

Research Article



An updated molecular phylogeny and Chinese species diversity of Tricholomataceae (Agaricales)

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Received: 13 October 2025 / Accepted: 25 May 2026 / Published: 25 July 2026

Abstract

Fungi of the Tricholomataceae are of great ecological and economic importance. Most species in this family are ectomycorrhizal fungi that play a crucial role in tree growth. Many species, such as *Tricholoma matsutake* and *T. bakamatsutake*, are highly regarded delicacies, while others, like *T. highlandense* and *T. pardinum*, are poisonous to humans. However, limited taxon sampling and insufficient molecular data have hindered our understanding of the species diversity of Tricholomataceae in many regions, including China. In this study, 371 specimens of Tricholomataceae from China were analysed using integrated approaches, including phylogenomic data, multi-gene phylogenetic evidence, morphological characteristics, and ecological features. Phylogenetic analysis of the concatenated dataset of nrLSU/ITS/nrSSU/RPB2 revealed that Tricholomataceae s. str. forms a monophyletic group, comprising 11 genera (*Albomagister*, *Corneriella*, *Dennisiomyces*, *Dermoloma*, *Leucopaxillus*, *Neodermoloma*, *Porpoloma*, *Pseudobaeospora*, *Pseudoporpoloma*, *Pseudotricholoma*, and *Tricholoma*). Among these, *Tricholoma* is the most species-rich genus within the family. Phylogenomic analysis utilizing 1,477 single-copy orthologous genes indicated that *Tricholoma* comprises five subgenera (subgen. *Tricholoma*, subgen. *Pardinicutis*, subgen. *Sericeicutis*, subgen. *Terrea*, and *Melleum* clade) and 15 section-level clades (sect. *Tricholoma*, sect. *Fucata*, sect. *Genuina*, sect. *Matsutake*, sect. *Muscaria*, sect. *Rigida*, sect. *Pardinicutis*, sect. *Lasciva*, sect. *Sericella*, sect. *Atrosquamosa*, sect. *Terrea*, Clades A, B, and C, and *Melleum* clade), with phylogenetic relationships among these clades fully resolved. Detailed morphological studies allowed for the identification of possible synapomorphies of *Tricholoma* and diagnostic characteristics for each subgenus and section. From China, 82 species of Tricholomataceae were documented, including 24 novel species and 58 known species from five genera. These findings were based on multi-gene analysis (ITS/RPB2/MCM7/EF1- α /mtSSU), ITS phylogenetic inference, morphological characteristics, and ecological data. Comprehensive descriptions, illustrations, and identification keys for these species are provided. Among the 82 species recognized in China, 52 were originally described from East Asia, while 30 originated from Europe or North America, suggesting that over 60% of the family's species are probably endemic to (East) Asia.

Keywords: Classification, Phylogenomic analysis, Single-copy orthologous genes, Species richness, Tricholomatoid fungi

Citation: Cui, Y.Y., Li, J., Fan, X.P., Liu, J.W., Ding, X.X., Xu, X., Zhu, X.T., Deng, C.Y., Guo, T., Che, N.J., Zhao, Q., Li, Y.C., Yang, Z.L., Cai, Q. (2026) An updated molecular phylogeny and Chinese species diversity of Tricholomataceae (Agaricales). Fungal Diversity 136: 136010. [https:// doi.org/10.65390/fdiv.2026.136010](https://doi.org/10.65390/fdiv.2026.136010)

Introduction

Fungi of the Tricholomataceae family hold significant ecological, commercial, and scientific importance. Most species form ectomycorrhizal symbiosis with various trees (e.g., Fagaceae, Pinaceae, Salicaceae, and Nothofagaceae), and play important ecological roles in forest ecosystems (Christensen & Heilmann-Clausen 2013; Sánchez-García &

Matheny 2017; Vaario et al. 2017; Cosme 2023). In addition, the family comprises numerous edible fungi that are culturally and economically valued in different regions, such as *Tricholoma populinum* J.E. Lange, *T. magnivelare* (Peck) Redhead, and *T. portentosum* (Fr.) Quél. are consumed in Europe and North America (Bessette et al. 2013; Christensen & Heilmann-Clausen 2013), as well as the highly prized *T. matsutake* (S. Ito & S. Imai) Singer and *T. bakamatsutake* Hongo in East Asia (Vaario et al. 2017; Wang et al. 2017).

Notably, *T. matsutake* is currently listed as Vulnerable by the International Union for Conservation of Nature (IUCN) due to substantial population declines driven by habitat loss, pine forest diseases, and land-use change (Brandrud 2020). Conversely, Tricholomataceae also includes several toxic species (e.g. *T. equestre* (L.) P. Kumm., *T. highlandense* Zhu L. Yang et al., *T. pardinum* (Pers.) Quél., and *T. saponaceum* (Fr.) P. Kumm.), of which can cause poisoning in humans, highlighting the importance of accurate taxonomy understanding within this family (Anand et al. 2009; Christensen & Heilmann-Clausen 2013; Chen et al. 2016; Laubner & Mikulevičienė 2016; Wan et al. 2023).

Taxonomically, Tricholomataceae sensu Singer (1986) was broadly circumscribed to include 98 genera, characterized by pale spore prints, various types of lamellar attachment and trama structures, amyloid or inamyloid basidiospores, and a wide range of ecological habitats. Due to its morphologically diverse characters and broad delimitation, this family has long been considered one of the most problematic groups within Agaricales. The application of molecular phylogenetics has profoundly reshaped the circumscription of this family. Based on multi-gene phylogenetic analyses, Sánchez-García et al. (2014) redefined Tricholomataceae s.str. and demonstrated that the family comprises seven genera, including *Leucopaxillus* Boursier, *Tricholoma* (Fr.) Staude, *Pseudotracholoma* (Singer) Sánchez-García & Matheny, *Porpoloma* Singer, *Dennisiomyces* Singer, *Corneriella* Sánchez-García, and *Albomagister* Sánchez-García, Birkebak & Matheny. This narrow circumscription of Tricholomataceae is followed in the present study. Notably, only four of these genera (*Tricholoma*, *Porpoloma*, *Dennisiomyces*, and *Leucopaxillus*) are congruent with Tricholomataceae sensu Singer (1986). Subsequent studies have further refined the systematic framework of Tricholomataceae s.str. *Pseudoporpoloma* Vizzini & Consiglio was described as a new genus within Tricholomataceae s.str. (Vizzini et al. 2016). *Dermoloma* J.E. Lange ex Herink and *Pseudobaeospora* Singer were later supported as members of the family based on multi-gene phylogenetic evidence (Sánchez-García et al. 2021). The placement of *Albomagister* within Tricholomataceae s.str. was further corroborated and defined by the description of four new species from eastern North America (Matheny et al. 2024). More recently, Vizzini et al. (2025) proposed a subdivision of the family into two subfamilies, Tricholomatoideae and Pseudobaeosporoideae, and the new genus *Neodermoloma* Sánchez-García, Matheny & Adamčík was established shortly thereafter (Adamčíková et al. 2025). At present, Tricholomataceae s.str. comprises two subfamilies (Tricholomatoideae and Pseudobaeosporoideae) and eleven genera (*Albomagister*, *Corneriella*, *Dennisiomyces*, *Dermoloma*, *Leucopaxillus*, *Neodermoloma*, *Porpoloma*, *Pseudobaeospora*, *Pseudoporpoloma*, *Pseudotracholoma*, and *Tricholoma*) (Sánchez-García et al. 2014, 2021; Vizzini et al. 2016; Matheny et al. 2024; Adamčíková et al. 2025; Vizzini et al. 2025). However, to date, only two genera (*Tricholoma* and *Pseudobaeospora*) have been documented from China with molecular support (Wu et al. 2017; Ding et al. 2023), and the actual generic diversity of Tricholomataceae s. str. in China remains poorly understood due to the lack of comprehensive systematic studies of this family.

With respect to species diversity, more than 1,000 published species names have been listed under Tricholomataceae sensu Singer (1986). However, under the recent

circumscription of Tricholomataceae s.str., only approximately half of these names are currently accepted as belonging to the family (Fungal Names; Index Fungorum). Historically, investigations of species diversity within this group have focused primarily on Europe and North America, resulting in numerous papers and monographs (Ovrebo 1973, 1980; Bon 1984; Riva 1988, 2003; Christensen & Noordeloos 1999; Bessette et al. 2013; Christensen & Heilmann-Clausen 2013; Landry et al. 2022). In China, early taxonomic studies of the family relied predominantly on morphological data, with molecular evidence incorporated more recently (Zang 1990; Cao 2003; Deng 2005; Wu et al. 2017; Yu et al. 2006; Yu 2007, 2011; Hosen et al. 2016; Yang et al. 2017; Reschke et al. 2018; Xu et al. 2020; Cui et al. 2022; Ding et al. 2022; Zhao et al. 2022; Yang et al. 2023). To date, more than 100 species names of Tricholomataceae have been reported from China (Zang 1990; Cao 2003; Deng 2005; Yu 2011). Nevertheless, most of these records represent misapplications of European or North American taxa that do not actually occur in the region, and only 21 species (approximately 20%) were originally described from Chinese collections (Wu et al. 2017; Ding et al. 2023). Some species, such as *T. virgatum* (Fr.) P. Kumm., *T. portentosum*, and *T. focale* (Fr.) Ricken, are widely distributed across the Northern Hemisphere (Ding et al. 2023). In contrast, other species have a more restricted distribution in East Asia, including *T. sinoacerbum* Li et al., *T. highlandense*, and *T. nigrosquamosum* (P.G. Liu) Zhu L. Yang & G.S. Wang (Hosen et al. 2016; Yang et al. 2017; Wang et al. 2024). Moreover, recent studies in the region have shown that many species of this family, especially in the genus *Tricholoma* have not yet been described scientifically (Ding et al. 2023). These findings highlight the need for comprehensive species delimitation of Chinese Tricholomataceae s.str. based on integrated molecular, morphological, and ecological evidence.

Within Tricholomataceae s.str., *Tricholoma* represents one of the most species-rich and taxonomically complex genera, and it has therefore been the primary focus of taxonomically systemic studies within the family. Various classification systems have been proposed, including those by Bon (1984, 1991), Riva (1988), Singer (1986), and Noordeloos & Christensen (1999) prior to the molecular era. Molecular phylogenetic studies, such as those by Heilmann-Clausen et al. (2017) and Reschke et al. (2018), have significantly advanced the taxonomy of this genus. Recently, Ding et al. (2023) inferred the phylogeny of *Tricholoma* using a combined dataset of 50 loci generated through extensive PCR experiments, and proposed a taxonomic framework comprising four subgenera and 11 sections. However, this approach is labor-intensive, relies on limited analysis tools, and is generally best suited to fresh specimens, which restricts the number of genes that can be obtained. As a result, the phylogenetic relationships among several major clades of the genus remain unresolved. In this context, the application of next-generation sequencing (NGS) to retrieve single-copy orthologous genes (SOGs) directly from genome data has opened new opportunities for resolving both deep and shallow phylogenetic relationships in macrofungi (Dentinger et al. 2016; He et al. 2023; Kraisitudomsook et al. 2024; Wang et al. 2024; Qu et al. 2025). This genome-based approach is more efficient, supported by a wide range of analytical tools, applicable to older herbarium specimens, and capable of generating large numbers of genes, thereby

offering further avenues for research on *Tricholoma* evolution and taxonomy.

The objectives of this study are: (1) to identify and delimit the genera of Tricholomataceae occurring in China using four-gene phylogenetic analyses, morphological characters and ecological data; (2) to construct a robust phylogenomic framework of *Tricholoma* based on numerous SOGs and to define diagnostic characteristics for its infrageneric classification, particularly at the levels of subgenera and sections; and (3) to assess and delimit the species diversity of Tricholomataceae in China based on multi-locus phylogenetic analyses, ITS data, and morphological evidence.

Materials and methods

Abbreviations of generic names used in this study

The generic names of Tricholomataceae s.str. used in this paper are abbreviated as follows: *A.* = *Albomagister*, *C.* = *Corneriella*, *D.* = *Dennisiomyces*, *De.* = *Dermoloma*, *L.* = *Leucopaxillus*, *N.* = *Neodermoloma*, *Po.* = *Porpoloma*, *P.* = *Pseudobaespora*, *Ps.* = *Pseudoporpoloma*, *Pse.* = *Pseudotricholoma*, and *T.* = *Tricholoma*.

Sample collection

In total, 371 specimens of Tricholomataceae s. str. from China were examined. Among these, 352 specimens were collected between 1999 and 2023 for this study, and 19 specimens were borrowed from fungaria and collected between 1972 and 2017. In addition, six specimens from other parts of the world (Belarus, Canada, and Germany) were included. All specimens were deposited in the Herbarium of Cryptogams at the Kunming Institute of Botany, Chinese Academy of Sciences (KUN-HKAS), the Fungarium of Institute of Microbiology, Chinese Academy of Sciences (HMAS), the Herbarium of Mycology, Jilin Agricultural University, Changchun, Jilin, China (HMJAU), Alpine Fungarium, Tibet Plateau Institute of Biology (AF), the Herbarium Marburgense, Philipps-Universität Marburg, Marburg, Germany (MB), and the Mycological Herbarium of Tarim University, Aral, China (HMUT).

DNA extraction, sequencing, and data processing

Total DNA was extracted from silica gel-dried material or air-dried specimens using the Ezup Column Fungi Genomic DNA Purification Kit (Sangon Biotech, Shanghai, China). Seven gene fragments were employed in the phylogenetic analyses, including the internal transcribed spacers 1 and 2 with the 5.8S rDNA (ITS), the large and small subunit of nuclear ribosomal RNA (nrLSU and nrSSU), the mitochondrial small subunit rDNA (mtSSU), partial sequences of the second-largest subunit of RNA polymerase (RPB2), the translation elongation factor 1- α (EF1- α), and the minichromosome maintenance protein 7 (MCM7). The primer pairs ITS1F and ITS4 (White et al. 1990; Gardes & Bruns 1993) were employed to amplify the ITS sequences, LR0R/LR5 (Vilgalys & Hester 1990) were used for the nrLSU region, PNS1/NS8, PNS1/NS41 and NS51/NS8NS19 (White et al. 1990; Hibbett 1996) for nrSSU, MS1 and MS2 (White et al. 1990) for mtSSU, bRPB2-6F and bRPB2-7.1R (Matheny et al. 2007) for RPB2, 983F/1567R (Rehner & Buckley 2005) for EF1- α , as well as

bMCM7-709F/bMCM7-1348R and MCM7-T1F/MCM7-T1R for MCM7 (Ding et al. 2023). The PCR amplification and sequencing protocols followed those employed by Ding et al. (2023). Sequences newly generated in this study and their GenBank (<http://www.ncbi.nlm.nih.gov>) accession numbers are shown in Supplementary Tables S1–3.

Using a genome skimming approach, 45 samples representing 38 species of *Tricholoma* and five species of *Albomagister*, *Leucopaxillus*, *Pseudotricholoma*, and *Pseudobaespora* were sequenced on an Illumina Hi-seq platform. The raw sequence data of each sample were deposited in the Genome Sequence Archive in National Genomics Data Center, China National Center for Bioinformation/Beijing Institute of Genomics, Chinese Academy of Sciences (Accession no. CRA022587). Protocols for DNA extraction, library preparation, and library pooling for genome sequencing followed those described by Zeng et al. (2018). The raw sequencing reads were preprocessed using Trimmomatic v0.33 (Bolger et al. 2014), which involved trimming adapters and removing low-quality bases. The processed reads were then assembled de novo using SPAdes (Bankevich et al. 2012) with automatic K selection based on read length. The completeness of the genome assembly was evaluated using Benchmarking Universal Single-Copy Orthologs (BUSCO v3) (Manni et al. 2021), with the Agaricales OrthoDB v10 database (Zdobnov et al. 2021) as a reference. Thereafter, SOGs for each sample were retrieved from the genome using the results from the BUSCO analysis. Of these gene fragments, 1,652 shared by more than 95% of the representative samples were employed for further phylogenetic analyses. They were also blasted to the genome of *T. matsutake* in JGI to ascertain that they were single-copy genes.

Four datasets were built from sequences generated in this study and retrieved from GenBank (Supplementary Tables S1–3). Dataset I (nrLSU, ITS, nrSSU, and RPB2) aimed to investigate the genus and species diversity of Tricholomataceae in China. *Pseudolaccaria pachyphylla* (Fr.) Vizzini & Contu, *Xerophorus olivascens* (Boud.) Vizzini et al., *Macrocybe titans* (H.E. Bigelow & Kimbr.) Pegler et al., *Callistosporium elegans* Desjardin & B.A. Perry of Callistosporiaceae were employed as outgroups according to previous phylogenetic studies (Sánchez-García et al. 2014; Vizzini et al. 2020a; He & Yang 2022). Dataset II (single-copy orthologous genes) aimed to resolve the phylogeny of *Tricholoma* and to investigate the potential evolutionary patterns of key morphological traits within the genus. Five species of the other four genera of Tricholomataceae, *Albomagister*, *Leucopaxillus*, *Pseudotricholoma*, and *Pseudobaespora*, were selected as outgroups. The SOGs were applied exclusively to *Tricholoma* rather than the entire Tricholomataceae due to the lack of available genomic data from *Corneriella*, *Dennisiomyces*, *Dermoloma*, *Neodermoloma*, *Porpoloma*, and *Pseudoporpoloma*. Dataset III (ITS, EF1- α , RPB2, MCM7, and mtSSU) was constructed to explore the species diversity of *Tricholoma* and the phylogenetic relationships among them. The dataset mainly included collections of the genus from China because most species of the genus described from other areas are only represented by ITS sequence data in GenBank. Two species of *Leucopaxillus* were employed as outgroups. Dataset IV (ITS) aimed to uncover the species diversity of *Tricholoma* and to elucidate the phylogenetic relationships between the species

from China and those from other parts of the world. In the dataset, two species of *Leucopaxillus* were selected as outgroups.

Phylogenetic analyses

For Datasets I, III, and IV, the sequences of each gene fragment were aligned with MAFFT 7.402 using the E-INS-I strategy, manually optimized with BioEdit 7.0.9.0, and then concatenated with Geneious Prime 2020.0.5 (Hall 1999; Kearse et al. 201; Katoh & Standley 2013). The three datasets were then analyzed with both Maximum Likelihood (ML) and Bayesian Inference (BI) methods using RAxML v8.2.4 (Stamatakis 2014) and MrBayes v3.2.6 (Ronquist et al. 2012), respectively. The optimal substitution models for each gene fragment of the three datasets were determined with MrModeltest 2.3 based on the Akaike Information Criterion (AIC). The selected substitution models for each gene fragment were as follows: GTR + I + G for nrLSU, ITS, nrSSU and RPB2 in Dataset I, GTR + I + G for ITS, mtSSU, and MCMC7 in Dataset III, SYM + I + G for EF1- α and RPB2 in Dataset III, GTR + I + G for ITS in Dataset IV. In the ML analyses, the statistical supports were obtained using rapid bootstrapping with 1,000 replicates, and the other parameters were set to the default settings. Some of the selected models could not be implemented in RAxML; thus, the GTR + I + G model, which included all the parameters of the chosen model, was used for all datasets. For BI analyses, four Markov Chain Monte Carlo (MCMC) chains were run simultaneously for 5 to 20 million generations under the best-fit models (Dataset I: 5 million generations; Dataset III: 20 million generations; Dataset IV: 20 million generations). The trees were sampled every 1,000 generations. Chain convergence was determined using Tracer v1.5 (<http://tree.bio.ed.ac.uk/software/tracer/>) to confirm sufficiently large ESS values (>200). Subsequently, the sampled trees were summarized, and posterior probabilities (PP) were obtained by discarding the first 25% of generations as burn-in.

For Dataset II, the 1,652 SOGs shared by more than 95% of samples were aligned using MAFFT v7.505 (Katoh & Standley 2013) under the L-INS-I setting. Three of them, with a length of less than 100 aligned amino acids, were excluded from further phylogenetic analyses. The ambiguously aligned regions of the remaining alignments were then trimmed using trimAl v1.4.rev15 (Capella-Gutiérrez et al. 2009). To investigate the potential effects of sequence biases in the dataset on the phylogenetic reconstruction, several related tests were performed using TreSpEx (Struck 2014), which was recently developed to detect possible sequence biases, including long branch attraction (LBA) and saturation. A total of 1,477 SOGs were included in the final analyses. Phylogenetic analyses were then performed based on the concatenated dataset of these SOGs using both concatenation and coalescence methods. For the concatenation analysis, the SOGs were concatenated using PhyKIT (Steenwyk et al. 2021) and then subjected to the ML analysis using IQ-TREE v2.0-rc1 with automatic detection for the best-fit model with the “-MFP” option (Nguyen et al. 2015). Branch supports were generated with 1,000 UFBoot (ultrafast bootstrap) replicates (Hoang et al. 2018). For the coalescent analysis, sequences with more than 60% gap characters were removed from each SOG to improve the accuracy of

individual gene trees (Sayyari et al. 2017). Individual gene trees were then generated by IQ-TREE with 1,000 UFBoot replicates under the best substitution model. We also contracted branches with very low support (less than 20% UFBoot support) from each gene tree to improve accuracy (Zhang et al. 2017; Zhang et al. 2018). Based on these individual gene trees, the species tree was estimated using Astral v5.7.3 (Zhang et al. 2018) with local posterior probabilities (LPP) (Sayyari & Mirarab 2016).

Morphological studies

Macroscopic characteristics were recorded from fresh basidioma, detailed field notes, and photographs. Particular attention was paid to traits, such as pileus size, color, and surface texture, lamellae attachment and spacing, stipe size and features, and color changes or reactions to bruising or exposure. Color codes (e.g. 1A1) of each species were obtained from Kernerup & Wanscher (1981). The microscopic features were sectioned under a stereomicroscope (ZEISS Stemi 305), and then observed under a light microscope (ZEISS Axioi Scope A1) after mounting in 5% KOH solution. Congo red was applied for dyeing when necessary. Melzer's reagent was applied to test the amyloidity of the basidiospores. In addition to basidiospores, other microscopic structures, including basidia, pleurocystidia, cheilocystidia, and pileipellis, were carefully examined under a light microscope with a phase contrast objective at 1,000 $\times$ magnification. These characters were documented based on repeated observations and illustrated by freehand drawings, and their diagnostic features were described qualitatively following standard taxonomic practice. Quantitative measurements and statistical analyses were applied only to basidiospores. In the descriptions of basidiospores, the abbreviation (n/m/p) means n basidiospores measured from m basidioma of p collections; the dimensions of basidiospores were presented in the form of (a–) b–c (–d), the range b–c indicates a minimum of 90% of the measured values, a and d in parentheses stands for extreme values if exists; Q means “length/width ratio” of a basidiospore in side view; Qm represents the mean Q of all basidiospores $\pm$ sample standard deviation. SigmaPlot 10.0 (Systat Software, San Jose, California) was applied to analyze these values. The scanning electron microscopy (ZEISS Sigma 300 scanning electron microscope, Oberkochen, Germany) was also applied to observe the basidiospores of some species.

Results

Phylogenetic analyses

Dataset I comprised 92 nrLSU sequences (928 bp), 119 ITS sequences (1,046 bp), 35 nrSSU sequences (1,743 bp) and 66 RPB2 sequences (749 bp), which were derived from 117 representative samples of Tricholomataceae and four outgroup species of Callistosporiaceae. Among these, 18 samples were collected from China with 59 sequences. The dataset comprised 1,347 parsimony informative sites with a total length of 4,466 positions. Dataset III included 215 ITS sequences (714 bp), 180 EF1- α sequences (764 bp), 159 RPB2 sequences (655 bp), 142 MCMC7 sequences (602 bp) and 169 mtSSU sequences (871 bp) from 228 representative collections of *Tricholoma* and two outgroup species of

Leucopaxillus. The total length of the dataset is 3,606 bp with 1,541 parsimony informative sites. Dataset IV consisted of 639 ITS sequences (775 bp), with 478 parsimony informative sites. In the three datasets, 373 sequences were newly generated in this study. Dataset II included 45 collections representing 43 species with a total length of 593,898 amino acid positions from 1,477 single-copy orthologous gene fragments. The phylogenetic trees inferred from the ML, BI, or coalescent-based analyses were similar in topology. Therefore, only the trees obtained from the ML analyses were presented (Figs. 1–4).

In the phylogenetic tree inferred from Dataset I (nrLSU/ITS/nrSSU/RPB2), Tricholomataceae s.str. was supported to be a monophyletic group, and 11 genus-level clades were included in the family (Fig. 1). All clades corresponded to the 11 well-circumscribed genera of the family. Among these genera, *Dermoloma* was sister to *Pseudoporpoloma* (MLB=67%). The two genera were closely related to *Pseudotracholoma*, forming a clade that was then sister to *Tricholoma* (MLB=82%, PP=1.0). *Corneriella* was closely related to the clade formed by *Porpoloma* and *Dennisiomyces* (Fig. 1). The collections from China, except *Tricholoma*, were clustered in *Leucopaxillus*, *Albomagister*, *Pseudobaesopora*, and *Pseudotracholoma*. Based on the results combined with morphological studies, these samples represent eight species, with five of them being described as new species in this study (Fig. 1).

Based on molecular phylogenetic analyses of Dataset II (SOGs) and Dataset III (ITS/RPB2/MCMC/EF1- α /mtSSU), along with morphological observations, *Tricholoma*, the most species-rich genus of the family, was divided into five subgenus-level clades and 15 section-level clades (Figs. 2, 3). The phylogenetic relationships among these subgenera and sections were highly resolved in the tree inferred from Dataset II (Fig. 2). *Tricholoma* subgen. *Tricholoma* was closely related to *T.* subgen. *Terrea* Ding et al. The two subgenera were then sister to *T.* subgen. *Sericeicutis* Singer, followed by *Melleum* Clade and *T.* subgen. *Pardincutis* Singer (Fig. 2). In the subgenus *Tricholoma*, the seven section-level clades were grouped into three monophyletic groups with high support values. *Tricholoma* sect. *Muscaria* Reschke was closely related to sect. *Fucata* Ding et al., and the two sections were then sister to sect. *Matsutake* Ding et al. The group formed by the three sections was sister to the group formed by sect. *Rigida* (Fr.) Quél. and sect. *Tricholoma*, followed by the group consisting of sect. *Genuina* (Fr.) Sacc. and Clade C. The phylogeny of the subgenus was also supported in the tree generated from Dataset III (Fig. 3). In the subgenus *Terrea*, sect. *Terrea* was sister to Clade B, followed by sect. *Atrosquamosa* Kühner ex Bon and Clade A (Fig. 2). However, the phylogenetic relationships among them were not supported with strong supports in the tree based on Dataset III (Fig. 3). The sister relationship between sect. *Sericella* (Fr.) Quél. and sect. *Lasciva* Bon, which was strongly supported in the tree generated from Dataset II, was also not elucidated in the tree based on Dataset III (Figs. 2, 3). There were 286 collections from China included in the tree generated from Datasets III and IV (Figs. 3, 4). Based on these results, along with morphological studies, these samples

represented 76 *Tricholoma* species from China, and 19 of them were described as new species in this study.

Morphological observations

The 371 Chinese specimens examined in this study represented 82 species of Tricholomataceae s.str. Of these 58 are known species, while 24 taxa are new to science. Most of the taxa (74) belong to the genus *Tricholoma*, while the remaining species are allocated to *Albomagister* (2 species), *Leucopaxillus* (3 species), *Pseudobaesopora* (1 species), and *Pseudotracholoma* (2 species).

Among the Chinese representatives of Tricholomataceae s. str., *Tricholoma* includes the largest and most well-represented genus of species. Therefore, we have provided a summary of the morphological features of each structure within *Tricholoma*, as detailed below.

Basidioma: Most basidioma of *Tricholoma* species are small to medium-sized, robust, and fleshy; some are large to very large (e.g., *T. orienticolossum* X. Xu et al.), and others are very small to small (e.g., *T. triste* (Scop.) Quél.). According to Bas (1969), the size of basidioma is categorized based on pileus diameter: very small (≤ 3 cm), small (3–5 cm), medium-sized (5–9 cm), large (9–15 cm), and very large (≥ 15 cm). These categories were applied throughout this study.

Pileus: The pileus of *Tricholoma* species is initially conical to convex, later becoming plano-convex to applanate, often irregular with a wavy appearance. Some species possess a distinct papillate umbo at the center of the pileus, a feature significant for section divisions within the genus (Fig. 14b). For example, species in sect. *Muscaria* and sect. *Fucata* often have papillate-umbonate pilei (Fig. 14b). The pileal margin is involute when young, with most species becoming straight at maturity. Pileus is dry or viscid, and its coloration is highly variable—white, yellow, brown, grey, or olivaceous. The surface can be glabrous (Fig. 5a), squarrose (Fig. 5b–d), squamose (Fig. 5e, f), or radially fibrillose (Fig. 5g, h), features valuable for subgenus division (Fig. 14a).

Lamellae: The lamellae of *Tricholoma* species are sinuate with lamellulae. The edge may be entire or not and is often easily broken. The spacing between them is crowded (Fig. 6a), close (Fig. 6b) to distant (Fig. 6c), which have played a certain role in the classification of subgenera and sections of *Tricholoma* (Fig. 14). For instance, species in subgen. *Sericeicutis* generally have close to distant lamellae, while sect. *Rigida* features close to distant lamellae and sect. *Genuina* has crowded lamellae (Fig. 14). Lamellae coloration ranges from white, cream-colored, yellow, grey to brown, with some species exhibiting color changes upon aging or bruising, including turning yellow (Fig. 7a, b), grey or with dark-grey to grey spots (Fig. 7c, d), brown or with brown spots (Fig. 7e, f), or red to reddish (Fig. 7g, h).

Stipe: The stipe is cylindrical, subcylindrical, clavate, or subclavate, with the center being solid, stuffed, or hollow. While stipe shape appears to have limited taxonomic value, stipe ornamentation can be informative for recognition in some species. For example, *Tricholoma orienticolossum* possesses brownish to red-brown, fibrillose squamules on the stipe surface.

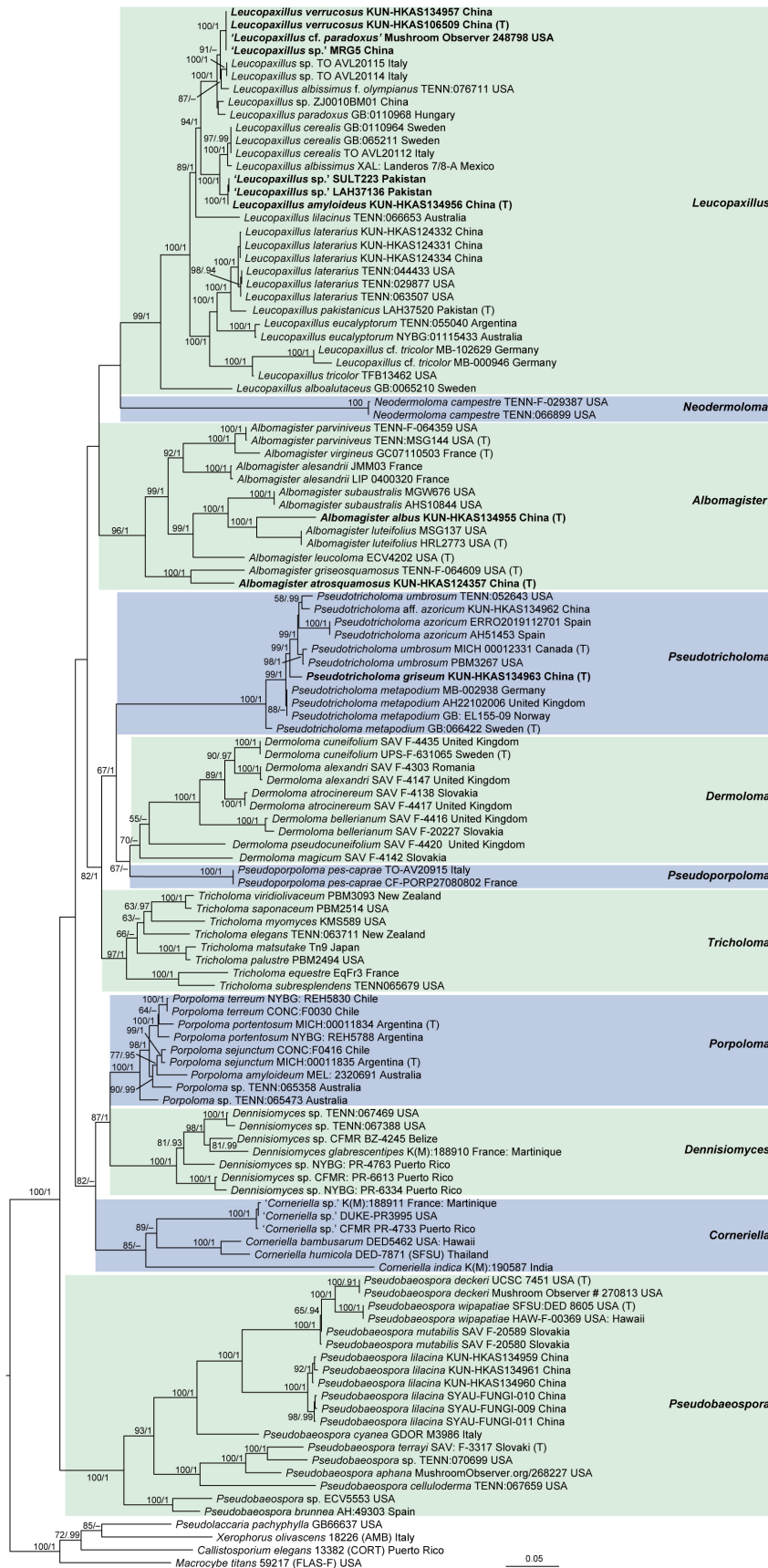


Fig. 1 Phylogenetic tree of Tricholomataceae inferred from Maximum Likelihood analyses based on Dataset I (nrLSU/ITS/nrSSU/RPB2). Bootstrap values (MLB) over 50% and posterior probabilities (PP) over 0.90 are shown along the branches. Sequences from type collections are marked with (T) and new species are indicated in bold.

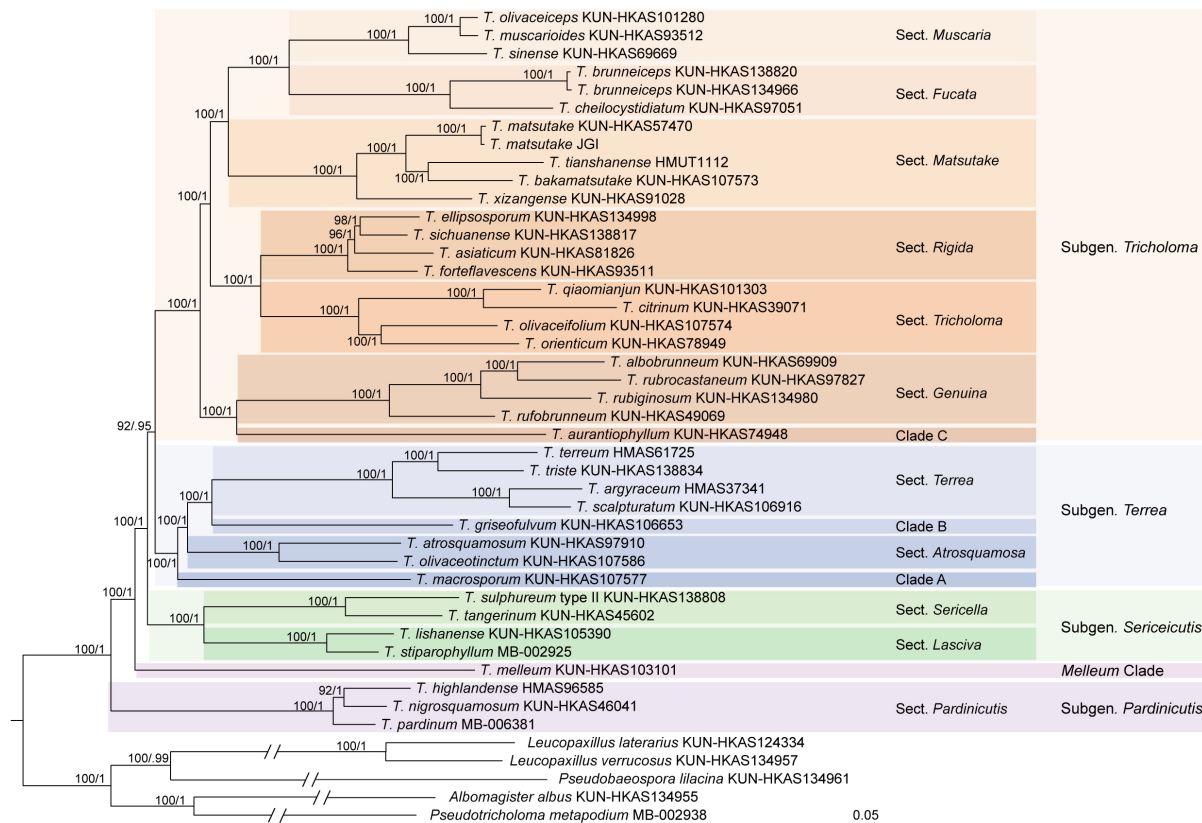


Fig. 2 The concatenation-based species tree of *Tricholoma* inferred by IQ-TREE based on Dataset II (1,477 SOGs). Numbers associated with nodes are the ultrafast bootstrapping values and ASTRAL local posterior probabilities.

Annulus: Most *Tricholoma* species lack an annulus, but some possess one near the top of the stipe. Annuli can be categorized into three types based on texture: (1) a pseudoannular zone—a white zone at the stipe apex that may be sharply delimited, unevenly or faintly delimited, or occasionally relieved and prominent, particularly in sect. *Genuina* (Fig. 8a, b), as exemplified by *T. aurantium* (Schaeff.) Ricken and *T. albobrunneum* (Pers.) P. Kumm.; (2) a cobwebby zone—cobweb-like cortina or remnants at the stipe apex (Fig. 8c, d), observed in *T. argyraceum* (Bull.) Gillet and *T. scalpturatum* (Fr.) Quél. (sect. *Terrea*); and (3) a distinct annulus—a large, cottony to woolly structure at the stipe apex (Fig. 8e, f), as found in species of sect. *Matsutake*, *T. cingulatum* (Almfelt ex Fr.) Jacobasch (sect. *Terrea*), and *T. focole* (sect. *Genuina*).

Taste and odour: Species of *Tricholoma* often exhibit distinctive tastes and odors, which are critical for species identification. The most common odor and taste is farinaceous. Unusual odors have been reported. For example, *T. bakamatsutake* has a slightly pungent, tongue-numbing taste and sweet odor; *T. sulphureum* (Bull.) P. Kumm. has an unpleasant taste and a strong gas or almond odor; and *T. mastoideum* Y.Y. Cui & Zhu L. Yang has a mild taste with an oak-like odor. However, organoleptic data are lacking for most Chinese collections, largely because such characters were insufficiently documented in earlier field studies. This highlights the necessity of systematically recording taste and odor in future field investigations.

Basidiospores: The size of basidiospores is a critical character in the division of *Tricholoma* sections and the

definition of some species (Fig. 14b). In this study, basidiospores were divided into three groups based on their mean length and mean width: (1) small (mean length $\leq 6.5 \mu\text{m}$, mean width $\leq 4.5 \mu\text{m}$) (Fig. 9a), characteristic of most species in sect. *Rigida*, sect. *Genuina*, sect. *Atrosquamosa* and sect. *Lasciva*; (2) medium-sized ($6.5 \mu\text{m} < \text{mean length} \leq 9 \mu\text{m}$, $4.5 \mu\text{m} < \text{mean width} \leq 5.5 \mu\text{m}$) (Fig. 9b), typical of most species in sect. *Tricholoma*, sect. *Muscaria*, sect. *Fucata* and sect. *Matsutake*; and (3) large (mean length $> 9 \mu\text{m}$, mean width $> 5.5 \mu\text{m}$) (Fig. 9c), such as most species in sect. *Sericella*.

Bas (1969) categorized basidiospore shapes into six types: (1) globose ($Q = 1.0\text{--}1.05$); (2) subglobose ($Q = 1.05\text{--}1.15$); (3) broadly ellipsoid ($Q = 1.05\text{--}1.3$); (4) ellipsoid ($Q = 1.3\text{--}1.6$); (5) elongate ($Q = 1.6\text{--}2.0$); and (6) cylindrical ($Q = 2.0\text{--}3.0$). The basidiospores of *Tricholoma* species are predominantly broadly ellipsoid (Fig. 10b), ellipsoid (Fig. 10c), or elongate (Fig. 10d), occasionally subglobose (Fig. 10a). Additionally, amygdaliform spores (Fig. 10e) are present in species of sect. *Sericella*. Spore shape plays a pivotal role in distinguishing subgenera, sections, and certain species within *Tricholoma* (Fig. 14).

The basidiospores of this genus are inamyloid (Lebeuf et al. 2024; this study), a diagnostic feature that distinguishes *Tricholoma* from other genera within Tricholomataceae.

Discoloration of hymenophoral surface: In most species of sect. *Genuina*, the lamellae develop brown spots, eventually turning entirely brown with age or bruising. Microscopically, this discoloration results from pigment formation in hymenial cells, followed by cell gelatinization and degradation (Fig. 11).

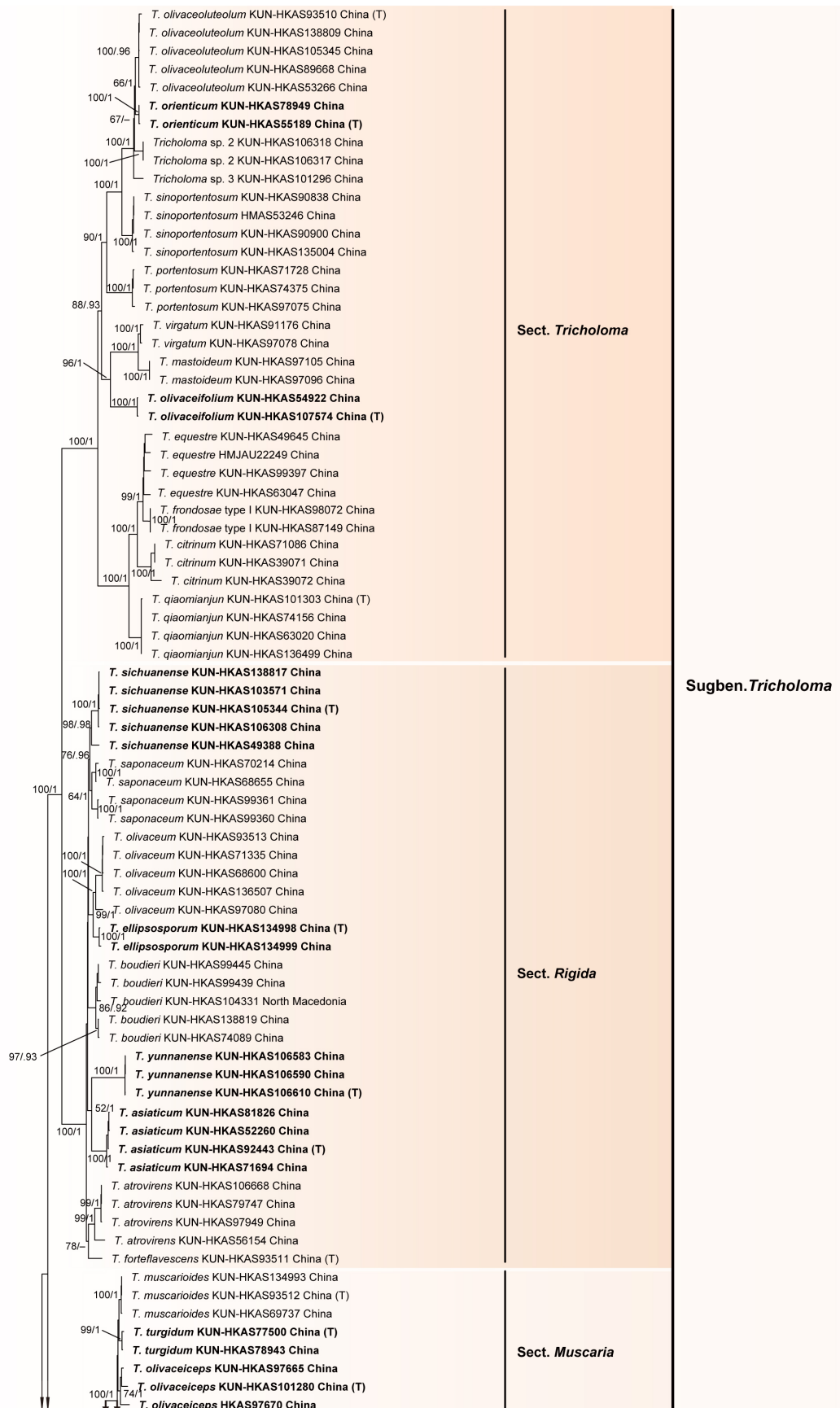


Fig. 3 Phylogenetic tree of *Tricholoma* inferred from Maximum Likelihood analyses based on Dataset III (ITS/RPB2/MCM7/EF1- α /mtSSU). Bootstrap values (MLB) over 50% and posterior probabilities (PP) over 0.90 are shown along the branches. Sequences from type collections are marked with (T) and new species are indicated in bold.



Fig. 3 (continued)

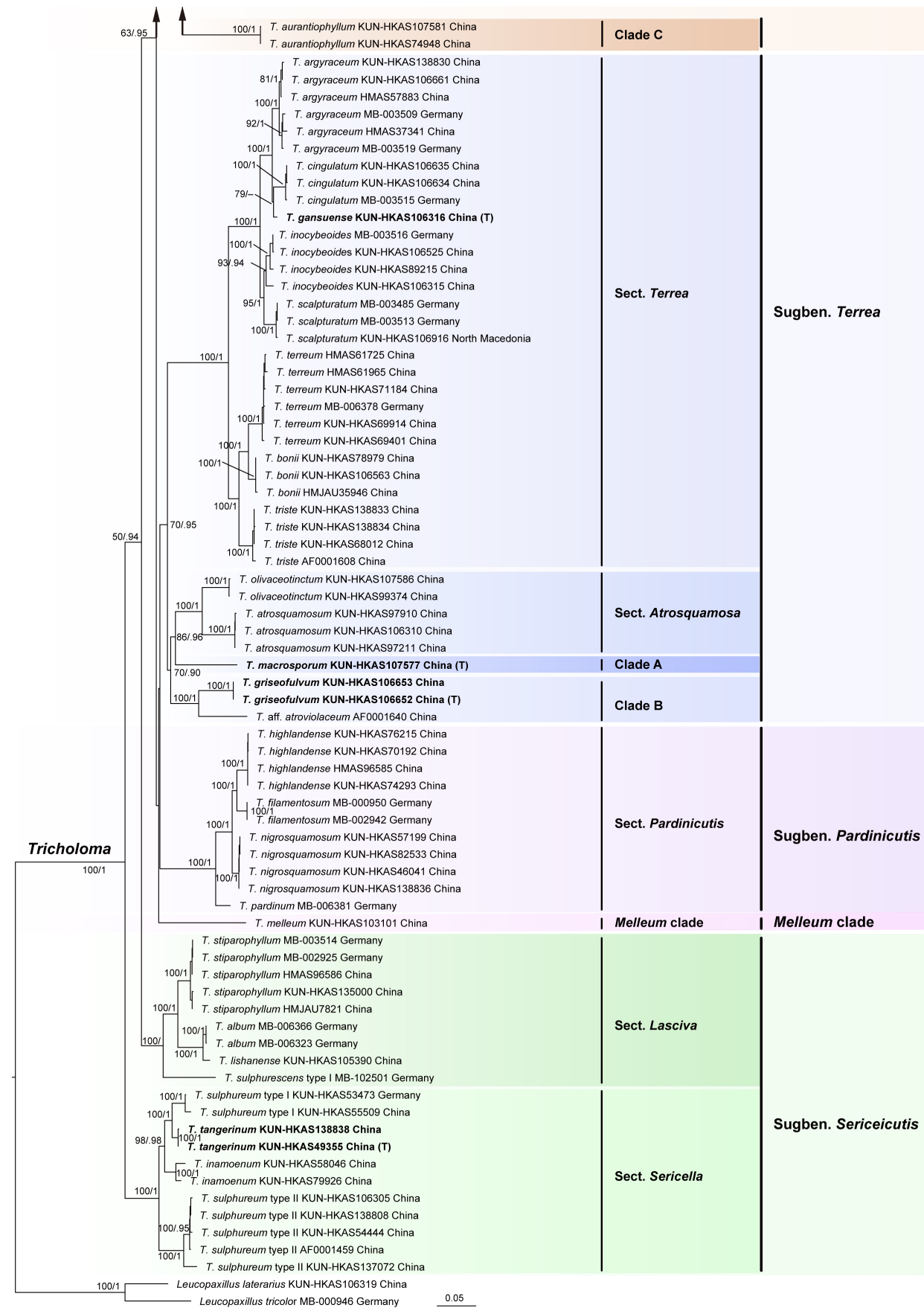


Fig. 3 (continued)

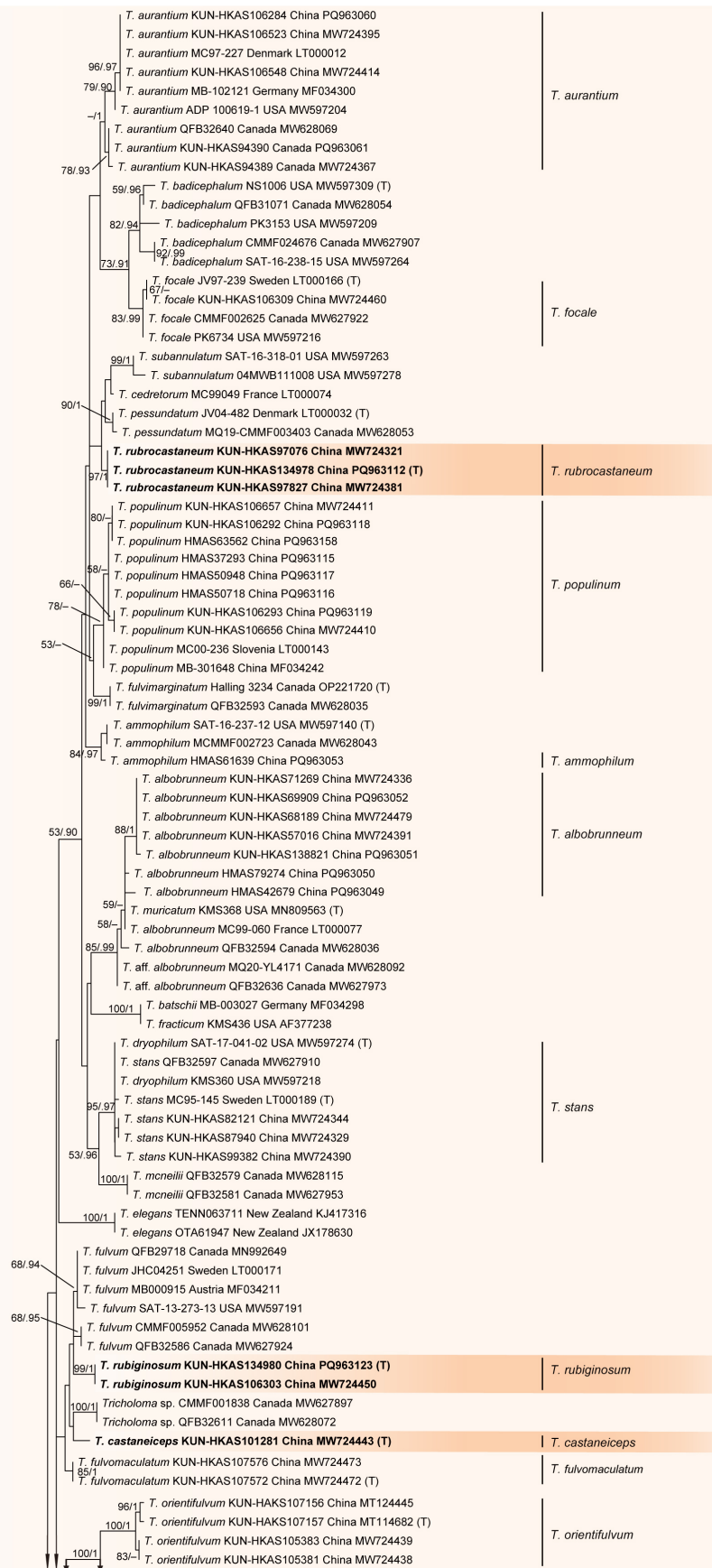


Fig. 4 Phylogenetic tree of *Tricholoma* inferred from Maximum Likelihood analyses based on Dataset IV (ITS). Bootstrap values (MLB) over 50% and posterior probabilities (PP) over 0.90 are shown along the branches. Sequences from type collections are marked with (T) and new species are indicated in bold.

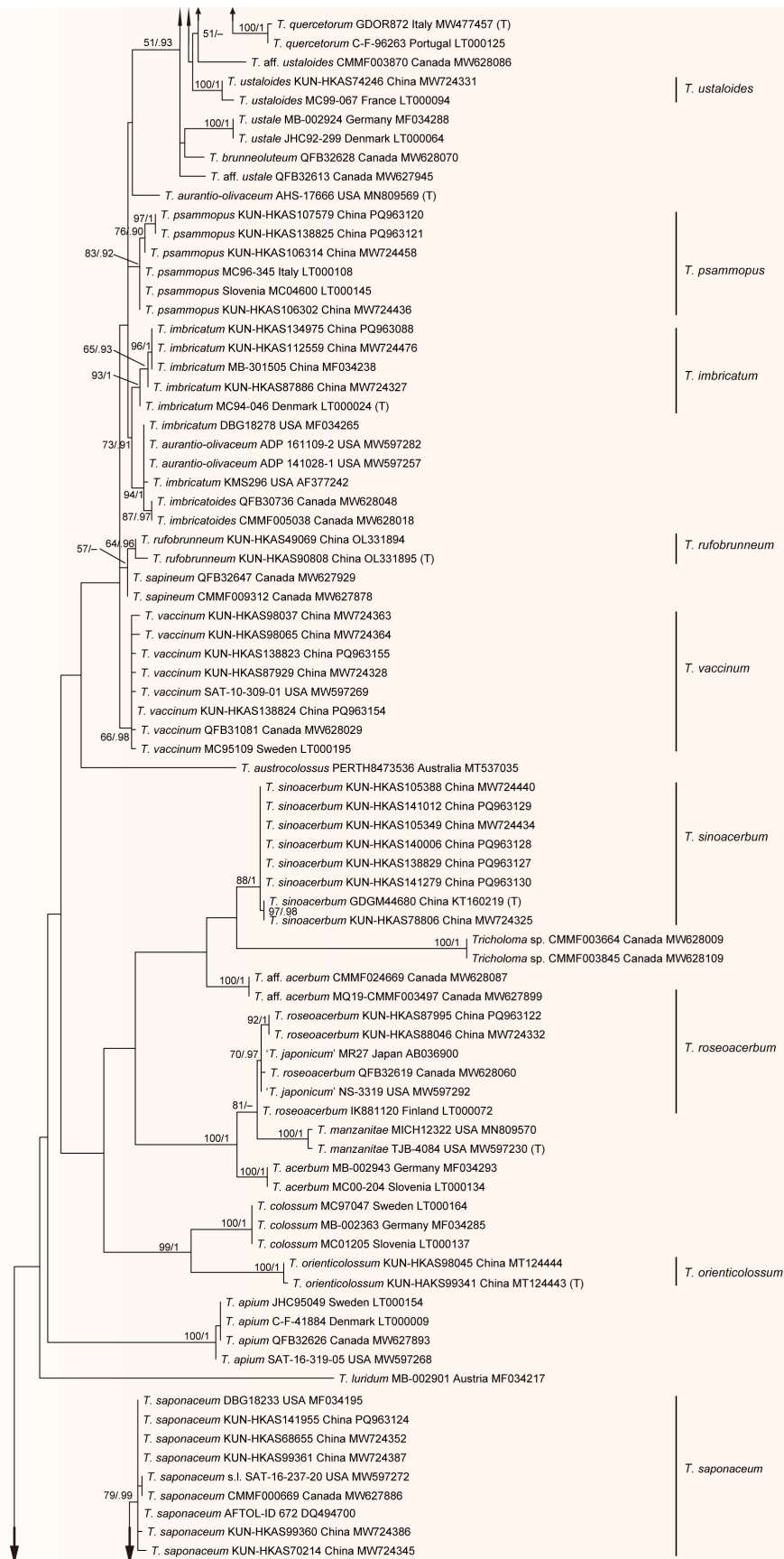


Fig. 4 (continued)



Fig. 4 (continued)

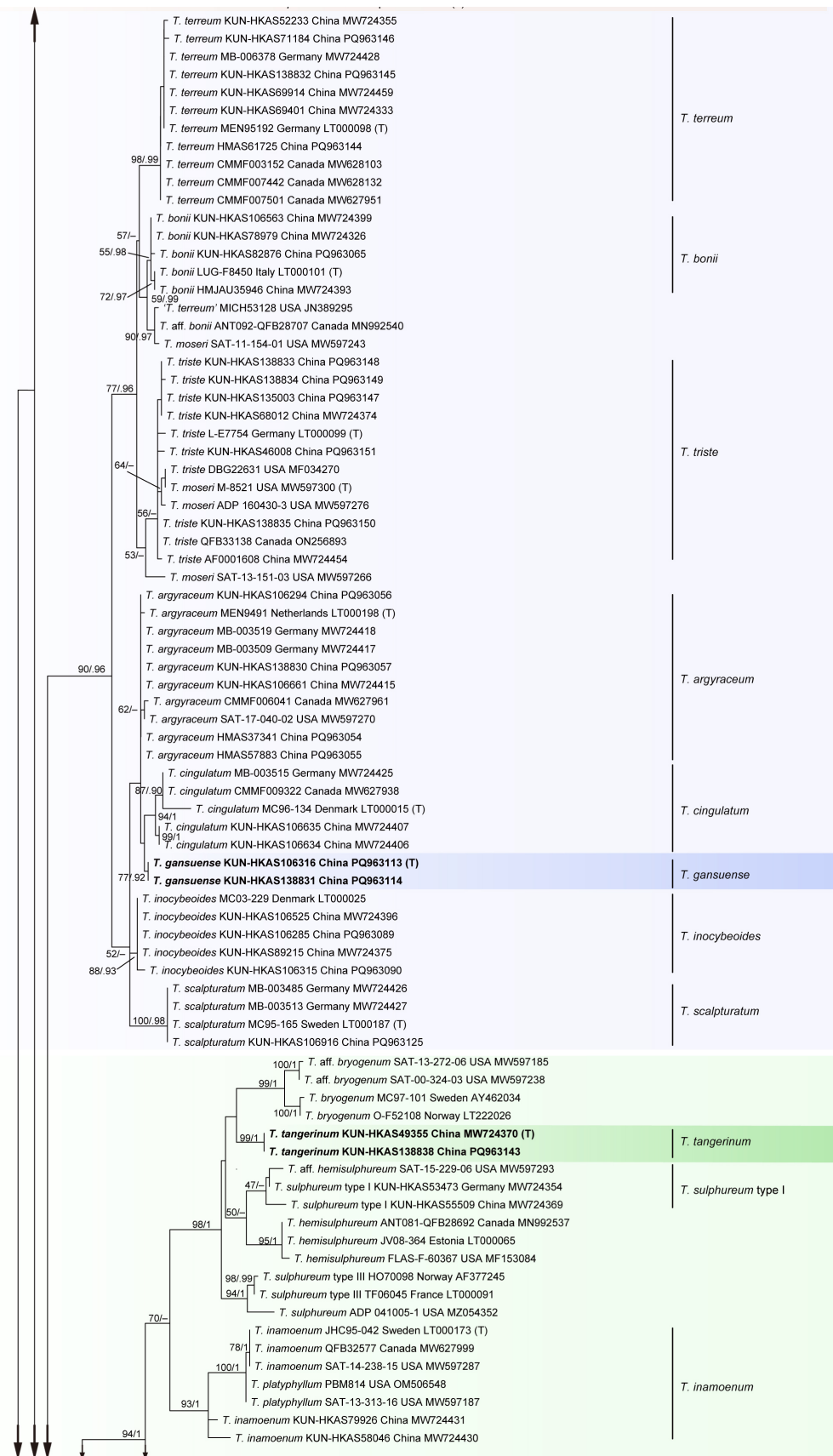


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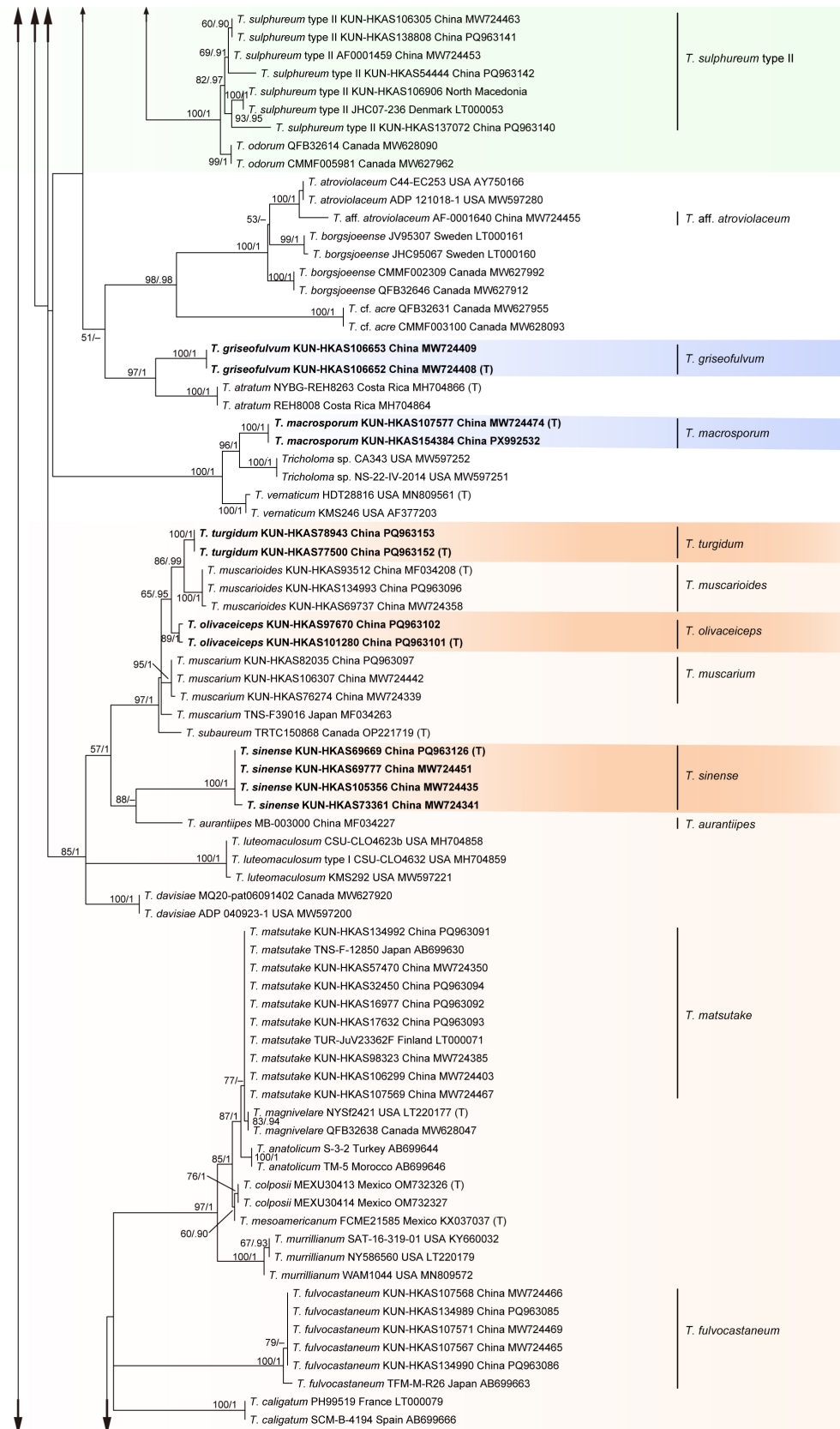


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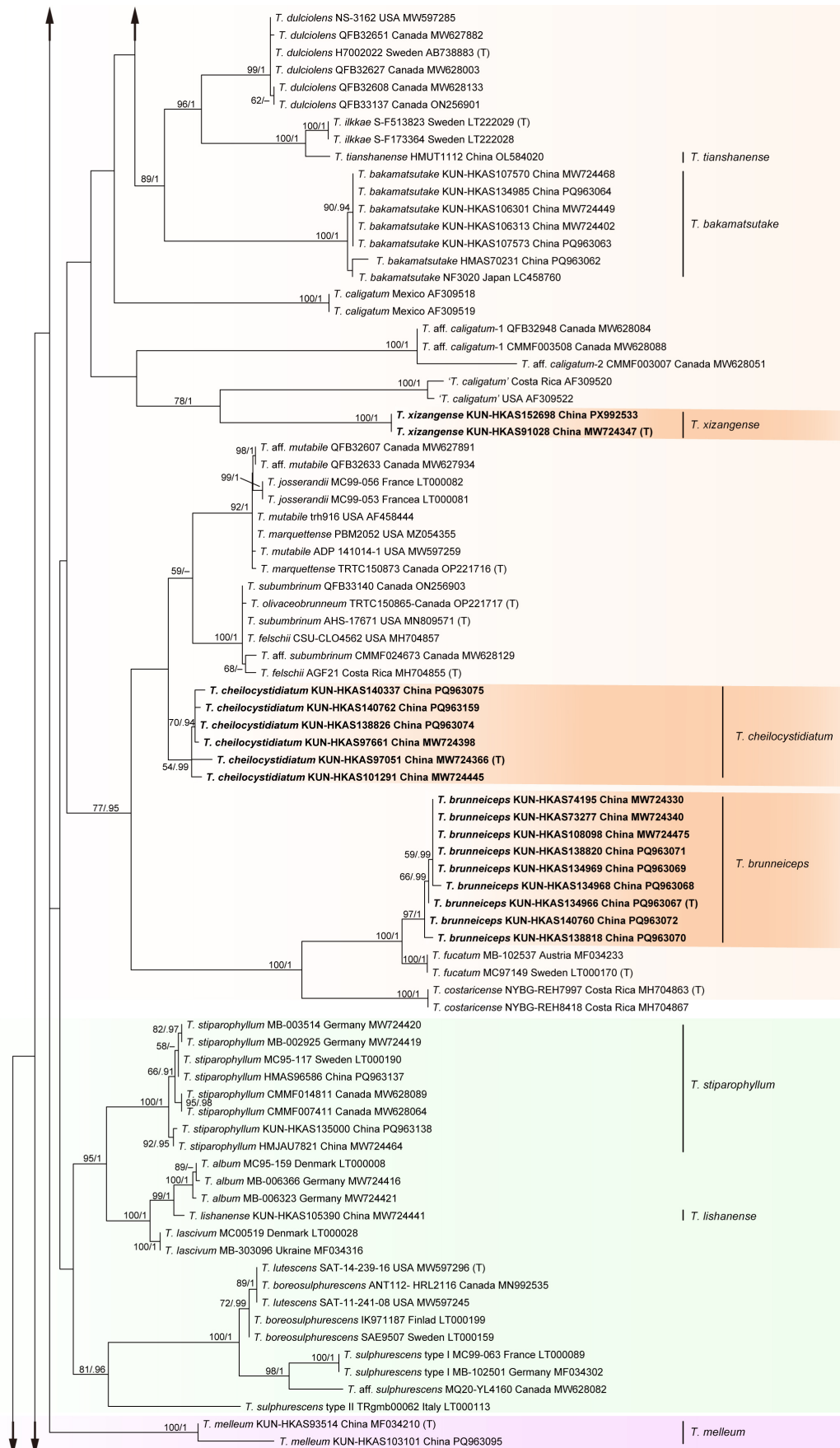


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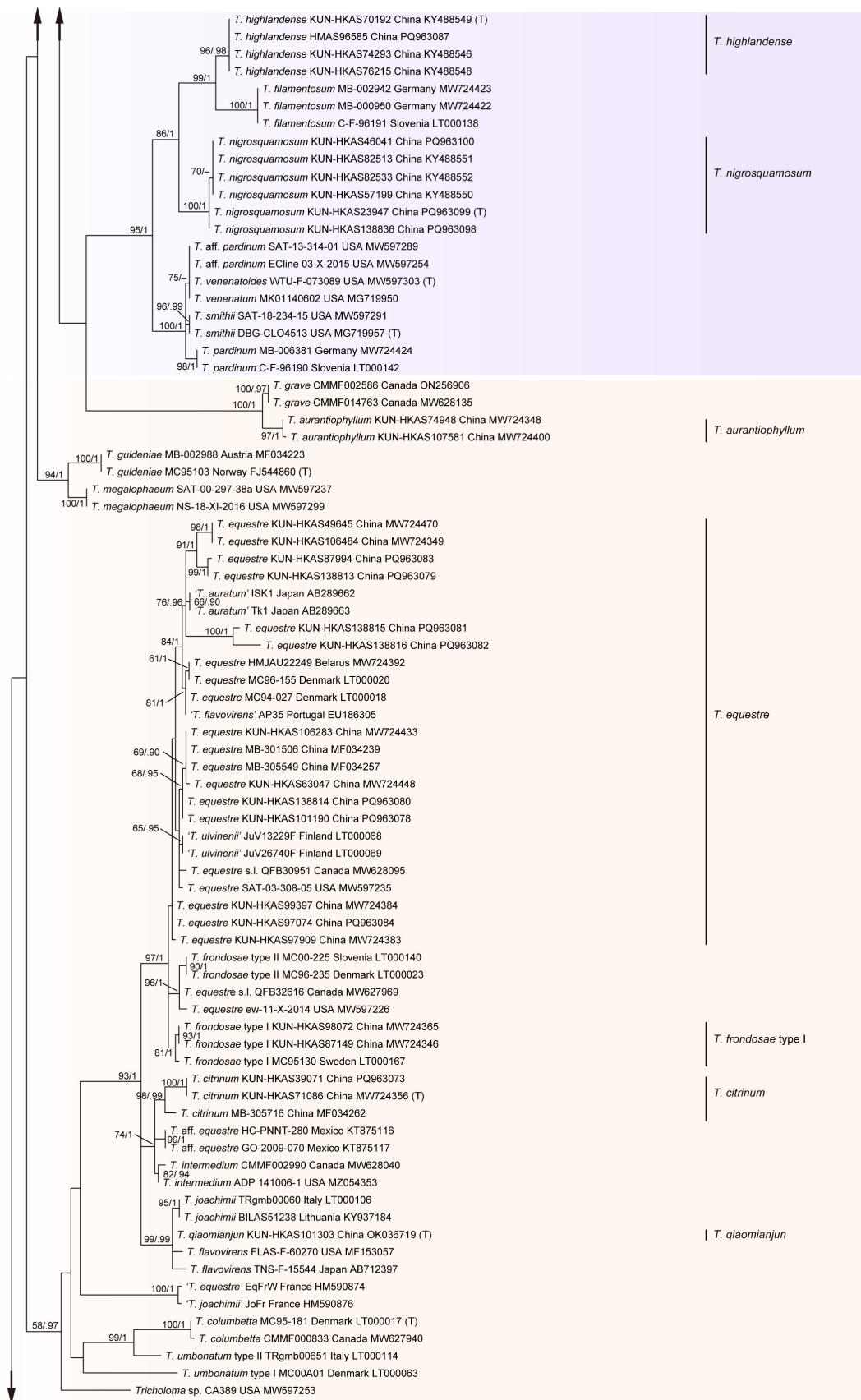


Fig. 4 (continued)

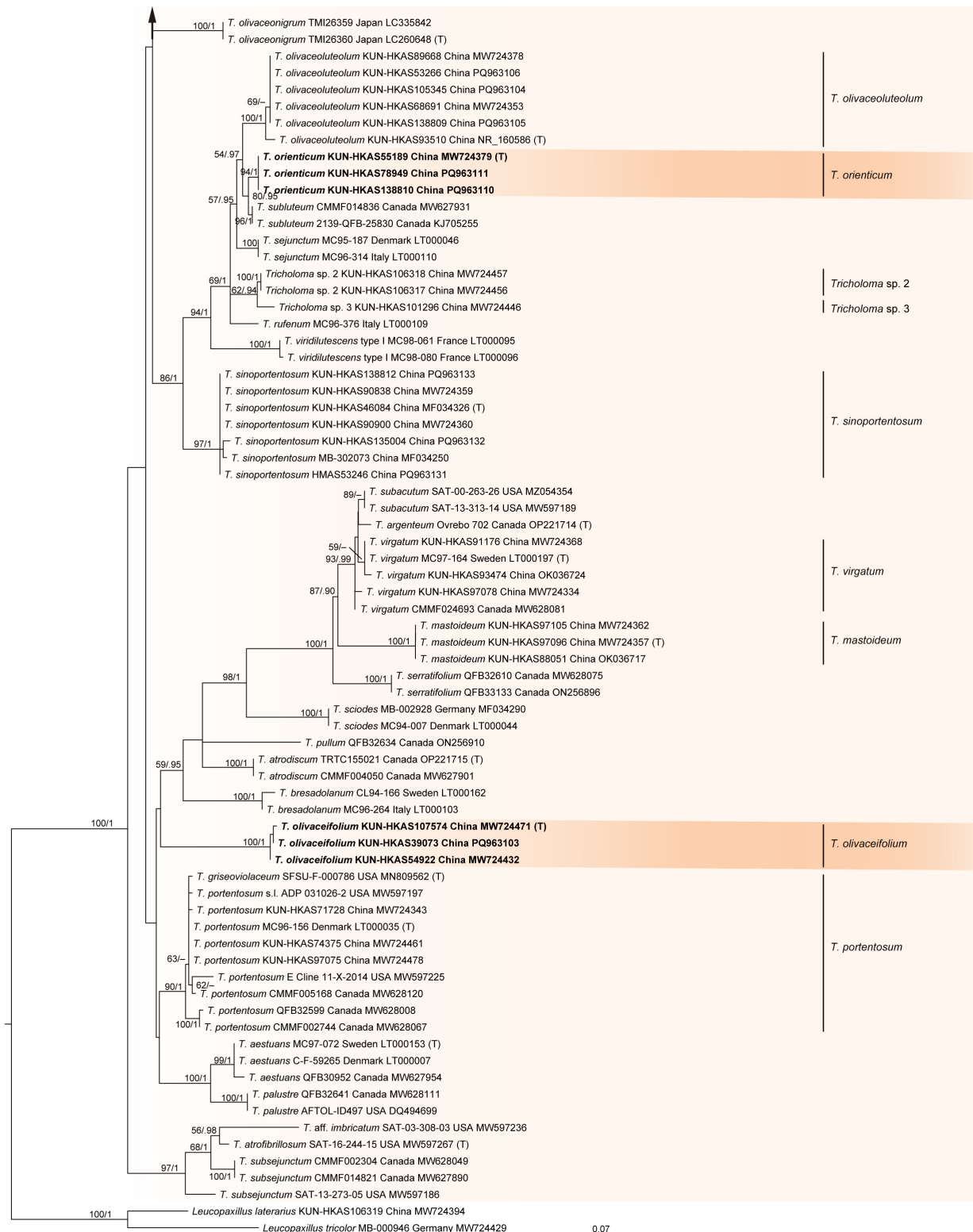


Fig. 4 (continued)

Basidia: The basidia in *Tricholoma* are clavate to narrowly clavate, predominantly 4-spored, occasionally mixed with 1-, 2-, or 3-spored ones. They are typically 20–50 µm long and 5–12 µm wide, with limited taxonomic significance.

Cystidia: Pleurocystidia are usually absent in *Tricholoma*. For cheilocystidia, in most cases they are poorly differentiated and may often merely represent marginal cells emerging

from the underlying gill trama. Sometimes the cheilocystidia are conspicuous and range in shape from broadly clavate (Fig. 12a), cylindrical (Fig. 12b), fusiform (Fig. 12c) to filamentous (Fig. 12d). Although the cheilocystidia may vary within some species, they are somewhat useful for species recognition in the genus.

Lamellar trama: The lamellar trama of *Tricholoma* varies from regular to subregular. Most species exhibit parallel-arranged, clavate, cylindrical, or filamentous hyphae, while some have distinctly inflated cells that range from ellipsoid to fusiform.

Pileipellis: The pileipellis structure is a crucial diagnostic feature for identifying subgenera, sections, and species within *Tricholoma* (Fig. 14). Hyphae in the pileipellis are mostly radially arranged, occasionally somewhat erect. The pileipellis can be categorized into eight structural types (Fig. 13).



Fig. 5 The characters of the pileal surface of *Tricholoma* species. a glabrous (*T. atrovirens*, KUN-HKAS80796). b–d squarulose (b small fibrillose squamules in *T. citrinum*, KUN-HKAS71086; c felty to woolly squamules in *T. triste*, KUN-HKAS135003; d densely arranged, small, reflexed squamules in *T. atosquamosum*, KUN-HKAS97211). e, f squamose (e large, reflexed scales in *T. nigrosquamosum*, KUN-HKAS98053; f large, appressed, fibrillose scales in *T. fulvocastaneum*, KUN-HKAS107568). g, h innately radially fibrillose (g *T. virgatum*, KUN-HKAS98358; h *T. brunneiceps*, KUN-HKAS108098).



Fig. 6 The spacing between lamellae in *Tricholoma* species. a crowded (*T. sinoacerbum*, KUN-HKAS136950). b close (*T. atosquamosum*, KUN-HKAS97910). c distant (*T. olivaceum*, KUN-HKAS83119).



◀ **Fig. 7** The color change of lamellae in *Tricholoma* species when bruised or aged. a, b turning yellow (a *T. portentosum*, KUN-HKAS99381; b *T. sinoportentosum*, KUN-HKAS136951). c, d turning grey or with dark grey to grey spots (c *T. cheilocystidium*, KUN-HKAS97661; d *T. virgatum*, KUN-HKAS98081). e, f turning brown or with brown spots (e *T. fulvomaculatum*, holotype, KUN-HKAS107572; f *T. rubrocastaneum*, KUN-HKAS97827). g, h turning red to reddish (*Tricholoma* sp., KUN-HKAS101282).



Fig. 8 Three different types of annulus in *Tricholoma*. a, b a pseudoannular zone (a *T. aurantium*, KUN-HKAS94389; b *T. albobrunneum*, KUN-HKAS70133). c, d a cobwebby zone (c *T. sculpturatum*, KUN-HKAS106916; d *T. argyraceum*, KUN-HKAS105357). e, f a distinct annulus (e *T. bakamatsutake*, KUN-HKAS106301; f *T. cingulatum*, KUN-HKAS106635).

Clamps: Clamps may be absent or present in *Tricholoma* species. When present, they are typically abundant at the bases of basidia but may occur less frequently elsewhere in the basidioma. The presence or absence of clamps among different collections in the same species is consistent. This feature holds significant value for distinguishing sections and species within the genus (Fig. 14b).

Results

Taxonomy

The taxonomic system of Tricholomataceae

Building on findings of previous studies (Sánchez-García et al.

2014, 2021; Vizzini et al. 2016; Ding et al. 2023; Adamčíková et al. 2025) combined with our phylogenomic, morphological and ecological data, we hereby present the taxonomic system of Tricholomataceae in alphabetic order:

Tricholomataceae R. Heim ex Pouzar

Type: *Tricholoma* (Fr.) Staude

I. Albomagister Sánchez-García et al.

Type: *A. subaustralis* (A.H. Sm. & Hesler) Sánchez-García et al.

II. Corneriella Sánchez-García

Type: *C. bambusarum* (Desjardin & Hemmes) Sánchez-García

III. Dennisiomyces Singer

Type: *D. glabrescentipes* Singer

IV. Dermoloma J.E. Lange ex Herink

Type: *De. cuneifolium* (Fr.) Singer ex Bon

i. Subgen. *Dermoloma*

Type: *De. cuneifolium* (Fr.) Singer ex Bon

1. Sect. *Dermoloma*

Type: *De. cuneifolium* (Fr.) Singer ex Bon

2. Sect. *Conica* Adamčík

Type: *De. bellerianum* Bon

ii. Subgen. *Amylospora* Adamčík

Type: *De. phaeopodium* P.D. Orton

3. Sect. *Atrobrunnea* Singer ex Contu

Type: *De. atrobrunneum* (Dennis) Singer ex Bon

4. Sect. *Nigrescentia* Adamčík

Type: *De. magicum* Arnolds

V. *Leucopaxillus* Boursier

Type: *L. paradoxus* (Costantin & L.M. Dufour) Boursier

VI. *Neodermoloma* Sánchez-García, Matheny & Adamčík

Type: *N. campestre* Sánchez-García, Matheny & Adamčík

VII. *Porpoloma* Singer

Type: *Po. sejunctum* Singer

VIII. *Pseudobaeospora* Singer

Type: *P. oligophylla* (Singer) Singer

IX. *Pseudoporpoloma* Vizzini & Consiglio

Type: *Ps. pes-caprae* (Fr.) Vizzini & Consiglio

X. *Pseudotracholoma* (Singer) Sánchez-García & Matheny

Type: *Pse. umbrosum* (A.H. Sm. & M.B. Walters) Sánchez-García & Matheny

XI. *Tricholoma* (Fr.) Staude

Type: *T. equestre* (L.) P. Kumm.

i. Subgen. *Tricholoma*

Type: *T. equestre* (L.) P. Kumm.

1. Sect. *Tricholoma*

Type: *T. equestre* (L.) P. Kumm.

2. Sect. *Fucata* X.X. Ding et al.

Type: *T. fucatum* (Fr.) P. Kumm.

3. Sect. *Genuina* (Fr.) Sacc.

Type: *T. vaccinum* (Schaeff.) P. Kumm.

4. Sect. *Matsutake* X.X. Ding et al.

Type: *T. matsutake* (S. Ito & S. Imai) Singer

5. Sect. *Muscaria* Reschke

Type: *T. muscarium* Kawam. ex Hongo

6. Sect. *Rigida* (Fr.) Quél.

Type: *T. saponaceum* (Fr.) P. Kumm.

ii. Subgen. *Pardinicutis* Singer

Type: *T. pardinum* (Pers.) Quél.

7. Sect. *Pardinicutis*

Type: *T. pardinum* (Pers.) Quél.

iii. Subgen. *Sericeicutis* Singer

Type: *T. sulphureum* (Bull.) P. Kumm.

8. Sect. *Lasciva* Bon

Type: *T. lascivum* (Fr.) Gillet

9. Sect. *Sericella* (Fr.) Quél.

Type: *T. sulphureum* (Bull.) P. Kumm.

iv. Subgen. *Terrea* Ding et al.

Type: *T. terreum* (Schaeff.) P. Kumm.

10. Sect. *Atrosquamosa* Kühner ex Bon

Type: *T. atrosquamosum* Sacc.

11. Sect. *Terrea*

Type: *T. terreum* (Schaeff.) P. Kumm.

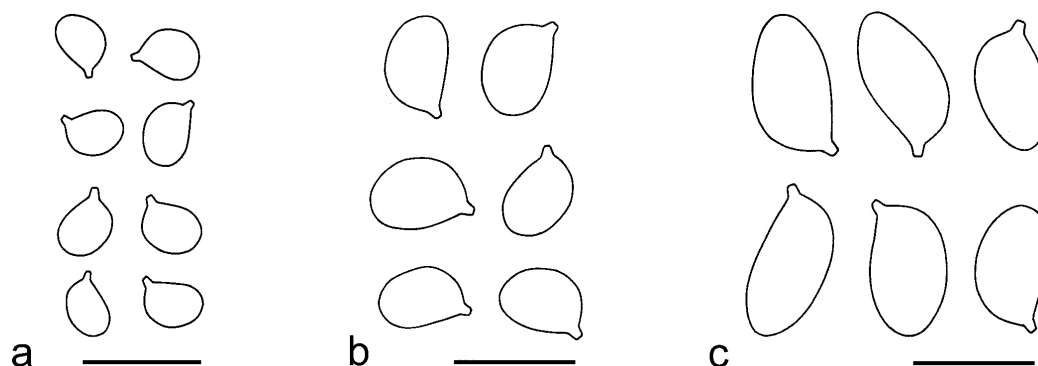


Fig. 9 The size of basidiospores in *Tricholoma*. a small (*T. sinoacerbum*, KUN-HKAS105349). b medium-sized (*T. matsutake*, KUN-HKAS98323). c large (*T. inamoenum*, KUN-HKAS79926). Scale bars = 10 μ m.

Infrageneric classification of *Tricholoma*

Within Tricholomataceae s. str., *Tricholoma* is the best-known and one of the most species-rich genus. In China, it has the highest species diversity among the family, and our sampling for this genus is the most complete. Therefore, we conducted a detailed study of the infrageneric classification of *Tricholoma* based on 1,477 phylogenomic data and morphological observations. Members of *Tricholoma* are characterized by tricholomatoid basidioma, inamyloid basidiospores, absence of pleurocystidia, and pileipellis composed primarily of repent hyphal elements (Fig. 14a).

Tricholoma can be divided into five subgenera (subgen. *Tricholoma*, subgen. *Pardinicutis*, subgen. *Sericeicutis*, subgen. *Terrea*, and *Melleum* clade) and 15 section-level clades (sect. *Tricholoma*, sect. *Fucata*, sect. *Genuina*, sect. *Matsutake*, sect. *Muscaria*, sect. *Rigida*, sect. *Pardinicutis*, sect. *Lasciva*, sect. *Sericella*, sect. *Atrosquamosa*, sect. *Terrea*, Clades A, B, C, and *Melleum* clade) (Fig. 14). These divisions are supported by both phylogenomic and morphological evidence. According to our morphological observations, each subgenus-level clade can be distinguished by a combination of features, including pileus color, pileus squamules, lamellar spacing, basidiospore shape, and the arrangement of pileipellis (Fig. 14a). Similarly,

the 15 section-level clades can be delimited using a suite of characters, such as the shape of pileus center, pileus color and squamules, lamellar spacing, presence or absence of annulus, basidiospore shape and size, presence or absence of cheilocystidia, arrangement of pileipellis, and presence or absence of clamps (Fig. 14b). Clades A, B, C, and the *Melleum* clade were not treated taxonomically due to limited material.

The taxonomy of the genera and species of Tricholomataceae from China

Below we provided the taxonomy of the genera and species diversity of Tricholomataceae s.str. from China in alphabetic order:

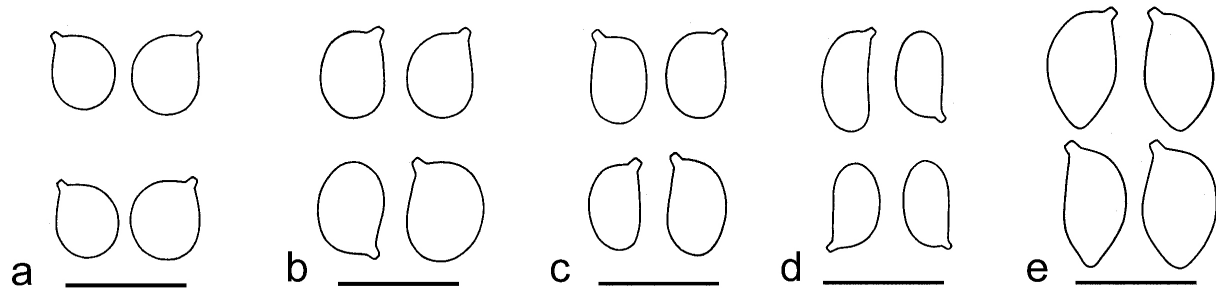


Fig. 10 The shape of basidiospores in *Tricholoma*. a subglobose (*T. bakamatsutake*, KUN-HKAS107573). b broadly ellipsoid (*T. mastoideum*, KUN-HKAS97096). c ellipsoid (*T. muscarioides*, holotype, KUN-HKAS93512). d elongate (*T. inocybeoides*, KUN-HKAS106315). e amygdaliform (*T. tangerinum*, holotype, KUN-HKAS49355). Scale bars = 10 μm.

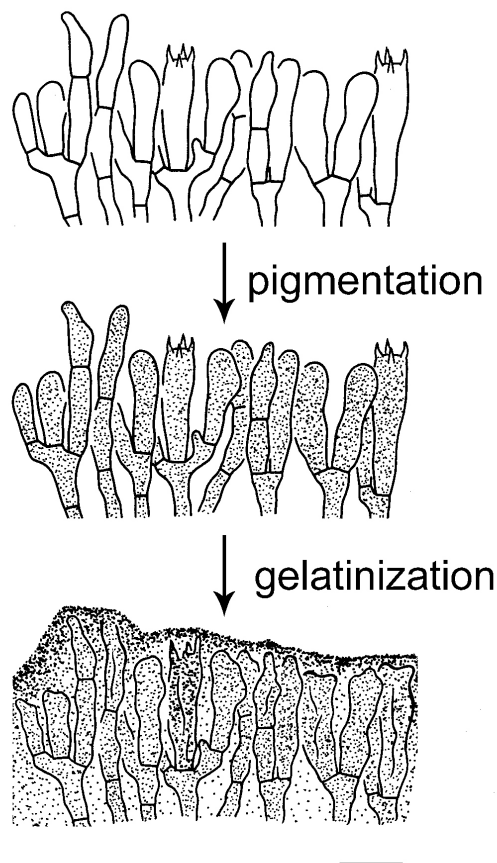


Fig. 11 Schematic illustrations of microscopic changes corresponding to the brown spots in the lamellar edge of *T. albobrunneum* observed under light microscope ($\times 1,000$ magnification) (KUN-HKAS69909). Scale bar = 10 μm.

Tricholomataceae R. Heim ex Pouzar, *Česká Mykol.* 37(3): 175 (1983)

Type: *Tricholoma* (Fr.) Staude, Schwämme Mitteldeutschl. 1: xxviii, 125 (1857).

Description: Basidioma mostly tricholomatoid, occasionally mycenoid to collybioid, currently no sequestrate forms or taxa of Tricholomataceae present. Pileus plano-convex to applanate, umbonate or not, convex, glabrous, squarrose, squamose or radially fibrillose. Lamellae adnate, adnexed, sinuate, emarginate to decurrent. Annulus mostly absent, sometimes present as a distinct annulus, a pseudoannular zone or a cobwebby zone. Basidiospores subglobose, broadly ellipsoid, ellipsoid to elongate, sometimes amygdaliform, mostly smooth, sometimes verrucose,

amyloid or inamyloid, mostly non-dextrinoid, sometimes dextrinoid, thin-walled in most species and hyaline in all. Pleurocystidia present or absent. Cheilocystidia present or absent. Lamellar trama regular. Clamps present or absent.

Ecology: Ectomycorrhizal or saprotrophic on soil in forests or in grasslands.

Known distribution: Almost cosmopolitan. Most in temperate areas, and some in tropical areas.

Genera included: *Albomagister*, *Corneriella*, *Dennisiomyces*, *Dermoloma*, *Leucopaxillus*, *Neodermoloma*, *Porpoloma*, *Pseudobaeospora*, *Pseudoporpoloma*, *Pseudotricholoma* and *Tricholoma*.

Notes: Among the 11 genera (Fig. 1), *Albomagister*, *Leucopaxillus*, *Pseudobaeospora*, *Pseudotricholoma* and *Tricholoma* are found in China.

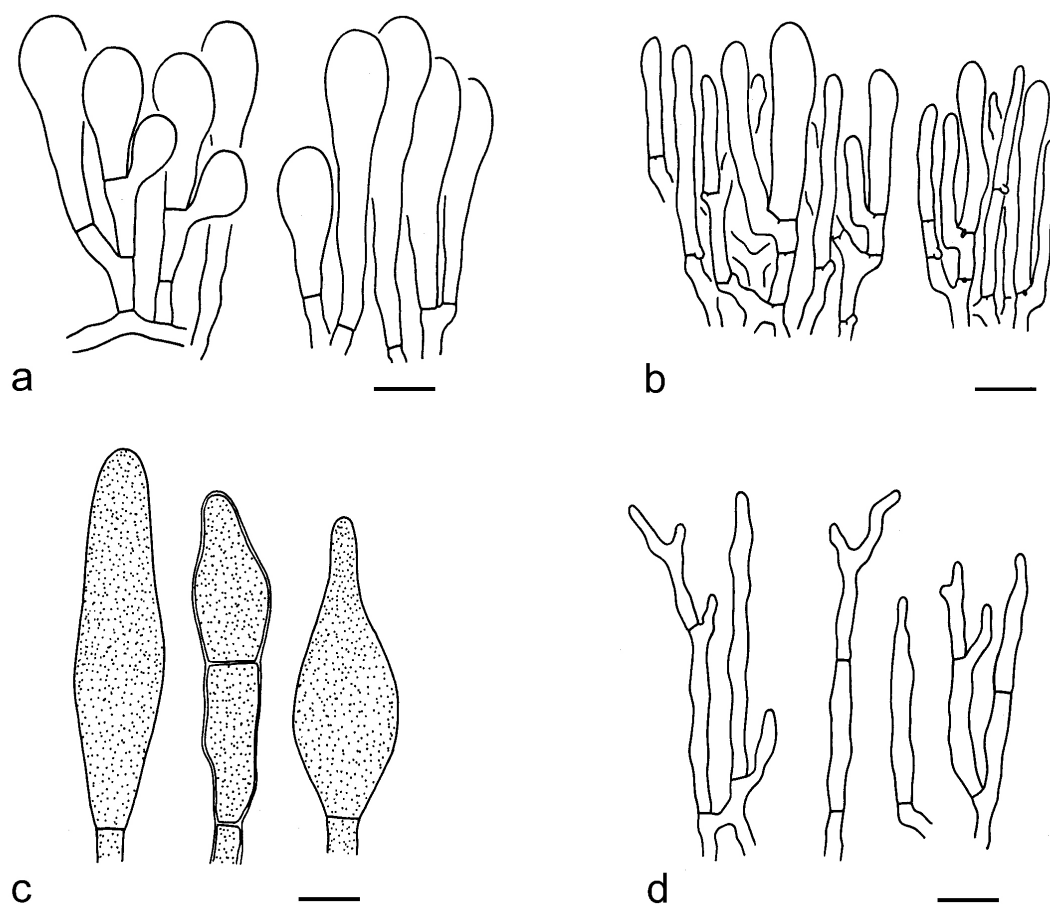


Fig. 12 The shape of cheilocystidia in *Tricholoma*. a broadly clavate (*T. triste*, KUN-HKAS135003). b cylindrical (*T. inamoenum*, KUN-HKAS79926). c fusiform (*T. brunneiceps*, holotype, KUN-HKAS134966). d filamentous (*T. aurantium*, KUN-HKAS94390). Scale bars = 10 µm.

Key to the genera of Tricholomataceae

1. Basidioma large with thick flesh; basidiospores verrucose; pleurocystidia absent; cheilocystidia present... *Leucopaxillus*
1. Basidioma small to large without obviously thick flesh; basidiospores smooth; pleurocystidia present or absent; cheilocystidia present or absent.....2
2. Basidiospores inamyloid to indistinctly amyloid, sometimes dextrinoid3
2. Basidiospores distinctly amyloid6

3. Pleurocystidia absent; basidiospores at first thin-walled, then becoming thick-walled and more or less dextrinoid when mature *Pseudobaeospora*
3. Pleurocystidia absent or present; basidiospores thin-walled, non-dextrinoid.....4
4. Pileipellis a hymeniderm, pluristratous hymeniderm or transitional to an epithelium, composed of one or more layers of inflated cells; context becoming black or without color change when bruised; clamps present..... *Dermoloma*
4. Pileipellis mostly a cutis or ixo-cutis; context without distinct color change when bruised; clamps present or absent5

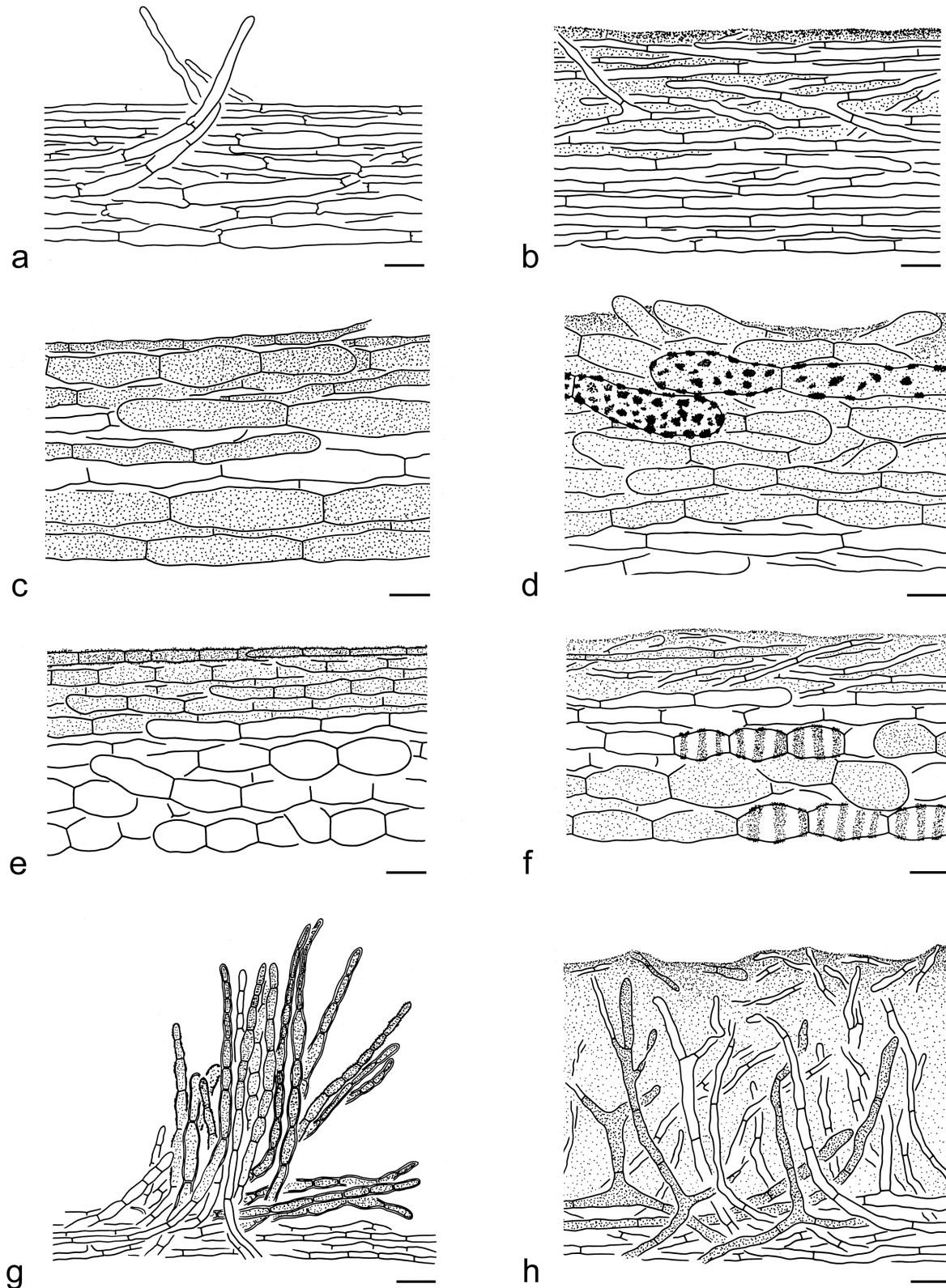


Fig. 13 The types of pileipellis in *Tricholoma*. a cutis composed of filamentous hyphae (*T. sichuanense*, holotype, KUN-HKAS105344). b a ixocutis composed of gelatinizing filamentous hyphae (*T. stans*, KUN-HKAS99382). c a cutis with slightly inflated (clavate to cylindrical) hyphae (*T. vaccinum*, KUN-HKAS87929). d an ixocutis with gelatinizing, slightly inflated (clavate to cylindrical) hyphae (*T. rufobrunneum*, holotype, KUN-HKAS90808). e a cutis with its subpellis made of inflated cells (*T. muscarum*, KUN-HKAS106307). f an ixocutis with its subpellis made of inflated cells (*T. cheilocystidiatum*, holotype, KUN-HKAS97051). g a cutis with its upper hyphae somewhat erected, thick-walled and inflated or not (*T. atosquamosum*, KUN-HKAS97910). h an ixotrichoderm with gelatinizing filamentous hyphae (*T. auratum*, KUN-HKAS94390). Scale bars: a–f, h = 20 μ m, g = 50 μ m.

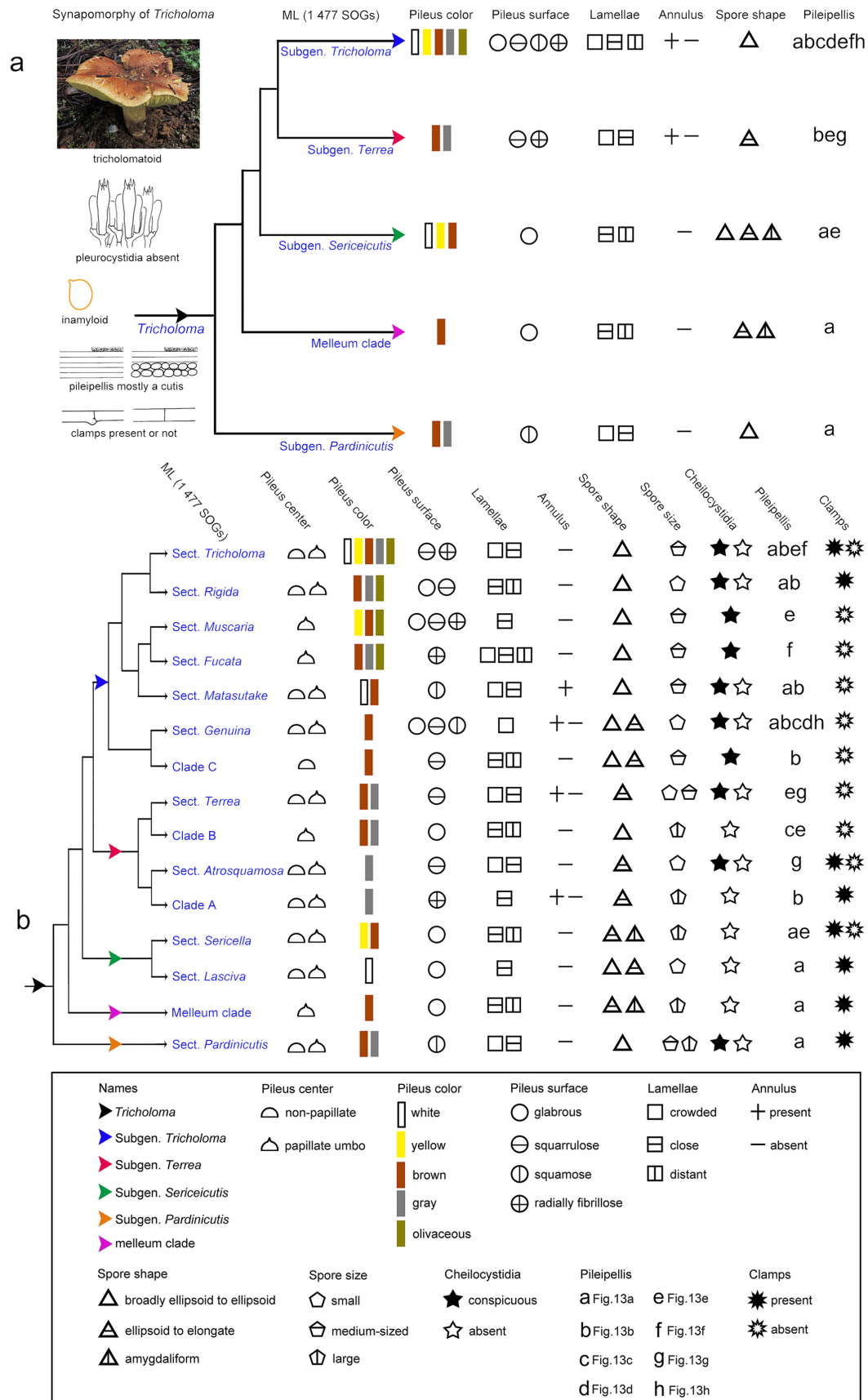


Fig. 14 Schematic diagram of five subgenus- (a) and 15 section-level clades (b) division of *Tricholoma* based on phylogenomic and morphological evidence. The phylogenetic tree is inferred by IQ-TREE based on Dataset II (1,477 SOGs). Morphological data come from this study.



Fig. 15 Basidiomata of species in Tricholomataceae. a *Albomagister albus* (holotype, KUN-HKAS134955). b *A. atosquamosus* (holotype, KUN-HKAS124357). c *Leucopaxillus amyloideus* (holotype, KUN-HKAS134956). d *L. laterarius* (KUN-HKAS124334). e *L. verrucosus* (holotype, KUN-HKAS106509). f, g *Pseudobaeospora lilacina* (KUN-HKAS134959). h, i *Pseudotracholoma* aff. *azoricum* (KUN-HKAS134962). j, k *Pse. griseum* (holotype, KUN-HKAS134963). l, m *Tricholoma citrinum* (holotype, KUN-HKAS71086). n, o *T. equestre* (KUN-HKAS87994).

5. Basidioma small with thin flesh, white or grey; pleurocystidia present and conspicuous in most species, sometimes absent; cheilocystidia present; clamps present *Albomagister*
5. Basidioma medium-sized to large with thick flesh, various in color, white, yellow, brown, grey to olivaceous; pleurocystidia absent; cheilocystidia present or absent; clamps present or absent *Tricholoma*
6. Pileipellis a hymeniderm, pluristratous hymeniderm or transitional to an epithelium, composed of one or more layers of inflated cells 7
6. Pileipellis not a hymeniderm 8
7. Basidioma grey-brown; pileipellis with relatively larger inflated elements *Dermoloma*
7. Basidioma pale grey; pileipellis with relatively smaller inflated elements *Neodermoloma*
8. Lamellae becoming red then blacking when bruised; pleurocystidia absent *Pseudotracholoma*
8. Lamellae without color change when bruised; pleurocystidia present or absent 9
9. Cheilocystidia rare and absent *Pseudoporpholoma*
9. Cheilocystidia present and conspicuous 10
10. Pleurocystidia present *Dennisiomyces*
10. Pleurocystidia absent 11
11. Basidioma distributed in tropical regions *Corneriella*
11. Basidioma mainly distributed in the Southern Hemisphere, but also recorded in Europe *Porpoloma*

Albomagister Sánchez-García et al., Taxon 63(5): 1000 (2014)

Type: *Albomagister subaustralis* (A.H. Sm. & Hesler) Sánchez-García et al., Taxon 63(5): 1000 (2014).

Description: Basidioma very small to small, with pileus ca. 2–4 cm in diam. Pileus mostly white, sometimes grey and scaly. Lamellae white. Basidiospores small, thin-walled, smooth and inamyloid. Pleurocystidia present and conspicuous in most species, sometimes absent. Cheilocystidia present and conspicuous. Clamps present.

Ecology: Putatively ectomycorrhizal on soil in forests with *Quercus*, *Tsuga*, *Pinus*, and *Eucalyptus*, but European species occur among non-ectomycorrhizal plants (Sánchez-García et al. 2014; Moreau et al. 2015; Sánchez-García & Matheny 2017; Matheny et al. 2024). Also collected in bamboo forests in China.

Known distribution: Known from Europe (Moreau et al. 2015; Corriol & Jargeat 2018), North America (Sánchez-García et al. 2014; Matheny et al. 2024) and Eastern China.

Notes: To date, seven species were described in this genus, only *A. albus* and *A. atosquamosus* are found in China (see below).

Key to the species of *Albomagister* from China

1. Basidioma white; pleurocystidia fusiform to subfusiform; lamellar edge fertile with scattered cheilocystidia; caulocystidia colorless, narrowly clavate to clavate *A. albus*
1. Basidioma white but densely covered with dark to grey, fibrillose squamules; pleurocystidia broadly clavate with a mucronate apex; lamellar edge sterile with clustered cheilocystidia; caulocystidia grey-brown, fusiform, subfusiform to ventricose *A. atosquamosus*

1. *Albomagister albus* Y.Y. Cui, T. Guo & Zhu L. Yang, sp. nov. Figs. 15a, 16

Fungal Names: FN 572328

Etymology: *albus* = white, referring to its white basidioma.

Diagnosis: Similar to *A. subaustralis* (A.H. Sm. & Hesler) Sánchez-García et al., but differs in having slightly broader basidiospores and is found only in China.

Type: CHINA. Anhui Province, Huangshan, in a subtropical evergreen broad-leaved forest, altitude 540 m, 21 Oct. 2020, Ting Guo 2213 (holotype, KUN-HKAS134955).

Description: Basidioma very small. Pileus 1–2 cm in diam., convex; surface dry, white (1A1), covered with white (1A1), fibrillose-silky squamules; margin slightly revolute, sometimes splitting. Lamellae emarginate, white (1A1), distant. Stipe 1.5–3 × 0.1–0.3 cm, subcylindrical to cylindrical, white (1A1), glabrous, exannulate. Taste and odour not recorded.

Basidiospores [30/1/1] 4.5–6 × 4–5 µm (mean length = 5.2 µm, mean width = 4.4 µm), Q = (1.06–) 1.15–1.26 (–1.32), Qm = 1.2 ± 0.06, broadly ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 20–30 × 5–8 µm, clavate, 4-spored, hyaline; sterigmata 3–5 µm long; basal septa with clamps. Pleurocystidia 55–85 × 10–15 µm, abundant, scattered, fusiform to subfusiform, slightly thick-walled (0.5–1 µm). Cheilocystidia 45–70 × 8–15 µm, conspicuous, abundant, scattered, fusiform to subfusiform, slightly thick-walled (0.5–1 µm). Subhymenium composed of 2–4 µm wide filamentous hyphae. Lamellar trama regular, composed of colorless, cylindrical to filamentous hyphae 5–20 µm wide. Pileipellis a cutis, composed of radially arranged, 2–20 µm wide, colorless hyphae; terminal cells in the upper layer fusiform to ventricose, often thick-walled (ca. 1 µm). Caulocystidia 40–100 × 8–10 µm, narrowly clavate to clavate, thin- to thick-walled up to 1 µm. Clamps present in all parts of basidioma.

Ecology: On soil in a subtropical evergreen broad-leaved forest.

Known distribution: Currently only known from Eastern China.

Notes: *Albomagister albus* is characterized by its very small, white basidioma with a fibrillose pileus, distant lamellae, broadly ellipsoid basidiospores, and fusiform, slightly thick-walled pleuro- and cheilocystidia. This species is related to *A. luteifolius* Lebeuf et al. (Fig. 1), but the latter has a stipitipellis without caulocystidia and is currently only found in eastern North America (Matheny et al. 2024).

Albomagister subaustralis, *A. alesandrii* P.A. Moreau et al. and *A. virgineus* G. Corriol & P. Jargeat are similar to the new species. However, *A. subaustralis* has slightly narrower basidiospores (5–6.5 × 3–4 µm) and is currently only found in North America (Hesler & Smith 1963; Sánchez-García et al. 2014). The European *A. alesandrii* differs from *A. albus* by its faintly amyloid basidiospores sometimes thick-walled, and thin-walled pleuro- and cheilocystidia (Moreau et al. 2015). *Albomagister virgineus* differs by its slightly larger basidiospores (5.8–6.7 × 4.9–6 µm) with few thick-walled, the absence of pleurocystidia and is currently only collected from Europe to date (Corriol & Jargeat 2018).

2. *Albomagister atosquamosus* Y.Y. Cui, L.K. Jia & Zhu L. Yang, sp. nov. Figs. 15b, 17

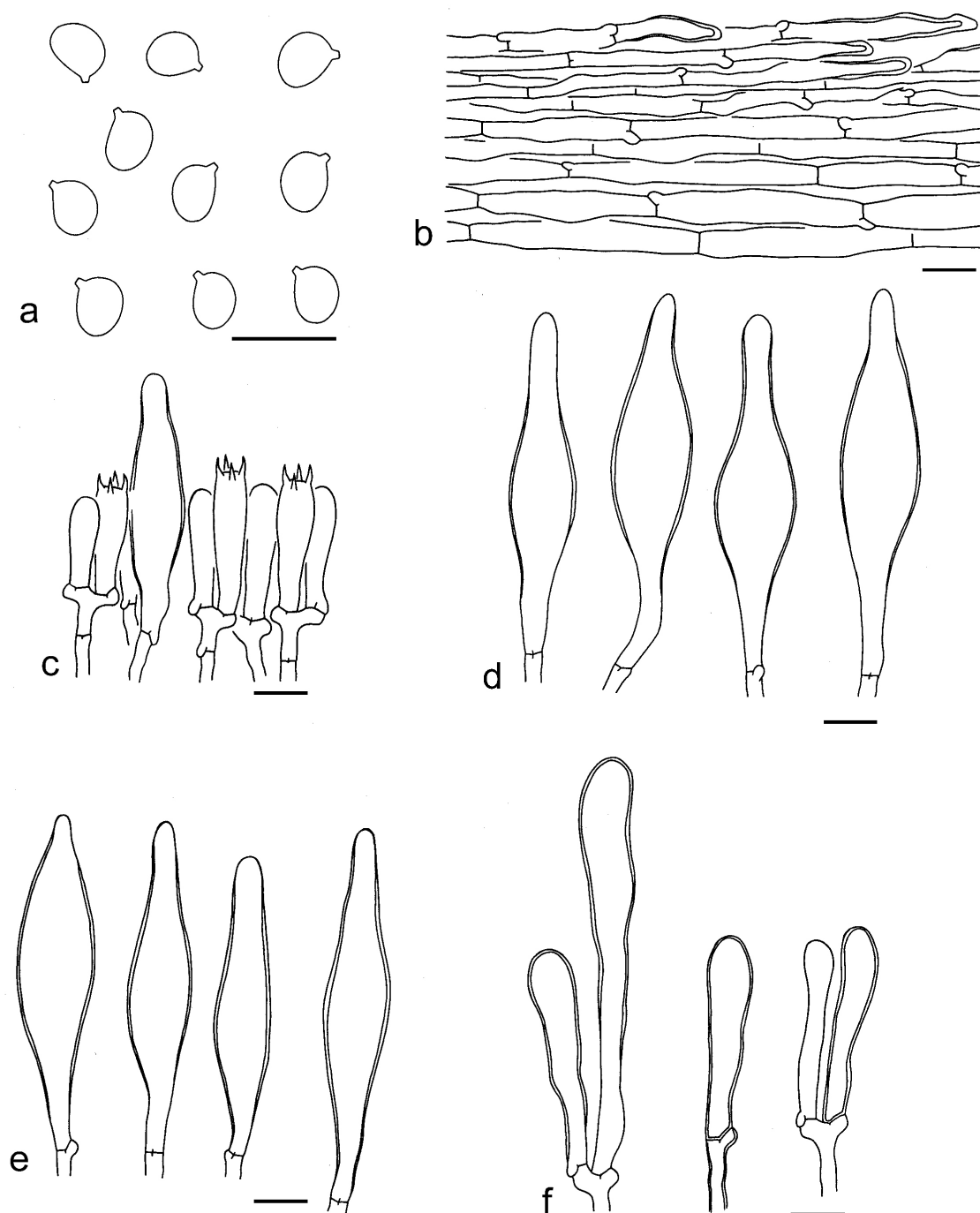


Fig. 16 Microscopic features of *Albomagister albus* (holotype, KUN-HKAS134955). a Basidiospores. b Pileipellis. c Hymenium and subhymenium. d Pleurocystidia. e Cheilocystidia. f Caulocystidia. Scale bars: a, c–f = 10 μ m, b = 20 μ m.

Fungal Names: FN 572329

Etymology: *atrosquamosus* = black squamules, referring to its basidioma densely covered with black squamules.

Diagnosis: Related to *A. griseosquamosus* Lebeuf et al., but differs by having smaller basidiospores ($4.5\text{--}6 \times 3.5\text{--}5 \mu\text{m}$).

Type: CHINA. Zhejiang Province, Lishui, Jingning She Autonomous County, in a subtropical forest with bamboos, altitude 687 m, 24 Jun. 2021, 331127MF-JLK1608 (holotype, KUN-HKAS124357).

Description: Basidioma small. Pileus ca. 3.5 cm in diam., applanate; surface dry, background white (1A1), densely covered with black (1F1–4) to grey (2F1–3), fibrillose squamules over the entire disk; margin straight. Lamellae sinuate to adnate, white (1A1) to dirty white (1B1–2), subclose to close; lamellar edges white (1A1) to dirty white (1B1–2), sometimes with grey (1C1–3) stains. Stipe ca. 5×0.9 cm, subcylindrical, white (1A1) background covered with black (1F1–4) to grey (2F1–3), fibrillose squamules, exannulate. Taste and odour not recorded.

Basidiospores [20/1/1] $4.5\text{--}6 \times 3.5\text{--}5 \mu\text{m}$ (mean length = $5.1 \mu\text{m}$, mean width = $4.2 \mu\text{m}$), $Q = (1.1\text{--}) 1.15\text{--}1.29$ (-1.37), $Q_m = 1.22 \pm 0.07$, broadly ellipsoid, occasionally subglobose or ellipsoid, inamyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $20\text{--}30 \times 5\text{--}7 \mu\text{m}$, clavate, 4-spored, hyaline; sterigmata $3\text{--}5 \mu\text{m}$ long; basal septa with clamps. Pleurocystidia $50\text{--}60 \times 18\text{--}23 \mu\text{m}$, abundant, scattered, broadly clavate with a mucronate apex, thick-walled (ca. $1 \mu\text{m}$), colorless, hyaline. Cheilocystidia $55\text{--}65 \times 10\text{--}15 \mu\text{m}$, abundant, clustered, fusiform, broadly fusiform to ventricose, sometimes broadly clavate with a mucronate apex, thin- to thick-walled ($0.5\text{--}2 \mu\text{m}$), colorless, hyaline. Subhymenium composed of $2\text{--}4 \mu\text{m}$ wide filamentous hyphae. Lamellar trama regular, composed of colorless, ellipsoid, cylindrical, clavate to filamentous hyphae $5\text{--}35 \mu\text{m}$ wide. Pileipellis a cutis, composed of radially arranged, colorless or grey-brown to grey, $8\text{--}15 \mu\text{m}$ wide, slightly thick-walled ($0.5\text{--}1 \mu\text{m}$), cylindrical hyphae with lanceolate to cylindrical terminal cells; subpellis composed of radially arranged, colorless, $5\text{--}10 \mu\text{m}$ wide, thin-walled, cylindrical to filamentous hyphae. Stipitipellis a trichoderm-like layer, composed of erected arranged, clavate to subclavate, thin- to slightly thick-walled ($0.5\text{--}1 \mu\text{m}$), grey-brown, septate elements $5\text{--}20 \mu\text{m}$ wide, mixed with scattered, thick-walled (ca. $1 \mu\text{m}$), grey-brown, lanceolate, subfusiform to ventricose caulocystidia. Clamps present in all parts of basidioma.

Ecology: On soil in a subtropical forest with bamboos.

Known distribution: Currently only known from Eastern China.

Notes: *Albomagister atosquamosus* is well delimited by its grey scaly basidioma, broadly ellipsoid basidiospores ($4.5\text{--}6 \times 3.5\text{--}5 \mu\text{m}$), thick-walled, broadly clavate pleurocystidia with a mucronate apex, clustered, thin- to thick-walled, fusiform, broadly fusiform to ventricose cheilocystidia, and the presence of clamps. This species is closely related to *A. griseosquamosus* (Fig. 1), but the latter species has larger basidiospores ($6\text{--}7.1\text{--}8 \times 4.5\text{--}5.6\text{--}6.7 \mu\text{m}$) and is currently distributed in eastern North America (Matheny et al. 2024).

Albomagister atosquamosus can be easily separated from *A. subaustralis*, *A. alesandrii* and *A. virgineus* by its grey scaly basidioma. In addition, *A. alesandrii* has faintly amyloid, sometimes thick-walled basidiospores, thin-walled pleurocystidia, and thin-walled, sparse cheilocystidia (Moreau et al. 2015). *Albomagister virgineus* has relatively larger, few thick-walled basidiospores ($5.8\text{--}6.7 \times 4.9\text{--}6 \mu\text{m}$), and no pleurocystidia (Corriol & Jargeat 2018). *Albomagister albus* has fusiform pleurocystidia, fertile lamellar edges with scattered cheilocystidia, and narrowly clavate to clavate caulocystidia. *Tricholoma atosquamosum* Sacc. is somewhat similar to this species but can be easily separated by its larger basidioma with a glabrous stipe, ellipsoid to elongate basidiospores ($5.5\text{--}7 \times 3.5\text{--}4.5$), and the absence of pleuro- and cheilocystidia, and clamps (this study). *Pogonoloma spinulosum* (Kühner & Romagn.) Sánchez-García is comparable to *A. atosquamosus*. However, the former species can be easily separated by its amyloid basidiospores (Sánchez-García et al. 2014; Læssøe & Petersen 2019).

Corneriella Sánchez-García, *Taxon* 63(5): 1000 (2014)

Type: *Corneriella bambusarum* (Desjardin & Hemmes) Sánchez-García, *Taxon* 63(5): 1000 (2014).

Description: Lamellae white when young, then becoming darker. Basidiospores smooth, thin-walled, and amyloid. Cheilocystidia present and conspicuous. Pleurocystidia absent. Pileipellis a cutis with suberect to erect terminal cells. Clamps present.

Ecology: Saprotrophic (Sánchez-García et al. 2014; Raj et al. 2015). On soil and humus in tropical regions (Sánchez-García et al. 2014; Raj et al. 2015).

Known distribution: The known species of this genus is distributed in India, Malaysia, Thailand, and USA (Sánchez-García et al. 2014; Raj et al. 2015).

Notes: Only three species are recorded in *Corneriella* (Sánchez-García et al. 2014; Raj et al. 2015). Currently no species of this genus has been found in China. The description above is a summary of Sánchez-García et al. (2014) and Raj et al. (2015).

Dennisiomyces Singer, *Anais Soc. Biol. Pernambuco* 13(1): 225 (1955)

Type: *Dennisiomyces glabrescentipes* Singer, *Anais Soc. Biol. Pernambuco* 13(1): 225 (1955).

Description: Basidiospores smooth, thin-walled, and amyloid. Pleurocystidia present. Cheilocystidia present and conspicuous. Clamps present.

Ecology: Saprotrophic, on soil with various trees (Singer 1989; Sánchez-García & Matheny 2017; Corriol & Jargeat 2019).

Known distribution: Known from Europe, Caribbean Basin, Central America, Eastern U.S., and South America (Singer 1955a, b, 1989; Sánchez-García et al. 2014; Corriol & Jargeat 2019; Fig. 1)

Notes: To date, five species, including *D. fibrillosus* G. Corriol & P. Jargeat, *D. fuscoalbus* Singer, *D. glabrescentipes* Singer, *D. griseus* (Dennis) Singer and *D. rionegrensis* Singer, are recorded under *Dennisiomyces* (Singer 1955a, b, 1956, 1989; Corriol & Jargeat 2019). Only three of them (*D. fibrillosus*, *D. glabrescentipes* and *D. griseus*) are confirmed with molecular evidence (Sánchez-García et al. 2014; Corriol & Jargeat 2019), and the descriptions of this genus are a summary on these three species (Singer 1955a, b, 1956; Corriol & Jargeat 2019). No species of *Dennisiomyces* are found in China.

Dermoloma J.E. Lange ex Herink, *Sb. severočesk. Mus., Hist. Nat.* 1: 62 (1958)

Type: *Dermoloma cuneifolium* (Fr.) Singer ex Bon, *Docums Mycol.* 17(no. 65): 51 (1986).

Description: Context becoming black or without color change when bruised. Basidiospores smooth, thin-walled, amyloid or inamyloid. Pileipellis a hymeniderm, pluristratous hymeniderm or transitional to an epithelium, composed of one or more layers of inflated cells. Clamps present.

Ecology: Reported as a member of CHEGD (acronym of Clavariaceae, *Hygrocybe* s.l., *Entoloma*, Geoglossaceae, *Dermoloma*) fungi, which have a biotrophic lifestyle and probably form an unspecified symbiosis with vascular plants (Halbwachs et al. 2013, 2018; Adamčíková et al. 2025; Caboňová et al. 2025).

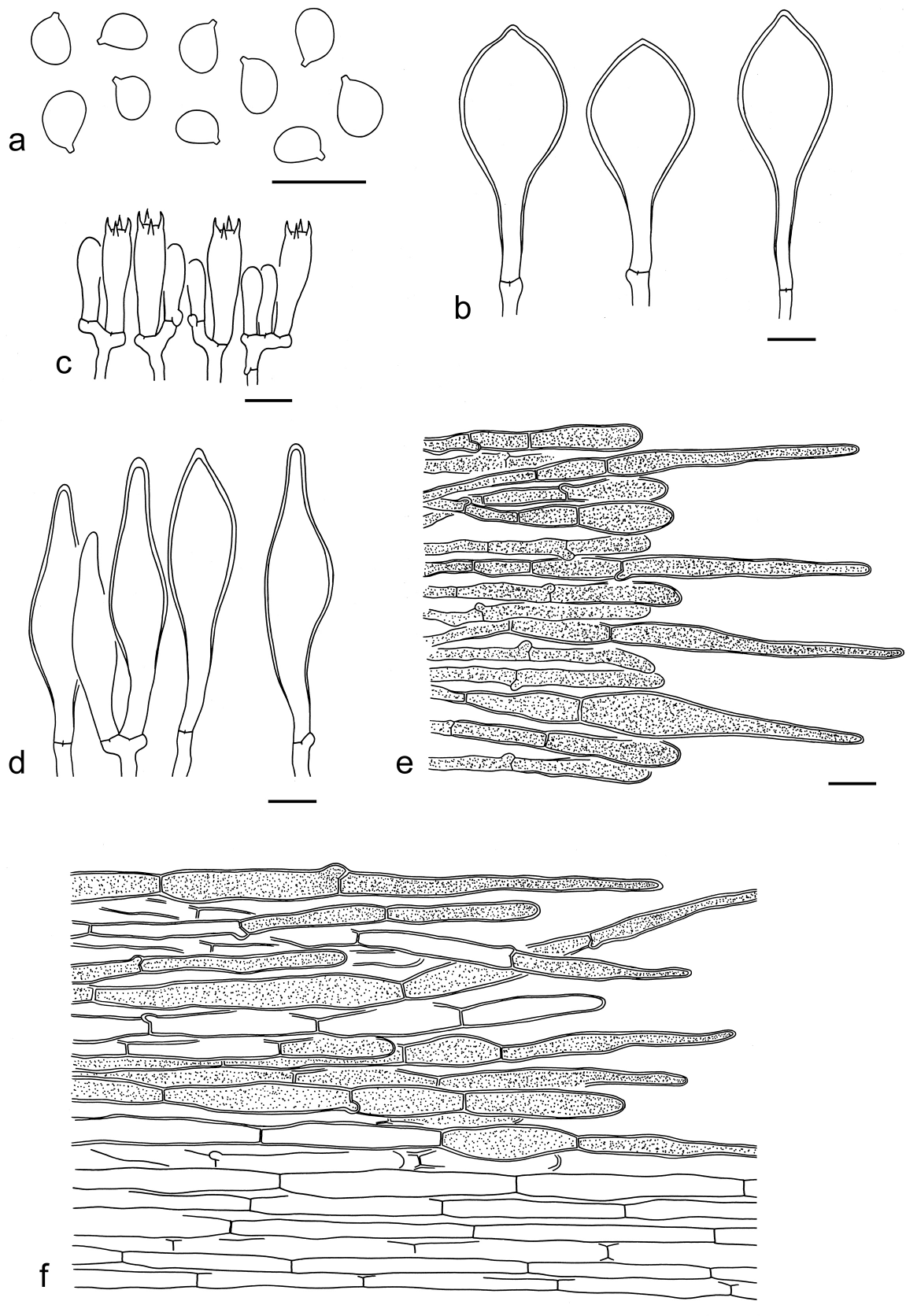


Fig. 17 Microscopic features of *Albomagister atosquamosus* (holotype, KUN-HKAS124357). a Basidiospores. b Pleurocystidia. c Hymenium and subhymenium. d Cheilocystidia. e Stipitipellis. f Pileipellis. Scale bars: a–d = 10 μ m, e, f = 20 μ m.

Known distribution: Almost cosmopolitan. Known from Africa, Asia, Australia and Oceania, Europe, and North America (Sánchez-García et al. 2021; Adamčíková et al. 2025; Caboňová et al. 2025).

Notes: Many mycologists have contributed to the study of *Dermoloma* based on morphological characters since its publication (Singer 1962a, 1975, 1986; Bon 1979, 1986, 1998; Arnolds 1992, 1993; Contu et al. 2008; Vesterholt 2008, 2012). Sánchez-García et al. (2021) provided the first phylogenetic study of *Dermoloma* based on DNA sequence analysis of four gene fragments and supported the subdivision of this genus into two subgenera (subgen. *Dermoloma* and subgen. *Amylospora*) and four sections (sect. *Dermoloma*, sect. *Conica*, sect. *Atrobrunnea* and sect. *Nigrescentia*). Later, Adamčíková et al. (2025) validated this finding, however the subgenera splitting was not retrieved with molecular evidence, implying that the delimitation of subgenera was mainly based on morphological data and required more investigations. Here, we follow the studies of Sánchez-García et al. (2021) and Adamčíková et al. (2025). So far, no species of *Dermoloma* has been found in China.

***Leucopaxillus* Boursier, Bull. trimest. Soc. mycol. Fr. 41(3): 393 (1925)**

Type: *Leucopaxillus paradoxus* (Costantin & L.M. Dufour) Boursier [as 'paradoxa'], Bull. trimest. Soc. mycol. Fr. 41(3): 393 (1925).

Description: Basidioma robust and fleshy. Pileus white, beige to brown, finely velvety. Lamellae crowded and narrow, often forked. Basidiospores verrucose and amyloid. Pleurocystidia absent. Cheilocystidia present. Pileipellis a cutis composed of radially arranged hyphae mixed with interwoven to more or less erected hyphae. Clamps present.

Ecology: Probably saprotrophic (Sánchez-García & Matheny 2017). Solitary to scattered on soil with various trees.

Known distribution: Almost cosmopolitan. Known from Asia, Europe, North America, Oceania, and South America (Singer & Smith 1943; Bougher 1987; Hubregtse & Hubregtse 2012; Vizzini et al. 2012).

Notes: *Leucopaxillus*, typified by *L. paradoxus* (Costantin & L.M. Dufour) Boursier, belongs to Tricholomataceae (Sánchez-García et al. 2014). There were 110 names recorded under this genus ([Index Fungorum](#); Singer & Smith 1943, 1947; Bougher 1987; Kibby et al. 2009; Isık & Türkeul 2018), but many species were subsequently moved into other genera, such as *Aspropaxillus* Kühner & Maire, *Giacomia* Vizzini & Contu, *Notholepista* Vizzini & Contu and *Pseudoclitopilus* Vizzini & Contu (Vizzini et al. 2012; He & Yang 2022). Recent molecular phylogenetic analyses indicated that *Leucopaxillus* is a well-supported monophyletic group (Sánchez-García et al. 2014, 2021). Species in this genus can be separated from the other members of Tricholomataceae by its verrucose and amyloid basidiospores. To date, three species are found in China (see below).

Key to the species of *Leucopaxillus* from China

1. Pileus brown; basidiospores smaller, with length less than 5.5 μm *L. laterarius*
1. Pileus white, cream to brownish; basidiospores larger, with length most more than 5.5 μm 2

2. Pileus white, often with cream tinge; basidiospores ellipsoid to elongate, $Q = 1.35\text{--}1.69$, $Q_m = 1.52 \pm 0.11$ *L. amyloideus*
2. Pileus white to brownish; basidiospores broadly ellipsoid to ellipsoid, $Q = 1.17\text{--}1.48$, $Q_m = 1.32 \pm 0.12$ *L. verrucosus*

3. *Leucopaxillus amyloideus* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 15c, 18, 19

Fungal Names: FN 572330

Etymology: amyloideus = amyloid, referring to its amyloid basidiospores.

Diagnosis: Similar to *L. cerealis* (Lasch) Singer, but differs by its bulbous stipe base.

Type: CHINA. Xinjiang, Tacheng, Shawan, altitude ca. 1700 m, Jian-Wei Liu 645 (holotype, KUN-HKAS134956).

Description: Basidioma medium-sized. Pileus ca. 6 cm in diam., hemispherical, convex to plano-convex; surface dry, white (1A1), often with cream (1A2–4) to brownish (3B2–4) tints, glabrous or slightly fibrillose; margin incurved, often ribbed in ages; context white (1A1). Lamellae subdecurrent, crowded, narrow, often forked, white (1A1) to beige white (1A2); edges entire. Stipe ca. 6 $\times$ 1.5–2.5 cm, firm, solid, cylindrical, often slightly tapering downwards, white (1A1), exannulate; basal mycelium white (1A1). Taste and odour not recorded.

Basidiospores [60/3/1] 6–8 (–8.5) $\times$ 4–5.5 μm (mean length = 7.2 μm , mean width = 4.7 μm), $Q = (1.24\text{--}) 1.35\text{--}1.69$ (–1.89), $Q_m = 1.52 \pm 0.11$, ellipsoid to elongate, occasionally broadly ellipsoid, amyloid, colorless, hyaline, thin-walled, verrucose, sometimes glabrous. Basidia 30–45 $\times$ 10–12 μm , clavate, 4-spored, thin- to slightly thick-walled, hyaline; sterigmata ca. 4 μm long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia 30–55 $\times$ 3–7 μm , scattered, irregularly fusiform to filiform, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 μm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless; thin-walled hyphae 3–8 μm wide. Pileipellis a cutis, composed of radially arranged, 2–8 μm wide, thin-walled, colorless hyphae, often mixed with more or less erected hyphae. Clamps present in all parts of basidioma.

Ecology: On soil in a temperate forest with trees of *Picea*.

Known distribution: Currently known from Northwestern China and probably Pakistan.

Additional specimen examined: CHINA. Xinjiang, Tacheng, Shawan, altitude ca. 1800 m, Jian-Wei Liu (KUN-HKAS152699).

Notes: *Leucopaxillus amyloideus* is characterized by its white and fleshy basidioma, amyloid, verrucose basidiospores and the presence of clamps. This species is similar to *L. cerealis*, *L. monticola* (Singer & A.H. Sm.) Bon and *L. paradoxus*. *Leucopaxillus cerealis* can be separated by its white stipe often with a bulbous base (Singer & Smith 1943; Singer 1962b; Hubregtse & Hubregtse 2012). *Leucopaxillus monticola* differs from *L. amyloideus* by its collybioid or clitocyboid habit, fairly crowded lamellae and abundant cheilocystidia (Singer & Smith 1947; Vizzini & Contu 2009). *Leucopaxillus paradoxus* possesses slightly smaller basidiospores (5–7.5 $\times$ 3.3–4.8 μm) and no cheilocystidia (Singer & Smith 1943). Molecular phylogenetic analysis indicated that *L. amyloideus* also occur in Pakistan (Fig. 1).

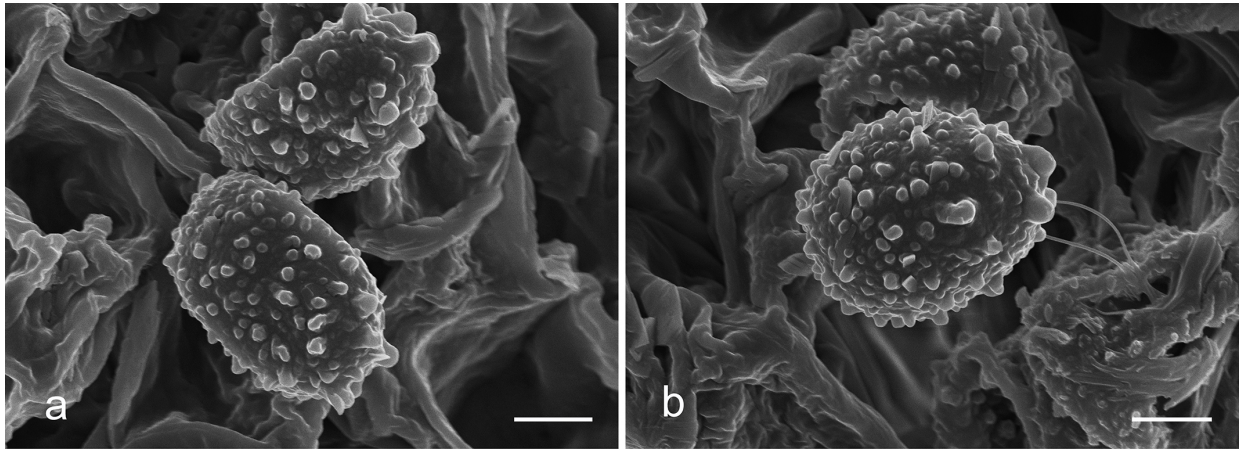


Fig. 18 Basidiospores of *Leucopaxillus amyloideus* (holotype, KUN-HKAS134956) under SEM. Scale bars = 2 μ m.

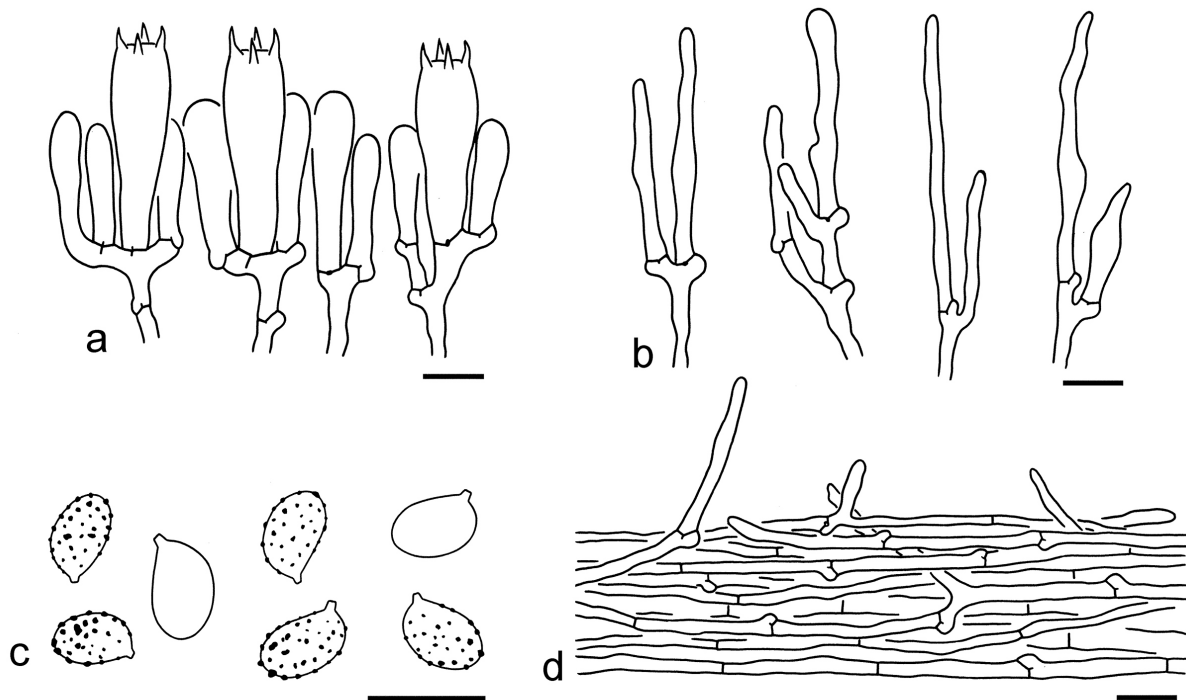


Fig. 19 Microscopic features of *Leucopaxillus amyloideus* (holotype, KUN-HKAS134956). a Hymenium and subhymenium. b Cheilocystidia. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 μ m, d = 20 μ m.

4. *Leucopaxillus laterarius* (Peck) Singer & A.H. Sm., Pap. Mich. Acad. Sci. 28: 117 (1943) [1942]. Figs. 15d, 20, 21

Basionym: *Agaricus laterarius* Peck, Bull. Buffalo Soc. nat. Sci. 1(2): 43 (1873) [1873-1874].

Description: Basidioma small to medium-sized, clustered, and robust. Pileus 2–5 cm in diam., convex to applanate, sometimes obtusely umbonate; surface dry, brown (5D4–6),

matted-fibrillose, in ages sometimes becoming scurfy or cracking into small pieces around the disc; margin incurved, often ribbed or grooved; context white (1A1). Lamellae adnate, sinuate to decurrent, very crowded, narrow, often forked, white (1A1), with brownish (5A2–5) color in age; edges entire, concolor. Stipe 6–8 $\times$ 0.8–1.2 cm, very firm, solid, clavate, often inflated at base, white (1A1), sometimes with brown (5A2–5, 5B3–5) color, exannulate; basal mycelium white (1A1). Taste and odour not recorded.

Basidiospores [60/3/3] $4\text{--}5.5 \times 3\text{--}4.5$ (~ 5) μm (mean length = $4.8 \mu\text{m}$, mean width = $3.8 \mu\text{m}$), $Q = 1.1\text{--}1.45$ (~ 1.57), $Q_m = 1.28 \pm 0.09$, broadly ellipsoid to ellipsoid, occasionally subglobose, amyloid, colorless, hyaline, thin-walled, verrucose. Basidia $25\text{--}35 \times 6\text{--}8 \mu\text{m}$, clavate, 4-spored, hyaline; sterigmata ca. $4 \mu\text{m}$ long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia $15\text{--}55 \times 2\text{--}4 \mu\text{m}$, scattered or clustered, filiform, occasionally branching, thin-

walled, colorless, hyaline. Subhymenium composed of $2\text{--}4 \mu\text{m}$ wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled hyphae $2\text{--}7 \mu\text{m}$ wide. Pileipellis a cutis, composed of radially arranged, $2\text{--}7 \mu\text{m}$ wide, thin-walled, colorless to yellowish hyphae, often mixed with more or less erected hyphae. Clamps present in all parts of basidioma.

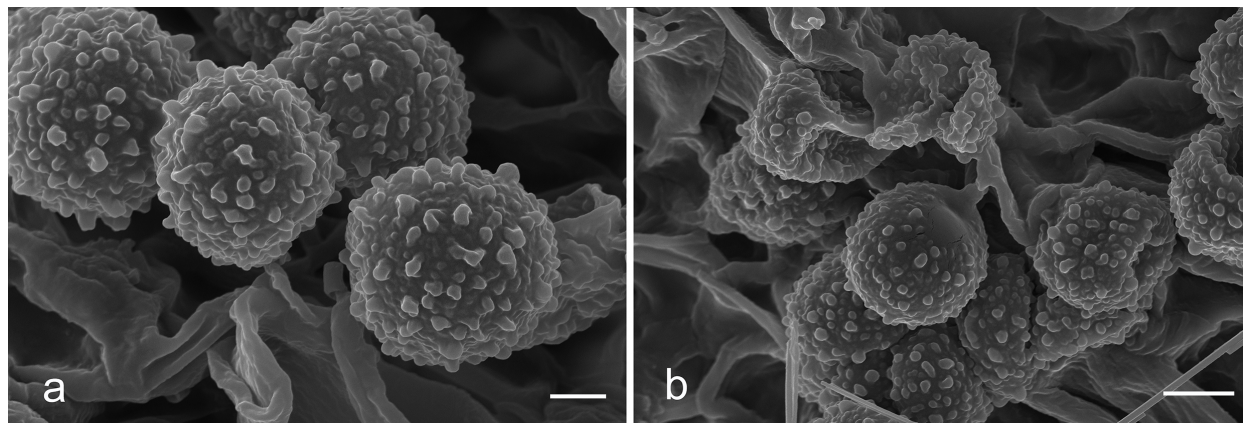


Fig. 20 Basidiospores of *Leucopaxillus laterarius* (KUN-HKAS124334) under SEM. Scale bars = $2 \mu\text{m}$.

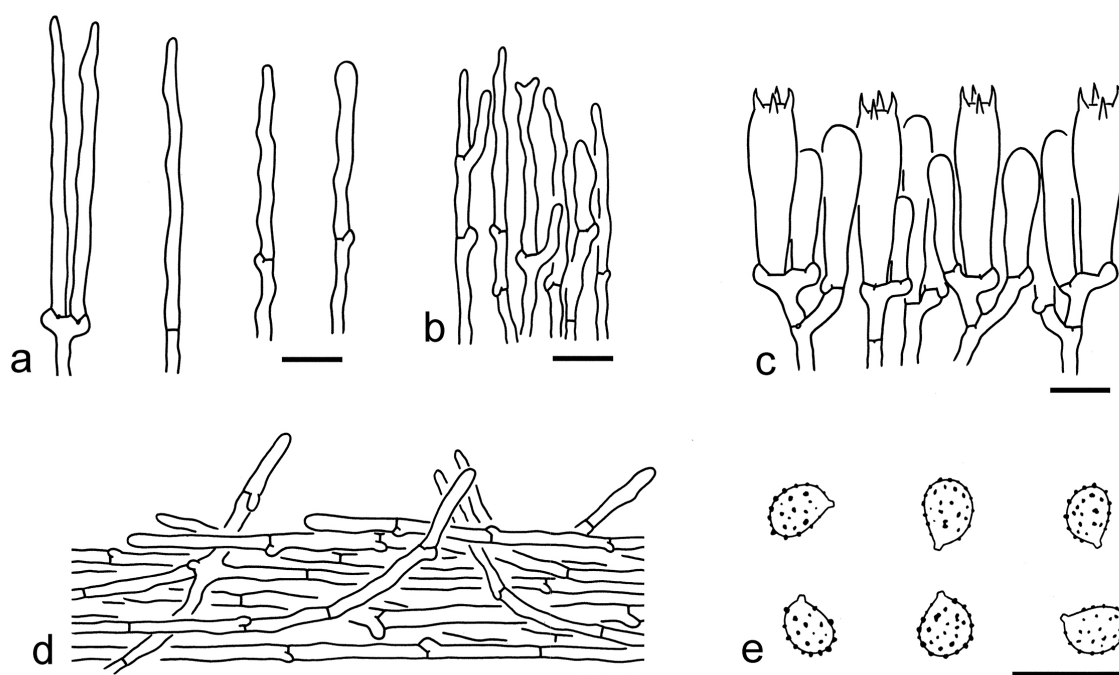


Fig. 21 Microscopic features of *Leucopaxillus laterarius*. a, b Cheilocystidia (a KUN-HKAS124334; b KUN-HKAS124331). c Hymenium and subhymenium (KUN-HKAS124334). d Pileipellis (KUN-HKAS124334). e Basidiospores (KUN-HKAS124334). Scale bars: a–c, d = $20 \mu\text{m}$, e = $10 \mu\text{m}$.

Ecology: On soil in temperate forests.

Known distribution: Our molecular data indicated this species occurs in North America and East Asia (Northwestern China).

Specimens examined: CHINA. Xinjiang, altitude 1865 m, 3 Aug. 2021, Jin Li 112 (KUN-HKAS124334); Changji Hui Autonomous Prefecture, Jimusaer, altitude 1987 m, 18 Jul.

2021, Jin Li 73 (KUN-HKAS124332); Urumqi, altitude 1885 m, 18 Jul. 2021, Jin Li 59 (KUN-HKAS124331).

Notes: *Leucopaxillus laterarius* was described from New York (Singer & Smith 1943) and is well separated by its small, broadly ellipsoid to ellipsoid basidiospores ($4\text{--}5.5 \times 3\text{--}4.5 \mu\text{m}$, mean length = $4.8 \mu\text{m}$, mean width = $3.8 \mu\text{m}$) (this study). *Leucopaxillus eucalyptorum* (Cleland) Grgur. is related to *L. laterarius* (Fig. 1), but the former species grows in *Eucalyptus*

forests of New Zealand (Grgurinovic 1997; Hubregtse 2019). *Leucopaxillus pulcherrimus* (Peck) Singer & A.H. Sm. is similar to *L. laterarius*, but differs by its subglobose basidiospores ($4\text{--}5.8 \times 3.5\text{--}4.5 \mu\text{m}$) (Singer & Smith 1943, 1947).

5. *Leucopaxillus verrucosus* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 15e, 22, 23

Fungal Names: FN 572331

Etymology: *verrucosus* = verrucose, referring to its verrucose basidiospores.

Diagnosis: Similar to *L. laterarius*, but differs by its larger basidiospores.

Type: CHINA. Xinjiang, Huocheng County, Guozigou, altitude ca. 2000 m, 5 Jul. 2017, Xiao-Xia Ding 167 (holotype, KUN-HKAS106509).

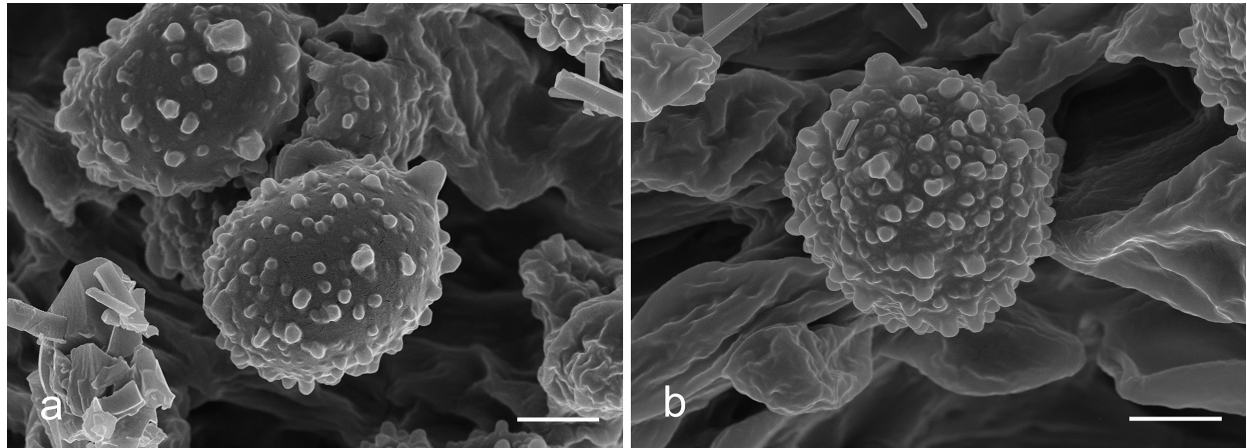


Fig. 22 Basidiospores of *Leucopaxillus verrucosus* (holotype, KUN-HKAS106509) under SEM. Scale bars = 2 μm .

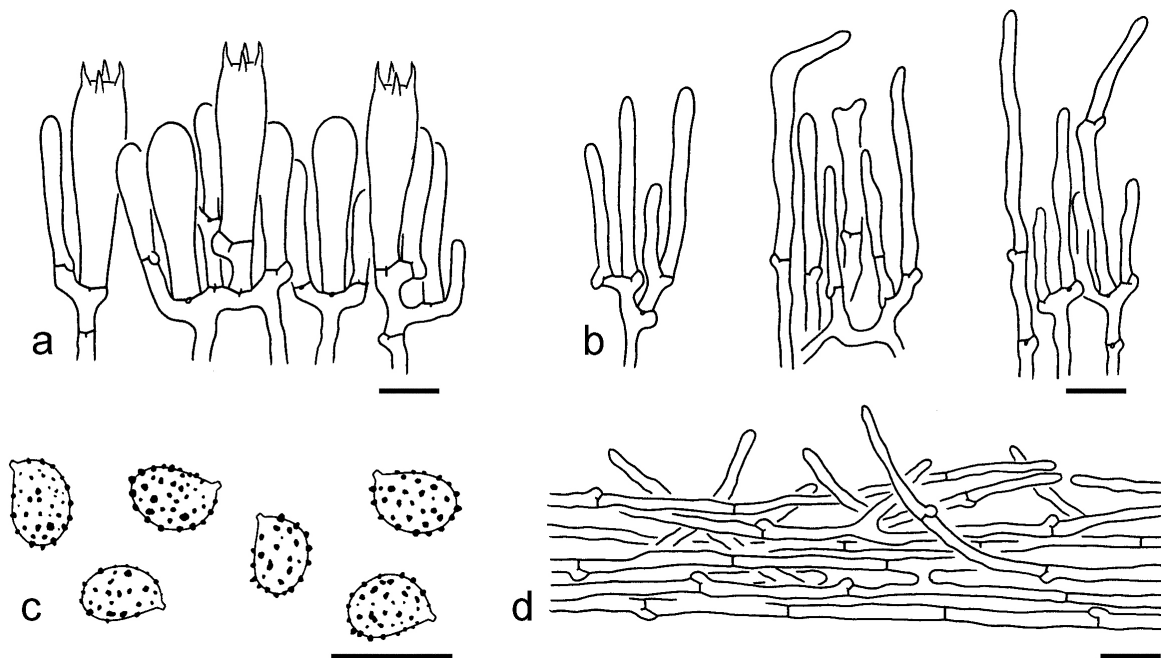


Fig. 23 Microscopic features of *Leucopaxillus verrucosus*. a Hymenium and subhymenium (KUN-HKAS134957). b Cheilocystidia (KUN-HKAS134957). c Basidiospores (holotype, KUN-HKAS106509). d Pileipellis (KUN-HKAS134957). Scale bars: a–c = 10 μm , d = 20 μm .

Description: Basidioma small to medium-sized, clustered. Pileus ca. 3.5 cm in diam., hemispherical, convex to plano-convex; surface dry, white (1A1), cream (1A2–4) to brownish (2B3–5), glabrous to fibrillose, in ages sometimes cracking into small pieces around the disc; margin incurved, often ribbed; context white (1A1). Lamellae subdecurrent, crowded, very narrow, sometimes forked, white (1A1) to pinkish (7A2);

edges entire, concolor. Stipe ca. $4 \times 1.5 \text{ cm}$, firm, solid, subclavate to clavate, white (1A1); basal mycelium white (1A1). Taste and odour not recorded.

Basidiospores $[40/2/1] (5\text{--}) 5.5\text{--}7.5 \times 4.5\text{--}6 \mu\text{m}$ (mean length = 6.7 μm , mean width = 5.1 μm), $Q = (1.02\text{--}) 1.17\text{--}1.48$ (~ 1.56), $Q_m = 1.32 \pm 0.12$, broadly ellipsoid to ellipsoid, amyloid, colorless, hyaline, thin-walled, verrucose. Basidia

30–45 × 7–9 µm, clavate, 4-spored, thin-walled, sometimes slightly thick-walled, hyaline; sterigmata 3–6 µm long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia 20–50 × 2–5 µm, often clustered, subcylindrical to filiform, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 µm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless; thin-walled hyphae 2–7 µm wide. Pileipellis a cutis, composed of radially arranged to interwoven, 3–6 µm wide, thin-walled, colorless hyphae, often mixed with more or less erected hyphae. Clamps present in all parts of basidioma.

Ecology: On soil in temperate forests with trees of *Picea*.

Known distribution: Currently known from Northwestern China.

Additional specimen examined: CHINA. Xinjiang, Tacheng, Shawan County, forest type not recorded, altitude ca. 1600 m, 2 Jul. 2017, Qi Zhao 2767 (KUN-HKAS134957).

Notes: *Leucopaxillus verrucosus* is delimited by its brownish pileus, amyloid, verrucose, broadly ellipsoid to ellipsoid basidiospores (5.5–7.5 × 4.5–6 µm) and abundant cheilocystidia. No closely related species were detected based on our currently data (Fig. 1). *Leucopaxillus laterarius* is similar to this species due to their brown pileus but can easily be separated by its smaller basidiospores (4–5.5 × 3–4.5 µm) (this study).

***Neodermoloma* Sánchez-García, Matheny & Adamčík, IMA Fungus 16(e157337): 120 (2025)**

Type: *Neodermoloma campestre* Sánchez-García, Matheny & Adamčík, IMA Fungus 16(e157337): 120 (2025).

Description: Basidiospores smooth, amyloid. Pileipellis an epithelium composed of inflated cells. Clamps present.

Known distribution: North America (Adamčíková et al. 2025).

Notes: Sánchez-García et al. (2021) identified a "Dermoloma-like" clade within the Tricholomataceae (Supplementary Table S4). Adamčíková et al. (2025) described this clade as a new genus named *Neodermoloma* (Supplementary Table S4). This study follows the study of Adamčíková et al. (2015). There have been no *Neodermoloma* species discovered in China thus far.

***Porpoloma* Singer, Sydowia 6(1–4): 198 (1952)**

Type: *Porpoloma sejunctum* Singer, Sydowia 6(1–4): 198 (1952).

Description: Basidioma tricholomatoid. Basidiospores smooth, thin-walled, amyloid. Clamps present.

Ecology: Ectomycorrhizal (Garrido 1988; Tedersoo et al. 2010; Sánchez-García & Matheny 2017). On soil in forests with Myrtaceae and *Nothofagus* (Singer 1952; Sánchez-García & Matheny 2017).

Distribution: Mainly distributed in the Southern Hemisphere (Singer 1952; Sánchez-García & Matheny 2017), but also recorded in Europe (Hausknecht & Zuccherelli 1999; Arauzo 2012).

Notes: *Porpoloma* was described and divided into three subgenera (Singer 1952). Sánchez-García et al. (2014) promoted the subgen. *Pogonoloma* Singer and subgen. *Pseudotracheloma* (Singer) Singer to independent genera, as *Pogonoloma* (Singer) Sánchez-García and *Pseudotracheloma* (Singer) Sánchez-García & Matheny with molecular evidence

respectively. Species of *Porpoloma* are mainly distributed in the Southern Hemisphere, but a few are recorded in Europe (Singer 1952; Hausknecht & Zuccherelli 1999; Arauzo 2012). To date, 12 species were described under this genus (<https://nmdc.cn/fungalnames/currentfungal?searchval=porpoloma&radiosearch=2>), but only three of them (*Po. portentosum* Singer, *Po. sejunctum* Singer and *Po. terreum* Singer) are supported by both molecular and morphological evidence (Sánchez-García et al. 2014). Currently no species of *Porpoloma* are found in China and the aforementioned descriptions are a summary based on the three species.

***Pseudobaeospora* Singer, Lloydia 5: 129 (1942)**

Type: *Pseudobaeospora oligophylla* (Singer) Singer, Lilloa 22: 438 (1951) [1949].

Description: Basidioma mycenoid to collybioid, very small to small. Pileus mostly violaceous, purple to purple-brown, glabrous to slightly squamulose. Lamellae concolorous with pileus or sometimes paler. Stipe subcylindrical, often concolorous with pileus. Basidiospores very small to small, smooth, at first thin-walled, then becoming thick-walled and more or less dextrinoid when mature. Cheilocystidia present or absent. Pileipellis with color change or not in 5% KOH, composed of radical or erected chains of inflated cells, or sometimes separated into two layers, with a suprapellis made of radically arranged filamentous hyphae and a subpellis composed of chains of inflated cells. Clamps mostly present, but absent in some species.

Ecology: Probably non-ectomycorrhizal (Bas 2003). Solitary to scattered on soil in various environments (Bas 2002, 2003; Arnolds et al. 2004; Desjardin 2004; Vellinga 2009; Desjardin et al. 2014; Wu et al. 2017; Craig et al. 2023).

Known distribution: Probably cosmopolitan (Singer 1986; Bas 2002, 2003; Arnolds et al. 2004; Desjardin 2004; Adamčík et al. 2007; Vellinga 2009; Adamčík & Jančovičová 2011; Schwarz 2012; Desjardin et al. 2014; Wu et al. 2017; Gisotti et al. 2021; Craig et al. 2023).

Notes: Vizzini et al. (2025) described a new subfamily named Pseudobaeosporoideae for the genus *Pseudobaeospora* within Tricholomataceae, with the remaining members placed in another suborder Tricholomatoideae. However, this work has not followed thus far because the Tricholomatoideae clade did not receive strong support in our phylogenetic analysis (Fig. 1).

Pseudobaeospora, typified by *P. oligophylla* (Singer) Singer (originally as *Baeospora oligophylla* Singer), was proposed by Singer (1942), and species in this genus have thick-walled and dextrinoid basidiospores when mature (Bas 2002, 2003). *Pseudobaeospora* was placed in Tricholomataceae or different tribus of Agaricaceae based on morphological characters (Singer 1942, 1951, 1986; Kühner 1980; Bas 2003), and molecular evidence supported this genus in Tricholomataceae (Sánchez-García & Matheny 2017; Sánchez-García et al. 2021; this study).

In regard to the subdivision within this genus, Bas (2003) divided it into five groups (*Albidula* group, *Celluloderma* group, *Pyrifera* group, *Frieslandica* group and *Pillodii* group) according to the color of basidioma, the presence or absence of clamps and cheilocystidia, and the structure of pileipellis, while Voto (2009) proposed an infrageneric systematic organization of *Pseudobaeospora* based on the structure of pileipellis. Both studies were relied on morphological data

only. To date, Fungal Names database (<https://nmdc.cn/fungalnames/currentfungal?searchval=Pseudobaeospora&radiosearch=2>) listed 35 species names under the genus. Only one species, *P. lilacina* X.D. Yu et al., was found in China (see below).

6. *Pseudobaeospora lilacina* X.D. Yu et al., Mycotaxon 132(2): 332 (2017) [2016]. Figs. 15f, g, 24

Description: Basidioma very small to small, single or in small groups. Pileus 2–4.5 cm in diam., subhemispherical, convex to plano-convex, becoming applanate when mature,

umbonate or not; surface dry, red-violet (13B3–6), rosy brown (11D3–5, 13D3–5) to purple-brown (6E2–5, 13E1–3), glabrous to slightly squamulose, sometimes cracking into small pieces in some specimens; margin straight, sometimes exceeding lamellae. Lamellae adnexed, sinuate to emarginate, sometimes emarginate with decurrent adnexed, purplish (14B3–6), purplish brown (14D2–4), or foggy grey (14B1–2), with attenuate lamellae, close. Stipe 3.5–6 × 0.3–0.8 cm, subcylindrical, purplish (14A2–4), dull purple (13C2–5) to purple-brown (14D2–4), longitudinal fibrils, with white (1A1) felted mycelium at base. Taste and odour not recorded.

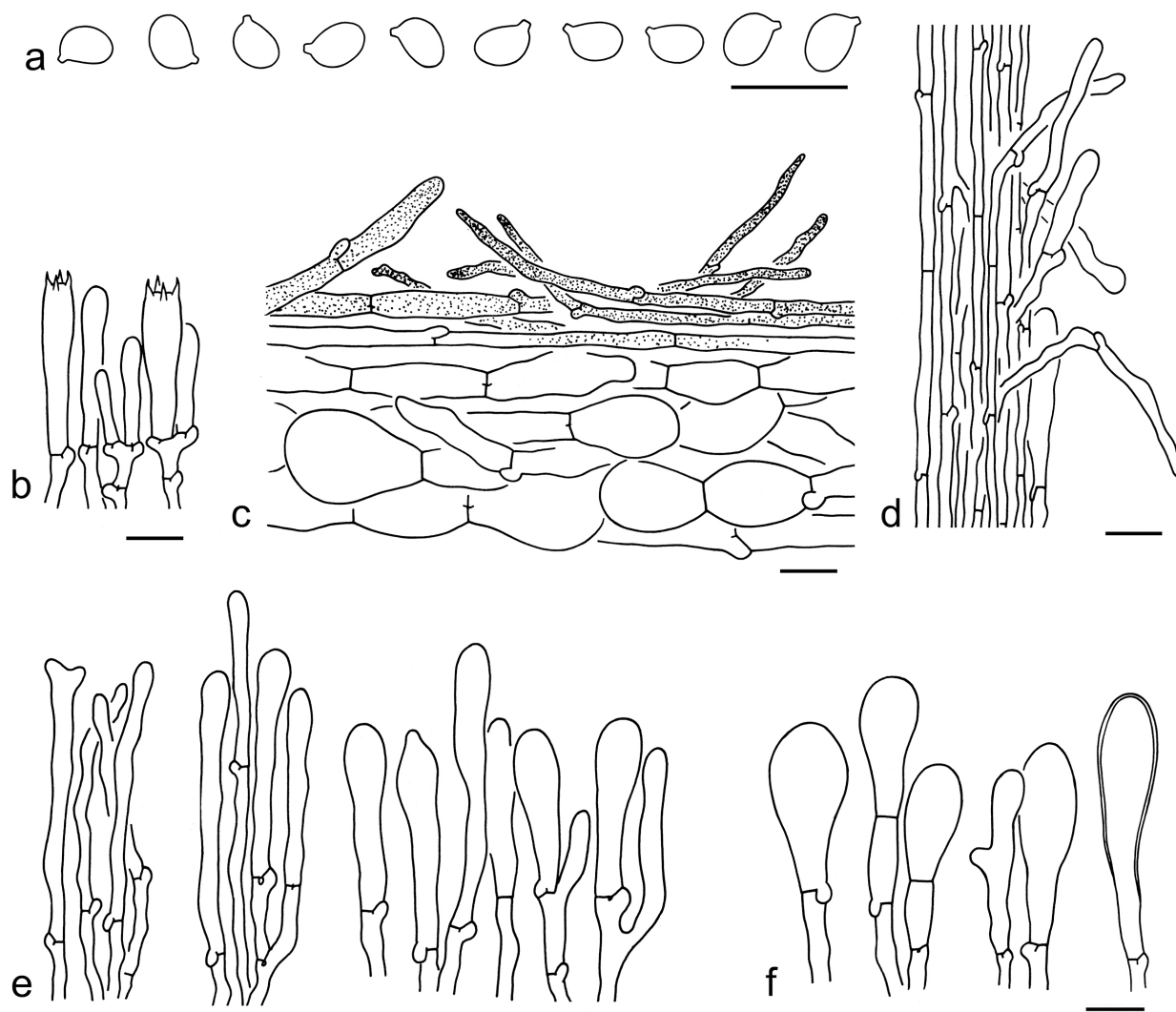


Fig. 24 Microscopic features of *Pseudobaeospora lilacina*. a Basidiospores (KUN-HKAS134959). b Hymenium and subhymenium (KUN-HKAS134959). c Pileipellis (KUN-HKAS134961). d Stipipellis (KUN-HKAS134960). e, f Cheilocystidia (e KUN-HKAS134961; f KUN-HKAS134959). Scale bars: a, b, e, f = 10 µm, c, d = 20 µm.

Basidiospores [84/4/4] 3.5–5 (–6) × 3–4 µm (mean length = 4.5 µm, mean width = 3.4 µm), Q = 1.16–1.53, Qm = 1.34 ± 0.08, broadly ellipsoid to ellipsoid, non-amyloid, mostly dextrinoid and thick-walled. Basidia 25–30 × 5–7 µm, clavate, 4-spored, hyaline; sterigmata 2–4 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 25–50 × 3–15 µm, conspicuous, scattered to clustered, filamentous,

subcylindrical, cylindrical to clavate, thin-walled, sometimes slightly thick-walled (ca. 1 µm), colorless, hyaline. Subhymenium composed of 2–4 µm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, filamentous, cylindrical, ellipsoid to clavate hyphae 5–35 µm wide. Pileipellis composed of two layers; suprapellis thin, greyish, grey-brown, grey-green to green in KOH, consisting

of thin-walled, 2–10 µm wide, repent hyphae with scattered, interwoven to somewhat erected, filamentous, subcylindrical to clavate terminal cells, which sometimes gathered as clusters at regular intervals with the cracking of pileus in appearances; subpellis made of chains of inflated cells, 30–50 × 15–40 µm, colorless, thin- to slightly thick-walled, clavate, ellipsoid to subglobose. Clamps present in all parts of basidioma.

Ecology: On naked soil or on soil with mosses or grasses in subtropical forests.

Known distribution: Known from Southern and South-western China.

Specimens examined: CHINA. Guangdong Province, Guangzhou, Baiyun District, 28 May 2013, Xiao-Dan Yu 3450 (SYAU FUNGI-010); same province, Zhaoqing, Fengkai County, 3 Jun. 2013, Xiao-Dan Yu 5546 (SYAU FUNGI-011). Yunnan Province, Baoshan, Longling County, on naked soil, altitude 1500 m, 26 Jul. 2022, GLG-WGS 223 (KUN-HKAS134959); Dehong Dai and Jingpo Autonomous Prefecture, Ruili, on soil with mosses, altitude ca. 1800 m, 17 Jul. 2022, Xue-Ping Fan 208 (KUN-HKAS134960); same prefecture, Longchuan County, on soil with mosses, altitude 1900 m, 18 Jul. 2022, Xue-Ping Fan 239 (KUN-HKAS134961).

Notes: *Pseudobaeospora lilacina* is characterized by its reddish violet, rosy brown to purple-brown basidioma, broadly ellipsoid to ellipsoid basidiospores (3.5–5 × 3–4 µm), conspicuous cheilocystidia, a cutis becoming grey-brown to green in KOH with a well differentiated subpellis, and the presence of clamps (Wu et al. 2017; this study).

One of the generic characters of *Pseudobaeospora* is that the basidiospores become thick-walled and dextrinoid when mature, but this phenomenon only can be found from the basidiospores on the surface of the pileus and the apical part of the stipe (Bas 2002, 2003). In our study, both non-dextrinoid and thick-walled, dextrinoid basidiospores was observed in preparations of fragments of lamellae; and thick-walled and dextrinoid basidiospores are dominant on the pileipellis and on the apex of stipe. The size of basidiospores of this species provided in this paper mostly refer to these thick-walled ones.

The color change of pileipellis in KOH, the structure of pileipellis, and the presence or absence of cheilocystidia are key characters for species delimitation in this genus (Bas 2002, 2003). The pileipellis of *P. lilacina* becomes grey-brown to green in KOH, and is made up of a suprapellis with repent, filamentous hyphae and a subpellis with chains of inflated cells (Fig. 24). The cheilocystidia of *P. lilacina* are present and conspicuous, but variable from filamentous, cylindrical to clavate, mostly thin-walled, sometimes thick-walled (Fig. 24).

***Pseudoporpoloma* Vizzini & Consiglio, Phytotaxa 243(3): 274 (2016)**

Type: *Pseudoporpoloma pes-caprae* (Fr.) Vizzini & Consiglio, Phytotaxa 243(3): 274 (2016).

Description: Basidioma tricholomatoid. Pileus conical, dry, radially fibrillose. Basidiospores smooth, thin-walled, amyloid. Pleurocystidia absent. Cheilocystidia rare or absent. Pileipellis a cutis. Clamps present.

Ecology: Probably saprotrophic and on soil in grasslands (Vizzini et al. 2016).

Known distribution: Widespread in Europe (Vizzini et al. 2016).

Notes: *Pseudoporpoloma* was described by Vizzini et al. (2016) and contains only a single species, namely *Ps. pes-caprae*. To date, no species are found in China and the aforementioned descriptions are based on the study of Vizzini et al. (2016).

***Pseudotracheloma* (Singer) Sánchez-García & Matheny, Taxon 63(5): 1000 (2014)**

Basionym: *Cantharellula* subgen. *Pseudotracheloma* Singer, Sydowia 2(1-6): 30 (1948).

Type: *Pseudotracheloma umbrosum* (A.H. Sm. & M.B. Walters) Sánchez-García & Matheny, Taxon 63(5): 1000 (2014).

Description: Basidioma brown to grey, covered with grey to dark grey, felted to tomentose squamules. Lamellae dirty white, brownish to greyish, becoming red then black when bruised. Basidiospores thin-walled, smooth, amyloid. Pleurocystidia absent. Cheilocystidia present or absent. Clamps present.

Ecology: Recorded as possibly ectomycorrhizal in Sánchez-García et al. (2014), and then listed as non-ectomycorrhizal taxa in Sánchez-García & Matheny (2017). On soil in woods and grasslands (Sánchez-García et al. 2014).

Known distribution: Distributed in Northern Hemisphere (Sánchez-García et al. 2014).

Notes: *Pseudotracheloma*, typified by *Pse. umbrosum*, was proposed by Sánchez-García et al. (2014). To date, only two species are found in China (see below).

Key to the species of *Pseudotracheloma* from China

1. Basidiospores longer, mostly elongate, 6–8 × 3.5–4.5 µm (mean length = 7.2 µm, mean width = 3.9 µm), Q = 1.62–2, Qm = 1.83 ± 0.15; cheilocystidia poorly differentiated..... *Pse. aff. azoricum*
1. Basidiospores mostly ellipsoid, 5.5–7 × 4–5 µm (mean length = 6.5 µm, mean width = 4.4 µm), Q = 1.35–1.65, Qm = 1.49 ± 0.08; cheilocystidia present *Pse. griseum*

7. *Pseudotracheloma aff. azoricum* P. Iglesias et al., Errotari 18: 279 (2021). Fig. 15h, i

Description: Basidioma small. Pileus 3–5 cm in diam., hemispherical to convex; surface dry, brown-grey (3D2–4), densely covered with brown-grey (3D2–5) to dark grey (2E1–3), felted to tomentose squamules; margin incurved. Lamellae brownish (2B2–4), brownish grey (2C2–4) to greyish (2D1–3), close. Stipe 5–9 × 1–2 cm, subcylindrical to cylindrical, white (1A1) to dirty white (2B1) background with longitudinally arranged, grey (2C1–3) fibrils, exannulate. The color change when bruised or cut not recorded. Taste and odour not recorded.

Basidiospores [27/1/1] 6–8 × 3.5–4.5 µm (mean length = 7.2 µm, mean width = 3.9 µm), Q = (1.59–) 1.62–2 (–2.2), Qm = 1.83 ± 0.15, mostly elongate, amyloid, colorless, hyaline, thin-walled, smooth.

Ecology: Solitary to scattered on soil in a temperate forest.

Known distribution: Southwestern China.

Specimen examined: CHINA. Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-La, in a subalpine temperate forest, 9 Aug. 2020, MF399 (KUN-HKAS134962).

Notes: Through years of field collections, a specimen of *Pseudotracheloma* (KUN-HKAS134962) somewhat sister to

Pse. azoricum P. Iglesias et al. was collected from Yunnan, China (Fig. 1). Unfortunately, the bad status of this specimen hindered us from detailed studying on it, we therefore treated it as *Pse. aff. azoricum* for the time being.

8. *Pseudotracholoma griseum* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 15j, k, 25

Fungal Names: FN 572332

Etymology: *griseum* = grey, referring to the grey basidioma.

Diagnosis: Similar to *Pse. umbrosum*, but differs by its conspicuous cheilocystidia.

Type: CHINA. Yunnan Province, Nujiang Lisu Autonomous Prefecture, Lushui, in a bamboo forest, altitude 2590–2690 m, 6 Aug. 2022, GLG-LJ024 (holotype, KUN-HKAS134963).

Description: Basidioma very small. Pileus ca. 2 cm in diam., broadly conical, conical to hemispherical; surface dry, white (1A1), dirty white (1B1) to greyish (2B1) background with grey (1C1, 1D1) to dark grey (2E1, 4E1–3), felted to tomentose squamules; margin incurved. Lamellae greyish (3C1, 3D1) to grey (4E1), close; lamellulae attenuate. Stipe ca. 3.5×1 cm, subcylindrical to cylindrical, white (1A1), dirty white (1B1) to greyish (2B1) background with grey (1C1, 1D1) to greyish

brown (4D1–3), furfuraceous squamules, exannulate. The color change when bruised or cut not recorded. Taste and odour not recorded.

Basidiospores [20/1/1] $5.5\text{--}7 \times 4\text{--}5$ μm (mean length = 6.5 μm , mean width = 4.4 μm), $Q = 1.35\text{--}1.65$, $Q_m = 1.49 \pm 0.08$, mostly ellipsoid, occasionally elongate, amyloid, colorless, hyaline, thin-walled, smooth. Basidia $25\text{--}45 \times 7\text{--}10$ μm , clavate, 4-spored, colorless to brown, hyaline; sterigmata $4\text{--}7$ μm long; basal septa with clamps. Pleurocystidia absent, but some narrowly cylindrical hyphae or clavate with apex mucronate cells present with a cystidioid appearance. Cheilocystidia $20\text{--}35 \times 6\text{--}10$ μm , clavate to fusiform or narrowly cylindrical to flexuose $2\text{--}4$ μm wide, thin-walled, colorless to brown. Subhymenium composed of $2\text{--}4$ μm wide filamentous hyphae, clamps present. Lamellar trama subregular to regular, composed of brown, cylindrical to filamentous hyphae $2\text{--}6$ μm wide. Pileipellis with a suprapellis composed of brown, $5\text{--}20$ μm wide, thin- to slightly thick-walled, cylindrical to clavate hyphae often more or less erected to irregularly arranged; a subpellis made of radially arranged, colorless, thin-walled, subcylindrical to filamentous hyphae $5\text{--}10$ μm wide. Clamps present in all parts of basidioma.

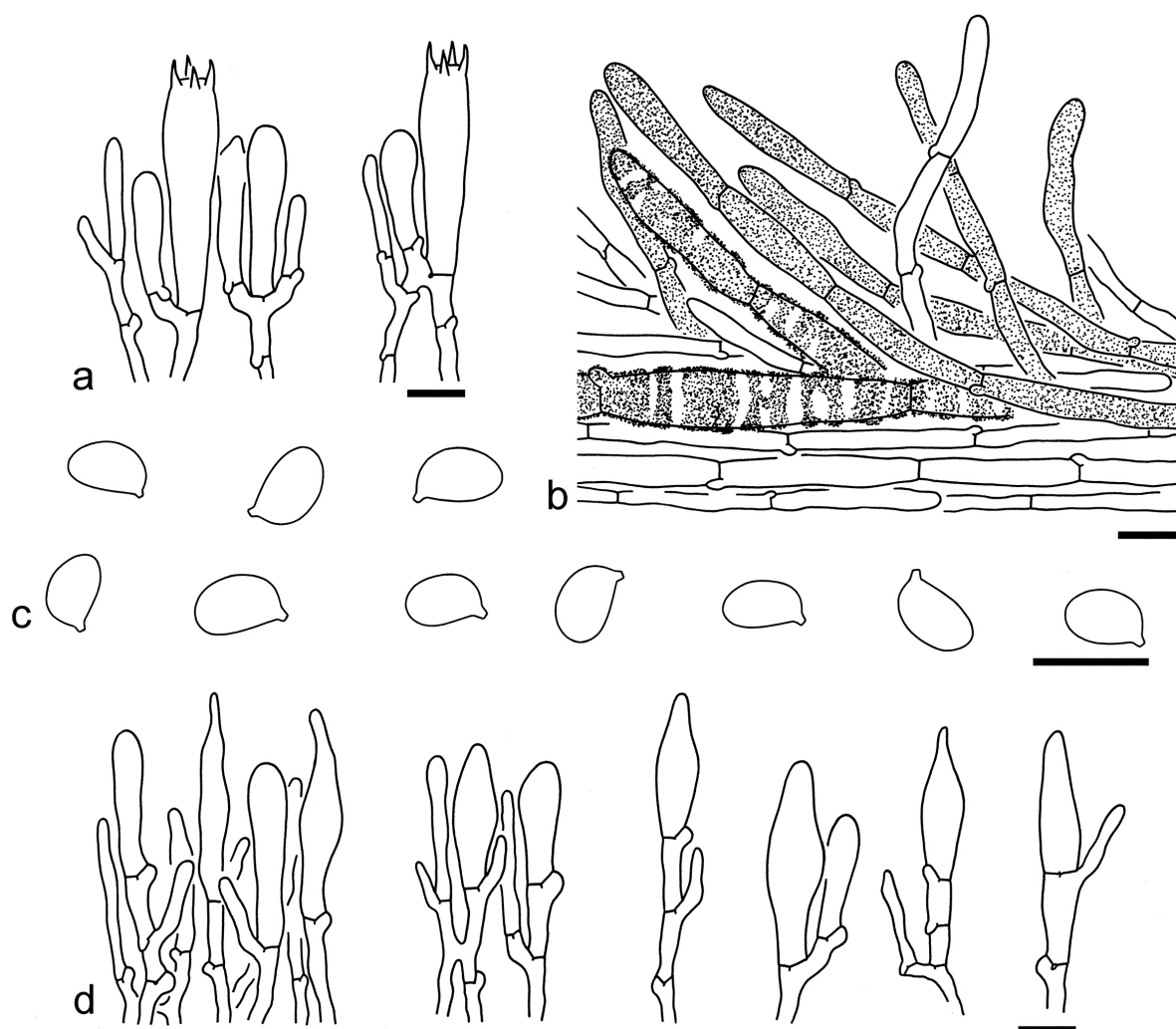


Fig. 25 Microscopic features of *Pseudotracholoma griseum* (holotype, KUN-HKAS134963). a Hymenium and subhymenium. b Pileipellis. c Basidiospores. d Cheilocystidia. Scale bars: a, c, d = 10 μm , b = 20 μm .

Ecology: Solitary to scattered on soil in a subtropical bamboo forest.

Distribution: Currently only known from Southwestern China.

Specimen of *Pse. metapodium* examined: MB002938.

Notes: To accelerate the understanding of the species diversity of *Pseudotracholoma*, we describe *Pse. griseum* based on molecular and morphological evidence, although only a single specimen is available. *Pseudotracholoma griseum* is characterized by its dark grey, felted to tomentose pileus, grey lamellae, ellipsoid basidiospores ($5.5\text{--}7 \times 4\text{--}5 \mu\text{m}$), presence of cheilocystidia, a suprapellis composed of more or less erected to irregularly arranged, cylindrical to clavate hyphae, and presence of clamps (this study).

This species is related to *Pse. umbrosum*, *Pse. azoricum* and *Pse. aff. azoricum* (Fig. 1). However, *Pse. umbrosum* has poorly differentiated cheilocystidia (Smith & Walters 1943). *Pseudotracholoma azoricum* differs from *Ps. griseum* by its dark brown to reddish brown pileus and slightly narrower basidiospores ($6.1\text{--}7.2 \times 3.4\text{--}3.8 \mu\text{m}$) (Iglesias et al. 2021). *Pseudotracholoma aff. azoricum* can be separated from *Pse. umbrosum* by its mostly elongate basidiospores ($6\text{--}8 \times 3.5\text{--}4.5 \mu\text{m}$) (this study).

Pseudotracholoma metapodium (Fr.) Sánchez-García & Matheny, originally described in Europe and listed as an endangered species in the IUCN Red List of Threatened Species (Jordal & Olariaga Ibarguren 2019), has not been found in China but is similar to *Pse. griseum*. We examined a specimen of *Ps. metapodium* (MB002938), and found that *Ps. metapodium* can be separated from *Pse. griseum* by its relatively longer basidiospores, which are often elongate to cylindrical with its size as $[26/1/1] 7\text{--}9 \times 3.5\text{--}4.5 \mu\text{m}$ (mean length = $8 \mu\text{m}$, mean width = $3.9 \mu\text{m}$), $Q = 1.82\text{--}2.28$ (-2.34), $Q_m = 2.05 \pm 0.15$ (this study).

***Tricholoma* (Fr.) Staude, Schwämme Mitteleurop. 1: xxviii, 125 (1857)**

Basionym: *Agaricus* trib. *Tricholoma* Fr., Syst. mycol. (Lundae) 1: 9, 36 (1821).

Type: *Tricholoma equestre* (L.) P. Kumm., Führ. Pilzk. (Zerbst): 130 (1871).

Description: Basidioma tricholomatoid. Pileus umbonate or not, white, yellow, brown, grey or olivaceous, glabrous, squarrose, squamose or radially fibrillose. Lamellae sinuate, lamellar trama regular. Annulus present or absent. Basidiospores broadly ellipsoid, ellipsoid to elongate, thin-walled, inamyloid, smooth. Pleurocystidia absent. Cheilocystidia conspicuous or poorly differentiated. Pileipellis mostly a cutis composed of more or less radially arranged elements, sometimes gelatinized. Clamps present or absent.

Ecology: Ectomycorrhizal. On soil with various trees (e.g. Fagaceae, Pinaceae and Salicaceae et al.). Some species are specific ectomycorrhizal with a single tree genus (e.g. *T. populinum* with *Populus* and *T. orienticolossum* with *Abies*), while others are associated with a wide range of plant partners.

Known distribution: Widely distributed and nearly cosmopolitan.

Notes: *Tricholoma* is one of the most species-rich genus in the family Tricholomataceae. Phylogenomic study and morphological characters supported the division of *Tricholoma* into four subgenera and 11 sections (Figs. 2, 14),

which was consistent with Ding et al. (2023). Our study also found four unnamed clades in China, and they may represent a new subgenus (*T. melleum* clade) and three new sections (Clade A, Clade B and Clade C) (Figs. 2, 14). However, in this study no taxonomical treatments are made to them due to limited taxa sampling. Here, 74 species of this genus found in China are described and reported. In addition, a comparison between the Chinese *Tricholoma* species reported in this work and Ding et al. (2023) are provided in Supplementary Table S5.

Key to the subgenera and the sections in *Tricholoma*

1. Pileus glabrous; lamellae close to distant; annulus absent; basidiospores often amygdaliform (subgen. *Sericeiculis*)..... 2
1. Pileus glabrous, squarrose, squamose or radially fibrillose; lamellae mostly crowded to close; annulus present or absent; basidiospores not amygdaliform..... 3
2. Pileus yellow to brown; lamellae close to distant; basidiospores large, often amygdaliform; clamps present or absent..... sect. *Sericella*
2. Pileus white colored; lamellae close; basidiospores small, not as amygdaliform shape; clamps present sect. *Lasciva*
3. Pileus mostly squarrose; pileipellis often a cutis with somewhat erected, thick-walled hyphae inflated or not, occasionally an ixo-cutis or with its subpellis composed of inflated cells; basidiospores mostly ellipsoid to elongate (subgen. *Terrea*)..... 4
3. Pileus glabrous, squarrose, squamose or radially fibrillose; pileipellis not with erected, thick-walled hyphae; basidiospores mostly broadly ellipsoid to ellipsoid..... 5
4. Basidioma small to medium-sized; pileus brown to grey, tomentose to felty or squamulose; basidiospores small to medium-sized sect. *Terrea*
4. Basidioma medium-sized to large; pileus grey, covered with fibrillose scales; basidiospores small..... sect. *Atrosquamosa*
5. Pileus brown to grey colored, squamose; annulus absent; pileipellis a cutis (subgen. *Pardincutis*) sect. *Pardincutis*
5. Pileus white, yellow, brown, grey or olivaceous, glabrous, squarrose, squamose or radially fibrillose; annulus absent or present; pileipellis various (subgen. *Tricholoma*) 6
6. Pileus mostly brown, occasionally white, squamose, densely covered with distinctly fibrillose squamules; annulus present and distinct, cottony sect. *Matsutake*
6. Pileus white, yellow, brown, grey or olivaceous, glabrous, squarrose or radially fibrillose; annulus mostly absent, occasionally present and retain a ring zone at stipe, not obvious..... 7
7. Pileus umbonate at center, mostly radially fibrillose; cheilocystidia conspicuous; pileipellis a cutis to an ixo-cutis with its subpellis differentiated and composed of inflated cells 8
7. Pileus umbonate or not, mostly glabrous to squarrose; cheilocystidia absent or conspicuous; pileipellis mostly with its subpellis poorly differentiated..... 9
8. Pileipellis not gelatinized..... sect. *Muscaria*
8. Pileipellis gelatinized sect. *Fucata*
9. Pileus mostly with olivaceous color; lamellae close to subdistant; basidiospores small; clamps present sect. *Rigida*
9. Pileus various in color, sometimes with olivaceous color; lamellae crowded to close; basidiospores small to medium-sized; clamps present or absent..... 10

10. Pileus various in color; lamellae white, yellow or grey, sometimes becoming yellow when old; annulus absent; basidiospores medium-sized; clamps absent or presentsect. *Tricholoma*
 10. Pileus brown; lamellae white to yellowish, with brown spots when old; annulus absent or sometimes retain a ring zone; basidiospores small; clamps absent.....sect. *Genuina*

Tricholoma subgen. *Tricholoma*

Type: *Tricholoma equestre* (L.) P. Kumm., Führ. Pilzk. (Zerbst): 130 (1871).

Description: Basidioma tricholomatoid. Pileus various in color, white, yellow, brown, grey or olivaceous, glabrous, squarrose, squamose or radially fibrillose. Lamellae crowded, close to distant. Annulus present or absent. Basidiospores broadly ellipsoid to ellipsoid, thin-walled, smooth, inamyloid. Pleurocystidia absent. Cheilocystidia present or absent. Clamps present or absent.

Ecology: Ectomycorrhizal. On soil with various trees.

Known distribution: Almost cosmopolitan.

Notes: *Tricholoma* subgen. *Tricholoma* forms a monophyletic group and comprises six sections, including sect. *Tricholoma*, sect. *Rigida*, sect. *Muscaria*, sect. *Fucata*, sect. *Matasutake* and sect. *Genuina* (Figs. 2, 14). This subgenus is sister to subgen. *Terrea* (Figs. 2, 14). However, members in subgen. *Terrea* have brown to grey, squarrose to squamose pilei and ellipsoid to elongate basidiospores. To date, 53 species of subgen. *Tricholoma* are found in China (see below).

Tricholoma sect. *Tricholoma*

Type: *Tricholoma equestre* (L.) P. Kumm., Führ. Pilzk. (Zerbst): 130 (1871).

Description: Basidioma tricholomatoid. Pileus various in color, mostly yellow, olivaceous, brown or grey, occasionally white, squarrose to radially fibrillose. Lamellae often white, yellow or grey, crowded to subclose. Annulus absent. Basidiospores medium sized, broadly ellipsoid to ellipsoid, smooth, thin-walled, inamyloid. Pleurocystidia absent. Cheilocystidia present or absent. Pileipellis a cutis or an ixocutis occasionally with a subpellis slightly differentiated. Clamps present or absent.

Ecology: Ectomycorrhizal. Solitary to scattered on soil with various trees.

Known distribution: To date, mainly distributed in Europe, North America, and Asia.

Notes: To date, 11 species, including two new and nine known species, were found in China (see below).

Key to the species of *Tricholoma* sect. *Tricholoma* from China

1. Pileus with yellow tinges, yellow, lemon yellow, sulphur-yellow, olivaceous yellow, yellowish brown to orange-brown, without innately radially fibrillose structure2
1. Pileus with grey to brown tinges, greyish, grey, grey-brown, brown, dark brown to dark grey, with innately radially fibrillose structure7
2. Pileus with broadly umbo at center; lamellae white to slightly cream; basidiospores subglobose to broadly ellipsoid with Q value 1.1–1.2.....3

2. Pileus without umbo at center; lamellae yellow, lemon yellow, sulphur-yellow to greenish yellow; basidiospores broadly ellipsoid, ellipsoid to elongate with Q value 1.1–2....4
3. Pileus brown to orange-brown, with obvious olive color; pileipellis strongly gelatinized, composed of interwoven to somewhat erected filamentous hyphae, often with clavate terminal cells at lower layer.....*T. olivaceoluteolum*
3. Pileus brown to olivaceous yellow; pileipellis gelatinized, composed of radially arranged filamentous hyphae*T. orienticum*
4. Basidioma with dirty yellow tinges, sulphur-yellow to olivaceous yellow; basidiospores relatively smaller, 5–7 × 3.5–5 µm (mean length = 5.9 µm, mean width = 4 µm) . *T. citrinum*
4. Basidioma chrome yellow, olivaceous yellow, yellowish brown to orange-brown; basidiospores relatively larger, with mean length > 6 µm and mean width > 4 µm5
5. Basidiospores relatively shorter, ellipsoid shaped, with mean length < 7 µm; clamps observed and present*T. qiaomianjun*
5. Basidiospores relatively longer, broadly ellipsoid, ellipsoid to elongate, with mean length > 7 µm; clamps absent6
6. Pileus orange-brown to brown when mature; basidiospores broadly ellipsoid, ellipsoid to elongate, 6.5–9 × 4–5.5 µm, Q = 1.15–1.95, Qm = 1.54 ± 0.23; dominantly distributed on nutrient poor soil (often sandy soil) in pine forests, sometimes also in broad-leaved or mixed forests..... *T. equestre*
6. Pileus yellow to brownish colored when mature; basidiospores predominantly elongate, 7–8.5 × 4–5 µm, Q = 1.66–2, Qm = 1.83 ± 0.14; dominantly distributed on rich nutrient soil in broad-leaved forests..... *T. frondosae*
7. Pileus pale colored, yellow-brown to grey-brown at center, greyish to white towards margin; lamellae white, without distinct color change when old or damage..... *T. mastoideum*
7. Pileus dark colored, greyish, grey, dark brown, dark grey to mouse grey; lamellae ivory to green-brown, or white to greyish, becoming yellowish to yellow when old or damaged8
8. Lamellae ivory to olivaceous brown; basidiospores relatively larger with mean length ≥ 8 µm, mean width ≥ 6 µm *T. olivaceifolium*
8. Lamellae white to greyish; basidiospores relatively smaller with mean length < 8 µm, mean width < 6 µm9
9. Pileus with distinct yellow colors at least at the margin; basidiospores broadly ellipsoid, 6–8 × 5–6.5 µm, Q = 1.17–1.36, Qm = 1.27 ± 0.08; clamps present...*T. sinoportentosum*
9. Pileus without distinct yellow colors; basidiospores broadly ellipsoid, ellipsoid to oblong; clamps absent10
10. Pileus broadly umbonate, dark grey at center and greyish towards margin, sticky when wet and greasy when dry; taste mild; basidiospores ellipsoid to oblong, 6–7.5 × 4–5 µm, Q = 1.44–1.88, Qm = 1.66 ± 0.12..... *T. portentosum*
10. Pileus acutely umbonate, grey, not sticky or greasy; taste acrid to bitter; basidiospores broadly ellipsoid to ellipsoid, 7–10 × 5–7 µm, Q = 1.25–1.6, Qm = 1.43 ± 0.1 *T. virgatum*

9. *Tricholoma citrinum* Y.Y. Cui & Zhu L. Yang, Mycol. Progr. 21(35): 6 (2022). Figs. 15l, m, 26

Description: Basidioma medium-sized. Pileus 4–7 cm in diam., convex, plano-convex to applanate, without an umbo or depression at center; surface dry, brownish yellow (4B4–6), sulphur-yellow (1B4–7, 2B3–6) to olivaceous yellow (2C5–8, 30A4–6, 30B5–7), often darker at center, with dirty yellow

(3C3–5) tinges, often covered with brownish grey (3E6–8, 4D5–8) squamules; margin slightly uplifted and straight; context cream (1A2). Lamellae adnexed to sinuate, sulphur-yellow (2B6–8) to olivaceous yellow (1B5–8, 30A3–6), with dirty yellow (3C3–5) tinges, moderately crowded to subclose; edges smooth, undulate, sulphur-yellow (2B6–8) to olivaceous yellow (1B5–8, 30A3–6). Stipe 6–10 × 0.5–1 cm, subcylindrical, slightly enlarged downwards, yellowish (1A2–5, 3A4–6) to sulphur-yellow (2B2–7), but paler at basal part, smooth or covered with sulphur-yellow (2B4–7) to brownish grey (2C4–7) fibrillose squamules, exannulate. Taste and odour not recorded.

Basidiospores [57/5/1] 5–7 × 3.5–5 µm (mean length = 5.9 µm, mean width = 4 µm), $Q = 1.25\text{--}1.7$ (-1.75), $Q_m = 1.47 \pm 0.13$, predominately ellipsoid, sometimes broadly ellipsoid or elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 25–40 × 7–9 µm, clavate, 4-spored, hyaline; sterigmata 4–6 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 20–40 × 3–8 µm, poorly differentiated, clavate to subclavate, thin-walled, colorless, hyaline. Subhymenium composed of 2–5 µm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae 2–20 µm wide. Pileipellis an ixocutis, gelatinized, composed of radially arranged to interwoven, 2–8 µm wide, thin-walled, brown to reddish brown filamentous hyphae; subpellis poorly differentiated, non-gelatinized. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in coniferous forests with Pinaceae.

Known distribution: Known from Southwestern China.

Specimen examined: CHINA. Yunnan Province, Kunming, Fangwang Forest Farm, in a subtropical forest with *Pinus armandii*, altitude 2000 m, 22 Oct. 2011, Zhu L. Yang 5601 (holotype, KUN-HKAS71086); Kunming, Qiongzhusi, in a forest of *Pinus*, altitude 2000 m, 4 Sep. 2000, Fu-Qiang Yu 407 (KUN-HKAS39072); Chuxiong, Zixishan, in a forest of *Pinus*, altitude 2200 m, 30 Aug. 2000, Fu-Qiang Yu 333 (KUN-HKAS39071).

Notes: *Tricholoma citrinum* is characterized by its sulphur-yellow basidioma, ellipsoid basidiospores (5–7 × 3.5–5 µm, $Q = 1.25\text{--}1.7$, $Q_m = 1.47 \pm 0.13$), the absence of clamps and associations with coniferous trees (Cui et al. 2022; this study). In the tree generated from the ITS sequences, *T. citrinum* is somewhat close to *T. intermedium* Peck (Fig. 4), but the latter differs from the former by its white to whitish lamellae and variously shaped cheilocystidia (Bessette et al. 2013; Landry et al. 2022).

In China, *T. equestre*, *T. frondosae* Kalamees & Shchukin and *T. qiaomianjun* Y.Y. Cui & Zhu L. Yang can be confused with *T. citrinum* due to their yellow pileus and lamellae. However, *T. equestre* differs by its relatively larger basidiospores (6.5–9 × 4–5.5 µm) (this study). *Tricholoma frondosae* has a warmer colored pileus, longer basidiospores (7–8.5 × 4–5 µm) and is distributed in broad-leaved forests (Christensen & Heilmann-Clausen 2013; Cui et al. 2022; this study). *Tricholoma qiaomianjun* is different from *T. citrinum* by its yellowish brown to orange-brown pileus and presence of clamps (Cui et al. 2022; this study).

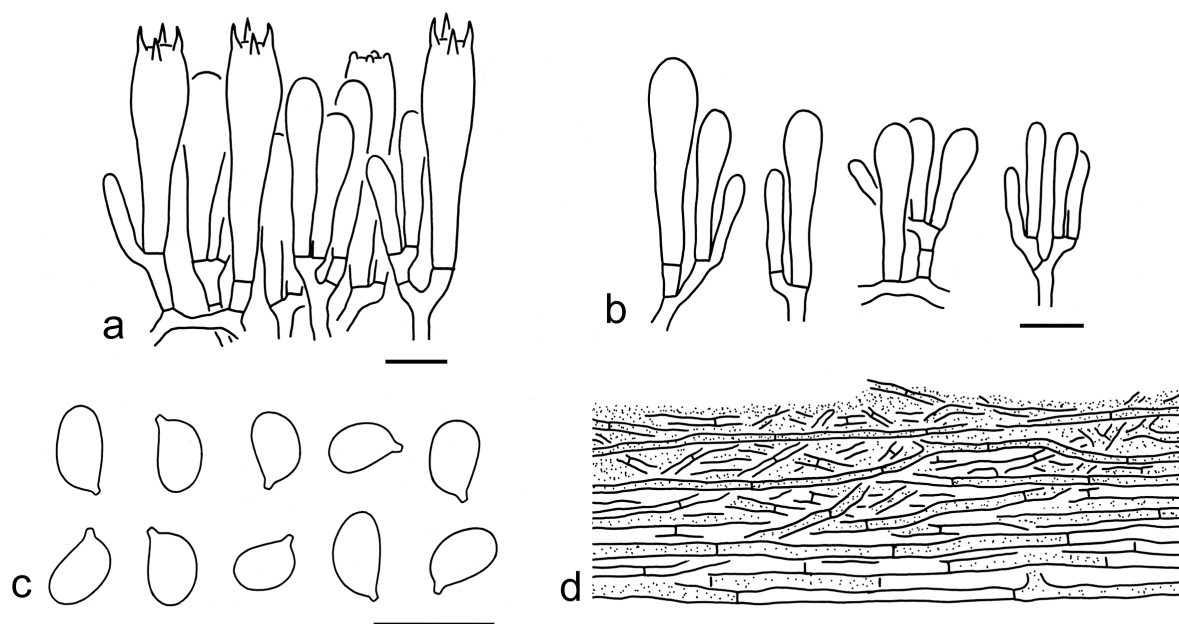


Fig. 26 Microscopic features of *Tricholoma citrinum* (holotype, KUN-HKAS71086). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm. Cited from Cui et al. (2022)

10. *Tricholoma equestre* (L.) P. Kumm., Führ. Pilzk. (Zerbst): 130 (1871). Figs. 15n, o, 27

Basionym: *Agaricus equestris* L., Sp. pl. 2: 1173 (1753).

Description: Basidioma small to medium-sized. Pileus 3.5–8 cm in diam., convex-applanate to applanate, without an obvious umbo or depression at center; surface dry, orangish brown (6C4–6, 5C5–7), often brownish (4B3–5) to yellow (3A2–5) towards margin, covered with orange-brown (5C5–7),

fibrillose squamules; margin at first incurved, then straight; context cream (1A2). Lamellae sinuate, yellow (1A4–6), sulphur-yellow (2A6–8) to olivaceous yellow (30A4–6), crowded to subclose; edges concolor. Stipe 3–9 × 1–3 cm, cylindrical to subcylindrical, yellowish (1A2–4), olivaceous yellow (30A4–6) to brownish (5B3–5), glabrous to slightly fibrillose, solid to stuffed, exannulate. Taste and odour not recorded.

Basidiospores [239/9/6] (6–) 6.5–9 (–10) × 4–5.5 (–6) µm (mean length = 7.3 µm, mean width = 4.8 µm), $Q = (1.13–) 1.15–1.95$ (–2.25), $Q_m = 1.54 \pm 0.23$, broadly ellipsoid, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 30–40 × 7–12 µm, clavate, 4-spored, colorless or red brown, hyaline; sterigmata 3–6 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 15–40 × 3–8 µm, poorly differentiated, clavate, subclavate to cylindrical, thin-walled, colorless or red-brown, hyaline. Subhymenium composed of 2–4 µm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae 2–20 µm wide. Pileipellis a cutis, non- to very slightly gelatinized, composed of radially arranged to interwoven, 2–10 µm wide, thin-walled, yellow-brown to red-brown filamentous hyphae, often with transition to a trichoderm at regular intervals forming squamules; subpellis poorly differentiated, non-gelatinized. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered in *Pinus* forests and often on sandy soil, also collected in broad-leaved or mixed forests.

Known distribution: Known from Europe (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013), North America (Bessette et al. 2013) and Asia (Reschke et al. 2018).

Specimens examined: BELARUS. Gomel, in mixed forests, altitude unknown, 10 Aug. 2009, Tolgor Bau (HMJAU22249). CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Daocheng County, in a subalpine forest with *Quercus semicarpifolia*, altitude 4000 m, 12 Sep. 2016, Xiao-

Xia Ding 131 (KUN-HKAS97074); same prefecture, Kangding, Gonggashan Village, in a broad leaved forest, altitude 3550 m, 5 Sep. 2016, KD-FB 44 (KUN-HKAS99397); same location, in a mixed forest with *Quercus* and *Pinus*, altitude 3700 m, 5 Sep. 2016, KD-LJW 41 (KUN-HKAS97834); same city, Waze Village, in a coniferous forest, altitude 3860 m, 8 Sep. 2016, KD-LJW 116 (KUN-HKAS97909). Yunnan Province, Baoshan, Tengchong, in a forest dominated with *Pinus yunnanensis*, altitude 1900 m, 10 Aug. 2010, Li-Ping Tang 1227 (KUN-HKAS63047); Diqing Tibetan Autonomous Prefecture, Shangri-La, in a mixed forest with *Pinus* and *Quercus*, altitude 3480 m, 23 Aug. 2014, Qi Zhao 2228 (KUN-HKAS87994); Kunming, Panlong District, Jindian, in a forest with *Pinus yunnanensis*, altitude 2000 m, 4 Nov. 2005, Yan-Chun Li 433 (KUN-HKAS49645); Lijiang, Yulong Naxi Autonomous County, Shitou Village, in a forest with *Pinus yunnanensis*, altitude 2600 m, 12 Aug. 2008, Qi Zhao 8188 (KUN-HKAS55183); Nujiang Lisu Autonomous Prefecture, Lanping Bai and Pumi Autonomous County, in a forest dominated by *Pinus yunnanensis*, altitude 2240–2350 m, 15 Aug. 2011, Gang Wu 722 (KUN-HKAS75037).

Notes: *Tricholoma equestre* is widely consumed as wild edible mushrooms in Southwestern China, but intoxications of rhabdomyolysis were reported in some countries (Bedry et al. 2001; Anand et al. 2009; Laubner & Mikulevičienė 2016; Yang et al. 2021). Christensen & Heilmann-Clausen (2013) reported its smell as weak but strongly farinaceous when cut, and its taste as mild and farinaceous. However, taste and odour were not recorded for Chinese collections. This species belongs to a species complex comprising several *Tricholoma* taxa with yellow pileus and lamellae. However, the delimitations within this complex remain unclear. To avoid unnecessary nomenclatural confusions, this study follows the treatment of *T. equestre* in Christensen & Heilmann-Clausen (2013), Reschke et al. (2018) and Cui et al. (2022).

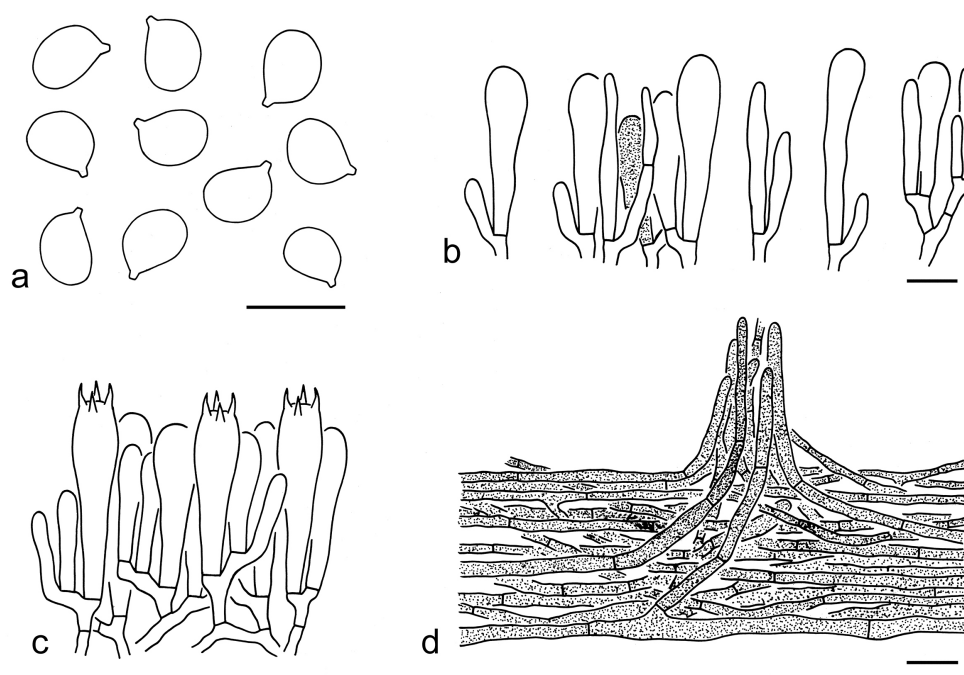


Fig. 27 Microscopic features of *Tricholoma equestre* (KUN-HKAS87994). a Basidiospores. b Marginal cells. c Hymenium and subhymenium. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm.



Fig. 28 Fresh basidiomata of the species in *Tricholoma*. a *T. frondosae* (KUN-HKAS98072). b *T. mastoideum* (holotype, KUN-HKAS97096). c *T. olivaceifolium* (holotype, KUN-HKAS107574). d *T. olivaceoluteolum* (KUN-HKAS134965). e *T. orienticum* (holotype, KUN-HKAS55189). f *T. portentosum* (KUN-HKAS97075). g *T. qiaomianjun* (holotype, KUN-HKAS101303). h *T. sinoportentosum* (KUN-HKAS58002). i, j *T. virgatum* (i KUN-HKAS 98081; j KUN-HKAS135006). k, l *T. brunneiceps* (k holotype, KUN-HKAS134966; l KUN-HKAS134968). m *T. cheilocystidiatum* (holotype, KUN-HKAS97051). n *T. albobrunneum* (KUN-HKAS68189). o *T. aurantium* (KUN-HKAS94389).

11. *Tricholoma frondosae* Kalamees and Shchukin, Folia Cryptogamica Estonica 38: 14 (2001). Figs. 28a, 29

Description: Basidioma medium-sized. Pileus 5–8 cm in diam., at first convex to convex-applanate, then applanate, often with a broadly low umbo at center; surface dry, reddish brown (6C5–7, 6B4–6), becoming brownish yellow (5A3–5, 4B3–5) to yellow (3A3–6) towards margin, with olivaceous (30A4–6) color, covered with red-brown (6C5–7) to brown (5C5–7) squamules; margin involute when young, then straight; context white (1A1) to yellowish (1A2–4). Lamellae sinuate, yellowish (1A2–4), yellow (2A3–5) to sulphur-yellow (3A5–7), often with olivaceous (30A4–6) color, crowded; edges concolor. Stipe 5–8 × 1–2 cm, cylindrical to subcylindrical, hollow, yellowish (2A2–4), olivaceous yellow (30A4–6, 1B4–6) to brownish (3B3–5), basal mycelium white (1A1), often with fine fibrils, solid to stuffed, exannulate. Taste and odour not recorded.

Basidiospores [40/2/1] 7–8.5 × 4–5 µm (mean length = 7.7 µm, mean width = 4.2 µm), $Q = (1.5\text{--}1.66\text{--}2\text{--}2.1)$, $Q_m = 1.83 \pm 0.14$, predominately elongate, sometimes ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 25–40 × 8–10 µm, clavate, 4-spored, colorless, hyaline; sterigmata 3–6 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 15–40 × 5–12 µm, poorly differentiated, clavate to subclavate, sometimes septate, thin-walled, hyaline, colorless or yellowish. Subhymenium composed of 2–5 µm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of yellow, thin-walled, ellipsoid, clavate, cylindrical to filamentous hyphae 3–25 µm wide. Pileipellis an ixo-cutis, gelatinized, composed of radially arranged, interwoven to more or less erected, 2–5 µm wide, thin-walled,

yellow-brown filamentous hyphae; subpellis poorly differentiated, non-gelatinized, composed of radially arranged to interwoven, 3–7 µm wide, thin-walled, yellow-brown filamentous hyphae. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered in broad-leaved forests.

Known distribution: Known from Europe (Christensen & Heilmann-Clausen 2013; Heilmann-Clausen et al. 2017), North America (Heilmann-Clausen et al. 2017) and East Asia.

Specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Daocheng County, in a subalpine sclerophyllous evergreen forest dominated by *Quercus semicarpifolia*, altitude 3960 m, 7 Aug. 2016, Jian-Wei Liu 493 (KUN-HKAS98072). Yunnan Province, Lijiang, Yulong Naxi Autonomous County, in a subalpine sclerophyllous evergreen forest dominated by *Quercus semicarpifolia*, altitude 3500 m, 8 Aug. 2014, Xiao-Bin Liu 504 (KUN-HKAS87149).

Notes: *Tricholoma frondosae* was described by Kalamees (2001), and then separated into two types (*T. frondosae* type I and II) according to Heilmann-Clausen et al. (2017). *Tricholoma frondosae* type I can be found in China and is characterized by its reddish brown pileus, sulphur-yellow lamellae, mostly elongate basidiospores (7–8.5 × 4–5 µm, $Q = 1.66\text{--}2$, $Q_m = 1.83 \pm 0.14$), absence of clamps, and associations with broad-leaved trees (this study). This species is mixed within *T. equestre* in our molecular analyses (Figs. 3, 4), but can be separated by its warm colored basidioma, mostly elongate basidiospores and being ectomycorrhizal with broad-leaved forests (Christensen & Heilmann-Clausen 2013). Here we follow the treatment of Christensen & Heilmann-Clausen (2013) and Heilmann-Clausen et al. (2017) for the time being.

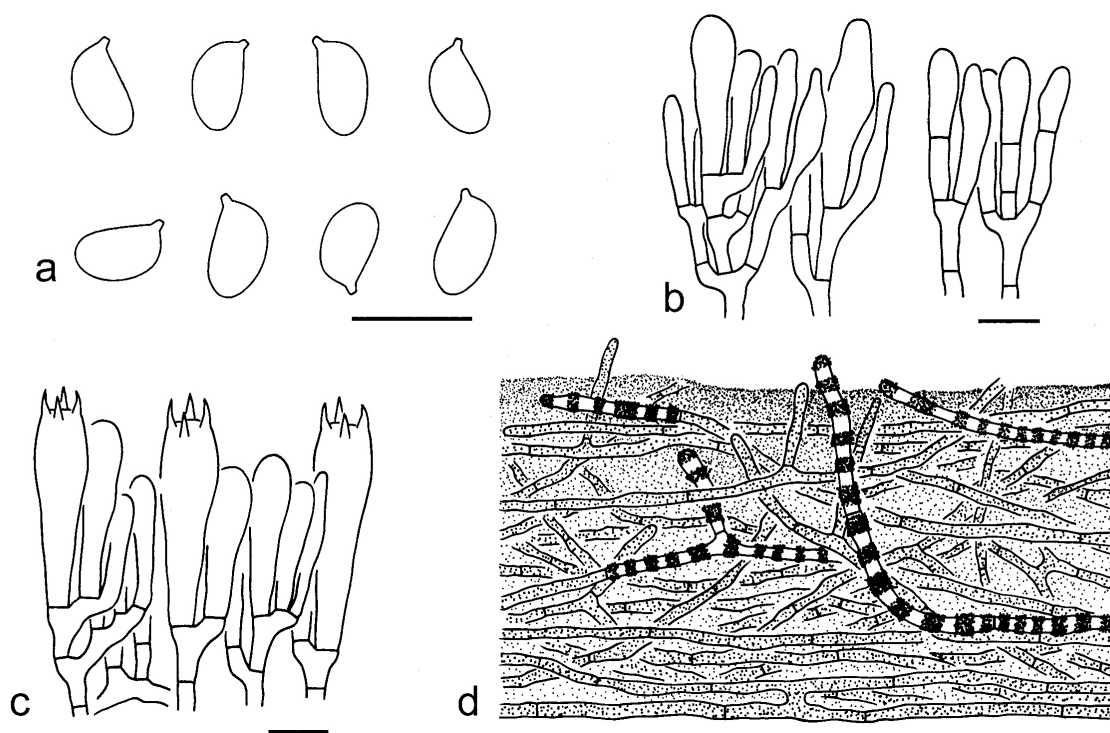


Fig. 29 Microscopic features of *Tricholoma frondosae* (KUN-HKAS98072). a Basidiospores. b Marginal cells. c Hymenium and subhymenium. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm.

12. *Tricholoma mastoideum* Y.Y. Cui & Zhu L. Yang, Mycol. Progr. 21(35): 8 (2022). Figs. 28b, 30

Description: Basidioma small to medium-sized. Pileus 3–9 cm in diam., convex when young, applanate when mature, broadly umbonate at center; surface dry, often yellowish brown (5C5–7, 5D5–8), brown (5E5–7) to greyish brown (5D2–4, 5E3–5) at center, becoming greyish (1B1–3) to white (1A1) towards margin, sometimes greyish (1B1–3) to brownish grey (3B2–4, 4B3–5) over the entire surface, covered with concolor fibrillose squamules; margin undulating and slightly incurved; context white (1A1) to dirty white (1B1–3). Lamellae adnexed to sinuate, white (1A1) to dirty white (1B2), crowded; edges white (1A1) to dirty white (1B2). Stipe 6.5–9 × 1–1.5 cm wide, stuffed, subcylindrical to cylindrical, enlarged downwards, white (1A1) to dirty white (2B2–3), exannulate. Taste mild. Odour like trees of oaks.

Basidiospores [191/11/3] (6–) 7–9 × (4.5–) 5–7 µm (mean length = 7.4 µm, mean width = 5.9 µm), $Q = (1.04\text{--}) 1.15\text{--}1.38$ (–1.56), $Q_m = 1.26 \pm 0.08$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth, apiculus relatively large. Basidia 30–40 × 9–12 µm, clavate, 4-spored, hyaline; sterigmata 3–5 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 15–40 × 10–15 µm, clavate, thin- to slightly thick-walled, colorless and hyaline. Subhymenium composed of 2–4 µm wide filamentous hyphae,

clamps absent. Lamellar trama regular, composed of colorless, thin- to slightly thick-walled hyphae 3–35 µm wide. Pileipellis an ixocutis to cutis, non- to slightly gelatinized, composed of radially arranged, 2–5 µm wide, thin-walled, colorless to yellowish filamentous hyphae; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in subalpine coniferous, broad-leaved or mixed forests with altitude 2500–3600 m.

Known distribution: Known from Southwestern China.

Specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, in a subalpine forest, altitude 3550 m, 5 Sep. 2016, KD-Ding 15 (holotype, KUN-HKAS97096); same location, in a subalpine sclerophyllous evergreen forest with *Quercus semicarpifolia*, altitude 3550 m, 5 Sep. 2016, KD-Ding 24 (KUN-HKAS97105); same city, in a subalpine forest, altitude 3550 m, 5 Sep. 2016, Bang Feng 32 (KUN-HKAS99385) same city, in a subalpine forest, altitude 3500 m, 6 Sep. 2016, Bang Feng 62 (KUN-HKAS99415). Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-La, in a subalpine mixed forest with trees of *Pinus*, *Quercus* and *Betula*, altitude 3000 m, 25 Aug. 2014, Qi Zhao 2284 (KUN-HKAS88051); Lijiang, Yulong Naxi Autonomous County, in a subalpine forest, altitude 2700 m, 3 Sep. 2019, Jian-Wei Liu 1876 (KUN-HKAS115907).

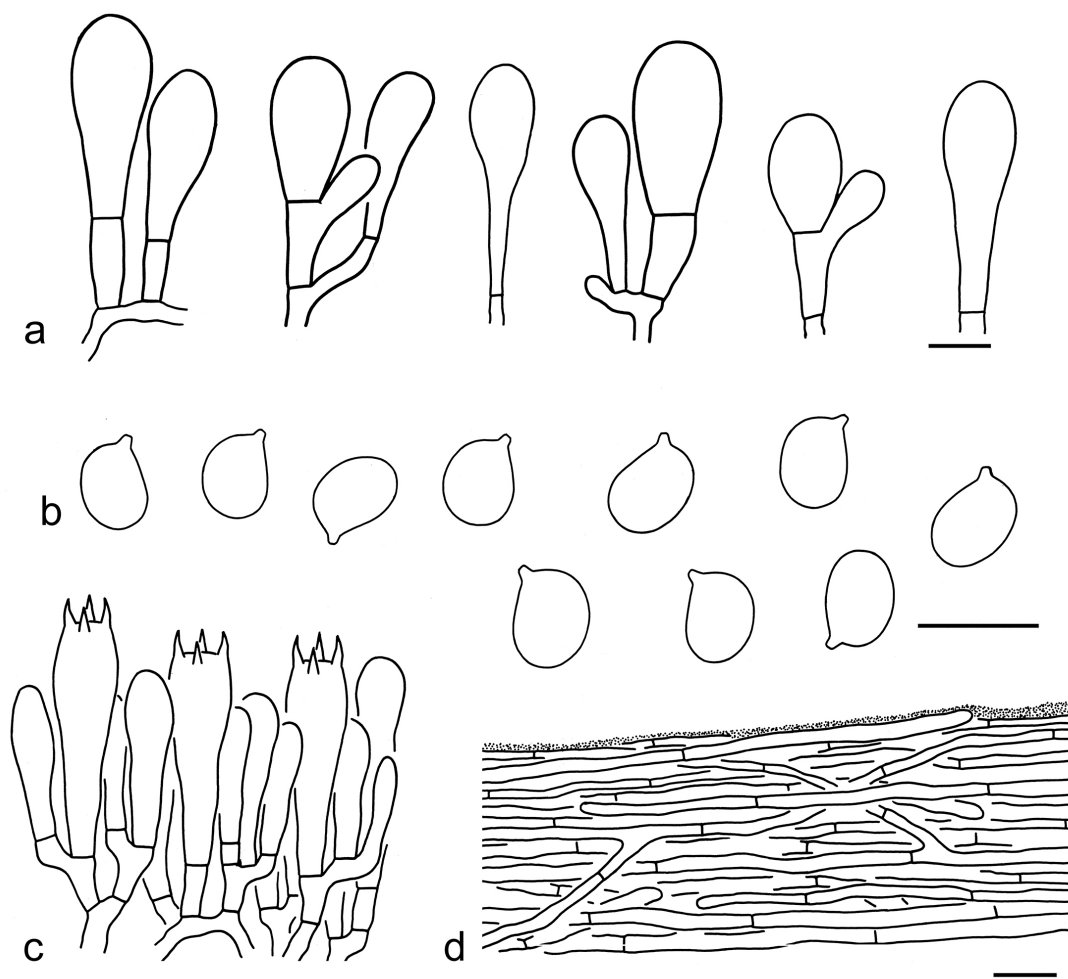


Fig. 30 Microscopic features of *Tricholoma mastoideum* (holotype, KUN-HKAS97096). a Marginal cells. b Basidiospores. c Hymenium and subhymenium. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm. Cited from Cui et al. (2022).

Notes: *Tricholoma mastoideum* is well delimited by its umbonate pileus often yellowish brown to greyish brown at center and greyish to white towards margin, broadly ellipsoid to ellipsoid basidiospores ($7\text{--}9 \times 5\text{--}7 \mu\text{m}$, $Q = 1.15\text{--}1.38$, $Q_m = 1.26 \pm 0.08$), and absence of clamps. Molecular data indicated that *T. virgatum* is closely related (Fig. 3), but differs by its grey, silvery shiny pileus and white to greyish lamellae becoming brownish when old (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013; this study). *Tricholoma guldeniae* Mort. Chr. is somewhat similar to *T. mastoideum*, but has a greyish yellow pileus and heterogeneously sized basidiospores (Christensen & Heilmann-Clausen 2013).

13. *Tricholoma olivaceifolium* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 28c, 31

Fungal Names: FN 572342

Etymology: *olivaceifolium* = olivaceous lamellae, referring its lamellae with green color.

Diagnosis: Similar to *T. portentosum*, but differs in its brownish grey pileus often with yellow tinge, larger basidiospores and a non-gelatinized pileipellis.

Type: CHINA. Xizang Autonomous Region, Linzhi, Bayi District, in a subalpine forest with *Picea* and *Rhododendron*, altitude 3995 m, 20 Jul. 2019, Gen-Shen Wang 454 (holotype, KUN-HKAS107574).

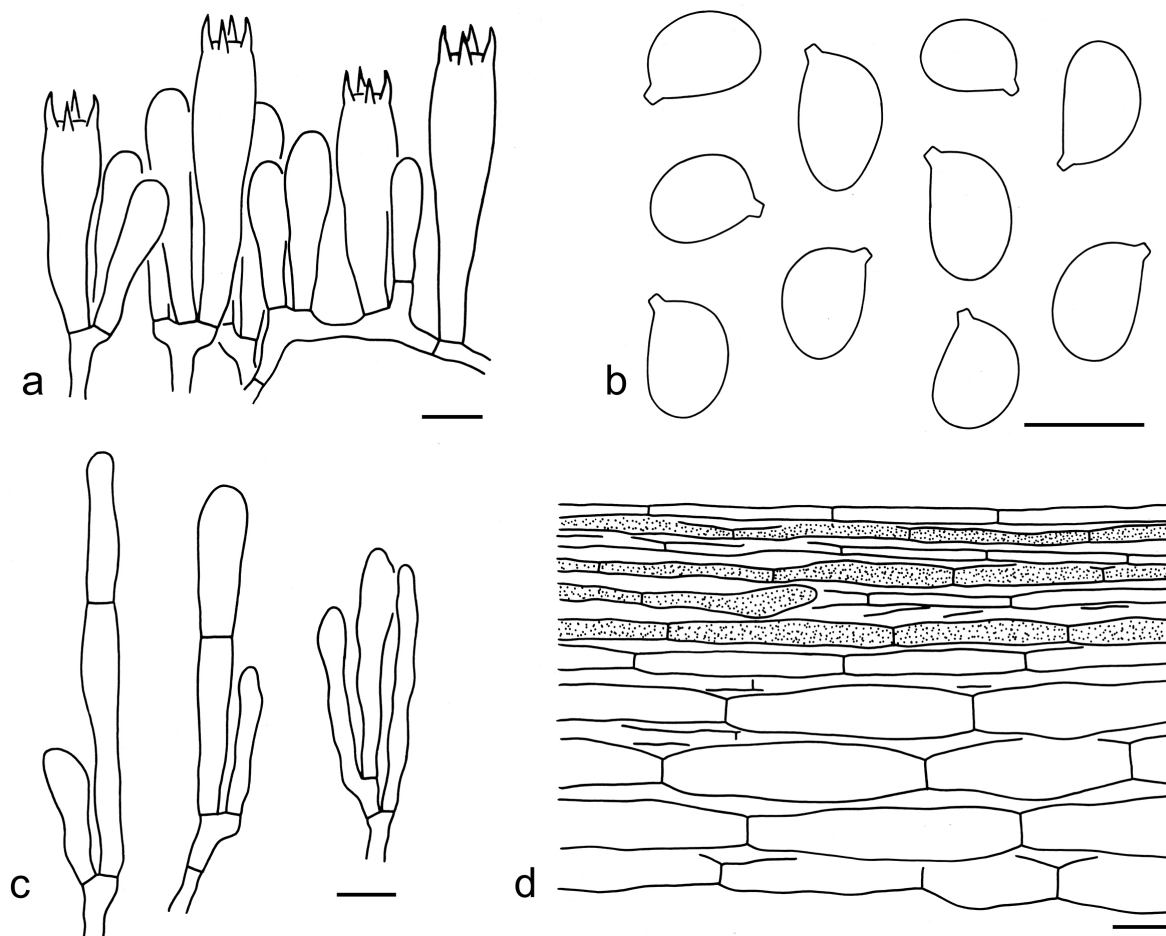


Fig. 31 Microscopic features of *Tricholoma olivaceifolium* (holotype, KUN-HKAS107574). a Hymenium and subhymenium. b Basidiospores. c Cheilocystidia. d Pileipellis. Scale bars: a–c = 10 μm , d = 20 μm .

Description: Basidioma small to medium-sized. Pileus 4–7 cm in diam., conical, convex to plano-convex, papillate at center, often acute; surface dry, greyish (1B1, 2B1), grey (1D1) to brownish grey (2E1–4), sometimes with yellow (1A2–4) tinge, covered with grey (1D1) to brownish grey (2E1–4) fibrillose squamules; margin inflexed to straight; context grey (2E1–3), greyish (2D1–3) to dirty yellow (1B2–4). Lamellae adnexed, light ivory (1A2–3), ivory (2A2–4) to olivaceous brown (30A2–4, 30B2–4), subcrowded to subclose; edges ivory (2A2–4), sometimes brown (2E4–7). Stipe 5–8 $\times$ 0.5–1.5 cm, subcylindrical to subclavate, greenish yellow (30A2–5), glabrous or with brown (2E3–5) to greenish yellow (30A2–5)

fibrils, stuffed, fistulose to hollow, exannulate. Taste and odour not recorded.

Basidiospores $[20/1/1] 7.9\text{--}10 (-12) \times 6\text{--}8 \mu\text{m}$ (mean length = 9.4 μm , mean width = 7 μm , $Q = 1.21\text{--}1.5 (-1.59)$, $Q_m = 1.35 \pm 0.11$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 30–50 $\times$ 9–12 μm , clavate, 4-spored, occasionally 2-spored, hyaline; sterigmata 5–7 μm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 25–45 $\times$ 3–9 μm , clavate to filamentous, often septate, sometimes branching, thin-walled, colorless, hyaline. Subhymenium composed of 3–5 μm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of

colorless, thin-walled filamentous hyphae 3–10 µm wide. Pileipellis a cutis, composed of radially arranged, 3–8 µm wide, thin-walled, colorless or brown filamentous hyphae; subpellis slightly differentiated, composed of cylindrical, clavate to ellipsoid inflated cells 10–25 µm wide. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered in subalpine forests.

Known distribution: Known from Southwestern China.

Additional specimens examined: CHINA. Yunnan Province, Diqing Tibetan Autonomous Prefecture, in a subalpine forest, altitude 3300 m, 22 Aug. 2008, Li-Ping Tang 690 (KUN-HKAS54922); Lijiang, Yulong Naxi Autonomous County, in a subalpine forest, altitude 3750 m, 31 Jul. 2005, Yan-Chun Li 255 (KUN-HKAS48488).

Notes: *Tricholoma olivaceifolium* is characterized by its papillate, grey to brownish grey, fibrillose pileus, ivory to olivaceous brown lamellae, broadly ellipsoid to ellipsoid basidiospores ($7.9\text{--}10 \times 6\text{--}8$ µm, $Q = 1.21\text{--}1.5$, $Q_m = 1.35 \pm 0.11$) and a cutis pileipellis with its lower layer composed of cylindrical to ellipsoid elements. No closely related species were found according to the phylogenetic analysis based on the ITS sequences (Fig. 4). Morphologically, *T. portentosum* is similar to this species, but has a darker coloured pileus, white, olivaceous yellow to yellow lamellae, smaller basidio-

spores ($4.5\text{--}7.7 \times 3.2\text{--}5.3$ µm) and a gelatinized pileipellis (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013; Landry et al. 2022; this study). *Tricholoma palustre* A.H. Sm. sometimes can be confused with *T. olivaceifolium*, but differs in its non-papillate pileus and smaller basidiospores ($6.2\text{--}7.6 \times 5.2\text{--}5.7$ µm) (Ovrebo 1989; Bessette et al. 2013; Landry et al. 2022).

14. *Tricholoma olivaceoluteolum* Reschke et al., Mycologia 110(6): 1100 (2018). Figs. 28d, 32

Description: Basidioma small to medium-sized. Pileus 4–8 cm in diam., convex to plano-convex, often subumbonate at center; surface viscid, often dark brown (5F3–5) at center, becoming orangish brown (5D6–8) to yellow-brown (4D3–5) towards margin, with obviously olive (30B4–6) color, sometimes with a white (1A1) margin, fibrillose; margin undulating and slightly incurved; context white (1A1). Lamellae adnexed to sinuate, white (1A1), sometimes yellow (2A2–4) at the very margin, crowded; edges white (1A1), sometimes yellow (2A2–4). Stipe 5–12 $\times$ 0.5–1.5 cm wide, stuffed to hollow, cylindrical to clavate, white (1A1), often olivaceous yellow (30A2–4) in the middle part, exannulate. Taste slightly bitter. Odour not recorded.

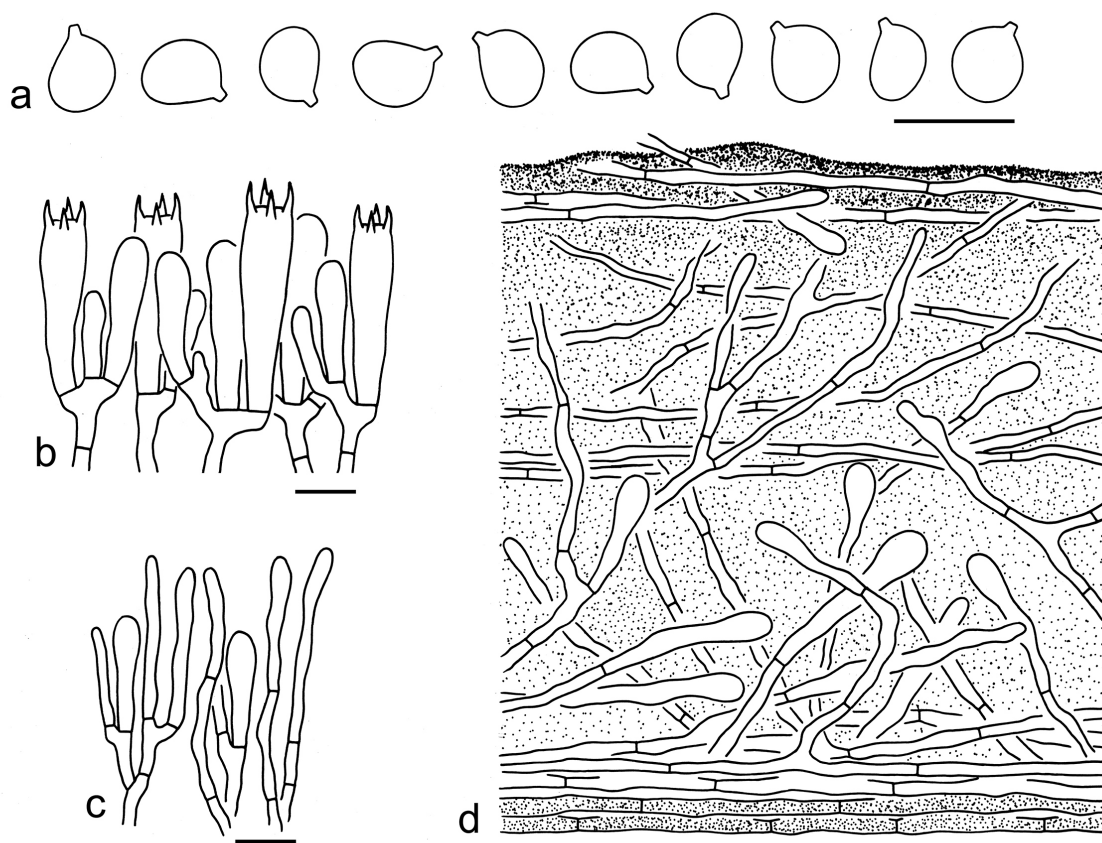


Fig. 32 Microscopic features of *Tricholoma olivaceoluteolum* (KUN-HKAS134964). a Basidiospores. b Hymenium and subhymenium. c Marginal cells. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm.

Basidiospores [60/3/3] $5.5\text{--}7.5$ (–9) $\times$ (4.5--) $5\text{--}7$ (–8) µm, (mean length = 6.5 µm, mean width = 5.7 µm), $Q = (1.01\text{--}) 1.05\text{--}1.25$ (–1.4), $Q_m = 1.15 \pm 0.08$, subglobose to broadly ellipsoid,

non-amyloid, colorless, hyaline, thin-walled, smooth, apiculus relatively large. Basidia $25\text{--}35 \times 7\text{--}10$ µm, clavate, 4-spored, hyaline; sterigmata 3–6 µm long; basal septa without

clamps. Pleurocystidia absent. Cheilocystidia $20\text{--}30 \times 2\text{--}5 \mu\text{m}$, filamentous to clavate, thin thick-walled, colorless, and hyaline. Subhymenium composed of $2\text{--}4 \mu\text{m}$ wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae $3\text{--}20 \mu\text{m}$ wide. Pileipellis an ixocutis, strongly gelatinized, upper layer composed of more or less radially arranged to interwoven, $2\text{--}7 \mu\text{m}$ wide, thin-walled, colorless filamentous hyphae; lower layer composed of interwoven to somewhat erected, thin-walled, colorless filamentous hyphae, often with clavate terminal cells up to $15 \mu\text{m}$ wide. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in subtropical coniferous or broad-leaved forests.

Known distribution: Known from Southwestern China.

Specimens examined: CHINA. Yunnan Province, Baoshan, Longling County, in a subtropical coniferous forest, altitude 2100 m, 31 Aug. 2022, GLG-FXP858 (KUN-HKAS134964); same location and date, GLG-TJY610 (KUN-HKAS134965); Puer, Jingdong Yi Autonomous County, in a subtropical broad-leaved forest dominated by *Quercus* and *Lithocarpus*, altitude 2500 m, 20 Jul. 2006, MR 50 (holotype, KUN-HKAS93510).

Notes: *Tricholoma olivaceoluteolum* is characterized by its umbonate, olivaceous brown pileus, white lamellae sometimes yellow at the very margin, subglobose to broadly ellipsoid basidiospores ($5.5\text{--}7.5 \times 5\text{--}7 \mu\text{m}$, $Q = 1.05\text{--}1.25$, $Q_m = 1.15 \pm 0.08$) and a strongly gelatinized pileipellis (this study). This species is related to *T. orienticum* Y.Y. Cui & Zhu L. Yang in the phylogenetic analysis based on five gene fragments (Fig. 3), but the latter species has poorly differentiated cheilocystidia and an ixo-cutis pileipellis with its subpellis composed of repent filamentous hyphae (this study).

Tricholoma sejunctum (Sowerby) Qué. looks like *T. olivaceoluteolum*, but the former differs from the latter by its more greenish pileus, medium spaced to distant lamellae and broadly ellipsoid to ellipsoid basidiospores (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013). *Tricholoma olivaceoluteolum* may be confused as a member of sect. *Muscaria*, but species in sect. *Muscaria* have subclose to close lamellae, conspicuous cheilocystidia, a non-gelatinized pileipellis with its subpellis well differentiated and composed of inflated cells.

15. *Tricholoma orienticum* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 28e, 33

Fungal Names: FN 572343

Etymology: *orienticum* = eastern, namely after its type locality from East Asia.

Diagnosis: Related to *T. olivaceoluteolum*, but differs by its poorly differentiated cheilocystidia and an ixo-cutis pileipellis with its subpellis composed of repent filamentous hyphae.

Type: CHINA. Yunnan Province, Lijiang, Yulong County, in a mixed forest with Fagaceae and Pinaceae, altitude 3200 m, 14 Aug. 2008, Qi Zhao 8198 (holotype, KUN-HKAS55189).

Description: Basidioma small to medium-sized. Pileus $4\text{--}7 \text{ cm}$ in diam., plano-convex to applanate, broadly umbonate at center; surface dry, slightly viscid when wet, brown (1E3–5, 1F6–8) at center, becoming olivaceous yellow (30A6–8) towards margin, sometimes olivaceous yellow (30A6–8) overall, innately fibrillose or covered with brown (1F6–8),

brownish (1E6–8), olivaceous brown (30E6–8) squamules, margin straight; context white (1A1) to yellowish (1A2–4). Lamellae adnexed to sinuate, white (1A1), sometimes yellow (30A3–5) at the very margin, crowded; edges white (1A1) to yellow (30A3–5). Stipe $5\text{--}8 \times 1\text{--}1.5 \text{ cm}$, cylindrical, white (1A1) to olivaceous yellow (30A3–5, 2A5–7), glabrous, stuffed to hollow, exannulate. Taste not recorded. Odour pleasant.

Basidiospores $[47/2/2] (5.5\text{--}) 6\text{--}7 \times (4\text{--}) 5\text{--}6 \mu\text{m}$ (mean length = $6.1 \mu\text{m}$, mean width = $5.2 \mu\text{m}$), $Q = (1.05\text{--}) 1.1\text{--}1.28$ (-1.4), $Q_m = 1.19 \pm 0.07$, subglobose to broadly ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $35\text{--}40 \times 7\text{--}9 \mu\text{m}$, clavate, 4-spored, hyaline; sterigmata $4\text{--}6 \mu\text{m}$ long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia not observed. Subhymenium composed of $2\text{--}5 \mu\text{m}$ wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled, cylindrical hyphae $3\text{--}15 \mu\text{m}$ wide. Pileipellis an ixocutis, gelatinized, composed of radially arranged, $3\text{--}8 \mu\text{m}$ wide, thin-walled, colorless or brownish filamentous hyphae; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered in coniferous or mixed forests.

Known distribution: Known from Southwestern China.

Additional specimen examined: CHINA. Yunnan Province, Lijiang, Yulong County, in a coniferous forest with *Pinus yunnanensis*, altitude 3269 m, 17 Sep. 2012, Qi Zhao 1691 (KUN-HKAS78949).

Notes: *Tricholoma orienticum* is well delimited by its basidioma with olivaceous yellow color, white lamellae with yellow color at the very margin, and subglobose to broadly ellipsoid basidiospores ($6\text{--}7 \times 5\text{--}6 \mu\text{m}$, $Q = 1.1\text{--}1.28$, $Q_m = 1.19 \pm 0.07$). Our multi-gene phylogenetic analysis (Fig. 3) suggested that *T. olivaceoluteolum* is related to *T. orienticum*. For comparison, see notes under that name. *Tricholoma subluteum* Peck is closely related (Fig. 4) and similar to *T. orienticum*, but has a dull orange or golden-yellow to yellow pileus and is currently only recorded from North America (Peck 1904; Murrill 1914; Bessette et al. 2013).

Tricholoma subsejunctum Peck can be confused with *T. orienticum*, but the former species has relatively smaller basidiospores ($5\text{--}6 \times 4\text{--}5 \mu\text{m}$ in the protologue), and is a rare species currently only known from North America (Peck 1912; Ammirati & Ovrebo 1979; Landry et al. 2022; Trudell et al. 2022). *Tricholoma atrofibrillosum* S.A. Trudell et al. also looks like, but differs by its ixocutis pileipellis with its lower layer composed of cylindrical to moderately inflated elements and only found in North America (Trudell & Parker 2021; Trudell et al. 2022). *Tricholoma sejunctum*, *T. viridilutescens* M.M. Moser and *T. viridifucatum* Bon are similar to *T. orienticum*. However, *T. sejunctum* has broadly ellipsoid to ellipsoid basidiospores and an ixocutis pileipellis with its lower layer composed of cylindrical to slightly inflated elements (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013). *Tricholoma viridilutescens* differs by its medium spaced to rather distant lamellae, slightly larger basidiospores (average $6.3\text{--}8 \times 5.3\text{--}6.6 \mu\text{m}$) and a subpellis with rather short inflated hyphae (Christensen & Heilmann-Clausen 2013). *Tricholoma viridifucatum* has medium-spaced lamellae and broadly ellipsoid to ellipsoid basidiospores (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013).

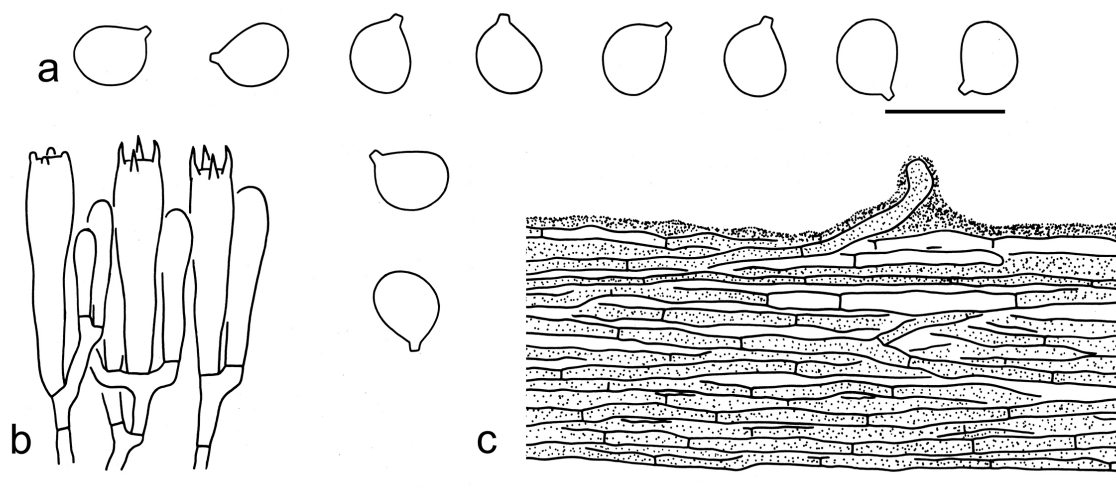


Fig. 33 Microscopic features of *Tricholoma orienticum* (holotype, KUN-HKAS55189). a Basidiospores. b Hymenium and subhymenium. c Pileipellis. Scale bars: a, b = 10 μ m, c = 20 μ m.

16. *Tricholoma portentosum* (Fr.) Quél., Mémoires de la Société d'émulation de Montbéliard, Sér. 2 5: 338 (1873). Figs. 28f, 34

Basionym: *Agaricus portentosus* Fr., Syst. mycol. (Lundae) 1: 39 (1821).

Description: Basidioma medium-sized. Pileus 5–9 cm in diam., convex-applanate to applanate, sometimes with a broadly low umbo at center; surface viscid when wet, greasy when dry, dark grey (2F1–3), grey (1E1–3) to grey-brown (4E4–6), often darker (1F1–3) at center, glabrous or finely squamulose; margin straight; context white (1A1) to dirty white (1B1–2). Lamellae sinuate, white (1A1) to greyish (1B2), then olivaceous yellow (30A3–5) to yellow (1A4–6), crowded; edges concolor or brown (4E6–8). Stipe 4–11 $\times$ 1–2.5 cm, subcylindrical to cylindrical, white (1A1) to olivaceous yellow (30A2–4), fibrillose, solid, exannulate. Taste and odour indistinct.

Basidiospores [61/3/2] 6–7.5 (–8) $\times$ 4–5 μ m (mean length = 6.8 μ m, mean width = 4.1 μ m), $Q = (1.33\text{--}1.44\text{--}1.88\text{--}1.95)$, $Q_m = 1.66 \pm 0.12$, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 25–40 $\times$ 6–8 μ m, clavate, 4-spored, hyaline; sterigmata 3–5 μ m long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 20–35 $\times$ 3–5 μ m and filiform or 30–50 $\times$ 10–15 μ m and clavate, thin-walled, colorless, hyaline. Subhymenium composed of 2–5 μ m wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled, more or less inflated to filamentous hyphae 2–20 μ m wide. Pileipellis an ixo-cutis, gelatinized, composed of radially arranged to interwoven, 2–5 μ m wide, thin-walled, colorless filamentous hyphae; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered dominated in coniferous or broad-leaved forests.

Known distribution: Known from Europe (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013; Heilmann-Clausen et al. 2017), North America (Heilmann-Clausen et al. 2017;

Bessette et al. 2013) and East Asia (Hongo 1988; Ushijima et al. 2021; this study).

Specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Daocheng County, in a forest with *Quercus semicarpifolia*, altitude 4000 m, 12 Sep. 2016, Xiao-Xia Ding 132 (KUN-HKAS97075); Ganzi Tibetan Autonomous Prefecture, Kanding, forest and altitude not recorded, 5 Sep. 2016, Bang Feng 28 (KUN-HKAS99381). Yunnan Province, Kunming, in a forest with *Pinus armandii* and *Pinus yunnanensis*, altitude 2200 m, 22 Oct. 2011, Yan-Jia Hao 619 (KUN-HKAS71728).

Notes: *Tricholoma portentosum* is characterized by its dark grey to grey pileus often viscid when wet and greasy when dry, yellow color on lamellae and stipe, and ellipsoid to elongate basidiospores (6–7.5 $\times$ 4–5 μ m, $Q = 1.44\text{--}1.88$, $Q_m = 1.66 \pm 0.12$) (this study). This species was reported by Christensen & Heilmann-Clausen (2013) to have a weak but distinctly farinaceous smell when cut, and a rather mild, farinaceous taste. However, no distinct odour or taste have been observed in Chinese collections.

Phylogenetically, no closely related species were detected (Figs. 3, 4). *Tricholoma sinoportentosum* Zhu L. Yang et al. is similar to *T. portentosum*. However, *T. sinoportentosum* differs by its greenish yellow color on pileus, broader basidiospores (6–8 $\times$ 5–6.5 μ m, $Q = 1.17\text{--}1.36$, $Q_m = 1.27 \pm 0.08$), and the clamped basidia (Reschke et al. 2018; this study).

17. *Tricholoma qiaomianjun* Y.Y. Cui & Zhu L. Yang, Mycological Progress 21(35): 10 (2022). Figs. 28g, 35

Description: Basidioma medium-sized. Pileus 4–8 cm diam., convex, plano-convex to applanate, often broadly umbonate; surface dry, slightly viscid when wet, greenish yellow (30A6–8), chrome yellow (2B6–8, 3B7–8), yellowish brown (3C6–8, 4C5–8) to orangish brown (5D8, 5E6–8, 6D5–8), covered with olivaceous brown (30D3–5, 30E4–6), orangish brown (5D8, 5E6–8, 6D5–8) to brown (6E6–8, 6F8) squamules; margin straight; context white (1A1). Lamellae adnexed to sinuate, pale yellow (1A1–3), yellow (2A4–6), citron yellow

(3A6–8) to greenish yellow (30A4–7), crowded; edges pale yellow (1A1–3), citron yellow (3A6–8) to greenish yellow (30A3–6). Stipe 4–8 × 0.5–2 cm, subcylindrical to cylindrical, enlarged downwards, dry, cream (2A2–3) at apex, pale yellow (1A1–3), yellowish (3A2–4) to pale greenish yellow (30A2–6) below, covered with greenish yellow (30A6–8), brownish (3B5–8, 4C6–8) to orangish brown (5C6–8) fibrillose and more or less reflexed squamules, solid, exannulate. Taste and odour not recorded.

Basidiospores [80/4/4] 5.5–7 (–7.5) × 4–5 µm (mean length = 6.2 µm, mean width = 4.3 µm), $Q = (1.2\text{--}) 1.3\text{--}1.58$ (–1.7), $Q_m = 1.44 \pm 0.1$, ellipsoid, occasionally broadly ellipsoid or elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 35–45 × 7–9 µm,

clavate, mostly 4-spored, rarely 2-spored, or 1-spored, hyaline; sterigmata 5–8 µm long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia 25–60 × 3–10 µm, subcylindrical, cylindrical, subclavate to clavate, often septate, sometimes branching, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 µm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled hyphae 3–25 µm wide, branching, sometimes anastomosing. Pileipellis an ixocutis with transition to an ixotrichoderm, composed of radially, interwoven to more or less erectly arranged filamentous hyphae, 2–8 µm wide, thin-walled, colorless to brownish; subpellis not gelatinized, poorly differentiated. Clamps present in all parts of basidioma.

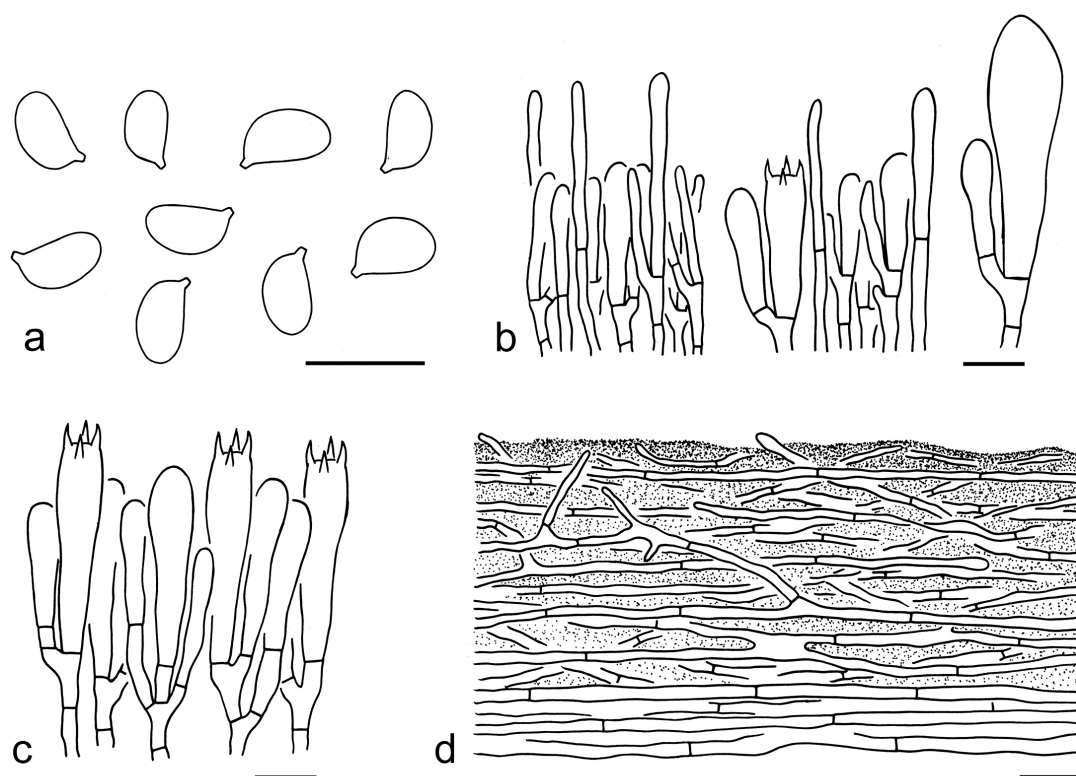


Fig. 34 Microscopic features of *Tricholoma portentosum* (KUN-HKAS71728). a Basidiospores. b Marginal cells. c Hymenium and subhymenium. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm.

Ecology: Solitary to scattered on soil in coniferous or mixed forests with trees of Pinaceae and Fagaceae.

Known distribution: Known from early summer to late autumn in Southwestern China.

Specimens examined: CHINA. Yunnan Province, Baoshan, in a forest with Pinaceae, altitude 1900 m, 9 Aug. 2010, Yan-Jia Hao 211 (KUN-HKAS69195); the same city, Longyang, in a mixed forest with Pinaceae and Fagaceae, altitude 1700 m, 8 Aug. 2011, Qi Zhao 1203 (KUN-HKAS74156); the same city, Changning County, in a mixed forest of *Pinus yunnanensis*, *Lithocarpus* and *Rhododendron*, altitude 1800 m, 25 Jun. 2009, Yan-Chun Li 1801 (KUN-HKAS59548); Dali Bai Autonomous Prefecture, Yunlong County, in a forest with *Pinus armandii*, altitude 2370 m, 8 Aug. 2010, Li-Ping Tang 1201 (KUN-HKAS63020); Kunming, bought from Ciba Market, 23 Jul. 2017, Xiao-Xia Ding 220A (KUN-HKAS106561); same location, bought from Ciba Market, altitude unknown, 27 Jul.

2020, Yang-Yang Cui 378 (KUN-HKAS115902); same city, bought from Mushuihua Market, altitude unknown, 7 Oct. 2019, Yang-Yang Cui 346 (KUN-HKAS115901); Puer, Lancang Lahu Autonomous County, in a mixed forest with Pinaceae and Fagaceae, altitude 1090 m, 12 Nov. 2017, Zhu L. Yang 6114 (holotype, KUN-HKAS101303); same city, Jingdong Yi Autonomous County, Ailao Mountain, in a forest with *Pinus yunnanensis*, altitude 2500 m, 10 Aug. 2019, Zhu L. Yang 6243 (KUN-HKAS106855). Xizang Autonomous Region, Nyingchi, Bome County, in a subalpine sclerophyllous evergreen forest dominated by *Quercus* spp., altitude 2760 m, 17 Jul. 2019, Zhu L. Yang 6190 (KUN-HKAS106802).

Notes: *Tricholoma qiaomianjun* is widely consumed in Southwestern China and has been reported as “*Tricholoma* aff. *flavovirens*” in Yang et al. (2021). This species is well delimited by its greenish yellow to orange-brown pileus, yellow lamellae, ellipsoid basidiospores (5.5–7 × 4–5 µm, $Q =$

1.3–1.58, $Q_m = 1.44 \pm 0.1$) and presence of clamps (Cui et al. 2022; this study).

Besides *T. qiaomianjun*, *T. equestre*, *T. frondosae* and *T. citrinum* from sect. *Tricholoma* also share yellow pileus and lamellae and can be collected from China. However, the latter three species can be easily differentiated from *T. qiaomianjun* by their absence of clamps. In addition, *T. equestre* has

relatively longer basidiospores ($6.5\text{--}9 \times 4\text{--}5.5 \mu\text{m}$, mean length = $7.3 \mu\text{m}$) (this study). *Tricholoma frondosae* differs by its longer basidiospores ($7\text{--}8.5 \times 4\text{--}5 \mu\text{m}$, mean length = $7.7 \mu\text{m}$) and associations with broad-leaved trees (this study). *Tricholoma citrinum* possesses sulphur-yellow pileus (Cui et al. 2022; this study).

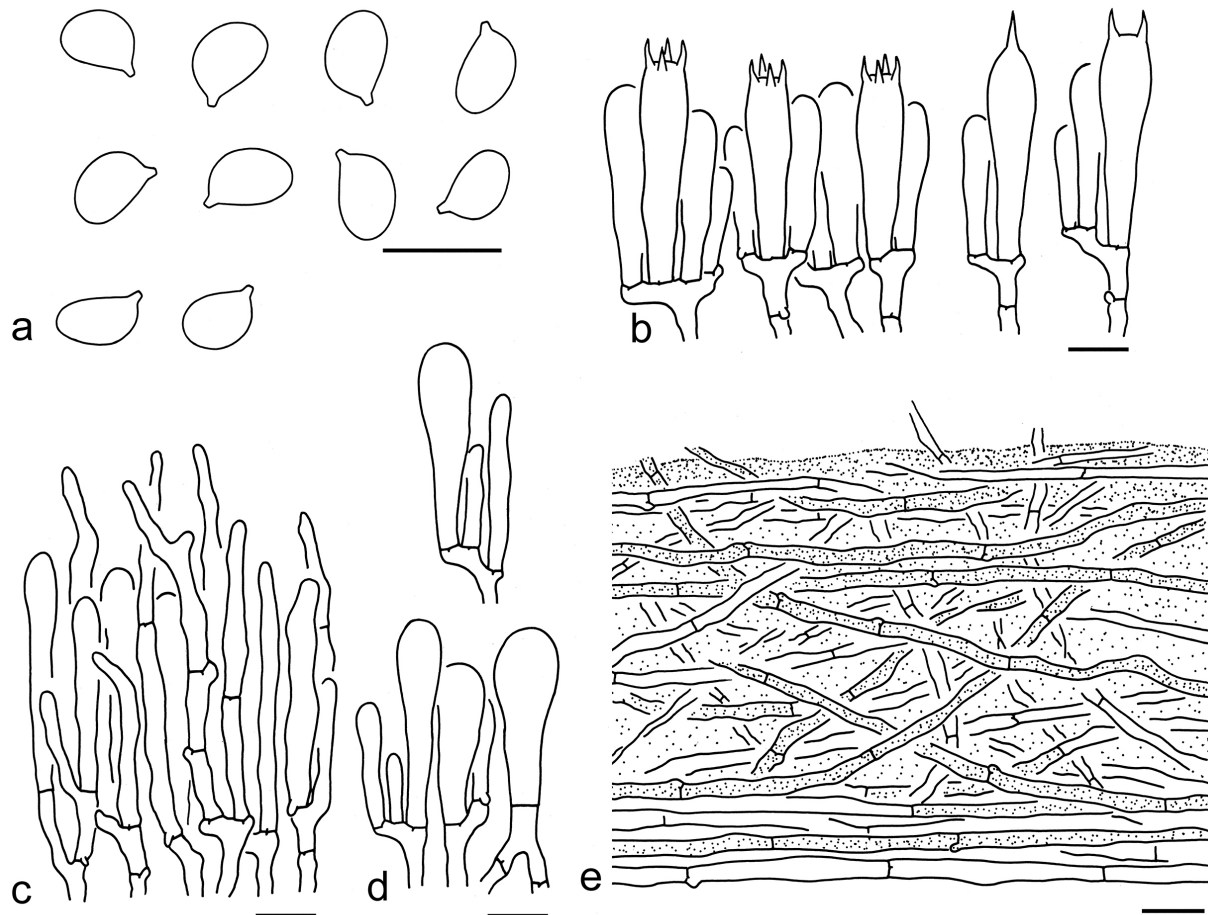


Fig. 35 Microscopic features of *Tricholoma qiaomianjun*. a Basidiospores (holotype, KUN-HKAS101303). b Hymenium and subhymenium (holotype, KUN-HKAS101303). c, d Marginal cells (c holotype, KUN-HKAS101303; d KUN-HKAS106855). e Pileipellis (holotype, KUN-HKAS101303). Scale bars: a–d = $10 \mu\text{m}$, e = $20 \mu\text{m}$. Cited from Cui et al. (2022).

18. *Tricholoma sinoportentosum* Zhu L. Yang et al., Mycologia 110(6): 1098 (2018). Figs. 28h, 36

Description: Basidioma small, medium-sized to large. Pileus 3–12 cm in diam., convex to plano-convex, often irregularly convex, often acutely papillate or papillate at center; surface dry, often dark brown (1F1–3), grey-brown (2E4–5, 4E6–8) to greyish brown (2D3–5), with greenish yellow (30B5–7) color, sometimes grey-brown (2F6–8) at center, becoming olivaceous yellow (30B5–7) to olivaceous brown (30C5–7) towards margin, covered with blackish (1F1–3), dark grey (1F1–3) to brown (3E6–8) squamules; margin straight; context white (1A1). Lamellae sinuate, white (1A1), cream (1B2–4) to olivaceous yellow (30A4–6), subclose; edges concolor. Stipe 5–13 $\times$ 1–3 cm, subcylindrical to cylindrical,

olivaceous yellow (30A4–6) to olivaceous brown (30C3–6), glabrous to fibrillose, exannulate. Taste and odour indistinct.

Basidiospores $[40/2/1] 6\text{--}8\text{--}(8.5) \times (4.5\text{--}) 5\text{--}6.5 \mu\text{m}$ (mean length = $7.1 \mu\text{m}$, mean width = $5.6 \mu\text{m}$), $Q = (1.08\text{--}) 1.17\text{--}1.36$ (~ 1.45), $Q_m = 1.27 \pm 0.08$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $25\text{--}40 \times 6\text{--}8 \mu\text{m}$, clavate, 4-spored, also 1-, 2- to 3-spored, hyaline; sterigmata $3\text{--}6 \mu\text{m}$ long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia $20\text{--}35 \times 5\text{--}9 \mu\text{m}$, poorly differentiated, clavate to narrowly clavate, sometimes subfusiform, thin-walled, colorless or brownish, hyaline. Subhymenium composed of 2–5 μm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled, filamentous or inflated hyphae 3–25 μm wide. Pileipellis a cutis, slightly gelatinized or not, composed of radially arranged, 3–5 μm wide, thin-walled, yellow to brownish filamentous hyphae; subpellis

poorly differentiated, non-gelatinized. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered dominated with *Picea* and *Pinus*.

Known distribution: Known from East Asia (Reschke et al. 2018; this study).

Specimens examined: CHINA. Sichuan Province, Ngawa Tibetan and Qiang Autonomous Prefecture, Hongyuan County, in a subalpine forest, altitude 3350 m, 19 Jul. 2014, Jian-Wei Liu 106 (KUN-HKAS90900). Xizang Autonomous Region, Qamdo, Jomda County, in a forest with *Picea*, altitude 3900 m, 4 Aug. 2009, Zhu L. Yang 5460 (KUN-HKAS58002); Nyingchi, Mainling, in a broad-leaved forest, altitude unknown, 27 Aug. 1983, Xiao-Lan Mao 1364 (HMAS53246); Changdu, Zhuge, on ground under *Picea* spp., altitude 4200 m, 7 Aug. 2004, Zai-Wei Ge (holotype, KUN-

HKAS46084). Yunnan Province, Dali Bai Autonomous Prefecture, Yunlong County, in a pine forest, altitude 1800 m, 8 Aug. 2010, Ting Guo 92 (KUN-HKAS69084); Diqing Tibetan Autonomous Prefecture, Shangri-La, in a subalpine forest, altitude 3950 m, 14 Jul. 2014, Jian-Wei Liu 44 (KUN-HKAS90838); Chuxiong, bought from restaurant, Chuxiong-Lv1 (KUN-HKAS136951).

Notes: *Tricholoma sinoportentosum* is well delimited by its papillate, dark brown to brown pileus, presence of clamps and broadly ellipsoid to ellipsoid basidiospores ($6\text{--}8 \times 5\text{--}6.5 \mu\text{m}$, $Q = 1.17\text{--}1.36$, $Q_m = 1.27 \pm 0.08$) (Yang et al. 2018; this study). In addition, this species grows in coniferous forests with *Pinus* (Yang et al. 2018; this study). *Tricholoma portentosum* is similar to *T. sinoportentosum*. For comparison of the two species, see notes under the name.

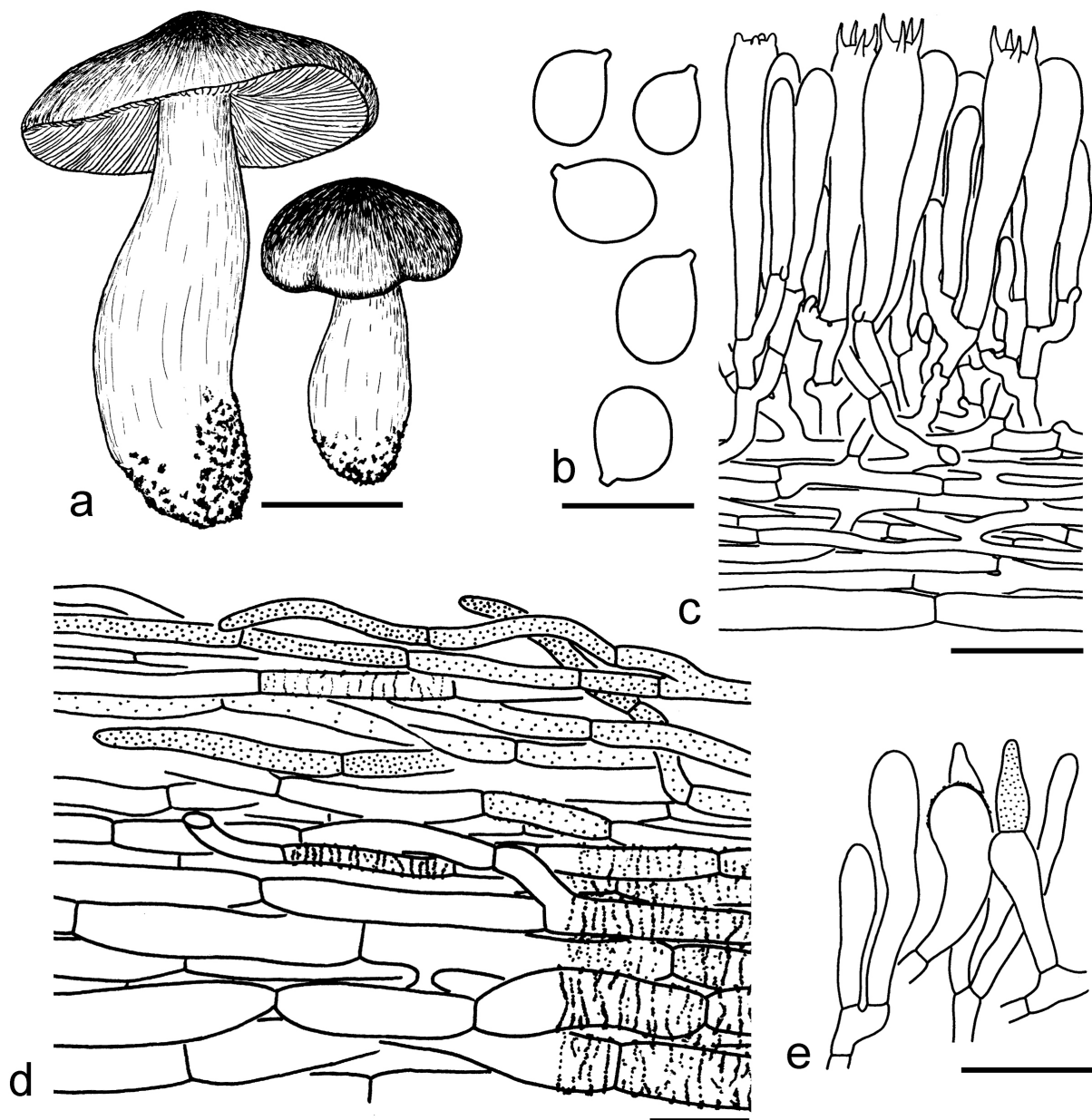


Fig. 36 Microscopic features of *Tricholoma sinoportentosum* (holotype, KUN-HKAS46084). a Basidioma. b Basidiospores. c Hymenial structure. d Pileipellis. e Young basidia and marginal cells. Scale bars: a = 3 cm, b = 10 μm , c–e = 20 μm . Cited from Reschke et al. (2018).

19. *Tricholoma virgatum* (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 134 (1871). Figs. 28i, j, 37

Basionym: *Agaricus virgatus* Fr., Observ. mycol. (Havniae) 2: 113 (1818).

Description: Basidioma small to medium-sized. Pileus 3–10 cm in diam., conical, convex to plano-convex, with an acute papilla or papilla at center; surface dry, often silvery shiny (1B1), sometimes dark grey (1F1–3) to grey (2D1–3), darker at center, glabrous or covered with dark grey (1F1–3) squamules; margin straight; context dirty white (1B1) to greyish (2B1–3). Lamellae sinuate, white (1A1) to greyish (2B1, 2C1), becoming greyish brown (1D2–4) to brownish (1C3–5) when old, crowded to subclose; edges white (1A1), grey (2E1–3) to brownish (1C3–5). Stipe 7–15 × 0.7–1.5 cm, cylindrical, often twisted, white (1A1), greyish (1B1–3), greyish brown (2B2–4) to brownish (4B2–4), glabrous to fibrillose, stuffed to hollow, exannulate. Taste not recorded. Odour unpleasant.

Basidiospores [240/12/7] (6–) 7–10 (–11) × 5–7 (–8) µm (mean length = 7.9 µm, mean width = 5.6 µm), Q = (1.17–) 1.25–1.6 (–1.73), Qm = 1.43 ± 0.1, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 30–50 × 8–11 µm, clavate, 4-spored, hyaline; sterigmata 4–6 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 15–50 × 7–13 µm, clavate to subclavate, often septate, thick- to slightly thick-walled (ca. 0.3–0.8 µm), colorless, hyaline. Subhymenium composed of 2–5 µm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled, clavate, cylindrical to filamentous hyphae 2–20 µm

wide. Pileipellis a cutis, very slightly gelatinized, composed of radially arranged, 2–5 µm wide, thin-walled, colorless or yellow brown filamentous hyphae; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered in coniferous, broad-leaved, or mixed forests.

Known distribution: Known from Europe (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013; Heilmann-Clausen et al. 2017), North America (Bessette et al. 2013) and East Asia.

Specimens examined: CHINA. Hubei Province, Yichang, Shennongjia Forest District, in a mixed forest, altitude 2300 m, 7 Aug. 2015, Xing He 3 (KUN-HKAS91176). Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, in a subalpine forest, altitude 3450 m, 8 Sep. 2016, Bang Feng 98 (KUN-HKAS99452); the same county, in a mixed forest, altitude 3370 m, 9 Sep. 2016, KD-LJW 128 (KUN-HKAS97921); same county, in a mixed forest, altitude 3370 m, 9 Sep. 2016, KD-WPM 103 (KUN-HKAS98358). Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-La, in a mixed forest, altitude 4000 m, 13 Sep. 2016, Xiao-Xia Ding 136 (KUN-HKAS97079); the same location, in a mixed forest, altitude 4000 m, 13 Sep. 2016, Xiao-Xia Ding 135 (KUN-HKAS 97078); the same location, in a subalpine forest with *Abies* and *Picea*, altitude 3600 m, 30 Aug. 2021, Yang-Yang Cui 463 (KUN-HKAS135006); the same location, in a subalpine forest with *Abies* and *Picea*, altitude 3910 m, 8 Aug. 2016, Jian-Wei Liu 502 (KUN-HKAS98081); Kunming, Mushuihua Market, in a mixed forest, altitude unknown, 30 Aug. 2015, Pan-Meng Wang 468 (KUN-HKAS93474).

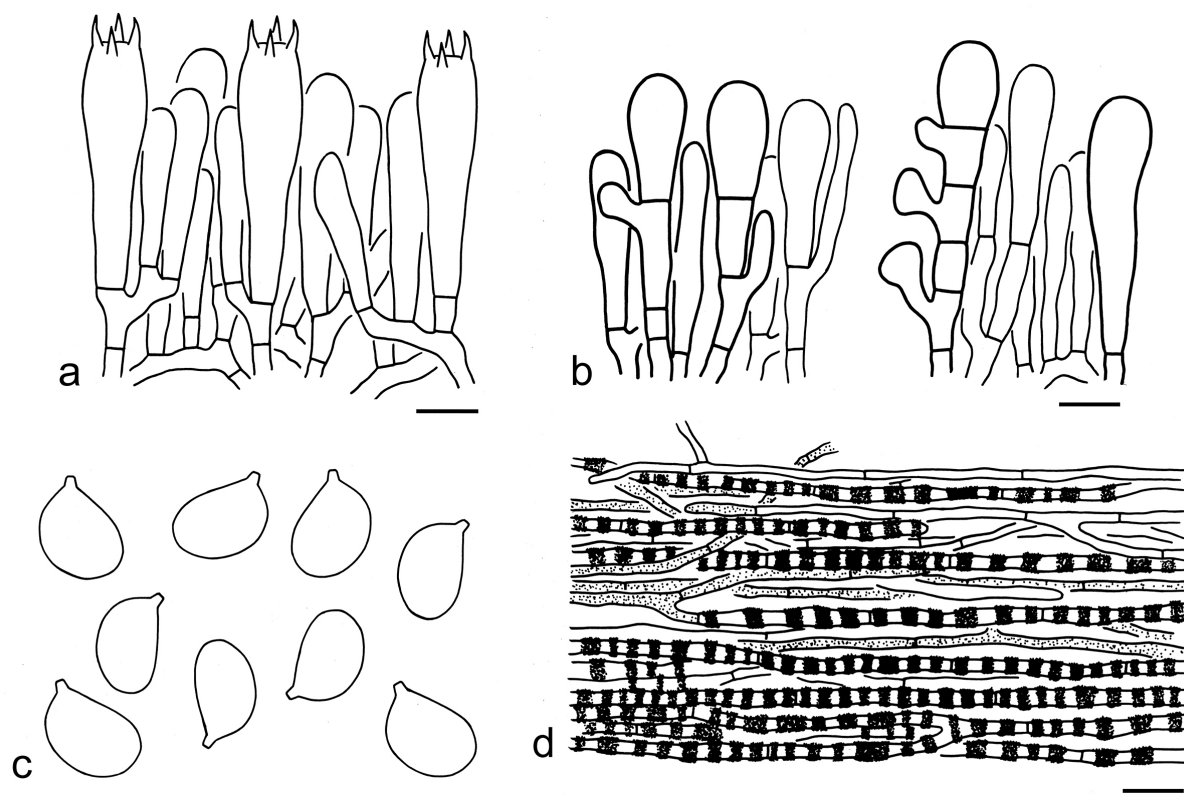


Fig. 37 Microscopic features of *Tricholoma virgatum* (KUN-HKAS99452). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm.

Notes: *Tricholoma virgatum* is characterized by its papillate, grey to silvery shiny pileus, a white to greyish stipe often twisted, broadly ellipsoid to ellipsoid basidiospores ($7\text{--}10 \times 5\text{--}7 \mu\text{m}$, $Q = 1.25\text{--}1.6$, $Q_m = 1.43 \pm 0.1$) and absence of clamps (this study). Christensen & Heilmann-Clausen (2013) reported that this species has an indistinct or slightly spicy odour, and a taste that is initially mild but gradually becomes slightly to strongly acrid or bitterish. For the Chinese collections of this species, taste was not recorded, and odour was reported as unpleasant in the field.

In the phylogenetic tree based on five gene fragments (Fig. 3), *T. mastoideum* is sister to *T. virgatum*, and their differences have been discussed under its notes part. Morphologically, *T. sciodes* (Pers.) C. Martín can be confused. However, *T. sciodes* has darker colored basidioma, white to brownish lamellae without brown tinge, relatively longer basidiospores ($5.6\text{--}8.3 \times 4.5\text{--}7 \mu\text{m}$) and is associated with broad-leaved trees (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013).

Tricholoma sect. *Fucata* X.X. Ding et al.

Type: *Tricholoma fucatum* (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 130 (1871).

Description: Basidioma tricholomatoid. Pileus papillate at center, brown, grey or olivaceous, radially fibrillose. Lamellae white, dirty white, greyish or brownish. Annulus absent. Basidiospores medium-sized, broadly ellipsoid to ellipsoid, thin-walled, smooth, inamyloid. Pleurocystidia absent. Cheilocystidia present and conspicuous. Pileipellis an ixo-cutis with its lower layer composed with inflated cells. Clamps absent.

Ecology: Ectomycorrhizal. On soil with various trees.

Known distribution: Molecular evidence indicates that species from this section are found in Europe, North America, and Asia.

Notes: To date, two species, here newly describes as *T. brunneiceps* Y.Y. Cui & Zhu L. Yang and *T. cheilocystidiatum* Y.Y. Cui & Zhu L. Yang are known from China (see below).

Key to the species of *Tricholoma* sect. *Fucata* from China

1. Pileus dark grey to grey; lamellae white to dirty white, sometimes with grey edge; stipe dirty white, greyish to dirty brownish *T. cheilocystidiatum*
1. Pileus dark brown, brown to yellow-brown; lamellae white, cream to brownish, edges without grey color; stipe brownish to yellowish brown *T. brunneiceps*

20. *Tricholoma brunneiceps* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 28k, l, 38

Fungal Names: FN 572334

Etymology: brunneiceps = brown-headed, referring to its brown pileus.

Diagnosis: Closely related to *T. fucatum*, but differs in relatively smaller basidiospores and being associated with trees of Fagaceae.

Type: CHINA. Yunnan Province, Honghe Hani and Yi Autonomous Prefecture, Lvchun County, Amoebin Forest Park, in a broad-leaved forest with Fagaceae, altitude 1600 m, 23 Sep. 2019, 532531MF0521 (holotype, KUN-HKAS134966).

Description: Basidioma small. Pileus 2.5–5 cm in diam., plano-convex to applanate, with an acute to blunt papilla; surface viscid, innately fibrillose, often blackish (1F1–3) to grey-brown (1E1–4) at center, becoming brown (4E4–8) to brownish (4D4–8, 3C4–8) towards margin, occasionally brown (2D4–8) overall; margin straight to inflexed; context white (1A1) to brownish (4D3–5). Lamellae adnexed to sinuate, white (1A1), cream (3A2–3) to yellow brownish (3C4–7), crowded to subclose; edges entire, white (1A1), cream (3A2–3) to brownish (3C4–7). Stipe 6–11 $\times$ 0.5–1 cm, cylindrical, stuffed to hollow, brownish (4B2–5) to yellowish brown (4C3–6), covered with brown (4D3–6) fibrillose squamules, exannulate. Taste and odour not recorded.

Basidiospores $[100/5/4]$ $6\text{--}8.5$ ($\text{--}9$) $\times$ (4.5--) $5\text{--}6 \mu\text{m}$ (mean length = $7.2 \mu\text{m}$, mean width = $5.3 \mu\text{m}$), $Q = 1.17\text{--}1.56$ ($\text{--}1.73$), $Q_m = 1.37 \pm 0.1$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $30\text{--}40 \times 7\text{--}10 \mu\text{m}$, clavate, 4-spored, hyaline; sterigmata $3\text{--}5 \mu\text{m}$ long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia $15\text{--}65 \times 10\text{--}20 \mu\text{m}$, conspicuous, fusiform, subfusiform to clavate, sometimes septate, thin- to thick-walled, brownish to brown or colorless, hyaline. Subhymenium composed of $3\text{--}5 \mu\text{m}$ wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless to thin-walled hyphae $3\text{--}15 \mu\text{m}$ wide. Pileipellis an ixo-cutis, strongly gelatinized, composed of radially arranged, $3\text{--}10 \mu\text{m}$ wide, thin-walled, colorless or brownish to brown filamentous hyphae; subpellis composed of radially arranged inflated cells, ellipsoid, clavate to cylindrical, $30\text{--}90 \times 15\text{--}30 \mu\text{m}$, thin-walled, yellow-brown to brownish. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in subtropical broad-leaved forests with trees of Fagaceae.

Known distribution: Known from Southwestern China.

Additional specimens examined: CHINA. Yunnan Province, Baoshan, Tengchong, in a subtropical broad-leaved forest with Fagaceae, altitude 1700 m, 10 Aug. 2011, Jiao Qin 291 (KUN-HKAS73277); same city, in a subtropical mixed forest with Fagaceae and Pinaceae, altitude 1960 m, 26 Jul. 2022, GLG-JLK2282 (KUN-HKAS134968); same city, in a subtropical forest dominated by Fagaceae, altitude 1900 m, 26 Jul. 2022, GLG-FXP236 (KUN-HKAS134971); same city, in a subtropical forest dominated by Fagaceae, altitude 1580 m, 24 Jul. 2022, GLG-FXP167 (KUN-HKAS134972), same city, in a subtropical forest dominated by Fagaceae, altitude 1900 m, 26 Jul. 2022, GLG-FXP250 (KUN-HKAS134973); same city, in a subtropical forest dominated by Fagaceae, altitude 1900 m, 26 Jul. 2022, GLG-FXP229 (KUN-HKAS134974); same city, in a subtropical broad-leaved forest with Fagaceae, altitude 1700 m, 10 Aug. 2011, Qi Zhao 1242 (KUN-HKAS74195); Baoshan, Longling County, in a subtropical mixed forest, altitude 1960 m, 30 Aug. 2022, GLG-FXP825 (KUN-HKAS134969); same county, in a subtropical mixed forest, altitude 1960 m, 30 Aug. 2022, GLG-FXP824 (KUN-HKAS134970); Honghe Hani and Yi Autonomous Prefecture, Pingbian Miao Autonomous County, Daweishan Nature Reserve, in a subtropical broad-leaved forest with Fagaceae, altitude 2300 m, 14 Sep. 2019, 532531MF0479 (KUN-HKAS108098); same prefecture, Lvchun County, Amoebin Forest Park, in a subtropical broad-leaved forest with Fagaceae, altitude 1600 m, 23 Sep. 2019, 532531MF0504 (KUN-HKAS134967); same province, Kunming, Qiongzhu Temple, in a subtropical broad-leaved forest,

altitude 2200 m, 8 Aug. 2007, Bang Feng 32 (KUN-HKAS52753).

Notes: *Tricholoma brunneiceps* is characterized by its viscid and brown pileus, broadly ellipsoid to ellipsoid basidiospores ($6\text{--}8.5 \times 5\text{--}6 \mu\text{m}$, mean length = $7.2 \mu\text{m}$, mean width = $5.3 \mu\text{m}$, $Q = 1.17\text{--}1.56$, $Q_m = 1.37 \pm 0.1$), and occurrences in subtropical broad-leaved forests. *Tricholoma fucatum* (Fr.) P. Kumm. appears to be closely related to *T. brunneiceps* in the phylogenetic analysis based on the ITS sequences (Fig. 4). However, the former species is distin-

guished by having a basidioma often with olivaceous colors on cap and on the punctate squamulose stem, relatively larger basidiospores ($5.9\text{--}9.2 \times 4.6\text{--}7.3 \mu\text{m}$) and being associated with trees of *Picea* and possibly *Pinus* (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013). *Tricholoma costaricense* Ovrebo, K.W. Hughes & Halling is similar in brown pileus, but it has relatively larger basidiospores ($8\text{--}9.5 \times 6\text{--}6.5 \mu\text{m}$) and is distributed in Costa Rica (Ovrebo et al. 2019).

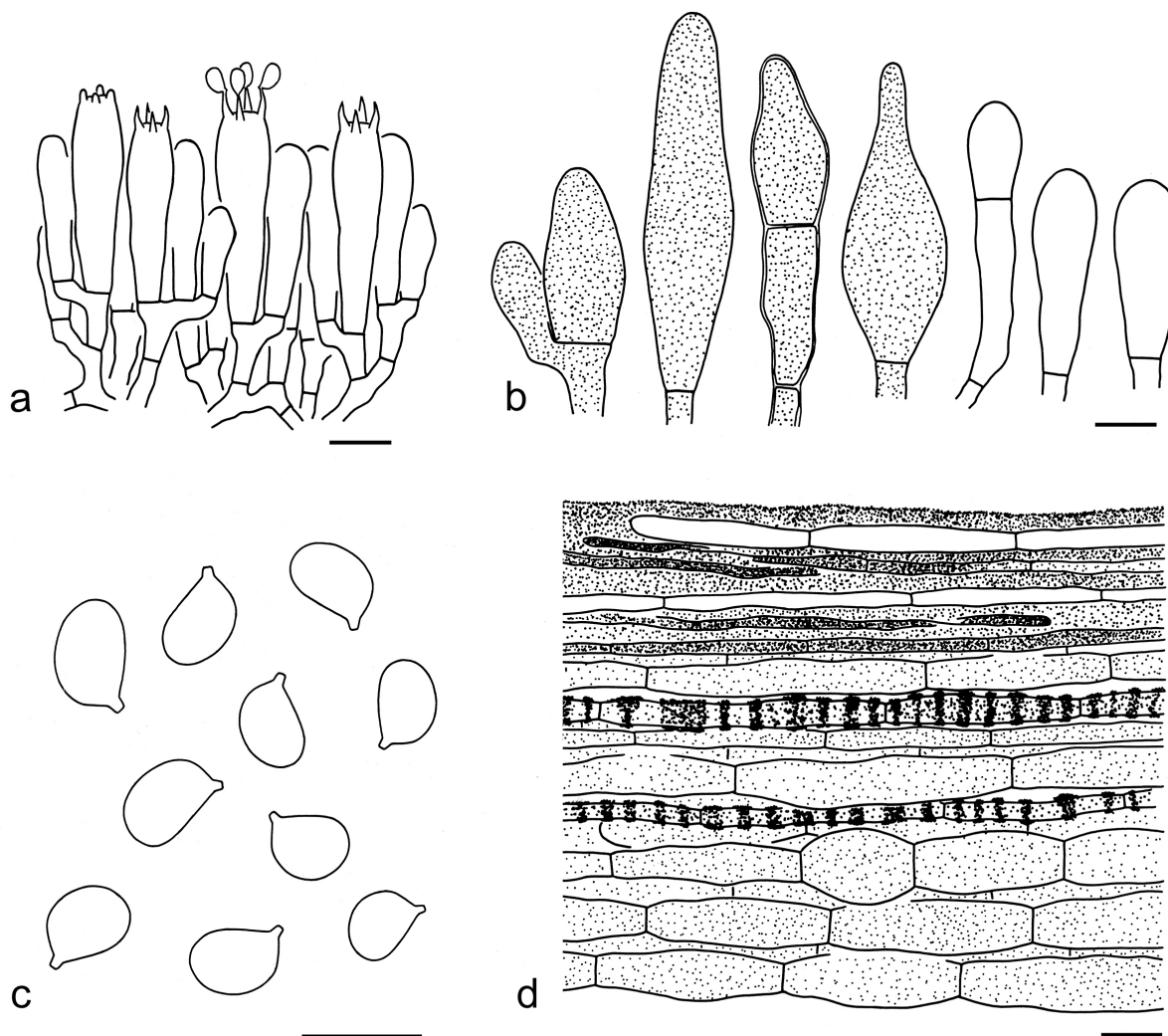


Fig. 38 Microscopic features of *Tricholoma brunneiceps* (holotype, KUN-HKAS134966). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = $10 \mu\text{m}$, d = $20 \mu\text{m}$.

21. *Tricholoma cheilocystidium* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 28m, 39

Fungal Names: FN 572336

Etymology: cheilocystidium = cheilocystidia, referring to its conspicuous cheilocystidia.

Diagnosis: Related to *T. brunneiceps*, but differs by its grey pileus, white to dirty white lamellae and a greyish stipe.

Type: CHINA. Yunnan Province, Chuxiong Yi Autonomous Prefecture, Nanhua County, in a subtropical broad-leaved

forest dominated by plants of Fagaceae, altitude 1950 m, 10 Aug. 2016, Xiao-Xia Ding 108 (holotype, KUN-HKAS97051).

Description: Basidioma small to medium-sized. Pileus 3–7 cm in diam., plano-convex to applanate, often with a low umbo; surface dry to slightly viscid, radially rugose, innately fibrillose, dark grey (1E1–3) to blackish (1F1–4) at center, often grey (1E1–3, 2E1–3) to brownish grey (1E3–6), sometimes greyish brown (2E5–8) to olivaceous yellow (3D4–7) towards margin; margin straight or slightly reflexed, sometimes radially rimose; context white (1A1). Lamellae adnexed to sinuate, white (1A1), dirty white (1C1–2) to cream (1A2, 1B2–4), crowded to subclose; edges slightly serrulate,

dirty white (1C1–2), cream (1A2, 1B2–4) to grey (2E1–2). Stipe 4–8 × 0.5–1.5 cm, cylindrical, hollow, dirty white (1B1–3), greyish (1C1–2) to dirty brownish (1B2–4), fibrillose, exannulate. Taste unknown. Odour like almond.

Basidiospores [140/7/2] 6–9 (–10) × 4–6 (–6.8) μm (mean length = 7.2 μm , mean width = 5.0 μm), $Q = 1.18\text{--}1.75$ (–1.8), $Q_m = 1.46 \pm 0.13$, mostly ellipsoid, sometimes broadly ellipsoid or elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 25–40 × 7–10 μm , clavate, 1-, 2- to 4-spored, hyaline; sterigmata 4–8 μm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 15–40 × 8–15 μm , conspicuous, subclavate, clavate, fusiform to ellipsoid, sometimes irregular shaped, sometimes septate, thin- to slightly thick-walled, colorless, hyaline. Subhymenium composed of 2–5 μm wide filamentous hyphae, clamps absent. Pileipellis an ixo-cutis, gelatinized, composed of radially arranged, 4–8 μm wide, thin-walled, colorless to brown filamentous hyphae; subpellis composed of radially arranged inflated cells, fusiform, ellipsoid to cylindrical, 25–55 × 10–25 μm , thin-walled, colorless to brown. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in subtropical broad-leaved forests with trees of Fagaceae.

Known distribution: Known from Southwestern China.

Additional specimens examined: CHINA. Yunnan Province, Puer, Lancang Lahu Autonomous County, in a broad-leaved

forest, altitude 1400 m, 25 Sep. 2016, LC-LJW157 (KUN-HKAS97661); same locality, in a broad-leaved forest, altitude 1300 m, 11 Sep. 2017, Zhu L. Yang 6102 (KUN-HKAS101291).

Notes: *Tricholoma cheilocystidiatum* is recognized by its dark grey to grey pileus which is slightly viscid, white to dirty white lamellae sometimes with grey edges, and ellipsoid basidiospores (6–9 × 4–6 μm , mean length = 7.2 μm , mean width = 5.0 μm , $Q = 1.18\text{--}1.75$, $Q_m = 1.46 \pm 0.13$). In our phylogenetic analysis based on five gene fragments (Fig. 3), this species is sister to *T. brunneiceps*. However, *T. brunneiceps* can be easily separated by its brown to yellow-brown pileus, white, cream to brownish lamellae and a brownish to yellowish brown stipe (this study).

Tricholoma felschii Ovrebo et al. is similar to *T. cheilocystidiatum*. However, *T. felschii* differs by having relatively smaller basidiospores (6–7.5 × 5–5.5 μm) and being found in the USA and Costa Rica (Ovrebo et al. 2019). *Tricholoma mutabile* Shanks and *T. josserandii* Bon can be confused with *T. cheilocystidiatum*. However, *T. mutabile* has a violet color on pileus, especially in old specimens, smaller basidiospores (5.8–7.7 × 4.3–5.8 μm) and is distributed in the USA (Shanks 1996; Bessette et al. 2013). *Tricholoma josserandii* is different from *T. cheilocystidiatum* in its shiny pileus and relatively narrower basidiospores (5.2–8 × 4.5–6.2 μm , $Q = 1\text{--}1.4$) (Riva 1988; Christensen & Heilmann-Clausen 2013).

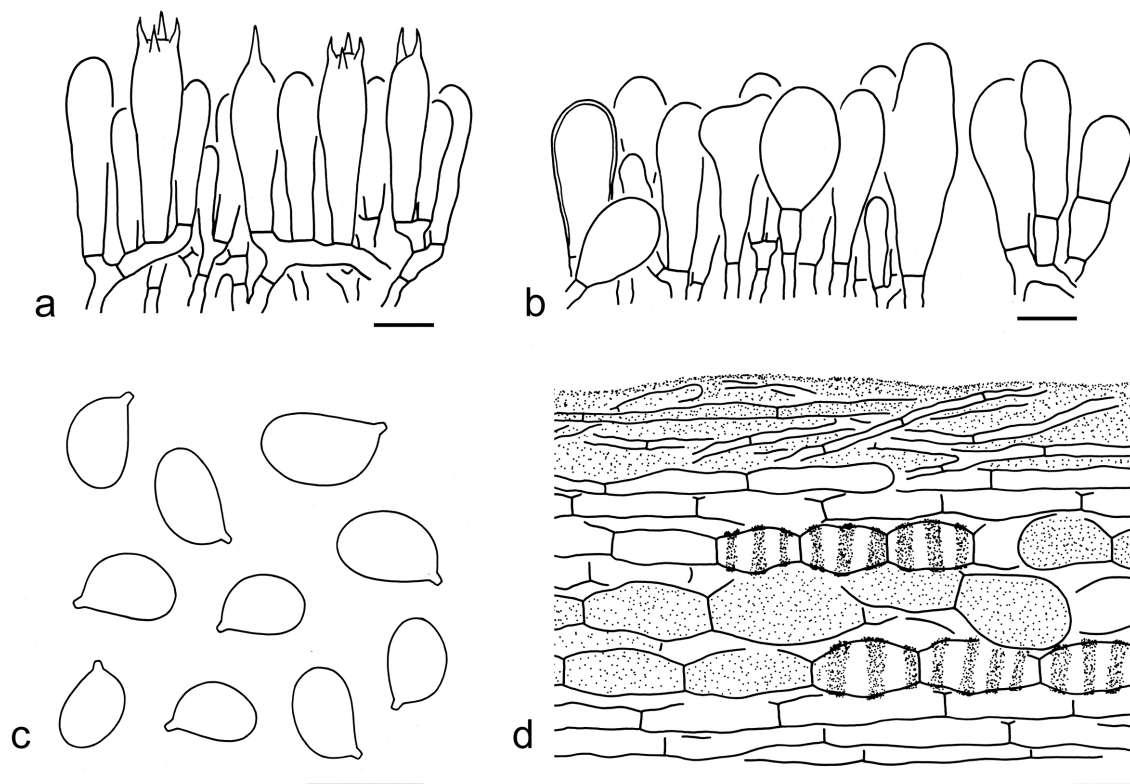


Fig. 39 Microscopic features of *Tricholoma cheilocystidiatum* (holotype, KUN-HKAS97051). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 μm , d = 20 μm .

Tricholoma sect. *Genuina* (Fr.) Sacc.

Type: *Tricholoma vaccinum* (Schaeff.) P. Kumm., Führ. Pilzk. (Zerbst): 133 (1871).

Description: Basidioma tricholomatoid. Pileus umbonate or not, often with an involute margin especially in young stage, orange-brown to brown, glabrous, squarrose to squamosa. Lamellae crowded, often with brown stains when damaged or old. Stipe cylindrical to subcylindrical, often without or

occasionally with an evanescent ring. Basidiospores small, broadly ellipsoid, ellipsoid to elongate, thin-walled, smooth, inamyloid. Pleurocystidia absent. Cheilocystidia present or absent, elements in lamellar edge often gelatinized and pigmented. Pileipellis mostly a cutis or an ixo-cutis. Clamps absent.

Ecology: Ectomycorrhizal. Solitary to scattered on soil with various trees.

Distribution: Molecular data indicated members from this section are currently found in Europe, North America, Oceania, and Asia.

Notes: To date, 18 species, including three novel and 15 known ones, are found in China with both molecular and morphological evidence (see below).

Key to the species of *Tricholoma* sect. *Genuina* from China

1. Stipe with an obviously woolly to skin-like ring on the apical part of stipe *T. focale*
1. Stipe exannulate 2
2. Pileus yellowish to yellowish brown, with more yellow color; cheilocystidia poorly differentiated; distributions dominated in *Larix* or broad-leaved forests 3
2. Pileus pinkish brown, orange-brown to reddish brown, with more orange color; cheilocystidia conspicuous or poorly differentiated; distributions in coniferous, broad-leaved or mixed forests 4
3. Pileus fibrillose-felty to fibrillose, with obvious squamules; basidioma associations in forests with trees of *Larix* *T. psammopus*
3. Pileus without distinct squamules; basidioma associations in forests with broad-leaved trees *T. sinoacerbum*
4. Pileus pinkish to pinkish brown at center, whitish towards margin; stipe shorter than pileus diameter, with pinkish brown color *T. roseoacerbum*
4. Pileus red-brown, orange-brown to brown; stipe often longer than pileus diameter, without pinkish brown color 5
5. Basidioma relatively robust, large to very large; pileal margin strongly involute; basidiospores relatively larger, with mean length > 8 µm, mean width > 6 µm... *T. orienticolossum*
5. Basidioma often medium-sized to large; pileal margin often involute when young, deflexed when mature; basidiospores relatively smaller, with mean length < 8 µm, mean width < 6 µm 6
6. Stipe with distinct apricot orange, ochraceous to brown squamules breaking into girdles; cheilocystidia conspicuous; pileipellis an ixo-trichoderm *T. aurantium*
6. Stipe glabrous or fibrillose, without distinct girdles; cheilocystidia conspicuous or poorly differentiated; pileipellis an ixo-cutis, cutis or ixo-trichoderm 7
7. Pileus dry, coarsely fibrillose to fibrillose-tomentose, with obvious squamules 8
7. Pileus dry or viscid when wet, glabrous or with distinct squamules 10
8. Basidiospores relatively narrower, with mean width < 5 µm; cheilocystidia poorly differentiated *T. imbricatum*
8. Basidiospores relatively broader, with mean width ≥ 5 µm; cheilocystidia conspicuous 9
9. Pileus tomentose, fibrillose-tomentose to fibrillose-hairy, often with a shaggy margin; lamellae white when young *T. vaccinum*

9. Pileus fibrillose-tomentose, without a shaggy margin; lamellae cream to yellowish colored when young *T. rufobrunneum*
10. Lamellae yellowish to yellow when young 11
10. Lamellae white to whitish when young 13
11. Pileal margin somewhat ribbed when mature; basidiospores slightly shorter, with mean length < 6 µm; cheilocystidia not observed *T. orientifulum*
11. Pileal margin not ribbed; basidiospores slightly longer, with mean length ≥ 6 µm; cheilocystidia present 12
12. Basidiospores slightly larger (6–7.5 × 4–5.5 µm, mean length = 6.6 µm, mean width = 4.8 µm); associations with *Picea* and *Quercus* *T. fulvomaculatum*
12. Basidiospores slightly smaller (5–7 × 4–5 µm, mean length = 6 µm, mean width = 4.3 µm); associations with *Castanopsis* and *Pinus* *T. castaneiceps*
13. Associations with *Populus* *T. populinum*
13. Associations in conifers, broad-leaved or mixed forests with Pinaceae and Fagaceae 14
14. Stipe without a white zone at top 15
14. Stipe with a white zone at top 17
15. Basidiospores relatively broader, subglobose to broadly ellipsoid; pileipellis not gelatinized; associations in broad-leaved forests *T. rubiginosum*
15. Basidiospores relatively narrower, broadly ellipsoid, ellipsoid to elongate; pileipellis gelatinized; associations in coniferous, broad-leaved or mixed forests 16
16. Pileus with dark brown spots; pileal margin not ribbed *T. rubrocastaneum*
16. Pileus without dark brown spots; pileal margin somewhat ribbed *T. stans*
17. Basidiospores relatively larger (6–7 × 4.5–5.5 µm, mean length = 6.3 µm, mean width = 5 µm); associations in coniferous or broad-leaved forests *T. ustaloides*
17. Basidiospores relatively smaller (5–7 × 3.5–5 µm, mean length = 5.7 µm, mean width = 4 µm); associations dominated with *Pinus* *T. albobrunneum*

22. *Tricholoma albobrunneum* (Pers.) P. Kumm., Führ. Pilzk. (Zerbst): 130 (1871). Figs. 28n, 40

Basionym: *Agaricus albobrunneus* Pers., Syn. meth. fung. (Göttingen) 2: 293 (1801).

Description: Basidioma small to medium-sized. Pileus 2–10 cm in diam., at first convex, then plano-convex to applanate, often slightly umbonate; surface dry, but viscid when wet, reddish brown (6C4–8, 6B4–6) to brown (4C4–6), darker at center, covered with reddish brown (6C4–8, 6B4–6) to brown (4C4–6), fine squamules; margin involute when young, deflexed when mature; context white (1A1) to cream (1A2). Lamellae sinuate, white (1A1) to cream (1A2), with brownish (5C3–5) spots then entirely brown (5D5–7), crowded; edges white (1A1) to brownish (5C3–5). Stipe 3–7 × 0.3–2 cm, cylindrical to subcylindrical, stuffed to hollow, whitish (1A1) to brownish (5C3–5), often white (1A1) at apical part, basal mycelium white (1A1), covered with brownish (5C3–5) fibrillose squamules, exannulate. Taste mild. Odour not recorded.

Basidiospores [113/5/4] (4–) 5–7 (–8) × (3–) 3.5–5 µm (mean length = 5.7 µm, mean width = 4 µm), Q = 1.15–1.75 (–2), Qm = 1.44 ± 0.16, broadly ellipsoid, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 20–30 × 6–8 µm, clavate, 4-

or 2-spored, at first colorless, then yellow brown to brown, hyaline; sterigmata 3–7 μm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 10–30 $\times$ 3–7 μm , poorly differentiated, clavate, sometimes septate, occasionally branching, thin-walled, hyaline, colorless when young, then brownish, at last gelatinized. Subhymenium composed of 2–5 μm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae 2–8 μm wide. Pileipellis an ixo-cutis, gelatinized, composed of radially arranged, 3–9 μm wide, thin-walled, yellow-brown, brown to brownish filamentous hyphae; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in subtropical, sometimes temperate forests dominated with *Pinus*, sometimes mixed with *Quercus*.

Known distribution: Known from Europe and China.

Specimens examined: CHINA. Qinhai, Qilian, on ground in mixed woods, 1 Aug. 1996, Shu-Xiao Sun, Hua-An Wen & Xiao-Lan Mao 9019 (HMAS79274). Yunnan Province, Baoshan, Longyang District, Xiyi Village, in a forest with *Pinus yunnanensis*, altitude 1650 m, 12 Aug. 2015, Pan-Meng Wang 355 (KUN-HKAS93315); Baoshan, Tengchong, forest and altitude not recorded, 7 Jun. 2022, GLG-FXP 75 (KUN-HKAS138821); Lijiang, Gucheng, forest and altitude not recorded, 3 Aug. 2011, Qing Cai 537 (KUN-HKAS70133); Diqing Tibetan Autonomous Prefecture, Shangri-La,

Jinmulong, in a forest with *Pinus* and *Quercus*, altitude 3480 m, 23 Aug. 2014, Qi Zhao 2229 (KUN-HKAS87995); Lijiang, Yulong Naxi Autonomous County, Laojun Mountain, in a temperate forest with *Pinus* and *Quercus*, altitude 3400 m, 1 Aug. 2005, Zhu L. Yang 4505 (KUN-HKAS48671); same county, Longpan Village, in a forest with *Pinus yunnanensis*, altitude 2164 m, 4 Aug. 2011, Li-Ping Tang 1448 (KUN-HKAS69909); same county, Ningli Village, in a forest dominated with *Pinus yunnanensis*, altitude 2422 m, 8 Aug. 2011, Li-Ping Tang 1520 (KUN-HKAS69981); same location, in a forest dominated with *Pinus yunnanensis*, altitude 2422 m, 8 Aug. 2011, Ting Guo 399 (KUN-HKAS71295); same city, Ninglang Yi Autonomous County, Luoshui Village, Lugu Lake, in a forest with *Pinus yunnanensis*, altitude 2740 m, 10 Jul. 2010, Xue-Tai Zhu 13 (KUN-HKAS68189).

Notes: *Tricholoma albobrunneum* is distinguished by its reddish brown to brown pileus and broadly ellipsoid, ellipsoid to elongate basidiospores (this study). In China, this species can be found not only in coniferous forest, but also in mixed forest with both *Pinus* and *Quercus*. According to Christensen & Heilmann-Clausen (2013), this species has a strongly farinaceous odour and a mild, farinaceous to slightly bitter taste, whereas taste and odour were not recorded in the Chinese specimens.

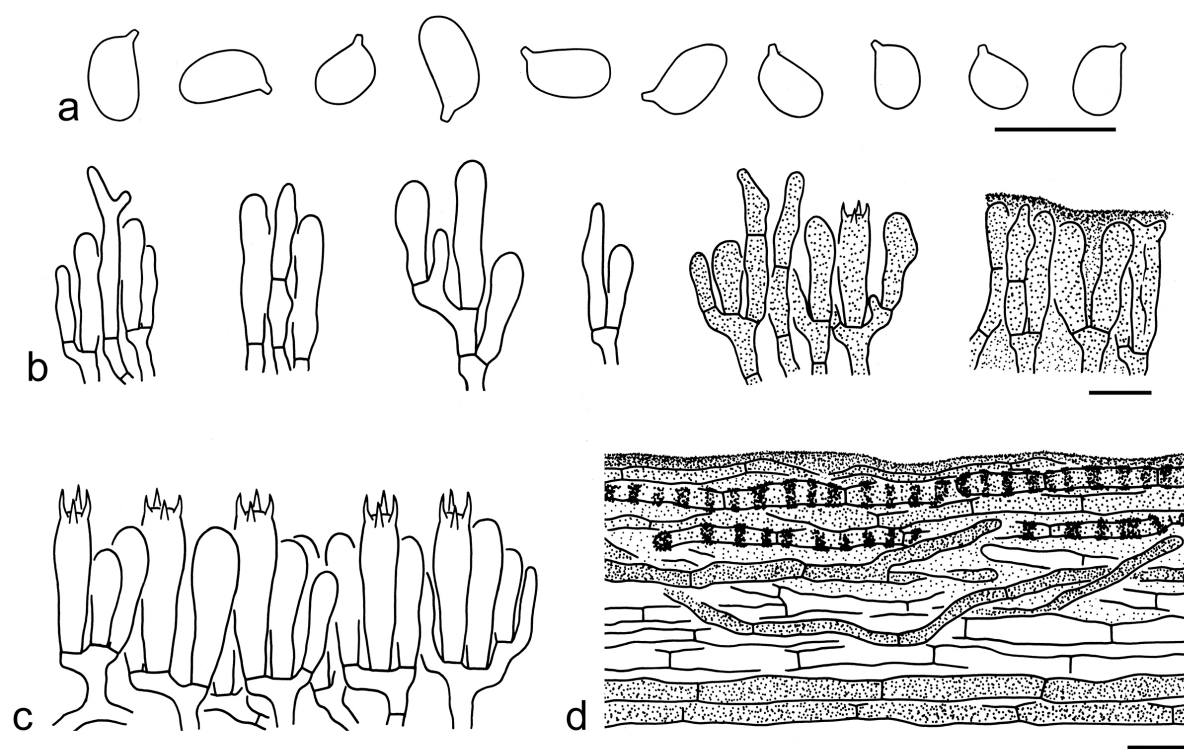


Fig. 40 Microscopic features of *Tricholoma albobrunneum* (KUN-HKAS69909). a Basidiospores. b Marginal cells. c Hymenium and subhymenium. d Pileipellis. Scale bars: a–c = 10 μm , d = 20 μm .

According to current data, no closely related species were discovered (Figs. 3, 4). *Tricholoma stans* (Fr.) Sacc. is similar to it, but has a more robust basidioma, a somewhat ribbed pileal margin and is distributed in coniferous and mixed forests (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013; Landry et al. 2022; this study). *Tricholoma*

rubrocastaneum Y.Y. Cui & Zhu L. Yang can be confused with it. For comparison, see notes under that name. *Tricholoma fulvum* (DC.) Bigeard & H. Guill. and *T. ustaloides* Romagn. are similar to *T. albobrunneum*. However, *T. fulvum* has distinct yellowish context (Christensen & Heilmann-Clausen 2013; Landry et al. 2022). *Tricholoma ustaloides* differs by its

slight ring zone more obvious than *T. albobrunneum*, slightly larger basidiospores ($6\text{--}7 \times 4.5\text{--}5.5 \mu\text{m}$, mean length = $6.3 \mu\text{m}$, mean width = $5 \mu\text{m}$) and association with only deciduous hosts (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013; this study). *Tricholoma batschii* Gulden also similar to *T. albobrunneum*, but the former species has shorter and more broadly ellipsoid basidiospores (Christensen & Heilmann-Clausen 2013).

23. *Tricholoma aurantium* (Schaeff.) Ricken, Die Blätterpilze: 332 (1914). Figs. 28o, 41

Basionym: *Agaricus aurantius* Schaeff., Fung. bavar. palat. nasc. (Ratisbonae) 4: 18 (1774).

Description: Basidioma medium-sized to large. Pileus 4–12 cm in diam., convex to plano-convex, sometimes with a

broadly low umbo; surface viscid when wet, often cracking into squamules when dry, apricot orange (1B4–6), ochraceous (5B5–7) to brown (5C5–7); margin involute, later inflexed; context white (1A1) to dirty white (1B2). Lamellae adnexed to sinuate, at first white (1A1) to cream (1A2), with brownish (5B3–5) to brown (5E6–8) spots when old, crowded; edges white (1A1) to cream (1A2), later with brown (5E6–8) spots or entirely brown (5E6–8). Stipe 3–10 $\times$ 0.5–3 cm, cylindrical to clavate, white (1A1) at apical part, a white (1A1) background covered with apricot orange (1B4–6), ochraceous (5B5–7) to brown (5C5–7) squamules often breaking into girdles, basal mycelium white (1A1), exannulate. Taste not recorded. Odour like cucumber.

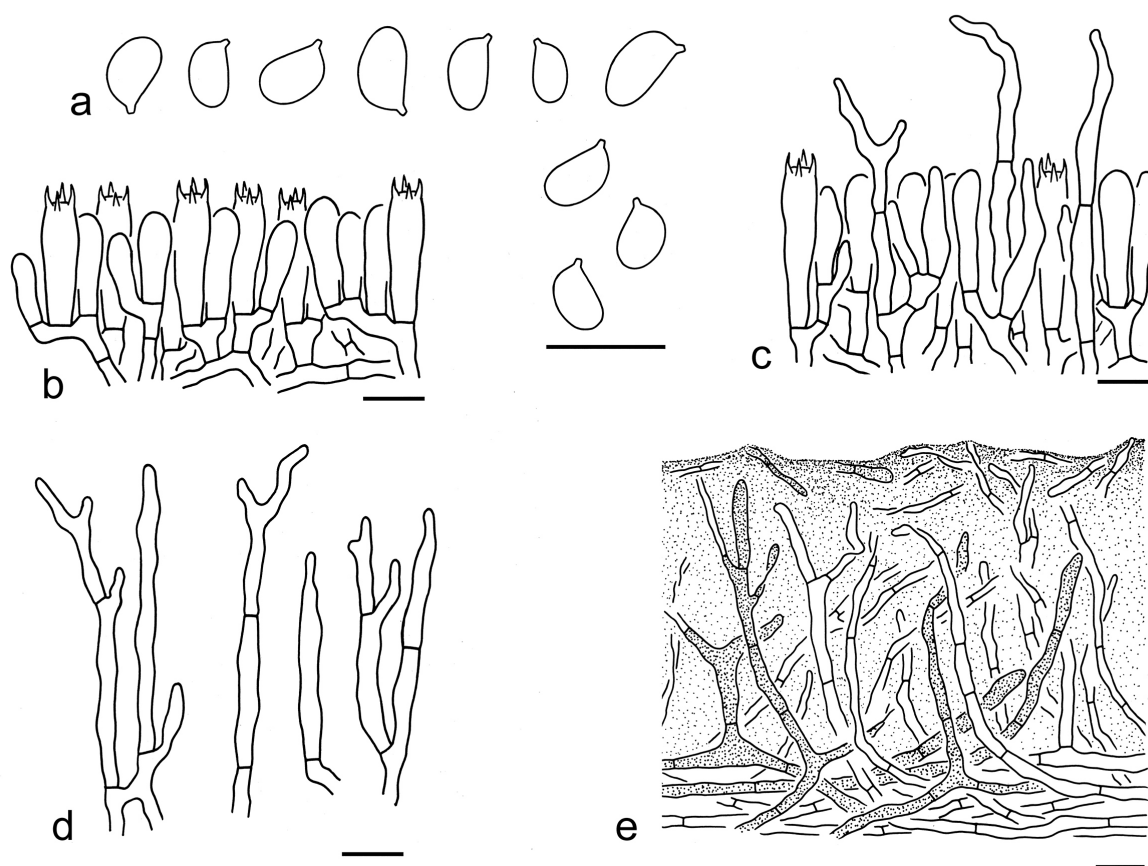


Fig. 41 Microscopic features of *Tricholoma aurantium* (KUN-HKAS94390). a Basidiospores. b Hymenium and subhymenium. c Hymenium near lamellar edge. d Cheilocystidia. e Pileipellis. Scale bars: a–d = $10 \mu\text{m}$, e = $20 \mu\text{m}$.

Basidiospores $[90/5/2] 5\text{--}7$ (–8) $\times$ $3\text{--}4$ (–4.5) μm (mean length = $5.9 \mu\text{m}$, mean width = $3.7 \mu\text{m}$), $Q = 1.32\text{--}1.9$ (–2.1), $Q_m = 1.6 \pm 0.14$, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $15\text{--}35 \times 5\text{--}7 \mu\text{m}$, clavate, 4-spored, hyaline; sterigmata 2–4 μm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia $30\text{--}60 \times 2\text{--}6 \mu\text{m}$, conspicuous, cylindrical to filiform, often branching, sometimes septate, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 μm wide filamentous hyphae, clamps absent. Lamellar trama regular,

composed of colorless, thin-walled hyphae 2–8 μm wide. Pileipellis an ixo-trichoderm, strongly gelatinized, composed of more or less vertically arranged, 2–6 μm wide, colorless or yellowish filamentous hyphae; subpellis non-gelatinized, composed of radially arranged, 3–7 μm wide, thin-walled, colorless to yellowish hyphae. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in temperate coniferous forests with *Abies* and *Picea*.



Fig. 42 Fresh basidiomata of the species in *Tricholoma*. a *T. castaneiceps* (holotype, KUN-HKAS101281). b, c *T. focale* (KUN-HKAS106309). d, e *T. fulvomaculatum* (d holotype, KUN-HKAS107572; e KUN-HKAS107576). f *T. imbricatum* (KUN-HKAS134975). g, h *T. orienticolossum* (g KUN-HKAS98645; h holotype, KUN-HKAS99341). i, j *T. orientifulvum* (i KUN-HKAS107156; j KUN-HKAS105381). k *T. rubrocastaneum* (holotype, KUN-HKAS134978). l *T. populinum* (KUN-HKAS106656). m *T. psammopus* (KUN-HKAS106302). n *T. roseoaccerbum* (KUN-HKAS88046). o *T. rubiginosum* (holotype, KUN-HKAS134980).

Distribution: Known from Europe (Christensen & Heilmann-Clausen 2013), North America (Bessette et al. 2013) and East Asia, distributed in Northern and Northwestern China.

Specimens examined: CANADA. Ontario, Bruce peninsula National Park, near the Emmett Lake, in a coniferous forest with *Abies*, altitude 200 m, 12 Sep. 2015, Bang Feng 1997 (KUN-HKAS94389); same location, in a coniferous forest with *Abies*, altitude 200 m, 12 Sep. 2015, Bang Feng 1998 (KUN-HKAS94390). CHINA. Inner Mongolia, Hulunbuir City, Genhe, altitude 800 m, 29 Aug. 2014, collector unknown (HMJAU28452). Xinjiang Uygur Autonomous Region, Yili Kazak Autonomous Prefecture, in a temperate coniferous forest with *Picea*, altitude 2300 m, 9 Jul. 2017, Xiao-Xia Ding 194 (KUN-HKAS106536).

Notes: *Tricholoma aurantium* can be easily delimited by its apricot orange pileus, apricot orange girdles on stipe surface, ellipsoid to elongate basidiospores, conspicuous cheilocystidia and an ixo-trichoderm pileipellis (this study). Christensen & Heilmann-Clausen (2013) recorded this species as having a strongly farinaceous or linseed-oil-like odour and a strongly farinaceous to rancid-bitter taste. In the Chinese collections of this species, however, taste was not recorded, and the odour was described as cucumber-like in the field.

This species is sister to *T. focale* on the phylogenetic tree inferred from five gene fragments (Fig. 3), but the latter species has a coarsely radially fibrillose pileus, a woolly to skin-like ring and relatively shorter basidiospores ($4\text{--}5.5 \times 3\text{--}4 \mu\text{m}$, mean length = $4.8 \mu\text{m}$, mean width = $3.5 \mu\text{m}$) (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013; this study). *Tricholoma batschii* Gulden ex Mort. Chr. & Noordel. and *T. stans* (Fr.) Sacc. are somewhat similar to *T. aurantium*, but

these two species have no girdles on stipe surface (Riva 1988; Christensen & Heilmann-Clausen 2013; Landry et al. 2022). Moreover, *T. batschii* has a thin, but distinct skin-like ring when young (Christensen & Heilmann-Clausen 2013). *Tricholoma stans* possesses poorly differentiated cheilocystidia and an ixo-cutis pileipellis (this study).

24. *Tricholoma castaneiceps* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 42a, 43

Fungal Names: FN 572335

Etymology: *castaneiceps* = chestnut-headed, referring to its chestnut-colored pileus.

Diagnosis: Similar to *T. fulvum*, but differs by its non-ribbed pileal margin, presence of cheilocystidia and associations with subtropical trees of *Castanopsis* and *Pinus*.

Type: CHINA. Yunnan Province, Puer, Lancang Lahu Autonomous County, Qianliu Village, in a forest with *Castanopsis* and *Pinus kesiya* var. *langbianensis*, altitude 1300 m, 10 Nov. 2017, Zhu L. Yang 6092 (holotype, KUN-HKAS101281).

Description: Basidioma very small to small. Pileus 2–5 cm in diam., applanate to plano-concave, slightly umbonate at center; surface dry or viscid when wet, fulvous (5C4–7), often darker at center, covered with fulvous (5C4–7) fibrillose squamules; margin deflexed; context dirty white (1A1) to cream (1A2). Lamellae adnexed to sinuate, pale sulphur-yellow (3A2–4), crowded; edges often reddish (6A2–4) to brownish (5C4–6) when injured. Stipe 4–6 $\times$ 0.5–0.8 cm, cylindrical, attenuate upwards, brownish (5C4–6), covered with brown (5D6–8) squamules, basal mycelium dirty white (1A1) to pinkish (6A2), exannulate. Taste and odour not recorded.

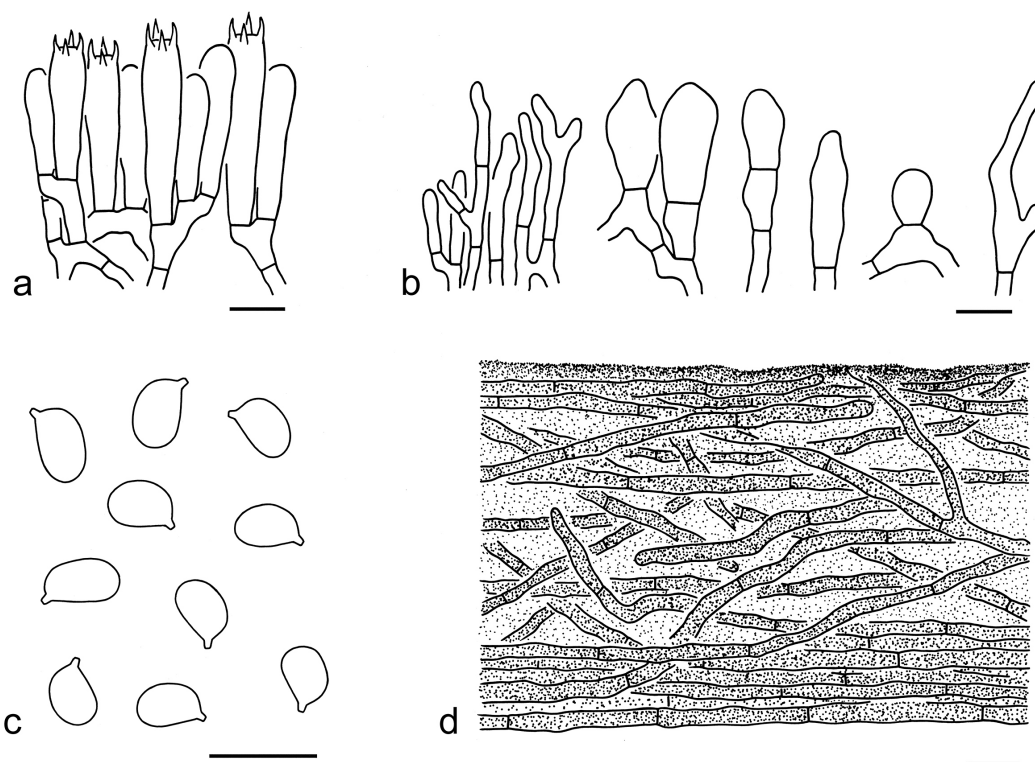


Fig. 43 Microscopic features of *Tricholoma castaneiceps* (KUN-HKAS101281). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 μm , d = 20 μm .

Basidiospores [80/4/1] $5\text{--}7 \times 4\text{--}5 \mu\text{m}$ (mean length = $6 \mu\text{m}$, mean width = $4.3 \mu\text{m}$), $Q = (1.2\text{--}) 1.3\text{--}1.5$ (-1.75), $Q_m = 1.41 \pm 0.1$, ellipsoid, sometimes broadly ellipsoid or elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $20\text{--}40 \times 5\text{--}8 \mu\text{m}$, clavate, 4-spored, sometimes 2- or 1-spored, hyaline; sterigmata $3\text{--}7 \mu\text{m}$ long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia $10\text{--}45 \times 3\text{--}10 \mu\text{m}$, conspicuous, clavate, cylindrical to filamentous, often branching or septate, thin-walled, colorless, hyaline. Subhymenium composed of $2\text{--}5 \mu\text{m}$ wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae $2\text{--}15 \mu\text{m}$ wide. Pileipellis an ixo-cutis, gelatinized, composed of radially arranged to interwoven, $2\text{--}5 \mu\text{m}$ wide, thin-walled, yellow-brown filamentous hyphae; subpellis poorly differentiated, non-gelatinized, composed of radially arranged, $4\text{--}7 \mu\text{m}$ wide, yellow-brown filamentous hyphae. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in subtropical mixed forests with *Castanopsis* and *Pinus kesiya* var. *langbianensis*.

Known distribution: Known from Southwestern China.

Additional specimen examined: CHINA. Yunnan Province, Qin Cai 11 (KUN-HKAS138822).

Notes: *Tricholoma castaneiceps* is characterized by its fulvous pileus, ellipsoid basidiospores, conspicuous cheilocystidia and associations with subtropical trees of *Castanopsis* and *Pinus*. It is closely related to *T. rubiginosum* Y.Y. Cui & Zhu L. Yang and *T. fulvomaculatum* X.X. Ding et al. (Fig. 3). However, *T. rubiginosum* differs by its subglobose to broadly ellipsoid basidiospores with $Q = 1.08\text{--}1.29$, and a non-gelatinized pileipellis. *Tricholoma fulvomaculatum* has slightly larger basidiospores ($6\text{--}7.5 \times 4\text{--}5.5 \mu\text{m}$, mean length

= $6.6 \mu\text{m}$, mean width = $4.8 \mu\text{m}$) and is associated with *Picea* and *Quercus* (Ding et al. 2022; this study). This species is similar to *T. fulvum*, but the latter species differs by a somewhat ribbed pileal margin when mature, absence of cheilocystidia and associations with *Betula*, *Abies* and *Picea* (Christensen & Heilmann-Clausen 2013; Landry et al. 2022). *Tricholoma orientifulvum* X. Xu et al. Yang is comparable to *T. castaneiceps*, but possesses relatively smaller basidiospores ($5\text{--}6 \times 4\text{--}4.5 \mu\text{m}$, mean length = $5.3 \mu\text{m}$, mean width = $4.2 \mu\text{m}$) and lacks cheilocystidia (Xu et al. 2020; this study).

25. *Tricholoma focale* (Fr.) Ricken, Die Blätterpilze: 332 (1914). Figs. 42b, c, 44

Basionym: *Agaricus focalis* Fr., Epicr. syst. mycol. (Upsaliae): 20 (1838) [1836-1838].

Description: Basidioma large. Pileus ca. 10 cm in diam., at first hemispherical, then plano-convex; surface dry, orange-brown (5B5-7), covered with appressed, orange-brown (5B5-7), fibrillose squamules, often with cottony remnants at margin; margin involute to inflexed; context white (1A1) to brownish (5A2-4). Lamellae adnate, adnexed to sinuate, white (1A1) to brownish (5B3-5), crowded; edges entire, white (1A1), sometimes with brownish (5B3-5) to brown (5C4-6) spots when mature. Stipe ca. $10 \times 2.5 \text{ cm}$, cylindrical, sometimes slightly tapering downwards, solid to fistulose, with an orange-brown (5B5-7), cottony to fibrillose annulus on the apical part, white (1A1) above annulus, white (1A1) backgrounds densely covered with appressed, orange-brown (5B5-7), fibrillose squamules below annulus. Taste and odour not recorded.

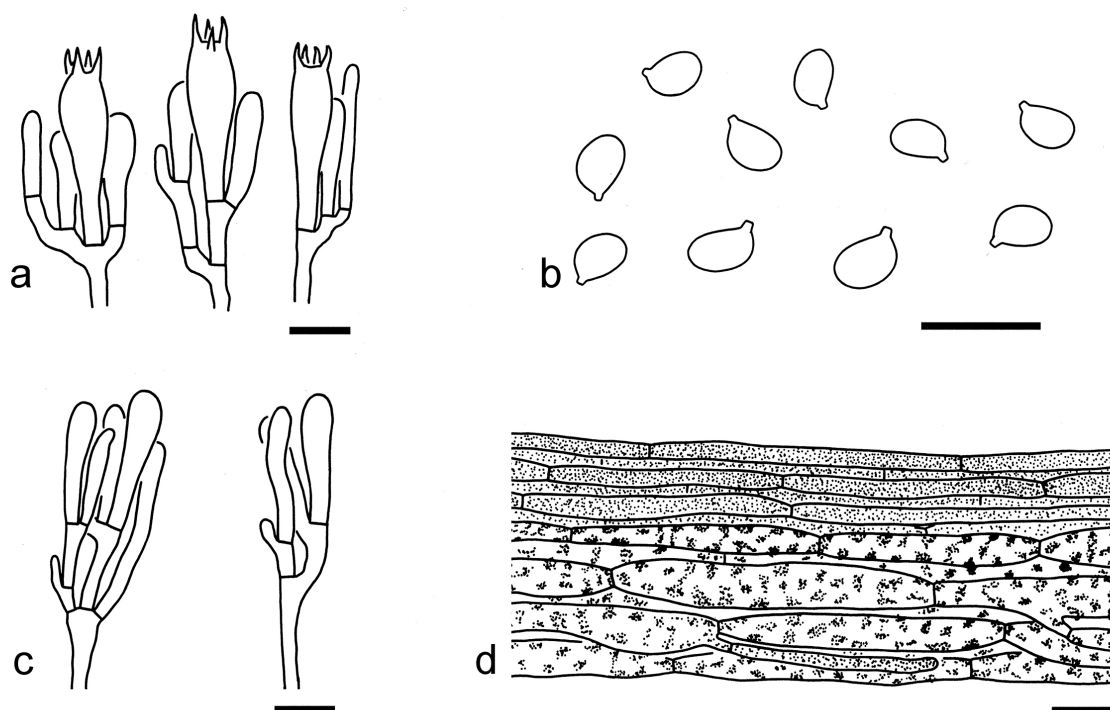


Fig. 44 Microscopic features of *Tricholoma focale* (KUN-HKAS138827). a Hymenium and subhymenium. b Basidiospores. c Marginal cells. d Pileipellis. Scale bars: a-c = $10 \mu\text{m}$, d = $20 \mu\text{m}$.

Basidiospores [20/1/1] $4\text{--}5.5 \times 3\text{--}4 \mu\text{m}$ (mean length = $4.8 \mu\text{m}$, mean width = $3.5 \mu\text{m}$), $Q = 1.26\text{--}1.47$, $Q_m = 1.37 \pm 0.08$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $25\text{--}40 \times 5\text{--}8 \mu\text{m}$, clavate, 4-spored, hyaline; sterigmata $4\text{--}6 \mu\text{m}$ long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia $15\text{--}30 \times 3\text{--}5 \mu\text{m}$, poorly differentiated, clavate to subclavate, thin-walled, colorless, hyaline. Subhymenium composed of $2\text{--}5 \mu\text{m}$ wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae $3\text{--}10 \mu\text{m}$ wide. Pileipellis a cutis, composed of radially arranged, $2\text{--}5 \mu\text{m}$ wide, thin-walled, brown filamentous hyphae; subpellis poorly differentiated, composed of radially arranged, $4\text{--}20 \mu\text{m}$ wide, brown cylindrical hyphae. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in coniferous forests.

Known distribution: Known from Europe (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013), North America (Bessette et al. 2013) and Southwestern China.

Specimens examined: CHINA. Yunnan Province, Nujiang Lisu Autonomous Prefecture, Lanping Bai and Pumi Autonomous County, in a coniferous forest, altitude 2700 m, 31 Aug. 2018, Jian-Wei Liu 1428 (KUN-HKAS106309); Diqing Tibetan Autonomous Prefecture, Shangri-La, in a mixed forest with *Pinus* and *Quercus*, altitude 3540 m, 11 Aug. 2023, Zi-Rui Wang 198 (KUN-HKAS138827).

Notes: *Tricholoma focale* is characterized by an orange-brown pileus covered with appressed, concolorous fibrillose squamules, and an orange-brown, cottony to fibrillose annulus on the apical part of the stipe (this study). Christensen & Heilmann-Clausen (2013) reported a weak, sweetish-spicy odour becoming distinctly farinaceous to rancid after cutting, and a distinctly farinaceous taste, but taste and odour were not recorded in the field for the Chinese collections of this species.

In the phylogenetic analysis based on the ITS sequences (Fig. 4), this species is related to *T. badicephalum* (Zeller) N. Siegel, S.A. Trudell & M.J. Gordon, but *T. badicephalum*, originally described from Oregon, USA, is associated with spruce (Landry et al. 2022). In the tree generated from five gene fragments, it is closely related to *T. aurantium* (Fig. 3). However, *T. aurantium* can be easily separated by its more orange colors basidioma, absence of annulus, relatively longer basidiospores ($5\text{--}7 \times 3\text{--}4 \mu\text{m}$, mean length = $5.9 \mu\text{m}$, mean width = $3.7 \mu\text{m}$), cylindrical to filiform cheilocystidia often branching, and an ixo-trichoderm pileipellis (this study).

26. *Tricholoma fulvomaculatum* X.X. Ding et al., Mycol. Progr. 21(37): 6 (2022). Figs. 42d, e, 45

Description: Basidioma small to medium-sized. Pileus $3\text{--}7 \text{ cm}$ in diam., convex to plano-convex, slightly subumbonate or broadly umbonate at center; surface dry or viscid when wet, orange-brown (6B4–7, 6C6–8), often darker at center, covered with dark brown (6E6–8, 6F6–8) to orange-brown (6B4–7, 6C6–8) fibrillose squamules; margin involute to deflexed; context cream (2A2). Lamellae sinuate, yellowish (2A2–4), with orange-brown (6B4–7, 6C6–8) spots when injured or old, crowded; edges yellowish (2A2–4) to orange-brown (6B4–7, 6C6–8). Stipe $5\text{--}10 \times 1\text{--}2 \text{ cm}$, subcylindrical, slightly inflated downwards, orange-brown (6B4–7, 6C6–8), often yellowish (2A2–4) at apical part, covered with orange-

brown (6B4–7, 6C6–8) fibrillose squamules, basal mycelium white (1A1), solid, exannulate. Taste and odour not recorded.

Basidiospores [60/3/2] ($5.5\text{--}6\text{--}7.5\text{--}8 \times 4\text{--}5.5\text{--}6 \mu\text{m}$) (mean length = $6.6 \mu\text{m}$, mean width = $4.8 \mu\text{m}$), $Q = 1.2\text{--}1.55\text{--}1.67$, $Q_m = 1.37 \pm 0.11$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $25\text{--}40 \times 6\text{--}9 \mu\text{m}$, clavate, 4-spored, hyaline; sterigmata $4\text{--}7 \mu\text{m}$ long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia $15\text{--}45 \times 2\text{--}7 \mu\text{m}$, subcylindrical to clavate, sometimes septate or branching, thin-walled, colorless to yellowish, hyaline. Subhymenium composed of $2\text{--}5 \mu\text{m}$ wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled, filamentous, cylindrical, clavate to elongate hyphae $4\text{--}25 \mu\text{m}$ wide. Pileipellis an ixo-cutis, gelatinized, composed of radially arranged to interwoven, $3\text{--}10 \mu\text{m}$ wide, thin-walled, yellow-brown to brownish filamentous hyphae; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in subalpine temperate forests dominated by *Picea* and *Quercus*.

Known distribution: Known from Southwestern China.

Specimens examined: CHINA. Sichuan Province: Ganzi Tibetan Autonomous Prefecture, Danba County, altitude 2100 m, 23 Jul. 2007, Zai-Wei Ge 1493 (KUNHKAS53579). Xizang Autonomous Region, Nyingchi, in a forest dominated by *Picea* and *Quercus*, altitude 3000 m, 18 Jul. 2019, Zhu L. Yang 6203 (KUN-HKAS106815); same city, Bayi District, Lulang Town, in a forest dominated by *Picea likiangensis* var. *rubescens* and *Quercus aquifolioides*, altitude 2850 m, 21 Jul. 2019, Geng-Shen Wang 479 (holotype, KUN-HKAS107572); same district, Nyingchi Town, in a forest dominated by *Picea* and *Quercus*, altitude 3000 m, 22 Jul. 2019, Geng-Shen Wang 506 (KUN-HKAS107576).

Notes: *Tricholoma fulvomaculatum* is characterized by its orange-brown basidioma, a yellowish zone at the top of stipe, cream context, yellowish lamellae when young and broadly ellipsoid to ellipsoid basidiospores (Ding et al. 2022; this study). *Tricholoma rubiginosum* is related to this species (Fig. 3), but can be separated by its subglobose to broadly ellipsoid basidiospores with $Q = 1.08\text{--}1.29$, and a non-gelatinized pileipellis (this study).

Tricholoma ustaloides Romagn. and *T. fulvum* can be confused with *T. fulvomaculatum*. However, cheilocystidia from the former two species have not been observed (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013; Landry et al. 2022). Moreover, *T. ustaloides* has white lamellae when young, white context and a white zone at top of stipe (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013). *Tricholoma fulvum* possesses a ribbed pileal margin when mature (Christensen & Heilmann-Clausen 2013; Landry et al. 2022). *Tricholoma rufobrunneum* X.X. Ding et al. is similar to *T. fulvomaculatum*, but differs by its more fibrillose-tomentose pileus and an ixo-cutis pileipellis with cylindrical hyphae (Ding et al. 2022; this study). *Tricholoma ligusticum* M. Carbone, Boccardo & Calleda, *T. quercetorum* Contu and *T. ustale* (Fr.) P. Kumm. are also comparable to *T. fulvomaculatum*, but the former three species can be easily separated by their white context and more white colored lamellae with brown spot or becoming brown when old (Contu 2004; Christensen & Heilmann-Clausen 2013; Carbone et al. 2020; Overall 2021).

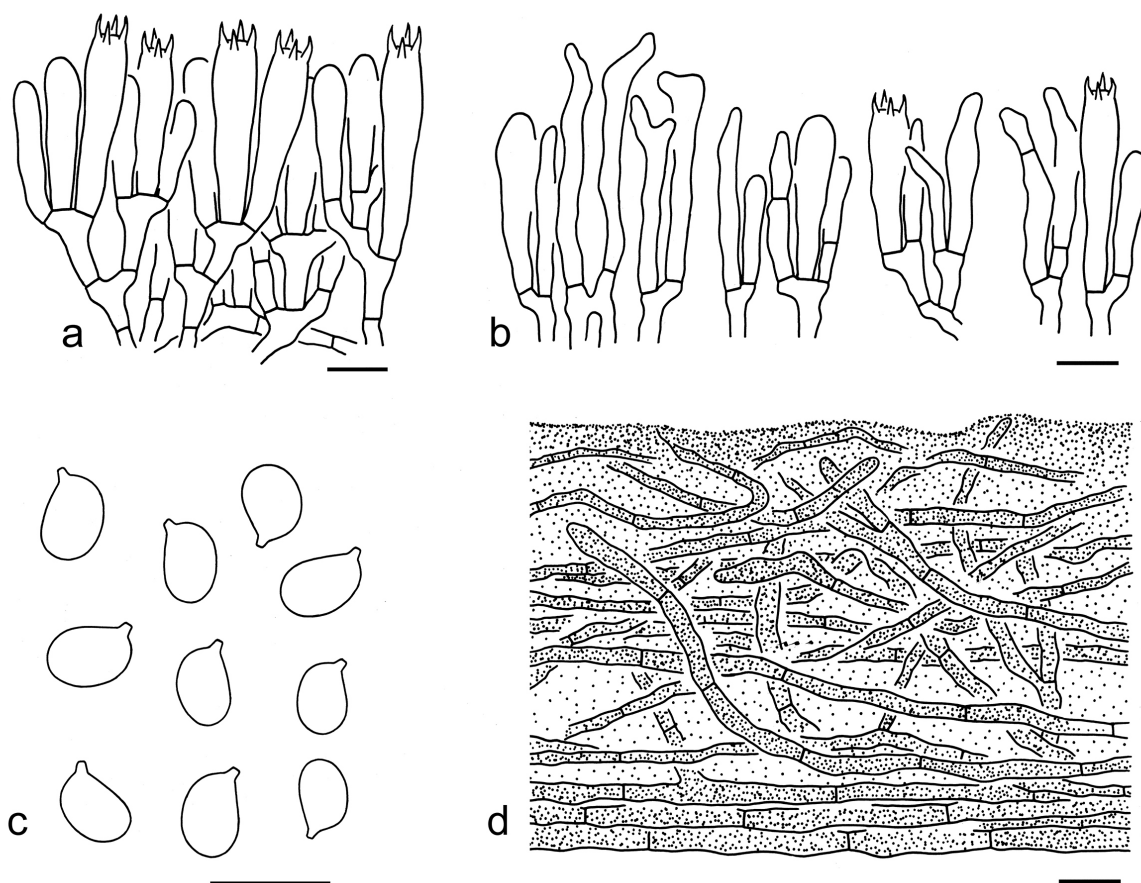


Fig. 45 Microscopic features of *Tricholoma fulvomaculatum* (KUN-HKAS107572). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 μ m, d = 20 μ m. Cited from Ding et al. (2022).

27. *Tricholoma imbricatum* (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 133 (1871). Figs. 42f, 46

Basionym: *Agaricus imbricatus* Fr., Observ. mycol. (Havniae) 1: 27 (1815).

Description: Basidioma medium-sized to large. Pileus 4–12 cm in diam., at first convex, then plano-convex to applanate, sometimes with a broadly low umbo at center surface dry, dark brown (6F6–8), cinnamon (6E6–8) to orange-brown (6D5–7), covered with dark brown (6F6–8) to orange-brown (6D5–7) fibrillose squamules; margin involute to deflexed; context white (1A1). Lamellae adnexed to sinuate, white, with brownish (6C2–4) to brown (6D2–4) stains, crowded to subclose; edges brownish (6C2–4) to brown (6D2–4). Stipe 6–12 $\times$ 1–2 cm, cylindrical, dirty white (6B1), brownish (5B2–4) to orangish brown (6C3–5), basal mycelium white (1A1), fibrillose, exannulate. Taste and odour not recorded.

Basidiospores [70/3/2] (4.5–) 5.5–7 (–8) $\times$ (3.5–) 4–5 μ m (mean length = 6.2 μ m, mean width = 4.2 μ m), $Q = (1.11–) 1.2–1.75 (–1.9)$, $Q_m = 1.48 \pm 0.15$, ellipsoid to elongate, sometimes broadly ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 30–40 $\times$ 5–7 μ m, clavate, 4-spored, hyaline; sterigmata 4–6 μ m long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia not observed. Subhymenium composed of 2–4 μ m wide filamentous hyphae, clamps absent. Lamellar trama regular,

composed of colorless, thin-walled, ellipsoid, cylindrical to filamentous hyphae 5–20 μ m wide. Pileipellis a cutis, made of radially arranged, 5–10 μ m wide, thin-walled, yellow-brown filamentous hyphae; subpellis poorly differentiated, composed of colorless filamentous hyphae 10–20 μ m wide. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil dominated in coniferous, also found in broad-leaved or mixed forests with *Pinus* and *Quercus*.

Known distribution: Known from Europe, North America, Japan, and Southwestern China.

Specimens examined: CHINA. Xizang Autonomous Region, Nyingchi, Mainling County, Qiangna Village, in a forest with *Pinus*, altitude 2950 m, 29 Jul. 2014, Qi Zhao 2120 (KUN-HKAS87886). Yunnan Province, Lijiang, Yulong Naxi Autonomous County, Lijiang Alpine Botanic Garden, in a forest dominated by *Pinus*, mixed with *Quercus*, altitude 2700 m, 29 Sep. 2019, Jian-Wei Liu 2170 (KUN-HKAS134975); same location, in a forest with *Quercus*, altitude 2700 m, 9 Oct. 2019, Jian-Wei Liu 2226 (KUN-HKAS112559); same location, in a mixed forest with *Pinus* and *Quercus*, altitude 2700 m, 29 Sep. 2019, Jian-Wei Liu 2171 (KUN-HKAS134976).

Notes: *Tricholoma imbricatum* is recognized by its cinnamon, squamulose pileus, ellipsoid to elongate basidiospores and associations dominated with coniferous trees (this study). Christensen & Heilmann-Clausen (2013) reported that this species has an indistinct or fruity odour and a farinaceous, mild to slightly bitter taste. However, for the

Chinese collections of this species, taste and odour were not recorded in the field.

This species is closely related with *T. vaccinum* (Schaeff.) P. Kumm. and *T. rufobrunneum* (Fig. 3). However, *T. vaccinum* differs by having pileus scales exceeding the cap margin, conspicuous cheilocystidia and a pileipellis composed of slightly inflated hyphae (Riva 1988; Christensen

& Heilmann-Clausen 2013; Landry et al. 2022; this study). *Tricholoma rufobrunneum* is similar to *T. imbricatum*, but has slightly broader basidiospores ($6\text{--}7.5 \times 5\text{--}6 \mu\text{m}$, mean length = $6.7 \mu\text{m}$, mean width = $5.2 \mu\text{m}$), presence of cheilocystidia and a gelatinized pileipellis composed of cylindrical hyphae (Ding et al. 2022; this study).

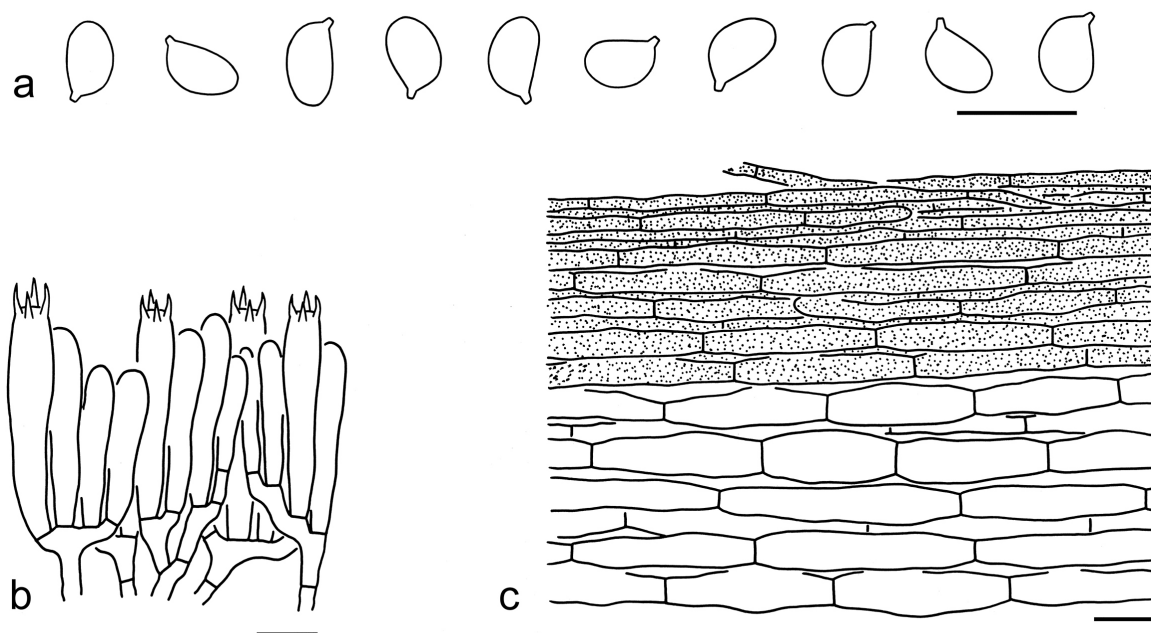


Fig. 46 Microscopic features of *Tricholoma imbricatum* (KUN-HKAS134975). a Basidiospores. b Hymenium and subhymenium. c Pileipellis. Scale bars: a, b = $10 \mu\text{m}$, c = $20 \mu\text{m}$.

28. *Tricholoma orienticolossum* X. Xu et al., Phytotaxa 443 (2): 159 (2020). Figs. 42g, h, 47

Description: Basidioma large to very large. Pileus 13–18 cm in diam., convex to plano-convex, sometimes slightly depressed at center; surface dry, red-brown (6D6–8) to brown (6C5–7), covered with dark brown (6F6–8) to red-brown (6D6–8) squamules; margin strongly incurved; context white (1A1). Lamellae adnexed to sinuate, white (1A1) to cream (1A2), later becoming reddish brown (6C5–7), crowded; edges cream (1A2) to brown (6D6–8). Stipe 9–15 $\times$ 4.5–6.5 cm, robust, clavate, dirty white (1A1), covered with brownish (4A2–4) to red-brown (4C6–7), fibrillose squamules, basal mycelium white (1A1), exannulate. Taste and odour indistinct.

Basidiospores [40/2/2] (8–) $8.5\text{--}10$ (–10.5) $\times$ (6–) $6.5\text{--}7.5$ (–8) μm (mean length = $9.1 \mu\text{m}$, mean width = $6.8 \mu\text{m}$), $Q = (1.24\text{--}) 1.29\text{--}1.46$ (–1.54), $Q_m = 1.35 \pm 0.06$, ellipsoid, sometimes broadly ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 60–70 $\times$ 9.5–11 μm , clavate, 4-spored, rarely 2-spored, hyaline; sterigmata up to 7 μm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 50–120 $\times$ 4–8 μm , conspicuous, subcylindrical, often septate and slightly capitate, thin-walled, colorless or yellow to brownish, hyaline. Subhymenium composed of 3–5 μm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae 3–10 μm wide. Pileipellis a cutis with transition to a trichoderm at regular intervals, composed of loosely and more or less

radially arranged, 3–8 μm wide, thin-walled filamentous hyphae; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in subalpine temperate forests dominated by *Abies*.

Known distribution: Known from Southwestern China.

Specimens examined: CHINA. Sichuan Province, Daofu County, Bamei Town, in a forest dominated by *Abies*, altitude 3800 m, 4 Aug. 2016, Bang Feng 2051 (holotype, KUN-HKAS99341); same location, in a forest dominated by *Abies*, altitude 3800 m, 4 Aug. 2016, Jian-Wei Liu 466 (KUN-HKAS98645).

Notes: *Tricholoma orienticolossum* is well delimited by large to very large, robust basidioma, a red-brown to brown pileus with an incurved margin, ellipsoid basidiospores and conspicuous cheilocystidia (this study). In the phylogenetic analysis based on the ITS sequences (Fig. 4), this species is sister to *T. colossus* (Fr.) Quél., but the latter species has a woolly-fibrillose ring that disappears as a zone with age, and relatively smaller and narrower basidiospores ($6.8\text{--}9.4 \times 5\text{--}6.4 \mu\text{m}$, average $7.7\text{--}8.7 \times 5.7\text{--}5.9 \mu\text{m}$) (Riva 1988; Christensen & Heilmann-Clausen 2013). *Tricholoma batschii* is similar to *T. orienticolossum*, but has relatively smaller basidioma, a distinct ring when young and smaller basidiospores ($3.8\text{--}6.4 \times 3.1\text{--}5.4 \mu\text{m}$, average $4.6\text{--}5.5 \times 3.8\text{--}4.5 \mu\text{m}$) (Riva 1988; Christensen & Heilmann-Clausen 2013).

29. *Tricholoma orientifulvum* X. Xu et al., Phytotaxa 443 (2): 161 (2020). Figs. 42i, j, 48

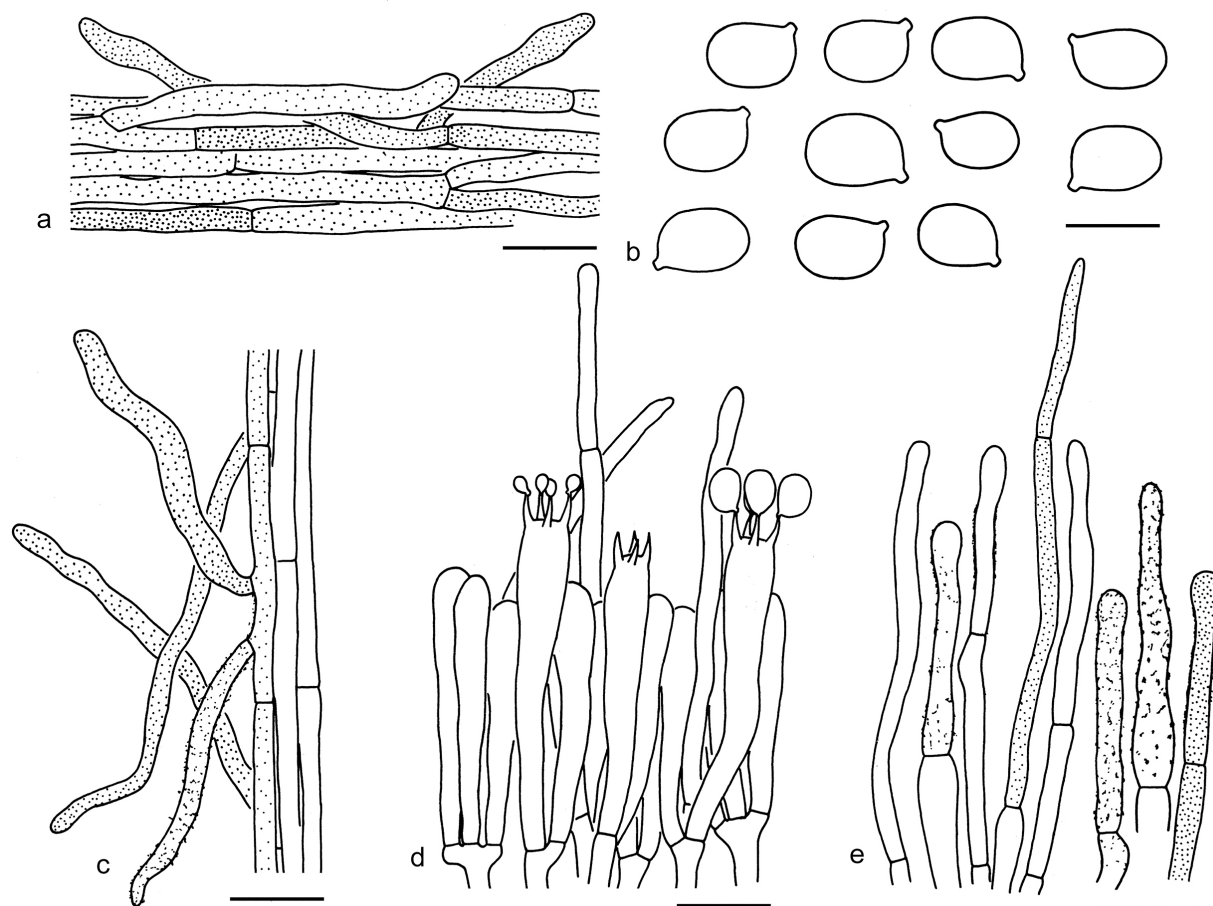


Fig. 47 Microscopic features of *Tricholoma orienticolosum* (holotype, KUN-HKAS99341). a Pileipellis. b Basidiospores. c Caulocystidia and stipitipellis. d Hymenium near the lamellar edge with pleurocystidia. e Cheilocystidia. Scale bars: a, c–e = 20 μ m, b = 10 μ m. Cited from Xu et al. (2020).

Description: Basidioma medium-sized to large. Pileus 4–11 cm in diam., at first convex, then plano-convex to applanate, sometimes with a broadly low umbo; surface viscid when wet, red-brown (6E6–8) to dark brown (6F6–8) at center, becoming reddish brown (6D6–8), yellow-brown (4C6–8) to yellowish (1A2–4) towards margin, glabrous; margin deflexed, often ribbed; context white (1A1). Lamellae adnate to sinuate, olivaceous yellow (30A3–5) to yellow-brown (1A3–5), with brown (5C5–7) stains when damaged or old, crowded; edges olivaceous yellow (30A3–5) with brown (5C5–7) stains. Stipe 8–11 $\times$ 0.8–1.2 cm, cylindrical, dirty white (1A1, 1B2), yellowish brown (2A3–5), reddish brown (6A2–4) to brownish (5B3–6), with concolor fibrils, basal mycelium white (1A1), hollow, exannulate. Taste not recorded. Odour like soap.

Basidiospores [40/2/2] (4.5–) 5–6 (–6.5) $\times$ (3.5–) 4–4.5 (–5) μ m (mean length = 5.3 μ m, mean width = 4.2 μ m), Q = 1.11–1.42 (–1.46), Qm = 1.26 $\pm$ 0.1, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 18–30 $\times$ 5–7 μ m, clavate, 4-spored, hyaline; sterigmata 3–5 μ m long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia not observed. Subhymenium composed of 2–5 μ m wide filamentous hyphae, clamps absent. Pileipellis an ixo-cutis, composed of radially arranged to interwoven, 3–6 μ m wide, thin-walled, brownish

filamentous hyphae; subpellis poorly differentiated, non-gelatinized. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in subtropical mixed forests with Fagaceae and Pinaceae.

Known distribution: Known from Southwestern and Northeastern China.

Specimens examined: CHINA. Yunnan Province, Puer, Simao, in a subtropical mixed forest with *Lithocarpus*, *Quercus* and *Pinus*, altitude 1230 m, 31 Aug. 2019, Xiao-Xia Ding 632 (holotype, KUN-HKAS107157); same location, in a mixed forest with *Lithocarpus*, *Quercus* and *Pinus*, altitude 1230 m, 31 Aug. 2019, Xiao-Xia Ding 642 (KUN-HKAS107156). Liaoning Province, Dandong, Kuandian Manchu Autonomous County, in a temperate broad-leaved forest, 29 Jul. 2018, Xiao-Xia Ding 371 (KUN-HKAS105381).

Notes: *Tricholoma orientifulum* is characterized by its red-brown to dark brown pileus becoming reddish brown to yellow-brown and somewhat ribbed towards margin, yellow lamellae when young, broadly ellipsoid to ellipsoid basidiospores and soap odour (Xu et al. 2020; this study). In the phylogenetic analysis based on the ITS sequences, this species is closely related to *T. quercetorum* Contu (Fig. 4), but the latter has a relatively robust basidioma and white to pinkish lamellae when young (Contu 2004; Casas et al. 2015;

Carbone et al. 2020; Overall 2021). *Tricholoma fulvum* can be easily confused with *T. orientifulvum*, but differs by its slightly larger basidiospores ($4.7\text{--}7.4 \times 3.6\text{--}6.1 \mu\text{m}$, average $5.4\text{--}6.4$

$\times 4.3\text{--}5.1 \mu\text{m}$), lack of soap odour and associations with *Betula*, *Abies* and *Picea* (Christensen & Heilmann-Clausen 2013; Landry et al. 2022).

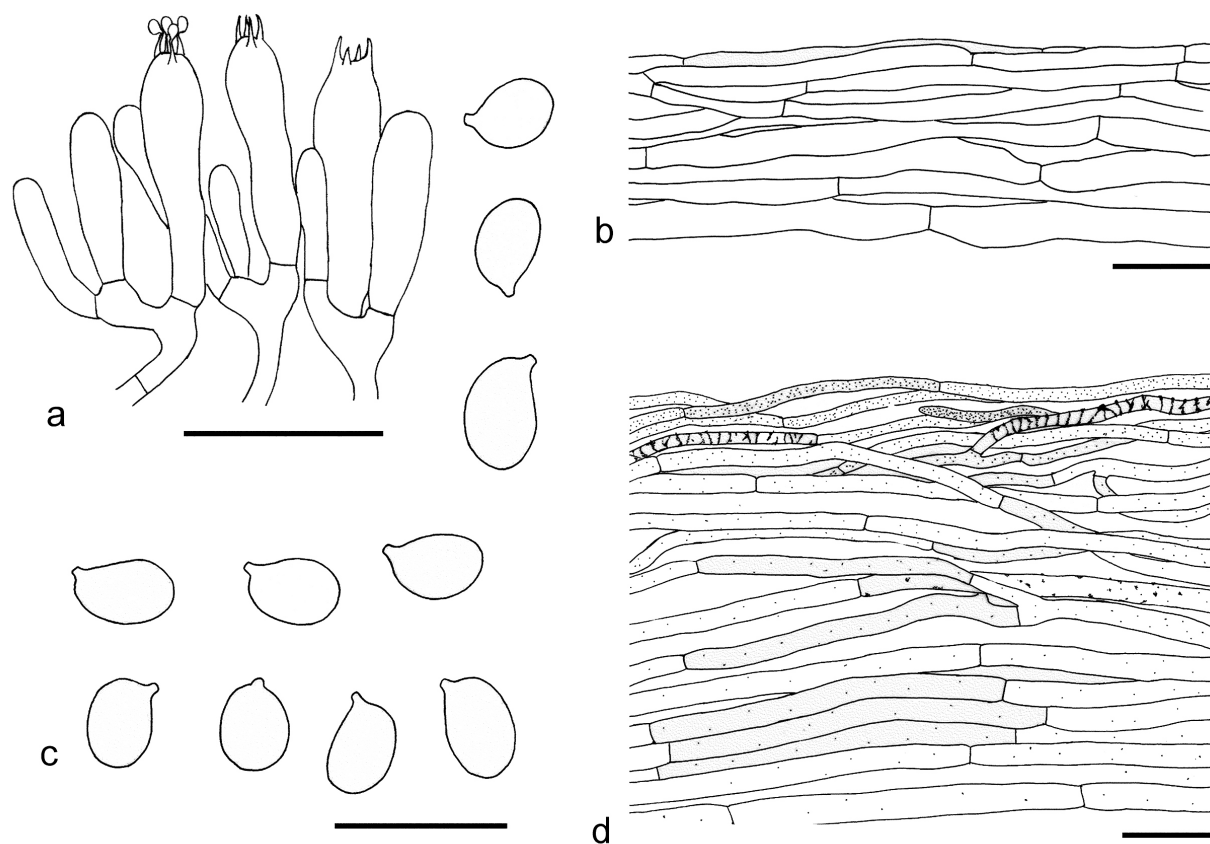


Fig. 48 Microscopic features of *Tricholoma orientifulvum* (holotype, KUN-HKAS107157). a Basidia. b Lamellar trama. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 μm , d = 20 μm . Cited from Xu et al. (2020).

30. *Tricholoma rubrocastaneum* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 42k, 49

Fungal Names: FN 572344

Etymology: rubrocastaneum referring to its red-brown pileus.

Diagnosis: Related to *T. populinum*, but differs by its red-brown to orange-brown pileus often with dark brown spots concentrated near margin and associations with *Quercus*, *Pinus*, *Picea* and *Abies*.

Type: CHINA. Yunnan Province, Lijiang, Yulong Naxi Autonomous County, Lijiang Alpine Botanic Garden, in a subalpine temperate forest dominated by *Quercus semicarpifolia*, mixed with *Pinus*, altitude 2700 m, 24 Aug. 2019, Jian-Wei Liu 1783 (holotype, KUN-HKAS134978).

Description: Basidioma medium-sized to large. Pileus 5–12 cm in diam., convex, plano-convex to applanate, center without umbo, often slightly depressed; surface dry or viscid when moist, red-brown (6B6–8) to orange-brown (5B6–8, 5C6–8), becoming paler towards margin, often with dark brown (5E6–8, 5F6–8) spots mainly concentrated near margin; margin involute, becoming deflexed when mature; context white (1A1) to dirty white (1A2, 1B2). Lamellae adnexed, white (1A1), dirty white (1B2) to cream (1A2), becoming brownish (5B3–5) to brown (5C5–7) when handed, damaged or old, very

crowded; edges white (1A1), brownish (5B3–5) to brown (5C5–7). Stipe 4–7 $\times$ 1–2 cm, cylindrical to clavate, white (1A1), brownish (5B3–5) to brown (5C5–7), fibrillose, base white (1A1), solid, exannulate. Odour like cucumber. Taste indistinct.

Basidiospores [90/4/4] (4–) $4.5\text{--}6.5$ (–7) $\times$ $3\text{--}4.5 \mu\text{m}$ (mean length = $5.4 \mu\text{m}$, mean width = $3.5 \mu\text{m}$), $Q = (1.2\text{--}) 1.32\text{--}1.81$ (–2), $Q_m = 1.56 \pm 0.15$, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 20–35 $\times$ 4–6 μm , clavate, 4-spored, hyaline; sterigmata 2–4 μm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 15–30 $\times$ 3–5 μm , poorly differentiated, cylindrical to clavate, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 μm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae 2–7 μm wide. Pileipellis is an ixocutis, strongly gelatinized, composed of irregularly to more or less radially arranged, 2–6 μm wide, thin-walled, yellow-brown filamentous hyphae; subpellis poorly differentiated, composed of radially arranged filamentous hyphae. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in subalpine temperate forests dominated by various trees, including *Quercus*, *Pinus*, *Picea* and *Abies*.

Known distribution: Known from Southwestern China.

Additional specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Daocheng County, Sangdui Village, in a forest with *Quercus semicarpifolia*, altitude 4000 m, 12 Sep. 2016, Xiao-Xia Ding 133 (KUN-HKAS97076); Ganzi Tibetan Autonomous Prefecture, Kangding, forest and altitude not recorded, 5 Sep. 2016, KD-LJW 34 (KUN-HKAS97827). Yunnan Province, Lijiang, Yulong Naxi Autonomous County, Lijiang Alpine Botanic Garden, in a forest dominated by *Quercus semicarpifolia*, mixed with *Pinus*, altitude 2700 m, 22 Sep. 2019, Jian-Wei Liu 2075 (KUN-HKAS134977); same location, in a forest dominated by *Quercus semicarpifolia*, altitude 2700 m, 30 Sep. 2019, Jian-Wei Liu 2186 (KUN-HKAS134979).

Notes: *Tricholoma rubrocastaneum* is characterized by its red-brown to orange-brown pileus often with dark brown spots concentrated near margin and ellipsoid to elongate basidiospores. This species is related to *T. populinum* in the five-gene phylogenetic analysis (Fig. 3), but the latter has a pileus without dark brown spots near margin and is

associated with *Populus* (Riva 1988; Christensen & Heilmann-Clausen 2013).

Tricholoma pessundatum can be confused, but differs by its slightly smaller basidiospores ($4.2\text{--}4.8 \times 2.8\text{--}3.1 \mu\text{m}$) and distribution in Europe and North America (Christensen & Heilmann-Clausen 2013). *Tricholoma stans*, *T. ustaloides* and *T. albobrunneum* are similar to *T. rubrocastaneum*. However, the former three species have no dark brown spots near pileal margin (Riva 1988; Christensen & Heilmann-Clausen 2013; Landry et al. 2022). In addition, *T. stans* has a more or less ribbed pileal margin (Riva 1988; Christensen & Heilmann-Clausen 2013; Landry et al. 2022). *Tricholoma ustaloides* possess relatively larger basidiospores ($6\text{--}7 \times 4.5\text{--}5.5 \mu\text{m}$, mean length = $6.3 \mu\text{m}$, mean width = $5 \mu\text{m}$) (this study). *Tricholoma albobrunneum* has slightly broader basidiospores with mean width ca. $4 \mu\text{m}$ and associated dominated with *Pinus* (Christensen & Heilmann-Clausen 2013; Landry et al. 2022; this study).

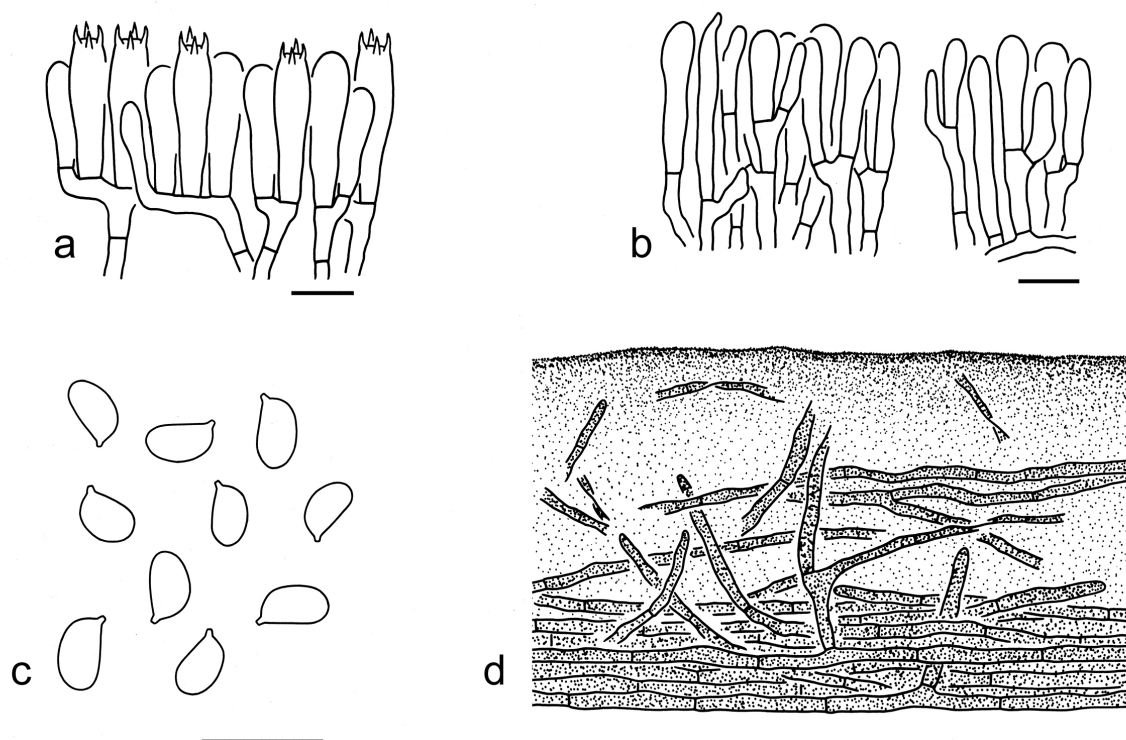


Fig. 49 Microscopic features of *Tricholoma rubrocastaneum*. a Hymenium and subhymenium (holotype, KUN-HKAS134978). b Marginal cells (holotype, KUN-HKAS134978). c Basidiospores (KUN-HKAS97076). d Pileipellis (KUN-HKAS134978). Scale bars: a–c = $10 \mu\text{m}$, d = $20 \mu\text{m}$.

31. *Tricholoma populinum* J.E. Lange, Dansk bot. Ark. 8(no. 3): 14 (1933). Figs. 421, 50

Description: Basidioma medium-sized to large. Pileus 4–12 cm in diam., convex to plano-convex, sometimes with a low, broad umbo; surface viscid when wet, shiny when dry, dark brown (6F6–8), brown (6D3–6, 5E6–8) to brownish (6C2–4, 5C3–5), often relatively paler towards margin, glabrous; margin involute when young, becoming inflexed to deflexed when mature; context white (1A1). Lamellae adnexed, dirty white (1B2), cream (2B2) to brownish (5B2–5), with brown (6C3–6) spots, crowded; edges dirty white (1B2) to brownish

(5B2–5), with brown (6C3–6) areas. Stipe 3–10 $\times$ 1–4 cm, clavate, brownish (6C3–6), fibrillose, basal mycelium white (1A1), solid, exannulate. Taste not recorded, with a strong farinaceous odour.

Basidiospores [$100/5/2$] ($4.5\text{--}5.7$ (-7.5) $\times$ ($3\text{--}3.5\text{--}4$ (-4.5) μm (mean length = $5.7 \mu\text{m}$, mean width = $3.8 \mu\text{m}$), $Q = (1.11\text{--}1.3\text{--}1.67$ (-1.88), $Q_m = 1.48 \pm 0.14$, ellipsoid to elongate, non-amylid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 20–35 $\times$ 5–7 μm , clavate, 4-spored, hyaline; sterigmata 3–6 μm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 10–30 $\times$ 3–7 μm , clavate, sometimes septate, thin-walled, yellow-brown, hyaline. Subhymenium composed of 2–4 μm wide filamentous hyphae,

clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae 2–5 µm wide. Pileipellis an ixo-cutis, strongly gelatinized, composed of radially arranged to interwoven, 2–6 µm wide, thin-walled, yellow-brown filamentous hyphae; subpellis poorly differentiated, composed of radially arranged, yellow-brown filamentous hyphae 3–8 µm wide.

Ecology: Solitary to scattered on soil in forests dominated with *Populus*.

Known distribution: Known from Europe (Grubisha et al. 2012; Christensen & Heilmann-Clausen 2013), North America (Grubisha et al. 2012; Bessette et al. 2013), Japan (Hongo 1988) and Southwestern China.

Specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, Waze Village, in a forest with *Populus*, altitude 3500 m, 18 Sep. 2017, Xiao-Xia Ding 315 (KUN-HKAS106656); same location, in a forest with *Populus*, altitude 3500 m, 18 Sep. 2017, Xiao-Xia Ding 316 (KUN-HKAS106657).

Notes: *Tricholoma populinum* is characterized by a dark brown to brown basidioma, ellipsoid to elongate basidiospores and is distributed in forests dominated with *Populus* (this study). Christensen & Heilmann-Clausen (2013) reported that European collections of this species have a faintly farinaceous odour that becomes strongly farinaceous after

cutting, resembling linseed oil or cucumber, and a mild, strongly farinaceous taste. However, in the Chinese collections of this species, taste was not recorded in the field, and the odour was strongly farinaceous.

This species is closely related to *T. fulvimarginatum* Ovrebo & Halling in the tree generated from the ITS sequences (Fig. 4). However, *T. fulvimarginatum*, originally described from Massachusetts, USA, has a lighter reddish brown pileus and not found in China (Bessette et al. 2013; Landry et al. 2022). *Tricholoma stans* is similar to *T. populinum*, but has a somewhat ribbed pileal margin and is distributed in coniferous, broad-leaved or mixed forests (Riva 1988; Christensen & Heilmann-Clausen 2013; this study). *Tricholoma albobrunneum* is also similar to it, but differs by a white zone at the top of stipe and distributions in forests dominated by *Pinus* (Christensen & Heilmann-Clausen 2013; Landry et al. 2022). *Tricholoma ustaloides* is somewhat comparable, but can be separated by a white zone at the top of stipe, relatively larger basidiospores (6–7 × 4.5–5.5 µm, mean length = 6.3 µm, mean width = 5 µm) and associations with Fagaceae and Pinaceae (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013; this study).

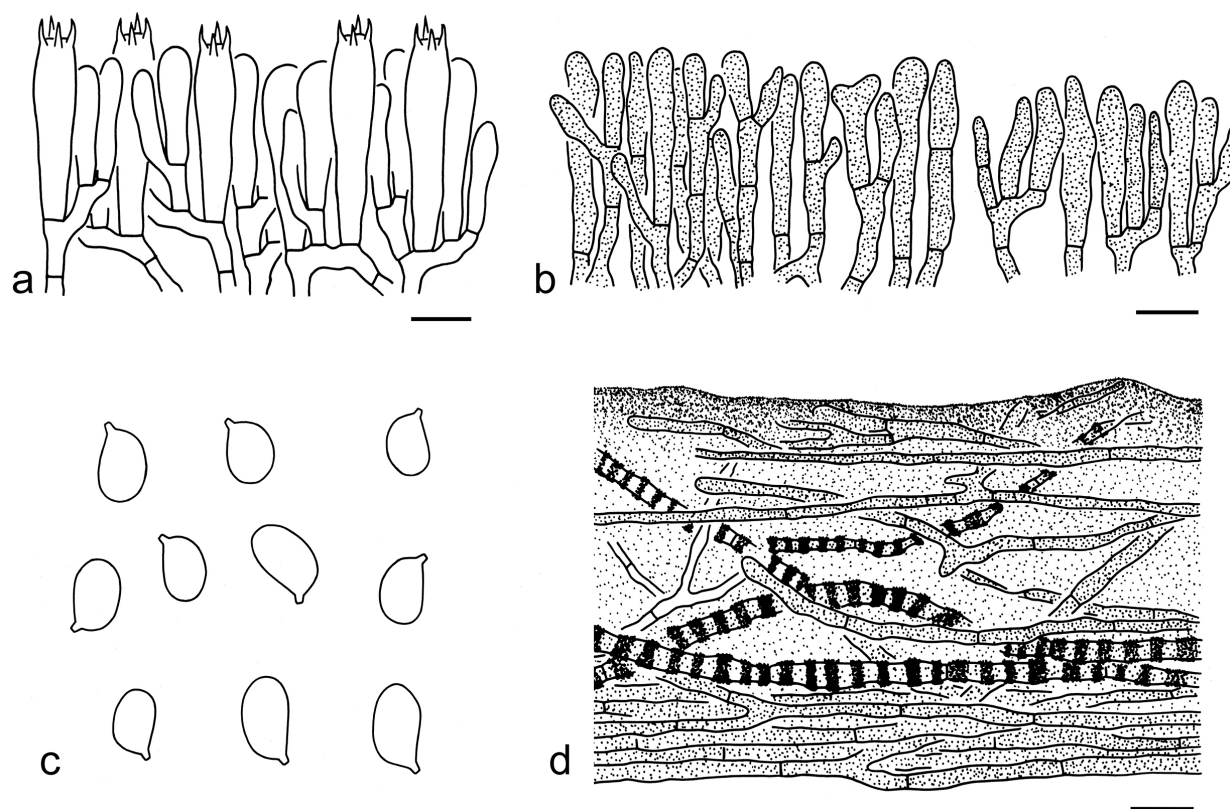


Fig. 50 Microscopic features of *Tricholoma populinum* (KUN-HKAS106657). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm.

32. *Tricholoma psammopus* (Kalchbr.) Quél., Mém. Soc. Émul. Montbéliard, Sér. 2 5: 433 (1875). Figs. 42m, 51

Basionym: *Agaricus psammopus* Kalchbr., Icon. Sel. Hymenomyc. Hung. (Budapest) 1: tab. 3 (1873).

Description: Basidioma small to medium-sized. Pileus 2–7 cm in diam., convex to plano-convex, sometimes with a broad low umbo; surface dry, yellowish (3A2–4) to yellowish

brown (3B3–5), covered with yellowish brown (3B3–5) to brown (4B4–6) fibrillose-felty to fibrillose squamules; margin involute to deflexed; context white (1A1) to cream (1A2). Lamellae adnate, cream (1A2–4) to brownish (5B3–5), often with brown (6A2–4) stains, subclose; edges brownish (5B3–5) to brown (6A2–4). Stipe 5–12 × 0.5–1 cm, subcylindrical to clavate, dirty white (1A1, 1B1) background covered with brownish (5B3–5) fibrillose squamules, often white (1A1) at apical part, stuffed to hollow, exannulate. Taste and odour not recorded.

Basidiospores [60/2/2] 5–6 (–6.5) × 4–5 µm (mean length = 5.4 µm, mean width = 4.2 µm), $Q = (1.04\text{--}) 1.16\text{--}1.37$ (–1.5), $Q_m = 1.26 \pm 0.09$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 25–35 × 5–8 µm, clavate, 4-spored, hyaline; sterigmata 3–5 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 20–30 × 3–6 µm, poorly differentiated, clavate to subclavate, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 µm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled, filamentous, cylindrical to subellipsoid hyphae 3–25 µm wide. Pileipellis a cutis, composed of radially to sometimes erected arranged, 3–8 µm wide, thin-walled, yellow-brown filamentous hyphae; subpelis made of radially arranged, colorless, filamentous to cylindrical hyphae 5–25 µm wide. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in coniferous forests.

Distribution: Known from Europe, East Asia (Japan, and Northwestern and Northern China).

Specimens examined: CHINA. Gansu Province, Pingliang, in a coniferous forest, altitude 2160 m, 15 Jul. 2016, Xue-Tai Zhu 1797 (KUN-HKAS106314); same location, Xue-Tai Zhu 1536 (KUN-HKAS107579). Inner Mongolia, Hulunbuir, Genhe, altitude 840 m, 17 Aug. 2017, Gang Wu 2307 (KUN-HKAS106302).

Notes: *Tricholoma psammopus* is characterized by a yellowish to yellowish brown, fibrillose-felty pileus and broadly ellipsoid to ellipsoid basidiospores (this study). Christensen & Heilmann-Clausen (2013) reported that the taste of this species is initially mild, later becoming bitterish-astringent, but taste was not recorded in the Chinese collections.

Phylogenetically, it is closely related to the clade formed by *T. imbricatum*, *T. vaccinum* and *T. rufobrunneum* (Fig. 3). However, the latter three species can easily be separated by their dark brown to orange brown basidioma. In addition, *T. imbricatum* has longer basidiospores (5.5–7 × 4–5 µm, mean length = 6.2 µm, mean width = 4.2 µm) (this study). *Tricholoma vaccinum* possesses longer basidiospores (6–7.5 × 4.5–6 µm, mean length = 6.7 µm, mean width = 5 µm), conspicuous and gelatinized cheilocystidia, and a pileipellis with inflated cells (this study). *Tricholoma rufobrunneum* has larger basidiospores (6–7.5 × 5–6 µm, mean length = 6.7 µm, mean width = 5.2 µm) and a gelatinized pileipellis with cylindrical hyphae (this study).

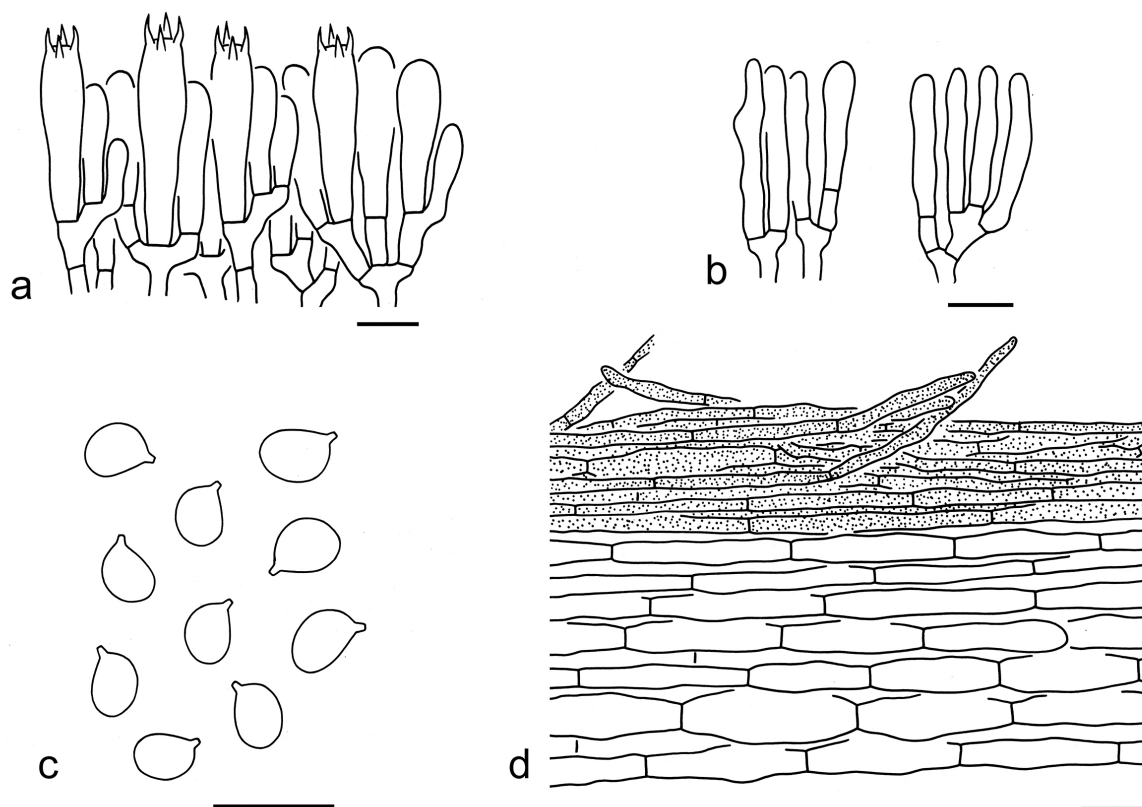


Fig. 51 Microscopic features of *Tricholoma psammopus* (KUN-HKAS107579). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm.

Morphologically, *T. sinoacerbum*, *T. acerbum* (Bull.) Quél. and *T. apium* Jul. Schäff. are similar to *T. psammopus*. However, *T. sinoacerbum* differs by its yellow-brown pileus without obvious squamules and associations dominated with broad-leaved trees (Hosen et al. 2016). *Tricholoma acerbum* has a much more robust and shorter stipe, more crowded lamellae and forms mycorrhizal relationships with *Quercus*, *Castanea* and other deciduous trees (Riva 1988; Christensen & Heilmann-Clausen 2013). *Tricholoma apium* possesses a much more robust and shorter stipe, relatively smaller basidiospores ($3.4\text{--}5.6 \times 2.9\text{--}4.6\text{ }\mu\text{m}$, average $4.3\text{--}5 \times 3.5\text{--}4\text{ }\mu\text{m}$) and a strong smell of lovage (Riva 1988; Christensen & Heilmann-Clausen 2013).

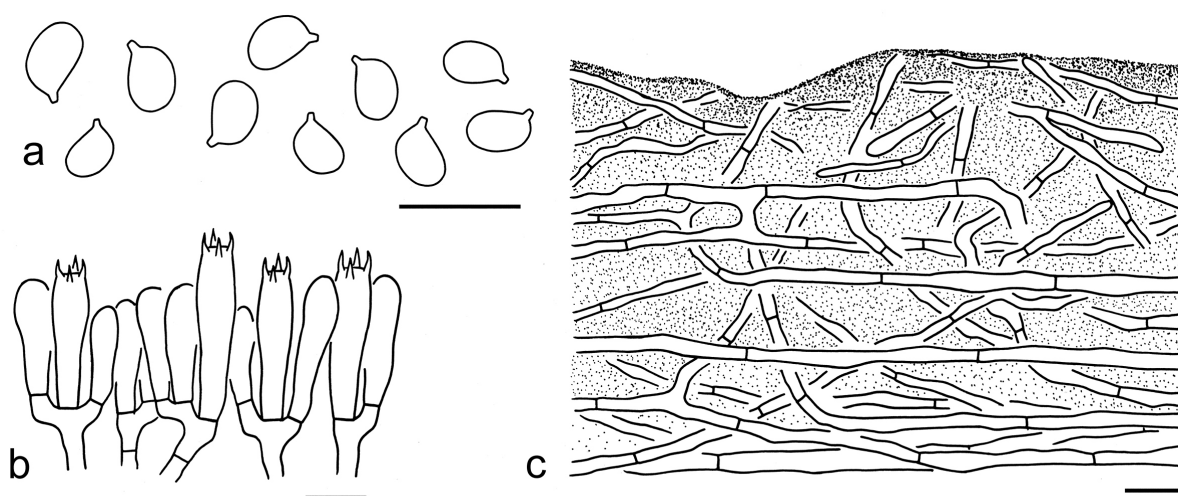


Fig. 52 Microscopic features of *Tricholoma roseoacerbum* (KUN-HKAS88046). a Basidiospores. b Hymenium and subhymenium. c Pileipellis. Scale bars: a, b = 10 μm , c = 20 μm .

Basidiospores [20/1/1] (4–) $4.5\text{--}5.5$ (–6) $\times 3\text{--}4\text{ }\mu\text{m}$ (mean length = 5 μm , mean width = 3.6 μm), $Q = 1.25\text{--}1.57$, $Q_m = 1.4 \pm 0.1$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $20\text{--}30 \times 5\text{--}7\text{ }\mu\text{m}$, clavate, 4-spored, hyaline; sterigmata $3\text{--}5\text{ }\mu\text{m}$ long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia not observed. Subhymenium composed of $2\text{--}4\text{ }\mu\text{m}$ wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled, cylindrical, clavate to filamentous hyphae $2\text{--}10\text{ }\mu\text{m}$ wide. Pileipellis gelatinized, composed of loosely arranged, interwoven to more or less erectly arranged, $2\text{--}5\text{ }\mu\text{m}$ wide, thin-walled, colorless filamentous hyphae; subpellis non-gelatinized, made of radially arranged, colorless filamentous hyphae $5\text{--}7\text{ }\mu\text{m}$ wide. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in mixed forests with *Pinus*, *Quercus* and *Betula*.

Known distribution: Known from Europe (Christensen & Heilmann-Clausen 2013), North America (Bessette et al. 2013), East Asia (Japan and Southwestern China).

Specimen examined: CHINA. Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-La, Namucuo, in a forest with *Pinus*, *Quercus* and *Betula*, altitude 3400 m, 25 Aug. 2014, Qi Zhao 2279 (KUN-HKAS88046).

Notes: *Tricholoma roseoacerbum* is well recognized by a pinkish to pinkish brown pileus becoming whitish to strongly

33. *Tricholoma roseoacerbum* A. Riva, Mycol. helv. 1(3): 179 (1984). Figs. 42n, 52

Replaced synonym: *Tricholoma pseudoimbricatum* var. *roseobrunneum* A. Riva, Schweiz. Z. Pilzk. 57(1): 2 (1979).

Description: Basidioma small to medium-sized. Pileus $3\text{--}9\text{ cm}$ in diam., convex, without an umbo or a depression at center; surface viscid when wet, pinkish (7A2–4) to pinkish brown (6B3–6) at center, whitish (1A1, 5A2) towards margin; with white (1A1) fibrillose squamules; margin strongly involute; context white (1A1). Lamellae sinuate to emarginate, cream (2A2–4), crowded; edges cream (2A2–4). Stipe $4\text{--}6 \times 1\text{--}2.5\text{ cm}$, solid, clavate, white (1A1), with pinkish brown (6A2–4) hues, basal mycelium white (1A1), exannulate. Taste and odour not recorded.

involute towards margin, broadly ellipsoid to ellipsoid basidiospores and associations with coniferous and broad-leaved trees (this study). Christensen & Heilmann-Clausen (2013) recorded this species as having a weak odour and a farinaceous to slightly bitterish taste, but these characters were not recorded in the field for the Chinese collections.

This species is sister to *T. manzanitae* T.J. Baroni & Ovrebo in the phylogenetic analysis based on the ITS sequences (Fig. 4). However, *T. manzanitae* has relatively larger basidiospores ($5\text{--}7 \times 4\text{--}5.5\text{ }\mu\text{m}$) (Bessette et al. 2013). *Tricholoma acerbum* is similar to *T. roseoacerbum*, but differs by its relatively paler, often cream to buff pileus and associations with deciduous trees (Riva 1988; Christensen & Heilmann-Clausen 2013).

34. *Tricholoma rubiginosum* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 42o, 53a, 54

Fungal Names: FN 572346

Etymology: *rubiginosum* = rust-colored, referring to its white lamellae with rust-colored stains when old.

Diagnosis: Related to *T. fulvomaculatum*, but can be separated by its white lamellae, subglobose to broadly ellipsoid basidiospores with $Q = 1.08\text{--}1.29$ and a non-gelatinized pileipellis.



Fig. 53 Fresh basidiomata of the species in *Tricholoma*. a *T. rubiginosum* (holotype, KUN-HKAS134980). b *T. rufobrunneum* (holotype, KUN-HKAS90808). c *T. sinoacerbum* (KUN-HKAS134981). d *T. stans* (KUN-HKAS87940). e *T. ustaloides* (KUN-HKAS74246). f *T. vaccinum* (KUN-HKAS87929). g *T. bakamatsutake* (KUN-HKAS106301). h *T. xizangense* (holotype, KUN-HKAS91028). i *T. fulvocastaneum* (KUN-HKAS134988). j *T. matsutake* (KUN-HKAS87930). k, l *T. muscarioides* (KUN-HKAS134994). m *T. muscarium* (KUN-HKAS106307). n *T. olivaceiceps* (holotype, KUN-HKAS101280). o *T. sinense* (holotype, KUN-HKAS69669).

Type: CHINA. Yunnan Province, Baoshan, Tengchong, in a broad-leaved forest, altitude 2000 m, 25 Jul. 2022, GLG-FXP221 (holotype, KUN-HKAS134980).

Description: Basidioma medium-sized. Pileus 5–8 cm in diam., convex to plano-convex, without obviously umbo or depression at center; surface viscid when wet, orange-brown (6D6–8) to brown (6B3–5), sometimes dark brown (6E6–8) at center when old, glabrous or covered with orange-brown (6D6–8), fibrillose squamules; margin involute; context dirty white (1B1). Lamellae adnate, white (1A1), with brown (6C5–7) stains or spots when old, crowded; edges white (1A1), with brown (6C5–7) stains. Stipe 8–12 × 1–2 cm, slender, cylindrical, white (1A1) background with dark brown (6E6–8), orange-brown (6D6–8) to brown (6B3–5), fibrillose squamules, basal mycelium white (1A1), exannulate. Taste and odour not recorded.

Basidiospores [20/1/1] 5.5–7 × 4.5–6.5 µm (mean length = 6.1 µm, mean width = 5.1 µm), Q = (1.03–) 1.08–1.29, Qm = 1.19 ± 0.07, subglobose to broadly ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 25–45 × 6–8 µm, clavate, 4-spored, hyaline; sterigmata 3–5 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 15–40 × 2–5 µm, narrowly clavate, clavate, fusiform to irregular-shaped, sometimes with a long narrow slender neck or a capitate apex,

sometimes septate, colorless to brownish. Subhymenium composed of 2–4 µm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled, ellipsoid, clavate to filamentous hyphae 4–15 µm wide. Pileipellis a cutis, non-gelatinized, composed of radially arranged, interwoven to more or less erected, 2–10 µm wide, thin-walled, brown filamentous hyphae; subpellis poorly differentiated, brown or colorless. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in subtropical broad-leaved forests.

Known distribution: Known from Southwestern China.

Additional specimen examined: CHINA. Yunnan Province, Dali Bai Autonomous Prefecture, Dali, in a broad-leaved forest, altitude 2300 m, 1 Sep. 2017, Gang Wu 2467 (KUN-HKAS106303).

Notes: *Tricholoma rubiginosum* is characterized by its orange-brown pileus, white lamellae with brown spots when old, subglobose to broadly ellipsoid basidiospores (5.5–7 × 4.5–6.5 µm) and associations with broad-leaved trees. *Tricholoma fulvomaculatum* is related to this species in our four-gene phylogenetic analysis (Fig. 3), but has yellowish lamellae, broadly ellipsoid to ellipsoid basidiospores with Q = 1.2–1.55 and a gelatinized pileipellis (this study).

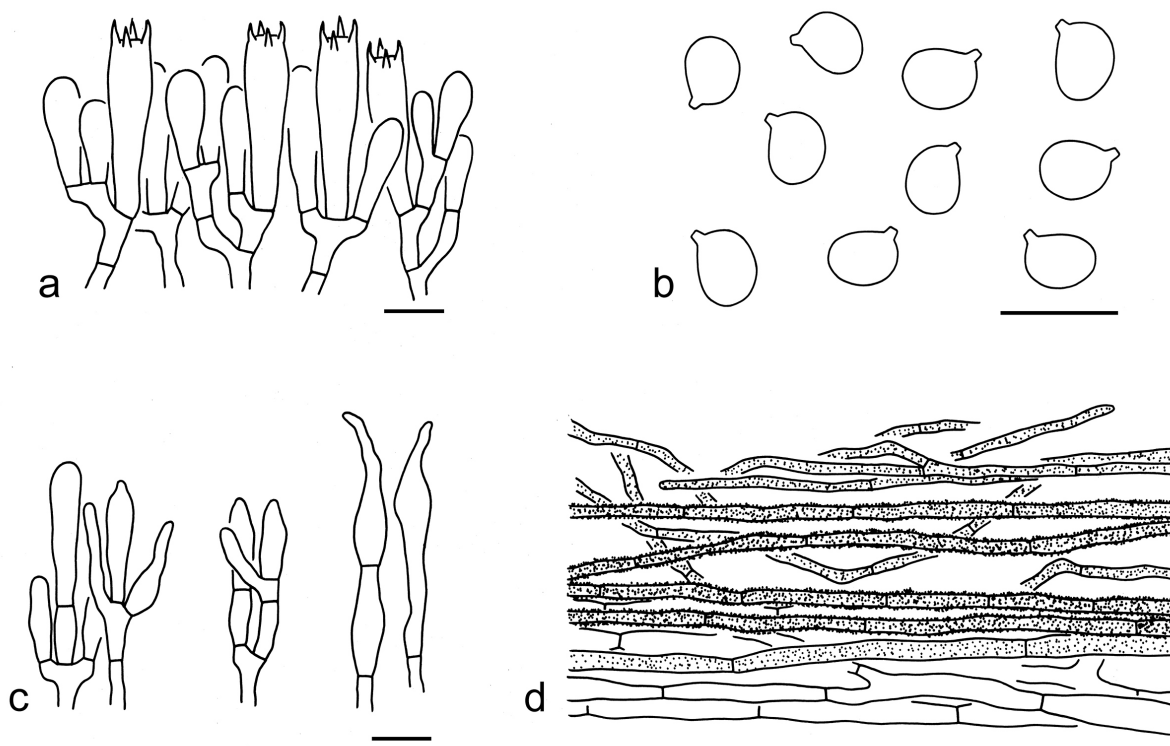


Fig. 54 Microscopic features of *Tricholoma rubiginosum* (holotype, KUN-HKAS134980). a Hymenium and subhymenium. b Basidiospores. c Marginal cells. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm.

Tricholoma castaneiceps can be confused with *T. rubiginosum*, but differs by its pale sulphur-yellow lamellae, relatively narrower and ellipsoid basidiospores (5–7 × 4–5 µm), and a gelatinized pileipellis. *Tricholoma orientifulvum* and *T. fulvum* are similar to *T. rubiginosum*. However, *T. orientifulvum* can be separated by its olivaceous yellow to yellow-brown lamellae, narrower basidiospores with mean

width ca. 4.2 µm and a gelatinized basidiospores. *Tricholoma fulvum* has pale yellow lamellae, broadly ellipsoid to ellipsoid basidiospores (4.7–7.4 × 3.6–6.1 µm), a gelatinized pileipellis, and associations with *Betula*, *Abies* and *Picea* (Christensen & Heilmann-Clausen 2013; Landry et al. 2022). *Tricholoma ustale* (Fr.) P. Kumm. and *T. ustaloides* are also similar to *T. rubiginosum*. However, *T. ustale* has cream to warm buff

lamellae, broadly ellipsoid to ellipsoid basidiospores ($5.3\text{--}7.7 \times 4.4\text{--}6.4 \mu\text{m}$), and a gelatinized pileipellis (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013). *Tricholoma ustaloides* can be distinguished from *T. rubiginosum* by its broadly ellipsoid to ellipsoid basidiospores ($6\text{--}7 \times 4.5\text{--}5.5 \mu\text{m}$) and a gelatinized pileipellis (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013; this study).

35. *Tricholoma rufobrunneum* X.X. Ding et al., Mycol. Progr. 21(37): 8 (2022). Figs. 53b, 55

Description: Basidioma medium-sized to large. Pileus 5–12 cm in diam., convex to plano-convex, obtusely umbonate; surface dry or viscid when wet, dark brown (6E6–8) to orange-brown (6C5–8), densely covered with dark brown (6E6–8), fibrillose-tomentose squamules; margin involute; context dirty white (1B1). Lamellae sinuate, cream (1A2) to yellowish (2A2–4), with brown (7D5–7) stains when damaged or old, crowded to subclose; edges yellowish (2A2–4). Stipe 5–9 $\times$ 0.8–1.5 cm, cylindrical to subcylindrical, brownish (5B3–5) to brown (5C5–7), often yellowish (1A2) at apical part, covered

with concolorous fibrillose squamules. Taste and odour not recorded.

Basidiospores [40/2/1] ($5.5\text{--}6\text{--}7.5 \times (4.5\text{--}) 5\text{--}6 \mu\text{m}$ (mean length = $6.7 \mu\text{m}$, mean width = $5.2 \mu\text{m}$), $Q = (1.09\text{--}) 1.17\text{--}1.4$ (–1.5), $Q_m = 1.29 \pm 0.1$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $20\text{--}30 \times 6\text{--}10 \mu\text{m}$, clavate, 4-spored, sometimes 2-spored, colorless to brownish, hyaline; sterigmata $3\text{--}6 \mu\text{m}$ long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia $10\text{--}90 \times 3\text{--}10 \mu\text{m}$, clavate, cylindrical to subcylindrical, sometimes septate, thin-walled, colorless or brownish, hyaline. Subhymenium composed of $2\text{--}5 \mu\text{m}$ wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae $2\text{--}10 \mu\text{m}$ wide. Pileipellis an ixo-cutis, slightly gelatinized, composed of radially arranged, interwoven to more or less erectly arranged, thin-walled, brownish to brown cylindrical hyphae ($30\text{--}100 \times 10\text{--}25 \mu\text{m}$); subpellis poorly differentiated, non-gelatinized, composed of radially arranged, colorless or brownish hyphae $10\text{--}20 \mu\text{m}$ wide. Clamps absent in all parts of basidioma.

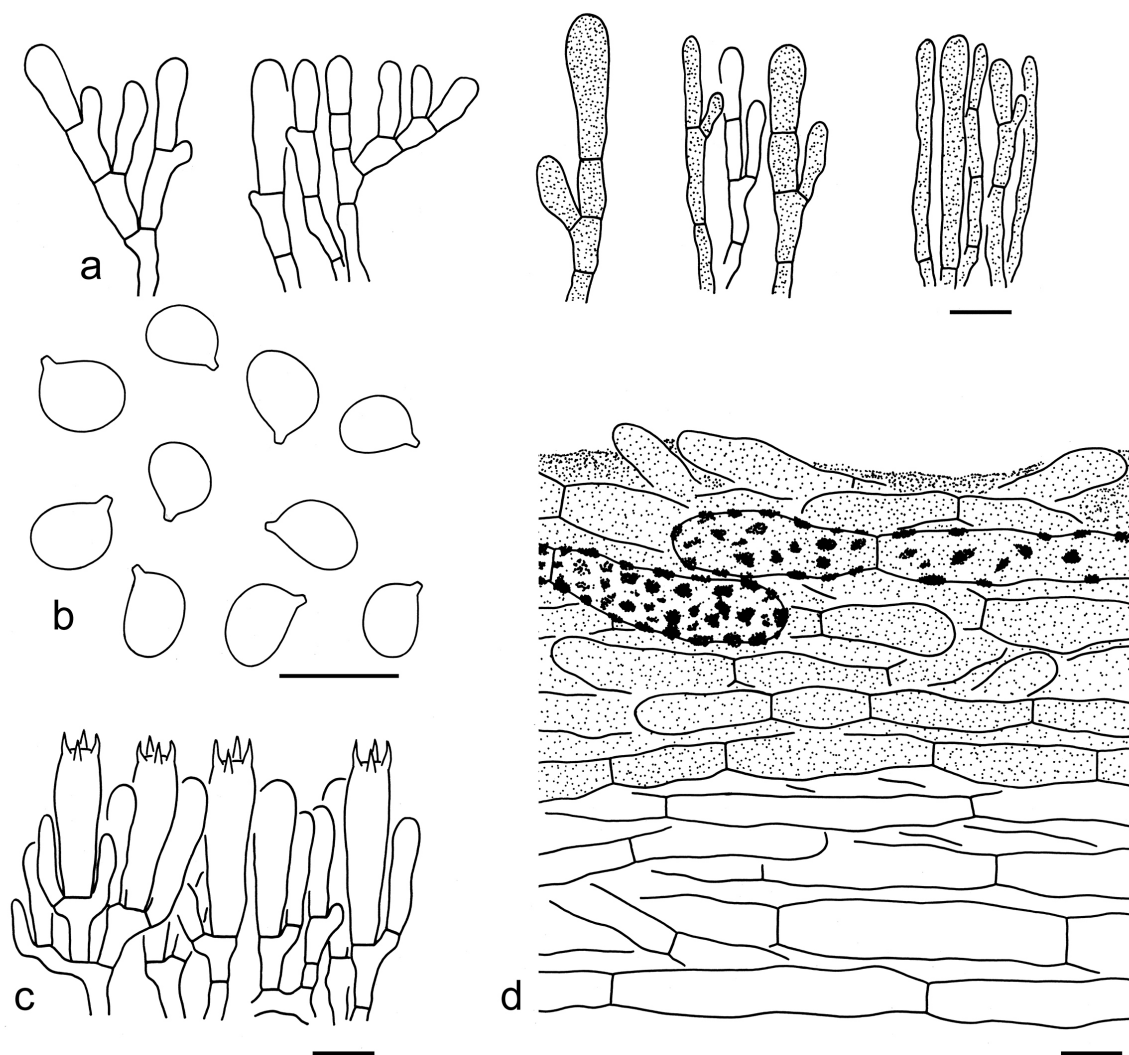


Fig. 55 Microscopic features of *Tricholoma rufobrunneum* (holotype, KUN-HKAS90808). a Marginal cells. b Basidiospores. c Hymenium and subhymenium. d Pileipellis. Scale bars: a–c = $10 \mu\text{m}$, d = $20 \mu\text{m}$. Cited from Ding et al. (2022).

Ecology: Solitary to scattered on soil in subalpine temperate forests with *Quercus*, *Abies*, *Picea* and *Salix*.

Known distribution: Known from Southwestern China.

Specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Jiulong County, Tanggu Village, in a mixed forest with *Quercus*, *Abies*, *Picea*, *Salix*, adjacent meadow and boggy marsh, altitude 3600 m, 19 Jul. 2005, Zai-Wei Ge 574 (KUN-HKAS49069). Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-La, Tian Lake, in a forest dominated by *Abies*, altitude 3700 m, 9 Jul. 2014, Jian-Wei Liu 14 (holotype, KUN-HKAS90808).

Notes: *Tricholoma rufobrunneum* is characterized by an orange-brown, fibrillose-tomentose pileus, cream to yellowish lamellae when young, broadly ellipsoid to ellipsoid basidiospores and a gelatinized pileipellis with cylindrical hyphae (Ding et al. 2022; this study). It is closely related to *T. imbricatum* and *T. vaccinum* (Fig. 3). However, *T. imbricatum* differs by its ellipsoid to elongate basidiospores with $Q = 1.2\text{--}1.75$, and a non-gelatinized pileipellis composed of filamentous hyphae (this study). *Tricholoma vaccinum* has gelatinized cheilocystidia and a non-gelatinized pileipellis (this study). *Tricholoma fulvum* and *T. fulvomaculatum* share cream to yellowish lamellae and can be confused, but these two species have indistinct squamules on pileus and gelatinized pileipellis with filamentous hyphae (Christensen & Heilmann-Clausen 2013; Ding et al. 2022; Landry et al. 2022). Moreover, *T. fulvum* has a somewhat ribbed pileal margin when mature (Christensen & Heilmann-Clausen 2013; Landry et al. 2022). *Tricholoma imbricatum* is similar to *T. rufobrunneum*. For comparison, see notes under that name.

36. *Tricholoma sinoacerbum* T.H. Li et al., *Mycoscience* 57 (4): 234 (2016). Figs. 53c, 56

Description: Basidioma small, medium-sized to large. Pileus 3–15 cm in diam., at first convex to plano-convex, then applanate to plano-concave, slightly umbonate at center; surface dry or viscid when wet, yellow-brown (3A2–4), brown (5C4–6) to brownish (5B4–6); margin involute to deflexed when young, becoming straight to reflexed when mature; context white (1A1) to cream (1A2). Lamellae sinuate to subdecurrent, dirty white (1B1) to cream (1A2), with brownish (5C4–6) stains when damaged or old, crowded; edges cream (1A2) to brownish (5C4–6). Stipe 3–11 × 0.7–3 cm, clavate to cylindrical, dirty white (1A1, 2A2, 2B2), covered with brownish (3B3–5) to brown (3C3–5) fibrillose squamules, basal mycelium white (1A1), solid, exannulate. Odour fragrant. Taste bitter.

Basidiospores [80/3/3] (4–) 4.5–5.5 (–6) × 3–4 µm (mean length = 5 µm, mean width = 3.7 µm), $Q = 1.18\text{--}1.5$ (–1.67), $Q_m = 1.35 \pm 0.11$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 20–30 × 5–7 µm, clavate, 4-spored, hyaline; sterigmata 3–5 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia not observed. Subhymenium composed of 2–4 µm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae 4–10 µm wide. Pileipellis strongly gelatinized, composed of radially to more or less erectly arranged, 2–5 µm wide, colorless filamentous hyphae; subpellis not gelatinized, made of interwoven to radially arranged filamentous hyphae 3–7 µm wide. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil, mainly in broad-leaved forests, occasionally in coniferous forests.

Known distribution: Known from Northeastern, Central, Southern and Southwestern China.

Specimens examined: CHINA. Anhui Province, Lu'an, Jinzhai County, in a mixed forest with Fagaceae and Pinaceae, altitude 940 m, Yan-Jia Hao 1686 (KUN-HKAS134981); Huangshan, forest type not recorded, altitude 1625 m, 12 Sep. 2018, Ting Guo 1401 (KUN-HKAS136950). Hubei Province, Yichang, Shennongjia Forest District, Muyu Town, in a forest with *Quercus*, *Acer* and *Betula*, altitude 1500 m, Qi Zhao 1454 (KUN-HKAS78713); same district, Hongping Town, in a forest with *Quercus*, altitude 1850 m, 15 Jul. 2012, Qi Zhao 1547 (KUN-HKAS78806). Liaoning Province, Dandong, Kuandian Man Autonomous County, Sipingjie Village, in a broad-leaved forest, altitude 600 m, 29 Aug. 2018, Xiao-Xia Ding 378 (HKAS105388); same location, in a broad-leaved forest, altitude 600 m, 29 Aug. 2018, Xiao-Xia Ding 379 (KUN-HKAS105389). Yunnan Province, Baoshan, Longling County, Santai Village, in a broad-leaved forest, altitude 2000 m, 17 Jun. 2014, Xiao-Bin Liu 334 (KUN-HKAS86986); Kunming, Panlong District, Aziying Village, in a forest with *Quercus*, altitude 2000 m, 12 Jul. 2018, Xiao-Xia Ding 339 (KUN-HKAS105349); Lijiang, Yulong Naxi Autonomous County, Lijiang Alpine Botanic Garden, in a broad-leaved forest, altitude 2700 m, 22 Sep. 2019, Jian-Wei Liu 2089 (KUN-HKAS122161); Nujiang Lisu Autonomous Prefecture, Lushui, Luzhang Town, in a forest with *Pinus yunnanensis* and *Keteleeria fortunei*, altitude 2000 m, 7 Aug. 2010, Qing Cai 307 (KUN-HKAS67869).

Notes: *Tricholoma sinoacerbum* is characterized by its yellow-brown pileus, dirty white and very crowded lamellae, bitter taste, broadly ellipsoid to ellipsoid basidiospores and associations with broad-leaved trees (Hosen et al. 2016; this study). In the five-gene phylogenetic analysis (Fig. 3), this species is sister to the clade formed by *T. roseoacerbum* and *T. orienticolossum*. However, *T. roseoacerbum* has a pinkish to pinkish brown pileus with a whitish, involute margin and is distributed in mixed forests (this study). *Tricholoma orienticolossum* can be easily separated from *T. sinoacerbum* by its large to very large basidioma with a red-brown pileus, larger basidiospores (8.5–10 × 6.5–7.5 µm) and a non-gelatinized pileipellis (this study).

Tricholoma psammopus is similar to *T. sinoacerbum*. For comparison, see notes under that name. The pileus color of *T. sinoacerbum* can be comparable to *T. acerbum*. However, *T. acerbum* has a relatively larger, robust basidioma and an involute, ribbed pileal margin (Riva 1988; Christensen & Heilmann-Clausen 2013).

37. *Tricholoma stans* (Fr.) Sacc., *Syll. fung. (Abellini)* 5: 94 (1887). Figs. 53d, 57

Basionym: *Agaricus pessundatus* subsp. *stans* Fr., C. r. Congr. Soc. sav., Paris Dépts, Sec. Sci. 1(3): 25, tab. 28 (1869).

Description: Basidioma medium-sized to large. Pileus 4–14 cm in diam., at first convex, then plano-convex to applanate, without obvious umbo or depression at center; surface viscid, orange-brown (5B4–7), often relatively paler, sometimes ribbed towards margin, covered with orange-brown (5B4–7), fine squamules; margin involute to deflexed; context white (1A1). Lamellae adnate to sinuate, at first white (1A1) to cream (1A2), later brownish (5C5–7), crowded; edges

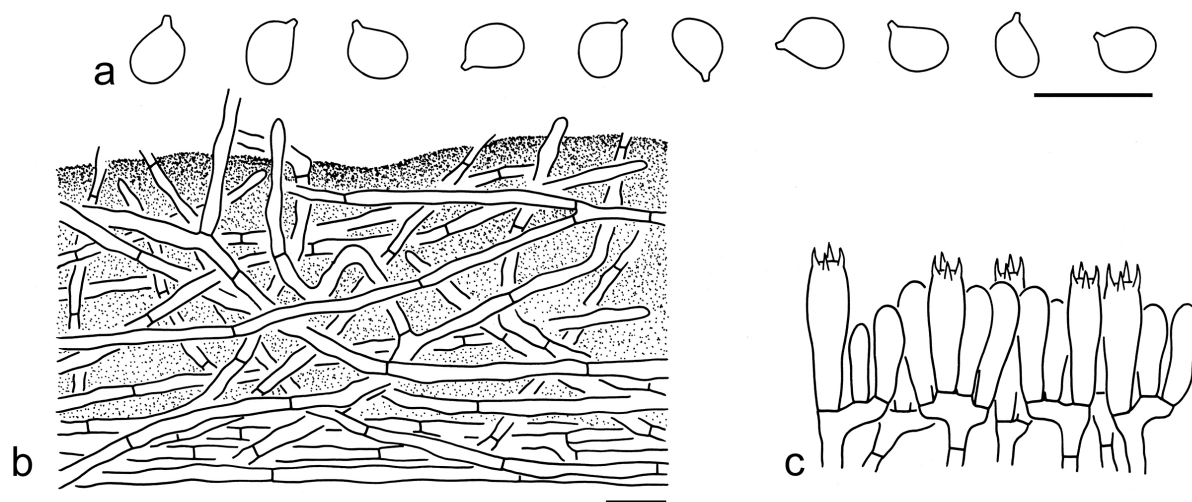


Fig. 56 Microscopic features of *Tricholoma sinoacerbum* (KUN-HKAS105349). a Basidiospores. b Pileipellis. c Hymenium and subhymenium. Scale bars: a, c = 10 μ m, b = 20 μ m.

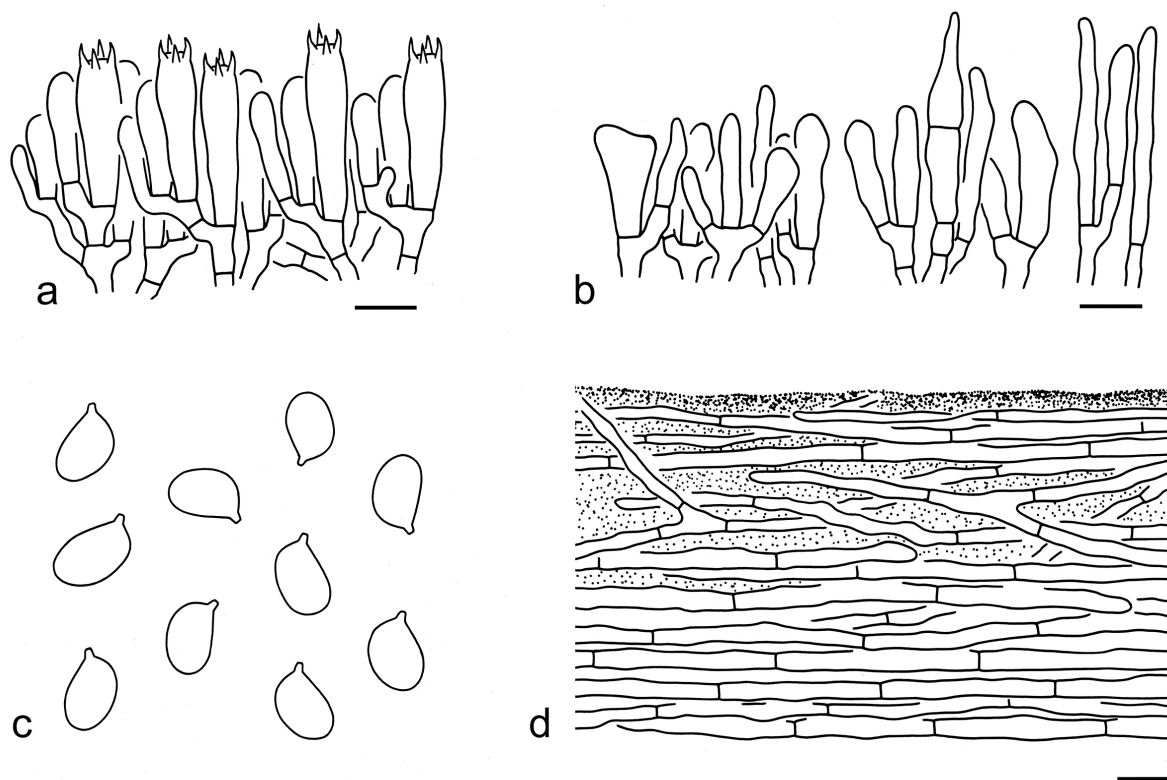


Fig. 57 Microscopic features of *Tricholoma stans* (KUN-HKAS99382). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 μ m, d = 20 μ m

brownish (5C5–7). Stipe 3–10 $\times$ 1–2.5 cm, cylindrical to clavate, brownish (5C5–7) to orange-brown (5B4–7), covered with concolorous, fibrillose squamules, stuffed, exannulate. Taste not recorded. Odour with slightly almond.

Basidiospores [92/5/5] 5–6.5 (–7.5) $\times$ 3.5–4.5 μ m (mean length = 5.7 μ m, mean width = 4 μ m), $Q = 1.2$ –1.63 (–1.88), $Q_m = 1.42 \pm 0.13$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively

large. Basidia 20–35 $\times$ 5–8 μ m, clavate, 4-spored, hyaline; sterigmata 3–5 μ m long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 20–30 $\times$ 3–10 μ m, poorly differentiated, clavate, cylindrical to filamentous or irregular-shaped, sometimes septate, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 μ m wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae 2–20 μ m wide.

Pileipellis is an ixo-cutis with transition to an ixo-trichoderm at regular intervals, gelatinized, composed of 2–7 μm wide, thin-walled, colorless to brownish filamentous hyphae, often radially arranged, but becoming interwoven to more or less vertically arranged at regular intervals; subpellis poorly differentiated, composed of radially arranged, non-gelatinized, 4–10 μm wide filamentous hyphae. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in coniferous, broad-leaved or mixed forests.

Known distribution: Known from Europe and Southwestern China.

Specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, Gonggashan Village, in a subalpine temperate forest with *Quercus*, altitude 3550 m, 5 Sep. 2016, Bang Feng 29 (KUN-HKAS99382); same location, in a subalpine temperate forest with *Quercus*, altitude 3550 m, 5 Sep. 2016, KD-WPM 31 (KUN-HKAS98286). Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-La, Bitahai, in a subalpine temperate forest with Pinaceae and Fagaceae, altitude 3600 m, 20 Aug. 2014, Qi Zhao 2174 (KUN-HKAS87940).

Notes: *Tricholoma stans* is characterized by an orange-brown pileus with a somewhat ribbed margin when mature and broadly ellipsoid to ellipsoid basidiospores (this study). In Europe, this species is exclusively known from coniferous hosts (Christensen & Heilmann-Clausen 2013). In China, we discovered that it may also be collected in broad-leaved or mixed forests (this study). Christensen & Heilmann-Clausen (2013) reported the smell as indistinct, becoming distinctly

farinaceous after cutting, and the taste as farinaceous, mild to slightly bitter. For the Chinese collections examined in the field, taste was not recorded, and the odour was slightly almond-like.

Tricholoma mcneilii Lebeuf et al. is related to *T. stans* in the phylogenetic tree inferred from the ITS sequences (Fig. 4), but differs by its subglobose to broadly ellipsoid basidiospores (Trudell et al. 2022). *Tricholoma populinum* and *T. rubrocastaneum* may be confused with *T. stans*. For comparison, see notes under that name. *Tricholoma ustaloides* is similar to it, but has a non-ribbed pileus when mature and slightly larger basidiospores ($6\text{--}7 \times 4.5\text{--}5.5 \mu\text{m}$, mean length = 6.3 μm , mean width = 5 μm) (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013; this study).

38. *Tricholoma ustaloides* Romagn., Bull. Soc. nat. Oyonnax 8: 76 (1954). Figs. 53e, 58

Description: Basidioma medium-sized. Pileus 5–8 cm in diam., convex to plano-convex, without obvious umbo or depression at center; surface viscid when wet, orange-brown (6C4–8), darker at center; margin involute; context white (1A1). Lamellae adnexed to sinuate, dirty white (1A2), with brown (5F6–8) stains or spots when damaged or old, crowded; edges dirty white (1A1–2), with brown (5F6–8) stains. Stipe 4–8 $\times$ 1–2 cm, subcylindrical, orange-brown (6C4–8) to grey-brown (5F6–8), often white (1A1) to dirty white (1B1) at apical part, fibrillose, with a faint, poorly demarcated ring zone, basal mycelium white (1A1), stuffed. Taste and odour not recorded.

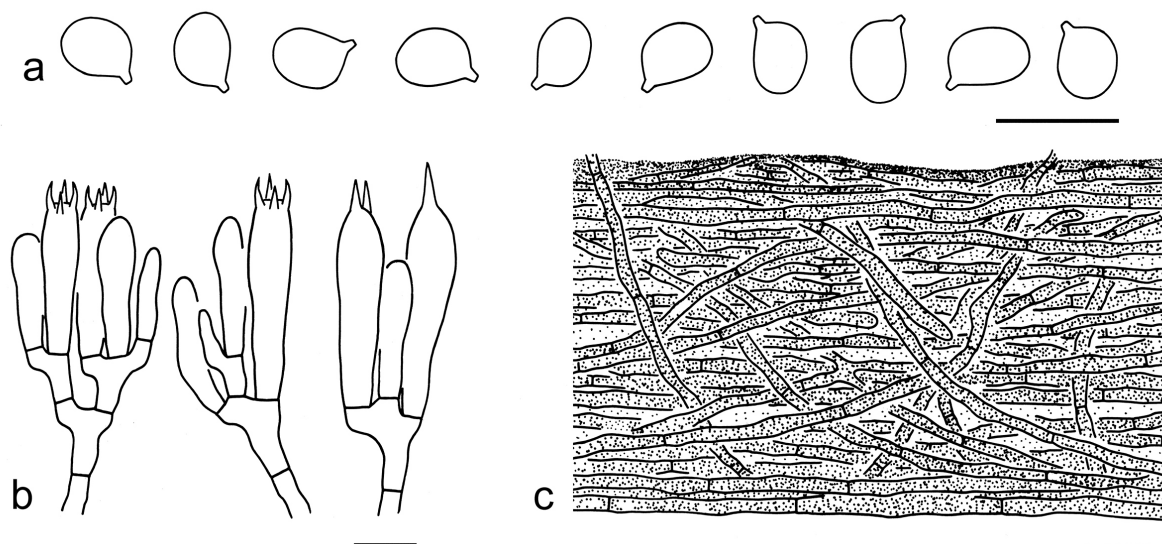


Fig. 58 Microscopic features of *Tricholoma ustaloides* (KUN-HKAS74246). a Basidiospores. b Hymenium and subhymenium. c Pileipellis. Scale bars: a, b = 10 μm , c = 20 μm .

Basidiospores [40/2/1] (5.5–) $6\text{--}7 \times 4.5\text{--}5.5 \mu\text{m}$ (mean length = 6.3 μm , mean width = 5 μm), $Q = (1.09\text{--}) 1.15\text{--}1.4$ (–1.46), $Q_m = 1.27 \pm 0.09$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $25\text{--}40 \times 6\text{--}9 \mu\text{m}$, clavate, 4-spored, sometimes 2- or 1-spored, hyaline; sterigmata 3–8 μm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia not observed. Subhymenium composed of 2–

5 μm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled, filamentous, cylindrical to clavate hyphae 3–30 μm wide. Pileipellis an ixo-cutis to an ixo-trichoderm, more or less gelatinized, composed of radially arranged, interwoven to more or less erected, 2–6 μm wide, thin-walled, brownish to brown filamentous hyphae; subpellis poorly differentiated, not gelatinized. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in coniferous or broad-leaved forests.

Known distribution: Known from Europe and China.

Specimens examined: CHINA. Hubei Province, Shennongjia, on ground in a broad-leaved forest, altitude unknown, 5 Sep. 1984, Xiao-Qing Zhang & Shu-Xiao Sun 435 (HMAS54035). Yunnan Province, Baoshan, Longyang District, Wayao Village, in a forest with *Pinus yunnanensis*, altitude 1800 m, 13 Aug. 2011, Qi Zhao 1293 (KUN-HKAS74246).

Notes: *Tricholoma ustaloides* is characterized by its orange-brown pileus, broadly ellipsoid to ellipsoid basidiospores and associations with *Quercus* in Europe and *Pinus* in southwestern China. According to Christensen & Heilmann-Clausen (2013), this species has a rather weak odour that becomes distinctly farinaceous after cutting, and a strongly farinaceous, bitter taste. For the Chinese collections of this species, however, these characters were not recorded in the field.

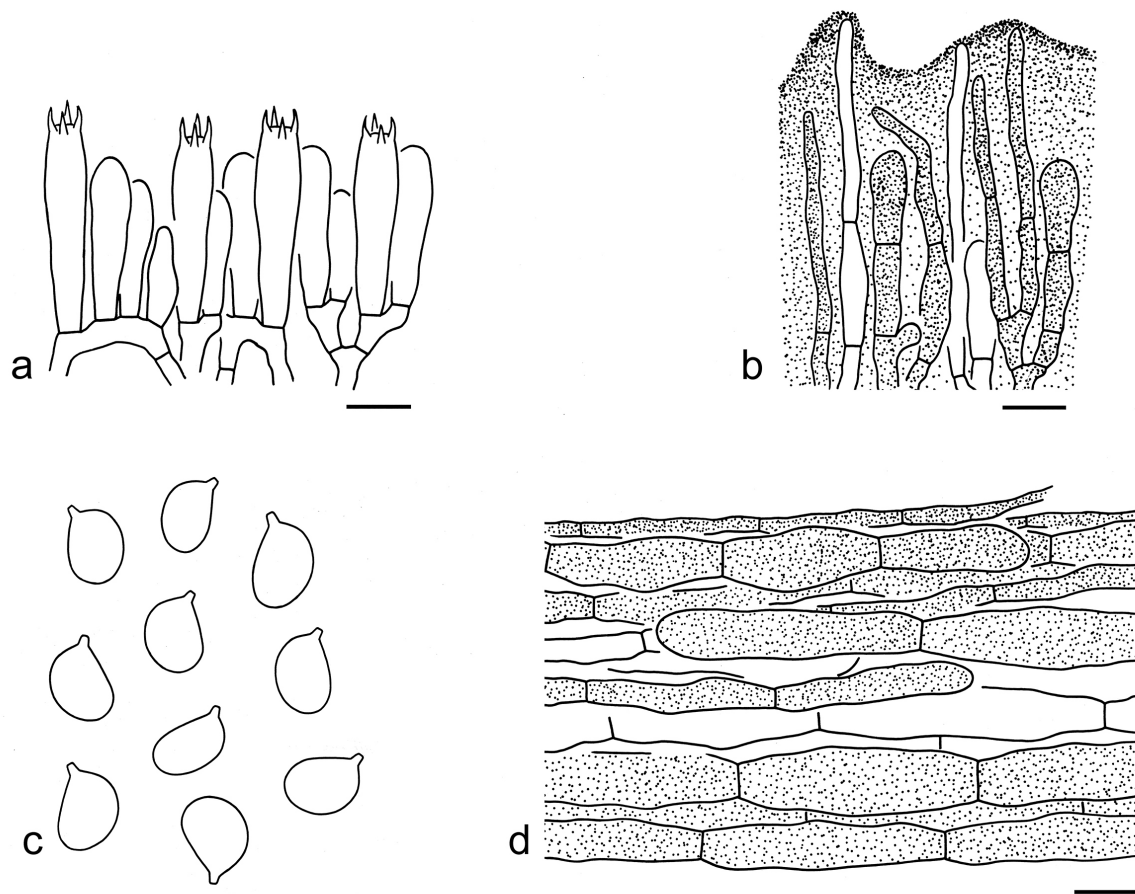


Fig. 59 Microscopic features of *Tricholoma vaccinum* (KUN-HKAS87929). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 μ m, d = 20 μ m.

No closely related species were detected based on our current data (Figs. 3, 4). *Tricholoma ustale* could be confused with *T. ustaloides*, but differs by its stipe without a white zone at top and more viscid pileus (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013). *Tricholoma castaneiceps* is similar to *T. ustaloides*, but has slightly smaller basidiospores ($5\text{--}7 \times 4\text{--}5 \mu\text{m}$, mean length = $6 \mu\text{m}$, mean width = $4.3 \mu\text{m}$) and conspicuous cheilocystidia (this study). *Tricholoma batschii* is also similar to it, but can be separated by a distinct skin-like ring at stipe when young and slightly smaller basidiospores ($3.8\text{--}6.4 \times 3.1\text{--}5.4 \mu\text{m}$, average $4.6\text{--}5.5 \times 3.8\text{--}4.5 \mu\text{m}$) (Riva 1988; Christensen & Heilmann-Clausen 2013). *Tricholoma albobrunneum* and *T. populinum* also can be comparable. For comparison, see notes under these names. *Tricholoma ligusticum* and *T. quercetorum* can be comparable to *T. ustaloides*, but the former two species have a stipe without any ring zone, and often in broad-leaved forests (Carbone 2020; Overall 2021).

39. *Tricholoma vaccinum* (Schaeff.) P. Kumm., Führ. Pilzk. (Zerbst): 133 (1871). Figs. 53f, 59

Basionym: *Agaricus vaccinus* Schaeff., Fung. bavar. palat. nasc. (Ratisbonae) 4: 13 (1774).

Description: Basidioma small to medium-sized. Pileus 3–10 cm in diam., convex to plano-convex, sometimes slightly umbonate at center; surface dry, dark brown (5E6–8) to orange-brown (6C5–7) at center, orangish brown (6B4–6) to brownish (4B3–5) towards margin, densely covered with concolorous squamules, often tomentose at center, fibrillose-tomentose to fibrillose-hairy at margin; margin involute, often deflexed when mature; context white (1A1), dirty white (1B1) to dirty cream (1B2). Lamellae sinuate to subdecurrent, white (1A1) at first, later cream (1A2) to brownish (5B3–6), with brown (5E6–8) stains or spots when injured or old, crowded; edges cream (1A2) to brownish (5B3–6). Stipe $3.5\text{--}12 \times 0.7\text{--}$

2.5 cm, cylindrical to subcylindrical, white (1A1), dirty white (1B1), brownish (5B3–6) to orange-brown (6C5–7), often white (1A1) at apical part, covered with concolorous fibrillose squamules, basal mycelium white (1A1), hollow, exannulate. Taste not recorded. Odour fresh.

Basidiospores [80/4/4] (5.5–) 6–7.5 (–8) $\times$ (4–) 4.5–6 μm (mean length = 6.7 μm , mean width = 5 μm), $Q = 1.18\text{--}1.53$ (–1.63), $Q_m = 1.35 \pm 0.11$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 30–40 $\times$ 6–8 μm , clavate, 4-spored, hyaline; sterigmata 3–5 μm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 10–25 $\times$ 2–10 μm , conspicuous, often gelatinized, filamentous to clavate, often septate, thin-walled, colorless or brownish to brown, hyaline. Subhymenium composed of 2–5 μm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled, ellipsoid, clavate, subglobose to cylindrical cells (25–90 $\times$ 10–35 μm) and filamentous hyphae (4–8 μm wide). Pileipellis a cutis, composed of radially arranged, slightly inflated hyphae (3–30 μm wide), which are often clavate to cylindrical, sometimes filamentous, thin-walled, yellow-brown, brownish to brown; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in forests dominated by *Picea*.

Known distribution: Known from Europe, North America, Japan and Southwestern China.

Specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Dege County, Yulonglacuo, in a forest with *Picea*, *Salix*, *Lonicera* and *Sorbus*, altitude 4000 m, 17 Aug. 2006, Zai-Wei Ge 1295 (KUN-HKAS50875); same location, in a forest with *Picea*, altitude 4000 m, 9 Aug. 2013, Kuan Zhao 339 (KUN-HKAS80764); same prefecture, Daofu County, Bamei Town, Kama Village, in a forest with *Abies* and *Pinus*, altitude 3812 m, 4 Aug. 2016, Jian-Wei Liu 458 (KUN-HKAS98037); same prefecture, Kangding, Tagong Town, in a forest with *Picea*, altitude 4021 m, Bang Feng 146 (KUN-HKAS99500). Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-La, Bitahai, in a forest dominated with *Picea*, altitude 3600 m, 20 Aug. 2014, Qi Zhao 2163 (KUN-HKAS87929).

Notes: *Tricholoma vaccinum* is well delimited by its orange brown, obviously squamulose pileus, broadly ellipsoid to ellipsoid basidiospores, conspicuous cheilocystidia and associations dominated with *Picea* (this study). This species is related to *T. imbricatum* (Fig. 3). For comparison, see notes under that name.

Tricholoma sect. *Matsutake* X.X. Ding et al.

Type: *Tricholoma matsutake* (S. Ito & S. Imai) Singer, Annls mycol. 41(1/3): 77 (1943).

Description: Basidioma tricholomatoid. Pileus umbonate or not, mostly brown, occasionally white, squamose. Lamellae crowded to close. Stipe covered with a cottony to fibrillose annulus on the apical part. Basidiospores medium-sized, broadly ellipsoid to ellipsoid, thin-walled, smooth, inamyloid. Pleurocystidia absent. Cheilocystidia present or absent. Pileipellis a cutis or an ixo-cutis. Clamps absent.

Ecology: Ectomycorrhizal. On soil with various trees.

Distribution: Molecular data indicated species from this section are distributed in Europe, North America and Asia.

Notes: Matsutakes and its allies are a group of the most widely known edible mycorrhizal mushrooms and highly prized in Japan and China (Yang et al. 2008; Vaario et al. 2017; Wang et al. 2017). Because high demands outstrip supplies in Japan, more than 1,000 tonnes of matsutake are imported from China annually (Yang et al. 2008; Vaario et al. 2017; Wang et al. 2017). Apart from the Japanese common name “Matsutake”, it is also called “songkoumo”, “songrong”, “songmaojun” and “qinggangjun” in China (Zang 1990; Wang et al. 2004; Wang et al. 2017). Traditionally, Matsutake growing under conifers are considered as the true, while these associated with broad-leaved trees are treated as false. According to the previous studies, Matsutake group harbours more than one species widely distributed in Asia, Europe, North America and North Africa and associated with both coniferous and broad-leaved trees (Zang 1990; Chapela & Garbelotto 2004; Ota et al. 2012; Bessette et al. 2013; Christensen & Heilmann-Clausen 2013; Trudell et al. 2017; Vaario et al. 2017). To date, seven species, including one new and six known species, are found in China (see below).

Key to the species of *Tricholoma* sect. *Matsutake* from China

1. Lamellae pale to creamy lavender *T. lavendulophyllum*
1. Lamellae white, cream to brownish 2
2. Pileus less coarse, squamules mainly concentrated in central part; basidioma currently only collected from northwestern China *T. tianshanense*
2. Pileus densely covered with appressed, brown, fibrillose squamules; basidioma is not restricted to northwestern China 3
3. Basidiospores relatively larger, 6.5–10 $\times$ 4.5–6.5 μm , with mean length > 7.2 μm 4
3. Basidiospores relatively smaller, 6–8 $\times$ 4–6.5 μm , with mean length $\leq$ 7.2 μm 5
4. Basidioma distributed in subalpine coniferous forest; basidiospores relatively smaller, 7–9 $\times$ 4.5–6 μm *T. xizangense*
4. Basidioma only distributed in alpine broad-leaved forests; basidiospores relatively larger, 6.5–10 $\times$ 5–6.5 μm ... *T. zangii*
5. Basidiospores relatively larger, ellipsoid, with mean length > 7 μm ; basidioma distributed in Europe, North America and Asia associated with both coniferous and broad-leaved trees *T. matsutake*
5. Basidiospores relatively smaller, subglobose, broadly ellipsoid to ellipsoid, with mean length < 7 μm ; basidioma distributed in Asia associated with broad-leaved trees 6
6. Basidiospores subglobose to broadly ellipsoid shaped, 6–8 $\times$ 4.5–6.5 μm , $Q = 1.08\text{--}1.33$, $Q_m = 1.21 \pm 0.09$; cheilocystidia cylindrical, fusiform, subclavate to irregularly shaped, sometimes septate *T. bakamatsutake*
6. Basidiospores broadly ellipsoid to ellipsoid, 6–8 $\times$ 4–6 μm , $Q = 1.15\text{--}1.5$, $Q_m = 1.32 \pm 0.09$; cheilocystidia poorly differentiated *T. fulvocastaneum*

40. *Tricholoma bakamatsutake* Hongo, J. Jap. Bot. 49(10): 294 (1974). Figs. 53g, 60

Description: Basidioma medium-sized. Pileus 4–9 cm in diam., at first hemispherical to convex, then plano-convex to applanate, sometimes with a broadly umbo; surface dry, dark brown (4F6–8), red-brown (6E6–8), yellow-brown (4E5–8) to

brown (3E5–8), sometimes brownish (3D6–8) to white (1A1) at margin, densely covered with appressed, dark brown (4F6–8) to brown (4D5–8, 4E5–8), fibrillose squamules; margin involute to inflexed; context white (1A1). Lamellae adnexed, at first white (1A1) to cream (1A2), then red-brownish (5A2–4) to red-brown (5C3–6), crowded; edges entire, fragile, white (1A1) when young, becoming brown (5E6–8) when mature. Stipe 8–14 × 1–2 cm, cylindrical, often tapering or sometimes slightly inflated downwards, solid, with a cream (1A2), brownish (4B2–5) to brown (4E6–8, 4F6–8), cottony to fibrillose annulus on the apical part, white (1A1) to brownish (4B2–4) above annulus, white (1A1) backgrounds densely covered with appressed, dark brown (4F6–8), yellow-brown (4E6–8) to reddish brown (5E6–8), fibrillose squamules below annulus. Taste slightly spicy and tongue-numbing. Odour strong, sweetish.

Basidiospores [112/6/6] (5.5–) 6–8 (–9) × (4–) 4.5–6.5 (–7) μm (mean length = 6.5 μm , mean width = 5.4 μm), $Q = (1.03\text{--}1.08\text{--}1.33\text{--}1.5)$, $Q_m = 1.21 \pm 0.09$, subglobose to broadly ellipsoid, sometimes ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 30–40 × 6–8 μm , clavate, 4-spored, hyaline; sterigmata 4–6 μm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 15–60 × 4–10 μm , conspicuous, cylindrical,

fusiform, subclavate to irregularly shaped, sometimes septate, thin-walled, colorless, hyaline. Subhymenium composed of 2–5 μm wide filamentous hyphae, clamps absent. Pileipellis a cutis, composed of 3–12 μm wide, thin-walled, brown, filamentous hyphae; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in broad-leaved forests with trees of Fagaceae.

Known distribution: Known from Japan (Hongo 1974) and China.

Specimens examined: CHINA. Gansu Province, Longnan, Wudu, the type of forest and altitude unknown, the year of 1993, Mao-Lin Tian (HMAS70231). Yunnan Province, Kunming, Guandu District, Mushuihua Market, the type of forest and altitude unknown, 12 Jul. 2019, Xiao-Xia Ding 482 (KUN-HKAS134983); same location and date, Xiao-Xia Ding 474 (KUN-HKAS134984); same location and date, Xiao-Xia Ding 477 (KUN-HKAS134985); same location and date, Xiao-Xia Ding 478 (KUN-HKAS134986); same location and date, Xiao-Xia Ding 481 (KUN-HKAS107573); same location and date, Xiao-Xia Ding 480 (KUN-HKAS134987); Wenshan Zhuang and Miao Autonomous Prefecture, Malipo County, in a broad-leaved forest, altitude 1100 m, 28 Jul. 2017, Gang Wu 2261 (KUN-HKAS106301).

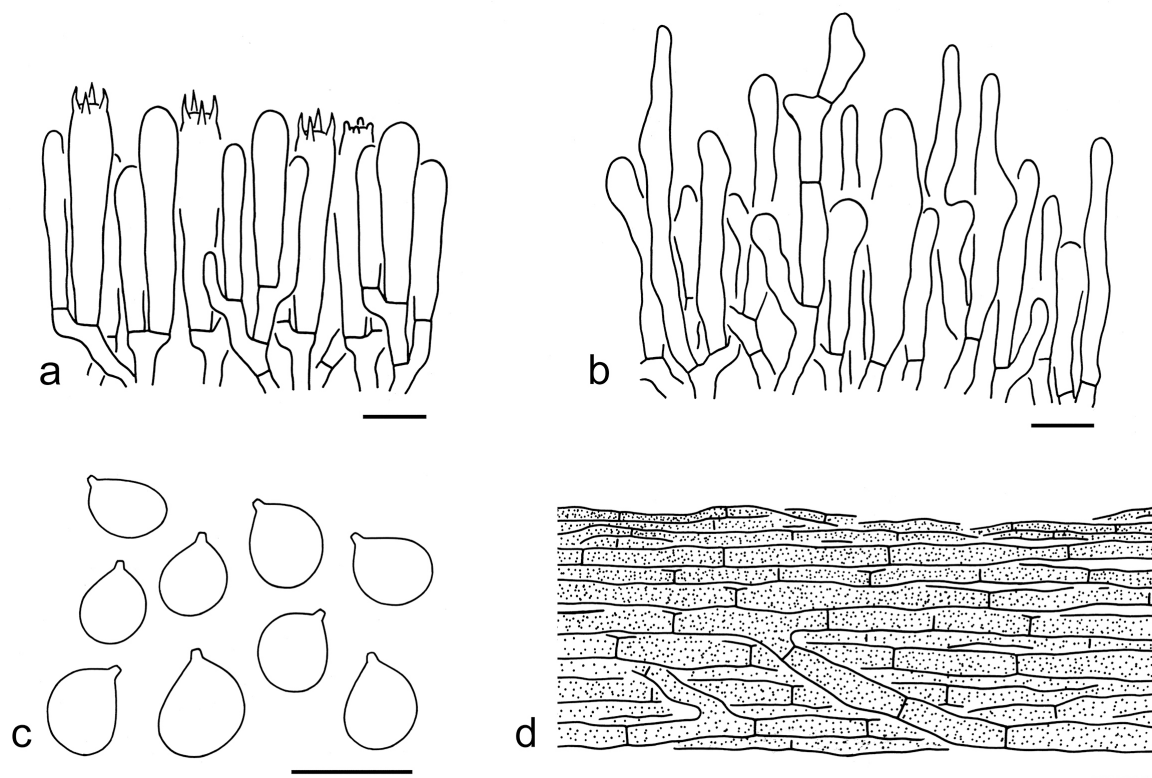


Fig. 60 Microscopic features of *Tricholoma bakamatsutake* (KUN-HKAS107573). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 μm , d = 20 μm .

Notes: *Tricholoma bakamatsutake* was originally described from Japan in forests with *Quercus* (Hongo 1974), it also occurs in China and commonly called “jiasongrong”, “jiasongkoumo” and “lirong” in markets. This species is characterized by its dark brown, red-brown to brown pileus densely covered with concolor, appressed, fibrillose

squamules, subglobose to broadly ellipsoid basidiospores (6–8 × 4.5–6.5 μm , $Q = 1.08\text{--}1.33$, $Q_m = 1.21 \pm 0.09$), cylindrical, subclavate to irregularly shaped, sometimes septate cheilocystidia, numbing and spicy tastes and strong odours.

In the phylogenetic analyses based on the ITS sequences (Fig. 4), *T. bakamatsutake* is closely related to the clade formed by *T. dulciolens* Kytöv., *T. ilkkæ* Mort. Chr. et al. and *T. tianshanense* Zhao et al. However, these latter three relative species all grow with conifers (Christensen & Heilmann-Clausen 2013; this study). *Tricholoma dulciolens* can be easily distinguished from *T. bakamatsutake* by its pale brown basidioma, and predominantly broadly ellipsoid basidiospores ($4.4\text{--}7.9 \times 3.7\text{--}5.8 \mu\text{m}$, $Q = 1\text{--}1.6$) (Kytövuori 1988; Christensen & Heilmann-Clausen 2013). *Tricholoma ilkkæ* has a distinct ring at the margin of pileus and relatively smaller basidiospores ($4.5\text{--}6.7 \times 3.9\text{--}5.5 \mu\text{m}$, average $5.1\text{--}6 \times 4.4\text{--}4.9 \mu\text{m}$) (Christensen & Heilmann-Clausen 2013; Heilmann-Clausen et al. 2017). *Tricholoma tianshanense* differs by its broadly ellipsoid to ellipsoid basidiospores and poorly differentiated cheilocystidia (this study).

Tricholoma fulvocastaneum Hongo occurs in broad-leaved forests and can be confused with *T. bakamatsutake*, but the former one has broadly ellipsoid to ellipsoid basidiospores ($6\text{--}8 \times 4\text{--}6 \mu\text{m}$, $Q = 1.15\text{--}1.5$, $Q_m = 1.32 \pm 0.09$) and poorly differentiated cheilocystidia (Hongo 1960; this study). *Tricholoma matsutake* is similar to *T. bakamatsutake*, but differs by its strong odour, proportionally robust stipe, ellipsoid basidiospores ($6.5\text{--}8 \times 5\text{--}6 \mu\text{m}$, $Q = 1.3\text{--}1.5$, $Q_m = 1.39 \pm 0.09$) and associations with both coniferous and broad-leaved trees (this study).

41. *Tricholoma xizangense* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 53h, 61

Fungal Names: FN 572338

Etymology: xizangense = Xizang Autonomous Region, named due to its type locality.

Diagnosis: Similar to *T. matsutake*, but differs in its relatively larger basidiospores and clavate cheilocystidia.

Type: CHINA. Xizang Autonomous Region, Qamdo, Baxoi County, Ranwu Town, in a subalpine temperate forest, altitude 3900 m, 4 Aug. 2014, Jian-Wei Liu 220 (holotype, KUN-HKAS91028).

Description: Basidioma medium-sized to large. Pileus ca. 10 cm in diam., at first hemispherical to convex, then plano-convex to applanate; surface dry, a white (1A1) background densely covered with appressed, dark brown (5F5–8) to brown (5E5–8), tomentose, floccose to fibrillose squamules, often becoming brownish (5D5–8) to cream (3B2) at margin; margin involute; context white (1A1). Lamellae adnexed to sinuate, white (1A1), crowded; edges entire, white (1A1). Stipe ca. 12×2 cm, cylindrical, solid, with a white (1A1) to brownish (5C3–6), cottony to fibrillose annulus on the apical part. white (1A1) above annulus, white (1A1) backgrounds densely covered with appressed, blackish (5F6–8), dark brown (5E5–8) to brown (4F6–8), fibrillose squamules below annulus. Taste bitter. Odour not recorded.

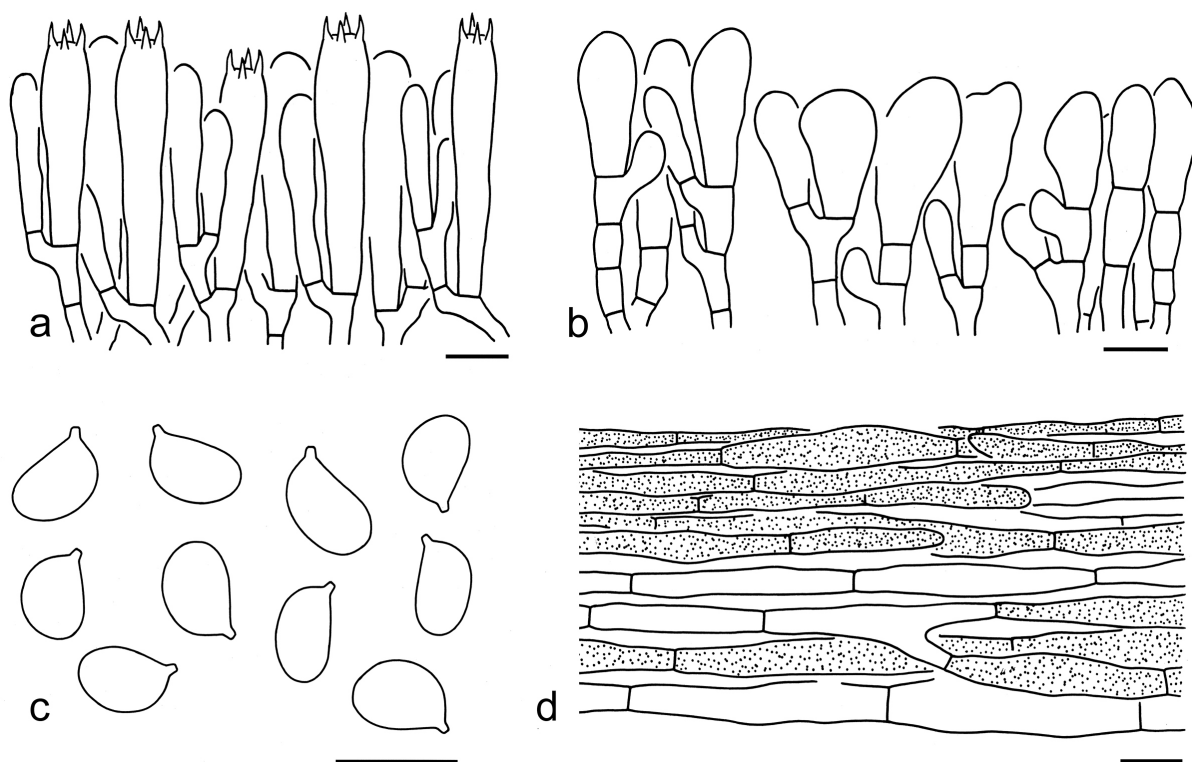


Fig. 61 Microscopic features of *Tricholoma xizangense* (holotype, KUN-HKAS91028). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = $10 \mu\text{m}$, d = $20 \mu\text{m}$.

Basidiospores [30/1/1] (6–) $7\text{--}9 \times 4.5\text{--}6 \mu\text{m}$ (mean length = $7.6 \mu\text{m}$, mean width = $5.3 \mu\text{m}$), $Q = 1.17\text{--}1.69$ (–1.78), $Q_m = 1.43 \pm 0.15$, broadly ellipsoid to ellipsoid, sometimes elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $35\text{--}50 \times 7\text{--}9 \mu\text{m}$, clavate, 4-

spored, hyaline; sterigmata $3\text{--}5 \mu\text{m}$ long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia $15\text{--}35 \times 8\text{--}15 \mu\text{m}$, conspicuous, subclavate, clavate to irregularly shaped, sometimes septate, thin-walled, colorless, hyaline. Subhymenium composed of $2\text{--}5 \mu\text{m}$ wide filamentous hyphae, clamps

absent. Pileipellis a cutis, composed of 3–20 μm wide, thin-walled, yellow-brown to brownish, filamentous to cylindrical hyphae; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in subalpine forests.

Known distribution: Southwestern China.

Additional specimen examined: CHINA. Xizang Autonomous Region, Qamdo, Baxoi County, in a subalpine temperate forest, altitude 3800 m, Jian-Wei Liu (KUN-HKAS152698).

Notes: *Tricholoma xizangense* is characterized by its dark brown to brown basidioma, broadly ellipsoid to ellipsoid basidiospores ($7\text{--}9 \times 4.5\text{--}6 \mu\text{m}$, $Q = 1.17\text{--}1.69$, $Q_m = 1.43 \pm 0.15$) and distributed in subalpine forests (this study). In the tree based on the ITS sequences, it is related to two samples which labelled as *T. caligatum* in GenBank (Fig. 4).

Morphologically, *T. matsutake* is similar to *T. xizangense*, but differs by its relatively smaller basidiospores ($6.5\text{--}8 \times 5\text{--}6 \mu\text{m}$) and filiform, cylindrical to narrowly cylindrical cheilocystidia (this study). *Tricholoma caligatum* also can be confused with it, but has relatively darker colored basidioma, relatively smaller basidiospores (average $6.5\text{--}7.1 \times 5.3\text{--}5.6 \mu\text{m}$) and is not distributed in China (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013).

42. *Tricholoma fulvocastaneum* Hongo, J. Jap. Bot. 35: 86 (1960). Figs. 53i, 62

Description: Basidioma medium-sized. Pileus 5–9 cm in diam., at first hemispherical to convex, then plano-convex to

applanate, often with a broadly low umbo; surface dry, red-brown (6D4–8) to brown (5D5–8, 5E6–8), densely covered with appressed, red-brown (6D4–8) to brown (5D5–8, 5E6–8), fibrillose squamules; margin involute to inflexed, often splitting to expose white (1A1) flesh; context white (1A1). Lamellae adnexed to sinuate, white (1A1) to cream (1A2, 1B2), crowded; edges entire, fragile, white (1A1) to cream (1A2, 1B2). Stipe 8–15 $\times$ 1.5–2 cm, cylindrical, often tapering downwards, solid, with a dirty white (5B2), brown (5D5–8, 5E6–8) to red-brown (6D4–8), cottony annulus on the apical part, white (1A1) above annulus, white (1A1) backgrounds densely covered with appressed, brown (5D5–8, 5E6–8) to red-brown (6D4–8), fibrillose squamules below annulus. Taste slightly spicy and tongue-numbing. Odour strong, sweetish.

Basidiospores [$80/4/4$] ($5.5\text{--}6.8 \times 4\text{--}6$ (~ 6.5) μm (mean length = 6.8 μm , mean width = 5.1 μm), $Q = 1.15\text{--}1.5$ (~ 1.56), $Q_m = 1.32 \pm 0.09$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $30\text{--}40 \times 6\text{--}8 \mu\text{m}$, clavate, 4-spored, hyaline; sterigmata 4–6 μm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia $15\text{--}40 \times 3\text{--}7 \mu\text{m}$, poorly differentiated, filiform, cylindrical, subclavate to clavate, sometimes septate, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 μm wide filamentous hyphae, clamps absent. Pileipellis a cutis, often more or less lightly gelatinized, composed of 3–15 μm wide, thin-walled, brown, filamentous to cylindrical hyphae; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in broad-leaved forests with trees of Fagaceae.

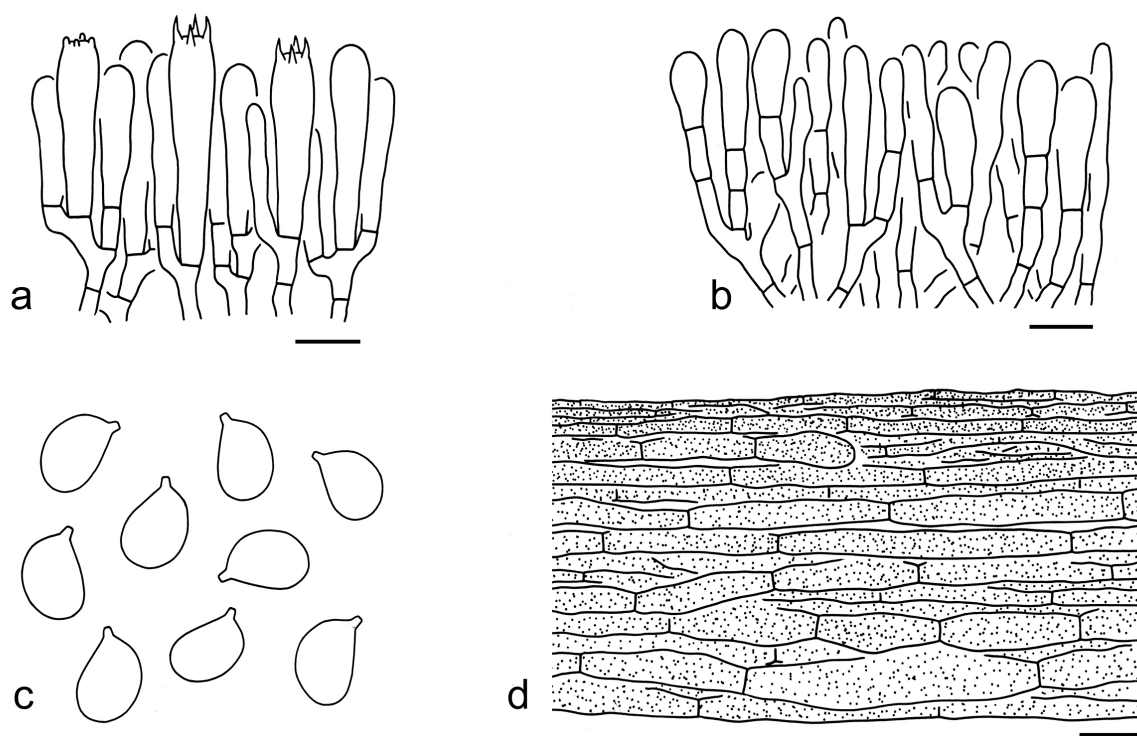


Fig. 62 Microscopic features of *Tricholoma fulvocastaneum* (KUN-HKAS134988). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 μm , d = 20 μm .

Known distribution: Known from Japan, Northern Thailand (Sanmee et al. 2007) and Southwestern China.

Specimens examined: CHINA. Yunnan Province, Kunming, Guandu District, bought from Mushuihua Market, 12 Jul. 2019, Xiao-Xia Ding 462 (KUN-HKAS134988); Xiao-Xia Ding 463

(KUN-HKAS134989); Xiao-Xia Ding 465 (KUN-HKAS107568); Xiao-Xia Ding 472 (KUN-HKAS134990); Xiao-Xia Ding 476 (KUN-HKAS107571).

Notes: *Tricholoma fulvocastaneum* was originally described from Japan (Hongo 1960) and also found in northern Thailand (Sanmee et al. 2007) and southwestern China (Zang 1990; Wang et al. 2004; Yu 2007). This species is characterized by its red-brown to brown pileus densely covered with appressed, concolor, fibrils squamules, broadly ellipsoid to ellipsoid basidiospores ($6-8 \times 4-6 \mu\text{m}$, $Q = 1.15-1.5$, $Q_m = 1.32 \pm 0.09$), poorly differentiated cheilocystidia and broad-leaved associations.

Phylogenetically, *T. fulvocastaneum* is closely related and morphologically similar to the clade formed by *T. matsutake*, *T. bakamatsutake* and *T. tianshanense* (Fig. 3). However, *T. matsutake* has strong odour, proportionally robust stipe, conspicuous cheilocystidia and is associated with both coniferous and broad-leaved trees. The comparisons between *T. bakamatsutake* and *T. fulvocastaneum* are provided under the notes of the former species. *Tricholoma tianshanense* is distributed in coniferous forests.

43. *Tricholoma lavendulophyllum* F.Q. Yu, Mycotaxon 95: 306 (2006)

Description: Pileus 4.5–7.5 cm in diam., hemispherical to convex when young, becoming subumbonate to plano-convex when mature; surface slightly viscid when wet, chestnut brown to fuscous in the center, with appressed dark brown zoned scales, often becoming broken up into rather indistinct pieces; margin brown to whitish brown, inrolled when young; context white, taste sweetish. Lamellae adnate, sinuate or arcuate, then separating from stem, pale to creamy lavender, with some lamellulae. Stipe 8–9.5 $\times$ 1.2–1.5 cm, equal or enlarged at the base, with a persistent but inconspicuous annulus on the upper part, 1.5–2.2 cm downward from the lamellae; concolorous with the pileus below the ring, with dark brown, appressed scales, whitish above the ring.

Pileipellis a layer of interwoven and thin-walled hyphae, 5–13 μm in diam., light yellowish brown, terminal elements subclavate to clavate, 7.5–9 $\times$ 22.5–67.5 μm . Lamellar trama subparallel, hyphae mostly 3–12 μm in diam., thin-walled, hyaline. Basidia 40–50 $\times$ 7.5–15 μm , clavate, hyaline, 4-spored, rarely 2- and 1-spored, sterigmata 2–5 μm long. Cystidia absent, but some clavate free hyphal ends present at the gill edge. Basidiospores (5.5–) 6–7.5 $\times$ (4.5–) 5–5.5 (–6) μm , $Q = (1.18-)$ 1.25–1.33, broadly ellipsoid, thin-walled, hyaline, smooth, inamyloid. Stipitipellis with longitudinally arranged, appressed, parallel hyphae, 4–12 μm in diam., thin-walled, whitish brown to yellowish brown, terminal elements scattered, cylindrical, 6.8–9 $\times$ 30–54 μm , periclinal arranged.

Ecology: On soil in a broad-leaved forest (Yu et al. 2006).

Known distribution: Currently only known from Southwestern China (Yu et al. 2006).

Specimen examined: CHINA. Yunnan Province, Kunming City, Wujing Road, wild edible mushroom market, 23 Jul. 2005, F. Q. Yu 1273 (holotype, HKAS49804).

Notes: The description above and the citation of the holotype are from Yu et al. (2006). *Tricholoma lavendulophyllum* was described from Kunming, Yunnan, China, and is characterized by its lavender-colored lamellae (Yu et al. 2006). Although Yu et al. (2006) did not provide molecular evidence,

Yu (2007) mentioned that this species possessed an ITS sequence and was labelled as 'T19, *T. lavendulophyllum*, Yunnan' in the MP tree analysis. Additionally, 'T19, *T. lavendulophyllum*, Yunnan' and '*T. bakamatsutake*' form a monophyletic group with significant support, suggesting that *T. lavendulophyllum* may be a member of *T. bakamatsutake* group (Yu 2007). Unfortunately, the sequence was not submitted to a public database for additional confirmatory investigation.

Tricholoma lavendulophyllum was described based on two collections purchased from the wild edible mushroom markets in Kunming, namely F.Q. Yu1273 (HKAS49804, holotype) and F.Q. Yu1310B (HKAS49796). However, HKAS49796 was F.Q. Yu1310A, and was cited under the name *T. bakamatsutake* by Yu (2007). ITS phylogenetic analysis indicated that F.Q. Yu1310A (HKAS49796) is *T. bakamatsutake* (Yu 2007). Unfortunately, the type specimen for this species (F.Q. Yu1273, HKAS49804) and F.Q. Yu1310B were not traced.

44. *Tricholoma matsutake* (S. Ito & S. Imai) Singer, Annls mycol. 41(1/3): 77 (1943). Figs. 53j, 63

Basionym: *Armillaria matsutake* S. Ito & S. Imai, Bot. Mag. Tokyo: 327 (1925).

Description: Basidioma medium-sized, large to very large. Pileus 5–17 cm in diam., at first hemispherical to convex, becoming convex, plano-convex to applanate when mature, sometimes with a broadly low umbo; surface dry, clay buff (3D3–5), grey-brown (3F4–6, 4E3–6) to brown (4C5–8, 5D4–6), sometimes greyish brown (4E3–6) to brown (4C5–8, 5D4–6) at center, becoming paler towards margin, densely covered with appressed, dark greyish brown (3F4–6, 4E3–6), clay buff (3D3–5) to brown (4C5–8, 5D4–6), fibrillose squamules; margin involute when young, later inflexed to deflexed, often splitting to expose white flesh; context white (1A1). Lamellae adnexed to emarginate, dirty white (1B1), white (1A1) to cream (1A2), with brown (4D3–6) spots when old, crowded; edges entire, white (1A1) to cream (1A2). Stipe 6–13 $\times$ 1.5–3.5 cm, cylindrical, sometimes tapering downwards, robust and solid, covered with a large, white (1A1), brownish (3C2–4) to brown (4C5–8, 5D4–6), cottony annulus, white (1A1) with snake-shaped squamules above annulus, white (1A1) background with grey-brown (3F4–6, 4E3–6), clay buff (3D3–5) to brown (4C5–8, 5D4–6), fibrillose squamules below annulus. Taste mild. Odour strong, sweetish.

Basidiospores [40/1/1] (6–) 6.5–8 $\times$ (4.5–) 5–6 μm (mean length = 7.2 μm , mean width = 5.2 μm), $Q = (1.17-)$ 1.3–1.5 (–1.63), $Q_m = 1.39 \pm 0.09$, ellipsoid, sometimes broadly ellipsoid or elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 35–50 $\times$ 7–10 μm , clavate, 4-spored, hyaline; sterigmata 4–6 μm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 40–60 $\times$ 3–6 μm , conspicuous, filiform, cylindrical, narrowly cylindrical to subclavate, sometimes forked, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 μm wide filamentous hyphae, clamps absent. Pileipellis a cutis to a more or less trichoderm, composed of 7–15 μm wide, thin-walled, yellow-brown to brown, cylindrical to filamentous hyphae; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in coniferous, broad-leaved or mixed forests.

Known distribution: Widely distributed throughout Northern Hemisphere, known from Europe, North America, and Asia.

Specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, Pusharong Village, in a broad-leaved forest, altitude 3500 m, 6 Sep. 2016, Pan-Meng Wang 68 (KUN-HKAS98323). Xizang Autonomous Region, Nyingchi, Bayi District, Lulang Town, Zhaxigang Village, in a broad-leaved forest, altitude 2850 m, 1 Aug. 2014, Bang Feng 1683 (KUN-HKAS94067). Yunnan Province, Chuxiong Yi Autonomous Prefecture, Nanhua County, Wujie Town, in a broad-leaved forest, altitude 2500 m, 13 Aug. 2017, Jian-Wei Liu 912 (KUN-HKAS106299); Dali Bai Autonomous Prefecture, Jianchuan County, Shanglan Village, altitude 2500 m, 31 Aug. 2009, Bang Feng 741 (KUN-HKAS57470); Kunming, Guandu District, Mushuihua Market, the type of forest and altitude unknown, 12 Jul. 2019, Xiao-Xia Ding 468 (KUN-HKAS134991); Lijiang, Ninglang Yi Autonomous County, the type of forest unknown, altitude 2200 m, 6 Aug. 2011, Li-Ping Tang 1457 (KUN-HKAS69918); same city, Yulong Naxi Autonomous County, Lijiang Alpine Botanic Garden, in a broad-leaved forest, altitude 2700 m, 13 Sep. 2019, Jian-Wei Liu 1979 (KUN-HKAS134992); Diqing Tibetan Autonomous Prefecture: Shangri-La, Potatso National Park, in a coniferous forest, altitude 3500 m, 20 Aug. 2014, Qi Zhao 2164 (KUN-HKAS87930).

Notes: *Tricholoma matsutake* is a famous edible mushroom with significant commercial value and ecological

importance, particularly in East Asia. This species is popularly consumed in Japan and China for its distinct spicy-aromatic odour and distinctive taste (Yang et al. 2008; He 2010; Vaario et al. 2017).

In Japan, *T. matsutake* is mainly associated with the Japanese red pine (*Pinus densiflora*) and also called Matsutake or pine mushroom (Murata & Minamide 1989; Murata et al. 2001; Vaario et al. 2017), whereas in China can be collected from northeastern and eastern regions with conifers and in southwestern areas under both conifers and broad-leaved trees (Yu 2007; Vaario et al. 2017; Wang et al. 2017). In regarding to this kind of mushrooms from Taiwan, Sawada (1931) circumstanced it as *Armillaria matsutake* var. *formosana* Sawada, which is treated as a synonym of *T. matsutake* (Yu 2007).

In the phylogenetic analysis based on the ITS sequences, *T. magnivelare* (Peck) Redhead is clustered within *T. matsutake* (Fig. 4). However, *T. magnivelare* has a paler colored basidioma (beige to tan), slightly smaller basidiospores ($5\text{--}7.5 \times 3.5\text{--}5.5 \mu\text{m}$, mean $6.1 \times 4.5 \mu\text{m}$) and currently only known from North America (Bessette et al. 2013; Trudell et al. 2017). *Tricholoma caligatum*, *T. bakamatsutake* and *T. fulvocastaneum* can be confused with *T. matsutake*. However, *T. caligatum* has a relatively darker (dark greyish brown to dark reddish brown or dark brick) pileus (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013). For comparisons with *T. bakamatsutake* and *T. fulvocastaneum*, see notes under that these names.

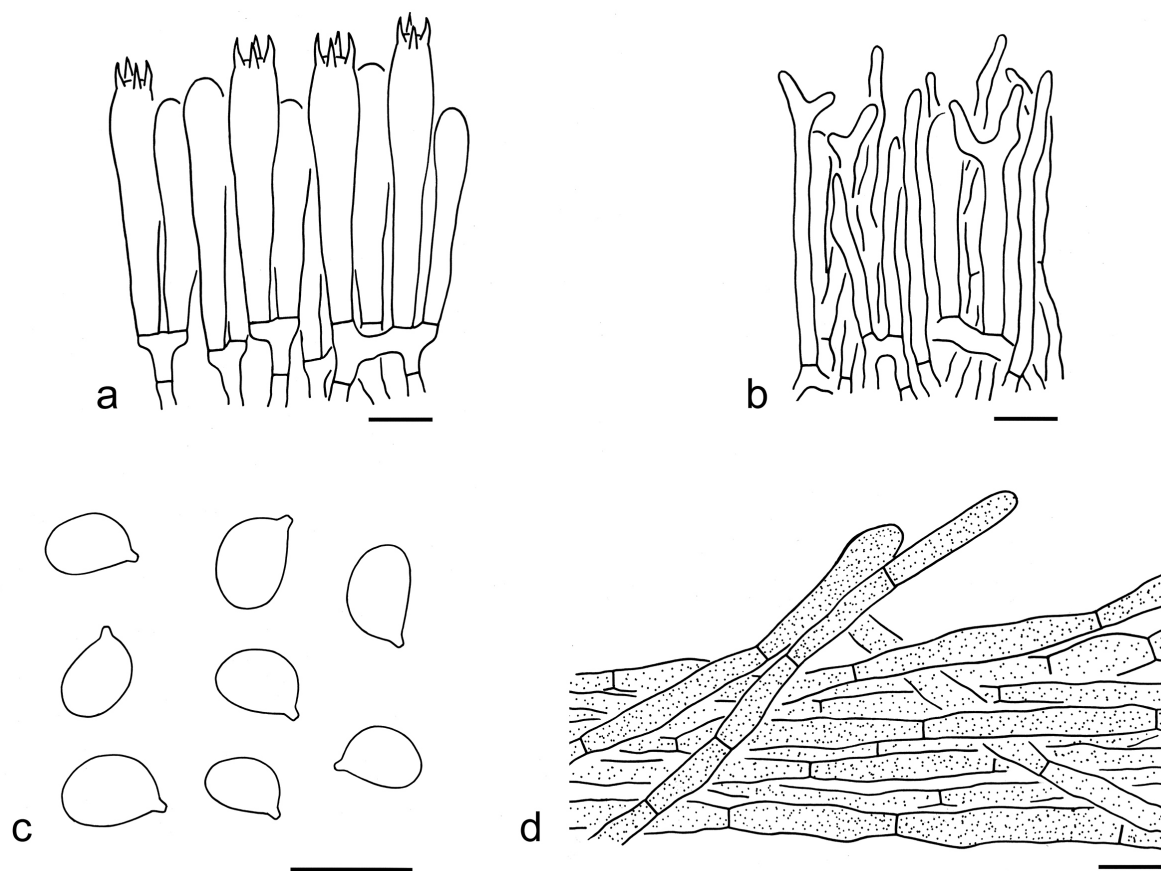


Fig. 63 Microscopic features of *Tricholoma matsutake* (KUN-HKAS98323). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 μm , d = 20 μm . Cited from Ding et al. (2023).

45. *Tricholoma tianshanense* Z.X. Zhao et al., Phytotaxa 549(1): 26 (2022). Fig. 64

Description: Basidioma medium-sized. Pileus 4–9 cm in diam., at first hemispherical, then plano-convex to applanate; surface dry, white (1A1) background covered with appressed, dark brown (4F6–8), brown (4E3–5) to brownish (4D4–6), fibrillose squamules; margin involute to inflexed; context white (1A1). Lamellae adnexed, white (1A1), crowded; edges entire, white (1A1). Stipe 5–10 × 2–2.5 cm, cylindrical, solid, with a brownish (4D4–6) to brown (4E3–5), cottony to fibrillose annulus on the apical part, white (1A1) above annulus, white (1A1) backgrounds covered with appressed, dark brown (4F6–8), brown (4E3–5) to brownish (4D4–6), fibrillose squamules below annulus. Taste not recorded. Odour very strong, like perfume.

Basidiospores [40/1/1] 6–7.5 × (4–) 4.5–6 µm (mean length = 6.7 µm, mean width = 5.2 µm), Q = 1.15–1.41 (–1.5), Qm = 1.28 ± 0.08, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 30–50 × 6–9 µm, clavate, 4-spored, hyaline; sterigmata 3–4 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia not observed. Subhymenium composed of 2–5 µm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless; thin-walled, filamentous to cylindrical hyphae 3–20 µm wide. Pileipellis a cutis, composed of 7–25 µm wide, thin-walled, colorless or brown, filamentous, cylindrical to clavate hyphae, sometimes ellipsoid; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in coniferous forests.

Known distribution: Currently only known from North-western China.

Specimen examined: CHINA. Xinjiang Province, Hejing County, in a coniferous forest dominated by *Picea schrenkiana*, altitude 2650 m, 11 September 2020, Z.X. Zhao & B. Xu (holotype, HMUT1112).

Notes: *Tricholoma tianshanense* is characterized by its white pileus densely covered with appressed, brown, fibrillose squamules, a white stipe with a brown cottony annulus on the apical part and covered with brown squamules below annulus, broadly ellipsoid to ellipsoid basidiospores (6–7.5 × 4.5–6 µm), and absence of clamps (this study). Zhao et al. (2022) reported that clamps are present in the species but rare. Our re-examination on the holotype cited above indicated that no clamps are present in the species. To our knowledge, no species of sect. *Matsutake* possesses clamps.

This species is related to *T. ilkkae* in phylogenetic tree based on the ITS sequences (Fig. 4), but the latter species has a more squamulose pileus and relatively smaller basidiospores (4.5–6.7 × 3.9–5.5 µm, average 5.1–6 × 4.4–4.9 µm) (Christensen & Heilmann-Clausen 2013; Heilmann-Clausen et al. 2017). *Tricholoma dulciolens* looks like *T. tianshanense*, but differs in its pale colored (brownish) basidioma, relatively smaller basidiospores (4.4–7.9 × 3.7–5.8 µm, average 5.7–6.3 × 4.7–4.9 µm) and has not been found in China (Christensen & Heilmann-Clausen 2013; Landry et al. 2022).

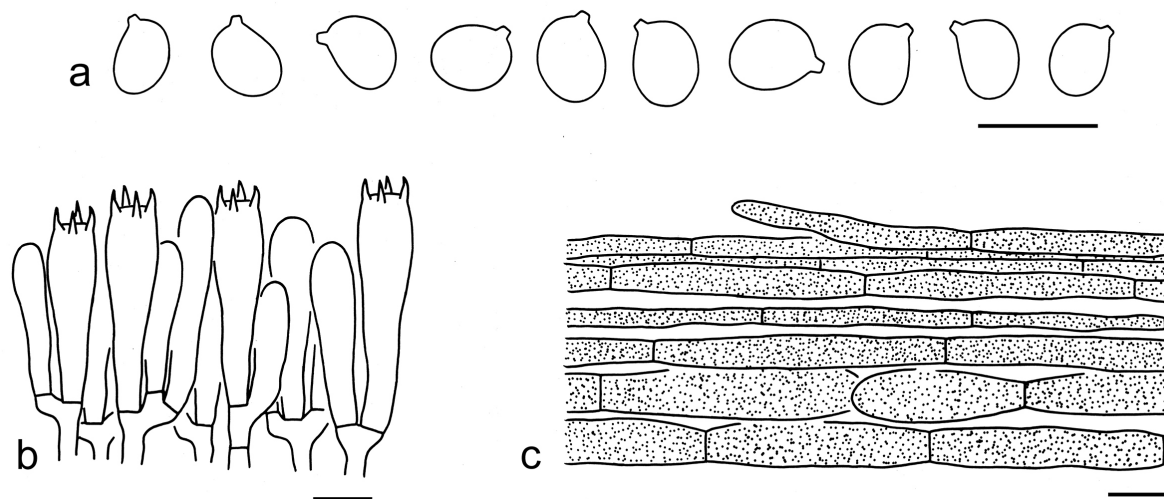


Fig. 64 Microscopic features of *Tricholoma tianshanense* (holotype, HMUT1112). a Basidiospores. b Hymenium and subhymenium. c Pileipellis. Scale bars: a, b = 10 µm, c = 20 µm.

46. *Tricholoma zangii* Z.M. Cao et al., Mycotaxon 85: 161 (2003)

Replaced synonym: *Tricholoma quercicola* M. Zang, Acta Mycol. Sin. 9(2): 123 (1990).

Competing homonym: non *Tricholoma quercicola* (Murrill) Murrill, Lloydia 12: 67 (1949).

Description: Pileus 6–12 cm in diam., convex to plano-convex; surface light brown to pale grey, sometimes darker at center, dry, with light brown and appressed squamules; margin inrolled, entire, appendiculate. Lamellae sinuate-adnexed, adnexed to emarginate, crowded, whitish, 2.5–4 cm broad, with lamellulae of two lengths. Stipe 6–10 × 1.5–2.5 cm, robust, cylindrical, equal or slightly tapering towards the base; surface whitish and with small granules above the annulus, concolorous with pileus and scabrous below.

Annulus apical, membranous. Context thick, whitish, comprising of thin-walled hyphae, 5–10 µm diam., lacking clamps-connections. Odour strong, sweetish. Taste mild, pleasant.

Basidiospores 6.5–10 × 5–6.5 µm, Q = 1.27, ellipsoid, hyaline, inamyloid, thin-walled, with a prominent hilar appendix. Basidia 16–26 × 7–12 µm, clavate, bearing four sterigmata. Lamellar edge heteromorphous, often with scattered cheilocystidia. Cheilocystidia 25–30 × 13–19 µm, clavate or ventricose-rostrate. Hymenophoral trama regular, hyaline, comprising parallel hyphae, 4–11 µm diam. Pileipellis a repent epicutis of tightly woven hyphae, 4–7 µm diam.

Ecology: Solitary to scattered on soil in broad-leaved forests.

Known distribution: Known from Southwestern China (Zang 1990; Cao et al. 2003).

Specimen examined: CHINA. Sichuan Province, Miyi, under *Quercus pannosa*, altitude 3000 m, 27 Jul. 1984, Ming-sheng Yuan 381 (holotype, KUN-HKAS19947).

Notes: The description above and specimen citation are from Zang (1990) and Cao et al. (2003). Zang (1990) described this matsutake from alpine *Quercus* forests in southwestern China as a new species, namely, *T. quercicola* M. Zang. Before that, Tominaga et al. (1988) proposed a variety, viz. *T. matsutake* var. *qinggang* Tominaga, based on matsutake mushrooms growing under alpine *Quercus* forests in Barkam, Sichuan Province, China. However, there is no Latin diagnosis or description, therefore this name is invalid (Turland et al. 2018). Cao et al. (2003) proposed a new name *T. zangii* to replace *T. quercicola* M. Zang 1990, which is a later homonym of *T. quercicola* (Murrill) Murrill 1949.

Seven specimens of this species were cited from Sichuan and Yunnan in Zang (1990) and Cao et al. (2003) (holotype, KUN-HKAS19947; KUN-HKAS16977; KUN-HKAS18210; KUN-HKAS14644; KUN-HKAS17632; KUN-HKAS32450 and KUN-HKAS32449). We traced five of them in the herbarium (KUN-HKAS17632; KUN-HKAS16977; KUN-HKAS32450; KUN-HKAS14644 and KUN-HKAS32449) and generated ITS sequences from the collections. ITS phylogenetic data indicated that they should be treated as *T. matsutake*. The sample KUN-HKAS18210, which was collected from alpine broad-leaved forests in Aba (Ngawa) Tibetan and Qiang Autonomous Prefecture, Sichuan Province, China, was not found. Unfortunately, the holotype (KUN-HKAS19947) for this species has not been traced, and, thus, no sequence from the holotype is available. The collections of *T. zangii* are probably populations of *T. matsutake* instead of an independent species. For the time being, *T. zangii* is listed here.

Tricholoma sect. *Muscaria* Reschke

Type: *Tricholoma muscarium* Kawam. ex Hongo, Mem. Fac. lib. Arts Educ. Shiga Univ., Nat. Sci. 9: 62 (1959).

Description: Basidioma tricholomatoid. Pileus more or less umbonate at center, yellow, brown or olivaceous, glabrous, squarrose or radially fibrillose. Lamellae subclose to close. Basidiospores medium-sized, broadly ellipsoid to ellipsoid, thin-walled, smooth, inamyloid. Pleurocystidia absent. Cheilocystidia present and conspicuous. Pileipellis with a differentiated subpellis made of inflated cells. Clamps absent.

Ecology: Ectomycorrhizal. On soil with various trees.

Known distribution: Molecular data indicated species from this section are distributed in North America and Asia.

Notes: To date, six species, including three species described as new in this paper, occur in China (see below).

Key to the species of *Tricholoma* sect. *Muscaria* from China

1. Stipe with obvious orange color *T. aurantiipes*
1. Stipe white, dirty white, greyish, brownish, without orange color 2
2. Pileal margin bright yellow, yellow, dirty yellow to yellowish 3
2. Pileal margin without obvious yellow color 4
3. Pileal center with obvious olivaceous color, olive-grey to olivaceous brown *T. muscarioides*
3. Pileal center without obvious olivaceous color, dark brown, grey-brown to brown *T. muscarium*
4. Pileus without obvious olivaceous color, yellow-brown, grey-brown to brown; lamellae at first dirty white, greyish to grey, later becoming yellowish brown to brownish; stipe greyish, yellowish brown to brownish, with brownish stains after bruised *T. sinense*
4. Pileus with olivaceous color; lamellae white to cream; stipe white to dirty white 5
5. Basidioma medium-sized; pileus dark brown, grey-brown to brown at center, olivaceous brown, brown to brownish towards margin, without obvious squamules; basidiospores relatively shorter, with mean length = 6.3 µm *T. turgidum*
5. Basidioma small to medium-sized; pileus olivaceous, densely covered with olivaceous brown squamules; basidiospores relatively longer, with mean length = 6.9 µm *T. olivaceiceps*

47. *Tricholoma aurantiipes* Hongo, Trans. Mycol. Soc. Japan 32(4): 464 (1991)

Ecology: On soil under deciduous trees (Hongo 1991).

Known distribution: Currently known from East Asia (Hongo 1991, Ko et al. 2012, Reschke et al. 2018).

Notes: *Tricholoma aurantiipes* was originally described from Japan (Hongo 1991), and reported from Korea (Ko et al. 2012). Reschke et al. (2018) provided an ITS sequence (MF034227) from a specimen (MB-003000) collected from Yunnan, China and delimited as *T. aurantiipes*. Because no additional material is available for this study, we follow the treatment of Reschke et al. (2018). The detailed morphological characters of *T. aurantiipes* was not provided here due to lack of specimens.

48. *Tricholoma muscarioides* Reschke et al., Mycologia 110 (6): 1096 (2018). Figs. 53k, l, 65

Description: Basidioma medium-sized. Pileus 5–9 cm in diam., convex, plano-convex to applanate, papillate; surface dry, olive-grey (1D2–4, 2D3–5) to olivaceous brown (3D3–5, 3E3–6) at center, becoming bright yellow (1A2–6) to yellow (2B3–7) towards margin, sometimes greyish brown (2D4–6, 3D4–7) to brown (4D3–6) overall, covered with olivaceous brown (3D3–5, 3E3–6) to greyish brown (2D4–6, 3D4–7) fibrillose squamules; margin irregularly undulating and slightly reflexed, sometimes radially splitting; context white (1A1). Lamellae sinuate, white (1A1) to cream (1B3), subclose

to close; edges entire, white (1A1) to cream (1B3). Stipe 8–16 × 1–2.5 cm, cylindrical, sometimes tapering downwards, at first solid, then stuffed to hollow, white (1A1) to brownish (3B2–4), fibrillose, exannulate. Taste slightly bitter. Odour not recorded.

Basidiospores [20/1/1] 6.5–7.5 × 4–5 µm (mean length = 6.9 µm, mean width = 4.7 µm), $Q = (1.3\text{--})1.35\text{--}1.56\text{--}(1.67)$, $Q_m = 1.46 \pm 0.1$, predominantly ellipsoid, occasionally broadly ellipsoid or elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 30–40 × 7–10 µm, clavate, 4-spored, hyaline; sterigmata 4–6 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 15–60 × 5–20 µm, conspicuous, cylindrical, clavate, subclavate, fusiform to irregular shaped, sometimes septate, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 µm wide filamentous hyphae, clamps absent. Pileipellis a cutis, composed of radially arranged, 5–15 µm wide, thin-walled, brownish filamentous hyphae; subpellis composed of radially arranged inflated cells, subfusiform, fusiform to

ellipsoid to cylindrical, 25–35 × 8–20 µm, thin-walled, colorless. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in subtropical forests dominated with trees of Fagaceae, or sometimes mixed with conifers.

Known distribution: Known from Southwestern China.

Specimens examined: CHINA. Yunnan Province, Honghe Hani and Yi Autonomous Prefecture, Lvchun County, Amoebin Forest Park, in a broad-leaved forest, altitude 1600 m, 22 Sep. 2019, 532531MF0354 (KUN-HKAS134993); same location, 23 Sep. 2019, 532531MF0484 (KUN-HKAS134994); same location; Lijiang, Yulong Naxi Autonomous County, Lijiang Alpine Botanic Garden, in a mixed forest with *Quercus* and *Pinus*, altitude 2700 m, 10 Sep. 2019, Jian-Wei Liu 1954 (KUN-HKAS134995); same city, Gucheng, Longshan Village, in a broad-leaved forest, altitude 2700 m, 21 Aug. 2010, Qi Zhao 1016 (KUN-HKAS69737); Puer, Jingdong Yi Autonomous County, Ailao Mountain, in a *Quercus* dominated broad-leaved forest, altitude 2500 m, 15 Jul. 2007, K. Donges, G. Kost and K.-H. Rexer (holotype, KUN-HKAS93512).

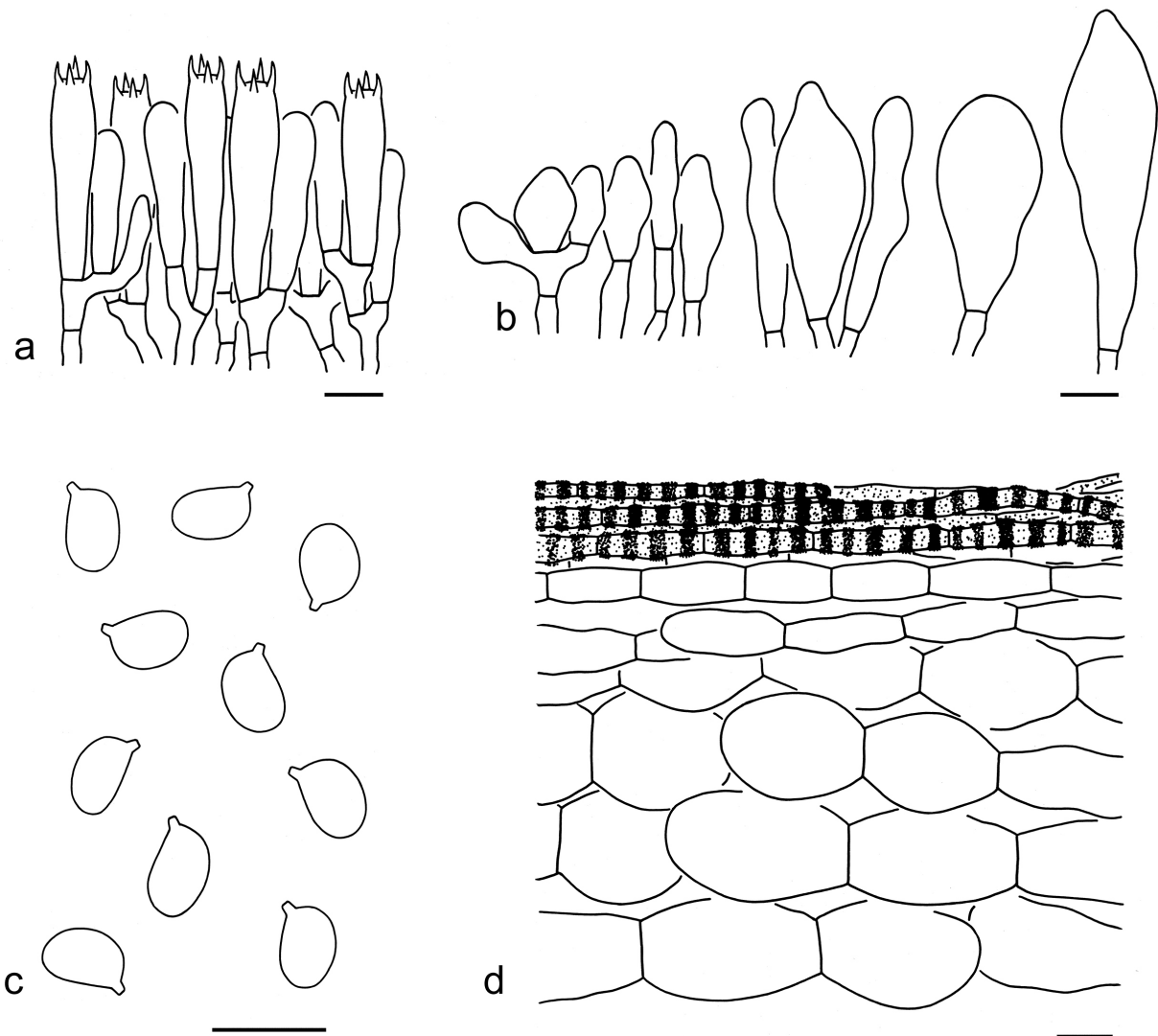


Fig. 65 Microscopic features of *Tricholoma muscarioides* (holotype, KUN-HKAS93512). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm.

Notes: *Tricholoma muscarioides* was described by Reschke et al. (2018). This species is recognized by an papillate pileus with an olive-grey to olivaceous brown center and a bright yellow to yellow margin, and the main occurrence in broad-leaved forests (this study). Based on the tree inferred from the ITS sequences, *T. muscarioides* is closely related to *T. turgidum* Y.Y. Cui & Zhu L. Yang (Fig. 4), but the latter has a pileus without bright yellow color, which is grey-brown at center and brown to brownish at margin. In addition, *T. turgidum* is mainly distributed in conifers-dominated forests.

Tricholoma muscarioides can be confused with *T. muscarium* Kawam. ex Hongo due to its yellow pileal margin. However, the latter species has a dark brown, grey-brown to brown pileal center without obviously olivaceous color. *Tricholoma davisiae* Peck is somewhat similar to *T. muscarioides*, but has a relatively larger basidioma (3–16 cm), develops pink orange stains on the stipe and lamellar edges, and grows with conifers (Bessette et al. 2013).

49. *Tricholoma muscarium* Kawam. ex Hongo, Mem. Fac. lib. Arts Educ. Shiga Univ., Nat. Sci. 9: 62 (1959). Figs. 53m, 66

Description: Basidioma small to medium-sized. Pileus 4–9 cm in diam., convex to applanate, often papillate at center; surface dry, dark brown (4E3–6), grey-brown (2E4–7) to brown (4D3–6) at center, becoming yellow (4A4–6), dirty yellow (3B4–

7) to yellowish (1A2–5) towards margin, sometimes with a white (1A1) marginal zone, covered with minute, brown (4D3–6) to greyish brown (3D3–6) squamules, margin straight to deflexed; context white to cream-colored. Lamellae sinuate, white (1A1) to cream (1A2–4), subclose to close; edges entire, white (1A1) to cream (1A2–4). Stipe 8–10 × 1.5–2 cm, cylindrical, dry, stuffed to hollow, white (1A1), glabrous or with white (1A1) fibrils, exannulate. Taste and odour not recorded.

Basidiospores [40/2/2] 6–8 × 4–5.5 µm (mean length = 7 µm, mean width = 4.8 µm), Q = (1.27–) 1.3–1.6 (–1.63), Qm = 1.45 ± 0.08, ellipsoid, occasionally broadly ellipsoid or elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 35–50 × 7–9 µm, clavate, 4-spored, hyaline; sterigmata 4–6 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 10–60 × 5–12 µm, conspicuous, clavate to subclavate, sometimes irregularly shaped, often septate, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 µm wide filamentous hyphae; clamps absent. Pileipellis a cutis, composed of radially arranged, 5–15 µm wide, thin-walled, brownish to brown filamentous hyphae, terminal elements subcylindrical, with round apex; subpellis composed of radially arranged inflated cells, ellipsoid, fusiform to clavate, 30–100 × 15–50 µm, thin-walled, yellowish to colorless. Clamps absent in all parts of basidioma.

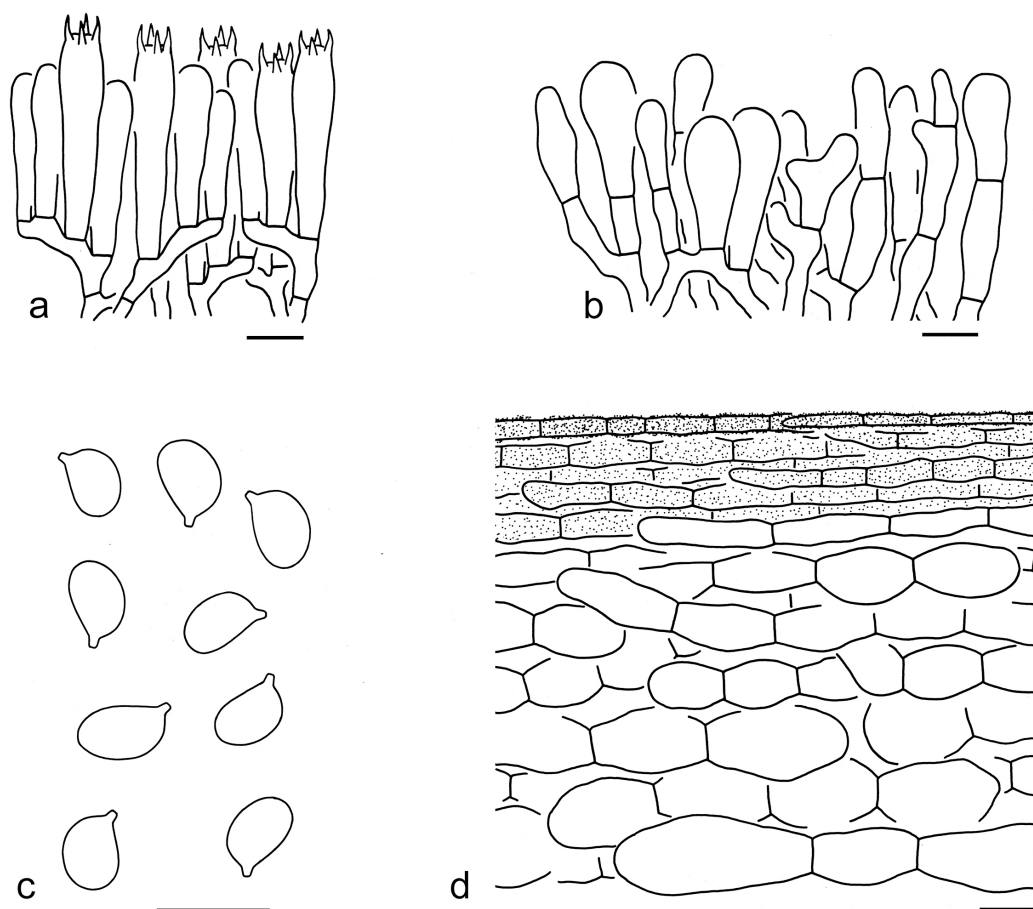


Fig. 66 Microscopic features of *Tricholoma muscarium* (KUN-HKAS106307). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm.

Ecology: Solitary to scattered on soil in subtropical broad-leaved forests.

Known distribution: Reported from Japan (Hongo 1959) and China (Deng et al. 2004).

Specimens examined: CHINA. Yunnan Province, Chuxiong Yi Autonomous Prefecture, Nanhua County, in a broad-leaved forest with trees of Fagaceae, altitude 2300 m, 12 Aug. 2017, Jian-Wei Liu 899 (KUN-HKAS106307); Kunming, Shuanglong Village, Yeyahu Lake, in a broad-leaved dominated forest, altitude 2100 m, 18 Aug. 2012, Hui Chen 40 (KUN-HKAS134996); same location, in a broad-leaved forest, altitude 2100 m, 18 Aug. 2012, Ting Guo 582 (KUN-HKAS76274).

Notes: *Tricholoma muscarium* was published by Hongo (1959) from Japan, and then reported from China (Deng et al. 2004). This species can be recognized by its papillate, dark brown, grey-brown to brown pileal center and yellow, dirty yellow to yellowish pileal margin. *Tricholoma olivaceiceps* Y.Y. Cui & Zhu L. Yang resembles *T. muscarium*, but the former has an olivaceous pileus densely covered with olivaceous brown squamules. *Tricholoma muscarioides* and *T. davisiae* are similar in their yellow color at the pileal margin. However, *T. muscarioides* has a pileus with obvious olivaceous colors, often olive-grey to olivaceous brown at center. *Tricholoma davisiae* can be separated by its relatively larger basidioma (3–16 cm), pink-orange stains on the stipe and lamellar edges, and associations with conifers (Bessette et al. 2013).

50. *Tricholoma olivaceiceps* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 53n, 67

Fungal Names: FN 572341

Etymology: *olivaceiceps* = olive-headed, referring to its olivaceous pileus.

Diagnosis: Similar to *T. turgidum*, but differs by its relatively smaller basidioma (3–7 cm), densely olivaceous brown squamules on pileal surface and association dominated with broad-leaved trees.

Type: CHINA. Yunnan Province, Puer, Lancang Lahu Autonomous County, Qianliu Village, in a forest with trees of *Castanopsis* and *Pinus*, altitude 1300 m, 10 Nov. 2017, Zhu L. Yang 6091 (holotype, KUN-HKAS101280).

Description: Basidioma small to medium-sized. Pileus 3–7 cm diam, plano-convex to applanate, papillate at center; surface dry, olivaceous (1D4–8, 30C4–7), but darker at center, densely covered with minute, olivaceous brown (1D3–6, 30D4–7) squamules; margin straight; context whitish. Lamellae sinuate, at first with greyish tinge, becoming whitish to cream when mature, subclose; edges white (1B1–2), dirty white (1A1, 1B2) to cream (1B2–3). Stipe 5–7 × 0.5–1 cm, cylindrical to subcylindrical, dry, dirty white (2B1–3), with grey (1B1) to greyish (1B2–3) fibrils, exannulate. Taste not recorded, odour indistinct.

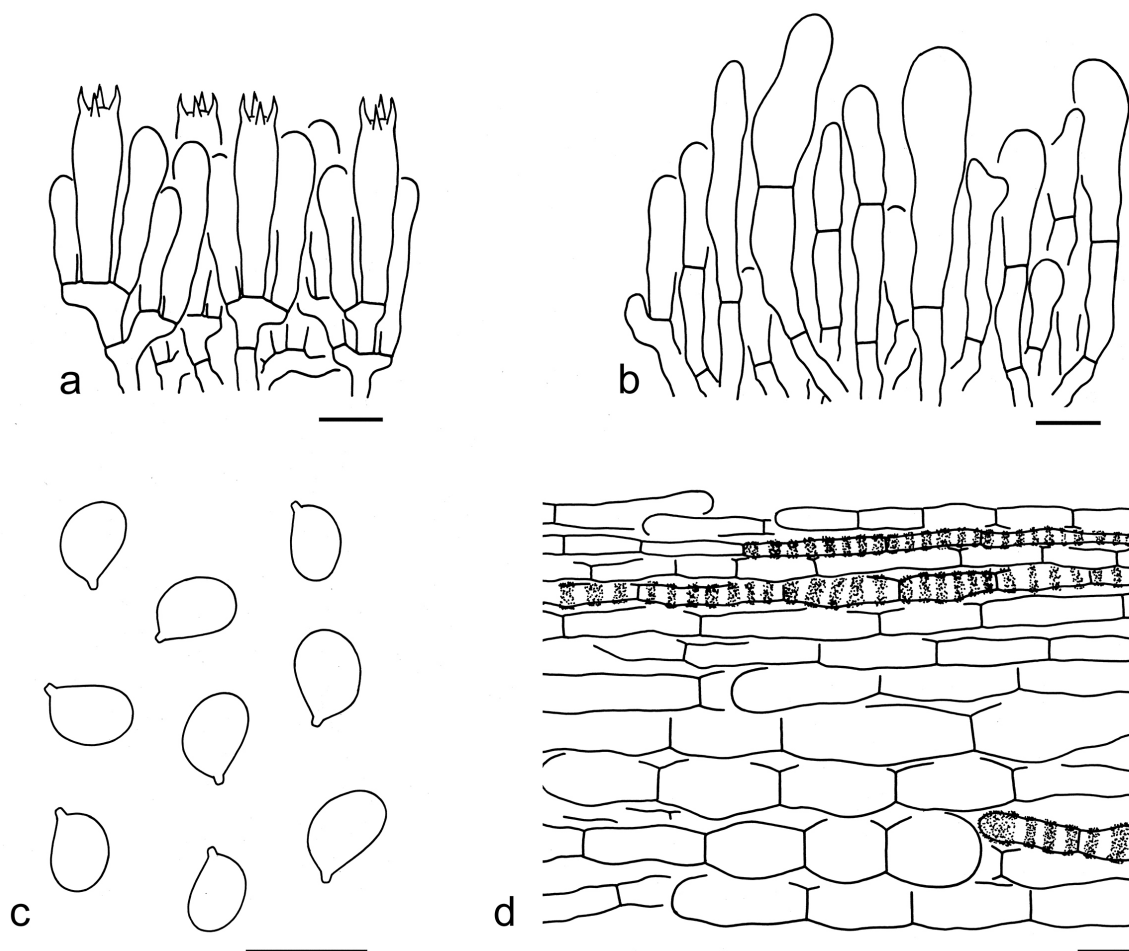


Fig. 67 Microscopic features of *Tricholoma olivaceiceps* (holotype, KUN-HKAS101280). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 μ m, d = 20 μ m.

Basidiospores [60/3/2] $6\text{--}8 \times 4\text{--}6 \mu\text{m}$ (mean length = $6.9 \mu\text{m}$, mean width = $4.8 \mu\text{m}$), $Q = 1.2\text{--}1.67$ (-1.71), $Q_m = 1.43 \pm 0.11$, broadly ellipsoid to ellipsoid, occasionally elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $25\text{--}40 \times 7\text{--}9 \mu\text{m}$, clavate, 4-spored, rarely 2-spored or 1-spored, hyaline; sterigmata $4\text{--}7 \mu\text{m}$ long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia $20\text{--}40 \times 6\text{--}15 \mu\text{m}$, conspicuous, clavate to subclavate, often septate, thin- or slightly thick-walled, brownish, hyaline. Subhymenium composed of $3\text{--}6 \mu\text{m}$ wide filamentous hyphae; clamps absent. Lamellar trama regular, composed of colorless, thin-walled, ellipsoid, fusiform, clavate to filamentous hyphae $3\text{--}30 \mu\text{m}$ wide. Pileipellis a cutis, composed of radially arranged, $5\text{--}10 \mu\text{m}$ wide, thin-walled, brownish to brown filamentous hyphae, terminal elements subcylindrical, with round apex; subpellis composed of radially arranged inflated cells, ellipsoid, subfusiform to clavate, $30\text{--}65 \times 10\text{--}30 \mu\text{m}$, thin-walled, brownish to brown or colorless. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in broad-leaved dominated forests.

Known distribution: Known from autumn in Southwestern China.

Additional specimen examined: CHINA. Yunnan Province, Puer, Lancang Lahu Autonomous County, Fazhanhe Village, in a subtropical broad-leaved forest, altitude 1400 m, 25 Sep. 2016, MF-LJW166 (KUN-HKAS97670).

Notes: *Tricholoma olivaceiceps* can be recognized by its olivaceous pileus densely covered with olivaceous brown squamules, and white to dirty white lamellae. It is closely related to *T. turgidum* and *T. muscarioides* (Figs. 3, 4). *Tricholoma turgidum* is similar but can be separated. For comparisons, see notes under that that name. *Tricholoma muscarioides* differs from *T. olivaceiceps* by its bright yellow to yellow color on pileal margin.

Morphologically, *T. luteomaculosum* A.H. Sm. is similar to *T. olivaceiceps*. However, *T. luteomaculosum* has a mostly dark brownish grey or bluish grey pileus without olivaceous color, and its lamellar edges often stain dark brownish grey to blackish (Ovrebo 1986; Bessette et al. 2013).

51. *Tricholoma sinense* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 53o, 68

Fungal Names: FN 572347

Etymology: sinense = chinese, referring its type locality from China.

Diagnosis: Similar to *T. luteomaculosum*, but differs by its relatively smaller basidioma and a greyish, yellowish brown to brownish stipe covered with grey, grey-brown to yellow-brown fibrils.

Type: CHINA. Yunnan Province, Lijiang, Dadong Village, in a subtropical mixed forest with *Pinus armandii* and *Quercus semicarpifolia*, altitude 2500 m, 18 Aug. 2010, Qi Zhao 948 (holotype, KUN-HKAS69669).

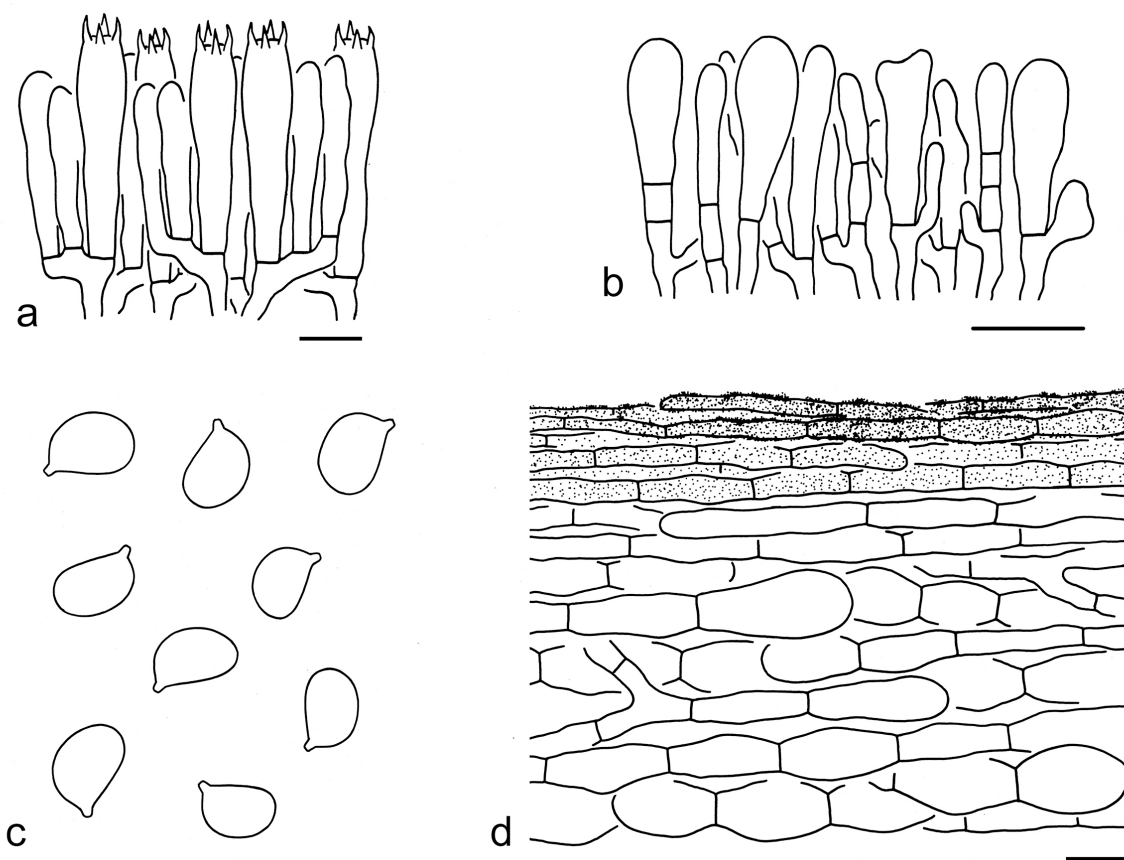


Fig. 68 Microscopic features of *Tricholoma sinense* (holotype, KUN-HKAS69669). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = $10 \mu\text{m}$, d = $20 \mu\text{m}$.



Fig. 69 Fresh basidiomata of the species in *Tricholoma*. a *T. turgidum* (holotype, KUN-HKAS77500). b *T. asiaticum* (holotype, KUN-HKAS92443). c *T. atrovirens* (KUN-HKAS80796). d *T. boudieri* (KUN-HKAS99445). e *T. ellipsosporum* (KUN-HKAS134999). f *T. olivaceum* (KUN-HKAS83119). g *T. saponaceum* (KUN-HKAS99361). h *T. sichuanense* (holotype, KUN-HKAS105344). i *T. yunnanense* (KUN-HKAS106610). j *T. highlandense* (type, KUN-HKAS70192). k *T. nigrosquamosum* (KUN-HKAS89643). l *T. lishanense* (KUN-HKAS105390). m *T. stiparophyllum* (KUN-HKAS135000). n *T. inamoenum* (KUN-HKAS79926). o *T. sulphureum* type I (KUN-HKAS53473).

Description: Basidioma small to medium-sized. Pileus 3–8 cm diam, plano-convex to applanate, sometimes slightly broadly umbonate at center; surface dry, yellow-brown (4C4–7), grey-brown (4D3–5, 3D2–6) to brown (5D3–6), densely covered with minute, yellow-brown (4C4–7), grey-brown (4D3–5, 3D2–6) to brown (5D3–6) squamules; margin slightly incurved; context white (1A1). Lamellae sinuate, at first dirty white (1B1), greyish (1B1) to grey (2B1–3), becoming yellowish brown (4B2–4) to brownish (3C2–4) with age, subclose to close; edges smooth, entire to slightly undulate, greyish, yellow-brown (4B2–4) to brownish (3C2–4). Stipe 4–11 × 1–2 cm, cylindrical to subclavate, stuffed, dirty white (1B2–3), greyish (1B1), yellowish brown (4B2–4) to brownish (3C2–4), bruising brownish (4B2–4) after touch, covered with grey (1D1), grey-brown (3D2–4), yellow-brown (4D2–5) fibrils, exannulate. Taste not recorded. Odour similar to that of *T. matsutake*.

Basidiospores [120/6/4] (5.5–) 6–8 (–8.5) × 4–6 µm (mean length = 6.7 µm, mean width = 5 µm), Q = 1.18–1.55 (–1.73), Qm = 1.36 ± 0.09, broadly ellipsoid to ellipsoid, occasionally elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 30–45 × 7–9 µm, clavate, 4-spored, hyaline; sterigmata 3–5 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 20–35 × 5–10 µm, clavate to subclavate, often septate, thin-walled, colorless, hyaline. Subhymenium composed of 3–5 µm wide filamentous hyphae; clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae 2–20 µm wide. Pileipellis a cutis, composed of radially arranged, 5–12 µm wide, thin-walled, brownish filamentous hyphae, terminal elements subcylindrical, with round apex; subpellis composed of radially arranged inflated cells, ellipsoid, fusiform to clavate, 15–50 × 10–20 µm, thin-walled, colorless. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered dominated in subtropical coniferous or mixed forests with trees of *Pinus* and *Fagaceae*.

Known distribution: Known from Southwestern China.

Additional specimens examined: CHINA. Yunnan Province, Kunming, Aziying, in a mixed forest, altitude 2050 m, 12 Jul. 2018, Xiao-Xia Ding 346 (KUN-HKAS105356); Lijiang, Qihe Village, in a pine forest with *Pinus yunnanensis*, altitude 2423 m, 27 Jul. 2011, Li-Ping Tang 1316 (KUN-HKAS69777); Nujiang Lisu Autonomous Prefecture, Lanping Bai and Pumi Autonomous County, in a pine forest with *Pinus yunnanensis*, altitude 2200 m, 15 Aug. 2011, Jiao Qin 375 (KUN-HKAS73361).

Notes: *Tricholoma sinense* is characterized by its yellow-brown, grey-brown to brown pileus densely covered with concolorous squamules, and dirty white, greyish to grey lamellae becoming yellowish brown to brownish with age. It is related to *T. aurantiipes* with moderate support (Fig. 4).

Tricholoma luteomaculosum has a similar pileal color and its stipe with brownish staining after touch. However, this species differs from *T. sinense* by its relatively larger basidioma (4–12 cm) and relatively light colored stipe (white to pale grey) without obvious squamules (Ovrebo 1986; Bessette et al. 2013). *Tricholoma olivaceiceps* also somewhat resembles, but has an olivaceous pileus with olivaceous brown squamules, white to cream lamellae and a white stipe without color change.

52. *Tricholoma turgidum* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 69a, 70

Fungal Names: FN 572348

Etymology: *turgidum* = inflated, referring to its inflated cells in subpellis.

Diagnosis: Related and similar to *T. muscarioides*, but differs in its greyish brown to brown pileal margin without yellow color and the association with coniferous trees.

Type: CHINA. Yunnan Province, Lijiang, Yulong Naxi Autonomous County, Yulong Snow Mountain, in a forest with *Pinus yunnanensis*, altitude 2490 m, 16 Sep. 2012, Kuan Zhao 147 (holotype, KUN-HKAS77500).

Description: Basidioma medium-sized. Pileus 6–9 cm in diam., convex, plano-convex to applanate, sometimes with a pronounced or low papilla; surface dry, grey-brown (3D2–4, 3E5–8) to dark brown (3E2–4, 2E2–4) in the central part, greyish brown (2C2–5), brown (3C4–7) to brownish (3B3–5) towards margin, sometimes greyish brown (2C2–5), greyish yellow (2D2–5) to brown (3C4–7) overall, often with olivaceous (30B4–6) tinge over the entire part, covered with brown (3C4–7), minutely granular squamules; margin irregularly undulating; context white (1A1) to cream (1A2). Lamellae adnexed to sinuate, white (1A1) to cream (1A2, 1B3), subclose to close; edges entire, white to cream. Stipe 6–9 × 0.7–1.5 cm, cylindrical to subcylindrical, equal, stuffed to hollow, white (1A1), bruising brownish (3B2–4) after touch, smooth or fibrillose, exannulate. Taste not recorded. Odour like soap.

Basidiospores [160/8/4] 5–7 (–9) × 4–5.5 (–6) µm (mean length = 6.3 µm, mean width = 4.5 µm), Q = (1.13–) 1.2–1.6 (–1.95), Qm = 1.4 ± 0.12, broadly ellipsoid to ellipsoid, occasionally elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 28–40 × 7–10 µm, clavate, 4-spored, hyaline; sterigmata 4–6 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 20–40 × 5–15 µm, conspicuous, cylindrical, subclavate to clavate, often septate, thin- to slightly thick-walled (≤ 1 µm), colorless, hyaline. Subhymenium composed of 2–4 µm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin- to slightly thick-walled, clavate, cylindrical to filamentous hyphae 5–30 µm wide. Pileipellis a cutis, composed of radially arranged, 5–18 µm wide, thin-walled, yellow-brown to brownish filamentous hyphae; subpellis composed of radially arranged inflated cells, subglobose, subfusiform, fusiform to ellipsoid, 25–80 × 15–35 µm, thin-walled, colorless. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil dominated in forests with trees of *Pinus*, sometimes mixed with broad-leaved trees.

Known distribution: Known from Southwestern China.

Additional specimens examined: CHINA. Yunnan Province, Kunming, bought from Aziying Village, altitude 2050 m, 12 Jul. 2018, Xiao-Xia Ding 340 (KUN-HKAS 105350); Lijiang, Gucheng, Jinshan Village, in a forest with *Pinus yunnanensis*, altitude 2300 m, 16 Sep. 2012, Qi Zhao 1685 (KUN-HKAS78943); same city, Yulong Naxi Autonomous County, Lijiang Alpine Botanic Garden, in a broad-leaved forest, altitude 2700 m, 24 Aug. 2019, Jian-Wei Liu 1776 (KUN-HKAS134997).

Notes: *Tricholoma turgidum* is characterized by its papillate pileus, which is dark brown, grey-brown to brown in the central part and olivaceous brown, brown to brownish towards margin. It is predominantly associated with trees of conifers. *Tricholoma turgidum* is sister to *T. muscarioides* in the tree generated from the ITS sequences (Fig. 4), but differs

by its non-yellow pileal margin and the association with conifers.

Morphologically, *T. luteomaculosum* and *T. olivaceiceps* are similar to *T. turgidum*, but can be separated. *Tricholoma luteomaculosum* has a pileus mostly dark brownish or bluish grey overall, and its lamellar edges often stain dark brownish

grey to blackish (Ovrebo 1986; Bessette et al. 2013). *Tricholoma olivaceiceps* differs by its relatively smaller basidioma (3–7 cm), densely olivaceous brown squamules on pileal surface and association dominated with broad-leaved trees.

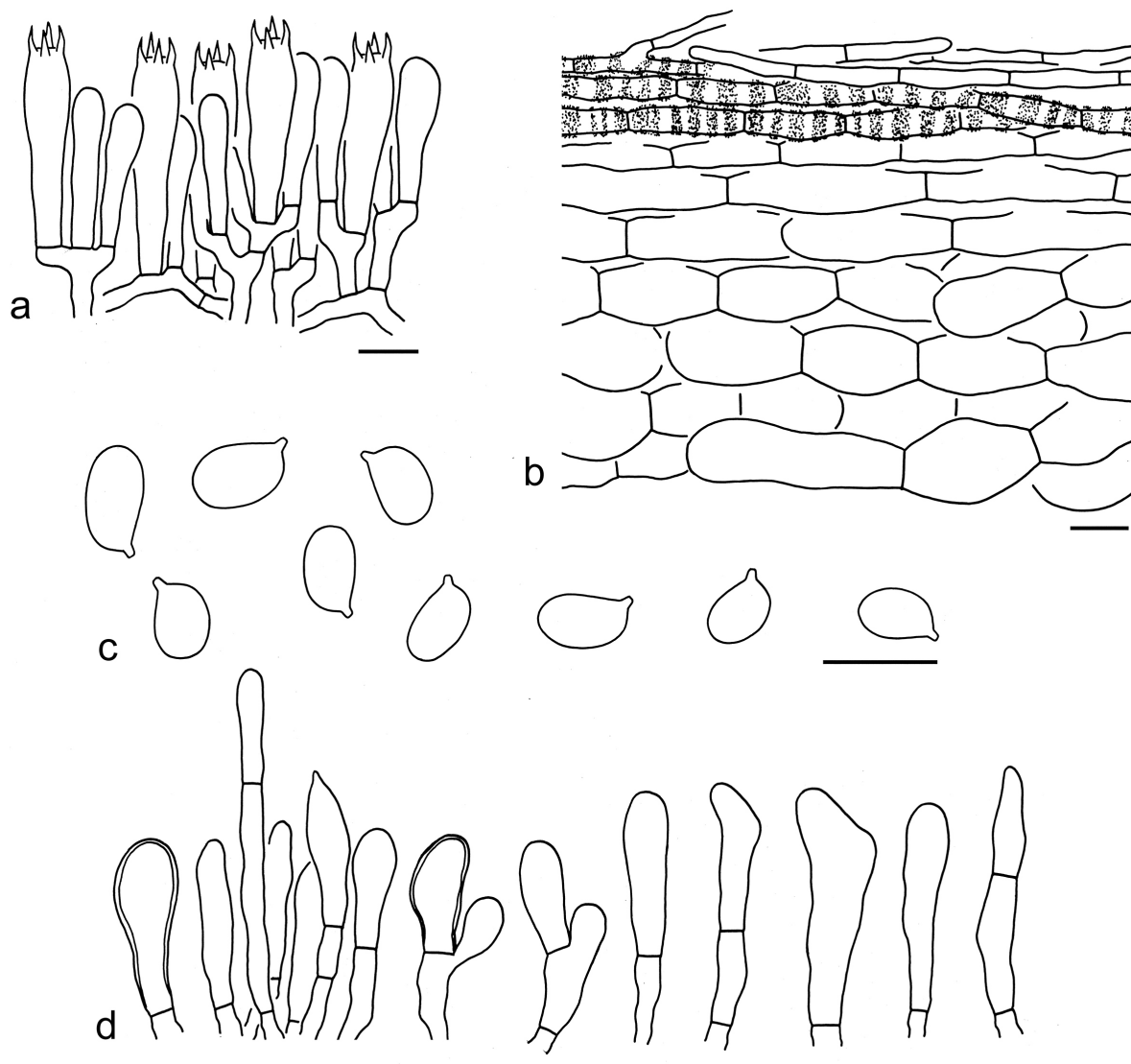


Fig. 70 Microscopic features of *Tricholoma turgidum* (holotype, KUN-HKAS77500). a Hymenium and subhymenium. b Pileipellis. c Basidiospores. d Marginal cells. Scale bars: a, c, d = 10 µm, b = 20 µm.

Tricholoma sect. *Rigida* (Fr.) Quél.

Type: *Tricholoma saponaceum* (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 133 (1871).

Description: Basidioma tricholomatoid. Pileus umbonate or not, grey-brown, yellow-brown to brown pileus, mostly glabrous and with greenish color. Lamellae close to subdistant. Stipe subcylindrical to cylindrical, without annulus. Basidiospores small, broadly ellipsoid to ellipsoid, thin-walled, smooth, inamyloid. Pleurocystidia absent. Cheilocystidia present or absent. Pileipellis a cutis or an ixocutis. Clamps present.

Ecology: Ectomycorrhizal. On soil with various trees.

Known distribution: Molecular data indicated species from this section are distributed in Europe, North America, and Asia.

Notes: Species in sect. *Rigida* are challenging to differentiate due to their similar morphologies. Compared with the phylogenetic analysis based on the ITS sequences, the analyses based on the five gene fragments are more accurate in recognizing the phylogenetic species of this section by using the GCPSR criteria. Based on the multi-gene phylogenetic analyses, morphological characters, and ecological data, nine species from this section, including four new and five known ones, are identified (see below).

Key to the species of *Tricholoma* sect. *Rigida* from China

1. Basidioma staining yellow when old, damaged or touched *T. forteflavescens*
1. Basidioma without yellow change when old, damaged or touched 2
2. Basidioma often with strong reddening reaction with age and when damaged *T. boudieri*
2. Basidioma without strong reddening 3
3. Subpellis composed of more or less slightly inflated hyphae, ellipsoid, cylindrical, cylindrical to filamentous; distributions in subalpine forests with *Abies* *T. saponaceum*
3. Subpellis composed of filamentous hyphae; distributions in coniferous, broad-leaved or mixed forests 4
4. Pileus blackish grey, grey-brown, brown to greyish white, without green tinge; basidiospores relatively smaller, mean length < 5.5 μm , mean width < 4 μm 5
4. Pileus grey-brown to yellow-brown, with green tinge; basidiospores relatively larger, mean length > 5.5 μm , mean width > 4 μm 7
5. Pileus dark blackish grey, greyish brown to brown, finely tomentose *T. asiaticum*
5. Pileus brown, grey-brown or greyish white, glabrous 6
6. Pileus paler, grey-brown to greyish white *T. atrovirens*
6. Pileus brown *T. yunnanense*
7. Basidiospores larger, with mean length up to 7 μm , mean width up to 5 μm *T. ellipsosporum*

7. Basidiospores relatively smaller, with mean length less than 7 μm , mean width less than 5 μm 8
8. Cheilocystidia conspicuous *T. sichuanense*
8. Cheilocystidia poorly differentiated *T. olivaceum*

53. *Tricholoma asiaticum* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 69b, 71

Fungal Names: FN 572333

Etymology: asiaticum = Asiatic, referring to its type locality from Asia.

Diagnosis: Somewhat related to *T. yunnanense* Y.Y. Cui & Zhu L. Yang, but differs by its greyish brown to brown pileus often finely tomentose.

Type: CHINA. Yunnan Province, Wenshan Zhuang and Miao Autonomous Prefecture, Guangnan County, Nanping Town, in a mixed forest with Pinaceae and Fagaceae, altitude 1300 m, 7 Aug. 2015, Kuan Zhao 813 (holotype, KUN-HKAS92443).

Description: Basidioma small to medium-sized. Pileus 3–10 cm in diam., convex to convex-applanate, slightly umbonate or not; surface dry, dark blackish grey (3E1–3), greyish brown (4D3–5) to brown (5C4–6), finely tomentose; margin straight; context white (1A1). Lamellae sinuate, white (1A1) to brownish (4B3–5), subclose to close; edges concolor. Stipe 3–8 $\times$ 1–2 cm, cylindrical to subclavate, greyish (1B1–3), basal part brownish (5B3–6) to pinkish (6A2), solid, exannulate. Taste not recorded. Odour slightly gas-like.

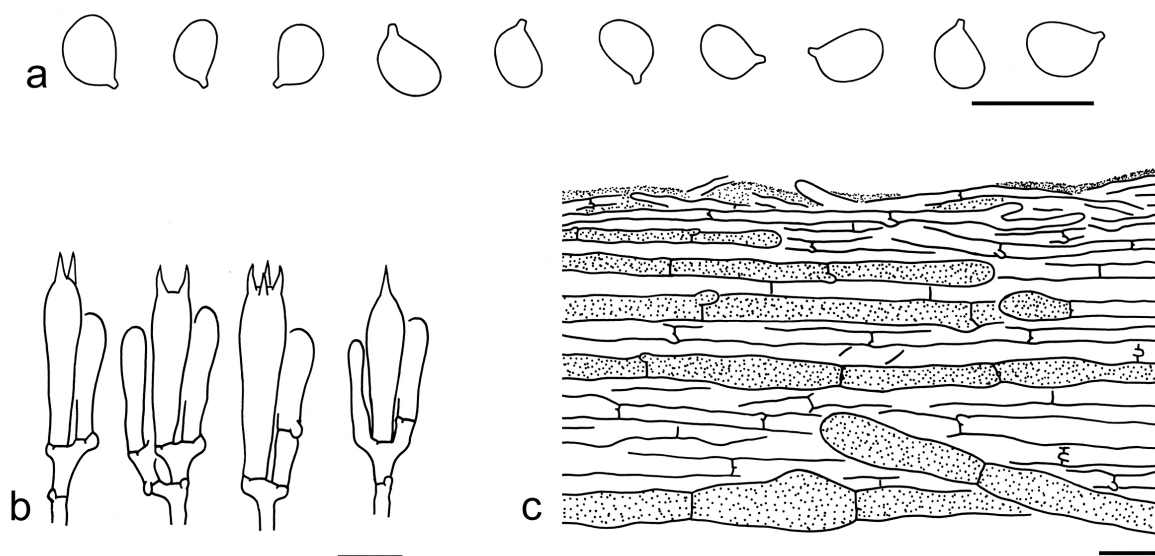


Fig. 71 Microscopic features of *Tricholoma asiaticum* (holotype, KUN-HKAS92443). a Basidiospores. b Hymenium and subhymenium. c. Pileipellis. Scale bars: a, b = 10 μm , c = 20 μm .

Basidiospores [60/3/1] 4–6 $\times$ 3–4.5 μm (mean length = 5.2 μm , mean width = 3.6 μm), $Q = (1.15\text{--}) 1.3\text{--}1.57$ (–1.67), $Q_m = 1.43 \pm 0.13$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 25–35 $\times$ 5–7 μm , clavate, 1-, 2- to 4-spored, hyaline; sterigmata 4–7 μm long; basal septa with clamps. Pleurocystidia and cheilocystidia absent. Subhymenium composed of 2–5 μm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-

walled, clavate, cylindrical to filamentous hyphae 3–25 μm wide. Pileipellis a cutis, slightly gelatinized, composed of radially arranged, 3–8 μm wide, thin-walled, yellowish to brownish, filamentous hyphae; subpellis poorly differentiated, composed of radially arranged, colorless, yellowish to brownish, clavate to filamentous hyphae 5–20 μm wide. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in mixed forests with Pinaceae and Fagaceae.

Known distribution: Southwestern China.

Additional specimen examined: CHINA. Yunnan Province, Kunming, Panlong District, Jindian, in a mixed forest with *Pinus* and *Quercus*, altitude 1900 m, 1 Sep. 2007, Zhu L. Yang 4943 (KUN-HKAS52260); Kunming, Panlong District, Heilongtan, forest and altitude not recorded, 4 Sep. 2011, Yan-Jia Hao 585 (KUN-HKAS71694); Kunming, Xishan District, Xishan, forest and altitude not recorded, 22 Sep. 2012, Ting Guo 624 (KUN-HKAS81826).

Notes: *Tricholoma asiaticum* can be well separated from other species of sect. *Rigida* by its dark blackish grey to greyish brown and tomentose pileus, and broadly ellipsoid to ellipsoid basidiospores ($4\text{--}6 \times 3\text{--}4.5 \mu\text{m}$). This species is somewhat related to *T. yunnanense* in the five-gene analysis (Fig. 3), and has been compared under the latter species.

54. *Tricholoma atrovirens* (Pers.) Sacc., Syll. fung. (Abellini) 5: 106 (1887). Figs. 69c, 72

Description: Basidioma small to medium-sized. Pileus 4–8 cm in diam., convex, plano-convex to applanate, somewhat slightly umbonate; surface dry, grey-brown (2E2–5) to greyish brown (1D2–4) at center, becoming brownish (2B2–4), yellowish (1A2–4) to white (1A1) towards margin, glabrous;

margin straight; context white (1A1). Lamellae sinuate, white (1A1) to brownish (1B2–4), close; edges concolorous. Stipe 6–9 $\times$ 0.5–1.5 cm, cylindrical, brownish (4B2–4), hollow, exannulate. Taste not recorded. Odour unpleasant.

Basidiospores [20/1/1] $4.5\text{--}6 \times 3\text{--}4 \mu\text{m}$ (mean length = $5.1 \mu\text{m}$, mean width = $3.7 \mu\text{m}$), $Q = 1.24\text{--}1.51$ (-1.87), $Q_m = 1.38 \pm 0.14$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $25\text{--}40 \times 6\text{--}8 \mu\text{m}$, clavate, 4-spored, hyaline; sterigmata $2\text{--}4 \mu\text{m}$ long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia $25\text{--}50 \times 3\text{--}5 \mu\text{m}$, conspicuous, clavate, cylindrical to filiform, often branching, thin-walled, colorless, hyaline. Subhymenium composed of $2\text{--}4 \mu\text{m}$ wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled, cylindrical to filamentous hyphae $4\text{--}15 \mu\text{m}$ wide. Pileipellis a cutis, non- to slightly gelatinized, composed of radially arranged, $2\text{--}10 \mu\text{m}$ wide, thin-walled, colorless filamentous hyphae; subpellis poorly differentiated. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in broad-leaved or mixed forests with Fagaceae and Pinaceae.

Known distribution: Known from Europe and Southwestern China.

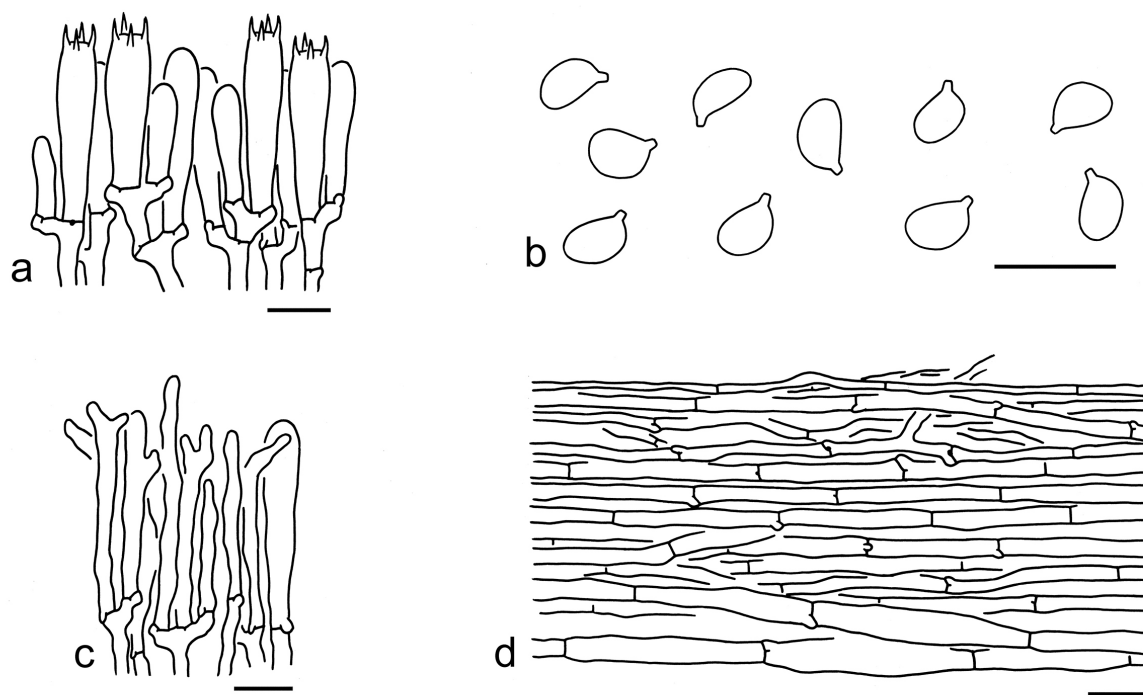


Fig. 72 Microscopic features of *Tricholoma atrovirens* (KUN-HKAS80796). a Hymenium and subhymenium. b Basidiospores. c Marginal cells. d Pileipellis. Scale bars: a–c = $10 \mu\text{m}$, d = $20 \mu\text{m}$.

Specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, Pengta Village, in a broad-leaved forest, altitude 3100 m, 10 Sep. 2016, KD-LJW 156 (KUN-HKAS97949). Yunnan Province, Lijiang, Yulong Naxi Autonomous County, Lijiang Observatory, in a mixed forest with *Lithocarpus*, *Picea* and *Pinus armandii*, altitude 2400 m, 31 Aug. 2013, Kuan Zhao 371 (KUN-HKAS80796).

Notes: *Tricholoma atrovirens* collected from China has a pileus often grey-brown at center and dirty white towards margin, broadly ellipsoid to ellipsoid basidiospores ($4.5\text{--}6 \times 3\text{--}4 \mu\text{m}$), conspicuous cheilocystidia and the presence of clamps (this study). This species was delimited as *T. saponaceum* in Heilmann-Clausen et al. (2017), but it is morphological similar and appears to be *T. atrovirens* (<https://svampe.databasesen.org/taxon/72030>). While the ITS

sequence DQ494700 seem to be the best candidate for the true *T. saponaceum* and has been recorded below.

In the phylogenetic analysis based on the ITS sequences (Fig. 4), *T. rapipes* (Krombh.) Heilm.-Claus. & Mort. Chr. was clustered together with *T. atrovirens*, but can be separated by its more yellow colored pileus and associations with *Abies* and *Picea* (Christensen & Heilmann-Clausen 2013; Heilmann-Clausen et al. 2017). Because no more gene fragments of *T. rapipes* are available for multi-locus phylogenetic analysis, this study treats them as two independent species for the time being. *Tricholoma yunnanense* is similar to *T. atrovirens*, but differs by its more brown pileus. *Tricholoma sudum* (Fr.) Quél. may be confused with it, but has slightly larger basidiospores ($5.1\text{--}7.9 \times 3.3\text{--}5.1 \mu\text{m}$) (Riva 1988; Christensen & Heilmann-Clausen 2013).

55. *Tricholoma boudieri* Barla, Bull. Soc. mycol. Fr. 3: 205 (1887). Figs. 69d, 73

Description: Basidioma medium-sized. Pileus 4–11 cm in diam., at first convex, then plano-convex to applanate, often concave when mature; surface dry, blackish (2E1–3, 2F1–3) to grey-brown (3E6–8) at center, becoming brown (4D2–4), brownish (4C2–4) to dirty white (1B1–2) towards margin, sometimes with greenish tinge (30A2–4), glabrous or covered

with dark brown (2E1–3, 2F1–3) fibrillose scales often concentrated at center; margin at first involute, often straight to reflexed when mature; context white (1A1) to dirty white (1B1–2), sometimes with strong reddening reaction with age and when damaged. Lamellae sinuate, white (1A1), dirty white (2B1), cream (1A2) to greenish yellow (30A2–4), subclose; edges concolor. Stipe 7–12 $\times$ 1–2.5 cm, cylindrical to subcylindrical, greenish yellow (30A2–4), brownish (30B2–4) to brown (5B3–5), stuffed to hollow, exannulate. Taste not recorded. Odour strong, unpleasant, like cucumber.

Basidiospores [100/5/3] 5–7 (–8) $\times$ 3.5–5 μm (mean length = 6.1 μm , mean width = 4.1 μm), $Q = (1.2\text{--}) 1.33\text{--}1.6$ (–1.78), $Q_m = 1.47 \pm 0.12$, ellipsoid, sometimes broadly ellipsoid or elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 30–40 $\times$ 5–8 μm , clavate, 4-spored, colorless to yellowish, hyaline; sterigmata 3–5 μm long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia poorly differentiated. Subhymenium composed of 2–4 μm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless to yellowish, thin-walled, cylindrical to filamentous hyphae 4–20 μm wide. Pileipellis a cutis, composed of radially arranged, 2–10 μm wide, thin-walled, brownish filamentous hyphae; subpellis poorly differentiated. Clamps present in all parts of basidioma.

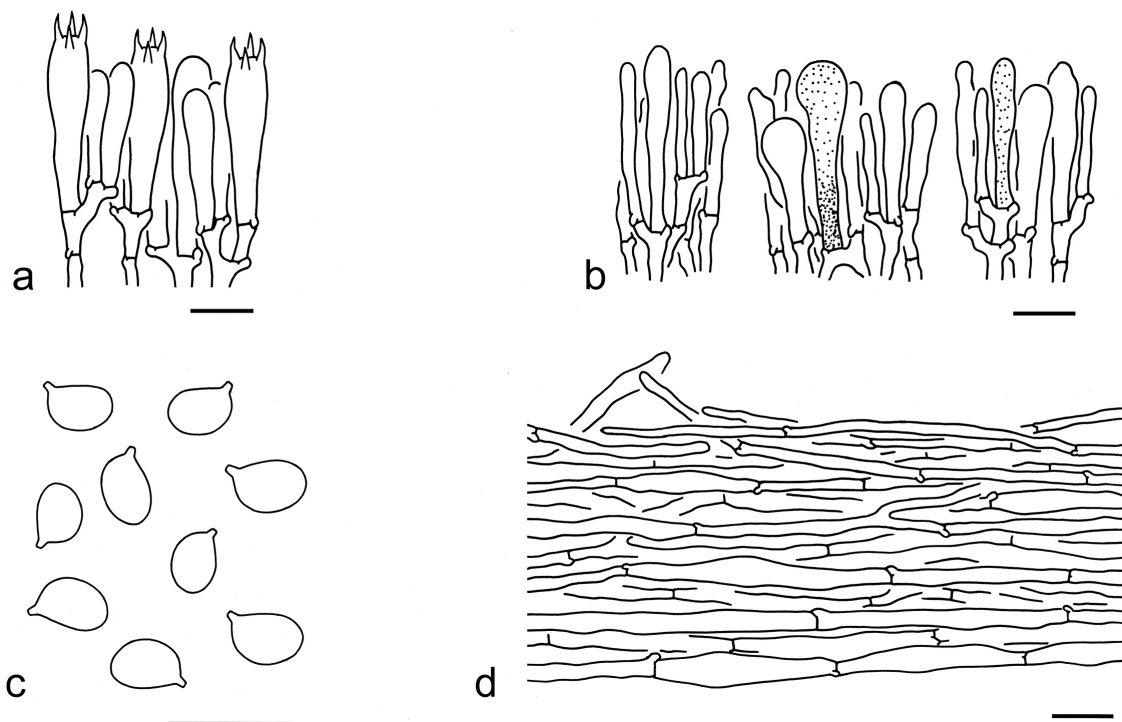


Fig. 73 Microscopic features of *Tricholoma boudieri* (KUN-HKAS99445). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 μm , d = 20 μm .

Ecology: Solitary to scattered on soil in forests with Fagaceae and Pinaceae.

Known distribution: Known from Europe, North America, and Southwestern China.

Specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, Waze Village, in a forest with *Abies*, altitude 3450 m, 8 Sep. 2016, KD-FB92

(KUN-HKAS99445); same location, in a mixed forest with Fagaceae and Pinaceae, altitude 3450 m, 8 Sep. 2016, KD-Ding 76 (KUN-HKAS97157); same location, in a mixed forest with Fagaceae and Pinaceae, altitude 3450 m, 8 Sep. 2016, Bang Feng 92 (KUN-HKAS99445); same city, Yala Village, in a mixed forest with Fagaceae and Pinaceae, altitude 3800 m, 9 Sep. 2016, KD-Ding 104 (KUN-HKAS97185), same city,

forest and altitude not recorded, 10 Sep. 2016, Bang Feng 86 (KUN-HKAS99439). Yunnan Province: Lijiang, Ninglang, forest type not recorded, altitude 3610 m, 22 Sep. 2019, Xiang-Hua Wang 6872 (KUN-HKAS138819). NORTH MACEDONIA. The forest type and altitude not recorded, 2 Oct. 2018, Zhu L. Yang MK4 (KUN-HKAS104331).

Notes: *Tricholoma boudieri* is a morphological variable species, and has a grey, grey-brown, yellow-brown to olivaceous brown pileus, and white, dirty white, yellowish to olivaceous yellow lamellae (this study). Our field observations revealed that the reddening reaction is unstable; certain basidioma of this species exhibit a pronounced reddening reaction with age or injury, while others do not. No closely related species of *T. boudieri* were detected in our phylogenetic analyses (Figs. 3, 4). *Tricholoma atrovirens* is morphologically similar to it, but differs from it by its basidioma without reddish color change and relatively smaller basidiospores ($4.5\text{--}6 \times 3\text{--}4 \mu\text{m}$, mean length = $5.1 \mu\text{m}$, mean width = $3.7 \mu\text{m}$) (this study).

56. *Tricholoma ellipsosporum* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 69e, 74

Fungal Names: FN 572337

Etymology: ellipsosporum = ellipsoid, referring to its broadly ellipsoid to ellipsoid basidiospores.

Diagnosis: Related to *T. olivaceum* Reschke et al., but the latter species has close lamellae, smaller basidiospores and poorly differentiated cheilocystidia.

Type: CHINA. Yunnan Province, Baoshan, Longling County, in a mixed forest, altitude 1900 m, 11 Aug. 2022, GLG-FXP 648 (holotype, KUN-HKAS134998).

Description: Basidioma very small, small to medium-sized. Pileus 1–8 cm in diam., conical to convex, often broadly umbonate; surface dry, olivaceous grey (30C5–8), often darker at center, glabrous; margin involute; context whitish. Lamellae white (1A1), crowded; edges white (1A1). Stipe 4–9 $\times$ 0.5–3 cm, subclavate, white (1A1) to greyish (1B1), covered with grey (2E2–4) squamules, exannulate. Taste and odour not recorded.

Basidiospores $[24/1/1] 6\text{--}8 \times 4\text{--}6 \mu\text{m}$ (mean length = $7 \mu\text{m}$, mean width = $5 \mu\text{m}$), $Q = (1.19\text{--}) 1.24\text{--}1.56$ (–1.63), $Q_m = 1.4 \pm 0.12$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $25\text{--}35 \times 5\text{--}7 \mu\text{m}$, clavate, 4-spored, sometimes 2-spored, hyaline; sterigmata 2–5 μm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia $25\text{--}45 \times 3\text{--}6 \mu\text{m}$, conspicuous, filiform, cylindrical, clavate to irregular shaped, sometimes branching, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 μm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled, ellipsoid, clavate, cylindrical to filamentous hyphae 2–20 μm wide. Pileipellis a cutis, composed of radially arranged, 2–8 μm wide, colorless filamentous hyphae; subpellis poorly differentiated. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in forests with *Abies* and *Picea*.

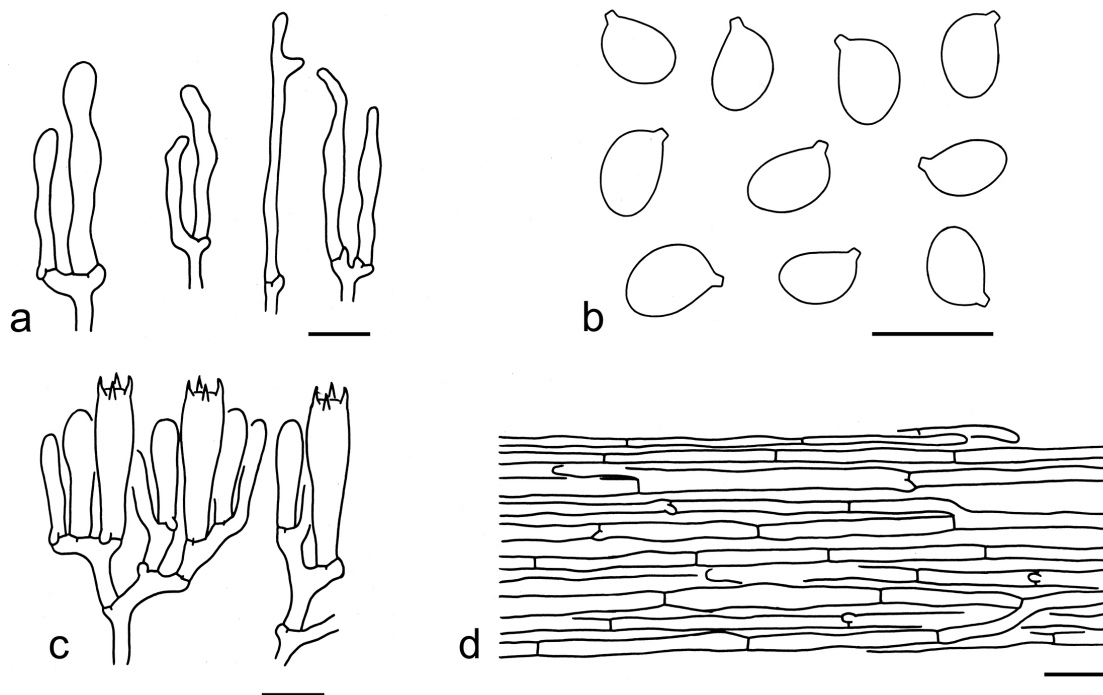


Fig. 74 Microscopic features of *Tricholoma ellipsosporum* (holotype, KUN-HKAS134998). a Marginal cells. b Basidiospores. c Hymenium and subhymenium. d Pileipellis. Scale bars: a–c = $10 \mu\text{m}$, d = $20 \mu\text{m}$.

Known distribution: Known from Southwestern China.

Additional specimen examined: CHINA. Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-La, in a forest with *Picea* and *Abies*, altitude 3900 m, 4 Aug. 2018, Kui Wu 129 (KUN-HKAS134999).

Notes: *Tricholoma ellipsosporum* is well delimited by its olivaceous grey pileus, broadly ellipsoid to ellipsoid basidiospores ($6\text{--}8 \times 4\text{--}6 \mu\text{m}$), conspicuous cheilocystidia and presence of clamps. *Tricholoma olivaceum* is sister to *T. ellipsosporum* in the phylogenetic analysis based on five

gene fragments (Fig. 3). However, *T. olivaceum* has close lamellae, smaller basidiospores ($5\text{--}6.5 \times 3.5\text{--}5 \mu\text{m}$) and poorly differentiated cheilocystidia (Reschke et al. 2018; this study).

57. *Tricholoma forteflavescens* Reschke et al, Mycologia 110(6): 1102 (2018). Fig. 75

Description: Basidioma medium-sized. Pileus 4–8 cm in diam., convex to plano-convex, without an umbo or depression at center; surface dry, light grey (1C1, 1D1) to silver grey (1B1), often darker at center and becoming paler towards margin, sometimes with reddish (7B4) tinge, staining yellow (3B4–6) when old, damaged or touched, glabrous or often centrally cracking; margin at first involute, then straight; context white (1A1) to greyish (1B1–2). Lamellae sinuate, greyish cream (3B2–4) to grey (1B1–2), staining yellow (3A3–5) when old or after damage, subclose; edges concolor. Stipe 5–10 $\times$ 1–2.5 cm, cylindrical to subclavate, greyish white (2B2–4), covered with dark grey (2E1–3) to grey (1D1–3) fibrils, staining yellow (3A3–5) after touch, solid, exannulate. Taste weak. Odour like unperfumed soap.

Basidiospores [20/1/1] (5–) 6–8 (–8.5) $\times$ 3.5–4 μm (mean length = 6.7 μm , mean width = 3.9 μm), $Q = (1.25\text{--}) 1.5\text{--}1.9$ (–2.13), $Q_m = 1.71 \pm 0.24$, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively

large. Basidia 25–35 $\times$ 5–7 μm , clavate, 4-spored, hyaline; sterigmata 2–4 μm long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia 15–25 $\times$ 2–5 μm , subclavate, cylindrical to filiform, often branching, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 μm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled, clavate, cylindrical to filamentous hyphae 5–20 μm wide. Pileipellis a cutis, non- to slightly gelatinized, composed of radially arranged, 2–10 μm wide, thin-walled, colorless, cylindrical to filamentous hyphae; subpellis poorly differentiated. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in mixed forests with *Pinus* and *Quercus*.

Known distribution: Known from Southwestern China.

Specimen examined: CHINA. Yunnan Province, Yulong Snow Mountain, in a forest with *Quercus aquifolioides* and *Pinus* sp., altitude 3500 m, 20 Aug. 2013, G. Kost & F. Popa FP1006 (holotype, KUN-HKAS93511).

Notes: *Tricholoma forteflavescens* is easily recognized in sect. *Rigida* by its yellow color change with age and when damaged and ellipsoid to elongate basidiospores (6–8 $\times$ 3.5–4 μm). *Tricholoma atrovirens* is related to this species with moderate support (Fig. 3), but differs by its basidioma without yellow discoloration and smaller basidiospores (4.5–6 $\times$ 3–4 μm) (this study).

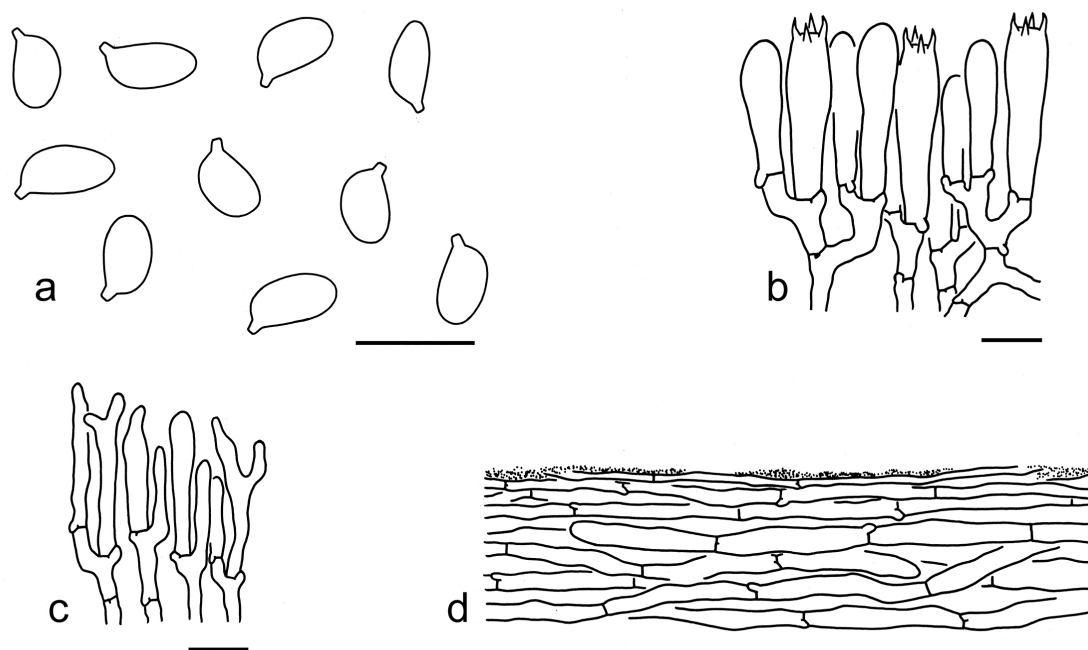


Fig. 75 Microscopic features of *Tricholoma forteflavescens* (holotype, KUN-HKAS93511). a Basidiospores. b Hymenium and subhymenium. c Marginal cells. d Pileipellis. Scale bars: a–c = 10 μm , d = 20 μm .

58. *Tricholoma olivaceum* Reschke et al., Mycologia 110(6): 1101 (2018). Figs. 69f, 76

Description: Basidioma small to medium-sized. Pileus 2–7 cm in diam., convex to plano-convex, sometimes umbonate at center; surface dry, grey (1E1–3), grey-brown (2E3–5) to yellow-brown (2C4–6), with distinct greenish (30B6–8) colors, glabrous; margin at first involute, then inflexed; context white

(1A1). Lamellae adnexed to sinuate, white (1A1) to greenish yellow (30A4–6), close to subdistant; edges concolorous. Stipe 3–11 $\times$ 0.5–1.5 cm, cylindrical, often taper downwards, grey-brown (2E3–5) to brownish (1B2–4), with greenish (30B6–8) colors, exannulate. Taste not recorded. Odour like almond or cucumber.

Basidiospores [80/4/4] (4–) 5–6.5 (–8) $\times$ (3–) 3.5–5 μm (mean length = 5.6 μm , mean width = 4.0 μm), $Q = (1.2\text{--}) 1.25\text{--}1.55$ (–1.83), $Q_m = 1.40 \pm 0.12$, broadly ellipsoid to ellipsoid,

non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $25\text{--}35 \times 5\text{--}7 \mu\text{m}$, clavate, 4-spored, hyaline; sterigmata $3\text{--}5 \mu\text{m}$ long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia poorly differentiated. Subhymenium composed of $2\text{--}4 \mu\text{m}$ wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled hyphae $3\text{--}20 \mu\text{m}$ wide. Pileipellis a cutis, non- to slightly gelatinized, composed of radially arranged, $2\text{--}8 \mu\text{m}$ wide, thin-walled, yellowish filamentous hyphae; subpellis poorly differentiated. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in subtropical broad-leaved, coniferous or mixed forests with Fagaceae and Pinaceae.

Known distribution: Known from Southwestern China.

Specimens examined: CHINA. Yunnan Province, Puer, Jingdong Yi Autonomous County, Taizhong Village, Ailao Mountain, in a broad leaved forests dominated with Fagaceae, altitude 2576 m, 6 Aug. 2014, Yan-Jia Hao 1328 (KUN-

HKAS83119); Kunming, Xishan District, Qiongzhu Temple, in a broad-leaved forest, altitude 2200 m, 1 Aug. 2015, Pan-Meng Wang 309 (KUN-HKAS93269); Nujiang Lisu Autonomous Prefecture, Lanping Bai and Pumi Autonomous County, Jinding Town, in a forest dominated by *Pinus yunnanensis*, altitude 2200 m, 14 Aug. 2010, Bang Feng 819 (KUN-HKAS68600); Dali Bai Autonomous Prefecture, Binchuan County, Jizushan Town, in a coniferous forest, altitude 2100 m, 11 Aug. 2011, Ting Guo 439 (KUN-HKAS71335).

Notes: *Tricholoma olivaceum* is delimited by its grey-brown to yellow-brown pileus with obviously greenish tinge, close and white to greenish yellow lamellae, broadly ellipsoid to ellipsoid basidiospores ($5\text{--}6.5 \times 3.5\text{--}5 \mu\text{m}$) and presence of clamps (this study). Our phylogenetic analysis based on five gene fragments indicated that it is sister to *T. ellipso sporum* (Fig. 3). For comparison, see notes under that name.

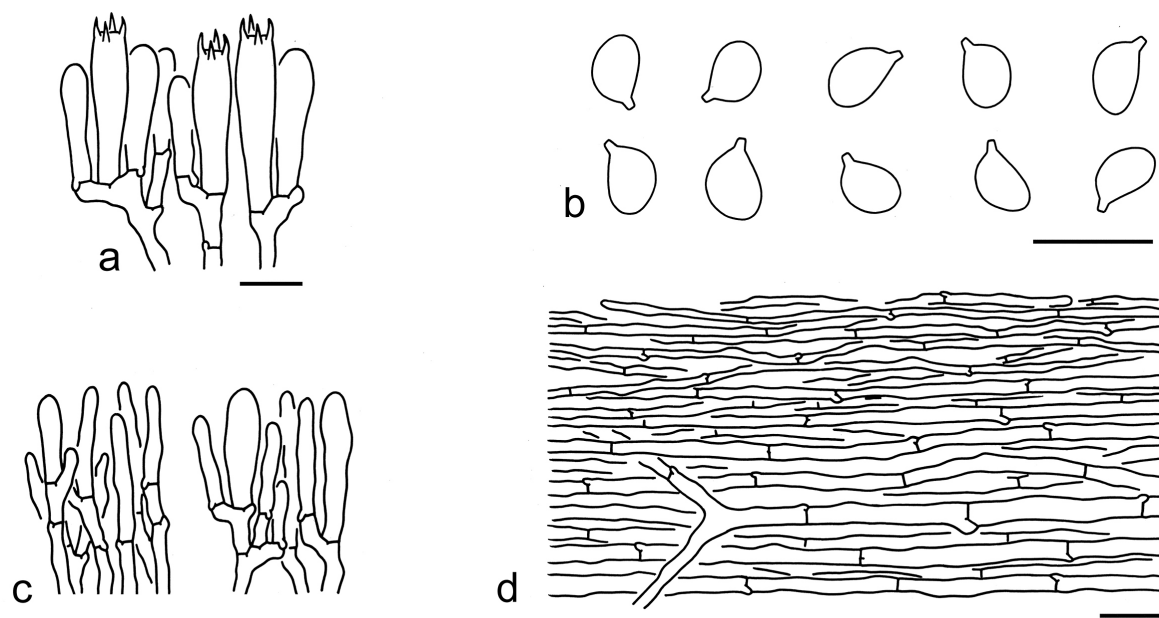


Fig. 76 Microscopic features of *Tricholoma olivaceum*. a Hymenium and subhymenium (KUN-HKAS93269). b Basidiospores (KUN-HKAS71335). c Marginal cells (KUN-HKAS93269). d Pileipellis (KUN-HKAS71335). Scale bars: a–c = $10 \mu\text{m}$, d = $20 \mu\text{m}$.

59. *Tricholoma saponaceum* (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 133 (1871). Figs. 69g, 77

Description: Basidioma medium-sized, with weaker reddish discoloration. Pileus $5\text{--}10 \text{ cm}$ in diam., plano-convex to applanate, umbonate at center; surface dry, greyish brown (4E6–8) to brown (5E6–8, 5D6–8) at center, becoming yellowish brown (2B2–4), brownish (5C3–5) to yellowish grey (3B2–4) towards margin; margin straight; context dirty white (2B2) to white (1A1). Lamellae sinuate, cream (1A2) to yellowish (4A2–3), subdistant; edges cream (1A2) to yellowish (4A2–3). Stipe $8\text{--}12 \times 1\text{--}2 \text{ cm}$, subcylindrical, yellowish (1A2–4) to brownish (5C5–7), longitudinally striate, stuffed, exannulate. Taste not recorded. Odour like rotten wood.

Basidiospores $[31/2/2] (5\text{--}) 6\text{--}7.5 \times 3.5\text{--}5 \mu\text{m}$ (mean length = $6.5 \mu\text{m}$, mean width = $4.5 \mu\text{m}$), $Q = 1.32\text{--}1.61$ (~ 1.75), $Q_m =$

1.46 ± 0.1 , ellipsoid, occasionally elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $25\text{--}40 \times 6\text{--}8 \mu\text{m}$, clavate, 4-spored, hyaline; sterigmata $4\text{--}6 \mu\text{m}$ long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia $25\text{--}50 \times 2\text{--}5 \mu\text{m}$, conspicuous, filiform, subclavate to clavate, often septate, thin-walled, colorless, hyaline. Subhymenium composed of $2\text{--}4 \mu\text{m}$ wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled, cylindrical, subcylindrical to filamentous hyphae $5\text{--}35$ (~ 60) μm wide. Pileipellis a cutis, composed of radially arranged, $5\text{--}10 \mu\text{m}$ wide, thin- to slightly thick-walled, colorless to brownish filamentous hyphae; subpellis composed of radially arranged, more or less slightly inflated hyphae, ellipsoid, cylindrical, cylindrical to filamentous, $5\text{--}25 \mu\text{m}$ wide, thin-walled, colorless to brownish. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in forests with trees of *Abies*.

Distribution: Known from Southwestern China.

Specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, Gonggashan Village, in a forest with *Abies*, altitude 3650 m, 4 Sep. 2016, KD-FB 8 (KUN-HKAS99361); same location, in a forest with *Abies*, altitude 3650 m, 4 Sep. 2016, KD-FB 7 (KUN-HKAS99360).

Notes: *Tricholoma saponaceum* is delimited according to the ITS sequence of DQ494700. This species is characterized by its basidioma with weaker reddish discoloration, grey-

brown to yellow-brown pileus, subdistant lamellae, conspicuous cheilocystidia, mostly ellipsoid basidiospores ($6\text{--}7.5 \times 3.5\text{--}5 \mu\text{m}$), a subpellis with more or less slightly inflated hyphae, presence of clamps and associations with *Abies* (this study). *Tricholoma sichuanense* Y.Y. Cui & Zhu L. Yang is closely related and similar to *T. saponaceum*, but has more yellow colored lamellae and a non-differentiated subpellis (Fig. 3). *Tricholoma yunnanense* can be confused, but differs by its white lamellae often with brown or pinkish tinge when old, slightly smaller basidiospores ($4.5\text{--}6 \times 3\text{--}4 \mu\text{m}$, mean length = $5 \mu\text{m}$, mean width = $3.6 \mu\text{m}$), and a non-differentiated subpellis.

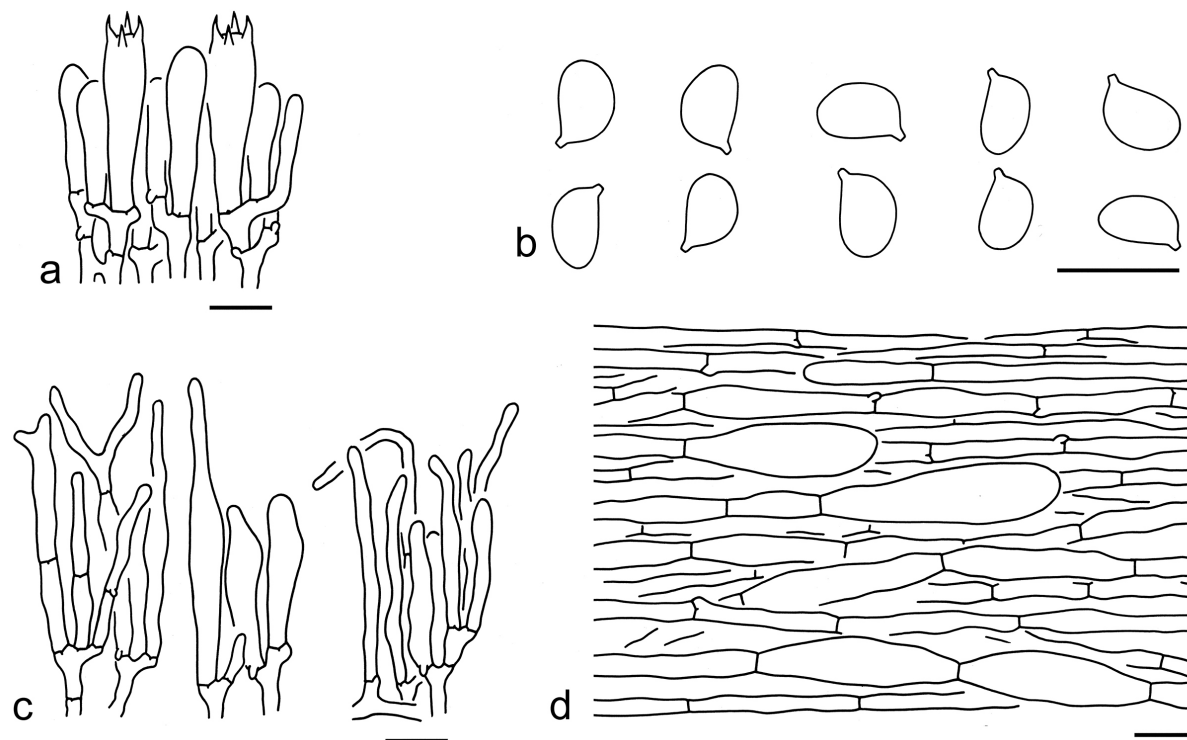


Fig. 77 Microscopic features of *Tricholoma saponaceum* (KUN-HKAS99361). a Hymenium and subhymenium. b Basidiospores. c Marginal cells. d Pileipellis. Scale bars: a–c = $10 \mu\text{m}$, d = $20 \mu\text{m}$.

60. *Tricholoma sichuanense* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 69h, 78

Fungal Names: FN 572349

Etymology: sichuanense = Sichuan Province, referring to its type locality.

Diagnosis: Similar to *T. olivaceum*, but differs in its pileus often with squamules at center and occurrence in subalpine forests dominated with *Picea*.

Type: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, Gonggashan Village, in a forest with *Picea* and *Rhododendron*, altitude 4000 m, 21 Sep. 2017, Xiao-Xia Ding 331 (holotype, KUN-HKAS105344).

Description: Basidioma small to medium-sized. Pileus 3–7 cm in diam., convex to plano-convex, slightly umbonate or not; surface dry, often grey-brown (2F6–8) to brown (4E6–8) at center, becoming olivaceous yellow (1C6–8) towards margin, sometimes grey-brown (2F6–8) overall, covered with grey-brown (2F6–8) to brown (4E6–8) squamules; margin at

first involute, then straight; context white (1A1) to cream (1A2). Lamellae sinuate, white (1A1) to pale olivaceous yellow (1B2–4), sometimes with pinkish (7A2–4) hues, subclose; edges concolorous. Stipe 7–10 $\times$ 0.5–1.5 cm, cylindrical to subcylindrical, dirty white (1B1), greyish olivaceous (1B2–4), brownish (4B3–5) to pinkish (7A2–4), exannulate. Taste and odour not recorded.

Basidiospores [50/3/2] 5–7 (–8) $\times$ 4–5 μm (mean length = $6.4 \mu\text{m}$, mean width = $4.5 \mu\text{m}$), $Q = 1.23\text{--}1.6$ (–1.7), $Q_m = 1.42 \pm 0.11$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 25–35 $\times$ 6–8 μm , clavate, 4-spored, hyaline; sterigmata 4–6 μm long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia 15–35 $\times$ 3–8 μm , filiform, subclavate to clavate or irregular shaped, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 μm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled hyphae 5–25 μm wide. Pileipellis a cutis, sometimes slightly gelatinized, composed of radially arranged, 3–15 μm wide, thin-walled, yellowish to yellowish

brown filamentous hyphae; subpellis poorly differentiated. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in subalpine temperate forests dominated with *Picea*.

Known distribution: Known from Southwestern China.

Additional specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, Gonggashan Village, in a forest with *Picea*, altitude 3650 m, 4 Sep. 2016, KD-WPM15 (KUN-HKAS98270); same city, Yala Village, in a forest with *Picea*, altitude 3290 m, 21 Aug. 2017, Jian-Wei Liu 933 (KUN-HKAS106308).

Notes: *Tricholoma sichuanense* is characterized by its grey-brown to olivaceous yellow pileus often with obvious

squamules at center, subclose, white to olivaceous yellow lamellae, broadly ellipsoid to ellipsoid basidiospores ($5\text{--}7 \times 4\text{--}5 \mu\text{m}$), presence of clamps and associations with subalpine temperate forests. *Tricholoma saponaceum* is related to this species in the five-gene phylogenetic analysis (Fig. 3). However, *T. saponaceum* has a basidioma with weaker reddish discoloration, a glabrous pileus, and a slightly differentiated subpellis with more or less inflated hyphae (this study). *Tricholoma olivaceum* can be confused with *T. sichuanense*, but has an almost glabrous pileus and is distributed in subtropical forests (Reschke et al. 2018; this study).

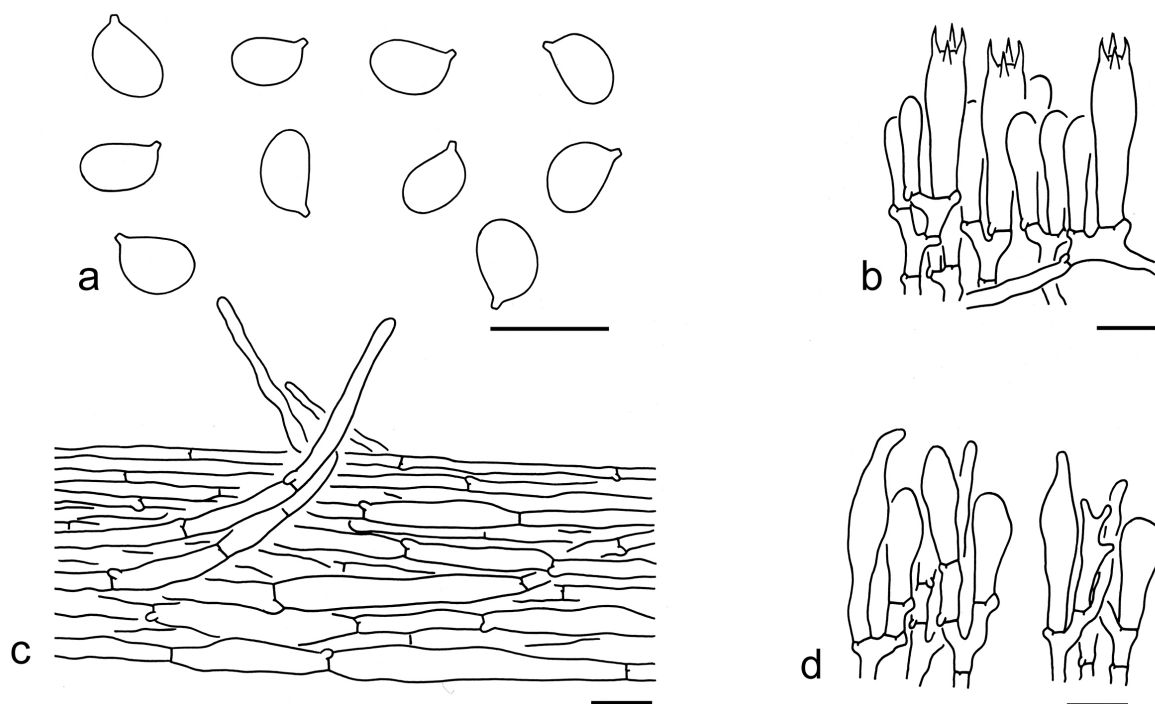


Fig. 78 Microscopic features of *Tricholoma sichuanense* (holotype, KUN-HKAS105344). a Basidiospores. b Hymenium and subhymenium. c Pileipellis. d Marginal cells. Scale bars: a, b, d = 10 μm , c = 20 μm .

61. *Tricholoma yunnanense* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 69i, 79

Fungal Names: FN 572351

Etymology: *yunnanense* = Yunnan, referring its type locality from Yunnan province.

Diagnosis: Related to *T. asiaticum*, but differs by its glabrous and brown, brownish to dirty white pileus.

Type: CHINA. Yunnan Province, Kunming, Panlong District, Shuanglong Village, Yeya Lake, in a mixed forest with Fagaceae and Pinaceae, altitude 2100 m, 1 Sep. 2013, Jiao Qin 847 (holotype, KUN-HKAS81285).

Description: Basidioma medium-sized. Pileus 4–10 cm in diam., at first convex, then convex-applanate, without an umbo or depression at center; surface dry, grey-brown (3E1–3) to brown (6E3–5) at center, becoming brownish (5D3–5) to dirty white (1B2) towards margin, sometimes brown (5D4–6) overall, glabrous; margin straight; context dirty white (1B2) to pinkish (5A2–3). Lamellae sinuate, white (1A1), staining brown

(4B2–4) to pinkish (5A2–3) tinge when old, close; edges concolor. Stipe 6–9 $\times$ 0.7–2 cm, cylindrical to subcylindrical, dirty white (1A1, 1B1), greyish (1B2–3) to brownish (5B2–4), hollow, exannulate. Taste not recorded. Odour like sesame paste.

Basidiospores [20/1/1] (4–) $4.5\text{--}6 \times 3\text{--}4 \mu\text{m}$ (mean length = 5 μm , mean width = 3.6 μm), $Q = (1.13\text{--}) 1.25\text{--}1.57 (-1.83)$, $Q_m = 1.4 \pm 0.18$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 20–30 $\times$ 5–7 μm , clavate, 4-spored, hyaline; sterigmata 3–5 μm long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia not observed. Subhymenium composed of 2–5 μm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled, cylindrical hyphae 5–15 μm wide. Pileipellis a cutis, non- to slightly gelatinized, composed of radially arranged, 3–7 μm wide, thin-walled, colorless filamentous hyphae; subpellis poorly differentiated. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in subtropical conifers or mixed forests with Pinaceae and Fagaceae.

Known distribution: Known from Southwestern China.

Additional specimen examined: CHINA. Yunnan Province, Puer City, Lancang Lahu Autonomous County, Nuofu Village, in a coniferous forest with *Pinus*, altitude 2100 m, 1 Sep. 2013, Xiao-Xia Ding 268 (KUN-HKAS106610).

Notes: *Tricholoma yunnanense* is characterized by its brown pileus without olivaceous colour, close and white lamellae with brown to pinkish tinge when old, and broadly

ellipsoid to ellipsoid basidiospores ($4.5\text{--}6 \times 3\text{--}4 \mu\text{m}$). This species is related to *T. asiaticum* with moderate support (Fig. 3). However, *T. asiaticum* can be easily distinguished by its more darker (dark blackish grey to greyish brown) and tomentose pileus. Morphologically, *T. saponaceum* is similar to it, but can be separated by its relatively larger basidiospores ($6\text{--}7.5 \times 3.5\text{--}5 \mu\text{m}$, mean length $6.5 \mu\text{m}$, mean width $4.5 \mu\text{m}$), a slightly differentiated subpellis and associations with *Abies* (this study).

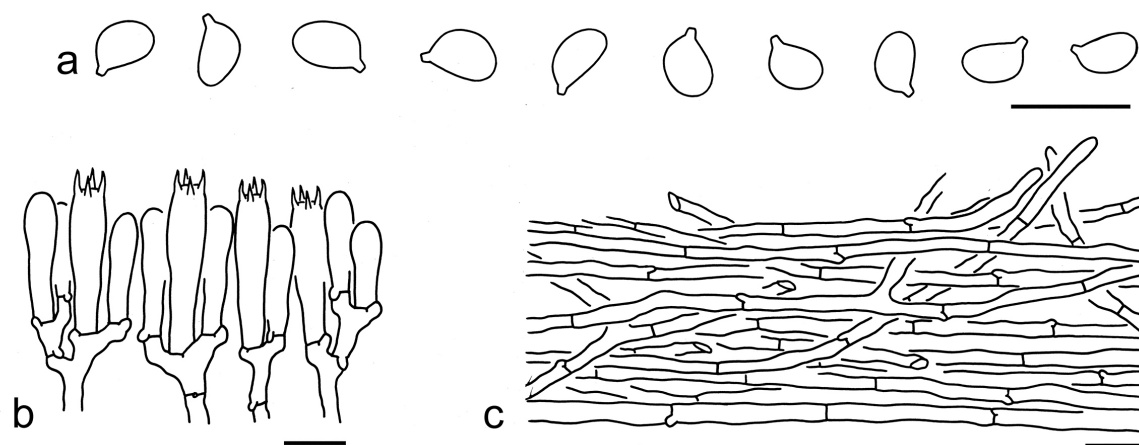


Fig. 79 Microscopic features of *Tricholoma yunnanense* (holotype, KUN-HKAS81285). a Basidiospores. b Hymenium and subhymenium. c Pileipellis. Scale bars: a, b = 10 μm , c = 20 μm .

Tricholoma subgen. *Pardincutis* Singer

Type: *Tricholoma pardinum* (Pers.) Quél., Mém. Soc. Émul. Montbéliard, Sér. 2 5: 339 (1873).

Description: Basidioma tricholomatoid. Pileus mostly brown or grey, squamose. Lamellae crowded to close. Annulus absent. Basidiospores broadly ellipsoid to ellipsoid, thin-walled, smooth, inamyloid. Pileipellis a cutis composed of repent filamentous hyphae.

Ecology: Ectomycorrhizal. On soil with various trees.

Known distribution: Molecular data indicated species from this subgenus are found in Europe, North America, and Asia.

Notes: *Tricholoma* subgen. *Pardincutis* is supported to be a monophyletic group and comprises only one section named sect. *Pardincutis*. Currently, two species of this subgenus are found in China (see below).

Tricholoma sect. *Pardincutis*

Type: *Tricholoma pardinum* (Pers.) Quél., Mém. Soc. Émul. Montbéliard, Sér. 2 5: 339 (1873).

Description: Basidioma tricholomatoid and robust. Pileus umbonate or not, whitish, greyish to brownish, squamose. Lamellae crowded to close. Annulus absent. Basidiospores medium-sized to large, broadly ellipsoid to ellipsoid, thin-walled, smooth, inamyloid. Pleurocystidia absent. Cheilocystidia conspicuous or absent. Pileipellis a cutis composed of repent filamentous hyphae. Clamps present.

Ecology: Ectomycorrhizal. On soil with various trees.

Known distribution: Molecular data indicated that species from this section are collected from Europe, North America, and Asia.

Notes: To date, *T. highlandense* and *T. nigrosquamosum* are found in China (see below).

Key to the species of *Tricholoma* sect. *Pardincutis* from China

1. Basidiospores relatively smaller ($6.5\text{--}8 \times 5\text{--}6 \mu\text{m}$, mean length = $7.3 \mu\text{m}$, mean width = $5.5 \mu\text{m}$); cheilocystidia clavate or mucronate; associations mainly with *Pinus* *T. highlandense*
1. Basidiospores relatively larger ($8.5\text{--}10.5 \times 6.5\text{--}7.5 \mu\text{m}$, mean length = $9.3 \mu\text{m}$, mean width = $6.9 \mu\text{m}$); cheilocystidia clavate without mucronate shaped; associations mainly in forests with trees of *Picea* *T. nigrosquamosum*

62. *Tricholoma highlandense* Zhu L. Yang et al., Phytotaxa 305(1): 5 (2017). Figs. 69j, 80

Description: Basidioma medium-sized to large. Pileus 5–10 cm in diam., plano-convex to applanate, broadly umbonate or not; surface dry, white (1A1), dirty white (3B1) to brownish (1B2–4), covered with brown (2C2–4) to grey-brown (2E3–5), somewhat reflexed scales; margin involute to inflexed; context white (1A1). Lamellae adnexed to sinuate, white (1A1), dirty white (1B1) to cream (1B2), crowded; edges white (1A1) to cream (1B2). Stipe 3–9 $\times$ 1–3 cm, cylindrical, often slightly inflated at base, white (1A1) to cream (1B2), covered with dirty white (1B1) to brownish (3C2–5) fibrillose

squamules, exannulate. Taste and odour indistinct or farinaceous.

Basidiospores [60/3/3] $6.5\text{--}8\text{ (} -9.5) \times 5\text{--}6\text{ (} -6.5) \mu\text{m}$ (mean length = $7.3 \mu\text{m}$, mean width = $5.5 \mu\text{m}$), $Q = (1.12\text{--}) 1.21\text{--}1.46\text{ (} -1.50)$, $Q_m = 1.33 \pm 0.08$, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $37\text{--}50 \times 8\text{--}10 \mu\text{m}$, clavate, 4-spored, rarely 2-spored, hyaline; sterigmata $4\text{--}5 \mu\text{m}$ long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia $40\text{--}50 \times 8\text{--}10 \mu\text{m}$, conspicuous, clavate, often mucronate, thin-walled, colorless, hyaline. Subhymenium composed of $2.5\text{--}5 \mu\text{m}$ wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled hyphae $3\text{--}15 \mu\text{m}$ wide. Pileipellis a cutis with transition to trichoderm at regular intervals, composed of radially arranged, $3\text{--}8 \mu\text{m}$ wide, thin-walled, yellowish to brownish filamentous hyphae; subpellis poorly differentiated. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in subtropical evergreen mixed or coniferous forests.

Known distribution: Known from Southwestern China (Yang et al. 2007).

Specimens examined: CHINA. Sichuan Province, Liangshan Yi Autonomous Prefecture, Muli Tibetan Autonomous County, Liziping Village, in a forest with *Pinus*, altitude 2450

m, 31 Jul. 2012, Ting Guo 523 (KUN-HKAS76215). Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-La, in a mixed forest with *Pinus* and Fagaceae, altitude 3000 m, 26 Jul. 2004, Hui Deng 450 (HMAS96585); Ninglang County, Xinyingpan Town, in a forest dominated by *Pinus yunnanensis*, altitude 2500–2600 m, 7 Aug. 2011, Qing Cai 596 (type, KUN-HKAS70192); same county, Hexi Town, in a forest of *Pinus yunnanensis*, altitude 2400 m, 16 Aug. 2011, Qi Zhao 1340 (KUN-HKAS74293); Lijiang, in a forest dominated by *Pinus yunnanensis* mixed with broad-leaved plants, altitude 2800 m, 30 Jul. 2011, Ting Guo 258 (KUN-HKAS71156); same city, Heilongtan Park, in a mixed forest with *Pinus* and Fagaceae, altitude 2460 m, 22 Aug. 2011, Qi Zhao 1028 (KUN-HKAS69749).

Notes: *Tricholoma highlandense* is characterized by its white pileus covered with coarsely brown to grey-brown scales, broadly ellipsoid to ellipsoid basidiospores, clavate to mucronate cheilocystidia, and the presence of clamps (this study). In the phylogenetic analyses (Figs. 3, 4), this species is sister to *T. filamentosum* (Alessio) Alessio, but the latter has a shiny pileus with little contrasting-coloured scales, which are pale grey or olivaceous buff or smoke grey, poorly differentiated cheilocystidia and are mainly with deciduous trees (Christensen & Heilmann-Clausen 2013).

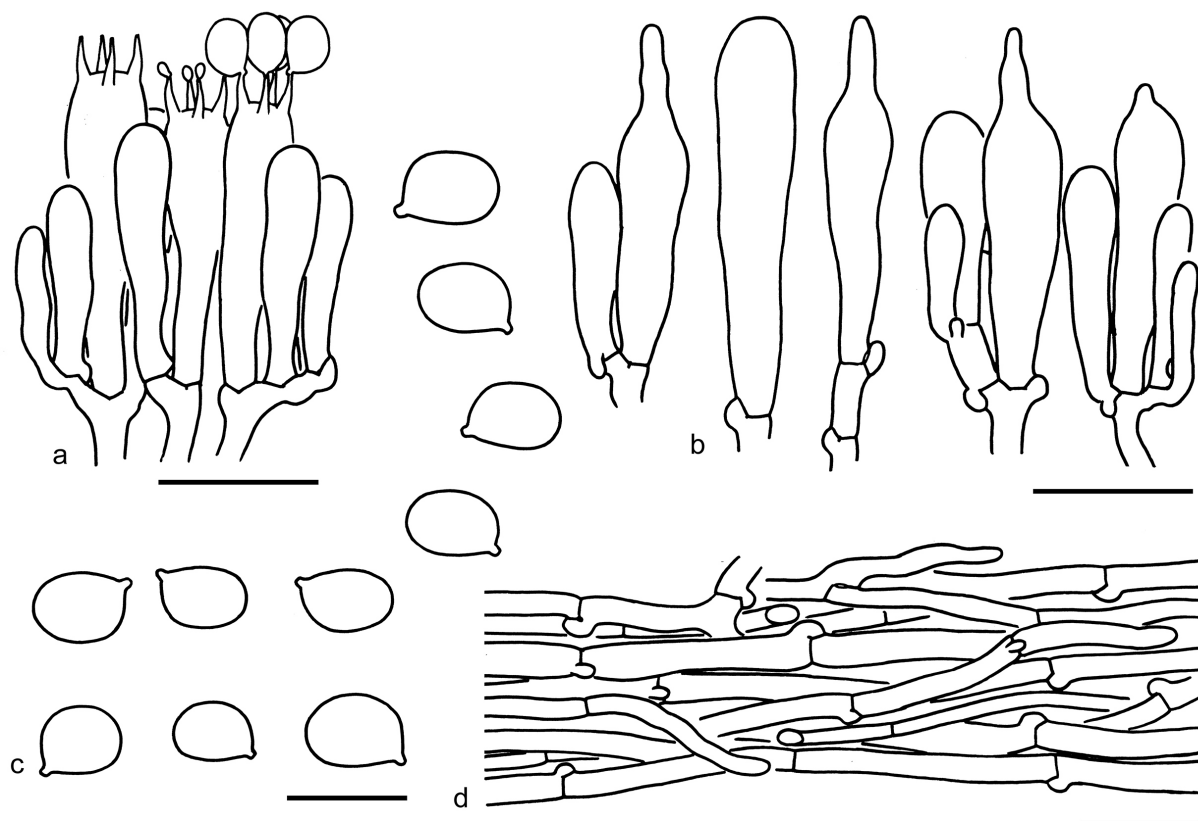


Fig. 80 Microscopic features of *Tricholoma highlandense* (type, KUN-HKAS70192). a Basidia at different stages of development and subhymenium elements. b Mucronate or clavate cheilocystidia. c Basidiospores. d Pileipellis. Scale bars: a, b = $20 \mu\text{m}$, c = $10 \mu\text{m}$, d = $30 \mu\text{m}$. Cited from Yang et al. (2017).

Tricholoma nigrosquamosum can be confused, but differs by its relatively larger basidiospores ($8.5\text{--}10.5 \times 6.5\text{--}7.5 \mu\text{m}$, mean length = $9.3 \mu\text{m}$, mean width = $6.9 \mu\text{m}$), clavate cheilocystidia without mucronate shapes, and associations

with subalpine temperate forests (Yang et al. 2017; Wang et al. 2024; this study). *Tricholoma highlandense* is also similar to *T. pardinum*. However, *T. pardinum* has relatively larger basidiospores ($7.5\text{--}9.5 \times 5.5\text{--}6.5 \mu\text{m}$, mean length = $8.5 \mu\text{m}$,

mean width = 6.1 μm), poorly differentiated cheilocystidia and forms mycorrhizal relationships with *Fagus* and *Abies* on calcareous soil (Riva 1988; Bessette et al. 2013; Christensen & Heilmann-Clausen 2013; Yang et al. 2017).

63. *Tricholoma nigrosquamosum* (P.G. Liu) Zhu L. Yang & G.S. Wang, *Mycology* 15(2): 205 (2023) [2024]. Figs. 69k, 81

Basionym: *Tricholomopsis nigrosquamosa* P.G. Liu, *Acta Mycol. Sin.* 13(3): 183 (1994).

Synonymy: *Tricholoma sinopardinum* Zhu L. Yang et al., *Phytotaxa* 305(1): 6 (2017).

Description: Basidiomata medium-sized to large. Pileus 5–11 cm in diam., at first convex, then plano-convex to applanate, often broadly umbonate; surface dry, white (1A1), dirty white (1B1–3) to greyish (2B1–3), covered with brown (2B2–4, 3C2–4) to dark brown (3D2–4, 3E2–4), fibrillose scales; margin involute to inflexed; context white (1A1) to cream (1A2). Lamellae adnexed to sinuate, white (1A1), dirty white (1B1) to cream (1B2–3), crowded; edges brownish (4B3–5) to yellow-brown (3B3–5). Stipe 5–18 $\times$ 1–3 cm, cylindrical to clavate, often slightly inflated at base, white (1A1) to brownish (3B2–4), covered with brownish (3B2–4) to brown (3D2–4), fibrillose squamules, exannulate. Taste and odour indistinct or farinaceous or fishlike.

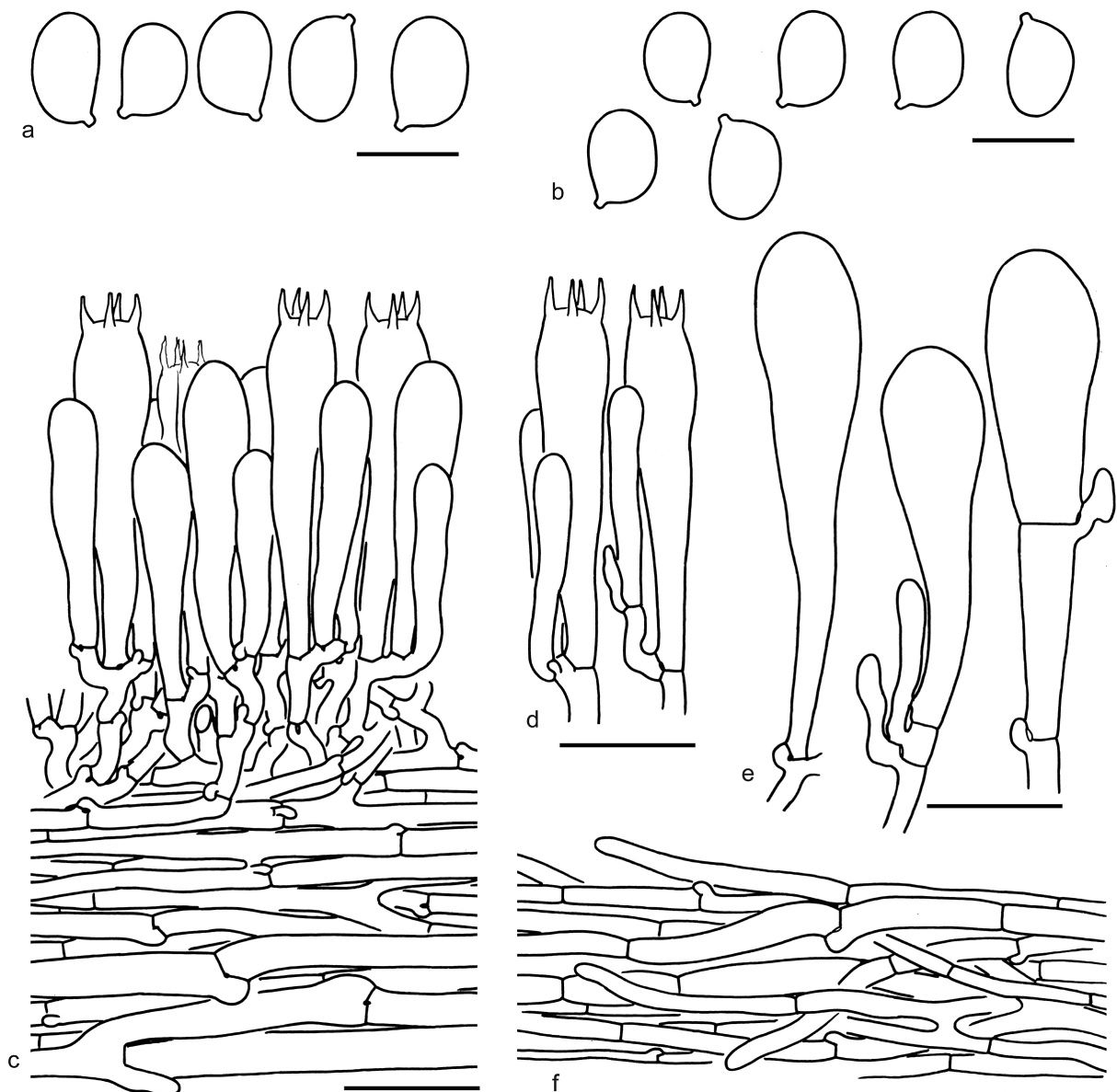


Fig. 81 Microscopic features of *Tricholoma nigrosquamosum*. a Basidiospores (KUN-HKAS46041). b Basidiospores (KUN-HKAS82533). c Hymenium, subhymenium and lamellar trama (KUN-HKAS46041). d Basidia (KUN-HKAS82533). e Cheilocystidia (KUN-HKAS82533). f Pileipellis (KUN-HKAS45529). Scale bars: a, b = 10 μm , c–e = 20 μm , f = 30 μm . Cited from Yang et al. (2017).

Basidiospores [115/6/5] (8–) 8.5–10.5 (–11.5) $\times$ (5.5–) 6.5–7.5 (–8) μm (mean length = 9.3 μm , mean width = 6.9 μm), $Q = (1.20\text{--}) 1.25\text{--}1.50$ (–1.62), $Q_m = 1.36 \pm 0.09$, mostly ellipsoid, sometimes broadly ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 45–55 (–65) $\times$ 9–11 (–15) μm , clavate, 4-spored, rarely 2-spored, hyaline; sterigmata 4–5 μm long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia 40–75 $\times$ 15–25 μm , conspicuous, clavate, sometimes septate, thin- to slightly thick-walled ($\leq 0.5 \mu\text{m}$), colorless, sometimes brownish or yellowish, hyaline. Subhymenium composed of 2.5–4 μm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled hyphae 3–30 μm wide. Pileipellis a cutis with transition to a trichoderm at regular intervals, composed of radially arranged, 3–10 (–15) μm wide, thin-walled, yellowish to brownish filamentous hyphae; subpellis poorly differentiated. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in subalpine forests dominated by *Picea*, sometimes mixed with *Betula*, *Populus* or *Quercus*.

Known distribution: known from Southwestern China and Nepal.

Specimens examined: CHINA. Xizang Autonomous Region, Jiangda County, Jiangda Town, in a forest dominated by *Picea* and *Populus*, altitude 3500 m, 8 Aug. 2013, Bang Feng 1427 (KUN-HKAS82533); same town, in a forest dominated by *Picea* and *Betula*, altitude 4100 m, 4 Aug. 2009, Zhu L. Yang 5459 (KUN-HKAS58001); same county, Tongpu Town, in a forest dominated by *Picea*, altitude 3300 m, 2 Aug. 2004, Zai-Wei Ge 261 (KUN-HKAS46041); Mangkang County, on the way to Sichuan, in a forest dominated by *Picea likiangensis*, altitude unknown, 16 Jul. 2009, Bang Feng 470 (KUN-HKAS57199); Xiangcheng County, Reda Town, in a forest dominated by *Picea* and *Quercus*, altitude 3600 m, 16 Jul. 2004, Zhu L. Yang 4143 (KUN-HKAS45529). Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Luhuo County, in a forest dominated by *Picea*, altitude 3100 m, 16 Jul. 2014, Kuan Zhao 551 (KUN-HKAS89214); Litang County, in a forest dominated by *Picea*, altitude 4000 m, 8 Aug. 2014, Kuan Zhao 712 (KUN-HKAS89643); same county, forest type and altitude not recorded, 5 Aug. 2016, Jian-Wei Liu 474 (KUN-HKAS98053).

Notes: *Tricholoma nigrosquamosum* is delimited by its white pileus covered with brown to dark brown scales, mostly ellipsoid basidiospores, clavate cheilocystidia, the presence of clamps and associated with subalpine temperate forests dominated by *Picea* (this study). *Tricholoma nigrosquamosum* is closely related to the clade formed by *T. highlandense* and *T. filamentosum* in the phylogenetic analyses (Figs. 3, 4). Indeed, *T. nigrosquamosum* can be confused with *T. highlandense*, and the differences between them has been discussed under *T. highlandense*. *Tricholoma filamentosum* has a shiny pileus with little contrasting colored scales, relatively smaller basidiospores (6.6–9.8 $\times$ 4.7–7.1 μm , average 7.6–8.5 $\times$ 5.8–6.2 μm), poorly differentiated cheilocystidia and is mainly with deciduous trees (Christensen & Heilmann-Clausen 2013). *Tricholoma pardinum* is similar to *T. nigrosquamosum*, but the former has relatively smaller basidiospores (7.5–9.5 $\times$ 5.5–6.5 μm , mean length = 8.5 μm , mean width = 6.1 μm) and poorly differentiated cheilocystidia (Riva 1988; Bessette et al. 2013; Christensen & Heilmann-Clausen 2013; Yang et al. 2017).

Tricholoma subgen. *Sericeicutis* Singer

Type: *Tricholoma sulphureum* (Bull.) P. Kumm., Führ. Pilzk. (Zerbst): 133 (1871).

Description: Basidioma tricholomatoid. Pileus umbonate or not, white, yellow or brown, glabrous. Lamellae close to distant. Annulus absent. Basidiospores variable in shape and size, broadly ellipsoid, ellipsoid to elongate, sometimes amygdaliform, thin-walled, smooth, inamyloid. Pileipellis a cutis, sometimes with its subpellis composed of more or less inflated hyphae. Clamps present or absent.

Ecology: Ectomycorrhizal. On soil with various trees.

Known distribution: Molecular data showed that species from this subgenus are collected from Europe, North America, and Asia.

Notes: *Tricholoma* subgen. *Sericeicutis* is proved to be a monophyletic group and includes two sections named sect. *Sericella* and sect. *Lasciva*. To date, six species of subgen. *Sericeicutis* are collected from China (see below).

Tricholoma sect. *Lasciva* Bon

Type: *Tricholoma lascivum* (Fr.) Gillet, Hyménomycètes (Alençon): 111 (1874) [1878].

Description: Basidioma tricholomatoid and pale colored. Pileus umbonate or not, white, glabrous. Lamellae close. Annulus absent. Basidiospores small, broadly ellipsoid, ellipsoid to elongate, smooth, inamyloid. Cheilocystidia absent. Pileipellis a cutis with repent filamentous hyphae. Clamps present.

Ecology: Ectomycorrhizal. On soil with various trees.

Known distribution: Molecular data indicated species from this section are found in Europe, North America, and Asia.

Notes: To date, *Tricholoma lishanense* L. Fan & J.J. Yang and *T. stiparophyllum* (N. Lund) P. Karst. have been reported from China (see below).

Key to the species of *Tricholoma* sect. *Lasciva* from China

1. Pileus relatively smaller, 3–5 cm in diam.; context with a honey-like smell; associations with *Quercus* *T. lishanense*
1. Pileus relatively larger, 6–12 cm in diam.; context with an unpleasant smell; associations with *Betula* *T. stiparophyllum*

64. *Tricholoma lishanense* L. Fan & J.J. Yang, Phytotaxa 598(1): 92 (2023). Figs. 69l, 82

Description: Basidioma small. Pileus 3–5 cm in diam., convex to plano-convex, sometimes slightly umbonate at center; surface dry, smooth, glabrous, white (1A1) to cream (1A2); margin straight; context white (1A1). Lamellae sinuate, white (1A1), very crowded; edges white (1A1). Stipe 4–7 $\times$ 0.5–0.8 cm, cylindrical, slightly widen at base, white (1A1), glabrous, exannulate. Taste not recorded. Odour like honey.

Basidiospores [40/2/1] 5.5–6.5 (–7) $\times$ (3–) 3.5–4.0 μm (mean length = 6.0 μm , mean width = 3.8 μm), $Q = 1.37\text{--}1.75$ (–1.83), $Q_m = 1.55 \pm 0.1$, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 25–30 $\times$ 6–8 μm , clavate, 4-spored, hyaline;

sterigmata 3–5 μm long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia 20–35 $\times$ 4–8 μm , poorly differentiated, narrowly clavate to clavate, thin-walled, colorless, hyaline. Subhymenium composed of 3–5 μm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled hyphae 3–10 μm wide. Pileipellis a cutis, composed of radially arranged to interwoven, 2–8 μm wide, thin-walled, colorless filamentous hyphae; subpellis poorly differentiated. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in broad-leaved forests with *Quercus*.

Known distribution: Known from northern (Yang et al. 2023) and Northeastern China.

Specimen examined: CHINA. Liaoning Province, Dandong, Kuandian Man Autonomous County, Sipingjie Village, in a broad-leaved forest, altitude 1000 m, 29 Aug. 2018, Xiao-Xia Ding 380 (KUN-HKAS105390).

Notes: *Tricholoma lishanense* is characterized by its small, white basidioma, ellipsoid to elongate basidiospores (5.5–6.5 $\times$ 3.5–4.0 μm , $Q = 1.37$ –1.75, $Q_m = 1.55 \pm 0.1$), honey-like smells and associations with *Quercus* (this study). This species is closely related and very similar to *T. album* (Schaeff.) P. Kumm (Figs. 3, 4), but differs by its very crowded lamellae.

Tricholoma lascivum (Fr.) Gillet is similar to *T. lishanense*, but has a pale greyish yellow pileus and a rancid smell (Riva 1988, 2003; Christensen & Noordeloos 1999; Christensen & Heilmann-Clausen 2013). *Tricholoma stiparophyllum* has a whitish basidioma and can be confused with *T. lishanense*. However, *T. stiparophyllum* has relatively larger basidioma and an unpleasant smell (Christensen & Noordeloos 1999; Christensen & Heilmann-Clausen 2013).

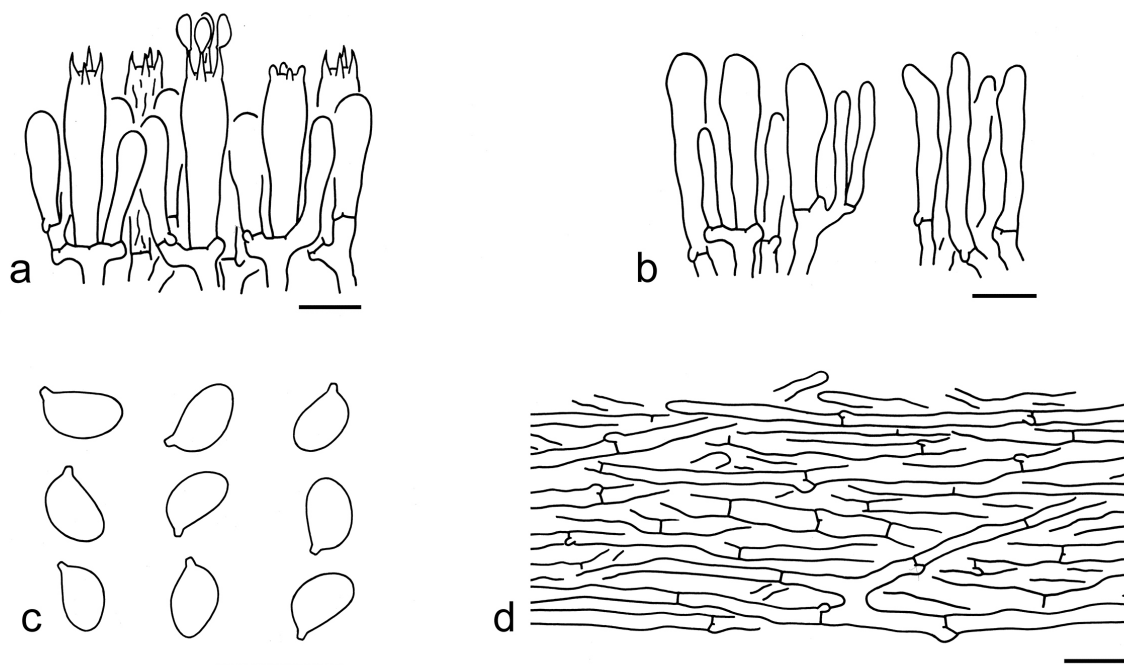


Fig. 82 Microscopic features of *Tricholoma lishanense* (KUN-HKAS105390). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 μm , d = 20 μm .

65. *Tricholoma stiparophyllum* (N. Lund) P. Karst., Meddn Soc. Fauna Flora fenn. 5: 42 (1879). Figs. 69m, 83

Basionym: *Agaricus stiparophyllus* N. Lund, Consp. Hymen. Holm (Christianiae): 10 (1845).

Description: Basidioma medium-sized to large. Pileus 6–12 cm in diam., convex to plano-convex, sometimes slightly umbonate at center; surface dry, smooth, glabrous, yellowish (2A2–4) to cream (1A2–4) at center, becoming pale cream (1A2) to white (1A1) towards margin; margin involute when young, becoming inflexed to straight when mature; context white (1A1). Lamellae adnate to sinuate, white (1A1) to cream (1A2–4), with brownish (4B4) spots when damaged or old, crowded; edges concolor. Stipe 8–11 $\times$ 1–2.5 cm, cylindrical,

white (1A1) to cream (1A2–4), glabrous, exannulate. Taste not recorded. Odour unpleasant.

Basidiospores [20/1/1] 6–7 $\times$ 3.5–4.5 μm (mean length = 6.5 μm , mean width = 4 μm), $Q = (1.47$ –) 1.5–1.8 (–1.91), $Q_m = 1.65 \pm 0.12$, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 30–40 $\times$ 6–9 μm , clavate, 4-spored, hyaline; sterigmata 3–5 μm long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia 35–50 $\times$ 3–5 μm , narrowly cylindrical to filamentous, thin-walled, colorless, hyaline. Subhymenium composed of 3–5 μm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled hyphae 3–15 μm wide. Pileipellis a cutis, composed of radially arranged, 3–10 μm wide, thin-walled, colorless filamentous hyphae; subpellis poorly differentiated. Clamps present.

Ecology: Solitary to scattered on soil in broad-leaved forests with *Betula*.

Known distribution: Known from Europe (Christensen & Noordeloos 1999; Christensen & Heilmann-Clausen 2013), North America (Trudell et al. 2022) and China.

Specimens examined: CHINA. Inner Mongolia, Hinggan League, Arxan, 30 Aug. 2006, HMGU7829; same location and date, HMGU7821. Xinjiang Uygur Autonomous Region, Altay Prefecture, forest unknown, altitude 1100 m, 6 Aug. 2003, Man-Shu Song 043 (HMAS96586). Xizang Autonomous Region, Zayü County, forest unknown, altitude 3585 m, 25 Aug. 2018, Xiang-Hua Wang 5825 (KUN-HKAS135000).

Notes: *Tricholoma stiparophyllum* is characterized by its cream to white basidioma, ellipsoid to elongate basidiospores ($6\text{--}7 \times 3.5\text{--}4.5 \mu\text{m}$) and presence of clamps (this study). In Chinese collections of this species, taste was not recorded and the odour was unpleasant. By contrast, European collections (Christensen & Heilmann-Clausen 2013)

exhibit a complex odour, mostly nauseating and rancid with floral to chemical notes, reminiscent of old kitchen waste or parsnip, and a farinaceous to rancid, slightly acrid taste.

This species forms a strongly supported clade with *T. album*, *T. lishanense*, and *T. lascivum* (Figs. 3, 4). However, *T. album* has medium-spaced lamellae and association with *Quercus* (Riva 1988; Christensen & Heilmann-Clausen 2013). *Tricholoma lishanense* differs by its relatively smaller basidioma, honey-like smell and associations with *Quercus* (this study). *Tricholoma lascivum* has a pale greyish yellow basidioma and larger basidiospores ($4.8\text{--}9.7 \times 3\text{--}5.7 \mu\text{m}$) (Riva 1988; Christensen & Heilmann-Clausen 2013). *Tricholoma sulphurescens* Bres. is morphologically comparable to *T. stiparophyllum*, but can be separated by its white basidioma strongly yellowing when touched and broadly ellipsoid basidiospores ($4.5\text{--}7.6 \times 3.9\text{--}6 \mu\text{m}$) (Riva 1988; Christensen & Heilmann-Clausen 2013).

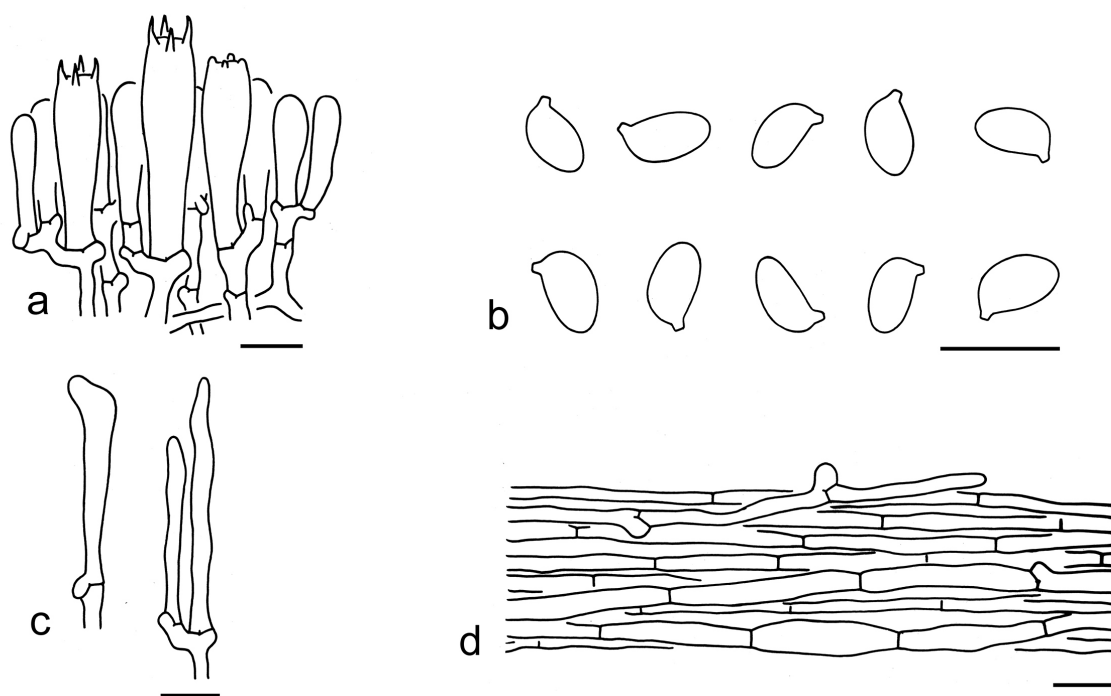


Fig. 83 Microscopic features of *Tricholoma stiparophyllum* (KUN-HKAS135000). a Hymenium and subhymenium. b Basidiospores. c Marginal cells. d Pileipellis. Scale bars: a–c = 10 μm , d = 20 μm .

Tricholoma sect. *Sericella* (Fr.) Quél.

Type: *Tricholoma sulphureum* (Bull.) P. Kumm., Führ. Pilzk. (Zerbst): 133 (1871).

Description: Basidioma tricholomatoid. Pileus umbonate or not, whitish, cream, pinkish, sulphur-yellow, orangish brown to brown, glabrous. Lamellae close to distant, white, cream to sulphur-yellow. Annulus absent. Basidiospores large, ellipsoid to elongate, often somewhat amygdaliform, smooth, inamyloid. Cheilocystidia poorly differentiated. Pileipellis a cutis with its subpellis composed of radially arranged filamentous hyphae or inflated cells. Clamps present or absent.

Ecology: Ectomycorrhizal. On soil with various trees.

Known distribution: In Europe, North America, and Asia.

Notes: To date, four species have been reported from China (see below).

Key to the species of *Tricholoma* sect. *Sericella* from China

1. Basidioma paler colored, off-white, ivory to brownish colored; subpellis with obviously inflated cells..... *T. inamoenum*
1. Basidioma sulphur-yellow, orangish brown to brown; subpellis poorly differentiated, mostly composed of radially arranged filamentous hyphae, occasionally with slightly inflated cells..... 2
2. Pileus orangish brown to brown at center and brownish to white at margin; lamellae white to cream..... *T. tangerinum*
2. Pileus sulphur-yellow; lamellae sulphur-yellow 3

3. Basidiospores relatively larger ($10\text{--}12 \times 5.5\text{--}7 \mu\text{m}$, mean length = $10.6 \mu\text{m}$, mean width = $6.2 \mu\text{m}$); subpellis composed of radially arranged slightly inflated cells.....
.....*T. sulphureum* type I
3. Basidiospores relatively smaller ($9\text{--}11.5 \times 5\text{--}6.5 \mu\text{m}$, mean length = $9.9 \mu\text{m}$, mean width = $5.4 \mu\text{m}$); subpellis composed of radially arranged filamentous hyphae.....
.....*T. sulphureum* type II

66. *Tricholoma inamoenum* (Fr.) Gillet, Hyménomycètes (Alençon): 112 (1874) [1878]. Figs. 69n, 84

Description: Basidioma small to medium-sized. Pileus 3–7 cm in diam., convex to plano-convex, with or without a broadly low umbo; surface dry, smooth to finely rugosus, off-white (1B1), ivory (1A2–3, 2A2–3), pale chrome to pale ochraceous (2B1, 3B1) to brownish (3B2–4); margin inflexed to straight, often waved; context off-white (1A1, 1B1). Lamellae sinuate, off-white (1A1, 1B1) to ivory (1A2–3, 2A2–3), distant; edges entire, off-white (1A1, 1B1) to ivory (1A2–3, 2A2–3). Stipe 6–12 $\times$ 0.7–1.2 cm, cylindrical, stuffed, off-white (1B1) to ivory (1A2–3, 2A2–3), with brownish (2B3–5) colors, fibrillose, exannulate. Taste mild. Odour strong of bitter almond.

Basidiospores [60/3/1] (9–) $10\text{--}12 \times (5\text{--}) 5.5\text{--}7 \mu\text{m}$ (mean length = $10.7 \mu\text{m}$, mean width = $6.1 \mu\text{m}$), $Q = (1.46\text{--}) 1.52\text{--}2$, $Q_m = 1.76 \pm 0.13$, elongate, occasionally ellipsoid, often somewhat amygdaliform, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 30–50 $\times$ 8–12 μm , clavate, 4-spored, hyaline; sterigmata 4–6 μm long; basal septa with clamps. Pleurocystidia absent.

Cheilocystidia 20–35 $\times$ 3–10 μm , poorly differentiated, subclavate, clavate, cylindrical to filiform, occasionally septate, thin-walled, colorless, hyaline. Subhymenium composed of 3–6 μm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless; thin-walled hyphae 2–20 μm wide. Pileipellis a cutis, composed of radially arranged, 3–6 μm wide, thin-walled, colorless hyphae; subpellis composed of radially arranged inflated cells, fusiform, ellipsoid, clavate to cylindrical, 15–50 $\times$ 8–15 μm , thin-walled, colorless. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in subalpine temperate forests with trees of *Abies*.

Known distribution: Known from southwestern China.

Specimens examined: CHINA. Xizang Autonomous Region, Qamdo, Markam County, Hongla Mountain, in a forest dominated by *Abies*, altitude 4200 m, 4 Aug. 2013, Xiao-Bin Liu 225 (KUN-HKAS79926). Yunnan Province, Diqing Tibetan Autonomous Prefecture, Daxueshan, in a forest dominated by species of *Picea*, *Quercus* and *Rhododendron*, altitude 4100 m, 8 Aug. 2009, Zhu L. Yang 5504 (KUN-HKAS58046).

Notes: Two Chinese specimens (KUN-HKAS79926 and KUN-HKAS58046) clustered with the neotype of *T. inamoenum* as a monophyletic group (Fig. 4). Because subtle morphological and ecological differences were observed among them, the Chinese collections are regarded as *T. inamoenum* for the time being. *Tricholoma inamoenum* is well recognized by its off-white to ivory basidioma, inflated cells in subpellis and associations with *Abies* and *Picea* trees (this study).

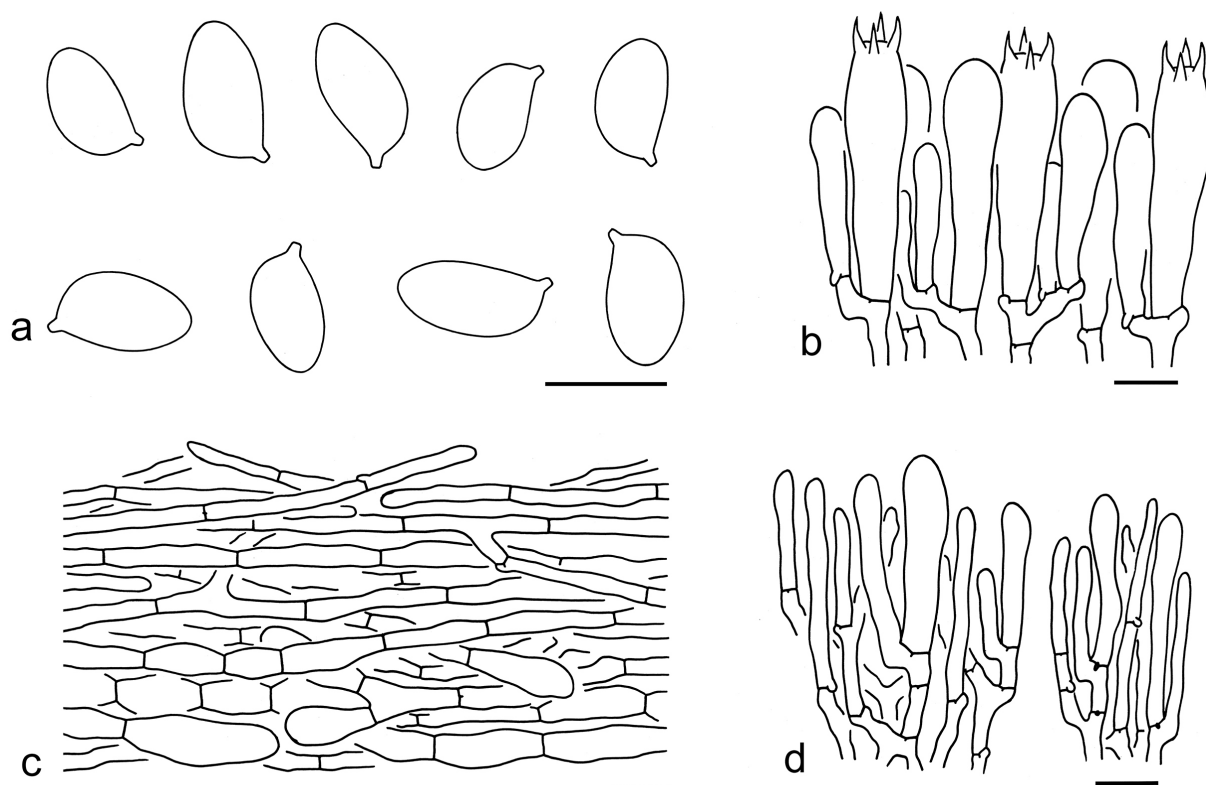


Fig. 84 Microscopic features of *Tricholoma inamoenum* (KUN-HKAS79926). a Basidiospores. b Hymenium and subhymenium. c Pileipellis. d Marginal cells. Scale bars: a, b, d = 10 μm , c = 20 μm .

67. *Tricholoma sulphureum* (Bull.) P. Kumm. type I, Führ. Pilzk. (Zerbst): 133 (1871). Figs. 69o, 85

Basionym: *Agaricus sulphureus* Bull., Herb. Fr. (Paris) 4: pl. 168 (1784) [1783–84].

Description: Basidioma small to medium-sized. Pileus 4–8 cm in diam., at first convex, then applanate, sometimes concave, sometimes slightly umbonate; surface dry, glabrous, sulphur-yellow (2A4–6, 2B2–5) with pale ochraceous (4C3–5) tinge; margin straight to slightly reflexed; context cream (1A2). Lamellae sinuate, yellow (1A2–4) to sulphur-yellow (1B4–7), often with grass greenish yellow (30A2–4) tinge, close; edges yellow (1A2–4) to sulphur-yellow (1B4–7). Stipe 7–10 × 0.8–1.5 cm, cylindrical, yellow (1A2–4) to sulphur-yellow (1B4–7), fibrillose, base with white-yellowish (1A2–3) hairs, exannulate. Taste unpleasant. Odour with strong gas or almond.

Basidiospores [40/2/2] (8.5–) 10–12 (–14) × (5–) 5.5–7 µm (mean length = 10.6 µm, mean width = 6.2 µm), Q = (1.21–) 1.6–1.83 (–2), Qm = 1.71 ± 0.13, elongate, often somewhat amygdaliform, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 30–50 × 9–12 µm, clavate, 4-spored, hyaline; sterigmata 5–8 µm long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia 15–30 × 3–7 µm, poorly differentiated, clavate, cylindrical to filiform, sometimes septate, thin-walled, colorless, hyaline. Subhymenium composed of 2–4 µm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled hyphae 2–4 µm wide. Pileipellis a cutis, composed of radially arranged to interwoven, 3–7 µm wide, thin-walled, colorless to brownish filamentous hyphae; subpellis composed of radially arranged, more or less slightly inflated hyphae, cylindrical, clavate to ellipsoid, 8–20 µm wide,

thin-walled, colorless. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in broad-leaved forests.

Known distribution: Known from Europe, North America, and East Asia.

Specimens examined: CHINA. Yunnan Province, Kunming, Panlong District, Shuanglong Village, Yeya Lake, the type of forest unknown, altitude 2100 m, 8 Sept. 2008, Xi-Hui Du 57 (KUN-HKAS55509). GERMANY. Hessen, Marburg, in a broad-leaved forest with *Fagus*, altitude 300 m, 2 Dec. 2006, Zhu L. Yang M10 (KUN-HKAS53473).

Notes: Our phylogenetic inference based on the ITS sequences (Fig. 4) indicated that *T. sulphureum* s. l. is not monophyletic but clusters into three clades (*T. sulphureum* type I, II and III) (Comandini et al. 2004; Christensen & Heilmann-Clausen 2013; Heilmann-Clausen et al. 2017). Because no epitype of *T. sulphureum* is selected, the phylogenetic position of this species remains unclear. Among the three clades, the samples collected in China were grouped in *T. sulphureum* type I and II, and the two types can be separated by their size of basidiospores and structure of subpellis. *Tricholoma sulphureum* type III is currently only known in Europe. *Tricholoma sulphureum* type I is recognized by its sulphur-yellow basidioma, elongate to amygdaliform basidiospores (10–12 × 5.5–7 µm, mean length = 10.6 µm, mean width = 6.2 µm, Q = 1.6–1.83, Qm = 1.71 ± 0.13), slightly inflated hyphae in subpellis and a strong odour. *Tricholoma sulphureum* type II is characterized by its sulphur yellow basidioma, elongate to amygdaliform basidiospores (9–11.5 × 5–6.5 µm, mean length = 9.9 µm, mean width = 5.4 µm, Q = 1.64–2, Qm = 1.82 ± 0.12) and a strong odour.

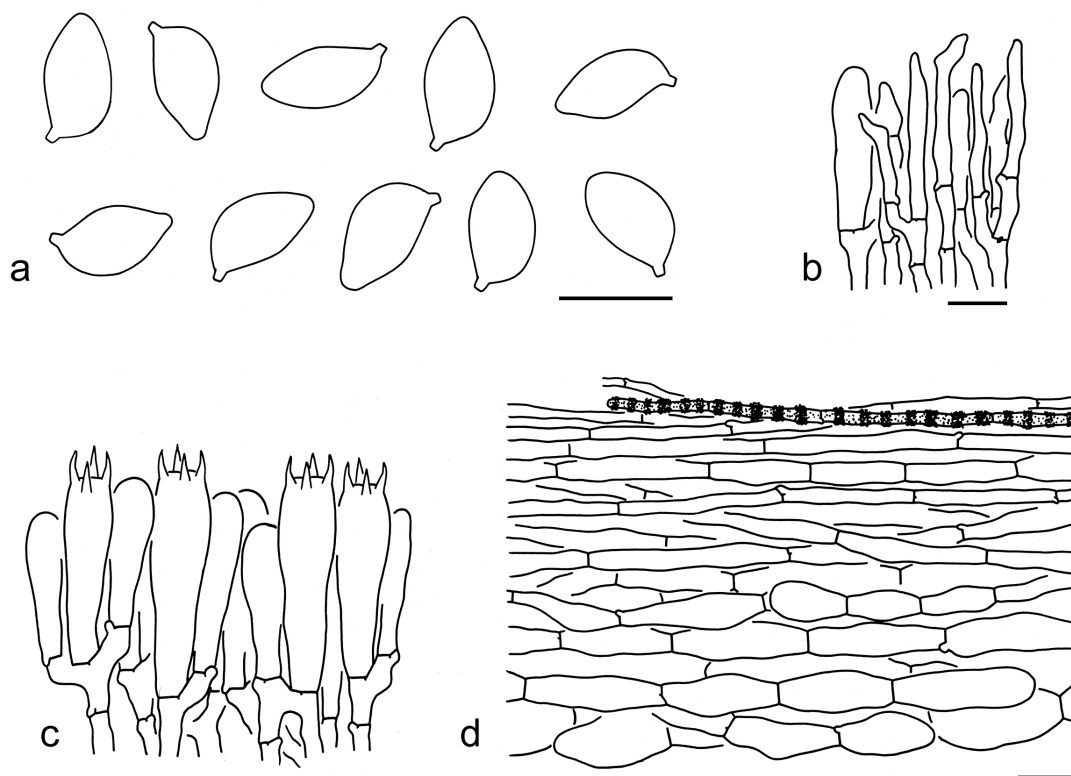


Fig. 85 Microscopic features of *Tricholoma sulphureum* type I. a Basidiospores (KUN-HKAS55509). b Marginal cells (KUN-HKAS53473). c Hymenium and subhymenium (KUN-HKAS55509). d Pileipellis (KUN-HKAS53473). Scale bars: a–c = 10 µm, d = 20 µm.



Fig. 86 Fresh basidiomata of the species in *Tricholoma*. a *T. sulphureum* type II (KUN-HKAS106305). b *T. tangerinum* (holotype, KUN-HKAS49355). c *T. atosquamosum* (KUN-HKAS106310). d *T. olivaceotinctum* (KUN-HKAS107583). e *T. argyraceum* (KUN-HKAS70098). f *T. bonii* (KUN-HKAS78979). g *T. cingulatum* (KUN-HKAS106634). h *T. inocybeoides* (KUN-HKAS106525). i *T. gansuense* (holotype, KUN-HKAS106316). j *T. terreum* (KUN-HKAS135002). k *T. triste* (KUN-HKAS135003). l *T. macrosporum* (holotype, KUN-HKAS107577). m *T. griseofulvum* (holotype, KUN-HKAS106652). n *T. aurantiophyllum* (KUN-HKAS151533). o *T. melleum* (KUN-HKAS103101).

Tricholoma hemisulphureum (Kühner) A. Riva ex Boffelli is sister to *T. sulphureum* type I with low support (Fig. 4), but the former has a pinkish pileus, pale pinkish lamellae and a poorly differentiated subpellis (Riva 2003; Christensen & Heilmann-Clausen 2013). *Tricholoma bryogenum* Mort. Chr., Heilm.-Claus. & Vauras is somewhat similar to this, but differs by its pileus with a pinkish buff to ochraceous orange center and a chrome margin, a poorly differentiated subpellis and absence of clamps (Christensen & Heilmann-Clausen 2013; Heilmann-Clausen et al. 2017).

68. *Tricholoma sulphureum* (Bull.) P. Kumm. type II, Führ. Pilzk. (Zerbst): 133 (1871). Figs. 86a, 87

Basionym: *Agaricus sulphureus* Bull., Herb. Fr. (Paris) 4: pl. 168 (1784) [1783–84].

Description: Basidioma small to medium-sized. Pileus 3–12 cm in diam., at first bell-shaped to convex, soon plano-convex to applanate, occasionally with a low umbo; surface dry, smooth, pruinose to tomentose, orangish brown (4A6–8, 5A4–7), sulphur-yellow (3A4–7) to greenish yellow (30A3–6), often darker at center, context white (1A1), cream (1A2) to yellow (2A3–5); margin inflexed to involute. Lamellae sinuate to emarginate, sulphur-yellow (2A4–6), lemon yellow (1A5–7) to greenish yellow (30A4–6), crowded; edges entire, sulphur-yellow (2A4–6). Stipe 4–12 × 0.5–2 cm, cylindrical, orangish yellow (4A3–5), sulphur-yellow (1A4–6) to greenish yellow (30A2–5), fibrillose, exannulate. Taste and odour strong, unpleasant.

Basidiospores [40/2/2] (8.5–) 9–11.5 × (4–) 5–6.5 µm (mean length = 9.9 µm, mean width = 5.4 µm), Q = 1.64–2 (–2.25), Qm = 1.82 ± 0.12, elongate, often somewhat amygdaliform, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia (30–) 35–45 (–50) × 9–11 µm, clavate,

4-spored, hyaline; sterigmata 4–6 µm long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia 20–40 × 2–10 µm, poorly differentiated, clavate, narrowly clavate to filiform, sometimes septate, thin-walled, colorless, hyaline. Subhymenium composed of 2–5 µm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled hyphae 4–15 µm wide. Pileipellis a cutis, composed of radially arranged to interwoven, 3–8 µm wide, thin-walled, brownish to colorless filamentous hyphae; subpellis poorly differentiated. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil dominated in broad-leaved forests.

Known distribution: Known from Europe, North America, and East Asia.

Specimens examined: CHINA. Xizang Autonomous Region, Xigaze, Gyirong County, the type of forest and altitude unknown, 11 Aug. 2017, Ai-Guo Xu 2076 (AF0001459). Yunnan Province, Kunming, Kunming Botanical Garden, in a broad-leaved forest, altitude 1950 m, 25 Sep. 2018, Jian-Wei Liu 1640 (KUN-HKAS106305). NORTH MACEDONIA. The type of forest not recorded, altitude 1400 m, 12 Oct. 2019, Zhu L. Yang 6294 (KUN-HKAS106906); same location, 22 Oct. 2019, Pan-Meng Wang 2666 (KUN-HKAS131889).

Notes: As mentioned under *T. sulphureum* type I, *T. sulphureum* s. l. is a polyphyletic group and separated into three clades (*T. sulphureum* type I, II and III). *Tricholoma odorum* Peck is closely related to *T. sulphureum* type II (Fig. 4), but differs by its relatively paler, yellowish buff to yellowish tan pileus and close lamellae (Bessette et al. 2013; Landry et al. 2022). *Tricholoma hemisulphureum* is somewhat similar to *T. sulphureum* type II, but the former differs by its pinkish color in pileus and lamellae (Riva 2003; Christensen & Heilmann-Clausen 2013).

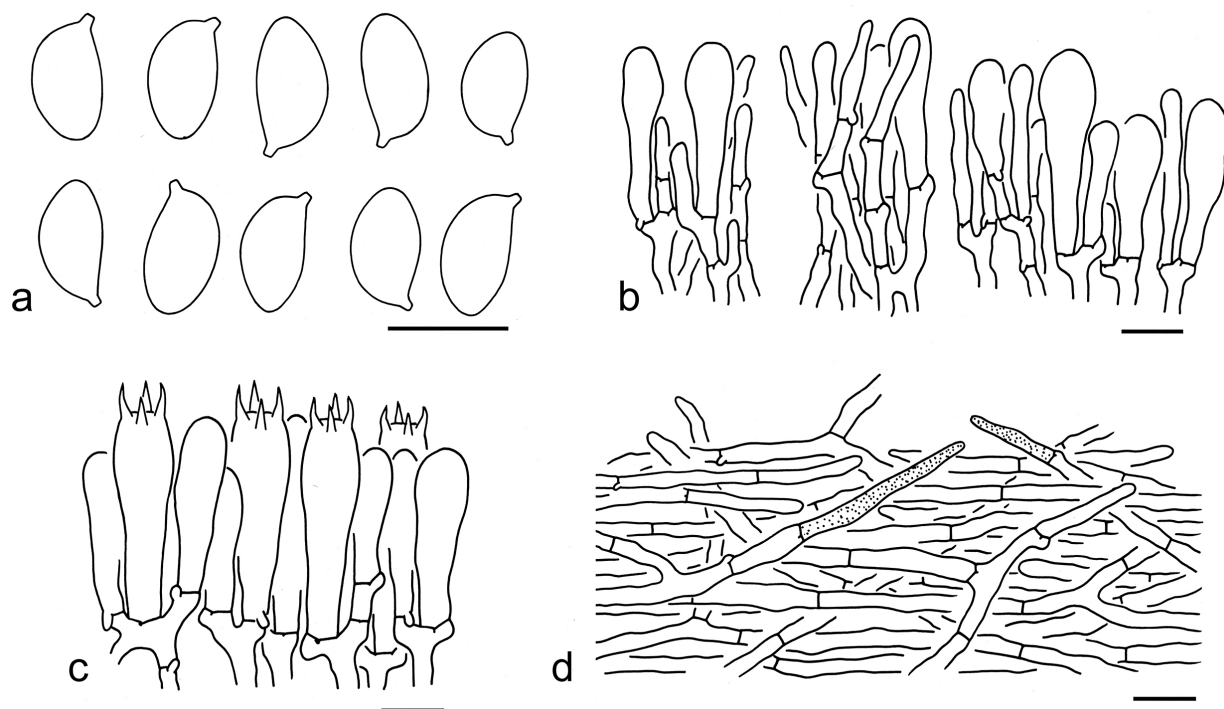


Fig. 87 Microscopic features of *Tricholoma sulphureum* type II (KUN-HKAS106305). a Basidiospores. b Marginal cells. c Hymenium and subhymenium. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm.

69. *Tricholoma tangerinum* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 86b, 88

Fungal Names: FN 572350

Etymology: tangerinum = orange colored, referring to its orange colored pileal center.

Diagnosis: Related to *T. sulphureum* type I, but differs by its orangish brown pileus and smaller basidiospores ($9\text{--}10 \times 5\text{--}6 \mu\text{m}$, mean length = $9.7 \mu\text{m}$, mean width = $5.8 \mu\text{m}$).

Type: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Seda County, Huoxi Village, in a subalpine forest, altitude 3650 m, 11 Aug. 2005, Zai-Wei Ge 860 (holotype, KUN-HKAS49355).

Description: Basidioma small to medium-sized. Pileus 5–7 cm in diam., convex, with a broadly umbo; surface dry, smooth, orangish brown (5A4–6, 4A6–8) to brown (4B6–8) at center, brownish (5B3–4, 3B3–5) to white (1A1) towards margin; margin straight. Lamellae sinuate to emarginate, white (1A1) to cream (1A2), close; edges entire, white (1A1) to cream (1A2). Stipe 6–9 $\times$ 0.5–1.5 cm, cylindrical, brownish (3B2–5), fibrillose, exannulate. Taste and odour not recorded.

Basidiospores [$20/1/1$] $9\text{--}10 \times 5\text{--}6 \mu\text{m}$ (mean length = $9.7 \mu\text{m}$, mean width = $5.8 \mu\text{m}$), $Q = 1.5\text{--}1.85$ (–2), $Q_m = 1.68 \pm 0.14$, ellipsoid to elongate, often somewhat amygdaliform, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $40\text{--}50 \times 8\text{--}12 \mu\text{m}$, clavate, 4-spored, hyaline; sterigmata $4\text{--}6 \mu\text{m}$ long; basal septa with clamps.

Pleurocystidia and cheilocystidia absent. Subhymenium composed of 2–4 μm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled, cylindrical to filamentous hyphae 3–15 μm wide. Pileipellis a cutis, composed of radially arranged to interwoven, 4–10 μm wide, thin-walled, brown, brownish to colorless hyphae; subpellis poorly differentiated. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in subalpine forests.

Known distribution: Known from Southwestern China.

Additional specimen examined: CHINA. Gansu Province, Gannan, Lintan County, in a forest with trees of *Abies*, *Betula* and *Prunus*, altitude 2670 m, 26 Oct. 2020, Xin Xu 419 (KUN-HKAS138838).

Notes: *Tricholoma tangerinum* is characterized by an orangish brown to brown pileus with a paler margin, and ellipsoid, elongate to amygdaliform basidiospores ($9\text{--}10 \times 5\text{--}6 \mu\text{m}$, mean length = $9.7 \mu\text{m}$, mean width = $5.8 \mu\text{m}$, $Q = 1.5\text{--}1.85$, $Q_m = 1.68 \pm 0.14$). This species is related to *T. sulphureum* type I based on the five-gene phylogenetic inference (Fig. 3). However, *T. sulphureum* type I has a sulphur basidioma and larger basidiospores ($10\text{--}12 \times 5.5\text{--}7 \mu\text{m}$, mean length = $10.6 \mu\text{m}$, mean width = $6.2 \mu\text{m}$). *Tricholoma hemisulphureum* is similar, but differs from *T. tangerinum* by its coarsely velutinous pileus and relatively larger basidiospores ($8.1\text{--}13 \times 5.5\text{--}8.2 \mu\text{m}$) (Riva 2003; Christensen & Heilmann-Clausen 2013).

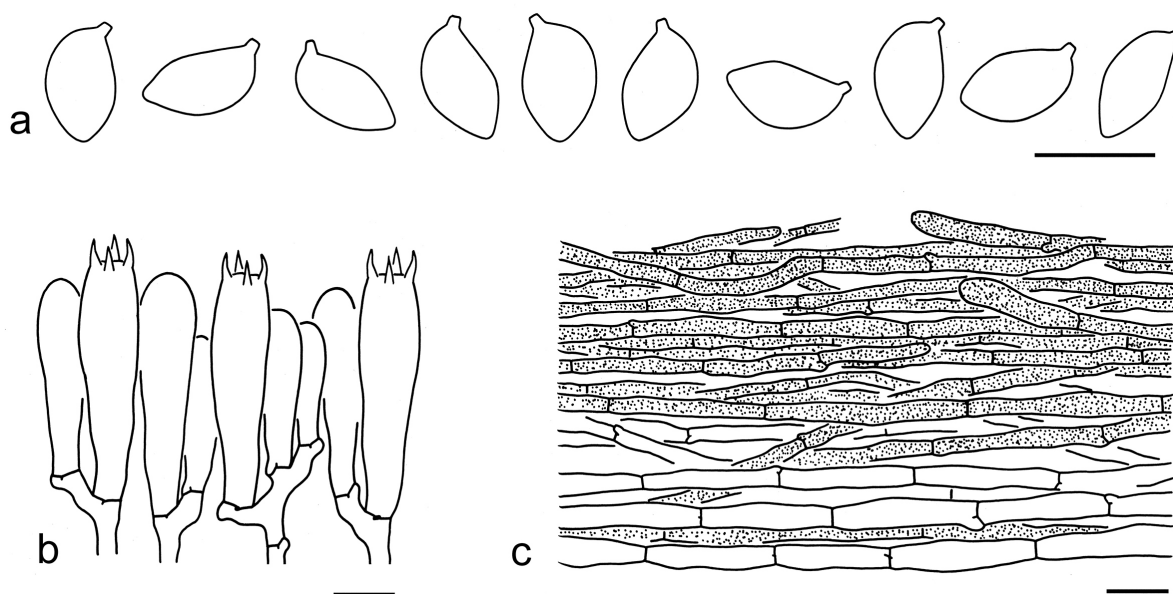


Fig. 88 Microscopic features of *Tricholoma tangerinum* (holotype, KUN-HKAS49355). a Basidiospores. b Hymenium and subhymenium. c Pileipellis. Scale bars: a, b = $10 \mu\text{m}$, c = $20 \mu\text{m}$.

***Tricholoma* subgen. *Terrea* Ding et al.**

Type: *Tricholoma terreum* (Schaeff.) P. Kumm., Führ. Pilzk. (Zerbst): 134 (1871).

Description: Basidioma tricholomatoid. Pileus umbonate or not, brown or grey, radially fibrillose or squarrose. Lamellae crowded to close. Annulus present or absent. Basidiospores small, medium-sized to large, ellipsoid to elongate, smooth, inamyloid. Cheilocystidia present or absent. Pileipellis an ixo-cutis with filamentous hyphae, a

cutis with its subpellis composed of inflated cells, or a cutis with somewhat erected, thick-walled hyphae. Clamps present or absent.

Ecology: Ectomycorrhizal. On soil with various trees.

Known distribution: Molecular data indicates species from this subgenus are found in Europe, North America, and Asia.

Notes: *Tricholoma* subgen. *Terrea* forms a clade sister to subgen. *Sericeicutis* (Figs. 2, 14). Members in this subgenus can be divided into two sections (sect. *Atrosquamosa* and sect. *Terrea*) and two unnamed clades (clades A and clade B).

Currently, nine species of this subgenus are found in China (see below).

Tricholoma sect. *Atrosquamosa* Kühner ex Bon

Type: *Tricholoma atrosquamosum* Sacc., Syll. fung. (Abellini) 5: 104 (1887).

Description: Basidioma tricholomatoid. Pileus umbonate or not, dirty white to greyish, densely covered with dark grey to black squamules to scales. Lamellae crowded to close. Annulus absent. Basidiospores small, ellipsoid to elongate, smooth, inamyloid. Cheilocystidia conspicuous or absent. Pileipellis a cutis with transition to a trichoderm at regular intervals, composed of thick-walled hyphae, subpellis composed of radially arranged, thin-walled hyphae. Clamps present or absent.

Ecology: Ectomycorrhizal. On soil with various trees.

Known distribution: Molecular data shows species from this section are distributed in Europe, North America, and Asia.

Notes: *Tricholoma atrosquamosum* and *T. olivaceotinctum* Heilm.-Claus. & Mort. Chr. are found in China (see below).

Key to the species of *Tricholoma* sect. *Atrosquamosa* from China

1. Pileus white to dirty white background without olivaceous color; cheilocystidia poorly differentiated; clamps absent.....
.....*T. atrosquamosum*

1. Pileus cream, yellow-grey to olivaceous grey background with obvious olivaceous color; cheilocystidia conspicuous; clamps present *T. olivaceotinctum*

70. *Tricholoma atrosquamosum* Sacc., Syll. fung. (Abellini) 5: 104 (1887). Figs. 86c, 89

Replaced synonym: *Agaricus atrosquamosus* Chevall., Strauch- und Laubflechten Mitteleur. 1: 45 (1837).

Competing homonym: non *Agaricus atrosquamosus* Batsch, Elench. fung. (Halle): 81, tab. 6, fig. 27 (1783).

Description: Basidioma medium-sized. Pileus 5–10 cm in diam., plano-convex to applanate, sometimes with a broadly low umbo; surface dry, a white (1A1) to dirty white (1B1–2) background densely covered with greyish (1B1), grey (1C1, 2C1) to dark grey (1E1–3, 1F1), more or less recurved, fibrillose scales; margin often radially splitting; context white (1A1). Lamellae sinuate, dirty white (1B2) to greyish (1B1), subclose; edges greyish (1B1) to cream (2B2) often with black (1F8) spots. Stipe 6–9 × 1–1.5 cm, cylindrical, stuffed, white (1A1) to dirty white (1B2), glabrous, exannulate. Taste not recorded. Odour sweet.

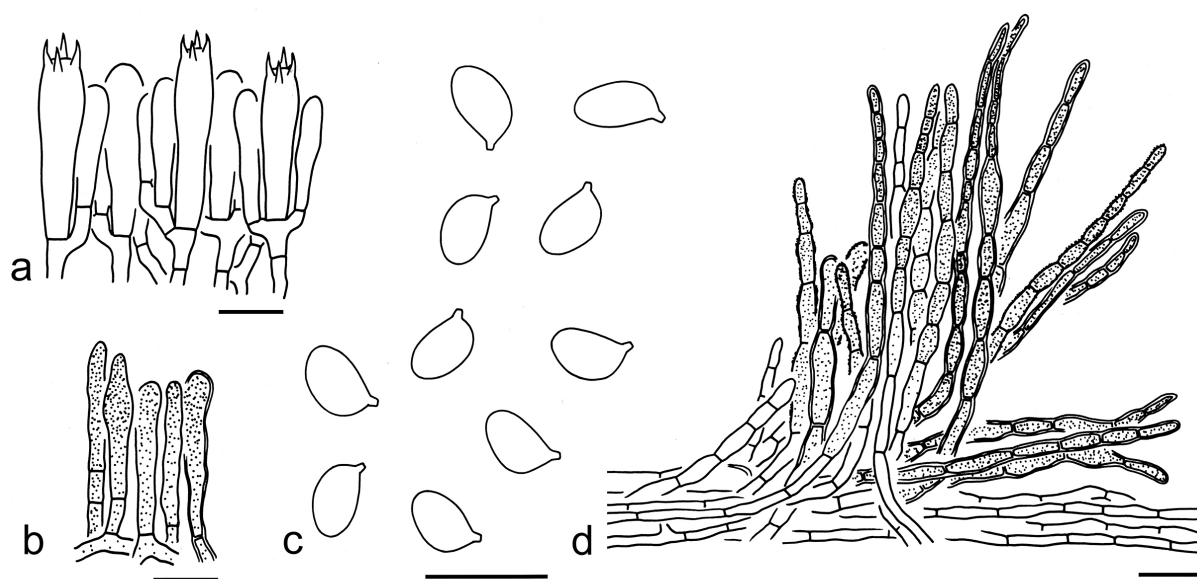


Fig. 89 Microscopic features of *Tricholoma atrosquamosum* (KUN-HKAS97910). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 µm, d = 50 µm.

Basidiospores [60/3/2] (5–) 5.5–7 (–8) × (3–) 3.5–4.5 µm (mean length = 6.4 µm, mean width = 4 µm), $Q = (1.25\text{--}) 1.4\text{--}1.8$ (–2), $Q_m = 1.6 \pm 0.14$, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 25–35 × 5–8 µm, clavate, 4-spored, hyaline; sterigmata 3–6 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia poorly differentiated. Subhymenium composed of 2–4 µm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae 2–6 µm wide. Pileipellis a cutis with transition to a trichoderm at regular intervals, composed

of 5–25 µm wide, thick-walled (ca. 1 µm), yellow-brown, cylindrical to filamentous hyphae; subpellis poorly differentiated, composed of radially arranged, thin-walled hyphae. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in broad-leaved or coniferous forests.

Known distribution: Known from Europe (Riva 1988, Christensen & Heilmann-Clausen 2013), North America (Bessette et al. 2013, Trudell et al. 2022) and Southwestern China.

Specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, Waze Village, in a forest with *Picea*, altitude 386 m, 8 Sep. 2016, KD-LJW 117 (KUN-HKAS97910); same city, Xinduqiao Town, in a broad-leaved forest, altitude 3500 m, 11 Sep. 2016, KD-Ding 130 (KUN-HKAS97211). Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-La, the type of forest unknown, altitude 3500 m, 5 Sep. 2018, Jian-Wei Liu 1596 (KUN-HKAS106310).

Notes: *Tricholoma atosquamosum* is characterized by its white to dirty white pileus covered with greyish, grey to dark grey scales, ellipsoid to elongate basidiospores ($5.5\text{--}7 \times 3.5\text{--}4.5 \mu\text{m}$, $Q = 1.4\text{--}1.8$, $Q_m = 1.6 \pm 0.14$) and sweet odour (this study). In the five-gene phylogenetic analyses (Fig. 3), it is closely related to *T. olivaceotinctum*. However, *T. olivaceotinctum* differs by its yellow-grey to olivaceous grey pileus with obvious olivaceous color, conspicuous cheilocystidia and presence of clamps. *Tricholoma squarrulosum* Bres. is similar to *T. atosquamosum*, but the former has distinct brownish to blackish squamules on stipe surface and relatively larger basidiospores (Hongo 1988; Riva 1988; Bessette et al. 2013; Christensen & Heilmann-Clausen 2013). *Tricholoma orirubens* Qué. can be confused with *T.*

atosquamosum. However, the Chinese specimens of *T. atosquamosum* differs by its slightly longer basidiospores ($5.5\text{--}7 \times 3.5\text{--}4.5 \mu\text{m}$, mean length = $6.4 \mu\text{m}$, mean width = $4 \mu\text{m}$, $Q = 1.4\text{--}1.8$, $Q_m = 1.6 \pm 0.14$) and absence of clamps at all part during all stage of development (this study).

71. *Tricholoma olivaceotinctum* Heilm.-Claus. & Mort. Chr., Mycotaxon 107: 436 (2009). Figs. 86d, 90

Description: Basidioma small, medium-sized to large. Pileus 3–10 cm in diam., at first hemispherical to convex, then plano-convex to applanate, slightly umbonate at center; surface dry, a cream (1A2), yellow-grey (1B3–5) to olivaceous grey (30B3–5, 30C4–6) background densely covered with dark grey (1E1–3) to black (1F1–3), recurved fibrillose scales; margin inflexed to straight; context white (1A1). Lamellae adnexed to sinuate, white (1A1), cream (1A2) to olivaceous (30B4–6), subclose; edges cream (1A2) to olivaceous grey (30D6–8). Stipe 7–13 $\times$ 0.7–2 cm, cylindrical, sometimes slightly inflated at base, white (1A1) to olivaceous grey (30B3–5, 30C4–6) often with a white (1A1) base, covered with brownish grey (1D4–6) to olivaceous grey (30B3–5, 30C4–6) fibrils, exannulate. Taste and odour not recorded.

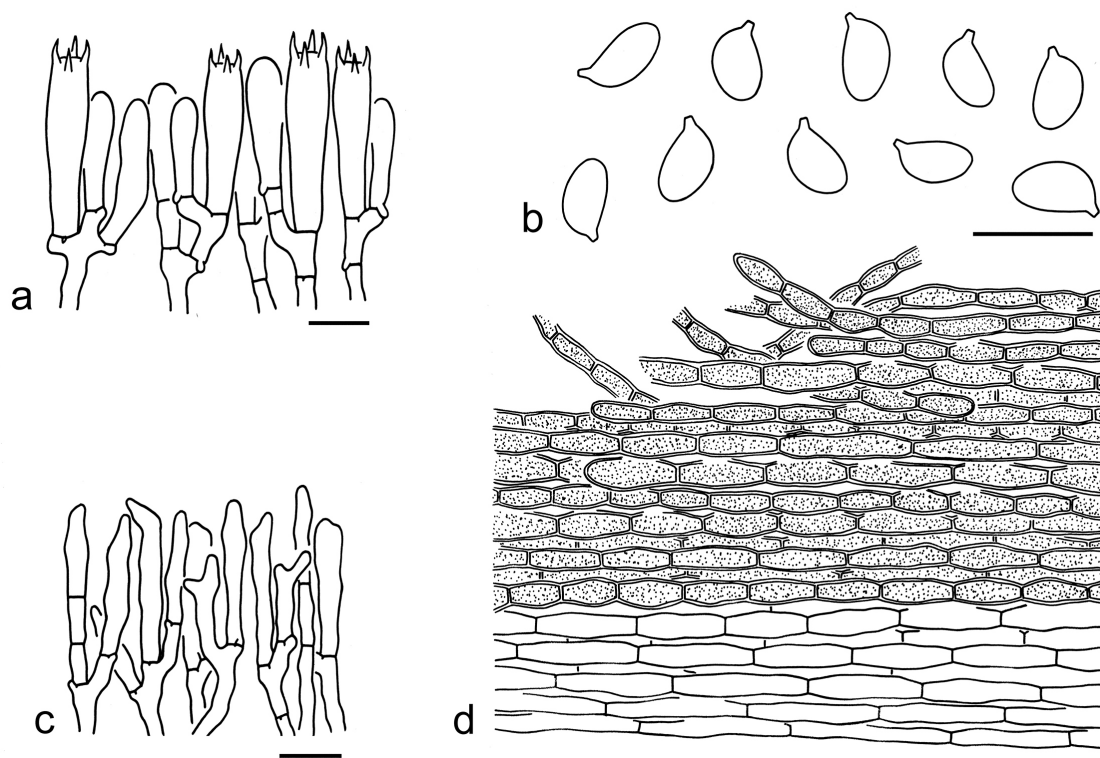


Fig. 90 Microscopic features of *Tricholoma olivaceotinctum* (KUN-HKAS107583). a Hymenium and subhymenium. b Basidiospores. c Marginal cells. d Pileipellis. Scale bars: a–c = 10 μm , d = 50 μm .

Basidiospores [40/2/2] $6\text{--}7.5 \times 3.5\text{--}5 \mu\text{m}$ (mean length = $6.5 \mu\text{m}$, mean width = $4.1 \mu\text{m}$), $Q = (1.2\text{--}) 1.33\text{--}1.88$ (–2), $Q_m = 1.6 \pm 0.17$, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $25\text{--}35 \times 6\text{--}8 \mu\text{m}$, clavate, 4-spored, hyaline; sterigmata $3\text{--}5 \mu\text{m}$ long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia $15\text{--}30 \times 3\text{--}5 \mu\text{m}$, conspicuous, cylindrical to subclavate, thin-walled, colorless, hyaline. Subhymenium

composed of 2–4 μm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless, thin-walled hyphae 2–5 μm wide. Pileipellis a cutis, composed of radially arranged, ellipsoid, clavate to cylindrical hyphae, often breaking up into curved trichoderm scales, 5–25 μm wide, thick-walled (ca. 1 μm), yellow-brown; subpellis poorly differentiated, composed of radially arranged, thin-walled hyphae. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in temperate forests with trees of *Picea*.

Known distribution: Known from Europe (Christensen & Heilmann-Clausen 2009, 2013) and Southwestern China.

Specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, Xiaba Village, in a subalpine forest, altitude 3750 m, 23 Aug. 2017, Jian-Wei Liu 959 (KUN-HKAS107586); same city, Tagong Town, in a subalpine forest, altitude 3700 m, 22 Aug. 2017, Jian-Wei Liu 948 (KUN-HKAS107583); Ngawa Tibetan and Qiang Autonomous Prefecture, Hongyuan County, Shuajingsi Town, in a subalpine forest with *Picea*, altitude 3300 m, 12 Aug. 2013, Kuan Zhao 357 (KUN-HKAS80782).

Notes: *Tricholoma olivaceotinctum* is well delimited by its olivaceous grey pileus covered with dark grey to black scales, ellipsoid to elongate basidiospores ($6\text{--}7.5 \times 3.5\text{--}5 \mu\text{m}$, $Q = 1.33\text{--}1.88$, $Q_m = 1.6 \pm 0.17$), the presence of clamps and associations with trees of *Picea* (this study). In the protologue of *T. olivaceotinctum*, the absence of clamps was described (Christensen & Heilmann-Clausen 2009). However, clamps were found in the Chinese specimens (Fig. 90), which clustered well with the holotype of *T. olivaceotinctum* (Fig. 4). Although the taste and odour of the Chinese collections of this species were not recorded in the field, European collections were reported to have a weak but distinctly spicy and sweetish odour, reminiscent of honey and often intermixed with components similar to ground black pepper, becoming faintly to strongly farinaceous after cutting; the taste was mild to slightly bitter, and distinctly farinaceous (Christensen & Heilmann-Clausen 2013).

In the phylogenetic analyses based on the ITS sequences (Fig. 4), *T. olivaceotinctum* is related to *T. squarulosum*, *T. michiganense* A.H. Sm. and *T. basirubens* (Bon) A. Riva & Bon. However, *T. squarulosum* differs by its tomentose to squarulose, dark greyish brown to black pileus often paler towards margin, relatively larger basidiospores ($4.8\text{--}10.5 \times 2.8\text{--}6.4 \mu\text{m}$), the absence of clamps, and associations with deciduous trees (Hongo 1988; Riva 1988; Bessette et al. 2013; Christensen & Heilmann-Clausen 2013). *Tricholoma michiganense* possesses a dark grey pileus without olivaceous color and is associated with oak (Trudell et al. 2022). *Tricholoma basirubens* has a pale cream to buff pileus background without olivaceous color, the absence of clamps and associations with deciduous trees (Riva 1988; Christensen & Heilmann-Clausen 2013).

Tricholoma sect. *Terrea*

Type: *Tricholoma terreum* (Schaeff.) P. Kumm., Führ. Pilzk. (Zerbst): 134 (1871).

Description: Basidioma tricholomatoid. Pileus umbonate or not, white, grey, brown to black, densely covered with felty, tomentose to somewhat fibrillose squamules. Lamellae crowded to close. Veil absents or somewhat present especially in young basidioma. Basidiospores small to medium-sized, ellipsoid to elongate. Pleurocystidia absent. Cheilocystidia present or absent. Pileipellis a cutis with transition to a trichoderm at regular intervals composed of thick-walled, filamentous to cylindrical hyphae with poorly or well differentiated subpellis. Clamps absent.

Ecology: Ectomycorrhizal. On soil with various trees.

Known distribution: Molecular data indicates species from this section are distributed in Europe, North America, and Asia.

Notes: To date, seven species, *T. argyraceum*, *T. bonii* asso & Candusso, *T. cingulatum*, *T. inocybeoides* A. Pearson, *T. terreum*, *T. triste* and *T. gansuense* Y.Y. Cui & Zhu L. Yang, occur in China. Among them, *T. cingulatum* and *T. terreum* are widely distributed in Europe, North America and Asia, *T. gansuense* is currently only collected in China, while the remaining four species can be found in Europe and Asia.

Key to the species of *Tricholoma* sect. *Terrea* from China

1. A white stipe with a white, felty to cottony annulus on the upper part *T. cingulatum*
1. A stipe with or without a cobweb-like zone in the upper part 2
2. Veil is more or less present, often form a cobweb-like zone in the upper part of stipe; subpellis poorly differentiated with radially arranged filamentous hyphae 3
2. Veil absent, without a cobweb-like zone in the upper part of stipe; subpellis composed of inflated cells 5
3. Basidiospores relatively longer, elongate, $6\text{--}8 \times 3.5\text{--}4 \mu\text{m}$, mean length = $7.1 \mu\text{m}$, mean width = $3.9 \mu\text{m}$ $Q = 1.63\text{--}2$, $Q_m = 1.82 \pm 0.15$ *T. inocybeoides*
3. Basidiospores relatively shorter, ellipsoid to elongate, with mean length less than $5.5 \mu\text{m}$ 4
4. Veil weakly developed, only distinct in very young basidioma; cheilocystidia poorly differentiated *T. gansuense*
4. Veil developed, often form a cobweb-like zone in the upper part of stipe; cheilocystidia conspicuous *T. argyraceum*
5. Pileus dark colored, black, dark grey to grey, with a distinct, white to dirty white zone at margin *T. triste*
5. Pileus relatively paler, greyish, grey, brownish, brown, brownish grey to dark grey, without a distinct, white to dirty white zone at margin 6
6. Basidiospores relatively longer, $6\text{--}9 \times 4\text{--}6 \mu\text{m}$, mean length = $7.2 \mu\text{m}$; cheilocystidia conspicuous *T. bonii*
6. Basidiospores relatively shorter, $6\text{--}7 \times 3.5\text{--}5 \mu\text{m}$, mean length = $6.2 \mu\text{m}$; cheilocystidia poorly differentiated *T. terreum*

72. *Tricholoma argyraceum* (Bull.) Gillet, Hyménomycètes (Alençon): 103 (1874) [1878]. Figs. 86e, 91

Basionym: *Agaricus argyraceus* Bull., Herb. Fr. (Paris) 9: tab. 423 (1789).

Description: Basidioma small to medium-sized. Pileus 2–6 cm in diam., at first hemispherical to convex, then plano-convex to applanate, often slightly umbonate at center; surface dry, pale grey (1C1–3), grey-brown (2E3–6), brown (4D3–6, 4E5–7, 5D3–6) to dark brown (4E2–4, 4F6–8), covered with grey-brown (2E3–6) to dark brown (4E2–4, 4F6–8), felty-tomentose, tomentose to fibrillose squamules; margin straight to inflexed; context white (1A1). Lamellae sinuate to emarginate, white (1A1), grey-white (1B1) to pale grey (1B1–3), becoming brown (4E6–8) to yellow-brown (4D6–8) when old or damaged, crowded to subclose; edges entire, white (1A1) to grey-white (2E3–6). Stipe 3–8 cm long $\times$ 0.5–1 cm wide, cylindrical, white (1A1), grey-white (2E3–6) to brownish (4D2–5), glabrous, sometimes with a white (1A1) to dark

brown (4E2–4, 4F6–8) cobweb-like zone on the upper part. Taste and odour not recorded.

Basidiospores [60/3/3] (4.5–) 5–6.5 $\times$ 3–4 μ m (mean length = 5.4 μ m, mean width = 3.4 μ m), $Q = (1.25\text{--}) 1.3\text{--}2$, $Q_m = 1.6 \pm 0.15$, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth, apiculus relatively large. Basidia 20–40 $\times$ 5–7 μ m, clavate, 4-spored, hyaline; sterigmata 3–5 μ m long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 15–40 $\times$ 3–6 μ m, conspicuous, filiform, narrowly cylindrical, narrowly clavate to clavate, sometimes fusiform, often septate, thin-walled, colorless and hyaline. Subhymenium composed of 3–6 μ m wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae 2–25 μ m wide. Pileipellis a cutis with transition to a trichoderm at regular intervals, composed of 3–8 μ m wide, thick- (ca. 1 μ m) to thin-walled, colorless, brown to yellow-brown filamentous hyphae, terminal elements subcylindrical with round or abrupt apex; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in temperate or subtropical forests with a wide range of trees (*Pinus*, *Populus* and *Picea* et al.).

Known distribution: Known from Europe and China.

Specimens examined: CHINA. Beijing, Changping District, Yangfang, in a forest with *Populus*, altitude unknown, 5 Aug. 1989, Ju-Fang Wen 892b (HMAS57883); Mentougou District, Qingshui Town, Jiangshuihe Village, Ling Mountain, the type of forest unknown, altitude unknown, date unknown, Xiao-Xia Ding 403 (KUN-HKAS135001). Heilongjiang Province, Longjiang County, forest and altitude unknown, Sep. 1972, Lian-Wang Xu & Xiao-Lan Mao 262 (HMAS37341); Qiqihaer, Meilisi Daur District, Mingyuedao, the type of forest unknown, altitude 150 m, 28 Jul. 2005, collecting no. unknown (HMJAU4263). Sichuan Province, Ganzi Tibetan Autonomous Prefecture, from Dege County to Luhuo County, forest and altitude not recorded, 13 Jul. 2019, Liu-Kun Jia 232 (KUN-HKAS138830); Ganzi Tibetan Autonomous Prefecture,

Kangding, Waze Village, in a forest of *Populus*, altitude 3500 m, 18 Sep. 2017, Xiao-Xia Ding 319 (KUN-HKAS106294); same location and date, Xiao-Xia Ding 320 (KUN-HKAS106661). Yunnan Province, Lijiang, in a forest of *Pinus yunnanensis*, altitude 2450 m, 2 Aug. 2011, Qing Cai 502 (KUN-HKAS70098); Kunming, Yeyahu, forest and altitude not recorded, 12 Jul. 2018, Xiao-Xia Ding 347 (KUN-HKAS105357).

Notes: *Tricholoma argyraceum* is characterized by its pale grey, grey-brown, brown to dark brown pileus covered with grey brown to dark brown, felty-tomentose, tomentose to fibrillose squamules, a white to dark brown, cobweb-like zone often on the upper part of stipe, ellipsoid to elongate basidiospores (5–6.5 $\times$ 3–4 μ m, $Q = 1.3\text{--}2$, $Q_m = 1.6 \pm 0.15$). Even though taste and odour were not recorded in the field for the Chinese collections, Christensen & Heilmann-Clausen (2013) noted a strongly farinaceous odour after cutting and a farinaceous to rancid taste for the European ones.

Tricholoma argyraceum is related to *T. cingulatum* and *T. gansuense* based on the five-gene phylogenetic analysis (Fig. 3). However, *T. cingulatum* has a relatively paler colored pileus, a white, felty to cottony annulus in the upper part of stipe and poorly differentiated cheilocystidia (Riva 1988, 2003; Bessette et al. 2013; Christensen & Heilmann-Clausen 2013; this study). *Tricholoma gansuense* differs by a poorly developed veil only present as cortina on the upper part of stipe in young stage, and poorly differentiated cheilocystidia.

A cobweb-like zone also can be found in young basidioma of *T. sculpturatum* (Fr.) Quél., but it differs from *T. argyraceum* by its indistinctly broad and low umbo at pileus center, and relatively broader basidiospores ($Q = 1.2\text{--}8$, average $Q = 1.4\text{--}1.54$) (Riva 1988; Christensen & Heilmann-Clausen 2013). *Tricholoma inocybeoides* A. Pearson also has a weakly developed veil only distinct in very young basidioma and somewhat similar to *T. argyraceum*, but has relatively longer basidiospores (6–8 $\times$ 3.5–4 μ m, mean length = 7.1 μ m) and poorly differentiated cheilocystidia (this study).

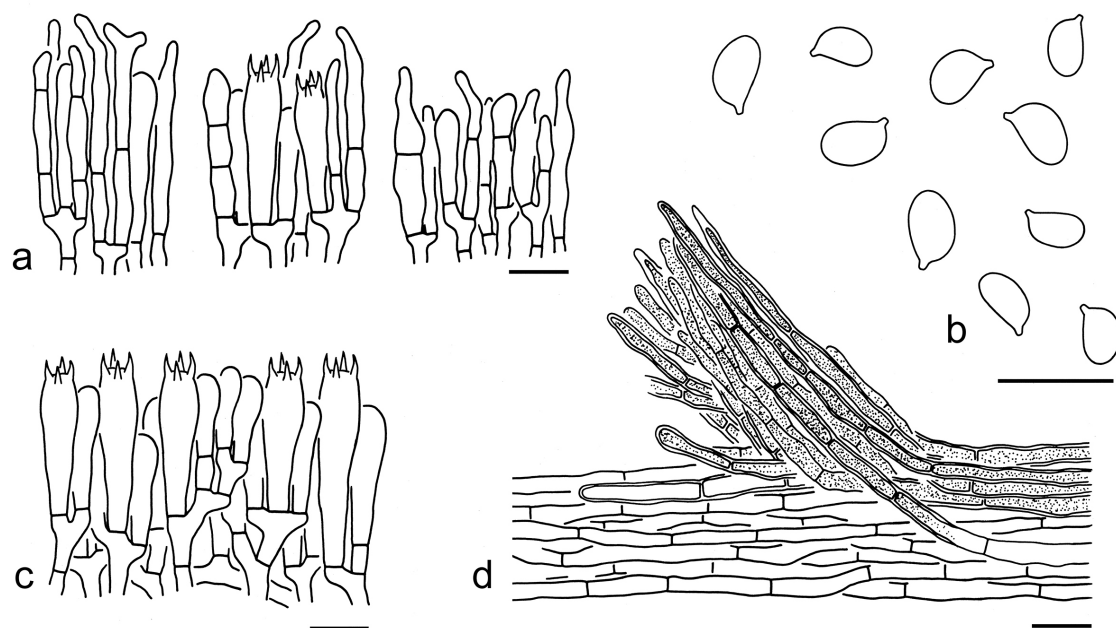


Fig. 91 Microscopic features of *Tricholoma argyraceum* (KUN-HKAS106294). a Marginal cells. b Basidiospores. c Hymenium and subhymenium. d Pileipellis. Scale bars: a–c = 10 μ m, d = 20 μ m.

73. *Tricholoma bonii* Basso & Candusso, Docums Mycol. 27(no. 107): 64 (1997). Figs. 86f, 92

Description: Basidioma small to medium-sized. Pileus 2–7 cm in diam., at first conical to broadly conical, then plano-convex to applanate, often acutely umbonate at center; surface dry, grey-brown, grey to dark grey, covered with dark grey, felty-tomentose to tomentose squamules, often fibrillose at margin; margin straight; context greyish. Lamellae adnexed to sinuate, white, dirty white to greyish, subclose; edges entire to slightly undulate, white to greyish. Stipe 4–8 cm long $\times$ 0.5–1 cm wide, cylindrical, stuffed to hollow, white, dirty white to brownish, glabrous or covered with greyish to brownish fibrillose squamules. Taste and odour not recorded.

Basidiospores [110/5/3] (5.5–) 6–9 (–10) $\times$ 4–6 μ m (mean length = 7.2 μ m, mean width = 4.6 μ m), $Q = (1.15\text{--}) 1.33\text{--}1.8$ (–2.14), $Q_m = 1.56 \pm 0.15$, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth, apiculus relatively large. Basidia 25–35 $\times$ 7–9 μ m, clavate, 4-spored; hyaline; sterigmata 3–6 μ m long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 25–40 $\times$ 7–18 μ m, conspicuous, cylindrical, fusiform, clavate to broadly clavate, often septate, thin-walled, colorless and hyaline. Subhymenium composed of 3–5 μ m wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled hyphae 3–40 μ m wide. Pileipellis a cutis with transition to a trichoderm at regular intervals, composed of 4–10 μ m

wide, thick- (ca. 1 μ m) to thin-walled, colorless to brownish filamentous hyphae, terminal elements subcylindrical with round apex; subpellis composed of radially arranged inflated cells, subglobose, ellipsoid, broadly ellipsoid, oblong to cylindrical, (20–) 30–60 (–120) $\times$ 10–35 μ m, thin-walled, colorless. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in temperate or subtropical coniferous or mixed forests.

Known distribution: Known from Europe and China.

Specimens examined: CHINA. Heilongjiang Province, Heihe, Wudalianchi, the type of forest unknown, altitude 300 m, 26 Sep. 2014, collecting no. unknown (HMJAU35946). Inner Mongolia, Chifeng, Ar Horqin Banner, the type of forest unknown, altitude 500 m, 14 Aug. 2014, collecting no. unknown (HMJAU34437). Liaoning Province, Dandong, Kuandian Man Autonomous County, Sipingjie Village, altitude 500 m, 29 Aug. 2018, Xiao-Xia Ding 385 (KUN-HKAS105395). Yunnan Province, Dali Bai Autonomous Prefecture, Binchuan County, Zhusheng Temple, in a forest with *Pinus yunnanensis*, altitude 2000 m, 20 Sep. 2012, Qi Zhao 1722 (KUN-HKAS78979); Kunming, Panlong District, bought from Ciba market, forests and altitude unknown, 23 Jul. 2017, Xiao-Xia Ding 221 (KUN-HKAS106563). Sichuan Province, Ngawa Tibetan and Qiang Autonomous Prefecture, Jiuzhaigou, in a mixed forest of *Picea*, *Pinus* and *Fagaceae*, altitude 2431 m, 20 Jun. 2014, Yan-Jia Hao 1085 (KUN-HKAS82876).

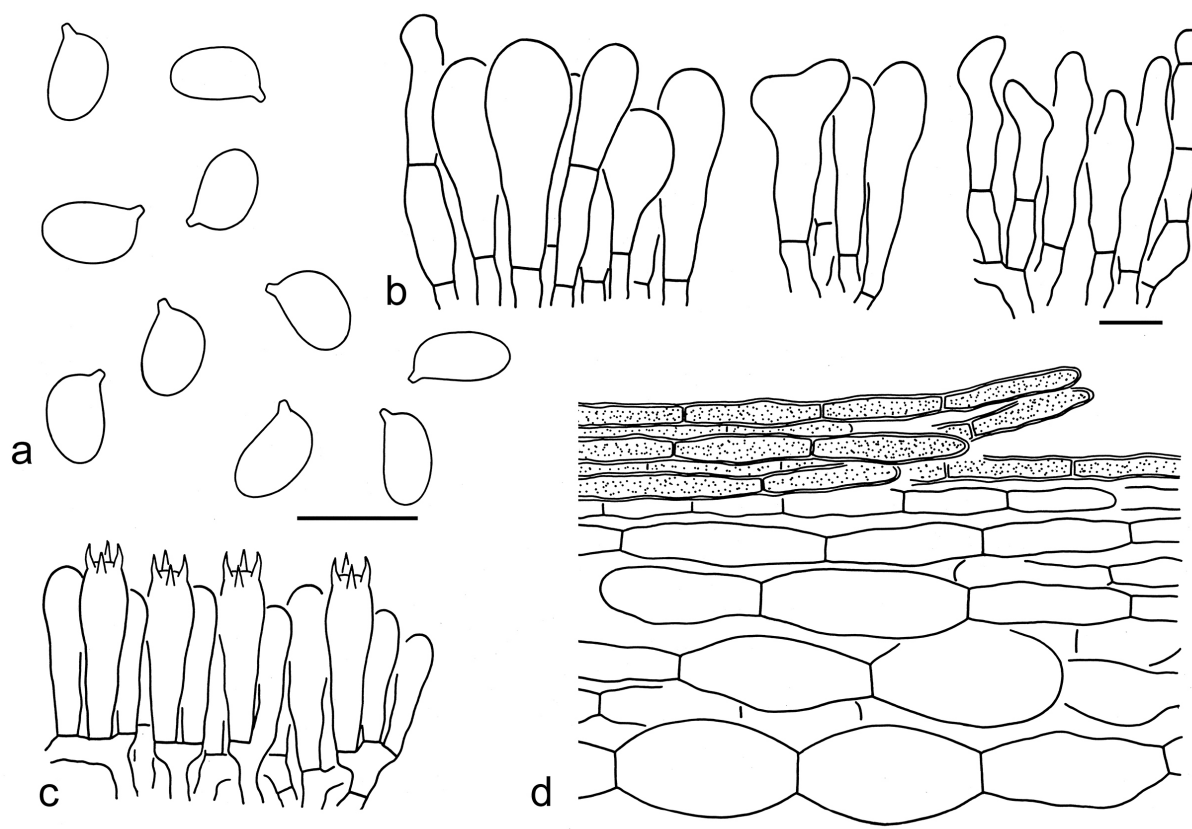


Fig. 92 Microscopic features of *Tricholoma bonii*. a Basidiospores (KUN-HKAS82876). b Marginal cells (KUN-HKAS106563). c Hymenium and subhymenium (KUN-HKAS82876). d Pileipellis (KUN-HKAS106563). Scale bars: a–c = 10 μ m, d = 20 μ m.

Notes: *Tricholoma bonii* is well defined by its grey-brown, grey to dark grey pileus covered with dark grey, felty-tomentose to tomentose squamules, a well differentiated subpellis with inflated cells, and ellipsoid to elongate basidiospores ($6\text{--}9 \times 4\text{--}6 \mu\text{m}$, $Q = 1.33\text{--}1.8$, $Q_m = 1.56 \pm 0.15$). *Tricholoma terreum* is closely related to *T. bonii* (Fig. 3), and these two species are indeed similar to each other in their color of basidioma and structure of pileipellis. However, *T. terreum* has relatively smaller basidiospores ($6\text{--}7 \times 3.5\text{--}5 \mu\text{m}$, mean length = $6.2 \mu\text{m}$, mean width = $4 \mu\text{m}$) and poorly differentiated cheilocystidia (Riva 1988; Bessette et al. 2013; Christensen & Heilmann-Clausen 2013; this study).

Morphologically, *T. sculpturatum* and *T. inocybeoides* resemble *T. bonii* in their color of basidioma. However, *T. sculpturatum* differs by its cobweb-like ring in young basidioma, poorly differentiated subpellis with filamentous hyphae, and relatively smaller basidiospores ($3.9\text{--}6.8 \times 2.5\text{--}4.5 \mu\text{m}$, average $4.9\text{--}5.6 \times 3.2\text{--}3.8 \mu\text{m}$) (Riva 1988; Christensen & Heilmann-Clausen 2013). *Tricholoma inocybeoides* has a weakly developed veil in young basidioma, pileipellis with filamentous hyphae, poorly differentiated cheilocystidia, and relatively narrower basidiospores ($6\text{--}8 \times 3.5\text{--}4 \mu\text{m}$, mean length = $7.1 \mu\text{m}$, mean width = $3.9 \mu\text{m}$, $Q = 1.63\text{--}2$, $Q_m = 1.82 \pm 0.15$) (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013; this study).

74. *Tricholoma cingulatum* (Almfelt ex Fr.) Jacobashch, Verh. bot. Ver. Prov. Brandenb. 33: 59 (1892). Figs. 86g, 93

Basionym: *Agaricus cingulatus* Almfelt ex Fr., Linnaea 5: 507 (1830).

Description: Basidioma small to medium-sized. Pileus 4–8 cm in diam., at first hemispherical to convex, then plano-convex to applanate, sometimes with a broadly low umbo; surface dry, dirty white (1B1–3), greyish (2B1–3) to greyish brown (3C1–5), often white (1A1) to dirty white (1B1–3) towards margin, occasionally white (1A1) overall, covered with brown (4C3–6) to greyish brown (5C3–6), tomentose to fibrillose squamules; margin involute when young, becoming straight to inflexed when mature; context dirty white (1B2–4). Lamellae adnexed to sinuate, white (1A1) to dirty white (1B1–3), crowded; edges white (1A1) to dirty white (1B1–3). Stipe 6–9 $\times$ 0.8–1 cm, cylindrical, white (1A1) to dirty white (1B1–3), brownish (4C4–6) in lower part, with a white (1A1), felty to cottony annulus on the upper part, glabrous above annulus,

densely covered with felty to silky fibrillose squamules below annulus. Taste not recorded. Odour like soap.

Basidiospores [$61/3/2$] (4–) $4.5\text{--}6$ ($\text{--}6.5$) $\times$ (2.5--) $3\text{--}4 \mu\text{m}$ (mean length = $5.2 \mu\text{m}$, mean width = $3.1 \mu\text{m}$), $Q = 1.4\text{--}2$, $Q_m = 1.7 \pm 0.15$, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $20\text{--}30 \times 5\text{--}7 \mu\text{m}$, clavate, 4-spored, colorless, hyaline; sterigmata $4\text{--}6 \mu\text{m}$ long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia poorly differentiated. Subhymenium composed of $2\text{--}4 \mu\text{m}$ wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin- to slightly thick-walled (ca. $1 \mu\text{m}$), clavate to cylindrical cells, $35\text{--}150 \times 15\text{--}25 \mu\text{m}$, mixed with filamentous hyphae $4\text{--}7 \mu\text{m}$ wide. Pileipellis a cutis, composed of radially arranged to interwoven, $4\text{--}10 \mu\text{m}$ wide, slightly thick-walled (ca. $0.5\text{--}1 \mu\text{m}$), colorless or yellow-brown to brownish filamentous hyphae; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in temperate forests with Fagaceae, Pinaceae and *Salix*.

Known distribution: Known from Europe (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013; this study), North America (Bessette et al. 2013) and Asia (Kudo & Nagasawa 1998; Deng et al. 2004).

Specimens examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, Gonggashan Village, in a mixed forest with Fagaceae and Pinaceae, altitude 2700 m, 16 Sep. 2017, Xiao-Xia Ding 292 (KUN-HKAS106634); same location, in a mixed forest with Fagaceae and Pinaceae, altitude 2700 m, 16 Sep. 2017, Xiao-Xia Ding 293 (KUN-HKAS106635); Pingwu County, along a roadside in a mixed forest, altitude 2500 m, 12 Oct. 1999, Zhu L. Yang 2848 (KUN-HKAS34313). Yunnan Province, Shangri-La, Wongsui Village, in a coniferous forest, altitude 3400 m, 21 Aug. 2000, Zhu L. Yang 2962 (KUN-HKAS36663).

Notes: *Tricholoma cingulatum* is well delimited by its pale colored pileus covered with brown to greyish brown, tomentose to fibrillose squamules, a white stipe with a white, felty to cottony annulus on the upper part, and ellipsoid to elongate basidiospores ($4.5\text{--}6 \times 3\text{--}4 \mu\text{m}$, $Q = 1.4\text{--}2$, $Q_m = 1.7 \pm 0.15$). In Europe this species is exclusively associated with *Salix*, while it can also be found in coniferous or mixed forests with Fagaceae and Pinaceae in China. In the molecular phylogenetic analyses (Figs. 3, 4), *T. gansuense* is closely related to *T. cingulatum*. For morphological comparison, see notes under that name.

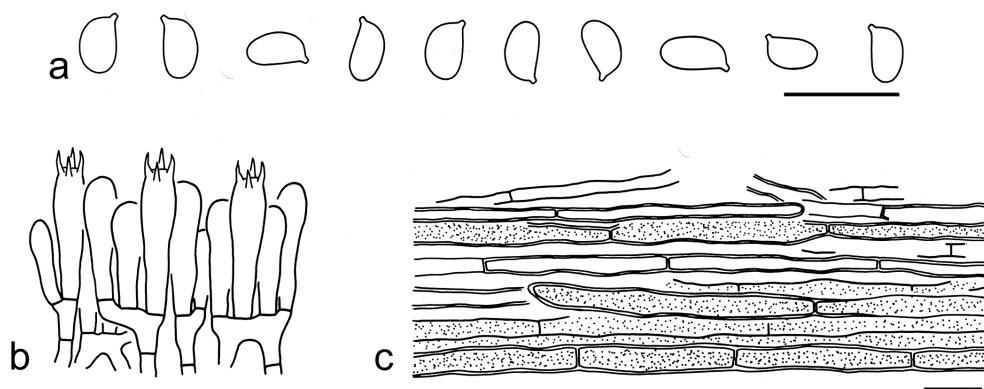


Fig. 93 Microscopic features of *Tricholoma cingulatum* (KUN-HKAS106635). a Basidiospores. b Hymenium and subhymenium. c Pileipellis. Scale bars: a, b = $10 \mu\text{m}$, c = $20 \mu\text{m}$.

75. *Tricholoma inocybeoides* A. Pearson, Trans. Br. mycol. Soc. 22(1-2): 29 (1938). Figs. 86h, 94

Description: Basidioma very small to small. Pileus 2–5 cm in diam., at first broadly conical, then convex to plano-convex, umbonate at center; surface dry, greyish (1B1, 1C1), brownish (4B2–4), grey (1D1–4) to brownish grey (3D2–5), covered with dark grey (1E1–4), grey (1D1–4) to brown (3E6–8), fibrillose squamules; margin involute when young, straight when mature; context white (1A1). Lamellae adnexed, white (1A1) to dirty white (1B1–3), subclose; edges white (1A1), dirty white (1B1–3) to brownish (3B2–4). Stipe 4–6 × 0.5–1 cm, cylindrical, stuffed to hollow, white (1A1), greyish (1B1, 1C1) to brownish (3B2–4). Taste not recorded. Odour like soap.

Basidiospores [20/1/1] 6–8 (–9) × (3–) 3.5–4 µm (mean length = 7.1 µm, mean width = 3.9 µm), Q = 1.63–2 (–2.25), Qm = 1.82 ± 0.15, elongate, occasionally cylindrical, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 20–30 × 5–7 µm, clavate, 4-spored, occasionally 1- or 2-spored, colorless, hyaline; sterigmata 3–5 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 10–40 × 2–7 µm, poorly differentiated, filamentous, cylindrical to clavate, thin-walled, colorless and hyaline. Subhymenium composed of 2–5 µm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled, filamentous to cylindrical hyphae 3–25 µm wide. Pileipellis a cutis to a trichoderm, composed of radially arranged, interwoven to more or less vertically arranged, 8–20 µm wide, thick-walled (ca. 1 µm), colorless to yellowish, clavate to cylindrical hyphae; subpellis poorly differentiated, composed of radially arranged, thin-walled, colorless, hyaline, filamentous hyphae 5–10 µm wide. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in temperate forests with *Picea*, *Betula*, *Populus* and *Pinus* (Jargeat et al. 2010; Christensen & Heilmann-Clausen 2013).

Known distribution: Known from Europe (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013) and China.

Specimens examined: CHINA. Gansu Province, Longnan, Wen County, Jianshan Village, in a forest with *Quercus*, altitude 1000 m, 15 Aug. 2018, Xue-Tai Zhu 2495 (KUN-HKAS106315). Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Luhuo County, Renda Village, in a subalpine forest, altitude 3100 m, 16 Jul. 2014, Kuan Zhao 552 (KUN-HKAS89215). Xizang Autonomous Region, Nyingchi City, Bome County, in a subalpine sclerophyllous evergreen forest dominated by *Quercus* spp., altitude 2760 m, 17 Jul. 2019, Zhu L. Yang 6188 (KUN-HKAS106800). Xinjiang Uygur Autonomous Region, Yili Kazak Autonomous Prefecture, in a forest with *Picea*, altitude 2300 m, 8 Jul. 2017, Xiao-Xia Ding 183 (KUN-HKAS106525); same location, in a forest with *Picea*, altitude 2300 m, 8 Jul. 2017, Xiao-Xia Ding 184 (KUN-HKAS106526); same location, in a forest with *Picea*, altitude 2300 m, 8 Jul. 2017, Xiao-Xia Ding 185 (KUN-HKAS106527).

Notes: *Tricholoma inocybeoides* is characterized by its greyish, brownish, grey to brownish grey pileus covered with dark grey, grey to brown, fibrillose squamules, a weakly developed veil only distinct in very young basidioma, and elongate basidiospores (6–8 × 3.5–4 µm, Q = 1.63–2, Qm = 1.82 ± 0.15) (this study). *Tricholoma inocybeoides* is closely related to *T. sculpturatum* in the five-gene phylogenetic analyses (Fig. 3), but the latter has conspicuous cheilocystidia, and relatively shorter basidiospores (average 4.9–5.6 × 3.2–3.8 µm) (Riva 1988; Christensen & Heilmann-Clausen 2013). Besides *T. inocybeoides* and *T. sculpturatum*, *T. argyraceum* also has a dark colored basidioma with a more or less developed veil. For comparison, see notes under that name. *Tricholoma terreum* is similar to *T. inocybeoides*, but differs by its well differentiated subpellis with inflated cells, and relatively shorter basidiospores (6–7 × 3.5–5 µm, mean length = 6.2 µm, mean width = 4 µm, Q = 1.3–1.8, Qm = 1.55 ± 0.12) (Riva 1988; Bessette et al. 2013; Christensen & Heilmann-Clausen 2013; this study).

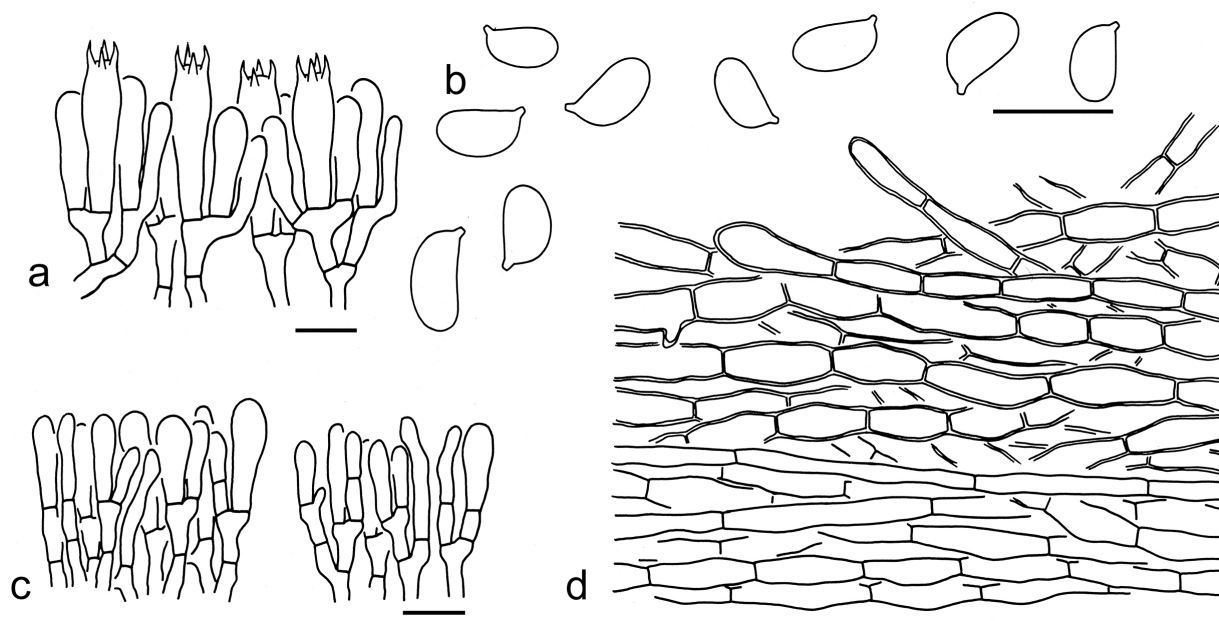


Fig. 94 Microscopic features of *Tricholoma inocybeoides* (KUN-HKAS106315). a Hymenium and subhymenium. b Basidiospores. c Marginal cells. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm.

76. *Tricholoma gansuense* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 86i, 95

Fungal Names: FN 572345

Etymology: gansuense referring to its type locality.

Diagnosis: Related to *T. cingulatum*, but differs in its poorly developed cortina present on the upper part of stipe in young basidioma only.

Type: CHINA. Gansu Province, Wuwei, Tianzhu Zangzu Autonomous County, in a temperate forest with *Picea*, altitude 2735 m, 29 Aug. 2018, Xue-Tai Zhu 2803 (holotype, KUN-HKAS106316).

Description: Basidioma small to medium-sized. Pileus 2–5 cm in diam., at first hemispherical to convex, then plano-convex to applanate, slightly umbonate or not; surface dry, greyish (2D1–3), grey (1D1–4) to grey-brown (2E3–6), covered with grey-brown (2E3–6) to dark brown (4E2–4, 4F6–8) squamules; margin incurved when young, then straight to inflexed; context white (1A1). Lamellae sinuate to emarginate, white (1A1) to grey-white (1B1), crowded; edges entire, white (1A1) to grey-white (2E3–6). Stipe 4–8 cm long $\times$ 0.5–1 cm wide, cylindrical, white (1A1) to grey-white (2E3–6), glabrous, cortina present on the upper part in young stage. Taste and odour not recorded.

Basidiospores [20/1/1] $4.5\text{--}6 \times 3\text{--}4 \mu\text{m}$ (mean length = $5.2 \mu\text{m}$, mean width = $3.2 \mu\text{m}$), $Q = (1.42\text{--}) 1.5\text{--}1.75 (-2)$, $Q_m = 1.63 \pm 0.13$, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $18\text{--}28 \times 5\text{--}7 \mu\text{m}$, clavate, 4-spored, colorless, hyaline; sterigmata $2\text{--}3 \mu\text{m}$ long; basal septa without clamps. Pleurocystidia absent.

Cheilocystidia not observed. Subhymenium composed of 2–4 μm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled, filamentous to cylindrical hyphae $2\text{--}20 \mu\text{m}$. Pileipellis a cutis, composed of radially arranged to interwoven, $5\text{--}20 \mu\text{m}$ wide, thin- to slightly thick-walled, colorless to brownish filamentous to cylindrical hyphae; subpellis poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: On soil in a temperate coniferous forest with *Picea*.

Known distribution: Currently only known from northwestern China.

Additional specimen examined: CHINA. Gansu Province, Xue-Tai Zhu 2793 (KUN-HKAS138831).

Notes: *Tricholoma gansuense* is well separated by its grey to grey-brown pileus, a white stipe often with white cortina on the upper part in young stage and small basidiospores ($4.5\text{--}6 \times 3\text{--}4 \mu\text{m}$). This species is sister to *T. cingulatum* (Figs. 3, 4), but the latter species has a white, felty to cottony annulus on the upper part of stipe. *Tricholoma inocybeoides* and *T. argyraceum* resembles *T. gansuense*. However, *T. inocybeoides* differs by its larger basidiospores ($6\text{--}8 \times 3.5\text{--}4 \mu\text{m}$) (this study). *Tricholoma argyraceum* has a developed veil often form a cobweb-like zone on the upper part of stipe, and conspicuous cheilocystidia. *Tricholoma sculpturatum* (Fr.) Quél. can be confused with *T. gansuense*, but the former species is mainly associated with deciduous trees and currently not found in China (Christensen & Heilmann-Clausen 2013).

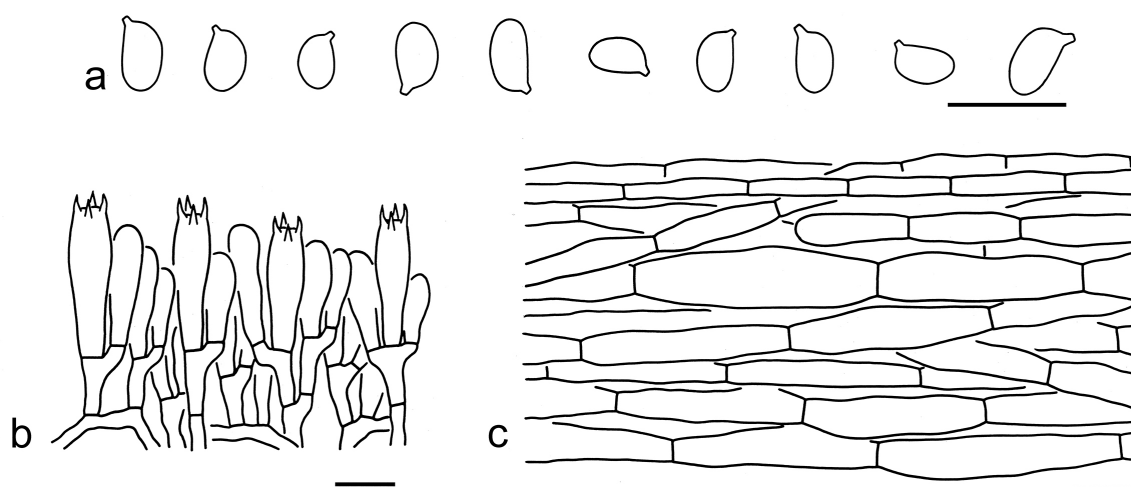


Fig. 95 Microscopic features of *Tricholoma gansuense* (holotype, KUN-HKAS106316). a Basidiospores. b Hymenium and subhymenium. c Pileipellis. Scale bars: a, b = $10 \mu\text{m}$, c = $20 \mu\text{m}$.

77. *Tricholoma terreum* (Schaeff.) P. Kumm., Führ. Pilzk. (Zerbst): 134 (1871). Figs. 86j, 96

Basionym: *Agaricus terreus* Schaeff., Fung. bavar. palat. nasc. (Ratisbonae) 4: 28 (1774).

Description: Basidiomata small to medium-sized. Pileus 3–8 cm in diam., at first convex, then plano-convex to applanate, often slightly umbonate at center; surface dry, greyish (1B1–3), grey (1D1–3), brownish (3B2–4) to brown (4C3–5), covered with grey (1C1–3), brown (4C3–5), grey-

brown (4D1–4) to dark grey (1D1–3), felty to tomentose, sometimes fibrillose squamules; margin involute when young, straight to slightly inflexed when mature; context white (1A1), dirty white (1B1) to grey (1C1). Lamellae adnexed to sinuate, white (1A1) to greyish (1B1–3), becoming yellowish (3A2–3) when old or damaged, close to subdistant; edges entire or undulate to undate, white (1A1) to greyish (1B1–3), becoming brownish (3B2–4) to brown (4B2–4) when damaged or old. Stipe 4–7 cm long $\times$ 0.3–1.5 cm wide, stuffed to hollow, cylindrical, white (1A1), dirty white (1B1) to greyish (1B2–4),

glabrous or sometimes covered with greyish (1B1–3) to brownish (3B2–4) fibrils. Taste and odour not obvious.

Basidiospores [40/2/2] (5–) 6–7 × 3.5–5 µm (mean length = 6.2 µm, mean width = 4 µm), $Q = (1.08\text{--}) 1.3\text{--}1.8$ (–2), $Q_m = 1.55 \pm 0.12$, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth, apiculus relatively large. Basidia 20–30 × 6–9 µm, clavate, 4-spored, colorless, hyaline; sterigmata 4–6 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 15–30 × 3–9 µm, poorly differentiated, cylindrical to clavate, thin-walled, colorless and hyaline. Subhymenium composed of 2–5 µm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless to yellowish, thin-walled hyphae 4–15 µm wide. Pileipellis a cutis with transition to a trichoderm at regular intervals, composed of 4–15 µm wide, mostly thin-walled, sometimes thick-walled (ca. 1 µm), yellow brown filamentous hyphae; subpellis composed of radially arranged inflated cells, ellipsoid, broadly ellipsoid, elongate to cylindrical, 40–80 × 10–40 µm, thin-walled, colorless. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in coniferous or mixed forests with trees of *Pinus* and Fagaceae.

Known distribution: Known from Europe (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013), North America (Bessette et al. 2013) and Asia.

Specimens examined: CHINA. Hebei Province, Zhangjiajie, Xiaowutaishan, forest and altitude unknown, 24 Aug. 1990, Hua-An Wen & Bin Li 113 (HMAS61965). Shaanxi Province, Hanzhong, forest and altitude unknown, Sep. 1991, Xiao-Lan Mao M3953 (HMAS61725). Sichuan Province, Tibetan and Qiang Autonomous Prefecture, Xiaojin County, Meiwo Village, in a mixed forest with Fagaceae and Pinaceae, altitude 2600

m, 27 Jul. 2007, Zai-Wei Ge 1574 (KUN-HKAS53660). Yunnan Province, Kunming, Panlong District, Jindian, the type of forest unknown, altitude 2000 m, 4 Nov. 2005, Yan-Chun Li 436 (KUN-HKAS49648); Kunming, Xishan District, Qiongzhu Temple, in a mixed forest with Fagaceae and Pinaceae, altitude 2000 m, 28 Jul. 2013, Yang-Yang Cui 53 (KUN-HKAS79820); Lijiang, Yulong Naxi Autonomous County, Longpan Village, in a pine forest of *Pinus*, altitude 2164 m, 4 Aug. 2011, Li-Ping Tang 1453 (KUN-HKAS69914); same county, in a pine forest of *Pinus*, altitude 3097 m, 11 Jul. 2010, Qi Zhao 680 (KUN-HKAS69401); same county, Lijiang Alpine Botanic Garden, in a mixed forest with Fagaceae and Pinaceae, altitude 2700 m, 2 Aug. 2019, Jian-Wei Liu 1658 (KUN-HKAS135002).

Notes: *Tricholoma terreum* is characterized by its greyish, grey, brownish to brown pileus decorated with grey, brown, grey-brown to dark grey, felty to tomentose squamules, a differentiated subpellis with inflated cells, and ellipsoid to elongate basidiospores (6–7 × 3.5–5 µm, $Q = 1.3\text{--}1.8$, $Q_m = 1.55 \pm 0.12$). It is closely related to *T. bonii* in the five-gene phylogenetic analysis (Fig. 3). For comparison, see notes under that name.

Tricholoma argyraceum, *T. inocybeoides* and *T. sculpturatum* morphologically somewhat resemble *T. terreum*. However, the former three species have more or less developed veils and clearly farinaceous smell. The comparisons with *T. argyraceum* and *T. inocybeoides* have provided under each notes part. In addition, *T. sculpturatum* is different from *T. terreum* in its conspicuous cheilocystidia and a poorly differentiated subpellis with filamentous hyphae (Riva 1988; Christensen & Heilmann-Clausen 2013).

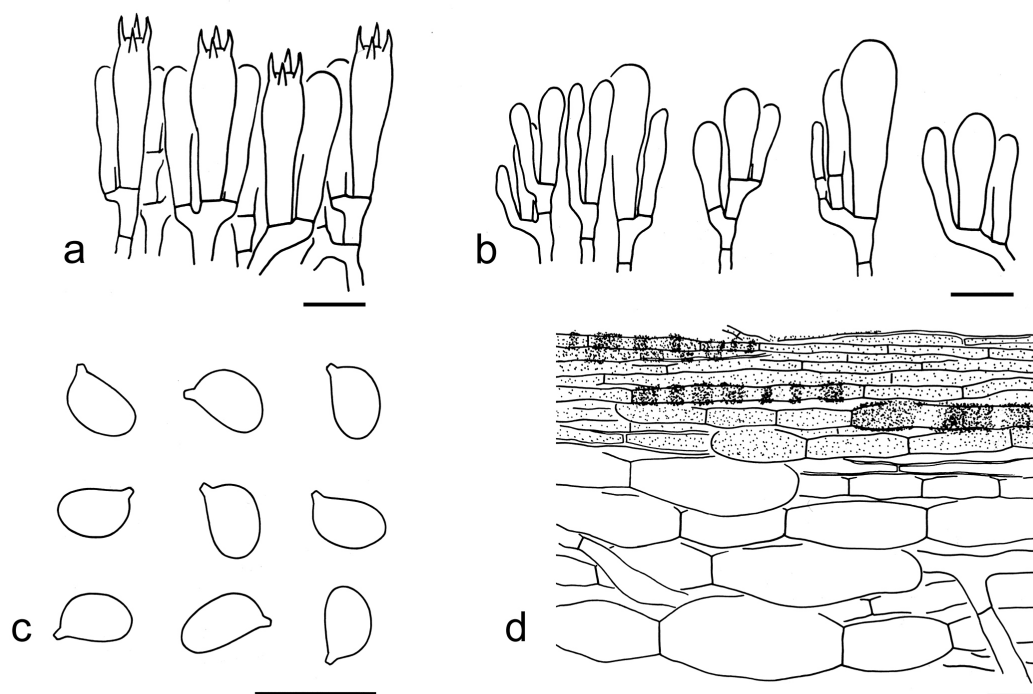


Fig. 96 Microscopic features of *Tricholoma terreum*. a Hymenium and subhymenium (KUN-HKAS69401). b Marginal cells (KUN-HKAS69914). c Basidiospores (KUN-HKAS69401). d Pileipellis (KUN-HKAS69914). Scale bars: a–c = 10 µm, d = 20 µm. Cited from Ding et al. (2023).

78. *Tricholoma triste* (Scop.) Quél., Mém. Soc. Émul. Montbéliard, Sér. 2 5: 79 (1872). Figs. 86k, 97

Basionym: *Agaricus tristis* Scop., Fl. carniol., Edn 2 (Wien) 2: 438 (1772).

Description: Basidioma very small to small. Pileus 2–5 cm in diam., convex to plano-convex, sometimes broadly umbonate at center; surface dry, black (2F6–8), dark grey (4E1–4) to grey (3D1, 2E1–3), densely covered with dark grey (4E1–4) to grey (3D1, 2E1–3), felty to woolly squamules, with a distinct, white (1A1) to dirty white (1B1, 2B1), woolly to fibrillose zone at margin; margin involute when young, later straight to inflexed; context white (1A1) to dirty white (1B1). Lamellae sinuate, dirty white (1B1) to greyish (3B1–2), sometimes with grey (2D1, 2E1) spots, with brown (3C2–4) color when old, subclose; edges serrulate, greyish (3B1–2), often with grey (2D1) to blackish (2E1) spots. Stipe 3–6 × 0.3–0.8 cm, cylindrical, hollow, white (1A1), dirty white (1B1) to greyish (2B1), covered with greyish (2B1) to brownish (1B2–4) fibrils. Taste not recorded. Odour fishy.

Basidiospores [100/5/2] 6–8 (–9) × 4–5 µm (mean length = 7.1 µm, mean width = 4.5 µm), $Q = (1.24\text{--}1.33\text{--}1.87\text{--}2)$, $Q_m = 1.59 \pm 0.14$, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 25–35 × 6–8 µm, clavate, 4-spored, colorless, hyaline; sterigmata 3–5 µm long; basal septa without clamps.

Pleurocystidia absent. Cheilocystidia 20–75 × 7–12 µm, conspicuous and abundant, clavate, sometimes septate, thin-walled, colorless and hyaline. Subhymenium composed of 2–4 µm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless, thin-walled, filamentous to cylindrical hyphae 3–20 µm. Pileipellis a cutis, composed of radially arranged to interwoven, 5–15 µm wide, slightly thick-walled (ca. 1–2 µm), dark brown filamentous hyphae; subpellis composed of fusiform, ellipsoid to clavate inflated cells, 30–75 × 20–35 µm, thin-walled, colorless to yellow-brown. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in temperate coniferous forests.

Known distribution: Known from Europe (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013) and Asia.

Specimens examined: CHINA. Xizang Autonomous Region, Xigaze, Gyirong County, the type of forest unknown, altitude 4700 m, 13 Aug. 2017, Ai-Guo Xu 2225 (AF0001608). Yunnan Province, Kunming, Xishan District, Qiongzhu Temple, the type of forest unknown, altitude 2200 m, 15 Jun. 2008, Zai-Wei Ge 2023 (KUN-HKAS54219); Lijiang, Yulong Naxi Autonomous County, in a coniferous forest with *Pinus armandii*, altitude 2400 m, 13 Jul. 2010, Yan-Jia Hao 40 (KUN-HKAS68012); same county, Lijiang Alpine Botanic Garden, in a coniferous forest, altitude 2700 m, 30 Sep. 2019, Jian-Wei Liu 2193 (KUN-HKAS135003).

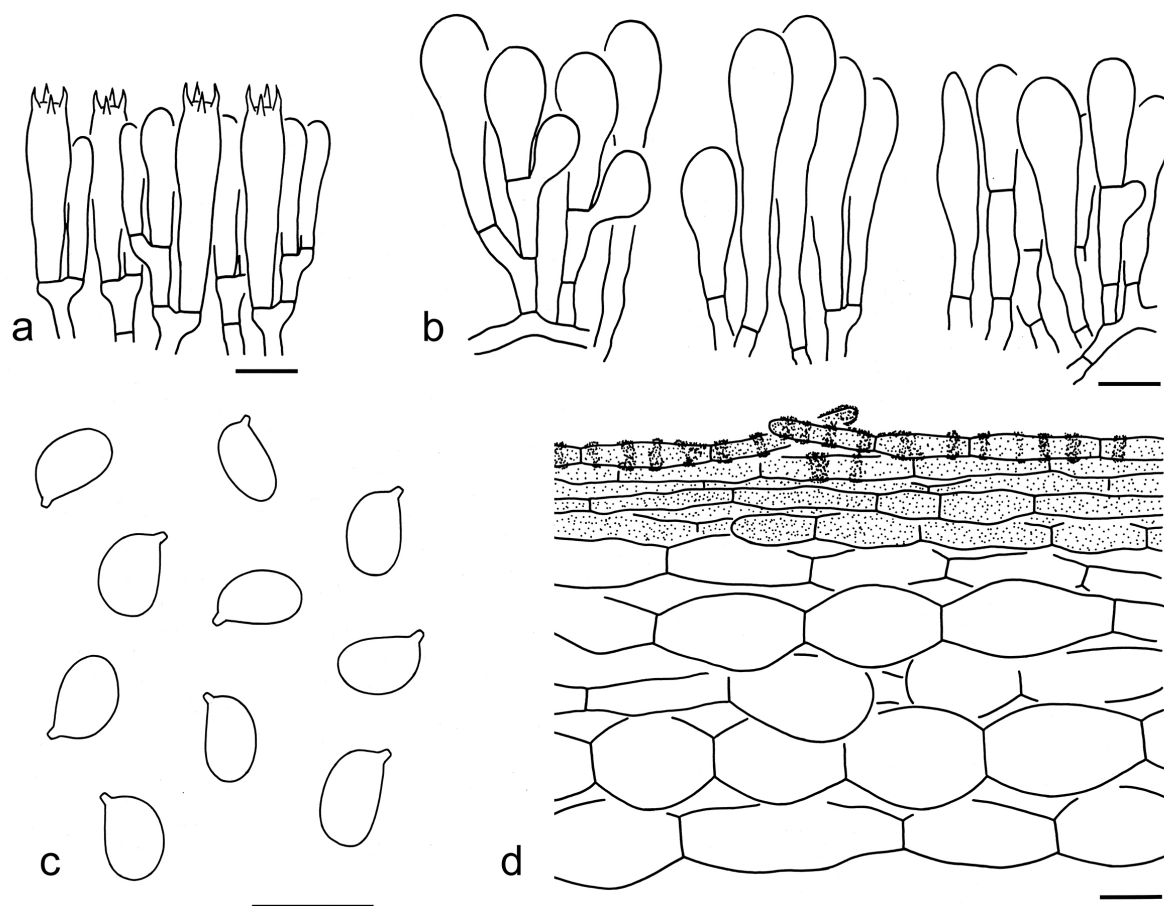


Fig. 97 Microscopic features of *Tricholoma triste* (KUN-HKAS135003). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = 10 µm, d = 20 µm.

Notes: *Tricholoma triste* is well characterized by its dark colored pileus with a distinct, white to dirty white, woolly to fibrillose zone at margin, a well differentiated subpellis with inflated cells, and ellipsoid to elongate basidiospores ($6\text{--}8 \times 4\text{--}5 \mu\text{m}$, $Q = 1.33\text{--}1.87$, $Q_m = 1.59 \pm 0.14$). In the five-gene phylogenetic analysis, it is closely related to the clade formed by *T. bonii* and *T. terreum* (Fig. 3). Indeed, they are similar to *T. triste*. However, *T. bonii* has a grey-brown, grey to dark grey pileus without a distinct zone at margin. *Tricholoma terreum* differs by its relatively paler colored pileus (grey, brown, grey-brown to dark grey) without a distinct zone at margin, poorly differentiated cheilocystidia, and relatively shorter basidiospores ($6\text{--}7 \times 3.5\text{--}5 \mu\text{m}$, mean length = $6.2 \mu\text{m}$) (Riva 1988; Bessette et al. 2013; Christensen & Heilmann-Clausen 2013; this study).

Species of *Tricholoma* with uncertain taxonomic position

Within the genus *Tricholoma*, there are still four clades found in China with unassigned taxonomic status, and they may represent a new subgenus (*T. melleum* clade) or new sections (clade A, clade B and clade C) (Figs. 2, 14). Due to the limited specimens and species available for the study, no taxonomic ranks for the four clades were proposed in this study. The species collected from China belonging to these clades are described below to facilitate comparison in subsequent studies.

Tricholoma clade A

Tricholoma clade A forms a monophyletic group with evident supports based on phylogenetic analyses (Figs. 2, 3, 4, 14). To date, only *T. macrosporum* Y.Y. Cui & Zhu L. Yang and *T. vernaticum* Shanks were detected in this clade, and are characterized by their robust basidioma with solid stipes, ellipsoid to elongate basidiospores and presence of clamps. Apart from clade A, sect. *Terrea*, sect. *Atrosquamosa* and clade B are found in subgen. *Terrea* based on the phylogenomic analysis (Figs. 2, 14). However, species in sect. *Terrea* differs from clade A by their felty, tomentose to somewhat fibrillose squamules on pileus, small to medium-sized basidiospores, and the absence of clamps. Members in sect. *Atrosquamosa* have densely squamules to scales on pileus and small basidiospores. Species from clade B can be separated from clade A by its glabrous pileus, broadly ellipsoid to ellipsoid basidiospores and the absent of clamps. Clade A may represent a novel section in subgen. *Terrea*. To date, only *T. macrosporum* was reported from China (see below).

79. *Tricholoma macrosporum* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 86l, 98

Fungal Names: FN 572340

Etymology: macrosporum = large basidiospores, referring to its large basidiospores.

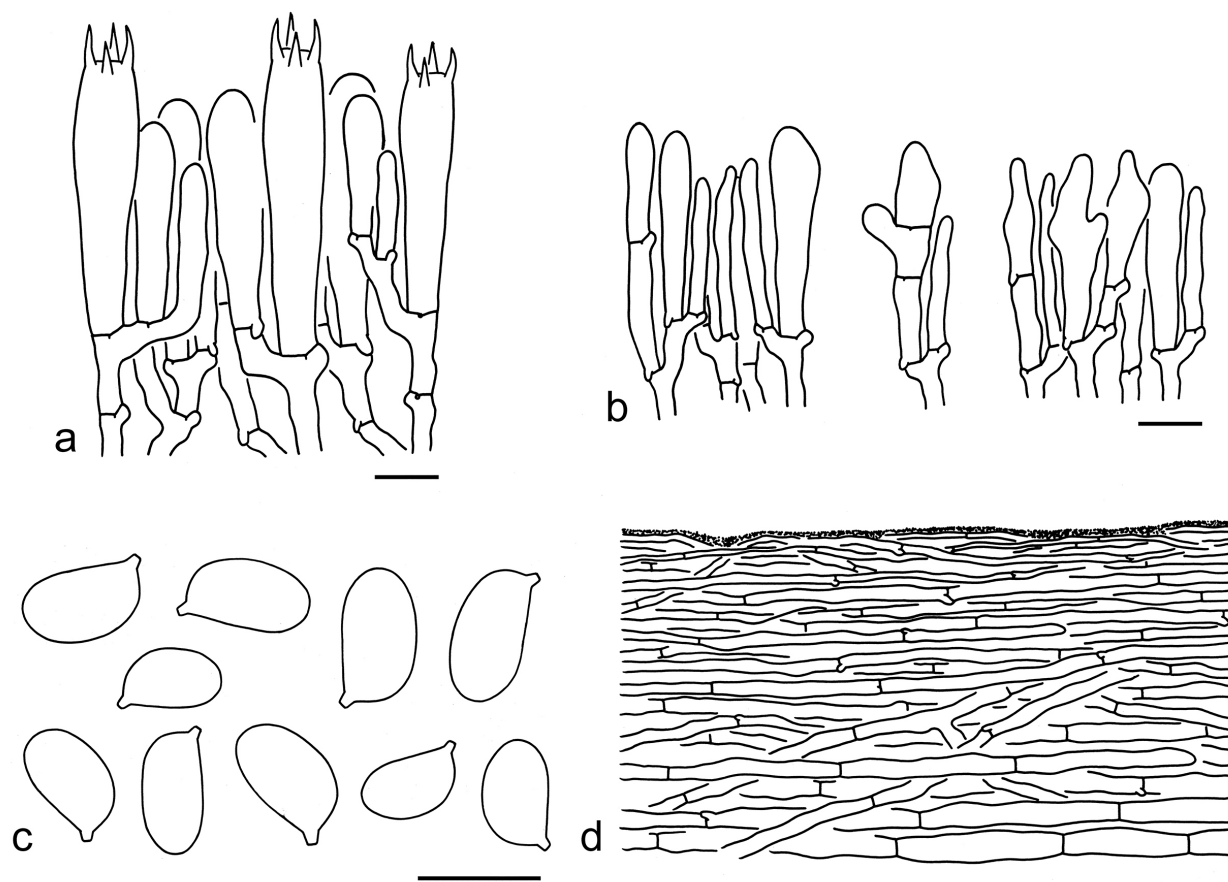


Fig. 98 Microscopic features of *Tricholoma macrosporum* (holotype, KUN-HKAS107577). a Hymenium and subhymenium. b Marginal cells. c Basidiospores. d Pileipellis. Scale bars: a–c = $10 \mu\text{m}$, d = $20 \mu\text{m}$.

Diagnosis: Related to *T. vernaticum* Shanks, but differs by its greyish lamellae and a ringless stipe.

Type: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Luhuo County, Renda Village, in a forest with *Abies*, altitude 3100 m, 1 Aug. 2019, Geng-Shen Wang 573 (holotype, KUN-HKAS107577).

Description: Basidioma medium-sized. Pileus ca. 6 cm in diam., conical to broadly conical, acutely umbonate; surface dry, grey-brown (2E4–6), greyish brown (2D2–4) to grey-white (1B1–3), glabrous to finely fibrillose; margin straight; context greyish (1B1–2, 1C1–2). Lamellae sinuate, greyish (1B1, 1C1), sometimes with brown (5E6–8) stains, subclose; edges concolor. Stipe 7–10 × 2–3.5 cm, subclavate, solid, dirty white (1B1–2) to pale brownish (5A2, 5B3), fibrillose, exannulate. Taste and odour not recorded.

Basidiospores [30/1/1] (7.5–) 8–11 × 5–6 µm (mean length = 9.4 µm, mean width = 5.7 µm), Q = (1.38–) 1.5–1.83 (–2), Qm = 1.66 ± 0.14, ellipsoid to elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 40–50 × 9–11 µm, clavate, 4-spored, thin- to slightly thick-walled, colorless to yellowish, hyaline; sterigmata 4–7 µm long; basal septa with clamps. Pleurocystidia absent. Cheilocystidia 15–35 × 3–10 µm, clavate, cylindrical to irregular shaped, sometimes septate, thin-walled, colorless to yellowish, hyaline. Subhymenium composed of 3–5 µm wide filamentous hyphae, clamps present. Lamellar trama regular, composed of colorless to yellowish, thin-walled, ellipsoid, cylindrical, clavate to filamentous hyphae 5–25 µm wide. Pileipellis an ixo-cutis, gelatinized, composed of radially arranged, 2–10 µm wide, thin-walled, colorless to yellowish filamentous hyphae; subpellis poorly differentiated. Clamps present in all parts of basidioma.

Ecology: Solitary to scattered on soil in forests with *Abies*.

Known distribution: Known from Southwestern China.

Additional specimen examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Luhuo County, Renda Village, in a forest with *Abies*, altitude 3000 m, 1 Aug. 2019, Geng-Shen Wang (KUN-HKAS154384).

Notes: *Tricholoma macrosporum* is characterized by its conical, grey-brown to grey-white pileus, ellipsoid to elongate basidiospores (8–11 × 5–6 µm, Q = 1.5–1.83, Qm = 1.66 ± 0.14), and the presence of clamps. In the phylogenetic analysis based on the ITS sequences, it is closely related to an undescribed species from USA and followed by *T. vernaticum* (Fig. 4). However, *T. vernaticum* differs by its white lamellae and a clavate stipe often with a median to superior ring (Shanks 1996; Bessette et al. 2013).

Morphologically, *T. virgatum* and *T. guldeniae* look like *T. macrosporum*. However, *T. virgatum* has a slender basidioma with a cylindrical, stuffed to hollow, somewhat twisted stipe, relatively shorter, broadly ellipsoid to ellipsoid basidiospores (7–10 × 5–7 µm, mean length = 7.9 µm), and the absence of clamps (Riva 1988, 2003; Christensen & Heilmann-Clausen 2013). *Tricholoma guldeniae* possesses a cylindrical stipe, heterogeneous basidiospores in size and shape (average 8–9.2 × 6–7.3 µm), and the absence of clamps (Christensen & Heilmann-Clausen 2013).

Tricholoma clade B

Tricholoma clade B forms a monophyletic group in phylogenetic analyses (Figs. 2, 3, 4, 14). This clade is sister to sect. *Terrea* (Figs. 2, 14), but can be easily separated by its

glabrous pileus and broadly ellipsoid to ellipsoid basidiospores. Clade B may represent a novel section in subgen. *Terrea*. Species in this clade are characterized by its grey-brown and glabrous pileus often umbonate at center, close lamellae, absent of annulus, broadly ellipsoid to ellipsoid basidiospores, poorly differentiated cheilocystidia and absent of clamps. To date, only *T. griseofulvum* was collected from China (see below).

80. *Tricholoma griseofulvum* Y.Y. Cui & Zhu L. Yang, sp. nov. Figs. 86m, 99

Fungal Names: FN 572339

Etymology: griseofulvum = grey-brown, referring to its grey-brown pileus.

Diagnosis: Related to *T. atratum* Ovrebo, K.W. Hughes & Halling, but differs by its larger basidiospores and associations with trees of *Picea*.

Type: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, Yala, Mugecuo, in a forest with *Picea*, altitude 3350 m, 17 Sep. 2017, Xiao-Xia Ding 310 (holotype, KUN-HKAS106652).

Description: Basidioma small to medium-sized. Pileus 3–5.5 cm in diam., convex to plano-convex, often acutely umbonate; surface dry, greyish brown (5E2–5) to reddish brown (6E3–6), sometimes grey-brown (6F5–7) at center, becoming greyish brown (5E2–5) to reddish brown (6E3–6) towards margin, glabrous; margin straight; context white (1A1). Lamellae sinuate, white (1A1) to dirty white (5B1), close to subdistant; edges concolor. Stipe 4.5–10 × 0.5–1 cm, subclavate, hollow when mature, greyish white (4D1) to grey white (4C1), exannulate. With strong soapy taste.

Basidiospores [45/2/2] 10–12 (–13) × (7–) 7.5–9.5 (–10) µm (mean length = 10.8 µm, mean width = 8.3 µm), Q = 1.17–1.44, Qm = 1.3 ± 0.07, broadly ellipsoid to ellipsoid, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia 50–65 × 12–15 µm, clavate, 4-spored, thin-walled, colorless, hyaline; sterigmata 6–9 µm long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia 20–50 × 3–10 µm, poorly differentiated, clavate to subclavate, thin-walled, colorless, hyaline. Subhymenium composed of 3–5 µm wide filamentous hyphae, clamps absent. Lamellar trama regular, composed of colorless thin-walled, cylindrical, clavate to filamentous hyphae 3–15 µm wide. Pileipellis a cutis, composed of radially arranged, 5–15 µm wide, thin-walled filamentous hyphae; subpellis made of radially arranged, ellipsoid, clavate to cylindrical hyphae. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in forests with *Picea*.

Known distribution: Known from Southwestern China.

Additional specimen examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, Yala, Mugecuo, in a forest with *Picea*, altitude 3350 m, 17 Sep. 2017, Xiao-Xia Ding 311 (KUN-HKAS106653).

Notes: *Tricholoma griseofulvum* is characterized by its greyish brown to reddish brown pileus often accurately umbonate at center, close to subdistant lamellae, broadly ellipsoid to ellipsoid basidiospores (10–12 × 7.5–9.5 µm) and the absence of clamps. *Tricholoma atratum* is closely related to this species in the tree generated from the ITS sequences (Fig. 4). However, *T. atratum* has smaller basidiospores (8–9 × 6–7.5 µm) and is distributed in Costa Rica in forests under *Quercus copeyensis* and *Q. seemannii* (Ovrebo et al. 2019).

Morphologically, *T. brunneiceps* is similar to *T. griseofulvum*, but differs by its smaller basidiospores ($6\text{--}8.5 \times 5\text{--}6 \mu\text{m}$), conspicuous cheilocystidia, a pileipellis with its lower part composed of inflated cells, and associations with trees of Fagaceae.

Tricholoma clade C

Tricholoma clade C clustered as an independent clade with evident support based on phylogenetic analyses (Figs. 2, 3, 4, 14), this clade is closely related to sect. *Genuina* in phylogenetic analysis (Figs. 2, 14). Presently only *T. grave* Peck and *T. aurantiophyllum* L.P. Tang et al. were detected in Clade C and are characterized by their robust basidioma and pale brown to brown lamellae. One species was found in China (see below).

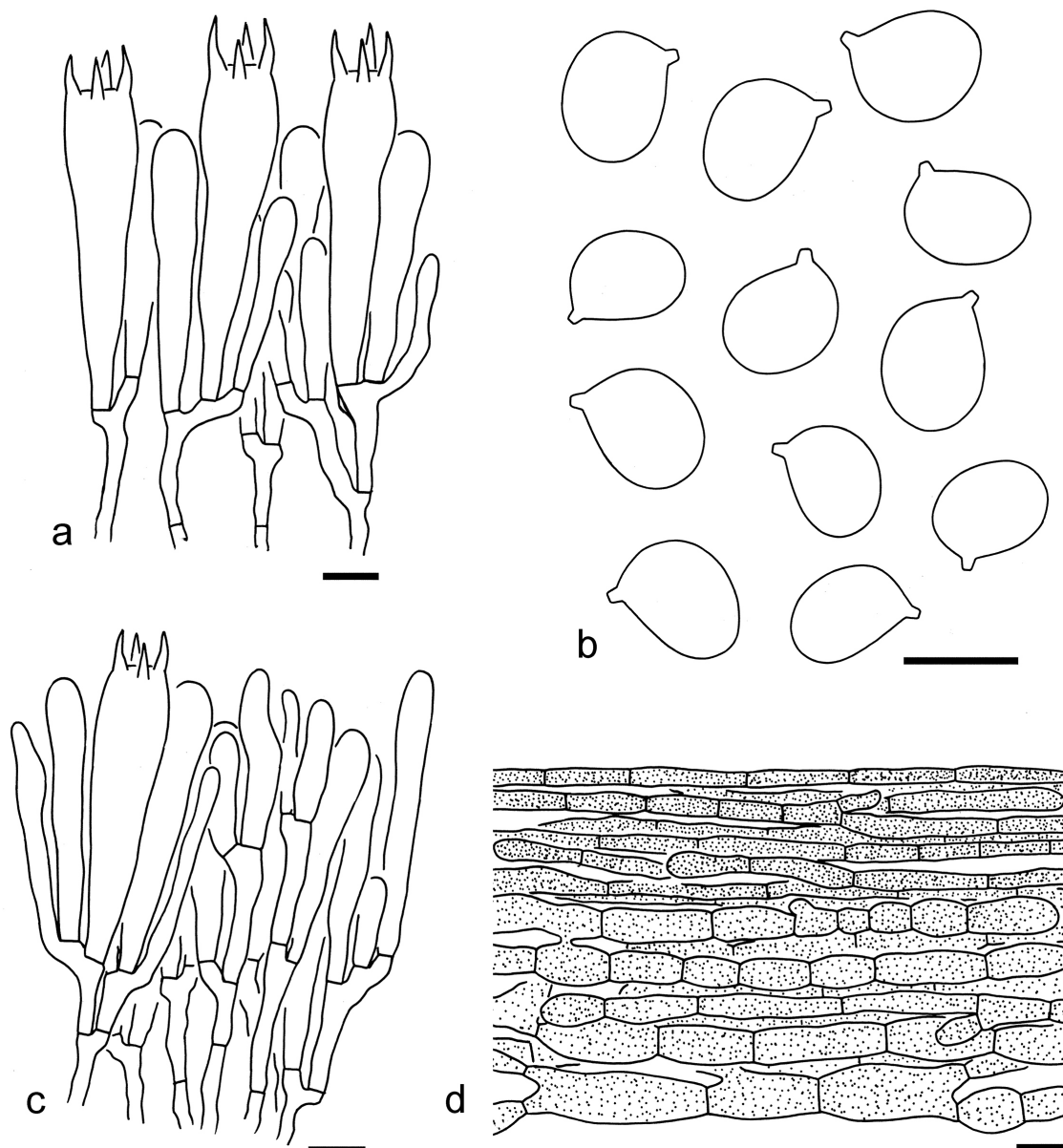


Fig. 99 Microscopic features of *Tricholoma griseofulvum* (holotype, KUN-HKAS106652). a Hymenium and subhymenium. b Basidiospores. c Marginal cells and basidia. d Pileipellis. Scale bars: a–c = $10 \mu\text{m}$, d = $20 \mu\text{m}$.

81. *Tricholoma aurantiophyllum* L.P. Tang, H.Y. Huang, F.Q. Yu & R. Wang, Phytotaxa 664 (3): 184. Figs. 86n, 100

Replaced synonym: *Hygrophorus robustus* F.Q. Yu, Mycotaxon 100: 170, Figs. 1–5 (2007).

Description: Basidioma medium-sized to large. Pileus 8–13 cm in diam., convex to plano-convex, without an umbo or depression at center; surface dry, brown, grey-brown (5B5–7) to brownish (5A3–5), often covered with brown (5B5–7), fibrillose squamules; margin straight; context white (1A1) to dirty white (5A1), up to 1.5 cm in thickness, stout. Lamellae adnate to sinuate, brown to pale brown (5C4–8), distant; edges concolorous or paler. Stipe 8–18 $\times$ 1.5–3.5 cm,

cylindrical, dirty white (5A1–2) to brownish (5A3–5), fibrillose, exannulate or with an incomplete annulate zone near the apex of stipe, solid and compact. Taste and odour indistinct.

Basidiospores $[20/1/1]$ $7\text{--}8\text{--}(10) \times 5\text{--}6\text{ }\mu\text{m}$ (mean length = $7.7\text{ }\mu\text{m}$, mean width = $5.3\text{ }\mu\text{m}$), $Q = 1.33\text{--}1.6\text{--}(1.8)$, $Q_m = 1.47 \pm 0.11$, predominantly ellipsoid, sometimes elongate, non-amyloid, colorless, hyaline, thin-walled, smooth; apiculus relatively large. Basidia $35\text{--}60 \times 9\text{--}11\text{ }\mu\text{m}$, clavate, 4-spored, hyaline; sterigmata $4\text{--}6\text{ }\mu\text{m}$ long; basal septa without clamps. Pleurocystidia absent. Cheilocystidia $20\text{--}60 \times 5\text{--}10\text{ }\mu\text{m}$, clavate, cylindrical to irregularly shaped, sometimes septate, thin-walled, colorless to yellowish. Subhymenium composed of $2\text{--}4\text{ }\mu\text{m}$ wide filamentous hyphae, clamps absent. Pileipellis a cutis, non- to slightly gelatinized, composed of radially arranged, $3\text{--}15\text{ }\mu\text{m}$ wide, thin-walled, yellow brown filamentous hyphae; subpellis non-gelatinized, poorly differentiated. Clamps absent in all parts of basidioma.

Ecology: Solitary to scattered on soil in subtropical mixed forests with broad-leaved plants, and *Pinus armandii* or *P. yunnanensis*.

Known distribution: Known from Southwestern China.

Specimens examined: CHINA. Yunnan Province, Kunming, Wujing Road, wild edible mushroom market, 23 Jul. 2005, Fu-Qiang Yu 1271 (holotype of *Hygrophorus robustus*, KUN-

HKAS49785); Baoshan, Longyang District, Haitangwa Village, in a mixed forest with Fagaceae and *Pinus armandii*, altitude 2400 m, 12 Aug. 2011, Gang Wu 634 (KUN-HKAS74948); Chuxiong Yi Autonomous Prefecture, Nanhua County, Majie Town, in a mixed forest, altitude 2240 m, 9 Aug. 2017, Jian-Wei Liu 776 (KUN-HKAS107581); Tengchong, Mingguang Town, alt. 2140 m, 2 Sept. 2025, Zhu L. Yang 7765 (KUN-HKAS151533).

Notes: *Hygrophorus robustus* was described from Southwestern China by Yu et al. (2007), and later transferred to *Tricholoma* as *T. aurantiophyllum* by Huang et al. (2024). According to our investigation, consumption of this species can cause headaches, eye pain, and severe vomiting in some individuals.

Tricholoma aurantiophyllum is characterized by its robust basidioma with a brown to grey-brown pileus, a rather stout context, subdistant and brown to brownish lamellae, mostly ellipsoid basidiospores ($7\text{--}8 \times 5\text{--}6\text{ }\mu\text{m}$) and the absence of clamps. In the phylogenetic analysis based on the ITS sequences (Fig. 4), *T. grave* Bessette et al. is closely related to this species. However, *T. grave* has pale brown lamellae and is distributed in North America (Bessette et al. 2013; Landry et al. 2022).

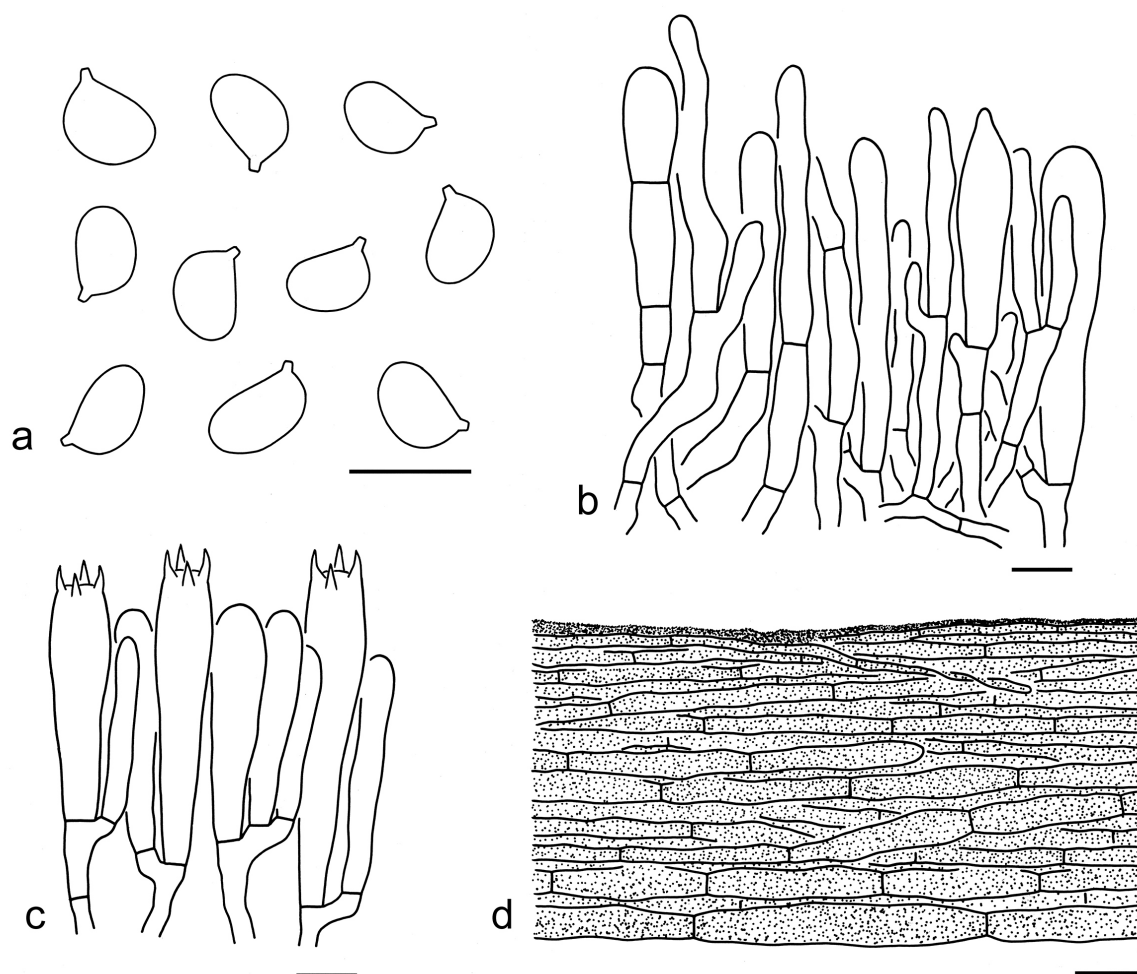


Fig. 100 Microscopic features of *Tricholoma aurantiophyllum* (KUN-HKAS74948). a Basidiospores. b Marginal cells. c Hymenium and subhymenium. d Pileipellis. Scale bars: a–c = $10\text{ }\mu\text{m}$, d = $20\text{ }\mu\text{m}$.

Tricholoma melleum clade

Tricholoma melleum represents an unassigned clade and may be a separate subgenus according to phylogenomic analysis (Figs. 2, 14). To date, only *T. melleum* Reschke et al. is known from this clade, as described below.

82. *Tricholoma melleum* Reschke et al., *Mycologia* 110(6): 1103 (2018). Fig. 86o

Description: Basidioma medium-sized to large. Pileus 4–11 cm in diam., convex to plano-convex, more or less umbonate; surface dry, orange-brown (5B4–7), covered with orange-brown (5B4–7) to light orange (5A2–5), fibrillose squamules; margin involute when young, becoming straight when mature. Lamellae sinuate, cream (4A2), subclose; edges entire, cream (4A2). Stipe 6–15 × 1–2.5 cm, cylindrical, cream (4A2), yellowish (4A3–5) to orangish brown (5B4–7), exannulate. Taste and odour like dishwater.

Ecology: Solitary to scattered on soil in broad-leaved or mixed forests.

Known distribution: Known from southwestern China (Reschke et al. 2018).

Specimen examined: CHINA. Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Kangding, altitude 3300 m, 21 August 2017, 513301MF0583 (KUN-HKAS103101).

Notes: Reschke et al. (2018) described *T. melleum* based on the holotype (KUN-HKAS93514) from China with an unassigned section. The holotype was not traced in the herbarium. We have collected another specimen (KUN-HKAS103101) which matches well with this species (Figs. 3, 4). Unfortunately, KUN-HKAS103101 has been used up and only macroscopic character of this species is given above. Its precise microscopic traits will be provided with more specimens available.

Discussion

Phylogeny of Tricholomataceae s.str.

Tricholomataceae in its narrow sense (Sánchez-García et al. 2014) is a monophyletic group and likely closely related to Callistosporiaceae Vizzini et al. (Vizzini et al. 2020a; He et al. 2023; Vizzini et al. 2024). Our study supports that members of this family have tricholomatoid basidioma with glabrous, squarrose, squamose, or radially fibrillose pilei; adnate, adnexed, sinuate, emarginate to decurrent lamellae; cylindrical stipes mostly lacking an annulus; subglobose, broadly ellipsoid, ellipsoid to elongate basidiospores, sometimes amygdaliform, that are mostly smooth, occasionally verrucose, and either amyloid or inamyloid (Fig. 14).

Our phylogenetic analysis based on Dataset I (nrLSU/ITS/nrSSU/RPB2) revealed that Tricholomataceae s.str. comprises eleven genera (Fig. 1). However, the relationships among most genera were not well resolved. Among them, *Pseudoporpoloma*, proposed by Vizzini et al. (2016) to describe members of the ‘pes-caprae clade’ in Sánchez-García et al. (2014), was not included in the study by Sánchez-García et al. (2021) and Adamčíková et al. (2025). Our findings support the inclusion of *Pseudoporpoloma* as a valid genus within Tricholomataceae s.str. (Fig. 1, Supplementary Table S4).

Albomagister is closely related to two undetermined clades (‘undet small white clade’ and ‘undet grey scaly clade’) identified by Sánchez-García et al. (2014, 2021). Later, Matheny et al. (2024) reclassified these clades under *Albomagister*, which is also supported in this study (Fig. 1, Supplementary Table S4). The *Corneriella*-like clade in Sánchez-García et al. (2021) clustered with *Corneriella* in our analysis (Fig. 1), and we have treated them as *Corneriella* for now (Fig. 1, Supplementary Table S4). Regarding the *Dermoloma*-like clade, we follow the treatment of Adamčíková et al. (2025) as *Neodermoloma* (Fig. 1, Supplementary Table S4).

Phylogeny of *Tricholoma* and the key characteristics of the infrageneric divisions

Tricholoma is the most famous genus within Tricholomataceae s.str. and presents significant challenges for taxonomy. Its subdivisions have been a subject of ongoing debate. In recent years, various sequencing strategies have been employed to elucidate the phylogeny of this genus, yielding substantial progress (Heilmann-Clausen et al. 2017; Reschke et al. 2018; Landry et al. 2022; Trudell et al. 2022; Ding et al. 2023).

Our study compared phylogenetic analyses of *Tricholoma* based on ITS sequences, five gene fragments (ITS/RPB2/MCM7/EF1- α /mtSSU), and 1,477 SOGs (Fig. S1). The results indicate that ITS sequences effectively identify most species, except for those in sect. *Rigida* and sect. *Matsutake*. At the sectional level, only six sections (sect. *Rigida*, sect. *Terrea*, Clade A, sect. *Sericella*, sect. *Genuina*, and sect. *Fucata*) are supported by ITS sequences, and their phylogenetic relationships remain unresolved (Fig. S1). Phylogenetic analysis using five gene fragments provides better resolution at the section level and improves species identification but fails to clarify the boundaries of subgenera and relationships among major clades (Fig. S1). Notably, phylogenomic analyses based on 1,477 SOGs successfully resolved all subgenera and sections of *Tricholoma* (Fig. S1). Ding et al. (2023) provided deep insights into the phylogenetic relationships among four subgenera and 14 section-level clades of *Tricholoma* using a 50-locus dataset. However, the relationships between subgen. *Terrea* and subgen. *Tricholoma*, as well as between the clade formed by sect. *Tricholoma* and sect. *Rigida*, and the clade that includes sect. *Muscaria*, sect. *Fucata* and sect. *Matsutake*, were poorly resolved, particularly in the ML analysis (MLB=70% and MLB=66%) (Ding et al. 2023). In addition, within subgen. *Terrea*, the sister group relationship between sect. *Atrosquamosa* and clade A was not supported (MLB=42% and PP=0.93) (Ding et al. 2023). In our research, four subgenera and one subgenus-level clade, and 15 section-level clades were identified. The phylogenetic relationships among these subgenera and clades were highly resolved in the tree constructed with 1,477 SOGs (Fig. 2). Sect. *Atrosquamosa* was indicated to be sister to the clade formed by sect. *Terrea* and clade B. Furthermore, clade A was found to be closely related to the clade that includes the aforementioned two sections and clade B (Fig. 2). It could be concluded that our research, based on genomic data, successfully resolved the phylogeny of *Tricholoma*, providing an evolutionary perspective for future studies on *Tricholoma* taxonomy and evolution (Fig. 2).

Molecular and morphological evidence suggests that the diagnostic characteristics of *Tricholoma* include tricholomatoid basidioma, absence of pleurocystidia, a cutis pileipellis primarily composed of repent hyphae, and smooth inamyloid basidiospores. Vizzini et al. (2020b) proposed a novel standardized method (including heating the sample in Melzer's reagent and different recipes for Melzer's exist) to test for spore amyloidity in *Tricholoma*. They suggested that basidiospores of this genus are latently amyloid. However, our study followed traditional methods due to their simplicity and widespread use in fungal taxonomy. Using this approach, we observed visibly inamyloid basidiospores in all studied *Tricholoma* species. These findings align with recent observations by Lebeuf et al. (2024), which also support the inamyloid nature of *Tricholoma* basidiospores.

Combining phylogenomic and morphological evidence, we support the division of *Tricholoma* into 11 sections. These sections are characterized by features such as pileal center morphology, pileus color and squamules, lamellar density, presence or absence of an annulus, basidiospore size and shape, presence or absence of cheilocystidia, pileipellis structure, and clamp connections. While these characteristics have been highlighted by Bon (1984), Singer (1986), Riva (1988), and Noordeloos & Christensen (1999), their taxonomic significance varies. Heilmann-Clausen et al. (2017) emphasized that pileus color, pileipellis structure, clamp presence, and basidiospore size are conserved within sections, whereas annulus presence and host specificity are more variable. Our study highlights additional diagnostic features, such as the presence or absence of an umbo on the pileal center, which may distinguish sections. For instance, species in sect. *Fucata* and sect. *Muscaria* exhibit a prominent papilla. Similarly, cheilocystidia presence is a critical marker, as species in sect. *Fucata* and sect. *Muscaria* have conspicuous cheilocystidia, whereas those in sect. *Lasciva* have poorly differentiated cheilocystidia.

The pileipellis structure remains a valuable taxonomic characteristics, as previously emphasized by Bon (1984), Singer (1986), Riva (1988), and Noordeloos & Christensen (1999). For example, members of sect. *Fucata* have a cutis with a strongly differentiated subpellis composed of inflated cells, while species in sect. *Atrosquamosa* possess a pileipellis with somewhat erect, thick-walled hyphae forming squamules on the pileus. These findings deepen our understanding of *Tricholoma* classification from an evolutionary perspective and underscore the importance of integrating phylogenomic, phylogenetic, and morphological data in fungal taxonomy.

Species diversity of Tricholomataceae s.str. from China

Presently, approximately 500 species are regarded as members of the family Tricholomataceae in its narrow sense. In China, members of Tricholomataceae s.str. are found in only five genera (*Tricholoma*, *Leucopaxillus*, *Pseudobaecyspora*, *Albomagister*, and *Pseudotracholoma*).

Due to morphological similarities and phenotypic plasticity, accurately identifying species in Tricholomataceae s.str. based on morphology alone is challenging. Some newly described species in this study were misidentified in the past. For instance, *T. mastoideum* was misidentified as *T. virgatum*, and *T. sichuanense* was mistaken for *T. saponaceum*. This

highlights the necessity of using both morphological and molecular evidence to delimit species within this family. For herbarium collections, generating DNA sequences using Sanger sequencing can be difficult. Fortunately, next-generation sequencing (NGS) combined with optimized library construction processes has enabled the extraction of DNA from historical specimens, providing solid evidence for the accurate recognition of fungal species (Zeng et al. 2018; Wang et al. 2024).

In this study, we identified 82 species of Tricholomataceae s.str. distributed in China. Of these, 30 were originally described from Europe or the USA, five from Japan, and 47 from China. This indicates a rich diversity of Tricholomataceae s.str. in China, with over 60% of species originally described from Asia or even East Asia. This pattern hints at a potentially high level of endemism in East Asia, but further biogeographic studies are needed to confirm whether these species are truly restricted to this region. Additionally, several unique clades labeled as *Tricholoma* sp. 2 and sp. 3 in Figures 3 and 4 may represent unnamed species. However, further collections are required before these can be formally described. These findings provide a strong foundation for future studies on the diversity and distribution patterns of Tricholomataceae.

Edibility and toxicity of species of Tricholomataceae s.str.

The family Tricholomataceae s.str., particularly the genus *Tricholoma*, includes both edible and poisonous species (Bresinsky 1990; Anand et al. 2009; Bessette et al. 2013; Christensen & Heilmann-Clausen 2013; Chen et al. 2016; Laubner & Mikulevičienė 2016; Yang et al. 2021; Wan et al. 2023). Accidental ingestion of toxic species Tricholomataceae s.str. primarily leads to three types of poisoning symptoms: rhabdomyolysis, acute liver damage, and gastroenteritis-type poisoning (Bresinsky 1990; Anand et al. 2009; Christensen & Heilmann-Clausen 2013; Chen et al. 2016; Laubner & Mikulevičienė 2016; Wan et al. 2023). Rhabdomyolysis poisoning has only been reported in Europe following the consumption of large quantities of *T. equestre* (Anand et al. 2009; Laubner & Mikulevičienė 2016). No such cases have been reported in China. Gastroenteritis-type poisoning, however, is associated with species primarily distributed in sect. *Fucata*, sect. *Genuina*, sect. *Sericella*, sect. *Lasciva*, sect. *Pardinicutis*, and clade C (Bresinsky 1990; Christensen & Heilmann-Clausen 2013; Chen et al. 2016; Yang et al. 2021; Wan et al. 2023; Bau et al. 2025; this study). Here, we highlight *T. aurantiophyllum* in clade C, as ingestion of this species has been reported to cause headaches and severe vomiting in some individuals (Huang et al. 2024; this study). Notably, accidental ingestion of toxic species in sect. *Pardinicutis* can cause severe acute liver damage, as seen with *T. nigrosquamosum* and *T. sinoportentosum*, both found in southwestern China (Wan et al. 2023).

Despite these risks, many Tricholomataceae s.str. mushrooms are sold in markets across China, particularly in the southwestern areas. Our results, show that mushrooms of Tricholomataceae sold in markets can be grouped into four categories comprising 18 species. These are commonly known as: "songrong" (including *T. matsutake*, *T. fulvocastaneum*, *T. bakamatsutake*, *T. xizangense*, *T. tianshanense* and *T. zangii*), "qiaomianjun" (including *T. citrinum*, *T.*

equestre, *T. frondosae* and *T. qiaomianjun*), “huihuijun” (including *T. terreum*, *T. bonii*, *T. triste* and *T. virgatum*), and “beifengjun” (including *T. saponaceum*, *T. olivaceum*, *T. sichuanense* and *T. sinoportentosum*). Despite their popularity, studies on the edibility and toxicity of these fungi remain limited. Further research is necessary to identify poisonous species, determine the types of toxins, and understand their distribution patterns within this family. Such investigations will raise public awareness of the safety of Tricholomataceae mushrooms and provide a scientific basis for food safety regulations.

Acknowledgments

We thank the curators of the herbaria HMAS, HMJAU, AF, MB, and HMUT for the loan of specimens. We are grateful to Dr. Zhuo Du (Institute of Microbiology, Chinese Academy of Sciences), Prof. Gerhard Kost (University of Marburg), Dr. Xiao-Juan Deng (North Minzu University), Mr. Ai-Guo Xu (Tibet Plateau Institute of Biology), Prof. Biao Xu (Zhongkai University of Agriculture and Engineering), and Dr. Xiao-Dan Yu (Shenyang Agricultural University) for their assistance with loan requests. We also appreciate the comments and advice from Prof. Bau Tolgor (Jilin Agricultural University), Prof. Tai-Hui Li, and Dr. Chao-Qun Wang (Institute of Microbiology, Guangdong Academy of Sciences). Special thanks to Mr. Zhi-Jia Gu (Kunming Institute of Botany, Chinese Academy of Sciences) for providing SEM images. Thanks are also due to the anonymous reviewers for their professional suggestions, important comments and valuable criticisms. The authors would like to express their gratitude to EditSpring (https://www.editsprings.cn) for the expert linguistic services provided. This work was supported by the Science and Technology Fundamental Resources Investigation Program, Ministry of Science and Technology of China (2023FY101303), the Joint Funds of the National Natural Science Foundation of China and Yunnan Provincial Government (U2202205), the Yunnan Revitalization Talent Support Program: Science & Technology Champion Project (202305AB350004), Yunnan Revitalization Talent Support Program “Young Talent” Project (XDYC-QNRC-2022-0509), Caiyun Postdoctoral Program, Yunnan Provincial High-Level Talents Support Program (YNWR-QNBJ-2020-295), the “Talent Introduction Program” of Kunming Institute of Botany, Chinese Academy of Sciences, the Second Tibetan Plateau Scientific Expedition and Research Program (2024QZKK02010303), and the Major Science and Technology Special Project of Yunnan Province (202502AE090044).

Author contributions

The authors confirm contribution to the paper as follows: Conceptualization: Cui YY, Yang ZL; Data curation: Cui YY, Li J, Fan XP, Che NJ; Formal analysis: Cui YY, Li J, Cai Q, Fan XP, Yang ZL, Che NJ; Funding acquisition: Yang ZL, Cui YY, Cai Q, Zhao Q; Investigation: Cui YY, Cai Q, Yan-Chun Li, Fan XP, Yang ZL, Liu JW, Ding XX, Xu X, Zhu XT, Deng CY, Guo T, Che NJ, Zhao Q; Methodology: Cui YY, Li J, Fan XP, Che NL, Cai Q; Project administration: Cui YY; Resources: Cui YY, Li J, Cai Q, Yan-Chun Li, Fan XP, Yang ZL, Liu JW, Ding XX, Xu X, Zhu XT, Deng CY, Guo T, Che NJ, Zhao Q; Software: Cui YY, Li J, Cai Q; Supervision: Yang ZL; Validation: Cui YY,

Li J, Cai Q; Visualization: Cui YY, Li J, Che NJ, Cai Q; Writing—original draft preparation, Cui YY, Cai Q; Writing—review & editing: Cui YY, Yang ZL, Cai Q. All authors have read and agreed to the published version of the manuscript.

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Conflict of interest statement

The author list includes members of the Editorial Board of Fungal Diversity. They were not involved in the journal’s review of, or decisions related to, this manuscript. The authors declare no competing interests.

Supplementary Information

The online version contains supplemental information available at <https://doi.org/10.65390/fdiv.2026.136010>.

Supplementary Figure S1 A comparison of the three *Tricholoma* trees inferred from Dataset II (1,477 SOGs), Datasets III (ITS/RPB2/MCM7/EF1- α /mtSSU) and IV (ITS).

Supplementary Table S1 Voucher information and GenBank accession numbers of the samples used in the phylogenetic analyses of Tricholomataceae (Dataset I). New Species described in this study are indicated in bold.

Supplementary Table S2 Voucher information of the samples used in the next-generation sequencing of Tricholomataceae (Dataset II).

Supplementary Table S3 Voucher information and GenBank accession numbers of the samples used in the phylogenetic analyses of *Tricholoma* (Datasets III and IV). New Species described in this study are indicated in bold.

Supplementary Table S4 Comparisons of several significant Tricholomataceae systems.

Supplementary Table S5 A comparison between the Chinese *Tricholoma* species reported in this work and Ding et al. (2023).

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