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ORIGINAL ARTICLE

The detection of major clades and new species of *Mallocybe* (*Inocybaceae*, *Agaricales*) from China with elongate cheilocystidia

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Abstract
Mallocybe, a member of the ectomycorrhizal mushroom family *Inocybaceae*, is a newly elevated genus based on *Inocybe* subg. *Mallocybe*. Although new species of *Mallocybe* have continuously been discovered worldwide during recent decades, species native to China are poorly documented. Members of the genus are frequently characterized by the presence of phaseoliform basidiospores and short, catenate cheilocystidia. Here, we describe three new *Mallocybe* species from China featuring elongate cheilocystidia that were revealed through morphological and molecular analyses: *M. pallidipes* collected from *Populus* in northeastern China, *M. aurantiodisca* discovered in subtropical evergreen broad-leaved forests dominated by *Castanopsis* in Zhejiang and Guizhou provinces, and *M. longicystis* found in fagaceous forests in tropical and subtropical China. According to a multi-gene phylogenetic analysis, which resolved the genus into three major clades, the three new species group with three North American species in a fully supported clade. Finally, we discuss the systematic position of the new species and infrageneric phylogeny of the genus.

Keywords *Inocybaceae* · Molecular phylogeny · New taxa · taxonomy · China

Introduction

Kuyper (1986) first carried out a morphological cladistic analysis to classify members of the genus *Inocybe* (Fr.) Fr. on the basis of three characters: presence or absence of pleurocystidia, the developmental source of cheilocystidia, and the presence or absence of yellow pigmentation in basidia. *Inocybe* has accordingly been divided into subg. *Mallocybe* Kuyper, subg. *Inosperma* Kühner, and subg. *Inocybe* (Fr.) Fr. (Kuyper 1986; Stangl 1989). With the discovery of diverse new species, the genus has been continuously expanded. As a consequence, Matheny et al. (2020) recently reassigned subg. *Mallocybe* as one of seven genera under *Inocybaceae* Jülich based on a six-gene phylogeny.

Members of *Mallocybe* (Kuyper) Matheny, Vizzini & Esteve-Rav. are characterized by the presence of generally small basidiomata and an often woolly, squamulose pileus that has a noticeably dark appearance upon application of ammonium hydroxide. Other important characteristics are adnate to subdecurrent lamellae with non-reddening

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Jian-Hua Hu and Wen-Jie Yu contributed equally to this work.

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features; phaseoliform, amygdaliform, cylindric to elliptic spores; a small, non-distinctive apiculus; short, thin-walled cheilocystidia originating from hymenophoral trama; and 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. In addition, certain species are associated with the mycoheterotrophic orchid *Epipogium aphyllum* (F. W. Schmidt) Sw. (Roy et al. 2009).

Mallocybe as currently recognized includes nearly all species previously assigned to subg. *Mallocybe*, with 64 entries present in the Index Fungorum database (www.indexfungorum.org, retrieved May 15, 2022). The elevation of *Mallocybe* to the genus rank has been followed by the discovery of new species, five of which were published in the past 2 years (Aïgnon et al. 2021; Bandini et al. 2022; Mao et al. 2022). In East Asia, species in *Mallocybe* have been poorly documented. Four species have been reported in Japan, namely, *M. gymnocarpa* (Kühner) Matheny & Esteve-Rav., *M. malenconii* (R. Heim) Matheny & Esteve-Rav., *M. leucoblema* (Kühner) Matheny & Esteve-Rav., and *M. terrigena* (Fr.) Matheny, Vizzini & Esteve-Rav. (Kobayashi 2002, 2005). One of these species, *M. malenconii*, has also been recently documented in South Korea (Cho et al. 2021). Only five species have been verified in China: *M. depressa* L. Fan, H. Zhou & N. Mao, *M. leucoblema*, *M. leucoloma* (Kühner) Matheny & Esteve-Rav., *M. piceae* L. Fan & N. Mao, and *M. terrigena* (Fan and Bau 2016; Mao et al. 2022). In addition to the scarcity of species described from Asia, relatively little attention has been paid to infrageneric relationships in *Mallocybe* (Matheny et al. 2020).

Species of *Mallocybe* usually have short cheilocystidia which appear in short, catenate, *Opuntia*-like chains. During a study of *Mallocybe* in China, however, collections with elongate-ellipsoid basidiospores and cheilocystidia attracted our attention. According to our phylogenetic and morphological analyses, these species are new to science. In this paper, we therefore describe three new species inferred from morphological studies and a multi-gene molecular analysis of combined nuclear ribosomal internal transcribed spacer region (ITS), the nuclear ribosomal large subunit (nrLSU), and the nuclear second-largest subunit of RNA polymerase II (*RPB2*) sequence data. Finally, we discuss the systematic position and infrageneric relationships of the genus.

Materials and methods

Specimens collected and microscopic observations

Fresh samples were collected from Hainan, Jilin, Yunnan, Guizhou, and Zhejiang Provinces of China. Ecological images were photographed using a digital camera in the field, including measurement data of fruiting bodies sooner 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, the Herbarium of Guizhou Academy of Sciences (HGAS), and the Mycological Herbarium of Kunming Medical University (MHKMU).

Macrofeatures were described based on field notes and digital images. Microscopic observations were conducted using a light microscope (Olympus CX23). Dried specimens were sliced and rehydrated in 5% KOH, and also 1% Congo red solution when necessary. Basidiospores, basidia, hymenophoral trama, cheilocystidia, pileipellis/pileal trama, and stipitipellis/stipe trama were examined and measured. The side views of at least 20 mature 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" collections. The 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. 2021). 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 ± sample standard deviation), was obtained (Na et al. 2022; 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). PCR reactions were conducted using the primer pairs ITS1-F/ITS4 for ITS (Gardes and Bruns 1993), LR0R/LR7 for LSU (Vilgalys and Hester 1990), and RPB2-6F/RPB2-7.1R for *RPB2* (Matheny 2005). Specifically, the PCR amplification setup was a 25 μL mixture comprising 10 μL ddH$_2$O, 12 μL of 2 × Taq Plus MasterMix (Dye), 1 μL of each primer, and 1 μL template DNA. 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 2011; Ariyawansa et al. 2015; Horak et al. 2015; Brugaletta et al. 2017; Matheny and Bougher 2017; Matheny and Kudzma 2019; Aïgnon et al. 2021; Mao et al. 2022) were selected and downloaded from the NCBI database for phylogenetic analyses. Specifically, representatives from *Auritella*, *Inosperma*, and *Tubariomyces* served as outgroups (Matheny et al. 2020). 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). 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). Bayesian analysis (BI) was performed using MrBayes v.3.2.7a (Ronquist et al. 2012). For this analysis, a total of 2,150,000 generations were run using four Metropolis-Coupled Monte Carlo Markov chains to calculate posterior probabilities and the standard deviation of the split frequencies was terminated at 0.009975. 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 14 collections were generated and submitted to GenBank. The final combined dataset comprised 104 samples representing 63 taxa (Table 1) and 3037 nucleotide sites (957 bp ITS, 1420 bp LSU, and 660 bp *RPB2*). For the phylogenetic analysis, the best substitution model for each of the three data partitions was GTR+I+G (lset nst = 6, rates = invgamma; prset statefreqpr = Dirichlet [1,1,1,1]). Because phylogenetic trees inferred from ML and BI analyses were nearly identical, with only a few statistical differences, the optimal ML tree with combined support data is presented in Fig. 1.

In the tree shown in Fig. 1, all members of *Mallocybe* are divided into three major clades (A–C). Clade A, which is only weakly supported (PP = 0.71/BP = 57%), comprises 55 accessions and is divided into three subclades. In the first subclade, 40 accessions are grouped together with strong support (PP = 0.98/BP = 90%). The second subclade, which is moderately supported (PP = 0.74/BP = 82%), contains eight accessions corresponding to *M. arenaria* (Kühner) Matheny & Esteve-Rav., *M. velutina* Saba & Khalid, *M. tomentosula* Matheny & Esteve-Rav., and *M. errata* (E. Horak, Matheny & Desjardin) Haelew. Finally, seven samples from *M. piceae* L. Fan & N. Mao, *M. arthrocystis* (Kühner) Matheny & Esteve-Rav., *M. fuscomarginata* (Kühner) Matheny & Esteve-Rav., and *M. gymnocarpa* (Kühner) Matheny & Esteve-Rav. are grouped in the third, moderately supported subclade (PP = 0.74/BP = 90%). Eleven accessions from Australia are grouped together with full support (PP = 1.0/BP = 100%) in clade B. Similarly, 20 accessions, including our three new species, are fully supported (PP = 1.0/BP = 100%) as members of clade C.

Within clade C, the Chinese materials form three independent lineages. Seven accessions from Hainan Province and one from Yunnan Province, all representing *M. longicystis*, constitute a fully supported lineage that is sister to a subclade consisting of three *M. aurantiodisca* accessions from Zhejiang Province. In addition, two accessions of *M. pallidipes* collected from Jilin Province form a fully supported lineage that is sister to the subclade comprising *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 and 3

MycoBank: **MB**844269

Etymology: refers to its long 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, Wuzhishan City, Shuiman Town, 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. 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

Table 1 Information on taxa used in the phylogenetic analysis

Taxa	Voucher	GenBank accession number			Country	Reference
		ITS	LSU	*RPB2*		
Auritella brunnescens	PBM3174	KJ702344	JQ313571	KJ702349	Australia	Matheny et al. (2020)
A. dolichocystis	T24844		AY380371	AY337371	Australia	Matheny et al. (2020)
A. foveata	TBGT9631	GU062740	GU062739	GU062738	India	Matheny et al. (2020)
A. fulvella	AQ669492	KJ702355	KJ702352	KJ702357	Australia	Matheny et al. (2020)
A. hispida	TH10009	KT378203	KT378207	KT378215	Cameroon	Matheny et al. (2020)
A. robusta	I163	KJ702359	KJ702358	KJ702360	Tasmania	Matheny et al. (2020)
A. serpentinocystis	PBM3188	KJ729858	JQ313559	KJ756402	Australia	Matheny et al. (2020)
A. spiculosa	TH9866	KT378204	KT378206	KT378214	Cameroon	Matheny et al. (2020)
Inocybe dulcamara	CLC1333	GU980635	GU980635		USA	Cripps et al. (2010)
Inoc. dulcamara	EL59-05	GU980643	GU980643		Norway	Cripps et al. (2010)
Inosperma adaequatum	JV16501F	JQ801381	JQ815407	AY333771	Finland	Matheny et al. (2020)
Inos. calamistratum	PBM1105	JQ801386	JQ815409	JQ846466	USA	Matheny et al. (2020)
Inos. calamistratum aff.	SAT9826004	JQ801387	JQ815410	JQ846467	USA	Matheny et al. (2020)
Inos. carnosibulbosum	TBGT12047	KT329448	KT329454	KT329443	Thailand	Matheny et al. (2020)
Inos. misakaense	PC96234	JQ801409	EU569874	EU569873	Zambia	Matheny et al. (2020)
Inos. mutatum	PBM2542	MG773837	AY732212	DQ472729	USA	Matheny et al. (2020)
Inos. rimosoides	PBM2459	DQ404391	AY702014	DQ385884	USA	Matheny et al. (2020)
Inos. virosum	TBGT753	KT329452	KT329458	KT329446	India	Matheny et al. (2020)
Mallocybe agardhii	AB980912	HM209790	HM209790		Denmark	Vauras and Larsson (2011)
M. arenaria	EL25008	FN550937	FN550937		France	Ryberg et al. (2010)
M. aurantiodisca	**2020ZD01**	**OM179937**			**China**	**The present study**
M. aurantiodisca	**NJ3109**	**OM179935**	**OM138834**	**OM835751**	**China**	**The present study**
M. aurantiodisca	**NJ3396**	**OM179936**	**OM138835**	**OM835752**	**China**	**The present study**
M. arthrocystis	EL9207	FN550941	FN550941		Sweden	Ryberg et al. (2010)
M. caesariata	NAMA272	EU819498			USA	Palmer et al. (2008)
M. caesariata	JMP0105	EU819473			USA	Palmer et al. (2008)
M. crassivelata	MCVE29561	MN536812	MN537138		Slovenia	Crous et al. (2020)
M. cf. *squarrosoannulata*	CLC1844	GU980611	GU980611		USA	Cripps et al. (2010)
M. cf. *subtilior*	PERTH:08383081	KP641629	KP171084	KM656125	Australia	Matheny and Bougher (2017)
M. depressa	BJTC FM1300	OM801895	OM801900	OM780099	China	Mao et al. (2022)
M. errata	DED8022		EU569844		Thailand	Matheny et al. (2009)
M. errata	ZT10108 (SFSU)		GQ892935		Thailand	Horak et al. (2015)
M. fibrillosa	LVK14371	MN178498	MN178526	MN203517	USA	Matheny unpublished
M. fibrillosa	LVK14390	MN178499	MN178527	MN203518	USA	Matheny unpublished
M. fulviceps	PBM4533	MZ404928	MZ375430		USA	Matheny unpublished
M. fulviceps	PBM4542	MZ404929	MZ375431		USA	Matheny unpublished
M. fulvipes	EL3705	AM882858			Norway	Ryberg et al. (2008)
M. fulvipes	EL8307	FN550935	FN550935		Sweden	Ryberg unpublished
M. fulvipes	EL99-07	GU980600	GU980600		Sweden	Cripps et al. (2010)
M. fulvoumbonata	PBM4537	MZ404931	MZ375433		USA	Matheny unpublished
M. fuscomarginata	BJ890718	GU980656	GU980656		Sweden	Cripps et al. (2010)
M. fuscomarginata	EL10906	FN550940	FN550940		Sweden	Ryberg et al. (2010)
M. granulosa	EL138-09	KR029727	KR029727		Sweden	Ariyawansa et al. (2015)
M. granulosa	SJ84030	KR029725	KR029725		Sweden	Ariyawansa et al. (2015)

Table 1 (continued)

Taxa	Voucher	GenBank accession number			Country	Reference
		ITS	LSU	*RPB2*		
M. gymnocarpa	16413	JF908161			Italy	Osmundson et al. (2013)
M. gymnocarpa	SJ980707	AM882866	AM882866		Sweden	Ryberg et al. (2008)
M. isabellina	PERTH:07699255	KP171137	KP170915	KJ811581	Australia	Matheny and Bougher (2017)
M. isabellina	PERTH:08096635	KP171138	KP170916	KJ811582	Australia	Matheny and Bougher (2017)
M. latispora	EL190-08	KR029724	KR029724		Not given	Ariyawansa et al. (2015)
M. latispora	JV19640F	MN178503	MN178529	MN203520	Finland	Matheny and Kudzma (2019)
M. leucoblema	JV2898	HM209789	HM209789		Finland	Vauras and Larsson (2011)
M. leucoblema	SM2324	GU980630	GU980630		Sweden	Cripps et al. (2010)
M. leucoloma	Kuhner63-36Type	GU980614			Geneva	Cripps et al. (2010)
M. leucoloma	EL41-07	GU980622	GU980622		Sweden	Cripps et al. (2010)
M. leucoloma	Ohenoja 880810	HM209786	HM209786		Svalbard	Vauras and Larsson (2011)
M. longicystis	**FYG2015407**	**OM179933**			**China**	**The present study**
M. longicystis	**FYG6371**	**OM179926**	**OM135609**	**OM835746**	**China**	**The present study**
M. longicystis	**FYG6373**	**OM179927**	**OM135610**	**OM747850**	**China**	**The present study**
M. longicystis	**FYG6374**	**OM179928**	**OM135611**	**OM835747**	**China**	**The present study**
M. longicystis	**FYG6376**	**OM179929**	**OM135612**	**OM835745**	**China**	**The present study**
M. longicystis	**FYG6378**	**OM179930**	**OM135613**	**OM835748**	**China**	**The present study**
M. longicystis	**FYG6501**	**OM179934**			**China**	**The present study**
M. longicystis	**FYG6880**	**OM179931**	**OM135614**	**OM858853**	**China**	**The present study**
M. longicystis	**HT370**	**OM179932**	**OM135615**		**China**	**The present study**
M. malenconii	JV23101	HM209787	HM209787		Finland	Vauras and Larsson (2011)
M. malenconii	PAM98941302	HM209788	HM209788		France	Vauras and Larsson (2011)
M. multispora	CO4248	MN178509	MN178540		USA	Matheny unpublished
M. myriadophylla	EL121-08	HM209792	HM209792		Sweden	Vauras and Larsson (2011)
M. myriadophylla	JV5968	HM209794	HM209794		Finland	Vauras and Larsson (2011)
M. myriadophylla	JV19652	HM209791	HM209791		Finland	Vauras and Larsson (2011)
M. myriadophylla	JV19678	HM209793	HM209793		Finland	Vauras and Larsson (2011)
M. pallidipes	**FYG3726**	**OM179924**	**OM137052**	**OM835749**	**China**	**The present study**
M. pallidipes	**FYG3727**	**OM179925**		**OM835750**	**China**	**The present study**
M. picea	BJTC FM555	OM801896	OM801901	OM780096	China	Mao et al. (2022)
M. picea	BJTC FM569	OM801897	OM801903	OM780097	China	Mao et al. (2022)
M. pygmaea	EL48-05	GU980628	GU980628		Norway	Cripps et al. (2010)
M. pygmaea	J. Favre76bis Type	GU980629			Norway	Cripps et al. (2010)
M. pyrrhopoda	TENN: 066987	KP308813	KP170983	KM406223	Australia	Matheny and Bougher (2017)
M. pyrrhopoda	PERTH: 08383278	KP308814	KP170984	KM406224	Australia	Matheny and Bougher (2017)
M. pyrrhopoda	PERTH: 08557764	KP308815	KP170986	KM406226	Australia	Horak et al. (2015)
M. sabulosa	PERTH: 07680732	KP308822	JN974916	KM406235	Australia	Matheny and Bougher (2017)
M. sabulosa	PERTH: 08320322	KP308821	KP170994	KM406234	Australia	Matheny and Bougher (2017)
M. siciliana	AMB18274	MG757417	MG757419		Italy	Brugaletta et al. (2017)
M. siciliana	M73	MW354997			Hungary	Csizmar et al. (2021)
M. squarrosoannulata	K63-236 Type	HM209795			Geneva	Vauras and Larsson (2011)
M. squamosodisca	LVK20133	MZ404935	MZ375436		USA	Matheny unpublished
M. subdecurrens	REH10168	MH024850	MH024886	MH577503	USA	Matheny et al. (2020)
M. subflavospora	NLB1078	MN178515	MN178544	MH577504	Australia	Matheny and Bougher (2017)
M. subflavospora	TENN: 067023	KP641620		KM656119	Australia	Matheny and Bougher (2017)
M. substraminipes	EL12-08	GU980607	GU980607		USA	Cripps et al. (2010)

Table 1 (continued)

Taxa	Voucher	GenBank accession number			Country	Reference
		ITS	LSU	*RPB2*		
M. substraminipes	K70-148	GU980601	GU980601		USA	Cripps et al. (2010)
M. subtilior	PERTH: 08095388	KP641628	KP171082		Australia	Matheny and Bougher (2017)
M. subtomentosa	LVK17005	MN178520			USA	Matheny unpublished
M. subtomentosa	PBM2460	MN178521	MN178549	MN203531	USA	Matheny unpublished
M. terrigena	EL24-08	GU980648			USA	Cripps et al. (2010)
M. terrigena	EL117_04	AM882864	AM882864		Sweden	Larsson et al. (2009)
M. tomentosula	PBM4138	MG773814	MK421969	MH577506	USA	Matheny et al. (2020)
M. umbrinofusca	Kuhner70-38 Type	GU980613			Geneva	Cripps et al. (2010)
M. unicolor	PBM2589	EU523555			USA	Matheny unpublished
M. unicolor	PBM2974	MN178524	JQ313569	MN203532	USA	Matheny unpublished
M. velutina	MSM # 0048	MK990129	MK999927		Pakistan	Saba and Khalid (2020)
M. velutina	MSM # 0049	MK990130	MK999928		Pakistan	Saba and Khalid (2020)
M. velutina	MSM # 0050	MK990131	MK999929		Pakistan	Saba and Khalid (2020)
Tubariomyces inexpectatus	AH20390	GU907095	EU569855	GU907088	Spain	Matheny et al. (2020)
T. sp.	BB6018	MK421965	EU600887	EU600886	Zambia	Matheny et al. (2020)

(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 lamellulae, 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, yellow to pale amber towards stipe base; 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 sweety, lightly earthy or not distinct.

Basidiospores: [160/8/8] (8)8.5–**9.7**–10(11) × (4)4.5–**5.1**–5.5(8) µm, Q = (1.52)1.59–2.20(2.64), Q_m ± SD = 1.92 ± 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 wide 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.

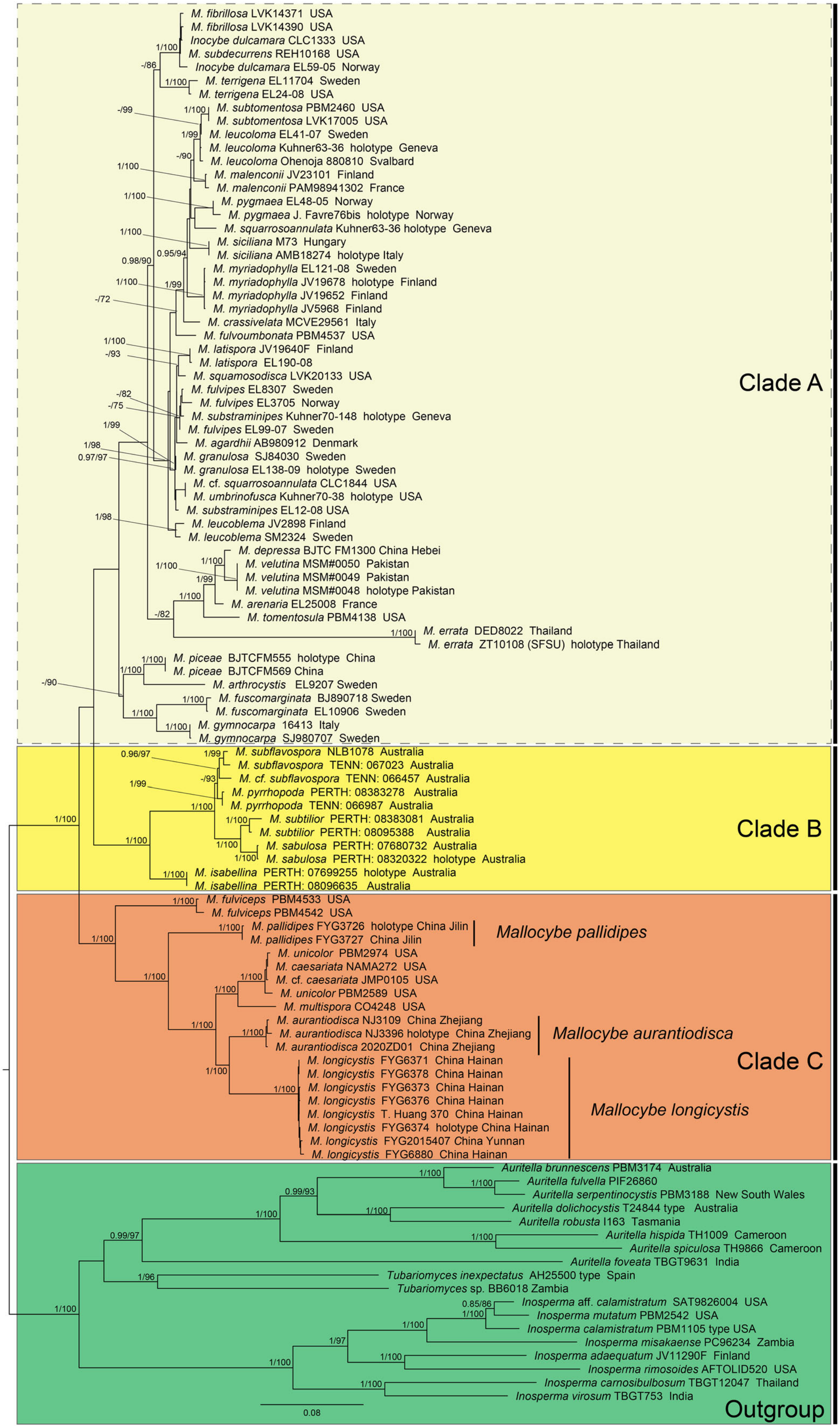

Fig. 1 Phylogram generated from the combined dataset sequence of nuclear genes (rDNA-ITS, nLSU, and *RPB2*). Bayesian inference posterior probabilities (BI-PP) ≥ 0.95 and ML bootstrap proportions ML-BP ≥ 70 are expressed by (BI-PP) / (ML-BP), respectively

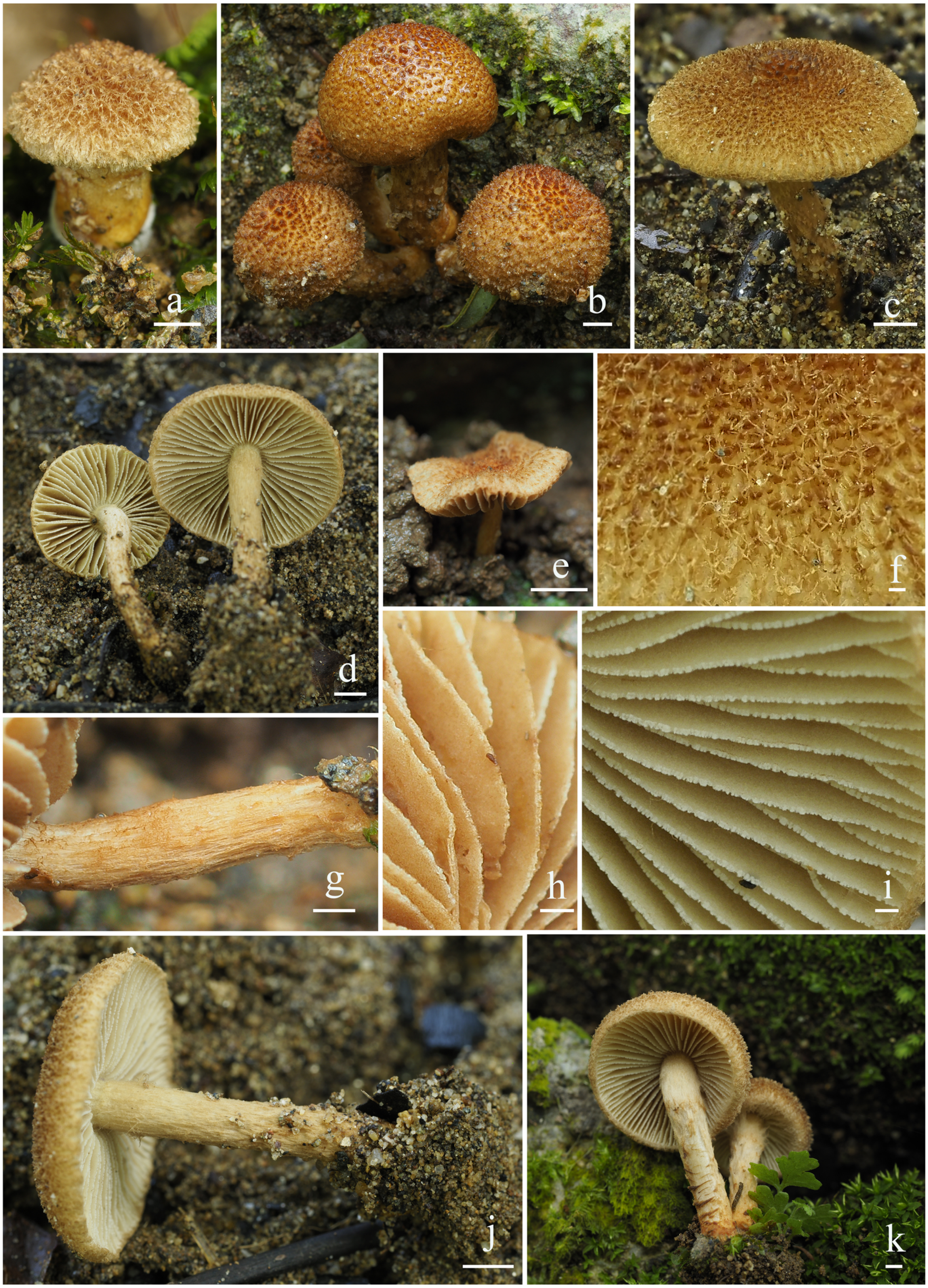

Fig. 2 Basidiomata of *Mallocybe longicystis*. **a**–**c**, **e** Basidiomata. **d**, **h**, **i** Lamellae. **f** Pileus. **g**, **j**, **k** Stipe surface. **a**, **c**, **d**, **f**, **i**–**k** FYG6374 (holotype); **b** FYG6373; **e**, **g**, **h** FYG6378. Scale bars: **a**–**b**, **f**–**i**, **k** = 1 mm; **c**–**e**, **j** = 5 mm. Photos by Y.-G. Fan

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),

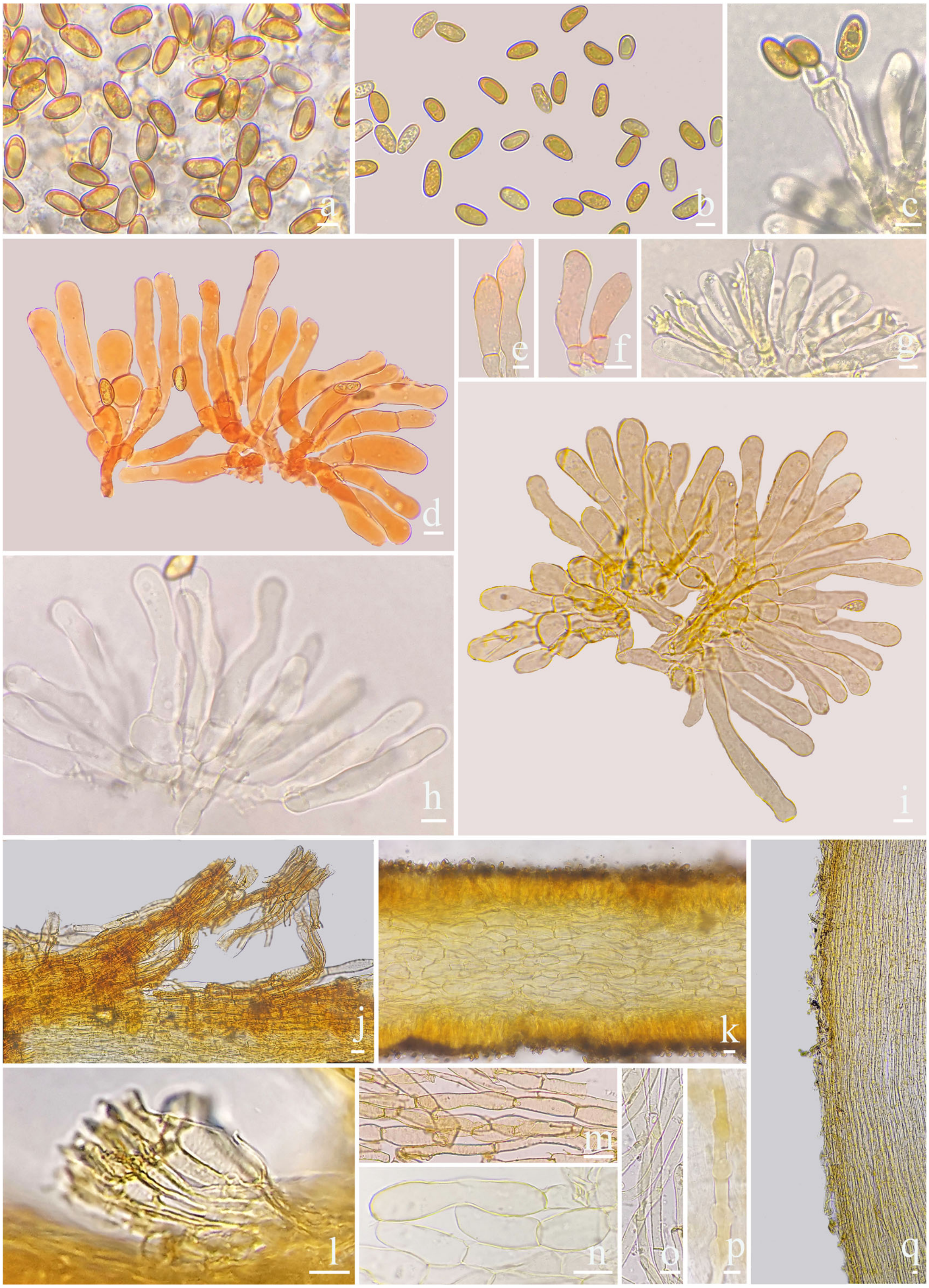

Fig. 3 Microscopic features of *Mallocybe longicystis* (FYG6374, holotype). **a**–**b** Basidiospores. **c**, **g** Basidia. **d**–**f**, **h**–**i** Cheilocystidia. **j** Pileipellis. **k** Transverse section of the lamella. **l** Terminal hyphae at the pileus. **m** Pileipellis hyphae. **n** Hymenophoral trama hyphae. **o** Stipitipellis hyphae. **p** Oleiferous hyphae. **q** Stipitipellis. Scale bars: **a**–**i**, **p** = 5 µm; **j**–**o**, **q** = 20 µm. Photos by J.-H. Hu

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. It usually has erected scales on the disc of the pileus, but certain individual has only appressed squamules on the disc. 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 and 5

MycoBank: MB844271

Etymology: refers to its pallid stipe.

Diagnosis: differs from *M. aurantiodisca* by its isabelline pileus, pallid stipes, more cylindrical basidiospores, and an association with trees of *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 trees of *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. 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 crowed, 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, yellowish (6B5) towards the base; 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, taste bitter.

Basidiospores [100/4/2] (9)10–**11.3**–13(13.5) × (4)4.3–**5.0**–5.5(6) µm, Q = (1.88)2.00–2.65(2.84), $Q_{\mathrm{m}} \pm \mathrm{SD} = 2.30 \pm 0.020$, 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 60–185 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. Oleiferous 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 trees of *Populus* in temperate zone.

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. 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 basidiospore

Fig. 4 Basidiomata of *Mallocybe pallidipes*. **a** Basidiomata. **b** 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

outlines, and elongate cheilocystidia, but differs by its reddish orange tinged basidiomata, narrower lamellae, smaller basidiospores, and ecology in subtropical forest. *Mallocybe unicolor*, originally described from New York, shares fibrillose-fleshy context in stipes, elongate-ellipsoid basidiospores, and long cheilocystidia, but differs in most cylindrical to cylindrical-flexuose cheilocystidia (Kuo 2017). *Mallocybe pallidotomentosa* E. Ludw., a species described from

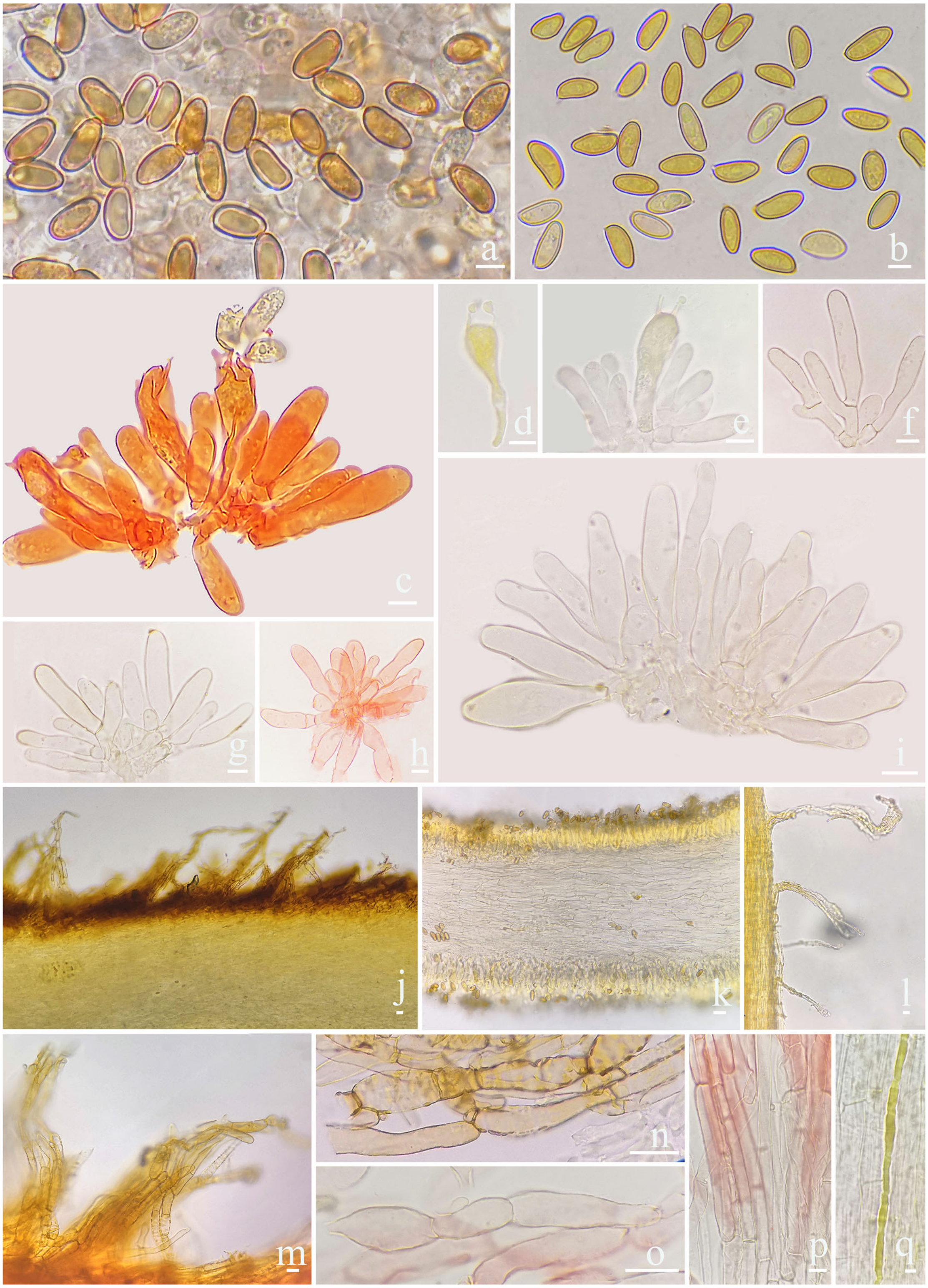

Fig. 5 Microscopic features of *Mallocybe pallidipes* (FYG3727, holotype). **a**–**b** Basidiospores. **c**–**e** Basidia. **f**–**i** Cheilocystidia. **j** Pileipellis and pileal trama. **k** Transverse section of the lamella. **l** Stipitipellis. **m** Terminal hyphae at the pileus. **n** Pileipellis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

Germany, is similar in outwards appearance and occurs under *Populus* and *Betula*, but it differs in smaller and often phaseoliform basidiospores measuring 6.5–9.5 × 4–5 µm and mostly catenate cheilocystidia (Ludwig 2017).

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

MycoBank: MB844273

Etymology: refers to the orange tinge on the disc of the 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. 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 grayish white (6B2), becoming yellowish white (6B4) to ochraceous brown (6C5), edge whitish (6B3) and fimbricate. Stipe 24–30 × 2–3 mm, cylindrical or slightly tapering towards base, solid at first, then becoming fistulose, dirty white (6A2) to pale orange (6B5), surface fibrillose with appressed velar remnants, yellowish (5B5) to pale orange (5B7) towards the base, 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] 8–**9.1**–10(12) ×4–**5.0**–5.5(6) μm, Q = (1.52)1.58–2.13(2.29), $Q_m \pm$ SD = 1.85 ± 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. Stipitipellis 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. Oleiferous 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 in subtropical evergreen broad-leaved forests dominated by *Castanopsis* in subtropical zone.

Distribution: Known from the two localities in Zhejiang Province and one locality in Guizhou 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 Fgaceae 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); Guizhou Province, Tongren City, Jiangkou County, Fanjing Mountain Scenic Area, 27°53′49″N, 108°43′21′′E, 1118 m asl., under fagaceous trees, 2 July 2020, C.Y. Deng, J. Zhang & H. Gao, D2663 (HGAS MF01-9312); Tongren City, Jiangkou County, Taiping Town, Fanjingshan Village, 27°53′49′′N, 108°43′21″E, 1110 m asl., under fagaceous trees, 30 July 2020, C.Y. Deng, J. Zhang & H. Gao, D3188 (HGAS MF01-9582).

Remarks: The new species is known so far from Zhejiang and GuiZhou Provinces of China. 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*. 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* above).

Discussion

Major clades in *Mallocybe*

Kuyper (1986) established the subgenus *Mallocybe* to accommodate species having necropigmented basidia and thin-walled cheilocystidia that originate from hymenial hyphae. Molecular phylogenetic studies have confirmed the monophyletic status of *Mallocybe* and supported its assignment as one of seven major clades in *Inocybaceae* (Matheny 2005; Matheny et al. 2009, 2020). Other recent studies on *Mallocybe* have mainly focused on new species discovery or on ectomycorrhizal associations of this genus with plants (Saba and Khalid 2020; Aïgnon et al. 2021; Daskalopoulos et al. 2021). Although molecular studies have uncovered some

Fig. 6 Basidiomata of *Mallocybe aurantiodisca*. **a** Basidiomata. **b** Pileus. **c** Lamellae. **d**–**e** Stipe surface. **a**–**d** NJ3396 (holotype); **e** NJ3109. Scale bars: **a**–**e** = 5 mm. Photos by Y.-P. Ge

specific clades, infrageneric relationships in *Mallocybe* have not been investigated in depth and require further clarification.

In the multi-gene phylogenetic analysis of *Mallocybe* described in this paper, we identified two strongly supported clades and one weakly supported one. Clade A, which is weakly supported (BP = 0.71/BI = 57) in the tree in Fig. 1, comprises 55 accessions belonging to at least 29 taxa, all from the Northern Hemisphere. We thus consider this clade to be the most diverse in

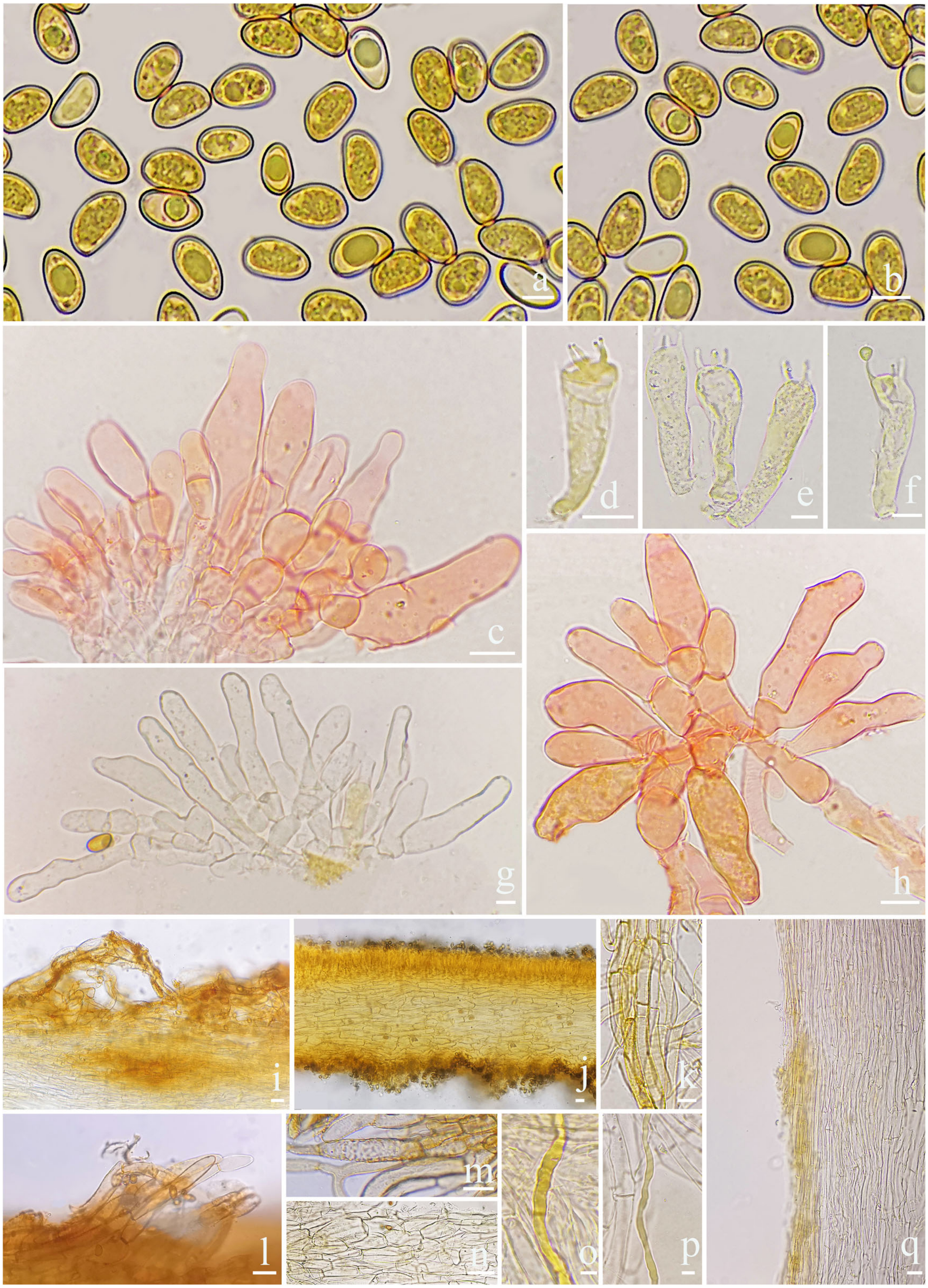

Fig. 7 Microscopic features of *Mallocybe aurantiodisca* (NJ3396, holotype). **a**–**b** Basidiospores. **d**–**f** Basidia. **c**, **g**, **h** Cheilocystidia. **i** Pileipellis and pileal trama. **j** Transverse section of the lamella. **k** Stipitipellis hyphae. **l** Terminal hyphae at the pileus. **m** Pileipellis hyphae. **n** Hymenophoral trama hyphae. **o**–**p** Oleiferous hyphae. **q** Stipe trama. Scale bars: **a**–**b**, **e**–**g**, **o**–**p** = 5 µm; **c**–**d**, **h** = 10 µm; **i**–**n**, **q** = 20 µm. Photos by J.-H. Hu

terms of major *Mallocybe* taxa. We also observed that the taxa in this clade are associated with a diverse range of plants, including angiosperms and gymnosperms. To date, most taxa in this clade have been described from Europe and North America. Few taxa have yet been described from East Asia. Interestingly, clade B (PP = 1/BP = 100%) comprises 11 accessions corresponding to at least five known species from Australia. These five species have been reported to have associations with *Eucalyptus*, *Allocasuarina*, and *Acacia* in temperate/tropical Australia (Matheny and Bougher 2017). Clade C, which includes the three new species described in the present paper, is also strongly supported (PP = 1/BP = 100%) in our phylogenetic tree.

Species with elongate-ellipsoid basidiospores and long cheilocystidia

Mallocybe species usually have catenate, thin-walled cheilocystidia. In this paper, we described three new *Mallocybe* species with elongate, thin-walled cheilocystidia. Our phylogenetic analysis placed these species in clade C along with three interesting North American species. The first species, *Mallocybe unicolor*, originally described from New York, is common under *Quercus* and widely distributed in eastern North America (Matheny 2014). Second, *M. multispora* (Murrill) Matheny & Esteve-Rav., first described from Florida (USA), occurs in open and mixed woods and is sister to *M. unicolor* in the phylogenetic tree. The species has oblong-ellipsoid basidiospores measuring 10–13 × 4–6 μm (Murill 1945). Two unpublished sequences (MZ404934 and MN178509) of *M. multispora* identified by Dr. Matheny were collected in Florida and Oklahoma (USA), respectively, reflecting the subtropical to temperate distribution of this species in North America. Finally, *M. fulviceps* (Murrill) Matheny & Esteve-Rav., originally described from Florida, likewise has elongate-ellipsoid basidiospores measuring 10–12 × 5–6 μm, but detailed morphological features were not provided in the original description (Murrill 1945).

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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., L-P.T., C-Y. D., 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., C-Y.D., 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. The final alignment was included in Supplemental Material.

Declarations

Ethics approval and consent to participate Not applicable.

Conflict of interest The authors declare that no competing interests.

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