-differentiated sterile elements, including cystidia (Heilmann-Clausen et al. 2017). Around 210 species are currently described in the genus (Wijayawardene et al. 2020).

Sequence comparison of newly generated ITS sequences showed—among the top 20 BLAST results—that the new species was most closely related to *T. moseri* Singer (99.42 % shared identity), *T. myomyces* (Pers.) J.E. Lange (98.83–99.71 %), *T. terreum* (Schaeff.) P. Kumm. (99.71 %), and *T. triste* (Scop.) Quél. (99.25–99.85 %). Comparison of the LSU locus led to the following top 20 BLAST results: *T. argyraceum* (Bull.) Gillet [including synonym *T. inocybeoides* A. Pearson] (98.89–99.22 % shared identity), *T. cingulatum* (Almfelt ex Fr.) Jacobashch (98.89 %), *T. moseri* (100 %), *T. (cf.) myomyces* (99.66–100 %), *T. sculpturatum* (Fr.) Quél. (98.89–99.00 %), and *T. terreum* (98.78–99.66 %). In our phylogenetic tree based on the concatenated ITS–LSU dataset of 64 isolates (Fig. 32), ex-holotype sequences of *T. kenanii* forms a separate clade sister to *T. moseri* with maximum support (BIPP=1). This clade (*T. kenanii*, *T. moseri*) is sister to a cluster with representatives of *T. bonii*, *T. myomyces*, *T. terreum*, and *T. triste*.

*Tricholoma kenanii* is characterized by the typical greyish brown and scaly pileus structure of sect. *Terrea*; its stipe is markedly clavate and has a slightly rooted structure; basidiospores are (6.1–) 7.0–9.1 × 4.0–5.5 µm, elliptic, globose; and basidia are 26.5–36.5 × 6–9 µm, cylindrical-clavate, without basal clamp connection. Sister species *T. moseri* is differentiated from *T. kenanii* by slightly different measurements for basidiospores (6.5–10.6 × 3.3–5.8 µm) and basidia (28–43 × 6.7–8.6 µm). *Tricholoma moseri* is an American species with reports in California and Mexico (type), found particularly under *Abies magnifica* and *Pinus hartwegii* (Singer 1989; Shanks 1996, 1997; Bessette et al. 2013). *Tricholoma triste* can be morphologically separated from the new species by the lack of cystidia, whereas *T. kenanii* has abundant cheilocystidia. In addition, the pileus color is different between both species: sometimes almost black in *T. triste* (Christensen & Noordeloos 1999) vs. greyish brown in *T. kenanii*. *Tricholoma myomyces* is morphologically easily distinguished from *T. kenanii*, by its basidiospores (5.0–10.5 × 3.5–6.0 µm), which are ellipsoid to ovoid, and 2-spored basidia (Bessette et al. 2013, Desjardin et al. 2015).

Authors: I. Acar, S. Aldemir & A. Dizkırıcı

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

#### Ascomycota, Laboulbeniomycetes, Laboulbeniales, Laboulbeniaceae

*Arthrorhynchus eucampsipodae* Thaxt., Proc. Am. Acad. Arts Sci. 36: 409 (1901). – Fig. 33b

Material examined. – RWANDA. Northern Province, Musanze District, Ruhengeri, on female *Eucampsipoda africanum* Theodor, 1955 (Diptera, Nycteribiidae) collected from female *Rousettus aegyptiacus*, UP498/D. Haelew. 1498 [bat fly labels], 10 December 2008, leg. W. Markotter, slide PUL F27651; *Ibid.*, on female *E. africanum*, UP404 [bat fly label], 10 December 2008, slide PUL F27653; *Ibid.*, 10 December 2008, on female *E. africanum*, UP478 [bat fly label], slide PUL F27652; *Ibid.*, on female *E. africanum*, UP508 [bat fly label], 11 December 2008, slide PUL F27650; *Ibid.*, on female *E. africanum*, UP541 [bat fly label], 13 December 2008, slide PUL F27647. – SOUTH AFRICA. Limpopo, on female *E. africanum* collected from male *R. aegyptiacus*, UP5917 [bat fly label], 26 October 2015, leg. W. Markotter, slide PUL F27649; *Ibid.*, on female *E. africanum* collected from female *R. aegyptiacus*, UP7190 [bat fly label], 1 November 2016, slide PUL F27648.

Material sequenced. – BULGARIA. Lovech Province, Chavdartsı village, Mandrata Cave, 43°14'30.9336"N, 24°58'02.3664"E, on female *Nycteribia vexata* Westwood, 1835 (Diptera, Nycteribiidae) collected from male adult *Myotis blythii*, A1003L [bat fly label] A1003 [bat label], 9 September 2017, leg. A. Sándor & Á. Péter, isolate D. Haelew, 1491a

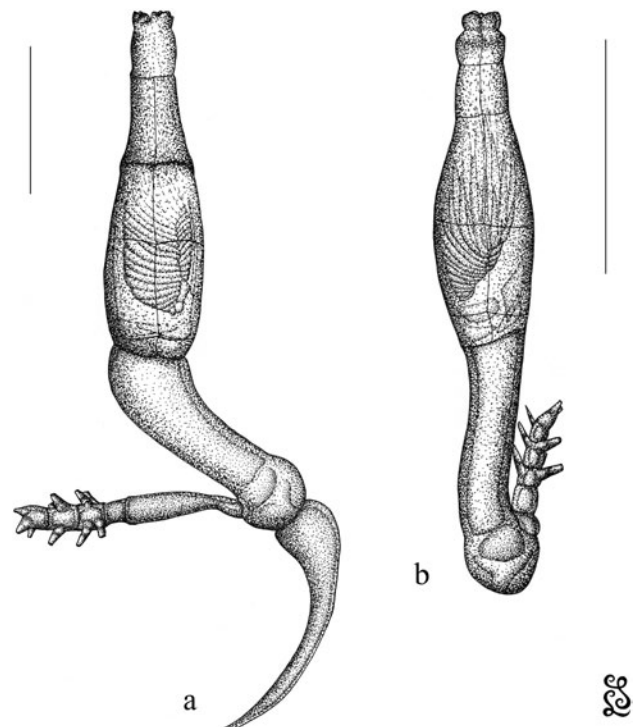


Fig. 33. *Arthrorhynchus* species. a. *Arthrorhynchus nycteribiidae*. b. *Arthrorhynchus eucampsipodae*. Scale bars a 200 µm, b 100 µm, del. J. Liu.

(3 adult thalli, left metacoxal cavity), MT241715 (LSU). – RWANDA. Northern Province, Musanze District, Ruhengeri, on female *E. africanum* collected from female *R. aegyptiacus*, UP498 [bat fly label], 10 December 2008, leg. W. Markotter, isolate D. Haelew. 1498a (2 adult thalli), MT235694 (SSU), MT235717 (LSU); *Ibid.*, isolate D. Haelew. 1498b (2 adult thalli), MT235695 (SSU), MT235718 (LSU). – SLOVAKIA. Banská Bystrica Region, Nandraž, near Jelšava, on *N. schmidlii* (Diptera, Nycteribiidae) collected from adult female *Miniopterus schreibersii*, AB04 [bat label], 6 December 2009, leg. M. Ševčík & P. Hohti, isolate D. Haelew. 1499a (9 thalli), MT235696 (SSU), MT235719 (LSU).

**Hosts and distribution.** – Currently known from temperate and tropical biomes of the Eastern Hemisphere, with records in many countries in Europe (France, Hungary, Italy, Slovakia, Spain, the UK), Africa (Egypt, Gabon, Kenya, Sierra Leone, Tunisia), and Asia (India, Indonesia, Israel, Myanmar, Peninsular Malaysia, Taiwan, Thailand). Reported hosts are *Basilina pumila* (Scott, 1914), *Leptocyclopodia ferrarii* (Rondani, 1878), *Eucampsipoda* spp., *Nycteribia* spp., and *Penicillidia dufourii* (Westwood, 1835) (Speiser 1901; Thaxter 1901; Balazuc 1971; Blackwell 1980a, 1980b; Haelewaters et al. 2017; Szentiványi et al. 2018a). Host bats include sedentary tropical, sedentary temperate, and migrating species.

**Notes.** – Laboulbeniales are obligate biotrophic fungi of arthropods. About 80 % of described Laboulbeniales taxa are known from beetles (Coleoptera), but these fungi are found on a wide variety of hosts, including ants (Hymenoptera: Formicidae), harvestmen (Opiliones), millipedes (Diplopoda), mites (Acari), true bugs (Hemiptera), and flies (Diptera) – including the ectoparasitic bat flies (Enghoff & Santamaría 2015; Haelewaters et al. 2017, 2020a; Santamaría et al. 2017). Bat flies are obligate hematophagous parasites of bats (Mammalia: Chiroptera) belonging to two families, Nycteribiidae and Streblidae. Both families show a worldwide distribution but nycteribiids have a higher diversity in the Eastern Hemisphere, whereas streblids show a higher diversity in the Western Hemisphere. Currently, about 21 nycteribiid genera with 275 species and 31 streblid genera with 227 species are described (Dick & Patterson 2006).

Four genera of bat fly-associated Laboulbeniales are known: *Arthrorhynchus* Kolen., *Dimeromyces* Thaxt., *Gloeandromyces* Thaxt. and *Nycteromyces* Thaxt. (Dogonniuck et al. 2019, Haelewaters et al. 2020a). *Arthrorhynchus* species are restricted to the Eastern Hemisphere. There are currently four described species in the genus, all parasitizing nycteribiid bat flies: *Arthrorhynchus acrandros* Merola, *A. cyclopodiae* Thaxt., *A. eucampsipodae* Thaxt.,

and *A. nycteribiae* (Peyr.) Thaxt. [although *A. acrandros* is disputed (Haelewaters et al. 2017)].

The here presented records of *A. eucampsipodae* from Bulgaria, Rwanda, and South Africa are new country records. *Arthrorhynchus eucampsipodae* has thus far been found on *E. africanum* in Gabon, Rwanda, Sierra Leone and South Africa (Blackwell 1980a, Balazuc 1971, this study). *Eucampsipoda africanum* has a wide distribution in sub-Saharan Africa, where its main bat host *R. aegyptiacus* occurs. Additionally, *E. africanum* occasionally parasitizes other cave-dwelling bat species such as *Eidolon helvum*, *Hipposideros caffer*, *H. gigas*, and *Mi. inflatus* (Theodor 1967, Obame-Nkoghe et al. 2016). In a recent study, Szentiványi et al. (2018a) focused on bat flies collected from the cave-dwelling bat *Mi. schreibersii* in Europe and found *A. eucampsipodae* only from *N. schmidlii* bat flies (23 infected specimens out of 468). This species of *Arthrorhynchus* seems to have a wide host spectrum but mostly occurs on bat flies associated with cave-dwelling bat species.

We generated 894–523 bp LSU sequences from different isolates of *A. eucampsipodae*, which share 98.53–100 % identity to one another, and 96.58–98.10 % identity with *A. nycteribiae*. In the LSU phylogeny (Fig. 34), *A. eucampsipodae* forms two clades, each clade consisting of isolates sampled from the same host genus (*Eucampsipoda*, *Nycteribia*). Sequences for the two isolates from *E. africanum* share 100 % identity but this “*Eucampsipoda*” clade only received moderate support (MLBS=69). The “*Nycteribia*” clade receives maximum support and consists of two isolates, one from *N. schmidlii* (GenBank accession no. MT235719), and the other from *N. vexata* (MT241715). Although these results may be premature to draw strong conclusions, they point to *A. eucampsipodae* being a complex of multiple species segregated by host genus. This presumed speciation pattern is similar to what was recently shown for *Hesperomyces virescens* Thaxt., a parasite of ladybirds in various genera (Coleoptera, Coccinellidae) (Haelewaters et al. 2018a). It is clear that the two clades of *A. eucampsipodae* are representative of segregation (speciation) but we must incorporate material from *E. hyrtlui* (Kolenati, 1856), the bat fly host on which *A. eucampsipodae* was originally described (Thaxter 1901), before making taxonomic decisions. Until we know what is the relation of *A. eucampsipodae* s.s. to the two clades uncovered by this study, we refrain from describing new species in the complex.

**Authors:** D. Haelewaters, J. Liu, T. Szentiványi, W.P. Pfliegler, A.D. Sándor, Á. Péter, W. Markotter, P. Christe, O. Glazot & M.C. Aime

## Ascomycota, Laboulbeniomycetes, Laboulbeniales, Laboulbeniaceae

*Arthrorhynchus nycteribiae* (Peyr.) Thaxt., in Clements & Shear, The genera of fungi, Ed. 2 (New York): 243 (1931). – Fig. 33a

**Basionym.** – *Helminthophana nycteribiae* Peyr., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 68: 250 (1873).

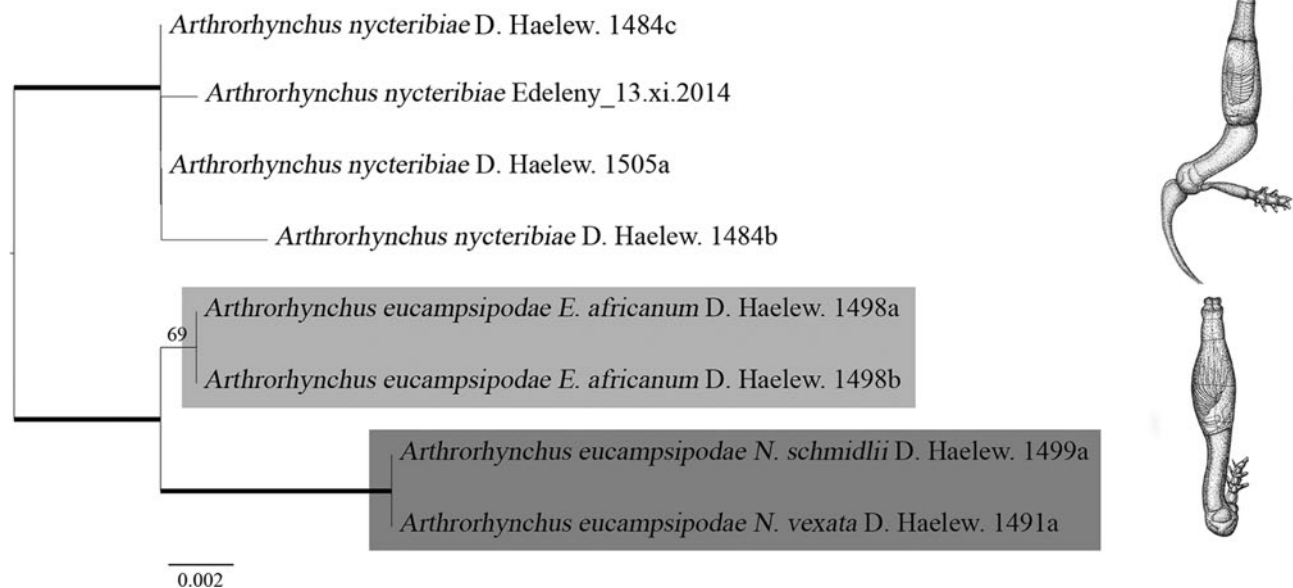
**Material examined.** – BULGARIA. Lovech Province, Chavdarts village, Mandrata Cave, 43°14'30.9336"N, 24°58'02.3664"E, 9 September 2017, on female *Penicillidia conspicua* Speiser, 1901 (Diptera, Nycteribiidae) collected from male adult *Mi. schreibersii*, A0974L/D. Haelew. 1484 [bat fly labels] A0974 [bat label], leg. A. Sandor & Á. Péter, slide PUL F25989. – SOUTH AFRICA. Limpopo, Muhave Cave, 24°06'53.892"S, 30°07'17.436"E, on male *E. africanum* collected from male *R. aegyptiacus*, UP8089 [bat fly label], 27 September 2017, leg. W. Markotter, slide PUL F27654. – TANZANIA. Serengeti National Park, Banagi, on *P. pachymela* (Diptera, Nycteribiidae) collected from *Hipposideros caffer*, 811–830/D. Haelew. 1496 [bat fly labels], 14 April 1971, leg. J.D. Hawkins, slide PUL F27646; Serengeti National Park, Kilima Fedha, on *P. pachymela* collected from *Rhinolophus* sp., 530–537/D. Haelew. 1497 [bat fly labels], 22 October 1970, leg. J.D. Hawkins, slide PUL F27655.

**Material sequenced.** – BULGARIA. Lovech Province, Chavdarts village, Mandrata Cave, 43°14'30.9336"N, 24°58'02.3664"E, on female *P. conspicua* Speiser, 1901 (Diptera, Nycteribiidae) collected from male adult *Mi. schreibersii*, A0974L [bat fly label] A0974 [bat label], 9 September 2017, leg. A. Sándor & Á. Péter, isolate D. Haelew. 1484b (2 adult thalli, tergites), MT235715 (LSU); *Ibid.*, isolate D. Haelew. 1484c (4 adult thalli, tergites), MT235716 (LSU); Montana

Province, Chiprovtsi Municipality, near Gorna Luka, Misin Kamak, 43°27'45.1692"N, 22°53'15.2952"E, 7 November 2017, on male *P. conspicua* collected from adult male *Mi. schreibersii*, A0841L [bat fly label] A0841 [bat label], leg. A. Sándor & Á. Péter, isolate D. Haelew. 1505a (2 adult thalli, left-hand side of last sternite), MT235697 (SSU), MT235720 (LSU).

**Hosts and distribution.** – Known from many countries in Europe: Austria, “Bulgaria and/or Slovakia” (Samšišáková 1960), Czech Republic, Croatia, Denmark, France, Georgia, Hungary, Italy, the Netherlands, Poland, Portugal, Romania, Russia (Kaliningrad; Speiser 1901), Serbia, Slovakia, Spain, Sweden, and Switzerland (Haelewaters et al. 2017; Szentiványi et al. 2018a, 2018b). There are also a few records from Africa (Kenya, Zambia), Asia (Sri Lanka), and Australia (Blackwell 1980a, 1980b). Reported hosts are *Nycteribia* spp., *Penicillidia* spp., and *Phthiridium* spp.

**Notes.** – The here presented records of *A. nycteribiae* from Tanzania and South Africa are new country records, and the material from Bulgaria represents the first undoubtful records for this country (Samšišáková 1960). Our records of *A. nycteribiae* were found on *E. africanum*, *P. conspicua*, and *P. pachymela*. Of these, *P. conspicua* has been cited as the main host of *A. nycteribiae*; Haelewaters et al. (2017) reported 38 infected bat flies out of 152 (prevalence of 25.0 %) from Hungary and Romania. Similarly, during their study of Laboulbeni-



**Fig. 34.** Preliminary phylogeny of *Arthrorhynchus* isolates reconstructed from an LSU dataset. The topology is the result of ML inference performed with IQ-TREE. Thick branches represent maximum bootstrap support. Light shading shows isolates of *A. eucampsipodae* originating from *Eucampsipoda africanum*, whereas darker shading shows isolates from either *Nycteribia schmidlii* or *N. vexata*.

**Tab. 2.** Published records of bat fly-associated Laboulbeniales from the African continent. Records in boldface are newly reported here.

Species	Country	Host
<i>Arthrorhynchus eucampsipodae</i>	Egypt	<i>Eucampsipoda hyrtlII</i> (Kolenati, 1856)
<i>Arthrorhynchus eucampsipodae</i>	Gabon	<i>Eucampsipoda africanum</i> Theodor, 1955
<i>Arthrorhynchus eucampsipodae</i>	Kenya	<i>Nycteribia schmidlii</i> Schiner, 1853
<b><i>Arthrorhynchus eucampsipodae</i></b>	<b>Rwanda</b>	<b><i>Eucampsipoda africanum</i> Theodor, 1955</b>
<i>Arthrorhynchus eucampsipodae</i>	Sierra Leone	<i>Eucampsipoda africanum</i> Theodor, 1955
<b><i>Arthrorhynchus eucampsipodae</i></b>	<b>South Africa</b>	<b><i>Eucampsipoda africanum</i> Theodor, 1955</b>
<i>Arthrorhynchus eucampsipodae</i>	Tunisia	<i>Nycteribia vexata</i> Westwood, 1835
<i>Arthrorhynchus nycteribiae</i>	Kenya	<i>Penicillidia fulvida</i> (Bigot, 1885)
<i>Arthrorhynchus nycteribiae</i>	Kenya	<i>Penicillidia fulvida</i> (Bigot, 1885)
<b><i>Arthrorhynchus nycteribiae</i></b>	<b>South Africa</b>	<b><i>Eucampsipoda africanum</i> Theodor, 1955</b>
<b><i>Arthrorhynchus nycteribiae</i></b>	<b>Tanzania</b>	<b><i>Penicillidia pachymela</i> Speiser, 1901</b>
<i>Arthrorhynchus nycteribiae</i>	Zambia	<i>Penicillidia pachymela</i> Speiser, 1901
<i>Dimeromyces capensis</i>	South Africa	<i>Brachytarsina africana</i> (Walker, 1849)
<i>Nycteromyces orientalis</i>	Tanzania	<i>Brachytarsina alluaudi</i> (Falcoz, 1923)

ales associated with bat flies from *Mi. schreibersii* bats in eight European countries, Szentiványi et al. (2018a) sampled 144 *P. conspicua*, of which 33 were infected with *A. nycteribiae* (prevalence of 22.9 %). In Europe, this fungus is predominantly associated with bat flies parasitizing migratory *Mi. schreibersii* (Moesz 1931; Thaxter 1931; Balcells 1954, 1955; Samšičáková 1960; Balazuc 1971; Blackwell 1980a, 1980b; Haelewaters et al. 2017; Szentiványi et al. 2018a).

The majority of bat fly-associated Laboulbeniales are reported from the neotropics and Europe (Thaxter 1917, Blackwell 1980a, 1980b, Haelewaters et al. 2017, Szentiványi et al. 2018a, Dogonniuck et al. 2019, Haelewaters & Pfister 2019). African records are rare (Tab. 2), with *A. eucampsipodae* previously known in Egypt, Gabon, Kenya, Sierra Leone, and Tunisia (Speiser 1901; Thaxter 1901; Balazuc 1971; Blackwell 1980a, 1980b); *A. nycteribiae* in Kenya and Zambia (Blackwell 1980a, 1980b); *Dimeromyces capensis* in South Africa; and *Nycteromyces orientalis* in Tanzania (Dogonniuck et al. 2019). Of the 55 African bat flies screened at the entomology collection of the California Academy of Sciences, only two specimens of *P. pachymela* from Tanzania were infected.

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### Basidiomycota, Agaricomycetes, Agaricales, Agaricaceae

***Calvatia lilacina*** (Mont. & Berk.) Henn., *Hedwigia* 43(3): 205 (1904). – Figs. 35–37.

*Basionym.* – *Bovista lilacina* Mont. & Berk., London J. Bot. 4: 64 (1845).

*Synonyms.* – *Globaria lilacina* (Mont. & Berk.) Speg., Anal. Soc. Cient. Argent. 9(4): 187 (1880).

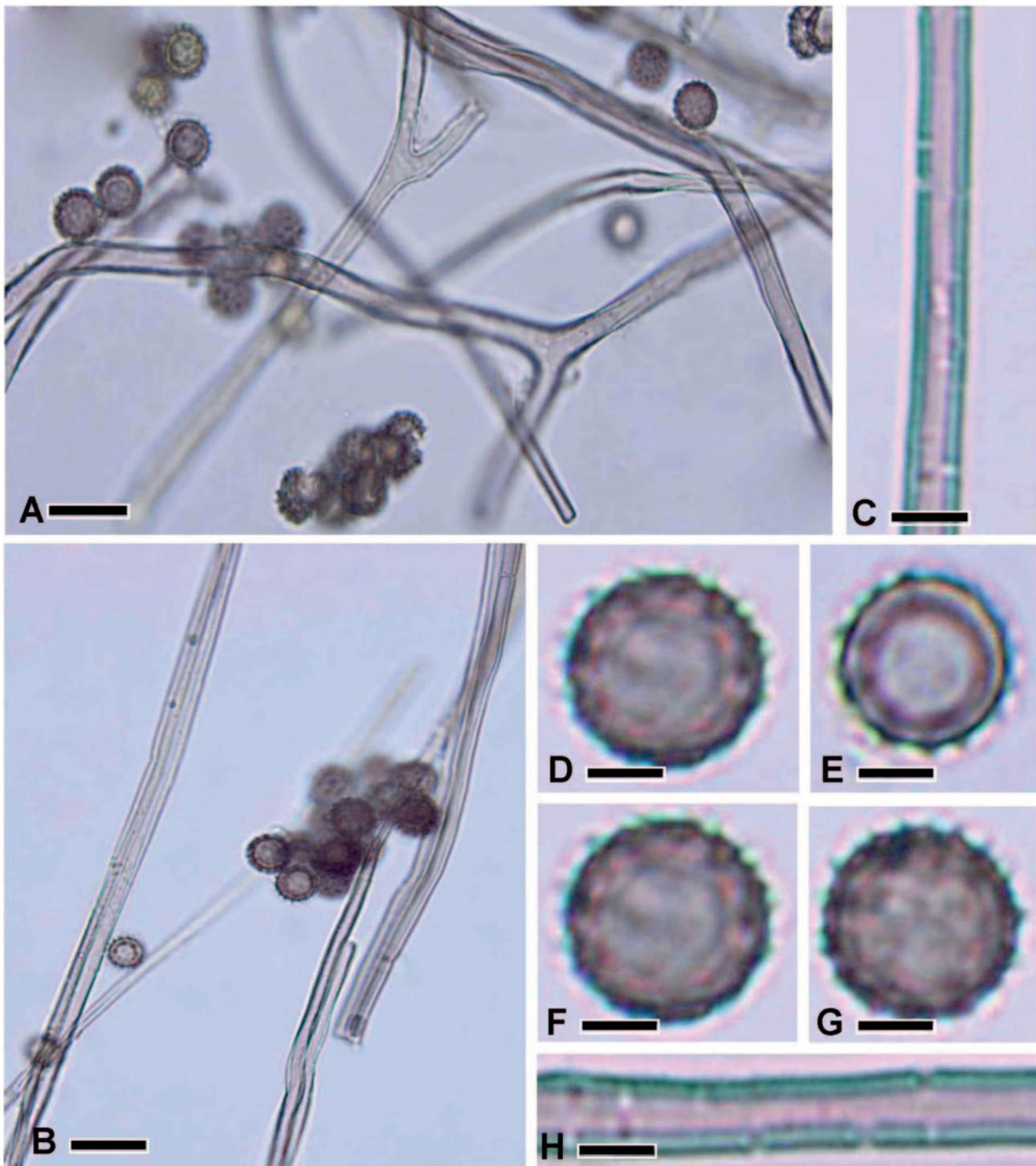
*Lycoperdon lilacinum* (Mont. & Berk.) Speg., Anal. Mus. Nac. Hist. Nat. B. Aires 12(3–6): 252 (1881).

*Material examined.* – PAKISTAN. Khyber Pak-tunkhwa Province, Mansehra District, Oghi, 975 m a.s.l., on soil under *Pinus wallichiana* (Pinales, Pinaceae), 1 September 2008, leg. M. Fiaz, NYG207 (LAH 10000082); Autonomous Territory of Gilgit-Baltistan, Deosai Plains, Deosai National Park, 4114 m a.s.l., in grass, 10 September 2011, leg. A.R. Niazi, CPK1 (LAH 10000083).

*Description.* – Basidiomata growing in groups, 60–90 mm wide × 45–60 mm high, subglobose to broadly obpyriform to obovoid, slightly tapering at the base, sometimes forming a pseudo-stipe below. – Peridium evanescent, violaceous brown at maturity; attached to the substrate by thick rhizomorphs. – Rhizomorphs brown densely encrusted with the particles of soil. – Subgleba with diaphragm, well-developed, compact, cottony, occupying two-third of basidioma, separated from glebal portion by diaphragm. – Diaphragm distinct, greyish brown, slightly depressed from the center, center rough, cracked with



**Fig. 35.** *Calvatia lilacina*. **A.** Different views of basidiomata, collection LAH 10000083. **B-C.** Mature basidioma, collection LAH 10000082. Scar bars 1.7 cm.

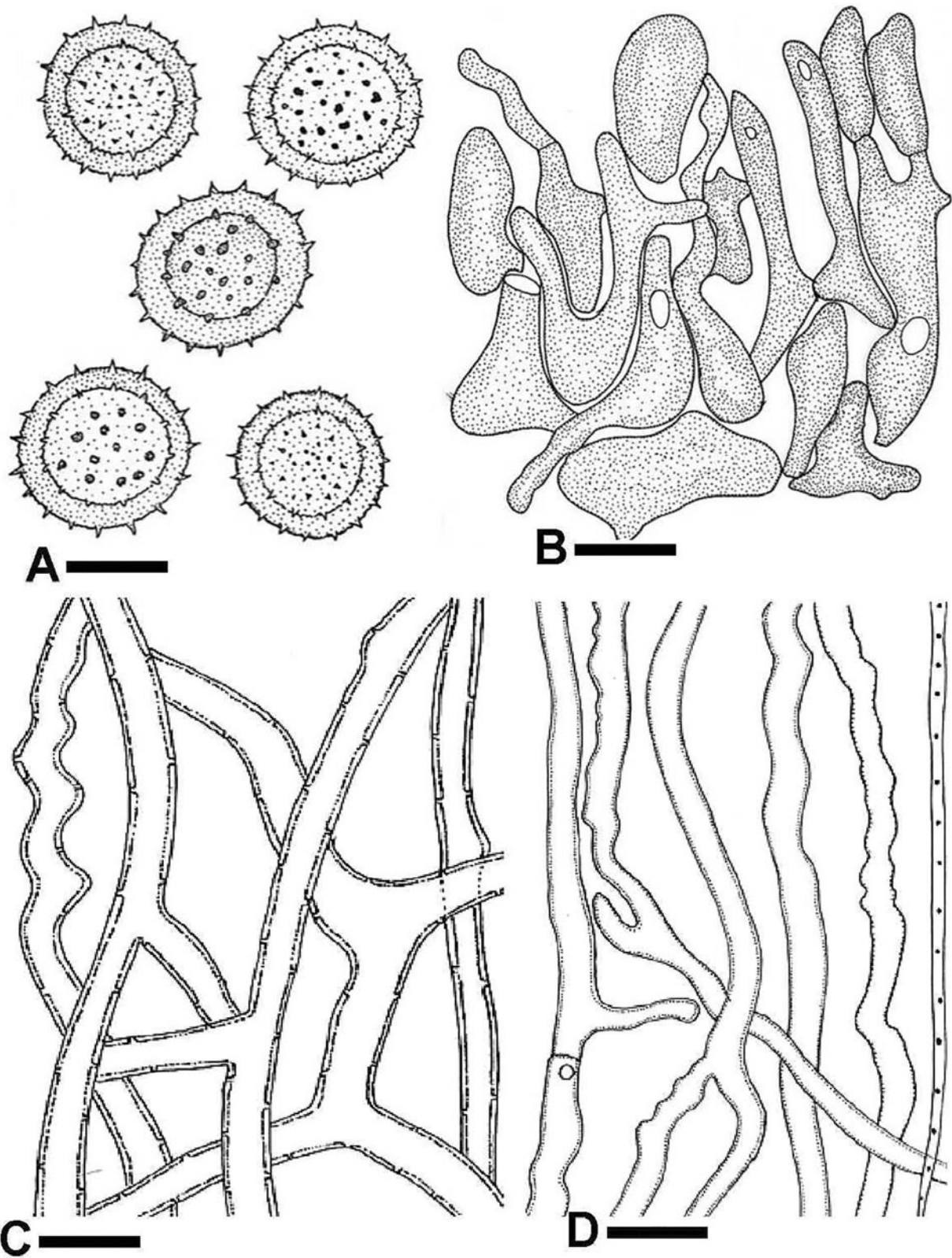


**Fig. 36.** *Calvatia lilacina*. **A–C, H.** Pitted *Calvatia*-type capillitium. **D–G.** Echinulate basidiospores. Scale bars **A–B** 12  $\mu\text{m}$ ; **C, H** 10  $\mu\text{m}$ ; **D–G** 3.2  $\mu\text{m}$ .

age after exposure, margins extend outwards, wavy.  
 – Gleba violaceous brown, lanose, pulverulent with age. – Basidiospores globose, echinulate, 7.0–8.5  $\mu\text{m}$  in diam. (including echines), 4.5–5.4

$\mu\text{m}$  in diam. (excluding echines), pedicel absent or rudimentary, brown in both water and 5 % KOH mounts. – Eucapillitium *Calvatia*-type, brown, non-elastic, up to 6.4  $\mu\text{m}$  in diam., with wall thick-





**Fig. 37.** Micromorphological features of *Calvatia lilacina*. **A.** Echinulate basidiospores. **B.** Exoperidial elements. **C.** Pitted capillitial hyphae. **D.** Endoperidial hyphae (bar = 10  $\mu\text{m}$ ). Scale bars A 4  $\mu\text{m}$ ; B, D 10  $\mu\text{m}$ ; C 7  $\mu\text{m}$ ; *del.* N.Yousaf.

ness up to 1  $\mu\text{m}$ , smooth to slightly encrusted, straight to subundulate, often bulging at some points, frequently branched, tapering at the ends up to 1.2  $\mu\text{m}$  thin; septa rarely seen, hypha broken where septa present; brown in water mounts. – Pits numerous, small to medium sized, circular. – P a r a c a p i l l i t i u m scarce, branched, hyaline, septate. – E x o p e r i d i u m composed of subglobose, oval to ellipsoid, elongated to irregular shaped hyphal elements, brown, thick-walled. – E n d o p e r i d i u m composed of thin-walled, branched and aseptate (rarely joint-like septa present) brown hyphae.

Habitat and distribution. – Known from five continents: North America (USA), South America (Argentina, Brazil, Chile), Europe (Spain), Asia (India, the Philippines, Taiwan), and Oceania (Australia, New Zealand). Growing solitary to gregarious in forests and grasslands.

Notes. – The genus *Calvatia* Fr. was established by Fries (1849) with *C. craniiformis* (Schwein.) Fr. as type species. The genus is characterized by medium to large basidiomata that have a reduced to well-defined subgleba. Dehiscence occurs by irregular rupturing of peridium and not through a definite pore (Li 2011, Cortez et al. 2012). *Calvatia* has been extensively studied throughout the years (Kreisel 1992, 1994; Lange 1990, 1993, 1994; Calonge 1998; Gube 2007; Kasuya & Kotumoto 2008; Cortez & Alves 2012). The number of *Calvatia* species is 44 thus far (Kirk et al. 2008; Suárez et al. 2009; Alves & Cortez 2013; Alfredo et al. 2014; Crous et al. 2018, 2019; Gunasekaran et al. 2018) but more species are awaiting description (e.g., Yousaf 2014). In Pakistan, the genus is represented by four species: *Calvatia ahmadii* Khalid & S.H. Iqbal, *C. craniiformis*, *C. cyathiformis* (Bose) Morgan, and *C. excipuliformis* var. *excipuliformis* (Scop.) Perdeck (Ahmad 1956; Khalid & Iqbal 1996, 2004; Ahmad et al. 1997). *Calvatia lilacina* is reported here a new record for the country. This species is characterized by the following characters: a well-developed sterile base (subgleba) of up to 60 mm in diam. with conspicuous diaphragm; fragile peridium that encloses the upper glebal part, weathering away at maturity; violaceous gleba; globose, strongly echinulate basidiospores; and pitted capillitium.

*Calvatia lilacina* is morphologically quite distinct but it may be confused with *C. cyathiformis* and *C. fragilis* (Quél.) Morgan. Although these three species have been synonymized by several authors in the past due to the presence of violaceous gleba in all three (Bottomley 1948; Zeller & Smith 1964; Liu 1984; Kreisel 1992, 1994; Moyersoen & Demoulin 1996; Wartchow & Silva 2007; Bates et al. 2009;

Chakraborty et al. 2012), they exhibit striking differences. The color of basidiomata is one morphological feature by which *C. cyathiformis* and *C. lilacina* can be separated: reddish-brown in *C. cyathiformis* vs. violaceous brown in *C. lilacina*. After rupture of the peridium and dispersal of spores, a cup-shaped structure is left, which is a characteristic for *C. cyathiformis*, but not found in *C. lilacina*. Finally, a distinct diaphragm separating the upper fertile glebal portion from the lower subgleba becomes evident after spore dispersal—this is a distinct feature of *C. lilacina* (Baseia 2003) not found in *C. cyathiformis*.

Both *C. fragilis* and *C. lilacina* have large basidiomata, violaceous gleba, and a fragile peridium, which breaks away at maturity from the upper portion only leaving remnants of the upper glebal portion. One striking difference is that *C. fragilis* lacks a well-developed subgleba and a distinct diaphragm—both of which are present in *C. lilacina*. Another difference are the basidiospores, which are finely echinulate in *C. fragilis* vs. strongly echinulate in *C. lilacina*. In the literature, several authors have considered *C. cyathiformis*, *C. fragilis*, and *C. lilacina* as synonyms. However, recent molecular phylogenetic studies suggest that these species are distinct taxa (Crous et al. 2018, 2019). Below, we provide a morphological key of *Calvatia* species of sect. *Hippoperdon* to resolve morphological misperceptions of these species.

*Calvatia lilacina* also shares some of its morphological features with *C. brasiliensis* R.J. Ferreira, R.L. Oliveira, B.D.B. Silva, M.P. Martín & Baseia and *C. caatinguensis* R.L. Oliveira, R.J. Ferreira, B.D.B. Silva, M.P. Martín & Baseia, both recently described from Brazil (Crous et al. 2018, 2019). *Calvatia brasiliensis* is similar in its violet-brown gleba, similar to *C. lilacina*. However, *C. brasiliensis* has smaller basidiomata, reduced subgleba, *Lycoperdon*-type capillitium, and smaller basidiospores (5.8–6.6  $\times$  5.2–6.5  $\mu\text{m}$  vs. 7.0–8.5  $\times$  7.0–8.5  $\mu\text{m}$ ). The second Brazilian species, *C. caatinguensis*, shares with *C. lilacina* a well-developed subgleba with distinct color band at the apex (diaphragm) and *Calvatia*-type capillitium. *Calvatia caatinguensis* can be separated from *C. lilacina* by its smaller, subglobose basidiospores (5.4–7.4  $\times$  5.1–6.7  $\mu\text{m}$  vs. 7.0–8.5  $\times$  7.0–8.5  $\mu\text{m}$ ).

During our study, two collections of *Calvatia* were identified as *C. lilacina* based on a unique combination of morphological features (well-developed subgleba, distinct diaphragm, globose basidiospores). We also generated ITS sequences that were included in a dataset of similar sequences (Tab. 1).

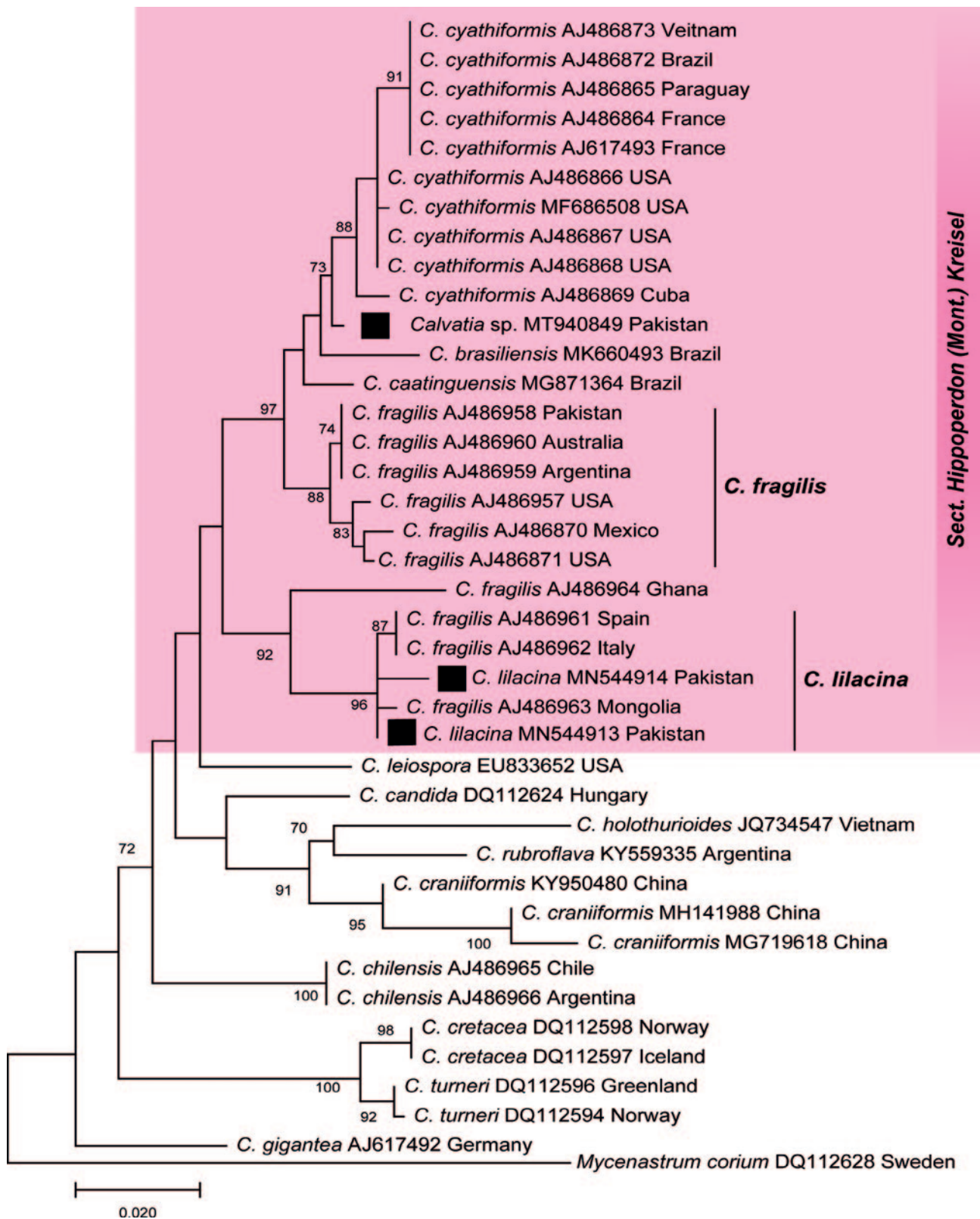
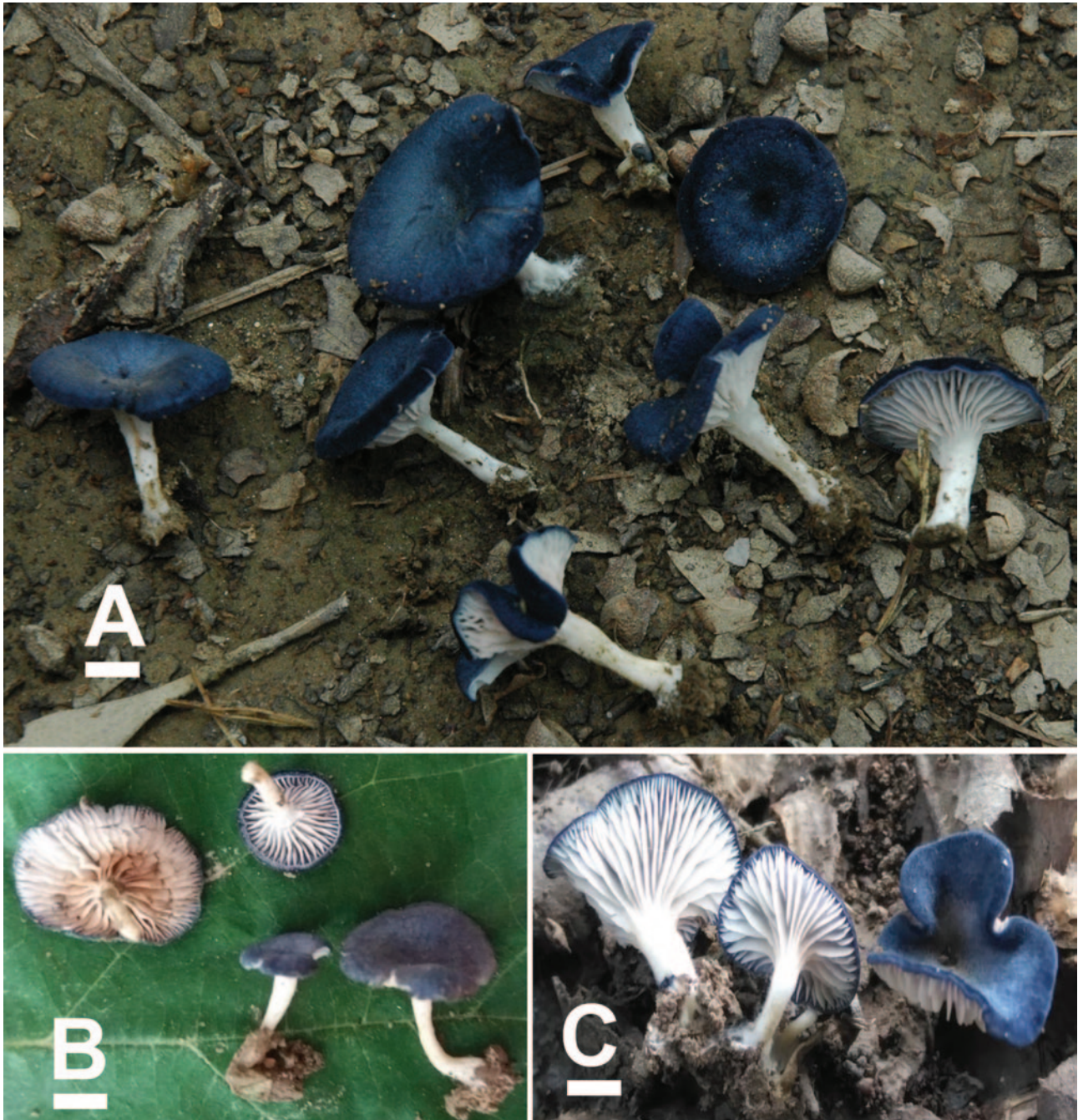


Fig. 38. Phylogeny of *Calvatia* sect. *Hippoperdon* reconstructed from an ITS dataset. The topology is the result of ML inference performed with MEGA X. Newly generated sequences are highlighted with black squares. MLBS  $\geq 70$  are indicated at the nodes.

The final alignment consisted of 691 characters, of which 494 were constant and 101 were parsimony-informative. In the resulting tree, our isolates of *C. lilacina* were placed in the *C. fragilis* clade of Crous et al. (2019) (Fig. 38). This clade includes what Crous et al. considered an ex-type for *C. fragilis* but this is not an actual type collection. We are convinced by

our morphological study that the Pakistani material we investigated represents *C. lilacina*. This was also confirmed by G. Moreno (personal communication). As a result, we renamed the clades from Crous et al. (2019) (the *C. fragilis* clade from Crous et al. is *C. lilacina*, and vice versa). It is obvious that the entire group of *Calvatia* sect. *Hippoperdon* is in ur-



**Fig. 39.** *Entoloma shandongense*. A–C. Basidiomata *in situ*, multiple collections. Scale bars A 0.4 cm, B–C 0.5 cm.

gent need of revision, including morphological investigations of herbarium collections, including the types, thorough phylogenetic study, and international collaboration.

**Key to closely related taxa of *Calvatia* section *Hippoperdon***

1. Sub-gleba well-developed .....2
- 1\*. Sub-gleba poorly developed or reduced .....4
2. Diaphragm absent .....*C. cyathiformis*
- 2\*. Diaphragm present .....3
3. Basidiospores subglobose, echinulated, 5.4–7.4 × 5.1–6.7 μm ..... *C. caatinguensis*
- 3\*. Basidiospores globose, echinulated, 7.0–8.5 μm in diam. .... *C. lilacina*
4. *Lycoperdon*-type capillitium; basidiospores globose to subglobose, echinulated, 5.8–6.6 × 5.2–6.5 μm ..... *C. brasiliensis*
- 4\*. *Calvatia*-type capillitium; basidiospores globose, finely echinulated, 4.0–5.5 μm in diam. .... *C. fragilis*

Authors: N. Yousaf, M. Fiaz, A.R. Niazi, H. Ahmad & A.N. Khalid

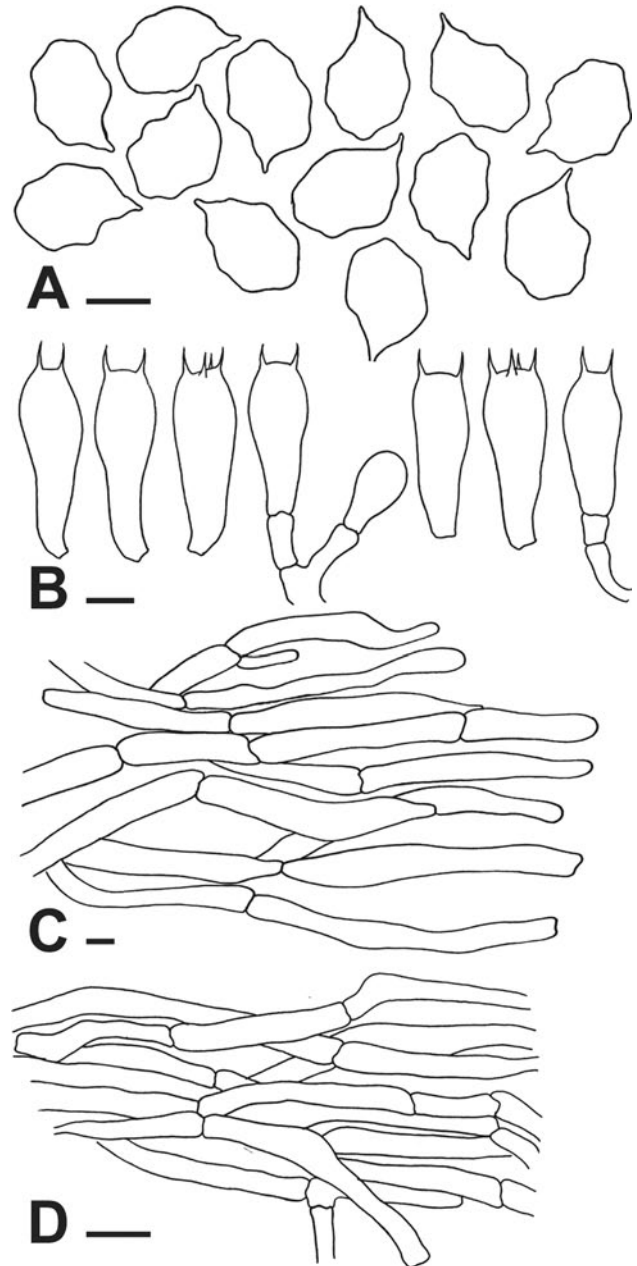
**Basidiomycota, Agaricomycetes, Agaricales, Entolomataceae**

***Entoloma shandongense*** T. Bau & J.R. Wang, Mycotaxon 124: 165–171 (2013). – Figs. 39–40

**Material examined.** – PAKISTAN. Punjab Province, Lahore District, Lahore, University of the Punjab, Quaid-i-Azam Campus, New Campus Botanical Garden, 31°29'57.98"N, 74°17'59.07"E, 217 m a.s.l., 16 July 2013, leg. T. Qasim & A.N. Khalid, T35 (LAH 36554); *Ibid.*, hostel road along the water channel under *Bombax ceiba* (Malvales, Malvaceae) and *Morus alba* (Rosales, Moraceae), 18 July 2018, leg. M. Ali, MA10 (LAH 36555); *Ibid.*, hostel road along the water channel near Main Library at 31°29'57.85"N, 74°18'20.39"E, 15 July 2019, leg. M. Ali, MA15 (LAH 36556); Punjab Province, Dera Ghazi Khan Division, Muzaffargarh District, in the vicinity of Taunsa Barrage, 65 m a.s.l., in soil under hardwood trees, 11 August 2019, leg. M. Ali & H. Nawaz, J1 (LAH 36560).

**Description.** – Basidiomata small, omphalinoid. – Pileus 0.5–1.5 cm in diam., convex to deeply umbilicate, infundibuliform with inflexed margins, non-hygrophanous, non-translucent, non-striate margins, irregularly lobed, uplifted and undulating when older; surface dry, shiny, silky, fibrillose, dark blue (7.5PB 2/18) with appressed fibrils, margins equal, entire, involute, cracked irregularly at maturity. – Context thin, white (10R 8/1). – Lamellae adnate, slightly decurrent up to 1–2 mm along the stipe, thin, distant, white (10R 8/1), margin entire, lamellulae present alternating with lamellae. – Stipe 0.7–1.7 × 0.1–0.2 cm, central, un-

equal in diameter, broader upwards gradually tapering towards base, fistulose, depressed angular, surface smooth, white tomentose covered with minute white hairs, base slightly swollen. – Annulus absent. – Volva absent. – Basidiospores [30/1/1] (6.5–)7.1–9.8(–10) × (5.8–)6.0–9.2(–9.5) μm, average 8.75 × 6.8 μm, Q=1.05–1.35, Q<sub>av</sub>=1.29±0.089, subisodiametric, angular with 5–8 irregular angles,



**Fig. 40.** Microscopic characters of *Entoloma shandongense*. A. Basidiospores. B. Basidia. C. Pileipellis. D. Stipitipellis. Scale bars A 5.3 μm, B 10.2 μm, C 20 μm, D 8.2 μm, del. M. Ali.

thick walled, apiculate, hyaline with light greenish or bluish tinge in 2 % KOH, non-dextrinoid, non-congophilous; single guttule with contents present. – Basidia (23.6–)24.4–29.5(–30.6) × (7.9–)8.2–9.8(–10.1) μm, average 26.5 × 9 μm, clavate to broadly clavate, thin-walled, smooth, hyaline in 2 % KOH, 2–4-spored, sterigmata with pointed ends, no clamps or short cells found at base. – Cheilocystidia not found. – Pleurocystidia absent. – Pileipellis a cutis made up of hyphae 4.2–12 μm wide, average 8.83 μm, hyaline with bluish tinge, septate, parallel to somewhat irregular in arrangement, smooth; terminal elements subclavate, cylindrical with apical papilla found occasionally, clamp connections absent. – Stipitipellis a cutis made up of hyphae 2.2–4.9 μm wide, average 3.48 μm, thin-walled, hyaline in 2 % KOH, smooth, septate, branched, parallel to overlapping in arrangement, clamp connections absent, no modified terminal ends or caulocystidia present.

**Distribution and habitat.** – Known from *Poa pratensis* (Poales, Poaceae) grassland in China (Wang & Bau 2013), under *Ficus religiosa* (Rosales, Moraceae) in India (Acharya et al. 2015), and on humus-rich soil or under angiosperm trees in Pakistan (this paper).

**Notes.** – Entolomataceae (Agaricales) is one of the largest euagaric families, with representatives being widely distributed around the world from the arctic to tropical regions. More than 1500 species of *Entoloma* have been described worldwide (Co-David et al. 2009, He et al. 2019, Wijayawardene et al. 2020). Despite being diverse in climate, geography, and flora, Pakistan is still understudied with regard to its fungal diversity (Hussain et al. 2018, Saba et al. 2020). The number of *Entoloma* species reported from Pakistan is only six. These are: *Entoloma cetratum* (Fr.) M.M. Moser, *E. gnaphalodes* (Berk. &

Broome) E. Horak, *E. incanum* (Fr.) Hesler, *E. mougeotii* (Fr.) Hesler, *E. papillatum* (Bres.) Dennis, and *E. sericeum* Quél. (Ahmad et al. 1997, Sultana et al. 2011). In this study, one more species is added as a new record for Pakistan, *E. shandongense*.

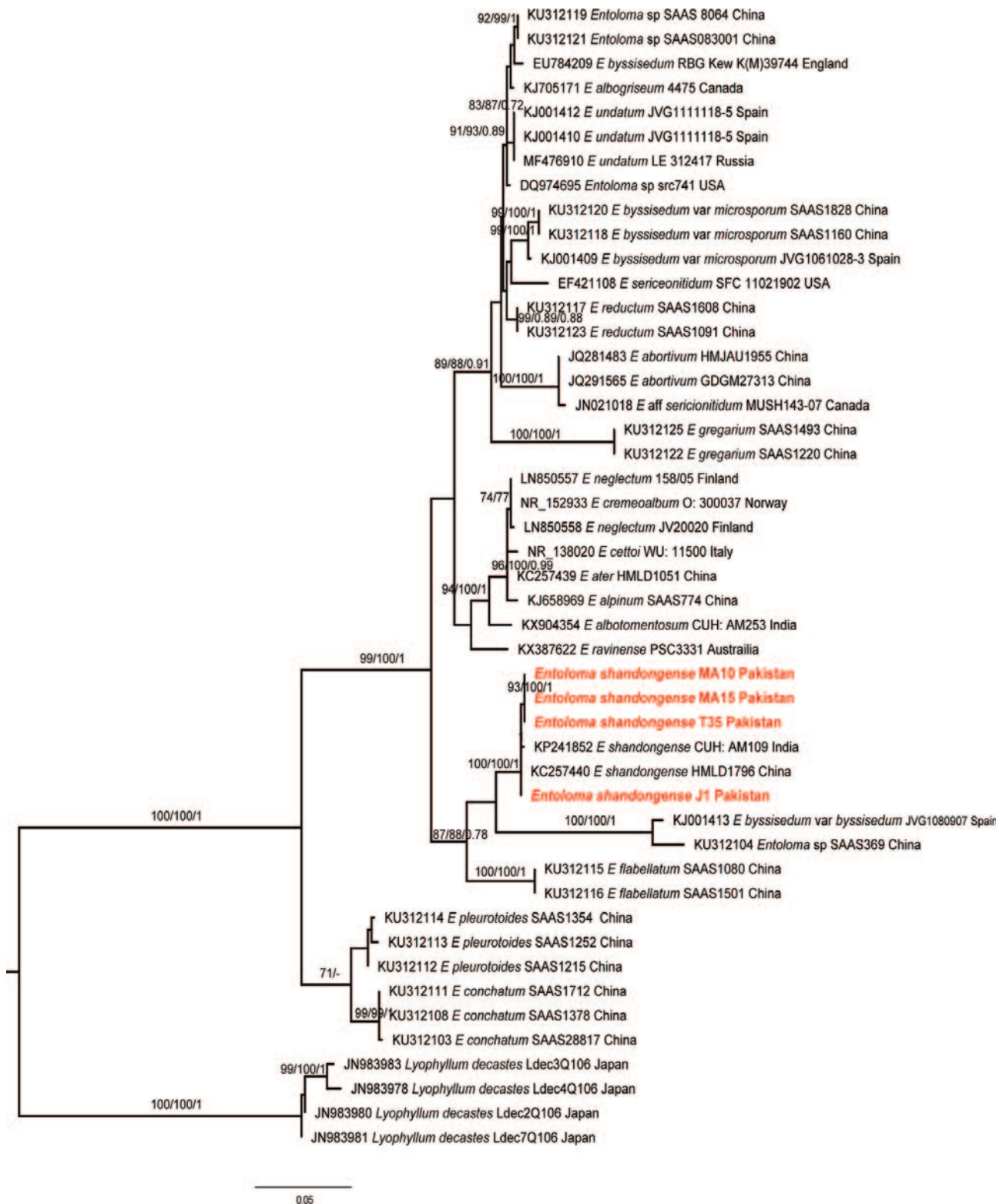
Our newly generated ITS sequences of *E. shandongense* were 660–674 bp in length and shared 99.52–98.87% identity with the Chinese (GenBank accession no. KC257440) and Indian (KP241852) sequences of this species. Phylogenetic analyses of an ITS dataset with 48 isolates placed sequences from Pakistani collections among a clade with *E. shandongense* isolates with maximum support (Fig. 41). Across the ITS region, there were eight nucleotide polymorphisms among existing isolates of *E. shandongense*. Of these, three were substitutions (A–T, C–Y, G–T); the others were deletions (Tab. 3).

The Pakistani material matches morphologically with previous descriptions of *E. shandongense*, described from China (Wang & Bau 2013) and later only reported in India (Acharya et al. 2015). *Entoloma shandongense* is mainly characterized by omphalinoid basidiomata, blue pileus, 5–8-angled, nodulose basidiospores, and the lack of all types of cystidia and clamp connections. Whereas many species of *Entoloma* have a blue pileus, they are rarely omphalinoid in habitus. *Entoloma ater* (Hongo) Hongo & Izawa resembles *E. shandongense* in its omphalinoid basidioma, but it can be separated by its often-purplish pileus and larger basidiospores (Hongo 1958, Li et al. 2009, He et al. 2012). Thus far, neither blue-colored *Entoloma* species nor species of subgenus *Claudopus* had been reported from Pakistan (Catcheside et al. 2016). Here, we add *E. shandongense* and a new subgenus of *Entoloma* (*Claudopus*) to the Funga of Pakistan.

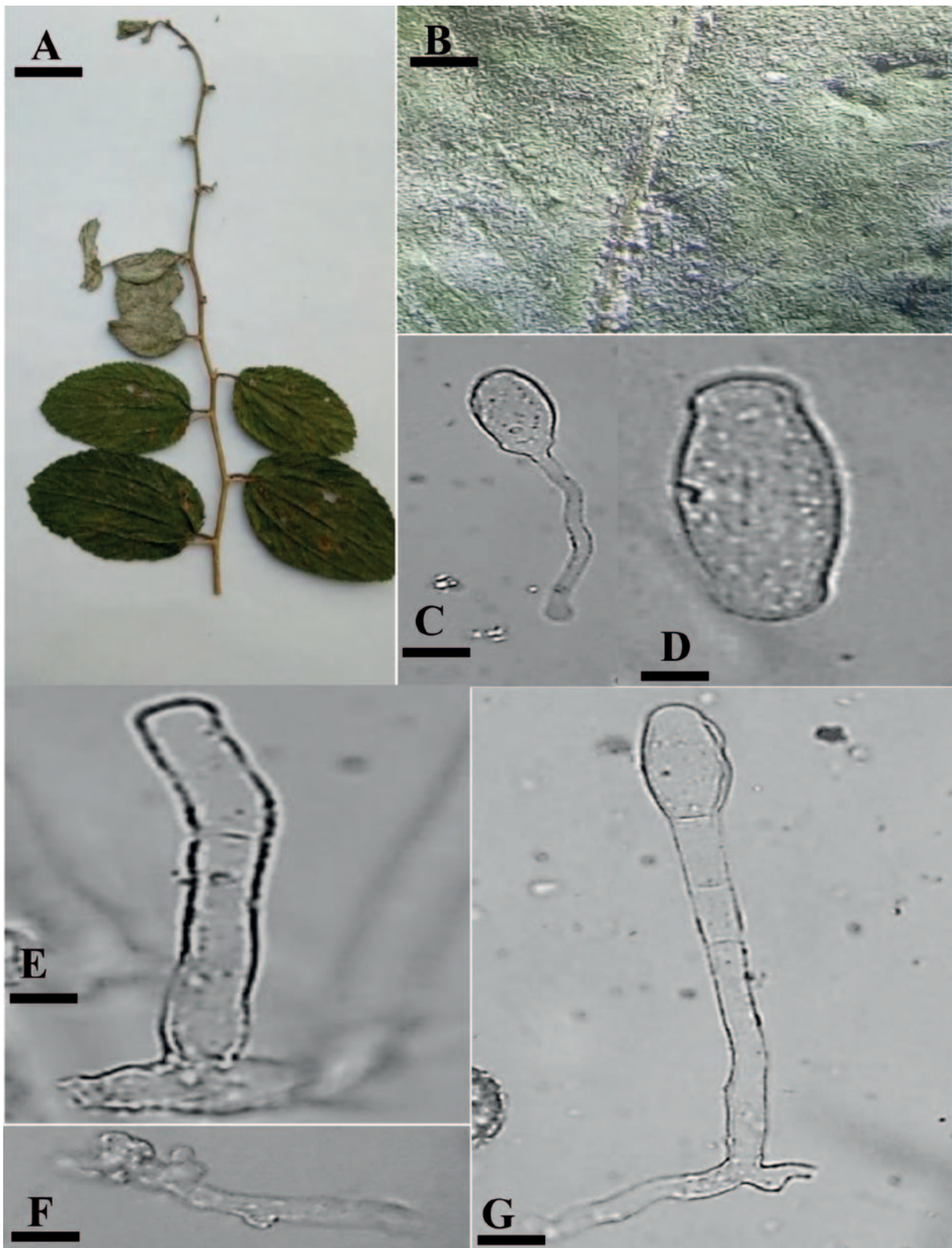
**Authors:** M. Ali, T. Qasim, H. Nawaz, A.R. Niazi & A.N. Khalid

**Tab. 3.** Polymorphic nucleotides from aligned ITS sequences showing variation among isolates of *Entoloma shandongense* from China (type), India, and Pakistan.

Isolate	Position							
	14	44	76	99	161	334	509	596
J1, Pakistan	A	G	C	A	A	C	T	T
MA10, Pakistan	A	G	-	T	A	Y	T	T
MA15, Pakistan	A	G	-	T	A	Y	T	T
T35, Pakistan	A	G	-	T	A	Y	T	T
KP241852, India	-	-	-	A	-	C	G	-
KC257440, China (type)	A	G	-	A	A	C	T	-



**Fig. 41.** Phylogeny of the genus *Entoloma* reconstructed from an ITS dataset of 48 isolates, with *Lyophyllum decastes* as out-group. The topology is the result of ML inference performed with RAxML. For each node, MLBS ( $\geq 70$ )/MPBS ( $\geq 70$ )/BIPP ( $\geq 0.7$ ) are presented above the branch leading to that node. Sequences of *E. shandongense* generated during this study are highlighted in red.



**Fig. 42.** *Erysiphe quercicola* on *Ziziphus jujuba*. **A.** Infected host plant. **B.** Infection viewed under stereomicroscope. **C.** Germinating conidium. **D.** Conidium. **E.** Foot cells. **F.** Appressoria. **G.** Conidiophore. Scale bars A 4 cm, B 8 mm, C–D 8  $\mu$ m, E 7  $\mu$ m, F 2  $\mu$ m, G 12  $\mu$ m.



## Ascomycota, Leotiomycetes, Helotiales, Erysiphaceae

***Erysiphe quercicola*** S. Takam. & U. Braun, in Takamatsu et al., Mycol. Res. 111: 819 (2007). – Fig. 42

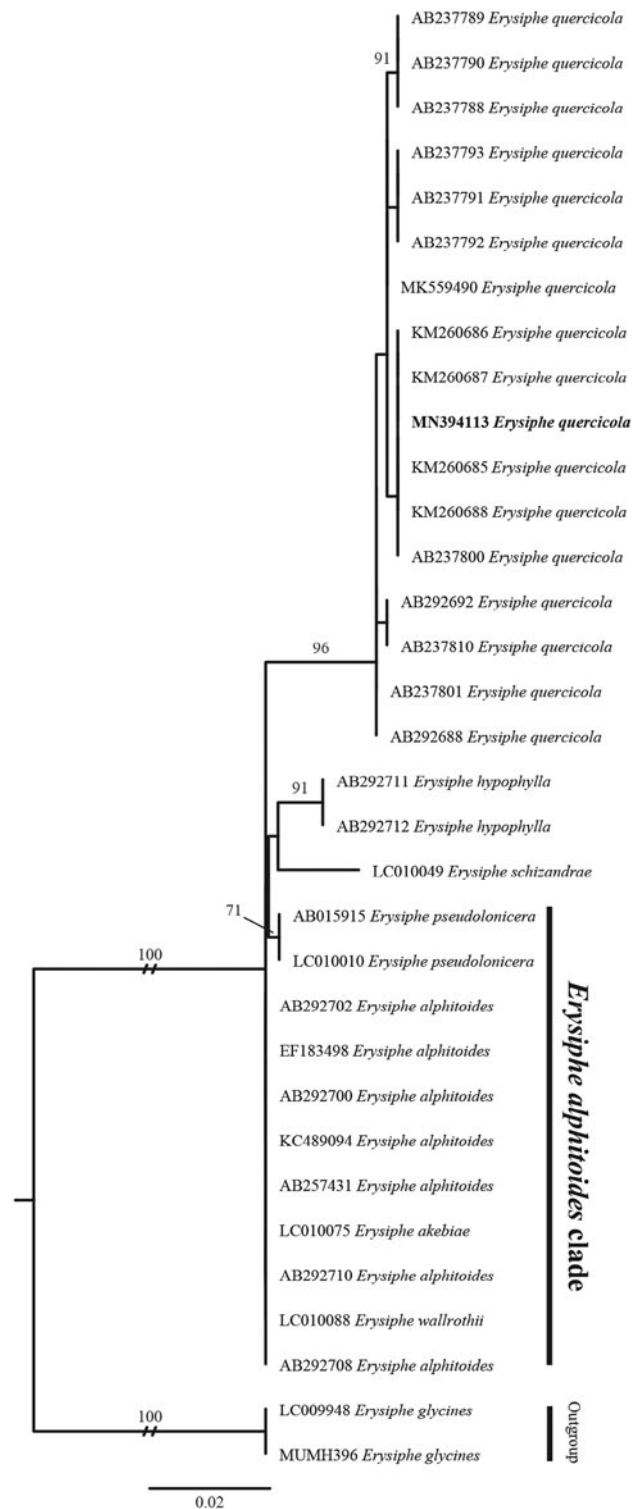
**Material examined.** – PAKISTAN. Khyber Pakhtunkhwa Province, Hazara Division, Abbottabad, Abbottabad District, Ayubia National Park, Mukshpuri, 34°03'36.72"N, 73°25'50.88"E, 2800 m a.s.l., on leaves of *Ziziphus jujuba* (Rosales, Rhamnaceae), 13 August 2018, leg. N.S. Afshan & J. Majeed, JP#5 (LAH 36141).

**Description.** – Mycelium amphigenous, persistent, dense, white, forming patches or effuse, epigenous, foliicolous, in patches, evanescent. – Hyphae about 4–7 µm wide; hyphal appressoria bilobed, distinct in pairs. – Conidiophores arising from the upper surface of superficial hyphae, erect, about 80–151 µm. – Foot cells cylindrical, straight, 44–74 × 7–10 µm; followed by 1 longer cell and 2–3 shorter cells. – Conidia catenulent, doliiform, subcylindrical to ellipsoid, 24–48 × 16–20 µm.

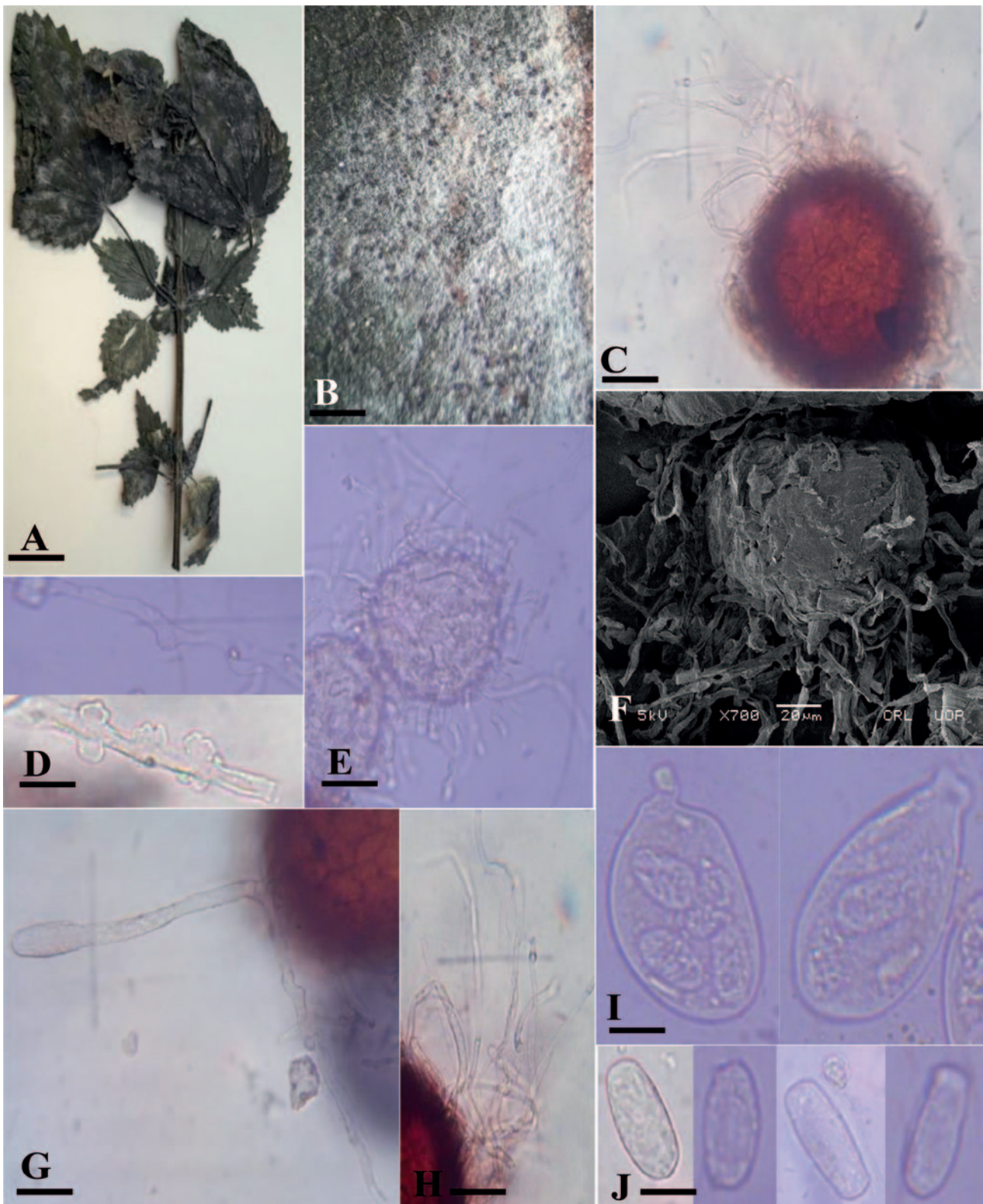
**Habitat and distribution.** – Known on *Acacia* spp., *Anacardium occidentale*, *Bixa orellana*, *Citrus* spp., *Hevea brasiliensis*, *Mangifera indica*, and *Quercus* spp. from many countries in South America, Europe, Africa, Asia, and Australia (Braun & Cook 2012); on *Ailanthus excels* from India; on *Cinnamomum camphora*, *Delonix regia*, and *Rumex crispus* from Brazil; on *Cyclobalanopsis* sp. and *Nephelium lappaceum* from Indonesia and Japan; on *Durio zibethinus* from Indonesia; and on *Murraya paniculata* from Taiwan (Farr & Rossman 2019).

**Notes.** – The genus *Erysiphe* consists of 478 species according to Wijayawardene et al. (2020) and belongs to the family Erysiphaceae in Helotiales s.l. (sensu Johnston et al. 2019). Morphology and molecular data point at *E. quercicola* as the identification for our fungus from *Z. jujuba* leaves. Our initial BLAST search found that our newly generated ITS sequence (GenBank accession no. MN394113) shares 99.69–100 % identity with the top 10 results—all *E. quercicola*. Our phylogenetic tree based on ITS (Fig. 43) retrieved our isolate in a cluster with 17 other isolates of *E. quercicola* with high support (BS=96). Inoculated leaves during pathogenicity test developed symptoms of *E. quercicola* after 7 days, whereas control plants remained symptomless. This report is the first one of a powdery mildew fungus from *Z. jujuba* in Pakistan.

**Authors:** N.S. Afshan, M. Riaz, J. Majeed & A.N. Khalid



**Fig. 43.** Phylogeny of the genus *Erysiphe* reconstructed from an ITS dataset of 31 isolates. The topology is the result of ML inference performed with RAxML. For each node, MLBS (if >60) is presented above/below the branch leading to that node. The sequence of *E. quercicola* generated during this study is highlighted in boldface.



**Fig. 44.** *Erysiphe urticae* on *Urtica dioica*. **A.** Infected host plant. **B.** Infection viewed under stereomicroscope. **C.** A Chasmothecium. **D.** Appressoria. **E.** Immature chasmothecium. **F.** Chasmothecium (SEM). **G.** Conidiophore. **H.** Chasmothecial appendages. **I.** asci. **J.** Conidia. Scale bars A 0.75 cm, B 0.08 mm, C 0.03  $\mu\text{m}$ , D 0.07  $\mu\text{m}$ , E 0.03  $\mu\text{m}$ , G 0.07  $\mu\text{m}$ , H 0.05  $\mu\text{m}$ , I 0.07  $\mu\text{m}$ , J 0.14  $\mu\text{m}$ .

**Ascomycota, Leotiomycetes, Helotiales, Erysiphaceae**

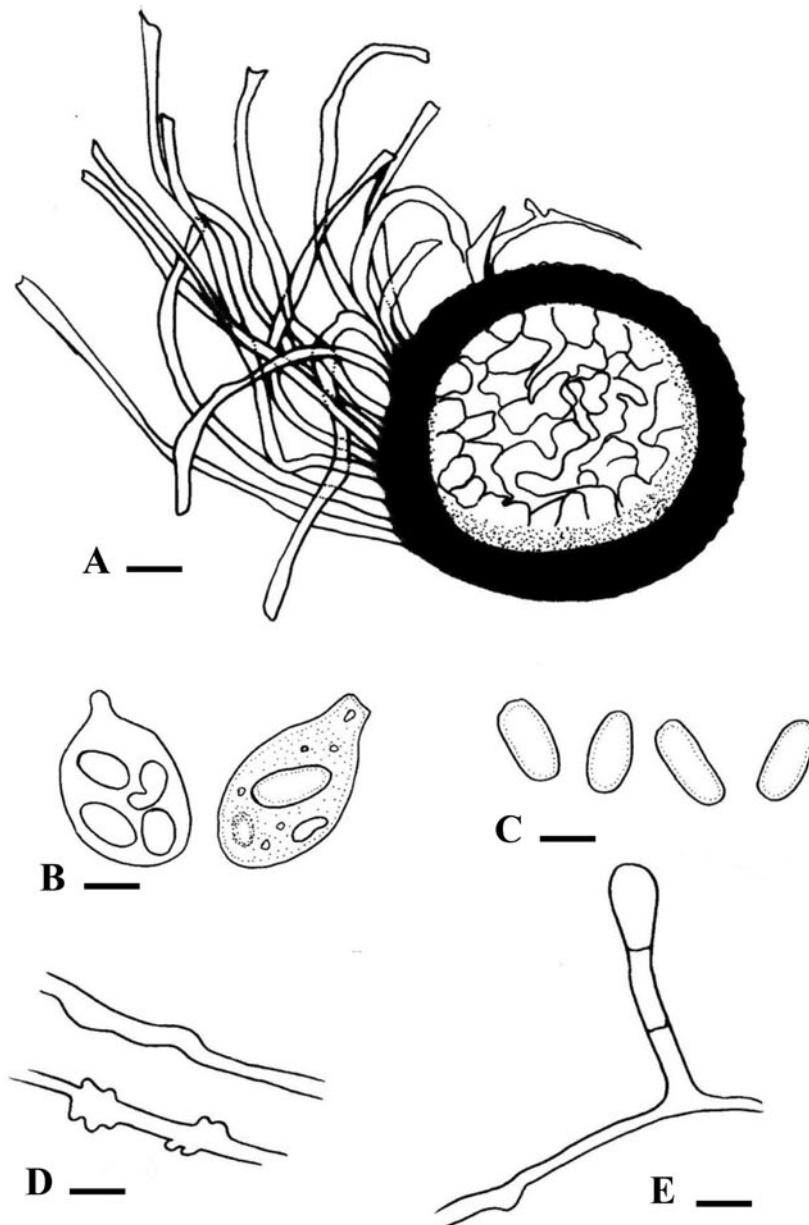
***Erysiphe urticae*** (Wallr.) S. Blumer, Beitr. Kryptfl. Schweiz 7(1): 224 (1933). – Figs. 44–45

**Basionym.** – *Alphitomorpha urticae* Wallr., Ann. Wetter. Gesellsch. Ges. Naturk. 4: 238 (1819).

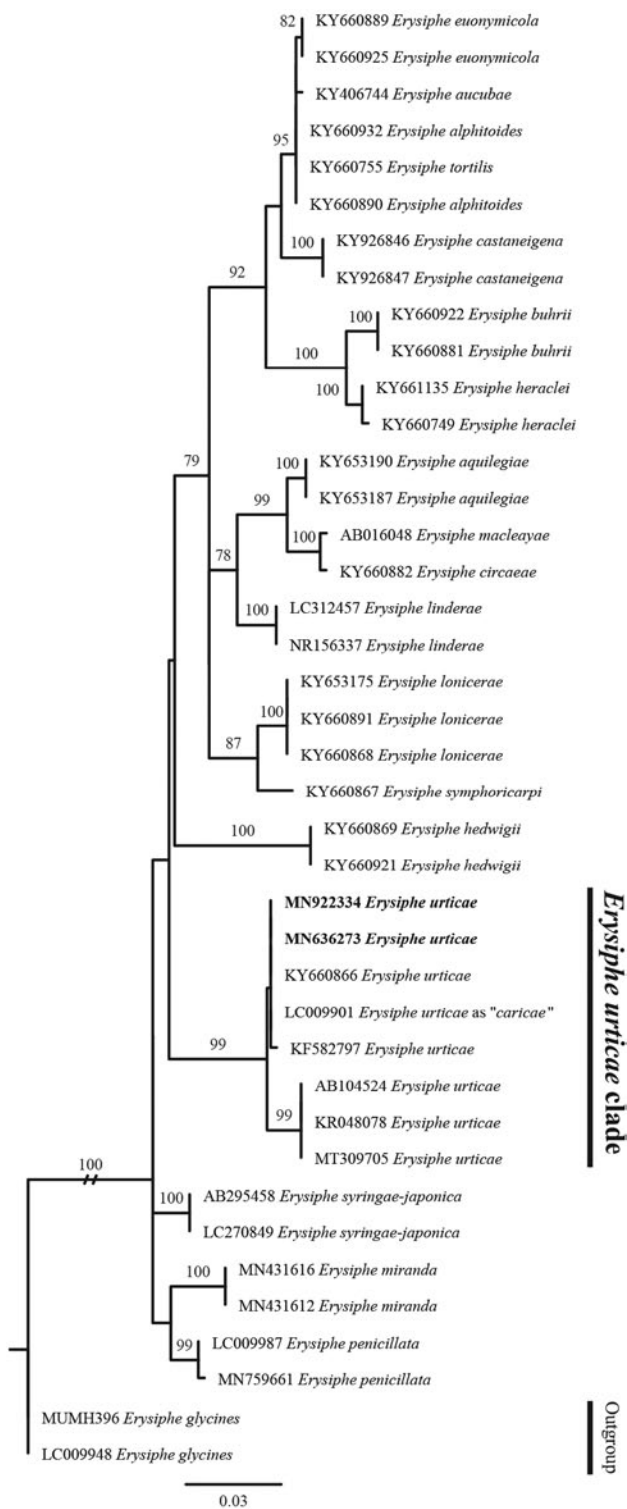
**Material examined.** – PAKISTAN. Khyber Pakhtunkhwa Province, Hazara Division, Haripur District, near Khun, 33°51'54.83" N, 73°8'19.57" E, 2438 m a.s.l., on leaves of *Urtica dioica* (Rosales, Urticaceae), 28 October 2018, leg. N.S. Afshan & M. Riaz, MA #08 (LAH 35663); Khyber Pakhtunkh-

wa Province, Hazara Division, Abbottabad District, Ayubia National Park, Mukshpuri, 34°04'N, 73°23'E, 2800 m a.s.l., on leaves of *U. dioica*, 30 October 2017, leg. N.S. Afshan & M. Riaz, ZM #21 (LAH 36173); Khyber Pakhtunkhwa Province, Hazara Division, Abbottabad District, Ayubia National Park, Khanspur, 34°00'60.00"N, 73°24'59.99"E, 2250 m a.s.l., on leaves of *U. dioica*, 29 October 2017, leg. N.S. Afshan, JP #20 (LAH 36156).

**Description.** – Mycelium epiphyllous, forming dense, thick white patches. – Hyphae hyaline, thin walled, smooth; hyphal appressoria in opposite pairs multilobed to nipple shaped. – Con-



**Fig. 45.** *Erysiphe urticae*. **A.** Chasmothecium. **B.** Asci with ascospores. **C.** Conidia. **D.** Appressoria. **E.** Conidiophore. Scale bars A 0.04  $\mu\text{m}$ , B 0.05  $\mu\text{m}$ , C 0.02  $\mu\text{m}$ , D 0.12  $\mu\text{m}$ , E 0.06  $\mu\text{m}$ , del. M. Riaz.



**Fig. 46.** Phylogeny of the genus *Erysiphe* reconstructed from an ITS dataset of 36 isolates. The topology is the result of ML inference performed with RAxML. For each node, the ML bootstrap (if >60) is presented above/below the branch leading to that node. Sequences of *E. urticae* generated during this study are highlighted in boldface.

idiophores arising from the upper surface of a hyphal mother cells, 44–105 µm in length. – Foot cells cylindrical, somewhat straight, 5–7 × 20–55 µm; followed by 1–2 shorter cells. – Conidia formed singly or in chains, ellipsoid to cylindrical, 17–18 × 34–40 µm. – Chasmothecia scattered to gregarious, hyaline when immature to light brown to dark brown at maturity, 125–166 µm in diam.; peridium cells irregularly shaped; appendages numerous, mycelioid, branched, 3–5 µm in diam., aseptate, hyaline, thin-walled, smooth. – Asci 2–7 per chasmothecium, ellipsoid to ovoid, 26–48 × 60–64 µm, stalked, 2–5-spored. – Ascospores ellipsoid to ovoid, 11–17 × 18–25 µm, hyaline.

**Habitat and distribution.** – Known from China, India, Iran, Israel, Lebanon, Russia, Siberia, Saudi Arabia, South Korea, Sri Lanka, and Turkey (Braun & Cook 2012; Farr & Rossman 2019). Reported host plants are *Urtica cannabina* L., *U. dioica*, *U. fissa* E. Pritz, *U. kioviensis* Rogow., *U. pilulifera* L., *U. urens* L., and outside of Europe also *Pilea glaberrima* (Blume) Blume (Urticaceae) (Ellis 2020, F.L. Zhang & C.W. Li unpublished). *Boehmeria gracilis* C.H. Wright (Urticaceae) is listed as the plant host for a Chinese collection of *E. urticae* in an NCBI GenBank sequence (L. Bai unpublished).

**Notes.** – Our newly generated ITS sequences (GenBank accession nos. MN922334, MN636273) resulting from our work towards the *Erysiphaceous Fungi of Ayubia* support identification as *E. urticae*. The sequences shared 99.57–100 % identity with an isolate from the UK (GenBank accession no. KY660866), 99.53–99.65 % with an isolate from China (KF582797), and 98.79 % with isolates from China and Iran (AB104524, KR048078, MT309705), all from either *U. dioica*, *U. fissa*, or *Boehmeria gracilis* (Tab. 1). Our ITS-based phylogenetic tree (Fig. 46) retrieved our Pakistani isolates in a cluster with other isolates of *E. urticae* (BS=99). One of the isolates in this cluster, however, is identified as *E. caricae* (LC009901). As the only ITS sequence that is available in Genbank for this species, it is unfortunate that the authors who generated it, did not provide morphological descriptions (Takamtsu et al. 2015). *Erysiphe caricae* is reported on members of Caricaceae (Brassicales) whereas known hosts of *E. urticae* belong to family Urticaceae (Rosales) (Braun & Cook 2012). Our pathogenicity assay on *U. dioica* shows symptoms of disease after 7 days, whereas control plants remained symptomless. *Erysiphe urticae* is reported here as a new country record for Pakistan.

**Authors:** N.S. Afshan, M. Riaz, J. Majeed & A.N. Khalid

**Ascomycota, Laboulbeniomycetes, Laboulbeniales, Laboulbeniaceae**

***Fanniomyces ceratophorus*** (Whisler) T. Majewski, *Acta Mycol.* 8(2): 230 (1972). – Fig. 47

**Basionym.** – *Stigmatomyces ceratophorus* Whisler, *Mycologia* 60(1): 68 (1968).

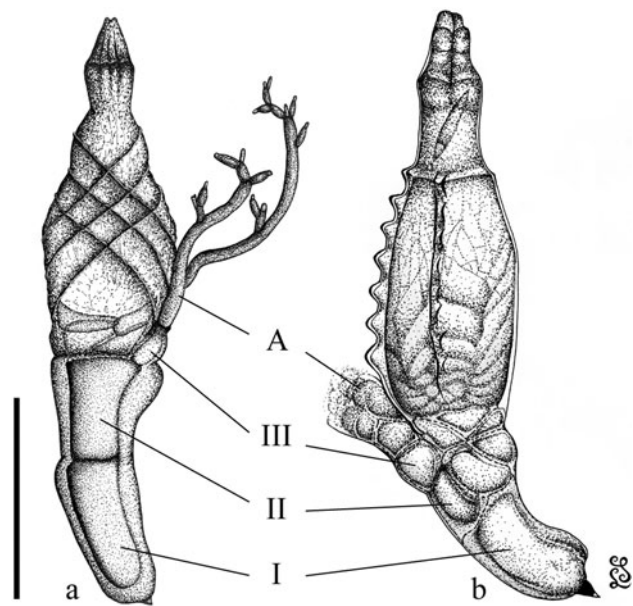
**Material examined.** – THE NETHERLANDS. Gelderland Province, Ede, Oude Kerkplein, 52°02'44.5"N, 5°40'17.6"E, on *Fannia canicularis* (Linnaeus, 1761) (Diptera, Fanniidae), D. Haelew. 135 [host label], 18 October 2012, *leg.* J. van Erkelens, slides FH 00313224 (4 thalli from abdominal tergites) and FH 00313225 (8 thalli from abdominal tergites).

**Material sequenced.** – USA. California, Alameda County, Oakland, 37°48'14.2"N, 122°15'55.7"W, on *F. canicularis*, D. Haelew. 1136 [host label], iNaturalist ID 3291539, 24 May 2016, *leg.* D. Tighe, isolate D. Haelew. 1136h (8 mature thalli, thorax), MG958013 (SSU), MH145384 (LSU).

**Hosts and distribution.** – Known from *Fannia canicularis* (lesser house fly) in five continents: North America (USA), South America (Guatemala), Europe (Czech Republic, Poland, Portugal, Spain), Asia (Lebanon, Turkey), and Oceania (New Zealand) (Whisler 1968; Majewski 1972; Tavares 1985; Hughes et al. 2004; Santamaría 2006; Rossi et al. 2013, 2019; Rossi 2016).

**Notes.** – *Stigmatomyces* H. Karst. as currently recognized is the second-largest genus of Laboulbeniales, with 176 described species (Species Fungorum 2020). Majewski (1972) established the genus *Fanniomyces* T. Majewski to accommodate *S. ceratophorus* on the basis of the highly branched appendage, which is different from the compact, single-axis appendage of most species in *Stigmatomyces*. Later, *F. burdigalensis* Balazuc from France (Balazuc 1979) and *F. copromyzae* Huldén from Finland (Huldén 1983) were added to *Fanniomyces*. Weir & Rossi (1995) synonymized *F. copromyzae* under *F. burdigalensis* based on morphological and morphometric data. In the same paper, the authors also considered *Fanniomyces* as a junior synonym of *Stigmatomyces* because the latter is variable in the structure of its appendage. Tavares (1985) presented *Stigmatomyces oecothaeae* Thaxt. (Thaxter 1931) as an example of a species with long appendage cells and elongate antheridia. However, without molecular data, it is unknown whether *S. oecothaeae* is representative of *Stigmatomyces* s.s. Phenotypic plasticity, polymorphism, position-induced morphological adaptations, and cryptic diversity in Laboulbeniales can hinder delimitation of natural groups by morphology alone (e.g., Goldmann & Weir 2012; Goldmann et al. 2013; Haelewaters et al. 2018a, 2018b, 2019b; Haelewaters & Pfister 2019).

This study presents the first-ever molecular phylogenetic analysis focused on *Stigmatomyces* s.l.



**Fig. 47.** Thalli of *Stigmatomyces* sensu lato. **a.** *Fanniomyces ceratophorus*, mature thallus from slide FH 00313225. **b.** *Gloeandromyces hilleri*, mature thallus from holotype slide FH 00313744 (Liu et al. 2020). Shown are cells I, II, and III of the receptacle and the appendage (A). Scale bar 100  $\mu$ m, *del.* J. Liu.

Our two-locus phylogenetic tree retrieved *Stigmatomyces* s.l. as paraphyletic, congruent with the prior studies of Haelewaters et al. (2018b) and Liu et al. (2020). Four major clades were retrieved, each with maximum support. Clade I included *S. burdigalensis* and *S. ceratophorus*—the type of *Fanniomyces*. Clade II included *S. gregarius*, *S. scaptomyzae*, and *S. entomophila*—the type of *Appendiculina*. Clade III was comprised of species of *Gloeandromyces*, including the type *G. streblae* (f. *sigmomorphus*). Clade IV included five species of *Stigmatomyces*.

*Fanniomyces* was erected to accommodate species with highly branched appendage and elongate antheridia (Majewski 1972, 1994). This genus is the earliest diverging lineage of the *Stigmatomyces* complex, represented by clade I in our phylogenetic tree (Fig. 48). Given the results of our phylogenetic reconstruction, *Fanniomyces* is reinstated here. The appendage structure (Tab. 4) associated with these species appears to be a characteristic feature for this lineage. *Fanniomyces ceratophorus* is here for the first time reported from the Netherlands. Our sequenced material was sampled in Oakland, California—a city neighboring Berkeley, the type locality.

*Appendiculina* Berl. was erected by Berlese (1889) to correct Peck's (1885) mistake of describing

**Tab. 4.** Overview of characters of four genera within *Stigmatomyces* sensu lato, including geographic distribution, host genus and classification up to subsection, and morphological features of the receptacle, appendage, and antheridia.

Clade	Genus	Species	Authors	Geographic distribution	Host family/-ies (genus/genera)	Host superfamily/-ies	Host subsection	Receptacle	Appendage	Antheridia																																																																																																																	
I	<i>Fanniomyces</i>	<i>burdigalensis</i>	Balazuc	Europe	Sphaeroceridae ( <i>Copromyza</i> , <i>Crumomyia</i> )	Sphaeroceroidae	Acalyptratae	Cell II elongated; cells I and VI never in contact	Highly branched	Elongate																																																																																																																	
	<i>Fanniomyces</i>	<i>ceratophorus</i>	(Whisler) T. Majewski	North and South America, Europe, Asia, Oceania	Fanniidae ( <i>Fannia</i> )	Muscoidea	Calypttratae				II	<i>Appendiculina</i>	<i>entomophila</i>	Peck (Berl.)	North and South America, Caribbean, Europe	Drosophilidae ( <i>Drosophila</i> )	Ephydroidea	Acalyptratae		Un-branched	Short	<i>Appendiculina</i>	<i>gregaria</i>	(W. Rossi) Haelew. & Aime	Africa	Diopsidae ( <i>Diopsis</i> )	Diopsoidea	Acalyptratae	<i>Appendiculina</i>	<i>scaptomyzae</i>	(Thaxt.) Haelew. & Aime	North and South America, Europe, Africa	Drosophilidae ( <i>Scaptomyza</i> )	Ephydroidea	Acalyptratae	IV	<i>Stigmatomyces</i>	<i>borealis</i>	Thaxt.	North America	Ephydriidae ( <i>Parydra imitans</i> )	Ephydroidea	Acalyptratae				<i>Stigmatomyces</i>	<i>chamaemyiae</i>	W. Rossi & M. Leonardi	Europe	Chamaemyiidae ( <i>Chamaemyia</i> )	Lauxanioidea	Acalyptratae	<i>Stigmatomyces</i>	<i>limnophorae</i>	Thaxt.	North and South America, Caribbean, Europe, Africa, Asia	Anthomyiidae (gen. & sp. indet.), Calliphoridae ( <i>Calliphora</i> , <i>Lucilia</i> ), Muscidae ( <i>Dasyphora</i> , <i>Heliographa</i> , <i>Leucomelina</i> , <i>Limnophora</i> ), Rhiniidae ( <i>Fainia</i> , <i>Isomyia</i> , <i>Rhyncomya</i> , <i>Sumatria</i> ), Sarcophagidae ( <i>Sarcophaga</i> )	Muscoidea (Anthomyiidae, Muscidae), Oestroidea (Calliphoridae, Rhiniidae, Sarcophagidae)	Calypttratae	<i>Stigmatomyces</i>	<i>protrudens</i>	Thaxt.	North America	Ephydriidae ( <i>Parydra pinguis</i> )	Ephydroidea	Acalyptratae	<i>Stigmatomyces</i>	<i>rugosus</i>	Thaxt.	North and South America, Caribbean, Europe, Africa, Asia, Oceania	Ephydriidae ( <i>Clanoneurum</i> , <i>Leptopsilopa</i> , <i>Psilopa</i> )	Ephydroidea	Acalyptratae	<i>Stigmatomyces</i>	<i>baeri</i> (type)	(Knoch) Peyr.	Europe	Muscidae ( <i>Musca</i> )	Muscoidea	Calypttratae	III	<i>Gloeandromyces</i>	<i>dickii</i>	Haelew.	Central and South America	Streblidae ( <i>Trichobius</i> )	Hippoboscoidea	Calypttratae	Cell II short; cells I and VI always in contact	Fan-like	Short, gelatinous	<i>Gloeandromyces</i>	<i>nycteribidarum</i>	(Thaxt.) Thaxt.	Caribbean, Central America	Streblidae ( <i>Megistopoda</i> , <i>Trichobius</i> )			<i>Gloeandromyces</i>	<i>pageanus</i> f. <i>alarum</i>	Haelew.	Central America	Streblidae ( <i>Trichobius</i> )			<i>Gloeandromyces</i>	<i>pageanus</i> f. <i>pageanus</i>	Haelew.	Central America	Streblidae ( <i>Trichobius</i> )			<i>Gloeandromyces</i>	<i>pageanus</i> f. <i>polymorphus</i>	Haelew.	Central America	Streblidae ( <i>Trichobius</i> )			<i>Gloeandromyces</i>	<i>streblae</i> f. <i>sigmomorphus</i>	Haelew.
II	<i>Appendiculina</i>	<i>entomophila</i>	Peck (Berl.)	North and South America, Caribbean, Europe	Drosophilidae ( <i>Drosophila</i> )	Ephydroidea	Acalyptratae		Un-branched	Short																																																																																																																	
	<i>Appendiculina</i>	<i>gregaria</i>	(W. Rossi) Haelew. & Aime	Africa	Diopsidae ( <i>Diopsis</i> )	Diopsoidea	Acalyptratae																																																																																																																				
	<i>Appendiculina</i>	<i>scaptomyzae</i>	(Thaxt.) Haelew. & Aime	North and South America, Europe, Africa	Drosophilidae ( <i>Scaptomyza</i> )	Ephydroidea	Acalyptratae																																																																																																																				
IV	<i>Stigmatomyces</i>	<i>borealis</i>	Thaxt.	North America	Ephydriidae ( <i>Parydra imitans</i> )	Ephydroidea	Acalyptratae																																																																																																																				
	<i>Stigmatomyces</i>	<i>chamaemyiae</i>	W. Rossi & M. Leonardi	Europe	Chamaemyiidae ( <i>Chamaemyia</i> )	Lauxanioidea	Acalyptratae																																																																																																																				
	<i>Stigmatomyces</i>	<i>limnophorae</i>	Thaxt.	North and South America, Caribbean, Europe, Africa, Asia	Anthomyiidae (gen. & sp. indet.), Calliphoridae ( <i>Calliphora</i> , <i>Lucilia</i> ), Muscidae ( <i>Dasyphora</i> , <i>Heliographa</i> , <i>Leucomelina</i> , <i>Limnophora</i> ), Rhiniidae ( <i>Fainia</i> , <i>Isomyia</i> , <i>Rhyncomya</i> , <i>Sumatria</i> ), Sarcophagidae ( <i>Sarcophaga</i> )	Muscoidea (Anthomyiidae, Muscidae), Oestroidea (Calliphoridae, Rhiniidae, Sarcophagidae)	Calypttratae																																																																																																																				
	<i>Stigmatomyces</i>	<i>protrudens</i>	Thaxt.	North America	Ephydriidae ( <i>Parydra pinguis</i> )	Ephydroidea	Acalyptratae																																																																																																																				
	<i>Stigmatomyces</i>	<i>rugosus</i>	Thaxt.	North and South America, Caribbean, Europe, Africa, Asia, Oceania	Ephydriidae ( <i>Clanoneurum</i> , <i>Leptopsilopa</i> , <i>Psilopa</i> )	Ephydroidea	Acalyptratae																																																																																																																				
	<i>Stigmatomyces</i>	<i>baeri</i> (type)	(Knoch) Peyr.	Europe	Muscidae ( <i>Musca</i> )	Muscoidea	Calypttratae																																																																																																																				
III	<i>Gloeandromyces</i>	<i>dickii</i>	Haelew.	Central and South America	Streblidae ( <i>Trichobius</i> )	Hippoboscoidea	Calypttratae	Cell II short; cells I and VI always in contact	Fan-like	Short, gelatinous																																																																																																																	
	<i>Gloeandromyces</i>	<i>nycteribidarum</i>	(Thaxt.) Thaxt.	Caribbean, Central America	Streblidae ( <i>Megistopoda</i> , <i>Trichobius</i> )																																																																																																																						
	<i>Gloeandromyces</i>	<i>pageanus</i> f. <i>alarum</i>	Haelew.	Central America	Streblidae ( <i>Trichobius</i> )																																																																																																																						
	<i>Gloeandromyces</i>	<i>pageanus</i> f. <i>pageanus</i>	Haelew.	Central America	Streblidae ( <i>Trichobius</i> )																																																																																																																						
	<i>Gloeandromyces</i>	<i>pageanus</i> f. <i>polymorphus</i>	Haelew.	Central America	Streblidae ( <i>Trichobius</i> )																																																																																																																						
	<i>Gloeandromyces</i>	<i>streblae</i> f. <i>sigmomorphus</i>	Haelew.	Central America	Streblidae ( <i>Trichobius</i> )																																																																																																																						

*Appendicularia* to accommodate *A. entomophila* Peck. The genus *Appendicularia* was illegitimate because it had already been applied to a genus in the plant family Melastomataceae, a genus that remains in use even today (Da Rocha et al. 2018). However, by recombining *A. entomophila* in *Stigmatomyces*, Thaxter (1896) reduced the monospecific genus *Appendiculina* in synonymy. Since *S. entomophilus*—the former type species of the genus *Appendiculina*—is represented in clade II of our phylogenetic reconstruction, we here reinstate the genus and add two species to it.

*Gloeandromyces* (Fig. 47) was erected to accommodate species with fan-like appendage, consisting of a basal cell that carries two short branches of dichotomously dividing cells, the final cells being antheridial. At maturity, the antheridia become gelatinous, “losing their identity more or less completely” (Thaxter 1931: 112). Another morphological character, unnoted by Thaxter in his generic description but consistent among described species of *Gloeandromyces* is the short cell II (Tavares 1985), allowing cells I and VI to be in contact (Thaxter 1917, 1931; Haelewaters & Pfister 2019; Liu et al. 2020). These morphological features do not occur in any of the species of *Fanniomyces* or *Stigmatomyces* (Tab. 4). In addition, LSU sequences of the *Gloeandromyces* species in our final (aligned and trimmed) dataset are 89.24–100 % identical, whereas they are 82.73–85.07 % identical with *Fanniomyces* spp. and 80.34–85.68 % with *Stigmatomyces* spp. (*S. protrudens* excluded because of low query coverage). This points at a barcode “gap” of minimum 3.56–4.17 % distinguishing inter- from intra-generic variability. We regard *Gloeandromyces* as an independent radiation on neotropical bat flies (Thaxter 1931, Haelewaters et al. 2018, Haelewaters & Pfister 2019) and the generic description is emended here.

*Stigmatomyces* s.s. – still the largest genus by far in the *Stigmatomyces* complex – represents the crown radiation, comprising 171 species (Species Fungorum 2020) and represented in our phylogenetic reconstruction by clade IV (Fig. 48). This situation needs confirmation by the inclusion of sequences of *Stigmatomyces baeri* (Knoch) Peyr, the type species of the genus. As long as these data are not available it is impossible to predict which of the current and potentially more clades in this diverse group should carry the name *Stigmatomyces* s.s. We recognize that our current sampling is poor (14 of 180 species included in our phylogenetic reconstruction of *Stigmatomyces* s.l.) but this work is only a starting point to resolve the taxonomy of this clade.

Our taxonomic circumscription of genera within the *Stigmatomyces* complex results in four monophyletic genera. For *Appendiculina*, *Fanniomyces*, and *Gloeandromyces*, the type species are present in the representative clades. Also in Laboulbeniales research, molecular phylogenetic work helps us to better understand evolutionary patterns. In the *Stigmatomyces* complex, this involves the recognition of a radiation in the Neotropics (*Gloeandromyces*), hinting at a temperate origin for this group, et cetera. The only way to further elaborate on these patterns and to attain a fully stable taxonomy of *Stigmatomyces* s.l. is by doing more collecting.

***Appendiculina*** Berl., Malpighia 3: 59 (1889).

Synonym. – *Appendicularia* Peck, Ann. Rep. N.Y. State Mus. Nat. Hist. 38: 95 (1885), nom. illegit.

Notes. – *Appendiculina* comprises species in clade II (Fig. 48), which is composed of *A. entomophila* (type species) and two more species that were formerly placed in the genus *Stigmatomyces* (Thaxter 1901, Rossi 1982). Its SSU is 92.93–96.40 % identical with *Fanniomyces*, 85.51–96.16 % identical with *Gloeandromyces*, and 83.25–95.71 % identical with *Stigmatomyces*; compared to other genera in *Stigmatomyces* s.l., unique molecular synapomorphies at positions 175, 176, 211, 226, 247, 250, 631, 634, 654, 675, 728.

Species included.

***Appendiculina entomophila*** (Peck) Berl., Malpighia 3: 59 (1889).

Basionym. – *Appendicularia entomophila* Peck, Ann. Rep. N.Y. St. Mus. nat. Hist. 38: 96 (1885).

***Appendiculina gregaria*** (W. Rossi) Haelew. & Aime, **comb. nov.** MycoBank no.: MB 835861.

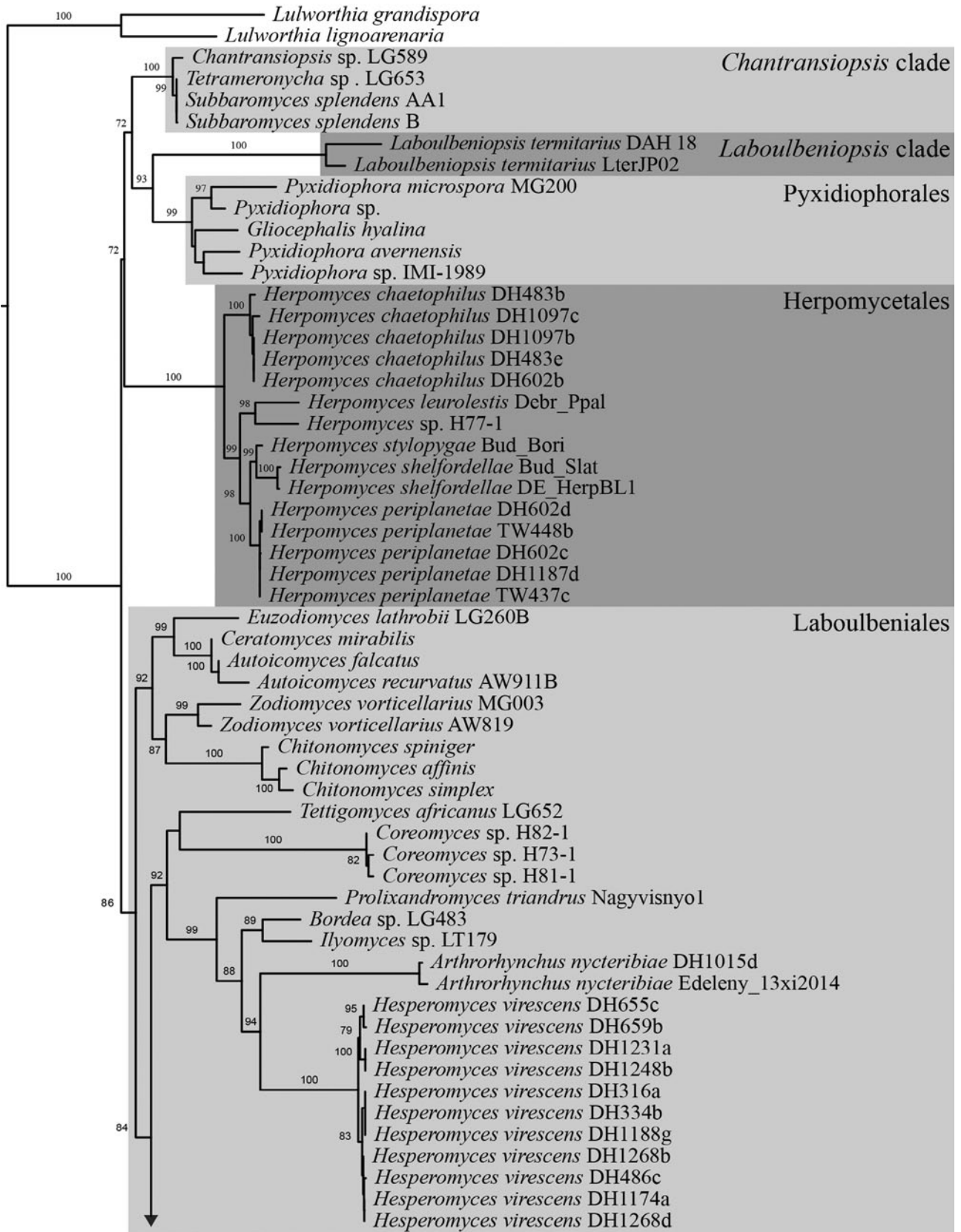
Basionym. – *Stigmatomyces gregarius* W. Rossi, Quad. Accad. Naz. Lincei 255: 19 (1982).

***Appendiculina scaptomyzae*** (Thaxt.) Haelew. & Aime, **comb. nov.** MycoBank no.: MB 835862.

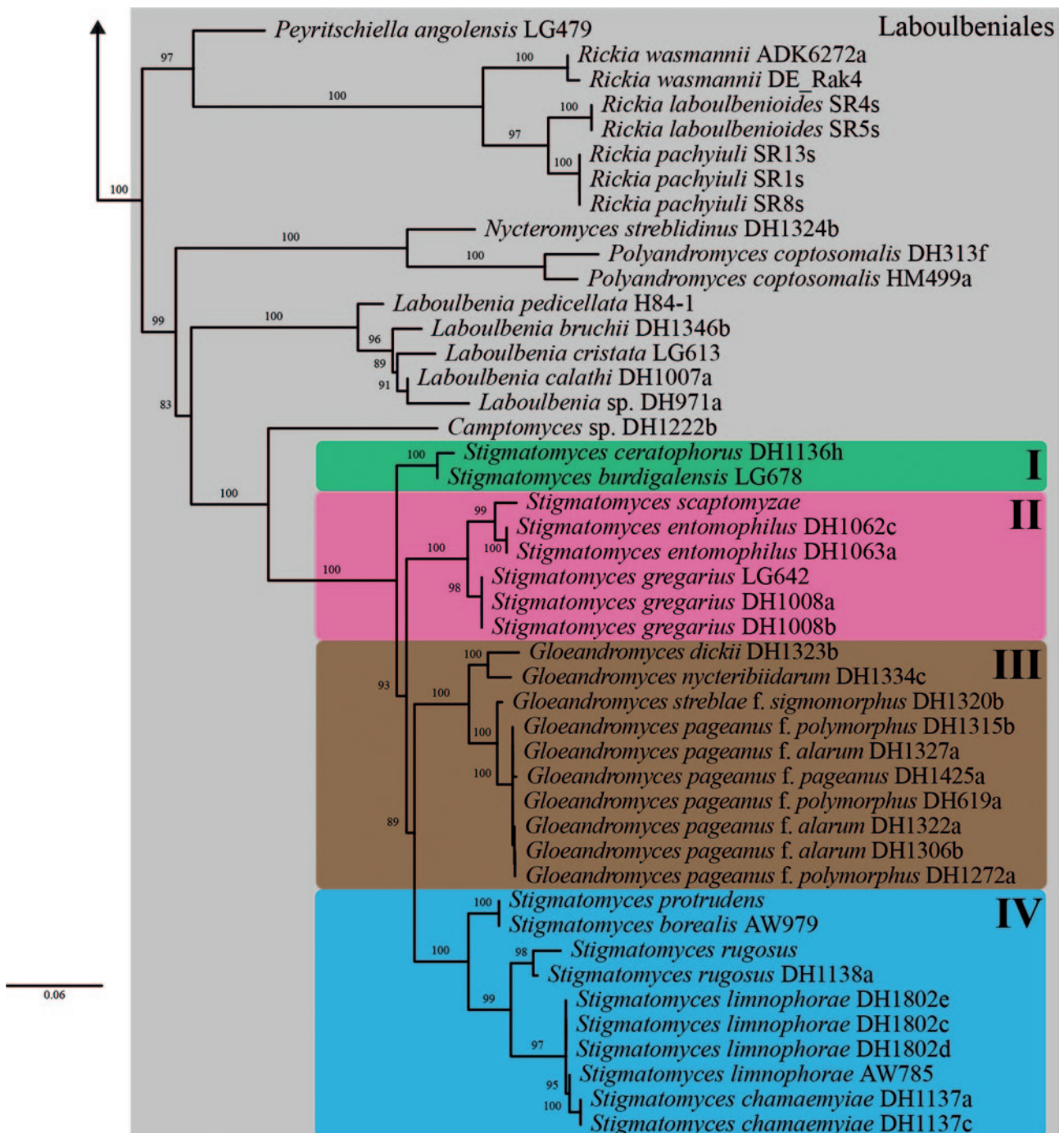
Basionym. – *Stigmatomyces scaptomyzae* Thaxt., Proc. Am. Acad. Arts Sci. 36(23): 400 (1901).

***Fanniomyces*** T. Majewski, Acta Mycol. 8(2): 229 (1972). – Fig. 47

Notes. – *Fanniomyces* comprises the two species in clade I (Fig. 48), *F. burdigalensis* and *F. ceratophorus* (type species). Its LSU is 82.73–85.07 % identical with *Gloeandromyces*, and 81.63–88.89 % identical with *Stigmatomyces*; compared to other genera in *Stigmatomyces* s.l., unique molecular synapomorphies at positions 79, 93, 100, 149, 205, 363, 411, 412, 423, 426, 428, 444, 447, 459, 460, 483, 488, 496, 502, 503, 505, 517, 544, 550, 563, 662. Its







**Fig. 48.** Phylogeny of Laboulbeniomycetes isolates reconstructed from a combined SSU–LSU dataset. The topology is the result of ML inference performed with IQ-TREE. For each node, MLBS (if >70) is presented above/below the branch leading to that node. The colored clades are representative of *Stigmatomyces* sensu lato, including four genus-level lineages, labeled clade I (= *Fanniomyces*), clade II (= *Appendiculata*), clade III (= *Gloeandromyces*), and clade IV (= *Stigmatomyces* sensu stricto).

SSU is 92.93–96.40% identical with *Appendiculina*, 93.12–97.62% identical with *Gloeandromyces*, and 74.57–97.42% identical with *Stigmatomyces*; com-

pared to other genera in *Stigmatomyces* s.l., unique molecular synapomorphies at positions 56, 266, 639, 671, 726, 827, 837, 840.

Species included.

*Fanniomyces burdigalensis* Balazuc, Revue Mycol., Paris 43: 402 (1979).

*Fanniomyces ceratophorus* (Whisler) T. Majewski, Acta Mycol. 8(2): 230 (1972).

Basionym. – *Stigmatomyces ceratophorus* Whisler, Mycologia 60(1): 68 (1968).

*Gloeandromyces* Thaxt., Mem. Am. Acad. Arts Sci. 16: 112 (1931). **emend.** Haelew. – Fig. 47

Description. – Receptacle with three cells; cell I longer than broad, sometimes bent or kinked, in contact with cell VI; cell II short, separated from cell III by an oblique septum; cell III broadly trapezoidal or triangular. – Appendage with basal cell broadly pentagonal, carrying two short, dichotomously dividing branches, terminal cells antheridial; appendage fan-like in structure. – Antheridia gelatinous at maturity, distally disintegrating towards below. – Cell VI broader than long, obliquely positioned between cells II and VII. – Perithecium with four tiers of vertical wall cells; intraspecific plasticity is observed regarding the presence of perithecial projections, undulations, bumps, or prominences; in certain species this plasticity can be linked to growing on a particular position of the host.

Notes. – *Gloeandromyces* comprises five species, of which four are included in clade III of our phylogeny (Fig. 48), including the type species, *G. streblae* (f. *sigmomorphus*). Its LSU is 82.73–85.07 % identical with *Fanniomyces*, and 80.34–85.68 % identical with *Stigmatomyces*; compared to other genera in *Stigmatomyces* s.l., unique molecular synapomorphies at positions 100, 114, 128, 138, 163, 193, 218, 409, 410, 428, 447, 460, 461, 494, 526, 544, 550, 556, 661. Its SSU is 85.51–96.16 % identical with *Appendiculina*, 93.12–97.62 % identical with *Fanniomyces*, and 85.12–97.42 % identical with *Stigmatomyces*; compared to other genera in *Stigmatomyces* s.l., unique molecular synapomorphies at positions 262, 266, 441, 481, 630, 646, 667, 677, 687, 731, 763, 804, 823, 827.

Species included.

*Gloeandromyces dickii* Haelew., in Haelewaters & Pfister, Fungal Syst. Evol. 3: 22 (2019).

*Gloeandromyces hilleri* Haelew. & Pfliegler, Mycologia in press (2020).

*Gloeandromyces nycteribiidarum* (Thaxt.) Thaxt., Mem. Am. Acad. Arts Sci. 16: 113 (1931).

Basionym. – *Stigmatomyces nycteribiidarum* Thaxt., Proc. Am. Acad. Arts Sci. 52(10): 702 (1917).

*Gloeandromyces pageanus* Haelew., in Haelewaters et al., Nova Hedwig. 105(3–4): 272 (2017).

*Gloeandromyces pageanus* f. *alarum* Haelew., in Haelewaters & Pfister, Fungal Syst. Evol. 3: 26 (2019).

*Gloeandromyces pageanus* f. *pageanus* Haelew., in Haelewaters et al., Nova Hedwig. 105(3–4): 272 (2017).

*Gloeandromyces pageanus* f. *polymorphus* Haelew., in Haelewaters & Pfister, Fungal Syst. Evol. 3: 28 (2019).

*Gloeandromyces streblae* (Thaxt.) Thaxt., Mem. Am. Acad. Arts Sci. 16: 113 (1931).

Basionym. – *Stigmatomyces streblae* Thaxt., Proc. Am. Acad. Arts Sci. 52(10): 700 (1917).

*Gloeandromyces streblae* f. *sigmomorphus* Haelew., in Haelewaters & Pfister, Fungal Syst. Evol. 3: 29 (2019).

*Gloeandromyces streblae* f. *streblae* Thaxt., Mem. Am. Acad. Arts Sci. 16: 113 (1931).

Authors: D. Haelewaters, A. De Kesel, J. Liu & M.C. Aime

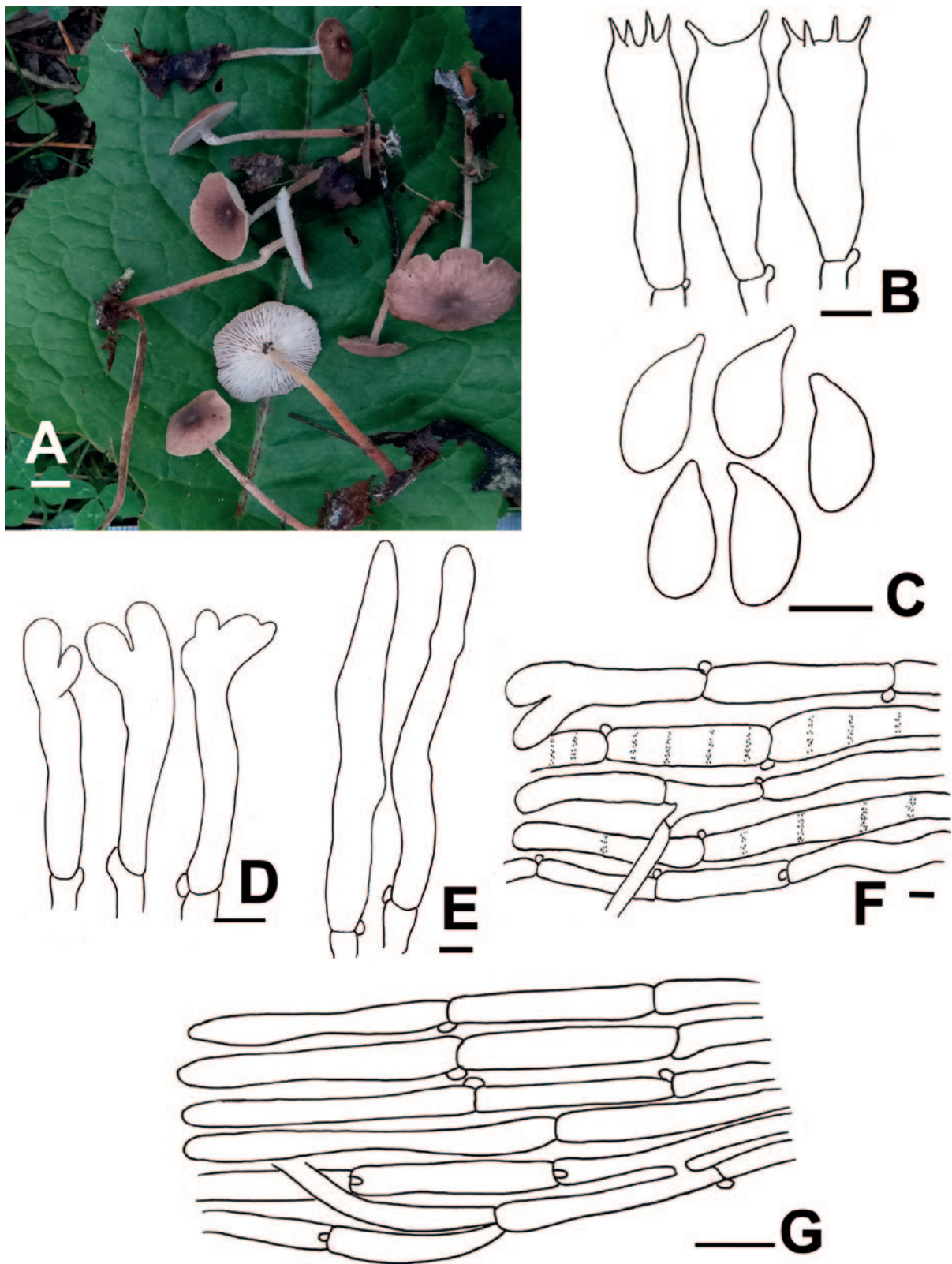
#### Basidiomycota, Agaricomycetes, Agaricales, Omphalotaceae

*Marasmiellus bififormis* (Peck) J.S. Oliveira, in Oliveira et al., Mycol. Progr. 18(5): 734 (2019). – Fig. 49

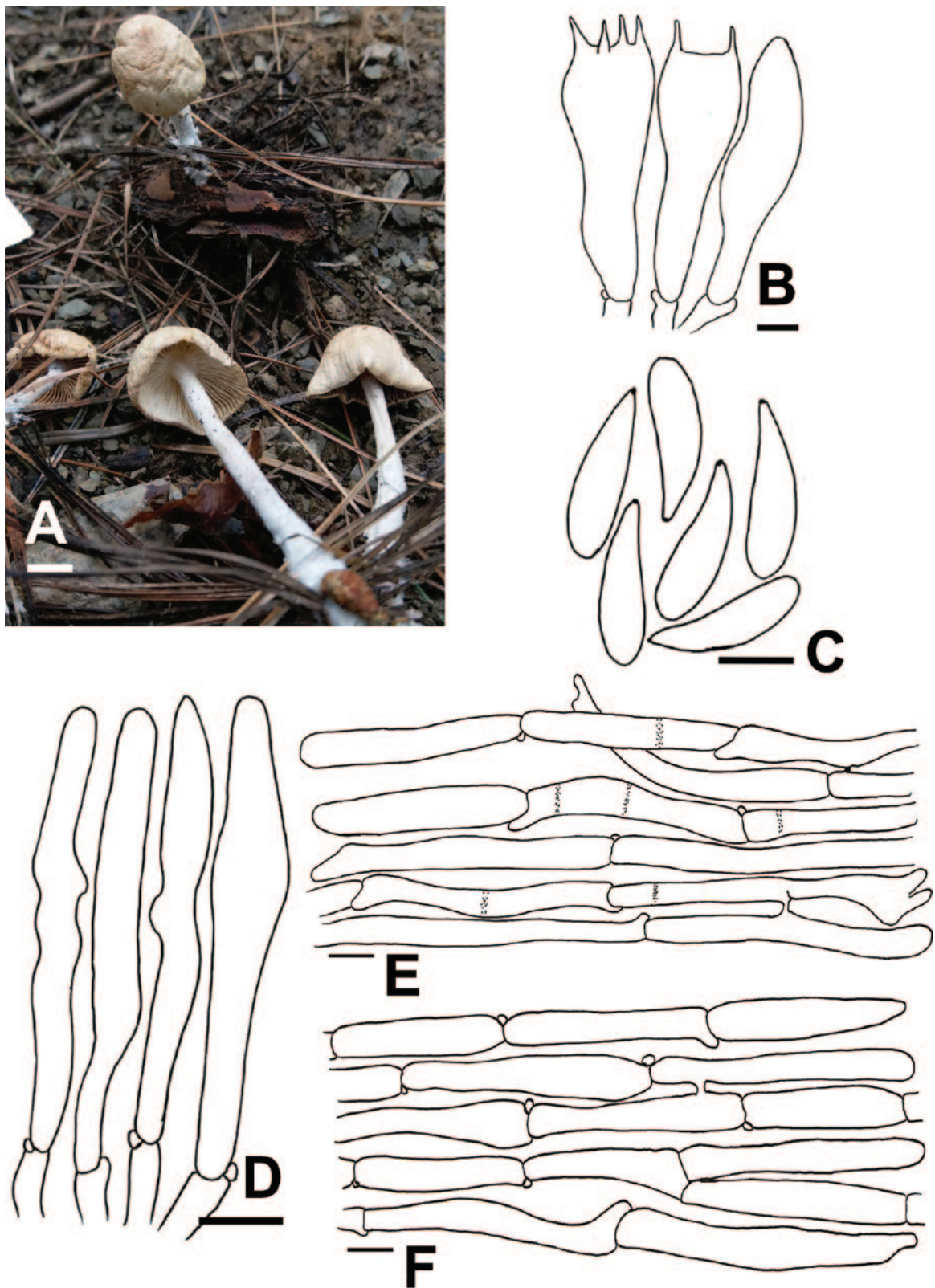
Basionym. – *Marasmius bififormis* Peck, Bull. N.Y. State Mus. 67: 25 (1904) [1903].

Material examined. – PAKISTAN. Khyber Pakhtunkhwa Province, Abbottabad District, Ayubia National Park, 33°51'54.83"N, 73°8'19.57"E, 2400 m a.s.l., 15 July 2017, leg. M. Ali & A.R. Niazi, KH 117 (LAH 36408); *Ibid.*, 16 July 2017, leg. M. Ali & A.R. Niazi, KH 122 (LAH 36409).

Description. – Pileus 10–28 mm in diam., medium-sized, convex with incurved and entire margin when young, becoming plane or depressed to umbilicate on disc, rugulose sulcate on the margin; surface dry, non-hygrophanous, glabrous, reddish brown (10R4/6) when young to leather brown (10R6/4) when mature. – Context white, thin, 0.4–1 mm thick. – Lamellae adnate, sub-distant to close, thin, narrow to moderately broad, white to white grayish or, pale pinkish with age. – Stipe 20–55 × 2.0–3.5 mm, centrally attached, equal, slender, cylindrical, rarely flattened, tough; surface dry, white near cap, tawny (2.5YR) to leather brown (10R6/4) toward the base, densely pubescent, pubescence whitish above and dark brown towards base. – Basidiospores (6.0–) 6.4–7.8(–8.7) × (3.0–)3.1–4.4(–4.5) μm, Q=1.4–1.8, Q<sub>av</sub>=1.5 μm, slightly ellipsoid to lacrymoid or obovoid, smooth, thin-walled, hyaline, inamyloid, acyanophilous. – Basidia 17.5–30 × 3.5–6.0 μm, clavate, bisporic to tetrasporic, hyaline,



**Fig. 49.** *Marasmiellus biformis*. **A.** Basidiomata *in situ*. **B.** Basidia. **C.** Basidiospores. **D.** Cheilocystidia. **E.** Caulocystidia. **F.** Pileipellis. **G.** Stipitipellis. Scale bars A 1 cm; B–C, E–F 5  $\mu\text{m}$ ; D, G 10  $\mu\text{m}$ ; *del.* M. Ali.



**Fig. 50.** *Marasmiellus subnudus*. **A.** Basidiomata *in situ* among pine needles. **B.** Basidia. **C.** Basidiospores. **D.** Cheilocystidia. **E.** Pileipellis. **F.** Stipitipellis. Scale bars A 1.5 cm, B–C 5  $\mu\text{m}$ , D–F 10  $\mu\text{m}$ , *del.* M. Ali.

thin walled. – Pleurocystidia absent. – Cheilocystidia 21.5–51 µm long, cylindrical, contorted, variously lobed to strangulated, thin walled. – Pileipellis a cutis made of cylindric and parallel hyphae, branched, septate, frequently encrusted, 2.0–6.5 µm in diam., with diverticulate or broadly round terminal elements. – Stipitipellis a layer of parallel and cylindrical hyphae, 2.0–5.5 µm in diam., rarely with inconspicuous encrusted, occasionally branched, smooth, thin-walled, frequently septate, terminal elements with rounded ends. – Caulocystidia differently shaped, cylindrical, contorted to strangulated, up to 19–55 µm, hyaline, thin-walled. – Clamp connections frequently present in all tissues.

**Habitat and distribution.** – Thus far reported from northeastern USA and eastern Asia (Japan). In Pakistan found growing scattered or in bunches on decomposing leaves or needles in pine-dominated moist temperate forests.

**Notes.** – In the ITS tree (Fig. 20), our sequences of Pakistani collections KH117 and KH122 are clustered with *M. biformis* with maximum support. Three sequences of *M. “biformis”* (GenBank accession nos. KM083047, KM083048, MG407676) form a separate clade (MLBS=84) sister to *M. biformis*. These are sequences from China (H. Tian unpublished) and South Korea (J.S. Lee et al. unpublished) that may be representative of another undescribed species, although no morphological information is available. The Pakistani material resembles *M. biformis* in both macromorphology and microscopic characters (Fig. 49). The only noted differences are the slightly larger pileus (10–28 mm) compared to eastern North American and Japanese collections, and slightly larger caulocystidia (6.0–8.5 µm) compared to Japanese material (Halling 1983, 2004; Miyamoto et al. 1998). North American collections of *M. biformis* are found mostly on soil and only rarely on decaying leaves or needles (Halling 1983). In contrast, Miyamoto et al. (1998) studied *M. biformis* in Japan collected from leaf or needle litter. Our collections were found on decomposing leafy materials.

**Authors:** M. Ali, H. Bashir, A.R. Niazi & A.N. Khalid

### Basidiomycota, Agaricomycetes, Agaricales, Omphalotaceae

***Marasmiellus subnudus*** (Ellis ex Peck) J.S. Oliveira, in Oliveira et al, Mycol. Progr. 18(5): 735 (2019). – Fig. 50

**Basionym.** – *Marasmius subnudus* Ellis ex Peck., Bull. Torrey Bot. Club 25: 287 (1898).

**Material examined.** – PAKISTAN. Khyber Pakhtunkhwa Province, Abbottabad District, Ayubia National Park, 33°51'54.83"N, 73°8'19.57"E, 2,400 m a.s.l., 15 July 2017, leg. M. Ali & A.R. Niazi, KH 317 (LAH36410).

**Description.** – Pileus 15–37 mm in diam., obtusely convex to broadly sub-umbonate becoming broadly convex to plane with a centrally depressed disc; surface dry, glabrous to fibrillose with age, more or less even on the disc, wrinkled towards the margin, very pale brown (10YR7/4). – Margin usually entire, incurved when young, becoming decurved when mature. – Context thin, whitish, tough. – Lamellae adnate to adnexed, subdistant to distant, thin or moderately thick, infrequently anastomosed, whitish when young, becoming light pale brown at maturity. – Stipe 20–70 × 3.0–5.0 mm, cylindrical or somewhat compressed, nearly equal or broader towards base, straight, surface dry, slightly pubescent towards base, concolorous with lamellae. – Basidiospores (7.7–)8.7–10.9(–11.5) × 3.1–4.1(–4.3) µm, lacrymoid to ellipsoid, smooth, inamyloid, hyaline, thin-walled. – Basidia clavate to subclavate, bisporic to tetrasporic with basal clamps, thin-walled, 20–36.5 × 5.0–11 µm. – Pleurocystidia absent. – Cheilocystidia variously shaped, ventricose-fusoid to somewhat mucronate, occasionally fusoid, sometimes lobed, thin walled, hyaline, 27–39(–53) × 7.5–9.0 µm. – Pileipellis a cutis of loosely arranged cylindric hyphae, thin walled, frequently encrusted; 3.0–7.5 µm in diam. with broadly round, occasionally diverticulate terminal elements. – Stipitipellis a layer of parallel arranged cylindric hyphae, thin-walled, cells 2.0–6.7 µm in diam., with sharply rounded terminal elements. – Clamp connections frequent in all tissues.

**Habitat and distribution.** – Reported from eastern North America (Morgan 1905), South Korea (Jang et al 2016), and Pakistan (this study). Gregarious or scattered in leaf litter, pine needles, and decaying/dead twigs in forests.

**Notes.** – The newly generated ITS sequence of collection KH 317 shares 99 % identity with *M. subnudus* (GenBank accession nos. KX513747, KX513748). In our ITS-based phylogenetic reconstruction of *Marasmiellus*, the Pakistani sequence is retrieved among isolates of *M. subnudus* with strong support: MLBS=95 (Fig. 20). Our collection KH 317 is micromorphologically similar to *M. subnudus* reported from South Korea by Jang et al. (2016). The holotype collection of *M. subnudus* from eastern North America is different macromorphologically only in its slightly smaller (10–35 mm), cinnamon-

brown to cinnamon pileus (Bañares et al. 2007). The Pakistani collection was sampled from leaf litter, pine needles, and decaying twigs in a mixed pine forest (Fig. 50A), which is in line with previous collections for this species. Eastern North American and South Korean collections of *M. subnudus* were also found in litter of leaves and dead twigs in mixed and deciduous forests (Jang et al. 2016).

*Authors:* M. Ali, H. Bashir, A.R. Niazi & A.N. Khalid

#### Ascomycota, Pezizomycetes, Pezizales, Morchellaceae

*Morchella anatolica* Işıloğlu, Spooner, Allı & Solak, Mycologia 102(2): 455 (2010). – Fig. 51

*Synonym.* – *Morchella lanceolata* Clowez & Illescas in Clowez, Bull. Soc. Mycol. France 126(3–4): 282 (2012), nom. inval. (“ad int.”, no diagnosis, no type designated).

*Material examined.* – TURKEY. Antalya Province, Kemer district, near Beydağları Coastal National Park, *P. brutia* forest, among moss growing on calcareous rocks, 36°35′38.1″N, 30°30′29.4″E, 354 m a.s.l., 17 April 2015, leg. O. Kaygusuz, OKA2001 (OKA-1B); *Ibid.*, 36°35′38.1″N, 30°30′29.7″E, 335 m a.s.l., 18 April 2015, leg. Ö.F. Çolak, ÖFÇ1249 (OKA-2B).

*Description.* – Ascomata 35–60 mm high. Hymenophore 25–40 mm high, 8–14 mm wide, usually conical to acutely conical when mature, with ribs longitudinally arranged, 0.4–0.9 mm wide, thick, fleshy, occasionally forked, forming large elongate pits. – Pits short when young but becoming vertically elongated on maturity, glabrous, widening and deepening with aging; surface dark lilac-grey when young, dark grayish to pale when mature, especially when exposed to sunlight, hollow when cut longitudinally. – Stipe 8–15 mm high, 6–8 mm wide, cylindrical or thicker at the base, hollow; surface puberulent, nearly coarsely granular, lilac-grey towards the base, upper parts whitish, occasionally with dark brownish stains. – Context elastic. – Smell weak to undetermined. – Ascospores (23.5–)25.0–28.5(–29.0) × (13.0–)14.0–16.5(–17.0) µm,  $L_{av} \times W_{av} = 26.5 \times 15.5$  µm,  $Q = (1.5–)1.6–1.8(–1.9)$  µm,  $Q_{av} = 1.7$  µm, ellipsoid, thick-walled, hyaline, distinctively striate lengthwise. – Ascii 250–300 × 16–24 µm, cylindrical to clavate, hyaline, 8-spored, uniseriate, sometimes also biseriate, inamyloid. – Paraphyses 90–210 × 15–35 µm, hyaline, (0–)1–2 septate in the lower half, usually enlarged towards the apices, cylindrical to narrowly clavate, apex sometimes narrowed, obtuse, supcapitae and fusiform apices. – Heteropara-

physes present in some collections, irregular. – Acroparaphyses 65–220 × 17–35 µm, predominantly fusiform to cylindrical, apically rounded or somewhat narrowed, thin-walled, hyaline. – Stipe cortex a textura globosa, composed of variously sized, irregularly arranged catenulate elements, clavate to capitate, cylindrical, lageniform or ampulliform, with 1–3 septa, measuring 30–170 × 10–55 µm.

*Habitat and distribution.* – Growing solitary between late March and mid-April at 100–700 m a.s.l., often among damp mosses, in warm, strongly calcareous forests, possibly associated with *Pinus brutia* Ten. and other Mediterranean vegetation. Thus far only known from Spain (Clowez 2012, as “*M. lanceolata*”; Richard et al. 2015; Palazón et al. 2017) and Turkey (Işıloğlu et al. 2010).

*Notes.* – Recent multilocus DNA studies have demonstrated the existence of ~80 species of *Morchella* around the world (Loizides 2017), but new species and new transcontinental records have been published since (Baroni et al. 2018, Du et al. 2019, Clowez et al. 2020). Whereas certain species show a high degree of continental endemism or provincialism (O’Donnell et al. 2011; Taşkın et al. 2012; Clowez et al. 2014, 2015), phylogenetic studies have revealed that, many others species are found on more than one continent (Taşkın et al. 2010, 2016; Du et al. 2012a, 2012b; Ku et al. 2012; Loizides et al. 2015, 2016; Richard et al. 2015; Voitek et al. 2016; Loizides 2017).

In recent molecular phylogenetic studies, three major clades of *Morchella* can be discriminated: the */Rufobrunnea* clade or “white morels” with *M. anatolica* Işıloğlu, Spooner, Allı & Solak and *M. rufobrunnea* Guzmán & F. Tapia; the */Esculenta* clade or “yellow morels” with *M. esculenta* (L.) Pers. and others; and the */Elata* clade of “black morels” with *M. elata* Fr. and others (Guzmán & Tapia 1998, O’Donnell et al. 2011, Taşkın et al. 2012, Richard et al. 2015, Loizides 2017, Clowez & Moreau 2018). The */Rufobrunnea* clade, which dates back to the late Jurassic, is represented by two distinct species, *M. rufobrunnea* and *M. anatolica* (Işıloğlu et al. 2010, Taşkın et al. 2012). These two species are often found on treeless, disturbed substrates and wood chippings in the Mediterranean basin, as well as under olive trees (Loizides et al. 2015).

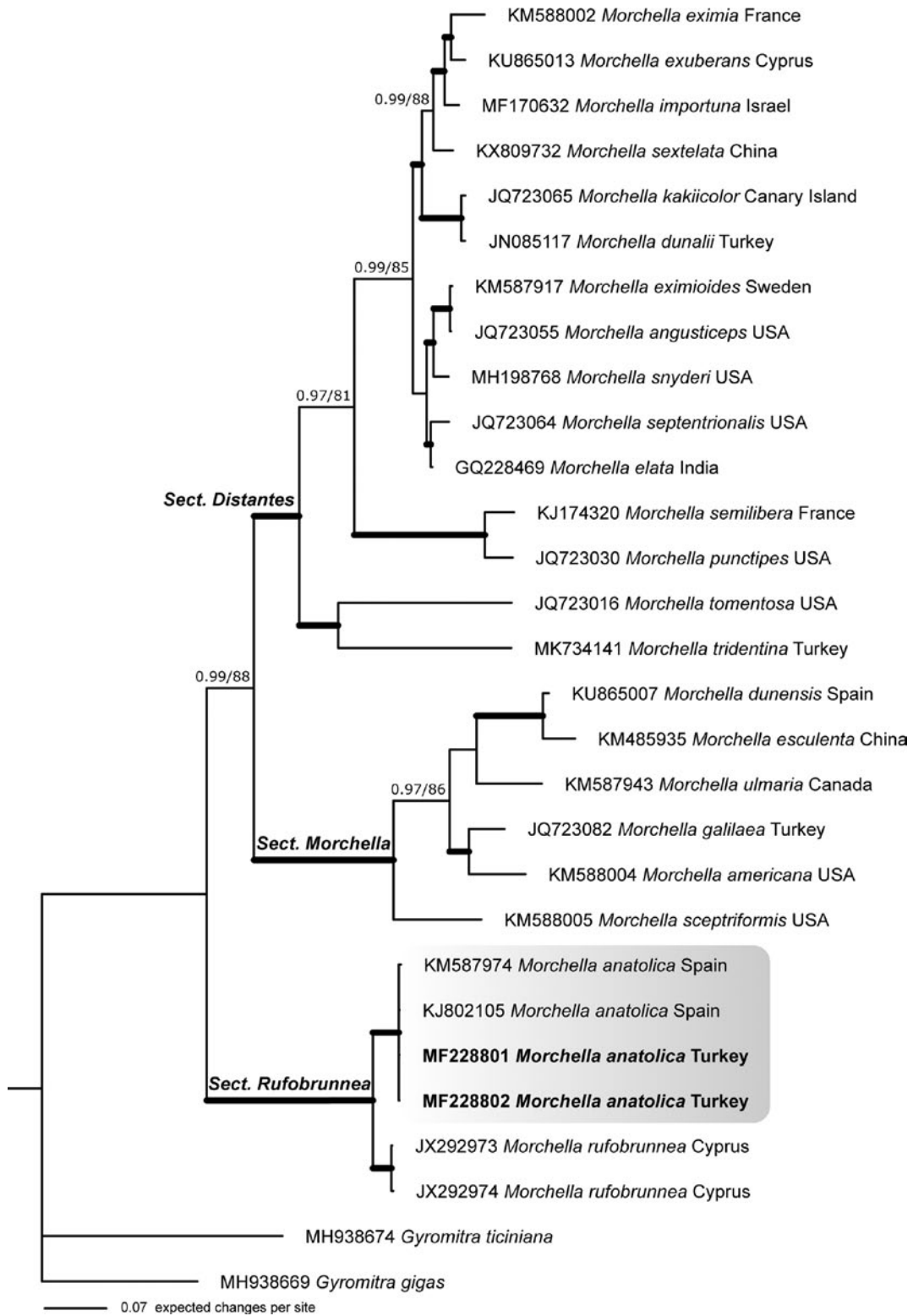
In our phylogenetic tree (Fig. 52), the basal-most monophyletic branch was the */Rufobrunnea* clade. The */Elata* and */Esculenta* clades were highly supported as sister clades. The */Esculenta* clade (sect. *Morchella* Dill. ex Pers.) (MLBS=99, BIPP=1.00) consisted of *M. americana* Clowez & Matherly, *M.*



**Fig. 51.** *Morchella anatolica*. a–f. Fresh ascomata, on natural substrate. g. Ascospores. h. Asci. i. Paraphyses. j. Acroparaphyses. k. Stipe hairs. Scale bars a–f 10 mm, g–k 25  $\mu$ m, del. O. Kaygusuz.

*dunensis* (Castañera, J.L. Alonso & G. Moreno) Clowez, *M. esculenta*, *M. galilaea* Masaphy & Clowez, *M. sceptriformis* Clowez & Matherly, and *M. ulmaria* Clowez. The /*Elata* clade (sect. *Dis-*

*tantes* Boud.) (MLBS=96, BIPP=0.99) was composed of *M. angusticeps* Peck, *M. dunalii* Boud., *M. elata*, *M. eximia* Boud., *M. eximioides* Jacquet., *M. exuberans* Clowez, Hugh Sm. & S. Sm., *M. importuna*



**Fig. 52.** Phylogeny of *Morchella* reconstructed from an ITS dataset. The topology is the result of Bayesian inference performed with MrBayes. *Gyromitra gigas* and *G. ticiniana* serve as outgroup taxa. For each node, BIPP (if  $\geq 0.95$ ) and MLBS (if  $\geq 80$ ) are shown the branch leading to that node. Branches in bold indicate BIPP  $\geq 0.95$  and MLBS  $\geq 90$ . Newly generated sequences from Turkey are in boldface.



M. Kuo, O'Donnell & T.J. Volk, *M. kakiicolor* (Clowez & L. Romero) Clowez, L. Romero, P. Alvarado & Loizides, *M. punctipes* Peck, *M. semilibera* DC., *M. septentrionalis* M. Kuo, J.D. Moore & Zordani, *M. sextelata* M. Kuo, *M. snyderi* M. Kuo & Methven, *M. tomentosa* M. Kuo, and *M. tridentina* Bres. Finally, the */Rufobrunnea* clade (sect. *Rufobrunnea* Clowez & Courtec.) (MLBS=99, BIPP=1.00) was composed of *M. anatolica* and *M. rufobrunnea* (Fig. 52). Phylogenetically, *M. anatolica* is closely related to but clearly distinct from *M. rufobrunnea* based on the ITS. Our newly generated sequences of *M. anatolica* from Turkey clustered with those of collections from Spain. *Morchella anatolica* was highly supported in both analyses MLBS=99, BIPP=1.00). The results of our ITS phylogeny agree with the topologies by Richard et al. (2015), Loizides et al. (2016), and Clowez & Moreau (2018).

*Morchella anatolica* is the sister species of *M. rufobrunnea* both morphologically and molecularly. Morphologically, the ascocarp surface of *M. anatolica* is rather rose and purplish to rufescent, similar to *M. rufobrunnea*. However, the dimensions of the ascocarp (up to 60 mm vs. up to 210 mm) and stipe (up to 25 mm vs. 90 mm) of *M. anatolica* (Işiloğlu et al. 2010, Palazón et al. 2017) are much smaller than those of *M. rufobrunnea* (Guzmán & Tapia 1998, Loizides et al. 2015). The absence of diagonal ribs in *M. anatolica* and its very few anastomosing longitudinal ribs also distinguish it from *M. rufobrunnea* and other taxa of the genus (Işiloğlu et al. 2010). Microscopically, *M. anatolica* can be easily distinguished from *M. rufobrunnea* by its relatively large ascospores (<30 µm) (Işiloğlu et al. 2010, Palazón et al. 2017, Clowez & Moreau 2018, this study).

The two species in the */rufobrunnea* clade are vastly different in their geographical distribution patterns. Compared to *M. rufobrunnea*, *M. anatolica* has a much narrower distribution. *Morchella anatolica* has thus far only been reported from Spain and Turkey (Işiloğlu et al. 2010, Clowez 2012, Richard et al. 2015, Palazón et al. 2017). Its known distribution suggests that might be limited to the Mediterranean area. Our report of *M. anatolica* is from southern Turkey. It is the second country record, and the first for Antalya Province, which borders Muğla Province where the first Turkish record of *M. morchella* was reported by Işiloğlu et al. (2010). On the other hand, *M. rufobrunnea* has been reported from the USA, Mexico, Cyprus, Israel, and Australia, and is known as a cosmopolitan species (Guzmán & Tapia 1998, Kuo 2008, Masaphy et al. 2010, Clowez 2012, Kuo et al. 2012, Elliot et al. 2014, Loizides et al. 2015, Richard et al. 2015).

In the original description, *M. anatolica* was reported to occur in forests of *Pinus brutia*, on stream bed mosses (Işiloğlu et al. 2010). The species was later found in Spain, under or in the vicinity of *Fraxinus angustifolia* Vahl, *Fraxinus* sp., *Nerium oleander* L., *Olea europaea* var. *sylvestris* (Mill.) Lehr., *Phyllirea latifolia* L., *Quercus faginea* Lam., and *Quercus* sp. (Clowez 2012, Richard et al. 2015, Palazón et al. 2017). The ecology of the collections obtained in our study is similar to the report of Işiloğlu et al. (2010). Contrary to *M. anatolica*, *M. rufobrunnea* is often found under olive trees (Loizides et al. 2015). A more complete knowledge of the ecology and hosts of *M. anatolica* and other species could be important from taxonomic and evolutionary points of view. *Morchella rufobrunnea* is known as a mainly saprophytic species—and was also the first morel to be cultured and grown commercially (Ower 1982, Kuo 2008, Loizides 2017). Our observations, along with those presented by Işiloğlu et al. (2010), suggest that *M. anatolica* may also be saprophytic and that culturing may be possible—as a species that is ecologically very close to *M. rufobrunnea*.

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#### Ascomycota, Sordariomycetes, Hypocreales, Ophiocordycipitaceae

***Ophiocordyceps ditmarii*** (Quél.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, in Sung et al., *Stud. Mycol.* 57: 42 (2007) – Figs. 53–54

**Basionym.** – *Cordyceps ditmarii* Quél. [as “ditmari”], *Bull. Soc. bot. Fr.* 24: 330 (1878) [1877].

**Synonyms.** – *Cordyceps forquignonii* Quél., *C. r. Assoc. Franç. Avancem. Sci.* 16(2): 591 (1888).

*Ophiocordyceps forquignonii* (Quél.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, in Sung et al., *Stud. Mycol.* 57: 43 (2007).

*Polycephalomyces ditmarii* Van Vooren & Audibert, *Bull. mens. Soc. linn. Lyon* 74(7–8): 231 (2005).

**Material examined.** – AUSTRIA. Steiermark, Hartberg, Ringwarte, in mixed forest of *Picea abies*, *Abies alba*, and *Fagus sylvatica*, on *Vespula vulgaris* (Linnaeus, 1758) (Hymenoptera, Vespidae), 7 September 2019, leg. A. Nagy, DB-2020-09-07-1 (WU-42993).

**Description.** – Asexual morph. – Synnemata numerous or solitary, single or branched, arising from different parts of the host, yellowish white, darkening at the base; each branch terminated by a small subspherical, orange-yellow head with an irregular surface, more or less covered with a fine whitish powder; context of the conidial mass somewhat cottony, homogeneous, pale cream. – Phialides produced on the heads, elongated,



**Fig. 53.** *Ophiocordyceps ditmarii*, collection WU-42993. Anamorphic synemmata on *Vespula vulgaris*. **a.** *In situ*. **b–c.** Under stereomicroscope.

cylindrical, tapering to the top,  $18\text{--}25 \times 1.6\text{--}2.3 \mu\text{m}$ . – Conidia subellipsoid to subclavate, smooth, hyaline,  $3.21\text{--}3.34 \times 1.37\text{--}1.6 \mu\text{m}$ . – Context formed of intertwined, hyaline, segmented hyphae,  $3\text{--}5 \mu\text{m}$  wide.

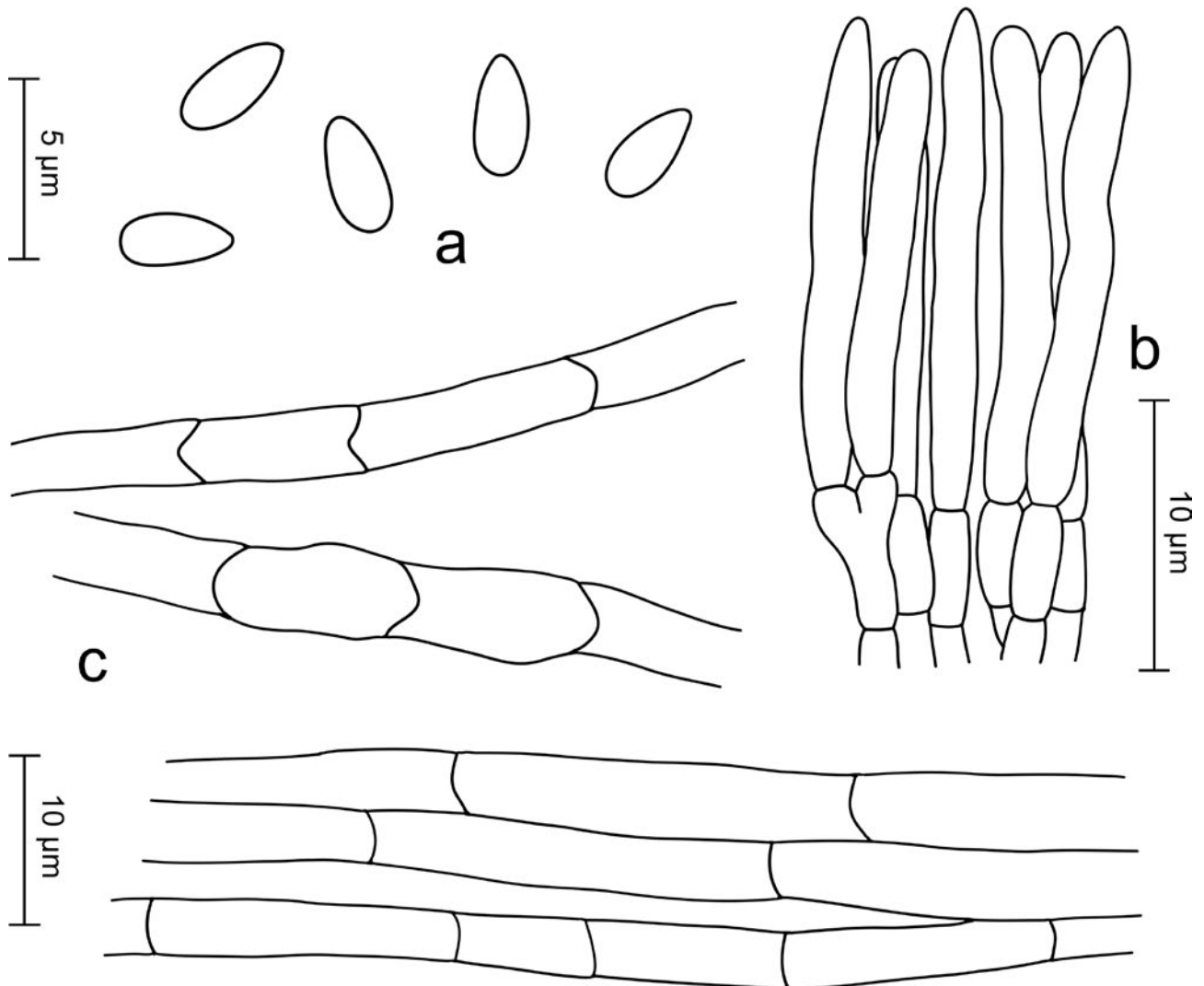
**Notes.** – The sequenced specimen recently found in Austria (WU-42993) is identical to *Polycephalomyces ditmarii* Van Vooren & Audibert, based on the host preference and the morphological characteristics of the synemmata (Van Vooren & Audibert 2005, Matočec et al. 2014, Shrestha et al. 2017). The anamorphic species, *P. ditmarii*, was described by Van Vooren & Audibert (2005) based on a

historical specimen collected by Quélet in 1876 in the Jura Mountains (France). In addition to the type locality, *P. ditmarii* was also reported from the Czech Republic, Germany, Italy, and Poland (Van Vooren & Audibert 2005). However, due to the misinterpretations of this species, and its teleomorphic stage, further studies are needed to circumscribe its real geographic distribution. *Polycephalomyces ditmarii* was considered as the potential anamorphic stage of *Cordyceps ditmarii* Quélet. (Van Vooren & Audibert 2005), a teleomorphic species described from similar host and same locality (Quélet 1877). Based on a systematic revision of *Cordyceps* s.l.,

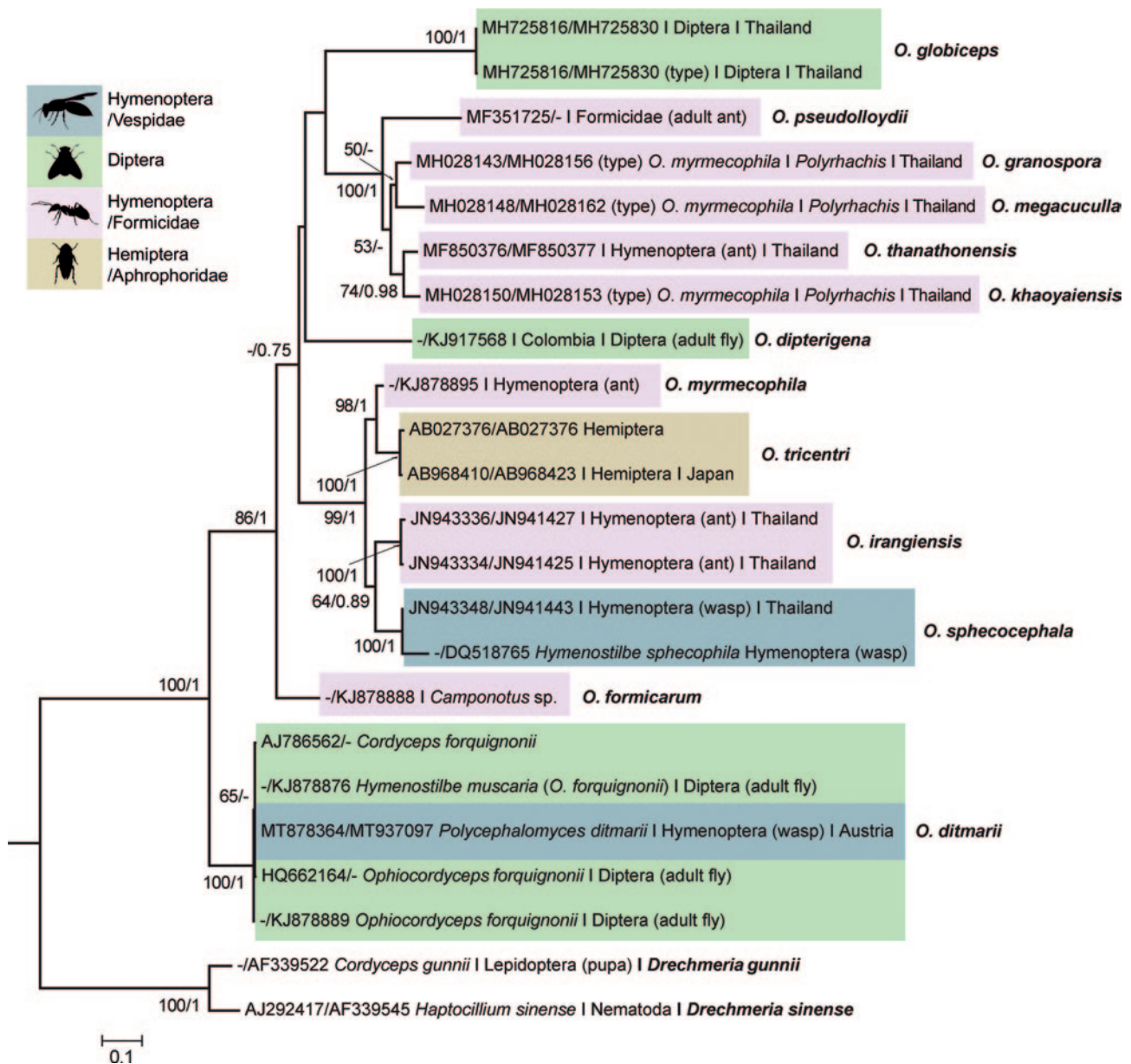
Sung et al. (2007) transferred *C. ditmarii* to the genus *Ophiocordyceps* Petch (family Ophiocordycipitaceae). However, they did not provide sequence data for this species. A molecular study by Kepler et al. (2013) based on a concatenated five-locus dataset retrieved *Polycephalomyces* as sister to Ophiocordycipitaceae with low support. It was later considered as the most basal lineage within the family with high support (Quandt et al. 2014). As a result, Quandt et al. (2014) accepted both the anamorph and teleomorph forms present in this clade as *Polycephalomyces* Kobayasi, based on the inclusion of the type species *P. formosus* Kobayasi. Kepler et al. (2013) accepted *P. ditmarii* in *Polycephalomyces*, although it was not confirmed by phylogenetic evidence. Matočec et al. (2014) queried the identity of

*P. ditmarii* and *Ophiocordyceps ditmarii*, until firm connection between these two species is demonstrated. Therefore, they considered *P. ditmarii* as an anamorphic species with *Polycephalomyces*-type synnemata, which has an unknown sexual state.

Our phylogeny shows that *P. ditmarii* does not belong to the genus *Polycephalomyces* (Fig. 55), although it has a similar type of synnemata (Figs. 53–54). In our two-locus (ITS–LSU) phylogenetic reconstruction, *P. ditmarii* forms a separate lineage in the *Ophiocordyceps sphecocephala* (Klotzsch ex Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora group, which is characterized by *Hymenostilbe*- and *Stilbella*-like anamorphs (Hywel-Jones 1995, Araújo & Hughes et al. 2017, Qu et al. 2018). Furthermore, the ITS and LSU sequences of our



**Fig. 54.** *Ophiocordyceps ditmarii*, collection WU-42993. Microscopic features of synnemata. **a.** Conidia. **b.** Phialides. **c.** Contextual hyphae from the stipe. Scale bars a 5 µm, b–c 10 µm, *leg.* V. Papp.



**Fig. 55.** Phylogeny of the *Ophiocordyceps sphecocephala* clade derived from ML analysis based on an ITS–LSU dataset. MLBS >50 and BIPP >0.7 are shown at the nodes. Isolates are color-coded by host substrate.

specimen (WU-42993) collected on a wasp species (Fig. 53) is identical with sequences of *O. forquignonii* (Quél.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, a species on dipteran hosts (Fig. 55). Our results suggest that *P. ditmarii* is the anamorphic stage of *O. ditmarii*, and this species is identical to *O. forquignonii*. The identity of these two species is also confirmed by the observations of Van Vooren & Audibert (2006), who concluded that *O. forquignonii* is probably a synonym of *O. ditmarii* based on

morphological examinations. However, without molecular data, in their study, they treated the two species separately by their host preference. Further type and molecular studies are needed both on sexual and asexual morphs to estimate the taxonomic relationships among the *O. sphecocephala* group and other *Ophiocordyceps* species parasitizing hymenopteran and hemipteran insects.

As far as we know, there are no specimens of *O. ditmarii* and *O. forquignonii* known in Austria. How-

ever, there remains a bit of uncertainty because some specimens could still be present in major herbaria—such as the Museum of Natural History in Vienna—because these collections have not yet been included in the Database of Austrian Fungi, which is run by the Austrian Mycological Society (<http://www.austria.mycodata.net>). Some records may also be hidden in the thirteen specimens of *Sphaeria sphecocephala* Klotzsch ex Berk. currently present in the database. At least in five of these, wasps are mentioned as substrate. None of them has been sequenced. The years of these reports span from 1969 to 2006. Wasps parasitized by *Ophiocordyceps* seem to be rare or are probably also overlooked. Two further Austrian finds of cordycipitaceous fungi on *Diphyus* Kriechbaumer 1890 cave wasps (Hymenoptera, Ichneumonidae) belong to *Polycephalomycetes ramosus* (Peck) Mains (WU-42995, GenBank accession no. MT937090) and *Lecanicillium coprophilum* Lei Su, Hua Zhu & C. Qin (WU-42994, MT940859).

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#### Ascomycota, Leotiomycetes, Rhytismatales, Rhytismataceae

*Parvacoccum pini* R.S. Hunt & A. Funk, Mycotaxon 33: 52 (1988). – Figs. 56–57

*Material examined.* – AUSTRIA. Salzburg, Lungau, Muhr, Sticklerhütte, 1800 m a.s.l., on dead corticated branch of *Pinus cembra* (Pinales, Pinaceae), 18 June 2019, leg. H. Voglmayr (WU 40042, culture TRY).

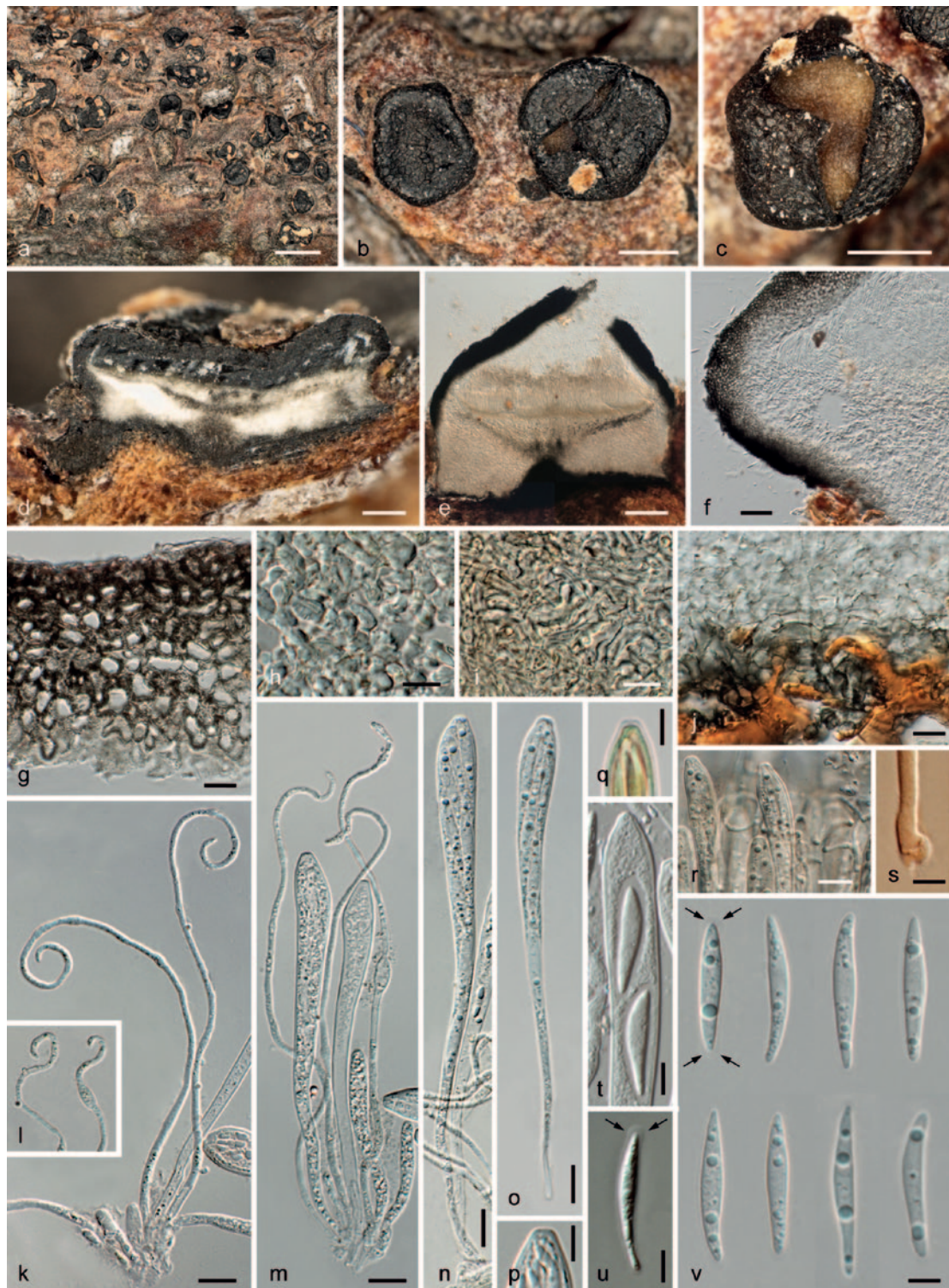
*Description.* – Ascomata apothecial, 0.7–2.1 mm diam., 0.6–0.7 mm high, erumpent from host bark, solitary to gregarious, sessile, more or less circular from above, depressed in the centre when dry. – Outer surface black, shiny, areolated by a reticulum of fine cracks, often with adherent bark remnants, with the excipular covering opening by irregular splits when hydrated, exposing the yellow hymenial surface. – Covering excipulum 40–110 µm thick in transverse section, more or less consistent in thickness, outermost layer highly melanised, intergrading to less melanized (subhyaline) cells toward the inner surface, of textura globulosa-angularis composed of thick-walled, dark brown to subhyaline cells 3–12 µm wide, walls 1.0–2.5 µm thick. – Basal layer black, 40–100 µm thick, of textura intricata composed of dark brown hyphae 3–6 µm wide, mixed with remnants of host tissue. – Medullary excipulum 100–300 µm thick, of textura globulosa-angularis composed of thin-walled, hyaline to pale

brown cells 3–16 µm wide. – Subhymenium 40–170 µm thick, of textura intricata of hyaline hyphae 2.0–4.5 µm diam., with a darker pigmented zone towards the medullary excipulum. – Paraphyses (130–)135–160(–175) × 1.5–2.5 µm (n=15), filiform, hyaline, smooth, aseptate, unbranched, with sinuous to circinate tips, often with subapical vesicular inflations up to 4.5 µm wide. – Asci (dead) (110–)115–137(–150) × (7–)8–10(–11) µm (n=23), thin-walled, clavate, with a basal crozier, a long stipe and an obtuse inamyloid apex, (living and dead) containing 8 obliquely uniseriate to irregularly biseriate ascospores. – Ascospores (20–)21–25(–29) × (2.5–)3.0–3.5(–4) µm, l/w=(5.8–)6.2–8.0(–9.2) (n=40), fusiform, hyaline, aseptate, thin-walled, multiguttulate, with narrowly rounded to subacute ends, within asci (in water) surrounded by a gel sheath becoming indistinct in released ascospores, occasionally with faint globular gelatinous appendages in water and 3 % KOH. – Conidiomata 150–600 µm diam. (n=30), developing close to the ascomata, solitary to aggregated, circular to polyangular in outline, black, with tubercular-wrinkled surface, erumpent from bark and opening by irregular splits. In vertical section wall 20–80 µm thick at base, plurilocular, loculi 80–140 µm diam. – Conidiomatal tissues textura globulosa-angularis composed of dark brown to greenish cells 5–10 µm wide. – Conidiogenous cells (10–)16–23(–27) × 3–4(–4.7) µm (n=23), lining the basal parts of the wall of the loculi, enteroblastic, phialidic, irregularly lageniform to cylindrical, hyaline, thin-walled, smooth. – Conidia (18–)33–44(–48) × (3.0–)3.3–4.0(–4.5) µm, l/w=(5.4–)8.8–12.5(–14) (n=30), curved to falcate, hyaline, smooth, aseptate, multiguttulate, with narrowly rounded tapering ends.

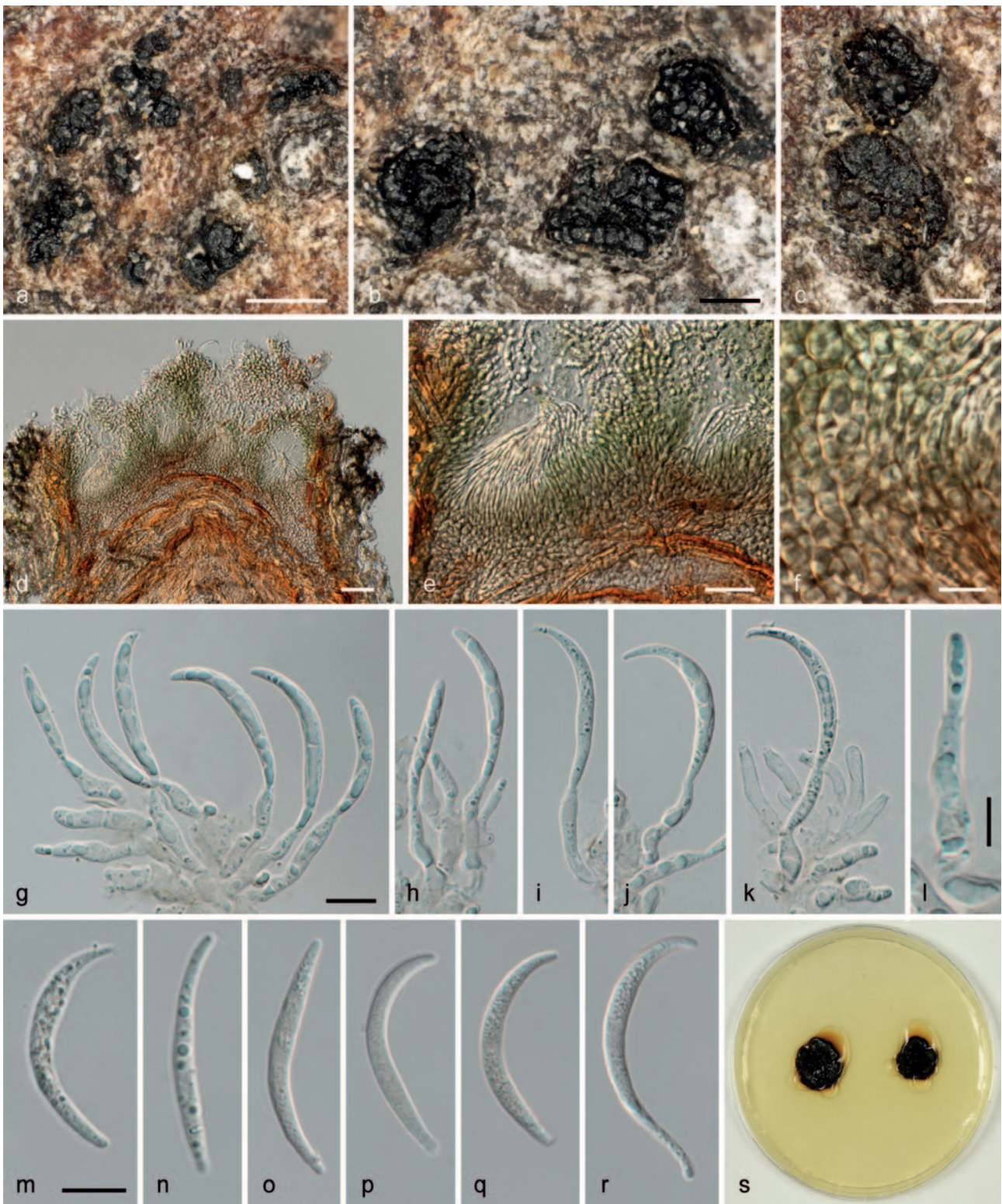
*Culture characteristics.* – On CMD very slow-growing, reaching 15 mm diam. after 2 months of growth at 22 °C, surface blackish brown, without aerial mycelium, covered in brownish mucous exudates, margins wavy, secreting diffusible pigments that stain the agar pale yellow, reverse black.

*Habitat and distribution.* – On dead corticated branches of *Pinus monticola* (type host) and *P. cembra* still attached to the tree. Only known from two localities in British Columbia, Canada (type) and Austria (this study); probably widespread but overlooked on species of *Pinus* subgen. *Strobus*.

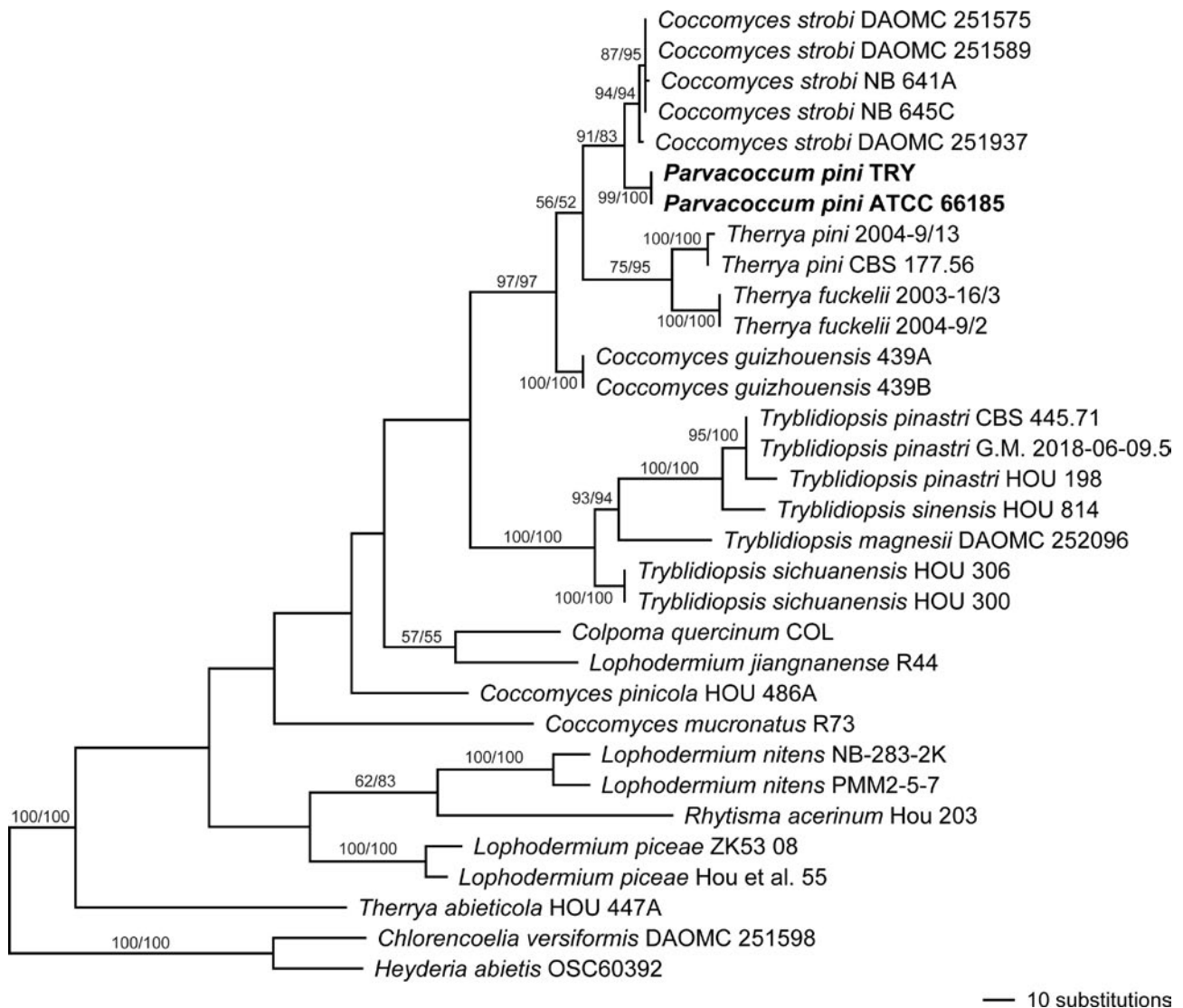
*Notes.* – *Parvacoccum* is a monotypic genus in the Rhytismataceae family (Wijayawardene et al. 2020). Its single species, *Pa. pini*, was described from a *Pinus monticola* (Pinaceae) that was killed



**Fig. 56.** *Parvacoccum pini*, collection WU 40042. Sexual morph. **a–c.** Apothecia in face view (**a**, **b** dry, **c** rehydrated). **d–f.** Apothecia in vertical section. **g.** Covering excipulum. **h.** Medulla. **i.** Subhymenium. **j.** Basal tissues with host cells. **k.** Paraphyses. **l.** Paraphysis tips. **m.** Immature asci and paraphyses. **n, o.** Mature asci. **p, q.** Ascus apices. **r.** Ascus apices and paraphyses tips. **s.** Crozier at ascus base. **t.** Ascus apex with ascospores surrounded by gel sheath. **u, v.** Ascospores; arrows denoting faint gel sheath and terminal appendages. All microstructures in dead state. All in 3 % KOH, except **h, i, q** in Lugol's solution after 3 % KOH pretreatment; **s** in Congo Red; **t, u** in water. Scale bars **a** 2 mm; **b, c** 500  $\mu$ m; **d, e** 200  $\mu$ m; **f** 50  $\mu$ m; **g–o, q, r**; 10  $\mu$ m; **p, q, s–t** 5  $\mu$ m.



**Fig. 57.** *Parvacoccum pini*, collection WU 40042). Asexual morph. **a–c.** Conidiomata in face view (**a, b** dry, **c** rehydrated). **d, e.** Plurilocular conidiomata in vertical section. **f.** Basal conidiomatal tissue. **g–l.** Conidiogenous cells with conidia; in **l** showing enteroblastic phialidic conidiation. **m–r.** Conidia. **s.** Culture on CMD (2 months, 22 °C). All microstructures in dead state and mounted in 3 % KOH. Scale bars a 300 µm; b, c 200 µm; d 50 µm; e 30 µm; f–k, m–r 10 µm; l 5 µm.



**Fig. 58.** Phylogeny of Rhytismataceae reconstructed from a combined ITS–LSU dataset (2224 characters, of which 362 parsimony-informative), with *Chlorencoelia versiformis* and *Heyderia abietis* (Cenangiaceae) as outgroup taxa. The position of *Parvacoccum pini* is highlighted in boldface. For each node, the MPBS/MLBS values (if >50) are presented above or below the branch leading to that node.

by blister rust (*Cronartium ribicola*), in British Columbia, western Canada (Hunt & Funk 1988). Until this study, only two collections of *Pa. pini* were known from the type locality (DAVFP 23419 and DAVFP 23420 [holotype]). The ITS sequence from the ex-type strain of *Pa. pini* (ATCC:66185, UNITE accession no. UDB035391) is identical to that of the here reported Austrian strain. However, the Austrian and Canadian material differ in ascus and ascospore sizes, which are distinctly larger in the Austrian collection compared to those given by Hunt & Funk (1988): Asci: 110–150 × 7–11 µm (Austrian) vs. 71–116 × 4.0–6.5 (Canadian). Ascospores: 20–29 ×

2.5–4.0 (Austrian) vs. 16–18 × 2 µm (Canadian). In addition, the paraphyses are wider in the Austrian collection (1.5–2.5 vs. 0.7–1.5 µm). The illustrations provided by Hunt & Funk (1988) indicate that the studied ascomata may have been immature. This material should be re-examined, which was not possible for this study due to loan problems generated by the COVID-19 pandemic. No asexual morph was mentioned in the original description of *Pa. pini*, but the asexual morph here reported matches those of related Rhytismataceae.

The Austrian find is remarkable, considering it was found on another continent from the type col-



lection. The host of the Austrian collection, *Pi. cembra*, is a member of *Pinus* subgen. *Strobos* and closely related to the type host, *Pi. monticola*. It appears unlikely that *Pi. pini* was introduced to Europe from North America, considering the occurrence of *Pi. cembra* in the timberline of the alpine and subalpine zone in remote, undisturbed mountainous areas (Caudullo & de Rigo 2016). Therefore, *Pa. pini* may be rare but widely distributed on additional related pine species in the boreonemoral temperate zone. It may have been overlooked due to its inconspicuous ascomata and little sampled hosts. In this regard, particularly *Pi. pumila* and *Pi. sibirica*, close relatives of *Pi. cembra*, should be considered—they largely bridge the distributional gap by their range from Siberia to the northern Far East Asia. Alternatively, *Pa. pini* may have been accidentally introduced from North America with living plants of the type hosts, *Pi. monticola*, or other closely related potential hosts, e.g. the Eastern North American *Pi. strobus*, which may have remained unnoticed. However, *Pa. pini* has not been reported from *Pi. strobus* in eastern North America, and it is unknown whether it occurs on this host. Additional evidence is necessary to clarify this distribution gap.

Our MP and ML analyses (Fig. 58) support that current morphology-based generic concepts within Rhytismataceae do not agree with molecular phylogenetic relationships (Lantz et al. 2011). Genera like *Coccomyces*, *Lophodermium*, and *Therrya* are retrieved as polyphyletic, indicating the need for future generic reclassification, which, however, is hampered by the lack of (i) multilocus data and (ii) sequences for generic type species (e.g. in *Coccomyces*) (Johnston et al. 2019). ITS–LSU data alone are unsuitable for generic classification, as topologies of nodes with no to moderate support change significantly depending on the taxon selection included in the analysis (data not shown). In the phylogenetic tree (Fig. X3), *Parvacoccum pini* groups with *Coccomyces strobi* with high support and forms a highly supported clade with *Therrya* (*T. fuckelii*, *T. pini*) and *Coccomyces guizhouensis*, which all occur on pine twigs. *Coccomyces strobi* is a common branch saprotroph and needle endophyte of *Pi. strobus* that likely plays a role in natural twig pruning (McMullin et al. 2019), and *Pa. pini* may occupy a similar niche. Currently, no sequence data are available for the generic type species, *Coccomyces coronatus*, but its ecology and morphology indicate that it may not be closely related to the *Coccomyces/Parvacoccum* clade. If this hypothesis is supported, *C. strobi* may be combined in *Parvacoccum*.

Author: H. Voglmayr

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