

Resolving the polyphyletic origins of *Pholiotina* s.l. (Bolbitiaceae, Agaricales) based on Chinese materials and reliable foreign sequences

Song HB and Bau T*

Key Laboratory of Edible Fungal Resources and Utilization (North), Ministry of Agriculture and Rural Affairs, Jilin Agricultural University, Changchun 130118, China

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Abstract

In Bolbitiaceae, the polyphyletic origin of *Pholiotina* sensu lato has led to the classification of many species of *Pholiotina* under *Conocybe*, causing confusion among researchers. This study aimed to reconcile morphology and phylogeny using Chinese materials and reliable gene sequences. To reconstruct the relationships of *Pholiotina* sensu lato, we conducted maximum likelihood and Bayesian analyses using a combined dataset of nuclear ribosomal DNA internal transcribed spacer region (nrITS), nuclear ribosomal DNA 28S subunit (nrLSU), and translation elongation factor 1-alpha (*tef1-α*). The analysis revealed three major clades within *Pholiotina* sensu lato: *Pholiotina* Clade 1, *Pholiotina* Clade 2, and *Pholiotina* Clade 3. A new genus named *Conocybula* was established within *Pholiotina* Clade 1, sister to *Galerella nigeriensis*. *Conocybula* comprises the *Conocybula* section *Cyanopodae* and *Conocybula* section *Conocybula*. *Pholiotina* Clade 2 was identified as a new genus called *Conobolbitina*, which includes *Conobolbitina* section *Conobolbitina*, *Conobolbitina* section *Aeruginosa*, and *Conobolbitina* section *Verrucisporae*. Based on the revision of Hausknecht's definition of *Pholiotina*, the monophyletic group of *Pholiotina* Clade 3, characterised by the presence of a veil, is considered a true *Pholiotina*. Therefore, *Pholiotina* now includes only *Pholiotina* section *Pholiotina*, *Pholiotina* section *Vestitae*, and *Pholiotina* section *Intermediae*. This study discovered 30 new taxonomic groups, including two new genera, 17 new species, 11 new combinations, and two new records from China. Keys for the genera, sections, and species within the family Bolbitiaceae in China are compiled. Morphological descriptions and line drawings of the 17 new species and two newly recorded species are provided. By resolving the delimitation of genera, sections, and species within *Pholiotina* sensu lato, we addressed possible phylogenetic relationships and evolutionary trends among genera and infrageneric ranks in Bolbitiaceae.

Keywords – Bolbitiaceae – morphology – *Pholiotina* s.l. – phylogenetics – Polyphyletic

INTRODUCTION

The genus *Pholiotina* Fayod classified under Bolbitiaceae Singer derives its name from the Greek word “pholis”, meaning “squamosae”, signifies the presence of a veil (Fayod 1889). These fungi are classified as saprophytic, and are commonly found on fertile soils, herbivore dung, and plant remains (Matheny et al. 2006, Tóth et al. 2013). Certain species within the *Pholiotina* s.l. contain toxic substances, such as psilocybin, phallotoxins, and amatoxins, which can have neuropsychotropic, gastroenteric, and hepatotoxic effects and it is worth noting that these toxic substances also exhibit potential pharmacological activities (Wu et al. 2019).

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***Corresponding Author:** Tolgor Bau – e-mail – junwusuo@126.com

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In 1889, Fayod established *Pholiotina* as a genus and defined its species based on the presence of a ring on the stipe (Fayod 1889). However, for an extended period, *Pholiotina* was considered a subgenus of *Conocybe* Fayod. Kühner (1935) observed that differences in the lamella trama were insufficient for a distinct generic classification and proposed *Pholiotina* as a subgeneric rank within *Conocybe*. This perspective found support from several scholars (Walting 1965, Kits van Waveren 1970, Walting 1982). Singer's (1951) adaption to Fayod's perspective elevates *Pholiotina* to a generic level and expanded Fayod's original definition (Fayod 1889) by transferring the sect. *Piliferae* Kühner ex Singer from *Conocybe* to *Pholiotina*, considering the presence of non-lecythiform cheilocystidia, although sect. *Piliferae* lack veils. Singer also included sect. *Togulares* Konrad & Maublanc which are characterised by a veil residue on the pileus margin and a ring on the stipe within *Pholiotina* (Singer 1951). Watling (1965) introduced the sect. *Vestitae* (Watling) Hausks. & Krisai for *Pholiotina* species lacking a ring but with non-lecythiform cheilocystidia. Watling (1971) established the sect. *Intermediae* (Watling) Singer for species possessing lecythiform cheilocystidia and caulocystidia, serrulate veil remnants on the pileus margin, and phaseoliform-to-reniform basidiospores (Watling 1965, 1971). Kits van Waveren (1970) proposed a distinction between *Pholiotina* and *Conocybe* based on the loss of red pigment in *Pholiotina* during drying, which could not be recovered upon rehydration. Through extensive specimen observations, Kits van Waveren (1970) identified significant variations in the length and depth of the striations on the pileus surface within the species. These variations often became indistinct when the specimens were dried. Consequently, Kits van Waveren disagreed with Kühner's (1935) proposal of using pileus striations as a classification criterion for *Pholiotina*. Singer (1973) established sect. *Cyanopodae* Singer for *Pholiotina* species exhibiting a bluish-green colouration at the base of the stipe or a bluish colouration on the pileus (containing psilocybin), and sect. *Verrucisporae* Singer for species with basidiospores featuring cristate-punctate surfaces (Singer 1973). Singer argued for the separation of *Conocybe* from *Pholiotina*, emphasising the differentiation based on the structure of the lamellar trama (Singer 1986). In 2002, Horak and Hausknecht introduced the sect. *Vesiculosae* Horak & Hauskn. for *Pholiotina* species characterised by spheropedunculate cheilocystidia (Horak & Hausknecht 2002). Hausknecht (2009) presented a comprehensive summary of the classification hierarchy within *Pholiotina*, incorporating traditional morphological criteria, which received broad recognition and acceptance. In this article, the authors have revised the definition of *Pholiotina*, as detailed in the results section.

The advent of molecular techniques has revealed discrepancies between traditional morphological classifications and phylogenetic relationships in fungal taxonomy, prompting a shift towards integrating morphology and systematics. Moncalvo et al. (2000) discovered that *Conocybe* and *Bolbitius* Fr. formed a monophyletic group, with *Pholiotina* closely related to *Bolbitius* as its sister group (Moncalvo et al. 2002). This finding was further confirmed by Matheny et al. (2006) through analysis of six gene regions (*rpb1*, *rpb1*-intron2, *rpb2*, 18S, 25S and 5.8S). Recent systematic molecular studies on *Pholiotina* have been conducted by various researchers. Tóth et al. (2013) constructed a phylogenetic framework for *Conocybe* and *Pholiotina* using the nrITS, nrLSU, and *tefl- α* gene regions. The results indicate that *Conocybe* and *Bolbitius* formed a monophyletic group, whereas *Pholiotina* and *Galerella* Earle had multiple origins. *Descolea* Singer is identified as the basal lineage within this group. This study also revealed an important issue: *Pholiotina* could be divided into three clades. According to the definition of *Pholiotina*, which includes species with well-developed veils and rings on the stipe, only *Pholiotina* Clade 3 (consisting of species from sect. *Pholiotina* Fayod sect. *Intermediae*, and sect. *Vestitae*) fit this definition. Consequently, *Pholiotina* should be limited to *Pholiotina* Clade 3, whereas species with indistinct or absent veils, including those from sect. *Cyanopodae*, sect. *Piliferae*, and sect. *Verrucisporae* should be excluded. However, the authors did not provide a further taxonomic classification for *Pholiotina* clades 1 and *Pholiotina* Clade 2 (Tóth et al. 2013). Recognising this issue, Karich (2020) suggested that *Pholiotina* Clade 1 and *Pholiotina* Clade 2 be split into one or two separate genera while retaining the name *Pholiotina* for the clade exhibiting a distinct veil.

The results from Liu (2018) and Song & Bau (2023) support the findings of Tóth et al. (2013) and further extend the analysis to encompass samples from northeastern China, providing additional insights into the phylogenetic framework of this group. These studies confirmed that *Pholiotina* is polyphyletic and adopted the clade designations proposed by Tóth et al. (2013). It was observed that *Pholiotina* Clade 1 and *Pholiotina* Clade 2 are sister groups to *Galerella* and *Bolbitius*, respectively. Notably, the species from sect. *Cyanopodae*, characterised by their blue colouration, were identified in both *Pholiotina* Clades 1 and *Pholiotina* Clade 2 with strong support, indicating the polyphyletic nature of this section. Therefore, relying solely on blue colouration as the basis for subdivision is insufficient (Tóth et al. 2013, Liu 2018). Both Tóth et al. (2013) and Song et al. (2023) found that some species currently classified under *Pholiotina* Clade 3 still retain the genus name *Conocybe*, such as *C. dentatomarginata* Watling, *C. aporos* Kits van Wav., and *C. serrata* T. Bau & J. Liu. This suggests that although the independent status of *Pholiotina* as a genus has been recognised, issues arise owing to historical reasons and the indistinct boundary between *Pholiotina* and *Conocybe*. Song et al. (2023) followed the viewpoints of Kühner (1935) and Hausknecht (2009) to clarify the boundaries between *Pholiotina* and *Conocybe* in China, and recombined *C. serrata* into *P. serrata* (T. Bau & J. Liu) T. Bau & H. B. Song. However, a drawback of this approach is that *Pholiotina* remains polyphyletic.

Pholiotina species are relatively uncommon, with a documented total of 55 species worldwide reported by Hausknecht (2007), encompassing multiple polyphyletic clades. In recent years, only a handful of species have been added to the *Pholiotina* genus, such as *P. calongei* Siquier, E. Suárez, Salom, & Planas, *P. mediterranea* Siquier & Salom, *P. pleurocystidiata* Hauskn. & Krisai, *P. pseudoampullaceocystis* Karich, *P. serrata* and *P. sphagnicola* T. Bau & Burenbaatar G. (Siquier & Salom 2017, Siquier et al. 2021, Hausknecht & Krisai-greilhuber 2020, Karich 2020, Song et al. 2023, Burenbaatar et al. 2024). Presently, the Index Fungorum lists 129 records of *Pholiotina* (29 June 2024); however, some cases still exist in which *Pholiotina* species are listed under the genus name *Conocybe*, leading to confusion. China, with its vast territory and diverse ecological types, provides excellent natural conditions for *Pholiotina* species. However, the number of reported *Pholiotina* species in China is much lower than those in Europe and North America (Song et al. 2023). Many records in China still rely on the names of species reported in Europe and America and lack precise verification using polyphasic classification methods. In this study, we aim to address the polyphyletic nature of *Pholiotina* by reconstructing the phylogenetic relationships of *Pholiotina* s.l. using specimens collected in China and reliable foreign sequences, integrating macroscopic morphological and phylogenetic analyses to achieve this goal.

MATERIALS AND METHODS

Samplings and Morphological Analyses

Specimens for this study were collected from China. Field habitat photographs were taken, and specimens were deposited at the Fungarium Mycology of Jilin Agricultural University (HMJAU). The specify of the specimens were treated with 5% Potassium hydroxide (KOH) solution and 1% Congo red solution, and an ammonia reaction was carried out using a 25% ammonia solution (Hausknecht 2009). Observations were made using a Carl Zeiss Primo Star optical microscope (Jena, Germany). The basidiospores were captured using a ZEISS MERLIN electron microscope with an accelerating voltage of EHT 1-5Kv. The color of fresh basidioma was described using the color-coding system developed by the German Institute for Quality Assurance and Certification (Reichs-Ausschuss für Lieferbedingungen und Gütesicherung, <https://www.ral-guetezeichen.de/>).

To provide accurate measurements, the basidiospore measurements in this study do not include the apiculus. They are presented as '(a)b–c(d)', where 'b–c' represents the minimum of 90% of the measured values, and 'a' and 'd' represent the extreme values. The main body (excluding sterigmata or excrescences) of the basidia, cheilocystidia, caulocystidia, and pileipellis were measured (if present) to record their dimensions accurately. The notation (n/m/p) indicates that

measurements were made on "n" randomly selected basidiospores from "m" basidiomata of "p" collections. This sampling method ensures a representative measurement sample. Q is the ratio of length divided by width, providing a measure of the elongation of the spores. Qm represents the average quotient (length/width ratio) \pm standard deviation, giving an overall average value with variation.

DNA Extraction, PCR Amplification, and Sequencing

Genomic DNA extraction and the polymerase chain reaction (PCR) procedures were conducted following the protocol outlined by Mou & Bau (2021). To amplify specific sequences, we utilized the primer pairs ITS1F/ITS4 (Gardes & Bruns 1993), LR0R/LR7 (Moncalvo et al. 2000), and EF1-983F/EF1-2218R (Rehner & Buckley 2005) for the nrITS, nrLSU, and *tef1- α* sequences, respectively. Following the amplification, sequencing services were performed by Sangon Biotech (Shanghai) Co., Ltd., resulting in the acquisition of sequence data.

Phylogenetic Analyses

A total of 146 sequences were generated in this study and those have been submitted to NCBI GenBank. In addition to these new sequences, relevant sequences were obtained following (Table 1) from GenBank and UNITE for constructing the phylogenetic trees (<https://www.ncbi.nlm.nih.gov/>, <https://unite.ut.ee/>). The nrITS, nrLSU, and *tef1- α* sequences were aligned using the G-INS-i algorithm with two iterative cycles only. The alignment was performed using the online Mafft version 7 (<https://mafft.cbrc.jp/alignment/server/>) and then manually refined and trimmed using MEGA7. The concatenated alignment was generated using PhyloSuite (Zhang et al. 2020). The best-fit partition model (edge-unlinked) was selected using the BIC criterion with ModelFinder (Kalyaanamoorthy et al. 2017). Maximum likelihood phylogenies were inferred using IQ-TREE under the edge-linked partition model. The analysis included 5000 ultrafast bootstraps and the Shimodaira-Hasegawa-like approximate likelihood-ratio test (Nguyen et al. 2015, Guindon et al. 2010). Bayesian inference phylogenies were inferred using MrBayes 3.2.6 under the partition model. The analysis involved two parallel runs and 1,000,000 generations (Ronquist et al. 2012), with the initial 25% of the sampled data discarded as burn-in, average standard deviation of split frequencies is 0.006774. Gene structures were analyzed using the GSDS online software (<http://gsds.gao-lab.org/index.php>). The final figures were edited using iTOL (Letunic & Bork 2019), Adobe Photoshop 2021, and Adobe Illustrator 2021.

Table 1 Information on the DNA sequences used to reconstruct phylogenetic trees.

Taxon	Voucher ID	nrITS	nrLSU	<i>tef1-α</i>	Origin	References
<i>Bolbitius coprophilus</i>	HMJAU64958	OQ780315	OQ758216	–	China	Song & Bau (2023)
<i>B. coprophilus</i>	SZMC-NL-2640	DQ234567	DQ234567	DQ234567	Hungary	Tóth et al. (2013)
<i>B. reticulatus</i>	WU30001	JX968249	JX968366	JX968455	Hungary	Tóth et al. (2013)
<i>B. subvolvatus</i>	WU28379	JX968248	JX968365	JX968454	Italy	Tóth et al. (2013)
<i>Conobolbitina aeruginosa</i>	WU27104	JX968247	JX968364	–	Germany	Tóth et al. (2013)
<i>Con. dasypus</i>	HMJAU62002	OR995661	OR995711	PP000854	China	This study
<i>Con. dasypus</i>	SZMC-NL-2279	JX968152	JX968269	JX968385	Hungary	Tóth et al. (2013)
<i>Con. micheliana</i>	HMJAU65015	OR995677	OR994080	PP000869	China	This study
<i>Con. micheliana</i>	HMJAU65016	OR995678	OR994081	PP000870	China	This study
<i>Con. ochroleuca</i>	HMJAU65017	OR995679	OR994082	PP000871	China	This study
<i>Con. ochroleuca</i>	HMJAU65018	OR995680	OR994083	PP000872	China	This study
<i>Con. pygmaeoaffinis</i>	WU16600	JX968149	JX968382	–	Austria	Tóth et al. (2013)
<i>Conobolbitina</i> sp.1	HMJAU65106	OR995670	PP001410	PP000863	China	This study

Table 1 Continued.

Taxon	Voucher ID	nrITS	nrLSU	<i>tef1-α</i>	Origin	References
<i>Conobolbitina</i> sp.2	HMJAU65107	OR995671	PP001411	PP000864	China	This study
<i>Conocybe alkovii</i>	LE262841	JQ247196	–	–	Russia	Malysheva (2012)
<i>C. antipus</i>	WU19791	JX968215	JX968332	JX968432	Austria	Tóth et al. (2013)
<i>C. ceracea</i>	HMJAU64951	OQ758110	OQ758218	OQ758305	China	Song & Bau (2023)
<i>C. coniferarum</i>	LE313009	NR_155030	–	–	Russia	Malysheva (2017)
<i>C. crispella</i>	WU27367	JX968208	JX968325	JX968426	Australia	Tóth et al. (2013)
<i>C. cylindrospora</i>	HMJAU42440	MG250375	OQ758203	–	China	Liu & Bau (2018), Song & Bau (2023)
<i>C. deliquescens</i>	HMJAU61998	OP373403	OQ758204	OQ758292	China	Song & Bau (2023)
<i>C. enderlei</i>	WU21272	JX968163	JX968279	–	Italy	Tóth et al. (2013)
<i>C. gigasperma</i>	SZMC-NL-3972	JX968179	JX968295	JX968403	Slovakia	Tóth et al. (2013)
<i>C. hausknechtii</i>	LE253998	JQ247194	–	–	Russia	Malysheva (2013)
<i>C. hornana</i>	SZMC-NL-3499	JX968178	JX968294	JX968402	Slovakia	Tóth et al. (2013)
<i>C. incerta</i>	LE313017	NR_155031	–	–	Russia	Malysheva (2017)
<i>C. leporina</i>	SZMC-NL-2380	JX968177	JX968293	JX968401	Hungary	Tóth et al. (2013)
<i>C. olivaceopileata</i>	LE313106	NR_155028	–	–	Russia	Malysheva (2017)
<i>C. parapilosella</i>	JLS3063/WU30224	MN872706	–	–	Spain	Siquier & Salom (2021)
<i>C. pilosella</i>	HMJAU64957	OQ780306	OQ758206	OQ758295	China	Song & Bau (2023)
<i>C. praticola</i>	HMJAU64965	OQ780303	–	–	China	Song & Bau (2023)
<i>C. pseudocrispa</i>	HMJAU64944	OQ780308	OQ758211	OQ758298	China	Song & Bau (2023)
<i>C. pubescens</i>	WU20759	JX968170	JX968286	JX968396	Italy	Tóth et al. (2013)
<i>C. rostellata</i>	SZMC-NL-2499	JX968162	JX968278	JX968390	Sweden	Tóth et al. (2013)
<i>C. rufostipes</i>	HMJAU64937	OQ758120	OQ758227	OQ758317	China	Song & Bau (2023)
<i>C. semiglobata</i>	WU8794	JX968188	JX968304	JX968168	Austria	Tóth et al. (2013)
<i>C. siennophylla</i>	HMJAU64966	OQ780312	OQ758210	OQ758297	China	Song & Bau (2023)
<i>C. singeriana</i>	WU22129	JX968166	JX968282	JX968393	Austria	Tóth et al. (2013)
<i>C. volvicystidiata</i>	LIP0001212	KY346827	–	–	France	Hausknecht & Broussal (2016)
<i>C. watlingii</i>	WU22744	JX968172	JX968288	JX968398	Finland	Tóth et al. (2013)
<i>Conocybula coprophila</i>	SZMC-NL-2176	JX968156	JX968273	–	Hungary	Tóth et al. (2013)

Table 1 Continued.

Taxon	Voucher ID	nrITS	nrLSU	<i>tef1-a</i>	Origin	References
<i>Co. coprophila</i>	HMJAU62008	OR995662	OR995712	PP000855	China	This study
<i>Co. cyanopus</i>	WU2134	JX968157	JX968274	JX968388	Austria	Tóth et al. (2013)
<i>Co. cyanopus</i>	HMJAU62007	OR995663	OR995713	PP000856	China	This study
<i>Co. longistipitata</i>	LE312984	KY627842	KY627843	–	Russia	Crous et al. (2017)
<i>Co. longistipitata</i>	HMJAU64974	OR995664	OR995714	PP000857	China	This study
<i>Co. smithii</i>	HMJAU62001	OP373407	OQ758215	OQ758300	China	Song & Bau (2023)
<i>Co. smithii</i>	CCB185	KF830097	KF830088	–	USA	Direct Submission
<i>Conocybula</i> sp.1	HMJAU65104	OR995672	PP001412	PP000865	China	This study
<i>Conocybula</i> sp.2	HMJAU65105	OR995673	PP001413	PP000866	China	This study
<i>Descolea antarctica</i>	NZ5182	AF325647	–	–	USA	Peintner & Bougher (2001)
<i>D. quercina</i>	HMJAU64959	OQ780313	OQ758213	OQ758299	China	Song & Bau (2023)
<i>Galerella nigeriensis</i>	CNF1/5859	JX968251	JX968368	JX968457	Nigeria	Tóth et al. (2013)
<i>Pholiotina aberrans</i>	SZMC-NL-3161	JX968256	JX968373	JX968459	Sweden	Tóth et al. (2013)
<i>P. aporos</i>	SZMC-NL-1241	JX968260	JX968376	JX968462	Hungary	Tóth et al. (2013)
<i>P. arrhenii</i>	SZMC-NL-2509	JX968261	JX968377	–	Sweden	Tóth et al. (2013)
<i>P. arrhenii</i>	HMJAU65103	OR995665	OR995715	PP000858	China	This study
<i>P. bambusicola</i>	HMJAU65054	OR995681	OR994084	PP000873	China	This study
<i>P. bambusicola</i>	HMJAU65055	OR995682	OR994085	PP000874	China	This study
<i>P. bifurcaticystidia</i>	HMJAU65030	OR995683	OR994086	PP000875	China	This study
<i>P. bifurcaticystidia</i>	HMJAU65032	OR995684	OR994087	PP000876	China	This study
<i>P. bispora</i>	HMJAU65070	OR995685	OR994088	PP000877	China	This study
<i>P. bispora</i>	HMJAU65072	OR995686	OR994089	PP000878	China	This study
<i>P. brevipila</i>	HMJAU65082	OR995687	OR994090	PP000879	China	This study
<i>P. brevipila</i>	HMJAU65084	OR995688	OR994091	PP000880	China	This study
<i>P. brunnea</i>	GLM-F39772	MK412353	–	–	Germany	Karich (2020)
<i>P. brunnea</i>	OF254586	UDB035771	–	–	Norway	Karich (2020)
<i>P. brunnea</i>	S2805	MT909555	–	–	Germany	Karich (2020)
<i>P. brunnea</i>	SZMC-NL-1216	JX968259	JX968375	JX968461	Hungary	Tóth et al. (2013)
<i>P. calongei</i>	98486	NR_182947	OK256958	–	Spain	Siquier et al. (2021)
<i>P. changbaishanensis</i>	HMJAU65101	OR995689	OR994092	PP000881	China	This study
<i>P. changbaishanensis</i>	HMJAU65102	OR995690	OR994093	PP000882	China	This study
<i>P. communis</i>	HMJAU65038	OR995691	OR994094	PP000883	China	This study
<i>P. communis</i>	HMJAU65039	OR995692	OR994095	PP000884	China	This study
<i>P. dentatmarginata</i>	SZMC-NL-2921	JX968258	JX968374	JX968460	Hungary	Tóth et al. (2013)
<i>P. eburnea</i>	HMJAU65034	OR995693	OR994096	PP000885	China	This study
<i>P. eburnea</i>	HMJAU65035	OR995694	OR994097	PP000886	China	This study
<i>P. exannulata</i>	GLM-F42368	MK412399	–	–	Germany	Karich (2020)
<i>P. exannulata</i>	HMJAU45107	OR995666	OR995716	PP000859	China	This study
<i>P. excrescenticystidiata</i>	HMJAU65021	OR995695	OR994098	PP000887	China	This study
<i>P. excrescenticystidiata</i>	HMJAU65022	OR995696	OR994099	PP000888	China	This study

Table 1 Continued.

Taxon	Voucher ID	nrITS	nrLSU	<i>tef1-α</i>	Origin	References
<i>P. filaris</i>	MSC378482	AY194542	–	–	USA	Hallen et al. (2003)
<i>P. gracilenta</i>	PDD:87363	KM975419	KM975382	–	New Zealand	Direct Submission
<i>P. hadrocystis</i>	WU10748	MF142251	–	–	Spain	Siquier & Salom (2017)
<i>P. horchinensis</i>	HMJAU65097	OR995697	OR994100	PP000889	China	This study
<i>P. horchinensis</i>	HMJAU65098	OR995698	OR994101	PP000890	China	This study
<i>P. indica</i>	WU20891	JX968263	JX968378	JX968464	India	Tóth et al. (2013)
<i>P. intermedia</i>	HMJAU62014	OR995667	OR995717	PP000860	China	This study
<i>P. liudingshanensis</i>	HMJAU65052	OR995699	OR994102	PP000891	China	This study
<i>P. liudingshanensis</i>	HMJAU65053	OR995700	OR994103	PP000892	China	This study
<i>P. longicystidiata</i>	HMJAU65056	OR995701	OR994104	PP000893	China	This study
<i>P. longicystidiata</i>	HMJAU65060	OR995702	OR994105	PP000894	China	This study
<i>P. mediterranea</i>	MA:Fungi:89945	NR_158849	–	–	Spain	Siquier & Salom (2017)
<i>P. micropora</i>	HMJAU65076	OR995703	OR994106	PP000895	China	This study
<i>P. micropora</i>	HMJAU65080	OR995704	OR994107	PP000896	China	This study
<i>P. parvula</i>	GLM-F39727	MK412362	–	–	Germany	Direct Submission
<i>P. pleurocystidiata</i>	WU40666	NR_176740	–	–	Austria	Hausknecht & Krisai-greilhuber (2020)
<i>P. pseudoampullaceocystis</i>	AK20191010	MT903471	–	–	Germany	Karich (2020)
<i>P. rostellulata</i>	HMJAU65049	OR995705	OR994108	PP000897	China	This study
<i>P. rostellulata</i>	HMJAU65050	OR995706	OR994109	PP000898	China	This study
<i>P. rufidispora</i>	HMJAU65027	OR995707	OR994110	PP000899	China	This study
<i>P. rufidispora</i>	HMJAU65029	OR995708	OR994111	PP000900	China	This study
<i>P. septentrionalis</i>	JDRG3010201101	MN449431	MN449432	–	Spain	Hallen et al. (2003)
<i>P. serrata</i>	HMJAU42442	MG250376	–	–	China	Liu & bau (2018)
<i>P. serrata</i>	HMJAU62006	OP538570	OQ758217	OQ758301	China	Song & Bau (2023)
<i>Pholiotina</i> sp.	137771707	OP743631	–	–	USA	Direct Submission
<i>Pholiotina</i> sp.	DM30-03805	OM212973	–	–	USA	Direct Submission
<i>Pholiotina</i> sp.	G4516	UDB0414885	–	–	Estonia	Karich (2020)
<i>Pholiotina</i> sp.1	HMJAU65108	OR995674	PP001414	–	China	This study
<i>Pholiotina</i> sp.2	HMJAU65109	OR995675	PP001415	PP000867	China	This study
<i>Pholiotina</i> sp.3	HMJAU65110	OR995676	PP001416	PP000868	China	This study
<i>P. sphagnicola</i>	HMJAU64971	PP034263	PP034265	PP034744	Mongolia	Burenbaatar et al. (2024)
<i>P. striipes</i>	WU26997	JX968150	JX968267	JX968383	Austria	Tóth et al. (2013)
<i>P. sulcata</i>	SZMC-NL-1975	JX968153	JX968270	JX968386	Hungary	Tóth et al. (2013)
<i>P. sulciceps</i>	HMJAU65099	OR995709	OR994112	PP000901	China	This study
<i>P. sulciceps</i>	HMJAU65100	OR995710	OR994113	PP000902	China	This study
<i>P. teneroides</i>	SZMC-NL-3501	JX968264	JX968379	JX968465	Slovakia	Tóth et al. (2013)

Table 1 Continued.

Taxon	Voucher ID	nrITS	nrLSU	<i>tef1-α</i>	Origin	References
<i>P. utricystidiata</i>	WU20164	JX968262	JX968463	–	Germany	Tóth et al. (2013)
<i>P. utricystidiata</i>	HMJAU45885	OR995668	OR995718	PP000861	China	This study
<i>P. vestita</i>	SZMC-NL-2191	JX968266	JX968381	JX968467	Hungary	Tóth et al. (2013)
<i>P. vexans</i>	SZMC-NL-3967	JX968265	JX968380	JX968466	Slovakia	Tóth et al. (2013)
<i>P. vexans</i>	HMJAU45078	OR995669	OR995719	PP000862	China	This study
<i>Psathyrella leucotephra</i>	SZMC-NL-1953	FM163226	FM160683	FM897219	Hungary	Nagy et al. (2011)
<i>Ps. piluliformis</i>	HMJAU37922	MG734716	MW413364	MW411001	China	Yan & Bau (2018)

Note: “–” means no relevant genetic information, and the new species are represented in bold.

RESULTS

Phylogenetic analyses

The ML phylogenetic tree was constructed based on a combined dataset of nrITS, nrLSU, and *tef1- α* , while the Bayesian tree was not presented due to their consistent topology. Support values were indicated on the tree nodes. All Bayesian posterior probabilities and ML bootstrap values (PP/MLbs) were retained (Fig. 1). The multi-locus dataset (nrITS + nrLSU + *tef1- α*) of *Pholiotina* s.l. comprised 901 bp for nrITS, 1299 bp for nrLSU, and 1193 bp for *tef1- α* . The alignment included 124 sequences with 3393 columns, resulting in 1643 distinct patterns, 1244 parsimony-informative sites, 195 singleton sites, and 1953 constant sites. During the construction of ML phylogenetic trees, the best-fit models, GTR+F+R5, were selected for nrITS, nrLSU, and *tef1- α* based on the BIC. Similarly, for Bayesian phylogenetic trees, the best-fit models according to the BIC were GTR+F+I+G4 for nrITS and nrLSU, SYM+I+G4 for *tef1- α* .

The phylogenetic tree of *Pholiotina* s.l. (Figs 1, 2) included *Psathyrella* (Fr.) Quél. as the outgroup at the base of the tree. The tree revealed that *Pholiotina* was polyphyletic, comprising *Pholiotina* Clade 1, *Pholiotina* Clade 2, and *Pholiotina* Clade 3. On the other hand, *Bolbitius*, and *Conocybe* were identified as monophyletic groups. *Pholiotina* Clade 1 (1/89) includes the new genera *Conocybula* T. Bau & H. B. Song and *Galerella* (1/100), demonstrating strong support. *Conocybula* consists of *Co.* sect. *Cyanopodae* (Singer) T. Bau & H. B. Song (1/99) and *Co.* sect. *Conocybula*. *Pholiotina* Clade 2 (1/99) is now recognized as the new genus *Conobolbitina* T. Bau & H. B. Song, encompassing *Con.* sect. *Conobolbitina* (= *P.* sect. *Piliferae*), *Con.* sect. *Aeruginosa* (Hauskn. & Krisai) T. Bau & H. B. Song, and *Con.* sect. *Verrucisporae* (Singer) T. Bau & H. B. Song. *Pholiotina* Clade 3 (0.99/98) corresponds to the traditional *Pholiotina*, comprising only *P.* sect. *Pholiotina*, *P.* sect. *Vestitae*, and *P.* sect. *Intermediae*. In total, 30 new taxa were discovered, including two new genera, 17 new species, 11 new combinations, and two new records.

Fitting morphology with phylogenetics

In Fig. 2, the analysis of morphological characteristics in conjunction with phylogenetics revealed distinctive features among different taxa. *Conocybula* species were observed to have stipes lacking a ring, pileus without blue-green hues, elliptical basidiospores devoid of cristate-punctate ornamentation, featuring a smooth surface with a germ pore. Cheilocystidia were found to be non-lecythiform, co-occurring with sub-lecythiform, lageniform, and nettle hair-shaped elements, while no excrescences were present. Caulocystidia displayed a non-lecythiform shape, and pileocystidia were detected, interspersed with nettle hair-shaped elements. Similarly, for *Conobolbitina* species, the stipes were found to be devoid of a ring, basidiospores exhibited an elliptical shape with a germ pore, and cheilocystidia were non-lecythiform. *Pholiotina* species were characterized by the

presence of a veil, pileus and stipes lacking blue-green hues, and basidiospores being smooth without cristate-punctate ornamentation. Further details can be found in “Fig. 2 and Taxonomy”.

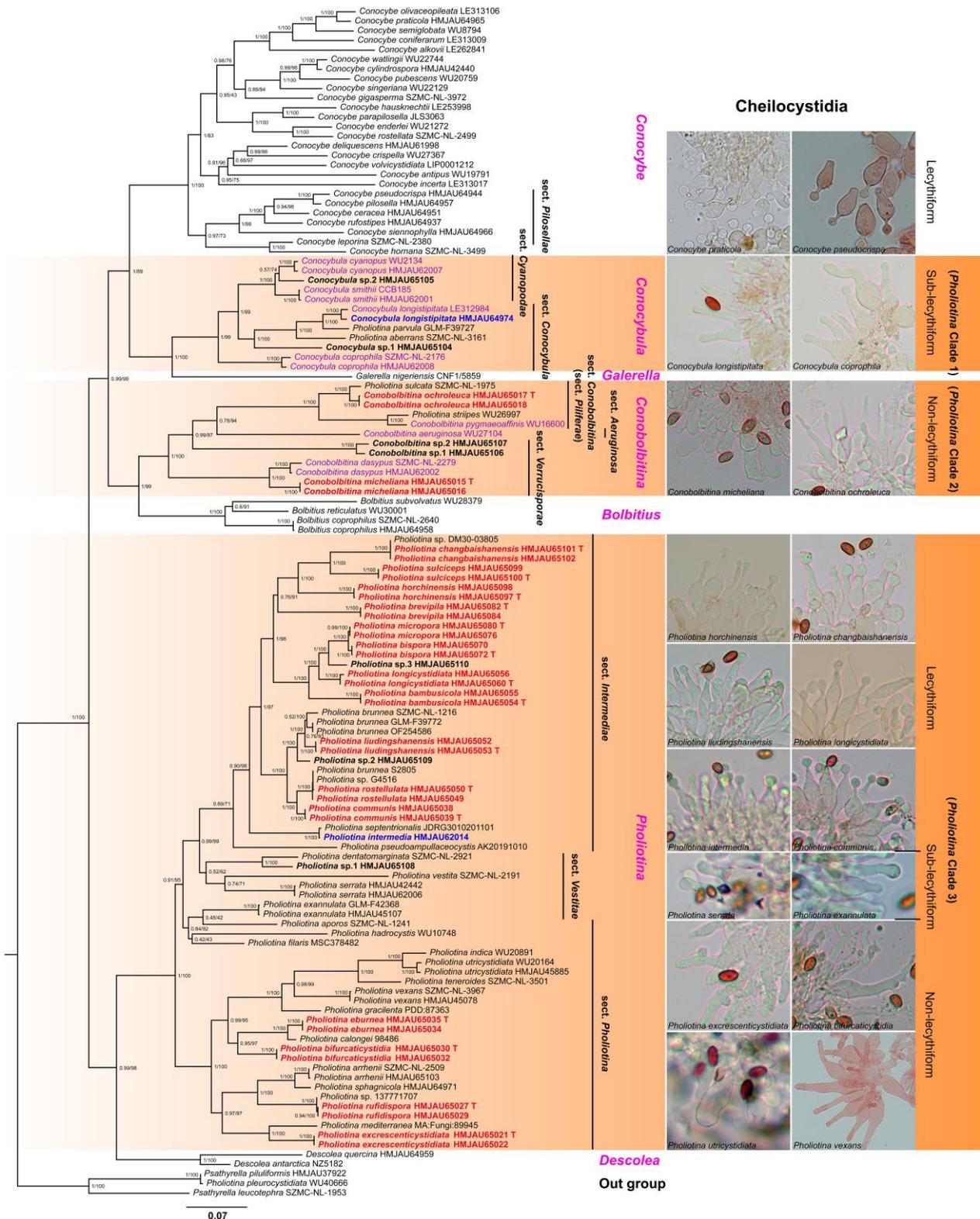


Figure 1 – The phylogenetic relationships of *Pholiotina* s.l. in Bolbitiaceae using Bayesian inference and maximum likelihood methods based on a multi-locus dataset (nrITS, nrLSU, and *tef1-α*). Nodes with PP values and ML boot-strap support values are indicated in the phylogenetic tree, the newly described taxa are highlighted in bold red font for new species, bold blue font for

new records in China, purple font for new combinations, and bold black font for hypothesized species. T denotes the sequence of the type species.

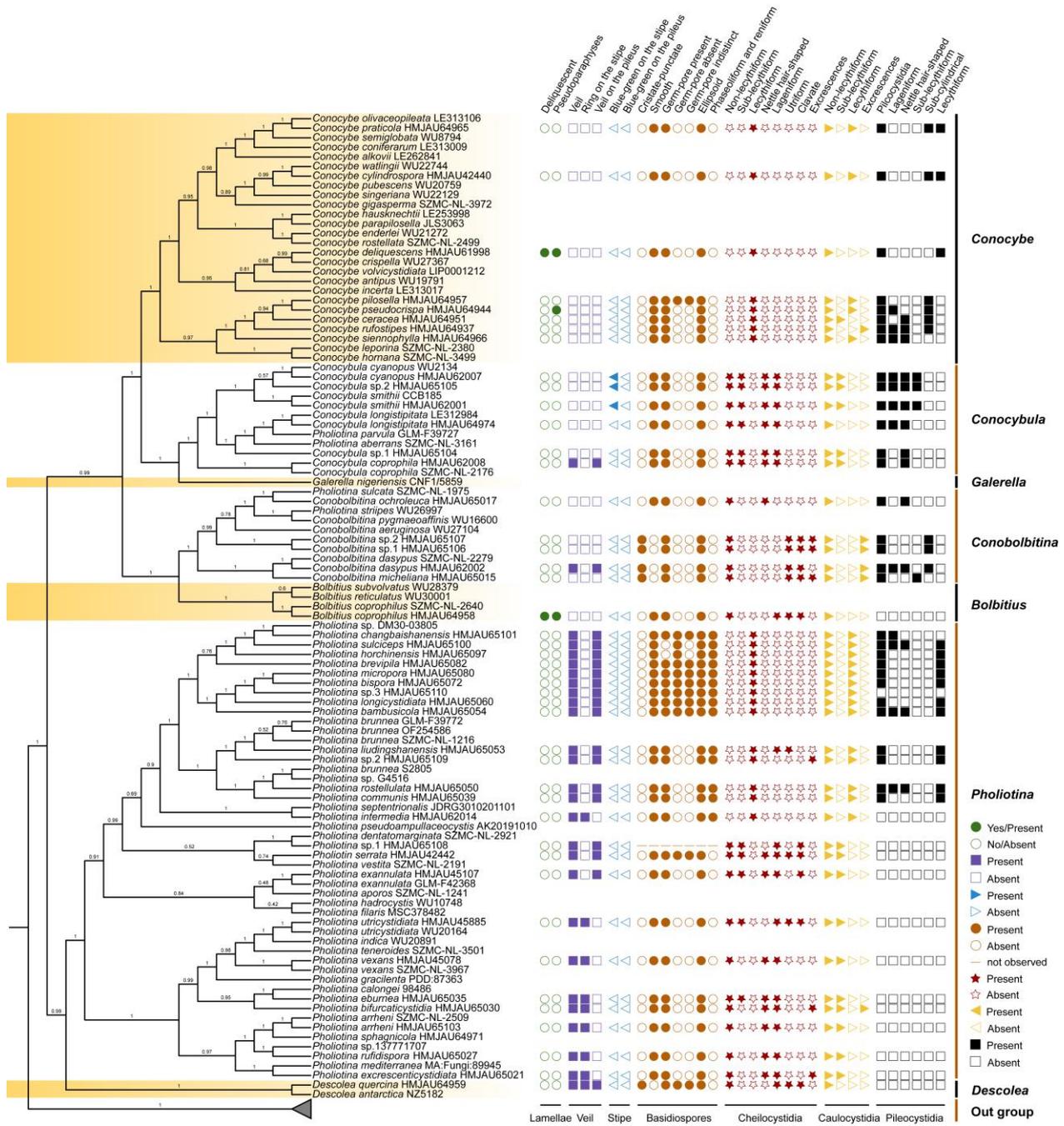


Figure 2 – *Pholiotina* s.l. was fitted with a morphology using a Bayesian phylogenetic tree based on a multi-locus dataset (nrITS, nrLSU, *tef1-α*), and PP values are labeled on the nodes.

Taxonomy

Conocybula T. Bau & H. B. Song, gen. nov.

Mycobank number: MB851475; Facesoffungi number: FoF15316

Etymology – “*Conocybula*” is composed of the two parts “*Conocybe*” and “*ula*”, indicating its correlation with *Conocybe*.

Type species – *Conocybula longistipitata* (E.F. Malysheva & Kiyashko) T. Bau & H. B. Song

Basidioma small, mycenoid. Pileus conical to obtusely conical, campanulate, hemispherical, convex, parabolic, surface smooth, hygrophanous, greasy or non-greasy, distinctly pubescent, with

or without striae. Context thin, beige (RAL1001), sandy yellow (RAL1002), or the same color as the pileus, odor indistinct. Lamellae adnexed to narrowly adnate, loosely to crowded, unequal, maize yellow (RAL1006), ochre brown (RAL8001), clay brown (RAL8003), copper brown (RAL8004), smooth or slightly serrated at the margin. Stipe cylindrical, slightly swollen or bulbous at the base. After injury, the stipe turns pastel blue (RAL5024), light blue (RAL5012), or remains uncolored. Surface of the stipe is covered with powdery frost and pubescence, with longitudinal fibrous striations. The pileus has a veil only in the early stages, which quickly disappears or becomes absent.

Basidiospores smooth, ellipsoid to oblong, slightly amygdaliform, occasionally phaseoliform to reniform, with a distinct germ pore, and some are eccentrically positioned. Basidia clavate, spheropedunculate, 4- or 2-spored, with vacuolar contents. Cheilocystidia are variable, lageniform, with slightly capitate apex, sub-lecythiform. Lamellar edges are sterile, and pseudoparaphyses may be present or absent. Pleurocystidia absent. Caulocystidia are polymorphic and irregular, including lageniform, long-necked lageniform with curved necks, sub-lecythiform, utriform, fusiform, clavate, subcylindrical, subcapitate, spheropedunculate, nettle hair-shaped, conical (like an icicle), or hair-like. Pileipellis hymeniform, composed of sphaeropedunculate elements and nearly clavate elements, with yellow pigments at the base. Pileocystidia present, lageniform, long-necked lageniform with curved necks, sub-lecythiform, hair-like, nettle hair-shaped to conical (like an icicle), relatively large, with a length of up to 200 µm. Some of them are filled with yellow pigment. Clamp connections present or absent. It can react negatively or positively with ammonia solution, and if positive, it forms rhomboid crystals. At the genetic level, the first intron of the *tef-1α* (983–2218) region is missing in species within this genus, which can serve as a classification criterion (Fig. 3).

Habitat – Grows on feces, on the forest floor between coniferous and broad-leaved trees, and on moist mossy layers.

Known distribution – It is widely distributed worldwide.

Notes – *Conocybula* was originally classified within the *Pholiotina* Clade 1 and is considered a lineage derived from *Pholiotina*. However, some scholars argue that *Conocybula* should be placed within *Conocybe* (Kühner 1935). This is because *Conocybula* is morphologically closer to *Conocybe*. Nonetheless, there are distinguishing factors between the two genera. The cheilocystidia of *Conocybe* are lecythiform, and the presence of filamentous hyphae in the trama allows for differentiation (Song et al. 2023). In contrast, Hausknecht (2009) considered *Conocybula* as part of *Pholiotina*. However, this treatment has resulted in *Pholiotina* being polyphyletic. In this study, we adopted a combined approach of morphology and molecular analysis, which led to the conclusion that *Pholiotina* Clade 1 (excluding *Galerella*) should be classified as *Conocybula*.

Key to sections of *Conocybula* in China

1. No color change in the stipe after injury *Co. sect. Conocybula*
1'. Bluing of the stipe after injury *Co. sect. Cyanopodae*

Conocybula section *Conocybula*

Etymology – “*Conocybula*” is composed of the two parts “*Conocybe*” and “*ula*”, indicating its correlation with *Conocybe*.

Basidioma small, mycenoid. Pileus conical to obtusely conical, campanulate, hemispherical, convex, parabolic, surface smooth, hygrophanous, greasy or non-greasy, distinctly pubescent, with or without striae. Context thin, beige (RAL1001), sandy yellow (RAL1002), or the same color as the pileus, odor indistinct or without specific odor. Lamellae adnexed to narrowly adnate, loosely to crowded, unequal, maize yellow (RAL1006), ochre brown (RAL8001), clay brown (RAL8003), copper brown (RAL8004), smooth or slightly serrated at the margin. Stipe cylindrical, slightly swollen or bulbous at the base. No color change in the stipe after injury. Surface of the stipe is

covered with powdery frost and pubescence, with longitudinal fibrous striations. The pileus has a veil only in the early stages, which quickly disappears or becomes absent.

Basidiospores smooth, ellipsoid to oblong, slightly amygdaliform, occasionally phaseoliform to reniform, with a germ pore, and some are eccentrically positioned. Basidia clavate, spheropedunculate, 4- or 2-spored, with vacuolar contents. Cheilocystidia are variable, lageniform, with slightly enlarged apex, sub-lecythiform. Lamellar edges are sterile, and pseudoparaphyses present or absent. Pleurocystidia absent. Caulocystidia are polymorphic and irregular, including lageniform, long-necked lageniform with curved necks, sub-lecythiform, utriform, fusiform, clavate, subcylindrical, subcapitate, spheropedunculate, nettle hair-shaped, conical (like an icicle), or hair-like. Pileipellis hymeniform, composed of sphaeropedunculate elements and nearly clavate elements, with yellow pigments at the base. Pileocystidia present, lageniform, long-necked lageniform with curved necks, sub-lecythiform, hair-like, nettle hair-shaped to conical (like an icicle), relatively large, with a length of up to 200 μm . Some of them are filled with yellow pigment. Clamp connections present or absent. It can react negatively or positively with ammonia solution, and if positive, it forms rhomboid crystals. At the genetic level, the first intron of the *tef-1 α* (983–2218) region is missing in species within this section (Fig. 3).

Habitat – Grows on feces, on the forest floor between coniferous and broad-leaved trees, and on moist mossy layers.

Known distribution – It is widely distributed worldwide.

Notes – Species within *Conocybula* section *Conocybula* were previously classified under *Pholiotina* section *Piliferae*, which can cause confusion (Hausknecht & Krisai-Greilhuber 2007). However, *P.* sect. *Piliferae* is characterized by cheilocystidia that are lageniform, long-necked lageniform, or nettle hair-shaped, and never capitate enlarged at the apex.

Key to *Conocybula* section *Conocybula* in China

1. Stipe long and slender, basidiospores less than 11 μm in length..... *Co. longistipitata*
- 1'. Stipe slightly short and thick, basidiospores can reach up to 14 μm in length
2. The base of the pileipellis is colorless
- 2' The base of the pileipellis has a yellow-brown pigment

Conocybula longistipitata (E.F. Malysheva & Kiyashko) T. Bau & H. B. Song, comb. nov.
Figs 4A, 5

Mycobank number: MB851640; Facesoffungi number: FoF15317

Basionym – *Pholiotina longistipitata* E.F. Malysheva & Kiyashko, in Crous et al., *Persoonia* 38: 361 (2017)

Pileus diameter 0.3–1.5 cm, initially paraboloid to hemispherical, later obtusely conical, campanulate, center ochre brown (RAL8001), copper brown (RAL8004) to orangebrown (RAL8023), margin is a pastel yellow (RAL1034), beige (RAL1001), and ochre brown (RAL8001). Pileus hygrophonous, surface smooth, covered with fine, short pubescence, margin striated, reaching 4/5 of the way to the center. Context thin, beige (RAL1001), no distinct odor. Lamellae adnexed, ventricose, slightly spaced, unequal in length, ranging from beige (RAL1001) to sandy yellow (RAL1002), margin slightly serrated. Stipe 2.0–6.0 cm long, 0.5–2.0 mm thick, cylindrical, slightly bulbous at the base, reaching up to 2 mm. Stipe light ivory (RAL1015), ranging from oyster white (RAL1013) to cream (RAL9001), covered with a powdery coating and short hairs, with longitudinal fibrous striations.

Basidiospores (60/3/3) (8–)8.4–9.9(–10.7) \times (4.8–)5–5.9(–6.2) μm , Q = (1.5–)1.58–1.84(–1.95), Qm = 1.71(\pm 0.07), slightly ellipsoid to oblong, amygdaliform, occasionally phaseoliform to reniform, with thick walls, containing oil droplets, germ pore diameter less than 1.5 μm , some basidiospores are eccentric. Basidiospores appear ochre brown (RAL8001) to copper brown (RAL8004) in KOH solution. Basidia (17–)18–27(–29) \times 7–10(–11) μm , clavate, 4-spored, sterigmata 2–6 μm long, with vacuolar contents. Cheilocystidia (24–)24–48(–50) \times (7–)8–14(–16)

µm, lageniform to long-necked lageniform, some with slightly swollen tips, sub-lecythiform, interspersed with utriform and spheropedunculate elements, lamellae margin sterile. Pleurocystidia absent. Caulocystidia (37–)39–110(–115) × (8–)9–17(–18) µm, lageniform to long-necked lageniform, nettle hair-shaped, nearly cylindrical, ice cone-shaped. Pileipellis hymeniform consisting of sphaeropedunculate elements, (23–)27–57(–60) × 10–23(–24) µm, and yellow pigments at the base. Pileocystidia (34–)37–70(–73) × 8–15(–17), lageniform, long-necked lageniform, nettle hair-shaped, nearly cylindrical, ice cone-shaped, similar to caulocystidia. All structures have clamp connections. It exhibits a weak positive reaction with ammonia, forming rhombic crystals.

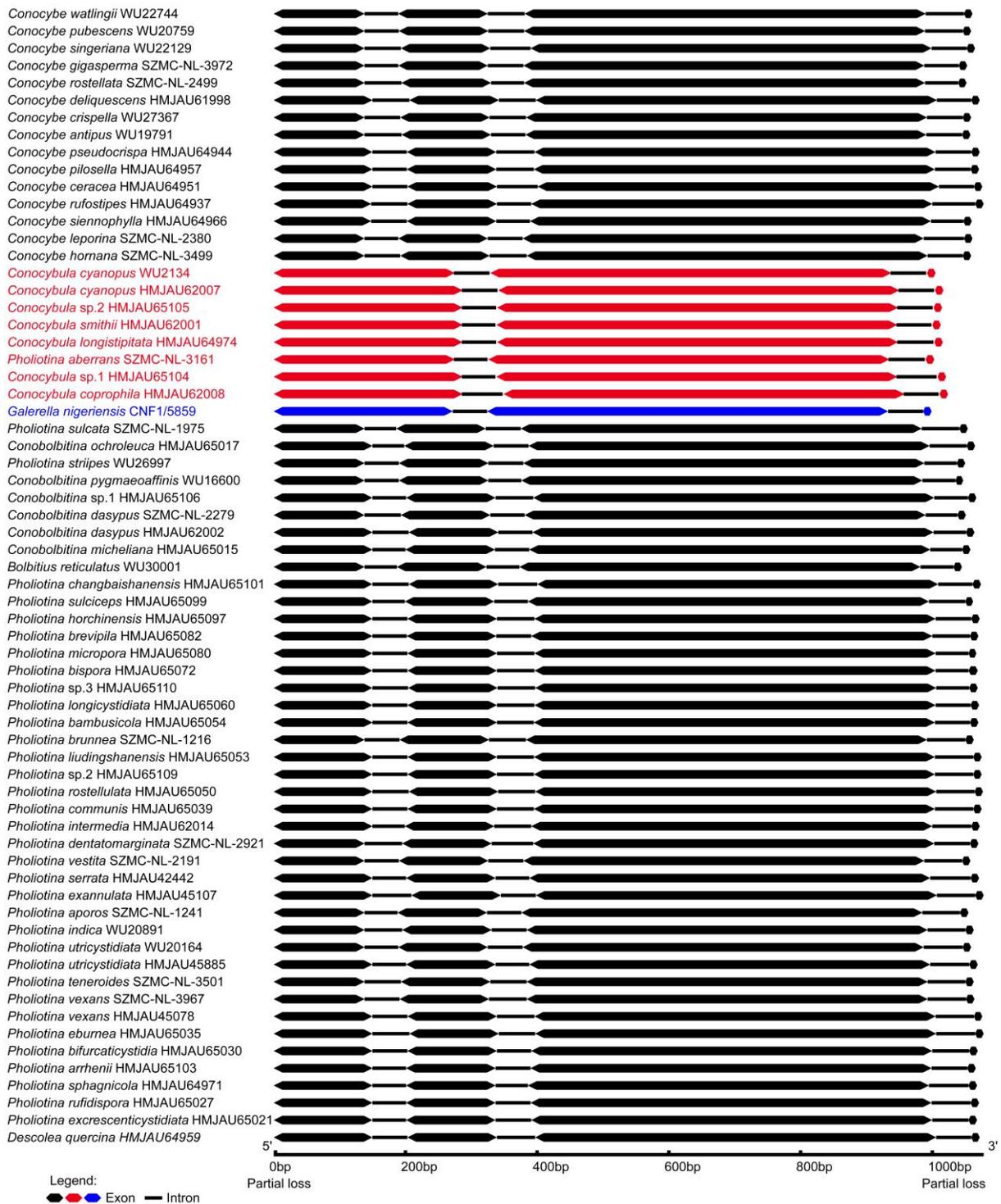


Figure 3 – Schematic diagram of the intron structure of *tef-1α* (983–2218).

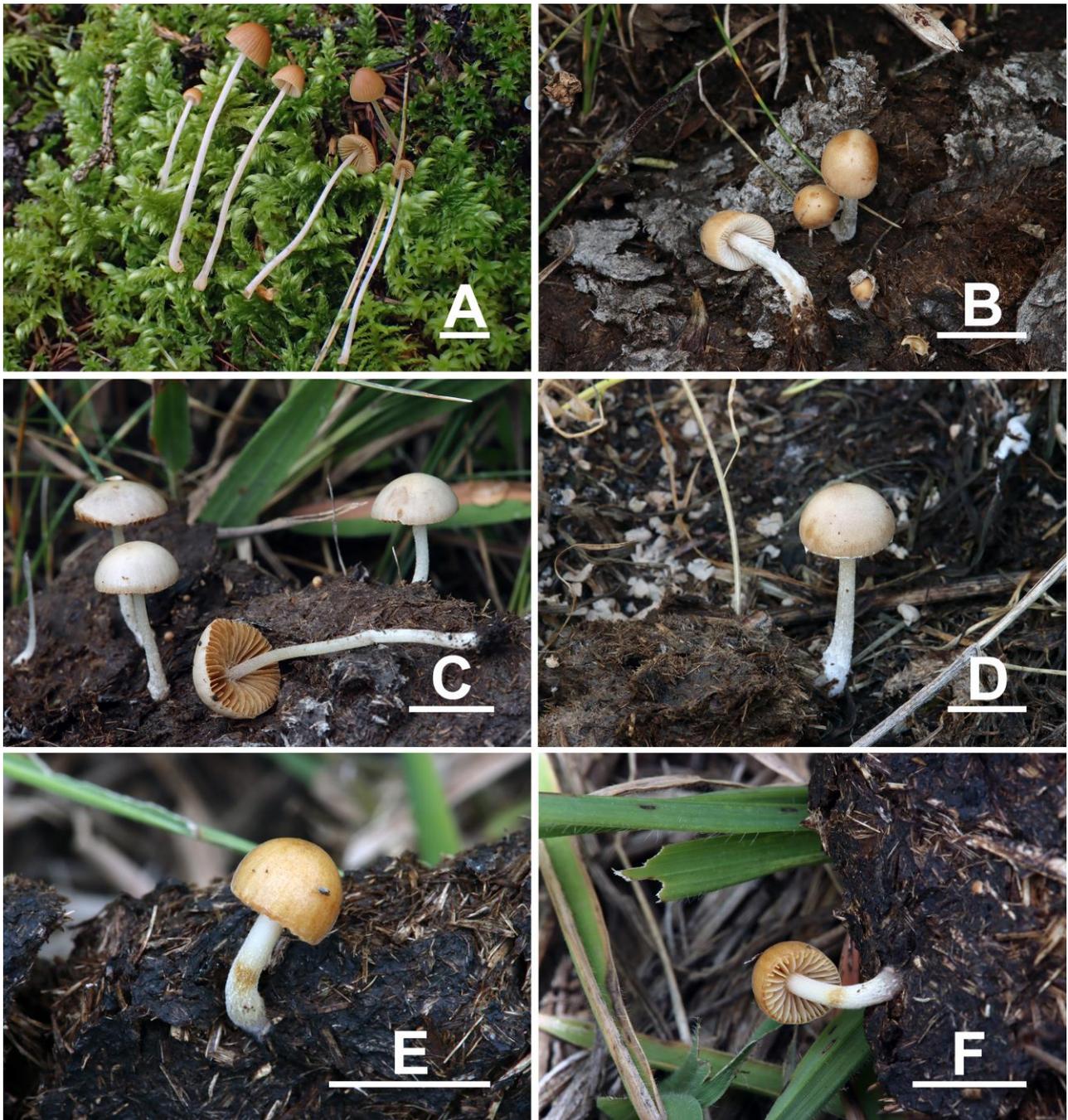


Figure 4 – Basidiomata of *Co.* sect. *Conocybula* species. A *Co. longistipitata* (HMJAU64974). B *Co. coprophila* (HMJAU64986). C *Co. coprophila* (HMJAU64987). D *Co. coprophila* (HMJAU64988). E, F *Conocybula* sp.1 (HMJAU65104). Scale bars = 1 cm. These pictures are copyright of the collectors of specimens.

Habitat – It grows scattered on the moss layer of coniferous forests.

Known distribution – China, Russia (type).

Collections examined – China, Inner Mongolia Autonomous Region, Chifeng City, Baiyinaobao National Nature Reserve, 1 August 2013, 117°11'41"E, 43° 30' 56"N, alt. 1336 m, T. Bau & L. Mu, HMJAU26286. Xinjiang Uyghur Autonomous Region, Altay Prefecture, Burqin County, Kanas Scenic Area, 15 August 2021, 87°03'05"E, 48°37'10"N, alt. 1474 m, T. Bau & X. L. Liu, L081512 (HMJAU64973), L081516 (HMJAU64974).

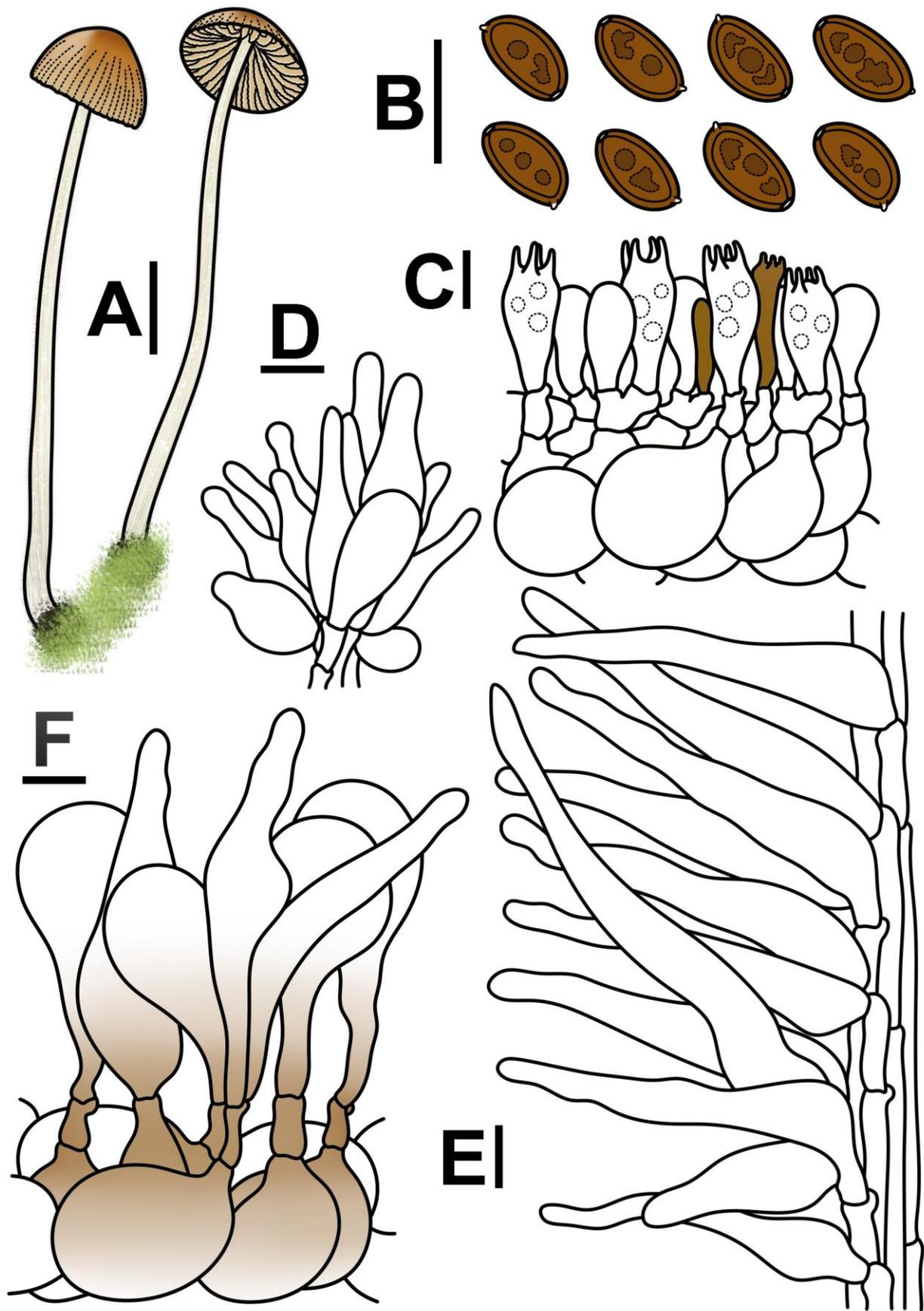


Figure 5 – *Conocybula longistipitata* (HMJAU64974). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipells. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

Notes – *Conocybula longistipitata* is a newly recorded species from China. In previous classifications, *Co. longistipitata* was grouped under *P. sect. Piliferae* (Crous et al. 2017). This classification was based on the shared characteristics of long-necked lageniform and nettle hair-shaped cheilocystidia, as well as abundant pileocystidia. However, in the present study, *Co. longistipitata* has been reclassified within *Co. sect. Conocybula* and designated as the type species. This reclassification is supported by the presence of cheilocystidia with sub-lecythiform elements, which are transitional in nature. In contrast, species within *P. sect. Piliferae* possess lageniform to long-necked lageniform, nettle hair-shaped cystidia without sub-lecythiform elements, and their apices do not swell (Hausknecht 2009). These differences allow for clear differentiation between the two groups. It is worth noting that *Co. longistipitata* is phylogenetically closer to *P. parvula* (Døssing & Watling) Bon and *P. aberrans* (Kühner) Singer. However, as no specimens of *P. parvula* and *P. aberrans* were collected for this analysis, they are currently not included.

Conocybula coprophila (Kühner) T. Bau & H. B. Song, comb. nov.

Fig. 4B–D

Mycobank number: MB851641; Facesoffungi number: FoF15318

Basionym – *Galera coprophila* Kühner, Botaniste 17(1-4): 169 (1926)

Synonymy – *Conocybe coprophila* (Kühner) Kühner, Encyclop. Mycol. 7: 125 (1935).

Galerula coprophila (Kühner) Maire, Publ. Inst. Bot. Barcelona 3(no. 4): 98 (1937). *Pholiotina coprophila* (Kühner) Singer, Acta Inst. bot. Komarov. Acad. Sci., Pl. Crypt, ser. 2 6: 434 (1950)

Collections examined – China, Jilin Province, Changchun City, Xincheng Street, 8 September 2016, 125°24'17"E, 43°48'43"N, alt. 221 m, T. Bau & J. Liu, HMJAU45087. Inner Mongolia Autonomous Region, Hulunbuir City, Ewenki Autonomous Banner, 5 September 2016, 119°47'54"E, 48°37'21"N, alt. 695 m, J. Liu, HMJAU45088, HMJAU45889. Tongliao City, Horqin Left Back Banner, 7 August 2021, 122°14'32"E, 43°12'27"N, alt. 286 m, X. Wang, WX218702 (HMJAU64975). Hulunbuir City, New Barag Left Banner, 7 August 2022, 118°17'33"E, 48°17'47"N, alt. 705 m, H. B. Song, S22080709 (HMJAU64976), S22080710 (HMJAU64977). Hulunbuir City, New Barag Left Banner, 8 August 2022, 118°14'36"E, 48°07'19"N, alt. 674 m, H. B. Song, S22080801 (HMJAU64978), S22080802 (HMJAU64979). Xinjiang Uyghur Autonomous Region, Altay Prefecture, Burqin County, Kanas Scenic Area, 15 August 2021, 87°03'03"E, 48°37'09"N, alt. 1400 m, Q. Q. Ye, HMJAU62008. Ili Kazakh Autonomous Prefecture, Tekes County, 11 August 2023, 81°50'26"E, 43°11'58"N, alt. 1204 m, H. B. Song, S23081102 (HMJAU64980), S23081106 (HMJAU64981), S23081109 (HMJAU64982). Ili Kazakh Autonomous Prefecture, Zhaosu County, 12 August 2023, 81°43'57"E, 43°20'35"N, alt. 2211 m, H. B. Song, S23081201 (HMJAU64983), S23081202 (HMJAU64984), S23081205 (HMJAU64985). Ili Kazakh Autonomous Prefecture, Zhaosu County, 13 August 2023, 81°11'1"E, 43°7'27"N, alt. 1796 m, H. B. Song, S23081307 (HMJAU64986), S23081316 (HMJAU64987), S23081322 (HMJAU64988).

Notes – *Conocybula coprophila* grows on dung, and its basidia are clavate to spheropedunculate. It bears resemblance to *Conocybula* sp.1 (Fig. 4E, F), but the latter has yellow-brown pigmentation at the base of pileipellis and has only been observed as an individual basidioma in Xinjiang. However, the stipe of *Co. coprophila* does not change color when injured, and it is macroscopically and microscopically similar to *Conocybula* sp.1. Therefore, it is temporarily classified under *Co. sect. Conocybula*. If more species of this clade are discovered in the future and stable classification features are identified, *P. ser. Coprophila* can be combine into *Co. sect. Coprophila*, which is not addressed in this article. Previous studies shown that that *Co. coprophila* lacks a veil, however, in the present study discovered the presence of a residual veil in a single basidioma collected in Xinjiang in 2023 (Fig. 4D). Therefore, it is considered that *Co. coprophila* is also a group in which the veil gradually disappears.

Conocybula section Cyanopodae (Singer) T. Bau & H. B. Song, comb. nov.

Mycobank number: MB851642

Type species – *Conocybula cyanopus* (G.F. Atk.) T. Bau & H. B. Song

Basionym – *Pholiotina* section *Cyanopodae* Singer, Beih. Sydowia 7: 79 (1973)

Synonymy – *Pholiotina* subsection *Cyanopodinae* (Singer) Arnolds, Persoonia 18(2): 229 (2003)

Based on the revision by Hausknecht (2009): Basidiocarp mycenoid. Pileus hygrophanous, smooth, in one species with faint, fibrillous, quickly vanishing veil. Stipe base with blue-green to blue colours (presence of psilocybin). Stipe slightly fibrillous, not entirely pruinose-hairy. Spores medium, thin-to slightly thick-walled, smooth, with germ-pore. Cheilocystidia vary, lageniform, nettle hair-shaped, with subcapitate apex, mixed with sub-leythiform. Caulocystidia are polymorphic and irregular, similar to cheilocystidia. Pileipellis with pileocystidia, some filled with yellow pigments. Gene fragment *tef-1a* (983-2218) region's first intron is missing (Fig. 3).

Habitat – Forest soil, meadows, grassland.

Known distribution – It is widely distributed worldwide.

Notes – *Conocybula* section *Cyanopodae* originally belonged to *Pholiotina* and included species like *Pholiotina aeruginosa* (Romagn.) M.M. Moser, which have a bluish-green tint on pileus. However, based on morphological and systematic considerations, the group of species with pileus displaying a bluish-green tint has been separated, as described in the following text.

Key to *Conocybula* section *Cyanopodae* in China

1. Pileus has distinct grooves and undulate margin..... *Conocybula* sp.2
- 1'. Pileus has distinct striae and lacks undulate margin..... 2
2. Cheilocystidia less than 50 µm, pileocystidia less than 70 µm *Co. cyanopus*
- 2' Cheilocystidia can reach 60 µm, pileocystidia can reach 150 µm *Co. smithii*

Conocybula cyanopus (G.F. Atk.) T. Bau & H. B. Song, comb. nov.

Fig. 6A–C

Mycobank number: MB851643; Facesoffungi number: FoF15320

Basionym – *Galerula cyanopus* G.F. Atk., Proc. Am. phil. Soc. 57(5): 367 (1918)

Synonymy – *Conocybe cyanopus* (G.F. Atk.) Kühner [as 'cyanopoda'], Encyclop. Mycol. 7: 128 (1935). *Pholiotina cyanopus* (G.F. Atk.) Singer, Trudy Bot. Inst. Akad. Nauk SSSR, ser. 2, Sporov. Rast. 6: 425 (1950)

Collections examined – China, Jilin Province, Changchun City, Jingyuetan National Forest Park, 10 August 2017, 125°28'01"E, 43°46'09"N, alt. 264 m, T. Bau & J. Liu, HMJAU45092. Changchun City, Jingyuetan National Forest Park, 2 September 2021, 125°28'23"E, 43°47'25"N, alt. 274 m, H. B. Song, HMJAU62007. Changchun City, Xincheng Avenue, 1 September 2022, 125°24'05"E, 43°48'38"N, alt. 215 m, H. B. Song, S22090108 (HMJAU64989). Liaoning Province, Dandong City, Zhenxing District, 1 July 2023, 124°23'26"E, 40°7'11"N, alt. 8 m, H. B. Song, S23070107 (HMJAU64990).

Notes – *Conocybula cyanopus* is characterized by the stipe changing to a bluish-green color when injured. It is recognized as the type species of *Co.* sect. *Cyanopodae*. According to Hausknecht (2009), *Co. cyanopus* typically develops a veil in its early stage. However, the specimens observed in this study did not exhibit any veil, suggesting that it may have disappeared.

Conocybula smithii (Watling) T. Bau & H. B. Song, comb. nov.

Fig. 6D–F

Mycobank number: MB854540; Facesoffungi number: FoF15319

Basionym – *Conocybe smithii* Watling, Lloydia 30(2): 152 (1967)

Synonymy – *Pholiotina smithii* (Watling) Enderle, in Enderle & Hübner, Z. Mykol. 65(1): 16 (1999)

Collections examined – China, Jilin Province, Changchun City, Jingyuetan National Forest Park, 18 September 2021, 125°28'17"E, 43°47'26"N, alt. 272 m, L. Y. Zhu, Z21091802 (HMJAU62001). Jilin City, Panshi City, Dongshan Park, 8 August 2022, 126°4'42"E, 42°56'25"N, alt. 427 m, F. Guo & X. Wang, gf196 (HMJAU64991), 22WX1840808 (HMJAU64992).

Changchun City, Jingyuetan National Forest Park, 12 August 2022, 125°28'38"E, 43°47'20"N, alt. 266 m, L. Y. Zhu, Z22081203 (HMJAU64993). Changchun City, Jingyuetan National Forest Park, 18 August 2022, 125°27'0"E, 43°45'54"N, alt. 275 m, H. B. Song, S22081816 (HMJAU64994). Changchun City, Jingyuetan National Forest Park, 24 August 2022, 125°27'47"E, 43°45'28"N, alt. 311 m, H. B. Song, S22082405 (HMJAU64995). Changchun City, Jingyuetan National Forest Park, 12 July 2023, 125°27'45"E, 43°45'50"N, alt. 315 m, H. B. Song, S23071213 (HMJAU64996), S23071214 (HMJAU64997). Jilin City, Jiaohe City, Shansongling, 28 July 2023, 127°12'0"E, 43°40'51"N, alt. 429 m, T. Bau & S. E. Wang, E2307195 (HMJAU64998). Heilongjiang Province, Yichun City, Wuying National Forest Park, 26 July 2023, 129°12'22"E, 48°14'57"N, alt. 424 m, H. B. Song, S23072612 (HMJAU64999), S23072605 (HMJAU65000). Inner Mongolia Autonomous Region, Tongliao City, Horqin Left Middle Banner, 21 August 2022, 123°17'31"E, 43°47'27"N, alt. 261 m, T. Bau & S. E. Wang, E2208246 (HMJAU65001).

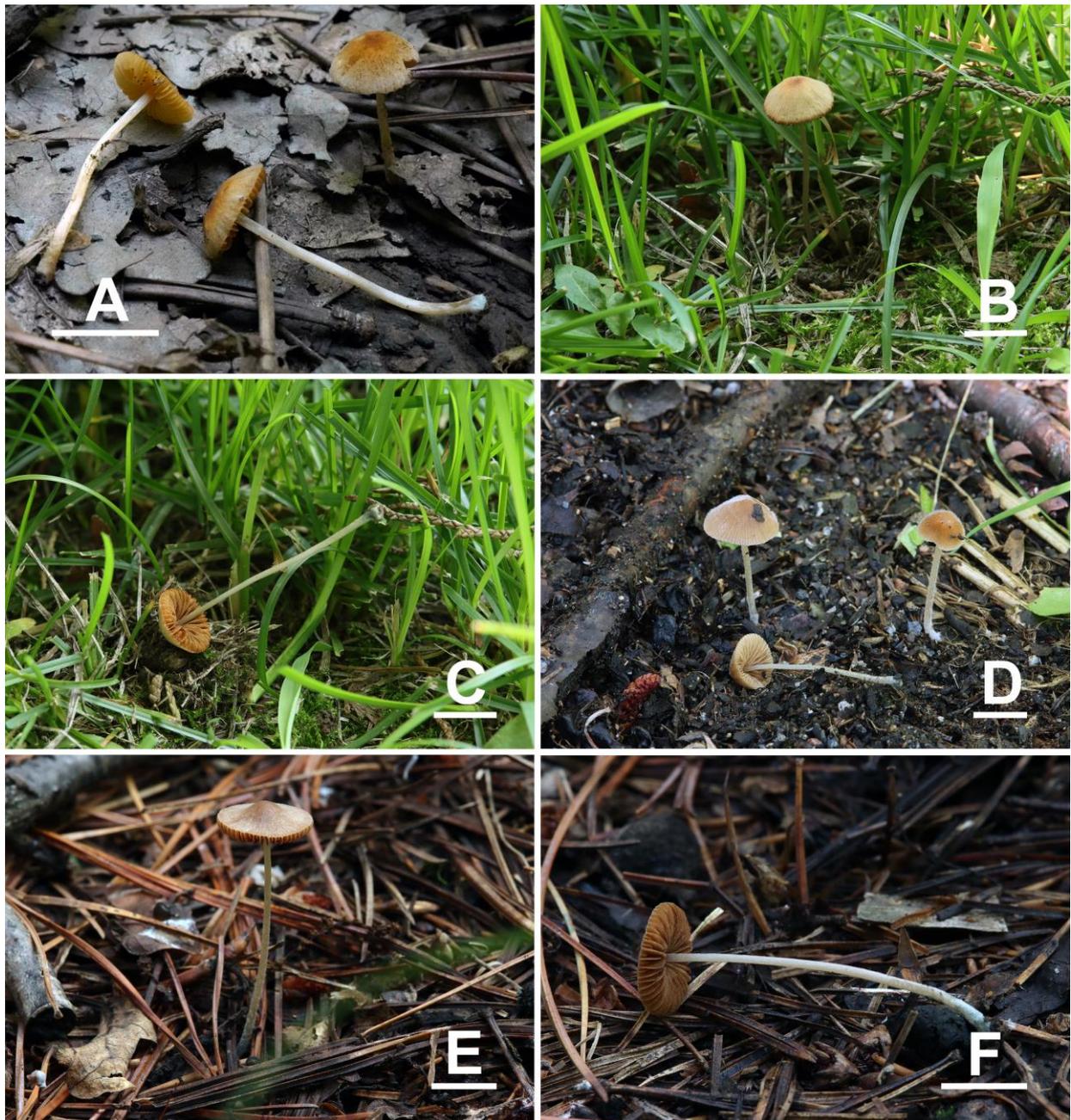


Figure 6 – Basidiomata of *Co.* sect. *Cyanopodae* species. A *Co. cyanopus* (HMJAU62007). B, C *Co. cyanopus* (HMJAU64990). D *Co. smithii* (HMJAU65000). E, F *Co. smithii* (HMJAU64997), Scale bars = 1 cm. These pictures are copyright of the collectors of specimens.

Notes – In the *Conocybula* section *Cyanopodae*, the current inclusion consists of only three species: *Pholiotina sulcatipes* (Peck) Kühner, *Conocybula smithii*, and *Conocybula cyanopus*. However, a study conducted by Horak & Hausknecht (2002) examined the type and concluded that the stipe of *P. sulcatipes* does not exhibit a blue coloration. Therefore, the only species with stipes displaying a bluish-green tint are *Co. smithii* and *Co. cyanopus*. Nevertheless, there remains an ongoing controversy regarding whether *Co. smithii* is synonymous of *Co. cyanopus*, as Hausknecht (2009) does not consider *Co. smithii* as a synonym of *Co. cyanopus*. Furthermore, Benedict et al. (1967) described the differences between *Co. smithii* and *Co. cyanopus*, which lie in the color of the lamellae, the width of basidiospores, and the width of cheilocystidia. However, Song et al. (2023), due to a small number of specimens, using pileus shape as distinguishing criteria was deemed incorrect. In our study, we identified a species that closely resembles *Co. cyanopus* but can be differentiated in the phylogenetic tree, clustering together with *Co. smithii* CCB185 (although it remains unclear how Matheny identified it). Considering these findings, besides *Co. cyanopus*, we only can consider *Co. smithii*. Although classification is not solely based on the process of elimination, we adhere to identifying this species as *Co. smithii*. Additionally, we have also determined distinguishing features based on microscopic structures, particularly the length of cheilocystidia and pileocystidia.

Conobolbitina T. Bau & H. B. Song, gen. nov.

Mycobank number: MB851476; Facesoffungi number: FoF15321

Etymology – “*Conobolbitina*” refers to an intermediate group between *Pholiotina* and *Conocybe*, and it is closely related to *Bolbitius*.

Type species – *Conobolbitina pygmaeoaffinis* (Fr.) T. Bau & H. B. Song

Basidiomata mycenoid, ranging from small to medium-sized. Pileus hemispherical or conical, obtusely conical, convex, appanate with a central projection or depression. Pileus exhibits light blue (RAL5012), oxide red (RAL3009), golden yellow (RAL1004) to signal yellow (RAL1003), ochre brown (RAL8001), chestnut brown (RAL8015), and the margin displays a pastel yellow (RAL1034) coloration. Pileus hygrophanous, smooth or rugosus, greasy or non-greasy, when moist, it shows distinct striations, and with or without a pubescent surface. Context thin, ranging from ivory (RAL1014) to sandy yellow (RAL1002), or it matches the color of the pileus, without specific odor. Lamellae adnexed to narrowly adnate, ventricose, sparsely or densely distributed, unequal in length, with a fine serrated or smooth edge. Stipe cylindrical, slightly swollen at the base or bulbous, and does not change color when damaged. The lower part of the stipe may have white fluffy mycelium. The surface of the stipe is covered with powdery frost and short pubescence, displaying longitudinal fibrous striations. During its early stages, it develops a veil but does not form a ring, which quickly disappears or is absent.

Basidiospores smooth or cristate-punctate, ellipsoid to oblong, slightly amygdaliform, with some being reniform to phaseoliform, and possess a distinct germ pore. Basidia clavate, containing vacuolar contents, 4- or 2-spored. Cheilocystidia exhibit a wide range of morphologies, including non-lecythiform, lageniform, long-necked lageniform, nettle hair-shaped, partially subcapitate at the tip, spheropedunculate, utriform, capitate, clavate, subcylindrical, with slightly bifurcated heads, resembling femoral heads, and some with excrescences, edges of lamellae are sterile. Pleurocystidia absent. Caulocystidia exhibit a diverse range of shapes, similar to cheilocystidia but slightly larger, spheropedunculate, lageniform, nettle hair-shaped, capitate, clavate, subcylindrical, with slightly bifurcated heads, resembling femoral heads, and some with excrescences. Pileipellis hymeniform and consists of sphaeropedunculate elements and nearly clavate elements, with yellow pigments at the base. Pileocystidia present or absent. If present, pileocystidia are lageniform, long-necked lageniform, nettle hair-shaped, sub-lecythiform, hair-like, and similar to caulocystidia. Clamp connections present or absent. It can exhibit a negative or positive reaction to ammonia, forming diamond-shaped crystals when positive.

Habitat – Growing on meadow, the litter layer of broad-leaved forests, or decaying wood in coniferous forests.

Known distribution – It is widely distributed worldwide.

Notes – *Conobolbitina* was originally classified under *Pholiotina*. The species of *Conobolbitina* display diverse morphological characteristics. The macroscopic and microscopic features of *Con. sect. Verrucisporae* and *Con. sect. Aeruginosa* are more similar to *Bolbitius*. On the other hand, the macroscopic and microscopic features of *Con. sect. Conobolbitina* resemble *Conocybula*, but *Conobolbitina* species do not exhibit deliquescent properties, which allows them to be distinguished from *Bolbitius* (Arnolds 2005). Furthermore, the cheilocystidia of *Con. sect. Conobolbitina* are lageniform to long-necked lageniform, nettle hair-shaped, and never sub-lythyiform, which sets them apart from *Conocybula*.

Key to sections of *Conobolbitina* in China

1. Basidiospores with cristate-punctate. *Con. sect. Verrucisporae*
- 1'. Basidiospores smooth 2
2. Pileus blue-green, with deep blue hues..... *Con. sect. Aeruginosa*
- 2' Pileus without blue-green hues *Con. sect. Conobolbitina*

Conobolbitina* section *Verrucisporae (Singer) T. Bau & H. B. Song, comb. nov.

Mycobank number: MB851644

Type species – *Conobolbitina verrucispora* (Singer) T. Bau & H. B. Song

Basionym – *Pholiotina* section *Verrucisporae* Singer, Beih. Sydowia 7: 79 (1973)

Synonymy – *Pholiotina* subsection *Verrucisporae* (Singer) Arnolds, Persoonia 18(2): 229 (2003)

Notes – *Conobolbitina* section *Verrucisporae*, originally classified under *Pholiotina*, has basidiospores with cristate-punctate, distinguishing it from other sections. Its cheilocystidia are similar to *Bolbitius*, but *Bolbitius* has pseudoparaphyses and exhibits deliquescence, making it easy to differentiate. The difference between *Con. sect. Verrucisporae* and *Con. sect. Aeruginosa* is that *Con. sect. Aeruginosa* has smooth basidiospores and a blue-green hue on the pileus. Conversely, the difference between *Con. sect. Verrucisporae* and *Con. sect. Conobolbitina* is that *Con. sect. Conobolbitina* has smooth basidiospores and cheilocystidia that are long-necked lageniform, approaching nettle hair-shaped. Within this section, only four species are currently known: *Con. verrucispora*, *Con. dasypus*, *P. australis* Singer, and *P. glutinosa* E. Horak & Hauskn. (Singer 1969, Horak & Hausknecht 2002).

Key to *Conobolbitina* section *Verrucisporae* in China

1. Pileus applanate, with an umbo, growing on decaying wood..... 2
- 1'. Pileus hemispherical, conical, growing in the leaf litter of broadleaf forests..... 3
2. Pileocystidia with yellow pigment or transparent at the apex *Conobolbitina* sp.1
- 2' Pileocystidia with dark purple pigment at the apex *Conobolbitina* sp.2
3. Pileus golden yellow *Con. micheliana*
- 3'. Pileus beige *Con. dasypus*

Conobolbitina verrucispora (Singer) T. Bau & H. B. Song, comb. nov.

Mycobank number: MB851645; Facesoffungi number: FoF15322

Basionym – *Pholiotina verrucispora* Singer, Beih. Nova Hedwigia 29: 213 (1969)

Synonymy – *Conocybe verrucispora* (Singer) Watling, in Watling & Gregory, Bibliotheca Mycol. 82: 148 (1981)

Notes – The combination of *Pholiotina* section *Verrucisporae* under *Conobolbitina* has resulted in the reassignment of the type species. However, it is unfortunate that *Con. verrucispora* has not yet been found or collected in China.

Conobolbitina dasypus (Romagn.) T. Bau & H. B. Song, comb. nov.

Figs 7A, B, 8A, B

Mycobank number: MB851646; Facesoffungi number: FoF15323

Basionym – *Naucoria dasypus* Romagn., Bull. trimest. Soc. mycol. Fr. 53: 121 (1937)

Synonymy – *Alnicola dasypus* (Romagn.) Romagn., Bull. trimest. Soc. mycol. Fr. 58: 126 (1944) [1942]. *Hebeloma dasypus* (Romagn.) Singer, Lilloa 22: 538 (1951) [1949]. *Pholiotina dasypus* (Romagn.) P. -A. Moreau, Fungal Diversity 20: 135 (2005)

Collections examined – China, Jilin Province, Yanbian Korean Autonomous Prefecture, Antu County, June 16, 2016, 128°06'43" E, 42°25'56" N, alt. 701 m, T. Bau & J. Liu, HMJAU45098. Changchun City, Jingyuetan National Forest Park, July 7, 2017, 125°28'01" E, 43°47'59" N, alt. 286 m, T. Bau & J. Liu, HMJAU45099, HMJAU45102, HMJAU45103. Changchun City, Jingyuetan National Forest Park, July 18, 2017, 128°06'54" E, 42°26'04" N, alt. 703 m, T. Bau & J. Liu, HMJAU45100, HMJAU45104, HMJAU45105. Changchun City, Jingyuetan National Forest Park, August 10, 2017, 125°27'49" E, 43°46'44" N, alt. 249 m, T. Bau & J. Liu, HMJAU45095, HMJAU45096. Changchun City, Jilin Agricultural University, May 30, 2022, 125°24'23" E, 43°48'34" N, alt. 223 m, T. Bau, HMJAU62002. Changchun City, Jilin Agricultural University, May 31, 2022, 125°24'23" E, 43°48'34" N, alt. 223 m, T. Bau & H. B. Song, HMJAU62003. Changchun City, Jilin Agricultural University, June 30, 2022, 125°24'29" E, 43°48'23" N, alt. 294 m, F. Guo, gf2206301 (HMJAU65002). Jilin City, Jiaohe City, July 26, 2022, 127°43'18" E, 43°58'5" N, alt. 495 m, F. Guo, gf22723102 (HMJAU65003), gf2272398 (HMJAU65004). Yanbian Korean Autonomous Prefecture, Antu County, July 31, 2022, 128°06'32" E, 42°25'51" N, alt. 698 m, H. B. Song, S22073101 (HMJAU65005), S22073102 (HMJAU65006). Jilin City, Jiaohe City, Shansongling, June 25, 2023, 127°42'42" E, 43°57'39" N, alt. 412 m, H. B. Song, S23062501 (HMJAU65007), S23062502 (HMJAU65008), S23062506 (HMJAU65009). Changchun City, Jilin Agricultural University, July 11, 2023, 125°24'35" E, 43°48'19" N, alt. 231 m, L. Y. Zhu, Z23071107 (HMJAU65010). Changchun City, Jingyuetan National Forest Park, July 12, 2023, 125°27'40" E, 43°46'27" N, alt. 251 m, H. B. Song, S23071219 (HMJAU65011). Changchun City, Jingyuetan National Forest Park, July 19, 2023, 125°28'0" E, 43°45'28" N, alt. 375 m, H. Cheng, C2371308 (HMJAU65012), C2371307 (HMJAU65013), C2371311 (HMJAU65014).

Notes – Arnolds (2005) stated that *Conocybe subnuda* Kühner is a synonymous name for *Conocybe utrififormis* P.D. Orton. Hausknecht (2009) indicated that both *C. utrififormis* and *C. subnuda* are synonymous names for *P. dasypus* (Romagn.) P. -A. Moreau. Moreau (2005), when revising Romagnesi's *Naucoria* specimens, found that the earliest valid description of this taxonomic unit was made by Romagnesi (1937). Therefore, it should be named *P. dasypus*. In this study, to address the issue of the polyphyletic origin of *Pholiotina*, the taxonomic unit is classified under *Conobolbitina*.

Conobolbitina micheliana T. Bau & H. B. Song, sp. nov.

Figs 7C, D, 8C, D, 9

Mycobank number: MB853969; Facesoffungi number: FoF15324

Etymology – “*micheliana*” refers to the species that grows in the humus layer of *Michelia maudiae* (Dunn) Figlar.

Type – China, Yunnan Province, Kunming City, Kunming Botanical Garden, 26 June 2023, 102°44'30" E, 25°08'25" N, alt. 1948 m, T. Bau & L. Y. Zhu, Z23062609 (HMJAU65015, holotype).

Basidioma small-sized, with a pileus diameter of 0.5–2 cm. Pileus hemispherical, convex to plano-convex, initially oxidized red (RAL3009) to pearl orange (RAL2013), later turning golden yellow (RAL1004) to signal yellow (RAL1003), with a margin ranging from pastel yellow (RAL1034) to orange (RAL1017). Pileus hygrophanous, smooth and slightly greasy when moist, with distinct striations on the margin that extend up to half of the center. When dry, it becomes rugosus and non-greasy, with shallow striations only at the edges. Context thin, ranging in color from ivory (RAL1014) to sandy yellow (RAL1002), with an indistinct odor. Lamellae adnexed to narrowly adnate, ventricose, moderately dense, of uneven length, and range in color from golden yellow (RAL1004) to signal yellow (RAL1003), with serrulate edges. Stipe 1.5–5 cm long and 1.0–

3.0 mm thick, cylindrical, ranging in color from ivory (RAL1014) to honey yellow (RAL1005) to pastel orange (RAL2003), surface is covered with a powdery pubescence, longitudinally fibrous striations, and a slightly swollen base with white cottony mycelium.

Basidiospores (60/3/2) (8–)8.4–10.2(–10.7) × (4.7–)4.8–5.6(–6) μm, Q = (1.57–)1.64–1.9(–1.98), Qm = 1.77(± 0.08), oblong, occasionally phaseoliform to reniform, they appear smooth under an optical microscope but show cristate-punctate (slightly reticulate) features under a scanning electron microscope, with thick walls and contain oil droplets, germ pore diameter 0.5–1.5 μm, partially indistinct, and brown beige (RAL1011) to copper brown (RAL8004) in KOH. Basidia (17–)18–26(–27) × 7–11 μm, broadly clavate to clavate, 4(2)-spored, sterigmata 2–5 μm long, with vacuolar contents. Cheilocystidia (20–)21–37(–40) × 6–12 μm, exhibiting various shapes such as spheropedunculate, lageniform, utriform, capitate, clavate, and subcylindrical, with slightly bifurcated heads known as caput femoris, some of which have excrescences, lamellae edges are sterile. Pleurocystidia absent. Caulocystidia (23–)25–55(–60) × 6–14 μm, exhibiting various shapes similar to Cheilocystidia but slightly larger, spheropedunculate, lageniform, capitate, clavate, and subcylindrical, with slightly bifurcated heads known as caput femoris, some of which have excrescences. Pileipellis hymeniform and consists of sphaeropedunculate elements (21–)23–43(–45) × (14–)16–25(–26) μm, with brown red (RAL3011) pigments at the base in KOH. Pileocystidia rare. Gelatinous layer thin. All structures have clamp connections. Weak positive reaction with ammonia, forming diamond-shaped crystals.

Habitat – During the summer, it grows singly or in clusters on the humus layer of *Michelia maudiae* (Dunn) Figlar.

Known distribution – China, Yunnan Province.

Additional specimens measured – China, Yunnan Province, Kunming City, Kunming Botanical Garden, 26 June 2023, 102°44'30" E, 25°08'25" N, alt. 1948 m, T. Bau & L. Y. Zhu, T3C2 (HMJAU65016).

Notes – Basidiospores of *Conobolbitina micheliana* possess cristate-punctate ornamentation (slightly reticulate), indicating their classification into the *Conobolbitina* section *Verrucisporae*. Although *Con. micheliana* shares the same cristate-punctate ornamentation with *Con. dasypus* basidiospores, they can be easily distinguished due to the beige pileus of *Con. dasypus* and its growth on the humus layer of broad-leaved forests. A distinguishing factor between *Con. micheliana* and *Conobolbitina* sp.1 (Figs 7E, F, 8E, F) and *Conobolbitina* sp.2 (Figs 7G, H, 8G, H) is that the basidiospores of *Conobolbitina* sp.1 and *Conobolbitina* sp.2 have cristate-punctate ornamentation (pointed), making them easily differentiable. Another difference is observed between *Con. micheliana* and *Con. verrucispora*, where *Con. verrucispora* exhibits larger pileocystidia. Furthermore, *P. glutinosa* can be distinguished from *Con. micheliana* due to its appanate, slightly depressed pileus. Lastly, *Con. micheliana* differs from *P. australis* in terms of the common occurrence of pileocystidia in *P. australis* (Singer 1969, Horak & Hausknecht 2002).

Conobolbitina* section *Aeruginosa (Hauskn. & Krisai) T. Bau & H. B. Song, comb. & stat. nov.

Mycobank number: MB851647

Type species – *Conobolbitina aeruginosa* (Romagn.) T. Bau & H. B. Song

Basionym – *Pholiotina* series *Aeruginosa* Hauskn. & Krisai, Öst. Z. Pilzk. 16: 135 (2007)

Notes – *Conobolbitina* section *Aeruginosa*, originally classified as *Pholiotina* section *Cyanopodae* series *Aeruginosa*, is distinguishable from *Conocybula* based on its bluish-green colored pileus, both in terms of morphology and phylogenetic relationships. Specifically, *Co. sect. Cyanopodae* refers to the stipe turning blue after injury, making it easily distinguishable. Although *Con. sect. Aeruginosa* shares similar marginal cheilocystidia with *Con. sect. Conobolbitina*, its characteristic bluish-green coloration and distinct clade in phylogeny support the establishment of a section. Unfortunately, no specimens of this section have been collected in China. However, *Con. aeruginosa* (WU27104) has been recorded by Hausknecht (2007) and includes genetic sequences along with habitat photographs (Tóth et al. 2013).



Figure 7 – Basidiomata of *Con.* sect. *Verrucisporae* species. A *Con. dasypus* (HMJAU65008). B *Con. dasypus* (HMJAU65009). C, D *Con. micheliana* (HMJAU65015). E, F *Conobolbitina* sp.1 (HMJAU65106). G, H *Conobolbitina* sp.2 (HMJAU65107). Scale bars = 1 cm. These pictures are copyright of the collectors of specimens.

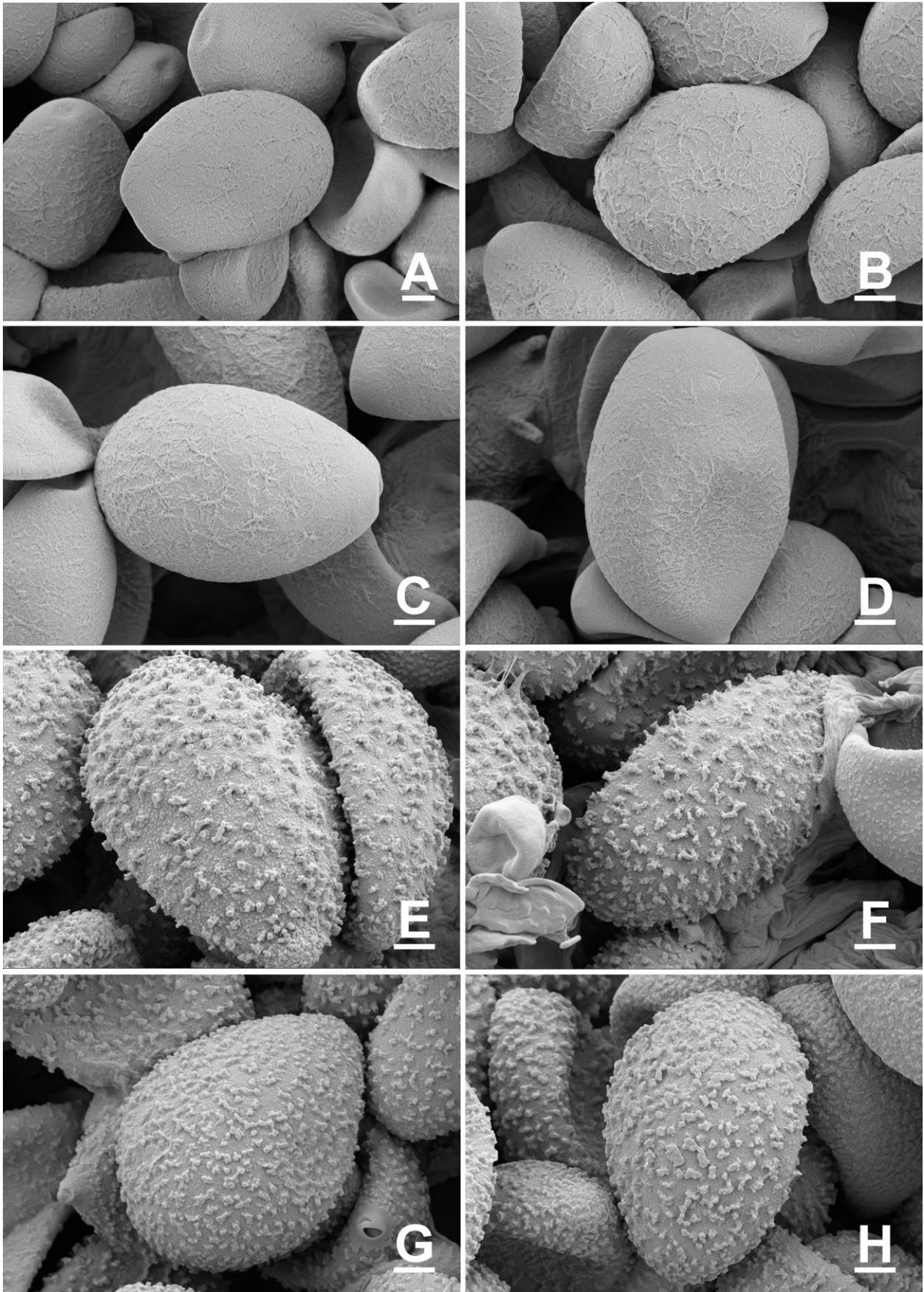


Figure 8 – Basidiospores under electron microscopy of *Con.* sect. *Verrucisporae* species. A, B *Con. dasypus* (HMJAU62002). C, D *Con. micheliana* (HMJAU65015). E, F *Conobolbitina* sp.1 (HMJAU65106). G, H *Conobolbitina* sp.2 (HMJAU65107). Scale bars = 1 μ m. These pictures are copyright of Song HB.

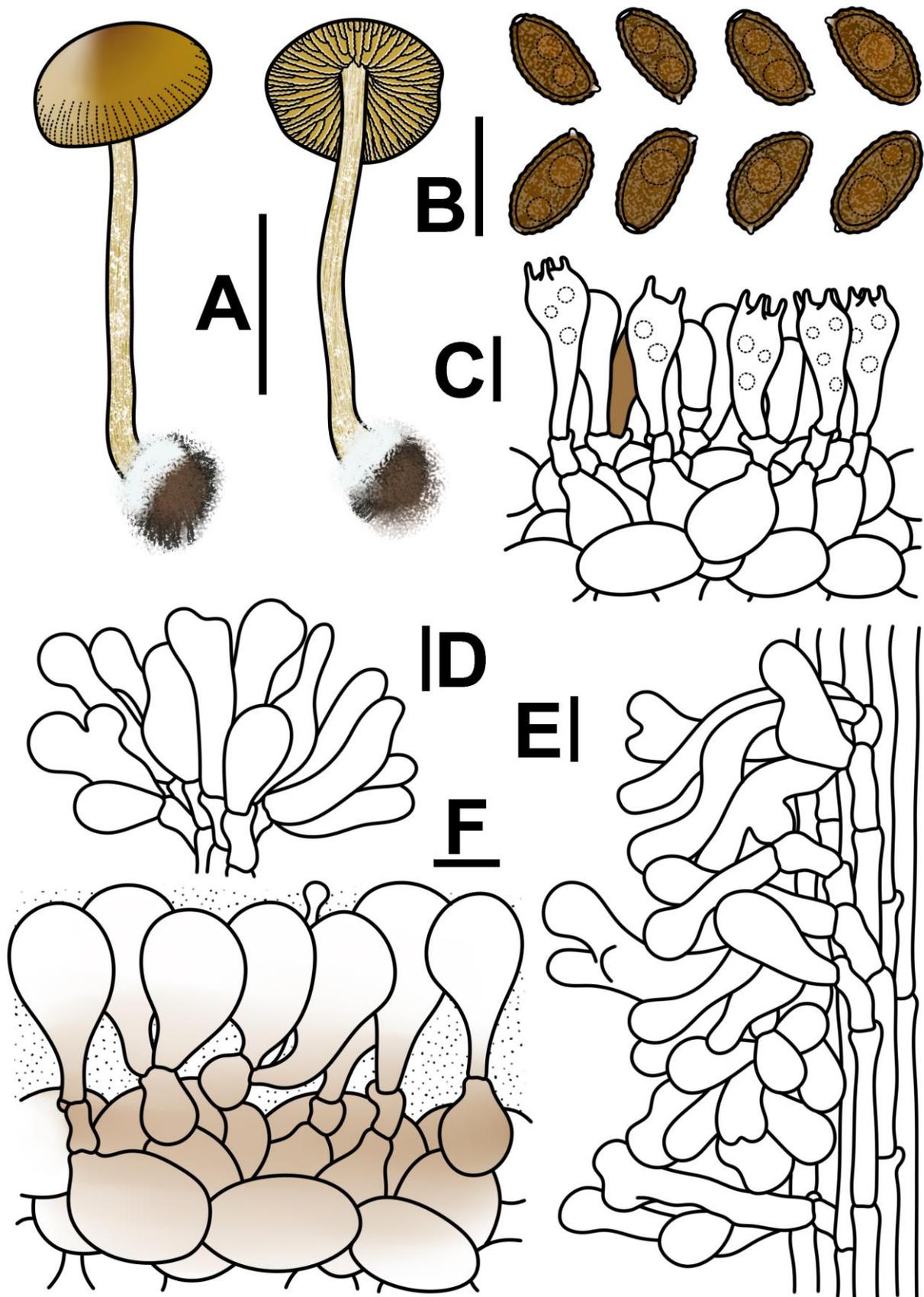


Figure 9 – *Conobolbitina micheliana* (HMJAU65015). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipells. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

Conobolbitina aeruginosa (Romagn.) T. Bau & H. B. Song, comb. nov.

Mycobank number: MB851649; Facesoffungi number: FoF15327

Basionym – *Conocybe aeruginosa* Romagn., Bull. trimest. Soc. mycol. Fr. 84: 368 (1969) [1968]

Synonymy – *Pholiotina aeruginosa* (Romagn.) M.M. Moser, in Gams, Kl. Krypt. – Fl., Edn 4 (Stuttgart) 2b/2: 283 (1978)

Notes – *Conobolbitina aeruginosa* (WU27104) belongs to the genus *Conobolbitina* and forms an independent clade within the genus. However, no specimens or sequences of other species within *Con. sect. Aeruginosa* have been obtained, limiting our knowledge of the other species within this section.

Conobolbitina* section *Conobolbitina

Etymology – “*Conobolbitina*” refers to an intermediate group between *Pholiotina* and *Conocybe*, and it is closely related to *Bolbitius*.

Synonymy – *Pholiotina* section *Piliferae* Hauskn. & Krisai, Öst. Z. Pilzk. 16: 136 (2007)

Based on Hausknecht (2007) with revisions: Basidiocarp mycenoid, veil absent, no blue or blue-green colours, very large to very small. Pileus smooth, mostly hygrophanous, often pruinose, striate or not, in one species distinctly crenulate at margin. Spores small to large, thin- to thick-walled, mostly with distinct germ-pore, hyaline yellow to rubiginous. Cheilocystidia lageniform to long-necked lageniform, approaching nettle hair-shaped, subcylindrical or utriform without well-delimited capitulum, without sub-lecythiform elements. Caulocystidia remarkable and large, mostly covering the entire stipe. Pileocystidia normally present and well-developed, only in a few species absent.

Habitat – Forests, meadows, grassy roadsides, dung, compost.

Known distribution – It is widely distributed worldwide.

Notes – Species that were previously included in *Conobolbitina* section *Conobolbitina* have been separated based on several characteristics. These characteristics include the presence of sub-lecythiform elements in the cheilocystidia and the capitate enlargement at the apex, as well as the absence of the first intron in the *tef-1a* (983–2218) region and differences in their systematic position. These species now belong to *Co. sect. Conocybula*. The type species of *Conobolbitina* is *Con. pygmaeoaffinis* (Hausknecht 2009). Specimens, such as *Con. pygmaeoaffinis* (WU16600), have been examined and photographed (Hausknecht 2009). Tóth et al. (2013) subsequently obtained sequences of *Con. pygmaeoaffinis* (WU16600) and used them to construct a phylogenetic tree, which revealed that this section is part of *Conobolbitina* and is closely related to *Con. sect. Aeruginosa*.

Conobolbitina pygmaeoaffinis (Fr.) T. Bau & H. B. Song, comb. nov.

Mycobank number: MB851651; Facesoffungi number: FoF15328

Basionym – *Agaricus pygmaeoaffinis* Fr. [as ‘pygmaeo-affinis’], Monogr. Hymenomyc. Suec. (Upsaliae) 1: 389 (1857).

Synonymy – *Conocybe pygmaeoaffinis* (Fr.) Kühner, Encyclop. Mycol. 7: 133 (1935). *Pholiotina pygmaeoaffinis* (Fr.) Singer, Acta Inst. bot. Komarov. Acad. Sci., Pl. Crypt, ser. 2 6: 435 (1950)

Notes – *Conobolbitina pygmaeoaffinis* (WU16600) belongs to the *Conobolbitina* in terms of its systematic position. However, no specimens or sequences of other known species within *Con. sect. Conobolbitina* have been obtained. The classification of these species solely relies on morphology, specifically the characteristics of cheilocystidia, whether they are lageniform, long-necked lageniform, or nettle hair-shaped. Nevertheless, this approach lacks rigor as it is highly prone to confusion when distinguishing between species within *Con. sect. Conobolbitina* and *Co. sect. Conocybula*. Therefore, an accurate delineation requires a combination of morphology and phylogenetic analysis, and based on the presence or absence of the first intron in the *tef-1a* (983–

2218) region. As a result, the other known species within *Con.* sect. *Conobolbitina* have not been addressed in this study.

Conobolbitina ochroleuca T. Bau & H. B. Song, sp. nov.

Figs 10A–F, 11

Mycobank number: MB853970; Facesoffungi number: FoF15329

Etymology – “*ochroleuca*” refers to the color of the basidioma.

Type – China, Jilin Province, Changchun City, Jingyuetan National Forest Park, August 24, 2022, 125°27'54"E, 43°45'32"N, alt. 313 m, H. B. Song, S22082410 (HMJAU65017, holotype).

Basidioma small. Pileus diameter 0.5–1 cm, initially convex mirror, approaching convex to plano-convex with a slight umbo, center pastel yellow (RAL1034), maize yellow (RAL1006), ochre brown (RAL8001), edges light ivory (RAL1015), ivory (RAL1014). Pileus hygrophanous, surface smooth, covered in powdery, short pubescence, edges with striations reaching half the pileus center. Context thin, same color as pileus, no distinct odor. Lamellae adnexed, ventricose, loosely, uneven lengths, ivory (RAL1014), pastel yellow (RAL1034) to ochre brown (RAL8001), with serrulate edges. Stipe long 1.5–2.5 cm, thick 0.5–1.0 mm, cylindrical, slightly bulbous at the base, reaching up to 2 mm, stipe ivory (RAL1014), beige (RAL1001), pastel yellow (RAL1034), covered in powdery frost and short pubescence, longitudinally striated with fibrous texture.

Basidiospores (60/3/3) (6.6–)6.7–8.5(–8.8) × (3.8–)3.9–4.5(–4.8) μm, Q = (1.51–)1.57–1.9(–1.97), Qm = 1.76(± 0.10), slightly ellipsoid to oblong, amygdaliform, occasionally phaseoliform to reniform, thick walls, containing oil droplets, eccentric germ pore with a diameter less than 1 μm. Basidiospores ochre brown (RAL8001) to copper brown (RAL8004) in KOH solution. Basidia 16–22(–24) × 6–9(–10) μm, clavate, 4(2)–spored, sterigmata 3–5 μm in length, with vacuolar contents. Cheilocystidia (24–)25–45(–46) × (5–)6–10 μm, lageniform to long-necked lageniform, nearly nettle hair-shaped in shape, edge of the lamellae is sterile. Pleurocystidia absent. Caulocystidia (21–)23–61(–65) × (7–)9–15 μm, lageniform to long-necked lageniform, occasionally exhibiting spheropedunculate and clavate elements. Pileipellis hymeniform, composed of arranged sphaeropedunculate elements (14–)15–30 × (8–)10–18(–19) μm, with the base exhibiting an ivory (RAL1014) pigment in KOH solution, slightly lighter in color. Pileocystidia (25–)26–60(–65) × (7–)8–14(–15), lageniform, long-necked lageniform, nearly nettle hair-shaped, similar to caulocystidia. All structures have clamp connections. Negative reaction to ammonia.

Habitat – It grows singly or scattered in mixed forests during the summer and autumn seasons.

Known distribution – Northeast China.

Additional specimens measured – China, Changchun City, Jilin Agricultural University, September 5, 2022, 125°24'18"E, 43°48'34"N, alt. 223 m, T. Bau & L. Y. Zhu, Z22090501 (HMJAU65018). Changchun City, Jilin Agricultural University, September 7, 2022, 125°24'03"E, 43°48'43"N, alt. 217 m, T. Bau & L. Y. Zhu, Z22090708 (HMJAU65019).

Notes – The cheilocystidia of *Conobolbitina ochroleuca* are lageniform and long-necked lageniform, nearly nettle hair-shaped. It belongs to *Con.* sect. *Conobolbitina*. *Con. ochroleuca* and *P. sulcata* Arnolds & Hauskn. are sister groups, but *P. sulcata* is distinguished by its distinct crenulate-striate pileus and sparse subcylindrical pileocystidia (Arnolds & Hausknecht 2003). To differentiate *Con. ochroleuca* from *Con. pygmaeoaffinis*, one should observe the campanulate and slightly involute pileus of *Con. pygmaeoaffinis*. The distinction between *Con. ochroleuca* and *P. alba* (Enderle) Hauskn. & Enderle lies in the milk-white pileus of *P. alba* without striations (Hausknecht 2009). Combination novum was not performed on *P. alba* and *P. sulcata* in this study due to the absence of their collection in China.

Pholiotina Fayod, Annl. Sci. Nat., Bot., sér. 7 9: 359 (1889)

Type species – *Pholiotina blattaria* (Fr.) Fayod = *Pholiotina vexans* (P.D. Orton) Bon

Based on the revision by Hausknecht (2007): Basidiocarp mycenoid, pileus usually hygrophanous, dry or slightly greasy, glabrous or pruinose, rarely sulcate; lamellae narrowly adnate to adnexed, pale brown, orangebrown to rubiginous when mature; stipe central, slender, often subbulbous, apex

or entirely pruinose, often fibrillose striate downwards; partial veil present and then leaving a membranaceous annulus at stipe or floccs adhering to margin of pileus; spore printpale brown, orange-brown to rubiginous. Spores smooth, thin- or rather thick-walled, yellow, yellow-brown to orange-brown, very rarely yellowish hyaline, usually with germ-pore but pore absent in some species; basidia clavate, 4- or 2-spored; cheilocystidia present, lageniform, long-necked lageniform, nettle hair-shaped, fusiform, subcylindrical, utriform, lecythiform, sub-lecythiform with globose capitulum, some species with excrescences, in one species with resinaceous content; pleurocystidia absent. Hymenophoral trama consisting of a distinct central strand of cylindrical hyphae surrounded by inflated elements; pileipellis an epitheloid hymenoderm consisting of pyriform to spheropedunculate or clavate elements, some species mixed with pileocystidia; stipitipellis a thin cutis, often entirely covered with caulocystidia or at apex only; clamp-connections present

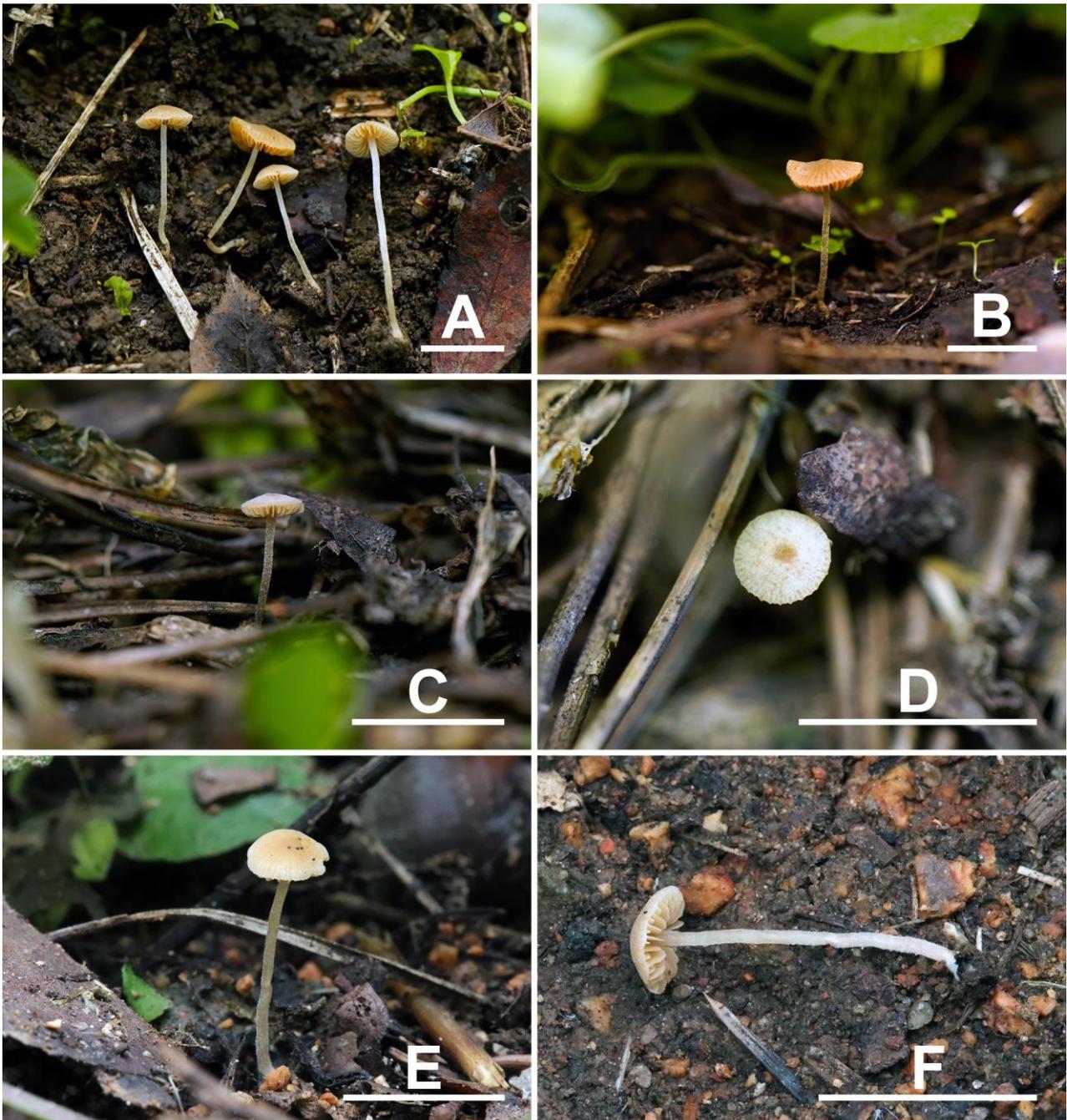


Figure 10 – Basidiomata of *Con.* sect. *Conobolbitina* species. A, B *Con. ochroleuca* (HMJAU65018). C, D *Con. ochroleuca* (HMJAU65017). E, F *Con. ochroleuca* (HMJAU65019). Scale bars = 1 cm. These pictures are copyright of the collectors of specimens.

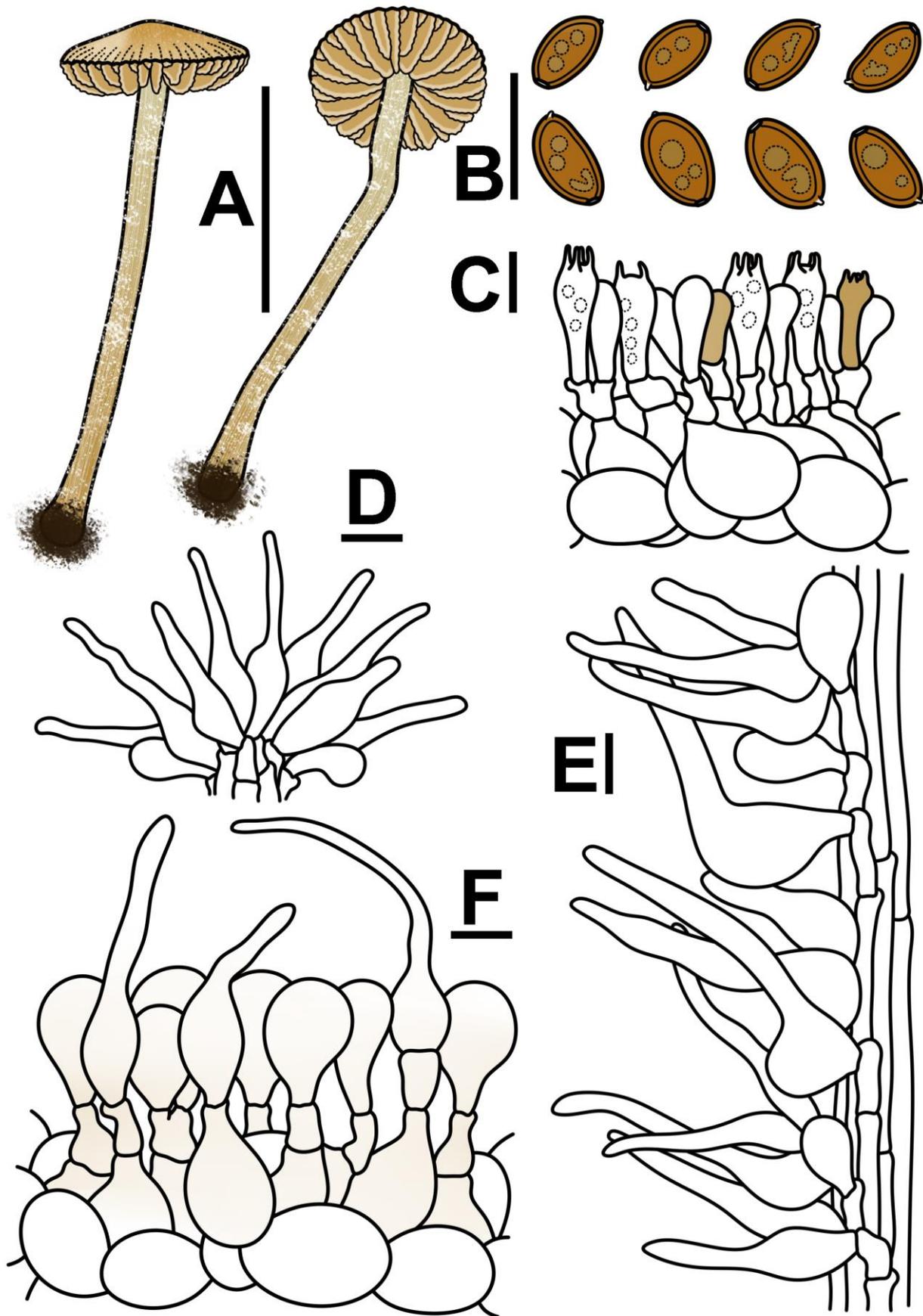


Figure 11 – *Conobolbitina ochroleuca* (HMJAU65017). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipellis. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

in most species, sometimes only in primordial stages. Development in most species paravelangiocarp.

Habitat – Saprotrophic on soil, litter, humus, dung, and small pieces of wood, solitary or gregarious, usually on subneutral to basic substrates rich in nutrients.

Known distribution – Widespread, with worldwide distribution.

Notes – Fayod (1889) initially proposed a classification that included only species with a ring. Later, Arnolds (2005) added European species characteristics to this classification. However, the designation of *Agaricus blattarius* Fr.:Fr. as the type species for *Pholiotina* was uncertain, as it had been used for almost all ringed species of *Pholiotina*. Consequently, *P. blattaria* (Fr.) Fayod was considered a nomen dubium. Hausknecht & Krisai-Greilhuber (2007) identified the lectotype designated by Fayod in France as *P. vexans* (P.D. Orton) Bon. As a result, *P. vexans* was used as the type species, and *Pholiotina* was revised based on Hausknecht (2007). This study further revises *Pholiotina* to address the polyphyletic nature of the genus. The two distinct lineages, *Pholiotina* Clade 1 (excluding *Galerella*) and *Pholiotina* Clade 2, are separated, and two new genera, *Conocybula* and *Conobolbitina*, are established. Both *Conocybula* and *Conobolbitina* include species with easily disappearing veils, but neither of them forms a ring on the stipe, making them easily distinguishable.

Key to sections of *Pholiotina* in China

- 1. Cheilocystidia lecythiform..... *P. sect. Intermediae*
- 1'. Cheilocystidia non-lecythiform 2
- 2. Veil forms a ring on the stipe *P. sect. Pholiotina*
- 2' Veil residue present on the edge of the pileus *P. sect. Vestitae*

Pholiotina section *Pholiotina*

Notes – *Pholiotina* section *Pholiotina* consists of species within the *Pholiotina* that possess a ring, as referenced by Arnolds (2005) and Hausknecht (2007).

Key to *Pholiotina* section *Pholiotina* in China

- 1. Pileus pale ivory to ivory, without distinct striae *P. eburnea*
- 1'. Pileus pale yellow to reddish-brown, with striated margin 2
- 2. Cheilocystidia mixed with utriform elements..... *P. utricystidiata*
- 2' Cheilocystidia without utriform elements..... 3
- 3. Cheilocystidia with excrescences 4
- 3'. Cheilocystidia without excrescences 5
- 4. Caulocystidia with excrescences *P. bifurcaticystidia*
- 4'. Caulocystidia without excrescences. *P. excrescenticystidiata*
- 5. Basidiospores less than 10 μm in length..... *P. arrhenii*
- 5'. Basidiospores can reach a length of 12 μm 6
- 6. Ring large and thick, cheilocystidia have thin walls *P. vexans*
- 6'. Ring small and thin, some cheilocystidia have thick walls at the top *P. rufidispora*

Pholiotina excrescenticystidiata T. Bau & H. B. Song, sp. nov.

Figs 12E–H, 13

Mycobank number: MB854541; Facesoffungi number: FoF15330

Etymology – “*excrescenticystidiata*” refers to cheilocystidia with excrescences.

Type – China, Jilin Province, Changchun City, Jilin Agricultural University, 9 September 2022, 125°24'29"E, 43°48'26"N, alt. 229 m, H. B. Song, S22090904 (HMJAU65021, holotype).

Basidioma very small, Pileus diameter 0.5–1.5 cm, initially hemispherical to paraboloid, later campanulate, convex, young pileus yellow orange (RAL2000) to red orange (RAL2001), mature pileus center bright red orange (RAL2008), pearl copper (RAL8029), ochre yellow (RAL1024) to

ochre brown (RAL8001). Pileus hygrophanous, surface smooth, striate. Context thin, ochre yellow (RAL1024) to sandy yellow (RAL1002), odor none. Lamellae adnexed to narrowly adnate, ventricose, moderately crowded, unequal length, saffron yellow (RAL1017), pastel yellow (RAL1034) to ochre brown (RAL8001), edge white serrulate. Stipe length 1.0–2.5 cm, thick 1–2.0 mm, cylindrical, slightly swollen at the base. Upper part of the stipe sandy yellow (RAL1002) to pastel yellow (RAL1034), lower part red brown (RAL8012) to chestnut brown (RAL8015). Stipe slightly covered with a powdery pubescence, exhibiting white longitudinal fibrous striations. Ring positioned in the middle, membranous, small and thin, sandy yellow (RAL1002) to pastel yellow (RAL1034), with undulate sulcate on the upper surface and smooth on the lower surface.

Basidiospores (60/3/3) (7.5–)7.7–9(–9.3) × (4.3–)4.5–5.2(–5.3) μm, Q = (1.58–)1.61–1.87(–1.97), Qm = 1.74(± 0.08), oblong, amygdaliform, suprahilar depression, thick-walled, containing oil droplets, germ pore diameter 0.5–1.5 μm, basidiospores red orange (RAL2001) to copper brown (RAL8004) in KOH. Basidia (16–)17–26(–27) × (7–)8–10(–11) μm, clavate, 4(2)-spored, sterigmata long 1–7 μm, with vacuolar contents. Cheilocystidia (20–)23–42(–45) × (4–)6–12(–13) μm, lageniform to long-necked lageniform, narrowly utriform, subcylindrical, neck often curved, some with excrescences, lamellae edge sterile. Pleurocystidia absent. Stipitipellis (above ring) of caulocystidia 16–52 × 6–20 μm, spheropedunculate, nearly clavate, lageniform, long-necked lageniform, narrowly utriform, fusiform, irregular lageniform, and irregular lecythiform. Pileipellis hymeniform and consists of spheropedunculate elements 26–49(–53) × 14–25(–28) μm, with brown red (RAL3011) pigments at the base in KOH. Pileocystidia absent. Gelatinous layer indistinct or absent. All structures have clamp connections. Weak positive reaction with ammonia.

Habitat – Solitary or scattered in broad-leaved forests or damp meadow during autumn.

Known distribution – Northeast China.

Additional specimens measured – China, Jilin Province, Changchun City, Jilin Agricultural University, 7 September 2022, 125°24'00"E, 43°48'39"N, alt. 229 m, T. Bau & L. Y. Zhu, Z22090709 (HMJAU65020). Changchun City, Jilin Agricultural University, 9 September 2022, 125°24'29"E, 43°48'26"N, alt. 229 m, H. B. Song, S22090905 (HMJAU65022), S22090906 (HMJAU65023), S22090907 (HMJAU65024), S22090917 (HMJAU65025), S22090918 (HMJAU65026).

Notes – Within the *Pholiotina* section *Pholiotina*, several distinctions can be made among different species. Firstly, *P. aporos* (Kits van Wav.) Cléménçon can be differentiated from *P. excrescenticystidiata* by the absence of a germ pore in its basidiospores. Secondly, *P. arrhenii* (Fr.) Singer is characterized by a white, easily detachable ring and thick-walled cheilocystidia at their apex, distinguishing it from *P. excrescenticystidiata*. Thirdly, the variable cheilocystidia of *P. hadrocystis* (Kits van Wav.) Courtec., which can be utriform, spheropedunculate, or subcylindrical, sets it apart from *P. excrescenticystidiata*. Another distinction is observed between *P. excrescenticystidiata* and *P. rugosa* (Peck) Singer, with *P. rugosa* having larger basidiospores, reaching a length of up to 12 μm. *P. excrescenticystidiata* can also be differentiated from *P. vexans* by the larger basidiospores of *P. vexans*, as well as its larger and thicker ring. Additionally, *P. excrescenticystidiata* can be distinguished from *P. utricystidiata* Enderle & H.-J. Hübner and *P. teneroides* (J.E. Lange) Singer by the predominance of spheropedunculate and utriform cheilocystidia in *P. utricystidiata* and *P. teneroides* (Hausknecht 2009). Furthermore, while both *P. excrescenticystidiata* and *P. bifurcaticystidia* T. Bau & H. B. Song have cheilocystidia with excrescences, the presence of excrescences on the caulocystidia distinguishes *P. bifurcaticystidia*. Lastly, in terms of phylogenetic relationship, *P. excrescenticystidiata* and *P. mediterranea* Siquier & Salom are sister taxa, but the cheilocystidia of *P. mediterranea* lack excrescences.

Pholiotina rufidispora T. Bau & H. B. Song, sp. nov.

Figs 14A–C, 15

Mycobank number: MB854543; Facesoffungi number: FoF15331

Etymology – “*rufidispora*” refers to basidiospores that are slightly reddish or have a faint red color.

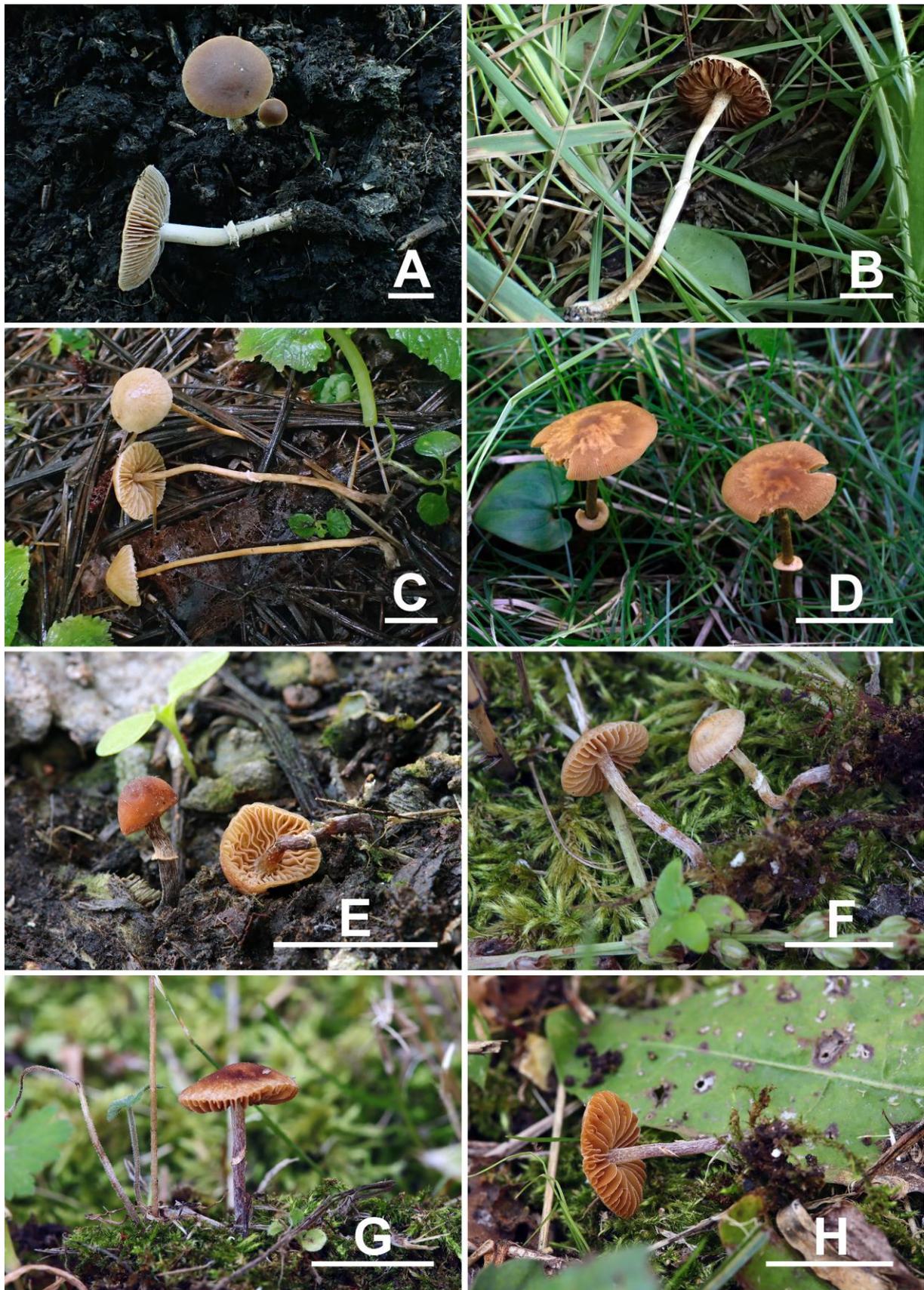


Figure 12 – Basidiomata of *P.* sect. *Pholiotina* species. A *P. utricystidiata* (HMJAU65112). B *P. utricystidiata* (HMJAU65111). C *P. arrhenii* (HMJAU65103). D *P. vexans* (HMJAU42439). E *P. excrescenticystidiata* (HMJAU65026). F *P. excrescenticystidiata* (HMJAU65023). G, H *P. excrescenticystidiata* (HMJAU65021). Scale bars = 1 cm. These pictures are copyright of the collectors of specimens.

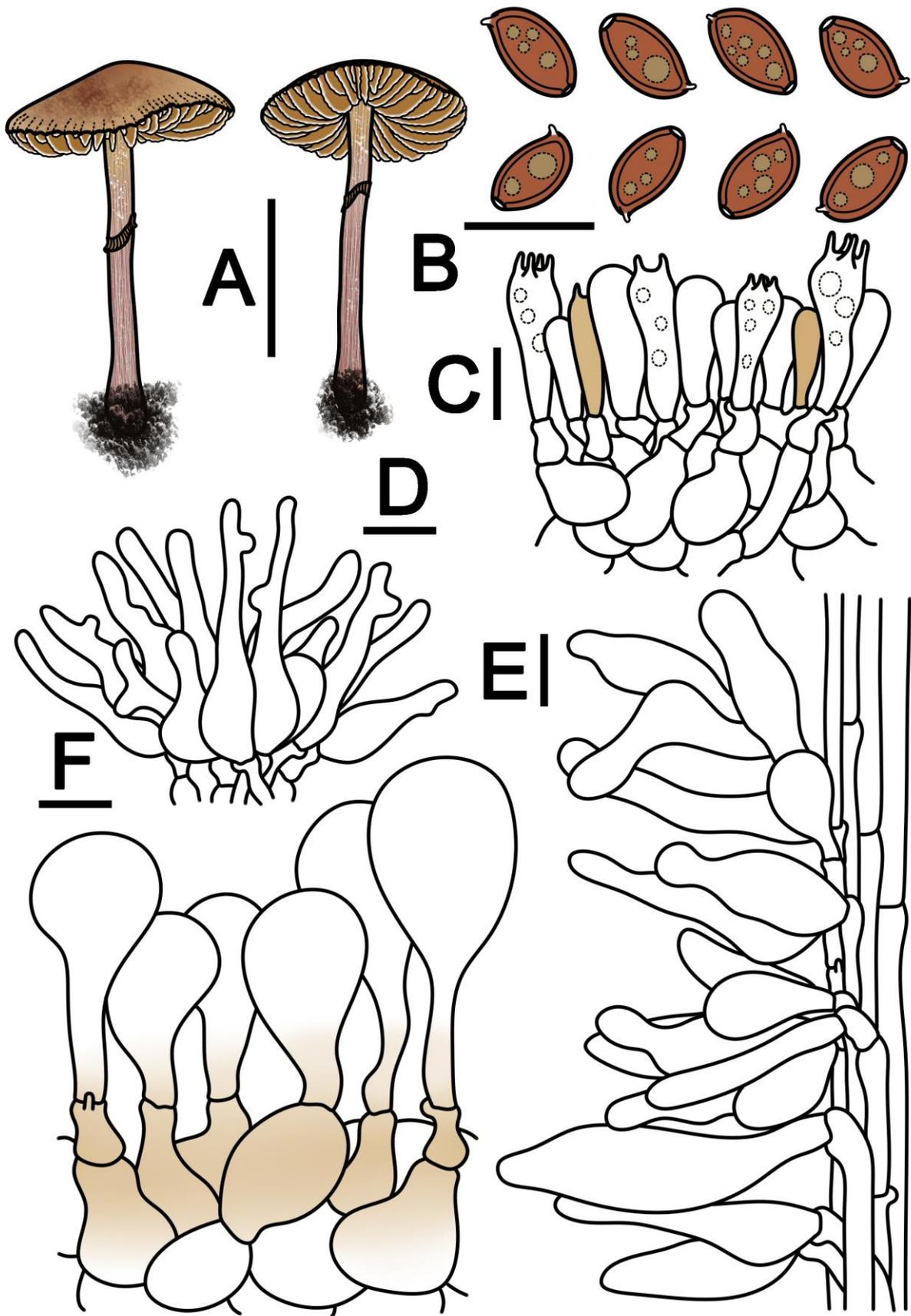


Figure 13 – *Pholiotina excrescenticystidiata* (HMJAU65021). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipells. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

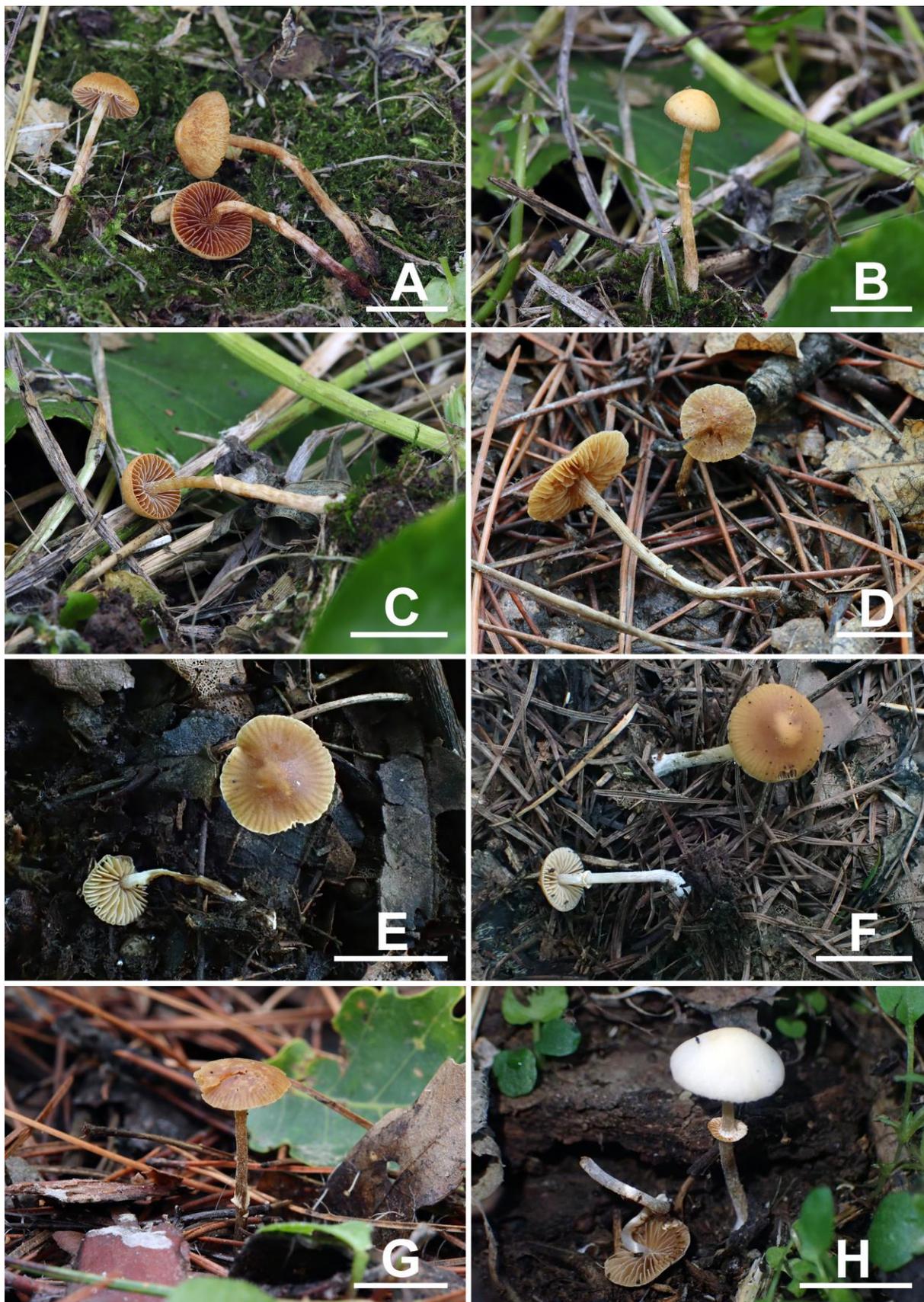


Figure 14 – Basidiomata of *P.* sect. *Pholiotina* species. A *P. rufidispora* (HMJAU65028). B, C *P. rufidispora* (HMJAU65027). D *P. bifurcaticystidia* (HMJAU65030). E *P. bifurcaticystidia* (HMJAU65033). F *P. bifurcaticystidia* (HMJAU65032). G *P. bifurcaticystidia* (HMJAU65031). H *P. eburnea* (HMJAU65035). Scale bars = 1 cm. These pictures are copyright of the collectors of specimens.

Type – China, Jilin Province, Changchun City, Jilin Agricultural University, 9 September 2022, 125°24'30"E, 43°48'31"N, alt. 225 m, H. B. Song, S22090908 (HMJAU65027, holotype).

Basidioma small-sized, Pileus diameter 0.5–1.5 cm, hemispherical to paraboloid, convex, slightly obtusely conical, subumbonate, ivory (RAL1014), pastel yellow (RAL1034) to dahlia yellow (RAL1033). Pileus hygrophanous, initially with shallow striations on the edge, gradually disappearing, surface smooth, slightly viscid. Context thin, ivory (RAL1014) to sandy yellow (RAL1002), without any distinctive odor. Lamellae adnexed to narrowly adnate, ventricose, moderately crowded, unequal length, saffron yellow (RAL1017) to red orange (RAL2001), serrulate white at the edge. Stipe length 2.0–3.5 cm, thick 1.5–3.0 mm, cylindrical, gradually widening towards the base, initially oyster white (RAL1013) to light ivory (RAL1015), later saffron yellow (RAL1017) to red orange (RAL2001), ochre brown (RAL8001), longitudinally fibrous striated, slightly pruinose above the ring. Ring positioned at the middle, small and thin, the same color as the stipe, with undulate sulcate on the upper surface and smooth on the lower surface.

Basidiospores (60/3/3) (9.2–)9.4–11.1(–12.1) × (5.2–)5.4–6(–6.2) μm, Q = (1.64–)1.68–1.95(–2.09), Qm = 1.80(± 0.09), oblong, amygdaliform, slightly suprahilar depression, thick walls, containing oil droplets, germ pore diameter 0.5–1.5 μm, red orange (RAL2001) to copper brown (RAL8004) in KOH solution. Basidia (15–)16–26(–27) × (7–)8–11 μm, clavate, 4(2)-spored, sterigmata long 2–6 μm, basidia with vacuolar contents. Cheilocystidia (23–)24–45(–46) × (6–)7–11(–12) μm, lageniform to long-necked lageniform, narrowly utriform, subcylindrical, neck often curved, some with thick walls, lamellae edge sterile. Pleurocystidia absent. Stipitipellis (above ring) of caulocystidia spheropedunculate, near clavate, lageniform, long-necked lageniform, narrowly utriform, capitate, and irregular lecythiform, up to 60 × 20 μm. Pileipellis hymeniform, consists of sphaeropedunculate elements (18–)22–47(–51) × (16–)17–24(–27) μm, with brown red (RAL3011) pigments at the base in KOH. Pileocystidia absent. Thin gelatinous layer. All structures have clamp connections. Negative reaction with ammonia.

Habitat – Growing solitarily or scattered in damp meadow during autumn.

Known distribution – Northeast China.

Additional specimens measured – China, Jilin Province, Changchun City, Jilin Agricultural University, 9 September 2022, 125°24'30"E, 43°48'31"N, alt. 225 m, H. B. Song, S22090909 (HMJAU65028), S22090910 (HMJAU65029).

Notes – *Pholiotina rufidispora* and *Pholiotina aporos* differ in terms of their basidiospores. Specifically, the basidiospores of *Pholiotina aporos* lack a germ pore. In the phylogenetic context, *P. rufidispora* and *P. arrhenii* are closely related; however, the basidiospores of *P. arrhenii* are smaller than 9 μm and exhibit a weak positive reaction with ammonia, forming diamond-shaped crystals. Another distinction is observed between *P. rufidispora* and *P. hadrocystis*. *P. hadrocystis* may sometimes possess a double-layered ring, and the length of its basidiospores is smaller than 9 μm. Furthermore, *P. rufidispora* differs from *P. rugosa*, as the latter species features a medium-sized basidioma and a slightly rugose pileus. Moving on to *P. vexans*, the difference lies in the size and thickness of the ring, with *P. vexans* exhibiting a larger and thicker ring. Additionally, the germ pore of *P. vexans* can reach 2 μm. Lastly, the primary distinction between *P. rufidispora* and *P. utricystidiata* as well as *P. teneroides* is evident in the cheilocystidia. In *P. utricystidiata* and *P. teneroides*, the cheilocystidia are predominantly lageniform and utriform (Hausknecht 2009).

Pholiotina bifurcaticystidia T. Bau & H. B. Song, sp. nov.

Figs 14D–G, 16

Mycobank number: MB854544; Facesoffungi number: FoF15332

Etymology – “*bifurcaticystidia*” refers to cheilocystidia with bifurcated tips.

Type – China, Jilin Province, Changchun City, Jingyuetan National Forest Park, 12 July 2023, 125°27'44"E, 43°45'27"N, alt. 316 m, H. B. Song, S23071203 (HMJAU65030, holotype).

Basidioma small-sized. Pileus diameter 0.5–2 cm, initially hemispherical to campanulate, later convex, subumbonate, center orange brown (RAL8023) to signal brown (RAL8002), margin pastel yellow (RAL1034) to ochre brown (RAL8001). Pileus hygrophanous, surface smooth,

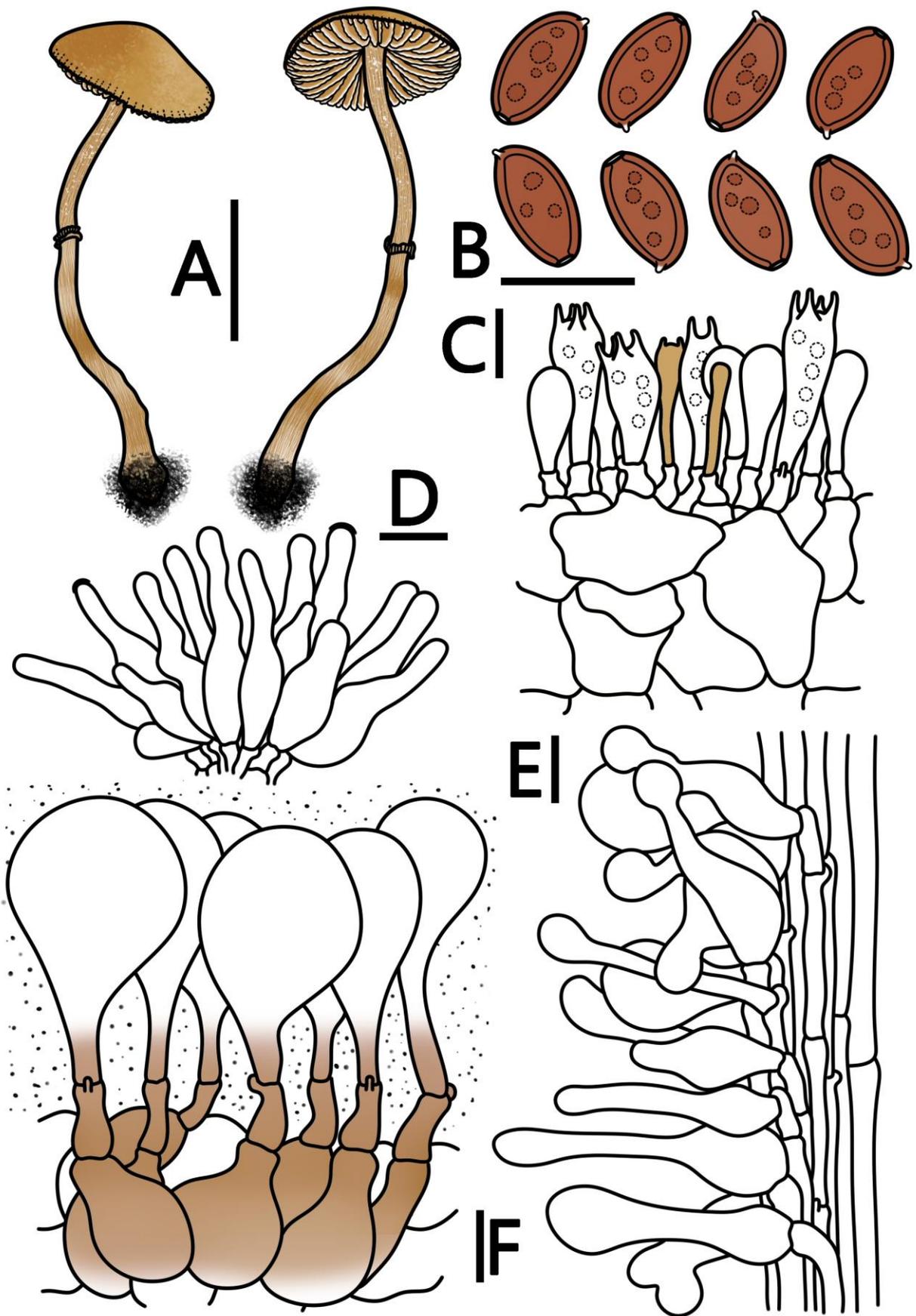


Figure 15 – *Pholiotina rufidispora* (HMJAU65027). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipellis. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

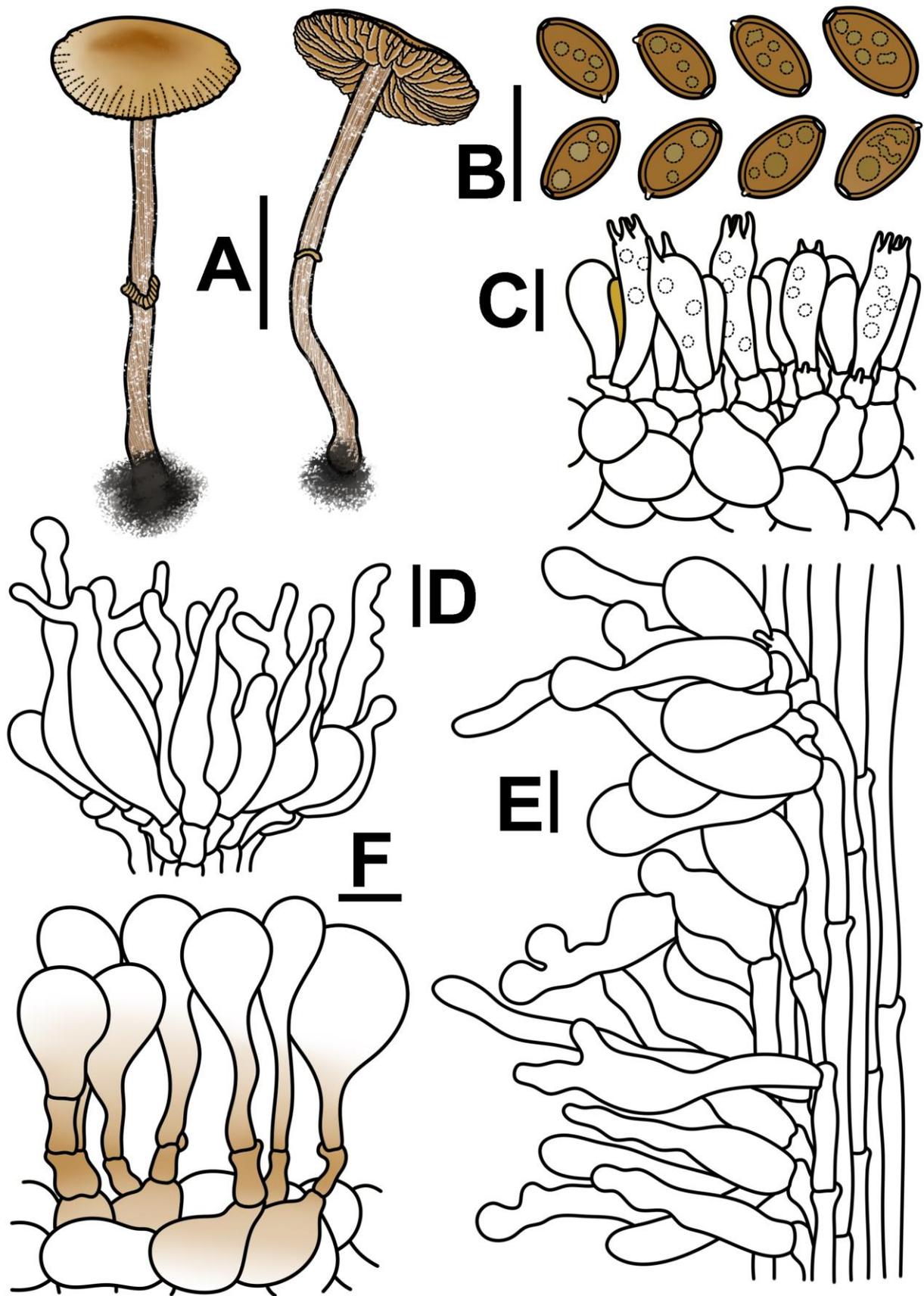


Figure 16 – *Pholiotina bifurcaticystidia* (HMJAU65030). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia, E Stipitipells. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

slightly viscid, margin with distinct striations, reaching up to half the radius of the pileus. Context thin, same color as pileus, without distinctive odor. Lamellae adnexed to narrowly adnate, ventricose, moderately crowded, unequal length, initially ivory (RAL1014), later pastel yellow (RAL1034) to ochre brown (RAL8001), with white serrulate edges. Stipe length 1.5–4 cm, diameter 1.0–2.5 mm, cylindrical, slightly swollen at the base, initially sand yellow (RAL1002), later ochre brown (RAL8001) to signal brown (RAL8002), covered with pruinose and fine pubescence, longitudinally fibrous striated. Ring at the middle, easily detachable when mature, same color as stipe, upper surface with undulate sulcate, lower surface smooth.

Basidiospores (60/3/3) (7.4–)7.6–9.4(–10.1) × (4–)4.4–5.4(–5.6) μm, Q = (1.52–)1.57–1.86(–2), Qm = 1.71(± 0.09), slightly ellipsoid to oblong, subcylindrical, slightly amygdaliform, thick walls, containing oil droplets, germ pore diameter 0.5–1.5 μm, in KOH solution ochre brown (RAL8001) to copper brown (RAL8004). Basidia (16–)17–23(–25) × (6–)7–10 μm, clavate, 4(2)-spored, sterigmata length 2–5 μm, basidia with vacuolar contents. Cheilocystidia (18–)20–59(–62) × (6–)8–12(–14) μm, diverse and irregular in shape, lageniform to long-necked lageniform, neck slightly curved, bifurcated or slightly swollen at the apex, some with excrescences, narrowly utriform, nettle hair-shaped, slightly curved, some bifurcated or with excrescences, spheropedunculate, sub-lecythiform, lamellae edge sterile. Pleurocystidia absent. Stipitipellis (above ring) of caulocystidia (23–)26–62(–66) × (5–)7–15(–16) μm, similar to cheilocystidia, diverse and irregular in shape, spheropedunculate, clavate, subcylindrical, hair-like, lageniform to long-necked lageniform, neck slightly curved, bifurcated or slightly swollen at the apex, some with excrescences, nettle hair-shaped, slightly curved, some bifurcated or with excrescences. Pileipellis hymeniform and consists of sphaeropedunculate elements 21–43(–46) × (7–)10–25(–26) μm, with brown red (RAL3011) pigments at the base in KOH. Pileocystidia absent. Gelatinous layer indistinct or absent. All structures have clamp connections. Negative reaction with ammonia.

Habitat – Growing singly or scattered in mixed forests during the summer and autumn seasons.

Known distribution – Northeast China.

Additional specimens measured – China, Jilin Province, Changchun City, Jingyuetan National Forest Park, 12 July 2023, 125°27'44"E, 43°45'27"N, alt. 316 m, H. B. Song, S23071204 (HMJAU65031). Jilin City, Jiaohe City, Laoyeling, 28 July 2023, 127°12'3"E, 43°40'52"N, alt. 425 m, S. E. Wang, E2307190 (HMJAU65032). Jilin City, Jiaohe City, Shansongling, 29 July 2023, 127°1'41"E, 43°32'18"N, alt. 576 m, S. E. Wang, E2307265 (HMJAU65033).

Notes – *Pholiotina bifurcaticystidia* can be distinguished from *Pholiotina excrescenticystidiata* by the difference in their caulocystidia. In *P. excrescenticystidiata*, the caulocystidia lacks excrescences. On the other hand, *P. bifurcaticystidia* shares a similarity with *P. rufidispora* in terms of caulocystidia. However, the cheilocystidia of *P. rufidispora* lack excrescences. In *P. sect. Pholiotina*, the presence or absence of excrescences on the cheilocystidia is a distinguishing characteristic that sets *P. bifurcaticystidia* apart from other species. Although closely related, *P. bifurcaticystidia* and *P. calongei* differ in their habitat and growth characteristics. *P. calongei* is found in Spain and typically grows on cow dung (Siquier et al. 2021).

Pholiotina eburnea T. Bau & H. B. Song, sp. nov.

Figs 14H, 17

Mycobank number: MB854546; Facesoffungi number: FoF15333

Etymology – “*eburnean*” refers to the color of the pileus as ivory.

Type – China, Jilin Province, Changchun City, Jilin Agricultural University, 15 September 2021, 125°24'14"E, 43°48'34"N, alt. 222 m, L. Zhu, Z21091501 (HMJAU65035, holotype).

Small-sized basidioma. Pileus diameter 0.5–1.5 cm, hemispherical to obtusely conical, convex, central light ivory (RAL1015) to ivory (RAL1014) in color, margin light ivory (RAL1015) to oyster white (RAL1013). Pileus hardly hygrophanous, indistinct or absent striations, surface smooth. Context thin, ivory (RAL1014) to sandy yellow (RAL1002), no distinctive odor. Lamellae adnexed to narrowly adnate, ventricose, moderately crowded, unequal length, sandy yellow

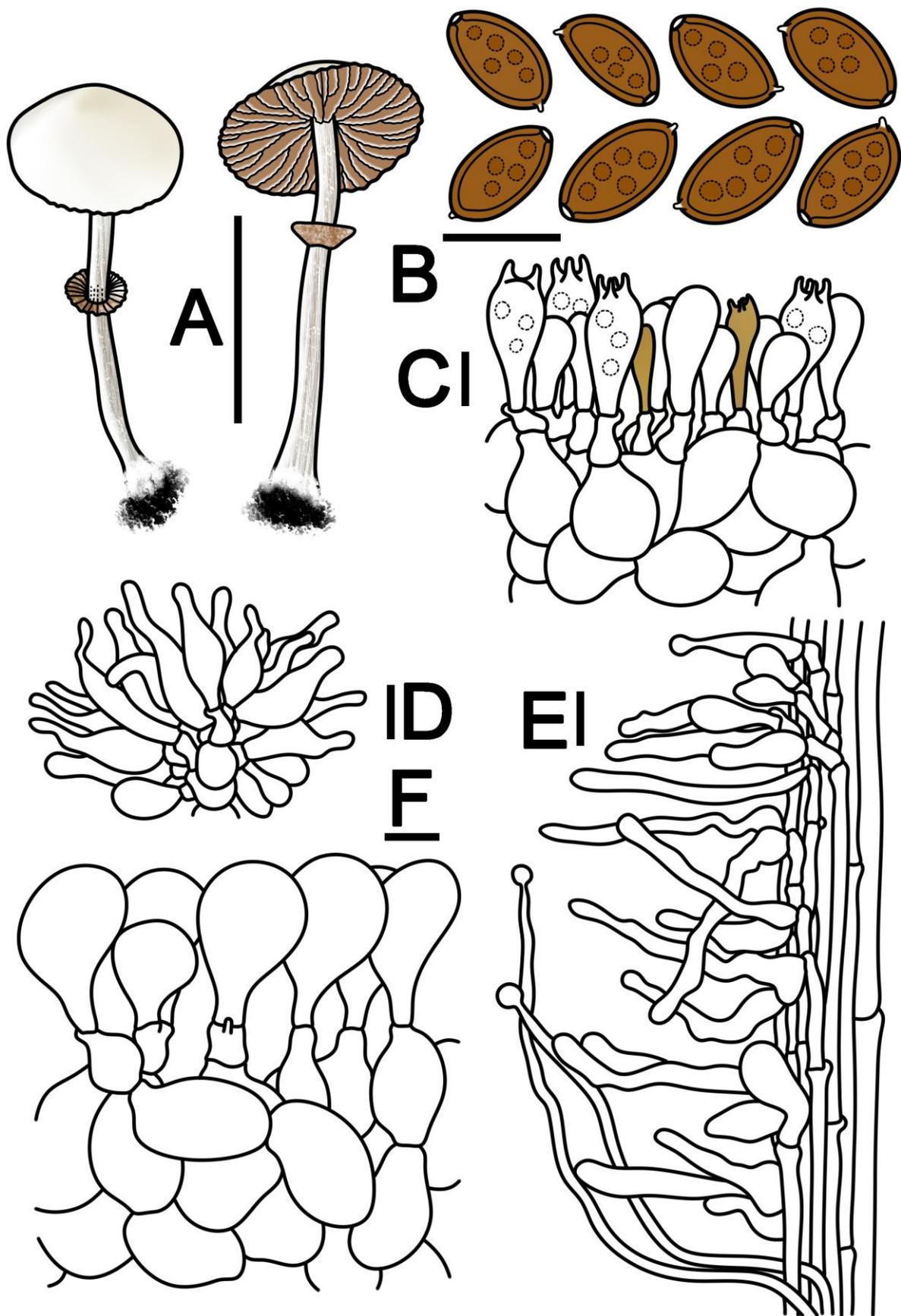


Figure 17 – *Pholiotina eburnea* (HMJAU65035). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipellis. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

(RAL1002) to brown beige (RAL1011), ochre brown (RAL8001), with white serrulate edge. Stipe 1.5–3 cm in length, thick 0.5–1.5 mm, cylindrical, gradually widening towards the base, oyster white (RAL1013) to light ivory (RAL1015), green beige (RAL1000), possessing a white metallic luster, slightly pruinose, longitudinally fibrous striated. Ring at the middle, approximately 3 mm in diameter, thin, membranous, with undulate sulcate on the upper surface and smooth on the lower surface.

Basidiospores (60/3/3) (9.7–)10.2–13.2(–13.8) × (6.1–)6.3–7.5(–7.9) μm, Q = (1.55–)1.56–1.86(–1.89), Qm = 1.71(± 0.08), slightly ellipsoid to oblong, slightly amygdaliform, thick-walled, oil droplets present, germ pore diameter less than 1.5 μm, basidiospores ochre brown (RAL8001) to copper brown (RAL8004) in KOH solution. Basidia (18–)19–28(–29) × 9–12 μm, clavate, 4(2)-spored, sterigmata 2–5 μm long, basidia with vacuolar contents. Cheilocystidia (20–)22–35(–36) × (5–)6–10(–11) μm, lageniform to long-necked lageniform, irregular lageniform, neck often curved, partially inflated, narrowly utriform, lamellae edge sterile. Pleurocystidia absent. Stipitipellis (above ring) of caulocystidia 15–53 × 5–12 μm, spheropedunculate, near clavate, subcylindrical, lageniform, long-necked lageniform, narrowly utriform, fusiform, and irregular lecythiform, hair-like elements with spherical apex, up to 100× 3 μm. Pileipellis hymeniform and consists of sphaeropedunculate elements (25–)27–41(–45) × (15–)16–24(–27) μm, lacking pigmentation at the base in KOH. Pileocystidia absent. Gelatinous layer indistinct or absent. All structures have clamp connections. Weakly positive reaction with ammonia.

Habitat – Found singly in autumn on decaying willow wood.

Known distribution – Northeast China.

Additional specimens measured – China, Jilin Province, Changchun City, Jilin Agricultural University, 13 September 2021, 125°24'19"E, 43°48'37"N, alt. 222 m, L. Y. Zhu, S92401H (HMJAU65034).

Notes – The main characteristics of *Pholiotina eburnea* are a pileus that is pale ivory to oyster white, and the pileipellis lacks pigmentation at the base. Within the *P. sect. Pholiotina*, *P. eburnea* differs from *P. arrhenii* by the presence of a white, easily detachable ring in *P. arrhenii*, and the thick-walled apex of cheilocystidia in *P. arrhenii*. *P. eburnea* can be differentiated from *P. vexans* by the yellow-brown pileus of *P. vexans* and the larger germ pore on the basidiospores, which can reach up to 2 μm (Hausknecht 2009). *P. eburnea* and *P. calongei* are sister taxa in terms of phylogenetic relationships, but *P. calongei* is found in Spain, and the type specimen was collected on cow dung (Siquier et al. 2021).

Pholiotina section Vestitae (Watling) Hauskn. & Krisai, Öst. Z. Pilzk. 16: 141 (2007)

Type species – *Pholiotina vestita* (Fr.) Singer

Basionym – *Conocybe* subgenus *Pholiotina section Vestitae* Watling, Note Roy. Bot. Garden Edinburgh 26: 298 (1965).

Notes – *Pholiotina section Vestitae* in *Pholiotina* is characterized by the presence of veil remnants on the pileus, which easily vanish. Cheilocystidia mixed with sub-lecythiform elements, based on the perspectives of Arnolds (2005) and Hausknecht (2009). The habitat pictures of *P. serrata* in *P. sect. Vestitae* are as follows (Fig. 18A–D).

Key to *Pholiotina section Vestitae* in China

- 1. Growing on decayed wood *Pholiotina* sp.1
- 1'. Growing in meadow 2
- 2. Basidiospores with distinct germ pore *P. exannulata*
- 2' Basidiospores without germ pore or indistinct *P. serrata*

Pholiotina section Intermediae (Watling) Singer, Sydowia Beiheft 7: 79 (1973)

Basionym – *Conocybe section Intermediae* Watling, Persoonia 6: 328 (1971)



Figure 18 – Basidiomata of *P.* sect. *Vestitae* species. A *P. serrata* (HMJAU65113). B *P. serrata* (HMJAU65114). C *P. serrata* (HMJAU65115). D *P. serrata* (HMJAU65116). Scale bars = 1 cm. These pictures are copyright of Song HB.

Notes – Within the *Pholiotina* section *Intermediae*, species possess a veil that can form a ring on the stipe or remain at the edge of the pileus, but it easily disappears. The *cheilocystidia* in this section are primarily lecythiform, as described by Arnolds (2005) and Hausknecht (2009). Previously, only four species were known within *P.* sect. *Intermediae*: *P. intermedia* (A.H. Sm.) Singer, *P. brunnea* (J.E. Lange & Kühner ex Watling) Singer, *P. caricicola* Singer, and *P. pseudoampullaceocystis* (Singer 1989, Karich 2020).

Key to *Pholiotina* section *Intermediae* in China

1. Veil forms a ring on stipe *P. intermedia*
- 1'. Veil remnants on pileus, not forming a ring 2
2. Basidiospores without germ pore 3
- 2' Basidiospores with distinct or indistinct germ pore..... 4
3. Pileocystidia mix lageniform and lecythiform *P. sulciceps*
- 3'. Pileocystidia only lecythiform, rare *P. horchinensis*
4. 2-spored *P. bispora*
- 4' 4(2)-spored..... 5
5. Cheilocystidia with excrescences *Pholiotina* sp.2
- 5'. Cheilocystidia without excrescences 6
6. Cheilocystidia mix lecythiform with a few utriform and lageniform..... *P. liudingshanensis*

6' Cheilocystidia only lecythiform.....	7
7. Pileipellis composed of clavate, spheropedunculate cells, some arranged in a mucronate or beak-like fashion.....	8
7'. Pileipellis composed of clavate, spheropedunculate arrangement.....	9
8. Growing in coniferous forests	<i>P. rostellulata</i>
8' Growing in bamboo forests.....	<i>P. bambusicola</i>
9. No pileocystidia observed.....	<i>Pholiotina</i> sp.3
9'. Pileocystidia present	10
10. Pileocystidia lageniform	<i>P. changbaishanensis</i>
10' Pileocystidia lecythiform	11
11. Distinct germ pore, diameter 0.5–1.5 µm	<i>P. communis</i>
11'. Germ pore smaller than 1 µm, partially indistinct	12
12. Cheilocystidia length can reach over 40 µm.....	<i>P. longicystidiata</i>
12' Cheilocystidia length less than 40 µm	13
13. Pileus without pubescence	<i>P. micropora</i>
13' Pileus covered with fine pubescence	<i>P. brevipila</i>

Pholiotina intermedia (A.H. Sm.) Singer, Beih. Botan. Centralbl., Abt. B 56: 170 (1936)
Figs 19A–B, 20

Basionym – *Pholiota intermedia* A.H. Sm., Annls mycol. 32(5/6): 479 (1934).

Synonymy – *Pholiota septentrionalis* A.H. Sm., Mycologia 27(2): 227 (1935). *Conocybe intermedia* Kühner, Encyclop. Mycol. 7: 143 (1935). *Conocybe septentrionalis* (A.H. Sm.) Bon & Courtec., Docums Mycol. 18(no. 69): 38 (1987)

Basidioma small. Pileus diameter 2.5 cm, broadly conical to obtusely conical, nearly convex, subumbonate, center yellow orange (RAL2000) to orange-brown (RAL8023), margin signal yellow (RAL1003) to maize yellow (RAL1006). Pileus hygrophanous, viscid, striated indistinct or absent. Context thin, ivory (RAL1014) to sand yellow (RAL1002), without distinctive odor. Lamellae adnexed to narrowly adnate, very crowded, unequal length, ivory (RAL1014) to beige (RAL1001), serrulate margin. Stipe 4 cm long, 3–4 mm thick, cylindrical, gradually swollen towards the base, beige (RAL1001) to pastel yellow (RAL1034), fibrous, hollow, above the ring the stipe has longitudinal sulcate, below the ring the stipe has floccose squamulose. Ring positioned upper-middle, large and slightly thick, same color as pileus, upper surface sulcate, lower surface smooth.

Basidiospores (20/1/1) (6.8–)6.7–7.9(–8.2) × (4.3–)4.4–4.8(–5.1) µm, Q = (1.38–)1.43–1.66(–1.68), Qm = 1.57(± 0.07), ellipsoid, slightly oblong, reniform to phaseoliform, thick walls, containing oil droplets, germ pore diameter 0.5–1.5 µm, basidiospores in KOH solution ochre brown (RAL8001) to pastel yellow (RAL1034). Basidia 19–24 × 6–9 µm, clavate, 4(2)-spored, sterigmata long 1–3 µm, basidia with vacuolar contents. Cheilocystidia (20–)21–27(–30) × 7–9(–10) µm, lecythiform, with 4–7 µm wide capitula, lamellae edge sterile. Pleurocystidia absent. Stipitipellis (above ring) of caulocystidia spheropedunculate, cylindrical to clavate, lageniform, predominantly lecythiform, 20–36(–40) × (4–)5–12(–13) µm, with 5–8 µm wide capitula. Pileipellis hymeniform, composed of arranged clavate and sphaeropedunculate elements (28–)30–58(–60) × 12–20 µm, with ochre brown (RAL8001) pigment at the base in KOH solution. Pileocystidia absent. Gelatinous layer present. All structures have clamp connections. Weakly positive reaction with ammonia forming rhomboid crystals.

Habitat – Summer and autumn growing in broad-leaved forests.

Known distribution – China, United States (type), Belgium, Switzerland, France, Argentina, Canada.

Collections examined – China, Jilin Province, Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 21 August 2021, 128°0'25" E, 42°31'20" N, alt. 721 m, T. Bau & Q. Q. D, DQQ10 (HMJAU62014).

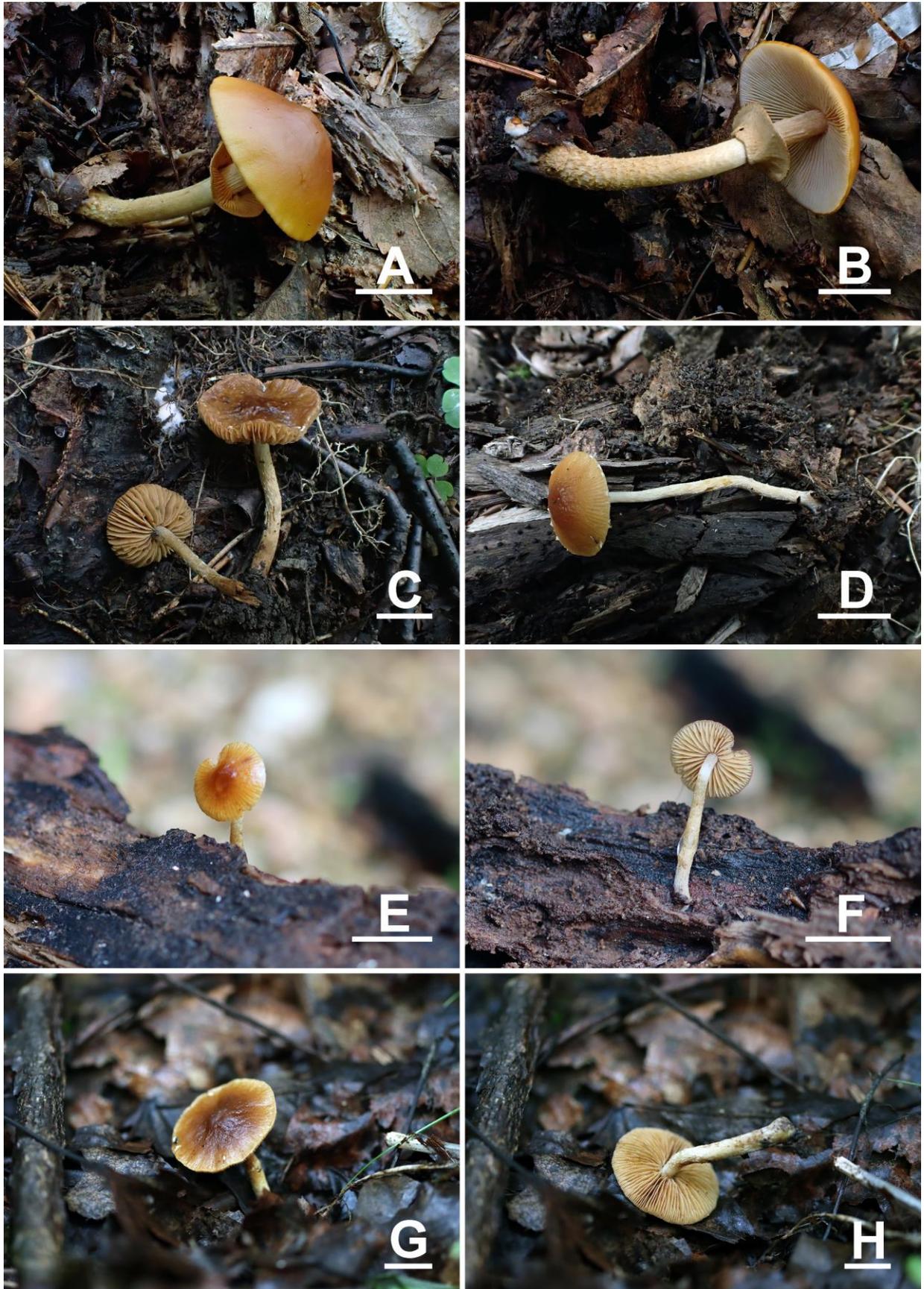


Figure 19 – Basidiomata of *P.* sect. *Intermediae* species. A, B *P. intermedia* (HMJAU62014). C *P. communis* (HMJAU65047). D *P. communis* (HMJAU65046). E, F *P. communis* (HMJAU65038). G, H *P. communis* (HMJAU65039). Scale bars = 1 cm. These pictures are copyright of the collectors of specimens.

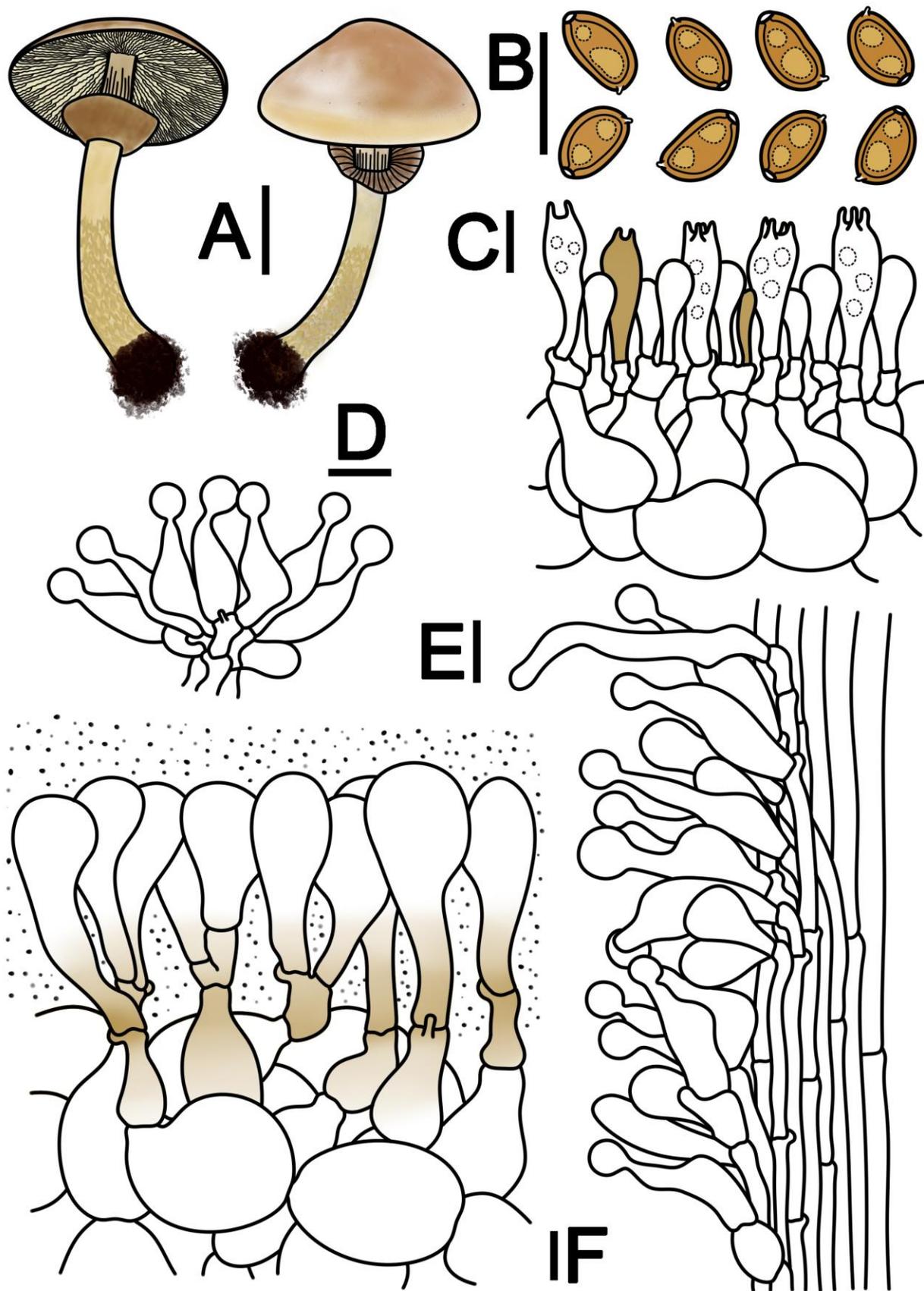


Figure 20 – *Pholiotina intermedia* (HMJAU62014). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipells. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

Notes – *Pholiotina intermedia* is a newly recorded species from China characterized by distinct features, including a prominent ring and lecythiform cheilocystidia. Among species in *P. sect. Intermediae*, it is currently the only one possessing a ring, making it easily distinguishable from others in the same section. Although *P. intermedia* shares morphological similarities with certain species in *P. sect. Pholiotina*, such as *P. teneroides* and *P. utricystidiata*, their cheilocystidia exhibit a non-lecythiform form, enabling clear differentiation from *P. intermedia* (Hausknecht 2009).

Pholiotina communis T. Bau & H. B. Song, sp. nov.

Figs 19C–H, 21

Mycobank number: MB851654; Facesoffungi number: FoF15334

Etymology – “*communis*” is widely distributed in northeastern China.

Type – China, Jilin Province, Jilin City, Jiaohe City, Shansongling, 24 July 2022, 127°02'00" E, 43°32'25" N, alt. 525 m, H. B. Song, S22072422 (HMJAU65039, holotype).

Basidioma small. Pileus diameter 1–3 cm, convex to plano-convex, campanulate to subumbonate. Pileus center pure orange (RAL2004), pearl copper (RAL8029) to chestnut brown (RAL8015), edge beige (RAL1001), pastel yellow (RAL1034) to ochre brown (RAL8001). Pileus hygrophanous, surface smooth, slightly greasy, with shallow striations along the edge, initially covered in veil remnants that gradually disappear. Context thin, beige (RAL1001) to sandy yellow (RAL1002), no distinctive odor. Lamellae adnexed to narrowly adnate, ventricose, moderately crowded, unequal length, pastel yellow (RAL1034) to ochre brown (RAL8001), serrulate at the edge. Stipe length 1.5–4.5 cm, thick 2.0–3.5 mm, cylindrical, gradually widening towards the base, slightly bulbous, stipe ivory (RAL1014), pastel yellow (RAL1034) to ochre brown (RAL8001), slightly pruinose, longitudinally fibrous striated.

Basidiospores (60/3/3) (7–)7.2–8.9(–9.3) × (4.2–)4.3–5.1(–5.7) μm, Q = (1.46–)1.6–1.88(–1.91), Qm = 1.73(± 0.09), slightly ellipsoid to oblong, reniform to phaseoliform, thick walls, containing oil droplets, germ pore diameter 0.5–1.5 μm, basidiospores in KOH solution red orange (RAL2001) to ochre brown (RAL8004). Basidia (16–)17–25(–26) × 6–9 μm, clavate, 4(2)-spored, sterigmata length 3–6 μm, basidia with vacuolar contents. Cheilocystidia (23–)24–38(–41) × 7–11(–12) μm, lecythiform, with capitula 4–7 μm wide, lamellae edge sterile. Pleurocystidia absent. Caulocystidia spheropedunculate, cylindrical to clavate, lageniform, and irregular lecythiform, mainly lecythiform, (20–)21–44(–46) × 6–10(–11) μm, with capitula 4–7 μm wide. Pileipellis hymeniform and consists of sphaeropedunculate and clavate elements (24–)28–54 × 11–22 μm, with brown red (RAL3011) pigments at the base in KOH. Pileocystidia (33–)35–49(–52) × 7–15(–16), lecythiform, with capitula 3–7 μm wide. Pileus residual veil composed of irregular lecythiform to lecythiform elements, in a string-like to chain-like arrangement. Gelatinous layer indistinct or absent. All structures have clamp connections. Weakly positive reaction with ammonia, forming rhombic to hexagonal crystals.

Habitat – Summer and autumn seasons, solitary or scattered on decaying wood in mixed forests.

Known distribution – Northeast China.

Additional specimens measured – China, Jilin Province, Yanbian Korean Autonomous Prefecture, Longjing City, Baixin Township, 24 August 2020, 129°33'59" E, 42°29'24" N, alt. 589 m, T. Bau & L. Y. Zhu, 082403 (HMJAU65036). Jilin City, Jiaohe City, Shansongling, 24 July 2022, 127°02'00" E, 43°32'25" N, alt. 525 m, H. B. Song, S22072418 (HMJAU65037), S22072420 (HMJAU65038). Jilin City, Jiaohe City, Shansongling, 25 July 2022, 127°03'11" E, 43°32'15" N, alt. 489 m, H. B. Song, S22072522 (HMJAU65040). Baishan City, Fusong County, G201, 28 July 2022, 128°01'12" E, 43°09'19" N, alt. 605 m, X. Wang, 63W (HMJAU65041). Yanbian Korean Autonomous Prefecture, Erdaobaihe Town, 31 July 2022, 128°06'38" E, 42°25'34" N, alt. 713 m, L. Y. Zhu, Z22073127 (HMJAU65042). Jilin City, Jiaohe City, Shansongling, 29 July 2023, 127°03'09" E, 43°32'21" N, alt. 566 m, X. Wang, W23072931 (HMJAU65043). Jilin City, Jiaohe City, Shansongling, 29 July 2023, 127°03'07" E, 43°32'17" N, alt. 533 m, S. E. Wang, E2307250 (HMJAU65044). Jilin City, Jiaohe City, Shansongling, 29 July 2023, 127°03'10" E, 43°32'21" N,

alt. 521 m, S. E. Wang, E2307245 (HMJAU65045). Jilin City, Jiaohe City, Shansongling, 30 July 2023, 127°01'45" E, 43°32'17" N, alt. 557 m, S. E. Wang, E2307283 (HMJAU65046). Jilin City, Shansongling, 26 August 2023, 127°01'56" E, 43°32'30" N, alt. 566 m, H. Cheng, C2382608 (HMJAU65047). Jilin City, Huadian City, Hongshi National Forest Park, 27 August 2023, 127°08'12" E, 42°49'57" N, alt. 498 m, H. Cheng, C2382707 (HMJAU65048).

Notes – The distinction between *Pholiotina communis* and *Pholiotina brunnea* lies in the fact that *P. brunnea* is 4-spored and lacks pileocystidia (Hausknecht 2009). On the other hand, *P. communis* differs from *P. caricicola* in that the basidiospores of *P. caricicola* can reach a length of 13 µm (Singer 1989). Furthermore, *P. communis* can be differentiated from *P. liudingshanensis* T. Bau & H. B. Song based on the utriform, lageniform, and predominantly lecythiform cheilocystidia found in *P. liudingshanensis*. Another species, *P. bispora* T. Bau & H. B. Song, sets itself apart from *P. communis* by having 2-spored basidia. In contrast, *P. micropora* T. Bau & H. B. Song and *P. brevipila* T. Bau & H. B. Song can be distinguished from *P. communis* by their germ pore diameter, which is less than 1 µm or at times indistinct or absent. Additionally, *P. horchinensis* T. Bau & H. B. Song lacks germ pore on its basidiospores, providing a distinguishing characteristic. Lastly, while *P. communis* and *P. rostellulata* T. Bau & H. B. Song are sister taxa, the latter stands out due to its spheropedunculate pileipellis, resembling bird beaks, making it easily recognizable.

Pholiotina rostellulata T. Bau & H. B. Song, sp. nov.

Figs 22A–D, 23

Mycobank number: MB851655; Facesoffungi number: FoF15335

Etymology – “*rostellulata*” refers to pileipellis consisting of spheropedunculate elements, some of which have a “small beak” or “little rostrum”.

Type – China, Jilin Province, Baishan City, Fusong County, Changbai Mountain Ancient Tree Park, July 30, 2022, 128°00'15"E, 42°32'23"N, alt. 655 m, H. B. Song, S22073006 (HMJAU65050, holotype).

Basidioma small. Pileus diameter 0.5–1.5 cm, obtusely conical to broadly conical, plano-convex, subumbonate, center red orange (RAL2001), copper brown (RAL8004), margin ivory (RAL1014), pastel yellow (RAL1034) to ochre brown (RAL8001). Pileus hygrophanous, surface smooth, viscid, margin striated, veil remnants on the edge of pileus, pure white (RAL9010), serrate to triangular. Context thin, beige (RAL1001) to sandy yellow (RAL1002), odorless. Lamellae adnexed to narrowly adnate, ventricose, crowded, unequal length, beige (RAL1001) to ivory (RAL1014), ochre brown (RAL8001), margin serrulate. Stipe length 2.5–4.5 cm, thick 1.0–3.0 mm, cylindrical, gradually enlarged at the base, without a bulbous structure, light ivory (RAL1015), maize yellow (RAL1006), ochre brown (RAL8001), slightly pruinose, longitudinally fibrous striated.

Basidiospores (60/3/3) (6.1–)6.4–8.1(–8.4) × (4.1–)4.2–4.9(–5.1) µm, Q = (1.43–)1.51–1.81(–1.84), Qm = 1.64 (± 0.09), ellipsoid to oblong, reniform to phaseoliform, thick walls, containing oil droplets, germ pore diameter 0.5–1 µm, basidiospores in KOH solution ochre brown (RAL8001) to copper brown (RAL8004). Basidia (17–)18–27(–28) × 6–9 µm, clavate, 4(2)-spored, sterigmata length 3–7 µm, basidia with vacuolar contents. Cheilocystidia (21–)22–33 × (6–)7–11 µm, lecythiform, with capitula 3–7 µm wide, lamellae margin sterile, mixed with clavate elements. Pleurocystidia absent. Caulocystidia spheropedunculate, cylindrical to clavate, lageniform, predominantly lecythiform, (20–)21–39(–45) × (5–)6–12(–13) µm, with 4–6 µm wide capitula. Pileipellis hymeniform, composed of arranged clavate, spheropedunculate elements, some of which have little rostrum and small beak, measuring 24–45(–49) × (9–)10–20(–21) µm, with a brown red (RAL3011) pigment at the base in KOH solution. Pileocystidia 30–50(–65) × (8–)9–14(–17), long-necked lageniform, lecythiform, with 3–8 µm wide capitula. Pileus residual veil composed of irregular lecythiform to lecythiform elements, arranged in a string-like to chain-like pattern. Gelatinous layer present. All structures have clamp connections. Weakly positive reaction with ammonia, forming rhomboid crystals.

Habitat – Growing solitarily in the humus layer of coniferous forests during summer.

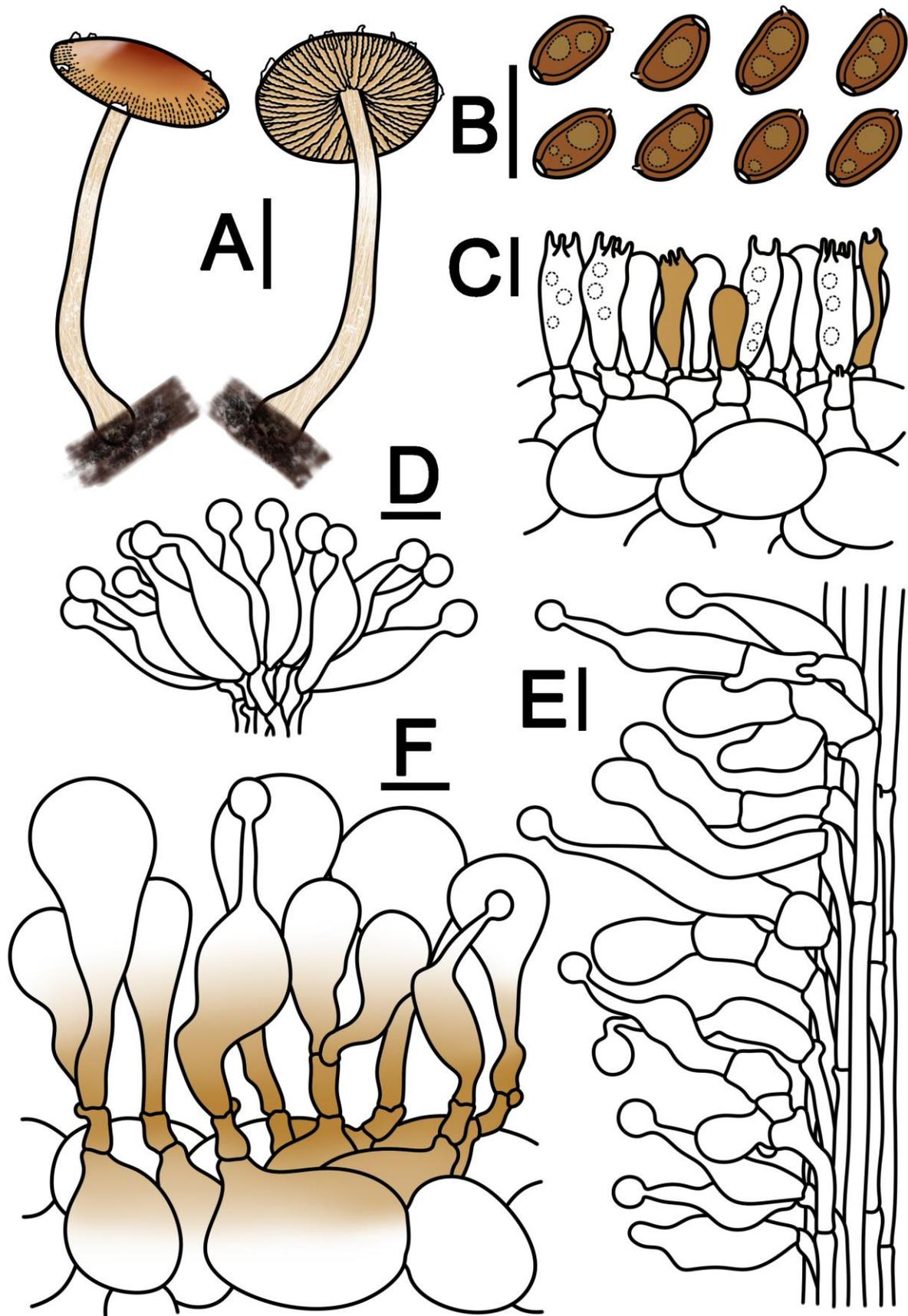


Figure 21 – *Pholiotina communis* (HMJAU65039). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipells. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

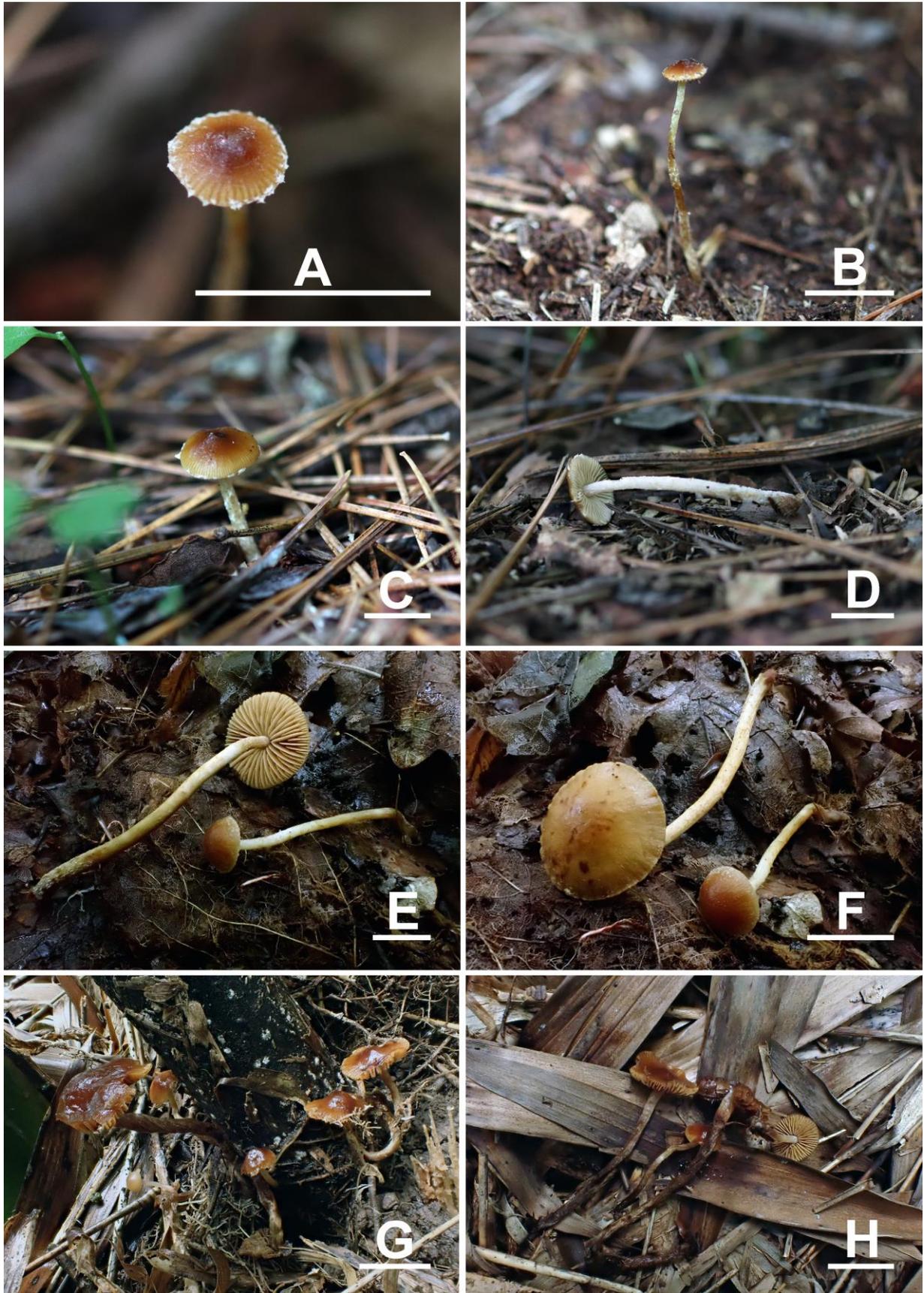


Figure 22 – Basidiomata of *P.* sect. *Intermediae* species. A, B *P. rostellulata* (HMJAU65049). C, D *P. rostellulata* (HMJAU65050). E, F *P. liudingshanensis* (HMJAU65053). G, H *P. bambusicola* (HMJAU65054). Scale bars = 1 cm. These pictures are copyright of the collectors of specimens.

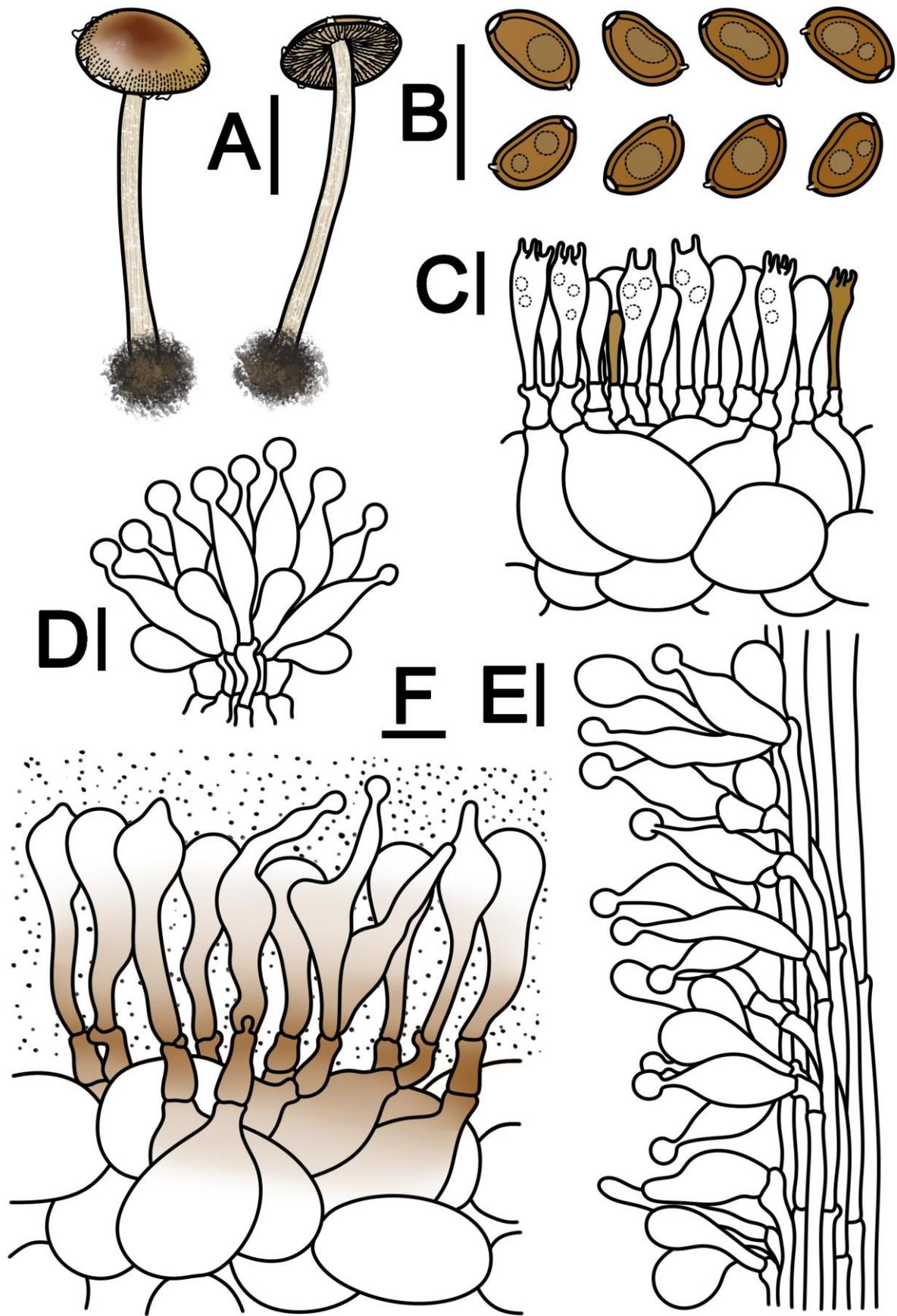


Figure 23 – *Pholiotina rostellulata* (HMJAU65050). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia, E Stipitipells. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

Known distribution – Northeast China.

Additional specimens measured – China, Jilin Province, Baishan City, Fusong County, Changbai Mountain Ancient Tree Park, July 30, 2022, 128°00'18"E, 42°32'17"N, alt. 661 m, H. B. Song, S22073005 (HMJAU65049), S22073007 (HMJAU65051).

Notes – *Pholiotina rostellulata* and *Pholiotina bambusicola* T. Bau & H. B. Song both have a pileipellis with a small beak or little rostrum. However, *P. bambusicola* is distinguishable because it grows in bamboo forests. In contrast, *P. rostellulata* can be differentiated from other species in *P. sect. Intermediae* based on the presence of a small beak or little rostrum in its pileipellis (Hausknecht 2009). Although *P. rostellulata* and *P. communis* are sister taxa, they can be easily distinguished because *P. communis* has a clavate to spheropedunculate pileipellis.

Pholiotina liudingshanensis T. Bau & H. B. Song, sp. nov.

Figs 22E–F, 24

Mycobank number: MB851657; Facesoffungi number: FoF15336

Etymology – “*liudingshanensis*” refers to the type specimen originating from Liuding Mountain.

Type – China, Jilin Province, Dunhua City, Liuding Mountain, July 28, 2022, 128°8'20"E, 43°12'27"N, alt. 770 m, T. Bau & H. B. Song, S22072820 (HMJAU65053, holotype).

Basidioma very small. Pileus diameter 1–2 cm, initially hemispherical, obtusely conical, later convex, subumbonate, center copper brown (RAL8004), ochre brown (RAL8001), margin pastel yellow (RAL1034) to sandy yellow (RAL1002). Pileus hygrophorous, slightly greasy, margin shallowly striated. Veil remnants present at the pileus margin, gradually disappearing. Context thin, beige (RAL1001) to sandy yellow (RAL1002), without distinctive odor. Lamellae adnexed to narrowly adnate, ventricose, moderately crowded, unequal length, pastel yellow (RAL1034), maize yellow (RAL1006), serrulate at the margin. Stipe 4–6.5 cm long, thick 1.0–2.0 mm, cylindrical, slightly swollen at the base, light ivory (RAL1015), pastel yellow (RAL1034) to maize yellow (RAL1006), slightly pruinose, longitudinally fibrillose striated.

Basidiospores (60/3/2) (7–)7.5–8.5(–8.7) × (4–)4.2–5.1(–5.3) μm, Q = (1.48–)1.56–1.84(–1.93), Qm = 1.68 (± 0.09), slightly ellipsoid, oblong, reniform to phaseoliform, with thick walls and containing oil droplets, germ pore diameter 0.5–1 μm. Basidiospores in KOH solution range from ochre brown (RAL8001) to copper brown (RAL8004). Basidia 17–24(–25) × (6–)7–10 μm, clavate, 4(2)-spored, with sterigmata 2–6 μm, basidia containing vacuolar contents. Cheilocystidia (20–)22–33(–35) × 7–10(–13) μm, utriform, lageniform, predominantly lecythiform, with capitula 3–6 μm wide, lamellae edges are sterile. Pleurocystidia absent. Caulocystidia spheropedunculate, clavate, lageniform, fusiform, narrowly utriform, predominantly lecythiform, 22–42(–45) × (6–)7–14(–15) μm, with 5–8 μm wide capitula. Pileipellis hymeniform, composed of arranged spheropedunculate elements 24–43(–45) × 14–23(–25) μm, with a brown red (RAL3011) pigment at the base in KOH solution. Pileocystidia lecythiform, reaching up to 50 × 20 μm, with 5–7 μm wide capitula. Pileus residual veil composed of irregular lecythiform to lecythiform elements, arranged in a string-like to chain-like pattern. Gelatinous layer is indistinct or absent. All structures have clamp connections. Weakly positive reaction with ammonia, forming rhomboid crystals.

Habitat – Summer and autumn, solitary or scattered in broad-leaved forests.

Known distribution – Northeast China.

Additional specimens measured – China, Jilin Province, Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, August 21, 2021, 128°6'21"E, 42°24'19"N, alt. 832 m, T. Bau & Q. Q. D, DQQ (HMJAU65052).

Notes – The cheilocystidia of *Pholiotina liudingshanensis* and *Pholiotina caricicola* exhibit a mixed type. However, *P. caricicola* is specifically found on mosses in the Andes Mountains, and its basidiospores can reach a length of up to 13 μm. On the other hand, *P. liudingshanensis* differs from *P. pseudoampullaceocystis* in that the basidiospores of *P. pseudoampullaceocystis* lack germ pore (Karich 2020). Within *P. sect. Intermediae*, *P. liudingshanensis* can be distinguished from other species by the presence of utriform and lageniform elements in its cheilocystidia. Although *P. liudingshanensis* is closely related to *P. brunnea* in the phylogenetic tree, the cheilocystidia of

P. brunnea are exclusively lecythiform, with no pileocystidia, making them easily distinguishable (Hausknecht 2009).

Pholiotina bambusicola T. Bau & H. B. Song, sp. nov.

Figs 22G–H, 25

Mycobank number: MB851658; Facesoffungi number: FoF15337

Etymology – “*bambusicola*” refers to an organism that inhabits bamboo forests.

Type – China, Guizhou Province, Tongren City, Jiangkou County, Yamugou Scenic Area, June 21, 2022, 108°44'0"E, 27°47'12"N, alt. 627 m, M. C. Pan, PMC136 (HMJAU65054, holotype).

Basidioma small, Pileus diameter 0.5–2 cm, initially hemispherical, obtusely conical to campanulate, plano-convex, applanate with umbo, center copper brown (RAL8004), brown red (RAL3011), margin pastel yellow (RAL1034) to ochre brown (RAL8001). Pileus hygrophane, greasy, surface smooth, margin undulate, with distinct striations, initial veil remnants on the pileus margin, later gradually disappearing. Context thin, beige (RAL1001) to sandy yellow (RAL1002), no distinct odor. Lamellae adnexed to narrowly adnate, ventricose, moderately crowded, unequal length, pastel yellow (RAL1034) to ochre brown (RAL8001), serrulate margin. Stipe length 2–4 cm, thick 1.0–2.0 mm, cylindrical, slightly swollen at the base, pastel yellow (RAL1034), ochre brown (RAL8001) to copper brown (RAL8004), slightly pruinose and with short pubescence, longitudinally fibrous striations.

Basidiospores (60/3/2) (7.2–)7.5–8.8(–9.3) × (4.3–)4.5–5.2(–5.4) μm, Q = (1.5–)1.58–1.83(–1.85), Q_m = 1.7(± 0.07), slightly ellipsoid, oblong, reniform to phaseoliform, thick walls, containing oil droplets, germ pore less than 1 μm, partially indistinct or absent germ pore, basidiospores in KOH solution ochre brown (RAL8001) to copper brown (RAL8004). Basidia (18–)19–25(–26) × 7–10(–11) μm, clavate, 4(2)-spored, sterigmata length 2–6 μm, basidia with vacuolar contents. Cheilocystidia (20–)22–33(–34) × 7–11 μm, lecythiform, with capitula 3–6 μm wide, mixed with spheropedunculate elements, 12–18 × 8–11 μm. Pleurocystidia absent. Caulocystidia lecythiform, lageniform, clavate, spheropedunculate, hair-like, predominantly lecythiform, 22–34(–37) × 7–11 μm, with capitula 3–6 μm wide, hair-like elements can reach 80 × 6 μm. Pileipellis hymeniform, consisting of clavate and spheropedunculate elements (22–)23–56(–60) × (9–)10–17(–19) μm, partially arranged in long or short pointed rows, with brown red (RAL3011) pigment at the base in KOH solution. Pileocystidia 24–56(–60) × 9–14(–15), lageniform, long-necked lageniform, with curved necks, lecythiform, with capitula 2–7 μm wide. Gelatinous layer present. Pileus residual veil composed of irregular lecythiform to lecythiform elements, arranged in a string-like to chain-like pattern. All structures have clamp connections. Weak positive reaction with ammonia, forming rhomboid crystals.

Habitat – Growing gregariously in the humus layer of bamboo forests during summer.

Known distribution – Southwest China.

Additional specimens measured – China, Guizhou Province, Tongren City, Jiangkou County, Yamugou Scenic Area, June 21, 2022, 108°44'0"E, 27°47'12"N, alt. 627 m, M. C. Pan, PMC136_2 (HMJAU65055).

Notes – The basidiospores of *Pholiotina bambusicola* possess germ pore, although some may be indistinct or absent. The pileipellis is composed of clavate and spheropedunculate elements, some of which have long or short pointed structures. This characteristic can lead to confusion with *P. rostellulata*. However, in *P. rostellulata*, the basidiospores have distinct germ pore, and it typically grows in the humus layer of red pine forests, making it distinguishable. The presence or absence of long or short pointed structures in the pileipellis is a distinguishing feature of *P. bambusicola* from other species in *P. sect. Intermediae* (Hausknecht 2009). *P. bambusicola* is closely related to *P. longicystidiata* T. Bau & H. B. Song, but in *P. longicystidiata*, the cheilocystidia can reach lengths of up to 40 μm, aiding in its differentiation.

Pholiotina longicystidiata T. Bau & H. B. Song, sp. nov.

Figs 26A–H, 27

Mycobank number: MB851659; Facesoffungi number: FoF15338

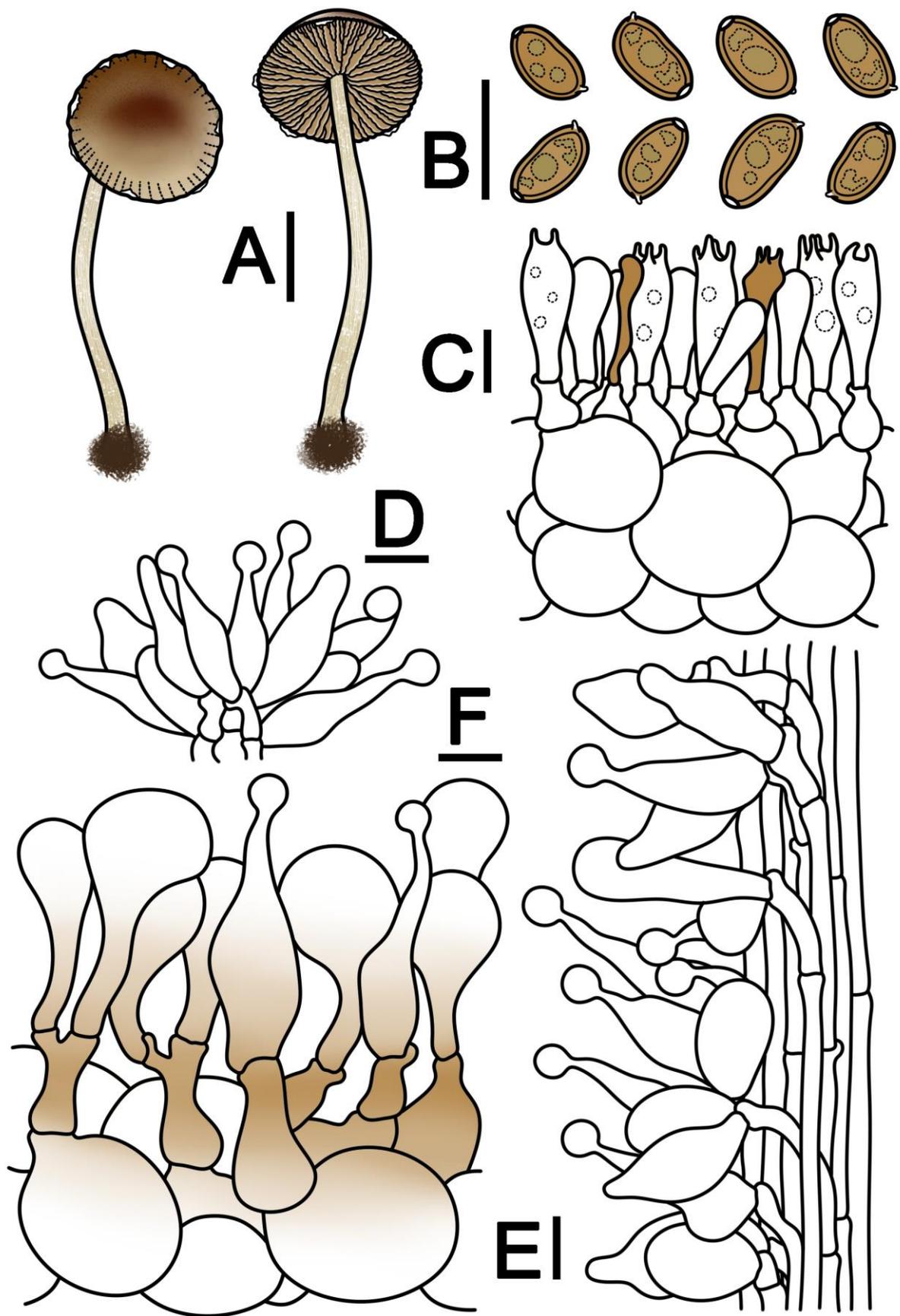


Figure 24 – *Pholiotina liudingshanensis* (HMJAU65053). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipells. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

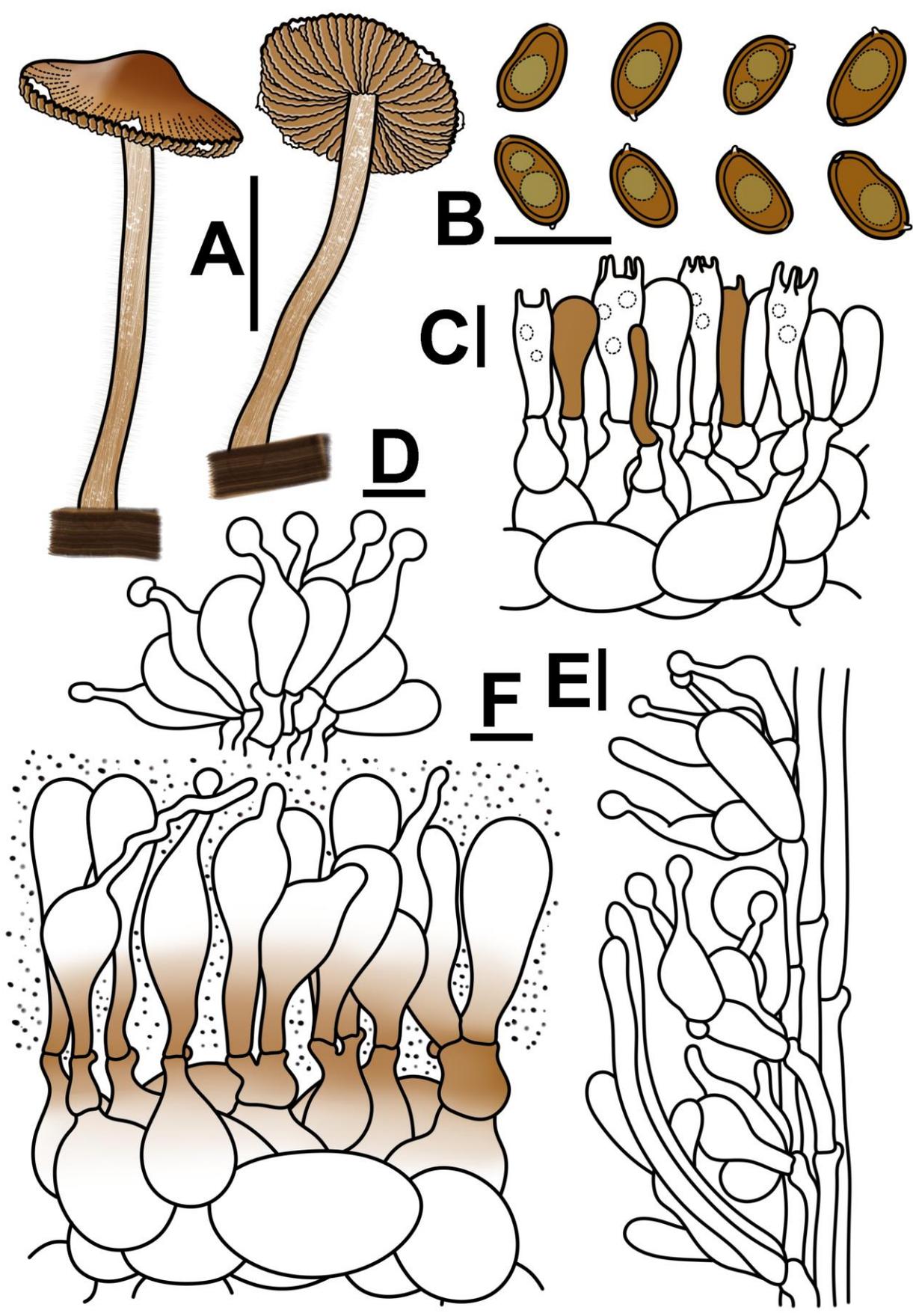


Figure 25 – *Pholiotina bambusicola* (HMJAU65054). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipells. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

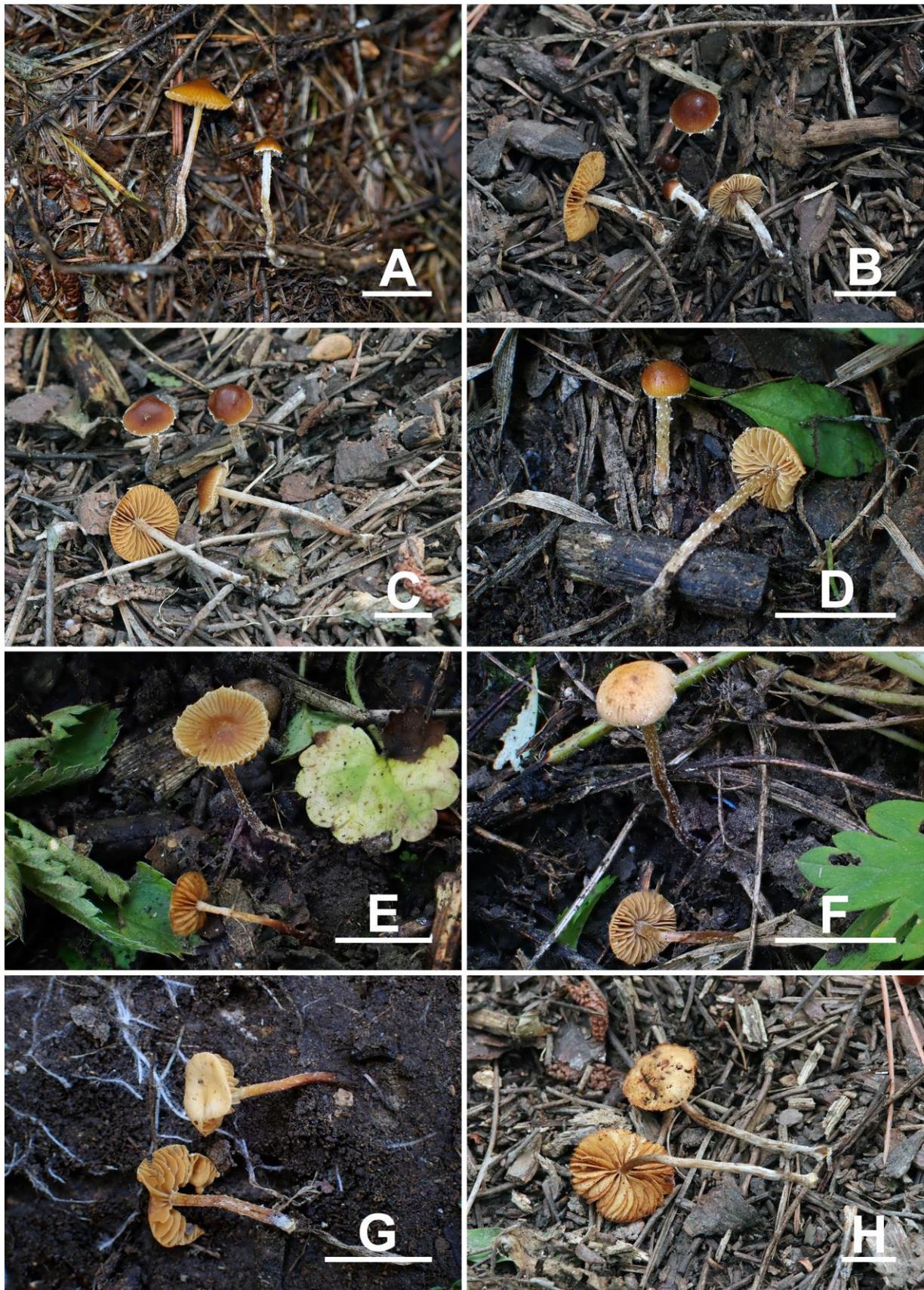


Figure 26 – Basidiomata of *P.* sect. *Intermediae* species. A *P. longicystidiata* (HMJAU65057). B *P. longicystidiata* (HMJAU65059). C *P. longicystidiata* (HMJAU65060). D *P. longicystidiata* (HMJAU65068). E *P. longicystidiata* (HMJAU65065). F *P. longicystidiata* (HMJAU65062). G *P. longicystidiata* (HMJAU65068). H *P. longicystidiata* (HMJAU65061). Scale bars = 1 cm. These pictures are copyright of the collectors of specimens.

Etymology – “*longicystidiata*” refers to having elongated cheilocystidia.

Type – China, Changchun City, Jingyuetan National Forest Park, August 24, 2022, 125°28'21"E, 43°47'30"N, alt. 290 m, H. B. Song, S22082412 (HMJAU65060, holotype).

Basidioma small. Pileus diameter 0.5–2 cm, initially parabolic to hemispherical, later obtusely conical, slightly campanulate to convex, subumbonate, center pastel yellow (RAL1034), pastel orange (RAL2003), copper brown (RAL8004) to chestnut brown (RAL8015), margin beige (RAL1001), signal yellow (RAL1003), copper brown (RAL8004) to ochre brown (RAL8001). Pileus hygrophorous, surface smooth, margin striated. Veil remains at the edge of the pileus, gradually disappearing. Context thin, beige (RAL1001) to ochre brown (RAL8001), no distinctive odor. Lamellae adnexed to narrowly adnate, ventricose, slightly crowded, unequal length, sand yellow (RAL1002), ochre brown (RAL8001) to orange brown (RAL8023), margin serrulate. Stipe length 1–4.5 cm, thick 1.0–2.0 mm, cylindrical, base swollen bulbous, stipe maize yellow (RAL1006), ochre brown (RAL8001), copper brown (RAL8004) to chestnut brown (RAL8015), covered with pruinose and short pubescence, longitudinally fibrous striated.

Basidiospores (60/3/3) (6.9–)7.3–8.6(–9.3) × (4.1–)4.3–5.1(–5.4) μm, Q = (1.51–)1.59–1.84(–1.92), Qm = 1.71(± 0.07), slightly ellipsoid, oblong, reniform to phaseoliform, thick walls, containing oil droplets, germ pore less than 1 μm, some germ pore indistinct or absent, basidiospores in KOH solution ochre brown (RAL8001) to copper brown (RAL8004). Basidia (15–)16–25(–26) × (7–)8–10 μm, clavate, 4(2)-spored, sterigmata long 2–7 μm, basidia with vacuolar contents. Cheilocystidia (24–)25–43(–45) × (6–)7–11(–12) μm, lecythiform, with 3–6 μm wide capitula, lamellae edge sterile. Pleurocystidia absent. Caulocystidia lecythiform, spheropedunculate, clavate, predominantly lecythiform, (21–)23–39(–40) × (6–)7–9(–10) μm, with 4–7 μm wide capitula, non-lecythiform elements (14–)15–27(–28) × 7–10(–11) μm. Pileipellis hymeniform, composed of clavate and spheropedunculate elements (23–)24–63(–65) × 13–20(–23) μm, base exhibiting brown-red (RAL3011) pigment in KOH solution. Pileocystidia 32–50 × 9–13, lecythiform, with 4–8 μm wide capitula. Gelatinous layer present. Pileus residual veil composed of irregular lecythiform to lecythiform elements, arranged in a string-like to chain-like pattern. All structures have clamp connections. Weakly positive reaction to ammonia, forming rhomboid crystals.

Habitat – Summer and autumn growing in the litter layer of mixed forests, on decaying wood.

Known distribution – Northeast China.

Additional specimens measured – China, Jilin Province, Changchun City, Jingyuetan National Forest Park, August 10, 2021, 125°27'18"E, 43°47'28"N, alt. 312 m, X. Wang, WX2181011 (HMJAU65056). Changchun City, Jingyuetan National Forest Park, August 16, 2022, 125°27'38"E, 43°47'45"N, alt. 288 m, L. Y. Zhu, Z22081604 (HMJAU65057), Z22081608 (HMJAU65058). Changchun City, Jingyuetan National Forest Park, August 24, 2022, 125°28'21"E, 43°47'30"N, alt. 290 m, H. B. Song, S22082411 (HMJAU65059), S22082413 (HMJAU65061). Siping City, Yitong Manchu Autonomous County, September 6, 2023, 125°12'17"E, 43°37'26"N, alt. 206 m, H. B. Song, S23090602 (HMJAU65062), S23090603 (HMJAU65063), S23090604 (HMJAU65064). Siping City, Yitong Manchu Autonomous County, September 7, 2023, 125°12'12"E, 43°36'2"N, alt. 277 m, H. B. Song, S23090712 (HMJAU65065), S23090713 (HMJAU65066), S23090714 (HMJAU65067), S23090715 (HMJAU65068), S23090716 (HMJAU65069).

Notes – *Pholiotina longicystidiata* has longer cheilocystidia, with lengths reaching over 40 μm. In *P. sect. Intermediae*, both *P. communis* and *P. bispora* can also have cheilocystidia lengths of up to 40 μm, making them easily confused. The difference between *P. longicystidiata* and *P. communis* is that *P. communis* has distinct basidiospore germ pore. The difference between *P. longicystidiata* and *P. bispora* is that *P. bispora* is 2-spored, making it easy to distinguish. *P. longicystidiata* is closely related to *Pholiotina* sp.3, but *Pholiotina* sp.3 has rare or absent pileocystidia, making it easy to differentiate.

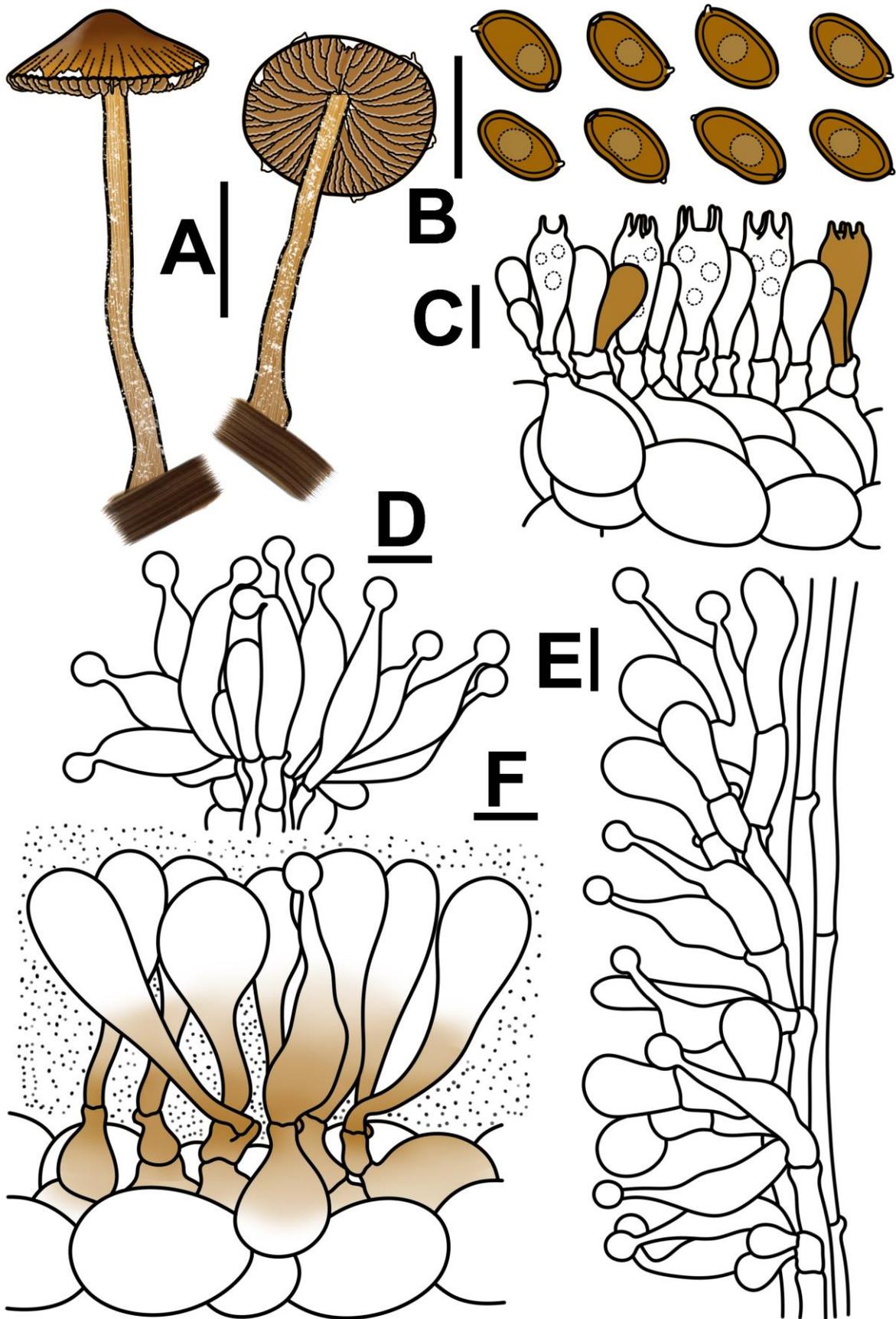


Figure 27 – *Pholiotina longicystidiata* (HMJAU65060). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipells. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

Pholiotina bispora T. Bau & H. B. Song, sp. nov.

Figs 28A–B, 29

Mycobank number: MB851660; Facesoffungi number: FoF15339

Etymology – “*bispora*” refers to basidia that are 2-spored.

Type – China, Jilin Province, Jilin City, Jiaohe City, Qianjin Forest Farm, 25 August 2023, 127°42'42"E, 43°57'39"N, alt. 658 m, H. Cheng, C2382506 (HMJAU65072, holotype).

Basidioma small. Pileus diameter 0.5–2 cm, broadly conical, plano-convex, subumbonate, center copper brown (RAL8004), red brown (RAL8012), margin pastel yellow (RAL1034) to ochre brown (RAL8001). Pileus hygrophorous, slightly viscous, surface smooth, with distinct striations, initial veil remains at the edge of the pileus, gradually disappearing. Context thin, beige (RAL1001) to sand yellow (RAL1002), no distinctive odor. Lamellae adnexed to narrowly adnate, ventricose, slightly crowded, unequal length, ivory (RAL1014), pastel yellow (RAL1034) to ochre brown (RAL8001), margin serrulate. Stipe length 1.5–4 cm, thick 1.0–2.0 mm, cylindrical, base slightly swollen, initially light ivory (RAL1015), sand yellow (RAL1002), later nut brown (RAL8011) to mahogany brown (RAL8016), slightly pruinose and pubescent, longitudinally fibrous striated.

Basidiospores (60/3/3) (8–)8.9–10.7(–11.3) × (4.4–)4.9–5.6(–5.8) μm, Q = (1.67–)1.69–2.04(–2.09), Qm = 1.87(± 0.10), oblong to subcylindrical, reniform to phaseoliform, thick walls, containing oil droplets, germ pore diameter less than 1 μm, some germ pore indistinct, basidiospores in KOH solution ochre brown (RAL8001) to copper brown (RAL8004). Basidia (16–)17–22(–23) × (6–)7–9 μm, clavate, 2-spored, sterigmata long 2–5 μm, basidia with vacuolar contents. Cheilocystidia 21–39(–41) × 5–10(–11) μm, lecythiform, with 3–6 μm wide capitula, mixed with spheropedunculate elements, lamellae edge sterile. Pleurocystidia absent. Caulocystidia (15–)16–43(–45) × (7–)8–12(–14) μm, lecythiform, irregular lecythiform, clavate, spheropedunculate, predominantly lecythiform, with 4–7 μm wide capitula. Pileipellis hymeniform, composed of clavate and spheropedunculate elements (17–)18–54(–58) × 10–18(–20) μm, base exhibiting brown red (RAL3011) pigment in KOH solution. Pileocystidia (30–)35–50(–52) × 7–13(–15), lecythiform, with 3–7 μm wide capitula. Thin gelatinous layer. Pileus residual veil composed of irregular lecythiform to lecythiform elements, arranged in a string-like to chain-like pattern. All structures have clamp connections. Negative reaction to ammonia.

Habitat – In summer, it grows singly or in clusters in the humus layer of broad-leaved forests.

Known distribution – Northeast China.

Additional specimens measured – China, Jilin Province, Tonghua City, Liuhe County, Sanxianjia National Forest Park, 12 August 2022, 125°51'37"E, 42°16'30"N, alt. 672 m, X. Wang, WX227 (HMJAU65070). China, Jilin Province, Tonghua City, Liuhe County, Sanxianjia National Forest Park, 12 August 2022, 125°51'37"E, 42°16'30"N, alt. 658 m, F. Guo, gf22812192 (HMJAU65071).

Notes – *Pholiotina bispora* in *Pholiotina* section *Intermediae* is often mistaken for species with 2-spored basidia. Another species in *P.* sect. *Intermediae*, *P. pseudoampullaceocystis*, also possesses 2-spored basidia (Karich 2020). However, the distinguishing feature between *P. bispora* and *P. pseudoampullaceocystis* is the presence of lageniform and nettle hair-shaped elements in the cheilocystidia of *P. pseudoampullaceocystis*. *P. bispora* is closely related to *P. micropora*, but unlike *P. bispora*, *P. micropora* has 4(2)-spored basidia, making it easily distinguishable.

Pholiotina micropora T. Bau & H. B. Song, sp. nov.

Figs 28C–H, 30

Mycobank number: MB851661; Facesoffungi number: FoF15340

Etymology – “*micropora*” refers to basidiospores with a germ pore diameter small, with some germ pore being indistinct or absent.

Type – China, Jilin Province, Songyuan City, Fuyu City, Songhuajiang Village, 27 August 2023, 125°15'22"E, 45°8'13"N, alt. 186 m, H. B. Song, S23082719 (HMJAU65080, holotype).

Basidioma small, pileus diameter 0.3–1 cm, initially paraboloid to hemispherical, later convex, plano-convex with an umbo, center signal brown (RAL8002) to chestnut brown (RAL8015), ochre brown (RAL8001) to orange brown (RAL8023), margin pastel yellow (RAL1034) to ochre brown

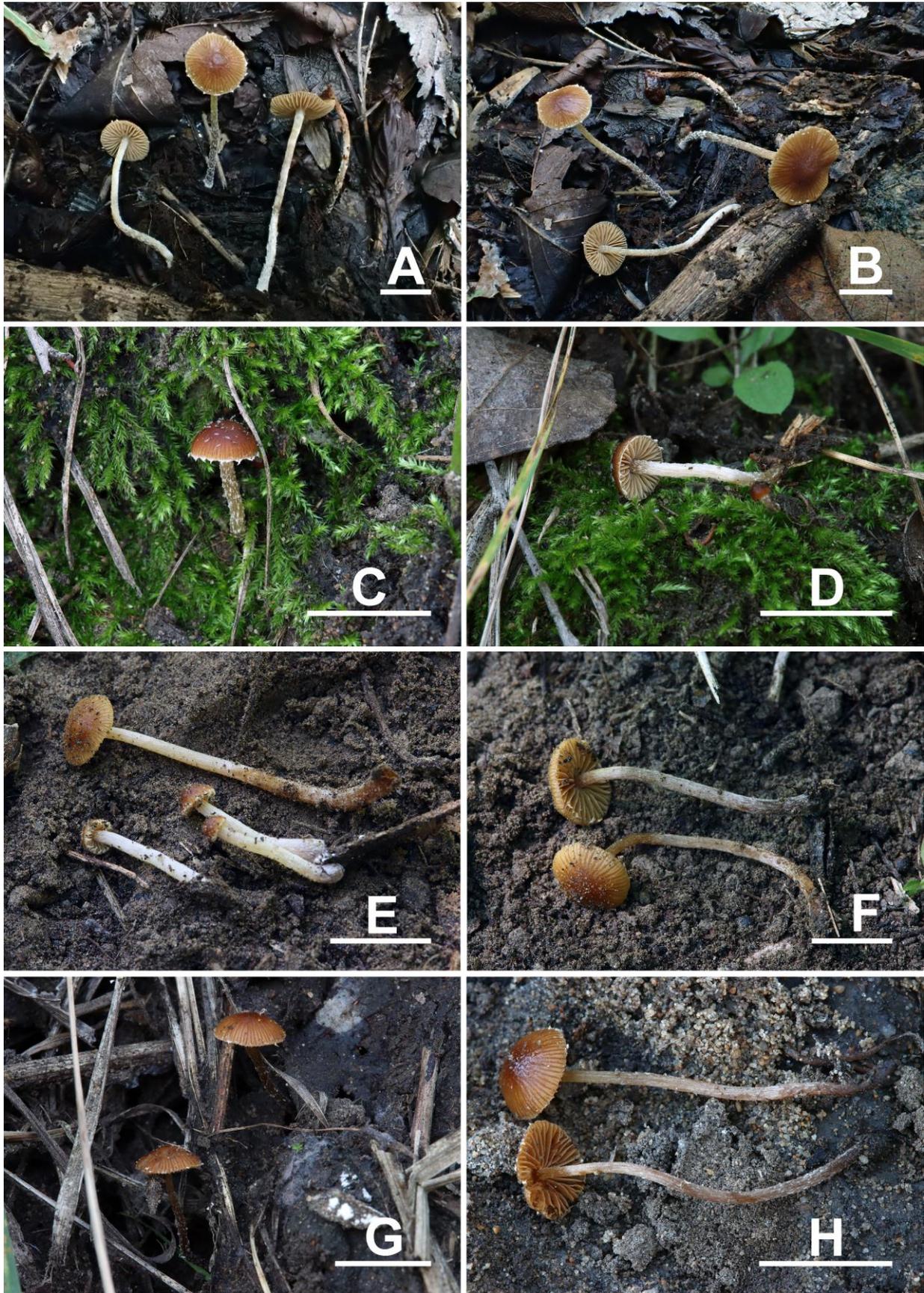


Figure 28 – Basidiomata of *P.* sect. *Intermediae* species. A, B *P. bispora* (HMJAU65072). C, D *P. micropora* (HMJAU65081). E *P. micropora* (HMJAU65077). F *P. micropora* (HMJAU65076). G, H *P. micropora* (HMJAU65080). Scale bars = 1 cm. These pictures are copyright of the collectors of specimens.

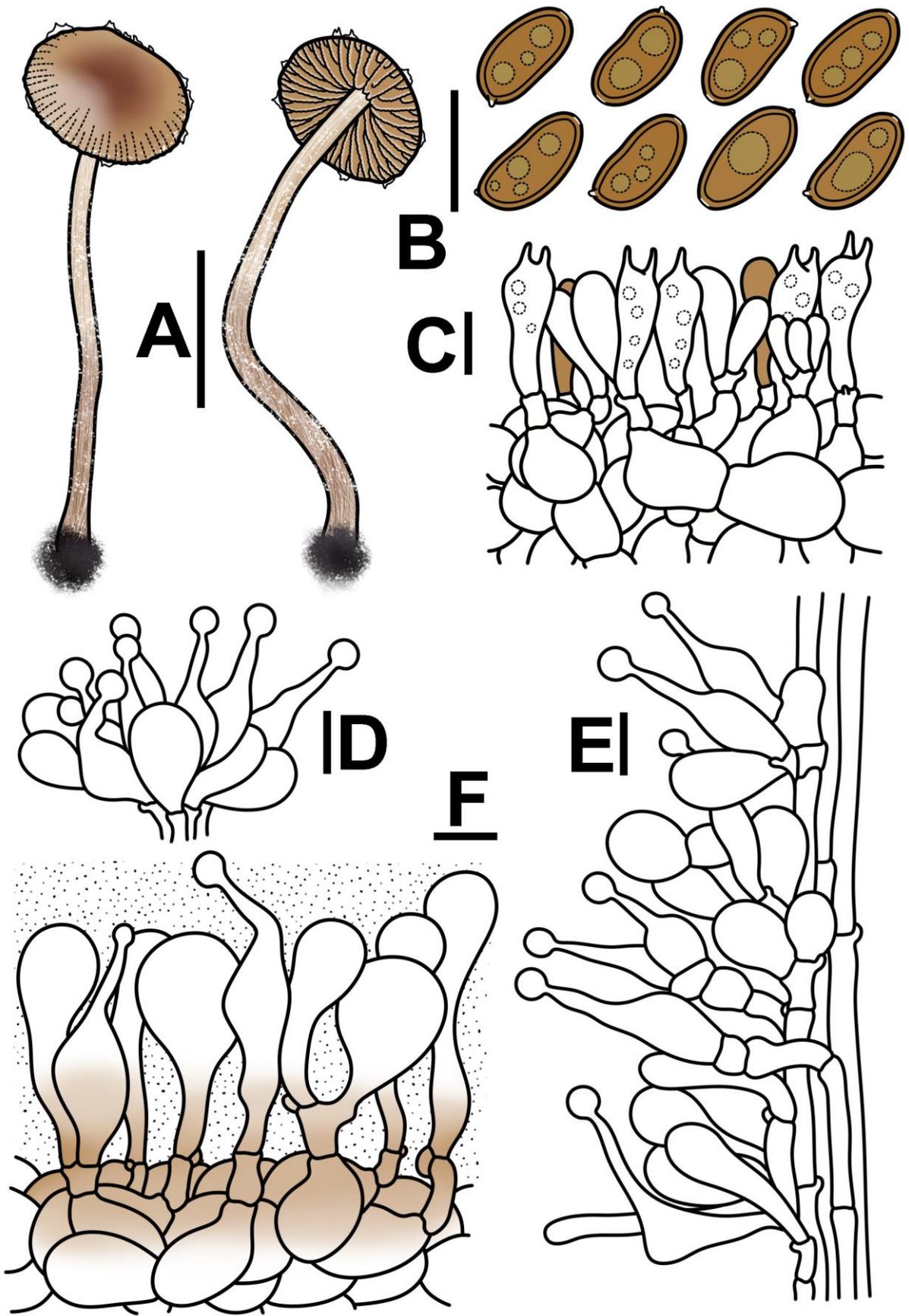


Figure 29 – *Pholiotina bispora* (HMJAU65072). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipells. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

(RAL8001). Pileus hygrophanous, viscid, with a smooth surface and distinct striations. Veil remains at the edge of the pileus and gradually disappears. Context is thin, beige (RAL1001) to sand yellow (RAL1002), without distinctive odor. Lamellae adnexed to narrowly adnate, ventricose, slightly loosely, unequal length, ivory (RAL1014) to ochre brown (RAL8001), clay brown (RAL8003), with a serrulate margin. Stipe 1.5–4 cm long, thick 1.0–2.0 mm, cylindrical, with a slightly swollen base, light ivory (RAL1015) or honey yellow (RAL1005), later transitioning to clay brown (RAL8003) to chestnut brown (RAL8015), slightly pruinose and with short pubescence, longitudinally fibrous striated.

Basidiospores (60/3/3) (7–)7.1–8.6(–8.8) × 4.4–5(–5.2) μm, Q = (1.42–)1.52–1.76(–1.86), Qm = 1.62 (± 0.08), ellipsoid to oblong, reniform to phaseoliform, thick walls, containing oil droplets, germ pore diameter smaller than 1 μm, some germ pore indistinct or absent, basidiospores in KOH solution ochre brown (RAL8001) to copper brown (RAL8004). Basidia (14–)15–25(–28) × (6–)7–10 μm, clavate, 4(2)-spored, sterigmata long 3–7 μm, basidia with vacuolar contents. Cheilocystidia 21–30(–33) × 7–12(–13) μm, lecythiform, with 2–7 μm wide capitula, mixed with spheropedunculate elements, lamellae edge sterile. Pleurocystidia absent. Caulocystidia 15–45(–47) × (7–)8–12(–14) μm, lecythiform, clavate, spheropedunculate, predominantly lecythiform, with 3–7 μm wide capitula. Pileipellis hymeniform, composed of clavate and spheropedunculate elements (22–)23–44(–47) × (10–)11–19 μm, arranged in KOH solution, showing a brown red (RAL3011) pigment at the base. Pileocystidia (32–)33–46 × 9–14, lecythiform, with 3–7 μm wide capitula. Thin gelatinous layer. Pileus residual veil composed of irregular lecythiform to lecythiform elements, arranged in a string-like to chain-like pattern. All structures exhibit clamp connections. Negative reaction with ammonia solution.

Habitat – It grows singly or in clusters on decaying wood in broad-leaved forests during summer.

Known distribution – Northeast China.

Additional specimens measured – China, Jilin Province, Changchun City, Jingyuetan National Forest Park, 12 August 2022, 125°28'34"E, 43°47'18"N, alt. 257 m, H. B. Song, Z22081211S (HMJAU65073); Jilin City, Longtan Mountain Park, 14 August 2022, 126°36'25"E, 43°52'58"N, alt. 277 m, S. Y. Li, L68 (HMJAU65074); Songyuan City, Qian Gorlos Mongol Autonomous County, Hada Mountain, 27 August 2023, 121°54'56"E, 45°37'31"N, alt. 259 m, H. B. Song, S23082707 (HMJAU65075), S23082708 (HMJAU65076), S23082709 (HMJAU65077), S23082710 (HMJAU65078); Songyuan City, Fuyu City, Bailing Village, 27 August 2023, 125°7'51"E, 45°9'19"N, alt. 180 m, T. Bau & H. B. Song, S23082715 (HMJAU65079); Songyuan City, Fuyu City, Songhuajiang Village, 27 August 2023, 125°15'22"E, 45°8'13"N, alt. 186 m, H. B. Song, S23082720 (HMJAU65081).

Notes – Species within *Pholiotina* section *Intermediae* that possess lecythiform pileocystidia can be easily confused with *Pholiotina micropora*. However, *P. micropora* can be distinguished from *P. communis* by the presence of a distinct germ pore in *P. communis* basidiospores. Another species, *P. liudingshanensis*, can be differentiated from *P. micropora* by the presence of a mixture of utriform and lageniform elements in its cheilocystidia. Furthermore, *P. micropora* differs from *P. longicystidiata* in that the cheilocystidia of *P. longicystidiata* are longer. Additionally, *P. bispora* can be distinguished from *P. micropora* by having 2-spored basidia. *P. brevipila* is characterized by a velutinous pileus and caulocystidia containing a mixture of lageniform and fusiform elements, which sets it apart from *P. micropora*. Unlike *P. micropora*, *P. horchinensis* lacks a germ pore in its basidiospores. While *P. micropora* and *Pholiotina* sp.3 are closely related on the phylogenetic tree, the absence or rarity of pileocystidia in *Pholiotina* sp.3 allows for easy differentiation. The lecythiform cheilocystidia of *P. micropora* occasionally exhibit a short nettle hair-shaped structure, resembling basidia with a single sterigmata or incompletely developed cheilocystidia with a ball-like apex. However, this structure is considered a remnant or a result of breakage and is not considered a defining characteristic for the classification of *P. micropora*.

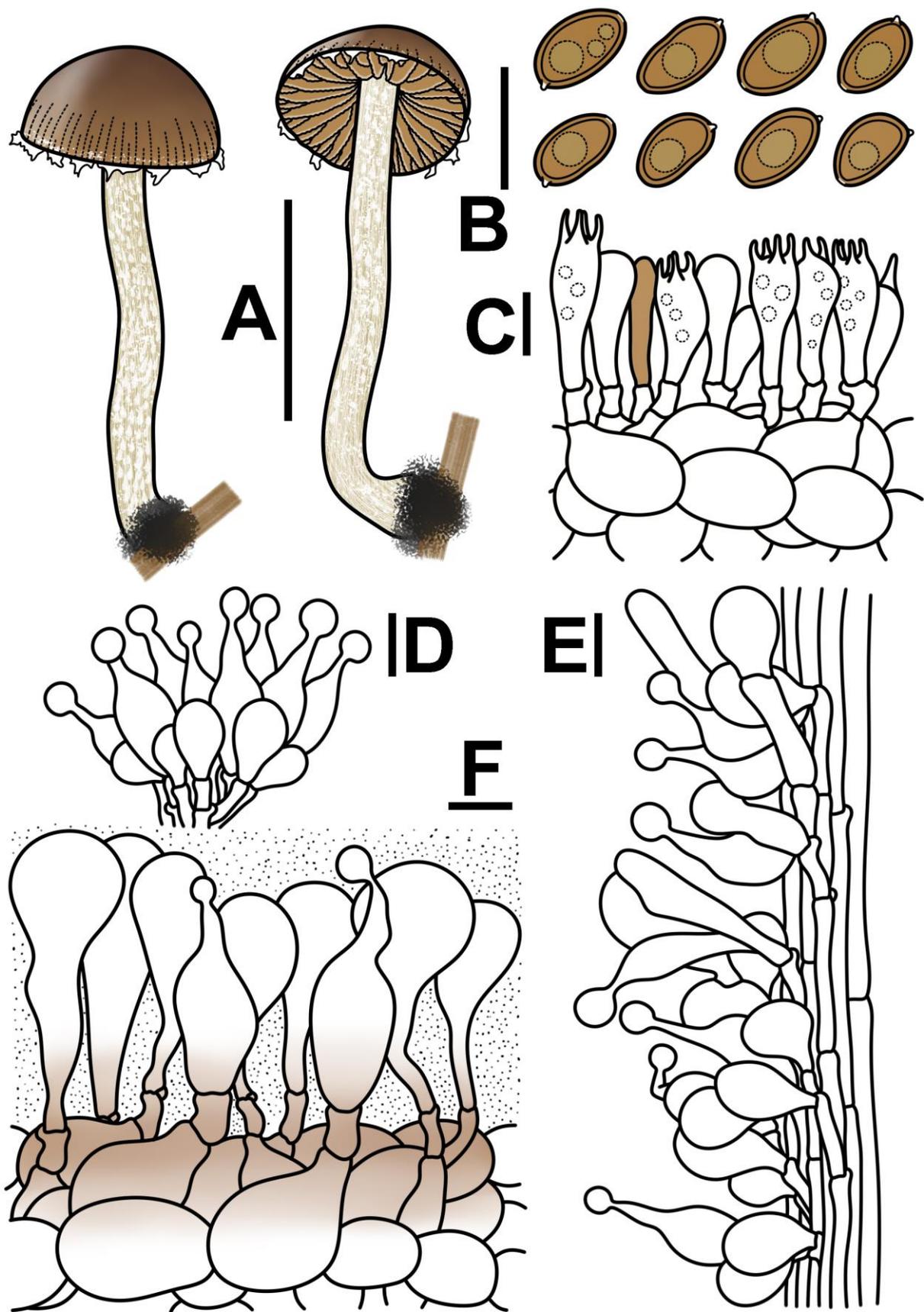


Figure 30 – *Pholiotina micropora* (HMJAU65080, HMJAU65081). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipellis. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

Pholiotina brevipila T. Bau & H. B. Song, sp. nov.

Figs 31A–H, 32

Mycobank number: MB851662; Facesoffungi number: FoF15341

Etymology – “*brevipila*” refers to the pileus having short hairs.

Type – China, Jilin Province: Changchun City, Nanhu Park, 17 August 2022, 125°17'56"E, 43°51'22"N, alt. 218 m, L. Y. Zhu, Z22081704 (HMJAU65082, holotype).

Basidioma very small. Pileus diameter 0.2–1.2 cm, initially paraboloid to hemispherical, obtusely conical, later convex, applanate, subumbonate, initially ivory (RAL1014), orange brown (RAL8023), later red brown (RAL8012) to chestnut brown (RAL8015), with a pastel yellow (RAL1034) to ochre brown (RAL8001) margin. Pileus hygrophanous, surface smooth, with striate on the edge when moist, covered with short pubescence, initially veil remnants present on the pileus edge, gradually disappearing later. Context thin, beige (RAL1001) to sandy yellow (RAL1002), without distinctive odor. Lamellae adnexed to narrowly adnate, ventricose, loosely, unequal length, sandy yellow (RAL1002), ochre brown (RAL8001), serrulate margin. Stipe 1–3 cm long, 1.0–2.0 mm thick, cylindrical, slightly swollen at the base, upper part of the stipe light ivory (RAL1015), sandy yellow (RAL1002) to ochre brown (RAL8001), lower part red brown (RAL8012) to chestnut brown (RAL8015), slightly pruinose and covered with short pubescence, longitudinally fibrous-striated.

Basidiospores (60/3/3) (6.8–)7.1–8.8 × (4.1–)4.2–5(–5.2) μm, Q = (1.51–)1.57–1.84(–1.92), Qm = 1.7(± 0.08), slightly ellipsoid, oblong, reniform to phaseoliform, thick walls, containing oil droplets, germ pore diameter less than 1 μm, some germ pore indistinct or absent, basidiospores turn ochre brown (RAL8001) to copper brown (RAL8004) in KOH solution. Basidia (17–)18–25(–26) × 6–9 μm, clavate, 4(2)-spored, sterigmata elongated 2–7 μm, basidia with vacuolar contents. Cheilocystidia (22–)23–30(–33) × 7–11 μm, lecythiform, with capitula 3–7 μm wide, containing spheropedunculate elements, reaching up to 20 × 15 μm, lamellae edge sterile. Pleurocystidia absent. Caulocystidia lageniform, fusiform, clavate, predominantly lecythiform and spheropedunculate, lecythiform elements (27–)28–37(–40) × 5–13 μm, with capitula 4–7 μm wide, spheropedunculate elements (17–)18–42(–51) × (8–)10–18(–23) μm. Pileipellis hymeniform, composed of clavate and spheropedunculate elements (21–)23–43(–45) × 11–18(–20) μm, with brown red (RAL3011) pigment at the base in KOH. Pileocystidia (29–)30–55(–58) × (7–)10–14(–15), lecythiform, with capitula 4–6 μm wide. Gelatinous layer indistinct or absent. Pileus residual veil composed of irregular lecythiform to lecythiform elements, arranged in a string-like to chain-like pattern. All structures have clamp connections. Weak positive reaction with ammonia, forming diamond-shaped crystals.

Habitat – In summer and autumn, it is solitary or scattered in the humus layer and decaying wood of broad-leaved forests.

Known distribution – Northeast China.

Additional specimens measured – China, Jilin Province: Changchun City, Nanhu Park, 17 August 2022, 125°17'56"E, 43°51'22"N, alt. 218 m, L. Y. Zhu, Z22081706 (HMJAU65083), Z22081707 (HMJAU65084), Z22081716 (HMJAU65085). Changchun City, Jingyuetan National Forest Park, 18 August 2022, 125°26'58"E, 43°47'36"N, alt. 224 m, H. B. Song, S22081806 (HMJAU65086), S22081807 (HMJAU65087). Siping City, Yitong Manchu Autonomous County, 7 September 2023, 125°12'12"E, 43°35'58"N, alt. 283 m, H. B. Song, S23090705 (HMJAU65088), S23090706 (HMJAU65089), S23090707 (HMJAU65090), S23090708 (HMJAU65091); Jilin City, Jiaohe City, 25 August 2023, 127°41'54"E, 43°57'2"N, alt. 444 m, X. Wang & M. Liu, W23082501 (HMJAU65092), W23082513 (HMJAU65093), LM230845 (HMJAU65094). Inner Mongolia, Tongliao City, 6 September 2023, 122°15'20"E, 43°37'53"N, alt. 174 m, S. E. Wang, E2309424 (HMJAU65095), E2309425 (HMJAU65096).

Notes – *Pholiotina brevipila* can be easily confused with species in *Pholiotina* section *Intermediae* that have caulocystidia mixed with lageniform elements. The difference between *P. brevipila* and *P. communis* is that *P. communis* has distinct germ pore. Additionally, *P. rostrellulata* can be differentiated from *P. brevipila* by the presence of beak-like elements

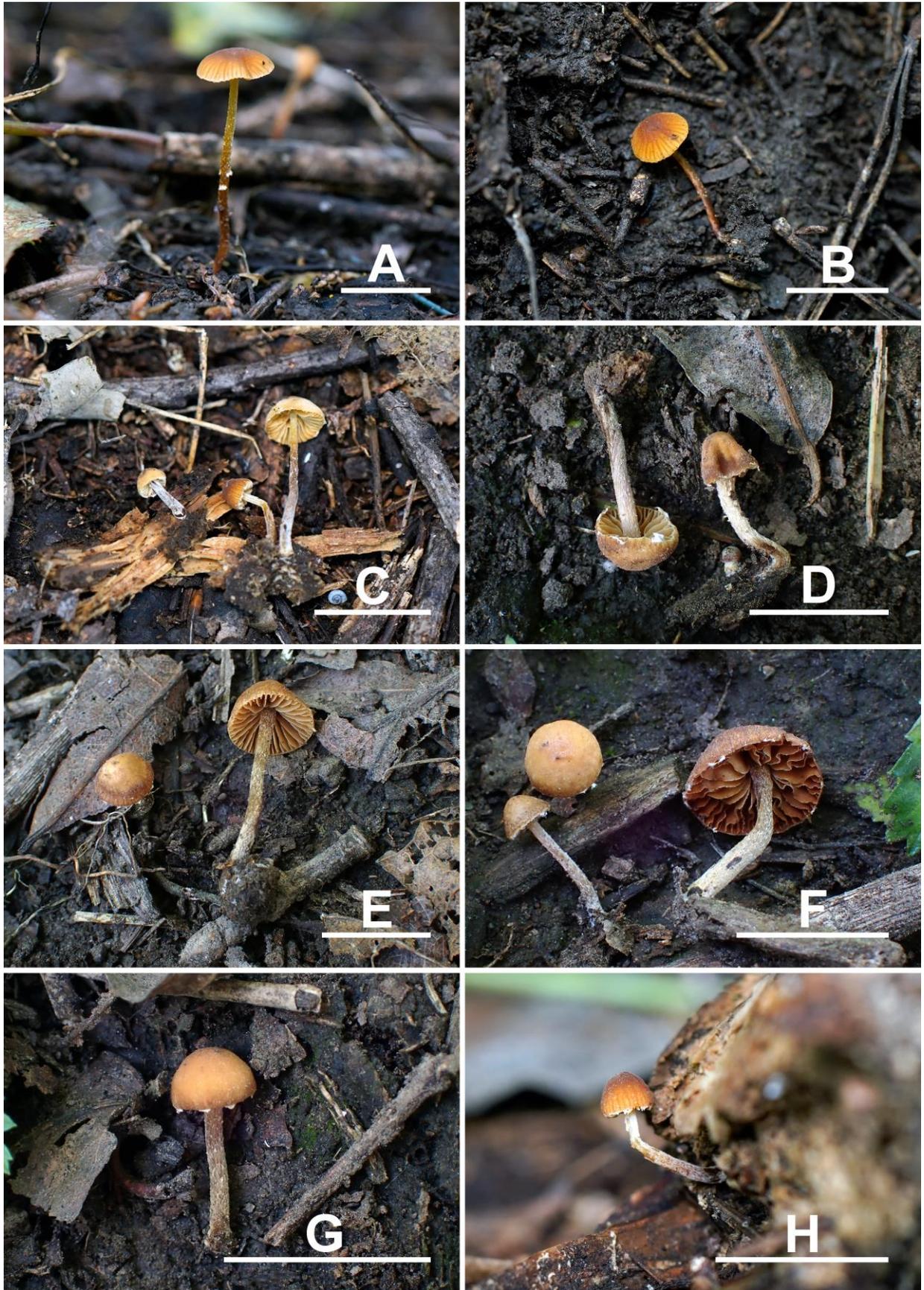


Figure 31 – Basidiomata of *P.* sect. *Intermediae* species. A *P. brevipila* (HMJAU65082). B *P. brevipila* (HMJAU65085). C *P. brevipila* (HMJAU65084). D *P. brevipila* (HMJAU65088). E *P. brevipila* (HMJAU65089). F, G *P. brevipila* (HMJAU65091). H *P. brevipila* (HMJAU65083). Scale bars = 1 cm. These pictures are copyright of the collectors of specimens.

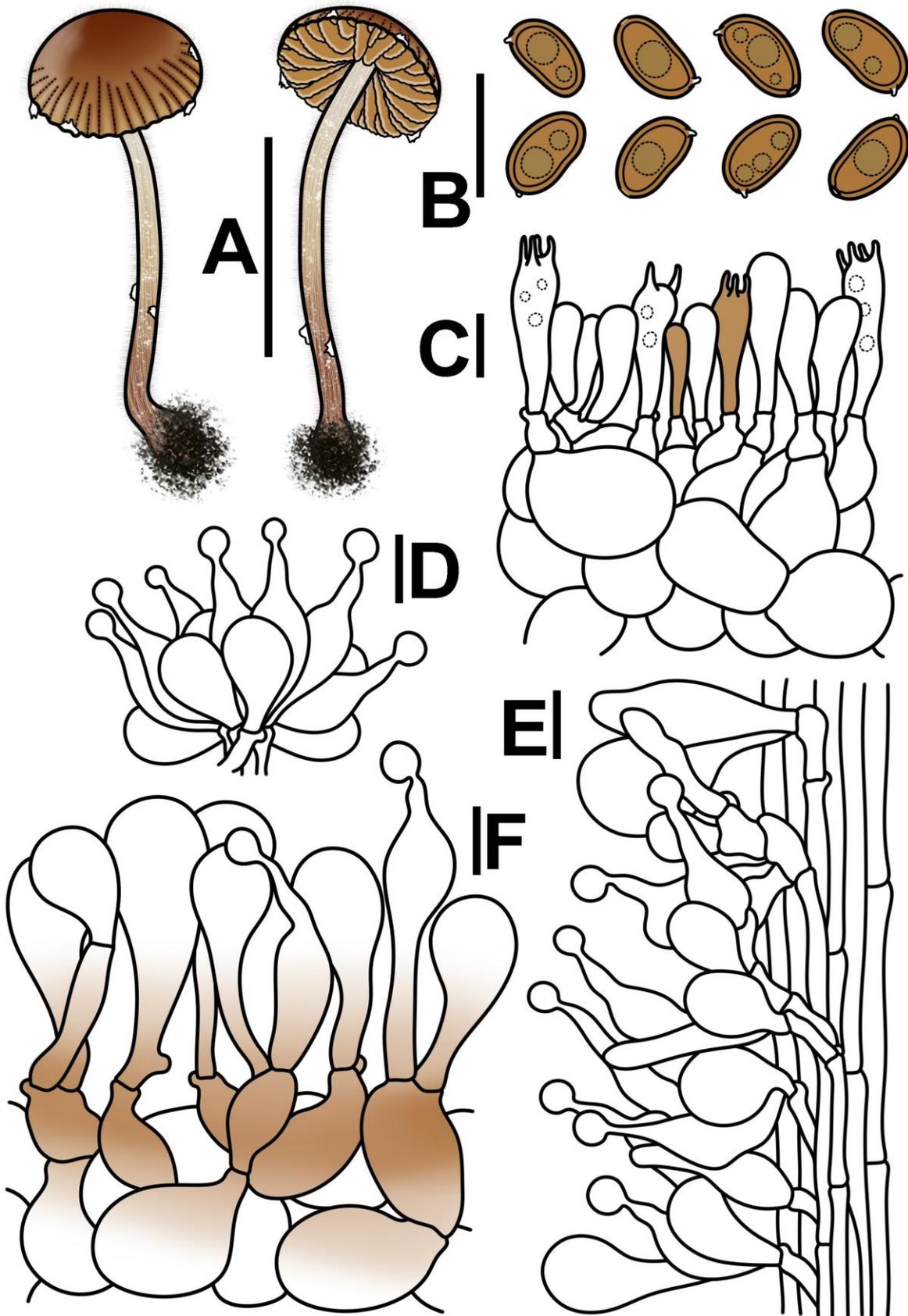


Figure 32 – *Pholiotina brevipila* (HMJAU65082). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipellis. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

in its pileipellis. Furthermore, *P. liudingshanensis* can be distinguished from *P. brevipila* by the presence of utriform and lageniform elements in its cheilocystidia. Similarly, *P. sulciceps* differs from *P. brevipila* in that *P. sulciceps* basidiospores lack germ pore. While *P. brevipila* shares a close relationship with *P. horchinensis*, it is easy to distinguish *P. horchinensis* due to the absence of germ pore in its basidiospores. The cheilocystidia of *P. brevipila* are lecythiform and occasionally exhibit short nettle hair-shaped structures. These structures may resemble basidia with a single sterigmata or incompletely developed cheilocystidia with ball-shaped heads. However, they are considered remnants or results of breakage and should not be considered defining characteristics for the classification of *P. brevipila*.

Pholiotina horchinensis T. Bau & H. B. Song, sp. nov.

Figs 33A–C,34

Mycobank number: MB851663; Facesoffungi number: FoF15342

Etymology – “*horchinensis*” refers to the type specimen originating from Horqin Left Back Banner.

Type – China, Inner Mongolia Autonomous Region, Tongliao City, Horqin Left Back Banner, 23 August 2022, 122°10'1"E, 42°48'5"N, alt. 210 m, T. Bau & L. Y. Zhu, Z22082312 (HMJAU65097, holotype).

Basidioma small. Pileus diameter 1–1.5 cm, hemispherical to obtusely conical, convex, center dahlia yellow (RAL1033), daffodil yellow (RAL1007), edge pastel yellow (RAL1034) to ochre brown (RAL8001), ivory (RAL1014) to beige (RAL1001) after dehydration. Pileus hygrophanous, slightly viscid, surface smooth, edge shallowly striated, initial veil remnants on the edge of pileus, gradually disappearing later. Context thin, beige (RAL1001) to sandy yellow (RAL1002), without specific odor. Lamellae adnexed to narrowly adnate, ventricose, slightly crowded, unequal length, melon yellow (RAL1028) to dahlia yellow (RAL1033), beige (RAL1011), green brown (RAL8000), with serrulate margin. Stipe length 2–4 cm, thick 1.0–2.0 mm, cylindrical, slightly swollen at the base, initially light ivory (RAL1015), daffodil yellow (RAL1007), later ochre brown (RAL8001) to fawn brown (RAL8007), slightly pruinose and pubescent, longitudinally fibrous striated.

Basidiospores (40/2/2) (6.5–)6.7–8.3(–8.5) × (4.2–)4.3–4.8(–5) μm, Q = (1.46–)1.48–1.84(–1.88), Qm = 1.67 (± 0.10), ellipsoid to oblong, reniform to phaseoliform, thick walls, containing oil droplets, lacking germ pore, basidiospores in KOH solution ochre brown (RAL8001) to copper brown (RAL8004). Basidia (16–)18–24(–26) × 7–10 μm, clavate, 4(2)-spored, sterigmata length 3–6 μm, basidia contain vesicular contents. Cheilocystidia 20–36(–37) × (6–)7–10(–11) μm, lecythiform, with capitula 3–6 μm wide, including elements of spheropedunculate, lamellae edge sterile. Pleurocystidia absent. Caulocystidia lecythiform, clavate, spheropedunculate, predominantly lecythiform (18–)20–34(–36) × 7–12 μm, with capitula 2–7 μm wide, spheropedunculate elements (10–)12–23(–25) × 8–15 μm. Pileipellis hymeniform, composed of clavate and spheropedunculate elements (24–)26–52(–56) × 12–22(–26) μm, with brown red (RAL3011) pigment at the base in KOH solution. Pileocystidia lecythiform, reaching a length of up to 60 μm, rarely observed. Thin gelatinous layer. Pileus residual veil composed of irregular lecythiform to lecythiform elements, arranged in a string-like to chain-like pattern. All structures have clamp connections. Weakly positive reaction with ammonia, forming diamond-shaped crystals.

Habitat – Summer, solitary, growing on the litter layer of broad-leaved forests.

Known distribution – Northeast China.

Additional specimens measured – China, Jilin Province, Jiaohe City, 24 August 2023, 127°42'42"E, 43°57'39"N, alt. 412 m, H. Cheng, C2382404 (HMJAU65098).

Notes – *Pholiotina horchinensis* can be easily confused with species in *Pholiotina* section *Intermediae* that have basidiospores without germ pore. The distinction between *P. horchinensis* and *P. pseudoampullaceocystis* lies in the presence of lageniform, nettle hair-shaped elements in the cheilocystidia of *P. pseudoampullaceocystis* (Karich 2020). While *P. horchinensis* and *P. sulciceps* T. Bau & H. B. Song are closely related and share the absence of germ pore in their

basidiospores, they can be differentiated by the presence of lageniform elements in the pileocystidia of *P. sulciceps*. Additionally, *P. horchinensis* is closely related to *P. brevipila*; however, *P. brevipila* can be distinguished by the short pubescence on its pileus.

Pholiotina sulciceps T. Bau & H. B. Song, sp. nov.

Figs 33D–H, 35

Mycobank number: MB851664; Facesoffungi number: FoF15343

Etymology – “*sulciceps*” refers to the pileus having distinct long striations.

Type – China, Jilin Province, Siping City, Yitong Manchu Autonomous County, 7 September 2023, 125°12'13"E, 43°36'27"N, alt. 283 m, L. J. Zhao, S23090717 (HMJAU65100, holotype).

Small-sized basidioma with pileus diameter of 0.5–1 cm, initially broadly conical to obtusely conical, later convex to applanate. Center of the pileus clay brown (RAL8003) to signal brown (RAL8002), slightly oxide red (RAL3009), while the margin pastel yellow (RAL1034) to ochre brown (RAL8001). Pileus hygrophanous, slightly viscid, with a smooth surface, exhibiting striated patterns from the margin to the center. Veil flocculose, remaining on the pileus margin and gradually disappearing. Context thin, same color as the pileus, without distinct odor. Lamellae adnexed to narrowly adnate, ventricose, loosely, unequal length, pastel yellow (RAL1034) to ochre brown (RAL8001), with serrulate edges. Stipe is 1.5–2.5 cm long and 0.5–1.5 mm thick, cylindrical, subbulbous at the base, stipe light ivory (RAL1015) to ivory (RAL1014), sandy yellow (RAL1002), and close to maize yellow (RAL1001), covered slight pruinose and short pubescence, with longitudinally fibrous striations.

Basidiospores (60/3/2) (6.5–)7–8.6(–9) × (3.9–)4.1–5.1(–5.3) μm, Q = (1.44–)1.51–1.80(–1.89), Qm = 1.65(± 0.09), ellipsoid to oblong, reniform to phaseoliform, thick walls, containing oil droplets, lacking germ pore, basidiospores in KOH solution ochre brown (RAL8001) to copper brown (RAL8004). Basidia (14–)15–25 × 6–9 μm, clavate, 4-spored, Sterigmata length 2–6 μm, basidia contain vacuolar contents. Cheilocystidia (21–)23–32(–33) × 7–10 μm, lecythiform, with capitula 3–6 μm wide, including elements of spheropedunculate, lamellae edge sterile. Pleurocystidia absent. Caulocystidia (18–)20–40(–44) × 6–11(–13) μm, lecythiform, lageniform, clavate, subcylindrical, spheropedunculate, fusiform, predominantly lecythiform, with capitula 5–8 μm wide, including cylindrical elements reaching a length of up to 60 μm. Pileipellis hymeniform, composed of clavate and spheropedunculate elements (17–)20–48(–50) × (9–)10–27(–28) μm, with brown red (RAL3011) pigment at the base in KOH solution. Pileocystidia (21–)25–55(–60) × 8–13 μm, lageniform, lecythiform, with capitula 5–8 μm wide. Thin gelatinous layer. Pileus residual veil composed of irregular lecythiform to lecythiform elements, arranged in a string-like to chain-like pattern. All structures have clamp connections. Weakly positive reaction with ammonia, forming diamond-shaped crystals.

Habitat – In autumn, solitary or scattered, growing on the litter layer of broad-leaved forests.

Known distribution – Northeast China.

Additional specimens measured – China, Jilin Province, Siping City, Yitong Manchu Autonomous County, 7 September 2023, 125°12'12"E, 43°35'57"N, alt. 290 m, S. Z. Song, S23090711 (HMJAU65099).

Notes – *Pholiotina sulciceps* can be easily confused with species in *Pholiotina* section *Intermediae* that have basidiospores without germ pore (Hausknecht 2009, Karich 2020). The distinction between *P. sulciceps* and *P. pseudoampullaceocystis* lies in the presence of lageniform and nettle hair-shaped elements in the cheilocystidia of *P. pseudoampullaceocystis*. Additionally, *P. sulciceps* shares a close relationship with *P. horchinensis*; however, *P. horchinensis* can be distinguished by having pileocystidia that are all lecythiform. Similarly, *P. sulciceps* is closely related to *P. brevipila*; however, *P. brevipila* can be differentiated by the presence of a short pubescence on the pileus and basidiospores with germ pore.

Pholiotina changbaishanensis T. Bau & H. B. Song, sp. nov.

Figs 36A–B, 37

Mycobank number: MB851665; Facesoffungi number: FoF15344

Etymology – “*Changbaishanensis*” refers to the type specimen discovered in Changbaishan.

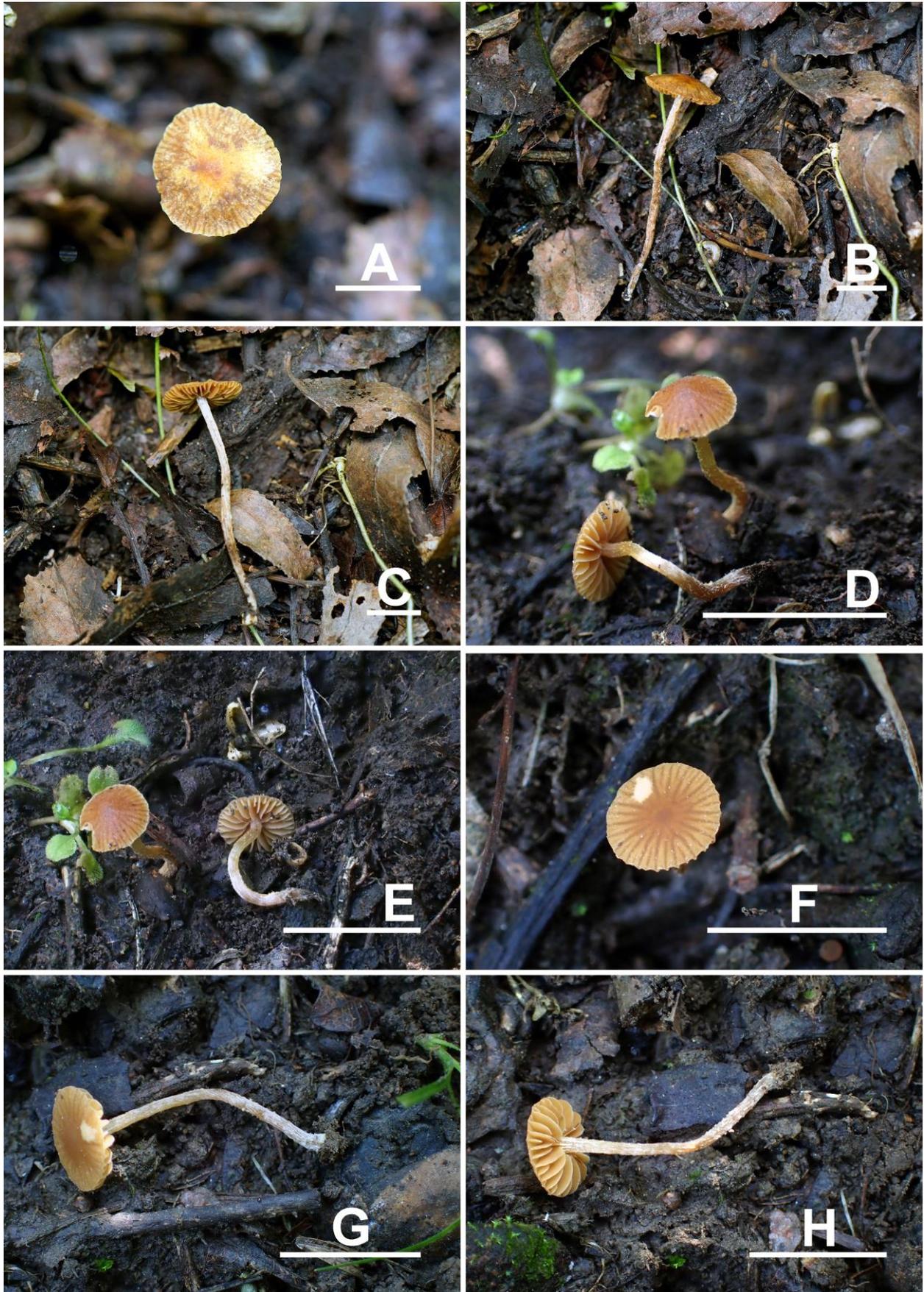


Figure 33 – Basidiomata of *P.* sect. *Intermediae* species. A, B, C *P. horchinensis* (HMJAU65101). D, E *P. sulciceps* (HMJAU65100). F, G, H *P. sulciceps* (HMJAU65099). Scale bars = 1 cm. These pictures are copyright of the collectors of specimens.

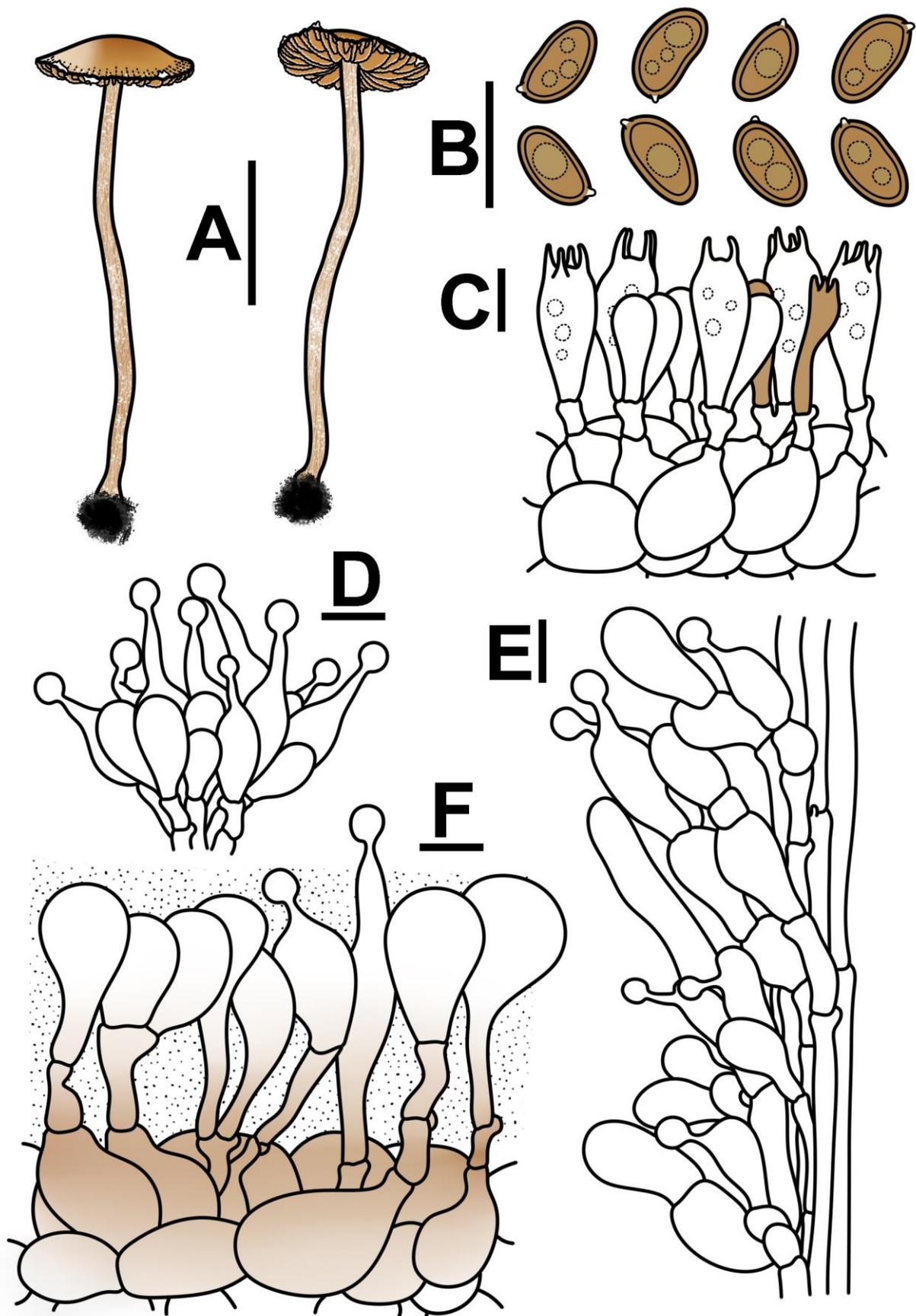


Figure 34 – *Pholiotina horchinensis* (HMJAU65097). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipells. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

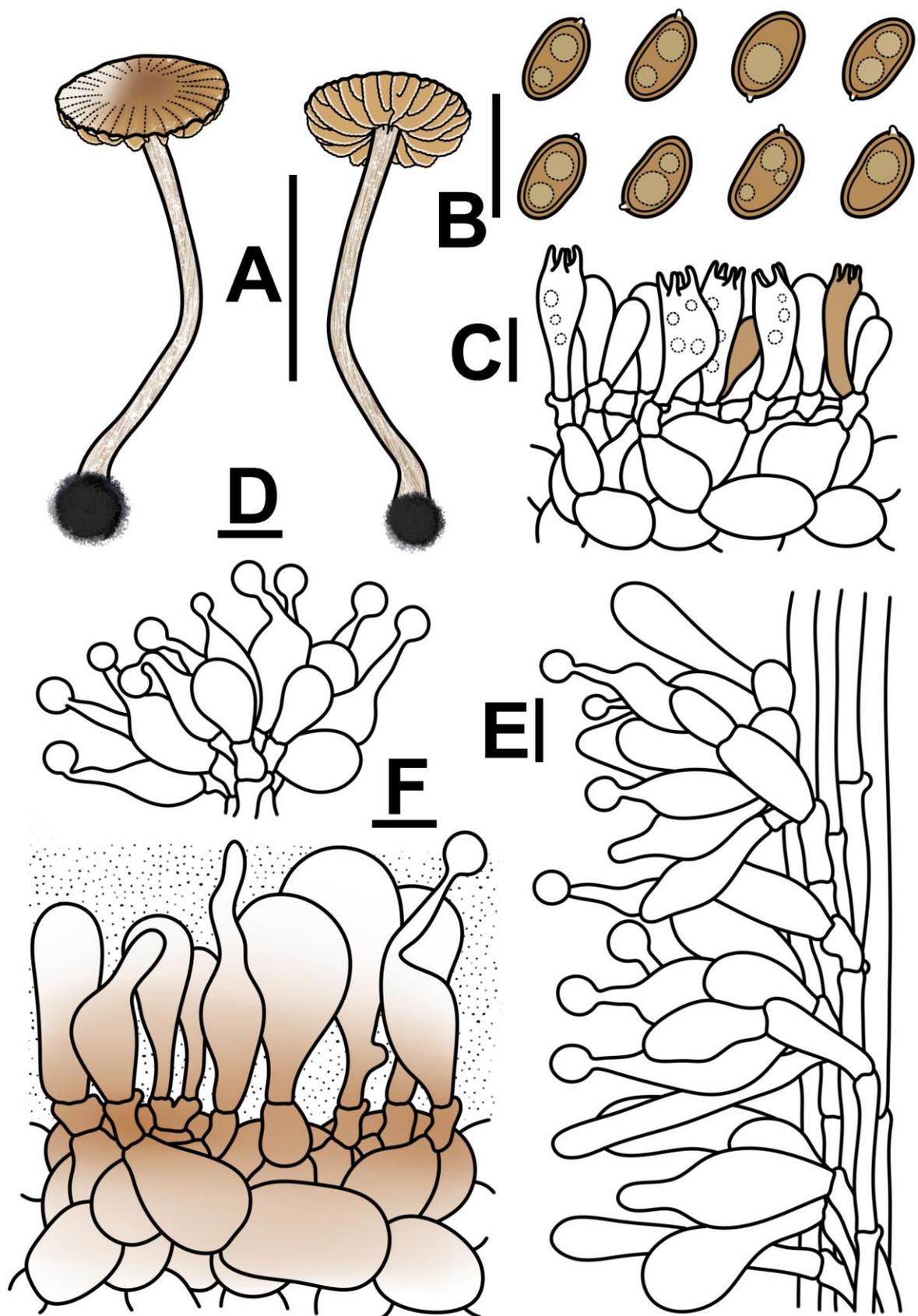


Figure 35 – *Pholiotina sulciceps* (HMJAU65099, HMJAU65100). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipellis. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.



Figure 36 – Basidiomata of *P.* sect. *Intermediae* species. A *P. changbaishanensis* (HMJAU65101). B *P. changbaishanensis* (HMJAU65102). C, D *Pholiotina* sp.2 (HMJAU65109). E, F *Pholiotina* sp.3 (HMJAU65110). Scale bars = 1 cm. These pictures are copyright of the collectors of specimens.

Type – China, Jilin Province, Yanbian Korean Autonomous Prefecture, Antu County, 31 July 2022, 128°06'45"E, 42°26'01"N, alt. 695 m, H. B. Song, S22073104 (HMJAU65101, holotype).

Basidioma small. Pileus diameter 0.5–1.5 cm, initially paraboloid to hemispherical, later convex, center ochre brown (RAL8001), copper brown (RAL8004) to chestnut brown (RAL8015), margin ochre brown (RAL8001) to clay brown (RAL8003). Pileus hygrophanous, with shallow striate, veil remnants on the pileus edge, serrulate, triangular. Context thin, beige (RAL1001) to sandy yellow (RAL1002), no distinctive odor. Lamellae adnexed to narrowly adnate, ventricose, moderately crowded, unequal length, beige (RAL1001) to ochre brown (RAL8001), serrulate edge. Stipe length 1–3 cm, thick 2.0–3.5 mm, cylindrical, slightly swollen at the base, stipe ivory (RAL1014), beige (RAL1001), fawn brown (RAL8007) to olive brown (RAL8008), initially covered with floccose squamose, later disappearing, covered longitudinally fibrous striated.

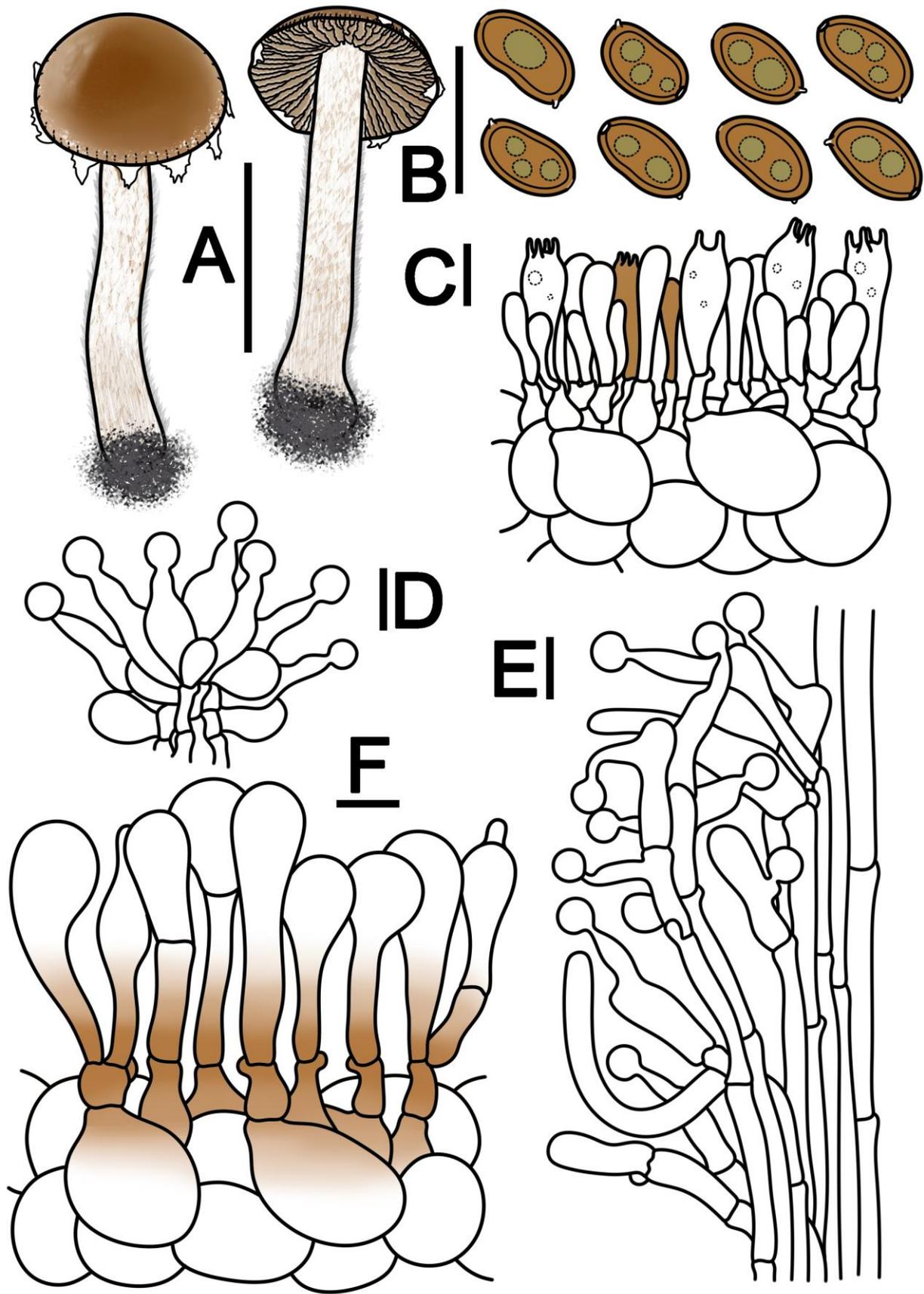


Figure 37 – *Phliotina changbaishanensis* (HMJAU65101). A Basidiomata. B Basidiospores in KOH. C Hymenium and subhymenium. D Cheilocystidia. E Stipitipells. F Pileipellis. Scale bars: A = 1 cm, B–F = 10 μ m.

Basidiospores (60/3/2) (6.1–)6.6–7.8(–8) × 4–4.8 μm, Q = (1.47–)1.51–1.79(–1.83), Qm = 1.64 (± 0.08), ellipsoid to oblong, reniform to phaseoliform, thick walls, containing oil droplets, germ pore diameter less than 1 μm, some germ pore indistinct or absent, basidiospores in KOH solution ochre brown (RAL8001) to copper brown (RAL8004). Basidia (17–)19–26(–28) × (6–)7–9 μm, clavate, 4(2)-spored, sterigmata length 2–5 μm, basidia contain vacuolar contents. Cheilocystidia (21–)24–34(–35) × 6–10 μm, lecythiform, with capitula 5–8 μm wide, lamellae edge sterile, with clavate to spheropedunculate elements. Pleurocystidia absent. Caulocystidia clavate, subcylindrical, irregular lecythiform to lecythiform, (12–)15–46(–48) × 5–9(–10) μm, with capitula 4–8 μm wide. Pileipellis transition between hymeniderm and epithelium, composed of clavate to spheropedunculate elements (19–)20–45(–47) × (9–)10–15(–17) μm, with brown red (RAL3011) pigment at the base in KOH solution. Pileocystidia lageniform, rare. Pileus residual veil composed of irregular lecythiform to lecythiform elements, arranged in a string-like to chain-like pattern. All structures have clamp connections. Negative reaction with ammonia.

Habitat – Growing singly or in groups during the summer in the litter layer beneath the *Syringa*.

Known distribution – Northeast China.

Additional specimens measured – China, Jilin Province, Yanbian Korean Autonomous Prefecture, Antu County, 31 July 2022, 128°06'45"E, 42°26'01"N, alt. 695 m, H. B. Song, S22073105 (HMJAU65102).

Notes – *Pholiotina changbaishanensis* shares similarities with *Pholiotina micropora* in terms of pileus morphology; however, *P. micropora* can be distinguished by its lecythiform pileocystidia. On the other hand, *P. bambusicola* can be differentiated from *P. changbaishanensis* by its habitat, as *P. bambusicola* specifically grows in bamboo forests. While both *P. changbaishanensis* and *P. rostellulata* have lageniform pileocystidia, *P. rostellulata* has a pileipellis that partially resembles a bird's beak, making it easily distinguishable. Furthermore, *P. changbaishanensis* shares a close relationship with *P. sulciceps*; however, *P. sulciceps* can be differentiated by its basidiospores lacking germ pore.

Hypothesized Species of *Pholiotina* s.l. in China

1. *Conocybula* sp.1 (Fig. 4E, F)

Collection: China, Xinjiang Uyghur Autonomous Region, Ili Kazakh Autonomous Prefecture, Zhaosu County, 12 August 2023, 81°43'57"E, 43°20'35"N, alt. 2211 m, H. B. Song, S23081206 (HMJAU65104).

2. *Conocybula* sp.2

Collection: China, Jiangsu Province, Nanjing City, Purple Mountain, 29 October 2023, 118°51'13"E, 32°04'02"N, alt. 258 m, X. Chen, 829 (HMJAU65105).

3. *Conobolbitina* sp.1 (Figs 7E, F, 8E, F)

Collection: China, Jilin Province, Jilin City, Jiaohe City, Qianjin Forest Farm, 24 June 2021, 127°42'7"E, 43°57'10"N, alt. 650 m, Q. Q. Ye, Y2408 (HMJAU65106).

4. *Conobolbitina* sp.2 (Figs 7G, H, 8G, H)

China, China, Jilin Province, Jilin City, Huadian City, 27 August 2023, 127°08'17"E, 42°49'30"N, alt. 483 m, H. Cheng, C2382702 (HMJAU65107).

5. *Pholiotina* sp.1

Collection: China, Hubei Province, Enshi Tujia and Miao Autonomous Prefecture, Shennongjia National Nature Reserve, 26 June 2022, 110°23'48"E, 31°27'39"N, alt. 1180 m, L. Y. Zhu, Z22062613 (HMJAU65108).

6. *Pholiotina* sp.2 (Fig. 36C, D)

Collection: China, Inner Mongolia Autonomous Region, Hulunbuir City, New Barag Left Banner, 7 August 2022, 118°17'35"E, 48°17'49"N, alt. 700 m, H. B. Song, S22080705 (HMJAU65109).

7. *Pholiotina* sp.3 (Fig. 36E, F)

Collection: China, Jilin Province, Jilin City, Jiaohe City, Qianjin Forest Farm, 25 August 2023, 127°41'54"E, 43°57'03"N, alt. 444 m, X. Wang, 3R11 (HMJAU65110).

DISCUSSION

Using the phylogenetic framework established by Tóth et al. (2013) and the morphological classification of Hausknecht (2009), we integrated genetic sequences from Chinese materials with combined nrITS, nrLSU, and *tef1- α* datasets to reconstruct the phylogenetic relationships of *Pholiotina* s.l. in Bolbitiaceae. The results revealed the polyphyletic nature of *Pholiotina*, including *Pholiotina* Clade 1, *Pholiotina* Clade 2, and *Pholiotina* Clade 3. In this study, *Pholiotina* Clade 3 was identified as *Pholiotina*, representing a monophyletic group. *Pholiotina* encompasses *P.* sect. *Pholiotina*, *P.* sect. *Vestitae*, and *P.* sect. *Intermediae*. We found that within *Pholiotina* Clade 1, there is a new genus that is sister to *Galerella nigeriensis* Tkalčec, Mešić & Čerkez. Based on this finding, we propose the establishment of a new genus, *Conocybula*, for *Pholiotina* Clade 1 (excluding *G. nigeriensis*). *Conocybula* includes *Co.* sect. *Cyanopodae* and *Co.* sect. *Conocybula*. Furthermore, *Pholiotina* Clade 2 was sister to *Bolbitius*, leading us to propose a new genus, *Conobolbitina*, for *Pholiotina* Clade 2. *Conobolbitina* comprises *Con.* sect. *Verrucisporae*, *Con.* sect. *Aeruginosa*, and *Con.* sect. *Conobolbitina*. Additionally, we have developed a key for the genera within the Bolbitiaceae family.

Key to Bolbitiaceae

1. Cheilocystidia non-lecythiform. 2
- 1'. Cheilocystidia containing sub-lecythiform to lecythiform elements 4
2. Pileus viscid, deliquescent, pseudoparaphyses present *Bolbitius*
- 2' Pileus viscid or non-viscid, non-deliquescent, basidiospores cristate-punctate or smooth 3
3. Veil distinct, forming a ring on the stipe *Descolea*
- 3'. Veil ephemeral or absent, not forming a ring *Conobolbitina*
4. Lamellar trama center filiform..... *Conocybe*
- 4'. Lamellar trama center vacuolar 5
5. Veil distinct, forming a ring or remaining at the edge of the pileus..... *Pholiotina*
- 5'. Veil ephemeral or absent, not forming a ring, with pileocystidia..... 6
6. Pileus smooth..... *Conocybula*
- 6'. Pileus with rugose or sulcate *Galerella*

Discussion as on *Conocybula*

Conocybula is sister to *Galerella nigeriensis*. It is characterized by a pileus with distinct pubescence, lamellae that are slightly serrulate or laevis, and a stipe that bruises blue or not change color. The cheilocystidia exhibit polymorphism and are lageniform and nettle hair-shaped, with a capitate apex, including sub-lecythiform elements. The caulocystidia resemble the cheilocystidia. Abundant pileocystidia are present, some of which are filled with yellow pigment. In *Conocybula* species, the first intron of the *tef-1 α* (983-2218) region is absent. *Conocybula* comprises *Co.* sect. *Cyanopodae* and *Co.* sect. *Conocybula*, with the stipe of *Co.* sect. *Conocybula* not bruising.

In *Conocybula* section *Conocybula*, both *Conocybula coprophila* and *Conocybula* sp.1 are coprophilous and have basidia that are nearly spheropedunculate to clavate, the macroscopic and microscopic structures are similar, with the difference lying in the pigmentation at the base of the pileipellis. Therefore, *Co. coprophila* is classified within *Co.* sect. *Conocybula*. According to Hausknecht (2009), *P. aberrans* is considered a synonym of *P. filipes* (G.F. Atk.) Singer. *P. aberrans* (SZMC-NL-2279) lacks a veil and its stipe does not bruise. The cheilocystidia of *P. aberrans* contain sub-lecythiform elements, and the first intron of the *tef-1 α* (983-2218) region is missing, which is consistent with the characteristics of *Co.* sect. *Conocybula*. However, since no specimens of *P. aberrans* have been collected in China, no new combination has been proposed. Similarly, no specimens of *P. parvula* have been collected. *Co. longistipitata* is reported for the first time in China and serves as the type species for *Conocybula*. Only one immature fruiting body of *Conocybula* sp.1 was collected in Xinjiang, growing on horse dung. According to the morphological descriptions by Hausknecht (2009), species such as *P. arnoldsii* Hauskn., *P. filipes*,

P. mairei Singer, *P. parvula*, and *P. sulcata* var. *oreina* Hauskn. are suspected to belong to *Co.* sect. *Conocybula*. However, relying solely on morphological characteristics for classification is not advisable, and further clarification requires molecular systematic studies.

In the *Conocybula* section *Cyanopodae*, species within this section typically show blue bruising at the base of the stipe. For the purpose of this study, taxa exhibiting a blue coloration on the pileus have been excluded from *Co.* sect. *Cyanopodae*. While Hausknecht (2009) considered *Co. cyanopus* and *Co. smithii* as synonymous, our study reveals clear morphological and systematic distinctions between them. The only limitation is that the identification of the collected specimens as *Co. smithii* was based solely on morphology speculation. Although Hausknecht (2009) reported the presence of veil remnants in specimens of *Co. cyanopus* and *Co. smithii*, this study did not observe any in our specimens. Additionally, *Conocybula* sp.2, collected in Nanjing, can be distinguished from *Co. cyanopus* and *Co. smithii* due to its pileus with groove, but unfortunately, only one basidioma was available for examination.

In the study conducted by Tóth et al. (2013), *Galerella*, was represented by only two species sequences: *Galerella floriformis* Hauskn. and *Galerella nigeriensis*. While *G. floriformis* has been assigned to *Psathyrella* (Voto 2021), *G. nigeriensis* is closely related to *Conocybula* and shows strong support for this relationship. It is worth noting that *G. nigeriensis* lacks the first intron of the *tef-1a* (983-2218) region and possesses a distinct sulcate pileus, distinguishing it from *Conocybula*. Considering the possibility of *Galerella* having multiple origins and not converging at the base of *Pholiotina* Clade 1, we propose placing *G. nigeriensis* within *Conocybula*. If other species of *Galerella* converge with *G. nigeriensis*, then this clade should be named *Galerella*, as its distinct sulcate pileus can distinguish it from *Conocybula*. Fortunately, there are well-documented type specimens and sequences available for *G. nigeriensis* (Tkalčec 2010). Previous research by Hausknecht (2003) has been conducted on *Galerella*, but some species have been excluded from the genus. The remaining *Galerella* species are morphologically inferred as potential members of *Pholiotina* Clade 1, with *G. plicatella* being a suspected species. However, since we did not obtain specimens or sequences of *G. plicatella*, it is not addressed in this particular study.

Discussion as on *Conobolbitina*

Conobolbitina, the sister group to *Bolbitius*, is characterized by several distinguishing features. These include the presence or absence of a blue-green coloration on the pileus, a viscid or non-viscid texture, and the presence or absence of pubescence. The stipe of *Conobolbitina* is cylindrical and does not undergo color changes when bruised. During its juvenile stage, it possesses a veil that does not form a ring and quickly disappears or is absent. Basidiospores have a smooth or cristate-punctate surface and display a distinct germ pore. The cheilocystidia of *Conobolbitina* are non-leythiform and polymorphic, while the caulocystidia resemble cheilocystidia but are slightly larger in size. Pileocystidia present or absent. *Conobolbitina* comprises three sections: *Con.* sect. *Verrucisporae*, *Con.* sect. *Aeruginosa*, and *Con.* sect. *Conobolbitina*. The distinction between *Conobolbitina* and *Conocybula* lies in the presence of sub-leythiform cheilocystidia in *Conocybula*. Additionally, species within the genus *Conocybula* lack the first intron of the *tef-1a* (983–2218) region.

Within the *Conobolbitina* section *Verrucisporae*, the basidiospores display cristate-punctate ornamentation, while the cheilocystidia are non-leythiform. Among the specimens in this section, *Con. micheliana* from Yunnan, it features shallowly slightly reticulate basidiospores and rarely observed sub-leythiform pileocystidia. *Con. micheliana* is closely related to *Con. dasypus*. Two other specimens, *Conobolbitina* sp.1 and *Conobolbitina* sp.2, were collected from Jilin. Their basidiospores exhibit pointed ornamentation, which distinguishes them easily from *Con. micheliana* and *Con. dasypus*. Notably, both *Conobolbitina* sp.1 and *Conobolbitina* sp.2 share the same pointed ornamentation as described in Horak & Hausknecht (2002) for *P. glulinosa*. However, the morphological description of *P. glulinosa* indicates a pileus color similar to that of *Conobolbitina* sp.2, but its pileocystidia lack purple-black pigments and are transparent at the apex, aligning with *Conobolbitina* sp.1. Due to the collection of only one specimen for both

Conobolbitina sp.1 and *Conobolbitina* sp.2, they were not classified as new species. Regarding *P. australis*, no specimens or sequences were obtained, and no combination novum was proposed. Nevertheless, based on its morphological description, it can be inferred that *P. australis* belongs to the species within *Con.* sect. *Verrucisporae*, as stated by Singer (1969).

In the *Conobolbitina* section *Aeruginosa*, all the pileus display a blue-green coloration. Initially, *Con.* sect. *Aeruginosa* was classified under *Co.* sect. *Cyanopodae*. Among the species in *Con.* sect. *Aeruginosa*, only *Con. aeruginosa* has available molecular sequences. Considering the length of the clade, it can be treated as a separate section, resulting in its combination novum. The taxa *P. aeruginosa* var. *caeruleopallida* Hauskn. and *P. atrocyanea* Esteve-Rav., Hauskn. & Rejos mentioned in Hausknecht (2009) are suspected to belong to this section of species (Esteve-Raventós et al. 2007, Hausknecht 2007).

In *Conobolbitina* section *Conobolbitina* (= *P.* sect. *Piliferae*), cheilocystidia do not exhibit terminal swelling and lack a mixture of sub-lecythiform to lecythiform elements. Based on the systematic position of the type species *Con. pygmaeoaffinis*, the clade is classified as *Con.* sect. *Conobolbitina*. *Con. pygmaeoaffinis* (WU16600) has reliable sequences and detailed morphological descriptions, which greatly assist in distinguishing between *Con.* sect. *Conobolbitina* and *Co.* sect. *Conocybula*. Unfortunately, specimens of *P. sulcata* and *P. striipes* were not collected in China. *Con. ochroleuca*, found in Jilin, is closely related to *P. sulcata*, however, *P. sulcata* can be easily differentiated by its distinct sulcate features on the pileus. The species *P. alba*, *P. striipes* (Cooke) M.M. Moser, *P. sulcata*, and *P. mairei* var. *stercorea* Tkalčec, Mešić & Hauskn. mentioned in Hausknecht (2009) are suspected to be species within *Con.* sect. *Conobolbitina* (Tkalčec et al. 2009).

Discussion as on *Pholiotina*

Pholiotina and *Descolea* are sister taxa. *Pholiotina* is distinguished by the presence of a veil, which forms a ring on the stipe or remains on the surface of the pileus but can easily disappear. In *Pholiotina*, the cheilocystidia display a polymorphic and irregular morphology, varying from clavate, subcylindrical, spheropedunculate, capitate, fusiform, utriform, sub-lecythiform to lecythiform, lageniform to long-necked lageniform, and nettle hair-shaped. They often have a curved neck or a swollen apex, and some may possess excrescences. The lamellar edges are sterile. *Pholiotina* comprises three sections: *P.* sect. *Pholiotina*, *P.* sect. *Vestitae*, and *P.* sect. *Intermediae*. According to the revision, *Pholiotina* excludes species belonging to *Conocybula* and *Conobolbitina*.

Within the *Pholiotina* section *Pholiotina*, species in this group display a veil that forms a ring on the stipe. Four new species have been discovered in China belonging to *P.* sect. *Pholiotina*: *P. excrescenticystidiata*, *P. rufidispora*, *P. bifurcaticystidia*, and *P. eburnea*. *P. excrescenticystidiata* and *P. rufidispora* share similar habitats, but their distinguishing feature lies in the cheilocystidia of *P. excrescenticystidiata*, which possess excrescences, while both cheilocystidia and caulocystidia of *P. bifurcaticystidia* exhibit excrescences. On the other hand, *P. eburnea* stands apart with its distinct ivory-white pileus. *P. aporos* and *P. exannulata* (Kühner & Watling) M.M. Moser ex Courtec. are sister taxa, albeit with low support. *P. exannulata*, classified within *P.* sect. *Vestitae*, belongs to the non-annulate species. In Karich (2020), *P. exannulata* is considered the basal group within *P.* sect. *Vestitae*. However, the classification of this clade raises questions, suggesting the necessity for further research and the inclusion of additional sequences to address this issue.

In the *Pholiotina* section *Vestitae*, the remnants of the veil are present on the surface of the pileus and easily disappear. The cheilocystidia exhibit a mixture of sub-lecythiform elements. *Pholiotina* sp.1 is considered a sister taxon to *P. dentatmarginata* (Watling) Enderle, and suspected that *Pholiotina* sp.1 is *P. novae-zelandiae* (Watling & G.M. Taylor) Hauskn. (Krieglsteiner & Enderle 1986, Hausknecht 2007). However, *Pholiotina* sp.1 consists of only one basidiome, possibly representing a variant with albinism, characterized by white lamellae, but no

basidiospores were found. The low support for the clade of *P. sect. Vestitae* suggests that there are likely undiscovered species within this section.

In the *Pholiotina* section *Intermediae*, the remnants of the veil are found on the surface of the pileus or form a ring of the stipe, and they easily disappear. The cheilocystidia primarily exhibit a lecythiform morphology. Prior to this study, only four species were known within *P. sect. Intermediae*, namely *P. intermedia*, *P. brunnea*, *P. caricicola*, and *P. pseudoampullaceocystis* (Karich 2020). *P. pseudoampullaceocystis* and *P. intermedia* form separate clades as basal groups within *P. sect. Intermediae*, and they show strong support. The cheilocystidia of *P. pseudoampullaceocystis* consist of a combination of lecythiform and non-lecythiform elements, and it is temporarily classified within *P. sect. Intermediae*. If additional species are discovered within this clade, it is recommended to establish a new section specifically for this clade. *P. intermedia* serves as the type species of *P. sect. Intermediae* and is currently the only species within the section that possesses a ring. If other species with lecythiform cheilocystidia and a ring are found, it is suggested to consider them as *P. sect. Intermediae* and reclassify no ring species like *P. brunnea* into a new section. This recommendation is based on the limited number of species previously known within *P. sect. Intermediae* and the addition of 11 new species and 2 hypothesized species in this study, which significantly enriches the species diversity of *P. sect. Intermediae*. The main distinguishing features among the new taxa within *P. sect. Intermediae* include the presence or absence of germ pore, distinct or indistinct characteristics, the morphology and size of cheilocystidia, the shape of pileocystidia, and their habitat preferences.

Evolution of Bolbitiaceae

Furthermore, our study suggests a pattern of veil evolution in *Pholiotina*, where it transitions from present to absent, gradually becoming weaker until it disappears completely. This phenomenon is also observed in related clades such as *Conocybula*, and *Conobolbitina*. In *Conocybula*, the basal species *Co. coprophila* initially possesses a veil in its juvenile stage but quickly loses it. Another species, *Co. cyanopus*, is also documented to have a present veil, while in *Pholiotina* Clade 1, the basal species *G. nigeriensis* possesses a veil. Finally, in *Conobolbitina*, the basal species *Con. dasypus* has a veil during its juvenile stage, but it also disappears. These findings provide further support for our viewpoint.

This study suggests that the evolutionary direction of cheilocystidia in *Pholiotina* is from non-lecythiform to lecythiform. This pattern is also observed in the clade spanning from *Bolbitius* to *Conocybe*. In *P. sect. Pholiotina*, the cheilocystidia are non-lecythiform. In *P. sect. Vestitae*, species exhibit a combination of sub-lecythiform cheilocystidia. Conversely, in *P. sect. Intermediae*, the cheilocystidia are lecythiform. Within the clades of *Bolbitius* and *Conobolbitina*, the cheilocystidia consistently remain non-lecythiform. In the clades of *Conocybula* and *G. nigeriensis*, the cheilocystidia display a mixture of sub-lecythiform elements. Notably, in *Conocybe*, the cheilocystidia are exclusively lecythiform. These findings demonstrate that the evolution of cheilocystidia in both *Pholiotina* and its sister clades follows a progression from non-lecythiform to lecythiform, which serves as an important distinguishing feature among different clades (Fig. 1).

Based on the results and observations, we point that pleurocystidia are absent in species of *Pholiotina*, *Conocybe*, *Conocybula*, and *Conobolbitina*. According to Song & Bau (2023), *Conocybe* pleurocystidia are described as a type of chrysocystidia, which are basidia and basidioles. These structures are believed to form when basidia and basidioles age and become filled with yellow pigments or as a result of a yellowing reaction with a KOH solution. Hausknecht (2020) identified a species, *P. pleurocystidiata* Hauskn. & Krisai, with pleurocystidia that is closely related to *Psathyrella piluliformis*, showing a high sequence alignment similarity of 99%. Furthermore, *P. pleurocystidiata* and *Ps. piluliformis* (Bull.) P.D. Orton exhibit identical pleurocystidia morphology (Yan 2018, Hausknecht & Krisai-Greilhuber 2020). Therefore, we propose considering *P. pleurocystidiata* as a synonymous name for *Ps. piluliformis*. Currently, the only species known to possess pleurocystidia is *C. punjabensis* A. Izhar, H. Bashir & Khalid, as described by Izhar

(2019). However, we maintain a skeptical stance towards this species. *C. punjabensis* is phylogenetically sister to *C. karinae* Gubitz & Hauskn., which is closely related and morphologically similar. However, *C. karinae* lacks pleurocystidia, and resolving this issue would require verification through examination of the type specimens.

Conclusions and future directions

Overall, this study focuses on addressing the issue of the polyphyly of *Pholiotina*. To achieve this, the phylogenetic relationships among species within *Pholiotina* s.l. were reconstructed using Chinese materials and reliable molecular and type sequences from abroad. The findings of this study led to the establishment and description of two new genera, 17 new species, 11 new combinations, and two new records. Moving forward, the research will shift its focus to investigating the unresolved issues within *Conocybe*. Previous results from Tóth et al. (2013) indicate that the six clades of *Conocybe* do not correspond well with the morphological sections. Specifically, *C. sect. Conocybe* Fayod, *C. sect. Pilosellae*, and *C. sect. Mixtae* Singer are not monophyletic, suggesting that caulocystidia morphology alone may not be a reliable criterion for subsection classification. In the morphological classification system of *Conocybe*, caulocystidia play a crucial role in delineating infrageneric ranks. However, it is important to note that their morphology undergoes changes during different stages of individual development. Therefore, relying solely on caulocystidia for infrageneric classification may introduce biases (Hausknecht 2009). To address this, it becomes necessary to establish infrageneric ranks within *Conocybe* based on more stable morphological characteristics.

DATA AVAILABILITY STATEMENT

All the sequences have been deposited in GenBank (<https://www.ncbi.nlm.nih.gov>). Fungal Name Registration has been submitted to either Index Fungorum (<https://www.indexfungorum.org>), Mycobank (<https://www.mycobank.org>) and Faces of Fungi (<http://www.facesoffungi.org>). The data presented in this study are deposited in the Zenodo repository (Doi: 10.5281/zenodo.10477544), as well as TreeBASE (<http://treebase.org>). The reviewer access URL is <http://purl.org/phylo/treebase/phyloWS/study/TB2:S31114?x-access-code=9821fff8c8fbf83b2f0056fb309b5f42&format=html>.

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