



## Species clarification of fairy inkcap ("*Coprinellus disseminatus*") in China

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### ABSTRACT

*Coprinellus disseminatus* and other morphologically similar species are widely dispersed worldwide and are commonly referred to as "fairy inkcap". Based on the molecular phylogenetic study and morphological observation, a thorough investigation was carried out utilising 74 collections of related species that were gathered from seventeen provinces and five Chinese fungaria between 1998 and 2023 and revealed 11 lineages of "fairy inkcap", nine of which were found in China, and which belonged to the two genera *Coprinellus* and *Tulosesus*. In sect. *Disseminati*, genetic diversities ( $\pi$ ), and fixation index (Fst) amongst lineages were computed, and a haplotype-based network was established to ascertain the relationships amongst each clade. A new section of *Coprinellus*, sect. *Aureodisseminati*, were discovered. In addition, four new species (*C. aureodisseminatus*, *C. austrodisseminatus*, *C. parvus*, and *C. velutipes*), a new subspecies of *C. disseminatus*, a new combination (*Tulosesus pseudodisseminatus*), the first discovery of epigamous type of *C. magnoliae* and a new record to China (*T. subdisseminatus*) were also identified and thoroughly described with accompanying illustrations. Their differences in macro- and micro-features, as well as their character sequence, were discussed.

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Taxonomy; phylogeny; species recognition; population genetics; biogeography; DNA barcoding


## 1. Introduction

The genus *Coprinellus* P. Karst, a notable member of coprinoid fungi, is classified under the family Psathyrellaceae of the order Agaricales (Basidiomycota). Wächter and Melzer (2020) divided *Coprinellus* into nine sections, with one of them being named sect. *Disseminati*, containing species with charming names such as "fairy inkcap" or "fairies bonnets". Currently, three legitimate species have been identified (*C. disseminatus*, *C. disseminatus-similis*, and *C. magnoliae*), along with more than five phylopecies confirmed through recent studies, as do not cluster with any known species (Hussain et al. 2018; Wächter and Melzer 2020; de Silva et al. 2021). Species in this section exhibit tiny to small, pale basidiomata and stand out from other coprinoid fungi due to their non-deliquestent lamellae (Wächter and Melzer 2020). They are typically found in large groups on living trees, stumps, rotten wood, and surrounding soil. While they predominantly exist as saprophytes, they also form mycorrhiza associations with orchid plants (e.g. *Cremastra appendiculata*) and aid in their seed germination (Yagame et al. 2008; Gao et al. 2022).

As the type and representative species of this section, *Coprinellus disseminatus* (Per.) J.E. Lange was initially recorded by Schaeffer (1774) (as *Agaricus pallescens* or *Agaricus digitaliformis*). Schaeffer described this species as having small basidiomata, conical greyish-brown pileus with radial stripes, slender white stipes, without rings, and growing in large clusters. Bulliard (1790–1798) illustrated the macroscopic morphology of this species (as *Agaricus digitaliformis*), showing a light brownish-yellow pileus. Based on Schaeffer's description, Persoon (1801) formally named it *Agaricus disseminatus* (dis-, as in all directions, and -seminare, meaning to propagate) due to its prolific nature. In 1821, Gray further categorised it within *Coprinus*. However, this species was chosen as the lectotype for *Psathyrella* (Clements and Shear 1931) and was also thought to belong to the genus *Psathyrella* due to its non-deliquestent traits (Quélet 1872). By dividing the non-autolysed species of *Coprinus*, Kühner (1928) established *Pseudocoprinus*, and this species was selected as the type of this new genus. For its small-sized basidiomata, Lange (1938) originally ascribed it to *Coprinellus*; however, he

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subsequently concurred with Kühner's assessment (Lange 1939). Given that their pseudoparaphyses are not as inflated as those of other coprinoid fungi, he thought that this species represented a transitional group between *Psathyrella* and *Coprinus*. In 1978, Kühner and Romagnesi classified it under the *Coprinus* sect. *Setulosi* according to the presence of both pileocystidia and caulocystidia; Uljé et al. (2005) also accepted this categorisation.

Based on the phylogenetic results obtained by Hopple et al. in 1994 and 1999, Redhead et al. (2001) confirmed the taxonomic status of the genus *Coprinellus*, which includes *C. disseminatus* and *C. micaceus* (Bulliard) Vilgalys, Hopple & Jacq. Johnson. These species share common characteristics such as the presence of veils (mostly composed of globose elements) and/or lageniform cystidia on the pileus. Nagy et al. (2012) confirmed the polyphyletic nature of haired coprinoid fungi through phylogenetic analysis and demonstrated the close relationship between *C. disseminatus* and *C. micaceus*, suggesting removing *C. disseminatus* from sect. *Setulosi* and placing it into sect. *Micacei*, which has a veil in the form of glistening mica-like granules (composed of globose cells microscopically) introduced by Schafer (2010). These findings were further validated by phylogenetic studies conducted by Hussain et al. (2018), who also discovered the second "fairy inkcap", *C. disseminatus-similis*, which is currently only found in Pakistan. Recently, Wächter and Melzer (2020) established sect. *Disseminati* due to distinctive morphological differences and long divergence in phylogenetic frameworks between this section and other species in sect. *Micacei*. They proposed that this section could be characterised by a veil composed of chains of pigmented thick-walled subcylindrical or globose cells, the absence of pleurocystidia, the presence of large-sized pileocystidia and caulocystidia, and the absence of clamp connection.

Our team previously reported a widely distributed species in the Northern Hemisphere, *Coprinellus pseudodisseminatus* M. Huang & T. Bau, which is macroscopically almost indistinguishable from *C. disseminatus*, not only due to the similar size and colour of their basidiomata, but also due to the minute hairs on their pileus and stipes. This species is also common on living standing trees and rotten wood (Huang and Bau 2018). However, compared to *C. disseminatus*, it has a veil

composed of narrow, branched cells and presents clamp connections, contradicting the description of sect. *Disseminati*, indicating that the taxonomic attribution has yet to be resolved. In addition, the number of sect. *Disseminati* members present a challenging issue. Ko et al. (2001) noticed that "*C. disseminatus*" collected from Hawaii and East Asia involved at least three species using ITS sequences. James et al. (2006) found that Japanese homokaryons of "*C. disseminatus*" were unable to mate with any of them from Europe and North America, indicating potential differences in species. Additionally, we have encountered some undetermined specimens, though with obvious divergence from *C. disseminatus* collected from Europe, which were still treated as the latter, further suggesting potential species diversity within the so-called "*C. disseminatus*" in China (Hubregtse 2019; Wächter and Melzer 2020; Zhu et al. 2022).

Evolutionary divergences result in differentiation among populations, subspecies, species, and other higher classification units (Dobzhansky 1940). Population genetics studies the structure within and between lineages, while phylogenetics reconstructs relationships and evolution patterns. Taxonomy, on the other hand, classifies, nominates, and describes operational taxonomic units. Elucidating population structures, divisions, and relationships is crucial for understanding speciation and species delimitation (Wiens 2007). Such combined studies of taxonomy, phylogeny and population genetics have been extensively utilised in research on plants, animals and microorganisms (Huysse et al. 2005; Pinzón and Lajeunesse 2011; Medrano et al. 2014; Ikabanga et al. 2017; Winker 2018; Folt et al. 2019; Dvořák et al. 2023), while the integration of such approaches is rare in macro-basidiomycetes (Liang et al. 2009; Jargeat et al. 2010; Li et al. 2017; Wang et al. 2018). Species recognition in sect. *Disseminati* remains ambiguous, and a comprehensive study could enhance our understanding of the evolutionary histories of these lineages at the species level and below.

The objectives of this study were to 1) reconstruct a phylogenetic framework to verify the attribution of so-called "fairy inkcap"; 2) clarify the taxonomic status of lineages in sect. *Disseminati*; and 3) identify morphological, geographical, and other characteristics to distinguish species of "fairy inkcap" in China.



## 2. Materials and methods

### 2.1. Sampling and morphological characterization

A collection of “fairy inkcap” specimens from various regions in China was conducted over more than 25 years, from 1998 to 2023. The samples were gathered in Heilongjiang Province, Jilin Province, Inner Mongolia Autonomous Region, Shaanxi Province, Xizang Autonomous Region, Sichuan Province, Chongqing City, Guizhou Province, Yunnan Province, Jiangsu Province, Shanghai City, Hunan Province, Zhejiang Province, Guangxi Zhuang Autonomous Region, Hainan Province, and Guangdong Province of China. During fieldwork, the specimens were photographed, tagged, and accompanied by ecological information. The photos were aimed to capture multiple basidiomata and provide comprehensive details such as habitat, pileus, lamellae, and stipes. Colour descriptions were based on the Methuen Handbook of Colour (Kornerup and Wanscher 1978). The specimens were desiccated using silica gel for at least 12 h and stored in zip-lock bags. Voucher specimens were deposited in the Herbarium of Mycology of Jilin Agricultural University (HMJAU).

The detailed characteristics of the specimens were observed under stereoscope (Stemi 2000C, Zeiss Co. Ltd., Jena, Germany), including examining several large and small lamellae and the base of the stipe. Hand-sectioned slices were studied under a light microscope (BX53, Olympus Co. Ltd., Tokyo, Japan). Water and 5% aqueous KOH were used to prepare slides, with additional staining applied if necessary using 1% Congo Red solution or 1% phloxine B stain. Microscopic features, including the size, shape, and colour of basidiospores, basidia, pseudoparaphyses, cheilocystidia, pleurocystidia, pileocystidia, caulocystidia, pileipellis, stipipellis, gill trama, stipe trama, and hyphae of mycelial rhizomorphs, were measured. At least 40 structures for new species and 20 for known species were examined, and the presence of clamp connection was observed in each sample. Free mature basidiospores collected from the surface of the pileus or stipes were selected for observation in front view and/or side view using 1,000× magnification and measured with software EP viewer (Olympus Co. Ltd., Japan) with a precision of 0.01 µm. The germ pore diameter was also measured and the length of spores were excluding the hilum under any circumstance. The results of the measurements were presented in the form of (a) b–c

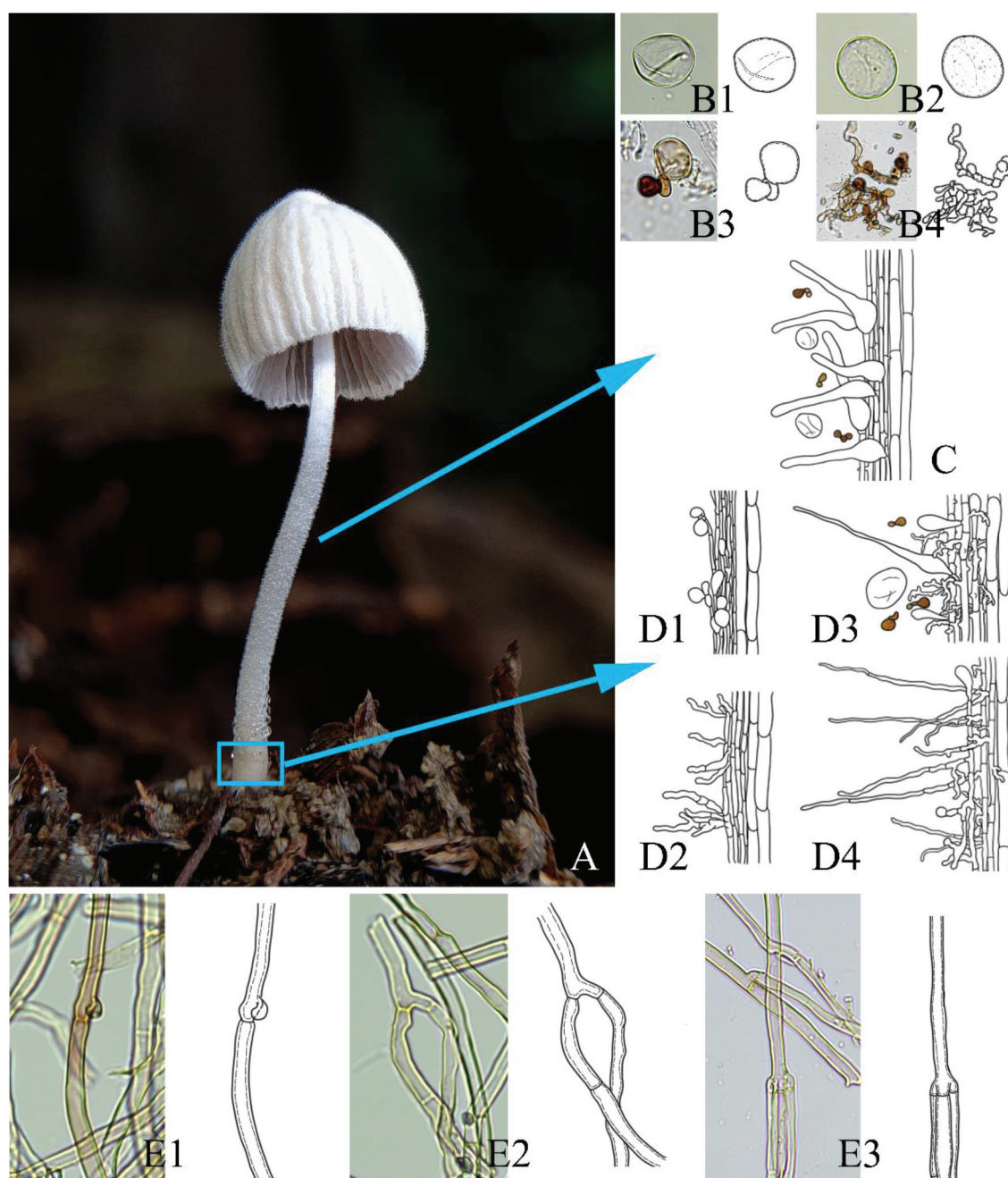
(d), where b–c represented the 90% confidence interval; (a) and (d) represented minimum and maximum values, respectively. Basidiospore sizes were presented as follows: Length range × breadth range × width range. The Q values were calculated as the ratio of length divided by width; when measuring breadth range, Q1 was calculated as the ratio of length divided by breadth range, and Q2 was calculated as the ratio of length divided by width (Ujlé and Bas 1991; Nagy et al. 2011). The shape terms corresponding to the Q value were described following Bas (1969). Terminology for descriptive terms followed Vellinga (1988) and Cléménçon (2012). Other structures were measured and described using 400× magnification. For basidia, the length of sterigma was excluded from the measurement; the measured values of cystidia and veil elements included the amorphous incrustation on the surface; the value of the widest point was chosen as the widest length of cystidia and basidia. The mycelial rhizomorphs referred to thick-walled, red-brown, or yellow-brown mycelia at the base of stipes, which were previously studied by Buller (1924). Additionally, percurrent, thin-walled hyphae harbouring these mycelial rhizomorphs were also recorded if present. Pseudoclamp or short branches near septa resembling clamp connection, along with different types of elements of veil and caulopellis at the lower part of stipes, were first photographed and illustrated. Figure 1 provides a detailed view of these structures.

### 2.2. DNA extraction, PCR amplification, and DNA sequencing

DNA extraction, PCR amplification, and sequencing procedures followed established protocols by Bau and Yan (2021), Mou and Bau (2021), and references therein. The ITS and LSU regions were amplified using specific primers, namely ITS1F/ITS4 (White et al. 1990) and LR0R/LR7 (Hopple and Vilgalys 1994), respectively. Sangon Biotech Co. Ltd. (Shanghai, China) conducted the DNA sequencing, and all newly generated sequences were deposited in GenBank ([www.ncbi.nlm.nih.gov/genbank](http://www.ncbi.nlm.nih.gov/genbank)) (Table 1).

### 2.3. Alignment and phylogenetic analyses

Newly generated sequences were edited using Sequencher 4.1.4 (Gene Codes, Ann Arbor, MI, USA), and haplotypes of heterozygotes were resolved based



**Figure 1.** Illustration of part morphological features covered in this study. (A) Basidiomata (represented by *Coprinellus parvus* HMJAU67155); (B) Veil elements: (B1) Smooth colorless globose cells; (B2) Encrusted colorless globose cells; (B3) Chains of brown (sub)globose cells; (B4) Chains of brown cylindrical cells. (C) Vaulopellis of middle-upper part of stipes. (D) Caulopellis of lower part of stipes: (D1) Only with (sub)globose or utriform terminal elements; (D2) Narrow cylindrical terminal elements with short branches; (D3) Mixed with utriform and short-branched cylindrical elements; (D4) Mostly with long-branched terminal cells. (E) Pseudoclamps or short branches near septa which resembling clamp connections: (E1) pseudoclamp; (E2) short branch resembling clamp connections; (E3) verticillate short branches resembling clamp connections. Bars: A = 1 cm; B1–B4, C, D1–D4 = 20  $\mu$ m; E1–E3 = 10  $\mu$ m.

on Hughes et al. (2013). Missing or ambiguous loci were denoted as “N”. Additional sequences for phylogenetic analyses were retrieved from GenBank following Thorn et al. (1996), Keirle et al. (2004), Lygis et al. (2005), Larsson and Örstadius (2008), Arhipova et al. (2011), Bakys et al. (2011), Nagy et al. (2010, 2011, 2012), Tóth et al. (2013),

Örstadius et al. (2015), Desjardin and Perry (2016), Huang and Bau (2018), Hussain et al. (2018), Yan and Bau (2018), Wächter and Melzer (2020), Bau and Yan (2021), de Silva et al. (2021), Schafer et al. (2022), Wang et al. (2022), and Zhu et al. (2022) (Table 1). The combined dataset was aligned with MAFFT v.7.245 (Katoh and Standley 2016)



**Table 1.** Fungal species and sequences used in phylogenetic analyses.

Species	Seq.-ID	Location	ITS	LSU	Reference
<i>Brizeliomyces multipedata</i>	LÖ237-04	Sweden	KC992888	KC992888	Örstadius et al. 2015
<i>B. supernula</i>	LÖ250-04	Sweden	KC992867	KC992867	Örstadius et al. 2015
<i>Candolleomyces candolleanus</i>	LÖ38-00	Sweden	DQ389720	DQ389720	Larsson and Örstadius 2008
<i>Candolleomyces luteopallida</i>	Sharp20863 (type)	Sweden	KC992884	KC992884	Örstadius et al. 2015
<i>Candolleomyces subsingeri</i>	HMJAU37811	China	MG734715	-	Yan and Bau 2018
<i>Coprinellus aureodissemminatus</i>	HMJAU67119 (JIM43)	China-Shanghai	OR436416	OR436373	This study
	HMJAU67120 (ZJQY1)	China-Zhejiang	OR436414	OR436374	This study
	HMJAU67121 (YH076)	China-Yunnan	OR436415	OR436375	This study
	E145121	Ecuador	KM265563	-	Wächter and Meizer 2020
<i>C. aureodissemminatus</i>	PERTHE8297	USA	MK077862	-	-
	NLB 1363	Australia	MT537065	-	-
	E8297	Australia	MT537045	-	-
	420526MF0012	China-Jiangsu	MG719770	-	-
	RF21	China-Guizhou	OP902415	-	-
	9Y-G71	China-Guizhou	MT138591	-	-
<i>C. aureogramulatus</i>	CBS973.95	The Netherlands	GQ249274	GQ249283	Nagy et al. 2011
<i>C. aureogramulatus</i>	HMJAU67111	China-Guangdong	OR436413	OR436376	This study
<i>C. austrodissimminatus</i>	HMJAU25112	China-Hunan	OR436394	OR436377	This study
	HMJAU67134	China-Guangdong	OR436393	OR436378	This study
<i>C. curtoides</i>	SFSU DEH630	Hawaii (USA)	AY461834	-	Keirle et al. 2004
<i>C. curtus</i>	SZMC-NL-1490	Hungary	JN159569	JN159589	Nagy et al. 2011
<i>C. deminutus</i>	SZMC-NL-0761	Hungary	JN159572	JN159592	Nagy et al. 2011
<i>C. disseminatus</i>	LE-BIN 2127	Russia	MG722732	-	Wächter and Meizer 2020
	SZMC-NL-0786	Hungary	JN159560	-	Nagy et al. 2011
	863	Lithuania	GU934607	-	Bakys et al. 2011
	I241	Latvia	GU062268	-	Ahipova et al. 2011
	olrim (SUAS)	Lithuania	AY787669	-	Lygis et al. 2005
	R175	Sweden	JN689938	-	Wächter and Meizer 2020
<i>C. disseminatus</i> subsp. <i>orientalis</i>	HMJAU22008	China-Jilin	OR436408	OR436379	This study
<i>C. disseminatus</i> subsp. <i>orientalis</i>	HMJAU67127	China-Shanxi	OR436412	-	This study
	HMJAU67128	China-Jilin	OR436409	-	This study
	HMJAU67129	China-Jilin	OR436410	-	This study
	HMJAU67130	China-Jilin	OR436411	OR436380	This study
	KUC11047	China	KJ714005	-	Wächter and Meizer 2020
<i>C. disseminatisimilis</i>	SHCr3w (type)	Pakistan	MH753670	-	Hussain et al. 2018
	SWAT SH-Cr3-b	Pakistan	MH753669	-	Hussain et al. 2018
<i>C. domesticus</i>	SZMC-NL-1292	Hungary	FN396102	HQ847132	Nagy et al. 2011
<i>C. flocculosus</i>	SZMC-NL-1567	Hungary	FN430683	JN159593	Nagy et al. 2011

(Continued)

Table 1. (Continued).

Species	Seq-ID	Location	ITS	LSU	Reference
<i>C. heptemerus</i>	X-22	USA	KC176321	KC176321	Thorn et al. 1996
<i>C. magnoliae</i>	MFLUCC 18-0942 WZ-433	Thailand	MW244022	–	de Silva- et al. 2021
	HMJAU67122 (Z21062505)	China-Jiangsu	OP163480	–	–
	HMJAU46307	China-Guangxi	OR436401	OR436383	This study
	HMJAU49305	China-Guangdong	OR436399	OR436381	This study
	WkRe_2	China-Hainan	OR436400	OR436382	This study
<i>C. micaceus</i>	SZMC-NL-3656	China-Taiwan	KC416185	–	–
<i>C. parvus</i>	HMJAU46315	Hungary	JN159567	JN159588	Nagy et al. 2011
	HMJAU46320	China-Guangdong	OR436404	OR436384	This study
	HMJAU46323	China-Guangxi	OR436402	OR436385	This study
	HMJAU67132	China-Guangxi	OR436403	OR436386	This study
	HMJAU67133	China-Guangdong	OR436406	OR436387	This study
<i>C. radians</i>	SZMC-NL-3986	China-Guangdong	OR436405	–	This study
<i>C. silvaticus</i>	SZMC-NL-3035	Hungary	JN943117	JN159594	Nagy et al. 2011
<i>C. sp.</i>	ZD1102-1	Hungary	HQ846986	HQ847072	Nagy et al. 2011
<i>C. sp.</i>	BAB-3624	USA	KC514901	–	Wächter and Melzer 2020
<i>C. sp.</i>	BLBS 107	India	KU504290	–	Wächter and Melzer 2020
<i>C. sp.</i>	DWM51	Brazil	MK843955	–	Wächter and Melzer 2020
<i>C. sp. (as "C. disseminatus")</i>	SZMC-NL-1101	China-Yunnan	KM357334	–	Wächter and Melzer 2020
<i>C. truncorum</i>	HMJAU67123	Hungary	JN159562	FM876262	Nagy et al. 2010
<i>C. velutipes</i>	HMJAU67124	China-Zhejiang	OR436398	–	This study
<i>C. velutipes</i>	HMJAU67125	China-Jiangsu	OR436396	–	This study
	HMJAU67126	China-Hunan	OR436397	OR436388	This study
	SZMC-NL-2146	China-Hunan	OR436395	OR436389	This study
<i>C. verrucispermus</i>	SFSU BAP 619 (type)	Hungary	JN159577	–	Nagy et al. 2011
<i>Coprinopsis afronivea</i>	SZMC-NL-0564	Sao Tome and Principe	NR_148105	–	Desjardin and Perry 2016
<i>Coprinopsis sclerotiorum</i>	SZMC-NL-0774A	Hungary	HQ847039	HQ847124	Nagy et al. 2011
<i>Coprinopsis strossmayeri</i>	Ramsholm800927	Hungary	HQ847048	HQ847129	Nagy et al. 2012
<i>Cystogargaricus hirtosquamulosus</i>	WUJ22833	Sweden	KC992945	KC992945	Örstadius et al. 2015
<i>Hausknechtia floriformis</i>	HMJAU37802 (type)	Vanuatu	JX968254	JX968371	Wächter and Melzer 2020
<i>Heteropsathyrella macrocystidia</i>	HFJAU1352 (type)	China	MW405102	MW413359	Bau and Yan 2021
<i>Iugisporipathyra reticulopilae</i>	LÖ223-90	China	ON207138	ON207137	Wang et al. 2022
<i>Kauffmania larga</i>	HMJAU67114	Sweden	DQ389694	DQ389694	Larsson and Örstadius 2008
<i>Narcissea cordispora</i>	HMJAU67113	China-Zhejiang	OR436423	–	This study
	HMJAU67112	China-Zhejiang	OR436424	–	This study
	HMJAU46343	China-Jilin	OR436425	–	This study
<i>N. ephemerioidea</i>	HMJAU67115	China	MW832859	OL375252	Zhu et al. 2022
<i>N. patouillardii</i>		China	OR436422	–	This study

(Continued)





Table 1. (Continued).

Species	Seq.-ID	Location	ITS	LSU	Reference
<i>Psathyrella amygdalinospora</i>	HMJAU67116	China	OR436421	–	This study
<i>P. fagetophila</i>	HMJAU46343 (type)	China	MW405104	MW413361	Bau and Yan 2021
<i>P. fennoscandica</i>	LÖ210-85 (type)	Sweden	KC992902	KC992902	Örstadius et al. 2015
<i>P. noli-tangere</i>	LÖ484-05 (type)	Sweden	KC992903	KC992903	Örstadius et al. 2015
<i>P. seminuda</i>	LÖ83-03 (neotype)	Sweden	DQ389713	DQ389713	Larsson and Örstadius 2008
<i>P. warrenensis</i>	Smith34091 (type)	USA	KC992907	–	Örstadius et al. 2015
<i>Punjabia pakistanica</i>	Smith70162 (type)	USA	KC992906	–	Örstadius et al. 2015
<i>Tulosesus amphithallus</i>	LAH35323 (type)	Pakistan	MH366736	–	Hussain et al. 2018
<i>T. angulatus</i>	L128	Hungary	HQ846978	HQ847065	Nagy et al. 2012
<i>T. bisporiger</i>	SZMC-NL-1934	Hungary	HQ846994	HQ847082	Nagy et al. 2012
<i>T. aff. bisporiger</i>	WU7403	Hungary	HQ846974	–	Nagy et al. 2012
<i>T. bisporus</i>	HMJAU67201	China	OR762027	–	This study
<i>T. brevisetulosus</i>	SZMC-NL-2512	Hungary	FN396107	–	Nagy et al. 2011
<i>T. aff. brevisetulosus</i>	SZMC-NL-1956	Hungary	GU227709	FN396154	Nagy et al. 2011
	HMJAU67202	China	OR762034	OR762002	This study
	HMJAU67204	China	OR762035	OR762003	This study
<i>T. callinus</i>	HMJAU67205	China	OR762036	OR762004	This study
	SZMC-NL-1931	Hungary	FN396105	FN396158	Nagy et al. 2011
	HMJAU67198	China	OR762022	OR761997	This study
<i>T. canistri</i>	OT1-232	Portugal	KT804062	–	–
	Walley 877	Hungary	HQ846985	–	Nagy et al. 2012
<i>T. christianopolitanus</i>	LÖ141-08 (type)	Sweden	KC992944	KC992944	Örstadius et al; Nagy et al. 2012
<i>T. cinereopallidus</i>	SZMC-NL-0177 (type)	Hungary	HQ847001	HQ847090	Nagy et al. 2012
	HMJAU67178	China	OR762044	OR762011	This study
<i>T. congregatus</i>	SZMC-NL-0588	Hungary	JN943129	JQ045866	Nagy et al. 2012
<i>T. doverii</i>	SZMC-NL-1035	Hungary	HQ846983	HQ847070	Nagy et al. 2012
<i>T. fuscocystidiatus</i>	HMJAU67196	China	OR762019	–	This study
	HMJAU67194	China	OR762015	OR761994	This study
	SZMC-NL-2720 (type)	Hungary	HQ846977	HQ847064	Nagy et al. 2012
<i>T. heterosetulosus</i>	SZMC-NL-1059	Hungary	GU227708	HQ847075	Nagy et al. 2012
<i>T. heterothrix</i>	Ulje 1063	The Netherlands	HQ847000	HQ847088	Nagy et al. 2012
<i>T. hiascens</i>	SZMC-NL-2536	Hungary	FM878018	FM876275	Nagy et al. 2012
<i>T. impartiens</i>	SZMC-NL-0968	Hungary	JN943132	JQ045876	Wächter and Meizer 2020
<i>T. limicola</i>	Ulje 1009b (type)	The Netherlands	HQ847003	HQ847092	Nagy et al. 2012
<i>T. marculentus</i>	SZMC-NL-1167	Hungary	GU227706	HQ847089	Nagy et al. 2012
	HMJAU67189	China	OR762040	–	This study
	HMJAU67191	China	OR762030	–	This study
<i>T. maritimus</i>	ML21131CM (type)	Cyprus	MG857119	MG857116	Schafer et al. 2022
<i>T. mitrinodulisporum</i>	type	Italy	HQ180171	–	Doveri et al. 2010

(Continued)

Table 1. (Continued).

Species	Seq.-ID	Location	ITS	LSU	Reference
<i>T. pellucidus</i>	SZMC-NL-2344	Hungary	GU227715	FM876280	Nagy et al. 2010
<i>T. pellucidus</i>	HMJAU67206	China	OR762031	OR761999	This study
<i>T. plagioporus</i>	SZMC-NL-1365	Hungary	HQ846981	HQ847068	Nagy et al. 2012
	SZMC-NL-1086	Hungary	JN159512		Nagy et al. 2012
	HMJAU67177	China	OR762041	OR762008	This study
<i>T. pseudoamphithallus</i>	Ulje 1288 (type)	The Netherlands	HQ846973	HQ847059	Nagy et al. 2012
<i>T. pseudodissemminatus</i>	HMJAU46298 (type)	China-Guangdong	MH379147	–	Huang and Bau 2018
	HMJAU46301	China-Jilin	MH379149	–	Huang and Bau 2018
	HMJAU46303	China-Guangdong	MH379151	–	Huang and Bau 2018
<i>T. pseudodissemminatus</i>	HMJAU46312	China-Guangdong	OR436417	OR436392	This study
	HMJAU46321	China-Guangxi	OR436418	OR43639	This study
	HMJAU67136	China-Guangxi	OR436419	OR436390	This study
<i>T. radiceilus</i>	SZMC-NL-3168 (type)	Sweden	GU227719	HQ847077	Nagy et al. 2012
<i>T. sabulicola</i>	SZMC-NL-2906	Hungary	JN159559	–	Nagy et al. 2012
	HMJAU67176	China	OR762039	OR762007	This study
<i>T. sassii</i>	SZMC-NL-1495	Hungary	FN396101	FN396155	Nagy et al. 2011
	HMJAU67200	China	OR762038	OR762006	This study
<i>T. sclerocystidiosus</i>	SZMC-NL-1018	Hungary	HQ846991	HQ847079	Nagy et al. 2012
<i>T. sp. 1</i>	SZMC-NL-0636	Hungary	JN159514	–	Nagy et al. 2012
<i>T. sp. 2</i>	SZMC-NL-3854	Hungary	HQ846999	HQ847087	Nagy et al. 2012
<i>T. sp. 3</i>	SZMC-NL-1349	Hungary	JN159525	–	Nagy et al. 2012
<i>T. sp. 4</i>	SZMC-NL-1070	Hungary	HQ846987	HQ847073	Nagy et al. 2012
<i>T. sp. 5</i>	SZMC-NL-2887	Hungary	HQ847004	HQ847093	Nagy et al. 2012
<i>T. sp. 6</i>	Hojjer 95067	Hungary	HQ846990	HQ847078	Nagy et al. 2012
<i>T. sp. 7</i>	SZMC-NL-2617	Hungary	HQ846996	HQ847084	Nagy et al. 2012
<i>T. subdissemminatus</i>	SZMC-NL-1482	Hungary	HQ847005	HQ847094	Nagy et al. 2012
	HMJAU67117	China	OR436420	–	This study
<i>T. subimpatiens</i>	SZMC-NL-0162	Hungary	JN159542	–	Nagy et al. 2012a
<i>T. cf. subimpatiens</i>	ML41582C5	Cyprus	OL630113	–	Schafer et al. 2022
<i>T. ulje</i>	SZMC-NL-0157	Hungary	HQ846982	HQ847069	Nagy et al. 2012a
<i>T. velatopruinatus</i>	M330	Hungary	HQ847002	HQ847091	Nagy et al. 2012a
	HMJAU67184	China	OR762033	OR762001	This study
	HMJAU67185	China	OR762023	–	This study

and manually adjusted in MEGA7 (Kumar et al. 2016). Sequences of *Coprinopsis afronivea* Desjardin & B.A. Perry, *Coprinopsis sclerotiorum* (P.D. Orton) Redhead, Vilgalys & Moncalvo, and *Coprinopsis strossmayeri* (Schulzer) Redhead, Vilgalys & Moncalvo were selected as outgroup taxa.

Phylogenetic analyses were performed using maximum likelihood (ML) and Bayesian inference (BI) methods on the combined and individual ITS and LSU datasets. ML analyses employed the GTRGAMMAI substitution model with 1,000 bootstrap resamples by RAxML-HPC BlackBox on Cipres or raxmlGUI2.0 (Miller et al. 2010; Stamatakis 2014). The best-fit models for BI analyses were determined by MrMoedeltest v.2.3 (Nylander 2004). MrBayes v.3.2.6 (Ronquist et al. 2012) conducted the BI analysis, running four Markov chains for 3,000,000 generations, sampling every 100 generations until the split deviation frequency value was less than 0.01 (Ronquist and Huelsenbeck 2003). Statistical support thresholds were defined as Bootstrap support (BS) > 70% for ML analyses and Bayesian posterior probabilities (BPP) > 0.95 for BI analyses (Huelsenbeck and Hillis 1993; Leaché et al. 2002).

#### 2.4. Population genetics structure in sect. *Disseminati*

To assess population genetics structure in sect. *Disseminati*, molecular variation estimates were obtained from the constructed haplotype dataset of the ITS region, including homozygous sequences and disassembled heterozygous sequences with or without cloning. DNASP 6.12.03 (Rozas et al. 2017) was employed to calculate population diversity parameters such as number of segregating sites (*S*), number of polymorphic sites, number of haplotypes (*h*), haplotype diversity (*H<sub>d</sub>*), nucleotide diversity ( $\pi$ ), average number of nucleotide differences (*k*), average number of nucleotide differences between populations (*K%*), average number of nucleotide substitutions per site within and between populations (*D<sub>xy</sub>*), and fixation index (*F<sub>st</sub>*). The *F<sub>st</sub>* value indicates the degree of genetic differentiation between populations: (1) 0–0.05 indicates that the genetic differentiation between populations is small and can be ignored; (2) 0.05–0.15 refers to a moderate differentiation; (3) 0.15–0.25 represents a clear differentiation; (4) >0.25 means a significant genetic differentiation; and >0.30 means different species (Hartl and Clark 1997; Frankham et al. 2002, 2010). A median-joining

haplotype network was created using NETWORK 4.6.1.6 (Fluxus Technology Ltd., Colchester, UK).

### 3. Results

#### 3.1. Molecular phylogenies

In the concatenated dataset of ITS-LSU, a total of 128 sequences (86 for ITS and 42 for LSU) from 86 collections were included. Among these, 77 sequences (47 for ITS and 30 for LSU) were newly generated in this study. The alignment length of the dataset was 2,086 characters, including gaps (799 characters for ITS and 1,287 characters for LSU). The variable characters of the phylogenetic clade in sect. *Disseminati* in the ITS region are listed in Table 2. The best models for BI analysis of both the concatenated dataset and single locus dataset were determined as GTR + F + I + G4. Similar topologies to the BI framework (shown in Figures 2 and 3) were also obtained from ML analysis.

In China, the species commonly known as “fairy ink-cap” is not monophyletic and could be classified into four main clades belonging to the genera *Coprinellus* and *Tulosesus*. *T. subdisseminatus*, a new record for China, forms a strong cluster with materials from Europe (SZMC-NL-1482) without significant divergence (BPP/ML = 1.00/100). The species previously referred to as “*Coprinellus pseudodisseminatus*” is nested within *Tulosesus* and is closely related to *T. velatopruinatus* with robust evidence (BPP/ML = 1.00/100). Therefore, it is considered as a new combination within *Tulosesus*.

In *Coprinellus*, the species identified as “*Coprinellus disseminatus*” in China belongs to two sections. *Coprinellus aureodisseminatus*, a novel species discovered in this study, forms a distinct clade within this genus, which may share a common ancestor with sect. *Aureogranulati*, although statistical support is lacking. Due to significant morphological differences and substantial phylogenetic divergence, it is classified as a new section, sect. *Aureodisseminati*.

The specimens collected in China cluster within sect. *Disseminati* with robust evidence (BPP/ML = 1.00/100), and along with downloaded sequences, form eight clades, and four of which do not match any known species. Therefore, three novel species are identified: *C. austrodisseminatus*, *C. parvus*, and *C. velutipes* based on phylogenetic and morphological evidence. Additionally, sequences obtained from several specimens collected in south and

**Table 2.** Alignment including variable sites appearing in ITS region.

		ITS1																																	
		2	5	7	9	11	12	14	22	27	28	30	39	43	51	53	58	60	62	65	68	70	71	79	84	87	89	92	93	100	107	108	115	117	
A	C	-	-	-	G	T	G	-	G	T	G	C	-	C	G	C	A	T	G	T	A	C	C	C	A	A	A	T	T	A	G	C	C	C	T
B	T	-	-	-	A	A	C	-	A	T	T	-	G	G	A	G	C	C	A	T	T	T	T	A	C	C	C	A	A	-	A	T	A	C	T
C	C	-	-	-	A	A	C	-	C	T	T	-	C	Y	T	G	G	C	A	T	T	T	T	A	A	A	A	C	A	-	G	A	A	C	T
D	C	-	-	-	A	A	C	-	C	T	T	-	C	C	T	G	G	C	A	T	T	T	T	A	A	A	A	C	A	-	G	A	A	C	C
E	C	-	-	-	A	A	C	T	C	T	T	C	C	T	T	G	C	C	A	T	T	T	T	A	A	A	A	C	A	-	G	A	A	C	T
F	-	-	-	-	-	-	-	-	C	T	T	-	C	C	T	G	G	C	A	T	T	T	A	A	A	A	C	A	-	G	A	A	T	T	T
G	C	-	-	-	A	A	C	-	C	C	T	-	C	C	T	G	G	C	A	T	T	T	A	A	A	A	C	A	-	G	A	A	T	T	T
H	C	G	G	-	A	A	C	-	C	T	-	-	C	C	T	G	G	C	A	T	T	T	A	A	A	A	C	A	-	G	A	A	C	C	T

		ITS1																																	
		118	119	124	127	133	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	
A	T	T	T	T	G	A	-	-	-	-	G	T	G	-	-	-	-	-	A	G	-	-	-	-	-	-	-	-	G	T	T	-	-	-	C
B	T	T	G	T	G	T	T	T	G	C	G	T	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	T	T	-	-	-	-
C	T	C	G	T	G	T	T	T	G	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D	T	C	G	T	G	T	T	T	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E	C	C	G	T	G	T	T	T	G	C	G	T	-	T	-	C	G	T	-	-	-	-	-	-	-	-	-	-	G	T	T	-	-	-	C
F	C	C	G	T	G	T	T	T	G	C	G	T	-	-	G	C	G	A	G	C	C	G	G	C	G	C	C	-	T	T	T	C	G	C	
G	C	T	G	T	G	T	T	T	G	C	A	T	G	T	G	C	G	A	A	G	C	A	C	T	G	C	C	G	T	T	T	C	G	C	
H	C	C	G	T	G	T	T	T	G	C	G	T	G	T	G	C	G	-	-	-	-	-	-	-	-	-	-	-	G	T	T	-	-	-	C

(Continued)



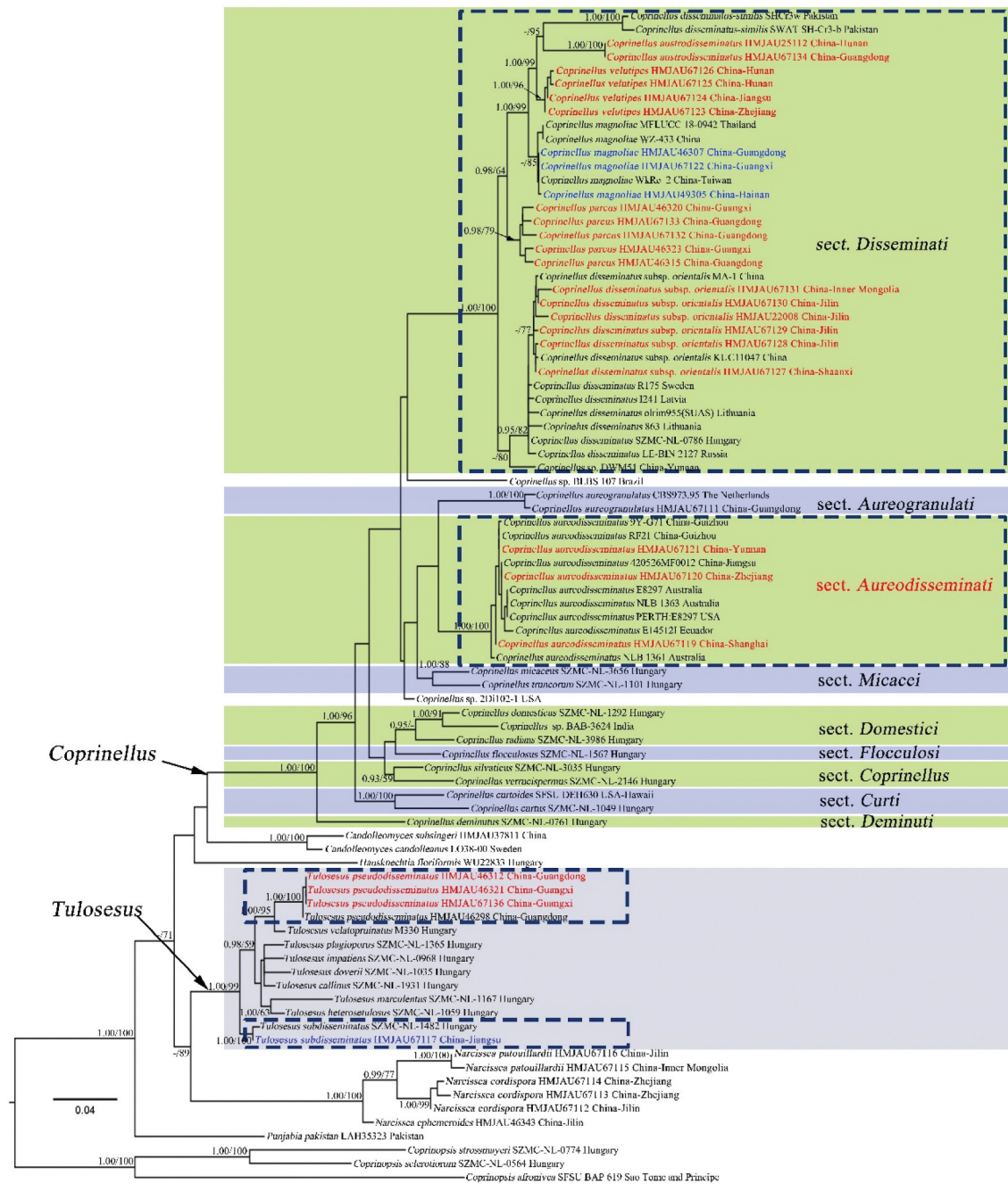
Table 2. (Continued).

		ITS1																												ITS2																											
		163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	179	180	181	182	184	185	188	189	190	191	206	212	217	219	224	226	240	264																							
A	-	-	-	-	-	-	-	-	-	-	-	C	G	C	G	G	G	C	G	A	C	G	C	T	-	-	G	C	C	T	C	C	T	-																							
B	-	-	-	-	-	-	-	-	-	-	-	C	G	C	G	G	G	C	A	A	C	G	C	T	-	-	G	C	C	T	C	C	T	-																							
C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	G	C	A	A	C	G	C	T	-	-	G	G	C	C	T	T	T	-																							
D	-	-	-	-	-	-	-	-	-	-	-	-	G	C	G	G	G	C	A	A	C	G	C	T	-	-	G	C	C	T	C	C	T	-																							
E	G	C	A	-	-	-	-	-	-	-	-	-	-	-	-	-	G	T	G	A	C	G	T	-	A	G	C	C	T	C	C	T	A																								
F	G	C	G	C	C	G	T	T	-	-	-	G	C	G	G	A	A	G	G	-	-	-	-	-	A	A	C	T	T	C	C	T	-																								
G	G	C	A	C	C	G	T	T	G	C	G	T	G	G	G	A	A	G	G	-	-	C	T	-	A	A	C	T	T	C	C	C	-																								
H	G	C	-	-	-	G	T	T	-	-	-	G	C	C	G	A	A	G	G	-	-	C	T	-	-	A	T	C	T	A	C	T	-																								

		ITS1																												ITS2																											
		265	267	449	461	473	479	480	500	509	510	518	540	553	557	558	563	577	578	579	595	598	609	610	629	631	643	645	649	650	653	655																									
A	T	C	C	C	G	C	C	C	C	T	C	C	C	-	-	-	G	G	G	T	G	G	T	-	T	C	A	-	G	A	C	A																									
B	T	C	C	G	G	C	C	C	C	T	C	C	C	-	-	-	G	T	A	A	A	T	-	T	A	A	-	T	G	A	T	T																									
C	T	C	C	G	G	C	C	C	C	T	C	C	C	-	-	-	G	G	G	T	G	G	T	-	Y	C	A	-	T	G	A	T																									
D	T	C	C	G	G	C	C	C	T	T	C	C	C	-	-	-	G	G	G	T	G	G	T	-	T	C	-	T	G	A	T	T																									
E	A	A	C	C	G	C	-	A	T	C	C	T	-	-	-	A	A	A	G	T	G	G	T	T	T	C	A	-	T	G	A	T																									
F	T	A	C	C	C	G	C	C	T	C	C	T	-	-	-	A	A	A	G	T	G	G	T	-	T	C	A	T	T	G	A	T																									
G	T	A	M	C	C	G	C	C	T	C	T	T	-	-	-	A	A	A	G	T	G	G	T	-	T	C	A	T	T	G	A	T																									
H	T	A	C	A	T	-	-	A	T	C	C	T	-	-	-	A	A	A	G	T	G	G	T	T	T	C	A	-	T	G	A	T																									

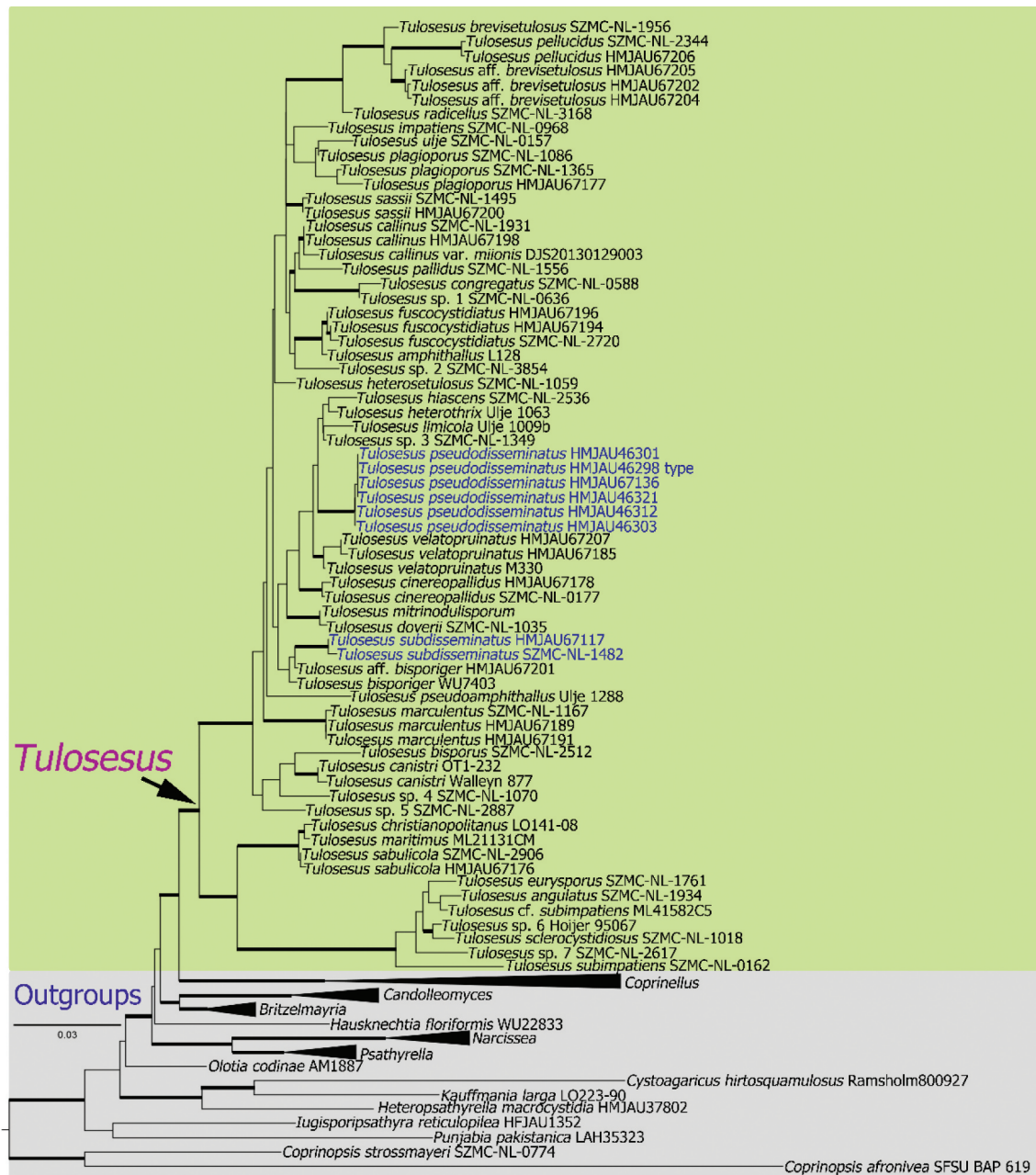
The alignment includes one sequence representing *C. disseminatissimilis* (A), *C. austrodisseminatus* (B), *C. velutipes* (C), *C. magnoliae* (D), *C. parvus* (E), *C. disseminatus* (F), *C. disseminatus* subsp. *orientalis* (G) and *C. sp.* (H). The degenerate sites A-C were replaced by M and C-T were by Y in the table.



**Figure 2.** Phylogenetic framework inferred from BI with combined ITS and LSU datasets. Posterior probability values  $\geq 0.90$  (left) and bootstrap values  $\geq 50$  (right) are indicated at nodes. Taxa that should be treated as “fairy inkcap” are boxed out with deep blue dotted boxes. The proposed new section, new species, and new combination are indicated in red. New record species in China are in blue.

southwest China (HMJAU46307, HMJAU49305, and HMJAU67122) cluster with *C. magnoliae*, previously reported only as anamorphic species in Thailand; this finding represents the first record of the sexual stage of this species. Materials from north and northeast China show close relatedness to *C.*

*disseminatus* from Europe but exhibit divergences and variable sites in the ITS region (listed in Table 2), indicating 16 INDELS and 7 mutational sites. Considering the results of population genetics in section 3.2, this clade is treated as a subspecies of *C. disseminatus*.

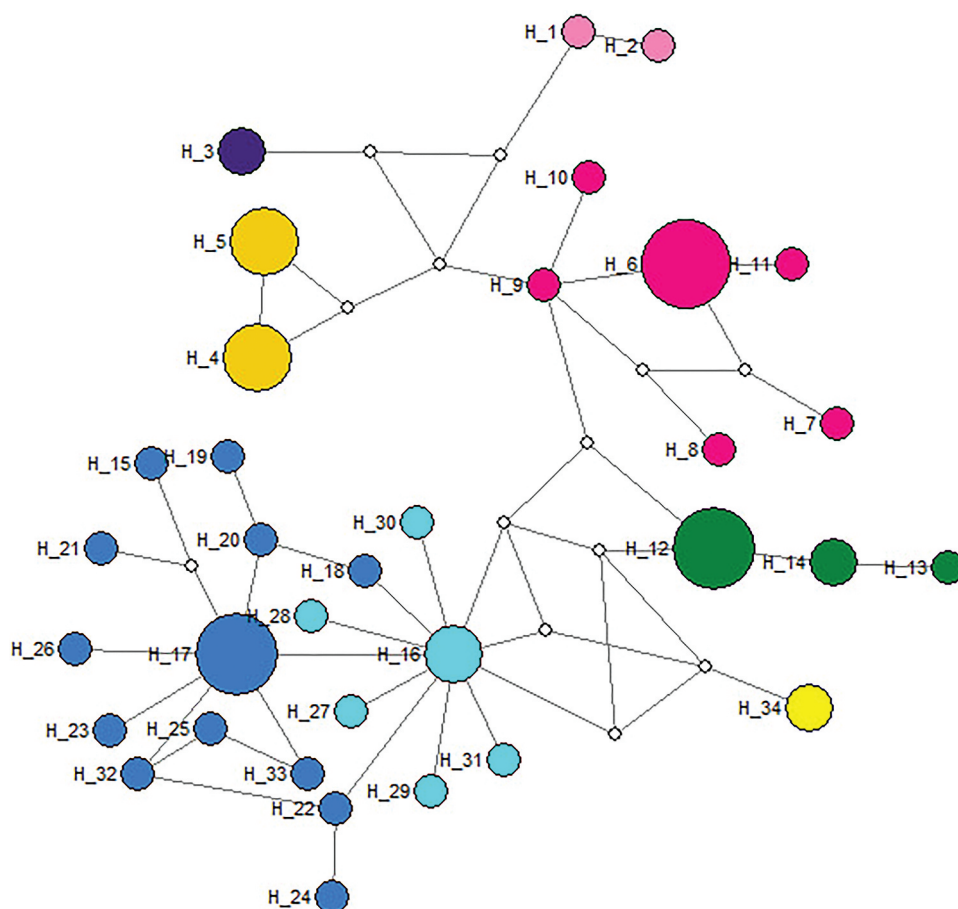


**Figure 3.** Phylogenetic framework of *Tulosesus* inferred from BI with combined ITS and LSU datasets. Nodes with robust support (posterior probability values  $\geq 0.95$  and/or bootstrap values  $\geq 75$ ) are shown with bold lines. Taxa treated as "fairy inkcap" are shown in blue.

### 3.2. Identification of phylogenetic species in sect. Disseminati

According to the combined phylogenetic framework (Figure 2) and haplotype network of sect. *Disseminati* with the ITS region (Figure 4), eight phylogenetic groups were revealed. While three clades of them were previously recognised as independent species with legitimate names in former studies, most of them were formerly thought to be "*Coprinellus disseminatus*" due to their high morphological similarity. However,

our results indicate that, except for the clade of *C. disseminatus* subsp. *orientalis*, which showed connections with *C. disseminatus* through various haplotypes (Haplotype 16-17, Haplotype 16-18-20-17, and Haplotype 16-22-32-17), the remaining populations are distinct from each other and exhibit clear species boundaries. *C. disseminatus* subsp. *orientalis* is considered a subspecies of *C. disseminatus*, but there is a dominant population (Haplotype 17) within it that is independent of *C. disseminatus* from Europe (Haplotype



**Figure 4.** Network analyses of ITS region haplotypes of known species and collections from China in sect. *Disseminati*. Each colour-filled circle represents a haplotype, and the size of the circle is proportional to haplotype frequency. The little unfilled circle represents a presumed median vector, while the dominant haplotype in each population is located in the middle. The ligature indicates the genetic relationship. The different colours of circles represent clades, as follows: *C. austrodisseminatus* (purple), *C. disseminatus* (sky blue), *C. disseminatus* subsp. *orientalis* (blue), *C. disseminatisimilis* (pink), *C. magnoliae* (deep pink), *C. parvus* (dark green), *C. velutipes* (deep yellow), and an unknown species found in Yunnan Province of China (haplotype 34) (lemon yellow).

16). In line with these results, the  $F_{st}$  value between *C. disseminatus* and *C. disseminatus* subsp. *orientalis* was less than 0.30 ( $F_{st} = 0.17526$ ), indicating some genetic differentiation but still suggesting subspecific relationship. On the other hand, the  $F_{st}$  values between other populations were all greater than 0.7, suggesting significant intraspecific differentiation and interspecific divergence (refer to Table 4 for detailed  $F_{st}$  values).

### 3.3. Haplotype analyses and genetic diversity in sect. *Disseminati*

The haplotype dataset of ITS region isolated from materials of sect. *Disseminati* contained 60 sequences, encompassing 34 types of haplotypes and 48 polymorphic sites (as shown in Table 3). Nucleotide diversity ( $\pi$ ) was employed to assess sequence variation

within and between clades (as indicated in Tables 3 and 4). Within each divergent clade (excluding *C. sp.* due to the use of only one sequence), the nucleotide diversity ranged from 0.00000 to 0.00607 (with an average  $\pi$  of 0.00316), which is considerably lower than the values between different clades, ranged from 0.00694 to 0.04596 (with an average  $\pi$  of 0.01804).

Table 3 also presents the number of haplotypes ( $h$ ) and haplotype diversity ( $H_d$ ), used as measures of gene diversity. Among all clades, *C. disseminatisimilis*, *C. disseminatus*, and *C. disseminatus* subsp. *orientalis* exhibits relatively high gene diversity.

### 3.4. Geographical distribution of “fairy inkcap” in China

Aside from the widespread occurrence of *T. pseudo-disseminatus*, the distribution of other species in



**Table 3.** Genetic diversities of the 8 divergent clades in sect. *Disseminati* based on ITS sequences.

	All	A	B	C	D	E	F	G	H
No. of sequences	60	2	2	8	12	9	8	18	1
S	48	1	0	1	7	3	8	14	0
h	34	2	1	2	6	3	7	14	1
No. of polymorphic sites	48	6	0	4	14	17	18	14	0
Hd	0.96230	1.00000	0.00000	0.57143	0.68182	0.55556	0.96429	0.93464	0.00000
$\pi$	0.01725	0.00249	0.00000	0.00142	0.00417	0.00303	0.00496	0.00607	0.00000

A: *C. disseminatissimilis*; B: *C. austrodisseminatus*; C: *C. velutipes*; D: *C. magnoliae*; E: *C. parvus*; F: *C. disseminatus*; G: *C. disseminatus* subsp. *orientalis*; H: *C. sp.*

Table 4. Statistical data calculated based on ITS region at the intergroup levels for clades in sect. *Disseminati*.

	Number of polymorphic sites	Number of fixed differences	$\pi$	k	K%	Dxy	Fst
A-B	37	32	0.03896	24,000	34,500	0.05601	0.95238
A-C	33	25	0.01916	11,689	28,750	0.04713	0.89820
A-D	38	19	0.01468	9,187	25,750	0.04394	0.86699
A-E	52	30	0.02683	16,473	37,889	0.06171	0.91632
A-F	53	30	0.01818	11,092	38,750	0.06352	0.88930
A-G	30	15	0.01789	7,530	17,900	0.04252	0.89902
A-H	43	37	0.04596	27,667	40,000	0.04342	0.97143
B-C	25	23	0.01497	9,778	23,750	0.03637	0.93443
B-D	31	17	0.01306	7,769	20,167	0.03389	0.89756
B-E	45	30	0.02260	14,982	34,444	0.05196	0.94330
B-F	42	25	0.01518	9,379	30,750	0.04976	0.90598
B-G	27	13	0.01598	6,758	15,400	0.03641	0.91603
B-H	36	36	0.03744	24,000	36,000	0.05616	1.00000
C-D	23	4	0.00972	5,784	8,500	0.01429	0.71456
C-E	29	12	0.01695	11,000	17,139	0.02641	0.86029
C-F	31	12	0.01631	9,964	18,000	0.02946	0.83243
C-G	23	10	0.01778	7,379	12,300	0.02556	0.85714
C-H	20	16	0.01217	7,644	17,750	0.02605	0.95745
D-E	32	7	0.01317	7,781	11,833	0.02002	0.77942
D-F	38	7	0.01501	8,735	14,229	0.02445	0.77321
D-G	28	6	0.01630	6,701	10,717	0.02607	0.86951
D-H	26	12	0.01041	6,154	14,500	0.02453	0.92696
E-F	40	8	0.01687	10,527	17,160	0.02750	0.70520
E-G	30	7	0.01911	8,140	12,267	0.02879	0.71500
E-H	28	10	0.01529	9,891	15,889	0.02456	0.89423
F-G	23	0	0.00694	2,978	3,163	0.00737	0.17526
F-H	24	7	0.00799	4,850	9,563	0.01575	0.80977
G-H	21	5	0.01017	4,424	6,800	0.01563	0.82258

A: *C. disseminatisimilis*; B: *C. austrodisseminatus*; C: *C. velutipes*; D: *C. magnoliae*; E: *C. parvus*; F: *C. disseminatus*; G: *C. disseminatus* subsp. *orientalis*; H: *C. sp.*

China appears to display certain regional characteristics. Specifically, *C. disseminatus* subsp. *orientalis* is mainly found in northeast and northern China, while *C. velutipes* is predominantly discovered in the eastern and central regions of the country. On the other hand, the remaining species, appear to favour tropical and subtropical regions (located south of the Yangtze River), with no clear geographical segregation among them.

### 3.5. Taxonomy

#### *Coprinellus* sect. *Aureodisseminati* sect. nov.

T. Bau & L.Y. Zhu

*Mycobank*: MB 849760.

*Type species*: *Coprinellus aureodisseminatus* T. Bau & L.Y. Zhu.

*Description*: Basidiomata small-sized, lignicolous, or terrestrial, in groups or caespitose. Lamellae never deliquescent. Ozonium present at the base of the stipe. Pilei yellow-brown when young, white-grey at mature; pileipellis spherocystoderm at ridge, paraderm at groove; subpileipellis thin, without obvious context. Veil sparse, powdery, or scaly, most in globose cells at pilei and in hypha-like cells at stipe, brown, slightly thick-walled. Basidiospores medium-sized, ovoid in frontal view, amygdaliform with acute apex in side view, with a central germ pore. Basidia trimorphological, 4-spored. Cheilocystidia narrow lageniform. Pleurocystidia absent. Pileipellis in spherocystoderm at ridge part and in paraderm in groove part, consisting of subglobose cells. Clamps absent but pseudocystidia present and short side-branches of hyphae near septa which resemble clamp connections often observed.

*Notes*: Wächter and Melzer (2020) initially classified *C. aureodisseminatus* as an unidentified species within sect. *Micacei*. However, our results contradict this classification, as they indicate that sect. *Micacei* is polyphyletic. Moreover, our results suggest that *C. aureodisseminatus* is more closely related to species in sect. *Aureoconulati* and sect. *Disseminati*. It is also supported by our morphological observation, which indicates that this clade may represent a transitional position between these two sections. Given the substantial genetic divergence, we propose that it should be designated as a distinct section within *Coprinellus*. Currently, only the type species of this section has been discovered, the further discovery of additional species may enhance our

understanding of its phylogenetic position. In conjunction with existing literature and our observations, we compiled macro-morphological and micro-morphological features of known 10 sections of *Coprinellus*, including sect. *Aureodisseminati* in Tables 5 and 6, respectively (Lange and Smith 1953; Ujlé and Bas 1991; Enderle 2004; Nagy 2005; Nagy et al. 2012; Laessøe and Petersen 2019; Wächter and Melzer 2020).

#### *Coprinellus aureodisseminatus* T. Bau & L.Y. Zhu, sp. nov, Figures 5–7

*Mycobank*: MB 849759.

*Etymology*: The prefix “aureo” refers to the yellow-brown colour of its young basidiomata and veil which is similar to the species in sect. *Aureoconulati*, while “disseminatus” indicates that the species is morphologically close to *C. disseminatus*.

*Diagnosis*: Pileus yellow-brown when young and become whitish when mature with not obvious radial grooves; lamellae undeliquencing at age; stipe attached to a cream to rust-brown ozonium-state; basidiospores ovoid in frontal view, amygdaliform with the acute apex in side view; basidia trimorphological; cheilocystidia lageniform; pileipellis in spherocystoderm at ridge part and in paraderm in groove part; elements of the veil at pileus most in subglobose to globose and on stipe mostly consisted of the hyphae-like cell, slightly thick-walled, yellow-brown to dark brown; clamp connection absent.

*Type*: China: Shanghai City: Jiading District, Jiabei Country Park, on mud ground near rotten wood in artificial camphor forest, 9 April 2023, Jia-Ming Cai, HMJAU67119 (ITS: OR436416; LSU: OR436373).

*Description*: Basidiomata small-sized. Pileus 0.5–1.5 cm, first subglobose, ellipsoid or ovoid, obtuse conical when mature, sometimes with a rounded umbo; light yellow-brown (1B5) or deep yellow (4B5) when young covered with white (2A1) to cream (3A2), powdery or scaly veil, then become (sub)white (2A2, 3A2) at the margin and light yellow-brown (1B5) at the centre, finally become grey-white (1B1) at age, only with brown hue at centre and margin, pubescent; the radial grooves not obvious when young, and extended to the top 1/4 of the cap after maturation, without a clear line at the folding part. Context very thin, only present at the centre part, white (1A2) to cream (1A3). Lamellae narrow adnate, L = 18–24, I = 0 or 1, 0.1–0.2 cm in wide, first white (1A1) to cream (1A3), then brown-grey

Table 5. Comparison of macro-morphological and habitat of known sections of *Coprinellus*.

Section name	Basidiomata size	Pileus colour	Radial grooves on pileus	Veil	Lamellae	Ring- or volva-like part at middle part or base of stipe	Yellow-brown mycelium at base of stipe	Habitat
Sect. <i>Deminuti</i>	Tiny- to small-sized	White to pale yellowish	Present	Minute yellow-brown granular	Distant, free with a distinct pseudocollar	Absent	Absent	Soil
Sect. <i>Hepthemeri</i>	Tiny-sized	Pale yellow to yellow-brown at centre, paler towards margin	Present	Minute pellicid yellow-brown granular	Rather distant, free; deliquescent	Absent	Absent	Dung
Sect. <i>Curri</i>	Tiny- to small-sized	Cream, yellow-brown at centre	Not obvious	Minute brown granule	Adnate or free, deliquescent or withering	Absent	Absent	Dung
Sect. <i>Flocculoci</i>	Medium- to large-sized	Pale dirty ochre, grey-ochre	Not obvious	Cream to light brown, woolly flocks	Free, deliquescent	Present	Absent	Wood chips, rotten grass, dung
Sect. <i>Domestici</i>	Medium-sized	Cream, pale ochre, yellow-brown, bright grey-ochre	Not obvious	Whitish, cream, yellow-brown, felty, woolly flocks, become small red-brown or dark brown scales at age	Adnate or almost free, deliquescent	Present	Present	Rotten wood, humus layer of broad-leaved forest
Sect. <i>Coprinellus</i>	Small- to medium-sized	Pale yellow-brown, bright grey-ochre, bright ochre-grey	Present or not obvious	Minute, granular, brown, or ochre flocks	Adnate or almost free, deliquescent	Present	Absent	Clayey soil
Sect. <i>Aureoconulati</i>	Small- to medium-sized	Yellow-brown to orange-brown	Not obvious	Minute, granular, brown, or ochre flocks	Adnate or almost free, deliquescent	Absent	Present	Soil
Sect. <i>Aureodisseminati</i>	Small-sized	Cream, light yellow-brown at centre	Not obvious when young and present at mature	Sparse, not obvious whitish to cream granule	Adnate or almost free, withering	Absent	Present	Base of trunk, soil
Sect. <i>Micacei</i>	Medium-sized	Light brown to brown, light ochre	Absent or not obvious	Minute, granular, whitish flocks	Adnate or almost free, deliquescent	Present	Absent	Base of trunk, soil
Sect. <i>Disseminati</i>	Tiny- to small-sized	Whitish, cream, light yellow-brown	Present	Sparse, minute, colourless, and/or brown granule, only seen when young	Adnate or almost free, withering, or deliquescent in the moist environment	Absent	Present or absent	Base of trunk, soil



Table 6. Micro-morphological characteristics comparison of known sections of *Coprinellus*.

Section name	Basidiospores	Basidia	Cheilocystidia	Pleurocystidia	Veil elements	Pileipellis	Pileocystidia	Caulocystidia	Clamp connection
Sect. <i>Deminuti</i>	Ellipsoid, smooth, germ pore central	4-spored, dimorphological	Clavate, ellipsoid	Absent	Chains of cylindrical-fusoid cells, encrusted, colourless to bright brown, thick-walled	Unknown	Absent	Present (not mentioned in previous literature)	Absent
Sect. <i>Hepthemerii</i>	Ellipsoid to oblong, smooth, germ pore distinctly eccentric	4-spored, trimorphological	Ellipsoid, utriform	Absent	Globose cells, often with long spine-like projections, thin- to thick-walled	Spherocysto-derm	Present	Present	Absent
Sect. <i>Curri</i>	Ellipsoid or ovoid, smooth, germ pore distinctly eccentric	4-spored, dimorphological	Ellipsoid, utriform	Absent	Globose cells, slightly thick-walled to thick-walled	Spherocysto-derm to paraderm	Present	Present	Present?
Sect. <i>Flocculaci</i>	Ellipsoid to oblong, smooth, germ pore eccentric	4-spored, dimorphological	(Sub)globose, ellipsoid, ovoid	Broadly utriform or subcylindrical	Chains of cylindrical cells, colourless, sometimes encrusted, thin-walled	Paraderm	Absent	Absent	Absent
Sect. <i>Domestici</i>	Ellipsoid, smooth, germ pore central or slightly eccentric	4-spored, trimorphological	Utriform, subglobose, ellipsoid, lageniform	Subglobose, broadly utriform or subcylindrical	Chains of subcylindrical cells or subglobose cells, brown, often thick-walled, sometimes encrusted	Paraderm	Absent	Present	Absent, only pseudoclamp present
Sect. <i>Coprinellus</i>	Ovoid or ellipsoid in front view, amygdaliform in side view, ornamented, germ pore central	4- or 2-spored, trimorphological	(Sub)globose to ellipsoid, lageniform	Present or absent	Globose cells or short chains of subglobose or subcylindrical cells, colourless to pale brown, slightly thick-walled, encrusted	Paraderm	Present	Present	Present or absent
Sect. <i>Aureogramma-lati</i>	Subcylindrical ellipsoid in front view, phaseoliform in side view	4-spored, trimorphological	Lageniform with cylindrical neck	Absent	Chains of subglobose or subcylindrical cells, brown or ochre, thick-walled, encrusted	Spherocysto-derm to paraderm	Present	Present	Absent
Sect. <i>Aureodisse-riminati</i>	Ovoid	4-spored, trimorphological	Lageniform	Absent	Globose cells or chains of hyphae-like cells, yellow-brown or light ochre, slightly thin-walled to thick-walled	Spherocysto-derm to paraderm	Present	Present	Absent, but short branches of hyphae near septa, resembling clamp connections abundant
Sect. <i>Micarei</i>	Ellipsoid, ovoid, mitriform	4-spored, trimorphological	Subglobose, ellipsoid, or ovoid	Ellipsoid, ovoid, or subcylindrical	Globose cells, colourless to light brown or light ochre, slightly thick-walled	Paraderm	Present or absent	Present or absent	Absent, only pseudoclamp present
Sect. <i>Disseminati</i>	Ovoid	4-spored, mono-, di- or trimorphological	Absent in most species, the presence still in doubt in <i>C. disseminatussemi-flis</i>	Absent	Two types: 1) chains of small, thick-walled, cream to dark brown, ellipsoid to subglobose elements; 2) globose cells, colourless, thin-walled to slightly thick-walled	Spherocysto-derm	Present	Present	Absent, but short branches of hyphae near septa, resembling clamp connections abundant



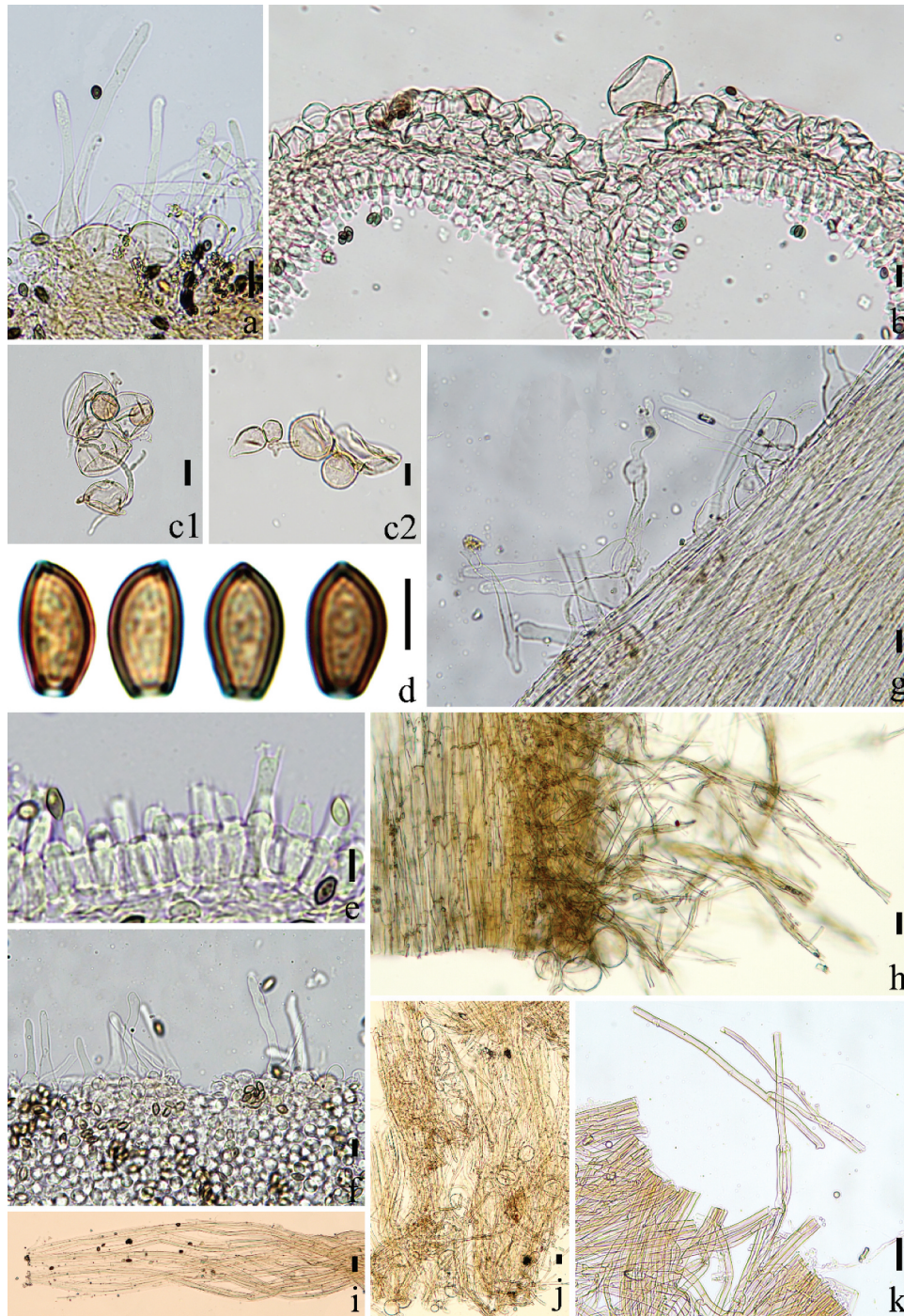
**Figure 5.** Photographs of fresh fruiting body of *Coprinellus aureodisseminatus*. (a–d) HMJAU67119; (e–f) HMJAU67120; (g–h) HMJAU67118.

(5D3), finally blackish (6F4), not deliquescent at age. Stipe 1.5 – 4.5 × 0.1 – 0.2 cm, white (1A2) to cream (1A3), sometimes with a brown hue at the lower part of the stipe, hollow, crispy, pubescent, without a volva-like margin, often attached to a cream (1A3) to rust-brown (7E8) ozonium-state.

Basidiospores [78, 7, 4] (7.9)9.0 – 9.2(10.1) × (5.2) 5.4 – 5.6(6.1) × (4.7)5.3 – 5.4(5.8)  $\mu\text{m}$ ,  $Q_1 = 1.49 – 1.83$ ,  $Q_2 = 1.53 – 1.92$ , ovoid in frontal view, amygdaliform with acute apex in side view, dark red-brown (7E8) in

water and blackish (7F7) in 5% KOH solution; germ pore central, 1.7 – 2.4  $\mu\text{m}$  in wide. Basidia trimorphologic, 15 – 37 × 5 – 8  $\mu\text{m}$ , short clavate to clavate, usually constricted at the middle part, 4-spored, sterigmata 3 – 6  $\mu\text{m}$  in length; each basidium surrounded with 4 – 6 pseudoparaphyses. Cheilocystidia lageniform, 16 – 68 × 10 – 18  $\mu\text{m}$ , with 5 – 7  $\mu\text{m}$  wide, tapering neck, sometimes with 3 – 5  $\mu\text{m}$ , lanceolate or 5 – 8  $\mu\text{m}$ , obtuse or subcapitate apex. Pleurocystidia unseen. Hymenophoral trama regular. Pileipellis in

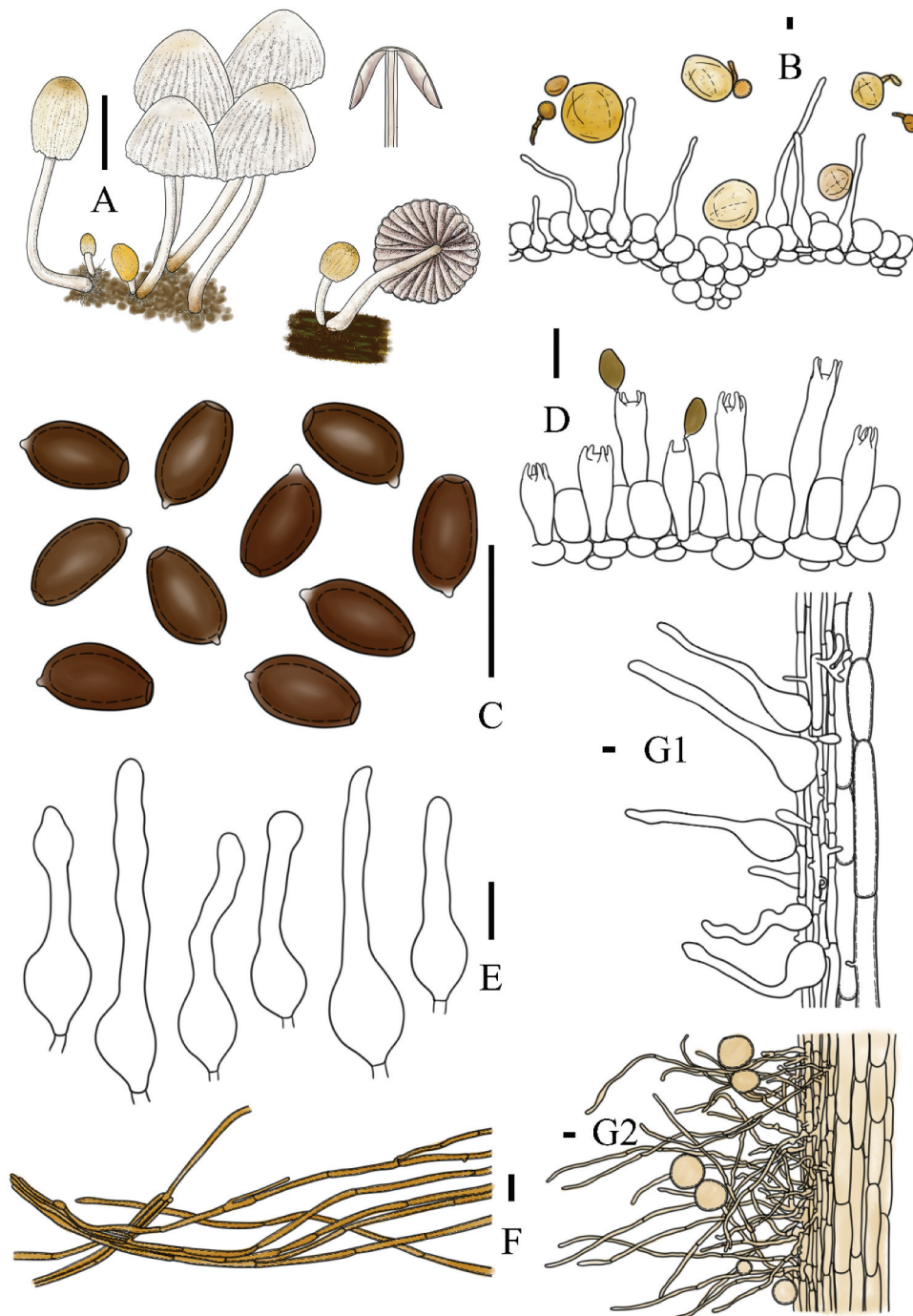




**Figure 6.** Micromorphological features of *Coprinellus aureodisseminatus*. (a) Pileocystidia; (b) Pileipellis; (c1–c2) Veils composed of yellow-brown globose cells; (d) Basidiospores; (e) Basidia; (f) Cheilocystidia; (g) Caulopellis of the upper part of stipes; (h) Longitudinal section of the lower part of stipes; (i) Colorless to light yellow mycelium at base of stipes; (j) Top view of the lower part of stipes; (k) Hyphae of ozonium at base of stipes. Bars: a–b, c1–c2, e–k = 20 µm; d = 5 µm.

spherozystoderm at ridge part and in paraderm in groove part, consisting of subglobose cells,  $18 - 72 \times 15 - 67 \mu\text{m}$ , hyaline to light yellow-brown (5A5), thin-walled to slightly thick-walled; pileocystidia slender lageniform,  $63 - 138 \times 8 - 23 \mu\text{m}$ , with  $6 - 12 \mu\text{m}$  wide, tapering neck, sometimes subcapitate apex, hyaline or

with brown hue at the base, thin-walled to slightly thick-walled. Caulopellis hyphae  $3 - 8 \mu\text{m}$  wide, hyaline to yellow-brown (6C7), strongly multiple-branched and diverticulate which usually with septa, thin-walled; hyphae of stipe trama  $13 - 27 \mu\text{m}$  wide, hyaline, thin-walled to somewhat thick-walled; caulocystidia



**Figure 7.** *Coprinellus aureodisseminatus*. (A) Basidiomata; (B) Pileipellis; (C) Basidiospores; (D) Basidia; (E) Cheilocystidia; (F) Hyphae of ozonium; (G) Longitudinal section of stipes: (G1) Middle and upper part of stipes; (G2) Lower part of stipes. Bars: A = 1 cm; B–G = 10  $\mu$ m.

lageniform, 25 – 174  $\times$  11 – 13  $\mu$ m, with 5 – 9  $\mu$ m wide, erect or bender, tapering neck, usually with capitate apex (sometimes in shape like thanatophidia head), same colour with hyphae of caulopellis. Elements of veil at pileus most in subglobose to globose, 16 – 70  $\times$  16 – 55  $\mu$ m, occasionally attached with a 2 – 5  $\mu$ m, short hyphae-like cell; elements of veil on stipe mostly consisted of hyphae-like cell, 4 – 6  $\mu$ m in width, some

subglobose to ellipsoid cells also present, 13 – 40  $\times$  12 – 27  $\mu$ m, slightly thick-walled, yellow-brown to dark brown. Hyphae of ozonium parallel dense arrangement, 3 – 6  $\mu$ m, slightly thick-walled to thick-walled, cream (1A3) to rust-brown (7E7), darker in 5% KOH solution. Clamp connection absent, but pseudocystidia present, and short side-branches of hyphae near septa which resemble clamp connections are often observed.



*Habitat:* In groups or caespitose on the bark of the broad-leaved tree or ground of a forest. Usually occurs in late spring to early autumn.

*Distribution:* Southeast and Southwest China.

*Additional specimens examined:* China: Zhejiang Province: Lishui City, Qingyuan County, Qingyuan Town, Baishanzu National Park, on rotten wood of broad-leaved tree, 15 August 2015, Tolgor Bau, HMJAU67120 (ITS: OR436414; LSU: OR436374); same location, on moss layer on the trunk of the broad-leaved tree, 25 August 2023, Yong Zhou, HMJAU67119; Yunnan Province: Kunming City, Yeya Lake, on rotten wood of the broad-leaved tree, 7 August 2016, Tolgor Bau and Jun-Qing Yan, HMJAU67121 (ITS: OR436415; LSU: OR436375).

*Notes:* *C. aureodisseminatus* displays macroscopic similarities to *C. disseminatus* when mature, however, the pileus of the latter is initially whitish and exhibits a distinct line or groove when young. Microscopically, *C. disseminatus* lacks cheilocystidia, and its pileipellis consists of spherocystoderm, whether at the ridge or the groove. Additionally, the veil elements are comprised of two types of cells: one type is (sub)globose, hyaline, and thin-walled, while the other type mainly consists of chains of ellipsoid or subglobose, brown or ochre, thick-walled cells. It is worth noting that *C. aureodisseminatus* has been discovered in Australia, initially as "*C. disseminatus*" (Hubregtse 2019), and in Ecuador as endophytes. These findings indicate that this species might have a widespread presence in subtropical or tropical areas (unpublished).

***Coprinellus parvus* T. Bau, L.Y. Zhu & M. Huang sp. nov., Figures 8–10**

*Mycobank:* MB 849761.

*Etymology:* "*parvus*" refers to the relatively small size of this species in sect. *Disseminati*.

*Diagnosis:* Basidiomata tiny-sized; pileus almost without brown hue, white to pearl white when young and become grey-white at age; basidia dimorphologic, most in short clavate; terminal cells of caulopellis at the lower part of stipes most in globose to ellipsoid, or utriform; usually seen in grassland and distributed in southern China.

*Type:* China: Guangdong Province: Zhaoqing City, Dinghu Mountain National Nature Reserve, on moss layer on stone in broad-leaved forest, 11 May 2017,

Mei Huang, HMJAU46316 (ITS: OL355008; LSU: OL375245).

*Description:* Basidiomata tiny-sized. Pileus 0.3–0.9 cm, first subglobose or ovoid, semisphere to obtuse conical when mature, sometimes with a rounded umbo; white to pearl white (2A2) when young, become grey-white (6B1, 6B2) at age, sometimes white (1A2) to cream (1A3) at centre; the radial grooves extended to the top 1/3 of the cap after maturation, with a clear line at the folding part; pubescent. Context is very thin, only present at the centre part, white to cream. Lamellae narrow adnate,  $L = 18 - 22$ ,  $l = 0$  or  $1$ , 0.1 cm in wide, first white (1A2) to cream (1A3), then brown-grey (6D4), finally blackish (6E2), not deliquescent at age. Stipe  $1.8 - 3.9 \times 0.05 - 0.1$  cm, white (1A2) to cream (1A3), hollow, crispy, pubescent, without a volva-like margin, often attached to a cream (1A3) ozonium-state.

Basidiospores  $[60, 6, 6] (6.0)7.1 - 7.3(8.3) \times (4.1) 4.6 - 4.7(5.1) \times (3.8)4.3 - 4.5(4.9) \mu\text{m}$ ,  $Q_1 = 1.43 - 1.77$ ,  $Q_2 = 1.54 - 1.75$ , ovoid in frontal view, amygdaliform with acute apex in side view, obconical at base and truncate at apex, dark red-brown (7E7) in water and blackish (7E4) in 5% KOH solution; germ pore central to slightly eccentric,  $0.6 - 1.7 \mu\text{m}$  in wide. Basidia dimorphological,  $10 - 20 \times 6 - 8 \mu\text{m}$ , most in short clavate, 4-spored, sterigmata  $2 - 4 \mu\text{m}$  in length; each basidium surrounded with 3–5 pseudoparaphyses. Cheilocystidia and pleurocystidia absent. Hymenophoral trama regular, trama hyphae  $10 - 18 \mu\text{m}$  in wide. Pileipellis spherocystoderm at ridge part and groove part, consisting of subglobose cells,  $15 - 54 \times 12 - 43 \mu\text{m}$ , hyaline, thin-walled to slightly thick-walled; pileocystidia clavate to slender lageniform,  $121 - 259 \times 11 - 32 \mu\text{m}$ , with  $9 - 14 \mu\text{m}$  wide, tapering neck, sometimes subcapitate apex, hyaline or with brown hue at base, thin-walled to slightly thick-walled. Caulopellis hyphae  $2 - 6 \mu\text{m}$  wide, hyaline, sometimes branched and diverticulate, thin-walled to slightly thick-walled; hyphae of stipe trama  $10 - 18 \mu\text{m}$  wide, hyaline, thin-walled to somewhat thick-walled. Caulocystidia lageniform to long lageniform,  $28 - 170 \times 17 - 18 \mu\text{m}$ , with  $4 - 6 \mu\text{m}$  wide, erect or bender, tapering neck; terminal cells of caulopellis at lower part of stipes most in globose to ellipsoid, or utriform,  $14 - 56 \times 8 - 24 \mu\text{m}$ , sometimes with  $4 - 6 \mu\text{m}$  wide stem, same colour with hyphae of caulopellis. Elements of the veil at pileus most in subglobose to globose,  $16 - 53 \times 5 - 7 \mu\text{m}$ , hyaline, thin-walled to slightly thick-walled; elements of the veil



**Figure 8.** Photographs of fresh fruiting bodies of *Coprinellus parvus*. (a–b) HMJAU67133; (c–d) HMJAU67155; (e–g) HMJAU67132.

on stipe mostly consisted of single or chains of subglobose to globose elements,  $12 - 41 \times 9 - 35 \mu\text{m}$  when colourless,  $6 - 12 \times 5 - 7 \mu\text{m}$  and with a constricted middle part when yellow-brown (6C7) to dark brown (6D8), sometimes attached with a hyphae-like element,  $2 - 7 \mu\text{m}$  in width, usually branched and diverticulate, thin-walled to slightly thick-walled. Clamp connection and pseudoclamps absent.

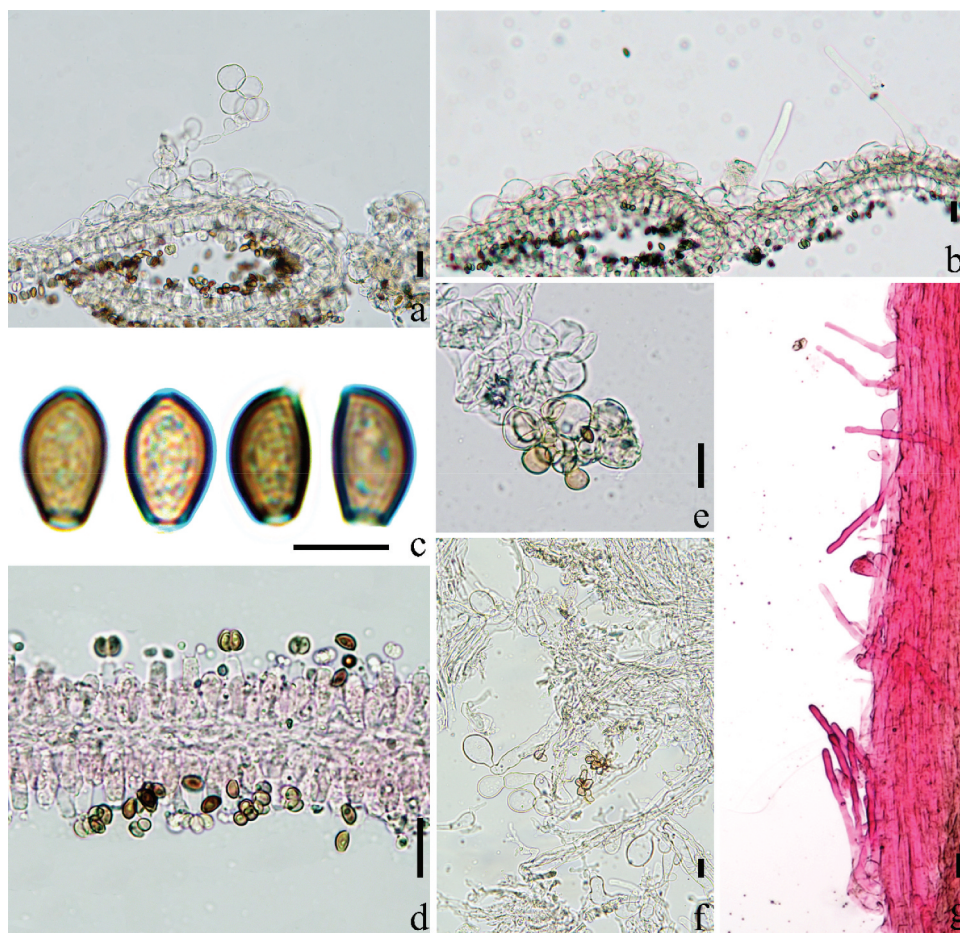
**Habitat:** In groups or caespitose in grassland or on the bark of a broad-leaved tree. Usually occurs in the middle spring to summer.

**Distribution:** South China.

**Additional specimens examined:** China: Guangdong Province: Zhaoqing City, Dinghu Mountain National Nature Reserve, on moss layer on stone in the broad-leaved forest, 11 May 2017, Mei Huang, HMJAU46315

(ITS: OR436404; LSU: OR436384); Guangzhou City, a campus of South China Agricultural University, in grassland, 11 April 2023, Jia-Yin Lin and Kun-Long Yang, HMJAU67133 (ITS: OR436405); Guangzhou City, Tianhe District, Huolushan Forest Park, on soil near *Ficus microcarpa*, 15 May 2023, An-Fei Zeng, HMJAU67137; Guangzhou City, Huangpu District, Niutou Mountain, on deciduous leaves of broad-leaved tree, 13 November 2023, Yu-Rong Liang, HMJAU67155; Shenzhen City, Longgang District, Furong Garden of Lotus Villa, in grassland, 26 April 2023, Li Yin, HMJAU67132 (ITS: OR436406; LSU: OR436387). Guangxi: Chongzuo City, Longzhou county, Nonggang National Nature Reserve, on rotten wood of broad-leaved tree, 17 May 2017, Tolgor Bau, Mei Huang, and Guang-Fu Mou, HMJAU46320 (ITS: OR436402; LSU: OR436385); same location, on soil





**Figure 9.** Micromorphological features of *Coprinellus parvus*. (a) Veil cells attaching pileus; (b) Pileipellis; (c) Basidiospores; (d) Basidia; (e) Veils composed of short chains of light yellow-brown to dark brown, subglobose to ellipsoid cells; (f) Veils and subglobose to ellipsoid caulocystidia; (g) Longitudinal section of stipes. Bars: a–b, d–g = 20 µm; c = 5 µm.

under broad-leaved forest, 16 May 2017, Tolgor Bau, Mei Huang, and Guang-Fu Mou, HMJAU46323 (ITS: OR436403; LSU: OR436386).

*Notes:* *C. austrodisseminatus* is similar to *C. parvus* in terms of colour and distribution, however, it could be distinguished by the latter by its larger pileus size, and its basidium is surrounded by 4–6 pseudoparaphyses, short-branched cylindrical terminal cells of caulopellis at the lower part of stipes, moreover, its caulocystidia and pileocystidia are relatively short which up to 140 µm. *C. magnoliae* is also found in southern China, it differs from *C. austrodisseminatus* in that its lamellae are relatively sparser, with a range of  $L = 16\text{--}19$ . Furthermore, *C. magnoliae* exhibits a trimorphological basidia.

***Coprinellus austrodisseminatus*** T. Bau & L.Y. Zhu sp. nov, Figures 11–13

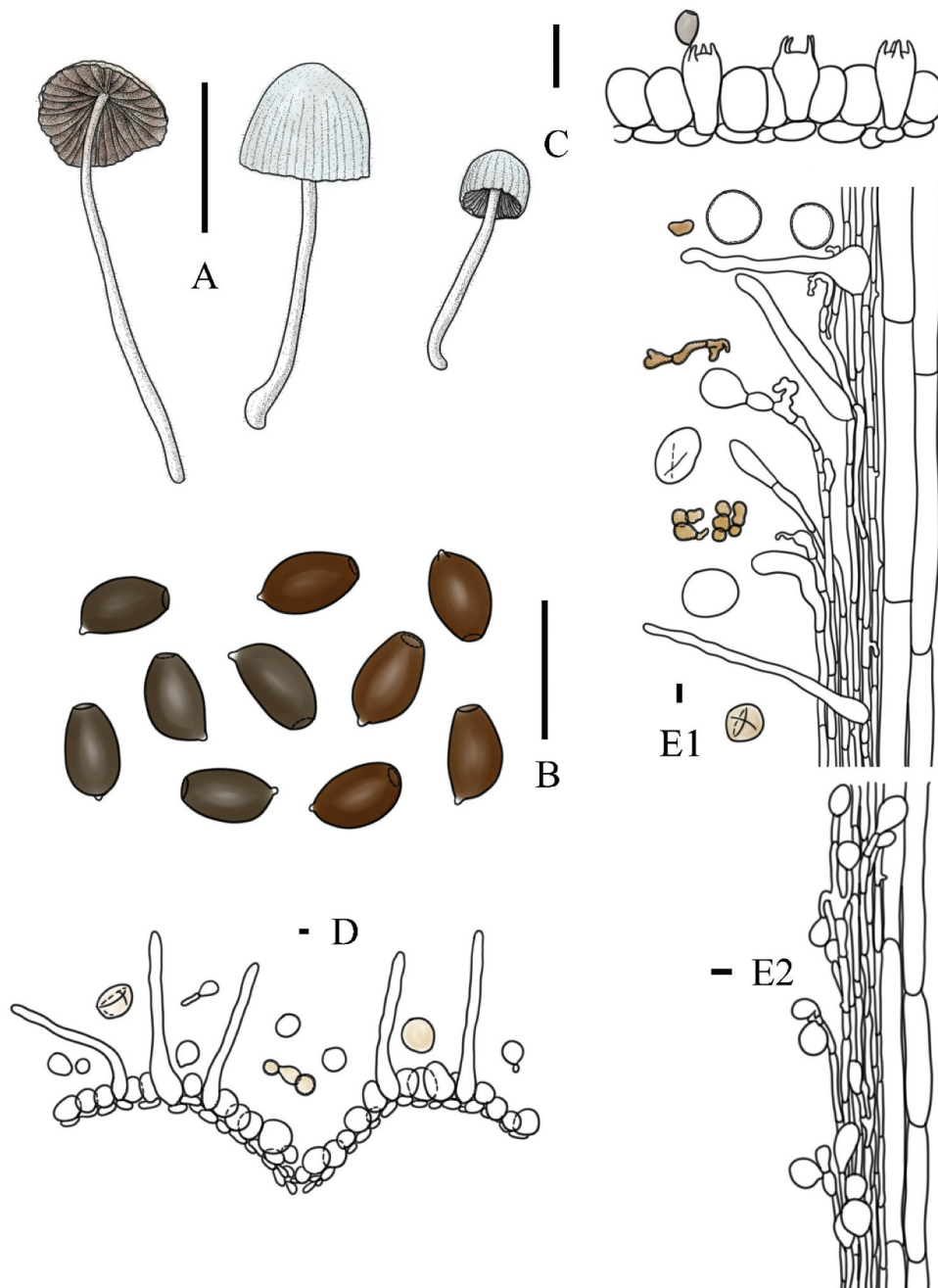
*Mycobank:* MB 849762.

*Etymology:* The prefix “austro” indicates that this species is distributed in southern China, while “disseminatus” indicates that the species is morphologically close to *C. disseminatus*.

*Diagnosis:* Basidiomata relatively large in sect. *Disseminati*, pileus usually over 1 cm in diameter, whitish from young to mature; basidia dimorphological; caulocystidia and pileocystidia relatively short which up to 140 µm, most in clavate to narrow lageniform; terminal cells of caulopellis at the lower part of stipes mostly in short-branched cylindrical; distributed in southern China.

*Type:* China: Guangdong Province: Guangzhou City, Tianhe District, Linhe Street, Mingyayuan Community, on grassland, 25 April 2023, Hong-Sheng Wang, HMJAU67134 (ITS: OR436393; LSU: OR436378).

*Description:* Basidiomata small-sized. Pileus 0.7–1.5 cm, first ovoid, obtuse conical when mature, with a rounded umbo; pearl white (1A2) when young,



**Figure 10.** *Coprinellus parvus*. (A) Basidiomata; (B) Basidiospores; (C) Basidia; (D) Pileipellis; (E) Longitudinal section of stipes: (E1) Middle and upper part of stipes; (E2) Lower part of stipes. Bars: A = 1 cm; B–E = 10  $\mu$ m.

become grey-white (1B2) at age, cream (1A3) at the centre; the radial grooves extended to the top 1/4 of the cap after maturation, with a clear line at the folding part; pubescent. Context is very thin, only present at the centre part, white to cream. Lamellae narrow adnate,  $L=17-26$ ,  $l=1-3$ , 0.1 cm in wide, first white (1A2) to cream (1A3), then pink-brown (7B3, 7C3), finally dark brown (7E4), not deliquescent at age. Stipe 3.3–5.6  $\times$  0.1 cm, white (1A1) to cream

(1A3), hollow, crispy, pubescent, without a volva-like margin.

Basidiospores [70, 4, 2] (6.2) 7.6–7.9 (9.1)  $\times$  (4.3) 4.8–5.0 (5.8)  $\times$  (3.8) 4.6–4.8 (5.5)  $\mu$ m,  $Q_1=1.41-1.76$ ,  $Q_2=1.44-1.81$ , long ovoid in frontal view, amygdaliform with the acute apex in side view, obconical at the base and truncate at apex, dark red-brown (8E6, 8E8) in water and deep olivaceous (2F7) to blackish (2F3) in 5% KOH

solution; germ pore central to slightly eccentric, 1.3 – 2.7  $\mu\text{m}$  in wide. Basidia dimorphologicals, 10 – 19  $\times$  6 – 9  $\mu\text{m}$ , short clavate, 4- or 2- spored, sterigmata 2 – 5  $\mu\text{m}$  in length; each basidium surrounded with 4 – 6 pseudoparaphyses. Cheilocystidia and pleurocystidia absent. Hymenophoral trama regular, trama hyphae 2 – 5  $\mu\text{m}$  in wide. Pileipellis spherocystoderm at ridge part and groove part, consisting of subglobose cells, 20 – 53  $\times$  17 – 47  $\mu\text{m}$ , hyaline, thin-walled to slightly thick-walled; pileocystidia clavate to slender lageniform, 40 – 132  $\times$  13 – 23  $\mu\text{m}$ , with 7 – 12  $\mu\text{m}$  wide, with subcapitate apex, hyaline or with brown hue at base, thin-walled to slightly thick-walled. Caulopellis hyphae 3 – 8  $\mu\text{m}$  wide, hyaline, sometimes branched and diverticulate, thin-walled to slightly thick-walled; hyphae of stipe trama 9 – 33  $\mu\text{m}$  wide, hyaline, thin-walled to somewhat thick-walled. Caulocystidia most in clavate, occasionally in lageniform, 37 – 132  $\times$  13 – 23  $\mu\text{m}$ , with 7 – 12  $\mu\text{m}$  wide; terminal cells of caulopellis at the lower part of stipes mostly in short-branched cylindrical, 22 – 50  $\mu\text{m}$  in length, with obtuse apex. Elements of the veil at the centre of the pileus are composed of chains of thick-walled, cream (1A3) to dark brown (5E7), ellipsoid to subglobose elements, 7 – 31  $\times$  4 – 31  $\mu\text{m}$ ; elements of the veil at the margin of pileus composed of thin-walled, hyaline, subglobose to globose elements, 22 – 74  $\times$  20 – 60  $\mu\text{m}$ . Hyphae of ozonium parallel dense arrangement, 3 – 6  $\mu\text{m}$ , slightly thick-walled to thick-walled, cream (1A3) to light brown (4B5), darker in 5% KOH solution. Clamp connection and pseudoclamps are absent.

*Habitat:* In groups or caespitose in grassland or on the bark of broad-leaved tree. Usually occurs in the middle spring to summer.

*Distribution:* Southern China.

*Additional specimens examined:* China: Hunan Province: Changsha City, Yuelu Mountain Scenic Area, on soil in the broad-leaved forest, 19 July 2012, Tolgor Bau, HMJAU25112 (ITS: OR436394; LSU: OR436377).

*Notes:* *C. austrodisseminatus* is the sister of *C. disseminatisimilis*, a species that has been reported in Pakistan. However, the pileus of *C. disseminatisimilis* is usually greyish-brown when mature, and its basidiospores have relatively small germ pores (0.5 – 1.0  $\mu\text{m}$  in diameter). *C. magnoliae* and *C. parvus* are also distributed in southern China, however, they are relatively small-

sized macroscopically (diameter of pileus usually less than 0.7 cm) and possess longer pileocystidia and caulocystidia (up to 170  $\mu\text{m}$ ). Additionally, *C. magnoliae* exhibits trimorphological basidia.

***Coprinellus magnoliae*** N.I de Silva, Lumyong & K.D. Hyde, Figures 14–16

*Description:* Basidiomata tiny-sized. Pileus 0.4 – 0.7 cm, first ellipsoid, semisphere when mature, without a rounded umbo; (sub)white (3A1) when young, become grey-white (5B1) or light purple-brown (7B2) to purple-grey (9D2) at age, without brown hue at the centre; the radial grooves extended to the top of the cap after maturation, with a clear line at the folding part which is slightly darker than other parts; pubescent. Context very thin, only present at the centre part, white (1A2) to cream (1A3). Lamellae narrow adnate, L = 16 – 19, l = 1, 0.1 – 0.2 cm in wide, first white (1A2) to light grey-white (9B1), finally dark brown-grey (7E3), usually deliquescent at age especially in moist environment. Stipe 2.8 – 4.0  $\times$  0.1 cm, white (1A1) to cream (1A3), hollow, crispy, pubescent, without a volva-like margin.

Basidiospores [80, 4, 4] (6.2) 7.4 – 7.6 (8.4)  $\times$  (3.9) 4.3 – 5.4 (4.7)  $\times$  (3.4) 4.1 – 4.3 (4.6)  $\mu\text{m}$ ,  $Q_1 = 1.55 – 1.91$ ,  $Q_2 = 1.62 – 2.04$ , long ovoid in frontal view, amygdaliform with acute apex in side view, obconical at base and truncate at apex, dark red-brown (6E5) in water and brown-grey (6E3) in 5% KOH solution; germ pore central to slightly eccentric, 0.8 – 1.8  $\mu\text{m}$  in wide. Basidia trimorphologic, 13 – 31  $\times$  4 – 7  $\mu\text{m}$ , short clavate to clavate, sometimes bulging in middle part, 4- or 2- spored, sterigmata 3 – 5  $\mu\text{m}$  in length; each basidium surrounded with 4 – 6 pseudoparaphyses. Cheilocystidia and pleurocystidia absent. Hymenophoral trama regular, trama hyphae 3 – 9  $\mu\text{m}$  in wide. Pileipellis spherocystoderm at ridge part and groove part, consisting of subglobose, ellipsoid or utriform cells, 22 – 53  $\times$  14 – 52  $\mu\text{m}$ , hyaline, thin-walled; pileocystidia clavate, lageniform to slender lageniform, 38 – 183  $\times$  11 – 29  $\mu\text{m}$ , with 10 – 17  $\mu\text{m}$  wide, with subcapitate apex, hyaline, thin-walled. Caulopellis hyphae 3 – 6  $\mu\text{m}$  wide, hyaline, sometimes branched and diverticulate, thin-walled; hyphae of stipe trama 11 – 26  $\mu\text{m}$  wide, hyaline, thin-walled to somewhat thick-walled. Caulocystidia clavate to narrow lageniform, 82 – 170  $\times$  14 – 67  $\mu\text{m}$ , with





**Figure 11.** Photographs of the fresh fruiting body of *Coprinellus austrodisseminatus*. (a–b) HMJAU67134.

6–16  $\mu\text{m}$  wide, could be found until the lower part of the stipes. Elements of the veil have two types: 1) chains of ellipsoid to subglobose elements, 19–38  $\times$  12–25  $\mu\text{m}$ , thick-walled, cream (1A3) to dark brown (6E8); 2) free subglobose to globose elements, 18–45  $\times$  13–41  $\mu\text{m}$ , thin-walled, hyaline. Hyphae of ozonium parallel dense arrangement, 2–5  $\mu\text{m}$ , slightly thick-walled to thick-walled, cream (1A3) to yellow-brown (5C6), darker in 5% KOH solution. Clamp connection and pseudoclamps are absent. The conidiophores are short and unbranched, constricted at the septa with swollen bases, hyaline, thick-walled, and around 2  $\mu\text{m}$  in wide, the apical cell of each conidiophore could produce one subulate phialide, 8–9  $\times$  3–4  $\mu\text{m}$ , with a puncta apex. Conidium unseen.

**Habitat:** In groups or caespitose soil, moss layer, or rotten wood in broad-leaved trees. Usually occurs in the middle of spring to summer.

**Distribution:** Southern and eastern Asia (China, Thailand).

**Additional specimens examined:** China: Guangdong Province: Shaoguan City, Chebaling National Nature Reserve, on rotten wood in broad-leaved forest, 7 May 2017, Tolgor Bau and Mei Huang, HMJAU46308, HMJAU46311; same location, on moss layer, HMJAU46307 (ITS: OR436399; LSU: OR436381); Hainan Province: Baisha County, Wuzhishan National Nature Reserve, on rotten wood in broad-leaved forest, Tolgor Bau and Qin Na, 6 June 2018, HMJAU49305 (ITS: OR436400; LSU: OR436382); Guizhou Province: Qiandongnan Mao and Dong Autonomous Prefecture, Leigong Mountain National Forest Park, dead branches of broad-leaved tree, Jun-Qing Yan; Guangxi: Baise City, Leye Courty, Yachang Orchid National Nature Reserve,

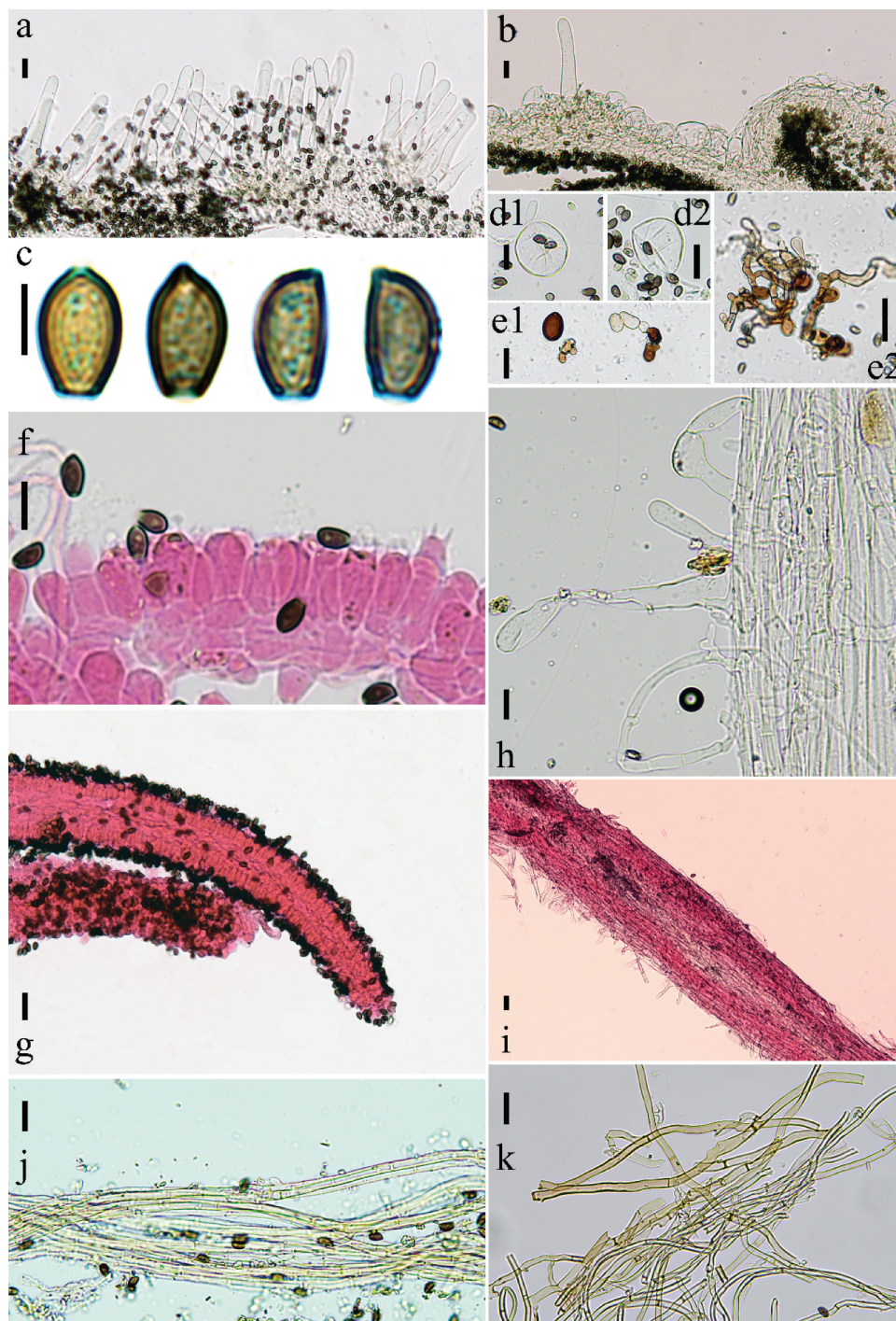
Niuping Protection Station, clayed soil in broad-leaved forest, Xiao-Liang Liu, Guang-Fu Mou and Li-Yang Zhu, 25 June 2021, HMJAU67122 (ITS: OR436401; LSU: OR436383); Yunnan Province: Kunming City, on rotten woods, October, 2017, Hai-Ying Bau, HMJAU49302; Kunming City, Kunming Botanical Garden, Fuligong Greenhouse, humus layer of *Alocasia macrorrhizos*, Tolgor Bau and Li-Yang Zhu, NaN Invalid Date NaN, HMJAU67135.

**Note:** This species was initially identified as an asexual endophytic fungus isolated from healthy leaves of *Magnolia garrettii* in Thailand and here we present the first description of its sexual stage. The main recognition feature of this species is the purple-grey pileus when mature, with the centre of the pileus lacking a brownish-yellow hue. Additionally, the caulocystidia of this species is relatively longer compared to other species in this section, typically measuring 120–170  $\mu\text{m}$  in length, and could also be found even at the lower part of stipes. *C. velutipes* is close to *C. magnoliae*, however, it has long-branched terminal cells of caulopellis (105–190  $\mu\text{m}$  in length) at the lower part of the stipes as well as clamp connection and pseudoclampe. The lower part of the stipes of *C. parvus* has distinct subglobose or utriform terminal cells that could be distinguished from *C. magnoliae*.

***Coprinellus velutipes* T. Bau & L.Y. Zhu sp. nov,**  
**Figures 17–19**

**Mycobank:** MB 849765.

**Etymology:** “*velutipes*” refers to its stipes with fine tomentum.



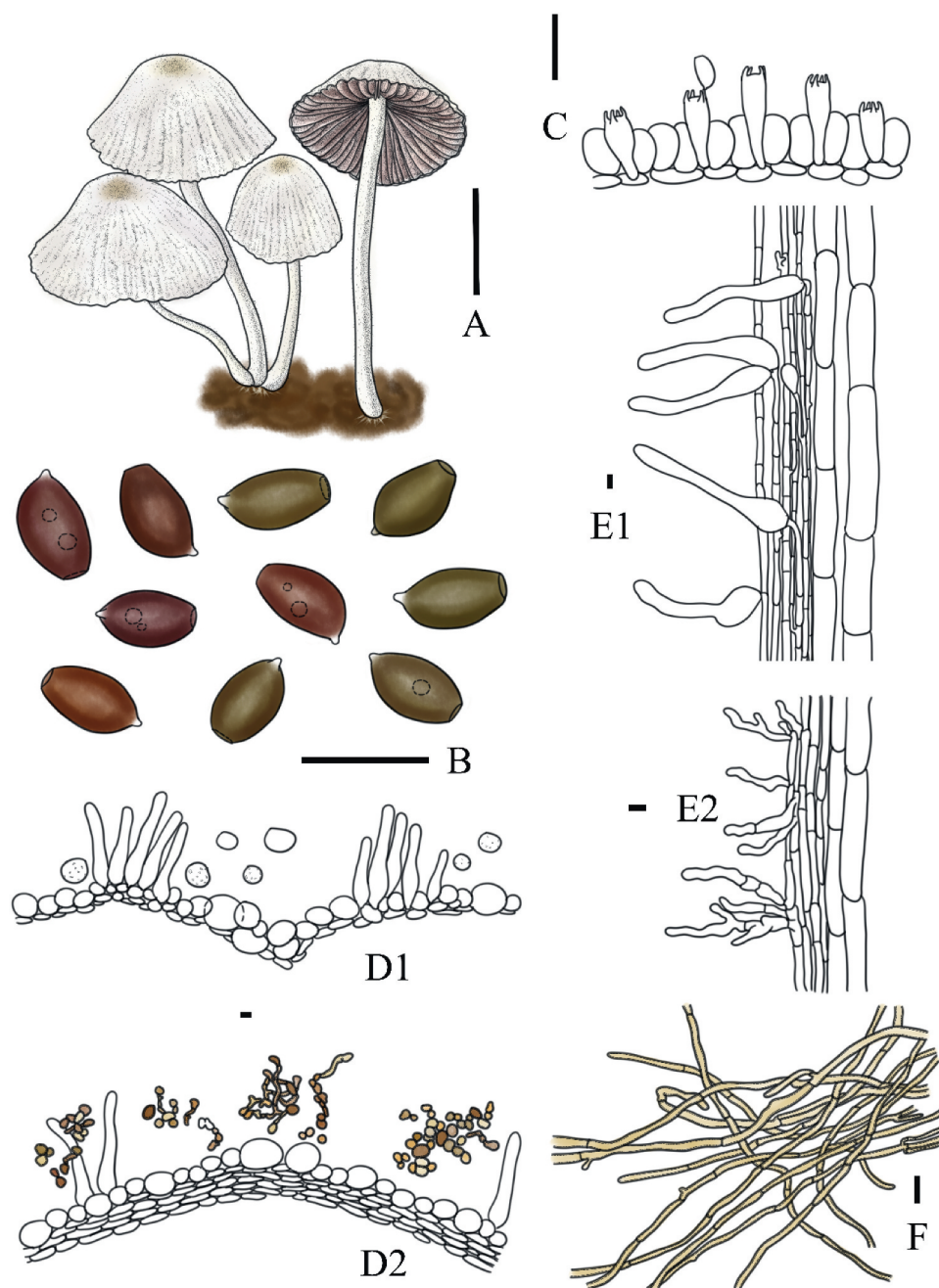
**Figure 12.** Micromorphological features of *Coprinellus austrodisseminatus*. (a) Pileocystidia; (b) Pileipellis; (c) Basidiospores; (d1–d2) Freely exfoliated veil cells; (e1–e2) Veils composed of short chains of light yellow-brown to dark brown, subglobose to ellipsoid cells; (f) Basidia; (g) Longitudinal section of lamellae; (h) Longitudinal section of stipes; (i) Colorless to light yellow mycelium at base of stipes; (j–k) Hyphae of ozonium at base of stipes. Bars: a–b, d1–d2, e1–e2, f–k = 20  $\mu\text{m}$ ; c = 5  $\mu\text{m}$ .

*Diagnosis:* Basidiomata tiny-sized; lower part of stipes with fine tomentum which is composed of long-branched cells usually with tapering apex microscopically; with cream to light brown ozonium at base of stipes; basidia trimorphological; clamp connection

present but rare and only seen in hyphae of subpileipellis or hymenophoral trama, pseudoclamps abundant in all part.

*Type:* China: Jiangsu Province: Nanjing City, a greenhouse in the south garden of Nanjing Botanical Garden





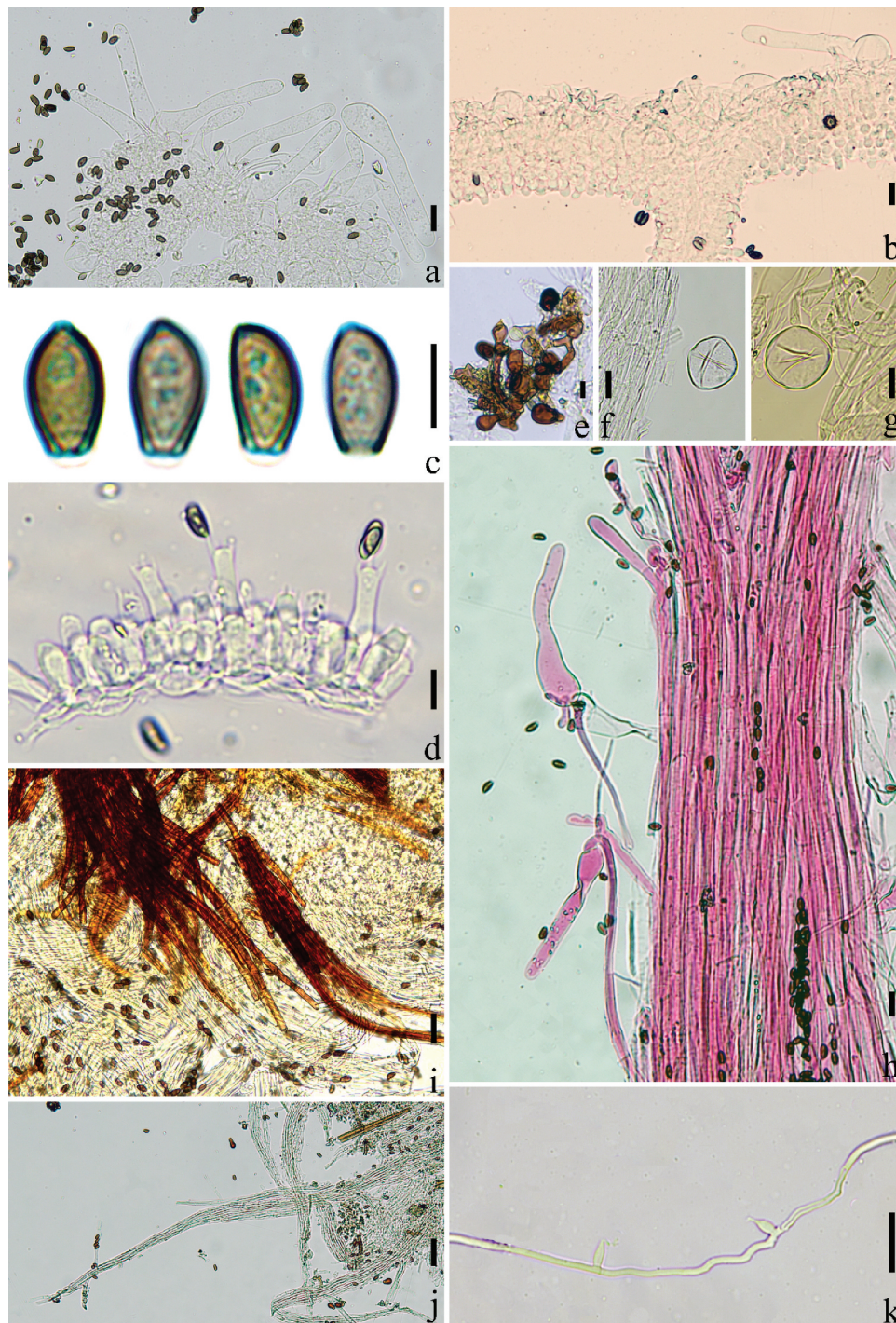
**Figure 13.** *Coprinellus austrodisseminatus*. (A) Basidiomata; (B) Basidiospores; (C) Basidia; (D1–D2) Pileipellis: (D1) Margin of pileus; (D2) Central of pileus; (E) Longitudinal section of stipes: (E1) Middle and upper part of stipes; (E2) Lower part of stipes; (F) Hyphae of ozonium. Bars: A = 1 cm; B–F = 10  $\mu$ m.

Mem. Sun Yat-Sen, on humus layer of Orchidaceae plant, 2 May 2022, Zi-Han Zhang, HMJAU67124 (ITS: OR436396).

**Description:** Basidiomata tiny-sized. Pileus 0.3 – 1.3 cm, first subglobose or campaniform, semi-globose to obtuse conical when mature, sometimes with a rounded umbo; white (1A1) to pearl white (2A2) when young, become grey-white (1B1), light purple-grey (14B2) or yellow cream (2A3) at age, light brown yellow (3B3) at the centre; the radial

grooves extended to the top, with a clear line at the folding part; pubescent. Context is very thin, only present at the centre part, white (1A1) to cream (3A2). Lamellae narrow adnate,  $L = 17 - 26$ ,  $l = 0$  or  $1$ , 0.1 cm in wide, first white (1A1) to cream (3A2), then pink-brown (7B2), finally blackish (7F4), undeliquescing at age. Stipe 2.8 – 5.3  $\times$  0.1 – 0.15 cm, white (1A2) to cream (3A2), hollow, crispy, pubescent, and with fine tomentum, without a volva-like margin and usually attach to cream to light brown ozonium.





**Figure 14.** Micromorphological features of *Coprinellus magnoliae*. (a) Pileocystidia; (b) Pileipellis; (c) Basidiospores; (d) Basidia; (e) Veils composed of short chains of light yellow-brown to dark brown, subglobose to ellipsoid cells; (f–g) Freely exfoliated veil cells; (h) Longitudinal section of stipes; (i) Hyphae of ozonium at base of stipes; (j) Colorless mycelium at base of stipes; (k) Conidiophores. Bars: a–b, d–k = 20  $\mu\text{m}$ ; c = 5  $\mu\text{m}$ .

Basidiospores [120, 6, 4] (6.5) 8.3 – 8.6 (10.7)  $\times$  (4.4) 4.9 – 5.1 (6.2)  $\times$  (4.2) 4.7 – 4.8 (5.5)  $\mu\text{m}$ ,  $Q_1 = 1.38 – 2.03$ ,  $Q_2 = 1.49 – 2.08$ , ovoid to long ovoid in frontal view, amygdaliform with acute apex in side view, obconical at the base and truncate at apex, dark red-brown (6E8) in water and blackish (5E3) in 5% KOH solution; germ pore

central to slightly eccentric, 0.9 – 1.9  $\mu\text{m}$  in wide. Basidia trimorphological, 14 – 26  $\times$  6 – 10  $\mu\text{m}$ , short clavate to clavate, 4- or 2- spored, sterigmata 3 – 5  $\mu\text{m}$  in length; each basidium surrounded with 4 – 6 pseudoparaphyses. Cheilocystidia and pleurocystidia absent. Hymenophoral trama regular, trama hyphae 2 – 7  $\mu\text{m}$  in wide. Pileipellis





**Figure 15.** Photographs of the fresh fruiting body of *Coprinellus magnoliae*. (a–d) HMJAU67122.

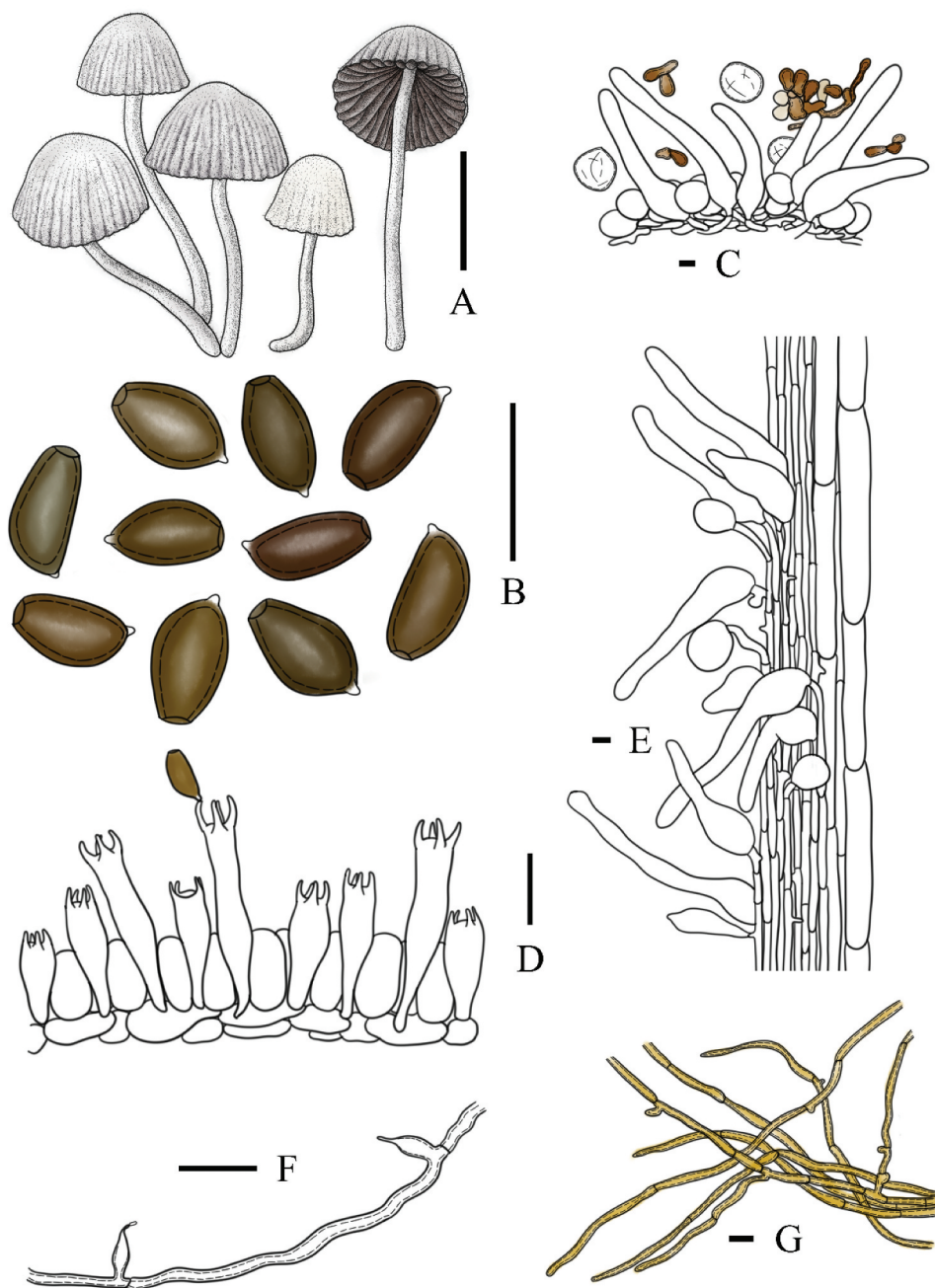
spherozystoderm at ridge part and groove part, consisting of subglobose cells,  $20 - 53 \times 17 - 47 \mu\text{m}$ , hyaline, thin-walled to slightly thick-walled; pileocystidia clavate to lageniform,  $23 - 169 \times 17 - 47 \mu\text{m}$ , with  $9 - 19 \mu\text{m}$  wide, tapering neck, sometimes subcapitate apex, hyaline or with brown hue at base, thin-walled, sometimes slightly thick-walled at base. Caulopellis hyphae  $4 - 7 \mu\text{m}$  wide, hyaline, rare diverticulate at middle and upper part and multiple-branched ( $29 - 336 \mu\text{m}$  in length) and diverticulate at lower part, thin-walled; hyphae of stipe trama  $10 - 20 \mu\text{m}$  wide, hyaline, thin-walled to somewhat thick-walled. Caulocystidia multi-shaped: 1) long lageniform to clavate,  $81 - 143 \times 13 - 22 \mu\text{m}$ , with  $7 - 15 \mu\text{m}$  wide, erect or bender, tapering neck; or 2) subglobose to ellipsoid,  $16 - 54 \times 10 - 20 \mu\text{m}$ , thin-walled to slightly thick-walled. The veil on pileus and stipes only composed of colourless, subglobose to globose cells,  $16 - 49 \times 10 - 20 \mu\text{m}$ , hyaline, thin-walled to slightly thick-walled; terminal cells of caulopellis at the lower part of stipes long-branched,  $105 - 190 \mu\text{m}$  in length, usually with tapering apex. Hyphae of ozonium parallel dense arrangement,  $4 - 6 \mu\text{m}$ , slightly thick-walled to thick-walled, cream (5A2) to rust-brown (6D8), darker in 5% KOH solution. Clamp connection is rare and only be seen in hyphae of subpileipellis or hymenophoral trama, pseudoclamps abundant in all parts.

*Habitat:* In groups or caespitose on the humus layer of Orchidaceae plant or on or near a living tree or the bark of the broad-leaved tree. Usually occurs in summer.

*Distribution:* Eastern and central China.

*Additional specimens examined:* China: Zhejiang Province: Hangzhou City, Zijingang Campus of Zhejiang University, on living tree of *Styphnolobium japonicum*, 5 July 2021, Tolgor Bau, Wen-Fei Lin, and Li-Yang Zhu, HMJAU67123 (ITS: OR436398); Hunan Province: Changsha City, Yuelu Mountain, on soil near *Platanus hispanica*, 8 July 2022, Li-Yang Zhu, Han-Bing Song, HMJAU67126 (ITS: OR436395; LSU: OR436389); Shaoyang City, Shidai Park, on bark of broad-leaves tree, 3 July 2022, Li-Yang Zhu, Han-Bing Song, HMJAU67125 (ITS: OR436397; LSU: OR436388).

*Notes:* This species is characterised by its clamp connections and flocculent stipes, while lacking brown veil elements (which were not even observed in young basidiomata in our study). Currently, this species has only been found in eastern and central China. The cream to light brown ozonium of this species is relatively dense on the humus layer of orchids, but scarcer on other substrates. *C. disseminatus* subsp. *orientalis* is similar to *C. velutipes*, while this species lacks clamp connection and has brown thick-walled veil



**Figure 16.** *Coprinellus magnoliae*. (A) Basidiomata; (B) Basidiospores; (C) Pileipellis; (D) Basidia; (E) Longitudinal section of stipes; (F) Conidiophores; (G) Hyphae of ozonium. Bars: A = 1 cm; B–G = 10  $\mu$ m.

elements. Furthermore, *C. disseminatus* subsp. *orientalis* is only found in northern China.

***Coprinellus disseminatus* subsp. *orientalis*** T. Bau & L. Y. Zhu subsp. nov, Figures 20–22

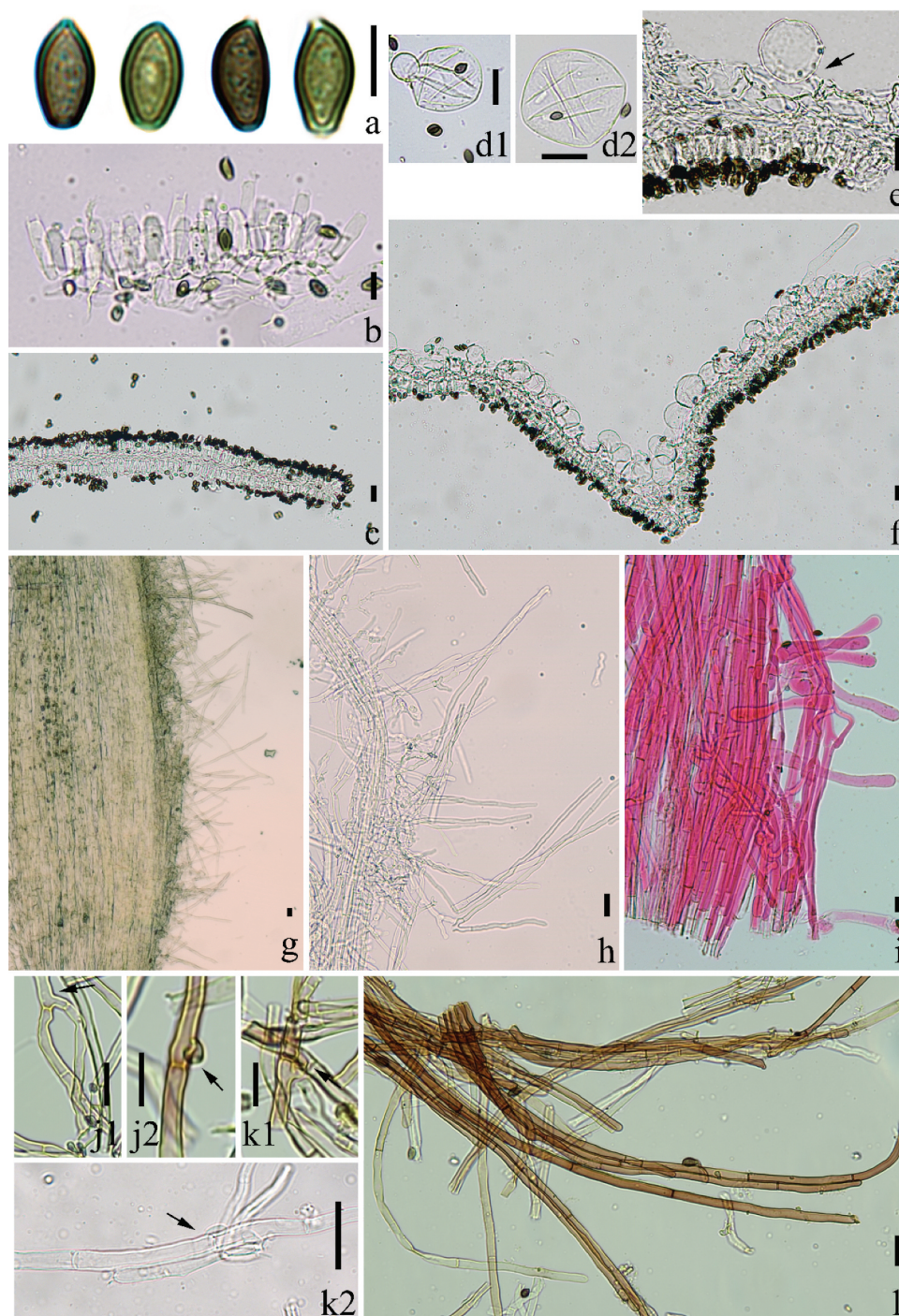
*Mycobank*: MB 849766.

*Etymology*: “*orientalis*” indicates that this new subspecies is distributed in northeast Asia.

*Diagnosis*: Basidiomata tiny-sized; pileus light grey to grey when mature, mostly without brown hue; lamellae relatively sparse ( $L=14-19$ ); basidia trimorphological; terminal cells of caulopellis at the lower part of stipes mixed with short-branched, long-branched and urtiform or ellipsoid cells; distributed in northeast Asia.

*Type*: China: Jilin Province: Changchun City, a campus of Jilin Agricultural University, on the base of the living tree of *Salix* spp., 16 September 2020, Li-Yang Zhu, HMJAU67128 (ITS: OR436409).

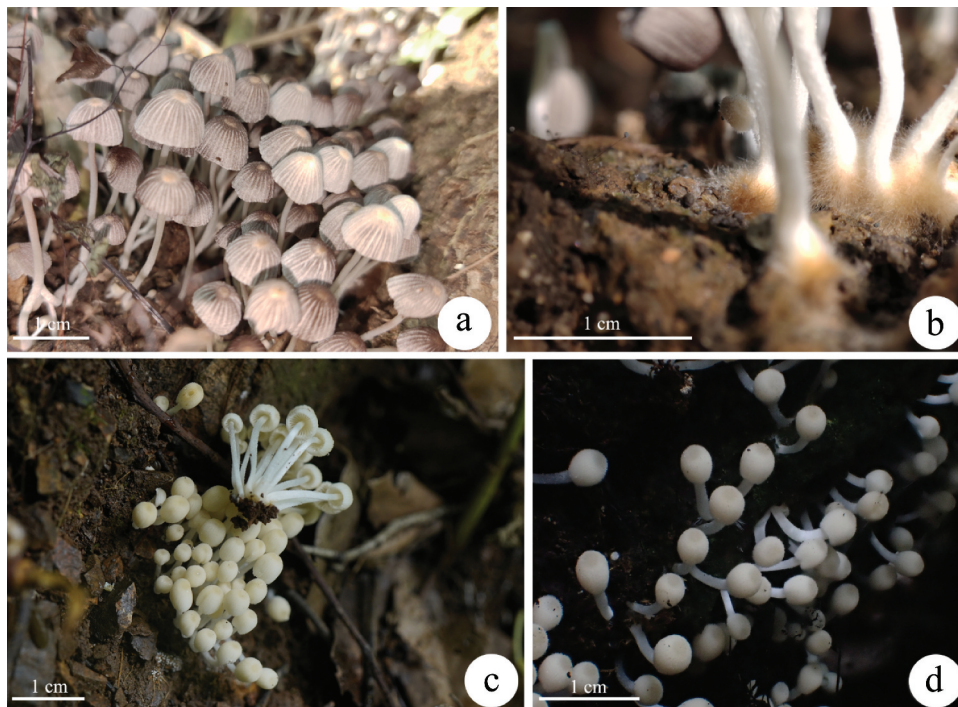




**Figure 17.** Micromorphological features of *Coprinellus velutipes*. (a) Basidiospores; (b) Basidia; (c) Longitudinal section of lamellae; (d1–d2) Freely exfoliated veil cells; (e) Veil cells attaching pileus; (f) Longitudinal section of pilei; (g) Longitudinal section of lower part of stipes; (h) Long branches of hyphae of caulopellis of lower part of stipes; (i) Longitudinal section of upper part of stipes; (j1–j3) Short branches of hyphae near septa, resembling clamp connections; (k) Clamp connection; (l) Hyphae of ozonium. Bars: a = 5  $\mu$ m; b–l = 20  $\mu$ m.

**Description:** Basidiomata tiny-sized. Pileus 0.3 – 0.9 cm, first subglobose, pearl white to pale grey, cover with yellow-brown to dark brown powdery or finely scaly scales; then become ellipsoid or campaniform, white (1A1), cream (3A2) to light

yellow-brown (3B3), the colour on the centre of pileus usually darker; obtuse conical when mature, light grey (1B1) to grey, mostly without brown hue; the radial grooves extended to the top, with a clear line at the folding part; pubescent. Context is very



**Figure 18.** Photographs of the fresh fruiting body of *Coprinellus velutipes*. (a–b) HMJAU67124; (c) HMJAU67125; (d) HMJAU67123.

thin, only present at the centre part, white (1A1) to cream (3A2). Lamellae narrow adnate,  $L = 14 - 19$ ,  $l = 0 - 3$ , 0.1 cm in wide, first white (1A1) to cream (3A2), then purple-brown (7B2), finally blackish (7F4), mostly non-deliquescent at age except in moist environment. Stipe  $1.3 - 3.8 \times 0.1 - 0.15$  cm, white (1A2) to cream (3A2), hollow, crispy, pubescent, and with fine tomentum at the middle and lower part of the stipe, without a volva-like margin. Ozonium at the base of the stipe is absent most time.

Basidiospores  $[60, 6, 5] (6.3) 7.9 - 8.2 (9.0) \times (4.4) 4.9 - 5.1 (5.6) \times (4.5) 4.8 - 5.0 (5.7) \mu\text{m}$ ,  $Q_1 = 1.36 - 1.77$ ,  $Q_2 = 1.47 - 1.83$ , ovoid to long ovoid in frontal view, amygdaliform with the acute apex in side view, obconical at the base and truncate at apex, dark red-brown (6E8) in water and blackish (5E3) in 5% KOH solution; germ pore central to slightly eccentric,  $1.0 - 1.9 \mu\text{m}$  in wide. Basidia trimorphological,  $11 - 31 \times 4 - 8 \mu\text{m}$ , short clavate to clavate, 4-spored, sterigmata  $3 - 4 \mu\text{m}$  in length; each basidium surrounded with 4–6 pseudo-paraphyses. Cheilocystidia and pleurocystidia absent. Hymenophoral trama regular, trama hyphae  $2 - 11 \mu\text{m}$  in wide. Pileipellis spherocystoderm at ridge part and groove part, consisting of subglobose cells,  $20 - 57 \times 18 - 46 \mu\text{m}$ , hyaline, thin-walled to slightly thick-walled; pileocystidia clavate to lageniform,  $71 - 211 \times 8 - 29 \mu\text{m}$ , with  $9 - 16 \mu\text{m}$  wide, tapering

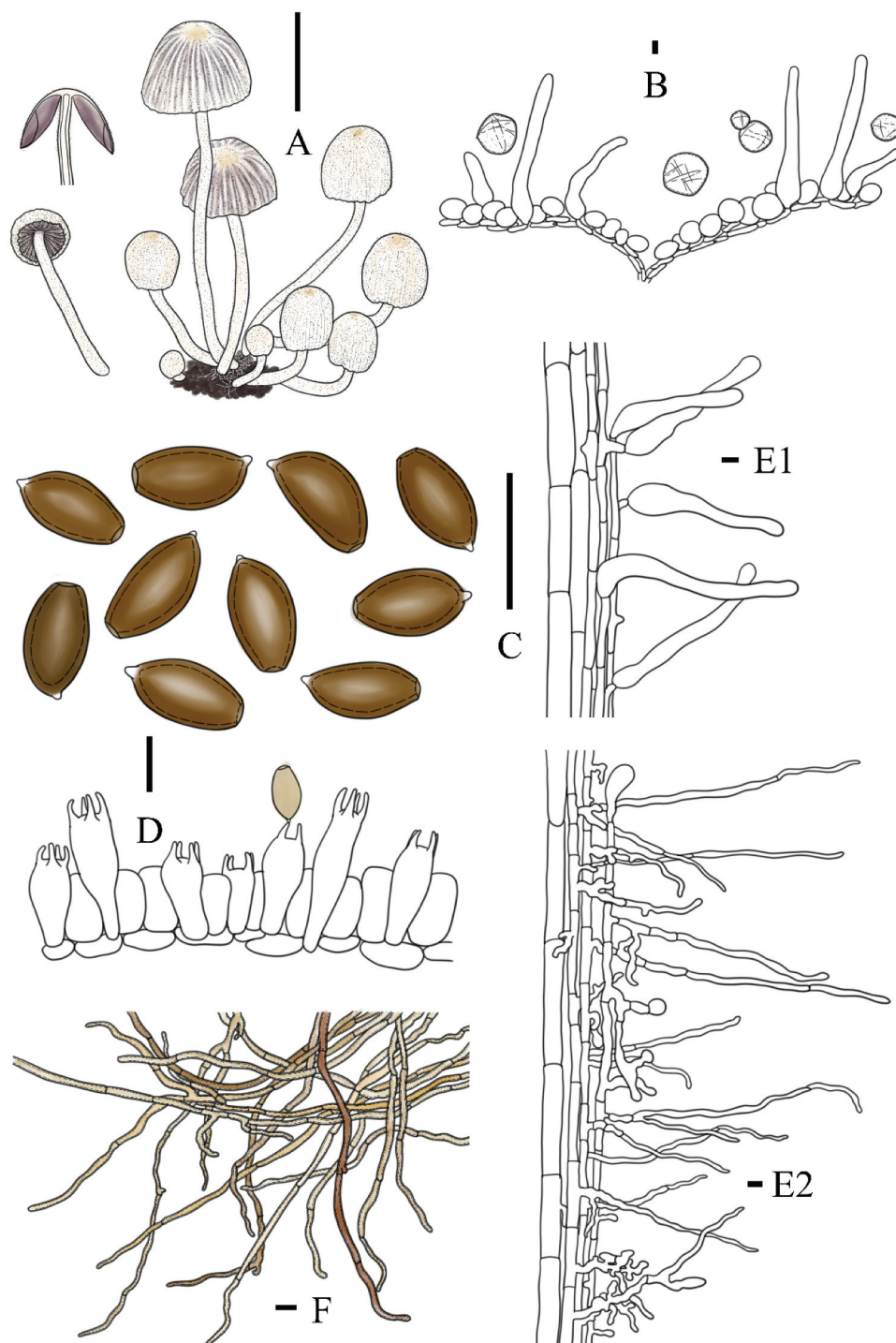
neck, sometimes subcapitate apex, hyaline or with brown hue at base, thin-walled, sometimes slightly thick-walled at base. Caulopellis hyphae  $2 - 6 \mu\text{m}$  wide, hyaline, rare diverticulate at middle and upper part and multiple-branched ( $16 - 96 \mu\text{m}$  in length) and diverticulate at lower part, thin-walled; hyphae of stipe trama  $10 - 22 \mu\text{m}$  wide, hyaline, thin-walled to somewhat thick-walled. Caulocystidia long lageniform to clavate,  $41 - 180 \times 16 - 33 \mu\text{m}$ , with  $6 - 13 \mu\text{m}$  wide, erect or bender, tapering neck; terminal cells of caulopellis at the lower part of stipes mixed with short-branched, long-branched and urtiform or ellipsoid cells. The veil on pileus and stipes dimorphologic: (1) colourless, subglobose to globose cells,  $16 - 49 \times 10 - 20 \mu\text{m}$ , hyaline, thin-walled to slightly thick-walled; (2) chains of light yellow-brown to dark brown, subglobose to ellipsoid cells,  $6 - 20 \times 6 - 15 \mu\text{m}$ , thick-walled. Clamp connection absent.

*Habitat:* In groups or caespitose on the base of the trunk or near living trees or bark of broad-leaved trees. Usually occurs in summer to autumn.

*Distribution:* North and Northeast China.

*Additional specimens examined:* China: Heilongjiang Province: Yichun City, Liangshuihe National Forest Park, on rotten woods, 29 August 2015, Tolgor Bau, HMJAU46466, HMJAU46467; Jiamusi City, Fuyuan City, Tongjiang Town, Dongfa Village, on moss layer on





**Figure 19.** *Coprinellus velutipes*. (A) Basidiomata; (B) Pileipellis; (C) Basidiospores; (D) Basidia; (E1–E2) Longitudinal section of stipes: (E1) Middle to upper part of stipes; (E2) Lower part of stipes; (F) Hyphae of ozonium. Bars: A = 1 cm; B–F = 10  $\mu$ m.

trunk of living tree of *Quercus mongolica*, 29 July 2023, Li-Yang Zhu and Wei-Nan Hou, HMJAU67140; Inner Mongolia Autonomous Region: Tongliao City, Daqinggou National Nature Reserve, on bark of living tree, 1997, Tolgor Bau, HMJAU1651; same location, on rotten wood, 16 June 2018, Tolgor Bau and Mei Huang, HMJAU46427; same location, on bark of living tree, 6

August 2021, Tolgor Bau and Li-Yang Zhu, HMJAU67131 (ITS: OR436407); Jilin Province: Changchun City, Jingyuetan National Forest Park, on bark of willow (*Salix* spp.) tree, Jian-Rui Wang, 24 June 2005, HMJAU3734, HMJAU3744; same location, on rotten woods, 25 June 2017, Qin Na and Ming-Zheng Duan, HMJAU46334; same location, on rotten woods,



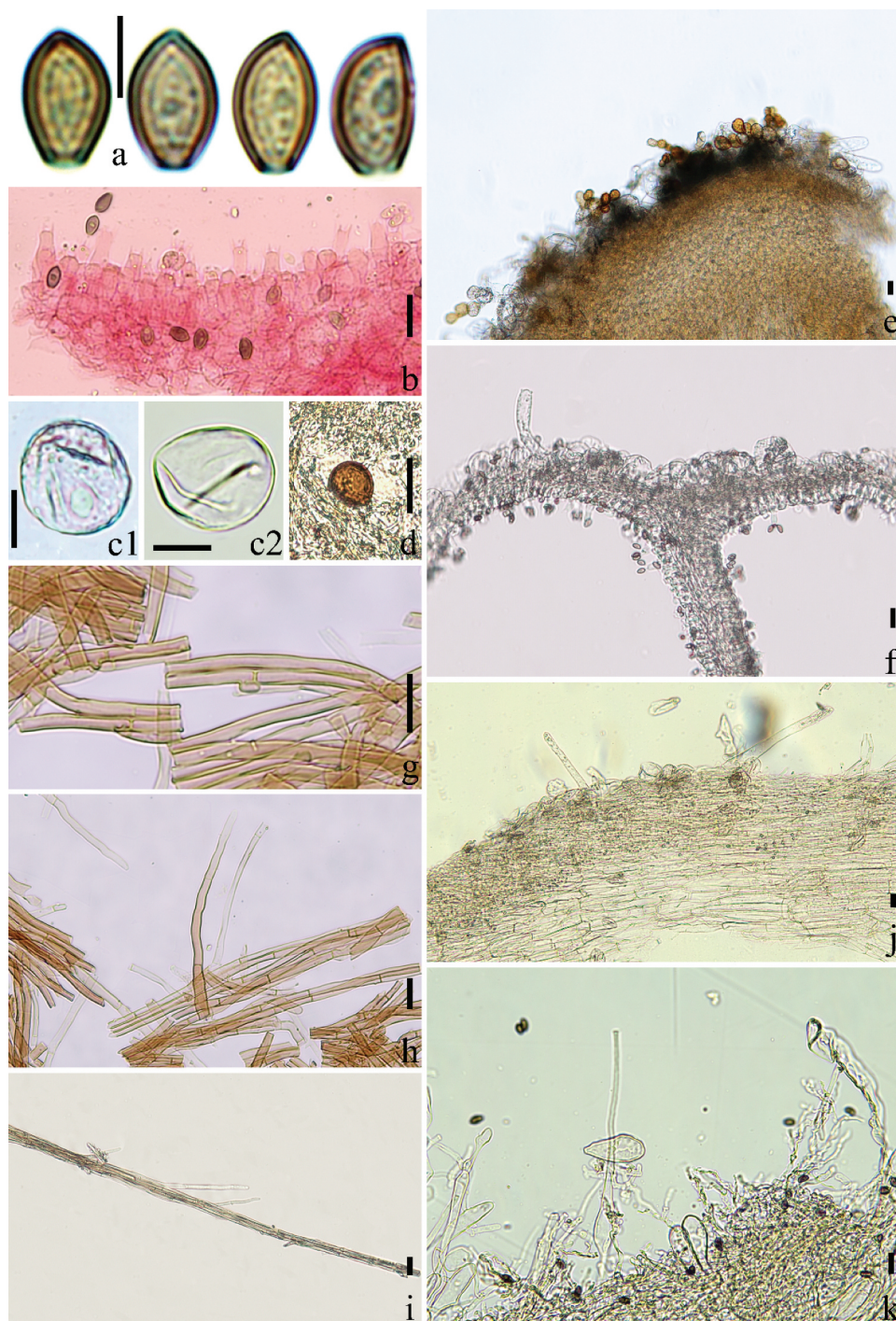


**Figure 20.** Photographs of the fresh fruiting body of *Coprinellus disseminatus* subsp. *orientalis*. (a) HMJAU67140; (b) HMJAU67141; (c) HMJAU67131; (d) HMJAU67139; (e–h) HMJAU67128 (type).

7 July 2017, Mei Huang, HMJAU46362; Changchun City, campus of Jilin Agricultural University, on base of broad-leaved tree, 15 July 2023, Li-Yang Zhu and Jun-Lin Wei, HMJAU67141; Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, on rotten wood, 18 July 2001, Tolgor Bau, HMJAU5168; same location, on rotten wood, 30 July 2014, Tolgor Bau, HMJAU35909; Yanbian Korean Autonomous

Prefecture, Dunhua City, Hancongling State Forest Farm, on root of *Pinus koraiensis*, 27 July 2022, Tolgor Bau and Li-Yang Zhu, HMJAU67130 (ITS: OR436411; LSU: OR436380); Yanbian Korean Autonomous Prefecture, Fusong County, Lushui River Hunting Ground, 25 June 2009, Tolgor Bau, HMJAU22008 (ITS: OR436408; LSU: OR436379); Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe

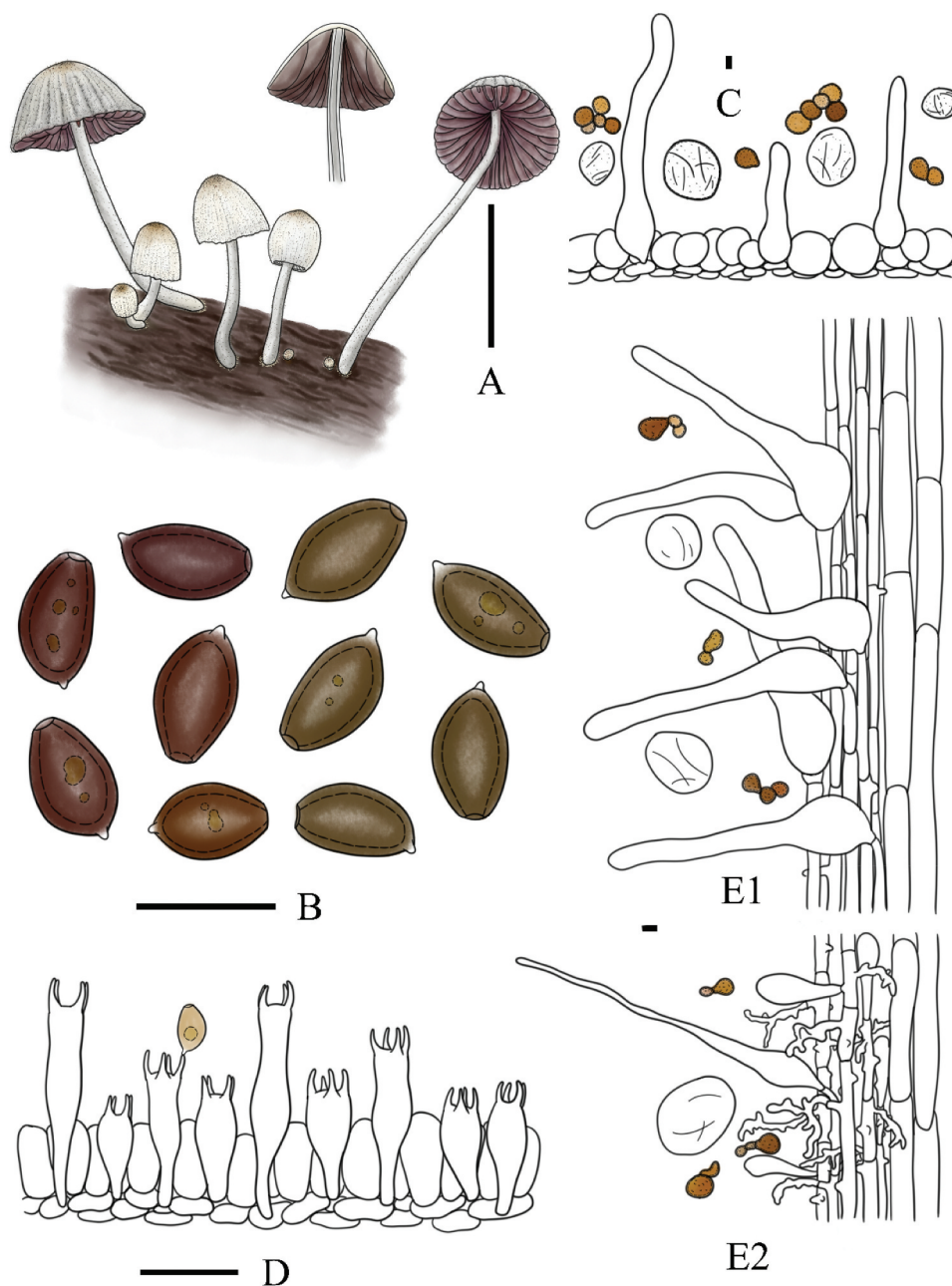




**Figure 21.** Micromorphological features of *Coprinellus disseminatus* subsp. *orientalis*. (a) Basidiospores; (b) Basidia; (c1–c2) Freely exfoliated veil cells; (d) Dark brown, subglobose to ellipsoid veil cells; (e) Longitudinal section pileus of the young fruiting body; (f) Longitudinal section of pileus of the mature fruiting body; (g) Short branches of hyphae near septa, resembling clamp connections; (h) Hyphae of ozonium; (i) Colorless to light yellow mycelium at base of stipes; (j) Longitudinal section of the upper part of stipes; (k) Longitudinal section of the lower part of stipes. Bars: a = 5  $\mu\text{m}$ ; b–k = 20  $\mu\text{m}$ .

Town, Heping Forest Farm, on rotten woods, 26 July 2017, Yu-Peng Ge, HMJAU67143; Yanbian Korean Autonomous Prefecture, Helong City, Bajiazi Town, Xianfeng National Forest Park, on the base of broad-leaved tree, 22 August 2020, Tulgor Bau and Li-Yang

Zhu, HMJAU67139; Jilin City, Jiaohe City, Laoyeling Mountain, on ground under forest, 13 June 2009, Tolgor Bau, HMJAU21901; Jilin City, Jiaohe City, Qianjin Forest Farm, 26 June 2017, Tolgor Bau and Mei Huang, HMJAU46339; Jilin City, Jiaohe City,



**Figure 22.** *Coprinellus disseminatus* subsp. *orientalis*. (A) Basidiomata; (B) Basidiospores; (C) Pileipellis; (D) Basidia; (E1–E2) Longitudinal section of stipes: (E1) Middle to upper part of stipes; (E2) Lower part of stipes. Bars: A = 1 cm; B–F = 10  $\mu$ m.

Shengli River Forest Farm, on stump of broad-leaved tree, 27 June 2017, Tolgor Bau and Mei Huang, HMJAU46345, HMJAU46346; Jilin City, Jiaohe City, Shansongling Mountain, on root of fallen broad-leaved tree, 26 July 2022, Tolgor Bau and Li-Yang Zhu, HMJAU67129 (ITS: OR436410); Shaanxi Province: Yangling Agricultural Hi-tech Industries Demonstration Zone, campus of Northwest A&F University, on the ground around with *Albizia*

*julibrissin*, 20 September 2020, Hui-Ning Peng, HMJAU67127 (ITS: OR436412).

*Notes:* The distribution in Northeast Asia is a significant distinguishing characteristic of this subspecies. The pileus of the original subspecies found in Europe was previously described as pale brown, yellow-brown, or ochre, but the colour of materials we collected usually lacked the yellow-brown hue. Additionally, the basidia of the original subspecies



are relatively larger (16–41 µm) than those of the specimens we observed here. The presence of multiple-branched and diverticulate caulopellis hyphae at the lower part of the stipes was not reported in the original subspecies, but we found it to be a relatively stable characteristic in *C. disseminatus* subsp. *orientalis*. *C. velutipes* also possess similar structures, while their branches are much longer, measuring up to 336 µm in length.

Furthermore, we identified a unique 54 bp length sequence in the hyper-variable ITS1 domain (5'-TTGCRGTGCGTAGCRCTGCGTGTCGCGCRGTTGCG-TTGGCTACGGGCTC(T)A-3', site 135 to 190; shown in Table 2) for this subspecies. This sequence could also distinguish this Northeast Asian subspecies from the original subspecies from Europe. The blast result with this sequence (Figure S2) revealed that the most similar sequences were all located in Northeast Asia. Therefore, we consider these fragments as the DNA barcode of this subspecies.

***Tulosesus pseudodisseminatus*** (T. Bau & M. Huang) T. Bau & L.Y. Zhu comb. nov

*Mycobank*: MB 849767.

*Basionym*: *Coprinellus pseudodisseminatus* T. Bau & M. Huang, in Huang & Bau, *Phytotaxa* 374(2): 119–28 (2018).

*Etymology*: The prefix “pseudo” means false and “disseminatus” means the morphological similarity between this species and *C. disseminatus*.

*Type*: China: Jilin Province, Lushuihe National Forest Park, Baishan City, August 7, 17, Tolgor Bau and Mei Huang, HMJAU46301.

*Additional specimens examined*: China: Heilongjiang Province: Yichun City, Liangshuihe National Forest Park, on rotten woods, 16 July 2016, Jun-Qing Yan and Qin Na, HMJAU46303; Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, Mountain near Academy of Sciences of Changbai Mountain, rotten woods, 6 August 2017, Tolgor Bau and Mei Huang, HMJAU46300; Guangdong Province: Shaoguan City, Chebaling National Nature Reserve, on rotten woods, 8 May 2017, Mei Huang, HMJAU46312; Zhaoqing City, Dinghushan National Nature Reserve, on rotten woods, 10 May 2017, Mei Huang, HMJAU46298; Chongqing City: Fuling District,

Baihe Forest Park, on bark of living tree, 2 October 2017, Mei Huang, HMJAU46302; Hainan Province: Yuedong County, Jianfengling National Nature Reserve, Mingfeng Valley, on rotten woods, 28 June 2018, Tolgor Bau and Qin Na, HMJAU46442; Guangxi Zhuang Autonomous Region: Chongzuo City, Longzhou County, Nonggang National Nature Reserve, on rotten woods, 16 May 2017, Mei Huang, HMJAU46299; same location, on rotten woods, 17 May 2017, Mei Huang, HMJAU46321.

*Notes*: *T. pseudodisseminatus* is phylogenetic close to *T. velatopruinatus*, and these two species share similar ellipsoid to oblong basidiospores and cylindrical veil elements that differ from “fairy inkcap” in *Coprinellus*. However, *T. velatopruinatus* mostly grows on grassland, with pileus that are usually tussle-shaped to flat when mature, and cheilocystidia that are mostly globose to ellipsoid. In comparison, *T. subdisseminatus* mainly grows on grassland and lacks cheilocystidia.

***Tulosesus subdisseminatus*** (M. Lange) D. Wächt. & Melzer, Figures 23, 24

*Description*: Basidiomata tiny-sized. Pileus 0.4–0.7 cm, first ellipsoid, semisphere when mature, without a rounded umbo; cream (1A2) when young, become grey-white (1B1) or light purple-grey (11D2) at age, light orange-brown (6B5) at the centre; the radial grooves extended to the top of the cap after maturation; pubescent. Context very thin, only present at the centre part, white (1A1) to cream (1A2). Lamellae narrow adnate, L = 16–19, l = 1, 0.1 cm in wide, first white to light grey-white (9B1), finally light red-brown (9D5), non-deliquescent at age. Stipe 2.1–3.0 × 0.1 cm, white (1A1) to cream (1A2), hollow, crispy, pubescent, without a volva-like margin.

Basidiospores [40, 3, 1] (10.6) 11.8–12.3 (14.9) × (5.7) 6.2–6.6 (7.3) × (5.3) 5.9–6.3 (7.3) µm, Q<sub>1</sub> = 1.58–2.52, Q<sub>2</sub> = 1.68–2.40, oblong to cylindrical in front and side view, dark red-brown (8E8) in water and deep olivaceous (28F4) or dark brown-grey (30F5) in 5% KOH solution; germ pore eccentric, 1.7–3.2 µm in wide. Basidia dimorphologicals, 17–34 × 6–10 µm, short clavate to clavate, 4- or 2- spored, sterigmata 4–7 µm in length; each basidium surrounded with 4–6 pseudoparaphyses.

Cheilocystidia and pleurocystidia unseen. Hymenophoral trama regular, trama hyphae 3–12 µm in wide. Pileipellis spherocystoderm at ridge part and groove part, consisting of subglobose, ellipsoid or utriform cells, 16–71 × 14–51 µm, hyaline, thin-walled; pileocystidia clavate, lageniform to slender lageniform, 56–159 × 13–19 µm, with 7–14 µm wide, hyaline and with brown hue (5B3) at base, thin-walled. Caulopellis hyphae 3–9 µm wide, hyaline, thin-walled; hyphae of stipe trama 11–26 µm wide, hyaline, thin-walled. Caulocystidia clavate to slender lageniform, 95–134 × 13–25 µm, with 7–12 µm wide, thin-walled, hyaline. Elements of veil unseen. Sclerocystidia absent. Clamp connection present.

*Habitat:* in groups in grassland. Occur in summer.

*Specimens examined:* China: Jiangsu Province: Nanjing City, Zhongshan Hill Scenic Area, on lawn, 18 June 2022, Wei-Jie Li, HMJAU67117.

*Distribution:* Europe (Denmark, the Netherlands, Hungary) (Lange and Smith 1953; Ujlé and Bas 1991), Asia (China).

*Note:* This species was previously believed to be closely related to *C. disseminatus* (Lange and Smith 1953; Ujlé and Bas 1991; Ujlé et al. 2005). However, Wachter and Melzer's phylogenetic results in 2020 confirmed that

it should be classified as *Tulosesus*. During our study, we did not observe any cheilocystidia, while previous studies based on European materials (Lange and Smith 1953; Ujlé and Bas 1991; Ujlé et al. 2005) have described the presence of cheilocystidia. This species is relatively rare and is mostly found on wet sticks and other vegetable substrates, as reported in previous studies.

### Key

1. Veil present. .... 2
1. Veil absent. .... *T. subdisseminatus*
2. Veil only composed of chains of narrow, branched, hyaline cells. .... *T. pseudodisseminatus*
2. Veil mostly composed of hyaline or brown (sub) globose cells. .... 3
3. Hyaline veil cells absent; pileipellis in spherocystoderm at ridge part and in paraderm in groove part. .... *C. aureodisseminatus*
3. Hyaline veil cells present; pileipellis in spherocystoderm at ridge part and groove part. .... 4
4. Cheilocystidia present. .... *C. disseminatus-similis*
4. Cheilocystidia absent. .... 5
5. Basidia monomorphological or dimorphological. .... 6
5. Basidia trimorphological, sometimes constricted in the middle part. .... 7

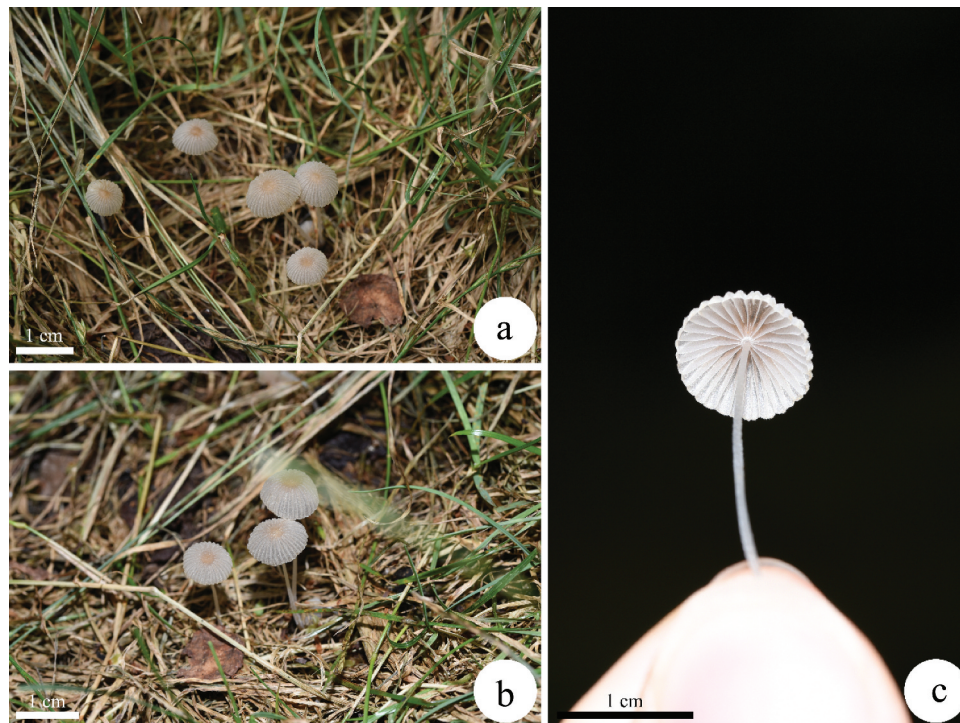
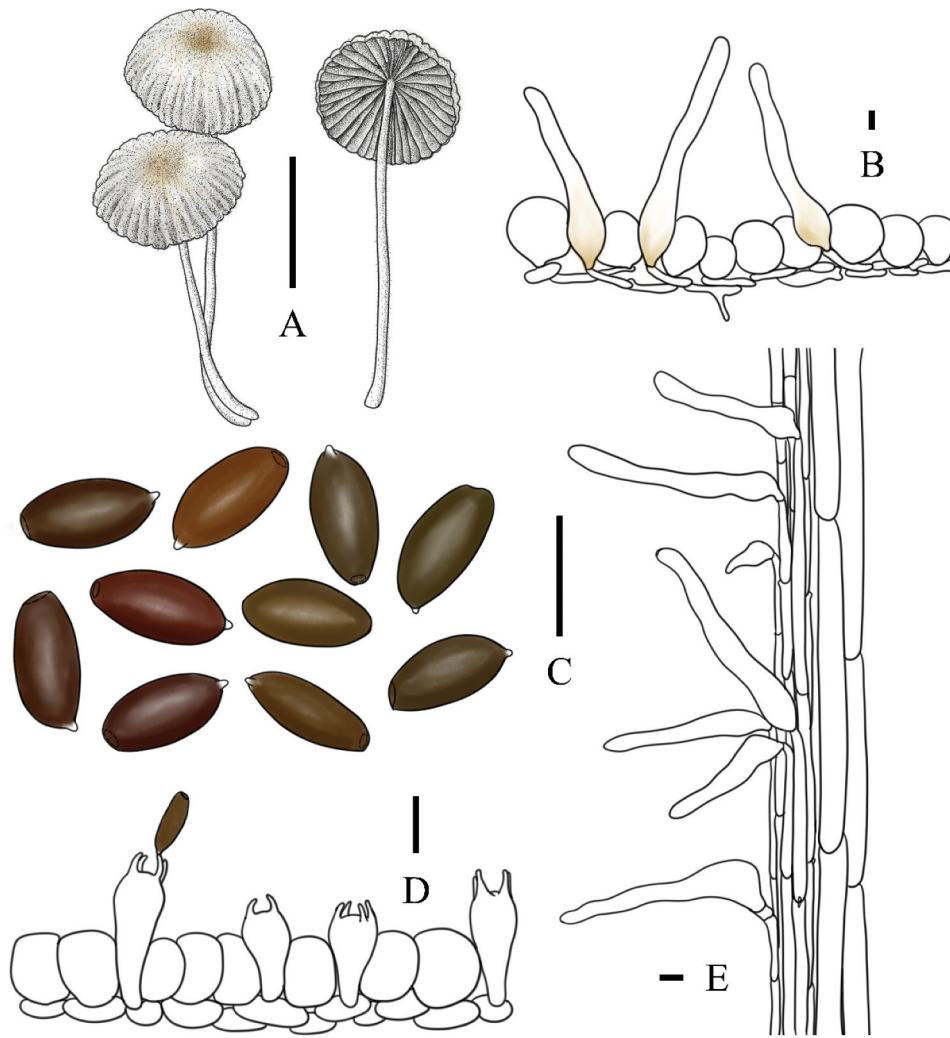


Figure 23. Photographs of the fresh fruiting body of *Tulosesus subdisseminatus*. (a–c) HMJAU67117.



**Figure 24.** *Tulosesus subdisseminatus*. (A) Basidiomata; (B) Pileipellis; (C) Basidiospores; (D) Basidia; (E) longitudinal section of stipes. Bars: a = 1 cm; B–E = 10 µm.

- 6. Pileus mostly larger than 1.0 cm; pseudoparaphyses 4 – 6 per basidium; terminal cells of caulopellis at the lower part of stipes most in narrow cylindrical with short branches; hyphae of stipitrama 19 – 33 µm in wide. .... *C. austrodisseminatus*
- 6. Pileus mostly less than 0.7 cm; pseudoparaphyses 3 – 5 per basidium; germ pore basidiospores in average 1.2 µm in wide; terminal cells of caulopellis at the lower part of stipes globose, ellipsoid or utriform; hyphae of stipitrama 10 – 18 µm in wide. .... *C. parvus*

- 7. Lower part of the stipe obviously puberulent which is composed of multi-branched hyphae. .... 8
- 7. Lower part of the stipe is not obviously puberulent. .... *C. magnoliae*
- 8. Veil cells monomorphological, only composed of hyaline (sub)globose cells; clamp connection present at subpileipellis and gill trama. .... *C. velutipes*
- 8. Veil cells diomorphological, composed of hyaline (sub)globose cells and short chains of brown or ochre globose cells; clamp connection absent. ... 9



9. Pileus with brown hue when mature. . . . .  
 . . . . . *C. disseminatus* subsp. *disseminatus*  
 (9) Pileus with white-grey to grey hue when  
 mature. . . . . *C. disseminatus* subsp. *orientalis*

## 4. Discussions

### 4.1. Morphological features and amendment of description of sect. *Disseminati*

Diverging from previous studies, *C. disseminatus* subsp. *orientalis* and *C. magnoliae* were observed to autolyse in humid environments. Combining these observations, we propose four revisions to the description of sect. *Disseminati*, in addition to the original definition by Wächter and Melzer (2020): 1) Lamellae are generally not deliquescent under most conditions, except for high humidity; 2) Veils consist of two types of elements: Chains of brown, thick-walled subglobose or cylindrical cells (unseen in *C. velutipes*) and free hyaline thin-walled globose cells; 3) Cheilocystidia are absent in most species; 4) Clamp connections are absent in most species, but short side-branches of hyphae near septa, resembling clamps, are often observed.

Although previous descriptions of species in “fairy inkcap” have used basidia types, the criteria for these have not been clearly defined. In this study, we employed numerical classification to cluster the lengths of basidia based on scatter coordinates (Figure S1). Based on our observation of the longitudinal section of gills, we propose that the clustering of basidia length could serve as a taxonomic feature in this section. For example, basidia lengths concentrated in one range could be classified as “monomorphological”, while two non-adjacent ranges indicate “dimorphological”, and so on. Additionally, the caulopellis of lower stipes and the number of pseudoparaphyses around each basidium differ among species in this section (3–5 in *C. parvus* and 4–6 in other species in this section), and these features could aid in distinguishing this complex.

Another noteworthy finding is the cream to yellow-brown ozonium state at the base of stipes, which resembles species in sect. *Domestici*, sect. *Aureoconulati*, and our new reported sect.

*Aureodisseminati*. This characteristic, often observed when the fruit body grows on the humus layer of Orchidaceae or the rotten wood of broad-leaved trees, is described here in sect. *Disseminati*. However, further research is needed to determine whether this feature can be regarded as a classification standard.

In comparison with other coprinoid fungi, species in the “fairy inkcap” group are not easily deliquescent. Morphologically, we speculate that this may be due to the absence of cheilocystidia and pleurocystidia. Pseudoparaphyses in this group are narrower than those in other coprinoid fungi, which might also contribute to the difficulty of autodigestion.

### 4.2. A case of fungal evolution

Our study confirms that the “fairy inkcap” is derived from two genera, yet they do share similar macro- and microscopic characteristics, as well as habitats and growth substrates, suggesting the presence of convergent evolution. Although the functions of pileocystidia and caulocystidia have not been verified, these structures likely play a role in protecting the basidiomata and preventing the adhesion of gills to stipes during development (Nagy et al. 2012). Based on our observation, these hair-like cells likely originate from the pileipellis or caulopellis cells, or in other words, they could be seen as specialised terminal cells of pileus or stipes. Thus, the aforementioned characteristics are preserved in several lineages in coprinoid fungi or have originated in Psathyrellaceae multiple times. Within in genus *Coprinellus*, similar convergent processes occur, as the presence of such structures is not consistently observed between sister sections (Nagy et al. 2011; Hussain et al. 2018; Wächter and Melzer 2020; Zhu et al. 2022), objectively leading to the difficulties in morphological identification of this type of species.

A high level of genetic diversity was observed in species of sect. *Disseminati*, with haplotype diversity ( $H_d$ )  $\geq 0.500$  per population, except for *C. austrodisseminatus* and *C. sp.* (refer to Table 3). This was coupled with relatively low nucleotide diversity ( $\pi$ )  $< 0.005$  per population (refer to Table 3). This phenomenon might be attributed to the similarities in nucleotide sequences among haplotypes, indicating a high potential for dispersal, as

observed in other taxa with population expansion (Uthicke and Benzie 2003; Brown et al. 2004; Ma et al. 2015; Van Doren et al. 2017). Ancient hybridisation in this section is supported by both network analysis (Figure 4) and mutation sites of the ITS region (Table 2). For example, *C. disseminatus-similis* exhibits significant divergence from *C. disseminatus* and is relatively close to *C. austrodisseminatus* and *C. velutipes*. However, the nucleotide sequences of sites 139–141, 147–148, and 157–159 in the highly variable region of the ITS1 domain of *C. disseminatus-similis* are identical to those of the former species, despite the distant relationship. These genetic exchanges among populations could contribute to diversification and accelerate the evolution of this lineage.

The speciation process in sect. *Disseminati* likely involves geographic isolation, which may be the primary factor leading to the formation of *C. disseminatus-similis* and the division of different subspecies of *C. disseminatus*. Additionally, the presence of numerous rare variants (Table 2) in *C. austrodisseminatus*, *C. magnoliae*, and *C. parvus*, which share similar distributions and habitats, likely contribute to the differentiation of these three species. These two evolutionary events may represent typical cases of allopatric and sympatric speciation, respectively.

Notably, several specimens we collected, as well as the original materials of the download sequences, are closely related to Orchidaceae. Previous studies on species in this section have suggested that they might be mycorrhizal fungi of orchids and promote orchid seed germination. We speculate that this clade may be undergoing a transformation process from saprophytic to symbiotic trophic types or expanding into additional ecological niches.

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Liyang Zhu: Collection, design of methodology, illustration, and writing original draft; Tolgor Bau: Collection, instruction, review, and editing of the original draft.

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