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Systematic arrangement within the family Clitocybaceae (Tricholomatineae, Agaricales): phylogenetic and phylogenomic evidence, morphological data and muscarine-producing innovation

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Abstract

The Clitocybaceae is a recently established family. Currently, the infrafamilial divisions and relationships within the family are vague due to limited sampling and genes employed for phylogenetic analysis. Some mushrooms of the family contain the neurotoxic muscarine, which has caused many severe and even deadly poisonings worldwide. However, the taxonomic distribution and evolution of the toxin within the family is largely unknown. In this study, phylogenetic analyses based on nucleotide sequences of ITS and of six molecular loci (ITS, LSU, *TEF1*, *RPB1*, *RPB2* and *ATP6*), plus a phylogenomic analysis based on 485 single-copy orthologous genes, were performed to reconstruct the framework of Clitocybaceae. BEAST analysis was used to estimate the divergence times within the family. Additionally, biochemical analysis for muscarine was conducted of 32 representative species. Based on these analyses, an updated classification of Clitocybaceae into six genera (*Clitocybe*, *Collybia*, *Dendrocollybia*, *Lepista*, *Pseudolyophyllum*, and *Singerocybe*) is proposed. The genus *Collybia* is emended to accommodate four subgenera (*Collybia*, *Crassicyme*, *Leucocalocybe*, and *Macrosporocybe*). Seventeen new Chinese species and 15 new combinations are proposed. Keys to the genera of Clitocybaceae and the subgenera of *Collybia*, as well as to the known species of *Clitocybe* and *Collybia* subgen. *Collybia* in China, are presented. In addition, muscarine was detected in 18 species, and these muscarine-containing species formed a major monophyletic clade within *Collybia* subgen. *Collybia*. Finally, our phylogenetic, phylogenomic, chemotaxonomic and molecular dating results indicate that the Clitocybaceae is a natural group estimated to have arisen some 60 million years ago, and in this family, muscarine has evolved only once circa 20 million years ago without later losses.

Keywords *Clitocybe* · Clitocyboid · *Collybia* · Muscarine · Phylogenomic analysis · Single-copy gene

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Introduction

The Clitocybaceae Vizzini, Consiglio & M. Marchetti is one of the ten families currently recognized in the suborder Tricholomatineae Aime, Dentinger & Gaya (Kalichman et al. 2020; Vizzini et al. 2020b; Mou and Bau 2021; He and Yang 2022). The family includes at least five genera: *Clitocybe* (Fr.) Staude, *Collybia* (Fr.) Staude, *Dendrocollybia* R.H. Petersen & Redhead, *Lepista* (Fr.) W.G. Sm., and *Singerocybe* Harmaja, according to the phylogenetic analyses over the past 20 years (Moncalvo et al. 2002; Matheny et al. 2006; Binder et al. 2010; Alvarado et al. 2018b; He and Yang 2022). Members of the family are saprotrophic or mycoparasitic, occur worldwide and are generally characterized by the production of clitocyboid, collybioid or lepistoid basidiomes without veils, inamyloid basidiospores, the

absence of pleurocystidia and cheilocystidia, and the presence of clamp connections (Vizzini et al. 2020a).

The Clitocybaceae was first referred to as ‘Clitocybées’ by Roze (1876), but this name had a French rather than a Latin ending and was therefore invalid according to Art. 18.4 of the code 2018 (Shenzhen Code) (Turland et al. 2018). Vizzini et al. (2020a) validly published the name Clitocybaceae, corresponding to the clade representing Clitocybeae Fayod. Nevertheless, the taxonomic status of the different lineages within Clitocybaceae remains contradictory. For instance, several clades of *Clitocybe* and *Lepista* group together with *Collybia* s.str. (Sánchez-García et al. 2014; Alvarado et al. 2018a, b). Since only a limited number of species, genera and genes were used to date, the monophyly of Clitocybaceae received low support in previous phylogenetic analyses (Alvarado et al. 2018a, b; Vizzini et al. 2020b).

In recent years, nuclear single-copy orthologous genes have been demonstrated to be capable of molecular markers for fungal phylogenetic and evolutionary inferences (Sato et al. 2017; Sato and Toju 2019; Li et al. 2020a, b). Because the genomes of Basidiomycota are very small (about 50 Mbp/1C on average, Mohanta and Bae 2015; Li et al. 2018), shallow whole genome sequencing has been employed as an efficient and low-cost strategy to obtain single-copy gene data from them (Liimatainen et al. 2022). Compared to traditionally mono- or multigenic phylogeny, phylogenomics can provide a much higher resolution of deep internal branches (Li et al. 2021a, b, c, d). As relied on a few loci or lineages, previous molecular phylogenetic analyses of Clitocybaceae displayed unstable and ambiguous topologies (Alvarado et al. 2015; Cooper 2016; He and Yang 2022). Therefore, it is necessary to use the genomic approach with high-coverage sampling to recover the poorly resolved relationships within Clitocybaceae.

Muscarine, a toxic alkaloid that stimulates the parasympathetic nervous system, is found in basidiomes of many species of the genera *Amanita* Pers., *Clitocybe*, *Entoloma* (Fr.) P. Kumm., *Inocybe* (Fr.) Fr., *Mycena* (Pers.) Roussel, and *Omphalotus* Fayod, etc. (Peredy and Bradford 2014). The toxin was first isolated and characterized in *A. muscaria* (L.) Lam., but the amount in this species is very low, only 0.0003% by weight (Eugster and Schleusener 1969). In comparison, the toxin concentration is particularly high in species of *Clitocybe* and *Inocybe*, up to 1.6% by weight (Peredy and Bradford 2014; Puschner 2018). In China, basidiomes of *Clitocybe* species caused ten reported cases of mushroom poisoning involving 51 patients from 2019 to 2022 (Li et al. 2020a, b, 2021a, b, c, d, 2022b, 2023). However, most of such poisonous clitocybes in China are currently unstudied and not correctly or accurately recognized. This seriously hampers prevention of poisonings caused by *Clitocybe* species.

To the best of our knowledge, more than 100 species of Inocybaceae have been confirmed to contain muscarine (Kosentka et al. 2013; Xu et al. 2020; Li et al. 2021a, b, c, d; Deng et al. 2021, 2022; Zhang et al. 2022; Zhao et al. 2022; Yan et al. 2022). Surprisingly, in the Clitocybaceae, only three species, namely *Cli. dealbata* (Sowerby) P. Kumm., *Cli. phyllophila* (Pers.) P. Kumm. and *Cli. rivulosa* (Pers.) P. Kumm., have been reported positive for muscarine (Swenberg et al. 1967; Genest et al. 1968). Accordingly, the distribution and evolution of muscarine within Clitocybaceae remains largely unknown.

The aims of this study are (i) to reconstruct the phylogenetic framework of Clitocybaceae with single-locus, multi-locus and genomic data, respectively; (ii) to ascertain the distribution pattern of muscarine within the resulting framework; (iii) to recircumscribe the genera belonging to the family based on a well-supported phylogeny; (iv) to estimate divergence times of the family and muscarine; and (v) to document species of Clitocybaceae in China using morphological characters, phylogenetic evidence, ecological data and toxin detection.

Materials and methods

Specimens

A total of 80 collections of Clitocybaceae and 11 related collections of Tricholomatineae were involved in this study. These specimens were collected from Southwestern (61), Northwestern (16), Northeastern (9) and Central (3) China, plus two from France and Germany. The fresh basidiomes were dehydrated using heat or silica gel. Most specimens are deposited in the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN-HKAS), while other three labeled with MHHNU come from the Mycological Herbarium of Hunan Normal University and four labeled with HMJAU from the Herbarium of Mycology, Jilin Agricultural University. Information regarding the specimens, including species name, GenBank accession number, voucher and location, is provided in Table S1 (Suppl. material 1).

Morphological study

Macroscopic characters of the species studied were described based on fresh specimens and photographs. The size of basidiomes, as determined by pileus width, was described as tiny (< 1.5 cm), small (1.5–3 cm), medium-sized (3–5 cm) or large (> 5 cm). The color codes cited in the descriptions are from Kornerup and Wanscher (1978). Sections of different parts of dried specimens were mounted in either a 5% KOH solution or distilled water. Subsequently,

basidiospores, basidia, lamella trama, pileipellis and stipitipellis were observed under a phase contrast microscope. Basidiospores, basidia and pileipellis were illustrated by hand drawing.

In the description of basidiospores, the abbreviation [n/m/p] means that n basidiospores were measured from m basidiomes of p collections. The range notation (a)b–c(d) stands for the dimensions of basidiospores, in which b–c contains a minimum of 90% of the measured values, while a and d are the extreme values. The Q value represents the length/width ratio of basidiospores, and the Q_m value is the average Q ± standard deviation. The shape of basidiospores was described following the terminology employed by Bas (1969) and Vellinga et al. (2018). Melzer's reagent was employed to test the amyloidity of basidiospores.

The abbreviations of the genera names used in our study are as follows: *Amanita* = 'A.', *Agaricus* = 'Aga.', *Clitocybe* = 'Cli.', *Collybia* = 'C.', *Dendrocollybia* = 'D.', *Hygrophorus* = 'H.', *Inosperma* = 'I.', *Lepista* = 'L.', *Lepistella* = 'Lpl.', *Leucocalocybe* = 'Leu.', *Paxillus* = 'Pax.', *Pseudolyophyllum* = 'P.', *Singerocybe* = 'S'.

DNA extraction, PCR and Sanger-sequencing

Total genomic DNA was extracted using an Ezup Column Fungi Genomic DNA Purification Kit (Sangon Biotech, Shanghai, China) in accordance with the manufacturer's instructions. For the PCR amplification, the following primers were employed: (i) ITS5 and ITS4 (White et al. 1990) were used for the internal transcribed spacer (ITS); (ii) LR0R and LR5 (Vilgalys and Hester 1990) for the nuclear ribosomal large subunit (LSU); (iii) EF1-983F and EF1-1953R or EF1-1567R (Matheny et al. 2007), or the newly designed primers *Collybia*-TEF1-F (5'-AGGAGACCTCTG GCTTCATC-3') and *Collybia*-TEF1-R (5'-CAGACATTT CCACGACGAAT-3') for the translation elongation factor 1- α (*TEF1*); (iv) RPB1-Af and RPB1-Cr (Matheny et al. 2002) or the newly designed primers *Collybia*-RPB1-F (5'-ACGAGGTTGYGTGGTGAAAT-3') and *Collybia*-RPB1-R (5'-GGAGGNGGDACHGGCATNA-3') for the DNA-directed RNA polymerase II subunit 1 (*RPB1*); (v) RPB2-6F and RPB2-7.1R (Matheny 2005) or the newly designed primers *Collybia*-RPB2-F (5'-ATYTCYGTGGT TCTTAYTC-3') and *Collybia*-RPB2-R (5'-GAARGGAAAT RATACTRGCRCA-3') for the DNA-directed RNA polymerase II subunit 2 (*RPB2*); and (vi) ATP6-3 (Kretzer and Bruns 1999) and ATP6-6r (Binder and Hibbett 2003) or the newly designed primers *Collybia*-ATP6-F (5'-TTGAAYGCT CCAATYTTAGG-3') and *Collybia*-ATP6-R (5'-ATTTAA THCCATGTATYGAT-3') for the ATP synthase subunit 6 (*ATP6*).

The PCR mixtures contained 1 × PCR buffer, 1.5 mM MgCl₂, 0.2 mM dNTPs, each primer at 0.4 μ M, 1.25U of

Taq polymerase (Sangon Biotech, Shanghai, China), and 1 μ L of DNA template in a total volume of 25 μ L. Amplification reactions were performed with the following program: initial denaturation at 94 °C for 5 min, 35 cycles at 94 °C for 30 s, 50 °C (*ATP6*), 52 °C (LSU, *TEF1*, *RPB1* and *RPB2*) or 54 °C (ITS) for 30 s, and 72 °C for 30 s (ITS and *ATP6*), 50 s (LSU and *RPB2*) or 75 s (*TEF1* and *RPB1*), and for terminal elongation, the reaction batches were incubated at 72 °C for 10 min. All PCR products were examined by electrophoresis on 2% agarose gels and subsequently sent to the Kunming branch of Tsingke Biological Technology Co., Ltd. (Beijing, China) for sequencing.

Sequence alignment and phylogenetic analysis

For the phylogenetic analysis of Tricholomatineae, the newly generated sequences from the present work and representative lineages from Mou and Bau (2021) and He and Yang (2022) were used. *Hygrophorus hypothejus* (Fr.) Fr. and *H. xiangjun* H.Y. Huang & L.P. Tang (Hygrophorineae) were selected as outgroups. These sequences (Table S1) were aligned using MAFFT v7.471 (Kato and Standley 2016), and then manually adjusted in BioEdit v7.2.5 (Hall 1999). The intron regions of *TEF1*, *RPB1* and *RPB2* were manually removed, except for the conserved *RPB1*-intron 2. The ambiguously aligned regions of ITS, LSU and *RPB1* were removed in Gblocks v0.91b (Castresana 2000).

A six-locus matrix for Tricholomatineae (Dataset I, Suppl. material 2), containing sequences of ITS, LSU, *TEF1*, *RPB1*, *RPB2* and *ATP6*, was generated by Sequence-Matrix 1.7.8 (Vaidya et al. 2011). According to the AIC criterion in MrModeltest v2.4 (Nylander 2004), GTR + I + G was selected as the best-fit model for all the six partitions. Bayesian inference (BI) analysis was performed in MrBayes v3.2.7 (Ronquist and Huelsenbeck 2003) with the selected model, two simultaneous runs, four Markov Chain Monte Carlo (MCMC) chains, sampling every 100 generations and a total of two or eight million generations to ensure standard deviation of split frequencies below the 0.01 threshold. The first 25% generations were discarded as burn-in, and the convergence of runs was visually assessed using the trace function in Tracer v1.7.2 (Rambaut et al. 2018). Maximum likelihood (ML) analysis with 1,000 bootstrap replicates was computed in RAxML v8.0.20 (Stamatakis 2014) using the GTR + G + I model for the entire dataset.

For the phylogenetic analysis of Clitocybaceae, two datasets were individually analyzed following the procedure described above. One dataset comprised sequences of ITS, LSU, *TEF1*, *RPB1*, *RPB2* and *ATP6* (Dataset II, Suppl. material 3), while the other dataset contained only ITS sequences (Dataset III, Suppl. material 4). *Atractosporocybe* aff. *inornata* and *Rhizocybe alba* Y.X. Ding & E.J. Tian were selected as outgroups because of their external positions to

Clitocybaceae (Alvarado et al. 2015; He and Yang 2022). To build the ITS tree, all the representative Clitocybaceae sequences available in GenBank (<http://www.ncbi.nlm.nih.gov>) and UNITE (<https://unite.ut.ee/>) were included. In the BI analysis based on six loci, GTR + I + G was selected as the best-fit model for ITS, LSU, *RPB1*, *RPB2* and *ATP6*, whereas SYM + I + G was chosen for *TEF1*. In the other BI analysis based on ITS, GTR + I + G was the best-fit model. The SYM + I + G model was not implementable in RAXML, thus the GTR + I + G model was employed for ML analysis instead.

Genetic distance calculation

Mean genetic distances between and within clades were calculated using MEGA v11.0.13 (Tamura et al. 2021), with Dataset II serving as input file. The options of the analysis were configured with the following settings: bootstrap method with 1000 replications for variance estimation, nucleotide type, pairwise (p) distance method (Nei and Kumar 2000), substitutions to include both transitions and transversions, uniform rates among sites, homogeneous pattern among lineages and pairwise deletion for gaps or missing data.

Genomic library preparation and NGS sequencing

A modified CTAB protocol introduced by Li et al. (2013) was used to extract genomic DNA from material dried with silica gel. DNA was quantified using a Qubit 3.0 Fluorometer (Life Technologies, Carlsbad, CA, USA), and its integrity was assessed by electrophoresis on 1% agarose gel. Paired-end (PE) libraries (Insert size: 400 bp) were prepared using a Hieff NGS® OnePot DNA Library Prep Kit for Illumina® (Yeasen Biotech, Shanghai, China), following the manufacturer's protocol. The concentration and size of the prepared libraries were detected using Qubit 3.0 and Q-sep1 (Bioptic, Changzhou, China), respectively. Next generation sequencing (NGS) was performed on Illumina Novaseq 6000, PE150 systems (Illumina, San Diego, CA, USA) at the laboratories of Wuhan Igenebook Biotechnology Co., Ltd. and Shanghai Personalbio Technology Co., Ltd. (China). The amount of sequencing data for each sample was 5 Gbase.

Data filtering and genome assembly

FastQC v0.11.9 (Andrews 2010) was used to control the quality of raw data. Then the raw data was filtered using Trimmomatic v0.36 (Bolger et al. 2014) to obtain clean data, according to the following parameters: ILLUMINA-CLIP: adapters.fa:2:30:10; LEADING: 3; TRAILING: 3; SLIDINGWINDOW: 4:15; MINLEN: 20. The clean data was assessed using FastQC and SOAPec v2.03 (Kmer = 17,

Luo et al. 2012), and subsequently as an input file to run de-novo assembly using A5-miseq v[08/25/2016] (Coil et al. 2014) and SPAdes v3.13.1 (Prjibelski et al. 2020). Pilon v1.18 (Walker et al. 2014) was used for assembly correction. After assembly, Assembly-stats v1.0.1 (<https://pypi.org/project/assembly-stats/>) was used to check the basic assembly information, and BUSCO v5.2.2 (Manni et al. 2021) was used to assess the assembly completeness. The assembly statistics of 38 representative samples of Clitocybaceae and two outgroup samples are presented in Table S2 (Suppl. material 1).

Single-copy gene extraction and phylogenomic analysis

Red v[05/22/2015] (Girgis 2015) was used to screen out repeated sequences, and Augustus v3.3.3 (Keller et al. 2011), GlimmerHMM v3.0.1 (Majoros et al. 2004), GeneMark-ES v4.35 (Ter-Hovhannisyan et al. 2008) and Exonerate v2.2 (Slater and Birney 2005) were used to perform gene prediction. The resulting prediction was then integrated with EVidenceModeler v[06/25/2012] (Haas et al. 2008). The protein prediction was extracted by gffread v0.12.7 (Perte and Perte 2020). Using BUSCO analysis, single-copy genes of 43 sample (Table S3, Suppl. material 1) were retrieved by comparing the obtained predicted proteins against the lineage dataset Agaricales_odb10. A total of 485 shared single-copy genes (Table S4, Suppl. material 1) were selected to carry out the phylogenomic analysis. The aforementioned softwares MAFFT and Gblocks were employed for aligning amino acid sequences and extracting conserved sequences, respectively. The shared single-copy gene sequences were concatenated to form the final Dataset IV (Suppl. material 5). Finally, ML analysis with 1,000 bootstrap replicates was performed with FastTree v2.1.11 (Price et al. 2010) using the LG + CAT model.

Divergence time estimation

A two-step calibration procedure was performed to estimate node ages using BEAST v1.10.4 (Suchard et al. 2018), following Zhao et al. (2016) and Wilson et al. (2017). The marasmioid clade node based on a 90 million years ago (Mya) fossil *Archaeomarasmius legetti* from mid-Cretaceous amber (Hibbett et al. 1997), and the Suillineae node based on a 50 Mya permineralized suilloid ECM fossil associated with pine roots (LePage et al. 1997), were set for calibration.

Dataset V of Agaricomycetidae (Suppl. material 6) contained sequences of LSU, *TEF1*, *RPB1*, *RPB2* and *ATP6* from representatives of Tricholomatineae, marasmioid clade and Boletales (Table S5, Suppl. material 1). The sequences of *TEF1*, *RPB1*, *RPB2*, and *ATP6* were trimmed to start in the first codon position, and introns of the four genes were

removed. The ambiguously aligned regions of LSU were removed from the dataset. The xml file was generated in BEAUti v1.10.4 with settings as follows: GTR + G + I substitution model for each partition, uncorrelated lognormal relaxed clock (Drummond et al. 2006), tree prior as Yule Process speciation (Gernhard 2008), lognormal prior distribution with 1.0 stdev in real space and offset ages of 90 and 50 Mya for marasmioid clade and Suillineae, 200 million length of chain, every 1,000 log parameters. The output log files of two runs were compared in Tracer to assess convergence and ensure effective sample sizes (ESS) \geq 200. The first 10% sampled states were discarded as burn-in using TreeAnnotator v1.10.4. The generated maximum-clade-credibility (MCC) tree was viewed to obtain the stem age of Clitocybaceae + Tricholomataceae.

Dataset VI of Clitocybaceae (Suppl. material 7), containing ITS, LSU, *TEF1*, *RPB1*, *RPB2* and *ATP6*, were analyzed following a similar procedure as above for Dataset VI. Node ages were calibrated by using the highest posterior density (HPD) age values for the Clitocybaceae + Tricholomataceae divergence. A normal distribution prior on the treeModel.rootHeight parameter was used, which had a 1.0 stdev.

Toxin extraction and detection

Sixty-eight dried mushroom samples (Table 1, 25 mg per sample) were individually ground into powder. The powder was mixed with 1 mL of methanol-deionized H₂O (7:3, v/v), then treated with an ultrasonic bath for 30 min and vortexed at 1,200 rpm for 30 min at 10 °C. After centrifugation (4 °C, 18,000 rpm, 25 min), the supernatant was blow dried under nitrogen, and redissolved in 250 μ L acetonitrile in a vortex (10 °C, 1,200 rpm, 30 min). One hundred times dilution of the resulting supernatants from each sample were used for ultrahigh performance liquid chromatography-tandem mass spectrometry (UPLC-MS/MS) analysis. Pure acetonitrile was used as a blank control. Two to three duplicates of each species were used for extraction, although in some cases the available material only permitted a single extraction.

The UPLC-MS/MS analysis was performed with a ACQUITY UPLC-Xevo TQ-S system (Waters, Milford, MA, USA). (i) Chromatographic conditions: The model of column was ACQUITY UPLC BEH Amide (100 mm \times 2.1 mm, 1.7 μ m; Waters). The mobile phase A (0.05% formic acid aqueous solution) and B (acetonitrile) with a flow rate of 0.4 mL/min were used to run the following gradient elution program: 0–0.2 min, 10–30% A and 90–70% B; 0.2–1 min, 30–90% A and 70–10% B; 1–2 min, 90–30% and 10–70% B; 2–5 min, 30% A and 70% B. The column and sample were set to 40 °C and 10 °C, respectively, and the injection volume was 2.0 μ L. (ii) Mass spectrometry conditions: ESI⁺ mode, capillary at 3 kV, cone at 18 V, collision at 16 V, desolvation temperature at 500 °C, desolvation gas flow at 1000

L/h, cone gas flow at 150 L/h, collision gas flow at 11.4 L/h and other parameters at default values. In the multiple reaction monitor, protonated molecular ion ($[M + H]^+$) of 174.13 was the parent ion, and two daughter ions of 56.81 and 96.93 were used for qualitative and quantitative detection, respectively.

The standard of muscarine (C₉H₂₀NO₂.Cl, 209.7, CAS. No. 2303-35-7, 98% purity) was purchased from Good Laboratory Practice Bioscience Co., Ltd (Glpbio, CA, USA). Serial dilutions of the standard (500, 100, 50, 25, 12.5, 6.25, 3.125, 1.625, 0.8125 and 0.40625 ng/ml) were analyzed to obtain the retention time and response peak areas. Based on the obtained data, the linear equation of calibration curve for quantitative analysis and its correlation coefficient were calculated. Muscarine was scored as present or absent by comparing sample chromatograms to the standard, and the content by dry weight was converted to mg/kg.

Results

Phylogenetic analysis

As shown in Table S1, a total of 1,013 sequences (206 ITS, 204 LSU, 167 *TEF1*, 147 *RPB1*, 185 *RPB2* and 104 *ATP6*) from 209 samples were used in the phylogenetic analysis of Tricholomatineae, 492 (86 ITS, 86 LSU, 82 *TEF1*, 79 *RPB1*, 80 *RPB2* and 79 *ATP6*) of which were newly generated in the present study. The combined dataset ITS-LSU-*TEF1*-*RPB1*-*RPB2*-*ATP6* of Tricholomatineae comprised a total of 4,543 positions. In the phylogenetic analyses of Clitocybaceae, the six-locus dataset comprised 534 sequences (102 ITS, 101 LSU, 90 *TEF1*, 78 *RPB1*, 91 *RPB2* and 72 *ATP6* from 103 samples) and 4,669 positions, and the ITS dataset comprised 287 sequences and 874 positions. The ML and BI analyses of these datasets do not show conflicts in any clades of the trees.

The overall topology of Tricholomatineae obtained in this study (Fig. 1) is consistent with that of previous work conducted by Alvarado et al. (2018b), Vizzini et al. (2020a, b), and He and Yang (2022). The Clitocybaceae represents a monophyletic lineage (71% BP, 0.90 PP), separated from seven other major familial lineages: Lyophyllaceae Jülich s.str. (100% BP, 1.00 PP), Asproinocybaceae T. Bau & G.F. Mou (100% BP, 1.00 PP), Entolomataceae Kotl. & Pouzar (91% BP, 1.00 PP), Tricholomataceae R. Heim ex Pouzar (87% BP, 1.00 PP), Callistosporiaceae Vizzini, Consiglio, M. Marchetti & P. Alvarado (100% BP, 1.00 PP), Biannulariaceae Jülich (95% BP, 1.00 PP), and Pseudoclitocybaceae Vizzini et al. (98% BP, 1.00 PP).

As shown in the phylogenetic analyses of Clitocybaceae (Figs. 2 and 3), we divide the family into six groups recognized as the following genera: (i) *Collybia* [type: *C.*

Table 1 Determination of muscarine in Clitocybaceae species

| Genus and subgenus | Species | Voucher | Amount of muscarine (mg/kg) |
|---|-----------------------------|------------------------------|-----------------------------|
| <i>Clitocybe</i> | <i>C. epixyla</i> | KUN-HKAS 105576, basidiome 1 | – |
| | | KUN-HKAS 105576, basidiome 2 | – |
| | <i>C. nebularis</i> | KUN-HKAS 105556 | – |
| | <i>C. tomentosa</i> | KUN-HKAS 123096 | – |
| | | KUN-HKAS 123097 | – |
| <i>Collybia</i> subgen. <i>Collybia</i> | <i>C. alboclitocyboides</i> | KUN-HKAS 123098 | – |
| | | KUN-HKAS 105616 | 6.47 |
| | | KUN-HKAS 123099 | 22.47 |
| | <i>C. asiatica</i> | KUN-HKAS 123100 | 11.07 |
| | | KUN-HKAS 123119, basidiome 1 | 81.42 |
| | <i>C. bisterigmata</i> | KUN-HKAS 123119, basidiome 2 | 18.86 |
| | | KUN-HKAS 77538 | 378.84 |
| | | KUN-HKAS 123102 | 72.40 |
| | <i>C. brunneoumbilicata</i> | KUN-HKAS 123103 | 31.46 |
| | | KUN-HKAS 123104 | 18.38 |
| | | KUN-HKAS 123105 | 22.57 |
| | <i>C. cirrhata</i> | KUN-HKAS 123106 | 21.37 |
| | | HMJAU 44754 | 17.33 |
| | | HMJAU 44755 | 55.80 |
| | <i>C. dryadicola</i> | HMJAU 44756 | 18.42 |
| | | KUN-HKAS 116076 | 40.34 |
| | | <i>C. humida</i> | KUN-HKAS 76368 |
| | <i>C. hunanensis</i> | KUN-HKAS 123108 | 23.08 |
| | | KUN-HKAS 123109 | 27.08 |
| | | MHHNU 31389, basidiome 1 | 164.66 |
| | <i>C. odora</i> | MHHNU 31389, basidiome 2 | 123.12 |
| | | KUN-HKAS 105638 | – |
| | | KUN-HKAS 123110 | – |
| | <i>C. pannosa</i> | KUN-HKAS 123111 | – |
| | | KUN-HKAS 115428 | 20.31 |
| | | KUN-HKAS 123113 | 15.65 |
| | <i>C. petaloidea</i> | KUN-HKAS 123114 | 14.82 |
| | | KUN-HKAS 101063 | 55.97 |
| | <i>C. phyllophila</i> | KUN-HKAS 106642 | 17.97 |
| | | KUN-HKAS 105547 | 35.30 |
| | | KUN-HKAS 103697 | 86.83 |
| | <i>C. piceata</i> | KUN-HKAS 123115 | 19.19 |
| KUN-HKAS 123117 | | 40.72 | |
| KUN-HKAS 123118 | | 36.70 | |
| <i>C. sp.</i> | KUN-HKAS 106644 | 18.93 | |
| | KUN-HKAS 123120 | 106.56 | |
| | KUN-HKAS 123121 | 46.89 | |
| <i>C. tibetica</i> | KUN-HKAS 123124 | 86.77 | |
| | KUN-HKAS 115436 | 72.19 | |
| | KUN-HKAS 123101 | 99.88 | |
| <i>C. tomentostipes</i> | KUN-HKAS 123125 | 16.78 | |
| | KUN-HKAS 123126 | 14.12 | |
| <i>C. tuberosa</i> | HMJAU 44757 | 49.56 | |
| <i>C. xylogena</i> | KUN-HKAS 54966, basidiome 1 | 100.21 | |

Table 1 (continued)

| Genus and subgenus | Species | Voucher | Amount of muscarine (mg/kg) |
|---|---------------------------------|------------------------------|-----------------------------|
| <i>Collybia</i> subgen. <i>Crassicybe</i> | <i>C. irina</i> | KUN-HKAS 54966, basidiome 2 | 37.47 |
| | | KUN-HKAS 82928 | – |
| <i>Collybia</i> subgen. <i>Leucocalocybe</i> | <i>C. nuda</i> | KUN-HKAS 105553 | – |
| | | KUN-HKAS 71083 | – |
| | | KUN-HKAS 93478 | – |
| <i>Collybia</i> subgen. <i>Macrosporocybe</i> | <i>C. sordida</i> | KUN-HKAS 123127, basidiome 1 | – |
| | | KUN-HKAS 123127, basidiome 2 | – |
| | | KUN-HKAS 123128 | – |
| <i>Lepista</i> | <i>L. panaeolus</i> | KUN-HKAS 123129 | – |
| | | KUN-HKAS 105370 | – |
| <i>Pseudolyophyllum</i> | <i>L. sp.</i> | KUN-HKAS 76295 | – |
| | | <i>P. macrobasidium</i> | KUN-HKAS 123130 |
| <i>Singerocybe</i> | <i>S. alboinfundibuliformis</i> | KUN-HKAS 123131 | – |
| | | KUN-HKAS 123133, basidiome 1 | – |
| | | KUN-HKAS 123133, basidiome 2 | – |
| | | KUN-HKAS 123134 | – |
| | | KUN-HKAS 123135 | – |
| <i>Singerocybe</i> | <i>S. umbilicata</i> | KUN-HKAS 123136 | – |
| | | KUN-HKAS 123137 | – |
| | | | – |

‘–’ Means muscarine is not detected in a sample

tuberosa (Bull.) P. Kumm.], (ii) *Pseudolyophyllum* [type: *P. metachroa* (Fr.) Raithelh.], (iii) *Lepista* [type: *L. densifolia* (J. Favre) Singer & Cléménçon], (iv) *Dendrocollybia* [type: *D. racemosa* (Pers.) R.H. Petersen & Redhead], (v) *Singerocybe* [type: *S. viscida* Harmaja (not sequenced)], and (vi) *Clitocybe* [type: *Cli. nebularis* (Batsch) P. Kumm.].

Sequences of *Clitocybe* species in the old sense are distributed in four clades: (i) *Collybia* subgen. *Collybia* (100% BP, 1.00 PP in Fig. 2), (ii) *Collybia* subgen. *Macrosporocybe* (100% BP, 1.00 PP in Fig. 2 and 93% BP, 1.00 PP in Fig. 3), (iii) *Pseudolyophyllum* (100% BP, 1.00 PP in Fig. 2 and 57% BP, 0.90 PP in Fig. 3), and (iv) *Clitocybe* s.str. (100% BP, 1.00 PP in Fig. 2 and 64% BP in Fig. 3). Meanwhile, Sequences of *Lepista* species in the old sense group in three clades: (i) *Collybia* subgen. *Leucocalocybe* (100% BP, 1.00 PP in Fig. 2 and 95% BP, 1.00 PP in Fig. 3), (ii) *Collybia* subgen. *Crassicybe* (100% BP, 1.00 PP in Fig. 2 and 83% BP in Fig. 3), and (iii) *Lepista* s.str. (100% BP, 1.00 PP in Fig. 2 and 75% BP, 1.00 PP in Fig. 3).

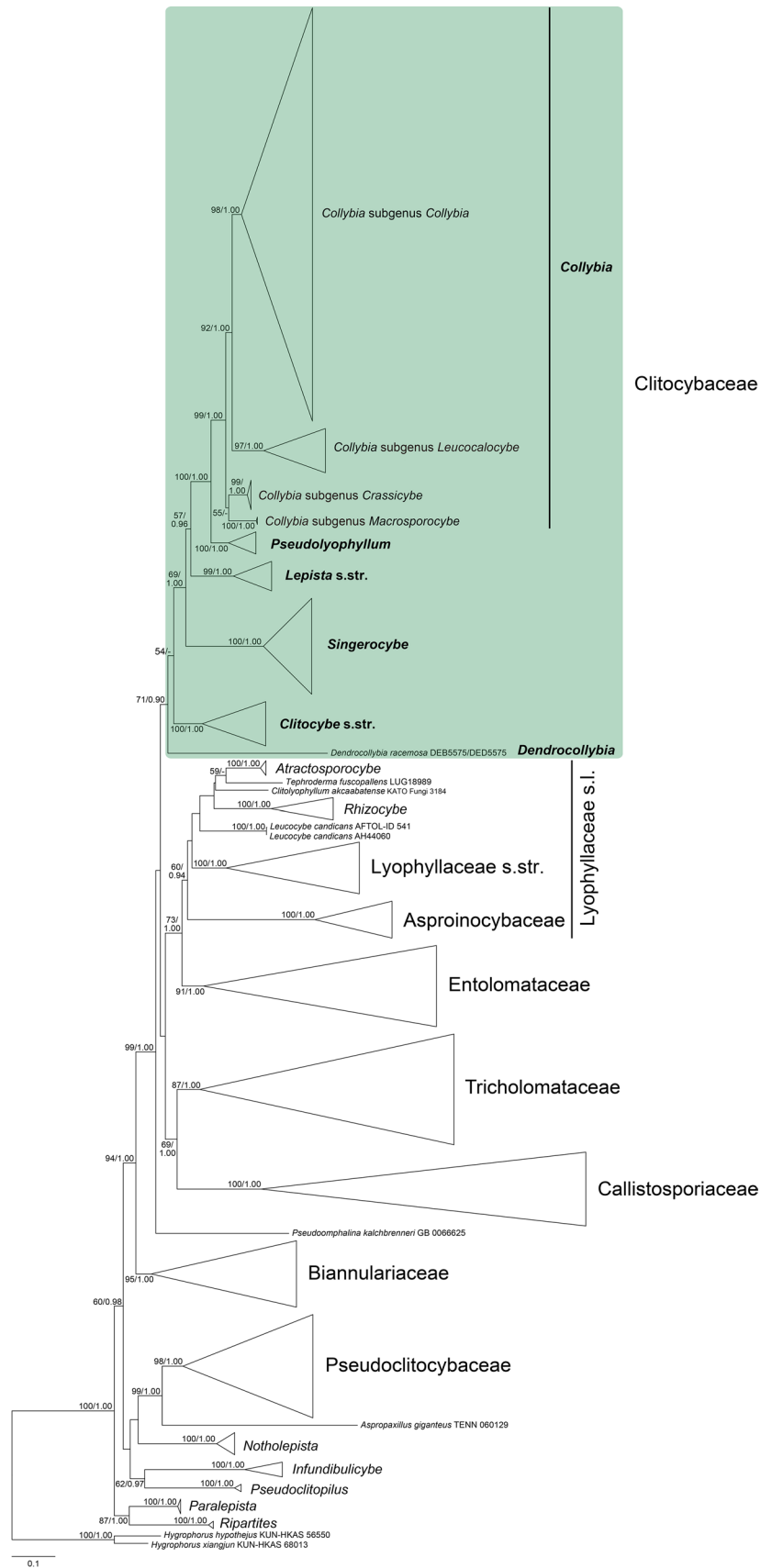
To accommodate the clades deviating from *Clitocybe* s.str. and *Lepista* s.str. (Figs. 2 and 3), we propose the recognition of a clade for *Pseudolyophyllum* Raithelh., and expand the delimitation of *Collybia* and divide the genus in four subgenera: (i) subgenus *Collybia* is proposed to accommodate the clade containing previous *Collybia* s.str. and a large number of previous *Clitocybe* species, such as *Cli. dealbata*, *Cli. odora* (Bull.) P. Kumm. and *Cli. phyllophila*;

(ii) two new subgenera, *Macrosporocybe* and *Crassicybe*, are proposed to accommodate a lineage with two species of *Clitocybe* and another one with *Lepista irina* (Fr.) H.E. Bigelow, respectively; (iii) *Leucocalocybe* is reclassified as subgenus to accommodate the clade composed of *Leucocalocybe mongolica* (S. Imai) X.D. Yu & Y.J. Yao and the closely related *Lepista* section *Spongiosa* (Fr.) Kühner. The ITS tree (Fig. 3) shows 64 clades, 17 of which represent the newly proposed Chinese *Collybia* (14), *Clitocybe* (2) and *Pseudolyophyllum* (1) species, which are also supported by the six-locus phylogenetic analysis (Fig. 2).

Phylogenomic analysis

In order to resolve the generic relationships of *Clitocybe*-baceae, the subgeneric relationships of *Collybia* and the infrasubgeneric relationships of *Collybia* subgen. *Collybia*, a phylogenomic analysis of the family based on 485 single-copy genes was performed. The genomic dataset comprised 258,291 amino acid sites from 43 samples. The nodes that lacked support or had weak support in the six-locus tree (Fig. 2) were significantly supported in the 485-gene tree (Fig. 4), and a well resolved topology was obtained. According to the two trees, the species-rich subgen. *Collybia* was further divided into eight clades. In the six-locus phylogenetic analysis (Fig. 4A), Clade II (100% BP), IV (100% BP), V (100% BP), VI, VII (99% BP) and VIII (100% BP) were

Fig. 1 ML phylogenetic tree of Tricholomatineae based on the concatenated dataset (ITS-LSU-TEF1-RPB1-RPB2-ATP6), with *Hygrophorus hypothejus* and *H. xiangjun* (Hygrophorineae) as outgroups. Bootstrap values (BP) $\geq 50\%$ from ML analysis and Bayesian posterior probabilities (PP) ≥ 0.90 from BI analysis are shown at nodes



strongly to fully supported. However, Clade I (67% BP) and III (78% BP) was weakly to moderately supported, the arrangement of the clades was indeterminate. In the phylogenomic analysis (Fig. 4B), all clades were supported with 100% bootstrap values except for Clade I with 96% bootstrap, and the arrangement of these clades was clear.

Toxin detection

According to the external standard method, the resulting equation of calibration curve for muscarine was $y = 2499.74x + 6.33452$ ($R^2 = 0.999884$) with a dynamic range of 0.4–500 ng/mL (y : the peak area; x : muscarine concentration, ng/mL; R^2 : correlation coefficient) and the retention time was 1.36 min (Fig. S1). A total of 68 samples from the genera *Collybia* (52), *Pseudolyophyllum* (4), *Lepista* (2), *Singerocybe* (4) and *Clitocybe* (6) were analyzed using UPLC-MS/MS. The detection results for each sample are provided in Table 1.

Phylogenetic distribution of characters

The results obtained by phylogenetic and chemical analyses of Clitocybaceae are integrated in Fig. 2. The six-locus phylogram shows that all muscarine-containing species are exclusively found in *Collybia*, forming a monophyletic clade within *Collybia* subgen. *Collybia* with only weak support (50% BP). Nevertheless, the monophyly of muscarine distribution is further confirmed by the 485-gene phylogram with 100% BP support (Fig. 4).

Besides muscarine, the adhesion of basidiospores and the growth substrate were used as characters to correlate with the phylogenetic structure of subgen. *Collybia*. In the six-locus and 485-gene phylograms (Fig. 4), (i) species belonging to Clades I to VII contain muscarine, whereas *C. odora* in the earliest diverging Clade VIII does not; (ii) species belonging to Clades I and VIII have basidiospores mostly in tetrads, while those in Clades III and V have some basidiospores adhering in tetrads except for the 2-spored species, *C. bisterigmata*; (iii) species belonging to Clades II, IV and VII have basidiospores which are almost always single, while 2-spored *C. xylogena* in Clade VI has basidiospores which are always single; (3) species of subgen. *Collybia* exhibit a decreasing trend in substrate preference, with broad leaf litter being the most preferred followed by needle leaf litter, soil and mushroom remnants.

Molecular dating

The MCC tree of Agaricomycetes (Fig. S2, Suppl. material 1) supported that the median stem age of Clitocybaceae + Tricholomataceae was 65.89 Mya. Based on the MCC tree of Clitocybaceae (Fig. 5), the divergence time

of the family was further estimated to be 60.14 Mya (95% HPD: 46.90–67.08 Mya). The divergence times of the genera *Clitocybe* (median: 33.01 Mya, 17.20–50.24 Mya), *Collybia* (median: 30.25 Mya, 21.27–39.34 Mya), *Lepista* (median: 17.90 Mya, 9.16–28.25 Mya), *Pseudolyophyllum* (median: 16.30 Mya, 6.21–28.43 Mya), and *Singerocybe* (median: 24.56 Mya, 14.95–35.38 Mya) were estimated as well. In addition, muscarine acquisition was estimated to have occurred at 20.18 Mya (13.99–26.91 Mya) within the family.

P-distance calculation

As shown in Fig. 6, six possible generic divisions for the nine clades shown in Fig. 2 were displayed. Using the six-locus Dataset II, the mean p-distances between and within different generic clades for each division were calculated, and the resulting values of the genetic distances are provided in Table S6–S11 (Suppl. material 8).

Taxonomy

Based on our phylogenetic, morphological, ecological, and chemical evidence, we hereby present an updated classification and arrangement of the family Clitocybaceae, accompanied by detailed descriptions of the species discovered in China.

Clitocybaceae Vizzini, Consiglio & M. Marchetti, Index Fungorum 462: 1 (2020).

The family is emended here based on Vizzini et al. (2020a) and our results.

Diagnosis: Shares several morphological traits with Tricholomataceae and Pseudoclitocybaceae, but can be discriminated because its members all possess inamyloid basidiospores and clamp connections, and usually do not possess pleurocystidia and cheilocystidia.

Type genus: *Clitocybe* (Fr.) Staude, Schwämme Mitteldeutschl. 1: xxviii, 122 (1857).

Description: Habit clitocyboid, collybioid or tricholomatoid, gymnocarpic. Basidiomes vary from very small to large. Pileus convex, umbonate, applanate or depressed to funnel-shaped, hygrophanous, subhygrophanous or non-hygrophanous. Lamellae adnexed, adnate, emarginate, sinuate or decurrent. Stipe usually central, hollow, solid or stuffed, without or with conidiogenous branches (*Dendrocollybia*), without or with sclerotia (*Dendrocollybia*, several species of *Collybia*) attached to base. Spore-deposit often white to cream, also pinkish, yellowish, salmon. Basidiospores hyaline, smooth or punctate, tuberculate, verrucose to spinose, thin-walled, inamyloid, cyanophilic or acyanophilic. Basidia clavate to narrowly clavate, usually 4-spored, rarely 2-spored. Lamella trama regular or subregular. Pleurocystidia and cheilocystidia absent or inconspicuous. Pileipellis usually a cutis, rarely

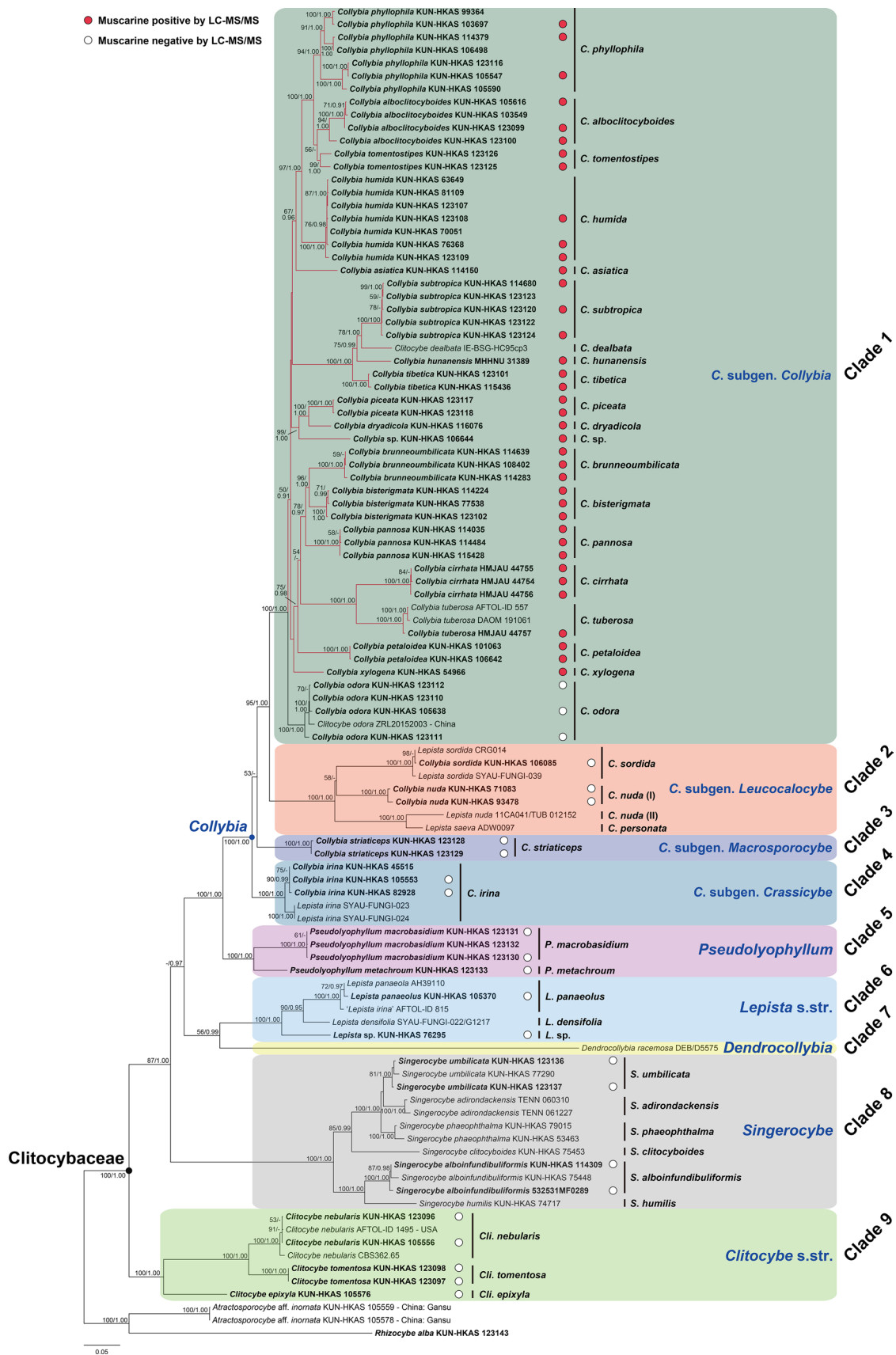


Fig. 2 ML analysis of Clitocybaceae based on the combined ITS-LSU-TEF1-RPB1-RPB2-ATP6 sequence data, with *Atractosporocybe* aff. *inornata* and *Rhizocybe alba* (Lyophyllaceae s.l.) as outgroups. Bootstrap values (BP) $\geq 50\%$ from ML analysis and Bayesian posterior probabilities (PP) ≥ 0.90 from BI analysis are shown at nodes. Newly generated sequences are shown in bold and muscarine-producing branches are shown in red. Red and white circles indicate the presence and absence of muscarine, respectively

becoming trichodermal, without or with vesicles (*Singerocybe*), occasionally with pileocystidia. Stipitipellis usually a cutis, occasionally with caulocystidia. Clamp connections present. Muscarine present or absent.

Ecology: Generally gregarious, even forming fairy rings, also scattered or solitary, saprotrophic or fungicolous, on soil, broad leaf or needle litter, rotten wood or remnants of decaying fungal basidiomes; in all seasons.

Distribution: Cosmopolitan.

Genera included: *Clitocybe*, *Collybia*, *Dendrocollybia*, *Lepista*, *Pseudolyophyllum*, and *Singerocybe*.

Notes: The monophyletic status of Clitocybaceae was previously revealed in phylogenetic analyses by Alvarado et al. (2018a, b) and Vizzini et al. (2020b). However, the support values were low and only a limited number of species and genera from the family were included. In our six-locus phylogenetic analysis of Tricholomatineae, the latest available data (521 sequences from GenBank) and 492 sequences newly generated in the present work were analyzed. Our result confirms that the Clitocybaceae forms a monophyletic lineage (71% BP, 0.90 PP, Fig. 1), clearly separated from other major families Lyophyllaceae, Asproinocybaceae, Entolomataceae, Tricholomataceae, Callistosporiaceae, Biannulariaceae and Pseudoclitocybaceae with improved support. The main topology recovered in this study (Fig. 1) is consistent with those inferred from LSU-RPB2-TEF1-SSU analyses in previous works, indicating that the topology is stable despite the use of different combinations of gene datasets.

Vizzini et al. (2020a) included the genus *Lepistella* T.J. Baroni & Ovrebo in Clitocybaceae. Its only member, *Lpl. ocula* T.J. Baroni & Ovrebo, has a pale pink to pinkish buff spore print and inamyloid, cyanophilic, verrucose basidiospores (Ovrebo and Baroni 2007), features that match *Lepista* in the old sense well. Even so, the lignicolous habit and the striking gelatinized tissues in the context are quite different from *Lepista*. *Lepistella* could represent an independent clade separated from all known clades of *Lepista* in the Clitocybaceae. However, a separate phylogenetic analysis of LSU data conducted by us (not shown) was insufficient to show that. Due to lack of other available DNA fragments for analysis, *Lepistella* is not considered in the present work.

Key to the genera of the family Clitocybaceae

- 1 Basidiomes usually large (pileus > 5 cm wide) with thick flesh (> 0.3 cm thick)2
- 1 Basidiomes usually not large (pileus \leq 5 cm wide) with thin flesh (\leq 0.3 cm thick)3
- 2 Basidiospores smooth.....*Clitocybe*
- 2 Basidiospores verruculose.....*Lepista*
- 3 Stipe with conidiogenous branches.....*Dendrocollybia*
- 3 Stipe without conidiogenous branches.....4
- 4 With swollen elements in epicutis of pileus.....*Singerocybe*
- 4 Without swollen elements in epicutis of pileus.....5
- 5 Lamellae usually dark to pale gray or gray-brown*Pseudolyophyllum*
- 5 Lamellae usually white to whitish, cream or lilac.....*Collybia*

Clitocybe (Fr.) Staude, Schwämme Mitteledeutschl.: xxviii, 122 (1857).

Basionym: *Agaricus* trib. *Clitocybe* Fr., Syst. mycol. (Lundae) 1: 9, 78 (1821).

Diagnosis: Differs from *Collybia* and *Pseudolyophyllum* generally by its relatively larger basidiomes with non-hygrophanous pilei and thicker flesh. Differs from *Lepista* s.str. by its smooth basidiospores. Differs from *Harmajaea* by its abundance of clamp connections.

Type species: *Clitocybe nebularis* (Batsch) P. Kumm., Führ. Pilzk. (Zerbst): 124 (1871).

Description: Basidiomes large, clitocyboid. Pileus convex to plane, somewhat depressed or depressed, sometimes with slight umbo at center, white, yellowish brown, gray-brown to beige-gray, smooth to fibrillose, glabrous or tomentose to hirsute, somewhat pruinose or not, not hygrophanous. Flesh white or whitish, thick. Lamellae decurrent, white, cream or yellowish. Stipe central, cylindrical, solid or hollow, concolorous with pileus or paler, fibrillose to tomentose. Basidiospores in general ellipsoid, hyaline, smooth, thin-walled, inamyloid, cyanophilic. Lamella trama regular or subregular. Pleurocystidia and cheilocystidia absent. Clamp connections present in all parts of basidiome. Muscarine absent.

Ecology: Usually gregarious, or in fairy rings, on soil, broad leaf or needle litter, rarely on rotten wood; mainly in autumn.

Distribution: Widespread in the Northern Hemisphere, also reported from New Zealand (Cooper 2016).

Notes: A number of species were designated as lectotypes of *Clitocybe*, viz. *Cli. clavipes* (Pers.) P. Kumm. (Bigelow 1982), *Cli. gibba* P. Kumm. (Clements and Shear 1931) and *Cli. nebularis* (Donk 1949, 1962). The species *Cli. clavipes* and *Cli. gibba* have been excluded since phylogenetic evidence suggests they are in their own independent generic lineages, viz. *Ampulloclitocybe* (Hygrophoraceae) and *Infundibulicybe* (incertae sedis, Tricholomatineae), and are distantly related to *Clitocybe* (Redhead et al. 2002; Matheny

Fig. 3 ML analysis of Clitocybaceae based on ITS sequence data, with *Atractosporocybe* aff. *inornata* (Lyophyllaceae s.l.) as out-group. Bootstrap values (BP) \geq 50% from ML analysis and Bayesian posterior probabilities (PP) \geq 0.90 from BI analysis are shown at nodes. Newly generated sequences are highlighted in bold and newly proposed species names are marked in blue. GenBank accession numbers of public sequences are given in parentheses and their geographic origins are shown, if available

et al. 2006). Although *Cli. nebularis* belongs to a different clade from a great number of previous *Clitocybe* species, it still falls within Clitocybaceae (Fig. 2). *Clitocybe nebularis* was reaffirmed as the type species of *Clitocybe* by Harmaja (2003), and is currently accepted by most modern authors (e.g., Ammirati et al. 2007; Vizzini et al. 2010; Alvarado et al. 2015, 2018b; Cooper 2016). Thus, the clades containing *Cli. nebularis* (highlighted in grass green boxes, Figs. 2 and 3) represent *Clitocybe* s.str. Muscarine was not detected in species of *Clitocybe* s.str. (Table 1), and *Cli. nebularis* is listed as an edible and medicinal fungus in China (Wu et al. 2019). The large fleshy basidiomes and cyanophilic basidiospores distinguish *Clitocybe* s.str. from the small, thin, muscarine-containing *Clitocybe* taxa (in the old sense) with cyanophobic or weakly cyanophilic basidiospores, which are transferred to *Collybia* subgen. *Collybia* in the present work.

Based on the above-mentioned features, *Cli. nebularis* and related species were once considered in *Lepista* by Harmaja (1974, 1976). *Clitocybe* in the current concept can indeed recall *Lepista* s.str., but the former has smooth basidiospores while in the latter the basidiospores are verrucose. The ITS phylogenetic tree (Fig. 3) reveals that the four samples of *Cli. robusta* (LC370436, LC370435, MK573913 and JN021001) should also be identified as *Cli. nebularis*. This implies that *Cli. robusta* is most likely just a whitish form of *Cli. nebularis*, as previously suggested by Kühner and Romagnesi (1953) and Harmaja (1969). However, additional genes should be analyzed to check for differences before confirming this hypothesis.

Key to the known *Clitocybe* species in China

- 1 Growing on rotten wood.....*Cli. epixyla*
- 1 Growing on soil, broad leaf or needle litter.....2
- 2 Pileus fibrillose.....*Cli. nebularis*
- 2 Pileus tomentose to hirsute.....*Cli. tomentosa*

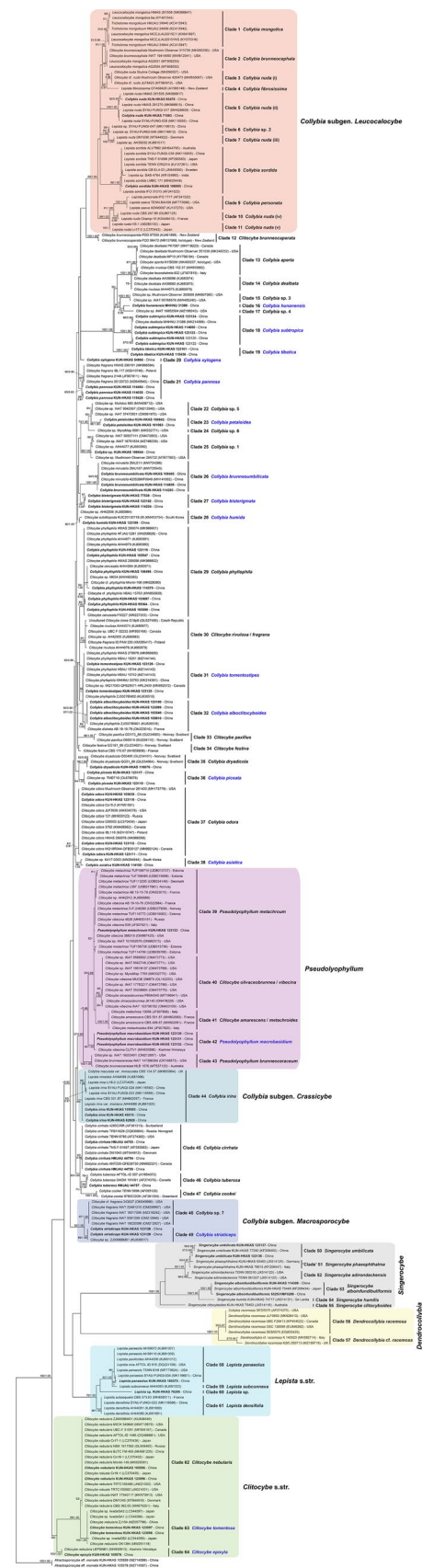
Clitocybe epixyla Z.M. He & Zhu L. Yang, sp. nov. Figures 7a and 8

Mycobank: MB 847224.

Etymology: ‘*epixyla*’ (Greek), referring to the habitat on wood.

Diagnosis: Differs from other known species of the genus by its lignicolous habit.

Type: CHINA. GANSU PROVINCE: Zhuoni County, Donggou, on a decaying stump of *Picea* sp., alt. 3,082 m, 10 Sep 2021, S.P. Jian 251 (KUN-HKAS 105576, holotype).



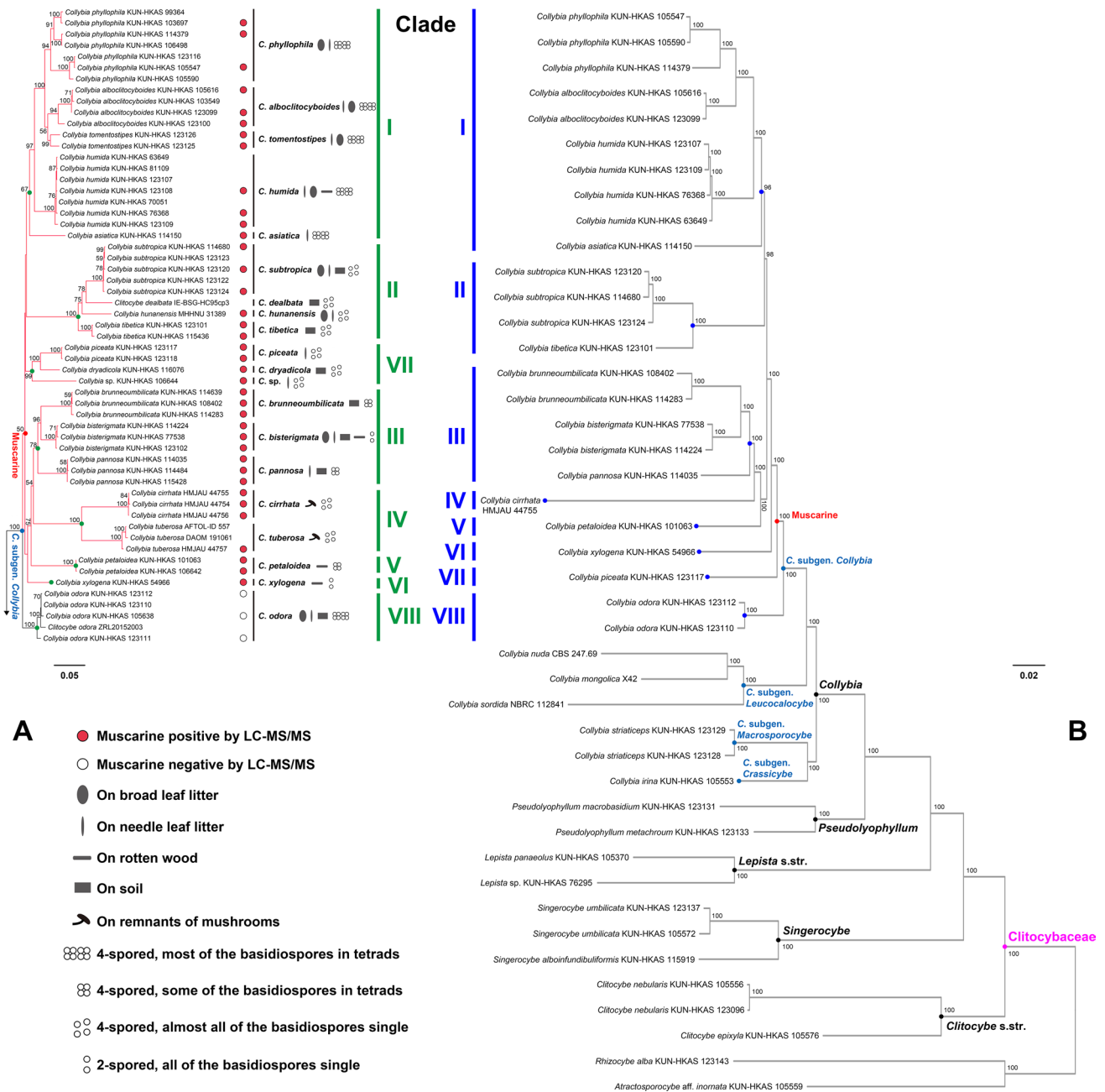


Fig. 4 ML analyses of Clitocybeaceae based on six-locus (A, partially displayed) and 485-gene (B) datasets showing generic relationships of the family, subgeneric relationships of *Collybia* and other supraspecific morpho-ecological groups of *Collybia* subgen. *Collybia*

Description: Basidiomes large, clitocyboid. Pileus 5–7 cm in diam, applanate with slightly depressed disc and faint umbo at center; surface white-pruinose, gray-brown (6C2–5), not hygrophanous; margin striate at very edge, straight; context moderately thick (0.3–0.5 cm thick), whitish (2A1). Lamellae decurrent, crowded, cream (1A2), broad (up to 0.5 cm high), at times forked, not intervenose; edges smooth. Stipe 4–5 × 0.6–0.8 cm, nearly equal, hollow; surface longitudinally whitish-fibrillose or slightly tomentose

with grayish (4B2) background; base not inflated, strongly white-tomentose; context whitish (2A1).

Basidiospores [60/3/1] (4.5)5–6.5(7) × 3–4.5(5) μm, Q = (1.11)1.27–1.67(1.71), Qm = 1.48 ± 0.11, ellipsoid in majority, smooth, hyaline, thin-walled, inamyloid, almost always single. Basidia 23–33 × 5–7 μm, clavate, 4-spored, hyaline, thin-walled; sterigmata up to 5 μm long. Cystidia absent. Lamella trama more or less regular; hyphae 3–8(11) μm wide, hyaline, cylindrical, thin-walled. Pileipellis a cutis made up of nearly parallel, thin-walled, cylindrical hyphae

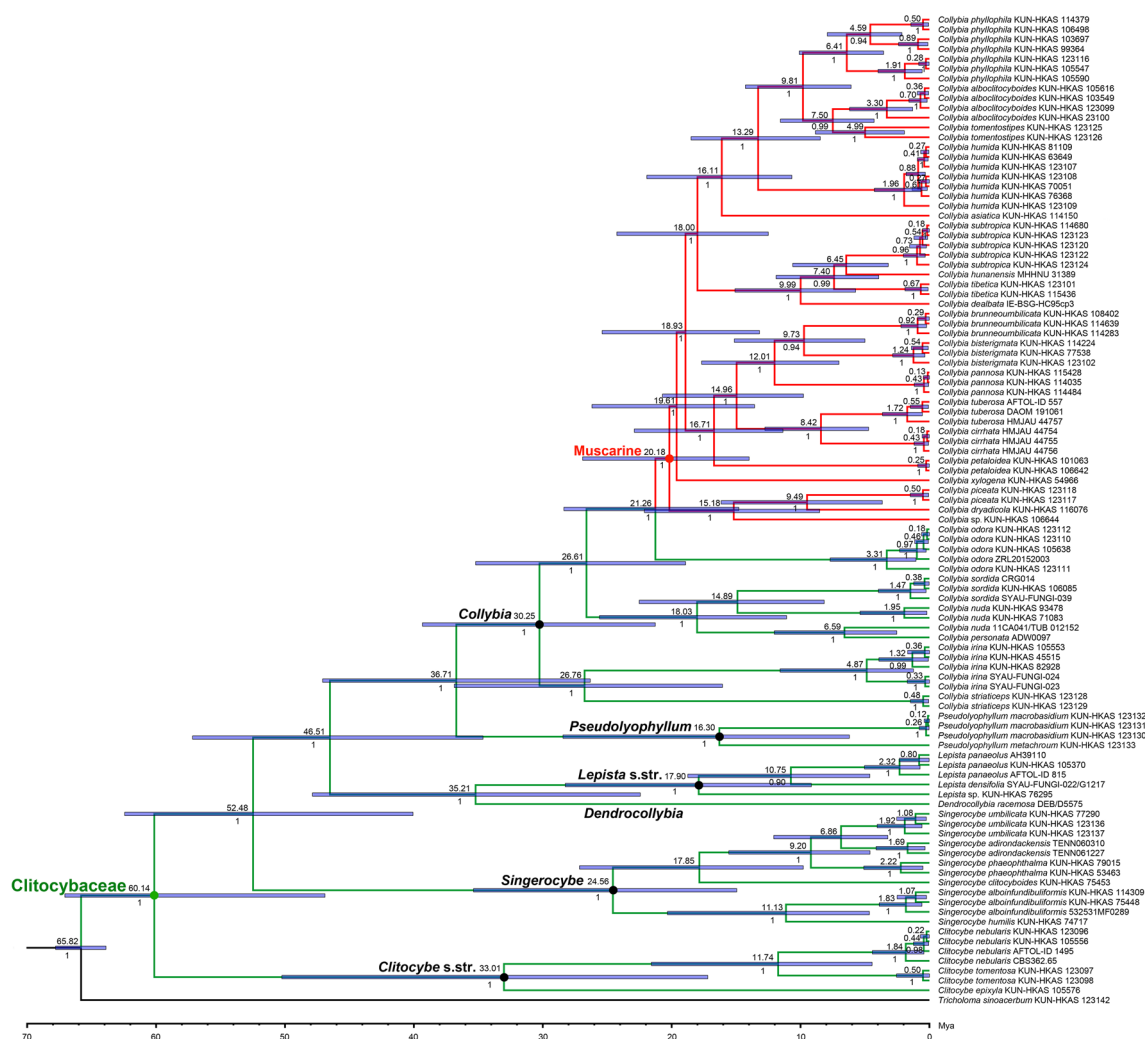


Fig. 5 MCC tree of Clitocybeaceae based on the combined ITS-LSU-TEF1-RPB1-RPB2-ATP6 dataset, with *Tricholoma sinoacerbum* (Tricholomataceae) as outgroup. The estimated median divergence times and Bayesian posterior probabilities ≥ 0.90 are above and below

2.5–5 μm wide. Stipitipellis a cutis made up of parallel, thin-walled, cylindrical hyphae 2–6 μm wide, with some hyphoid caulocystidia 10–50 \times 2–3 μm and some of them forked. Clamp connections present in all parts of basidiome.

Ecology: Gregarious, on rotten wood, in high-montane zones; autumn.

Distribution: Known from temperate zones of North-western China and Kashmir Himalaya.

Notes: It is the only lignicolous member of *Clitocybe* s.str. so far. We found this species at a highland above 3,000 m. According to the phylogenetic analysis of ITS (Fig. 3), another sample from Kashmir Himalaya (MH930913) should be identified as *Cli. epixyla* as well (pairwise identity value = 99.83%). The collection sites imply that the species inhabits high-altitude environments.

each node, respectively. The 95% highest posterior density of divergence time is indicated as blue node bar. Red and green branches mean the presence and absence of muscarine, respectively

Clitocybe tomentosa Z.M. He & Zhu L. Yang, sp. nov. Figures 7c and 9

Mycobank: MB 847225.

Etymology: ‘*tomentosa*’ (Lat.), referring to the tomentose pileus surface.

Diagnosis: Differs from *Cli. nebularis* by its tomentose to hirsute pileus and two-layer pileipellis made up of an irregular suprapellis and a regular subpellis. Differs from *Cli. epixyla* by its terrestrial habit and basidiospores which often occur in tetrads.

Type: CHINA. YUNNAN PROVINCE: Nanhua County, Ailao Mountain, on broad leaf and needle litter, alt. 2,422 m, 18 Aug 2021, J.W. Liu 2318 (KUN-HKAS 123097, holotype).

Description: Basidiomes large, clitocyboid. Pileus 2–12 cm in diam, at first nearly applanate, then concave,

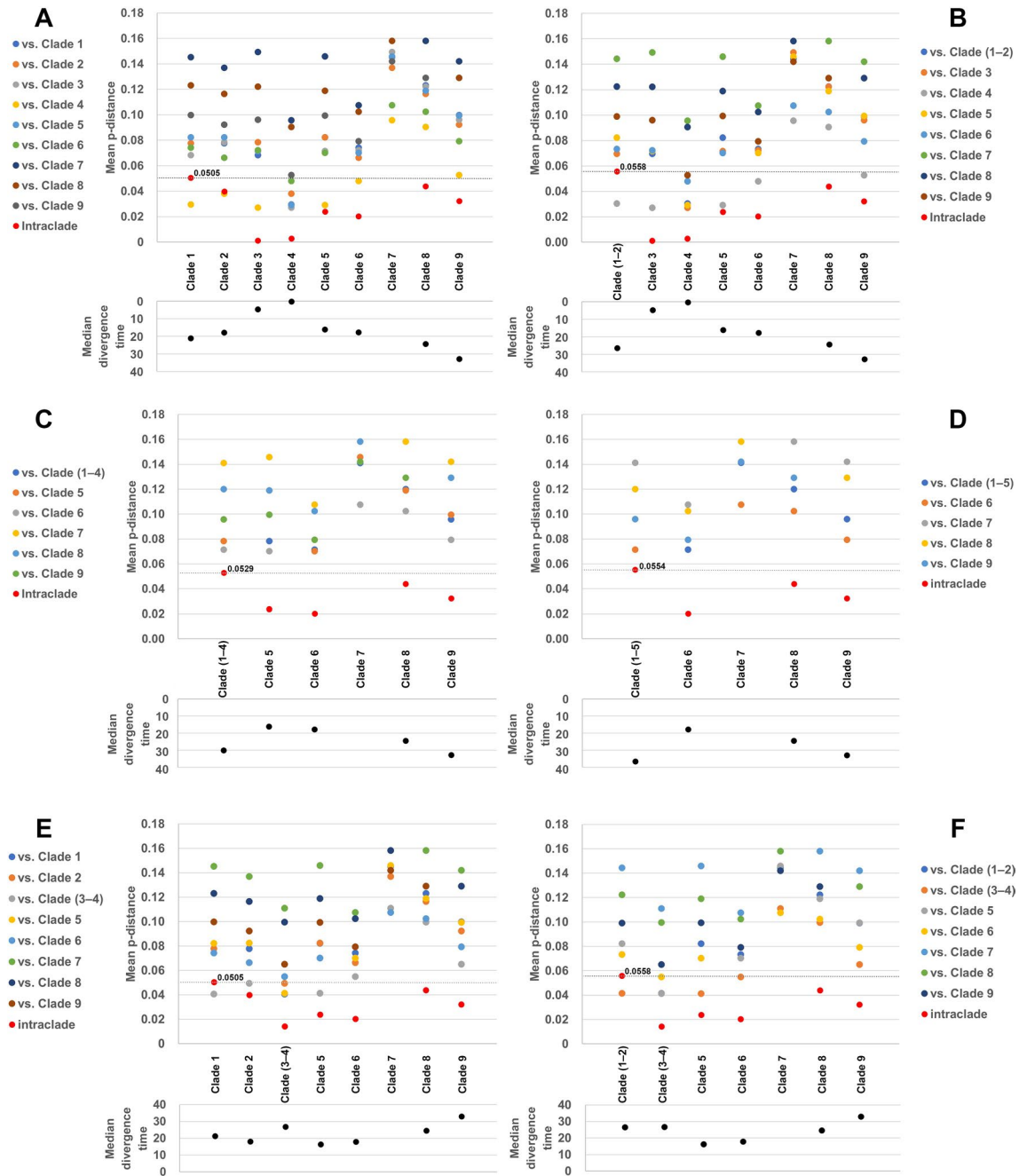


Fig. 6 Mean p-distances between and within different clades of Clitocybeae, as well as the median divergence times of the corresponding clades, calculated based on the combined ITS-LSU-*TEF1-RPB1-RPB2-ATP6* dataset

finally infundibuliform; surface tomentose, yellowish brown (5A2–5) to grayish brown (1B2–4), not hygrophanous; margin not striate, acute, at first inrolled, then incurved for a long time, becoming straight to reflexed and broadly undulate in age, with tomentose to spiny squamules; center depressed, sometimes inconspicuously gibbous, more or less darker in color than rest of pileus; context thick in center (up to 0.5 cm thick), nearly concolorous with pileus surface. Lamellae deeply decurrent, close, whitish (2A1) to

buff (1A2), narrow (about 0.2 cm high), at times forked; edges smooth. Stipe 3–9 × 1–3 cm, central, equal, hollow; surface fibrillose to tomentose, concolorous with pileus surface; base not inflated, strongly white-tomentose; context concolorous with stipe surface background.

Basidiospores [60/3/2] 4–5(5.5) × 2.5–3 μm, Q = (1.33)1.43–1.81(1.85), Qm = 1.62 ± 0.11, ellipsoid to elongate, smooth, hyaline, thin-walled, inamyloid, often adhering and appearing in tetrads. Basidia 23–33 × 5–6 μm,



Fig. 7 Basidiomes of representative species of Clitocybeaceae. **a** *Clitocybe epixyla* (KUN-HKAS 105576); **b** *Clitocybe nebularis* (KUN-HKAS 123096); **c** *Clitocybe tomentosa* (KUN-HKAS 123097); **d** *Collybia alboclitocybooides* (KUN-HKAS 123099); **e** *Collybia asiatica* (KUN-HKAS 114150); **f** *Collybia bisterigmata* (KUN-HKAS 77538); **g** *Collybia brunneoumbilicata* (KUN-HKAS 108402); **h** *Collybia cookei* (photographed by G. Wu); **i** *Collybia humida* (KUN-HKAS 76368); **j** *Collybia hunanensis* (MHHNU 31389); **k** **l** *Collybia irina* (KUN-HKAS 105553); **m** *Collybia nuda* (KUN-HKAS 71083); **n** *Collybia odora* (KUN-HKAS 123111); **o** *Collybia pannosa* (KUN-HKAS 115428); **p** *Collybia petaloidea* (KUN-HKAS 101063); **q** *Collybia phyllophila* (KUN-HKAS 105547); **r** *Collybia piceata* (KUN-HKAS 123117); **s** *Collybia striaticeps* (KUN-HKAS 123129); **t** *Collybia subtropica* (KUN-HKAS 123120); **u** *Collybia tibetica* (KUN-HKAS 115436); **v** *Collybia tomentostipes* (KUN-HKAS 123126); **w** *Collybia xylogena* (KUN-HKAS 54966); **x** *Lepista panaeolus* (KUN-HKAS 105370); **y** *Lepista* sp. (KUN-HKAS 76295); **z** *Pseudolyophyllum macrobasidium* (KUN-HKAS 123130); **aa** *Pseudolyophyllum metachroum* (KUN-HKAS 123133); **bb** *Singerocybe alboinfundibuliformis* (KUN-HKAS 114309); **cc** *Singerocybe umbilicata* (KUN-HKAS 123137). Bars = 3 cm

cylindro-clavate, 4-spored, hyaline, thin-walled; sterigmata up to 4 µm long. Cystidia absent. Lamella trama subregular; hyphae 3–8(10) µm wide, hyaline, cylindrical, thin- to slightly thick-walled (up to 0.5 µm). Pileipellis composed of thin- to slightly thick-walled (up to 0.5 µm), cylindrical hyphae 3–6(8) µm wide, distinctly divided into two layers, outer layer a 5–15 µm thick suprapellis made up of extremely irregular elements, exhibiting compactly arranged, trichodermal elements at margin of pileus; subpellis made up of parallel elements. Stipitipellis composed of thin- to slightly thick-walled (up to 0.5 µm), cylindrical hyphae 3–7 µm wide; elements irregularly arranged in 5–10 µm thick suprapellis but becoming regularly arranged in subpellis. Clamp connections present in all parts of basidiome.

Ecology: Generally gregarious, more rarely solitary, sometimes in fairy rings, on broad leaf or needle litter, in mixed broad-leaved and coniferous forests; late summer and early autumn.

Distribution: Known from subtropical zones of Central and Southwestern China, also in Japan (Harada et al. 2021).

Additional specimen examined: CHINA. HUNAN PROVINCE: Sangzhi County, Badagong Mountain, on needle litter of *Cunninghamia lanceolata* (Lamb.) Hook., alt. 1,600 m, 17 Sep 2019, Z.H. Chen, MHHNU 31581. YUNNAN PROVINCE: Yulong County, Tianchi National Nature Reserve, on needle and broad leaf litter, alt. 2,500 m, 29 Sep 2019, X.H. Wang 7537 (KUN-HKAS 123098).

Notes: This species is easily recognized by the tomentose to spiny squamules on its pileus surface. According to the phylogenetic analysis of ITS (Fig. 3), three Japanese samples (LC544097, LC544096 and LC544099), one Chinese sample (MZ057798) and another one probably from South Korea (MW291118) should also be identified as *Clitocybe*.

tomentosa (pairwise identity value $\geq 99.56\%$), indicating its wide distribution in East Asia.

Collybia (Fr.) Staude, Schwämme Mitteledeutschl. 1: xxviii, 119 (1857).

Basionym: *Agaricus* trib. *Collybia* Fr., Syst. mycol. (Lundae) 1: 9, 129 (1821).

= *Microcollybia* Lennox, Mycotaxon 9(1): 187 (1979).

= *Rubeolarius* Raitheh., Die Gattung *Clitocybe* (Stuttgart) 1: 16 (1981), Nom. inval., Art. 29.1 (Shenzhen).

Based on Singer (1986) and our morphological, phylogenetic and chemical findings, the genus is emended here.

Diagnosis: Similar to *Clitocybe* s.str., but distinguished by the fact that species of this genus producing large fleshy basidiomes typically possess finely verrucose basidiospores, whereas those with smooth basidiospores usually produce small thin basidiomes with basidiospores that are either weakly cyanophilic or cyanophobic.

Type species: *Collybia tuberosa* (Bull.) P. Kumm., Führ. Pilzk. (Zerbst): 119 (1871).

Description: Basidiomes clitocyboid, collybioid or tricholomatoid, veils absent, very small to large, containing muscarine if poisonous. Pileus convex, umbonate, appanate or depressed to funnel-shaped, white, whitish, cream, buff, brown, gray, blue, violet, lilac, purple or flesh-colored, usually smooth, glabrous, rarely tomentose, sometimes pruinose, often hygrophanous. Lamellae adnexed, emarginate, adnate to (sub)decurrent, white, whitish, cream, buff, beige or lilac in color. Stipe central, hollow or solid; surface concolorous with pileus or paler, smooth to fibrillose; base often tomentose, developing sclerotia in particular species. Spore print white, cream, yellow or pink. Basidiospores ellipsoid, inamyloid, weakly cyanophilic or completely cyanophobic if smooth, cyanophilic if finely verrucose. Basidia clavate or more or less clavate, 4-spored or 2-spored. Cystidia usually absent. Lamella trama regular or subregular. Pileipellis and stipitipellis usually a cutis, rarely trichoderm or possessing gelatinized hyphae. Muscarine present or absent.

Ecology: Usually gregarious or scattered, mostly saprotrophic, some species mycoparasitic, on broad leaf or needle litter, rotten wood and mushroom remnants, also on bare soil; mainly in summer and autumn.

Distribution: Almost cosmopolitan, widespread, known from Asia, Europe, North and West Africa, America and Oceania.

Notes: The close phylogenetic relationships between the genera *Collybia* s.str., *Clitocybe* and *Lepista*, and polyphyly status of the traditional concept of the latter two genera have been shown in previous studies (Moncalvo et al. 2002; Matheny et al. 2006; Binder et al. 2010; Sánchez-García et al. 2014; Alvarado et al. 2015, 2018a, b; He and Yang 2022). Based on our ITS, six-locus and 485-gene

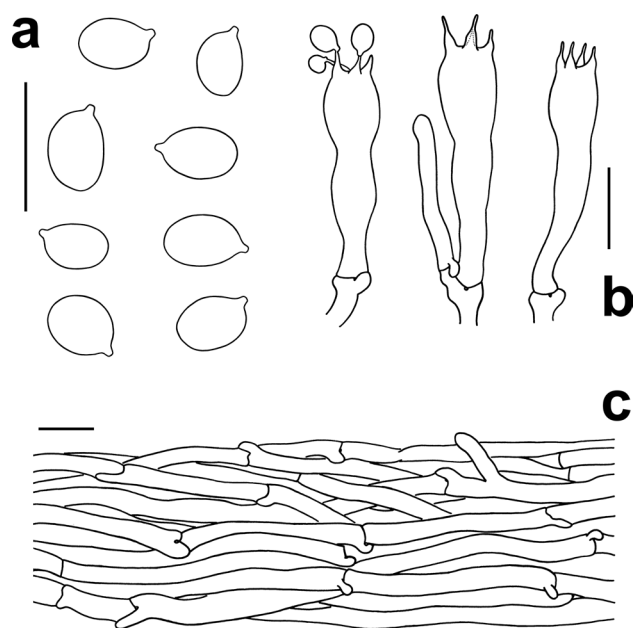


Fig. 8 Microscopic features of *Clitocybe epixyla* (KUN-HKAS 105576, holotype). **a** Basidiospores; **b** Basidia; **c** Pileipellis. Bars = 10 μ m

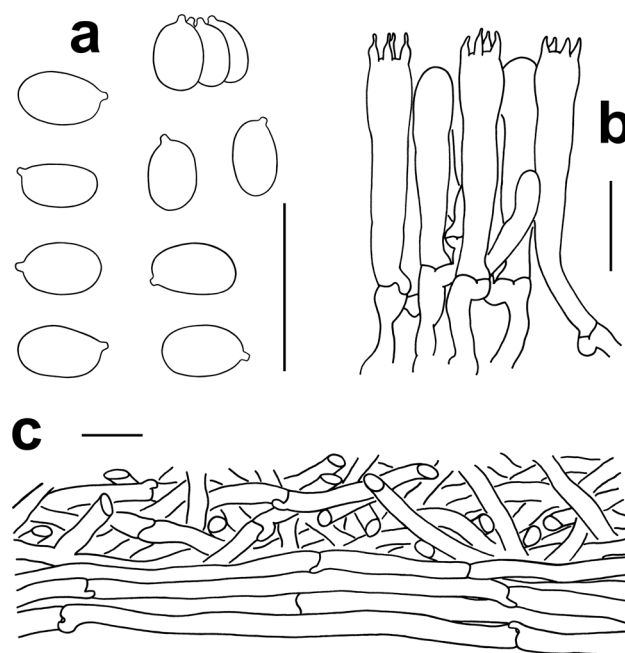


Fig. 9 Microscopic features of *Clitocybe tomentosa* (KUN-HKAS 123097, holotype). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μ m

phylogenetic analyses (Figs. 2, 3, 4), we have further clarified the positions of the three old genera and species distributions of these genera.

The results of the phylogenetic analyses of the DNA data suggest that five clades of previous *Clitocybe* (*C.* subgen. *Collybia* and *Macrosporocybe*, and *Pseudolyophyllum*) and *Lepista* (*C.* subgen. *Leucocalocybe* and *Crassicybe*) along with previous *Collybia* s.str. cluster together forming a monophyletic clade. Among these clades, the genetic distances between the first four nodes are low and distinctly less than that between the fourth node and the fifth node (Figs. 2 and 4B), which is an indication that the first four clades are closely related.

Traditionally, the primary characters used to distinguish between *Clitocybe* and *Lepista* were the attachment of the lamellae, spore print color, and ornamentation and cyanophily of the basidiospores (*Clitocybe*: decurrent, white, smooth, cyanophobic; *Lepista*: sinuate, pinkish, rough, cyanophilic). In fact, these morphological characters do not provide sufficient distinction between the first four clades of previous *Clitocybe* and *Lepista* species (Figs. 2 and 4B), because that: (i) lamellae of previous *Clitocybe* species (Clade 1) and *Lepista* species (Clade 4) can both be broadly adnate to subdecurrent (e.g., *Cli. dealbata* and *L. irina*, Breitenbach and Kränzlin 1991; Bigelow 1982); (ii) the spore print of *Leu. mongolica* nested in one *Lepista* clade (Clade 2) is white (Yu et al. 2011); (iii) basidiospores of *L. irina* (Clade 4) are slightly roughened or smooth (Bigelow and

Smith 1969); (iv) basidiospores of some previous *Clitocybe* species show a cyanophilic response to cotton blue (e.g., in *Cli. phyllophila* and *Cli. odora*, Harmaja 1976). However, clitocyboid taxa of the fifth clade, *Pseudolyophyllum*, can be differentiated from those of the other four clades generally by the gray-brown colors of the basidiomes, in particular of the lamellae.

We were surprised to find that not only clitocybes, but also *Collybia* s.str. species contain muscarine (Table 1). The concept of *Collybia* is expanded here to further encompass the first four clitocyboid and lepistoid clades previously treated as *Clitocybe*, *Collybia*, and *Lepista*, but exclude the fifth clade (Figs. 2 and 4B). These four clades are here considered subgenera of *Collybia* and are described in details below.

Key to the subgenera of *Collybia*

- 1 All of the basidiospores smooth.....2
- 1 All or some of the basidiospores not smooth.....3
- 2 Basidiospores usually 3–6 μ m long
.....*Collybia* subgen. *Collybia*
- 2 Basidiospores usually 6–10 μ m long
.....*Collybia* subgen. *Macrosporocybe*
- 3 Habit tricholomatoid; lamellae adnexed to emarginate
.....*Collybia* subgen. *Leucocalocybe*
- 3 Habit clitocyboid to tricholomatoid; lamellae adnate to (sub)decurrent*Collybia* subgen. *Crassicybe*

Collybia (Fr.) Staude subgenus *Collybia*

Diagnosis: Differs from subgen. *Crassicybe* and *Leucoalocybe* by the clitocyboid or collybioid basidiomes and smooth basidiospores. Differs from subgen. *Macrosporocybe* by the relatively smaller basidiospores. The vast majority of species in the subgenus are poisonous because of the presence of the neurotoxin muscarine.

Type species: *Collybia tuberosa* (Bull.) P. Kumm., Führ. Pilzk. (Zerbst): 119 (1871).

Description: Basidiomes clitocyboid or collybioid, gymnocarpic, tiny to large, but mostly small, containing or not containing (*C. odora*) muscarine. Pileus convex, umbonate, applanate or depressed to funnel-shaped, usually dull in color, such as white, whitish, cream, brownish and grayish, rarely bright in color (blue-green in *C. odora*), sometimes pruinose, often hygrophanous. Lamellae adnexed, emarginate, adnate to decurrent, white, whitish or other pale color. Clitocyboid species often depressed at center of pileus with adnate to decurrent lamellae while collybioid species usually developing convex to applanate pileus, sometimes somewhat depressed, with indistinctly decurrent but adnexed to emarginate lamellae. Stipe central, solid when young, later hollow; surface concolorous with pileus or paler, often longitudinally whitish-fibrillose; base often covered with white to whitish tomentum, developing sclerotia in particular species (*C. tuberosa* and *C. cookei*). Spore print usually white to cream. Basidiospores often small in size, single or in tetrads, more or less ellipsoid, hyaline, smooth, thin-walled, inamyloid, weakly cyanophilic or cyanophobic. Basidia clavate to narrowly clavate, usually 4-spored, rarely 2-spored. Cystidia usually absent. Lamella trama regular, rarely subregular. Pileipellis and stipitipellis usually arranged as a cutis, rarely an ixocutis.

Ecology: Usually clustered, grouped or scattered, more rarely solitary, saprotrophic or mycoparasitic, often on broad leaf or needle litter, also on soil, decaying logs and stumps or on fungal basidiomes; mainly growing in summer and autumn.

Distribution: Almost globally distributed, and especially widely distributed in temperate and subtropical zones of Asia, Europe and North America.

Notes: In previous studies (Noordeloos 1995; Hughes et al. 2001), *Collybia* s.str. referred to tiny, white-spored and sclerotium-producing fungi (except for *C. cirrhata*) growing on decayed remains of other fungi; it consisted of *C. tuberosa* (type species of the genus), *C. cookei* and *C. cirrhata*. Under this concept, *Collybia* is a monophyletic group, but here it is shown that it is nested in a larger monophyletic clade (*Collybia* subgen. *Collybia*) that also includes many subclades of previous *Clitocybe* species (Figs. 2 and 4), such as the well-known poisonous muscarine-containing species, *Cli. dealbata* and *Cli. phyllophila* (Genest et al. 1968).

Collybia subgen. *Collybia* clade is unique because all its members previously placed in *Clitocybe* and *Collybia* produce muscarine, except for the earliest diverging species *Cli. odora* (Table 1). Interestingly, this pattern is very similar to amanitin-producing *Amanita* sect. *Phalloideae* (Fr.) QuéL., in which the earliest diverging species of the sectional clade, *A. zangii* Zhu L. Yang, T.H. Li & X.L. Wu, does not contain amanitin (Cai et al. 2014).

Despite the distinct macroscopic and nutritional differences among the taxa in *Collybia* subgen. *Collybia*, they (i) share small, smooth, inamyloid and at least not strongly cyanophilic basidiospores; (ii) form a strongly supported monophyletic clade and exhibit close phylogenetic relationships; (iii) and all taxa (with one exception) contain the compound muscarine.

Key to the known species of *Collybia* subgenus *Collybia* in China

- | | |
|--|-----------------------------|
| 1 Basidiomes tiny (pileus ≤ 1.5 cm in diam) | 2 |
| 1 Basidiomes not tiny (pileus > 1.5 cm in diam) | 4 |
| 2 Sclerotia absent | <i>C. cirrhata</i> |
| 2 Sclerotia present | 3 |
| 3 Sclerotia fusiform or ellipsoid, dark purplish brown or reddish brown | <i>C. tuberosa</i> |
| 3 Sclerotia irregularly shaped, yellow–brown | <i>C. cookei</i> |
| 4 Basidiomes small (pileus 1.5–3 cm in diam) | 5 |
| 4 Basidiomes not small (pileus > 3 cm in diam) | 16 |
| 5 Habit lignicolous | <i>C. xylogena</i> |
| 5 Habit not lignicolous | 6 |
| 6 Basidia 2-spored | <i>C. bisterigmata</i> |
| 6 Basidia 4-spored | 7 |
| 7 Basidiospores in tetrads | 8 |
| 7 Basidiospores almost exclusively single | 11 |
| 8 Most of the basidiospores in tetrads; stipe surface tomentose to floccose | 9 |
| 8 Some of the basidiospores in tetrads; stipe surface fibrillose | 10 |
| 9 Pileus infundibuliform; pileus center deeply depressed | <i>C. asiatica</i> |
| 9 Pileus not infundibuliform; pileus center slightly depressed | <i>C. tomentostipes</i> |
| 10 Pileus felty; basidiospores ellipsoid to elongate; pileocystidia and caulocystidia absent | <i>C. pannosa</i> |
| 10 Pileus smooth; basidiospores elongate to cylindrical; pileocystidia and caulocystidia present | <i>C. brunneoumbilicata</i> |
| 11 Habitat alpine | 12 |
| 11 Habitat not alpine | 13 |
| 12 Pileus brown in color | <i>C. tibetica</i> |
| 12 Pileus white in color | <i>C. dryadicola</i> |
| 13 In open habitats | <i>C. dealbata</i> |
| 13 In forests | 14 |
| 14 In temperate zones | <i>C. piceata</i> |
| 14 In subtropical zones | 15 |

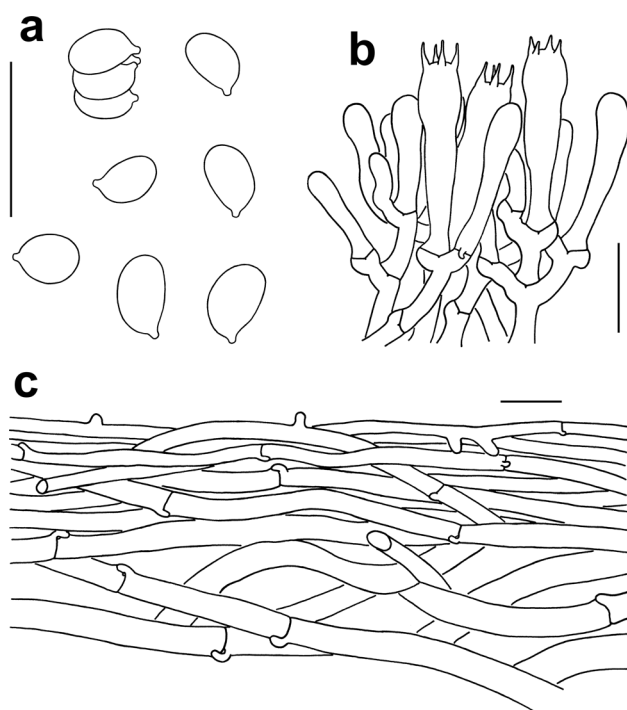


Fig. 10 Microscopic features of *Collybia alboclitocyboides* (KUN-HKAS 123099, holotype). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μ m

- 15 Pileus margin white *C. subtropica*
 15 Pileus margin yellowish brown *C. hunanensis*
 16 Basidiomes medium-sized (pileus 3–5 cm in diam) 17
 16 Basidiomes large (pileus > 5 cm in diam) 19
 17 Basidiomes blue-green *C. odora*
 17 Basidiomes brownish 18
 18 Only on rotten wood; basidiospores in tetrads and single *C. petaloidea*
 18 Mainly on needle or broad leaf litter; basidiospores mostly in tetrads *C. humida*
 19 Lamella trama regular; pileipellis with trichodermal hyphae *C. phyllophila*
 19 Lamella trama subregular; pileipellis without trichodermal hyphae *C. alboclitocyboides*

Collybia alboclitocyboides Z.M. He & Zhu L. Yang, sp. nov. Figures 7d and 10

Etymology: ‘*alboclitocyboides*’ (Lat.), referring to the white clitocyboid basidiome.

Diagnosis: Differs from *C. phyllophila* by its subregular lamella trama and completely repent hyphae in pileipellis.

Type: CHINA. YUNNAN PROVINCE: Shangri-La County, Bigutianchi, on needle litter, in a mixed coniferous forest of *Abies* sp. and *Picea* sp., alt. 3,844 m, 5 Sep 2018, J.W. Liu 1598 (KUN-HKAS 123099, holotype).

Description: Basidiomes medium-sized to large, clitocyboid. Pileus 3–8 cm in diam, plano-convex to applanate,

with slightly depressed center when mature; surface smooth, white (1A1) to dirty white (2A1), with brownish (5B2–5) to pinkish brown (5A2–3) spots or areas when watersoaked, slightly hygrophanous; margin not striate, at first involute, then uplifted and slightly undulate, becoming lobate and sometimes split when old; context thin at margin but thick at disc (up to 0.4 cm thick), light brown (4B2–3), watery. Lamellae (sub)decurrent, crowded, white (1A1) or appearing buff-tinged, arcuate, not broad (0.2–0.4 cm high), not forked; edges smooth. Stipe 2.5–5 \times 0.3–0.5 cm, central, equal or slightly enlarged at base, hollow; surface watersoaked, appearing light brown (4B4–6), covered with longitudinal white (1A1) fibrils; base sometimes white-tomentose; context light brown (5B2–4), watery.

Basidiospores [60/3/3] (3.5)4–5 \times 2.5–3(3.5) μ m, $Q = (1.27)1.29–1.67$, $Q_m = 1.52 \pm 0.13$, ellipsoid, smooth, hyaline, thin-walled, inamyloid, often in tetrads. Basidia 18–24 \times 4–5 μ m, clavate, 4-spored, hyaline, thin-walled; sterigmata up to 4 μ m long. Cystidia absent. Lamella trama subregular; hyphae 2–7(9) μ m wide, hyaline, cylindrical, thin-walled. Pileipellis nearly parallel-arranged, in places with some small outgrowths sometimes, becoming loose in subpellis, composed of thin- to slightly thick-walled (up to 0.5 μ m), cylindrical hyphae 2–8(10) μ m wide. Stipitipellis a cutis composed of slightly thick-walled (0.4–1 μ m) cylindrical hyphae 2–6(8) μ m wide. Clamp connections present in all parts of basidiome.

Ecology: Usually gregarious, rarely solitary, often on needle litter, in montane coniferous forests; autumn.

Distribution: Known from montane zones of Western China, also in France.

Additional specimens examined: CHINA. GANSU PROVINCE: Zhuoni County, on broad leaf and needle litter, in a mixed forest of *Abies* sp., *Picea* sp. and *Betula* sp., alt. 3,203 m, 12 Sep 2018, S.P. Jian 291 (KUN-HKAS 105616). SICHUAN PROVINCE: Kangding County, Waze Township, on needle litter, in a coniferous forest, alt. 3,487 m, 18 Sep 2017, S.P. Jian, 513301MF1051 (KUN-HKAS 103549). YUNNAN PROVINCE: Deqin County, Baimaxueshan Nature Reserve, on needle litter, in a coniferous forest, alt. 4,222 m, 3 Oct 2020, X.H. Wang 9495 (KUN-HKAS 123100).

Notes: Macroscopically, *C. alboclitocyboides* recalls *C. phyllophila* because of the large white basidiomes. The six-locus and 485-gene phylogenetic analyses (Figs. 2 and 4) show that the two taxa are closely related. However, *C. phyllophila* differs from *C. alboclitocyboides* by having regular lamella trama and upright or trichodermial hyphae in some places of pileipellis. *Collybia tomentostipes* is sister to *C. alboclitocyboides* (Figs. 2, 3, 4), but it can be easily differentiated by its smaller basidiomes than those of *C. alboclitocyboides*. The ITS phylogenetic tree of Clitocybaceae (Fig. 3) reveals that ‘*C. phyllophila*’ (KU836518) was misidentified and should be named *C. alboclitocyboides* (pairwise identity = 100%).

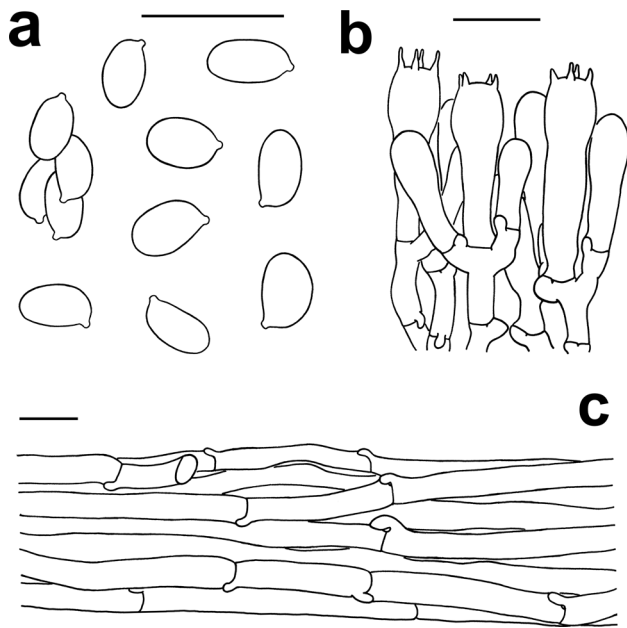


Fig. 11 Microscopic features of *Collybia asiatica* (KUN-HKAS 114150, holotype). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μ m

The ITS sequences of *C. alboclitocyboides* exhibit a 99.43% similarity to a French sequence identified as '*Clitocybe diatreta*' (GenBank No.: ON323016). *Clitocybe diatreta* (Fr.) P. Kumm. can be distinguished from *C. alboclitocyboides* by its smaller pileus, which appears pinkish or vinaceous when moist and pale pinkish on drying (Bigelow 1982; Kuyper 1995). The other relevant species, *Clitocybe leucodiatreta* Bon, differs from *C. alboclitocyboides* by its habitat preference for sandy soils and bare or grassy areas, slightly larger basidiospores, as well as the pileus color, which is pink-brown when moist and beige when dry (Breitenbach and Kränzlin 1991; GÜNGÖR et al. 2014).

Collybia asiatica Z.M. He & Zhu L. Yang, sp. nov. Figures 7e and 11

Mycobank: MB 847231.

Etymology: '*asiatica*' (Lat.), referring to the distribution of the species in Asia.

Diagnosis: Similar to *C. tomentostipes*, but differs from the latter in having an infundibuliform pileus with deeply depressed center, and the pileipellis is a regular cutis.

Type: CHINA. YUNNAN PROVINCE: Baoshan County, Wafang Township, Shiquan, on needle (*Pinus* sp.) and broad leaf litter, in a coniferous and broad-leaved mixed forest, alt. 2,199 m, 6 Aug 2019, Y.R. Ma 143 (KUN-HKAS 114150, holotype).

Description: Basidiomes small, clitocyboid. Pileus 2.5–3.5 cm in diam, at first convex, later expanding to appanate and center depressed with age to appear

infundibuliform; surface smooth, glabrous, whitish (2B1), with brown (5C2–6) spots or areas when watersoaked, slightly hygrophanous; margin not striate, usually strongly involute or at least incurved, becoming broadly undulate and split when old; context thin (0.1–0.2 cm thick), brownish (2B2). Lamellae decurrent, crowded, butter yellow (2A2), rarely forked, not broad (0.2–0.35 cm high), not intervenose; edges smooth. Stipe 2.5–3.5 \times 0.2–0.35 cm, central, equal, hollow, sometimes slightly curved; surface with whitish longitudinal fibrils on brownish (5B2–4) and watery background, white-floccose at apex; base covered with quite thick whitish mycelium.

Basidiospores [60/3/1] (4)4.5–6(6.5) \times (2.5)3–3.5(4) μ m, $Q = (1.29)1.38–1.93(2.1)$, $Q_m = 1.63 \pm 0.19$, ellipsoid to elongate, rarely cylindrical, smooth, hyaline, thin-walled, inamyloid, often occurring in tetrads. Basidia 15–26 \times 5–6.5 μ m, clavate, 4-spored, hyaline, thin-walled; sterigmata up to 3 μ m long. Cystidia absent. Lamella trama regular to subregular, with vacuoles in some hyphae; hyphae 3–8 μ m wide, hyaline, cylindrical, thin- to slightly thick-walled (0.5–0.8 μ m). Pileipellis a cutis made up of parallel, thin- to slightly thick-walled (0.5 μ m), cylindrical hyphae 3–6(8) μ m wide. Stipitipellis a cutis made up of parallel, thin- to slightly thick-walled (0.5 μ m), cylindrical hyphae 2.5–6(9) μ m wide. Clamp connections present in all parts of basidiome.

Ecology: Gregarious, on needle or broad leaf litter, in montane forests; summer.

Distribution: Known from subtropical zones of Southwestern China, also found in South Korea (Cho et al. 2020).

Notes: According to our phylogenetic analysis based on ITS sequences (Fig. 3), the Chinese sample of *C. asiatica* and the Korean sample of '*Clitocybe* sp.' (MN294844, Clade 38) are conspecific.

Collybia bisterigmata Z.M. He & Zhu L. Yang, sp. nov. Figures 7f and 12

Mycobank: MB 847227.

Etymology: '*bisterigmata*' (Lat.), referring to the basidia with two sterigmata.

Diagnosis: It differs from *C. subtropica* by having 2-spored basidia and many inflated hyphae in the lamella trama.

Type: CHINA. Tibet: Motuo County, Gelin Village, on broad leaf and needle litter, in a mixed broad-leaved and coniferous forest, alt. 1,800 m, 12 Dec 2018, X. Xu 412 (KUN-HKAS 123102, holotype).

Description: Basidiomes small, clitocyboid. Pileus 2–3.2 cm in diam, plano-convex to appanate, also infundibuliform sometimes; surface glabrous, often with some white pruina, especially at margin, off-white (1A2) when dry, becoming light brown (4B2) at places where are moist, hygrophanous; margin sometimes striate when wet, often

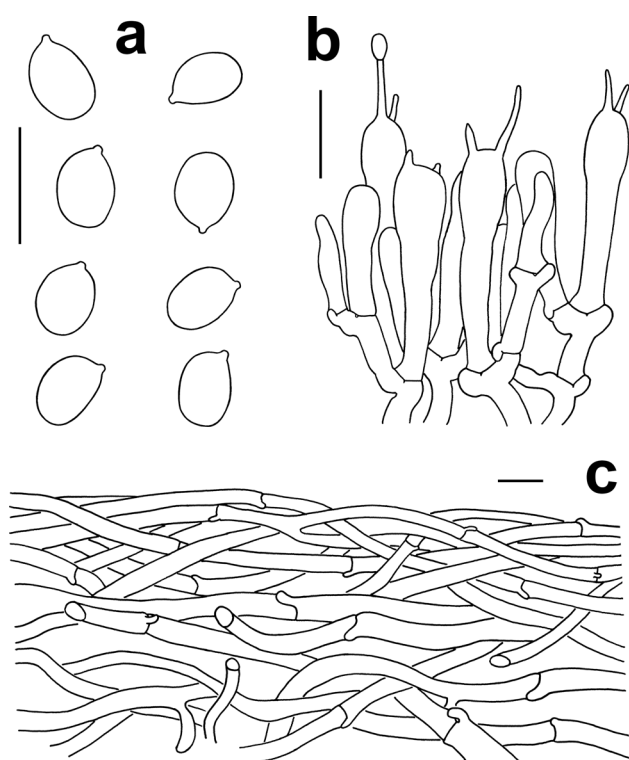


Fig. 12 Microscopic features of *Collybia bisterigmata* (KUN-HKAS 123102, holotype). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μ m

incurved; context thin (0.1–0.2 cm thick), concolorous with pileus surface. Lamellae subdecurrent, subdistant to crowded, white (1A1), arcuate, narrow (0.1–0.2 cm high); edges even. Stipe 2.5–3.2 \times 0.2–0.3 cm, central, equal, hollow, sometimes somewhat curved; surface and inside concolorous with pileus; base sometimes tomentose.

Basidiospores [60/3/3] 6–7.5(8) \times 4–6 μ m, $Q = (1.16)1.18–1.55(1.7)$, $Q_m = 1.33 \pm 0.13$, broadly ellipsoid (a large proportion) to ellipsoid, rarely elongate, smooth, hyaline, thin-walled, inamyloid, single. **Basidia** 18–32 \times 5–8 μ m, cylindro-clavate, 2-spored, hyaline, thin-walled; sterigmata up to 16 μ m long. **Cystidia** absent. **Lamella trama** subregular, loose; **hyphae** 4–30 μ m wide, hyaline, thin- to slightly thick-walled (0.5 μ m), cylindrical and many inflated. **Pileipellis** a cutis, subregularly arranged, becoming somewhat loose in subpellis, made up of thin- to slightly thick-walled (0.5–1 μ m) cylindrical hyphae 2–10 μ m wide. **Stipitipellis** a cutis made up of thin- to slightly thick-walled (0.5 μ m), cylindrical, 3–8 μ m wide hyphae. **Clamp connections** present in all parts of basidiome.

Ecology: Usually in clusters of 2–3 basidiomes, on ground litter or soil; autumn and winter.

Distribution: Only known from subtropical zones of Southwestern China.

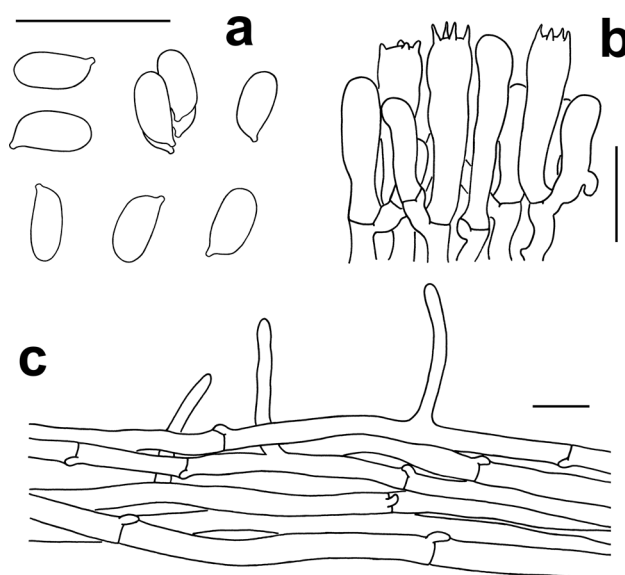


Fig. 13 Microscopic features of *Collybia brunneoumblicata* (KUN-HKAS 108402, holotype). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μ m

Additional specimens examined: CHINA. YUNNAN PROVINCE: Binchuan County, Jizu Mountain, on rotten wood, in a mixed broad-leaved and coniferous forest of *Lithocarpus* sp., *Castanopsis* sp., *Pinus yunnanensis* Franch., *P. armandii* Franch. and *P. tabuliformis* Carrière, alt. 2,280 m, 20 Sep 2012, K. Zhao 188 (KUN-HKAS 77538); Fugong County, Yaping Village, on soil among herbs, at the edge of a forest of *Quercus* sp., alt. 2,485 m, 19 Aug 2020, Y.R. Ma 246 (KUN-HKAS 114224).

Notes: This species can be found on various substrates, such as needle or broad leaf litter, soil and rotten wood. It clusters together with *C. brunneoumblicata* and *C. pannosa* forming Clade III of *Collybia* subgen. *Collybia* (Fig. 4). The members of this clade have basidiospores which present both in tetrads and single, while *C. bisterigmata* is exceptional, with single basidiospores possibly caused by its 2-spored feature. It differs from another macroscopically similar species *C. subtropica* by having 2-spored basidia, and differs from the other 2-spored species *C. xylogena* by having many inflated hyphae in the lamella trama.

Collybia brunneoumblicata Z.M. He & Zhu L. Yang, sp. nov. Figures 7g and 13

Mycobank: MB 847228.

Etymology: ‘*brunneoumblicata*’ (Lat.), referring to the brownish umbilicate pileus.

Diagnosis: Differs from other species of the subgenus by the presence of hyphoid pileocystidia and caulocystidia, as well as elongated to cylindrical basidiospores, some of which adhere in tetrads.

Type: CHINA. YUNNAN PROVINCE: Lvchun County, on rich soil among herbs, in a broad-leaved forest, alt. 1,841 m, 13 Aug 2019, Q. Cai, 532531MF0294 (KUN-HKAS 108402, holotype).

Description: Basidiomes small, clitocyboid. Pileus 1.5–4 cm in diam, (sub)umbilicated; surface smooth, sometimes covered with a white pruina, brownish (5B3–6) to pinkish brown (5A2–3), hygrophonous, whitish (2A1) when dry; margin usually translucently striate, inrolled or incurved; context thin (0.1–0.2 cm thick), watery, concolorous with pileus surface. Lamellae (sub)decurrent, spaced to somewhat crowded, whitish (2A1), appearing buff (1A2) or yellowish brown (4A2–3) tinge, arcuate, narrow (0.1–0.2 cm high), not forked or intervenose; edges smooth. Stipe 2–6 × 0.15–0.4 cm, central, equal, often slightly curved, fragile, hollow; surface nearly smooth, finely white-fibrillose longitudinally, concolorous with pileus surface; base not inflated, faintly tomentose; context concolorous with stipe surface, watery.

Basidiospores [60/3/3] 4–5(5.5) × 2–2.5(3) μm, Q = (1.67)1.7–2.43(2.5), Qm = 2.02 ± 0.21, elongate to cylindrical, smooth, hyaline, thin-walled, inamyloid, some of them in tetrads. Basidia 15–20 × 4–5 μm, narrowly clavate to cylindrical, 4-spored, hyaline, thin-walled; sterigmata up to 4 μm long. Pleurocystidia and cheilocystidia absent. Lamella trama regular; hyphae 3–9(12) μm wide, hyaline, cylindrical, thin- to slightly thick-walled (up to 0.5 μm). Pileipellis nearly parallel-arranged, with intracellular light brown pigment, in place with solitary or clustered, narrowly cylindrical pileocystidia 20–25 × 2–2.5 μm, composed of thin- to slightly thick-walled (about 0.5 μm), cylindrical hyphae 3–8(10) μm wide. Stipitipellis a cutis, existing some curved hyphoid caulocystidia (15–36 × 2–2.5 μm) at outer surface, composed of parallel, thin- to slightly thick-walled (0.5–1 μm), cylindrical hyphae 2–7(10) μm wide. Clamp connections present in all parts of basidiome.

Ecology: Gregarious, on soil of broad-leaved forests; late summer.

Distribution: Known from subtropical zones of Southwestern China.

Additional specimens examined: CHINA. YUNNAN PROVINCE: Lushui County, Pianma Town, on soil, under trees of *Alnus nepalensis* D. Don, alt. 2,499 m, 4 Aug 2019, T.X. Xu 272 (KUN-HKAS 114639); Lushui County, Pianma Town, on soil among mosses, under trees of *Castanopsis delavayi* Franch., alt. 2,097 m, 24 Aug 2020, Y.R. Ma 307 (KUN-HKAS 114283).

Notes: The elongate to cylindrical basidiospores, and presence of pileocystidia and caulocystidia make *C. brunneoumbilicata* unique among the *Collybia* species which generally have ellipsoid basidiospores and no cystidia. In the phylogenetic analysis of ITS (Fig. 3), the three Chinese samples of '*Cli. minutella*' (MW725545, MW724286 and

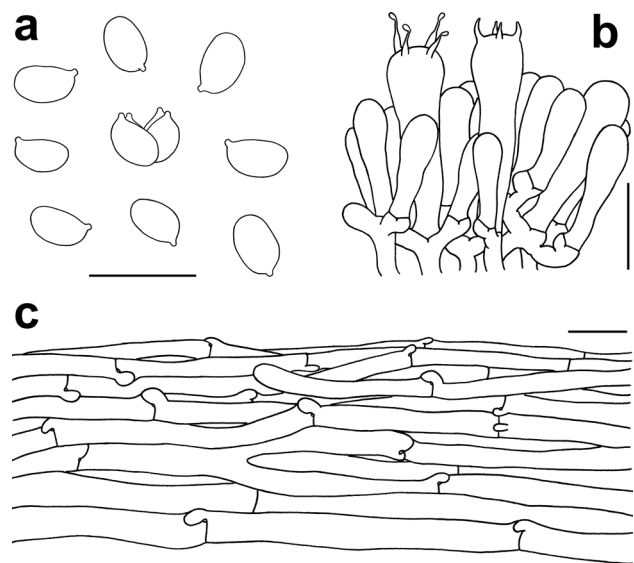


Fig. 14 Microscopic features of *Collybia humida* (KUN-HKAS 123107, holotype). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μm

MH141992) should also be identified as *C. brunneoumbilicata* because they cluster together with the new species almost without genetic differences (pairwise identity value > 99%). *Clitocybe minutella* Har. Takahashi, originally described from Japan, has a tiny non-hygrophonous pileus, 1- or 2-spored basidia, and basidiospores measuring 6–7.5 × 3.5–4 μm (Takahashi 2003). In contrast, *C. brunneoumbilicata* has a small hygrophonous pileus, 4-spored basidia, and basidiospores measuring 4–5 × 2–2.5 μm.

Collybia humida Z.M. He & Zhu L. Yang, sp. nov. Figures 7i and 14

MycoBank: MB 847230.

Etymology: '*humida*' (Lat.), referring to the very wet basidiomes.

Diagnosis: Characterized by its smoky grayish brown basidiomes, which are usually in watery condition; resembles *C. brunneoumbilicata* but differs in having ellipsoid to elongate basidiospores and the lack of pileocystidia and caulocystidia.

Type: CHINA. YUNNAN PROVINCE: Kunming City, Qipan Mountain, on needle litter, in a subtropical forest, alt. 1,920 m, 25 Jul 2020, Z.M. He 34 (KUN-HKAS 123107, holotype).

Description: Basidiomes medium-sized, clitocyboid. Pileus 1–5.5 cm in diam, convex to applanate; surface smooth, glabrous, brownish (1B2–6) at margin and smoky grayish brown (4D3–6) at disc in moist condition, strongly hygrophonous and becoming whitish (2A1) on drying; center often slightly depressed, or shallowly umbonate, distinctly darker in color; margin often revolute, usually distinctly

or not distinctly striate when wet, but striation disappearing when dry; context watery, thin (about 0.2 cm thick), concolorous with pileus surface. Lamellae subdecurrent, crowded, white (1A1) or appearing light buff (1A2), arcuate, narrow (about 0.2 cm high), sometimes furcate; edges even. Stipe 2–7 × 0.2–1 cm, central, (sub)cylindrical, sometimes slightly flexuous, hollow; surface smooth, watery, glabrous, finely longitudinally striate, concolorous with pileus; context watery, concolorous with stipe surface; base not inflated, finely tomentose. Odor fungoid and pleasant.

Basidiospores [60/3/3] 5–6.5(7) × 3–4 μm, $Q = (1.39)1.42–1.87(1.88)$, $Q_m = 1.65 \pm 0.14$, (broadly) ellipsoid to elongate, somewhat amygdaliform, smooth, hyaline, thin-walled, inamyloid, often in tetrads. **Basidia** 18–27 × 5–6 μm, clavate, 4-spored, hyaline, thin-walled; sterigmata up to 4 μm long. **Cystidia** absent. **Lamella trama** regular; hyphae 4–16 μm wide, hyaline, cylindrical, thin-walled. **Pileipellis** a cutis made up of parallel, thin- to slightly thick-walled (about 0.5 μm), cylindrical hyphae 3–16 μm wide. **Stipitipellis** a cutis made up of parallel, thin- to slightly thick-walled (0.5–1 μm), cylindrical hyphae 3–18 μm wide. **Clamp connections** present in all parts of basidiome.

Ecology: Usually gregarious in clusters of 2–5 basidiomes, rarely solitary, on decaying fallen needles or leaves, rarely on wood, in subtropical forests; summer.

Distribution: Known from Southwestern China, also in Europe ((Alvarado et al. 2015).

Additional specimens examined: CHINA. YUNNAN PROVINCE: Kunming City, Qiongzhusi, on broad leaf litter, in a mixed broad-leaved forest, alt. 1,900 m, 25 Jul 2020, Z.M. He 24 (KUN-HKAS 123109); Kunming City, Qipan Mountain, on broad leaf litter, in a mixed broad-leaved and coniferous forest, alt. 1,900 m, 25 Jul 2020, Z.M. He 32 (KUN-HKAS 123108); Kunming City, around Yeya Lake, on needle litter, in a mixed forest dominated by conifers, alt. 2,000 m, 9 Jul 2013, J. Qin 671 (KUN-HKAS 81109); Lijiang City, Xiang Mountain, among underlayer of Fagaceae, in a forest dominated by *Pinus yunnanensis*, alt. 2,500 m, 30 Jul 2011, Q. Cai 455 (KUN-HKAS 70051); Ninglang County, around Lugu Lake, on needle litter, in a mixed broad-leaved and coniferous forest, alt. 2,650 m, 10 Jul, 2010, J. Qin 14 (KUN-HKAS 63649). SICHUAN PROVINCE: Muli County, on a tree trunk, in a mixed broad-leaved and coniferous forest consisting of *Quercus semecarpifolia* Sm., *Picea* sp. and Ericaceae sp., alt. 3,500 m, 1 Aug 2012, Y.J. Hao 710 (KUN-HKAS 76368).

Notes: This species is widespread in Southwestern China. It is capable of thriving on both leaf litter and wood substrates. Basidiomes of *C. humida* are always strongly hygrophanous, making it easily to be recognized. Phylogenetically, it is nested in Clade I of *Collybia* subgen. *Collybia* (Fig. 4), a group whose members have basidiospores mostly in tetrads. According to our analysis of ITS sequences

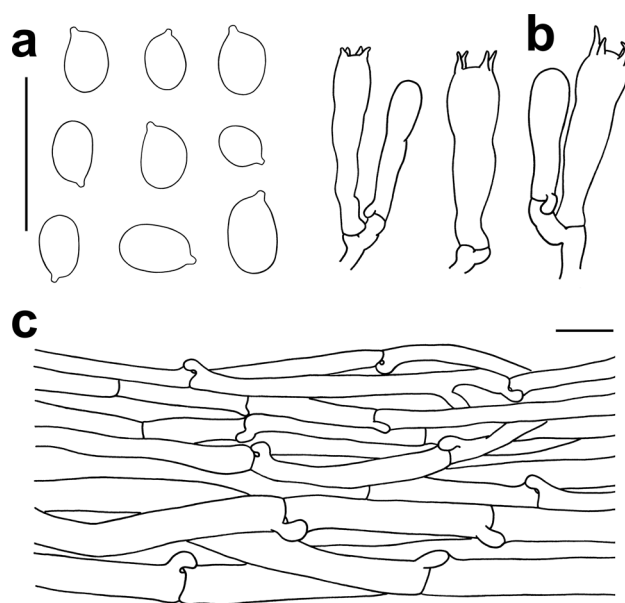


Fig. 15 Microscopic features of *Collybia hunanensis* (MHHNU 31389, holotype). **a** Basidiospores; **b** Basidia; **c** Pileipellis. Bars = 10 μm

(Fig. 3), sequence KJ680984 (from collection AH42906) shares a 99% similarity with the sequence of the new species, and could be identified as *C. humida* as well. This means that the species is widely distributed and could also occur in Europe. The ITS sequence similarity between *C. humida* and '*Cli. subditopoda*' (KM453734) ranges from 98.79% to 99.55%. However, *Cli. subditopoda* Peck can be distinguished from *C. humida* by its gray lamellae and farinaceous odor (Bigelow 1982).

Collybia hunanensis Z.M. He, Z.H. Chen & Zhu L. Yang, sp. nov. Figures 7j and 15

Mycobank: MB 847240.

Etymology: '*hunanensis*' (Lat.), referring to the type locality in Hunan Province, China.

Diagnosis: Similar to *C. dealbata* and *C. subtropica*, but differs in having a yellowish brown pileus lacking pruina on the surface.

Type: CHINA. HUNAN PROVINCE: Zixing County, on needle and broad leaf litter, alt. ca. 800 m, 21 Nov 2018, Z.H. Chen, MHHNU 31389 (holotype).

Description: Basidiomes small, clitocyboid. Pileus 1.5–3 cm in diam, applanate with slightly depressed center; surface smooth, glabrous, yellowish brown (4B4–8), hygrophanous; margin not distinctly striate, straight to reflexed, undulate and split in age; context thin, watery, concolorous with pileus surface. Lamellae (deeply) decurrent, crowded, off-white (1B1) to light brown (3B3), narrow to slightly broad (0.2–0.4 cm high), sometimes forked, not intervenose; edges smooth. Stipe 2–3 × 0.3–0.8 cm,

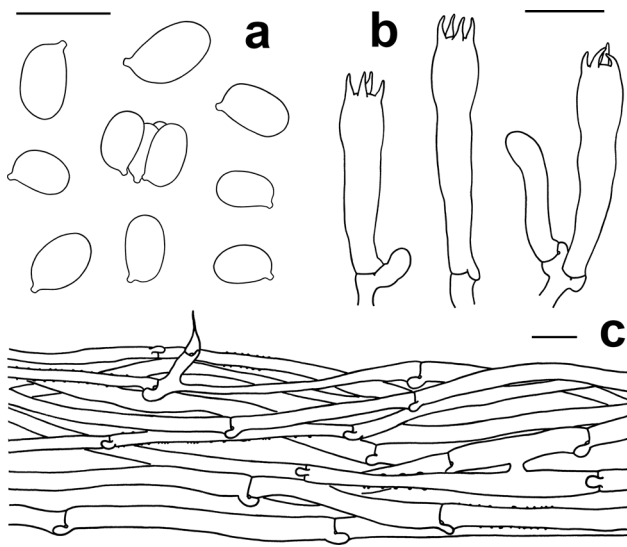


Fig. 16 Microscopic features of *Collybia odora* (KUN-HKAS 123111). **a** Basidiospores; **b** Basidia; **c** Pileipellis. Bars = 10 μ m

subcylindrical, enlarged at base, hollow, sometimes curved; surface smooth, glabrous, concolorous with pileus surface; base inflated, slightly whitish-tomentose; context watery, concolorous with stipe surface.

Basidiospores [60/3/1] (3)3.5–5 \times 2–3 μ m, $Q=(1.3)1.3$ –1.75(1.82), $Q_m=1.5 \pm 0.13$, mostly ellipsoid, also elongate sometimes, smooth, hyaline, thin-walled, inamyloid, single. Basidia 16–20 \times 4–5 μ m, clavate, 4-spored, hyaline, thin-walled; sterigmata up to 4 μ m long. Cystidia absent. Lamella trama more or less regular; hyphae 2–6(8) μ m wide, hyaline, cylindrical, thin-walled. Pileipellis a cutis made up of parallel, thin- to slightly thick-walled (up to 0.5 μ m), cylindrical hyphae 3–8(10) μ m wide. Stipitipellis a cutis made up of parallel, thin- to slightly thick-walled (about 0.5 μ m), cylindrical hyphae 3–8 μ m wide. Clamp connections present in all parts of basidiome.

Ecology: Gregarious, on needle or broad leaf litter, in mixed broad-leaved and coniferous forests; Autumn.

Distribution: Only known from subtropical zones of Central China.

Notes: In China, the consumption of *C. hunanensis* basidiomes led to a mushroom poisoning and hospitalization of seven individuals (Li et al. 2021a, b, c, d). The sample MHHNU 31389 was collected by us from the scene, and here we have confirmed its muscarine content to be up to 165 mg/kg (dry weight, Table 1) using LC–MS/MS analysis.

Collybia odora (Bull.) Z.M. He & Zhu L. Yang, comb. nov. Figures 7n and 16

Mycobank: MB 847233.

Basionym: *Agaricus odorus* Bull., Herb. Fr. (Paris) 4: tab. 176 (1784) [1783–84].

\equiv *Gymnopus odorus* (Bull.) Gray, Nat. Arr. Brit. Pl. (London) 1: 606 (1821).

\equiv *Clitocybe odora* (Bull.) P. Kumm., Führ. Pilzk. (Zerbst): 121 (1871).

\equiv *Lepista odora* (Bull.) Harmaja, Karstenia 15: 15 (1976).

\equiv *Rubeolarius odorus* (Bull.) Raithelh., Die Gattung *Clitocybe* (Stuttgart) 1: 17 (1981).

\equiv *Agaricus trogii* Fr., Epicr. syst. mycol. (Upsaliae): 59 (1838).

\equiv *Clitocybe trogii* (Fr.) Sacc., Syll. fung. (Abellini) 5: 153 (1887).

\equiv *Agaricus virens* Scop., Fl. carniol., Edn 2 (Wien) 2: 437 (1772).

\equiv *Mycena virens* (Scop.) Quéél., Forh. Vidensk.-Selsk. Kristiania: 35 (1886).

\equiv *Clitocybe virens* (Scop.) Sacc., Syll. fung. (Abellini) 5: 152 (1887).

\equiv *Agaricus viridis* Huds., Fl. Angl., Edn 2 2: 614 (1778).

\equiv *Clitocybe viridis* (Huds.) Gillet, Hyménomycètes (Alençon): 158 (1874) [1878].

\equiv *Agaricus moschatus* J.F. Gmel., Syst. Nat., Edn 13 2(2): 1416 (1792).

\equiv *Agaricus anisatus* Pers., Observ. mycol. (Lipsiae) 1: 44 (1796).

Diagnosis: Differs from other species of the subgenus by its blue-green basidiomes and absence of muscarine.

Description: Basidiomes medium-sized, clitocyboid. Pileus 3–5 cm in diam, at first convex, later plano-convex to applanate; surface finely radially fibrillose, usually blue-green (25A3–6), sometimes pallid to whitish (2A1), not or indistinctly hygrophanous; margin not striate, inrolled or incurved, becoming undulate in age; center shallowly depressed or gibbous; context not thick (0.2–0.3 cm thick), whitish (2A1). Lamellae adnate to subdecurrent, usually crowded to close, sometimes appearing subdistant when young, cream (1A2) or sometimes light gray-green (24A2), not broad (0.2–0.4 cm high), rarely forked or intervenose; edges slightly undulate. Stipe 3–6 \times 0.5–1 cm, central, cylindrical, sometimes slightly curved, hollow; surface longitudinally whitish-fibrillose or slightly tomentose with light brown (4B2–3) or bluish green (25A3) background; base not inflated, strongly white-tomentose. Odor strong, like anise.

Basidiospores [60/3/3] (5.5)6–8.5(10.5) \times (3.5)4–5(6) μ m, $Q=(1.33)1.46$ –1.85(2), $Q_m=1.64 \pm 0.17$, ellipsoid to elongate, smooth, hyaline, thin-walled, inamyloid, sometimes in tetrads. Basidia 23–33 \times 6–8 μ m, clavate, 4-spored, hyaline, thin-walled; sterigmata up to 5 μ m long. Pleurocystidia and cheilocystidia absent. Lamella trama regular; hyphae 2–12(16) μ m wide, hyaline, cylindrical, thin-walled. Pileipellis nearly parallel-arranged, made up of thin-walled cylindrical hyphae 2–6 μ m wide, some of which with faint epiparietal grainy pigment. Stipitipellis a cutis made up of parallel thin-walled cylindrical hyphae 2–7 μ m wide, also

with some narrowly cylindrical or filamentous caulocystidia $8\text{--}45 \times 2\text{--}3 \mu\text{m}$ on the surface. Clamp connections present in all parts of basidiome.

Ecology: Gregarious or scattered, on broad leaf or needle litter, also on soil; summer and autumn.

Distribution: Widespread in temperate and subtropical zones of the Northern Hemisphere.

Specimens examined: CHINA. GANSU PROVINCE: Zhuoni County, on soil, in a coniferous forest, alt. 2,990 m, 30 Aug 2020, S.W. Zhou, ZSW-GS (KUN-HKAS 123112). JILIN PROVINCE: Antu County, Erdaobaihe Town, on broad leaf litter, in a mixed broad-leaved and coniferous forest, alt. 750 m, 25 Aug 2018, X.X. Ding 358 (KUN-HKAS 105638); Antu County, Erdaobaihe Town, on broad leaf and needle litter, 25 Aug 2018, X. Xu 213 (KUN-HKAS 123110). YUNNAN PROVINCE: Yulong County, Lijiang Alpine Botanical Garden, on leaf litter of *Quercus aquifolioides* Rehd. & E. H. Wils., alt. 3,481 m, 10 Aug 2019, J.W. Liu, LJW-LJ (KUN-HKAS 123111).

Notes: Muscarine was not detected in basidiomes of *C. odora* as expected (Table 1), which is consistent with its descriptions of edibility in some field guides (Bon 1988; Phillips 1990). *Collybia odora* may hold significant evolutionary significance as the sole species lacks muscarine as basal within the *Collybia* subgen. *Collybia* clade. This species is easy to be identify because of its strong anise-like odor and distinctive bluish green to grayish green pileus colors. In our study, the ITS sequence of a collection with white basidiomes (KUN-HKAS 123110), microscopically indistinguishable from the blue-green ones (KUN-HKAS 105638, 123,111 and 123,112), is 100% similar to the ITS of blue-green basidiomes, indicating that both white and blue-green basidiomes of *C. odora* are present in the nature.

Collybia pannosa Z.M. He & Zhu L. Yang, sp. nov. Figures 7o and 17

MycoBank: MB 847234.

Etymology: ‘*pannosa*’ (Lat.), referring to the felty pileus surface.

Type: CHINA. TIBET: Chayu County, Zitaer, on needle litter of *Pinus* sp., alt. 3,110 m, 28 Jul 2019, Y.J. Hou, Zitaer1-36 (KUN-HKAS 115428, holotype).

Diagnosis: Similar to *Cli. fragrans*, but differs from the latter in having felty pileus, relatively smaller basidiospores and irregular-arranged pileipellis.

Description: Basidiomes small, clitocyboid. Pileus 1–3.5 cm in diam, (sub)infundibuliform; surface felty, more or less pruinose, whitish (2A1) when dry, yellowish brown (4A2–4) to brownish (4B2–4) at areas where are watersoaked, hygrophanous; margin not striate, at first inrolled, later incurved for a long time, rarely straight; center (slightly) depressed, distinctly darker in color; context thin (0.1–0.2 cm thick), watery, concolorous with pileus surface.

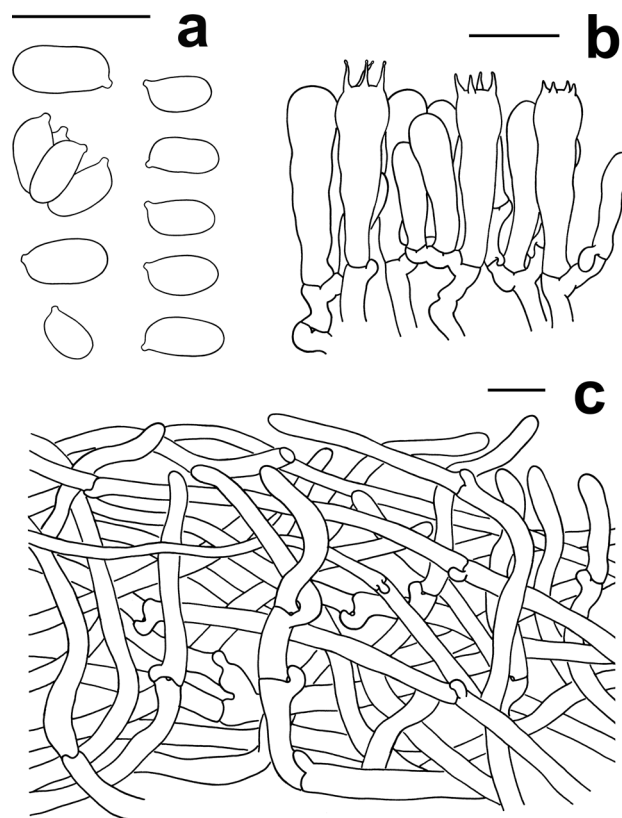


Fig. 17 Microscopic features of *Collybia pannosa* (KUN-HKAS 115428, holotype). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μm

Lamellae deeply decurrent, crowded, whitish (2A1), arcuate, narrow (0.1–0.2 cm high), sometimes forked, not interve-nose; edges smooth. Stipe 2–4 \times 0.15–0.4 cm, central, equal, hollow; surface covered with whitish longitudinal fibrils on yellowish brown (4A2) background; base not inflated, whitish-tomentose; context concolorous with stipe surface background, watery. Odor slightly fragrant.

Basidiospores [60/3/3] 4–6(7) \times 2.5–4 μm , $Q = (1.13)1.37\text{--}2.1(2.19)$, $Q_m = 1.74 \pm 0.24$, mostly elongate, also ellipsoid or cylindrical sometimes, smooth, hyaline, thin-walled, inamyloid, sometimes adhering in tetrads. Basidia 17–24 \times 4.5–6.5 μm , clavate, 4-spored, hyaline, thin-walled; sterigmata up to 3.5 μm long. Cystidia absent. Lamella trama regular; hyphae 2–7 μm wide, hyaline, cylindrical, thin-walled. Pileipellis composed of irregular, thin-walled, cylindrical hyphae 2–6 μm wide, with many erect hyphae and exserted ends. Stipitipellis composed of compactly parallel, thin- to slightly thick-walled (0.5 μm), cylindrical hyphae 2–6 μm wide. Clamp connections present in all parts of basidiome.

Additional specimens examined: CHINA. YUNNAN PROVINCE: Gongshan County, Bingzhongluo, on soil among mosses and herbs, alt. 2,450 m, 25 Jul 2019, T.X.

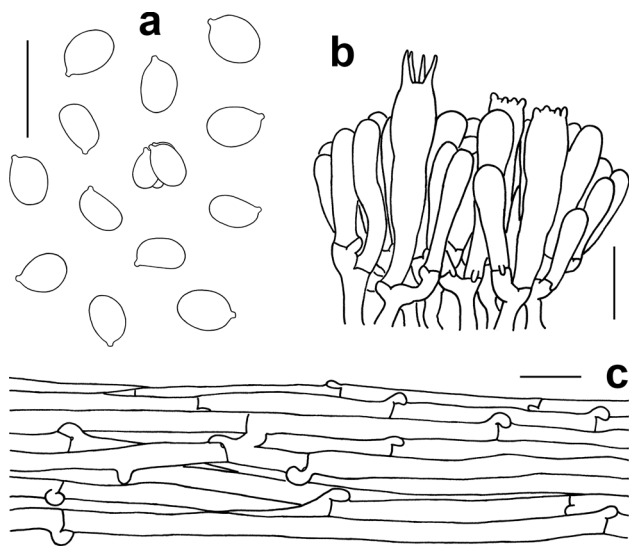


Fig. 18 Microscopic features of *Collybia petaloidea* (KUN-HKAS 101063, holotype). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μ m

Xu 102 (KUN-HKAS 114484); Gongshan County, Bingzhongluo, on needle litter of *Pinus* sp., alt. 2,455 m, 25 Jul 2019, Y.R. Ma 19 (KUN-HKAS 114035).

Ecology: Gregarious, on needle litter or soil, growing under montane pines; summer.

Distribution: Found in subtropical zones of Southwestern China, also reported in Poland and Italy (Osmundson et al. 2013).

Notes: The phylogenetic analysis based on ITS (Fig. 3) suggests that the four sequences (MZ410746, MK966594, MZ645940 and JF907811) of '*Cli. fragrans*' cluster together with our three Chinese sequences of the new species and these should be identified as *C. pannosa* (pairwise identity value > 99%). Among them, MZ410746 and JF907811 are respectively isolated from Poland and Italy, indicating *C. pannosa* is distributed in Europe as well. *Clitocybe fragrans* (With.) P. Kumm. differs from *C. pannosa* by its significantly larger basidiospores and basidia (Harmaja 1969: 6.2–8.6 \times 3.4–4.6 μ m; Bigelow 1982: 6.5–8.5 \times 3.5–4.5 μ m and 25–35 \times 5–8 μ m; Breitenbach and Kränzlin 1991: 6.4–9.5 \times 4–5.3 μ m and 25–33 \times 6.5–7.5 μ m; Kuyper 1995: 6.5–9 \times 3.5–5 μ m and 21–32 \times 5–8 μ m). *Clitocybe anisata* Velen. differs from *C. pannosa* in that its lamellae are conspicuously distant and broader, measuring up to 0.6 cm high (Harmaja 1969).

Collybia petaloidea Z.M. He & Zhu L. Yang, sp. nov. Figures 7p and 18

Mycobank: MB 847235.

Etymology: '*petaloidea*' (Lat.), referring to the petaloid pileus margin.

Diagnosis: Differs from the other lignicolous species *C. xylogena* by its petaloid pileus margin, 4-spored basidia, and ellipsoid basidiospores that occur both in tetrads and singly.

Type: CHINA. SICHUAN PROVINCE: Kangding County, Gonggashan Township, on a stump, in a mixed forest, alt. 2,829 m, 16 Sep 2017, S.P. Jian 74 (KUN-HKAS 101063, holotype).

Description: Basidiomes medium-sized, clitocyboid. Pileus 3–5.5 cm in diam, nearly applanate when young, then plano-convex, with depressed to subumbilicated center; surface smooth, glabrous, dark brown (5C6–8) at very center, (light) brown (5B2–4) elsewhere and whitish (2A1) to nearly buff (2A2) at very margin, sometimes hygrophanous; margin not striate, wavy when mature; context thin (0.1–0.2 cm thick), concolorous with pileus surface. Lamellae decurrent, crowded, white (1A1), arcuate, very narrow (about 0.1 cm high), at times forked; edges even. Stipe 4–6 \times 0.4–0.7 cm, central, nearly equal, tend to be slightly enlarged at base, hollow, often curved; surface finely white-tomentose, concolorous with pileus surface; context concolorous with stipe surface. Odor fresh and sweet.

Basidiospores [60/3/2] (4.5)5–6 \times 3–4(4.5) μ m, $Q = (1.25)1.32$ –1.76(1.88), $Q_m = 1.55 \pm 0.15$, ellipsoid to elongate, smooth, hyaline, thin-walled, inamyloid, some of them in tetrads. Basidia 22–30 \times 5–6 μ m, cylindro-clavate, 4-spored, hyaline, thin-walled; sterigmata up to 6 μ m long. Cystidia absent. Lamella trama more or less regular; hyphae 3–10(14) μ m wide, hyaline, cylindrical, thin- to slightly thick-walled (0.5–1 μ m). Pileipellis a cutis made up of parallel, thin- to slightly thick-walled (0.5–1 μ m), cylindrical hyphae 2–8(14) μ m wide. Stipitipellis a cutis made up of thin- to slightly thick-walled (0.5–1 μ m) cylindrical hyphae 2–8(12) μ m wide. Clamp connections present in all parts of basidiome.

Ecology: Gregarious on decaying downed logs or stumps, in subtropical forests; autumn.

Distribution: Only known from Southwestern China.

Additional specimen examined: CHINA. SICHUAN PROVINCE: Kangding County, Gonggashan Township, on a downed log, in a mixed forest of *Larix* sp. and broad-leaved trees, alt. 2,700 m, 16 Sep 2017, X.X. Ding 300 (KUN-HKAS 106642).

Notes: *Collybia petaloidea* is one of the lignicolous *Collybia* species which are rare in the genus. It differs from the other known lignicolous *Collybia* species, *C. bisterigmata* and *C. xylogena*, by having distinctly larger basidiomes and 4-spored basidia, and *C. humida* by its distinctly lower frequency of adhering basidiospores. Phylogenetically, it represents Clade V of *Collybia* subgen. *Collybia* (Fig. 4) and it clusters together with three American samples of Clade 22 (OM212948, MW408712 and OM391975) and another one of Clade 24 (MK532771) in the ITS tree (73% BP, 1.00 PP, Fig. 3), indicating that the four American samples treated

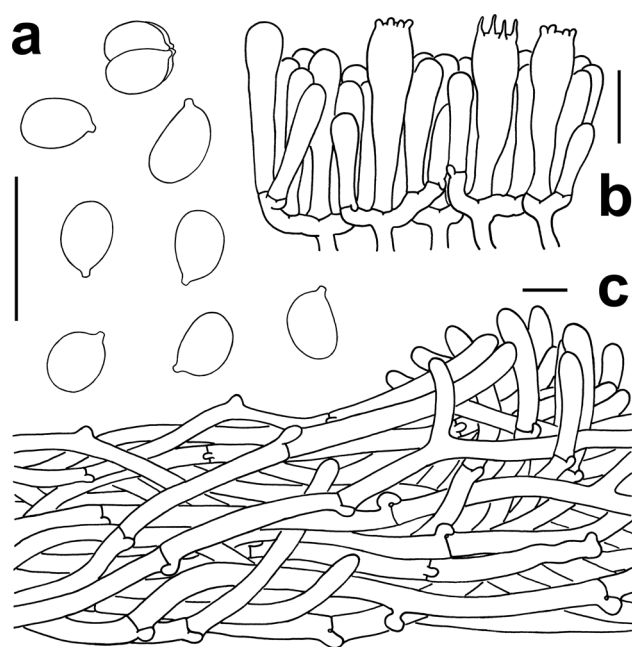


Fig. 19 Microscopic features of *Collybia phyllophila* (KUN-HKAS 114379). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μ m

as *Clitocybe* should be transferred to *Collybia* subgen. *Collybia*.

Collybia phyllophila (Pers.) Z.M. He & Zhu L. Yang, comb. nov. Figures 7q and 19

Mycobank: MB 847236.

Basionym: *Agaricus phyllophilus* Pers., Syn. Meth. Fung. (Göttingen) 2: 457 (1801).

≡ *Omphalia phyllophila* (Per.) Quélet, Enchir. Fung. (Paris): 22 (1886).

≡ *Lepista phyllophila* (Pers.) Harmaja, Karstenia 15: 15 (1976).

≡ *Clitocybe phyllophila* (Pers.) P. Kumm., Führ. Pilzk. (Zerbst): 122 (1871).

= *Agaricus cerussatus* Fr., Syst. Mycol. (Lundae) 1: 92 (1821).

= *Clitocybe cerussata* (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 122 (1871).

= *Omphalia cerussata* (Fr.) Quélet, Enchir. Fung. (Paris): 22 (1886).

= *Agaricus pithyophilus* Secr. ex Fr., Epicr. Syst. Mycol. (Upsaliae): 62 (1838).

= *Clitocybe pithyophila* (Secr. ex Fr.) Gillet, Hyménomycètes (Alençon): 152 (1874) [1878].

Diagnosis: Characterized by having large white basidiomes, ellipsoid to elongate basidiospores that predominantly adhere in tetrads, and pileipellis with short outgrowths. Very similar to *C. alboclitocyboides*, but differs from the latter by its pileipellis with trichodermal hyphal ends.

Description: Basidiomes medium-sized to large, clitocyboid. Pileus 3–11 cm in diam, at first convex, later plano-convex to appanate and with slightly depressed center; surface smooth to slightly tuberculate-wrinkled, white (1A1) or whitish (1B1), with brownish (5B2–4) spots or areas when watersoaked, often hygrophanous; margin not striate, at first inrolled, then expanding to incurved for a long time, finally becoming broadly undulate in age; context thin at margin but quite thick at disc (0.3–0.6 cm thick), concolorous with pileus surface. Lamellae broadly adnate to sub-decurrent, crowded to close, white (1A1) to cream (3A2), narrow to moderately broad (0.2–0.6 cm high), rarely forked; edges smooth. Stipe 2.5–6.5 \times 0.5–1.6 cm, central, equal or enlarged at base, hollow; surface often watersoaked and appearing brownish (5B2–4) overall, longitudinally whitish-fibrillose; base often rather tomentose; context concolorous with stipe surface. Odor spicy and fragrant.

Basidiospores [60/6/6] (4)4.5–6(7) \times (2.5)3–4 μ m, $Q = (1.25)1.33$ –1.97(2), $Q_m = 1.64 \pm 0.17$, ellipsoid to elongate, smooth, hyaline, thin-walled, inamyloid, predominantly adhering in tetrads. Basidia 17–32 \times 5–8 μ m, clavate, 4-spored, hyaline, thin-walled; sterigmata up to 5 μ m long. Cystidia absent. Lamella trama almost regular; hyphae 2–15 μ m wide, hyaline, cylindrical, thin-walled. Pileipellis subregular- to irregular-arranged, in places trichodermal in appearance, with some short outgrowths, becoming slightly loose in subpellis, made up of thin- to slightly thick-walled (0.5 μ m), cylindrical hyphae 3–10(12) μ m wide. Stipitipellis a cutis made up of parallel, thin- to slightly thick-walled (0.5–1 μ m), cylindrical hyphae 3–8(12) μ m wide. Clamp connections present in all parts of basidiome.

Ecology: Gregarious, on broad leaf or needle litter in forests; summer and autumn.

Distribution: Widespread in temperate and subtropical zones of the Northern Hemisphere.

Specimens examined: CHINA. GANSU PROVINCE: Zhuoni County, Huangjianzi, on broad leaf and needle litter, in a mixed broad-leaved and coniferous forest of *Abies* sp., *Larix* sp., *Picea* sp. and *Betula* sp., alt. 2,917 m, 11 Sep 2018, S.P. Jian 265 (KUN-HKAS 105590). SICHUAN PROVINCE: Kangding County, Gonggashan Township, on needle litter, in a dark coniferous forest, alt. 3,527 m, 4 Sep 2016, B. Feng 11 (KUN-HKAS 99364); Jiulong County, Jichou Mountain, on broad leaf litter, in a mixed broad-leaved and coniferous forest, alt. 4,300 m, 21 Sep 2017, X.X. Ding, 513301MF1199 (KUN-HKAS 103697). TIBET: Mangkang County, Wutuntang, on decaying cones of *Picea*, alt. 3,946 m, 21 Aug 2020, H. Qu 167 (KUN-HKAS 114379). XINJIANG: Shawan County, Dongdatang, on needle litter of *Picea* sp., alt. ca. 2,000 m, 4 Jul 2017, X.X. Ding 156 (KUN-HKAS 106498). YUNNAN PROVINCE: Deqin County, around No. 214 National Highway, on leaf litter of *Quercus semecarpifolia*, alt. 3,696 m, 17 Aug 2018, S.P. Jian

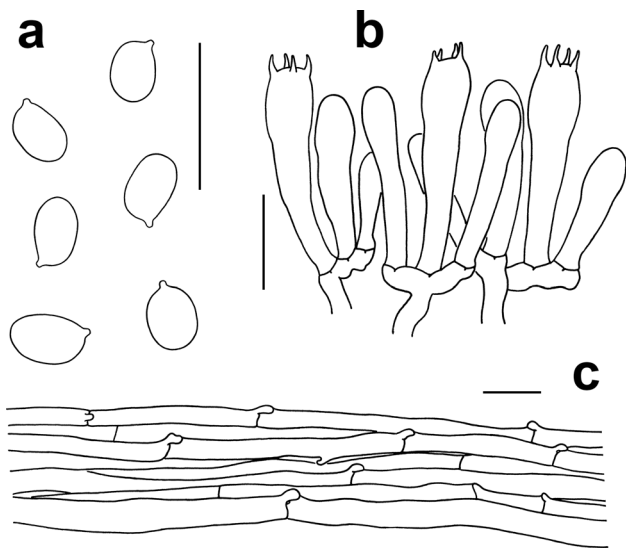


Fig. 20 Microscopic features of *Collybia piceata* (KUN-HKAS 123117). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μ m

219 (KUN-HKAS 105547); Shangri-La County, Pudacuo National Park, on broad leaf litter, in a mixed broad-leaved and coniferous forest, alt. 3,548 m, 28 Sep 2020, X.H. Wang 9110 (KUN-HKAS 123116).

Notes: This common species stands out in *Collybia* subgen. *Collybia* for its distinctly large white basidiomes. As shown in the six-locus phylogenetic analysis (Fig. 2), collections named *C. phyllophila* are recovered into three clades. Despite showing 1%–2% mean p-distances (Table S12, Suppl. material 8) between them, we still treat them as the same species, since no distinct macroscopical or microscopical differences were found, and all the three clades of *C. phyllophila* contain muscarine according to our LC–MS/MS detection method. The phylogenetic analysis of ITS (Fig. 3) suggests that a further three sequences, viz. MW485565 (*Clitocybe* sp.), MK028380 (*Clitocybe* cf. *phyllophila*), and MW855939 (*Clitocybe* cf. *phyllophila*), should also be identified as belonging to *C. phyllophila*.

Collybia piceata Z.M. He & Zhu L. Yang, sp. nov. Figures 7r and 20

Mycobank: MB 847237.

Etymology: ‘*piceata*’ (Lat.), referring to the spruce.

Diagnosis: Differs from *C. dryadicola* by the absence of coralloid hyphal ends in pileipellis and its forest habitat.

Type: CHINA. XINJIANG: Shawan County, Dongdatang, on needle litter of *Picea* sp., alt. 1,650 m, 4 Jul 2017, Q. Zhao 2786 (KUN-HKAS 123117, holotype).

Description: Basidiomes small, clitocyboid. Pileus 1–3.5 cm in diam, at first convex, later plano-convex to nearly appanate; surface smooth, pruinose, beige (1A2–4),

slightly hygrophanous; margin not striate, inrolled or incurved; context thin (0.1–0.2 cm thick), white (1A1); center slightly depressed when mature. Lamellae adnate to subdecurrent, moderately crowded, white (1A1) to cream (1A2), arcuate, narrow (0.1–0.2 cm high), not forked or intervenose; edges smooth. Stipe 2–4 \times 0.3–0.7 cm, central, equal, sometimes slightly curved, hollow; surface nearly smooth, yellowish (1A2–3) to yellowish brown (4A2–4), also appearing whitish (2A1) if covered with longitudinal white fibrils; base not inflated, covered with white mycelium.

Basidiospores [60/3/2] 4–5.5(6) \times 3–3.5(4) μ m, $Q = (1.21)1.3$ –1.67, $Q_m = 1.47 \pm 0.12$, ellipsoid, smooth, hyaline, thin-walled, inamyloid, almost always single. Basidia 15–25 \times 5–6 μ m, clavate, 4-spored, hyaline, thin-walled; sterigmata up to 5 μ m long. Cystidia absent. Lamella trama regular; hyphae 4–10(12) μ m wide, hyaline, cylindrical, thin-walled. Pileipellis a cutis composed of parallel, thin-walled, cylindrical hyphae 3–7(9) μ m wide. Stipitipellis a cutis composed of parallel, thin- to slightly thick-walled (0.5 μ m), cylindrical hyphae 2–5(7) μ m wide. Clamp connections present in all parts of basidiome.

Ecology: Gregarious, mainly on needle litter of *Picea*; summer.

Distribution: Known from Northwestern China.

Additional specimen examined: CHINA. XINJIANG: Shawan County, Dongdatang, on needle litter of *Picea* sp., alt. ca. 1,700 m, 4 Jul 2017, Q. Zhao 2802 (KUN-HKAS 123118).

Notes: As shown in Fig. 4, *C. piceata* belongs to Clade VII of *Collybia* subgen. *Collybia* whose members have basidiospores that are almost exclusively single. As *C. piceata* and *C. dryadicola* are phylogenetical sisters (100% BP, 1.00 PP, Fig. 2), they are very similar morphologically, sharing small white pruinose basidiomes and ellipsoid basidiospores of similar size (4.4–5.7 \times 2.4–3.2 μ m in *C. dryadicola*, Breitenbach and Kränzlin 1991). However, they can be easily distinguished from each other by their different habitats. *Collybia piceata* grows in subalpine coniferous forests, while *C. dryadicola* grows in alpine meadows (Breitenbach and Kränzlin 1991). In addition, our ITS phylogenetic analysis (Fig. 3) suggests that the sample of ‘*Clitocybe* sp.’ (OL678076), probably from China, should also be identified as *C. piceata* as well (pairwise identity value = 99.55%).

Collybia subtropica Z.M. He, Z.H. Chen & Zhu L. Yang, sp. nov. Figures 7t and 21

Mycobank: MB 847238.

Etymology: ‘*subtropica*’ (Lat.), referring to the subtropical habitat.

Diagnosis: Differs from *C. dealbata* by its subtropical forest habitat and differs from *C. rivulosa* by its basidiospores appearing almost always single.

Type: CHINA. YUNNAN PROVINCE: Kunming City, Heilongtan Park, on soil, under trees of *Quercus* sp. and

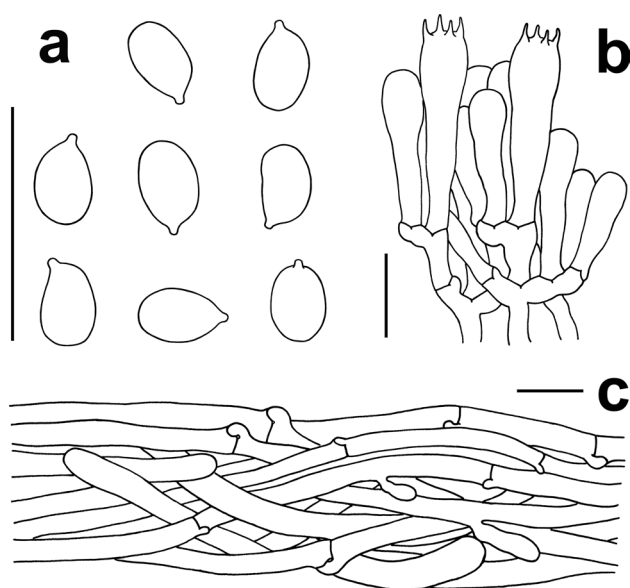


Fig. 21 Microscopic features of *Collybia subtropica* (KUN-HKAS 123124, holotype). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μ m

Pinus sp., alt. 2,000 m, 23 Aug 2020, Z.L. Yang 6389 (KUN-HKAS 123124, holotype).

Description: Basidiomes small, clitocyboid. Pileus 1.5–4 cm in diam, at first convex, then appanate, finally umbilicate to slightly infundibuliform; surface nearly smooth, glabrous, brownish (1B2–4) to brownish pink (5A2–3), hygrophanous; center depressed with age, more or less darker in color than rest of pileus; margin not striate, always white-pruinose and incurved to inrolled; context thin, concolorous with pileus surface. Lamellae adnate to (sub)decurrent, (sub)crowded, white (1A1), arcuate, narrow (up to 0.2 cm high), at times forked; edges smooth. Stipe 2–5 \times 0.15–0.6 cm, central, subcylindrical or sometimes flexuous, hollow; surface finely fibrillose, concolorous with pileus; base covered with white mycelium; context concolorous with stipe surface.

Basidiospores [60/3/3] 3–4(4.5) \times 2–3 μ m, $Q = (1.24)1.26$ – $1.75(1.82)$, $Q_m = 1.5 \pm 0.15$, ellipsoid to elongate, smooth, hyaline, thin-walled, inamyloid, almost always single. Basidia 19–27 \times 4.5–6 μ m, clavate, 4-spored, hyaline, thin-walled; sterigmata up to 4 μ m long. Cystidia absent. Lamella trama regular; hyphae 3–14 μ m wide, hyaline, cylindrical, thin-walled. Pileipellis a cutis, (sub)parallel-arranged, made up of thin-walled cylindrical hyphae 2–8 μ m wide. Stipitipellis a cutis made up of thin-walled cylindrical hyphae 3–8 μ m wide. Clamp connections present in all parts of basidiome.

Ecology: Generally gregarious, on soil or ground litter (primarily on broad leaf litter), in subtropical broad-leaved or mixed broad-leaved and coniferous forests, mainly

associated with hardwoods, such as *Alnus* Mill., *Castanea* Mill., *Cinnamomum* Schaeff. and *Quercus* L.; summer and autumn.

Distribution: Only known from subtropical zones of Central and Southwestern China.

Additional specimens examined: CHINA. HUNAN PROVINCE: Changsha County, Jiangbei Town, under trees of *Cinnamomum* sp., alt. ca. 150 m, 9 Nov 2018, Z.H. Chen, MHHNU 31386. YUNNAN PROVINCE: Baoshan City, Taibaoshan Forest Park, under trees of *Castanea* sp. and *Pinus* sp., alt. 1,730 m, 7 Aug 2019, T.X. Xu 319 (KUN-HKAS 114680); Baoshan City, Taibaoshan Forest Park, 7 Aug 2019, J.Y. Wu 184 (KUN-HKAS 123123); Fugong County, Zhiziluo, under trees of *Castanea* sp. and *Pinus* sp., alt. 2,050 m, 1 Aug 2019, T.X. Xu 199 (KUN-HKAS 123120); Gongshan County, Bingzhongluo, under trees of *Alnus nepalensis*, alt. 2,394 m, 25 Jul 2019, J.Y. Wu 14 (KUN-HKAS 123122).

Notes: This species is a sister taxon to *C. dealbata*, and nested in the Clade II of *Collybia* subgen. *Collybia* (Fig. 4), whose members have basidiospores appearing almost always single. Indeed, *C. subtropica* is morphologically very similar to *C. dealbata* and *C. rivulosa*, producing white-pruinose pileus whose margin is usually strongly inrolled, white lamellae and small basidiospores. However, *C. subtropica* has smaller basidiospores (3–4 \times 2–3 μ m) than *C. dealbata* (Harmaja 1969: 4–6 \times 2.5–3.3 μ m; Bigelow 1982: 4–4.5 \times 2–3 μ m; Breitenbach and Kränzlin 1991: 4–5.3 \times 3–3.3 μ m) and *C. rivulosa* (Kuyper 1995 and Læssøe and Petersen 2019: 4.5–6 \times 3–4 μ m). Furthermore, basidiospores are almost always single in *C. subtropica* and *C. dealbata* but predominantly occurring in tetrads in *C. rivulosa*.

In addition, the habitat is also a very important diagnostic character. *Collybia subtropica* is found under arbors such as trees of *Alnus*, *Castanea*, *Quercus* and *Pinus*, in subtropical forests of China, while *C. dealbata* and *C. rivulosa* are found in open habitats of temperate Europe, i.e., on various kinds of bare and nutrient-rich soil, among grasses and herbs or and mosses, in meadows, fields and waysides, etc. (Hamaja 1969; Breitenbach and Kränzlin 1991; Kuyper 1995; Læssøe and Petersen 2019).

Sometimes, it is also confusing between *C. subtropica* and *C. phyllophila*, because of their forest habitats and morphological similarity in the moist condition (especially small basidiomes of the latter). However, microscopically, the two species can be easily differentiated by their characters of basidiospores. *Collybia phyllophila* has larger basidiospores that predominantly occur in tetrads (Harmaja 1969: 4.3–6 \times 2.8–3.8 μ m; Bigelow 1982: 4–5 \times 2.5–3.5 μ m; Breitenbach and Kränzlin 1991: 4.3–6 \times 2.8–2.9 μ m; Kuyper 1995: 4–5 \times 3–3.5 μ m; our study: 4.5–6 \times 3–4 μ m).

Collybia subtropica was responsible for a mushroom poisoning incident in November 2018 in Hunan Province,

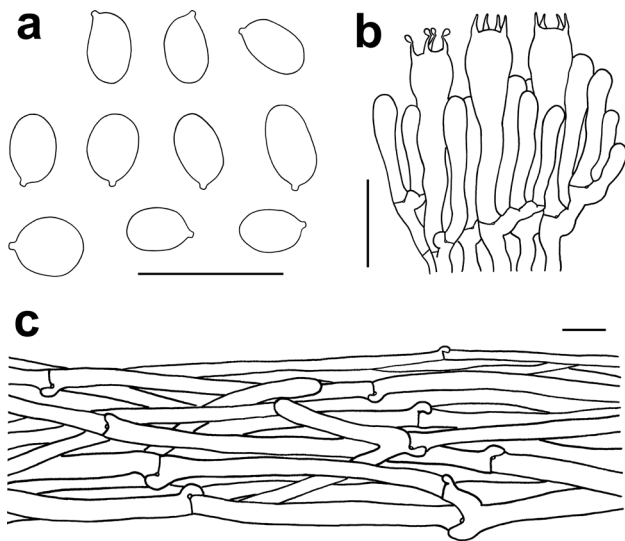


Fig. 22 Microscopic features of *Collybia tibetica* (KUN-HKAS 115436, holotype). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μ m

Central China. Three people ate its basidiomes (MHHNU 31386) and subsequently displayed neurotoxic symptoms (Li et al. 2021a, b, c, d). In this study, we have confirmed that the basidiomes of this species contain muscarine (viz., 46–107 mg/kg, dry weight).

Collybia tibetica Z.M. He & Zhu L. Yang, sp. nov. Figures 7u and 22

Mycobank: MB 847232.

Etymology: ‘*tibetica*’ (Lat.), referring to the distribution of the species in Tibet, China.

Diagnosis: Differs from the other alpine species *C. dryadicola* by having cylindrical hyphal ends in pileipellis rather than coralloid ones. It is only distributed in Tibet plateau of China by now.

Type: CHINA. TIBET: Mangkang County, Bangda Town, on rich soil among grasses and lichens, at the edge of a forest of *Picea* sp., alt. ca. 4,000 m, 26 Jul 2019, H. Qu, Alinla 1–20 (KUN-HKAS 115436, holotype).

Description: Basidiomes small, clitocyboid. Pileus 2.5–4 cm in diam, slightly depressed; surface glabrous, brown (5C3–5) to grayish brown (5D5–8), slightly darker in color at center, hygrophanous, brownish (5B2–3) when dry; margin not striate, incurved, strongly pruinose when young, later slightly pruinose; context thin (up to 0.3 cm thick), watery, light brown (5B2). Lamellae adnate to subdecurrent, moderately crowded, off-white (1A2) to brownish (4B2–3), arcuate, narrow (0.1–0.25 cm high); edges smooth. Stipe 2–3.5 \times 0.3–0.5 cm, central, subcylindrical, slightly enlarged at apex and slightly tapering at base, stuffed (filled with light brown watery tissue); surface longitudinally pruinose, nearly

concolorous with pileus; base not inflated, nearly not tomentose; context off-white (3A1) to brownish (4B2).

Basidiospores [60/3/2] (4) 4.5–6 \times 3–4 μ m, $Q = (1.25)1.31$ – $1.73(1.88)$, $Q_m = 1.57 \pm 0.14$, ellipsoid to elongate in side view, sometimes subglobose in frontal view, smooth, hyaline, thin-walled, inamyloid, not adherent, almost always single. Basidia 20–30 \times 5–6 μ m, clavate, 4-spored, hyaline, thin-walled; sterigmata up to 4 μ m long. Cystidia absent. Lamella trama regular; hyphae 2–11 μ m wide, hyaline, cylindrical, thin-walled. Pileipellis a cutis, parallel-arranged, made up of thin-walled cylindrical hyphae 2–10 μ m wide. Stipitipellis a cutis made up of thin-walled cylindrical hyphae 3–10 μ m wide. Clamp connections present in all parts of basidiome.

Ecology: Scattered on rich soil among herbs, and mosses or lichens, rare, associated with conifers, such as *Picea* Dietr. and *Sabina* Mill.; summer.

Distribution: Only known from alpine zones of Southwestern China.

Additional specimen examined: CHINA. TIBET: Dingqing County, on rich soil among mosses and herbs, in a forest of *Sabina* sp., alt. ca. 3,870 m, 29 Jul 2019, L.K. Jia 205 (KUN-HKAS 123101).

Notes: This Chinese species macroscopically resembles European *C. rivulosa*, which is confined to open, nutrient-rich and grassy habitats (Læssøe and Petersen 2019). However, the former differs from the latter by its alpine forest habitat as well as basidiospores that are almost always single.

Collybia tomentostipes Z.M. He & Zhu L. Yang, sp. nov. Figures 7v and 23

Mycobank: MB 847239.

Etymology: ‘*tomentostipes*’ (Lat.), referring to the tomentose stipe.

Diagnosis: Differs from *C. dealbata* and *C. subtropica* by its tomentose stipes and the basidiospores which frequently remain in tetrads.

Type: CHINA. TIBET: Yanjing County, on needle and broad leaf litter, in a coniferous and broad-leaved mixed forest, alt. 3,559 m, 12 Aug 2018 X.H. Wang 5206 (KUN-HKAS 123126, holotype).

Description: Basidiomes small, clitocyboid. Pileus 1–3 cm in diam, plano-convex to applanate; surface smooth, glabrous, whitish (2A1) when dry, brownish (5B2–4) to grayish brown (5D5–7) when wet, hygrophanous; margin sometimes striate, always inrolled or at least incurved; center slightly depressed, distinctly darker in color whether surface is wet or dry; context thin (0.1–0.2 cm thick), watery, concolorous with pileus surface. Lamellae (sub)decurrent, crowded, cream (2A1), appearing light brown (3B2) when wet, arcuate, narrow (0.1–0.25 cm high), not intervenose, at times forked; edges smooth. Stipe 2–2.5 \times 0.2–0.3 cm,

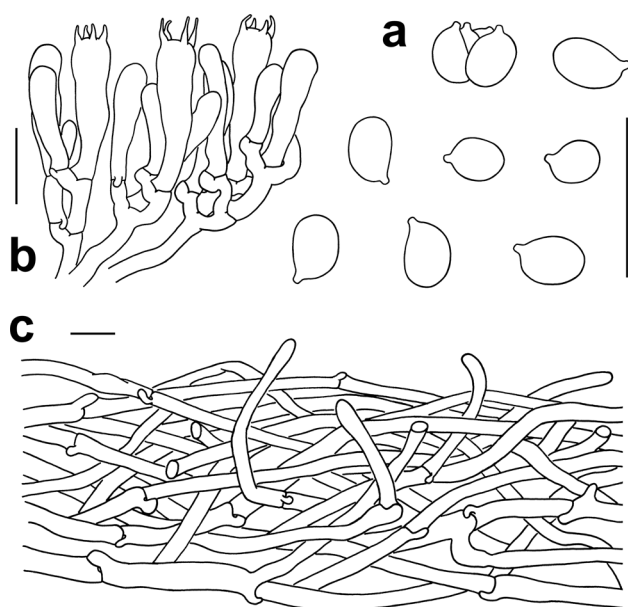


Fig. 23 Microscopic features of *Collybia tomentostipes* (KUN-HKAS 123126, holotype). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μ m

central, cylindrical, hollow; surface covered with whitish longitudinal tomentum or floc on background concolorous with pileus; base not inflated, whitish-tomentose; context concolorous with stipe surface background, watery.

Basidiospores [60/3/3] (3)3.5–4.5(5) \times 2.5–3 μ m, $Q = (1.07)1.17$ –1.59(1.67), $Q_m = 1.38 \pm 0.13$, broadly ellipsoid to ellipsoid, rarely subglobose or elongate, smooth, hyaline, thin-walled, inamyloid, often adhering in tetrads. Basidia 14–23 \times 4.5–6 μ m, clavate, 4-spored, hyaline, thin-walled; sterigmata up to 4 μ m long. Cystidia absent. Lamella trama regular; hyphae 3–10(15) μ m wide, hyaline, cylindrical, thin-walled, some of which have contents inside. Pileipellis a cutis composed of slightly irregular, thin-walled, cylindrical hyphae 2–6 μ m wide, with some exserted ends but not differentiated. Stipitipellis a cutis composed of thin-walled cylindrical hyphae 2–7 μ m wide. Clamp connections present in all parts of basidiome.

Ecology: Gregarious, on needle or broad leaf litter, in montane coniferous or coniferous and broad-leaved mixed forests; late summer and early autumn.

Distribution: Found in Southwestern China, also reported in Canada.

Additional specimen examined: CHINA. YUNNAN PROVINCE: Shangri-La County, on needle litter among mosses, alt. ca. 3,500 m, 30 Sep 2020, X.H. Wang 9228 (KUN-HKAS 123125).

Notes: Sometimes, *C. tomentostipes* could be confused with the small basidiomes of *C. alboclitocyboides* and *C. phyllophila*. However, the former one can be distinguished

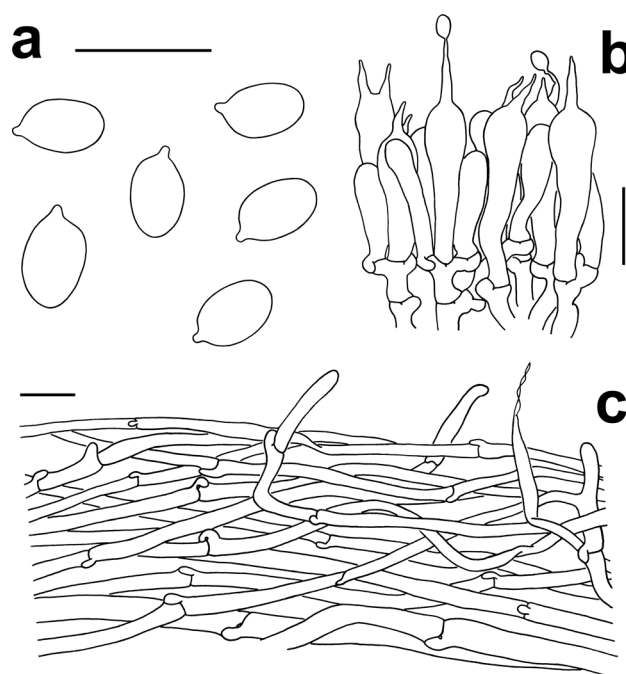


Fig. 24 Microscopic features of *Collybia xylogena* (KUN-HKAS 54966, holotype). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μ m

from the latter ones by its distinct tomentum on stipe surface and floc forming at apex of stipe. As shown in the ITS tree (Fig. 3), the six samples of '*C. phyllophila*' (MZ144144, MZ144142, MZ144143, MK966600, KU836519 and MK214391) and one sample of '*Clitocybe* sp.' (MN992572) are grouped together with the new species forming two subclades but exhibiting a very short genetic distance. This indicates that they should be considered as belonging to the same species; therefore, all seven samples should be identified as *C. tomentostipes*. *Clitocybe phyllophila* can be distinguished from *C. tomentostipes* by its distinctly larger basidiomes and longer basidiospores (Harmaja 1969; Bigelow 1982; Breitenbach and Kränzlin 1991; Kuyper 1995). Based on information from the GenBank database, sequence MN992572 was obtained from a Canadian sample, suggesting that this new species is also distributed in North America.

The ITS sequences of *C. tomentostipes* show a 99% similarity to a sequence identified as '*Cli. diatreta*' (GenBank No.: ON323016). However, they should not belong to *Cli. diatreta* or the related species *Cli. leucodiatreta*. Collections of *C. tomentostipes* do not exhibit pilei that are pinkish, vinaceous or pink-brown when moist and pale pinkish or beige when dry, which are the characters of the latter two species (Bigelow 1982; Breitenbach and Kränzlin 1991; Kuyper 1995; Gungör et al. 2014).

Collybia xylogena Z.M. He & Zhu L. Yang, sp. nov. Figures 7w and 24

MycoBank: MB 847241.

Etymology: ‘*xylogena*’ (Gk.), referring to growing on wood.

Diagnosis: Differs from *C. bisterigmata* by not having inflated hyphae in lamella trama.

Type: CHINA. YUNNAN PROVINCE: Kunming City, Baoziqing, on rotten wood of *Camellia* sp., alt. 2,000 m, 28 Sep 2008, L.P. Tang 729 (KUN-HKAS 54966, holotype).

Description: Basidiomes small, clitocyboid. Pileus about 2 cm in diam when mature, convex to broadly convex when young, later at disc depressed or expanding to shallowly umbilicate; surface glabrous, cream (4A2) to brown (4B5) or grayish brown (4C5) from margin to disc, distinctly darker at center, hygrophanous; margin not striate, incurved, pruinose at very edge; context thin (0.1–0.2 cm thick), concolorous with surface. Lamellae decurrent, moderately crowded, cream (4A2), arcuate, very narrow (about 0.1 cm high); edges smooth. Stipe 2–4 × 0.2–0.5 cm, central, equal, flexible, concolorous with pileus, hollow and concolorous inside; base not inflated, with white strigose mycelium.

Basidiospores [60/3/1] (4.5)5–8(10) × 3–4.5(5) μm, Q = (1.25)1.31–1.89(2.5), Qm = 1.57 ± 0.22, ellipsoid to elongate, smooth, hyaline, thin-walled, inamyloid, single. Basidia 15–22 × 5–6 μm, clavate, mostly 2-spored or sometimes single-spored, hyaline, thin-walled; sterigmata up to 8 μm long. Cystidia absent. Lamella trama subregular, very narrow (12–20 μm thick), appearing slightly gelatinized; hyphae 2–5 μm wide, hyaline, cylindrical, thin-walled. Pileipellis a cutis, more or less parallel-arranged, made up of thin-walled cylindrical hyphae 1.5–5 μm wide, occasionally with exserted ends. Stipitipellis a cutis, compactly parallel-arranged, made up of thin-walled cylindrical hyphae 2–5 μm wide. Clamp connections present in all parts of basidiome.

Ecology: Gregarious on downed decaying logs, in subtropical broad-leaved forests; autumn.

Distribution: Only known from the type locality in Southwestern China.

Notes: Phylogenetically, *C. xylogena* represents Clade VI of *Collybia* subgen. *Collybia* (Fig. 4) and no samples from GenBank are found to be clustered with *C. xylogena* (Fig. 3). In the field, *Lepistella ocula* can recall *C. xylogena* because of its small, brown, broadly depressed and glabrous pileus with a brown disc and habit of growing in dense clusters on downed decaying logs (Ovrebø and Baroni 2007). Even so, *C. xylogena* can be easily recognized by its white-pruinose margin and smooth basidiospores (verrucose in *Lpl. ocula*). Besides, the gelatinized collapsing hyphae in lamella trama and pileus context of *Lpl. ocula* are also diagnostic to distinguish *Lpl. ocula* from *C. xylogena* (Ovrebø and Baroni 2007).

In addition to the 15 species described above, we propose three additional new combinations in *Collybia* subgen. *Collybia* according to our ITS and six-locus phylogenetic analyses (Figs. 2 and 3) and known morphological data (Harmaja 1969; Bigelow 1982; Breitenbach and Kränzlin 1991).

Besides, we also transfer *Clitocybe rivulosa* to *Collybia* subgen. *Collybia* for its presence of muscarine (Swenberg et al. 1967; Genest et al. 1968) and morphological features (Kuyper 1995; Læssøe and Petersen 2019), although we are not sure of its exact phylogenetic placement.

Collybia aperta (Peck) Z.M. He & Zhu L. Yang, comb. nov.
MycoBank: MB 847242.

Basionym: *Agaricus apertus* Peck, Ann. Rep. N.Y. St. Mus. nat. Hist. 30: 38 (1878) [1877].

≡ *Clitocybe aperta* (Peck) Sacc., Syll. fung. (Abellini) 5: 164 (1887).

≡ *Clitocybula aperta* (Peck) Singer, Sydowia 8(1–6): 110 (1954).

Collybia dealbata (Sowerby) Z.M. He & Zhu L. Yang, comb. nov.

MycoBank: MB 847243.

Basionym: *Agaricus dealbatus* Sowerby, Col. fig. Engl. Fung. Mushr. (London) 2(no. 13): tab. 123 (1799).

≡ *Clitocybe dealbata* (Sowerby) P. Kumm., Führ. Pilzk. (Zerbst): 121 (1871).

Collybia dryadicola (J. Favre) Z.M. He & Zhu L. Yang, comb. nov.

MycoBank: MB 847244.

Basionym: *Clitocybe rivulosa* var. *dryadicola* J. Favre, Ergebn. wiss. Unters. schweiz. Natn Parks 5(33): 199 (1955).

≡ *Clitocybe dryadicola* (J. Favre) Harmaja, Karstenia 15: 17 (1976).

Collybia rivulosa (Pers.) Z.M. He & Zhu L. Yang, comb. nov.

MycoBank: MB 847245.

Basionym: *Agaricus rivulosus* Pers., Syn. meth. fung. (Göttingen) 2: 369 (1801).

≡ *Clitocybe rivulosa* (Pers.) P. Kumm., Führ. Pilzk. (Zerbst): 122 (1871).

≡ *Omphalia rivulosa* (Pers.) Quél., Enchir. fung. (Paris): 22 (1886).

Collybia* subgenus *Crassicybe Z.M. He & Zhu L. Yang, subgen. nov.

MycoBank: MB 847246.

Etymology: ‘*Crassi*’ (Gk.), thick; ‘*cybe*’ (Gk.), head; that is a *Clitocybe*-like subgenus with thick flesh.

Diagnosis: Differs from *Collybia* subgen. *Leucocalocybe* by possessing adnate to subdecurrent lamellae.

Type species: *Collybia irina* (Fr.) Z.M. He & Zhu L. Yang.

Description: Basidiomes medium-sized to large, clitocyboid to tricholomatoid, more or less flesh-colored in tone. Pileus convex to plane, umbonate, smooth, hygrophanous. Flesh white to whitish, thick in center, thin towards margin,

odor faintly aromatic. Lamellae adnate to subdecurrent, crowded. Stipe solid, fibrillose. Basidiospores finely verruculose to smooth, ellipsoid, inamyloid, cyanophilic if ornamentation present. Pileipellis and stiptipellis a cutis. Lamella trama regular. Cheilocystidia sometimes present, other sorts of cystidia absent. Clamp connections present. Muscarine absent.

Ecology: Usually in clusters, groups or fairy rings, on bare soil or humus, in hardwood and coniferous forests or grassland, from the lowlands to montane habitats, common; summer and autumn.

Distribution: Widespread in Asia, Europe, North America, North Africa and Oceania.

Notes: As shown in the six-locus and ITS phylogenetic analyses (Figs. 2 and 3), *L. irina* forms a monophyletic clade that is distinct from other clades of previous *Lepista* but belongs to the current *Collybia* clade. Moreover, its microscopic feature of presenting both smooth and finely verruculose basidiospores (Bigelow and Smith 1965; Noordeloos and Kuyper 1995) distinguishes it from other clitocyboids of the current *Collybia*. We propose the new subgenus *Crassicybe* for *L. irina*, corresponding with Clade 4 (Fig. 2), and the new combination is made below.

Collybia irina (Fr.) Z.M. He & Zhu L. Yang, comb. nov.

Mycobank: MB 847247.

Basionym: *Agaricus irinus* Fr., Epicr. syst. mycol. (Upsaliae): 48 (1838) [1836–1838].

≡ *Gyrophila irina* (Fr.) Quél., Enchir. fung. (Paris): 17 (1886).

≡ *Tricholoma irinum* (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 132 (1871).

≡ *Rhodopaxillus irinus* (Fr.) Métrod, Revue Mycol., Paris 7(Suppl. Colon. no. 2): 29 (1942).

≡ *Lepista irina* (Fr.) H.E. Bigelow, Can. J. Bot. 37: 775 (1959).

≡ *Clitocybe irina* (Fr.) H.E. Bigelow & A.H. Sm., Brittonia 21: 172 (1969).

Collybia subgenus *Leucocalocybe* (X.D. Yu & Y.J. Yao) Z.M. He & Zhu L. Yang, stat. nov.

Mycobank: MB 847248.

Basionym: *Leucocalocybe* X.D. Yu & Y.J. Yao, in Yu, Deng & Yao, Afr. J. Microbiol. Res. 5(31): 5751 (2011).

Based on Harmaja (1978), Singer (1986), Yu et al. (2011), and our phylogenetic analyses, the taxon *Leucocalocybe* is emended here.

Diagnosis: Differs from *Collybia* subgen. *Crassicybe* by possessing adnexed to emarginate lamellae.

Type species: *Collybia mongolica* (S. Imai) Z.M. He & Zhu L. Yang.

Description: Basidiomes more or less tricholomatoid, most large, white, brown, blue, violet, lilac or purple in color, gymnocarpic. Pileus convex to plane, non-pruinose.

Lamellae adnexed to emarginate. Flesh white or whitish, thick in center, thin towards margin, odor not unpleasant. Stipe central, solid. Spore print in most species pinkish, also white. Basidiospores ellipsoid, hyaline, smooth, thin-walled, inamyloid, finely verruculose, cyanophilic, sometimes in tetrads. Basidia cylindrical to clavate, 4-spored. Cystidia absent. Lamella trama more or less regular. Pileipellis a cutis or ixocutis. Clamp connections present. Muscarine absent.

Ecology: Usually gregarious, in clusters, groups, rows or fairy rings, more rarely solitary, in meadows, pastures, along forest edges or in forests; summer and autumn, more rarely in spring.

Distribution: Documented in Asia, Europe, North America, North Africa and Oceania.

Notes: Before our study, *Leucocalocybe* only harbored for *Leu. mongolica*, an edible agaric from Northern China and Mongolia (Yu et al. 2011). According to our phylogenetic analysis based on ITS (Fig. 3), *Lepista personata* (Fr.) Cooke, five subclades of *L. nuda* (Bull.) Cooke, *L. fibrosissima* Singer, *L. sordida* (Schumach.) Singer, *Leucocalocybe mongolica* and *Clitocybe brunneocephala* H.E. Bigelow cluster together, forming a strongly supported monophyletic clade (BP=95%, PP=1.00). Furthermore, our six-locus phylogenetic analysis (Fig. 2) shows *L. sordida*, *L. nuda* and *L. saeva* (Fr.) P.D. (= *L. personata*) cluster together, also representing a monophyletic clade within the current *Collybia*. Unfortunately, we were not able to solve the puzzle which subclade in Figs. 2 and 3 could represent the true *L. nuda*; but we can say that all putative subclades of *L. nuda* are nested in *Collybia* subgen. *Leucocalocybe*.

In our view, *Leu. mongolica* is merely unique for the white color of its basidiomes and spore print but morphologically similar in other aspects to its allies, producing large fleshy tricholomatoid basidiomes, convex to plane pileus, adnexed to emarginate lamellae, solid stipe and inamyloid, finely verruculose basidiospores. Another brown species *Clitocybe brunneocephala* from western North America also conforms to these generic features (Bigelow 1982). *Leucocalocybe* is recircumscribed here to further include *Cli. brunneocephala* plus previous *Lepista* species with bluish, lilac or purplish colors in stipe, pileus or lamellae, namely *Lepista* sect. *Spongiosa* (Singer 1986) (= *Lepista* sect. *Nuda* Harmaja, Harmaja 1978). All the necessary new combinations in *Collybia* are made.

Collybia brunneocephala (H.E. Bigelow) Z.M. He & Zhu L. Yang, comb. nov.

Mycobank: MB 847249.

Basionym: *Clitocybe brunneocephala* H.E. Bigelow, Beih. Nova Hedwigia 72: 176 (1982).

Collybia fibrosissima (Singer) Z.M. He & Zhu L. Yang, comb. nov.

Mycobank: MB 847250.

Basionym: *Lepista fibrosissima* Singer, Sydowia (1–6): 104 (1954).

Collybia mongolica (S. Imai) Z.M. He & Zhu L. Yang, comb. nov.

Mycobank: MB 847251.

Basionym: *Tricholoma mongolicum* S. Imai, Proc. Imper. Acad. Tokyo 13: 282 (1938).

≡ *Leucocalocybe mongolica* (S. Imai) X.D. Yu & Y.J. Yao [as ‘*mongolicum*’], in Yu, Deng & Yao, Afr. J. Microbiol. Res. 5(31): 5751 (2011).

Collybia nuda (Bull.) Z.M. He & Zhu L. Yang, comb. nov.

Mycobank: MB 847252.

Basionym: *Agaricus nudus* Bull., Herb. Fr. (Paris) 10: tab. 439 (1790).

≡ *Cortinarius nudus* (Bull.) Gray, Nat. Arr. Brit. Pl. (London) 1: 628 (1821).

≡ *Tricholoma nudum* (Bull.) P. Kumm., Führ. Pilzk. (Zerbst): 132 (1871).

≡ *Lepista nuda* (Bull.) Cooke, Handb. Brit. Fungi 1: 192 (1871).

≡ *Gyrophila nuda* (Bull.) Quél., Enchir. fung. (Paris): 17 (1886).

≡ *Rhodopaxillus nudus* (Bull.) Maire, Anns mycol. 11(4): 338 (1913).

≡ *Clitocybe nuda* (Bull.) H.E. Bigelow & A.H. Sm., Brittonia 21(1): 52 (1969).

= *Agaricus bicolor* Pers., Syn. meth. fung. (Göttingen) 2: 281 (1801).

= *Cortinarius bicolor* Gray, Nat. Arr. Brit. Pl. (London) 1: 628 (1821).

= *Agaricus tyrianthinus* Fr., Icon. Desc. Fung. Min. Cognit. (Leipzig) 2: 91 (1818).

= *Clitocybe tyrianthina* (Fr.) P. Karst., Bidr. Känn. Finl. Nat. Folk 32: 60 (1879).

= *Omphalia tyrianthina* (Fr.) Quél., Enchir. fung. (Paris): 21 (1886).

= *Agaricus bulbosus* Bolton, Hist. fung. Halifax, App. (Huddersfield) 3: 147 (1792) [1791].

= *Collybia lilacea* Quél., Mém. Soc. Émul. Montbéliard, Sér. 2 5: 434 (1875).

Collybia personata (Fr.) Z.M. He & Zhu L. Yang, comb. nov.

Mycobank: MB 847253.

Basionym: *Agaricus personatus* Fr., Observ. mycol. (Havniae) 2: 89 (1818).

≡ *Lepista personata* (Fr.) Cooke, Handb. Brit. Fungi 1: 193 (1871).

≡ *Tricholoma personatum* (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 132 (1871).

≡ *Rhodopaxillus personatus* (Fr.) Singer, Anns mycol. 41(1/3): 92 (1943).

= *Agaricus anserinus* (Fr.) Eeden, in Kops, Fl. bat. 19(288–330): tab. 1514 (1893).

= *Tricholoma anserinum* (Fr.) Sacc., Syll. fung. (Abellini) 11: 8 (1895).

= *Rhodopaxillus saevus* (Fr.) Maire, Anns mycol. 11(4): 338 (1913).

= *Tricholoma saevum* (Fr.) Gillet, Anns mycol. 18(1/3): 65 (1920).

= *Lepista saeva* (Fr.) P.D. Orton, Trans. Br. mycol. Soc. 43(2): 177 (1960).

= *Clitocybe saeva* (Fr.) H.E. Bigelow & A.H. Sm., Brittonia 21: 169 (1969).

Collybia sordida (Schumach.) Z.M. He & Zhu L. Yang, comb. nov.

Mycobank: MB 847254.

Basionym: *Agaricus sordidus* Schumach., Enum. pl. (Kjbenhavn) 2: 341 (1803).

≡ *Tricholoma sordidum* (Schumach.) P. Kumm., Führ. Pilzk. (Zerbst): 134 (1871).

≡ *Gyrophila sordida* (Schumach.) Quél., Enchir. fung. (Paris): 18 (1886).

≡ *Rhodopaxillus sordidus* (Schumach.) Maire, Anns mycol. 11(4): 338 (1913).

≡ *Melanoleuca sordida* (Schumach.) Murrill, Mycologia 6(1): 3 (1914).

≡ *Lepista sordida* (Schumach.) Singer, Lilloa 22: 193 (1951) [1949].

Collybia subgenus *Macrosporocybe* Z.M. He & Zhu L. Yang, subgen. nov.

Mycobank: MB 847255.

Etymology: ‘*Macrosporo*’ (Gk.), large spore; ‘*cybe*’ (Gk.), head; that is a *Clitocybe*-like subgenus with large basidiospores.

Diagnosis: Differs from *Collybia* subgen. *Collybia* by possessing relatively large basidiospores.

Type species: *Collybia striaticeps* Z.M. He & Zhu L. Yang.

Description: Basidiomes small to medium-sized, clitocyboid. Pileus convex to applanate, yellowish brown, grayish brown or beige-gray, smooth, glabrous, non-pruinose, with dark-colored depressed center and striate margin, hygrophonous. Flesh thin, watery, odor fragrant. Lamellae adnate to subdecurrent, dirty white, cream or buff. Stipe central, (sub) cylindrical, hollow, concolorous with pileus or paler, finely longitudinally fibrillose, base white-tomentose. Basidiospores relatively large, 6.5–10 × 4–5.5 μm, elongate to cylindrical, hyaline, smooth, thin-walled, inamyloid. Basidia clavate. Cystidia absent. Lamella trama regular. Pileipellis and stipitipellis a cutis. Clamp connections present. Muscarine absent.

Ecology: Grouped, scattered or solitary, on soil, needle or broad leaf litter, planar to (sub)alpine; mainly in summer and autumn, also in spring and winter.

Distribution: At least in Asia and North America.

Notes: As suggested by the six-locus and ITS phylogenetic analyses, *Collybia* subgen. *Macrosporocybe* represents

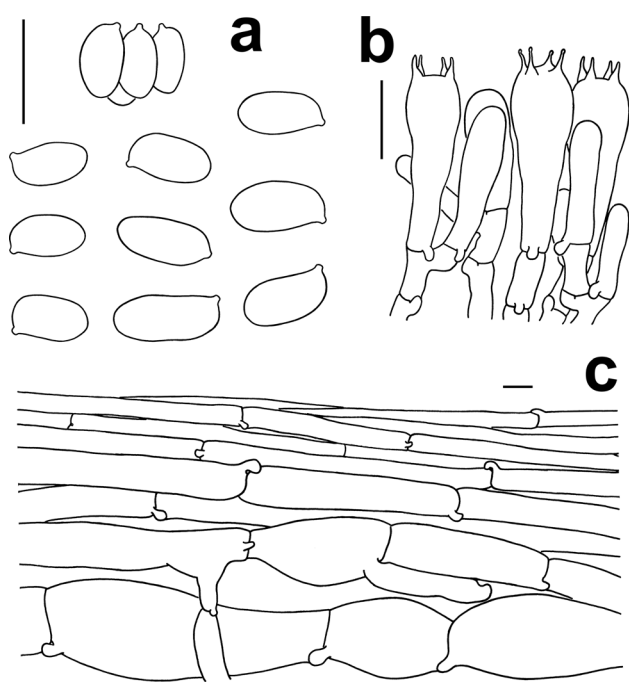


Fig. 25 Microscopic features of *Collybia striaticeps* (KUN-HKAS 123129, holotype). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μ m

an independent clade in the current *Collybia* (Fig. 2: 100% BP, 1.00 PP; Fig. 3: 93% BP, 1.00 PP). Microscopically, the taxa included in this subgenus have basidiospores $6\text{--}10 \times 3.5\text{--}5.5 \mu\text{m}$, significantly larger than those of previous *Clitocybe* taxa in *Collybia* subgen. *Collybia* (except for *C. odora* and *C. xylogena*). These results support the new proposed subgenus. Moreover, muscarine was not detected in *Collybia* subgen. *Macrosporocybe*, which is consistent with its placement separated from the poisonous *Collybia* subgen. *Collybia* clade (Fig. 2).

Collybia striaticeps Z.M. He & Zhu L. Yang, sp. nov. Figures 7s and 25

Mycobank: MB 847256.

Etymology: ‘*striaticeps*’ (Lat.), referring to the striate pileus.

Diagnosis: Differs from *Cli. fragrans* by having numerous inflated hyphae in lamella trama and pileipellis.

Type: CHINA. YUNNAN PROVINCE: Deqin County, Baimaxueshan Nature Reserve, on needle litter, in a mixed forests of *Picea* sp. and *Quercus semecarpifolia*, alt. 4,106 m, 5 Oct 2020, X.H. Wang 9638 (KUN-HKAS 123129, holotype).

Description: Basidiomes small, clitocyboid. Pileus 1–2 cm in diam, plano-convex to nearly applanate; surface smooth, glabrous, not pruinose, yellowish brown (4A2) to grayish brown (4B3–5), hygrophanous; margin distinctly striate, at first strongly inrolled, later straight; center

slightly depressed and distinctly darker in color; context thin (0.1–0.2 cm thick), watery, concolorous with pileus surface. Lamellae adnate to subdecurrent, subdistant, dirty white (2B1) to buff (1A2), arcuate, narrow (0.15–0.3 cm high), not forked or intervenose; edges smooth. Stipe $2\text{--}3.5 \times 0.3\text{--}0.5$ cm, central, subcylindrical, slightly enlarged towards to base, hollow; surface nearly smooth, concolorous with pileus or paler, with finely white fibrils longitudinally; base not inflated, covered with some white mycelium; context concolorous with stipe surface, watery. Odor like anise, pleasant.

Basidiospores [60/3/2] $7\text{--}10 \times 4\text{--}5 \mu\text{m}$, $Q = (1.52)1.66\text{--}2.22(2.38)$, $Qm = 1.89 \pm 0.18$, elongate to cylindrical, smooth, hyaline, thin-walled, inamyloid, sometimes in tetrads. Basidia $22\text{--}32 \times 7\text{--}8 \mu\text{m}$, broadly clavate, 4-spored, hyaline, thin-walled; sterigmata up to 4 μm long. Cystidia absent. Lamella trama regular, hyaline, composed of thin-walled cylindrical hyphae $3\text{--}10 \mu\text{m}$ wide, also inset with numerous inflated hyphae $15\text{--}40 \mu\text{m}$ wide. Pileipellis parallel-arranged; hyphae $4\text{--}40 \mu\text{m}$ wide, thin-walled, cylindrical in superapellis, but many of which becoming inflated in subpellis. Stipitipellis a cutis composed of parallel, thin- to slightly thick-walled (about 0.5 μm), cylindrical hyphae $2\text{--}8 \mu\text{m}$ wide. Clamp connections present in all parts of basidiome.

Additional specimen examined: CHINA. YUNNAN PROVINCE: Shangri-La County, Hongshan, on soil among mosses and herbs, under trees of *Quercus semecarpifolia*, alt. ca. 4,100 m, 17 Aug 2019, X.H. Wang 6169 (KUN-HKAS 123128).

Ecology: Scattered or Solitary on needle litter or soil, in high-montane forests; summer and autumn.

Distribution: Only known from subtropical zones of Southwestern China.

Notes: The phylogenetic analysis of ITS (Fig. 3) shows that *Cli. fragrans* from North America and *C. striaticeps* are sister taxa (BP = 80%, PP = 0.89), exhibiting a sequence similarity ranging from 98.66% to 98.81%. Moreover, the morphological features of *Cli. fragrans* as described in European and North American monographs conform to the definition of the new subgenus *Macrosporocybe*, which produces brownish to brownish gray, hygrophanous, clitocyboid basidiomes and relatively large basidiospores (Harmaja 1969: $6.2\text{--}8.6 \times 3.4\text{--}4.6$; Bigelow 1982: $6.5\text{--}8.5 \times 3.5\text{--}4.5$; Kuyper 1995: $6.5\text{--}9 \times 3.5\text{--}5 \mu\text{m}$; Breitenbach and Kränzlin 1991: $6.4\text{--}9.5 \times 4\text{--}5.3 \mu\text{m}$). Despite having similar spore sizes ($7\text{--}10 \times 4\text{--}5 \mu\text{m}$ in *C. striaticeps*), the presence of numerous abnormally inflated hyphae (up to 40 μm wide) in lamella trama and subpellis easily distinguishes *C. striaticeps* from *Cli. fragrans*.

Considering its close phylogenetic relationship with *C. striaticeps* (Fig. 3), it is unlikely for *Cli. fragrans* from North America to contain muscarine, as supported by the absence

of muscarine in *C. striaticeps* (Table 1). Bon (1988) and Laux (2002) classify *Cli. fragrans* as poisonous, while Phillips (1990) and Davis et al. (2012) consider it edible. Hence, it can be inferred that *Cli. fragrans* from North America and Europe may not belong to the same species, and at least *Cli. fragrans* from North America should be classified under *Collybia* subgen. *Macrosporocybe*. Similar to *Cli. fragrans*, *C. striaticeps* may be mistaken for *C. rivulosa*, which lacks the characteristic anise scent (Bigelow 1982) and possesses smaller basidiospores measuring $4.5\text{--}6 \times 3\text{--}4 \mu\text{m}$ (Kuyper 1995). It also resembles the whitish variety of *C. odora*, but differs from the latter by having intracellular pigment rather than incrusting one in pileipellis (Breitenbach and Kränzlin 1991).

Dendrocollybia R.H. Petersen & Redhead, Mycol. Res. 105(2): 169 (2001).

Type species: *Dendrocollybia racemosa* (Pers.) R.H. Petersen & Redhead, Mycol. Res. 105(2): 169 (2001).

Notes: Both ITS and LSU phylogenetic analyses of Hughes et al. (2001) demonstrated the separation of *Dendrocollybia* from previous *Collybia* s.str. Our own phylogenetic results (Figs. 2, 3, 4) support this conclusion and further specify that *Dendrocollybia* corresponds to Clade 7 of Clitocybaceae in Fig. 2.

Lepista (Fr.) W.G. Sm., J. Bot., Lond. 8: 248 (1870).

Basionym: *Paxillus* sect. *Lepista* Fr., Summa veg. Scand., Sectio Post. (Stockholm): 306 (1849).

= *Rhodopaxillus* Maire, Anns mycol. 11(4): 338 (1913).

Diagnosis: Differs from *Clitocybe* s.str. by having verruculose basidiospores.

Type species: *Lepista densifolia* (J. Favre) Singer & Clémenceçon, Nova Hedwigia 23(2–3): 308 (1973) [1972].

Description: Basidiomes usually large, sometimes medium-sized, clitocyboid to tricholomatoid. Pileus at first convex, later plane with depressed center; surface smooth, glabrous or fibrillose, not dark in color, white, cream, grayish-white, grayish-buff or grayish-brown, not hygrophalous. Flesh thick in center, white or tinged pinkish, brownish or grayish, odor pleasant. Lamellae adnate to decurrent, crowded to close, narrow to moderately broad, forked at times. Stipe central, cylindrical with or without bulbous base, solid or hollow; base white-tomentose. Spore print not white, pinkish, pinkish buff or pinkish cream. Basidiospores subglobose or ellipsoid, verruculose, inamyloid, cyanophilic. Basidia clavate, 4-spored. Cystidia absent. Lamella trama subregular to regular. Pileipellis a cutis. Clamp connections present. Muscarine absent.

Ecology: Gregarious, on humus, broad leaf or needle litter, also in grasslands; summer and autumn, rarely in winter.

Distribution: Widespread in the Northern Hemisphere, also documented in Oceania (Young 2000; Cooper 2016).

Notes: The genus *Lepista* was proposed by Smith (1870), who elevated *Paxillus* sect. *Lepista* to genus. The type species of *Lepista* are as controversial as the identity of *Paxillus lepista* Fr. Donk (1962) recognized *Agaricus lepista* Fr. (\equiv *Pax. lepista*) as type of *Lepista*. Singer (1962) at first suggested that *L. subaequalis* (Britzelm.) Singer and *Pax. lepista* were conspecific, and then Singer (1975, 1976, 1986) and Kühner (1976) thought that *L. densifolia* was the same as *Pax. lepista* and accepted it as the type species of *Lepista*. While Harmaja (1974, 1976) expressed the opinion that *L. subconnexa* (Murrill) Harmaja could be *Pax. lepista* or a very closely related species. Nowadays, *L. panaeolus* is given as the current name for *Pax. lepista* according to the Index Fungorum database (<http://www.indexfungorum.org/>).

Anyhow, one thing is clear that the monophyletic clade (75% BP, 1.00 PP) highlighted with a sky-blue box in Fig. 3 represents *Lepista* s.str., as all aforementioned lectotype species are encompassed within this clade. Similarly, in the six-locus tree (Fig. 2, Clade 6), *L. densifolia*, *L. panaeolus* and an unnamed *Lepista* species constitute a monophyletic clade (100% BP, 1.00 PP) separated from the other two clades of previous *Lepista* (Clade 2 and 4) in Clitocybaceae, thus truly representing *Lepista* s.str.

In the present study, we follow the suggestion of Singer (1986) to accept *L. densifolia* as the lectotype of *Lepista*, since this species is representative for *Lepista* and consistent to the original description of *Aga. lepista* by Fries (1821). Taxa in *Lepista* s.str. have more or less white-toned basidiomes, overall duller and lighter in color and more decurrent lamellae compared to species in the other two *Lepista* clades, viz., *Collybia* subgen. *Leucocalocybe* and *Crassicybe*. Based on these results, *Lepista* s.str. currently contains at least three members: *L. densifolia*, *L. panaeolus* and *L. subconnexa*.

Pseudolyophyllum Raithelth., Metrodiana 6(3): 71 (1977).

\equiv *Clitocybe* subgen. *Pseudolyophyllum* Singer [as ‘*Pseudo-Lyophyllum*’], Anns mycol. 41(1/3): 41 (1943).

\equiv *Pseudolyophyllum* (Singer) Raithelth., Metrodiana 8(2–3): 53 (1979), Nom. inval., Art. 41.1 (Shenzhen).

Diagnosis: Differs from *Clitocybe* s.str. by its hygrophalous basidiomes and pale to gray or brown-toned lamellae.

Type species: *Pseudolyophyllum metachroum* (Fr.) Raithelth. ex Z.M. He & Zhu L. Yang.

Description: Basidiomes mostly medium-sized, rarely large, clitocyboid. Pileus convex, umbonate, appanate to infundibuliform; surface smooth, glabrous, dry to slightly viscid, dull-colored, grayish brown to gray-brown, hygrophalous. Lamellae decurrent to deeply decurrent, crowded, pale, grayish or brownish to gray or brown. Stipe central, (sub)cylindrical, longitudinally fibrillose, solid or hollow, concolorous with pileus or paler; base tomentose. Basidiospores generally ellipsoid to elongate, hyaline, smooth,

thin-walled, inamyloid, single or in tetrads. Basidia clavate, 4-spored. Pleurocystidia and cheilocystidia absent. Lamella trama regular to subregular. Pileipellis a cutis or ixocutis. Clamp connections present. Muscarine absent.

Ecology: Gregarious, on needle or broad leaf litter, also on soil, nitrophilic, in coniferous and broad-leaved mixed forests; summer and autumn.

Distribution: Known from America, Asia, Europe, and Oceania.

Notes: *Pseudolyophyllum* was established as a subgenus of *Clitocybe* by Singer (1943). Harmaja (1969) and Bigelow (1982) maintained this division despite with different treatments of subdivision. It was first elevated to the genus rank by Raithelhuber (1977) without citing the basionym, thus interpreting it as the name of a new taxon. According to the both six-locus and ITS phylogenetic analyses (Figs. 2 and 3), *Pseudolyophyllum* forms a monophyletic clade that includes the type species *P. metachroum*, which is separated from other generic clades within Clitocybaceae.

The phylogenetic analysis of ITS (Fig. 3) also suggests that a clade named *Cli. brunneoceracea* Cleland is positioned at the base of *Pseudolyophyllum* with significant support (Fig. 3, BP = 57%, PP = 0.90). The specimen (GenBank No.: MT537122) has been taxonomically identified by Bougher and Barrett (2020). This Australian species has brown hygrophanous pileus, grayish-brown lamellae, slightly white-floccose stipe base, and smooth, ellipsoid to elongate, inamyloid basidiospores (Grgurinovic 1997), all of which conform to the diagnosis features of *Pseudolyophyllum*. Therefore, this species should be classified under *Pseudolyophyllum*, and the new combination is made below.

Pseudolyophyllum brunneoceraceum (Cleland) Z.M. He & Zhu L. Yang, comb. nov.

MycoBank: MB 847260.

Basionym: *Clitocybe brunneoceracea* Cleland, Trans. Roy. Soc. S. Australia 51: 300 (1927).

Pseudolyophyllum macrobasidium Z.M. He & Zhu L. Yang, sp. nov. Figures 7z and 26

MycoBank: MB 847261.

Etymology: ‘*macrobasidium*’ (Gk.), referring to the large basidia.

Diagnosis: Differs from *P. metachroum* by its relatively larger basidia, non-gelatinized pileipellis, and basidiospores that occur singly.

Type: CHINA. GANSU PROVINCE: Zhuoni County, Yeliguan National Forest Park, on needle litter of *Picea* sp., alt. 2,991 m, in a mixed forest dominated by *Abies* sp., *Larix* sp., *Picea* sp. and *Betula* sp., 14 Sep 2020 M.X. Li 148 (KUN-HKAS 123131, holotype).

Description: Basidiomes medium-sized to large, clitocyboid. Pileus 1–7 cm in diam, at first convex, soon plano-convex with obtuse umbo when young, later depressed and

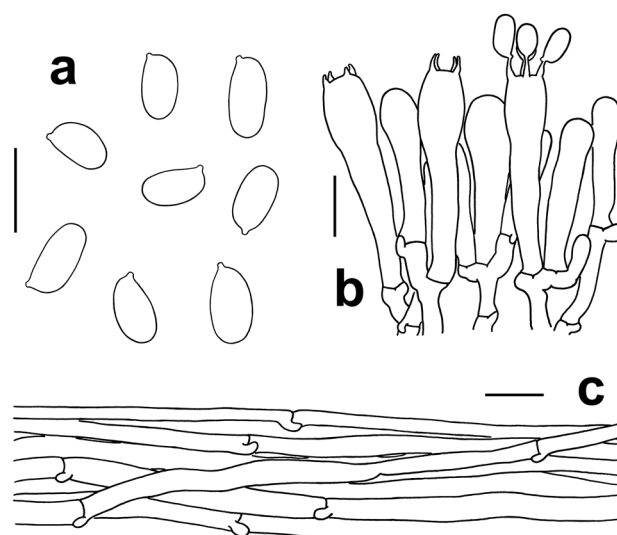


Fig. 26 Microscopic features of *Pseudolyophyllum macrobasidium* (KUN-HKAS 123131, holotype). **a** Basidiospores; **b** Hymenium and subhymenium; **c** Pileipellis. Bars = 10 μ m

subinfundibuliform; surface smooth, glabrous, not pruinose, tan (4B4–8) to brownish gray (4B2–3), hygrophanous; margin acute, non-striate even when wet, at first inrolled, later straight to reflexed; center distinctly darker in color; context thin (0.2–0.3 cm thick), watery, concolorous with pileus surface. Lamellae decurrent to deeply decurrent, crowded, brownish (2B3) to grayish (3B2), arcuate, not broad (0.2–0.4 cm high), never intervenose, at times forked near stipe apex; edges smooth. Stipe 2–7 \times 0.2–0.8 cm, central, cylindrical, hollow; surface concolorous with pileus, usually with white longitudinal fibrils and white-floccose at apex; base not inflated, covered with some white mycelium; context concolorous with stipe surface, watery. Odor fungoid.

Basidiospores [60/3/3] (6)7–9.5(11) \times 3.5–5 μ m, $Q = (1.56)1.71–2.18(2.2)$, $Q_m = 1.92 \pm 0.16$, elongate to cylindrical, smooth, hyaline, thin-walled, inamyloid, single. Basidia 28–44 \times 6–8 μ m, clavate, 4-spored, hyaline, thin-walled; sterigmata up to 4 μ m long. Pleurocystidia and cheilocystidia absent. Lamella trama regular to subregular; hyphae 2–8(12) μ m wide, hyaline, cylindrical, thin-walled. Pileipellis composed of almost parallel-arranged, thin-walled cylindrical hyphae 2–6(8) μ m wide. Stipitipellis a cutis composed of parallel, thin- to slightly thick-walled (about 0.5 μ m), cylindrical hyphae 2–5(7) μ m wide; occasionally with hyphoid caulocystidia 12–22 \times 2–3 μ m on the surface. Clamp connections present in all parts of basidiome.

Ecology: Usually gregarious, on needle or broad leaf litter, in coniferous and broad-leaved mixed forests; late summer and early autumn.

Distribution: Known from Western China and Kashmir Himalaya.

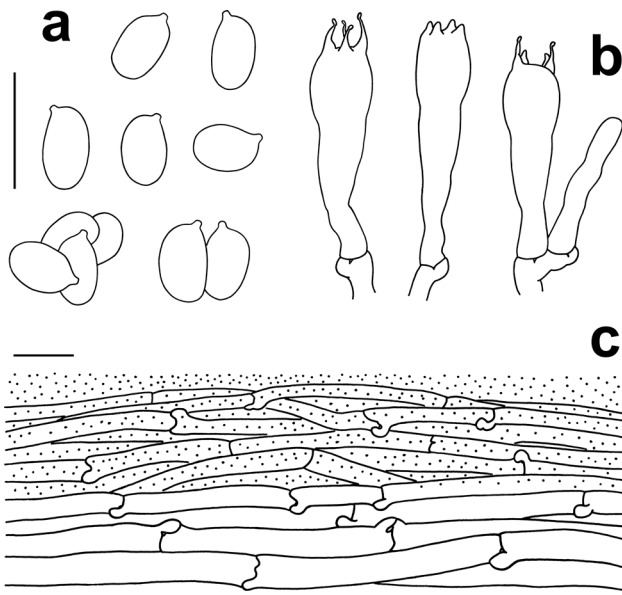


Fig. 27 Microscopic features of *Pseudolyophyllum metachroum* (KUN-HKAS 123133). **a** Basidiospores; **b** Basidia; **c** Pileipellis. Bars = 10 μ m

Additional specimens examined: CHINA. SICHUAN PROVINCE: Hongyuan County, Hongshan, on needle and broad leaf litter, in a coniferous and broad-leaved mixed forest, alt. ca. 3,500 m, 24 Aug 2019, X.H. Wang 6450 (KUN-HKAS 123132). TIBET: Leiwuqi County, on needle and broad leaf litter, in a coniferous and broad-leaved mixed forest, alt. ca. 3,700 m, 16 Aug 2018, X.H. Wang 5322 (KUN-HKAS 123130).

Notes: Judging from the ITS tree (Fig. 3), the sample of '*Clitocybe vibecina*' (MH930886) from Kashmir Himalaya should also be identified as *P. macrobasidium*, because it clusters together with the new species with very low genetic differences (pairwise identity value = 99.8%). This taxon should be a high-montane species, as its specimens were collected from forests at high altitudes. *Clitocybe vibecina* (Fr.) Quél. differs from *P. macrobasidium* by its rancid-farinaceous odor, slightly gelatinized pileipellis, and smaller basidiospores (Harmaja 1969: 5–7 \times 2.9–3.6 μ m; Breitenbach and Kräenzlin 1991: 5.2–6.8 \times 3–4.1 μ m; Kuyper 1995: 4.5–7 \times 3.5–4.5 μ m).

Pseudolyophyllum metachroum (Fr.) Raitelh. ex Z.M. He & Zhu L. Yang, comb. nov. Figures 7aa and 27

Mycobank: MB 847258.

Basionym: *Agaricus metachrous* Fr., Observ. mycol. (Havniae) 2: 110 (1818).

\equiv *Agaricus metachrous* Fr., Syst. mycol. (Lundae) 1: 172 (1821).

\equiv *Clitocybe metachroa* (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 120 (1871).

\equiv *Omphalia metachroa* (Fr.) Quél., Enchir. fung. (Paris): 25 (1886).

\equiv *Omphalia mortuosa* (Fr.) Quél., Enchir. fung. (Paris): 25 (1886).

\equiv *Collybia metachroa* (Fr.) Costantin & L.M. Dufour, Nouv. Fl. Champ., Edn 1 (Paris): 22 (1891).

\equiv *Tricholoma metachroum* (Fr.) Lapl., Dictionnaire iconographique de Champignons supérieures (Hyménomycètes) (Paris): 337 (1894) \equiv *Lepista metachroa* (Fr.) Harmaja, Karstenia 15: 14 (1976).

\equiv *Pseudolyophyllum metachroum* (Fr.) Raitelh. [as '*metachroa*'], Metrodiana 6(3): 71 (1977), Nom. inval., Art. 41.5 (Shenzhen).

\equiv *Pseudolyophyllum metachroum* (Fr.) Raitelh. [as '*metachroa*'], Metrodiana 7(3–4): 73 (1978), Nom. inval., Art. 41.5 (Shenzhen).

= *Agaricus mortuosus* (Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 79 (1838) [1836–1838].

= *Clitocybe mortuosa* (Fr.) Gillet, Hyménomycètes (Alençon): 168 (1874) [1878].

Diagnosis: Differs from *P. macrobasidium* by its relatively smaller basidia, gelatinized pileipellis, and predominance of basidiospores occurring in tetrads.

Description: Basidiomes medium-sized, clitocyboid. Pileus 2.5–5 cm in diam, plano-convex to applanate and with depressed center, infundibuliform or umbilicate; surface glabrous, gray-brown (5C2–6) at spots or areas which are wet, dark gray-brown (6D2) at center, hygrophanous and becoming whitish (2A1) on drying; margin striate, acute, incurved or expanding to even when mature, becoming broadly undulate in age; context watery, concolorous with pileus surface but paler. Lamellae decurrent, crowded, beige (2B1) to brownish (1B2), narrow to moderately broad (0.2–0.6 cm high), sometimes forked near stipe apex; edges smooth. Stipe 3.5–6.5 \times 0.5–0.8 cm, central, nearly equal, solid when young, later becoming hollow; surface concolorous with pileus but paler near apex, sometimes finely whitish-fibrillose longitudinally; base not inflated, usually white-tomentose; context watery, nearly concolorous with stipe surface. Odor fungoid, not pungent.

Basidiospores [60/3/1] (5)5.5–9(10) \times (3)3.5–5(5.5) μ m, Q = (1.38)1.45–1.97(2), Qm = 1.65 \pm 0.15, mostly ellipsoid, also elongate sometimes, smooth, hyaline, thin-walled, inamyloid, predominantly in tetrads. Basidia 23–32 \times 5–8 μ m, clavate, 4-spored, hyaline, thin-walled; sterigmata up to 5 μ m long. Cystidia absent. Lamella trama regular; hyphae 3–8(12) μ m wide, hyaline, cylindrical, thin-walled. Pileipellis a slightly developed ixocutis, made up of parallel to slightly interwoven, thin- to slightly thick-walled (0.3–0.7 μ m), cylindrical hyphae 2–6(8) μ m wide, with intracellular pigment. Stipitipellis a cutis made up of thin-

slightly thick-walled (0.3–0.6 μm), cylindrical hyphae 2–5 μm wide. Clamp connections present in all parts of basidiome.

Ecology: Gregarious, generally on needle litter, sometimes on broad leaf litter, also on soil but not often; autumn.

Distribution: Widespread in Europe, North America and Asia.

Specimen examined: CHINA. YUNNAN PROVINCE: Yulong County, Lijiang Alpine Botanical Garden, on broad leaf and needle litter, alt. ca. 2,800 m, 29 Sep 2019, J.W. Liu 2174 (KUN-HKAS 123133).

Notes: The basidiospore size of the Chinese sample (5.5–9 \times 3.5–5) is comparable to that of European *Cli. metachroa* described by Harmaja (1969) (6.4–9.5 \times 3.5–4.2 μm) and Kuyper (1995) (5.5–8.5 \times 3.5–5 μm). The other typical features observed from the Chinese sample, such as a gray-brown, marginally striate, glabrous, hygrophanous pileus, brownish gray lamellae, a stipe that is whitish at apex but becomes dark towards base, a slightly gelatinized pileipellis, and ellipsoid to elongate basidiospores that predominantly occur in tetrads, also correspond well with their descriptions.

The phylogenetic analysis based on ITS (Fig. 3) shows that the Chinese sample KUN-HKAS 123133, along with nine samples from Estonia, Denmark, France and Norway identified as *Cli. metachroa* (UNITE No.: UDB015698, UDB015736, UDB015737, UDB019582, UDB034149, UDB037939, and UDB039788) and four samples from France, Italy, Russia, and USA identified as '*Cli. vibecina*' (GenBank No.: ON322984, JF907821, MH930181, and OM987425), form a clade. The ITS sequence of the Chinese sample exhibits a similarity ranging from 99.25% to 99.72% with respect to these European and North American samples, indicating that they are conspecific. However, the clade should be recognized as *Cli. metachroa* rather than *Cli. vibecina*, because that the latter has rancid to farinaceous smell and shorter, predominantly single basidiospores (Harmaja 1969: 5–7 μm long; Kuyper 1995: 4.5–7 μm). These features are clearly distinct from our sample. Hence, the Chinese material is identified as *P. metachroum* (\equiv *Cli. metachroa*). The ITS tree (Fig. 3) also indicates the inclusion of sequences named *Cli. amarescens* Harmaja, *Cli. metachroides* Harmaja, *Cli. olivaceobrunnea* H.E. Bigelow, and *Cli. vibecina* within *Pseudolyophyllum*. However, we are unable to determine their specific clades. It is evident that these morphologically related species previously placed in *Clitocybe* subgen. *Pseudolyophyllum* (Harmaja 1969; Singer 1986) would eventually be transferred to *Pseudolyophyllum*, which needs further confirmation in subsequent work.

Singerocybe Harmaja, Karstenia 27(2): 71 (1988) [1987].

Type species: *Singerocybe viscida* Harmaja, Karstenia 27(2): 72 (1988) [1987].

Notes: The monophyly of *Singerocybe* has been shown by Qin et al. (2014), and our phylogenetic analyses have further elucidated its accurate placement within the phylogeny of Clitocybaceae (Clade 8, Figs. 2 and 4). The type species of the genus, *S. viscida*, has not yet undergone DNA-based phylogenetic analysis, which necessitates future confirmation. It is not surprising that no muscarine has been detected in *Singerocybe* by LC–MS/MS, since one of its members, viz. *S. alboinfundibuliformis* (Seok et al.) Zhu L. Yang et al., is often eaten by local mycophagists in Guizhou and Yunnan Provinces, China (Deng 2016; Yang et al. 2021).

Discussion

The monophyly of Clitocybaceae

The monophyly of Clitocybaceae was not well-supported in previous studies. An LSU phylogenetic analysis by Moncalvo et al. (2002) and a three-locus phylogeny (LSU, SSU and *RPB2*) by Sánchez-García et al. (2014) suggested that the Clitocybaceae formed a monophyletic clade, but without support. Four-locus phylogenetic analyses (LSU, SSU, *TEF1* and *RPB2*) could support the familial clade, but with weak support, such as 56% BP, 0.93 PP in Alvarado et al. (2018a), 57% BP, 0.93 PP in Alvarado et al. (2018b), and 0.95 PP in Vizzini (2020b). A six-locus (ITS, LSU, *TEF1*, *RPB1*, *RPB2*, and *ATP6*) analysis by He and Yang (2022) further improved the support to 76% BP, 0.98 PP, but only seven species and 11 samples of the family were involved.

In the present work, an updated six-locus phylogenetic analysis was performed with 41 species of Clitocybaceae from 100 samples as well as all other available representatives of Tricholomatineae. The resulting phylogram moderately supports (71% BP and 0.90 PP, Fig. 1) the conclusion that the Clitocybaceae is monophyletic, even though such a large dataset is used. In future, designing a phylogenomic analysis to cover as many major lineages of Tricholomatineae as possible could fully support the monophyly of Clitocybaceae.

The rearrangement within Clitocybaceae

Despite the proposal of Clitocybaceae by Vizzini (2020a), the molecular phylogenetic basis for its subdivision remains ambiguous. Previous phylogenetic studies conducted in the past two decades have shown the inclusion of five genera in the Clitocybaceae, namely *Clitocybe*, *Collybia*, *Dendrocollybia*, *Lepista* and *Singerocybe*; however, it is noteworthy that both *Clitocybe* and *Lepista* were found to be polyphyletic (Moncalvo et al. 2002; Walther et al. 2005; Matheny et al. 2006; Binder et al. 2010; Sánchez-García et al. 2014; Cooper 2016; Alvarado et al. 2015, 2018a, b; He and Yang 2022).

Furthermore, previous multi-locus phylogenetic analyses did not target at the Clitocybaceae, and only included a few species and genera of the family. While an ITS-LSU phylogeny by Alvarado et al. (2015) and an ITS phylogeny by Cooper (2016) recovered the species and genera of the family to some extent, the nucleotide sequences of one or two DNA regions were insufficient to resolve the specific and generic relationships correctly.

In the present work, mutually supported phylogenetic analyses based on ITS, six loci and 485 genes with a significantly improved taxon sampling (ITS: 285 samples from 64 species; six-locus: 100 samples from 41 species; 485-gene: 41 samples from 27 species), were carried out to recover the species, genera and infrafamilial relationships of Clitocybaceae as comprehensively as possible. Our molecular evidence suggests that the family can be classified into nine clades (Fig. 2). Clades 6 to 9 are recognized as the genera *Lepista* s.str., *Dendrocollybia*, *Singerocybe*, and *Clitocybe* s.str., respectively. Clades 1 to 5, containing species previously treated as *Clitocybe* or *Lepista*, require taxonomic revision due to their deviation from *Lepista* s.str. and *Clitocybe* s.str. The focal point of concern lies in the classification of Clades 1 to 5, which are being considered as either genera or subgenera here.

Based on the phylogenetic and phylogenomic results (Figs. 2 and 4), six alternative taxonomic treatments for the group comprising Clades 1 to 5 are possible: (i) treating each clade as an independent genus; (ii) grouping Clades 1 and 2 under the genus *Collybia*, while assigning different genera to the other three clades; (iii) recognizing Clades 1 to 4 as subgenera of *Collybia*, with Clade 5 treated as a separate genus; (iv) considering all five clades together as a single genus; (v) treating Clades 3 and 4 together as a genus, while considering the other three clades as different genera; or (vi) recognizing Clades 1 and 2, and Clades 3 and 4, as two genera, while treating Clade 5 as a distinct genus. We exclude options (i), (ii), (v) and (vi) due to the close phylogenetic relationship between Clades 1 to 4, as well as the fact that not all mean p-distances between genera exhibit higher values than those within genera if divided in such ways (Fig. 6A, B, E and F, Table S6, S7, S10 and S11). Moreover, in our perspective, the morphological characters traditionally used to distinguish *Clitocybe* from *Lepista*, such as spore ornamentation and spore cyanophily, cannot be considered basis of generic classification for Clades 1 to 5 consisting of previous *Clitocybe* or *Lepista* species.

Bigelow and Smith (1965) and Bigelow (1982) placed *Lepista* as a section of *Clitocybe* and thought that the rough-spored species could not be unified into a single evolutionary lineage. Our phylogenetic analyses (Figs. 1, 2, 3) also support that rough-spored *Lepista* s.l. species are accommodated in four distinct clades (Clades 2, 4, 6, and the genus

Paralepista). *Lepista irina* has finely ornamented to smooth basidiospores under a light microscope or electron microscope (Bigelow and Smith 1965; Pegler and Young 1971; Bigelow 1981). The Chinese materials (KUN-HKAS 45515, 82928 and 105553, Clade 2) examined by us also show a significant proportion of smooth basidiospores when viewed under an oil immersion lens.

Harmaja (1976) transferred a number of *Clitocybe* species to *Lepista*, such as *Cli. phyllophila* and *Cli. odora* (in Clade 1), *Cli. metachroa* and *Cli. metachroides* (in Clade 5), based on their cyanophilous spore wall. However, our phylogenetic analyses (Figs. 1 and 2) report that the spore cyanophily cannot have a phylogenetic signal at genus level. Clades 1 and 3 comprise species with basidiospores that are either completely acyanophilous or weakly cyanophilous, while Clades 2 and 4 include species possessing strongly cyanophilous basidiospores. In contrast, Clade 5 contains species with basidiospores ranging from weakly to moderately cyanophilous (Harmaja 1978).

The production of muscarine, studied here in details, is not suitable for generic classification either. This is because it is exclusively found in taxa belonging to Clade 1 and does not occur in all species within this clade (Figs. 2 and 4). Although both options (iii) and (iv) satisfy the condition of having intergeneric mean p-distances greater than intrageneric mean p-distances (Fig. 6C and D, Table S8 and S9), we prefer to option (iii), viz. treating Clades 1 to 4 together as the genus *Collybia*, while recognizing Clade 5 as the genus *Pseudolyophyllum*. We have the following five reasons. Firstly, option (iii) displays lower intrageneric p-distances in comparison to option (iv), while exhibiting a higher disparity between intrageneric and intergeneric p-distances. Secondly, the median divergent times of the genera in option (iii) exhibit a higher degree of proximity compared to option (iv). Thirdly, there is a clear increase in genetic distance between nodes when Clade 5 is connected (Figs. 2 and 4). Fourthly, Clade 5 comprises taxa previously classified in *Clitocybe* subgen. *Pseudolyophyllum*, characterized by pilei and lamellae in shades of pale to dark gray, gray-brown or brown-gray with intraparietal or incrusting pigment (Harmaja 1969; Bigelow 1982; Singer 1986). The color of the basidiomes, particularly the lamellae, distinguishes them from other previous *Collybia*, *Clitocybe* and *Lepista* species in Clades 1 to 4, whose lamellae are white, whitish, cream, lilac or lightly tinted with yellowish, buff or pinkish, but never gray to gray brown. Fifthly, if option (iv) was to be pursued, it would result in the concealment of many genetic variations and evolutionary lineages, thereby impeding our comprehension of the evolutionary patterns within the major clades of this family.

In addition, we suggest to avoid erecting unnecessary new genera (Vellinga et al. 2015), since Clades 1 to 4 are so closely phylogenetic related and morphologically similar in

various aspects. According to our genetic distance analysis, the mean p-distances between the genera of Clitocybaceae ranged from 7.02% to 15.81% (Table S8). As a reference, we calculated the mean p-distances between the 59 generic clades of Boletaceae divided by Wu et al. (2014), and the resulting values were greater than or equal to 6.18% (data not shown). Therefore, 7% genetic distance could be considered as the intergeneric boundary for Clitocybaceae. The main framework we propose is to recognize six genera in the Clitocybaceae: *Collybia* (a conserved name listed in Appendix IIIB, ICBN), *Pseudolyophyllum*, *Lepista*, *Dendorcollybia*, *Singerocybe*, and *Clitocybe*, and further to divide the newly emended *Collybia* into four subgenera corresponding with Clades 1 to 4 in Fig. 2.

The taxonomic distribution and evolution of muscarine within Clitocybaceae

Analyses aimed to resolve the relationship between phylogeny and muscarine production within Clitocybaceae have never been performed before. Based on our phylogenetic framework of Clitocybaceae (Fig. 2), we provide a comprehensive species of the family assayed for muscarine. Although the collections analyzed are all from China, they represent almost all the clades of the ITS tree inferred from publicly available sequences of Clitocybaceae (Fig. 3), including some species originally described from North America and Europe that also occur in China. In the literature, only three species of Clitocybaceae, *Cli. dealbata*, *Cli. phyllophila* and *Cli. rivulosa*, have been confirmed to contain muscarine (Genest et al. 1968). We have reviewed edible species involved in this family, which can be considered to be muscarine-lacking, namely *Cli. nebularis*, *Cli. odora*, *L. irina*, *L. nuda*, *L. personata*, *L. sordida*, *Leu. mongolica*, and *S. alboinfundibuliformis* (Bon 1988; Phillips 1990, 2005; Courtecuisse and Duhem 1995; Laux 2002; Dai et al. 2010; Deng 2016; Wu et al. 2019; Yang et al. 2021). On this basis, we add new data from assays of 68 collections from 32 species (Table 1), which are distributed in eight of the nine clades of Clitocybaceae (Fig. 2).

According to our phylogenetic and biochemical findings (Figs. 2 and 4), muscarine-containing species of Clitocybaceae are only restricted to the *Collybia* subgen. *Collybia* clade, while being absent from the other clades. Furthermore, the taxonomic distribution of muscarine is monophyletic. These results thus indicate that (i) the muscarine pathway should have evolved independently in the Clitocybaceae, and (ii) the presence of muscarine is a synapomorphy of those poisonous collybias. It should be pointed out that we were not able to include *Dendorcollybia* in the muscarine assays. It is necessary to check species of this genus in the future.

The distribution of muscarine in the Clitocybaceae shows a much stronger correlation with phylogeny than that observed in the Inocybaceae. In the Clitocybaceae, the presence of muscarine is ancestral for a monophyletic clade (Clades I to VII of *Collybia* subgen. *Collybia*, Fig. 4) without later losses. Meanwhile, in the Inocybaceae, muscarine is found in five of its seven major genera: *Inocybe*, *Nothocybe* Matheny & K.P.D. Latha, *Pseudosperma* Matheny & Esteve-Rav., *Mallocybe* (Kuyper) Matheny, Vizzini & Esteve-Rav., and *Inosperma* (Kühner) Matheny & Esteve-Rav., in which muscarine has evolved independently on several occasions, together with several losses (Kosentka et al. 2013; Deng et al. 2021; Yan et al. 2022; Zhao et al. 2022). Interestingly, the phylogenetic distribution pattern of muscarine within *Collybia* subgen. *Collybia* is strikingly similar to that of alpha-amanitin within *Amanita* sect. *Amanita*. Both toxins are individually present in every species of the two groups, except for the earliest diverging species (i.e., *C. odora* and *A. zangii*, respectively) (Cai et al. 2014). As muscarine is a highly conserved trait for the monophyletic clade of poisonous collybias in the Clitocybaceae, sequencing can serve as a more convenient and low-cost alternative way to deduce whether muscarine is present in an unknown or unfamiliar Clitocybaceae species than LC–MS/MS.

Toxicity and harmfulness of poisonous Clitocybaceae species

Muscarine-producing species of Clitocybaceae are those clitocyboids belonging to *Collybia* subgen. *Collybia* (except for *C. odora*). In our biochemical study, muscarine was detected positive in 18 *Collybia* species from 41 samples and the resulting concentrations in dry basidiomes ranged from 6 to 379 mg/kg (average value = 55 mg/kg, Table 1). The muscarine concentration values of collybias obtained by us are of the same order of magnitude as those measured in a previous study of Genest et al. (1968), in which samples of *Clitocybe cerussata* (Fr.) P. Kumm. (= *Collybia phyllophila*), *Clitocybe dealbata* (= *Collybia dealbata*) and *Clitocybe rivulosa* (= *Collybia rivulosa*) were found to contain 120, (100, 830, 1,800) and 350 mg/kg muscarine (dry weight), respectively.

The lethal dose of muscarine for humans is not precisely known, with estimates ranging from 180 to 300 mg (Bresinsky and Besl 1990) and 40 to 495 mg (Benjamin 1995). Based on the concentration data, *Collybia* species usually do not induce fatal poisonings. The concentration of muscarine in members of Inocybaceae appear much higher compared to that found in species belonging to Clitocybaceae. Many Inocybaceae species, such as *Inocybe squarrosolutea* (Corner & E. Horak) Garrido (up to 1,683 mg/kg, Li et al. 2021a, b, c, d) and *Pseudosperma umbrinellum* (Bres.) Matheny &

Esteve-Rav. (3022 to 4002 mg/kg, Zhang et al. 2022), contain thousands mg/kg of muscarine. The concentrations can sometimes exceed 10,000 mg/kg, as observed in *Inosperma muscarium* Y.G. Fan et al. and *I. hainanense* Y.G. Fan et al. (16,030 and 11,870 mg/kg, Deng et al. 2021), thus eating a single mushroom can be lethal. As far as we know, only *C. dealbata* has been detected to have 1,800 mg/kg muscarine (Genest et al. 1968), the highest value that has been recorded in the Clitocybaceae so far. Consequently, muscarine-containing Clitocybaceae species overall seem to be less dangerous than muscarine-containing Inocybaceae species.

Species diversity of Clitocybaceae

Approximately 300 species names of Clitocybaceae have been reported in the literature (Harmaja 1969; Bigelow 1982; Breitenbach and Kränzlin 1991; Bas et al. 1995). Many of them have been or would be excluded from the family or reduced to synonymy based on molecular approaches (Redhead et al. 2002; Ammirati et al. 2007; Vizzini et al. 2010, 2012; Lavorato et al. 2015; Alvarado et al. 2015, 2018a, b; Matheny et al. 2020; He and Yang 2021). Nevertheless, many clitocyboid species remain to be found and studied. In this study, 32 species of Clitocybaceae s.str. from China are recognized, of which 19 (including two unnamed species), namely about 60%, are new to science.

In China, except for *Singerocybe* (Qin et al. 2014), taxa of Clitocybaceae were rarely reported or studied in depth before our study. Many of the new taxa from China have been misidentified as other named species from Europe and North American due to their similar morphology. For example, the newly discovered *C. subtropica* and *C. pannosa* were always named *C. dealbata* and *Cli. fragrans* (Li et al. 2022a; Gu et al. 2022). In fact, due to the insufficiently informative diagnostic characters caused by interspecific similarities and intraspecific phenotypic plasticity, many species of Clitocybaceae are difficult to be identified to species level without DNA data. As a result, other clitocyboid taxa previously reported in Chinese scientific literature and identified as European or North American species names, such as *Cli. rivulosa* and *Cli. dealbata* var. *sudorifa* Pec (i.e., Mao 2000), should be further verified by sequencing. Additionally, our worldwide phylogenetic analysis of ITS (Fig. 3) suggests that there are at least nine different unnamed clades, which may represent potentially novel taxa.

In the Clitocybaceae, *Collybia* subgen. *Collybia* is a particularly species-rich group, with several useful diagnostic morphological, chemical, and ecological characters. Macroscopical dimensions and colors, hygrophanity, adhesion and length of basidiospores, 2- or 4-spored basidia,

presence or absence of muscarine, and substrates for growth, can be useful characters to distinguish different clades within the subgenus (Fig. 4). As shown in Figs. 2 and 3, the species diversity of *Collybia* subgen. *Collybia* in China or even all over the world, is obviously richer than that of the other three subgenera, even compared with the other five genera in the family. Almost all species of *Collybia* subgen. *Collybia* produce muscarine, but the earliest diverging species *C. odora* is an exception (Figs. 2 and 4). The ability to produce muscarine could be a factor to accelerate or promote speciation.

Most species of Clitocybaceae are saprotrophic while species of Clade IV in *Collybia* subgen. *Collybia* (*C. cirrhata*, *C. cookei* and *C. tuberosa*) and *Dendrocollybia* (*D. racemosa*) are fungicolous (Harmaja 2003; Læssøe and Petersen 2019). The relative long genetic distances observed between *C. cirrhata* and other species of *Collybia* subgen. *Collybia* in the 485-gene phylogenetic analysis (Fig. 4B), as well as between *Dendrocollybia* and other genera of Clitocybaceae in the six-locus phylogenetic analysis (Fig. 2) could be caused by their unique ecological niche.

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Author contributions Z-MH conceived, designed and complete the experiments under the guidance of ZLY. Z-MH wrote the manuscript and ZLY revised it. Z-HC investigated two cases of mushroom poisoning and identified two specimens of *Collybia* collected from the scene. TB collected and identified four very critical specimens of *Collybia*. Z-MH and G-SW did the genome assemble and phylogenomic analysis.

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Data availability The DNA sequences obtained in this study have been submitted to GenBank.

Declarations

Competing interests The authors declare no competing interests.

References

- Alvarado P, Moreno G, Vizzini A, Consiglio G, Manjón JL, Setti L (2015) *Atractosporocybe*, *Leucocybe* and *Rhizocybe*: three new clitocyboid genera in the Tricholomatoid clade (Agaricales) with notes on *Clitocybe* and *Lepista*. *Mycologia* 107:123–136. <https://doi.org/10.3852/13-369>
- Alvarado P, Moreau PA, Sesli E, Khodja LY, Contu M, Vizzini A (2018a) Phylogenetic studies on *Bonomyces* (Tricholomatineae, Agaricales) and two new combinations from *Clitocybe*. *Cryptogam Mycol* 39:149–168. <https://doi.org/10.7872/crym/v39.iss2.2018.149>
- Alvarado P, Moreau PA, Dima B, Vizzini A, Consiglio G, Moreno G, Setti L, Kekki T, Huhtinen S, Liimatainen K, Niskanen T (2018b) Pseudoclitocybaceae fam. nov. (Agaricales, Tricholomatineae), a new arrangement at family, genus and species level. *Fungal Divers* 90:109–133. <https://doi.org/10.1007/s13225-018-0400-1>
- Ammirati JF, Parker AD, Matheny PB (2007) *Cleistocybe*, a new genus of Agaricales. *Mycoscience* 48:282–289. <https://doi.org/10.1007/s10267-007-0365-5>
- Andrews S (2010) FastQC: a quality control tool for high throughput sequence data. *Babraham Bioinformatics*. <https://www.bioinformatics.babraham.ac.uk/projects/fastqc/>. Accessed 26 April 2010
- Bas C (1969) Morphology and subdivision of *Amanita* and a monograph of its section *Lepidella*. *Persoonia* 5:285–579
- Bas C, Kuyper TW, Noordeloos ME, Vellinga EC (1995) *Flora Agaricina Neerlandica*, vol 3. A.A. Balkema, Rotterdam
- Benjamin DR (1995) *Mushrooms poisons and panaceas: a handbook for naturalists, mycologists and physicians*. W.H. Freeman, New York
- Bigelow HE (1981) Spore ornamentation in the Tricholomataceae I. *Mycologia* 73:128–140. <https://doi.org/10.1080/00275514.1981.12021326>
- Bigelow HE (1982) North American species of *Clitocybe*, Part I. Strauss & Cramer GmbH, Vaduz
- Bigelow HE, Smith AH (1969) The status of *Lepista*—a new section of *Clitocybe*. *Brittonia* 21:144–177. <https://doi.org/10.2307/2805523>
- Binder M, Hibbett DS (2003) Oligonucleotides. The Education Network of Clark University. http://www.clarku.edu/faculty/dhibbett/Protocols_Folder/Primers/Primers.htm. Accessed 18 Sep 2003
- Binder M, Larsson KH, Matheny PB, Hibbett DS (2010) Amylocorticiales ord. nov. and Jaapiales ord. nov.: early diverging clades of Agaricomycetidae dominated by corticioid forms. *Mycologia* 102:865–880. <https://doi.org/10.3852/09-288>
- Bolger AM, Lohse M, Usadel B (2014) Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics* 30:2114–2120. <https://doi.org/10.1093/bioinformatics/btu170>
- Bon M (1988) *Pareys Buch der Pilze*. Verlag Paul Parey, Hamburg
- Bougher NL, Barrett MD (2020) Fungi and slime molds recorded in surveys at Kings Park and Bold Park—urban bushlands Perth, Western Australia. *West Aust Nat* 31:191–251
- Breitenbach J, Kränzlin F (1991) *Fungi of Switzerland 3: Boletales and Agaricales*. Mykologia, Luzern
- Bresinsky A, Besl H (1990) Muscarine syndrome. In: Bresinsky A, Besl H (eds) *A colour atlas of poisonous fungi*. Wolfe, London, pp 71–73
- Cai Q, Tulloss RE, Tang LP, Tolgor B, Zhang P, Chen ZH, Yang ZL (2014) Multi-locus phylogeny of lethal amanitas: implications for species diversity and historical biogeography. *BMC Evol Biol* 14:143. <https://doi.org/10.1186/1471-2148-14-143>
- Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Mol Bio Evol* 17:540–552. <https://doi.org/10.1093/oxfordjournals.molbev.a026334>
- Cho SE, Kwag YN, Jo JW, Han SK, Oh SH, Kim CS (2020) Macro-fungal diversity of urbanized areas in southern part of Korea. *J Asia-Pac Biodivers* 13:189–197. <https://doi.org/10.1016/j.japb.2020.01.005>
- Clements FE, Shear CL (1931) *The genera of fungi*. H.W. Wilson Co., New York
- Coil D, Jospin G, Darling AE (2014) A5-miseq: an updated pipeline to assemble microbial genomes from Illumina MiSeq data. *Bioinformatics* 31:587–589. <https://doi.org/10.1093/bioinformatics/btu661>
- Cooper J (2016) *Mycological Notes 36: notes on NZ Clitocybe and allies (Clitocybaceae)*. The Fungal Network of New Zealand. https://www.funnz.org.nz/sites/default/files/2016-MycNotes36-Clitocybaceae_1.pdf. Accessed 19 Dec 2016
- Courtecuisse R, Duhem B (1995) *Mushrooms and toadstools of Britain and Europe*. Harper Collins Publishers, New York
- Dai YC, Zhou LW, Yang ZL, Wen HA, Bau T, Li TH (2010) A revised checklist of edible fungi in China. *Mycosystema* 29:1–21. <https://doi.org/10.13346/j.mycosystema.2010.01.022>
- Davis RM, Sommer R, Menge JA (2012) *Field guide to mushrooms of Western North America*. University of California Press, Berkeley
- Deng CY (2016) A new genus recorded to Guizhou—*Singerocybe*. *Guizhou Sci* 34:29–31
- Deng LS, Kang R, Zeng NK, Yu WJ, Chang C, Xu F, Deng WQ, Qi LL, Zhou YL, Fan YG (2021) Two new *Inosperma* (Inocybaceae) species with unexpected muscarine contents from tropical China. *Mycosyst* 85:87–108. <https://doi.org/10.3897/mycokeys.85.71957>
- Deng LS, Yu WJ, Zeng NK, Zhang YZ, Wu XP, Li HJ, Xu F, Fan YG (2022) A new muscarine-containing *Inosperma* (Inocybaceae, Agaricales) species discovered from one poisoning incident occurring in tropical China. *Front Microbiol* 13:923435. <https://doi.org/10.3389/fmicb.2022.923435>
- Donk MA (1949) Nomenclatural notes on generic names of agarics (Fungi: Agaricales). *Bull Jard Bot Buitenzorg* 18:271–402
- Donk MA (1962) The generic names proposed for Agaricaceae. J. Cramer, Weinheim
- Drummond AJ, Ho SYW, Phillips MJ, Rambaut A (2006) Relaxed phylogenetics and dating with confidence. *PLoS Biol* 4:e88. <https://doi.org/10.1371/journal.pbio.0040088>
- Eugster CH, Schleusener E (1969) Stereomere Muscarine kommen in der Natur vor. Gas-chromatographische Trennung der Norbasen. *Helv Chim Acta* 52:708–715. <https://doi.org/10.1002/hlca.19690520319>
- Fries EM (1821) *Systema Mycologicum, Volumen I. Ex Officina Berlingiana, Lundæ*
- Genest K, Hughes DW, Rice WB (1968) Muscarine in *Clitocybe* species. *J Pharmacol Sci* 57:331–333. <https://doi.org/10.1002/jps.2600570223>
- Gernhard T (2008) The conditioned reconstructed process. *J Theor Biol* 253:769–778. <https://doi.org/10.1016/j.jtbi.2008.04.005>
- Girgis HZ (2015) Red: an intelligent, rapid, accurate tool for detecting repeats de-novo on the genomic scale. *BMC Bioinform* 16:227. <https://doi.org/10.1186/s12859-015-0654-5>
- Grgurinovic CA (1997) Larger fungi of South Australia. Botanic Gardens of Adelaide and State Herbarium and The Flora and Fauna of South Australia Handbooks Committee, Adelaide
- Gu DD, Shi LY, Liu HX, Zhang JX, Yao QG, Wang LA (2022) Biological characteristics and cultivation of *Clitocybe fragrans*. *Mycosystema* 41:647–657. <https://doi.org/10.13346/j.mycosystema.210307>
- Güngör H, Solak MH, Alli H, Işıloğlu M, Kalmiş E (2014) New macrofungi records to the Turkish mycobiota. *Biol Divers Conserv* 7:126–129

- Haas BJ, Salzberg SL, Zhu W, Pertea M, Allen JE, Orvis J, White O, Buell CR, Wortman JR (2008) Automated eukaryotic gene structure annotation using EVIDENCEModeler and the Program to Assemble Spliced Alignments. *Genome Biol* 9:R7. <https://doi.org/10.1186/gb-2008-9-1-r7>
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for windows 95/98/NT. *Nucleic Acids Symp Ser* 41:95–98
- Harada E, Tada N, Kamei I, Morizono T, Matsuda Y (2021) Development of cultivation method for *Leucopaxillus giganteus* fruiting bodies in *Cryptomeria japonica* artificial forests. *J for Res* 26:386–394. <https://doi.org/10.1080/13416979.2021.1935550>
- Harmaja H (1969) The genus *Clitocybe* (Agaricales) in Fennoscandia. *Karstenia* 10:5–121. <https://doi.org/10.29203/ka.1969.62>
- Harmaja H (1974) A revision of the generic limit between *Clitocybe* and *Lepista*. *Karstenia* 14:82–92. <https://doi.org/10.29203/ka.1974.91>
- Harmaja H (1976) A further revision of the generic limit between *Lepista* and *Clitocybe*. *Karstenia* 15:13–15. <https://doi.org/10.29203/ka.1976.106>
- Harmaja H (1978) The division of the genus *Lepista*. *Karstenia* 18:49–54. <https://doi.org/10.29203/ka.1978.137>
- Harmaja H (2003) Notes on *Clitocybe* s. lato (Agaricales). *Ann Bot Fenn* 40:213–218
- He ZM, Yang ZL (2021) A new clitocyboid genus *Spodocybe* and a new subfamily Cuphophylloideae in the family Hygrophoraceae (Agaricales). *MycKeys* 79:129–148. <https://doi.org/10.3897/mycokeys.79.66302>
- He ZM, Yang ZL (2022) The genera *Bonomyces*, *Harmajaea* and *Notholepista* from Northwestern China: two new species and a new record. *Mycol Prog* 21:26. <https://doi.org/10.1007/s11557-022-01786-0>
- Hibbett DS, Grimaldi D, Donoghue MJ (1997) Fossil mushrooms from Cretaceous and Miocene ambers and the evolution of homobasidiomycetes. *Am J Bot* 84:981–991. <https://doi.org/10.2307/2446289>
- Hughes KW, Petersen RH, Johnson JE, Moncalvo JM, Vilgalys R, Redhead SA, Thomas T, McGhee LL (2001) Infragenic phylogeny of *Collybia* s. str. based on sequences of ribosomal ITS and LSU regions. *Mycol Res* 105:164–172. <https://doi.org/10.1017/S0953756200003415>
- Katoh K, Standley DM (2016) A simple method to control over-alignment in the MAFFT multiple sequence alignment program. *Bioinformatics* 32:1933–1942. <https://doi.org/10.1093/bioinformatics/btw108>
- Kalichman J, Kirk PM, Matheny PB (2020) A compendium of generic names of agarics and Agaricales. *Taxon* 69:425–447. <https://doi.org/10.1002/tax.12240>
- Keller O, Kollmar M, Stanke M, Waack S (2011) A novel hybrid gene prediction method employing protein multiple sequence alignments. *Bioinformatics* 27:757–763. <https://doi.org/10.1093/bioinformatics/btr010>
- Kornerup A, Wanscher JH (1978) *Methuen handbook of colour*, 3rd edn. Eyre Methuen, London
- Kosentka P, Sprague SL, Ryberg M, Gartz J, May AL, Campagna SR, Matheny PB (2013) Evolution of the toxins muscarine and psilocybin in a family of mushroom-forming fungi. *PLoS ONE* 8:e64646. <https://doi.org/10.1371/journal.pone.0064646>
- Kretzer AM, Bruns TD (1999) Use of *atp6* in fungal phylogenetics: an example from the Boletales. *Mol Phylogenet Evol* 13:483–492. <https://doi.org/10.1006/mpev.1999.0680K>
- Kühner R (1976) *Agaricales de la zone alpine*. *Lépistées Bull Trimest Soc Mycol France* 92:5–32
- Kühner R, Romagnesi H (1953) *Flore analytique des champignons supérieurs*. Masson et Cie, Paris
- Kuyper TW (1995) Genus *Clitocybe*. In: Bas C, Kuyper TW, Noordeloos ME, Vellinga EC (eds) *Flora Agaricina Neerlandica*, vol 3. A.A.Balkema, Rotterdam, pp 42–62
- Læssøe T, Petersen JH (2019) *Fungi of temperate Europe*. Princeton University Press, Princeton
- Laux HE (2002) *Der neue Kosmos PilzAtlas*. Franckh-Kosmos Verlags GmbH, Stuttgart
- Lavorato C, Vizzini A, Ge ZW, Contu M (2015) Redescription of *Clitocybe umbrinopurpurascens* (Basidiomycota, Agaricales) and revision of *Neohygrophorus* and *Pseudoomphalina*. *Phytotaxa* 219:43–57. <https://doi.org/10.11646/phytotaxa.219.1.3>
- LePage BA, Currah RS, Stockey RA, Rothwell GW (1997) Fossil ectomycorrhizae from the Middle Eocene. *Am J Bot* 84:410–412. <https://doi.org/10.2307/2446014>
- Li H, Wu S, Ma X, Chen W, Zhang J, Duan S, Gao Y, Kui L, Huang W, Wu P, Shi R, Li Y, Wang Y, Li J, Guo X, Luo X, Li Q, Xiong C, Liu H, Gui M, Sheng J, Dong Y (2018) The genome sequences of 90 mushrooms. *Sci Rep* 8:9982. <https://doi.org/10.1038/s41598-018-28303-2>
- Li HJ, Zhang YZ, Liu ZT, Zheng FS, Zhao B, Wu G (2022a) Species diversity of poisonous mushrooms causing poisoning incidents in Yunnan Province, Southwest China. *Mycosystema* 41:1416–1429. <https://doi.org/10.13346/j.mycosysrema.210488>
- Li HJ, Zhang HS, Zhang YZ, Zhou J, Yin Y, He Q, Jiang SF, Ma PB, Zhang YT, Yuan Y, Lang N, Cheng BW, Wang M, Sun CY (2022) Mushroom poisoning outbreaks—China, 2021. *China CDC Wkly* 4:35–40. <https://doi.org/10.46234/ccdcw2022.010>
- Li HJ, Zhang YZ, Zhang HS, Zhou J, Liang JQ, Yin Y, He Q, Jiang SF, Zhang YT, Yuan Y, Lang N, Cheng BW, Wang M, Sun CY (2023) Mushroom poisoning outbreaks—China, 2022. *China CDC Wkly* 5:45–50. <https://doi.org/10.46234/ccdcw2023.009>
- Li HJ, Zhang HS, Zhang YZ, Zhang KP, Zhou J, Yin Y, Jiang SF, Ma PB, He Q, Zhang YT, Wen K, Yuan Y, Lang N, Lu JJ, Sun CY (2020) Mushroom poisoning outbreaks—China, 2019. *China CDC Wkly* 2:19–24. <https://doi.org/10.46234/ccdcw2020.005>
- Li HJ, Zhang HS, Zhang YZ, Zhou J, Yin Y, He Q, Jiang SF, Ma PB, Zhang YT, Wen K, Yuan Y, Lang N, Cheng BW, Lu JJ, Sun CY (2021) Mushroom poisoning outbreaks—China, 2020. *China CDC Wkly* 3:41–45. <https://doi.org/10.46234/ccdcw2021.014>
- Li J, Han LH, Liu XB, Zhao ZW, Yang ZL (2020b) The saprotrophic *Pleurotus ostreatus* species complex: late Eocene origin in East Asia, multiple dispersal, and complex speciation. *IMA Fungus* 11:10. <https://doi.org/10.1186/s43008-020-00031-1>
- Li JL, Wang S, Yu J, Wang L, Zhou SL (2013) A modified CTAB protocol for plant DNA extraction. *Chin Bull Bot* 48:72–78. <https://doi.org/10.3724/SP.J.1259.2013.00072>
- Li SN, Xu F, Jiang M, Liu F, Wu F, Zhang P, Fan YG, Chen ZH (2021b) Two new toxic yellow *Inocybe* species from China: morphological characteristics, phylogenetic analyses and toxin detection. *MycKeys* 81:185–204. <https://doi.org/10.3897/mycokeys.81.68485>
- Li WW, Pires SM, Liu ZT, Liang JJ, Wang YF, Chen W, Liu CW, Liu JK, Han HH, Fu P, Guo YC (2021) Mushroom poisoning outbreaks—China, 2010–2020. *China CDC Wkly* 3:518–522. <https://doi.org/10.46234/ccdcw2021.134>
- Li Y, Steenwyk JL, Chang Y, Wang Y, James TY, Stajich JE, Spatafora JW, Groenewald M, Dunn CW, Hittinger CT, Shen XX, Rokas A (2021d) A genome-scale phylogeny of the kingdom Fungi. *Curr Biol* 31:1653–1665.e5. <https://doi.org/10.1016/j.cub.2021.01.074>
- Liimatainen K, Kim JT, Pokorny L, Kirk PM, Dentinger B, Niskanen T (2022) Taming the beast: a revised classification of Cortinariaceae based on genomic data. *Fungal Divers* 112:89–170. <https://doi.org/10.1007/s13225-022-00499-9>
- Luo R, Liu B, Xie Y, Li Z, Huang W, Yuan J, He G, Chen Y, Pan Q, Liu Y, Tang J, Wu G, Zhang H, Shi Y, Liu Y, Yu C, Wang B, Lu Y, Han C, Cheung DW, Yiu SM, Peng S, Xiaoqian Z, Liu G,

- Liao X, Li Y, Yang H, Wang J, Lam TW, Wang J (2012) SOAPdenovo2: an empirically improved memory-efficient short-read de novo assembler. *Gigascience* 1:18. <https://doi.org/10.1186/2047-217X-1-18>
- Majoros WH, Pertea M, Salzberg SL (2004) TigrScan and Glimmer-HMM: two open-source ab initio eukaryotic gene-finders. *Bioinformatics* 20:2878–2879. <https://doi.org/10.1093/bioinformatics/bth315>
- Manni M, Berkeley MR, Seppely M, Simão FA, Zdobnov EM (2021) BUSCO update: novel and streamlined workflows along with broader and deeper phylogenetic coverage for scoring of eukaryotic, prokaryotic, and viral genomes. *Mol Biol Evol* 38:4647–4654. <https://doi.org/10.1093/molbev/msab199>
- Mao XL (2000) The macrofungi in China. Henan Science and Technology Press, Zhengzhou
- Matheny PB (2005) Improving phylogenetic inference of mushrooms with *RPB1* and *RPB2* nucleotide sequences (*Inocybe*; Agaricales). *Mol Phylogenet Evol* 35:1–20. <https://doi.org/10.1016/j.ympev.2004.11.014>
- Matheny PB, Liu YJ, Ammirati JF, Hall BD (2002) Using *RPB1* sequences to improve phylogenetic inference among mushrooms (*Inocybe*, Agaricales). *Am J Bot* 89:688–698. <https://doi.org/10.3732/ajb.89.4.688>
- Matheny PB, Hughes KW, Kalichman J, Lebeuf R (2020) *Pulverulina*, a new genus of Agaricales for *Clitocybe ulmicola*. *Southeast Nat* 19:447–459
- Matheny PB, Hofstetter V, Aime MC, Moncalvo JM, Ge ZM, Yang ZL, Slot JC, Ammirati JF, Baroni TJ, Bougher NL, Hughes NW, Lodge DJ, Kerrigan R, Seidl MT, Aanen DK, DeNitis M, Daniele GM, Desjardin DE, Kropp BR, Norvell LL, Parker A, Vellinga EC, Vilgalys R, Hibbett DS (2006) Major clades of Agaricales: a multilocus phylogenetic overview. *Mycologia* 98:982–995. <https://doi.org/10.1080/15572536.2006.11832627>
- Matheny PB, Wang Z, Binder M, Curtis JM, Lim YW, Nilsson H, Hughes KW, Hofstetter V, Ammirati JF, Schoch CL, Langer E, Langer G, McLaughlin DJ, Wilson AW, Frøslev T, Ge ZW, Kerrigan RW, Slot JC, Yang ZL, Baroni TJ, Fischer M, Hosaka K, Matsuura K, Seidl MT, Vauras J, Hibbett DS (2007) Contributions of *rpb2* and *tefl* to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). *Mol Phylogenet Evol* 43:430–451
- Mohanta TK, Bae H (2015) The diversity of fungal genome. *Biol Proc Online* 17:8. <https://doi.org/10.1186/s12575-015-0020-z>
- Moncalvo JM, Vilgalys R, Redhead SA, Johnson JE, James TY, Aime MC, Hofstetter V, Verduin SJW, Larsson E, Baroni TJ, Thorn RG, Jacobsson S, Clémenceçon H, Miller OK Jr (2002) One hundred and seventeen clades of euagarics. *Mol Phylogenet Evol* 23:357–400. [https://doi.org/10.1016/S10557903\(02\)00027-1](https://doi.org/10.1016/S10557903(02)00027-1)
- Mou GF, Bau T (2021) *Asproinoocybaceae* fam. nov. (Agaricales, Agaricomycetes) for accommodating the genera *Asproinoocybe* and *Tricholosporum*, and description of *Asproinoocybe sinensis* and *Tricholosporum guangxiense* sp. nov. *J Fungi* 7:1086. <https://doi.org/10.3390/jof7121086>
- Nei M, Kumar S (2000) Molecular evolution and phylogenetics. Oxford University Press, New York
- Noordeloos ME, Kuyper TW (1995) Genus *Lepista*. In: Bas C, Kuyper TW, Noordeloos ME, Vellinga EC (eds) Flora Agaricina Neerlandica, vol 3. A.A. Balkema, Rotterdam, pp 67–75
- Noordeloos ME (1995) Genus *Collybia*. In: Bas C, Kuyper TW, Noordeloos ME, Vellinga EC (eds) Flora Agaricina Neerlandica, vol 3. A.A. Balkema, Rotterdam, pp 106–122
- Nylander JAA (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala
- Osmundson TW, Robert VA, Schoch CL, Baker LJ, Smith A, Robich G, Mizzan L, Garbelotto MM (2013) Filling gaps in biodiversity knowledge for macrofungi: contributions and assessment of an herbarium collection DNA barcode sequencing project. *PLoS ONE* 8:e62419. <https://doi.org/10.1371/journal.pone.0062419>
- Ovrebo CL, Baroni TJ (2007) New taxa of Tricholomatataceae and Entolomatataceae (Agaricales) from Central America. *Fungal Divers* 27:157–170
- Pegler DN, Young TWK (1971) Basidiospore morphology in the Agaricales. J. Cramer, Lehre
- Peredy T, Bradford H (2014) Mushrooms, muscarine. In: Wexler P (ed) Encyclopedia of toxicology, 3rd edn. Academic Press, Waltham, pp 416–417. <https://doi.org/10.1016/B978-0-12-386454-3.00758-2>
- Pertea G, Pertea M (2020) GFF Utilities: GffRead and GffCompare. *F1000Res* 9:ISCB Comm J-304. <https://doi.org/10.12688/f1000research.23297.2>
- Phillips R (1990) Der Kosmos PilzAtlas. Franckh-Kosmos, Stuttgart
- Phillips R (2005) Mushrooms and other fungi of North America. Firefly Books, Richmond Hill
- Price MN, Dehal PS, Arkin AP (2010) FastTree 2—approximately maximum-likelihood trees for large alignments. *PLoS ONE* 5:e9490. <https://doi.org/10.1371/journal.pone.0009490>
- Prjibelski A, Antipov D, Meleshko D, Lapidus A, Korobeynikov A (2020) Using SPAdes de novo assembler. *Curr Protoc Bioinform* 70:e102. <https://doi.org/10.1002/cpbi.102>
- Puschner B (2018) Mushroom toxins. In: Gupta RC (ed) Veterinary toxicology, 3rd edn. Academic Press, Waltham, pp 955–966
- Qin J, Feng B, Yang ZL, Li YC, Ratkowsky D, Gates G, Takahashi H, Rexer KH, KostGW KSC (2014) The taxonomic foundation, species circumscription and continental endemisms of *Singerocybe*: evidence from morphological and molecular data. *Mycologia* 106:1015–1026. <https://doi.org/10.3852/13-338>
- Raithelhuber J (1979) Supplementum descript. fungorum 2—(Validations of not validly published specimens). *Metrodiana* 8:52–54
- Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Syst Biol* 67:901–904. <https://doi.org/10.1093/sysbio/syy032>
- Redhead SA, Lutzoni F, Moncalvo JM, Vilgalys R (2002) Phylogeny of agarics: partial systematics solutions for core omphalinoid genera in the Agaricales (euagarics). *Mycotaxonomy* 83:19–57
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574. <https://doi.org/10.1093/bioinformatics/btg180>
- Roze E (1876) Catalogue des Agaricinées observées aux environs de Paris. *Bull Soc Bot Fr* 23:108–115
- Sánchez-García M, Matheny PB, Palfner G, Lodge DJ (2014) Deconstructing the Tricholomatataceae (Agaricales) and introduction of the new genera *Albomagister*, *Corneriella*, *Pogonoloma* and *Pseudotracheloma*. *Taxonomy* 63:993–1007. <https://doi.org/10.12705/635.635.3>
- Sato H, Toju H (2019) Timing of evolutionary innovation: scenarios of evolutionary diversification in a species-rich fungal clade, Boletales. *New Phytol* 222:1924–1935. <https://doi.org/10.1111/nph.15698>
- Sato H, Tanabe AS, Toju H (2017) Host shifts enhance diversification of ectomycorrhizal fungi: diversification rate analysis of the ectomycorrhizal fungal genera *Strobilomyces* and *Afroboletus* with an 80-gene phylogeny. *New Phytol* 214:443–454. <https://doi.org/10.1111/nph.14368>
- Singer R (1962) The Agaricales in modern taxonomy, 2nd edn. J. Cramer, Weinheim
- Singer R (1975) The Agaricales in modern taxonomy, 3rd edn. J. Cramer, Vaduz
- Singer R (1976) Le genre *Lepista* et la nomenclature correcte. *Bull Trimest Soc Mycol Fr* 92:127–128
- Singer R (1986) The Agaricales in modern taxonomy, 4th edn. Koeltz Scientific Books, Koenigstein

- Slater GS, Birney E (2005) Automated generation of heuristics for biological sequence comparison. *BMC Bioinform* 6:31. <https://doi.org/10.1186/1471-2105-6-31>
- Smith WG (1870) *Clavis Agaricorum*. *J Bot Lond* 8:246–252
- Stamatakis A (2014) RAXML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30:1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Suchard MA, Lemey P, Baele G, Ayres DL, Drummond AJ, Rambaut A (2018) Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evol* 4:vey016. <https://doi.org/10.1093/ve/vey016>
- Swenberg ML, Kelleher WJ, Schwarting AE (1967) Muscarine: isolation from cultures of *Clitocybe rivulosa*. *Science* 155:1259. <https://doi.org/10.1126/science>
- Takahashi H (2003) New species of *Clitocybe* and *Crepidotus* (Agaricales) from eastern Honshu, Japan. *Mycoscience* 44:103–107. <https://doi.org/10.1007/s10267-003-0091-6>
- Tamura K, Stecher G, Kumar S (2021) MEGA 11: molecular evolutionary genetics analysis version 11. *Mol Biol Evol* 38:3022–3027. <https://doi.org/10.1093/molbev/msab120>
- Ter-Hovhannisyantsyan V, Lomsadze A, Chernoff YO, Borodovsky M (2008) Gene prediction in novel fungal genomes using an ab initio algorithm with unsupervised training. *Genome Res* 18:1979–1990. <https://doi.org/10.1101/gr.081612.108>
- Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber WH, Li DZ, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. *Regnum Vegetabile* 159. Koeltz Botanical Books, Glashütten. <https://doi.org/10.12705/Code.2018>
- Vaidya G, Lohman DJ, Meier R (2011) Sequencematrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics* 27:171–180. <https://doi.org/10.1111/j.1096-0031.2010.00329.x>
- Vellinga EC, Verbeke A, Noordeloos ME (2018) Glossary. In: Noordeloos ME, Kuyper TW, Somhorst I, Vellinga EC (eds) *Flora Agaricina Neerlandica*, vol 7. Candusso Editrice, Milan, pp 6–65
- Vellinga EC, Kuyper TW, Ammirati J, Desjardin DE, Halling RE, Justo A, Læssøe T, Lebel T, Lodge DJ, Matheny PB, Methven AS, Moreau PA, Mueller GM, Noordeloos ME, Nuytinck J, Ovrebo CL, Verbeke A (2015) Six simple guidelines for introducing new genera of fungi. *IMA Fungus* 6:A65–A68. <https://doi.org/10.1007/BF03449356>
- Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *J Bacteriol* 172:4238–4246. <https://doi.org/10.1128/jb.172.8.4238-4246.1990>
- Vizzini A, Ercole E (2012) *Paralepistopsis* gen. nov. and *Paralepista* (Basidiomycota, Agaricales). *Mycotaxonomy* 120:253–267. <https://doi.org/10.5248/120.253>
- Vizzini A, Musumeci E, Murat C (2010) *Trichocybe*, a new genus for *Clitocybe puberula* (Agaricomycetes, Agaricales). *Fungal Divers* 42:97–105. <https://doi.org/10.1007/s13225-010-0030-8>
- Vizzini A, Consiglio G, Marchetti M (2020a) Index Fungorum 462:1
- Vizzini A, Consiglio G, Marchetti M, Alvarado P (2020b) Insights into the Tricholomatineae (Agaricales, Agaricomycetes): a new arrangement of Biannulariaceae and *Callistosporium*, Callistosporiaceae fam. nov., *Xerophorus* stat. nov., and *Pleurocollybia* incorporated into *Callistosporium*. *Fungal Divers* 101:211–259. <https://doi.org/10.1007/s13225-020-00441-x>
- Walker BJ, Abeel T, Shea T, Priest M, Abouelliel A, Sakthikumar S, Cuomo CA, Zeng Q, Wortman J, Young SK, Earl AM (2014) Pilon: an integrated tool for comprehensive microbial variant detection and genome assembly improvement. *PLoS ONE* 9:e112963. <https://doi.org/10.1371/journal.pone.0112963>
- Walther G, Garnica S, Weiß M (2005) The systematic relevance of conidiogenesis modes in the gilled Agaricales. *Mycol Res* 109:525–544. <https://doi.org/10.1017/S0953756205002868>
- White TJ, Bruns TD, Lee SB, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) *PCR protocols: a guide to methods and applications*. Academic Press, New York, pp 315–322. <https://doi.org/10.1016/b978-0-12-372180-8.50042-1>
- Wilson AW, Hosaka K, Mueller GM (2017) Evolution of ectomycorrhizas as a driver of diversification and biogeographic patterns in the model mycorrhizal mushroom genus *Laccaria*. *New Phytol* 213(4):1862–1873. <https://doi.org/10.1111/nph.14270>
- Wu F, Zhou LW, Yang ZL, Bau T, Li TH, Dai YC (2019) Resource diversity of Chinese macrofungi: edible, medicinal and poisonous species. *Fungal Divers* 98:1–76. <https://doi.org/10.1007/s13225-019-00432-7>
- Wu G, Feng B, Xu JP, Zhu XT, Li YC, Zeng NK, Hosen MI, Yang ZL (2014) Molecular phylogenetic analyses redefine seven major clades and reveal 22 new generic clades in the fungal family Boletaceae. *Fungal Divers* 69:93–11. <https://doi.org/10.1007/s13225-014-0283-8>
- Xu F, Zhang YZ, Zhao YH, Guan GY, Zhang KP, Li HJ, Wang JJ (2020) Mushroom poisoning from *Inocybe serotina*: a case report from Ningxia, northwest China with exact species identification and muscarine detection. *Toxicology* 179:72–75. <https://doi.org/10.1016/j.toxicol.2020.03.003>
- Yan YY, Zhang YZ, Vauras J, Zhao LN, Fan YG, Li HJ, Xu F (2022) *Pseudosperma arenarium* (Inocybaceae), a new poisonous species from Eurasia, based on morphological, ecological, molecular and biochemical evidence. *MycologyKeys* 92:79–93. <https://doi.org/10.3897/mycokeys.92.86277>
- Yang ZL, Wu G, Li YC, Wang XH, Cai Q (2021) Common edible and poisonous mushrooms of Southwestern China. Science Press, Beijing
- Young, (2000) *Common Australian fungi: a bushwalker's guide*, rev. University of New South Wales Press, Sydney
- Yu XD, Deng H, Yao YJ (2011) *Leucocalocybe*, a new genus for *Tricholoma mogolicum*. *Afr J Biomed Res* 5:5750–5756. <https://doi.org/10.5897/AJMR11.1228>
- Zhang YZ, Yan YY, Li HJ, Fan YG, Xu F (2022) Toxin screening of *Pseudosperma umbrinellum* (Agaricales, Basidiomycota): First report of phalloidin in Inocybaceae mushroom. *Toxicol* 217:155–161. <https://doi.org/10.1016/j.toxicol.2021.155-161>
- Zhao LN, Yu WJ, Deng LS, Hu JH, Ge YP, Zeng NK, Fan YG (2022) Phylogenetic analyses, morphological studies, and muscarine detection reveal two new toxic *Pseudosperma* (Inocybaceae, Agaricales) species from tropical China. *Mycol Prog* 21:75. <https://doi.org/10.1007/s11557-022-01822-z>
- Zhao RL, Zhou JL, Chen J, Margaritescu S, Sánchez-Ramírez S, Hyde KD, Callac P, Parra LA, Li GJ, Moncalvo JM (2016) Towards standardizing taxonomic ranks using divergence times—a case study for reconstruction of the *Agaricus* taxonomic system. *Fungal Divers* 78:239–292. <https://doi.org/10.1007/s13225-016-0357-x>

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