

ARTICLE

The revision of the taxonomic system of *Lycoperdaceae*

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Abstract

The members of *Lycoperdaceae*, commonly known as puffballs, are widely distributed as saprotrophic fungi. The current taxonomic system of this family has been extensively debated, primarily due to conflicts between morphological based system and the phylogenetics one. In this study, we reconstructed a comprehensive phylogeny of *Lycoperdaceae*, represented by 96 species across 19 genera, using multiple gene sequences; internal transcribed spacer (ITS), large ribosomal subunit (nrLSU), the second largest RNA polymerase subunit (*rpb2*), and translation elongation factor 1- α (*tef1- α*). Additionally, we estimated the divergence times for each taxon, considering it as an additional criterion for taxonomic ranking. Based on updated phylogenetic results and examination of morphological characters, *Lycoperdaceae* is divided into a total of 19 genera, with a divergence time range of 26.7–75.5 Ma. This includes the identification of five new genera: *Fuscospina*, *Leptocaulis*, *Lycoperdiscus*, *Pseudoperdon*, and *Sinoperdon*. Four previously known *Lycoperdon* s.l. subgenera (*Bovistella*, *Morganella*, *Utraria* and *Vascellum*) and *Bovista* subg. *Globaria* were elevated to the generic level. Moreover, we proposed and described 22 new species and 25 new combinations from the genera *Bovista*, *Calvatia*, *Globaria* and *Lycoperdon* s.l. Simultaneously, morphological examination revealed key features, such as capillitium types and paracapillitium, which could potentially be informative to delineate species at the generic level. This study enhances the understanding of the phylogeny and evolution of *Lycoperdaceae*, bridging diversity gaps within Asia and contributing to the global species diversity of *Lycoperdaceae*.

Keywords – Divergence times – *Lycoperdon* – Phylogenetics – Puffball – Taxonomy

INTRODUCTION

Fungi belonging to *Lycoperdaceae* F. Berchtold & J. Presl are commonly known as puffballs. They feature globose to subglobose basidiomes and mature gleba, releasing a powdery mass of spores passively through the apical opening of the endoperidium. These species are widely distributed in temperate, arid, and tropical climates, found on the forest floor, rotting wood, or open meadows (Pegler et al. 1995). Some species within this family have culinary and medicinal value. For instance, *Calvatia craniiformis* (Schwein.) Fr. ex De Toni and *C. cyathiformis* (Bosc) Morgan are used as food in the UK, while *C. gigantea* (Batsch) Lloyd, *C. lilacina* (Mont. & Berk.) Henn are used in traditional medicine for their hemostatic properties and to treat various ailments (Van Wyk & Coetzee 2009). Terrestrial saprophytic species, like *Lycoperdon perlatum* Pers.; and *Bovistella utriformis* (Bull.) Demoulin & Rebriev, contribute to organic matter decomposition and heavy metal enrichment

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(Petkovšek & Pokorny 2013).

Lycoperdaceae, established by F. Berchtold and J. Presl in 1820, originally encompassed 18 genera and around 150 species. Initially this family was considered synonymous with *Agaricaceae* (Kirk et al. 2008), molecular phylogenetic analyses later revealed *Lycoperdaceae* to be a monophyletic gasteroid lineage distinct from *Agaricaceae* (Hibbett et al. 1997, Krüger et al. 2001, Moncalvo et al. 2002, Vellinga 2004). Subsequent studies identified four main subclades within *Lycoperdaceae*, representing the genera *Bovista*, *Calvatia*, *Disciseda*, and *Lycoperdon sensu lato* (Larsson & Jeppson 2008). Notably, some rare taxa including *Holocotylon*, *Abstoma*, and *Bryoperdon* were not included in these analyses. In the recent taxonomic system of Basidiomycota, *Lycoperdaceae* is treated as a distinct family comprising the genera *Apioperdon* (Kreisel & D. Krüger) Vizzini, *Bovista* Pers., *Bryoperdon* Vizzini, *Calvatia* Fr., *Calbovista* Morse ex M.T. Seidl., *Gastropila* Homrich & J.E. Wright, *Lycoperdon* Pers., *Morganella* Zeller (He et al. 2019). However, certain puffball-like genera such as *Abstoma* G. Cunn., *Acutocapillitium* P. Ponce de Leo'n., *Arachnion* Schwein., *Calvatiopsis* Hollo's, *Disciseda* Czern., *Glyptoderma* R. Heim & Perr. – Bertr., *Japonogaster* Kobayasi, and *Lycoperdopsis* Henn. were still accommodated within *Agaricaceae* (He et al. 2019). Conversely, a recent compendium of generic names for agarics and Agaricales proposed the concept of *Agaricaceae* s.l., which includes five families: *Lycoperdaceae*, *Agaricaceae* s.str., *Coprinaceae*, "*Lepiotaceae*" (temporarily due to nom. invalid.), and *Tulostomataceae* (Kalichman et al. 2020). While historically treated as synonymous with *Agaricaceae* (Kirk et al. 2008), *Lycoperdaceae* has more recently been acknowledged as an independent family (He et al. 2019, Kalichman et al. 2020).

Historically, the genera of *Lycoperdaceae* were classified by morphological characters such as: the presence of capillitium or paracapillitium, the type of capillitium (*Lycoperdon*-type, *Bovista*-type, *Calvatia*-type, intermediate *Bovista-Lycoperdon* type, and *Mycenastrum*-type), the apical opening type of endoperidium and the presence or absence of the pseudostipe (Kreisel 1969, Kreisel 1993, Pegler et al. 1995, Sarasini 2005, Larsson & Jeppson 2008). Although some morphological characters, such as the presence of *Calvatia*-type capillitium in *Calvatia*, appear to be phylogenetically significant in generic segregation (Rebriev 2013), *Mycenastrum*-type in *Mycenastrum* (Gurgel et al. 2017), while in genera more than one, distinctive features can be observed, such as in *Bovista* species where two types of capillitiums are present: the *Lycoperdon*-type and the *Bovista*-type (Bautista-Hernández et al. 2012, Rebriev et al. 2020, Krakhmalnyi et al. 2023). In addition, *Vascellum* F. Šmarda and *Morganella* Zeller are morphologically distinct, however, they are both currently assigned to *Lycoperdon* s.l. (Larsson & Jeppson 2008). Therefore, an updated DNA based phylogeny coupled with a re-examination of morphological characters is needed to reassess the current classification scheme of these genera.

The species richest genus within *Lycoperdaceae* is the type genus *Lycoperdon* Pers. Molecular phylogenetics conducted by Larsson & Jeppson (2008) has recommended a wide sense concept of *Lycoperdon*, which incorporates some traditional genera such as *Bovistella*, *Morganella*, and *Vascellum*, to date, *Lycoperdon*, as circumscribed in the current classification, was divided into five subgenera, and they were subgs. *Bovistella*, *Lycoperdon*, *Morganella*, *Utraria* and *Vascellum*. However, some recent studies showed the taxonomic arrangement of those five subgenera did not fit well with some taxa. For example, *L. caudatum* and *L. nigrescens* were temporarily treated in the subg. *Utraria* with its phylogenetic position was out of this subgenus (Bates et al. 2009, Gube & Piepenbring 2009, Jeppson & Larsson 2010, Alfredo et al. 2017). In addition, Vizzini & Ercole (2017) had raised *Lycoperdon* subg. *Apioperdon* into generic level with the type species of *Apioperdon pyriforme* (Schaeff.) Vizzini (= *Lycoperdon pyriforme* Schaeff.). However, some scholars disagree with these findings due to the relatively small number of samples involved (Alfredo et al. 2017). Therefore, a comprehensive reevaluation of *Lycoperdon* based on extensive research is necessary.

The delineation of genera within the *Lycoperdaceae*, as well as the familial placement within the order, has undergone significant changes through the integration of morphological characteristics. (Kreisel 1969, Hibbett et al. 1997, Krüger et al. 2001, Moncalvo et al. 2002, Krüger & Kreisel 2003,

Bates 2004, Vizzini & Ercole 2017, Krakhmalnyi et al. 2023). With the contributions of numerous prominent mycologists, the taxonomic system of *Lycoperdaceae* is converging toward a comprehensive understanding of its natural divergence history. The first molecular phylogenetic analysis of *Lycoperdaceae*, utilizing ITS and nrLSU sequences, was conducted in 2008 (Larsson & Jeppson 2008). The family *Lycoperdaceae* includes genera like *Lycoperdon*, *Bovista*, *Calvatia*, and *Disciseda* (Krüger et al. 2001, Krüger & Kreisel 2003, Larsson & Jeppson 2008, Bates et al. 2009, Larsson et al. 2009, Jeppson & Larsson 2010, Alfredo et al. 2017). The largest genus, *Lycoperdon*, is divided into subgenera *Bovistella*, *Morganella*, and *Vascellum*, despite distinguished morphological differences (Larsson & Jeppson 2008, Bates et al. 2009, Alfredo et al. 2017, Krakhmalnyi et al. 2023). *Bovista* is subdivided into two subgenera, *Bovista* and *Globaria*, while *Calvatia* is classified into two subgenera, *Langermannia* and *Calvatia* (Larsson & Jeppson 2008, Rebriev et al. 2020, Krakhmalnyi et al. 2023). However, this taxonomic system heavily relies on specimens from Europe and America, with scarce representation from Asia, especially China. Additionally, some genera, such as *Abstoma* G. Cunn. and *Arachnion* Schwein, have not been subjected to molecular phylogenetic studies, necessitating clarification of their taxonomic status.

In this study, an extensive collection of specimens, particularly from China, was utilized. The taxonomic framework of *Lycoperdaceae*, with a particular focus on intricate genera such as *Lycoperdon*, *Bovista*, *Globaria*, and *Calvatia*, was revised based on molecular phylogeny employing multiple gene sequences (ITS, nrLSU, *rpb2*, and *tef1- α*). The assessment of taxa above the species level was conducted through the phylogenetic analyses, morphological characteristics, and supplemented with divergence time estimates (Zhao et al. 2017, He et al. 2019).

MATERIALS AND METHODS

Morphological study

Specimens were collected from 13 provinces at 21 sites in the field. Upon on-site photography, aluminum foil was utilized to wrap specimens, preventing mixing or crushing. Macro-morphological features and chemical reactions of fresh specimens were promptly documented upon return. Subsequently, the specimens were thoroughly dried with a food drier at 50 °C, sealed in plastic bags, and deposited in the Herbarium Mycologicum Academiae Sinicae, Beijing, China (HMAS).

Anatomical and cytological features including basidiospores, basidia, capillitium, eucapillitial threads and paracapillitial threads, exoperidium and endoperidium elements were observed. Dried specimens were examined following the protocols of Largent et al (1986). Additionally, basidiospore ornamentations and other microstructures were observed using a JEM-1400 scanning electron microscope (SEM), following previous studies (Hosen et al. 2017, Xu et al. 2019, Wang et al. 2024). Staining reactions were performed using 95% ethanol, 5% KOH, and 10 mg/mL Congo Red. More than twenty measurements of microscopic features (basidiospores) were recorded, including $\bar{x}$ (the mean length by width $\pm$ SD), Q (the quotient of basidiospore length to width), and Q_m (the mean of Q -values $\pm$ SD) (Largent et al. 1986).

DNA extraction PCR amplification and sequencing

DNA extraction from dried specimens was performed using a Broad-spectrum plant Rapid Genomic DNA Kit (Biomed) following the manufacturer's protocol. For the internal transcribed spacer (ITS), primers ITS4 and ITS5 were employed, while primers LROR and LR5 were used for the large ribosomal subunit (nrLSU). The *rpb2* gene was amplified and sequenced using primers brpb2-6F/brpb2-7.1R (Matheny 2005), and the *tef1- α* gene was targeted with primers EF1-983F/EF1-1567R (Renner 2005).

PCR cycling conditions included an initial denaturation for 5 minutes at 94 °C, followed by 35 cycles of denaturation at 94 °C for 50 seconds, annealing at 50 °C (LSU, *tef1- α*), 52 °C (ITS), or 55 °C (*rpb2*) for 50 seconds, and extension at 72 °C for 1 minute (He et al. 2019, Li et al. 2021, Ling et al. 2021). The PCR products were sent to a Biomed Biotechnology commercial company for purification and sequencing. The contiguous sequences were assembled using SeqMan, implemented

in Lasergene v7.1 (DNASTAR Inc., USA). All available sequences of *Lycoperdaceae* in this research are provided in Tables 1–6.

Phylogenetic analyses

In this section, a four-gene combined dataset (ITS–nrLSU–*rpb2*–*tef1- α* dataset) was created. Raw sequences were individually aligned using MAFFT V7.310 (Kato & Standley 2013), manually adjusted in BioEdit (Hall 1999), and then concatenated using SequenceMatrix v1.7.8 (Vaidya et al. 2011). Missing data and ambiguous regions were coded as “N.” Additionally, introns of *rpb2* and *tef1-a* were excluded. MrModeltest v2.3 (Nylander et al. 2004) was employed to select the best-fitted substitution model based on the Akaike Information Criterion (AIC). Consequently, GTR+I+G was chosen as the best model for ITS and nrLSU, TVM+I+G for *rpb2*, and SYM+I+G for *tef1- α* .

Both Maximum Likelihood (ML) and Bayesian Inference (BI) methods were executed. Firstly, the ML tree was constructed using RAxML v7.2.6 with the GTR+G+I model of site substitution, which includes the estimation of Gamma-distributed rate heterogeneity and a proportion of invariant sites (Stamatakis 2006). Statistical supports were obtained through nonparametric bootstrapping with 1000 replicates. Secondly, BI analyses were performed with MrBayes 3.2.2 (Ronquist & Huelsenbeck 2003), utilizing a general time reversible (GTR) model of DNA substitution and a gamma distribution rate variation across sites (Ronquist & Huelsenbeck 2003). Four chains were processed with the generation set at 10 million for each gene. Trees were sampled every 100 generations, and chain convergence was assessed using Tracer v1.7.1 (Rambaut et al. 2018) (<http://tree.bio.ed.ac.uk/software/tracer/>) to ensure sufficiently large Effective Sample Size (ESS) values. The stop rule was applied when parallel MCMC runs converged (ESS value > 200). Finally, 15 million generations were considered for convergence. The first 25% of the sampled trees were discarded as burn-in, and the remaining trees were used to reconstruct a majority rule consensus and calculate Bayesian posterior probabilities (BPP) for the clades. The resulting trees were visualized using iTOL v5 (Letunic & Bork 2021).

Estimation of Divergence times

The divergence-time analysis followed the methodology outlined in previous studies (Renner 2005, Zhao et al. 2017, He et al. 2019). Utilizing a secondary calibration method, two separate analyses were conducted to estimate the divergence times of *Lycoperdaceae* and the incorporated genera (Renner 2005, Sánchez-Ramírez et al. 2015, Aime et al. 2018).

To assess the time of *Lycoperdaceae*, a separate monophyletic gasteroid lineage within the lepiotoid fungi in *Agaricaceae*, a mean stem age of approximately 125 Myr for *Agaricaceae* s.l. was utilized based on previous studies (Hibbett & Thorn 2001, Krüger et al. 2001, Vellinga 2004, He et al. 2019). For this calibration, 84 samples representing 34 genera of *Agaricaceae*, seven genera of *Lycoperdaceae*, and other closely related taxa were selected. Sequence data for this part are provided in Table 7.

Similarly, the divergence times of genera within *Lycoperdaceae* were estimated based on the results obtained above. This analysis involved 199 samples representing 19 genera within this family, with *Mycenastrum corium* set as the outgroup taxon.

Divergence time analyses were conducted using BEAST v1.10.4 (Suchard et al. 2018). XML files were constructed with BEAUti v1.10.4 by importing separate NEXUS files for each gene partition. Gene partitions were set to be unlinked for substitution and molecular-clock models but linked (concatenated) for gene trees. Substitution models for nucleotides were determined using jModelTest v2, with the following settings: GTR+I+G for ITS and nrLSU, SYM+I+G for *tef1- α* , TVM+I+G for *rpb2*. An uncorrelated log-normal distributed clock model and a Yule speciation model were selected as priors to assume a constant speciation rate per lineage. The prior for the ucl.d.mean parameter was gamma-distributed (shape = 1.0; scale = 0.001; offset = 0.0) for all genes. Secondary calibrations were conducted using a normally distributed calibration of the treeModel.rootHeight parameter (SD, 1; the mean value was determined by fossil node calibrations, like 125 Myr for *Agaricaceae* s.l., 83 Myr for *Lycoperdaceae*). Four independent Markov chain

Monte Carlo (MCMC) chains of 50,000,000 generations with a sampling frequency of 10,000 were performed. Log files were checked for convergence and mixing in Tracer v1.7.1 (Rambaut et al. 2018) (<http://tree.bio.ed.ac.uk/software/tracer/>) to ensure effective sample size (ESS) values were at least 200. An ultrametric maximum clade credibility (MCC) tree with mean and 95% HPD node ages and per-clade posterior probabilities was summarized using TreeAnnotator 1.10.4, with 25% burn-in and a 0.8 posterior limit (PP value). The resulting trees were visualized using iTOL v5 (Letunic & Bork 2021).

RESULTS

The phylogeny of *Lycoperdaceae*

This study generated 362 new sequences, including 105 ITS, 105 nrLSU, 78 *rpb2*, and 82 *tef1-α*. The comprehensive dataset, which includes all available sequences of *Lycoperdaceae* in this research along with 170 sequences retrieved from GenBank, comprises 209 samples. These samples represent 96 species from nineteen genera of *Lycoperdaceae*, with *Mycenastrum corium* chosen as the outgroup taxon. Sequence data for this part are provided in Table 1. The best-fitted model for this combined dataset, estimated and applied in the Bayesian Inference (BI) analysis, was GTR+I+G. The Maximum Likelihood (ML) trees constructed exhibited similar topologies to the BI tree, and the Maximum Clade Credibility (MCC) tree is presented in Fig. 1.

The phylogenetic analysis revealed that *Lycoperdaceae* forms a monophyletic clade with robust statistical support (Fig. 1). Twenty subclades, each representing a distinct genus, were identified with high statistical support (Posterior Probabilities [PP] displaying full values, Bootstrap [BS] values ranging from 70% to 100%). These genera include *Abstoma*, *Apioperdon*, *Arachnion*, *Bryoperdon*, *Calvatia*, *Disciseda*, and *Lycoperdon* (in the sense of Larsson et al. 2008) (Larsson & Jeppson 2008). Notably, the genus *Bovista* appeared as a paraphyletic group, comprising two strongly supported subclades represented by *Bovista* subg. *Globaria* and *Bovista* subg. *Bovista* separately (Fig. 1). In this study, subg. *Globaria* has been elevated to the generic level within *Lycoperdaceae*, as indicated by red asterisks in Fig. 1, while subg. *Bovista* has been proposed to be recognized as the true *Bovista*.

As depicted in Fig. 1, *Lycoperdon* s.l., constitutes a well-supported lineage (PP = 1.00), predominantly encompassing genera within *Lycoperdon*. This broader category, previously identified as *Lycoperdon* s.l., can now be phylogenetically subdivided into eleven subclades, each with robust statistical support (Fig. 1, *Lycoperdon* s.l.). Notably, the genus *Holocotylon* forms a distinct subclade, while five subclades align with the subgenera *Bovistella*, *Lycoperdon*, *Morganella*, *Utraria* and *Vascellum* as identified in prior research (Larsson & Jeppson 2008, Alfredo et al. 2017). However, the remaining five subclades (highlighted with red asterisks in Fig. 1) currently lack corresponding subgenera to accommodate the respective *Lycoperdon* species. Given the significant morphological differences among the known subgenera *Bovistella*, *Lycoperdon*, *Morganella*, *Utraria*, and *Vascellum*, and considering the results of the phylogenetic analysis and subsequent molecular clock analyses, this study proposes the restoration of the known subgenera *Bovistella*, *Morganella*, *Utraria*, and *Vascellum* to the generic level. Additionally, five new genera viz. *Fuscospina*, *Leptocaulis*, *Lycoperdiscus*, *Pseudoperdon*, and *Sinoperdon* have been established, as indicated in Fig. 1 with red asterisks.

The divergence times of *Lycoperdaceae* and genera

Two independent datasets were analyzed to estimate the divergence times of *Lycoperdaceae* and various genera. The first dataset comprised 81 species from 34 genera of *Agaricaceae* s.l., utilizing four-gene sequences (ITS, nrLSU, *rpb2*, *tef1-α*). Six species from the families *Inocybaceae* and *Crepidotaceae* were designated as the outgroup. Sequence data for this part are provided in Table 7. The Maximum Clade Credibility (MCC) tree (Fig. 2) revealed well-defined lineages for six families (*Agaricaceae* s. str., *Coprinaceae*, *Lycoperdaceae*, *Mycenastraceae*, *Phelloriniaceae*, and *Tulostomataceae*) with strong statistical support. However, the support for “*Lepiotaceae*” was not

robust. Additionally, these seven families exhibited close divergence times ranging from 80 to 118.3 million years, with *Lycoperdaceae* having a divergence time of 82.6 million years, represented by nine species from its main subclades.

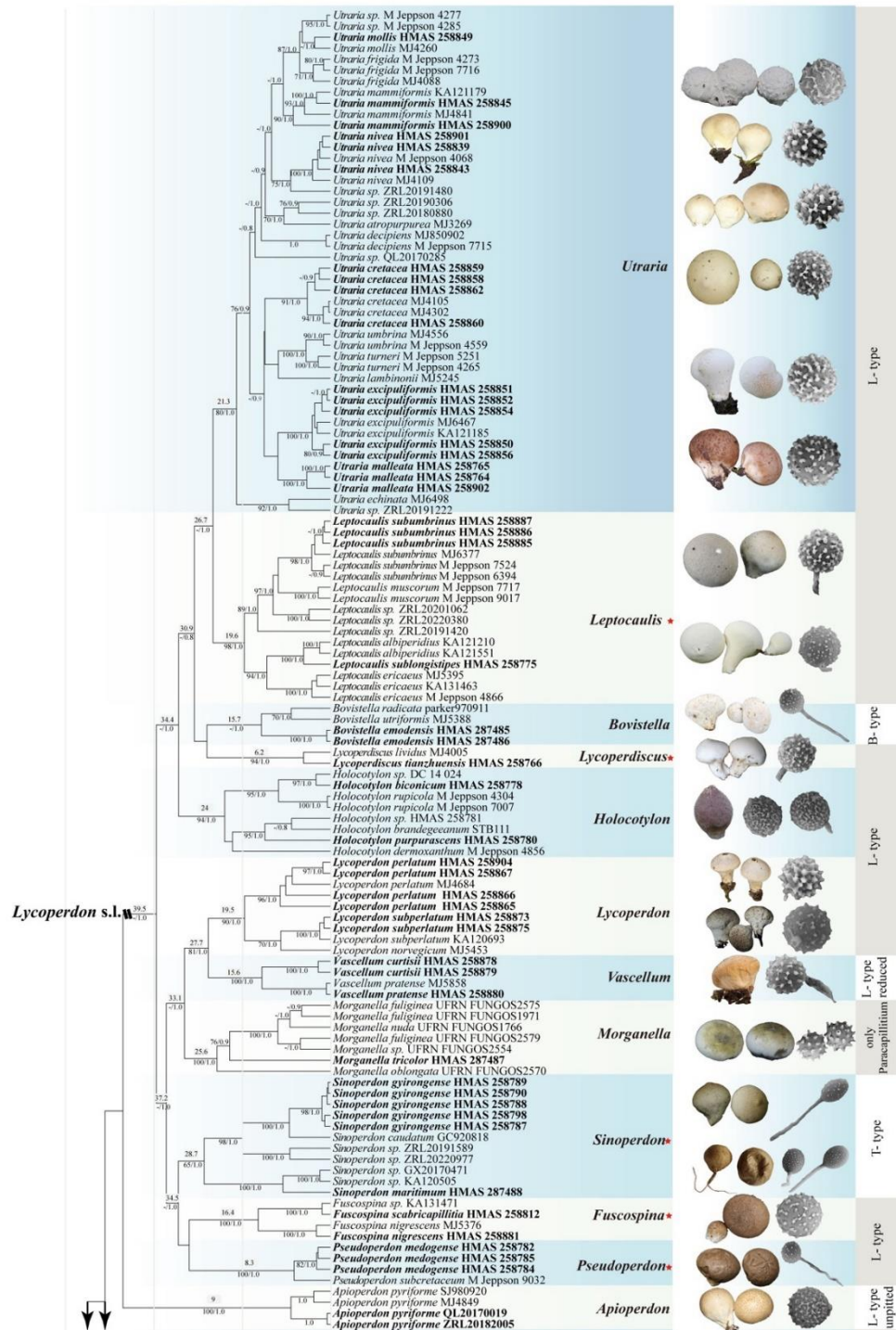


Figure 1 – Maximum Clade Credibility tree depicting the phylogeny of *Lycoperdaceae* based on ITS, nrLSU, *rpb2*, and *tef1-α* sequences. 19 genera of *Lycoperdaceae* were included, with the genus *Mycenastrum* from *Mycenaceae* serving as the outgroup. Branches supported by both Bootstrap (BS) values $\geq 70\%$ or Bayesian posterior probabilities (PP) ≥ 0.80 are indicated. The mean stem age of various genera is annotated at the internodes. Five newly proposed genera and *Globaria* are marked with red asterisks. The letters “M,” “C,” “T,” “B,” and “L” refer to the type of Capillitium, representing “*Mycenastrum*-type,” “*Calvatia*-type,” “transitional type,” “*Bovista*-type,” and “*Lycoperdon*-type,” respectively.

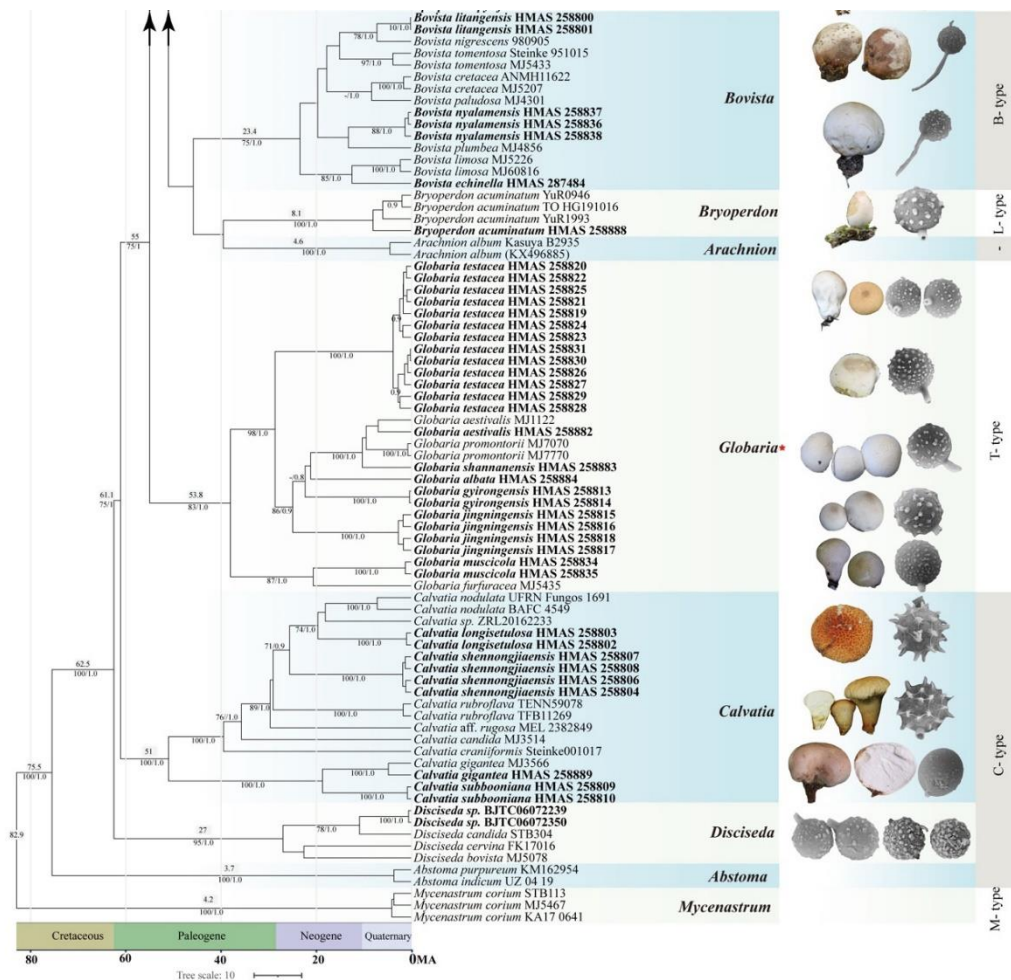


Figure 1 – Continued.

The second dataset comprised 199 specimens from 19 genera of *Lycoperdaceae*, utilizing a combined four-gene sequence, with *Mycenastrum corium* chosen as the outgroup. In this analysis, the calibration point for the root of *Lycoperdaceae* was set at 83 million years. The mean stem age of diverse genera was also annotated in the Maximum Clade Credibility tree of *Lycoperdaceae* (Fig. 1). Details on the estimated divergence times within *Lycoperdaceae*, with abbreviations corresponding to the different genera, are also provided in Table 8.

Lycoperdon s.l., appeared as a well-supported monophyletic lineage, along with eight other genera that received full support (PP value), with divergence times ranging from 26.7 to 75.5 million years. Notably, the genera *Abstoma*, *Disciseda*, and *Calvatia* diverged relatively early, ranging from 61.1 to 75.5 million years (Fig. 1). Additionally, *Apioperdon*, *Bryoperdon*, *Bovista*, and *Globaria* were estimated to have similar divergence times of around 55 million years (Table 8). Consequently, *Globaria* was elevated to the genus level due to its similar divergence times compared to others. The type genus *Lycoperdon* showed a more recent division around 27.7 million years, and the 11 genera within *Lycoperdon* s.l., shared roughly similar divergence times (26.7–34.5 million years, Fig. 1) with full support (PP = 1). The five known genera, namely *Bovistella*, *Lycoperdon*, *Morganella*, *Utraria*, and *Vascellum*, exhibited divergence times of 30.9, 27.7, 33.1, 26.7, and 27.7 million years, respectively. Additionally, the monophyletic genus *Holocotylon* diverged around 34.4 million years. The five newly proposed genera, *Fuscospina*, *Pseudoperdon*, and *Sinoperdon*, showed a similar divergence time of 34.5 million years, while *Leptocaulis* and *Lycoperdiscus* diverged around 26.7 and 30.9 million years, respectively. The broadly similar divergence times, combined with phylogenetic results and morphological differences, support the ranking of these 11 lineages within *Lycoperdon* s.l. as genera.

Table 1 Taxa, vouchers, and GenBank accession numbers in the phylogeny of *Lycoperdaceae*.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-α</i>	References
<i>Utraria frigida</i>	MJ4088	DQ112564	–	–	–	Larsson & Jeppson (2008)
<i>Utraria</i> sp.	M Jeppson 4285	DQ112573	–	–	–	Larsson & Jeppson (2008)
<i>Utraria frigida</i>	M Jeppson 4273	DQ112562	–	–	–	Larsson & Jeppson (2008)
<i>Utraria frigida</i>	M Jeppson 7716	DQ112561	–	–	–	Larsson & Jeppson (2008)
<i>Utraria</i> sp.	M Jeppson 4277	DQ112574	–	–	–	Larsson & Jeppson (2008)
<i>Utraria mollis</i>	MJ4260	DQ112566	–	–	–	Larsson & Jeppson (2008)
<i>Utraria mollis</i>	HMAS 258849	OR792733	OR831337	–	PP392957	this study
<i>Utraria mammiiformis</i>	MJ4841	DQ112567	–	–	–	Larsson & Jeppson (2008)
<i>Utraria mammiiformis</i>	KA121179	KP340187	–	–	–	Kim et al. (2016)
<i>Utraria mammiiformis</i>	HMAS 258845	OR792712	OR831331	OR853814	PP387681	this study
<i>Utraria mammiiformis</i>	HMAS 258900	OR792708	OR831333	OR853816	PP387684	this study
<i>Utraria nivea</i>	MJ4109	DQ112570	–	–	–	Larsson & Jeppson (2008)
<i>Utraria nivea</i>	M Jeppson 4068	DQ112571	–	–	–	Larsson & Jeppson (2008)
<i>Utraria nivea</i>	HMAS 258843	OR792727	OR831311	–	–	this study
<i>Utraria nivea</i>	HMAS 258901	OR792729	OR831310	OR853818	–	this study
<i>Utraria nivea</i>	HMAS 258839	OR792730	OR831312	OR853817	PP351995	this study
<i>Utraria</i> sp.	ZRL20191480	OR792736	OR831332	–	PP387678	this study
<i>Utraria</i> sp.	ZRL20180880	OR792735	OR831335	OR853811	PP387686	this study
<i>Utraria</i> sp.	ZRL20190306	OR792724	OR831334	OR853810	PP387687	this study
<i>Utraria atropurpurea</i>	MJ3269	DQ112586	–	–	–	Larsson & Jeppson (2008)
<i>Utraria decipiens</i>	MJ850902	DQ112583	–	–	–	Larsson & Jeppson (2008)
<i>Utraria decipiens</i>	M. Jeppson 7715	DQ112583	–	–	–	Larsson & Jeppson (2008)
<i>Utraria</i> sp.	QL20170285	OR792713	OR831319	OR853821	PP387683	this study
<i>Utraria cretacea</i>	MJ4302	DQ112598	–	–	–	Larsson & Jeppson (2008)
<i>Utraria cretacea</i>	MJ4105	DQ112597	–	–	–	Larsson & Jeppson (2008)
<i>Utraria cretacea</i>	HMAS 258858	OR792715	OR831264	OR853819	PP387680	this study
<i>Utraria cretacea</i>	HMAS 258859	OR792716	OR831323	–	–	this study
<i>Utraria cretacea</i>	HMAS 258860	OR792718	OR831320	OR853820	–	this study
<i>Utraria cretacea</i>	HMAS 258862	OR792717	OR831321	–	PP352000	this study
<i>Utraria malleata</i>	HMAS 258764	OR792722	OR831308	OR853812	PP352002	this study

Table 1 Continued.

Species	Voucher/specimen numbers	ITS	LSU	rpb2	tef1- α	References
<i>Utraria malleata</i>	HMAS 258765	OR792721	OR831307	OR853813	PP352001	this study
<i>Utraria excipuliformis</i>	MJ6467	DQ112590	–	–	–	Larsson & Jeppson (2008)
<i>Utraria excipuliformis</i>	KA121185	KP340186	–	KU764390	–	Kim et al. (2016)
<i>Utraria excipuliformis</i>	HMAS 258850	OR792705	OR831326	–	PP351997	this study
<i>Utraria excipuliformis</i>	HMAS 258851	OR792703	OR831328	–	PP387677	this study
<i>Utraria excipuliformis</i>	HMAS 258852	OR792704	OR831327	–	–	this study
<i>Utraria excipuliformis</i>	HMAS 258854	OR792706	OR831329	–	PP387676	this study
<i>Utraria excipuliformis</i>	HMAS 258856	OR792707	OR831325	–	PP351996	this study
<i>Utraria turneri</i>	M Jeppson 4265	DQ112595	–	–	–	Larsson & Jeppson (2008)
<i>Utraria turneri</i>	M Jeppson 5251	DQ112594	–	–	–	Larsson & Jeppson (2008)
<i>Utraria umbrina</i>	MJ4556	DQ112591	–	–	–	Larsson & Jeppson (2008)
<i>Utraria umbrina</i>	M Jeppson 4559	DQ112592	–	–	–	Larsson & Jeppson (2008)
<i>Utraria lambinonii</i>	MJ5245	DQ112576	–	–	–	Larsson & Jeppson (2008)
<i>Utraria malleata</i>	HMAS 258902	OR792723	OR831309	–	–	this study
<i>Utraria echinata</i>	MJ6498	DQ112578	–	–	–	Larsson & Jeppson (2008)
<i>Utraria</i> sp.	ZRL20191222	OR792701	OR831330	OR853809	PP351994	this study
<i>Leptocaulus subumbrinus</i>	HMAS 258885	OR792673	OR831315	OR853828	PP351998	this study
<i>Leptocaulus subumbrinus</i>	HMAS 258886	OR792675	OR831317	OR853830	PP351999	this study
<i>Leptocaulus subumbrinus</i>	HMAS 258887	OR792674	OR831316	OR853829	–	this study
<i>Leptocaulus subumbrinus</i>	MJ6377	DQ112602	–	–	–	Jeppson et al. (2012)
<i>Leptocaulus subumbrinus</i>	M. Jeppson 7524	JN572907	–	–	–	Jeppson et al. (2012)
<i>Leptocaulus subumbrinus</i>	M. Jeppson 6394	DQ112601	–	–	–	Jeppson et al. (2012)
<i>Leptocaulus muscorum</i>	M. Jeppson 7717	DQ112604	–	–	–	Jeppson et al. (2012)
<i>Leptocaulus muscorum</i>	M. Jeppson 9017	JN572905	–	–	–	Jeppson et al. (2012)
<i>Leptocaulus</i> sp.	ZRL20201062	OR792749	OR831314	–	–	this study
<i>Leptocaulus</i> sp.	ZRL20220380	OR792747	OR831313	OR853826	PP392956	this study
<i>Leptocaulus</i> sp.	ZRL20191420	OR792748	OR831298	OR853827	PP352003	this study
<i>Leptocaulus sublongistipes</i>	HMAS 258775	OR792741	OR831318	OR853825	–	this study
<i>Leptocaulus albiperidia</i>	KA121210	KP340182	–	KU764391	–	Kim et al. (2016)
<i>Leptocaulus albiperidia</i>	KA121551 t	KP340183	–	–	KU764399	Kim et al. (2016)

Table 1 Continued.

Species	Voucher/specimen numbers	ITS	LSU	rpb2	tef1- α	References
<i>Leptocaulus ericaea</i>	MJ 5395	DQ112605	–	–	–	Larsson & Jeppson (2008)
<i>Leptocaulus ericaea</i>	KA131463	KP340185	–	KU764396	KU764404	Kim et al. (2016)
<i>Leptocaulus ericaea</i>	M. Jeppson 4866	DQ112606	–	–	–	Larsson & Jeppson (2008)
<i>Lycoperdiscus tianzhuensis</i>	HMAS 258766	OR792725	OR831324	OR853822	–	this study
<i>Lycoperdiscus lividus</i>	MJ4005	DQ112600	–	–	–	Larsson & Jeppson (2008)
<i>Bovistella radicata</i>	parker970911	DQ112608	–	–	–	Larsson & Jeppson (2008)
<i>Bovistella utriformis</i>	MJ5388	DQ112607	–	–	–	Larsson & Jeppson (2008)
<i>Bovistella emodensis</i>	HMAS 287485	PP175744	PP175752	PP351955	PP351962	this study
<i>Bovistella emodensis</i>	HMAS 287486	PP175745	PP175753	PP351956	PP351963	this study
<i>Holocotylon biconicum</i>	HMAS 258778	OR792667	OR831266	–	–	this study
<i>Holocotylon</i> sp.	DC 14 024	KU167031	–	–	–	Unpublished
<i>Holocotylon rupicola</i>	MJ4304	DQ112580	–	–	–	Jeppson et al. (2012)
<i>Holocotylon rupicola</i>	M. Jeppson 7007	JN572902	–	–	–	Jeppson et al. (2012)
<i>Holocotylon</i> sp.	HMAS 258781	OR792672	OR831267	OR853805	PP387664	this study
<i>Holocotylon purpurascens</i>	HMAS 258780	OR792671	OR831300	OR853806	–	this study
<i>Holocotylon dermoxanthum</i>	MJ4856	DQ112579	–	–	–	Larsson & Jeppson (2008)
<i>Holocotylon brandegeeanum</i>	STB111	EU833660	–	–	–	Bates et al. 2009
<i>Lycoperdon perlatum</i>	MJ4684	DQ112630	–	–	–	Larsson & Jeppson (2008)
<i>Lycoperdon perlatum</i>	HMAS 258865	OR792758	OR831262	OR853791	PP387672	this study
<i>Lycoperdon perlatum</i>	HMAS 258866	OR792763	OR831257	OR853792	PP387673	this study
<i>Lycoperdon perlatum</i>	HMAS 258867	OR792760	OR831263	–	PP387671	this study
<i>Lycoperdon perlatum</i>	HMAS 258904	OR792759	OR831265	–	–	this study
<i>Lycoperdon subperlatum</i>	HMAS 258873	OR792751	OR831261	OR853789	PP387670	this study
<i>Lycoperdon subperlatum</i>	HMAS 258875	OR792750	OR831260	OR853790	–	this study
<i>Lycoperdon subperlatum</i>	KA120693	KP340207	–	KU764388	–	Kim et al. (2016)
<i>Lycoperdon norvegicum</i>	MJ5453	DQ112631	–	–	–	Larsson & Jeppson (2008)
<i>Vascellum curtisii</i>	HMAS 258878	OR792665	OR831258	OR853787	–	this study
<i>Vascellum curtisii</i>	HMAS 258879	OR792666	OR831259	OR853788	–	this study
<i>Vascellum pratense</i>	MJ5858	DQ112556	–	–	–	Larsson & Jeppson (2008)

Table 1 Continued.

Species	Voucher/specimen numbers	ITS	LSU	rpb2	tef1- α	References
<i>Vascellum pratense</i>	HMAS 258880	OR792664	PP175749	PP351953	–	this study
<i>Morganella fuliginea</i>	UFRN-Fungos 2575	KU958325	KU958326	–	–	Alfredo et al. (2017)
<i>Morganella fuliginea</i>	UFRN-Fungos 2579	KU958349	KU958350	–	–	Alfredo et al. (2017)
<i>Morganella fuliginea</i>	UFRN-Fungos 1971	KU958321	KU958322	–	–	Alfredo et al. (2017)
<i>Morganella nuda</i>	UFRN-Fungos 1766	KU958315	KU958316	–	–	Alfredo et al. (2017)
<i>Morganella oblongata</i>	UFRN-Fungos 2570	KU958355	KU958356	–	–	Alfredo et al. (2017)
<i>Morganella tricolor</i>	HMAS 287487	PP175741	PP175750	–	PP351959	this study
<i>Morganella</i> sp.	UFRN-Fungos 2554	KU958309	KU958310	–	–	Alfredo et al. (2017)
<i>Sinoperdon gyirongense</i>	HMAS 258798	OR792682	OR831247	–	–	this study
<i>Sinoperdon gyirongense</i>	HMAS 258787	OR792686	OR831248	OR853801	PP351990	this study
<i>Sinoperdon gyirongense</i>	HMAS 258788	OR792699	OR831243	OR853799	PP387666	this study
<i>Sinoperdon gyirongense</i>	HMAS 258789	OR792696	OR831246	OR853800	PP387667	this study
<i>Sinoperdon gyirongense</i>	HMAS 258790	OR792695	OR831249	–	–	this study
<i>Sinoperdon caudatum</i>	GC920818	DQ112633	–	–	–	Jeppson & Larsson (2010)
<i>Sinoperdon</i> sp.	ZRL20191589	OR792677	OR831236	OR853793	PP387663	this study
<i>Sinoperdon</i> sp.	ZRL20220977	OR792676	OR831235	OR853794	–	this study
<i>Sinoperdon</i> sp.	GX20170471	OR792627	OR831233	OR853808	PP387668	this study
<i>Sinoperdon</i> sp.	KA120505	KP340215	–	KU764387	–	Kim et al. (2016)
<i>Sinoperdon maritimum</i>	HMAS 287488	OR792626	OR831234	OR853807	PP387669	this study
<i>Fuscospina</i> sp.	KA131471	KP340188	–	–	–	Kim et al. (2016)
<i>Fuscospina scabricapillitia</i>	HMAS 258812 T	OR792678	PP175748	PP351958	PP351961	this study
<i>Fuscospina nigrescens</i>	MJ5376	DQ112577	–	–	–	Larsson & Jeppson (2008)
<i>Fuscospina nigrescens</i>	HMAS 258881	OR792702	OR831256	PP351957	PP351964	this study
<i>Pseudoperdon medogense</i>	HMAS 258782	OR792742	OR831253	–	PP387675	this study
<i>Pseudoperdon medogense</i>	HMAS 258784	OR792745	OR831254	OR853823	PP387674	this study
<i>Pseudoperdon medogense</i>	HMAS 258785	OR792746	OR831255	OR853824	–	this work
<i>Pseudoperdon subcretaceum</i>	M. Jeppson 9032	JN572908	–	–	–	Jeppson et al. (2012)
<i>Apioperdon pyriforme</i>	SJ980920	DQ112557	–	–	–	Larsson & Jeppson (2008)

Table 1 Continued.

Species	Voucher/specimen numbers	ITS	LSU	rpb2	tef1- α	References
<i>Apioperdon pyriforme</i>	MJ4849	DQ112558	–	–	–	Larsson & Jeppson (2008)
<i>Apioperdon pyriforme</i>	QL20170019	PP175742	PP175746	–	–	this study
<i>Apioperdon pyriforme</i>	ZRL20182005	PP175743	PP175747	–	PP351960	this study
<i>Bovista litangensis</i>	HMAS 258800	OR792635	OR831301	OR853765	PP351969	this study
<i>Bovista litangensis</i>	HMAS 258801	OR792636	OR831302	OR853764	PP351968	this study
<i>Bovista tomentosa</i>	MJ5433	DQ112616	–	–	–	Larsson & Jeppson (2008)
<i>Bovista tomentosa</i>	Steinke 951015	DQ112617	–	–	–	Larsson & Jeppson (2008)
<i>Bovista nigrescens</i>	S&JJ980905	DQ112612	–	–	–	Larsson & Jeppson (2008)
<i>Bovista limosa</i>	MJ60816	EU915075	–	–	–	Larsson et al. (2009)
<i>Bovista limosa</i>	MJ5226	DQ112615	–	–	–	Larsson & Jeppson (2008)
<i>Bovista echinella</i>	HMAS 287484	OR792634	OR831289	–	–	this study
<i>Bovista nyalamensis</i>	HMAS 258836	OR792637	OR831304	OR853767	PP351972	this study
<i>Bovista nyalamensis</i>	HMAS 258837	OR792638	OR831306	OR853766	PP351971	this study
<i>Bovista nyalamensis</i>	HMAS 258838	OR792639	OR831305	OR853768	PP351970	this study
<i>Bovista plumbea</i>	MJ4856	DQ112613	–	–	–	Larsson & Jeppson (2008)
<i>Bovista cretacea</i>	ANMH11622	DQ112611	–	–	–	Larsson & Jeppson (2008)
<i>Bovista cretacea</i>	MJ5207	DQ112610	–	–	–	Larsson & Jeppson (2008)
<i>Bovista paludosa</i>	MJ4301	DQ112609	–	–	–	Larsson & Jeppson (2008)
<i>Bryoperdon acuminatum</i>	YuR0946	MH628567	–	–	–	Rebriev et al. (2020)
<i>Bryoperdon acuminatum</i>	YuRI993	MH628573	–	–	–	Rebriev et al. (2020)
<i>Bryoperdon acuminatum</i>	TO HG191016	KY581201	KY581199	–	–	Vizzini & Ercole (2017)
<i>Bryoperdon acuminatum</i>	HMAS 258888	OR792632	OR831232	–	PP351973	this study
<i>Globaria testacea</i>	HMAS 258819	OR792656	OR831280	OR853778	–	this study
<i>Globaria testacea</i>	HMAS 258820	OR792655	OR831283	–	–	this study
<i>Globaria testacea</i>	HMAS 258821	OR792653	OR831251	OR853779	–	this study
<i>Globaria testacea</i>	HMAS 258822	OR792654	OR831282	OR853783	–	this study
<i>Globaria testacea</i>	HMAS 258823	OR792651	OR831275	OR853781	–	this study
<i>Globaria testacea</i>	HMAS 258824	OR792657	OR831286	OR853782	–	this study
<i>Globaria testacea</i>	HMAS 258825	OR792658	OR831279	OR853780	–	this study
<i>Globaria testacea</i>	HMAS 258826	OR792647	OR831284	OR853776	–	this study

Table 1 Continued.

Species	Voucher/specimen numbers	ITS	LSU	rpb2	tef1- α	References
<i>Globalia testacea</i>	HMAS 258827	OR792648	OR831285	OR853773	–	this study
<i>Globalia testacea</i>	HMAS 258828	OR792646	OR831281	OR853777	–	this study
<i>Globalia testacea</i>	HMAS 258829	OR792649	OR831278	–	–	this study
<i>Globalia testacea</i>	HMAS 258830	OR792652	OR831277	OR853774	–	this study
<i>Globalia testacea</i>	HMAS 258831	OR792650	OR831276	OR853775	–	this study
<i>Globalia aestivalis</i>	MJ1122	DQ112620	–	–	–	Larsson & Jeppson (2008)
<i>Globalia promontorii</i>	MJ7070	DQ112621	–	–	–	Larsson & Jeppson (2008)
<i>Globalia gyirongensis</i>	HMAS 258813	OR792660	OR831288	OR853785	PP351977	this study
<i>Globalia gyirongensis</i>	HMAS 258814	OR792661	OR831287	OR853786	PP351976	this study
<i>Globalia shannanensis</i>	HMAS 258883	OR792662	OR831303	–	–	this study
<i>Globalia albata</i>	HMAS 258884	OR792659	OR831270	OR853784	–	this study
<i>Globalia jingningensis</i>	HMAS 258815	OR792644	OR831273	–	–	this study
<i>Globalia jingningensis</i>	HMAS 258816	OR792645	OR831272	OR853770	–	this study
<i>Globalia jingningensis</i>	HMAS 258817	OR792642	OR831271	OR853769	PP351967	this study
<i>Globalia jingningensis</i>	HMAS 258818	OR792643	OR831274	–	–	this study
<i>Globalia muscicola</i>	HMAS 258834	OR792640	OR831269	OR853772	PP351974	this study
<i>Globalia muscicola</i>	HMAS 258835	OR792641	OR831268	OR853771	PP351975	this study
<i>Globalia furfuracea</i>	MJ5435	DQ112622	–	–	–	Larsson & Jeppson (2008)
<i>Calvatia</i> sp.	ZRL20162233	OR792619	OR831231	–	–	this study
<i>Calvatia longisetulosa</i>	HMAS 258802	OR792617	OR831229	OR853757	PP351981	this study
<i>Calvatia longisetulosa</i>	HMAS 258803	OR792618	OR831230	OR853758	PP351982	this study
<i>Calvatia nodulata</i>	UFRN Fungos 1691	KP751206	–	–	–	Alfredo et al. (2014)
<i>Calvatia nodulata</i>	BAFC 4549	KY366490	–	–	–	Alfredo et al. (2014)
<i>Calvatia rubroflava</i>	TENN59078	AF485064	–	–	–	Krüger et al. (2003)
<i>Calvatia rubroflava</i>	TFB11269	KY559335.1	–	–	–	Senthilarasu et al. (2018)
<i>Calvatia</i> aff. <i>rugosa</i>	MEL 2382849	KP012724.1	–	–	–	Senthilarasu et al. (2018)
<i>Calvatia shennongjiaensis</i>	HMAS 258804	OR792621	OR831294	OR853761	PP351978	this study
<i>Calvatia shennongjiaensis</i>	HMAS 258806	OR792623	OR831291	OR853759	PP351979	this study

Table 1 Continued.

Species	Voucher/specimen numbers	ITS	LSU	rpb2	tef1- α	References
<i>Calvatia shennongjiaensis</i>	HMAS 258807	OR792624	OR831293	–	PP351966	this study
<i>Calvatia shennongjiaensis</i>	HMAS 258808	OR792625	OR831292	OR853760	PP351980	this study
<i>Calvatia candida</i>	MJ3514	DQ112624.1	–	–	–	Larsson & Jeppson (2008)
<i>Calvatia craniiformis</i>	Steinke001017	DQ112625	–	–	–	Larsson & Jeppson (2008)
<i>Calvatia shennongjiaensis</i>	HMAS 258804	OR792621	OR831294	OR853761	PP351978	this study
<i>Calvatia shennongjiaensis</i>	HMAS 258806	OR792623	OR831291	OR853759	PP351979	this study
<i>Calvatia shennongjiaensis</i>	HMAS 258807	OR792624	OR831293	–	PP351966	this study
<i>Calvatia shennongjiaensis</i>	HMAS 258808	OR792625	OR831292	OR853760	PP351980	this study
<i>Calvatia candida</i>	MJ3514	DQ112624.1	–	–	–	Larsson & Jeppson (2008)
<i>Calvatia craniiformis</i>	Steinke001017	DQ112625	–	–	–	Larsson & Jeppson (2008)
<i>Calvatia gigantea</i>	MJ3566	DQ112623	–	–	–	Larsson & Jeppson (2008)
<i>Calvatia subbooniana</i>	HMAS 258809	OR792631	OR831296	–	–	this study
<i>Calvatia subbooniana</i>	HMAS 258810	OR792630	OR831297	–	–	this study
<i>Disciseda candida</i>	STB304	EU833654	–	–	–	Bates et al. (2009)
<i>Disciseda cervina</i>	FK17016	MN338568	–	–	–	Unpublished
<i>Disciseda bovista</i>	M. Jeppson 5078	DQ112627	–	–	–	Larsson & Jeppson (2008)
<i>Disciseda</i> sp.	BJTC06072350	OR792633	OR831295	OR853763	PP351965	this study
<i>Disciseda</i> sp.	BJTC06072239	–	PP175751	PP351954	–	this study
<i>Abstoma purpureum</i>	KM162954	GQ981488	–	–	–	Unpublished
<i>Abstoma indicum</i>	UZ-04-19	MN231720	–	–	–	Altaf et al. (2022)
<i>Mycenastrum corium</i>	STB113	EU833666	–	–	–	Bates et al. 2009
<i>Mycenastrum corium</i>	MJ5467	DQ112628	–	–	–	Larsson & Jeppson (2008)
<i>Mycenastrum corium</i>	KA17 0641	MK351723	–	–	–	Kim et al. (2016)

Table 2 Taxa, vouchers, and GenBank accession numbers in the phylogeny of *Lycoperdon* s.l.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-a</i>	References
<i>Utraria frigida</i>	MJ4088	DQ112564	–	–	–	Larsson & Jeppson (2008)
<i>Utraria</i> sp.	M Jeppson 4285	DQ112573	–	–	–	Larsson & Jeppson (2008)
<i>Utraria frigida</i>	Lange 191	DQ112559	–	–	–	Larsson & Jeppson (2008)
<i>Utraria frigida</i>	M Jeppson 4273	DQ112562	–	–	–	Larsson & Jeppson (2008)
<i>Utraria frigida</i>	M Jeppson 7716	DQ112561	–	–	–	Larsson & Jeppson (2008)
<i>Utraria</i> sp.	M Jeppson 4277	DQ112574	–	–	–	Larsson & Jeppson (2008)
<i>Utraria mollis</i>	MJ4260	DQ112566	–	–	–	Larsson & Jeppson (2008)
<i>Utraria mollis</i>	HMAS 258848	OR792734	–	–	–	this study
<i>Utraria</i> sp.	ZRL20190897	OR792731	OR831336	–	PP387682	this study
<i>Utraria</i> sp.	ZRL20191234	OR792732	OR831338	OR853815	PP387685	this study
<i>Utraria mammiformis</i>	HMAS 258900	OR792708	OR831333	OR853816	PP387684	this study
<i>Utraria mammiformis</i>	MJ4841	DQ112567	–	–	–	Larsson & Jeppson (2008)
<i>Utraria mammiformis</i>	KA121179	KP340187	–	–	–	Kim et al. (2016)
<i>Utraria mammiformis</i>	HMAS 258845	OR792712	OR831331	OR853814	PP387681	this study
<i>Utraria mammiformis</i>	HMAS 258846	OR792711	–	–	–	this study
<i>Utraria mammiformis</i>	HMAS 258899	OR792710	–	–	–	this study
<i>Utraria nivea</i>	MJ4109	DQ112570	–	–	–	Larsson & Jeppson (2008)
<i>Utraria nivea</i>	M Jeppson 4068	DQ112571	–	–	–	Larsson & Jeppson (2008)
<i>Utraria nivea</i>	HMAS 258843	OR792727	OR831311	–	–	this study
<i>Utraria nivea</i>	HMAS 258844	OR792728	–	–	–	this study
<i>Utraria nivea</i>	HMAS 258901	OR792729	OR831310	OR853818	–	this study
<i>Utraria nivea</i>	HMAS 258839	OR792730	OR831312	OR853817	PP351995	this study
<i>Utraria</i> sp.	ZRL20191480	OR792736	OR831332	–	PP387678	this study
<i>Utraria pulcherrima</i>	stb066	EU833663	–	–	–	Bates et al. 2009
<i>Utraria</i> sp.	ZRL20211761	OR792709	–	–	–	this study
<i>Utraria</i> sp.	ZRL20180880	OR792735	OR831335	OR853811	PP387686	this study
<i>Utraria</i> sp.	ZRL20190306	OR792724	OR831334	OR853810	PP387687	this study
<i>Utraria atropurpurea</i>	MJ3269	DQ112586	–	–	–	Larsson & Jeppson (2008)
<i>Utraria rimulata</i>	STB112	EU833664	–	–	–	Bates et al. 2009
<i>Utraria rimulata</i>	FFUI_-1	MN596942	–	–	–	Unpublished

Table 2 Continued.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-a</i>	References
<i>Utraria decipiens</i>	MJ850902	DQ112583	–	–	–	Larsson & Jeppson (2008)
<i>Utraria decipiens</i>	M. Jeppson 7715	DQ112583	–	–	–	Larsson & Jeppson (2008)
<i>Utraria</i> sp.	QL20170285	OR792713	OR831319	OR853821	PP387683	this study
<i>Utraria cretacea</i>	MJ4302	DQ112598	–	–	–	Larsson & Jeppson (2008)
<i>Utraria cretacea</i>	MJ4105	DQ112597	–	–	–	Larsson & Jeppson (2008)
<i>Utraria cretacea</i>	HMAS 258857	OR792714	OR831322	–	–	this study
<i>Utraria cretacea</i>	HMAS 258858	OR792715	OR831264	OR853819	PP387680	this study
<i>Utraria cretacea</i>	HMAS 258859	OR792716	OR831323	–	–	this study
<i>Utraria cretacea</i>	HMAS 258860	OR792718	OR831320	OR853820	–	this study
<i>Utraria cretacea</i>	HMAS 258861	OR792719	–	–	–	this study
<i>Utraria cretacea</i>	HMAS 258862	OR792717	OR831321	–	PP352000	this study
<i>Utraria malleata</i>	HMAS 258764	OR792722	OR831308	OR853812	PP352002	this study
<i>Utraria malleata</i>	HMAS 258765	OR792721	OR831307	OR853813	PP352001	this study
<i>Utraria altimontana</i>	MJ4270	DQ112588	–	–	–	Larsson & Jeppson (2008)
<i>Utraria excipuliformis</i>	MJ6467	DQ112590	–	–	–	Larsson & Jeppson (2008)
<i>Utraria excipuliformis</i>	KA121185	KP340186	–	KU764390	–	Kim et al. (2016)
<i>Utraria excipuliformis</i>	HMAS 258850	OR792705	OR831326	–	PP351997	this study
<i>Utraria excipuliformis</i>	HMAS 258851	OR792703	OR831328	–	PP387677	this study
<i>Utraria excipuliformis</i>	HMAS 258852	OR792704	OR831327	–	–	this study
<i>Utraria excipuliformis</i>	HMAS 258854	OR792706	OR831329	–	PP387676	this study
<i>Utraria excipuliformis</i>	HMAS 258856	OR792707	OR831325	–	PP351996	this study
<i>Utraria turneri</i>	Lange 0895	DQ112596	–	–	–	Larsson & Jeppson (2008)
<i>Utraria turneri</i>	M Jeppson 4265	DQ112595	–	–	–	Larsson & Jeppson (2008)
<i>Utraria turneri</i>	M Jeppson 5251	DQ112594	–	–	–	Larsson & Jeppson (2008)
<i>Utraria umbrina</i>	MJ4556	DQ112591	–	–	–	Larsson & Jeppson (2008)
<i>Utraria umbrina</i>	M Jeppson 4559	DQ112592	–	–	–	Larsson & Jeppson (2008)
<i>Utraria lambinonii</i>	MJ5245	DQ112576	–	–	–	Larsson & Jeppson (2008)
<i>Utraria lambinonii</i>	Demoulin 4622	DQ112575	–	–	–	Larsson & Jeppson (2008)
<i>Utraria lambinonii</i>	HMAS 258863	OR792720	–	–	–	this study
<i>Utraria malleata</i>	HMAS 258902	OR792723	OR831309	–	–	this study

Table 2 Continued.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-a</i>	References
<i>Utraria echinate</i>	MJ6498	DQ112578	–	–	–	Larsson & Jeppson (2008)
<i>Utraria</i> sp.	ZRL20191222	OR792701	OR831330	OR853809	PP351994	this study
<i>Leptocaulus subumbrinus</i>	HMAS 258885	OR792673	OR831315	OR853828	PP351998	this study
<i>Leptocaulus subumbrinus</i>	HMAS 258886	OR792675	OR831317	OR853830	PP351999	this study
<i>Leptocaulus subumbrinus</i>	HMAS 258887	OR792674	OR831316	OR853829	–	this study
<i>Leptocaulus subumbrinus</i>	MJ6377	DQ112602	–	–	–	Jeppson et al. (2012)
<i>Leptocaulus subumbrinus</i>	M. Jeppson 7524	JN572907	–	–	–	Jeppson et al. (2012)
<i>Leptocaulus subumbrinus</i>	M. Jeppson 6394	DQ112601	–	–	–	Jeppson et al. (2012)
<i>Leptocaulus</i> cf. <i>umbrinus</i>	STB098B	EU833665	–	–	–	Larsson & Jeppson (2008)
<i>Leptocaulus muscorum</i>	MPM2673	JN572904	–	–	–	Jeppson et al. (2012)
<i>Leptocaulus muscorum</i>	M. Jeppson 7717	DQ112604	–	–	–	Jeppson et al. (2012)
<i>Leptocaulus muscorum</i>	M. Jeppson 9017	JN572905	–	–	–	Jeppson et al. (2012)
<i>Leptocaulus</i> sp.	ZRL20201062	OR792749	OR831314	–	–	this study
<i>Leptocaulus</i> sp.	ZRL20220380	OR792747	OR831313	OR853826	PP392956	this study
<i>Leptocaulus</i> sp.	ZRL20191420	OR792748	OR831298	OR853827	–	this study
<i>Leptocaulus sublongistipes</i>	HMAS 258768	OR792740	–	–	–	this study
<i>Leptocaulus sublongistipes</i>	HMAS 258769	OR792738	–	–	+	this study
<i>Leptocaulus sublongistipes</i>	HMAS 258770	OR792739	–	–	+	this study
<i>Leptocaulus sublongistipes</i>	HMAS 258771	OR792737	–	–	–	this study
<i>Leptocaulus sublongistipes</i>	HMAS 258775	OR792741	OR831318	OR853825	–	this study
<i>Leptocaulus albiperidia</i>	KA121210	KP340182	–	KU764391	–	Kim et al. (2016)
<i>Leptocaulus albiperidia</i>	KA121551 t	KP340183	–	–	KU764399	Kim et al. (2016)
<i>Leptocaulus ericaea</i>	MJ 5395	DQ112605	–	–	–	Larsson & Jeppson (2008)
<i>Leptocaulus ericaea</i>	KA131463	KP340185	–	KU764396	KU764404	Kim et al. (2016)
<i>Leptocaulus ericaea</i>	M. Jeppson 4866	DQ112606	–	–	–	Larsson & Jeppson (2008)
<i>Lycoperdiscus tianzhuensis</i>	HMAS 258766	OR792725	OR831324	OR853822	–	this study
<i>Lycoperdiscus tianzhuensis</i>	HMAS 258767	OR792726	–	–	–	this study
<i>Lycoperdiscus lividus</i>	Dobremez 19740514	DQ112599	–	–	–	Larsson & Jeppson (2008)

Table 2 Continued.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-α</i>	References
<i>Lycoperdiscus lividus</i>	MJ4005	DQ112600	–	–	–	Larsson & Jeppson (2008)
<i>Bovistella radicata</i>	parker970911	DQ112608	–	–	–	Larsson & Jeppson (2008)
<i>Bovistella utriformis</i>	MJ5388	DQ112607	–	–	–	this study
<i>Bovistella emodensis</i>	HMAS 287485	PP175744	PP175752	PP351955	PP351962	this study
<i>Bovistella emodensis</i>	HMAS 287486	PP175745	PP175753	PP351956	PP351963	this study
<i>Holocotylon biconicum</i>	HMAS 258776	OR792668	–	–	–	this study
<i>Holocotylon biconicum</i>	HMAS 258777	OR792669	–	–	–	this study
<i>Holocotylon biconicum</i>	HMAS 258778	OR792667	OR831266	–	–	this study
<i>Holocotylon</i> sp.	DC 14 024	KU167031	–	–	–	Unpublished
<i>Holocotylon rupicola</i>	MJ4304	DQ112580	–	–	–	Jeppson et al. (2012)
<i>Holocotylon rupicola</i>	M. Jeppson 7007	JN572902	–	–	–	Jeppson et al. (2012)
<i>Holocotylon rupicola</i>	Vetter 407	DQ112581	–	–	–	Jeppson et al. (2012)
<i>Holocotylon</i> sp.	HMAS 258781	OR792672	OR831267	OR853805	PP387664	this study
<i>Holocotylon purpurascens</i>	HMAS 258779	OR792670	–	–	PP392955	this study
<i>Holocotylon purpurascens</i>	HMAS 258780	OR792671	OR831300	OR853806	–	this study
<i>Holocotylon dermoxanthum</i>	MJ4856	DQ112579	–	–	–	Larsson & Jeppson (2008)
<i>Lycoperdon perlatum</i>	HE21023	KC505543	–	–	–	Unpublished
<i>Lycoperdon perlatum</i>	TNSKasuya B780	KF551249	–	–	–	Kasuya et al. (2013)
<i>Lycoperdon perlatum</i>	ASIS22671	KF668322	–	–	–	Unpublished
<i>Lycoperdon perlatum</i>	KA130555	KP340193	–	KU764393	KU764403	Kim et al. (2016)
<i>Lycoperdon perlatum</i>	TENN58040	AJ237627	–	–	–	Krüger et al. (2001)
<i>Lycoperdon perlatum</i>	MJ4684	DQ112630	–	–	–	Larsson & Jeppson (2008)
<i>Lycoperdon perlatum</i>	HMAS 258864	OR792764	–	–	–	this study
<i>Lycoperdon perlatum</i>	HMAS 258865	OR792758	OR831262	OR853791	PP387672	this study
<i>Lycoperdon perlatum</i>	HMAS 258866	OR792763	OR831257	OR853792	PP387673	this study
<i>Lycoperdon perlatum</i>	HMAS 258867	OR792760	OR831263	–	PP387673	this study
<i>Lycoperdon perlatum</i>	HMAS 258868	OR792756	–	–	–	this study
<i>Lycoperdon perlatum</i>	HMAS 258869	OR792757	–	–	–	this study
<i>Lycoperdon perlatum</i>	HMAS 258870	OR792765	–	–	–	this study
<i>Lycoperdon perlatum</i>	HMAS 258871	OR792762	–	–	–	this study

Table 2 Continued.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-α</i>	References
<i>Lycoperdon perlatum</i>	HMAS 258872	OR792761	—	—	—	this study
<i>Lycoperdon perlatum</i>	HMAS 258904	OR792759	OR831265	—	—	this study
<i>Lycoperdon subperlatum</i>	HMAS 258873	OR792751	OR831261	OR853789	PP387670	this study
<i>Lycoperdon subperlatum</i>	HMAS 258875	OR792750	OR831260	OR853790	—	this study
<i>Lycoperdon subperlatum</i>	HMAS 258876	OR792755	—	—	—	this study
<i>Lycoperdon subperlatum</i>	HMAS 258877	OR792754	—	—	—	this study
<i>Lycoperdon subperlatum</i>	HMAS 258905	OR792752	—	—	—	this study
<i>Lycoperdon subperlatum</i>	HMAS 258906	OR792753	—	—	—	this study
<i>Lycoperdon subperlatum</i>	KA120918 t	KP340208	—	—	KU764400	Kim et al. (2016)
<i>Lycoperdon subperlatum</i>	KA120693	KP340207	—	KU764388	—	Kim et al. (2016)
<i>Lycoperdon marginatum</i>	parker750822	DQ112632	—	—	—	Larsson & Jeppson (2008)
<i>Lycoperdon marginatum</i>	stb072	EU833661	—	—	—	Bates et al. 2009
<i>Lycoperdon norvegicum</i>	MJ5453	DQ112631	—	—	—	Larsson & Jeppson (2008)
<i>Vascellum curtisii</i>	HMAS 258878	OR792665	OR831258	OR853787	—	this study
<i>Vascellum curtisii</i>	HMAS 258879	OR792666	OR831259	OR853788	—	this study
<i>Vascellum curtisii</i>	NCP49	HQ235048	—	—	—	Miller et al. (2011)
<i>Vascellum curtisii</i>	NCP9	HQ235045	—	—	—	Miller et al. (2011)
<i>Vascellum curtisii</i>	HIP1	HQ235043	—	—	—	Miller et al. (2011)
<i>Vascellum curtisii</i>	AMP085	KY777489	—	—	—	Peli (2018)
<i>Vascellum pratense</i>	MJ5858	DQ112556	—	—	—	Larsson & Jeppson (2008)
<i>Vascellum pratense</i>	HMAS 258880	OR792664	PP175749	PP351953	—	this study
<i>Morganella fuliginea</i>	UFRN-Fungos 2575	KU958325	KU958326	—	—	Alfredo et al. (2017)
<i>Morganella fuliginea</i>	UFRN-Fungos 2579	KU958349	KU958350	—	—	Alfredo et al. (2017)
<i>Morganella fuliginea</i>	UFRN-Fungos 1971	KU958321	KU958322	—	—	Alfredo et al. (2017)
<i>Morganella fuliginea</i>	UFRN-Fungos 2568	KU958313	KU958314	—	—	Alfredo et al. (2017)
<i>Morganella nuda</i>	UFRN-Fungos 1766	KU958315	KU958316	—	—	Alfredo et al. (2017)
<i>Morganella</i> sp.	UFRN-Fungos 2554	KU958309	KU958310	—	—	Alfredo et al. (2017)
<i>Morganella</i> sp.	R-83	KR135347	—	—	—	Alfredo et al. (2017)
<i>Morganella oblongata</i>	UFRN-Fungos 2570	KU958355	KU958356	—	—	Alfredo et al. (2017)
<i>Morganella subincarnata</i>	EG106	AJ237626	—	—	—	Alfredo et al. (2017)

Table 2 Continued.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-α</i>	References
<i>Morganella subincarnata</i>	TNS Kasuya B286	KF551244	–	–	–	Alfredo et al. (2017)
<i>Morganella tricolor</i>	HMAS 287487	PP175741	PP175750		PP351959	this study
<i>Morganella sosinii</i>	YR2013	KC591769	–	–	–	Alfredo et al. (2017)
<i>Morganella purpurascens</i>	MEL 2382736	KP012918	–	–	–	Alfredo et al. (2017)
<i>Sinoperdon gyirongense</i>	HMAS 258791	OR792683	OR831252	OR853798	PP351984	this study
<i>Sinoperdon gyirongense</i>	HMAS 258792	OR792681	OR831238	OR853797	PP387665	this study
<i>Sinoperdon gyirongense</i>	HMAS 258798	OR792682	OR831247	–	–	this study
<i>Sinoperdon gyirongense</i>	HMAS 258799	OR792680	OR831237	OR853802	PP351989	this study
<i>Sinoperdon gyirongense</i>	HMAS 258789	OR792696	OR831246	OR853800	PP387667	this study
<i>Sinoperdon gyirongense</i>	HMAS 258787	OR792686	OR831248	OR853801	PP351990	this study
<i>Sinoperdon caudatum</i>	GC920818	DQ112633	–	–	–	Jeppson & Larsson (2010)
<i>Sinoperdon</i> sp.	ZRL20191589	OR792677	OR831236	OR853793	PP387663	this study
<i>Sinoperdon</i> sp.	ZRL20220977	OR792676	OR831235	OR853794	–	this study
<i>Sinoperdon</i> sp.	GX20170471	OR792627	OR831233	OR853808	PP387668	this study
<i>Sinoperdon</i> sp.	KA120505	KP340215	–	KU764387	–	Kim et al. (2016)
<i>Sinoperdon maritimum</i>	HMAS 287488	OR792626	OR831234	OR853807	PP387669	this study
<i>Fuscospina</i> sp.	KA131471	KP340188	–	–	–	Kim et al. (2016)
<i>Fuscospina scabricapillitia</i>	HMAS 258812 T	OR792678	PP175748	PP351958	PP351961	this study
<i>Fuscospina nigrescens</i>	MJ5376	DQ112577	–	–	–	Larsson & Jeppson (2008)
<i>Fuscospina nigrescens</i>	HMAS 258881	OR792702	OR831256	PP351957	PP351964	this study
<i>Pseudoperdon medogense</i>	HMAS 258782	OR792742	OR831253	–	PP387675	this study
<i>Pseudoperdon medogense</i>	HMAS 258783	OR792744	–	–	–	this study
<i>Pseudoperdon medogense</i>	HMAS 258784	OR792745	OR831254	OR853823	PP387674	this study
<i>Pseudoperdon medogense</i>	HMAS 258785	OR792746	OR831255	OR853824	–	this study
<i>Pseudoperdon medogense</i>	HMAS 258786	OR792743	–	–	–	this study
<i>Apioperdon pyriforme</i>	SJ980920	DQ112557	–	–	–	Larsson & Jeppson (2008)
<i>Apioperdon pyriforme</i>	MJ4849	DQ112558	–	–	–	Larsson & Jeppson (2008)
<i>Apioperdon pyriforme</i>	AFTOL-ID 480	AY854075	–	AY218495	AY883426	Vellinga et al. (2011)
<i>Apioperdon pyriforme</i>	EG181091Os	AJ237620	–	–	–	Vizzini & Ercole (2017)

Table 3 Taxa, vouchers, and GenBank accession numbers in the phylogeny of *Bovista*.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-α</i>	References
<i>Bovista tomentosa</i>	ML96.28	MT303138	—	—	—	Rebriev et al. (2020)
<i>Bovista tomentosa</i>	YuR3115	MH628581	—	—	—	Rebriev et al. (2020)
<i>Bovista tomentosa</i>	LE253893	MH628564	—	—	—	Rebriev et al. (2020)
<i>Bovista helenae</i>	LE253875	MH628572	—	—	—	Rebriev et al. (2020)
<i>Bovista altaica</i>	LE314839	MH628583	—	—	—	Rebriev et al. (2020)
<i>Bovista tomentosa</i>	MJ5433	DQ112616	—	—	—	Larsson & Jeppson (2008)
<i>Bovista hollosii</i>	P. Finy45	KT958937	—	—	—	Jeppson et al. (2016)
<i>Bovista hollosii</i>	MJ6045	KT958938	—	—	—	Jeppson et al. (2016)
<i>Bovista subcatastoma</i>	LE314841	MH628584	—	—	—	Rebriev et al. (2020)
<i>Bovista disciseda</i>	LE314840	MH628582	—	—	—	Rebriev et al. (2020)
<i>Bovista</i> sp.	YuR2470	MH628576	—	—	—	Rebriev et al. (2020)
<i>Bovista</i> sp.	YuR2255	MH628575	—	—	—	Rebriev et al. (2020)
<i>Bovista pezica</i>	APBP100	MK966425	—	—	—	Caffot et al. (2020)
<i>Bovista pezica</i>	LSD3232	MT444003	—	—	—	Caffot et al. (2020)
<i>Bovista pezica</i>	LSD3230	MT444002	—	—	—	Caffot et al. (2020)
<i>Bovista pila</i>	WBCooke52813	MT303139	—	—	—	Rebriev et al. (2020)
<i>Bovista pila</i>	OSC40127	MT444004	—	—	—	Rebriev et al. (2020)
<i>Bovista litangensis</i>	HMAS 258800	OR792635	OR831301	OR853765	PP351969	this study
<i>Bovista litangensis</i>	HMAS 258801	OR792636	OR831302	OR853764	PP351968	this study
<i>Bovista nigrescens</i>	S&JJ980905	DQ112612	—	—	—	Larsson & Jeppson (2008)
<i>Bovista nigrescens</i>	YuR3672	MT303137	—	—	—	Rebriev et al. (2020)
<i>Bovista graveolens</i>	Widgren 030816	DQ112618	—	—	—	Larsson & Jeppson (2008)
<i>Bovista graveolens</i>	YuR2923	MH628578	—	—	—	Rebriev et al. (2020)
<i>Bovista limosa</i>	EL4 06	EU915074	—	—	—	Larsson et al. (2009)
<i>Bovista limosa</i>	MJ60816	EU915075	—	—	—	Larsson et al. (2009)
<i>Bovista limosa</i>	YuR1649	MT303140	—	—	—	Rebriev et al. (2020)
<i>Bovista limosa</i>	MJ5226	DQ112615	—	—	—	Larsson & Jeppson (2008)
<i>Bovista echinella</i>	HMAS 287484	OR792634	OR831289	—	—	this study
<i>Bovista pusilla</i>	MJ8305	EU915072	—	—	—	Larsson et al. (2009)
<i>Bovista pusilla</i>	MJ8365	EU915073	—	—	—	Larsson et al. (2009)

Table 3 Continued.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-a</i>	References
<i>Bovista pusilla</i>	BMJ3971	DQ112614	—	—	—	Larsson & Jeppson (2008)
<i>Bovista nyalamensis</i>	HMAS 258836	OR792637	OR831304	OR853767	PP351972	this study
<i>Bovista nyalamensis</i>	HMAS 258837	OR792638	OR831306	OR853766	PP351971	this study
<i>Bovista nyalamensis</i>	HMAS 258838	OR792639	OR831305	OR853768	PP351970	this study
<i>Bovista</i> sp.	YuR1346	MT279450	—	—	—	Rebriev et al. (2020)
<i>Bovista plumbea</i>	MJ4856	DQ112613	—	—	—	Larsson & Jeppson (2008)
<i>Bovista plumbea</i>	NYGD01	JX183694	—	—	—	Yousaf et al. (2013)
<i>Bovista cretacea</i>	ANMH11622	DQ112611	—	—	—	Larsson & Jeppson (2008)
<i>Bovista cretacea</i>	MJ5207	DQ112610	—	—	—	Larsson & Jeppson (2008)
<i>Bovista cretacea</i>	YuR3725	MT303135	—	—	—	Rebriev et al. (2020)
<i>Bovista paludosa</i>	YuR1344	MH628568	—	—	—	Rebriev et al. (2020)
<i>Bovista paludosa</i>	MJ4301	DQ112609	—	—	—	Larsson & Jeppson (2008)
<i>Calvatia craniiformis</i>	Steinke001017	DQ112625	—	—	—	Larsson & Jeppson (2008)
<i>Calvatia candida</i>	MJ3514	DQ112624	—	—	—	Larsson & Jeppson (2008)

Table 4 Taxa, Vouchers, and GenBank Accession Numbers in the Phylogeny of *Globalia*.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-a</i>	References
<i>Globalia polymorpha</i>	TENN58028	AJ237613	—	—	—	Krüger et al. (2001)
<i>Globalia aestivalis</i>	HMAS 258882	OR792663	OR831290	—	—	this study
<i>Globalia aestivalis</i>	MJ3860	DQ112619	—	—	—	Larsson & Jeppson (2008)
<i>Globalia aestivalis</i>	STB0124	FJ438477	—	—	—	Bates et al. (2009)
<i>Globalia aestivalis</i>	MJ1122	DQ112620	—	—	—	Larsson & Jeppson (2008)
<i>Globalia gyirongensis</i>	HMAS 258813	OR792660	OR831288	OR853785	PP351977	this study
<i>Globalia gyirongensis</i>	HMAS 258814	OR792661	OR831287	OR853786	PP351976	this study
<i>Globalia shannanensis</i>	HMAS 258883	OR792662	OR831303	—	—	this study
<i>Globalia albata</i>	HMAS 258884	OR792659	OR831270	OR853784	—	this study
<i>Globalia promontorii</i>	MJ7070	DQ112621	—	—	—	Larsson & Jeppson (2008)

Table 4 Continued.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-α</i>	References
<i>Globalia himalaica</i>	MH 2011	JX183689	–	–	–	Yousaf et al. (2013)
<i>Globalia himalaica</i>	NYGL5 T	JX183690	–	–	–	Yousaf et al. (2013)
<i>Globalia himalaica</i>	NYG3	JX183693	–	–	–	Yousaf et al. (2013)
<i>Globalia jingningensis</i>	HMAS 258815	OR792644	OR831273	–	–	this study
<i>Globalia jingningensis</i>	HMAS 258816	OR792645	OR831272	OR853770	–	this study
<i>Globalia jingningensis</i>	HMAS 258817	OR792642	OR831271	OR853769	PP351967	this study
<i>Globalia jingningensis</i>	HMAS 258818	OR792643	OR831274	–	–	this study
<i>Globalia testacea</i>	HMAS 258819	OR792656	OR831280	OR853778	–	this study
<i>Globalia testacea</i>	HMAS 258820	OR792655	OR831283	–	–	this study
<i>Globalia testacea</i>	HMAS 258821	OR792653	OR831251	OR853779	–	this study
<i>Globalia testacea</i>	HMAS 258822	OR792654	OR831282	OR853783	–	this study
<i>Globalia testacea</i>	HMAS 258823	OR792651	OR831275	OR853781	–	this study
<i>Globalia testacea</i>	HMAS 258824	OR792657	OR831286	OR853782	–	this study
<i>Globalia testacea</i>	HMAS 258825	OR792658	OR831279	OR853780	–	this study
<i>Globalia testacea</i>	HMAS 258826	OR792647	OR831284	OR853776	–	this study
<i>Globalia testacea</i>	HMAS 258827	OR792648	OR831285	OR853773	–	this study
<i>Globalia testacea</i>	HMAS 258828	OR792646	OR831281	OR853777	–	this study
<i>Globalia testacea</i>	HMAS 258829	OR792649	OR831278	–	–	this study
<i>Globalia testacea</i>	HMAS 258830	OR792652	OR831277	OR853774	–	this study
<i>Globalia testacea</i>	HMAS 258831	OR792650	OR831276	OR853775	–	this study
<i>Globalia furfuracea</i>	MJ5435	DQ112622	–	–	–	Larsson & Jeppson (2008)
<i>Globalia furfuracea</i>	YuR3037	MH628579	–	–	–	Rebriev et al. (2020)
<i>Globalia muscicola</i>	HMAS 258834	OR792640	OR831269	OR853772	PP351974	this study
<i>Globalia muscicola</i>	HMAS 258835	OR792641	OR831268	OR853771	PP351975	this study
<i>Calvatia craniiformis</i>	Steinke001017	DQ112625	–	–	–	Larsson & Jeppson (2008)
<i>Calvatia candida</i>	MJ3514	DQ112624	–	–	–	Larsson & Jeppson (2008)

Table 5 Taxa, Vouchers, and GenBank Accession Numbers in the Phylogeny of *Calvatia*.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-α</i>	References
<i>Calvatia candida</i>	Strain PB101	GU939632.1	—	—	—	Unpublished
<i>Calvatia</i> sp.	ZRL20162233	OR792619	OR831231	—	—	this study
<i>Calvatia holothurioides</i>	LE 287408	JQ734547.1	—	—	—	Rebriev et al. (2013)
<i>Calvatia holothurioides</i>	KA11-0287	KJ909662.1	—	—	—	Kim et al. (2016)
<i>Calvatia longisetulosa</i>	HMAS 258802	OR792617	OR831229	OR853757	PP351981	this study
<i>Calvatia longisetulosa</i>	HMAS 258803	OR792618	OR831230	OR853758	PP351982	this study
<i>Calvatia nodulata</i>	UFRN Fungos 1691	KP751206	—	—	—	Alfredo et al. (2014)
<i>Calvatia nodulata</i>	BAFC 4549	KY366490	—	—	—	Alfredo et al. (2014)
<i>Calvatia</i> sp.	HMAS 258833	OR792620	—	—	—	this study
<i>Calvatia rubroflava</i>	TENN59078	AF485064	—	—	—	Krüger et al. (2003)
<i>Calvatia rubroflava</i>	TFB11269	KY559335.1	—	—	—	Senthilarasu et al. (2018)
<i>Calvatia</i> aff. <i>rugosa</i>	MEL 2382849	KP012724.1	—	—	—	Senthilarasu et al. (2018)
<i>Calvatia shennongjiaensis</i>	HMAS 258804	OR792621	OR831294	OR853761	PP351978	this study
<i>Calvatia shennongjiaensis</i>	HMAS 258805	OR792622	—	—	—	this study
<i>Calvatia shennongjiaensis</i>	HMAS 258806	OR792623	OR831291	OR853759	PP351979	this study
<i>Calvatia shennongjiaensis</i>	HMAS 258807	OR792624	OR831293	—	PP351966	this study
<i>Calvatia shennongjiaensis</i>	HMAS 258808	OR792625	OR831292	OR853760	PP351980	this study
<i>Calvatia craniiformis</i>	TNS Kasuya B734	KF551248.1	—	—	—	Senthilarasu et al. (2018)
<i>Calvatia candida</i>	MJ3514	DQ112624.1	—	—	—	Larsson & Jeppson (2008)
<i>Calvatia craniiformis</i>	Steinke001017	DQ112625	—	—	—	Larsson & Jeppson (2008)
<i>Calvatia fragilis</i>	AH 24114	AJ486959.1	—	—	—	Senthilarasu et al. (2018)
<i>Calvatia fragilis</i>	AH 25227	AJ486958.1	—	—	—	Senthilarasu et al. (2018)
<i>Calvatia fragilis</i>	K 56043	AJ486960.1	—	—	—	Senthilarasu et al. (2018)
<i>Calvatia fragilis</i>	AH 18553	AJ486870.1	—	—	—	Senthilarasu et al. (2018)
<i>Calvatia fragilis</i>	Sydow 941 (M)	AJ486871.1	—	—	—	Bates et al. (2009)
<i>Calvatia fragilis</i>	Cragin 523NY	AJ486957.1	—	—	—	Senthilarasu et al. (2018)
<i>Calvatia cyathiformis</i>	Strain JTT10	MF686508.1	—	—	—	Senthilarasu et al. (2018)
<i>Calvatia cyathiformis</i> var. <i>cyathiformis</i>	AH 25225	AJ486866.1	—	—	—	Bates et al. (2009)
<i>Calvatia cyathiformis</i>	MP12	KY706183.1	—	—	—	Senthilarasu et al. (2018)

Table 5 Continued.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-α</i>	References
<i>Calvatia cyathiformis</i> var. <i>cyathiformis</i>	AH 25232	AJ486864.1	–	–	–	Senthilarasu et al. (2018)
<i>Calvatia cyathiformis</i> var. <i>crucibulum</i>	HAJB 2811	AJ486869.1	–	–	–	Senthilarasu et al. (2018)
<i>Calvatia fragilis</i>	AH 21915	AJ486961.1	–	–	–	Senthilarasu et al. (2018)
<i>Calvatia fragilis</i>	PAD 3309	AJ486962.1	–	–	–	Senthilarasu et al. (2018)
<i>Calvatia fragilis</i>	AH 25228	AJ486963.1	–	–	–	Senthilarasu et al. (2018)
<i>Calvatia pachydermica</i>	AN014692	EU833653.1	–	–	–	Bates et al. (2009)
<i>Calvatia fenzlii</i>	Strain Jz01	FJ772413.1	–	–	–	Senthilarasu et al. (2018)
<i>Calvatia</i> cf. <i>leiospora</i>	AN014671	EU833652.1	–	–	–	Bates et al. (2009)
<i>Calvatia bicolor</i>	LMG75658	EU833651	–	–	–	Bates et al. (2009)
<i>Calvatia gigantea</i>	MJ3566	DQ112623	–	–	–	Larsson & Jeppson (2008)
<i>Calvatia gigantea</i>	HMAS 258889	OR792628	OR831299	OR853762	PP351983	this study
<i>Calvatia subbooniana</i>	HMAS 258809	OR792631	OR831296	–	–	this study
<i>Calvatia subbooniana</i>	HMAS 258810	OR792630	OR831297	–	–	this study
<i>Calvatia subbooniana</i>	HMAS 258811	OR792629	–	–	–	this study
<i>Disciseda candida</i>	STB304	EU833654	–	–	–	Bates et al. (2009)
<i>Disciseda cervina</i>	FK17016	MN338568	–	–	–	Unpublished
<i>Disciseda cervina</i>	FK1802	MN338569	–	–	–	Unpublished
<i>Disciseda cervina</i>	FK1801	MN338570	–	–	–	Unpublished
<i>Disciseda</i> sp.	BJTC06072350	OR792633	OR831295	OR853763	PP351965	this study
<i>Disciseda</i> sp.	BJTC06072239	–	PP175751	PP351954	–	this study

Table 6 Taxa, vouchers, and GenBank accession numbers in the phylogeny of *Morganella*.

Species	Voucher/specimen numbers	ITS	LSU	References
<i>Morganella fuliginea</i>	UFRN-Fungos 2579	KU958349	KU958350	Alfredo et al. (2017)
<i>Morganella fuliginea</i>	UFRN-Fungos 2582	KU958339	KU958340	Alfredo et al. (2017)
<i>Morganella fuliginea</i>	UFRN-Fungos 2586	KU958343	KU958344	Alfredo et al. (2017)

Table 6 Continued.

Species	Voucher/specimen numbers	ITS	LSU	References
<i>Morganella nuda</i>	UFRN-Fungos 2565	KU958311	KU958312	Alfredo et al. (2017)
<i>Morganella nuda</i>	UFRN-Fungos 1766	KU958315	KU958316	Alfredo et al. (2017)
<i>Morganella nuda</i>	UFRN-Fungos 2568	KU958313	KU958314	Alfredo et al. (2017)
<i>Morganella nuda</i>	ICN 154541	KU958317	KU958318	Alfredo et al. (2017)
<i>Morganella nuda</i>	UFRN-Fungos 1765	KU958319	KU958320	Alfredo et al. (2017)
<i>Morganella allostipitata</i>	INPA 239563	KU958363	KU958364	Alfredo et al. (2017)
<i>Morganella allostipitata</i>	UFRN-Fungos 2249	KU958361	KU958362	Alfredo et al. (2017)
<i>Morganella allostipitata</i>	UFRN-Fungos 2569	KU958357	KU958358	Alfredo et al. (2017)
<i>Morganella allostipitata</i>	UFRN-Fungos 2572	KU958359	KU958360	Alfredo et al. (2017)
<i>Morganella oblongata</i>	UFRN-Fungos 2570	KU958355	KU958356	Alfredo et al. (2017)
<i>Morganella tricolor</i>	HMAS 287487	PP175741	PP175750	this study
<i>Morganella purpurascens</i>	MEL 2382736	KP012918	–	Alfredo et al. (2017)
<i>Morganella sosinii</i>	YR2013	KC591769	–	Alfredo et al. (2017)
<i>Morganella sosinii</i>	VLA 15520	KC59176	–	Alfredo et al. (2017)
<i>Morganella subincarnata</i>	EG106	AJ237626	–	Alfredo et al. (2017)
<i>Morganella subincarnata</i>	TNS Kasuya B286	KF551244	–	Alfredo et al. (2017)
<i>Vascellum curtisii</i>	HMAS 258878	OR792665	OR831258	this study
<i>Vascellum curtisii</i>	HMAS 258879	OR792666	OR831259	this study
<i>Vascellum</i> sp.	UFRN-Fungos 814	KU958375	KU958376	Alfredo et al. (2017)
<i>Vascellum pratense</i>	MJ5858	DQ112556	–	Larsson & Jeppson (2008)
<i>Vascellum pratense</i>	HMAS 258880	OR792664	PP175749	this study
<i>Lycoperdon arenicola</i>	UFRN Fungos 656	KU958291	KU958292	Alfredo et al. (2017)
<i>Lycoperdon arenicola</i>	UFRN Fungos 1006	KU958303	KU958304	Alfredo et al. (2017)
<i>Lycoperdon arenicola</i>	UFRN Fungos 649	KU958297	KU958298	Alfredo et al. (2017)
<i>Lycoperdon</i> sp.	UFRN Fungos 655	KU958307	KU958308	Alfredo et al. (2017)
<i>Lycoperdon</i> sp.	UFRN Fungos 2554	KU958309	KU958310	Alfredo et al. (2017)
<i>Lycoperdon norvegicum</i>	MJ5453	DQ112631	–	Larsson & Jeppson (2008)
<i>Lycoperdon perlatum</i>	MJ4684	DQ112630	–	Larsson & Jeppson (2008)
<i>Lycoperdon perlatum</i>	HMAS 258865	OR792758	OR831262	this study
<i>Lycoperdon perlatum</i>	HMAS 258866	OR792763	OR831257	this study

Table 6 Continued.

Species	Voucher/specimen numbers	ITS	LSU	References
<i>Lycoperdon perlatum</i>	HMAS 258867	OR792760	OR831263	this study
<i>Lycoperdon perlatum</i>	HMAS 258904	OR792759	OR831265	this study
<i>Lycoperdon subperlatum</i>	HMAS 258873	OR792751	OR831261	this study
<i>Lycoperdon subperlatum</i>	HMAS 258875	OR792750	OR831260	this study
<i>Lycoperdon subperlatum</i>	KA120918	KP340208	–	Kim et al. (2016)
<i>Lycoperdon subperlatum</i>	KA120693	KP340207	–	Kim et al. (2016)
<i>Apioperdon pyriforme</i>	QL20170019	PP175742	PP175746	this study
<i>Apioperdon pyriforme</i>	ZRL20182005	PP175743	PP175747	this study
<i>Apioperdon pyriforme</i>	UFRN Fungos 155	KU958365	KU958366	Alfredo et al. (2017)
<i>Apioperdon pyriforme</i>	MJ4849	DQ112558	–	Larsson & Jeppson (2008)
<i>Bovista paludosa</i>	MJ4301	DQ112609	–	Larsson & Jeppson (2008)
<i>Bovista cretacea</i>	ANMH11622	DQ112611	–	Larsson & Jeppson (2008)

Table 7 Taxa, sequence data for estimation of divergence times in *Agaricaceae* s.l.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-α</i>	References
<i>Leucoagaricus cf. rubrotinctus</i>	HKAS54240	JN944081	JN940295	JN993684	–	Unpublished
<i>Leucoagaricus rubroconfusus</i>	ZT13003	KP300875	–	HM488853	HM488916	Ge et al. (2015)
<i>Leucoagaricus subcrystallifer</i>	Z.W. Ge 878 T	KP096236	–	KP096240	–	Ge et al. (2015)
<i>Leucoagaricus subpurpureolilacinus</i>	Z.W. Ge 406 T	KP096233	–	KP096241	–	Ge et al. (2015)
<i>Leucoagaricus pakistaniensis</i>	LAH SJF13 T	KU647727	KU900515	KY965808	KU900512	Hussain et al. (2018)
<i>Leucoagaricus lahorensiformis</i>	LAH SH L2 T	KU647729	KU900517	KU900509	KU900511	Hussain et al. (2018)
<i>Leucoagaricus sultanii</i>	LAH SH 115 T	KU647733	KU900519	KU900523	KU900513	Hussain et al. (2018)

Table 7 Continued.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-α</i>	References
<i>Leucoagaricus orientiflavus</i>	HKAS 54260 T	GU084262	JN940290	JN993687		Ge (2010)
<i>Lepiota flammeotincta</i>	ecv3315	GU136165	–	HM488831	HM488904	Vellinga et al. (2011)
<i>Leucoagaricus barssii</i>	ecv3126	DQ911600	DQ911601	DQ911602	HM488924	Vellinga et al. (2011)
<i>Termiticola</i> sp.	TL6106	AY176352	AY176353	–	–	Vellinga (2004)
<i>Leucoagaricus pardalotus</i>	ecv3313 T	GQ258479	–	HM488829	–	Vellinga et al. (2011)
<i>Leucoagaricus sabinae</i>	ANGE305 Paratype	KM983666	KM983668	–	–	Justo et al. (2015a)
<i>Leucocoprinus</i> sp.	LE2017034	PP151904	–	–	–	this study
<i>Micropsalliot delicatula</i>	ZRL2015249 T	MT671229	–	–	–	this study
<i>Micropsalliot digitatocystis</i>	ZRL20180564 T	MT671239	MT671250	–	–	this study
<i>Podaxis pistillaris</i>	PREM 34405	KT844877	KT844831	–	–	Conlon et al. (2016)
<i>Podaxis rugospora</i>	PREM 27280	KT844863	KT844827	–	–	Conlon et al. (2016)
<i>Pseudolepiota zangmui</i> T	Ge2106	KY768927	–	–	–	Ge & Yang (2017)
<i>Pseudolepiota zangmui</i>	FLU100515	KX904355	–	–	–	Ge & Yang (2017)
<i>Pseudolepiota zangmui</i>	Ge2175	KY768928	MG742049	KY768929	MG742106	Ge & Yang (2017)
<i>Coniolepiota spongodes</i> T	ecv3898	HM488755		HM488798	HM488882	Vellinga et al. (2011)
<i>Coniolepiota spongodes</i>	ZRL2012204	PP158529	PP152291	–	–	this study
<i>Hymenagaricus saisamornaeg</i>	LD2012186	KM982451	KM982453	–	–	Kumla et al. (2021)
<i>Hymenagaricus</i> sp.	glgs20170163	PP158531	PP152283	–	–	this study
<i>Heinemannomyces splendidissima</i> T	ecv3586	HM488760	HM488769	HM488793	–	Vellinga et al. (2011)
<i>Agaricus kerriganii</i>	LAPAG808	KT951306	KT951442	KT951528	KT951589	Zhao et al. (2017)
<i>Agaricus augustus</i>	ZRL2012598	KT951373	KT951477	–	KT951629	Zhao et al. (2017)
<i>Barcheria willisiana</i>	MEL2177563	JF495036	AY372216	–	–	Lebel & Syme (2012)
<i>Barcheria willisiana</i>	Bougher H7564	JF495038	JF495019	–	–	Lebel & Syme (2012)
<i>Clarkeinda trachodes</i>	ZRL2013322	PP158530	PP152287	–	–	this study
<i>Eriocybe chionea</i> T	ecv3560	HM488752	HM488773	HM488800	–	Vellinga et al. (2011)
<i>Chlorophyllum globosum</i>	LE2019002	PP217292	PP152290	–	–	this study
<i>Chlorophyllum hortense</i>	GX20170707	PP217294	PP152289	–	–	this study

Table 7 Continued.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-α</i>	References
<i>Chlorophyllum sphaerosporum</i>	ZRL20191953	PP217293	PP152284	–	–	this study
<i>Macrolepiota orientiexcoriata</i>	HKAS 45863 Type	NR_119833	JN940279	JN993682	–	Ge (2010)
<i>Macrolepiota colombiana</i>	NY-EFM694	U85311.1	U85276.1	–	–	Ge (2010)
<i>Calvatia gigantea</i>	Strain 9 7A	HM237179	–	–	–	Unpublished
<i>Calvatia cyathiformis</i> var. <i>cyathiformis</i>	AH 25225	AJ486866.1	–	–	–	Bates et al. (2009)
<i>Disciseda bovista</i>	MJ5078	DQ112627	–	–	–	Larsson & Jeppson (2008)
<i>Bovista aestivalis</i>	MJ1122	DQ112620	–	–	–	Larsson & Jeppson (2008)
<i>Apioperdon pyiforme</i>	QL20170019	PP175742	PP175746	–	–	this study
<i>Bryoperdon acuminatum</i>	TOHG201016	KY581202	KY581200	–	–	Vizzini & Ercole (2017)
<i>Bryoperdon acuminatum</i>	TOHG191016	KY581201	KY581199	–	–	Vizzini & Ercole (2017)
<i>Lycoperdon ericaeum</i>	KA131463	KP340185	–	KU764396	KU764404	Kim et al. (2016)
<i>Abstoma purpureum</i>	UZ-04-19	MN231720	–	–	–	Altaf et al. (2022)
<i>Abstoma purpureum</i>	KM162954	GQ981488	–	–	–	Unpublished
<i>Mycenastrum corium</i>	MJ5467	DQ112628	–	–	–	Larsson & Jeppson (2008)
<i>Mycenastrum corium</i>	KA17 0641	MK351723.1	–	–	–	Kim et al. (2016)
<i>Melanophyllum haemospermum</i>	E.C. Vellinga 2249	AF391038	–	–	–	Vellinga et al. (2011)
<i>Cystolepiota pseudofumosifolia</i>	HMAS276122	KF804000	–	–	–	Xu et al. (2016)
<i>Chamaemyces fracidus</i>	TAA172045	–	AM946419	–	–	Vellinga et al. (2011)
<i>Melanophyllum eyrei</i>	TL6692	AY176493	–	–	–	Kasuya & Knudsen (2003)
<i>Cystolepiota</i> aff. <i>seminuda</i>	HKAS 92275	MN810149	MN810101	MN820980	MN820926	Hou & Ge (2020)
<i>Echinoderma flavidoasperum</i>	HKAS 87905	MN810147	MN810098	MN820969	MN820903	Hou & Ge (2020)
<i>Echinoderma asperum</i>	HKAS 84240	MN810136	MN810090	MN820965	MN820909	Hou & Ge (2020)
<i>Smithiomyces asiaticus</i>	HKAS 54324	MW522981	–	–	–	Ge et al. (2021)
<i>Smithiomyces lepiotoides</i>	HKAS 54388	MW522982	–	–	–	Ge et al. (2021)

Table 7 Continued.

Species	Voucher/specimen numbers	ITS	LSU	<i>rpb2</i>	<i>tef1-α</i>	References
<i>Smithiomyces dominicanus</i>	CA18	KR604686	–	–	–	Justo et al. (2015b)
<i>Smithiomyces mexicanus</i>	UTC258259	JX409901	JX409900	–	–	Justo et al. (2015b)
<i>Lepiota</i> aff. <i>Carinii</i>	NL2202	MK277953	MK277953	–	–	Hou & Ge (2020)
<i>Lepiota alba</i>	HKAS 90371	MN810115	MN810075	MN820946	MN820930	Hou & Ge (2020)
<i>Lepiota brunneoincarnata</i>	LE2017053	PP152237	PP152288	–	–	this study
<i>Lepiota geocarpa</i>	UTC00143916	HQ020412	EU130550	MN820945	MN820935	Hou & Ge (2020)
<i>Lepiota jacobii</i>	HKAS 48802	MN810138	GU199356	MN820953	–	Hou & Ge (2020)
<i>Lepiota maculans</i>	JMB 05080918	HM222939	HQ832458	HQ832436	–	Hou & Ge (2020)
<i>Lepiota menegi</i>	UTC00253524	MN810131	MN810082	MN820942	MN820936	Hou & Ge (2020)
<i>Lepiota omninoflava</i>	HKAS 106734	MN810157	MN810092	MN820951	MN820923	Hou & Ge (2020)
<i>Lepiota venenata</i>	HKAS 105751	MN810128		MN820958	MN820927	Hou & Ge (2020)
<i>Coprinus</i> sp.	ZRL20152555	PP152257	PP152285	–	–	this study
<i>Coprinus comatus</i>	ZRL20181306	PP152258	PP152286	–	–	this study
<i>Phellorinia herculanea</i>	BCC-MPM1050	AF097753	–	–	–	Martin et al. (2000)
<i>Phellorinia longistriatica</i>	LE2017059	MZ047792	MZ047794	–	–	this study
<i>Dictyocephalos attenuatus</i>	AH 19028	AF095688	–	–	–	Martin et al. (2000)
<i>Dictyocephalos xinjiangensis</i>	ZRL20151108	MZ047791	MZ047793	–	–	this study
<i>Chlamydopus meyenianus</i>	AH 18743	AF097755	–	–	–	Martin et al. (2000)
<i>Tulostoma beccarianum</i>	Finy 2	KU519076	KU519076	–	KU843959	Jeppson et al. (2017)
<i>Tulostoma calcareum</i>	Jeppson 6965 T	KU519086	KU519086	–	KU843881	Jeppson et al. (2017)
<i>Crepidotus</i> cf. <i>applanatus</i>	PBM 717	DQ202273	AY380406	AY333311	–	Matheny et al. (2007)
<i>Neopaxillus dominicanus</i>	MCVE 26928	JN033216.1	JN033217.1	–	–	Vizzini et al. (2012)
<i>Simocybe serrulata</i>	AFTOL_ID_970	DQ494696	AY745706	DQ484053	–	Matheny et al. (2006)
<i>Inocybe jarrahae</i>	PBM 2207	–	AY380381	AY337382	–	Matheny et al. (2006)
<i>Inocybe</i> sp.	ZT 8944	–	EU600903	EU600902	–	Matheny (2005)
<i>Pleuroflammula praestans</i>	ZRL2015066	LT716043	KY418859	KY419005	–	Zhao et al. (2017)

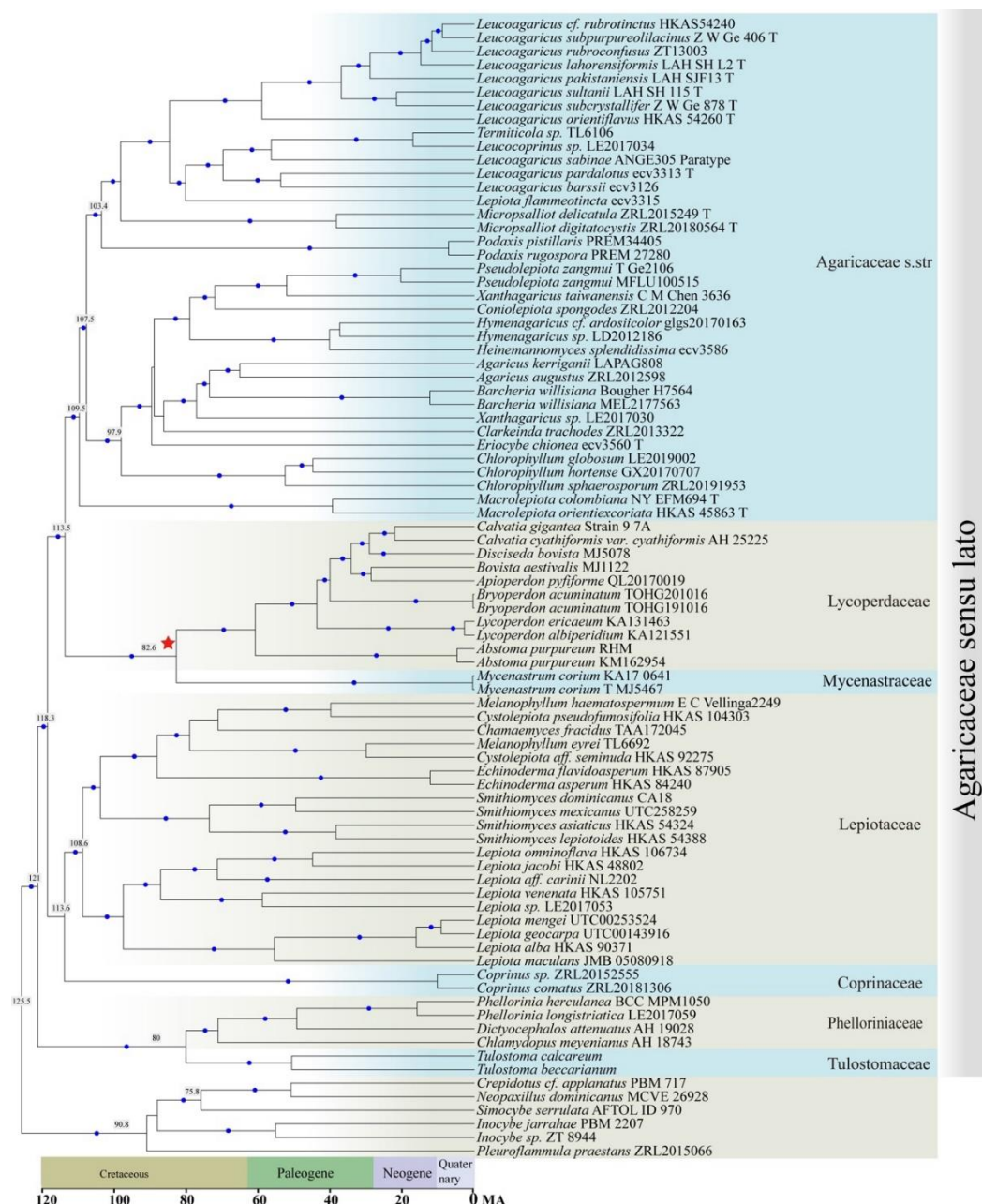


Figure 2 – Maximum Clade Credibility tree of *Agaricaceae* s.l. based on ITS, nrLSU, *rpb2*, and *tef1- α* genes, with outgroup species selected from *Crepidotaceae* and *Inocybaceae*. Nodes indicate the divergence times of *Agaricaceae* s.str., *Coprinaceae*, “*Lepiotaceae*”, *Mycenastraceae*, *Phelloriniaceae* and *Tulostomataceae*, with *Lycoperdaceae* marked by red asterisks. Branches supported by both (BS) $\geq 70\%$ or (PP) ≥ 0.80 are highlighted.

Table 8 Estimated divergence times in *Lycoperdaceae*, with abbreviations corresponding to different genera.

Genera recognized in this study	Abbreviations	Mean of stem age (Myr)	PP values
<i>Abstoma</i> G. Cunn. 1926	<i>Ab.</i>	75.5	1
<i>Apioperdon</i> (Kreisel & D. Krüger) Vizzini 2017	<i>Ap.</i>	55	1
<i>Arachnion</i> Schwein. 1822	<i>Ar.</i>	55	1
<i>Bovista</i> Pers. 1794	<i>Ba.</i>	55	1

Table 8 Continued.

Genera recognized in this study	Abbreviations	Mean of stem age (Myr)	PP values
<i>Bovistella</i> Morgan 1892	<i>Be.</i>	30.9	0.8
<i>Bryoperdon</i> Vizzini 2017	<i>Br.</i>	55	1
<i>Calvatia</i> Fr. 1849	<i>C.</i>	61.1	1
<i>Disciseda</i> Czern. 1845	<i>D.</i>	62.5	1
<i>Fuscospina</i> R.L. Zhao & J.X. Li, gen. nov.	<i>F.</i>	34.5	1
<i>Globaria</i> Quél. 1873	<i>G.</i>	55	1
<i>Holocotylon</i> Lloyd 1906	<i>H.</i>	34.4	1
<i>Leptocaulis</i> R.L. Zhao & J.X. Li, gen. nov.	<i>Le.</i>	26.7	1
<i>Lycoperdiscus</i> R.L. Zhao & J.X. Li, gen. nov.	<i>Li.</i>	30.9	0.8
<i>Lycoperdon</i> Pers. 1794	<i>Lo.</i>	27.7	1
<i>Morganella</i> Zeller 1948	<i>M.</i>	33.1	1
<i>Pseudoperdon</i> R.L. Zhao & J.X. Li, gen. nov.	<i>P.</i>	34.5	1
<i>Sinoperdon</i> R.L. Zhao & J.X. Li, gen. nov.	<i>S.</i>	34.5	1
<i>Utraria</i> Quél. 1873	<i>U.</i>	26.7	1
<i>Vascellum</i> F. S. marda 1958	<i>V.</i>	27.7	1

Phylogeny of *Lycoperdon* s.l.

A combined dataset of four-gene sequences was utilized to deduce the phylogeny of *Lycoperdon*, encompassing 443 sequences (198 for ITS, 122 for nrLSU, 57 for *rpb2*, 66 for *tef1- α*) from 198 specimens. The dataset also incorporated 153 sequences retrieved from GenBank, primarily generated by (Larsson & Jeppson 2008, Larsson et al. 2009, Jeppson et al. 2012, Kim et al. 2016). Sequence data for this part are provided in Table 2. The GTR+I+G model was determined as the best fit for this combined dataset and was employed in the Bayesian inference (BI) analysis. Both Maximum Likelihood (ML) and BI analyses yielded nearly identical topologies, with minimal variation in statistical support values. The BI tree was selected for display in Fig. 3.

The phylogenetic analysis indicates that the previously identified *Lycoperdon* s.l. forms a monophyletic group, strongly supported by both bootstrap values and posterior probabilities. The results reveal that *Lycoperdon* s.l. is subdivided into eleven subclades, all of which are elevated to the generic level in this study. Among these, five were previously recognized as *Lycoperdon* subgenera, namely *Bovistella*, *Lycoperdon*, *Morganella*, *Utraria*, and *Vascellum*. Additionally, six subclades were newly identified in this study, corresponding to a monophyletic genus *Holocotylon* and five newly proposed genera named *Fuscospina*, *Leptocaulis*, *Lycoperdiscus*, *Pseudoperdon*, and *Sinoperdon*.

As depicted in Fig. 3, *Lycoperdon*, together with *Morganella* and *Vascellum*, forms a core lineage with strong support (PP values = 0.9), consistent with previous studies (Bates et al. 2009, Gube 2009, Alfredo et al. 2017). Additionally, *Holocotylon*, historically a genus accommodating only one species, *Holocotylon brandegeeanum* Lloyd, clusters with *Holocotylon dermoxanthum* (= *Lycoperdon dermoxanthum* Vittad.) and *Holocotylon rupicola* (= *Lycoperdon rupicola* Jeppson, E. Larss. & M.P. Martín), forming a subclade.

The newly proposed genus *Sinoperdon* forms a distinct lineage with high support in BI values (PP = 0.9), represented by *Sinoperdon caudatum* (= *Lycoperdon caudatum* J. Schröt.) and several closely related taxa. The phylogenetic position of *Sinoperdon caudatum* was previously unclear in previous studies (Larsson & Jeppson 2008, Alfredo et al. 2017). To address this, a new genus is

proposed here to better categorize these taxa. The second proposed genus, *Pseudoperdon*, is established to accommodate *Pseudoperdon subcretaceum* (= *Lycoperdon subcretaceum* (Zeller) Jeppson & E. Larss.) and *Pseudoperdon medogense* R.L. Zhao & J.X. Li sp. nov. This genus forms a subclade that receives full support in both ML and BI analyses. The third newly proposed genus includes *Fuscospina scabroscapillitium* R.L. Zhao & J.X. Li sp. nov. and *Fuscospina nigrescens* (= *Lycoperdon nigrescens* Pers). In previous phylogenetic studies, *F. nigrescens* was tentatively placed in *Lycoperdon* subg. *Utraria* due to its separation from most species of *Utraria* and its more distant location.

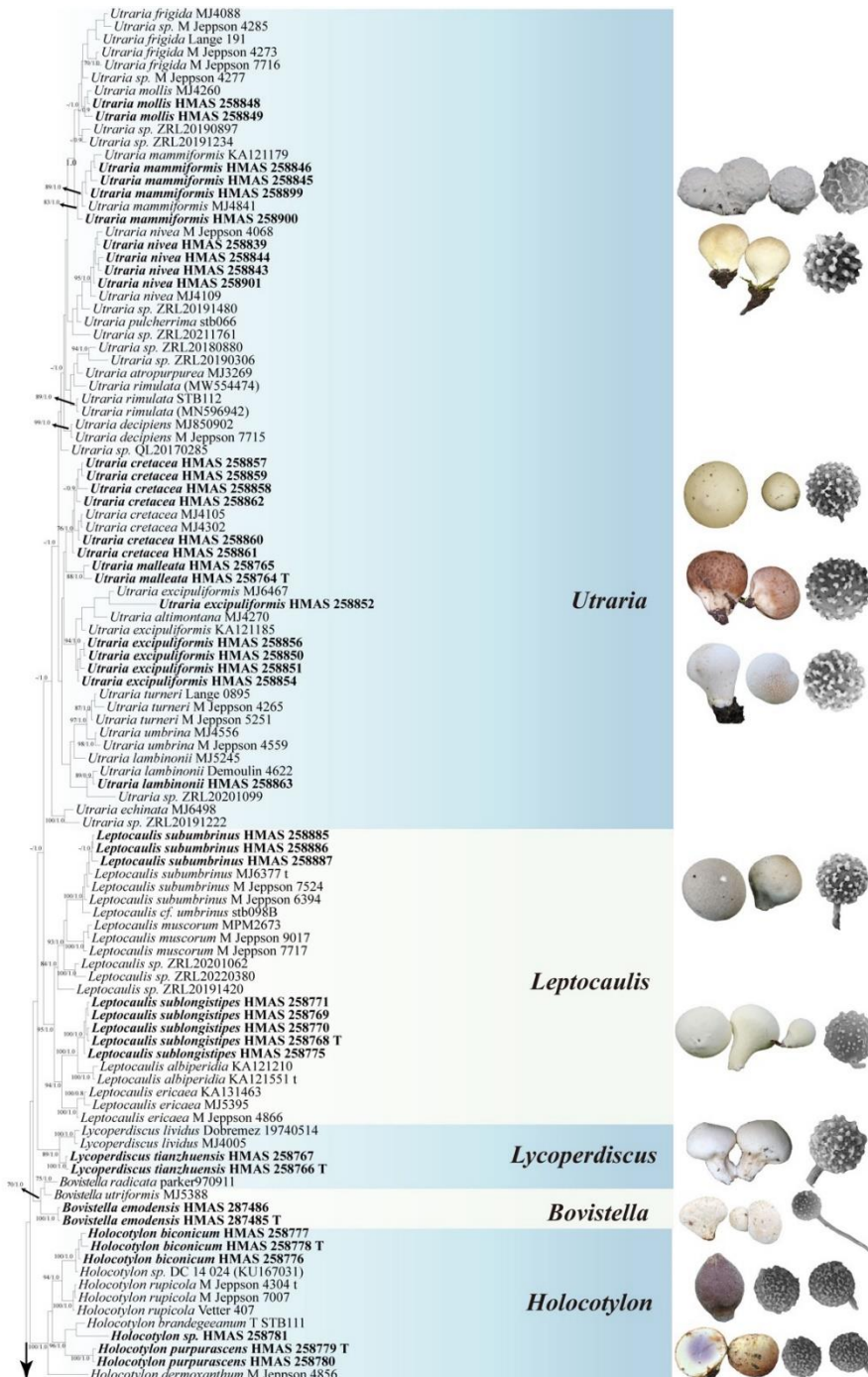


Figure 3 – Phylogenetic tree of *Lycoperdon* s.l. inferred from ITS, nrLSU, *rpb2*, and *tef1-α* sequences, rooted by *Apiopedon pyriforme*. Branches supported by both (BS) ≥ 70% and (PP) ≥ 0.80 are indicated. Eleven generic names are labeled, with newly proposed names marked by a red asterisk. The examined specimens in this study are in bold.

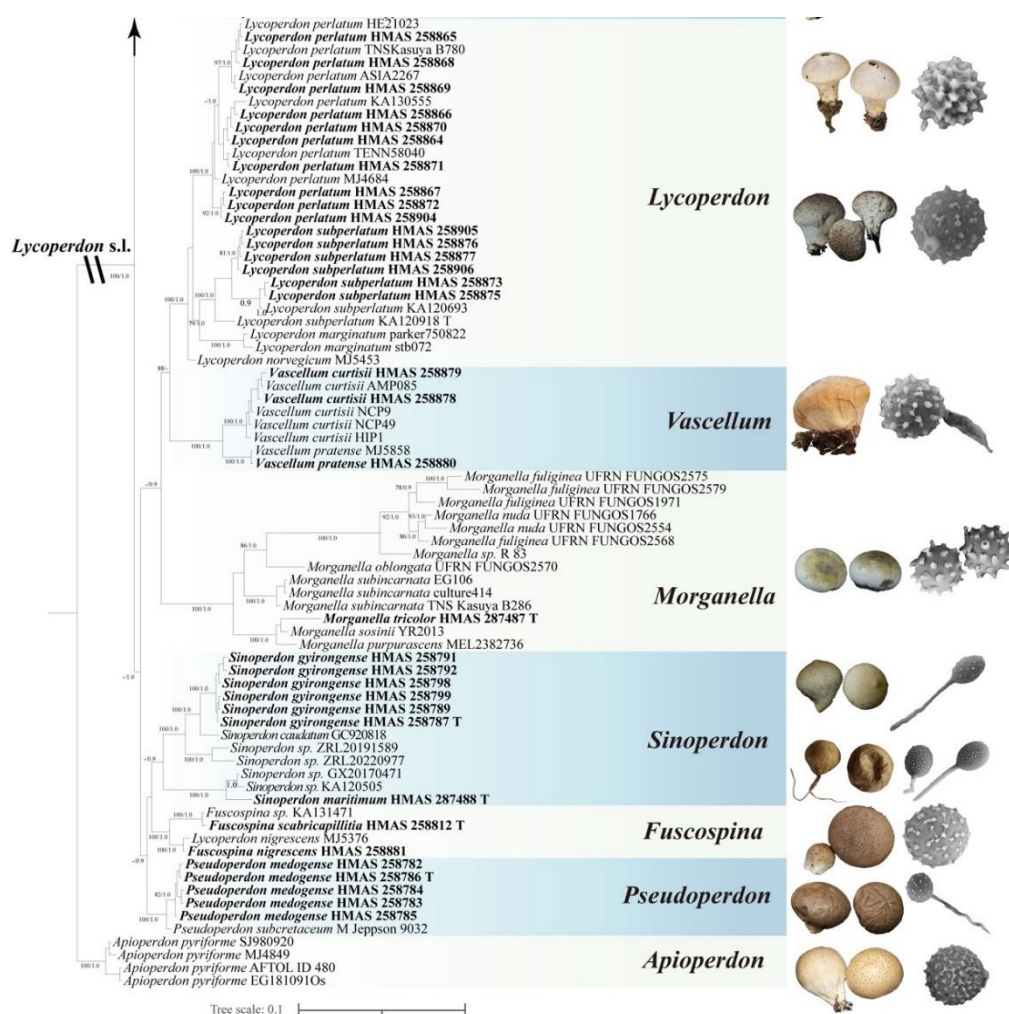


Figure 3 – Continued.

Additionally, the newly proposed *Leptocaulis* and *Lycoperdiscus* were previously classified within *Lycoperdon* subg. *Utraria* without statistical support (Larsson & Jeppson 2008, Alfredo et al. 2017). This study suggests that the previously designated *Utraria* can be further divided into three monophyletic subclades. The one containing the type species of *Utraria* [*Utraria excipuliformis* (Scop.) Quél] is retained as *Utraria*. The subclade represented by *Lycoperdiscus nivea* (= *Lycoperdon lividum* Pers.) and *Lycoperdiscus tianzhuensis* R.L. Zhao & J.X. Li sp. nov. is proposed as *Lycoperdiscus*. The last subclade, represented by *Leptocaulis albiperidius* (= *Lycoperdon albiperidium* Chang S. Kim) and *Leptocaulis subumbrinus* (= *Lycoperdon subumbrinum* Jeppson & E. Larss.), is proposed as *Leptocaulis*. Detailed descriptions of these newly recommended taxonomic taxa, as well as new species, are provided in the following section on “Taxonomy.”

Phylogeny of *Bovista*

The phylogeny of *Lycoperdaceae* has revealed that the previous genus *Bovista* was not a monophyletic group (Fig. 1). One *Bovista* subg. *Bovista*, with the type species *Ba. plumbea* Pers., was retained as *Bovista*. In this analysis, a combined four-gene dataset was employed to infer the phylogenetics in *Bovista*, comprising 89 sequences (45 for ITS, 34 for nrLSU, five for *rpb2*, five for *tef1-α*) from 45 specimens. Sequence data for this part are provided in Table 3. The best model for this combined dataset, estimated and applied in the Bayesian Inference (BI) analysis, was JC. Both Maximum Likelihood (ML) and BI analyses generated almost identical topologies with minimal variation in statistical support values, and the BI tree was selected for display (Fig. 4). Phylogenetics indicated that the newly defined *Bovista* was monophyletic, strongly supported by both bootstrap

value (BS = 100%) and posterior probability (PP = 1). Two new species were proposed, and one known species, *Ba. echinella* Pat, was re-defined.

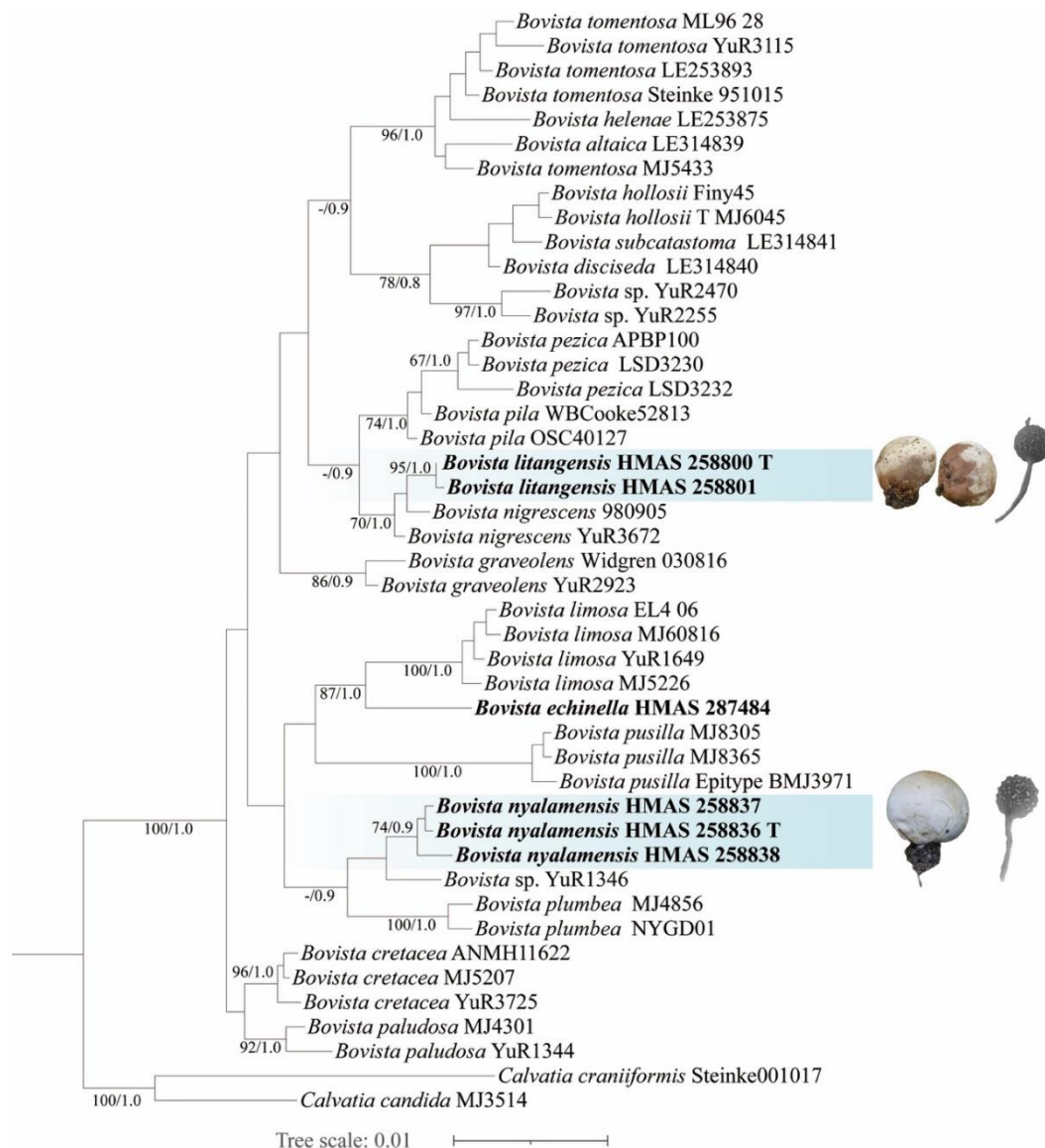


Figure 4 – Phylogenetic tree of *Bovista* inferred from ITS, nrLSU, *rpb2* and *tef1-α* sequences data, rooted with *Calvatia craniiformis* and *C. candida*. Branches supported by both BS $\geq 70\%$ and PP ≥ 0.90 were labeled. The examined specimens in this study are in bold.

Phylogeny of *Globaria*

Phylogenetic analysis of *Lycoperdaceae* in this study revealed that *Globaria* (previously *Bovista* subgenus *Globaria*) forms a monophyletic group and should be elevated to the generic level. A combined four-gene sequences dataset was used to infer the phylogeny of *Globaria*, which included 89 sequences (37 for ITS, 33 for nrLSU, 18 for *rpb2*, 21 for *tef1-α*) from 37 specimens. Sequence data for this part are provided in Table 4. The best model for this combined dataset was estimated and applied in the Bayesian Inference (BI) analysis using the JC model. Both Maximum Likelihood (ML) and BI analyses generated almost identical topologies with minimal variation in statistical support values, and the BI tree is displayed in Fig. 5. Phylogenetic analysis indicated that *Globaria* is monophyletic, supported by both bootstrap and posterior probability values. Here, six new species and two new combinations are proposed.

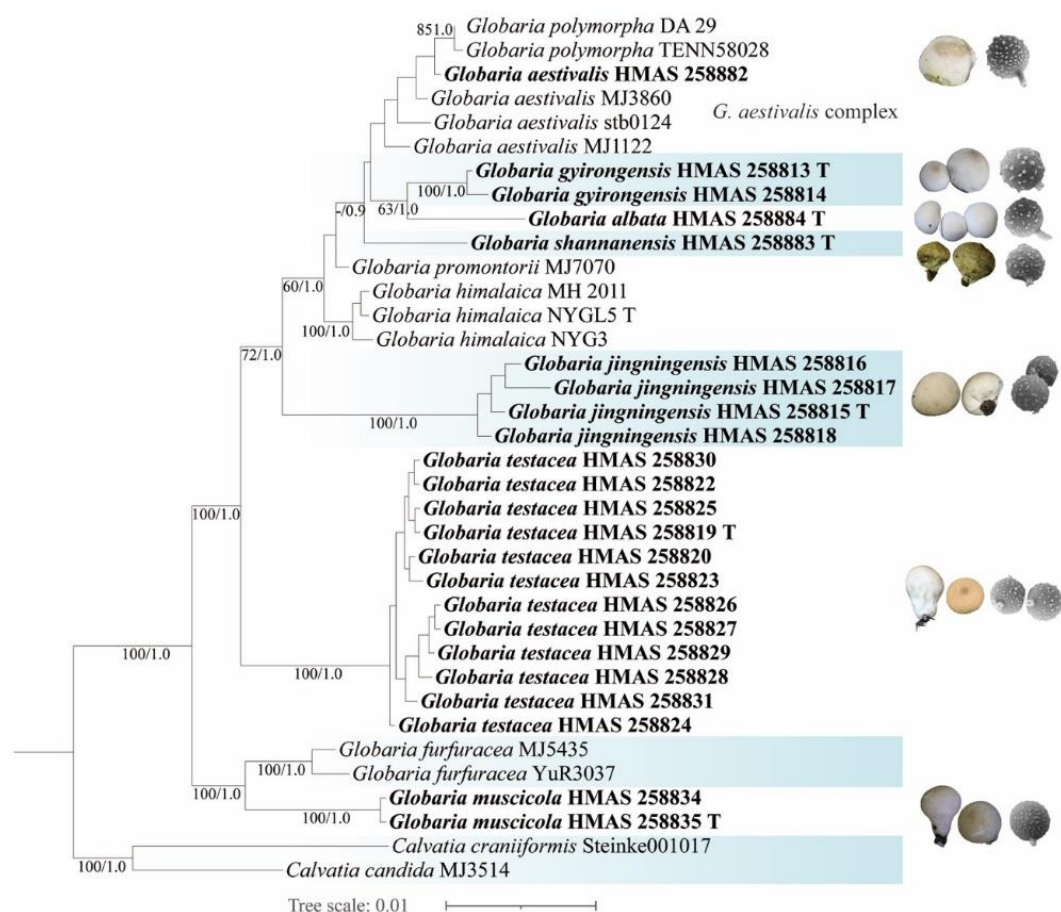


Figure 5 – Phylogenetic tree (ML) of *Globaria* inferred from ITS, nrLSU, *rpb2* and *tef1- α* sequences, rooted with *Calvatia craniiformis* and *C. candida*. Branches supported by both BS $\geq$ 50% and PP $\geq$ 0.90 were labeled. The examined specimens in this study are in bold.

Phylogeny of *Calvatia*

A dataset comprising combined four-gene sequences was utilized to investigate the phylogenetic relationships of *Calvatia*. This dataset included 81 sequences (50 for ITS, 16 for nrLSU, seven for *rpb2*, and eight for *tef1- α*) from 37 specimens. Sequence data for this part are provided in Table 5. The best model for this combined dataset was estimated and applied in the Bayesian Inference (BI) analysis using the JC model. Both Maximum Likelihood (ML) and BI analyses generated nearly identical topologies with minimal variation in statistical support values, and the BI tree is displayed in Fig. 6. Phylogenetic results revealed that *Calvatia* is monophyletic and is strongly supported by both bootstrap values and posterior probability. Two main subclades were identified corresponding to *Calvatia* subg. *Calvatia* and subg. *Langermannia*. The former accommodates the majority of species, including fourteen species, two of which are new viz *C. shennongjiaensis* sp. nov. and *C. longisetulosa* sp. nov. Subg. *Langermannia* comprises five species, including one new species – *C. subbooniana* sp. nov. All proposed new species received full statistical support.

Phylogeny of *Morganella*

A combined dataset of ITS and nrLSU sequences was employed for the phylogenetic inference of *Morganella*, encompassing 69 sequences (36 for ITS, 33 for nrLSU) and including eight *Morganella* species. Sequence data for this part are provided in Table 6. The best model for this combined dataset was estimated and applied in the Bayesian Inference (BI) analysis using the JC model. Both Maximum Likelihood (ML) and BI analyses yielded nearly identical topologies, with the BI tree displayed in Fig. 7. The results revealed that *Morganella* was fully supported as a monophyletic group (PP = 1). The proposed new species, *M. tricolor* sp. nov., nested with

M. purpurascens (Berk. & M.A. Curtis) Kreisel & Dring and *M. sosinii* Rebriev & Bulakh 2015, forming a distinct lineage with full support (Fig. 7).

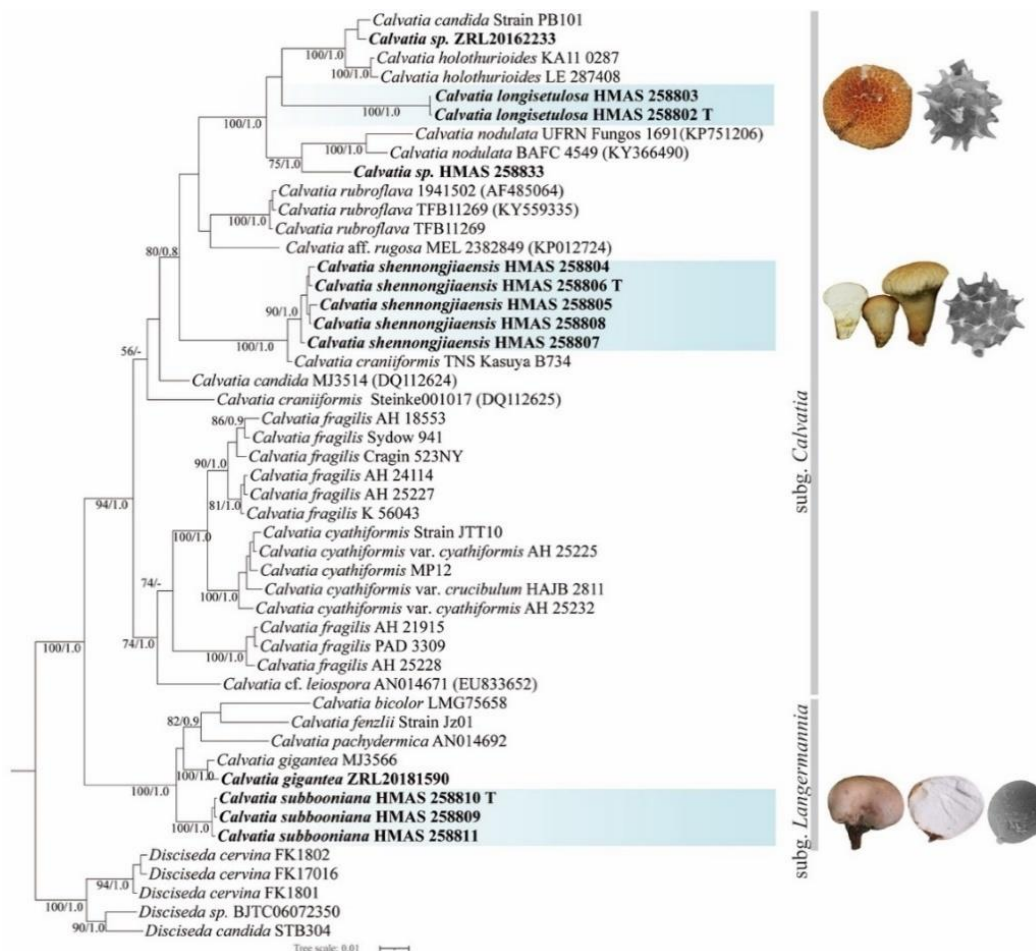


Figure 6 – Phylogenetic tree of *Calvatia* inferred from ITS, nrLSU, *rpb2* and *tef1-α* sequences data, rooted with *Disciseda*. Branches supported by both BS $\geq 70\%$ and PP ≥ 0.90 were labeled. The examined specimens in this study are in bold.

Taxonomy

***Lycoperdaceae* F. Berchtold & J. Presl 1820**

Note – In this study, leveraging information from phylogeny, divergence times, and morphology, *Lycoperdon* s.l. is restructured into 11 genera. The previous subgenera *Bovostella*, *Morganella*, *Utraria*, and *Vascellum* have been elevated to the genus level; *Lycoperdon* is redefined to encompass the clade with the type species *L. perlatum*; and five new genera have been proposed to accommodate unnamed clades (Figs 1–3).

Nineteen major clades are well-supported, with divergence times spanning 26.7–75.5 Myr. These clades correspond to 14 known genera (*Abstoma*, *Apioperdon*, *Arachnion*, *Bovista*, *Bovistella*, *Bryoperdon*, *Calvatia*, *Disciseda*, *Globaria*, *Holocotylon*, *Lycoperdon*, *Morganella*, *Utraria*, *Vascellum*), and the five newly established genera in this study: *Fuscospina*, *Leptocaulis*, *Lycoperdiscus*, *Pseudoperdon*, and *Sinoperdon*. Additionally, seven genera (*Acutocapillitium* P. Ponce de León, *Calvatiopsis* Hollós, *Calbovista* Morse ex M.T. Seidl, *Gastropila* Homrich & J.E. Wright, *Glyptoderma* R. Heim & Perr. – Bertr., *Japonogaster* Kobayasi, *Lycoperdopsis* Henn.) were provisionally included in *Lycoperdaceae* due to the absence of molecular data. Herein, *Lycoperdaceae* encompasses 26 genera as given below;

Abstoma G. Cunn. 1926

Acutocapillitium P. Ponce de León 1976
Apioperdon (Kreisel & D. Krüger) Vizzini 2017
Arachnion Schwein. 1822
Bovista Pers. 1794
Bovistella Morgan 1892
Bryoperdon Vizzini 2017
Calvatiopsis Hollós 1929
Calbovista Morse ex M.T. Seidl 1995
Calvatia Fr. 1849
Disciseda Czern. 1845
Fuscospina J.X. Li, R.L. Zhao. gen. nov. 2024
Gastropila Homrich & J.E. Wright 1973
Globaria Qué'l. 1873
Glyptoderma R. Heim & Perr. –Bertr. 1971
Japonogaster Kobayasi 1989
Holocotylon Lloyd 1906
Leptocaulis J.X. Li, R.L. Zhao. gen. nov. 2024
Lycoperdiscus J.X. Li, R.L. Zhao. gen. nov. 2024
Lycoperdon Pers. 1794
Lycoperdopsis Henn. 1900
Morganella Zeller 1948
Pseudoperdon J.X. Li, R.L. Zhao. gen. nov. 2024
Sinoperdon J.X. Li, R.L. Zhao. gen. nov. 2024
Utraria Qué'l. 1873
Vascellum F. Šmarda 1958

In the present study, 17 genera out of 26 accepted genera have been studied for morphological characterization. Among these, five genera are reported as new, and six have been recovered. Furthermore, 22 new species have been introduced, and 24 new combinations have been made. The details are as follows.

Abstoma G. Cunn., Trans. Proc. N.Z. Inst. 57: 206 (1926)

Fungal Name: FN19001

Type species – *Abstoma purpureum* (Lloyd) G. Cunn., Trans. Proc. N.Z. Inst. 57: 206 (1926).

Abstoma, established by Cunningham (1926), is mainly characterized by basidiomes lacking a determined stoma and peridium irregularly rupturing, with basidiospores exhibiting reticulate ornamentation and conspicuous to obsolete pedicels. The capillitium is of *Calvatia*-type (Cunningham 1926, Wright & Suárez 1990, Krüger et al. 2001, Gube & Dörfelt 2011). The type species, *Ab. purpureum*, was included in this study, and the phylogenetic results indicated that this genus was fully supported as a monophyletic group appearing to be basal within *Lycoperdaceae*. Molecular clock analyses inferred its divergence around 75.5 Myr (Fig. 1).

Apioperdon (Kreisel & D. Krüger) Vizzini, Phytotaxa 299(1): 81 (2017)

Fungal Name: FN819913

Type species – *Apioperdon pyriforme* (Schaeff.) Vizzini, in Vizzini & Ercole, Phytotaxa 299(1): 81 (2017)

The genus *Apioperdon* currently consists of only one species. It is mainly characterized by clustered, obovoid to obpyriform basidiomes with a cellular subgleba, conspicuous white rhizomorphs, unpitted *Lycoperdon*-type capillitium, abundant paracapillitium, and basidiospores that are smooth to minutely ornamented (Kreisel 1962, Demoulin 1971, Pegler et al. 1995, Calonge 1998, Krüger & Kreisel 2003, Sarasini 2005, Vizzini & Ercole 2017, He et al. 2019). The type species,

Ap. pyriforme, was included in this study, and the phylogenetic results indicated that this genus was fully supported as a monophyletic group that diverged around 55 Myr (Fig. 1).

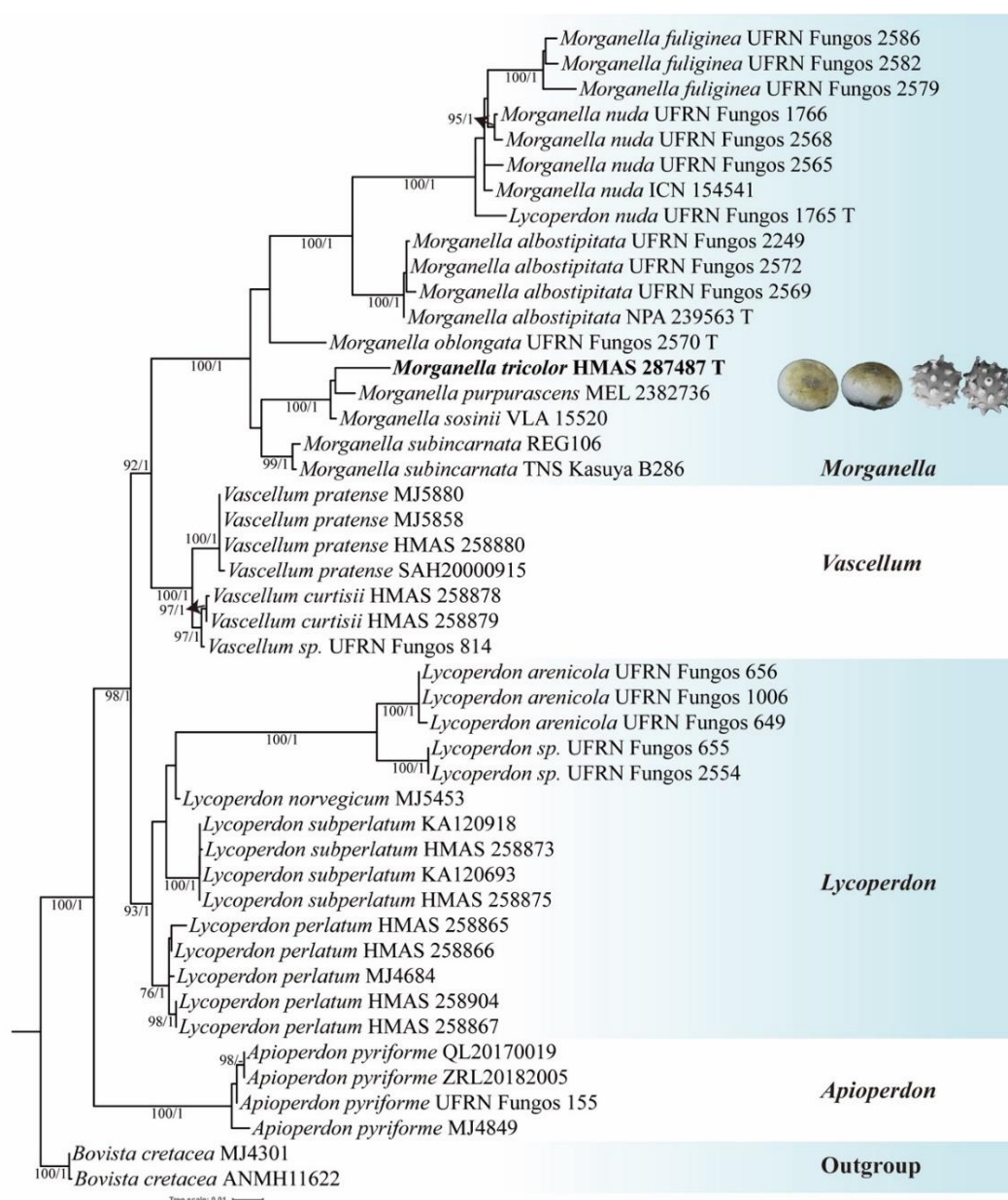


Figure 7 – Phylogenetic tree of *Morganella* inferred from ITS and nrLSU sequences data, rooted with *Ba. cretacea*. Branches supported by both BS $\geq$ 70% and PP $\geq$ 0.90 were labeled. The examined specimens in this study are in bold.

Arachnion Schwein., Schr. naturf. Ges. Leipzig 1: 59 [33 of repr.] (1822)

Fungal Name: FN19017

Type species – *Arachnion album* Schwein., Schr. naturf. Ges. Leipzig 1: 59 (1822)

The genus *Arachnion* is characterized by small-sized basidiomes, an endoperidium that disintegrates at maturity, and a gleba that develops minute peridioles resembling sand grains. The capillitium is either absent or poorly developed, and the basidiospores exhibit reticulate ornamentation (Underwood 1899, Kreisel 1962, Wright & Suárez 1990, Cortez et al. 2010b). The type species, *Ar. album*, was included in this study, and the phylogenetic results indicated that this genus was fully supported as a monophyletic group that diverged around 55 Myr (Fig. 1).

Bovista Pers., Neues Mag. Bot. 1: 86 (1794)

Fungal Name: FN19036

Type species – *Bovista plumbea* Pers., Ann. Bot. (Usteri) 15: 4 (1795)

The puffball genus *Bovista*, typified by *Ba. plumbea* Pers., was established in 1794 and comprises approximately 58 species based on the current classification system (He et al. 2019). Morphologically, this genus is distinguished by basidiomes usually with persistent spines on the exoperidium, the presence or absence of a subgleba, *Bovista*-type capillitium or an intermediate *Bovista-Lycoperdon* type, and usually ellipsoid, pedicellate spores (Larsson & Jeppson 2008, Larsson et al. 2009, Rebriev et al. 2020). Kreisel divided this genus into two subgenera based on these morphological characteristics: subgenus *Bovista* with the type species *Ba. plumbea* and subgenus *Globaria* with the type species *G. aestivalis* (Bonord.) (Kreisel 1964).

In this study, the multigene phylogeny of *Lycoperdaceae* indicated that the previous genus *Bovista* was not a monophyletic group; the subgenus *Bovista* and subgenus *Globaria* were well-supported, respectively (Fig. 1). Additionally, their divergence time of 55 Myr falls within the range of all other genera of *Lycoperdaceae*. Consequently, these two subgenera are elevated to the rank of two genera, respectively. *Bovista* is re-defined as the genus with the type species *Ba. plumbea*. The main morphological features distinguishing *Bovista* from *Globaria* include the absent or reduced subgleba, *Bovista*-type capillitium, and pedicellate spores. *Globaria*, on the other hand, includes species with more characteristics of *Lycoperdon*, such as developing a subgleba and an intermediate *Bovista-Lycoperdon* type capillitium (Kreisel 1964, Larsson & Jeppson 2008, Rebriev et al. 2020).

Bovista litangensis R.L. Zhao & J.X. Li sp. nov.

Fig. 8

Fungal Name: FN571698; Facesoffungi number: FoF15155

Etymology – referring to the Litang County, Sichuan Province, where the holotype was collected.

Type – China, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Litang County, Nimagong Shenshan, 100°45'44.68"N, 30°3'49.26"E, 4300m, 17 Aug. 2020, R.L. Zhao, ZRL20200963 (holotype HMAS 258800).

Diagnosis – This species is characterized by its globose to subglobose basidiomes, developing an indistinct pseudostipe. The exoperidium is initially whitish but turns dark brown at the lower part when mature. The basidiospores are globose to subglobose, densely ornamented with coarse, minute verrucae, and have a long pedicel. The capillitium is *Bovista*-type and thick-walled.

Macroscopic description – *Basidiomes* globose to subglobose, 13–32 mm with, 15–25 mm height. *Pseudostipe* reduced or indistinct. Rhizomorphs sparse, white, often densely embedded in the substrate. *Peridium* layered. Exoperidium initially whitish, densely covered with minutely smooth granular verrucose, gradually cracking but not falling off, and the lower part turn dark brown when mature, irregular opening at the tip. *Endoperidium* smooth, off-white, yellowish-white, fragile and papery. *Gleba* pulverulent, initially white, turning dark brown as it matures, fibrous, pulverulent. *Subgleba* absent.

Microscopic description – *Basidiospores* globose to subglobose, 4.2–5.4 µm in diameter [$x = 4.8 \pm 0.3$, $n = 30$], thick-walled, with an oil drop central, light brown in 5% KOH, usually with a long pedicel (8.5–10.5 µm in Length, $n = 30$), often the long pedicel with vertical grooves. Under SEM, densely ornamented coarse minute verrucae, irregularly. *Capillitium* of *Bovista*-type, (1.3)3.8–12 µm in width, dark brown, thick-walled, tapering towards the tips, and often undulate at the end, intertwined and branches abundant, elastic, no pores and septa observed, dark brown in 5% KOH. *Paracapillitium* absent. Exoperidium composed of chains of inflated cells, slightly thick-walled, variety of shapes, subglobose to globose, oblong to pyriform, cylindrical, 7.8–37.2 µm in width, 14.6–49.3 µm in length. hyaline in 5% KOH. *Endoperidium* made up of intertwined hyaline hyphae, hardly branches, straight to slight undulate, 1.3–3.0 µm in width, septa not observed.

Ecology and distribution – It's assumed that this species occurs in the higher elevations of the state, altitude over 4300m, within the alpine meadow. It often fruiting in humus soils, socially in a habitat full of low-growing herbs. known from China.

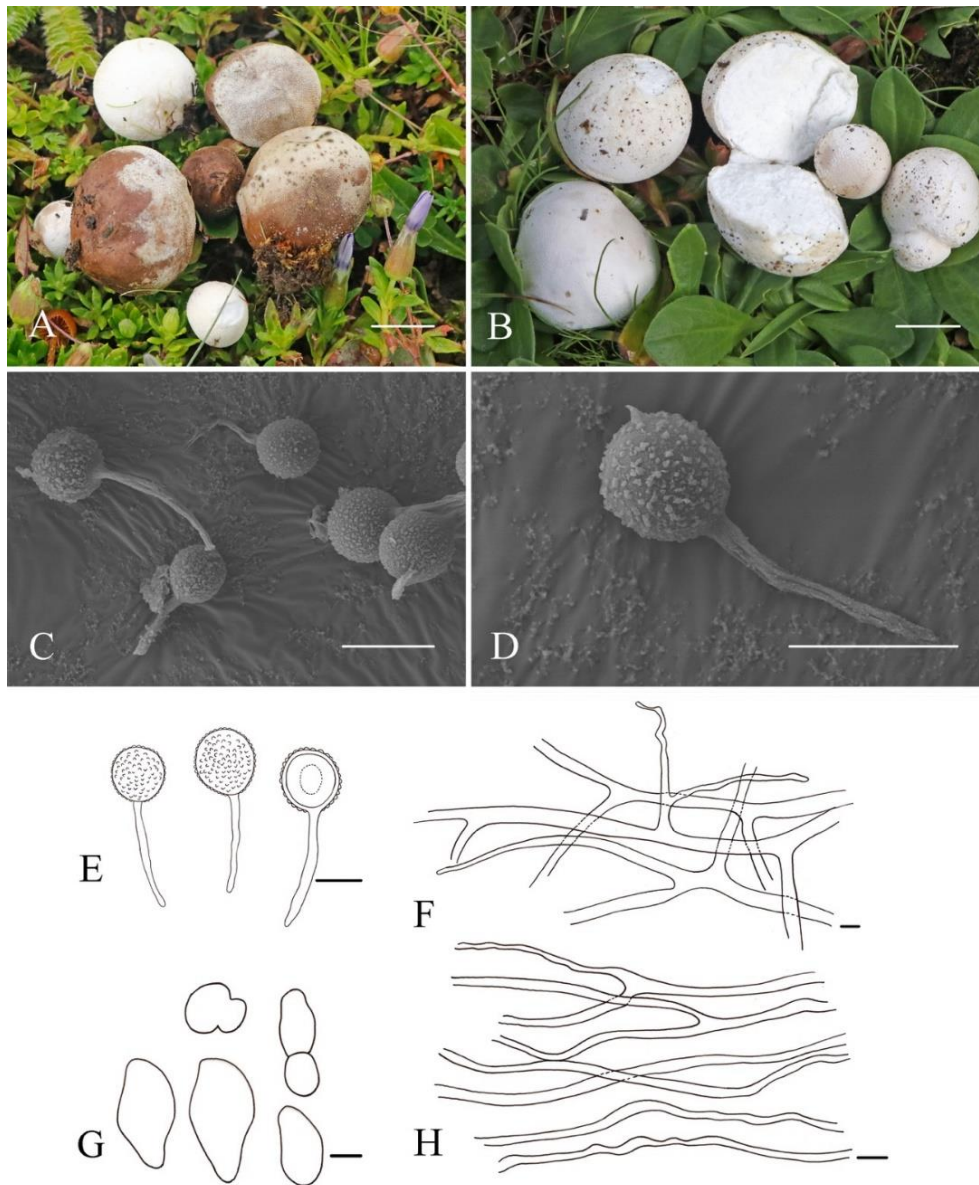


Figure 8 – Morphology of *Bovista litangensis*. A gasterocarps (holotype, HMAS 258800). B gasterocarps (HMAS 258801). C, D basidiospores under SEM. E basidiospores. F exoperidial elements (sphaerocysts). G capillitial threads. H endoperidial hyphae. Scale bars: A–B = 1 cm, C–H = 5 μ m.

Additional material examined – China, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Litang County, Zaga Shenshan, 20 Aug. 2020, R.L. Zhao, ZRL20201295 (HMAS 258801).

Notes – Ecologically, this new species occurs at high altitudes (over 4,000 meters) on moist grassy ground in alpine meadow biomes. The phylogenetic analysis in this study indicates that this fungus is nested within *Bovista*, showing a sister relationship with *Ba. nigrescens*, a common species in most areas of North and West Europe (Larsson & Jeppson 2008). They share many macro features and spore size characteristics, such as the initially white exoperidium turning dark brown when mature and globose to subglobose basidiospores with a long pedicel (5.0–6.0 μ m in size in *Ba. nigrescens*, 4.2–5.4 μ m in diameter in *Ba. litangensis* sp. nov.) (Watling & Gregory 1977, Beig et al. 2008). The microscopic morphology of the spores sets them apart, with *Ba. nigrescens* possessing larger verrucae in the SEM sense of Rebriev et al. (Rebriev et al. 2020) and shorter pedicels up to 8 μ m long, while in *Ba. litangensis* sp. nov., minute warts or structures similar to point-like and longer pedicels (8.5–10.5 μ m in length) were observed. *Bovista plumbea* is very similar to

Ba. litangensis sp. nov., but can be easily recognized mainly by its white exoperidium, which, when removed, reveals the lead grey endoperidium (Bautista-Hernández et al. 2012). *Bovista bovistoides* and *Ba. limosa* are easily confused due to their similar appearance, with globose to subglobose basidiomes and an initially white exoperidium covered with small granules. However, the former can be distinguished by its basidiospores with a longer pedicel (10–18 µm in length) (Fan 2019), while the latter can be differentiated mainly by the presence of a delimited peristome, a peristomal depression, and a fimbriate, protruding stoma in *Ba. limosa* (Larsson et al. 2009).

***Bovista nyalamensis* R.L. Zhao & J.X. Li sp. nov.**

Fig. 9

Fungal Name: FN571699; Facesoffungi number: FoF15156

Etymology – referring to the Nyalam County, Shigatse City, Xizang Autonomous Region in China where the holotype was collected.

Type – China, Xizang Autonomous Region, Shigatse City, Nyalam County, Zhangmu Town, Zhangmugou, 4 Aug. 2022, R.L. Zhao, ZRL20220839 (holotype HMAS 258836).

Diagnosis – Macroscopically, this species is characterized by globose to subglobose basidiomes with a whitish or off-white exoperidium that is densely covered with minutely smooth granular verruculose. The capillitium is of the *Bovista*-type, and the globose to subglobose basidiospores usually have a long pedicel and are ornamented with cylindrical verruculose.

Macroscopic description – *Basidiomes* globose to subglobose, depressed globose, 20–32 mm with, 18–38 mm height. *Rhizomorphs* abundant, light brown, solid, heavily encrusted with particles of soil and stones. *Pseudostipe* absent or indistinct. *Peridium* layered. Exoperidium whitish, white to off-white, densely covered with minutely smooth granular verruculose, becoming light brown, yellowish white in the upper part of the basidiomes. *Endoperidium* smooth, off-white, fragile, papery, yellowish-white. *Gleba* pulverulent, initially white, turning dark brown as it matures, fibrous to cottony. *Subgleba* absent.

Microscopic description – *Basidiospores* globose, subglobose, sometimes ovoid, 3.5–4.0 µm in diameter (n = 30), thick-walled, with an oil drop central, dark olive green in 5% KOH, usually with a long pedicel (6.2–8.9 µm in Length, n = 30), sometimes the long pedicel is breakable. Under SEM, asperulate, densely ornamented with cylindrical warts, usually the apex of several verrucose connected. *Capillitium* of *Bovista*-type, 5.2–10.4 µm in width, dark brown, thick-walled (3.5–5 µm in width), tapering towards the tips, intertwined and many branches, elastic, no pores and septa observed. *Paracapillitium* absent. Exoperidium composed of chains of hyaline inflated cells, slightly thick-walled (up to 0.6 µm), variety of shapes, subglobose to globose, oblong to pyriform, cylindrical, 3.2–15.5 µm in width, 5.5–18.6 µm in length. *Endoperidium* made up of intertwined and unbranches hyaline hyphae, 1.1–4.0 µm in width, light olive green in 5% KOH, straight to slight undulate, septa not observed.

Ecology and distribution – It's assumed that this species occurs in the higher elevations of the state, often found on the grass, solitary or socially in a relatively humid environment. known from China.

Additional material examined – China, Xizang Autonomous Region, Shigatse City, Nyalam County, Zhangmu Town, Zhangmugou, 4 Aug. 2022, R.L. Zhao, ZRL20220626 (HMAS 258837); China, Xizang Autonomous Region, Shigatse City, Yadong County, Lower Yadong Town, Poroka meadow, 26 Jul. 2022, M.Q. He, ZRL20220040 (HMAS 258838).

Notes – Morphologically, *Ba. nyalamensis* sp. nov. forms medium-sized basidiomes that are globose to subglobose and lack a subgleba. The exoperidium is whitish to off-white, developing minutely smooth granules. The capillitium is of the *Bovista*-type, and its verrucose basidiospores usually have a long pedicel and are breakable. Phylogenetic analysis in this study indicated that *Ba. nyalamensis* sp. nov. falls near the type *Ba. plumbea*, sharing similar features. Both species have a white exoperidium and verrucose basidiospores. However, *Ba. plumbea* differs by having larger basidiospores (4.8–5.6 µm in diameter × 5.6–6.4 µm in length) and displaying a lead grey endoperidium (Fan 2019). Additionally, *Ba. paludosa* is morphologically similar to *Ba. nyalamensis* sp. nov. due to the white to off-white appearances of basidiomes. However, *Ba. paludosa* can be

distinguished by its restricted habitats, usually attached to living mosses, and more or less pear-shaped fruiting bodies (Bolshakov et al. 2018, Rebriev et al. 2020). In the field, the white exoperidium in *Ba. litangensis* sp. nov. may lead to misidentifications with *Ba. nyalamensis* sp. nov.; however, they differ as *Ba. litangensis* sp. nov. has an exoperidium that turns dark brown when mature and possesses larger spores (4.2–5.4 μm) with pedicels.

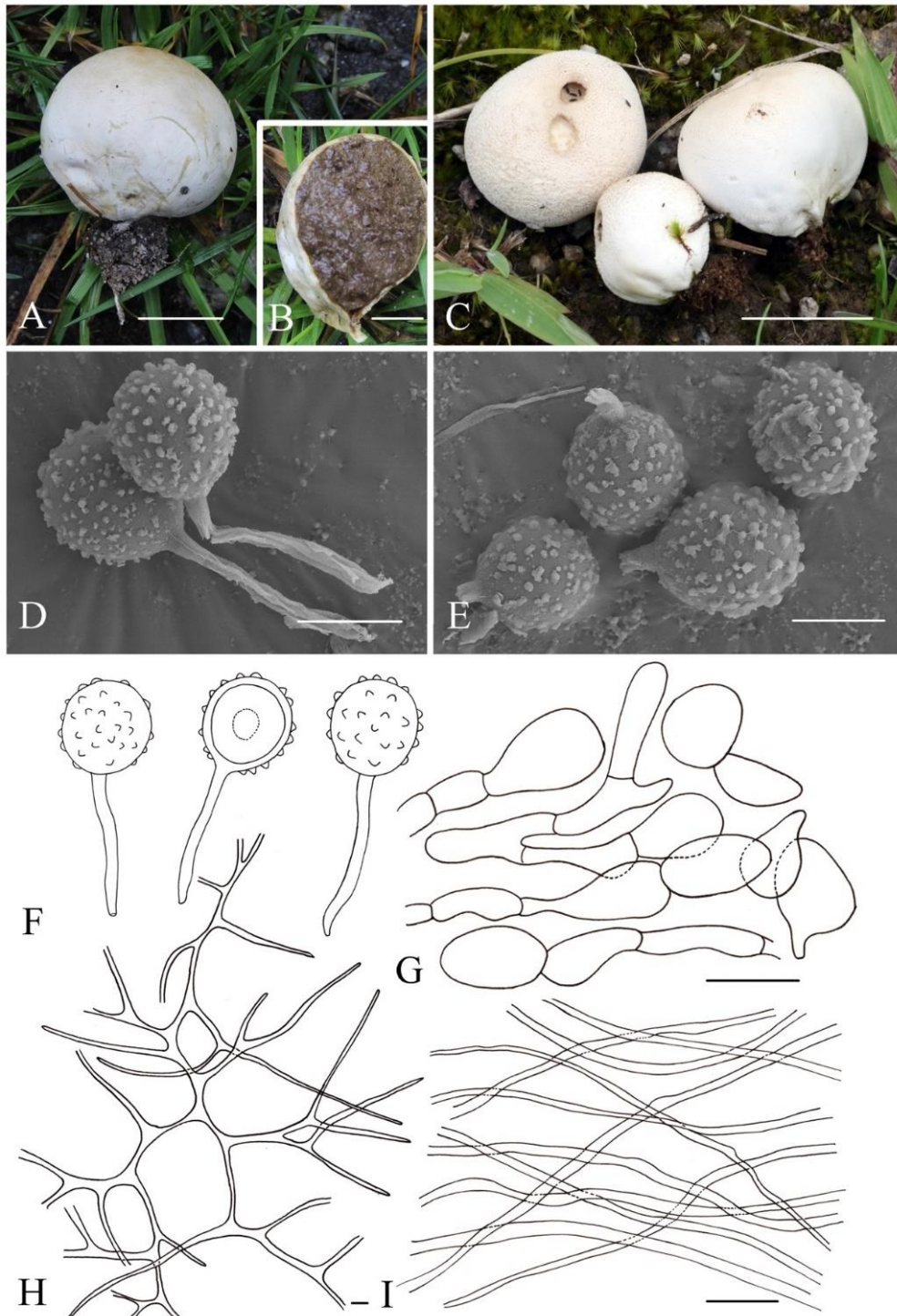


Figure 9 – Morphology of *Bovista nyalamensis*. A, B gasterocarps (holotype, HMAS 258836). C gasterocarps (HMAS 258838). D, E basidiospores under SEM. F basidiospores. G capillitial threads. H exoperidial elements (sphaerocysts). I endoperidial hyphae. Scale bars: A–C = 1 cm, D–E = 2 μm , F–I = 5 μm .

Bovista echinella Pat., in Patouillard & Lagerheim, Bull. Soc. mycol. Fr. 7: 165 (1891) 1891.

Fungal Name: FN203073

Diagnosis – This species is distinguished by globose to subglobose basidiomes surface with small spines, persistent. Capillitium of *Bovista*-type and with abundant Paracapillitium, globose to subglobose basidiospores ornamented with fine wart, present long pedicels.

Macroscopic description – *Basidiomes* globose, subglobose, 10–18 mm in diameter. *Pseudostipe* not indistinct, the base encrusted with soil around moss. *Peridium* layered. Exoperidium surface with granular or small spines, initially white, turn brown after maturity, not easily fall off. *Endoperidium* papery, smooth, brownish, tear shaped at the apical pore. *Gleba* powdery, yellowish-brown at maturity.

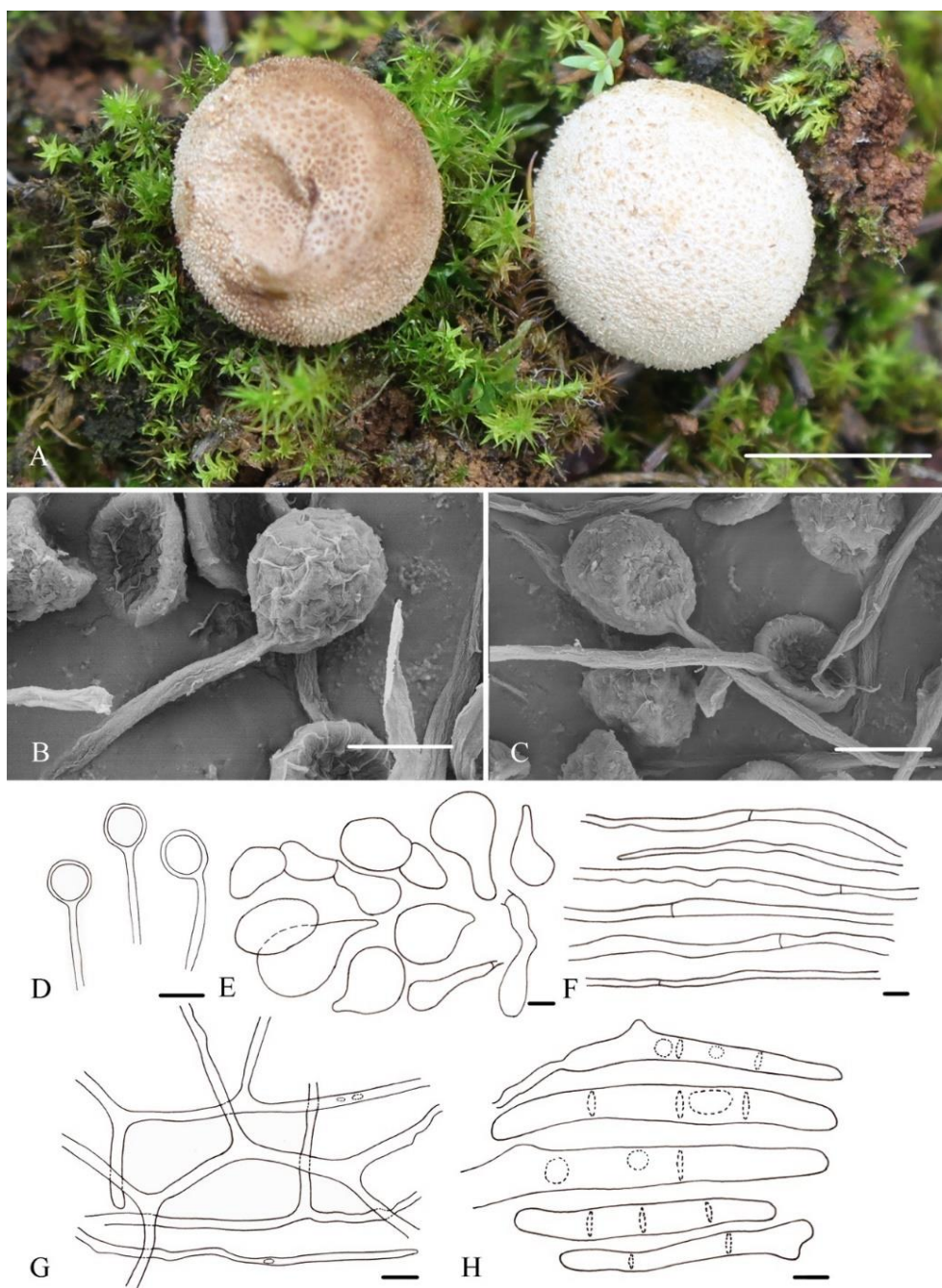


Figure 10 – Morphology of *Bovista echinella*. A gasterocarps (holotype, HMAS 287484). B, C basidiospores under SEM. D basidiospores. E exoperidial elements (sphaerocysts). F endoperidial hyphae. G capillitial threads. H Paracapillitium. Scale bars: A = 1 cm, B–E = 5 μ m, F = 2 μ m, (G–H) 5 μ m.

Microscopic description – *Basidiospores* globose to subglobose, 4.2–5.4 μm in diameter, [$x = 4.8 \pm 0.3$, $n = 30$], yellowish-brown, smooth in LM, verrucose in SEM, ornamented fine wart, with long pedicels, 8.5–12.7 μm . *Capillitium* of *Bovista*-type, dark brown, thick-walled, 2.7–9.5 μm , tapering towards the tips, no septa, and often undulate at the end. *Paracapillitium* short without branching, same color with capillitial threads, 6.8–18.5 μm , produce septa. Exoperidium composed of irregular sphaerocysts, thick-walled, hyaline in 5% KOH. *Endoperidium* composed of straight, interwoven hyaline hyphae, 1.8–3.5 μm .

Ecology – Terrestrial and found in broadleaf forest, growing solitary in the soil around moss.

Material examined – China, Sichuan Province, Liangshan Autonomous Prefecture, Yanyuan County, Xiamosuo Gou, 8 Aug. 2019, R.L. Zhao, ZRL20190374 (HMAS 287484).

Notes – *Bovista echinella* is characterized by its globose to subglobose basidiomes, featuring an exoperidium adorned with small, persistent spines, and basidiospores with fine warts and long pedicels. The examined specimen (HMAS 287484) closely aligns with the description of *Bovista echinella* (Fan 2019). The most morphologically similar species is *Ba. limosa* Rostr. The key distinction lies in the production of capillitium, which is of intermediate type in *Ba. limosa*, whereas it is *Bovista*-type in *Ba. echinella* (Fan 2019).

Bovistella Morgan, J. Cincinnati Soc. Nat. Hist. 14: 141 (1892)

Fungal Name: FN19038

Type species – *Mycenastrum ohiense* Ellis & Morgan, J. Mycol. 1: 89 (1885)

This genus is mainly characterized by the development of a distinct pseudo-diaphragm to separate the gleba from the subgleba, the production of a fragile capillitium, and walls with abundant pits of irregular outline (Larsson & Jeppson 2008, Fan 2019). *Bovistella utrifforme* and *Be. radiculatum* have been included in the phylogeny, and the results confirm that both taxa cluster together with high support (PP values = 1), regardless of which gene fragment is used. Therefore, *Bovistella* is fully supported as a monophyletic genus with a divergence time of 30.9 Myr (Fig. 1).

Bovistella emodensis R.L. Zhao & J.X. Li sp. nov.

Fig. 11

Fungal Name FN571822; Facesoffungi number: FoF15345

Etymology – referring to the holotype was collected in the Himalayan region, China

Type – China, Xizang Autonomous Region, Shigatse City, Yadong County, Pali Town, Plateau Meadow, 28 Jul. 2022, M.Q. He, ZRL20220383 (holotype HMAS 287485).

Diagnosis – This species is identified by basidiomes exhibiting irregular cracking at the upper part and flaky verrucae at the lower part. The basidiospores are globose to subglobose, featuring a long pedicel and an asperulate surface. It thrives in soils within the alpine meadow, specifically at altitudes exceeding 4300 m.

Macroscopic description – *Basidiomes* subglobose, depressed globose, sub-pyriform, 12–30 mm width, 20–25 mm height. *Pseudostipe* not indistinct. Rhizomorphs sparse, encrusted with soil. *Peridium* layered. Exoperidium whitish overall when young, the upperpart possesses irregular cracking, yellowish-brown, the lower part densely covered with flaky verrucose. *Endoperidium* whitish when young, fragile, papery. *Gleba* pulverulent or fibrous, initially whitish. *Subgleba* pulverulent.

Microscopic description – *Basidiospores* globose, subglobose, 4.0–5.2 μm in diameter, asperulate, surface densely ornamented with irregular-sized verruca, with long pedicel, 6.7–11.2 μm . *Capillitium* of *Lycoperdon*-type, 1.1–4.4 μm width, occasionally swollen in the middle, no pores and septa observed. *Paracapillitium* absent. Exoperidium made up of chains of inflated cells, slightly thick-walled, hyaline in 5% KOH. *Endoperidium* made up of hyaline inflated hyphae, interwoven, septa abundant.

Ecology and distribution – It's assumed that this species occurs in the higher elevations of the state, altitude over 4300 m. It often fruiting in soils within the alpine meadow, socially two or more in a habitat full of low-growing herbs. known from China.

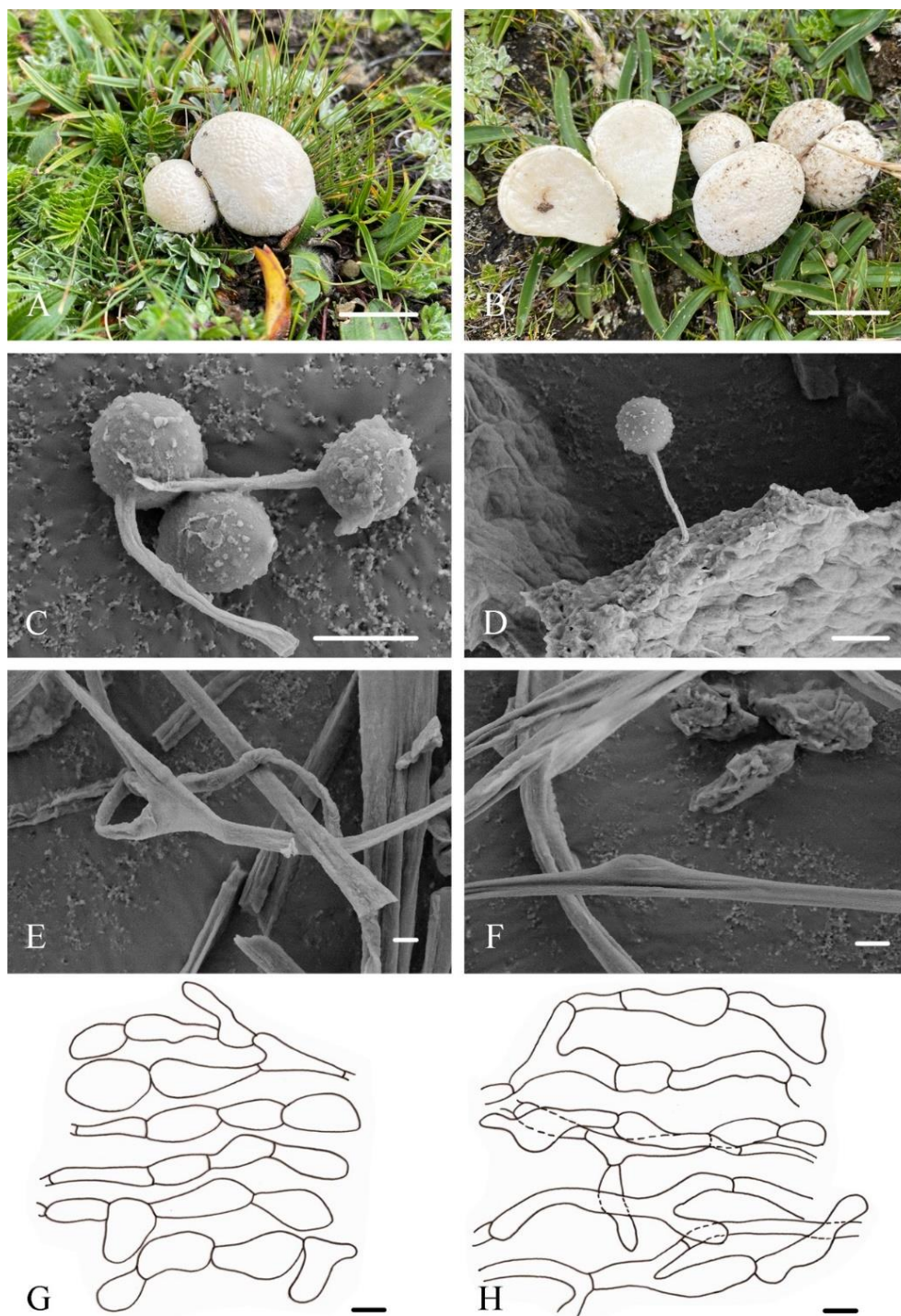


Figure 11 – Morphology of *Bovistella emodensis*. A, B gasterocarps (holotype, HMAS 287485 ZRL20220383). C, D basidiospores under SEM. E, F capillitial threads under SEM. G exoperidial elements (sphaerocysts). H endoperidial hyphae. Scale bars: A–B = 1 cm, C–D = 5 µm, E–F = 2 µm, G–H = 5 µm.

Additional material examined – China, Xizang Autonomous Region, Shigatse City, Yadong County, Pali Town, Plateau Meadow, 28 Jul. 2022, M.Q. He, ZRL20220385 (HMAS 287486).

Notes – Phylogenetic trees, generated using ITS, nrLSU, *rpb2*, and *tef1-α* sequences data (Fig. 3), indicate that *Be. emodensis* sp. nov. is nested within *Bovistella* with fully supported PP values. The morphological features of this new species align with those of the genus. *Bovistella emodensis* sp. nov. is characterized by basidiomes exhibiting irregular cracking at the upper part and asperulate basidiospores with long pedicels. In comparison to closely related species like *Be. radicata*

Pat. and *Be. utriformis* (Bull.) Demoulin & Rebriev, *Be. emodensis* sp. nov. shows significant morphological differences. For instance, *Be. radicata* has an echinulate exoperidium with granules or spines, distinguishing it from *Be. emodensis* sp. nov. Additionally, its basidiospores feature different verruca ornamentation (Fan 2019). *Bovistella utriformis* develops echinulate basidiomes with an exoperidium adorned with conical spines, further differentiating it from the cracking pattern observed in *Be. emodensis* sp. nov. (Kuragina & Krakhmaleva 2019). While *Be. sinensis* Lloyd shares morphological similarities with *Be. emodensis* sp. nov., its basidiomes exhibit irregular lobes at the apical portion, and a distinct pseudo-diaphragm is present (Fan 2019).

Bovistella radicata Pat., Bull. Soc. mycol. Fr. 15: 55 (1899)

Basionym – *Lycoperdon radicum* Durieu & Mont., in Durieu (1848).

Bovistella utriformis (Bull.) Demoulin & Rebriev, Lejeunia 197: 6 (2017)

Basionym – *Lycoperdon utriforme* Bull., Hist. Champ. France: 153 (1791).

Bryoperdon Vizzini, Phytotaxa 299(1): 80 (2017)

Fungal Name: FN819911

Type species – *Bryoperdon acuminatum* (Bosc) Vizzini, in Vizzini & Ercole, Phytotaxa 299(1): 80 (2017)

The genus *Bryoperdon* currently contains only one species, well characterized by small-sized oblong, conical basidiomes with white mycelial cords, *Lycoperdon*-type pitted capillitium, and minutely ornamented basidiospores (Kreisel & Dring 1967, Kreisel & Karasch 2005, Sarasini 2005, Poumarat 2007, Vizzini & Ercole 2017). In this study, a specimen collected from the Xizang Autonomous Region from China was identified as *Br. acuminatum* based on molecular phylogeny and morphological examinations (Fig. 1). This species is a new record from China, and its description follows.

Bryoperdon acuminatum (Bosc) Vizzini, in Vizzini & Ercole, Phytotaxa 299(1): 80 (2017)

Fig. 12

Fungal Name: FN819912

Macroscopic description – *Basidiomes* 1 cm broad, 1.3 cm high, ovoid, obovoid, with a pointed apex and rounded base. Initially whitish to cream, pale ochraceous when mature. Exoperidium covered with small, pyramidal spines. *Endoperidium* whitish when young, turn light to dark brown later. *Gleba* at first whitish then yellowish green to dark brown with age.

Microscopic description – *Basidiospores* globose to subglobose, 2.8–3.5 μm , [$x = 3.2 \pm 0.2$, $n = 30$], smooth to asperulate, slightly thick-walled, with an oil drop central, yellowish brown in 5% KOH, without a pedicel or short (up to 0.5 μm), under SEM ornamented with cylindrical to sub-cylindrical verrucae. *Capillitium* of *Lycoperdon*-type, 2–6 μm width, slightly thick-walled, less than 1 μm width, yellowish-brown in 5% KOH, smooth to asperulate on surface under SEM. *Paracapillitium* absent. Exoperidium was made up of inflated cells, globose to subglobose, thick-walled, smooth, hyaline in 5% KOH. *Endoperidium* was made up of straight hyphae, 1.3–5.3 μm width, rare branched. septa abundant.

Ecology and distribution – Terrestrial and often gregarious on moss or under coniferous forests. Known from North America, Europe, Asia.

Material examined – China, Xizang Autonomous Region, Shigatse City, Gyirong Country, Gyirong Gully, 2 Aug. 2022, M.Q. He, ZRL20220548 (HMAS 258888).

Notes – Vizzini et al. proposed *Bryoperdon* as a distinct genus due to its unique phylogenetic position relative to *Bovista* species (Vizzini & Ercole 2017). However, this classification was contested due to limited sample representation (Alfredo et al. 2017, Rebriev et al. 2020). The phylogenetic analysis in this study supports *Bryoperdon* as an independent genus (Fig. 1). *Bryoperdon acuminatum* is easily identified by its small, ovoid basidiome, the absence of a subgleba, *Lycoperdon*-type capillitium, and small globose to subglobose basidiospores with indistinct pedicels

(Vizzini & Ercole 2017). *Holocotylon rupicola* (= *Lycoperdon rupicola* Jeppson, E. Larss. & M.P. Martín) shares morphological similarities with *Br. acuminatum* but differs in having an exoperidium composed of sphaerocysts distinct from those of *Br. acuminatum*. Additionally, the finely warted globose basidiospores of *H. rupicola* are larger in size (4.0–4.5 µm in diameter) (Jeppson et al. 2012). *Holocotylon biconicum* sp. nov. may be confused with *Br. acuminatum* due to certain morphological similarities such as fusiform basidiomes and an exoperidium finely pointed at the apical part, featuring connected smallish slender spines. However, it can be distinguished from *Br. acuminatum* by its larger-sized basidiospores (3.9–4.4 µm in diameter) (Fig. 25).



Figure 12 – Morphology of *Bryoperdon acuminatum*. A gasterocarps (HMAS 258888). B basidiospores under SEM. C capillitiums under SEM. Scale bars: A = 1 cm, B–C = 2 µm.

Calvatia Fr., Summa veg. Scand., Sectio Post. (Stockholm): 442 (1849)

Fungal Name: FN19051

Type species – *Calvatia craniiformis* (Schwein.) Fr., Summa veg. Scand.: 442(1849).

The genus *Calvatia* is characterized by globose to pyriform, turbinate, epigeous basidiomes, gleba pulverulent to cottony, rudimentary to often well-developed subgleba, dehiscence of peridium occurring by irregular fragmentation, *Calvatia*-type capillitium, and basidiospores that are smooth to verrucose and echinate (Kreisel 1992, Krüger et al. 2001, Larsson & Jeppson 2008). Subgenus *Langermannia* is distinguished by medium to larger basidiomes without a subgleba (Kreisel 1992, Krüger et al. 2001). In this study, seventeen *Calvatia* species were involved in phylogenetic analyses using ITS, nrLSU, *rpb2*, and *tef1-α* sequences. The results indicated that the genus *Calvatia* formed a distinct monophyletic group, strongly supported (BS values = 100; PP values = 1), and its divergence was estimated around 61.1 Myr (Fig. 1). Furthermore, *Calvatia* split into two lineages corresponding to subg. *Calvatia* and subg. *Langermannia*, which diverged around 51 Myr respectively. Here, three new species are described as follows.

Calvatia longisetulosa R.L. Zhao & J.X. Li sp. nov.

Fig. 13

Fungal Name: FN571700; Facesoffungi number: FoF15109

Etymology – *longus* (long) and *setulosa* (setulose). The epithet refers to the densely arranged coniform spines adhered to the exoperidium.

Type – Thailand, Huai Kang Pla, 8 Jul. 2019, X.Y. Zhu, THAI20190073 (holotype HMAS 258802).

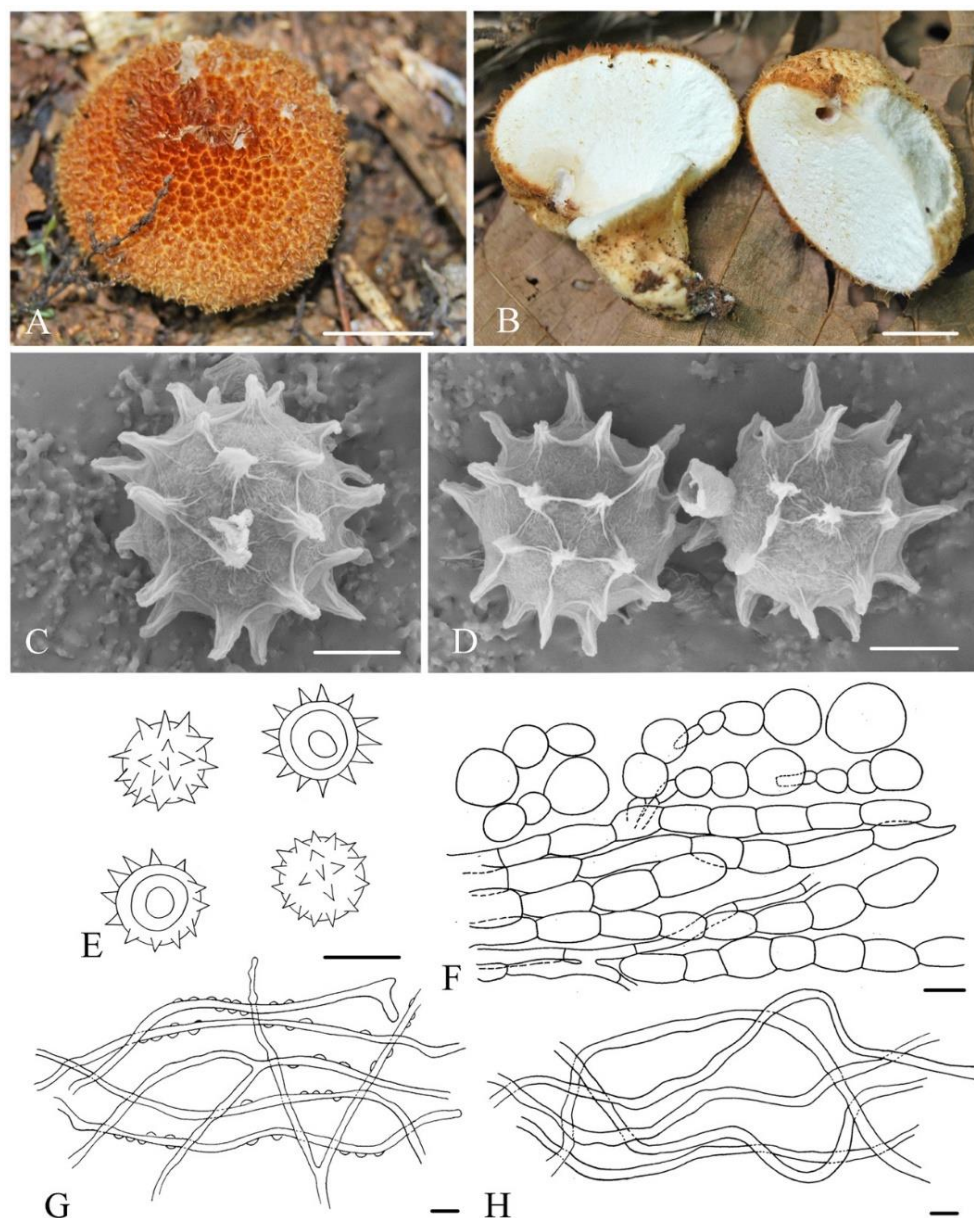


Figure 13 – Morphology of *Calvatia longisetulosa*. A, B gasterocarps (holotype, HMAS 258802). C, D basidiospores under SEM. E verrucose basidiospores. F exoperidial elements. G capillitial threads. H endoperidial hyphae. Scale bars: A–B = 1 cm, C–D = 1 µm, E = 3 µm, F–H = 2 µm.

Diagnosis – Macroscopically, this species features pyriform basidiomes that are yellowish-brown with a reddish-brown upper part. The basidiomes are adorned with robust coniform spines, densely arranged, and the apical part gradually falls off as they mature.

Macroscopic description – *Basidiomes* pyriform, depressed globose, 24–40 mm width, 20–35 mm height, *Pseudostipe* plicate, yellowish-white in lower part. Rhizomorphs scarce, whitish. *Peridium* layered. Exoperidium yellowish-white, yellowish-brown, dark brown to reddish-brown in upper part, densely with robust spines, coniform, sometimes with connected tips, gradually shed in

places at apex, to reveal a whitish *Endoperidium*, papery, fragile. *Gleba* initially whitish, grayish-brown, light-brown, pulverulent, cottony. *Subgleba* pulverulent, brownish, comprising one-third of the basidiomes, tapering at the base, attached to substrate.

Microscopic description – *Basidiospores* globose, 3.3–3.7 µm in diameter, distinctly ornamented echinate, echinate coniform in SEM, short pedicels present, up to 0.5–1 µm. *Capillitium* *Calvatia*-type, 1.4–3.6 µm diameter hyaline, colorless and transparent, thick-walls, less than 1.5 µm, often ornamented with numerous nodules, 0.5–1.5 µm height, straight, occasionally branched and septa. *Paracapillitium* absent. Exoperidium composed of chains of hyaline hyphae, ellipsoid, oblong, pyriform, occasionally globose to subglobose, sphaecysts, thick-walled. *Endoperidium* composed of unbranched interwoven hyaline hyphae.

Ecology and distribution – growing solitary or two basidiomes on soil under broad-leaved forest, known to data from Thailand.

Additional material examined – Thailand, Huai Kang Pla, 8 Jul. 2019, X.Y. Zhu, THAI20190067 (HMAS 258803).

Notes – *Calvatia longisetulosa* sp. nov. can be morphologically characterized by pyriform basidiomes, an exoperidium with distinct coniform robust spines, and echinate basidiospores. In the phylogenetic tree (Fig. 6), two specimens of this new species form a distinct lineage close to *C. candida* (Rostk.) Hollós and *C. holothuriodes* Rebriev. *Calvatia candida* differs from this new species due to basidiospores being ellipsoid (3.4–4.4 × 2.3–3.1 µm) and excipuliform turbinate to broadly shaped (Kshirsagar 2020). *Calvatia holothuroides* differs from this new species by having a thinner, fragile, yellowish-white to yellowish exoperidium, basidiospores that appear smooth under LM, and finely verrucose under SEM (Hollós 1902, Amira 2018). *Calvatia nodulata* Alfredo & Baseia, originally described from Brazil, shares some morphological features with this new species, such as punctate basidiospores and usually capillitium ornamented with spaced nodules. However, it differs with a granulose to pilose exoperidium, mature gleba in olive-brown color, and subgleba sometimes disappearing after maturity (Alfredo et al. 2014).

Calvatia shennongjiaensis R.L. Zhao & J.X. Li sp. nov.

Fig. 14

Fungal Name: FN571701; Facesoffungi number: FoF15110

Etymology – The epithet refers to the Shennongjia National Forestry Park of Hubei province, China where the holotype was collected.

Type – China, Hubei Province, Shennongjia Forestry District, Shennongding Area, Jizi Gully, 27 Aug. 2022, X.Y. Zhu, ZRL20221248 (holotype HMAS 258806).

Diagnosis – This species is characterized by large-sized basidiomes attached by a thick rhizomorph, featuring a well-developed subgleba. The basidiospores are globose to subglobose and echinate, and the capillitium is of the *Calvatia*-type.

Macroscopic description – *Basidiomes* 3.5 cm broad, 3 cm high, broadly obpyriform to turbinate, slightly tapering at the base and develop a rounded base, which attached by a thick rhizomorph. Exoperidium initially whitish, ochraceous to dark brownish when mature and breaking up into thin irregular-shaped flaky patches, and finally the upper part is completely detached. *Endoperidium* pale yellow, papery and fragile. *Gleba* initially whitish, pale brown to olive-yellow when mature, cottony.

Microscopic description – *Basidiospores* globose to subglobose, 3.2–4.0 µm, [$x = 3.6 \pm 0.2$, $n = 30$], spinose observed under LM, under SEM ornamented with distinct spines, dense, up to 2 µm, with a short pedicel (less than 3 µm). *Capillitium* of *Calvatia*-type, straight, rare branched, septate, fragile, under SEM smooth to asperulate. *Paracapillitium* absent. Exoperidium was made up of inflated cells, globose to subglobose or pear shaped, slightly thick-walled, smooth, hyaline in 5% KOH. *Endoperidium* was made up of tightly interwoven inflated cells.

Ecology and distribution – often occur on open grounds or meadows, growing alone or gregariously. known from China.

Additional material examined – China, Hubei Province, Shennongjia Forestry District, Shennongding Area, Jizi Gully, 27 Aug. 2022, M.Q. He, ZRL20220910 (HMAS 258807); China,

Hubei Province, Shennongjia Forestry District, Shennongding Area, Jizi Gully, 27 Aug. 2022, J.X. Li, *ZRL20221250* (HMAS 258808); China, Yunnan Province, Kunming City, Baoshan to Tengchong Stilwell Highway, 4 Jul. 2018, M.Q. He, *ZRL20180100* (HMAS 258805).



Figure 14 – Morphology of *Calvatia shennongjiaensis*. A gasterocarps (HMAS 258808). B gasterocarps (HMAS 258807). C gasterocarps (holotype, HMAS 258806). D basidiospores under SEM. E *capillitiums* under SEM. Scale bars: A–C = 2 cm, D–E = 2 μ m.

Notes – Phylogenetic studies based on ITS, nrLSU, *rpb2*, and *tef1- α* sequence data revealed that five specimens represented by *C. shennongjiaensis* sp. nov. clustered together, forming a distinct

lineage with strong support (BS = 100, PP = 1), falling into *Calvatia* subg. *Calvatia*. Morphologically, *C. shennongjiaensis* sp. nov. resembles the commonly known “Brain puffball” *C. craniiformis* (Schwein.) Fr. ex De Toni; both possess large-sized basidiomes, a dark dull yellow exoperidium, and globose to subglobose spinose basidiospores. However, they exhibit more than forty base site differences between our examined specimens of *C. shennongjiaensis* sp. nov. and *C. craniiformis* (Steinke001017 DQ112625) in the ITS sequence. *Calvatia craniiformis* displays variability in morphology across different countries. For instance, *C. craniiformis* from North-East India exhibits white to tan basidiomes when mature, with mostly elliptical basidiospores (3.2–4.8 µm in diameter, 4.0–4.8 µm in length) (Gogoi & Kumar 2020). However, *C. craniiformis* reported from Peninsular Malaysia exhibits a unique peridium rupturing pattern and differences in basidiospore size and shape; it can be distinguished by having light brown gleba when mature (Amira 2018).

***Calvatia subbooniana* R.L. Zhao & J.X. Li sp. nov.**

Fig. 15

Fungal Name: FN571702; Facesoffungi number: FoF15111

Etymology – *sub-*: under, close to, near, and “*booniana*” refers to the morphological features reminding of *Calvatia booniana* A.H. Sm.

Type – China, Inner Mongolia Autonomous Region, Baotou City, Olympic Park, 24 Aug. 2019, J.Y. Zhang, ZRL20191927. (holotype HMAS 258810).

Diagnosis – This species is characterized by large-sized basidiomes with a depressed globose or oviform shape, featuring a well-developed rhizomorph. The exoperidium exhibits smallish lamellar cracks, and the mature gleba adopts a dark olive color. Microscopically, it is distinguished by ovoid and oblong basidiospores, with a capillitium of the *Calvatia*-type.

Macroscopic description – *Basidiomes* globose, depressed globose, subovate, 30–80 mm width, 30–50 mm height. Rhizomorphs well-developed, robust, heavily incrustated with soil. *Peridium* layered. Exoperidium greenish-olive or sometimes light reddish-brown, thin, possess smallish lamellar cracks, deeper and wider when mature. Apical pore irregular cracking, large, often reveal a whitish papery *Endoperidium* and *Gleba*. Mature gleba yellowish-white, dark olive-brown, pulverulent.

Microscopic description – *Basidiospores* ovoid, oblong, $5.2\text{--}6.6 \times 3.7\text{--}5.1\mu\text{m}$, with an oil-drop central, smooth in LM, asperulate under SEM, short pedicel present, less than 0.5 µm. *Capillitium* *Calvatia*-type, 2.4–7.2 µm diameter, straight to slightly undulate, easily broken, yellowish-brown, thick-walled, occasionally branched and septa, constricted at the septa. *Paracapillitium* absent. Exoperidium made up of hyaline hyphae, branched, septa present, 2.5–10.1 µm, inflated cells irregular arrangement, pyriform, globose to subglobose, colorless and transparent. *Endoperidium* composed of undulate hyaline hyaline hyphae, occasionally branched, septa present, 1.8–4.9 µm.

Ecology and distribution – growing solitary or two basidiomes on grassland, known to data from China.

Additional material examined – China, Inner Mongolia Autonomous Region, Baotou City, Olympic Park, 24 Aug. 2019, J.Y. Zhang, ZRL20191930 (HMAS 258809); China, Inner Mongolia Autonomous Region, Baotou City, Olympic Park, 3 Oct. 2018, J.Y. Zhang, ZRL20182029 (HMAS 258811).

Notes – *Calvatia subbooniana* sp. nov. is primarily characterized by its large-sized basidiomes, and the exoperidium exhibits small flaky patches. Phylogenetic results indicate that three specimens cluster together, forming a distinct lineage of *C. subbooniana* sp. nov. within *Calvatia* subg. *Langermannia* (Fig. 6). Several species share morphological similarities with *C. subbooniana* sp. nov., including *C. pachydermica* (Speg.) Kreisel and *C. gigantea* (Batsch) Lloyd. However, *C. pachydermica* can be distinguished by its thin, fragile, papery exoperidium, which easily breaks and falls off, and basidiospores that are globose, subglobose, and smooth under SEM (Bates et al. 2009). *Calvatia gigantea* has verrucose basidiospores with small warts under SEM (Diego Calonge & Martín 1990, Li 2011). *Calvatia booniana* A.H. Sm. differs due to the presence of thick or irregularly shaped patches on the exoperidium and globose, subglobose basidiospores ($3.2\text{--}4.8 \times 4.0\text{--}$

4.8 μm) (Bates et al. 2009). *Calvatia sculpta* (Harkn.) Lloyd can be clearly distinguished by exhibiting pyramidal warts and possessing Bovista-type capillitium (Bates et al. 2009).

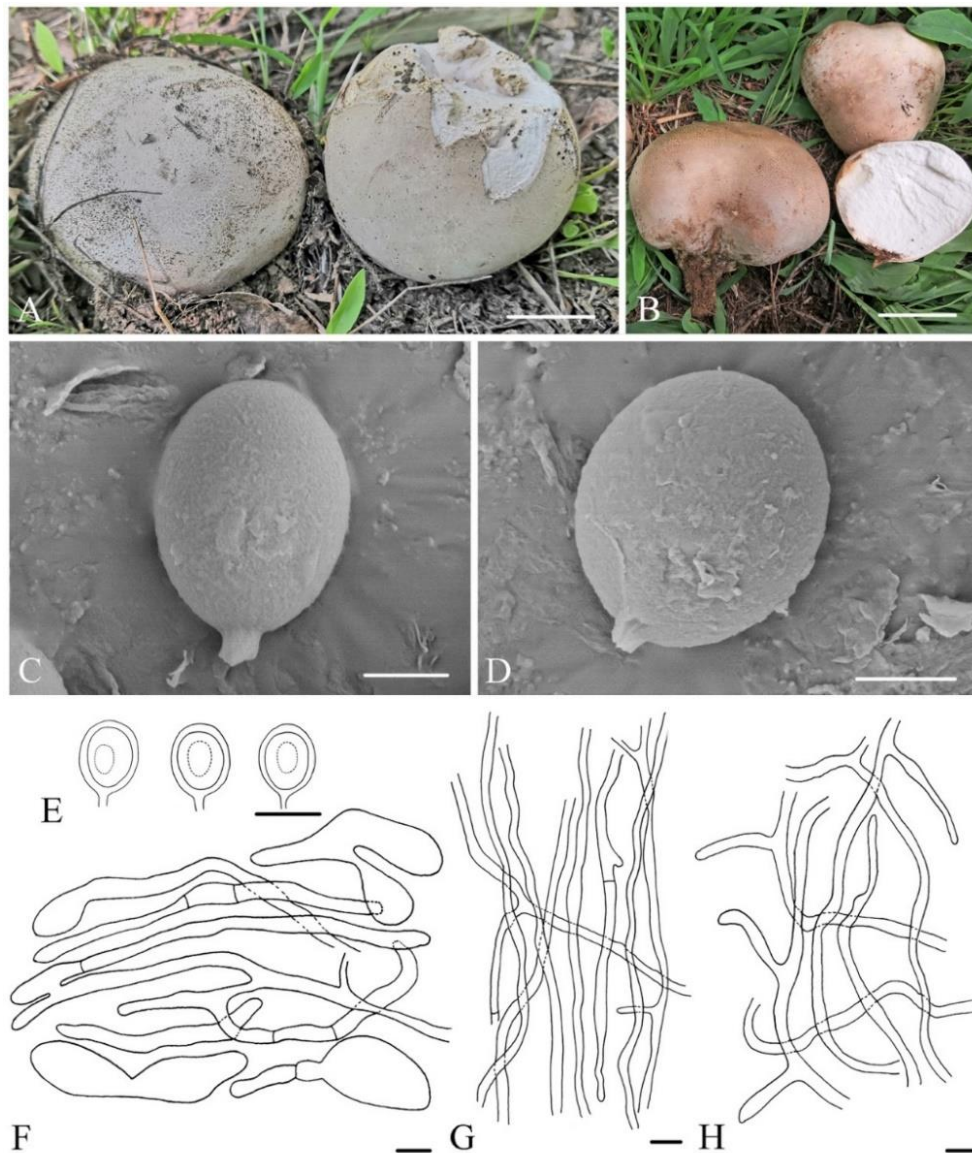


Figure 15 – Morphology of *Calvatia subbooniana*. A gasterocarps (holotype HMAS 258810). B gasterocarps (HMAS 258809). C, D basidiospores under SEM. E basidiospores. F exoperidial elements. G endoperidial hyphae. H capillitial threads. Scale bars: A–B = 1 cm, C–D = 2 μm , E–H = 5 μm .

Disciseda Czern., Bull. Soc. Imp. nat. Moscou 18(no. 3): 153 (1845)

Fungal Name: FN19104

Type species – *Disciseda collabescens* Czern. Bull. Soc. Imp. nat. Moscou 18(no. 3): 153 (1845).

This genus is mainly characterized by globose to globose-depressed basidiomes, with the lower half of the exoperidium covered by a sand case. The endoperidium features dehiscence through a small, fimbriate peristoma at the height of the septum. The capillitium is of the *Calvatia*-type, commonly wavy, and basidiospores are pedicellate, smooth to verrucose, and shortly pedicellate (Underwood 1899, Kreisel 1962, Kers 1975, Wright & Suárez 1990, Cortez et al. 2010b). Phylogenetic results strongly support this genus as a monophyletic group that diverged around 62.5 Myr (BS = 95, PP = 1) (Fig. 1).

Fuscospina R.L. Zhao & J.X. Li, gen. nov.

Fungal Name: FN571716; Facesoffungi number: FoF15150

Type species – *Fuscospina scabricapillitia* R.L. Zhao & J.X. Li

Etymology – *fuscus* (dark, dark brown) and *spina* (spine). The epithet refers to the dusky basidiomes with spined exoperidium.

Fuscospina gen. nov. is proposed to accommodate species exhibiting distinct morphological characteristics: lycoperdoid basidiomes with a dark brown appearance, an exoperidium adorned with conical and curved warts that persist longer than those of other lycoperdoid species, *Lycoperdon*-type capillitium with pits, and basidiospores covered with rounded warts. Previous phylogenetic studies suggested an uncertain placement of *F. nigrescens* (= *Lycoperdon nigrescens* Pers.), leading to its temporary assignment to *Lycoperdon* subg. *Utraria* (Larsson & Jeppson 2008, Larsson et al. 2009, Alfredo et al. 2017).

In this study, phylogenetic analysis involving two species, *F. scabricapillitia* sp. nov. and *F. nigrescens* (Pers.) R.L. Zhao & J.X. Li comb. nov., reveals this genus as a fully-supported distinct lineage (Figs 1, 3). Furthermore, divergence-time analysis suggests that *Fuscospina* diverged around 34.5 Myr, aligning with other estimates within *Lycoperdaceae* (Fig. 1). Ecologically, *F. nigrescens*, previously reported as a common species in Europe and recorded in South America, now represents its first record from China. Here, one new species and the new record for China are described as follows.

Fuscospina scabricapillitia R.L. Zhao & J.X. Li sp. nov.

Fig. 16

Fungal Name: FN571703; Facesoffungi number: FoF15166

Etymology – *scaber/scabra/scabrum* meaning coarse and the feminine of *capillitium*. The epithet refers to the gleba develop coarse *capillitium*.

Type – China, Guizhou Province, Tongren City, Taiping Town, Fanjingshan, 27°90'97"N, 108°67'03"E, 29 Sep. 2021, R.L. Zhao, ZRL20211919 (holotype HMAS 258812).

Diagnosis – The exoperidium is densely covered with brownish conical spines that easily fall off from the tip to the base, resulting in a depressed and rounded grid appearance on the endoperidium. Microscopically, basidiospores are globose to subglobose, verrucous, with a long pedicel. The capillitium presents a coarse surface covered with large pieces of flaky fibers under SEM. Macroscopic description – *Basidiomes* sub-pyriform to subglobose, depressed globose, 40 mm in diameter, 30 mm height. *Pseudostipe* indistinct. Rhizomorphs sparse, white, often densely embedded in the substrate. *Peridium* layered. Exoperidium echinate, densely with conical spines, brown to dark brown when mature, shedding from tip to base with age, reveal yellowish *Endoperidium*, membranous, papery, with rounded grid, slightly depressed. *Gleba* yellowish green when fully mature, fibrous to cottony, pulverulent.

Microscopic description – *Basidiospores* globose to subglobose, 3.6–4.5 μm , [$x = 4 \pm 0.2$, $n = 30$], thick-walled, with an oil drop central, yellowish brown 5% KOH, usually with a long pedicel (7.8–9.7 μm , $n = 30$), under SEM ornamented with cylindrical to sub cylindrical verrucae, often 2–3 connect or isolated with linear. *Capillitium* of *Lycoperdon*-type, 1.4–4.4 μm width, thick-walled, brownish, dark brown, straight to slightly undulate. under SEM, coarse surface covered with large pieces of flaky fibers which is easy to shed. no pores and septa observed. *Paracapillitium* absent. Exoperidium was made up of inflated cells, irregular, slightly thick-walled, smooth, hyaline in 5% KOH. *Endoperidium* made up of unbranched arrangement hyphae, pale brownish, straight, no septa observed.

Ecology and distribution – It's assumed that this species occurs in the higher elevations of the state, altitude over 2000m, within the mixed broadleaf forests, like *Camellia*, *Rhododendron*. It often fruiting on decaying wood, surrounded by moss, solitary in a relatively humid environment. known to data from China.

Notes – The distinctive feature of *F. scabricapillitia* sp. nov. lies in its exoperidium, which is initially covered by brownish conical spines that easily detach from the tip to the base. The basidiospores are ornamented with cylindrical to sub-cylindrical verrucae, measuring 3.6–4.5 μm ,

with a long pedicel. The capillitium is of the *Lycoperdon*-type, covered with large pieces of flaky fibers on the surface. Phylogenetic analysis indicates that it is the sister species to *F. nigrescens*. Despite sharing many morphological features, such as pyriform to subglobose, depressed globose basidiomes, and an exoperidium densely covered with conical spines, these two species can be distinguished by their micromorphological characteristics of basidiospores and capillitium. *Fuscospina nigrescens* has rounded warts on the surface of basidiospores (Baseia 2005), and capillitium threads develop vertical stripes on the surface (observed in this study) (Fig. 17). In contrast, spores of *F. scabricapillitia* are ornamented with cylindrical to sub-cylindrical verrucae, featuring a long pedicel, and the capillitium presents a coarse surface covered with large pieces of flaky fibers (Fig. 16).

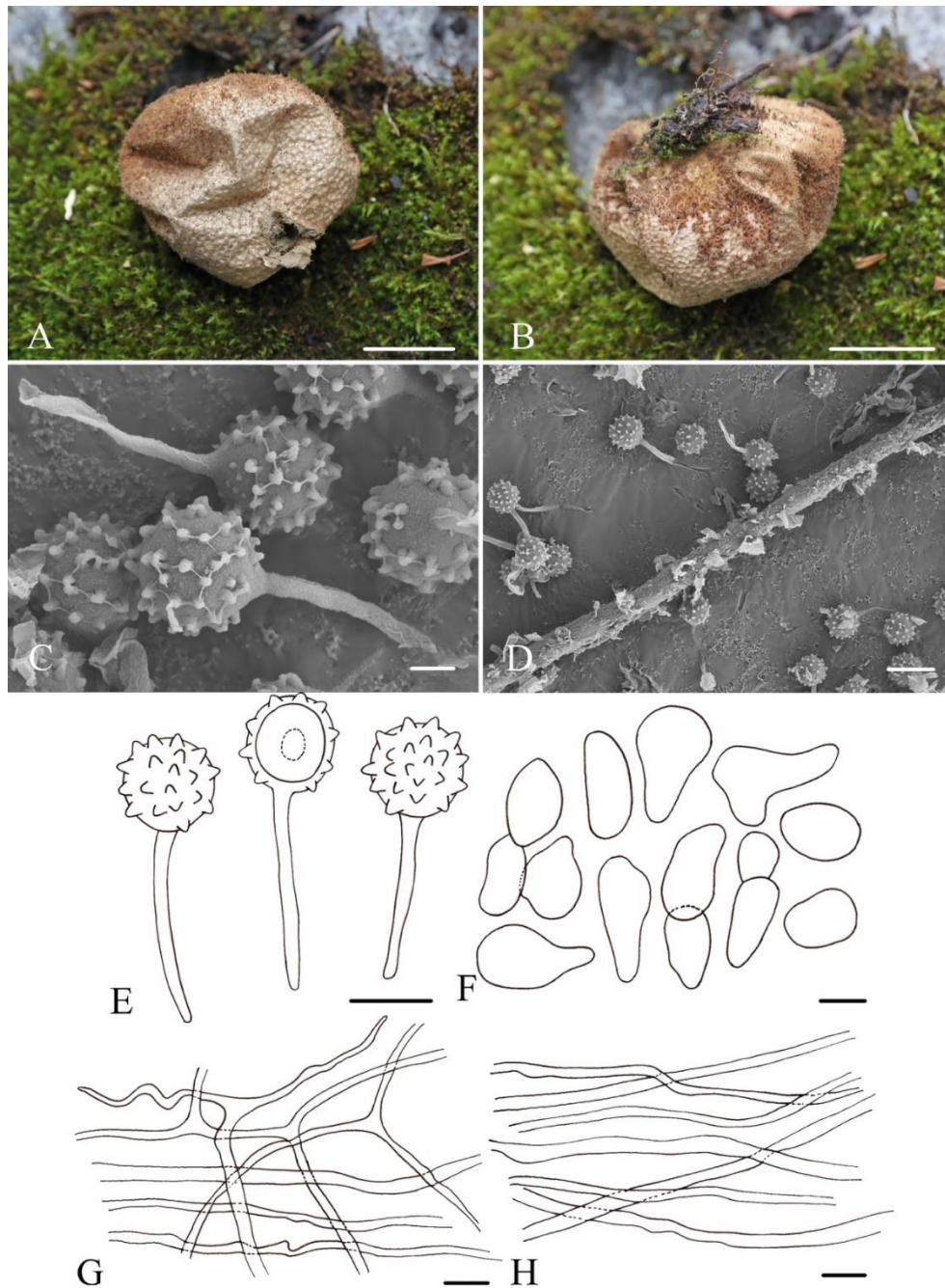


Figure 16 – Morphology of *Fuscospina scabricapillitia*. A, B gasterocarps (holotype, HMAS 258812). C basidiospores under SEM. D capillitium under SEM. E basidiospores under LM. F exoperidial elements (sphaerocysts). G capillitial threads. H endoperidial hyphae. Scale bars: A–B = 2 cm, C–D = 2 µm, E–H = 5 µm.

Fuscospina nigrescens (Pers.) R.L. Zhao & J.X. Li comb. nov.

Fig. 17

Fungal Name: FN571729

Basionym – *Lycoperdon nigrescens* Pers., Neues Mag. Bot.1: 87 (1794).

Macroscopic description – *Basidiomes* 3.5 cm broad, 3 cm high, turbinate to subglobose; exoperidium yellowish brown, spinose, spines up to 1 mm in length, dense, falling off from the top when mature. *Endoperidium* brown, papery. *Gleba* yellowish-brown. *Subgleba* of the same color.

Microscopic description – *Basidiospores* globose to subglobose, 3.7–4.5 μm , [$x = 4 \pm 0.2$, $n = 30$], smooth to asperulate in LM, slightly thick-walled, with an oil drop central, olive-green color in 5% KOH, without a pedicel or short (less than 2 μm), under SEM ornamented with cylindrical to sub-cylindrical verrucae. *Capillitium* of *Lycoperdon*-type, 1.4–7.2 μm width, olive green color in 5% KOH, under SEM it ornamented with vertical stripes. *Paracapillitium* absent. Exoperidium was made up of inflated cells, irregular, slightly thick-walled, smooth, hyaline in 5% KOH. *Endoperidium* was made up of unbranched arrangement hyphae, straight, no septa.

Ecology and distribution – Terrestrial and found in grassy areas, solitary on soil or litter. Known from North America, Europe, Asia.

Material examined – China, Sichuan Province, Liangshan Yi Autonomous Prefecture, Muli Tibetan Autonomous County, Duckbill Reserve, 8 Aug. 2019, R.L. Zhao, ZRL20190617 (HMAS 258881).



Figure 17 – Morphology of *Fuscospina nigrescens*. A gasterocarps (HMAS 258881). B basidiospores under SEM. C capillitiums under SEM. Scale bars: A = 1 cm. B–C = 5 μm .

Notes – Phylogenetic analysis in this study indicates that *F. nigrescens* is a member of the newly proposed genus *Fuscospina*. In comparison to another species in this subclade,

F. scabricapillitia, they share several common macroscopic features, such as a yellowish-brown exoperidium covered with dense spines, which fall off from the top with age. However, specific microscopic characteristics, such as basidiospores with long pedicels and capillitium composed of large pieces of flaky fibers, serve as distinctive identifiers (Diego Calonge & Syvokon 2008, Bates et al. 2009). While *Lycoperdon perlatum* Pers. appears morphologically closer to *F. nigrescens*, distinctions arise in the exoperidium composition, formed by conical but not curved spines, and the capillitium appearing yellow to pale brownish in 3% KOH, allowing for differentiation (Baseia 2005, Diego Calonge & Syvokon 2008, Kim et al. 2016).

Globaria Quél., Mém. Soc. Émul. Montbéliard, Sér. 2 5: 370 (1873)

Fungal Name: FN19143

Type species – *Globaria aestivalis* (Bonord.) Hazsl. 1877.

In this study, the phylogeny and divergence time analysis indicated that the formerly *Bovista* subgenus *Globaria* should be recognized as a distinct genus (Figs 1, 3). The main morphological characters see those described under *Bovista*. Here, six new species are introduced, and two new combinations are detailed as follows.

Globaria albata R.L. Zhao & J.X. Li sp. nov.

Fig. 18

Fungal Name: FN571820; Facesoffungi number: FoF15346

Etymology – referring to the whitish color of basidiomes.

Type – China, Heilongjiang Province, Yichun City, Wuyiling National Nature Reserve, 31 Aug. 2017, Z.L. Ling, ZRL20170966 (holotype HMAS 258884).

Diagnosis – Macroscopically, this species is characterized by basidiomes exhibiting a whitish color, with the exoperidium developing irregular cracking at the upper part. Microscopically, it possesses *Lycoperdon*-type capillitium and minutely verruculose basidiospores with inconspicuous pedicels.

Macroscopic description – *Basidiomes* subglobose, depressed globose, 15–25 mm width, 15–25 mm height. *Pseudostipe* not indistinct. *Peridium* layered. Exoperidium whitish almost overall, pale yellowish at the upperpart and develop irregular cracking with age. Sparsely with granular and smallish warts. *Endoperidium* smooth, fragile, papery, whitish. *Gleba* pulverulent, whitish. *Subgleba* absent.

Microscopic description – *Basidiospores* globose, subglobose, 2.9–4.1 μm in diameter [$x = 3.3 \pm 0.3$, $n = 30$], slightly thick-walled, with an oil drop central, hyaline in 5% KOH, under SEM surface densely ornamented with irregular-sized arrangements, the verruca occasionally connect with linear, short pedicel less than 0.5 μm . *Capillitium* of *Lycoperdon*-type, 3.4–7.3 μm width, dark brownish, thick-walled, unequal width, often swollen in the middle and tapering towards the tips, elastic, no pores and septa observed. *Paracapillitium* absent. Exoperidium made up of inflated cells, irregularly arranged, slightly thick-walled, hyaline in 5% KOH. *Endoperidium* made up of hyaline hyphae, 2.4–5.4 μm in width, short branched, produce septa.

Ecology and distribution – Solitary or in small groups around dried pine needles, known from China.

Notes – *Globaria albata* sp. nov. can be easily distinguished by its whitish basidiomes, with the exoperidium developing irregular cracking at the upper part. Phylogenetic trees based on ITS, nrLSU, *rpb2*, and *tef1- α* sequences data (Fig. 5) demonstrate that *G. albata* forms a distinct lineage and is sister to *G. gyirongensis* sp. nov. with full PP values (Fig. 5). Additionally, both species are closely related to the *G. aestivalis* complex. Morphologically, both species have whitish basidiomes; however, *G. gyirongensis* sp. nov. has an exoperidium covered with yellowish-white minutely verrucae without cracking, and it develops intermediate capillitial threads. In contrast, *G. albata* sp. nov. possesses capillitium of the *Lycoperdon*-type. Another closely related species, *G. aestivalis*, also exhibits whitish basidiomes at an early stage. However, its exoperidium is densely covered with yellowish warts at the upper part (Bautista-Hernández et al. 2012), and morphologically, it has intermediate capillitial threads and an exoperidium made up of chained cylindrical cells (Fig. 24).

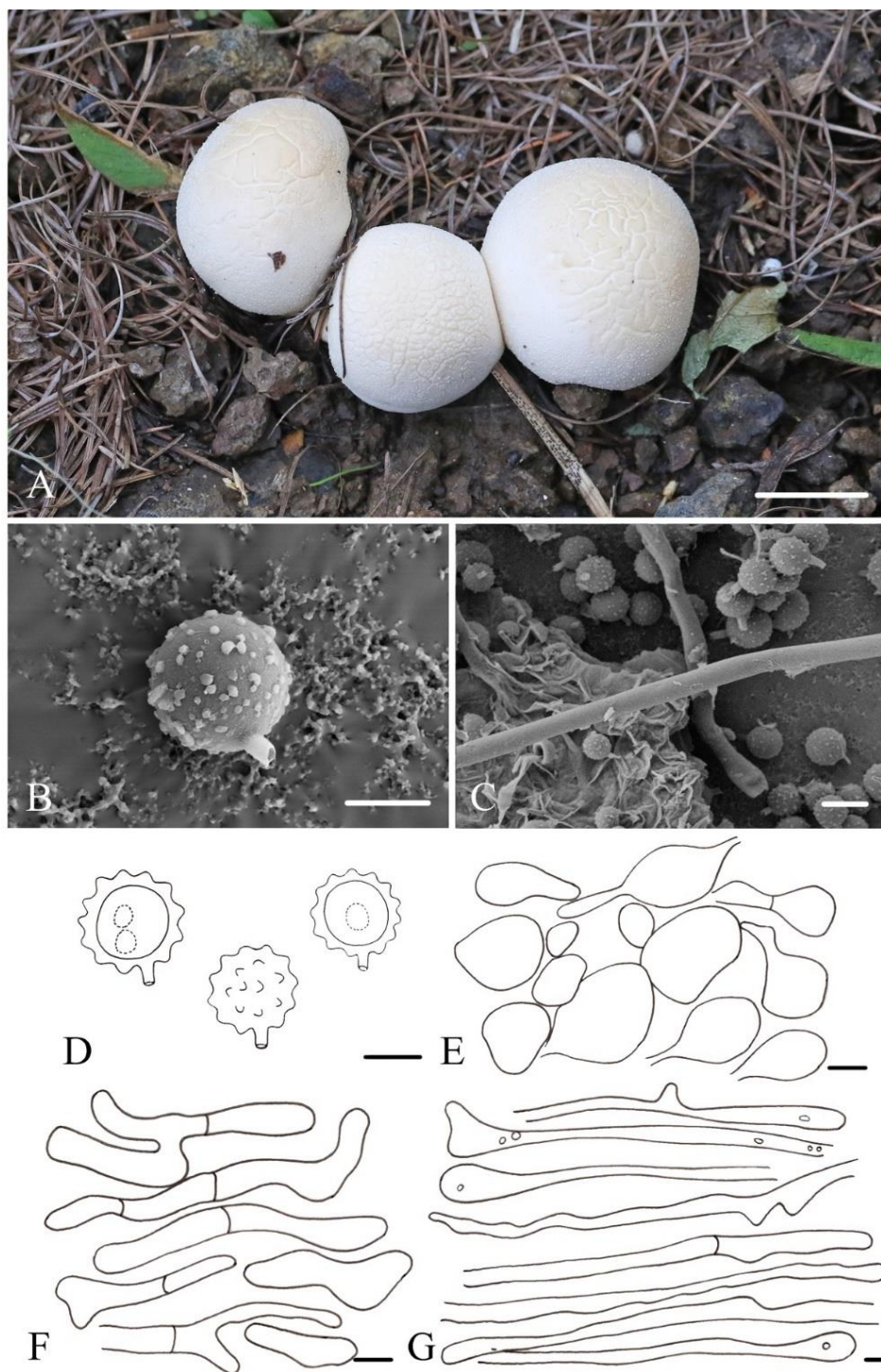


Figure 18 – Morphology of *Globaria albat*. A gasterocarps (holotype, HMA258884 ZRL20170966). B, C basidiospores and capillitial threads under SEM. D basidiospores. E exoperidial elements (sphaerocysts). F endoperidial hyphae. G capillitial threads. Scale bars: A = 1 cm, B = 2 μ m, C = 5 μ m, D = 2 μ m, E–G = 5 μ m.

Globaria gyirongensis R.L. Zhao & J.X. Li sp. nov.

Fig. 19

Fungal Name: FN571704; Facesoffungi number: FoF15157

Etymology – referring to the Gyirong County, Shigatse City, Xizang Autonomous Region from China where the holotype was collected.

Type – China, Xizang Autonomous Region, Shigatse City, Gyirong County, Gyirong Gully, 2 Aug. 2022, M.Q. He, ZRL20220680 (holotype HMAS 258813).

Diagnosis – Macroscopically, this species is characterized by globose to subglobose basidiomes with an exoperidium densely covered in yellowish-white minutely verrucae. The capillitium is of an intermediate type, generating globose to subglobose basidiospores with surfaces densely ornamented with conical warts.

Macroscopic description – *Basidiomes* globose to subglobose, 15–28 mm width, 15–26 mm height. Rhizomorphs sparse, white, solid, inserted with soil. *Pseudostipe* reduced or indistinct. *Peridium* layered. Exoperidium whitish, yellowish-white, becoming yellowish white to pale yellow when mature. densely covered with minutely verruculose, becoming slightly smooth near the base. *Endoperidium* smooth, fragile, papery, yellowish-brown, gray. *Gleba* pulverulent, initially white, turning yellowish-brown as it matures, fibrous to cottony. *Subgleba* absent or indistinct.

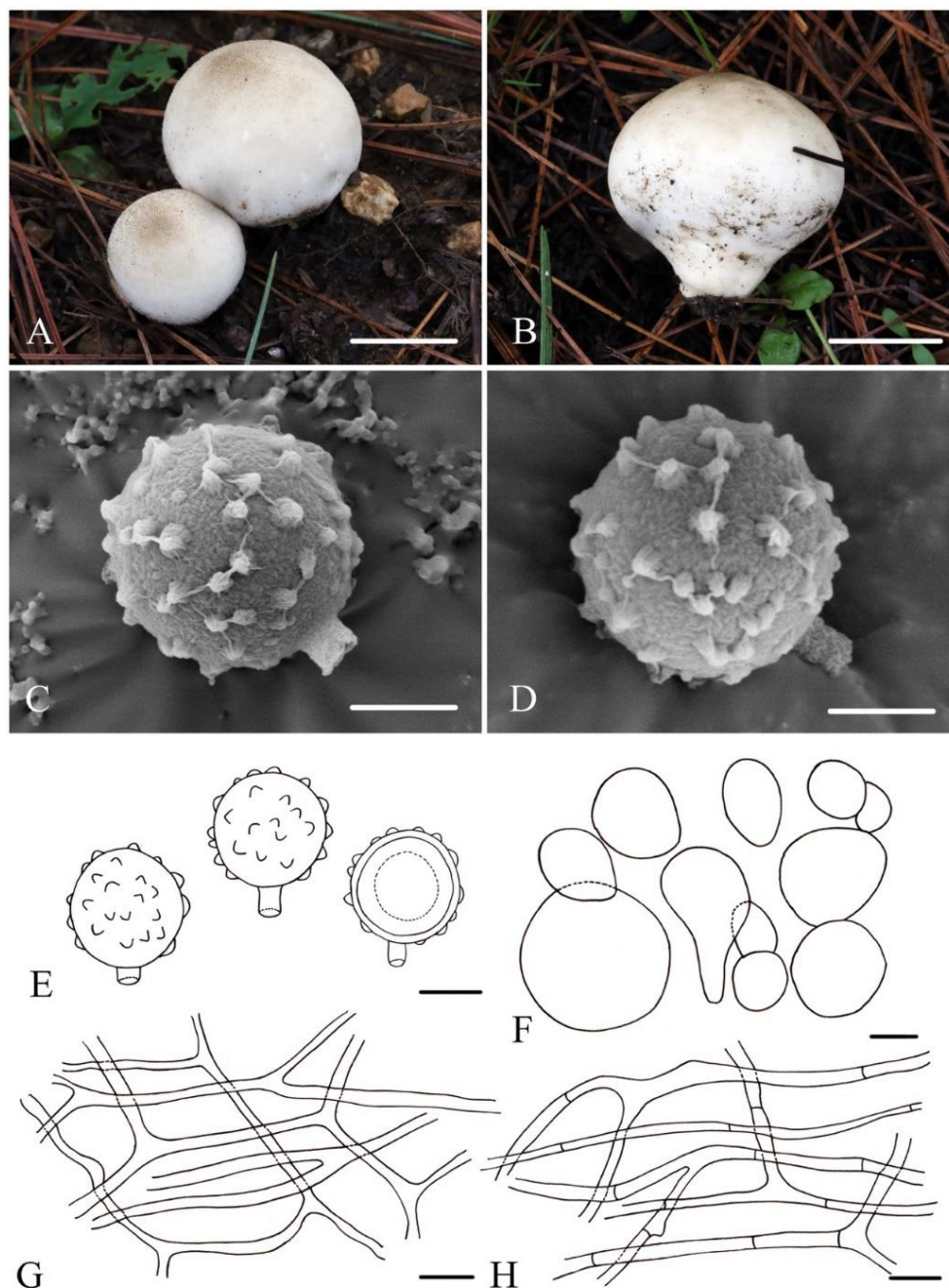


Figure 19 – Morphology of *Globaria gyirongensis*. A gasterocarps (holotype, HMAS 258813). B gasterocarps (HMAS 258814). C, D basidiospores under SEM. E basidiospores under LM. F exoperidial elements (sphaerocysts). G capillitial threads. H endoperidial hyphae. Scale bars: A–B = 1 cm, C–E = 1 μ m, F = 10 μ m, G–H = 5 μ m.

Microscopic description – *Basidiospores* globose, subglobose, 2.4–2.8 µm in diameter (n = 30), thick-walled, with an oil drop central, hyaline in 5% KOH, asperulate under SEM, rough surface densely ornamented conical warts, irregularly arrangement, verrucose usually connect with linear, short pedicel present (less than 0.5 µm). *Capillitium* of intermediate type, 2.1–4.7 µm width, pale brownish, thick-walled, unequal width, tapering towards the tips, elastic, straight to undulate, no pores and septa observed. *Paracapillitium* absent. Exoperidium made up of inflated cells, subglobose to globose, oblong to pyriform, 9.5–32.3 µm in width, 11.3–44.1 µm in length, slightly thick-walled (less than 0.5 µm), hyaline in 5% KOH. *Endoperidium* made up of hyaline hyphae, 1.5–3.3 µm in width, straight and slightly branched, produces septa not constricted.

Ecology and distribution – It's assumed that this species occurs in the higher elevations of the state, altitude over 3,500, within the coniferous forest, growing on the grass, often solitary in a relatively humid environment. known from China.

Additional material examined – China, Xizang Autonomous Region, Shigatse City, Jilong Country, Jilong Gully, 1 Aug. 2022, P. Dorji, ZRL20220682 (HMAS 258814).

Notes – Morphologically, *G. gyirongensis* sp. nov. can be easily distinguished by its subglobose or pear-shaped basidiomes, white to off-white exoperidium with minute verrucae, intermediate capillitium, and its globose to subglobose basidiospores. Phylogenetic analysis in *Globalia* indicates that the two specimens formed a distinct lineage with full support (Fig. 5) and nested in the *G. aestivalis* complex, near the type *G. aestivalis*. Although confusion may arise due to the whitish exoperidium and minute verrucae at times, they can be clearly differentiated based on spore morphology. *G. aestivalis*, for example, possesses larger basidiospores (3.1–5.4 µm) (Abrar et al. 2008). In reality, *G. gyirongensis* sp. nov. may be misidentified in the wild with *Ba. litangensis* and *Ba. nyalamensis* within the genus *Bovista* because they all have a white to off-white exoperidium and are covered with minute verrucae more or less. However, the basidiomes of *Ba. litangensis* turn dark brown when mature, and it has larger basidiospores (4.2–5.4 µm); meanwhile, *Ba. nyalamensis* can be distinguished by its basidiospores usually having a long pedicel (6.2–8.9 µm). Additionally, the capillitium of *Bovista*-type in these two *Bovista* species is also an important feature to distinguish them from this new species.

***Globalia jingningensis* R.L. Zhao & J.X. Li sp. nov.**

Fig. 20

Fungal Name: FN571705; Facesoffungi number: FoF15158

Etymology – referring to the region where the holotype was collected, Jingning She Autonomous County of Zhejiang Province in China.

Type – China, Zhejiang Province, Jingning She Autonomous County, Grass carp pond, 6 Sep. 2019, X.Y. Zhu, ZRL20191590 (holotype HMAS 258815).

Diagnosis – This species is characterized by subglobose, depressed globose basidiomes, with the exoperidium densely covered with granular verrucae, and the mature gleba exhibiting an olive-green color.

Macroscopic description – *Basidiomes* globose, subglobose, depressed globose 14–23mm width, 8–18mm height. Rhizomorphs thick and solid, white, unbranched, encrusted with humus and soil. *Peridium* layered. Exoperidium yellowish-white, yellowish-brown, densely covered with small granular warts, becoming slightly smooth near the base, turns brownish, dark brown when mature. *Endoperidium* smooth, fragile, papery, lacerate. *Gleba* pulverulent, initially white, turning light olive-green as it matures. *Subgleba* absent.

Microscopic description – *Basidiospores* globose to subglobose, 2.3–3.9 µm in diameter, verrucose with an oil drop central, cylindrical warts with rounded tips, occasionally isolated or 2–3 connected, short pedicels present, less than 0.5µm. *Capillitium* of *Lycoperdon*-type, yellowish-brown, straight to undulate, thick-walled, tapering towards the tips, 1.2–4.3 µm in diameter. *Paracapillitium* not observed. Exoperidium composed of numerous hyaline sphaerocysts, thick-walled, subglobose to globose, 13.2–23.8 µm in diameter. *Endoperidium* composed of filamentous interwoven hyphae, sometimes branched, medially expanded as a bulging parcel. Basidia can be observed at a young age, colorless and transparent, thin-walled, 6.1–12.1 × 4.8–6.3 µm.

Ecology and distribution – Terrestrial and found in open areas, growing solitary in the soil under coniferous forests, in a humid environment, sometimes surrounded by mosses. known from China.

Additional material examined – China, Zhejiang Province, Jingning She Autonomous County, Grass carp pond, 6 Sep. 2019, X.Y. Zhu, ZRL20191591 (HMAS 258816); ZRL20191595 (HMAS 258817); ZRL20191616 (HMAS 258818).

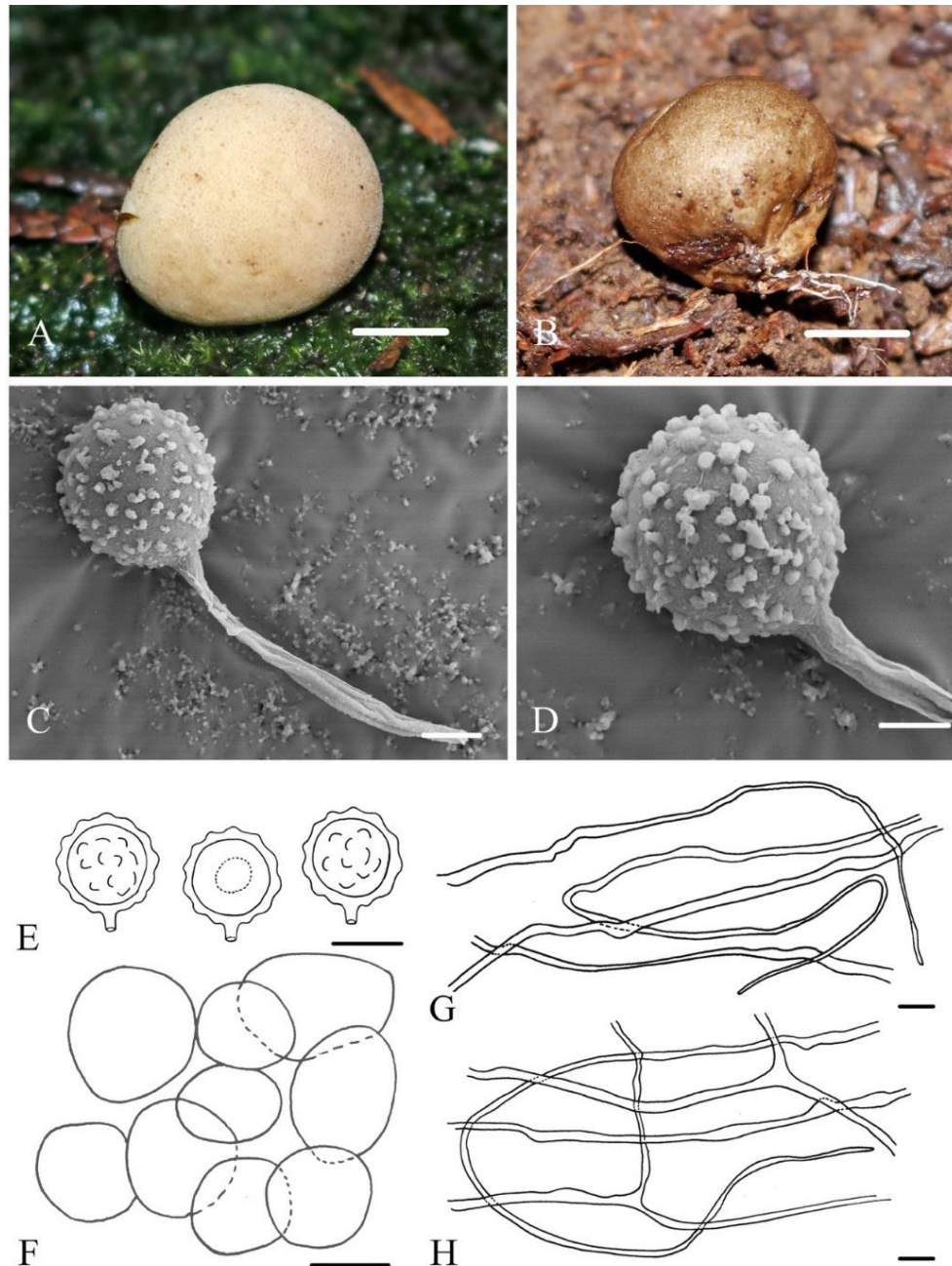


Figure 20 – Morphology of *Globaria jingningensis*. A gasterocarps (holotype HMAS 258815). B gasterocarps (HMAS 258817). C, D basidiospores under SEM. E basidiospores under LM. F exoperidial elements (sphaerocysts). G endoperidial hyphae. H capillitial threads. Scale bars: A–B = 1 cm, C–D = 1 µm, E = 3 µm, F = 5 µm, G–H = 2 µm.

Notes – The species is characterized by basidiomes that are yellowish-white to brown, covered with densely arranged granular warts, and the gleba turns pale olive when mature. In the phylogenetic tree (Fig. 5), four specimens of this new species form a distinct lineage with full support. In the field, *Ba. citrina* [= *Bovista citrina* (Berk. & Broome) Bottomley] and *Lo. asperum* Spg. may resemble

G. jingningensis sp. nov. However, *Ba. citrina* possesses intermediate-type capillitia, larger basidiospores (4–5 µm in diameter), and the gleba turns lemon yellow when mature (Fan 2019). The exoperidium of *Lo. asperum* presents warts and is easily detached (Kreisel & Hausknecht 2002). These features distinguish them from the new species.

Globalia testacea R.L. Zhao & J.X. Li sp. nov.

Fig. 21

Fungal Name: FN571706; Facesoffungi number: FoF15159

Etymology – referring to brownish color at the upperpart of the fruiting body, especially at apical part.

Type – China, Xizang Autonomous Region, Shigatse City, Gyirong County, Gyirong Town, 2 Aug. 2022, P. Dorji, ZRL20220726 (holotype HMAS 258819).

Diagnosis – This species is distinguished by its pyriform basidiomes. The exoperidium is granular or with verrucae, accompanied by whitish or brownish slender spines, which appear dark brown in the upper part.

Macroscopic description – *Basidiomes* pyriform, globose, subglobose, 14–23mm width, 8–18mm height. Rhizomorphs occasionally with white flocculent, encrusted with rotten wood. *Peridium* layered. Exoperidium initially white, granular with smallish warts, easily shed slender soft spines often dark to tan in upper part. *Endoperidium* fragile, papery, apical pore lacerate. *Gleba* initially cottony, whitish, light brown, becoming powdery, yellowish-brown at maturity.

Microscopic description – *Basidiospores* globose to subglobose, 3–3.9 µm in diameter, smooth to asperulate in LM, verrucose in SEM, pedicels less than 5 µm. *Capillitium* *Lycoperdon*-type, 1–3.7µm diam, yellowish-brown, straight to undulate, thick-walled, up to 1.5 µm, branched, tapering towards the tips, no septa. *Paracapillitium* absent. Exoperidium composed of numerous sphaerocysts, subglobose, depressed globose, pyriform, obpyriform, colorless and transparent, thick-walls, 10.3–39.2 × 8.7–25.8 µm. *Endoperidium* 1–4.4 µm, composed of straight, interwoven hyphae, hyaline to light brown in 5% KOH.

Ecology and distribution – Terrestrial and found in broadleaf forest, growing solitary in the soil, known from China.

Additional material examined – China, Xizang Autonomous Region, Shigatse City, Jilong County, Jilonggou, 1 Aug. 2022, M.Q. He, ZRL20220464 (HMAS 258820); China, Xizang Autonomous Region, Shigatse City, Jilong County, Jilong Town, 2 Aug. 2022, R.L. Zhao, ZRL20220727 (HMAS 258821); China, Xizang Autonomous Region, Shigatse City, Jilong County, Jilong Town, Zhangmugou, 2 Aug. 2022, B. Cao, ZRL20220825 (HMAS 258822); China, Xizang Autonomous Region, Shigatse City, Jilong County, Jilong Town, 2 Aug. 2022, M.Q. He, ZRL20220695 (HMAS 258823); China, Xizang Autonomous Region, Shigatse City, Jilong County, Jilong Town, 2 Aug. 2022, M.Q. He, ZRL20220687 (HMAS 258824); China, Xizang Autonomous Region, Shigatse City, Jilong County, Jilong Town, 2 Aug. 2022, P. Dorji, ZRL20220724 (HMAS 258825); China, Hubei Province, Shennongjia Forestry District, Shennongding Area, Guanyin Cave, 2 Sep. 2022, X.Y. Zhu, ZRL20221443 (HMAS 258826); China, Hubei Province, Shennongjia Forestry District, Shennongding Area, Guanyin Cave, 2 Sep. 2022, M.Q. He, ZRL20221459 (HMAS 258827); China, Sichuan Province, Liangshan Yi Autonomous Prefecture, Muli Tibetan Autonomous County, Shuiluo Town, 11 Aug. 2019, R.L. Zhao, ZRL20190919 (HMAS 258830); ZRL20190915 (HMAS 258831); China, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Batang County, Drukpa Cage Nature Reserve, 18 Aug. 2020, M.Q. He, ZRL20201152 (HMAS 258828), ZRL20201151 (HMAS 258832); China, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Batang County, Drukpa Cage Nature Reserve, 19 Aug. 2020, M.Q. He, ZRL20201534 (HMAS 258829).

Notes – Based on morphological characteristics, *G. testacea* sp. nov. can be distinguished by its dark brown upper basidiomes, with the exoperidium covered in finely granular verrucae or spiniform structures. In the phylogenetic tree (Fig. 5), twelve specimens of this new species form a distinct lineage with full support. *Lycoperdon asperum* (Lév.) Speg. appears macroscopically most similar to this new species; however, it differs due to its larger basidiospores (3.6–4.6 µm in

diameter), mature gleba presenting a clear olivaceous to ochraceous brown color, and the development of a long pedicel (9–20 μm) (Kreisel & Hausknecht 2002). Another resembling species is *G. jingningensis* sp. nov. as they both exhibit yellowish-brown basidiomes. Nevertheless, *G. jingningensis* sp. nov. has an exoperidium with granular verrucae, not slender spines, and the mature gleba is noticeably pale olive-green (Fig. 20).

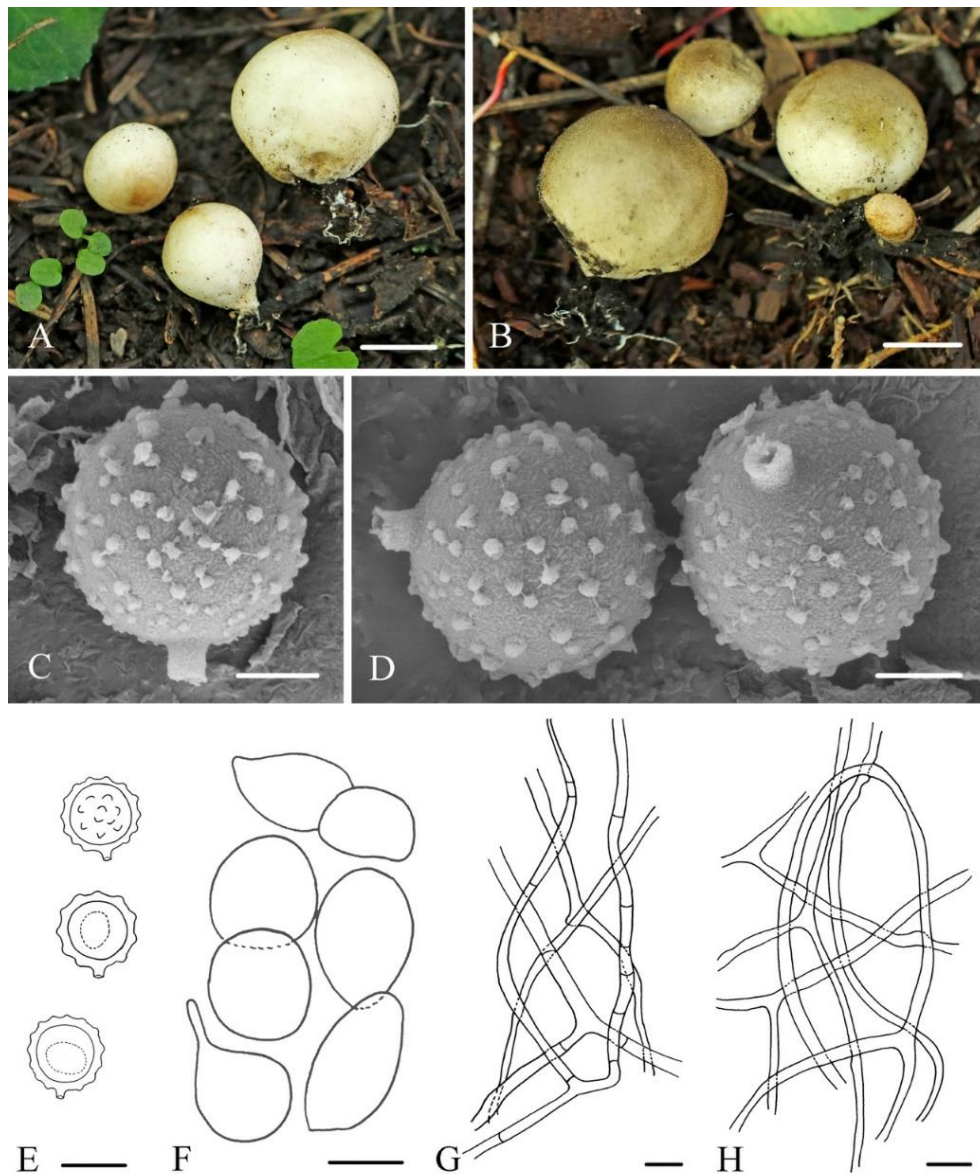


Figure 21 – Morphology of *Globaria testacea*. A gasterocarps (holotype HMAS 258819), B gasterocarps (HMAS 258831), C, D basidiospores under SEM, E basidiospores under LM, F exoperidial elements (sphaerocysts), G endoperidial hyphae, H capillitial threads. Scale bars: A–B = 1 cm, C–D = 1 μm , E = 3 μm , G–H = 5 μm .

Globaria shannanensis R.L. Zhao & J.X. Li sp. nov.

Fig. 22

Fungal Name: FN571821; Facesoffungi number: FoF15347

Etymology – referring to the region where the holotype was collected, Shannan City of Xizang Autonomous Region in China.

Type – China, Xizang Autonomous Region, Shannan City, Lhünzê County, Gatang Village, Xuesha Township, 17 Sep. 2015, X.Y. Zhu, ZRL20152235 (holotype HMAS 258883).

Diagnosis – This species is distinguishable by its yellowish basidiomes covered with small granules or warts. Microscopically, it exhibits globose to subglobose basidiospores without pedicels, minutely verruculose, and an intermediate-type capillitium.

Macroscopic description – *Basidiomes* subglobose, depressed globose, obpyriform, 10–15 mm width, 15–20 mm height. Rhizomorphs sparse, encrusted with soil. *Peridium* layered. Exoperidium yellowish, yellowish-brown, densely covered with small granular or warts, initially whitish, becoming yellowish-brown with age. *Endoperidium* smooth, papery, fragile. *Gleba* pulverulent, or fibrous to cottony, yellowish-brown, brownish when mature. *Subgleba* not indistinct, pulverulent, brownish.

Microscopic description – *Basidiospores* globose to subglobose, 3.1–4.1 μm in diameter, [$x = 3.6 \pm 0.3$, $n = 30$], thick-walled, dark-brown, with an oil drop central, pedicels short or inconspicuous, less than 0.5 μm , under SEM surface with cylindrical warts, random arrangement. *Capillitium* of intermediate type, 1.2–5.8 μm in diameter, thick-walled, yellowish-brown, dark-brown, tapering towards the tips, no pores and septa observed. *Paracapillitium* not observed. Exoperidium composed of numerous hyaline sphaerocysts, often subglobose to globose, pyriform, slightly thick-walled. *Endoperidium* composed of almost straight hyaline hyphae, 1.6–3.8 μm in width, produce septa.

Ecology and distribution – Terrestrial and growing solitary in the soil, known from China.

Notes – Phylogenetic analysis within this genus revealed that *G. shannanensis* sp. nov. formed a distinct clade, closely associated with *G. gyirongensis* sp. nov., *G. albata* sp. nov., and the type species *G. aestivalis* (Fig. 5), with support primarily indicated by PP values (PP = 0.9). Morphologically, *G. gyirongensis* sp. nov. and *G. shannanensis* sp. nov. share numerous characteristics, such as globose to subglobose basidiomes with exoperidia densely covered in yellowish-white minute granules or warts, and basidiospores exhibiting surface ornamentation with irregularly arranged warts, along with an intermediate-type capillitium. However, the size of spores serves as a distinguishing factor, with *G. gyirongensis* measuring 2.4–2.8 μm in diameter, while *G. shannanensis* ranges from 3.1–4.1 μm in diameter. In comparison to *G. aestivalis*, the presence of yellowish warts at the upper part of basidiomes differs, and the spores of *G. aestivalis* typically have short pedicels (Abrar et al. 2008, Rebriev et al. 2020), a feature not as conspicuous in *G. shannanensis* sp. nov. The other two species with yellowish basidiomes in this genus, *G. testacea* sp. nov. and *G. muscicola* sp. nov., can be distinguished from *G. shannanensis* by variations in spore size and ornamentation, as detailed in the corresponding descriptions within this genus.

Globaria muscicola R.L. Zhao & J.X. Li sp. nov.

Fig. 23

Fungal Name: FN571707; Facesoffungi number: FoF15160

Etymology – *muscus* refers to moss and *-cola* refers to dweller, so the epithet *muscicola* refers to the habit of growing on mossy rotting wood mostly.

Type – China, Zhejiang Province, Jingning She Autonomous County, Grass carp pond, 1 Sep. 2017, Z.L. Ling, ZRL20171015 (holotype HMAS 258835).

Diagnosis – This species features a well-developed pseudostipe, with the exoperidium covered in small granular verrucae and distinct inverted pyramidal slender spines. It predominantly grows on rotten wood, often surrounded by moss.

Macroscopic description – *Basidiomes* obpyriform, gyroscopic, 16–20 mm width, 20–23 mm height, has a well-developed pseudostipe. Rhizomorphs scarce, with rotten wood incrustated. *Peridium* layered. Exoperidium yellowish-white, yellowish-brown, smooth to asperulate, with connivant slender spines, inverted pyramidal, less than 1 mm. *Endoperidium* light white, pale yellow, papery, apical pore present, irregular lobed. *Gleba* soft, initially cream, yellowish at maturity, pulverulent, cottony. *Subgleba* occupying half of the basidiomes, tapering at the base attached to the substrate, yellowish, pulverulent, cottony.

Microscopic description – *Basidiospores* globose to subglobose, 3.1–4.5 μm in diameter, smooth to asperulate in LM, verrucose in SEM, isolated or in groups with rounded tips, pedicels straight, up to 5 μm . *Capillitium* Bovista-type, occasionally *Lycoperdon*-type, 1.6–9.5 μm diam, straight to undulate, brownish, unequal width, thick-walled, no septa, paracapillitium not observed.

Exoperidium composed of chains of inflated cells, colorless, transparent, thick-walled, subglobose, ellipsoid, irregularly oblong, $11.3\text{--}35.7 \times 9\text{--}14.6 \text{ }\mu\text{m}$. *Endoperidium* composed of straight, interwoven unbranched hyphae, hyaline, no septa elastic.

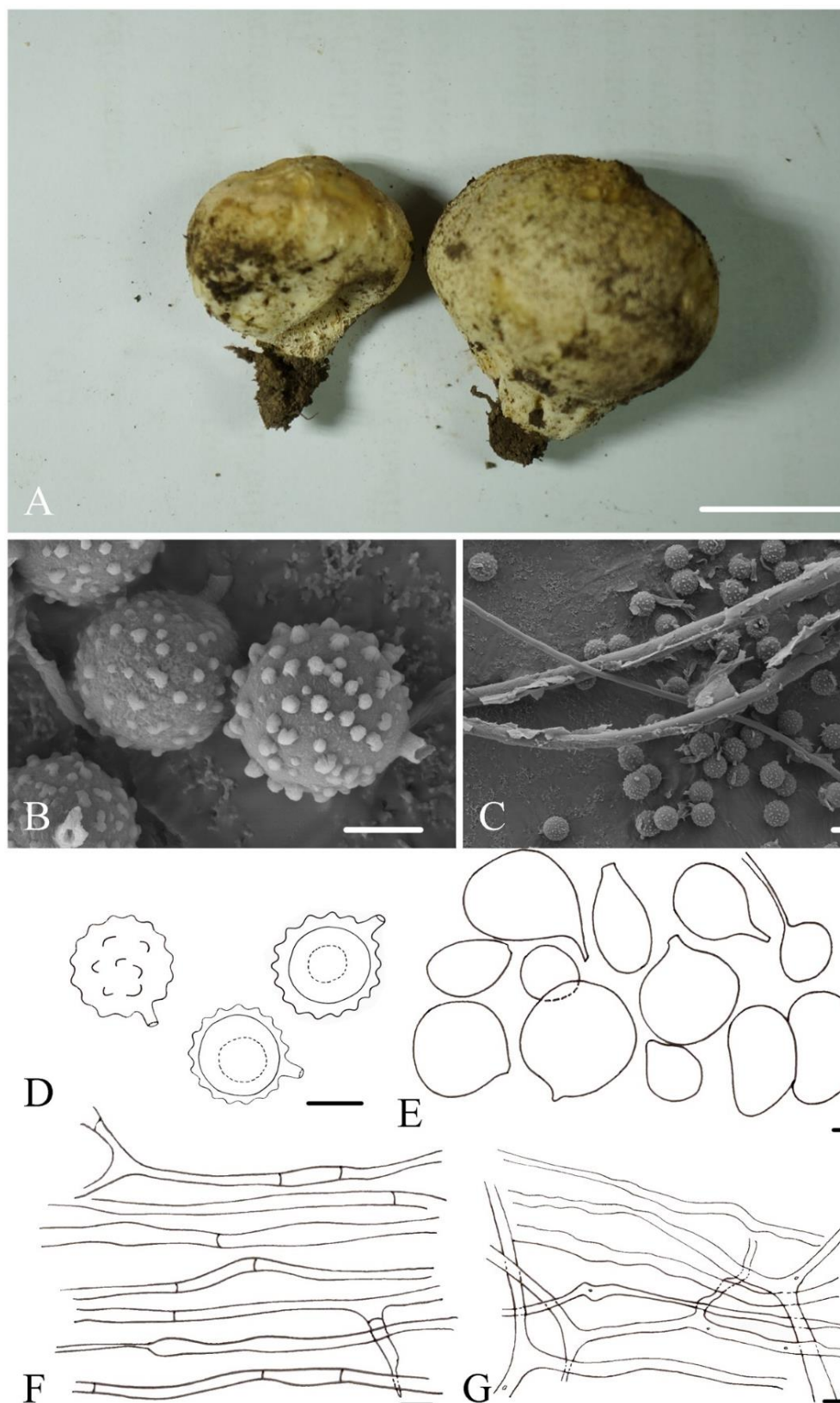


Figure 22 – Morphology of *Globaria shannanensis*. A gasterocarps (holotype, HMA258883 ZRL20152235). B, C basidiospores and capillitial threads under SEM. D basidiospores.

E exoperidial elements (sphaerocysts). F endoperidial hyphae. G capillitial threads. Scale bars: A = 1 cm, B = 2 μ m, C = 3 μ m, D = 2 μ m, E = 5 μ m, F–G = 2 μ m.

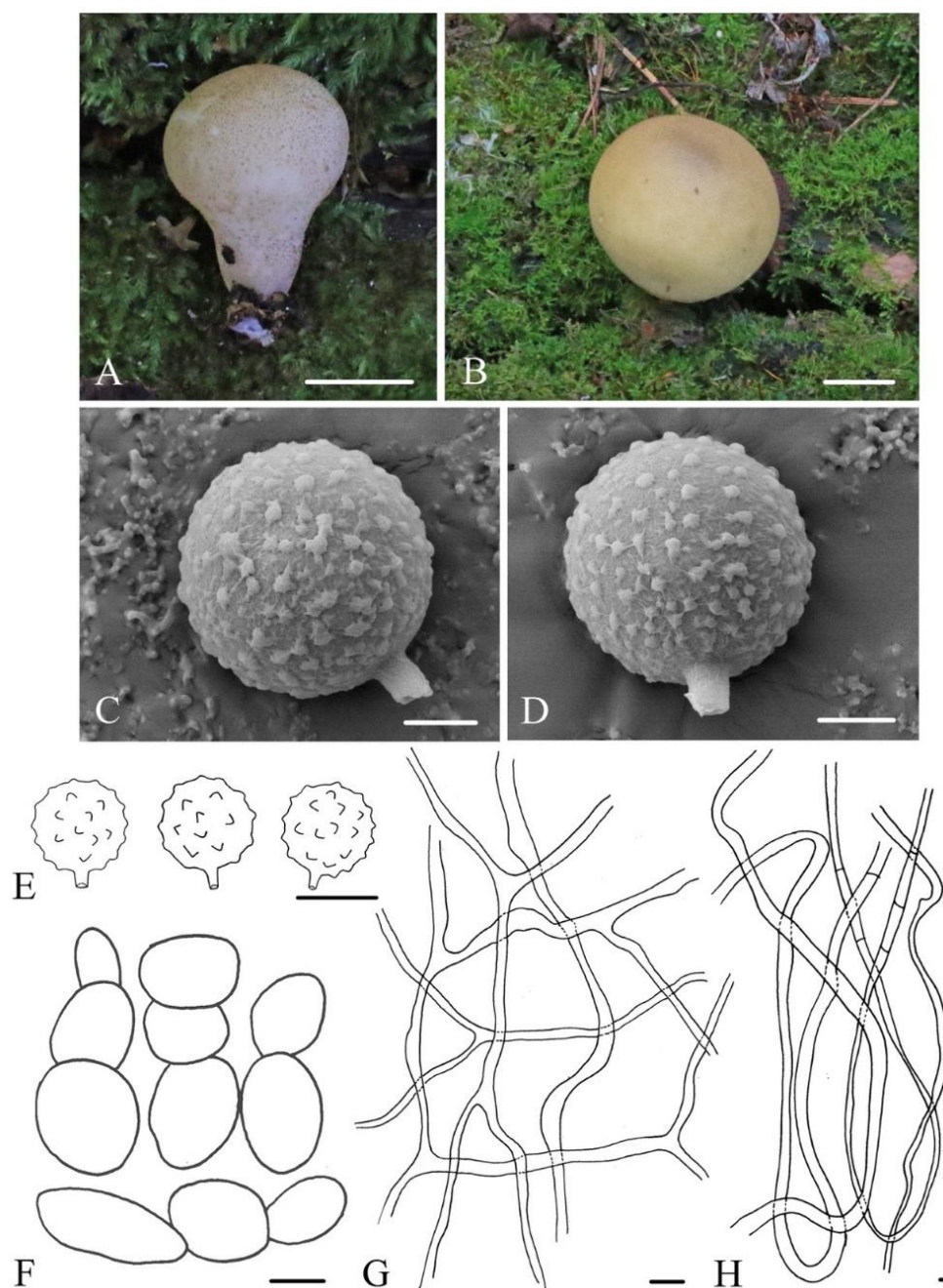


Figure 23 – Morphology of *Globaria muscicola*. A gasterocarps (holotype HMAS 258835). B gasterocarps (HMAS 258834). C, D basidiospores under SEM. E basidiospores under LM. F exoperidial elements (sphaerocysts). G capillitial threads. H endoperidial hyphae. Scale bars: A–B = 1 cm, C–D = 1 μ m, E = 4 μ m, G = 5 μ m, H = 2 μ m.

Ecology and distribution – growing solitary on decaying wood, usually among the mosses. known from China.

Additional material examined – China, Inner Mongolia Autonomous Region, Hulunbeier City, Genhe City, Jinhe Town, Daxinganling Khan Horse National Nature Reserve, 23 Aug. 2017, Z.L. Ling, ZRL20170441 (HMAS 258834).

Notes – Distinctive features of this new species in *Globaria* include a well-developed pseudostipe, granular verrucae, and pyramidal connivant spines on the exoperidium. In the

phylogenetic tree (Fig. 5), two specimens of this new species formed a sister branch with *G. furfuracea*. Morphologically, *G. furfuracea* differs from this new species by the absence of a pseudostipe, the presence of capillitia with numerous pores, and basidiospores that are finely warty and apedicellate (Larsson et al. 2009). *Holocotylon dermoxanthum* (= *Lycoperdon dermoxanthum* Vittad.) shares some similarities with this new species in morphology. However, *H. dermoxanthum* possesses granular to smallish verrucae on the exoperidium, persistent capillitia, and larger basidiospores (5.5–6.0 µm in diameter) (Jeppson 2008, Bates et al. 2009). In comparison to *G. jingningensis* sp. nov. and *G. testacea* sp. nov., *G. muscicola* sp. nov. presents a coniform exoperidium with slender spines (Fig. 23).

Globaria aestivalis (Bonord.) Hazsl., Verh. Kaiserl. -Könl. zool.-bot. Ges. Wien 26: 225 (1877).
Fig. 24

Fungal Name: FN654307

Basionym – *Bovista aestivalis* (Bonord.) Demoulin, Beih. Sydowia 8: 143 (1979).

Diagnosis – This species was widespread, developing subglobose to pyriform basidiomes, with capillitial threads of intermediate type, and globose basidiospores exhibiting an asperulate to verruculose surface.

Habitat – Terrestrial and found in grassy areas on the soil or on the forest floor.

Distribution – Known from Europe, Asia, North America, South America, Australia, Chian.

Material examined – China, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Batang County, Drukpa Cage Nature Reserve, 18 Aug. 2020, J.X. Li, ZRL20201238 (HMAS 258882).

Notes – *Globaria aestivalis* is the designated type species of *Globaria*; however, recent investigations suggest the existence of a complex of closely related taxa surrounding *G. aestivalis* (Jeppson 2018, Rebriev et al. 2020). Further detailed studies are essential to elucidate the *G. aestivalis* complex. In this context, we present both morphological features of *G. aestivalis* and molecular data represented by the examined specimen HMAS 258882 (ZRL20201238), providing a reference for subsequent in-depth research.

Globaria promontorii (Kreisel) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571812

Basionym – *Bovista promontorii* Kreisel, Beih. Nova Hedwigia 25: 225 (1967).

Globaria himalaica (Yousaf, Kreisel & Khalid) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571811

Basionym – *Bovista himalaica* Yousaf, Kreisel & Khalid, Mycol. Progr. 12(4): 570 (2012).

Globaria furfuracea (Schaeff.) Quél. 1873

Basionym – *Bovista furfuracea* Pers., Syn. meth. fung. (Göttingen) 1: 138 (1801).

Holocotylon Lloyd, Mycol. Writ. (Cincinnati) 2(Letter 21): 254 (1906).

Fungal Name: FN19158

Type species – *Holocotylon brandegeeanum* Lloyd, Mycological Notes 2: 254 (1906).

Holocotylon was initially described by Lloyd in 1906, featuring the type species *H. brandegeeanum* Lloyd. In this study, several species, including *H. rupicola* and *H. dermoxanthum*, along with a new species, *H. biconicum* sp. nov., have been assigned to *Holocotylon* based on phylogenetic data. The genus was strongly supported as a monophyletic group in the divergence times analysis, dating back to approximately 34.4 Myr (Fig. 1).

Morphologically, *H. brandegeeanum* is characterized by a mature gleba comprised of labyrinthiform and sinuous tramal plates, the absence of capillitium, and subglobose to ovoid basidiospores that are smooth to asperulate (Bates et al. 2009). However, several other taxa within this genus exhibit features that overlap to varying degrees: smallish and subglobose, pyriform fruiting bodies, capillitium in the mature gleba of *Lycoperdon*-type or *Lycoperdon-Bovista* type, with septa

and abundant small pits. A common characteristic among these taxa is their preference for fruiting among moss (Bates et al. 2009). Phylogenetically within this subclade, *H. dermoxanthum* formed a distinct lineage, while *H. biconicum* sp. nov. and *H. rupicola* appeared together as the sister group, well-separated from *H. brandegeeanum*. In this section, two new species are described as follows.

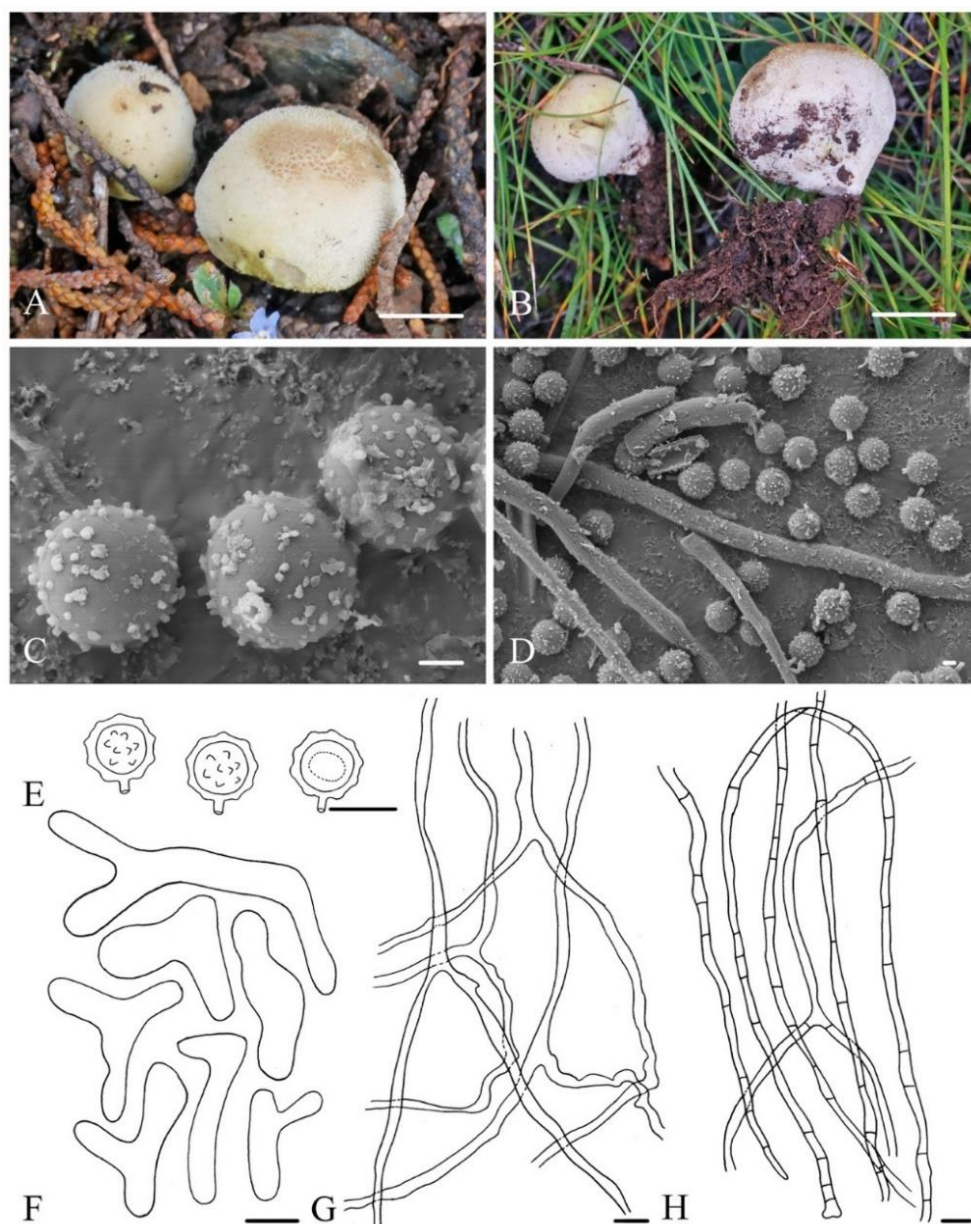


Figure 24 – Morphology of *Globaria aestivalis*. A, B gasterocarps (HMAS 258882). C, D basidiospores under SEM. E basidiospores. F exoperidial elements (sphaerocysts). G capillitial threads. H endoperidial hyphae. Scale bars: A–B = 1 cm. C–D = 1 µm, E = 4 µm, G = 5 µm, H = 2 µm.

Holocotylon biconicum R.L. Zhao & J.X. Li sp. nov.

Fig. 25

Fungal Name: FN571708; Facesoffungi number: FoF15167

Etymology – *biconicum* refers to the biconical shape of basidiomes in this species.

Type – China, Hubei Province, Shennongjia Forest Area Shennongding Tiziya Primeval Forest, 26 Aug. 2022, J.X. Li, ZRL20221202 (holotype HMAS 258778).

Diagnosis – This species is characterized by fusiform basidiomes with a yellowish-white exoperidium, turning yellowish-brown at the apical part, finely pointed, and adorned with small jointed slender spines.

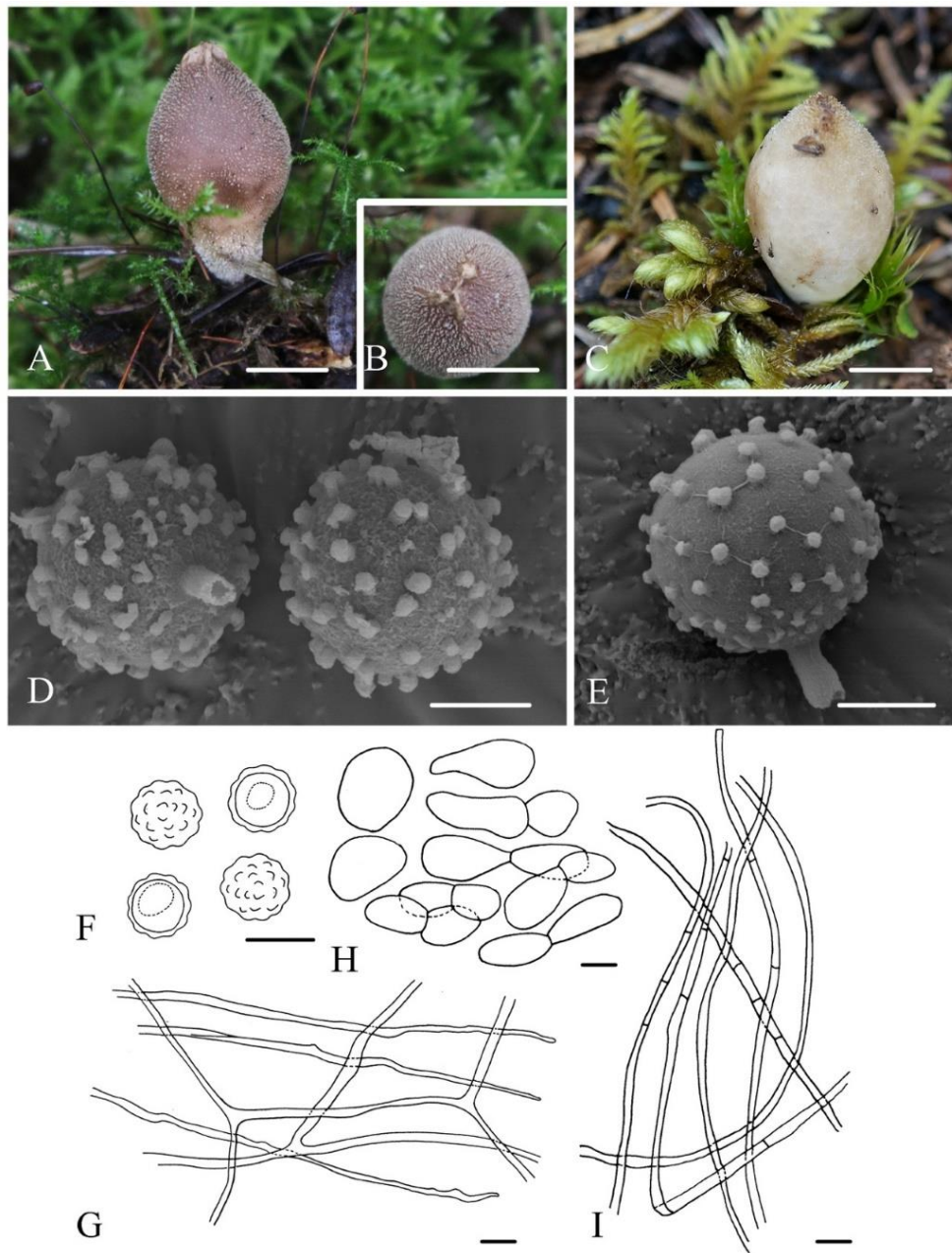


Figure 25 – Morphology of *Holocotylon biconicum*. A, B gasterocarps (holotype, HMAS 258778). C gasterocarps (HMAS 258777). D, E basidiospores under SEM. F basidiospores under LM. G capillitial threads. H exoperidial elements (sphaerocysts). I endoperidial hyphae. Scale bars: A–C = 1 cm, D–E = 2 μ m, F = 5 μ m, G = 2 μ m, H = 10 μ m, I = 5 μ m.

Macroscopic description – *Basidiomes* fusiform, obpyriform, 10–15mm in diameter, 20–25 mm height. Rhizomorphs sparse, white, thick, unbranched. *Peridium* layered. Exoperidium off-white, yellowish-white, ochre yellow in the upper part of the basidiomes, with slender spines and granular warts, conical-inverted, up to 0.1–0.2 mm, pyramid shape, gradually shedding in places with age. *Endoperidium* off-white, membranous, papery, stellate dehiscence at apical pore. *Gleba* off-white when young, yellowish-brown when fully mature, pulverulent. *Subgleba* indistinct.

Microscopic description – *Basidiospores* subglobose to globose, 3.9–4.4 μ m in diameter, asperulate, densely ornamented verrucae, irregularly arranged, thick-walled, short pedicel present (less than 0.5 μ m). *Capillitium* absent. Exoperidium composed of chains of hyaline inflated cells, slightly thick-walled, various in shape, fusiform, pyriform, cylindrical, vase-like. *Endoperidium*

composed of densely interwoven, unbranched hyphae, hyaline, thin-walled, 1.7–3.8 μm . *Gleba* possess persistent granular cells, oviform, globose, subglobose, 13.5–21.7 μm in diameter.

Ecology and distribution – It's assumed that this species occurs in the higher elevations of the state within the coniferous forest, often fruiting among moss, solitary in a relatively humid environment. known from China.

Additional material examined – China, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Litang County, Zagar sacred mountain, 20 Aug. 2020, X.Y. Zhu, ZRL20201357 (HMAS 258777); China, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Yajiang County, Geshegou Nature Reserve, 16 Aug. 2020, B. Cao, ZRL20200709 (HMAS 258776).

Notes – The fusiform basidiomes, connivant granular warts at the apical part, yellowish-brown color, and growth on moss are distinctive features of *H. biconicum* sp. nov. In the phylogenetic tree (Fig. 3), three specimens of this new species cluster together with a reference sequence (*Holocotylon* sp. KU167031), and both are sisters to *H. rupicola* (= *Lycoperdon rupicola* Jeppson, E. Larss. & M.P. Martín). In comparison, *H. rupicola* differs with its subglobose to pyriform basidiomes and an exoperidium constructed of spines (Jeppson et al. 2012); furthermore, they exhibit a difference of 15 base pairs in the ITS sequence. Formerly, *Lo. fusiforme* M. Zang has been reported from eastern China, showing similar fusiform basidiomes and exoperidium with granular verrucae. However, that species produces smaller basidiospores (2.4–3.7 μm in width) and broader capillitium (6–8.7 μm) (Zang 1980). In the field, *Le. ericaeum* (= *Lycoperdon ericaeum* Bonord) and *Li. niveua* (= *Lycoperdon lividum* Pers.) can also be easily confused with this new species because their basidiomes are covered with yellowish to brownish spines and granular warts. However, the former has larger basidiomes (15–30 mm diameter, 25–30 mm high), and the capillitium frequently presents irregular pores (Kim et al. 2016). The latter differs by having a white exoperidium that remains white even when mature (Eckblad & Ellingsen 1984, Kim et al. 2016, Krakhmalnyi et al. 2023), while *H. biconicum* becomes yellowish-brown when mature.

Holocotylon purpurascens R.L. Zhao & J.X. Li sp. nov.

Fig. 26

Fungal Name: FN571709; Facesoffungi number: FoF15168

Etymology – *purpurascens* meaning becoming purple, referring to the basidiomes with a gleba discoloring violet-purple in the center when cut.

Type – China, Sichuan Province, Panzhihua City, 7 Aug. 2019, R.L. Zhao, ZRL20190356 (holotype HMAS 258779).

Diagnosis – This species is characterized by subglobose to depressed globose basidiomes. The exoperidium exhibits yellowish-brown small patches to rugulose, while the gleba appears whitish to yellowish-white and discolors violet at the center.

Macroscopic description – *Basidiomes* globose, subglobose, depressed globose, rhizomorph white, thin, occasionally plicate at base, encrusted with particles of soil. *Peridium* layered. Exoperidium entirely white when young, glabrous to rugulose, small patches to rugulose adheres to the surface, when fully mature, yellowish, yellowish-brown. *Endoperidium* whitish, thin, membranous. Mature *Gleba* yellowish white, yellowish gray to dull yellow, violent at central, possess labyrinthiform, sinuous, tramal plates, forming numerous membranaceous locules. *Subgleba* normally absent.

Microscopic description – *Basidiospores* subglobose to ovoid, 3.3–3.9 μm in diameter, asperulate, densely ornamented verrucae, irregularly arrangement, thick-walled, short pedicel present (less than 0.5 μm). *Capillitium* absent. *Exoperidium* composed of chains of hyaline inflated cells, slightly thick-walled, various in shape, fusiform, pyriform, cylindrical, vase-like. *Endoperidium* composed of densely interwoven, unbranched hyphae, hyaline, thin-walled, 1.7–3.8 μm . *Gleba* possesses persistent granular cells, oviform, globose, subglobose, 13.5–21.7 μm in diameter.

Ecology and distribution – Terrestrial and found in soil, growing on solitary, under coniferous forest, in a higher elevation. known from China.

Additional material examined – China, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Batang County, Drukpa Cage Nature Reserve, 18 Aug. 2020, B. Cao, ZRL20201242 (HMAS 258780).

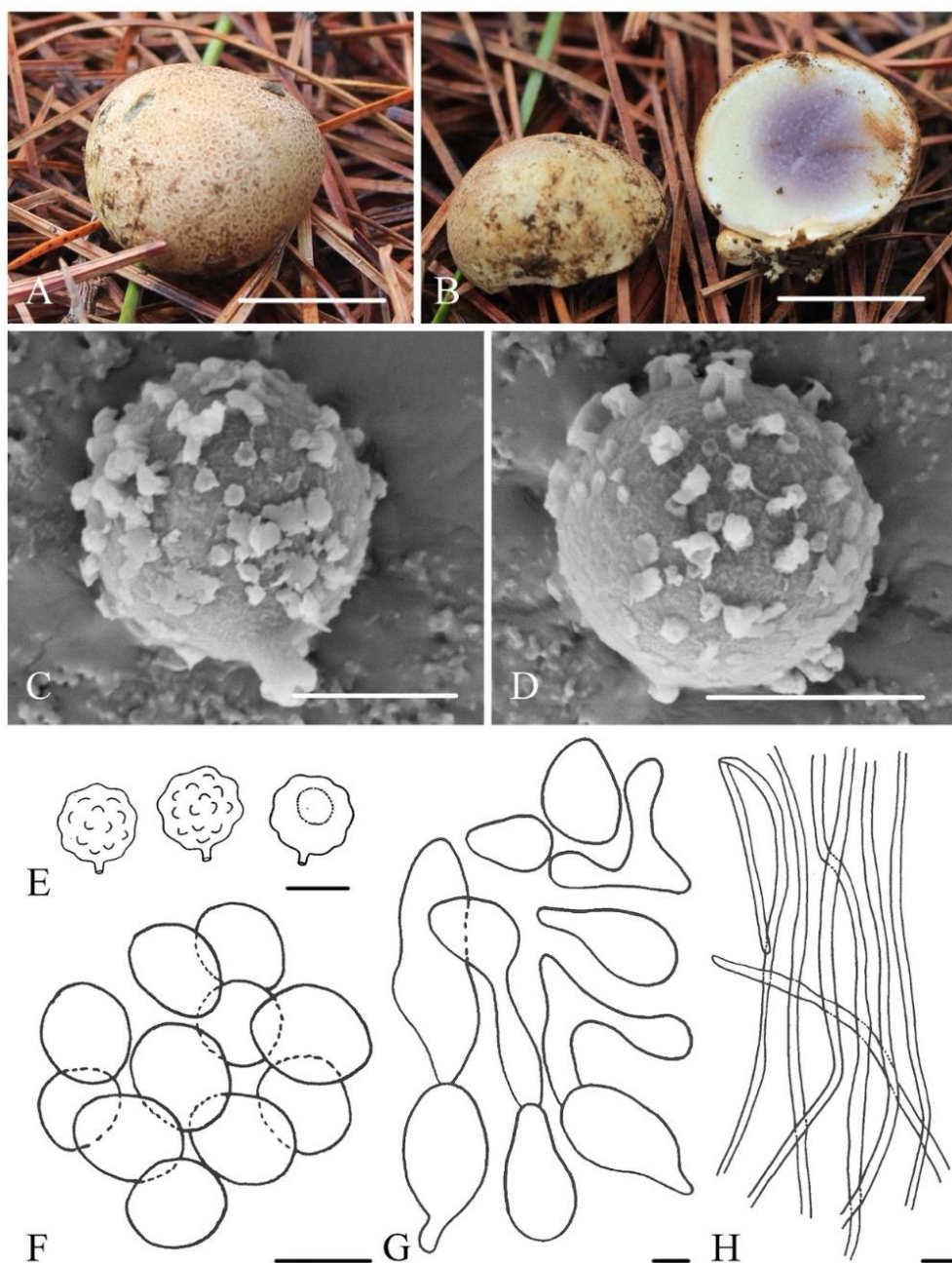


Figure 26 – Morphology of *Holocotylon purpurascens*. A, B gasterocarps (holotype, HMAS 258779). C–D basidiospores under SEM. E verrucose basidiospores under LM. F groups of globular elements. G exoperidial elements (sphaerocysts). H endoperidial hyphae. Scale bars: A–B = 1 cm, C–E = 5 µm, F–G = 10 µm, H = 2 µm.

Notes – In the phylogenetic tree (Fig. 3), two specimens of this new species clustered together, forming a sister group to *H. brandegeeanum*. The exoperidium of *H. brandegeeanum* is white to off-white, while that of *H. purpurascens* sp. nov. starts off white and discolors to pale yellow to yellowish-brown at maturity. The mature gleba of *H. brandegeeanum* appears grayish-yellow to olive-brown, whereas that of *H. purpurascens* sp. nov. is yellowish-white, yellowish-gray to dull yellow, with the center turning purple. Basidiospores of *H. brandegeeanum* are small ($4\text{--}5.6 \times 4\text{--}4.8$ µm), smooth to asperulate, with a long pedicel (0.8–8 µm in length) (Bates et al. 2009).

H. purpurascens sp. nov. produces larger basidiospores (7.7–10.7 µm in diameter) ornamented with cylindrical warts and presents a short pedicel (less than 0.5 µm). *Arachnion album* Schwein., another species resembling *H. purpurascens* sp. nov., however, has a gleba composed of numerous small peridioles (Bates et al. 2009).

Holocotylon rupicola (Jeppson, E. Larss. & M.P. Martín) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571809

Basionym – *Lycoperdon rupicola* Jeppson, E. Larss. & M.P. Martín, Mycol. Progr. 11(4): 892 (2012).

Holocotylon dermoxanthum (Vittad.) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571810

Basionym – *Lycoperdon dermoxanthum* Vittad., Monogr. Lycoperd. (Torino): 178 (34 of prepr.) (1842)

Holocotylon brandegeeanum Lloyd, Mycol. Writ. (Cincinnati) 2(Letter 21): 254 (1906).

Leptocaulis R.L. Zhao & J.X. Li, gen. nov.

Fungal Name: FN571717; Facesoffungi number: FoF15151

Type species – *Leptocaulis sublongistipes* R.L. Zhao & J.X. Li

Etymology – From the latinized Greek *lepto-* (slender) and *caulos* (stipe). The epithet refers to the basidiomes with a slender pseudostipe.

Formerly, species belonging to *Leptocaulis* were classified under *Lycoperdon* s.l. and assigned to *Lycoperdon* subg. *Utraria* (Larsson & Jeppson 2008, Alfredo et al. 2017). However, phylogenetic analyses of *Lycoperdaceae* and *Lycoperdon* s.l., conducted using ITS, nrLSU, *rpb2*, and *tef1-α* sequences data, indicated that *Leptocaulis* forms a fully-supported, monophyletic group (Figs 1, 3). Molecular clock analyses depicts its divergence around 26.7 Myr, a timeframe close to other genera in *Lycoperdaceae*, especially within *Lycoperdon* s.l. (26.7–34.5 Myr). Morphologically, members of this genus typically have basidiomes with well-developed pseudostipes, a feature particularly distinct in *Le. sublongistipes* sp. nov., *Le. albiperidius* (= *Lycoperdon albiperidium* Chang S. Kim) (Kim et al. 2016). Compared with the closely related *Utraria*, *Leptocaulis* species prefer fruiting on rotten wood, as seen in *Le. sublongistipes* sp. nov., *Le. albiperidium*, and *Le. subumbrinus* (= *Lycoperdon subumbrinum* Jeppson & E. Larss.) (Jeppson et al. 2012, Kim et al. 2016).

In this study, a new species, *Le. sublongistipes* sp. nov., is proposed, and three species, *Le. muscorum*, *Le. albiperidius*, and *Le. ericaeus*, previously classified under *Lycoperdon*, are transferred to this new genus.

Leptocaulis sublongistipes R.L. Zhao & J.X. Li sp. nov.

Fig. 27

Fungal Name FN571710; Facesoffungi number: FoF15162

Etymology – The epithet refers to the morphology of this new species similar to *Lycoperdon longistipes* M. Zang & M.S. Yuan.

Type – China, Zhejiang Province, Lishui City, Qingyuan Country, Baishanzu National Nature Reserve, 26 Aug. 2016, R.L. Zhao, ZRL20161749 (holotype HMAS 258768).

Diagnosis – This species possesses a well-developed long pseudostipe, numerous rhizomorphs attached to substrate, exoperidium with smallish verrucae, entirely white to cream-white when young, becoming yellowish to yellowish-brown when mature.

Macroscopic description – Basidiomes pyriform 15–30 mm in diameter, 17–35 mm high, possess a well-developed long pseudostipe, rhizomorphs attached to substrate, heavily encrusted with rotten wood and soil particles. *Peridium* layered. Exoperidium entirely white to cream-white when young, densely covered with smallish verrucae or occasionally with some erect white soft squamulose when fully mature, discolor yellowish to yellowish-brown. Apical pore irregularly lobed. *Endoperidium* ochre yellow, smooth, fragile, papery. *Gleba* first whitish, cream, pulverulent, flocculent, loosely, brownish, smoky yellow when mature. *Subgleba* brownish, pulverulent.

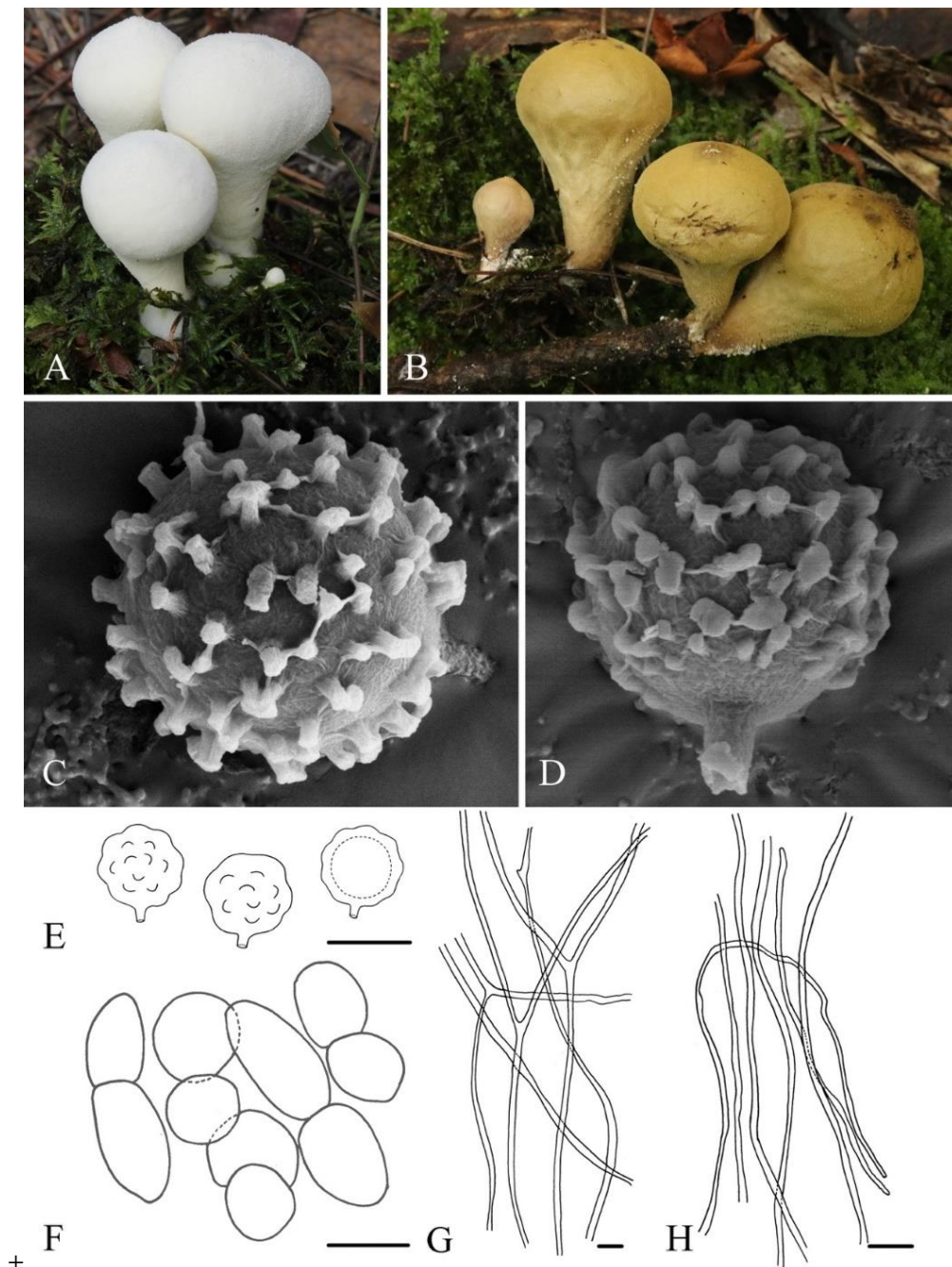


Figure 27 – Morphology of *Leptocaulis sublongistipes*. A gasterocarps (HMAS 258770). B gasterocarps (holotype HMAS 258768). C, D basidiospores under SEM. E basidiospores under LM. F exoperidial elements (sphaerocysts). G capillitial threads. H endoperidial hyphae. Scale bars: A–B = 1 cm, C–D = 2 µm, E = 5 µm, F = 10 µm, G–H = 5 µm.

Microscopic description – *Basidiospores* globose to subglobose, 3.3–3.9 µm in diameter, distinctly ornamented verrucae, cylindrical, rounded at apex, often 2–3 connect or isolated. Short pedicel present (less than 0.5 µm). Basidia not observed. *Capillitium* of *Lycoperdon*-type, 1.4–6.3 µm in diameter, thick-walled, brownish to yellowish-brown, straight, occasionally sub-undulate, dichotomous branching abundant. No irregular pores observed, no septa observed. Paracapillitium absent. Exoperidium composed of sphaerocysts 7.4–6.3 µm. *Endoperidium* composed of filamentous hyphae interweave, unbranched, thin-walled, 2.4–6.2 µm.

Ecology and distribution – Generally fruiting directly on rotten-wood, growing solitary or in small groups, surrounded among mosses under coniferous forest. known from China.

Additional material examined – China, Zhejiang Province, Lishui City, Qingyuan Country, Baishanzu National Nature Reserve, 26 Aug. 2016, R.L. Zhao, ZRL20161708 (HMAS 258770); China, Zhejiang Province, Jingning Country, Dayanghu Alpine Wetland Nature Reserve, 26 Aug. 2016, J.X. Li, ZRL20161530 (HMAS 258771); ZRL20161579 (HMAS 258769); China, Zhejiang Province, Jingning Country, Yujikeng, 7 Sep. 2019, J.X. Li, ZRL20191643 (HMAS 258775).

Notes – *Leptocaulis sublongistipes* sp. nov. is characterized by having basidiomes with a well-developed pseudostipe (10–15 mm in length, 5–10 mm in width). Exoperidium densely covered with white verrucae, becoming yellowish brown when fully mature. In the phylogenetic tree (Fig. 3), five specimens of this new species clustered together, which formed a distinct lineage with fully supported. *Lycoperdon longistipes* M. Zang & M.S. Yuan. often resembles this new species externally, for example, both possess well-developed pseudostipe, however, it has bigger basidiomes (30–40 mm in diam, 80–100 mm height), besides, its basidiospore present a long pedicel (Zang & Yuan 1999). *Lycoperdon perlatum*, which is a species often develop a large-sized pseudostipe too, but its exoperidium ornamented yellowish to brownish verrucose and echinulate (Bates et al. 2009, Kim et al. 2016, Fan 2019).

Leptocaulis subumbrinus (Jeppson & E. Larss.) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571730

Basionym – *Lycoperdon subumbrinum* Jeppson & E. Larss., Mycol. Progr. 11(4): 891 (2012).

Leptocaulis muscorum (Morgan) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571806

Basionym – *Lycoperdon muscorum* Morgan, J. Cincinnati Soc. Nat. Hist. 13:16 (1891).

Leptocaulis albiperidius (Chang S. Kim) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571807

Basionym – *Lycoperdon albiperidium* Chang S. Kim, in Kim, Jo, Kwag, Sung, Han, Shrestha, Oh, Kim, Shin & Han, Phytotaxa 260(2): 109 (2016).

Leptocaulis ericaeus (Bonord.) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN 571808

Basionym – *Lycoperdon ericaeum* Bonord., Bot. Zeitung (Berlin) 15: 596 (1857).

Lycoperdiscus R.L. Zhao & J.X. Li, gen. nov.

Fungal Name: FN571718; Facesoffungi number: FoF15152

Type species – *Lycoperdiscus tianzhuensis* R.L. Zhao & J.X. Li

Etymology – From the Greek meaning small-sized (suffix -iscus). The epithet refers to the small-sized basidiomes.

Formerly, species belonging to *Lycoperdiscus* were classified under *Lycoperdon* s.l., assigned to *Lycoperdon* subg. *Utraria* (Larsson & Jeppson 2008, Alfredo et al. 2017). However, phylogenetic analyses of *Lycoperdaceae* and *Lycoperdon* s.l. conducted using ITS, nrLSU, *rpb2*, and *tef1-α* sequences data indicated that *Lycoperdiscus* forms a fully-supported monophyletic group (Figs 1, 3). Molecular clock analyses inferred that *Lycoperdiscus* diverged around 30.9 Myr, a timeframe close to other genera in *Lycoperdaceae* and especially within *Lycoperdon* s.l. (26.7–34.5 Myr).

Currently, two species, *Li. tianzhuensis* sp. nov. and *Li. lividus* (= *Lycoperdon lividum* Pers.), are assigned to this genus. Morphologically, *Li. lividus* can be easily recognized by small-sized basidiomes, initially white, turning yellow-olive, and finally brown at maturity, with a small irregular apical pore, often found in grassland (Bates et al. 2009). *Lycoperdiscus tianzhuensis* sp. nov. develops pyriform basidiomes with a distinctive pseudostipe, exoperidium covered with slender spines and farinaceous granules, and often grows in soils around moss. Here, the proposed morphological features of this genus include small-sized lycoperdoid-basidiomes, exoperidium white in a young state, turning brown at maturity, and developing a small irregular apical pore.

Lycoperdiscus tianzhuensis R.L. Zhao & J.X. Li sp. nov.

Fig. 28

Fungal Name: FN571712; Facesoffungi number: FoF15163

Etymology – referring to Tianzhu Zangzu autonomous County of Gansu Province from China where the holotype was collected.

Type – China, Gansu Province, Wuwei City, Tianzhu Zangzu autonomous County, Kola Village, 19 Aug. 2018, J.X. Li, ZRL20181029 (holotype HMAS 258766).

Diagnosis – This species is characterized by pyriform basidiomes, a well-developed pseudostipe, and an exoperidium that is entirely white. The exoperidium is densely covered with slender spines and farinaceous granules, appearing white to pale brown overall but distinctly yellowish-brown at the pseudostipe when mature.

Macroscopic description – Basidiomes pyriform 12–20 mm in diameter, 25–30 mm high, with a well-developed pseudostipe, occasionally plicate. Rhizomorphs abundant, white, heavily encrusted with soil particles. *Peridium* layered. Exoperidium in young stages with a dense cover of white, pale brown slender spines, usually with farinaceous granules, yellowish brown, slightly rough when mature. Apical pore irregular lobed. *Endoperidium* white, pale yellow, papery, fragile. *Gleba* whitish, discolor brownish when mature, pulverulent to flocculent. *Subgleba* brownish, pulverulent.

Microscopic description – *Basidiospores* globose to subglobose, 3.4–3.9 μm in diameter, with a central oil drop, rough densely ornamented with verrucae, irregular and different size. Short pedicel present, 1–1.5 μm . *Capillitium* of *Lycoperdon*-type, 2.6–5.7 μm in diameter, thick-walled, brownish, straight to slightly subundulate, dichotomous branching abundant. No irregular pores observed, no septa observed. *Paracapillitium* absent. Exoperidium made up of sphaerocysts, thick-walled, hyaline in 3% KOH. *Endoperidium* made up of dense interwoven unbranched, hyphae, thin-walled, 2.2–3.3 in diameter.

Ecology and distribution – Terrestrial and found in grassy areas, often around moss and pine needles, sometimes herbaceous plants, growing solitary or in small groups, known from China.

Additional material examined – China, Gansu Province, Wuwei City, Tianzhu County, Kola Village, 19 Aug. 2018, J.X. Li, ZRL20181018 (HMAS 258767).

Notes – *Lycoperdiscus tianzhuensis* sp. nov. can be easily distinguished from others by its exoperidium covered densely with slender spines and granular, as well as the well-developed and often plicate pseudostipe. Microscopically, it features globose to subglobose basidiospores densely ornamented with verrucae and a short pedicel. Phylogenetic analyses based on ITS, nrLSU, *rpb2*, and *tef1- α* sequences data (Fig. 3) indicate that the two specimens of this new species form a distinct lineage and are sister to *Li. lividus* (BS = 89%, PP = 1). Morphologically, *Li. lividus* resembles *Li. tianzhuensis* sp. nov. by having a well-developed pseudostipe and an exoperidium occasionally with appressed flocculence, minute, echinate, or granular verrucae. However, microscopically, *Li. lividus* has larger basidiospores (3.2–)4.0–4.8 $\times$ (3.2–)4.0–4.8 μm , and its capillitial threads feature abundant large-sized pores (4.0–7.2 μm diam) (Bates et al. 2009). Furthermore, they differ by twelve base pairs in the ITS sequences. *Lycoperdon longistipes* M. Zang & M.S. Yuan and *Le. subongistipes* sp. nov. may sometimes resemble this new species, but the former often develops larger basidiomes (30–40 diameters, 80–100 mm height) and basidiospores with a long pedicel (Zang & Yuan 1999, Fan 2019). The latter differs in basidiospores presenting a short pedicel (less than 0.5 μm). Additionally, *Le. subongistipes* sp. nov. is distinct in fruiting on rotten wood or mosses (Fig. 27).

Lycoperdiscus lividus (Pers.) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571805

Basionym – *Lycoperdon lividum* Pers., J. Bot. (Paris) 2: 18 (1809).

Notes – As shown in Fig. 3, phylogenetic analyses based on ITS, nrLSU, *rpb2*, and *tef1- α* sequences data indicate that *Lycoperdon lividum* Pers. 1809 nested in the newly proposed *Lycoperdiscus*, and form a distinct lineage and are sister to type species *Li. tianzhuensis* sp. nov., (BS = 89%, PP = 1). Based on these phylogenetic results, we propose that *Lycoperdon lividum* should be transferred to *Lycoperdiscus*.

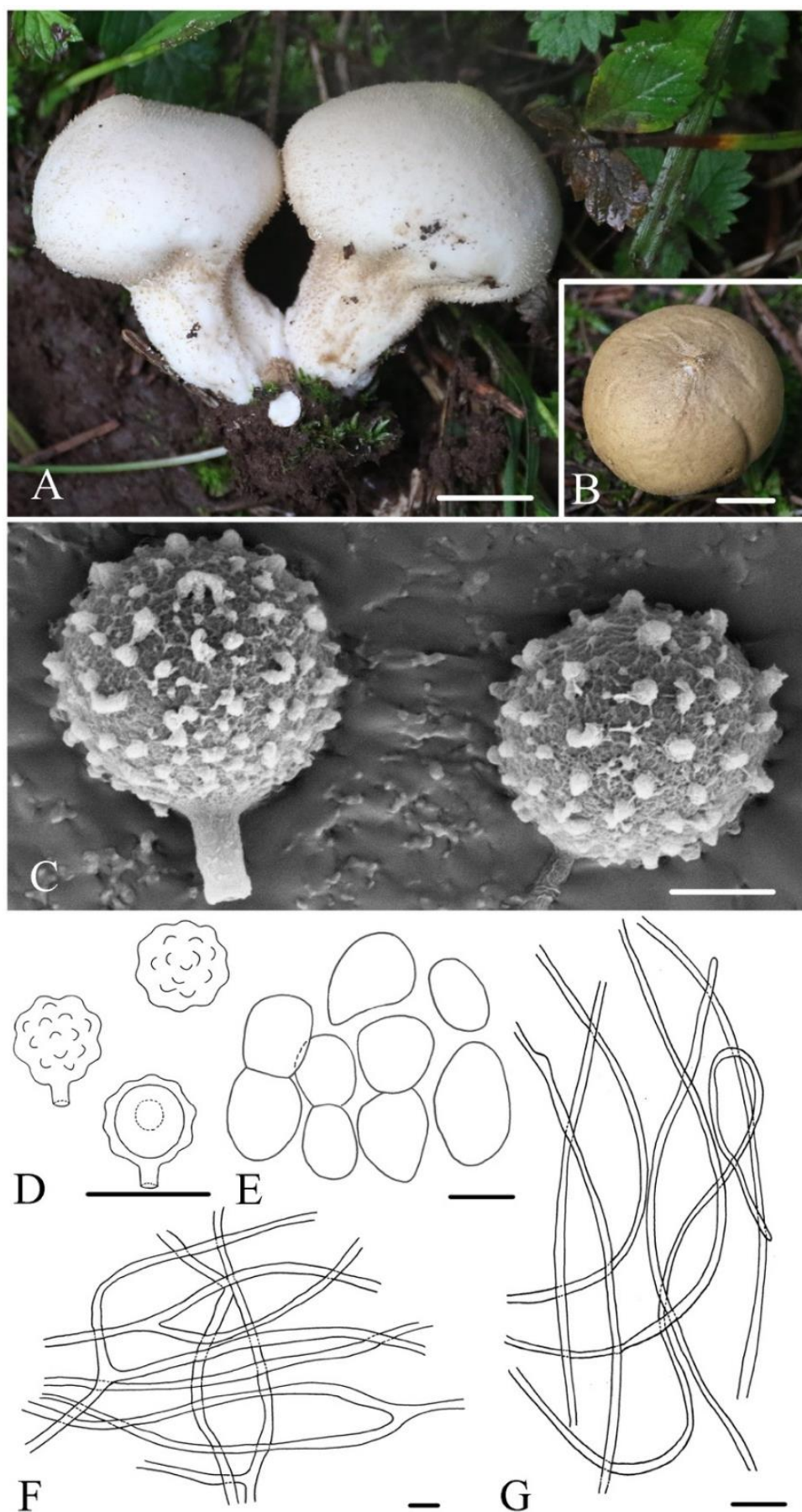


Figure 28 – Morphology of *Lycoperdiscus tianzhuensis*. A gasterocarps (holotype HMAS 258766). B gasterocarps (HMAS 258767). C basidiospores under SEM. D basidiospores under LM.

E exoperidial elements (sphaerocysts). F capillitial threads. G endoperidial hyphae. Scale bars: A–B = 1 cm, C–D = 5 µm, E, G–H = 5 µm. F = 10 µm.

Lycoperdon Pers., Ann. Bot. (Usteri) 15: 4 (1794)

Fungal Name: FN19207

Type species – *Lycoperdon perlatum* Pers., Observ. mycol. 1: 145 (1796): Pers., Syn. meth. fung.: 145 (1801).

Lycoperdon, represented here by the lineage containing the generic type *L. perlatum*, is morphologically characterized by a well-developed pseudostipe, echinate exoperidium, deciduous spines that irregularly expose the smooth, brown underlying surface, and basidiospores that are globose to subglobose, usually ornamented with minute warts (Bates et al. 2009, Cortez et al. 2013, Kim et al. 2016, Fan 2019, Krakhmalnyi et al. 2023). In the molecular phylogeny, *Lycoperdon* is the sister group to the genera *Morganella* and *Vascellum*, with a divergence time estimated at 27.7 Myr (Fig. 1).

Morganella Zeller, Mycologia 40(6): 650 (1948)

Fungal Name: FN19222

Type species – *Morganella mexicana* Zeller, Mycologia 40: 650 (1948).

Morganella is readily distinguished by several key characteristics: the basidiomes are depressed, globose to pyriform, composed of two layers of peridium, the gleba consists of abundant paracapillitium, and basidiospores are asperulate to echinulate. True capillitium is absent, and these fungi are typically found on wood (Kreisel & Dring 1967, Ponce de León 1971, Suárez & Wright 1996, Alfredo et al. 2017). The phylogenetic analysis supports the monophyly of this genus, with an estimated divergence time of 33.1 Myr (Fig. 1). Historically, *Morganella* had been considered a subgenus of *Lycoperdon* (Larsson & Jeppson 2008, Alfredo et al. 2017). However, in this study, we recognize it as a separate genus due to its older divergence time and distinct morphological features.

Morganella tricolor R.L. Zhao & J.X. Li sp. nov.

Fig. 29

Fungal Name: FN571823; Facesoffungi number: FoF15348

Etymology – referring to the basidiomes present three colors, ivory at the lower part, yellowish at the upperpart and deep brownish at apical part.

Type – China, Hubei Province, Shennongjia Forest District, Laojunshan area, Shanmuping, 29 Aug. 2022, J.X. Li, ZRL20221333 (holotype HMAS 287487).

Diagnosis – Macroscopically, this species is characterized by depressed globose basidiomes displaying three distinct colors: ivory at the lower part, yellowish to brownish at the upper part, and deep brownish at the apical part. Microscopically, it features basidiospores densely ornamented with coarse verrucae, an absent capillitium, and a paracapillitium composed of hyaline hyphae. This fungus is typically found growing on rotten wood.

Macroscopic description – *Basidiomes* subglobose, depressed globose, 10–13 mm in diameter. subgleba reduced. *Peridium* layered. Exoperidium surface with coarse granular, not easily fall off. ivory at the lower part, yellowish to brownish at the upperpart, deep brownish at apical part and possess large cracks at maturity. *Endoperidium* off-white, smooth, fragile. *Gleba* powdery or fibrous, brown.

Microscopic description – *Basidiospores* globose to subglobose, 3.2–3.6 µm in diameter [$x = 3.4 \pm 0.2$, $n = 30$], brownish, asperulate, thick-walled, with an oil drop central. Under SEM, densely ornamented coarse verrucae, cylindrical or inverted pyramid. *Capillitium* absent. *Paracapillitium* hyaline hyphae, straight without branches, 3.1–5.7 µm width, septa abundant. Exoperidium composed of irregular inflated cells, thick-walled, hyaline in 5% KOH. *Endoperidium* made up of intertwined hyaline hyphae, thick-walled, undulate, sometimes expand in the middle, 2.6–8.5 µm in width.

Ecology and distribution – solitary, growing on decaying wood, known from China.

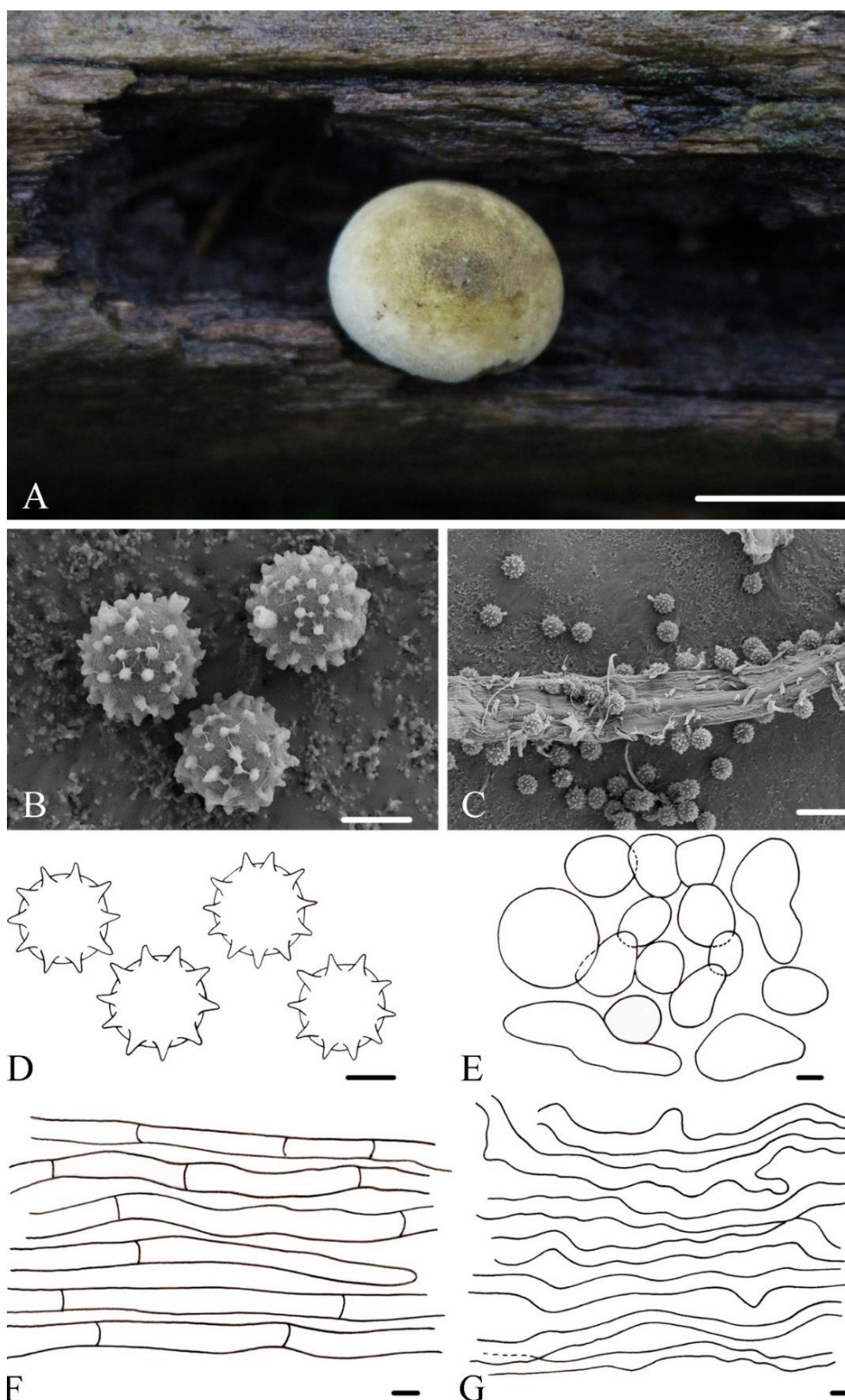


Figure 29 – Morphology of *Morganella tricolor*. A gasterocarps (holotype, HMAS 287487 ZRL20221333). B, C basidiospores under SEM. D basidiospores. E exoperidial elements (sphaerocysts). F paracapillitium. G endoperidial hyphae. Scale bars: A = 1 cm, B = 2 μ m, C = 10 μ m, D = 2 μ m, E–G = 5 μ m.

Notes – *Morganella tricolor* sp. nov. exhibits most of the characteristic features of *Morganella*, such as depressed globose basidiomes, a reduced subgleba, the absence of a true capillitium, a

paracapillitium composed of hyaline hyphae, and echinulate basidiospores. This fungus is typically found growing on rotten wood. In the phylogenetic trees based on ITS and nrLSU sequences data, *M. tricolor* sp. nov. forms a distinct lineage and clusters with *M. purpurascens* (Berk. & M.A. Curtis) Kreisel & Dring and *M. sosinii* Rebriev & Bulakh, with fully supported statistical values (Fig. 7). Morphologically, these species can be easily distinguished from each other. In comparison with *M. purpurascens*, significant differences are apparent, such as *M. purpurascens* having a warty exoperidium, dark grayish-brown to blackish-violet gray (Kumla et al. 2014, Alfredo et al. 2017). Contrasting with *M. sosinii*, *M. tricolor* sp. nov. displays exoperidium ornamentation composed of granules and spines (0.1–0.2 mm in length), and the endoperidium surface exhibits an “incomplete areolate pattern,” distinguishing it from *M. tricolor* sp. nov. (Rebriev & Bulakh 2015, Alfredo et al. 2017).

Morganella oblongata (Accioly, Baseia & M.P. Martín) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571804

Basionym – *Lycoperdon oblongatum* Accioly, Baseia & M.P. Martín, in Alfredo, Baseia, Accioly, Silva, Moura, Marinho & Martín, Mycol. Progr. 16(10): 977 (2017).

Morganella mengsongensis (L. Ye, P.E. Mortimer, & Karunarathna) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN572121

Basionym – *Lycoperdon mengsongense* L. Ye, P.E. Mortimer & Karunarathna, Chiang Mai J. Sci. 49(3): 646 (2022).

Notes – *Morganella mengsongensis* (= *Lycoperdon mengsongense* L. Ye, P.E. Mortimer, & Karunarathna) was originally described as a tropical species from Yunnan Province, China (Ye et al. 2022). Phylogenetic analysis showed that *M. mengsongensis* clusters with *M. purpurascens* (Berk. & M.A. Curtis) Kreisel & Dring and *M. sosinii* Rebriev & Bulakh with strong statistical support (Ye et al. 2022). Consequently, in this study, *M. mengsongensis* is transferred to the genus *Morganella*. Morphologically, this species is characterized by a small, light grey to grey exoperidium, distinguishing it from *Morganella tricolor* sp. nov. Additionally, its small basidiospores (2.8–3.7 µm in diameter) with dense and short spinous protrusions further differentiate it from *M. tricolor* sp. nov. described in this study (Ye et al. 2022).

Morganella fuliginea (Berk. & M.A. Curtis) Kreisel & Dring 1967

Basionym – *Lycoperdon fuligineum* Berk. & M.A. Curtis, in Berkeley, J. Linn. Soc., Bot. 10(no. 46): 345 (1868) [1869].

Morganella nuda Alfredo & Baseia 2014

Basionym – *Lycoperdon nudum* (Alfredo & Baseia) Baseia, Alfredo & M.P. Martín, in Alfredo, Baseia, Accioly, Silva, Moura, Marinho & Martín, Mycol. Progr. 16(10): 977 (2017).

Morganella subincarnata (Peck) Kreisel & Dring 1967

Basionym – *Lycoperdon subincarnatum* Peck, Ann. Rep. N.Y. St. Mus. 24: 83 (1872) [1871].

Morganella purpurascens (Berk. & M.A. Curtis) Kreisel & Dring 1967

Basionym – *Lycoperdon purpurascens* Berk. & M.A. Curtis, Proc. Amer. Acad. Arts & Sci. 4: 124 (1860).

Morganella sosinii Rebriev & Bulakh 2015

Basionym – *Lycoperdon sosinii* (Rebriev & Bulakh) Baseia, B.D.B. Silva, Alfredo & M.P. Martín, in Alfredo, Baseia, Accioly, Silva, Moura, Marinho & Martín, Mycol. Progr. 16(10): 982 (2017).

Pseudoperdon R.L. Zhao & J.X. Li, gen. nov.

Fungal Name: FN571719; Facesoffungi number: FoF15153

Type species – *Pseudoperdon medogense* R.L. Zhao & J.X. Li

Etymology – The epithet refers to the false appearance overlapping some similar morphological characters with the genus *Lycoperdon*.

Pseudoperdon has been newly proposed to accommodate *P. medogense* sp. nov. and *P. subcretaceum* [= *Lycoperdon subcretaceum* (Zeller) Jeppson & E. Larss.]. Earlier studies by Larsson and Jeppson indicated that the phylogenetic positions of *P. subcretaceum*, as well as *F. nigrescens*, were outside of “*Lycoperdon* subg. *Utraria*” and were related to the “subgs. *Lycoperdon*, *Vascellum*, and *Morganella*.” (Larsson & Jeppson 2008, Jeppson & Larsson 2010) The phylogenetic analysis in this study resulted in a similar topology, as shown in Figs 1, 3, where *Pseudoperdon* formed a distinct lineage with high statistical values and a divergence time of 34.5 Myr. The main distinguishing characteristics of this genus include basidiomes that are globose to subglobose when mature, the absence of a subgleba, and the presence of *Lycoperdon*-type capillitium with abundant large irregular pores.

Pseudoperdon medogense R.L. Zhao & J.X. Li sp. nov.

Fig. 30

Fungal Name: FN571713; Facesoffungi number: FoF15165

Etymology – referring to the Medog County of Xizang Autonomous Region province from China, where the holotype was collected.

Type – China, Xizang Autonomous Region, Medog Country, Xironggou Scenic Area, 24 Jul. 2021, X.Y. Zhu, ZRL20210823 (holotype HMAS 258786).

Diagnosis – This species is characterized by a yellowish-brown exoperidium covered with granular warts or finely slender spines, often displaying a star-shaped fold at the opening. The basidiospores possess a long pedicel and are ornamented with cylindrical verrucae, as observed under SEM, with a rounded apex.

Macroscopic description – Basidiomes slightly subglobose, depressed globose or sub-pyriform, 30–40 mm in diameter, 25–30 mm height. *Pseudostipe* usually not very developed. Rhizomorphs sparse, white, present a clear backbone attached to substrate, unbranched. *Peridium* layered. Exoperidium grey, brown, yellowish brown when nearing maturity, with densely granular warts or finely slender spines, residual white spot, fine flakes of cracking and gradually shedding in places with age, often star-shaped fold at the opening. *Endoperidium* light grey, yellowish brown, membranous, papery, stellate dehiscence at apical pore. *Gleba* yellowish-brown when fully mature, fibrous to cottony. *Subgleba* pulverulent.

Microscopic description – *Basidiospores* globose to subglobose, 3.9–4.4 µm in diameter, thick-walled, with an oil drop central, verrucose, with a long pedicel (7.1–9.8 µm, n = 30), pale yellow to brown in 5% KOH. Densely ornamented with verrucose under SEM, cylindrical, verrucose rounded at apex, often 2–3 connect or isolated with linear. *Capillitium* of *Lycoperdon*-type, 2.0–8.5 µm width, pale yellowish-brown, thick-walled, unequal width, tapering towards the tips, sometimes with bulging surface, elastic, straight to undulate, with abundant large irregular pores, no septa. Exoperidium made up of isolated or chains inflated cells, subglobose, oblong, pyriform, or cylindrical, 9.5–20.3 µm in width, 12.4–36.1 µm in length, thick-walled, less than 1 µm, hyaline in 3% KOH. *Endoperidium* made up of interwoven and unbranched arrangement hyphae, straight sometimes slightly undulate, no septa, hyaline in 3% KOH.

Ecology and distribution – Presently, this species only been found in the mixed coniferous forest with the elevations over 3,500m, growing on decaying wood, often solitary in a relatively humid environment. known from China.

Additional material examined – China, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Batang County, Zhubalong Nature Reserve, 19 Aug. 2021, X.Y. Zhu, ZRL20201528 (HMAS 258783); China, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Batang County, Zhubalong Nature Reserve, 19 Aug. 2020, J.X. Li, ZRL20201114 (HMAS 258784); China, Hubei Province, Shennongjia Forest Area, Shennongding, 26 Aug. 2022, J.X. Li HMAS 258785

(ZRL20221045); China, Xizang Autonomous Region, Yadong Country, Xiasima Town, 14 Sep. 2015, J.X. Li, ZRL20152148 (HMAS 258782).

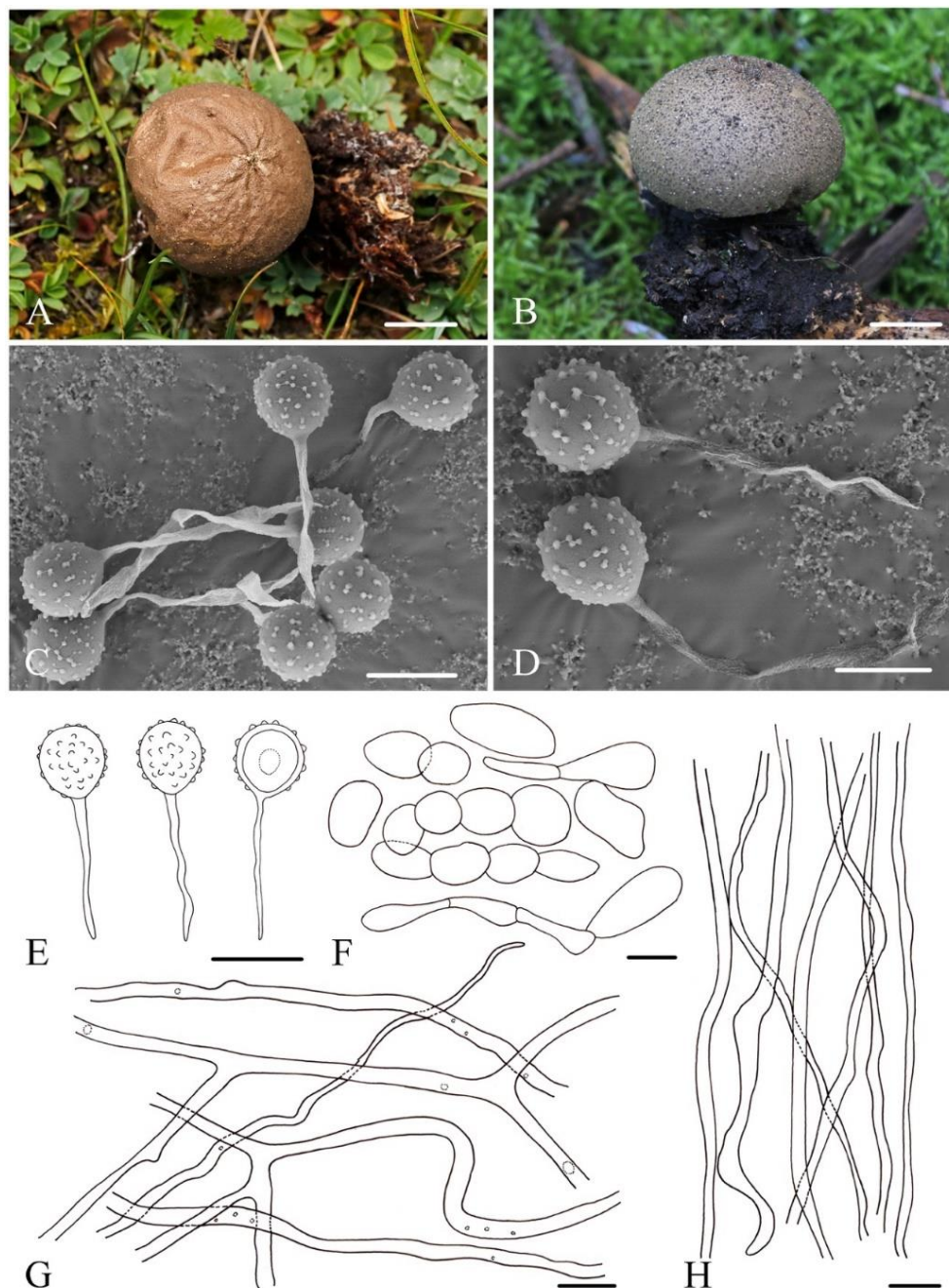


Figure 30 – Morphology of *Pseudoperdon medogense*. A gasterocarps (holotype, HMAS 258786). B gasterocarps (HMAS 258785). C, D basidiospores under SEM. E basidiospores under LM. F exoperidial elements (sphaerocysts). G capillitial threads. H endoperidial hyphae. Scale bars: A–B = 1 cm, C–D = 5 µm, E, G–H = 5 µm, F = 10 µm.

Notes – *Pseudoperdon* currently comprises two species: *P. subcretaceum* and the newly described *P. medogense* sp. nov. (Fig. 3). *Pseudoperdon subcretaceum*, once common in Europe, shares a similarity with this new species in its development of a wide apical opening at maturity. However, they differ in terms of basidiospores: *P. subcretaceum* features spherical spores with fine warts, lacking a pedicel (Jeppson & Larsson 2010), while *P. medogense* sp. nov. has globose to subglobose spores, densely covered with cylindrical to rounded verrucae, as observed under SEM, and possesses a long pedicel (7.1–9.8 µm) (Fig. 30).

Pseudoperdon subcretaceum (Zeller) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571819

Basionym – *Calvatia subcretacea* Zeller, Mycologia 39(3): 298 (1947).

Sinoperdon R.L. Zhao & J.X. Li, gen. nov.

Fungal Name: FN571720; Facesoffungi number: FoF15154

Type species – *Sinoperdon gyirongense* R.L. Zhao & J.X. Li

Etymology – *sino-* meaning from China, and *-perdon* meaning the genus name *Lycoperdon*.

The name refers to the type from China and having the similar morphology to the genus *Lycoperdon*.

In a previous molecular phylogenetic study, *S. caudatum* (= *Lycoperdon caudatum* J. Schröt. 1889), a common species from Europe, had an ambiguous position within *Lycoperdon* and was temporarily placed in *Lycoperdon* subg. *Utraria* (Larsson & Jeppson 2008, Jeppson & Larsson 2010, Alfredo et al. 2017). Based on the molecular phylogenetics in this study (Figs 1, 3), *S. caudatum*, along with other *Sinoperdon* species, clustered together as a monophyletic group with a divergence time of 34.5 Myr. Members of *Sinoperdon* can be diagnosed by the following characteristics: lycoperdoid basidiomes, echinate exoperidium covered with conical spines, *Lycoperdon*-type capillitium with thick walls, abundant paracapillitium, verrucose basidiospores with long pedicels.

Currently, *S. caudatum* (= *L. caudatum* J. Schröt.), *S. gyirongense* sp. nov., and *S. maritimum* sp. nov., as well as some unnamed specimens, have been identified as members of this genus (Fig. 3). Based on their geographic distribution, it can be inferred that this genus has a wide distribution, mainly found in North Europe, North America (Larsson & Jeppson 2008, Jeppson & Larsson 2010), Korea (Kim et al. 2016), China (ZRL20191589; ZRL20220977; GX20170471), and Thailand HMAS 287488 (LE2016125).

Sinoperdon gyirongense R.L. Zhao & J.X. Li sp. nov.

Fig. 31

Fungal Name: FN571714; Facesoffungi number: FoF15164

Etymology – referring to the Gyirong County of Xizang Autonomous Region Autonomous Region from China, where the holotype was collected.

Type – China, Xizang Autonomous Region Autonomous Region, Shigatse City, Gyirong Country, Gyirong Gully, 1 Aug. 2022, R.L. Zhao, ZRL20220551 (holotype HMAS 258787).

Diagnosis – The basidiomes of this species are pyriform to sub-pyriform, and the exoperidium is echinate, covered with brownish conical spines. Microscopically, it features small-sized, oblong basidiospores that are finely ornamented with verrucae, displaying conical warts when observed under SEM. This fungus typically grows on rotting wood.

Macroscopic description – *Basidiomes* pyriform to sub-pyriform, depressed globose to subglobose, 20–42 mm in diameter, 25–40 mm height. Usually develop a *Pseudostipe*, sometimes not distinct. Rhizomorphs sparse, white, mixed with humic substances. *Peridium* layered. Exoperidium echinate, densely with conical spines, singular, whitish when young, entirely brown to dark brown when old, and decreased with age, present a dark brown color at the center of the apex. *Endoperidium* off-white, yellowish brown when mature, membranous, papery. *Gleba* yellowish-brown, dark brown when fully mature, fibrous to cottony. *Subgleba* pulverulent.

Microscopic description – *Basidiospores* oblong, $5.2\text{--}6.5 \times 2.9\text{--}4.1\ \mu\text{m}$, [$x = 5.9 \pm 0.3 \times 3.5 \pm 0.3$, $Q = 1.4\text{--}1.9$, $Q_m = 1.7 \pm 0.1$, $n = 30$], thick-walled, with an oil drop central, light olive green in 5% KOH, usually with a long pedicel ($10.2\text{--}16.6\ \mu\text{m}$, $n = 30$), under SEM finely ornamented with verrucose, conical with different sizes. often 2–3 connect or isolated with linear. *Capillitium* of *Lycoperdon*-type, $1.3\text{--}3.7\ \mu\text{m}$ width, pale brownish, thick-walled, unequal width, elastic, straight to undulate, fewer pores observed, no septa. *Paracapillitium* abundant, interwoven and branched, thick-walled (up to $1\ \mu\text{m}$), pale brownish, $3.4\text{--}11.9\ \mu\text{m}$ width, similar to *Capillitium* but shorter in length. Exoperidium was made up of chains of inflated cells, subglobose to globose, oblong to pyriform, $5.5\text{--}24.9\ \mu\text{m}$ in width, $10.6\text{--}47.8\ \mu\text{m}$ in length, slightly thick-walled (up to $0.5\ \mu\text{m}$), hyaline in 5% KOH. *Endoperidium* made up of branched arrangement hyphae, produces many septa and constricted, slightly thick-walled and smooth, hyaline in 5% KOH.

Ecology and distribution – solitary or sometimes socially within the mixed coniferous forest, fruiting on decaying wood, often occurs in the higher elevations of the state, known from China.

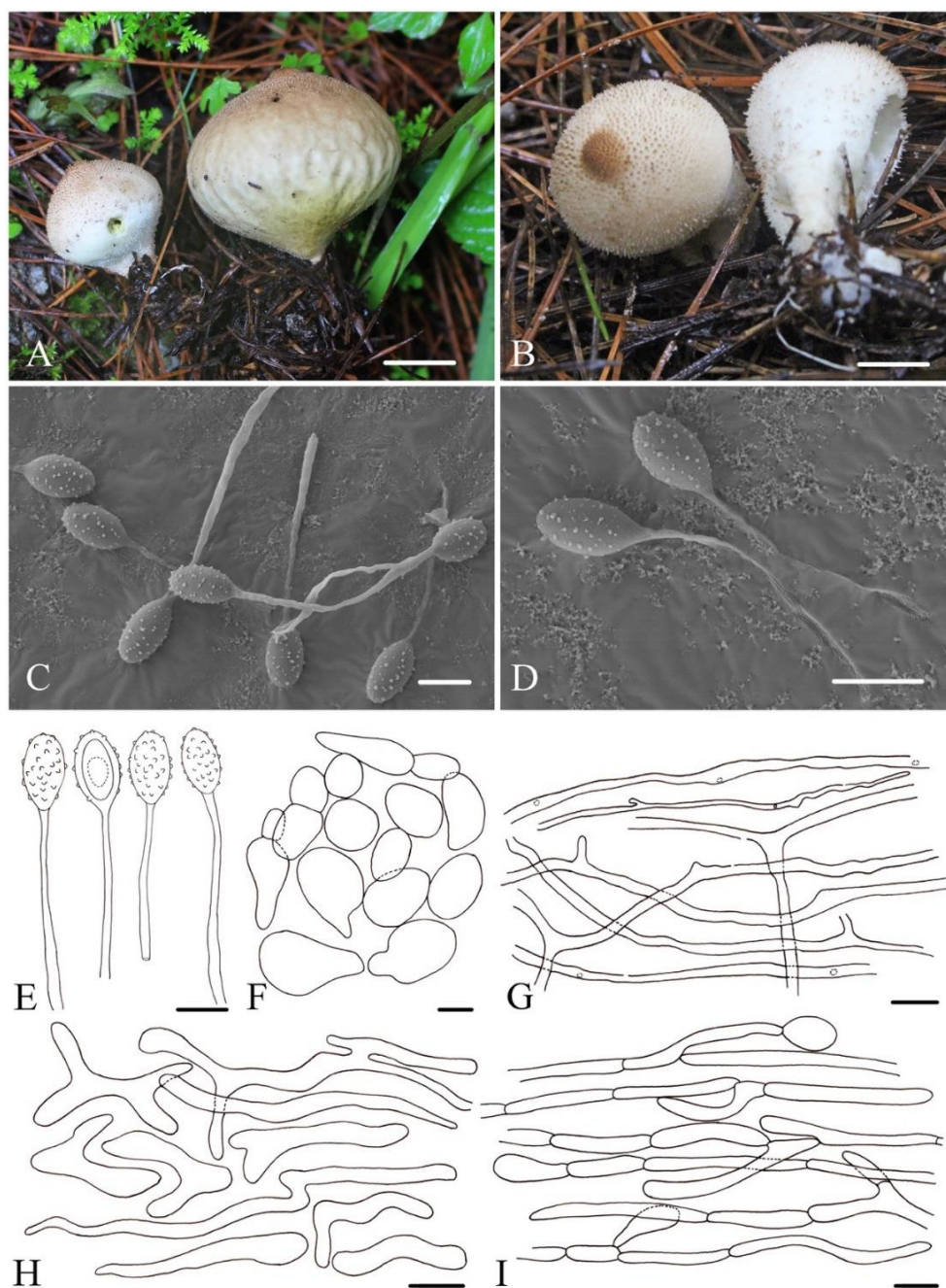


Figure 31 – Morphology of *Sinoperdon gyirongense*. A gasterocarps (holotype, HMAS 258787). B gasterocarps (HMAS 258789). C, D basidiospores under SEM. E basidiospores under LM. F exoperidial elements (sphaerocysts). G capillitial threads. H paracapillitium. I endoperidial hyphae. Scale bars: A–B = 1 cm, C–D = 5 µm, E–I = 5 µm.

Additional material examined – China, Xizang Autonomous Region Autonomous Region, Shigatse City, Dingjie Country, Chentang Town, 30 Jul. 2022, R.L. Zhao, ZRL20220495 (HMAS 258788); China, Xizang Autonomous Region Autonomous Region, Shigatse City, Gyirong Country, Gyirong Gully, 2 Aug. 2022, R.L. Zhao, ZRL20220759 (HMAS 258789); China, Xizang Autonomous Region Autonomous Region, Shigatse City, Yadong Country, Xiayadong Gully, 26 Jul. 2022, R.L. Zhao, ZRL20220176 (HMAS 258790); China, Hubei Province, Shennongjia Forest Area, Shennongding, 26 Aug. 2022, M.Q. He, ZRL20221001 (HMAS 258791); China, Hubei Province,

Shennongjia Forest Area, Shennongding, 26 Aug. 2022, R.L. Zhao, ZRL20221014 (HMAS 258792); China, Yunnan Province, Jingdong County, Ailao Mountain, 4 Jul. 2021, R.L. Zhao, ZRL20210190 (HMAS 258793); China, Chongqing City, Chengkou County, North Ping Mountain, Dabashan Mountain, 4 Sep. 2021, X.Y. Zhu, ZRL20211672 (HMAS 258794); China, Chongqing City, Chengkou County, North Ping Mountain, Dabashan Mountain, 4 Sep. 2021, X.Y. Zhu, ZRL20211733 (HMAS 258795); China, Chongqing City, Kaizhou County, Xuebaoshan National Nature Reserve, 11 Sep. 2021, X.Y. Zhu, ZRL20211506 (HMAS 258796); China, Chongqing City, Kaizhou County, Xuebaoshan National Nature Reserve, 13 Sep. 2021, X.Y. Zhu, ZRL20211651 (HMAS 258797); China, Sichuan Province, Ganzi Xizangan Autonomous Prefecture, Yajiang County, Gexigou Nature Reserve, 14 Aug. 2020, R.L. Zhao, ZRL20200350 (HMAS 258798); China, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Yajiang County, Gexigou Nature Reserve, 15 Aug. 2020, R.L. Zhao, ZRL20200469 (HMAS 258799).

Notes – In the phylogenetic topology (Fig. 3), *S. gyirongense* sp. nov. is positioned within the well-supported lineage of *Sinoperdon*, forming a sister relationship with the known species *S. caudatum*. While *S. gyirongense* sp. nov. shares morphological similarities with *S. caudatum*, such as having similar spines on the exoperidium and globose to elliptical spores with long pedicels, there are notable distinctions. Specifically, capillitiums in *S. caudatum* exhibit flaky, membranous appendages (Gorbunova & Rebriev 2018). Additionally, *S. gyirongense* sp. nov. features an abundance of paracapillitium, as depicted in Fig. 21. Another related species, *Lycoperdon ovalicaudatum* D. Bisht, J.R. Sharma & Kreisel, was described in the Western Himalaya. While it shares similarities with *S. gyirongense* sp. nov. in terms of an exoperidium covered by prominent spiny warts on the upper part and basidiospores with long pedicels, it differs in having hyaline, thin-walled paracapillitium and narrow, aseptate endoperidium hyphal (Bisht et al. 2006). Similarly, *Lycoperdon ovoidisporum* Cortez, Baseia & R.M.B. Silveira, described in Southern Brazil, bears resemblance to the new species. However, its basidiospores are mostly ovoid or broad ellipsoid, with absent or short pedicels (less than 0.7 µm in length), and it lacks paracapillitium (Cortez et al. 2011).

Sinoperdon maritimum R.L. Zhao & J.X. Li sp. nov.

Fig. 32

Fungal Name: FN571824; Facesoffungi number: FoF15349

Etymology – referring to this species has habitat by the seaside.

Type – Thailand, Chumphon Province, Noen Sai Chumphon, 2 Dec. 2016, M.Q. He, LE2016125 (holotype HMAS 287488).

Diagnosis – This species is readily distinguishable by its depressed globose basidiomes featuring non-persistent flaky verrucae. Under microscopic examination, the basidiospores exhibit an elliptical shape with a long pedicel, showcasing fine verrucae when observed under SEM. The capillitium is of either *Lycoperdon*-type or *Bovista*-type. This fungus is commonly found in proximity to seaside environments.

Macroscopic description – *Basidiomes* sugglobose, depressed globose, sub-pyriform, 13–26 mm width, 10–20 mm height. *Rhizomorphs* well developed, up to 35 mm, encrusted with soil. *Pseudostipe* not indistinct. *Peridium* layered. *Exoperidium* densely covered with flaky verrucae, falling off from the upperpart when mature. *Endoperidium* brownish, membranous, soft, split at the apical pore. *Gleba* powdery brown.

Microscopic description – *Basidiospores* elliptical, oblong, $4.4\text{--}5.2 \times 3.6\text{--}4.3$ µm, [$x = 4.8 \pm 0.3 \times 3.9 \pm 0.3$, $Q = 1.1\text{--}1.3$, $Q_m = 1.2 \pm 0.1$, $n = 30$], thick-walled, with an oil drop central, yellowish-brown in 5% KOH, with a long pedicel (8.1–15.6 µm, $n = 30$). Under SEM, surface densely ornamented fine verrucae, irregular. *Capillitium* of *Lycoperdon*-type mostly, 1.9–3.8 µm, sometimes *Bovista*-type, brownish, coarse under SEM, thick-walled, tapering towards the tips, no septa, and often undulate at the end. *Exoperidium* composed of irregular sphaerocysts, thick-walled, hyaline in 5% KOH. *Endoperidium* composed of straight hyaline hyphae, 1.3–3.4 µm, occasionally branching. *Rhizomorphs* composed of interwoven hyaline hyphae, 1.1–3.1 µm, straight to undulate.

Ecology and distribution – solitary, growing on the soil under forest, near the seaside, known from Thailand.

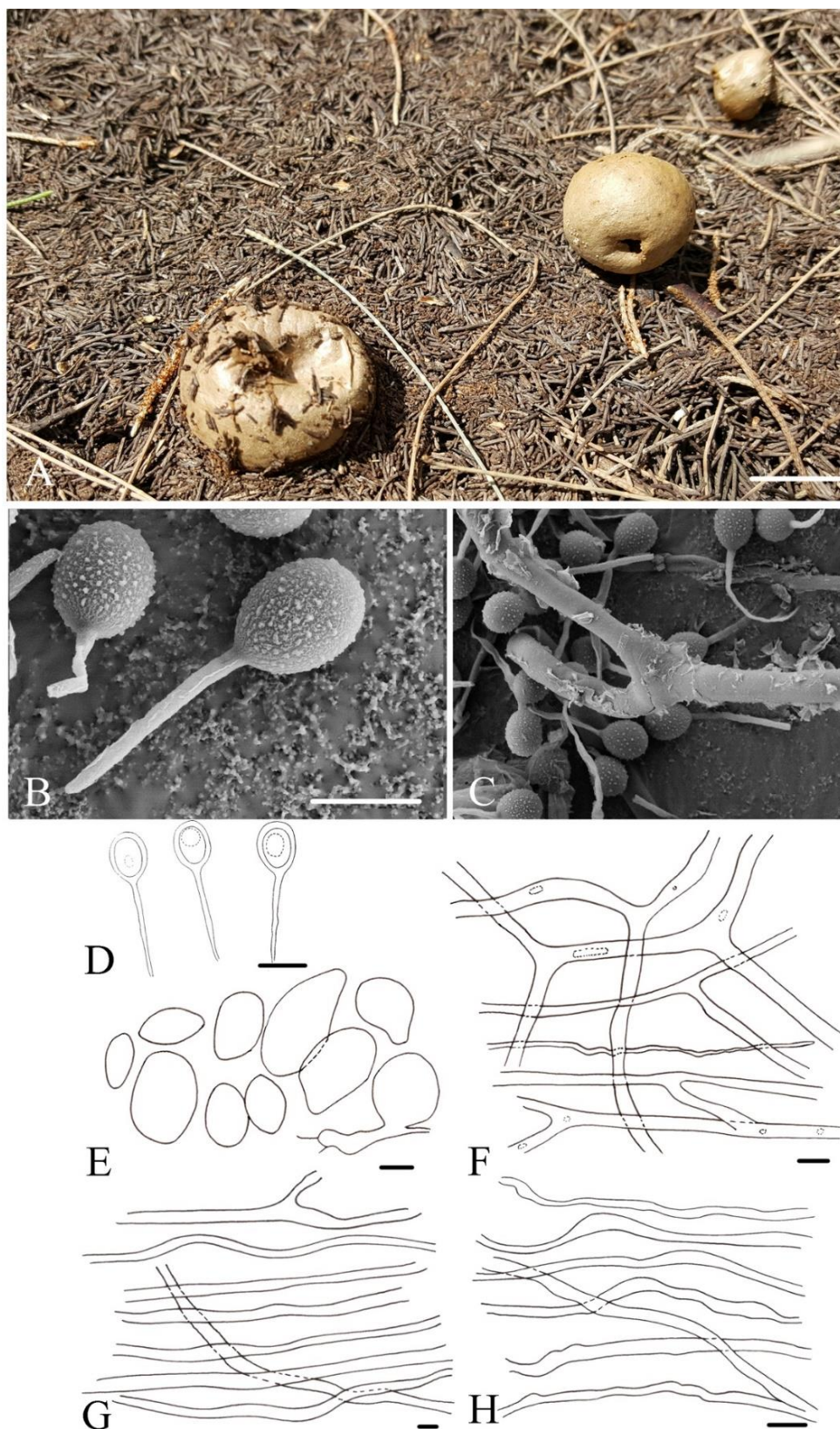


Figure 32 – Morphology of *Sinoperdon maritimum*. A gasterocarps (holotype, HMAS 287488 LE2016125). B, C basidiospores and capillitial threads under SEM. D basidiospores. E exoperidial elements (sphaerocysts). F capillitial threads. G endoperidial hyphae. H rhizomorphs hyphae. Scale bars: A = 1 cm, B = 5 µm, C = 2 µm, D = 5 µm, E–H = 2 µm.

Notes – The most distinctive features of *S. maritimum* sp. nov. include elliptical basidiospores with a long pedicel, adorned with fine verrucae, and depressed globose to pyriform basidiomes with

flaky verrucae, along with well-developed rhizomorphs. This species can be found in forests near the seaside. Phylogenetic analysis in this study revealed that *S. maritimum* sp. nov. forms a distinct lineage separate from the type species *S. gyirongense* sp. nov. and another species, *S. caudatum* (Fig. 3). In comparison, both *S. gyirongense* and *S. caudatum* exhibit echinulate basidiomes and exoperidium ornamentation composed of granules or spines, providing clear distinctions (Gorbunova & Rebriev 2018). Additionally, there are noticeable differences in the morphological features of basidiospores, despite all three species having long pedicels (Gorbunova & Rebriev 2018). *Sinoperdon maritimum* sp. nov. produces distinct spore shapes and ornamentations, with Q values of 1.1–1.3 and Qm of 1.2 ± 0.1 , showcasing densely ornamented fine verrucae. These unique phylogenetic position and morphological characteristics support the proposal of *S. maritimum* sp. nov. as a new species.

Sinoperdon caudatum (J. Schröt.) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571803

Basionym – *Lycoperdon caudatum* J. Schröt., in Cohn, Krypt-Fl. Schlesien (Breslau) 3.1(41): 698 (1889).

Utraria Quél., Mém. Soc. Émul. Montbéliard, Sér. 2 5: 366 (1873)

Fungal Name: FN19344

Type species – *Utraria excipuliformis* (Scop.) Quél., Mém. Soc. Émul. Montbéliard 5: 368 (1873).

Utraria was first proposed by Quél (1873). The type species, *U. excipuliformis* (Scop.) Quél., can be easily distinguished by the exoperidium covered with soft, pointed warts, which fall off at maturity, revealing a smooth, matte surface (Larsson & Jeppson 2008). It develops a well-supported pseudostipitate and warty spores (Yousaf et al. 2012). In the research by Larsson and Jeppson, *Utraria* was suggested as one subgenus of *Lycoperdon* s.l. (Larsson & Jeppson 2008). However, phylogenetic analyses in that study indicated that subg. *Utraria* was not monophyletic, with a wide range of combinations of morphological characters being defined. Under these circumstances, some widespread and traditionally reported taxa were included, such as *U. mollis* (= *Lycoperdon molle* Pers.), *U. atropurpurea* (= *Lycoperdon atropurpureum* Vittad.), *U. altimontana* (= *Lycoperdon altimontanum* Kreisel), *U. lambinonii* (= *Lycoperdon lambinonii* Demoulin), etc. (Larsson & Jeppson 2008, Alfredo et al. 2017).

Based on the molecular phylogenetics in this study (Fig. 3), the formerly *Lycoperdon* subg. *Utraria* (in the sense of Larsson & Jeppson 2008) formed three distinct lineages with strong support (Fig. 3). They are recommended as three distinct genera. Furthermore, molecular clock analyses resulted in the three having close divergence times, with the division ranging from 26.7 to 34.4 Myr. Among them, species nested with the type *U. excipuliformis* were restored as *Utraria* with a stem age of 26.7 Myr, and species within the two groups represented by *Li. tianzhuensis* sp. nov. and *Le. sublongistipes* sp. nov. were transferred into new genera *Lycoperdiscus* and *Leptocaulis*, respectively (Figs 1, 3). Macroscopically, these several species remaining in *Utraria* share common morphological features, such as being widely distributed, developing more or less subgleba, having the presence of *Lycoperdon*-type capillitium and absence of paracapillitium, and less prominently showing *Lycoperdon*-*Bovista*-type capillitium. In this part, one new species was described and eleven new combinations were detailed as follows.

Utraria malleata R.L. Zhao & J.X. Li sp. nov.

Fig. 33

Fungal Name: FN571715; Facesoffungi number: FoF15161

Etymology – The epithet refers to the concave-wrinkle gridded ornamented on the exoperidium when fully mature.

Type – China, Gansu Province, Wuwei City, Haxi Protection Station Spruce Forest, 22 Aug. 2018, B. Cao, ZRL20181345 (holotype HMAS 258764).

Diagnosis – This species is characterized by pyriform basidiomes with well-developed rhizomorphs attached to the substrate. The exoperidium exhibits a gridded wrinkle when mature, along with farinaceous granules.

Macroscopic description – *Basidiomes* pyriform 35–50 mm in diameter, 40–50 mm high, with or without Pseudostipitate, not well-developed, attached to the substrata by well-developed rhizomorphs, white, branched, and heavily encrusted with soil particles. Predium layered. Exoperidium brownish-white, pale-brown. In young stage possess gridded wrinkle, slightly concave with granular warts, wrinkle isolated or in groups, discolor dark-brown, blackish-brown when mature, granular warts persistent, discolor white. *Endoperidium* pale yellowish, papery, fragile. *Gleba* pale yellow to rusty-yellow at maturity, pulverulent. *Subgleba* present, pale yellowish, occasionally reduced, spongiform.

Microscopic description – *Basidiospores* globose to subglobose, 4.3–5.3 μm in diameter, with a central oil drop, pedicel present, up to 1–2 μm , distinctly ornamented with verrucous warts, cylindrical, verrucose rounded at apex. *Capillitium* of *Lycoperdon*-type, 3–8.5 μm in diameter, yellowish brown, brownish in 3% KOH, thick-walled, elastic to sub-elastic, straight to subundulate, abundantly dichotomous branching, no irregular pores observed, no septa observed. Paracapillitium not observed. Exoperidium composed of sphaerocysts, 22.4–32.7 $\times$ 15.8–23.1 μm , thick-walled, hyaline in 3% KOH. *Endoperidium* composed of dense interwoven unbranched, hyphae, 1.8–3.8 in diameter, thin-walled.

Ecology and distribution – Terrestrial and found in grassy areas, growing solitary in the soil among grass and moss, occurs under conifer forest, known from China.

Additional material examined – China, Gansu Province, Zhangye City, Shandan County, Army Horse Farm, 19 Aug. 2017, X.Y. Zhu, QL20170156 (HMAS 258765); China, Sichuan Province, Ganzi Tibetan Autonomous Prefecture, Batang County, Drukpa Cage Nature Reserve, 19 Aug. 2020, Bin Cao, ZRL20201099 (HMAS 258902).

Notes – *Utraria malleata* sp. nov. is discovered in China, featuring a gridded-wrinkled exoperidium and often developing brownish granular and slender spines. In the phylogenetic tree (Fig. 3), this new species forms a sister relationship with *U. lambinonii*. However, *U. lambinonii* can be easily distinguished, typically having a yellowish to yellowish-brown exoperidium ornamented with granulose, sometimes accompanied by convex spines (Gube 2007, Fan 2019). Macroscopically similar species to this new discovery include *Lo. perlatum*, *H. brandegeenum*, and *H. purpurascens* sp. nov., all sharing a wrinkled exoperidium. Nevertheless, *Lo. perlatum* exhibits regularly fused units at the tips encircled by numerous smallish echinated spines (Kim et al. 2016, Fan 2019); *H. brandegeenum* displays an exoperidium that is white to yellowish-white, composed of glabrous to rugulose, appressed flocculence (Bates et al. 2009); and *H. purpurascens* sp. nov. differs with its gleba stained purple and the presence of larger basidiospores (7.7–10.7 μm) (Fig. 26).

Utraria frigida (Demoulin) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571743

Basionym – *Lycoperdon frigidum* Demoulin, Lejeunia 62: 10 (1972).

Utraria mollis (Pers.) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571726

Basionym – *Lycoperdon molle* Pers., Observ. mycol. (Lipsiae) 2: 70 (1800).

Utraria nivea (Kreisel) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571725

Basionym – *Lycoperdon niveum* Kreisel, Khumbu Himal. 6(1): 30 (1969).

Utraria pulcherrima (Berk. & M.A. Curtis) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571795

Basionym – *Lycoperdon pulcherrimum* Berk. & M.A. Curtis, Grevillea 2(no. 16): 51 (1873).

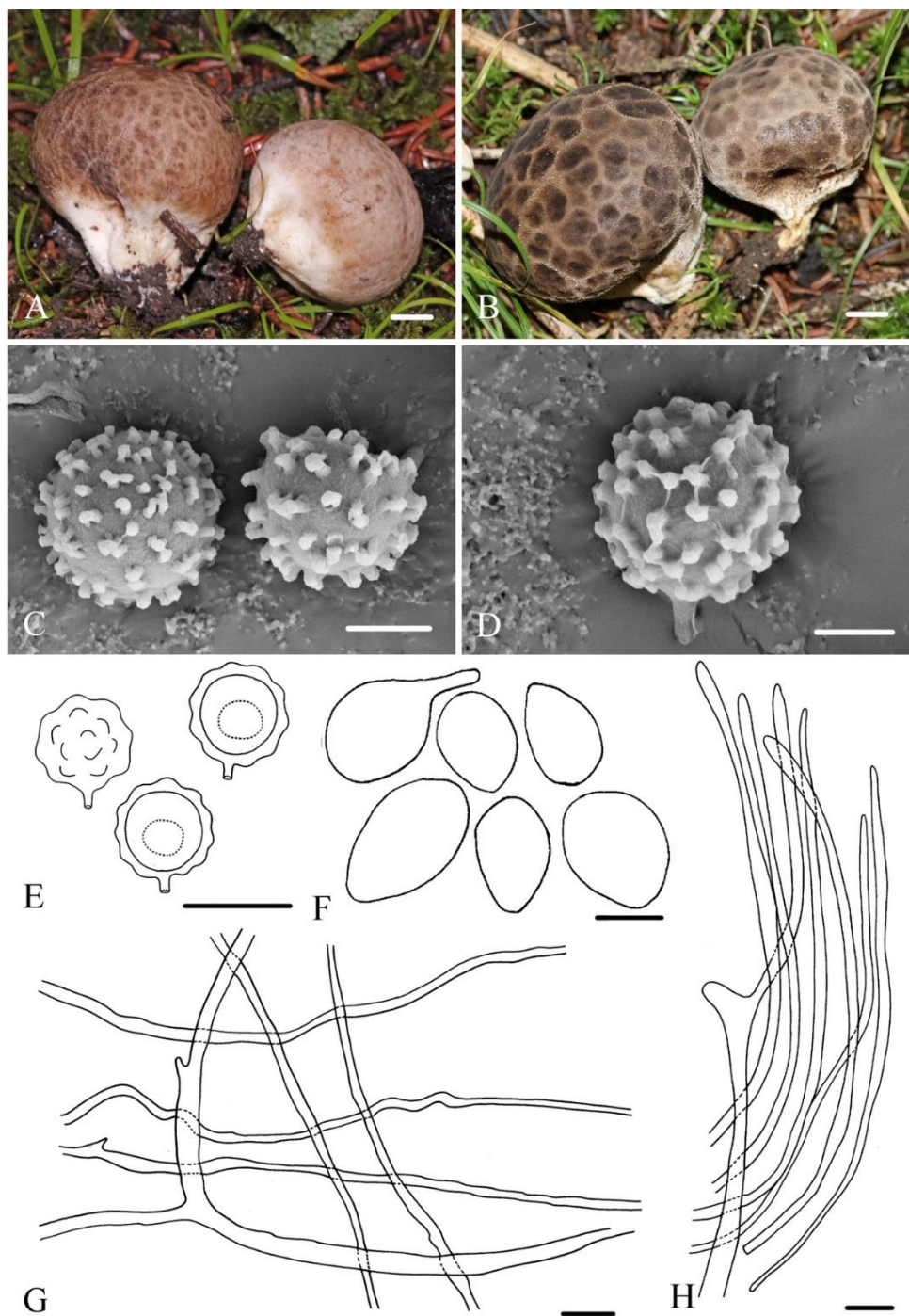


Figure 33 – Morphology of *Utraria malleata*. A gasterocarps (holotype HMAS 258764). B gasterocarps (HMAS 258765). C, D basidiospores under SEM. E basidiospores under LM. F exoperidial elements (sphaerocysts). G capillitial threads. H endoperidial hyphae. Scale bars: A–B = 1 cm, C–D = 2 μ m, E = 5 μ m, F–G = 10 μ m, H = 5 μ m.

Utraria rimulata (Peck) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571798

Basionym – *Lycoperdon rimulatum* Peck, in Morgan, Trans. Wis. Acad. Sci. Arts Lett. 7: 117 (1888).

Utraria decipiens (Durieu & Mont.) R.L. Zhao & J.X. Li comb. nov.

Fungal Name: FN571799

Basionym – *Lycoperdon decipiens* Durieu & Mont., Expl. sci. Algérie 1: 380 (1848).

- Utraria altimontana*** (Kreisel) R.L. Zhao & J.X. Li comb. nov.
 Fungal Name: FN571800
 Basionym – *Lycoperdon altimontanum* Kreisel, Feddes Repert. 87: 97 (1976).
- Utraria turneri*** (Ellis & Everh.) R.L. Zhao & J.X. Li comb. nov.
 Fungal Name: FN571801
 Basionym – *Lycoperdon turneri* Ellis & Everh., J. Mycol. 1(7): 87 (1885).
- Utraria umbrina*** (Pers.) R.L. Zhao & J.X. Li comb. nov.
 Fungal Name: FN571802
 Basionym – *Lycoperdon umbrinum* Pers., Ann. Bot. (Usteri) 11: 28 (1794).
- Utraria lambinonii*** (Demoulin) R.L. Zhao & J.X. Li comb. nov.
 Fungal Name: FN571728
 Basionym – *Lycoperdon lambinonii* Demoulin, Lejeunia, n.s. 62: 13 (1972).
- Utraria cretacea*** (Berk.) R.L. Zhao & J.X. Li comb. nov.
 Fungal Name: FN571727
 Basionym – *Lycoperdon cretaceum* Berk., J. Linn. Soc., Bot. 17: 15 (1880).
- Utraria echinata*** (Pers.) Quél. 1873
 Basionym – *Lycoperdon echinatum* Pers., Ann. Bot. (Usteri) 11: 28 (1794).
- Utraria excipuliformis*** (Scop.) Quél. 1886
 Basionym – *Lycoperdon excipuliforme* (Scop.) Pers., Syn. meth. fung.: 143 (1801).
- Utraria mammiformis*** (Pers.) Quél. 1886
 Basionym – *Lycoperdon mammiforme* Pers., Syn. meth. fung.: 145 (1801).
- Utraria atropurpurea*** (Vittad.) Quél. 1886
 Basionym – *Lycoperdon atropurpureum* Vittad., Monogr. Lycoperd.: 42 (1842).
- Vascellum*** F. Šmarda, Fl. ČSR, B-1, Gasteromycetes: 760 (1958)
 Fungal Name: FN19346
 Type species – *Lycoperdon pratense* Pers., Neues Mag. Bot. 1: 87 (1794).
 Currently, the genus *Vascellum* is distinguished from other genera by having a diaphragm to separate the gleba and subgleba, and by presenting both capillitium and paracapillitium (Cortez et al. 2013). This molecular phylogenetic analysis shows that this genus forms a well-supported clade with a divergence time of 27.7 Myr (Figs 1, 3).
- Vascellum curtisii*** (Berk.) Kreisel 1963
 Basionym – *Lycoperdon curtisii* Berk., Grevillea2(no. 16): 50 (1873).
- Vascellum pratense*** (Pers.) Kreisel 1962
 Basionym – *Lycoperdon pratense* Pers., Neues Mag. Bot. 1: 87 (1794).

DISCUSSION

Revision of the generic lineages of *Lycoperdaceae*

In this study, a concatenated dataset (ITS, nrLSU, *rpb2*, and *tef1-α*) was employed to revisit the classification of *Lycoperdaceae*. Phylogenetic results indicate that *Lycoperdaceae* forms a monophyletic group, revealing 19 well-recovered major clades corresponding to 14 known genera

and five newly established ones (see Fig. 1). Molecular clock analyses disclose that *Lycoperdaceae* diverged approximately 83 million years ago, with genera exhibiting a divergence range from 26.7 to 75.5 Myr. Notably, *Abstoma*, *Calvatia*, and *Disciseda* diverged relatively early compared to other genera (61.1–75.5 Myr, Fig. 1). The type genus, *Lycoperdon*, underwent a more recent division around 27.7 Myr, while the 11 genera involved in *Lycoperdon* s.l. shared roughly similar divergent times (26.7–34.5 Myr, Fig. 1). Two previously controversial genera, *Apioperdon* and *Bryoperdon*, diverged around 55 Myr, and formerly, *Bovista* two subgenera also diverged around 55 Myr.

Based on the results, a revision of the taxonomic system of *Lycoperdaceae* family into 26 genera is proposed. Nineteen genera are supported by molecular data, while seven genera (*Acutocapillitium*, *Calvatiopsis*, *Calbovista*, *Gastropila*, *Glyptoderma*, *Japonogaster*, *Lycoperdopsis*) lack temporarily available molecular data (Zhou & May 2023). The previously united *Lycoperdon* s.l. is now divided into 11 genera, with the recommendation of adopting the concept of *Lycoperdon* str. Former *Lycoperdon* s.l. subgenera (*Bovistella*, *Morganella*, *Utraria*, *Vascellum*) have been elevated to independent genera and restored to generic rank. Among them, the acceptance of *Holocotylon* is justified based on phylogenetic evidence, distinctive morphology, and divergence times. Additionally, five new genera (*Fuscospina*, *Leptocaulis*, *Lycoperdiscus*, *Pseudoperdon*, and *Sinoperdon*) are described as new to science based on their well-supported phylogenetic positions and divergence times. Furthermore, 22 novel species are proposed, along with 24 new combinations. The taxonomic classification of *Lycoperdaceae* is herein updated using multigene data.

Morphological characters with high phylogenetic significance in distinguishing genera

Within the *Lycoperdaceae*, morphological characters, such as the presence and type of capillitium, the presence or absence of paracapillitium, the presence and structure of subgleba, opening patterns of endoperidium, and peridium anatomy, serve as distinctive features for genera in this family (Cunningham 1944, Pegler et al. 1995, Calonge 1998, Krüger et al. 2001, Larsson & Jeppson 2008, Bates et al. 2009, Larsson et al. 2009, Jeppson & Larsson 2010, Kim et al. 2016, Fan 2019, Krakhmalnyi et al. 2023).

Our results indicate that morphological features, such as the presence and types of capillitia, are valuable in distinguishing genera within this family (see Fig. 1 for detailed morphological comparisons). Specifically, three closely related genera viz. *Abstoma*, *Calvatia*, and *Disciseda* develop *Calvatia*-type capillitium, which is a key marker for these genera in our phylogenetic analysis. In contrast, the genus *Globalaria* predominantly develops a transitional type capillitium (Figs 18–24), further distinguishing it from the aforementioned genera. The *Bovista*-type capillitium is mostly found in the genus *Bovista* (Figs 8–10), underscoring its importance as a phylogenetic marker. Additionally, several genera closely related to the type genus *Lycoperdon* mostly exhibit a broadly similar *Lycoperdon*-type capillitium (Figs 16–17, 25–27, 30, 33), except for *Morganella* spp., which differ by possessing only paracapillitium instead of the true capillitium, as clearly shown in Fig. 29. Furthermore, our results suggest that habitat could serve as an additional discriminable feature. For instance, species from the genus *Apioperdon* can be distinguished by their lignicolous habitat, while members of *Morganella* almost exclusively grow on wood (Fig. 29). Additionally, several species of *Disciseda* have been reported in sandy habitats (Krüger et al. 2001, Cortez et al. 2010a, Kumla et al. 2014, Alfredo et al. 2017). These morphological and ecological markers, when integrated with our phylogenetic analysis, provide a comprehensive framework for distinguishing genera within the *Lycoperdaceae*.

Meanwhile, morphological data in this study reveal that certain features, such as the presence or absence of subgleba and peridium anatomy, show less significance at a generic level. The presence or absence of a subgleba perhaps does not significantly differ among puffballs in this family. Almost all members of *Bovista* develop an inconspicuous subgleba, while all the other genera more or less present a subgleba. Even within one genus, some develop a distinct subgleba, while others do not. For instance, in *Globalaria*, *G. testacea* and *G. muscicola* have a well-developed subgleba, while *G. gyirongensis* and *G. albata* do not possess a distinct subgleba. The same holds true in *Calvatia*, where *C. shennongjiaensis* and *C. craniiformi* often develop a subgleba, while it is not distinct in

C. subbooniana. Furthermore, among these diverse genera, peridium microanatomical structures are almost uniform in most cases. The exoperidium is made up of sphaerocysts or chains of inflated cells, and the endoperidium is composed of interwoven hyaline hyphae in most situations. These features are therefore considered to have less significance in distinguishing diverse genera.

In summary, several key morphological characters are now recommended to distinguish diverse genera of the family *Lycoperdaceae*. These characters could include capillium type, paracapillium, opening patterns of endoperidium.

The hypothesis of evolution in *Lycoperdaceae*

Molecular clock analyses indicate that *Lycoperdaceae* diverged during the late Upper Cretaceous (around 83 Myr), with generic lineages branching throughout the Paleogene period (26.7–75.5 Myr). Notably, the genera *Abstoma*, *Calvatia*, and *Disciseda* experienced later divisions (75.5 Myr, 62.5 Myr, 61.1 Myr), while the type genus *Lycoperdon* and closely related genera diverged around the late Paleogene (26.7–34.5 Myr). The results suggest that most species originated during this period, as illustrated in Fig. 1. Members from *Utraria* diverged around 21.3 Myr, *Holocotylon* species around 24 Myr, *Lycoperdon* species around 19.5 Myr, and *Vascellum* species around 15.6 Myr. Based on the geological time scale and events, a hypothesis of evolution in *Lycoperdaceae* is proposed: during the transition from the Eocene to the Oligocene, particularly during the Great Ice Age at the beginning of the Oligocene, the global climate suddenly became colder and drier (Westerhold et al. 2020). As a result, a significant expansion of species within this family may have occurred. In response to these changes, gasteroid-basidiomes and more than two peridia may have evolved to adapt to the sudden cooling and drying environment.

This study also inferred the evolution of capillitium types and basidiospores within *Lycoperdaceae*. As shown in Fig. 1, almost all genera in this family develop different types of ornamental basidiospores, with more than half involving *Lycoperdon*-type capillitium. The analysis hypothesizes that features such as ornamented basidiospores and *Lycoperdon*-type capillitium may represent ancestral states of this family, serving as symplesiomorphic features for generic lineages. Additionally, the analysis suggests that the common ancestor of *Lycoperdaceae* possibly possessed *Calvatia*-type capillitium, evolving at least three times in genera like *Abstoma*, *Calvatia*, and *Disciseda*. Subsequently, transitional-type capillitium emerged (*Globaria*), and the most recent common ancestor gave rise to *Lycoperdon*-type and *Bovista*-type capillitium, leading to a high diversity among the former *Lycoperdon*-type. For instance, *Apioperdon* exhibits an unpitted *Lycoperdon*-type of capillitium, *Vascellum* diverged with a reduced *Lycoperdon*-type of capillitium, and the genus *Morganella* evolved only paracapillitium instead of the true capillitium.

Genera and Species diversity, distribution of *Lycoperdaceae* from China

Fungi from the family *Lycoperdaceae* are predominantly found worldwide. Previous research specimens were primarily sourced from Europe and the Americas (Bates 2004, Baseia 2005, Jeppson 2008, Larsson & Jeppson 2008, Bates et al. 2009, Larsson et al. 2009, Jeppson & Larsson 2010, Cortez et al. 2011, Jeppson et al. 2012, Rebriev & Assyov 2012, Cortez et al. 2013). In contrast, research on the family *Lycoperdaceae* in China has been comparatively limited. In 1984, Liu et al. conducted a systematic investigation, documenting 38 species across seven genera of *Lycoperdaceae* in China (Liu 1984). Subsequently, Mao et al. reported 29 species within seven genera of this family (Mao 2000). More recently, Li et al. recorded 16 species across four genera in “Atlas of Chinese macrofungal resources” (Li et al. 2016). Additionally, several new species from China have been reported, such as *Lo. fusiforme* M. Zang, *Lo. longistipes* M. Zang & M.S. Yuan (Zang 1980, Zang & Yuan 1999). In recent years, Fan et al. extensively studied Chinese specimens, documenting eight genera and around 52 species based solely on morphological examination (Fan et al. 2019). This study, however, recognized and supported 96 species in the world using molecular data. Among them, 41 species of 17 genera were identified in China.

Within *Lycoperdaceae*, genera in China exhibit significant variations in geographic distribution. Genera such as *Calvatia*, *Globaria*, *Lycoperdon*, *Sinoperdon*, and *Utraria* are widely

distributed across different regions of the country (Li et al. 2016, Fan et al. 2019). Additionally, in this study, we found that some species, particularly those from the genera *Holocotylon*, *Pseudoperdon*, and *Fuscospina*, display a marked preference for higher altitudes, often occurring at elevations above 3,500 meters. For example, *H. biconicum* sp. nov., *P. medogense* sp. nov., *F. scabricapillitia* sp. nov. were predominantly found in high-altitude areas, further reinforcing their ecological preference for such environments.

Previous studies have reported several puffballs from the Himalaya, including *Utraria nivea* (Kreisel) R.L. Zhao & J.X. Li (= *Lycoperdon niveum* Kreisel), *Utraria altimontana* (Kreisel) R.L. Zhao & J.X. Li (= *Lycoperdon altimontanum* Kreisel), and *Lo. yetisodale* Kreisel known from Nepal, *Lo. ovalicaudatum* D. Bisht, J.R. Sharma & Kreisel described from Western Himalaya (Kreisel 1969, Eckblad & Ellingsen 1984, Bisht et al. 2006, Larsson & Jeppson 2008). In this study, new species were recorded from the Himalayas, including *P. medogense* sp. nov., *S. gyirongense* sp. nov., and *G. gyirongensis* sp. nov., which were newly described and assigned to *Pseudoperdon*, *Sinoperdon*, and *Globaria*, respectively. These were collected from the border areas of Gyirong County and Medog County in the Xizang Autonomous Region of China. Additionally, *Bryoperdon acuminatum* (Bosc) Vizzini was reported for the first time from the Himalayas, China. In summary, this paper provides an updated worldwide checklist of *Lycoperdaceae*. However, the number of species identified so far is insufficient given the extensive population. To enhance our understanding of the distribution of *Lycoperdaceae* in the Himalayas, more intensive studies are imperative in this region.

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