

# The detection of four major clades and new species from China with elongated cheilocystidia: A contribution to the genus *Mallocybe* (Inocybaceae, Agaricales)

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## Research Article

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# Abstract

*Mallocybe* is a newly elevated genus of the ectomycorrhizal mushroom family, *Inocybaceae*, based on *Inocybe* subg. *Mallocybe*. Although new species in this genus have constantly been discovered worldwide during the past decades, species native to China is poorly documented. Moreover, as a characteristic feature, members of this genus often have phaseoliform basidiospores and short catenated cheilocystidia. Therefore, this study describes three new Chinese *Mallocybe* species with elongated cheilocystidia through morphological and molecular analyses. Of the identified species, while *M. pallidipes* was collected from *Populus* in northeastern China, *M. aurantiodisca* was discovered in subtropical evergreen broad-leaved forests dominated by *Castanopsis* in the Zhejiang Province, and *M. longsicystis* was discovered under fagaceous forests in tropical and subtropical China. From the multi-gene phylogenetic analysis, four major clades were also elucidated in the genus, of which three new species were grouped with three North American species in a full support clade. Finally, we discussed the systematic position of the new species and the genus's infrageneric phylogeny.

## Introduction

Kuyper (1986) first used the cladistic classification method to analyze the phylogenetic relationship between members of the genus *Inocybe* (Fr.) Fr. based on the presence or absence of pleurocystidia, the development source of cheilocystidia, and the presence or absence of a yellow pigment in basidia. It has also been reported that the genus *Inocybe* is divided into subg. *Mallocybe* Kuyper, subg. *Inosperma* Kühner, and subg. *Inocybe* (Fr.) Fr. However, because of the discovery of new species, the genus is constantly enriched. Therefore, Matheny et al. (2020) recently promoted subg. *Mallocybe* to one of the seven genera under *Inocybaceae* Jülich, based on a six-gene phylogeny. Members of *Mallocybe* (Kuyper) Matheny, Vizzini & Esteve-Rav. are characterized by small-sized basidiomata, often woolly squamulose and noticeably dark pileus appearance upon application of ammonium hydroxide. Furthermore, they are adnate to subdecurrent lamellae and have nonreddening features, phaseoliform basidiospores, short and thin-walled cheilocystidia originating from hymenophoral trama, including a necropigmented basidia (Kuyper 1986; Matheny et al. 2020). Ecologically, species of *Mallocybe* can associate with many symbiotic plants, including gymnosperms and angiosperms, and play an important role in forest ecosystems. Accordingly, certain species also associate with the mycoheterotrophic orchid, *Epipogium aphyllum* (F. W. Schmidt) Sw. (Roy et al. 2009).

Recently, genus *Mallocybe* reportedly comprised nearly all previously assigned species to the subg. *Mallocybe*, with 64 recorded taxa in the IndexFungorum database ([www.indexfungorum.org](http://www.indexfungorum.org), retrieved May 15, 2022). The recognition of *Mallocybe* in the genus rank has facilitated its new species discovery, four of which were published in the past two years (Aïgnon et al. 2021; Mao et al. 2022). However, *Mallocybe* species in China have been poorly documented, and only five species have been verified: *M. depressa* L. Fan, H. Zhou & N. Mao, *M. leucoblema* (Kühner) Matheny & Esteve-Rav., *M. leucobloma* (Kühner) Matheny & Esteve-Rav., and *M. piceae* L. Fan & N. Mao (Fan and Bau 2016; Mao et al. 2022). Moreover, the infrageneric phylogeny of *Mallocybe* has been less concerned (Matheny et al. 2020).

*Mallocybe* species usually have a short cheilocystidia and appear in short incrustated chains. However, during the study of *Mallocybe* in China, collections with elongated ellipsoid basidiospores and cheilocystidia attracted our attention. After phylogenetic and morphological analyses, they were proven to be new to the science. Therefore, this paper described three new species by adopting morphological studies and multi-gene molecular analysis of combined rDNA-ITS, nrLSU, and *RPB2* sequence data. Then, we discussed its systematic position and elucidated the infrageneric phylogeny of the genus.

## Materials And Methods

## Specimens collected and microscopic observations

Fresh samples were collected from Hainan, Jilin, Yunnan, and Zhejiang Provinces of China. Subsequently, ecological images were photographed using a digital camera in the field, including measurement data of fruiting bodies soon after fieldwork. Following a study by Kornerup and Wanscher (1978), color codes were subsequently assigned. Then, specimens were dried in a 45 °C electric oven overnight, sealed in plastic bags, and placed in a refrigerator for insecticidal treatment (Yu et al. 2020; Deng et al. 2021a, 2021b). After the study, the specimens were deposited at the Herbarium of the Changbai Mountain Natural Reserve (ANTU) with FCAS numbers and the Mycological Herbarium of Kunming Medical University (MHKMU).

Macrofeatures were subsequently described from ecological pictures and field notes. However, microscopic observations were conducted using a light microscope (Olympus CX23). Dried specimens were also sliced and rehydrated in 5% KOH and 1% Congo red solution (When necessary). Next, basidiospores, basidia, hymenophoral trama, cheilocystidia, pileipellis/pileal trama, and stipitipellisstipe trama were examined and measured. Then, the side views of at least 20 matured basidiospores for each specimen were measured, excluding apiculus, with the form [n/m/p], indicating the measurement of “n” basidiospores of “m” individuals from “p” specimens. Finally, measurement data were expressed in the form of (a) b–e–c (d), where “a” and “d” represent the minimum and maximum values in the measurement data, respectively, “b” and “c” represent the values when the species measurement data are arranged at 5% and 95% from small to large, and “e” represents the average value (Liu et al. 2021; Ge et al. 2021; Na et al. 2022a). Additionally, the roundness of spores from a certain length (Q) conveniently distinguished different species, represented by the formula:

$$Q = \text{spore length} / \text{spore width}$$

Subsequently,  $Q_m$ , the average Q of all basidiospores (presented as basidiospores  $\pm$  sample standard deviation), was obtained (Na et al. 2022b; Jean et al. 2022).

## DNA extraction, PCR, and sequencing

Genomic DNA was extracted from dried samples using the NuClean Plant Genomic DNA kit (ConWin Biotech Beijing). Then, PCR reactions were conducted using the primer pairs ITS1-F /ITS4 for ITS (Gardes and Bruns 1993), LR0R/LR7 for LSU (Vilgalys and Herster 1990), and *RPB2*-6F/*RPB2*-7.1R for *RPB2* (Matheny 2005). Specifically, the PCR amplification setup was a 25  $\mu$ L mixture comprising 10  $\mu$ L ddH<sub>2</sub>O, 12  $\mu$ L of 2 $\times$  Taq Plus MasterMix (Dye), 1  $\mu$ L of each primer, and 1  $\mu$ L template DNA. Moreover, the PCR reaction program was set as follows: 5 min at 95°C; 1 min at 95°C; 30 s at 65°C (addition of a–1°C per cycle), then 1 min at 72°C for 15 cycles, followed by 1 min at 95°C; 30 s at 50°C, and 1 min at 72°C for 20 cycle times, finally ending with 10 min at 72°C (Wang et al. 2021). Amplified products were subsequently sent to BGI Biotech (Guangdong), Ltd. for purification and sequencing.

## Phylogenetic analyses

Authentically identified sequences retrieved from previous studies (Ryberg et al. 2008; Cripps et al. 2010; Vauras and Larsson 2012; Ariyawansa et al. 2015; Matheny and Kudzma 2019; Aignon et al. 2021; Mao et al. 2022) were selected and downloaded from the NCBI database for phylogenetic analyses. Specifically, *Inocybe relicina* (Fr.) Quél. and *I. lanuginosa* (Bull.) P. Kumm. served as outgroups. After that, ITS, nrLSU, and *RPB2* sequences were aligned using the MAFFT online service (<https://mafft.cbrc.jp/alignment/server/>) (Katoh et al. 2019), then manually edited using BioEdit v.7.0.9.0 (Hall 1999). Next, Mrmodeltest v.2.3 selected the optimal evolutionary substitution model for each gene following the Akaike information criterion (Nylander 2004), after which Mega v.5.0 concatenated the three gene sequences into a multi-locus dataset, followed by the maximum likelihood (ML) analysis using the IQ-TREE web server

with 1000 duplicates (Trifinopoulos et al. 2016). Finally, Bayesian analysis (BI) was performed using MrBayes v.3.2.7a (Ronquist et al. 2012). For this analysis, four Markov chains were set for 100 million generations, sampling every 1000 generations with the stoprul and stopval commands when the standard deviation of the split frequencies fell below 0.01. After discarding the first quarter of all generations as the burn-in, the majority-rule consensus tree of all remaining trees was calculated.

## Results

### Phylogenetic analyses

Thirty-four sequences (14 ITS, 10 nLSU, and 10 *RPB2*) from fourteen specimens were produced and submitted to GenBank. The final combined dataset comprised 90 samples representing 44 taxa (Table 1) and 2992 nucleotide sites, with 895 bp ITS, 1402 bp LSU, and 659 bp *RPB2*. Subsequently, the best model, GTR + I + G (lset nst = 6, rates = invgamma; prset statefreqpr = Dirichlet (1,1,1,1)), was selected for each of the three datasets. Phylogenetic trees inferred from the ML and BI analyses were nearly identical but with a few statistical differences. As a result, an optimal scoring tree was provided using the ML with combined support data.

Table 1  
Information on taxa used in the phylogenetic analysis.

Taxa	Voucher	Genbank accession number			Country	Reference
		ITS	LSU	RPB2		
<i>Inocybe lanuginosa</i>	PBM956	HQ232480	KP170923	KM245992	Washington	Matheny et al. (2020)
<i>Inocybe relicina</i>	JV10258	AF325664	AY038324	AY333778	Finland	Matheny et al. (2020)
<i>Mallocybe africana</i>	BRF4123		MK908842		Benin	Unpublished
<i>M. africana</i>	HLA0462	MT458691	MT456364		Benin	Aignon et al. (2021)
<i>M. africana</i>	MR00358	MT476160	MT509360	MT628398	Benin	Aignon et al. (2021)
<i>M. africana</i>	MR00369	MT476162	MT509361		Burkina Faso	Aignon et al. (2021)
<i>M. africana</i>	MR00385	MN096194	MN097886	MT465593	Togo	Aignon et al. (2021)
<i>M. africana</i>	PC:0088767	MN178510	MN178542		Zambia	Unpublished
<i>M. agardhii</i>	AB980912	HM209790	HM209790		Denmark	Larsson and Vauras (2012)
<i>M. arenaria</i>	EL25008	FN550937	FN550937		France	Ryberg M et al. (2010)
<i>M. aurantiodisca</i>	<b>2020ZD01</b>	<b>OM179937</b>			<b>China</b>	<b>The present study</b>
<i>M. aurantiodisca</i>	<b>NJ3109</b>	<b>OM179935</b>	<b>OM138834</b>	<b>OM835751</b>	<b>China</b>	<b>The present study</b>
<i>M. aurantiodisca</i>	<b>NJ3396</b>	<b>OM179936</b>	<b>OM138835</b>	<b>OM835752</b>	<b>China</b>	<b>The present study</b>
<i>M. arthrocystis</i>	EL9207	FN550941	FN550941		Sweden	Ryberg et al. (2010)
<i>M. caesariata</i>	NAMA272	EU819498			USA	Palmer et al. (2008)
<i>M. caesariata</i>	JMP0105	EU819473			USA	Palmer et al. (2008)
<i>M. cf. dulcamara</i>	CLC1333	GU980635	GU980635		USA	Cripps et al. (2010)
<i>M. cf. squarrosoannulata</i>	CLC1844	GU980611	GU980611		USA	Cripps et al. (2010)
<i>M. cf. subtilior</i>	PERTH:08383081	KP641629	KP171084	KM656125	Australia	Matheny and Bougher (2014)

Taxa	Voucher	Genbank accession number			Country	Reference
<i>M. depressa</i>	BJTC FM1300	OM801895	OM801900	OM780099	China	Mao et al. (2022)
<i>M. dulcamara</i>	EL59-05	GU980643	GU980643		Norway	Cripps et al. (2010)
<i>M. errata</i>	DED8022		EU569844		Thailand	Matheny et al. 2009
<i>M. fibrillosa</i>	LVK14371	MN178498	MN178526	MN203517	USA	Unpublished
<i>M. fibrillosa</i>	LVK14390	MN178499	MN178527	MN203518	USA	Unpublished
<i>M. fulviceps</i>	PBM4542	MZ404929	MZ375431		USA	Unpublished
<i>M. fulvipes</i>	EL3705	AM882858			Norway	Ryberg et al (2008)
<i>M. fulvipes</i>	EL8307	FN550935	FN550935		Sweden	Unpublished
<i>M. fulvipes</i>	EL99-07	GU980600	GU980600		Sweden	Cripps et al. (2010)
<i>M. fulvoumbonata</i>	PBM4537	MZ404931	MZ375433		USA	Unpublished
<i>M. fuscomarginata</i>	BJ890718	GU980656	GU980656		Sweden	Cripps et al. (2010)
<i>M. fuscomarginata</i>	EL10906	FN550940	FN550940		Sweden	Ryberg et al. (2010)
<i>M. granulosa</i>	EL138-09	KR029727	KR029727		Sweden	Ariyawansa et al. (2015)
<i>M. granulosa</i>	SJ84030	KR029725	KR029725		Sweden	Ariyawansa et al. (2015)
<i>M. gymnocarpa</i>	16413	JF908161			Italy	Osmundson et al.(2013)
<i>M. gymnocarpa</i>	SJ980707	AM882866	AM882866		Sweden	Ryberg et al. (2008)
<i>M. isabellina</i>	PERTH:07699255	KP171137	KP170915	KJ811581	Australia	Unpublished
<i>M. isabellina</i>	PERTH:08096635	KP171138	KP170916	KJ811582	Australia	Unpublished
<i>M. latispora</i>	EL190-08	KR029724	KR029724		Not given	Ariyawansa et al. (2015)
<i>M. latispora</i>	JV19640F	MN178503	MN178529	MN203520	Finland	Matheny et al. (2019)
<i>M. leucoblema</i>	JV2898	HM209789	HM209789		Finland	Larsson and Vauras (2012)
<i>M. leucoloma</i>	Kuhner63-36Type	GU980614			Geneva	Cripps et al. (2010)
<i>M. leucoblema</i>	SM2324	GU980630	GU980630		Sweden	Cripps et al. (2010)

Taxa	Voucher	Genbank accession number			Country	Reference
<i>M. leucoloma</i>	EL41-07	GU980622	GU980622		Sweden	Cripps et al. (2010)
<i>M. leucoloma</i>	Ohenoja 880810	HM209786	HM209786		Svalbard	Larsson and Vauras (2012)
<i>M. longicystis</i>	<b>FYG2015407</b>	<b>OM179933</b>			<b>China</b>	<b>The present study</b>
<i>M. longicystis</i>	<b>FYG6371</b>	<b>OM179926</b>	<b>OM135609</b>	<b>OM835746</b>	<b>China</b>	<b>The present study</b>
<i>M. longicystis</i>	<b>FYG6373</b>	<b>OM179927</b>	<b>OM135610</b>	<b>OM747850</b>	<b>China</b>	<b>The present study</b>
<i>M. longicystis</i>	<b>FYG6374</b>	<b>OM179928</b>	<b>OM135611</b>	<b>OM835747</b>	<b>China</b>	<b>The present study</b>
<i>M. longicystis</i>	<b>FYG6376</b>	<b>OM179929</b>	<b>OM135612</b>	<b>OM835745</b>	<b>China</b>	<b>The present study</b>
<i>M. longicystis</i>	<b>FYG6378</b>	<b>OM179930</b>	<b>OM135613</b>	<b>OM835748</b>	<b>China</b>	<b>The present study</b>
<i>M. longicystis</i>	<b>FYG6501</b>	<b>OM179934</b>			<b>China</b>	<b>The present study</b>
<i>M. longicystis</i>	<b>FYG6880</b>	<b>OM179931</b>	<b>OM135614</b>	<b>OM858853</b>	<b>China</b>	<b>The present study</b>
<i>M. longicystis</i>	<b>HT370</b>	<b>OM179932</b>	<b>OM135615</b>		<b>China</b>	<b>The present study</b>
<i>M. malenconii</i>	JV23101	HM209787	HM209787		Finland	Larsson and Vauras (2012)
<i>M. malenconii</i>	PAM98941302	HM209788	HM209788		France	Larsson and Vauras (2012)
<i>M. multispora</i>	CO4248	MN178509	MN178540		USA	Matheny and Kudzma (2019)
<i>M. myriadophylla</i>	EL121-08	HM209792	HM209792		Sweden	Larsson and Vauras (2012)
<i>M. myriadophylla</i>	JV5968	HM209794	HM209794		Finland	Larsson and Vauras (2012)
<i>M. myriadophylla</i>	JV19652	HM209791	HM209791		Finland	Larsson and Vauras (2012)
<i>M. myriadophylla</i>	JV19678	HM209793	HM209793		Finland	Larsson and Vauras (2012)

Taxa	Voucher	Genbank accession number			Country	Reference
<i>M. pallidipes</i>	FYG3726	OM179924	OM137052	OM835749	China	The present study
<i>M. pallidipes</i>	FYG3727	OM179925		OM835750	China	The present study
<i>M. picea</i>	BJTC FM555	OM801896	OM801901	OM780096	China	Mao et al. (2022)
<i>M. picea</i>	BJTC FM569	OM801897	OM801903	OM780097	China	Mao et al. (2022)
<i>M. pygmaea</i>	EL48-05	GU980628	GU980628		Norway	Cripps et al. (2010)
<i>M. pygmaea</i>	J. Favre76bisType	GU980629			Norway	Cripps et al. (2010)
<i>M. pyrrhopoda</i>	TENN:066987	KP308813	KP170983	KM406223	Australia	Matheny and Bougher (2017)
<i>M. pyrrhopoda</i>	PERTH:08383278	KP308814	KP170984	KM406224	Australia	Matheny and Bougher (2017)
<i>M. pyrrhopoda</i>	PERTH:08557764	KP308815	KP170986	KM406226	Australia	Matheny and Bougher (2017)
<i>M. sabulosa</i>	PERTH:07680732	KP308822	JN974916	KM406235	Australia	Horak et al. (2015)
<i>M. sabulosa</i>	PERTH:08320322	KP308821	KP170994	KM406234	Australia	Unpublished
<i>M. siciliana</i>	AMB 18274	MG757417	MG757419		Italy	Unpublished
<i>M. siciliana</i>	M73	MW354997			Hungary	Consiglio et al. (2020)
<i>M. squarrosoannulata</i>	K63-236Type	HM209795			Geneva	Larsson and Vauras (2012)
<i>M. subdecurrens</i>	REH10168	MH024850	MH024886	MH577503	USA	Matheny et al. (2020)
<i>M. subflavospora</i>	NLB1078	MN178515	MN178544	MH577504	Australia	Unpublished
<i>M. subflavospora</i>	TENN:067023	KP641620		KM656119	Australia	Horak et al. (2015)
<i>M. substraminipes</i>	EL12-08	GU980607	GU980607		USA	Cripps et al. (2010)
<i>M. substraminipes</i>	K70-148	GU980601	GU980601		USA	Cripps et al. (2010)
<i>M. subtilior</i>	PERTH:08095388	KP641628	KP171082		Australia	Matheny and Bougher (2017)



Taxa	Voucher	Genbank accession number			Country	Reference
<i>M. squamosodisca</i>	LVK20133	MZ404935	MZ375436		USA	Unpublished
<i>M. subtomentosa</i>	LVK17005	MN178520			USA	Unpublished
<i>M. subtomentosa</i>	PBM2460	MN178521	MN178549	MN203531	USA	Unpublished
<i>M. terrigena</i>	EL24-08	GU980648			USA	Cripps et al. (2010)
<i>M. tomentosula</i>	PBM4138	MG773814	MK421969	MH577506	USA	Matheny et al. (2020)
<i>M. umbrinofusca</i>	Kuhner70-38Type	GU980613			Geneva	Cripps et al. (2010)
<i>M. unicolor</i>	PBM2589	EU523555			USA	Unpublished
<i>M. unicolor</i>	PBM2974	MN178524	JQ313569	MN203532	USA	Unpublished
<i>M. velutina</i>	MSM # 0048	MK990129	MK999927		Pakistan	Saba and Khalid (2020)
<i>M. velutina</i>	MSM # 0049	MK990130	MK999928		Pakistan	Saba and Khalid (2020)
<i>M. velutina</i>	MSM # 0050	MK990131	MK999929		Pakistan	Saba and Khalid (2020)
<i>M. terrigena</i>	EL11704	AM882864	AM882864		Sweden	Ryberg et al. (2008)

In Fig. 1, all members of *Mallocybe* are grouped and divided into four major clades, namely, clades A–D. Fifty-three samples grouped into clade A had a strong support (PP = 1/BP = 94). Of these samples in clade A, while 33 formed a subclade with another strong support (PP = 1/BP = 97), six samples each from *M. arenaria* (Kühner) Matheny & Esteve-Rav., *M. velutina* Saba & Khalid, and *M. tomentosula* Matheny & Esteve-Rav., clustered in a fully supported subclade separated from the others, whereas seven samples from *M. terrigena* (Fr.) Matheny, Vizzini & Esteve-Rav., and *M. fibrillosa* (Peck) Matheny & Esteve-Rav., clustered together, although with a moderate support (PP = 0.85 / BP = 72). Additionally, seven samples from *M. piceae*, *M. arthrocystis* (Kühner) Matheny & Esteve-Rav., *M. fuscomarginata* (Kühner) Matheny & Esteve-Rav., and *M. gymnocarpa* (Kühner) Matheny & Esteve-Rav., were also grouped in a strongly supported (PP = 0.95 / BP = 97) subclade. Contrastively, 11 samples from Australia were grouped in clade B with a full support. Therefore, clades A and B were grouped together with a strong support (PP = 0.99/ BP = 99). Similarly, while 20 samples were grouped into clade C with a full support where our three new species nested, six samples from Old World tropical regions clustered together in a full support clade, namely, clade D.

The Chinese materials formed three independent lineages and were all placed in clade C. Therefore, we labeled the clade the “longicystis clade.” in this study. Seven samples from Hainan Province and one from Yunnan Province also formed a full support lineage, representing *M. longicystis*. Thus, we propose that this lineage is sister to that of *M. aurantiodisca* with three samples from Zhejiang Province. Additionally, two samples of *M. pallidipes* collected from the Jilin Province formed a full support lineage. Hence, they were also proposed as sisters to the subclade, unifying *M.*

*aurantiodisca*, *M. longicystis*, *M. multispora* (Murrill) Matheny & Esteve-Rav., and *M. unicolor* (Peck) Matheny & Esteve-Rav.

## Taxonomy

*Mallocybe longicystis* T. Bau, Y.G. Fan, J.H. Hu & W.J. Yu, sp. nov., Figs. 2–3

**MycoBank:** MB844269

## Etymology

*longicystis* (Latin) refers to its cylindrical cheilocystidia.

## Diagnosis

differs from *M. pallidipes* by the lack of reddish orange tinge in basidiomata, its erected scales in pileus, and more cylindrical cheilocystidia.

**Holotype:** China, Hainan province, Shuiman Township, Wuzhishan City, Wuzhishan area of Hainan Tropical Rain Forest National Park, 18°51' 53" N, 109°40' 43" E, 695 m asl., 28 Jul. 2021, Y.-G. Fan & W.-J. Yu, FYG6374 (FCAS3535), GenBank accession number: ITS (OM179928), LSU (OM135611), and *RPB2* (OM835747).

## Description

Basidiomata small-sized. Pileus 16–30 mm diam. spherical to hemispherical when very young, becoming convex to broadly convex and nearly flattened when mature, sometimes turns up in a wavy shape, without umbo; margin incurved at first, then decurved for a long time, straight when mature, longer than lamellae; surface dry, covered with densely and radially arranged, thick, conical scales, erected towards center, becoming recurved outwards, nearly appressed to appressed-rimulose towards the margin; amber, burnt yellowish (4B6) to yellowish brown (5C7) at the center, darker towards the disc and slightly paler outwards; occasionally with a thin smoky-yellowish (5B6) filamentous veil remnants layer around the disc, sometimes not distinctly. Lamellae 2–4 mm wide, adnexed, crowded, subdecurrent, alternating with 3–4 tiers of lamellula, whitish (3A1) to grayish white (3B1) or dirty white (3B2) when young, beige (5B2), yellowish (5B4) to brownish (5C4) when mature, edges paler and fimbriate. Stipe 19–40 × 2–5 mm, solid at first, becoming fistulose with age, equal, truncate or pestle like and slightly swollen at the base; woolly or feltly from veil remnants, grayish white (3B2) to yellowish white (4C4) when young, yellowish brown (5B5) when mature; partial veil present when young, fugacious. Context solid and fleshy in pileus, white (5A1) to dirty whitish (4B2), 1–2 mm thick at middle radius, 2–3 mm thick at the center, fleshy to somewhat fibrous in the stipe, whitish (5A2) to yellow whitish (3B2), with light yellowish brown (5B4) tinge near the epidermis. Odor lightly sweet, lightly earthy or not distinct.

Basidiospores: [160/8/8] (8.2)8.8–**9.7**–10.2(10.8) × (3.9)4.3–**5.1**–5.6(8.2) µm,  $Q = (1.52)1.59–2.20(2.64)$ ,  $Q_m \pm SD = 1.92 \pm 0.015$ , ellipsoid to oblong, smooth, thick-walled, with blunt or slightly acute apex, golden yellowish to pale yellowish in KOH, apiculus small and indistinct, with one large ellipsoid oily droplet. Basidia 24–34 × 5–9 µm, slenderly clavate to clavate, blunt or rounded at apex, nearly truncate or pestle-like at the base, colorless at the initial stage, then golden yellowish and shriveled, 4- or 2-spored; necropigmented, sterigmata acute, 3–6 µm in length. Pleurocystidia absent. Lamellae edge sterile. Cheilocystidia 35–63 × 5–14 µm ( $n = 50$ ), abundant, in clusters, slenderly clavate or cylindrical-clavate, less often broadly clavate or ventricose, mostly enlarged and rounded at apex, occasionally utriform or ventricose, thin-walled or slightly thick-walled, walls bright yellow. Hymenophoral trama 65–150 µm thick, regular to subregular, yellowish to golden yellowish; trama hyphae 10–30 µm wide, smooth, concave, inflated at both ends of cell, cylindrical, thin-walled or slightly thick-walled, walls bright yellow. Stipitipellis a cutis often extended with irregularly and loosely arranged hyphae, golden yellowish in mass, composed of cylindrical inflated cells, 7–15 µm wide, smooth,

colorless to light yellowish. Stipe trama regularly arranged, light yellowish when aggregated, composed of smooth, cylindrical hyphae, colorless, 5–10 µm wide. Caulocystidia not observed. Pileipellis a cutis with emerged bundles of trichodermally arranged hyphae comprising scales, those bundles 93–140 µm wide, coniform, golden yellowish to yellowish brown when aggregated, composed of cylindrical to inflated encrusted, hyphae 7–18 µm wide, slightly thickened, bright yellow. Pileal trama 250–650 µm wide, subregular, yellowish in mass, composed of fleshy, cylindrical hyphae, colorless, 11–20 µm wide. Oleiferous hyphae 3–5 µm in length of two types: yellowish type often present in pileal trama, with oily inclusions, colorless type more often observed in stipe trama, smooth, with no oily inclusions. Clamp connections present in all tissues.

### Habitat

gregarious, caespitose in small groups or scattered along roadsides under fagaceous trees, on sandy or lateritic soil.

### Distribution

Known from Hainan and Yunnan Provinces, China.

### Specimens examined

China. Hainan Province, Wuzhishan City, Shuiman Town, 18°51' 53" N, 109°40' 43" E, 695 m asl., under fagaceous trees, 26 May 2022, Y.-G. Fan & W.-J. Yu, FYG6972 (FCAS3583), 1 May 2022, Y.-G. Fan & W.-J. Yu, FYG6963 (FCAS3581), FYG6964 (FCAS3582); same locality, 28 Jul. 2021, Y.-G. Fan & J.-H. Hu, FYG6371 (FCAS3533), FYG6373 (FCAS3534), FYG6376 (FCAS3536), Y.-G. Fan, L.-S. Deng, L.-N. Zhao & J.-H. Hu, FYG6378 (FCAS3537), Y.-G. Fan & W.-J. Yu, FYG6880 (FCAS3538), Y.-G. Fan & W.-J. Yu, same locality, 30 Jun 2021, T. Bau & Y.-G. Fan, FYG6501 (FCAS3541), same locality, 02 Aug 2020, MHKMU T. Huang 370 (FCAS3539); Yunnan Province, Kunming City, Kunming Botanic Garden, 25 Sep 2015, Y.-G. Fan & W.-J. Yu, FYG2015407 (FCAS3540).

### Remarks

This species fruits from late April to late September under fagaceous forests in tropical or subtropical China. The umber-colored basidiomata and erected squamules in pileus make it outstanding in the field. The pileus surface also exhibits nearly appressed scales in certain individuals, this phenotypic variation was largely induced by the weather. Microscopically, its basidiospores are mostly elongate-ellipsoid, but distinct larger basidiospores present and probably discharged from bisporic basidia measured 10.5–**11.1**–12.0 × (4.0) 5.0–**5.2**–6.0 µm (n = 21). The cylindrical cheilocystidia are striking and very abundant, a character that is atypical to the genus. *Mallocybe errata* (E. Horak, Matheny & Desjardin) Haelew, a tropical Asian species shares erected squamules in pileus and profile and size of basidiospores, but differs by its hazel brown to golden brown pileus, adnate to marinate-depressed lamellae, more robust stipe measured 10–35 × (3) 4–8 mm, and broadly clavate to vesiculose cheilocystidia (Horak et al. 2015). Phylogenetically, *M. longicystis* is sister to another new species *M. aurantiodisca* discovered in subtropical China and shares a similar outline and size of basidiospores (see description of *M. aurantiodisca*). However, the latter species has reddish orange tinged pileus with tomentose squamules, less cylindrical cheilocystidia, and occurring in subtropical evergreen broad-leaved forests dominated by *Castanopsis*.

*Mallocybe pallidipes* Y.G. Fan, J.H. Hu & W.J. Yu, sp. nov., Figs. 4–5

**MycoBank:** MB844271

### Etymology

pallidipes refers to its pallid stipe.

## Diagnosis

differs from *M. aurantiodisca* by its isabelline pileus, pallid stipes, more cylindrical basidiospores, and an association with *Populus*.

**Holotype:** China, Jilin Province, Changchun City, in the campus of Jilin Agricultural University, 43°48' 16" N, 125°24' 07" E, 220 m asl., under *Populus*, 26 Jul 2019, Y.-G. Fan & W.-J. Yu, FYG3726 (FCAS3542), GenBank accession number: ITS (OM179924); LSU (OM137052) and *RPB2* (OM835749).

## Description

Basidiomata small-sized. Pileus 5–17 mm diam, hemispherical when young, becoming convex to broadly convex or upon expanding, plano-convex to undulate-applanate with age, obtusely umbonate at the disc; margin initially inflexed, then depressed to straight with age; surface dry, fibrillose-tomentose to woolly tomentose with scurfy appressed squamules, not rimose; dirty-yellowish (5B3), brownish yellow (5B4), or ochraceous brown (5B6), darker around the center, paler outwards. Lamellae 3–5 mm wide, adnexed-emarginate, moderately crowded, alternated with 3–4 tiers of lamellulae; initially pale yellowish white (5A3) or pale grayish white (5B2), then yellowish brown (5B4) to brown (5B5) with age; edges pallid and fimbriate. Stipe 14–28 × 1–3 mm, cylindrical, solid at first, then becoming fistulose, beige (5A2) or yellowish white (5B4), sometimes concolorous with pileus; equal, dry, silky from veil remnants. Context dirty white (5A2) and fleshy in pileus, 1–2 mm wide at mid-radius, fleshy-fibrillose and shiny in stipe. Odor unpleasant, somewhat bitter.

Basidiospores [100/4/2] (9.2)10.1–**11.3**–13.1(13.4) × (4.2)4.3–**5.0**–5.2(5.8) µm, Q = (1.88)2.00–2.65(2.84),  $Q_m \pm SD = 2.30 \pm 0.020$ , smooth, thick-walled, yellowish to yellowish brown, very variable in shape, ellipsoid to subphaseoliform, sometimes phaseoliform in side view. Basidia 20–33 × 5–9 µm, clavate to slenderly clavate, necropigmented, 4-spored, sometime 2-spored, with inner olivaceous guttulae; sterigmata 3–5 mm long. Pleurocystidia absent. Lamellae edge sterile. Cheilocystidia 38–65 × 7–14 µm (n = 50), abundant, clavate to slenderly clavate, fusiform or utriform, apex rounded or slightly tapered, base truncate or tapered, colorless and hyaline, thin-walled. Hymenophoral trama 262–735 µm thick, regular to subregular, light yellowish, trama elements 11–16 µm wide, cylindrical to inflated or concave, thin-walled, smooth, hyaline. Stipitipellis a cutis often with extending hyphae, pale yellowish when aggregated, composed of cylindrical expanded hyphae, 6–10 µm wide, encrusted, hyaline. Stipe trama densely arranged, light yellowish when aggregated, composed of smooth, cylindrical hyphae, colorless, 6–11 µm wide. Caulocystidia absent. Pileipellis 90–122 µm thick, a cutis with emerging bundles of hyphae, golden yellow to yellowish brown when aggregated, composed of cylindrical to inflated and encrusted hyphae, 8–18 µm wide, slightly thick-walled, pale yellowish. Pileal trama hyaline, subregular, 300–560 µm thick, composed of several barbell cells or expanded cells of different sizes, 8–16 µm wide. Oieiferous hyphae exist in pileal and stipe trama, hyaline, 2–5 µm wide, with oval or spherical intracellular substances. Clamp connections present in all tissues.

## Habitat

solitary and scattered along roadsides on clay soil under *Populus*.

## Distribution

Known only from the type locality in Jilin Province, China.

## Specimen examined

CHINA. Jilin Province, in the campus of Jilin Agricultural University, 43°48' 16" N, 125°24' 07" E, 220 m asl., under *Populus*, 26 Jul 2019, Y.-G. Fan & W.-J. Yu, FYG3727 (FCAS3543).

## Remarks

*Mallocybe pallidipes* is a rare species collected in the Botanic Garden of Jilin Agricultural University, where there is a temperate climate. It occurs on the roadsides on clay soils in plantations of *Populus* and shrubs. The new species is characterized by Isabella-colored pileus with finely tomentose squamules, pallid stipe with fibrillose-fleshy context, dirty yellowish lamellae, and a bitter smell. Microscopically, its large cylindrical basidiospores, and cylindrical to fusiform cheilocystidia are distinct. Distinct large spores probably discharged from bisporic basidia are unfrequently observed and measured 12–**12.4**–14 × 4–**4.8**–6 µm (n = 27). *Mallocybe aurantiodisca* is similar in having finely squamules in pileus, pallid stipes, cylindrical basidiospores outlines, and elongate cheilocystidia, but differs by its reddish orange tinged basidiomata, narrower lamellae, smaller basidiospores, and ecology in a subtropical forest. *Mallocybe unicolor* (Peck) Matheny & Esteve-Rav. originally described from New York shares subdistant lamellae, fibrillose-fleshy context in stipes, elongate-ellipsoid basidiospores, and long cheilocystidia, but differs by slightly broader basidiospores measured 10–13 × 5–6 µm and most cylindrical to cylindrical-flexuose cheilocystidia (Kuo 2017). *Mallocybe pallidotomentosa* E. Ludw., a European species described from Germany, is similar in outwards appearance and occurs under *Populus* and *Betula*, but it differs in smaller and often phaseoliform basidiospores measured 6.5–9.5 × 4–5 µm and mostly catenate cheilocystidia (Ludwig 2017).

*Mallocybe aurantiodisca* Y.G. Fan, J.H. Hu, W.J. Yu, Y.P. Ge & W.F. Lin, sp. nov., Figs. 6–7

**MycoBank:** MB844273

## Etymology

*aurantiodisca* (Latin) refers to the orange tinge on pileus.

## Diagnosis

differs from *M. longicystis* by its reddish orange pileus with finely tomentose squamules and shorter cheilocystidia.

**Holotype:** CHINA. Zhejiang Province, Lishui City, Liandu District, 28°26' 9" N, 119°54' 14" E, 59 m asl., Under forest dominated by *Pinus*, 3 Jun. 2020. Y.-P. Ge & Q. Na, NJ3396 (FCAS3545), GenBank accession number: ITS (OM179936); LSU (OM138835) and *RPB2* (OM835752).

## Description

Basidiomata small-sized. Pileus 13–25 mm diam, convex when young, becoming plano-convex to broadly convex or upon expanding, becoming plano-convex to undulate-applanate with age, obtusely umbonate at the disc, margin initially inflexed, then deflexed, fibrillose-tomentose to woolly tomentose with scurfy appressed squamules, not rimose; initially brownish with orange tinge (6B4) or orange (6B5) to reddish brown (6B6), becoming pale yellow brown (6C6) or pale ochraceous yellow with orange tinge (6C7) at least around the disc. Lamellae 1–3 mm wide, adnate, narrow, initially pale greyish white (6B2), becoming yellowish white (6B4) to ochraceous brown (6C5), edge whitish (6B3) and fimbriate. Stipe 24–30 × 2–3 mm, cylindrical or slightly tapering towards base, solid at first, then becoming fistulose, dirty white (6A2) to pale yellow (6B5), surface fibrillose with appressed velar remnants, white (6A1) towards the base for the presence of a white (6A1) velipellis, whitish (6A1) cortina present in young basidiomes. Context creamy white (6B2) or pale yellowish white (6A2) in pileus, 1–2 mm thick, concolorous in stipe. Odor indistinct.

Basidiospores [100/5/3] (7.9)8.1–**9.1**–10.2 (11.8) × (4.1)4.2–**5.0**–5.4 (6.2) μm, Q = (1.52) 1.58–2.13 (2.29),  $Q_m \pm SD = 1.85 \pm 0.016$ , smooth, thick-walled, yellowish, thick-walled, ellipsoid, elongate ellipsoid to subphaseoliform. Basidia 27–38 × 6–10 μm, clavate to narrowly clavate, 4-spored, sometimes 2-spored, necropigmented, sterigmata up to 3–4 mm long. Pleurocystidia absent. Lamellae sterile. Cheilocystidia 28–62 × 6–18 μm (n = 52), mean 41 × 11 μm, abundant, subfusiform, subclavate, clavate to slenderly clavate, sometimes fusiform or cylindrical, septate and often constricted at septa, hyaline, thin-walled, Hymenophoral trama 92–141 μm, regular to subregular, colorless or somewhat yellowish, trama elements 13–20 μm wide, inflated or concave, cylindrical, thin-walled, hyaline. Stipitellis a cutis often with extending hyphae, yellowish when aggregated, composed of cylindrical expanded hyphae, 4–8 μm wide, encrusted, yellowish. Stipe trama densely arranged, light yellowish when aggregated, composed of smooth cylindrical hyphae, colorless, 5–8 μm wide. Caulocystidia absent. Pileipellis a cutis often with emerging bundles of hyphae, 98–225 μm thick, brownish to yellowish brown when aggregated, composed of cylindrical to expanded shell hyphae, 9–18 μm wide, slightly thickened, pale yellowish. Pileal trama 246–425 μm thick, hyaline, composed of several barbell-shaped cells or expanded cells of different sizes. Oieiferous hyphae 3–5 μm wide, hyaline, present in the epidermis of pileus and the stipe trama, exist oval or spherical substances. Clamp connections present in all tissues.

### Habitat

solitary or scattered on clay soils under subtropical evergreen broad-leaved forest dominated by *Castanopsis*.

### Distribution

Known from the two localities in Zhejiang Province, China.

### Specimen examined

China, Zhejiang Province, Lishui City, Liandu District., 28°30' 5" N, 119°42' 35" E, 166.4 m asl., in evergreen broad-leaved forests dominated by Fagaceae trees, 4 Aug 2021, Q. Na, NJ3109 (FCAS3544); Hangzhou City, Yutang District, 866 Hangtang Road, Campus of Zhejiang University, 30°18' 33" N, 120°5' 27" E, 666 m asl., under mixed broad-leaved forest, 3 Jun. 2020, W.-F. Lin, 2020ZD01 (FCAS3546).

### Remarks

The new species is known so far from two localities in Zhejiang Province of China, where there is a subtropical monsoon climate. It occurs on clay soils in a subtropical evergreen broad-leaved forest dominated by *Castanopsis* and on the campus of Zhejiang University. *Mallocybe aurantiodisca* is characterized by its reddish orange tinged basidiomata, tomentose-squamulose pileus, elongate-ellipsoid basidiospores, utriform, ventricose to cylindrical cheilocystidia that is usually flexuous. Phylogenetically, it is sister to *M. longicystis*, another new species discovered in tropical China. Both the two species share similar-sized basidiospores. However, the latter has umber colored pileus with erected squamules and more elongate cheilocystidia (see descriptions of *M. longicystis*).

## Discussion

### Major clades in Mallocybe

Kuyper established the subgenus *Mallocybe* in 1986 to accommodate species having necropigmented basidia and thin-walled cheilocystidia that originated from hymenial hyphae (Kuyper 1986). Then, molecular phylogenetic studies confirmed its monophyletic status and proved it as one of the seven major clades in Inocybaceae (Matheny 2005, Matheny et al. 2009, 2020). According to another biogeographic study, since the genus *Mallocybe* (treated as the Mallocybe clade) diversified during the Palaeocene, north temperate radiation was detected in the genus (Matheny et al.

2009). Recent studies on *Mallocybe* have also focused mainly on new species discovery or its ectomycorrhizal associations with plants (Saba and Khalid 2020; Aïgnon et al. 2021; Daskalopoulos et al. 2021). In these studies, certain clades were presented in their molecular phylogeny. However, the infrageneric phylogeny of *Mallocybe* has been less of a concern and should be clarified.

Therefore, this study resulted in a multi-gene phylogeny of *Mallocybe* and revealed four major clades in this genus. As shown in Fig. 1, clade A, a fully supported clade (BP = 1 / BI = 94), comprised 53 samples belonging to at least 28 taxa, all from the north temperate regions, including Europe, North America, and Asia. As a result, this clade was considered the most diverse with major *Mallocybe* taxa. We also observed that the taxa in this clade were associated with diverse plants, including angiosperms and gymnosperms. Currently, although most taxa in this clade were described from Europe and North America, many taxa from East Asia were still undescribed. Interestingly, however, clade B (BP = 1 / BI = 100) comprised 11 samples belonging to at least five known species from Australia. These five species were recorded to have associations with *Eucalyptus*, *Allocasuarina*, and *Accacia* in temperate Australia (Matheny and Bougher 2017). Furthermore, clade B was a sister to clade A, forming a strong support (BP = 0.99 / BI = 96). Alternatively, clade C, whose three new species were nested, was also strongly supported (BP = 1 / BI = 100) and was sister to the superclade comprising clades A and B. Moreover, while this clade (clade C in Fig. 1) comprised 19 samples belonging to six species, we present three new species in this paper. The other three species were from North America. Likewise, clade D was a fully supported clade (BP = 1 / BI = 100) comprising six samples that belonged to two species. A study recently described *Mallocybe africana* Aïgnon, Yorou & Ryberg as species from western Africa but described *M. errata* from Thailand and tropical India (Horak et al. 2015). Accordingly, two north temperate clades; one south temperate clade; and one Old World tropical clade; were retrieved in this study.

### **Species had elongated-ellipsoid basidiospores and long cheilocystidia**

*Mallocybe* species usually have catenae thin-walled cheilocystidia. Accordingly, this study described three new *Mallocybe* species with elongated thin-walled cheilocystidia. Phylogenetically, they were placed in clade C, among which three North American species are worth discussing. While *M. unicolor* was originally described from New York and considered a common species under *Quercus*, which had other broad-leaved trees, it is also widely distributed in eastern North America (Matheny 2014). In a study, while Peck (1897) reported that elongate-ellipsoid basidiospores measured  $8-10 \times 5-6 \mu\text{m}$ , Masee (1904) reported that they measured  $10-13 \times 5-6 \mu\text{m}$  and had long cheilocystidia that exceeded  $75 \mu\text{m}$  in length (Kuo 2017). It has also been reported that *M. multispora* (Murrill) Matheny & Esteve-Rav., a species originally described from Florida (USA), is sister to *M. unicolor* in the phylogeny and occurs in open and mixed woods. However, although it has oblong-ellipsoid basidiospores measuring  $10-13 \times 4-6 \mu\text{m}$ , as reported by Murrill (1945), there is limited information on its other microfeatures. Additionally, two submitted but unpublished sequences (MZ404934 & MN178509) of this species identified by Dr. Matheny were from Florida and Oklahoma (USA), respectively, indicating their subtropical to temperate distribution in North America. Nevertheless, another study by Murrill (1945) reported *M. fulviceps* (Murrill) Matheny & Esteve-Rav. as another species originally described from Florida (USA), sharing elongate-ellipsoid basidiospores that measured  $10-12 \times 5-6 \mu\text{m}$ . Other microcharacters were not mentioned in detail.

Based on current knowledge, clade C is a north temperate clade with a disjunct distribution between East Asia and North America. However, this study further observed three Chinese species distributed from temperate to subtropical or north tropics, including three American species. However, the microfeatures of the two American species, *M. multispora* and *M. fulviceps*, have been far poorly documented in original descriptions. Nevertheless, members of this clade comprise elongate-ellipsoid basidiospores and elongated cheilocystidia, which are atypical to *Mallocybe*.

## **Declarations**

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**Author contribution** Conceptualization: Y-G.F. and T.B. Methodology: Y-G.F. Performing the experiment: J-H.H. Formal analysis: J-H.H., W-J.Y., and L-S.D. Resources: Y-G.F., W-F.L. and T.B. Writing—original draft preparation: J-H.H. and W-J.Y. Writing—review and editing: Y-G.F. and T.B. Supervision: Y-G.F. and T.B. Project administration: Y-G.F. Funding acquisition: Y-G.F. and L-S.D. All authors have read and agreed to the published version of the manuscript.

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**Data availability** The sequence data generated in this study are deposited in NCBI GenBank.

**Ethics approval and consent to participate** Not applicable.

**Conflict of interest** The authors declare that no competing interests.

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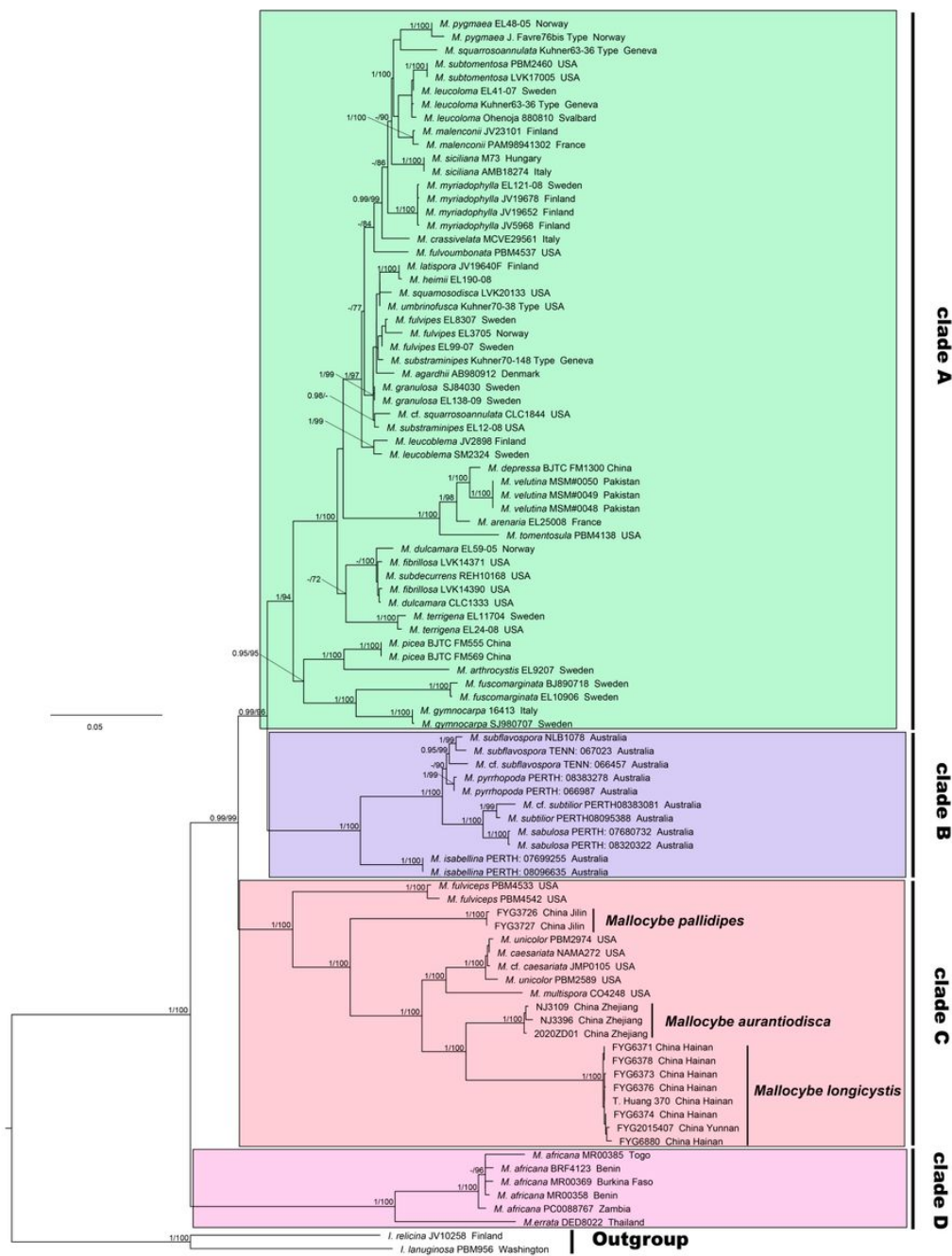
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## Figures



**Figure 1**

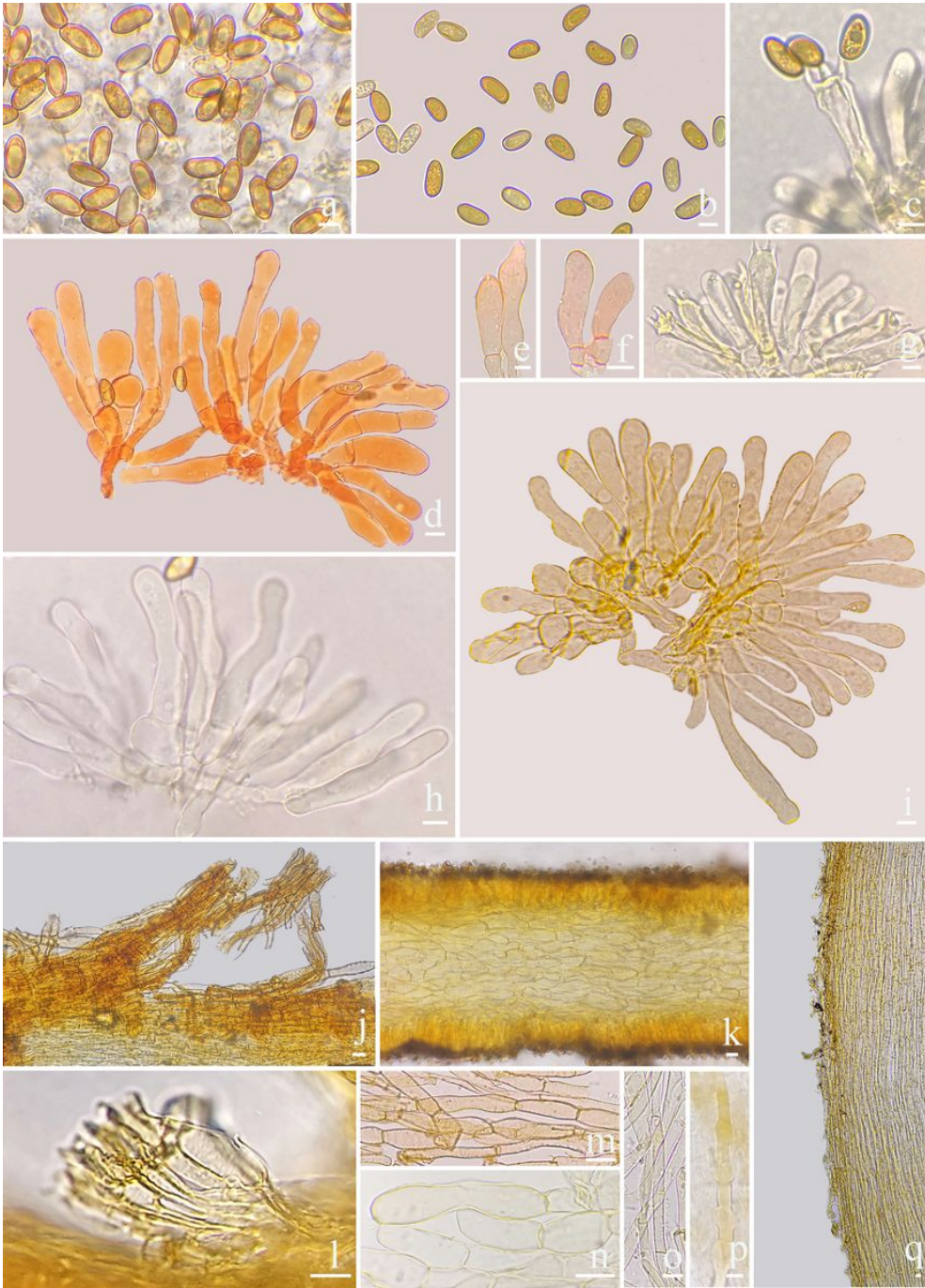
Phylogram generated from the combined dataset sequence of nuclear genes (rDNA-ITS, nLSU, and *RPB2*), rooted with *I. relicina* and *I. lanuginosa*. Bayesian inference posterior probabilities (BI-PP)  $\geq 0.95$  and ML bootstrap proportions ML-BP  $\geq 70$  are expressed by (BI-PP) / (ML-BP), respectively.



**Figure 2**

Basidiomata of *Mallocybe longicystis*. **a–c, e**. Basidiomata. **d, h, i**. Lamellae. **f**. Rimose to rimulose pileus. **g, j, k**. Stipe surface. **a, c, d, f, i–k**: FYG6374 (holotype); **b**: FYG6373; **e, g, h**: FYG6378. Scale bars: a–b, f–i, k = 1 mm; c–e, j = 5 mm. Photos by Y.-G. Fan.





**Figure 3**

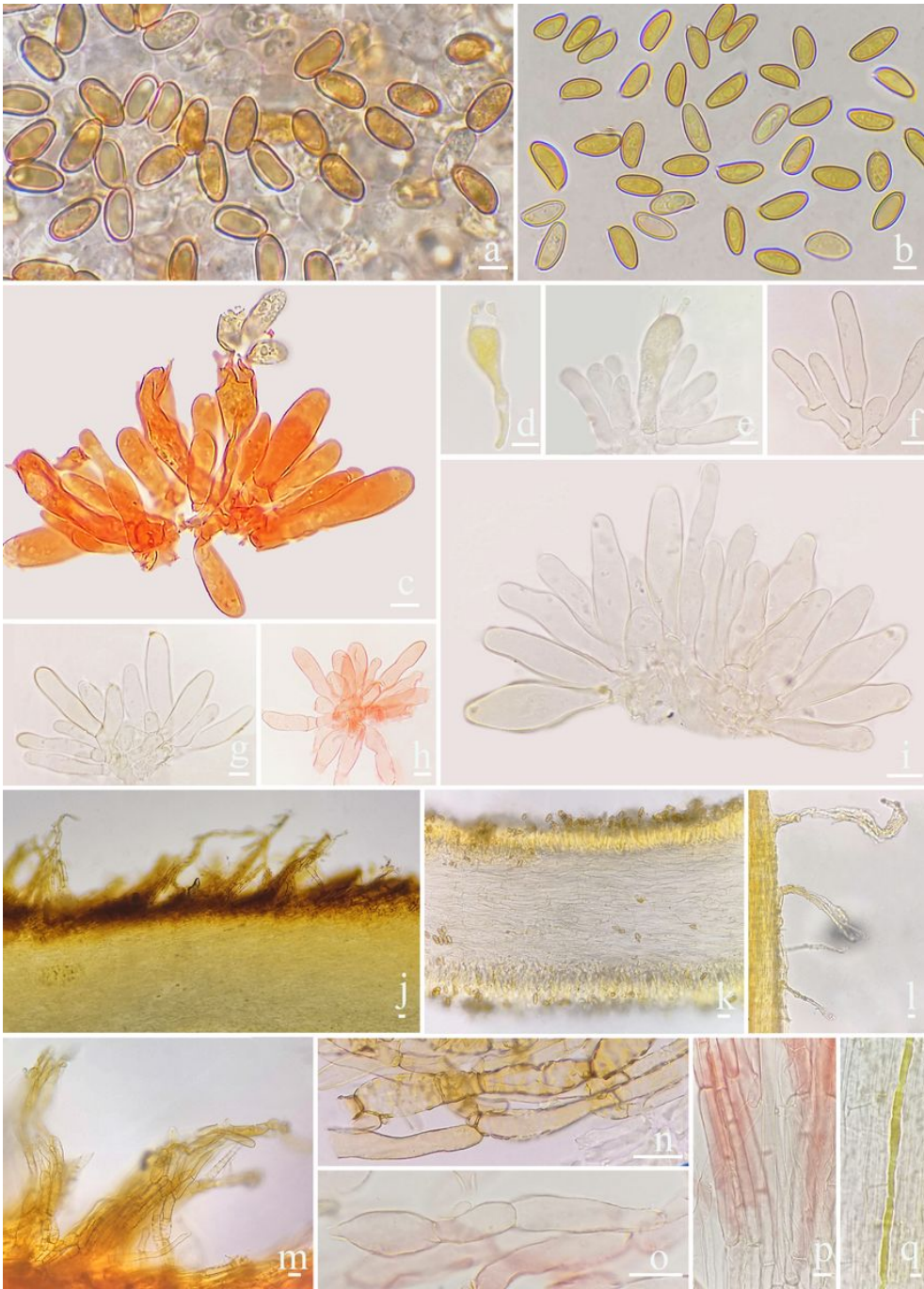
Microscopic features of *Mallocybe longicystis* (FYG6374, holotype). **a–b.** Basidiospores. **c, g.** Basidia. **d–f, h–i.** Cheilocystidia. **j.** Pileipellis. **k.** Transverse section of the lamella. **l.** Terminal hyphae at the pileus. **m.** Pileipellis hyphae. **n.** Hymenophoral trama hyphae. **o.** Stipitipellis hyphae. **p.** Oleiferous hyphae. **q.** Stipitipellis. Scale bars: a–i, p = 5 mm; j–o, q = 20 mm. Photos by J.-H. Hu.



**Figure 4**

Basidiomata of *Mallocybe pallidipes*. **a.** Basidiomata. **b.** Rimose to rimulose pileus. **c.** Lamellae. **d–e.** Stipe surface. **a–c:** FYG3727 (holotype); **d–e:** FYG3726. Scale bars: a, d = 5 mm; b–c, e = 2.5 mm. Photos by Y.-G. Fan.





**Figure 5**

Microscopic features of *Mallocybe pallidipes* (FYG3727, holotype). **a–b.** Basidiospores. **c–e.** Basidia. **f–i.** Cheilocystidia. **j.** Pileipellis and pileal trama. **k.** Transverse section of the lamella. **l.** Stipitipellis. **m.** Terminal hyphae at the pileus. **n.** Pileipellis hyphae. **o.** Hymenophoral trama hyphae. **p.** Stipitipellis hyphae. **q.** Oleiferous hyphae. Scale bars: a–f, q = 5 mm; g–i = 10 mm; j–p = 20 mm. Photos by J.-H. Hu.



**Figure 6**

Basidiomata of *Mallocybe aurantiodisca*. **a.** Basidiomata. **b.** Rimose to rimulose pileus. **c.** Lamellae. **d–e.** Stipe surface. **a–d:** NJ3396 (holotype); **e:** NJ3109. Scale bars: a–e = 5 mm. Photos by Y.-P. Ge.





**Figure 7**

Microscopic features of *Mallocybe aurantiodisca* (NJ3396, holotype). **a–b.** Basidiospores. **d–f.** Basidia. **c, g, h.** Cheilocystidia. **i.** Pileipellis and pileal trama. **j.** Transverse section of the lamella. **k.** Stipitipellis hyphae. **l.** Terminal hyphae at the pileus. **m.** Pileipellis hyphae. **n.** Hymenophoral trama hyphae. **o–p.** Oleiferous hyphae. **q.** Stipe trama. Scale bars: a–b, e–g, o–p = 5 mm; c–d, h = 10 mm; i–n, q = 20 mm. Photos by J.-H. Hu.