














Two novel species belonging to *Psathyrella* sections *Atomatae* and *Hydrophilae* (Psathyrellaceae, Agaricales) from Yunnan Province, China, based on morphological and multi-locus phylogenetic analyses

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Abstract

This study describes two collections of saprobic gilled mushrooms morphologically identified as *Psathyrella* and collected in Qujing, Yunnan Province, China. Based on multi-gene phylogenetic analyses of nrITS, nrLSU, and *tef-1α* sequences, two collections were confirmed to belong to the *Psathyrella* sections *Atomatae* and *Hydrophilae*. Morphologically, *Psathyrella qujinguniversitatica* (*Psathyrella* sect. *Atomatae*) is characterized by small basidiomata, a beige to light brown pileus, large basidiospores, and partially thick-walled cheilocystidia, while *P. yunnanensis* (*Psathyrella* sect. *Hydrophilae*) is characterized by a pileus that gradually changes from orange-brown to lighter towards the margin, with the edge light brown to brown, distinct striations, a fibrillose veil, larger basidia, and partially thick-walled cheilocystidia. Descriptions, illustrations, and phylogenetic analyses of the two new species are provided. In addition, the present study updates the number of *Psathyrella* species reported from China to 55, along with their known distribution.

Key words: Morphology, new species, phylogeny, psathyrelloid fungi, taxonomy



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Introduction

Psathyrella (Fr.) Quél. was initially described as *Psathyra* Fr., a tribe of the genus *Agaricus* L. (Fries 1821, 1838), and was subsequently treated as a subgenus within Agaricaceae Chevall (Fries 1849). Quelet (1872) raised it to the genus *Psathyrella*. Later, Singer (1951, 1975) revised the two genera *Drosophila* Quél. and *Psathyrella*, and incorporated the *Drosophila* species into *Psathyrella*. Based on phenotypic characteristics, Kits van Waveren (1985) divided *Psathyrella* into two subgenera and 12 sections, primarily according to spore size: species with spores larger than 10 µm were assigned to subgenus *Psathyra*; otherwise, they were placed in subgenus *Psathyrella*, which contained five sections. Previously, studies of *Psathyrella* have mainly focused on Europe and North America (Kits van Waveren 1987; Hansen and Knudsen 1992; Örstadius and Huhtinen 1996), largely following the classification scheme proposed by Kits van Waveren (1985). In addition, new *Psathyrella* species have been reported from other regions, including South America (Guzmán et al. 1988) and Asia (Natarajan 1978; Zheng 1988; Ying 1994; Takahashi 2000), with these studies primarily based on morphological characteristics.

With the development of molecular biology, Redhead et al. (2001b) and Padamsee et al. (2008) placed *Psathyrella* within Psathyrellaceae Vilgalys, Moncalvo & Redhead, and phylogenetic studies have shown that the genus *Psathyrella* is not monophyletic (Keirle et al. 2004; Walther et al. 2005; Matheny et al. 2006; Padamsee et al. 2008). However, molecular phylogeny based on nrITS and nrLSU sequences failed to adequately distinguish species within *Psathyrella*. For instance, *P. conopilus* (Fr.) A. Pearson & Dennis clusters with species of *Parasola* Redhead, Vilgalys & Hopple with strong support (BS 99% and PP 1.00); *P. marcescibilis* (Britzelm.) Singer and *P. pannucioides* A.H. Sm. cluster with the *Coprinopsis* P. Karst. species (Larsson and Örstadius 2008). Consequently, several authors proposed wholesale realignment of the group (Redhead et al. 2001a, b; Gams 2002; Larsson and Örstadius 2008).

Nagy et al. (2013) conducted a phylogenetic analysis of the four-loci (nrITS, nrLSU, *tef-1α*, and *btub*) dataset, and Örstadius et al. (2015) reclassified the genus *Psathyrella* based on this analysis. Although not all species classifications were well supported, the conclusion still serves as the basis for the classification of the genus *Psathyrella* (Örstadius et al. 2015). Yan (2018) examined 769 samples from China and identified 46 *Psathyrella* species; the results showed that the taxonomic boundaries were consistent with the two subgenera defined by Kits van Waveren (1985). Voto (2020) elevated *Psathyrella* subsect. *Lutenses* Kits van Wav. (*P. lutensis*) to the sectional level by extracting it from *Psathyrella* sect. *Spadiceogriseae* Kits van Wav. and emended the definition of *Psathyrella* sect. *Spadiceogriseae*. Based on subsequent in-depth studies of numerous specimens, combined with morphological and phylogenetic analyses, Wächter and Melzer (2020) revised the Psathyrellaceae and divided *Psathyrella* into 18 subclades, viz., sect. *Pennatae* (*P. pennata*), sect. *Cystopsathyra* (*P. kellermanii*), sect. *Noli-tangere* (*P. noli-tangere*), sect. *Hydrophilae* (*P. piluliformis*), sect. *Pygmaeae* (*P. pygmaea*), sect. *Saponaceae* (*P. saponacea*), sect. *Stridvalliorum* (*P. stridvallii*), sect. *Arenosae* (*P. arenosa*), sect. *Confusae* (*P. gordonii*), sect. *Obtusatae* (*P. obtusata*), sect. *Spadiceogriseae* (*P. spadiceogrisea*), sect. *Jacobssoniorum* (*P. jacobssonii*), sect. *Microrhizae* (*P. microrhiza*), sect. *Pseudostropharia* (*P. caput-medusae*), sect. *Lutenses* (*P. lutensis*), sect. *Psathyrella* (*P. gracilis*), sect. *Atomatae* (*P. prona*), sect.

Sinefibularum (*P. vinosofulva*) (Wächter and Melzer 2020). To date, excluding synonyms, variants, and varieties, Species Fungorum has recorded 674 *Psathyrella* species, with sequence data for at least half of them available in NCBI GenBank.

Psathyrella is a saprotrophic genus of fragile, hygrophanous agarics that leave a dark-brown spore deposit, invariably possess cheilocystidia, and exhibit the “fade-to-grey” reaction of basidiospores in concentrated H₂SO₄ (Kits van Waveren 1985; Örstadius et al. 2015; Wächter and Melzer 2020; Bhunjun et al. 2022). The species of *Psathyrella* most often occur on soil, wood, dung of cows and horses (Lange 1939; Smith 1972; Kits van Waveren 1985; Hansen and Knudsen 1992; Yan 2018). However, a few occur on old bonfires or in swamps (Pegler 1977; Kirk et al. 2008; Larsson and Örstadius 2008; Yan and Bau 2018a). Based solely on morphological studies, *Psathyrella* is similar to the genera *Candolleomyces* D. Wächt. & A. Melzer and *Kauffmania* Örstadius & E. Larss. (Örstadius et al. 2015; Wächter and Melzer 2020). However, *Candolleomyces* can be distinguished by the presence or absence of pleurocystidia (Wächter and Melzer 2020). In *Kauffmania*, only a single species has been recorded, similar to *Psathyrella*, and they cannot be distinguished by a single morphological feature (Örstadius et al. 2015; Wächter and Melzer 2020).

This study aims to describe two novel *Psathyrella* species from Yunnan Province, China, based on morphological and phylogenetic analyses. Detailed descriptions, illustrations, and phylogenetic results of the two new species are also provided.

Materials and methods

Sample collection and morphological observation

Fresh basidiomata were collected from Qujing City, Yunnan Province, China, in 2025. They were photographed *in situ*, and essential collection information was recorded (Rathnayaka et al. 2024). The basidiomata were placed in plastic collection boxes and taken to the mycology laboratory at Qujing Normal University. Macromorphological characteristics, such as pileus, lamella, and stipe, were recorded while the specimens were fresh. Color names and codes were based on the system developed by Kernerup and Wanscher (1978). The fresh specimens were dried at 40 °C in an electric oven (Hu et al. 2022). Dried specimens were sliced and mounted in a 5% KOH solution containing 1% Congo red solution for microstructure observation (Tarafder et al. 2025). The light Eclipse 80i microscope (Olympus, Japan) was used to view features of basidia, basidiospores, cystidia, and pileipellis, which were drawn using the drawing tube attached to the microscope. Micromorphological measurements were obtained using Adobe Photoshop 2019, with at least 40 sample data points for each structure. The basidiospore dimensions were reported as (a–) b–c (–d), where the range ‘b–c’ represented 90% or more of the measured value, and a and d are the extreme values. The meanings of “avL” and “avW” are average length and average width, respectively. The Q refers to the length/width ratio values of all measured basidiospores. Q_m refers to the average Q value with standard deviation. The dry specimens were deposited in the Herbarium of Guizhou Medical University, Guiyang (GMB-W), China. All line drawings of the microstructures were made freehand from rehydrated materials and subsequently modified in Adobe Photoshop 2019.

DNA extraction, PCR amplification, and sequencing

The genomic DNA was extracted from the lamellae of dried specimens using an Ezup Fungus Genomic DNA extraction kit (Sangon Biotech, Shanghai, China) according to the manufacturer's instructions. The primer pairs ITS1/ITS4, LR5/LR0R, and EF1-983F/EF1-2218R were used to amplify the internal transcribed spacer (nrITS) and partial large subunit (nrLSU) of ribosomal RNA and partial translation elongation factor 1-alpha (*tef-1α*) genes, respectively (Vilgalys and Hester 1990; White et al. 1990; Gardes and Bruns 1993; Örstadius et al. 2015). PCR amplification was performed in a 25 µL reaction volume containing 12.5 µL of 2 × Bench Top™ Taq Master Mix, 8.5 µL ddH₂O, 1 µL of each primer (10 µM), and 2 µL genomic DNA. The PCR thermal cycle programs for nrITS and nrLSU amplification were based on those described by Zheng et al. (2025), and the *tef-1α* cycle programs followed those described by Yan and Bau (2018a). After PCR amplification, the purification and sequencing of PCR products were completed by Sangon Biotech Engineering Technology (Shanghai) Co., Ltd. (Shanghai, China). The name of the new taxon was registered in Index Fungorum (2026) (<https://www.indexfungorum.org/Names/IndexFungorumRegister.htm>). All newly generated sequences in this study were deposited in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) and listed in Table 1.

Phylogenetic analyses

The assembly of the forward and reverse primers for the recently obtained sequences was accomplished using BioEdit version 7.0.5.3 and SeqMan version 7.0.0 software packages (DNASTAR, Madison, WI) (Plasterer 1997; Hall 1999). According to the latest studies, additional *Psathyrella* sequences were obtained from GenBank for phylogenetic analyses (Örstadius et al. 2015; Bau and Yan 2021a; Muñoz et al. 2022; Table 1). The sequences were aligned using the online multiple alignment program MAFFT version 7 (Katoh and Standley 2016; Katoh et al. 2019), followed by automatic trimming using TrimAl v. 1.3 with the gappyout method (0.4) (Katoh et al. 2019). Subsequently, the combined FASTA files of nrITS, nrLSU, and *tef-1α* sequences were converted to PHYLIP and NEXUS formats using the online Alignment Transformation Environment (<https://www.sing-group.org/ALTER/>) (Glez-Peña et al. 2010). Phylogenetic tree construction for both Maximum Likelihood (ML) and Bayesian Inference (BI) analyses was conducted on the CIPRES Science Gateway online platform (<https://www.phylo.org/portal2/home.action>) (Miller et al. 2012). ML analysis of the dataset was performed on the above platform using RAXML-HPC v.8 on AC-CESS with the GTRGAMMA substitution model and 1,000 bootstrap replicates (Stamatakis et al. 2005; Stamatakis 2006, 2014). BI analysis was performed using MrBayes on XSEDE v3.2.7a (Ronquist et al. 2012), with six simultaneous Markov chains running for 2,000,000 generations, sampling every 200th generation. The best-fitting model of sequence evolution (GTR+I+G) was determined using MrModelTest 2.2 (Nylander 2004). Topologies sampled below the 25% asymptote were excluded from the burn-in procedure. The phylogenetic trees were visualized and edited with FigTree v1.4.0 (Rambaut and Drummond 2012), and the final figure layouts were created in Adobe Illustrator CC 2021.

Table 1. Names, voucher numbers, and corresponding GenBank accession numbers of the taxa used in the phylogenetic analysis.

Taxon	Voucher number	Locality	GenBank accession number		
			nrITS	nrLSU	tef-1α
<i>Candolleomyces candolleanus</i>	LAS73030	Sweden	KM030175	KM030175	/
<i>Ca. candolleanus</i>	LÖ38-00	Sweden	DQ389720	DQ389720	/
<i>Ca. shennongdingicus</i>	HMAS 258917	China	OR822165	OR822147	OR819984
<i>Ca. shennongdingicus</i> ^T	HMAS 258918	China	OR822166	OR822148	OR819985
<i>Ca. sichuanicus</i> ^T	HMAS 287616	China	PP734617	PP734628	PP729330
<i>Ca. sichuanicus</i>	HMAS 287617	China	PP734618	PP734629	PP729331
<i>Ca. subcacao</i> ^T	HMJAU37807	China	MW301064	MW301092	MW314081
<i>Ca. subminutisporus</i> ^T	HMJAU37801	China	MW301066	MW301094	MW314083
<i>Coprinopsis cineraria</i> ^T	CBM-FB-24142	Japan	KC992962	/	/
<i>Co. uliginicola</i> ^T	Smith34903	USA	KC992960	KC992960	/
<i>Psathyrella agrariella</i>	MICH65241	USA	MF325951	/	/
<i>P. albescens</i>	MCVE29106	Italy	MF325953	/	MF521822
<i>P. albescens</i>	MCVE29107	Italy	MF326009	/	/
<i>P. almerensis</i>	LO379-06	Sweden	KC992873	KC992873	KJ732768
<i>P. almerensis</i>	LO31-04	Sweden	KC992874	KC992874	/
<i>P. ammophila</i>	SZMC-NL-1450	Hungary	FN396111	FN396162	FN396218
<i>P. ammophila</i>	LO359-11	Sweden	KC992872	KC992872	KJ732767
<i>P. bifrons</i>	CBS:299.47	France	MH856259	MH867794	/
<i>P. carinthiaca</i> ^T	MCVE25611	Austria	MF325963	/	/
<i>P. carinthiaca</i>	VER fu19	Slovenia	OQ296568	/	OQ687051
<i>P. carminei</i>	LO5-09	Italy	KC992880	KC992880	KJ732773
<i>P. clivensis</i>	LO182-03	Sweden	DQ389683	DQ389683	KJ732774
<i>P. clivensis</i>	SZMC-NL-1952	Hungary	FM163228	FM160681	FM897216
<i>P. corrugis</i>	SZMC-NL-1951	Hungary	FM878015	FM876272	FM897220
<i>P. dicrani</i>	LO207-04	Sweden	DQ389698	/	/
<i>P. fagetophila</i>	SZMC-NL-2530	Hungary	FM878003	FM876259	FM897222
<i>P. fatua</i>	LO132-97	Sweden	DQ389681	/	/
<i>P. fatua</i>	LO231-08	Sweden	KC992879	KC992879	KJ732772
<i>P. fimiseda</i> ^T	GB LO56-96	USA	NR_158879	/	/
<i>P. fusca</i>	SZMC-NL-0630/2157	Hungary	FM878030	FM876288	FM897217
<i>P. fusca</i>	LO287-04	Sweden	KC992892	KC992892	KJ732779
<i>P. griseovelata</i>	GM2055	Spain	MZ571481	MZ604935	/
<i>P. griseovelata</i>	GM2495	Spain	MZ571482	MZ604936	/
<i>P. impexa</i>	LO78-93	Sweden	KC992900	/	/
<i>P. kitsiana</i> ^T	GB LO217-85	USA	NR_158878	/	/
<i>P. lilliputana</i>	LO130-09	Sweden	KC992850	KC992850	KJ732756
<i>P. lilliputana</i>	GB LO130-09	Sweden	NR_167949	/	/
<i>P. lutulenta</i>	AH21379	Spain	KC992875	KC992875	/
<i>P. mammifera</i>	HMJAU 37882	China	MG734740	/	/
<i>P. marquana</i>	AM1693	Germany	MF668178	MF668178	/
<i>P. merdicola</i> ^T	GB LO45-02	Sweden	NR_158877	/	/
<i>P. microrhiza</i>	SZMC-NL-3059	Hungary	FN396130	FN396178	FN396230
<i>P. mycenoides</i>	HMJAU37993	China	MG734731	/	/
<i>P. mycenoides</i>	HMJAU37888	China	MG734730	/	/
<i>P. noli-tangere</i>	LÖ83-03	Sweden	DQ389713	DQ389713	FN396239
<i>P. oboensis</i>	HMJAU37936	China	MT429164	MW413366	/
<i>P. oboensis</i>	SFSU DED-8234	São Tomé	NR_148107	/	/

Taxon	Voucher number	Locality	GenBank accession number		
			nrITS	nrLSU	<i>tef-1α</i>
<i>P. orbicularis</i>	LO149-11	Sweden	KC992897	/	KJ732786
<i>P. orbicularis</i>	LO211-04	Sweden	DQ389692	/	/
<i>P. owyheensis</i>	HMAS 292422	China	OR237033	/	/
<i>P. owyheensis</i>	MICH5357	USA	MF325990	/	/
<i>P. panaeoloides</i>	LO44-03	Sweden	DQ389719	DQ389719	KJ732782
<i>P. pertinax</i>	LO259-91	Sweden	DQ389701	DQ389701	KJ732809
<i>P. pertinax</i>	HMJAU 6830	China	MG734735	/	/
<i>P. pervelata</i>	SZMC-NL-1950	Hungary	FN430694	FN396192	FM897221
<i>P. phlegophila</i>	SZMC-NL-3527	Hungary	FN396129	FN396198	FN396229
<i>P. piluliformis</i>	XC23-242	France	PV121594	PV121907	/
<i>P. piluliformis</i>	SZMC-NL-3923	Hungary	FN396136	FN396185	FN396235
<i>P. piluliformoides</i>	HMJAU37923	China	MW405106	MW413362	MW411002
<i>P. potteri</i>	AH33721	Spain	MF966495	MF962872	/
<i>P. prona</i>	LÖ237-00	Sweden	KJ939634	/	/
<i>P. pseudogracilis</i>	SZMC-NL-2142	Hungary	FM878025	FM876283	FM897249
<i>P. pygmaea</i>	SZMC-NL-2325	Hungary	FM878011	FM876267	FM897224
<i>P. qujinguniversitatica</i>^T	GMB-W1229	China	PX443606	PX443617	PX583848
<i>P. qujinguniversitatica</i>	GMB-W1230	China	PX443607	PX443618	PX583849
<i>P. rogersiae</i> ^T	MCVE29120	Italy	MF325995	/	/
<i>P. romagnesii</i>	LO85-98	Sweden	DQ389716	/	/
<i>P. sacchariolens</i>	SZMC-NL-3995	Hungary	FN396133	FN396182	FN396233
<i>P. scanica</i> ^T	GB LO183-09	Sweden	NR_167957	/	/
<i>P. scatophila</i> ^T	LO64-95	Sweden	DQ389703	/	/
<i>P. seminuda</i> ^T	Smith34091	USA	KC992907	/	/
<i>P. senex</i>	LÖ115-02	Germany	DQ389712	DQ389712	/
<i>P. spadiceogrisea</i>	MCVE29103	France	MF325997	/	MF521779
<i>P. spadiceogrisea</i>	LO102-98	Sweden	KC992878	KC992878	KJ732771
<i>P. squamosa</i>	HMJAU37816	China	MG367206	/	/
<i>P. squamosa</i>	LO104-95	Sweden	DQ389687	/	/
<i>P. tintinnabula</i>	HMLD2497	China	MK123930	/	/
<i>P. tintinnabula</i> ^T	HFJAU0711	China	MK123929	MK211206	/
<i>P. umbrina</i>	SZMC-NL-1949	Hungary	FM878004	FM876260	FM897226
<i>P. velatipes</i>	MICH12106	USA	MF326004	/	MF521774
<i>P. vestita</i>	SZMC-NL-2346	Hungary	FN430693	FM876260	FN430696
<i>P. warrenensis</i>	KA16-1043	Kyrgyzstan	MK351682	/	/
<i>P. warrenensis</i>	Smith70162	USA	KC992906	/	/
<i>P. yunnanensis</i>^T	GMB-W1231	China	PX443608	PX443619	PX583850
<i>P. yunnanensis</i>	GMB-W1232	China	PX443609	PX443620	PX583851

Notes: The newly generated sequences in this study are in bold; superscript "T" represents the type species; and "/" indicates unavailable sequences.

Results

Phylogenetic analyses

The combined nrITS, nrLSU, and *tef-1α* sequences were used to assess phylogenetic relationships among *Psathyrella* species. *Coprinopsis cineraria* (Har. Takah.) Örstadius & E. Larss. (CBM-FB-24142^T) and *Co. uliginicola* (McKnight & A.H. Sm.) Örstadius & E. Larss. (Smith34903^T) were used as the outgroup (Bau and Yan 2021a). The final concatenated dataset of nrITS, nrLSU, and *tef-1α* sequences, consisting of 85 nrITS, 50 nrLSU, and 42 *tef-1α* sequences, was used to conduct ML

and BI analyses. The phylogenetic trees generated by ML and BI were similar, and the results were consistent with those of previous studies by Yan (2018) and Wächter and Melzer (2020). Therefore, the phylogenetic tree obtained from ML analysis was chosen for presentation in Fig. 1. The RAxML tree was based on a combined dataset of nrITS, nrLSU, and *tef-1α* gene sequence data, which comprised 2,658 characters (LSU: 1–900, ITS: 901–1,656, *tef-1α*: 1,657–2,658), including gaps. The best-scoring RAxML tree with a final likelihood value of -19568.188807 is presented. Estimated base frequencies were as follows: A = 0.253834, C = 0.231013, G = 0.254215, T = 0.260938; substitution rates AC = 1.383986, AG = 2.887342, AT = 1.622628, CG = 0.727172, CT = 6.064389, GT = 1.000000.

In the phylogeny, our collections GMB-W1229^T and GMB-W1230 (*Psathyrella qujinguniversitatica*) were placed in *Psathyrella* sect. *Atomatae* Romagn. ex Singer and formed a distinct lineage closely related to *P. lilliputana* Örstadius & E. Larss. (LO130-09), with strong statistical support (99% BS and 1.00 PP; Fig. 1). The collections GMB-W1231^T and GMB-W1232 (*P. yunnanensis*), belong to *Psathyrella* sect. *Hydrophilae* Romagn. ex Singer and form a distinct lineage closely related to *P. carinthiaca* Voto (MCVE 25611^T) and *P. piluliformis* (Bull.) P.D. Orton (SZMC-NL-3923) being separated with statistical support of 98% BS and 1.00 PP (Fig. 1). Based on nucleotide comparisons, *P. qujinguniversitatica* (GMB-W1229^T) is different from *P. lilliputana* (LO130-09) by 38/622 bp (6.11%, without gap) of the nrITS, for nrLSU by 19/848 bp (2.24%, without gap), and by 97/661 bp (14.67%, without gap) of the *tef-1α*. *Psathyrella yunnanensis* (GMB-W1231^T) is different from *P. piluliformis* (SZMC-NL-3923) by 35/641 bp (5.46%, without gap) of the nrITS, for nrLSU by 26/798 bp (3.26%, without gap), and by 40/1,048 bp (3.82%, without gap) of the *tef-1α*. In addition, *P. yunnanensis* (GMB-W1231^T) is different from *P. carinthiaca* (MCVE 25611^T) by 25/639 bp (3.91%, without gap) of the nrITS and by 37/1,063 bp (3.91%, without gap) of the *tef-1α* (compared with *P. carinthiaca* VER fu19).

Taxonomy

Psathyrella qujinguniversitatica D.G. Zheng. & Karun., sp. nov.

Index Fungorum: IF904677

Figs 2a–c, 3

Etymology. Refers to 'Qujing Normal University', where the holotype was collected.

Holotype. China • Yunnan Province, Qujing City, Qujing Normal University, on grassland, 25°31'29"N, 103°44'39"E, elev. 1,882 m, 23 June 2025, D.G. Zheng (QJ25-05 = GMB-W1229).

Description. *Pileus* 4–6 mm in diameter, hemispherical when young and parabolic to broadly parabolic when mature, hygrophanous, beige (4C3) to light brown (5D4) at the center and yellowish gray (4B2) to grayish beige (4C2) towards the margin, smooth, faintly visible striations at the margin, with granules or powder on the surface of the pileus. *Veil* fibrillose, gradually disappearing in maturity stages. *Lamellae* adnexed to adnate, regular, yellowish gray (4B3–4). *Stipe* 21–30 × 0.3–0.4 mm, fragile, cylindrical, hollow, slender, equal, from the top to the base, the color gradually deeper from white (5A1) to light brown (5D5), without visible mycelium at the base. *Annulus* absent. **Odour and taste** were not determined.

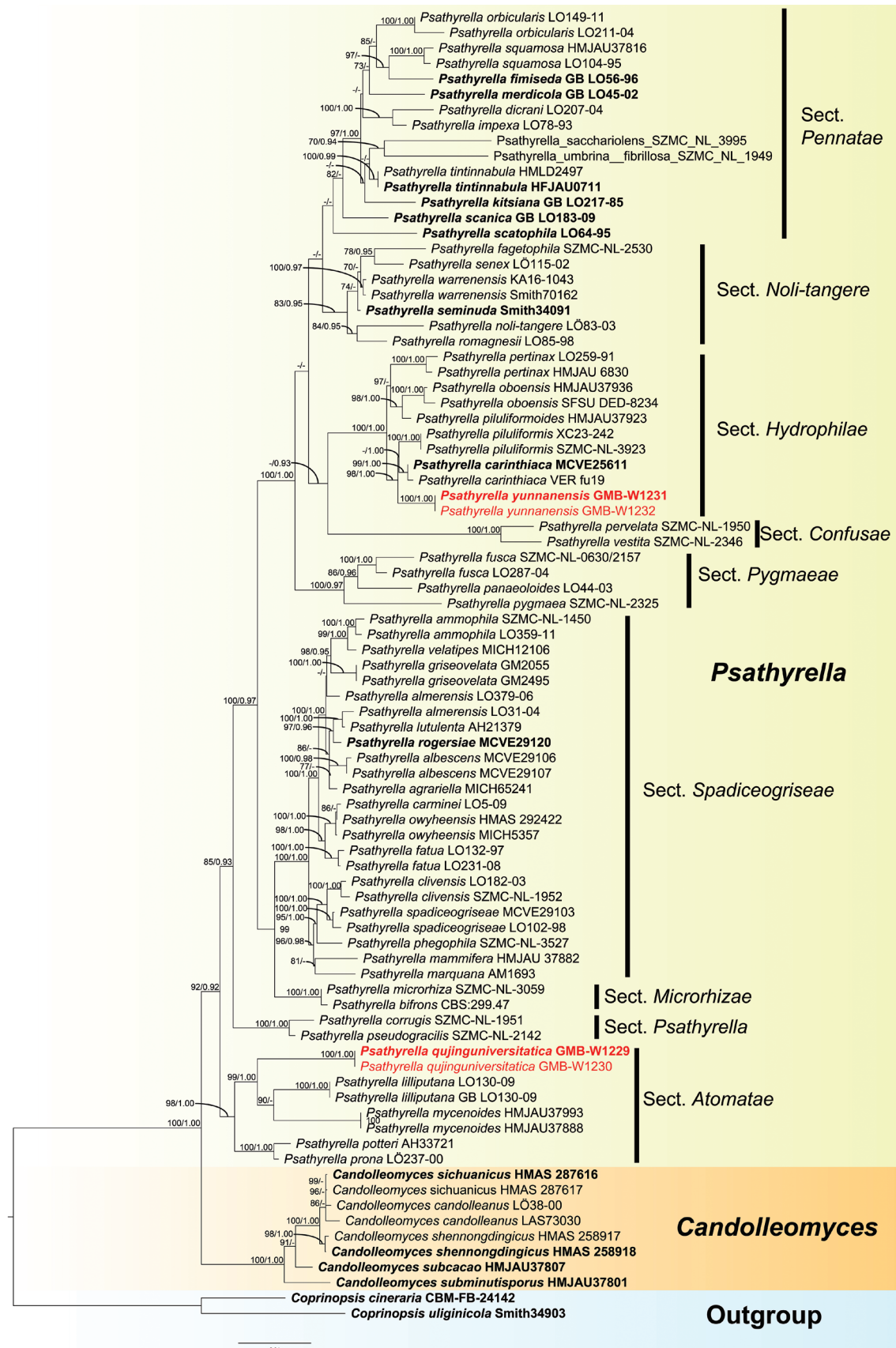


Figure 1. Phylogenetic tree for *Psathyrella* generated from the combined sequence dataset (nrITS, nrLSU, and *tef-1α*) using Maximum Likelihood (ML) analysis and Bayesian Inference (BI) analyses. The ML bootstrap values $\geq 70\%$ and BI posterior probabilities ≥ 0.90 are provided at relevant nodes (BS/PP). The new species are in red text. Type species are in bold.



Figure 2. Basidiomata of *Psathyrella qujinguniversitatica* (GMB-W1229, holotype) (**a–c**), and *Psathyrella yunnanensis* (GMB-W1231, holotype) (**d–f**). Scale bars: 1 cm (**a, b, d–f**); 1 mm (**c**).

Basidiospores (9.0–)9.7–11.3(–12.4) × (5.1–)5.6–6.7(–7.1) μm (avL = 10.4 μm, avW = 6.2 μm), Q = 1.46–1.90, Q_m = 1.69 ± 0.15, ellipsoid to oblong, pale brown to brown in water, deepening in 5% KOH, smooth, with germ pore central or slightly eccentric, 1.0–1.5 μm broad, and many canary yellow (2B7) oil drops. **Basidia** (17.3–)18.0–21.8(–24.1) × (6.6–)6.8–8.4(–8.8) μm, clavate, hyaline, 2- or 4-spored, occasionally 1-spored. **Pleurocystidia** (27.0–)27.7–41.9(–42.4) × (7.8–)10.1–14.7(–17.0) μm, scattered to rare, lageniform to fusiform, pyriform or utriform, thin-walled, not forked, with obtuse apex. **Cheilocystidia** (20.0–)25.2–35.2(–50.3) × (4.5–)5.6–9.6(–12.3) μm, numerous, utriform, pyriform, cylindrical to claviform, lageniform, partially thick-walled, hyaline. **Pileipellis** a one- to two-layered irregular epithelium composed of globose to subglobose or ellipsoid cells 22–38 × 18–32 μm, thin-walled, hyaline

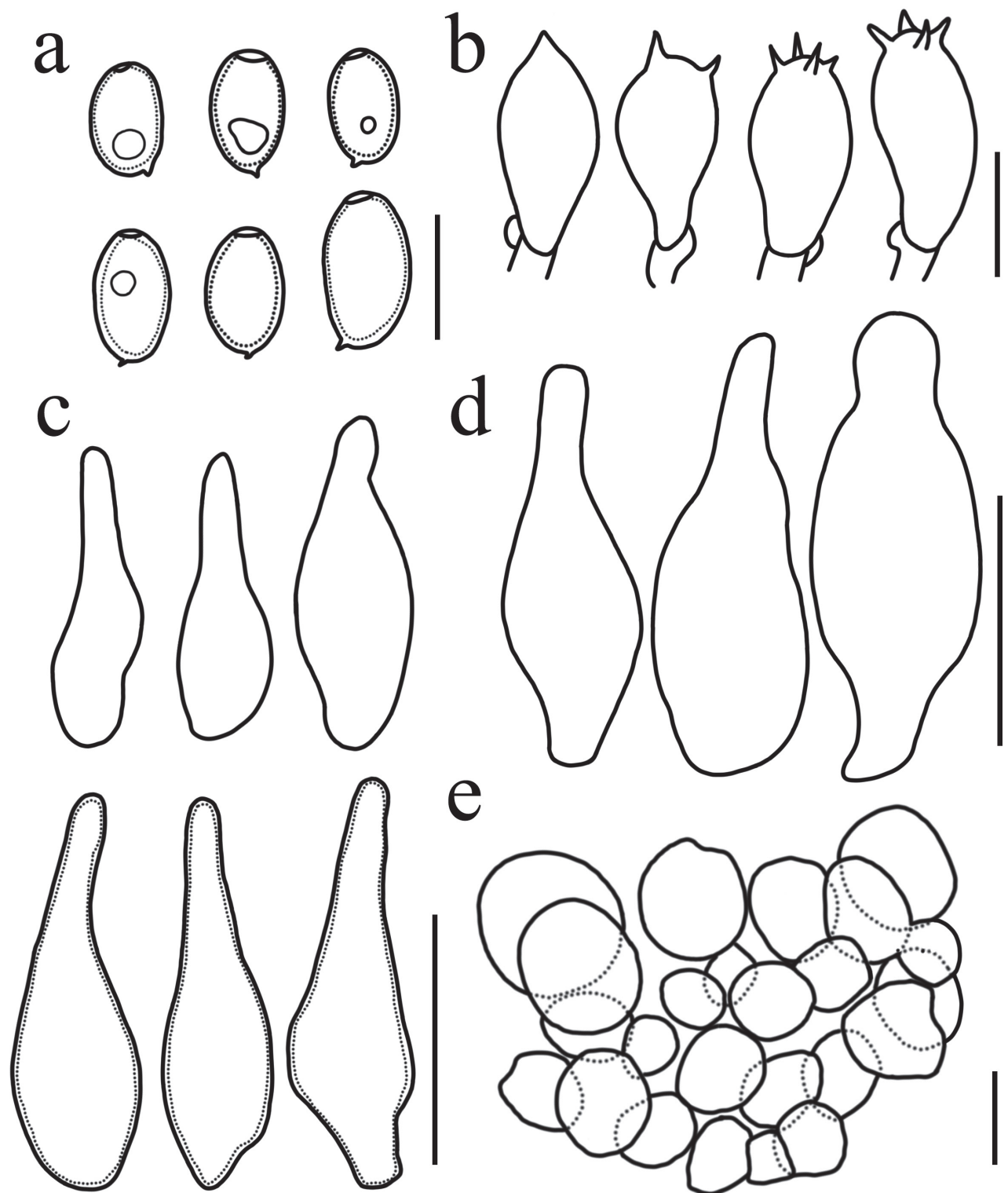


Figure 3. *Psathyrella qujinguniversitatica* (GMB-W1229, holotype). **a.** Basidiospores; **b.** Basidia; **c.** Cheilocystidia; **d.** Pleurocystidia; **e.** Pileipellis. (Micrographs are provided in Suppl. material 1: fig. S1). Scale bars: 10 μm (**a**, **b**), 20 μm (**c**–**e**).

in 5% KOH. ***Stipitipellis*** a cutis of parallel, slightly skewed, cylindrical, smooth hyphae, thin-walled, 5–12 μm wide. **Clamp connection** present.

Habitat. Solitary or gregarious in a grassland at Qujing Normal University in Yunnan Province, China.

Distribution. Only known from Yunnan, China.

Additional specimen examined. CHINA • Yunnan Province, Qujing City, Qujing Normal University, on grassland, 25°31'36"N, 103°44'49"E, elev. 1,889 m, 23 June 2025, D.G. Zheng & S.C. Karunarathna (QJ25-80 = GMB-W1230, isotype).

GenBank numbers. GMB-W1229: nrITS = PX443606, nrLSU = PX443617, *tef*-1 α = PX583848. GMB-W1230: nrITS = PX443607, nrLSU = PX443618, *tef*-1 α = PX583849.

Notes. In morphology, *P. qujinguniversitatica* differs from *P. lilliputana* by larger basidiomata, especially longer stipes (21–30 \times 0.3–0.4 mm vs. 6–8 \times 0.2–0.5 mm), longer basidia (18.0–21.8 \times 6.8–8.4 μ m vs. 16–19 \times 8–9 μ m), and slightly larger pileipellis cells (18–38 μ m vs. 15–30 μ m) (Örstadius et al. 2015). In addition, *P. lilliputana* is coprophilic and differs in having a semiglobate to convex pileus that is reddish-brown, and the stipe apex is pulverulent, with sparsely fibrillose veil remnants. In micromorphology, it can be easily distinguished from our species by its rarely forked pleurocystidia and cheilocystidia, and yellowish-red basidiospores, which are sometimes snout-like at the apex or irregular in outline (Örstadius et al. 2015). In the phylogenetic tree, *P. qujinguniversitatica* is closely related to *P. lilliputana* and *P. mycenoides* T. Bau. Their basidiomata are all less than 5.0 mm. However, *P. mycenoides* differs in having smaller basidia and a dirty white to pinkish pileus (Örstadius et al. 2015; Yan and Bau 2018a). Based on the above evidence, we identify our collection as *P. qujinguniversitatica* sp. nov.

***Psathyrella yunnanensis* D.G. Zheng. & Karun., sp. nov.**

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Figs 2d–f, 4

Etymology. “*yunnanensis*” refers to the type locality, Yunnan Province, China.

Holotype. CHINA • Yunnan Province, Qujing City, Malong County, on humus-rich soil among moss and woody debris, 25°18'57"N, 103°16'03"E, elev. 2,152 m, 12 July 2025, D.G. Zheng (MLX74 = GMB-W1231).

Description. **Pileus** 26–35 mm in diameter, parabolic or subumbonate when young, and subumbonate or convex when mature, slightly hygrophanous, brownish orange (6C5) at the center, the color gradually paler between the center and edges, but deeper at the edges, which are light brown (6D6) to brown (6E6) towards the margin, smooth, striations distinct at margin. **Veil** white (5A1), fibrillose, rarely on the edge of the pileus, and gradually disappearing in maturity stages. **Lamellae** adnexed to adnate, even, regular and with tiers, dull red (9C4) to reddish brown (9D4). **Stipe** 69–79 \times 6–7 mm, fragile, fistulose, cylindrical, hollow, flexuous, longitudinally fibrillose or flocculose, slightly thickened towards the middle, white (5A1) to white gray (5B1), with a little white mycelial tomentum at the base. **Annulus** absent. **Odor and taste** were not determined.

Basidiospores (5.8–)6.4–8.1(–9.5) \times (2.9–)3.2–4.4(–5.8) μ m (avL = 7.28 μ m, avW = 3.90 μ m), Q = 1.45–2.03, Q_m = 1.87 \pm 0.27, ellipsoid to oblong, slightly flexuous or irregular in outline, thick-walled, base often broadly truncate, pale brown to brown in water, and deepening in 5% KOH, smooth, with germ pore absent or partially present with medium guttules. **Basidia** (20.4–)25.2–32.6(–35.2) \times (5.8–)6.3–8.3(–9.2) μ m, clavate, hyaline, 4- or 2-spored, with granular content, have basidioles arranged in a regular pattern. **Pleurocystidia** (32–)44.0–62.8(–71.6) \times (6.4–)9.04–18.0(–22.6) μ m, abundant, narrowly clavate

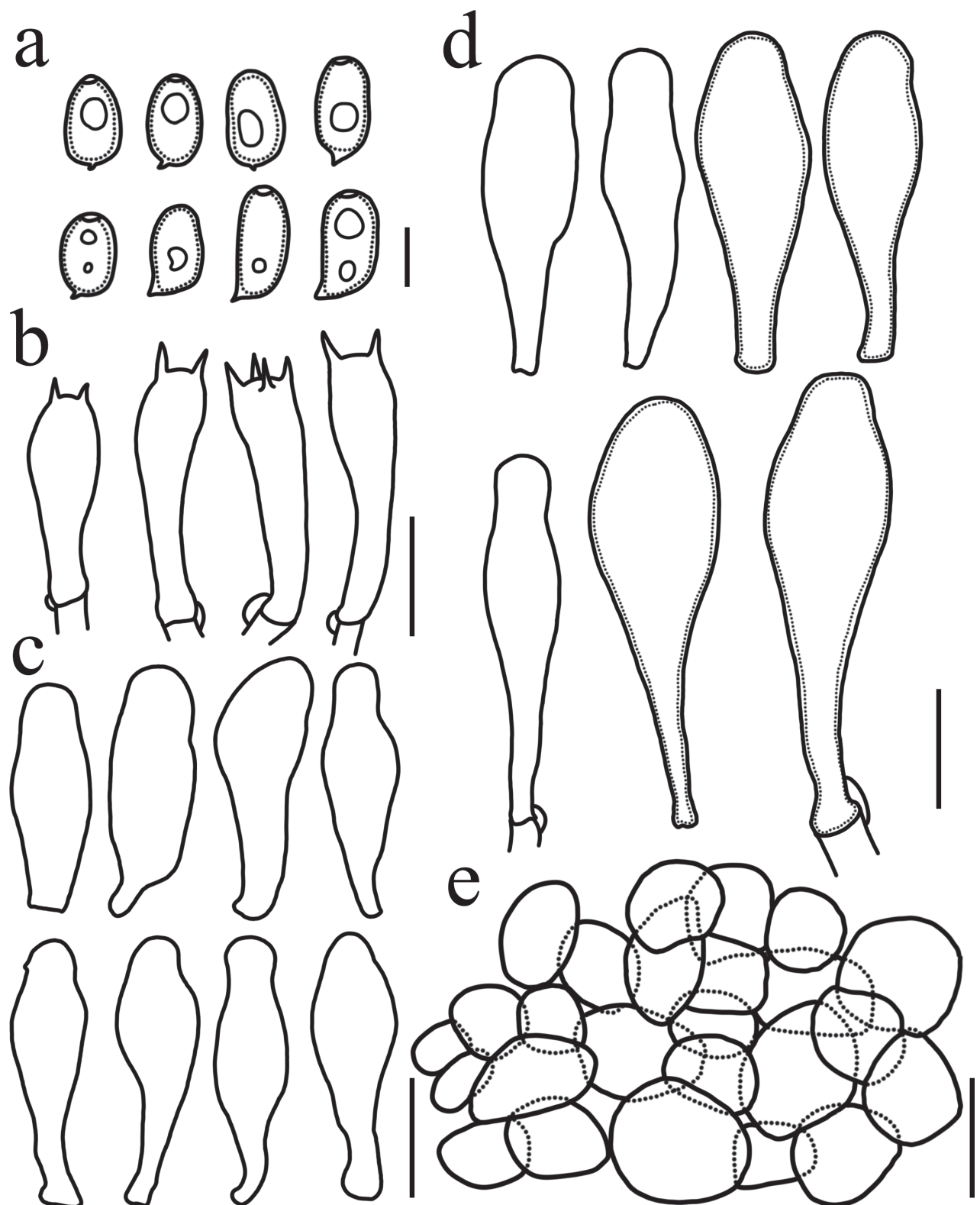


Figure 4. *Psathyrella yunnanensis* (GMB-W1231, holotype). **a.** Basidiospores; **b.** Basidia; **c.** Cheilocystidia; **d.** Pleurocystidia; **e.** Pileipellis. (Micrographs are provided in Suppl. material 1: fig. S2). Scale bars: 5 μ m (**a**); 20 μ m (**b–d**); 10 μ m (**e**).

to clavate, or narrowly utriform to utriform, thick-walled, apex broadly obtuse, dissolving in 5% KOH. **Cheilocystidia** (28.1–)33.1–46.7(–49.4) \times (7.5–)10.1–14.8(–15.9) μ m, utriform, oblong to claviform, partially thin-walled, hyaline. **Pileipellis** a one- to two-layered irregular epithelium composed of globose to sub-

globose or ellipsoid cells $28\text{--}40 \times 18\text{--}39 \mu\text{m}$, thin-walled, hyaline in 5% KOH. ***Stipitipellis*** a cutis of parallel, slightly skewed, cylindrical, smooth hyphae, thin-walled, $7\text{--}12 \mu\text{m}$ wide. **Clamp connection** present.

Habitat. Scattered or gregarious on humus-rich soil among moss and woody debris.

Distribution. Only known from Yunnan, China.

Additional specimen examined. CHINA • Yunnan Province, Qujing City, Malong County, on humus-rich soil among moss and woody debris, $25^{\circ}18'57''\text{N}$, $103^{\circ}16'03''\text{E}$, elev. 2,152 m, 12 July 2025, D.G. Zheng & S.C. Karunarathna (MLX126 = GMB-W1232, isotype).

GenBank numbers. GMB-W1231: nrITS = PX443608, nrLSU = PX443619, *tef-1 α* = PX583850. GMB-W1232: nrITS = PX443609, nrLSU = PX443620, *tef-1 α* = PX583851.

Notes. In morphology, *P. yunnanensis* differs from *P. piluliformis* by smaller basidiomata, especially the narrower pileus (25–35 mm vs. 30–70 mm), larger basidia ($25.2\text{--}32.6 \times 6.3\text{--}8.3 \mu\text{m}$ vs. $15\text{--}22 \times 5.0\text{--}8.0 \mu\text{m}$), and larger basidiospores ($6.4\text{--}8.1 \times 3.2\text{--}4.4 \mu\text{m}$ vs. $5.0\text{--}6.5 \times 3.5\text{--}4.0 \mu\text{m}$). It is also distinguished by its fibrillose veil, basidioles arranged in a regular pattern, and pale brown to brown basidiospores. *Psathyrella piluliformis* has a pileus that is brown to reddish brown or honey brown, hygrophanous, with blunt, rounded protrusions in the center, and faint, translucent stripes along the edge (Yan 2018; Kuo 2020). *Psathyrella yunnanensis* differs from *P. carinthiaca* in having a lighter-colored pileus, larger pleurocystidia ($44.0\text{--}62.8 \times 9.0\text{--}18.0 \mu\text{m}$ vs. $30\text{--}45 \times 8.0\text{--}13.7 \mu\text{m}$), larger cheilocystidia ($33.1\text{--}46.7 \times 10.1\text{--}14.8 \mu\text{m}$ vs. $17\text{--}37 \times 8\text{--}12 \mu\text{m}$), and larger basidia ($25.2\text{--}32.6 \times 6.3\text{--}8.3 \mu\text{m}$ vs. $10\text{--}18 \times 5\text{--}7 \mu\text{m}$). In contrast, *P. carinthiaca* is characterized by a reddish-brown to brick-red or brownish (pinkish-) violaceous pileus, blackish violaceous lamellae, and smaller basidiospores ($5.0\text{--}6.0 \times 3.0\text{--}3.7 \mu\text{m}$ vs. $6.4\text{--}8.1 \times 3.2\text{--}4.4 \mu\text{m}$) (Voto 2011; Voto et al. 2020). *Psathyrella pertinax* (Fr.) Örstadius has a pileus color ranging from reddish brown to ochraceous brown to yellow brown, and the pileus often becomes radially rugose, veined, or reticulate (Örstadius 2007). The main identifying feature of *P. oboensis* Desjardin & B.A. Perry is that the gills are extremely dense, slender, and 1.0–1.5 mm wide (Desjardin and Perry 2016). Based on the above evidence, we identify our collection as *P. yunnanensis* sp. nov.

Discussion

In this study, two new species exhibit all micromorphological characteristics consistent with the genus *Psathyrella*; notably, the presence of pleurocystidia is a key diagnostic feature distinguishing it from the genus *Candolleomyces*. Based on molecular data and morphological features, our two novel species are respectively accommodated in *Psathyrella* sect. *Atomatae* and sect. *Hydrophilae*. In the classification criteria of Wächter and Melzer (2020), *Psathyrella* sect. *Atomatae* is characterized by its very small to medium-sized basidiomata that are terrestrial or coprophilous, a drying pileus that is often with pink tones, large, dark basidiospores with a centrally located germ pore, 1-, 2- or 4-spored basidia, the cheilocystidia predominantly lageniform, subutriform or clavate, and rarely pleurocystidia. Compared with other species in *Psathyrella* sect. *Atomatae*, *P. qujinguniversitatica* can usually be distinguished by its small basidiomata, beige or light brown pileus,

and large basidiospores. Our species, *P. qujinguniversitatica*, meets all the characteristics of *Psathyrella* sect. *Atomatae* and forms an independent lineage in the phylogenetic tree (Fig. 1). This section has only one species recorded in China, *P. mycenoides*, which was described as a new species from Jilin Province. The proportion of species in *Psathyrella* sect. *Atomatae* found in China, compared to the global total, is 11% (Yan and Bau 2018a; Wächter and Melzer 2020).

Psathyrella sect. *Hydrophilae* is characterized by its small to medium-sized basidiomata that are all lignicolous; the veil is sparse to strongly developed; small, phaseoliform basidiospores without germ pores or indistinct germ pore; the marginal cells are lageniform, utriform, very often mucronate in the lamellar edge; and with moderately numerous clavate and sphaeropedunculate cells (Yan 2018; Wächter and Melzer 2020; Bau and Yan 2021a). Our new species, *P. yunnanensis*, meets the requirements of the above classification. However, our specimens were collected from humus-rich soil among moss and woody debris, rather than from the tree or wood itself. Moreover, in 2018, Yan recorded a specimen of *P. piluliformis* that was collected from the ground in a broadleaf forest in Heilongjiang Province, China (Yan 2018). This specimen also belongs to this section, but it was found growing in soil rather than lignicolous. In 2021, Bau and Yan (2021a) collected a new species, *P. piluliformoides*, which grew solitarily on moss and belongs to *Psathyrella* sect. *Hydrophilae*. This pattern may be associated with variations in geographical environments. The occurrence of these species suggests that the current circumscription of *Psathyrella* sect. *Hydrophilae* may not adequately reflect their ecological diversity (Padamsee et al. 2008; Bau and Yan 2021a). In particular, the habitat of *Psathyrella* sect. *Hydrophilae* is not confined to dead wood or other lignicolous substrates, but also encompasses humus-rich soils. This broader ecological amplitude indicates that the habitat range of *Psathyrella* sect. *Hydrophilae* is more diverse than previously assumed, and the possible existence of additional subsections within *Psathyrella* sect. *Hydrophilae*, underscoring the need for additional collections and data to better define its taxonomic characteristics. New species in *Psathyrella* sect. *Hydrophilae* continue to be discovered, and comprehensive datasets, including morphological characteristics, geographical distributions, and phylogenetic analyses, are being compiled. Although our new species, *P. yunnanensis*, has a different habitat, there is no doubt that it belongs to *Psathyrella* sect. *Hydrophilae*, from a phylogenetic and taxonomic point of view. This new information not only helps clarify the phylogenetic relationships among species within the sections but also provides key evidence for revising and improving the classification standards of the subgroup and for defining interspecies boundaries. In China, a total of four species from *Psathyrella* sect. *Hydrophilae* have been recorded, including one novel species, *P. piluliformoides* T. Bau & J.Q. Yan, representing 44% of the global diversity of this section (Wächter and Melzer 2020; Bau and Yan 2021a).

Before 2015, a total of 44 *Psathyrella* species had been reported from China. Yan (2018) re-examined these records and confirmed that 11 species were actually distributed within *Psathyrella*. Since then, continuous taxonomic investigations have considerably expanded the diversity of this genus in China, increasing the number of recorded species in China to 53 (Bi 1991; Mao 1997; Chang et al. 2006; Wang and Bau 2014; Wei 2017; Yan 2018; Cen et al. 2021; Bau and Yan 2021a, 2021b; Yan and Bau 2021; Li et al. 2023; Liang et al. 2023; Wang et al. 2024; Zhang 2024; Table 2). Notably, 11

Table 2. List of sections, species, and provinces of distribution of *Psathyrella* recorded in China.

Sections	Species	Provinces of distribution	References
<i>Atomatae</i>	<i>Psathyrella mycenoides</i>	Jilin	Yan (2018); Yan and Bau (2018a)
	<i>P. qujinguniversitatica</i>	Yunnan	This study
<i>Confusae</i>	<i>P. gordonii</i>	Jilin	Yan (2018); Yan and Bau (2017)
<i>Hydrophila</i>	<i>P. oboensis</i>	Yunnan	Yan (2018); Liang et al. (2023)
	<i>P. pertinax</i>	Jilin	Yan (2018)
	<i>P. piluliformis</i>	Liaoning, Heilongjiang, Fujian, Guangdong, Yunnan, Sicuang, Hunan, Jilin, Xinjiang, Shanxi, Xizang, Hong Kong, Taiwan	Cen et al. (2021); Li et al. (2023); Wang and Bau (2014); Yan (2018)
	<i>P. piluliformoides</i>	Yunnan, Jilin	Yan (2018); Bau and Yan (2021a)
	<i>P. yunnanensis</i>	Yunnan	This study
	<i>P. lutensis</i>	Neimenggu	Yan (2018)
<i>Microrhizae</i>	<i>P. boreifasciculata</i>	Neimenggu, Jilin, Heilongjiang	Yan (2018); Yan and Bau (2017)
	<i>P. microrhiza</i>	Ningxia	Mao (1997)
	<i>P. owyheensis</i>	Beijing	Wang et al. (2024)
<i>Noli-tangere</i>	<i>P. amygdalinospora</i>	Sicuang	Yan (2018); Bau and Yan (2021a)
	<i>P. fennoscandica</i>	Heilongjiang	Yan (2018)
	<i>P. senex</i>	Neimenggu, Jilin	Yan (2018); Yan and Bau (2017)
	<i>P. subterrestris</i>	Jilin, Hubei	Yan (2018)
<i>Obtusatae</i>	<i>P. obtusata</i>	Ningxia, Liaoning, Hong Kong, Neimenggu, Jilin, Sicuang	Mao (1997); Yan (2018)
<i>Pennatae</i>	<i>P. alpina</i>	Yunnan, Jiangxi	Yan (2018); Yan and Bau (2018b)
	<i>P. borealis</i>	Neimenggu, Jilin	Yan (2018)
	<i>P. conica</i>	Jilin	Yan (2018); Yan and Bau (2018a)
	<i>P. jilinensis</i>	Jilin	Yan (2018); Yan and Bau (2018a)
	<i>P. pennata</i>	Ningxia	Mao (1997)
	<i>P. rostellata</i>	Xinjiang	Yan (2018)
	<i>P. spintrigeroides</i>	Jilin	Yan (2018)
	<i>P. squamosa</i>	Hebei, Beijing, Neimenggu, Jilin, Heilongjiang, Liaoning, Guangdong, Ningxia	Yan (2018); Wang and Bau (2014); Wang et al. (2024); Cen et al. (2021); Wei (2017); Mao (1997)
	<i>P. tintinnabula</i>	Yunnan	Yan et al. (2019)
	<i>P. vesterholtii</i>	Sicuang	Yan (2018)
<i>Psathyrella</i>	<i>P. atomata</i>	Gansu	Zhang (2024)
	<i>P. bipellis</i>	Gansu, Jilin, Yunnan, Hebei	Zhang (2024); Wang et al. (2024); Yan (2018)
	<i>P. corrugis</i>	Gansu, Guangdong, Fujian, Sicuang, Neimenggu	Zhang (2024); Wang and Bau (2014); Yan (2018)
	<i>P. longicauda</i>	Ningxia	Li et al. (2023)
<i>Pygmaea</i>	<i>P. squarrosa</i>	Guangdong	Yan (2018); Yan and Bau (2021)
	<i>P. truncatisporoides</i>	Zhejiang	Yan (2018); Bau and Yan (2021a)
<i>Pygmaeae</i>	<i>P. amaura</i>	Jilin, Sicuang, Beijing	Yan (2018); Wang et al. (2024)
	<i>P. olympiana</i>	Jilin, Liaoning, Gansu, Beijing, Hebei	Cen et al. (2021); Zhang (2024); Wang et al. (2024)
	<i>P. pygmaea</i>	Jilin, Liaoning	Cen et al. (2021)
<i>Saponaceae</i>	<i>P. panaeoloides</i>	Xizang, Jilin	Yan (2018); Yan and Bau (2021)
	<i>P. saponacea</i>	Shanxi	Yan (2018); Yan and Bau (2021)
<i>Sinefibularum</i>	<i>P. effibulata</i>	Jilin	Yan (2018)

Sections	Species	Provinces of distribution	References
<i>Spadiceogriseae</i>	<i>P. bifrons</i>	Liaoning	Cen et al. (2021)
	<i>P. carmine</i>	Gansu, Neimenggu	Zhang (2024); Yan (2018)
	<i>P. mammiifera</i>	Jilin, Sicuang	Yan (2018)
	<i>P. marquana</i>	Gansu	Zhang (2024)
	<i>P. phegophila</i>	Beijing	Wang et al. (2024)
	<i>P. spadiceogrisea</i>	Guangdong, Guizhou, Liaoning	Cen et al. (2021)
	<i>P. subspadiceogrisea</i>	Jilin	Yan and Bau (2017)
Un-placement section	<i>P. armeniaca</i>	Fujian, Guangdong, Liaoning	Cen et al. (2021); Wei (2017)
	<i>P. campestris</i>	Guangdong, Hebei, Henan, Liaoning, Yunnan	Cen et al. (2018); Yan and Bau (2017)
	<i>P. lactobrunnescens</i>	Yunnan	Liang et al. (2023)
	<i>P. microspore</i>	Jilin, Sicuang	Wang and Bau (2014)
	<i>P. multissima</i>	Jilin, Yunnan	Chang et al. (2006); Liu et al. (2020)
	<i>P. rubiginosa</i>	Guangdong	Wang and Bau (2014)
	<i>P. rugocephala</i>	Hong Kong	Wang and Bau (2014)
	<i>P. subincerta</i>	Guangdong	Bi (1991)
	<i>P. tristis</i>	Guangdong	Wang and Bau (2014)

of these species have been described as novel species from China (Bi 1991; Yan and Bau 2017; Yan 2018; Yan et al. 2019; Bau and Yan 2021a, 2021b). In Yunnan Province, a total of nine *Psathyrella* species were recorded, viz. *P. alpina* T. Bau & J.Q. Yan, *P. bipellis* (Quél.) A.H. Sm., *P. campestris* (Earle) A.H. Sm., *P. lactobrunnescens* A.H. Sm., *P. oboensis*, *P. piluliformis*, *P. piluliformoides*, *P. spadiceogrisea* (Schaeff.) Maire, and *P. tintinnabula* J.Q. Yan (Yan 2018; Yan and Bau 2018b; Li et al. 2019; Yan et al. 2019; Bau and Yan 2021b; Liang et al. 2023; Zhang 2024). In this study, *P. qujinguniversitatica* and *P. yunnanensis* are described as new species. Therefore, a total of 55 *Psathyrella* species have been recorded in China. However, the nine species were identified only through morphological classification, which is insufficient for accurately assigning their taxonomic placement and requires molecular data to determine their section placement.

Yunnan Province, with its highly diverse ecological environments, harbors a wide range of organisms, including animals, plants, and fungi (Feng and Yang 2018; Wang et al. 2021; Li et al. 2024). Given this remarkable biodiversity, it is likely that numerous species remain undocumented. Consequently, further systematic surveys are essential to more comprehensively characterize the diversity and distribution of the genus *Psathyrella*. This study provides information on two new *Psathyrella* species, thereby enriching the current mycological research dataset on *Psathyrella* and providing evidence for future taxonomic, phylogenetic, and distributional studies.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Conceptualization: SCK, ST, JK, and WHL. Data curation: DGZ, JK, WHL, and LJZ. Formal analysis: SCK, ST, JK, and NS. Funding acquisition: SCK, ST, DDQ, and AME. Investigation: SCK, WHL, and DGZ. Methodology: DGZ, SCK, JK, KC, and EC. Project administration: SCK, ST. Resources: DGZ. Software: DGZ, WHL, MYH, JK, and LJZ. Supervision: SCK, JK, NK, and ST. Validation: SCK, JK, NK, and ST. Visualization: SCK, JK, and DGZ. Writing - original draft: DGZ. Review, and editing: SCK, ST, JK, NS, EC, WHL, AME, DQD, LJZ, and MYH.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary information

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Data type: docx

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