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Multi-gene phylogeny and morphological characters reveal seven new species of *Micropsalliota* (Agaricales, Agaricaceae) from southern China, with an updated key for the species distributed in China

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ABSTRACT

Species of *Micropsalliota* generally grow in the tropics and are characterised by small, slender basidiomes, brown basidiospores, and cheilocystidia that vary in shape with capitate or subcapitate apex, and pigmented pileipellis. Based on morphological characters and molecular evidence, here we describe seven new species from southern China, viz. *Micropsalliota ferruginea*, *M. fimbriata*, *M. gigaspora*, *M. longicystis*, *M. nana*, *M. squarrosa*, and *M. umbonata*. *Micropsalliota appendiculata*, a species recently described from Vietnam, was first recorded in China. The Maximum likelihood and Bayesian analyses based on multi-locus sequence datasets (the nuc rDNA internal transcribed spacer region ITS1-5.8S-ITS2, nrITS; the D1-D2 domains of nuc 28S rDNA, LSU; partial sequences of the most variable region of the second-largest subunit of RNA polymerase II, *rpb2*, and a portion of the translation-elongation factor 1-a, *tef1*) shows that the genus is separated into 11 major clades and subclades. To aid in diagnosis, a key to 32 species of *Micropsalliota* in China is provided.

ARTICLE HISTORY

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KEYWORDS

Agaricaceae; molecular phylogeny; new taxa; taxonomy

1. Introduction

The genus *Micropsalliota* Höhn. was established by Höhnel (1914) to accommodate species within *Agaricus* L. [syn. *Psalliota* (Fr.) P. Kumm. 1871:23] that form small and slender basidiomes. The generic concept was subsequently amended by Heinemann (1956), Pegler and Rayner (1969), and adopted by subsequent mycologists such as Singer (1975). In previous molecular systematics studies, Zhao et al. (2010) provided the first molecular phylogenetic study of the genus based on nrITS and nrLSU sequences. Based on combined nrITS and nrLSU sequences, or *rpb2*, the genera *Leucoagaricus* Locq. ex Singer, *Leucocoprinus* Pat., and *Micropsalliota* together form a monophyletic clade (BS = 100%, PP = 1) (Ge et al. 2015; Ma et al. 2022). Yan et al. (2022) reconstructed its phylogeny based on the three-gene dataset (nrITS, nrLSU, and *rpb2*) and separated the genus into 18 weakly to strongly supported clades and subclades.

Up to now, about 80 species of *Micropsalliota* are recorded worldwide (<https://www.speciesfungorum.org/>) (Al-Kharousi et al. 2022; Patil et al. 2022; Yan et al. 2022; Ji and He 2023), most of which are distributed in tropical and subtropical areas of Africa, India, America, Indonesia, and Malaysia (Heinemann 1980, 1983, 1988, 1989; Heinemann and Flower 1983; Guzmán-Dávalos 1992; Guzmán-Dávalos and Heinemann 1994), and few reports were from China (Wei et al. 2015; Li et al. 2021; Yan et al. 2022; Ji and He 2023). Since *Micropsalliota pseudoglobocystis* Li Wei & R.L. Zhao, the first new species from China, was reported (Wei et al. 2015), 11 new species, and 13 new records for China have been published recently (Wei et al. 2015; Xu et al. 2016; Wang et al. 2017; Chen et al. 2019; Sun et al. 2020; Li et al. 2021; Liu et al. 2022; Yan et al. 2022; Ji and He 2023).

In this paper, we explore the species diversity of *Micropsalliota* and describe seven new species and

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a new record from southern China based on morphological observations and molecular phylogenetic analyses.

2. Materials and methods

2.1. Morphological study

Macroscopic characters and habitat details of fresh basidiomes were photographed and recorded at the time of collecting. Odor and colour changes after bruising were recorded at the same time. GPS coordinates were documented for each collection site. To avoid mixing or crushing, aluminium foil was used for wrapping. Chemical reactions of fresh specimens were recorded soon after returning from the field. Colour terms and notations follow the Methuen Handbook of Colour (Kornerup and Wanscher 1978). Specimens were dried completely with a dehydrator at 50 Celsius degrees, then sealed in plastic bags, and deposited in the Herbarium of Cryptogams, Kunming Institute of Botany, Chinese Academy of Sciences (KUN, with HKAS accession numbers) (Table 1). Microscopic observations were performed on dried specimens. Tissues to be observed were mounted in 3% KOH, and then stained with 1% Congo Red reagent. When necessary, Melzer's reagent was used to test the amyloidity of basidiospores, and 10% NH₄OH was used to test the type of pigments. A minimum of 20 basidiospores, 10 basidia, and 10 cystidia per specimen were randomly measured using a LEICA DM2500 microscope (Leica, Bensheim, Germany). The notations [n/m/p] indicate that the measurements were taken on n basidiospores, from m basidiomes and p collections. Dimensions for basidiospores are given using (a) b – c (d). The b – c range contains at least 90% of the measured values, and (a) and (d) represent the extreme values whenever present. "av." stands for the average size of basidiospores, "Q" stands for the ratio of the length and width of a spore, and Q_m stands for the mean value of all basidiospores ± standard deviation of the samples (Largent 1986).

2.2. DNA extraction, PCR, and sequencing

DNA was extracted from the dried specimens using an Ezup Column Fungi Genomic DNA Purification Kit (Sangon Biotech, Shanghai, China) following the manufacturer's protocol. Polymerase chain reaction (PCR) was implemented on an ABI 2720 thermal cycler

(Applied Biosystems, Foster City, CA, USA). PCR amplification and sequencing procedures followed procedures described by Ge et al. (2021). Specifically, each PCR reaction mixture contained 1 µL (10 mmol/L) of each primer, 1 µL DNA template, 0.3 µL MgCl₂ (Sangon Biotech, Shanghai, China), 12.5 µL 2 × GS Taq PCR Mix (Genesand Biotech, Beijing, China) and ddH₂O up to 25 µL. Primers used to amplify the internal transcribed spacer (ITS) region, the large subunit (LSU) of the ribosomal DNA, the second largest RNA polymerase subunit (*rpb2*), and translation elongation factor 1-α (*tef1*) were ITS1F/ITS4 (White et al. 1990; Gardes and Bruns 1993), LR0R/LR5 (Vilgalys and Hester 1990; Cubeta et al. 1991), bRPB2-6F/bRPB2-7 R (Matheny 2005) and EF1-983F/EF1-1567 R (Rehner and Buckley 2005), respectively. The PCR program was set as follows: Pre-denaturation at 95 °C for 3 min; 35 cycles of denaturation at 95 °C for 25 s, annealing at appropriate temperature and time (ITS and LSU: 53 °C for 25 s, *rpb2* and *tef1*: 58 °C for 25 s) and extension at 72 °C for 15 s, followed by a final extension at 72 °C for 5 min. PCR products were sent to Biomed Biotechnology commercial company for sequencing.

2.3. Molecular phylogenetic study

Reference sequences were selected based on previous studies (Zhao et al. 2010; Wei et al. 2015; Xu et al. 2016; Parra et al. 2016; Wang et al. 2017; Chen et al. 2019; He et al. 2020; Sun et al. 2020; Li et al. 2021; Liu et al. 2022; Al-Kharousi et al. 2022; Patil et al. 2022; Yan et al. 2022). Sequences (ITS, LSU, *rpb2*, and *tef1*) of *Micropsalliota* in NCBI GenBank were downloaded and 185 out of the 359 sequences were retained after excluding redundant sequences from the same location and the sequences with low quality. Then additional 166 sequences generated from our newly collected specimens were incorporated into the data set. *Leucoagaricus barssii* (Zeller) Vellinga and *L. centricastaneus* Y.R. Ma, Z.W. Ge & T.Z. Liu were chosen as the outgroup taxon for rooting purposes based on data published by Ma et al. (2022). A total of 359 sequences including 145 ITS, 107 LSU, 67 *rpb2*, and 40 *tef1* sequences were used in subsequent analyses. Details of all sequences are listed in Table 1.

The sequences were aligned using MAFFT v7.453 (Katoh and Standley 2013) and then inspected and manually corrected using BioEdit v.7.0.9 (Hall 1999). TrimAl v.1.4.rev15 (Capella-Gutiérrez et al. 2009) was

Table 1. Taxa, vouchers, and GenBank accession numbers used in the molecular analyses for ITS, LSU, TEF1, and RPB2 datasets.

Taxa	Locality	Vouchers	GenBank accession numbers			
			ITS	LSU	rp _{b2}	tef1
<i>Micropsalliotia alba</i>	India		EF069420	-	-	-
<i>M. albella</i>	Thailand	LE2016123 T	MN294514	MN294516	-	-
<i>M. albofeline</i>	China, Yunnan	HKAS 70329	OR799877	OR799922	OR962218	OR962180
<i>M. albofeline</i>	Vietnam	LE312536 T	OK257212	OK257209	-	-
<i>M. albosericia</i>	Thailand	zrl3049	HM436644	-	-	-
<i>M. allantoidea</i>	Thailand	zrl2038 T	HM436648	HM436597	-	-
<i>M. appendiculata</i>	China, Yunnan	HKAS 131128	OR799910	OR799955	OR962246	OR962203
<i>M. appendiculata</i>	China, Yunnan	HKAS 54322	OR799911	-	-	-
<i>M. appendiculata</i>	China, Yunnan	HKAS 131127	OR799912	OR799956	OR962247	OR962204
<i>M. appendiculata</i>	Vietnam	LE F-315913 T	OR161109	OR161104	-	-
<i>M. appendiculata</i> as "M. sp."	Singapore	SL1948	OR434599	-	-	-
<i>M. arginea</i>	Thailand	zrl3090	-	HM436595	-	-
<i>M. arginophaea</i>	China, Hainan	HKAS 60309	OR799878	OR799923	OR962219	OR962208
<i>M. arginophaea</i>	Thailand	zrl3110	HM436617	HM436577	-	-
<i>M. arginophaea</i>	China, Jiangxi	JXSB1685	MK402219	MK402227	-	-
<i>M. arginophaea</i>	China, Guangxi	GX20170167	MT671226	MT671244	-	-
<i>M. bifida</i>	Thailand	zrl3067 T	HM436640	HM436591	-	-
<i>M. bifida</i>	China, Fujian	HFJAU2998	OM650272	OM650252	OM669858	-
<i>M. bifida</i>	China, Guangdong	HFJAU1348	OM650271	OM650251	OM669857	-
<i>M. brunneosquamatus</i>	Thailand	LD201236 T	KP316210	-	-	-
<i>M. cortinata</i>	China, Yunnan	HKAS 92221	OR799879	OR799924	OR962220	OR962183
<i>M. cortinata</i>	Thailand	zrl2129	HM436630	HM436593	-	-
<i>M. cortinata</i>	China, Jiangxi	HFJAU0713	MN508426	OM650253	OM669874	-
<i>M. delicatula</i>	China, Yunnan	HKAS 54332	OR799880	OR799925	OR962221	OR962209
<i>M. delicatula</i>	China, Yunnan	HKAS 101130	OR799881	OR799926	OR962222	OR962210
<i>M. delicatula</i>	China, Zhejiang	ZRL2015234 T	MT671229	-	-	-
<i>M. delicatula</i>	China, Zhejiang	ZRL2015249	MT671230	MT671243	-	-
<i>M. dentatomarginata</i>	China, Guangxi	GX20170202 T	MT671228	MT671242	-	-
<i>M. digitatocystis</i>	China, Yunnan	HKAS 114297	OR799882	OR799927	OR962223	OR962184
<i>M. digitatocystis</i>	China	HKAS 123832	OR799883	OR799928	OR962224	OR962185
<i>M. digitatocystis</i>	China, Yunnan	ZRL20180564 T	MT671239	MT671250	-	-
<i>M. digitatocystis</i>	China, Jiangxi	HFJAU1871	OM650273	-	OM669855	-
<i>M. ferruginea</i>	China, Yunnan	HKAS 70562 T	OR799884	OR799929	OR962225	OR962181
<i>M. ferruginea</i>	China, Yunnan	HKAS 131130	OR799885	OR799930	OR962226	OR962182
<i>M. fimbriata</i>	China, Hainan	HKAS 60241 T	OR799886	OR799931	OR962227	OR962198
<i>M. fimbriata</i>	China, Hainan	HKAS 60261	OR799887	OR799932	-	OR962199
<i>M. furfuracea</i>	China, Yunnan	HKAS 84374	OR799888	OR799933	OR962228	OR962200
<i>M. furfuracea</i>	China, Hainan	HKAS 60229	OR799889	OR799934	OR962229	OR962201
<i>M. furfuracea</i>	Thailand	zrl3006 T	HM436621	HM436603	-	-
<i>M. furfuracea</i>	China, Fujian	HFJAU3123	OM650276	OM650254	OM669873	-
<i>M. furfuracea</i>	China, Jiangxi	HFJAU1570	OM650275	-	OM669872	-
<i>M. geesterani</i>	The Netherlands	E.C. Vellinga 2263(L)	AF482857	AF482888	-	-
<i>M. geesterani</i>	England	LAPAG520	KM923965	KM923966	-	-
<i>M. gigaspora</i>	China, Yunnan	HKAS 131118	OR799890	OR799935	OR962230	-
<i>M. gigaspora</i>	China, Yunnan	HKAS 131119 T	OR799891	OR799936	OR962231	-
<i>M. globocystis</i>	China, Yunnan	HKAS 131120	OR799892	OR799937	-	OR962186
<i>M. globocystis</i>	China, Yunnan	HKAS 84379	OR799893	OR799938	OR962232	OR962187
<i>M. globocystis</i>	China, Yunnan	HKAS 92202	OR799894	OR799939	OR962233	OR962196
<i>M. globocystis</i>	China, Zhejiang	HKAS 131133	OR799895	OR799940	OR962234	OR962197
<i>M. globocystis</i>	China	ZRL2013465	LT716024	KY418839	KY418991	KY419046
<i>M. globocystis</i>	China, Fujian	HFJAU1518	OM650277	OM650255	OM669852	-
<i>M. globocystis</i>	Thailand	zrl3004	HM436634	HM436605	-	-
<i>M. globocystis</i>	Thailand	zrl2126	HM436633	-	-	-
<i>M. globocystis</i>	Laos	HNL501777	MW073389	-	-	-
<i>M. globocystis</i>	Laos	HNL501440	MW073388	-	-	-
<i>M. globocystis</i>	China, Zhejiang	ZRL2015164	MT671236	MT671251	-	-
<i>M. globocystis</i>	China, Zhejiang	ZRL2015243	MT671237	MT671252	-	-
<i>M. globocystis</i>	China, Hunan	MHHNU31093	MK239247	-	-	-
<i>M. globocystis</i>	China	K15091213	MH045832	-	-	-
<i>M. globocystis</i>	China, Jiangxi	JXBS819	MK402215	-	-	-
<i>M. globocystis</i>	China	K16053117	MH045833	-	-	-
<i>M. globocystis</i>	China	H16091312	MH045831	-	-	-
<i>M. globocystis</i>	China	H15060610	MH045830	-	-	-
<i>M. globocystis</i>	China, Jiangxi	JXSB819-1	MK402216	MK402224	-	-
<i>M. globocystis</i>	South Africa	VDW1278	MT304640	-	-	-
<i>M. globocystis</i>	China, Zhejiang	HFJAU2709	OM650278	OM650262	OM669856	-
<i>M. globocystis</i>	Thailand	zrl2049	HM436635	-	-	-
<i>M. gracilis</i>	Thailand	zrl2041	HM436647	HM436583	-	-
<i>M. gracilis</i>	Laos	HNL503432	MW192914	-	-	-
<i>M. inflata</i>	Vietnam	LE F-315912 T	OR161106	OR161106	-	-

(Continued)

Table 1. (Continued).

Taxa	Locality	Vouchers	GenBank accession numbers			
			ITS	LSU	rpb2	tef1
<i>M. jiangxiensis</i>	China, Jiangxi	SWFC_THJ20018	ON117420	ON117438	-	-
<i>M. jiangxiensis</i>	China, Jiangxi	SWFC_THJ20019A	ON117421	ON117439	-	-
<i>M. lateritia</i> var. <i>vinaceipes</i>	China, Yunnan	HKAS 131124	OR799896	OR799941	OR962235	OR962202
<i>M. lateritia</i> var. <i>vinaceipes</i>	Thailand	zrl2073 T	HM436631	-	-	-
<i>M. lateritia</i> var. <i>vinaceipes</i>	China, Jiangxi	HFJAU1885	OM650279	-	OM669877	-
<i>M. longicystis</i>	China, Yunnan	HKAS131121 T	OR799897	OR799942	OR962257	-
<i>M. longicystis</i>	China, Yunnan	HKAS131126	OR799898	OR799943	OR962258	-
<i>M. megarubescens</i>	China	HKAS 85001	OR799899	OR799944	OR962236	OR962188
<i>M. megarubescens</i>	China, Hainan	HKAS 60253	OR799900	OR799945	OR962237	OR962189
<i>M. megarubescens</i>	Thailand	zrl2086 T	HM436620	-	-	-
<i>M. megarubescens</i>	China, Zhejiang	ZRL2015251	MT671235	MT671247	-	-
<i>M. megarubescens</i>	Thailand	zrl2008	HM436618	HM436602	-	-
<i>M. megarubescens</i>	Singapore	SL1232	OR354982	-	-	-
<i>M. megaspora</i>	Thailand	zrl3068 T	HM436624	-	-	-
<i>M. megaspora</i>	China, Jiangxi	HFJAU1255	OM650282	OM650258	OM669876	-
<i>M. megaspora</i>	China, Jiangxi	HFJAU0712	OM650280	OM650256	OM669875	-
<i>M. minor</i>	China, Zhejiang	HFJAU2812 T	OM650293	-	OM669864	-
<i>M. minor</i>	China, Zhejiang	HFJAU2796	OM650294	OM650266	OM669865	-
<i>M. nana</i>	China, Yunnan	HKAS 114619	OR799901	OR799946	OR962238	OR962216
<i>M. nana</i>	China, Yunnan	HKAS 115226 T	OR799902	OR799947	-	OR962217
<i>M. ovalispora</i>	China, Zhejiang	HFJAU2010 T	OM650295	OM650269	OM669866	-
<i>M. ovalispora</i>	China, Zhejiang	HFJAU3179	OM650296	-	OM669867	-
<i>M. pileocystidiata</i>	India	AMH9975 T	MG917970	-	-	-
<i>M. pileocystidiata</i>	India	MMH1114	MZ598496	-	-	-
<i>M. pleurocystidiata</i>	Thailand	zrl2023	HM436636	-	-	-
<i>M. pseudoarginea</i>	China, Yunnan	HKAS 131125	OR799903	OR799948	OR962239	OR962212
<i>M. pseudoarginea</i>	China, Guangdong	HKAS 60358	OR799904	OR799949	OR962240	-
<i>M. pseudoarginea</i>	Thailand	zrl3069	HM436643	-	-	-
<i>M. pseudoarginea</i>	China, Zhejiang	HFJAU2122	OM650284	OM650260	OM669861	-
<i>M. pseudoarginea</i>	China, Zhejiang	HFJAU1715	OM650283	OM650259	OM669859	-
<i>M. pseudodelicatula</i>	China, Yunnan	HKAS 131129	OR799905	OR799950	OR962241	OR962213
<i>M. pseudodelicatula</i>	China, Yunnan	HKAS 131122	OR799906	OR799951	OR962242	OR962214
<i>M. pseudodelicatula</i>	China, Yunnan	HKAS 131123	OR799907	OR799952	OR962243	OR962215
<i>M. pseudodelicatula</i>	China, Zhejiang	HFJAU2228 T	OM650288	OM650264	OM669863	-
<i>M. pseudodelicatula</i>	China, Jiangxi	HFJAU1291	MN622758	OM650263	OM669862	-
<i>M. pseudoglobocystis</i>	China, Sichuan	HKAS 87127	OR799908	OR799953	OR962244	OR962190
<i>M. pseudoglobocystis</i>	China, Yunnan	HKAS 68165	OR799909	OR799954	OR962245	OR962191
<i>M. pseudoglobocystis</i>	China, Yunnan	ZRL2013321 T	KM889913	-	-	-
<i>M. pseudoglobocystis</i>	China, Guangxi	GX20172228	MT671233	MT671245	-	-
<i>M. pseudoglobocystis</i>	China, Fujian	HFJAU2433	OM650287	-	OM669854	-
<i>M. purpureobrunneola</i>	Thailand	LE2016124 T	MN294513	MN294517	-	-
<i>M. pusillissima</i>	Thailand	zrl3047 T	HM436645	HM436594	-	-
<i>M. repanda</i>	Togo	LAPAF8	KP739805	KP739804	-	-
<i>M. roseipes</i>	China, Fujian	HFJAU2494	OM650297	OM650270	OM669870	-
<i>M. rubrobrunnescens</i>	China, Yunnan	HKAS 63051	OR799913	OR799957	OR962248	OR962205
<i>M. rubrobrunnescens</i>	China, Yunnan	HKAS 96929	OR799914	OR799958	OR962249	OR962206
<i>M. rubrobrunnescens</i>	Thailand	zrl2120 T	HM436628	HM436588	-	-
<i>M. rubrobrunnescens</i>	China, Guangxi	GX20170540	MT671231	MT671240	-	-
<i>M. rubrobrunnescens</i>	Singapore	SL1143	OR434554	-	-	-
<i>M. rubrobrunnescens</i> var. <i>tibiicystis</i>	Thailand	zrl2121 T	HM436629	HM436589	-	-
<i>M. rufosquarrosa</i>	China, Jiangxi	HFJAU1236 T	OM650292	OM650268	OM669869	-
<i>M. rufosquarrosa</i>	China, Jiangxi	HFJAU1208	OM650291	OM650267	OM669868	-
<i>M. squarrosa</i>	China, Yunnan	HKAS 128633 T	OR799915	OR799959	OR962250	-
<i>M. squarrosa</i>	China, Yunnan	HKAS 128713	OR799916	OR799960	OR962251	-
<i>M. squarrosa</i> as " <i>M. globocystis</i> "	Thailand	zrl2133	HM436632	-	-	-
<i>M. subalba</i>	China, Guangdong	HKAS 105828	OR799917	OR799961	-	OR962211
<i>M. subalba</i>	China, Guangdong	RITF4594	MW454141	-	-	-
<i>M. subalba</i>	Thailand	zrl2080	HM436646	HM436596	-	-
<i>M. subarginea</i>	Thailand	zrl2052	HM436612	HM436573	-	-
<i>M. subarginea</i>	Thailand	zrl2092	HM436611	HM436574	-	-
<i>M. suricatoides</i>	Vietnam	LE F-348070	OR161114	OR161107	-	-
<i>M. suricatoides</i>	Vietnam	LE F-348071	OR161111	OR161105	-	-
<i>M. suricatoides</i>	Vietnam	LE F-348072 T	OR161112	-	-	-
<i>M. suthepensis</i>	Thailand	zrl3035 T	-	HM436584	-	-
<i>M. tenuipes</i>	China, Fujian	HFJAU1536 T	OM650289	-	-	-
<i>M. tenuipes</i>	China, Fujian	HFJAU3180	OM650290	OM650265	-	-
<i>M. umbonata</i>	China, Yunnan	HKAS 125689	OR799918	OR799962	OR962252	OR962192
<i>M. umbonata</i>	China, Yunnan	HKAS 131134	OR799919	OR799963	OR962253	OR962193
<i>M. umbonata</i>	China, Yunnan	HKAS 131131 T	OR799920	OR799964	OR962254	OR962194
<i>M. umbonata</i>	China, Yunnan	HKAS 131132	OR799921	OR799965	OR962255	OR962195

(Continued)

Table 1. (Continued).

Taxa	Locality	Vouchers	GenBank accession numbers			
			ITS	LSU	rpb2	tef1
<i>M. ventricocystidiata</i>	Oman	SQUH-GOB002 T	OM397374	OM630414	-	-
<i>M. ventricocystidiata</i>	Oman	SQUH-ATR004	OM397373	OM630413	-	-
<i>M. wuyishensis</i>	China, Fujian	HAFJAU3048 T	OM650298	-	OM669878	-
<i>M. xanthorubescens</i>	Thailand	NW1356	MW504965	-	-	-
<i>M. xanthorubescens</i>	Thailand	zrl3083	HM436638	HM436598	-	-
<i>Leucoagaricus badius</i>	Pakistan	SH148	DQ911600	DQ911601	DQ911602	GU187722
<i>L. centricastaneus</i>	China, Liaoning	SYAU FUNGI 076	OM976855	OM976871	OR962256	OR962207

Sequences derived in this study are in bold. Vouchers for type materials are designated by the letter "T".

used to remove sites that were vaguely aligned. The resulting alignments were examined and optimised manually in AliView 1.27 (Larsson 2014). Phylogenetic analysis was then performed based on the concatenated ITS-LSU-rpb2-tef1 dataset using PhyloSuite v1.2.2 (Zhang et al. 2020). Maximum likelihood (ML) analyses were performed in RAxML 8.2.12 (Stamatakis 2006) with the GTRGAMMA model as the best-fit likelihood model with 1,000 replicates (Silvestro and Michalak 2012). The BI phylogenies were tested in MrBayes v. 3.2.6 (Ronquist et al. 2012) and the best-fit model (GTR+F+I+G4) was selected using ModelFinder (Kalyaanamoorthy et al. 2017). 10,000,000 generations were run for four chains and sampled every 1,000 generations. The first 25% of generated trees were discarded as the burn-in, and the Bayesian posterior probabilities (BPPs) were calculated from the posterior distribution of the remaining phylogenetic trees. For phylogenetic tree visualisation, FigTree 1.4.4 (Rambaut 2018) was used and the tree was annotated using Adobe Illustrator CC2018.

3 Results

3.1. Phylogenetic results

The combined ITS-LSU-rpb2-tef1 dataset comprised 147 sequences, representing 41 described species, two varieties, and seven undescribed species of *Micropsalliota*, with two sequences from *Leucoagaricus* as outgroups. A total of 166 new sequences were generated in this study, including 45 ITS, 44 LSU, 41 rpb2, and 38 tef1 sequences (Table 1). The final dataset included 2,649 characters with 616 bp from ITS, 857 bp from LSU, 625 bp from rpb2, and 551 bp from tef1.

The results from RAxML and Bayesian analyses generated almost similar topologies, clades with a Bayesian posterior probability (BI-PP) ≥ 0.95 and

ML bootstrap support (ML-BP) $\geq 75\%$ were considered to be well-supported (Yan et al. 2022). Based on the phylogenetic analyses of the combined dataset, all taxa of *Micropsalliota* form a monophyletic clade (BI-PP = 1; MLBP = 100%).

As shown in the phylogenetic tree in Figure 1, all taxa of *Micropsalliota* formed a well-supported monophyletic clade (BI-PP = 1; MLBP = 100%). Based on the phylogenetic tree and previous studies (Zhao et al. 2010; Wei et al. 2015; Li et al. 2021; Al-Kharousi et al. 2022; Patil et al. 2022; Yan et al. 2022), 11 major Clades within the genus were identified: Clade albofelina, Clade bifida, Clade cortinata, Clade ferruginea, furfuracea, Clade globocystis, Clade jiangxiensis, Clade lateritia, Clade megaspora, Clade pleurocystidiata, and Clade ventricocystidiata. These major clades are described further below.

Clade globocystis was strongly supported (BI-PP = 1; MLBP = 100%) and included five known species (*Micropsalliota digitatocystis* R.L. Zhao, J.X. Li & M.Q. He, *Micropsalliota globocystis* Heinem., *Micropsalliota megarubescens* R.L. Zhao, Desjardin, Soytong & K.D. Hyde, *M. pseudoglobocystis*, *Micropsalliota purpureobrunneola* M.Q. He & R.L. Zhao) and three new species (*M. gigaspora*, *M. squarrosa*, and *M. umbonata*). The sequences in GenBank labelled as *M. globocystis* from China, South Africa, and Thailand formed five distinct lineages (Figure 1). One of the lineages, represented by "*Micropsalliota globocystis* voucher SFSU zrl 2133" in GenBank (HM436632), and referred to as "globocystis 5" in Yan et al. (2022), is clustered with *M. squarrosa*, a new species described in the present study, with strong support (BI-PP = 1; MLBP = 97%).

Clade lateritia (BI-PP = 0.97; MLBP < 75%) contained six species (varieties): *Micropsalliota inflata* D.D. Ivanova & O.V. Morozova, *Micropsalliota lateritia* var. *vinaceipes* R.L. Zhao, Desjardin, Soytong &

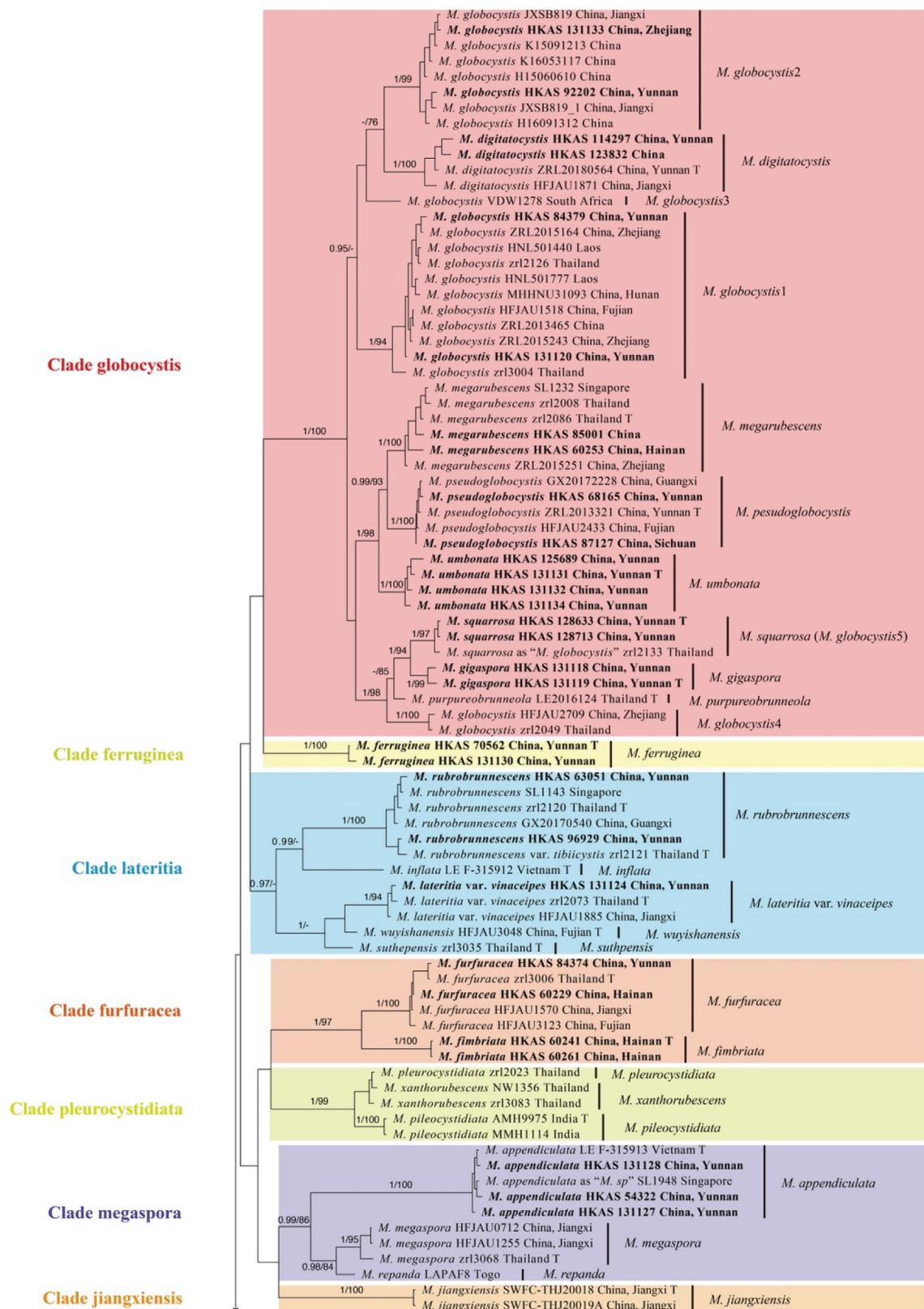


Figure 1. Phylogram of *Micropsalliota* generated by Bayesian inference (BI) analysis based on sequences of a concatenated data set from four nuclear genes (ITS, LSU, *rpb2*, and *tef1*). *Leucoagaricus centricastaneus* and *L. badius* are selected as outgroups. Posterior probabilities (BI-PP) ≥ 0.95 and ML bootstrap (ML-BP) $\geq 75\%$ are shown as PP/BP. The scale bar represents the substitutions per nucleotide site.

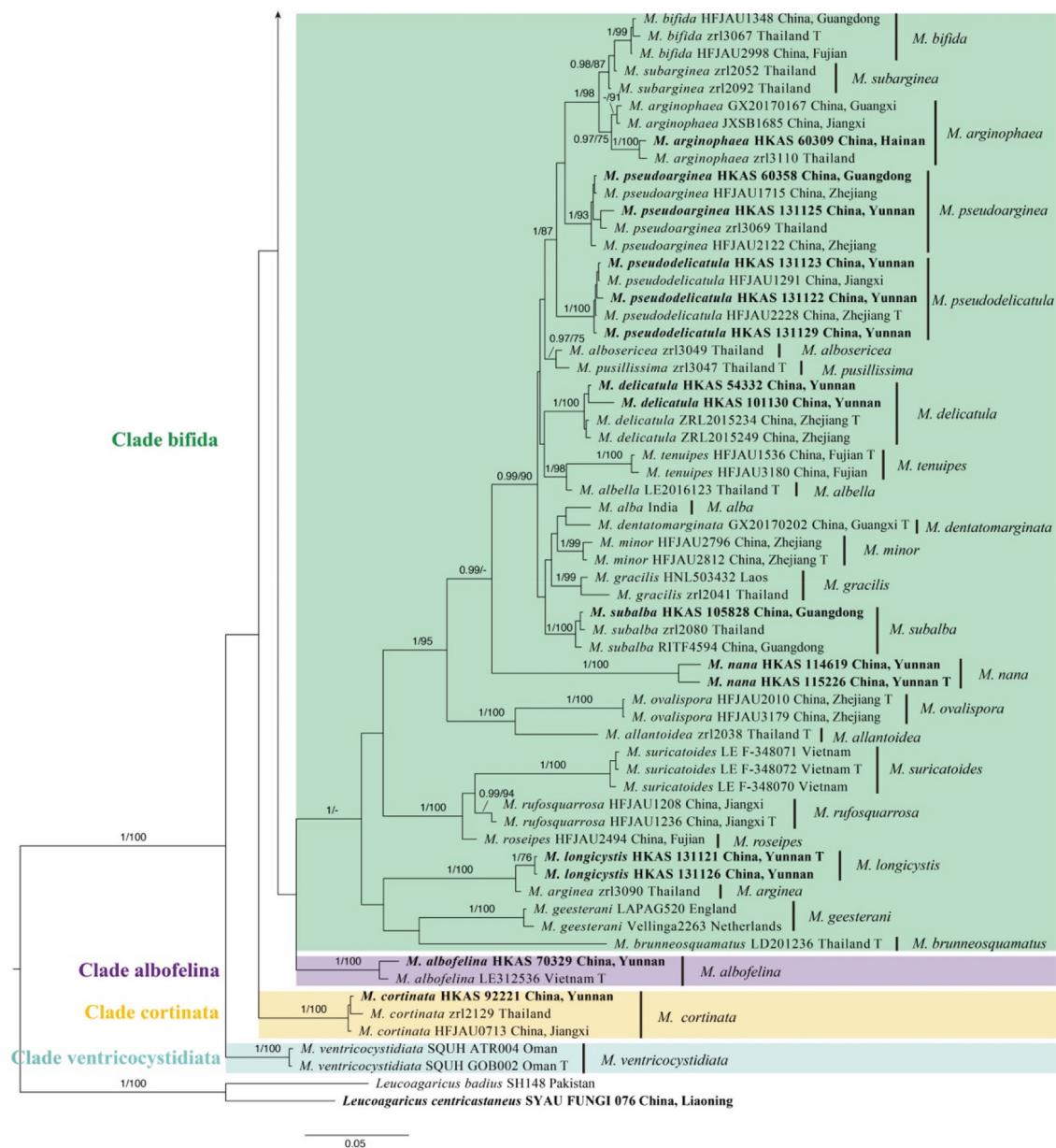


Figure 1. (Continued).

K.D. Hyde, *Micropsalliota rubrobrunnescens* R.L. Zhao, Desjardin, Soytong & K.D. Hyde, *Micropsalliota rubrobrunnescens* var. *tibiicystis* R.L. Zhao, Desjardin, Soytong & K.D. Hyde, *Micropsalliota suthepensis* R.L. Zhao, Desjardin, Soytong & K.D. Hyde, and *Micropsalliota wuyishanensis* J.Q. Yan.

Clade furfuracea (BI-PP = 1; MLBP = 97%) contained two species, *M. furfuracea* and the new species *Micropsalliota fimbriata* described in the present study.

Clade pleurocystidiata (BI-PP = 1; MLBP = 99%) consisted of *Micropsalliota pileocystidiata* P.B. Patil &

S.A. Vaidya, *Micropsalliota pleurocystidiata* Heinem. & Little Flower, and *Micropsalliota xanthorubescens* Heinem.

Clade megaspora was strongly supported (BI-PP = 0.99; ML-BP = 86%) and consisted of a newly recorded taxon of China (*Micropsalliota appendiculata* D.D. Ivanova & O.V. Morozova) and two known species: *Micropsalliota megaspora* R.L. Zhao, Desjardin, Soytong & K.D. Hyde and *Micropsalliota repanda* Heinem.

Clade bifida (BI-PP = 1; MLBP < 75%) consisted of 24 species. Among these, *Micropsalliota nana* and *M. longicystis* were new taxa.

Clade albofelia, Clade cortinata, Clade ferruginea, Clade jiangxiensis, and Clade ventricocystidiata consisted of a single species respectively.

3.2. Taxonomy

Micropsalliota appendiculata D.D. Ivanova & O.V. Morozova. Phytotaxa. 626(4):247–258. Figures 2a–c, 3

Macroscopic description: Pileus 3–11 mm in diam., convex or hemispherical in early stage, expanding to plano-convex with age, sometimes with apparent umbo, yellowish white (1A2); surface dry, densely covered with squamules, light yellow (5A4) or yellowish brown (5D8) when young, dark brown (6E6) when mature, margin with light yellow (5A4) or yellowish brown (5E6) appendiculate. Context thickened at the disc and thin towards the margin, white (1A1). Lamellae free, close, with 3–5 series of lamellulae, 1–1.5 mm broad, cream (5A2) to brown (6E6). Stipe 13–27 × 0.5–1 mm, cylindrical, straight, surface with tiny fibrils, cream (5A2) when young, with a light brown (5C4) tone with age. Annulus membranous, single, superior, up to 1–2 mm broad, cream (5A2) to dark brown (5F4), fragile, and disappears in age. No colour changes were observed when bruised or cut.

Microscopic description: Basidiospores [40/2/2] (5) 5.5–7 × 3.5–4 µm, av. = 6.15 × 3.85 µm, Q = (1.43) 1.50–1.75, $Q_m = 1.60 \pm 0.11$, amygdaliform to ellipsoid, with apical thickening, without germ pore, light brown, inamyloid. Basidia (13) 14–16 × 6–7 µm, clavate, hyaline, 4-spored, sometimes 2-spored. Pleurocystidia 35–52 (61) × 9–16 µm, broadly clavate to clavate-capitate, hyaline, smooth. Cheilocystidia 16–25 × 10–13 (14) µm, pyriform to subglobose, hyaline, smooth. Pileus squamules composed of hyphae 6–15 µm in diam., hyaline, smooth, cylindrical, slightly constricted at septa, with light brown membranous pigments.

Distribution: Vietnam and southwestern China (Yunnan).

Habit and habitat: Gregarious on soil in broad-leaved forest.

Known distribution: Vietnam and the tropical region of Yunnan Province, China.

Specimens examined: China, Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Jinghong City, Dadugang Township, 100.918056°E, 22.611111°N, alt. 1,370 m, 29 June 2008, Z.W. Ge 2112

(KUN-HKAS 54322); ibid. Mengla County, Menglun Township, Xishuangbanna Tropical Botanical Garden, Greenstone Forest Park, on soil under broad-leaved forest, 101.281291°E, 21.9102435°N, alt. 590 m, 8 July 2021, H. Qu 422 (KUN-HKAS 131127); ibid., 101.28188°E, 21.9120206°N, alt. 520 m, 8 July 2021, H. Qu 429 (KUN-HKAS 131128).

Notes: *Micropsalliota appendiculata*, which was originally described from Vietnam, is characterised by yellowish brown, squamulose pileus with apparent umbo, and pyriform to subglobose cheilocystidia. The morphology of three Chinese materials overall matches the description of the type specimen of *M. appendiculata* (Ivanova et al. 2023). The similarity of ITS sequences between Chinese collections and type specimens is higher than 99%. However, all the specimens collected from China possess broadly clavate to clavate-capitate pleurocystidia, which is described as absent in the protologue. Despite the differences, considering the similarity of other morphologies and ITS sequences, we identified the three specimens of Yunnan, China as *M. appendiculata*.

Considering the overall appearance, *Micropsalliota appendiculata* is similar to *Micropsalliota albosericea* Heinem. & Leelav., *M. allantoidea*, *Micropsalliota albella* M.Q. He & R.L. Zhao, and *Micropsalliota delicatula* R.L. Zhao, J.X. Li & M.Q. He. However, *M. albosericea* differs in forming pure white pileus and smaller basidiospores (4.5–6 × 3–4 µm) (Heinemann and Leelavathy 1991); *M. allantoidea* differs in forming sausage-shaped pileipellis elements (Zhao et al. 2010); *M. albella* differs in forming smaller basidiomes (pilei 2–5 mm in diam., stipe 5–13 × 0.3–0.6 mm) with glabrous pileus (He et al. 2020). *M. delicatula* R.L. Zhao, J.X. Li & M.Q. He differs in forming pure white squamules, and capitate cheilocystidia 26–36 µm long with capitulum 3–5 µm in diam. (Li et al. 2021).

In the phylogenetic tree (Figure 1), *Micropsalliota appendiculata* groups together with *M. megaspora* and *M. repanda*. However, *M. megaspora* differs in forming brown (7E6) to dark brown (8E4) pileus, bigger spores (6–8 × 3.8–4.5 µm) and the smaller basidia (11–15 × 6–7.5 µm) (Zhao et al. 2010); *M. repanda* differs in forming larger basidiomes (pilei 15–45 mm in diam., stipe 25–40 × 2–5 mm), purplish-red squamules and narrower cheilocystidia (broad 7–10 µm) (Heinemann 1980).

Micropsalliota ferruginea T. Gao & Z.W. Ge, sp. nov.
Figures 2d–e, 4



Figure 2. Basidiomata of *Micropsalliota* species. (a – c) *M. appendiculata*; (a) KUN-HKAS 54322; (b, c) KUN-HKAS 131127. (d, e) *M. ferruginea*; (d) KUN-HKAS 70562 (Holotype); (e) KUN-HKAS 131130. (f) *M. fimbriata*; KUN-HKAS 60241 (holotype). (g – i) *M. gigaspora*; (g, h) KUN-HKAS 131119 (Holotype); (i) KUN-HKAS 131118. (j, k) *M. longicystis*; KUN-HKAS 131126. (l, m) *M. nana*; (l) KUN-HKAS 114619; (m) KUN-HKAS 115226 (holotype). (n, o) *M. squarrosa*; (n) KUN-HKAS 128633 (Holotype); (o) KUN-HKAS 128713. (p, q) *M. umbonata*; (p) KUN-HKAS 125689; (q) KUN-HKAS 131134. Bars = 10 mm.

Fungal names: FN571731.

Etymology: Referring to its reddish-brown pileus.

Types: China, Yunnan Province, Honghe Hani and Yi Autonomous Prefecture, Gejiu City, on the trail to Shazhudi from Manhao in broad-leaved forest,

103.434444°E, 23.025556°N, alt. 860 m,

22 September 2011, Z.W. Ge 3058 (KUN-HKAS 70562, holotype). GenBank: ITS = OR799884, LSU = OR799929, rpb2 = OR962225, tef1 = OR962181.

Diagnosis: *Micropsalliota ferruginea* is distinguished from closely related species by the relatively large basidiomes with more or less recurved squamules that are

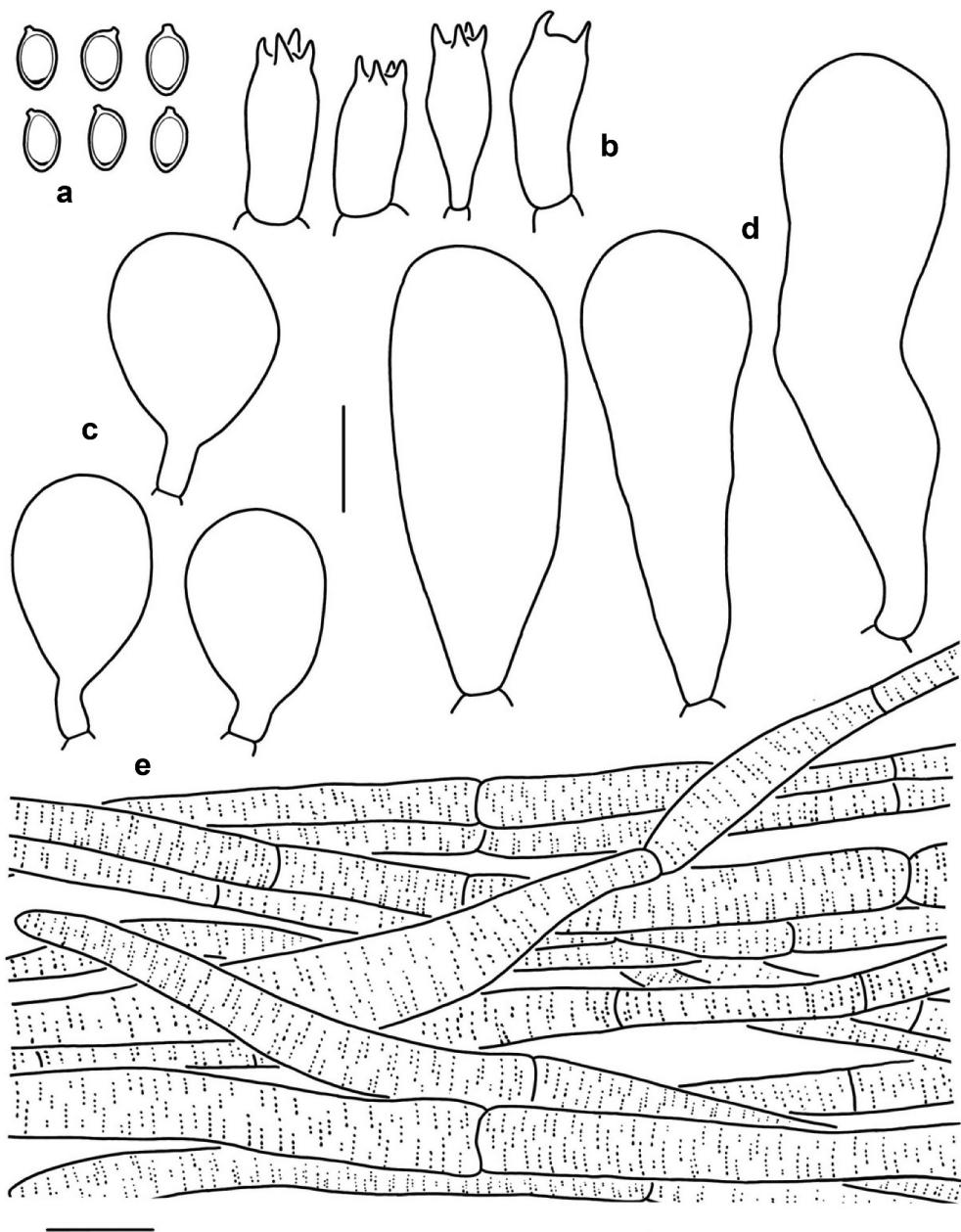


Figure 3. Microscopic features of *Micropsalliota appendiculata* (KUN-HKAS 54322). (a) Basidiospores. (b) Basidia. (c) Cheilocystidia. (d) Pleurocystidia. (e) Pileus squamules. Bars: a – d = 10 µm; e = 20 µm.

brown to dark brown, and has larger recurved squamules on the margin, lamellae staining slightly blue when bruised or cut.

Macroscopic description: Pileus 35–50 mm in diam., convex in early stage, plano-convex to applanate with age; squamules small, pointed, up to 1 mm high, more or less recurved, dense on the disc and scattered near the margin, reddish brown (7D7), brown (5E8) to dark brown (8F8) on the disc, turning white (1A1) to cream (4A3) towards the margin; larger squamules on margin, recurved, concolorous with the disc. Context

firm, up to 1 mm thick, cream (4A2). Lamellae free, crowded, with 3 series of lamellulae, 3–4 mm broad, light yellow (3A3) to greyish brown (3C2). Lamellae staining blue (23A4) when bruised or cut. Stipe 40–60 × 2–4 mm, cylindrical, hollow, with fibrillose to tiny reddish brown squamules, white or with reddish brown tone. Annulus pendent, single, superior, edge entire, persistent, membranous, white (1A1) in early stages, light brown (5B3) when mature.

Microscopic description: Basidiospores [20/1/1] (6) 6.5–7.5 × 3.5–4 µm, av. = 6.95 × 3.93 µm, Q = (1.50)

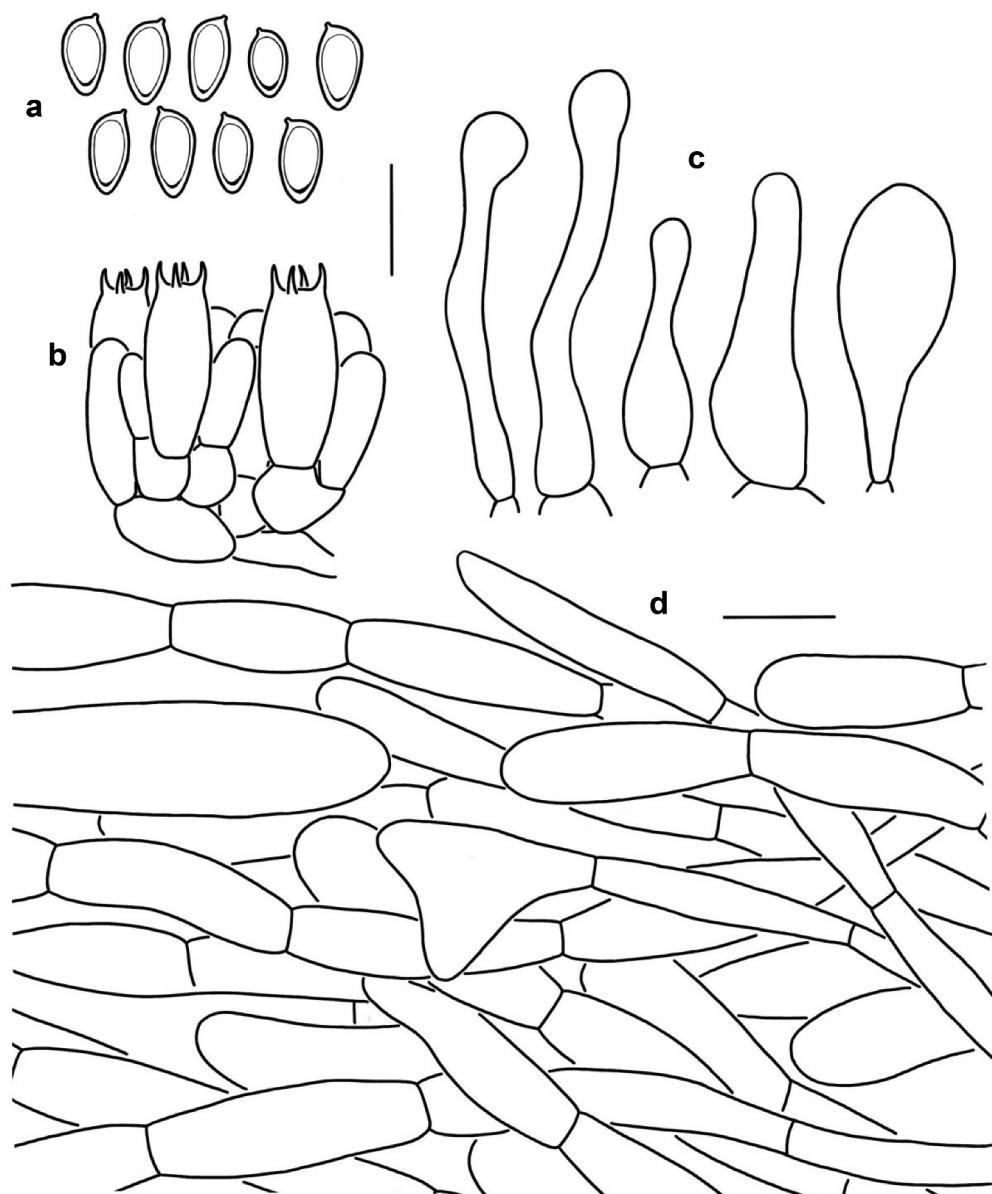


Figure 4. Microscopic features of *Micropsalliota ferruginea* (holotype, KUN-HKAS 70562). (a) Basidiospores. (b) Basidia. (c) Cheilocystidia. (d) Pileus squamules. Bars: a – c = 10 µm; d = 20 µm.

1.63–2.00 (2.14), $Q_m = 1.78 \pm 0.14$, amygdaliform to cym-biform, with apical thickening, without germ pore, light brown, inamyloid. Basidia 14.5–15.5 × 6–7 µm, clavate, hyaline, 4-spored. Pleurocystidia absent. Cheilocystidia 15–33 × 3–10 µm, tibiiform, cylindrical or slightly swollen near base and middle, with a narrower neck and apical capitulum (3) 4–6 µm in diam., hyaline, smooth. Pileus squamules composed of hyphae 11–20 µm in diam., hyaline, yellowish brown, smooth, cylindrical, constricted at the septa on some hyphae.

Distribution: Southwestern China (Yunnan).

Habit and habitat: Solitary or scattered on soils in broad-leaved forest.

Known distribution: Tropical region of Yunnan Province, China.

Additional specimens examined: China, Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Mengla County, Menglun Township, Xishuangbanna Tropical Botanical Garden, Greenstone Forest Park, on soil under evergreen broad-leaved forest, 101.28117°E, 21.910726°N, alt. 650 m, 25 June 2020, G.S. Wang 1017 (KUN-HKAS 131130).

Notes: *Micropsalliota ferruginea* is characterised by its relatively large basidiomes with more or less recurved, brown to dark brown pileus squamules, and lamellae staining a slightly blue when bruised or cut.

Micropsalliota ferruginea differs from *Micropsalliota albonuda* (Beeli) Heinem. in that the latter forms a blue-white and glabrous pileus, and smaller basidiospores ($5.1\text{--}5.8 \times 3.1\text{--}3.8 \mu\text{m}$) (Heinemann 1956). *Micropsalliota brunneosquamata* Linda J. Chen, R.L. Zhao & K.D. Hyde is similar to *M. ferruginea* by having reddish brown squamules. However, *M. brunneosquamata* differs in forming bigger squamules, the stipe below the annulus heavily covered by brown fibrils, and having smaller basidiospores measuring $5\text{--}6 \times 3\text{--}4 \mu\text{m}$ (Chen et al. 2016). *Micropsalliota furfuracea* R.L. Zhao, Desjardin, Soytong & K.D. Hyde, and *M. globocystis* have similar-sized pileus to that of *M. ferruginea*. However, *M. furfuracea* and *M. globocystis* stain strong reddish brown when bruised (Zhao et al. 2010). In addition, *M. ferruginea* forms a well-supported monophyletic clade (BI-PP = 1; MLBP = 100%) in the four-locus phylogeny (Figure 1).

***Micropsalliota fimbriata* T. Gao & Z.W. Ge, sp. nov.**
Figures 2f, 5

Fungal Names: FN571732.

Etymology: Referring to fimbriated fibrils of its pileus.

Types: China, Hainan Province, Wuzhishan National Nature Reserve, in broad-leaved forest, 109.579°E , 18.865°N , alt. 650 m, 31 July 2010, Z.W. Ge 2565 (KUN-HKAS 60241, holotype). GenBank: ITS = OR799886, LSU = OR799931, rpb2 = OR962227, tef1 = OR962198.

Diagnosis: *Micropsalliota fimbriata* is characterised by its reddish brown or greyish brown pileus with villous fibrils and appendiculate margin; whitish stipe with fibrillose surface, and clavate to capitate or subcapitate cheilocystidia.

Macroscopic description: Pileus 5–20 mm in diam., convex in early stage, plano-convex to applanate with age, surface dry, white (1A1) to whitish (1B1), covered with reddish brown (7D5) or greyish brown (6D3) villous fibrils, dense on the disc, margin appendiculate, fimbriated. Context less than 0.5 mm thick, white (1A1). Lamellae free, moderately distant, with 3–4 series of lamellulae, 1–2 mm broad, white (1A1). Stipe 20–35 × 1–2 mm, cylindrical, hollow, surface fibrillose, whitish (5A2). Annulus pendent, single, superior, persistent, edge entire, membranous, white (1A1). No colour change was observed when bruised or cut.

Microscopic description: Basidiospores [40/2/2] $6.5\text{--}7.5 \times (3) \quad 3.5\text{--}4 \mu\text{m}$, av. $= 6.88 \times 3.78 \mu\text{m}$, $Q = 1.63\text{--}2.00$ (2.17), $Q_m = 1.83 \pm 0.15$, amygdaliform, with apical thickening, without germ pore, light brown, inamyloid. Basidia (12) $13\text{--}17 \times 6\text{--}9 \mu\text{m}$, clavate, hyaline, 4-spored. Pleurocystidia absent. Cheilocystidia $25\text{--}44 \times 5\text{--}9 \mu\text{m}$, clavate to irregularly tibiiform, capitate or subcapitate with long narrow neck, capitulum $7\text{--}8.5$ (9) μm in diam., hyaline, smooth. Pileus squamules composed of hyphae $5\text{--}10 \mu\text{m}$ in diam., cylindrical, slightly constricted at septa, with reddish brown, distinctly incrusting, and membranous pigments (Figure 4d).

Distribution: Tropical regions of Southern China (Hainan).

Habit and habitat: Solitary on soil in broad-leaved forest.

Known distribution: Hainan Province, China.

Additional specimens examined: China, Hainan Province, Hainan Island, Wuzhishan National Nature Reserve, in broad-leaved forest, 109.579°E , 18.865389°N , alt. 650 m, 1 August 2010, Z.W. Ge 2585 (KUN-HKAS 60261).

Notes: *Micropsalliota fimbriata* is characterised by its pileus covered with reddish brown or greyish brown villous fibrils, appendiculate pileus margin, and clavate to capitate or subcapitate cheilocystidia.

Micropsalliota fimbriata is similar to *M. megaspora*. However, the latter forms a brown pileus, finely squamulose stipe, and ventricose-rostrate to pyriform cheilocystidia (Zhao et al. 2010). *Micropsalliota malabarensis* Heinem. & Little Flower and *Micropsalliota subalpina* Guzm.-Dáv. & Heinem. differ in forming different spores: the former forms cymbiform spores, measuring $5\text{--}6 \times 3\text{--}4 \mu\text{m}$ (Heinemann and Flower 1983), and the spores of the latter are ellipsoid to amygdaliform ($5.1\text{--}6.4 \times 3.2\text{--}3.7 \mu\text{m}$) (Guzmán-Dávalos and Heinemann 1994), in contrast to the amygdaliform spores with larger measurements ($6.5\text{--}7.5 \times 3.5\text{--}4 \mu\text{m}$) formed by *M. fimbriata*. *Micropsalliota cortinata* (Heinem.) Heinem. differs in forming cortinate partial veil that leaves remnants only on the pileus margin, cheilocystidia clavate to ventricose with a large base (Heinemann 1980).

Micropsalliota fimbriata, forming an independent clade (BI-PP = 1; MLBP = 100%) in Clade furfuracea, can be confused with *M. furfuracea* in overall appearance. However, *M. furfuracea* differs in forming

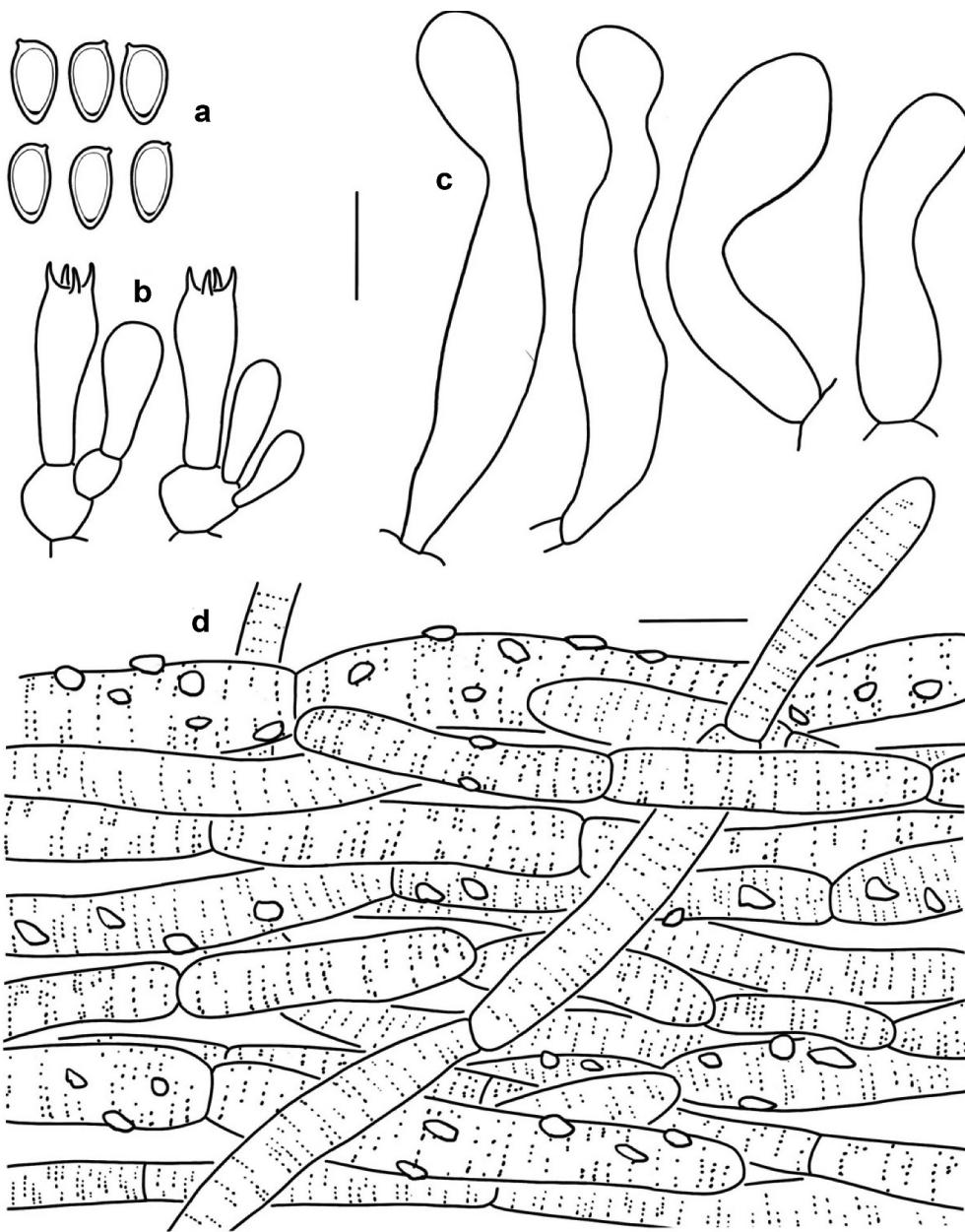


Figure 5. Microscopic features of *Micropsalliota fimbriata* (KUN-HKAS 60261). (a) Basidiospores. (b) Basidia. (c) Cheilocystidia. (d) Pileus squamules. Bars: a – c = 10 µm; d = 20 µm.

relatively bigger basidiomes, flake-like squamules, and flesh staining red when bruised or cut (Zhao et al. 2010).

Micropsalliota gigaspora T. Gao & Z.W. Ge, sp. nov.
Figures 2g–i, 6

Fungal Names: FN571733.

Etymology: Referring to the large basidiospores up to 9 µm long.

Types: China, Yunnan Province, Dehong Dai and Jingpo Autonomous Prefecture, Yingjiang County, Mangyun Town, Hongbeng River, on soil under evergreen broad-leaved forest, 97.601667°E, 24.449444°N, alt. 700 m, 19 July 2022, X.P. Fan 291 (KUN-HKAS 131119, holotype). GenBank: ITS = OR799891, LSU = OR799936, rpb2 = OR962231.

Diagnosis: *Micropsalliota gigaspora* is distinguished by small basidiomes (pilei 20–27 mm in diam., stipe

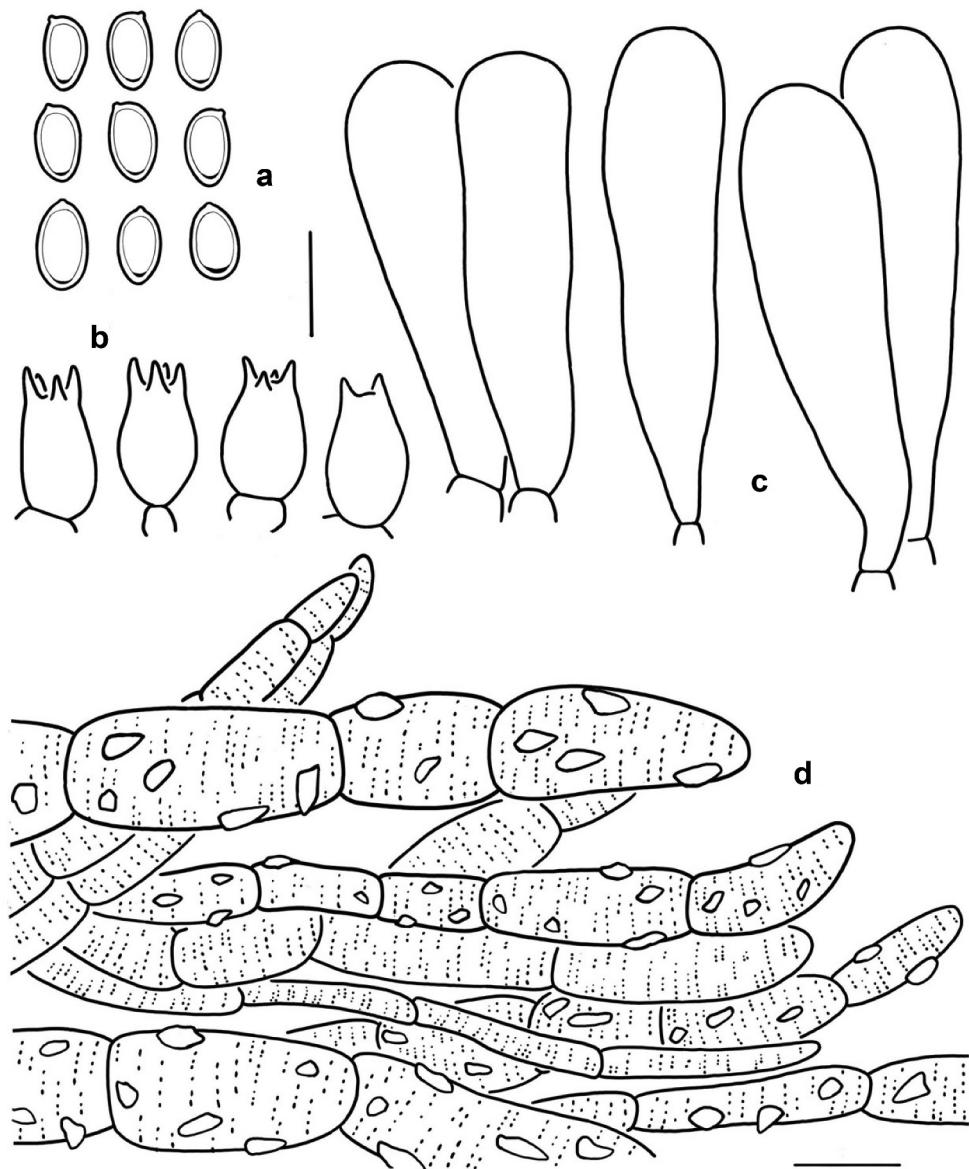


Figure 6. Microscopic features of *Micropsalliota gigaspora* (Holotype, KUN-HKAS 131119). (a) Basidiospores. (b) Basidia. (c) Cheilocystidia. (d) Pileus squamules. Bars: a – c = 10 µm; d = 20 µm.

35–50 × 2–3 mm), narrow and thick annulus, clavate cheilocystidia and large basidiospores (7–9 × 4–5.5 µm).

Macroscopic description: Pileus 20–27 mm in diam., conical, convex in early stage, applanate or subumbonate with age, margin crenate, surface dry, covered with fibrillose scales, slightly recurved, dense on the disc and scattered near the margin, reddish brown (7E7), background white (1A1) or light grey (1B1), turning light brown with age. Context firm, up to 1–2 mm thick at disc. Lamellae free, crowded, with 2–4 series of lamellulae, 1–2 mm broad, light yellow (6A3) to brown (6C5). Stipe 35–50 × 2–3 mm, cylindrical, hollow; light yellow (6A3) to brown (6C5), covered with white (1A1)

fibrils. Annulus persistent, superior, membranous, thick, white (1A1), edge entire, with light brown tone, 1–2 mm wide. No colour changes were observed when bruised or cut.

Microscopic description: Basidiospores [20/1/1] 7–9 × 4–5.5 µm, av. = 7.98 × 4.45 µm, Q = (1.40) 1.56–2.00, Q_m = 1.80 ± 0.16, ellipsoid, with apical thickening, without germ pore, light brown, inamyloid. Basidia 11–15 (20) × 7–8 (12) µm, short-clavate, hyaline, 4-spored, sometimes 2-spored. Pleurocystidia absent. Cheilocystidia 37–50 × 7–14 µm, broadly clavate to clavate, hyaline, smooth. Pileus squamules composed of hyphae 6–19 µm in diam., hyaline,

smooth, cylindrical, slightly constricted at septa, with reddish brown or light brown incrusting and membranous pigments.

Distribution: Southwestern China (Yunnan).

Habit and habitat: Solitary or scattered on soils.

Known distribution: West of Yunnan province, China.

Additional specimens examined: China, Yunnan Province, Dehong Dai and Jingpo Autonomous Prefecture, Yingjiang County, Mangyun Town, Hongbeng River, on soil under evergreen broad-leaved forest, 97.601667°E, 24.449444°N, alt. 700 m, 18 July 2022, X.P. Fan 258 (KUN-HKAS 131118).

Notes: *Micropsalliota gigaspora* is characterised by small basidiomes, a pileus covered with slightly recurved scales or fibrils, clavate cheilocystidia, and large basidiospores.

Micropsalliota brunneola Heinem. is morphologically similar to *M. gigaspora* in having similar-sized pileus and similar colour (Heinemann 1980). However, *M. brunneola* differs in forming shorter stipe (long 25 × 3.5 mm), and much smaller basidiospores (4.1–4.9 × 2.9–3.3 µm). *Micropsalliota digitatocystis* also have similar appearance but differ in forming larger basidiomes (pilei 16–72 mm in diam., stipe 60–90 × 5–8 mm), smaller spores (5.8–7.4 × 4–4.6 µm), and needle-like pleurocystidia (Li et al. 2021); *M. gigaspora* is also similar to several other species that have big basidiospores: *M. megarubescens*, however, has larger basidiomes (pilei 25–80 mm in diam.), white to cream and become light grey to greyish brown in age (Zhao et al. 2010). *M. megaspora* has smaller basidiomes (pilei 5–12 mm in diam.), and a paler fibrillose at disc (Zhao et al. 2010). *Micropsalliota ventricocystidiata* Al-Sadi & S. Hussain has a pale pileus (white to pale reddish-brown) and larger basidiomes (pilei 30–50 mm in diam., stipe 40–70 × 7–10 mm) (Al-Kharousi et al. 2022).

Micropsalliota gigaspora is sister to *M. purpureobrunneola* and *M. squarrosa* (this paper) in the molecular analyses (BI-PP < 0.95; MLBP = 85%). *M. purpureobrunneola* differs in forming smaller basidiomes (pilei 5–12 mm in diam.) and larger basidia (17.2–26 × 5.7–7.4 µm) (He et al. 2020); *M. squarrosa* differs in forming subcapitate cheilocystidia, which is clavate in *M. gigaspora*. Both *M. gigaspora* and *M. squarrosa* have large basidiospores. However, the basidiospores are longer in *M. gigaspora* (av. = 7.98 × 4.45 µm) but

wider in *M. squarrosa* (av. = 7.75 × 4.90 µm); *M. squarrosa* staining slightly yellow (4A4) or reddish brown (7C5) when bruised but *M. gigaspora* with no colour changes observed when bruised or cut.

***Micropsalliota longicystis* T. Gao & Z.W. Ge, sp. nov.**

Figures 2j–k, 7

Fungal names: FN571735.

Etymology: Referring to its long caulocystidia up to 78 µm in length.

Types: China, Yunnan Province, Kunming City, Kunming Botanical Garden, on soil under moss, 102.74099494°E, 25.14476019°N, alt. 1,970 m, 12 June 2023, T. Gao 206 (KUN-HKAS 131121, holotype). GenBank: ITS = OR799897, LSU = OR799942, rpb2 = OR962257.

Diagnosis: *Micropsalliota longicystis* is distinguished by the white glabrous pileus, stipe with white rhizomorphs at the base, staining yellow then reddish-brown when bruised, and a dark brown or olive-green reaction with KOH, the presence of pleurocystidia and caulocystidia, and caulocystidia with a very long and narrow neck.

Macroscopic description: Pileus 5–20 mm in diam., convex, expanding to broadly convex with age, surface dry, surface silky-fibrillose, white (1A1) overall in early stage, sometimes becoming cream (3A2) to pale grey (1C3) with age. Context firm, less than 0.5 mm thick. Lamellae free, close, with 3 series of lamellulae, 2–3 mm broad, light yellow, becoming light brown (7D5–7D6) when mature, edges paler. Stipe 15–30 × 1–2 mm, cylindrical, white (1A1) to brown (2E5), surface smooth or with slightly white (1A1) fibrillose, with white rhizomorphs at the base. Annulus single, superior, persistent, edge entire, white. Pileus and stipe staining yellow then reddish brown when bruised or cut. KOH reaction dark brown or olive-green.

Microscopic description: Basidiospores [40/4/2] 5–6 × 3–3.5 µm, av. = 5.7 × 3.0 µm, Q = 1.7–2.0, Q_m = 1.89 ± 0.16, ellipsoid, with apical thickening, without germ pore, light brown, inamyloid. Basidia (14) 15–17 (19) × 5–6.5 (8) µm, clavate, hyaline, 4-spored. Cheilocystidia and pleurocystidia common, similarly shaped, (25) 34–43 × 5–8 µm, clavate to clavate-capitate, sometimes subcapitate with long narrow neck, capitulum 4–5 µm in diam., hyaline, covered by light brown deposition. Caulocystidia 45–78 × 5–7 µm, tibiiform, capitate or subcapitate

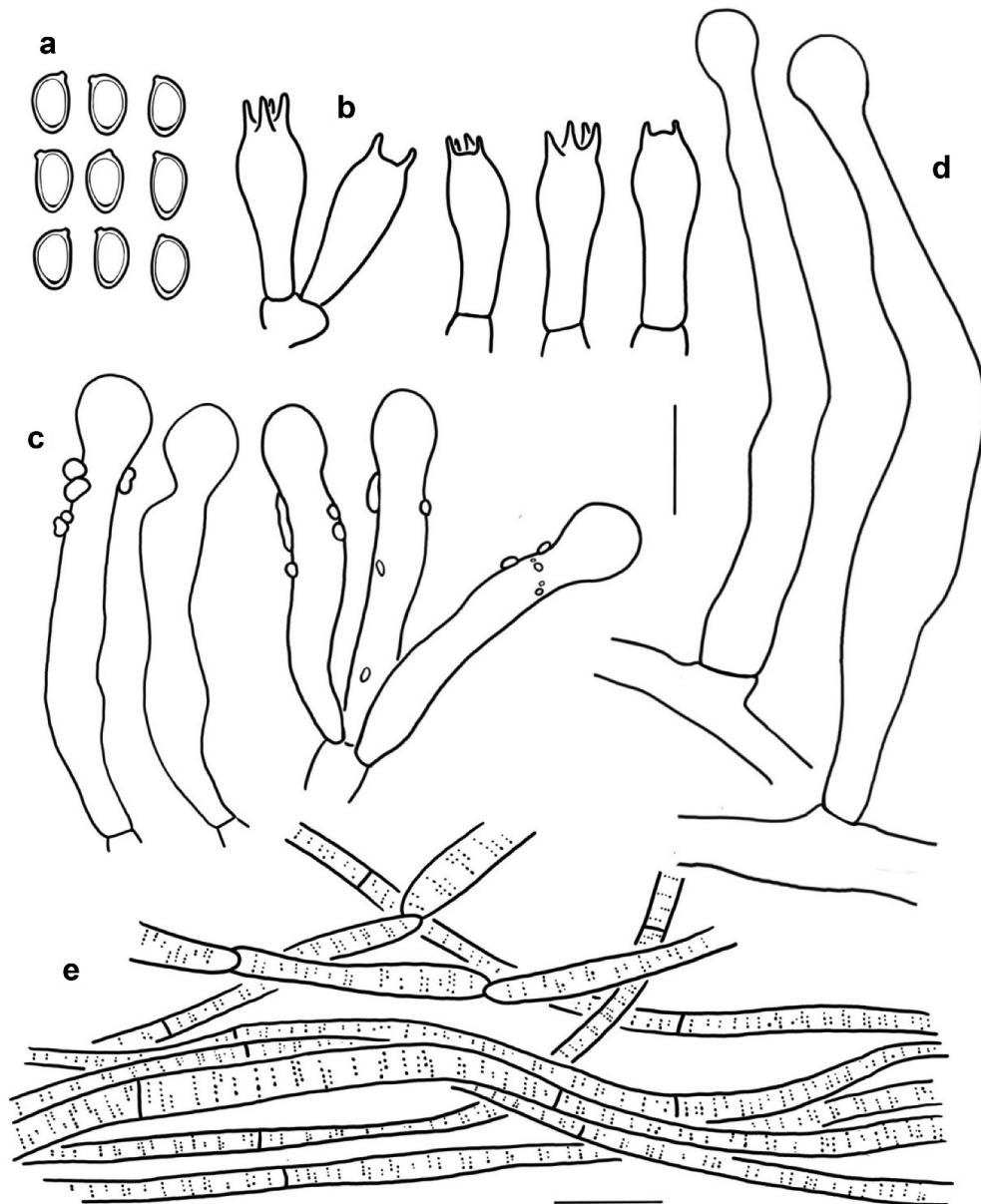


Figure 7. Microscopic features of *Micropsalliota longicystis* (holotype, KUN-HKAS 131121). (a) Basidiospores. (b) Basidia. (c) Cheilocystidia/pleurocystidia. (d) Caulocystidia. (e) Pileus squamules. Bars: a – d = 10 µm; e = 20 µm.

with long narrow neck, capitulum (3) 4–6 µm in diam., hyaline, smooth. Pileus squamules composed of hyphae 3–10 µm in diam., hyaline, smooth, cylindrical, slightly constricted at septa, with brown membranous pigments.

Distribution: Southwestern China (Yunnan).

Habit and habitat: Solitary or scattered on soils.

Known distribution: Central region of Yunnan province, China.

Additional specimens examined: China, Yunnan Province, Kunming City, Kunming Botanical Garden, on soil under moss, 102.74099494°E, 25.14476019°N, alt. 1,970 m, 17 June 2023, H. Qu 1075 (KUN-HKAS 131126).

Notes: *Micropsalliota longicystis* is characterised by a white silky-fibrillose pileus, stipe with white rhizomorphs at the base, presence of pleurocystidia and caulocystidia, and caulocystidia with a very long and narrow neck.

Micropsalliota longicystis forms a well-supported monophyletic clade (BI-PP = 1; MLBP = 100%) with *Micropsalliota arginea* (Berk. & Broome) Pegler & R.W. Rayner (only LSU sequences available for the Thai *M. arginea* zrl3090). Both species have capitate or subcapitate caulocystidia. However, *M. arginea* differs in forming smaller spores (4–5 × 2.5–3 µm) and smaller-sized cheilocystidia (25–35 × 3–6 µm) (Zhao et al. 2010).

Several species are similar in overall appearance to *Micropsalliota longicystis*. However, *Micropsalliota allantoidea* R.L. Zhao, Desjardin, Soytong & K.D. Hyde differs in forming slender basidiomes (pilei 5–10 mm in diam., stipe 10–20 × 0.5 mm) and sausage-shaped pileipellis elements (Zhao et al. 2010); *M. pseudoarginea* differs in forming a brown fibrillose-squamulose pileus, no staining reaction when bruised or cut, and a strong reddish brown reaction with KOH (Heinemann 1982; Zhao et al. 2010); *Micropsalliota bifida* R.L. Zhao, Desjardin, Soytong & K.D. Hyde differs in forming smaller basidiospores ($3.8\text{--}5 \times 2.3\text{--}3.2 \mu\text{m}$) and bifid cheilocystidia, and strong reddish brown reaction with KOH (Zhao et al. 2010); *Micropsalliota laeta* Heinem. differs in forming bigger basidiospores ($6.3\text{--}7.1 \times 3.6\text{--}4 \mu\text{m}$) and a white to light pink pileus (Heinemann 1980);

Micropsalliota lutescens Heinem. differs in forming longer stipe ($40\text{--}70 \times 1.5\text{--}2 \mu\text{m}$) and longer basidiospores (long $6.1\text{--}7.2 \mu\text{m}$) (Heinemann 1980). *Micropsalliota plumaria* (Berk. & Broome) Höhn. differs in forming a squamulose-floccose pileus and subciliate, broadly ventricose cheilocystidia without elongated neck (Pegler 1986); *Micropsalliota vinaceoumbrina* (A.H. Sm.) Heinem. differs in forming bigger basidiospores ($6\text{--}7 \times 5\text{--}5.5 \mu\text{m}$) and bigger basidia ($19\text{--}23 \times 7\text{--}8 \mu\text{m}$) (Smith 1944).

Micropsalliota nana T. Gao, H. Qu & Z.W. Ge, sp. nov.

Figures 2l–m, 8

Fungal Names: FN571734.

Etymology: Referring to its tiny pileus measuring 5–15 mm in diameter.

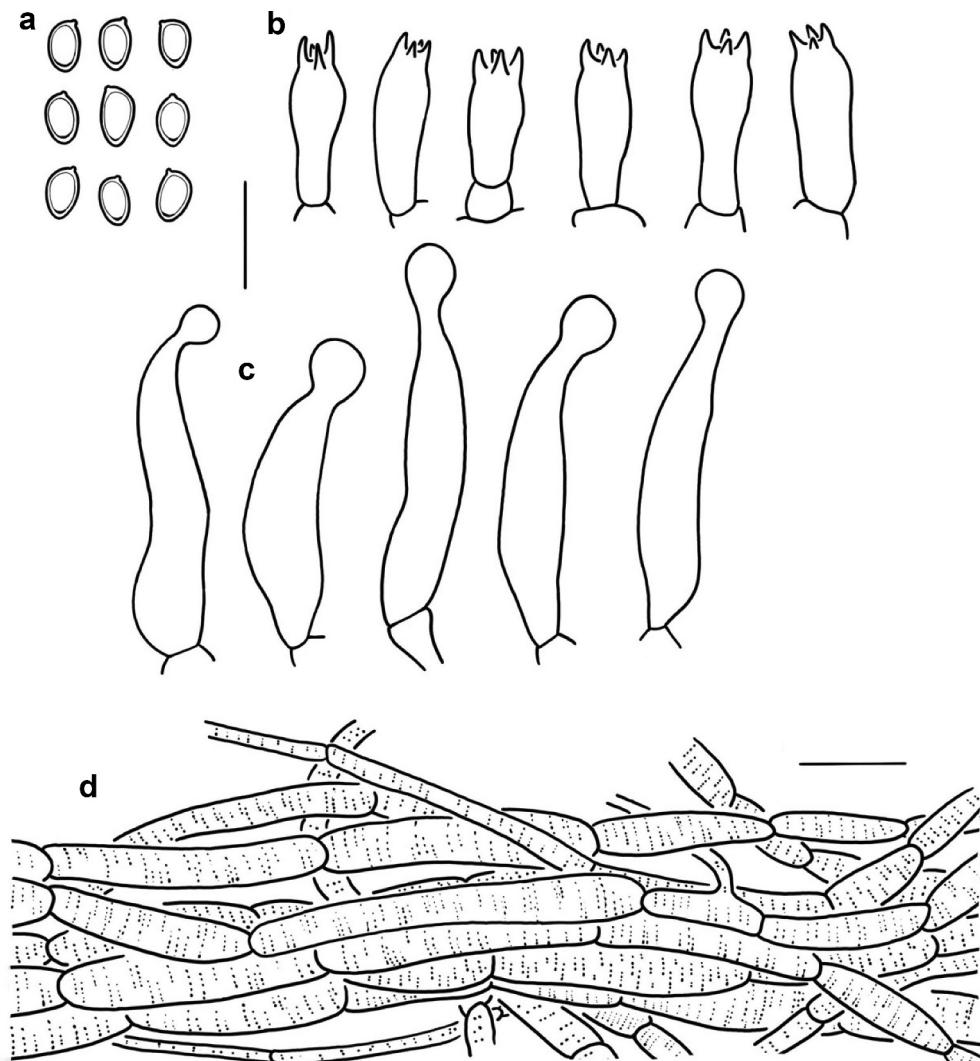


Figure 8. Microscopic features of *Micropsalliota nana* (holotype, KUN-HKAS 115226). (a) Basidiospores. (b) Basidia. (c) Cheilocystidia. (d) Pileus squamules. Bars: a – c = 10 μm ; d = 20 μm .

Types: China, Yunnan Province, Baoshan City, Tengchong City, Jietou Town, Goubianzhai, on soil under evergreen broad-leaved forest, 98.712175°E, 25.429414°N, alt. 1,910 m, 8 August 2019, L.R. Zhou 280 (KUN-HKAS 115226, holotype). GenBank: ITS = OR799902, LSU = OR799947, rrf1 = OR962217.

Diagnosis: *Micropsalliota nana* is distinguished by a white, glabrous to silky pileus that turns brown when bruised or cut, small basidiospores, and capitate or subcapitate cheilocystidia.

Macroscopic description: Pileus 5–15 mm in diam., convex in early stage, expanding to plane, with obtuse umbo, surface dry, silky to fibrillose, white (1A1) when young, cream (5A2) to light yellowish grey (5B2) or light brown with age, light salmon (6A4) at disc. Context less than 0.5 mm thick. Lamellae free, moderately distant, with 2 series of lamellulae, 0.5–0.7 mm broad, white (1A1), becoming brown (7E4–7E5) when mature. Stipe 15–40 × 1–1.5 mm, cylindrical, white (1A1) when young, turning brown (6E2) with age, surface with fine white (1A1) fibrils. Annulus superior, persistent, edge entire, white (1A1) at first, brown (7E4) when mature. Staining brown (7E4) when bruised or cut.

Microscopic description: Basidiospores [20/2/1] 4.5–6 × 3–4 µm, av. = 5.2 × 3.53 µm, Q = 1.25–1.71 (2.00), $Q_m = 1.49 \pm 0.20$, ellipsoid to amygdaliform, with apical thickening, without germ pore, light brown, inamyloid. Basidia 11–20 × (4) 5–6 µm, clavate, hyaline, 4-spored. Pleurocystidia absent. Cheilocystidia 29–45 (60) × 5–13 µm, ventricose to irregularly tibiiform, capitate or subcapitate on the top, followed by a long narrow neck, capitulum 4–8 (10) µm in diam., hyaline, smooth. Pileus squamules composed of hyphae 4–15 µm in diam., hyaline, smooth, cylindrical, with membranous pigments.

Distribution: Southwestern China (Yunnan).

Habit and habitat: Gregarious on soil in broad-leaved forest.

Known distribution: Subtropical area in the west of Yunnan Province, China.

Additional specimens examined: China, Yunnan Province, Nujiang Lisu Autonomous Prefecture, Lushui City, Liuku Town, Qingshan Park, on soil by the roadside under evergreen broad-leaved forest, 98.853353°E, 25.859708°N, alt. 820 m, 3 August 2019, T.X. Xu 251 (KUN-HKAS 114619).

Notes: In the phylogenetic tree (Figure 1), *Micropsalliota nana* forms a strongly supported clade

of its own in Clade bifida. It is characterised by a white, silky pileus that turns brown when bruised or cut, small spores, and capitate or subcapitate cheilocystidia.

Micropsalliota nana can be confused with the following species by having a tiny and relatively white pileus: *Micropsalliota alba* Heinem. & Little Flower, *M. bifida*, *Micropsalliota dentatomarginata* R.L. Zhao, J.X. Li & M.Q. He, *Micropsalliota minor* J.Q. Yan, *Micropsalliota pseudoarginea* Heinem., and *Micropsalliota subalba* Heinem. & Little Flower. However, *M. alba* has slender basidiomes (pilei 4–8 mm in diam., stipe 20–25 × 0.6 mm), brown annulus, and bigger basidiospores (5.5–7 × 3.2–4 µm) (Heinemann and Flower 1983); *M. bifida* differs in forming cheilocystidia with two irregular toe-like lobes (Zhao et al. 2010); *M. dentatomarginata* is distinguished from *M. nana* by its pure white pileus and the cheilocystidia with a thickened base (Li et al. 2021); *M. minor* differs by smaller basidiomes (pilei 2.5–6 mm in diam., stipe 12–17 × 0.3–0.6 mm) and forked cheilocystidia (Yan et al. 2022); *M. pseudoarginea* differs in forming smaller spores (4–5 × 2.5–3.2 µm) and smaller cheilocystidia (15–24 × 6.5–12 µm) (Heinemann 1982); *M. subalba* differs in forming bigger basidiomes (pilei 12–18 mm in diam., stipe 28–30 × 1–1.5 mm), bigger spores (5.2–7 × 3–4 µm), and slightly white fibrillose pileus that does not change colour when bruised (Heinemann and Flower 1983).

In addition, *Micropsalliota arginea* is also similar to *M. nana* in demonstrating a similar overall appearance. However, *M. arginea* forms longer stipe (17–25 mm), smaller basidiospores (4–5 × 2.5–3 µm), and capitate or subcapitate caulocystidia (Pegler and Rayner 1969).

***Micropsalliota squarrosa* T. Gao & Z.W. Ge, sp. nov.**

Figures 2n–o, 9

Fungal Names: FN571737.

Etymology: Referring to erect scales on its pileus.

Types: China, Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Menghai County, by the side of K16 highway heading into Bulangshan Bulang Ethnic Township, on soil under evergreen broad-leaved forest, 100.356683°E, 21.561704°N, alt. 1,290 m, 23 June 2020, Y.J. Lüli 119 (KUN-HKAS 128633, holotype). GenBank: ITS = OR799915, LSU = OR799959, rpb2 = OR962250.

Diagnosis: *Micropsalliota squarrosa* is characterised by the brown to reddish brown pileus covered with

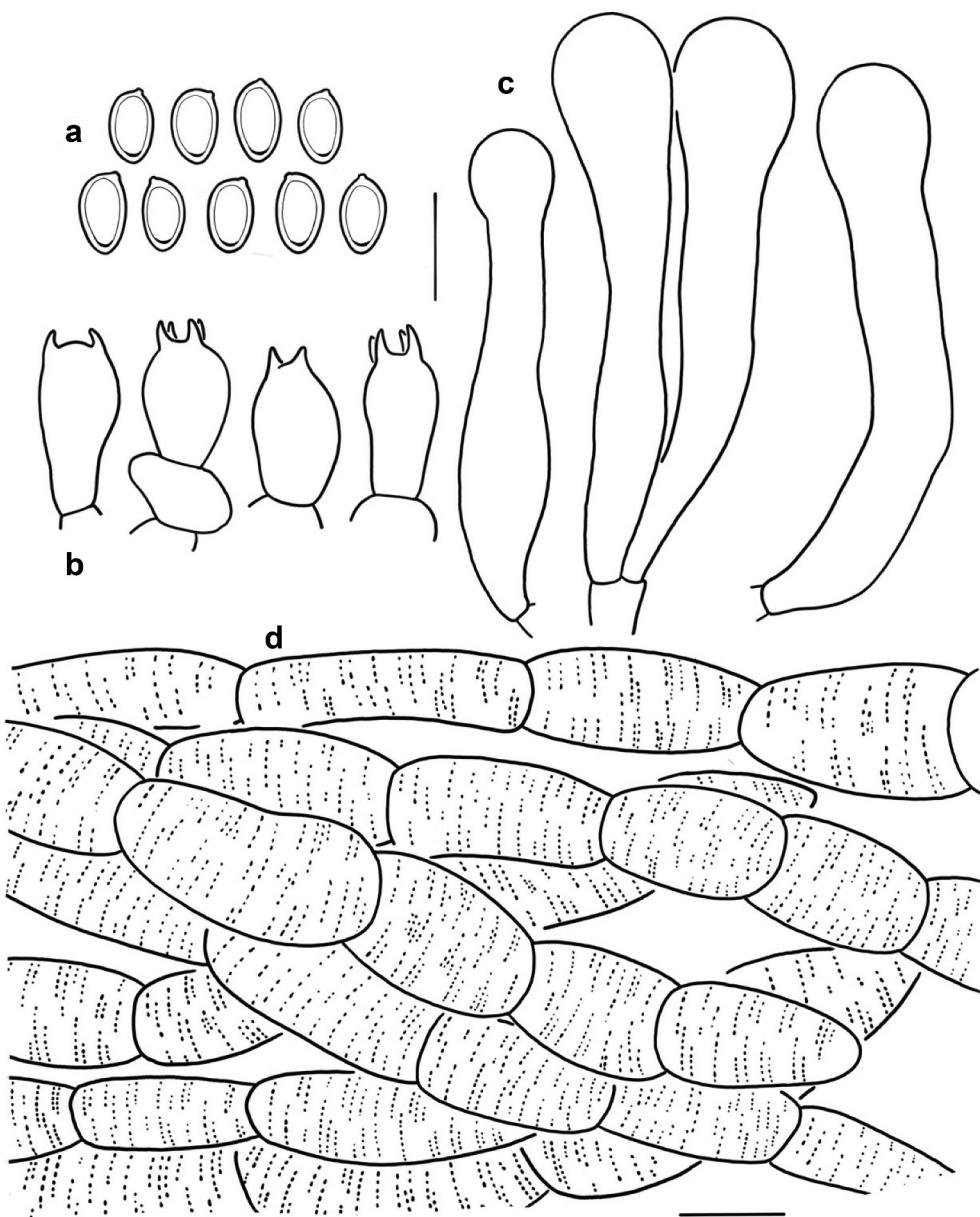


Figure 9. Microscopic features of *Micropsalliota squarrosa* (KUN-HKAS 128713). (a) Basidiospores. (b) Basidia. (c) Cheilocystidia. (d) Pileus squamules. Bars: a – c = 10 µm; d = 20 µm.

squamules, bigger basidiospores ($7-8 \times 4.5-5.5 \mu\text{m}$), clavate to clavate-capitate cheilocystidia, and tissues staining yellow or reddish brown when bruised.

Macroscopic description: Pileus 25–30 mm in diam., white (1A1), convex in early stage, plano-convex to applanate with age, covered with fibrillose brown (6E5) to reddish brown (6F4–6F6) squamules, denser at disc. Context firm, thickened at the disc, and thin near the margin. Lamellae free, crowded, with 2–4 series of lamellulae, 3–4 mm broad, white (1A1) at first, greyish white (1B1) to light brown (8E3) with age, edges paler. Stipe

55–60 × 3–4 mm, cylindrical, white (1A1) to brown (6D4), surface with white (1A1) fibrils, stipe base with white rhizomorphs. Annulus single, superior, persistent, edge entire, white (1A1). Pileus and stipe staining slightly yellow (4A4) or reddish brown (7C5) when bruised.

Microscopic description: Basidiospores [20/1/1] $7-8 (8.5) \times 4.5-5.5 \mu\text{m}$, av. = $7.75 \times 4.90 \mu\text{m}$, Q = (1.27) 1.40–1.78, $Q_m = 1.59 \pm 0.12$, ellipsoid, with apical thickening, without germ pore, light brown, inamyloid. Basidia (12) 13–15 (16) × 7–9 µm, clavate, hyaline, 4-spored. Pleurocystidia absent. Cheilocystidia (42)

$45\text{--}55 \times 6\text{--}9$ (10) μm , clavate to clavate-capitate, some subcapitate with long narrow neck, capitulum 7–13 μm in diam., hyaline, smooth. Pileus squamules composed of hyphae 4–15 μm in diam., hyaline, smooth, cylindrical, slightly constricted at septa, with membranous pigments.

Distribution: Southwestern China (Yunnan).

Habit and habitat: Solitary or scattered on soils.

Known distribution: Tropical region of Yunnan province, China.

Additional specimens examined: China, Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Jinghong City, Dadugang Township, on soil under evergreen broad-leaved forest, 100.91482° E, 22.28536°N, alt. 1,120 m, 27 June 2020, Y.J. Lüli 207 (KUN-HKAS 128713).

Notes: *Micropsalliota squarrosa* is characterised by brown to reddish brown pileus covered with squamules, bigger basidiospores (7–8 \times 4.5–5.5 μm), clavate to clavate-capitate cheilocystidia, and tissues staining yellow or reddish brown when bruised or cut.

Morphologically, *Micropsalliota squarrosa* is similar to *M. globocystis*, *M. digitatocystis*, and *M. pseudoglobocystis*. However, *M. globocystis* differs in forming smaller basidiospores (6–7 \times 3.5–4.2 μm) and staining reddish brown when bruised; *M. digitatocystis* differs in forming longer stipe (stipe 60–90 \times 5–8 mm), smaller basidiospores (5.8–7.4 \times 4–4.6 μm) and needle-like pleurocystidia (Li et al. 2021); *M. pseudoglobocystis* differs in forming larger basidiomes (pilei 25–55 mm in diam.) and forming needle-like pleurocystidia (Li et al. 2021).

Phylogenetically, *Micropsalliota squarrosa* is sister to *M. purpureobrunneola* and *M. gigaspora*. However, *M. purpureobrunneola* differs in forming smaller basidiomes (pilei 5–12 mm in diam.) and larger basidia (17.2–26 \times 5.7–7.4 μm) (He et al. 2020); while *M. gigaspora* differs in forming clavate, rather than subcapitate cheilocystidia, and demonstrating no colour staining when bruised or cut.

***Micropsalliota umbonata* T. Gao & Z.W. Ge, sp. nov.**

Figures 2p–q, 10

Fungal Names: FN571738.

Etymology: Referring to its pileus with obtuse umbo.

Types: China, Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Mengla County,

Shangyong Township, Niupeng Village, on soil under evergreen broad-leaved forest, 101.57251° E, 21.32043°N, alt. 1,080 m, 26 June 2020, G.S. Wang 1044 (KUN-HKAS 131131, holotype). GenBank: ITS = OR799920, LSU = OR799964, rpb2 = OR962254, tef1 = OR962194.

Diagnosis: *Micropsalliota umbonata* is distinguished from other *Micropsalliota* species by yellowish brown pileus covered with fibrillose, yellowish brown to brown squamules, pileus with obtuse umbo.

Macroscopic description: Pileus with a wide range of size, 15–50 mm in diam., campanulate at first, conical or broadly conical with age, with obtuse umbo, surface dry; white (1A1) to cream (1A2) when young, with reddish brown (7D5) tone in age; covered with fibrillose, light brown (5B4), yellowish brown (5D7) or brown (7E7) squamules, dense on the disc and scattered near the margin. Context firm, up to 3 mm thick, white. Lamellae free, crowded, 2–4 mm broad, white (1A1) at first, becoming greyish white (5B2) to greyish brown (5D2), edges paler, with 4–6 series of lamellulae. Stipe 80–130 \times 3–6 mm, cylindrical, hollow, smooth to tomentose, white (1A1) or with reddish brown (5F6) tone, surface heavily covered white (1A1) tomentose-flocculose fibrils. Annulus single, membranous, persistent, superior, up to 5 mm broad, white (1A1), sometimes brown (6E5) in margin. Upper part of annulus smooth or glabrous, lower part with flocculose fibrils. Pileus and stipe staining yellow (4A4) when bruised; context staining yellow (4A4) then red (7A2) or reddish brown (6E8) when cut.

Microscopic description: Basidiospores [40/2/2] (5.5) 6–7 \times 3–4 μm , av. = 6.13 \times 3.48 μm , Q = 1.50–2.00, $Q_m = 1.78 \pm 0.23$, ellipsoid to amygdaliform, with apical thickening, without germ pore, light brown, inamyloid. Basidia 15–19 \times (5.5) 6–7 μm , clavate, hyaline, 4-spored, sometimes 2-spored. Pleurocystidia absent. Cheilocystidia 42–60 (65) \times 7–10 (12) μm , apex 12–18 (22) μm in diam., broadly clavate to clavate-capitate, some subcapitate, rarely ventricose, hyaline, smooth. Pileus squamules composed of hyphae (4) 11–22 μm in diam., hyaline, smooth, cylindrical, slightly constricted at septa, with light brown membranous pigments.

Distribution: Southwestern China (Yunnan).

Habit and habitat: Cespiteous, gregarious, or occasionally solitary on soil.

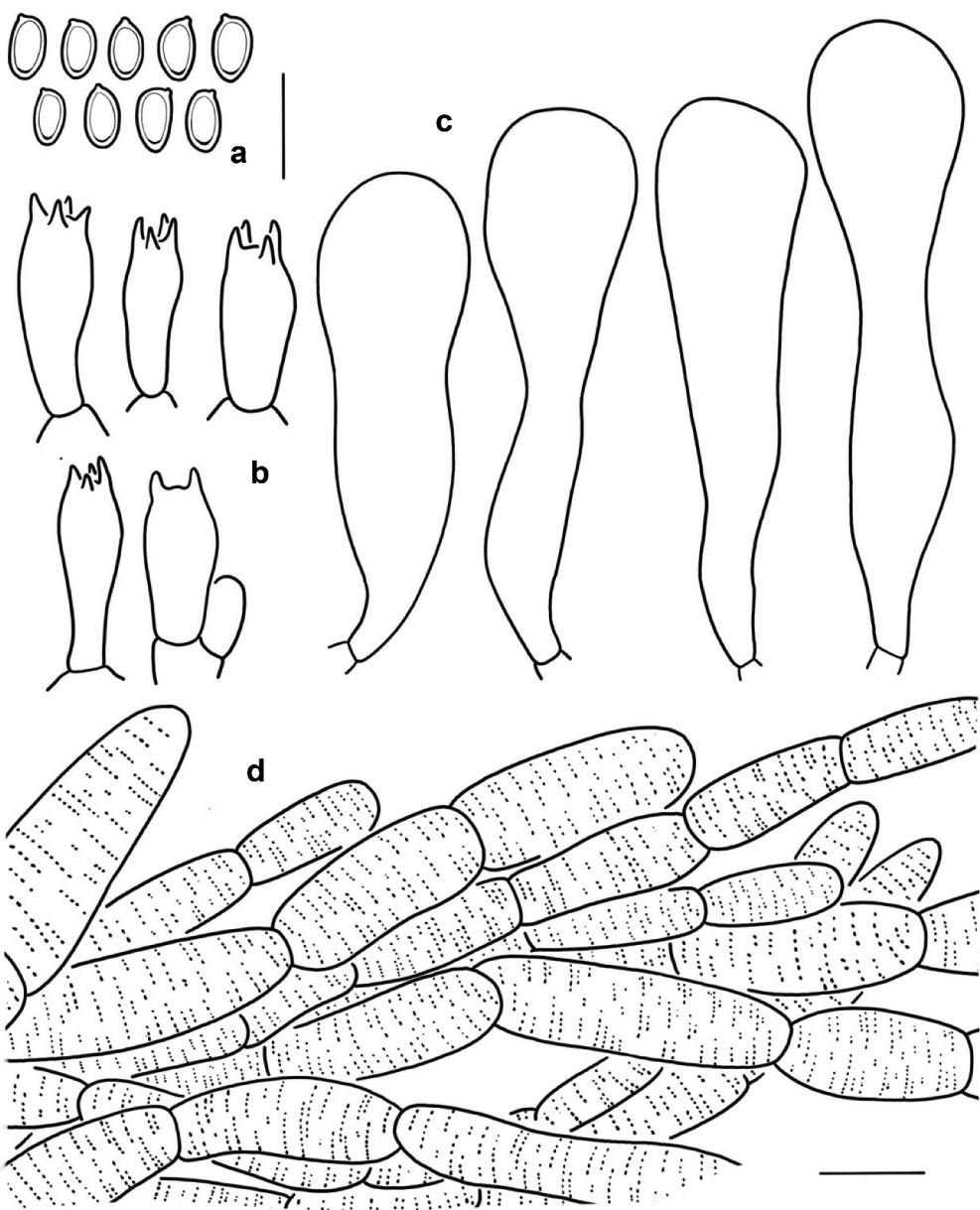


Figure 10. Microscopic features of *Micropsalliota umbonata* (holotype, KUN-HKAS 131131). (a) Basidiospores. (b) Basidia. (c) Cheilocystidia. (d) Pileus squamules. Bars: a – c = 10 μm ; d = 20 μm .

Known distribution: Tropical region of Yunnan Province, China.

Additional specimens examined: China, Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Mengla County, Shangyong Township, Niupeng Village, on soil under evergreen broad-leaved forest, 101.57251°E, 21.32043°N, alt. 1,080 m, 26 June 2020, P.C. Yuan 092 (KUN-HKAS 131134); ibid., L.K. Jia 878 (KUN-HKAS 125689); ibid. G.S. Wang 1048 (KUN-HKAS 131132).

Notes: *Micropsalliota umbonata* is distinguished by light brown to yellowish brown pilei covered with

yellowish brown to brown squamules, campanulate, conical to broadly conical pileus with obtuse umbo, and clavate to clavate-capitate cheilocystidia without a long neck.

The following species share similar morphological characters with *Micropsalliota umbonata*: *Micropsalliota bambusicola* (Heinem.) Heinem. which has shorter basidiospores ($5.5\text{--}5.9 \times 3.1\text{--}3.5 \mu\text{m}$), and much narrower cheilocystidia $20\text{--}35 \times 10\text{--}20 \mu\text{m}$ (Heinemann 1956); *Micropsalliota arginophaea* Heinem. have much smaller basidiomes (pilei 6–20 mm in diam.), and subcylindrical to clavate cheilocystidia with long elongated neck in

most cases (Heinemann 1980); *M. furfuracea* has brown flake-like scales on the pileus (Zhao et al. 2010), while *M. umbonata* has fibrillose, yellowish brown to brown squamules.

Micropsalliota umbonata, which forms an independent lineage in Clade globocystis, is sister to *M. megarubescens*, *M. digitatocystis*, *M. globocystis*, *M. pseudoglobocystis*, and *M. purpureobrunneola* in the molecular analyses (Figure 1). However, *M. megarubescens* colours white to cream and becomes light grey to greyish brown with age (Zhao et al. 2010); *M. digitatocystis* and *M. pseudoglobocystis* differs in having needle-like pleurocystidia (Li et al. 2021); *M. globocystis* has conical to convex or plano-convex, purple to purplish brown, greyish brown (8E3), or reddish brown (8E4) pilei (Zhao et al. 2010); *M. purpureobrunneola* differs in forming smaller basidiomes (pilei 5–12 mm in diam.) and purplish-brown pileus (He et al. 2020).

Key to *Micropsalliota* species distributed in China

- 1a. Pileus white to dirty white, glabrous to slightly fibrillose..... 2
- 1b. Pileus coloured, e.g. brown, red, or violet, silky to fibrillose-scaly..... 13
- 2a. Basidiomes medium-sized, pileus 20–80 mm in diam., stipe 70–120 mm long, strongly staining reddish brown when bruised or cut..... *M. megarubescens*
- 2b. Basidiomes small-sized, pileus less than 20 mm in diam., stipe less than 40 mm long..... 3
- 3a. Pileus less than 5 mm in diam..... 4
- 3b. Pileus 5–20 mm in diam..... 5
- 4a. Stipe < 15 mm long, basidiospores $4.3\text{--}5.5 \times 2.7\text{--}3.3 \mu\text{m}$ *M. pseudodelicatula*
- 4b. Stipe > 17 mm long, basidiospores $5.5\text{--}7.5 \times 3.5\text{--}4 \mu\text{m}$ *M. albofelia*
- 5a. Caulocystidia present; Stipe base with white rhizomorphs..... *M. longicystis*
- 5b. Caulocystidia absent; Stipe base without white rhizomorphs..... 6
- 6a. Cheilocystidia forked or bifid..... 7
- 6b. Cheilocystidia simple, utriform, tibiiform, or ventricose-capitate with a long flexuous neck..... 8
- 7a. Basidiomes tiny, pileus 2.5–6 mm in diam.; Cheilocystidia two types, tibiiform or forked with capitate or subacute apex..... *M. minor*
- 7b. Basidiomes larger, pileus 6–21 mm in diam.; Cheilocystidia bifid with two toe-like subcapitate lobes..... *M. bifida*
- 8a. Cheilocystidia non-capitate..... 9
- 8b. Cheilocystidia capitate, with a sinuous or straight neck..... 10
- 9a. Cheilocystidia broadly clavate or ventricose-clavate, hyaline, smooth; basidiospores $4\text{--}5 \times 2.5\text{--}3.2 \mu\text{m}$ *M. pseudoarginea*
- 9b. Cheilocystidia utriform, with broadly obtuse apex, covered by hyaline deposition; basidiospores $5.3\text{--}6.2 \times 3\text{--}3.5 \mu\text{m}$ *M. tenuipes*
- 10a. Cheilocystidia clavate to ventricose, capitate, without a thickened base..... 11
- 10b. Cheilocystidia capitate, with a sinuous or straight neck and a thickened base..... 12
- 11a. Pileus 5–12 mm in diam.; basidiospores $4.5\text{--}6 \times 3\text{--}4 \mu\text{m}$; flesh staining reddish brown when bruised or cut..... *M. nana*
- 11b. Pileus 12–18 mm in diam.; basidiospores $5.2\text{--}7.3 \times 3\text{--}4 \mu\text{m}$; flesh not staining when bruised or cut..... *M. subalba*
- 12a. Basidiospores $4\text{--}5 \times 2.5\text{--}3 \mu\text{m}$, ovoid in face view, amygdaliform in profile view..... *M. ovalispora*
- 12b. Basidiospores longer than $5 \mu\text{m}$, wider than $3 \mu\text{m}$, ellipsoid, sometimes amygdaliform..... 13
- 13a. Basidiomes larger, pileus 12–15 mm in diam., stipe 25–35 mm long..... *M. dentatomarginata*
- 13b. Basidiomes smaller, pileus 3–7 mm in diam., stipe 12–19 mm long..... *M. delicatula*
- 14a. Basidiomes medium-sized, pileus 20–80 mm in diam., stipe 35–130 mm long..... 15
- 14b. Basidiomes small-sized, pileus less than 20 mm in diam., stipe less than 40 mm long..... 22
- 15a. Pleurocystidia present, needle-like..... 16
- 15b. Pleurocystidia absent..... 17
- 16a. Basidiospores $4.5\text{--}6 \times 2.5\text{--}3.2 \mu\text{m}$; flesh staining bright yellow then reddish brown when bruised or cut..... *M. pseudoglobocystis*
- 16b. Basidiospores $5.8\text{--}7.4 \times 4\text{--}4.6 \mu\text{m}$; flesh staining yellowish brown when bruised or cut..... *M. digitatocystis*
- 17a. Pileus squamules flake-like, appressed, light brown to brown; flesh staining red when bruised or cut..... *M. furfuracea*

- 17b. Pileus squamules fibrillose-scaly, erect or recurved, reddish brown, greyish brown, purplish brown or dark brown; flesh staining yellow, reddish brown or blue..... 18
- 18a. Pileus squamules reddish brown, purplish brown or dark brown, background grey or yellowish brown; larger squamules in margin, recurved; lamellae staining blue when bruised or cut..... *M. ferruginea*
- 18b. Pileus squamules light brown, greyish brown purplish brown or reddish brown, background white or light grey; denser at disc, scanty towards the margin; flesh staining yellow or reddish brown when bruised or cut..... 19
- 19a. Basidiospores shorter than 7 µm, narrower than 4 µm..... 20
- 19b. Basidiospores longer than 7 µm, wider than 4 µm..... 21
- 20a. Pileus conical to broadly conical, with conspicuously obtuse umbo; squamules light brown, yellowish brown, or brown..... *M. umbonata*
- 20b. Pileus conical to broadly conical, convex or plano-convex and slightly umbonate; squamules purple to purplish brown, greyish brown or reddish-brown..... *M. globocystis*
- 21a. Stipe 55–65 × 3–4 mm; cheilocystidia subcapitate; stipe base with white rhizomorphs, basidiospores 7–8 (8.5) × 4.5–5.5 µm, av. = 7.75 × 4.90 µm..... *M. squarrosa*
- 21b. Stipe 35–50 × 2–3 mm; cheilocystidia non-capitate; stipe base without white rhizomorphs, basidiospores 7–9 × 4–5.5 µm, v. = 7.98 × 4.45 µm..... *M. gigaspora*
- 22a. Partial veil cortinate, remaining as fibrillose patches along pileus margin..... *M. cortinata*
- 22b. Partial veil forming a membranous annulus... 23
- 23a. Pileus pink, red to violet-red..... 24
- 23b. Pileus brown to dark brown, or with reddish brown tones on the disc..... 28
- 24a. Cheilocystidia utriform with obtuse, subcapitate, or capitate apex..... 25
- 24b. Cheilocystidia non-utriform..... 26
- 25a. Stipe dirty white with pink tone, cheilocystidia without deposit..... *M. cf. roseipes*
- 25b. Stipe white, cheilocystidia covered by light brown deposit..... *M. rufosquarrosa*
- 26a. Cheilocystidia hyphoid, often forked, up to 60 µm long; pileipellis hyphae with membranous pigments..... *M. wuyishanensis*
- 26b. Cheilocystidia simple, non-hyphoid, capitate or subcapitate; pileipellis hyphae with vacuolar pigments..... 27
- 27a. Basidiomes slender (pileus 6–22 mm in diam., stipe 18–42 mm long); pileus greyish red to dull red or reddish brown; stipe white..... *M. gracilis*
- 27b. Basidiomes stout (pileus 10–18 mm in diam., stipe 15–18 mm long); pileus violet brown; stipe violet red..... *M. lateritia* var. *vinaceipes*
- 28a. Basidiospores 4–5.5 × 2.5–3 µm..... *M. arginophaea*
- 28b. Basidiospores longer than 5.5 µm, wider than 3.5 µm..... 29
- 29a. Pileus white to cream with reddish brown stains, glabrous to silky..... *M. rubrobrunnescens*
- 29b. Pileus brown to dark brown, fibrillose to floccose or squamulose..... 30
- 30a. Pleurocystidia present; cheilocystidia pyriform to subglobose..... *M. appendiculata*
- 30b. Pleurocystidia absent; cheilocystidia capitate or subcapitate with long neck 31
- 31a. Pileus brown to dark brown; squamules erect or recurved; cheilocystidia ventricose with a long obtuse neck to pyriform, apex merely obtuse or seldom subcapitate..... *M. megaspora*
- 31b. Pileus reddish brown or greyish brown; squamules appressed; cheilocystidia clavate to irregularly tibiiform, capitate or subcapitate with long narrow neck..... *M. fimbriata*

4. Discussion

The results of our phylogenetic analyses are, to some extent, consistent with the previous studies (Zhao et al. 2010; Wei et al. 2015; Li et al. 2021; Al-Kharousi et al. 2022; Patil et al. 2022; Yan et al. 2022). However, compared to the previous studies (Yan et al. 2022; Ivanova et al. 2023), the present study resolved 6 more major clades based on the ITS, LSU, *rpb2*, and *tef1* sequence datasets, and some clades, for instance, Clade *lateritia*, and Clade *bifida*, had higher support values and were able to be combined with morphological features. Nevertheless, the backbone of the *Micropsalliota*

phylogeny remains poorly resolved. Based on our present study, *Micropsalliota* consists of 11 major clades.

Species in Clade *globcystis* share reddish brown to greyish brown fibrillose or squamulose on the white context (except for *M. megarubescens*), erect fibrillose or squamulose, basidiospores generally longer than 6 µm (except for *M. pseudoglobocystis*), cheilocystidia clavate to capitate and almost all staining reddish brown when bruised or cut (Heinemann and Leelavathy 1991; Zhao et al. 2010; Wei et al. 2015; Li et al. 2021).

Species in Clade *lateritia* have small-sized to medium-sized basidiomes, that are thick-fleshy and stout, and have deep red to violet brown fibrils on the white context (except for *M. rubrobrunnescens* and *M. rubrobrunnescens* var. *tibiicystis*, which have a white and silky pileus with reddish-brown stains) (Zhao et al. 2010; Yan et al. 2022; Ivanova et al. 2023).

Clade *ferruginea* is currently composed of only one species, *M. ferruginea*. It is distinguished from all other *Micropsalliota* species by relatively large basidiomes with erect to recurved squamules that are brown to dark brown, and lamellae staining a slightly blue when bruised or cut.

Species in Clade *furfuracea* share reddish brown appressed fibrillose or squamulose on the white context, vivid red to reddish brown staining, and rather large spores with a mean of 6.9×3.8 µm, distinguish them from other species (Zhao et al. 2010).

Species in Clade *pleurocystidiata* are characterised by robust basidiomes, presence of large pleurocystidia and brown scales on pileus, broadly clavate, utriform to broadly utriform cheilocystidia, which is similar to pleurocystidia (Heinemann 1980; Heinemann and Flower 1983; Zhao et al. 2010; Patil et al. 2022).

Species in Clade *megaspora* share small-sized basidiomes (pilei 3–13 mm in diam., except for *M. repanda*), fibrillose to floccose, light yellow, yellowish brown to dark brown squamules (Heinemann 1980; Zhao et al. 2010; Ivanova et al. 2023).

Clade *jiangxiensis* is characterised by its brownish, fibrillose scales on pileus, cylindrical to subclavate cheilocystidia, ellipsoid, and sometimes amygdaliform basidiospores (Ji and He 2023).

Clade *bifida* contains 24 species with different morphological characteristics. Except for *M. brunneosquamata* and *M. geesterani*, which form robust basidiomes and thick-fleshed pileus, all species in Clade *bifida* are slender

and very small. Most small species are white, only *M. arginophaea*, *M. gracilis*, *M. roseipes*, *M. rufosquarrosa*, and *Micropsalliota suricatoides* D.D. Ivanova, O.V. Morozova & T.H.G. Pham share coloured pilei (Heinemann and Flower 1983; Zhao et al. 2010; He et al. 2020; Li et al. 2021; Yan et al. 2022; Ivanova et al. 2023).

Clade *albofentina* is similar to Clade *bifida*, the only species, *M. albofentina* D.D. Ivanova & O.V. Morozova, is characterised by the following features: Delicate, tiny pristine white discolouring to brown basidiomes, cheilocystidia with a long neck, and well-distinguished capitulum. The most distinctive feature of this species is the presence of thin white hairs which cover the entire basidiome (Crous et al. 2021).

Clade *cortinata* contained only one species, *M. cortinata*, which is distinguished by cortinate partial veil that leaves remnants only on the pileus margin (Heinemann 1980, 1988; Zhao et al. 2010).

Clade *ventricocystidiata* contains only one species, *M. ventricocystidiata*, which is characterised by medium-sized, thick-fleshy, and stout basidiomes covered with reddish-brown squamules; amygdaliform basidiospores measuring $7.5\text{--}8.5 \times 4.5\text{--}5$ µm; and the cheilocystidia which are mostly ventricose, rarely more or less subcylindrical (Al-Kharousi et al. 2022).

In previous studies, *Micropsalliota* has approximately 80 species, of which 24 are known to be distributed in China (most were reported from Southwestern China). Based on multigene phylogeny and morphological studies on specimens collected from Yunnan and Hainan Provinces, seven new species and a newly recorded species of China were introduced in the present study, increasing the total number of *Micropsalliota* species found in China from 24 to 32. With further investigations and studies of macrofungi in China going on, more *Micropsalliota* species are expected to be discovered.

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