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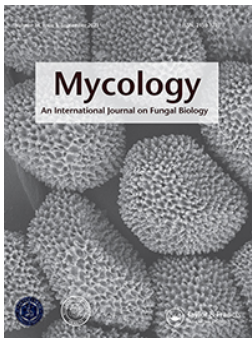
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# Phylogenetic and taxonomic updates of *Agaricales*, with an emphasis on *Tricholomopsis*

Geng-Shen Wang<sup>a,b,c</sup>, Qing Cai<sup>a,b</sup>, Yan-Jia Hao<sup>d</sup>, Tolgor Bau<sup>e</sup>, Zuo-Hong Chen<sup>f</sup>, Mei-Xiang Li<sup>g</sup>, Navarro David<sup>h,i</sup>, Nattapol Kraistudomsook<sup>j</sup> and Zhu-Liang Yang<sup>a,b</sup>

<sup>a</sup>Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany Chinese Academy of Sciences, Kunming, China; <sup>b</sup>Yunnan Key Laboratory for Fungal Diversity and Green Development, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, China; <sup>c</sup>College of Life Sciences, University of Chinese Academy of Sciences, Beijing, China; <sup>d</sup>School of Horticulture, Anhui Agricultural University, Hefei, China; <sup>e</sup>Engineering Research Centre of Chinese Ministry of Education for Edible and Medicinal Fungi, Jilin Agricultural University, Changchun, China; <sup>f</sup>Life Science College, Hunan Normal University, Changsha, China; <sup>g</sup>State Key Laboratory of Biocontrol, Guangdong Provincial Key Laboratory of Plant Resources and Southern Marine Science and Engineering Guangdong Laboratory (Zhuhai), School of Life Sciences, Sun Yat-Sen University, Guangzhou, China; <sup>h</sup>INRAE, Aix Marseille Université, UMR1163 Biodiversité et Biotechnologie Fongiques, Marseille, France; <sup>i</sup>INRAE, Aix Marseille Université, CIRM-CF, Marseille, France; <sup>j</sup>Department of Biology, Faculty of Science and Technology, Muban Chombueng Rajabhat University, Ratchaburi, Thailand

## ABSTRACT

The order *Agaricales* was divided into eight suborders. However, the phylogenetic relationships among some suborders are largely unresolved, and the phylogenetic positions and delimitations of some taxa, such as *Sarcomyaceae* and *Tricholomopsis*, remain unsettled. In this study, sequence data of 38 genomes were generated through genome skimming on an Illumina sequencing system. To anchor the systematic position of *Sarcomyaceae* and *Tricholomopsis*, a phylogenetic analysis based on 555 single-copy orthologous genes from the aforementioned genomes and 126 publicly accessible genomes was performed. The results fully supported the clustering of *Tricholomopsis* with *Phyllotopsis* and *Pleurocybella* within Phyllotopsidaceae, which formed a divergent monophyletic major lineage together with *Pterulaceae*, *Radulomycetaceae*, and *Macrotiophula* in *Agaricales*. The analysis also revealed that *Sarcomyaceae* formed a unique major clade. Therefore, two new suborders, *Phyllotopsidineae* and *Sarcomyxineae*, are proposed for the two major lineages. Analyses of 450 single-copy orthologous genes and four loci suggested that *Tricholomopsis* consisted of at least four clades. *Tricholomopsis* is subsequently subdivided into four distinct sections. Seventeen *Tricholomopsis* species in China, including six new species, are reported. *Conoloma* is established to accommodate *T. mucronata*. The substrate preference of *Tricholomopsis* species and the transitions of the pileate ornamentations among the species within the genus are discussed.

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## 1. Introduction

*Agaricales* Underw. is one of the most diverse orders of mushroom-forming fungi (Bánki et al. 2022). Based on multi-locus phylogenetic analyses (Matheny et al. 2006; Lodge et al. 2014; Zhao et al. 2017), the positions of many taxa in *Agaricales* have been anchored. To date, 8 suborders, 46 families, 482 genera, and more than 40,000 species have been allocated to the order (Vizzini et al. 2019; Kalichman et al. 2020; Mou and Bau 2021; Bánki et al. 2022).

According to Dentinger et al. (2016), *Agaricales* was phylogenetically divided into seven suborders:

*Agaricineae* Aime, Dentinger & Gaya, *Pluteineae* Aime, Dentinger & Gaya, *Tricholomatineae* Aime et al., *Marasmiineae* Aime et al., *Schizophyllineae* Aime et al., *Pleurotineae* Aime et al., and *Hygrophorineae* Aime, et al. Subsequently, Olariaga et al. (2020) further split *Hygrophorineae* into two suborders and additionally established *Clavariineae* Olariaga et al. based on six gene-loci analysis. Meanwhile, Olariaga et al. (2020) also broadened the taxonomic range of *Pleurotineae* so that it encompassed not only the previously recognised *Pleurotaceae* Kühner and *Pterulaceae* Corner but also *Phyllotopsidaceae* Olariaga et al., *Radulomycetaceae* Leal-

**CONTACT** Zhu-Liang Yang  [fungi@mail.kib.ac.cn](mailto:fungi@mail.kib.ac.cn)

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Dutra et al., *Stephanosporaceae* Oberw. & E. Horak, *Sarcomyxa* Olariaga et al., and *Typhulaceae* Jülich. However, the monophyletic clade *Pleurotineae* was less or not supported by Bayesian posterior probabilities (PP = 0.95) or maximum likelihood bootstrap proportion (ML-BP < 70%) (Olariaga et al. 2020), owing to the insufficient gene fragments.

*Sarcomyxa* P. Karst. includes four saprophytic and fan- or kidney-shaped species with prominent cheilocystidia and amyloid basidiospores (Cai et al. 2023). The genus was regarded as a new family based on a single species and was added to the suborder *Pleurotineae* (Olariaga et al. 2020).

The genus *Tricholomopsis* Singer has an undetermined phylogenetic affinity in *Agaricales*. *Tricholomopsis* includes a group of saprophytic, tricholomoid fungi with prominent cheilocystidia and is usually associated with decaying wood, growing on conifer wood, hardwood, or bamboo. Several studies have attempted to identify the phylogenetic position of the genus. Singer (1939) placed *Tricholomopsis* in *Tricholomataceae* R. Heim ex Pouzar based on its morphology. However, Moncalvo et al. (2002) clustered *Tricholomopsis rutilans* (Schaeff.) Singer and *T. aurea* (Beeli) Desjardin & B.A. Perry with *Clavulinopsis fusiformis* (Sowerby) Corner, whereas Matheny et al. (2006) clustered *Tricholomopsis decora* (Fr.) Singer with *Amanita* Pers. (Lodge et al. 2014) suggested that *T. rutilans* and *T. decora* were close to *Typhula* (Pers.) Fr., *Macrotyphula* R.H. Petersen, and *Phyllotopsis* E.-J. Gilbert & Donk ex Singer, and located in the basal clade to the hygrophoroid group. Kalichman et al. (2020) placed *Tricholomopsis* in *Typhulaceae* in the suborder *Hygrophorineae* along with *Typhula*, *Macrotyphula*, *Pleurocybella* Singer, and *Phyllotopsis*, whereas Olariaga et al. (2020) established the family *Phyllotopsidaceae* to accommodate *Phyllotopsis*, *Pleurocybella*, and *Macrotyphula* in the suborder *Pleurotineae* without discussing *Tricholomopsis*. These previous studies indicate that *Tricholomopsis* might be related to *Tricholomataceae*, *Clavulinopsis*, *Amanita*, *Typhulaceae*, or *Phyllotopsidaceae*. However, previous work has not provided firm evidence for the phylogenetic position of *Tricholomopsis*.

*Tricholomopsis* was once divided into two sections according to the colour of the pileus and lamellae: sect. *Tricholomopsis* and sect. *Platyphyllae* Singer (Singer 1943). Later, Smith (1960) further expanded the classification of *Tricholomopsis* by adding two additional sections based on the pileus colour: sect. *Lividae* A. H. Smith and sect. *Decoramentum* A. H. Smith. Sect. *Platyphyllae* was recently reassigned to *Megacollybia* Kotl. & Pouzar (Hughes et al. 2007). Jayawardena et al. (2022) divided *Tricholomopsis* into five clades: *Rubroaurantiaca*, *Decora*, *Rutilans*, *Scabra*, and *Aurea*. To date, approximately 40 species have been recognised from Africa (Pegler 1977; Desjardin 2017), Asia (Hongo 1959, 1960, 1966; He 1989; Liu 1994; Hosen et al. 2020; Mao et al. 2021; Wang and Yang 2023), Australia (Horak 1971; Cooper and Park 2016), Europe (Singer 1939; Holec 2009; Olariaga et al. 2015; Vizzini et al. 2019), North America (Singer 1943, 1951; Thiers 1958; Smith 1960), and South America (Singer 1953, 1989; Horak 1980; Pegler 1983; Garrido 1988; Singer et al. 1990; Jayawardena et al. 2022). In China, 14 species of *Tricholomopsis*, including eight novel species (*T. shulanensis* X. He, *T. lividipileata* P.G. Liu, *T. nigrosquamosa* P.G. Liu, *T. rubroaurantiaca* Hosen & T.H. Li, *T. galeata* L. Fan & N. Mao, *T. pallidolutea* L. Fan & N. Mao, *T. mitirubicunda* L. Fan & N. Mao, and *T. mucronata* Zhu L. Yang & G.S. Wang) and one novel variety (*T. bambusina* var. *megasporea* P.G. Liu) have been reported (He 1989; Liu 1994; Wang et al. 2018; Hosen et al. 2020; Mao et al. 2021; Wang and Yang 2023). However, species diversity is underestimated because of limited sampling and the morphological similarity of the different taxa.

This study aimed (1) to construct a phylogenetic framework of *Agaricales* using a robust phylogeny; (2) to clarify the phylogenetic positions of *Sarcomyxa* and *Tricholomopsis*; and (3) to elucidate the infrageneric relationships and species diversity within *Tricholomopsis*, and to infer the evolution of substrate preference and the pileate ornamentations of the species within *Tricholomopsis*.

## 2. Materials & methods

### 2.1. Taxon sampling

Ninety-eight samples collected during the last two decades, including 92 *Tricholomopsis*, three *Phyllotopsis*, one *Macrotyphula*, and two *Sarcomyxa* samples, were included in this study. Voucher specimens were deposited in the Cryptogamic Herbarium of the Herbaria of Kunming Institute of Botany, Chinese Academy of Sciences (KUN-HKAS), the Mycological Herbarium of Hunan Normal University (MHHNU), and the Herbarium of Mycological Institute of Jilin Agricultural University (HMJAU). Detailed information is provided in Supplementary Table S1.

### 2.2. Morphological observations

Macroscopic descriptions were based on field notes and digital images of basidiomata. Colors used in the descriptions are based on standard plates (Kornerup and Wanscher 1978). Microscopic characteristics were observed using the hand-sectioned tissues immersed in 5% KOH and stained in Congo red solution when necessary. The size of basidiospores is presented as (a–) b – c (–d). The range b – c contains a minimum of 90% of the measured values, whereas a and d refer to the extremities of all measurements. Q indicates the length/width ratio of basidiospores in the side view, with Q<sub>m</sub> representing the average Q of all basidiospores ± standard deviation. Descriptive terms are based on the work of Vellinga and Noordeloos (2001). The generic names used in this study are abbreviated as follows: “T.” for *Tricholomopsis*, “Ta.” for *Tricholoma*, “C.” for *Conoloma*, “Ph.” for *Phyllotopsis*, and “Pl.” for *Pleurocybella*.

### 2.3. DNA extraction, sequencing, and data processing

Sanger sequencing and next-generation sequencing were performed in this study. Protocols for DNA extraction, PCR amplification, and sequencing followed those described by Cai et al. (2014) and the references therein. The following four pairs of primers were used for PCR amplification and Sanger sequencing: ITS1F and ITS4 for the internal transcribed spacer (ITS), LROR and LR5 for the nuclear ribosomal large subunit (nrLSU), EF1-983F and EF1-1567R for the translation elongation factor 1- $\alpha$  (*tef1-a*) and Am-6F

and Am-7R for the DNA-directed RNA polymerase II second largest subunit 2 (*rpb2*). Sequencing traces were carefully verified using SeqMan NGen Version 17.2 (DNASTAR, Madison, WI, USA), and after the manual editing of the ends of the sequence, the paired-end sequences were assembled using DNASTAR. In total, 276 sequences were obtained and submitted to GenBank under the accession numbers listed in Table S1.

Following the genome skimming approach on an Illumina Hi-seq platform, 38 samples representing 24 species in four genera (*Phyllotopsis*, *Sarcomyxa*, *Tricholomopsis*, and *Macrotyphula*) were sequenced. Protocols for DNA extraction, library preparation, and library pooling for genome sequencing followed those described in Zeng et al. (2018). Fastp (Chen et al. 2018) was used to control the data quality and preprocess fastq files. Genome assembly was conducted using SPAdes (Bankevich et al. 2012) with automatic K selection based on read length. The completeness of the genome assembly was evaluated using Benchmarking Universal Single-Copy Orthologs (BUSCO v3) (Manni et al. 2021), with the *Agaricales* OrthoDB v10 database (Zdobnov et al. 2021) as a reference. Thereafter, single-copy orthologous genes for each sample were retrieved from the genome using the results from the BUSCO analysis.

### 2.4. Sequence data matrix construction

Three data matrices were generated for different purposes. The first matrix (Matrix I) comprised single-copy ortholog genes from 141 genomes of representatives of *Agaricales* and outgroups, including 126 publicly available genomes downloaded from A-WINGS (Yamamoto et al. 2014), the Joint Genome Institute (JGI), and the National Center for Biotechnology Information (NCBI), and 15 genomes generated in the present study. These were used to establish the framework of suborders and the phylogenetic positions of *Sarcomyxa* and *Tricholomopsis* within *Agaricales*. The second matrix (Matrix II) included single-copy orthologous genes from 37 genomes of *Tricholomopsis* and three genomes of *Phyllotopsis* as an outgroup and was used to elucidate the infrageneric classification of *Tricholomopsis* species. The last matrix (Matrix III) included four-locus sequences from *Tricholomopsis*,

*Phyllotopsis*, and *Pleurocybella* and was used to demonstrate the diversity of *Tricholomopsis*.

For Matrix I, we only retained single-copy orthologous genes that could be detected in 80% of the total samples and encoded proteins > 100 amino acids in length. For Matrix II, we retained genes that could be detected in 100% of samples and encoded proteins > 100 amino acids in length. Each single gene dataset was aligned using MAFFT v7.487 (Kato and Standley 2013) under the L-INS-I setting, and ambiguously aligned regions were trimmed using Gblocks 0.91b (Castresana 2000), with the minimum length of a block set as 2, allowing the gap positions when they occurred in half of the sequences. Subsequently, all datasets were concatenated using PhyKIT (Steenwyk et al. 2021) to form the final matrix.

For Matrix III, each single locus dataset was automatically aligned using MAFFT v7.487 (Kato and Standley 2013), manually adjusted and trimmed using Mega 7.0 (Kumar et al. 2016), and then concatenated using SequenceMatrix v1.8 (Vaidya et al. 2011). The dataset finally comprised 124 ITS sequences (761 bp), 116 nrLSU sequences (942 bp), 42 *rpb2* sequences (821 bp), and 79 *tef1-a* sequences (615 bp) from 155 representative samples (Table S1).

## 2.5. Phylogenetic analysis

For Matrix I, inconsistencies between genes (Shen et al. 2021) were first examined before performing the phylogenetic analysis. First, a single concatenated tree was constructed with the concatenated data matrix using IQ-TREE 2 (Minh et al. 2020) based on the single model LG+G4. For each gene, a gene tree was inferred using IQ-TREE 2 with automatic detection for the best-fitting model with the “-MFP” option, and branch support was evaluated based on 1,000 replicates of the ultrafast bootstrap. Low-supported branches (BS < 30%) in each gene tree were collapsed using Newick Utilities v1.6 (Junier and Zdobnov 2010). Subsequently, all gene trees were used to infer a coalescent tree using Astral 5.7.8 (Mirarab et al. 2014). Thereafter, IQ-TREE 2 and Astral 5.7.8 were used to infer the difference in gene-wise loglikelihood score ( $\Delta$ GLS) and gene-wise quartet score ( $\Delta$ GQS) (Shen et al. 2021) based on concatenated and coalescent trees. Genes were considered

consistent when their  $\Delta$ GLS and  $\Delta$ GQS were both > 0 or < 0. Finally, 555 consistent genes were filtered for the next analysis (Table S3). The final tree was built using IQ-TREE 2 with the LG+G4 model. BP (Kishino et al. 1990), one-sided Kishino-Hasegawa (Kishino and Hasegawa 1989), Shinodaira-Hasegawa (Shimodaira and Hasegawa 1999), expected likelihood weight (Strimmer and Rambaut 2002) and approximately unbiased (Shimodaira and Goldman 2002) topology tests were conducted using IQ-TREE 2 (Minh et al. 2020) with 10,000 RELL replicates. For Matrix II, we followed the analysis process of Matrix I, and 450 genes were filtered for the final tree.

For Matrix III, ML and Bayesian inference (BI) algorithms were employed. MrModeltest 2.3 (Nylander 2004) was used to identify the optimal model for each dataset based on the Akaike information criterion. The ML analysis was performed using raxmlGUI 2.0 beta (Edler et al. 2021) with the default parameters and bootstrapping with 1,000 replicates. The BI analysis was performed using MrBayes v3.2 (Ronquist et al. 2012) with the Markov chain Monte Carlo method. Three independent runs with four chains each were run for 3 million generations, and trees were sampled every 100 generations. Chain convergence was determined using Tracer v1.7 (Rambaut et al. 2018) to ensure sufficiently large effective sample sizes (>200). Trees were summarised and statistical values were obtained using the sump and sumt commands in MrBayes by discarding the first 25% of generations as burn-ins. The genealogical concordance phylogenetic species recognition (GCPSR) criterion (Taylor et al. 2000) was employed to infer species boundaries.

The ancestral states of pileate ornamentations and substrate preference were constructed using ape (Paradis et al. 2019) and phytools (Revell 2012) packages in R with stochastic character mapping 1,000 times under an equal-rates model based on the phylogenetic tree of Matrix II.

## 2.6. Data and code availability

The genomes of *Tricholomopsis* generated in this study were submitted to the NCBI database. Other genome assemblies were downloaded from the NCBI or JGI (Table S2). All scripts, data matrices, and

phylogenetic trees were deposited on GitHub (<https://github.com/jungleblack007/Tricholomopsis>).

### 3. Results

The ML tree of *Agaricales* inferred from 555 single-copy orthologous genes is shown in Figure 1. As indicated in the tree, *Agaricales* is monophyletic in origin with 100% BS support. This order is further divided into 12 well-supported major clades, including eight previously recognised suborders (*Agaricineae*, *Pluteineae*, *Tricholomatineae*, *Marasmiineae*, *Schizophyllineae*, *Pleurotineae* s. str., *Hygrophorineae*, and *Clavariineae*), a clade composing *Mycenaceae*, and three suborder-level lineages separated from suborder *Pleurotineae* s. l. The first lineage, representing the family *Typhulaceae*, is located between the suborders *Hygrophorineae* and *Clavariineae*. The second lineage comprises the families *Phyllotopsidaceae*, *Radulomycetaceae*, and *Pterulaceae* and genus *Macrotypula*, which diverged from *Hygrophoraceae*. The third lineage represents the family *Sarcomyaceae*. Interestingly, *Tricholomopsis*, along with *Phyllotopsis* and *Pleurocybella*, are within the family *Phyllotopsidaceae* with full statistical support.

To investigate whether the suborder *Pleurotineae*, second lineage, and third lineage were three truly separate major clades, 15 alternative topologies for the relationship between the three clades and other clades within *Agaricales* were evaluated (Figure 2). Only topology 1 was accepted, while the other 14 topologies were rejected by all the topology tests (Table 1), indicating that the three clades are certainly independent.

The ML tree of *Tricholomopsis* based on 450 single-copy orthologous genes is shown in Figure 3a. *Tricholomopsis* s. l. is divided into two deeply divergent clades. One represents the genus *Tricholomopsis* s. str., and the other forms a genus-level clade corresponding to the novel genus *Conoloma*. *Tricholomopsis* s. str. is divided into four clades, which are recognised as sections in this study.

Both ML and BI phylogenetic analyses based on four gene loci produced similar tree topologies; therefore, only the tree inferred from the Bayesian analysis is shown in Figure 3b. As indicated in the tree,

*Tricholomopsis* is divided into five clades, four of which correspond to the aforementioned sections of *Tricholomopsis*, and the remaining includes *T. ornaticeps* and *T. scabra* from New Zealand, which were not included in the analysis shown in Figure 3a because of the lack of genomic data. Based on the grouping and ranking criteria of the GCP SR method, 23 species of *Tricholomopsis* were delimited, and one single species of *Conoloma* was recognised.

Ancestral state reconstruction of *Tricholomopsis* (Figure 4) inferred that these species preferred Bamboo stumps. Subsequently, a transition occurred towards a preference for rotten wood or buried debris in forests of either *Angiosperms* or *Gymnosperms*. Finally, in the recently diverged lineages, some species gradually evolved a preference for growing on ferns or in meadows. The ancestral ornamentation on the pileus of *Tricholomopsis* was characterised by erect scales. Diversification occurred over time, resulting in various types of ornamentation, including glabrous, fibrillose, and granular scales. Ultimately, a derived state with tomentose scales became fixed in the recently diverged lineages.

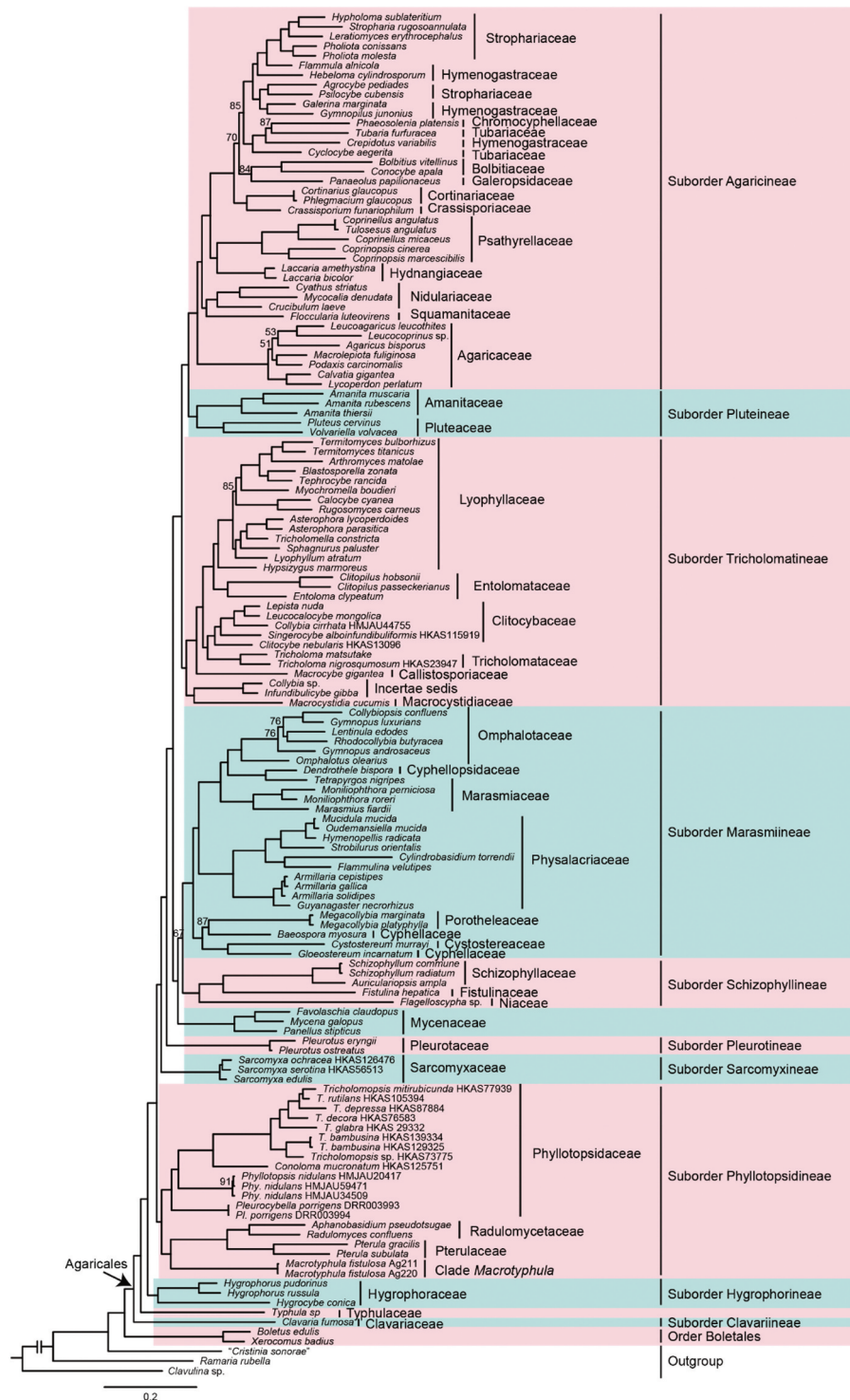
### 4. Discussion

#### 4.1. Phylogenetic framework of *Agaricales* and relationships among suborders

We generated the most comprehensive and robust phylogenetic framework for *Agaricales* to date through an in-depth phylogenomic analysis including 42 families and two family-level lineages (Figure 1). Ten suborders and one suborder-level lineage could be recognised in *Agaricales*, which were almost the same as those reported in previous studies on recently diverged lineages (Dentinger et al. 2016; Olariaga et al. 2020). However, *Mycenaceae* Overeem, once arranged in *Marasmiineae* with less support (ML-BP < 70), forms a clade sister to *Marasmiineae* and *Schizophyllineae*. The suborder *Pleurotineae* initially included only *Pleurotaceae* and *Pterulaceae* (Dentinger et al. 2016), but was expanded by Olariaga et al. (2020) to encompass five additional families: *Phyllotopsidaceae*, *Radulomycetaceae*, *Stephanosporaceae*, *Sarcomyaceae*, and *Typhulaceae*. In our study, *Pleurotineae* is delimited to include only *Pleurotaceae*, whereas

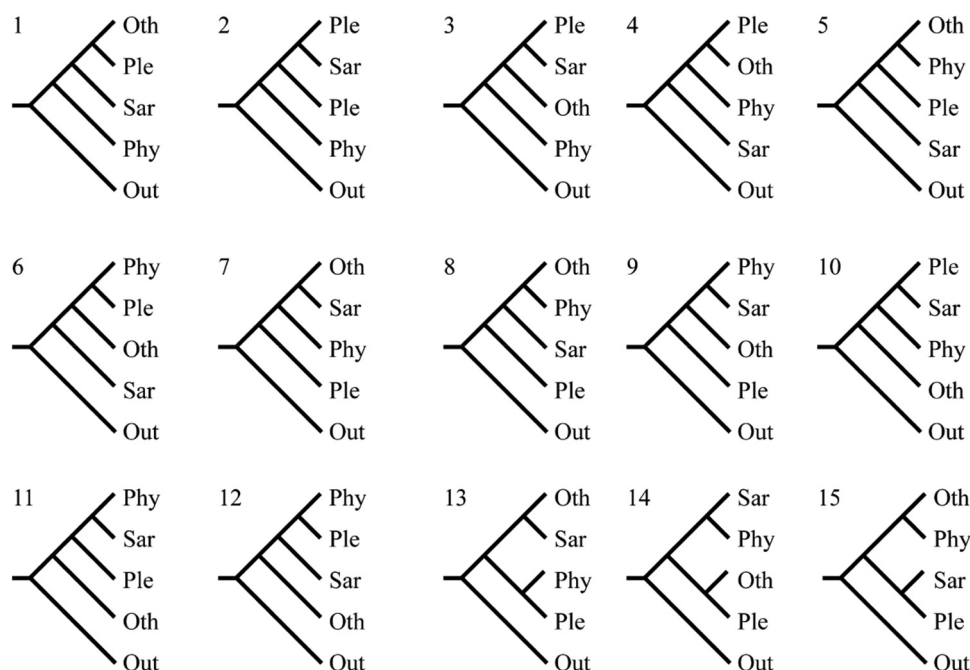
*Phyllotopsidaceae*, *Radulomycetaceae*, and *Pterulaceae* are grouped as a separate suborder (see Taxonomy section). *Sarcomyaceae*, typified by *Sarcomyxa serotina* (Pers.) V. Papp, is considered an independent suborder here due to its unique morphological

features and phylogenetic position (see Taxonomy section). *Typhulaceae*, typified by *Typhula incarnata* Lasch (Olariaga et al. 2022), was once also arranged in *Pleurotineae* s. l., but is identified as an independent suborder-level lineage in this study. However, the



**Figure 1.** Phylogeny of *Agaricales* inferred from a matrix containing 555 single-copy orthologs based on the maximum likelihood (ML) analysis method. Nodes without numeric labels are supported with 100% BS.





**Figure 2.** Fifteen alternative topologies of *Agaricales*. Out, outgroup and basal clades of *Agaricales* (including *Hygrophorineae*, *Typhulaceae*, *Clavariineae*, and outgroups); Phy, *Phyllostopsidaceae*; Sar, *Sarcomyxiineae*; Ple, *Pleurotineae*; Oth, other clades in *Agaricales* (including *Agaricineae*, *Pluteineae*, *Tricholomatineae*, *Marasmiineae*, and *Schizophyllineae*).

sampling of the family was not comprehensive enough to regard it as a new suborder (Shen et al. 2023). Additional studies are required to improve our understanding of the phylogenetic positions of the family *Stephanosporaceae* and the genus *Macrotyphula*.

Dentinger et al. (2016) treated *Hygrophoraceae* and *Clavariaceae* within the suborder *Hygrophorineae*. However, the findings of Olariaga et al. (2022) and the present study revealed that these two families do not represent a monophyletic group but rather two independent lineages, namely the suborders *Hygrophorineae* and *Clavariineae*. A comparison of the suborders in *Agaricales* among the three treatments (Dentinger et al. 2016; Olariaga et al. 2020; this study) is shown in Table 2.

#### 4.2. Phylogenetic position of *Tricholomopsis* and delimitation of *Phyllostopsidaceae*

In this study, we confirmed that *Tricholomopsis* is clustered within the family *Phyllostopsidaceae* of the suborder *Phyllostopsidaceae* (see Taxonomy section for *Phyllostopsidaceae*). *Tricholomopsis mucronata* Zhu L. Yang & G.S. Wang was distinct from the other *Tricholomopsis* species, indicating that it represents

a separate genus (Figure 3a). Morphologically, it differs from *Tricholomopsis* species by its mucronate umbo of the pileus and a cortiniform annulus on the upper part of the stipe. Therefore, the new genus, *Conoloma* (see Taxonomy section) is proposed to accommodate this unique species. The genus *Macrotyphula*, which was arranged in the same family with less support (Olariaga et al. 2020), forms a family-level sister clade to *Pterulaceae* and *Radulomycetaceae*. Therefore, the genus might be distinguished from *Phyllostopsidaceae*, but understanding whether it should be arranged as a separate family requires more in-depth analysis with more samples. Finally, *Phyllostopsidaceae* comprises *Conoloma*, *Phyllostopsis*, *Pleurocybella*, and *Tricholomopsis*. The common features of this family are the fleshy basidioma; hyaline, smooth, and non-amyloid basidiospores; prominent cheilocystidia; and the presence of clamp connections in the basidioma.

#### 4.3. Delimitation and evolution of infrageneric sections in *Tricholomopsis*

Molecular phylogenetic analyses based on the 450 single-copy orthologous genes concatenated dataset (Figure 3a) and ITS-nrLSU-*tef1-a-rpb2* concatenated

**Table 1.** Topology tests of 15 alternative hypotheses for the relationships among *Sarcomyxiineae*, *Pleurotineae*, *Phyllotopsidinae*, and the other clades within *Agaricales*.

Tree	logL	bp-RELL	p-KH	p-SH	c-ELW	p-AU
1	-101471281.2	1 +	1 +	1 +	1 +	1 +
2	-101475233	0 -	0 -	0 -	0 -	4.71E-05 -
3	-101472264.3	0 -	0 -	0.0001 -	2.01E-157 -	9.61E-10 -
4	-101473271.2	0 -	0 -	0 -	0 -	9.97E-07 -
5	-101479434.2	0 -	0 -	0 -	0 -	2.52E-63 -
6	-101479166.7	0 -	0 -	0 -	0 -	1.66E-49 -
7	-101477984.9	0 -	0 -	0 -	0 -	2.28E-106 -
8	-101479801	0 -	0 -	0 -	0 -	1.78E-06 -
9	-101477425.3	0 -	0 -	0 -	0 -	2.28E-51 -
10	-101476539.9	0 -	0 -	0 -	0 -	2.30E-05 -
11	-101478122.9	0 -	0 -	0 -	0 -	1.57E-42 -
12	-101479719	0 -	0 -	0 -	0 -	1.32E-05 -
13	-101478553.3	0 -	0 -	0 -	0 -	6.87E-28 -
14	-101472448.8	0 -	0 -	0 -	4.82E-272 -	8.35E-06 -
15	-101477106.8	0 -	0 -	0 -	0 -	2.11E-09 -

“+” signs denote the 95% confidence sets; “-” signs denote significant exclusion. logL, log likelihood; bp-RELL, bootstrap proportion using REll method; p-KH, p-value of one-sided Kishino-Hasegawa test; p-SH, p-value of Shimodaira-Hasegawa test; c-ELW, expected likelihood weight; p-AU, p-value of approximately unbiased (AU) test.

dataset (Figure 3b) supported four sections in *Tricholomopsis*, including sect. *Tricholomopsis*, sect. *Decoramentum*, sect. *Glabrae*, and sect. *Bambusinae* (see Taxonomy part). Among the four identified sections, sect. *Tricholomopsis* and sect. *Decoramentum* were mostly congruent with the work of Smith (1960), while *T. sulphureoides* and *T. flavescens* were moved from sect. *Tricholomopsis* to sect. *Decoramentum*. Sect. *Glabrae* and sect. *Bambusinae* are newly proposed in this study. Table 3 includes the comparisons among the four infrageneric treatments of *Tricholomopsis* (Singer 1943; Smith 1960; Jayawardena et al. 2022; this study).

Owing to the lack of genomic data, the phylogenomic four-section framework (Figure 3a) did not include two New Zealand species, *T. scabra* and *T. ornaticeps* (Cooper and Park 2016), which might belong to a unique section-level clade (Figure 3b), or the sect. *Lividae* proposed by Smith (1960). However, sect. *Lividae* can be easily distinguished from the above-mentioned sections by the livid colour of the pileus and lamellae and larger pleurocystidia. The phylogenetic positions of *T. scabra* and *T. ornaticeps* and *T. sect. Lividae* require further investigation.

Our data also revealed that two unique characteristics, substrate preference and ornamentations on the pileus surface, could help distinguish the four sections within *Tricholomopsis*. These distinctive features serve as valuable taxonomic markers, aiding in the classification and differentiation of various sections

within the genus. Moreover, the transition of substrate preference from bamboo to *Angiosperm/Gymnosperm* forests as well as grasslands and *Pteridium aquilinum* may provide a plausible explanation for the radiation and ecological niche differentiation observed in *Tricholomopsis* to some extent (Sato et al. 2017; Han et al. 2020; Li et al. 2020). However, to our knowledge, no previous studies have provided evidence of the ornamentation of pileus contributing to fungal adaptation to the environment. Nevertheless, the pileate ornamentation of *Tricholomopsis*, transitioning from erect scales to glabrous or fibrillose/granular scales and ultimately to tomentose scales, undoubtedly holds some degree of significance for the adaptation of fungi to their surroundings. These intriguing features of *Tricholomopsis* highlight the multifaceted nature of fungal adaptation and evolution. Further investigations into the genetic, ecological, and functional aspects of these characteristics may provide deeper insights into the ecological success and diversification of *Tricholomopsis* species.

## 5. Taxonomy

***Phyllotopsidinae*** Zhu L. Yang & G. S. Wang, subord. nov.

*Mycobank*: MB 849,776.

*Type genus*: *Phyllotopsis* E.-J. Gilbert & Donk ex Singer 1936.

*Etymology*: From the type genus *Phyllotopsis*.

**Table 2.** Comparisons of suborder divisions within *Agaricales* by different authors.

Dentinger et al. 2016	Olariaga et al. 2020	This study
<i>Agaricineae</i>	<i>Agaricineae</i>	<i>Agaricineae</i>
<i>Pluteineae</i>	<i>Pluteineae</i>	<i>Pluteineae</i>
<i>Tricholomatineae</i>	<i>Tricholomatineae</i>	<i>Tricholomatineae</i>
<i>Marasmiineae</i>	<i>Marasmiineae</i> + <i>Schizophyllineae</i>	<i>Marasmiineae</i>
<i>Schizophyllineae</i>		<i>Mycenaceae</i> clade
<i>Pleurotineae</i>	<i>Pleurotineae</i>	<i>Schizophyllineae</i>
		<i>Pleurotineae</i>
not included		<i>Phyllotopsidineae</i>
not included		<i>Sarcomyxiineae</i>
<i>Hygrophorineae</i>	<i>Hygrophorineae</i>	<i>Typhulaceae</i> clade
	<i>Clavariineae</i>	<i>Hygrophorineae</i>
		<i>Clavariineae</i>

**Diagnosis:** *Phyllotopsidineae* differs from other suborders of *Agaricales* by its saprophytic nutrient mode; usually small non-amyloid basidiospores; and the common presence of clamp connections and cheilocystidia.

**Description:** Basidioma corticoid, tricholomoid, pleurotoid, or clavarioid and sometimes arising from a sclerotium, small to large, fleshy or tough. Basidia cylindrical to clavate, usually 4-spored. Basidiospores small, globose to ellipsoid, cylindrical or allantoid, colourless and hyaline, smooth, and non-amyloid. Cheilocystidia usually present in tricholomoid and pleurotoid genera, and pleurocystidia sometimes present in tricholomoid genera. Pileipellis a cutis with a transition to a trichoderm in tricholomoid and pleurotoid genera. Clamp connections usually present.

**Known distribution:** Probably nearly cosmopolitan.

**Habitat:** Saprotrophic, on rotten wood above the ground or buried substrates.

**Families included:** *Phyllotopsidaceae* Olariaga et al. (2020), *Pterulaceae* Corner (1971), and *Radulomycetaceae* Leal-Dutra et al. (2020).

**Notes:** In previous work, these three families and the genus *Macrotyphula* were once treated in the suborder *Pleurotineae* (Dentinger et al. 2016; Kalichman et al. 2020; Olariaga et al. 2020). Based on the phylogenomic analysis in this study, these four taxa formed a lineage separated from the suborder *Pleurotineae*. Thus, it is considered as a new suborder.

***Phyllotopsidaceae*** Olariaga et al., *Stud. Mycol.* 96: 175 (2020)

**Type genus:** *Phyllotopsis* Singer 1936.

**Description:** Basidioma pleurotoid or tricholomoid, small to large, flesh. Spore prints white or pale pink.

Basidia cylindrical to clavate, usually 4-spored. Basidiospores small, globose to ellipsoid, cylindrical, or allantoid, colourless and hyaline, smooth, and non-amyloid. Cheilocystidia usually present and pleurocystidia sometimes present in tricholomoid genera. Pileipellis a cutis with the transition to a trichoderm. Clamp connections present.

**Known distribution:** Probably nearly cosmopolitan.

**Habitat:** Solitary or scattered on rotten wood above ground or buried substrates.

**Genera included:** *Pleurocybella*, *Phyllotopsis*, *Conoloma*, and *Tricholomopsis*.

**Notes:** Olariaga et al. (2020) placed *Phyllotopsis*, *Pleurocybella*, and *Macrotyphula* in the family *Phyllotopsidaceae*. Our analyses suggested that *Macrotyphula* forms a separate clade. *Tricholomopsis* and *Conoloma* in the family *Phyllotopsidaceae* were confirmed for the first time. All four genera of the family *Phyllotopsidaceae* share species with a saprotrophic nutrition mode, the presence of clamp connections, and a cutis pileipellis with a transition to a trichoderm.

***Conoloma*** Zhu L. Yang & G. S. Wang, gen. nov.

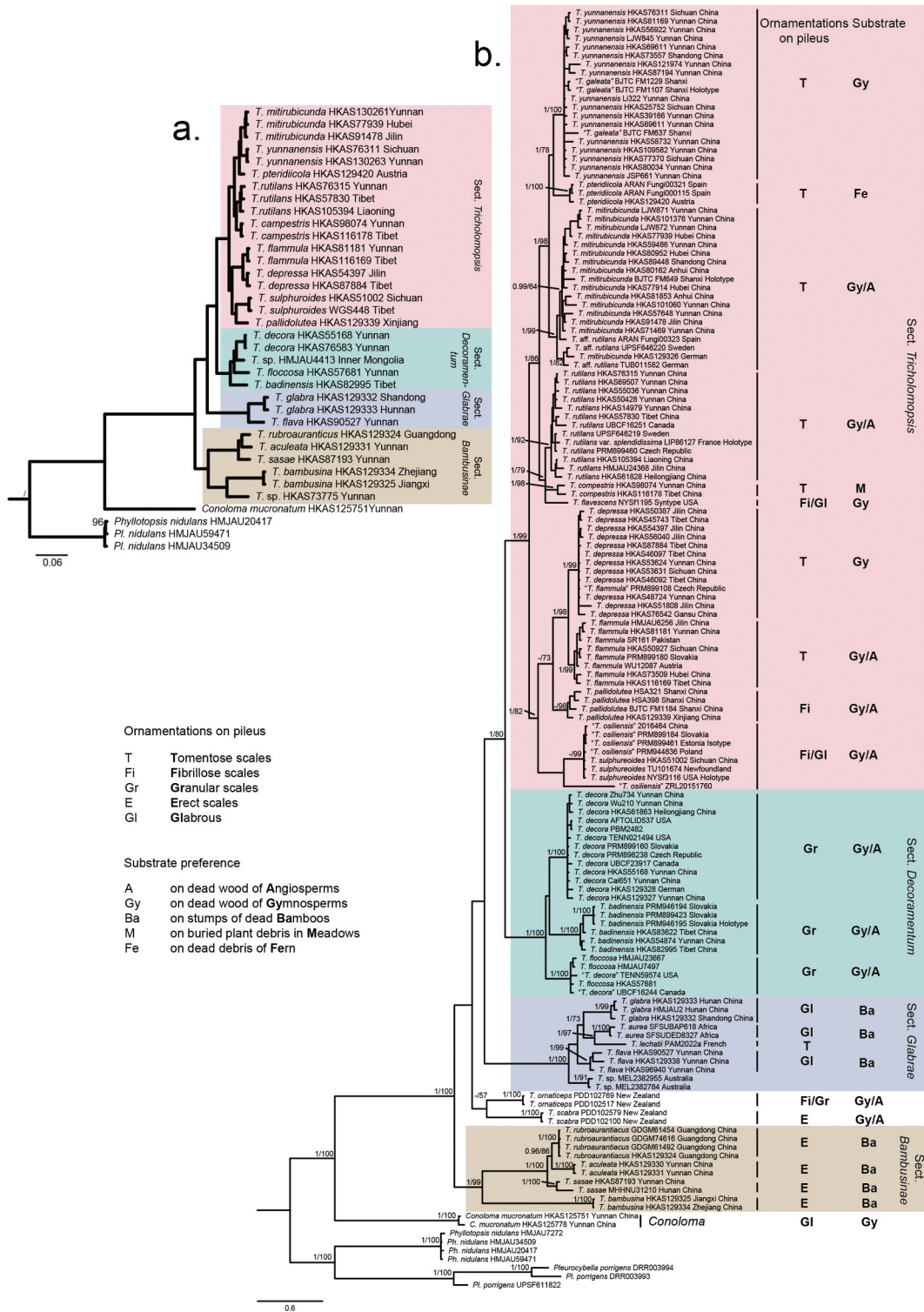
**Mycobank:** MB 849,787.

**Type species:** *Conoloma mucronatum* (Zhu L. Yang & G. S. Wang) Zhu L. Yang & G. S. Wang.

**Etymology:** The name "*Conoloma*" referring to the mucronate pileus of the basidioma.

**Diagnosis:** *Conoloma* differs from *Tricholomopsis* by its mucronate umbo of the pileus, fibrillose annuli-form zone on the upper part of the stipe, and smaller cheilocystidia.

**Description:** Basidioma tricholomoid, small to medium-sized, fleshy. Basidia cylindrical to clavate, usually



**Figure 3.** (a) phylogeny of *Tricholomopsis* inferred from a matrix containing 450 single-copy orthologous genes using the maximum likelihood (ML) analysis method. Nodes without numeric labels are supported with 100 BS. (b) phylogeny of *Tricholomopsis* inferred from a matrix consisting of ITS-nrLSU-*rpb2-tef1-a* using Bayesian inference (BI) analysis. BI (BPP  $\geq 0.90$ ) and ML bootstrap support values (ML  $\geq 70$ ) are shown (BPP/ML). The habitats and ornamentations of pileus are labelled after each species.

**Table 3.** Section divisions within *Tricholomopsis* by different authors.

Singer 1943	Smith 1960	Jayawardena et al. 2022	This study
sect. <i>Tricholomopsis</i>	sect. <i>Tricholomopsis</i> sect. <i>Decoramentum</i> sect. <i>Lividae</i> not included	clade <i>rutilans</i> clade <i>decora</i> not included clade <i>rubroaurantiaca</i>	sect. <i>Tricholomopsis</i> sect. <i>Decoramentum</i> sect. <i>Lividae</i> (no molecular evidence) sect. <i>Bambusinae</i>
not included	not included	clade <i>aurea</i>	sect. <i>Glabrae</i>
not included	not included	clade <i>scabra</i>	clade <i>scabra</i>
sect. <i>Platyphyllae</i>	sect. <i>Platyphyllae</i>	excluded	excluded

4-spored. Basidiospores small, globose to ellipsoid, colourless and hyaline, smooth, and non-amyloid. Cheilocystidia present. Pileipellis a cutis. Clamp connections present.

**Known distribution:** Only known from southwestern China.

**Habitat:** Saprotrophic, on rotten wood above the ground or buried wood.

**Notes:** *Conoloma mucronatum* was previously recognised as a species of *Tricholomopsis* (Wang and Yang 2023). However, based on our genomic analysis, this species formed a lineage sister but is distinct from *Tricholomopsis*. It is therefore considered as a separate genus.

***Conoloma mucronatum*** (Zhu L. Yang & G. S. Wang)  
Zhu L. Yang & G. S. Wang, comb. nov.

**Mycobank:** MB 849,788.

**Basionym:** *Tricholomopsis mucronata* Zhu L. Yang & G. S. Wang, in Wang & Yang, Journal of Fungal Research 21: 27 (2023).

***Tricholomopsis*** Singer, Schweiz. Z. Pilzk. 17: 56 (1939)

**Type species:** *T. rutilans* (Schaeff.) Singer.

**Diagnosis:** *Tricholomopsis* differs from other genera of *Phyllotopsidaceae* by its tricholomoid basidiomata, glabrous, tomentose to fibrillose pileus, and conspicuous cheilocystidia.

**Known distribution:** Probably nearly cosmopolitan

**Habitat:** Solitary or scattered on rotten wood above ground or underground, on substrates with dead bamboo, or on buried grass or litter.

**Notes:** Smith (1960) divided *Tricholomopsis* into four sections, among which *T. sect. Platyphylla* has been transferred to *Megacollybia* (Hughes et al.

2007), and *T. sect. Lividae* can be distinguished from the other sections by a livid pileus and lamellae and its large pleurocystidia. Our phylogenetic analysis confirmed the erections of sects. *Tricholomopsis*, *Decoramentum*, *Bambusinae* and *Glabrae*. There may well be another section including *T. ornaticeps* and *T. scabra* (Hosen et al. 2020; Jayawardena et al. 2022). To locate their exact position in *Tricholomopsis*, additional studies are necessary.

**Key to the sections of *Tricholomopsis* in China**

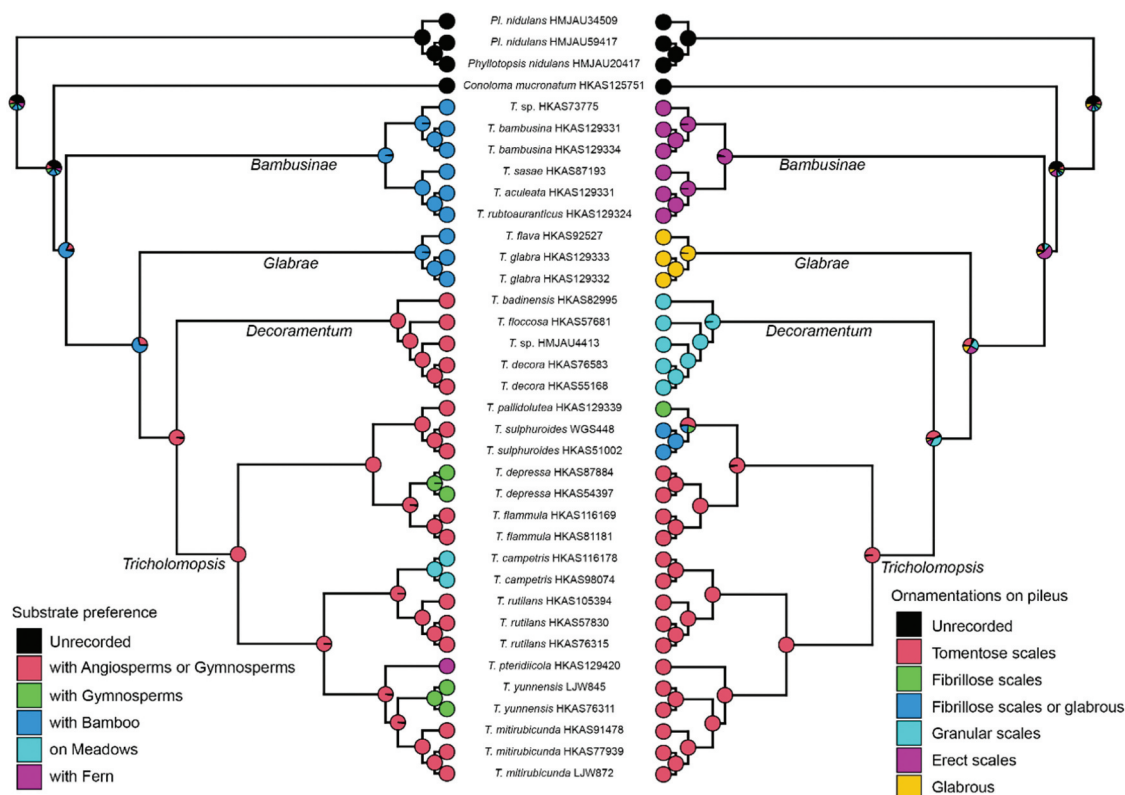
- (1) Occurring on dead stumps of bamboo; pleurocystidia absent or rarely present..... 2
- (2) Occurring on other plant debris; pleurocystidia present..... 3
- (3) Pileus yellow or yellowish; scales absent or velvety..... *T. sect. Glabrae*
- (4) Pileus brown to dark brown; scales present and erect..... *T. sect. Bambusinae*
- (5) Pileus surface covered with purplish to red, tomentose to fibrillose scales; stipe glabrous or covered with purplish scales.....  
..... *T. sect. Tricholomopsis*
- (6) Pileus surface covered with greyish minute scales; stipe glabrous or covered with greyish scales..... *T. sect. Tricholomopsis*

***Tricholomopsis sect. Bambusinae*** Zhu L. Yang & G. S. Wang, sect. nov.

**Mycobank:** MB 849,784.

**Type:** *Tricholomopsis bambusina* Hongo.

**Diagnosis:** *Tricholomopsis sect. Bambusinae* can be distinguished from the other sections of *Tricholomopsis* by its yellow, orange to brown pileus covered with erect fibrillose scales, sinuate to sub-decurrent lamellae, subglobose to broadly ellipsoid



**Figure 4.** Ancestral state reconstructions of substrate preference (left part) and ornamentalations on pileus (right part) of *Tricholomopsis* using ape and phytotools packages in R. The phylogenetic tree was based on the results of 450 single-copy orthologous genes, and pie chart of each node were summarised by stochastic character mapping under equal-rates model with 1,000 times. Names for each section in *Tricholomopsis* are labelled next to the corresponding branches.

basidiospores, and absence of pleurocystidia. Species of *T. sect. Bambusinae* prefer forests with bamboo.

**Description:** Basidioma medium-sized, tricholomoid; pileus applanate, densely covered with erect fibrillose scales; lamellae sinuate, adnate to subdecurrent; stipe cylindrical, hollow; basidiospores subglobose to broadly ellipsoid, smooth, inamyloid; basidia clavate, 4-spored; pleurocystidia absent; cheilocystidia prominent; pileipellis cutis to trichoderm; clamps present. Known from East Asia on stumps or buried substrate of bamboo.

**Notes:** Previous data and our multi-locus phylogenetic study indicated that *T. bambusina*, *T. sasae*, *T. rubroaurantiaca*, and *T. aculeata* (Hongo 1959, 1960; Hosen et al. 2020) formed the earliest divergent lineage of *Tricholomopsis*. We treated this lineage as a novel section. All species in this section live on stumps or buried substrates of bamboo.

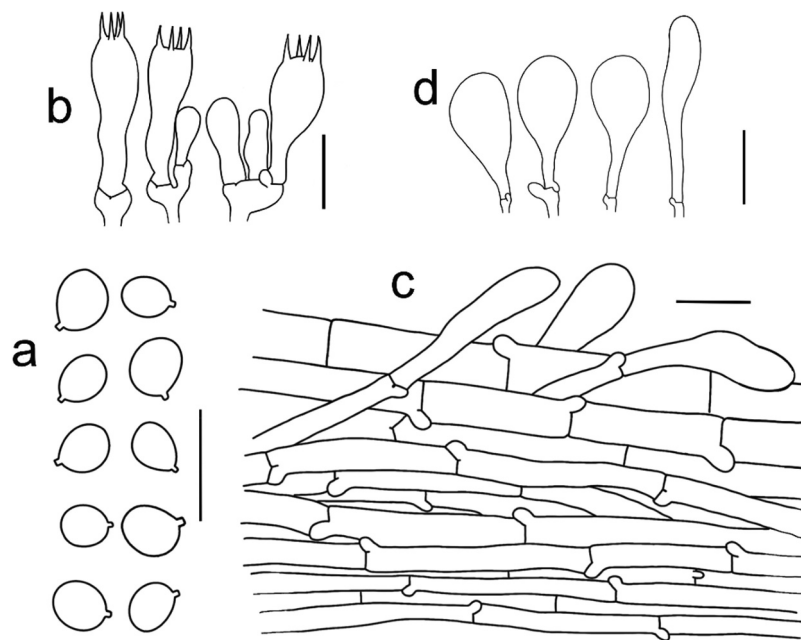
### Key to the species of *Tricholomopsis* sect. *Bambusinae* in China

- (1) Pileus dark yellow; scales dark red-brown..... *T. bambusina*
- (2) Pileus light yellow or light orange; scales reddish-brown..... 2
- (3) Pileus light yellow; basidiospores ellipsoid to ovoid..... *T. sasae*
- (4) Pileus light orange; basidiospores subglobose to broadly ellipsoid..... 3
- (5) Stipe > 4 cm in length; basidiospores > 6 µm in length..... *T. aculeata*
- (6) Stipe < 4 cm in length; basidiospores < 6 µm in length..... *T. rubroaurantiaca*

***Tricholomopsis aculeata*** Zhu L. Yang & G. S. Wang, sp. nov. Figures 5a-d, 6a

*Mycobank*: MB 849,785.

**Etymology:** *aculeata*, referring to the erect fibrillose or scales on the pileus.



**Figure 5.** Microscopic features of *Tricholomopsis aculeata* (type, HKAS 129,330). (a) Basidiospores; (b) Hymenium; (c) Pileipellis; (d) Cheilocystidia. Bars: a – b = 10  $\mu\text{m}$ , c – d = 20  $\mu\text{m}$ .

*Type:* China, Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Menghai County, Bulang Mountain, 1,000 m elev., on buried debris in a forest with bamboos, 23 June 2020, Geng-Shen Wang 982 (HKAS 129,330, holotype).

*Diagnosis:* *Tricholomopsis aculeata* differs from other species of sect. *Bambusinae* by its yellow to orange pileus, filamentous inner veils, segmentiform to adnate lamellae, longer basidiospores (6.5–8.5  $\times$  4–5.5  $\mu\text{m}$ ), and more robust basidia (22–32  $\times$  7–10  $\mu\text{m}$ ).

*Description:* Basidiomata small to medium-sized. Pileus 2–4.5 cm in diam., at first hemispherical to convex, then applanate to plano-concave, margin straight; surface dry, brown orange to buff (5C5–8) at centre, light orange, orange-white to white (6A1–6) towards margin; surface densely covered with radially erect fibrillose or scales, brown orange (5C7–8); inner veils filamentous. Lamellae segmentiform, sinuate to adnate with decurrent teeth, crowded, edges entire, white, yellow-white, pale yellow (4A1–3) to yellow-orange (4A6–8). Stipe 5–6  $\times$  0.4 cm, cylindrical, hollow, yellow-white, bright yellow (4A2–4) to light orange (5A3–4), glabrous.

Basidiospores [51/2/2] 6.5–8.5  $\times$  4–5.5  $\mu\text{m}$ , Q = (1.08–) 1.10–1.29 (–1.30), Qm = 1.19  $\pm$  0.05, subglobose to broadly ellipsoid, in-amyloid, colourless,

hyaline, thin-walled, smooth; apiculus relatively small. Basidia 22–32  $\times$  7–10  $\mu\text{m}$ , clavate, 4-spored, hyaline, sterigmata 2–4  $\mu\text{m}$  long. Pleurocystidia absent. Cheilocystidia 32–84  $\times$  12–24  $\mu\text{m}$ , broadly cylindrical, clavate to broadly clavate, thin-walled, colourless, hyaline. Pileipellis a cutis with the transition to a trichoderm at regular intervals, composed of 4–12  $\mu\text{m}$  wide, thin-walled, filamentous hyphae, terminal cells subcylindrical to clavate, 10–17  $\times$  25–58  $\mu\text{m}$ , with round apex. Clamps present at all parts of basidioma.

*Known distribution:* southwestern China.

*Habitat:* Scattered on buried substrates in forests with bamboo.

*Additional material examined:* China, Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Menghai County, Bulang Mountain, 1000 m elev., on buried debris in a forest with bamboos, 23 June 2020, Geng-Shen Wang 983 (HKAS 129,331).

*Notes:* *Tricholomopsis aculeata* is characterised by its light orange pileus with erect fibrils, while *T. bambusina* is a pale yellowish pileus with reddish brown scales and *T. sasae* is a yellowish-brown pileus with minute velvety-squamous scales. *Tricholomopsis aculeata* is similar to *T. rubroaurantiaca* but can be differentiated from the latter by its longer basidiospores and more robust basidia.



**Figure 6.** (a) *Tricholomopsis aculeata* (HKAS 129,330, photo by Gengshen Wang); (b) *T. bambusina* (HKAS 129,325, photo by Kuan Zhao); (c) *T. sasae* (HKAS 87,193, photo by Xiao-Bin Liu); (d) *T. rubroaurantiaca* (HKAS 129,324, photo by Jing-Wei Li). Bars: a – d = 1 cm.

***Tricholomopsis bambusina*** Hongo, J. Jap. Bot. 34: 239 (1959) Figure 6b

*Known distribution:* China and Japan (Hongo 1959; Liu 1994; this study).

*Habitat:* Scattered on buried substrates in forests with bamboo.

*Material examined:* China, Zhejiang Province, Lishui City, Songyang County, 122 m elev., in a forest with bamboo, 14 September 2021, Geng-Shen Wang 1856 (HKAS 129,334). Jiangxi Province, Jing'an County, Jiangxi Jiulingshan National Nature Reserve, 300 m elev., in a forest with bamboo, 14 July 2021, Jiulingshan 306 (HKAS 129,325).

*Notes:* *Tricholomopsis bambusina* is characterised by basidiomata covered with reddish-brown scales and small basidiospores, which differentiates it from other species in *T. sect. Bambusinae*.

***Tricholomopsis rubroaurantiaca*** Hosen & T. H. Li, in Hosen, Xu, Gates & Li, Mycoscience 61(6): 343 (2020) Figure 6d

*Known distribution:* South China (Hosen et al. 2020).

*Habitat:* Solitary or in small clusters on buried substrate in forests with bamboo.

*Material examined:* China, Guangdong Province, Zhaoqing City, Dinghushan Nature Reserve, 76 m elev., 21 June 2016, H16062103 (HKAS 129,324).

*Notes:* *Tricholomopsis rubroaurantiaca* was described in China; for descriptions and comparisons to other species, see Hosen et al. (2020).

***Tricholomopsis sasae*** Hongo, J. Jap. Bot. 35: 85 (1960) Figure 6c

*Known distribution:* Japan and China (Hongo 1960; Kasuya et al. 2015).

*Habitat:* scattered or clustered on roots of bamboo-grass or buried wood in forests with *Fagaceae* or coniferous forests.

*Material examined:* China, Yunnan Province, Longlin County, Zhenan Town, 2,100 m elev., in a forest with *Fagaceae*, 15 March 2014, Xiao-Bin Liu 641 (HKAS 87,193). Hunan Province, Yizhang County, Mang Mountain, 1,490 m elev., on rotten wood in a coniferous forest, 30 July 2018, MHHNU 31,210.



*Notes:* *Tricholomopsis sasae* was first described in Japan by Hongo (1960), and it is characterised by a yellowish-brown pileus covered with minute velvety-squamous scales. For comparisons between other species in *T.* sect. *Bambusinae*, see the notes on *T. aculeata* and *T. bambusina*.

***Tricholomopsis* sect. *Decoramentum*** A. H. Smith, *Brittonia* 12(1): 57 (1960)

*Type:* *Tricholomopsis decora* (Fr.) Singer.

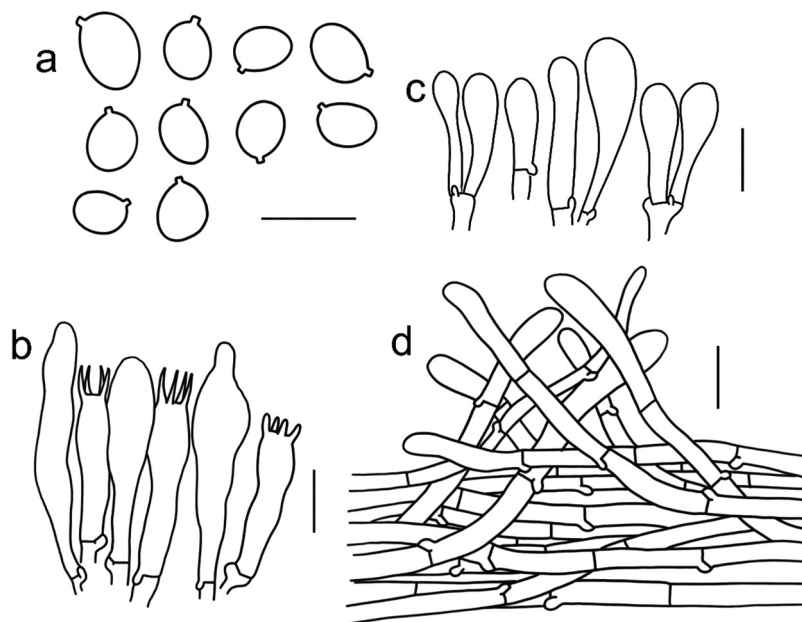
*Description:* Basidioma tricholomoid; pileus glabrous to covered with greyish minute fibrillose scales; basidiospores subglobose to oblong, smooth,

inamyloid; cheilocystidia prominent; pileipellis cutis to trichoderm; solitary or scattered on rotten wood or soil in coniferous or broad-leaved forests. *Tricholomopsis* sect. *Decoramentum* can be distinguished from the other sections by its greyish fibrillose scales on the pileus.

*Notes:* *Tricholomopsis* sect. *Decoramentum* was first described by Smith (1960). To date, three taxa of *T.* sect. *Decoramentum* have been recognised in the phylogenetic analyses. Our phylogenetic analysis indicated that *T. sulphureoides* and *T. flavescens* belong to sect. *Tricholomopsis* rather than sect. *Decoramentum*, as suggested by Figure 3b.



**Figure 7.** (a) *Tricholomopsis badinensis* (HKAS 83,622, photo by Qing Cai); (b) *T. decora* (HKAS 129,327, photo by Jianwei Liu); (c – d) *T. floccosa* (HKAS 57,681, photo by Gang Wu); (e) *T. flava* (HKAS 96,940, photo by Yan-Jia Hao 105); (f) *T. glabra* (HKAS 129,332, photo by Ting Guo).



**Figure 8.** Microscopic features of *Tricholomopsis floccosa* (type, HKAS 57,681). (a) Basidiospores; (b) Hymenium; (c) Cheilocystidia; (d) Pileipellis. Bars: a – b = 10  $\mu$ m, c – d = 20  $\mu$ m.

**Key to the species of *Tricholomopsis* sect. *Decoramentum* in China**

- (1) Stipe is >8 mm in width; basidiospores subglobose to ellipsoid..... *T. floccosa*
- (1) Stipe is <8 mm in width; basidiospores ellipsoid..... 2
- (2) Scales tiny and light; pileus dark yellow ..... *T. badinensis*
- (2) Scales grainy and dark; pileus bright yellow..... *T. decora*

***Tricholomopsis badinensis*** J. Holec, M. Kolařík & V. Kunca, in Holec, Kunca & Kolařík, *Mycol. Progr.* 18(3): 325 (2019) Figure 7a

*Known distribution:* Europe and Western China (Holec et al. 2019; this study).

*Habitat:* Scattered on rotten wood in coniferous and broad-leaved forests.

*Material examined:* China, Tibet Autonomous Region, Nyingchi, Bomi County, 2,462 m elev., in a forest with Fagaceae, Betulaceae, and *Pinus*, 2 July 2014, Yan-Jia Hao 1204 (HKAS 82,995); same locality, in a forest with Fagaceae, Betulaceae, and *Pinus*, 2 July 2014, Qing Cai 1162 (HKAS 83,622). Yunnan Province, Diqing Tibetan Autonomous Prefecture, Haba Snow Mountain,

2,800 m elev., on rotten wood, 15 August, Li-Ping Tang 643 (HKAS 54,874).

*Notes:* *Tricholomopsis badinensis* was described from Slovakia by Holec et al. (2019). *T. badinensis* differs from *T. decora* by its more muted background pileus colour, lighter scales, and longer basidia, and from *T. sulfureoides* by minute scales on the pileus and longer and ellipsoid spores.

***Tricholomopsis decora*** (Fr.) Singer, *Schweiz. Z. Pilzk.* 17: 56 (1939) Figure 7b

*Known distribution:* Europe, North America, and Asia (Smith 1960; Liu 1994; Holec and Kolařík 2011, 2013; Olariaga et al. 2015).

*Habitat:* Solitary to scattered on rotten wood in coniferous or broad-leaved forests.

*Material examined:* China, Heilongjiang Province, Yichun City, Yangwanghe Forest Park, 352 m elev., on rotten wood, 18 August, Xiang-Hua Wang 2666 (HKAS 61,863). Yunnan Province, Lijiang City, Yulong Mountain, 3,000 m elev., on rotten wood in a coniferous forest, 10 August, Qi Zhao 8171 (HKAS 55,168); Diqing Tibetan Autonomous Prefecture, Shangri-La, 3,611 m elev., on rotten wood, 20 January 2016, Jian-Wei Liu 1555 (HKAS 129,327). Austria: Kleinwalsertal, 1,300 m elev., on

rotten wood in a forest with *Picea* and *Abies*, 29 September 2016, Zhu-Liang Yang 5962 (HKAS 129,328).

*Notes:* *Tricholomopsis decora* presents a global distribution, and is found in the Holarctic realm (Smith 1960; Liu 1994; Holec and Kolařík 2013; Olariaga et al. 2015). *T. decora* can be distinguished from *T. floccosa* by its brighter pileus, tinier scales, slender basidiomata, and more elliptical basidiospores.

***Tricholomopsis floccosa* Zhu L. Yang & G. S. Wang, sp. nov.** Figures 7c-d, 8a-d

*Mycobank:* MB 849,779.

*Etymology:* *floccosa* referring to the floccus scales on the pileus.

*Type:* China, Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-La, 3,750 m elev., on rotten wood in a forest with *Abies*, 25 August, Gang Wu 149 (HKAS 57,681, holotype).

*Diagnosis:* *Tricholomopsis floccosa* differs from the other species of *T. sect. Decoramentum* by its tan to olive-brown scales on pileus, robust stipe (4.5–6 × 0.8–1.5 cm), and subglobose to ellipsoid basidiospores (5–7.5 × 4–5.5 μm).

*Descriptions:* Basidioma small to medium-sized. Pileus 6–7.5 cm in diam., plano-convex, margin exceeding lamellae; surface dry, bright yellow to yellow (2A5–7); scales tomentose-fibrillose, dense at the centre, becoming scarce towards the margin, tan (5E6–8) to olive-brown (4E6–8). Lamellae emarginate with decurrent teeth, crowded, edges entire, orange-white to light orange (5A2–4). Stipe 4.5–6 × 0.8–1.5 cm, central, hollow, cylindrical, bright yellow to yellow (2A5–7), with tan (5E6–8) to olive-brown (4E6–8) scales or fibrils.

Basidiospores [60/3/3] 5.5–7.5 × 4–5.5 μm, Q = (1.10–) 1.14–1.63 (–1.75), Qm = 1.35 ± 0.15, subglobose to ellipsoid, in-amyloid, colourless, hyaline, thin-walled, smooth; apiculus relatively small. Basidia 23–30 × 5–7 μm, clavate, 4-spored, hyaline, sterigmata 4.5–5.5 μm long. Pleurocystidia frequent, 32–47 × 5.5–9 μm, cylindrical to narrowly clavate, sometimes with mucronate apex, thin-walled, colourless, hyaline. Cheilocystidia 29–59 × 7–15 μm, narrowly cylindrical, cylindrical to clavate, thin-walled, colourless, hyaline. Pileipellis a cutis with the transition to

a trichoderm at regular intervals, composed of 3–9 μm wide, thin-walled, filamentous hyphae, terminal cells 4–11 × 30–57 μm, with round apex. Clamps present at all parts of basidioma.

*Known distribution:* Solitary to scattered on rotten wood in mixed coniferous broad-leaved forests.

*Habitat:* North America and East Asia (Holec et al. 2019; this study).

*Additional material examined:* China, Jilin Province, Baishan City, Lushuihe Forest farm, 786 m elev., on rotten wood in a mixed coniferous broadleaved forest, 12 July 2010, HMJAU 23,667; Baishan City, Jinjiang Grand Canyon, 1,049 m elev., on rotten wood in a mixed coniferous broadleaved forest, 19 August, HMJAU 7497.

*Notes:* *Tricholomopsis floccosa* was reported as a *T. decora* complex species (Holec et al. 2019) and it is characterised by a bright yellow to yellow pileus with olive-brown scales. It can be distinguished from *T. badinensis* by its more robust basidioma and shorter pleurocystidia and from *T. decora* by its darker pileus, coarser scales, more robust basidiomata, and subglobose to ellipsoid basidiospores.

***Tricholomopsis sect. Glabrae* Zhu L. Yang & G. S. Wang, sect. nov.**

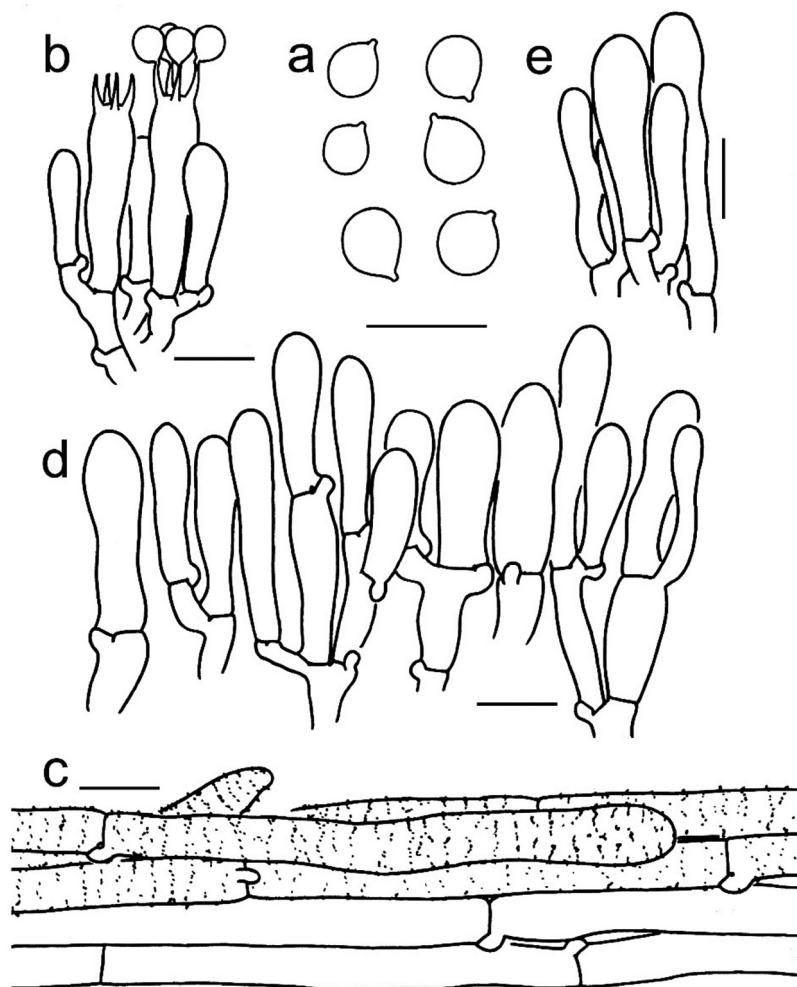
*Mycobank:* MB 849,780.

*Type:* *Tricholomopsis glabra* Zhu L. Yang & G. S. Wang.

*Diagnosis:* *Tricholomopsis sect. Glabrae* can be distinguished from the other sections of *Tricholomopsis* by its glabrous pileus, adnate to decurrent lamellae, slender stipe, and the absence of pleurocystidia. Species of sect. *Glabrae* prefer to live on stumps of bamboo.

*Description:* Basidioma small to medium-sized, tricholomoid; pileus yellow, glabrous, seldom tomentose; lamellae adnate; stipe clavate, hollow; basidiospores subglobose to ellipsoid, smooth, in-amyloid; basidia clavate, 4-spored; cheilocystidia prominent or absent; pleurocystidia absent or present; pileipellis cutis, seldom trichoderm; prefers forests with bamboo.

*Notes:* To date, four species of sect. *Glabrae* have been recognised via phylogenetic analyses. Three species in this section have a glabrous pileus, while *T. lechatii* has a tomentose or velvety pileus.



**Figure 9.** Microscopic features of *Tricholomopsis flava* (type, HKAS 96,940). (a) Basidiospores; (b) Basidia; (c) Pileipellis; (d) Cheilocystidia; (e) Caulocystidia. Bars: a – e = 10  $\mu$ m. Drawing by Zhu-Liang Yang.

**Key to the species of *Tricholomopsis* sect. *Glabrae* in China**

- (1) Pileus >4 cm in diam; stipe >5 cm in length..... *T. flava*  
 (1) Pileus <4 cm in diam; stipe <5 cm in length  
 ..... *T. glabra*

***Tricholomopsis flava* Zhu L. Yang & G. S. Wang, sp. nov. Figures 7e, 9a-e**

*Mycobank*: MB 849,781.

*Etymology*: *flava* referring to the yellow pileus.

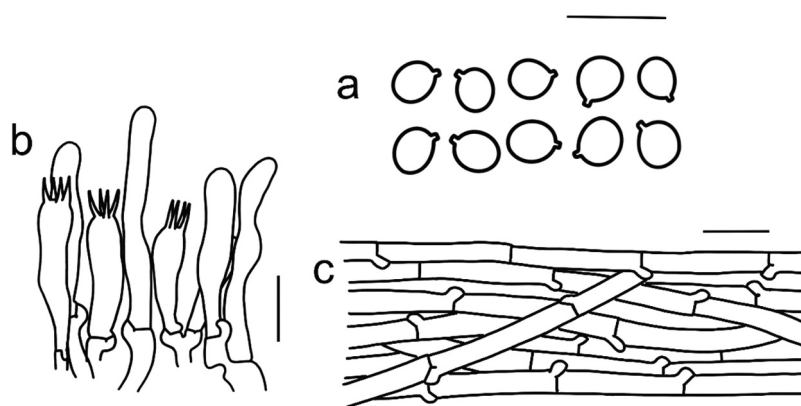
*Type*: China, Yunnan Province, Puer City, Lancang County, Mengben Village, 1,490 m elev., on stumps of bamboo, 22 August, Yan-Jia Hao 105 (HKAS 96,940, holotype).

*Diagnosis*: *Tricholomopsis flava* differs from the other species of sect. *Glabrae* by its larger pileus (4–9 cm),

robust stipe (6–8  $\times$  0.8–1 cm), subdecurrent to decurrent lamellae, and pileipellis cutis.

*Description*: Basidiomata small to medium-sized. Pileus 4–9 cm in diam., at first convex, plano-concave, sometimes with wavy-irregular margin; surface dry, light brown (4C6–8) at centre with radially light yellow (4A2) to white (2A3) striate, becoming sulphur yellow (2A5–8) towards the margin, surface glabrous. Lamellae subdecurrent to decurrent, crowded, edges even, pale yellow (3A2–3). Stipe 6–8  $\times$  0.8–1 cm, central, cylindrical, hollow, sometimes oblate or curved, sulphur yellow (2A5–8) with longitudinally light yellow (4A2) to white (2A1) striations.

Basidiospores [60/3/3] 4–6  $\times$  4–5  $\mu$ m, Q = 1–1.25 (–1.39), Q<sub>m</sub> = 1.13  $\pm$  0.09, globose to broadly ellipsoid, inamyloid, colourless, hyaline, thin-walled. Basidia 20–31  $\times$  5–9  $\mu$ m, cylindrical to clavate, 4-spored, hyaline, sterigmata 2–4  $\mu$ m long. Pleurocystidia absent.



**Figure 10.** Microscopic features of *Tricholomopsis glabra* (type, HKAS 129,332). (a) Hymenium; (b) Basidiospores; (c) Pileipellis. Bars: a – b = 10  $\mu$ m; c = 20  $\mu$ m.

Cheilocystidia frequent, 17–45  $\times$  5–24  $\mu$ m, cylindrical to clavate. Pileipellis a cutis of parallel cylindrical hyphae 4–9  $\mu$ m broad, with yellow pigments. Clamps present at all parts of basidioma.

*Known distribution:* China.

*Habitat:* Solitary to clustered on stumps of bamboo.

*Additional material examined:* China, Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Xishuangbanna Botanical Garden, 540 m elev., on stumps of bamboos, 7 August, Qi Zhao 2653 (HKAS 90,527); Puer City, Lancang County, 1,490 m elev., on stumps of bamboos, 22 August, Qing Cai 74 (HKAS 129,338).

*Notes:* *Tricholomopsis flava* is most phylogenetically similar to *T. aurea*. However, macro-morphologically, the pileus of *T. aurea* is smaller and the stipe is shorter than that of *T. flava*. Micro-morphologically, the cheilocystidia of *T. aurea* are longer than that of *T. flava*. *Tricholomopsis flava* is also similar to *T. badinensis*, *T. decora*, and *T. sulphureoides*, but it can be distinguished from the other three by its glabrous pileus. Furthermore, *T. flava* has a slenderer stipe, smaller and rounder basidiospores, and shorter cheilocystidia.

***Tricholomopsis glabra*** Zhu L. Yang & G. S. Wang, sp. nov. Figures 7f, 10a–c

*Mycobank:* MB 849,782.

*Etymology:* *glabra* referring to a glabrous pileus.

*Type:* China, Anhui Province, Huangshan City, Yungu Temple, 852 m elev., on stumps of bamboo, 15 July 2018, Ting Guo 1067 (HKAS 129,332, holotype).

*Diagnosis:* *Tricholomopsis glabra* differs from the other species of *T. sect. Glabrae* by its yellow-white

to pastel yellow glabrous pileus, adnate lamellae, slender stipe (3–4  $\times$  0.2–0.4 cm) presence of pleurocystidia, and absence of cheilocystidia.

*Description:* Basidiomata small to medium-sized. Pileus 2–4 cm in diam., at first hemispherical, then plano-convex, margin straight to inflexed; surface dry, yellow-white, pastel yellow (3A2–4) to bright yellow (3A6–8), sometimes olive (3E6–8) at the margin, glabrous. Lamellae adnate, crowded, edge entire, yellow-white, pastel yellow (3A2–4) to bright yellow (3A6–8). Stipe 3–4  $\times$  0.2–0.4 cm, cylindrical, hollow, yellow-white, pastel yellow (3A2–4) to bright yellow (3A6–8), glabrous.

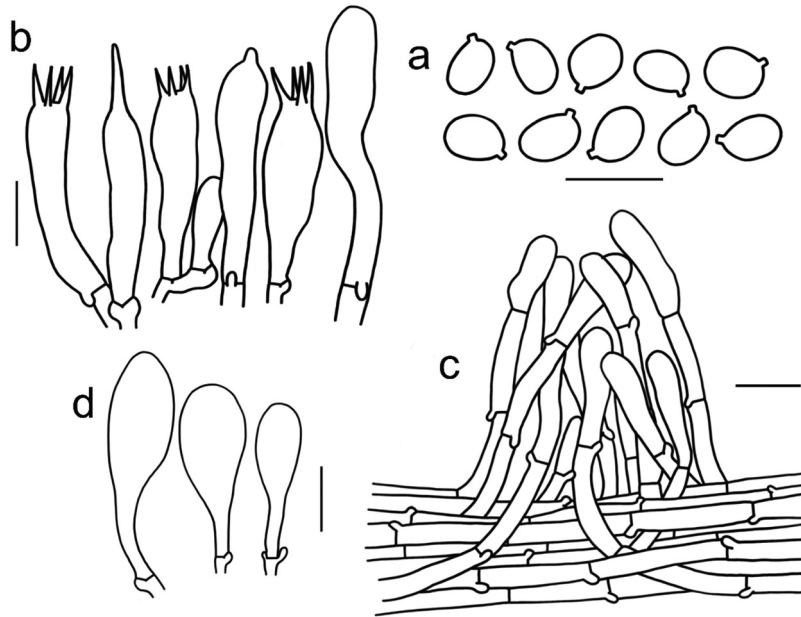
Basidiospores [41/2/2] 4–6  $\times$  3.5–5  $\mu$ m, Q = 1–1.4, Qm = 1.2  $\pm$  0.1, globose, broadly ellipsoid to ellipsoid, inamyloid, colourless, hyaline, thin-walled, smooth; apiculus relatively small. Basidia 17–27  $\times$  4.5–7  $\mu$ m, cylindrical to clavate, 4-spored, hyaline, sterigmata 3–4  $\mu$ m long. Pleurocystidia 22–38.5  $\times$  4–6  $\mu$ m, narrowly cylindrical to flexuose, thin-walled, colourless, hyaline. Cheilocystidia absent. Pileipellis a cutis to trichoderm, composed of 4–12  $\mu$ m wide, thin-walled, filamentous hyphae, terminal cells cylindrical 5–8  $\times$  20–45  $\mu$ m. Clamps present at all parts of basidioma.

*Known distribution:* China.

*Habitat:* Solitary to scattered on stumps of bamboo.

*Additional material examined:* China, Hunan Province, Yuelu Mountain, 208 m elev., on stumps of bamboo, 4 January 2017, Ping-Wu Luo (HKAS 129,333).

*Notes:* *Tricholomopsis glabra* is characterised by a pale yellow pileus without scales, slender basidiospores, and the absence of cheilocystidia. It has larger basidioma and more slender basidiospores



**Figure 11.** Microscopic features of *Tricholomopsis campestris* (type, HKAS 116,178). (a) Basidiospores; (b) Hymenium; (c) Pileipellis; (d) Cheilocystidia. Bars: a – b = 10  $\mu$ m, c – d = 20  $\mu$ m.

than *T. aurea* and smaller basidioma and paler pilei than *T. flava*. *Tricholomopsis glabra* also lacks cheilocystidia, while *T. flava* lacks pleurocystidia.

**Tricholomopsis sect. Tricholomopsis**

*Type:* *Tricholomopsis rutilans* (Schaeff.) Singer.

*Description:* Basidioma tricholomoid; pileus densely covered with purplish to red scales; basidiospores globose to oblong, smooth, inamyloid; cheilocystidia prominent; pileipellis a cutis to a trichoderm; solitary or scattered on rotten wood or soil in coniferous or broad-leaved forests, seldom on grassland.

*Notes:* *Tricholomopsis* sect. *Tricholomopsis* can be distinguished from the other sections by its purplish to red scales. To date, nine taxa of sect. *Tricholomopsis* have been identified via phylogenetic analyses, including two novel species and seven known taxa.

**Key to the species of Tricholomopsis sect. Tricholomopsis in China**

- (1) Pileus with brownish or darkish scales; stipe <0.5 cm in width..... 2
- (1) Pileus with purplish to red scales; stipe >0.5 cm in width..... 3
- (2) Basidiospores broadly ellipsoid to ellipsoid; pleurocystidia <50  $\mu$ m in length..... *T. sulphureoides*
- (2) Basidiospores ellipsoid to fusiform; pleurocystidia >50  $\mu$ m..... *T. pallidolutea*

- (3) Scales on pileus mealy, warped; stipe slender, less than 1 cm in width..... 4
- (3) Scales on pileus tomentose, adpressed; stipe robust, more than 1 cm in width..... 5
- (4) Pileus depressed; basidiospores wider than 4.5  $\mu$ m..... *T. depressa*
- (4) Pileus applanate; basidiospores narrower than 4.5  $\mu$ m..... *T. flammula*
- (5) On buried litter in meadows; scales dark blond to orange..... *T. campestris*
- (5) On rotten wood; scales red or purple-red..... 6
- (6) Pleurocystidia absent or scarce..... *T. rutilans*
- (6) Pleurocystidia present or abundant..... 7
- (7) Stipes covered with dense scales; scales purple-red..... *T. yunnanensis*
- (7) Stipes covered with scarce scales; scales brown..... *T. mitirubicunda*

**Tricholomopsis campestris** Zhu L. Yang & G. S. Wang, sp. nov. Figures 11a-d, 13a-b

*Mycobank:* MB 849,777.

*Etymology:* referring to the habitat of basidioma on buried litter on meadows.

*Type:* China, Tibet Autonomous Region, Nyingchi, Muduohuahai Scenic Area, 3,475 m elev.,

on buried litter in meadows, 21 July 2019, Geng-Shen Wang 476 (HKAS 116,178, holotype).

*Diagnosis:* *Tricholomopsis campestris* differs from the other species of sect. *Tricholomopsis* by its castaneous squamose pileus and stipe and stuffed stipe. It is the only species living on buried substrate in meadows above 3,400 m altitude.

*Description:* Basidiomata small to medium-sized. Pileus 4–8 cm in diam., plano-convex, with margin deflexed; surface dry, pale yellow (2A2–3) to bright yellow (3A3–5), surface densely covered with dark blond (5D4–5), tawny (5D6–8) to orange (6B6–8) tomentose-fibrillose scales or fibrils. Lamellae emarginate with decurrent teeth to subdecurrent, crowded, edges entire, white (1A1), yellow white (1A2–3) to pastel yellow (3A4), yellow (3A5). Stipe 4–5 × 1–1.5 cm, central, solid, cylindrical to slightly tapering upwards, pastel yellow (3A4–7), with dark blond (5D4–5), tawny (5D6–8) to orange (6B6–8) tomentose-fibrillose scales or fibrils.

Basidiospores [44/2/2] 5.5–7.5 × 4–5 μm, Q = 1.20–1.75(–1.80), Q<sub>m</sub> = 1.42 ± 0.09, broadly ellipsoid to ellipsoid, inamyloid, colourless, hyaline, thin-walled, smooth; apiculus relatively small. Basidia 22–32 × 6–8 μm, cylindrical to clavate, 4-spored, hyaline, sterigmata 6–8 μm long. Pleurocystidia frequent, 30–48 × 6–8 μm, cylindrical, with obtuse or rostrate apex, thin-walled, colourless, hyaline. Cheilocystidia 45–85 × 14–30 μm, narrowly clavate to clavate, thin-walled, colourless, hyaline. Pileipellis a cutis with the transition to a trichoderm at regular intervals, composed of 5–8 μm wide, thin-walled filamentous hyphae, terminal cells 20–45 × 6–13 μm, with round apex. Clamps present at all parts of basidioma.

*Known distribution:* southwestern China.

*Habitat:* Solitary on buried litter in meadows.

*Additional material examined:* China, Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-La, 4,251 m elev., on buried litter in meadow, 8 August, Jian-Wei Liu 495 (HKAS 98,074).

*Notes:* *Tricholomopsis campestris* formed a clade sister to *T. rutilans*. The castaneous scales on the pileus and stipe differentiate it from *T. rutilans*. In *Tricholomopsis*, most species have a hollow stipe, while *T. campestris* has a solid stipe. In addition, *T. campestris* is also the only known species in *Tricholomopsis* that lives on buried litter in meadows above 3,400–4,200 m altitude.

***Tricholomopsis depressa* Zhu L. Yang & G. S. Wang, sp. nov. Figures 12a-d, 13c**

*Mycobank:* MB 849,778.

*Etymology:* *depressa*, from *depressus* = depressed, referring to a depressed pileus.

*Type:* China, Tibet Autonomous Region, Garze, Daofu County, 3,000 m elev., on rotten wood in *Abies* forest, 25 July 2007, Zai-Wei Ge 1538 (HKAS 53,624, holotype).

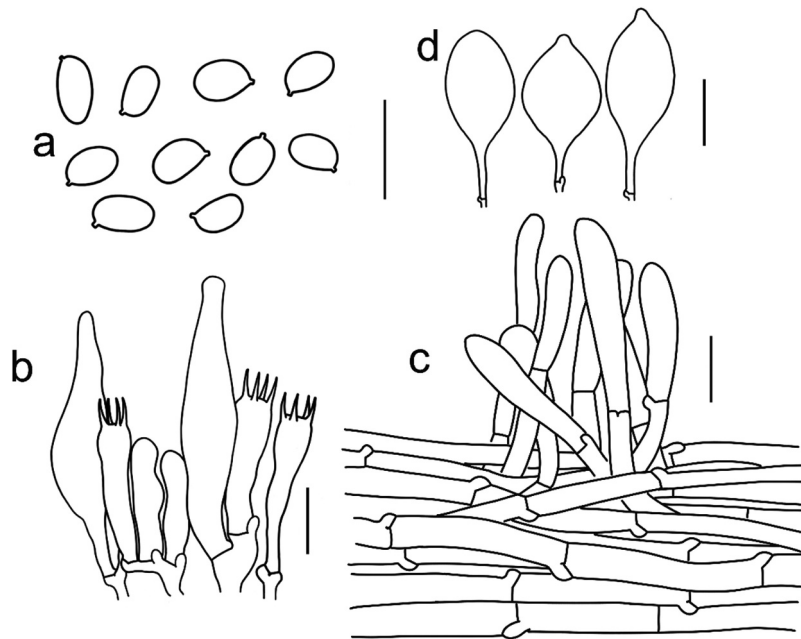
*Diagnosis:* *Tricholomopsis depressa* is characterised by its small to medium-sized basidioma, a depressed pileus covered with small, grey pink to pink scales, and a smooth stipe with yellowish to pink scales. It can be distinguished from *T. flammula* by a robust stipe and depressed pileus, while it can be distinguished from *T. rutilans* by a smaller and slender basidioma and elongated basidiospores.

*Description:* Basidioma small to medium-sized. Pileus 2–6 cm in diam., at first hemispherical to convex, then plano-convex, often depressed at centre, margin involute; surface dry, cream (3A2), yellowish (3A3–4) to grey yellow (3B5–7), densely covered with small, grey pink (11B4–6) to pink (12A3–6) scales. Lamellae adnate with decurrent teeth, crowded, edges entire, yellow-white (2A2–4) to yellowish (3A2–3). Stipe 2–7 × 0.5–1.2 cm, cylindrical, sometimes slightly tapering downwards, hollow, smooth or with yellow white (2A2–4) to yellowish (3A2–3), with grey pink (11B4–6) to pink (12A3–6) scales or fibrils.

Basidiospores [64/3/3] 5.5–7.5 × 3.5–5.0 μm, Q = (1.33–) 1.38–2.00, Q<sub>m</sub> = 1.64 ± 0.16, ellipsoid to elongate, in-amyloid, colourless, hyaline, thin-walled, smooth; apiculus relatively small. Basidia 21–36 × 5.5–8.5 μm, clavate, 4-spored, hyaline, sterigmata 2–4 μm long. Pleurocystidia frequent, 25–70 × 7–26 μm, ventricose-subfusiform, thin-walled, colourless, hyaline. Cheilocystidia 50–78 × 16–29 μm, clavate to spheropedunculate, apex sometimes mucronate, thin-walled, colourless, hyaline. Pileipellis a cutis with the transition to a trichoderm at regular intervals, composed of 5–11 μm wide, thin-walled, filamentous hyphae, terminal cells subcylindrical to cylindrical, 40–69 × 8–12 μm, with round apex. Clamps present at all parts of basidioma.

*Known distribution:* China and the Czech Republic.

*Habitat:* Solitary to scattered on rotten wood in *Abies* forests.



**Figure 12.** Microscopic features of *Tricholomopsis depressa* (type, HKAS 53,624). (a) Basidiospores; (b) Hymenium; (c) Pileipellis; (d) Cheilocystidia. Bars: a – b = 10  $\mu$ m, c – d = 20  $\mu$ m.

*Additional material examined:* China, Tibet Autonomous Region, Nyingchi, Milin Village, 2,950 m elev., on rotten wood in *Pinus* forest, 29 July 2014, Qi Zhao 2118 (HKAS 87,884); Riwoqe, Mengda Village, 4,100 m elev., on rotten wood in *Picea* forest, 9 August, Zai-Wei Ge 312 (HKAS 46,092); same locality, altitude 3900 m, on rotten wood in *Picea* forest, 10 August, Zai-Wei Ge 317 (HKAS 46,097); Riwoqe, Sangduo Village, 3900 m elev., on rotten wood in *Picea* forest, 11 August, Zhu-Liang Yang 4364 (HKAS 45,743). Sichuan Province, Xiaojin County, Shalong Village, 2723 m elev., on rotten wood in *Abies* forest, 26 July 2007, Zai-Wei Ge 1545 (HKAS 53,631). Gansu Province, Gannan City, Diebu, 3,000 m elev., on rotten wood in *Abies* forest, 12 August, Xue-Tai Zhu 693 (HKAS 76,542). Yunnan Province, Zhongdian County, 3,500 m elev., on rotten wood in *Picea* forest, 25 July 2006, Yan-Chun Li 633 (HKAS 50,387); same locality, 3,600 m elev., on rotten wood in *Picea* forest, 7 August, Zhu-Liang Yang 4560 (HKAS 48,724). Jilin Province, Xifeng County, 207 m elev., on rotten wood, 2 August, Yan-Chun Li 1186 (HKAS 56,040); Chibei District, Dayangcha Farmed Forest, 860 m elev., on rotten wood, 2 August, Zhu-Liang Yang 5101 (HKAS 54,397); Antu County, Erdaobaihe, Changbai Mountains Nature Reserve, Baishan Station, 490 m elev., on

rotten wood in mixed forests with *Pinus*, *Abies*, *Populus*, and *Betula*, 10 September 2006, Xiang-Hua Wang 2091 (HKAS 51,808).

*Notes:* One collection of *Tricholomopsis depressa* was once identified as *T. flammula* (Holec and Kolařík 2013). With additional analyses, we confirmed that *T. depressa* was a monophyletic clade sister to *T. flammula* and can be differentiated by its larger basidiomata and depressed pileus.

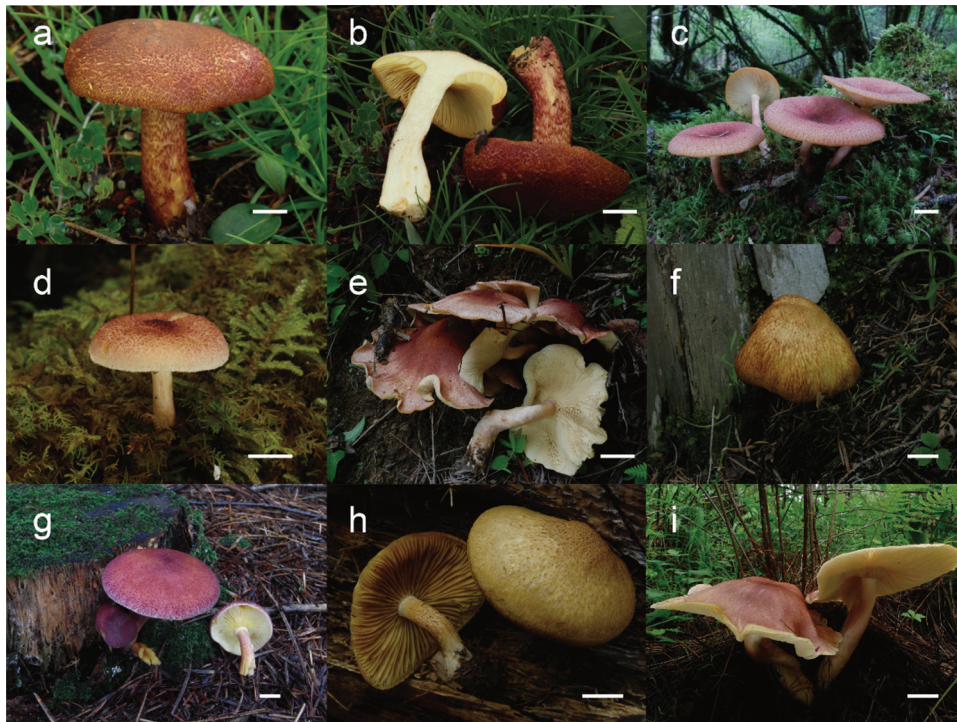
***Tricholomopsis flammula*** Métrod ex Holec, J. National Mus. (Prague), Nat. Hist. Ser. 178: 8 (2009) Figure 13d

*Known distribution:* Europe, East Asia, and North America (Métrod 1946; Smith 1960; Krisai-Greilhuber and Voglmayr 2000; Holec 2009; Holec and Kolařík 2011, 2013; Razaq et al. 2012; Wang et al. 2018; this study).

*Habitat:* Solitary to scattered on decaying wood chips or sawdust remnants in coniferous or broad-leaved forests.

*Material examined:* China, Hubei Province, Shennongjia, 2600 m elev., on rotten wood, 1 August, Xiang-Hua Wang 2494 (HKAS 73,509). Sichuan Province, Baiyu County, Marong Town, 3490 m elev., on rotten wood, 20 August, Zai-Wei Ge 1340 (HKAS 50,927). Tibet Autonomous Region, Nyingchi,





**Figure 13.** (a – b) *Tricholomopsis compestris* (HKAS 116,178, photo by Geng-Shen Wang); (c) *T. depressa* (HKAS 53,624, photo by Zai-Wei Ge); (d) *T. flammula* (HKAS 116,169, photo by Geng-Shen Wang); (e) *T. mitirubicunda* (HKAS 71,469, photo by Yan-Jia Hao); (f) *T. pallidolutea* (HKAS 129,339, photo by Jian-Wei Liu); (g) *T. rutilans* (HKAS 105,394, photo by Xiao-Xia Ding); (h) *Tricholomopsis sulfureoides* (HKAS 51,002, photo by Zaiwei Ge); (i) *T. yunnanensis* (HKAS 76,311, photo by Yanjia Hao). Bars: a – i = 1 cm.

Lulang Town, 3,400 m elev., on rotten wood in coniferous broad-leaved forests, 20 July 2019, Geng-Shen Wang 467 (HKAS 116,169). Yunnan Province, Dali Bai Autonomous Prefecture, Binchuan County, Jizu Mountain, 743 m elev., on rotten wood, 4 August, Jiao Qin 743 (HKAS 81,181).

*Notes:* *Tricholomopsis flammula* was first described in France by Métrod (1946) and then validly published by Holec (2009). It differs from *T. rutilans* by its smaller and much slender basidiocarps, smaller and finer scales, elongated basidiospores, and very abundant pleurocystidia.

***Tricholomopsis mitirubicunda*** L. Fan & N. Mao, in Mao, Xu & Fan, *Phytotaxa* 507(2): 161 (2021) Figure 13e

*Known distribution:* Europe and East Asia (Olariaga et al. 2015; Mao et al. 2021; this study).

*Habitat:* Solitary to scattered on rotten wood or buried wood in coniferous or broad-leaved forests.

*Material examined:* China, Hubei Province, Shennongjia Forestry District, Lishubao Town, 1,324 m elev., on buried debris in *Pinus* forest, 14 July 2012, Jiao Qin 513 (HKAS 77,914); Shennongjia Forestry District, Hongping Town, 1,900 m elev., on buried debris in *Pinus* forest, 15 July 2012, Jiao Qin 538 (HKAS 77,939); Shiyan City, Maojian District, 320 m elev., on buried debris in a forest with *Pinus* and *Quercus*, 1 July 2013, Qi Zhao 1842 (HKAS 80,952). Shandong Province, Taian City, Taishan Mountain, 982 m elev., on buried debris in *Pinus* forest, 4 August, Yan-Chun Li 2805 (HKAS 89,448). Yunnan Province, Baoshan City, Longyang County, 1,684 m elev., on buried debris in *Pinus* forest, 10 January 2003, Yan-Chun Li 1739 (HKAS 59,486); Zhaotong City, 1,900 m elev., on buried debris in *Pinus* forest, 17 August, Si-Peng Jian 71 (HKAS 101,060); Kunming City, Yeyahu, 2,100 m elev., in *Fagaceae* forest, 3 September 2017, Sai Gong 20 (HKAS 101,376); Lushui County, Pianma, 1,400 m elev., on rotten wood in a forest with *Fagaceae* and

*Theaceae*, 5 August, Yan-Jia Hao 360 (HKAS 71,469); Dali Bai Autonomous Prefecture, Cang Mountains, 2,900 m elev., on buried debris in coniferous forests, 22 August, Gang Wu 116 (HKAS 57,648). Anhui Province, Huoshan County, Taiyang Village, 600 m elev., on buried debris in a forest with *Pinus* and *Fagaceae*, 27 June 2013, Yan-Jia Hao 882 (HKAS 80,162); Huoshan County, Taiyang village, 446 m elev., on buried debris in *Pinus* forest, 27 June 2013, Ting Guo 651 (HKAS 81,853). Jilin Province, Changchun City, Jingyuetan Park, 350 m elev., on buried debris in a broadleaved and coniferous forest, 5 September 2015, Jing Li 376 (HKAS 91,478). AUSTRIA, Kleinwalsertal, 1,100 m elev., on rotten wood, 26 September 2016, Zhu-Liang Yang 5915 (HKAS 129,326).

*Notes:* *Tricholomopsis mitirubicunda* was regarded as "*T. aff. rutilans* 2" by Olariaga et al. (2015) and later published by Mao et al. (2021). It differs from *T. rutilans* by the presence of abundant pleurocystidia (Mao et al. 2021).

***Tricholomopsis pallidolutea*** L. Fan & N. Mao, in Mao, Xu & Fan, *Phytotaxa* 507(2): 160 (2021) Figure 13f

*Known distribution:* northwestern China (Mao et al. 2021; this study).

*Habitat:* solitary or scattered on trunks or buried wood in forests with *Picea* or *Larix*.

*Material examined:* China, Xinjiang Uygur Autonomous Region, Ili Kazakh Autonomous Prefecture, Zhaosu County, 1,886 m elev., solitary on soil in a forest with *Picea*, 14 July 2020, Jian-Wei Liu 752 (HKAS 129,339).

*Notes:* *Tricholomopsis pallidolutea*, *T. sulphureoides*, and *T. flavescens* are three species with brown fibrillose pileus scales. However, *T. pallidolutea* can be distinguished from *T. sulphureoides* and *T. flavescens* by its more elongated basidiospores and shorter pleurocystidia.

***Tricholomopsis rutilans*** (Schaeff.) Singer, *Schweiz. Z. Pilzk.* 17: 56 (1939) Figure 13g

*Known distribution:* Europe, North America, East Asia, and Australia (Smith 1960; Liu 1994; Holec and Kolařík 2013; Olariaga et al. 2015; Cooper and Park 2016).

*Habitat:* Solitary to scattered on rotten wood or buried wood in coniferous or broad-leaved forests.

*Material examined:* China, Sichuan Province, Luoji Town, Luoji Mountain, 2,000 m elev., on rotten wood in forests with *Pinus*, 28 July 2012, Yan-Jia Hao 657 (HKAS 76,315). Yunnan Province, Ninglang County, Zhanhe Country, 3,000 m elev., on rotten wood in mixed forests with *Quercus*, *Pinus*, and *Rhododendron*, 17 July 2010, Qi Zhao 786 (HKAS 69,507); Yulong County, Gaomeigu, 3,300 m elev., on rotten wood, 20 July 2008, Qi Zhao 835 (HKAS 55,036); Yulong County, Yulong Reservoir, 3,100 m elev., on rotten wood, 29 July 2006, Yan-Chun Li 674 (HKAS 50,428); Lijiang City, Yulong Mountain, 2,800 m elev., in a forest with *Pinus*, 1 August, Mu Zang 10,208 (HKAS14979). Tibet Autonomous Region, Zuogong County, Wangda Town, 3,900 m elev., on rotten wood, 18 July 2009, Zhu-Liang Yang 5287 (HKAS 57,830). Liaoning Province, Dandong City, Kuandian County, 500 m elev., on buried debris in a coniferous forest, 29 August, Xiao-Xia Ding 384 (HKAS 105,394). Heilongjiang Province, Yichun City, Dailing Town, 225 m elev., on rotten wood, 15 August, Xiang-Hua Wang 2631 (HKAS 61,828).

*Notes:* *Tricholomopsis rutilans* s. str. was designated a lectotype and an epitype by Olariaga et al. (2015). It is similar to *T. mitirubicunda* and *T. yunnanensis*. But *T. rutilans* has no or only scarce pleurocystidia, while *T. mitirubicunda* and *T. yunnanensis* have abundant pleurocystidia. The basidiospores of *T. mitirubicunda* are much more slender than those of *T. yunnanensis*. The *T. rutilans* is nearly distributed cosmopolitan, while *T. mitirubicunda* is distributed in Europe and East Asia, while *T. yunnanensis* is only known from southwestern China.

***Tricholomopsis sulphureoides*** (Peck) Singer, *Annls mycol.* 41(1/3): 69 (1943) Figure 13h

*Known distribution:* Europe, Asia, and North America (Smith 1960, Vauras 2009; Holec and Kolařík 2011, 2013; Holec 2012; Saar and Voitk 2015; this study).

*Habitat:* Solitary to scattered on rotten wood in coniferous or broad-leaved forests.

*Material examined:* China, Sichuan Province, Litang County, Junba Village, 4,280 m elev., on rotten wood, 26 August, Zai-Wei Ge 1416 (HKAS 51,002).

*Notes:* *Tricholomopsis sulphureoides* was first described in the United States as *Agaricus sulfur-oides* by (Peck 1872). Phylogenetic analysis

revealed that *T. sulphureoides* and *T. flavescens* formed two independent clades, although distinct morphological characteristics between them were not observed in the study by Saar and Voitk (2015). *Tricholomopsis sulphureoides* can be easily distinguished from *T. flammula*, *T. rutilans*, *T. depressa*, *T. yunnanensis*, and *T. pteridiicola* by minute brown or absent scales.

***Tricholomopsis yunnanensis*** (M. Zang) Li R. Liu, Yan C. Li & Zhu L. Yang, in Liu, Wang, Jia, Kang, Yang & Li, *Phytotaxa* 530(2): 184 (2022) Figure 13i

*Synonym:* *Tricholomopsis galeata* L. Fan & N. Mao, in Mao, Xu & Fan, *Phytotaxa* 507 (2): 160 (2021).

*Known distribution:* China (Zang and Zeng 1978; Mao et al. 2021; Liu et al. 2022).

*Habitat:* Solitary to scattered on rotten wood or buried wood in the forests of *Pinus*.

*Material examined:* China, Yunnan Province, Kunming City, Heilongtan Park, 2,700 m elev., on rotten wood, 2 September 1978, You-Feng Yu 3884 (HKAS 40,151); same locality, on rotten wood, 8 August, Wen-Qing Yin 931 (HKAS 28,976); same locality, on buried debris in *Pinus* forest, 9 August, Geng-Shen Wang 194 (HKAS 109,582); Kunming Botanical Garden, 1,990 m elev., on buried debris in *Pinus* forest, 18 August, Geng-Shen Wang 1335 (HKAS 121,974); Yeyahu, 2,100 m elev., on buried debris in *Pinus* forest, 1 September 2013, Zhu-Liang Yang 5757 (HKAS 80,034); Nujiang City, Lanping County, Xihe Village, 2,760 m elev., on buried debris in *Pinus* forest, 15 August, Qi Zhao 890 (HKAS 69,611); Chuxiong Yi Autonomous Prefecture, Nanhua County, Zixi Mountain, 2,250 m elev., on buried debris in *Pinus* forest, 12 July 2001, Xiang-Hua Wang 1230 (HKAS 39,166); Dali Bai Autonomous Prefecture, Yongping County, Longmen Village, 2,282 m elev., on buried debris in *Pinus* forest, 31 July 2009, Qing Cai 65 (HKAS 58,732); Nanjian County, 2,317 m elev., on buried debris in *Pinus* forest, 27 July 2009, Li-Ping Tang 965 (HKAS 56,922); Binchuan County, Jizu Mountain, on buried debris in *Pinus* forest, 2,450 m elev., 4 August, Jiao Qin 731 (HKAS 81,169); Lijiang City, Xiangshan Mountain, 2,600 m elev., on buried debris in *Pinus* forest, 5 August, Yan-Chun Li 322 (HKAS 48,555). Sichuan Province,

Xichang City, Jiluo Mountain, 2,000 m elev., on buried debris in a forest with broad-leaved and coniferous forest, 18 July 1992, Pei-Qiong Sun 1818 (HKAS25752); Puge County, Luoqi Mountain, 2,000 m elev., on buried debris in *Pinus* forest, 28 July 2012, Yan-Jia Hao 653 (HKAS 76,311); same locality, on buried debris in *Pinus* forest, 28 July 2012, Kuan Zhao 18 (HKAS 77,370). Shandong Province, Qingzhou City, Yangtianshan National Forest Park, 520 m elev., on buried debris in *Pinus* forest, 22 August, Xiang-Hua Wang 3008 (HKAS 73,557).

*Notes:* *Tricholomopsis yunnanensis* was first described in southwestern China as *Paxillus yunnanensis* by Zang and Zeng (1978). The type was restudied by Liu et al. (2022), who placed it into *Tricholomopsis* as *T. yunnanensis*. Phylogenetic analysis indicated that *T. yunnanensis* and *T. galeata* are conspecific. Although Mao et al. (2021) did not find any pleurocystidia in *T. galeata* and Liu et al. (2022) regarded the pileipellis as palisadoderm, we observed the presence of pleurocystidia and regarded the pileipellis as a cutis with transition to a trichoderm in *T. yunnanensis*.

***Tricholomopsis* sect. *Lividae*** A. H. Smith, *Brittonia* 12(1): 57 (1960)

*Type:* *Tricholomopsis totilivida* (Murrill) Singer.

*Notes:* This section contains only one species and can be easily distinguished from the other sections by its livid pileus and lamellae and its large pleurocystidia. It has only been known from Florida, USA. It may be close to *T. sect. Tricholomopsis* due to its squamous pileus. However, this section needs further research and molecular data to verify its position within *Tricholomopsis*.

### Other species

***Tricholomopsis lividipileata*** P. G. Liu, *Acta Mycol. Sin.* 13(3): 182 (1994)

*Known distribution:* China (Liu 1994).

*Habitat:* scattered or clustered in litterfall in forests with *Pinus*.

*Notes:* *Tricholomopsis lividipileata* was described in Sichuan, China, by Liu (1994), and it is an edible

species favoured by local people (Yuan & Sun 2007). However, subsequent visits by our expedition team to Sichuan failed to identify this species. The descriptions and illustrations of *T. lividipileata* are very similar to those of *Tricholoma olivaceum* by Rambaut et al. (2018). Both of them have an olive-brown pileus with fibrils, similar basidiospores, and cutis pileipellis, and they live in coniferous forests at similar altitudes. These clues suggested that *T. lividipileata* may belong to *Tricholoma* and be close to *Ta. olivaceum*. Whether they are conspecific remains an open question, because the type of *T. lividipileata* is missing.

***Tricholomopsis shulanensis*** X. He, *Acta Mycol. Sinica* 8(3): 202 (1989)

*Known distribution:* China (He 1989).

*Habitat:* Single or scattered, on rotting sticks buried in soil under hazel wood.

*Notes:* Specimens of *Tricholomopsis shulanensis* were not traced and studied in this study. Judging from the protologue, *T. shulanensis* is very similar to *T. flammula* with subtle differences. The identity of this species needs to be verified using molecular data in the future.

***Tricholoma nigrosquamosum*** (P. G. Liu) Zhu L. Yang & G. S. Wang, *comb. nov.*

*Mycobank:* MB 849,786.

*Basionym:* *Tricholomopsis nigrosquamosa* P. G. Liu, *Acta Mycol. Sinica* 13(3): 183 (1994).

*Synonymy:* *Tricholoma sinopardinum* Zhu L. Yang, X. X. Ding, G. Kost & Rexer, *Phytotaxa* 305(1): 6 (2017).

*Known distribution:* China (Liu 1994).

*Habitat:* Scattered under litter in forests with *Abies*.

*Material examined:* China, Sichuan Province, Rang Tang, 3,500 m elev., scattered under litterfall in a forest with *Abies*, 28 July 1991, Ming-Sheng Yuan 1434 (HKAS 23,947, type of *T. nigrosquamosum*). Tibet Autonomous Region, Jiangda County, Jiangda Town, 3,500 m elev., in forest dominated by *Picea* sp. and *Populus* sp., 8 August, Bang Feng 1427 (HKAS 82,533, type of *Ta. sinopardinum*).

*Notes:* *Tricholomopsis nigrosquamosum* was described from Sichuan by Liu (1994), while *Ta. sinopardinum* Zhu L. Yang et al. was described from Tibet by Yang et al. (2017). The type of *T. nigrosquamosum* (HKAS 23,947) was sequenced,

and the ITS identity between *T. nigrosquamosum* and *Ta. sinopardinum* was 100%. Morphologically, they are the same. Therefore, the new combination, *Ta. nigrosquamosum* is proposed.

***Sarcomyxiinae*** Zhu L. Yang & G. S. Wang, *subord. nov.*

*Mycobank:* MB 849,775.

*Type genus:* *Sarcomyxa* P. Karst. 1891.

*Etymology:* From the type genus *Sarcomyxa*.

*Diagnosis:* *Sarcomyxiinae* differs from the other suborders of *Agaricales* by its lignicolous habitat; fan- or kidney-shaped, viscid pileus with a pellicle easily peeling off from the context; lateral short stipe; prominent cheilocystidia; small allantoid to subcylindrical amyloid basidiospores; and the common presence of clamp connections.

*Description:* Basidioma pleurotoid, small to large, fan- or kidney-shaped, fleshy. Pileus viscid or velutinous; pellicle easily peeling off from the context. Lamellae decurrent, crowded. Stipe lateral, short, subcylindrical, floccose. Basidiospores allantoid or cylindrical, thin-walled, colourless and hyaline, smooth, amyloid; apiculus indistinct or very small. Basidia clavate, mostly 4-spored, thin-walled. Cheilocystidia clavate. Pleurocystidia clavate to nearly fusiform. Pileipellis a gelatinised plagiotrichoderm. Clamp connections present in all parts of basidioma.

*Known distribution:* Europe, North America, and Asia.

*Habitat:* Saprotrophic, on rotten wood in coniferous or broad-leaved forests.

*Family included:* *Sarcomyxiaceae* Olariaga et al.

*Notes:* *Sarcomyxiaceae* was once placed in the suborder *Pleurotineae* by Olariaga et al. (2020). Our phylogenomic analyses showed that *Sarcomyxiaceae* formed a unique suborder clade (Figures 1 and 2). Due to its unique phylogenetic position and morphological features, it is considered an independent suborder here. To date, four species have been described for the genus *Sarcomyxa* (Cai et al. 2023).

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