MYCOSPHERE 15(1): 365–472 (2024) www.mycosphere.org ISSN 2077 7019
Doi 10.5943/mycosphere/15/1/3

ARTICLE

New insights into *Gymnopus* s.l.: its systematic rearrangements and novel taxa

Hu JJ[1,2,3], Tuo YL[1,3], Yue L[1], Zhao GP[1] He XL[4], Song LR[5], Pu JB[6], Qi ZX[1], Qin WQ[7], Li TH[8], Jiang DH[2], Zhang B[1,3*], Li Y[1*], and Li X[1,3*]

[1] Engineering Research Center of Edible and Medicinal Fungi, Ministry of Education, Jilin Agricultural University, Changchun City, Jilin Province, 130118, China
[2] School of Life Science, Zhejiang Normal University, Jinhua City, Zhejiang Province, 321004, China
[3] Joint Laboratory of International Cooperation in Modern Agricultural Technology, Ministry of Education, Jilin Agricultural University, Changchun City, Jilin Province, 130118, China
4 Sichuan Institute of edible fungi, Chengdu City, Sichuan Province, 610066, China
[5] Gansu Engineering Laboratory of Applied Mycology, Hexi University, Zhangye City, Gansu Province, 734000, China
[6] Center for Medicinal Resources Research, Zhejiang Academy of Traditional Chinese Medicine, Hangzhou City, Zhejiang Province, 310012, China
[7] Jishou University, Zhangjiajie Campus, Zhangjiajie City, Hunan Province, 427000, China
[8] State Key Laboratory of Applied Microbiology Southern China, Guangdong Provincial Key Laboratory of Microbial Culture Collection and Application, Institute of Microbiology, Guangdong Academy of Sciences, Guangzhou City, Guangdong Province, 510070, China

Citation – Hu JJ, Tuo YL, Yue L, Zhao GP, He XL, Song LR, Pu JB, Qi ZX, Qin WQ, Li TH, Jiang DH, Zhang B, Li Y, Li X 2024 – New insights into *Gymnopus* s.l.: its systematic rearrangements and novel taxa. Mycosphere 15(1), 365–472, Doi 10.5943/mycosphere/15/1/3

Abstract

Gymnopus (sensu lato) is significant both economically and ecologically. However, the boundaries that demarcate these genera are indistinct, partly because of limited taxa sampling, and, also due to the insufficient use of gene fragments employed for phylogenetic analyses. Furthermore, species diversity in *Gymnopus* s.l. is likely to have been vastly underestimated, due to the lack of its detailed investigation outside of America and Europe, including in China and other countries. In this study, we examined 527 gymnopoid collections from China and performed a comprehensive phylogenetic analysis of both these collections and related genera within *Omphalotaceae* combined with ITS and nLSU sequences data. In this dataset, 159 sequences from 93 species were provided. Furthermore, sect. *Levipedes* and sect. *Impudicae* were newly recognized as independent genera by combined morphological and phylogenetic evidences and the relationships within *Omphalotaceae*, thus we propose accepting them as separate genera, namely: *Impudipilus* and *Levipedipilus*. Section *Vestipedes* was also found to share close affinity with *Collybiopsis*, which nests with it, while divided into three independent clades, for the reasons we propose accepting them as separate genera, namely: *Neomarasmius*, *Ligymopus*, and *Vestipedipilus*. The infrageneric analyses within *Impudipilus*, *Levipedipilus*, and *Gymnopus* were also performed. *Impudipilus* was divided into three sections – sect. *Impudicae*, sect. *Dysodes*, and sect. *Similis*. *Levipedipilus* was divided into three sections, namely sect. *Levipedes*, sect. *Erythropus*, and sect. *Alkalivirens*. *Gymnopus* was divided into six sections, based on the reactions with Melinda's reagent, namely sect. *Gymnopus*, sect. *Androsacei*, sect. *Efibulatus*, sect. *Omphalinoides*, sect. *Irresolutus*, and sect. *Brunneiniger*. Fifty-seven species of *Gymnopus* s.l. and allied from China were recorded, including 11 novel species and seven new records from China. In addition, we performed the first comprehensive divergence-times estimation between the genera within *Omphalotaceae*. Data from our molecular clock analyses suggest that the divergence of

Submitted: 30 October 2023; **Accepted:** 15 December 2023; **Published:** 28 February 2024
*__Corresponding Author:__ Bo Zhang – e-mail – zhangbofungi@126.com,
Yu Li – e-mail – fungi966@126.com,
Xiao Li – e-mail – lxmogu@126.com

Omphalotaceae probably occurred during the Jurassic period, while the divergence of *Gymnopus* s.l. likely occurred during the early Cretaceous period. This study also provides keys for the identification of the *Gymnopus* s.l. species.

Keywords – Biogeographic analysis – *Collybiopsis* – *Gymnopus* – *Impudipilus* – *Ligymnopus* – New genera and species – *Vestipedipilus*

INTRODUCTION

Gymnopus (Pers.) Gray s.l. species possess significant economic and ecological value (Wilson et al. 2004). However, the classification and boundaries defining the classification within the *Gymnopus* s.l., as well as the distinctions between closely related genera, have remained ambiguous. Therefore, it was deemed beneficial to conduct a comprehensive phylogenetic analysis on this group of species in the current study.

The epithet "*Gymnopus*" was proposed by Persoon in the early 19th century and initially regarded as a tribe within the genus *Agaricus* (Persoon 1801). Later, a contrasting viewpoint emerged that Fries (1821) proposed to establish trib. *Collybia* Fr. to represents a group of species that phenotypically exhibit "small, white-spored mushroom with a fleshy-membranous pileus and a hollow stipe" (Fries 1821, Antonín & Noordeloos 2010). The species of *Agaricus* trib. *Gymnopus* Pers. were incorporated into it accordingly. The tribe was divided into two distinct groups or sections, known as *Genuinae* Fr. and *Omphalariae* Fr. For an extended period, taxonomic research on this group has been conducted within *Collybia*, resulting in numerous taxonomic perspectives. Fries (1838) changed the boundaries of trib. *Collybia* to include more species. At the present moment, trib. *Collybia* encompasses species that display phenotypic characteristics such as "white spores, an incurved pileus margin, central cartilaginous stipes and putrescent basidiocarps" (Fries 1838, Antonín & Noordeloos 2010). All the species within trib. *Collybia* were further divided into four sections: sect. *Striipedes* Fr., sect. *Levipedes* Fr., sect. *Vestipedes* Fr., and sect. *Tephrophanae* Fr. Other mycologists commonly embraced this viewpoint until Staude (1857) established the genus *Collybia*. However, Staude's conception aligns more closely with Fries (1821) that the category should encompass not only the collybioid species, but also the marasmioid species (Antonín & Noordeloos 2010). Kümmer concurred with Staude's assertion that *Collybia* should be considered as a distinct genus. However, Kümmer's understanding of *Collybia* aligns more similar to Fries' (1838) perspectives as outlined. For an extended period, taxonomic research on this group was conducted within the genus *Collybia*, resulting in numerous taxonomic perspectives. However, Lennox (1979) proposed the establishment of *Microcollybia* Lennox, which led to the reclassification of only a limited number of species within *Collybia*. Later, Halling (1983) noted that the taxonomy of the genus *Collybia* was problematic and controversial, resulting in a lack of clear definition. This was also acknowledged by Antonín & Noordeloos (1993, 1997). Subsequently, Antonín et al. (1997) reclassified the sections and species, transferring them to *Gymnopus* and *Rhodocollybia* Singer. As a result, the genus *Collybia* was reduced to only four species.

However, after applying the molecular method to research *Gymnopus* and allied genera, it has been determined that *Gymnopus* is a monophyletic group and is now the focus of research. As a result, the boundaries of *Gymnopus* are changing (Fig. 1). Moncalvo et al. (2002) based on their phylogenetic analysis of *Agaricales* on the nLSU sequences and found that the genus *Gymnopus* was polyphyletic. Then, Mata et al. (2004) came to a similar conclusion, stating that *Gymnopus* is more closely related to *Marasmiellus* Murrill. Thus, *Marasmiellus* was treated as a synonym of *Gymnopus* in Mata et al.'s conception, due to the type species, *Marasmiellus juniperinus* Murrill, was confirmed to reside within it. Later, a similar result was conducted by Wilson & Desjardin (2005). Nevertheless, they disagreed with Mata et al. (2004), and pointed out that if *Marasmiellus* was treated as a synonym of *Gymnopus*, then *Rhodocollybia*, *Lentinula* Earle and *Mycetinis* Earle would also the synonym of *Gymnopus*. When the propose was rejection, Mata et al. (2006) point out that sect. *Gymnopus* (Pers.) Roussel and sect. *Androsacei* Kühner may compose the

monophyletic *Gymnopus*. More recently, Oliveira et al. (2019) redefined the genus *Gymnopus* into a smaller clade based on their combined ITS + nLSU phylogenetic analysis. As a result, sect. *Vestipedes* was segregated and placed within *Marasmiellus*. In addition, some *Gymnopus* species were transferred to two new genera: *Paramycetinis* R.H. Petersen and *Pseudomarasmius* R.H. Petersen & K.W. Hughes (Petersen & Hughes 2020).

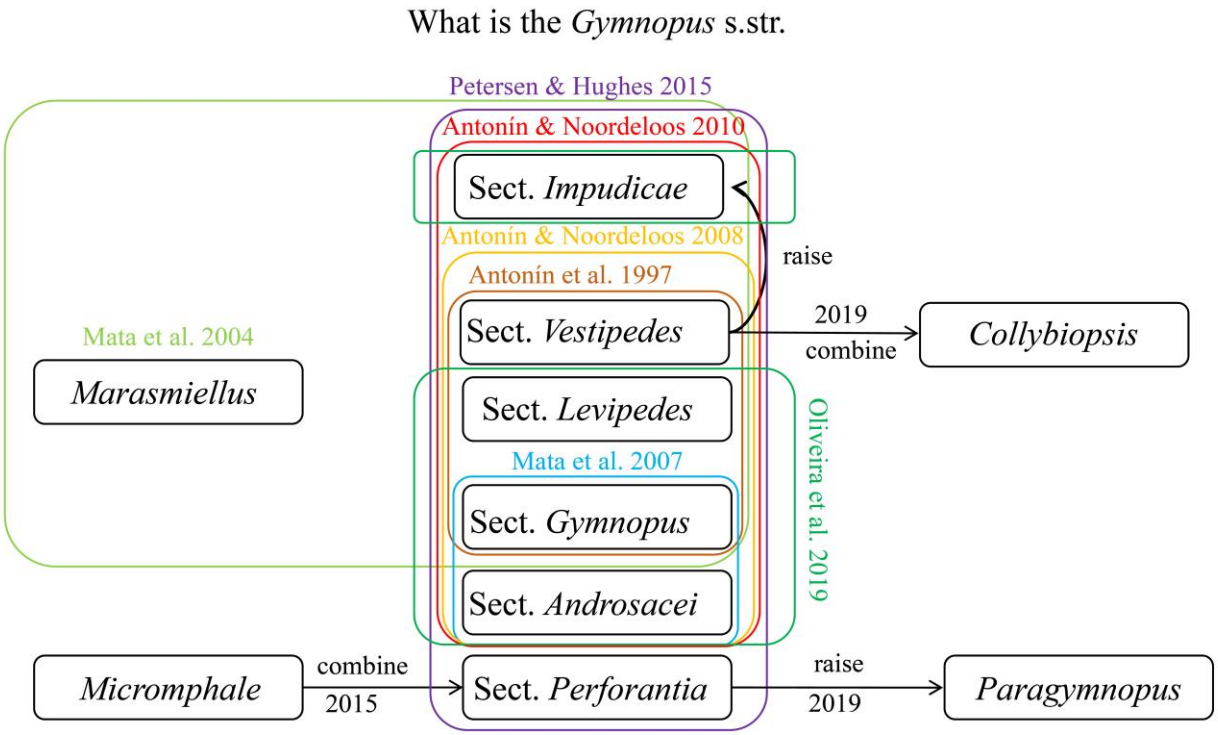

Figure 1 – The limits of genus *Gymnopus* s.str. proposed by mycologists.

Not only do the boundaries of *Gymnopus* fraught with controversy, but its infrageneric taxonomy also engenders extensive debates. Firstly, the taxonomic systems change within the genus *Collybia*. Patouillard (1900) revised the definition of sect. *Levipedes* and separated its species into two categories: those with or without annulus. Konrad & Maublanc (1935) then added two sections, sect. *Nitellinae* Konrad & Maublanc and sect. *Conigenae* Konrad & Maublanc.

Thereafter, an increasing number of mycologists have developed their own taxonomic ideas regarding these classifications. In the book, The *Agaricales* in Modern Taxonomy, Singer (1936, 1962, 1975, 1986) divided the genus *Collybia* into nine sections, namely sect. *Striipedes* (Fr.) Quél., sect. *Dictyoplocae* (Mont.) Sing., sect. *Iocephalae* Sing. ex Halling, sect. *Levipedes* (Fr.) Quél., sect. *Vestipedes* (Fr.) Quél., sect. *Subfumosae* Sing., sect. *Cystidiatae* Sing., sect. *Ixotrama* Sing., and sect. *Collybia* Sing. At the same time, Kühner & Romagnesi (1953) hold a different viewpoint, they applied features different from Singer's to divide *Collybia* into four sections, namely A-D. Then, Halling (1983) raised sect. *Striipedes* to subgenus *Rhodocollybia* (Sing.) Halling. From then on, the taxonomic systems proposed just rely on morphological studies. At the end of the 20th century, phylogenetic analysis began to help clarify taxonomic issues.

Because of the marasmioid appearance, sect. *Androsacei* belonged to *Marasmius* Fr. initially. Then, due to the presence of a non-hymeniform pileipellis, Antonín (1987) raised it to a genus rank – *Setulipes* Antonín. However, phylogenetic analysis shows that *Setulipes* have a closely affinity with *Gymnopus* (Moncalvo et al. 2002, Mata et al. 2004). Thus, Noordeloos & Antonín (2008) subsequently transferred it to *Gymnopus*, moreover, clear the limits between *Marasmius* and *Gymnopus*. Later, subsect. *Impudicae* Antonín & Noordel. (2010) was raised to a section rank. Then, Petersen & Hughes (2016) enlarges sect. *Perforantia* (Singer) R.H. Petersen and placed it

into *Gymnopus*, later, raised to a genus rank, *Paragymnopus* J.S. Oliveira (Oliveira et al. 2019). Till now, *Gymnopus* was mainly accepted as four sections, namely sect. *Androsacei* (Kühner) Antonín & Noordel., sect. *Gymnopus*, sect. *Impudicae* (Antonín & Noordel.) Antonín & Noordel., and sect. *Levipedes* (Quél.) Halling (Oliveira et al. 2019). But there is still significant controversy in each section.

Section *Androsacei* seems to be the least controversial, with unique broom cells in the pileipellis. However, some phylogenetic results show that sect. *Androsacei* is polyphyletic (i.g., Antonín et al. 2014, Li et al. 2021b, Oliveira et al. 2019). It seems that broom cells in pileipellis are not the one and only useful feature used for the classification of sect. *Androsacei* species.

Section *Levipedes* is another complicated group of species, and is dominated by *Gymnopus dryophilus* (Bull.) Murrill and its complex species. Furthermore, distinguishing between complex species based on morphology was difficult, as they had extremely similar appearances. Vilgalys & Miller Jr (1987a, 1987b) revealed that the combination of basidiospore size, pileus colour, and the shape of cheilocystidia, etc., could be used to distinguish themself. Then, Antonín et al. (2013) indicate that colour of lamellae and the shape of cheilocystidia are the key characteristics. In addition, *Gymnopus erythropus* (Pers.) Antonín, Halling, and Noordel. complex is always treated as a number of subsects. *Levipedes*, however, the phylogenetic analysis also shows these two complex form independent clades themself (Antonín et al. 2013, 2014, Hu et al. 2022b). Besides, there are some atypical species, such as *Gymnopus earleae* Murrill, *Gymnopus kauffmanii* (Halling) Halling, and *Gymnopus indoctoides* A.W. Wilson, Desjardin & E. Horak, and *Gymnopus vitellinipes* A.W. Wilson, Desjardin & E. Horak.

Section *Impudicae* is associated with a unique foetid smell. Cooper & Leonard (2013) reported three new foetid species from New Zealand. These species are characterized by their small and marasmioid basidiomata, propensity to grow on rotten wood, lack of cheilocystidia and pleurocystidia, and the presence of a gelatinized pileipellis (Hu et al. 2022a). These species, including *Gymnopus foetidus* (Sowerby) P.M. Kirk, are entirely different from the known species of sect. *Impudicae*, except for the foetid smell, and more fits the concept *Micromphale* Gray by Desjardin & Petersen (1989). *Gymnopus montagnei* (Berk.) Redhead also differed from the reported species in this section in its macro-morphology. Furthermore, there exist some species without distinctive smells viz. *Gymnopus atlanticus* V. Coimbra, Pinheiro, Wartchow & Gibertoni, *Gymnopus barbipes* R.H. Petersen & K.W. Hughes, and *Gymnopus salakensis* A.W. Wilson, Desjardin & E. Horak. For these reasons, Coimbra et al. (2015) considered that the conception put forth by Antonín & Noordeloos (2010) did not reflect all the morphological variability exhibited by members of the sect. *Impudicae*.

Section *Vestipedes* was proposed by Fries (1838), as a member of trib. *Collybia*, *Collybia*, or *Gymnopus*, due to their collybioid appearance, a cuits of pileipellis and white, inamyloid basidiospores (Singer 1986, Halling 1983, Antonín & Noordeloos 1997, 2010). But a few studies show that it is far from the genus *Gymnopus*, and clearly separate into several clades (Moncalvo et al. 2002, Wilson & Desjardin 2005, Mata et al. 2006). And the mycologists are attempting to trace the generic boundaries of *Collybiopsis* (*Marasimiellus*) (Singer 1986, Wilson & Desjardin 2005, Oliveira et al. 2019, Petersen & Hughus 2021). However, the species of sect. *Vestipedes* and the other species of *Collybiopsis* described by Petersen & Hughes (2021) expect *Collybiopsis hasanskyensis* are totally different in habitat, shape of basidiomata, pileipellis, present of pleurocystidia, and shape of cheilocystidia.

In China, *Gymnopus* s.l. is generally neglected, which contributes to many taxonomic issues. Furthermore, phylogenetic research only ever contains few sequences obtained from Chinese-derived materials. Thus, this paper aims to investigate and preliminary report on the *Gymnopus* s.l. species from China. We also aim to understand the evolutionary and phylogenetic relationships of *Gymnopus* s.l. and related genera after including the Chinese materials. In this paper, five new genera are proposed, and 11 new species are described in detail.

MATERIALS AND METHODS

Sampling and morphological study

The studied specimens were photographed *in situ*. The sizes of the basidiomata were measured when fresh. After examining and recording the fresh macroscopic characteristics, the specimens were dried in an electric drier at 40–45 °C.

Macroscopic characteristics were based on field notes and photographs, with colour descriptions corresponding to the Flora of British Fungi: colour identification chart (Royal Botanic Garden 1969). The dried specimens were rehydrated in 94% ethanol for microscopic examination before being mounted in 3% potassium hydroxide (KOH), 1% Congo red solution (0.1 g Congo red dissolved in 10 mL distilled water), and Melzer's reagent (1.5 g potassium iodide, 0.5 g crystalline iodine, and 22 g chloral hydrate dissolved in 20 mL distilled water) (César et al. 2018). They were then examined under a Zeiss Axio lab. A1 microscope at magnifications up to 1000×. All measurements were taken from sections mounted in 1% Congo red. For each specimen, a minimum of 40 basidiospores, basidia, cheilocystidia, or width of pileipellis elements were measured from at least two different basidiomata. When reporting the variation in the size of these characteristics, 5% of the obtained measurements were excluded from each extreme end of the range and then given in parentheses. The basidiospore measurements were taken as the length × width (L × W). Q denotes the variation in the ratio of L to W among the studied specimens. Qm denotes the average Q value of all the basidiospores ± the standard deviation. The specimens that were examined are deposited in the Fungarium of Jilin Agricultural University (HMJAU).

DNA extraction, PCR amplification, and sequencing

According to the manufacturer's instructions, the total DNA was extracted from the dried specimens or bio-materials using the NuClean Plant Genomic DNA Kit (Kangwei Century Biotechnology Company Limited, Beijing, China). Sequences of the internal transcribed spacer (ITS) region and nuclear large ribosomal subunits (nLSU) were used for phylogenetic analysis. The ITS sequence was amplified using the primer pair ITS1-F and ITS4-B (Gardes & Bruns 1993). The nLSU sequence was amplified using the primer pair LR0R and LR7 (Cubeta et al. 1991, Vilgalys & Hester 1990). The PCR reactions (25 μL) contained 8 μL 2 × EasyTaq® PCR SuperMix (TransGen Biotech Co., Ltd., Beijing, China), 1 μL 10 μM primer L, 1 μL 10 μM primer R, 3 μL DNA solution, and 12 μL dd H_2O (Hu et al. 2021a, b). The reaction programs were as follows: for ITS, an initial denaturation at 94 °C for 4 min, followed by 30 cycles at 94 °C for 1 min, 54 °C for 1 min, 72 °C for 1 min, and a final extension of 72 °C for 10 min (Coimbra et al. 2015); for nLSU, an initial denaturation at 95 °C for 3 min, followed by 30 cycles at 94 °C for 30 s, 47 °C for 45 s, 72 °C for 90 s, and a final extension of 72 °C for 10 min (Hu et al. 2022b, Ryoo et al. 2016). The PCR products were visualized under UV light after undergoing electrophoresis on 1.2% agarose gels stained with ethidium bromide and being purified using the Genview High-Efficiency Agarose Gels DNA Purification Kit (Gen-View Scientific Inc., Galveston, TX, USA). The purified PCR products were then sent to Sangon Biotech Limited Company (Shanghai, China) for sequencing using the Sanger method. For the species described here as new, two or more collections were sequenced for their ITS and nLSU sequences. The new sequences were deposited in GenBank (http://www.ncbi.nlm.nih.gov/genbank; Table 1).

Data analysis

NCBI was used to retrieve all the sequences belonging to *Gymnopus*, *Collybiopsis*, *Collybia*, and *Rhodocollybia*, which collectively represent the sequences of related genera. Representatives of published sequences from very close relatives to the new Chinese species (i.e., > 97% similar in BLASTn results) were also included (Table 1). A dataset of ITS and nLSU fragments comprised the sequences from this study, containing 159 sequences obtained from type species. This dataset included all *Gymnopus* sections that were determined by Oliveira et al. (including sect. *Androcacei*, sect. *Levipedes*, sect. *Impudicae*, and sect. *Gymnopus*) to further explore the relationships of the

newly sequenced Chinese specimens within the genus *Gymnopus*. Moreover, species within this genus and those within the allied genera were included (including *Lentinula*, *Rhodocollybia*, *Mycetinis*, *Marasmiellus*, and *Collybiopsis*). Also included those genera belonging to *Omphalotaceae*, i.g. *Neonothopanus* R.H. Petersen & Krisai, *Omphalotus* Fayod, and *Pusillomyces* J.S. Oliveira. Represent species belonging to *Marasmiaceae* (including *Marasmius* Fr., *Moniliophthora* H.C. Evans, Stalpers, Samson & Benny, and *Crinipellis* Pat.) were selected as out-groups (Petersen & Hughes 2016).

In the dataset, each gene region was aligned using either Clustal X (Thonpson 1997) or MAFFT 7.490 (Katoh & Standley 2013) before being manually checked in BioEdit 7.0.5.3 (Hall 1999). The datasets were first aligned before the ITS and nLSU sequences were combined with Phylosuite 1.2.2 (Zhang et al. 2020). The partition homogeneity test (PHT) (Farris et al. 1994) of the two-gene dataset was tested by PAUP 4.0b10 (Swofford 2002) using 1000 homogeneity replicates. The best-fit evolutionary model was estimated using ModelFinder (Kalyaanamoorthy et al. 2017). Bayesian inference (BI) algorithms were used following the models to perform the phylogenetic analysis. BI was calculated with MrBayes 3.2.6 with a general time-reversible DNA substitution model and gamma distribution rate variation across the sites (Ronquist & Huelsenbeck 2003). Four Markov chains were run for two runs from random starting trees until the split deviation frequency value was < 0.01; the trees were sampled every 100 generations. The first 25% of the sampled trees were discarded as burn-in, while all remaining trees were used to construct a 50% majority consensus tree and calculate the Bayesian posterior probabilities (BPPS). RaxmlGUI 2.0.6 (Edler et al. 2021) was used for maximum likelihood (ML) analysis along with 1000 bootstrap (BS) replicates using the GTRGAMMA algorithm to perform a tree inference and to search for the optimal topology (Vizzini et al. 2015). Then, FigTree 1.4.4 was used to visualize the resulting trees.

Molecular dating analysis

Given that several studies have used fossil records of fungi as calibration points to estimate the divergence time of fungi (Song & Cui 2017). We used the calibration point between *Ascomycota* and *Basidiomycota* inferred from *Paleopyrenomycites devonicus* Taylor, Hass, Kerp, M. Krings & Hanlin, which indicates that the estimated divergence time between *Ascomycota* and *Basidiomycota* is at least 400 Mya (Taylor et al. 1999, Taylor et al. 2005). Normal distribution was applied by setting the mean and standard deviation to 582.5 and 50.15, respectively. The parameter settings for the calibrations were the same as those reported by Feng (2012).

The ITS and nLSU sequences of *Gymnopus* s.l. were concatenated to estimate the divergence time and ancestral state reconstruction. ModelFinder was used to select the best evolution models using the hierarchical likelihood ratio test (Nylander 2004). The origin time of *Gymnopus* s.l. was estimated in BEAUti 1.10.4 (Drummond & Rambaut 2007) with the molecular clock and substitution models unlinked but with the trees linked for each gene partition. The uncorrelated lognormal relaxed molecular clock and Yule speciation prior set were used to estimate the divergence time and corresponding credibility intervals. Two independent MCMC runs were conducted for 1×10^8 generations, with sampling conducted every 5000 generations. Log files of the two runs were combined using LogCombiner by setting the 10% logs as burn-in. The convergence of the chains was confirmed using Tracer 1.7.4 (Rambaut et al. 2018). Samples from the posterior distributions were summarized using the program TreeAnnotator 1.10.4 to achieve a maximum clade credibility (MCC) tree (Drummond & Rambaut 2007).

FigTree 1.4.4 (Rambaut 2012) was used to visualize the MCC tree as well as to obtain the means and 95% HPD (Drummond & Rambaut 2007). A 95% HPD marks the shortest interval that contains 95% of the values sampled.

Biogeographic analysis

The geographic distributions of *Gymnopus* s.l. were delimited into seven areas: (A) Europe, (B) Southeast Asia, (C) Oceania, (D) Northeast Asia (including Northeast China, Russian Far-East,

Korea, and Japan), (E) North America, (F) Central America, and (G) Africa. Bayesian binary Markov chain Monte Carlo (BBM) analysis was implemented through RASP 3.2 (Yu et al. 2015) to infer ancestral areas by setting the generations to 10 million and discarding the first 10% of samples as burn-in; the other parameters were set to use were the default settings.

Table 1 Taxa and voucher sample information with their geographical location and GenBank accession numbers for sequence data used in this study.

Scientific name	Country	Voucher/specimen numbers	GenBank accession numbers	
			ITS	nLSU
Agaricostilbum hyphaenes	USA	CBS7811	AY789077	AY634278
Anthracophyllum archeri	Australia	PBM 2201 (WTU)	DQ404387	AY745709
A. lateritium	USA	TENN62043	FJ596892	
Boeltus nobilis	USA	BD239	JN020983	EU232002
B. edulis	USA	BD298	EU231985	EU232004
Calocera cornea	USA	GEL5359	AY789083	AY701526
Cantharellus yunnanensis	China	MHHNU32137	OM835795	OM319637
Clavaria zollingeri	USA	TENN58652		AY639882
Collybia cirrhata	**China**	**HMJAU61021**	**OQ597032**	**OQ594442**
C. cirrhata	Russia	TENN59595	DQ830805	
C. cookei	Russia	TENN58224	DQ830803	
C. tuberosa	USA	Duke1424	AF274377	
Collybiopsis billbowesii	Sao Tome	SFSU-BAP624	MF100990	
Co. californica	USA	SFSU-F-024539	MN413336	
Co. californica	Canada	TENN-F-052617	MN413338	
Co. fibrosipes	Costa Rica	TENN56660	AF505763	
Co. filamentipes	USA	TENN-F-065861	MN897832	MN897832
Co. foliiphila	India	CUH AM090	NR_154176	NG_060320
Co. fulva	USA	SFSU-DED4425	OL467259	OL462795
Co. furtiva	USA	SFSU-DED4425	DQ450031	AF042650
Co. gibbosus	Indonesia	SFSU-AWW12	AY263436	AY639415
Co. juniperinus	USA	TENN59540	AY256708	KY019637
Co. juniperinus	Argentina	TENN-F-58988	KY026661	KY026661
Co. koreana	Korea	SFC20120821-84	OL467269	OL546545
Co. melanopus	Indonesia	SFSU-AWW54	NR-137539	NG_060624
Co. minor	USA	TENN-F-059993	MN413334	MW396880
Co. pleurocystidiatus	Principe	SFSU-BAP 651	MF100977	
Co. quercophila	Slovakia	TENN-F-069267	KY026728	KY026728
Co. ramealis	Belgium	TENN-F-065145	MN413345	MN413345
Co. ramulicola	China	GDGM44256	KU321529	
Co. stenophyllus	USA	TENN-F-065943	MN413331	MW396886
Co. subpruinosus	USA	TENN59477	DQ450027	
Co. ugandensis	Sao Tome	SFSU-BAP 614	MF100986	
Coltricia perennis	China	Dai 20982	MZ484524	MZ437385
Colybiopsis dichra	USA	TENN-F-056721	KY026654	KY026654
Col. termiticola	Indonesia	SFSU-AWW106	AY263451	AY639430
Connopus acervatus	USA	TENN62824	GU318389	FJ750260
Craterellus badiogriseus	China	IFP019452	MW980548	MW979532
Cr. croceialbus	China	IFP019454	MW980572	MW979529
Crinipellis sp.	Guyana	MCA1527	AY916701	AY916699
Cri. zonata	USA	VPI3355	AY916692	AY916690
Cryptococcus neoformans	Japan	B-3501A	BR000310	BR000310
Dacryopinax spathularia	USA	GEL5052	AY854070	AY701525
Fomitiporia mediterranea	USA	AFTOL:688	AY854080	AY684157
Gautieria otthii	USA	REG636		AF393058
Gloeocantharellus papuanus	USA	PERTH4549		AY574667
Gl. purpurascens	USA	TENN14265		AY574684
Gomphus brunneus	USA	BR034190-46		AY574680

Table 1 Continued.

Scientific name	Country	Voucher/specimen numbers	GenBank accession numbers	
			ITS	nLSU
Go. clavatus	USA	OSC97616		AY574664
Gymnopanella nothofagi	Chile	SGO 163625	KT906425	KT906425
Gymnopus androsaceus	Russia	TENN-F-59594	KY026663	KY026663
G. androsaceus	France	CBS239.53	MH857174	MH868713
G. brunneiniger	Mexico	XAL-Cesar 49	MT232389	NG-075396
G. ceraceicola	New Zealand	PDD87181	KC248405	
G. cremeostipitatus	Korea	BRNM747547	KF251071	KF251091
G. efibulatus	China	HGASMF01-7052	OM970865	OM970865
G. foetidus	USA	TENN-F-65806	KY026682	KY026682
G. fusipes	Austria	TENN59300	AF505777	
G. fusipes	France	TENN59217	AY256710	AY256710
G. hakaroa	New Zealand	PDD87315	KC248410	
G. imbricatus	New Zealand	PDD95489	KC248390	
G. irresolutus	Sao Tome	SFSU-DED-8209	MF100973	
G. neobrevipes	USA	TENN-F-14505H1	MH673477	MH673477
G. omphalinoides	China	GDGM78318	MW134044	MW134730
G. pallipes	China	GDGM 81513	MW582856	OK087327
G. schizophyllus	China	GDGM77165	MW134043	MW134729
G. subsupinus	New Zealand	PDD96595	KM975399	KM975375
Hygrocybe conica	India	KUBOT-KRMK-2020-61	MW449855	MW449854
Hygrophoropsis aurantiaca	USA	AFTOL714	AY854067	AY662663
Impudipilus abruptibulbus	**China**	**HMJAU61050**	**OQ597084**	
I. abruptibulbus	**China**	**HMJAU61050-2**	**OQ597085**	
I. abruptibulbus	**China**	**HMJAU61050-3**	**OQ597086**	
I. albumistipticus	**China**	**HMJAU61032**	**OQ597081**	
I. albumistipticus	**China**	**HMJAU61032-2**	**OQ597082**	
I. albumistipticus	**China**	**HMJAU61032-3**	**OQ597083**	
I. alliifoetidissimus	China	GDGM76695	MT023344	MT017526
I. alliifoetidissimus	**China**	**HMJAU61026**	**OQ597033**	**OQ594443**
I. alpicola	Spain	BRNM705055		MK278102
I. atlanticus	Brazil	URM87728	KT222654	KY302698
I. barbipes	USA	TENN67855	KJ416269	NG_059733
I. brassicolens	Russia	TENN55550	DQ449989	
I. campanifomipileatus	**China**	**HMJAU61027**	**OQ597064**	**OQ594474**
I. campanifomipileatus	**China**	**HMJAU61028**	**OQ597065**	**OQ594475**
I. campanifomipileatus	**China**	**HMJAU61029**	**OQ597066**	**OQ594476**
I. cystidiosus	**China**	**HMJAU60992**	**ON259024**	**ON259036**
I. densilamellatus	Korea	BRNM714927	KP336685	KP336694
I. densilamellatus	China	HMJAU49128	MT023351	MT017529
I. densilamellatus	**China**	**HMJAU61015**	**ON259034**	**ON259045**
I. dysodes	**China**	**HMJAU61048**	**OQ597041**	**OQ594451**
I. dysodes	USA	TENN-F-61125	KY026666	
I. dysodes	Korea	VA12.117	KP336693	KP336701
I. dysodes	USA	TENN58367	DQ449987	
I. epiphyllus	**China**	**HMJAU60990**	**ON259030**	**ON259038**
I. graveolens	France	FF17084	MH422573	MH422572
I. impudicus	Russia	TENN60094	KJ416263	
I. iocephalus	USA	TENN52970	DQ449984	KY019630
I. iodes	China	HGASMF01-10068	OM970869	OM970869
I. minisporus	**China**	**HMJAU61030**	**OQ597070**	**OQ594480**
I. minisporus	**China**	**HMJAU61031**	**OQ597087**	
I. montagnei	Brazil	URM87715	KT222652	
I. polyphyllus	USA	TENN59455	AY256695	
I. polyphyllus	**China**	**HMJAU61047**	**OQ597049**	**OQ594459**
I. praeacutus	USA	TENN-F-059443	MN897828	

Table 1 Continued.

Scientific name	Country	Voucher/specimen numbers	GenBank accession numbers	
			ITS	nLSU
I. pygmaeus	Brazil	URM90003	KX869966	KY088273
I. salakensis	Indonesia	SFSU-AWW29	AY263447	
I. similis	**China**	**HMJAU61053**	**OQ597050**	**OQ594460**
I. similis	China	GDGM78308	MT023352	MT017530
I. similis	Korea	BRNM766739	KP336692	KP336699
I. sinopolyphyllus	China	HMJAU60386	OM970872	OM970872
I. subdensilamellatus	**China**	**HMJAU60997**	**ON259032**	**ON259042**
I. subpolyphyllus	**China**	**HMJAU60999**	**ON259028**	**ON259043**
I. talisiae	Brazil	URM87730	KT222655	KX958401
I. trabzonensis	Turkey	KATO Fungi 3375	KT271754	
I. variicolor	Korea	BRNM714959	LT594121	KP348011
Lactarius deceptivus	USA	PBM2462	AY854089	AY631899
Lentinula aciculospora	Costa Rica	TENN56421	NR176095	
L. boryana	Brazil	TENN58368	AY016440	
L. edodes	China	STCL125	AF031183	
L. lateritia	USA	RV95-376	AF031179	
L. novae-zelandiae	New Zealand	ICMP 18003	MZ325965	
L. raphanica	Brazil	INPA 289637	OL329824	
Levipedipiluis aquosus	**China**	**HMJAU61080**	**OQ597034**	**OQ594444**
L. brunneodiscus	**China**	**HMJAU61081**	**OQ597036**	**OQ594446**
L. ctrinoides	**China**	**HMJAU61069**	**OQ597053**	**OQ594463**
L. ctrinoides	**China**	**HMJAU61067**	**OQ597054**	**OQ594464**
L. dryophiloides	**China**	**HMJAU61082**	**OQ597038**	**OQ594448**
L. dryophiloides	**China**	**HMJAU61156**	**OQ597039**	**OQ594449**
L. dryophilus	**China**	**HMJAU61083**	**OQ597040**	**OQ594450**
L. inexpectatus	**China**	**HMJAU61087**	**OQ597044**	**OQ594454**
L. mimor	**China**	**HMJAU61064**	**OQ597051**	**OQ594461**
L. mimor	**China**	**HMJAU61063**	**OQ597052**	**OQ594462**
L. ocior	**China**	**HMJAU61157**	**OQ597047**	**OQ594457**
L. alkalivirens	USA	TENN51249	DQ450000	
L. alpinus	Latvia	CB16251	JX536168	
L. aquosus	Czech Republic	BRNM665362	JX536172	
L. aurantiipes	Indonesia	SFSU-AWW118	AY263432	AY639410
L. austrosemihirtipes	Indonesia	SFSU-AWW65	AY263422	
L. bicolor	Indonesia	SFSU-AWW116	AY263423	AY639411
L. bisporus	Spain	BCN-SCM B-4065	JN247551	JN247555
L. brunneodiscus	Korea	BRNM 808975	MH589975	MH589991
L. catalonicus	Spain	BCN-SCM B-4057	JN247552	JN247556
L. changbaiensis	**China**	**HMJAU60300**	**OM030272**	**OM033387**
L. dryophiloides	Korea	BRNM781447	MH589967	MH589985
L. dryophilus	Czech Republic	BRNM695586	JX536143	
L. dryophilus	Germany	BRNM737691	JX536139	
L. dryophilus	China	HMAS290095	MK966542	
L. dryophilus	Japan	Duke31	DQ480099	
L. earleae	USA	TENN-F-59140	DQ449994	KY019634
L. erythropus	Czech Republic	BRNM714784	JX536136	
L. erythropus	USA	JFA12910	DQ449998	
L. erythropus	Austria	TENN59329	AF505786	
L. fagiphilus	Czech Republic	BRNM707079	JX536129	
L. fagiphilus	**China**	**HMJAU61158**	**OQ597074**	
L. fuscopurpureus	Spain	BRNM-809119	MZ542559	MZ542563
L. globulosus	**China**	**HMJAU60307**	**OM030269**	**OM033406**
L. hemisphaericus	**China**	**HMJAU61077**	**OQ597057**	**OQ594467**
L. hemisphaericus	**China**	**HMJAU61077-1**	**OQ597058**	**OQ594468**
L. hybridus	Italy	BRNM695773	JX536177	

Table 1 Continued.

Scientific name	Country	Voucher/specimen numbers	GenBank accession numbers	
			ITS	nLSU
L. indoctoides	Singapore	AY263424	AY639419	
L. inexpectatus	Italy	545361	EU622905	EU622906
L. inusitatus	Spain	BCN-SCM B-4058	JN247553	JN247557
L. inusitatus var. *cystidiatus*	Hungary	BRNM737257	JN247550	JN247554
L. junquilleus	USA	TENN55224	NR_119582	
L. kauffmanii	USA	DUKE230	DQ450001	
L. lanipes	Spain	BRNM670686	JX536137	
L. loiseleurietorum	Sweden	URM 90060	KY321571	KY321572
L. longisterigmaticus	**China**	**HMJAU60288**	**OM030282**	**OM033403**
L. longus	**China**	**HMJAU60291**	**OM030285**	**OM033400**
L. luteofuscus	**China**	**HMJAU61071**	**OQ597062**	**OQ594472**
L. luteofuscus	**China**	**HMJAU61072**	**OQ597063**	**OQ594473**
L. macropus	Costa Rica	TENN58619	DQ449979	
L. macrosporus	**China**	**HMJAU60294**	**OM030266**	**OM033397**
L. maculatus	**China**	**HMJAU61070**	**OQ597059**	**OQ594469**
L. maculatus	**China**	**HMJAU61070-2**	**OQ597060**	**OQ594470**
L. maculatus	**China**	**HMJAU61070-3**	**OQ597061**	**OQ594471**
L. nubicola	Costa Rica	NYBG REH 8290	AF505781	
L. ocior	Czech Republic	BRNM699795	JX536166	
L. ocior	**China**	**HMJAU61159**	**OQ597076**	
L. pubipes	Spain	AH26931	MZ542558	MZ542562
L. semihirtipes	USA	TENN-F-07595	OK376741	
L. sepiiconicus	Indonesia	SFSU-AWW126	AY263449	
L. spongiosus	USA	TENN-F-68184	KY026706	KY026706
L. striatipileatus	**China**	**HMJAU61074**	**OQ597055**	**OQ594465**
L. striatipileatus	**China**	**HMJAU61074-1**	**OQ597056**	**OQ594466**
L. striatus	**China**	**HMJAU60297**	**OM030263**	**OM033384**
L. strigosipes	China	HMAS295796	OM970874	OM970874
L. subfasciatus	**China**	**HMJAU61089**	**OQ597067**	**OQ594477**
L. subfasciatus	**China**	**HMJAU61089-2**	**OQ597068**	**OQ594478**
L. subfasciatus	**China**	**HMJAU61089-3**	**OQ597069**	**OQ594479**
L. subsulphureus	USA	TENN56321	DQ449972	
L. subsulphureus	**China**	**HMJAU61091**	**OQ597071**	**OQ594482**
L. terginus	Hungary	NL-5265		MK278118
L. tiliicola	**China**	**HMJAU60305**	**OM030275**	**OM033393**
L. tomentosus	**China**	**HMJAU60303**	**OM030278**	**OM033390**
L. vitellinipes	Indonesia	SFSU-AWW127	AY263429	AY639432
Ligymnopus clavicystidiata	Korea	SFC20180705–84	OL467252	OL462817
Li. luxurians	USA	TENN-F-057910	AY256709	AY256709
Li. luxurians	**China**	**HMJAU61101**	**OQ597045**	**OQ594455**
Li. luxurians	**China**	**HMJAU61198**	**OQ597046**	**OQ594456**
Li. moseri	Indonesia	SFSU-AWW10	AY263431	AY639409
Li. polygrammus	Puerto Rico	TENN-F-056589	AY842954	
Li. polygrammus	**China**	**HMJAU61108**	**OQ597077**	
Li. polygrammus	**China**	**HMJAU61109**	**OQ597078**	
Li. pseudoluxurians	USA	TENN-F-068144	KY026702	
Li. sinoluxurians	**China**	**HMJAU61094**	**OQ597079**	
Li. sinoluxurians	**China**	**HMJAU61095**	**OQ597080**	
Li. subluxurians	**China**	**HMJAU61110**		**OQ594481**
Lig. trogioides	Indonesia	SFSU-AWW51	AY263428	AY639431
Marasmiellus bicoloripes	India	CAL1524	KY807129	KY817233
Ma. brunneigracilis	Indonesia	SFSU-AWW01	AY263434	AY639412
Ma. candidus	USA	Duke 83	DQ480088	
Ma. candidus	USA	CBS 252.39	MH856003	
Ma. carneopallidus	Italy	BRNM747442	OM522632	OM522624

Table 1 Continued.

Scientific name	Country	Voucher/specimen numbers	GenBank accession numbers	
			ITS	nLSU
Ma. celebanticus	Spain	TO HG2281	JF460781	
Ma. griseobrunneus	India	CAL1752	MK660191	MK660192
Ma. mesosporus	Korea	BRNM828732	OM522626	
Ma. pseudomphalodes	Costa Rica	NYBG-REH7348	AF505762	
Ma. tenerrimus	USA	TENN61596	FJ596840	
Ma. aff. *pluvius*	USA	TENN55766	DQ450029	
Marasmius aurantioferrugineus	Korea	BRNM714752	FJ904962	MK278334
M. brunneospermus	Korea	KPM-NC0005011	FJ904969	FJ904951
M. maximus	Korea	BRNM714570	FJ904976	FJ904958
M. nivicola	Korea	KPM-NC0006038	FJ904973	FJ904955
Moniliophthora perniciosa	Brazil	CMR UB 2041	AY317136	
Moniliophthora sp.	USA	MCA2500	AY916754	AY916752
Mycetinis alliaceus	Germany	TENN-F-67899	KY696765	KY696765
My. applanatipes	USA	SFSU DED6628	KY696775	KY696775
My. copelandii	USA	TENN-F-55408	KY696750	KY696750
My. curraniae	New Zealand	PDD 95301	KY696778	
My. ignobilis	Sao Tome	SFSU-DED 8207	MF100963	
My. opacus	USA	TENN-F-69200	KY696768	KY696768
My. prasiosmus	Sweden	UPS-F012968	KY696785	
My. querceus	Moravia	BRNM666586	KY696774	
My. salalis	USA	WTU-F-009308	KY696789	
My. scorodonius	Switzerland	TENN-F-50343	KY696725	KY696725
Neomarasmius albicantipes	Korea	SFC20170725-35	OL467272	OL462811
N. boreoorientalis	Russia	LE323323	MN597452	MN597444
N. cervinus	Principe	SFSU-DED8298	MF100984	
N. fuscotramus	China	GDGM26313	JF303730	
N. istanbulensis	Türkiye	KATO fungi 3596	KX184795	KX184796
N. lodgeae	Costa Rica	TENN58621	AF505757	
N. longistipes	Korea	BRNM714972	GU319113	
N. micromphaloides	USA	TENN68165	KJ416243	
N. mustachius	Sao Tome	SFSU-BAP 670	MF100987	
N. omphalodes	Costa Rica	TENN58629	AF505761	
N. orientisubnuda	Korea	NIBRFG0000500990	OL467262	OL546546
N. peronatus	Belgium	TENN-F-065120	KY026677	KY026677
N. peronatus	**China**	**HMJAU61092**	**OQ597048**	**OQ594458**
N. pseudolodgeae	Costa Rica	TENN-058601	NR_119462	
N. subnudus	USA	TENN-F-61138	KY026667	FJ750262
N vellerea	Korea	SFC20140821–29	OL467267	OL462810
Neonothopanus cystidiatus	Ghana	HMJAU48222	MW298683	MW250229
Ne. gardneri	Brazil	SP416340	JF344713	JF344714
Ne. hygrophanus	Ghana	HMJAU48223	MW298685	MW250231
Ne. nambi	Indonesia	7-SU-3-E-45(M)-B	KJ654574	
Neurospora crassa	USA	CBS:367.70	MH859714	MH871466
Omphalotus flagelliformis	China	HKAS76645	KC333363	
O. guepiniiformis	China	HKAS54190	KC333364	
O. illudens	USA	BR1830367	AF525047	
O. mexicanus	Mexico	TENN51283	AY313274	
O. nidiformis	China	CBS323.49	EU424307	EU365662
O. olearius	Hungary	CBS163.55	AF525049	
O. olivascens	USA	VT455	AF525063	
O. subilludens	USA	CBS660.85	AF525073	
Paragymnopus foliiphilus	USA	TENN-F-68183	KY026705	KY026705
P. perforans	Sweden	TENN-F-50319	KY026625	KY026625
P. pinophilus	USA	TENN-F-69207	KY026725	KY026725

Table 1 Continued.

Scientific name	Country	Voucher/specimen numbers	GenBank accession numbers	
			ITS	nLSU
P. sequoiae	USA	TENN-F- 69325	KY026740	KY026740
P. sublaccatus	Canada	UBC25212	KY026762	KY026762
Paramycetinis austrobrevipes	Australia	TENN-F-50135	KY026622	KY026622
P. caulocystidiatus	New Zealand	TENN-F-5405	KY026645	KY026645
Pseudomarasmius efibulatus	New Zealand	TENN-F-56187	MK268234	
Ps. glabrocystidiatus	Korea	BRNM718676	NR152899	NG060647
Ps. nidus-avis	Mexico	Cesar36	MH560576	
Ps. pallidocephalus	USA	TENN-F-52401	KY026635	KY026635
Ps. patagonianus	Chile	TENN-F-54424	KY352649	
Ps. quercophylloides	China	TENN-F-49177	MK268235	
Pusillomyces asetosus	Korea	BRNM715010	KF251066	KF251086
Pu. funalis	Korea	BRNM718747	KF251056	KF251077
Pu. manuripioides	Brazil	JO674	MK434210	MK434211
Ramaria rubella	USA	PBM 2408	AY854078	AY645057
Rhizopus oryzae	Japan	CBS 330.53	JN943054	MH868766
Rhodocollybia butyracea	**China**	**HMJAU61153**	**OQ597072**	**OQ594483**
R. butyracea	Sweden	TENN53580	AY313293	
R. butyracea	China	HFJAU0269	MN258680	
R. maculata	Dominican Republic	TFB11720	KT205402	
R. maculata	USA	TENN59459	AY313296	
Schizosaccharomyces pombe	Australia	UCDFST:65-116	MH595433	MH595188
Stereum hirsutum	USA	FPL8805	AF218400	AF393078
Suillus pictus	USA	MB03-002	AY854069	AY684151
Turbinellus floccosus	USA	MICH5588		AY574660
T. fujisanensis	USA	OSAMY1842		AY574669
Ustilago maydis	Canada	CBS:445.63	MH858320	MH869934
Vestipedepilus eneficola	**China**	**HMJAU61144**	**OQ597073**	
V. alnicola	Brazil	URM90019	KY302681	KY302682
V. biformis	USA	TENN58541	DQ450054	
V. biformis	**China**	**HMJAU61116**	**OQ597035**	**OQ594445**
V. collybioides	Costa Rica	TENN58020	AF505772	
V. confluens	**China**	**HMJAU61120**	**OQ597037**	**OQ594447**
V. confluens	Sweden	TENN50524	DQ450044	
V. confluens	Germany	TENN-F-067864	KP710296	KJ189573
V. confluens ssp. *americana*	Canada	TENN-F-069073	KP710278	KJ189585
V. confluens ssp. *americana*	USA	TENN-F-067822	KP710281	KJ189581
V. cylindricus	Costa Rica	TENN58097	AF505776	
V. diminutus	Sri Lanka	AR099-SFSU		AY639413
V. disjunctus	USA	TENN69172	KJ416252	
V. disjunctus	USA	TENN68136	KJ416253	KY019643
V. eneficola	Canada	TENN69123	KJ128264	KJ189586
V. eneficola	**China**	**HMJAU61141**	**OQ597042**	**OQ594452**
V. hariolorum	Netherlands	CBS250.48	MH856329	MH867883
V. hariolorum	**China**	**HMJAU61150**	**OQ597043**	**OQ594453**
V. hasanskyensis	Russia	TENN-F-060730	MN897829	
V. hirtelloides	Principe	SFSU-DED 8318	MF100975	
V. hirtellus	Principe	SFSU-DED 8299	MF100974	
V. hirtellus	**China**	**HMJAU61151**	**OQ597075**	
V. indoctus	Indonesia	SFSU-AWW17	AY263440	
V. menehune	USA	SFSU-DED5866	AY263426	
V. menehune	Indonesia	SFSU-AWW15	AY263443	AY639424
V. mesoamericanus	Costa Rica	TENN58613	DQ450035	KY019632
V. neotropicus	Costa Rica	TENN58110	AF505769	
V. nonnullus	USA	TENN-F-68133	KY026701	KY026701
V. nonnullus var. *attenuatus*	Indonesia	SFSU-AWW05	AY263445	AY639426

Table 1 Continued.

Scientific name	Country	Voucher/specimen numbers	GenBank accession numbers	
			ITS	nLSU
V. obscuroides	Norway	GB-0150514	KX958399	KX958399
V. obscuroides	Sweden	GB-0053811	KX958398	KX958398
V. parvulus	Costa Rica	TENN58113	DQ450060	
V. readiae	New Zealand	TENN61061	KJ416244	
V. rodhallii	Principe	SFSU-BAP 630	MF100981	
V. subcyathiformis	Brazil	URM-90022	KY404983	KY404983
V. subcyathiformis	Dominican Republic	TENN59550	DQ450042	
V. subumbilicata	Korea	SFC20140701–03	OL467232	OL462787
V. tamblinganensis	Indonesia	SFSU-AWW39	AY263450	
V. undulata	Korea	SFC20120821–04	OL467239	OL462813
V. villosipes	New Zealand	TENN60951	KJ416255	
Xanthoconium separans	USA	BD243	KC447046	EU232000

RESULTS

Phylogenetic analysis of *Omphalotaceae*

In the dataset, 509 sequences derived from two gene loci (ITS and nLSU) from 316 representing samples were used to build phylogenetic trees containing 2867 characters after being trimmed; 120 of these were newly generated, with 60 ITS sequences and 60 nLSU sequences. The combined ITS and nLSU dataset represented 244 taxa from *Omphalotaceae*. Representative species were chosen as out-groups from *Marasmiaceae* (including *Marasmius aurantioferrugineus* Hongo, *Marasmius brunneospermus* Har. Takah., *Marasmius maximus* Hongo, *Marasmius nivicola* Har. Takah., *Moniliophthora perniciosa* (Stahel) Aime & Phillips-Mora, *Moniliophthora* sp., *Crinipellis zonata* (Peck) Pat., and *Crinipellis* sp.). ModelFinder was used to select the best-fit model for the combined dataset; the best-fit model for BI was determined to be GTR+I+G. The Bayesian analysis was run for eight million generations, resulting in an average standard deviation of split frequencies of 0.031131. Then, Tracer 1.7.4 was used to check the log file, thus, determining that all ESS vale > 200. The same dataset and alignment were analyzed using the ML method. The phylogenetic construction performed via the ML and BI analysis methods for the two combined datasets showed a similar topology.

Three main clades, representing *Omphalotaceae*, *Marasmiaceae*, and *Tricholomataceae*, were obtained in the phylogenetic tree. Moreover, *Omphalotaceae* could be divided into 19 clades, representing *Anthracophyllum* Ces., *Collybiopsis* s.str., *Connopus* R.H. Petersen, *Gymnopanella* Sand. -Leiva, J.V. McDonald & Thorn, *Gymnopus* s.str., *Impudipilus*, *Lentinula*, *Levipedipilus*, *Ligymnopus*, *Mycetinis*, *Neomarasmius*, *Neonothopanus*, *Omphalotus*, *Paragymnopus*, *Paramycetinis*, *Pseudomarasmius*, *Pusillomyces*, *Rhodocollybia*, and *Vestipedipilus* (Figs 2, 3).

Furthermore, *Gymnopus* and *Marasmiellus* (now treated as *Collybiopsis*) delimited by Oliveira et al. (2019) were demonstrated to be polyphyletic groups. From our phylogenetic analysis, the genus *Gymnopus* was divided into three subclades, while *Collybiopsis* was divided into four subclades. The phylogenetic analyses for all 19 subclades of *Omphalotaceae* and two other clades are documented below.

(1) *Gymnopus* s.l. clade

The *Gymnopus* s.l. clade is comprised of 141 sequences, of which, 42 sequences were obtained from this study based on Chinese materials, and 52 sequences were obtained from type materials. Our collections fall into 24 well-supported branches, which are represented by nine common species, five new records from China, and 10 new species.

According to our study, the *Gymnopus* s.l. clade is split into three subclades, which refer to relationships with other genera in the phylogenetic analysis. Combined with the result of

morphological studies, we believe these three subclades represent three genera, namely *Gymnopus*, *Impudipilus*, and *Levipedipilus*.

In addition, *Levipedipilus* was also divided into three branches representing three sections, viz. sect. *Alkalivirens*, sect. *Levipedes*, and sect. *Erythropus*. *Impudipilus* consists of four branches representing three sections, viz. sect. *Impudicae*, sect. *Dysodes*, and sect. *Similis*. *Gymnopus* was split into six branches representing six sections: viz. sect. *Gymnopus*, sect. *Androsacei*, sect. *Efibulatus*, sect. *Omphalinoides*, sect. *Irresolutus*, and sect. *Brunneiniger* (Figs 2, 3).

(2) *Collybiopsis* s.l. clade

In former studies, the type species of *Marasmiellus* was gathered into one branch with species of *Gymnopus* sect. *Vestipedes.* Thus, *Marasmiellus* was treated as a synonym of *Gymnopus* (Mata et al. 2004). Then, owing to research published by Oliveira et al. (2019), it was proposed that transferring the species of sect. *Vestipedes* into *Marasmiellus.* More recently, Petersen & Hughes (2021) considered *Marasmiellus* as a synonym of *Collybiopsis*, according to the nomenclature, while the conceptions of *Collybiopsis* between Oliveira et al. and Petersen & Hughes are different. According to our former study (Hu et al. 2022b), *Collybiopsis* was divided into two clades, while the habitat, shape of basidiomata, shape of cheilocystidia, structure of pilepeillis, and present or absent of pleurocystidia between species of sect. *Vestipedes* and the type species clade of *Collybiopsis* are hugely different, especially the present of pleurocystidia, shape of cheilocystidia, and structure of pilepeillis, thus requiring further intensive study.

In the current study, we obtained all the sequences belonging to sect. *Vestipedes* and *Collybiopsis* from NCBI and 13 self-tested sequences. The phylogenetic analysis shows strong evidence that the sect. *Vestipedes* species closely related with type species clade of *Collybiopsis* s.l. And sect. *Vestipedes* is clearly divided into three subclades, and all the species belonging to these three clades are different in morphology, thus, we split it into three genera, namely *Ligymnopus*, *Neomarasmius*, and *Vestipedipilus*. In addition, the Chinese taxa were distinctly placed in ten well-supported clades represented by six common species, one new species, and three new records from China (Figs 2, 3).

(3) *Paragymnopus* clade

This subclade is comprised of five species. These species were previously considered as *Micromphale* sect. *Perforanita*. Then, due to having a similar pileipellis, Antonín & Noordeloos (2010) transferred them to *Gymnopus*. Based on phylogenetic analysis, Oliveira et al. proposed that this section be a genus rank – *Paragymnopus*. According to our result, we support *Paragymnopus* as an independent genus (Figs 2, 3).

(4) *Rhodocollybia* clade

This subclade is comprised of two species representing the genus *Rhodocollybia*. *Rhodocollybia* was previously considered a section (sect. *Striipedes*) belonging to *Collybia*. Then, Singer raised it to a genus rank due to its cream to pink spores disport and dextrinoid spores. According to our study, we support this genus as an independent genus that separately from *Collybia* (Figs 2, 3).

Bayesian estimation of *Omphalotaceae* divergence time

The alignment of the combined ITS + nLSU dataset was 2876 bp in length and consisted of 161 taxa. Analyses were calibrated based on the divergence between *Ascomycota* and *Basidiomycota* that occurred 582 million years ago (Mya). The mean ages, 95% HPD intervals, and Bayesian posterior probability values of all the labelled nodes are indicated in Table 2. Topologies obtained for the Bayesian consensus tree and BEAST analysis were found to be almost identical (Fig. 4). Bayesian dating results suggest that the stem age of *Agaricales* is estimated to be 165.3127 ± 0.2306 Mya (153.4271–189.0725 Mya, 95% HPD) during the Jurassic period, which is consistent with a previous inference (He et al. 2019). The data suggest that the stem age of *Omphalotaceae* is estimated to be 165.1802 ± 0.0.6342 Mya (141.3326–184.5799 Mya, 95% HPD), having occurred

during the transition from Jurassic to Cretaceous. The data suggest an ancient divergence of *Gymnopus* s.l. from allied genera during the late Cretaceous (88.8676 ± 0.4085 Mya, 76.8501–113.0027 Mya, 95% HPD).

The historical biogeography of *Gymnopus s.l.*

The inferred historical biogeographic scenario analyses through RASP are shown in Fig. 5. The Dispersal Extinction-Cladogenesis (DEC) analysis results suggest a complex biogeographic history for *Gymnopus* s.l. The ancestral area of *Gymnopus* s.l. has remained ambiguous. In the reconstruction of their ancestral geographic range, several areas contribute in different proportions. *Impudipilus* is highly likely to have originated in East Asia, with a probability of 67.56%. *Gymnopus* likely arose in East Asia, with a high probability of 95.50%. We obtained a 53.02% probability that *Levipedipilus* originated in East Asia, alongside a 29.98% probability that it originated in East Asia and North America.

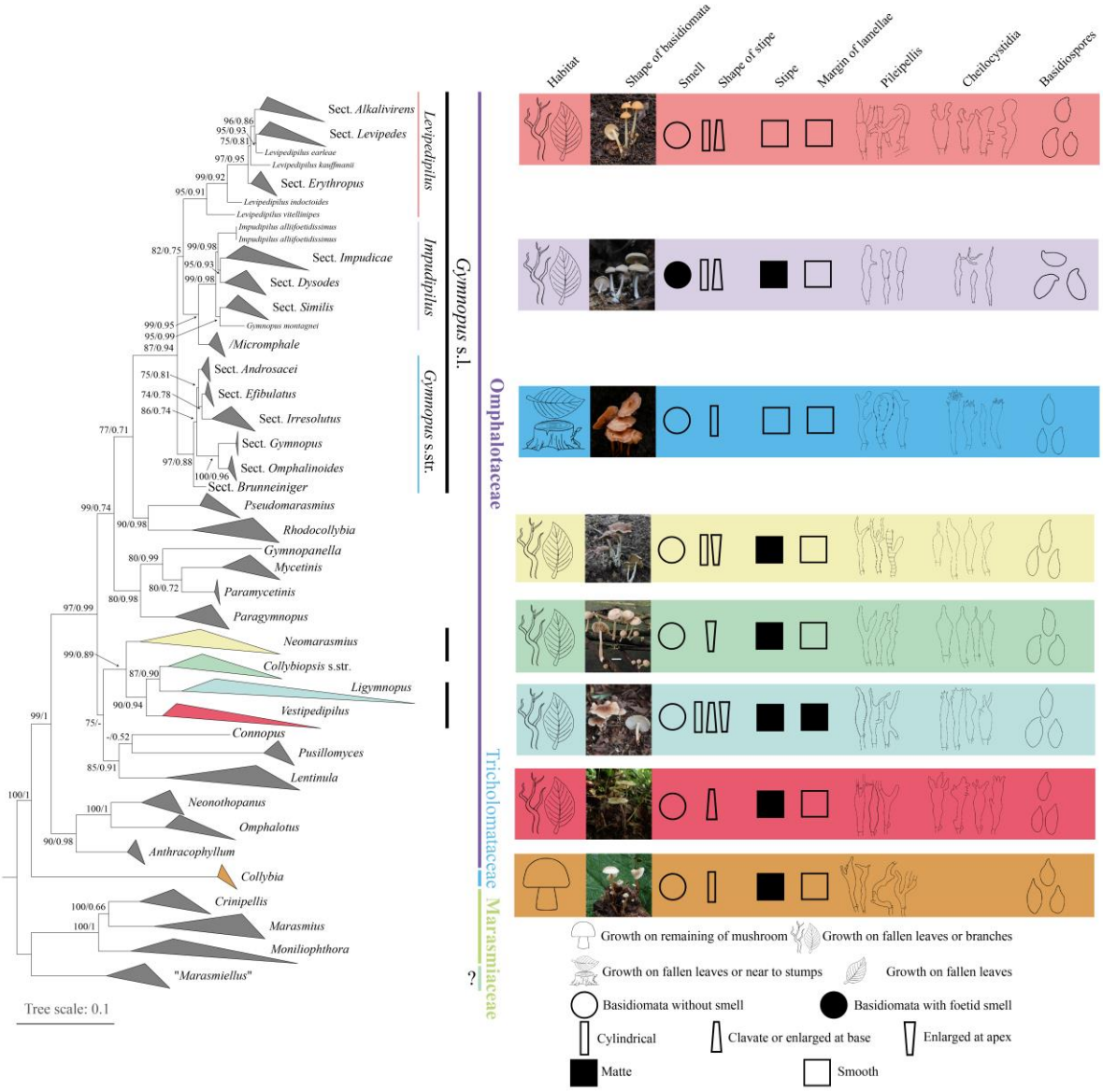

Figure 2 – Bayesian 50% majority-rule consensus tree from the ITS and nLSU analyses. Support values at the nodes consist of BP ≥ 0.50 and PP ≥ 50; unsupported nodes under BP 0.5 are collapsed. The major clade is simplified, representing genus-level groups, as depicted in the figure. The outgroup consists of members of *Marasmiaceae*.

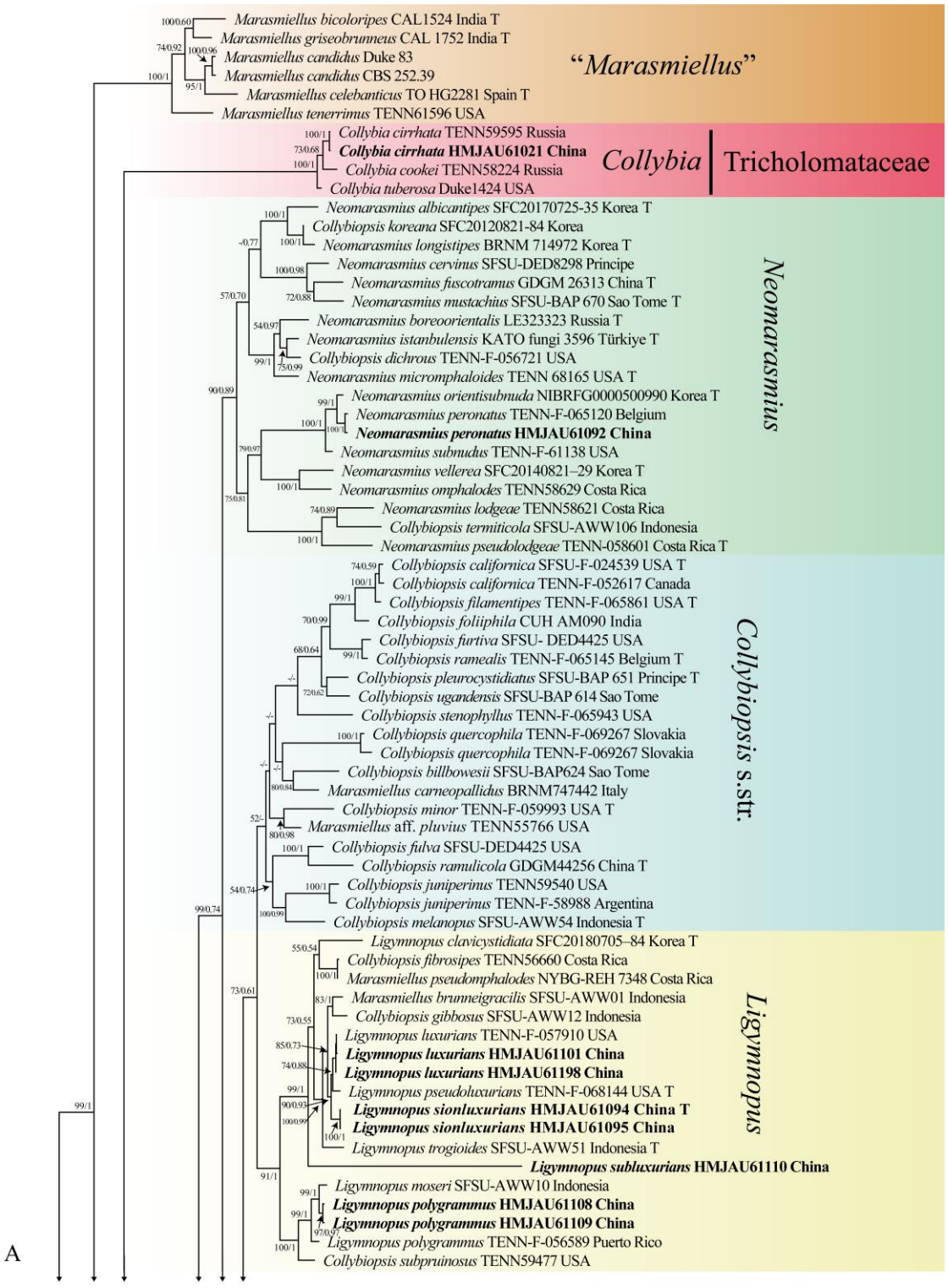

Figure 3 – Maximum likelihood phylogenetic tree generated from the ITS and nLSU dataset. Bootstrap values (PP) ≥ 50% from ML analysis and Bayesian posterior probabilities (BP) ≥ 0.50 are shown on the branches. Newly sequenced collections are indicated in bold, and the type specimens are denoted by (T).

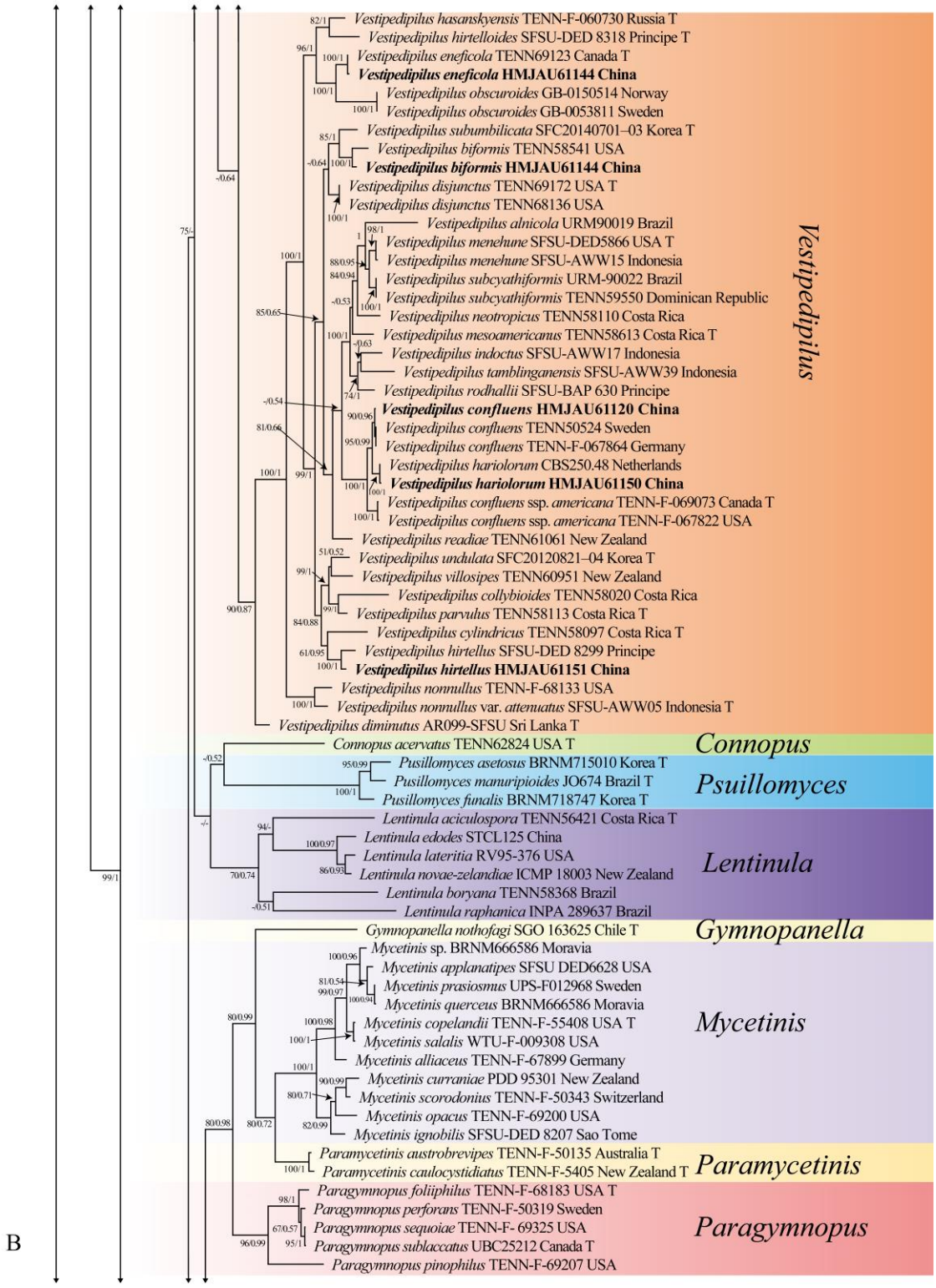

Figure 3 – Continued.

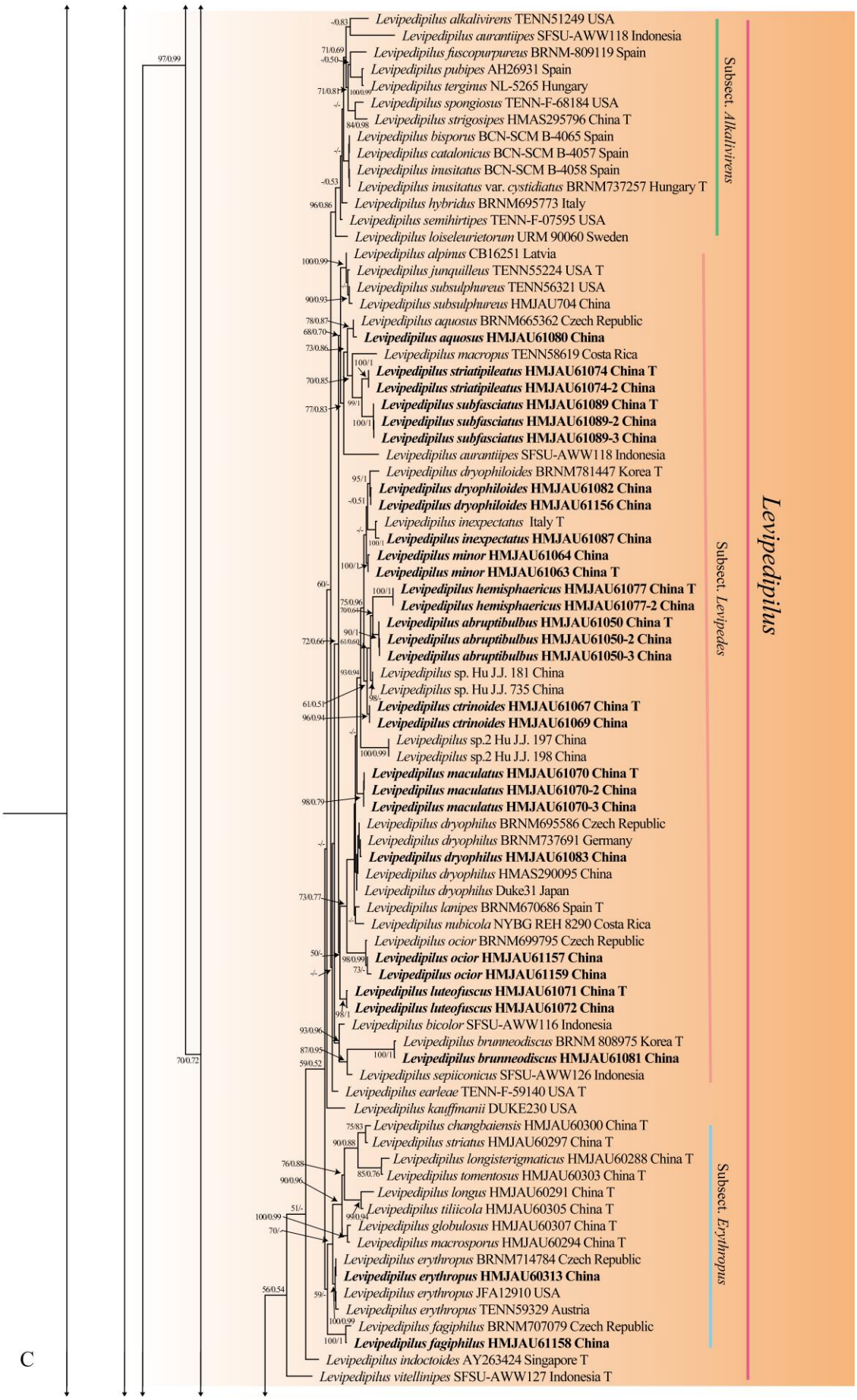

Figure 3 – Continued.

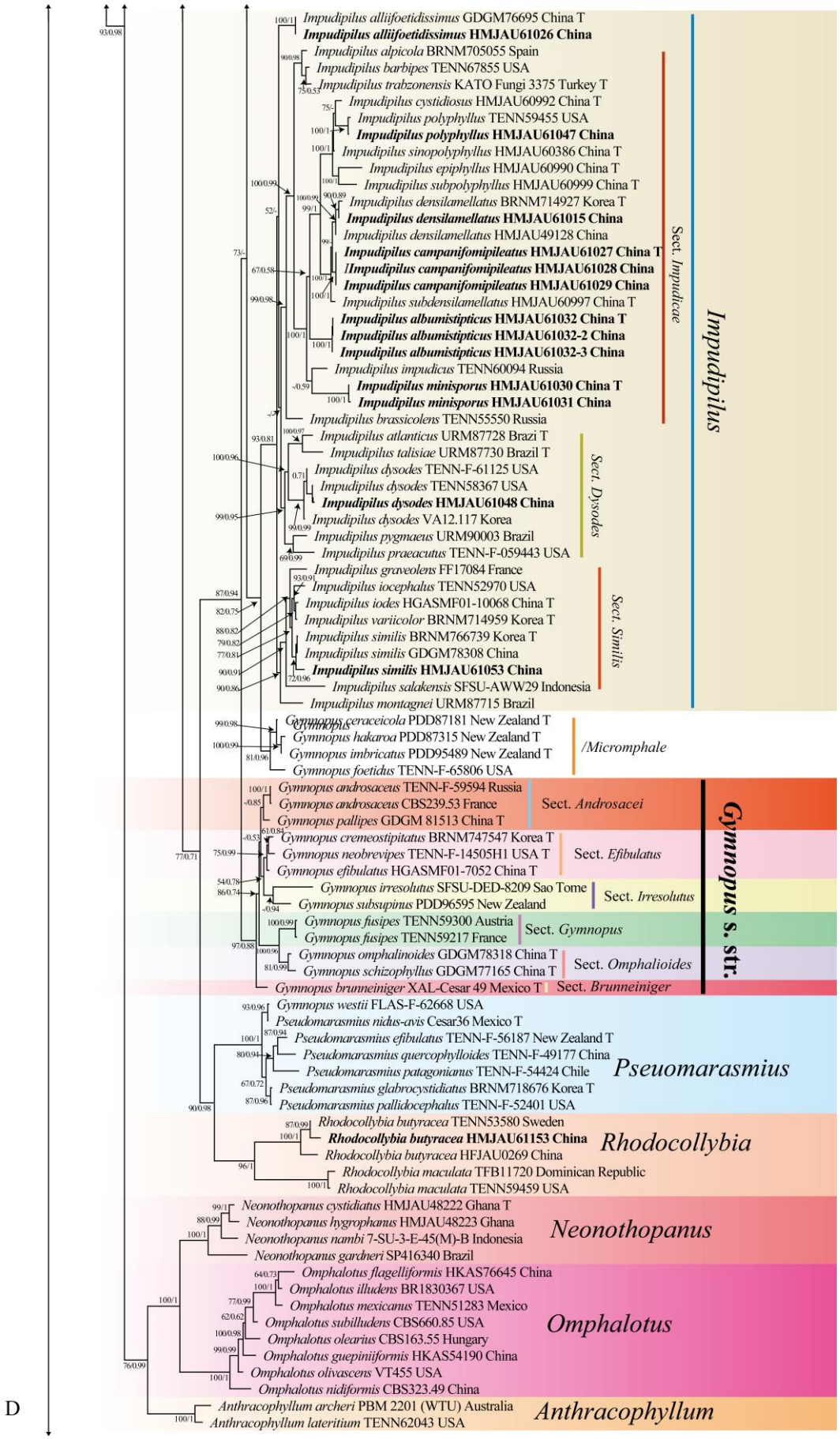

Figure 3 – Continued.

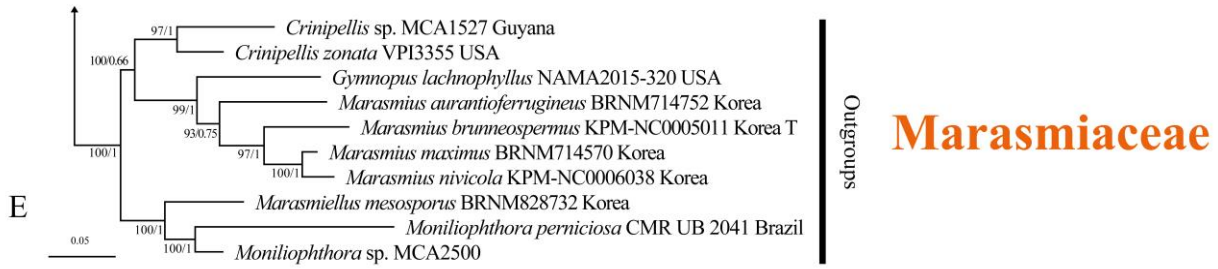

Figure 3 – Continued.

Morphological observations within *Gymnopus* s.l.

The phylogenetic analysis was relied on type sequences, reliable sequences, and our self-tested sequences, moreover, the specimens, including some type materials, were carefully examined. Then, these genera within *Gymnopus* s.l., viz. *Collybiopsis*, *Neomarasmius*, *Vestipedipilus*, *Gymnopus*, *Ligymnopus*, etc., were elucidated mainly based on the characters of habitat, shape of basidiomata, smelly, shape and smooth or matte of stipe, margin of lamellae, shape of pileipellis and cheilocystidia, and inamyloid or dextrinoid spores (Fig. 2).

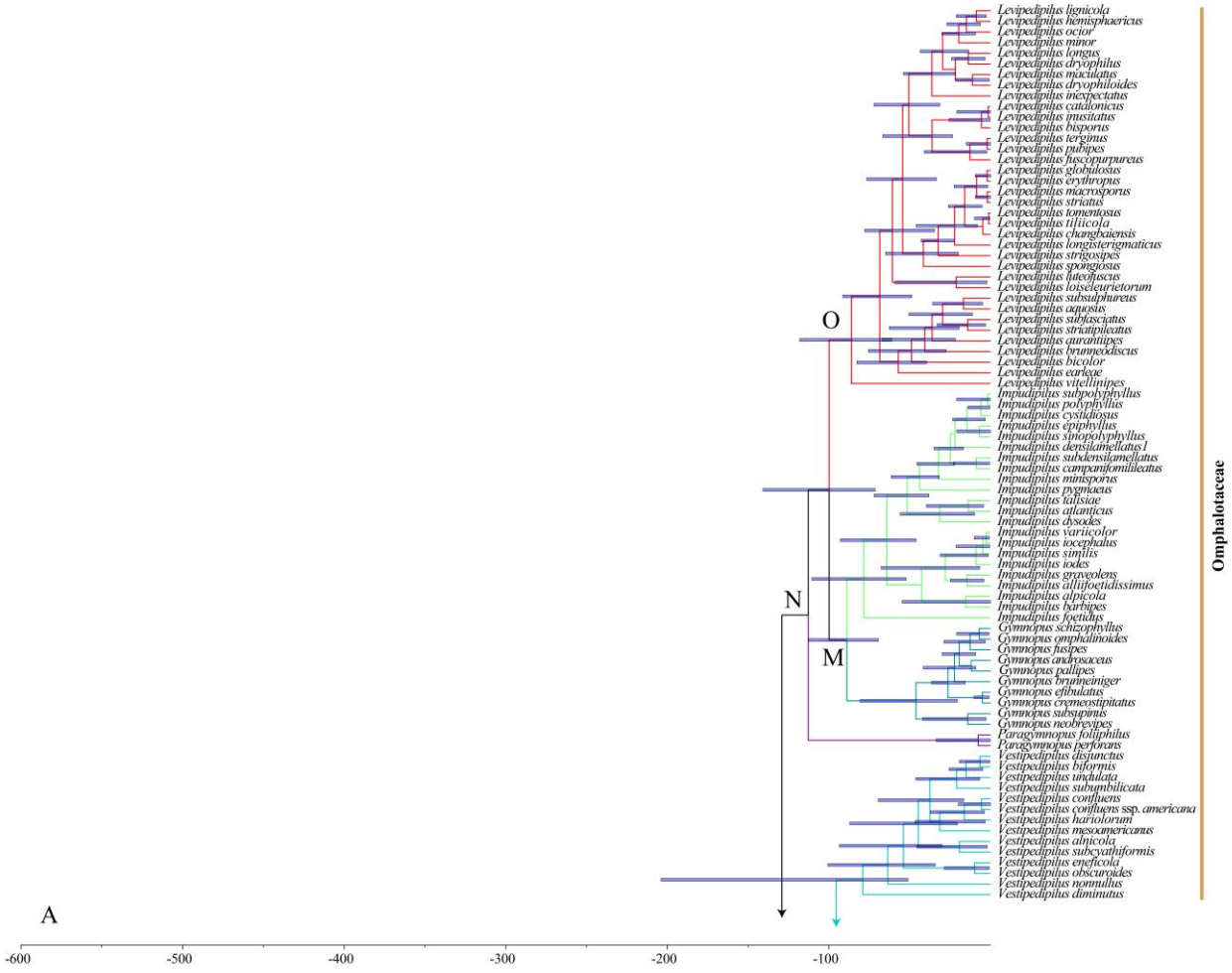

Figure 4 – Chronogram and estimated divergence times of *Omphalotaceae* generated from molecular clock analysis based on the ITS + nLSU data. The geological time scale is in millions of years ago (Mya).

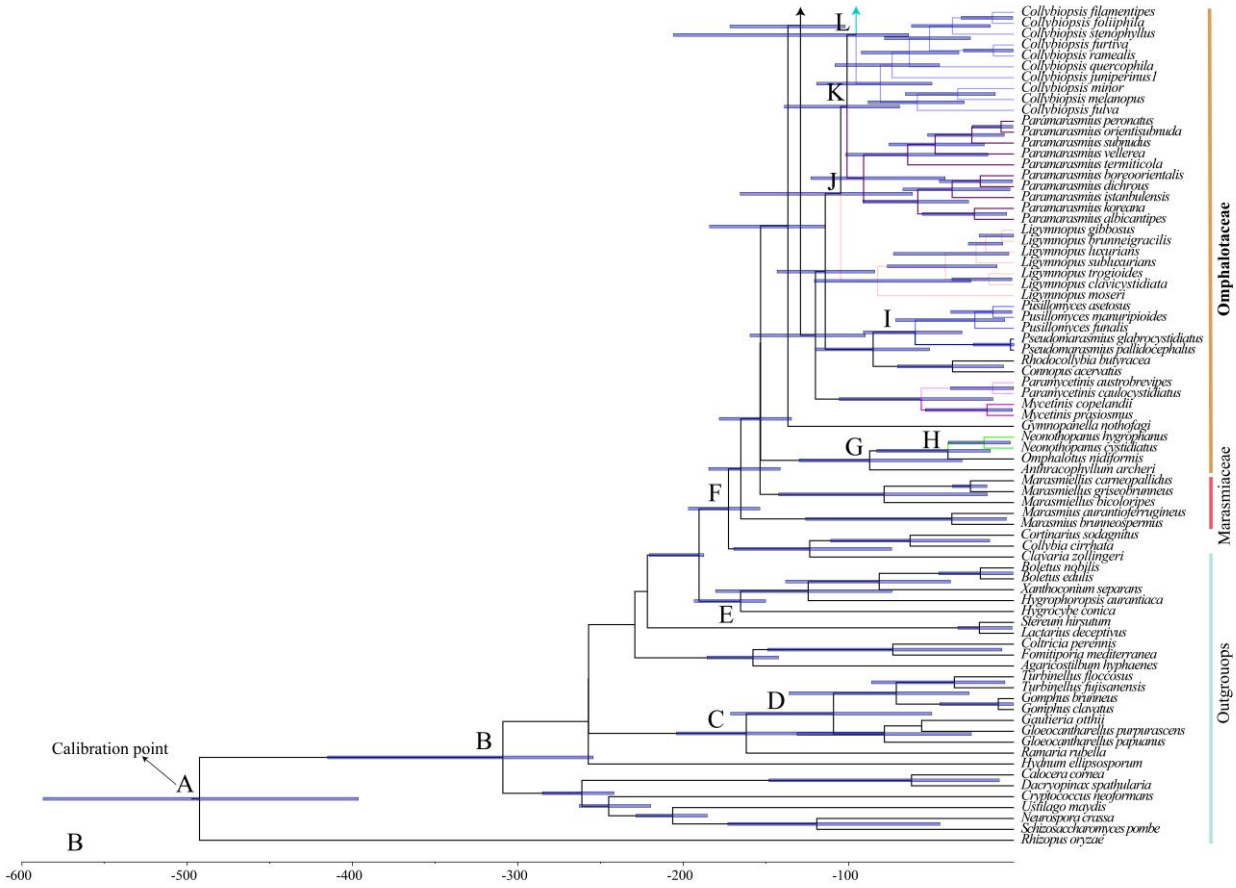

Figure 4 – Continued.

Table 2 Estimated divergence times of the main nodes.

Node	Mean ± standard error	95% HPD
A	492.5677 ± 1	396.4853–587.1236
B	309.1018 ± 1	254.4684–415.0397
C	161.8708 ± 0.5501	78.885–204.128
D	109.1376 ± 0.9194	49.6932–171.3855
E	165.3127 ± 0.2306	153.4271–189.0725
F	165.1802 ± 0.6342	141.3326–184.5799
G	87.2706 ± 0.7898	31.4–129.865
H	39.9068 ± 0.7848	14.2147–82.9897
I	59.71 ± 0.9021	31.4189–90.9928
J	105.7597 ± 0.737	61.3718–165.5979
K	100.9418 ± 0.1735	73.5270–137.0829
L	95.4694 ± 0.9083	63.7295–205.9148
M	88.8676 ± 0.4085	76.8501–113.0027
N	112.7686 ± 0.4356	
O	99.874 ± 0.9828	71.3192–140.8514

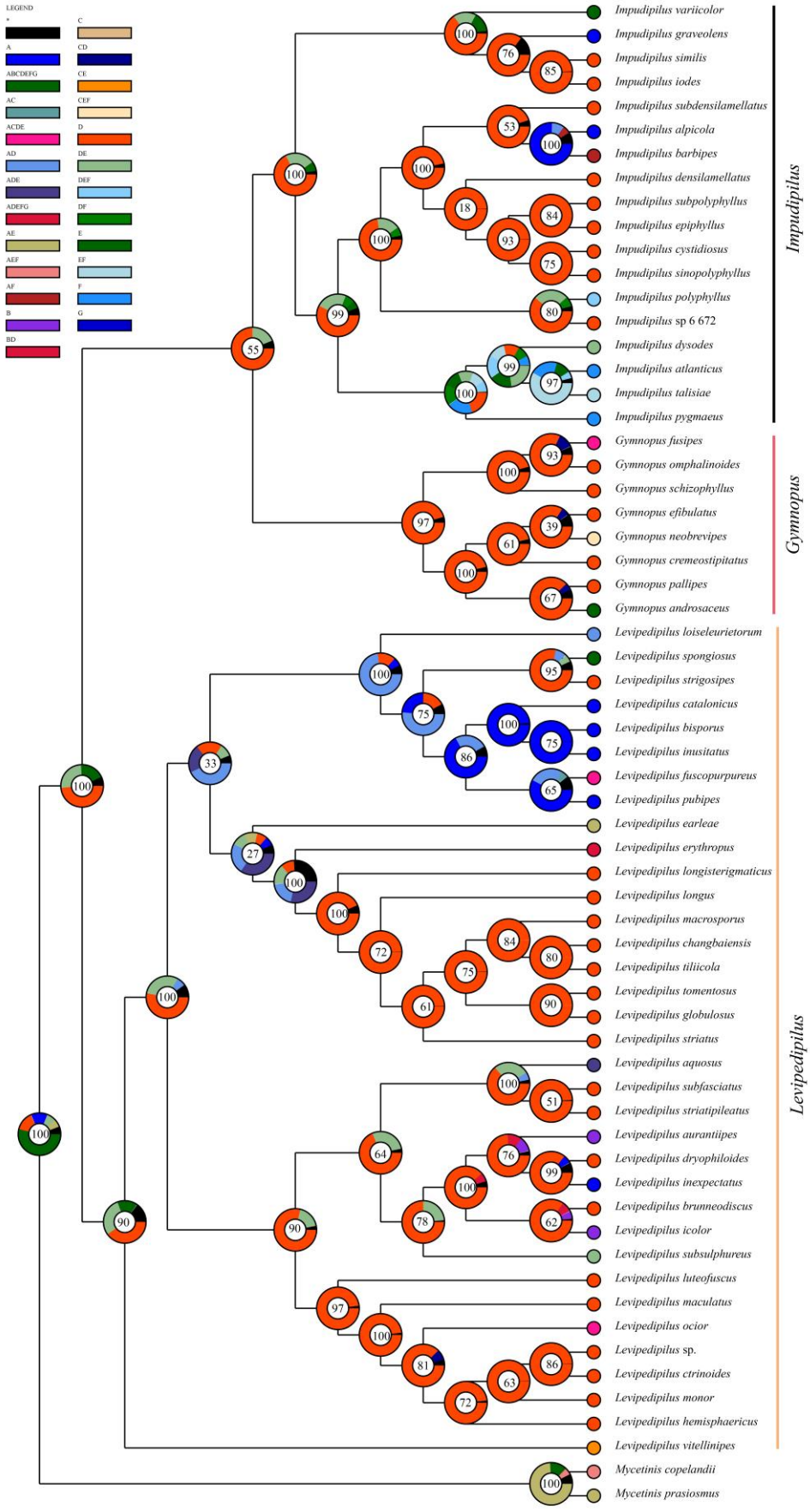

Figure 5 – Divergence time estimation and ancestral area reconstruction of *Gymnopus* based on ITS + nLSU sequences.

Taxonomy

Taxonomy characteristics

Basidiomata: Basidiomata of *Gymnopus* s.l. are small to large (He et al. 2023), collybioid to marasmioid (Antonín & Noordeloos 2010), and occasionally tricholomoid or mycenoid. The basidiomata of *Gymnopus* are marasmioid, sometimes collybioid, small, and occasionally large. The basidiomata of *Impudipilus* are collybioid, occasionally marasmioid, small to medium, and exhibit a foetid smell. The basidiomata of *Levipedipilus* are collybioid and small to medium. The basidiomata of *Collybia* are collybioid, and small. The basidiomata of *Rhodocollybia* are collybioid, occasionally tricholomoid, and small to medium. The basidiomata of *Neomarasmius* are marasmioid, occasionally collybioid or omphalinoid, and small. The basidiomata of *Ligymnopus* are collybioid, occasionally marasmioid, and small to medium. The basidiomata of *Vestipedipilus* are collybioid, occasionally marasmioid, and small (Fig. 6).

Figure 6 – Basidiomata characteristics of *Gymnopus* s.l.

Pileus: varies from nearly white to reddish or brown in colour. It is fresh, smooth, or slightly tomentose, striate, grooved, rugulose-striate, hygrophanus or not, not glutinous, hemispherical to convex or campaniform, and finally applanate or irregular, occasionally with an umbo at the disc. The margin is inrolled when young, then becomes straight, and is occasionally reflexed when mature. It is entire, lobed, or wavy, and may or may not be striate when moist (Fig. 7).

Figure 7 – Pileus characteristics of *Gymnopus* s.l.

Lamellae: white to light yellow, light brown, or yellow, uniform, distant to extremely crowded, free to adnate, unequal, not branched, narrow to wide, entire or serrated, and occasionally covered with pruinose or slightly tomentose at the edge (Fig. 8).

Stipe: cylindrical to clavate or enlarged at the base, hollow, fibrous, white to reddish brown, central, smooth, pruinose or tomentose, and occasionally striate (Fig. 9).

Habitat: *Gymnopus* s.l. grows on fallen leaves or branches, rotten wood, or on the ground. During our collections, we found that some specimens grew at the bases of living trees (Fig. 10).

Figure 8 – Lamellae characteristics of *Gymnopus* s.l.

Figure 9 – Stipe characteristics of *Gymnopus* s.l.

Figure 10 – Habitat of *Gymnopus* s.l.

Pileipellis: cuits to tricoderm, hyphae cylindrical, hyaline to brown, coralloid, branched, or lobed, sometimes with *Dryophila* structure or *Rameales* structure, diverticulate, and encrusted. The terminal cells are broom, coralloid, and can be flattened to spherical in shape. Sometimes layered, the upper layer flattened to spherical, diverticulate, sometimes encrusted, down layer flattened, branched, and encrusted. Clamp connections are present (Fig. 11).

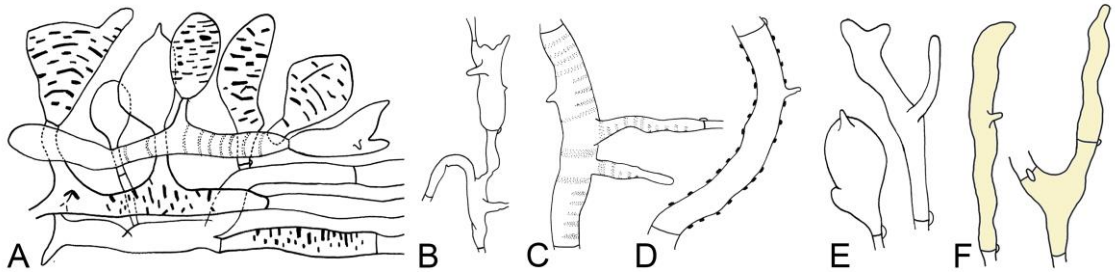

Figure 11 – Pileipellis characteristics of *Gymnopus* s.l. A layered pileipellis with bulbous terminal cells. B Coralloid pileipellis. C branched pileipellis with an annular pattern. D Encrusted pileipellis with diverticulate. E pileipellis inflate to bulbous. F light yellowish pileipellis with diverticulate.

Basidia: clavate to cylindrical, contains 1–4 sterigmate, either sterigmate short or extremely long, hyaline, thin-walled, and clamp connections present (Fig. 12A).

Basidiospores: cylindrical, oblong-elliptical to elliptical, or lacrymoid, sometimes pip-shaped, hyaline in 3% KOH, smooth, thin-walled, and inamyloid (Fig. 12C). Some of the basidiospores of *Rhodocollybia* are dextrinoid (Fig. 12B).

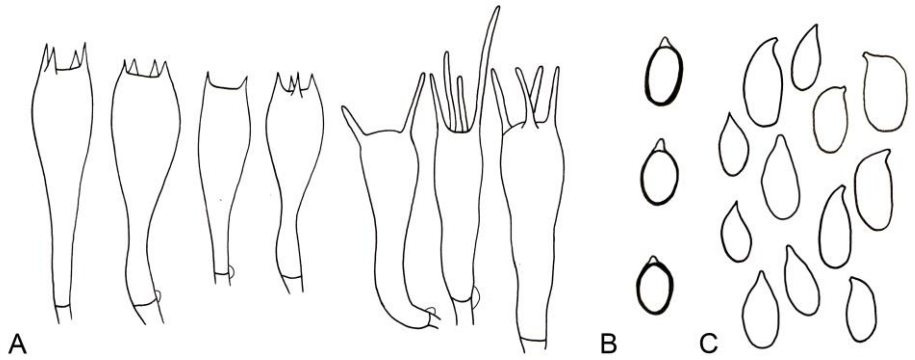

Figure 12 – Basidia and Basidiospores characteristics of *Gymnopus* s.l. A Basidia. B–C Basidiospores (B Dextrinoid basidiospores; C In-amyloid basidiospores).

Cheilocystidia: rare or abundant, hyaline, thin-walled, and exhibit a variety of shapes, clavate, irregular clavate, cylindrical, or clavate with an umbo, coralloid, or finger-like apex, and clamp connections present (Fig. 13).

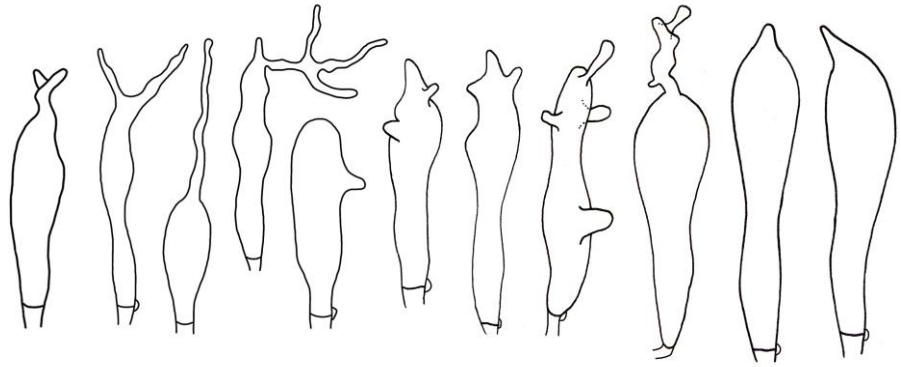

Figure 13 – Cheilocystidia characteristics of *Gymnopus* s.l.

Caulocystidia: absent to abundant, long clavate to cylindrical, occasionally branched or coralloid, hyaline, thin- to slightly thick-walled, and clamp connections present (Fig. 14).

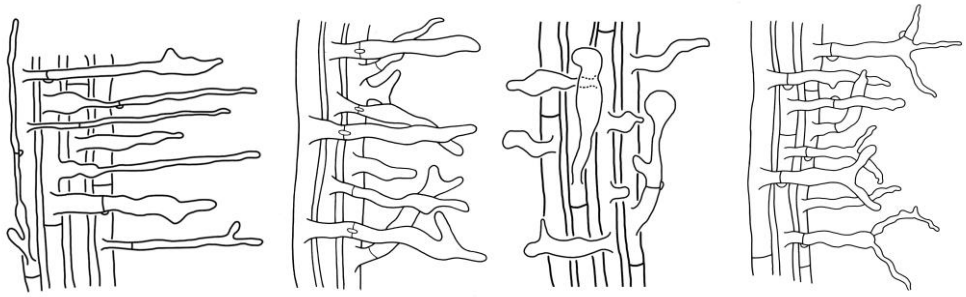

Figure 14 – Caulocystidia characteristics of *Gymnopus* s.l.

Key to the genera of *Gymnopus* s.l.

1 Basidiomata grows from sclerotium or decayed mushroom.....*Collybia*
1 Basidiomata does not grow from sclerotium or decayed mushroom.....2
2 Basidiomata dextrinoid.....*Rhodocollybia*
2 Basidiomata inamyloid.....3
3 Basidiomata marasmioid.....4
3 Basidiomata not marasmioid.....5
4 Stipe usually filiform.....*Gymnopus* s.str
4 Stipe not filiform.....*Neomarasmius*
5 Stipe smooth or covered with sparse tomentose.....*Levipedipilus*
5 Stipe covered with dense tomentose or pruinose.....6
6 Basidiomata with a strong smell reminding of rotten cabbage or onion …….....*Impudipilus*
6 Basidiomata without unpleasant smell.....7
7 Stipe with white mycelioid at the base.....*Vestipedipilus*
7 Stipe without white mycelioid at the base.....8
8 Cheilocystidia clavate, finger-like or coralloid at apex.....*Collybiopsis* s.str.
8 Cheilocystidia clavate, with an umbo at apex.....*Ligymnopus*

Collybia Fr.

Type species: *Collybia tuberosa* (Bull.) P. Kumm.

Collybia cirrhata (Schumach.) Quél. Figs 15, 16D–F

Basidiomata small, gregarious. Pileus convex to applanate-hemispherical, 0.1–0.6 cm diameter, white, deep colour at center, light yellow, umbo to slightly depressed at disc, striped, smooth; margin entire, wavy, white. Context extremely thin, fresh, odourless. Stipe central, cylindrical, 0.9–3.0 cm long and about 0.1 cm wide, flatten at apex, light yellow to fresh, farinose, covered with tomentose at base, fibrous. Lamellae distant, adnexed to adnate, white to light yellow, unequal.

Basidiospores subspherical to elliptical, 4.0–5.2(6.0) × (2.4)2.7–3.0(3.1) μm, Q = (1.33)1.37–1.71(2.00), Qm = 1.58 ± 0.16, hyaline, thin-walled, inamyloid. Basidia clavata, (12)14–19(20) × 3–5(6) μm, 2–4 spored, hyaline, thin-walled. Cheilocystidia and pleurocystidia absent. Pileipellis a cuits, made up of cylindrical hypha, coralloid, terminal hypha branched, diverticulate, 6–11(12) μm wide, hyaline, thin-walled, clamp connections abundant.

Habitat – Grows form decayed mushroom of *Cortinarius* s.l.

Specimens examined – China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, Shuangmu peak of Changbai Mountain, 21 August 2021, Jia-Jun Hu and Bo Zhang, HMJAU 61017 (Collcetion no. 871); Baishan City, Fusong County, Quanyang Town, 23 August 2021, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 61018 (Collcetion no. 884); Changchun City, Northeast Tiger Park, 14 September 2021, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 61019 (Collcetion no. 912); Inner Mongolia Autonomous Region: Hulunbuir City, Haolibao Forest Farm, 4 September 2021, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 61020 (Collcetion no. 899); Genhe City, Alongshan town, Alongshan forest farm, 5 September 2021, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 61021 (Collcetion no. 900); Heilongjiang Province: Mohe City, Guanyin Mountain, 6 September 2021, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 61022 (Collcetion no. 903); Mohe City, 28th Station Forest Farm, 8 September 2021, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 61023 (Collcetion no. 904).

Note – *Collybia cirrhata* is characterized by small and white to yellowish white basidiomata, a farinose to tomentose stipe, smooth basidiospores, absent of cheilocystidia and pleurocystidia, branched, coralloid, and diverticulate pileipellis, grow on the remains of decayed *Cortinarius* s.l. *Collybia cirrhata* is different from *C. tuberosa* (Bull.) P. Kumm. by the absent of cystidia and grow on remains of decayed *Cortinarius* s.l.

Before this study, *C. cirrhata* was usually reported as hosted on decayed *Russula* Pers. or *Lactarius* Pers. Through our investigation, the entire host was found and identified as *Cortinarus* s.l. Furthermore, this is the first time that *C. cirrhata* was recorded from Jilin Province, China.

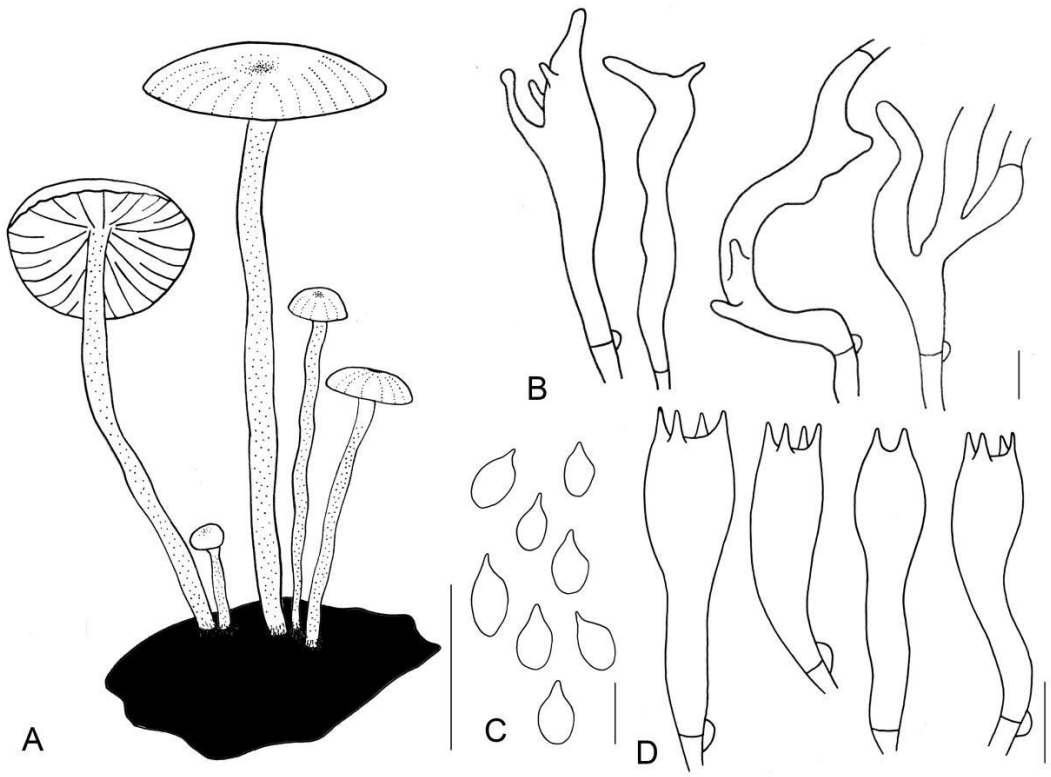

Figure 15 – Morphological character of *Collybia cirrhata* (HMJAU 61017). A Basidiomata. B Pileipellis elements. C Basidiospores. D Basidia. Scale bars: A = 0.5 cm, B = 10 μm, C, D = 5 μm.

Figure 16 – A–C *Rhodocollybia buyracea*. D–F *Collybia cirrhata*. G *Vestipedipilus hirtellus*. Scale bar = 1 cm.

Collybiopsis (J. Schröt.) Earle

Basidiomata collybioid, rare marasmioid, small. Pileus hemispherical, convex to applanate, striped or sulcate-striate, glabrous or rare tomentose. Lamellae adnate, adnaxed, free, or

subdecurrent, distant, white to light yellow. Stipe cylindrical, tapered downwards, tomentose or pruinose, lighter colour at apex.

Pileipellis a cuits, *Rameales*-structure or *Dryophila*-structure, encrusted, diverticulate. Basidiomata oblong-elliptical to cylindrical, occasionally lacrymoid, hyaline, smooth, inamyloid. Basidia clavate, 4-spored, rare 2-spored. Cheilocystidia clavate, wide clavate to irregular clavate, finger-like or coralloid at apex. Pleurocystidia present or not, clavate, slim fusiform, or wide clavate. Caulocystidia clavate, fusiform, or cylindrical.

Grows on fallen leaves or branches.

Type species: *Collybiopsis ramealis* (Bull.) Millsp.

Collybiopsis ramulicola (T.H. Li & S.F. Deng) J.S. Kim & Y.W. Lim Fig. 17

The macro-character was referred to the original description (Deng et al. 2016).

Basidiospores ellipsoid to oblong, 7.2–9.8 × 3.6–5.1 μm, Q = 1.53–2.00, Qm = 1.80 ± 0.15, hyaline, thin-walled, inamyloid. Basidia clavate to subcylindrical, (23)25–36 × 5–6(7) μm, 2- or 4-spored, hyaline, thin-walled. Cheilocystidia chavate, with a long umbo at apex, (24)27–38 × 4–6(8) μm, hyaline, thin-walled. Pleurocystidia and caulocystidia not observed. Pileipellis a cuits, made up of radially arranged cylindrical hyphae, 9–17(19) μm, diverticulate, hyaline, thin-walled. Clamp connections present.

Specimen examined – Hainan Province: Ledong County, Jianfengling National Forest Park, 29 June 2013, Chao-Qun Wang, GDGM 43884, holotype (!).

Note – This species was observed and description from China by Deng et al. (2016), and in its original description, the cheilocystidia were described as basidioles-like. However, when we rechecked the holotype, the clavate with a long umbo at apex cheilocystidia were found, which diverged from the original description. In addition, from our observations, the sizes of basidia and cheilocystidia were larger than those outlined in the original description.

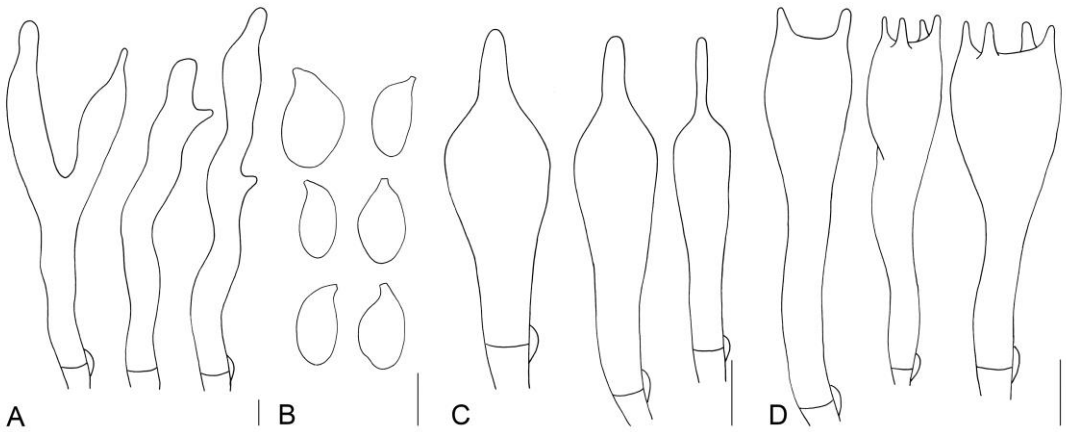

Figure 17 – Micro-morphological character of *Collybiopsis ramulicola* (GDGM 43884!). A Pileipellis elements. B Basidiospores. C Cheilocystidia. D Basidia. Scale bars: A = 10 μm, C–D = 5 μm.

Gymnopus (Pers.) Roussel

Basidiomata marasmioid, collybioid sometimes, small, gregarious. Pileus hemispherical to convex, finally applanate, depressed to umbilicate sometimes, smooth, striped, or sulcate-striate, furfuraceous sometimes. Lamellae adnate to free, distant, occasionally with cross vein, forming pseudocollarium sometimes, white to brown. Stipe filiform, cylindrical to fusiform sometimes, central, occasionally eccentric, smooth, glabrous, tomentose or pruinose, insititious or not. Rhizomorphs present or not.

Pileipellis a cuits, repent, radially, smooth or encrusted; terminal cells broom, coralloid, or *Rameales*-structure, hyaline, thin-walled. Basidiospores oblong-elliptical to elliptical or lacrymoid, smooth, hyaline, inamyloid. Cheilocystidia broom or irregular clavate, with an umbo or finger-like at apex, hyaline, thin-walled. Basidia clavate, 4-spored. Pleurocystidia and caulocystidia absent.

Grows on fallen leaves and branches or roots and stumps.

Type species: *Gymnopus fusipes* (Bull.) Gray

Key to the section of *Gymnopus*

1 Basidiomata marasmioid, stipe filiform.....2
1 Basidiomata collybioid, stipe fusiform.....Sect. *Gymnopus*
2 All parts do not react with Melzer's reagent.....3
2 Some parts react with Melzer's reagent.....4
3 Pileipellis with *Rameales* structure.....Sect. *Omphalinoides*
3 Pileipellis without *Rameales* structure .....Sect. *Irresolutus*
4 Pileipellis hyphae dextrinoid.....Sect. *Brunneiniger*
4 Pileipellis hyphae inamyloid.....5
5 Stipitipellis dextrinoid, and stipe trama inamyloid.....Sect. *Androsasei*
5 Stipitipellis and stipe trama dextrinoid.....Sect. *Efibulatus*

Gymnopus (Pers.) Roussel

I Sect. *Gymnopus* (Pers.) Roussel

Type species: *Gymnopus fusipes* (Bull.) Gray

II Sect. *Omphalinoides* J.J. Hu, B. Zhang & Y. Li

Type species: *Gymnopus Omphalinoides* J.P. Li, T.H. Li & Yu Li

III Sect. *Irresolutus* J.J. Hu, B. Zhang & Y. Li

Type species: *Gymnopus irresolutus* Desjardin & B.A. Perry

IV Sect. *Brunneiniger* J.J. Hu, B. Zhang & Y. Li

Type species: *Gymnopus brunneiniger* César, Bandala & Montoya

V Sect. *Androsasei* (Kühner) Antonín & Noordel.

Type species: *Gymnopus androsaceus* (L.) Della Magg. & Trassin.

VI Sect. *Efibulatus* J.J. Hu, B. Zhang & Y. Li

Type species: *Gymnopus efibulatus* J.P. Li, Chang Tian Li, Chun Y. Deng & Yu Li

Sect. Androsacei (Kühner) Antonín & Noordel.

Basidiomata small, marasmioid. Pileus membranous, hemispherical or convex to applanate, slightly depressed or depressed to umbilicate, grooved or sulcate-striate, glabrous. Lamellae adnate to adnaxed, distant, forming pseudocollarium sometimes, white to light brown. Stipe filiform, insititious, flatten at base, glabrous, lighter colour at apex. Rhizomorphs present. Pileipellis inamyloid or non-dextrinoid, terminal cells broom or not. Pileus trama inamyloid or non-dextrinoid. Cheilocystidia broom. Stipitipellis dextrinoid and stipe trama non-dextrinoid.

Grows on fallen leaves and branches.

Type species: *Gymnopus androsaceus* (L.) Della Magg. & Trassin.

Gymnopus androsaceus (L.) Della Magg. & Trassin.

For a detailed description see Antonín & Noordeloos (2010).

Gymnopus pallipes J.P. Li & Chun Y. Deng

For a detailed description see Li et al. (2021b).

Sect. *Brunneiniger* J.J. Hu, B. Zhang & Y. Li, sect. nov.

Etymology – Derived from the name of the type species of the section.

Fungal names: FN571345

Basidiomata small, marasmioid. Pileus convex to applanate-convex, radial striped. Lamellae adnate to free, transversal veins present. Stipe filiform, cylindrical, insititious, smooth. Pileipellis a cuits, broom cells absent, dextrinoid. Pileus trama some dextrinoid otherwise inamyloid. Cheilocystidia full with broom cells. Stipitipellis and stipe trama inamyloid. Rhizomorphs present.

Usually grows on fallen leaves in broad-leaf forests.

Type species: *Gymnopus brunneiniger* César, Bandala & Montoya

Gymnopus brunneiniger César, Bandala & Montoya

For a detailed description see César et al. (2020).

Sect. *Efibulatus* J.J. Hu, B. Zhang & Y. Li, sect. nov.

Etymology – Derived from the name of the type species of the section.

Fungal names: FN571346

Basidiomata marasmioid, small. Pileus hemispherical or convex to applanate, rugulose. Lamellae adnate, distant. Stipe filiform, cylindrical, smooth or tomentose. Rhizomorphs present or not. Pileipellis inamyloid and non-dextrinoid, terminal cells broom. Pileus trama inamyloid and non-dextrinoid. Stipitipellis and stipe trama dextrinoid.

Usually grows on fallen leaves or branches.

Type species: *Gymnopus efibulatus* J.P. Li, Chang Tian Li, Chun Y. Deng & Yu Li

Gymnopus cremeostipitatus Antonín, Ryoo & Ka

For a detailed description see Antonín et al. (2014).

Gymnopus neobrevipes R.H. Petersen

For a detailed description see Petersen & Hughes (2019).

Gymnopus efibulatus J.P. Li, Chang Tian Li, Chun Y. Deng & Yu Li Fig. 18

The macro-character was referred to the original description (Li et al. 2022b).

Basidiospores ellipsoid to oblong, 7–9 × (3.0)3.2–4.1(4.2) μm, Q = (1.67)1.85–2.24(2.33), Qm = 2.09 ± 0.16, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (20)21–30(33) × 4–8 μm, hyaline, thin-walled. Cheilocystidia clavate, with an umbo or finger-like at apex, hyaline, thin-walled. Pleurocystidia and caulocystidia not observed. Stipitipelis dextrinoid, thin- to thick-walled. Clamp connections present.

Specimen examined – China. Guizhou Province: Tongreng City, JiangKou County, Mt. Fanjin, 22 April 2020, Huan Gao, Jing Zhang, Zhong-Quan, Shu, De-Jun Ou HGASMF01-7052, holotype (!).

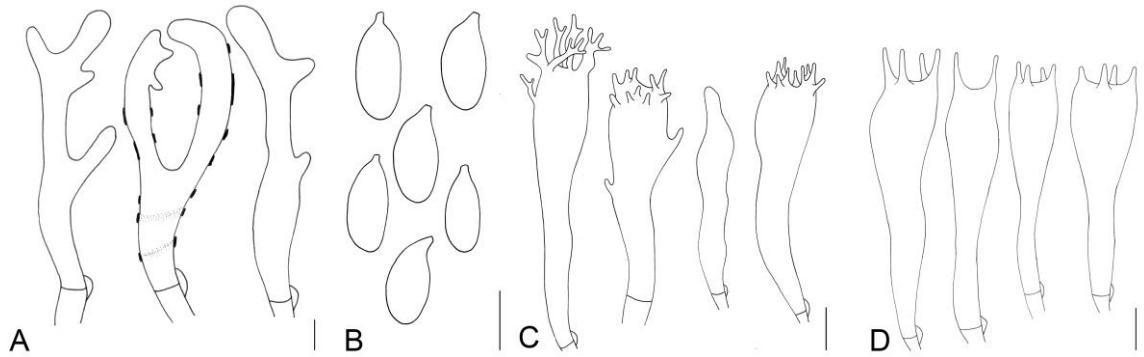

Figure 18 – Micro-morphological character of *Gymnopus efibulatus* (HGASMF01-7052!). A Pileipellis elements. B Basidiospores. C Cheilocystidia. D Basidia. Scale bars: A = 10 μm, C–D = 5 μm.

Sect. *Gymnopus* (Pers.) Roussel

Basidiocarps fleshy; stipe fusoid, deeply longitudinally striate to sulcate, forming a distinct pseudorrhiza; spore print white to pale ochraceous; cheilocystidia present; pileipellis a transition between cutis and trichoderm, made up of inflated, irregular, often coralloid elements, similar the *Dryophila*-structure, often slightly gelatinised Chemical reactions. No part of carpophores dextrinoid or cyanophilous (Antonín & Noordeloos 2010).

Type species: *Gymnopus fusipes* (Bull.) Gray

Gymnopus fusipes (Bull.) Gray

For a detailed description see Antonín & Noordeloos (2010).

Sect. *Irresolutus* J.J. Hu, B. Zhang & Y. Li, sect. nov.

Etymology – Derived from the name of the type species of the section.

Fungal names: FN571347

Basidiomata small, marasmioid. Pileus convex to applanate, glabrous. Lamellae adnate, distant, brown with gray or pink tone. Stipe cylindrical, filiform, minutely pruinose. Rhizomorphs absent. Pileipellis a cuits, broom cells and *Rameales*-structure absent. All tissues inamyloid.

Usually grows on fallen leaves or branches.

Type species: *Gymnopus irresolutus* Desjardin & B.A. Perr

Gymnopus irresolutus Desjardin & B.A. Perry

For a detailed description see Desjardin & Perry (2017).

Sect. *Omphalinoides* J.J. Hu, B. Zhang & Y. Li, sect. nov.

Etymology – Derived from the name of the type species of the section.

Fungal names: FN571348

Basidiomata small, marasmioid. Lamellae adnate, ventricose to broadly ventricose, distant, white to brown. Stipe cylindrical, glabrous, or tomentose when young, becoming smooth when old. Pileipellis a cuits, *Rameales*-structure present, absent of broom cells. Cheilocystidia irregularly clavate, enlarged, finger-like or diverticulate at apex. All tissues inamyloid.

Usually grows on stumps or rooting around the roots.

Type species: *Gymnopus omphalinoides* J.P. Li, T.H. Li & Y. Li

Gymnopus omphalinoides J.P. Li, T.H. Li & Y. Li

For a detailed description see Li et al. (2022a).

Gymnopus schizophyllus J.P. Li, T.H. Li & Y. Li

For a detailed description see Li et al. (2022a).

2.3.4 *Impudipilus* J.J. Hu, B. Zhang & Y. Li, gen. nov.

Etymology – *Impudipilus* referes to this genus is arise from sect. *Impudicae*.

Fungal names: FN571336

Basidiomata marasmioid to collybioid, small to large, solitary to gregarious, with a strong smell reminding of rotten cabbage or onion. Stipe tomentose or pruinose, cylindrical to clavate.

Pileipellis a cuits, cylindrical, diverticulate, not inflatten, encrusted, thin- or thick-walled. Basidiospores elliptical, thin-walled, hyaline, inamyloid. Cheilocystidia inconspicuous, clavate, clavate with branched or an umbo at apex. Clamp connection present.

Grows on fallen leaves, branches, or ground.

Type species: *Impudipilus impudicus* (Fr.) J.J. Hu, B. Zhang & Y. Li

Impudipilus J.J. Hu, B. Zhang & Y. Li

I Sect. *Similis* J.J. Hu, B. Zhang & Y. Li

Type species: *Impudipilus similis* (Antonín, Ryoo & Ka) J.J. Hu, B. Zhang & Y. Li

II Sect. *Impudicae* J.J. Hu, B. Zhang & Y. Li

Type species: *Impudipilus impudicus* (Fr.) J.J. Hu, B. Zhang & Y. Li

III Sect. *Dysodes* J.J. Hu, B. Zhang & Y. Li

Type species: *Impudipilus dysodes* (Halling) J.J. Hu, B. Zhang & Y. Li

Key to the section of *Impudipilus*

1 Basidiomata marasmioid, colour of lamellae variety, white, purple, purple-gary, gary-brown, etc., grows on ground.....Sect. *Similis*

1 Basidiomata collybioid, occasionally marasmioid, lamellae white to brown, grows on fallen leaves or branches.....2

2 Lamellae close to extremely crowded, stipe covered with tomentose or pruinose, with white tomentose or hispid.....Sect. *Impudicae*

2 Lamellae distant to close, stipe covered with pruinose or furfuraceous, cheilocystidia inconspicuous.....Sect. *Dysodes*

Impudipilus alliifoetidissimus (T.H. Li & J.P. Li) J.J. Hu, B. Zhang & Y. Li, comb. nov. Fig. 19

≡ *Gymnopus alliifoetidissimus* T.H. Li & J.P. Li

Fungal names: FN571349

Basidiomata small, gregarious. Pileus flat hemispherical to convex, or reflect, 0.35–0.55 cm in diameter, grooved, entirely white; margin entire, wavy sometimes, white. Context extremely thin, fresh, with a strong smell, reminding of garlic to shallot flavour. Stipe central or eccentric, 0.2–0.5 cm long and about 0.1 cm wide, white, pruinose, hollow, fibrous. Lamellae adnate, distant, unequal.

Basidiospores ellipsoid, (5.8)6.0–7.1(7.2) × 3.1–4.0 µm, Q = (1.50)1.60–2.19(2.23), Qm = 1.89 ± 0.20, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (16)18–25(26) × (3)4–6 µm, 2- or 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, with projections at apex sometimes, (17)18–30(31) × 3–6 µm, thin-walled, hyaline. Caulocystidia abundant, clavate, 59–100 × 3–7 µm, thin-walled, hyaline. Pileipellis a cuits, branched, hyaline to brown, 3–10(11) µm wide, clamp connections abundant.

Habitat – Saprophytic on decayed twigs or small branches in bamboo and pine mixed forests.

Specimens examined – China. Anhui Province: Lu'an City, Jinzhai County, Tiantangzhai Scenic Spot, 7 July 2022, Jia-Jun Hu, Yong-Lan Tuo, Yi-Ming Li, and Wei-Jun Li, HMJAU 61024 (Collection no.: 1027); Fujian Province: Wuyishan City, Wuyishan National Park, 7 July 2016, Yuan-Hao Ma, HMJAU 61025 (Collection no.: 950); Zhejiang Province: Shaoxing City, Keqiao County, Pingshui Town, 7 June 2020, Jia-Jun Hu, HMJAU 61026 (Collection no.: 507); Guangdong Province: Zhaoqing City, Dinghu District, Dinghushan National Nature Reserve, 12 July 2019, Ming Zhang, Ji-Peng Li, and Hua-Shu Wen, GDGM 76695, Holotype (!).

Note – This species was observed and described in Guangdong Province, China, by Li et al. (2021a). It is characterized by its small basidiomata, having a strong garlic- to shallot-like smell, being entirely white, growing from rotten wood (especially bamboo), having inconspicuous cheilocystidia, and the presence of caulocystidia. The current study is the first report of this species from Anhui, Zhejiang, and Fujian Province, China.

Sect. *Impudicae* (Antonín and Noordel.) J.J. Hu, B. Zhang & Y. Li, comb. nov.

Fungal names: FN571351

Basidiomata collybioid, marasmioid smoetimes, small to medium, gregarious. Pileus hemispherical, convex, or applanate-convex to applanate, smooth, glabrous, striped sometimes, tomentose at margin occasionally. Lamellae adnate to free, crowded to extremely crowded, withe to light brown. Stipe cylindrical or tapered downwards, flatten at base sometimes, tomentose or pruinose, white tomentose at base.

Pileipellis a cuits, repent, radically, smooth or encrusted; terminal cells branched, weakly coralloid or finger-like, diverticulate sometimes. Basidiospores oblong-elliptical to cylindrical, or lacrymoid, hyaline, thin-walled, inamyloid. Basidia clavate, 4-spored, hyaline, thin-walled. Cheilocystidia cylindrical to clavate, or irregular clavate, with an umbo, finger-like, or weakly coralloid at apex. Caulocystidia cylindrical to clavate, moniliform sometimes, with an umbo or forking.

Grows on fallen leaves or branches.

Type species: *Impudipilus impudicus* (Fr.) J.J. Hu, B. Zhang & Y. Li

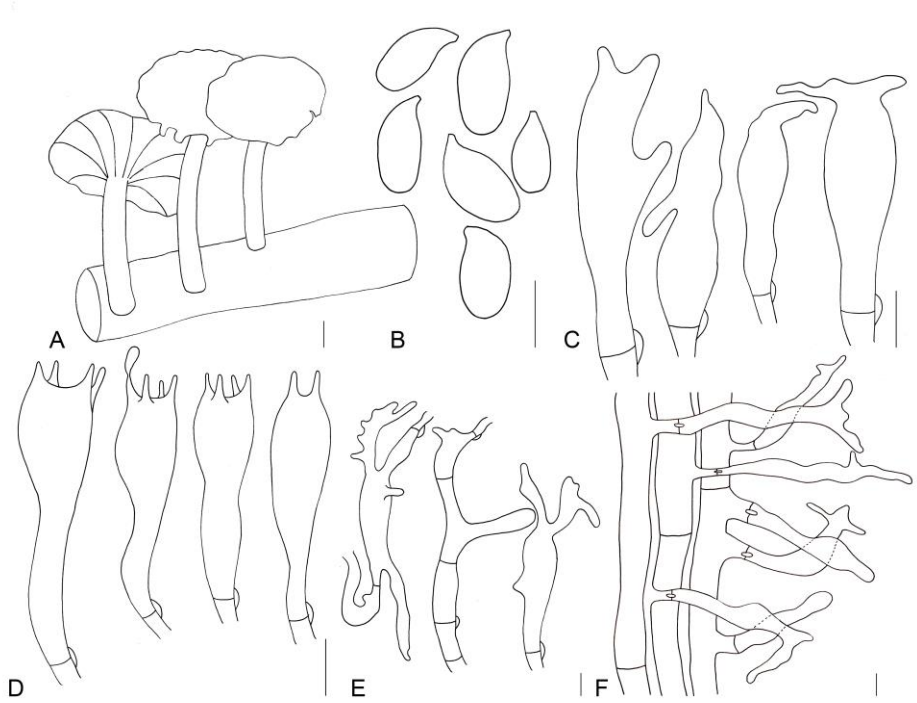

Figure 19 – Morphological characterize of *Impudipilus alliifoetidissimus* (HMJAU 61024). A Basidiomata. B Basidiospores. C Cheilocystidia. D Basidia. E Pileipellis. F Caulocystidia. Scale bars: A = 0.1 cm, B–D = 5 μm, E, F = 10 μm.

Key to the species of Sect. *Impudicae* present in this study

1 Basidiomata marasmioid.....*Imopudipilus* cf. *brassicolens*
1 Basidiomata collybioid.....2
2 Basidiomata large.....3
2 Basidiomata small to medium.....4
3 Pileus yellow when young, fading to yellowish white, light yellow at disc when mature.....
.....*Imopudipilus densilamellatus*
3 Pileus white when young, brown at disc when mature……*Imopudipilus albumistipticus*
4 Pleurocystidia presence.....*Imopudipilus cystidiosus*
4 Pleurocystidia absence.....5
5 Brown spots appear when old.....*Imopudipilus campanifomipileatus*
5 Spots would not show when old.....6
6 Stipe covered with bristle.....*Imopudipilus minisporus*
6 Stipe covered with tomentose or pruinose.....7
7 Surface of pileus smooth, glabrous.....*Imopudipilus subdensilamellatus*
7 Margin of surface covered with tomentose.....8
8 Basidiomata longer than 7 μm.....*Imopudipilus epiphyllus*
8 Basidiomata shorter than 7 μm.....*Imopudipilus subpolyphyllus*

Impudipilus campanifomipileatus J.J. Hu, Y.L. Tuo, B. Zhang & Y. Li, sp. nov. Figs 20, 34M–N

Fungal name: FN571352

Etymology – "campanifomipileatus" refers to the species with campanifom pileus.

Diagnosis – This species could be distinguished from other species by its white at first, then rust-brown to reddish brown pileus with brown spots when mature, striped margin, pruinose and striped stipe, and absence of caulocystidia.

Type – China. Jilin Province: Tonghua City, Ji'an city, Wunvfeng National Forest Park, 10 August 2019, Yong-Lan Tuo, HMJAU 61027 (Collection no.: Hu 367), holotype.

Basidiomata small to medium, solitary to gregarious. Pileus hemispherical, campaniform to convex, applanate or reflex when mature, 1.3–3.7 cm in diameter, smooth, glabrous, light yellow at disc, white outwards at first, rust-brown to reddish brown at disc, light yellowish brown to light rust-brown when mature, with brown spots; margin entire, slightly lobed, wavy sometimes, striped, white, with rust-brown spots. Context thin, white to fresh-pink, with a strong smell reminding of rotten cabbage or onion. Stipe central, clavate, 1.8–4.5 cm long and 0.2–0.5 cm wide, fresh-pink upwards, nearly white near base, striped, pruinose, hollow, fibrous. Lamellae adnate to adnexed, crowded, white, unequal, with rust-brown spots when mature.

Basidiospores ellipsoid, (5.0)5.1–8.2(10.0) × 2.8–3.2 µm, Q = (1.67)1.82–2.62(3.13), Qm = 2.21 ± 0.36, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (18)19–26 × 4–7(8) µm, 2- or 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, branched or with an umbo at apex, 18–31 × 4–8 µm, thin-walled, hyaline. Caulocystidia and pleurocystidia absent. Pileipellis a cuits, branched, hyaline, diverticulate, 5–11(15) µm wide, clamp connections abundant.

Habitat – Saprophytic on deciduous layer in broad-leaved forests.

Other specimens examined – China. Jilin Province: Tonghua City, Ji'an city, Wunvfeng National Forest Park, 12 August 2019, Yong-Lan Tuo, HMJAU 61028 (Collection no.: Hu 369); Tonghua City, Ji'an city, Wunvfeng National Forest Park, 24 August 2020, Yong-Lan Tuo, HMJAU 61029 (Collection no.: Hu 672).

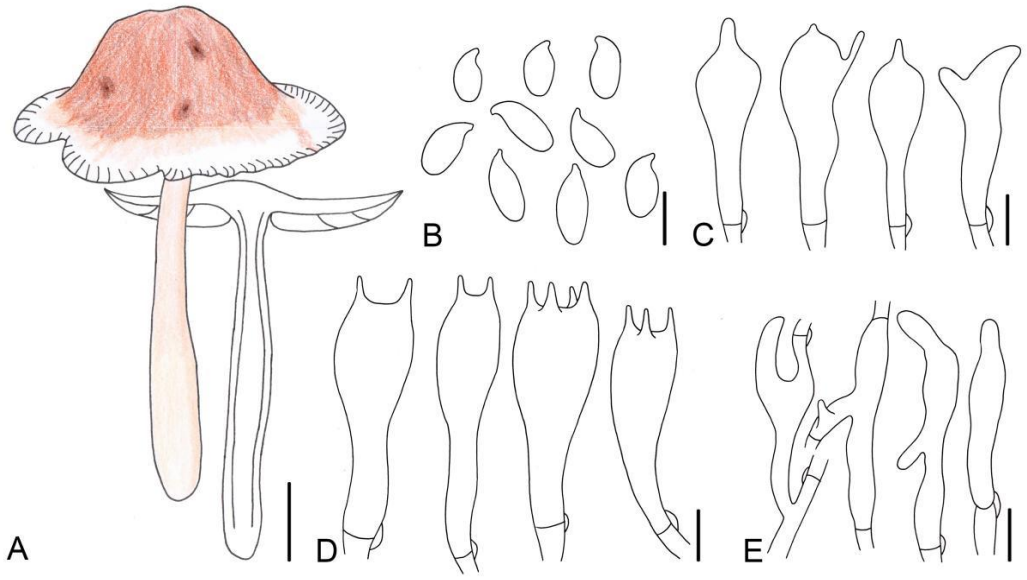

Figure 20 – Morphological characterize of *Impudipilus campanifomipileatus* (HMJAU 61027). A Basidiomata, B Basidiospores. C Cheilocystidia. D Basidia. E Pileipellis elements. Scale bars: A = 1 cm, B–D = 5 µm, E = 10 µm.

Note – This species is characterized by its white colour in the early stage, which then turns into a rust-brown to reddish brown pileus with brown spots when mature, having a striped margin, pruinose and striped stipe, a strong rotten cabbage- or onion-like smell, large basidiospores, and absence of caulocystidia.

Morphologically, *I. campanifomipileatus* is highly similar to *I. hariolorum*, as both exhibit a strong smell and white basidiomata. However, *I. campanifomipileatus* differs from *I. hariolorum* by being white in the early stage, then developing a rust-brown to reddish brown pileus, having adnate to adnexed lamellae, slighter larger basidiospores, 2- or 4-spored basidia, and absence of caulocystidia.

Impudipilus minisporus J.J. Hu, B. Zhang & Y. Li, sp. nov. Fig. 21

Fungal names: FN571353

Etymology – "minisporus" refers to this with small basidiospores.

Diagnosis – This species differs from other species by small basidiomata, hemispherical to convex pileus that pinkish brown at center and near white at margin, close lamellae, dense tomentose stipe, smaller basidiospores, branched or coralloid pileipellis with long and slim branches, clavate cheilocystidia with an umbo, branched, lobed, or finger-like at apex, clavate caulocystidia with branch or long and slim umbo at apex.

Type – China. Jilin Province: Baishan City, Fusong County, Lushuihe Town, Yongqing Forest Farm, 7 July 2018, Jia-Jun Hu, Ao Ma, and Xiao-Qi Xu, HMJAU 61030 (Collection no.: Hu 33), holotype.

Basidiomata small, solitary or scattered. Pileus hemispherical to convex, 1.6–2.0 cm in diameter, smooth, glabrous, hygrophanus, pinkish brown at disc, paler outwards, fresh-pink; margin entire, involute, wavy, hygrophanus, white to pinkish white. Contexy thin, fresh, odourless. Stipe central, cylindrical, 3.5–5.2 cm long and 0.2–0.3 cm wide, covered with dense tomentose, white to fresh-pink, deeper colour downwards, fistulose, fibrous. Lamellae adnate to adnexed, clos, white, unequal.

Basidiospores ellipsoid, (5.4)5.8–6.8(7.0) × 2.8–3.2(3.3) µm, Q = 1.87–2.14(2.33), Qm = 2.02 ± 0.12, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (14)17–26(28) × 4–6 µm, 2–4 spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, with an umbo at apex, branched, or projections sometimes, (15)17–40 × 3–6(7) µm, thin-walled, hyaline. Caulocystidia abundant, clavate, branched, (15)17–40 × 3–6(7) µm, thin-walled, hyaline. Pileipellis a cuits, branched, hyaline, 5–12(13) µm wide, clamp connections abundant.

Habitat – Saprophytic on the deciduous layer in broad-leaved forests.

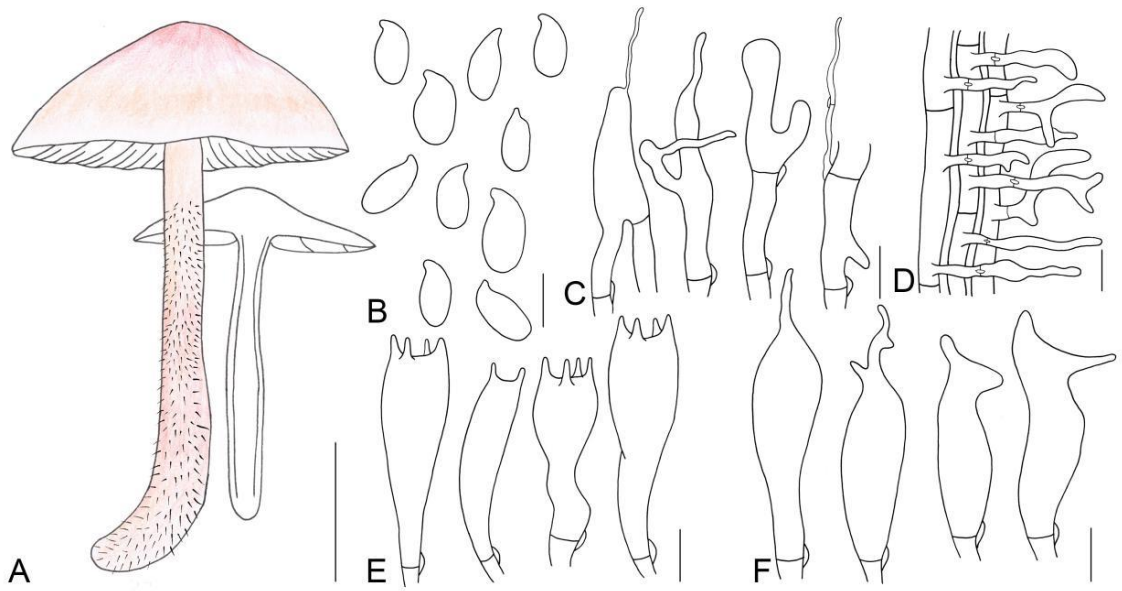

Figure 21 – Morphological characterize of *Impudipilus minisporus* (HMJAU 61030). A Basidiomata. B Basidiospores. C Pileipellis elements. D Caulocystidia. E Basidia. F Cheilocystidia. Scale bars: A = 1 cm, D = 15 µm, C = 10 µm, B, E, F = 5 µm.

Other specimen examined – China. Liaoning Province: Fushun City, Xinbin Manchu Autonomous County, Gangshan National Forest Park, Ao Ma and Jia-Jun Hu, HMJAU 61031 (Collection no.: Hu 121).

Note – This species is characterized by having small basidiomata, a hemispherical to convex pileus that is pinkish brown at the center and near white at the margin, close lamellae, a dense tomentose stipe, smaller basidiospores, a branched or coralloid pileipellis with long and slim branches, clavate cheilocystidia, with an umbo, branched, lobed, or finger-like at the apex, and having clavate caulocystidia with branches or a long and slim umbo at the apex.

This species is highly morphologically similar to *Vestipedipilus eneficola*. However, this species differs from *V. eneficola* by its dense tomemtose stipe, being without grooved, thin, smaller basidiospores, and having thin-walled pileipellis that has long and slim branches, as well as short caulocystidia.

Impudipilus albumistipticus J.J. Hu, B. Zhang & Y. Li, sp. nov. Figs 22, 34E

Fungal names: FN571354

Etymology – "albumistipticus" refers to this species with white stipe.

Diagnosis – This species could be distinguished from other species by the white pileus, brown at disc, white stipe and lamellae, tomentose stipe with cylindrical or clavate shape, with a rotten cabbage or onion smell, smaller basidiospores, flatten pileipellis, irregular and branched cheilocystidia.

Type – China. Jilin Province: Baishan City, Changbai Korean Autonomous County, Wangtian'er Scenic Area, 2 August 2019, Rui Ma and Zeng-Yi Bi, HMJAU 61032 (Collection no.: Hu 409).

Basidiomata medium to large, scattered to gregarious. Pileus convex, 3.7–5.6 cm in diameter, deep brown at disc, paler outwards, white to light pinkish brown, smooth, glabrous; margin entire, slightly lobed, wavy, hygrophanus, white. Context thin, white, fresh, with a strong smell reminding of rotten cabbage or onion. Stipe central, 5.1–7.3 cm long and 0.3–0.6 cm wide, cylindrical or clavate, pruinose, hollow, fibrous. Lamellae adnexed, close, white, unequal.

Basidiospores ellipsoid, (4.2)4.4–6.0 × (2.7)2.8–3.2(3.7) µm, Q = (1.48)1.56–2.00, Qm = 1.67 ± 0.14, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (15)16–26 × 4–6(7) µm, 2- or 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, branched or finger-like at apex, 16–30 × 3–5 µm, thin-walled, hyaline. Caulocystidia abundant, clavate or irregularly clavate, branched at apex, 40–77 × 3–4 µm, thin-walled, hyaline. Pleurocystidia absent. Pileipellis a cuits, branched or coralloid hyphae, flatten, hyaline, diverticulate, 9–20(25) µm wide, clamp connections abundant.

Habitat – Saprophytic on deciduous layer in broad-leaved forests.

Note – This species is characterized by its white pileus, being brown at the disc, having a white stipe and lamellae, a tomentose stipe that is cylindrical or clavate in shape, exhibiting a rotten cabbage- or onion-like smell, smaller basidiospores, a flattened pileipellis, and irregular and branched cheilocystidia.

Impudipilus albumistipticus is morphologically similar to *Impudipilus densilamellatus* due to sharing near-white basidiomata. However, *I. albumistipticus* differs from *I. densilamellatus* by its unchanging pileus colour, cylindrical or clavate and coarser stipe, and close, uncrowded lamellae. In micro-structure, *I. albumistipticus* differs by its smaller basidiospores, flattened pileipellis, and non-finger-like cheilocystidia.

Impudipilus* cf. *brassicolens (Romagn.) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 23, 34G

= *Gymnopus brassicolens* (Romagn.) Antonín & Noordel.

= *Collybia brassicolens* (Romagn.) Bon

= *Marasmius brassicolens* Romagn.

= *Micromphale brassicolens* (Romagn.) P.D. Orton

Fungal names: FN571355

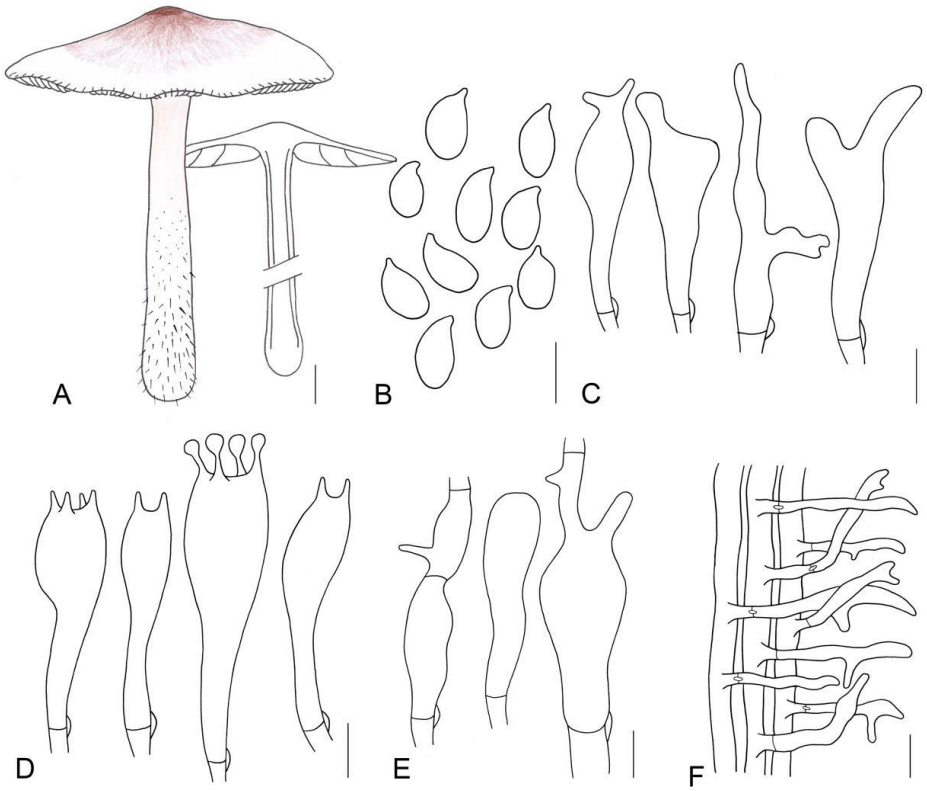

Figure 22 – Morphological characterize of *Impudipilus albumistipticus* (HMJAU 61032). A Basidiomata. B Basidiospores. C Cheilocystidia. D Basidia. E Pileipellis elements. F Caulocystidia. Scale bars: A = 1 cm, B–D = 5 μm, E = 10 μm, F = 15 μm.

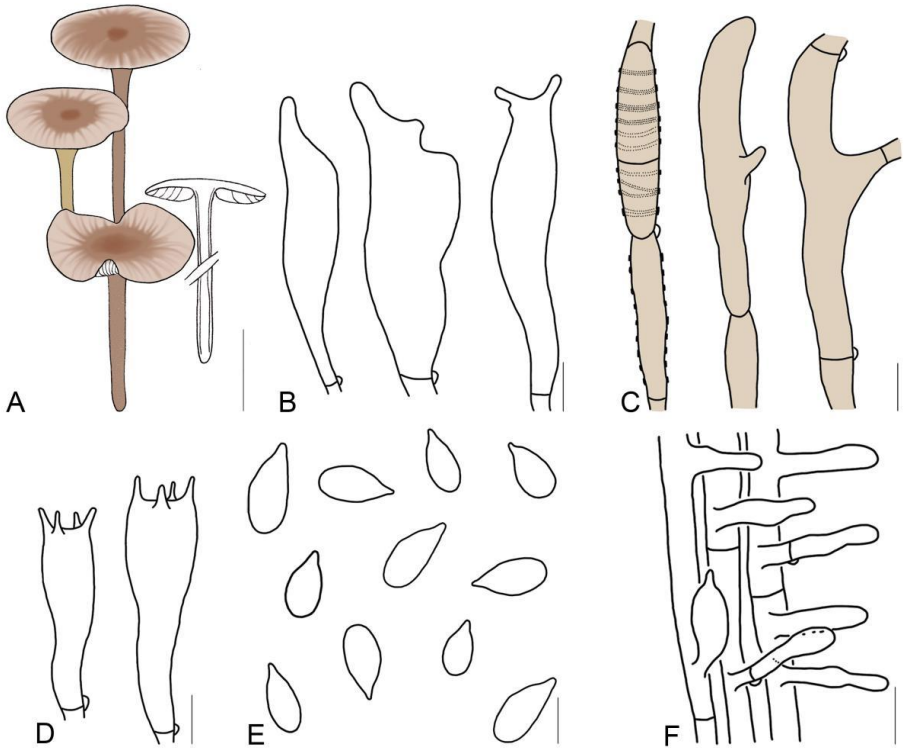

Figure 23 – Morphological characteristics of *Impudipilus* cf. *brassicolens* (HMJAU 61001). A Basidiomata. B Cheilocystidia. C Pileipellis elements. D Basidia. E Basidospores. F Caulocystidia. Scale bars: A = 1 cm, C = 10 μm, B, D, E = 5 μm, F = 20 μm.

Basidiomata small, gregarious. Pileus applanate to reflex, slightly depressed at the center, 1.5–2.5 cm wide, translucently striate up to the center, light brown at the center, light colour outwards; margin entire, inflexed, wavy sometimes, light brown to near white. Context very thin, with a strong smell reminding of rotten cabbage or onion. Stipe central, cylindrical, 5.0–6.5 cm long and about 0.1 cm wide, brown to dark brown, covered with tomentose entirely, hollow, fibrous. Lamellae subfree to adnexed, fairly distant, unequal.

Basidiospores ellipsoid, 5.0–8.0 × 3.0–4.2 µm, Q = 1.30–2.00, Qm = 1.70 ± 0.23, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 17–27 × 5–9 µm, 2- or 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, with projections in the upper part sometimes, (18)19–35(37) × (4)5–9(10) µm, thin-walled, hyaline. Caulocystidia abundant, clavate, 10–23 × 4–7 µm, thin-walled, hyaline. Pileipellis a cuits, branched, hyaline to brown, 5–9(10) µm wide, clamp connections abundant.

Habitat – Saprophytic on the deciduous layer in coniferous and broad-leaved mixed forest.

Specimen examined – China. Jilin Province: Tonghua City Ji'an County, Wunvfeng National Forest Park, 2 August 2020, Yong-Lan Tuo, HMJAU 61001 (Collection no.: Hu 638).

Note – This species was first recorded from Jiangxi Province, China by Deng (2016). There was no report about this species in China prior to the current study. During this time, we collected a specimen from Wunvfeng National Forest Park, Jilin Provence, which was found to be *I. brassicolens*. Thus, this species was originally observed and recorded from Jilin Provence, China.

Impudipilus cystidiosus (J.J. Hu, B. Zhang & Y. Li) J.J. Hu, B. Zhang & Y. Li, comb. nov.

Figs 24, 34J

≡ *Gymnopus cystidiosus* J.J. Hu, B. Zhang & Y. Li

Fungal names: FN571356

Basidiomata small, solitary to gregarious. Pileus convex to applanate, or reflex, 1.8–3.6 cm wide, glabrous, hygrophanous, brown to dark brown at the disc, yellow to light brown outwards; margin nearly white to light yellow then becoming light brown, straight at first then becoming reflex. Context thin, fresh, with a strong smell reminding of rotten cabbage or onion. Stipe central, cylindrical, tapering downwards sometimes, 2.4–4.5 cm long and 0.2–0.4 cm wide, yellow or fresh-coloured to pink-fresh, covered with pubescence entirely, tomentose at the base, hollow, fibrous. Lamellae adnexed to free, white, becoming dark brown when old, close, unequal.

Basidiospores ellipsoid to oblong ellipsoid, (5.1)5.2–6.4(7.0) × (2.8)3.0–4.0 µm, Q = (1.50)1.55–2.00(2.14), Qm = 1.79 ± 0.16, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 18–28 × 3–7 µm, 2-spored, occasionally 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, with a mucro that becomes elongated filiform with age, or projections like at apex, (15)19–32(34) × 3–5 µm, thin-walled, hyaline. Pleurocystidia scattered, pyriform to broadly fusoid-ventricose, 20–32 × (5)8–12(13) µm, thin-walled, hyaline. Caulocystidia clavate to branched, (15)27–50 × 3–5 µm, thin-walled, hyaline. Pileipellis a cuits, branched, hyaline, 7–15 µm wide; clamp connections abundant.

Habitat – Saprophytic on fallen leaves in broad-leaved forests.

Specimens examined – China. Jilin Province: Tonghua City, Ji'an County, Wunvfeng National Forest Park, 21 July 2020, Jia-Jun Hu and Yong-Lan Tuo, HMJAU 60992 (Collection no.: Hu 577); Tonghua City, Ji'an County, Wunvfeng National Forest Park, 21 July 2020, Jia-Jun Hu and Yong-Lan Tuo, HMJAU 60993 (Collection no.: Hu 578); Tonghua City, Ji'an County, Wunvfeng National Forest Park, 21 July 2020, Jia-Jun Hu and Yong-Lan Tuo, HMJAU 60994 (Collection no.: Hu 579); Tonghua City, Ji'an County, Wunvfeng National Forest Park, 21 July 2020, Jia-Jun Hu and Yong-Lan Tuo, HMJAU 60995 (Collection no.: Hu 581); Tonghua City, Ji'an County, Wunvfeng National Forest Park, 5 August 2020, Jia-Jun Hu and Yong-Lan Tuo, HMJAU 60996 (Collection no.: Hu 644).

Note – *Impudipilus cystidiosus* is characterized by its small basidiomata, glabrous pileus with a dark brown umbo and dark brown spots when old, having crowded and nearly white lamellae, fresh to pink and glabrous stipe, presence of pleurocystidia, and smaller basidiospores.

Impudipilus cystidiosus is closely related to *I. epiphyllus* in morphology and phylogeny due to having a pileus with an umbo. However, *I. cystidiosus* differs from *I. epiphyllus* by its glabrous pileus that has with brown spots when old, white and crowded lamellae, glabrous and fresh to pink stipe, presence of pleurocystidia, projected cheilocystidia, and smaller basidiospores.

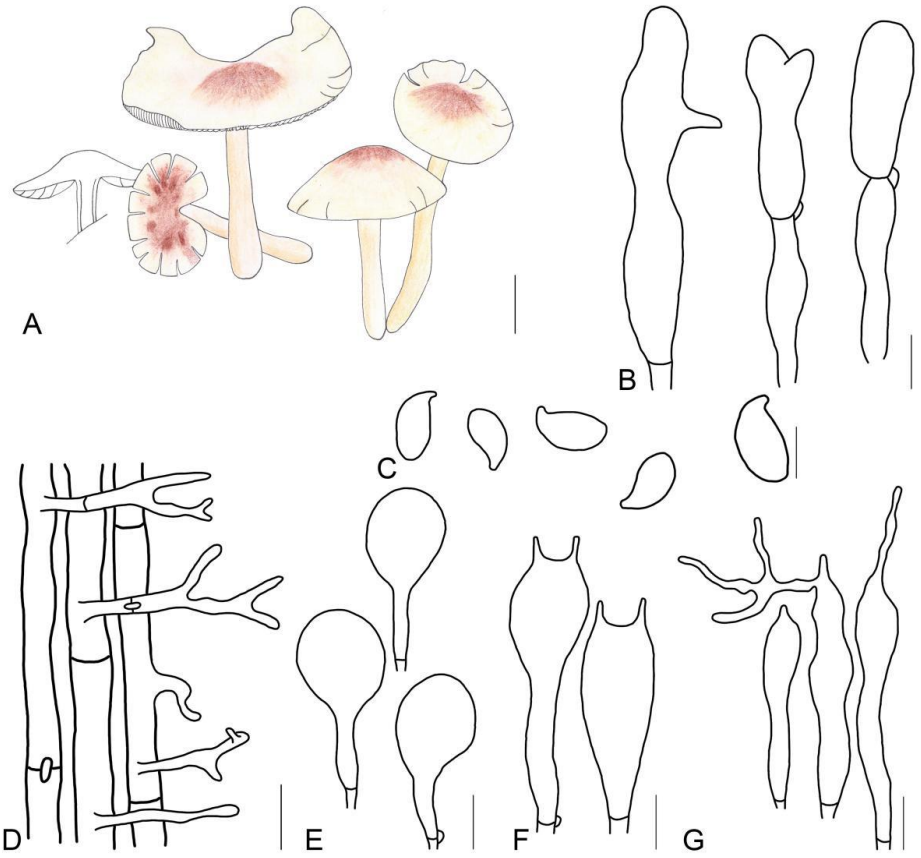

Figure 24 – Morphological characteristics of *Impudipilus cystidiosus* (HMJAU 60992, holotype). A Basidomata. B Pileipellis elements. C Basidiospores. D Caulocystidia. E Pleurocystidia. F Basidia. G Cheilocystidia. Scale bars: A = 1 cm, B, E = 10 μm, D = 20 μm, C, F, G = 5 μm.

Impudipilus densilamellatus (Antonín, Ryoo & Ka) J.J. Hu, B. Zhang & Y. Li, comb. nov.

Figs 25, 34I

= *Gymnopus densilamellatus* Antonín, Ryoo & Ka

Fungal names: FN571357

Basidiomata medium to large, gregarious. Pileis hemispherical or plano-hemispherical when young, then becoming convex, applanate when mature, 2.0–7.3 cm wide, brown or white sometimes when young, then paler, fading to light brown or yellowish-brown at the center, whitish towards, latter, white with a light brown center when mature, smooth, hygrophanous; margin entire, inflexed then straight, white, or brown at first then fading to white when mature. Context thin, white, fresh, with a strong smell reminding of rotten cabbage or onion. Stipe central, cylindrical, 2.2–10.3 cm long and 0.2–0.3 cm wide, white, with brown tone sometimes, smooth, tomentose sometimes, hollow, fibrous. Lamellae free, white to yellowish-white, brown when old, close to crowded, unequal.

Basidiospores ellipsoid, (5.2)5.6–8.0 × 2.8–4.0 μm, Q = (1.78)1.80–2.35(2.67), Qm = 2.11 ± 0.23, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (17)20–25 × 4–6 μm, 2- or 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, with projections, 17–23 × 3–6 μm, thin-walled, hyaline. Caulocystidia abundant, long clavate, branched, 30–170 × 3–8 μm, thin-

walled, hyaline. Pileipellis a cuits, branched, hyaline to brown, (6)7–13(15) μm wide, clamp connections abundant.

Habitat – Saprophytic on the deciduous layer in Coniferous and broad-leaved mixed forest.

Specimens examined – China. Jilin province, Baishan City Fusong County, Yongqing Forest Farm, 7 July 2018, Jia-Jun Hu and Ao Ma, HMJAU 61002 (Collection no.: Hu 31); Baishan City Fusong County, Beigang Town, 22 August 2021, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 61003 (Collection no.: Hu 881); Changchun City Jingyuetan National Forest Park, 15 July 2018, Jia-Jun Hu, HMJAU 61004 (Collection no.: Hu 49), HMJAU 61005 (Collection no.: Hu 50); 31 August 2018, Jia-Jun Hu, HMJAU 61006 (Collection no.: Hu 72); Jilin City Jiaohe county, Lafa mountain National Forest Park, 9 September 2018, Jia-Jun Hu and Bo Zhang, HMJAU 61007 (Collection no.: Hu 102); 19 August 2021, Jia-Jun Hu and Bo Zhang, HMJAU 61008 (Collection no.: Hu 866); Jilin City Jiaohe county, Zhuque mountain National Forest Park, 18 August 2021, Jia-Jun Hu, and Bo Zhang, HMJAU 61009 (Collection no.: Hu 841), HMJAU 61010 (Collection no.: Hu 845); Tonghua City Ji'an County, Wunvfeng National Forest Park, 21 August 2021, Yong-Lan Tuo, HMJAU 61011 (Collection no.: Hu 361), HMJAU 61012 (Collection no.: Hu 363); Jiangxi Province, Ji'an City Jinggangshan County, 19 July 2019, Bo Zhang, HMJAU 61013 (Collection no.: Hu 211); Gansu Province, Zhangye City Xishui Nature Reserve Station, 14 August 2019, Jia-Jun Hu, Wang Yang, and Zhi-Hui Luo, HMJAU 61014 (Collection no.: Hu 258);Henan Province, Zhumadian City Biyang County, Baiyun Mountain, 10 July 2021, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 61015 (Collection no.: Hu 772).

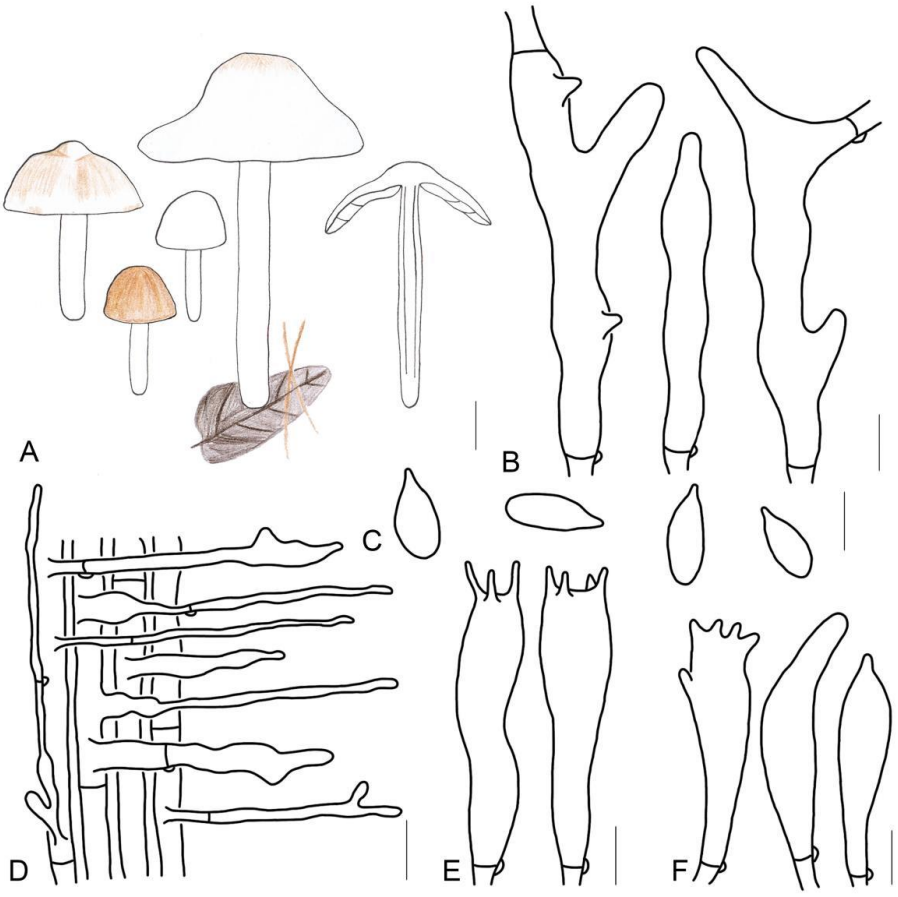

Figure 25 – Morphological characteristics of *Impudipilus densilamellatus* (HMJAU 61015). A Basidomata. B Pileipellis elements. C Basidiospores. D Caulocystidia. E Basidia. F Cheilocystidia. Scale bars: A = 2 cm, B = 10 μm, C, E, F = 5 μm, D = 20 μm.

Note – *Impudipilus densilamellatus* was initially described in South Korea (Ryoo et al. 2016). Subsequently, Li et al. (2021a) first observed and recorded it in China. In the current study, more than five specimens of *I. densilamellatus* were collected from Henan, Jiangxi, and Gansu Province, China.

Some differences were identified between the specimens we collected and the original description. According to the original description, the pileus is brown to reddish-brown at first, then becomes paler, brownish orange to brown at the center and outwardly whitish, and then eventually becomes more whitish, with an ochraceous brownish center when mature (Ryoo et al. 2016). During our investigation, some white basidiomata were found in young to mature specimens. The morphological characteristics were carefully examined.

Impudipilus epiphyllus (J.J. Hu, B. Zhang & Y. Li) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 26, 34F

≡ *Gymnopus epiphyllus* J.J. Hu, B. Zhang & Y. Li

Fungal names: FN571358

Basidiomata small, gregarious. Pileus convex to planate, 1.2–2.2 cm wide, tomentose, nearly white to light brown, with an umbo at disk and light brown to brown; margin nearly white to light brown, entire, involute, covered with dense tomentum. Context thin, fresh, with a strong smell reminding of rotten cabbage or onion. Stipe central, cylindrical, slightly expanded at base, 2.0–3.2 cm long and 0.2–0.3 cm wide, white, covered with pubescence entirely and tomentum at the base, hollow, fibrous. Lamellae adnexed to subfree, light brown, close, unequal.

Basidiospores oblong ellipsoid to cylindrical, 6.0–8.0 × 3.0–3.8(4.0) µm, Q = (1.72)1.88–2.30(2.32), Qm = 2.04 ± 0.15, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (13)17–31(32) × 4–6(7) µm, 2- or 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, with a mucro becoming elongated filiform with age, or with a projection at apex, 15–32(37) × 3–5 µm, thin-walled, hyaline. Caulocystidia numerous, clavate or irregularly clavate to branched, 40–65(75) × (3)4–6 µm, thin-walled, hyaline. Pileipellis a cuits; hyphal elements branched, hyaline, (3)5–12(13) µm wide; clamp connections abundant.

Habitat – Saprophytic on fallen leaves in broad-leaved forests.

Specimens examined – China. Jilin Province: Tonghua City, Ji'an County, Wunvfeng National Forest Park, 13 July 2020, Jia-Jun Hu and Yong-Lan Tuo, HMJAU 60990 (Collection no.: Hu 556); Tonghua City, Ji'an County, Wunvfeng National Forest Park, 13 July 2020, Jia-Jun Hu and Yong-Lan Tuo, HNJAU 60991 (Collection no.: Hu 560).

Note – *Impudipilus epiphyllus* is characterized by its small basidomata, yellowish-brown umbo and tomentose pileus, light khaki lamellae, white and tomentose stipe, and small basidiospores. Morphologically, *I. epiphyllus* is similar to *I. atlanticus*, due to having a pale brown pileus and light khaki lamellae. However, *I. epiphyllus* differs from *I. atlanticus* in having a tomentose pileus with a brown umbo at the disk, nearly white and tomentose stipe, not being pyriform, lageniform to somewhat sphaeropedunculate, versiform, or moniliform rostrum terminal elements of pileipellis (Coimbra et al. 2015), and having smaller basidiospores.

Impudipilus polyphyllus (Peck) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 27, 34C

= *Gymnopus polyphyllus* (Peck) Halling

= *Collybia polyphylla* (Peck) Singer ex Halling

= *Marasmius polyphyllus* Peck

Fungal names: FN571359

Basidiomata medium to large, gregarious. Pileus oblate hemispheric, 4.3–5.6 cm in diameter, smooth, grabrous, hygrophanus, fresh-pink to light brown at disc, paler colour outwards, white to fresh-pink; margin entire, wavy, involute, yellowish-white to light yellow. Context slightly thick, white, odourless. Stipe central, fusiform, 5.9–7.0 cm long and 0.7–1.0 cm wide, hollow, fibrous. Lamellae adnexed to subfree, white to fresh-pink, crowded, unequal.

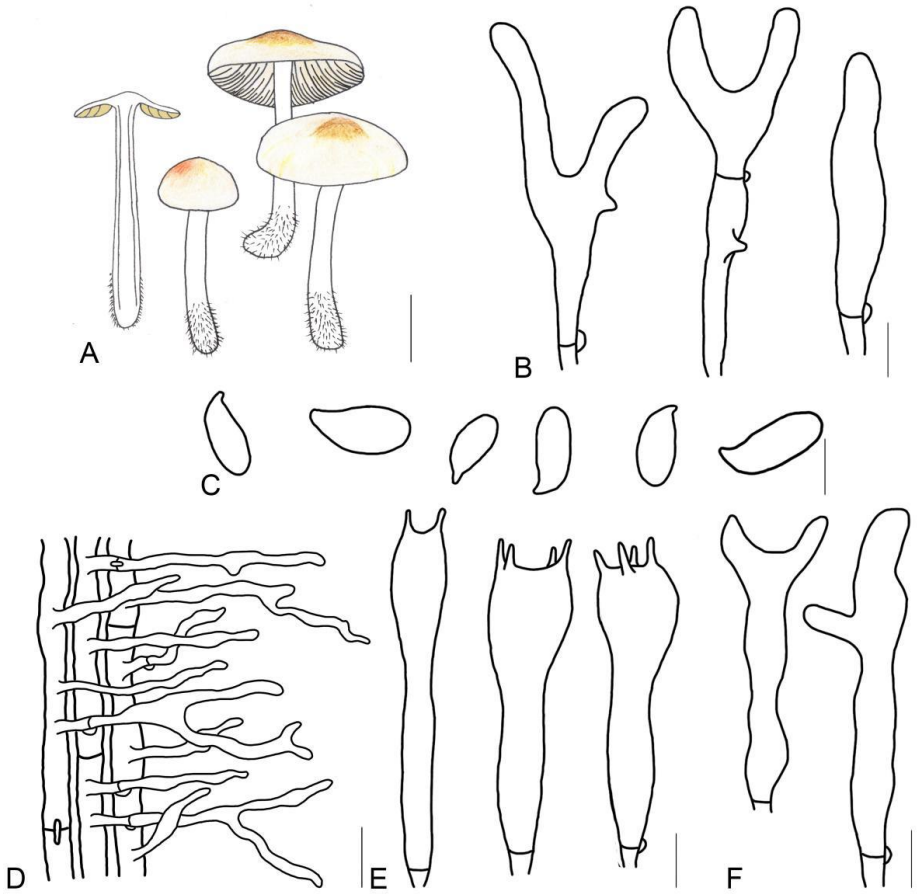

Figure 26 – Morphological characteristics of *Impudipilus epiphyllus* (HMJAU 60990, holotype). A Basidomata. B Pileipellis elements. C Basidiospores. D Caulocystidia. E Basidia. F Cheilocystidia. Scale bars: A = 1 cm, B = 10 µm, C, E, F = 5 µm, D = 20 µm.

Basidiospores oblong ellipsoid to cylindrical, (4.8)2.5–7.0(7.2) × 3.0–3.9(4.3) µm, Q = (1.50)1.58–2.16(2.23), Qm = 1.83 ± 0.19, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (17)21–29(31) × 4–8 µm, 2-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, with a mucro that becomes elongated filiform with age, or with projections sometimes, 23–25 × 3–8 µm, thin-walled, hyaline. Caulocystidia numerous, irregularly clavate, branched, (12)15–70 × 3–5 µm, thin-walled, hyaline. Pileipellis a cuits, branched, hyaline, (5)7–18(20) µm wide; clamp connections abundant.

Habitat – Saprophytic on fallen leaves in broad-leaved and coniferous mixed forest.

Specimen examined – China. Jilin Province, Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 4 September 2018, Jia-Jun Hu and Bo Zhang, HMJAU 61047 (Collection no.: Hu 88).

Note – This species initially belonged to sect. *Vestipedes* (*Collybiopsis*, in Petersen and Hughes' conception), while according to its morphological characteristics and phylogenetic analysis, it should be a member of sect. *Impudicae*. The species is characterized by its closed lamellae, rotten cabbage-like smell, diverticulate pileipellis hyphae, and propensity grows on leaf litter.

Impudipilus densilamellatus, described from South Korea in 2016, is similar to this species. However, it could be distinguished from *I. polyphyllus* by a the changing colour of its pileus, crowded lamellae, larger basidiospores, coralloid cheilocystidia, and propensity to grow on the ground. There were also have some differences between our collections and Halling's conception. Our collections with thick and fusiform stipes were 2-spored; in contrast, those in Halling's description were 4-spored.

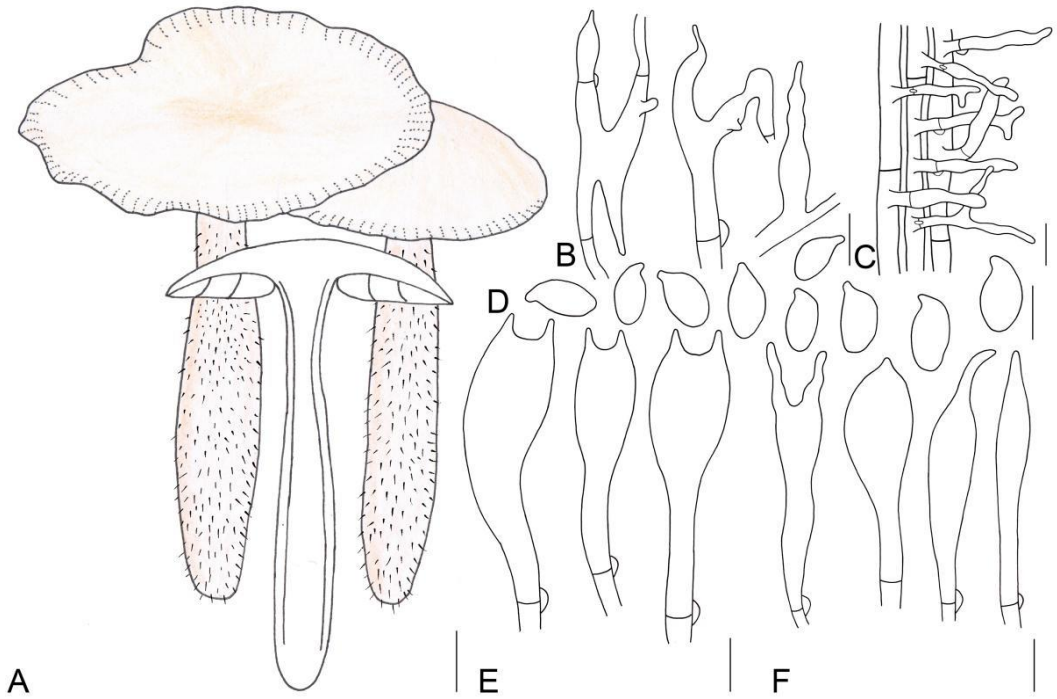

Figure 27 – Morphological characteristic of *Impudipilus polyphyllus* (HMJAU 61047). A Basidiomata. B pileipellis elements. C Caulocystidia. D Basidiospores. E Basidia. F Cheilocystidia. Scale bars: A = 1 cm, B, C = 10 μm, D–F = 5 μm.

Impudipilus subdensilamellatus (J.J. Hu, Y.L. Tuo, B. Zhang & Y. Li) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 28, 34B

≡ *Gymnopus subdensilamellatus* J.J. Hu, Y.L. Tuo, B. Zhang & Y. Li

Fungal names: FN571360

Basidiomata small to medium, gregarious. Pileus convex to applanate, 2.5–5.0 cm wide, glabrous, dark brown and slightly depressed at the center, pale coloured outwards at first, yellow to brown, dark brown when mature; margin nearly white to light yellow, entire, involute, wavy sometimes. Context thin, fresh, with a strong smell reminding of rotten cabbage or onion. Stipe central, cylindrical to clavate, 5.0–7.2 cm long and 0.2–0.7 cm wide, nearly white to dirty white, almost white to light reddish brown at apex, pruinose, covered with white tomentose at the base, with longitudinal striate, hollow, fibrous. Lamellae adnexed to sufree, white, extremely close, unequal.

Basidiospores oblong ellipsoid to cylindrical, 6.0–7.2(7.4) × 3.0–3.8(4.0) μm, Q = (1.75)1.82–2.07(2.19), Qm = 1.95 ± 0.10, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (16)17–28(30) × 4–6 μm, 2- to 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, with a mucro that becomes elongated filiform with age, or with projections sometimes, 20–28(30) × 4–7 μm, thin-walled, hyaline. Caulocystidia numerous, irregularly clavate, branched, (12)15–50 × 4–10(11) μm, thin-walled, hyaline. Pileipellis a cuits, branched, brown, 6–7(13) μm wide; clamp connections abundant.

Habitat – Saprophytic on fallen leaves in coniferous forest.

Specimen examined – China. Jilin Province: Tonghua City, Ji'an County, Wunvfeng National Forest Park, 4 September 2020, Yong-Lan Tuo, HMJAU 60997 (Collection no.: Hu 675); Tonghua City, Ji'an County, Wunvfeng National Forest Park, 4 August 2020, Yong-Lan Tuo, HMJAU 60998 (Collection no.: Hu 667).

Note – *Impudipilus subdensilamellatus* is characterized by its unchanging brown pileus with a white to light brown margin, crowded lamellae, white stipe that is light reddish brown at the apex, and smaller Qm.

Impudipilus subdensilamellatus differs from *I. densilamellatus* by its unchanging brown pileus (*I. densilamellatus* initially has a brown, then white pileus, with an ochraceous brownish center (Ryoo et al. 2016)), irregularly clavate caulocystidia, and mucro to projected cheilocystidia.

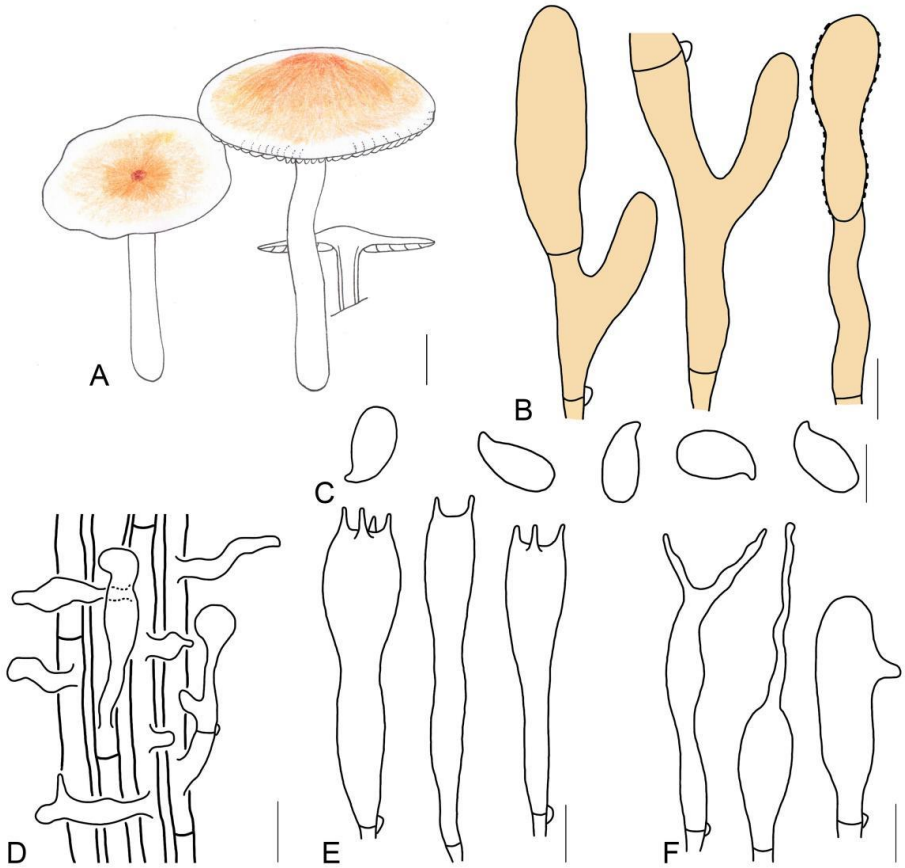

Figure 28 – Morphological characteristics of *Impudipilus subdensilamellatus* (HMJAU 60990, holotype). A Basidomata. B Pileipellis elements. C Basidiospores. D Caulocystidia. E Basidia. F Cheilocystidia. Scale bars: A = 1 cm, B = 10 µm, C, E, F = 5 µm, D = 20 µm.

Impudipilus subpolyphyllus (J.J. Hu, B. Zhang & Y. Li) J.J. Hu, B. Zhang & Y. Li, comb. nov.
Figs 29, 34A

≡ *Gymnopus subpolyphyllus* J.J. Hu, B. Zhang & Y. Li
Fungal names: FN571361

Basidiomata small, gregarious. Pileus plano-hemispherical to convex, 1.4–2.3 cm wide, glabrous, with an umbo sometimes, hygrophanous and pinkish brown when young, then brown to fresh-pink at the disc, pale coloured outwards; margin pinkish brown when young, then nearly white to light yellow, involute at first, then becoming straight, reflex sometimes, tomentum. Context thin, fresh, with a strong smell reminding of rotten cabbage or onion. Stipe central, cylindrical, 2.2–3.0 cm long and 0.2–0.3 cm wide, pinkish-brown when young, then pale reddish-brown, glabrous at the upper part at first, then entirely tomentose, hollow, fibrous. Lamellae adnexed, cream, close, unequal.

Basidiospores ellipsoid to cylindrical, (5.1)5.2–7.0 × (2.9)3.0–4.0 µm, Q = (1.48)1.58–2.19(2.33), Qm = 1.84 ± 0.20, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 17–27 × 4–6 µm, 2- or 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, with a mucro that becomes elongated filiform with age, or with projections sometimes, 18–29(30) × 3–6(7) µm, thin-walled, hyaline. Caulocystidia abundant, long clavate, branched, 40–90(100) × 3–6 µm, thin-walled, hyaline. Pileipellis a cuits; hyphal elements branched, hyaline to light yellow, (5)6–10(11) µm wide; clamp connections abundant.

Habitat – Saprophytic on fallen leaves in broad-leaved forests.

Specimens examined – China. Jilin Province: Tonghua City, Ji'an County, Wunvfeng National Forest Park, 13 July 2020, Jia-Jun Hu and Yong-Lan Tuo, HMJAU 60999 (Collection no.: Hu 561); Tonghua City, Ji'an County, Wunvfeng National Forest Park, 17 July 2020, Jia-Jun Hu and Yong-Lan Tuo, HMJAU 61016 (Collection no.: Hu 566); Tonghua City, Ji'an County, Wunvfeng National Forest Park, 17 July 2020, Jia-Jun Hu and Yong-Lan Tuo, HMJAU 61000 (Collection no.: Hu 572).

Note – *Impudipilus subpolyphyllus* is characterized by its small basidiomata, glabrous pileus occasionally with a light brown umbo, tomentose margin and stipe, cheilocystidia that are branched or projected at the apex, abundant, branched, and long caulocystidia, and small basidiospores.

Impudipilus subpolyphyllus is closely morphologically similar to *I. polyphyllus*. However, *I. subpolyphyllus* differs from *I. polyphyllus* by its glabrous pileus, cream lamellae, tomentose stipe, different cheilocystidia shape, and slightly wider basidiospores (Halling 1983).

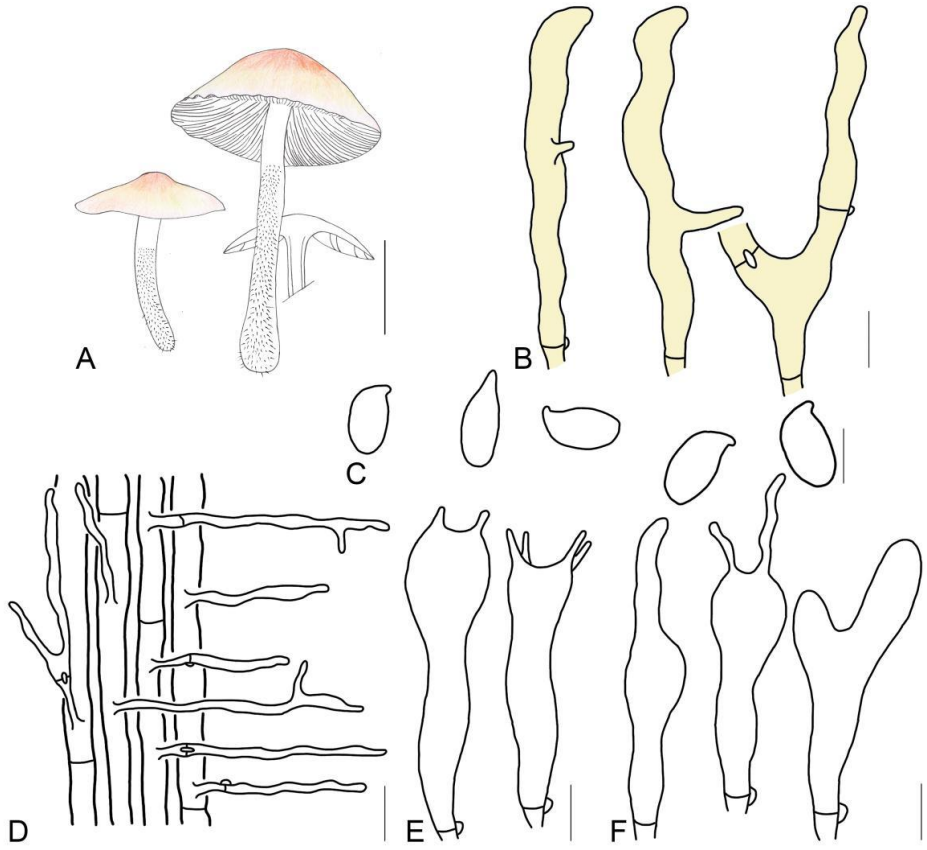

Figure 29 – Morphological characteristics of *Impudipilus subpolyphyllus* (HMJAU 60999, holotype). A Basidomata. B Pileipellis elements. C Basidiospores. D Caulocystidia. E Basidia. F Cheilocystidia. Scale bars: A = 1 cm, D = 20 µm, B = 10 µm, C, E, F = 5 µm.

Sect. *Dysodes* J.J. Hu, B. Zhang & Y. Li, sect. nov.

Etymology – Derived from the name of the type species of the section.

Fungal names: FN571338

Basidiomata marasmioid or collybioid, small, gregarious. Pileus campanaceous, convex to planate-convex, finally applanate, sulcate-striate, glabrous. Lamellae adnate to adnexed, distant to close, white to orange white. Stipe cylindrical, tapered downwards or flatten at base sometimes, pruinose to furfuraceous. Pileipellis a cuits, repent, *Rameales* structure sometimes. Basidiospores broad to narrow elliptical to pip-shaped, or lacrimoid, hyaline, thin-walled, inamyloid. Basidia

clavate, 4-spored, hyaline, thin-walled. Cheilocystidia extremely inconspicuous. Caulocystidia cylindrical, hyaline. Lamellae trama regular. Clamp connection present.

Grows on fallen leaves, branches, or rotten wood.

Type species: *Impudipilus dysodes* (Halling) J.J. Hu, B. Zhang & Y. Li

Impudipilus dysodes (Halling) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 30, 34O

= *Gymnopus dysodes* (Halling) Halling

= *Collybia dysodes* Halling

Fungal names: FN571362

Basidiomata small, solitary or scattered. Pileus hemispheric, 1.3–2.7 cm in diameter, tomentose, grooved (up to the center), chestnut coloured to chestnut brown, deeper colour at the center and groove, chestnut brown; margin entire, involute, chestnut coloured to chestnut brown. Context thin, light chestnut, fresh, with a strong smell reminding of rotten cabbage or onion. Stipe central, cylindrical, 1.7–2.5 cm long and 0.2–0.3 cm wide, light chestnut, chestnut to dark brown, hollow, fibrous. Lamellae adnexed to free, chestnut coloured to chestnut brown, rather distant, unequal.

Basidiospores ellipsoid, 5.0–7.0 × (2.4)2.6–3.2(3.4) µm, Q = 1.67–2.50(2.92), Qm = 1.98 ± 0.31, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 17–25(27) × 4–6(7) µm, 2- or 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, with a mucro that becomes elongated filiform with age, or projections at apex, 20–29(30) × (3)4–5(6) µm, thin-walled, hyaline. Caulocystidia absent. Pileipellis a cuits, branched, hyaline, (5)6–12 µm wide, clamp connections abundant.

Habitat – Saprophytic on the ground near to the *Salix* sp.

Specimen examined – China. Zhejiang Province: Shaoxing City, Keqiao County, Pinshui Town, Shangzao Village, 7 June 2020, Jia-Jun Hu, HMJAU 61048 (Collection no.: Hu 510).

Note – This species was initially described from USA by Halling (1983) as *Collybia dysodes* Halling, then, later transferred to *Gymnopus* (Antonín et al. 1997). This was the first time this species was recorded from China. It is characterized by chestnut-coloured to chestnut brown pileus, relatively distant lamellae, rotten cabbage-like smell, irregular or branched cheilocystidia with an umbo, and being bifurcated, or finger-like at the apex.

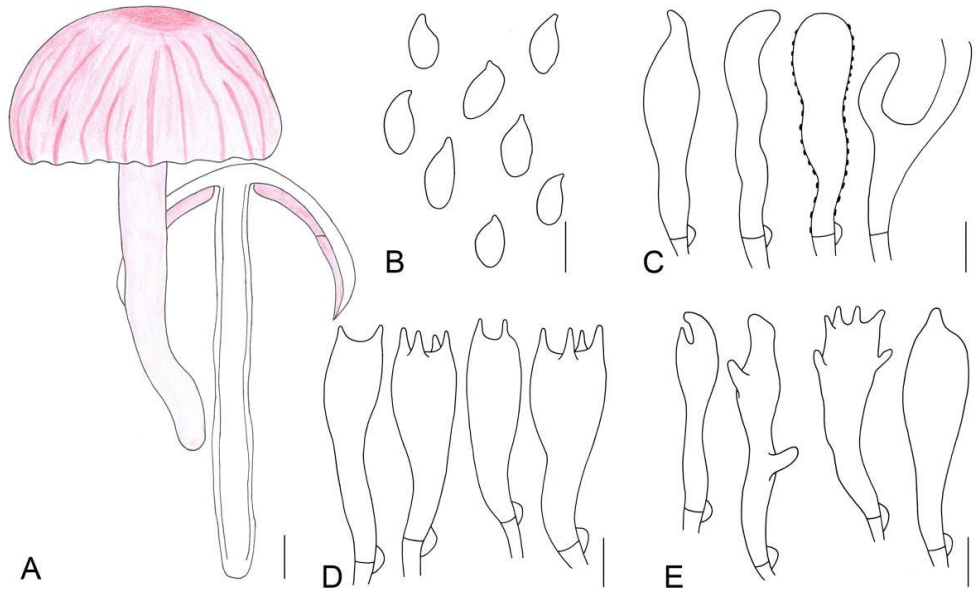

Figure 30 – Morphological character of *Impudipilus dysodes* (HMJAU 61048). A Basidiomata. B Basidiospores. C Pileipellis elements. D Basidia. E Cheilocystidia. Scale bars: A = 0.5 cm, C = 10 µm, B, D, E = 5 µm.

However, some differences were observed between our collections and Halling's description. Our collections are lack of Caulocystidia, which differs from the conception put forth by Antonín et al. (1997) and Ryoo et al. (2016). In addition, the basidiospores observed in our collections and those described by Ryoo et al. are similar in size, while they are smaller than Halling's.

Sect. *Similis* J.J. Hu, B. Zhang & Y. Li, sect. nov.

Etymology – Derived from the name of the type species of the section.

Fungal names: FN571339

Basidiomata marasmioid, occasionally collybiod, small. Pileus hemispherical, convex to planate-convex or applanate, slightly depressed at disc, with an umbo or mastoid sometimes, smooth or pruinose, striped or sulcate-striate. Lamellae adnate to free, or with a decurrent tooth, variety in colour, white, purple red, purple gray, or grayish brown etc., distant to crowded. Stipe cylindrical or tapered downwards, paler at apex, pruinose, furfuraceous, or tomentose.

Pileipellis a cuits, smooth or encrusted; terminal cells branched, finger-like or coralloid, diverticula sometimes, turn green or blue in 3% KOH sometimes. Basidiospores oblong-elliptical to pip-shaped, or lacrymoid, hyaline, thin-walled, smooth, in-amyloid. Basidia clavate, 4-spored, hyaline, thin-walled. Cheilocystidia present or not, cylindrical to clavate, or lageniform, finger-like or coralloid at apex. Caulocystidia cylindrical to fusiform, or moniliform, with an umbo or branched sometimes.

Grows on ground.

Type species: *Impudipilus similis* (Antonín, Ryoo & Ka) J.J. Hu, B. Zhang & Y. Li

Key to the species of Sect. *Similis* present in this study

1 Basidiomata marasmioid, stipe covered with white, dense tomentose.....*Impudipilus similis*
1 Basidiomata collybioid, stipe covered with spars, brown hairs.....*Impudipilus abruptibulbus*

Impudipilus abruptibulbus J.J. Hu, B. Zhang & Y. Li, sp. nov. Figs 31, 34H

Fungal names: FN571363

Etymology – "*abruptibulbus*" refers to this species with flatten to bulbus at the stipe.

Diagnosis – This species differentiated from other species by small and collybioid basidiomata, an irregular pileus with thick context, tomentose stipe with an enlarged base, small basidiospores, long and thin cheilocystidia, with an umbo, bifurcated, or finger-like at apex, smaller basidiospores, and abundant caulocystidia.

Type – China. Jilin Province: Baishan City, Fusong County, Songjianghe National Forest Park, 8 July 2018, Jia-Jun Hu, Ao Ma, and Xiao-Qi Xu, HMJAU 61049, holotype, (Collection no.: Hu 45).

Basidiomata small, scattered to gregarious. Pileus hemispherical, campaniform to convex, 0.5–3.0 cm in diameter, yellowish brown to reddish brown at disc, paler outwards, light yellowish brown to light reddish brown, smooth, glabrous, hygrophanus; margin entire, lobed, or wavy, yellowish white to light yellowish brown, involute, reflex sometimes. Context thin, light yellow to fresh-pink, with a strong smell reminding of rotten cabbage or onion. Stipe central, 3.6–4.2 cm long and 0.2–0.4 cm wide, cylindrical, tomentose, hollow, fibrous. Lamellae adnate, white to light yellowish brown or fresh-pink, closed, unequal.

Basidiospores ellipsoid, (4.8)4.9–6.0 × (2.3)2.4–3.1(3.2) µm, Q = (1.60)1.66–2.17(2.26), Qm = 1.84 ± 0.19, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (10)13–25(26) × 5–7 µm, 2- or 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, branched or finger-like at apex, (13)14–24(26) × (3)4–7 µm, thin-walled, hyaline. Caulocystidia abundant, clavate or irregularly clavate, branched at apex, 20–45 ×3–5 µm, thin-walled, hyaline. Pleurocystidia absent. Pileipellis a cuits, branched, hyaline, diverticulate, 6(7)–15(17) µm wide. Clamp connections abundant.

Habitat – Saprophytic on deciduous layer in broad-leaved forests.

Other specimens examined – China. Jilin Province: Baishan City, Fusong County, Songjianghe National Forest Park, 8 July 2018, Jia-Jun Hu, Ao Ma, and Xiao-Qi Xu, HMJAU 61050 (Collection no.: Hu 44); Jilin City, Jiaohe County, red leaf Valley, 5 September 2018, Jia-Jun Hu and Bo Zhang, HMJAU 61051 (Collection no.: Hu 96).

Note – This species is characterized by its small basidiomata, being collybioid, an irregular pileus with thick context, tomentose stipe with an enlarged base, small basidiospores, long and thin cheilocystidia with an umbo, being bifurcated or finger-like at the apex, and abundance of caulocystidia.

Impudipilus abruptibulbus is highly morphologically similar to *Levipedipilus dryophilus*. However, *I. abruptibulbus* differs from *L. dryophilus* by its irregular pileus with thick context, a close lamellae, tomentose stipe, abundant caulocystidia, long and thin cheilocystidia with an umbo, being bifurcated or finger-like at the apex, and not being coralloid (Antonín et al. 2013).

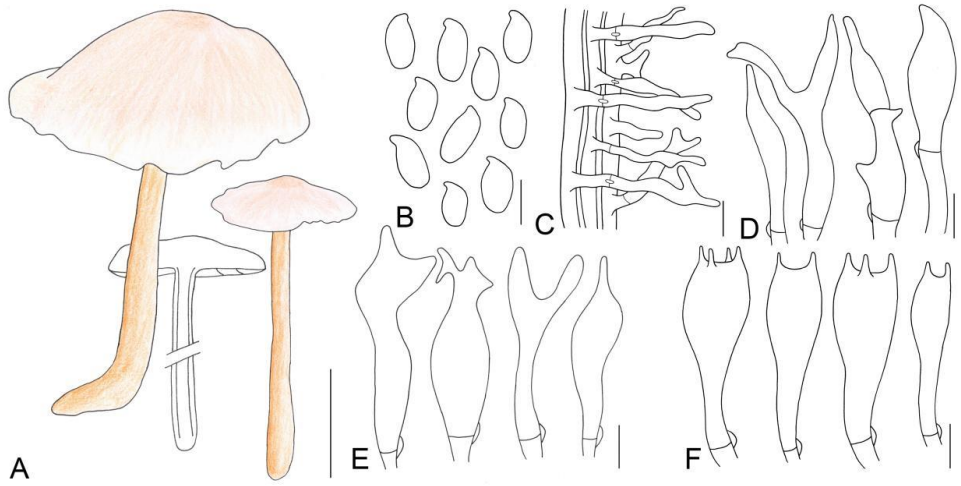

Figure 31 – Morphological characterize of *Impudipilus abruptibulbus* (HMJAU 61050). A Basidiomata. B Basidiospores. C Caulocystidia. D Pileipellis elements. E Cheilocystidia. F Basidia. Scale bars: A = 1 cm, C, D = 10 μm, B, E, F = 5 μm.

Impudipilus similis (Antonín, Ryoo & Ka) J.J. Hu, B. Zhang & Y. Li, comb. nov.

Figs 32, 34D

= *Gymnopus similis* Antonín, Ryoo & Ka

Fungal names: FN571364

Basidiomata small, scattered to gregarious. Pileus hemispherical to hat shaped, or convex, 0.5–2.3 cm in diameter, light brown to light reddish brown at disc, deeper colour outwards, light reddish brown, smooth, grabrous, grooved; margin entire, involute, reflex sometimes, grooved, light reddish brown. Context thin, fresh, with a strong smell reminding of rotten cabbage or onion. Stipe central, cylindrical, 3.7–4.3 cm long and 0.2–0.3 cm wide, tomentose, hollow, fibrous. Lamellae adnate to adnexed, rather distant, light brown, unequal.

Basidiospores oblong ellipsoid to cylindrical, (6.0)6.1–8.2(9.0) × (3.0)3.1–3.9(4.6) μm, Q = (1.56)1.57–2.50(2.90), Qm = 2.16 ± 0.31, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 19–27 × 4–6(7) μm, 2- to 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, with a mucro that becomes elongated filiform with age, (18)19–28(31) × (4)5–7 μm, thin-walled, hyaline. Caulocystidia numerous, irregularly clavate, branched, or diverticulae, (17)19–55(63) × (3)4–7(8) μm, thin-walled, hyaline. Pileipellis a cuits, branched, hyaline, (4)5–10 μm wide. Clamp connections abundant.

Habitat – Saprophytic on fallen leaves and branch in broad-leaved and coniferous mixed forest.

Specimens examined – China. Jilin Province: Yanbian Korean Autonomous Prefecture, Erdaobaihe Town, 5 July 2018, Jia-Jun Hu, Ao Ma, and Xiao-Qi Xu, HMJAU 61052 (Collection

no.: Hu 399); Yanbian Korean Autonomous Prefecture, Helong City, Bajiazi Forest Farm, 23 August 2018, Ye Ding, HMJAU 61053 (Collection no.: Hu 492); Baishan City, Fusong County, Lushuihe Town, Changbai Mountain ancient tree park, 7 July 2018, Jia-Jun Hu, Ao Ma, and Xiao-Qi Xu, HMJAU 61056 (Collection no.: Hu 414); Liaoning Province: Fushun City, Xinbin Manchu Autonomous County, Gangshan National Nature Reserve, 1 August 2018, Ao Ma, HMJAU 61060 (Collection no.: Hu 499); Benxi City, Tanggou green stone Valley National Forest Park, 13 July 2017, Yang Wang, HMJAU 61061 (Collection no.: Hu 895); Guangxi Zhuang Autonomous Region: Baise City, Leye County, National Nature Reserve of Orchidaceae, 14 July 2017, Jia-Jun Hu, Dai Dan, and Bo Zhang, HMJAU 61059 (Collection no.: Hu 426); Zhejiang Province: Shaoxing City, Keqiao County, Pingshui Town, Changfeng Village, 24 June 2020, Jia-Jun Hu, HMJAU 61062 (Collection no.: Hu 533).

Note – This species was initially described from South Koran (Ryoo et al. 2016), and, subsequently, Li et al. (2021a) recorded this species from China. It is characterized by its small and marasmioid basidiomata, being gregarious, distant lamellae, onion- or rotten cabbage-like smell, and relatively large basidiospores.

Some differences exist between our collections and the original description. Our cheilocystidia were clavate with an umbo at the apex, while the cheilocystidia described from South Koran were clavate and finger-like at the apex. In terms of the caulocystidia, our collections were irregularly clavate, branched, or diverticulae; in contrast, the caulocystidia described in the original description were cylindrical, subfusoid, (narrowly) clavate, sometimes irregular or branched, and obtuse.

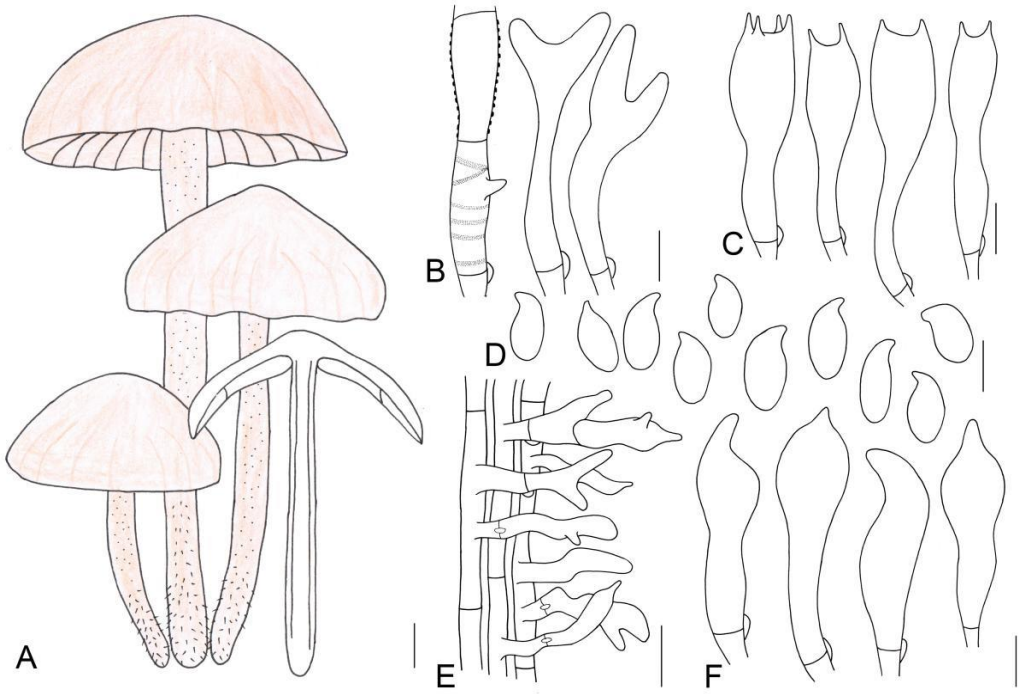

Figure 32 – Morphological characteristic of *Impudipilus similis* (HMJAU 61053). A Basidiomata. B Pileipellis elements. C Basidia. D Basidiospores. E Caulocystidia. F Cheilocystidia. Scale bars: A = 0.5 cm, B, E = 10 μm, C, D, F = 5 μm.

Impudipilus iodes (J.P. Li, Chang Tian Li, Chun Y. Deng & Yu Li) J.J. Hu, B. Zhang & Y. Li, comb. nov. Fig. 33

≡ *Gymnopus iodes* J.P. Li, Chang Tian Li, Chun Y. Deng & Yu Li

Fungal names: FN571365

The marco-morphological characters were referred to the original description (Li et al. 2022b).

Basidiospores ellipsoid to oblong, (5.6)6.0–8.0 × 3.2–4.0(4.2) μm, Q = (1.58)1.70–2.36(2.42), Qm = 1.94 ± 0.21, hyaline, smooth, thin-walled, inamyloid. Basidia clavate, 2- or 4-spored, 16–27(28) × 4–7 μm, hyaline, thin-walled. Cheilocystidia clavate, with an umbo at apex or bifurcate, 18–27(28) × 4–6 μm, hyaline, thin-walled. Pleurocystidia not observed. Caulocystidia abundant, clavate, with an unbo at apex, (30)31–55 × 4–6(7) μm, hyaline, thin-walled, diverticulate sometimes. Pileipellis a cuits, radically, made up of cylindrical hyphae, (5)6–10(11) μm, coralloid, diverticulate, hyaline, thin- to slightly thick-walled. Clamp connections present.

Habitat – Saprophytic on deciduous layer in broad-leaved forests.

Specimen examined – China. Guizhou Province: Qiandongnan Miao and Dong Autonomous Prefecture, Liping County, Taiping Mountain Forest Park, 28 August 2020, Ding-Fang Wei, Ming Wang, and Ji-Peng Li, HGASMF01-10068, holotype (!); Qiandongnan Miao and Dong Autonomous Prefecture, Liping County, Taiping Mountain Forest Park, 28 August 2020, Ding-Fang Wei, Ming Wang, and Ji-Peng Li, HGASMF01-10069.

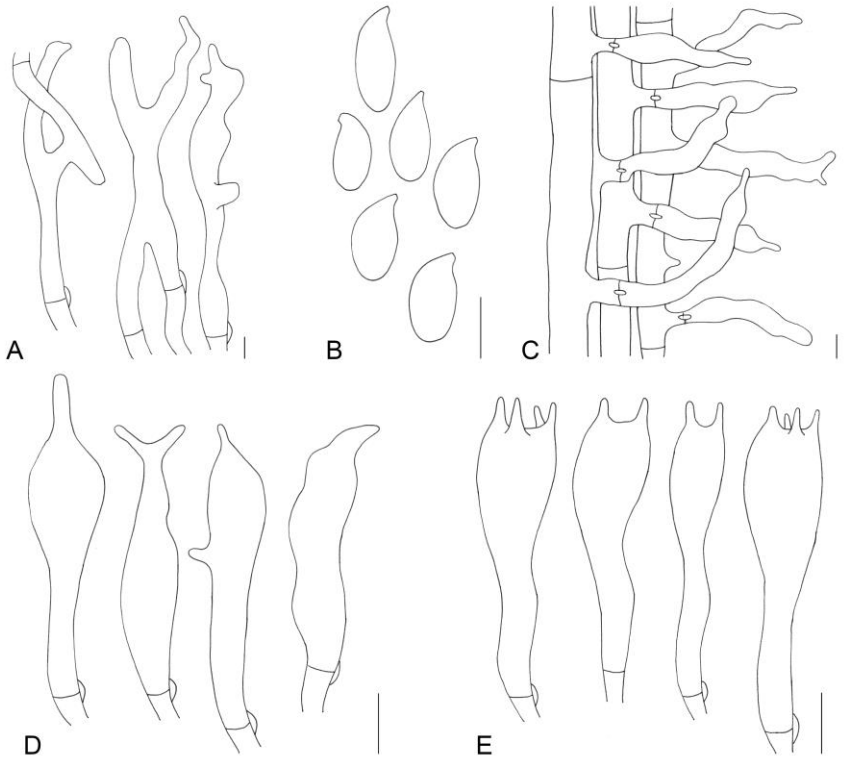

Figure 33 – Micro-morphological characteristic of *Impudipilus iodes* (HMASMF01-10068!). A Pileipellis elements B Basidiospores. C Caulocystidia. D Cheilocystidia. E Basidia. Scale bars: A, C = 10 μm, B, D, E = 5 μm.

2.3.5 *Levipedipilus* J.J. Hu, B. Zhang & Y. Li, gen. nov.

Etymology – *Levipedipilus* refers to this genus arising from sect. *Levipedes*.

Fungal names: FN571340

Basidiomata collybioid, occasionally marasmioid, small to medium, solitary to gregarious, odourless, convex to applanate, smooth, hygrophanus. Lamellae adnate to adnexed, close to crowded, white to light yellow. Stipe cylindrical, smooth, occasionally with sparse tomentose, fibrous, hollow.

Pileipellis a cutis, repent, radically, coralloid, branched, with *Dryophila* structure, smooth or encrusted, diverticulate, hyaline, thin- to slightly thick-walled. Cheilocystidia abundant, cylindrical or cylindrical with branched, finger-like or coralloid apex. Pleurocystidia and caulocystidia absent. Basidiospores elliptical, hyaline, thin-walled, inamyloid. Clamp connection present.

Grows on ground or fallen leaves or branches.
Types species: *Levipedipilus dryophilus* (Bull.) J.J. Hu, B. Zhang & Y. Li

Figure 34 – A *Impudipilus subpolyphyllus.* B *Impudipilus subdensilamellatus*. C *Impudipilus polyphyllus*. D *Impudipilus similis*. E *Impudipilus albumistipticus*. F *Impudipilus epiphyllus.* G *Impudipilus* cf. *Brassicolens*. H *Impudipilus abruptibulbus.* I *Impudipilus densilamellatus*. J *Impudipilus cystidiatus*. K–L *Impudipilus alliifoetidissimus*. M–N *Impudipilus campanifomipileatus.* O *Impudipilus dysodes*. Scale bars: A–J, K, L = 0.5 cm, M–O = 1 cm.

Levipedipilus J.J. Hu, B. Zhang & Y. Li
I Sect. *Levipedes* (Quél.) J.J. Hu, B. Zhang & Y. Li
Type species: *Levipedipilus dryophilus* (Bull.) J.J. Hu, B. Zhang & Y. Li
II Sect. *Alkalivirentes* (Antonín & Noordel.) J.J. Hu, B. Zhang & Y. Li
Type species: *Levipedipilus alkalivirens* (Singer) J.J. Hu, B. Zhang & Y. Li
III Sect. *Erythropus* J.J. Hu, B. Zhang & Y. Li
Type species: *Levipedipilus erythropus* (Pers.) J.J. Hu, B. Zhang & Y. Li

Key to the section of *Levipedipilus* present in this study

1 Mycelium turn green in KOH.....Sect. *Alkalivirentes*
1 Mycelium not turn green in KOH.....2
2 Stipe light yellow to brown, cheilocystidia clavate, branched, coralloid, or finger-like at apex .....Sect. *Levipedes*
2 Stipe reddish brown, cheilocystidia clavate, with an umbo at apex.....Sect. *Erythropus*

Sect. *Levipedes* (Quél.) J.J. Hu, B. Zhang & Y. Li, comb. nov.

Fungal names: FN571366

Basidiospores collybioid or marasmoid, small to medium, solitary to gregarious. Pileus convex, applanate finally, light yellow to yellow, smooth, hygrophanus. Lamellae adnexed, close to crowded, white to yellow. Stipe smooth, cylindrical to clavate, fibrous, hollow.

Pileipellis a cuits, *Dryophilia* structure, hyaline, thin-walled. Basidiospores elliptical, smooth, hyaline, thin-walled, inamyloid. Basidia clavate, hyaline, thin-walled. Cheilocystidia abundant, irregularly clavate to clavate, branched, finger-like, or coralloid at apex. Caulocystidia rare, clavate or irregular clavate, branched at apex.

Grows on ground, fallen leaves or branches.

Type species: *Levipedipilus dryophilus* (Bull.) J.J. Hu, B. Zhang & Y. Li

Key to the species of Sect. *Levipedes* present in this study

1 Basidiomata marasmioid.....2
1 Basidiomata collybioid.....3
2 Surface of pileus grooved, rugulose-striate.....*Levipedipilus cinnamomeus*
2 Surface of pileus with translucent striate.....*Levipedipilus striatipileatus*
3 Absence of cheilocystidia and pleurocystidia.....*Levipedipilus longistipes*
3 Presence of cheilocystidia.....4
4 Mastoid at disc of pileus that with brown spots.....*Levipedipilus maculatus*
4 Pileus lack of mastoid and spots.....5
5 Caulocystidia present.....6
5 Caulocystidia absent.....7
6 Cheilocystidia slim, finger-like or coralloid at apex.....*Levipedipilus inexpectatus*
6 Cheilocystidia clavate, occasionally with an umbo at apex.....*Levipedipilus hemisphaericus*
7 Colour of pileus darker, brown, grows at alpine meadow.....*Levipedipilus luteofuscus*
7 Colour of pileus paler, light yellow to yellowish brown, grows on ground, fallen leaves or branches.....8
8 Basidiomata entirely lemon yellow.....9
8 Basidiomata not lemon yellow.....10
9 Cheilocystidia clavate, with an umbo at apex.....*Levipedipilus minor*
9 Cheilocystidia clavate, diverticulate.....*Levipedipilus ctrinoides*
10 Stipe cylindrical or clavate.....11
10 Stipe cylindrical, enlarged at base.....13
11 Stipe light red.....*Levipedipilus aquosus*
11 Stipe light yellow to yellow.....12
12 Stipe deeper colour, yellow, covered with sparse tomentum.....*Levipedipilus brunneodiscus*
12 Stipe paler colour, light yellow, smooth, glabrous.....*Levipedipilus dryophilus*
13 Stipe paler colour, basidiomata smaller.....*Levipedipilus dryophilioides*
13 Stipe deeper colour, basidiomata bigger.....*Levipedipilus ocior*

Levipedipilus minor J.J. Hu, B. Zhang & Y. Li, sp. nov. Figs 35, 59Q

Fungal names: FN571367

Etymology – "*minor*" refers to this species with small basidiomata.

Diagnosis – This species is distinguished from closed species by medium basidiomata, smooth, glabrous, hemispherical pileus, with an umbo sometimes, entirely lemon-colour, flatten, coralliod, and encrusted pileipellis, smaller basidiospores.

Type – China. Jilin Province: Baishan city, Fusong County, Songjianghe Town, Songjianghe National Forest Park, 8 July 2018, Jia-Jun Hu, Ao Ma, and Xiao-Qi Xu, HMJAU 61063 (Collection no.: Hu 43), holotype.

Basidiomata medium, gregarious. Pileus hemispheric, 1.9–3.0 cm in diameter, smooth, glabrous, hygrophanus, lemon yellow to yellowish brown, with an umbo at disc sometimes; margin entire or serrated sometimes, involute, lemon yellow to yellowish brown. Context thin, fresh, odourless. Stipe central, cylindrical to fusiform, 6.5–7.5 cm long and 0.3–0.5 cm wide, lemon yellow or deeper colour downwards, yellowish brown, fistulose, fibrous. Lamellae adnexed, close, lemon yellow, unequal.

Basidiospores elliptic, (4.2)4.8–5.2(6.0) × (2.8)2.9–3.2 µm, Q = (1.40)1.56–1.79(1.88), Qm = 1.67 ± 0.09, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 13–21(22) × 4–6 µm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with an umbo at apex, (12)14–20 × 4–5 µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched or coralloid hyphae, diverticulate, flat, (6)7–15 µm wide, hyaline to light yellow, encrusting, smooth, thin- to thick-walled. clamp connections present.

Habitait – Grows on the deciduous layer in coniferous or broad-leaved forest.

Other specimen examined – China. Yanbian Korean Autonomous Prefecture, Dunhua City, Dapuchaihe Twon, Hancongling Scenic Spot, 6 July 2019, Jia-Jun Hu and Bo Zhang, HMJAU 61064 (Collection no.: Hu 204).

Note – This species is characterized by its medium basidiomata, smooth, glabrous, hemispherical pileus, the occasional presence of an umbo, being entirely lemon-coloured, flattened, coralloid, and encrusted pileipellis, and smaller basidiospores.

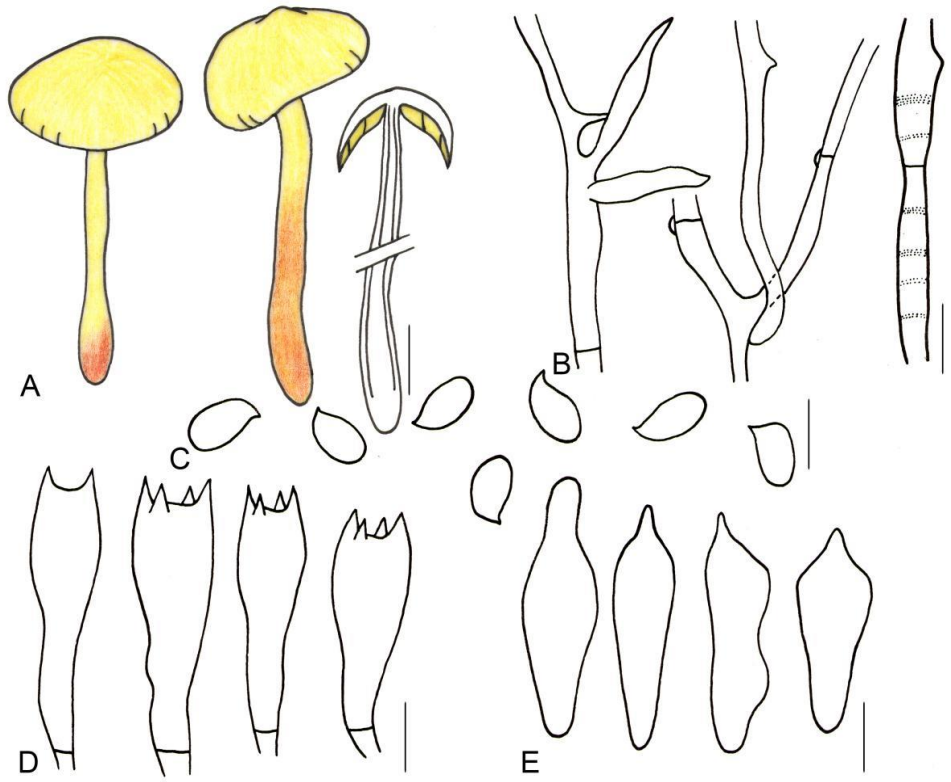

Figure 35 – Morphological characters of *Levipedipilus mimor* (HMJAU 61063). A Basidomata. B Pileipellis elements. C Basidospores. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B = 25 µm, C–E = 5 µm.

This species is easily confused with *Collybia citrina* B. Liu, Rong & H.S. Jin due to their highly similar morphology. However, *L. mimor* differs from *C. citrina* by its light yellow to lemon-colour, entire, and not wavy lamellae, smooth and fibrous stipe, smaller basidiospores, presence of cheilocystidia, and absence of pleurocystidia (Liu et al. 1984).

Levipedipilus ctrinoides J.J. Hu, B. Zhang & Y. Li, sp. nov. Figs 36, 59V

Fungal names: FN571368

Etymology – "*ctrinoides*" refers to this species similar to *Collybia ctrina*.

Diagnosis – This species could be distinguished from other species by small to large basidiomata, gregarious, yellowish brown at first, then yellow, yellowish brown at disc pileus, crowded and yellow lamellae, smooth and yellow stipe, happen in early spring or late Autumn, smaller basidiospores, weakly coralloid, diverticulate, or branched cheilocystidia, and a coralloid or clavate with long slender umbo at apex pileipellis.

Type – China. Jilin Province: Tonghua City, Liuhe County, Nanshan Park, 20 June 2021, Jia-Jun Hu and Zheng-Xiang Qi, HMJAU 61065 (Collection no.: Hu 719), holotype.

Basidiomata small to large, solitary, scattered, or gregarious. Pileus oblate semispherical to convex, or applanate, reflex sometimes, 0.8–4.3 cm in diameter, smooth, glabrous, hygrophanus, yellowish brown at first, yellowish brown at disc, yellow to lemon yellow outwards when mature, or always yellow to lemon yellow entirely; margin entire or serrated sometimes, wavy sometimes, hygrophanus, yellowish brown at first, yellow to lemon yellow when mature, or yellow to lemon yellow when mature all the time. Context thin, yellow to lemon yellow, fresh, odourless. Stipe central, cylindrical or clavate, 1.3–3.4 cm long and 0.2–0.8 cm wide, lemon yellow to yellowish brown, fistulose, fibrous. Lamellae adnate to adnexed, close, yellow to lemon yellow, unequal.

Basidiospores elliptic, 5.0–6.2(6.8) × (2.2)2.3–3.3(3.4) µm, Q = 1.67–2.22(2.27), Qm = 1.88 ± 0.18, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (13)17–23(27) × 4–6(7) µm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, finger-like, or diverticulate, (14)16–22 × 4–6 µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched or coralloid hyphae, diverticulate, flat, 7–11(13) µm wide, hyaline, smooth, thin-walled, clamp connections present.

Habitat – Grows on the deciduous layer in coniferous, broad-leaved, or broad-leaved and coniferous mixed forest.

Other specimens examined – China. Jilin Province: Changchun City, Campus of Jilin Agricultural University, 29 August 2019, Jia-Jun Hu, HMJAU 61066 (Collection no.: Hu 323); Changchun City, Jingyuetan National Forest Park, 8 August 2021, Jia-Jun Hu, Bo Zhang, Gui-Ping Zhao, and Zhen-Hao Zhang, HMJAU 61067 (Collection no.: Hu 806); Changchun City, Northeast Tiger Park, 14 September 2021, Jia-Jun Hu and Bo Zhang, HMJAU 61068 (Collection no.: Hu 908); Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 26 June 2021, Jia-Jun Hu and Zheng-Xiang Qi, HMJAU 61069 (Collection no.: Hu 746).

Note – This species is characterized by its small to large basidiomata, being gregarious, yellowish brown at first, which later develops into yellow, being yellowish brown at the disc pileus, crowded and yellow lamellae, smooth and yellow stipe, arising in the early Spring or late Autumn, relatively small basidiospores, weakly coralloid, diverticulate, or branched cheilocystidia, being coralloid or clavate, and having a long slender umbo at the apex pileipellis.

Levipedipilus ctrinoides is highly similar to *L. minor* based on its yellow to lemon basidiomata. However, *L. ctrinoides* differs from *L. minor* by being brown prior to turning yellow, being yellowish brown at the disc pileus, having crowded lamellae, occurring in the early Spring, larger basidiospores, weakly coralloid, diverticulate, or branched cheilocystidia, being coralloid or clavate, and having a long slender umbo at the apex pileipellis.

Levipedipilus maculatus J.J. Hu, B. Zhang & Y. Li, sp. nov. Figs 37, 59G

Fungal names: FN571369

Etymology – "*maculatus*" refers to this species with spots on pileus when mature.

Diagnosis – This species is differentiated from other species by small and light yellow basidiomata, with mastoid at the disc, without stripe, brown spots on the pileus when mature, wavy at margin, close lamellae with pinkish tone, cylindrical stipe with obviously flatten to spherical at base, smaller basidiospores, irregularly clavate, branched or finger-like, diverticulate cheilocystidia, branched or coralloid pileipellis.

Type – China. Jilin Province: Changchun City, Jingyuetan National Forest Park, 27 August 2022, Jia-Jun Hu and Bo Zhang, HMJAU 61070 (Collection no.: Hu 293).

Basidiomata small, gregarious. Pileus convex to bamboo-hat-like, 1.2–3.8 cm in diameter, light brown at disc, paler outwards, yellow, smooth, glabrous, hygrophanus, with brown spots when mature; margin entire, wavy, involute, yellow. Context thin, fresh, light yellow to white, odourless. Stipe central, cylindrical, obviously enlarged at base, 3.2–7.0 cm long and 0.2–0.6 cm wide, smooth, light yellow, deeper colour downwards, yellow to brown, or light reddish brown, fistulose, fibrous. Lamellae adnate or adnexed, white to light yellow, crowded, unequal.

Basidiospores elliptic, 4.8–5.2(8.0) × (2.4)2.7–3.0(3.1) µm, Q = (1.60)1.61–2.00, Qm = 1.76 ± 0.10, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (14)15–22 × (5)6–8 µm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, irregularly clavate, branched or finger-like, diverticulate, 13–27(30) × 3–7(8) µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched or coralloid hyphae, diverticulate, flatten, 5–13(14) µm wide, hyaline, smooth, thin-walled. clamp connections present.

Habitat – Grows on the deciduous layer in coniferous forest.

Note – This species is characterized by its small and light yellow basidiomata, being mastoid at the disc, brown spots on the pileus when mature, wavy margin, close lamellae, cylindrical stipe that is obviously flattened to spherical at the base, smaller basidiospores, being irregularly clavate, branched or finger-like, diverticulate cheilocystidia, and branched or coralloid pileipellis.

The light yellow basidiomata and the fact that it grows on fallen leaves make *L. maculatus* similar to both *L. dryophilus* and *L. ocior*. However, *L. maculatus* differs from *L. dryophilus* by its mastoid umbo at the disc of the pileus, without stripe, wavy margin, flattened to spherical base of the stipe, smaller basidiospores, and by growing on dead fallen leaves in coniferous forests. *Levipedipilus maculatus* differs from *L. ocior* by its paler pileus with brown spots and the fact that it happens in July (Antonín et al. 2013).

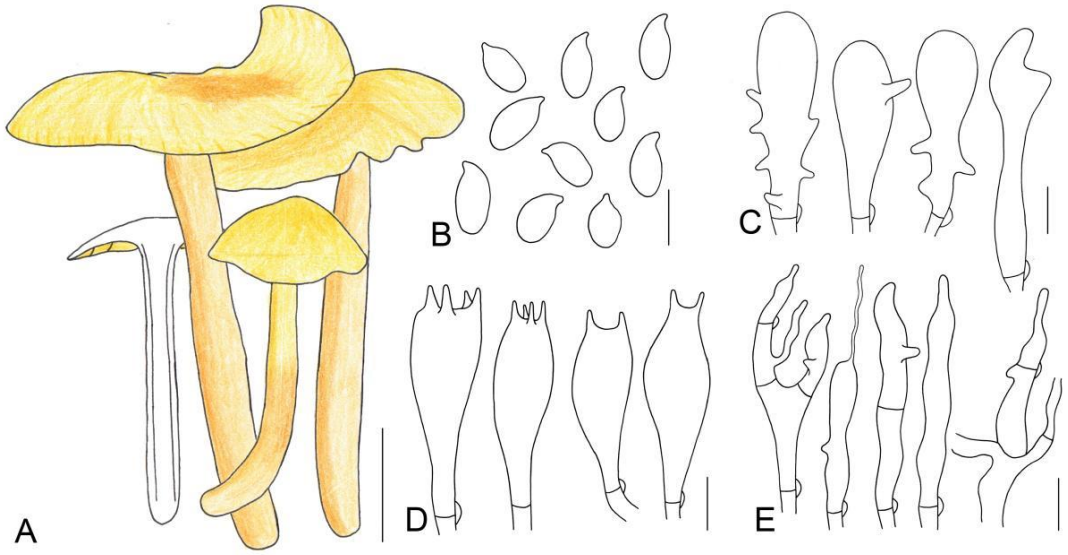

Figure 36 – Morphological characteristic of *Levipedipilus ctrinoides* (HMJAU 61065). A Basidiomata. B Basidiospores. C Cheilocystidia. D Basidia. E Pileipellis elements. Scale bars: A = 1 cm, E = 10 µm, B–D = 5 µm.

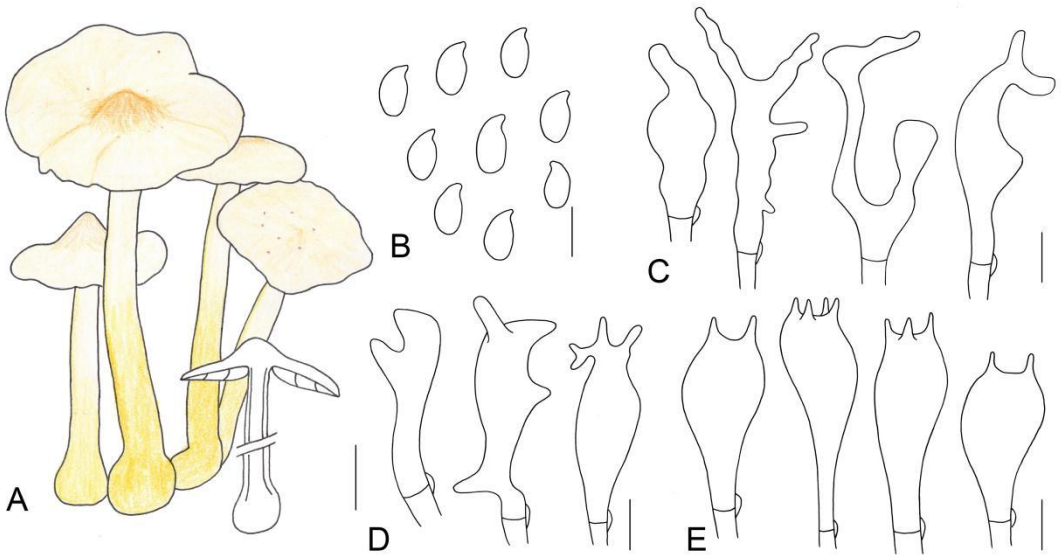

Figure 37 – Morphological characterize of *Levipedipilus maculatus* (HMJAU 61070). A Basidiomata. B Basidiospores. C Cheilocystidia. D. Pileipellis elements. E Basidia. Scale bars: A = 1 cm, D = 10 μm, B, C, E = 5 μm.

Levipedipilus luteofuscus J.J. Hu, B. Zhang & Y. Li, sp. nov. Figs 38, 59H

Fungal names: FN571370

Etymology – "*luteofuscus*" refers to this species with brown pileus and stipe.

Diagnosis – This species could be distinguished from other species by brown pileus and stipe, slight depressed at disc when mature, cylindrical or clavate stipe, close lamellae, flatten pileipellis that often coralloid, diverticulate, or long and slim branch with branched apex, clavate cheilocystidia with an umbo at apex, and bigger basidiospores.

Type – China. Yunnan Province: Qujing City, Huize County, Dahaicaoshan, 1 August 2019, Jia-Jun Hu and Bo Zhang, HMJAU 61071 (Collection no.: Hu 253).

Basidiomata small, gregarious. Pileus hemispheric to convex, slightly depressed at center to becoming shallow infundibuliform or reflex when mature, 1.7–3.7 cm in diameter, smooth, glabrous, hygrophanus, brown to dark brown or light brown; margin entire, wavy, yellow to light brown. Context thin, light yellow to light brown, fresh, odourless. Stipe central, cylindrical, 3.0–7.2 cm long and 0.3–0.4 cm wide, fistulose, fibrous. Lamellae adnexed, white to light yellowish brown, crowded, unequal.

Basidiospores elliptic, (5.3)5.4–7.0(7.1) × (2.6)2.9–3.8(3.9) μm, Q = (1.63)1.66–2.17(2.31), Qm = 1.92 ± 0.17, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (14)16–20(21) × 5–7(8) μm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, irregularly clavate, with an umbo at apex, 13–22 × 4–7(8) μm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched or coralloid hyphae, diverticulate, flat, 5–11(12) μm wide, hyaline, smooth, thin-walled, clamps present.

Habitait – Grows on alpine grassland.

Other specimen examined – China. Yunnan Province: Qujing City, Huize County, Dahaicaoshan, 1 August 2019, Jia-Jun Hu and Bo Zhang, HMJAU 61072 (Collection no.: Hu 254).

Note – This species is characterized by its brown pileus and stipe, slightly depressed disc when mature, cylindrical or clavate stipe, close lamellae, flattened pileipellis that is often coralloid, diverticulate, or with long and slim branches with a branched apex, clavate cheilocystidia with an umbo at the apex, and larger basidiospores.

Morphologically, the brown pileus and stipe render *L. luteofuscus* similar in apperance to *L. ocior*. However, *L. luteofuscus* differs from *L. ocior* by its brown pileus that is never reddish

brown, relatively sparse lamellae, cylindrical stipe, slightly larger basidiospores, and clavate cheilocystidia with an umbo at the apex (Antonín et al. 2013).

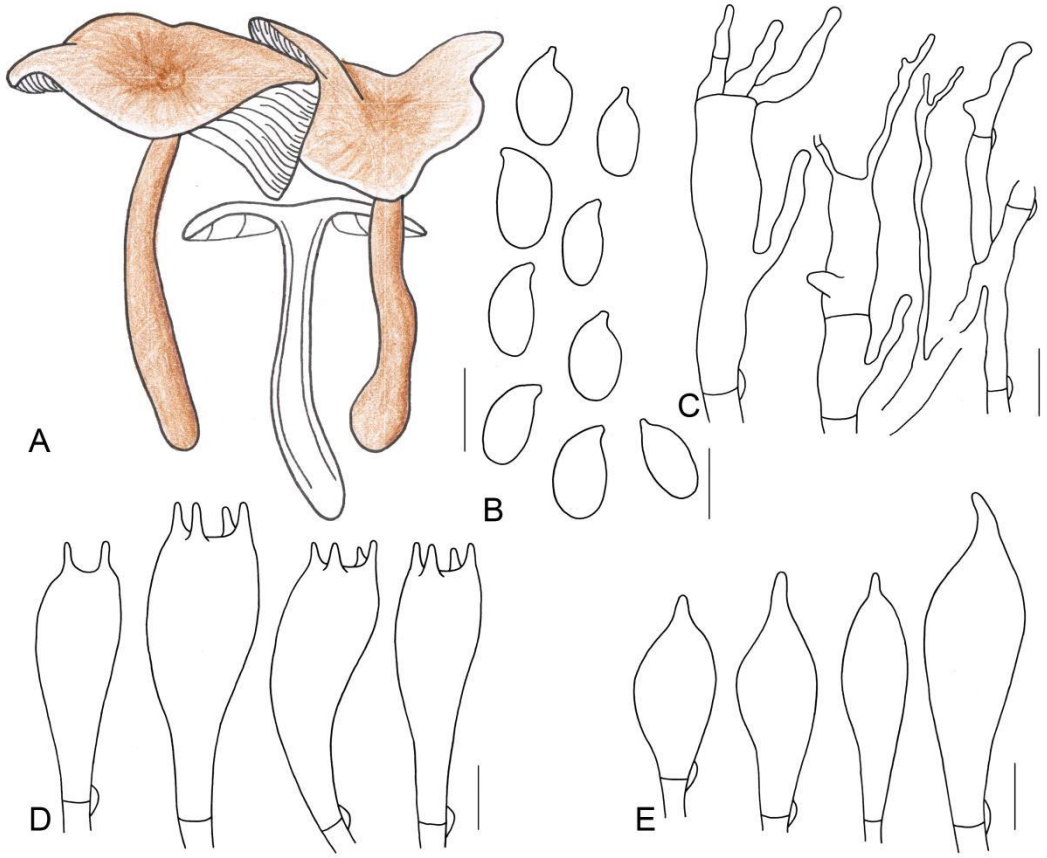

Figure 38 – Morphological characterize of *Levipedipilus luteofuscus* (HMJAU 61071). A Basidiomata. B Basidiospores. C Pileipellis elements. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B, D, E = 5 μm, C = 10 μm.

Levipedipilus hemisphaericus J.J. Hu, B. Zhang & Y. Li, sp. nov. Figs 39, 58O

Fungal names: FN571372

Etymology – "*hemisphaericus*" refers to this species with hemispherical pileus.

Diagnosis – This species differs from closed species by small to medium basidiomata, hemispherical pileus with an umbo at disc, entirely orange to yellow, pruinose on stipe, coralloid and diverticulate pileipellis, abundant caulocystidia that branched or coralloid, and irregular clavate or branched at apex cheilocystidia.

Type – China. Heilongjiang Province: Yichun City, Liangshui Nation Nature Reserve, 22 June 2019, Jia-Jun Hu and Di-Zhe Guo, HMJAU 61077 (Collection no.: Hu 148).

Basidiomata small to medium, gregarious. Pileus hemispherical to oblate hemispherical or convex, with an umbo sometimes, 2.1–5.6 cm wide, orange at first, yellowish brown when mature, hygrophanus, smooth, glabrous; margin entire, involute or reflex, orange at first, yellowish brown when mature, hygrophanus. Context thin, light yellowish brown, fresh, odourless. Stipe central to eccentric, 4.2–5.9 cm long and 0.2–0.7 cm wide, smooth or pruinose, fistulose, fibrous. Lamellae adnate to adnexed, close, yellowish brown, unequal.

Basidiospores elliptic, (4.8)5.0–6.0 × 2.9–3.1(3.2) μm, Q = (1.61)1.66–1.88(1.94), Qm = 1.73 ± 0.08, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 18–27 × 4–5 μm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, irregularly clavate, branched or finger-like on the top, (13)14–27(29) × 4–6 μm, thin-walled, smooth, hyaline. Caulocystidia abundant,

irregularly clavate, branched or finger-like, (38)40–100(125) × 3–6(25) µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched or weakly coralloid hyphae, flatten, 7–15 µm wide, hyaline, smooth, thin-walled. Clamp connections present.

Habitat – Grows on the deciduous layer in coniferous or broad-leaved forest.

Other specimens examined – China. Jilin Province: Baishan City, Fusong County, Lushuihe Town, Changbai Mountain ancient tree park, 5 July 2019, Jia-Jun Hu, Di-Zhe Guo, and Bo Zhang, HMJAU 61078 (Collection no.: Hu 187); Yanbian Korean Autonomous Prefecture, Dunhua City, Dapuchaihe Town, Hancongling Scenic Spot, Jia-Jun Hu, Di-Zhe Guo, and Bo Zhang, HMJAU 61079 (Collection no.: Hu 233).

Note – This species is characterized by its small to medium basidiomata, hemispherical pileus with an umbo at the disc, being entirely orange to yellow, pruinose on the stipe, coralloid and diverticulate pileipellis, abundant caulocystidia that are branched or coralloid, and irregular clavate or branched at the apex cheilocystidia.

This species is closely related to four species: *L. aurantiipes*, *L. fagiphilus*, *L. indoctoides* and *L. macropus*, due to the shared presence of caulocystidia in sect. *Levipedes*. However, *L. aurantiipes* and *L. fagiphilus* differ from this species by both featuring reddish brown stipes and larger basidiospores. *Levipedipilus indoctoides* differs from this species by its striped pileus and the presence of pileocystidia. *Levipedipilus macropus* differs from this species by its striped pileus, extremely long and slim stipe, and short-cylindrical cheilocystidia.

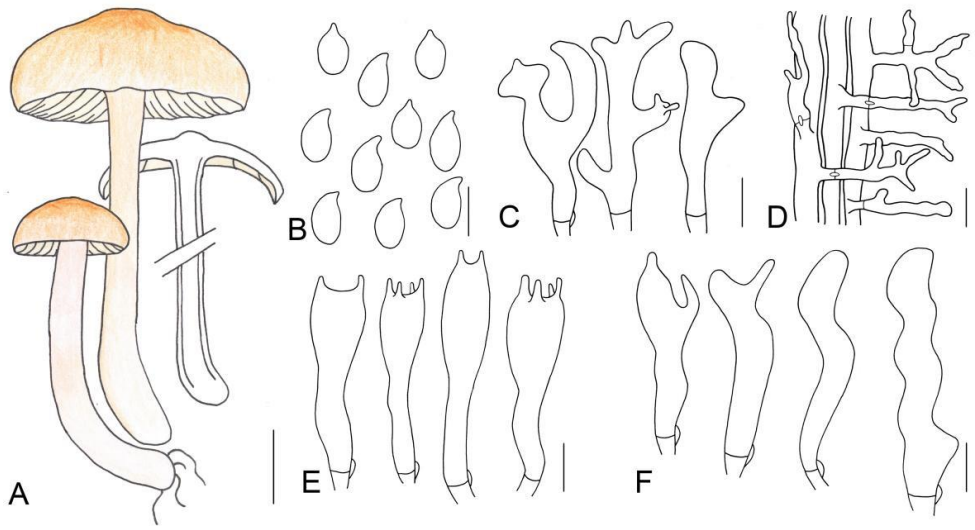

Figure 39 – Morphological characterize of *Levipedipilus hemisphaericus* (HMJAU 61077). A Basidiomata. B Basidiospores. C Pileipellis elements. D Caulocystidia. E Basidia. F Cheilocystidia. Scale bars: A = 1 cm, B, E, F = 5 µm, C = 10 µm, D = 20 µm.

Levipedipilus aquosus (Bull.) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 40, 58Y

= *Gymnopus aquosus* (Bull.) Antonín & Noordel.

= *Collybia aquosa* (Bull.) P. Kumm.

Fungal names: FN571373

Basidiomata collybioid, small to medium, gregarious. Pileus applanate, 3.6–5.7 cm, brown at disc, paler outwards, light brown to brown, smooth, glabrous; margin wavy, entire, yellowish white to light brown. Context thin, white to concolour with pileus, odourless. Lamellae adnate, extremely crowded, light brown to brown, unequal. Stipe central, cylindrical to clavate, 5.5–7.3 cm long and 0.5–1.1 cm wide, smooth, covered with brown sparse tomentose at base, fistulose, fibrous.

Basidiospores elliptic to oblong, (4.0)4.3–5.4(6.0) × (2.1)2.3–3.0(3.8) µm, Q = (1.33)1.48–2.00(2.38), Qm = 1.78 ± 0.19, smooth, hyaline, thin-walled, inamyloid. Basidia clavate, (17)18–29(35) × 5–6(7) µm, 2- or 4-spored, hyaline, thin-walled. Cheilocystidia irregular clavate or

clavate, with an umbo or finger-like at apex, (17)18–27(28) × 4–7(8) μm, thin-walled, hyaline. Pleurocystidia and caulocystidia not observed. Pileipellis a cuits, coralloid, diverticulate, flatted, made up of cylindrical hyphae; terminal hyphae coralloid or finger-like, flatted, thin-walled, 7–15 μm. Clamp connections present.

Habitat – Grows on the deciduous layer in coniferous and broad-leaved mixed forest.

Specimen examined – China. Hunan Province: Zhangjiajie City, Zhangjiajie Campus of Jishou University, 28 May 2021, Wei-Qiang Qin, HMJAU 61080 (Collection no.: 713).

Note – Some differences were noted between our collection and *L. aquosus* reported from Europe and North America, especially the lack of almost to the centre translucently striate and smaller basidiospores. *Levipedipilus aquosus* is easily confused with *L. dryophilus* and *L. ocior*, due to their highly similar appearance. However, *L. aquosus* can be distinguished from *L. dryophilus* by its enlarged to bulbus stipes with pinkish ochraceous rhizomorphs. In addition, *L. aquosus* can be differentiated from *L. ocior* by its pinkish ochraceous rhizomorphs and white to light yellow lamellae (Antonín & Noordeloos 2010, Antonín et al. 2013).

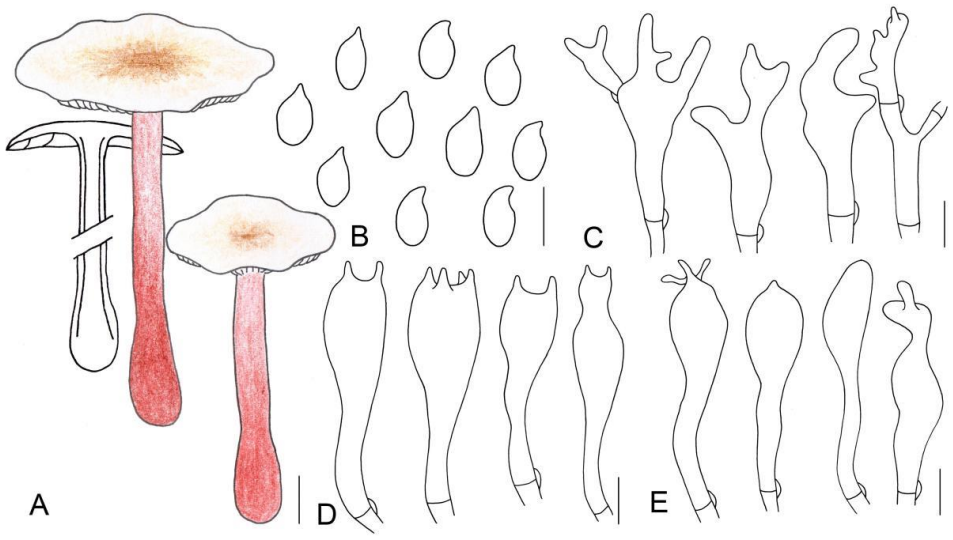

Figure 40 – Morphological characterize of *Impudipilus aquosus* (HMJAU 61080). A Basidiomata. B Basidiospores. C Pileipellis elements. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B, D, E = 5 μm, C = 10 μm.

Levipedipilus brunneodiscus (Antonín, Ryoo & Ka) J.J. Hu, B. Zhang & Y. Li, comb. nov.

Figs 41, 58T

= *Gymnopus brunneodiscus* Antonín, Ryoo & Ka

Fungal names: FN571374

Basidiomata small to large, scattered to gregarious. Pileus hemispheric to convex, smooth, dark brown at disc, brown outwards; margin light brown to yellow, entire. Context thin, white, odourless. Stipe central, cylindrical, 4.1–5.0 cm long and 0.3–0.4 cm wide, brown, paler at base, covered with tomentose, fistulose, fibrous. Lamellae adnexed to near free, white, close, unequal.

Basidiospores elliptic, (4.8)5.0–6.2(7.0) × 2.9–3.8 μm, Q = (1.34)1.58–2.06(2.07), Qm = 1.78 ± 0.16, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (17)18–25 × 4–6(7) μm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, branched, (14)15–25(27) × 4–6(7) μm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched or coralloid hyphae, diverticulate, flat, 7–12(15) μm wide, hyaline to brown, encrusting, smooth or rough, thin- to thick-walled. Clamp connections present.

Habitat – Grows on the deciduous layer in coniferous forest.

Specimen examined – China. Jilin Province: Tonghua City, Huinan County, 23 September 2021, Yang Wang, HMJAU 61081 (Collection no.: 990).

Note – This species is characterized by its light brown to brown pileus and stipe, being near white at the margin of the pileus, clavate cheilocystidia that are branched or coralloid at the apex, and having a *Dryophila* structure pileipellis. This species was described from South Koran in 2020 (Ryoo et al. 2020). Combined with morphological and phylogenetic study, our collection is conferred to be *L. brunneodiscus*. Moreover, this is the first time this species was recorded from China.

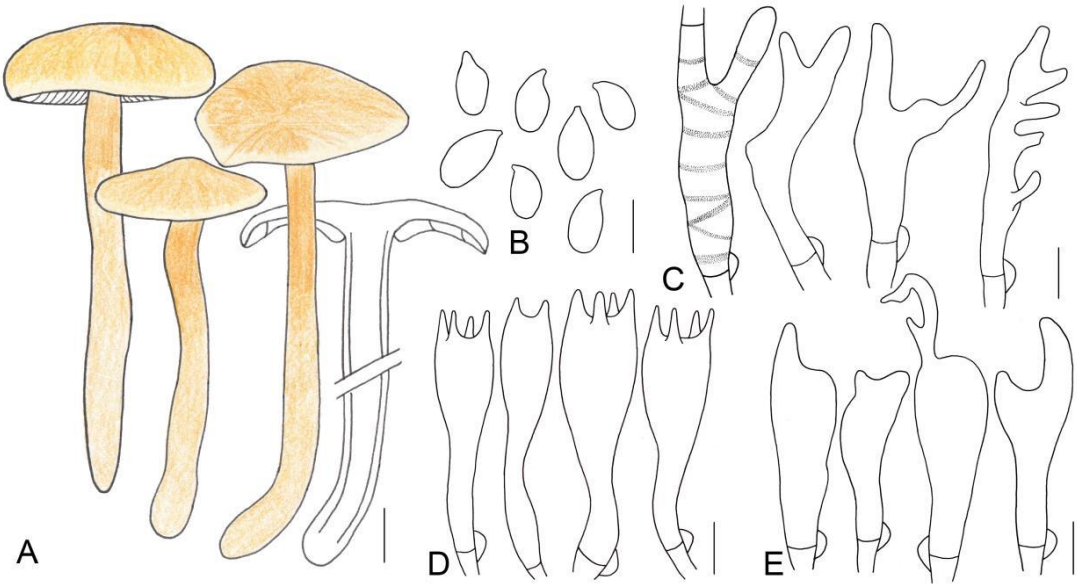

Figure 41 – Morphological characters of *Impudipilus brunneodiscus* (HMJAU 61081). A Basidomata. B Basidospores. C Pileipellis elements. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B, D, E = 5 µm, C = 25 µm.

Levipedipilus dryophiloides (Antonín, Ryoo & Ka) J.J. Hu, B. Zhang & Y. Li, comb. nov.

Figs 42, 58W

= *Gymnopus dryophiloides* Antonín, Ryoo & Ka

Fungal names: FN571375

Basidiomata collybioid, small, gregarious. Pileus hemispherical to oblate-semispherical, 0.5–2.3 cm, smooth, hygrophanus, yellowish brown when young, becoming yellow; margin entire, involute. Context thin, light yellow, odourless. Lamellae light yellow, adnexed, extreamly crowded, unequal. Stipe central, clavate, obviously enlarged at base, 1.5–5.1 cm, smooth, light yellow, fistulose, fibrous.

Basidiospores elliptic to oblong, 5.0–6.1(6.8) × 2.8–3.1(3.5) µm, Q = (1.65)1.71–2.03(2.19), Qm = 1.88 ± 0.13, hyaline, smooth, inamyloid, thin-walled. Basidia clavate, 14–21(23) × (4)5–7 µm, 2 or 4 spored, hyaline, thin-walled. Cheilocystidia irregularly clavate, labed, with an umbo or diverticulate at apex. Pleurocystidia and caulocystidia not observed. Pileipellis a cuits, made up of cylindrical hyphae, coralloid, diverticulate, 6–12(14) µm wide, hyaline to light yellow, thin-walled. Clamp connections present.

Habitat – Grows on the deciduous layer in coniferous forest.

Specimen examined – China. Jilin Province: Changchun City, Jingyuetan National Forest Park, 14 September 2021, Jia-Jun Hu, Bo Zhang, and Gui-Ping Zhao, HMJAU 61082 (Collection no.: Hu 905).

Note – This species was described from South Korea by Ryoo et al., while it has never previously been recorded from China. The species is characterized by its finely denticulate and pubescent edge of the lamellae, being slightly broader to sub-bulbose (up to 10 mm) at the base of

stipe, whiteish to pale (pinkish) ochraceous basal rhizoids, and smaller basidiospores ((4.0)4.5–6.0(6.5) × 2.5–3.5(4.0) mm) (Ryoo et al. 2020). There exist some differences between our collections and the original description. Our collections exhibited lamellae that were entirely at the edge, and 2- or 4-spored basidia, which are features that were not included in the original description.

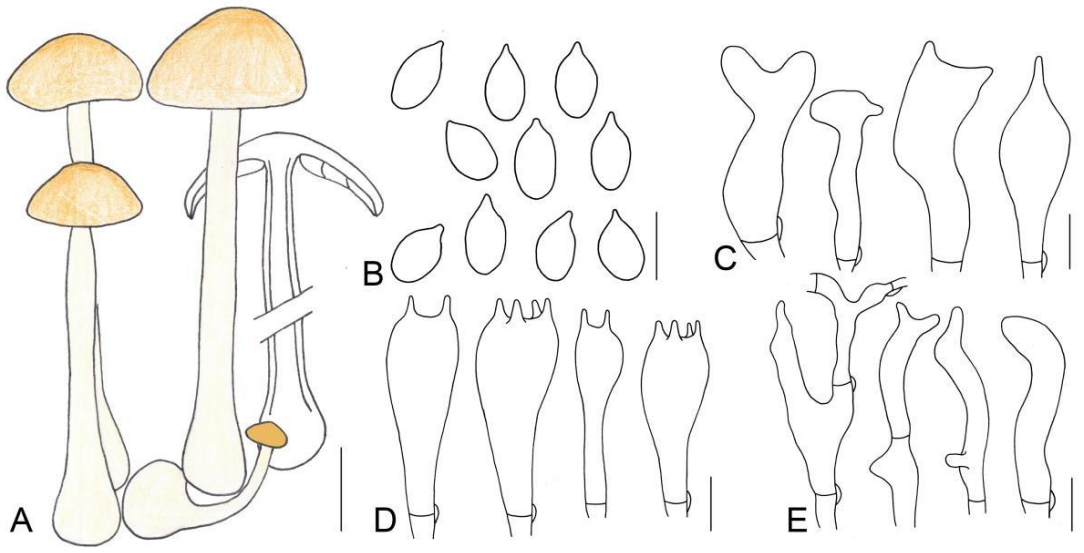

Figure 42 – Morphological characterize of *Impudipilus dryophilioides* (HMJAU 61082). A Basidomata. B Basidiospores. C Cheilocystidia. D Basidia. E Pileipellis elements. Scale bars: A = 1 cm, B–D = 5 μm, E = 10 μm.

Levipedipilus dryophilus (Bull.) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 43, 58X

= *Gymnopus dryophilus* (Bull.) Murrill

= *Collybia dryophila* (Bull.) P. Kumm.

= *Agaricus dryophilus* Bull.

Fungal names: FN571376

Basidiomata collybioid, small to medium, gregarious. Pileus oblate-semispherical, light yellow, 1.0–2.7 cm, smooth, glabrous, hygrophanus; margin entire, involute, light yellow. Context thin, white to light yellow, odourless. Stipe central, cylindrical, slightly enlarged at base, or clavate, 2.5–3.6 cm long and 0.3–0.6 cm wide, smooth, fistulose, fibrous. Lamellae adnate to adnexed, extremely crowded, yellowish white to light yellow, unequal.

Basidiospores elliptic to oblong, (4.2)4.8–6.0(6.3) × (2.2)2.8–3.2(3.4) μm, Q = (1.50)1.59–2.00, Qm = 1.75 ± 0.12, hyaline, smooth, inamyloid, thin-walled. Basidia clavate, (13)14–22(23) × 4–8 μm, 2- or 4-spored, hyaline, thin-walled. Cheilocystidia abundant, clavate, finger-like at apex, diverticulate, (13)14–22(23) × 4–8 μm, hyaline, thin-walled. Pleurocystidia and caulocystidia not observed. Pileipellis a cuits, made up of cylindrical hyphae, coralloid, diverticulate, 7–13(14) μm, hyaline, thin-walled. Clamp connections present.

Habitat – Grows on the deciduous layer in coniferous forest.

Specimens examined – China. Liaoning Province: Fushun City, Xinbin Manchu Autonomous County, Gangshan National Forest Park, 1 August 2017, Ao Ma, HMJAU 48370 (Collection no.: 448); Fushun City, Xinbin Manchu Autonomous County, Gangshan National Forest Park, 11 July 2017, Ao Ma, HMJAU 61083 (Collection no.: 442).

Note – This species is widespread, and has often been easily confused with *L. aquosus*, *L. ocior*, and *L. dryophilioides*, among others. Then, Antonín et al. pointed out that colour of the lamellae, and shape of the cheilocystidia are the key to distinguishing species belonging to the *Levipedipilus dryophilus* complex, though due to the variety of pileipellis, there is great difficulty in distinguishing these species (Antonín et al. 2013).

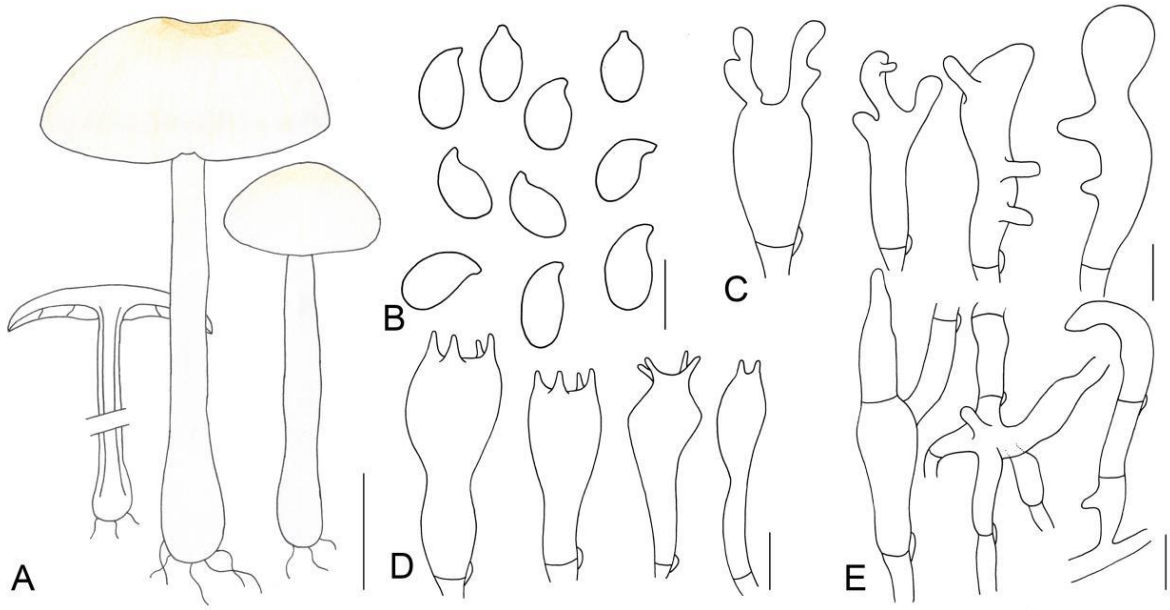

Figure 43 – Morphological characterize of *Impudipilus dryophilus* (HMJAU 48370). A Basidomata. B Basidiospores. C Cheilocystidia. D Basidia. E Pileipellis elements. Scale bars: A = 1 cm, B–D = 5 μm, E = 10 μm.

Levipedipilus inexpectatus (Consiglio, Vizzini, Antonín & Contu) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 44, 58I

= *Gymnopus inexpectatus* Consiglio, Vizzini, Antonín & Contu

Fungal names: FN571377

Basidiomata small to medium, gregarious. Pileus hemispherical to convex, 1.4–2.2 cm in diameter, smooth, light brown at disc, yellowish brown outwards; margin yellowish brown to beige, hgrophanous, entire. Context thin, white to light yellow, odourless. Stipe central, 2.3–4.2 cm long and 0.3–0.5 cm wide, light brown, paler at apex, smooth or tomentose at base, fistulose, fibrous. Lamellae adnate, white to fresh-pink, I = 3–5, L = 25–29, close, unequal.

Basidiospores elliptical, (4.4)4.8–6.0 × 2.8–3.2 μm, Q = (1.33)1.47–2.00(2.07), Qm = 1.75 ± 0.14, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 13–24 × 4–6(7) μm, 2- to 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with an umbo at apex, 14–22(23) × 4–5 μm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched or coralloid hyphae, diverticulate, flatten, (5)6–12(13) μm wide, yellow, smooth, thin-walled. Clamp connections present.

Habitat – Grows on the deciduous layer in coniferous and broad-leaved mixed forests.

Specimens examined – China. Jilin Province: Yanbian Korean Autonomous Prefecture, Dunhua City, Dapuchaihe Town, Hancongling Hongye Valley, 21 July 2019, Gu Rao, HMJAU 61084 (Collection no.: 695); Baishan City, Changbai Korean Autonomous County, Wangtian'e Scenic Spot, 24 July 2019, Rui Ma and Zeng-Yi Bi, HMJAU 61085 (Collection no.: 408); Sichuan Province: Diqing Tibetan Autonomous Prefecture, Shangri La City, Jiantang Town, Pudacuo National Forest Park, 13 August 2019, Di-Zhe Guo, HMJAU 61086 (Collection no.: 340); Diqing Tibetan Autonomous Prefecture, Shangri La City, Jiantang Town, Pudacuo National Forest Park, 13 August 2019, Di-Zhe Guo, HMJAU 61087 (Collection no.: 343).

Note – This species is characterized by its hemispherical to convex pileus that is yellow to yellowish brown, paler at the margin, being covered with brown spots when mature, yellowish brown and cylindrical stipe that is smooth or tomentose at the base, coralloid and flattened pileipellis, long and slim cheilocystidia that are clavate, being finger-like or coralloid at the apex, and the presence of cylindrical or clavate caulocystidia.

This species was originally described from Italy (Vizzini et al. 2008), however, it has never been recorded from China. This species belongs to the *L. dryophilus* complex, while, and due to the presence of caulocystidia, it differs from all other species within the complex.

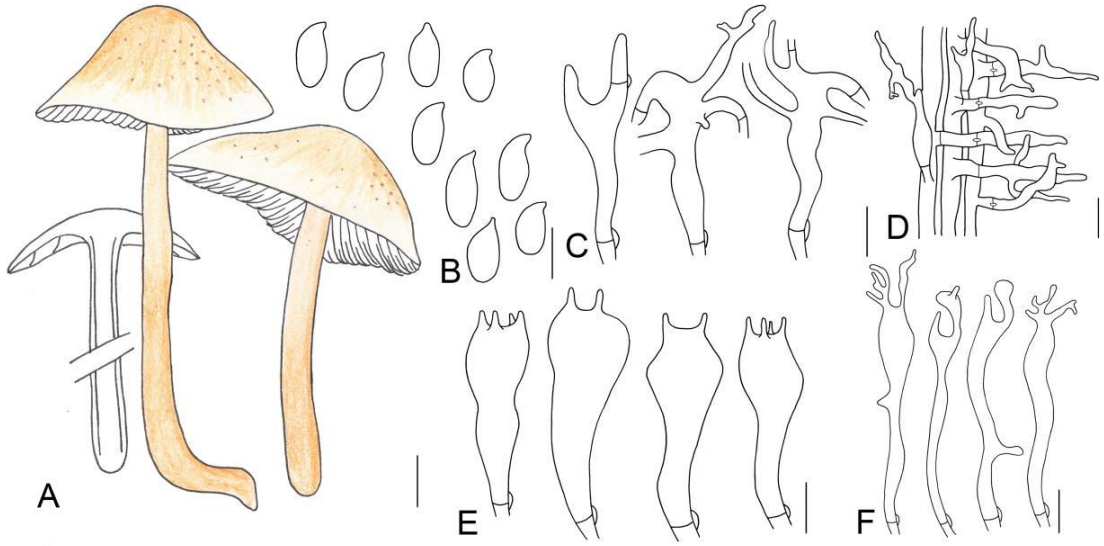

Figure 44 – Morphological characterize of *Levipedipilus inexpectatus* (HMJAU 61086). A Basidomata. B Basidiospores. C Pileipellis elements. D Caulocystidia. E Basidia. F Cheilocystidia. Scale bars: A = 1 cm, D = 20 μm, C = 10 μm, B, E, F = 5 μm.

Levipedipilus ocior (Pers.) J.J. Hu, B. Zhang & Y. Li, comb. nov. Fig. 45

= *Gymnopus ocior* (Pers.) Antonín & Noordel.

= *Collybia ocior* (Pers.) Vilgalys & O.K. Mill.

= *Agaricus ocior* Pers.

Fungal names: FN571378

Basidiomata collybioid, small to medium, solitary to gregarious. Pileus hemispherical to oblate-semispherical, 4.2–5.4 cm in diameter, smooth, glabrous, hygrophanus, orange-red to orange at disc, paler outwards, light yellow to orange; margin entire, reflex occasionally, yellowish white to light yellow. Context thin, yellowish white to concolour with the pileus, odourless. Lamellae adnate to adnexed, extremely crowded, yellowish white to light yellow, unequal. Stipe cylindrical to clavate, 5.0–6.7 cm long and 0.2–0.6 cm wide, smooth, yellow to orange-red, fistulose, fibrous, covered with sparse white mycelium at base.

Basidiospores elliptical, 4.0–6.2 × (2.8)2.9–3.8(4.1) μm, Q = (1.33)1.42–1.97(2.07), Qm = 1.67 ± 0.20, hyaline, smooth, thin-walled, inamyloid. Basidia clavate, (10)11–20 × (3)4–5(6) μm, 2 or 4 spored, hyaline, thin-walled. Cheilocystidia irregular clavate, lobed, bifurcate, or finger-like at apex, diverticulate, (11)12–23(26) × (2)3–6(7) μm, hyaline, thin-walled. Pleurocystidia not observed. Caulocystidia sparse, irregular clavate, branched, diverticulate, (30)33–80(100) × (3)4–9(10) μm, thin-walled, hyaline. Peliepellis a cuits, made up of cylindrical hyphae, branched or coralloid, diverticulate, 5–12(13) μm wide, hyaline, thin-walled.

Habitat – Grows on the deciduous layer in coniferous forest.

Specimens examined – China. Jilin Province: Changchun City, Jingyuetan National Forest Park, 21 June 2018, Jia-Jun Hu, HMJAU 61088 (Collection no.: 07).

Note – This species is characterized by its initially dark red or orange-brown pileus that then turns paler to reddish yellow or pinkish brown, being non-translucent or only translucent at margin, variable cheilocystidia, cylindrical or clavate, etc., and being branched or coralloid at the apex. The difference between our collections and the European and American specimens is the presence of caulocystidia in our collections.

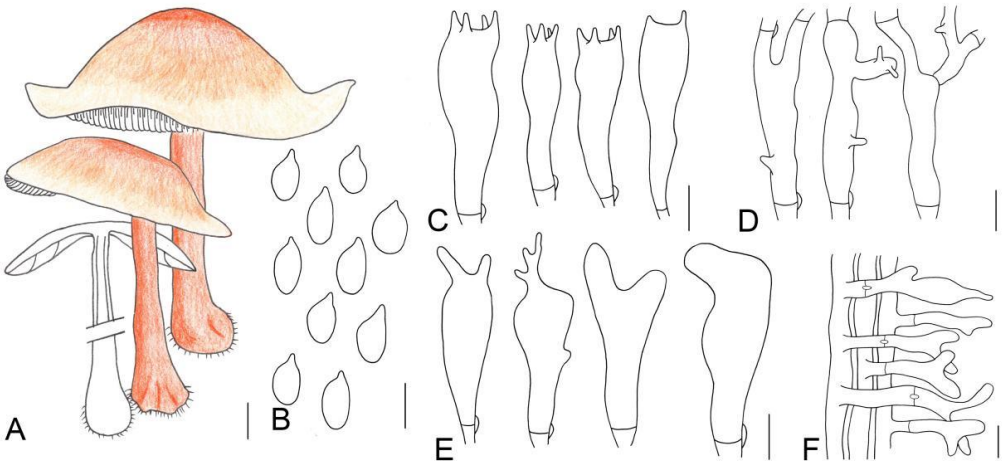

Figure 45 – Morphological characterize of *Levipedipilus ocior* (HMJAU 61088). A Basidomata. B Basidiospores. C Basidia. D Pileipellis elements. E Cheilocystidia. F Caulocystidia. Scale bars: A = 1 cm, B, C, E = 5 μm, D 10 μm, F = 20 μm.

Sect. *Erythropus* J.J. Hu, B. Zhang & Y. Li, sect. nov.

Etymology – Derived from the name of the type species of the section.

Fungal names: FN571341

Basidiospores collybioid, small to medium, scattered to gregarious. Pileus hemispherical to convex, applenate or slightly depressed at disc finally, smooth, glabrous, margin striped, smooth, or tomentose, inrolled to reflex. Lamellae adnate to adnexed, unequal. Stipe cylindrical, smooth, fibrous, hollow, light reddish brown to reddish brown.

Pileipellis a cuits, inflatten, cylindrical or subglobose, coralloid, smooth or encrusted; or layered, up layer inflatten to globose, encrusted, down layer inflatten, branched or coralloid, encrusted, diverticulate. Basidiospores oblong-elliptical to elliptical, smooth, hyaline, inamyloid, thin-walled. Cheilocystidia cylindrical to clavate, with an umbo or branched at apex.

Grows on ground, fallen leaves or branches, rotten woods or base of living trees.

Type species: *Levipedipilus erythropus* (Pers.) J.J. Hu, B. Zhang & Y. Li

Key to the species of Sect. *Erythropus* present in this study

1 Stipe covered with dense hairs at the base.....3
1 Stipe smooth, or covered with sparse hairs at the base.....2
2 Pileus red to reddish brown, grows on ground.....*Levipedipilus erythropus*
2 Pileus yellow to lemon yellow.....*Levipedipilus subsulphureus*
3 Basidia sterigmata extremely long.....4
3 Basidia sterigmata short.....6
4 Stipe smooth in upper part.....5
4 Stipe covered with brown farinose on the upper part.....*Levipedipilus longus*
5 Pileus pale colour, stipe colour uneven.....*Levipedipilus longisterigmaticus*
5 Pileus dark colour, stipe colour uniform.....*Levipedipilus macrosporus*
6 Growing on the deciduous layer or rotten branches.....7
6 Grows at the base of Tilia sp.....*Levipedipilus tiliicola*
7 Pileus pale colour, near white.....*Levipedipilus tomentosus*
7 Pileus deep color.....8
8 Stipe covered with longitudinal stripes.....*Levipedipilus striatus*
8 Stipe without longitudinal stripes.....9
9 Pileipellis a cuits, typically “Dryophila type”.....10
9 Pileipellis layered, hyphae inflated to spherical to prolate.....*Levipedipilus* globulosus
10 Lamellae crowded, smaller basidiospores, lack of caulocystidia.....*Levipedipilus changbaiensis*

10 Lamellae close, bigger basidiospores, presence of caulocystidia.....*Levipedipilus fagiphilus*

Levipedipilus subfasciatus J.J. Hu, Y.L. Tuo, B. Zhang & Y. Li, sp. nov. Figs 46, 58U

Fungal names: FN571379

Etymology – "*subfasciatus*" refers to this species closely related to *Levipedipilus fasciatus.*

Diagnosis – This species is distinguished from similar species by reddish brown to yellowish brown pileus, reddish brown stipe that paler at apex, smooth in upper part, tomentose at base, smaller basidiospores, rarely and clavate cheilocystidia with an umbo at apex, branched and encrusted pileipellis.

Type – China. Jilin Province: Tonghua City, Ji'an County, Wunvfeng National Forest Park, 2 July 2019, Jia-Jun Hu, Yong-Lan Tuo, and Bo Zhang, HMJAU 61089 (Collection no.: Hu 177)

Basidiomata small, gregarious. Pileus hemispherical to oblate hemispherical or convex, 1.9–2.6 cm in diameter, brick-red at disc, paler outwards, light reddish brown to yellowish brown, smooth, glabrous; margin entire, light yellow to light yellowish brown. Context thin, light yellow to light reddish brown, odourless. Stipe central, 3.5–5.3 cm long and 0.2–0.3 cm wide, cylindrical, slightly enlarged at base, reddish brown, paler colour upwards, yellowish brown to light reddish brown, smooth, tomentose downwards, fistulose, fibrous. Lamellae adnate to adnexed, close, white to fresh-pink, unequal.

Basidiospores ellipsoid, 5.0–6.0(6.1) × (2.8)2.9–3.1(3.4) µm, Q = (1.59)1.67–2.00(2.03), Qm = 1.77 ± 0.11, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (13)14–19(20) × (4)5–6(7) µm, 4-spored, thin-walled, hyaline. Cheilocystidia rarely, irregularly clavate, with an umbo at apex, or projections sometimes, (10)11–18(20) × 3–6 µm, thin-walled, hyaline. Caulocystidia abundant, clavate, branched, (30)35–92(95) × 4–6 µm, thin-walled, hyaline. Pileipellis a cuits, branched, diverticulate, hyaline, 5–12(15) µm wide. Clamp connections abundant.

Habitat – Saprophytic on the deciduous layer in broad-leaved forests.

Note – This species is characterized by its reddish brown to yellowish brown pileus, reddish brown stipe that is paler at the apex, being smooth in the upper part, tomentose at the base, relatively small basidiospores, rarely and clavate cheilocystidia with an umbo at the apex, and branched and encrusted pileipellis.

This species is similar to *L. castaneus* and *L. fasciatus* because they share a red to reddish brown pileus and stipe. However, this species differs from *L. castaneus* by its bigger basidiomata, downwardly tomentose stipe, smaller basidiospores, short basidia sterigmata, and the presence of cheilocystidia (Villarreal et al. 2002). *Levipedipilus fasciatus* differs in its free lamellae, smooth or slightly pruinose stipe, larger basidiospores ((5.4–)7.4–9.6 × 2.2–3.2 µm), and the absence of both pleurocystidia and cheilocystidia (Halling 1983).

Levipedipilus changbaiensis (J.J. Hu, B. Zhang & Y. Li) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 47, 58C

≡ *Gymnopus changbaiensis* J.J. Hu, B. Zhang & Y. Li

Fungal names: FN571380

Basidiomata small to medium, gregarious. Pileus hemispherical, deep reddish brown when young, convex or slightly depressed sometimes when mature, 2.1–3.4 cm diameter, smooth, hygrophanus, reddish brown at centre, light yellowish brown towards margin; margin beige to light yellow, striped, entire. Context thin, freshy, light yellowish brown, odourless. Stipe centre, cylindrical, 4.2–5.3 cm long and 0.2–0.3 cm wide, deep reddish brown to reddish brown, smooth in upper part, covered with light yellow to brown hairs up to 1/3 (from base upwards), fistulose, fibrous. Lamellae adnate, fresh-pink, I = 1–5, L = 19–24, crowded.

Basidiospores elliptic, (5.8)6.0–8.1(9.0) × 3.0–4.1(4.2) µm, Q = (1.41)1.53–2.40(2.50), Qm = 1.98 ± 0.24, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (19)20–29(32) × 5–8 µm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with obtuse on the top, (23)24–34(39) × (5)6–7(9) µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of

irregularly branched or weakly coralloid hyphae, flat, 8–23(25) µm wide, hyaline to light yellow, smooth, thin-walled. Clamp connections present.

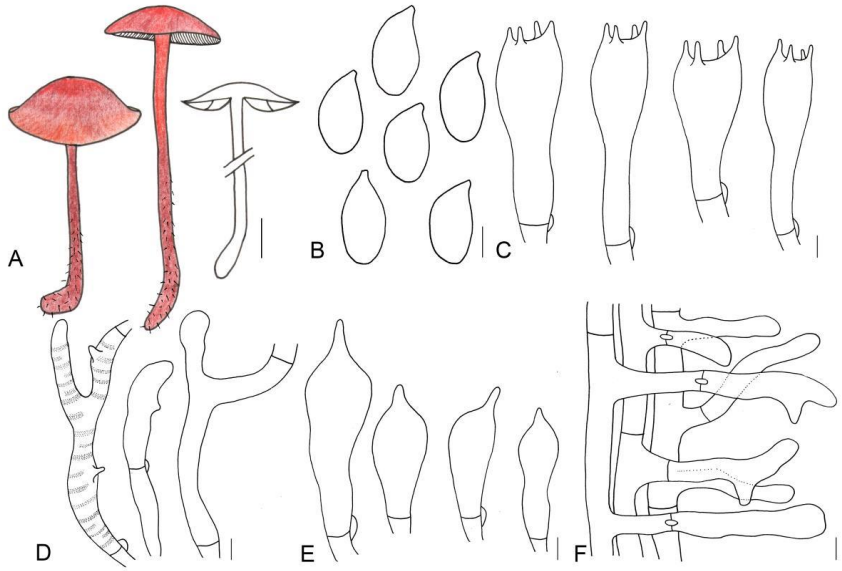

Figure 46 – Morphological characters of *Levipedipilus subfasciatus* (HMJAU 61089). A Basidiomata. B Basidiaspores. C Basidia Basidiaspores. D Pileipellis elements. E Cheilocystidia. F Caulocystidia. Scale bars: A = 1 cm, D, F = 10 µm, B, C, E = 5 µm.

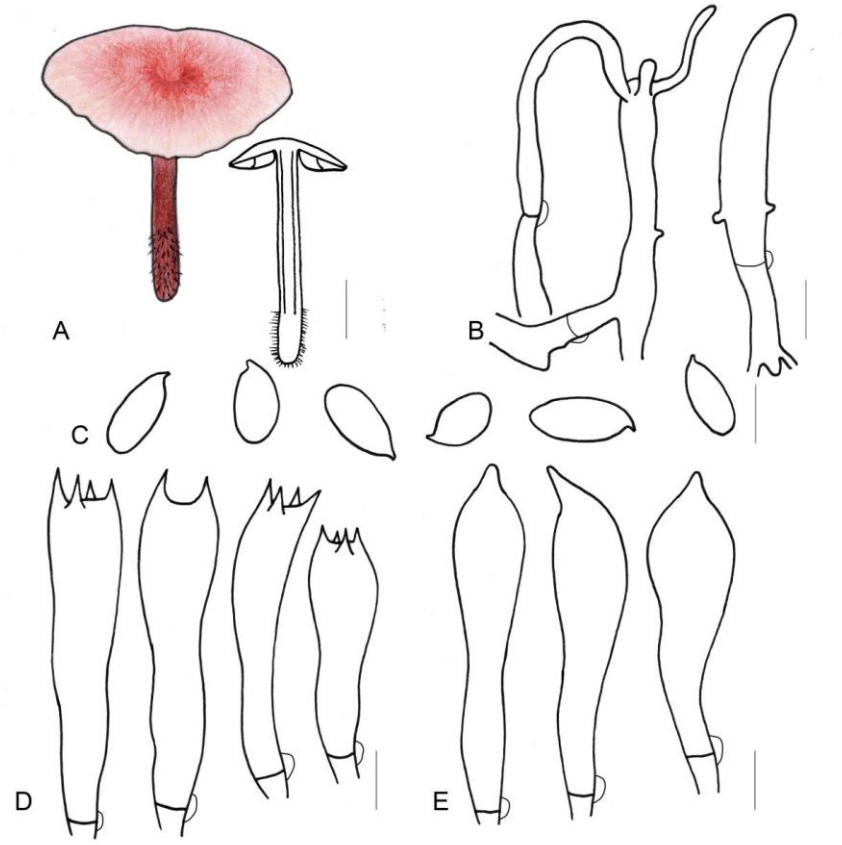

Figure 47 – Morphological characters of *Levipedipilus changbaiensis* (HMJAU 60300, holotype). A Basidomata. B Pileipellis elements. C Basidospores. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B = 25 µm, C–E = 5 µm.

Ecology – Grows on the deciduous layer or rotten branches in coniferous and broad-leaved mixed forests.

Specimens examined – China. Jilin Province: Baishan City, Changbai Korean Autonomous County, Wangtian'e Scenic Spot, 41.56° N, 127.95° E, 17 September 2020, Jia-Jun Hu, Gui-ping Zhao, and Bo Zhang, HMJAU 60300, holotype; Baishan City, Changbai Korean Autonomous County, Wangtian'e Scenic Spot, 41.56° N, 127.95° E, 9 September 2019, Jia-Jun Hu, Gui-ping Zhao, and Bo Zhang, HMJAU 60301; Baishan City, Changbai Korean Autonomous County, Wangtian'e Scenic Spot, 41.56° N, 127.95° E, 9 September 2019, Jia-Jun Hu, Gui-ping Zhao, and Bo Zhang, HMJAU 60302.

Note – *Levipedipilus changbaiensis* is highly morphologically similar to *L. fagiphilus* and *L. striatus* based on its reddish brown and tomentose stipe, and short basidia sterigmata. *Levipedipilus changbaiensis* can be distinguished from *L. fagiphilus* by its lighter and depressed pileus, denser and fresh to pink lamellae, and, in terms of microscopic characteristics, smaller basidiospores, non-coralloid cheilocystidia, and lack of caulocystidia. *Levipedipilus changbaiensis* differs from *L. striatus* by its pale colour, striped, depressed pileus, fresh-to-pink lamellae, non-striped stipe, relatively longer cheilocystidia, and coralloid pileipellis.

Levipedipilus erythropus (Pers.) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 48, 58K

= *Gymnopus erythropus* (Pers.) Antonín, Halling & Noordel.

= *Collybia erythropus* (Pers.) P. Kumm.

= *Agaricus erythropus* Pers.

Fungal names: FN571381

Basidiomata small to medium, scattered to gregarious. Pileus convex to applanate, 1.1–3.2 cm diameter, smooth, hygrophanus, reddish brown to brown at centre, light reddish brown to yellowish brown towards margin; margin beige to light yellow, entire, wavy sometimes. Context thin, freshy, light brown, odourless. Stipe centre, cylindrical, 4.1–10.0 cm long and 0.2–0.5 cm wide, deep reddish brown to light reddish brown, paler at apex, smooth, covered with scattered light yellow to brown hairs hairy at base, fistulose, fibrous. Lamellae adnate, fresh-pink, I = 3–5, L = 14–27, crowded.

Basidiospores elliptic, (5.0)6.0–8.2(10.0) × (2.1)3.0–5.0(6.0) µm, Q = (1.20)1.48–2.33(3.00), Qm = 1.87 ± 0.27, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (17)21–33(38) × (4)5–9(10) µm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with obtuse on the top, (15)21–33(39) × (3)4–8(9) µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregularly branched or weakly coralloid hyphae, flatten, (6)8–20(20) µm wide, hyaline to light yellow, smooth, thin-walled. Clamp connections present.

Habitat – Grows on the deciduous layer or rotten branches in coniferous and broad-leaved mixed forests.

Specimens examined – China. Jilin Province: Baishan City, Changbai Korean Autonomous County, Wangtian'e Scenic Spot, 41.56° N, 127.95° E, 8 September 2019, Jia-Jun Hu, Gui-ping Zhao, and Bo Zhang, HMJAU 60309; Baishan City, Changbai Korean Autonomous County, Wangtian'e Scenic Spot, 41.56° N, 127.95° E, 8 September 2019, Jia-Jun Hu, Gui-ping Zhao, and Bo Zhang, HMJAU 60315; Baishan City, Fusong County, Lushuihe Town, 42.53° N, 127.80° E, 8 September 2019, Jia-Jun Hu, Gui-ping Zhao, and Bo Zhang, HMJAU 60313; Yanbian Korean Autonomous Prefecture, Antu County, Edaobaihe Town, 42.39° N, 128.11° E, 4 September 2018, Jia-Jun Hu and Bo Zhang, HMJAU 60310; HMJAU 60311; HMJAU 60312; Liaoning Province: Jinzhou City, Yi County, Mt. Yiwulv, 24 September 2013, Di Wang, HMJAU 28892; Jinzhou City, Yi County, Mt. Yiwulv, 25 September 2013, Di Wang, HMJAU 28839.

Note – This species is widespread in China, however, has never been recorded from Jilin Province, China. This species is characterized by its yellow to reddish brown pileus and reddish-brown stipe that is smooth or covered with scattered tomentose.

During our investigation, we collected many specimens from different places in Jilin Province. However, the shape of the cheilocystidia observed from these was different from those

observed in the Europe specimens. The cheilocystidia of the European specimens were clavate to subclavate, coralloid, or with a mucro that became elongated and filiform at the apex. In contrast, our specimens were clavate with an umbo at the apex.

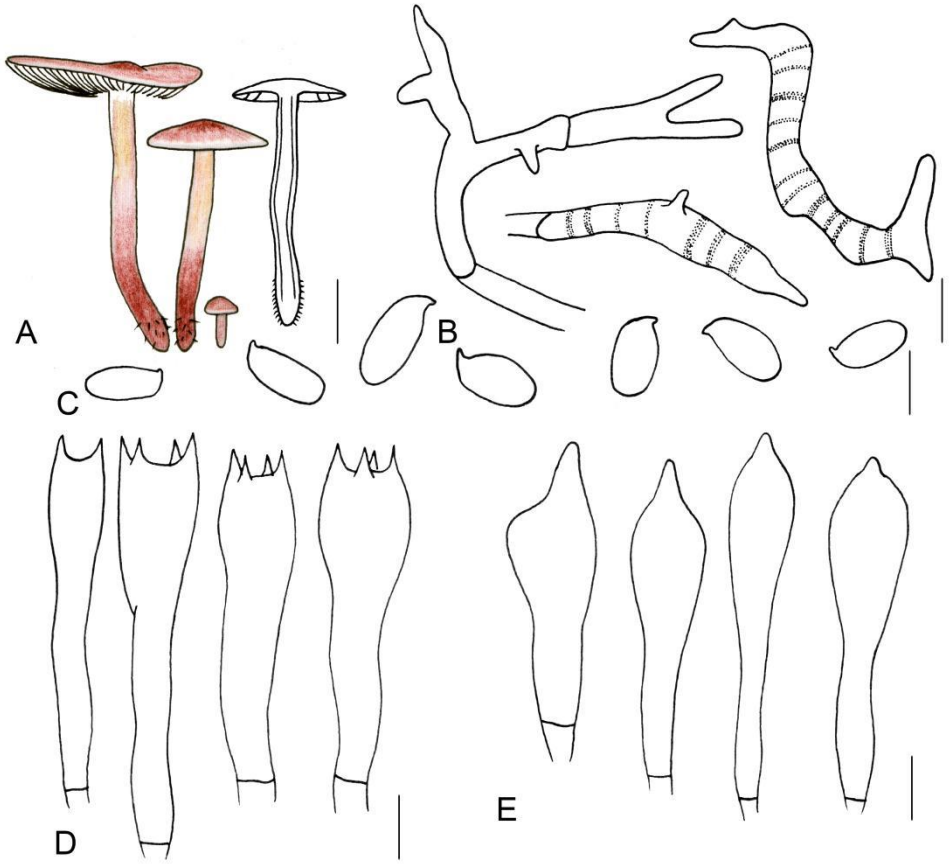

Figure 48 – Morphological characters of *Levipedipilus erythropus* (HMJAU 60313). A Basidomata. B Pileipellis elements. C Basidospores. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B = 25 µm, C–E = 5 µm.

Levipedipilus fagiphilus (Velen.) J.J. Hu, B. Zhang & Y. Li, comb. nov. Fig. 49

= *Gymnopus fagiphilus* (Velen.) Antonín, Halling & Noordel.

= *Collybia fagiphila* Velen.

Fungal names: FN571382

Basidiomata small to medium, gregarious. Pilus hemispherical to convex when young, then applanate, reflexed sometimes, 3.8–4.6 cm in diameter, reddish brown to light reddish brown, smooth, glabrous; margin entire, reflexed, light reddish brown to near white. Context thin, white, odourless. Lamellae adnate, crowded, white to light yellow, unequal. Stipe central, cylindrical to clavate, light reddish brown at apex, deeper coloured downwards, reddish brown at base, 2.0–3.4 cm long and 0.3–0.6 cm wide, pruinose at apex, tomentose at base, fistulose, fibrous.

Basidiospores elliptic, 6.0–8.0(8.4) × (3.0)3.2–4.2(4.9) µm, Q = 1.50–2.27(2.00), Qm = 1.84 ± 0.22, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 22–30 × (4)5–7 µm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with obtuse on the top, 23–32(40) × 5–10(11) µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched or weakly coralloid hyphae, flatten, 10–24(25) µm wide, light yellow, smooth, thin-walled. Clamp connections present.

Habitat – Grows on the deciduous layer or rotten branches in broad-leaved forest.

Specimens examined – China. Jilin Province: Yanbian Korean Autonomous Prefecture, Dunhua City, Dapuchaihe Town, 24 August 2020, Gu Rao, HMJAU 61089 (Collection no.: Hu 700).

Note – This species is characterized by its reddish brown to dark brown pileus and stipe, which is covered with tomentose, as well as non-striped, larger basidiospores, and its light yellow to yellowish brown pileipellis.

There exist some differences between our collections and the European collections. The cheilocystidia of the European collections are branched or coralloid at the apex, while our collections had an umbo at the apex.

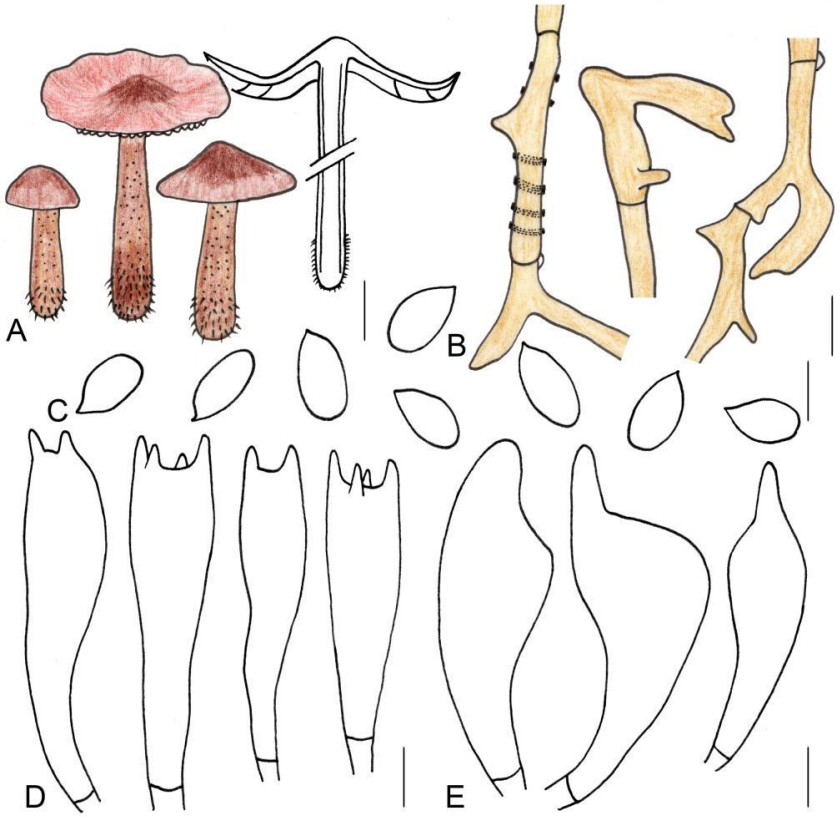

Figure 49 – Morphological characters of *Levipedipilus fagiphilus* (HMJAU 61089). A Basidiomata. B Pileipellis elements. C Basidiospores. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B = 25 μm, C–E = 5 μm.

Levipedipilus globulosus (J.J. Hu, Y.L. Tuo, B. Zhang & Y. Li) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 50, 58S

≡ *Gymnopus globulosus* J.J. Hu, Y.L. Tuo, B. Zhang & Y. Li

Fungal names: FN571383

Basidiomata small to medium, gregarious. Pileus convex to applanate, 4.5–5.5 cm diameter, smooth, deep reddish brown at centre, yellowish brown towards margin; margin white to light yellow, striped, entire, wavy. Context thin, freshy, brown, odourless. Stipe centre, clavate, 4.8–6.0 cm long and 0.6–0.8 cm wide, deep reddish brown, paler at apex, smooth, fistulose, fibrous. Lamellae adnexed to adnate, white to light yellowish green, I = 1–3, L = 9–15, crowded.

Basidiospores elliptic, (6.8)7.0–8.8(9.0) × (3.1)3.3–4.2(4.8) μm, Q = (1.63)1.75–2.20(2.26), Qm = 1.93 ± 0.16, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (23)25–32(33) × 6–9(11) μm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with an umbo on the top, (22)24–38(39) × 5–9(10) μm, thin-walled, smooth, hyaline. Pileipellis layered, flatted spherical to prolate hyphae, 15–33(47) μm wide, brown, smooth, thin-walled; down layer

made up of branched hyphae, flat, pigment light brown to brown incrusting in pileipellis thin- to thick-walled. Clamp connections present.

Habitat – Grows on rotten wood.

Specimens examined – China. Jilin Province: Tonghua City, Ji'an County, Wunvfeng National Forest Park, 41.28° N, 126.14° E, 28 August 2019, Yong-Lan Tuo and Jia-Jun Hu, HMJAU 60307, holotype; Tonghua City, Ji'an County, Wunvfeng National Forest Park, 41.28° N, 126.14° E, 3 September 2021, Yong-Lan Tuo and JiaJun Hu, HMJAU 60308.

Note – In terms of its morphology, *L. globulosus* resembles *L. erythropus* and *L. tiliicola* by having a red to dark red pileus and stipe. However, *L. globulosus* is distinguishable from *L. erythropus* due to its deeper-colored pileus, and light yellowish green lamellae, which is light yellow in *L. erythropus*. Regarding its micro-features, the pileipellis of *L. erythropus* is between a cutis and a trichoderm. In contrast, the pileipellis of *L. globulosus* is layered, with the upper layer inflated to spherical with prolate hyphae, while the lower layer is comprised of branched and inflated hyphae and larger basidiospores. *L. globulosus* differs from *L. tiliicola* by its deeper coloured pileus, light yellowish green lamellae, ability to grow on rotten wood, pileipellis with two layers, the terminal hyphae being inflated to spherical to prolate, and larger basidiospores.

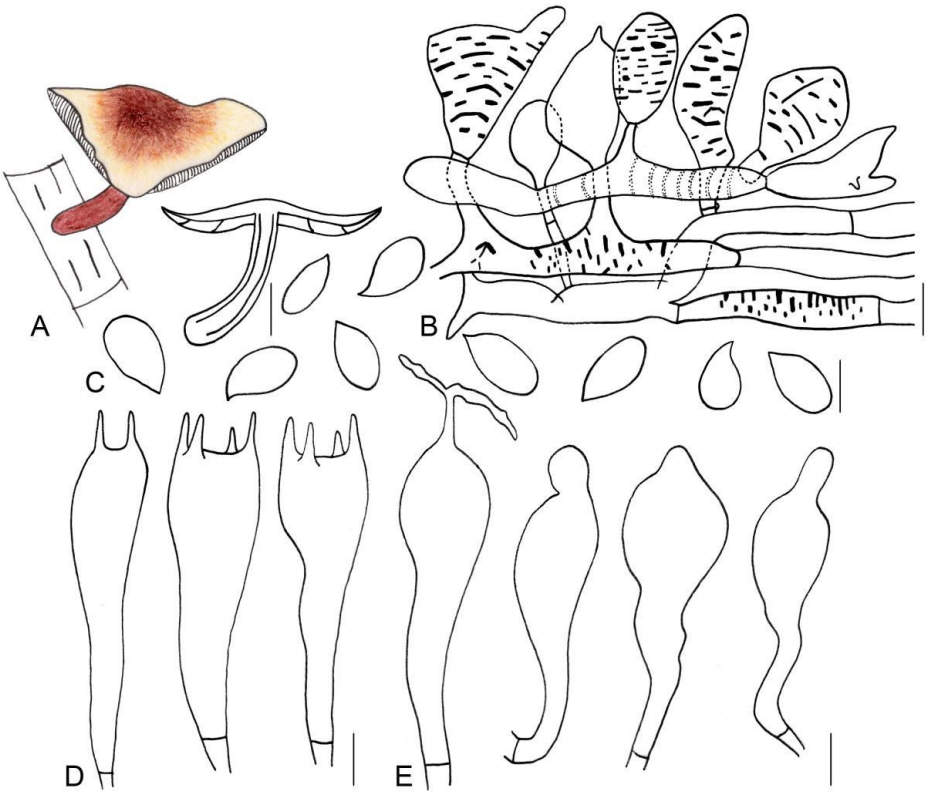

Figure 50 – Morphological characters of *Levipedipilus globulosus* (HMJAU 60307, holotype). A Basidomata. B Pileipellis. C Basidospores. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B = 25 µm, C–E = 5 µm.

Levipedipilus longisterigmaticus (J.J. Hu, B. Zhang & Y. Li) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 51, 58E

≡ *Gymnopus longisterigmaticus* J.J. Hu, B. Zhang & Y. Li

Fungal names: FN571384

Basidiomata small to medium, scattered to gregarious. Pileus convex to applanate, 1.5–3.2 cm diameter, smooth, hygrophanus, brown at the center, light brown to yellow towards the margin, margin light yellow to yellowish white, entire. Context thin, fleshy, light reddish brown, odourless.

Stipe center, cylindrical, 3.2–5.0 cm long and 0.2–0.3 cm wide, reddish brown, smooth, covered with white to light reddish-brown density hairs at base, fistulose, fibrous. Lamellae subfree to adnate, white to light yellow, I = 1–3, L = 15–18, crowded.

Basidiospores elliptic, (6.2) 6.7–9.0 × (3.0) 3.1–4.3 (5.0) μm, Q = (1.40) 1.67–2.25 (2.26), Qm = 1.93 ± 0.20, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (18) 19–27 (28) × (5) 6–10 μm, 4-spored, thin-walled, smooth, hyaline; sterigmata extremely long, up to 40 μm. Cheilocystidia abundant, clavate, with obtuse on the top, or branched, (16) 18–27 × (4) 5–8 (9) μm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregularly branched hyphae, inflated, 10–27 (35) μm wide, hyaline to light yellow, smooth or pigment yellowish brown incrusting in pileipellis, thin-walled. Clamp connections present.

Habitat – Grows on the deciduous layer or rotten branches in coniferous and broadleaved mixed forest.

Specimen examined – China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 4 September 2018, Jia-Jun Hu and Bo Zhang, HMJAU 60288, holotype; Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 13 September 2019, Jia-Jun Hu and Bo Zhang, HMJAU 60289; Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 13 September 2019, Jia-Jun Hu and Bo Zhang, HMJAU 60290.

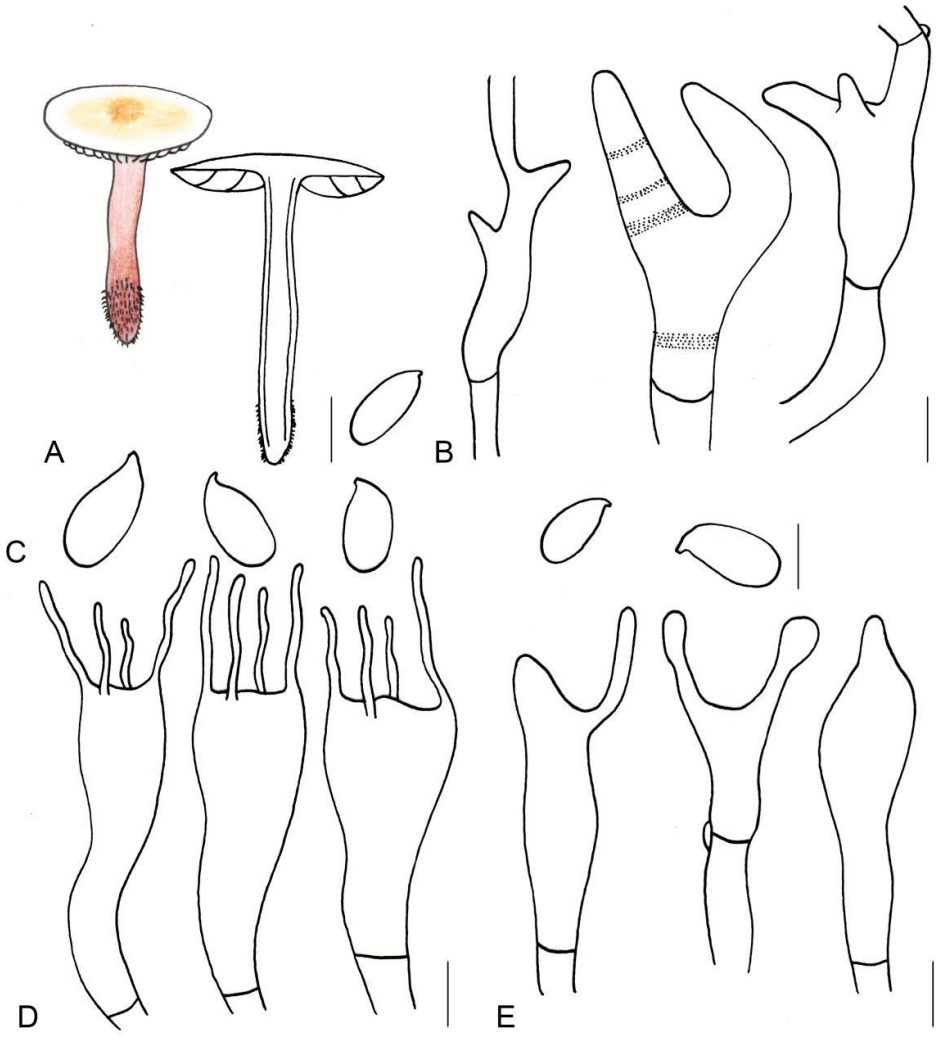

Figure 51 – Morphological characters of *Levipedipilus longisterigmaticus* (HMJAU 60288, holotype). A Basidomata. B Pileipellis elements. C Basidospores. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B = 25 μm, C–E = 5 μm.

Note – Morphologically, *L. longisterigmaticus* is similar to *L. erythropus* and *L. fagiphilus* due to its reddish-brown stipe. However, *L. longisterigmaticus* differs from *L. erythropus* by its light reddish brown and dense hairs on the stipe, extremely long basidiomata sterigmata (up to 40 μm), different cheilocystidia shape, and relatively larger basidiospores ((6.2) 6.7–9.0 × (3.0) 3.1–4.3 (5.0) μm).

Levipedipilus longisterigmaticus and *L. fagiphilus* are both covered with hairs on the stipe, however, the lamellae of *L. longisterigmaticus* are white to light yellow, while those of *L. fagiphilus* is pinkish brown to pinkish yellow. On the other hand, *L. longisterigmaticus* has extremely long sterigmata of the basidia and a lack of chaulocystidia. Moreover, the different shapes and sizes of the cheilocystidia can be used to differentiate *L. longisterigmaticus* from *L. fagiphilus*. The cheilocystidia of *L. fagiphilus* are irregularly clavate, often with a lobed apex or with a short-to-long rostrum, sometimes very slender and lageniform and relatively larger (15–40 (60) × 4.0–8.0 (10) μm) (Antonín et al. 2013), while the cheilocystidia of *G. longisterigmaticus* are clavate, branched, or obtuse.

Levipedipilus longus (J.J. Hu, B. Zhang & Y. Li) J.J. Hu, B. Zhang & Y. Li, comb. nov.

Figs 52, 58F

≡ *Gymnopus longus* J.J. Hu, B. Zhang & Y. Li

Fungal names: FN571385

Basidiomata small to medium, scattered to gregarious. Pileus 1.7–3.7 cm diameter, convex to applanate or revolute, smooth, hygrophanous, reddish brown at center, towards margin light reddish brown to brown; margin white to light yellow or light brown, entire. Context thin, freshy, light reddish brown, odourless. Stipe 3.7–4.3 cm long and 0.3–0.6 cm wide, cylindrical to clavate, reddish brown, with brown farinose on upper part, and white to light reddish brown tomentose at base, hollow, filiform. Lamellae adnate, white to light yellow, I = 5–7, L = 19–24, crowded.

Basidiospores (5.6)6.0–8.0 × (3.0)3.1–4.1(4.9) μm, Q = (1.27)1.47–2.19(2.58), Qm = 1.8 ± 0.24, oblong, smooth, hyaline, thin-walled, inamyloid. Basisia (19)20–28(29) μm, 2 or 4 spored, hyaline, thin-walled, clavate. Sterigmata extremely long, up to 33 μm long. Cheilocystidia (21)22–29(30) μm, mass, clavate, at apex with a mucro, hyaline, thin-walled, smooth. Pileipellis a translation between a cutis and a trichoderm, made up of irregularly interwoven, repent or ascending, inflated hyphae with inflated and irregularly branched terminal elements, encrusting in pileipellis. Clamp connections present.

Habitat – Grows on deciduous layer or rotten branch in coniferous and broad-leaved mixed forests.

Specimens examined – China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 4 September 2018, Jia-Jun Hu, Bo Zhang, and GuiPing Zhao, HMJAU 60291, holotype; Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 4 September 2018, Jia-Jun Hu, Bo Zhang, and Gui-Ping Zhao, HMJAU 60292; Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 31 August 2020, Jia-Jun Hu, Bo Zhang, and GuiPing Zhao, HMJAU 60293.

Note – *Levipedipilus longus* is morphologically similar to *L. erythropus*, *L. fagiphilus*, and *L. longisterigmaticus*, because of they shared red pileus and stipe. However, *L. longus* differs from *L. erythropus* by being covered with brown farinose on the upper part, being white to light reddish brown tomentose at the base, relatively thin basidiospores, smaller Qm, and extremely long sterigmata (up to 33 μm long).

Levipedipilus Longisterigmaticus differs from *L. longus* by its deeper coloured pileus, being covered with brown farinose on the stipe, smaller basidiospores, clavate with obtuse cheilocystidia, and pileipellis falling between a cutis and trichoderm types. *Levipedipilus longus* differs from *L. fagiphilus* by its farinose stipe, deeply coloured pileus and stipe, white lamellae, smaller basidiospores, lack of caulocystidia, and non-coralloid pileipellis.

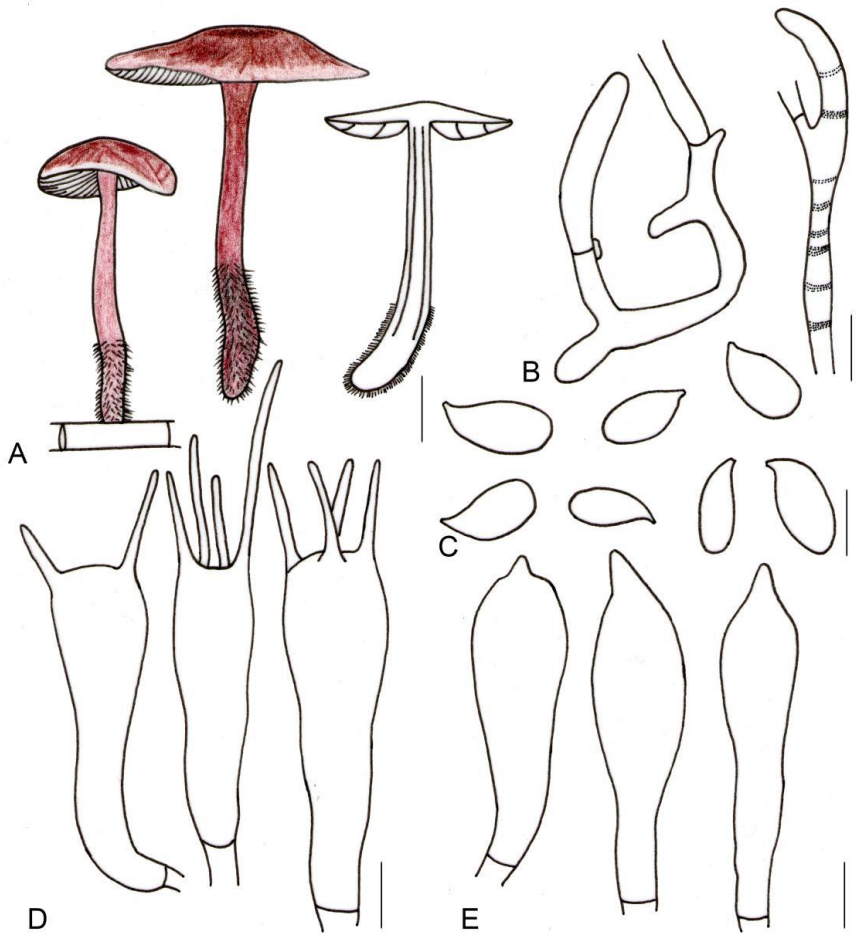

Figure 52 – Morphological characters of *Levipedipilus longus* (HMJAU 60291, holotype). A Basidomata. B Pileipellis elements. C Basidospores. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B = 25 μm, C–E = 5 μm.

Levipedipilus macrosporus (J.J. Hu, B. Zhang & Y. Li) J.J. Hu, B. Zhang & Y. Li, comb. nov.
Figs 53, 58P

≡ *Gymnopus macrosporus* J.J. Hu, B. Zhang & Y. Li

Fungal names: FN571386

Basidiomata small to medium, gregarious. Pileus convex to applanate, 1.2–4.6 cm diameter, smooth, hygrophanus, deep reddish brown at the center, reddish brown to yellowish brown towards margin; margin beige to light yellow, striped, entire, wavy. Context thin, fleshy, light reddish brown to light yellowish brown, odourless. Stipe centre, cylindrical, 7.8–9.5 cm long and 0.2–0.5 cm wide, deep reddish brown to reddish brown, smooth, fistulose, fibrous, and light yellow to light reddish brown tomentose at the base. Lamellae adnexed to adnate or near free, light yellow, I = 1–3, L = 13–17, crowded.

Basidiospores elliptic, (6.0) 6.8–7.9 (8.3) × (3.0) 3.1–4.2 (4.3) μm, Q = (1.63) 1.67–2.32 (2.37), Qm = 1.88 ± 0.18, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 20–29 × 6–9 μm, two- or four-spored, thin-walled, smooth, hyaline; sterigmata extremely long, up to 32 μm. Cheilocystidia abundant, clavate, with obtuse on the top, 20–28 (30) × 5 (6)–9 μm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched or weakly coralloid hyphae, inflated, 10–27 (35) μm wide, hyaline to light yellow, smooth, thin-walled. Clamp connections present.

Habitat – Grows on the deciduous layer or rotten branches in coniferous and broadleaved mixed forest.

Specimens examined – China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 4 September 2018, Jia-Jun Hu and Bo Zhang, HMJAU 60294, holotype; Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 4 September 2018, Jia-Jun Hu and Bo Zhang, HMJAU 60295; Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 13 September 2019, Jia-Jun Hu and Bo Zhang, HMJAU 60296.

Note – *Levipedipilus macrosporus* is morphologically similar to *L. longisterigmaticus* and *L. longus* due to its reddish brown, tomentose stipe, and long sterigmata of the basidia. *Levipedipilus macrosporus* differs from *L. longus* due to its pileus being a darker colour (deep reddish brown at the center, reddish brown to yellowish brown towards margin); margin being to beige to light yellow, striped characteristics, smooth texture on the upper part of the stipe, coralloid and non-encrusting pileipellis. These two *Levipedipilus* species share a similar basidiospore size; however, the Qm of *L. macrosporus* is larger than that of *L. longus*. *Levipedipilus longisterigmaticus* differs due to its smooth, pale colour, and unstriped pileus; relatively wider pileipellis, yellowish brown pigment encrusting in pileipellis, and larger basidiospores ((6.2) 6.7–9.0 × (3.0) 3.1–4.3 (5.0) µm).

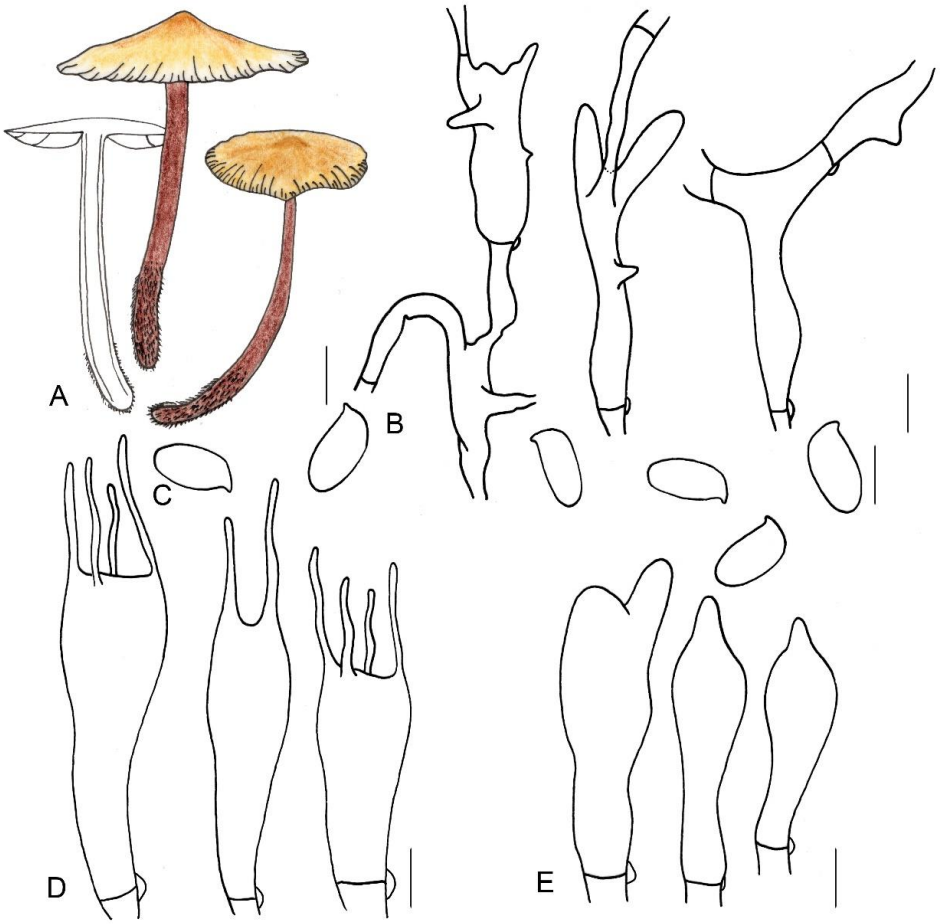

Figure 53 – Morphological characters of *Levipedipilus macrosporus* (HMJAU 60294, holotype). A Basidomata. B Pileipellis elements. C Basidospores. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B = 25 µm, C–E = 5 µm.

Levipedipilus subsulphureus (Peck) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 54, 58L, M

= *Gymnopus subsulphureus* (Peck) Murrill

= *Collybia subsulphurea* Peck

Fungal names: FN571387

Basidiomata small to large, gregarious. Pileus hemispherical to planate-hemispherical, mastoid when young, then becoming applanate, depressed when mature, 1.5–2.7 cm wide, light yellowish brown to sulphur, smooth at first, striped when mature. Context thin, light yellow, odourless. Stipe central, cylindrical, 4.5–5.7 cm long and 0.2–0.3 cm wide, smooth when young, smooth in upper part and covered with tomentose when mature, sulphur when young, becoming reddish yellow to reddish brown, fistulose, fibrous. Lamellae close, adnexed, unequal.

Basidiospores elliptic, 4.8–5.4(5.8) × (2.0)2.7–3.2 μm, Q = 1.5–2.5, Qm = 1.70 ± 0.15, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (15)17–25(29) × (4)5–6 μm, hyaline, thin-walled. Cheiocystidia clavate with an umbo at apex, (15)17–25(29) × (4)5–6 μm, hyaline, thin-walled. Pleurocystidia and caulocystidia absent. Pileipellis a cuits, coralloid or branched, flatten, hyaline to light yellow, 7–12(15) μm, thin-walled. Clamp connections present.

Habitat – Saprophytic on the deciduous layer in broad-leaved forest.

Specimens examined – China. Yunnan Province: Honghe Hani and Yi Autonomous Prefecture, Pingbian County, Daweishan National Nature Reserve, 9 June 2020, Chang-Ling Zhao, HMJAU 61090 (Collection no.: 681); Zhejiang Province: Wenzhou City, Taishun County Wuyanling National Nature Reserve, 9 April 2021, Jin-Bao Pu, HMJAU 61091 (Collection no.: 704).

Note – This species was never officially reported from China, only informally recorded on some websites from Taiwan, China; thus, this is the first time this species has been recorded from China. *Collybia subsulphurea* Peck was combined into *Gymnopus* by Murrill (1916). Subsequently, reports on this species were seldom provided worldwide, leading to the scarcity of knowledge of this species. In the current study, two specimens collected from Zhejiang and Yunnan Province, China were confirmed to be *L. subsulphureus* by combined morphological and molecular study. Thus, we have provided a detailed description of this species.

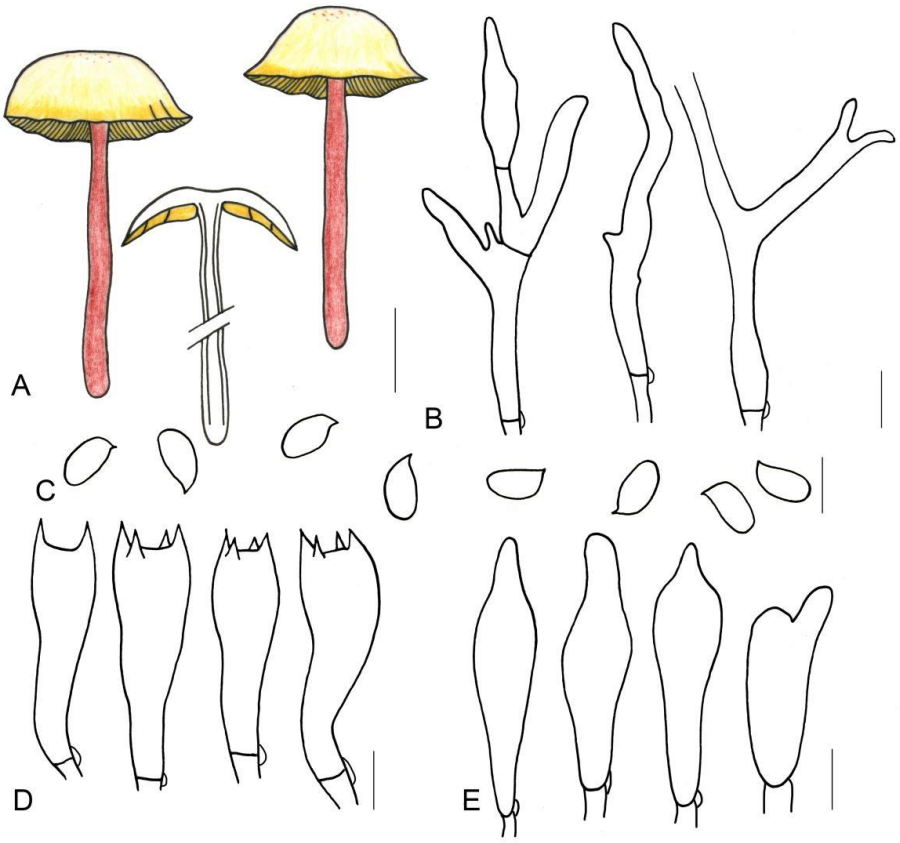

Figure 54 – Morphological characters of *Levipedipilus subsulphureus* (HMJAU 61090). A Basidomata. B Pileipellis elements. C Basidospores. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B = 25 μm, C–E = 5 μm.

Levipedipilus striatus (J.J. Hu, B. Zhang & Y. Li) J.J. Hu, B. Zhang & Y. Li, comb. nov.

Figs 55, 58R

≡ *Gymnopus striatus* J.J. Hu, B. Zhang & Y. Li

Fungal names: FN571388

Basidiomata small to medium, gregarious. Pileus convex to applanate, 2.3–4.1 cm diameter, smooth, hygrophanus, dark brown at centre, brown to light brown towards margin; margin white to light yellow, striped, entire, wavy. Context thin, freshy, light yellowish brown, odourless. Stipe centre, cylindrical to clavate, 5.5–7.0 cm long and 0.3–0.8 cm wide, deep reddish brown to reddish brown, smooth in upper part, longitudinal striped, covered with yellow to light brown hairs up to 1/3 (from base upwards), fistulose, fibrous. Lamellae adnate, yellow to light brown, I = 3–9, L = 17–23, crowded.

Basidiospores elliptic, 6.0–8.0(9.0) × 3.0–4.0 µm, Q = (1.50)1.58–2.50(2.60), Qm = 2.01 ± 0.25, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 20(21)–34(37) × 5–10 µm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with an umbo on the top, (17)20–30 × 4–8(10) µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched or weakly coralloid hyphae, flat, 10–30(35) µm wide, hyaline to light yellow, smooth, thin-walled. Clamp connections present.

Habitat – Grows on the deciduous layer or rotten branches in coniferous and broad-leaved mixed forests.

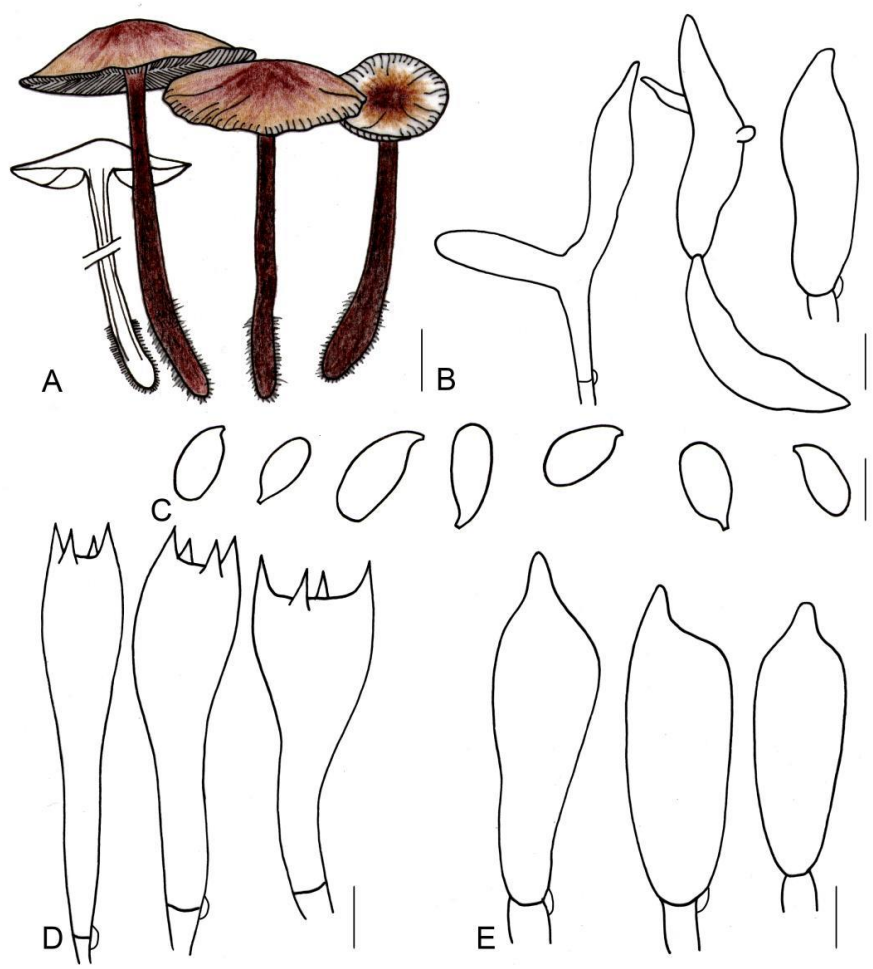

Figure 55 – Morphological characters of *Levipedipilus striatus* (HMJAU 60297, holotype). A Basidomata. B Pileipellis elements. C Basidospores. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B = 25 µm, C–E = 5 µm.

Specimens examined – China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 9 September 2019, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 60297, holotype; Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 18 September 2020, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 60298; Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 18 September 2020, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 60299.

Note – *Levipedipilus striatus* is easily confused with *L. longisterigmaticus*, *L. longus*, and *L. macrosporus* due to their highly similar morphology. However, *L. striatus* differs from the other three species by its deeper coloured lamellae, longitudinal stripes on the stipe, stripes on the margin of the pileus, larger Qm, and shorter basidia sterigmata. *Levipedipilus striatus* can easily be differentiated from *L. fagiphilus* by its deeper coloured pileus, uniformly coloured and longitudinally striped stipe, lack of caulocystidia, non-coralloid cheilocystidia, not encrusting in the pileipellis, and smaller basidiospores (Antonín et al. 2013).

Levipedipilus tiliicola (J.J. Hu, B. Zhang & Y. Li) J.J. Hu, B. Zhang & Y. Li, comb. nov.

Figs 56, 58J

≡ *Gymnopus tiliicola* J.J. Hu, B. Zhang & Y. Li

Fungal names: FN571389

Basidiomata medium to large, gregarious. Pileus convex, 3.0–6.7 cm diameter, smooth, deep rose red at centre, yellowish pink towards margin; margin white to light yellow, striped, entire, wavy. Context thin, freshy, white to pink, odourless. Stipe centre, cylindrical, 2.2–4.5 cm long and 0.3–0.7 cm wide, deep reddish brown, smooth, fistulose, fibrous. Lamellae adnexed to adnate, yellow, I = 1–3, L = 19–24, crowded.

Basidiospores elliptic, (6.0)6.9–8.0(8.2) × (3.0)3.1–4.0(4.2) µm, Q = (1.70)1.75–2.26(2.33), Qm = 1.93 ± 0.17, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 20–30 × 6–8 µm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with obtuse on the top, (20)21–27(28) × 5–7 µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched to weakly coralloid hyphae, flatten, (5)6–15(17) µm wide, light brown, smooth, thin-walled. Clamp connections present.

Habitat – Grows at the base of *Tilia* sp.

Specimens examined – China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 13 September 2019, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 60304, holotype; Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 31 August 2020, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 60305; Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 42.39° N, 128.11° E, 27 August 2021, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 60306.

Note – Morphologically, its rose-red to dark red pileus and stipe render *L. tiliicola* similar to *L. erythropus*. *Levipedipilus tiliicola* differs from *L. erythropus* by its lighter coloured and striped pileus and light pink to fresh and denser lamellae. Moreover, *L. tiliicola* grows at the base of *Tilia* sp., while *L. erythropus* grows on the deciduous layer or rotten branches. Concerning microfeatures, *L. tiliicola* differs from *L. erythropus* by its weakly coralloid pileipellis, non-coralloid cheilocystidia, larger basidiospores, and 2- or 4-spored basidia.

Levipedipilus tomentosus (J.J. Hu, B. Zhang & Y. Li) J.J. Hu, B. Zhang & Y. Li, comb. nov.

Figs 57, 58D

≡ *Gymnopus tomentosus* J.J. Hu, Y.L. Tuo, B. Zhang & Y. Li

Fungal names: FN571390

Basidiomata medium to large, scattered. Pileus convex, 1.6–3.0 cm diameter, smooth, tan at centre, light brown towards margin; margin white, tomentum, entire. Context thin, freshy, white to light yellow, odourless. Stipe centre, cylindrical, 3.3–4.3 cm long and 0.2–0.5 cm wide, blackish

green at apex, reddish brown below, covered with reddish brown hairs up to 1/4 (from base upwards), fistulose, fibrous. Lamellae adnexed, yellowish green, I = 3–7, L = 19–25, crowded.

Basidiospores elliptic, (6.0)6.2–8.2(9.0) × 3.0–4.1(4.2) µm, Q = (1.50)1.59–2.33(2.40), Qm = 1.92 ± 0.23, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 20–30(31) × 5–8 µm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with obtuse on the top, (20)22–30(32) × 5–7 µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched to weakly coralloid or bulbous hyphae, flatten, 10–18(21) µm wide, light brown, smooth, thin-walled. Clamp connections present.

Habitat – Grows on the deciduous layer in broad-leaved forest.

Specimens examined – China: Jilin Province, Jiaohe City, Lafa Mountain National Forest Park Red Leaf Valley Scenic Spot, 43.71° N, 127.08° E, 7 September 2019, Jia-Jun Hu, Gui-ping Zhao, and Bo Zhang, HMJAU 60303, holotype.

Note – Its reddish brown and tomentose stipe renders *L. tomentosus* morphologically similar to *L. fagiphilus*, *L. longisterigmaticus*, *L. longus*, *L. macrosporus*, *L. striatus*, and *L. changbaiensis*. However, *L. tomentosus* differentiates from *L. longisterigmaticus*, *L. longus*, *L. macrosporus*, *L. striatus*, and *L. changbaiensis* by its white-to-pale-yellow pileus with a tomentose margin and inflated bulbous terminal hyphae of the pileipellis. *Levipedipilus tomentosus* can be distinguished from *L. fagiphilus* by its near-white pileus with a tomentose margin, coralloid-to-bulbous pileipellis, smaller basidiospores, and lack of caulocystidia.

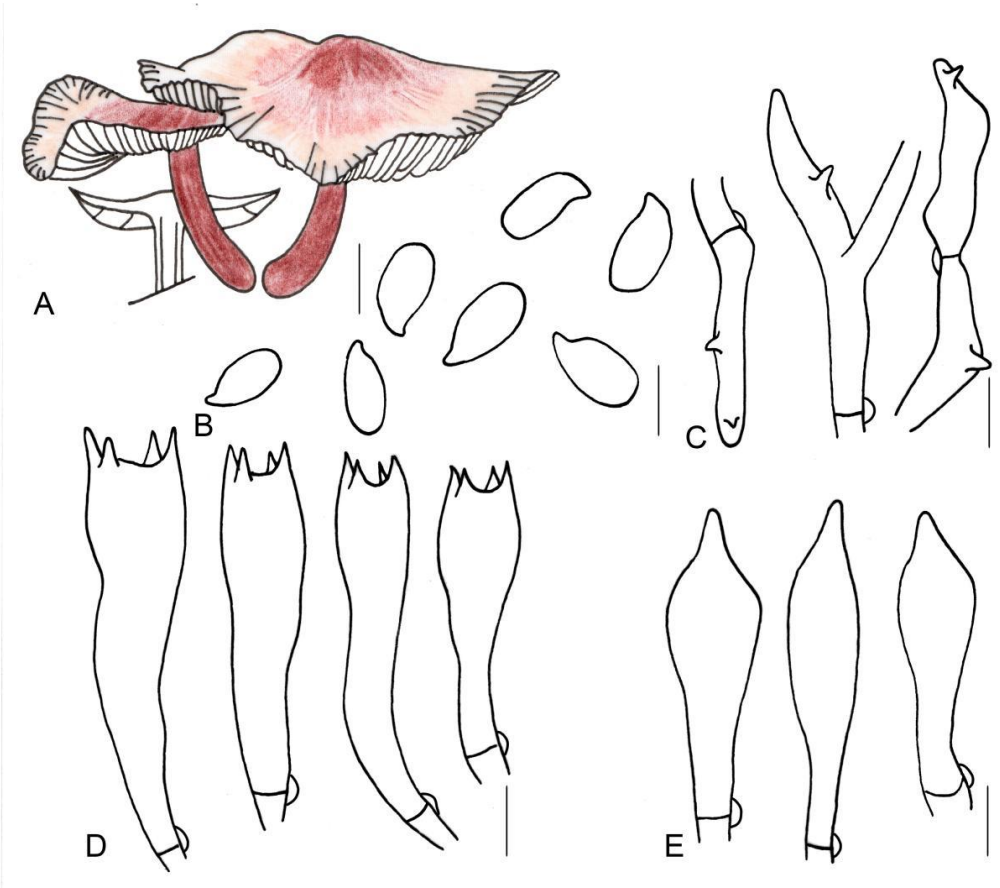

Figure 56 – Morphological characters of *Gymnopus tiliicola* (HMJAU 60305, holotype). A Basidomata. B Basidospores. C Pileipellis elements. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B, D, E = 5 µm, C = 25 µm.

Neomarasmius J.J. Hu, B. Zhang & Y. Li, gen. nov.

Etymology – Referes to the species of this genus are marasmioid.

Fungal names: FN571342

Basidiomata marasmioid, omphalinoid or collybioid sometimes, small, occasionally medium, solitary to scattered. Pileus hemispherical, campanaceous to convex at first, applanate to reflex or slightly depressed at disc, sometimes with an inconspicuous umbo, smooth, glabrous, or tomemtose, grooved, hygrophanus, translucent striped present when moist; margin entire or serrated. Lamellae adnate to adnexed, or narrowly adnate, occasionally free or adnate with a decurrent tooth, white to light yellow, light brown sometimes, distant. Stipe cylindrical or tapered downwards, becoming darker towards the base, velutinous, pubescent to tomentose, furfuraceous or pruinose.

Basidiospores elliptical, cylindrical, fusiform, or pip-shaped, hyaline, thin-walled, inamyloid. Basidia clavate to cylindrical, 4-spored, thin-walled, hyaline. Cheilocystidia abundant, variety in shape, clavate, pyriform, or irregular clavate, branched, lobed, finger-like, or coralloid at apex, thin-walled. Pleurocystidia rare. Lamellae trama non-dextrinoid. Caulocystidia abundant, cylindrical, fusiform, or clavate, thick-walled. Pileipellis a cuits, radically, cylindrical, rare branch, encrusted, thin- to thick-walled.

Grows on rotten branches, or fallen leaves.

Type species: *Neomarasmius fuscotramus* (Mešić, Tkalčec & Chun Y. Deng) J.J. Hu, B. Zhang & Y. Li

Key to the species of *Neomarasmius* present in this study

1 Basidiomata large, yellow lamellae, grows on ground.....*Neomarasmius peronatus*
1 Basidomata small, brown lamellae, grows on fallen branches.....*Neomarasmius fuscotramus*

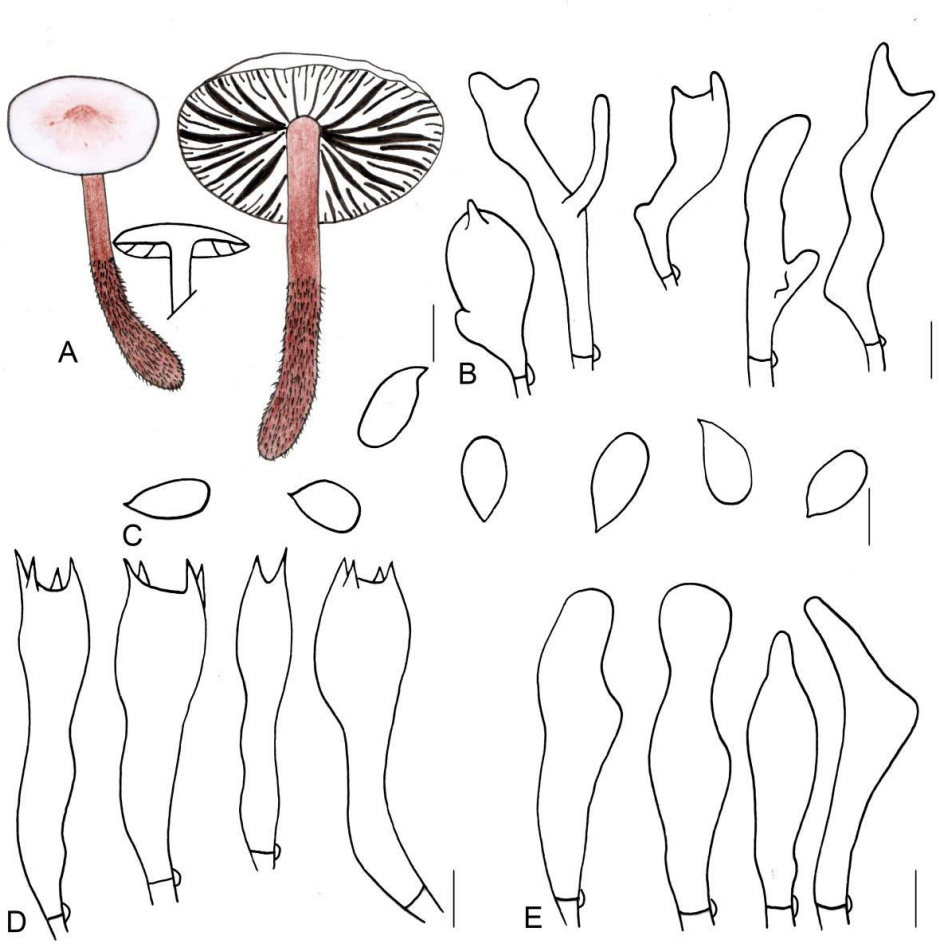

Figure 57 – Morphological characters of *Levipedipilus tomentosus* (HMJAU 60303, holotype). A Basidomata. B Pileipellis elements. C Basidospores. D Basidia. E Cheilocystidia. Scale bars: A = 1 cm, B = 25 µm, C–E = 5 µm.

Figure 58 – A *Levipedipilus cinnamomeus*. B *Levipedipilus longistipes*. C *Levipedipilus changbaiensis*. D *Levipedipilus tomentosus*. E *Levipedipilus longisterigmaticus*. F *Levipedipilus longus*. G *Levipedipilus maculatus*. H *Levipedipilus luteofuscus*. I *Levipedipilus inexpectatus*. J *Levipedipilus tiliicola*. K *Levipedipilus erythropus*. L–M *Levipedipilus subsulphureus*. N *Levipedipilus striatipileatus*. O *Levipedipilus hemisphaericus*. P *Levipedipilus macrosporus*. Q *Levipedipilus minor*. R *Levipedipilus striatus*. S *Levipedipilus globulosus*. T *Levipedipilus brunneodiscus*. U *Levipedipilus subfasciatus*. V *Levipedipilus citrinoides*. W *Levipedipilus dryophilioides*. X *Levipedipilus dryophilus*. Y *Levipedipilus aquosus*. Z *Levipedipilus strigosipes*. Scale bars: A, B, J, N, O–S, V, X, Y = 2 cm, C–M, T, U, W, Z = 1 cm.

Neomarasmius peronatus (Bolton) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 59, 61I

= *Gymnopus peronatus* (Bolton) Gray
= *Collybia peronata* (Bolton) P. Kumm.
= *Marasmius peronatus* (Bolton) Fr.
= *Marasmiellus peronatus* (Bolton) J.S. Oliveira
= *Collybiopsis peronata* (Bolton) R.H. Petersen
= *Agaricus peronatus* Bolton
Fungal names: FN571391

Basidiomata medium, gregarious. Pilus convex to reflexed to shallow infundibuliform, 3.7–4.6 cm wide, light reddish brown to brown, covered with white tomentose at disc, smooth outwards; margin entire, lobed occasionally, wavy, involute, light reddish brown. Context thin, odourless. Lamellae adnate to adnexed, yellow to yellowish brown, close, unequal. Stipe central,

5.2–7.4 cm long and 0.5–0.7 cm wide, yellow to yellowish brown, paler at apex and base, yellow, slightly enlarged at base, tomentose, denser at base.

Basidiospores elliptic, (6.8)6.9–11.0 × 3.0–4.0 µm, Q = (2.25)2.27–2.81(3.06), Qm = 2.55 ± 0.22, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (21)22–31 × 4–7 µm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, with obtuse on the top, (20)22–37(39) × 3–6 µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched to coralloid hyphae, 5–8(12) µm wide, hyaline, smooth, thin-walled, encrusted. Clamp connections present.

Habitat – Grows on the deciduous layer in broad-leaved forests.

Specimens examined – Jilin Province: Jilin City, Zhuque mountain, 18 August 2021, Jia-Jun Hu, Bo Zhang, and Gui-Ping Zhao, HMJAU 61092 (Collection no.: Hu 850); Yunnan Province: Pu'er City, Lancang County, 15 July 2017, Jia-Jun Hu and Ji-Ze Xu, HMJAU 61093 (Collection no.: Hu 998).

Note – This species is characterized by its medium to large basidiomata, being marasmioid, distant lamellae with a yellow to yellowish brown colour, yellow stipe covered with tomentose, and larger basidiospores.

There exist some differences between our collections and those from Europe. The cheilocystidia of our collections were clavate with an umbo at the apex, while the caulocystidia were clavate to irregular clavate. In contrast, the cheilocystidia of the European collections were clavate, finger-like, or coralloid at the apex, while the caulocystidia were cylindrical, sometimes strangulate, obtuse, and sometimes rostrate.

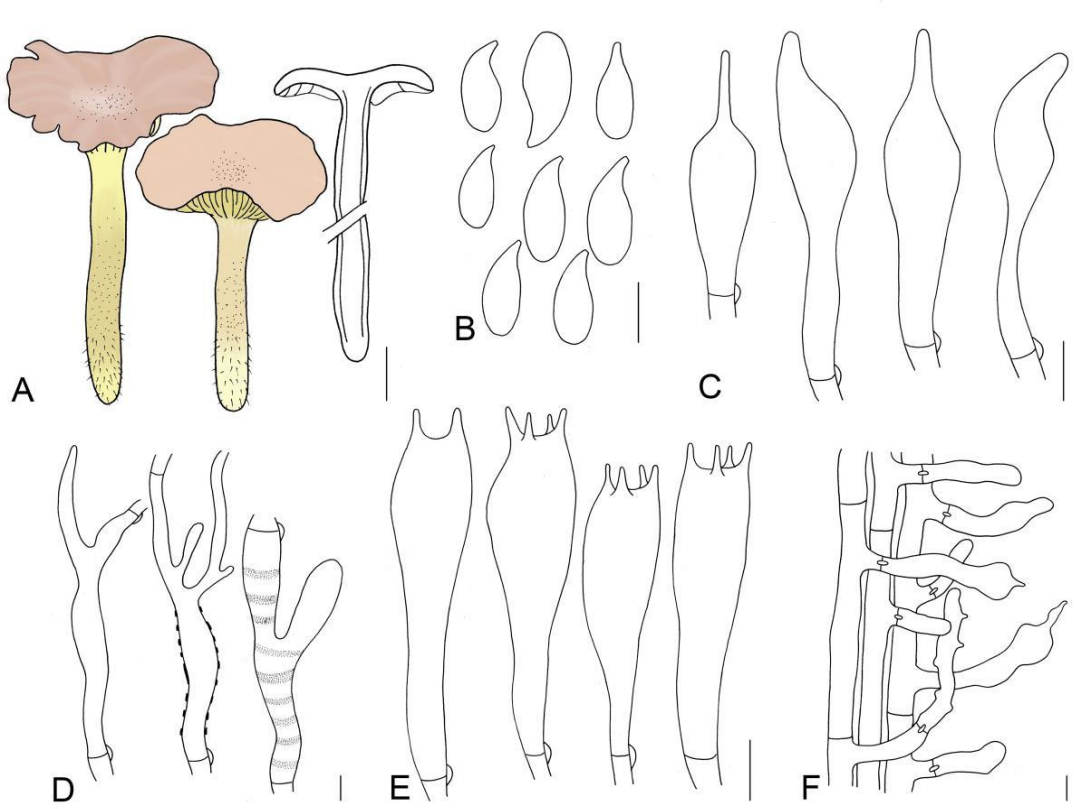

Figure 59 – Morphological characters of *Neomarasmius peronatus* (HMJAU 61093). A Basidomata. B Basidospores. C Cheilocystidia. D Pileipellis elements. E Basidia. F Caulocystidia. Scale bars: A = 1 cm, B, C, E = 5 µm, D, F = 10 µm.

Neomarasmius fuscotramus (Mešić, Tkalčec & Chun Y. Deng) J.J. Hu, B. Zhang & Y. Li, comb. nov. Fig. 60

≡ *Gymnopus fuscotramus* Mešić, Tkalčec & Chun Y. Deng

Fungal names: FN571392

The description of macro-character is referring to the original description (Mešić et al. 2011).

Basidiomata small, gregarious. Pilus campanulate, 1.2–2.1 cm, black-brown to black, sulcate almost to the center, glabrous; margin entire, reflex, brown. Context thin, grayish brown, odourless. Lamellae distant, free, brown, unequal. Stipe central, 1.5–3.0 cm long and about 0.1 cm long, cylindrical, black-brown to brown, entirely pale brown floccose-squamulose.

Basidiospores elliptic, (6.0)7.0–9.9(11.0) × (3.0)3.1–4.0(4.6) µm, Q = (1.75)1.94–2.75(2.94), Qm = 2.24 ± 0.28, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (21)22–30(31) × 4–6(7) µm, 2- or 4-spored, thin-walled, smooth, hyaline. Cheilocystidia abundant, clavate, coralloid or finger-like at apex, 21–25(29) × 4–6 µm, thin-walled, smooth, hyaline. Pileipellis a cutis, made up of irregular branched to coralloid hyphae, 3–5 µm wide, hyaline, smooth, thin-walled, encrusted. Clamp connections present.

Habitat – Grows on the fallen branches in broad-leaved forests.

Specimens examined – China. Guangxi Zhuang Autonomous Region: Guilin City, Xing'an County, Mao'ershan Nature Reserve, 29 May 2009, Chun-Ying Deng, GDGM 26313, Holotype (!).

Note – This species is characterized by its small basidiomata, campanulate pileus with brown to black-brown colour, distant lamellae, being concolour with the pileus or paler, dark brown to black stipe that is covered with pale brown floccose-squamulose, clavate cheilocystidia with a finger-like or coralloid apex, and larger basidiospores.

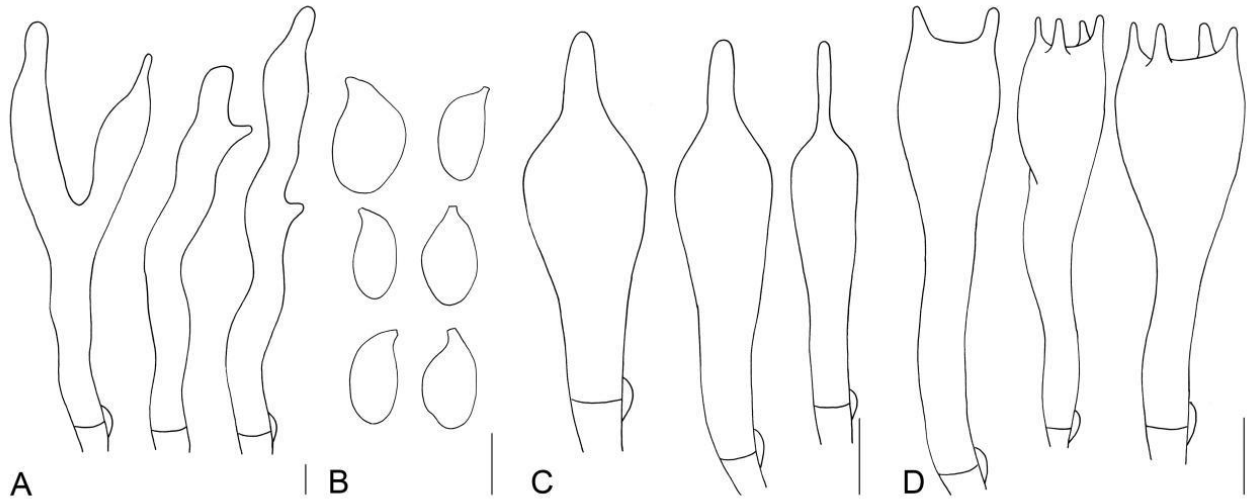

Figure 60 – Morphological characters of *Neomarasmius fuscotramus* (GDGM 26313, holotype). A Pileipellis elements. B Basidiospores. C Caulocystidia. D Basidia. E Cheilocystidia. Scale bars: A, C = 10 µm, B, D, E = 5 µm.

Ligymnopus J.J. Hu, B. Zhang & Y. Li, gen. nov.

Etymology – named after Prof. Yu Li, in honour of his outstanding contribution to the study of Chinese edible mushrooms, on the occasion of his 80th birthday.

Fungal names: FN571343

Basidiomata collybioid, rare marasmioid, small to medium, solitary to scattered. Pileus hemispherical to convex, applanate when mature, slightly depressed or with an umbo, smooth, glabrous, or with slightly tomentose, striped, margin inrolled, straight or reflex sometimes, entire, lobed sometimes. Lamellae adnate to adnexed, white to yellow, medium to close. Stipe cylindrical, flatten at apex or base, tomentose or pruinose, smooth sometimes, hollow.

Basidiospores oblong-elliptical, cylindrical, subfusiform, or elliptical. Basidia clavate, 4-spored, hyaline, thin-walled. Cheilocystidia abundant, variety in shape, cylindrical, clavate, or subfusiform. Pleurocystidia absent. Caulocystidia present or not, subfusiform, clavate, or

cylindrical, smooth, hyaline, thin-walled. Pileipellis a cuits to thrichoderm, branched, slightly flatten, smooth or encrusted.

Grows on rotten word, fallen branches, or ground.

Type species: *Ligymnopus luxurians* (Peck) J.J. Hu, B. Zhang & Y. Li

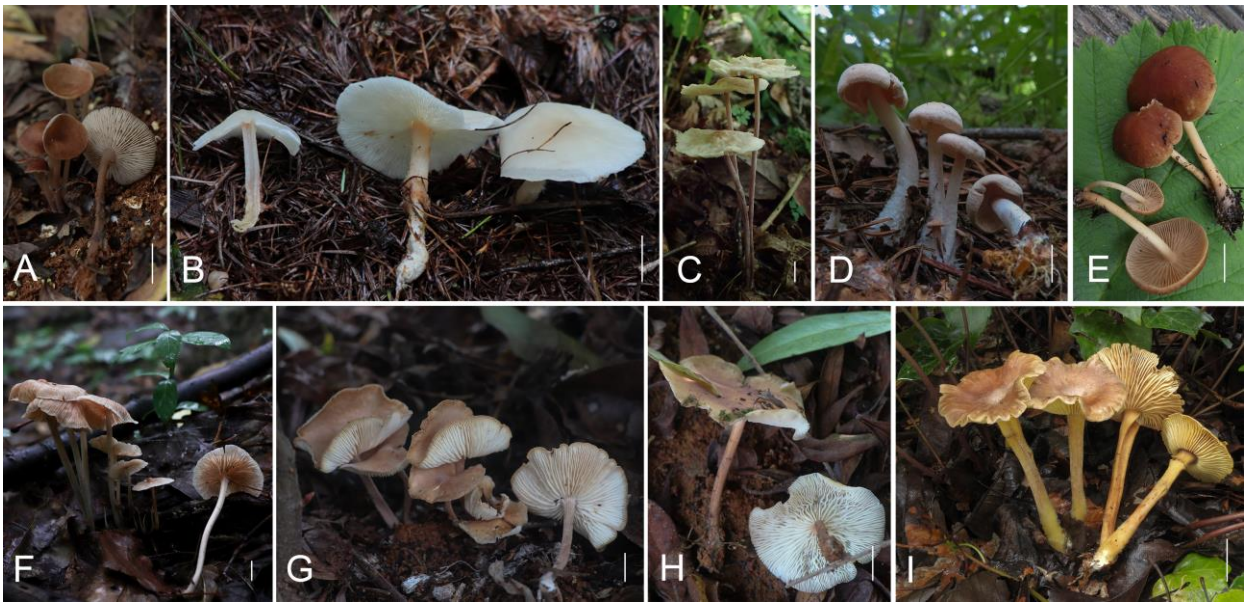

Figure 61 – A *Vestipedipilus biformis*. B *Vestipedipilus hariolorum*. C *Vestipedipilus confluens*. D *Vestipedipilus eneficola*. E *Vestipedipilus sinoluxurians*. F *Ligymnopus polygrammus*. G *Ligymnopus luxurians*. H *Ligymnopus subluxurians*. I *Neomarasmius peronatus*. Scale bars: 1 cm.

Key to the species of *Ligymnopus* present in this study

1 Surface of pileus with long striate, or rugulose-striate.....*Ligymnopu polygrammus*
1 Surface of pileus with striate, or inconspicuous.....2
2 Colour of pileus heterogeneous.....*Ligymnopu subluxurians*
2 Colour of pileus uniform.....3
3 Basidiomata larger, pileus brown.....*Ligymnopu luxurians*
3 Basidiomata smaller, pileus reddish brown.....*Ligymnopu sinoluxurians*

Ligymnopus sinoluxurians J.J. Hu, B. Zhang & Y. Li, sp. nov. Figs 62, 63E

Fungal names: FN571393

Etymology – sino = China, *sinoluxurians* refers to this species closely related to *Li. luxurians*.

Diagnosis – This species could be distinguished from other species by small basidiomata, hemispherical and reddish brown, distant lamellae, concolour with stipe, tomentose or furfuraceous stipe, branched or coralloid pileipellis, clavate cheilocystidia with an umbo at apex, bigger basidiospores, and caulocystidia absent.

Type – China. Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 4 July 2018, Jia-Jun Hu, Ao Ma, and Xiao-Qi Xu, HMJAU 61094 (Collection no.: Hu 11).

Basidiomata small, gregarious. Pileus hemispherical to convex, or reflex, 1.1–1.9 cm in diameter, smooth, glabrous, light reddish brown to reddish brown, hygrophanus; margin entire or slightly lobed, light brown to light reddish brown. Context thin, fresh, light yellow, odourless. Stipe central, cylindrical, 1.8–5.2 cm long and 0.2–0.3 cm wide, furfuraceous, tomentose at base, fistulose, fibrous. Lamellae adnate, close, yellow to light brown, unequal.

Basidiospores elliptic, 6.0–9.0 × (3.2)3.6–4.4(4.6) μm, Q = (1.43)1.46–2.09(2.25), Qm = 1.78 ± 0.18, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 20–25 × 6–9 μm, hyaline, thin-walled. Cheiocystidia clavate with an umbo at apex, 20–28 × 4–8 μm, hyaline, thin-walled.

Pleurocystidia and caulocystidia absent. Pileipellis a cuits, coralloid or branched, flatten, hyaline, encrusted, 9–18(23) μm, thin- to slightly thick-walled. Clamp connections present.

Habitat – Saprophytic on the deciduous layer in broad-leaved.

Other specimens examined – China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, Erdaobaihe Town, 8 September 2019, Jia-Jun Hu and Bo Zhang, HMJAU 61095 (Collection no.: Hu 17); Zhejiang Province: Shaoxing City, Keqiao County, Pingshui Town, Changfeng Village, 23 June 2020, Jia-Jun Hu, HMJAU 61096 (Collection no.: Hu 532).

Note – This species is characterized by its small basidiomata, hemispherical and reddish brown, distant lamellae, being concolour with the stipe, tomentose or furfuraceous stipe, branched or coralloid pileipellis, clavate cheilocystidia with an umbo at the apex, larger basidiospores, and absence of caulocystidia.

This species is highly morphologically similar to *Li. luxurians*. However, the species differs from *Li. luxurians* by its smaller basidiomata, reddish brown pileus, smaller basidiospores, and 2- or 4-spored basidia (Antonín & Herink 1999, Desjardin et al. 1999).

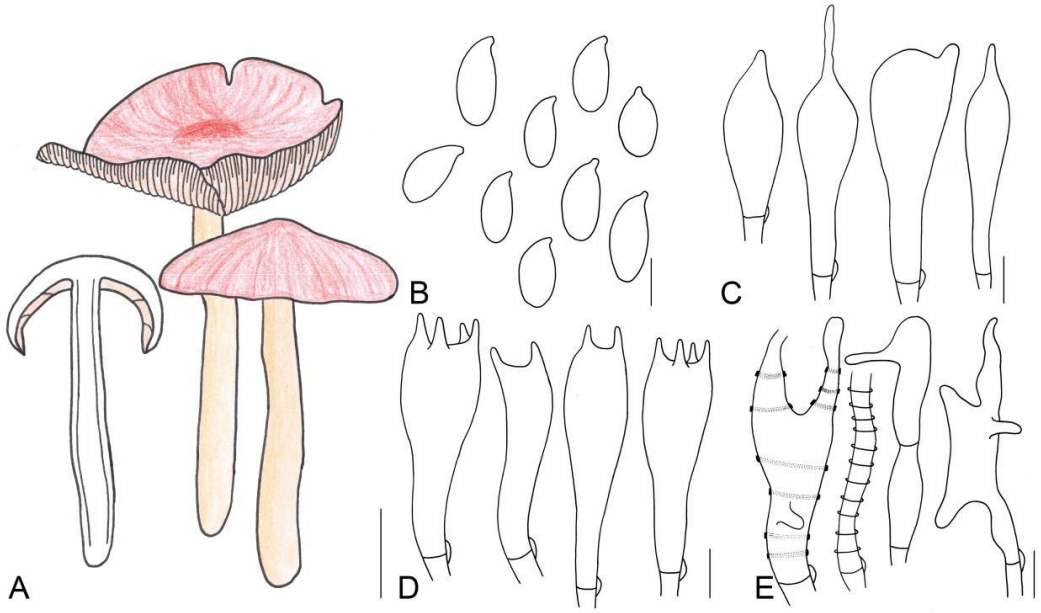

Figure 62 – Morphological characteristic of *Ligymnopus sinoluxurians* (HMJAU 61095). A Basidiomata. B Basidiospores. C Cheilocystidia. D Basidia. E Pileipeillis. Scale bars: A = 1 cm, B–D = 5 μm, E = 10 μm.

Ligymnopus luxurians (Peck) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 63, 61G

= *Gymnopus luxurians* (Peck) Murrill

= *Collybiopsis luxurians* (Peck) R.H. Petersen

= *Collybia luxurians* Peck

= *Collybidium luxurians* (Peck) Murrill

= *Marasmiellus luxurians* (Peck) J.S. Oliveira

Fungal names: FN571394

Basidiomata small- to medium, gregarious. Pileus hemispherical or campaniform to convex, or reflex, 4.4–6.9 cm diameter, smooth, mastoid at center sometimes, brown to reddish brown, light brown to brown outwards, hygrophanus; margin light yellow to light brown, entire, involute or reflex, wavy sometimes. Context thin, white to light yellow, odourless. Stipe central to eccentric, 4.0–6.3 cm long and 0.5–0.9 cm wide, cylindrical or slightly enlarged at base, white to brown, striped. Lamellae close, adnate, adnexed to subfree, white to light yellow, unequal.

Basidiospores ellipsoid, (6.0)7.0–9.0 × 4.0–5.2 μm, Q = (1.37)1.40–2.12(2.20), Qm = 1.77 ± 0.21, hyaline, thin-walled, inamyloid. Basidia clavate, 20–30 × (4)5–9 μm, 4-spored, occasionally

2-spored, hyaline, thin-walled. Cheilocystidia irregularly clavate, branched at apex sometimes, or coralliod, 21–36(38) × 4–8 μm, hyaline, thin-walled. Pleurocystidia and caulocystidia absent. Pileipellis a cuits, flatten, coralliod or branched, encrusted, light brown, thin-walled or slightly thick-walled, 6–15 μm. Clamp connections abundant.

Habitat – Saprophytic on ground in broad-leaved forests.

Specimens examined – China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, E'daobaihe Town, 15 July 2018, Jia-Jun Hu and Bo Zhang, HMJAU 61097 (Collection no.: 47); Tonghua City, Ji'an County, Wunvfeng National Forest Park, 12 August 2018, Yong-Lan Tuo, HMJAU 61098 (Collection no.: 918); Liaoning Province: Fushun City, Xinbin Manchu Autonomous County, Gangshan National Forest Park, 14 August 2017, Ao Ma, HMJAU 61099 (Collection no.: 498); Zhejiang Province: Shaoxing City, Keqiao County, Pingshui Town, 7 June 2020, Jia-Jun Hu, HMJAU 61100 (Collection no.: 509); Shaoxing City, Keqiao County, Pingshui Town, 7 June 2020, Jia-Jun Hu, HMJAU 61101 (Collection no.: 512); Shaoxing City, Keqiao County, Pingshui Town, 7 June 2020, Jia-Jun Hu, HMJAU 61102 (Collection no.: 515); Shaoxing City, Keqiao County, Pingshui Town, 7 June 2020, Jia-Jun Hu, HMJAU 61103 (Collection no.: 516); Shaoxing City, Keqiao County, Pingshui Town, 7 June 2020, Jia-Jun Hu, HMJAU 61104 (Collection no.: 518); Shaoxing City, Keqiao County, Pingshui Town, 7 June 2020, Jia-Jun Hu, HMJAU 61105 (Collection no.: 519); Shaoxing City, Keqiao County, Pingshui Town, 7 June 2020, Jia-Jun Hu, HMJAU 61106 (Collection no.: 521); Shaoxing City, Keqiao County, Pingshui Town, 7 June 2020, Jia-Jun Hu, HMJAU 61107 (Collection no.: 522).

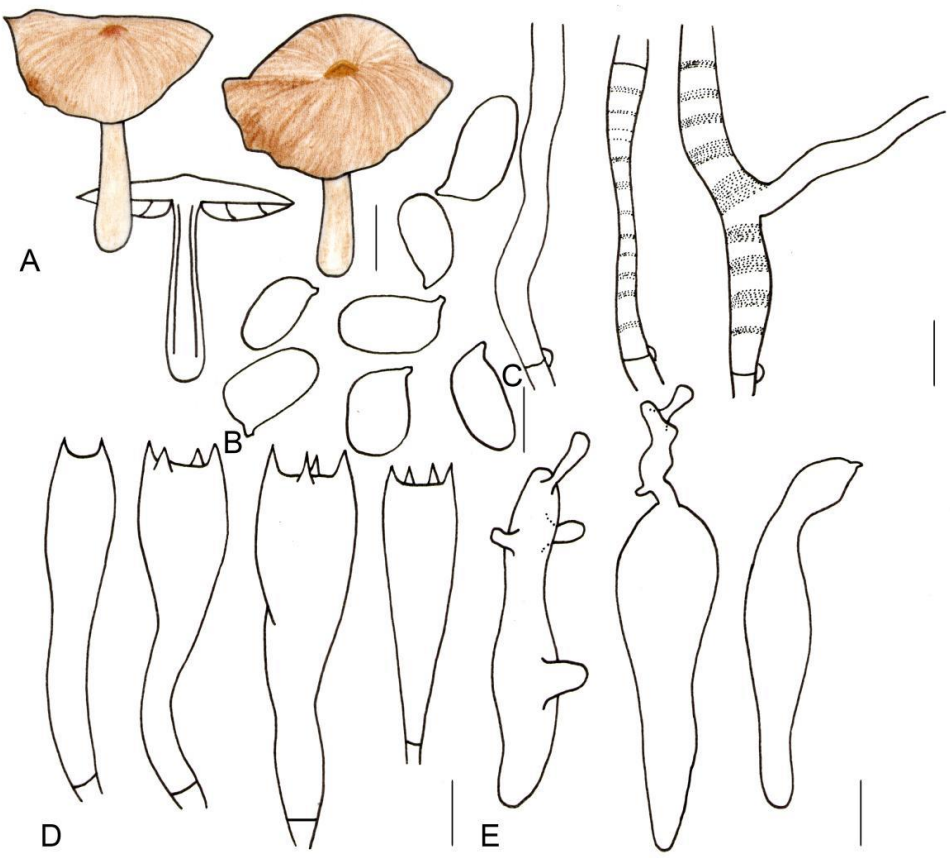

Figure 63 – Morphological characters of *Ligymnopus luxurians* (HMJAU 61107). A Basidomata. B Basidospores. C Pileipellis elements. D Basidia. E Cheilocystidia. Scale Scale bars: A = 1 cm, B, D, E = 5 μm, C = 25 μm.

Note – In this study, specimens of *Li. luxurians* were collected from Eastern China and Northeast China. We found that the specimens collected from Northeast China were larger and

deeper in colour than those collected from Eastern China. Our collections exhibited some differences from the specimens of the Hawaiian Islands, USA. The basidiospores of our collections were smaller, lacked caulocystidia, and the basidia were 4-spored and occasionally 2-spored. In contrast, the description based on the Hawaiian Islands collections described larger basidiospores, basidia that were 4-spored, and the presence of caulocystidia (Desjardin et al. 1999). Furthermore, the European specimens were described as having larger basidiomata and basidiospores, alongside the presence of caulocystidia (Antonín & Herink 1999).

Ligymnopus polygrammus (Mont.) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 64, 61F

= *Gymnopus polygrammus* (Mont.) J.L. Mata

= *Collybiopsis polygramma* (Mont.) R.H. Petersen

= *Chamaeceras polygrammus* (Mont.) Kuntze, Revis

= *Collybia polygramma* (Mont.) Dennis

= *Marasmiellus polygrammus* (Mont.) J.S. Oliveira

= *Marasmius polygrammus* Mont.

Fungal names: FN571395

Basidiomata small- to medium, gregarious. Pileus oblate-hemispheric to convex, or applanate, slightly depressed at center sometimes, smooth, glabrous, grooved, light brown to light reddish brown, deeper colour at disc, light reddish brown, matsoid at center; margin entire, reflexed, wavy sometimes, white to light brown. Context thin, white to light brown, fresh, odourless. Stipe centre to eccentric, cylindrical, pruinose to furfuraceous, fistulose, fibrous. Lamellae closed, adnate to adnexed, light brown, unequal.

Basidiospores elliptic, (6.8)7.0–10.0 × (4.9)5.0–6.1 μm, Q = (1.30)1.35–1.75(1.80), Qm = 1.51 ± 0.15, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 20–32 × 4–8 μm, hyaline, thin-walled. Cheiocystidia clavate with an umbo at apex, 20–45(48) × (4)6–8 μm, hyaline, thin-walled. Pleurocystidia absent. Caulocystidia clavate to irregular clavate, branched sometimes, (48)50–75(82) × 3–6 μm, hyaline, thin-walled. Pileipellis a cuits, coralloid or branched, flatten, hyaline to light yellow, 5–11 μm, thin-walled. Clamp connections present.

Habitat – Saprophytic on the deciduous layer in broad-leaved forest.

Specimens examined – China. Zhejiang Province: Quzhou City, Jiangshan County, Xianxialing Nature Reserve, 28 July 2020, Jin-Bao Pu, HMJAU 61108 (Collection no.: Hu 440); Jilin Province: Tonghua City, Ji'an County, Wunvfeng National Forest Park, 1 August 2020, Yong-Lan Tuo, HMJAU 61109 (Collection no.: Hu 633).

Note – This species is characterized by its small to medium basidiomata, pinkish brown to light reddish-brown pileus that is striped all over, becoming paler outwards, being near white at the margin, having an umbo at the apex, cylindrical and yellowish white stipe, pruinose to furfuraceous surface, being gregarious, flattened and coralloid pileipellis, irregular cheilocystidia, being coralloid or branched at the apex, and larger basidiospores.

Ligymnopus polygrammus is a highly controversial species. Furthermore, the type material only contained one basidiome and was in bad condition. Mata and Petersen re-checked the type material, and according to the pileipellis type, combined it from *Marasmius* to *Gymnopus* (Mata & Petersen 2003).

Our collections differed slightly from the published accounts of *Li. Polygrammus*. Namely, the pileus has previously been reported as brown-orange (Mata & Petersen 2003), initially garyish brown, then developing into brown to orange-brown (Desjardin & Perry 2017), or light brown (Jang et al. 2016), and having basidiospores that are 6.0–8.8 × 3.2–4.8 μm (Mata & Petersen 2003), which are smaller than our collections and those of Desjardin and Perry (Desjardin & Perry 2017). The shape of the cheilocystidia is also different: those from our specimens were clavate and coralloid or finger-like at the apex, while the cheilocystidia from the west African material were irregularly cylindrical to subfusoid, subclavate, narrowly ventricose or sinuous, often had one or more knob-like outgrowths, and were seldom lobed (Desjardin & Perry 2017).

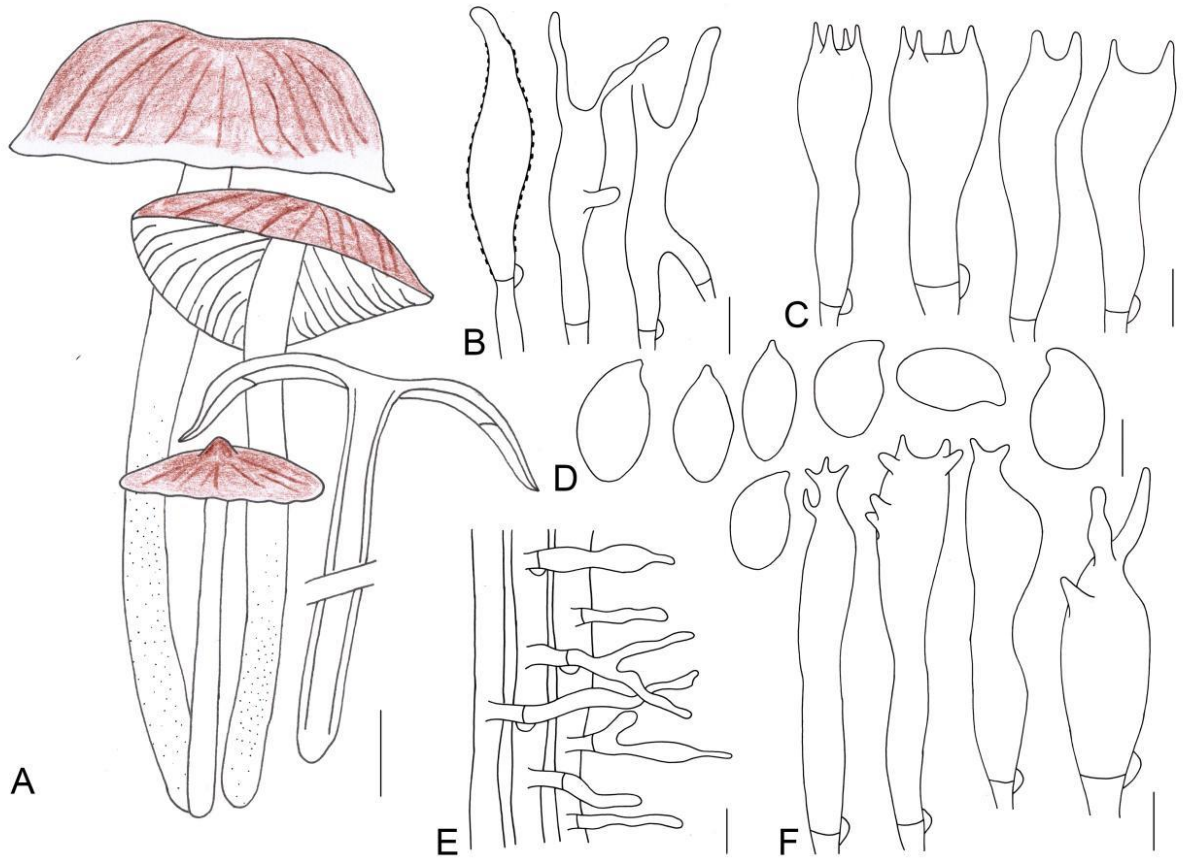

Figure 64 – Morphological characteristics of *Ligymnopus polygrammus* (HMJAU 61108). A Basidiomata. B Pileipellis elements. C Basidia. D Basidiospores. E Caulocystidia. F Cheilocystidia. Scale bars: A = 1 cm, B = 10 μm, C, D, F = 5 μm, E = 20 μm.

Ligymnopus subluxurians (Murrill) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 65, 61H

= *Gymnopus subluxurians* Murrill

= *Collybia subluxurians* (Murrill) Murrill

Fungal names: FN571396

Basidiomata small, solitary to scattered. Pileus convex, 3.6–5.2 cm in diameter, light yellow to brown, with brown spots when mature, smooth, glabrous, hygrophanus, striped; margin entire, striped, white to light yellow. Context thin, fresh, white to light yellow, odourless. Stipe central, cylindrical, 3.7–5.4 cm long and 0.2–0.5 cm wide, reddish brown, paler colour at apex, white to light brown, pruinose. Lamellae adnate to adnexed, white to light yellow, close, unequal.

Basidiospores elliptic, (6.0)6.8–8.8(9.1) × (3.2)3.4–4.8(4.9) μm, Q = (1.50)1.59–2.22(2.25), Qm = 1.97 ± 0.22, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 15–24(25) × (4)5–7(8) μm, hyaline, thin-walled. Cheiocystidia irregularly clavate, bifurcate bifurcation to finger-like, or with an umbo at apex, (15)17–26 × (4)5–8 μm, hyaline, thin-walled. Pleurocystidia absent. Caulocystidia abundant, clavate or irregularly clavate, branched or with an umbo at apex, (27)30–55(57) × 4–6 μm, hyaline, thin-walled. Pileipellis a cuits, coralloid or branched, flatten, hyaline, (5)7–13(15) μm, thin-walled. Clamp connections present.

Habitat – Saprophytic on the deciduous layer or branch in broad-leaved forest.

Specimens examined – China. Zhejiang Province: Shaoxing City, Keqiao County, Pingshui Town, Shangzao Village, 7 June 2020, Jia-Jun Hu, HMJAU 61110 (Collection no.: Hu 520); Shaoxing City, Keqiao County, Pingshui Town, Shangzao Village, 7 June 2020, Jia-Jun Hu, HMJAU 61111 (Collection no.: Hu 536); Henan Province: Zhumadian City, Biyang County, Baiyun Mountain, 11 July 2021, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 61112

(Collection no.: Hu 782); Jilin Province: Changchun City, Jingyuetan National Forest Park, Jia-Jun Hu, Gui-Ping Zhao, and Bo Zhang, HMJAU 61113 (Collection no.: Hu 803).

Note – This species was first described from USA by Murrill (1916), but since, there have seldom been new reports on this species. Prior to the current study, this species was never reported from China. The species is characterized by its medium basidiomata, being concolour with the stipe, being brown to reddish brown, becoming paler outwards, near white at the margin, long and slim stipe with longitudinal stripes, coralloid pileipellis, clavate cheilocystidia with an umbo, being finger-like or lobed at the apex, and smaller basidiospores.

This species is easily confused with *Li. luxurians* and *Li. pseudoluxurians* due to their similar appearance. However, this species can be distinguished from *Li. luxurians* by the uneven colour of pileus, thin stipe, and smaller basidiospores (Desjardin et al. 1999). *Ligymnopus pseudoluxurians* are differentiated by its smaller basidiomata, larger basidiospores, clavate cheilocystidia, and by being irregularly lumpy at the apex (Petersen & Hughes 2014).

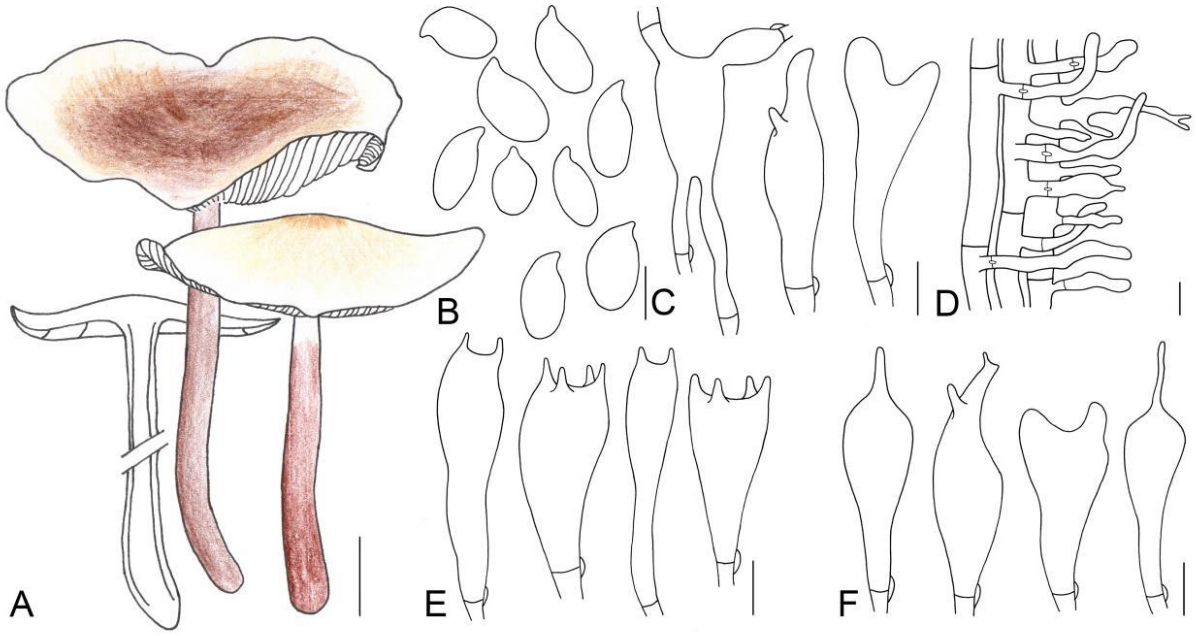

Figure 65 – Morphological characteristics of *Ligymnopus subluxurians* (HMJAU 61110). A Basidiomata. B Basidiospores. C Pileipellis elements. D Caulocystidia. E Basidia. F Cheilocystidia. Scale bars: A = 1 cm, B, E, F = 5 μm, C, D = 10 μm.

Vestipedipilus J.J. Hu, B. Zhang & Y. Li, gen. nov.

Etymology – *Vestipedipilus* refers to this genus arising from sect. *Vestipedes*.

Fungal names: FN571344

Basidiomata collybioid, rare marasmioid, small, medium occasionally, solitary to scattered. Pileus campaniform, convex, or planate-convex to applanate, slightly depressed or umbilicate at disc, striped, grooved, rugulose-striate, smooth, covered with pruinose or slightly tomentose. Lamellae adnate to free, with a decurrent tooth or subdecurrent, close to crowded, white to cream, pruinose or slightly tomentose at edge, forming a collar around the stipe smoetimes. Stipe cylindrical, flatten to clavate, tapered downwards sometimes, pruinose or tomentose, paler at apex, white mycelioid at the base, institious or not, rhizomorphs present or not.

Pileipellis a cuits, repent, radically, cylindrical, coralloid sometimes, smooth, encrusted or diverticulate sometimes. Basidiospores oblong-elliptical to cylindrical, or lacrymoid, thin-walled, smooth, hyaline, inamyloid. Basidia clavate, 4-spored, hyaline, thin-walled. Cheilocystidia cylindrical to clavate, finger-like, coralloid, or lobed at apex. Pleurocystidia absent, clavate to fusiform, hyaline, thin-walled. Pileocystidia present or not, clavate to cylindrical, smooth, hyaline,

thin-walled. Caulocystidia cylindrical, clavate, or irregular clavate, branched or with an umbo at apex, smooth, hyaline, thin- to thick-walled.

Grows on fallen leaves or branches.

Type species: *Vestipedipilus confluens* (Pers.) J.J. Hu, B. Zhang & Y. Li

Key to the species of *Vestipedipilus* present in this study

1 Basidiomata collybioid.....2
1 Basidiomata marasmioid.....*Vestipedipilus hirtellus*
2 Basidiomata with foetid smell.....*Vestipedipilus hariolorum*
2 Basidiomata without unpleasant smell.....3
3 Absence of caulocystidia.....*Vestipedipilus biformis*
3 Presence of caulocystidia.....4
4 Cheilocystidia clavate, finger-like or coralloid at apex.....*Vestipedipilus confluence*
4 Cheilocystidia clavate with an umbo at apex, or irregular clavate.....*Vestipedipilus* cf. *eneficola*

Vestipedipilus biformis (Peck) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 66, 61A

= *Collybiopsis biformis* (Peck) R.H. Petersen
= *Collybia biformis* (Peck) Singer
= *Gymnopus biformis* (Peck) Halling
= *Marasmiellus biformis* (Peck) J.S. Oliveira
= *Marasmius biformis* Peck
Fungal names: FN571397

Basidiomata small, gregarious. Pileus convex to reflexed, depressed at center sometimes, 0.7–2.1 cm in diameter, hygrophanus, striped; margin entire, involute or reflexed, wavy sometimes. Context extremely thin, odourless. Stipe central, cylindrical, 2.2–4.7 cm long and 0.2–0.3 cm wide, flatten at apex, light brown to brown, pruinose, pubescence at base, fistulose, fibrous. Lamellae adnexed to adnate, or subfree, white to light brown, crowded, unequal.

Basidiospores ellipsoid, 6.5–8.2 × (3.0)3.2–4.4 µm, Q = (1.83)1.90–2.01(2.03), Qm = 1.95 ± 0.11, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (18)19–30 × 6–8 µm, 2- or 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, with projections at apex sometimes, 20–28 × 4–7(8) µm, thin-walled, hyaline. Caulocystidia abundant, clavate, branched, 30–65(67) × 3–6 µm, thin-walled, hyaline. Pileipellis a cuits, branched, coralloid or diverticulate, hyaline to light yellow, 3–7(8) µm wide. Clamp connections abundant.

Habitat – Saprophytic on the deciduous layer or ground in broad-leaved or coniferous forests.

Specimens examined – China. Zhejiang province: Shaoxing City, Keqiao County, Pingshui Town, 7 June 2020, Jia-Jun Hu, HMJAU 61114 (Collection no.: 514); Shaoxing City, Keqiao County, Pingshui Town, 7 June 2020, Jia-Jun Hu, HMJAU 61115 (Collection no.: 517); Henan Province: Zhumadian City, Biyang County, Tongshan Lake Scenic Spot, 9 July 2021, Jia-Jun Hu and Bo Zhang, HMJAU 61116 (Collection no.: 761); Zhumadian City, Biyang County, Tongshan Lake Scenic Spot, 9 July 2021, Jia-Jun Hu and Bo Zhang, HMJAU 61117 (Collection no.: 764); Zhumadian City, Biyang County, Rock Botanical Garden, 12 July 2021, Jia-Jun Hu and Bo Zhang, HMJAU 61118 (Collection no.: 786).

Note – This species is characterized by its small basidiomata, light reddish brown to reddish brown or cinnamon pileus, white to light brown and close lamellae, and by growing on the ground.

Some differences were noted between our collections and Halling's conception. According to Halling's description, the lamellae usually formed a collar around the stipe, the species grew from July to September, and there was the presence of caulocystidia. In contrast, our collections lacked a collar between the lamellae and stipe, which occurred from June to July, and absent of caulocystidia (Halling 1983).

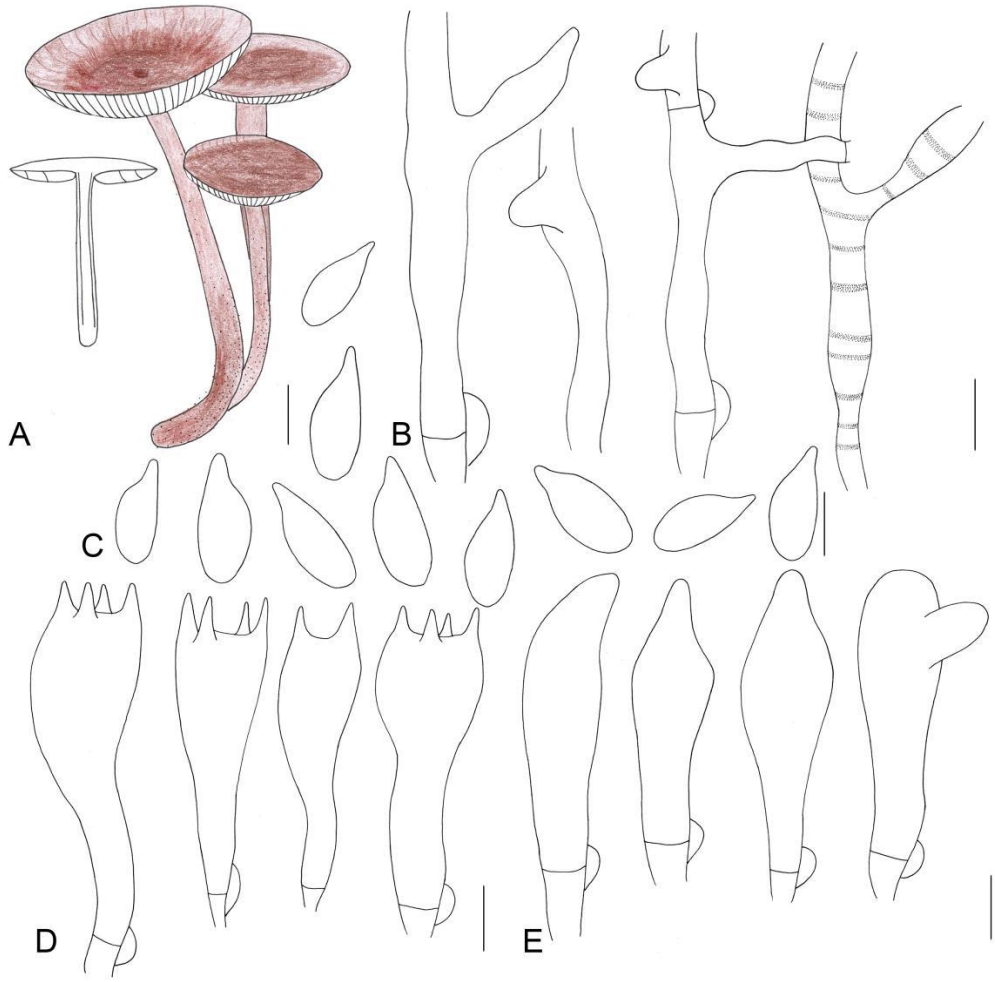

Figure 66 – Morphological character of *Vestipedipilus biformis* (HMJAU 61114). A Basidiomata. B Pileipellis elements. C Basidiospores. D Basidia. E Cheilocystidia. Scale bars: A = 0.5 cm, B = 10 μm, C–E = 5 μm.

Vestipedipilus confluens (Pers.) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 67, 61C

= *Collybiopsis confluens* (Pers.) R.H. Petersen
= *Agaricus confluens* Pers.
= *Chamaeceras archyropus* (Pers.) Kuntze
= *Collybia confluens* (Pers.) P. Kumm.
= *Gymnopus confluens* (Pers.) Antonín, Halling & Noordel.
= *Marasmiellus confluens* (Pers.) J.S. Oliveira
= *Marasmius archyropus* (Pers.) Fr.
= *Marasmius confluens* (Pers.) P. Karst.

Fungal names: FN571398

Basidiomata small, gregarious. Pileus convex to applanate, finally reflexed, 1.2–4.3 cm in diameter, smooth, with an umbo sometimes at center, light brown to yellowish white, or yellowish brown, deeper coloured at center; margin entire or slightly lobed, wavy sometimes, yellowish brown to yellowish white. Context thin, odourless. Stipe central, cylindral, 4.3–9.7 cm long and 0.2–0.3 cm wide, tomentose, fistulose, fibrous. Lamellae adnate to adnexed, white, crowded, unequal.

Basidiospores ellipsoid, (7.0)7.2–10.0 × 3.0–4.0 μm, Q = (1.75)1.90–3.33, Qm = 2.72 ± 0.42, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 16–28 × (5)6–8 μm, 2- or 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, with projections at apex sometimes, (18)19–25(33) × 5–7(8) μm, thin-walled, hyaline. Caulocystidia abundant, clavate, branched, 16–40(42) ×

3–5 µm, thin-walled, hyaline. Pileipellis a cuits, branched, coralloid or diverticulate, hyaline to light yellow, 5–12 µm wide. Clamp connections abundant.

Habitat – Saprophytic on the deciduous layer or ground in broad-leaved and coniferous mixed forests.

Specimens examined – China. Jilin Province: Baishan City, Fusong County, Lushuihe Town, Lushuihe international hunting ground, 30 August 2019, Jia-Jun Hu and Bo Zhang, HMJAU 61119 (Collection no.: Hu 322); Baishan City, Changbai Korean Autonomous County, Wangtiane Scenic Area, 23 July 2019, Rui Ma and Zeng Yi Bi, 61120 HMJAU (Collection no.: Hu 402); Tonghua City, Ji'an County, 24 July 2019, Yong-Lan Tuo, HMJAU 61123 (Collection no.: Hu 354); Tonghua City, Ji'an County, 22 July 2020, Jia-Jun Hu and Yong-Lan Tuo, HMJAU 61125 (Collection no.: Hu 582); Jilin City, Zhuque Mountain National Forest Park, 18 August 2121, Jia-Jun Hu, Gui-Ping Zhao, Zheng-Xiang Qi, and Bo Zhang, HMJAU 61135 (Collection no.: Hu 840); Liaoning Province: Fushun City, Xinbin Manchu Autonomous County, Gangshan National Forest Park, 31 July 2018, Ao Ma, HMJAU 61138 (Collection no.: Hu 463); Benxi City, Tanggou green stone Valley National Forest Park, 27 July 2017, Yang Wang, HMJAU 61139 (Collection no.: Hu 933).

Note – This species is characterized by its yellowish white to brown pileus, close to crowded lamellae, and long stipe that appears furfuraceous at first, then becomes tomentose.

Hughes & Petersen (2015) studied *V. confluence* from Europe and North America, finding some differences between the specimens. In this study, we only collected *V. confluence* specimens from Northeast China. In studying the collected specimens, we found that our collections were more similar to European ones.

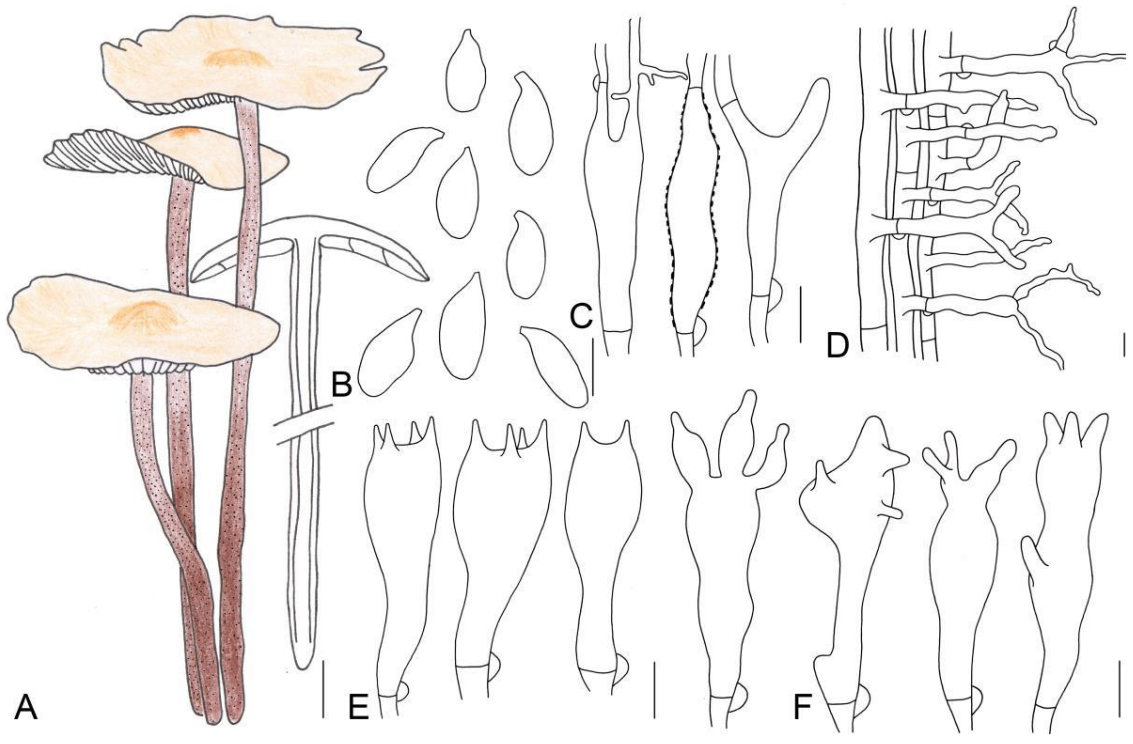

Figure 67 – Morphological character of *Vestipedipilus confluence* (HMJAU 61120). A Basidiomata. B Basidiospores. C Pileipellis elements. D Caulocystidia. E Basidia. F Cheilocystidia. Scale bars: A = 1 cm, B, E, F = 5 µm, C, D = 10 µm.

Vestipedipilus* cf. *eneficola (R.H. Petersen) J.J. Hu, B. Zhang & Y. Li, comb. nov.

Figs 68, 61D

= *Gymnopus eneficola* R.H. Petersen

= *Collybiopsis eneficola* (R.H. Petersen) R.H. Petersen

Fungal names: FN571399

Basidioma small to medium, solitary to gregarious. Pileus hemispherical to convex, 0.5–4.9 cm diameter, tomentose, with an umbo sometimes, light reddish brown at first, then fresh-pink, light pink to light brown, or light pinkish brown when mature, rose-red at center, light pink when dry; margin involute, entire, wavy sometimes, near white to light pink when young, light pink to light brown when mature, tomentose at first, then becoming smooth. Context white to light fresh, odourless. Stipe clavate, 2.8–3.9 cm long and 0.2–0.4 cm wide, pruinose at upper part, tomentose at base, fistulose, fibrous. Lamellae adnexed to adnate, close to crowded, fresh-pink to light brown, unequal.

Basidiospores elliptic, 5.0–6.2(6.8) × 3.0–4.0 μm, Q = (1.30)1.50–2.00, Qm = 1.78 ± 0.19, thin-walled, smooth, hyaline, inamyloid. Basidia clavate, (11)17–28(29) × (3)4–6 μm, 2–4 spored, hyaline, thin-walled. Cheilocystidia seldom, clavate to coralloid, 12–25 × 3–5 μm, hyaline, thin-walled. Pleurocystidia absent. Caulocystidia cylindrical to clavate, branched at apex sometimes, 23–47 × 3–5 μm. Pileipellis a cuits, flatten, weakly coralloid or branched, 5–11 μm wide, thin-walled, light yellow. Clamp connections present.

Habitat – Saprophytic on the deciduous layer in broad-leaved or coniferous forests.

Specimens examined – China. Jilin Province: Yanbian Korean Autonomous Prefecture, Antu County, E'daobaihe Town, 22 July 2018, Jia-Jun Hu and Bo Zhang, HMJAU 61141 (Collection no.: 60); Baishan City, Fusong County, Lushuihe Town, 23 July 2018, Jia-Jun Hu and Bo Zhang, HMJAU 61142 (Collection no.: 62); Baishan City, Fusong County, Lushuihe Town, 23 July 2018, Jia-Jun Hu and Bo Zhang, HMJAU 61143 (Collection no.: 63); Liaoning Province: Fushun City, Xinbin Manchu Autonomous County, Gangshan National Forest Park, 31 July 2017, Ao Ma, HMJAU 61144 (Collection no.: 447); Fushun City, Xinbin Manchu Autonomous County, Gangshan National Forest Park, 2 August 2017, Ao Ma, HMJAU 61145 (Collection no.: 449)

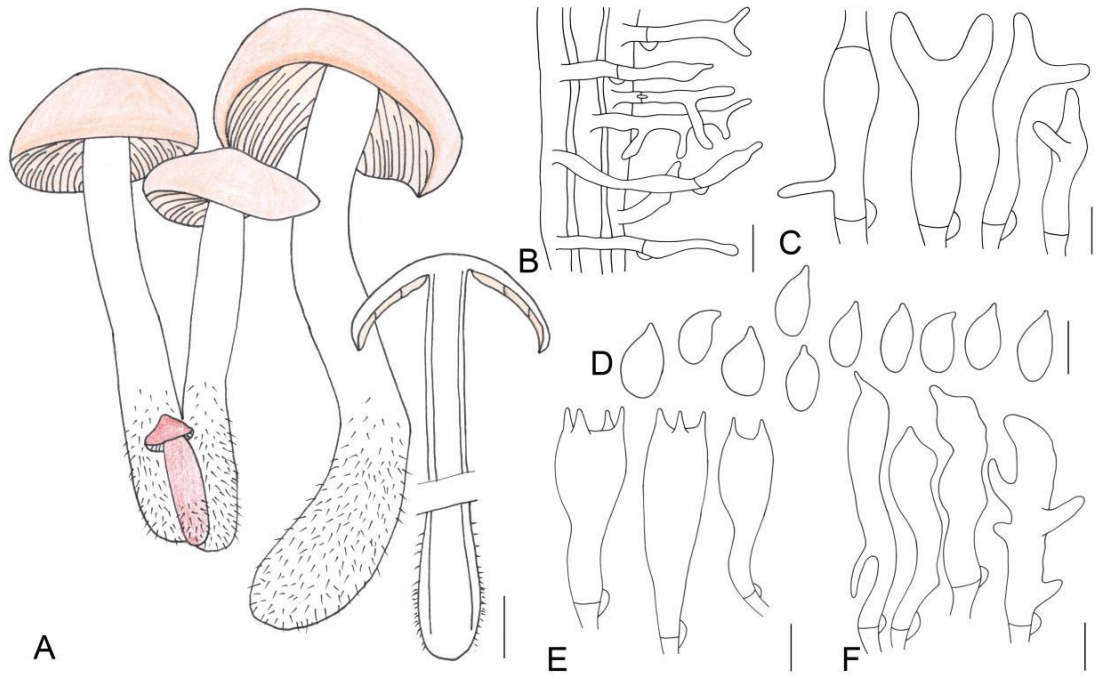

Figure 68 – Morphological characteristics of *Vestipedipilus eneficola* (HMJAU 61143). A Basidiomata. B Caulocystidia. C Pileipellis elements. D Basidiospores. E Basidia. F Cheilocystidia. Scale bars: A = 0.5 cm, B = 40 μm, C = 10 μm, D–F = 5 μm.

Note – This species was firstly described by Petersen in 2014 from Newfoundland, Canada. The current study is the first time this species has been recorded from China. However, there exist

some differences between our specimens and Petersen's description. In Petersen's description, the pileus of this species was always near white to light pink and with basidiospores in 7.5–9 × 3.5–5 μm (Petersen et al. 2014). In contrast, according to our specimens, the pileus are light reddish brown at first, then either light pink to light brown or light pinkish brown when mature, and with smaller basidiospores (5.0–6.2(6.8) × 3.0–4.0 μm).

Vestipedipilus hariolorum (Bull.) J.J. Hu, B. Zhang & Y. Li, comb. nov. Figs 69, 61B

= *Gymnopus hariolorum* (Bull.) Antonín, Halling & Noordel.

= *Agaricus hariolorum* Bull.

= *Collybia hariolorum* (Bull.) Quél.

= *Marasmius hariolorum* (Bull.) Quél.

Fungal names: FN571400

Basidiomata small, solitary to gregarious. Pileus hemispherical to convex or applanate, depressed at center sometimes, 2.1–3.7 cm wide, smooth, hygrophanous, brown to light brown at center, near white to light brown outwards; margin entire, inflexed or straight, white. Context thin, white, with a strong smell reminding of rotten cabbage or onion. Stipe central, clavate to cylindrical, 2.5–3.2 cm long and 0.2–0.4 cm wide, white to light brown, covered with white tomentose, fistulose, fibrous. Lamellae adnexed, white, close, unequal.

Basidiospores ellipsoid, 5.0–7.0 × 3.0–4.0 μm, Q = (1.50)1.67–2.26(2.27), Qm = 1.88 ± 0.17, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, (20)22–32(33) × 5–7 μm, 2- or 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, branched or with a long and slim umbo at apex, (20)23–36(37) × 4–7 μm, thin-walled, hyaline. Caulocystidia abundant, clavate, branched, 30–65(67) × 3–6 μm, thin-walled, hyaline. Pileipellis a cuits, branched, coralloid or diverticulate, hyaline to light yellow, 5–12 μm wide. Clamp connections abundant.

Habitat – Saprophytic on the deciduous layer in broad-leaved or coniferous forests

Specimens examined – China. Jilin Province: Yanbian Korean Autonomous Prefecture Antu County, Edaobaihe Town, 9 September 2019, Jia-Jun Hu and Bo Zhang, HMJAU 61146 (Collection no.: 22); Yanbian Korean Autonomous Prefecture Antu County, Edaobaihe Town, 9 September 2019, Jia-Jun Hu and Bo Zhang, HMJAU 61147 (Collection no.: 28); Yanbian Korean Autonomous Prefecture Antu County, Edaobaihe Town, 9 September 2019, Jia-Jun Hu, Dan Dai, and Bo Zhang, HMJAU 61148 (Collection no.: 30); Jiaohe City Hongye Valley Scenic Spot, 6 September 2019, HMJAU 61149 (Collection no.: 105); Tonghua City Ji'an County, Wunvfeng National Forest Park, 13 August 2019, HMJAU 61150 (Collection no.: 373).

Note – This species is characterized by its light brown to brown at the center, outwardly paler, close lamellae, being pruinose to tomentose at the base of stipe, exhibiting a foetid smell, having smaller basidiospores, and clavate basidia with long and slim branches or an umbo at the apex.

Some differences were noted between our collections and the conception of Antonín & Noordel. Our specimens included a cylindrical stipe with smaller basidiospores and clavate cheilocystidia with slim branches or an umbo at the apex. In contrast, the specimens collected from Europe featured a cylindrical stipe and a downwards border with larger basidiospores ((5.5)6.2–7.3 × 3.0–4.1 μm), irregular cheilocystidia, and being finger-like at the apex (Antonín & Noordeloos 2010).

Vestipedipilus hirtellus (Berk. & Broome) J.J. Hu, B. Zhang & Y. Li, comb. nov.

Figs 70, 16G

= *Gymnopus hirtellus* (Berk. & Broome) Desjardin & B.A. Perry

= *Chamaeceras hirtellus* (Berk. & Broome) Kuntze

= *Collybia hirtella* (Berk. & Broome) Dennis

= *Marasmiellus hirtellus* (Berk. & Broome) Pegle

= *Marasmius hirtellus* Berk. & Broome

Fungal names: FN571401

Basidiomata small, gregarious. Pileus oblate hemispheric to convex at first, reflexed finally, slightly depressed at disc, 1.3–2.1 cm in diameter, glabrous, grooved, light brown to brown, deeper colour at disc, dark brown; margin entire, involute at first, reflex finally, yellow to yellowish white. Context extremely thin, brown, odourless. Stipe central, cylindrical, 3.7–5.2 cm long and 0.1–0.2 cm wide, yellowish brown, brown to light dark brown, tomentose, hollow, fibrous. Lamellae adnate, rather distant, light yellow to light brown, unequal.

Basidiospores ellipsoid, (5.0)5.4–7.2(8.0) × 2.8–3.3(3.6) µm, Q = (1.74)1.78–2.40(2.50), Qm = 2.09 ± 0.23, smooth, hyaline, inamyloid, thin-walled. Basidia clavate, 17–25 × 4–7 µm, 2- or 4-spored, thin-walled, hyaline. Cheilocystidia irregularly clavate, with projections at apex sometimes, 17–32 × 4–6 µm, thin-walled, hyaline. Caulocystidia abundant, clavate, finger-like at apex, or branched, 35–60(62) × 4–6(7) µm, thin-walled, hyaline. Pileipellis a cuits, branched, hyaline to brown, 4–10(12) µm wide. Clamp connections abundant.

Habitat – Saprophytic on fallen leaves.

Specimen examined – China. Zhejiang Province: Hangzhou City, Hangzhou Botanical Garden, 10 June 2020, Jia-Jun Hu, HMJAU 61151 (Collection no.: Hu 523).

Note – This species was firstly described by Berkeley and Broome in 1875 from Sri Lanka. It belonged to *Marasmius* at first, and was subsequently transferred to *Gymnopus* by Desjardin and B.A. Perry as a new combination (Desjardin & Perry 2017). However, some differences were observed between our specimens collected from Hangzhou, China, and those included in Desjardin and B.A. Perry's conception. The caulocystidia of our specimens were clavate and finger-like, or branched at the apex, while in contrast, Desjardin and B.A. Perry's conception described them as cylindrical. Furthermore, according to their description, the shape of cheilocystidia was irregularly clavate and with 1–3(–4) broadly rounded apical lobes, while our specimens were observed to be irregularly clavate with an umbo at the apex. In addition, our current report is the first time this species has been recorded from China.

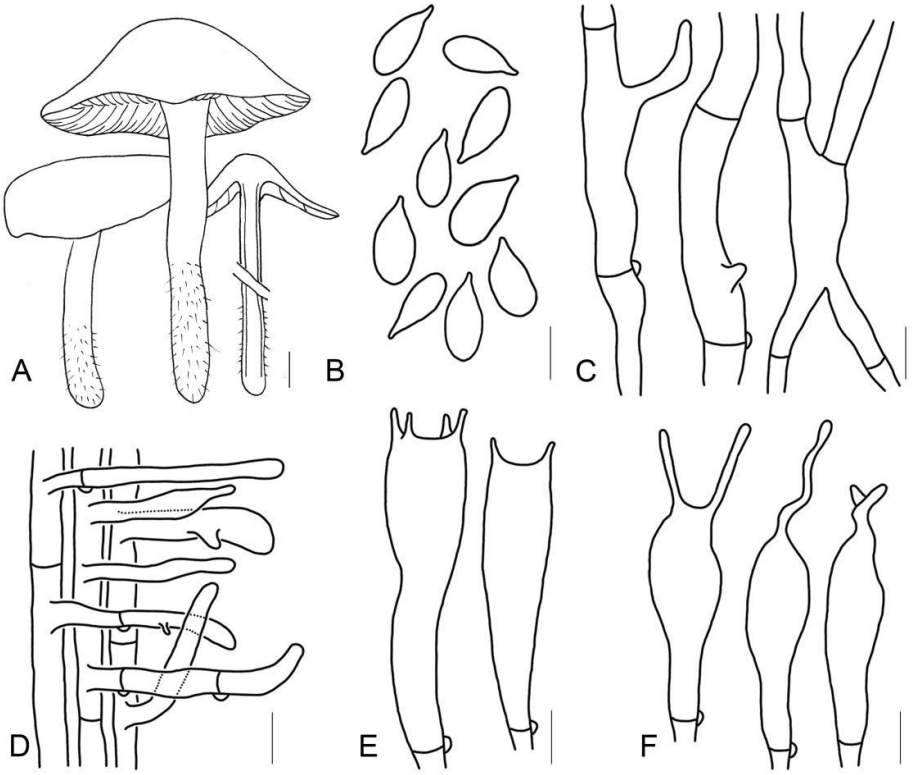

Figure 69 – Morphological characteristics of *Vestipedipilus hariolorum* (HMJAU 61150). A Basidiomata. B Basidospores. C Pileipellis elements. D Caulocystidia. E Basidia. F Cheilocystidia. Scale bars: A = 1 cm, B, E, F = 5 µm, C = 10 µm, D = 20 µm.

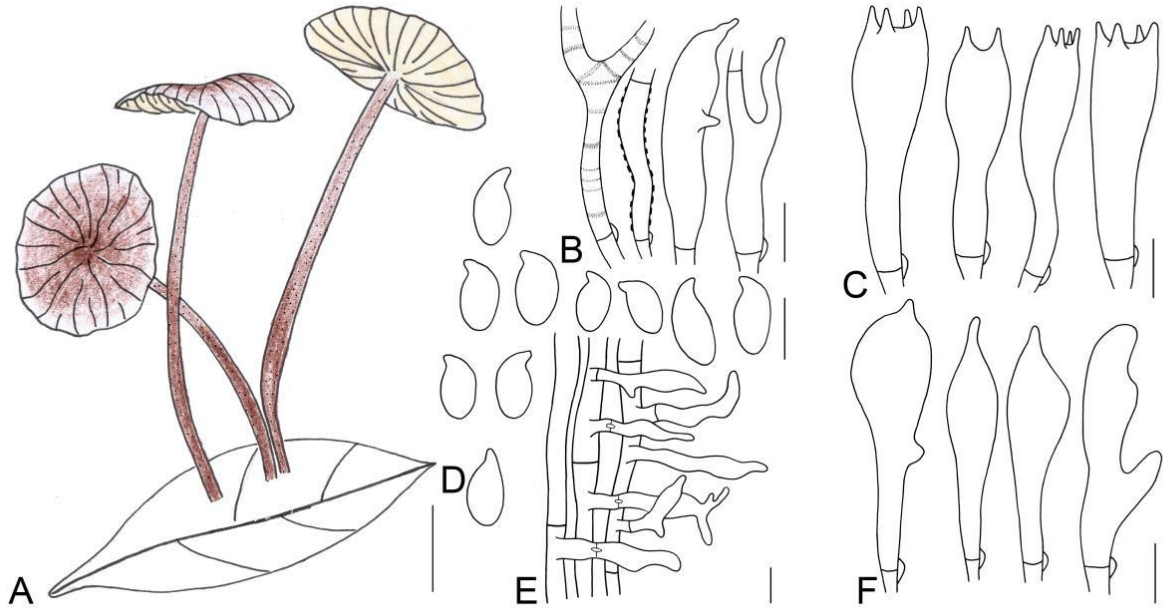

Figure 70 – Morphological characteristic of *Vestipedipilus hirtellus* (HMJAU 61151). A Basidiomata. B Pileipellis elements. C Basidia. D Basidiospores. E Caulocystidia. F Cheilocystidia. Scale bars: A = 1 cm, B, E = 10 μm, C, D, F = 5 μm.

Rhodocollybia Singer

Rhodocollybia butyracea (Bull.) Lennox Figs 71, 16A-C

≡ *Collybia butyracea* (Bull.) P. Kumm.

Basidiomata small to large, solitary to gregarious. Pileus hemispherical to convex, applanate to reflexed when mature, 1.3–4.1 cm diameter, brown to reddish brown, mastoid sometimes at centre, smooth; margin entire or lobed, involute, straight to reflexed, paler coloured, near white to light yellow or brown, inapparent striped sometimes. Context fresh, odourless. Stipe central, cylindrical to clavate, 3.3–6.1 cm long and 0.4–1.2 cm wide, smooth, covered with white tomentose at base, light brown. Lamellae closed, white to beige, adnexed to subfree, unequal.

Basidiospores elliptic, 6.0–8.0 × 3.0–4.0 μm, Q = 1.53–2.67, Qm = 2.08 ± 0.31, dextrinoid, hyaline, smooth, thin-walled. Basidia clavate, 18–23 × 5–7 μm, 2 or 4 spored, hyaline, thin-walled. Cheilocystidia clavate, whit an umbo at apex or branched, (15)19–27(30) × 3–5(7) μm, hyaline, thin-walled. Pleurocystidia basent. Pileipellis a cuits, weakly coralloid or branched, encrusted sometimes, (7)8–15(20) μm wide, thin- or thick-walled. Clamp connections present.

Habitat – Saprophytic on the deciduous layer in broad-leaved forests.

Specimens examined – China. Jilin Province: Baishan City, Fusong County, Songjianghe National Forest Park, 6 September 2019, Jia-Jun Hu and Bo Zhang, HMJAU 61152 (Collection no.: 40); Baishan City, Changbai Korean Autonomous County, Wangtian'e Scenic Spot, 9 September 2019, Jia-Jun Hu and Bo Zhang, HMJAU 61153 (Collection no.: 317); Yanbian Korean Autonomous Prefecture, Antu County, E'daobaihe Town, 9 September 2019, Jia-Jun Hu and Bo Zhang, HMJAU 61154 (Collection no.: 307); Liaoning Province: Fushun City, Xinbin Manchu Autonomous County, Gangshan National Forest Park, 2 October 2018, Jia-Jun Hu and Ao Ma, HMJAU 61155 (Collection no.: 117).

Note – This species is morphologically variable and characterized by a pileus with an umbo, variable colour from reddish brown to grayish brown, withe to light yellow lamellae, and having a longitudinally striped stipe that is slightly enlarged at the base.

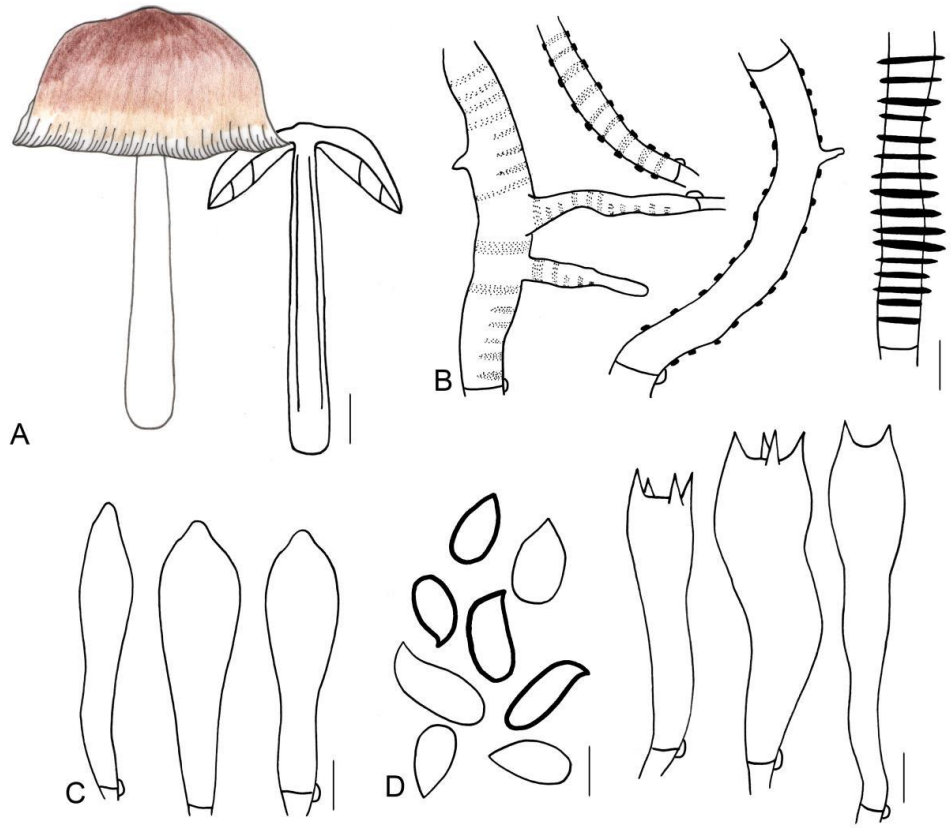

Figure 71 – Morphological characters of *Rhodocollybia butyracea* (HMJAU 61152). A Basidomata. B Pileipellis elements. C Cheilocystidia. D Basidospores. E Basidia. Scale bars: A = 1 cm, B = 25 µm, C–E = 5 µm.

New combinations
Impudipilus
Impudipilus montagnei (Berk.) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571404)
Gymnopus montagnei (Berk.) Redhead, Index Fungorum 148: 1 (2014)
Impudipilus alpicola (Bon & Ballarà) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571408)
Gymnopus alpicola (Bon & Ballarà) Esteve-Rav., V. González, Arenal & E. Horak, Z. Mykol. 64(1): 69 (1998)
Impudipilus barbipes (R.H. Petersen & K.W. Hughes) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571409)
Gymnopus barbipes R.H. Petersen & K.W. Hughes, N. Amer. Fung. 9(3): 2 (2014)
Impudipilus impudicus (Fr.) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571410)
Gymnopus impudicus (Fr.) Antonín, Halling & Noordel., Mycotaxon 63: 364 (1997)
Impudipilus trabzonensis (Vizzini, Antonín, Seslı & Contu) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571411)
Gymnopus trabzonensis Vizzini, Antonín, Seslı & Contu, Phytotaxa 226(2): 122 (2015)
Impudipilus atlanticus (V. Coimbra, Pinheiro, Wartchow & Gibertoni) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571412)
Gymnopus atlanticus V. Coimbra, Pinheiro, Wartchow & Gibertoni
Impudipilus pygmaeus (V. Coimbra, E. Larss., Wartchow & Gibertoni) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571413)
Gymnopus pygmaeus V. Coimbra, E. Larss., Wartchow & Gibertoni
Impudipilus talisiae (V. Coimbra, Pinheiro, Wartchow & Gibertoni) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571414)

Gymnopus talisiae V. Coimbra, Pinheiro, Wartchow & Gibertoni, Mycol. Progr. 14(no. 110): 5 (2015)
Impudipilus praeacutus (Ellis) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571415)
Marasmiellus praeacutus (Ellis) Halling, Syst. Bot. 12(3): 401 (1987)
Impudipilus iocephalus (Berk. & M.A. Curtis) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571416)
Gymnopus iocephalus (Berk. & M.A. Curtis) Halling, in Antonín, Halling & Noordeloos, Mycotaxon 63: 364 (1997)
Impudipilus salakensis (A.W. Wilson, Desjardin & E. Horak) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571417)
Gymnopus salakensis A.W. Wilson, Desjardin & E. Horak, Sydowia 56(1): 202 (2004)
Impudipilus variicolor (Antonín, Ryoo, Ka & Tomšovský, in Ryoo, Antonín, Ka & Tomšovský) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571418)
Gymnopus variicolor Antonín, Ryoo, Ka & Tomšovský, in Ryoo, Antonín, Ka & Tomšovský, Phytotaxa 268(2): 83 (2016)

Levipedipilus
Levipedipilus earleae (Murrill) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571419)
Gymnopus earleae Murrill, N. Amer. Fl. (New York) 9(5): 364 (1916)
Levipedipilus kauffmanii (Halling) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571420)
Gymnopus kauffmanii (Halling) Halling, in Antonín, Halling & Noordeloos, Mycotaxon 63: 364 (1997)
Levipedipilus vitellinipes (A.W. Wilson, Desjardin & E. Horak) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571421)
Gymnopus vitellinipes A.W. Wilson, Desjardin & E. Horak, Sydowia 56(1): 166 (2004)
Levipedipilus alpinus (Vilgalys & O.K. Mill.) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571422)
Gymnopus alpinus (Vilgalys & O.K. Mill.) Antonín & Noordel., in Antonín, Halling & Noordeloos, Mycotaxon 63: 363 (1997)
Levipedipilus aurantiipes (Corner) J.J. Hu, B. Zhang & Y. Li, comb. nov.
Gymnopus aurantiipes (Corner) A.W. Wilson, Desjardin & E. Horak, Sydowia 56(1): 153 (2004)
Levipedipilus bicolor (A.W. Wilson, Desjardin & E. Horak) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571423)
Gymnopus bicolor A.W. Wilson, Desjardin & E. Horak, Sydowia 56(1): 159 (2004)
***Levipedipilus* indoctoides** (A.W. Wilson, Desjardin & E. Horak) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571424)
Gymnopus indoctoides A.W. Wilson, Desjardin & E. Horak, Sydowia 56(1): 161 (2004)
Levipedipilus junquilleus (R.H. Petersen & J.L. Mata) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571425)
Gymnopus junquilleus R.H. Petersen & J.L. Mata, in Mata, Hughes & Petersen, Sydowia 58(2): 281 (2006)
Levipedipilus lanipes (Malençon & Bertault) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571426)
Gymnopus lanipes (Malençon & Bertault) Vila & Llimona, Revta Catal. Micol. 28: 180 (2006)
Levipedipilus macropus (Halling) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571427)
Gymnopus macropus Halling, Brittonia 48(4): 490 (1996)
Levipedipilus nubicola (Halling) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571428)
Gymnopus nubicola Halling, Brittonia 48(4): 492 (1996)
Levipedipilus sepiiconicus (Corner) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571429)
Gymnopus sepiiconicus (Corner) A.W. Wilson, Desjardin & E. Horak, Sydowia 56(1): 163 (2004)
Levipedipilus alkalivirens (Singer) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571430)
Gymnopus alkalivirens (Singer) Halling, in Antonín, Halling & Noordeloos, Mycotaxon 63: 363 (1997)
Levipedipilus austrosemihirtipes (A.W. Wilson, Desjardin & E. Horak) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571431)

Gymnopus austrosemihirtipes A.W. Wilson, Desjardin & E. Horak, Sydowia 56(1): 156 (2004)
Levipedipilus bisporus (J. Carbó & Pérez-De-Greg.) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571432)
Gymnopus bisporus (J. Carbó & Pérez-De-Greg.) J. Carbó & Pérez-De-Greg., Revta Catal. Micol. 28: 180 (2006)
Levipedipilus catalonicus (Vila & Llimona) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571433)
Gymnopus catalonicus (Vila & Llimona) Vila & Llimona, Revta Catal. Micol. 28: 180 (2006)
Levipedipilus fuscopurpureus (Pers.) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571434)
Gymnopus fuscopurpureus (Pers.) Antonín, Halling & Noordel., Mycotaxon 63: 364 (1997)
Levipedipilus hybridus (Kühner & Romagn.) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571435)
Gymnopus hybridus (Kühner & Romagn.) Antonín & Noordel., in Antonín, Halling & Noordeloos, Mycotaxon 63: 364 (1997)
Levipedipilus inusitatus (Vila & Llimona) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571436)
Gymnopus inusitatus (Vila & Llimona) Vila & Llimona, Revta Catal. Micol. 28: 180 (2006)
Levipedipilus loiseleurietorum (M.M. Moser, Gerhold & Tobies) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571437)
Gymnopus loiseleurietorum (M.M. Moser, Gerhold & Tobies) Antonín & Noordel., in Antonín, Halling & Noordeloos, Mycotaxon 63: 364 (1997)
Levipedipilus pubipes (Antonín, A. Ortega & Esteve-Rav.) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571438)
Gymnopus pubipes Antonín, A. Ortega & Esteve-Rav., in Ortega, Antonín & Esteve-Raventós, Mycotaxon 85: 69 (2003)
Levipedipilus semihirtipes (Peck) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571439)
Gymnopus semihirtipes (Peck) Halling, in Antonín, Halling & Noordeloos, Mycotaxon 63: 365 (1997)
Levipedipilus spongiosus (Berk. & M.A. Curtis) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571440)
Gymnopus spongiosus (Berk. & M.A. Curtis) Halling, Brittonia 48(4): 489 (1996)
Levipedipilus strigosipes (J.P. Li, Chang Tian Li, Yi Li & Yu Li) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571442)
Gymnopus strigosipes J.P. Li, Chang Tian Li, Yi Li & Yu Li, in Li, Pan, Li, Deng, Wang, Zhang, Li & Li, Journal of Fungi 8(4, no. 398): 11 (2022)
Levipedipilus terginus (Fr.) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571443)
Gymnopus terginus (Fr.) Antonín & Noordel., in Antonín, Halling & Noordeloos, Mycotaxon 63: 365 (1997)

Neomarasmius
Neomarasmius albicantipes (J.S. Kim & Y.W. Lim) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571444)
Collybiopsis albicantipes J.S. Kim & Y.W. Lim, in Kim, Cho, Park, Park, Kim, Kim & Lim, MycoKeys 88: 89 (2022)
Neomarasmius boreoorientalis (Kiyashko) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571445)
Collybiopsis boreoorientalis (Kiyashko) Bartrop & Haelew., Index Fungorum 515: 1 (2022)
Neomarasmius istanbulensis (E. Sesli, Antonín & K.W. Hughes) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571446)
Collybiopsis istanbulensis (E. Sesli, Antonín & K.W. Hughes) J.S. Kim & Y.W. Lim, in Kim, Cho, Park, Park, Kim, Kim & Lim, MycoKeys 88: 99 (2022)
Neomarasmius longistipes (Muh. Ali, Niazi & Khalid) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571448)
Collybiopsis longistipes (Muh. Ali, Niazi & Khalid) Bartrop & Haelew., Index Fungorum 515: 1 (2022)

Neomarasmius micromphaloides (R.H. Petersen & K.W. Hughes) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571449)
Collybiopsis micromphaloides (R.H. Petersen & K.W. Hughes) R.H. Petersen, in Petersen & Hughes, Index Fungorum 491: 1 (2021)
Neomarasmius orientisubnuda (J.S. Kim & Y.W. Lim) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571450)
Collybiopsis orientisubnuda J.S. Kim & Y.W. Lim, in Kim, Cho, Park, Park, Kim, Kim & Lim, MycoKeys 88: 94 (2022)
Neomarasmius vellerea (J.S. Kim & Y.W. Lim) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571451)
Collybiopsis vellerea J.S. Kim & Y.W. Lim, in Kim, Cho, Park, Park, Kim, Kim & Lim, MycoKeys 88: 98 (2022)
Neomarasmius cervinus (Henn.) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571452)
Gymnopus cervinus (Henn.) Desjardin & B.A. Perry, Mycosphere 8(9): 1377 (2017)
Neomarasmius lodgeae (Singer) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571454)
Gymnopus lodgeae (Singer) J.L. Mata, in Mata & Petersen, Mycotaxon 86: 313 (2003)
Neomarasmius mustachius (Desjardin & B.A. Perry) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571455)
Gymnopus mustachius Desjardin & B.A. Perry, Mycosphere 8(9): 1382 (2017)
Neomarasmius omphalodes (Berk.) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571456)
Gymnopus omphalodes (Berk.) Halling & J.L. Mata, in Mata, Halling & Petersen, Fungal Diversity 16: 122 (2004)
Neomarasmius pseudolodgeae (J.L. Mata) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571457)
Gymnopus pseudolodgeae J.L. Mata, in Mata, Halling & Petersen, Fungal Diversity 16: 120 (2004)
Neomarasmius subnudus (Ellis ex Peck) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571458)
Collybiopsis subnuda (Ellis ex Peck) R.H. Petersen, Index Fungorum 510: 1 (2022)

Ligymnopus
Ligymnopus clavicystidiata (J.S. Kim & Y.W. Lim) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571460)
Collybiopsis clavicystidiata J.S. Kim & Y.W. Lim, in Kim, Cho, Park, Park, Kim, Kim & Lim, MycoKeys 88: 91 (2022)
Ligymnopus moseri (Antonín & Noordel.) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571464)
Gymnopus moseri Antonín & Noordel., Libri Botanici 17: 50 (1997)
Ligymnopus pseudoluxurians (R.H. Petersen & K.W. Hughes) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571465)
Collybiopsis pseudoluxurians (R.H. Petersen & K.W. Hughes) R.H. Petersen, in Petersen & Hughes, Mycotaxon 136(2): 344 (2021)
Ligymnopus trogioides (A.W. Wilson, Desjardin & E. Horak) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571468)
Marasmiellus trogioides (A.W. Wilson, Desjardin & E. Horak) J.S. Oliveira, in Oliveira, Vargas-Isla, Cabral, Rodrigues & Ishikawa, Mycol. Progr. 18(5): 736 (2019)

Vestipedipilus
Vestipedipilus hasanskyensis (R.H. Petersen) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571469)
Collybiopsis hasanskyensis R.H. Petersen, in Petersen & Hughes, Mycotaxon 136(2): 309 (2021)
Vestipedipilus subumbilicata (J.S. Kim & Y.W. Lim) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571470)
Collybiopsis subumbilicata J.S. Kim & Y.W. Lim, in Kim, Cho, Park, Park, Kim, Kim & Lim, MycoKeys 88: 95 (2022)
Vestipedipilus undulatus (J.S. Kim & Y.W. Lim) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571471)

Collybiopsis undulata J.S. Kim & Y.W. Lim, in Kim, Cho, Park, Park, Kim, Kim & Lim, MycoKeys 88: 97 (2022)
Vestipedipilus alnicola (J.L. Mata & Halling) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571472)
Marasmiellus alnicola (J.L. Mata & Halling) J.S. Oliveira, in Oliveira, Vargas-Isla, Cabral, Rodrigues & Ishikawa, Mycol. Progr. 18(5): 734 (2019)
Vestipedipilus collybioides (Speg.) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571473)
Marasmiellus collybioides (Speg.) J.S. Oliveira, in Oliveira, Vargas-Isla, Cabral, Rodrigues & Ishikawa, Mycol. Progr. 18(5): 734 (2019)
Vestipedipilus cylindricus (J.L. Mata) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571474)
Gymnopus cylindricus (J.L. Mata) J.S. Oliveira, in Oliveira, Vargas-Isla, Cabral, Rodrigues & Ishikawa, Mycol. Progr. 18(5): 734 (2019)
Vestipedipilus diminutus (Berk. & Broome) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571475)
Collybiopsis diminuta (Berk. & Broome) R.H. Petersen, in Petersen & Hughes, Mycotaxon 136(2): 341 (2021)
Vestipedipilus disjunctus (R.H. Petersen & K.W. Hughes) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571476)
Collybiopsis disjuncta (R.H. Petersen & K.W. Hughes) R.H. Petersen & K.W. Hughes, in Petersen & Hughes, Mycotaxon 136(2): 341 (2021)
Vestipedipilus hirtelloides (Desjardin & B.A. Perry) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571477)
Gymnopus hirtelloides Desjardin & B.A. Perry, Mycosphere 8(9): 1361 (2017)
Vestipedipilus indoctus (Corner) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571478)
Collybiopsis indocta (Corner) R.H. Petersen, in Petersen & Hughes, Mycotaxon 136(2): 342 (2021)
Vestipedipilus menehune (Desjardin, Halling & Hemmes) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571479)
Collybiopsis menehune (Desjardin, Halling & Hemmes) R.H. Petersen, in Petersen & Hughes, Mycotaxon 136(2): 343 (2021)
Vestipedipilus mesoamericana (J.L. Mata) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571480)
Collybiopsis mesoamericana (J.L. Mata) R.H. Petersen, in Petersen & Hughes, Mycotaxon 136(2): 343 (2021)
Vestipedipilus neotropicus (Singer) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571481)
Marasmiellus neotropicus (Singer) J.S. Oliveira, in Oliveira, Vargas-Isla, Cabral, Rodrigues & Ishikawa, Mycol. Progr. 18(5): 735 (2019)
Vestipedipilus nonnullus (Corner) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571482)
Collybiopsis nonnulla (Corner) R.H. Petersen, in Petersen & Hughes, Mycotaxon 136(2): 343 (2021)
Vestipedipilus obscuroides (Antonín & Legon) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571483)
Collybiopsis obscuroides (Antonín & Legon) R.H. Petersen, in Petersen & Hughes, Mycotaxon 136(2): 343 (2021)
Vestipedipilus parvulus (J.L. Mata, R.H. Petersen & K.W. Hughes) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571484)
Collybiopsis parvula (J.L. Mata, R.H. Petersen & K.W. Hughes) R.H. Petersen, in Petersen & Hughes, Mycotaxon 136(2): 343 (2021)
Vestipedipilus readiae (G. Stev.) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571485)
Collybiopsis readiae (G. Stev.) R.H. Petersen, in Petersen & Hughes, Mycotaxon 136(2): 344 (2021)
Vestipedipilus rodhallii (Desjardin & B.A. Perry) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571486)
Collybiopsis rodhallii (Desjardin & B.A. Perry) Bartrop & Haelew., Index Fungorum 515: 1 (2022)
Vestipedipilus subcyathiformis (Murrill) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571487)
Collybiopsis subcyathiformis (Murrill) R.H. Petersen, in Petersen & Hughes, Mycotaxon 136(2): 344 (2021)

Vestipedipilus tamblinganensis (A.W. Wilson, Desjardin & E. Horak) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571488)
Gymnopus tamblinganensis A.W. Wilson, Desjardin & E. Horak, Sydowia 56(1): 193 (2004)
Vestipedipilus villosipes (Cleland) J.J. Hu, B. Zhang & Y. Li, comb. nov. (FN 571489)
Collybiopsis villosipes (Cleland) R.H. Petersen, in Petersen & Hughes, Mycotaxon 136(2): 345 (2021)

DISCUSSION

Gymnopus s.l. is one of the most confusing groups of macrofungi, with many of its species having significant ecological and economic values (Wilson & Desjardin 2005) establishing its accurate taxonomic boundaries has been pursued for an extensive time (Antonín et al. 1997, Mata et al. 2004, 2006, Wilson & Desjardin 2005, Oliveira et al. 2019). Although a large number of researches have focused on this group, the species diversity, phylogeny, and geographic distribution, etc., of its contained species still remain uncertain.

In the current study, we have observed collections or type materials and have combined them with a summary of the type species or reliable descriptions. Based on nine characteristics, viz., habitat, shape of basidiomata, smelly, and shape of pileipellis and cheilocystidia, etc. (Fig. 2), we have identified three distinct groups within the *Gymnopus*. And species of sect. *Vestipedes* are different from the type species of *Collybiopsis* – *Collybiopsis ramealis* (Bull.) Millsp. and its related species in the shape of basidiomata, especially the shape of cheilocystidia and present of pleurocystidia. Thus, in our conception, sect. *Vestipedes* is closely related to *Collybiopsis*, but does not nest with it.

Additionally, the phylogenetic analysis also reveals that species of *Gymnopus* were distributed among three distinct clades (Figs 2, 3), and sect. *Veastpedes* is also split into three independent clades. Furthermore, considering the relationships among *Omphalotaceae*, sect. *Levipedes* and sect. *Impudicae* were raised as separate genera, and sect. *Vestipedes* was redivided into three independent genera, *Neomarasmius*, *Ligymnopus*, and *Vestipedipilus*. Molecular dating analysis also supports to establish these genera. In addition, the boundaries of *Gymnopus* s.str. was restricted through our research. Furthermore, our phylogenetic analysis supports *Paramycetinis*, *Pseudomarasmius*, *Paragymnopus*, and *Psuillomyces* as separate genera. In some cases, we were faced with the choice to define genera in either a broader or narrower sense. Detailed descriptions of *Gymnopus* s.l. have also been provided in this study.

New conceptions of the *Gymnopus* s.l.

The discussion of *Gymnopus* s.str. is lasting for a long time, and the researchers provide their own opinions (Antonín et al. 1997, Mata et al. 2004, 2006, Oliveira et al. 2019). Conversely, in this study, the species belonging to *Gymnopus* were compared through nine characters, with particular focus on the following five characters, viz. Habitat, odour, texture (matte or smooth) of the stipe, shape of the pileipellis, and cheilocystidia (Fig. 2). Morphological studies show that the four sections differed in their reaction with Melinda's reagent, shape of basidiomata, odour, structure of pileipellis, and shape of cheilocystidia (Fig. 2). These differences go beyond the genus rank, suggesting that sect. *Levipedes* and sect. *Impudicae* should be treated as separate genera. And, meanwhile, *Gymnopus* also forms three independent clades, as indicated by our phylogenetic analysis. In addition, if sect. *Levipedes* and sect. *Impudicae* should continue to be treated as a member of *Gymnopus*. Similarly, species of *Pseudomarasmius* and *Rhodocollybia* should be treated within the same genus, as should *Paramycetinis* and *Mycetinis*. Moreover, molecular dating analysis shows that species of these three clades diverged in different periods. Thus, we proposed to raise the sect. *Levipedes* and sect. *Impudicae* to the genus rank, *Levipedipilus* and *Impudipilus*, leaving the sect. *Gymnopus* and sect. *Androsacei* in the genus *Gymnopus*. Mata et al. (2006) also note that these two sections may represent *Gymnopus* s.str. Furthermore, the infrageneric analysis is also performed.

Levipedipilus has historically been treated as a section of *Gymnopus* or *Collybia*. However, in this study, we separated sect. *Levipedes* from genus *Gymnopus*, due to its flattened, branched, or coralloid pileipellis (*Dryophila* structure), clavate to cylindrical cheilocystidia with an umbo, and forming finger-like to coralloid at the apex. Especially, the habitat, shape of cheilocystidia, and pileipellis separate sect. *Levipedies* from others (Fig. 2). According to the reaction with potassium hydroxide, colour of the stipe, and the shape of cheilocystidia, the genus *Levipedipilus* was divided into three sections. But there are some species, viz., *L. earleae*, *L. kauffmanii*, *L. indoctoides*, and *L. vitellinipes* were not belong to any section (Figs 2, 3). Additionally, these species have unique morphologies. *Levipedimyces earleae* differs by its absence or inconspicuous cheilocystidia and not diverticulate or coralloid pileipellis. The dense stipe vesture, inconspicuous cheilocystidia, and presence of caulocystidia allow *L. kauffmanii* separate from sect. *Levipedes*. The marasmioid appearance, cylindrical cheilocystidia, and the presence of pileocystidia reflect that *L. indoctoides* is far away from the other species of *Levipedipilus*. The gelatinous context, broadly clavate to subsphaeropedunculate cheilocystidia, and the absence of finger-like projections at the apex, as well as the presence of caulocystidia, indicate that *L. vitellinipes* is phylogenetically positioned at the outermost part of *Levipedipilus*.

Within this genus, species in the *L. dryophilus* complex are often confusing, and accurately recognizing them just relies on morphological characteristics is challenging. Mating studies, and combined with multigene phylogenetic analysis and morphological studies were used to distinguish these species from Europe and North America (Vilgalys & Miller Jr 1983, 1987a, b, Antonín et al. 2013). However, in China, these species are usually simply identified as *L. dryophilus*, without a detailed study.

Impudipilus was initially a subsection belonging to the sect. *Vestipedes* then it was raised to a section rank within *Gymnopus* (Antonín & Noordeloos 2010), consisting of species assigned to *Micromphale* Gray, *Marasmiellus* sect. *Gloeonemae* (Kühner) Antonín and Noordel., and *Marasmius* sect. *Gloeonemae* Kühner initially, and impressive due to its unique, foetid odour. But the conception held by Antonín & Noordeloos (2010) did not reflect all the morphological variability exhibited by members of sect. *Impudicae* (Coimbra et al. 2015), and some parts of it are filled with arguments. For example, *Impudipilus montagnei* was once treated as *Thelephoraceae* (Burt 1924) or *Podoscyphaceae* (Gibertoni et al. 2006). However, Moncalvo et al. (2002) and Mata et al. (2006) discussed the strong similarities between this species and gymnopoid fungi. However, no one had combined it into *Gymnopus* due to its atypically gymnopioid appearance. More recently, Redhead (2014) combined it into *Gymnopus*, and Coimbra et al. (2015) supported this conception.

Gymnopus foetidus (Sowerby) P.M. Kirk and *Gymnopus ceraceicola* J.A. Cooper & P. Leonard, *Gymnopus hakaroa* J.A. Cooper & P. Leonard, and *Gymnopus imbricatus* J.A. Cooper & P. Leonard, originally described from New Zeeland (Cooper & Leonard 2013), are unforgettable due to their marasmioid appearance, lack of cheilocystidia, and the gelatinous pileipellis, which distinguishes from all others in the group species. However, they perfectly fit in the conception of *Micromphale* according to Desjardin & Petersen (1989). Thus, we marked it as /*Micromphale* (Figs 2, 3), and look forward to a more intensive study. Moreover, in this section, some species do not record a significant foetid smell, including *I. atlanticus*, *I. barbipes*, and *I. salakensis*. Although we firmly believe it represents an independent genus, there still remain serious issues to solve.

Thus, we only left the sect. *Androsacei* and sect. *Gymnopus* remaining within the genus *Gymnopus* s.str., leading to a monophyletic genus, consistent with Mata et al. (2006). However, the relationships within the sect. *Gymnopus* and sect. *Androsacei* were still unclear. Section *Gymnopus* initially only contained the type species – *G. fusipes*, until Li et al. (2022a) added two more species to this section and emended its definition, thus leading a polyphyletic sect. *Gymnopus*. We cannot accept the conception of Li et al. (2022a) on sect. *Gymnopus*, and there exists a considerable difference between *G. fusipes* and these two species. We instead support Antonín & Noordeloos (2010) regarding sect. *Gymnopus*. Thus, a new section is proposed: sect. *Omphalinoides*.

In the current definition of sect. *Androsacei* renders it polyphyletic (Antonín et al. 2014, César et al. 2020, Li et al. 2022a, 2021b, Petersen & Hughes 2019). Moreover, some species do not fit the sectional circumscription well. *G. cremeostipitatus,* for instance, has a hairy and cream-colored stipe that with well-developed caulocystidia. Broom cells are considered to be significant characteristic features of sect. *Androsacei*. However, there are some species (viz. *Gymnopus irresolutus* Desjardin & B.A. Perry, *Gymnopus portoricensis* R.H. Petersen, *Gymnopus brunneiniger* César, Bandala & Montoya, and *Gymnopus pallipes* J.P. Li & Chun Y. Deng) lack broom cells in the pileipellis. Rhizmorphs are yet another major characteristic to distinguishes species from *Marasmius*, while *G. irresolutus, Gymnopus subsupinus* (Berk.) J.A. Cooper, *G. cremeostipitatus*, and *G. brunneiniger* without rhizomorphs. Thus, the broom cells in the pileipellis and the presence of rhizomorphs are not suitable for distinguishing sect. *Androsacei*. We summarized the characteristics of the species belonging to sect. *Androsacei* and re-checked the holotype of some species to determine whether dextrinoid hyphae in the pileipileis, pileus trama, stipitipillis, and stipe trama are the key characteristics in distinguishing sect. *Androsacei* species into four separate sections.

New conceptions of the limits between *Collybiopsis* s.l.

Collybiopsis, previously known as *Marasmiellus*, is also a genus that has been overlooked. However, the limits of *Collybiopsis* (*Marasmiellus*) s.str. is lasting for quite a while. In Singer's conception, "*Marasmiellus*" s.str. was composed of ten sections: sect. *Marasmiellus* Murrill, sect. *Dealbati* Sing., sect. *Rameales* Sing., sect. *Tricolores* Sing., sect. *Candidi* (Bat.) Sing., sect. *Stenophylloides* Sing., sect. *Nigripedes* Sing., sect. *Defibulati* Sing., sect. *Tetrachroi* Sing., and sect. *Distantifolii* Sing. Later, Wilson & Desjardin (2005) only consider *Collybia* sect. *Subfumosae*, *Collybia* sect. *Vestipedes*, sect. *Marasmiellus*, sect. *Dealbati*, and sect. *Tetrachroi* composed "*Marasmiellus*". However, Oliveira et al. (2019) hold a different opinion. They believed that species of sect. *Marasmiellus*, sect. *Dealbati*, sect. *Rameales*, sect. *Tricolores*, and sect. *Vestipedes* is the real "*Marasmiellus*" s.str. But Petersen & Hughes (2021) excluded species of sect. *Tricolores* in *Collybiopsis* s.str. In fact, Oliveira et al. (2019) and Petersen & Hughes (2021) all accept the sect. *Vestipedes* is a member of *Collybiopsis* (*Marasmiellus*) s.str. Then, it was also conferred as a multi-lineage genus (Hu et al. 2022b). Thus, it is clear that the limits of *Collybiopsis* s.str. is still needed for further clarification.

After that, based on morphological characteristics, we categorize them into four different types characterized by the following morphological features: (1) marasmioid basidiomata with a grooved pileus, distant lamellae, cylindrical or tapering down stipe that becomes increasingly paler downwards, irregular or regular to clavate cheilocystidia that are branched, lobed, finger-like, or coralloid at the apex, and the propensity to grow on rotten branches; (2) collybioid basidiomata with a smooth or striped pileus, cylindrical stipe that is flattened at the apex or base, cylindrical, clavate, or fusiform cheilocystidia, and the ability to grow on rotten wood, fallen branches, or on the ground; (3) collybiod basidiomata, with a striped, grooved, rugulose-striate pileus, a cylindrical stipe that is flattened at base, pruinose or tomentose, paler at the apex, white mycelioid at the base, cylindrical to clavate cheilocystidia being weakly coralloid, finger-like, or lobed at the apex, and the propensity to grow on fallen leaves; (4) collybioid basidiomata, with distant lamellae, tomentose or pruinose stipe, a pileipellis often having *Rameales*-like structure or *Dryophila*-like structure, wide clavate to clavate or irregular clavate, and coralloid or finger-like at the apex (Fig. 2). In summary, species of sect. *Vestipedes* are completely different from the *C. ramealis* and its allies, especially in terms of the shape of cheilocystidia and the presence of pleurocystidia.

Referring to the morphological results, a phylogenetic analysis is performed. The results implied that these species were clustered into four individual clades with robust support. Thus, three new genera, viz., *Neomarasmius*, *Ligymnopus*, and *Vestipedipileus*, were proposed, which contain the species prior to sect. *Vestipedes*. Since there were few collected specimens of this group, we have not performed a thorough study of the subsections within these genera.

Meanwhile, there are some differences in our phylogenetic analysis. Hughes & Petersen (2015) studied the differences between *V. confluens* populations in Europe and North America, and found that the North American and European populations were distinct at the species level. The North American populations were thus described as *Gymnopus confluens* subsp. *campanulatus* Petersen. However, according to our phylogenetic analysis, the sequences from these two regions were separate. In addition, we compared our collected *V. confluens* with Hughes & Petersen's study finding out that our collections are more closely related to the European materials, based on both their morphology and related molecular characteristics.

Muti-evidence applied in modern systematic analysis helps to better understand the affinities

Before the 1990s, research only relied on morphological studies, thus causing confusion regarding some groups. After applying phylogenetic analysis, the definition and boundaries of *Gymnopus* s.l. are becoming increasingly more and more precise. In this study, 509 sequences from 316 specimens were used in the phylogenetic analysis, including 159 sequences from type specimens. There were 120 sequences newly obtained and uploaded to GenBank, including 60 ITS sequences and 60 nLSU sequences. The reliability of these sequences was referenced by the existing literature and practical application. Consequently, these findings can now serve as a reference for future phylogenetic analyses of *Gymnopus* s.l.

Divergence times and historical biogeography were used as additional criteria for evaluating difficult-to-delimit genera. The results of the current study indicate that all the genera belonging to *Omphalotaceae* diverged during 165.18–39.91 Mya. *Gymnopus* s.l. diverged at 99.87 Mya, while *Collybiopsis* s.l. that diverged at 105.76 Mya, diverged earlier than *Gymnopus* s.l. Divergence times also helped to delimit certain genera in *Collybiopsis* s.l. and *Gymnopus* s.l. The molecular dating analysis also confirmed several genera that were delimited in previous studies. For example, two related genera, *Mycetinis* and *Paramycetinis*, were classified as *Mycetinis*, while the molecular dating analysis supports that they should be considered separate genera. In the future, molecular dating analysis could be applied to help clarify problematic genera or species.

The limitation in the taxonomic studies of *Gymnopus* s.l.

Based on the findings of the current study, we have evidence to suggest an increase in species diversity in *Gymnopus* s.l. than previously assumed. However, there is still extensive work to do. In this study, we only confirmed species with sequences, and all future analyses can rely on these sequences. Species without known sequences were not included in our study, and all of these will need to be rechecked to determine their appropriate taxonomic status, which is currently pending modification. Secondly, there are numerous sequences uploaded to GenBank with incorrect identification, consequently leading to misunderstandings in species identification when BLASTn is being used. Thus, a combination of morphological and molecular studies is required. Last but not least, a deep study of *Gymnopus* s.l. is still required, as the taxonomic system proposed by us is not the most accurate, and there are still some species that do not belong to any sections.

ACKNOWLEDGEMENT

The authors would like to give great thanks to Prof. Zhu-Liang Yang (Kunming Institute of Botany, Chinese Academy of Sciences), Wen-Fei Lin (Zhejiang University), Tie-Zheng Wei (Institute of Microbiology, Chinese Academy of Sciences), Chang-Lin Zhao (Southwest Forestry University), Drs. Chun-Ying Deng (Institute of Biology, Guizhou Academy of Sciences, China), Tao Deng (Kunming Institute of Botany, Chinese Academy of Sciences), Xue-Dan Xie (Kunming Institute of Botany, Chinese Academy of Sciences), Tian-Tian Han (Chinese Academy of Sciences), Mr. Jin Wang (Institute of Biology, Guizhou Academy of Sciences, China), Miss Min-Jun Zhao (Institute of Microbiology, Chinese Academy of Sciences) for the help during specimens' collections and renting.

This study is funded by Diversity and conservation of characteristic macrofungi resources in different vegetation zones in Changbai Mountain of China (20230202119NC), Youth Doctoral

Program of Zhejiang Normal University - Study on species diversity of macrofungi in Baishanzu National Park (2023QB043), Zhejiang Normal University Doctoral Initiation Fund, the Natural Science Foundation of China (Nos. 31970020), Investigation of macrofungal Resources in Tongjiang County, China, Investigation of macrofungal resources in Anhui Province, China (jwg202307), Construction of edible mushroom resource bank and Fungal Resource Conservation System, Accurate identification and evaluation of agro-microbiological resources (2023YFD1201601), and Gansu Provincial key research and development program (23YFNG0004).

REFERENCES

Antonín V. 1987 – *Setulipes*, a new genus of marasmioid fungi (*Tricholomatales*). Ceska Mykologie 41, 85–87.

Antonín V, Halling R, Noordeloos M. 1997 – Generic concepts within the groups of *Marasmius* and *Collybia* sensu lato. Mycotaxon 63, 359–368.

Antonín V, Herink J. 1999 – Notes on the variability of *Gymnopus luxurians* (*Tricholomataceae*). Czech Mycology 52(1), 41–49.

Antonín V, Noordeloos ME. 1993 – A monograph of *Marasmius*, *Collybia* and related genera in Europe. Part 1: *Marasmius*, *Setulipes*, and *Marasmiellus*. Libri Botanici 8, 1–229.

Antonín V, Noordeloos ME. 1997 – A monograph of *Marasmius*, *Collybia* and related genera in Europe. Part 2: *Collybia*, *Gymnopus*, *Rhodocollybia*, *Crinipellis*, *Chaetocalathus*, and additions to *Marasmiellus*. Libri Botanici 17, 1–256.

Antonín V, Noordeloos ME. 2010 – A monograph of marasmioid and collybioid fungi in Europe. Eching, Germany: IHW Verl.

Antonín V, Ryoo R, Ka KH. 2014 – Marasmioid and gymnopoid fungi of the Republic of Korea. 7. *Gymnopus* sect. *Androsacei*. Mycological progress 13(3), 703–718.

Antonín V, Sedlák P, Tomšovský M. 2013 – Taxonomy and phylogeny of European *Gymnopus* subsection *levipedes* (*Basidiomycota*, *Omphalotaceae*). Persoonia 31, 179–187.

Burt EA. 1924 – The *Thelephoraceae* of North America. XIII. *Cladoderris*, *Hypolyssus*, *Cymatella*, *Skepperia*, *Cytidia*, *Solenia*, *Matruchotia*, *Microstroma*, *Protocoronospora*, and *Asterostroma*. Annals of the Missouri Botanical Garden 11(1), 1–36.

César E, Bandala VM, Montoya L, Ramos A. 2018 – A new *Gymnopus* species with rhizomorphs and its record as nesting material by birds (*Tyrannideae*) in the subtropical cloud forest from eastern Mexico. MycoKeys (42), 21–34.

César E, Montoya L, Bandala VM, Ramos A. 2020 – Three new marasmioid-gymnopoid rhizomorph-forming species from Mexican mountain cloud forest relicts. Mycological progress 19(10), 1017–1029.

Coimbra VR, Pinheiro FG, Wartchow F, Gibertoni TB. 2015 – Studies on *Gymnopus* sect. *Impudicae* (*Omphalotaceae*, *Agaricales*) from Northern Brazil: two new species and notes on *G. montagnei*. Mycological progress 14(11), 1–9.

Cooper J, Leonard P. 2013 – Three new species of foetid *Gymnopus* in New Zealand. MycoKeys 7, 31–44.

Cubeta M, Echandi E, Abernethy T, Vilgalys R. 1991 – Characterization of anastomosis groups of binucleate Rhizoctonia species using restriction analysis of an amplified ribosomal RNA gene. Phytopathology 81(11), 1395–1400.

Deng SF. 2016 – Taxonomy of *Gymnopus* and preliminary study of *Marasmiaceae* resource in South China. South China Agricultural University, Guangdong Province, China.

Deng SF, Li TH, Jiang ZD, Song B. 2016 – *Gymnopus ramulicola* sp. nov., a pinkish species from southern China. Mycotaxon 131(3), 663–670.

Desjardin D, Perry B. 2017 – The gymnopoid fungi (*Basidiomycota*, *Agaricales*) from the Republic of São Tomé and Príncipe, West Africa. Mycosphere 8(9), 1317–1391.

Desjardin DE, Halling RE, Hemmes DE. 1999 – *Agaricales* of the Hawaiian Islands. 5. The genera

Rhodocollybia and *Gymnopus*. Mycologia 91(1), 166–176.
Desjardin DE, Petersen RH. 1989 – Studies on *Marasmius* from eastern North America. III. *Marasmius brevipes* and *Micromphale* sect. *Rhizomorphigena*. Mycologia 81(1), 76–84.
Drummond AJ, Rambaut A. 2007 – BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7(1), 564–591.
Edler D, Klein J, Antonelli A, Silvestro D. 2021 – RaxmlGUI 2.0: a graphical interface and toolkit for phylogenetic analyses using RAxML. Methods in Ecology and Evolution 12(2), 373–377.
Farris JS, Kallersjo M, Kluge AG, Bult C. 1994 – Testing significance of incongruence. Cladistics 10, 315–319.
Feng B. 2012 – Molecular Phylogeny and Biogeography of *Boletus* L. s.s. and *Hydnum* L. (PhD). Chinese Academy of Sciences, Beijing, China.
Fries E. 1821 – Systema mycologicum: sistens fungorum ordines, genera et species, huc usque cognitas (Vol. 1). Lund, Berling: Ex officina Berlingiana.
Fries E. 1838 – Epicrisis systematis mycologici, seu synopsis Hymenomycetum: Upsaliae, e Typographia Academica.
Gardes M, Bruns TD. 1993 – ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. Molecular ecology 2(2), 113–118.
Gibertoni T, Baptista Ryvarden L, Queiroz Cavalcanti M. 2006 – Steroid Fungi (*Basidiomycota*) of the atlantic rain forest in Northeast Brasil. Nova Hedwigia 82, 105–113.
Hall T. 1999 – BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp. Ser. 41, 95–98.
Halling RE. 1983 – The genus *Collybia* (*Agaricales*) in the northeastern United States and adjacent Canada. Mycologia 8, 1–148.
He MQ, Zhao RL, Hyde KD, Begerow D et al. 2019 – Notes, outline and divergence times of Basidiomycota. Fungal Diversity 99(1), 105–367.
He ZM, Chen ZH, Bau T, Wang GS, Yang ZL. 2023 – Systematic arrangement within the family *Clitocybaceae* (*Tricholomatineae*, *Agaricales*): phylogenetic and phylogenomic evidence, morphological data and muscarine-producing innovation. Fungal Diversity 123, 1–47.
Hu JJ, Li Y, Li X, Frederick SL et al. 2021a – New findings of *Neonothopanus* (*Marasmiaceae*, *Basidiomycota*) from Ghana. Phytotaxa 512(1), 57–67.
Hu JJ, Song LR, Tuo YL, Zhao GP et al. 2022a – Multiple evidences reveal new species and a new record of smelly *Gymnopus* (*Agaricales*, *Omphalotaceae*) from China. Frontiers in Microbiology 13, 968617.
Hu JJ, Zhao GP, Tuo YL, Dai D et al. 2021b – Morphology and molecular study of three new Cordycipitoid fungi and its related species collected from Jilin Province, northeast China. MycoKeys 83, 161–180.
Hu JJ, Zhao GP, Tuo YL, Rao G et al. 2022b – Morphological and Molecular Evidence Reveal Eight New Species of *Gymnopus* from Northeast China. Journal of Fungi 8(4), 349.
Hughes K, Petersen RH. 2015 – Transatlantic disjunction in fleshy fungi III: *Gymnopus confluens*. MycoKeys 9(1), 37–63.
Jang S, Jang Y, Lim YW, Kim C et al. 2016 – Phylogenetic identification of Korean *Gymnopus* spp. and the first report of 3 species: *G. iocephalus*, *G. polygrammus*, and *G. subnudus*. Mycobiology 44(3), 131–136.
Kalyaanamoorthy S, Minh BQ, Wong TK, Von Haeseler A et al. 2017 – ModelFinder: fast model selection for accurate phylogenetic estimates. Nature Methods 14(6), 587–589.
Katoh K, Standley DM. 2013 – MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular biology and evolution 30(4), 772–780.
Konrad P, Maublanc A. 1935 – Icones selectae fungorum (Vol. 5). Paris, Franch: Paul Lechevalier.
Kühner R, Romagnesi H. 1953 – Flore analytique des champignons supérieurs (agarics, bolets, chanterelles): comprenant les espèces de l'Europe occidentale et centrale ainsi que la plupart de celles de l'Algérie et du Maroc. Paris, Franch: Masson.
Lennox J. 1979 – Collybioid genera in the Pacific Northwest. Mycotaxon 9, 117–231.

Li JP, Antonín V, Gates G, Jiang L et al. 2022a – Emending *Gymnopus* sect. *Gymnopus* (*Agaricales*, *Omphalotaceae*) by including two new species from southern China. MycoKeys 87, 183–204.
Li JP, Li Y, Li TH, Antonin V et al. 2021a – A preliminary report of *Gymnopus* sect. *Impudicae* (*Omphalotaceae*) from China. Phytotaxa 497(3), 263–276.
Li JP, Pan MC, Li Y, Deng CY et al. 2022b – Morpho-Molecular Evidence Reveals Four Novel Species of *Gymnopus* (*Agaricales*, *Omphalotaceae*) from China. Journal of Fungi 8(4), 398.
Li JP, Song B, Feng Z, Wang J et al. 2021b – A new species of *Gymnopus* sect. *Androsacei* (*Omphalotaceae*, *Agaricales*) from China. Phytotaxa 521(1), 1–14.
Liu B, Rong FX, Jing HS, Cao JZ. 1984 – Three New Species of *Holobasidiomycetes* from China. Journal of shanxi university 4, 48–52.
Mata JL, Hughes KW, Petersen RH. 2004 – Phylogenetic placement of *Marasmiellus juniperinus*. Mycoscience 45(3), 214–221.
Mata JL, Hughes KW, Petersen RH. 2006 – An investigation of /*Omphalotaceae* (Fungi: Euagarics) with emphasis on the genus *Gymnopus*. Sydowia 58(2), 191–289.
Mata JL, Petersen R. 2003 – Type studies of neotropical *Collybia* species. Mycotaxon 86, 303–316.
Mešić A, Tkalčec Z, Deng CY, Li TH et al. 2011 – *Gymnopus fuscotramus* (*Agaricales*), a new species from southern China. Phytotaxa 117, 321–330.
Moncalvo JM, Vilgalys R, Redhead SA, Johnson JE et al. 2002 – One hundred and seventeen clades of euagarics. Molecular phylogenetics and evolution 23(3), 357–400.
Murrill WA. 1916 – *Agaricales*, *Polyporaceae-Agaricaceae*. North American Flora 9, 297–542.
Noordeloos ME, Antonín V. 2008 – Contribution to a monograph of marasmioid and collybioid fungi in Europe. Czech Mycology 60(1), 21–27.
Nylander J. 2004 – MrModeltest (Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden). In: Version.
Oliveira JJ, Vargas-Isla R, Cabral TS, Rodrigues DP et al. 2019 – Progress on the phylogeny of the *Omphalotaceae*: *Gymnopus* s. str., *Marasmiellus* s. str., *Paragymnopus* gen. nov. and *Pusillomyces* gen. nov. Mycological progress 18(5), 713–739.
Patouillard N. 1900 – Essai taxonomique sur les familles et les genres des Hyménomycètes. Lons-Le-Saunier, France: Lucien Declume.
Persoon CH. 1801 – Synopsis methodica fungorum 1. Göttingen, Germany: Apud Henricum Dieterich.
Petersen R, Hughes K. 2014 – New North American species of *Gymnopus*. North American Fungi 9, 1–22.
Petersen R, Hughes K, Voitk A. 2014 – *Gymnopus eneficola*-species nova from Newfoundland. Omphalina 5, 5–12.
Petersen RH, Hughes KW. 2016 – *Micromphale* sect. *Perforantia* (*Agaricales*, *Basidiomycetes*); expansion and phylogenetic placement. MycoKeys 18, 1–122.
Petersen RH, Hughes KW. 2019 – Two additional species of *Gymnopus* (Euagarics, *Basidiomycotina*). MycoKeys 45(45), 1–24.
Petersen RH, Hughes KW. 2020 – Two new genera of gymnopoid/marasmioid euagarics. Mycotaxon 135(1), 1–95.
Petersen RH, Hughes KW. 2021 – *Collybiopsis* and its type species, *Co. ramealis*. Mycotaxon 136(2), 263–349.
Rambaut A. 2012 – FigTree v1.4.0. Available at http://tree.bio.ed.ac.uk/software/figtree
Rambaut A, Drummond AJ, Xie D, Baele G et al. 2018 – Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67(5), 901–904.
Redhead S. 2014 – Nomenclatural novelties *Gymnopus montagnei* comb. nov., *Hypholoma australianum* nom. nov., *Pholiota nubigena*, *Protostropharia luteonitens* comb. nov. Index Fungorum 148, 1.
Ronquist F, Huelsenbeck JP. 2003 – MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19(12), 1572–1574.
Royal Botanic Garden E. 1969 – Flora of British fungi: colour identification chart. Edinburgh, UK:

HM Stationery Office.
Ryoo R, Antonín V, Ka KH. 2020 – Marasmioid and Gymnopoid Fungi of the Republic of Korea. 8. *Gymnopus* Section *Levipedes*. Mycobiology 48(4), 252–262.
Ryoo R, Antonín V, KA KH, Tomšovský M. 2016 – Marasmioid and gymnopoid fungi of the Republic of Korea. 8. *Gymnopus* section *Impudicae*. Phytotaxa 286(2), 75–88.
Singer R. 1936 – The *Agaricales* in modern taxonomy. Germany: Koeltz Scientific Books.
Singer R. 1962 – The *Agaricales* in modern taxonomy 2ED. Germany: J. Cramer.
Singer R. 1975 – The *Agaricales* in modern Taxonomy 3ED. Germany: J. Cramer.
Singer R. 1986 – The *Agaricales* in modern taxonomy 4ED. Germany: Koeltz Botanical Books.
Song J, Cui BK. 2017 – Phylogeny, divergence time and historical biogeography of *Laetiporus* (*Basidiomycota*, *Polyporales*). BMC Evolutionary Biology 17(1), 102.
Staude F. 1857 – Die Schwämme Mitteldeutschlands, insbesondere des Herzogtums Coburg (Vol. 1). Coburg, Germany: Dietz.
Swofford DL. 2002 – PAUP*: Phylogenetic Analysis Using Parsimony (and other methods) 4.0 b10. Sinauer Associates, Sunderland.
Taylor T, Hass H, Kerp H. 1999 – The oldest fossil *Ascomycetes*. Nature 399(6737), 648–648.
Taylor TN, Hass H, Kerp H, Krings M et al. 2005 – *Perithecial ascomycetes* from the 400 million-year-old Rhynie chert: an example of ancestral polymorphism. Mycologia 97(1), 269–285.
Thonpson J. 1997 – The CLUSTAL X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic acids research 24, 4876–4882.
Vilgalys R, Hester M. 1990 – Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. Journal of Bacteriology 172(8), 4238–4246.
Vilgalys R, Miller Jr O. 1987a – Mating relationships within the *Collybia dryophila* group in Europe. Transactions of the British Mycological Society 89(3), 295–300.
Vilgalys R, Miller Jr O. 1987b – Morphological studies on the *Collybia dryophila* group in Europe. Transactions of the British Mycological Society 88(4), 461–472.
Vilgalys R, Miller Jr OK. 1983 – Biological species in the *Collybia dryophila* group in North America. Mycologia 75(4), 707–722.
Villarreal M, Heykoop M, Esteve-Raventós F. 2002 – *Gymnopus castaneus*, a new Mediterranean species from Spain. Persoonia 17(4), 661–664.
Vizzini A, Antonin V, Sesli E, Contu M. 2015 – *Gymnopus trabzonensis* sp. nov. *Omphalotaceae* and *Tricholoma virgatum* var. *fulvoumbonatum* var. nov. *Tricholomataceae*, two new white-spored agarics from Turkey. Phytotax 226(2), 119–130.
Vizzini A, Consiglio G, Antonin V, Contu M. 2008 – A new species within the *Gymnopus dryophilus* complex (*Agaricomycetes*, *Basidiomycota*) from Italy. Mycotaxon 105, 43–52.
Wilson A, Desjardin D. 2005 – Phylogenetic relationships in the gymnopoid and marasmioid fungi (*Basidiomycetes*, euagarics clade). Mycologia 97(3), 667–679.
Wilson AW, Desjardin DE, Horak E. 2004 – *Agaricales* of Indonesia. 5. The genus *Gymnopus* from Java and Bali. Sydowia 56 (1), 137–210.
Yu Y, Harris AJ, Blair C, He X. 2015 – RASP (Reconstruct Ancestral State in Phylogenies): a tool for historical biogeography. Molecular phylogenetics and evolution 87, 46–49.
Zhang D, Gao F, Jakovlić I, Zou H et al. 2020 – PhyloSuite: an integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. Molecular Ecology Resources 20(1), 348–355.