

Exploring macrofungal diversity hotspot of the Qinghai–Xizang Plateau revealed by integrative taxonomy with 31 new species

Xixi Han^{1,2,3,4}, Ruilin Zhao^{2,5}, Bin Cao², Jiaxin Li^{2,5}, Rui Xing^{6,7}, Maoqiang He⁸, Haiying Feng^{2,5}, Shihui Wang^{2,9}, Kevin D. Hyde^{3,4}, Naritsada Thongklang^{3,4} and Dorji Phurbu^{1*}

¹ Xizang Key Laboratory of Plateau Fungi, Institute of Plateau Biology of Xizang Autonomous Region, Lhasa 850000, China

² State Key Laboratory of Microbial Diversity and Innovative Utilization, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, China

³ Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand

⁴ School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand

⁵ College of Life Sciences, University of Chinese Academy of Sciences, Beijing 100049, China

⁶ Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810008, China

⁷ Qinghai Provincial Key Laboratory of Crop Molecular Breeding, Xining 810008, China

⁸ College of Resource Sciences and Technology, Sichuan Agricultural University, Chengdu 611130, China

⁹ Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai 50200, Thailand

* Correspondence: puduo@126.com (Phurbu D)

Abstract

Macrofungi are key components of terrestrial ecosystems, yet their diversity remains poorly documented in high-elevation regions. The Qinghai–Xizang Plateau, characterized by strong environmental gradients and extreme conditions, provides an ideal system for investigating fungal diversity and adaptation. In this study, extensive field surveys conducted between 2015 and 2024 across multiple vegetation types were combined with morphological and multilocus phylogenetic analyses to assess macrofungal diversity. We describe 31 previously unknown species belonging to 10 genera of Agaricales, spanning multiple phylogenetic lineages and ecological guilds. Saprotrophic taxa dominate the assemblage, with ectomycorrhizal species also being well-represented. These findings indicate that macrofungal diversity in high-elevation ecosystems remains substantially underestimated and highlight the importance of integrative taxonomy for resolving species diversity. A subset of species exhibits a recurrent morphological pattern, characterized by robust basidiomata with relatively small, thick pileus and short, stout stipes, along with the occasional co-occurrence of two-spored and four-spored basidia. Based on these observations, we propose a preliminary hypothesis that coordinated shifts in structural and reproductive traits may occur in some macrofungi inhabiting high-elevation environments. Overall, this study expands current knowledge of macrofungal diversity on the Qinghai–Xizang Plateau and emphasizes the importance of mountain systems for understanding fungal diversification and ecological adaptation.

Keywords: Qinghai–Xizang plateau, Macrofungal diversity, Agaricales, Phylogeny, Morphology

Citation: Han XX, Zhao RL, Cao B, Li JX, Xing R, et al. 2026. Exploring macrofungal diversity hotspot of the Qinghai–Xizang Plateau revealed by integrative taxonomy with 31 new species. *Mycosphere* 17: e017 <https://doi.org/10.48130/mycosphere-0026-0017>

Introduction

Macrofungi constitute a fundamental yet still profoundly underexplored component of global terrestrial biodiversity^[1–4]. As dominant decomposers of lignocellulosic biomass, they play indispensable roles in organic matter turnover, nutrient mobilization, and soil formation across a wide range of ecosystems^[5–10]. In addition, numerous macrofungal taxa establish ectomycorrhizal symbioses with woody plants, thereby influencing plant productivity, vegetation dynamics, and ecosystem resilience^[11–14], and are important in other biotechnological applications including compound discovery^[15–17]. Through these ecological functions, macrofungi regulate carbon fluxes, mediate nutrient cycling, and contribute to the maintenance of ecosystem stability^[18–21]. Despite their ecological prominence and deep evolutionary history, global estimates indicate that only a small fraction of macrofungal diversity has been formally documented, with vast numbers of species remaining undescribed^[22–24]. This taxonomic knowledge gap is particularly pronounced in mountainous regions such as the Qinghai–Xizang Plateau, where pronounced environmental heterogeneity, arising from rugged topography, steep climatic gradients, and geographic isolation, is hypothesized to drive lineage diversification and endemic radiations^[25–27].

Traditionally, macrofungal taxonomy has relied primarily on phenotypic characterization, including macromorphological features of basidiomata and micromorphological traits such as basidiospore ornamentation, hymenophoral configuration, and hyphal structure^[28–30]. However, pervasive morphological plasticity across many fungal lineages, frequently driven by environmental factors such as substrate composition, moisture availability, temperature regimes, and altitude, can obscure species boundaries^[31–34]. Convergent evolution and parallel morphological adaptations further contribute to taxonomic frameworks that do not accurately reflect phylogenetic relationships^[24,31,35,36]. As a result, numerous historically described taxa circumscribed solely on morphological evidence lack phylogenetic support, leading to uncertain systematic placement and complicating the delimitation and recognition of newly discovered species^[37–39]. Such limitations may result in taxa being recovered as nested within established clades, generating paraphyly and persistent taxonomic instability^[40]. Over the past two decades, the rapid maturation of molecular systematics and the paradigm shift toward integrative taxonomy, which synthesizes phenotypic characters, ecological niches, and robust multilocus phylogenetic inference, have revolutionized fungal systematics and revealed extensive cryptic diversity across major macrofungal lineages^[34,37,41].

The Qinghai–Xizang Plateau represents the largest and highest alpine ecosystem on Earth, providing an exceptional setting for

studies of biodiversity and ecological processes^[42–44]. Shaped by a complex geological history and marked environmental gradients, the Plateau supports diverse alpine and montane vegetation types that create a wide range of fungal habitats^[45–47]. The extreme conditions of high-elevation environments, including low temperatures, intense ultraviolet radiation, fluctuating moisture regimes, and reduced oxygen availability, impose strong selective pressures that may drive adaptive divergence and lineage diversification in fungal populations^[48–53]. Owing to steep environmental gradients and topographic complexity, mountain systems function as major engines of diversification, promoting speciation through geographic isolation, ecological niche differentiation, and climatically driven range dynamics^[54–58]. Under these conditions, substantial fungal diversity, including cryptic taxa, may remain overlooked when relying solely on morphology-based identification. Consequently, integrative taxonomic investigations remain essential for revealing fungal diversity and improving our understanding of evolutionary processes in high-elevation ecosystems.

Although fungal diversity across parts of the Qinghai–Xizang Plateau and adjacent regions has received increasing attention in recent years^[59–63], current knowledge remains taxonomically fragmented and geographically uneven. Existing studies have largely focused on individual genera, specific ecological guilds, or restricted sampling areas^[64–67], resulting in an incomplete understanding of diversity patterns, lineage diversification, and systematic placement, particularly for taxa lacking multilocus phylogenetic assessment. Moreover, the scarcity of integrative studies spanning multiple phylogenetic lineages across vegetation belts and elevational gradients continues to constrain a comprehensive understanding of macrofungal diversity and diversification in high-elevation ecosystems^[25,26,68,69]. Here, we address these gaps through extensive plateau-wide field surveys and an integrative systematic investigation of 10 focal fungal lineages. By combining morphological, ecological, and multilocus phylogenetic evidence, this study provides a more robust evolutionary framework for species delimitation and taxonomic placement, thereby improving our understanding of macrofungal diversity and diversification on the Qinghai–Xizang Plateau. These findings also contribute to a broader understanding of how environmental heterogeneity and elevational gradients shape fungal diversification on the plateau.

Based on field collections made between 2015 and 2024 across multiple high-elevation habitats of the Qinghai–Xizang Plateau, this study uses an integrative taxonomic approach that combines morphological examination, ecological observations, and multilocus phylogenetic analyses to investigate macrofungal diversity. We describe 31 previously undocumented species belonging to 10 genera across 10 families of Agaricales, with specimens collected from multiple vegetation types, including coniferous forests, broad-leaved forests, mixed forests, alpine meadows, and shrublands. Although not intended as a comprehensive regional inventory, these findings highlight the presence of substantial, previously unrecognized taxonomic diversity across diverse high-elevation habitats. This work also provides a baseline framework for future studies addressing fungal diversity patterns, ecological associations, and evolutionary processes in mountain ecosystems.

Materials and methods

Sample collection and herbarium specimen preparation

Fresh basidiomata were collected during extensive field surveys conducted from 2015 to 2024 across the Qinghai–Xizang Plateau

and adjacent regions, including Xizang Autonomous Region, Qinghai, Sichuan, Gansu, and Yunnan Provinces. Collections were obtained from five major vegetation types, namely shrublands, alpine meadows, coniferous forests, broad-leaved forests, and mixed conifer and broad-leaved forests. Macromorphological features were documented from fresh specimens in the field and photographed before preservation. All collections were dehydrated at 50 °C, sealed, and deposited in the Mycological Herbarium of the Institute of Microbiology, Chinese Academy of Sciences (HMAS) and the Alpine Fungarium (AF).

Morphological studies

Morphological investigations were conducted using both fresh and dried materials. Macroscopic characters were recorded from mature basidiomata in the field, whereas microscopic structures were examined from rehydrated specimens^[66]. Colour descriptions followed the *Methuen Handbook of Colour*^[70]. Sections of pileus, lamellae, and stipe tissues were mounted in 5%–10% KOH and, when necessary, stained with Congo red. Microscopic observations were performed using an Olympus CX31 microscope following the procedures outlined by Largent et al.^[30]. Basidia, basidiospores, cystidia, and pileipellis structures were examined and measured, with a minimum of 50 measurements obtained for each character. Spore dimensions are expressed as $(a)b-c(d)$, where $b-c$ encompasses at least 90% of the observations. The notation $n/m/p$ refers to the number of spores measured, the number of basidiomata examined, and the number of collections studied, respectively. Q represents the spore length-to-width ratio and Qm its mean value $\pm$ standard deviation. Basidiospore ornamentation and other ultrastructural features were further examined using scanning electron microscopy (JEM-1400)^[66,71,72].

DNA extraction, amplification, and sequencing

Total genomic DNAs were isolated from fresh or dried basidiomata using a Broad-spectrum Plant Rapid Genomic DNA Kit (Beijing Biomed Gene Technology Co., Ltd., China), following the manufacturer's protocol with slight modifications. DNA extracts were stored at -20°C before PCR amplification. Four loci widely used in fungal phylogenetic studies include the internal transcribed spacer region (ITS1–5.8S–ITS2), the nuclear large subunit ribosomal DNA (LSU), partial sequences of the second largest subunit of RNA polymerase II (*rpb2*), and the translation elongation factor 1- α gene (*tef1 α*). The ITS region was amplified using ITS1-F (ITS5 or ITS1) and ITS4^[73,74]; LSU using LR0R and LR5 (or LR7)^[75,76]; *rpb2* using brpb2-6F (or frpb2-5F) and brpb2-7.1R^[77]; and *tef1 α* using 983F and 1567R (or 2218R)^[78]. For samples that failed to amplify with universal primers, specific or internal primers were used, following previous studies^[79,80].

PCR amplification was performed in a T30 Multi-Block Gradient PCR Thermocycler (Hangzhou LongGene Scientific Instruments Co., Ltd., China) using a total reaction volume of 25 μL containing 2 μL genomic DNA, 1 μL of each primer, 9 μL double-distilled water, and 12 μL 2 $\times$ Es Taq MasterMix (Dye) (Beijing ComWin Biotech Co., Ltd., China). PCR amplifications were carried out using the following thermal cycling programme: initial denaturation at 94 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 1 min, annealing at 48–55 °C for 1 min, and extension at 72 °C for 1.5 min, with a final extension at 72 °C for 10 min. For samples that failed to amplify under these conditions, gradient PCR was conducted using the same thermocycler with annealing temperatures ranging from 50 to 60 °C. PCR products were examined on 1.4% agarose gels stained with GoldenView. Successfully amplified products were purified and

sequenced using the same primers at BGI Genomics Co., Ltd. (Beijing, China). In a few cases when direct sequencing failed, PCR products were cloned into the pMD18-T vector (Takara Biomedical Technology Co., Ltd., Beijing, China) according to the manufacturer's instructions, then transformed into *Escherichia coli* DH5- α competent cells, and sequenced using M13F/M13R primers^[81]. Sequences were assembled and edited using SeqMan implemented in the DNASTAR software package (DNASTAR Inc., Madison, USA). All newly generated sequences were deposited in GenBank and are listed under 'Specimens examined' for each species in the Taxonomy. For new species described from single collections, PCR amplification and sequencing were independently repeated to minimize potential sequencing errors.

Phylogenetic analyses

Newly generated sequences were initially subjected to blastn searches in the GenBank database to identify closely related taxa. Sequences with query coverage > 90% and a percentage identity of 96% were selected, and one to three representative sequences per species were included for subsequent analyses. In addition, published sequences of morphologically similar taxa were incorporated into the final dataset. Individual loci were aligned separately using the online MAFFT v7 server (<https://mafft.cbrc.jp/alignment/server>)^[82] with the default strategy, and manually adjusted in BioEdit v7.1.3.0^[83]. The aligned datasets were subsequently concatenated using PhyloSuite v1.2.3^[84], with missing data and ambiguous regions coded as 'N'.

Phylogenetic relationships were inferred using Maximum Likelihood (ML) and Bayesian Inference (BI) methods. ML analyses were conducted on the CIPRES Science Gateway (www.phylo.org)^[85] using RAXML-HPC BlackBox v8.2.12^[86], and branch support was estimated based on 1,000 nonparametric bootstrap replicates. The best partitioning scheme and substitution models for BI analyses were determined using PartitionFinder2 v2.1.1^[87], implemented in PhyloSuite, applying the greedy algorithm and the AICc criterion. Bayesian analyses were performed on the CIPRES Science Gateway using MrBayes on ACCESS v3.2.7a^[88], with two independent runs and four Markov chains. For each group, the DNA loci used, analytical method(s), partitioning strategy, and outgroup(s) setting were described in the figure legend of the phylogenetic tree. The resulting phylogenetic trees were visualized using the tvBOT online platform (www.chiplot.online/tvbot.html)^[89] and further edited in Adobe Illustrator 2024.

Results

Taxonomy

Agaricales Underw.

Index Fungorum number: IF 90508

Agaricaceae Chevall.

Index Fungorum number: IF 80434

Type genus — *Agaricus* L.

Agaricus L.

Index Fungorum number: IF 17030

Type species — *Agaricus campestris* L.

Notes — *Agaricus* is widely distributed in temperate and tropical regions worldwide and currently comprises more than 600 described species, occurring on all continents except Antarctica^[90–92]. Approximately 200 species have been recorded in China, making it one of the most species-rich agaric genera in the country^[93]. Species of *Agaricus* are predominantly saprotrophic

and commonly occur in forest ecosystems and grasslands^[94,95]. Recently, studies have revealed that some species are lignicolous, such as *A. subiculosus*, which grows on decaying wood substrates^[96]. Basidiomata of *Agaricus* exhibit considerable variation in size and colour, typically possessing membranous annuli, free lamellae that become brown at maturity, as well as brown basidiospores^[97].

Based on multigene phylogenetic analyses combined with morphological studies, *Agaricus* is currently divided into six subgenera, including subg. *Agaricus*, subg. *Flavoagaricus*, subg. *Minores*, subg. *Minoriopsis*, subg. *Pseudochitonina*, and subg. *Spissicaules*^[95,98,99]. The above subgenera consist of 25 sections^[95,98–100]. In the present study, three new species belonging to the sect. *Agaricus* and sect. *Arvenses* are described based on morphological characteristics and phylogenetic analyses of ITS, LSU, and *tef1 α* sequences.

Agaricus albicrassipes R.L. Zhao & X.X. Han, sp. nov. Figs 1 and 4

Chinese Name: 白色粗柄蘑菇 (bai se cu bing mo gu)

Fungal Names: FN 573686; Facesoffungi number: FoF 20041

Etymology — *albicrassipes* (Latin), referring to the white basidiomata and the robust stipe of this species.

Diagnosis — differs from other species in this section by a thick stipe, broadly ellipsoid to narrowly ellipsoid (7.4–8.7 $\times$ 5.4–6.4 μ m), two- or four-spored basidia, and distinct DNA sequences.

Holotype — CHINA, Xizang, Lhasa City, Lhalu Wetland National Nature Reserve, 29°40'12.03" N, 91°5'38.79" E, 3,659 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests, 10 August 2023, Y. Zhang, ZRL20231653 (HMAS 259799 holotype; AF9574 isotype, GenBank no.: ITS PZ491328; LSU PZ495513; *tef1 α* PZ520019).

Pileus 24–94 mm diam., 5–23 mm thick at disc, initially hemispherical with involute margin, becoming convex to plano-convex when mature, fleshy, surface dry, smooth or covered with appressed fibrils, white (1A1) to yellowish white (1A2), nonstriate. Lamellae

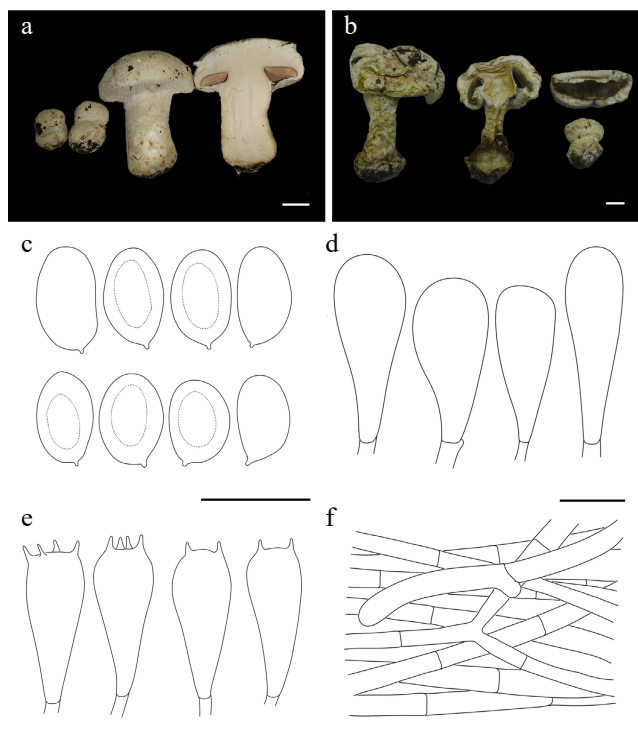


Fig. 1 *Agaricus albicrassipes* (a, b: ZRL20231653 holotype). (a, b) Basidiomata; (c) Basidiospores; (d) Basidioles; (e) Basidia; (f) Pileipellis. Scale bars: (a) = 1 cm; (c–f) = 10 μ m.

crowded, free, unequal, reddish white (8A2) to dull red (8B3), then brown to dark brown with age, even. Stipe 28–85 × 26–44 mm, cylindrical, central, equal, robust, hollow, smooth or slightly fibrillose. Annulus superior, membranous, attached at the margin of the pileus or entirely at the stipe, upper surface smooth and white, lower surface fibrillose, white, easily falling off. Context thick, white, pale brown when bruised, odour unknown.

Basidiospores [50/2/1] (6.5–)7.4–8.7(–9.8) × (5.0–)5.4–6.4(–6.8) μm , $Q = (1.17\text{--})1.22\text{--}1.53(1.75)$, $Q_m = 1.37 (\pm 0.16)$, broadly ellipsoid to narrowly ellipsoid, rarely oblong, smooth, light brown, thick-walled, usually containing an oil droplet. Basidia (19.6)21.9–26.6(29.2) × (8.2)8.6–10.5(12.4) μm , clavate or slightly truncate at the apex, hyaline, two- or four-spored. Cheilocystidia and pleurocystidia were not observed. Basidioles (11.1)17.2–30.3(37.4) × (4.4)5.7–11.3(13.3) μm , clavate to narrowly clavate, cylindrical. Lamella trama regular to subregular, hyphae 2–6 μm wide, cylindrical, thin-walled, hyaline. Pileipellis is a cutis with the transition to a trichoderm at regular intervals, thin-walled, hyphae 1–4 μm wide. Clamp-connections present.

Known distribution — Scattered on humus-rich ground within mixed coniferous and broad-leaved forests, in summer. So far found only in Xizang, China.

Notes — *Agaricus albicrassipes* belongs to *A. sect. Agaricus* and is morphologically similar to *A. argenteus* Braendle ex Peck of this section. However, *A. argenteus* has a thinner stipe (10–12 mm) and larger basidiospores (8.2–9.2 × 6.3–7.3 μm)^[101]. In the multigene phylogenetic tree, *A. albicrassipes* forms an independent clade (Fig. 4). Phylogenetically, the new species is related to *A. aristocratus*, *A. campestris*, *A. gastronevadensis*, and *A. zhangyensis*. *Agaricus aristocratus* differs by its slightly larger pileus (80–150 mm), thinner stipe (18–23 mm), and slightly wider basidiospores (5.8–6.7 μm)^[101]. *Agaricus campestris*, the type species of subg. *Agaricus*, has not been confirmed from China, as neither previous studies nor Asian sequences deposited in GenBank have demonstrated its occurrence in this region^[101]. Moreover, *A. campestris* has a white pileus with appressed squamules at the centre and smaller basidiospores (7.1 × 5.3 μm)^[102,103]. *Agaricus gastronevadensis*, originally described from the USA, differs in having a ventricose and slightly thinner stipe (20–35 mm), and wider basidiospores (6.9–7.3 μm)^[103]. *Agaricus zhangyensis*, originally described from Gansu Province, China, is distinguished by a thinner stipe (13–20 mm) and slightly longer basidiospores (6.4 μm)^[101].

Agaricus platifissus R.L. Zhao & X.X. Han, sp. nov. Figs 2 and 4

Chinese Name: 高原开裂蘑菇 (gao yuan kai lie mo gu)

Fungal Names: FN 573687; Facesoffungi number: FoF 20042

Etymology — *platifissus* (Latin), referring to the species' occurrence on the Qinghai–Xizang Plateau and its characteristically cracked pileus surface when mature.

Diagnosis — differs from other species in this section by a cracked pileus, broadly ellipsoid to ellipsoid basidiospores (6.8–7.8 × 5.4–6.2 μm), two- or four-spored basidia, the presence of cheilocystidia, alpine distribution, and distinct DNA sequences.

Holotype — CHINA, Xizang, Linzhi, Bomi County, along G318 from Egong Zangbu to Pu Zangbu, 29°40'17" N, 96°12'40" E, 3,133 m asl, growing on humus-rich ground within broad-leaved forests dominated by *Quercus*, 11 August 2023, M.Z. Zhang & X.X. Han, ZRL20231805 (HMAS 259800 holotype; AF9575 isotype, GenBank no.: ITS PZ491327; LSU PZ495512; *tef1α* PZ520021).

Pileus 26–60 mm diam., 4–7 mm thick at disc, convex when young, becoming plano-convex with age, surface dry, smooth or finely pruinose, usually cracked, fleshy, yellowish white (2A2) to greyish yellow (2C3) at the centre, white (2A1) to yellowish grey (2B2) towards margin, becoming greyish yellow (4C3) to olive brown

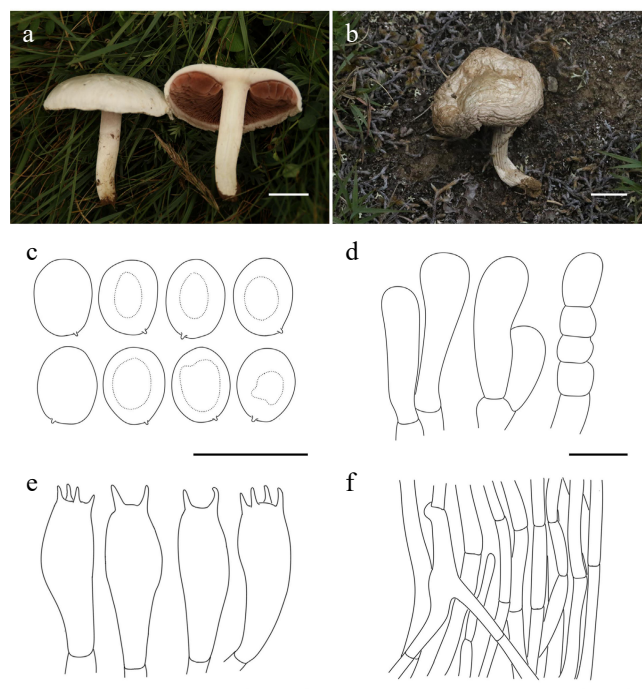


Fig. 2 *Agaricus platifissus* (a, ZRL20162141, b ZRL20231805 holotype). (a, b) Basidioma; (c) Basidiospores; (d) Cheilocystidia; (e) Basidia; (f) Pileipellis. Scale bars: (a, b) = 1 cm; (c–f) = 10 μm .

(4D5) when dry, deflexed, nonstriae. Lamellae crowded, free, unequal, pale red (8A3) to greyish red (8C5) initially, dark brown (8F5–8) with age, uneven. Stipe 34–53 × 5–10 mm, cylindrical, central, slightly tapering towards the base, with an annulus in its upper third, smooth above the annulus, fibrillose below the annulus. Annulus superior, white, membranous, attached at the margin of the pileus or entirely at the stipe, slightly pendant, simple, easily falling off. Context slightly thick, with an obscure central region of white pith, discolouration slightly pinkish near the connection between the stipe and pileus, odour unknown.

Basidiospores [50/2/2] (6.2–)6.8–7.8(–8.2) × (4.8–)5.4–6.2(–6.8) μm , $Q = (1.08\text{--})1.19\text{--}1.34(1.41)$, $Q_m = 1.26 (\pm 0.06)$, broadly ellipsoid to ellipsoid, rarely subglobose, smooth, light brown, thick-walled, usually containing an oil droplet. Basidia (21.0)23.6–28.6(30.8) × (7.5)8.4–10.0(10.6) μm , clavate, hyaline, two- or four-spored. Cheilocystidia (18.5)20.1–24.1(25.9) × (6.4)7.0–8.2(8.9) μm , clavate to narrowly clavate, subhyaline. Pleurocystidia not observed. Lamella trama subregular, hyphae 1.7–3.9 μm wide, cylindrical, thin-walled, hyaline. Pileipellis is a cutis with the transition to a trichoderm at regular intervals, thin-walled, hyphae 3.4–10.2 μm wide. Clamp-connections present.

Known distribution — Solitary on humus-rich ground within coniferous or broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Gansu, Zhangye City, Sunan County, Qilian Mountain National Nature Reserve, Dayekou Protection Station, 38°32'52" N, 100°14'31" E, 2,980 m asl, growing on humus-rich ground within coniferous forests dominated by *Picea crassifolia*, 1 September 2016, R.L. Zhao & X.M. Bai, ZRL20162141 (HMAS 280413, GenBank no.: ITS MN604414; LSU PZ495511; *tef1α* PZ520020).

Notes — *Agaricus platifissus* is nested within *A. sect. Agaricus*, which is typically characterized by a nonspecial odour, context often discolours pinkish or reddish near the stipe-pileus junction upon exposure, and cheilocystidia that are mostly absent or indistinguishable from immature basidia^[90,101,104].

Before *A. platifissus*, 17 species from this section have been reported from China, viz. *A. altipes* (F.H. Møller) F.H. Møller, *A. argenteus* Braendle ex Peck, *A. argyropotamicus* Speg., *A. aristocratus* Gulden, *A. campestris* L., *A. cantonotraminus* Kun L. Yang, Jia Y. Lin & Zhu L. Yang, *A. chionodermus* Pilát, *A. cupreobrunneus* (Jul. Schäff. & Steer) Pilát, *A. depauperatus* (F.H. Møller) Pilát, *A. fafuinus* P.H. Liu & S.E. Wang, *A. griseicephalus* Kerrigan, *A. jilinensis* R.L. Zhao & A.Q. Liu, *A. langei* (F.H. Møller) F.H. Møller, *A. porphyrocephalus* F.H. Møller, *A. rubribrunnescens* Murrill, *A. sinoagrocycloides* T. Bau & S.E. Wang, and *A. zhangyensis* R.L. Zhao & A.Q. Liu^[101,105–107].

In comparison with these species, *A. platifissus* is characterized by a white to yellowish-grey, smooth or finely pruinose, sometimes cracked pileus; a stipe slightly tapering towards the base; broadly ellipsoid to ellipsoid basidiospores measuring $6.8\text{--}7.8 \times 5.4\text{--}6.2\ \mu\text{m}$; and basidia that are two- or four-spored. Unlike most species of the section, *A. platifissus* possesses cheilocystidia and unique DNA sequences. Moreover, the species appears to occur solitarily and is, thus far, known only from the Qinghai–Xizang Plateau.

Agaricus submegacarpus R.L. Zhao & X.X. Han, sp. nov. Figs 3 and 4
Chinese Name: 拟大果蘑菇 (ni da guo mo gu)

Fungal Names: FN 573688; Facesoffungi number: FoF 20043

Etymology — referring to the resemblance to *A. megacarpus*.

Diagnosis — Phylogenetically and morphologically similar to *A. megacarpus*, but differs in having a paler stipe and smaller basidiospores and basidia, with distinct DNA sequences.

Holotype — CHINA, Qinghai, Haidong City, Huzhu Tu Autonomous County, Ganchan Temple, 402 m north of Weibei Highway, $37^{\circ}2'10''\text{N}$, $102^{\circ}20'56''\text{E}$, 2,701 m asl, growing on humus-rich ground within coniferous forests dominated by *Picea crassifolia* and *Sabina przewalskii*, 26 August 2023, M.Q. He & J.X. Li, ZRL20235671 (HMAS 259801 holotype; AF9580 isotype, GenBank no.: ITS PZ491324; LSU PZ495508)

Pileus 31–48 mm diam. in the early stage, 64–131 mm diam. at maturity, 8–33 mm thick at disc, initially hemispherical, later becoming obtusely conical to convex, and finally applanate, sometimes with a subumbonate at the centre and occasionally cracked, fleshy, surface dry, smooth at first, later covered by appressed thick fibrils, eventually breaking into appressed scales, white (1A1) to greyish green (1C3), paler towards the margin, turning brownish orange (5C5) with age, nonstriate. Lamellae crowded, free, unequal, pale red (8A3) to greyish red (8C5) initially, dark brown (8F5–8) with age, even. Stipe 62–122 $\times$ 13–26 mm, cylindrical, central, robust, hollow, slightly tapering towards the base or occasionally bulbous, smooth, or slightly fibrillose above the annulus, fibrillose when young, then fibrillose squamose below the annulus. Annulus superior, membranous, attached at the margin of the pileus or entirely at the stipe, upper surface smooth and white, lower surface floccose, white or light brown, easily falling off. Context thick, white or light brown, odour unknown.

Basidiospores $[50/2/2]$ $(5.4\text{--}5.8\text{--}6.5(-7.1) \times (4.0\text{--}4.3\text{--}4.9(-5.2)\ \mu\text{m}$, $Q = (1.09\text{--}1.26\text{--}1.42(-1.54))$, $Q_m = 1.34 (\pm 0.08)$, broadly ellipsoid to ellipsoid, rarely subglobose or narrowly ellipsoid, smooth, light brown, thick-walled, usually containing an oil droplet. Basidia $(13.7)15.6\text{--}19.1(20.8) \times (5.9)6.3\text{--}7.6(8.2)\ \mu\text{m}$, clavate or slightly truncate at the apex, hyaline, two- or four-spored. Cheilocystidia $(14.1)15.6\text{--}18.2(19.7) \times (5.6)6.0\text{--}7.0(7.4)\ \mu\text{m}$, clavate, hyaline. Pleurocystidia not observed. Lamella trama regular to subregular, hyphae $4.3\text{--}9.3\ \mu\text{m}$ wide, cylindrical, thin-walled, hyaline. Pileipellis is a cutis with the transition to a trichoderm at regular intervals, thin-walled, hyphae $3.6\text{--}12.1\ \mu\text{m}$ wide. Clamp-connections present.

Known distribution — Scattered or in pairs on humus-rich ground within coniferous or broad-leaved forests, summer to fall. So far found only in China.

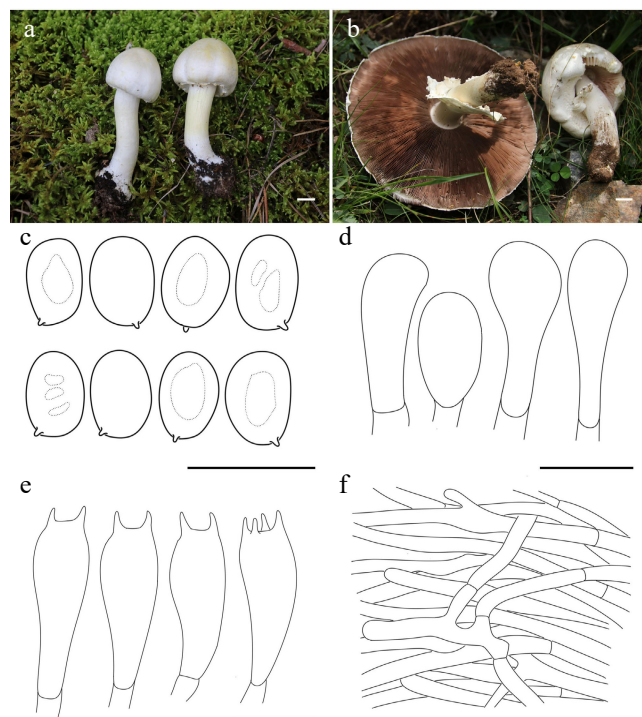


Fig. 3 *Agaricus submegacarpus* (a, ZRL20170661; b, ZRL20235671 holotype). (a, b) Basidiomata; (c) Basidiospores; (d) Cheilocystidia; (e) Basidia; (f) Pileipellis. Scale bars: (a, b) = 1 cm; (c–f) = 10 μm .

Material examined — CHINA, Xizang, Lhasa City, Qushui County, $29^{\circ}26'17.47''\text{N}$, $90^{\circ}57'17.53''\text{E}$, 3,794 m asl, growing on humus-rich ground within broad-leaved forests dominated by *Populus*, 15 August 2023, Y. Zhang, ZRL20236207 (HMAS 259802, GenBank no.: ITS PZ491325; LSU PZ495509; *tef1 α* PZ520016); Lhasa City, Lhunzhub County, $29^{\circ}53'8.26''\text{N}$, $91^{\circ}0'32.73''\text{E}$, 3,755 m asl, growing on humus-rich ground within broad-leaved forests dominated by *Populus*, 25 August 2023, Y. Zhang, ZRL20236208 (HMAS 259803, GenBank no.: ITS PZ491326; LSU PZ495510; *tef1 α* PZ520017).

Notes — *Agaricus submegacarpus* belongs to *A.* sect. *Arvenses*. Within this section, *A. submegacarpus* shares several morphological features with *A. griseopileatus* T. Bau & S.E. Wang, including whitish to pale yellow basidiomata, an occasionally cracked pileus, and broadly ellipsoid to ellipsoid basidiospores. Although the two species show only minor macroscopic differences, they can be clearly distinguished by their microscopic characteristics, as *A. griseopileatus* has larger basidiospores ($5.8\text{--}7.3\ \mu\text{m}$) and broader basidia ($7\text{--}9\ \mu\text{m}$), in addition to distinct molecular characters^[106]. Phylogenetic analyses further indicate that *A. submegacarpus* forms a sister lineage with *A. megacarpus* R.L. Zhao & B. Cao (Fig. 4). Compared with the new species, *A. megacarpus* possesses a slightly darker stipe and larger basidiospores ($7\text{--}8\ \mu\text{m}$) and basidia ($24.5\text{--}31.5\ \mu\text{m}$)^[108]. Moreover, the phylogenetic results (Fig. 4) show that specimens previously identified as '*Agaricus* sp.' (ZRL20170661 and HMJAU 67828), collected from Inner Mongolia and Jilin Province, China, are conspecific with *A. submegacarpus*.

Clitocybaceae Vizzini, Consiglio & M. Marchetti

Index Fungorum number: IF 557869

Type genus — *Clitocybe* (Fr.) Staude

Collybia (Fr.) Staude

Index Fungorum number: IF 17339

Type species — *Collybia tuberosa* (Bull.) P. Kumm.

Notes — *Collybia* is a cosmopolitan genus typified by *C. tuberosa*, with approximately 260 species currently recognized

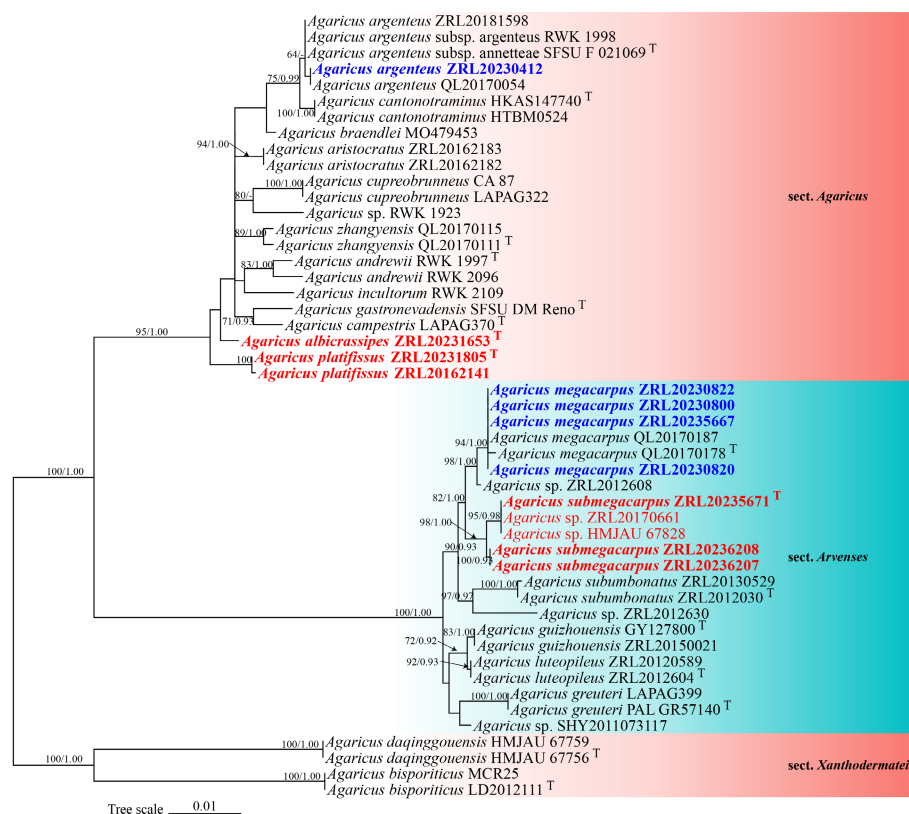


Fig. 4 Molecular phylogenetic analyses of *Agaricus* species by the maximum likelihood (ML) method based on combined ITS–LSU–*tef1α* sequences, rooted with *Agaricus daqinggouensis* and *Agaricus bisporiticus*. Maximum likelihood bootstrap support values (ML) $\geq 60\%$ and Bayesian posterior probabilities (PP) ≥ 0.90 are shown around nodes as ML/PP. 'T' refers to the type specimen. Sequences newly generated in this study are indicated in bold. New species described herein are shown in red, whereas other specimens newly collected in this study are shown in blue.

worldwide^[109]. Characteristically, it has a wide range of basidiomata, such as clitocyboid, collybioid, or tricholomatoid, with a convex, umbonate, applanate, or depressed to funnel-shaped pileus, ellipsoid basidiospores, and cystidia usually absent, pileipellis and stipitipellis usually a cutis, rarely as a trichoderm or composed of gelatinized hyphae^[109]. *Collybia* is widely distributed in both temperate and tropical regions^[27]. Most species are saprotrophic, whereas some exhibit mycoparasitic habits.

Phylogenetic and phylogenomic studies have transferred numerous species previously placed in *Clitocybe* and *Lepista* to *Collybia*, leading to a recircumscription of genera within Clitocybaceae and supporting the monophyly of *Collybia*^[109]. Accordingly, *Collybia* is divided into four subgenera, viz., subg. *Collybia*, subg. *Crassicybe*, subg. *Leucocalocybe*, and subg. *Macrosporocybe*^[109]. In China, 26 species of *Collybia* have been recognized^[27,109,110], several of which occur in the Qinghai–Xizang Plateau region and its surrounding areas. In the present study, two new species belonging to subg. *Collybia* are described based on morphological characteristics and phylogenetic analyses of ITS, LSU, *tef1α*, and *rpb2* sequences.

Collybia brevispora R.L. Zhao & X.X. Han, sp. nov. **Figs 5 and 7**

Chinese Name: 短孢金钱菌 (duan bao jin qian jun)

Fungal Names: FN 573689; Facesoffungi number: FoF 20044

Etymology — referring to the short basidiospores.

Diagnosis — differs from *Co. piceata* by its shorter basidiospores, solitary habit, and growth on mosses in mixed coniferous and broad-leaved forests.

Holotype — CHINA, Qinghai, Huzhu County, Beishan Forest Farm, Bazhaying Forest Management Area, 37°17' N, 102°21' 12" E, 2,551 m asl, growing on mosses within mixed coniferous and broad-leaved forests dominated by *Picea*, *Betula*, and *Acer*, 27

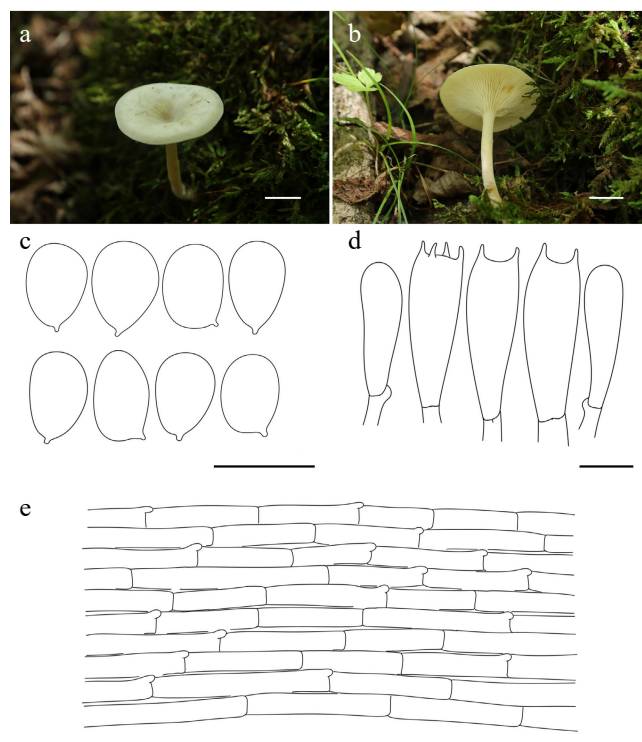


Fig. 5 *Collybia brevispora* (a, b: ZRL20235932 holotype). (a, b) Basidioma; (c) Basidiospores; (d) Basidia and Basidioles; (e) Pileipellis. Scale bars: (a, b) = 1 cm; (c) = 5 μm ; (d, e) = 10 μm .

August 2023, M.Q. He, J.X. Li, M.Y. Liu & H.M. Dai, ZRL20235932 (HMAS 259814 holotype; AF9583 isotype, GenBank no.: ITS PZ491490; LSU PZ491495; *tef1α* PZ520023; *rpb2* PZ520027).

Pileus 18–37 mm diam., nearly applanate when young, then plano-convex, with depressed to subumbilicated centre, smooth, glabrous, greyish green (1C3–D7) at very centre, yellowish white (1A2) to greyish yellow (1B3) elsewhere, slightly or not hygrophanous, margin nonstriate, straight, wavy when mature. Lamellae crowded, subdecurrent to decurrent, unequal, white (1A1) to pale yellow (1A3), concolorous, even. Stipe 26–39 × 3 mm, central, cylindrical, nearly equal or slightly twisted, surface finely pruinose, concolorous with pileus surface. Context slightly thin, concolorous with pileus surface, odour indistinct.

Basidiospores [50/2/2] (2.8–)3.4–4.6(–5.0) × (2.1–)2.4–3.4(–3.8) μm, Q = (1.20–)1.27–1.49(–1.58), Qm = 1.38 (± 0.11), broadly ellipsoid to narrowly ellipsoid, or lacrymoid, smooth, colourless, hyaline, thin-walled, almost always single. Basidia (12.8)13.9–17.6(21.8) × (3.6)4.2–5.4(6.6) μm, clavate, hyaline, four-spored. Basidioles (10.1)11.7–16.3(19.8) × (3.3)3.6–4.9(5.5) μm, clavate to narrowly clavate, cylindrical. Cheilocystidia and pleurocystidia not observed. Lamella trama subregular, hyphae 2–5 μm wide, cylindrical, thin-walled, colourless, hyaline. Pileipellis is a cutis with the transition to a trichoderm at regular intervals, thin-walled, hyphae 3–8 μm wide. Clamp-connections present.

Known distribution — Solitary on mosses within mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Qinghai, Huzhu County, Beishan Forest Farm, Bazhaying Forest Management Area, 37°17'N, 102°21'12" E, 2,551 m asl, growing on mosses within mixed coniferous and broad-leaved forests dominated by *Picea*, *Betula*, and *Acer*, 27 August 2023, M.Q. He, J.X. Li, M.Y. Liu & H.M. Dai, ZRL20235934 (HMAS 259815, GenBank no.: ITS PZ491489; LSU PZ491496; *tef1α* PZ520024; *rpb2* PZ520028).

Notes — This species is a sister taxon to *Collybia piceata*, and is nested within *Co.* subgen. *Collybia* (Fig. 7), whose members usually have basidiospores that are almost always single. Notably, *Co. brevispora*, *Co. piceata*, and *Co. dryadicola* share similar morphological features, including whitish to paler yellow basidiomata and ellipsoid basidiospores^[109,111]. However, *Co. piceata* is gregarious and primarily grows on needle litter of *Picea*, characterized by longer basidiospores (4–5.5 μm) and slightly larger basidia (15–25 × 5–6 μm)^[109], whereas *Co. dryadicola* occurs in alpine meadows and has longer basidiospores (4.4–5.7 μm)^[111,112].

Collybia yadongensis R.L. Zhao & X.X. Han, sp. nov. Figs 6 and 7

Chinese Name: 亚东金钱菌 (ya dong jin qian jun)

Fungal Names: FN 573690; Facesoffungi number: FoF 20045

Etymology — *yadongensis* (Latin) refers to the type locality.

Diagnosis — differs from *Co. tibetica* by the smaller, paler, not hygrophanous and cracked pileus, and smaller basidia.

Holotype — CHINA, Xizang, Shigatse, Yadong County, Pali Town, 27°45'23" N, 89°6'18" E, 4,330 m asl, growing on humus-rich ground in alpine meadows, 28 July 2022, M.Q. He & J.X. Li, ZRL20220382 (HMAS 259812 holotype; AF9567 isotype, GenBank no.: ITS PZ491491; LSU PZ491493; *tef1α* PZ520022; *rpb2* PZ520025).

Pileus 6–22 mm diam., convex to plano-convex, then applanate, becoming plano-concave with age, smooth or rugulose, sometimes slightly depressed, usually cracked centre, fleshy, margin nonstriate, slightly involute, then straight, light brown (6D5) to brown (6E7) when young, not hygrophanous, yellowish white (3A2) to greyish yellow (3B4) when mature, paler at the margin. Lamellae moderately crowded, adnate with slightly decurrent tooth to subdecurrent, orangish-white (5A2) to greyish orange (5B3),

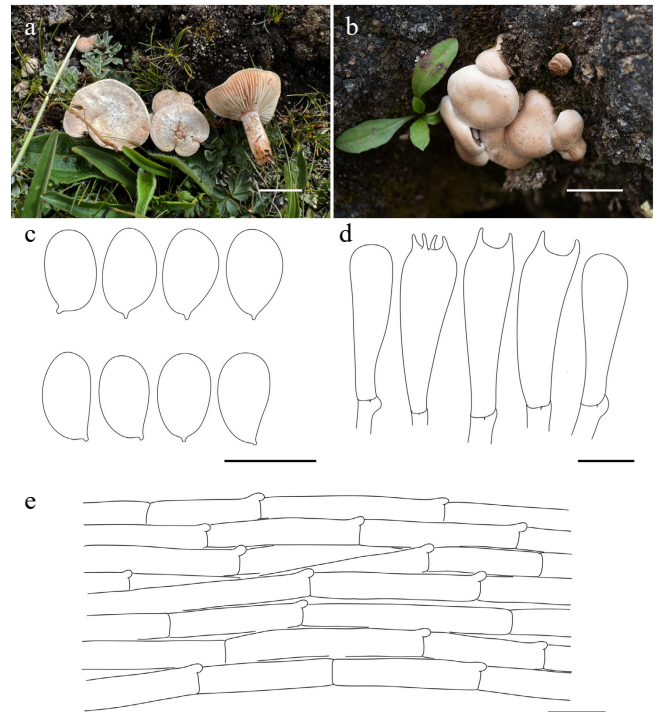


Fig. 6 *Collybia yadongensis* (a, ZRL20220382 holotype; b, ZRL20236670). (a, b) Basidiomata; (c) Basidiospores; (d) Basidia and Basidioles; (e) Pileipellis. Scale bars: (a, b) = 1 cm; (c) = 5 μm; (d, e) = 10 μm.

concolorous, even or uneven. Stipe 4–18 × 1–5 mm, central, cylindrical, robust, slightly tapering at the base, finely pruinose, yellowish white (3A2) to greyish yellow (3B4), nearly not tomentose. Context slightly thick, concolorous with stipe, odour indistinct.

Basidiospores [50/2/2] (3.6–)4.0–4.7(–5.2) × (2.3–)2.7–3.3(–3.5) μm, Q = (1.25–)1.36–1.55(–1.62), Qm = 1.46 (± 0.10), ellipsoid to narrowly ellipsoid, rarely broadly ellipsoid or oblong, smooth, colourless, hyaline, thin-walled, almost always single. Basidia (12.7)15.1–18.5(20.5) × (3.8)4.2–5.4(6.0) μm, clavate, hyaline, two- or four-spored. Basidioles (9.1)11.2–16.7(21.1) × (2.9)3.2–5.2(7.2) μm, clavate to narrowly clavate, cylindrical. Cheilocystidia and pleurocystidia not observed. Lamella trama subregular, hyphae 2–5 μm wide, cylindrical, thin-walled, colourless, hyaline. Pileipellis is a cutis with the transition to a trichoderm at regular intervals, thin-walled, hyphae 2–8 μm wide. Clamp-connections present.

Known distribution — Scattered on humus-rich ground in alpine meadows, summer to fall. So far found only in China.

Material examined — CHINA, Qinghai, Qilian County, Yeniugou Township, 38°31'23" N, 99°29'16" E, 3,385 m asl, growing on humus-rich ground in alpine meadows, 14 August 2021, R. Xing, ZRL20236670 (HMAS 259813, GenBank no.: ITS PZ491492; LSU PZ491494; *rpb2* PZ520026).

Notes — *Collybia yadongensis* is characterized by small basidiomata; a greyish-yellow, nonstriate, nonhygrophanous, cracked and fleshy pileus; ellipsoid to narrowly ellipsoid basidiospores measuring 4–4.7 × 2.7–3.3 μm; and small basidia that are two- or four-spored. This species is a sister taxon to *Co. tibetica* and is nested in *Collybia* subgen. *Collybia* (Fig. 7), whose members usually have basidiospores that occur singly. Although the two species both occur on the Qinghai–Xizang Plateau and have similar basidiospore sizes, *Co. tibetica* inhabits alpine forests and possesses larger pileus (25–40 mm), a darker and hygrophanous pileus, a longer stipe (20–35 mm), larger basidiospores (4.5–6 × 3–4 μm), and larger basidia (20–30 × 5–6 μm)^[109]. Consequently, they can be

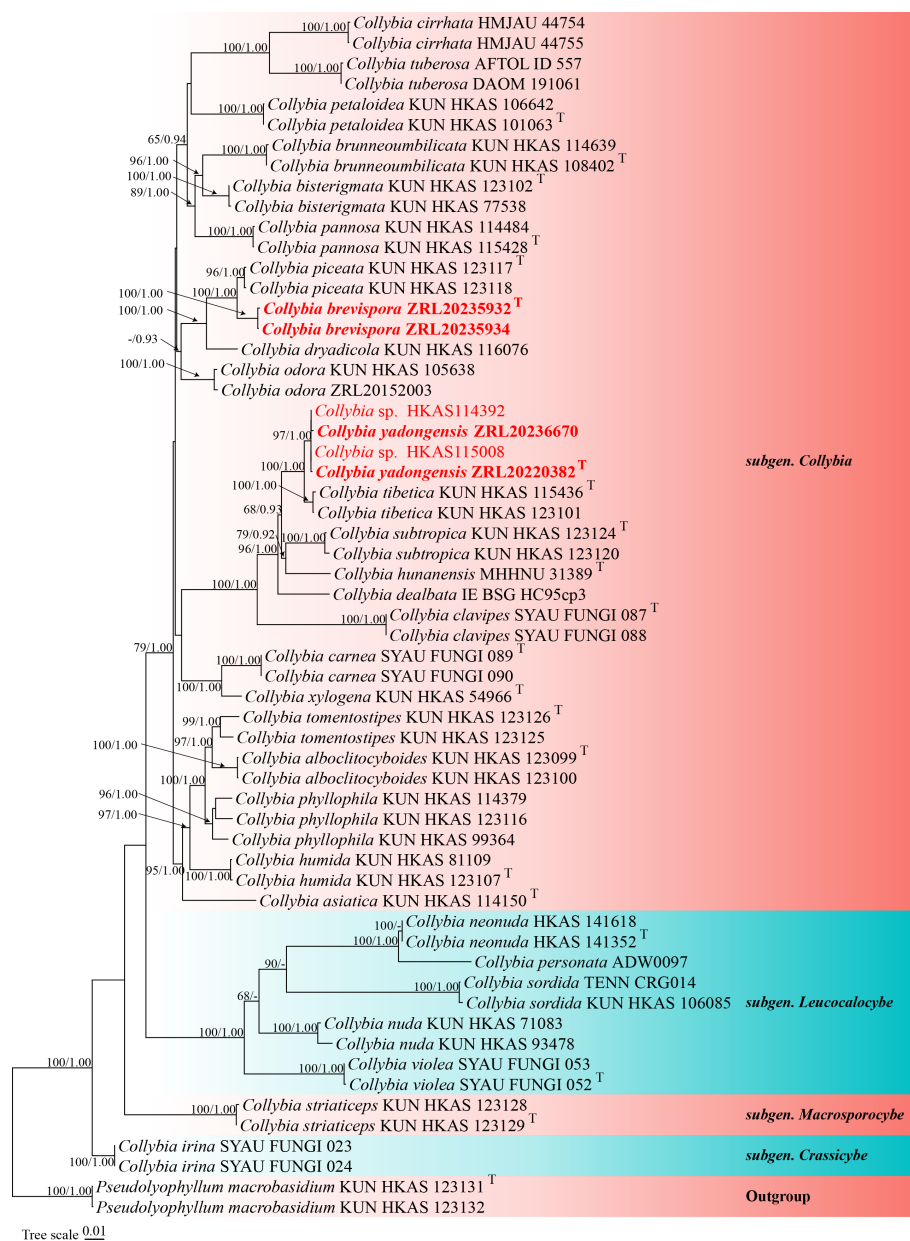


Fig. 7 Molecular phylogenetic analyses of *Collybia* species by the maximum likelihood (ML) method based on combined ITS–LSU–*tef1α*–*rpb2* sequences, rooted with *Pseudolyophyllum macrobasidium*. Maximum likelihood bootstrap support values (ML) $\geq 60\%$ and Bayesian posterior probabilities (PP) ≥ 0.90 are shown around nodes as ML/PP. 'T' refers to the type specimen. Bold indicates sequences newly generated in this study. Red font refers to the new species.

readily distinguished based on both phylogenetic analysis and morphological characteristics. Moreover, the phylogenetic analysis (Fig. 7) suggests that the specimens identified as '*Clitocybe* sp.' (HKAS114392 and HKAS115008), collected from China, are conspecific with *Co. yadongensis*.

Hydnangiaceae Gäm. & C.W. Dodge

Index Fungorum number: IF 80874

Type genus — *Hydnangium* Wallr.

Laccaria Berk. & Broome

Index Fungorum number: IF 17886

Type species — *Laccaria laccata* (Scop.) Cooke

Notes — *Laccaria* is a cosmopolitan ectomycorrhizal genus typified by *L. laccata*, with more than 100 species reported worldwide^[71,113]. Currently, about 50 species of *Laccaria* have been documented in China^[80,93,97,114–116]. Species of *Laccaria* are

characterized by collybioid to omphaloid basidiomata, a convex to plane or umbilicate pileus usually coloured orange, purple or flesh-coloured, thick and distant lamellae, and globose to subglobose basidiospores that are hyaline, echinulate, inamyloid, and cheilocystidia occur in most species^[97,117–120].

Species of *Laccaria* always form ectomycorrhizal associations with diverse woody plants^[121,122]. Previous infrageneric classifications of *Laccaria* were mainly morphology-based and lacked phylogenetic support^[114,123,124]. In recent years, several new species have been reported from China, mainly from southwestern regions, particularly Yunnan Province^[80,114–116,125,126]. In this study, nine new species are described based on morphology and phylogenetic analyses of ITS, LSU, *rpb2*, and *tef1α* sequences.

Laccaria alutacea R.L. Zhao & X.X. Han, sp. nov. Figs 8 and 17
Chinese Name: 淡棕蜡蘑 (dan zong la mo)

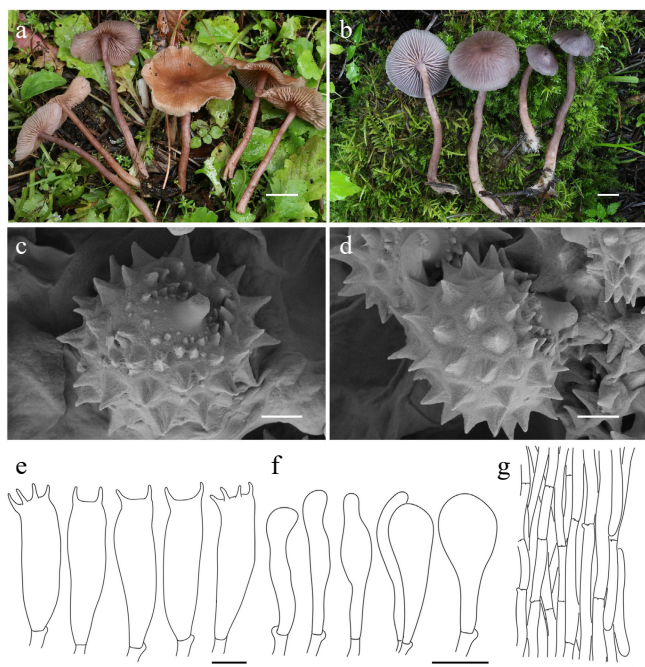


Fig. 8 *Laccaria alutacea* (a, ZRL20220420 holotype; b, ZRL20220777). (a, b) Basidiomata; (c, d) Basidiospores; (e) Basidia; (f) Cheilocystidia; (g) Pileipellis. Scale bars: (a, b) = 1 cm; (c, d) = 2 μm ; (e–g) = 10 μm .

Fungal Names: FN 573691; Facesoffungi number: FoF 20046

Etymology — *alutacea* (Latin), referring to the pale brown tones of the basidiomata.

Diagnosis — *Laccaria alutacea* is characterized by brown to orange-brown basidiomata, longer and thicker stipe, globose to subglobose basidiospores, and presence of cystidia, and differs from the morphologically similar *L. fagacicola* by its thinner stipe, shorter basidia, and slightly smaller basidiospores.

Holotype — CHINA, Xizang, Shigatse, Dingjie County, Chentang Township, Jiuyan hot spring, 27°55'15" N, 87°21'37" E, 3,060 m asl, growing on mosses within mixed coniferous and broad-leaved forests, 29 July 2022, M.Q. He, B. Cao, & J.X. Li, ZRL20220420 (HMAS 259883 holotype; AF9569 isotype, GenBank no.: ITS PZ494664; LSU PZ494210).

Pileus 12–58 mm diam., hemispherical to convex when young, becoming plano-convex to concave when mature, with broad obtuse umbo or a slightly depressed centre, hygrophanous, glabrous or finely fibrillose, margin inflexed to straight, or reflexed, translucently striate, occasionally radially rugulose, light brown (8D6) to dark brown (7F8) at the centre, fading towards margin, pale orange (6A2) to brownish grey (6C2), margin entire, sometimes becoming rimose with age. Lamellae slightly distant, narrowly adnate to slightly decurrent, unequal, edge entire to slightly eroded in some parts, concolorous, orange white (6A2) to brownish orange (6C5). Stipe 43–100 $\times$ 2–5 mm, central, cylindrical, equal or slightly broadened towards the base, surface subglabrous, with white longitudinal fibrils, slightly pruinose, concolorous with pileus or slightly paler, basal mycelium white. Context thin, odour indistinct.

Basidiospores [50/2/2] (5.7–)6.5–7.5(–7.8) $\times$ (5.3–)6.1–7.2(–7.8) μm , $Q = (0.98\text{--})1.00\text{--}1.10\text{--}(1.17)$, $Q_m = 1.05 (\pm 0.05)$, globose to subglobose, rarely broadly ellipsoid, echinulate, slightly thick-walled, hyaline, distant, spines 0.4–1.9 μm long. Basidia (32.6)36.7–47.3(54.4) $\times$ (9.6)10.5–13.2(14.6) μm , clavate, hyaline, two- or four-spored, sterigmata 3.5–7.7 μm long. Cheilocystidia (21.0)26.6–36.0(40.9) $\times$ (3.5)4.6–7.7(9.5) μm , narrowly clavate, filamentous to flexuose, thin-walled, hyaline. Pleurocystidia

(22.3)27.7–37.9(41.9) $\times$ (3.9)5.5–9.1(11.0) μm , narrowly clavate to filamentous, sometimes irregular, slightly thick-walled, hyaline. Lamella trama subregular, composed of slightly thick-walled, filamentous hyphae 2–6 μm wide. Stipitipellis is composed of appressed, parallel, thin-walled, hyaline to pale brown, caulocystidia not observed. Pileipellis is a cutis composed of repent to suberect, interwoven filamentous hyphae, 3–11 μm wide, thin- to slightly thick-walled, hyaline. Clamp-connections present.

Known distribution — Scattered on humus-rich ground within mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Xizang, Shigatse, Dingjie County, Chentang Township, Daguiwan, 27°54'58" N, 87°27'32" E, 3,188 m asl, growing on mosses within mixed coniferous and broad-leaved forests, 30 July 2022, R.L. Zhao & X.Y. Zhu, ZRL20220490 (HMAS 259884, GenBank no.: ITS PZ494663; LSU PZ494212; *tef1 α* PZ520035); *ibid.*, ZRL20220496 (HMAS 259885, GenBank no.: ITS PZ494667; LSU PZ494213; *tef1 α* PZ520038; *rpb2* PZ541195); Gyirong County, Gyirong Valley, 28°26'12" N, 85°15'39" E, 3,024 m asl, growing on mosses within mixed coniferous and broad-leaved forests, 1 August 2022, D. Phurba & J.X. Li, ZRL20220642 (HMAS 259886, GenBank no.: ITS PZ494668; LSU PZ494214; *tef1 α* PZ520037; *rpb2* PZ541196); Gyirong County, along the road from Gyirong Town to Zha Village, 28°23'45" N, 85°23'34" E, 3,441 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forest dominated by *Quercus*, 2 August 2022, R.L. Zhao & X.Y. Zhu, ZRL20220777 (HMAS 259887, GenBank no.: ITS PZ494666; LSU PZ494215; *tef1 α* PZ520036; *rpb2* PZ541197).

Notes — Phylogenetically, five specimens of *L. alutacea* formed a monophyletic lineage (99/1.00) that is closely related to *L. fulvogrisea* and *L. conifericola*. Although all three species share brownish-hued basidiomata, *L. fulvogrisea* has slightly darker basidiomata, four-spored basidia with sterigmata up to 10 μm long, larger basidiospores (8–10 $\times$ 8–11 μm) with longer spines (1.7–2.5 μm) and relatively longer pleurocystidia (30–50 μm)^[127]. In contrast, *L. conifericola* is distinguished by a shorter and thinner stipe (20–46 $\times$ 1–3 mm), slightly smaller basidia (30.3–40.7 $\times$ 9.3–12.0 μm), and its occurrence in coniferous forest habitats.

Laccaria bullipellis A.W. Wilson & G.M. Muell., *Laccaria fagacicola* Y.Y. Cui, Q. Cai & Zhu L. Yang and *L. versiformis* H.J. Cho & Y.W. Lim are morphologically similar to *L. alutacea* in having brown to orange-brown pileus. However, *L. bullipellis* possesses larger, globose basidiospores (av. 8.3 μm), slightly narrower basidia (10–11 μm), and grows solitary in mixed temperate alpine conifer forest^[128]. *Laccaria fagacicola* can be differentiated by a paler pileus, thicker stipe (5–6 mm), longer basidia (45–60 μm), and slightly larger basidiospores (av. 7.7 $\times$ 7.4 μm)^[129]. *Laccaria versiformis* has a shorter stipe (30–35 mm), larger basidiospores (7.5–10 $\times$ 7.5–9.5 μm), and slightly longer basidia (41–55 μm)^[130].

Laccaria angustistipes R.L. Zhao & X.X. Han, sp. nov. Figs 9 and 17

Chinese Name: 狭柄蜡蘑 (xia bing la mo)

Fungal Names: FN 573692; Facesoffungi number: FoF 20047

Etymology — *angustistipes* (Latin), composed of *angustus* (narrow, slender) and *stipes* (stipe), referring to the slender or narrow stipe of the new species.

Diagnosis — *Laccaria angustistipes* differs from other species in this genus by its brownish-orange-toned basidiomata, slender stipe, small basidiospores, presence of pleurocystidia, and distinct DNA sequences.

Holotype — CHINA, Xizang, Dingjie County, roadside from Dingjie County to Chentang Town, 27°54'58" N, 87°27'32" E, 3,188 m asl, growing on humus-rich ground within broad-leaved forests, 28 July 2022, R.L. Zhao, ZRL20220389 (HMAS 259846 holotype; AF9568

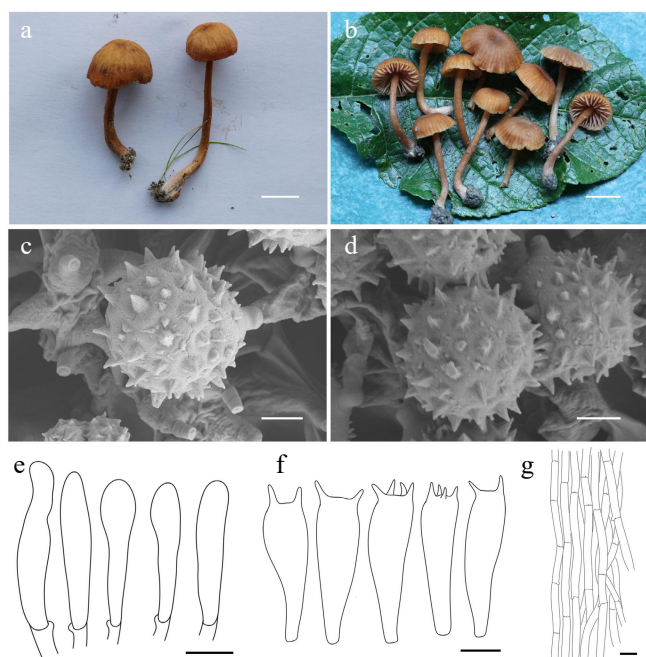


Fig. 9 *Laccaria angustistipes* (a, ZRL20152049; b, ZRL20220389 holotype). (a, b) Basidiomata; (c, d) Basidiospores; (e) Cheilocystidia; (f) Basidia; (g) Pileipellis. Scale bars: (a, b) = 1 cm; (c, d) = 2 μ m; (e–g) = 10 μ m.

isotype, GenBank no.: ITS PZ494630; LSU PZ494237; *tef1 α* PZ520039; *rpb2* PZ541209).

Pileus 10–20 mm diam., hemispherical to obtusely conical initially, then becoming convex to plano-convex, plane to slightly depressed at the centre when young, becoming depressed with age, dry or hygrophanous, margin translucently striate, glabrous, radially rugulose, margin straight, greyish orange (5B6) to brown (6E7) at the centre, sometimes paler towards the margin. Lamellae distant, adnate to narrowly adnate, unequal, entire, concolorous, pale red (9A3) to dull red (9B3). Stipe 25–47 $\times$ 2–4 mm, central, cylindrical, slightly broadened towards the base, occasionally finely longitudinally striate, subglabrous, surface finely pruinose, concolorous with pileus, basal mycelium white. Context thin, odour indistinct.

Basidiospores [50/3/2] (5.9–)6.3–7.1(–7.4) $\times$ (5.5–)6.0–6.8(–7.2) μ m, Q = (1.01–)1.02–1.09(–1.15), Q_m = 1.05 ($\pm$ 0.03), globose to subglobose, echinulate, thin- to slightly thick-walled, subhyaline, distant, spines 0.5–1.3 μ m long. Basidia (26.9)27.9–36.4(41.0) $\times$ (6.8)8.0–10.2(11.5) μ m, clavate, hyaline, two- or four-spored, sterigmata 3.5–6.7 μ m long. Cheilocystidia (23.0)26.5–35.4(39.0) $\times$ (4.1)5.1–6.8(7.5) μ m, filamentous to narrowly clavate, occasionally with a capitate apex, thin-walled, hyaline. Pleurocystidia (23.1)28.2–37.1(41.6) $\times$ (4.7)5.9–8.1(9.3) μ m, narrowly clavate to subclavate or filamentous, sometimes irregular, thin-walled, hyaline. Lamella trama regular to subregular, composed of slightly thick-walled, filamentous hyphae 4–7 μ m wide. Stipitipellis is composed of appressed, parallel, thin- to slightly thick-walled, hyaline to pale yellowish brown, caulocystidia not observed. Pileipellis is a cutis composed of appressed, parallel, hyaline to pale yellowish brown, thin-walled, cylindrical hyphae 3–7 μ m wide. Clamp-connections present.

Known distribution — In pairs or gregarious on humus-rich ground within broad-leaved forests or mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Xizang, Dingjie County, Chentang Town, 27°55'15" N, 87°21'37" E, 3,060 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests, 12

September 2022, SY Su, ZRL20152049 (HMAS 259845, GenBank no.: ITS PZ494631; LSU PZ494236; *tef1 α* PZ520040).

Notes — *Laccaria angustistipes* is phylogenetically and morphologically allied to *L. parva*. However, *L. parva* is distinguished by its thicker stipe (3–5 mm), larger basidiospores measuring 8–10 $\times$ 8.5–10 μ m, and larger basidia (44–56 $\times$ 12–15 μ m) with only four-spored^[130]. Several other species, such as *L. acanthospora* A.W. Wilson & G.M. Muell., *L. rubra* S.M. Tang, K.D. Hyde & Z.L. Luo, *L. laccata* (Scop.) Cooke, and *L. nanlingensis* Ming Zhang, share similar orange-toned basidiomata with *L. angustistipes*. *L. acanthospora* differs in its smaller basidiomata (pileus 4–15 mm in diam.), larger basidiospores (7–10 $\times$ 7–10 μ m), larger basidia (40–56 $\times$ 10–14 μ m), and the cheilo- and pleurocystidia^[128]. *Laccaria rubra* has a slightly larger pileus (18–24 mm in diam.), a thicker stipe (3.7–5.5 mm), larger basidiospores (7.2–10.3 $\times$ 7.3–9.4 μ m), and wider basidia (10–14 μ m)^[114]. Moreover, *L. laccata* is characterized by a thicker stipe (5–14 mm), and longer, broadly ellipsoid to ellipsoid basidiospores (7.5–9.4 $\times$ 6.0–7.5 μ m)^[131]. *Laccaria nanlingensis* has a larger pileus (30–55 mm in diam.), longer basidia (35–48 $\times$ 8–12 μ m), and longer cheilocystidia (40–60 μ m)^[126].

Laccaria dambaensis R.L. Zhao, B. Cao & X.X. Han, sp. nov. Figs 10 and 17

Chinese Name: 打坝蜡蘑 (da ba la mo)

Fungal Names: FN 573693; Facesoffungi number: FoF 20048

Etymology — *dambaensis* (Latin) refers to the type locality Damba, an officially standardized geographical name in the Zangnan region of Xizang Autonomous Region, China.

Diagnosis — *Laccaria dambaensis* differs from other species in this genus by its orange-toned basidiomata with a hemispherical to applanate, slightly depressed pileus and a translucently striate margin. Basidiospores are small, globose to subglobose. Cheilocystidia and pleurocystidia are present, and it occurs in high-elevation habitats (above 3,500 m).

Holotype — CHINA, Xizang, Linzhi, Chayu County, near Damba, 28°36'46" N, 98°05'22" E, 4,110 m asl, growing within mixed coniferous and broad-leaved forests, 21 July 2021, R.L. Zhao, M.Y. Zhu & B. Cao, ZRL20210538 (HMAS 259865 holotype; AF9563 isotype, GenBank no.: ITS PZ494676; LSU PZ494230; *tef1 α* PZ520057; *rpb2* PZ541217).

Pileus 14–39 mm diam., initially hemispherical to convex, becoming plano-convex to applanate at maturity, often slightly depressed at the centre, hygrophanous, glabrous to finely fibrillose, margin straight to inflexed, translucently striate, radially rugulose when young, greyish orange (6B6) to brown (7D8) at the centre, fading towards margin, margin entire to crenate, occasionally rimose with age. Lamellae distant, adnexed to adnate, unequal, edge entire or slightly eroded in some parts, concolorous, pale orange (5A3) to brownish orange (7C8). Stipe 41–89 $\times$ 3–6 mm, central, cylindrical, equal or slightly tapering upwards, sometimes twisted, surface slightly pruinose, with brownish orange (7C8) longitudinal fibrils, occasionally fading at the apex, concolorous with pileus or slightly paler, basal mycelium white. Context thin, odour indistinct.

Basidiospores [50/4/2] (4.9–)6.3–7.7(–8.2) $\times$ (4.3–)5.7–7.4(–7.9) μ m, Q = 1.00–1.16(–1.36), Q_m = 1.08 ($\pm$ 0.08), globose to subglobose, rarely broadly ellipsoid, echinulate, slightly thick-walled, hyaline, distant, spines 0.3–1.6 μ m long. Basidia (27.0)30.5–40.6(44.8) $\times$ (10.6)12.4–15.6(17.1) μ m, clavate, hyaline, two- or four-spored, sterigmata 3.6–8.0 μ m long. Cheilocystidia (12.5)16.7–24.9(28.0) $\times$ (2.7)3.4–5.7(6.5) μ m, narrowly clavate, filamentous to flexuose, thin-walled, hyaline. Pleurocystidia (17.0)18.7–24.5(29.2) $\times$ (3.6)4.0–5.9(6.9) μ m, narrowly clavate, filamentous to flexuose, slightly thick-walled, hyaline. Lamella trama regular to subregular,

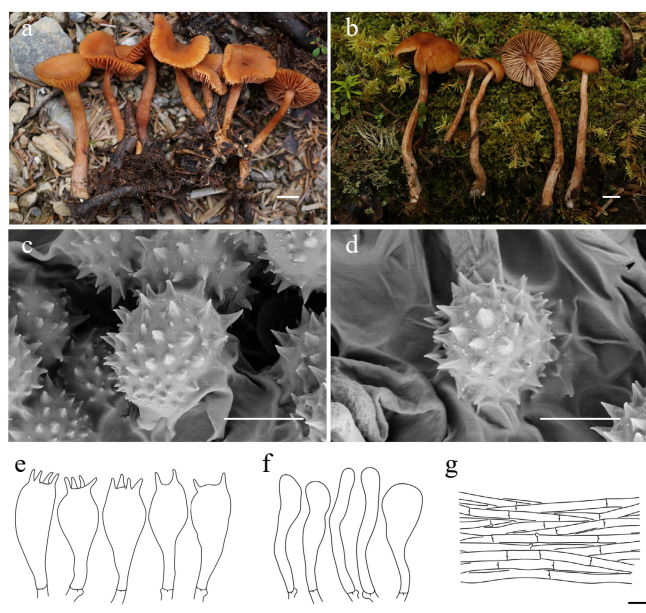


Fig. 10 *Laccaria dambaensis* (a, ZRL20210538 holotype; b, ZRL20210807). (a, b) Basidiomata; (c, d) Basidiospores; (e) Basidia; (f) Cheilocystidia; (g) Pileipellis. Scale bars: (a, b) = 1 cm; (c, d) = 5 μ m; (e–g) = 10 μ m.

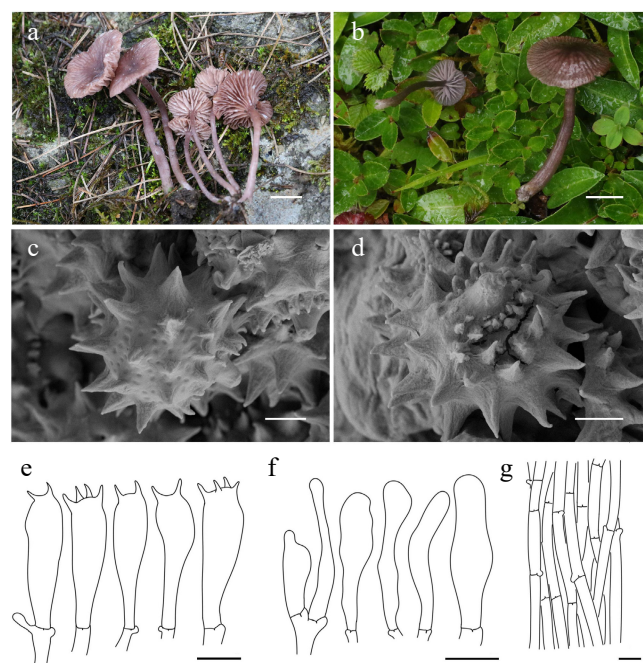


Fig. 11 *Laccaria conifericola* (a, ZRL20220145 holotype; b, ZRL20235012). (a, b) Basidiomata; (c, d) Basidiospores; (e) Basidia; (f) Cheilocystidia; (g) Pileipellis. Scale bars: (a, b) = 1 cm; (c, d) = 2 μ m; (e–g) = 10 μ m.

composed of slightly thick-walled, filamentous hyphae 2–7 μ m wide. Stipitipellis is composed of appressed, parallel, thin- to slightly thick-walled, hyaline to pale brown, caulocystidia not observed. Pileipellis is a cutis composed of repent to suberect, interwoven filamentous hyphae, 2.8–8.8 μ m wide, thick-walled, hyaline. Clamp-connections present.

Known distribution — Scattered on humus-rich ground within mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Xizang, Linzhi, Bomi County, along Zhamo Highway, 29°47'30" N, 95°41'50" E, 3,670 m asl, growing within mixed coniferous and broad-leaved forests, 24 July 2021, X.Y. Zhu & M.Z. Zhang, ZRL20210807 (HMAS 259866, GenBank no.: ITS PZ494678; LSU PZ494228; *tef1 α* PZ520056); Chayu County, along the banks of Lazhequ, 28°35'33" N, 97°57'10" E, 3,922 m asl, growing within mixed coniferous and broad-leaved forests, 9 August 2023, D. Phurba & X.H. Yu, ZRL20231459 (HMAS 259867, GenBank no.: ITS PZ494675; LSU PZ494231; *tef1 α* PZ520055).

Notes — Phylogenetically, the new species is closely related to *L. araneosa* H.J. Cho & Y.W. Lim, *L. trichodermophora* G.M. Muell., and *L. bicolor* (Maire) P.D. Orton. *Laccaria araneosa*, which was originally described from Korea, differs by its hyphal mat on the centre of the pileus, larger basidiospores (8–9 $\times$ 7.5–9 μ m), longer basidia (42–52 μ m), and the absence of cystidia^[130]. *Laccaria trichodermophora*, which was originally described from North America, has larger, subglobose to broadly ellipsoid basidiospores (7.4–9.2 $\times$ 6.4–8.3 μ m), narrower basidia (7.4–12.4 μ m), and the absence of cystidia^[119]. *Laccaria bicolor* has a long and stout stipe (72–144 $\times$ 4–7.5 mm), which is fibrillose-striate in the upper part, longer basidiospores (7–9 μ m), and narrower basidia (8–12 μ m)^[132].

Laccaria conifericola R.L. Zhao & X.X. Han, sp. nov. Figs 11 and 17
Chinese Name: 针叶蜡蘑 (zhen ye la mo)

Fungal Names: FN 573694; Facesoffungi number: FoF 20049

Etymology — refers to the coniferous forest habitat.

Diagnosis — differs from *L. fulvogrisea* by its shorter and thinner stipe, smaller basidiospores, and shorter basidia that are two- or four-spored.

Holotype — CHINA, Xizang, Shigatse, Dingjie County, Chentang Township, Jiuyan hot spring, 27°55'15" N, 87°21'37" E, 3,060 m asl, growing on mosses within coniferous forests, 29 July 2022, D. Phurba, ZRL20220145 (HMAS 259863 holotype; AF9565 isotype, GenBank no.: ITS PZ494671; LSU PZ494209; *tef1 α* PZ520043; *rpb2* PZ541187).

Pileus 12–26 mm diam., initially hemispherical to plano-convex, becoming applanate to plano-concave with a slightly depressed centre at maturity, hygrophanous, glabrous or finely fibrillose, margin straight to reflexed, translucently striate, sometimes radially rugulose, reddish brown (8E7) to dark brown (6F8) at the centre, fading towards margin, reddish grey (8B2) to light brown (7D4), margin entire to undulate, or occasionally becoming rimose with age. Lamellae distant, narrowly adnate to slightly decurrent, unequal, edge entire to slightly eroded in some parts, concolorous, reddish grey (7B2) to light brown (7D4). Stipe 20–46 $\times$ 1–3 mm, central, cylindrical, equal or slightly tapering upwards, surface subglabrous, longitudinally striate, slightly pruinose, concolorous with pileus or slightly paler, basal mycelium white. Context thin, odour indistinct.

Basidiospores [50/2/2] (5.7–)6.7–8.0(–8.5) $\times$ (5.7–)6.5–7.8(–8.5) μ m, Q = (0.95–)1.00–1.06(–1.09), Q_m = 1.04 ($\pm$ 0.03), globose to subglobose, echinulate, slightly thick-walled, hyaline, distant, spines 0.8–2.0 μ m long. Basidia (25.9)30.3–40.7(46.0) $\times$ (8.2)9.3–12.0(13.0) μ m, clavate, hyaline, two- or four-spored, sterigmata 3–6 μ m long. Cheilocystidia (21.7)24.4–35.0(41.0) $\times$ (4.0)4.8–8.2(9.4) μ m, narrowly clavate, filamentous to flexuose, thin-walled, hyaline. Pleurocystidia (24.3)29.9–39.7(44.0) $\times$ (7.0)7.9–10.0(11.1) μ m, narrowly clavate to filamentous, sometimes irregular, slightly thick-walled, hyaline. Lamella trama regular to subregular, composed of slightly thick-walled, filamentous hyphae 2–10 μ m wide. Stipitipellis is composed of appressed, parallel, thin-walled, hyaline to pale yellowish-brown, caulocystidia not observed. Pileipellis is a cutis composed of repent to suberect, interwoven filamentous hyphae, 4.0–13.4 μ m wide, thick-walled, hyaline. Clamp-connections present.

Known distribution — Scattered on humus-rich ground within coniferous forests, summer to fall. So far found only in China.

Material examined — CHINA, Xizang, Linzhi, Bomi County, Zhamu Town, along G559 (Motuo Highway), 29°46'26" N, 95°41'59" E, 3,743 m asl, growing on the ground within coniferous forests, 13 August 2023, M.Z. Zhang & L.H. Liu, ZRL20235012 (HMAS 259864, GenBank no.: ITS PZ494670; LSU PZ494208).

Notes — This Asian species is primarily characterized by greyish to brownish basidiomata, two- or four-spored basidia, globose to subglobose basidiospores, and a coniferous forest habitat. Morphologically and phylogenetically, *L. conifericola* is closely related to *L. fulvogrisea* Popa, Rexer & G. Kost. However, *L. fulvogrisea*, which occurs in mixed broad-leaved forests, differs in having a relatively long and stout stipe (30–70 × 3–5 mm), longer basidia (40–50 µm), and four-spored, larger basidiospores (8–10 × 8–11 µm) and longer cheilocystidia (30–50 µm)^[127].

Laccaria brunnea S.M. Tang, K.D. Hyde & Z.L. Luo, *L. dingjieensis*, and *L. murina* are morphologically similar to *L. conifericola* in having greyish to brownish basidiomata. However, *L. brunnea*, which occurs in broad-leaved forests dominated by *Fagus*, differs in having a darker pileus, a stout stipe (3.0–4.3 mm), shorter cheilocystidia (13–20 µm), and smaller pleurocystidia (12–18 µm)^[114]. *Laccaria dingjieensis* differs in having a paler pileus, and slightly smaller basidiospores (5.6–7.1 × 5.4–7.2 µm) with short spines (0.3–1.3 µm). In addition, *L. murina* is distinguished by its short stipe (15–25 mm) and slightly larger, globose basidiospores (7.5–10 µm)^[133].

Laccaria dingjieensis R.L. Zhao & X.X. Han, sp. nov. Figs 12 and 17

Chinese Name: 定结蜡蘑 (zhong hua chang bing la mo)

Fungal Names: FN 573695; Facesoffungi number: FoF 20050

Etymology — refers to the type locality, Dingjie County.

Diagnosis — differs from *L. negrimarginata* in having a brownish, glabrous pileus and smaller, globose to subglobose basidiospores.

Holotype — CHINA, Xizang, Shigatse, Dingjie County, Chentang Township, Jiuyan hot spring, 27°55'15" N, 87°21'37" E, 3,060 m asl, growing on mosses within mixed coniferous and broad-leaved forests, 29 July 2022, R.L. Zhao & X.Y. Zhu, ZRL20220313 (HMAS 259860 holotype; AF9566 isotype, GenBank no.: ITS PZ494627; LSU PZ494200; *tef1α* PZ520045; *rpb2* PZ541193).

Pileus 15–30 mm diam., convex to plano-convex when young, expanding to applanate to plano-concave with age, centre subumbonate to plane initially, eventually becoming slightly depressed, hygrophane, glabrous, margin straight to inflexed, translucently striate, sometimes radially rugulose, light brown (6D6) to dark brown (6F8) at the centre, fading towards margin, greyish orange (5B3) to brown (6E7), margin entire to undulate, or occasionally becoming rimose with age. Lamellae distant, adnexed to sinuate, unequal, edge entire to slightly eroded in some parts, concolorous, yellowish white (2A2) to greyish yellow (4B3). Stipe 27–64 × 1–3 mm, central, cylindrical, sometimes twisted, surface subglabrous, finely longitudinally striate, slightly pruinose, concolorous with pileus, basal mycelium white. Context thin, odour indistinct.

Basidiospores [50/2/2] (4.3–)5.6–7.1(–7.5) × (4.3–)5.4–7.2(–7.8) µm, *Q* = (0.90–)0.96–1.07(–1.10), *Qm* = 1.02 (± 0.05), globose to subglobose, echinulate, slightly thick-walled, hyaline, distant, spines 0.3–1.3 µm long. Basidia (28.2)33.1–41.2(46.2) × (9.1)10.6–12.9(13.7) µm, cylindrical, clavate, hyaline, two- or four-spored, sterigmata 3–6 µm long. Cheilocystidia (21.3)23.4–29.8(33.2) × (4.3)5.5–7.8(9.0) µm, filamentous to narrowly clavate, occasionally irregular, sometimes with a capitate apex, thin-walled, hyaline. Pleurocystidia (19.1)20.8–31.3(40.2) × (4.1)5.1–7.2(9.1) µm, narrowly clavate to filamentous, sometimes irregular, slightly thick-walled, hyaline. Lamella trama regular to subregular, composed of slightly thick-walled, filamentous hyphae 2.3–6.9 µm wide. Stipitipellis is

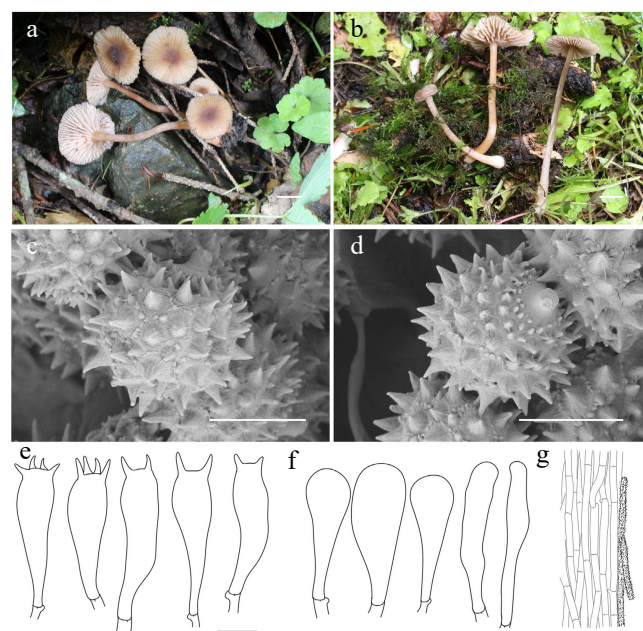


Fig. 12 *Laccaria dingjieensis* (a, ZRL20220313 holotype; b, ZRL20220418). (a, b) Basidiomata; (c, d) Basidiospores; (e) Basidia; (f) Cheilocystidia; (g) Pileipellis. Scale bars: (a, b) = 1 cm; (c, d) = 5 µm; (e–g) = 10 µm.

composed of appressed, parallel, thin- to slightly thick-walled, hyaline to pale yellowish-brown, caulocystidia not observed. Pileipellis is a cutis composed of repent to suberect, interwoven filamentous hyphae, 4.4–13.0 µm wide, thin- to slightly thick-walled, hyaline to slightly brownish. Clamp-connections present.

Known distribution — Scattered or gregarious on humus-rich ground within alpine meadows or mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Xizang, Shigatse, Dingjie County, Chentang Township, Jiuyan hot spring, 27°55'15" N, 87°21'37" E, 3,060 m asl, growing on mosses within mixed coniferous and broad-leaved forests, 29 July 2022, M.Q. He, B. Cao, & J.X. Li, ZRL20220418 (HMAS 259861, GenBank no.: ITS PZ494629; LSU PZ494199; *tef1α* PZ520046; *rpb2* PZ541194); Chentang Township, 27°54'58" N, 87°27'32" E, 3,188 m asl, growing on humus-rich ground in alpine meadows dominated by *Rhododendron*, 31 July 2022, R.L. Zhao, D. Phurba, & X.Y. Zhu, ZRL20220483 (HMAS 259862, GenBank no.: ITS PZ494628; LSU PZ494201; *tef1α* PZ520047; *rpb2* PZ541192).

Notes — In the phylogenetic analysis (Fig. 17), *L. dingjieensis* is sister to *L. negrimarginata*. Morphologically, *L. negrimarginata* differs from the new species by its orange-brown pileus covered with dark brown squamules, pink to pinkish-grey lamella with black edges, globose to subglobose-lacrymoid but larger basidiospores (7.8–9.0 × 8–9.5 µm), and four-spored basidia^[128]. Furthermore, the ITS sequence difference between the holotypes of *L. negrimarginata* (BAP360) and *L. dingjieensis* (ZRL20220313) is 2.88% (18/624, including gaps).

Laccaria friesii S. Choudhary, Y.P. Sharma & P. Uniyal, *L. murina* S. Imai, and *L. yunnanensis* Popa, Rexer, Donges, Zhu L. Yang & G. Kost also resemble *L. dingjieensis* in having a brownish pileus. However, *L. friesii*, originally described from India, is distinguished by its more robust stipe (62–85 × 5–13 mm), significantly larger basidiospores (av. 11.12 × 10.9 µm), and larger cheilocystidia (31.7–58.7 × 14.3–17 µm)^[134]. *Laccaria murina*, originally described from Japan, possesses smaller basidiomata and larger basidiospores

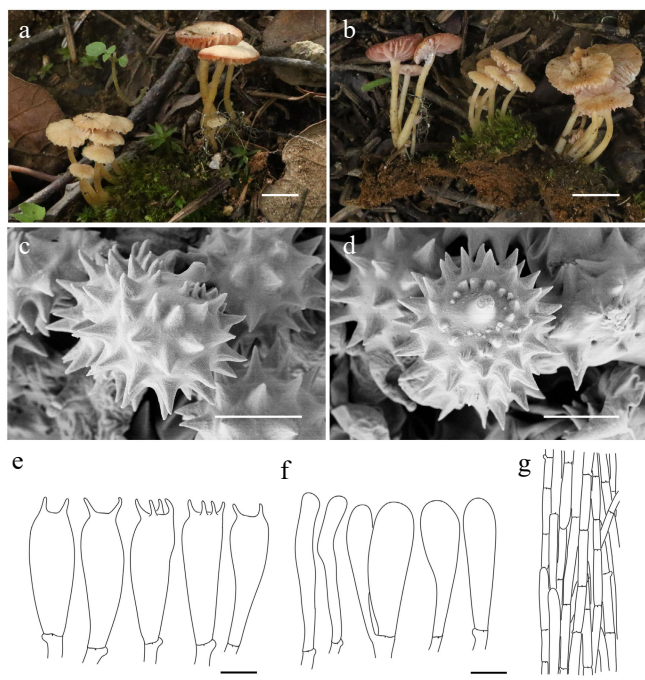


Fig. 13 *Laccaria fasciculata* (a, b: ZRL20235057 holotype). (a, b) Basidiomata; (c, d) Basidiospores; (e) Basidia; (f) Cheilocystidia; (g) Pileipellis. Scale bars: (a, b) = 1 cm; (c, d) = 5 µm; (e–g) = 10 µm.

(7.5–10 µm)^[133]. In contrast, *L. yunnanensis*, which inhabits broad-leaved forests dominated by *Dipterocarpus* and *Fagus*, differs by its more robust basidiomata, relatively longer basidia (41–53 µm), and larger basidiospores (av. 9.5 × 9.4 µm)^[71].

Laccaria fasciculata R.L. Zhao & X.X. Han, sp. nov. Figs 13 and 17

Chinese Name: 簇生蜡蘑 (cu sheng la mo)

Fungal Names: FN 573696; Facesoffungi number: FoF 20051

Etymology — refers to its fasciculate (gregarious) growth habit.

Diagnosis — *Laccaria fasciculata* differs from other species in this genus by its gregarious basidiomata exhibiting pale orange hues, slightly smaller pileus, globose to subglobose basidiospores, and the presence of cystidia.

Holotype — CHINA, Xizang, Linzhi, Bayi District, Lulang Town, along the route of G318, 29°50'37" N, 94°45'23" E, 2,976 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests, 14 August 2023, M.Z. Zhang & L.H. Liu, ZRL20235057 (HMAS 259882 holotype; AF9578 isotype, GenBank no.: ITS PZ494669; LSU PZ494220).

Pileus 6–17 mm diam., plano-convex when young, becoming applanate to plano-concave at maturity, sometimes with a slightly depressed centre, hygrophanous, glabrous or finely fibrillose, sometimes slightly pruinose, margin straight, translucently striate, sometimes radially rugulose, pale orange (5A3) to greyish orange (5B5) at the centre, occasionally fading towards margin, margin entire to undulate. Lamellae distant, narrowly adnate to slightly decurrent, unequal, edge entire to slightly eroded in some parts, concolorous, orange white (5A2) to brownish orange (7C5). Stipe 11–25 × 1–2 mm, central, cylindrical, equal or slightly broadened towards the base, glabrous, occasionally slightly pruinose, concolorous, yellowish white (4A2) to blond (4C4), basal mycelium white. Context thin, odour indistinct.

Basidiospores [50/4/1] (6.1–)6.8–8.2(–8.7) × (5.7–)6.4–7.8(–8.5) µm, $Q = (1.00–)1.01–1.08(–1.15)$, $Qm = 1.05 (\pm 0.03)$, globose to subglobose, echinulate, slightly thick-walled, hyaline, distant, spines 0.5–2.1 µm long. Basidia (22.8)29.2–37.8(42.0) ×

(7.6)9.3–12.6(14.6) µm, clavate, hyaline, two- or four-spored, sterigmata 2–6 µm long. Cheilocystidia (26.4)28.9–37.8(43.7) × (5.3)6.0–9.5(10.7) µm, narrowly clavate, filamentous to flexuose, thin-walled, hyaline. Pleurocystidia (29.0)31.4–44.8(51.5) × (7.0)8.5–12.0(13.3) µm, narrowly clavate to filamentous, sometimes irregular, slightly thick-walled, hyaline. Lamella trama regular, composed of thick-walled, filamentous hyphae 3–8 µm wide. Stipitipellis is composed of appressed, parallel, slightly thick-walled, hyaline to pale brown, caulocystidia not observed. Pileipellis is a cutis composed of repent to suberect, interwoven filamentous hyphae, 3–11 µm wide, slightly thick-walled, hyaline. Clamp-connections present.

Known distribution — Gregarious on humus-rich ground within mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Notes — *Laccaria fasciculata* is distinguished by its gregarious basidiomata exhibiting pale orange hues and a pileus ranging from plano-convex to plano-concave. Microscopically, it features globose to subglobose basidiospores ornamented with spines 0.5–2.1 µm in length. Additionally, the two- or four-spored basidia measure 29.2–37.8 × 9.3–12.6 µm, while cystidia are present. In the phylogenetic analysis (Fig. 17), *L. fasciculata* is closely related to *L. ganziensis*, *L. acanthospora*, *L. alutacea*, *L. conifericola*, and *L. fulvogrisea*. *Laccaria ganziensis* can be distinguished by its longer, thicker stipe (26–73 × 2–4 mm) and larger basidia (38.1–48.8 × 11.8–14.6 µm), as well as slightly shorter cheilocystidia (21.2–30.7 µm). In contrast, *L. acanthospora* differs in possessing a slighter darker basidiomata, a longer stipe (30–45 mm), larger basidiospores (7–10 × 7–10 µm), and larger basidia (40–56 × 10–14 µm) and has four-spored^[128]. Furthermore, *L. alutacea*, *L. conifericola*, and *L. fulvogrisea* are clearly separated by their predominantly brownish-hued basidiomata, which lack the distinct pale orange tones of *L. fasciculata*^[127].

Laccaria ganziensis R.L. Zhao & X.X. Han, sp. nov. Figs 14 and 17

Chinese Name: 甘孜蜡蘑 (gan zi la mo)

Fungal Names: FN 573697; Facesoffungi number: FoF 20052

Etymology — refers to the type locality, Ganzi Tibetan Autonomous Prefecture.

Diagnosis — differs from *L. acanthospora* in its pale orange, slightly broader pileus, smaller, globose to subglobose basidiospores, and two- or four-spored basidia bearing shorter sterigmata.

Holotype — CHINA, Sichuan, Ganzi Tibetan Autonomous Prefecture, Yajiang County, Gexigou Nature Reserve, Gexigou, 30°2'53" N, 100°57'13" E, 2,915 m asl, growing on the ground within broad-leaved forests dominated by *Quercus*, 14 August 2020, B. Cao & J.X. Li, ZRL20200134 (HMAS 259873 holotype; AF9558 isotype, GenBank no.: ITS PZ494651; LSU PZ494221; *tef1a* PZ520031; *rpb2* PZ541201).

Pileus 7–40 mm diam., initially hemispherical to convex, becoming plano-convex, applanate to plano-concave at maturity, sometimes with a slightly depressed centre, not or slightly hygrophanous, glabrous or pruinose, margin involute, inflexed to straight, sometimes with translucently striate, occasionally slightly sulcate at margin, yellowish grey (3B2–4B2), greyish orange (5B2) to yellowish brown (5D8), sometimes fading towards margin, margin entire to undulate, or occasionally becoming rimose with age. Lamellae distant, narrowly adnate to adnate with decurrent tooth, unequal, edge entire to slightly eroded in some parts, concolorous, grey (4B2) to brownish orange (6C5). Stipe 26–73 × 2–4 mm, central, cylindrical, equal or slightly broadened towards the base, sometimes twisted, surface subglabrous, with white longitudinal fibrils, slightly pruinose, concolorous with pileus or slightly paler, basal mycelium white. Context thin, odour indistinct.

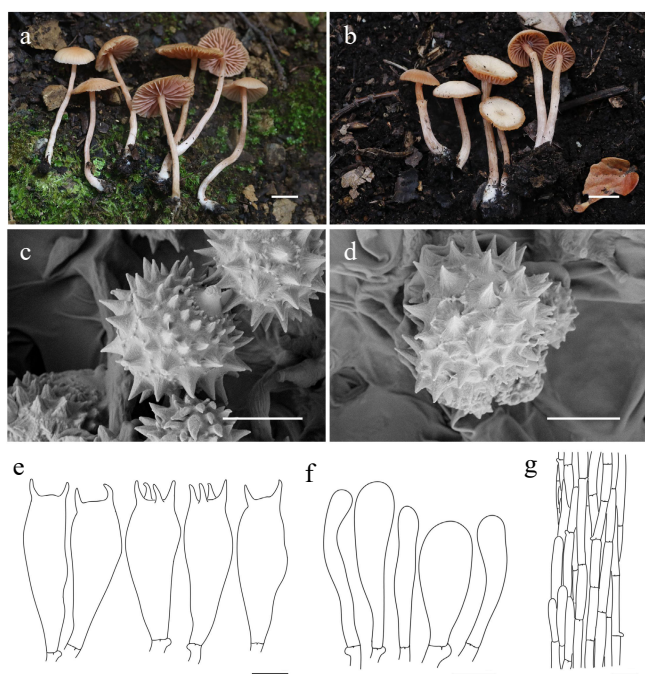


Fig. 14 *Laccaria ganziensis* (a, ZRL20200134 holotype; b, ZRL20201653). (a, b) Basidiomata; (c, d) Basidiospores; (e) Basidia; (f) Cheilocystidia; (g) Pileipellis. Scale bars: (a, b) = 1 cm; (c, d) = 5 µm; (e–g) = 10 µm.

Basidiospores [50/3/2] (5.6–)6.7–7.8(–8.1) × (5.5–)6.4–7.6(–8.2) µm, $Q = (0.98–)1.00–1.07(–1.12)$, $Q_m = 1.04 (\pm 0.03)$, globose to subglobose, echinulate, slightly thick-walled, hyaline, distant, spines 0.4–1.9 µm long. Basidia (33.9)38.1–48.8(54.7) × (10.7)11.8–14.6(16.1) µm, clavate, hyaline, two- or four-spored, sterigmata 2.6–7.2 µm long. Cheilocystidia (18.4)21.2–30.7(37.6) × (3.5)4.5–9.1(11.6) µm, narrowly clavate, filamentous to flexuose, thin- to slight thick-walled, hyaline. Pleurocystidia (21.9)26.7–36.6(43.7) × (4.6)6.7–12.3(14.1) µm, narrowly clavate to clavate, filamentous, sometimes irregular, slightly thick-walled, hyaline. Lamella trama regular to subregular, composed of slightly thick-walled, filamentous hyphae 2–8 µm wide. Stipitipellis is composed of appressed, parallel, thin-walled, hyaline to pale brown, caulocystidia not observed. Pileipellis is a cutis composed of repent to suberect, interwoven filamentous hyphae, 3–11 µm wide, thick-walled, hyaline. Clamp-connections present.

Known distribution — In pairs, gregarious or scattered on humus-rich ground in coniferous forests, broad-leaved forests or mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Sichuan, Ganzi Tibetan Autonomous Prefecture, Batang County, Zhubalong Nature Reserve, 29°39'37" N, 99°5'21" E, 4,101 m asl, growing on humus-rich ground within coniferous forests dominated by *Abies*, 19 August 2020, X.Y. Zhu & M.Z. Zhang, ZRL20201517 (HMAS 259875, GenBank no.: ITS PZ494662; LSU PZ494222); Zhubalong Nature Reserve, 29°40'6" N, 99°4'27" E, 3,368 m asl, growing on humus-rich ground within broad-leaved forests dominated by *Populus*, 19 August 2020, M.Q. He & M.Q. Wang, ZRL20201591 (HMAS 259876, GenBank no.: ITS PZ494650; LSU PZ494218; *tef1α* PZ520032; *rpb2* PZ541203); Derong County, Xiayong Nature Reserve, 28°22'46" N, 99°21'2" E, 3,399 m asl, growing on humus-rich ground within broad-leaved forests dominated by *Quercus*, 22 August 2020, X.X. Han & R.L. Zhao, ZRL20201653 (HMAS 259877, GenBank no.: ITS PZ494655; LSU PZ494205); *ibid.*, M.Q. He & M.Q. Wang, ZRL20201744 (HMAS 286060, GenBank no.: ITS PZ494653; LSU PZ494227), ZRL20201759

(HMAS 259878, GenBank no.: ITS PZ494648; LSU PZ494206), ZRL20201875 (HMAS 286062, GenBank no.: ITS PZ494659; LSU PZ494226; *tef1α* PZ520030; *rpb2* PZ541202); Xiangcheng County, Fozhu Gorge Nature Reserve, 29°3'46" N, 99°56'55" E, 3,288 m asl, growing on humus-rich ground within coniferous forests dominated by *Abies*, 15 August 2019, R.L. Zhao, B. Cao, & Z.L. Ling, ZRL20191123 (HMAS 259870, GenBank no.: ITS PZ494656; LSU PZ494217; *tef1α* PZ520034; *rpb2* PZ541200); Fozhu Gorge Nature Reserve, 29°4'49" N, 99°54'11" E, 3,000 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests dominated by *Pinus* and *Quercus*, 21 August 2020, B. Cao & J.X. Li, ZRL20201762 (HMAS 286061, GenBank no.: ITS PZ494649; LSU PZ494219); Fozhu Gorge Nature Reserve, 29°3'52" N, 99°56'16" E, 3,090 m asl, growing on humus-rich ground within broad-leaved forests dominated by *Quercus*, 21 August 2020, B. Cao & J.X. Li, ZRL20201900 (HMAS 259879, GenBank no.: ITS PZ494657; LSU PZ494223; *tef1α* PZ520033; *rpb2* PZ541198); Yajiang County, Gexigou Nature Reserve, Gexigou, 30°3'10" N, 100°56'35" E, 2,953 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests dominated by *Picea*, 14 August 2020, X.Y. Zhu & M.Z. Zhang, ZRL20200238 (HMAS 259874, GenBank no.: ITS PZ494652; LSU PZ494224; *tef1α* PZ520029; *rpb2* PZ541199); Yajiang County, Xinduqiao Town, 30°3'1" N, 100°57'15" E, 2,928 m asl, growing on humus-rich ground within broad-leaved forests dominated by *Quercus*, 13 August 2020, M.Q. He & M.Q. Wang, ZRL20200061 (HMAS 259871, GenBank no.: ITS PZ494661; LSU PZ494207); Xinduqiao Town, 30°3'1" N, 100°57'15" E, 2,998 m asl, growing on humus-rich ground within broad-leaved forests dominated by *Quercus*, 13 August 2020, X.Y. Zhu & M.Z. Zhang, ZRL20200113 (HMAS 259872, GenBank no.: ITS PZ494660; LSU PZ494204). Xizang, Linzhi City, Chayu County, Chawalong Township, Mengzha Village, 28°32'34" N, 98°14'36" E, 2,792 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests, 8 August 2023, X.X. Han & Y.Y. Zheng, ZRL20231211 (HMAS 259880, GenBank no.: ITS PZ494658; LSU PZ494216); Milin County, Milin Town, Bangzhong Village, 29°17'30" N, 94°19'46" E, 2,934 m asl, growing on humus-rich ground within broad-leaved forests dominated by *Quercus*, 15 August 2023, M.Z. Zhang & L.H. Liu, ZRL20235085 (HMAS 259881, GenBank no.: ITS PZ494654; LSU PZ494225).

Notes — Phylogenetically, the new species is closely related to *L. acanthospora*. Although both share orange-toned basidiomata, *L. acanthospora* differs in its slightly smaller and paler pileus, obellipsoid to globose, larger basidiospores (av. 8.3–8.4 × 8.9–9.2 µm) adorned with longer spines (2–6 µm), and relatively longer basidia (40–56 µm) bearing longer sterigmata (6–10 µm)^[128]. Other Asian *Laccaria* species exhibiting orange coloration and globose, echinate spores include *L. aurantiaca*, *L. carminostipes* Y.D. Xu & Z.M. He, and *L. fengkaiensis* Fang Li. *Laccaria aurantiaca* has slightly darker basidiomata, smaller basidia (30–40 × 7–10 µm), and narrower cheilocystidia (4–5 µm)^[114]. *Laccaria carminostipes* features a darker pileus, darker yet longer and thicker stipe (70–90 × 3–7 mm), plus an absence of cystidia^[80]. Whereas *Laccaria fengkaiensis* differs by paler and larger basidiomata, including a broader pileus (50–90 mm), and longer, thicker stipe (60–100 × 6–9 mm), along with smaller basidiospores (5.2–6.3 × 5.1–6.3 µm), and narrower basidia (6–8.5 µm)^[135].

Laccaria migpainsensis R.L. Zhao, B. Cao, & X.X. Han, sp. nov. Figs 15 and 17

Chinese Name: 米培蜡蘑 (mi pei la mo)

Fungal Names: FN 573698; Facesoffungi number: FoF 20053

Etymology — *migpainsensis* (Latin) refers to the type locality Migpain, an officially standardized geographical name in the Zangnan region of Xizang Autonomous Region, China.

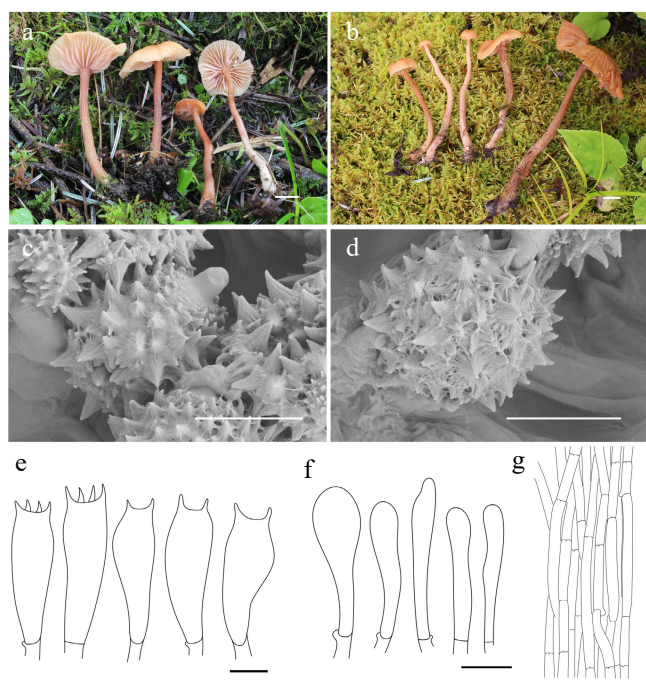


Fig. 15 *Laccaria migpainsensis* (a, ZRL20220224; b, ZRL20231870 holotype). (a, b) Basidiomata; (c, d) Basidiospores; (e) Basidia; (f) Cheilocystidia; (g) Pileipellis. Scale bars: (a, b) = 1 cm; (c, d) = 5 μ m; (e–g) = 10 μ m.

Diagnosis — differs from *L. longipes* by its broader basidia, globose to subglobose basidiospores, and higher elevation habitat (ca. 3,000 m).

Holotype — CHINA, Xizang, Linzhi, Motuo County, near Migpain, 29°43'42" N, 95°38'58" E, 3,182 m asl, growing on humus-rich ground in coniferous forest, 12 August 2023, X.X. Han & Y.Y. Zheng, ZRL20231870 (HMAS 259857 holotype; AF9576 isotype, GenBank no.: ITS PZ494646; LSU PZ494252; *rpb2* PZ541208).

Pileus 6–86 mm diam., hemispherical to plano-convex when young, expanding to applanate to plano-concave with age, centre slightly depressed to subumbonate initially, becoming umbilicate over time, hygrophanous, margin straight to inflexed, glabrous, translucently striate, and radially rugulose, brownish orange (5C6) to brown (6D8) at the centre, fading towards the margin, yellowish white (3A2) to pale orange (5A3), entire to undulate. Lamellae distant, narrowly adnate, adnate to adnate with decurrent tooth, unequal, edge entire to slightly eroded in some parts, concolorous or paler towards edge, pale orange (6A3) to brownish orange (7C6). Stipe 57–185 $\times$ 3–12 mm, central, cylindrical, sometimes twisted, slightly broadened towards the base, surface subglabrous, finely longitudinally striate and pruinose, concolorous with pileus, basal mycelium white. Context thin, odour indistinct.

Basidiospores [50/4/4] (5.7–)6.8–8.3(–8.9) $\times$ (5.6–)6.5–7.9(–8.7) μ m, Q = (1.00–)1.01–1.07(–1.15), Q_m = 1.04 ($\pm$ 0.03), globose to subglobose, echinulate, slightly thick-walled, hyaline, distant, spines 0.4–1.2 μ m long. Basidia (29.6)31.9–41.2(47.9) $\times$ (8.1)9.5–12.6(14.2) μ m, clavate, hyaline, two- or four-spored, sterigmata 4.3–7.9 μ m long. Cheilocystidia (18.8)23.6–33.7(43.7) $\times$ (2.9)3.9–6.1(7.7) μ m, filamentous to narrowly clavate, sometimes irregular, occasionally branched or with a capitate apex, thin-walled, hyaline. Pleurocystidia (16.7)20.2–28.0(30.9) $\times$ (4.7)5.3–7.1(8.0) μ m, narrowly clavate to filamentous, sometimes irregular, slightly thick-walled, hyaline. Lamella trama regular to subregular, composed of slightly thick-walled, filamentous hyphae 2–6 μ m wide. Stipitipellis

is composed of appressed, parallel, thin- to slightly thick-walled, hyaline to pale brown, caulocystidia not observed. Pileipellis is a cutis composed of repent to suberect, interwoven filamentous hyphae, 2.5–9.0 μ m wide, thin- to slightly thick-walled, hyaline to slightly brownish. Clamp-connections present.

Known distribution — Scattered or gregarious on humus-rich ground within coniferous forests or mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Xizang, Shigatse, Yadong County, Xiayadong Township, Renqinggang Village, Drinking Water Source Protection Area, 27°25'20" N, 88°55'6" E, 3,254 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forest, 27 July 2022, R.L. Zhao, X.Y. Zhu, & J.X. Li, ZRL20220224 (HMAS 259847, GenBank no.: ITS PZ494637; LSU PZ494263; *tef1 α* PZ520063; *rpb2* PZ541219); *ibid.*, M.Q. He & B. Cao, ZRL20220267 (HMAS 259848, GenBank no.: ITS PZ494639; LSU PZ494257; *tef1 α* PZ520068); Gyirong County, Gyirong Valley, 28°24'35" N, 85°18'54" E, 2,935 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forest, 1 August 2022, R.L. Zhao & X.Y. Zhu, ZRL20220564 (HMAS 259849, GenBank no.: ITS PZ494642; LSU PZ494255); *ibid.*, ZRL20220574 (HMAS 259850, GenBank no.: ITS PZ494643; LSU PZ494264); *ibid.*, D. Phurba & J.X. Li, ZRL20220609 (HMAS 259851, GenBank no.: ITS PZ494641; LSU PZ494256); *ibid.*, ZRL20220612 (HMAS 259852, GenBank no.: ITS PZ494638; LSU PZ494262; *tef1 α* PZ520066; *rpb2* PZ541220); Gyirong County, Gyirong Town, 1.7 km from Gyirong Town to Chongse Checkpoint, 28°22'39" N, 85°19'40" E, 2,780 m asl, growing on humus-rich ground in coniferous forest dominated by *Pinus*, 2 August 2022, D. Phurba & J.X. Li, ZRL20220705 (HMAS 259853, GenBank no.: ITS PZ494644; LSU PZ494259; *tef1 α* PZ520065; *rpb2* PZ541189); Gyirong County, along the road from Gyirong Town to Zha Village, 28°23'45" N, 85°23'34" E, 3,441 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forest dominated by *Quercus*, 2 August 2022, M.Q. He & B. Cao, ZRL20220821 (HMAS 259854, GenBank no.: ITS PZ494640; LSU PZ494261); Linzhi, Motuo County, near Migpain, 29°43'42" N, 95°38'58" E, 3,182 m asl, growing on humus-rich ground in coniferous forest, 12 August 2023, M.Z. Zhang & L.H. Liu, ZRL20231740 (HMAS 259855, GenBank no.: ITS PZ494635; LSU PZ494258; *tef1 α* PZ520067; *rpb2* PZ541205); *ibid.*, D. Phurba & X.H. Yu, ZRL20231840 (HMAS 259856, GenBank no.: ITS PZ494645; LSU PZ494254; *tef1 α* PZ520062; *rpb2* PZ541207); *ibid.*, ZRL20231887 (HMAS 259858, GenBank no.: ITS PZ494636; LSU PZ494253; *tef1 α* PZ520069; *rpb2* PZ541204); Motuo County, near Migpain, 29°43'36" N, 95°38'53" E, 3,151 m asl, growing on humus-rich ground in coniferous forest, 13 August 2023, X.X. Han & Y.Y. Zheng, ZRL20231893 (HMAS 259859, GenBank no.: ITS PZ494647; LSU PZ494260; *tef1 α* PZ520064; *rpb2* PZ541206).

Notes — In the multilocus phylogeny, 13 specimens of *L. migpainsensis* clustered together with 100/1.00 support (Fig. 17). Morphologically, *L. migpainsensis* resembles *L. aurantiaca* S.M. Tang, K.D. Hyde & Z.L. Luo, *L. longipes* G.M. Mueller, *L. nanlingensis*, and *L. torosa* H.J. Cho & Y.W. Lim by possessing soft orange basidiomata. However, *L. aurantiaca* is distinguished by its shorter stipe (46.0–55.1 mm), narrower basidia (av. 8 μ m), and smaller basidiospores (av. 6.9 $\times$ 6.5 μ m)^[114]. *Laccaria longipes*, originally described from Canada, differs by its narrower basidia (7–10 μ m) and subglobose to broadly ellipsoid basidiospores^[136]. *Laccaria torosa* H.J. Cho & Y.W. Lim, described from Korea, is characterized by a relatively shorter stipe (35–95 mm), larger basidiospores (8–9 $\times$ 8–9.5 μ m), and larger basidia (39–47 $\times$ 12.5–16.5 μ m)^[130]. *Laccaria nanlingensis* also differs in its shorter stipe (25–70 mm), smaller basidiospores (av. 6.95 $\times$ 6.37 μ m), four-spored basidia, and longer cheilocystidia (40–60 μ m)^[126].

Laccaria yadongensis R.L. Zhao & X.X. Han, sp. nov. Figs 16 and 17

Chinese Name: 亚东蜡蘑 (ni gui se la mo)

Fungal Names: FN 573699; Facesoffungi number: FoF 20054

Etymology — *yadongensis* (Latin) refers to the type locality.

Diagnosis — differs from *L. salmonicolor* by its smaller basidiospores with shorter spines, and two- or four-spored basidia.

Holotype — CHINA, Xizang, Shigatse, Yadong County, Xiasima Town, 27°23'13" N, 88°49'51" E, 2,945 m asl, growing on mosses within mixed coniferous and broad-leaved forests, 14 September 2015, X.M. Bai, ZRL20152140 (HMAS 259868 holotype; AF9554 isotype, GenBank no.: ITS PZ494632; LSU PZ494242; *rpb2* PZ541221).

Pileus 12–29 mm diam., initially plano-convex with a slightly depressed centre, becoming deeply infundibuliform at maturity, hygrophanous, glabrous, margin inflexed to reflexed, sometimes radially rugulose, yellowish grey (3B2), brownish orange (6C4) to brown (7E7) at the centre, fading towards margin, margin entire to undulate, occasionally rimose when mature. Lamellae distant, decurrent to deeply decurrent, unequal, edge entire, concolorous, reddish white (7A2), greyish orange (6B4) to brownish orange (6C7). Stipe 39–87 × 4–8 mm, central, cylindrical, equal or broadened towards the base, surface subglabrous, longitudinally striate, concolorous with pileus or slightly paler, basal mycelium white. Context thin, odour indistinct.

Basidiospores [50/3/2] (5.5–)6.4–7.5(–8.0) × (5.1–)6.3–7.3(–7.8) μm , $Q = (0.99\text{--}1.00\text{--}1.05\text{--}1.14)$, $Q_m = 1.03 (\pm 0.03)$, globose, rarely subglobose, echinulate, slightly thick-walled, hyaline, distant, spines 0.1–1.2 μm long. Basidia (32.4)37.6–45.5(47.1) × (11.1)12.3–14.9(16.3) μm , clavate, hyaline, two- or four-spored, sterigmata 3.2–7.4 μm long. Cheilocystidia (16.2)21.0–28.5(31.0) × (3.2)4.4–7.6(8.7) μm , narrowly clavate, filamentous to flexuose, thin-walled, hyaline. Pleurocystidia (27.8)30.3–36.1(40.3) × (5.0)6.1–8.5(9.8) μm , narrowly clavate to filamentous, sometimes irregular, slightly thick-walled, hyaline. Lamella trama regular to subregular, composed of slightly thick-walled, filamentous hyphae 2–6 μm wide. Stipitipellis is composed of appressed, parallel, slightly thick-walled, hyaline to pale yellowish-brown, caulocystidia not observed. Pileipellis is a cutis composed of repent to suberect,

interwoven filamentous hyphae, 3–9 μm wide, thin-walled, hyaline. Clamp-connections present.

Known distribution — Scattered on mosses within coniferous forests or mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Hubei, Shennongjia Forestry District, Shennongding, Taiziya, 31°27'14" N, 110°11'33" E, 2,588 m asl, growing on mosses within coniferous forests dominated by *Abies* and *Fargesia*, 26 August 2022, J.X. Li, R.L. Zhao, & X.X. Han, ZRL20221203 (HMAS 259869, GenBank no.: ITS PZ494633; LSU PZ494239; *tef1a* PZ520061; *rpb2* PZ541222).

Notes — In the field, *L. yadongensis* is easily confused with *L. salmonicolor* A.W. Wilson & G.M. Muell. due to their morphologically similar, brownish orange-hued basidiomata that fade to pale buff. *Laccaria salmonicolor* has globose, larger basidiospores (7.5–10 μm) with longer spines (1–3 μm), and four-spored basidia^[128]. In the phylogenetic analysis (Fig. 17), *L. yadongensis* is close to *L. proxima* (Boud.) Pat. and *L. guizhouensis* Jing Wang bis & Yi H. Yang. However, *L. proxima* has a convex to plano-convex and brick red to reddish brown pileus, larger but broadly ellipsoid basidiospores (7.3–9.8 × 6.8–8.8 μm), narrower basidia (8–11 μm)^[137]. *Laccaria guizhouensis* has a hemispherical to campanulate, orange-white to pinkish-white pileus, narrower stipe (2–3 mm), and smaller basidia (25–35 × 8–10 μm)^[97]. In addition to the collections from the Qinghai–Xizang Plateau, conspecific specimens were also identified from Shennongjia Forestry District, Hubei Province, extending the known distribution of *L. yadongensis* beyond the Plateau region.

Hygrophoraceae Lotsy

Index Fungorum number: IF 80877

Type genus — *Hygrophorus* Fr.

Cuphophyllus (Donk) Bon

Index Fungorum number: IF 25612

Type species — *Cuphophyllus pratensis* (Pers.) Bon

Notes — *Cuphophyllus* (Donk) Bon is a genus of waxcap fungi in the family Hygrophoraceae, typified by *Cu. pratensis*, with more than 50 species reported worldwide^[61,113,138–140]. More than 10 species have been recorded from China^[61,93,138,141]. Species of *Cuphophyllus* are typically characterized by clitocyboid basidiomata, decurrent lamellae. Basidiospores are smooth, inamyloid, and guttulate in KOH, while basidia are relatively long with basal clamp connections and cystidia are usually absent. The pileipellis consists of highly interwoven hyphae, occasionally forming a regular or subregular central strand^[142,143].

Cuphophyllus species usually grow on soil or forest litter and are commonly found in forests and grasslands, often preferring acidic and humus-rich soils^[143,144]. The genus is widely distributed worldwide, occurring from the nemoral zone to arctic–alpine regions^[145,146]. Molecular phylogenetic studies support *Cuphophyllus* as a monophyletic lineage within Hygrophoraceae^[142]. Accordingly, *Cuphophyllus* is divided into six sections, viz. sect. *Adonidi*, sect. *Cuphophyllus*, sect. *Fornicati*, sect. *Virginei*, and two additional unnamed sections^[142]. In this study, two new species are described based on morphology and phylogenetic analyses of ITS, LSU, and *rpb2* sequences.

Cuphophyllus alticola R.L. Zhao & X.X. Han, sp. nov. Figs 18 and 20

Chinese Name: 高原拱顶伞 (gao yuan gong ding san)

Fungal Names: FN 573700; Facesoffungi number: FoF 20055

Etymology — *alticola* (Latin), composed of 'altus' (high) and 'cola' (inhabitant), referring to the habitat of this species in high-altitude regions, where all specimens were collected at elevations above 4,100 m.

Diagnosis — differs from *Cu. dingjieensis* by its paler pileus, nearly white stipe, and larger basidia, and preference in mixed coniferous

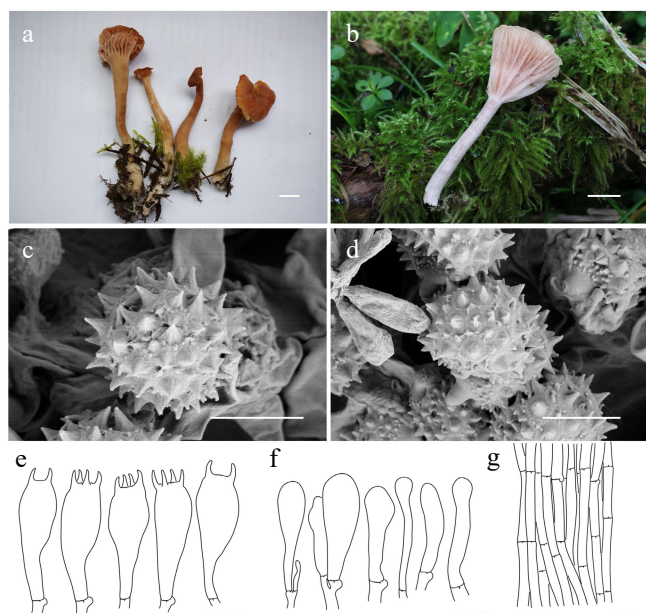


Fig. 16 *Laccaria yadongensis* (a, ZRL20152140 holotype; b, ZRL20221203). (a) Basidiomata; (b) Basidioma; (c, d) Basidiospores; (e) Basidia; (f) Cheilocystidia; (g) Pileipellis. Scale bars: (a, b) = 1 cm; (c, d) = 5 μm ; (e–g) = 10 μm .

and broad-leaved forests dominated by *Abies* at higher elevations (ca. 4,100 m).

Holotype — CHINA, Sichuan, Ganzi, Batang County, Zhubalong Nature Reserve, 29°39'36" N, 99°5'20" E, 4,101 m asl, growing on humus-rich ground in mixed coniferous and broad-leaved forests dominated by *Abies*, 19 August 2020, M.Z. Zhang & X.Y. Zhu, ZRL20201436 (HMAS 259819 holotype; AF9561 isotype, GenBank no.: LSU PZ491519; rpb2 PZ495424).

Pileus 16–30 mm diam., convex to plano-convex, becoming applanate, sometimes the margin is slightly involute, surface smooth, hygrophanous, striate up to halfway from the margin or indistinct when moist, greyish yellow (3C3) to olive (3D4) when young, dull yellowish white (3A2) to yellow (3B4) when mature, paling towards the margin. Lamellae subdistant, decurrent to deeply decurrent, unequal, with lamellulae, white (2A1) to yellowish white (2A2). Stipe 39–71 × 4–7 mm, slender, cylindrical, sometimes

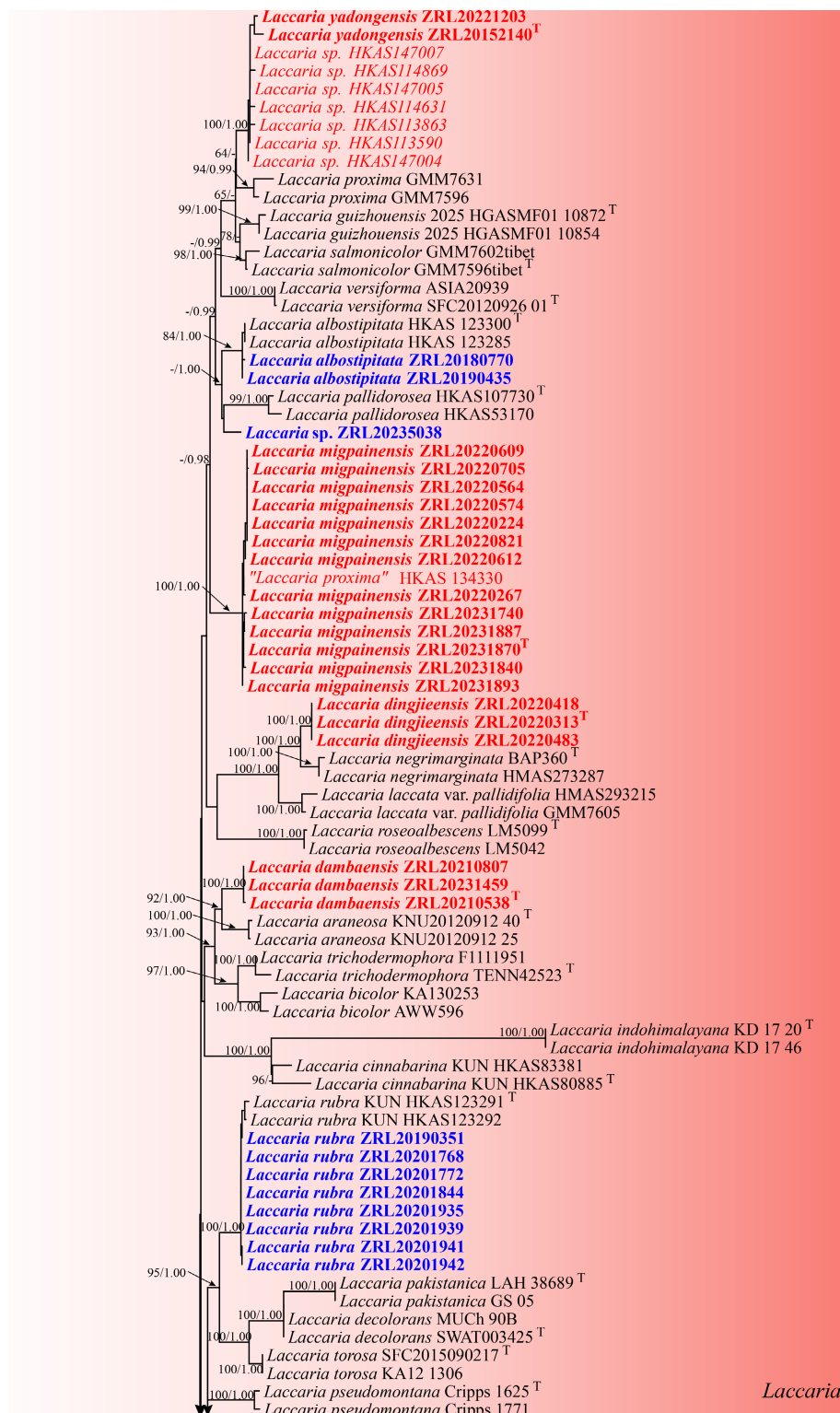
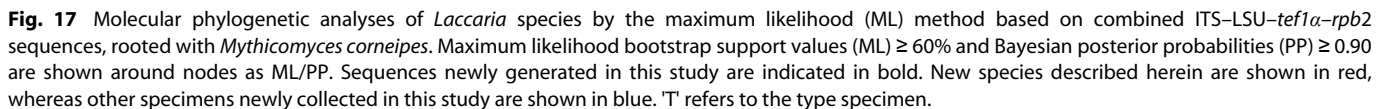


Fig. 17 to be continued



or lacrymoid, smooth, colourless, hyaline, sometimes containing an oil droplet. Basidia (36.3)41.3–51.8(58.4) $\times$ (8.2)8.8–10.2(10.8) μm , clavate, hyaline, colourless, hyaline, two- or four-spored. Basidioles (32.1)36.0–42.9(46.6) $\times$ (5.9)6.4–7.7(8.3) μm , colourless, hyaline, narrowly clavate. Pleurocystidia not observed. Cheilocystidia not

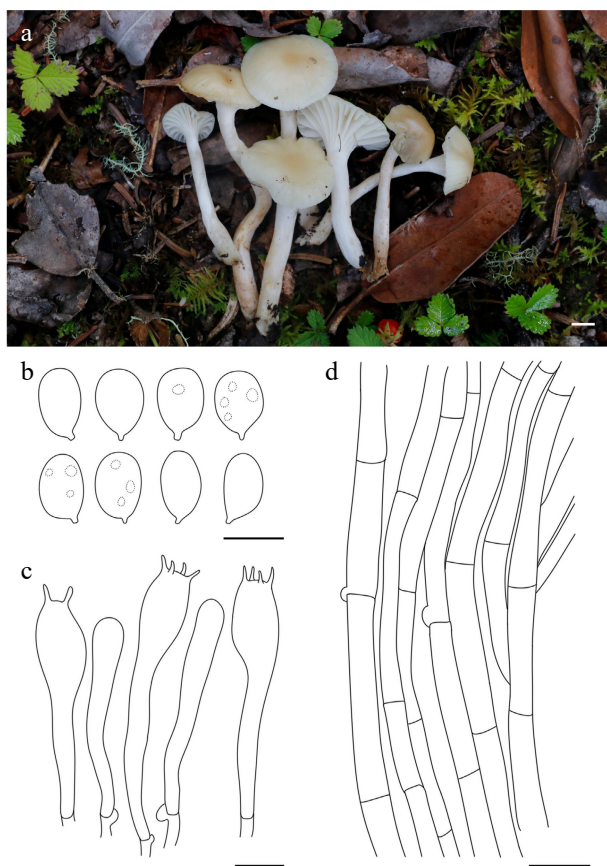


Fig. 18 *Cuphophyllus alticola* (a, ZRL20201436 holotype). (a) Basidiomata; (b) Basidiospores; (c) Basidia; (d) Pileipellis. Scale bars: (a) = 1 cm; (b–d) = 10 μ m.

observed. Pileipellis is a cutis with the transition to a trichoderm at regular intervals, composed of 2.5–6.8 μ m wide, thin-walled, filamentous hyphae. Clamp-connections present.

Known distribution — Solitary, in pairs or gregarious on humus-rich ground in mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Sichuan, Ganzi, Batang County, Zhubalong Nature Reserve, 29°39'36" N, 99°5'20" E, 4,101 m asl, growing on humus-rich ground in mixed coniferous and broad-leaved forests dominated by *Abies*, 19 August 2020, M.Q. He & M.Q. Wang, ZRL20201504 (HMAS 259820, GenBank no.: ITS PZ491508; LSU PZ491518; *rpb2* PZ495427), X.X. Han & R.L. Zhao, ZRL20201511 (HMAS 259821, GenBank no.: LSU PZ491520; *rpb2* PZ495426), M.Q. He & M.Q. Wang, ZRL20201513 (HMAS 259822, GenBank no.: ITS PZ491510; LSU PZ491521; *rpb2* PZ495428), M.Q. He & M.Q. Wang, ZRL20201529 (HMAS 259823, GenBank no.: ITS PZ491509; LSU PZ491514; *rpb2* PZ495425).

Notes — *Cuphophyllus alticola* is characterized by a pale yellow pileus that becomes lighter toward the margin and is striate up to halfway from the edge, a nearly white stipe, and larger basidia (41.3–51.8 $\times$ 8.8–10.2 μ m). In the multigene tree (Fig. 20), *Cuphophyllus alticola* formed a monophyletic sister clade to *Cu. fulvus* with high support. However, *C. alticola* has a pale yellow pileus, slender stipe (4–7 mm vs. 3–6 mm), and slightly longer basidiospores (7.0–8.3 μ m vs. 6.9–7.5 μ m). *Cuphophyllus alticola* is morphologically similar to *Cu. dingjieensis* but can be distinguished from the latter by its pale yellow pileus, whitish stipe, and larger basidia (41.3–51.8 $\times$ 8.8–10.2 μ m vs. 27–37 $\times$ 5–7 μ m)^[61].

Cuphophyllus fulvus R.L. Zhao & X.X. Han, sp. nov. Figs 19 and 20

Chinese Name: 浅黄褐拱顶伞 (qian huang he gong ding san)
Fungal Names: FN 573701; Facesoffungi number: FoF 20056
Etymology — *fulvus* (Latin) refers to the pale yellowish brown colours of the pileus.

Diagnosis — differs from other species of the genus by its pale yellowish brown, hygrophanous pileus, which is striate up to halfway from the margin, and ellipsoid to obovoid or lacrymoid basidiospores measuring 6.9–7.5 $\times$ 4.9–5.6 μ m.

Holotype — CHINA, Xizang, Dingjie County, Chentang Town, 27°54'58" N, 87°27'32" E, 3,188 m asl, growing on humus-rich ground in mixed coniferous and broad-leaved forests, 12 September 2015, X.M. Bai ZRL20152068 (HMAS 259817 holotype; AF9553 isotype, GenBank no.: ITS PZ491512; LSU PZ491516; *rpb2* PZ495422).

Pileus 14–17 mm diam., semi-globose, convex when young, becoming flattened and with a depressed centre when mature, inflexed margin, hygrophanous, striate up to halfway from the margin, sometimes surface covered with fine radial fibrils which are more evident when dry, greyish yellow (5A3) to brownish yellow (5C7), darker in the centre. Lamellae subdistant, decurrent, unequal, with lamellulae, white (2A1) to yellowish white (2A2). Stipe 36–50 $\times$ 3–6 mm, thick, cylindrical, usually curved and slightly enlarged at base, slightly fibrillose, surface smooth, white (5A1) to brownish orange (5C4). Context thin, white to orange white, fleshy, odour indistinct, taste mild.

Basidiospores [80/3/3] (5.5–)6.9–7.5(–9.4) $\times$ (4.4–)4.9–5.6(–6.0) μ m, $Q = (1.16–)1.32–1.56(–1.74)$, $Qm = 1.44 (\pm 0.12)$, ellipsoid to obovoid, or lacrymoid, smooth, colourless, hyaline, sometimes containing an oil droplet. Basidia (43.3)46.9–53.6(56.9) $\times$ (7.6)8.0–9.4(9.9) μ m, clavate, hyaline, colourless, two- or four-spored. Basidioles

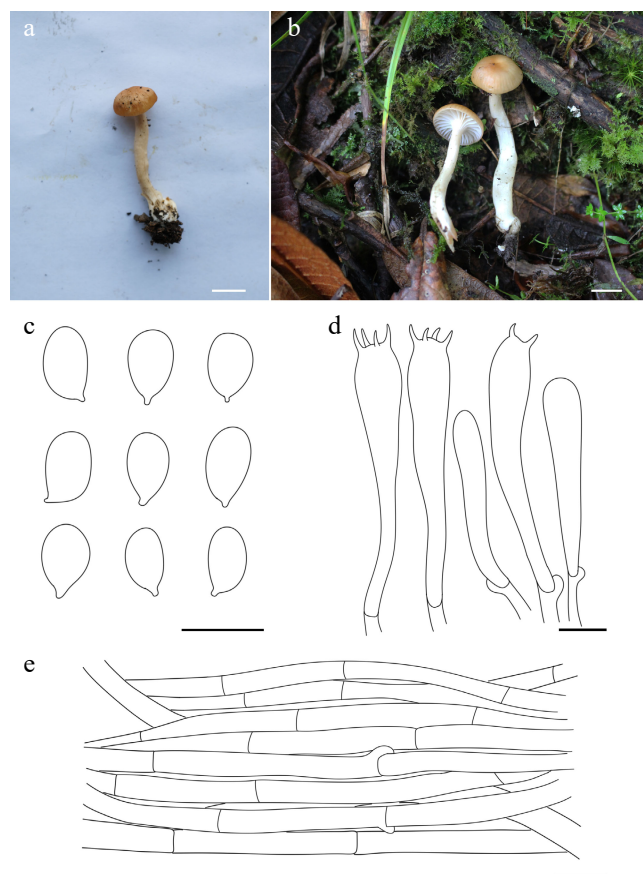


Fig. 19 *Cuphophyllus fulvus* (a ZRL20152068 holotype; b ZRL20220479). (a) Basidioma; (b) Basidiomata; (c) Basidiospores; (d) Basidia; (e) Pileipellis. Scale bars: (a, b) = 1 cm; (c–e) = 10 μ m.

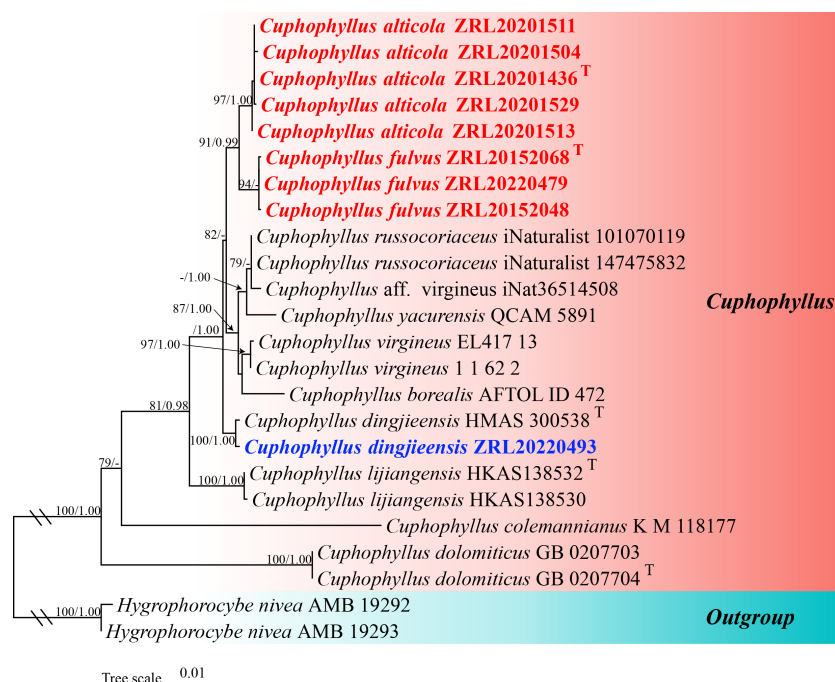


Fig. 20 Molecular phylogenetic analyses of *Cuphophyllus* species by the maximum likelihood (ML) method based on combined ITS–LSU–*rpb2* sequences, rooted with *Ampulloclitocybe clavipes* and *Clitocybe subclavipes*. Maximum likelihood bootstrap support values (ML) $\geq 60\%$ and Bayesian posterior probabilities (PP) ≥ 0.90 are shown around nodes as ML/PP. 'T' refers to the type specimen. Sequences newly generated in this study are indicated in bold. New species described herein are shown in red, whereas other specimens newly collected in this study are shown in blue.

(29.2)31.6–38.7(45.0) $\times$ (4.2)4.9–6.2(6.7) μm , colourless, hyaline, narrowly clavate. Pleurocystidia not observed. Cheilocystidia not observed. Pileipellis is a cutis with the transition to a trichoderm at regular intervals, composed of 3.2–7.1 μm wide, thin-walled, filamentous hyphae. Clamp-connections present.

Known distribution — Solitary or in pairs on humus-rich ground in mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Xizang, Dingjie County, Chentang Town, 27°54'58" N, 87°27'32" E, 3,188 m asl, growing on humus-rich ground in mixed coniferous and broad-leaved forests, 12 September 2015, X.M. Bai ZRL20152048 (HMAS 259816, GenBank no.: ITS PZ491513; LSU PZ491515; *rpb2* PZ495421; 30 July 2022, R.L. Zhao & X.Y. Zhu, ZRL20220479 (HMAS 259818, GenBank no.: ITS PZ491511).

Notes — *Cuphophyllus fulvus* can be easily distinguished from most other species within the genus by its small basidiomata, pale yellowish brown pileus, and two- or four-spored basidia. Although both *Cu. fulvus* and *Cu. dingjieensis* were collected from Dingjie County, Xizang, and are closely related phylogenetically, *Cu. dingjieensis* differs from *Cu. fulvus* in having a pale yellowish pileus, longer stipe (45–80 mm vs. 36–50 mm), and smaller basidia (27–37 $\times$ 5–7 μm vs. 46.9–53.6 $\times$ 8.0–9.4 μm)^[61]. Currently, *Cuphophyllus alticola*, *Cu. fulvus*, and *Cu. dingjieensis* are only known from the alpine regions of the southern Qinghai–Xizang Plateau, whereas other phylogenetically related species are predominantly distributed in lowland areas of North America and Europe^[143].

Omphalinaceae Vizzini, Consiglio & M. Marchetti

Index Fungorum number: IF 557851

Type genus — *Omphalina* Quél.

Infundibulicybe Harmaja

Index Fungorum number: IF 28751

Type species — *Infundibulicybe gibba* (Pers.) Harmaja

Notes — *Infundibulicybe* Harmaja, typified by *I. gibba* (Pers.) Harmaja was established to accommodate species formerly placed

in *Clitocybe*, with 28 species currently classified in the genus^[61,147]. At least 15 species have been reported from China^[61,93,147]. Species of *Infundibulicybe* are typically characterized by slightly depressed to infundibuliform pileus, decurrent lamellae, and smooth, mostly lacrymoid and cyanophobic basidiospores that do not adhere in tetrads, often with confluent bases^[148–150]. Molecular phylogenetic analyses have confirmed the independence of *Infundibulicybe* from *Clitocybe* and its placement in the suborder Tricholomatineae, where it is closely related to *Omphalina* and together they constitute Omphalinaceae^[35,150–152]. Members of the genus are mainly saprobic on leaf or needle litter and are largely confined to temperate, boreal, and alpine regions of the Northern Hemisphere^[148–150,153]. In this study, one new species is described based on morphological characters and phylogenetic analyses of ITS and LSU sequences.

Infundibulicybe jilongensis K. Wang, T.Z. Wei, & P. Hong **Figs 21 and 23**

Chinese Name: 吉隆漏斗伞 (ji long lou dou san)

Pileus 23–75 mm diam., at first plane to slightly depressed in the centre, infundibuliform when mature, surface dry, smooth, or finely felty, slightly hygrophanous, light orange (5A4) to brownish yellow (5C8), centre darker, margin slightly involute, undulate, always much paler context orange white (5A2). Lamellae decurrent to deeply decurrent, crowded, white (5A1) to orange white (5A2), concolorous, even, unequal, sometimes furcate at the margin of the pileus. Stipe (41)64–99 $\times$ 6–8 mm, central, subcylindrical to cylindrical, hollow, surface smooth, concolorous with the pileus, the base usually slightly coarser and covered with white tomentum. Context thin, and thinner towards the margin, fleshy, odour indistinct.

Basidiospores [50/3/3] (6.4–)6.8–7.8(–8.2) $\times$ (3.6–)3.9–4.6(–5.2) μm , $Q = (1.42–)1.58–1.84(–1.99)$, $Q_m = 1.71 (\pm 0.13)$, lacrymoid, rarely ellipsoid, smooth, thin-walled, hyaline, nonamyloid, guttulate. Basidia 31–43 $\times$ 6–8 μm , clavate, hyaline, two- or four-spored, sterigmata up to 6 μm long. Cheilocystidia and pleurocystidia

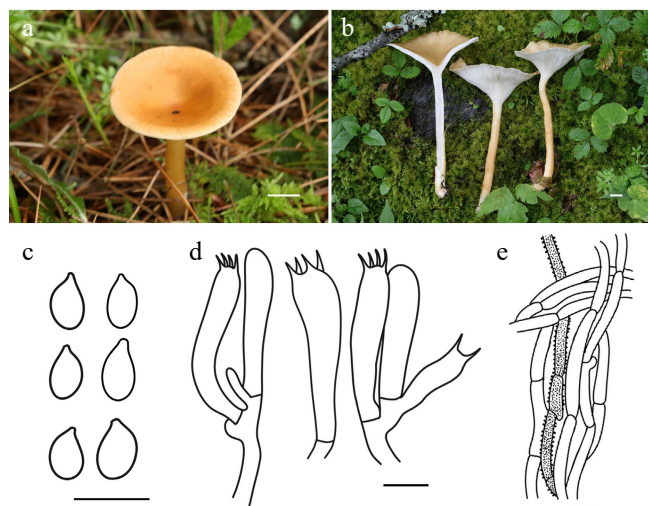


Fig. 21 *Infundibulicybe jilongensis* (a, b HMAS 259387). (a) Basidioma; (b) Basidiomata; (c) Basidiospores; (d) Basidia and Basidioles; (e) Pileipellis. Scale bars: (a, b) = 1 cm; (c–e) = 10 μ m.

not observed. Lamella trama subregular, hyphae 3–8 μ m diam., cylindrical, thin-walled, hyaline. Pileipellis is a cutis composed of subparallel, incrustated with abundant yellowish brown grainy epiparietal pigment, composed of thin- to slightly thick-walled (up to 0.7 μ m), cylindrical hyphae 4–9 μ m diam. Stipitipellis is a cutis composed of slightly thick-walled (0.5–1 μ m), cylindrical hyphae 4–7 μ m diam. Clamp-connections present.

Known distribution — Solitary, scattered on soil, in bush or deciduous coniferous forest, summer to fall. So far found only in China.

Material examined — CHINA, Xizang, Shigatse, Yadong County, Xiayadong Township, 27°25'17"N, 88°56'32"E, 3,024 m asl, growing on humus-rich ground within coniferous forests, 26 July 2022, D. Phurbu, ZRL20220109 (HMAS 259387. GenBank no.: ITS PP968407; LSU PP941771); *ibid.*, ZRL20220212 (HMAS 259388. GenBank no.: ITS PP968408; LSU PP941772); Dingjie County, Chentang Township, Jiuyan hot spring, 27°55'15"N, 87°21'37"E, 3,060 m asl, growing on mosses within mixed coniferous and broad-leaved forests, 29 July. 2022, M.Q. He, B. Cao, & J.X. Li, ZRL20220401 (HMAS 259389. GenBank no.: ITS PP968409; LSU PP941773).

Notes — *Infundibulicybe jilongensis* was originally collected by K. Wang, T.Z. Wei, and P. Hong from the litter layer or decaying branches in coniferous forests dominated by *Pinus* on the Qinghai–Xizang Plateau^[61]. Our phylogenetic analyses showed that the present collection clustered with *I. jilongensis* with 100% ML and 1.00 PP bootstrap support (Fig. 23). Macromorphologically, our specimens agree well with the original description of *I. jilongensis*. To further evaluate morphological variation, we measured 50 basidiospores from two basidiomata of the holotype specimen (HMAS 282369) following Largent^[29]. The holotype spores measured 5.8–6.4 $\times$ 4.0–4.7 μ m and ranged from subglobose to tear-shaped. In contrast, spores of our collection were distinctly longer, measuring 6.8–7.8 $\times$ 3.9–4.6 μ m, and were nearly uniformly tear-shaped. In addition, the basidia of our material were longer (31–43 $\times$ 6–8 μ m) compared with those of the type (22–28 $\times$ 6.0–7.2 μ m). In the field, the basidiomata of our collection also appeared darker, with a yellowish-brown pileus and stipe. These observations expand our understanding of morphological variability within *I. jilongensis*.

Infundibulicybe nanorobusta R.L. Zhao & X.X. Han, sp. nov. Figs 22 and 23

Chinese Name: 矮粗漏斗伞 (ai cu lou dou san)

Fungal Names: FN 573702; Facesoffungi number: FoF 20057

Etymology — *nanorobusta* (Latin), composed of 'nana' (dwarf, small) and 'robusta' (robust), referring to the characteristically small and stout basidiomata of the new species.

Diagnosis — differs by its small pileus with an involute margin, a short but robust stipe, basidia with two- or four-spored, and distinct DNA sequences.

Holotype — CHINA, Qinghai, Qilian County, Binggou Linhai, 38°7'8"N, 100°11'31"E, 3,160 m asl, growing on mosses within mixed coniferous and broad-leaved forests, 15 July 2023, R.L. Zhao, M.Y. Zhu, & M.Q. He, ZRL20230692 (HMAS 259843 holotype; AF9571 isotype, GenBank no.: ITS PZ494066; LSU PZ494069).

Pileus 15–34 mm diam., plano-concave when young, becoming infundibuliform when mature, centre depressed with age, margin involute, smooth or finely felty, slightly hygrophanous, nonstriate, fleshy, greyish orange (5B5) to golden brown (5D7), concolorous or slightly darker at the centre, occasionally split when mature. Lamellae decurrent to deeply decurrent, distant, white (5A1) to orange white (5A2), concolorous, even, sometimes furcate at the margin of the pileus. Stipe 21–51 $\times$ 5–11 mm, central, cylindrical, tough, finely yellowish brown-toned fibrillose longitudinally, greyish orange (5B3) to yellowish brown (5D8), sometimes twisted with a broadened base, concolorous, base with some white tomentum. Context slightly thick, white (5A1), fleshy, odour indistinct.

Basidiospores [50/2/2] (5.0–)6.3–8.0(–8.9) $\times$ (3.0–)3.7–4.9(–5.1) μ m, $Q = (1.40–)1.54–1.80(–1.95)$, $Q_m = 1.67 (\pm 0.13)$, narrowly ellipsoid to oblong, lacrymoid, smooth, colourless, hyaline, thin-walled. Basidia (16.6)18.4–22.5(24.4) $\times$ (4.7)5.4–7.0(7.9) μ m, clavate, hyaline, colourless, two- or four-spored, sterigmata up to 4 μ m long. Basidioles (16.4)18.4–24.2(27.5) $\times$ (4.9)5.1–6.2(6.8) μ m, colourless, hyaline, clavate. Cheilocystidia and pleurocystidia not observed. Lamella trama subregular, hyphae 2–5 μ m diam., cylindrical, thin-walled, colourless, hyaline. Pileipellis is a cutis composed of subparallel, incrustated with abundant greyish orange grainy epiparietal pigment, composed of thin- to slightly thick-walled (up to 0.4 μ m), cylindrical hyphae 3.5–6.6 μ m diam. Clamp-connections present.

Known distribution — Scattered or in pairs on humus-rich ground in mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

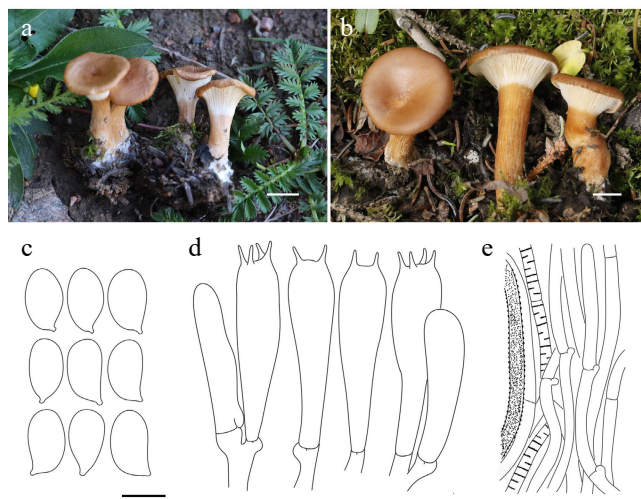


Fig. 22 *Infundibulicybe nanorobusta* (a ZRL20230632; b ZRL20230692 holotype). (a, b) Basidiomata; (c) Basidiospores; (d) Basidia and Basidioles; (e) Pileipellis. Scale bars: (a, b) = 1 cm; (c–e) = 5 μ m.

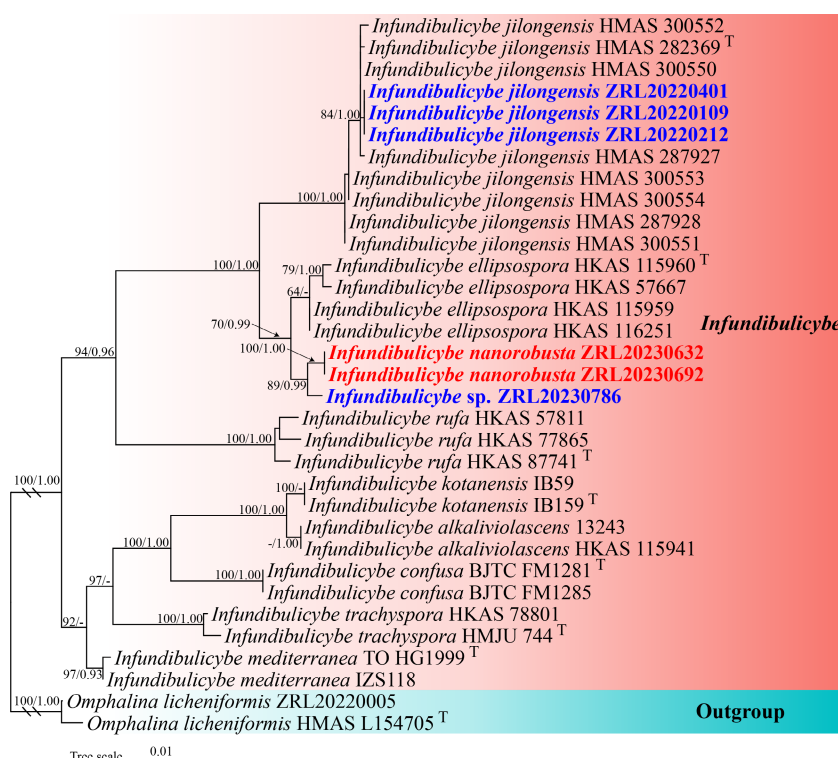


Fig. 23 Molecular phylogenetic analyses of *Infundibulicybe* species by the maximum likelihood (ML) method based on combined ITS–LSU sequences, rooted with *Omphalina licheniformis*. Maximum likelihood bootstrap support values (ML) $\geq 60\%$ and Bayesian posterior probabilities (PP) ≥ 0.90 are shown around nodes as ML/PP. 'T' refers to the type specimen. Sequences newly generated in this study are indicated in bold. New species described herein are shown in red, whereas other specimens newly collected in this study are shown in blue.

Material examined — CHINA, Qinghai, Qilian County, Binggou Linhai, 38°7'8" N, 100°11'31" E, 3,160 m asl, growing on mosses within mixed coniferous and broad-leaved forests, 15 July 2023, R.L. Zhao, M.Y. Zhu, & M.Q. He, ZRL20230632 (HMAS 259842, GenBank no.: ITS PZ494065; LSU PZ494068).

Notes — *Infundibulicybe nanorobusta* is characterized by its small, robust, and infundibuliform basidiomata, with a small and fleshy pileus and a short but slightly thick stipe. Microscopic features include narrowly ellipsoid to oblong basidiospores and basidia that are two- or four-spored. In the phylogenetic tree, *I. ellipsospora*, originally described from the Qinghai–Xizang Plateau, forms a sister clade with *I. nanorobusta*. Besides the macro differences in the small (15–34 mm vs. 35–60 mm) and robust basidiomata (21–51 × 5–11 mm vs. 55–80 × 5–7 mm), *I. nanorobusta* also has shorter basidia (18.4–22.5 μm vs. 26–40 μm) that are two- or four-spored^[153]. Our phylogenetic analyses are consistent with He & Yang (2023), showing that *I. ellipsospora* can be divided into two subclades based on its geographic distribution in Yunnan Province (HKAS 57667 and HKAS 115960) and Tibet (HKAS 115959 and HKAS 116251).

Omphalotaceae Bresinsky

Index Fungorum number: IF 81085

Type genus — *Omphalotus* Fayod

Gymnopus (Pers.) Gray

Index Fungorum number: IF 17703

Type species — *Gymnopus fusipes* (Bull.) Gray

Notes — *Gymnopus* (Pers.) Gray belongs to Omphalotaceae and is typified by *G. fusipes*, with approximately 300 species described worldwide^[154,155]. More than 79 species have been reported from China^[27,64,93,154–161]. The genus possesses notable ecological and economic importance^[162,163]. Species of *Gymnopus* are generally characterized by collybioid basidiomata, rarely tricholomatoid or

marasmoid, and a white spore print. Basidiospores are ellipsoid to short-oblong, occasionally subglobose, globose, or lacrymoid. Cheilocystidia are usually present and variable in shape. The pileipellis consists of a cutis or ixocutis composed of radially arranged cylindrical hyphae, sometimes appearing interwoven and resembling a trichoderm or ixotrichoderm with irregularly coralloid terminal elements^[164].

Members of the genus are predominantly saprotrophic, rarely parasitic, occurring in humus or on wood, and occasionally on dead roots or, less frequently, on living herbaceous or woody plants^[164,165]. *Gymnopus* has been extensively studied worldwide, with research originating in Europe and subsequently expanding to other regions, particularly North America^[162,164,166–169]. Most species have been documented from North America, Europe, and Asia, whereas comparatively few taxa are known from Oceania and Africa^[163,170]. Based on recent comprehensive phylogenetic studies, *Gymnopus* was divided into four sections, viz. sect. *Androsacei*, sect. *Gymnopus*, sect. *Levipedes*, and sect. *Impudicae*^[164,171]. In this study, four new species are described based on morphological characters and phylogenetic analyses of ITS and LSU sequences.

Gymnopus batangensis R.L. Zhao & X.X. Han, sp. nov. Figs 24 and 28

Chinese Name: 巴塘裸脚伞 (ba tang luo jiao san)

Fungal Names: FN 573703; Facesoffungi number: FoF 20058

Etymology — refers to the type locality, Batang County.

Diagnosis — distinguished by its brownish pileus with a slightly sulcate towards margin, a brownish stipe with pseudorrhiza, narrowly ellipsoid to oblong basidiospores (7.6–9.2 × 4.2–5.1 μm), and basidia with two- or four-spored.

Holotype — CHINA, Sichuan, Batang County, Zhubalong Nature Reserve, 29°39'36" N, 99°5'20" E, 4,102 m asl, growing on mosses within coniferous forests, 19 August 2020, X.Y. Zhu & M.Z. Zhang,

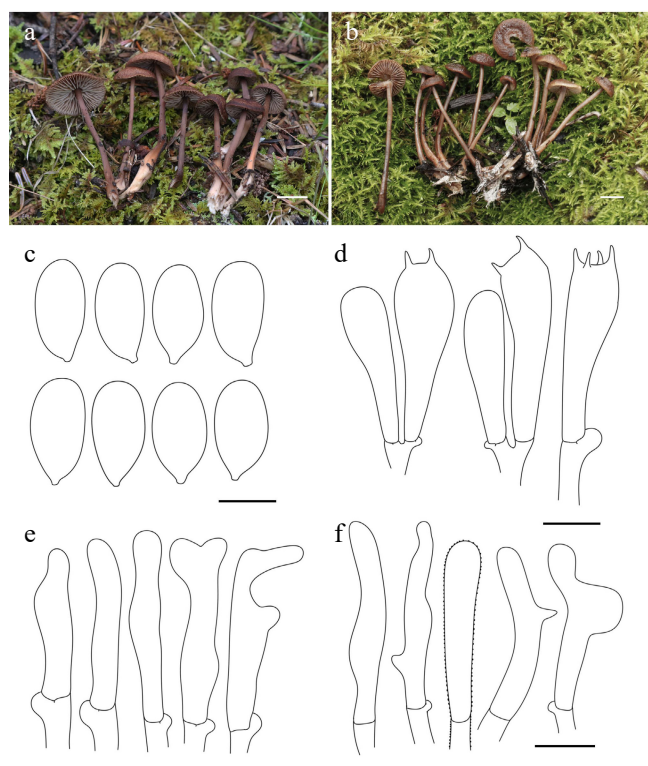


Fig. 24 *Gymnopus batangensis* (a, ZRL20201385 holotype, b ZRL20211060). (a, b) Basidiomata; (c) Basidiospores; (d) Basidia and Basidioles; (e) Cheilocystidia; (f) Pileipellis elements. Scale bars: (a, b) = 1 cm; (c) = 5 µm; (d-f) = 10 µm.

ZRL20201385 (HMAS 259833 holotype; AF9560 isotype, GenBank no.: ITS PZ492291; LSU PZ492304).

Pileus 7–26 mm diam., hemispherical when young, then convex to plano-convex, often slightly depressed or umbilicate at the centre, slightly sulcate towards margin, sometimes applanate when mature, margin deflexed, sometimes becoming reflexed margin when mature, hygrophanous, rugose, smooth, brownish orange (6C3) to brown (6E8), occasionally with a slightly paler margin. Lamellae moderately close, narrowly adnate to adnexed, orange white (5A2) to brownish orange (5C5), concolorous, even, unequal. Stipe 39–77 × 1–3 mm, central, cylindrical, sometimes twisted with a broadened base, or tapering towards the base forming a reduced pseudorrhiza, smooth or grooved lengthwise, hollow, brownish orange (6C5) to brown (6E7), becoming white at the pseudorrhiza. Context thin, and thinner towards the margin, odour indistinct.

Basidiospores [50/3/2] (5.9–)7.6–9.2(–10.3) × (3.1–)4.2–5.1(–5.6) µm, $Q = (1.50)–1.67–1.98(–2.38)$, $Qm = 1.83 (\pm 0.15)$, narrowly ellipsoid to oblong, subcylindrical, rarely lacrymoid, smooth. Basidia (18.8)21.2–30.5(39.7) × (6.5)7.5–9.0(10.0) µm, clavate to cylindrical, smooth, hyaline, two- or four-spored. Basidioles (15.4)20.3–26.1(27.5) × (3.8)4.9–7.4(8.1) µm, clavate to cylindrical. Cheilocystidia abundant, narrowly clavate to cylindrical, narrowly utriform, narrowly lageniform, (21.4)25.8–36.4(41.9) × (5.7)6.7–9.5(10.9) µm. Pleurocystidia not observed. Pileipellis is a cutis, sometimes intricate trichoderm at the centre, hyaline, cylindrical, 3.9–9.2 µm wide, thin- to slightly thick-walled. Clamp-connections present.

Known distribution — Scattered or gregarious on mosses within coniferous or broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Sichuan, Batang County, Zhubalong Nature Reserve, 29°39'36" N, 99°5'20" E, 4,102 m asl, growing on mosses within coniferous forests, 19 August 2020, M.Q. He & M.Q.

Wang, ZRL20201473 (HMAS 259834, GenBank no.: ITS PZ492294; LSU PZ492307). Xizang, Linzhi, Alpine Forest Ecosystem National Field Scientific Observation and Research Station, 29°39'2" N, 94°42'53" E, 3,880 m asl, growing on mosses in coniferous forests, 27 July 2021, X.Y. Zhu & B. Cao, ZRL20211060 (HMAS 259835, GenBank no.: ITS PZ492292; LSU PZ492306); *ibid.*, ZRL20211075 (HMAS 259836, GenBank no.: ITS PZ492293; LSU PZ492308); Chayu County, along the route of G219, 28°39'48" N, 97°27'44" E, 3,524 m asl, growing on mosses in broad-leaved forests, 6 August 2023, D. Phurba & X.H. Yu, ZRL20231047 (HMAS 259837, GenBank no.: ITS PZ492290; LSU PZ492305).

Notes — *Gymnopus batangensis* is characterized by a brownish orange to brown pileus that is slightly sulcate towards the margin, a brownish orange to brown stipe with pseudorrhiza, and the presence of cheilocystidia. In the field, its hygrophanous, sulcate-striate, brownish pileus and similarly coloured stipe may recall *G. variicolor*. However, *G. variicolor* differs from *G. batangensis* by having smaller basidiospores (6.7 × 3.8 µm) and exclusively four-spored basidia^[172], and the ITS sequences of their type specimens differ by more than 7% (BRNM 781307). Phylogenetically, the new species is related to *G. loiseleurietorum*, originally described from the alpine zone of Austria. However, it is distinct from the new species in morphology, characterized by a short stipe (20–30 mm), the absence of cheilocystidia, and hyphae that turn green in KOH^[173,174].

***Gymnopus ochraceoflavus* R.L. Zhao & X.X. Han, sp. nov. Figs 25 and 28**

Chinese Name: 赭黄裸脚伞 (zhe huang luo jiao san)

Fungal Names: FN 573704; Facesoffungi number: FoF 20059

Etymology — *ochraceoflavus* (Latin) refers to the ochre colour of the pileus.

Diagnosis — distinguished by its ochre-toned pileus, yellowish white to greyish yellow lamellae, stipe with whitish flocculose, and small basidiospores.

Holotype — CHINA, Qinghai, Qilian County, Binggou Linhai, 38°7'8" N, 100°11'31" E, 3,160 m asl, growing on mosses within mixed coniferous and broad-leaved forests, 15 July 2023, R.L. Zhao,

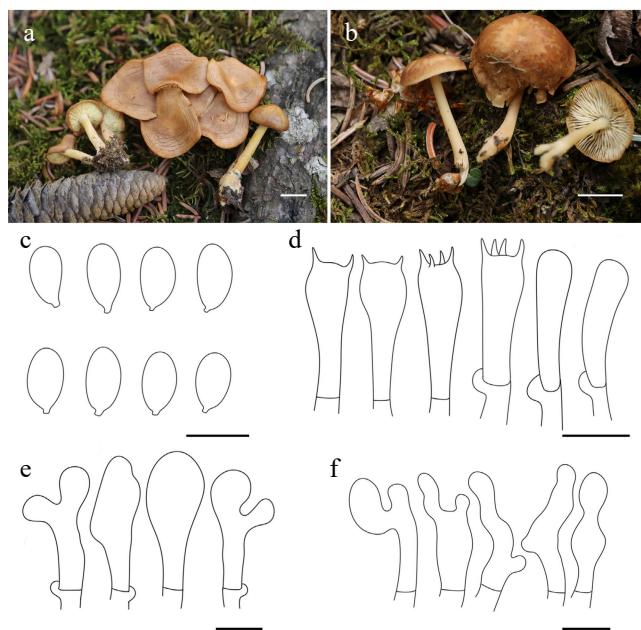


Fig. 25 *Gymnopus ochraceoflavus* (a, ZRL20230630 holotype, b ZRL20230683). (a, b) Basidiomata; (c) Basidiospores; (d) Basidia and Basidioles; (e) Cheilocystidia; (f) Pileipellis elements. Scale bars: (a, b) = 1 cm; (c) = 5 µm; (d-f) = 10 µm.

M.Y. Zhu, & M.Q. He, ZRL20230630 (HMAS 259831 holotype; AF9570 isotype, GenBank no.: ITS PZ492288; LSU PZ492309).

Pileus 13–29 mm diam., convex to plano-convex, becoming applanate when mature, with almost indistinct or rather distinct broad obtuse umbo at the centre, margin sometimes involute, sometimes becoming reflexed margin when mature, hygrophanous, usually nonstriate, smooth, brownish orange (6C5) to brown (6D8), sometimes with a slightly darker centre. Lamellae moderately close, adnate to adnexed, rarely emarginate and attached with a tooth, yellowish white (4A2) to greyish yellow (4B3), concolorous, even, unequal. Stipe 20–39 × 2–4 mm, central, cylindrical, sometimes slightly broadened at the base, pale orange (5A3) to greyish orange (5B6), with whitish flocculose. Context thin, and thinner towards the margin, odour indistinct.

Basidiospores [50/3/2] (4.3–)4.8–5.7(–6.4) × (2.9–)3.1–3.5(–3.8) µm, $Q = (1.36–)1.44–1.74(–1.96)$, $Qm = 1.59 (\pm 0.15)$, narrowly ellipsoid to oblong, rarely broadly ellipsoid or subcylindrical, hyaline, smooth. Basidia (14.8)16.4–20.3(21.7) × (4.9)5.8–7.2(8.1) µm, clavate to cylindrical, smooth, hyaline, two- or four-spored. Basidioles (10.8)14.2–17.3(18.6) × (3.9)4.5–6.1(7.4) µm, clavate to cylindrical. Cheilocystidia abundant, irregularly clavate to cylindrical, (14.3)18.4–26.8(31.4) × (4.7)4.9–7.1(8.5) µm, sometimes apically diverticulate, diverticulate or furcated, rarely ramose. Pleurocystidia not observed. Pileipellis is a cutis, hyaline, cylindrical, 2.9–6.7 µm wide, with branched, thin-walled. Clamp-connections present.

Known distribution — Scattered on mosses within mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Qinghai, Qilian County, Binggou Linhai, 38°7'8" N, 100°11'31" E, 3,160 m asl, growing on mosses within mixed coniferous and broad-leaved forests, 15 July 2023, R.L. Zhao, M.Y. Zhu, & M.Q. He, ZRL20230683 (HMAS 259832, GenBank no.: ITS PZ492289; LSU PZ492310).

Notes — *Gymnopus ochraceoflavus* is characterized by a hygrophanous, usually nonstriate, ochre-toned pileus, yellowish white to greyish yellow lamellae, stipe with whitish flocculose, and small basidiospores. In the molecular phylogenetic analysis, *G. ochraceoflavus* is related to *G. junquilleus*, *G. alpinus*, and *G. subsulphureus*. However, *G. junquilleus* differs by a brighter pileus, slightly longer basidiospores (5.2–6.4 µm), and longer basidia (20–26 µm)^[162]. *Gymnopus alpinus* is distinguished by a dark red-brown pileus, white lamellae, larger basidiospores (6.0–7.5 µm), and wider cheilocystidia (7–12 µm)^[175]. *Gymnopus subsulphureus* differs by a sulfur-yellow pileus with a depressed centre and longer basidiospores (6 µm)^[176]. *Gymnopus ochraceoflavus* has only been recorded from alpine regions above 3,000 m on the Qinghai–Xizang Plateau, whereas its phylogenetically close relatives mainly occur in low-altitude areas of Europe and North America.

Gymnopus planoconvexus R.L. Zhao & X.X. Han, sp. nov. Figs 26 and 28

Chinese Name: 平凸裸脚伞 (ping tu luo jiao san)

Fungal Names: FN 573705; Facesoffungi number: FoF 20060

Etymology — *planoconvexus* (Latin) refers to the plano-convex pileus of this species.

Diagnosis — similar to *G. yunnanensis*, but *G. planoconvexus* differs by slightly shorter basidiospores, longer basidia with two- or four-spored and distinct DNA sequences.

Holotype — CHINA, Xizang, Linzhi, Bayi District, Lulang Town, along the route of G318, 29°50'37" N, 94°45'23" E, 2,976 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests, 14 August 2023, M.Z. Zhang & L.H. Liu, ZRL20235063 (HMAS 259829 holotype; AF9579 isotype, GenBank no.: ITS PZ492296; LSU PZ492312).

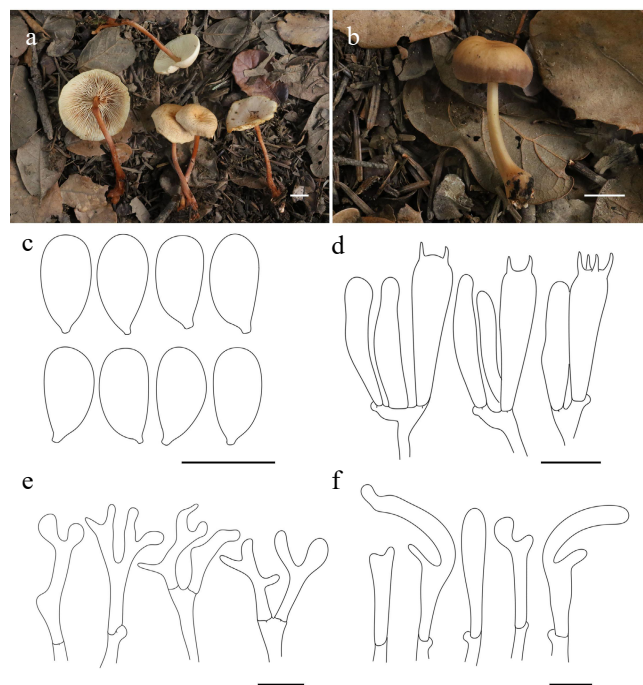


Fig. 26 *Gymnopus planoconvexus* (a, ZRL20235063 holotype, b ZRL20235065). (a) Basidiomata; (b) Basidioma; (c) Basidiospores; (d) Basidia and Basidioles; (e) Cheilocystidia; (f) Pileipellis elements. Scale bars: (a, b) = 1 cm; (c) = 5 µm; (d–f) = 10 µm.

Pileus 19–43 mm diam., hemispherical, convex to plano-convex, sometimes applanate, usually with a depressed centre, margin usually inflexed, hygrophanous, nonstriate, smooth, pale orange (5A3) to brownish yellow (5C8), sometimes with a darker margin, brownish yellow (5C7) to yellowish brown (5E8). Lamellae moderately close to close, narrowly adnate to adnexed, yellowish white (4A2) to pale yellow (4A3), concolorous, even, unequal. Stipe 38–69 × 2–4 mm, central, cylindrical, usually slightly broadened at the base, orange white (6A2) to brownish orange (7C8), with whitish flocculose. Context thin, and thinner towards the margin, odour indistinct.

Basidiospores [50/3/2] (4.6–)5.1–5.8(–6.2) × (2.7–)2.9–3.3(–3.7) µm, $Q = (1.37–)1.60–1.87(–2.11)$, $Qm = 1.73 (\pm 0.13)$, oblong to subcylindrical, or lacrymoid, hyaline, smooth. Basidia (19.3)21.8–25.6(26.7) × (5.4)5.6–6.6(7.0) µm, clavate to cylindrical, smooth, hyaline, two- or four-spored. Basidioles (16.6)17.9–22.0(23.6) × (3.1)3.8–5.1(6.3) µm, clavate to cylindrical. Cheilocystidia irregularly clavate to cylindrical, (17.1)19.3–23.6(26.3) × (3.8)4.5–5.9(7.5) µm, sometimes with an umbo at apex, diverticulate or furcated. Pleurocystidia and caulocystidia not observed. Pileipellis is a cutis, sometimes intricate trichoderm at the centre, hyaline, cylindrical, 4.7–12.1 µm wide, thin-walled. Clamp-connections present.

Known distribution — Solitary or scattered humus-rich ground within mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Xizang, Linzhi, Bayi District, Lulang Town, along the route of G318, 29°50'37" N, 94°45'23" E, 2,976 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests, 14 August 2023, M.Z. Zhang & L.H. Liu, ZRL20235065 (HMAS 259830, GenBank no.: ITS PZ492297; LSU PZ492313).

Notes — *Gymnopus planoconvexus* is characterized by a hygrophanous, nonstriate, often plano-convex pileus that ranges from pale orange to brownish yellow, oblong to subcylindrical basidiospores measuring 5.1–5.8 × 2.9–3.3 µm, and basidia bearing two- or four-spored. Phylogenetically, *G. planoconvexus* is related to *G.*

yunnanensis, *G. aurantiofuscus*, *G. ailaoensis*, *G. viridiscus*, and *G. viridocephalus*. All six species are originally distributed in China; *G. viridocephalus* occurs in eastern China, whereas the others originate from southwestern China. Notably, although *G. yunnanensis* was initially described from Yunnan, this study reports its presence in Xizang for the first time (ZRL20220270). *Gymnopus yunnanensis* differs by a slightly paler pileus, longer basidiospores (5–6.5 µm), and shorter basidia (16–22 µm) and has four-spored^[158]. *Gymnopus aurantiofuscus* is distinguished by a darker pileus, slightly larger basidiospores (av. 5.9 × 3.4 µm) and four-spored basidia^[177]. *Gymnopus ailaoensis* differs in having a darker pileus, shorter stipe (11.6–38.6 mm), and a preference for growing on dead wood^[160]. *Gymnopus viridiscus* is characterized by small basidiomata (17–19 mm) and a greyish green pileus^[161]. *Gymnopus viridocephalus* differs by translucently striate pileus with a yellowish green tint, longer basidiospores (5.6–7.5 µm), and four-spored basidia^[177].

Gymnopus sinopubescens R.L. Zhao & X.X. Han, sp. nov. Figs 27 and 28

Chinese Name: 中华绒柄裸脚伞 (zhong hua rong bing luo jiao san)

Fungal Names: FN 573706; Facesoffungi number: FoF 20061

Etymology — *sinopubescens* (Latin), composed of 'sino-' (Sīnae, 'Chinese') and 'pubescens', referring to the entirely pubescent stipe of this new species from China.

Diagnosis — similar to *G. fuscus*, but *G. fuscus* differs by longer basidiospores, longer basidia, and narrower cheilocystidia.

Holotype — CHINA, Sichuan, Xiangcheng County, Fozhu Gorge, 29°4'49" N, 99°54'11" E, 3,000 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests dominated by *Abies*, 15 August 2019, R.L. Zhao, B. Cao, & Z.L. Ling, ZRL20190949 (HMAS 259825 holotype; AF9555 isotype, GenBank no.: ITS PZ492303; LSU PZ492317).

Pileus 9–40 mm diam., hemispherical to plano-hemispherical when young, then obtusely conical to convex, applanate when

mature, sometimes slightly depressed at the centre, margin entire to slightly uneven, hygrophanous, smooth, sometimes rugose, reddish brown (8D4) to dark brown (8F8) at the centre, occasionally slightly sulcate at the margin, inflexed, becoming straight when mature, gradually fading reddish white (8A2) to reddish golden (6C7) towards the margin. Lamellae close, adnexed to free, white (5A1) to orange grey (5A2), concolorous, uneven, unequal. Stipe 18–53 × 2–4 mm, central, cylindrical, sometimes twisted with a broadened base, or tapering towards the base forming a reduced pseudorrhiza, usually covered with pubescence entirely, or sometimes pruinose, tomentose at the base, reddish grey (8B2) to reddish brown (8E8), becoming white at the pseudorrhiza. Context thin, and thinner towards the margin, odour indistinct.

Basidiospores [50/3/3] (4.2–)4.7–5.5(–6.1) × (2.6–)2.8–3.6(–4.2) µm, $Q = (1.30–)1.45–1.74(–1.91)$, $Qm = 1.59 (\pm 0.14)$, narrowly ellipsoid to oblong, rarely lacrymoid or subglobose, smooth. Basidia (12.7)13.8–17.8(20.0) × (4.6)5.3–6.4(7.0) µm, clavate to cylindrical, smooth, hyaline, two-spored. Basidioles (13.5)14.6–18.7(23.6) × (4.5)5.0–5.9(6.3) µm, clavate to cylindrical. Cheilocystidia abundant, irregularly clavate to cylindrical, narrowly utriform, sometimes apically diverticulate, diverticulate or furcated, (14.5)17.3–24.2(26.7) × (3.7)4.2–5.5(6.2) µm. Pleurocystidia not observed. Pileipellis is a cutis, sometimes intricate trichoderm at the centre, hyaline, cylindrical, 2.4–5.8 µm wide, thin- to slightly thick-walled. Clamp-connections present.

Known distribution — Solitary or scattered on humus-rich ground within mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Sichuan, Xiangcheng County, Fozhu Gorge, 29°4'49" N, 99°54'11" E, 3,000 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests dominated by *Abies*, 15 August 2019, R.L. Zhao, B. Cao, & Z.L. Ling, ZRL20191131 (HMAS 259826, GenBank no.: ITS PZ492300; LSU PZ492318); Yajiang County, Gexigou Nature Reserve, Hekou Town, Xiadu Village, 29°57'24" N, 100°57'35" E, 3,241 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests dominated by *Quercus* and *Pinus*, 15 August 2020, M.Q. He, B. Cao, & J.X. Li, ZRL20200433 (HMAS 259827, GenBank no.: ITS PZ492301; LSU PZ492316); *ibid.*, X.X. Han & X.Y. Zhu, ZRL20200605 (HMAS 259828, GenBank no.: ITS PZ492302; LSU PZ492315).

Notes — The new species resembles *G. fuscus*, which was originally described from the Qinghai–Xizang Plateau (Qinghai Province). However, *G. fuscus* can be readily distinguished by its longer basidiospores (6.5–8.2 µm), longer basidia (21.9–26.8 µm), and narrower cheilocystidia (2.3–3.9 µm)^[177]. Phylogenetic analyses indicate that the new species belongs to *G.* sect. *Impudicae*, although the characteristic odour was not recorded in the field. *Gymnopus sinopubescens* is phylogenetically close to *G. subdensilamellatus*, *G. densilamellatus*, *G. polyphyllus*, *G. subpolyphyllus*, *G. epiphyllus*, and *G. sinopolyphyllus*. Nevertheless, *G. sinopubescens* differs from these species by its reddish brown to dark brown pileus, reddish grey to reddish brown stipe that is covered with pubescence entirely, and narrowly ellipsoid to oblong basidiospores measuring 4.7–5.5 × 2.8–3.6 µm^[178].

Phyllotopsidaceae Locq. ex Olariaga, Huhtinen, Læssøe, J.H. Petersen & K. Hansen

Index Fungorum number: IF 831374

Type genus — *Phyllotopsis* E.-J. Gilbert & Donk ex Singer

Tricholomopsis Singer

Index Fungorum number: IF 18680

Type species — *Tricholomopsis rutilans* (Schaeff.) Singer.

Notes — The genus *Tricholomopsis* Singer, established in 1939, is currently placed in the family Phyllotopsidaceae and comprises

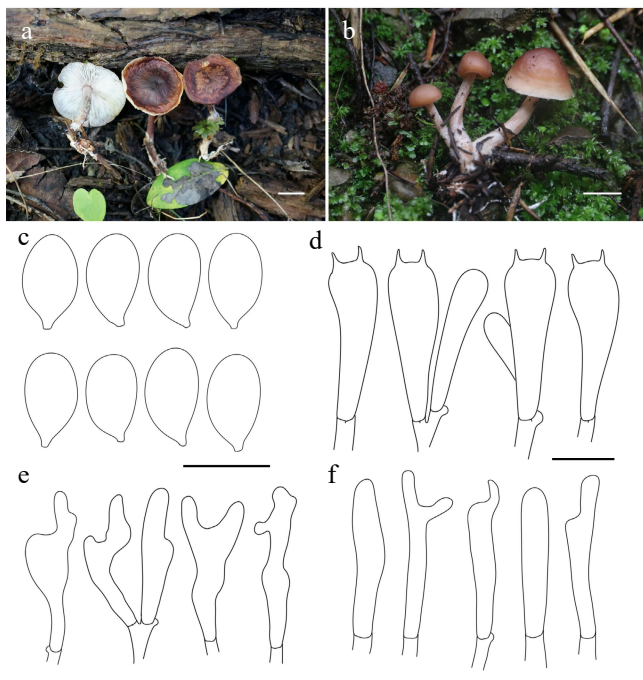


Fig. 27 *Gymnopus sinopubescens* (a, ZRL20190949 holotype, b ZRL20200605). (a, b) Basidiomata; (c) Basidiospores; (d) Basidia and Basidioles; (e) Cheilocystidia; (f) Pileipellis elements. Scale bars: (a, b) = 1 cm; (c) = 5 µm; (d–f) = 10 µm.

approximately 50 species with a probably nearly cosmopolitan distribution^[179,180]. Approximately 23 species have been confirmed in China based on morphological and molecular evidence^[93,181]. Species of *Tricholomopsis* are typically characterised by

tricholomoid, coloured basidiomata, usually yellow, with a glabrous to tomentose or fibrillose pileus, inamyloid basidiospores, conspicuous cheilocystidia, and clamp connections^[28,179,182]. Ecologically, members of the genus are saprotrophic, occurring solitary or

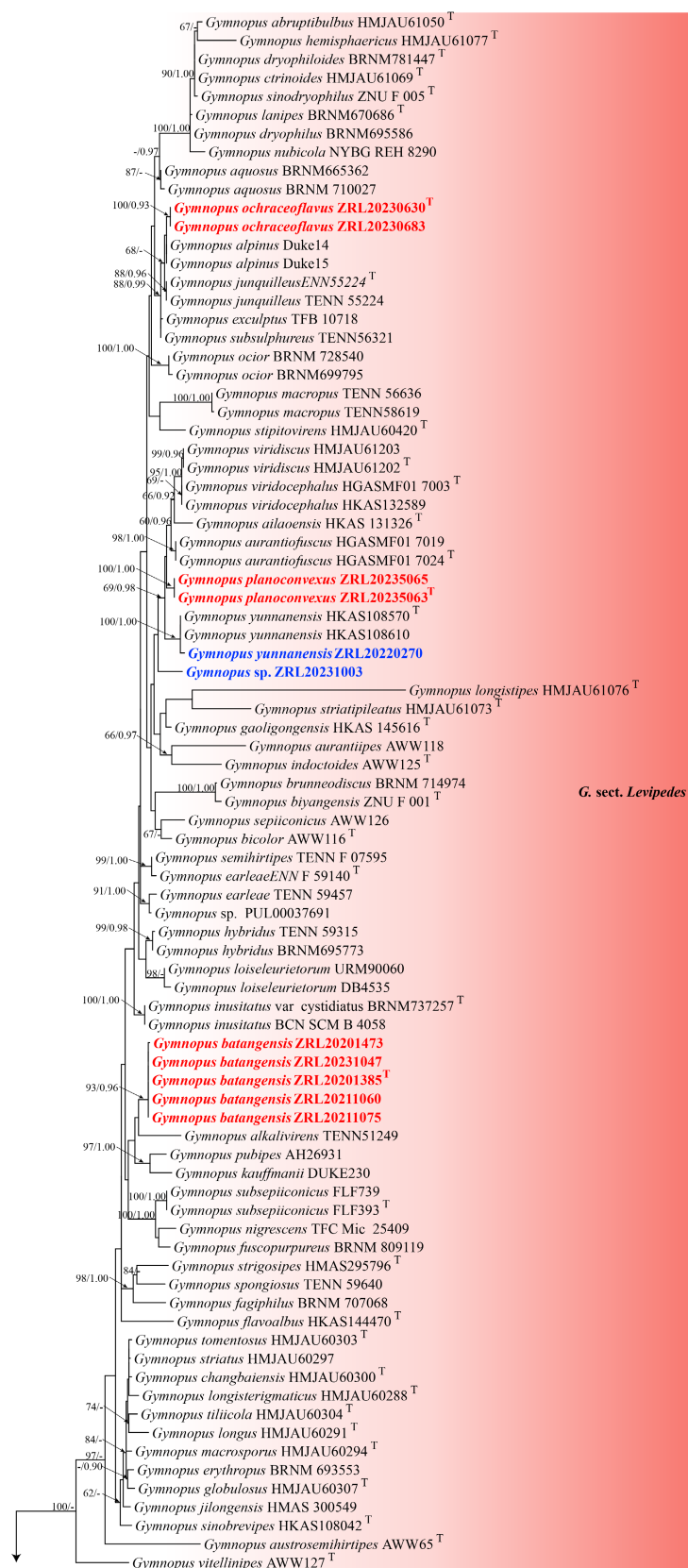


Fig. 28 to be continued



Fig. 28 Molecular phylogenetic analyses of *Gymnopus* species by the maximum likelihood (ML) method based on combined ITS–LSU sequences, rooted with *Marasmius medogensis*. Maximum likelihood bootstrap support values (ML) $\geq 60\%$ are shown around nodes as ML. Sequences newly generated in this study are indicated in bold. New species described herein are shown in red, whereas other specimens newly collected in this study are shown in blue. 'T' refers to the type specimen.

scattered on decaying wood of coniferous or broad-leaved forests, or on bamboo^[179,183]. The genus is currently divided into five sections, viz. sect. *Bambusinae*, sect. *Decoramentum*, sect. *Glabrae*, sect. *Lividae*, and sect. *Tricholomopsis*^[179]. To date, sect. *Decoramentum* comprises three reported species, namely *Tricholomopsis decora*, *T. floccosa*, and *T. badinensis*. In the present study, we describe a new species belonging to sect. *Decoramentum*.

Tricholomopsis dambaensis R.L. Zhao, B. Cao, & X.X. Han, sp. nov. Figs 29 and 30

Chinese Name: 打坝拟口蘑 (da ba ni kou mo)

Fungal Names: FN 573707; Facesoffungi number: FoF 20062

Etymology — *dambaensis* (Latin) refers to the type locality Damba, an officially standardized geographical name in the Zangnan region of Xizang Autonomous Region, China.

Diagnosis — differs from the other species of *T.* sect. *Decoramentum* by its light yellow to olive brown pileus with blond to olive brown scales, and ellipsoid to narrowly ellipsoid basidiospores ($7.4\text{--}8.5 \times 5.0\text{--}5.8 \mu\text{m}$).

Holotype — CHINA, Xizang, Linzhi, Chayu County, near Damba, $28^{\circ}36'46''\text{N}$, $98^{\circ}5'22''\text{E}$, 4,110 m asl, growing on rotten wood in mixed coniferous and broad-leaved forests, 21 July 2021, M.Z. Zhang & X.Y. Zhu, ZRL20210537 (HMAS 259918 holotype; AF9562 isotype, GenBank no.: ITS PZ499994; LSU PZ499985).

Basidioma is small to medium-sized. Pileus 42–93 mm diam., plano-convex, sometimes the margin is slightly involute, and nearly applanate with a slight central depression when mature; surface dry, light yellow (4A5) to olive brown (4E7), tomentose to finely scaly, dense at the centre and becoming scarce towards the margin, scales adpressed and slightly upturned when mature, blond (4C4) to olive brown (4E8). Lamellae moderately crowded with slightly decurrent teeth, sometimes emarginate, light yellow (4A5) to greyish yellow (4C7), sometimes the margin is darker, greyish yellow (4B4) to olive brown (4E7). Stipe 50–83 $\times$ 5–14 mm, central, hollow, cylindrical, often curved, greyish yellow (4B5) to dark brown (4C8), with greyish yellow (4C5) to olive brown (4E8) scales or fibrils.

Basidiospores $[80/3/2]$ $(7.0\text{--})7.4\text{--}8.5\text{--}(9.4) \times (4.7\text{--})5.0\text{--}5.8\text{--}(6.3) \mu\text{m}$, $Q = (1.32\text{--})1.38\text{--}1.57\text{--}(1.77)$, $Qm = 1.48 (\pm 0.10)$, ellipsoid to narrowly ellipsoid, colourless, hyaline, sometimes with one oil droplet, thin-walled, smooth, in-amyloid. Basidia $(21.6)29.1\text{--}38.6(45.3) \times (5.1)6.0\text{--}7.4(8.0) \mu\text{m}$, narrowly clavate to clavate, sterigmata 3.9–5.4 μm , two- or four-spored. Cheilocystidia $(32.4)37.8\text{--}54.1(68.0) \times (3.4)4.6\text{--}6.6(8.0) \mu\text{m}$, colourless, hyaline, thin-walled, varied in shape, narrowly clavate, clavate to sphaeropedunculate, sometimes obovoid or broadly ellipsoid. Pleurocystidia frequent, $(32.4)41.3\text{--}57.6(68.4) \times (7.9)13.1\text{--}18.5(20.3) \mu\text{m}$, cylindrical to narrowly clavate, colourless, hyaline, thin-walled. Pileipellis is a cutis with the transition to a trichoderm at regular intervals, composed of 3–7 μm wide, thin-walled, filamentous hyphae. Clamp-connections present.

Known distribution — Scattered or in pairs on rotten wood in mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Xizang, Linzhi, Chayu County, near Damba, $28^{\circ}36'46''\text{N}$, $98^{\circ}5'22''\text{E}$, 4,110 m asl, growing on rotten wood in mixed coniferous and broad-leaved forests, 21 July 2021, M.Q. He & Z.L. Ling, ZRL20210535 (HMAS 259917, GenBank no.: ITS PZ499993; LSU PZ499984).

Notes — *Tricholomopsis dambaensis* is characterized by a light yellow to olive brown pileus with blond to olive brown scales and slightly larger basidiospores ($7.4\text{--}8.5 \times 5.0\text{--}5.8 \mu\text{m}$). It has been reported as a member of the *T. decora* complex^[184]. Phylogenetically, *T. dambaensis* and *T. decora* are sister groups and share morphological similarities. However, *T. decora* can be distinguished

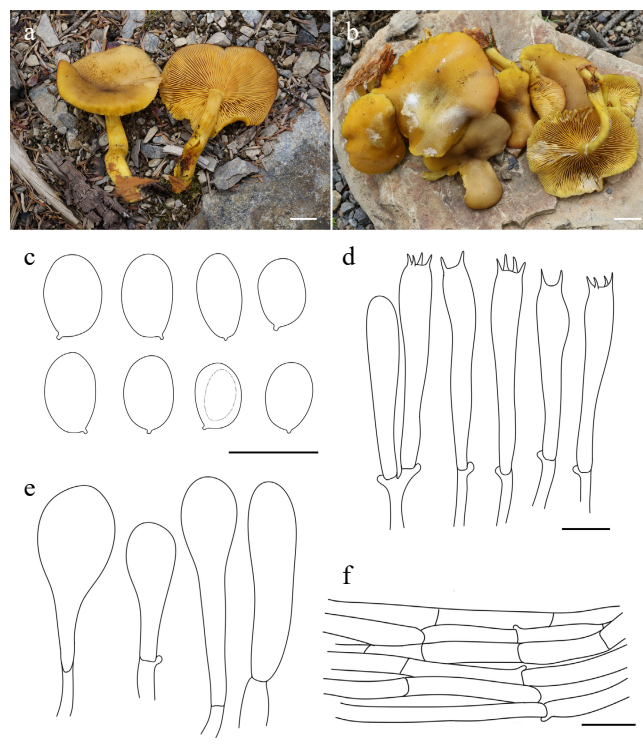


Fig. 29 *Tricholomopsis dambaensis* (a ZRL20210537 holotype; b ZRL20210535). (a, b) Basidiomata; (c) Basidiospores; (d) Basidia and Basidioles; (e) Cheilocystidia; (f) Pileipellis. Scale bars: (a, b) = 2 cm; (c–f) = 10 μm .

by its slightly brighter pileus and smaller basidiospores ($6\text{--}7.5 \times 4.7\text{--}5 \mu\text{m}$)^[185]. *Tricholomopsis floccosa* differs from *T. dambaensis* by possessing slightly more robust stipes ($45\text{--}60 \times 8\text{--}15 \text{ mm}$), darker pileus, smaller spores ($5.5\text{--}7.5 \times 4\text{--}5.5 \mu\text{m}$), and slightly shorter basidia ($23\text{--}30 \mu\text{m}$)^[179]. Additionally, *T. dambaensis* can be distinguished from *T. badinensis* by its slightly robust stipe ($50\text{--}83 \times 5\text{--}14 \text{ mm}$ vs. $50\text{--}70 \times 4\text{--}8 \text{ mm}$), shorter sterigmata ($3.9\text{--}5.4 \mu\text{m}$ vs. $5\text{--}7 \mu\text{m}$), and broader pleurocystidia ($13.1\text{--}18.5 \mu\text{m}$ vs. $6\text{--}7 \mu\text{m}$)^[183].

Melanoleucaceae Locq. ex Vizzini, Consiglio & P. Alvarado

Index Fungorum number: IF 851152

Type genus — *Melanoleuca* Pat.

Melanoleuca Pat.

Index Fungorum number: IF 18031

Type species — *Melanoleuca melaleuca* (Pers.) Murrill

Notes — *Melanoleuca* Pat. is a cosmopolitan genus with more than 410 legitimately described species (Index Fungorum, www.indexfungorum.org/names/Names.asp), of which approximately 80 taxa have been phylogenetically confirmed^[72,150,186–194]. In China, approximately 31 species have been recorded^[93]. Species are typically characterized by collybioid to tricholomatoid gymnocarpic basidiomata with indistinct brownish to greyish and convex to slightly depressed pileus^[150,186]. The pileipellis is a cutis to trichoderm, and basidiospores are hyaline, with amyloid ornamentation and a distinct suprahilar plage^[28]. Cheilocystidia are usually present, long and variable, including urticoid, septate, thin-walled forms or fusiform to lageniform, slightly thick-walled elements, sometimes with encrusting crystals at the apex; pleurocystidia, when present, resemble cheilocystidia, and clamp connections are absent^[150,186]. Molecular phylogenetic evidence indicates that the genus *Melanoleuca* belongs to Melanoleucaceae within suborder Pluteineae and represents a distinct monophyletic lineage closely related to *Giacomia* and other associated families^[150]. Species of

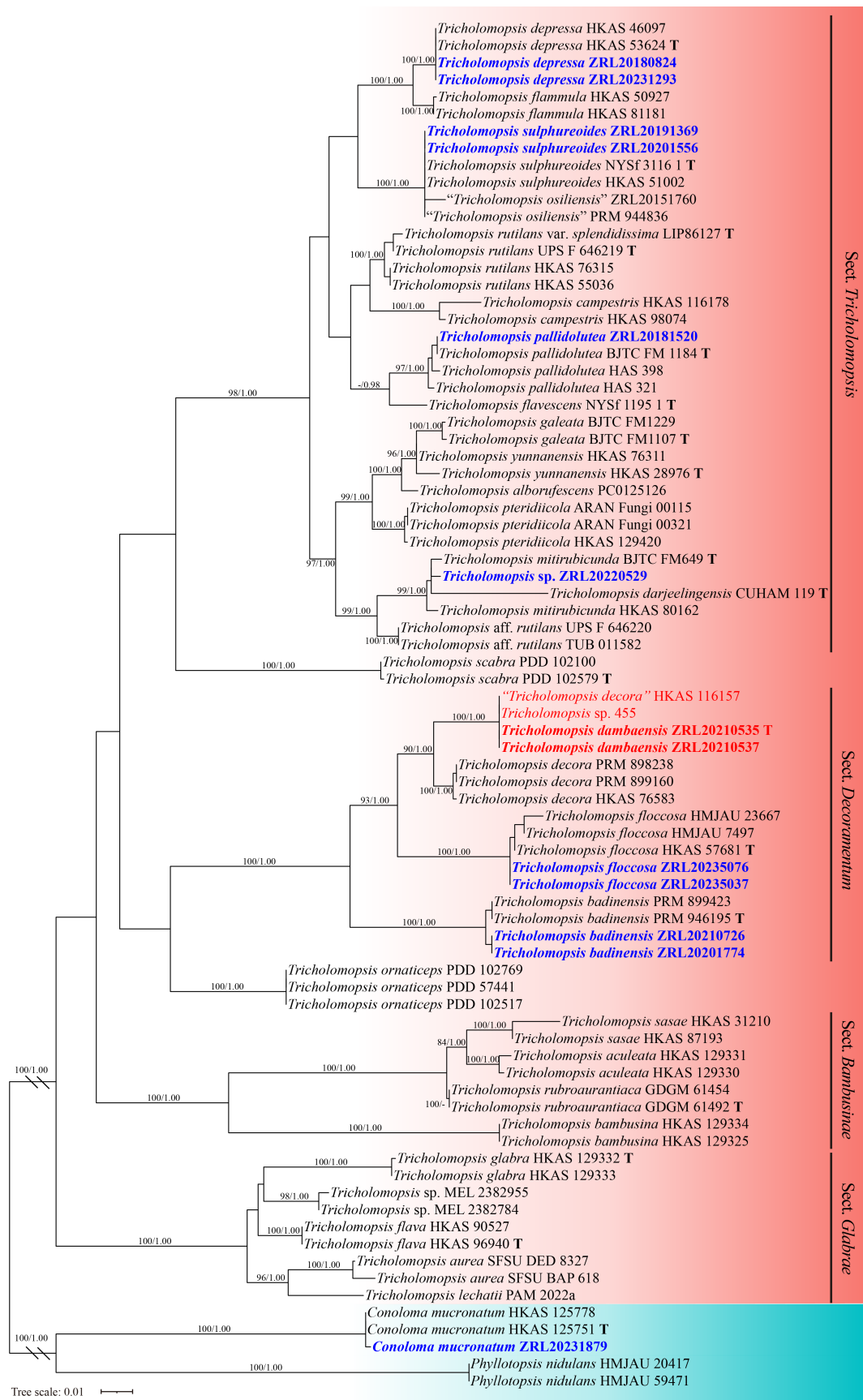


Fig. 30 Molecular phylogenetic analyses of *Tricholomopsis* species by the maximum likelihood (ML) method based on combined ITS–LSU sequences, rooted with *Conoloma mucronatum* and *Phyllotopsis nidulans*. Maximum likelihood bootstrap support values (ML) $\geq 80\%$ and Bayesian posterior probabilities (PP) ≥ 0.90 are shown around nodes as ML/PP. Sequences newly generated in this study are indicated in bold. New species described herein are shown in red, whereas other specimens newly collected in this study are shown in blue. 'T' refers to the type specimen.

Melanoleuca usually grow on humus-rich soils in meadow and forest habitats and are cosmopolitan in temperate to cold regions of both hemispheres^[28,113].

Melanoleuca guyutongensis R.L. Zhao, B. Cao, & X.X. Han, sp. nov. Figs 31 and 38

Chinese Name: 古玉通钨囊蘑 (gu yu tong xian nang mo)

Fungal Names: FN 573708; Facesoffungi number: FoF 20063

Etymology — *guyutongensis* (Latin) refers to the type locality Gǔyùtōng, an officially standardized geographical name in the Zangnan region of Xizang Autonomous Region, China.

Diagnosis — distinguished by its brownish orange to light brown pileus, which is applanate when young and becomes plano-concave to concave with age, long stipe, and basidia that are two- or four-spored.

Holotype — CHINA, Xizang, Linzhi, Chayu County, near Gǔyùtōng, 28°40'48" N, 97°44'54" E, 3,873 m asl, growing on humus-rich ground in coniferous forests dominated by *Juniperus*, 6 August 2023, D. Phurba & X.H. Yu, ZRL20231156 (HMAS 259906 holotype; AF9573 isotype, GenBank no.: ITS PZ496810; *tef1α* PZ523835; *rpb2* PZ541228).

Pileus 51–88 mm diam., applanate when young, becoming plano-concave to concave, with almost indistinct or rather distinct low broad obtuse umbo at the centre, sometimes depressed, long staying reflexed at the margin, not translucently striate, hygrophanous, smooth or very slightly rugulose at the centre, glabrous, brownish orange (6C5) to light brown (6D8), paler towards the margin. Lamellae rather close, emarginate with decurrent tooth, orange white (5A2) to greyish orange (5B4), concolorous, uneven. Stipe 97–161 × 7–11 mm, cylindrical, slightly broadened at apex, longitudinally fibrillose, central, sometimes with floccules of white at the base, brownish orange (6C4) to brown (6E7), sometimes slightly darker at the base. Context thin, orange white (5A2) to greyish orange (5B6), odour indistinct.

Basidiospores [50/3/2] (6.4–)7.1–8.2(–8.6) × (4.0–)4.2–4.7(–5.1) μm, $Q = (1.45–)1.62–1.84(–1.97)$, $Q_m = 1.73 (\pm 0.11)$, oblong, sometimes have one guttula, smooth, slightly thick-walled, with somewhat irregular small to large wart ornamentations. Basidia (22.5)24.1–29.9(32.7) × (7.8)8.4–9.5(9.9) μm, clavate, hyaline, two- or four-spored. Basidioles (16.1)17.6–23.3(26.9) × (5.8)7.0–8.8(10.0) μm, clavate to narrowly clavate, cylindrical. Cheilocystidia (45.1)51.9–67.6(78.2) × (10.7)12.2–15.6(18.6) μm, usually somewhat narrowly lageniform to lageniform, with acute or occasionally obtuse apex, sometimes with an apex usually encrusted by crystals. Pleurocystidia similar to Cheilocystidia. Trama hyphae thin-walled, subregular. Pileipellis hyphae cylindrical, 3.0–6.2 μm wide, with branched, somewhat intermediate between a cutis and intricate trichoderm, thin-walled. Clamp-connections absent.

Known distribution — Solitary or scattered on humus-rich ground within mixed coniferous and broad-leaved forests or coniferous forests, summer to fall. So far found only in China.

Material examined — CHINA, Xizang, Linzhi, Chayu County, near Gǔyùtōng, 28°35'33" N, 97°57'10" E, 3,922 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests, 9 August 2023, X.X. Han & Y.Y. Zheng, ZRL20231361 (HMAS 259907, GenBank no.: ITS PZ496811; *tef1α* PZ523836; *rpb2* PZ541227).

Notes — According to Vizzini et al.^[195], this species belonging to clade A5 and is close to *M. cognata* and *M. arcuata*. *Melanoleuca cognata*, which is primarily appears in spring, is distinguished by a clavate base of the pileus, slightly larger basidiospores (7.1–9.5 × 4.1–5.8 μm) that are ellipsoid to oblong, and basidia that are four-spored^[196]. *Melanoleuca arcuata* differs by having a fuliginous brown, sometimes fuliginous grey or vinaceous fuliginous pileus,



Fig. 31 *Melanoleuca guyutongensis* (a ZRL20231156 holotype; b, c ZRL20231361). (a) Basidioma; (b, c) Basidiomata; (d, e) Basidiospores; (f) Basidia and Basidioles; (g) Cheilocystidia; (h) Pileipellis. Scale bars: (a–c) = 2 cm; (d, e) = 5 μm; (f–h) = 10 μm.

with yellow-ochre lamellae only at maturity^[72,195]. Unlike other phylogenetically close species mainly distributed at low altitudes in Europe, *Melanoleuca guyutongensis* is currently known only from the alpine area of the southern Qinghai–Xizang Plateau^[72,196].

Melanoleuca conopileus R.L. Zhao & X.X. Han, sp. nov. Figs 32 and 38

Chinese Name: 锥盖钨囊蘑 (zhui gai xian nang mo)

Fungal Names: FN 573709; Facesoffungi number: FoF 20064

Etymology — *conopileus* (Latin), referring to the pileus of this species is conical.

Diagnosis — differs by a greyish orange to yellowish brown, obtusely conical to conical-convex pileus, basidia with two- or four-spored, small basidiospores and distinct DNA sequences.

Holotype — CHINA, Qinghai, Qilian Mountains National Park, Sigou Management Station, 37°7'50" N, 102°23'50" E, 2,678 m asl, growing on mosses within mixed coniferous and broad-leaved forests, 26 August 2023, M.Q. He, J.X. Li, M.Y. Liu, & H.M. Dai, ZRL20235721 (HMAS 259901 holotype; AF9581 isotype, GenBank no.: ITS PZ496804; *tef1α* PZ523849; *rpb2* PZ541232).

Pileus 20–38 mm diam., obtusely conical to conical-convex, sometimes with a subumbonate centre, later slightly reflexed at margin, hygrophanous, not translucently striate, smooth at centre, glabrous or pruinose at margin, lustrous, greyish orange (5B6) to yellowish brown (5D8), sometimes with a slightly darker or whitish outermost margin. Lamellae close, subventricose, emarginate, white (1A1) to yellowish white (1A2), with beige tinge or without it, concolorous, uneven. Stipe 53–88 × 5–8 mm, cylindrical, clavate or slightly bulbous at base, rather distinctly longitudinally fibrillose, central, solid, sometimes twisted, brownish orange (5C3) to yellowish brown (5E5), darker near apex. Context slightly thick, and thinner towards the margin, white (5A1) to yellowish brown (5B2), odour indistinct.

Basidiospores [50/2/1] (4.6–)5.1–6.2(–6.8) × (3.6–)3.9–4.8(–5.4) μm, $Q = (1.14–)1.23–1.39(–1.50)$, $Q_m = 1.31 (\pm 0.08)$, broadly ellipsoid to ellipsoid, rarely subglobose, with somewhat irregular small wart ornamentations. Basidia (33.0)35.0–42.4(45.9) × (8.9)9.3–11.5(13.4) μm, clavate, subhyaline, two- or four-spored. Basidioles (17.9)21.2–31.9(41.5) × (6.5)7.1–8.5(8.9) μm, clavate,

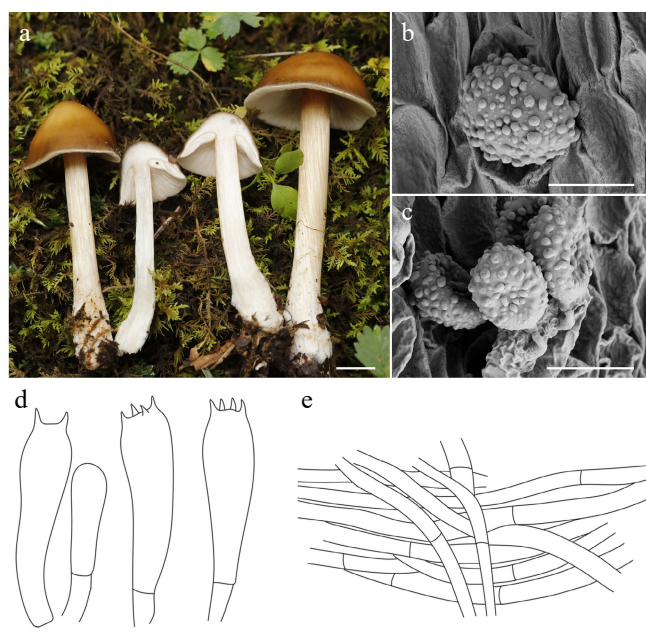


Fig. 32 *Melanoleuca conopileus* (a ZRL20235721 holotype). (a) Basidiomata; (b, c) Basidia; (d) Basidiospores; (e) Pileipellis. Scale bars: (a) = 1 cm; (b–d) = 5 μ m; (e) = 10 μ m.

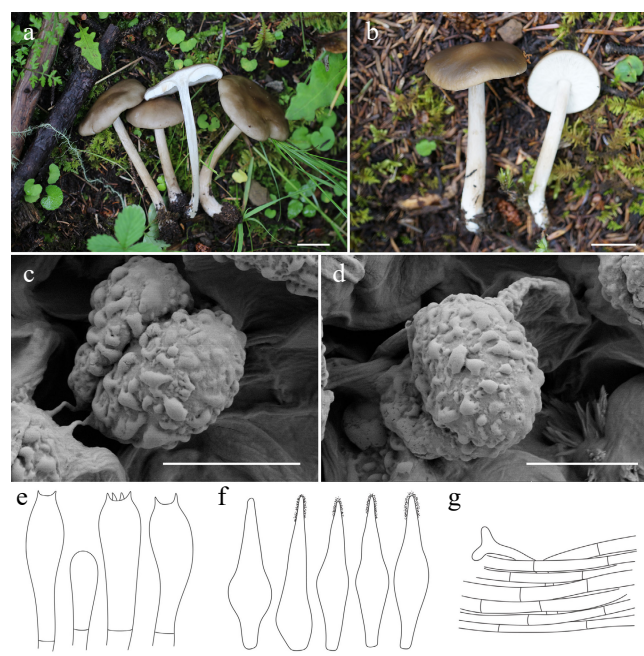


Fig. 33 *Melanoleuca piceicola* (a ZRL20200714 holotype; b ZRL20200921). (a, b) Basidioma; (c, d) Basidiospores; (e) Basidia and Basidioles; (f) Cheilocystidia; (g) Pileipellis. Scale bars: (a, b) = 2 cm; (c–e) = 5 μ m; (f, g) = 10 μ m.

cylindrical. Pleurocystidia and cheilocystidia not observed. Trama hyphae thin-walled, regular. Pileipellis hyphae cylindrical, 3.2–8.7 μ m wide, with numerous branched, intricate trichoderm, sometimes ixocutis, thin-walled. Clamp-connections absent.

Known distribution — Scattered on mosses within mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Notes — *Melanoleuca conopileus* can be easily distinguished from most other species of the genus by its greyish orange to yellowish brown, obtusely conical to conical-convex pileus, which is sometimes slightly darker or whitish outermost margin, and small basidiospores with irregular small warts. In the phylogenetic tree, *M. conopileus* closely relates to *M. monticola*, *M. brachyspora*, and *M. qilianensis* (Fig. 38). However, *M. monticola* differs by a relatively robust stipe (30–80 $\times$ 3–17 mm), a grey, grey-brown, or brown pileus, and larger basidiospores (5.5–10 $\times$ 4.0–6.5 μ m)^[197]. *Melanoleuca brachyspora* differs by brownish grey, brown to dark brown pileus, a pale grey-brown or light brown stipe, and larger basidiospores (av. 7.32 $\times$ 5.28 μ m)^[197]. *Melanoleuca qilianensis* differs by a yellowish grey to olive brown pileus, and larger basidiospores (6.5–7.5 $\times$ 4.7–5.3 μ m).

Melanoleuca piceicola R.L. Zhao & X.X. Han, sp. nov. Figs 33 and 38

Chinese Name: 云杉钹囊蘑 (yun shan xian nang mo)

Fungal Name: FN 573710; Facesoffungi number: FoF 20065

Etymology — refers to coniferous forest dominated by the genus *Picea* from which the new species was first collected.

Diagnosis — morphologically similar to *M. monticola*, but having smaller basidia with two- or four-spored, and the presence of cheilocystidia and pleurocystidia.

Holotype — CHINA, Sichuan, Yajiang County, Gexigou Nature Reserve, Hekou Town, Xiakezhong Village, 29°58'52" N, 100°54'28" E, 3,922 m asl, growing on humus-rich ground within coniferous forests dominated by *Picea*, 16 August 2020, X.Y. Zhu & M.Z. Zhang, ZRL20200714 (HMAS 286340 holotype; AF9559 isotype, GenBank no.: ITS PZ496814; *tef1 α* PZ523837; *rpb2* PZ541223).

Pileus 31–54 mm diam., convex to plano-convex, becoming applanate when mature, with almost indistinct or rather distinct low

broad obtuse umbo at the centre, margin inflexed, not translucently striate, not or slightly hygrophanous, smooth, glabrous or pruinose, olive brown (4D4–F8), grey (3B1) to greyish yellow (3C3) towards the margin. Lamellae rather close, emarginate or adnate with decurrent tooth, white (3A1) to yellowish white (3A2), concolorous, uneven. Stipe 64–87 $\times$ 6–8 mm, cylindrical, slightly broadened towards the base, longitudinally fibrillose, central, sometimes with floccules of white at the base, yellowish grey (4B2) to olive brown (4D5), sometimes slightly darker at the base. Context white (3A1) to yellowish grey (3C2), odour indistinct.

Basidiospores [50/2/2] (6.3–)7.0–8.1(–8.9) $\times$ (4.0–)4.4–5.4(–6.0) μ m, Q = (1.25–)1.44–1.65(–1.74), Q_m = 1.51 ($\pm$ 0.10), narrowly ellipsoid to oblong, rarely broadly ellipsoid, sometimes have guttula, usually smooth, slightly thick-walled, verruculose with connections, warts variable in size and shape. Basidia (25.5)27.7–32.0(36.7) $\times$ (8.3)9.1–10.4(11.0) μ m, clavate, hyaline, two- or four-spored. Basidioles (18.3)21.3–29.7(32.8) $\times$ (6.3)7.6–9.3(9.9) μ m, clavate to narrowly clavate, cylindrical. Cheilocystidia (42.5)51.9–64.5(66.7) $\times$ (9.5)11.8–15.5(19.3) μ m, narrowly lageniform to rarely lageniform, with acute or occasionally obtuse apex, sometimes with apex usually encrusted by crystals. Pleurocystidia similar to Cheilocystidia. Trama hyphae thin-walled, regular. Pileipellis hyphae cylindrical, 2.6–5.8 μ m wide, with branched, somewhat intermediate between a cutis and intricate trichoderm, thin-walled. Clamp-connections absent.

Known distribution — In pairs or scattered on humus-rich ground within coniferous forests, summer to fall. So far found only in China.

Material examined — CHINA, Sichuan, Yajiang County, Gexigou Nature Reserve, Suodi Village, 30°3'2" N, 100°46'50" E, 4,078 m asl, growing on humus-rich ground within coniferous forests dominated by *Picea*, 17 August 2020, J.X. Li & B. Cao, ZRL20200921 (HMAS 286343, GenBank no.: ITS PZ496815; *tef1 α* PZ523838; *rpb2* PZ541224).

Notes — *Melanoleuca piceicola* is characterized by an olive brown pileus and yellowish grey to olive brown stipe, which is slightly

broadened towards the base. The species produces small basidiospores that are verruculose with warts varying in size and shape. In the field, *M. piceicola* is easily confused with *M. monticola*. However, the latter has a relatively robust stipe (30–80 × 3–17 mm) and larger basidia (30–55 × 10–12 µm) that are four-spored^[197]. Phylogenetically, *M. piceicola* is related to *M. leucopoda*, which is normally saprobic on grass and was originally collected in north-eastern China. *Melanoleuca leucopoda* differs by having a slightly smaller (20–40 mm) and fawn-colored pileus, a whitish stipe, larger basidiospores (10–14 × 6–8 µm), and broader basidia (10–14 µm)^[198].

Melanoleuca dengkengquzongensis R.L. Zhao, B. Cao, & X.X. Han, sp. nov. Figs 34 and 38

Chinese Name: 登坑曲宗钨囊蘑 (deng keng qu zong xian nang mo)

Fungal Names: FN 573711; Facesoffungi number: FoF 20066

Etymology — *dengkengquzongensis* (Latin) refers to the type locality Dēngkēngqūzōng, an officially standardized geographical name in the Zangnan region of Xizang Autonomous Region, China.

Diagnosis — differs from the closely related *M. stridula* by its slightly robust basidiomata, slightly smaller basidiospores, and distinct DNA sequences.

Holotype — CHINA, Xizang, Linzhi, Chayu County, near Dēngkēngqūzōng, 28°48'6" N, 97°36'22" E, 3,960 m asl, growing on humus-rich ground in alpine meadows, 6 August 2023, M.Z. Zhang & L.H. Liu, ZRL20230996 (HMAS 259904 holotype; AF9572 isotype, GenBank no.: ITS PZ496806; *rpb2* PZ541236).

Pileus 26–37 mm diam., convex to plano-convex, becoming applanate when mature, with a less distinct broad central umbo, margin inflexed, sometimes becoming uplifted margin when mature, hygrophanous, not translucently striate, sometimes with small depressions, smooth, and lustrous, light brown (6D7) to dark brown (7F8), with a slightly darker margin. Lamellae moderately close, slightly arcuate, emarginate and attached with a tooth, white (2A1) to yellowish white (2A2), concolorous, uneven, with numerous lamellulae. Stipe cylindrical, 45–53 mm long, 5–7 mm thick from the mid-section to the apex, enlarged downwards to 8–13 mm in diam., central, solid, brownish orange (5C4) to light brown (5D6) on the upper part, brown (5E5–F8) towards the base, sometimes with a whitish flocculose apex, longitudinally striate, occasionally twisted. Context thin, and thinner towards the margin, white, odour indistinct.

Basidiospores [50/3/2] (5.5–)6.1–6.8(–7.2) × (4.1–)4.4–5.1(–5.7) µm, $Q = (1.15–)1.27–1.47(–1.56)$, $Q_m = 1.37 (\pm 0.10)$, broadly ellipsoid to ellipsoid, rarely subglobose or obovoid, with somewhat irregular small wart ornamentations. Basidia (29.3)31.0–36.6(41.5) × (7.9)8.5–9.4(9.5) µm, clavate, subhyaline, two- or four-spored. Basidioles (21.5)23.1–30.4(36.9) × (6.2)6.7–8.0(8.6) µm, clavate, cylindrical. Pleurocystidia and cheilocystidia not observed. Trama hyphae thin-walled, regular. Pileipellis hyphae cylindrical, 2.9–7.1 µm wide, with branched, thin-walled. Clamp-connections absent.

Known distribution — Solitary or scattered on soil rich in humus within alpine meadows or coniferous forests, summer to fall. So far found only in China.

Material examined — CHINA, Xizang, Linzhi, Chayu County, near Dēngkēngqūzōng, 28°36'26" N, 98°6'11" E, 3,848 m asl, growing on humus-rich ground in coniferous forests, 9 August 2023, D. Phurba & X.H. Yu, ZRL20231302 (HMAS 259905, GenBank no.: ITS PZ496805; *tef1α* PZ523847; *rpb2* PZ541235).

Notes — *Melanoleuca dengkengquzongensis* is characterized by the robust basidiomata, lustrous and light brown to dark brown pileus, stipe that is brownish orange to light brown on upper part and brown towards the base, and small basidiospores with irregular

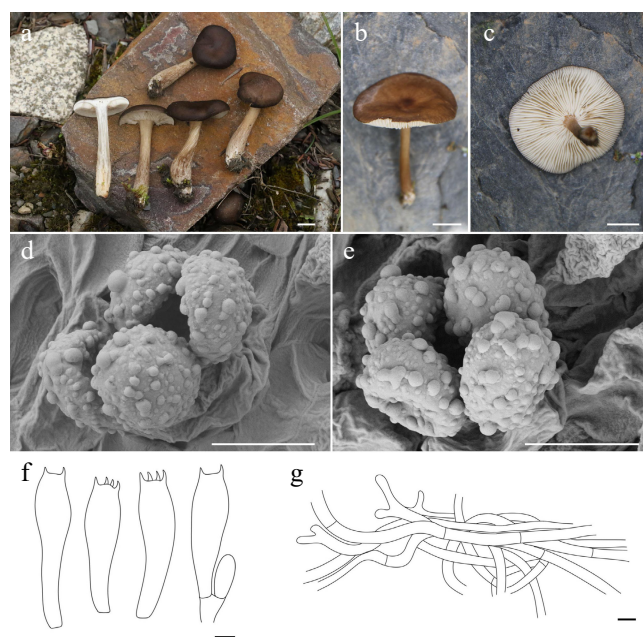


Fig. 34 *Melanoleuca dengkengquzongensis* (a ZRL20230996 holotype; b–c ZRL20231302). (a) Basidiomata; (b, c) Basidioma; (d, e) Basidia and Basidioles; (f) Pileipellis. Scale bars: (a–c) = 1 cm; (d–f) = 5 µm; (g) = 10 µm.

small warts. Phylogenetically, *M. dengkengquzongensis* and *M. stridula* are sister groups and share morphological similarities. However, *M. dengkengquzongensis* differs by robust basidiomata (45–53 × 5–7 mm vs. 40–95 × 2.5–6 mm), darker pileus, two- or four-spored basidia, and slightly smaller basidiospores (6.1–6.8 × 4.4–5.1 µm vs. 6.0–8.5 × 4.0–6.0 µm)^[197]. Currently, *M. dengkengquzongensis* is known only from alpine regions above 3,500 m on the Qinghai–Xizang Plateau, whereas its phylogenetically close relatives are mainly distributed in low-altitude areas of Europe^[197].

Melanoleuca qilianensis R.L. Zhao & X.X. Han, sp. nov. Figs 35 and 38

Chinese Name: 祁连钨囊蘑 (qi lian xian nang mo)

Fungal Names: FN 573712; Facesoffungi number: FoF 20067

Etymology — refers to the type locality, Qilian County.

Diagnosis — differs from *M. conopileus* in yellowish grey to olive brown pileus with an involute margin, large basidiospores, and distinct DNA sequences.

Holotype — CHINA, Qinghai, Qilian County, Binggou Linhai, 38°8'21" N, 100°11'9" E, 3,078 m asl, growing on mosses within mixed coniferous and broad-leaved forests, 30 August 2023, M.Q. He, J.X. Li, M.Y. Liu, & H.M. Dai, ZRL20235855 (HMAS 259899 holotype; AF9582 isotype, GenBank no.: ITS PZ496802; *rpb2* PZ541234).

Pileus 27–38 mm diam., plano-conical or plano-convex, then applanate, sometimes with a subumbonate centre, involute at the margin, hygrophanous, usually not striate, sometimes translucently striate, smooth or very slightly rugulose at the centre, glabrous or pruinose at the margin, lustrous, yellowish grey (4B2) to olive brown (4D6), sometimes with a slightly darker margin. Lamellae rather close, emarginate with decurrent tooth, white (4A1) to yellowish grey (4B2), concolorous, uneven. Stipe 37–89 × 6–8 mm, cylindrical, slightly broadened towards the base, rather distinctly longitudinally fibrillose, central, solid, sometimes with floccules of white at the base, yellowish grey (4B2) to blond (4C4), sometimes slightly darker at the apex. Context thin to slightly thick, white (4A1) to yellowish grey (4B2), odour indistinct.

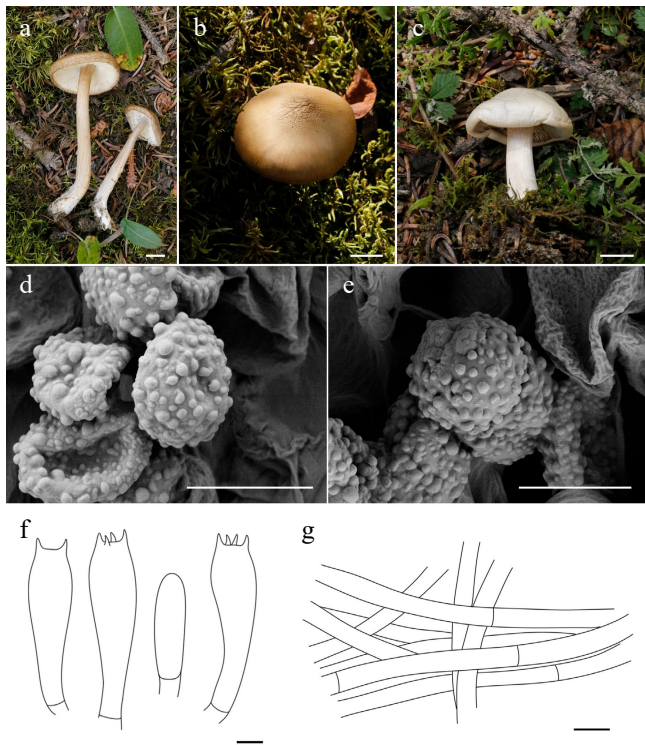


Fig. 35 *Melanoleuca qilianensis* (a, b ZRL20235855 holotype; c ZRL20235856). (a) Basidiomata; (b, c) Basidioma; (d, e) Basidiospores; (f) Basidia and Basidioles; (g) Pileipellis. Scale bars: (a-c) = 1 cm; (d-f) = 5 µm; (g) = 10 µm.

Basidiospores [50/2/2] (6.1–)6.5–7.5(–7.9) × (4.3–)4.7–5.3(–6.0) µm, $Q = (1.24–)1.32–1.48(–1.56)$, $Q_m = 1.40 (\pm 0.08)$, broadly ellipsoid, sometimes ellipsoid, with somewhat irregular small wart ornamentations. Basidia (29.4)30.3–35.4(38.2) × (7.7)8.2–9.4(9.9) µm, clavate, subhyaline, two- or four-spored. Basidioles (13.9)22.2–32.1(37.6) × (5.6)6.4–8.5(10.0) µm, narrowly clavate, cylindrical. Pleurocystidia and cheilocystidia not observed. Trama hyphae thin-walled, regular. Pileipellis hyphae cylindrical, 2.3–7.5 µm wide, with branched cutis, sometimes intricate trichoderm at centre, slightly thick-walled. Clamp-connections absent.

Known distribution — Scattered on mosses within mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Qinghai, Qilian County, Binggou Linhai, 38°8'21" N, 100°11'9" E, 3,078 m asl, growing on mosses within mixed coniferous and broad-leaved forests, 30 August 2023, M.Q. He, J.X. Li, M.Y. Liu, & H.M. Dai, ZRL20235856 (HMAS 259900, GenBank no.: ITS PZ496803; *tef1α* PZ523848; *rpb2* PZ541233).

Notes — *Melanoleuca qilianensis* is characterized by a yellowish grey to olive brown pileus with an involute margin, small basidiospores with irregular small warts, and basidia with two- or four-spored. Morphologically, it resembles *M. leucopoda*, a species also described from China, but differs in its whitish stipe, fusiform cystidia, larger (10–14 × 6–8 µm) and oblong basidiospores, and solitary growth habit^[198]. The closely related species *M. brachyspora* and *M. monticola* differ by having a darker pileus, slightly larger basidiospores (av. 7.32 × 5.28 µm and av. 7.15 × 5.10 µm), and basidia bearing only four spores. In contrast, *M. qilianensis* possesses basidia with two or four spores^[197]. The new species is distributed in the alpine area of Qinghai–Xizang Plateau.

Melanoleuca sinomelaleuca R.L. Zhao & X.X. Han, sp. nov. Figs 36 and 38

Chinese Name: 中华黑白钨囊蘑 (zhong hua hei bai xian nang mo)

Fungal Names: FN 573713; Facesoffungi number: FoF 20068

Etymology — refers to a Chinese endemic species that is similar to *M. melaleuca*.

Diagnosis — differs from the closely related *M. melaleuca* by its small basidiospores, small basidia that are two- or four-spored and distinct DNA sequences.

Holotype — CHINA, Xizang, Linzhi, Alpine Forest Ecosystem National Field Scientific Observation and Research Station, 29°39'2" N, 94°42'53" E, 3,880 m asl, growing on humus-rich ground in coniferous forests, 27 July 2021, X.Y. Zhu & B. Cao, ZRL20211077 (HMAS 259908 holotype; AF9564 isotype, GenBank no.: ITS PZ496818; *tef1α* PZ523840; *rpb2* PZ541226).

Pileus 23–96 mm diam., plano-convex to applanate when young, becoming plano-concave to concave when mature, with almost indistinct or rather distinct low broad obtuse umbo at the centre, sometimes slightly depressed, margin inflexed to straight when young, reflexed when mature, not translucently striate, not or slightly hygrophanous, smooth or somewhat rugulose at the centre, glabrous, brownish orange (5C5) to yellowish brown (5F8), with slightly darker centre, sometimes pruinose at the margin. Lamellae moderately close, sinuate with decurrent tooth, orange white (5A2) to brownish orange (5C3), concolorous, uneven. Stipe 39–83 × 4–9 mm, cylindrical, clavate at base, longitudinally fibrillose, central, finely pruinose or floccose, brownish orange (5C4) to yellowish brown (5E8), sometimes slightly darker at base. Context white (5A1) to brownish orange (5C3), odour indistinct.

Basidiospores [50/2/2] (6.3–)6.9–7.8(–8.6) × (4.3–)4.6–5.2(–5.5) µm, $Q = (1.24–)1.41–1.61(–1.71)$, $Q_m = 1.51 (\pm 0.10)$, ellipsoid to narrowly ellipsoid, rarely oblong, sometimes have guttula, smooth, slightly thick-walled, ornamentations consist of irregular, low, and isolated warts. Basidia (23.7)25.4–29.2(32.0) × (7.6)8.0–9.3(11.1) µm, clavate, hyaline, two- or four-spored. Basidioles (15.8)19.4–26.7(28.2) × (5.6)7.1–8.8(9.1) µm, clavate to narrowly clavate, cylindrical. Cheilocystidia (39.6)50.3–63.2(73.1) × (8.0)8.8–11.4(12.9) µm, narrowly

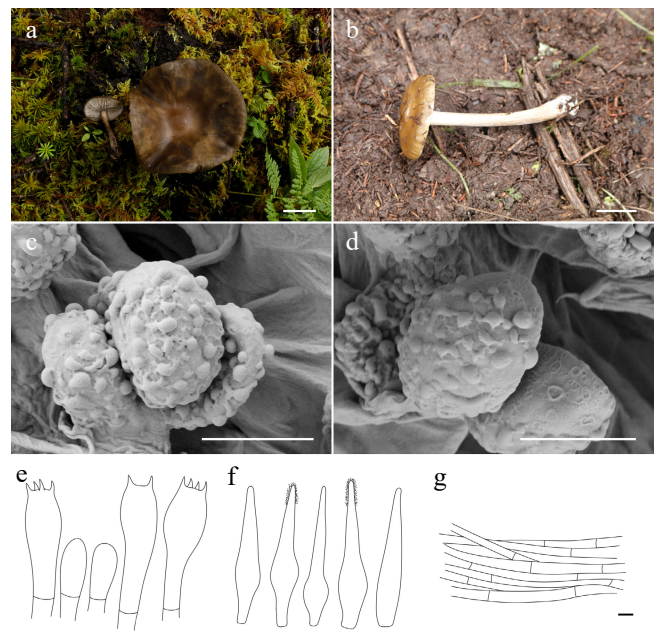


Fig. 36 *Melanoleuca sinomelaleuca* (a ZRL20211077 holotype; b ZRL20200829). (a) Basidiomata; (b) Basidioma; (c, d) Basidiospores; (e) Basidia and Basidioles; (f) Cheilocystidia; (g) Pileipellis. Scale bars: (a, b) = 2 cm; (c–e) = 5 µm; (f, g) = 10 µm.

conical, somewhat narrowly lageniform, rarely lageniform, with acute or occasionally obtuse apex, sometimes with apex usually encrusted by crystals. Pleurocystidia similar to Cheilocystidia. Trama hyphae thin-walled, subregular. Pileipellis hyphae cylindrical, 6.3–8.5 μm wide, with branched, somewhat intermediate between a cutis and intricate trichoderm, thin-walled. Clamp-connections absent.

Known distribution — Solitary or scattered on humus-rich ground within coniferous forests, summer to fall. So far found only in China.

Material examined — CHINA, Sichuan, Yajiang County, Gexigou Nature Reserve, Hekou Town, Xiakezong Village, 29°58'52" N, 100°54'28" E, 3,922 m asl, growing on humus-rich ground within coniferous forests dominated by *Picea*, 16 August 2020, R.L. Zhao & M.Q. He, ZRL20200829 (HMAS 286342, GenBank no.: ITS PZ496817; *tef1 α* PZ523841; *rpb2* PZ541225).

Notes — *Melanoleuca sinomelaleuca* is characterized by a brownish orange to yellowish brown pileus, with a margin that is inflexed to straight when young and becomes reflexed at maturity, a stipe clavate at the base, small basidiospores having irregular, low, and isolated ornamentations of warts, and cheilocystidia and pleurocystidia that are narrowly conical or somewhat narrowly lageniform. The new species clusters with *M. melaleuca* in phylogenetic analysis and is clearly separated from the other species (Fig. 38). In contrast to *M. melaleuca*, which is mainly distributed in low-altitude areas of Europe, *M. sinomelaleuca* is primarily distributed in the high-altitude regions of the southern Qinghai–Xizang Plateau, China^[72]. Furthermore, *M. sinomelaleuca* differs by having a pileus with an orange tint, smaller basidiospores (6.9–7.8 $\times$ 4.6–5.2 μm vs. 7.5–9.3 $\times$ 5.2–6.2 μm), and smaller basidia (25.4–29.2 $\times$ 8.0–9.3 μm vs. 34–40 $\times$ 11–13 μm) that are two- or four-spored.

Melanoleuca xunhuaensis R.L. Zhao & X.X. Han, sp. nov. Figs 37 and 38

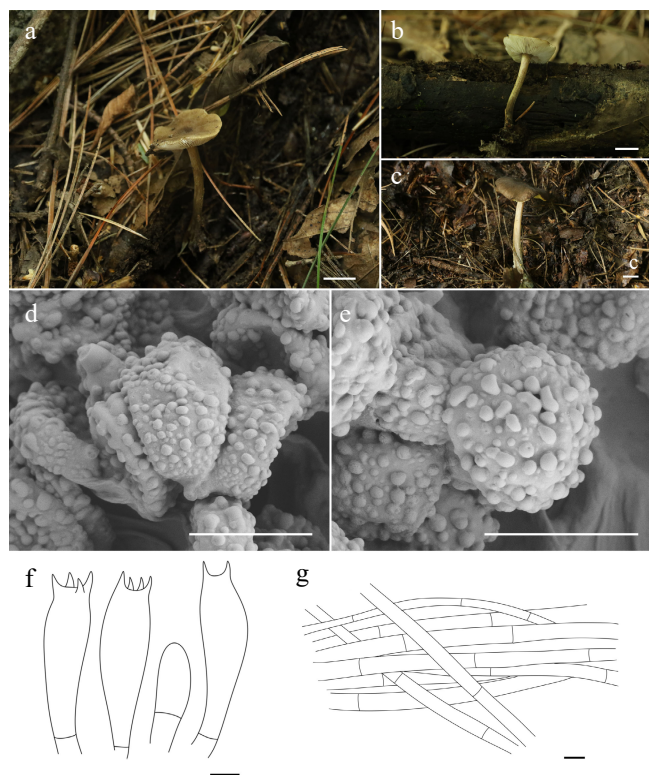


Fig. 37 *Melanoleuca xunhuaensis* (a, b ZRL20234605 holotype; c ZRL20234607). (a–c) Basidioma; (d, e) Basidiospores; (f) Basidia; (g) Pileipellis. Scale bars: (a–c) = 1 cm; (d–f) = 5 μm ; (g) = 10 μm .

Chinese Name: 循环钙囊蘑 (xun hua xian nang mo)

Fungal Names: FN 573714; Facesoffungi number: FoF 20069

Etymology — refers to the type locality, Xunhua County.

Diagnosis — distinguished by its yellowish-brown-toned pileus, small basidiospores, and basidia with two- or four-spored.

Holotype — CHINA, Qinghai, Xunhua County, Mengda Heavenly Lake, 35°47'49" N, 102°40'52" E, 2,384 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests, 24 August 2023, M.Q. He, J.X. Li, M.Y. Liu, & H.M. Dai, ZRL20234605 (HMAS 259902 holotype; AF9577 isotype, GenBank no.: ITS PZ496813; *tef1 α* PZ523846; *rpb2* PZ541237).

Pileus 22–37 mm diam., convex to plano-convex when young, then gradually applanate, with almost indistinct or rather distinct broad obtuse umbo at the centre, sometimes depressed, inflexed, later reflexed at the margin, not translucently striate, not hygrophanous, smooth, glabrous or finely granulose, yellowish brown (5E5–F8), sometimes paler at the margin. Lamellae moderately close, emarginate with decurrent tooth, white (5A1) to orange white (5A2), concolorous, uneven. Stipe 42–78 $\times$ 3–6 mm, cylindrical, slightly broadened at the apex, longitudinally fibrillose, central, sometimes with floccules of white at the base, greyish orange (5B3) to yellowish brown (5D5), sometimes slightly darker at the base. Context thin, white (5A1) to orange grey (5B2), odour indistinct.

Basidiospores [50/2/2] (5.0–)5.7–6.6(–7.0) $\times$ (3.7–)4.1–4.5(–4.8) μm , $Q = (1.23–)1.34–1.51(–1.70)$, $Q_m = 1.42 (\pm 0.09)$, ellipsoid to narrowly ellipsoid, rarely oblong, obovoid, with somewhat irregular small to large wart ornamentations. Basidia (24.1)25.8–29.6(31.2) $\times$ (6.9)7.3–8.2(8.7) μm , clavate, hyaline, two- or four-spored. Basidioles (17.7)21.4–26.9(29.7) $\times$ (6.1)6.6–8.1(8.7) μm , narrowly clavate, cylindrical. Pleurocystidia and cheilocystidia not observed. Trama hyphae thin-walled, regular. Pileipellis hyphae cylindrical, 4.6–8.8 μm wide, with branched, intricate trichoderm, thin-walled. Clamp-connections absent.

Known distribution — Solitary on humus-rich ground within mixed coniferous and broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Qinghai, Xunhua County, Mengda Heavenly Lake, 35°47'49" N, 102°40'52" E, 2,384 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests, 24 August 2023, M.Q. He, J.X. Li, M.Y. Liu, & H.M. Dai, ZRL20234607 (HMAS 259903, GenBank no.: ITS PZ496812; *tef1 α* PZ523845; *rpb2* PZ541238).

Notes — *Melanoleuca xunhuaensis* is characterized by its yellowish brown pileus with an inflexed then reflexed margin, greyish orange to yellowish brown stipe, small basidiospores, and basidia with two- or four-spored. In the phylogenetic tree, *M. xunhuaensis* is closely related to *M. subgriseoflava*. However, *M. subgriseoflava* has a slightly paler pileus, larger basidiospores (7–8 $\times$ 4–5 μm), and broader basidia (8 $\times$ 10 μm) with two- or four-spored, and it was originally collected from north-eastern China^[189]. *Melanoleuca lalsuhanraensis* is morphologically similar to *M. xunhuaensis* but can be distinguished by its shorter stipe (30–44 mm), and larger basidiospores (av. 8.2 $\times$ 5.4 μm) and basidia (33–43.03 $\times$ 9.03–10.39 μm), which are distributed only in the low-altitude areas of Pakistan^[199].

Porotheleaceae Murrill

Index Fungorum number: IF 81214

Type genus — *Porotheleum* Fr.

Clitocybula (Singer) Singer ex Métrod

Index Fungorum number: IF 17329

Type species — *Clitocybula lacerata* (Scop.) Métrod

Notes — *Clitocybula* (Singer) Singer ex Métrod belongs to Porotheleaceae and is typified by *Cl. lacerata*^[200,201], with

approximately 20 species currently accepted worldwide^[27,202,203]. In China, six species have been reported, namely *Cl. abundans*, *Cl. aperta*, *Cl. familia*, *Cl. fuscostriata*, *Cl. lacerata*, and *Cl. xizangensis*, of which only *Cl. fuscostriata* and *Cl. xizangensis* have been confirmed by molecular evidence^[27,203]. Species of *Clitocybula* are saprotrophic, and basidiomata are usually gregarious to caespitose, with convex to plane, or sometimes depressed to infundibuliform, pileus bearing radially fibrillose to squamulose surfaces. Their basidiospores are smooth and amyloid. Pileocystidia, cheilocystidia, caulocystidia, and

clamp connections are commonly present, whereas pleurocystidia may be absent in some taxa^[27,200–202,204]. Molecular phylogenetic analyses suggest that *Clitocybula*, in the traditional morphological circumscription, is not monophyletic, and several species have consequently been reassigned to other genera^[201,203,205]. In China, a few taxa have been reported, but only *Cl. fuscostriata* and *Cl. xizangensis* have been confirmed using molecular data^[27,203]. *Clitocybula microspora* represents the second record of the genus from the Qinghai–Xizang Plateau.



Melanoleuca

Fig. 38 to be continued

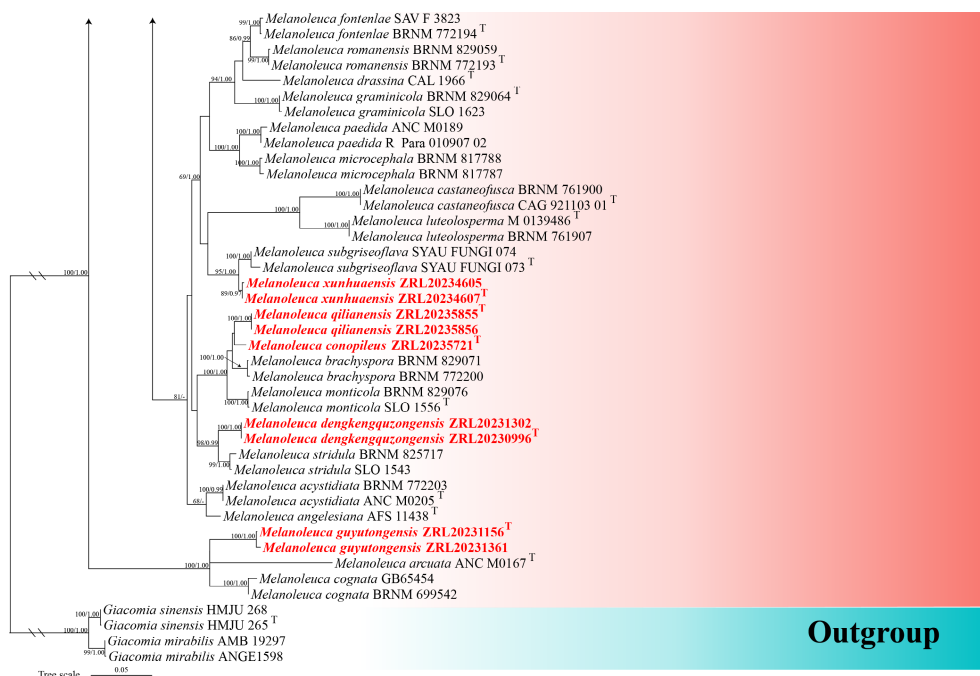


Fig. 38 Molecular phylogenetic analyses of *Melanoleuca* species by the maximum likelihood (ML) method based on combined ITS–*tef1α*–*rpb2* sequences, rooted with *Giacomia mirabilis* and *Giacomia sinensis*. Maximum likelihood bootstrap support values (ML) $\geq 60\%$ and Bayesian posterior probabilities (PP) ≥ 0.90 are shown around nodes as ML/PP. Sequences newly generated in this study are indicated in bold. New species described herein are shown in red, whereas other specimens newly collected in this study are shown in blue. 'T' refers to the type specimen.

Clitocybula microspora R.L. Zhao & X.X. Han, sp. nov. Figs 39 and 40

Chinese Name: 小孢小杯伞 (xiao bao xiao bei san)

Fungal Names: FN 573715; Facesoffungi number: FoF 20070

Etymology — referring to the small basidiospores.

Diagnosis — differs from other species by its brownish-orange pileus, smooth or sometimes very slightly innately fibrillose pileus, two- or four-spored basidia, slightly smaller basidiospores, and distinct DNA sequences.

Holotype — CHINA, Sichuan, Xiangcheng County, Fozhu Gorge, 29°3'27" N, 99°57'34" E, 3,380 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests dominated by *Abies*, 15 August 2019, R.L. Zhao, B. Cao, & Z.L. Ling, ZRL20191044 (HMAS 259809 holotype; AF9556 isotype, GenBank no.: ITS PZ491505; LSU PZ491662).

Pileus 14–36 mm diam., hemispherical to obtusely conical when young, then becoming convex to plano-convex with inflexed margin, and finally applanate with straight margin, centre plane to slightly depressed, sometimes with low broad umbo, hygrophanous, margin translucently striate, radially rugulose, slightly innately fibrillose or smooth, occasionally with cracked margin, brownish orange (5C4) to brownish yellow (5C7) at the centre, paler towards the margin. Lamellae moderately crowded, subdecurrent to emarginate with decurrent tooth with age, unequal, even, concolorous, white (5A1) to orange white (5A2). Stipe 43–98 × 2–4 mm, central, hollow, cylindrical, sometimes twisted, fragile, with occasionally finely longitudinally striate to shallowly sulcate, surface finely pruinose, white (5A1) to greyish orange (5B5). Context thin, concolorous with the surface, odour indistinct.

Basidiospores [50/3/2] (3.4–)3.7–4.4(–5.2) × (2.7–)2.9–3.6(–4.2) μm , $Q = (1.13\text{--})1.17\text{--}1.32(1.38)$, $Q_m = 1.25 (\pm 0.07)$, broadly ellipsoid, sometimes subglobose or ellipsoid, smooth, thin-walled, hyaline. Basidia (14.0)16.4–20.7(22.8) × (4.4)4.7–5.6(6.1) μm , clavate, hyaline, two- or four-spored, sterigmata 2.1–4.3 μm long. Basidioles (10.3)13.2–18.7(20.8) × (2.7)3.7–5.2(5.6) μm , clavate to

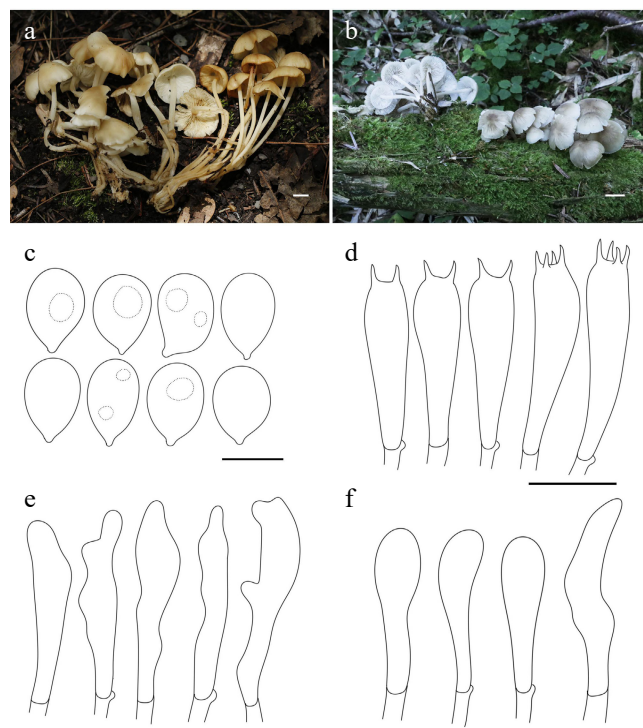


Fig. 39 *Clitocybula microspora* (a, ZRL20191044 holotype; b, ZRL20221237). (a, b) Basidiomata; (c) Basidiospores; (d) Basidia; (e) Cheilocystidia; (f) Caulocystidia. Scale bars: (a, b) = 1 cm; (c) = 5 μm ; (d–f) = 10 μm .

narrowly clavate, cylindrical. Cheilocystidia (16.0)16.5–19.6(22.1) × (3.8)4.2–5.2(5.7) μm , scattered, versiform, irregularly cylindrical, clavate, with apical papilla or subcapitate, thin-walled, hyaline. Lamella trama regular to subregular, hyphae 2.3–7.0 μm wide, cylindrical, thin- to slightly thick-walled. Pleurocystidia not

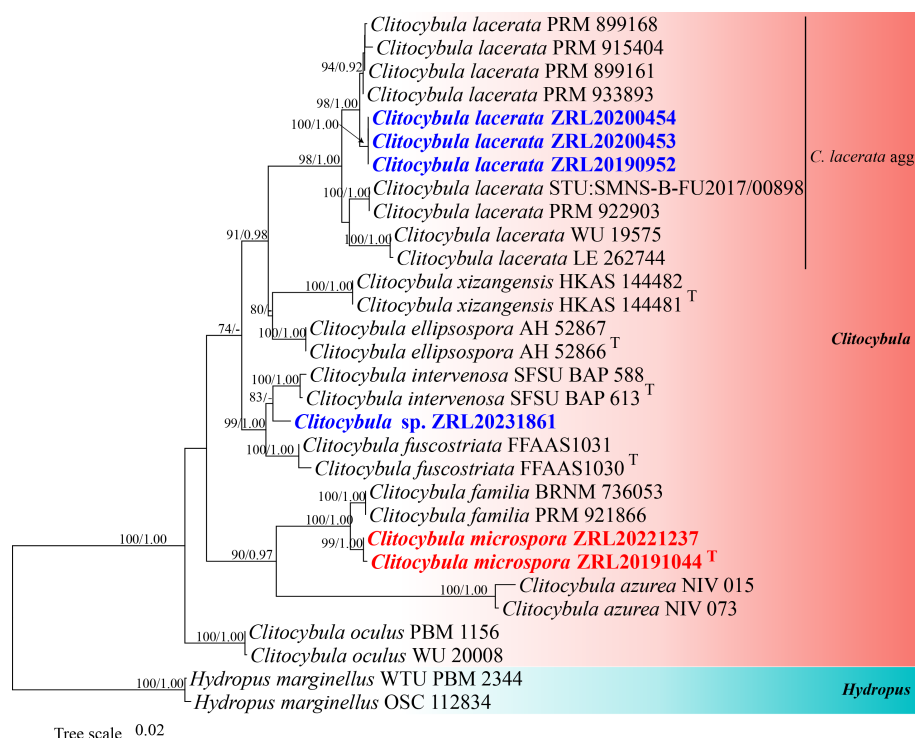


Fig. 40 Molecular phylogenetic analyses of *Clitocybula* species by the maximum likelihood (ML) method based on combined ITS–LSU sequences, rooted with *Hydrops marginellus*. Maximum likelihood bootstrap support values (ML) $\geq 60\%$ and Bayesian posterior probabilities (PP) ≥ 0.90 are shown around nodes as ML/PP. 'T' refers to the type specimen. Sequences newly generated in this study are indicated in bold. New species described herein are shown in red, whereas other specimens newly collected in this study are shown in blue.

observed. Caulocystidia (25.3)28.6–44.5(56.0) $\times$ (4.8)6.6–10.4(12.9) μm , cylindrical to clavate, occasionally with 2–3 lobes at the apex, rarely narrowly lageniform, thin- to slightly thick-walled. Pileipellis is a cutis of radially arranged, slightly thick-walled, smooth hyphae, 4.4–9.5 μm wide, hyaline. Pileocystidia (12.4)18.4–40.5(64.1) $\times$ (3.2)4.6–9.9(13.1) μm , irregular cylindrical to broadly clavate, rarely forked, slightly thick-walled, smooth, hyaline. Clamp-connections present.

Known distribution — Gregarious on humus-rich ground within mixed coniferous and broad-leaved forests dominated by *Abies*, summer to fall. So far found only in China.

Material examined — CHINA, Hubei, Shennongjia Forestry District, Shennongding, Taizi Ya, 31°27'14" N, 110°11'33" E, 2,588 m asl, growing on humus-rich ground within mixed coniferous and broad-leaved forests dominated by *Abies*, 26 August 2022, X.Y. Zhu & B. Cao, ZRL20221237 (HMAS 259810, GenBank no.: ITS PZ491506; LSU PZ491663).

Notes — *Clitocybula microspora* is distinct from other Chinese members of the genus by its brownish-orange pileus, usually not centrally depressed, smooth or sometimes very slightly innately fibrillose pileus, and broadly ellipsoid but smaller basidiospores measuring 3.7–4.4 $\times$ 2.9–3.6 μm . The newly described species is both morphologically and phylogenetically related to *Cl. familia*, which is primarily distributed in Europe and North America. Nevertheless, *Cl. familia* can be readily distinguished by its larger basidiospores (average 4.39 $\times$ 3.98 μm), broader basidia (5.0–7.5 μm) that are exclusively four-spored, and its tendency to grow in larger and denser clusters^[206].

Specimens ZRL20191044 from the Qinghai–Xizang Plateau and ZRL20221237 from Shennongjia, Hubei Province, form a single lineage in the phylogenetic analyses, supporting their treatment as the new species *Clitocybula microspora*. Specimen ZRL20191044 has a pileus with a light yellowish brown to yellowish brown centre and

a relatively long stipe, 75–98 mm long, whereas ZRL20221237 has a pileus with a light brown to brown centre and a shorter stipe, 34–43 mm long. In micromorphology, basidiospores of ZRL20191044 measure (3.4–)3.6–4.3(–4.7) $\times$ (2.7–)2.9–3.6(–4.2) μm ($n = 50$), $Q = (1.08\text{--})1.16\text{--}1.30(–1.41)$, $Q_m = 1.23 (\pm 0.07)$, whereas those of ZRL20221237 measure (3.5–)3.6–4.4(–5.0) $\times$ (2.8–)3.0–3.6(–4.2) μm ($n = 50$), $Q = (1.09\text{--})1.15\text{--}1.28(–1.38)$, $Q_m = 1.21 (\pm 0.06)$; the two collections are highly congruent in basidiospore size and Q values. Although there are slight differences in some macromorphological characters between these two populations, both phylogenetic analyses (Fig. 40) and micromorphological features support their assignment to a single species. Although currently known from only two collections, one from the Qinghai–Xizang Plateau and the other from Shennongjia Forestry District, Hubei Province, both morphological and phylogenetic evidence support their conspecificity, extending the known distribution of *Clitocybula microspora* beyond the Plateau region.

Tricholomataceae R. Heim ex Pouzar

Index Fungorum number: IF 81487

Type genus — *Tricholoma* (Fr.) Staude

Tricholoma (Fr.) Staude

Index Fungorum number: IF 18677

Type species — *Tricholoma terreum* (Schaeff.) P. Kumm.

Notes — *Tricholoma* (Fr.) Staude is an ectomycorrhizal genus widely distributed in temperate to subtropical ecosystems^[207,208], with more than 90 species reported from China^[93,209]. Species form symbiotic associations mainly with trees of Pinaceae, Betulaceae, Fagaceae, and Salicaceae, and several taxa are of considerable economic importance, including the well-known matsutake group^[210–212]. Basidiomata are typically fleshy with a central stipe, and white spore prints; lamellae are adnexed to emarginate, and basidiospores are subglobose to oblong and smooth; cystidia are usually poorly differentiated, and the pileipellis structure is

relatively simple^[28,207,210–215]. Recent multilocus phylogenetic analyses have led to a revised infrageneric classification of the genus, recognizing four subgenera and 11 sections^[207]. Although several important taxonomic studies on *Tricholoma* have been conducted in China in recent years^[179,209,216–219], the diversity of this genus on the vast and still underexplored Qinghai–Xizang Plateau remains poorly understood. Therefore, one new species is described here based on morphological characters and phylogenetic analyses of ITS and LSU sequence data.

Tricholoma fulvoochraceum R.L. Zhao & X.X. Han, sp. nov. Figs 41 and 42

Chinese Name: 赭黄松口蘑 (zhe huang song kou mo)

Fungal Names: FN 573716; Facesoffungi number: FoF 20071

Etymology — *fulvoochraceum* (Latin), composed of *fulvus* (tawny, yellow-brown) and *ochraceus* (ochre-coloured), referring to the tawny-ochraceous pileus of this species.

Diagnosis — differs from *Tr. aurantium* by its broadly ellipsoid to narrowly ellipsoid basidiospores, slightly wider basidia, the presence of clamp-connections and its distribution in broad-leaved forests.

Holotype — CHINA, Sichuan, Yajiang County, Gexigou Nature Reserve, Gexigou, 30°2'53" N, 100°57'13" E, 2,915 m asl, growing on humus-rich ground within broad-leaved forests, 14 August 2020, M.Z. Zhang & X.Y. Zhu, ZRL20200088 (HMAS 259913 holotype; AF9557 isotype, GenBank no.: ITS PZ500014; LSU PZ500004).

Pileus 19–56 mm diam., hemispherical to plano-hemispherical when young, becoming convex to plano-convex with age, with a slightly depressed or subumbonate centre, surface dry, golden yellow (5B7) to yellowish brown (5D8) at the centre, paler towards the margin, covered with brownish orange (6C7) to brown (6E8) reflexed fibrillose squamules, slightly or not hygrophanous, sometimes rugulose, margin nonstriate, slightly involute, then straight. Lamellae moderately crowded, adnexed to sinuate, unequal, yellowish white (2A2) when young, changes to light brown (6D6) to brown (6E8) on margin when mature, uneven. Stipe 39–100 × 7–13 mm, central, cylindrical to clavate, sometimes twisted and tapering towards the base, with brownish (5C6) to dark brown (6F8) appressed fibrillose scales densely covering the surface

except at the base, greyish orange (5B3) to yellowish brown (5D6). Context slightly thick, white, odour indistinct.

Basidiospores [50/2/2] (3.8–)4.4–5.3(–6.1) × (2.6–)3.1–3.8(–4.1) μm, $Q = (1.20–)1.30–1.52(–1.68)$, $Q_m = 1.41 (\pm 0.11)$, broadly ellipsoid to narrowly ellipsoid, rarely oblong, smooth, slightly thick-walled, almost always single. Basidia (21.8)23.1–25.8(26.8) × (5.5)6.1–6.7(6.8) μm, clavate, hyaline, two- or four-spored. Basidioles (12.2)15.7–22.5(26.8) × (3.6)4.1–5.6(6.3) μm, clavate to narrowly clavate, cylindrical. Cheilocystidia (18.7)19.9–23.1(26.0) × (3.9)4.5–5.7(6.5) μm, clavate to cylindrical with inflated apex, subhyaline. Pleurocystidia not observed. Lamella trama regular, hyphae 4.8–8.3 μm wide, cylindrical, thin-walled. Pileipellis is a cutis with the transition to a trichoderm at regular intervals, thin-walled, hyphae 2.5–5.3 μm wide. Clamp-connections present.

Known distribution — Solitary or in pairs on humus-rich ground within broad-leaved forests, summer to fall. So far found only in China.

Material examined — CHINA, Sichuan, Yajiang County, Gexigou Nature Reserve, Gexigou, 30°2'53" N, 100°57'13" E, 2,915 m asl, growing on humus-rich ground within broad-leaved forests, 14 August 2020, M.Q. He & M.Q. Wang, ZRL20200078 (HMAS 259912, GenBank no.: ITS PZ500015; LSU PZ500005); Gexigou, 30°3'10" N, 100°56'35" E, 2,953 m asl, growing on humus-rich ground within broad-leaved forests, 14 August 2020, X.X. Han & R.L. Zhao, ZRL20200309 (HMAS 286716, GenBank no.: ITS PZ500016; LSU PZ500006).

Notes — *Tricholoma fulvoochraceum* belongs to sect. *Genuina* (Fig. 42). Morphologically and phylogenetically, it is closely related to *Tr. aurantium*. Both species share a pileus with a yellowish-brown tint, yellowish white lamellae, and a stipe with brownish appressed fibrillose scales on the surface except at the base^[220,221]. However, *Tr. aurantium* differs by its subglobose basidiospores ($Q = 1.23$), slightly narrower basidia (4.5–6.0 μm), and the absence of clamp-connections^[220]. *Tricholoma vaccinum* (ZRL20191078, ZRL20191174) and *Tricholoma* sp. (ZRL20231809), the latter consisting of only one mature basidiome, both from this section, are also found on the Qinghai–Xizang Plateau. Moreover, *Tr. fulvoochraceum* can be readily distinguished from them by its golden yellow to yellowish-brown pileus with brownish orange reflexed fibrillose squamules and stipe with brownish appressed fibrillose scales. Furthermore, in contrast to the more common *Tr. vaccinum* associated with spruce forests and *Tr. sp.* (ZRL20231809) found in mixed coniferous and broad-leaved forests, the new species *Tr. fulvoochraceum* is exclusively distributed in broad-leaved forests^[210].

Discussion

In this study, an integrative taxonomic and phylogenetic assessment of macrofungi from the Qinghai–Xizang Plateau revealed 31 new species of Agaricales representing 10 families and 10 genera, substantially expanding the known macrofungal diversity in this globally significant yet still underexplored high-elevation region. From an ecological perspective, saprotrophic taxa dominate the assemblage, accounting for 19 species, whereas the remaining taxa are ectomycorrhizal^[92,113,222]. Notably, *Cuphophyllus* species (Hygrophoraceae) appear to be biotrophic and may form cryptic endophytic or symbiotic associations with the roots of herbaceous plants^[222,223].

Based on systematic collections accumulated over the past decade across multiple vegetation types, including coniferous forests, broad-leaved forests, mixed forests, alpine meadows,



Fig. 41 *Tricholoma fulvoochraceum* (a ZRL20200088 holotype). (a) Basidiomata; (b) Basidiospores; (c) Basidia and Basidioles; (d) Cheilocystidia. Scale bars: (a) = 1 cm; (b–d) = 5 μm.

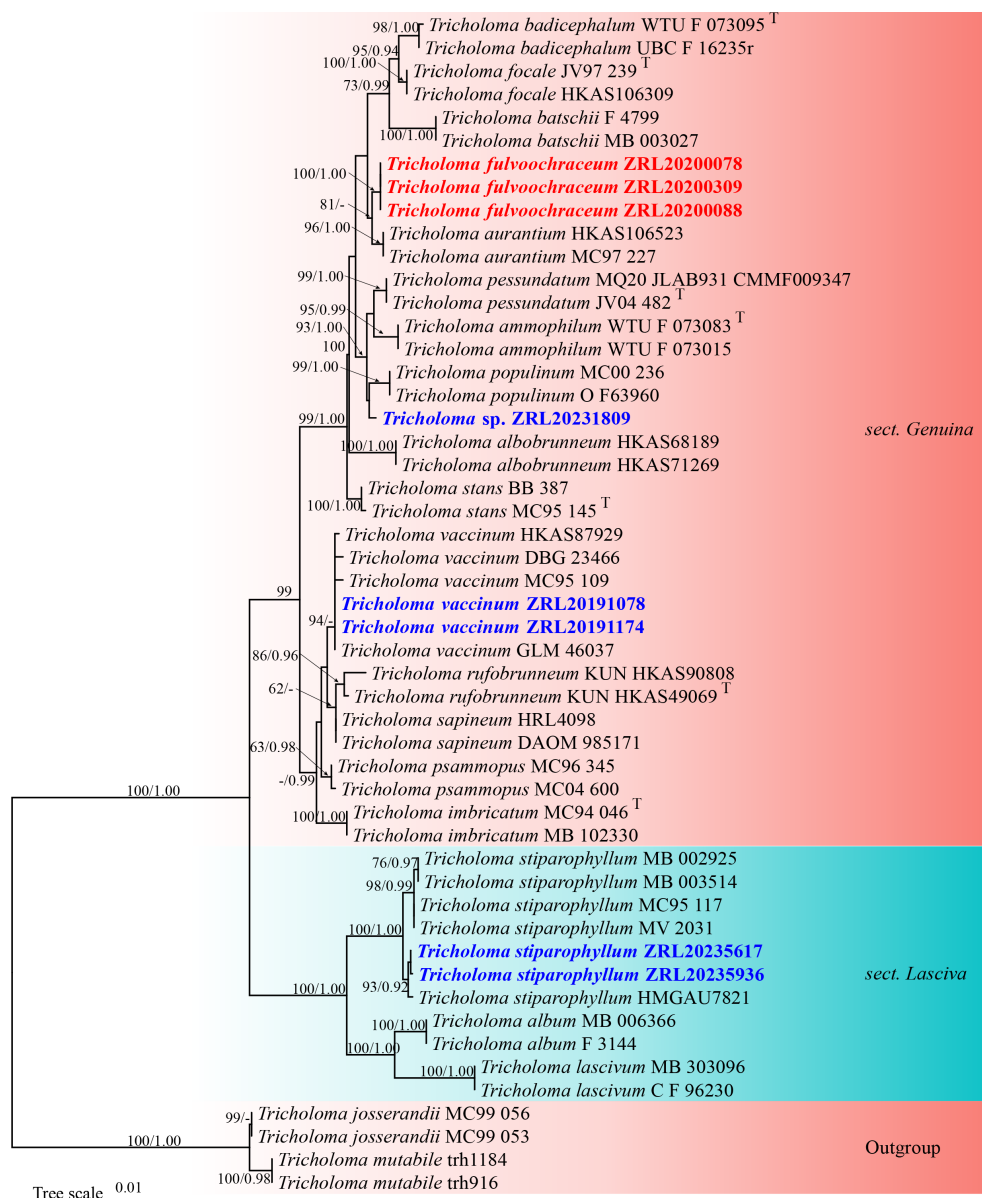


Fig. 42 Molecular phylogenetic analyses of *Tricholoma* species by the maximum likelihood (ML) method based on combined ITS–LSU sequences, rooted with *Tricholoma josserandii* and *Tr. mutabile*. Maximum likelihood bootstrap support values (ML) $\geq 60\%$ and Bayesian posterior probabilities (PP) ≥ 0.90 are shown around nodes as ML/PP. 'T' refers to the type specimen. Sequences newly generated in this study are indicated in bold. New species described herein are shown in red, whereas other specimens newly collected in this study are shown in blue.

and shrublands, the newly discovered taxa are distributed across multiple phylogenetic lineages. This pattern indicates that species-level diversity of Agaricales in alpine regions remains considerably underestimated^[27,184,224–226]. Overall, this taxonomically and ecologically broad sampling provides a preliminary framework for understanding Agaricales diversity on the Qinghai–Xizang Plateau and its surrounding areas, suggesting that high-elevation environments may be associated with increased lineage differentiation^[23,227–229].

These taxa were recorded across vegetation types spanning pronounced gradients in temperature, moisture, substrate continuity, and growing-season length. Such environmental heterogeneity may promote ecological specialization and trait-mediated community assembly^[230,231]. Recent studies further suggest that biodiversity patterns along elevational gradients are shaped not only by climatic filtering but also by biotic interactions,

evolutionary history, and dispersal dynamics operating across spatial and temporal scales^[232–236].

From a biogeographic perspective, these findings can be further interpreted in the context of the unique geographic setting of the Qinghai–Xizang Plateau. The plateau, particularly the southeastern and southern border regions of Xizang, represents an important transition zone linking the East Asian, Himalayan, and Southeast Asian biotas^[237]. Such mountainous transition zones, characterized by pronounced topographic complexity and strong climatic variability, are widely recognized as centres of endemism and evolutionary diversification^[238,239]. Environmental heterogeneity in these regions can generate a wide range of ecological niches and microrefugia, thereby promoting population isolation and speciation processes^[57,240,241]. These mechanisms have been proposed as general drivers shaping biodiversity patterns across montane ecosystems worldwide^[242–244].

Recent investigations of fungal diversity on the Qinghai–Xizang Plateau have revealed a remarkable number of previously undescribed taxa, highlighting the region as an important hotspot of fungal diversity^[59,245–250]. In the present study, we identified a noteworthy morphological trend among a subset of macrofungal species collected from the Qinghai–Xizang Plateau. Although a total of 31 new species across 10 genera were described, five species belonging to five genera, including *Agaricus albicrassipes*, *Collybia yadongensis*, *Infundibulicybe nanorobusta*, *Tricholomopsis dambaensis*, and *Tricholoma fulvoochraceum*, consistently exhibited a distinctive set of traits, characterized by structurally robust basidiomata with relatively small but thick pileus and short, stout stipes. Although this pattern is not universal across all taxa, its repeated occurrence in phylogenetically unrelated genera, together with similar observations from several high-elevation taxa in this region reported in our previous studies^[48,60,125,251], suggests that it is unlikely to be incidental. These convergent morphological features may reflect responses to multiple environmental constraints associated with high-elevation habitats, including strong winds, intense solar radiation, and pronounced fluctuations in moisture availability^[252–254]. Under such conditions, compact and reinforced basidiomata architectures may enhance mechanical stability, reduce desiccation risk, and prolong the period of spore release under environmentally unstable conditions^[255,256]. Moreover, the increasing prominence of these traits at higher elevations further supports the role of altitude-related environmental filtering in shaping macrofungal morphology^[257–260].

At the micromorphological level, most macrofungi are typically characterized by four-spored basidia^[261,262]. However, in several high-elevation species examined in this study, we observed the co-occurrence of two-spored and four-spored basidia within the same taxa. This pattern has also been documented in several alpine taxa^[27,61,184]. This pattern may indicate a shift in reproductive allocation, reflecting a trade-off between propagule number and resource investment per propagule. In harsh high-elevation environments, the production of fewer but potentially more resource-rich spores may enhance establishment success under limiting conditions^[263,264]. The recurrent, albeit limited, co-occurrence of reinforced macromorphology and modified reproductive traits suggests a possible coordination between structural investment and reproductive strategy along environmental gradients^[264]. Nevertheless, macroscopic features of the basidiome do not necessarily predict reproductive traits such as spore size, as these are additionally constrained by aerodynamic trade-offs and developmental processes^[265]. Accordingly, the observed patterns are more plausibly interpreted as the outcome of interacting environmental selection pressures and intrinsic developmental constraints^[256,265,266].

Based on these observations, we propose a preliminary hypothesis that high-elevation environments may promote coordinated adjustments in both morphological and reproductive traits of macrofungi, leading to a characteristic suite of functional attributes. This so-called "high elevation basidiomata syndrome" may be defined by enhanced morphological robustness coupled with shifts in reproductive strategies, potentially reflecting responses to alpine environmental conditions. Because the present study was not designed as a quantitative trait–elevation analysis, this pattern should be regarded as a hypothesis for future testing rather than evidence of confirmed adaptation. Testing this hypothesis will require integrative approaches that combine functional trait analyses, genomic data, and long-term monitoring across elevational gradients^[49,267–270]. More broadly, mountain ecosystems are increasingly recognized as multifunctional systems that can serve as refugia, centres of diversification, and early indicators of

climate-driven biotic reorganization^[242,271,272]. In this context, identifying and understanding potential adaptive trends of macrofungi in high-elevation environments will be essential for predicting future patterns of fungal diversity and their implications for ecosystem functioning under ongoing environmental change^[273].

Climate change is increasingly reshaping biodiversity patterns, leading to habitat shifts, range contractions, and, in some cases, species loss^[274,275]. Against this backdrop, systematic baseline inventories are essential for accurately documenting current diversity, establishing long-term monitoring frameworks, and anticipating future changes^[276,277]. At present, macrofungal cultivation on the Qinghai–Xizang Plateau relies largely on introduced or domesticated strains, whereas native fungal resources remain underutilized. In contrast, indigenous species, having evolved under conditions of low temperatures, strong radiation, and other environmental extremes, may exhibit greater adaptability and stability under low-input or even open-field cultivation systems. The taxa documented in this study also encompass a range of ecological functions and potential applications. However, the edibility, toxicity, and cultivation potential of the newly described species remain unknown and require targeted chemical, toxicological, and cultivation studies^[278,279]. In addition, ectomycorrhizal taxa such as *Laccaria* likely contribute to plant establishment and nutrient acquisition^[280], while saprotrophic groups, including *Gymnopus*, *Collybia*, *Clitocybula*, and *Melanoleuca*, play fundamental roles in organic matter decomposition and nutrient cycling^[281]. Collectively, advancing a systematic understanding of native macrofungal diversity is critical not only for biodiversity conservation but also for sustainable resource utilization and public health awareness.

The present study expands current knowledge of Agaricales diversity on the Qinghai–Xizang Plateau and underscores the region's importance as a natural system for investigating fungal diversification and ecological differentiation. Further efforts that integrate taxonomic resolution with macroecological and evolutionary perspectives will be crucial for advancing our understanding of the processes shaping diversity in environmentally extreme terrestrial ecosystems.

Ethical statements

Not applicable.

Author contributions

The authors confirm their contributions to the paper as follows: conceptualization, supervision, funding acquisition, and writing – review: Zhao R, Phurbu D, Cao B, Thongklang N, Hyde KD; field sampling: Han X, Cao B, Li J, Xing R, He M, Feng H, Wang S, Zhao R, Phurbu D; data collection: Han X, Cao B, Li J, Xing R, He M, Feng H, Wang S; analysis and interpretation of results: Han X, Zhao R, Thongklang N; draft manuscript preparation: Han X. All authors reviewed the results and approved the final version of the manuscript.

Data availability

The data that support the findings of this study are available in the National Center for Biotechnology Information (NCBI) databases and the Fungal Names repository.

Acknowledgments

The research was supported by the Science and Technology Projects of Xizang Autonomous Region, China (XZ202501ZY0019);

the Science and Technology Fundamental Resources Investigation Program, Ministry of Science and Technology of China (Grant No. 2023FY101303); the Macrofungal Diversity of Qinghai Province program (GHMB2024–18); the Projects of Science and Technology Programs of Tibet (Grant No. XZ202202YD0031C); the Biodiversity Survey and Assessment Project of the Ministry of Ecology and Environment, China (2019HJ2096001006); the Project of Background Resources Survey in Shennongjia National Park (SNJNP2022004); the Open Project Fund of Hubei Provincial Key Laboratory for Conservation Biology of Shennongjia Snub-nosed Monkeys (SNJGKL2022004); and the Mae Fah Luang University Research Grant (No. 7702(6)/414, no. 0460). The authors thank the Mycological Herbarium, Institute of Microbiology, Chinese Academy of Sciences (HMAS) for providing access to specimens. We thank Mingjun Zhao and Zhuo Du (HMAS) for their assistance with specimen deposition and providing accession numbers for our specimens at HMAS, and Ke Wang for guidance during the nomenclatural registration process in Fungal Names. We thank Areerat Manowong (Faces of Fungi Fungal Phyla) for assigning FOF numbers to the new taxa described in this study. We thank Zhengrong Ye (The Germplasm Bank of Wild Species) for assistance in plant identification. We thank Chunli Li (Senior Engineer, Institute of Microbiology, CAS) for technical guidance in morphological observations. We thank Shaun Pennycook (Manaaki Whenua: Landcare Research, New Zealand) for his valuable suggestions on fungal nomenclature. We thank Prof. Cheng Jin (Institute of Microbiology, CAS), Prof. Guojie Li (Hebei Agricultural University), Xuming Bai, Shengyu Su, Mingzhe Zhang, Meiqi Wang, Xihao Yu, Linhui Liu, Yanyan Zheng, Mingyue Liu, and Hongmei Dai for assistance in specimen collecting. We also appreciate generous specimen donations from mushroom enthusiasts Yu Zhang and Meng Li.

Conflict of interest

The authors declare that they have no conflict of interest.

Dates

Received 15 April 2026; Revised 18 June 2026; Accepted 8 July 2026; Published online 4 September 2026

References

- [1] Wu F, Zhou LW, Yang ZL, Bau T, Li TH, et al. 2019. Resource diversity of Chinese macrofungi: edible, medicinal and poisonous species. *Fungal Diversity* 98(1):1–76
- [2] Hawksworth DL. 1991. The fungal dimension of biodiversity: magnitude, significance, and conservation. *Mycological research* 95(6):641–655
- [3] Hibbett D, Nagy LG, Nilsson RH. 2025. Fungal diversity, evolution, and classification. *Current Biology* 35(11):R463–R469
- [4] Hawksworth DL, Lücking R. 2017. Fungal diversity revisited: 2.2 to 3.8 million species. *Microbiology Spectrum* 5(4):0052
- [5] Baldrian P. 2017. Forest microbiome: diversity, complexity and dynamics. *FEMS Microbiology Reviews* 41(2):109–130
- [6] Lundell TK, Mäkelä MR, Hildén K. 2010. Lignin-modifying enzymes in filamentous basidiomycetes—ecological, functional and phylogenetic review. *Journal of Basic Microbiology* 50(1):5–20
- [7] Gadd GM. 2021. Fungal biomineralization. *Current Biology* 31(24):R1557–R1563
- [8] Tedersoo L, Bahram M, Pölme S, Kõljalg U, Yorou NS, et al. 2014. Global diversity and geography of soil fungi. *Science* 346:1256688
- [9] Hyde K, Tavakol Noorabadi M, Thiagaraja V, He MQ, Johnston P, et al. 2024. The 2024 Outline of *Fungi* and fungus-like taxa. *Mycosphere* 15(1):5146–6239
- [10] Zhao H, Yuan HS, Cui YJ, Wang K, Dai YC, et al. 2026. Global polypore diversity and distribution patterns. *Fungal Diversity* 136:136002
- [11] Tedersoo L, Bahram M, Zobel M. 2020. How mycorrhizal associations drive plant population and community biology. *Science* 367(6480):eaba1223
- [12] van der Heijden MGA, Martin FM, Selosse MA, Sanders IR. 2015. Mycorrhizal ecology and evolution: the past, the present, and the future. *New Phytologist* 205(4):1406–1423
- [13] Steidinger BS, Crowther TW, Liang J, Van Nuland ME, Werner GDA, et al. 2019. Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature* 569:404–408
- [14] Cai Q, Codjia JEI, Buyck B, Cui YY, Ryberg M, et al. 2024. The evolution of ectomycorrhizal symbiosis and host-plant switches are the main drivers for diversification of Amanitaceae (Agaricales, Basidiomycota). *BMC Biology* 22(1):230
- [15] Niego AGT, Rapior S, Thongklang N, Raspé O, Hyde KD, et al. 2023. Reviewing the contributions of macrofungi to forest ecosystem processes and services. *Fungal Biology Reviews* 44:100294
- [16] Ling ZL, Ma XB, Zhao RL, Cao B, Huang CY, et al. 2025. Overview of the Chinese edible fungi industry of and developing trends analysis. *Mycosphere* 16(1):2712–2775
- [17] Manawasinghe I, Hyde K, Balasuriya A, Suwannarach N, Boonyuen N, et al. 2025. The emerging role of Fungi in sustainable farming and global food security. *Mycosphere* 16(1):4936–5064
- [18] Niego AGT, Lambert C, Mortimer P, Thongklang N, Rapior S, et al. 2023. The contribution of fungi to the global economy. *Fungal Diversity* 121(1):95–137
- [19] Song CG, Xu TM, Xu YH, Wang D, Long Z, et al. 2025. Systematic revision, molecular phylogeny and divergence times of Thelephorales (Basidiomycota). *Mycosphere* 16(1):296–422
- [20] Habib K, Li W, Ren Y, Liu L, Lu C, et al. 2025. Exploration of ascomycetous fungi revealing novel taxa in Southwestern China. *Mycosphere* 16(1):1412–1529
- [21] Dong JH, Chen ML, Chen M, Li Q, Zhu YJ, et al. 2025. Notes, outline, taxonomy and phylogeny of wood-inhabiting Agaricales. *Mycosphere* 16(1):2599–2711
- [22] Antonelli A, Fry C, Smith RJ, Eden J, Kersey PJ, et al. 2020. *State of the World's plants and fungi 2026*. doi: 10.34885/172
- [23] Varga T, Krizsán K, Földi C, Dima B, Sánchez-García M, et al. 2019. Megaphylogeny resolves global patterns of mushroom evolution. *Nature Ecology & Evolution* 3:668–678
- [24] Nagy LG, Branco S, Floudas D, Hibbett DS, Lofgren L, et al. 2026. The biodiversity, genomics, ecology and evolution of mushroom-forming fungi. *Nature Reviews Biodiversity* 2:24–39
- [25] Tedersoo L, Mikryukov V, Zizka A, Bahram M, Hagh-Doust N, et al. 2022. Global patterns in endemicity and vulnerability of soil fungi. *Glob Chang Biol* 28:6696–6710
- [26] Barbi F, Martinović T, Odriozola I, Machac A, Moravcová A, et al. 2025. Disentangling drivers behind fungal diversity gradients along altitude and latitude. *New Phytologist* 247(1):295–308
- [27] Wang XH, Cai Q, Yu FM, Yang ZL, Zhou SY, et al. 2025. New and notable taxa of Basidiomycota on the Qinghai-Xizang Plateau and its surrounding areas. *Fungal Diversity* 133(1):235–437
- [28] Singer R. 1986. *The Agaricales in modern taxonomy*. 4th ed. Koenigstein, Germany: Koeltz Scientific Books. pp. 1–981
- [29] Largent DL. 1986. *How to identify mushrooms to genus I: macroscopic features*. Eureka, California: Mad River Press. pp. 1–166
- [30] Largent DL, Johnson D, Watling R. 1977. *How to identify mushrooms to genus III: microscopic features*. Eureka, California: Mad River Press. pp. 1–148
- [31] Liu F, Wang SH, Cheewangkoon R, Zhao RL. 2024. Uneven distribution of prokaryote-derived horizontal gene transfer in fungi: a lifestyle-dependent phenomenon. *mBio* 16(1):e02855-24
- [32] Alster CJ, Allison SD, Johnson NG, Glassman SI, Treseder KK. 2021. Phenotypic plasticity of fungal traits in response to moisture and temperature. *ISME Communications* 1:43
- [33] Wrzosek M, Ruszkiewicz-Michalska M, Sikora K, Damszel M, Sierota Z. 2017. The plasticity of fungal interactions. *Mycological Progress* 16(2):101–108

- [34] Lin P, Kook M, Yi TH, Yan ZF. 2023. Current fungal taxonomy and developments in the identification system. *Current Microbiology* 80(12):375
- [35] Sánchez-García M, Ryberg M, Khan FK, Varga T, Nagy LG, et al. 2020. Fruiting body form, not nutritional mode, is the major driver of diversification in mushroom-forming fungi. *Proceedings of the National Academy of Sciences of the United States of America* 117(51):32528–32534
- [36] Virágh M, Merényi Z, Cséretics Á, Földi C, Sahu N, et al. 2021. Evolutionary morphogenesis of sexual fruiting bodies in Basidiomycota: toward a new evo-devo synthesis. *Microbiology and Molecular Biology Reviews* 86(1):e00019-21
- [37] Lücking R, Aime MC, Robbertse B, Miller AN, Aoki T, et al. 2021. Fungal taxonomy and sequence-based nomenclature. *Nature Microbiology* 6:540–548
- [38] de Queiroz K, Gauthier J. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Systematic Biology* 39(4):307–322
- [39] Tekpinar AD, Kalmer A. 2019. Utility of various molecular markers in fungal identification and phylogeny. *Nova Hedwigia* 109(1–2):187–224
- [40] Wiens JJ, Blomenkamp EG, Corliss M, Li X. 2026. Global biodiversity and the expanding tree of life. *Proceedings of the National Academy of Sciences of the United States of America* 123(12):e2530656123
- [41] Ke W, Lei C. 2023. 中国菌物分类学和多样性研究的历史与现状概况 [An overview of the historical and current status of fungal taxonomy and diversity in China]. *菌物学报 [Acta Mycologica Sinica]* 42(1):50–62 (in Chinese)
- [42] Mittermeier R, Gil PR, Hoffmann M, Pilgrim J, Brooks T, et al. 2004. *Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions*. Mexico City, Mexico: CEMEX
- [43] Yao T, Thompson LG, Mosbrugger V, Zhang F, Ma Y, et al. 2012. Third pole environment (TPE). *Environmental Development* 3:52–64
- [44] Mosbrugger V, Favre A, Muellner-Riehl A, Päckert M, Mulch A. 2018. Cenozoic evolution of geo-biodiversity in the Tibeto-Himalayan region. In *Mountains, Climate, and Biodiversity*, eds. Hoorn C, Perrigo A, Antonelli A. 1st ed. Hoboken, NJ: Wiley-Blackwell. pp. 429–449
- [45] Yang ZL. 2005. Diversity and biogeography of higher fungi in China. In *Evolutionary genetics of fungi*. Norfolk, UK: Horizon Bioscience. pp. 35–62
- [46] Tapponnier P, Zhiqin X, Roger F, Meyer B, Arnaud N, et al. 2001. Oblique stepwise rise and growth of the Tibet plateau. *Science* 294(5547):1671–1677
- [47] Feng B, Yang Z. 2018. Studies on diversity of higher fungi in Yunnan, southwestern China: a review. *Plant Diversity* 40(4):165–171
- [48] Han XX, Phurbu D, Cao B, Li JX, Zhu XY, et al. 2025. Molecular phylogeny and morphology reveal four new species of *Conocybe* (Bolbitiaceae, Agaricales) from the Qinghai–Xizang Plateau, China. *Journal of Fungi* 11(1):45
- [49] Naranjo-Ortiz MA, Gabaldón T. 2019. Fungal evolution: major ecological adaptations and evolutionary transitions. *Biological Reviews* 94(4):1443–1476
- [50] Körner C. 1995. Alpine plant diversity: a global survey and functional interpretations. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*, eds. Chapin FS, Körner C. Ecological Studies. Vol. 113. Berlin, Heidelberg: Springer. pp. 45–62 doi: [10.1007/978-3-642-78966-3_4](https://doi.org/10.1007/978-3-642-78966-3_4)
- [51] Shooner S, Davies TJ, Saikia P, Dekka J, Bharali S, et al. 2018. Phylogenetic diversity patterns in Himalayan forests reveal evidence for environmental filtering of distinct lineages. *Ecosphere* 9(5):e02157
- [52] Peay KG, Kennedy PG, Talbot JM. 2016. Dimensions of biodiversity in the Earth mycobiome. *Nature Reviews Microbiology* 14:434–447
- [53] Shen C, Gunina A, Luo Y, Wang J, He JZ, et al. 2020. Contrasting patterns and drivers of soil bacterial and fungal diversity across a mountain gradient. *Environmental Microbiology* 22(8):3287–3301
- [54] Vetaas OR. 2021. Mountain biodiversity and elevational gradients. *Frontiers of Biogeography* 13(3):e54146
- [55] Tenorio EA, Montoya P, Norden N, Rodríguez-Buritica S, Salgado-Negret B, et al. 2023. Mountains exhibit a stronger latitudinal diversity gradient than lowland regions. *Journal of Biogeography* 50(6):1026–1036
- [56] Costa FVD, Viana-Júnior AB, Aguiar R, Silveira FAO, Cornelissen TG. 2023. Biodiversity and elevation gradients: insights on sampling biases across worldwide mountains. *Journal of Biogeography* 50(11):1879–1889
- [57] Antonelli A, Kissling WD, Flantua SGA, Bermúdez MA, Mulch A, et al. 2018. Geological and climatic influences on mountain biodiversity. *Nature Geoscience* 11:718–725
- [58] Perrigo A, Hoorn C, Antonelli A. 2020. Why mountains matter for biodiversity. *Journal of Biogeography* 47(2):315–325
- [59] Cui YJ, Wu YD, Jiang YH, Zhu AH, Wu F, et al. 2025. Diversity of macrofungi in southeast Xizang 1. The wood-decay fungi. *Mycology* 16(2):635–669
- [60] Liu X, Chen Q, Xiang Q, Gu Y, Han X, et al. 2025. Additions to the *Entoloma* (Agaricales, Entolomataceae) from China: description of five species with one new to science. *Mycosphaera* 123:89–103
- [61] Wang K, Liu SL, Liu XZ, Hong P, Wei HW, et al. 2024. Catalogue of fungi in China 3. New taxa of macrofungi from southern Xizang, China. *Mycology* 16:91–123
- [62] Xu R, Hyde K, Li JN, Boonmee S, Liu NG, et al. 2025. Lignicolous freshwater fungi of the pan Qinghai-Xizang Plateau, China. *Fungal Diversity* 133(1):23–234
- [63] Zhu Y, Zhou L, Liu J, Yuan Y, Wei Y, et al. 2026. Thirty new species in Thelephorales and Hymenochaetales from the Eastern Himalayas and Southern China. *Mycosphere* 17:e001
- [64] Liu S, Pan M, Cui BK, Zhu B. 2025. Catalogue of fungi in China 5. Preliminary survey of macrofungi in Medog, Southwest China. *Mycology* 16(4):1589–1636
- [65] Wang SH, Li GJ, Phurbu D, He MQ, Zhang MZ, et al. 2024. Four new species of *Russula* from the Xizang Autonomous Region and other provinces of China. *Mycology* 15(2):210–237
- [66] Li JX, Cao B, Phurbu D, He MQ, Zhu XY, et al. 2024. The revision of the taxonomic system of Lycoperdaceae. *Mycosphere* 15(1):4919–5016
- [67] Xie ML, Dima B, Wang K, Phukhamsakda C, Li Y, et al. 2025. Taxonomy and phylogeny of *Cortinarius* sect. *Anomali* in China. *Persoonia* 54:225–263
- [68] Zhou Y, Jia X, Han L, Liu Z, Kang S, et al. 2021. Fungal community diversity in soils along an elevation gradient in a *Quercus aliena* var. *acuteserrata* forest in Qinling Mountains, China. *Applied Soil Ecology* 167:104104
- [69] Zhang Y, Zhou DQ, Zhao Q, Zhou TX, Hyde KD. 2010. Diversity and ecological distribution of macrofungi in the Laojun Mountain region, southwestern China. *Biodiversity and Conservation* 19(12):3545–3563
- [70] Kornerup A, Wanscher J. 1967. *Methuen handbook of colour*. London, UK: Eyre Methuen
- [71] Tang SM, Vadthanarat S, Raghoonundon B, Luo ZL, Zhu XY, et al. 2024. New species and new records of *Laccaria* (Agaricales, Basidiomycota) from Northern Thailand. *Mycosphaera* 107:189–217
- [72] Antonín V, Ďuriška O, Jančovičová S, Para R, Kudláček T, et al. 2022. Multilocus phylogeny and taxonomy of European *Melanoleuca* subgenus *Melanoleuca*. *Mycologia* 114(1):114–143
- [73] White TJ, Bruns T, Lee S, Taylor J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In *PCR protocols: a guide to methods and applications*, eds. Innis MA, Gelfand DH, Sninsky JJ, White TJ. Cambridge, UK: Academic Press. pp. 315–322 doi: [10.1016/b978-0-12-372180-8.50042-1](https://doi.org/10.1016/b978-0-12-372180-8.50042-1)
- [74] Gardes M, Bruns TD. 1993. ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2(2):113–118
- [75] Hopple Jr JS, Vilgalys R. 1999. Phylogenetic relationships in the mushroom genus *Coprinus* and dark-spored allies based on sequence data from the nuclear gene coding for the large ribosomal subunit RNA: divergent domains, outgroups, and monophyly. *Molecular Phylogenetics and Evolution* 13(1):1–19
- [76] Moncalvo JM, Lutzoni FM, Rehner SA, Johnson J, Vilgalys R. 2000. Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. *Systematic Biology* 49(2):278–305

- [77] Matheny PB. 2005. Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (*Inocybe*; Agaricales). *Molecular Phylogenetics and Evolution* 35(1):1–20
- [78] Rehner SA, Buckley E. 2005. A *Beauveria* phylogeny inferred from nuclear ITS and EF1- α sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. *Mycologia* 97(1):84–98
- [79] Antonín V, Ďuriška O, Jančovičová S, Tomšovský M. 2015. Identity of *Agaricus brevipes* Bull. (*Melanoleuca brevipes*, *Tricholomataceae*, Basidiomycota). *Mycological Progress* 14(11):107
- [80] Xu YD, Zhang P, Chen ZH, He ZM. 2025. Three new species and two new records of the genus *Laccaria* (Agaricales, Basidiomycota) from subtropical China based on morphological and multi-locus phylogenetic evidence. *Mycologia* 123:147–170
- [81] Long X, He B, Fang Y, Tang C. 2016. Identification and characterization of the glucose-6-phosphate dehydrogenase gene family in the para rubber tree, *Hevea brasiliensis*. *Frontiers in Plant Science* 7:215
- [82] Katoh K, Rozewicki J, Yamada KD. 2017. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 20(4):1160–1166
- [83] Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*. Vol. 41. pp. 95–98 doi: [10.14601/Phytopathol_Mediterr-14998u1.29](https://doi.org/10.14601/Phytopathol_Mediterr-14998u1.29)
- [84] Zhang D, Gao F, Jakovlić I, Zou H, Zhang J, et al. 2020. PhyloSuite: an integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. *Molecular Ecology Resources* 20(1):348–355
- [85] Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. 2010 Gateway Computing Environments Workshop (GCE), New Orleans, LA, USA, 14 November 2010. New York, NY: IEEE doi: [10.1109/GCE.2010.5676129](https://doi.org/10.1109/GCE.2010.5676129)
- [86] Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22(21):2688–2690
- [87] Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B. 2017. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* 34(3):772–773
- [88] Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, et al. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61(3):539–542
- [89] Xie J, Chen Y, Cai G, Cai R, Hu Z, et al. 2023. Tree Visualization By One Table (tvBOT): a web application for visualizing, modifying and annotating phylogenetic trees. *Nucleic Acids Research* 51(W1):W587–W592
- [90] Zhao RL, Zhou JL, Chen J, Margaritescu S, Sánchez-Ramírez S, et al. 2016. Towards standardizing taxonomic ranks using divergence times—a case study for reconstruction of the *Agaricus* taxonomic system. *Fungal Diversity* 78(1):239–292
- [91] Liang YS, Huang XX, Lin ZJ, He DL, Qiu LH. 2024. Three new species of *Agaricus* from Baiyun Mountain, Guangzhou, China. *Mycologia* 116(3):431–448
- [92] He MQ, Zhao RL, Liu DM, Denchev TT, Begerow D, et al. 2022. Species diversity of Basidiomycota. *Fungal Diversity* 114(1):281–325
- [93] Lin C, Liu B, Zhao M, Ma K, Ji L. 2025. Catalogue of life China: towards an index of known species present in China. *The Innovation Life* 3(3):100140
- [94] Zhao R, Karunarathna S, Raspé O, Parra LA, Guinberteau J, et al. 2011. Major clades in tropical *Agaricus*. *Fungal Diversity* 51(1):279–296
- [95] Chen J, Callac P, Parra LA, Karunarathna SC, He MQ, et al. 2017. Study in *Agaricus* subgenus *Minores* and allied clades reveals a new American subgenus and contrasting phylogenetic patterns in Europe and Greater Mekong Subregion. *Persoonia – Molecular Phylogeny and Evolution of Fungi* 38:170–196
- [96] Parra LA, Angelini C, Miller KO, Chen J. 2024. *Agaricus subiculosus*, a new species of the genus *Agaricus* sect. *Minores* from Puerto Rico (USA). *MycolObs - Mycological Observations* 8:33–43
- [97] Cao B, Phurbu D, Ralaivelarisoa A, Liimatainen K, Niskanen T, et al. 2025. Fungal diversity notes 1919–2016: taxonomic and phylogenetic contributions to fungal taxa. *Fungal Diversity* 132:425–651
- [98] Hussain S, Al-Kharousi M, Al-Muharabi MA, Al-Maqbali Da, Al-Shabibi Z, et al. 2022. Phylogeny of *Agaricus* subgenus *Pseudochitonina* with the description of a new section and a new species from Oman. *Mycological Progress* 21(8):72
- [99] Parra LA, Angelini C, Ortiz-Santana B, Mata G, Billette C, et al. 2018. The genus *Agaricus* in the Caribbean. Nine new taxa mostly based on collections from the Dominican Republic. *Phytotaxa* 345(3):219–271
- [100] He MQ, Chuankid B, Hyde KD, Cheewangkoon R, Zhao RL. 2018. A new section and species of *Agaricus* subgenus *Pseudochitonina* from Thailand. *Mycologia* 40:53–67
- [101] Liu AQ, Dai RC, Zhang MZ, Cao B, Xi YL, et al. 2020. Species of *Agaricus* section *Agaricus* from China. *Phytotaxa* 452(1):1–18
- [102] Parra Sánchez LA. 2008. *Fungi Europaei Agaricus L. Allopassillota, Nauta & Bas. Fungi Europaei*. Vol. 1. Alassio, Italy: Edizioni Candusso
- [103] Kerrigan RW. 2016. *Agaricus of North America*. New York: New York Botanical Garden Press
- [104] Liu AQ. 2020. 中国主要林区蘑菇属系统学研究 [*Phylogenetic study of Agaricus in main forests of China*]. Thesis. 中国科学院大学 [University of Chinese Academy of Sciences], Beijing, China (in Chinese). pp. 1–269
- [105] Yang KL, Lin JY, Li GM, Yang ZL. 2025. New and interesting fungi from Guangzhou City, South China. *Phytotaxa* 707(1):1–95
- [106] Wang SE, Bau T. 2024. Six new species of *Agaricus* (Agaricaceae, Agaricales) from Northeast China. *Journal of Fungi* 10(1):59
- [107] Wang SE, Chen SA, Huang HC, Lin DM, Liu PH. 2025. Three new species of *Agaricus* (Agaricaceae, Agaricales) from southern China. *Mycologia* 119:47–66
- [108] Cao B, He MQ, Ling ZL, Zhang MZ, Wei SL, et al. 2021. A revision of *Agaricus* section *Arvenses* with nine new species from China. *Mycologia* 113(1):191–211
- [109] He ZM, Chen ZH, Bau T, Wang GS, Yang ZL. 2023. Systematic arrangement within the family Clitocybaceae (Tricholomatineae, Agaricales): phylogenetic and phylogenomic evidence, morphological data and muscarine-producing innovation. *Fungal Diversity* 123(1):1–47
- [110] Qi Y, Xu A, Yang L, Guo H, Guo Y, et al. 2025. Multiple analyses reveal evidence for three new species of *Collybia* (Clitocybaceae, Basidiomycete) from China. *Journal of Fungi* 11(5):371
- [111] Breitenbach J, Kränzlin F. 1991. *Fungi of Switzerland 3: Boletales and Agaricales (Bolets and Agarics Pt. 1)*. Luzern: Mykologia
- [112] Ronikier M, Miśkiewicz A. 2002. *Clitocybe dryadicola* (J. Favre) Harmaja—a new species for Poland and the Carpathians recorded in Tatra mountains. *Cryptogamie Mycologie* 23(2):163–166
- [113] He MQ, Zhao RL, Hyde KD, Begerow D, Kemler M, et al. 2019. Notes, outline and divergence times of Basidiomycota. *Fungal Diversity* 99(1):105–367
- [114] Tang SM, Zhao G, Niu KY, Li RY, Yu FM, et al. 2025. Species Diversity of Edible Mushrooms I—four new *Laccaria* species from Yunnan Province, China. *Journal of Fungi* 11(3):189
- [115] Li J, Che NJ, Cui YY. 2024. Three new species of *Laccaria* (Agaricales, Basidiomycota) from Southwest China (Yunnan) based on morphological and multi-gene sequence data. *Frontiers in Microbiology* 15:1411488
- [116] Zhang SF, Gui Y, Zhu GS, Shang NJ, Li B, et al. 2024. *Laccaria guizhouensis* sp. nov. (Agaricales, Basidiomycota) from southwest China. *New Zealand Journal of Botany* 62(2–3):138–150
- [117] Singer R. 1962. The Agaricales in modern taxonomy. 2nd ed. Weinheim: J Cramer
- [118] Berkeley MJ, Broome CE. 1883. XLIII.—notices of British fungi. *Annals and Magazine of Natural History* 12(72):370–374
- [119] Mueller GM. 1984. New North American species of *Laccaria* (Agaricales). *Mycotaxon* 20(1):101–116
- [120] Mueller GM, Vellinga EC. 1986. Taxonomic and nomenclatural notes on *Laccaria* B. & Br. *Laccaria amethystea*, *L. fraterna*, *L. laccata*, *L. pumila*, and their synonyms. *Persoonia – Molecular Phylogeny and Evolution of Fungi* 13:27–43
- [121] Mueller GM. 1991. *Laccaria laccata* complex in North America and Sweden: intercollection pairing and morphometric analyses. *Mycologia* 83(5):578–594

- [122] Wilson AW, May TW, Mueller GM. 2017. Biogeography of the ectomycorrhizal mushroom genus *Laccaria*. In *Biogeography of Mycorrhizal Symbiosis*, ed. L Tedersoo. Ecological Studies. Cham: Springer International Publishing. pp. 273–297 doi: [10.1007/978-3-319-56363-3_13](https://doi.org/10.1007/978-3-319-56363-3_13)
- [123] Quan L, Shi L, Zhang S, Yao Q, Yang Q, et al. 2023. Ectomycorrhizal fungi, two species of *Laccaria*, differentially block the migration and accumulation of cadmium and copper in *Pinus densiflora*. *Chemosphere* 334:138857
- [124] Cullings K, Desimone J. 2020. Rapid response by the Ectomycorrhizal (ECM) community of a lodgepole pine forest to diesel application as indicated by Laccase gene fragment diversity. *Journal of Bioremediation & Biodegradation* 5:235
- [125] Hongsanan S, Khuna S, Manawasinghe IS, Tibpromma S, Chethana KWT, et al. 2025. Mycosphere notes 521–571: a special edition of fungal biodiversity to celebrate Kevin D. Hyde's 70th birthday and his exceptional contributions to Mycology. *Mycosphere* 16(2):2002–2180
- [126] Zhang M, Gao XL, Mu LQ, Deng WQ. 2023. Morphology and molecular phylogeny reveal five new species of *Laccaria* (Hydnangiaceae, Agaricales) from Southern China. *Journal of Fungi* 9(12):1179
- [127] Popa F, Rexer KH, Donges K, Yang ZL, Kost GW. 2014. Three new *Laccaria* species from Southwest China (Yunnan). *Mycological Progress* 13(4):1105–1117
- [128] Wilson AW, Hosaka K, Perry BA, Mueller GM. 2013. *Laccaria* (Agaricomycetes, Basidiomycota) from Tibet (Xizang Autonomous Region, China). *Mycoscience* 54(6):406–419
- [129] Cui YY, Cai Q, Li J, Yang ZL. 2021. Two new *Laccaria* species from China based on molecular and morphological evidence. *Mycological Progress* 20(4):567–576
- [130] Cho HJ, Park MS, Lee H, Oh SY, Wilson AW, et al. 2018. A systematic revision of the ectomycorrhizal genus *Laccaria* from Korea. *Mycologia* 110(5):948–961
- [131] Dovana F, Scali E, Lopez Del Visco C, Moreno G, Para R, et al. 2025. Solving the enigma of the identity of *Laccaria laccata*. *Journal of Fungi* 11(8):575
- [132] Orton PD. 1960. New check list of British Agarics and Boleti: part III. Notes on genera and species in the list. *Transactions of the British Mycological Society* 43(2):159–384
- [133] Imai S. 1938. Studies on the Agaricaceae of Hokkaido I. *Journal of the Faculty of Agriculture, Hokkaido Imperial University* 43(1):1–178
- [134] Choudhary S, Pal Sharma Y, Uniyal P. 2025. *Laccaria friesii* sp. nov. (Hydnangiaceae), a new species from northwestern Himalaya of Uttarakhand, India. *Nordic Journal of Botany* 2025(5):e04617
- [135] Li F. 2020. Two new species of *Laccaria* from South China, with a note on *Hodophilus glaberipes*. *Mycological Progress* 19(5):525–539
- [136] Mueller G. 1991. *Laccaria longipes*, a new North American species of the *Laccaria laccata* complex. *Mycotaxon* 40:145–150
- [137] McNabb RFR. 1972. The Tricholomataceae of New Zealand 1. *Laccaria* Berk. & Br. *New Zealand Journal of Botany* 10(3):461–484
- [138] Ye L, Mortimer PE, Tang SM, Tao Q, He G, et al. 2025. *Cuphophyllus lijiangensis* sp. nov. (Hygrophoraceae, Agaricales) from Yunnan, China. *New Zealand Journal of Botany* 63(2–3):354–369
- [139] Latha KPD, Varsha MK, Abhimanyu C, Ajmal M. 2025. *Cuphophyllus aureus*—a new species from Kerala state, India. *Phytotaxa* 721:265–276
- [140] Crous PW, Catcheside DEA, Catcheside PS, Alfenas AC, Alfenas RF, et al. 2025. Fungal Planet description sheets: 1781–1866. *Persoonia – Molecular Phylogeny and Evolution of Fungi* 54:327–587
- [141] Xia W, Wang C, Li T, Deng W, Yue H, Zhang M. 2025. *Cuphophyllus striatus* (Cuphophyllaceae, Agaricales), a new species from southwestern China. *Phytotaxa* 701(2):207–215
- [142] Lodge DJ, Padamsee M, Matheny PB, Aime MC, Cantrell SA, et al. 2014. Molecular phylogeny, morphology, pigment chemistry and ecology in Hygrophoraceae (Agaricales). *Fungal Diversity* 64(1):1–99
- [143] Voitk A, Saar I, Lodge DJ, Boertmann D, Berch SM, et al. 2020. New species and reports of *Cuphophyllus* from northern North America compared with related Eurasian species. *Mycologia* 112(2):438–452
- [144] Griffith GW, Easton GL, Jones AW. 2002. Ecology and diversity of waxcap (*Hygrocybe* spp.) Fungi. *Botanical Journal of Scotland* 54(1):7–22
- [145] Bon M. 1984. Le genre *Cuphophyllus* (Donk) sp. nov. *Documents Mycologiques* 14(56):9–12
- [146] Boertmann D. 2010. *The genus Hygrocybe. 2nd revised edition. Fungi of Northern Europe*. Vol. 1. Denmark: Svampetryk. pp. 200
- [147] Zhang YX, Mao N, Li T, Fan L. 2024. Two new species of *Infundibulicybe* (Omphalinaceae, Agaricales) from northern China. *Phytotaxa* 649(2):193–210
- [148] Harmaja H. 2003. Notes on *Clitocybe* s. lato (Agaricales). *Annales Botanici Fennici* 40(3):213–218
- [149] Vizzini A, Contu M, Musumeci E, Ercole E. 2011. A new taxon in the *Infundibulicybe gibba* complex (Basidiomycota, Agaricales, Tricholomataceae) from Sardinia (Italy). *Mycologia* 103(1):203–208
- [150] Vizzini A, Alvarado P, Consiglio G, Marchetti M, Xu J. 2024. Family matters inside the order Agaricales: systematic reorganization and classification of incertae sedis clitocyboid, pleurotoid and tricholomatoid taxa based on an updated 6-gene phylogeny. *Studies in Mycology* 107:67–148
- [151] Binder M, Larsson KH, Matheny PB, Hibbett DS. 2010. Amylocorticiales ord. nov. and Jaapiiales ord. nov.: early diverging clades of Agaricomycetidae dominated by corticioid forms. *Mycologia* 102(4):865–880
- [152] He ZM, Yang ZL. 2022. The genera *Bonomyces*, *Harmajaea* and *Notholepista* from Northwestern China: two new species and a new record. *Mycological Progress* 21(2):26
- [153] He ZM, Yang ZL. 2023. A contribution to the knowledge of the genus *Infundibulicybe* (Tricholomatineae, Agaricales) in China: two new species and five redescribed taxa. *Mycologia* 115(5):693–713
- [154] Wijesinghe SN, Deng Y, Yuan Q, Zhou H, Wang L, et al. 2025. Mycosphere Notes 572–624: exploring the hidden diversity of fungi and fungilike taxa in different terrestrial microhabitats. *Mycosphere* 16(1):2975–3129
- [155] Hu JJ, Tuo YL, Qi ZX, Jiang DH, Li Y, Zhang B. 2025. Two new species of *Gymnopus* sect. *Levipedes* (Omphalotaceae, Agaricales) from Central and North China. *MycoKeys* 118:19–34
- [156] Li JP, Gao J, Li Y, Xie ML, Li CT. 2026. New additions to *Omphalotaceae* (Agaricales, Basidiomycota): two new rhizomorph-forming species from China. *MycoKeys* 131:41–59
- [157] Deng CY, Wang WK, Li JP, Antonín V. 2025. Morphology and phylogeny reveal *Gymnopus pseudoandrosaceus* sp. nov. (Agaricales, Basidiomycota) from southwest China. *Phytotaxa* 683(3):218–228
- [158] Feng WC, Li XY, Cui YY, Cai Q. 2025. Species diversity of *Gymnopus* section *Levipedes* in southwestern China, with a description of three new species. *Journal of Fungi* 11(2):88
- [159] Fan LF, Wang BY, Ma TF, Li B, Ma JW, et al. 2024. Three new species of *Gymnopus* and *Mycena* (Agaricales, Basidiomycota) from Northwestern China. *Frontiers in Microbiology* 15:1487598
- [160] Manawasinghe IS, Hyde KD, Wanasinghe DN, Karunarathna SC, Maharachchikumbura S, et al. 2025. Fungal diversity notes 1818–1918: taxonomic and phylogenetic contributions on genera and species of fungi. *Fungal Diversity* 130(1):1–261
- [161] Hu JJ, Tuo YL, Qi ZX, Li XF, Jiang DH, et al. 2024. The combination of morphological and phylogenetic evidence reveals four new *Gymnopus* species and new distribution. *Journal of Fungi* 10(10):672
- [162] Mata JL, Hughes KW, Petersen R. 2006. An investigation of /omphalotaceae (Fungi: Euagarics) with emphasis on the genus *Gymnopus*. *Sydowia* 58:191–289
- [163] Hu JJ, Zhang B. 2023. 广义金钱菌属真菌研究概况 [Overview of research on fungi of the genus *Flococcus* in a broad sense]. *菌物学报 [Acta Mycologica Sinica]* 42(1):143–159 (in Chinese)
- [164] Oliveira JJS, Vargas-Isla R, Cabral TS, Rodrigues DP, Ishikawa NK. 2019. Progress on the phylogeny of the Omphalotaceae: *Gymnopus* s. str., *Marasmiellus* s. str., *Paragymnopus* gen. nov. and *Pusillomyces* gen. nov. *Mycological Progress* 18(5):713–739
- [165] Noordeloos ME, Antonín V. 2008. Contribution to a monograph of marasmoid and collybioid fungi in Europe. *Czech Mycology* 60:21–27
- [166] Fries E. 1821. *Systema mycologicum : sistens fungorum ordines, genera et species, huc usque cognitae, quas ad normam methodi naturalis determinavit*. Lundae: Ex Officina Berlingiana doi: [10.5962/bhl.title.5378](https://doi.org/10.5962/bhl.title.5378)

- [167] Antonín V, Halling RE, Noordeloos ME. 1997. Generic concepts within the groups of *Marasmius* and *Collybia* sensu lato. *Mycotaxon* 63:359–368
- [168] Antonín V, Ryoo R, Ka KH. 2014. Marasmioid and gymnopoid fungi of the Republic of Korea. 7. *Gymnopus* sect. *Androsacei*. *Mycological Progress* 13:703–718
- [169] Desjardin DE, Halling RE, Hemmes DE. 1999. Agaricales of the Hawaiian Islands. 5. The genera *Rhodocollybia* and *Gymnopus*. *Mycologia* 91:166–176
- [170] Sun YL, Luo Y, Bau T. 2021. 吉林省担子菌补记 (十) [Notes on basidiomycetes of Jilin province (X)]. 菌物研究 *[Journal of Fungal Research]* 19:139–147 (in Chinese)
- [171] Petersen RH, Hughes KW. 2021. *Collybiopsis* and its type species, *Collybiopsis ramealis*. *Mycotaxon* 136(2):263–349
- [172] Ryoo R, Antonín V, Ka KH, Tomšovský M. 2016. Marasmioid and gymnopoid fungi of the Republic of Korea. 8. *Gymnopus* section *Impudicae*. *Phytotaxa* 286(2):75–88
- [173] Sesli E. 2022. *Gymnopus impudicus* (Fr.) Antonín, Halling & Noordel.: a new record for the Turkish mycota. *Biological Diversity and Conservation* 15:103–106
- [174] Antonín V, Noordeloos ME. 2010. A monograph of marasmioid and collybioid fungi in Europe: with 131 figures and 130 coloured plates. Eching, Germany: IHW-Verlag
- [175] Antonín V, Sedláč P, Tomšovský M. 2013. Taxonomy and phylogeny of European *Gymnopus* subsection *levipedes* (Basidiomycota, Omphalotaceae). *Persoonia – Molecular Phylogeny and Evolution of Fungi* 31:179–187
- [176] The New York Botanical Garden. 1907. *North American flora*. New York: New York Botanical Garden
- [177] Li JP, Oliveira J, Pan MC, Deng CY, Antonín V, et al. 2024. Notes on all genera of Omphalotaceae: expanding the taxonomic spectrum in China and revisiting historical type specimens. *Mycosphere* 15(1):1522–1594
- [178] Hu JJ, Song LR, Tuo YL, Zhao GP, Yue L, et al. 2022. Multiple evidences reveal new species and a new record of smelly *Gymnopus* (Agaricales, Omphalotaceae) from China. *Frontiers in Microbiology* 13:968617
- [179] Wang GS, Cai Q, Hao YJ, Bau T, Chen ZH, et al. 2023. Phylogenetic and taxonomic updates of Agaricales, with an emphasis on *Tricholomopsis*. *Mycology* 15(2):180–209
- [180] Thapa A, Tamang J, Acharya K. 2023. A new species of *Tricholomopsis* (Agaricales) from Darjeeling Hills, India. *Italian Journal of Mycology* 52:144–153
- [181] Wang G, Guo T, Chen X, Liao J, Ma Y, et al. 2026. Two new species of *Tricholomopsis* (Agaricales) from China based on molecular phylogenetic and morphological evidence. *MycoKeys* 131:235–249
- [182] Hosen MI, Xu JY, Li T, Gates G, Li TH. 2020. *Tricholomopsis rubroaurantiaca*, a new species of Tricholomataceae from southern China. *Myco-science* 61(6):342–347
- [183] Holec J, Kunca V, Kolařík M. 2019. *Tricholomopsis badinensis* sp. nov. and *T. sulphureoides*—two rare fungi of European old-growth forests. *Mycological Progress* 18(3):321–334
- [184] Lu JR, Lei L, Yu FM, Zhu XT, Liang JF, et al. 2025. Diversity of macrofungi in southeast Xizang, China 2. *Mycology* 17(1):1–57
- [185] Smith AH. 1960. *Tricholomopsis* (Agaricales) in the Western hemisphere. *Brittonia* 12:41–70
- [186] Choudhary S, Mehmood T, Sharma YP, Uniyal P. 2025. Two novel species of genus *Melanoleuca* (Agaricales) from Indian Himalaya. *Feddes Repertorium* 136(4):277–286
- [187] Antonín V, Ďuriška O, Jančovičová S, Kudláček T, Para R, et al. 2022. *Melanoleuca monticola* and *M. romanensis*, two new European species of *Melanoleuca*, and comments to *M. graminicola* group. Preprint
- [188] Voto P, Maraia G, Milanese V. 2021. *Melanoleuca chalcibasis* sp. nov. from the Bosco Nordio (Italy). *Mycological Observations* 1:35–43
- [189] Qi Y, Li CH, Song YM, Zhang M, Guo HB, et al. 2022. *Melanoleuca subgriseoflava* and *M. substridula*—two new *Melanoleuca* species (Agaricales, Basidiomycota) described from China. *PeerJ* 10:e13807
- [190] Antonín V, Ševčíková H, Para R, Ďuriška O, Kudláček T, et al. 2021. *Melanoleuca galbuserae*, *M. fontenlae* and *M. acystidiata*—three new species in subgenus *Urticocystis* (Pluteaceae, Basidiomycota) with Comments on *M. castaneofusca* and related species. *Journal of Fungi* 7(3):191
- [191] Pei Y, Guo HB, Liu TZ, Qin WQ, Zhao D, et al. 2021. Three new *Melanoleuca* species (Agaricales, Basidiomycota) from north-eastern China, supported by morphological and molecular data. *MycoKeys* 80:133–148
- [192] Armada F. 2020. Quelques basidiomycètes nouveaux ou rares pour l'Andalousie, découverts près de Grenade dans la Sierra Nevada (Espagne). *Bulletin Mycologique et Botanique Dauphiné-Savoie* 239:67–78
- [193] Crous PW, Cowan DA, Maggs-Kölling G, Yilmaz N, Larsson E, et al. 2020. Fungal Planet description sheets: 1112–1181. *Persoonia – Molecular Phylogeny and Evolution of Fungi* 45:251–409
- [194] Ullah Z, Khurshid R, Khan MB, Ahmad I, Jabeen S, et al. 2020. *Melanoleuca kashmirensis* sp. nov. in subg. *Urticocystis* from Pakistan. *Phytotaxa* 434(1):89–100
- [195] Vizzini A, Para R, Fontenla R, Ghignone S, Ercole E. 2012. A preliminary ITS phylogeny of *Melanoleuca* (Agaricales), with special reference to European taxa. *Mycotaxon* 118(1):361–381
- [196] Boekhout T. 1988. Notulae ad floram agaricinam neerlandicam—XVI. New taxa, new combinations in *Melanoleuca* Pat. and notes on rare species in the Netherlands. *Persoonia – Molecular Phylogeny and Evolution of Fungi* 13(4):397–431
- [197] Antonín V, Ďuriška O, Jančovičová S, Kudláček T, Para R, et al. 2023. Two new European species of *Melanoleuca* (Fungi, Agaricales) with comments on the *M. graminicola* group. *Systematics and Biodiversity* 21:2218375
- [198] Yu XD, Lv SX, Ma D, Li FF, Lin Y, et al. 2014. Two new species of *Melanoleuca* (Agaricales, Basidiomycota) from northeastern China, supported by morphological and molecular data. *Myco-science* 55(6):456–461
- [199] Elahi H, Niazi AR. 2024. *Melanoleuca lalsuhanraensis*, a new species from Lal Suhanra National Park, Punjab, Pakistan. *Nordic Journal of Botany* 7:e04245
- [200] Bigelow HE. 1973. The genus *Clitocybula*. *Mycologia* 65(5):1101–1116
- [201] Antonín V, Borovička J, Holec J, Piltaver A, Kolařík M. 2019. Taxonomic update of *Clitocybula* sensu lato with a new generic classification. *Fungal biology* 123(6):431–447
- [202] Santamaría N, Rubio Casas L, Zamora JC. 2022. *Clitocybula ellipsospora*, a new species found in the Iberian Peninsula. *Fungi Iberici* 2:75–88
- [203] Na Q, Zeng H, Hu Y, Ding H, Ke B, et al. 2024. Morphological and phylogenetic analyses reveal five new species of Porothelaeaceae (Agaricales, Basidiomycota) from China. *MycoKeys* 105:49–95
- [204] Singer R. 1978. Keys for the identification of the species of Agaricales II. *Sydowia* 31(1–6):193–237
- [205] Malysheva E, Morozova O, Contu M. 2011. New combinations in *Clitocybula*: a study of cystidiate *Pseudoomphalina* species (Basidiomycota, Agaricomycetes). *Sydowia* 63(1):85–104
- [206] Antonín V, Beran M, Borovička J, Dvořák D, Holec J. 2011. *Clitocybula familia* (Fungi, Agaricales)—taxonomy, distribution, ecology and first records in the Czech Republic and Slovakia. *Czech Mycology* 63(1):1–11
- [207] Ding XX, Xu X, Cui YY, Kost G, Wang PM, et al. 2023. A fifty-locus phylogenetic analysis provides deep insights into the phylogeny of *Tricholoma* (Tricholomataceae, Agaricales). *Persoonia – Molecular Phylogeny and Evolution of Fungi* 50:1–26
- [208] Tedersoo L, May TW, Smith ME. 2010. Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. *Mycorrhiza* 20(4):217–263
- [209] Mao N, Yang JJ, Zhang YX, Li T, Fan L. 2025. Species diversity of *Tricholoma* (Agaricales, Tricholomataceae) from Shanxi Province of northern China with the description of four new species. *MycoKeys* 112:59–80
- [210] Bessette AE, Bessette AR, Roody WC, Trudell SA. 2013. *Tricholomas of North America: a mushroom field guide*. Austin: University of Texas Press. pp. 1–220 doi: 10.7560/742338
- [211] Heilmann-Clausen J, Christensen M, Frøslev TG, Kjoller R. 2017. Taxonomy of *Tricholoma* in northern Europe based on ITS sequence data

- and morphological characters. *Persoonia - Molecular Phylogeny and Evolution of Fungi* 38:38–57
- [212] Reschke K, Popa F, Yang ZL, Kost G. 2018. Diversity and taxonomy of *Tricholoma* species from Yunnan, China, and notes on species from Europe and North America. *Mycologia* 110(6):1081–1109
- [213] Kost G. 1981. *Vergleichende morphologische, anatomische und feinstrukturelle Merkmalsstudien an Arten der Gattung Tricholoma (Fr.) Staude, Sektion Genuina (Fr.) Sacc.* PhD dissertation. Eberhard-Karls-Universität, Tübingen, Germany. pp. 1–152
- [214] Christensen M, Noordeloos ME. 1999. Notulae ad Floram agaricinam neerlandicam—XXXVI. *Tricholoma*. *Persoonia—Molecular Phylogeny and Evolution of Fungi* 17(Part 2):295–317
- [215] Christensen M, Heilmann-Clausen J. 2013. *The genus Tricholoma*. 1st ed. Denmark: Svampetryk. pp.1–228
- [216] Ding XX, Cui YY, Yang ZL. 2022. Two new species of *Tricholoma* sect. *Genuina* (Agaricales) from China based on molecular phylogenetic and morphological evidence. *Mycological Progress* 21(3):37
- [217] Huang HY, Wang R, Zhang WH, Yu FQ, Tang LP. 2024. Phylogeny and taxonomic revision of *Hygrophorus robustus* (Hygrophoraceae, Agaricales) from southwestern China. *Phytotaxa* 664(3):181–190
- [218] Yang JJ, Xu YY, Lv JC, Fan L. 2023. *Tricholoma lishanense* (Tricholomataceae, Agaricales), a new species from China revealed by morphology and phylogenetic analysis. *Phytotaxa* 598(1):89–96
- [219] Cui YY, Ding XX, Kost GW, Yang ZL. 2022. *Tricholoma* sect. *Tricholoma* (Tricholomataceae) from China: molecular phylogeny and taxonomy. *Mycological Progress* 21(3):35
- [220] Kaur M, Rather H, Malik N. 2021. Morphoanatomical characterization of an ectomycorrhizal species of *Tricholoma* (Tricholomataceae) from Kashmir Himalaya, India. *Open Access Journal of Agricultural Research* 6(1):16000262
- [221] Ovrebo CL, Halling RE, Hughes KW, Kuo M. 2021. New species and records of *Tricholoma* (Agaricales: Tricholomataceae) sections *Genuina* and *Megatracholoma* from Costa Rica and United States. *Journal of the Botanical Research Institute of Texas* 15(2):545–557
- [222] Pölme S, Abarenkov K, Henrik Nilsson R, Lindahl BD, Clemmensen KE, et al. 2020. FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. *Fungal Diversity* 105(1):1–16
- [223] Seitzman BH, Ouimette A, Mixon RL, Hobbie EA, Hobbie DS. 2011. Conservation of biotrophy in Hygrophoraceae inferred from combined stable isotope and phylogenetic analyses. *Mycologia* 103(2):280–290
- [224] Song HB, Bau T. 2024. Resolving the polyphyletic origins of *Pholiotina* s.l. (Bolbitiaceae, Agaricales) based on Chinese materials and reliable foreign sequences. *Mycosphere* 15(1):1595–1674
- [225] Dong J, Li Q, Yuan Q, Luo Y, Zhang X, et al. 2024. Species diversity, taxonomy, molecular systematics and divergence time of wood-inhabiting fungi in Yunnan-Guizhou Plateau, Asia. *Mycosphere* 15(1):1110–1293
- [226] Guo MJ, Zhuo L, Wang S, Sui XN, Zhou H, et al. 2024. Hyperdiverse *Rhytismatales* on twigs of *Rhododendron* spp. *Mycosphere* 15(1):764–880
- [227] Li JX, Zhao RL, Phurbu D, Xing R, Liu DM, et al. 2025. Disentangling taxonomic chaos in Agaricaceae s.l.: an integrative phylogenomic framework with divergence dating reconstructs classification. *Fungal Diversity* 135(1):745–881
- [228] Kumar S, Das R, Sharma P, Tamang S, Ranjan RK, et al. 2023. Evaluation of fungal diversity in high altitude soils in different temperature conditions. *Journal of Climate Change* 9(2):65–75
- [229] Meng Q, Xie Z, Xu H, Guo J, Tang Y, et al. 2022. Out of the Qinghai-Tibetan plateau: origin, evolution and historical biogeography of *Morchella* (both Elata and Esculenta clades). *Frontiers in Microbiology* 13:1078663
- [230] Loughnan D, Gilbert B. 2017. Trait-mediated community assembly: distinguishing the signatures of biotic and abiotic filters. *Oikos* 126(8):1112–1122
- [231] Wang Y, Ma YH, Wu G, Yang XY, Liu YJ, et al. 2024. Polyphasic taxonomy clarifies the relationships between *Butyriboletus* and *Exsudoporus*, and new taxa and reports of Boletaceae from China. *Mycosphere* 15:881–953
- [232] Zhou Q, Cai Y, Zhou L, Zhang H, Li J, et al. 2026. Strategic and diversified soil microbes: unraveling the belowground control of plant multi-diversity-productivity relationships across elevation. *CATENA* 262:109613
- [233] Lin H, Wang X, Zhong M, Tang K, Du Y, et al. 2024. Elevational patterns and assembly processes of multifaceted bird diversity in a subtropical mountain system. *Journal of Biogeography* 51(7):1276–1289
- [234] Wang X, Zhong M, Yang S, Jiang J, Hu J. 2022. Multiple β -diversity patterns and the underlying mechanisms across amphibian communities along a subtropical elevational gradient. *Diversity and Distributions* 28(12):2489–2502
- [235] Wambulwa MC, Milne R, Wu ZY, Spicer RA, Provan J, et al. 2021. Spatiotemporal maintenance of flora in the Himalaya biodiversity hotspot: current knowledge and future perspectives. *Ecology and Evolution* 11(16):10794–10812
- [236] Liu F, Li JX, Yang WQ, He MQ, Cao B, et al. 2025. Evolution and horizontal transfer of the psilocybin biosynthetic gene cluster drive the diversification of magic mushrooms. *Mycosphere* 16(1):3673–3694
- [237] Xie Y, MacKinnon J, Li D. 2004. Study on biogeographical divisions of China. *Biodiversity & Conservation* 13:1391–1417
- [238] Päckert M, Favre A, Schnitzler J, Martens J, Sun YH, et al. 2020. "Into and Out of" the Qinghai-Tibet Plateau and the Himalayas: centers of origin and diversification across five clades of Eurasian montane and alpine passerine birds. *Ecology and Evolution* 10(17):9283–9300
- [239] Wen J, Zhang JQ, Nie ZL, Zhong Y, Sun H. 2014. Evolutionary diversifications of plants on the Qinghai-Tibetan Plateau. *Frontiers in Genetics* 5:4
- [240] Rahbek C, Borregaard MK, Antonelli A, Colwell RK, Holt BG, et al. 2019. Building mountain biodiversity: geological and evolutionary processes. *Science* 365(6458):1114–1119
- [241] Tzedakis PC, Lawson IT, Frogley MR, Hewitt GM, Preece RC. 2002. Buffered tree population changes in a quaternary refugium: evolutionary implications. *Science* 297(5589):2044–2047
- [242] Rahbek C, Borregaard MK, Colwell RK, Dalsgaard B, Holt BG, et al. 2019. Humboldt's enigma: what causes global patterns of mountain biodiversity? *Science* 365(6458):1108–1113
- [243] Kemppinen J, Lembrechts JJ, Van Meerbeek K, Carnicer J, Chardon NI, et al. 2024. Microclimate, an important part of ecology and biogeography. *Global Ecology and Biogeography* 33(6):e13834
- [244] Sun H, Zhang J, Deng T, Boufford DE. 2017. Origins and evolution of plant diversity in the Hengduan Mountains, China. *Plant Diversity* 39(4):161–166
- [245] Dai YC, Yu CJ, Wang HC. 2007. Polypores from eastern Xizang (Tibet), western China. *Annales Botanici Fennici* 44(2):135–145
- [246] Dai YC, Yang ZL, Cui BK, Wu G, Yuan HS, et al. 2021. 中国森林大型真菌重要类群多样性和系统学研究 [Diversity and systematics of the important macrofungi in Chinese forests]. *菌物学报 [Mycosystema]* 40(4):770–805 (in Chinese)
- [247] Yuan Y, Chen JJ, Korhonen K, Martin F, Dai YC. 2021. An updated global species diversity and phylogeny in the forest pathogenic genus *Heterobasidium* (Basidiomycota, Russulales). *Frontiers in Microbiology* 11:596393
- [248] Zhang QY, Liu HG, Papp V, Zhou M, Dai YC, et al. 2023. New insights into the classification and evolution of *Favolaschia* (Agaricales, Basidiomycota) and its potential distribution, with descriptions of eight new species. *Mycosphere* 14(1):777–814
- [249] Zhang X, Zhou HM, Tu ZH, Zeng GY, Dai YC. 2026. Morphological and phylogenetic evidence reveal two new *Pseudohydnum* (Auriculariales, Basidiomycota) species from Guangxi and Xizang, China. *Mycosystema* 131:251–264
- [250] Zhou M, Dai YC, Vlasák J, Liu HG, Yuan Y. 2023. Updated systematics of *Trichaptum* s.l. (Hymenochaetales, Basidiomycota). *Mycosphere* 14(1):815–917
- [251] He MQ, Yang WQ, Phurbu D, Liu F, Li JX, et al. 2026. Systematic study of *Panaeolus* (Agaricales, Galeropsidaceae) sensu lato and psilocybin-producing traits of species from China. *IMA Fungus* 17:e167329
- [252] Gu Y, Meng L, Wang Y, Wu Z, Pan Y, et al. 2025. Uncovering the role of solar radiation and water stress factors in constraining decadal

- intra-site spring phenology variability in diverse ecosystems across the Northern Hemisphere. *New Phytologist* 246(5):1986–2003
- [253] Zhang H, Zhang Y, Miralles DG, Tai X, Koppa A, et al. 2026. Increase in plant reliance on past precipitation associated with greening and drying. *Nature Ecology & Evolution* 10(4):689–699
- [254] Liu M, Peñuelas J, Trugman AT, Vargas GG, Yang L, et al. 2025. Diverging responses of terrestrial ecosystems to water stress after disturbances. *Nature Climate Change* 15(1):73–79
- [255] Krah FS, Hagge J, Schreiber J, Brandl R, Müller J, et al. 2022. Fungal fruit body assemblages are tougher in harsh microclimates. *Scientific Reports* 12:1633
- [256] Halbwachs H, Brandl R, Bässler C. 2015. Spore wall traits of ectomycorrhizal and saprotrophic agarics may mirror their distinct lifestyles. *Fungal Ecology* 17:197–204
- [257] Liu JW, Zhao WQ, Ren ML, Liu YQ, Xu Y, et al. 2022. Contrasting elevational patterns and underlying drivers of stream bacteria and fungi at the regional scale on the Tibetan Plateau. *FEMS Microbiology Ecology* 98(6):fiac050
- [258] Guo M, Xia Z, He X, Wan S, Wang Y, et al. 2026. High-throughput sequencing reveals endophytic bacterial differentiation of common truffles (*Tuber* spp.) in China: diversity, biogeographical patterns, and fungal health implications. *Microbiology Spectrum* 14(2):e01866-25
- [259] Kraft NJB, Adler PB, Godoy O, James EC, Fuller S, et al. 2015. Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* 29(5):592–599
- [260] Dorjey K, Kumar S, Sharma YP. 2023. The adaptations of high-altitude mushrooms in the cold desert of Ladakh. In *Environmental Change and Development in Ladakh, Indian Trans-Himalaya*, eds. Humbert-Droz B, Dame J, Morup T. Advances in Asian Human-Environmental Research. Cham: Springer Nature Switzerland. pp. 95–110 doi: 10.1007/978-3-031-42494-6_7
- [261] Halbwachs H, Bässler C. 2015. Gone with the wind—a review on basidiospores of lamellate agarics. *Mycosphere* 6(1):78–112
- [262] Linder DH. 1940. Evolution of the basidiomycetes and its relation to the terminology of the basidium. *Mycologia* 32(4):419–447
- [263] Sonnenberg ASM, Sedaghat-Telgerd N, Lavrijssen B, Hendrickx PM, Scholtmeijer K, et al. 2021. Mapping recombination landscape and basidial spore number in the button mushroom *Agaricus bisporus*. *Frontiers in Fungal Biology* 2:711330
- [264] Pehim Limbu S, Stürmer SL, Zahn G, Aguilar-Trigueros CA, Rogers N, et al. 2025. Climate-linked biogeography of mycorrhizal fungal spore traits. *Proceedings of the National Academy of Sciences U. S. A.* 122(29):e2505059122
- [265] Meerts. 1999. The evolution of spore size in Agarics: do big mushrooms have big spores? *Journal of Evolutionary Biology* 12(1):161–165
- [266] Crandall SG, Saarman N, Gilbert GS. 2020. Fungal spore diversity, community structure, and traits across a vegetation mosaic. *Fungal Ecology* 45:100920
- [267] Zanne AE, Abarenkov K, Afkhami ME, Aguilar-Trigueros CA, Bates S, et al. 2020. Fungal functional ecology: bringing a trait-based approach to plant-associated fungi. *Biological Reviews* 95(2):409–433
- [268] Dawson SK, Boddy L, Halbwachs H, Bässler C, Andrew C, et al. 2019. Handbook for the measurement of macrofungal functional traits: a start with basidiomycete wood fungi. *Functional Ecology* 33(3):372–387
- [269] Wang XW, Varga T, Li QS, G. Nagy LG, Zhou LW. 2025. Complex evolutionary history of the fungal order Hymenochaetales revealed by analyses of trait evolution and diversification. *Mycosphere* 16(1):517–535
- [270] Zhao H, Cui YJ, Guan QX, Wang K, Zhuang L, et al. 2025. Global fungal diversity and distribution patterns within the order Hymenochaetales (Agaricomycetes, Basidiomycota). *Mycosphere* 16(1):3257–3280
- [271] Cao GL, Li XQ, Xiang KL, Erst AS, Jabbour F, et al. 2025. Formation of three great Asian plateaus, climate change, and biodiversity. *Trends in Ecology & Evolution* 40(10):970–982
- [272] Chen YH, Lenoir J, Chen IC. 2025. Limited evidence for range shift-driven extinction in mountain biota. *Science* 388(6748):741–747
- [273] Runnel K, Tedersoo L, Krah FS, Piepenbring M, Scheepens JF, et al. 2025. Toward harnessing biodiversity-ecosystem function relationships in fungi. *Trends in Ecology & Evolution* 40(2):180–190
- [274] Sun Y, Deng Y, Yao S, Sun Y, Degen AA, et al. 2025. Distribution range and richness of plant species are predicted to increase by 2100 due to a warmer and wetter climate in northern China. *Global Change Biology* 31(7):e70334
- [275] Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, et al. 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355(6332):eaai9214
- [276] Han XX, Cao B, He MQ, Zhu XY, Li JX, et al. 2024. 中国西南地区沙鲁里山系大型真菌物种多样性 [Species diversity of macrofungi in Shaluli Mountains, southwest China]. *菌物学报 [MYCOSYSTEMA]* 43(3): 206–219 (in Chinese)
- [277] Liu DM, Wang SH, Wang K, Li JX, Yang WQ, et al. 2025. Species diversity and resource status of macrofungi in Beijing: insights from natural and urban habitats. *Journal of Fungi* 11(8):607
- [278] Glamočlija J, Stojković D, Nikolić M, Ćirić A, Reis FS, et al. 2015. A comparative study on edible *Agaricus* mushrooms as functional foods. *Food & function* 6(6):1900–1910
- [279] He MQ, Wang MQ, Chen ZH, Deng WQ, Li TH, et al. 2022. Potential benefits and harms: a review of poisonous mushrooms in the world. *Fungal Biology Reviews* 42:56–68
- [280] Shi J, Wang X, Wang E. 2023. Mycorrhizal symbiosis in plant growth and stress adaptation: from genes to ecosystems. *Annual review of plant biology* 74:569–607
- [281] Martin F, Tan H. 2025. Saprotrophy-to-symbiosis continuum in fungi. *Current Biology* 35(11):R469–R475



Copyright: © 2026 by the author(s). Published by Maximum Academic Press, Fayetteville, GA. This article is an open access article distributed under Creative Commons Attribution License (CC BY 4.0), visit <https://creativecommons.org/licenses/by/4.0/>.