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Two new *Lycoperdon* species collected from Korea: *L. albiperidium* and *L. subperlatum spp. nov.*

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Abstract

Thirty-four *Lycoperdon* specimens from Korea were examined with the internal transcribed spacer (ITS) region of ribosomal DNA sequence data. The result of the ITS sequences phylogenetic analysis indicated that the Korean specimens represented nine different species. To confirm the taxonomic position of these species, we conducted an intensive morphological investigation, and additional phylogenetic investigation of the protein coding regions RNA polymerase subunit II (RPB2) and translation elongation factor 1-alpha (TEF1). We discovered two new species (*L. albiperidium* and *L. subperlatum*) and one (*L. ericaeum*) newly discovered in Korea. *Lycoperdon albiperidium* is closely related to *L. ericaeum* based on ITS, RPB2 and TEF1 sequence data, but these species were distinguishable by morphological characteristics, especially the shape of the basidiocarps, the diameter of the eucapillitial threads and the size of the basidospores. *Lycoperdon subperlatum* is quite similar to the European and American *L. perlatum* based on morphological characteristics. However, *L. subperlatum* is clearly distinct from European and American *L. perlatum* based on ITS, RPB2 and TEF1 sequence data, and somewhat differs from them in macro- and microscopic characteristics. Based on morphological characteristics, *L. ericaeum* is related to *L. subumbrinum* and *L. lividum* but it is distinguishable by the presence of fragile, eucapillitial threads, the diameters of the threads and ITS sequences. Here, we describe four *Lycoperdon* species collected in Korea.

Keywords Agaricaceae, gasteroid, morphology, phylogeny, taxonomy

Introduction

Lycoperdaceae Chevall. (Agaricales, Agaricomycetes) is a large family of puffballs that traditionally contains eight genera: *Bovista* Pers., *Bovistella* Morgan, *Calvatia* Fr., *Disciseda* Czern., *Langermannia* Rostk., *Lycoperdon* Pers., *Morganella* Zeller and *Vascellum F*. Šmarda (Larsson & Jeppson 2008). Among them, *Lycoperdon* Pers. is composed of about 50 species of cosmopolitan puffballs (Kirk *et al.* 2008). This genus is characterized by small- to medium-sized basidiomata (*ca*. 10–100 mm diam.); spores usually released through an apical pore; frequent presence of a well-developed stem-like sterile base; and spores coated with spines, warts, or fine particles (Arora 1986).

In many cases, closely related species and/or complex groups of macrofungi may be morphologically indistinguishable, even microscopically (Larsson & Jeppson 2008; Cao *et al*. 2012; Sotome *et al.* 2013). To resolve this issue, many mycologists now use molecular phylogenetics to determine taxonomic relationships (Hibbett *et al*. 1997; Moncalvo *et al.* 2002; Larsson & Jeppson, 2008; Morgado *et al*. 2013). According to recent molecular phylogenetic studies of *Lycoperdon*, the generic type *L. perlatum* clusters with *Morganella*, *Vascellum*, and some other *Lycoperdon* species (Larsson & Jeppson 2008; Bates *et al*. 2009). Therefore, Larsson & Jeppson (2008) suggested a wide sense concept of this genus to minimize name changes and transferred genera *Morganella* and *Vascellum* to *Lycoperdon*. Here, we followed this concept to re-evaluate and describe two new Korean *Lycoperdon* species.

In Korea, only 14 species of *Lycoperdon* have been reported [*L. caudatum* J. Schröt., *L. colossus* A. Kawam., *L. echinatum* Pers., *L. excipuliforme* (Scop.) Pers. (= *Calvatia excipuliformis* (Scop.) Perdeck), *L. mammiforme* Pers., *L.*

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muscorum Morgan, *L. nigrescens* Pers., *L. perlatum* Pers., *L. pratense* Pers., *L. pusillum* Batsch, *L. pyriforme* Schaeff., *L. rimulatum* Peck, *L. lividum* Pers. (= *L. spadiceum* Pers.), and *L. umbrinum* Pers.] (The Korean Society of Mycology 2013). These species were mostly identified by morphology. However, many *Lycoperdon* species are morphologically indistinguishable, especially when immature. For that reason, we used the modern taxonomic concept, for which a combination of molecular and morphological data is used for accurate identification and description.

During a Korean mushroom diversity survey from 2012 to 2013, we collected 34 *Lycoperdon* specimens. In this study, we evaluate the phylogenetic placement of Korean *Lycoperdon* specimens and the relationship between two new *Lycoperdon* species and related species based on the internal transcribed spacer (ITS) region of ribosomal DNA, RNA polymerase subunit II (RPB2) and translation elongation factor 1-alpha (TEF1) sequences. In addition, we investigate their morphological characteristics. Herein, we provide taxonomic descriptions and macroscopic and microscopic pictures of *L. ericaeum*, *L. perlatum* and two new species *L. albiperidium* and *L. subperlatum*.

Materials and methods

Specimens and morphological observations

The 35 *Lycoperdon* specimens used in this study (34 Korean specimens and one Chinese specimen) are listed in Table 1, and the dried specimens were deposited in the Korea National Arboretum Herbarium (KH). The specimens were collected between June and October in 2012 and 2013. Macro-morphological characters were determined based on field notes and color photos of basidiomata. Micro-morphological characters were obtained from the dried specimens after sectioning and rehydration, which followed the protocols described by Largent *et al*. (1977). Basidiospores and capillitium were mounted in Cotton blue + lactophenol (CL) and heated to boiling for a few seconds or in 3% KOH. All basidiospore measurements exclude ornamentation. Basidiospore wall ornamentation was characterized as four types (A: smooth or very faintly ornamented; B: faintly verrucose; C: verrucose; D: strongly verrucose) in accordance with Demoulin (1972a, b). Peridial structures were studied in 3% KOH. An Olympus BX53 microscope and Jenoptik ProgRes C14 Plus camera (Jenoptik Corporation, Jena, Germany) were used for microscopic observation. ProgRes Capture Pro v.2.8.8 (Jenoptik Corporation) was used to measure microscopic characters.

TABLE 1. *Lycoperdon* specimens examined in this study.

Species	Specimen No.	Locality	GenBank No.			
			Coll. Date	ITS	RPB2	TEF1
L. albiperidium sp. nov.	KA12-1210	Korea, Chungnam Prov., Mt. Seodae	29 Aug. 2012	KP340182	KU764391	–
	KA12-1551	Korea, Chungnam Prov., Mt. Jinak	25 Sep. 2012	KP340183	–	KU764402
L. ericaeum	KA12-0761	Korea, Chungnam Prov., Mt. Seodae	18 Jul. 2012	KP340184	–	KU764399
	KA13-1463	Korea, Gyeongnam Prov., Mt. Gibaek	16 Oct. 2013	KP340185	KU764396	KU764404
L. excipuliforme	KA12-1185	Korea, Chungnam Prov., Mt. Jinak	28 Aug. 2012	KP340186	KU764390	–
L. mammiforme	KA12-1179	Korea, Chungnam Prov., Mt. Jinak	28 Aug. 2012	KP340187	KU764389	–
L. nigrescens	KA13-1471	Korea, Gyeongnam Prov., Mt. Udu	17. Oct. 2013	KP340188	–	–
L. perlatum	KA12-0186	Korea, Gangwon Prov., Daegwanryeong Natural Recreation Forest	09 Jun. 2012	KP340189	–	–
	KA12-0871	Korea, Gyeonggi Prov., Gwangneung Forest	26 Jul. 2012	KP340190	–	–
	KA12-1435	Korea, Gyeonggi Prov., Gwangneung Forest	12 Sep. 2012	KP340191	KU764392	–

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TABLE 1. (Continued)

Species	Specimen No.	Locality	GenBank No.			
			Coll. Date	ITS	RPB2	TEF1
	KA12-1506	Korea, Gyeonggi Prov., Saneum Natural Recreation Forest	19 Sep. 2012	KP340192	–	–
	KA13-0555	China, Xinjiang Prov., Mt. Tianshan, Heaven Pool Scenic Area	15 Jul. 2013	KP340193	KU764393	KU764403
	KA13-0608	Korea, Gyeonggi Prov., Gwangneung Forest	25 Jul. 2013	KP340194	–	–
	KA13-0619	Korea, Gyeonggi Prov., Gwangneung Forest	26 Jul. 2013	KP340195	–	–
	KA13-0646	Korea, Gyeonggi Prov., Gwangneung Forest	26 Jul. 2013	KP340196	–	–
	KA13-1148	Korea, Gyeonggi Prov., Gwangneung Forest	16 Sep. 2013	KP340197	–	–
	KA13-1188	Korea, Gyeonggi Prov., Gwangneung Forest	16 Sep. 2013	KP340198	–	–
	KA13-1270	Korea, Gyeonggi Prov., Gwangneung Forest	30 Sep. 2013	KP340199	–	–
	KA13-1542	Korea, Gyeonggi Prov., Gwangneung Forest	14 Oct. 2013	KP340200	KU764397	–
L. subperlatum sp. nov.	KA12-0281	Korea, Chungnam Prov., Mt. Jinak	20 Jun. 2012	KP340201	–	–
	KA12-0322	Korea, Chungnam Prov., Mt. Seodae	22 Jun. 2012	KP340202	–	KU764398
	KA12-0494	Korea, Jeonbuk Prov., Daejang-island	09 Jul. 2012	KP340203	–	–
	KA12-0533	Korea, Jeonbuk Prov., Seonyu-island	11 Jul. 2012	KP340204	–	–
	KA12-0594	Korea, Gyeonggi Prov., Gwangneung Forest	13 Jul. 2012	KP340205	–	–
	KA12-0627	Korea, Chungbuk Prov., Mt. Minjuji	16 Jul. 2012	KP340206	–	–
	KA12-0693	Korea, Chungnam Prov., Mt. Jinak	17 Jul. 2012	KP340207	KU764388	–
	KA12-0918	Korea, Gyeonggi Prov., Gwangneung Forest	27 Jul. 2012	KP340208	–	KU764400
	KA12-1105	Korea, Gyeonggi Prov., Gwangneung Forest	24 Aug. 2012	KP340209	–	KU764401
	KA12-1427	Korea, Gyeonggi Prov., Gwangneung Forest	12 Seq. 2012	KP340210	–	–
	KA13-0209	Korea, Gyeongnam Prov., Mt. Gibaek	19 Jun. 2013	KP340211	–	–

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TABLE 1. (Continued)

Species	Specimen No.	Locality	GenBank No.			
			Coll. Date	ITS	RPB2	TEF1
	KA13-0692	Korea, Gyeonggi Prov., Gwangneung Forest	08 Aug. 2013	KP340212	–	–
	KA13-0967	Korea, Gyeongnam Prov., Mt. Daebong	09 Sep. 2013	KP340213	KU764394	–
	KA13-0979	Korea, Gyeongnam Prov., Mt. Gibaek	10 Sep. 2013	KP340214	KU764395	–
Lycoperdon sp. 1	KA12-0505	Korea, JeonBuk Prov., Munyeo Island	10 Jul. 2012	KP340215	KU764387	–
Lycoperdon sp. 2	KA12-1218	Korea, Chungnam Prov., Mt. Seodae	29 Aug. 2012	KP340216	–	–

PCR amplification and sequencing

DNA was isolated from fresh fruiting bodies (approximately 0.1 g) using a DNeasy plant mini kit (Qiagen, Valencia, USA), following the manufacturer's recommendations. To amplify the ITS region of ribosomal RNA, the ITS5 and ITS4 primers were used. To amplify the protein-coding region, RNA polymerase subunit II (RPB2) and translation elongation factor 1-alpha (TEF1), the fRPB2-5F/bRPB2-7R and EF1-983F/EF1-2218R primer sets were used, respectively. PCR mixtures contained 0.5 pM of each primer, 0.25 mM dNTPs, 10 mM Tris-HCl, 50 mM KCl, 1.5 mM $MgCl_2$, 2.5 U of *Taq* DNA polymerase, and 15 ng of template DNA. PCR conditions for ITS and TEF1 were as follows: an initial denaturation step at 94°C for 4 min; followed by 34 cycles of 94°C for 40s, 55°C for 40s, and 72°C for 60s; and a final elongation step at 72°C for 8 min. For RPB2, the annealing temperature was lowered to 50°C. PCR products were purified and sequenced by Macrogen Inc. (Seoul, Korea). Unfortunately, some sequences of RPB2 and TEF1 of our specimens were not sequenced due to weak amplification or intragenomic heterogeneity. New sequence data (ITS, RPB2 and TEF1) were submitted to GenBank (Table 1).

Phylogenetic analyses

Raw sequences were proofread, edited, and assembled using PHYDIT 3.2 (Chun 1995). DNA sequences were aligned using ClustalX 1.81 (Thompson *et al.* 1997) and then manually adjusted using PHYDIT 3.2.

In the case of the ITS sequences data set, MrBayes 3.1 (Ronquist & Huelsenbeck 2003) was used to construct phylogenies under Bayesian inference. For the Bayesian approach, best-fit models of nucleotide substitution were first selected for ITS sequences data set using Akaike information criterion (AIC) in jModelTest2 software (Darriva *et al.* 2008). Posterior probabilities (PP) were approximated using metropolis-coupled Markov Chain Monte Carlo. Two parallel runs were conducted with one cold and three heated chains for 5 million generations, starting with a random tree. The trees were sampled every 100 generations. We determined that the two independent runs had converged when the average standard deviation of the split frequencies dropped below 0.01. The trees obtained before the convergence were discarded as burn-in, and the remaining trees were used to calculate a 50% majority consensus tree and estimate PP. Maximum parsimony (MP) analysis was conducted by heuristic search in PAUP* 4.0 (Swofford 2002) with the following settings: all characters were equally weighted, gaps were treated as missing characters, starting trees were obtained by random addition with 1000 replicates, and tree bisection-reconnection branch swapping algorithm. Nodal support for MP was determined by nonparametric bootstrapping of 1000 replicates (maximum parsimony bootstrap support value, MPBS), with a heuristic search consisting of 100 stepwise random addition replicates and tree bisection-reconnection branch swapping for each bootstrap replicate. Based on previous studies by Larsson & Jeppson (2008), Bates *et al*. (2009), and Kasuya *et al*. (2013), we retrieved reference ITS sequences to construct the phylogenetic tree.

In the case of RPB2 and TEF1 sequence set, we generated the Neighbor-Joining (NJ) trees only due to the lack of RPB2 and TEF1 sequences of reference specimens in GenBank. Bootstrap support values for nodes were computed from 1,000 replicates (Neighbor-Joining bootstrap support value, NJBS).

Results and discussion

Phylogenetic analysis of Korean *Lycoperdon* species based on ITS sequences.

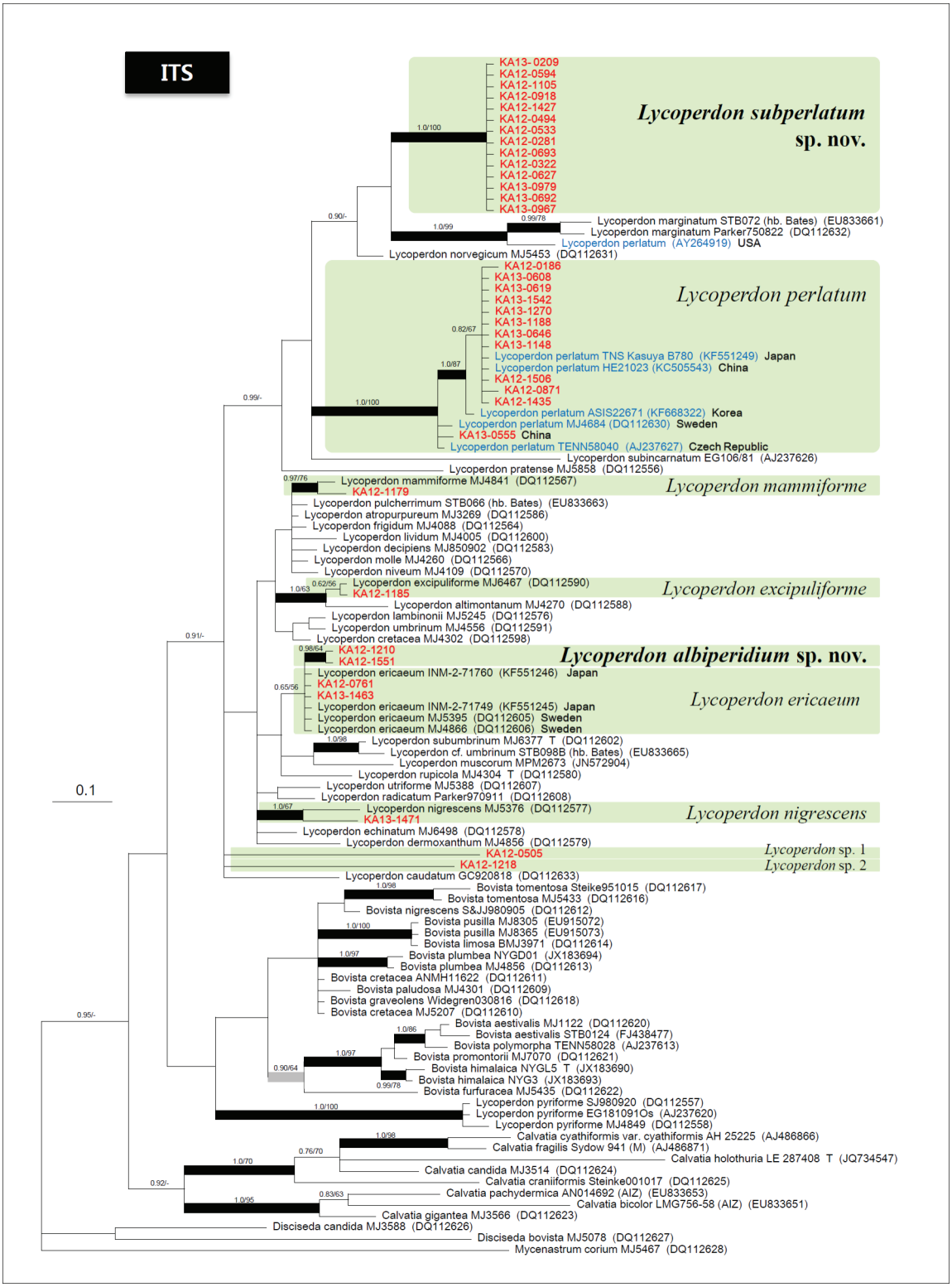

FIGURE 1. Bayesian 50% majority-rule consensus topology based on ITS sequence data. Bayesian posterior probabilities (PP) and 1000 bootstrap replicates in MP analysis (MPBS) are indicated as PP/MPBS above or below branches. Broad black branches indicate PP >0.95 and MPBS >60%. Broad gray branches indicate 0.89<PP<0.95 and MPBS >50%.

TABLE 2. Morphological comparison *Lycoperdon albiperidium sp. nov., L. subperlatum sp. nov*. and *L. ericaeum* with their related species.

Character	Species									
	L. subperlatum sp. nov. (this study)	Korean *L. perlatum* (this study)	European *L. perlatum* (refer to Breitenbach & Kränzlin 1986)	American *L. perlatum* (refer to Bates *et al*. 2009)	*L. marginataum* (refer to Bates *et al*. 2009)	*L. albiperidium* sp. nov. (this study)	*L. ericaeum* (this study)	*L. rupicola* (refer to Jeppson *et al*. 2012)	*L. subumbrinum* (refer to Jeppson *et al*. 2012)	*L. lividum* (refer to Breitenbach & Kränzlin 1986; Bate *et al*. 2009)
Basidiocarps shape	subglobose, pyriform to turbinate	subglobose, pyriform to turbinate	pyriform to turbinate	subglobose, obovoid, obpyriform to pseudostipitate	obovoid, depressed globose to obpyriform	pyriform to turbinate	subglobose, to obpyriform	subglobose to pyriform	pyriforme	subpyriform to obpyriform
Diameter (mm)	20–45	25–35	30–80	15–55	10–45 (65)	20–40	15–30	15–30	20–30	15–30
Height (mm)	25–60	25–40	up to 60	18–67	10–35 (55)	35–60	25–30	ND[a]	ND	15–25
Color	whitish when young, entirely brown to dark brown when old	whitish when young, brown to dark brown when old	whitish when young, then ocherish-brownish, olive-brown when old	white to off-white when young, yellowish white, pale yellow to brownish orange when old	whitish when young, whitish or becoming yellowish white to grayish orange when old	entirely white to grayish, becoming grayish yellow when old	white to grayish when young, becoming grayish brown to brown when old	off-white to pale ochraceous when young, becoming brown to yellowish brown	grayish-white to pale ochraceous when young, becoming yellowish brown	white to off-white when young, becoming grayish yellow to brownish orange when old
Gleba color at mature	olive-brown to yellowish brown	olive-brown to yellowish brown	olive to olive-brown	olive-brown to yellowish brown	grayish orange to yellowish brown	grayish brown to dark brown	olive-brown to dark brown	yellowish brown	yellowish brown	grayish yellow to olive-brown
Subgleba color at mature	grayish yellow to yellowish	grayish yellow to yellowish	olive to olive-brown	grayish yellow to grayish orange	grayish yellow to grayish orange	grayish yellow to violaceous gray	grayish yellow to yellowish	pale grayish brown	violaceous gray	yellowish gray to grayish yellow

...*Continued on next page*

TABLE 2. (Continued)

Character	Species									
	L. subperlatum sp. nov. (this study)	Korean *L. perlatum* (this study)	European *L. perlatum* (refer to Breitenbach & Kränzlin 1986)	American *L. perlatum* (refer to Bates *et al*. 2009)	*L. marginataum* (refer to Bates *et al*. 2009)	*L. albiperidium* sp. nov. (this study)	*L. ericaeum* (this study)	*L. rupicola* (refer to Jeppson *et al*. 2012)	*L. subumbrinum* (refer to Jeppson *et al*. 2012)	*L. lividum* (refer to Breitenbach & Kränzlin 1986; Bate *et al*. 2009)
Eucapillitial threads	subelastic to elastic	elastic	elastic	elastic	subelastic to elastic	fragile	fragile	subelastic	elastic	fragile
Diameter (µm)	3.5–5.2	3.8–4.8	2.5–7	3.2–5.6	3.2–5.6	3.0–5.4	2.2–3.4	ND	3.0–5.0	4.0–7.2
Thickness	up to 2.5 µm, thick	up to 1.7 µm, thick	thick	up to 1.0 µm, thick	up to 0.8 µm, thick	up to 1.3 µm	up to 1.2 µm, thick	ND	thick (≥1 µm)	up to 0.8 µm, thick
Pores	abundant	occasional	occasional	abundant	abundant	abundant	abundant	abundant	abundant	abundant
Paracapillitial threads										
Diameter (µm)	3.0–4.9	2.4–4.0	ND	ND	ND	3.0–4.2	1.9–2.3	ND	not observed	ND
Thickness	up to 1.0 µm, thin	up to 0.6 µm; thin	ND	thin	ND	thin	thin	ND	not observed	ND
Basidiospores shape	globose to subglobose, smooth to very faintly ornamented	globose to subglobose, faintly ornamented to faintly verrucose	globose, finely verrucose	globose to subglobose, faintly ornamented to faintly verrucose	globose, very faintly ornamented to faintly verrucose	globose to subglobose, faintly ornamented to faintly verrucose	globose to subglobose, faintly ornamented to faintly verrucose	globose, finely verrucose	globose, faintly ornamented to faintly verrucose	globose to subglobose, finely verrucose
Size (µm)	3.4–3.9 × 3.2–3.7	3.9–4.5 × 3.8–4.2	3.5–4.5	4.0–4.8 × 4.0–4.8	4.0–4.8 × 4.0–4.8	3.7–4.2 × 3.6–4.1	4.5–5.0 × 4.2–4.8	4.0–4.5	4.5–5.0	3.5–4.5× 3.5–4.0
Pedicel	up to 0.7 µm long	up to 0.8 µm long	not observed	up to 0.8 µm long	up to 0.8 µm long	up to 1.6 µm long	up to 2.3 µm long	absent	absent	absent or minute
Color in water or KOH	pale yellow	pale yellow to brown	brown	hyaline to yellow	pale yellowish brown	pale yellow	pale yellow to yellow	ND	ND	yellow to brownish yellow

[a], ND: not described

Bayesian analysis using a GTR+I+G model of evolution for 5 million generations was performed on the ITS sequence dataset. BI revealed a set of four chains that reached convergence after about 2 million generations, and therefore the first 20,000 trees in each parallel run were discarded as burn-in; the remaining 60,002 trees (representing 3 million generations) were used to calculate a 50% majority consensus tree and determine PP. The likelihoods (ln L) of the best states for cold chains of the two runs were −4144.66 and −4180.74. MP analysis of the ITS sequence data resulted in four most-parsimonious trees of 577 steps [106 taxa, 597 characters, 135 parsimony-informative characters, consistency index = 0.5130, retention index = 0.8181, homoplasy index = 0.4870] (Fig. 1).

Based on ITS sequence analysis, our 35 specimens (34 Korean specimens and one Chinese specimen) represented nine species (*L. albiperidium*, *L. ericaeum*, *L. excipuliforme*, *L. mammiforme*, *L. nigrescens*, *L. perlatum*, *L. subperlatum*, *Lycoperdon sp*. 1, and *Lycoperdon sp*. 2) (Fig. 1). Among them, the 14 *L. subperlatum* specimens grouped together with strong support (PP/MPBS = 1.0/100). This species was most closely related to American *L. perlatum* (GenBank accession No. AY264919; derived from Kasuya *et al*. 2013), with an ITS sequence identity of *ca*. 97%. However, our specimens were morphologically distinguishable from American *L. perlatum* (le 2). Twelve Korean *L. perlatum* specimens clustered with Chinese (*L. perlatum* HE21023 and KA13-0555), Japanese (*L. perlatum* TNS Kasuya B780), and European *L. perlatum* (*L. perlatum* MJ4684 and *L. perlatum* TENN58040). However, American *L. perlatum* did not belong to this clade, but was instead related to *L. marginatum*. The type locality of *L. perlatum* is Europe (Cunningham 1944) and American *L. perlatum* may be an unrecognized new species or belong to *L. marginatum*. Three specimens, KA12-1179, KA12-1185, and KA13-1471, genetically and macro-morphologically matched *L. mammiforme*, *L. excipuliforme*, and *L. nigrescens*, respectively, although they were immature (morphological comparison using Breitenbach & Kränzlin (1986) and Kasuya & Katumoto (2006)) (Figs. 1, 3). KA12-0505 and KA12-1218 formed an independent clade (Fig. 1).

Among the reported 14 species of *Lycoperdon* in Korea, we confirmed four species based on ITS sequences and morphological study (*L. excipuliforme*, *L. mammiforme*, *L. nigrescens*, and *L. perlatum*). It is still doubtful that the other 10 reported species (*L. caudatum*, *L. colossus*, *L. echinatum*, *L. lividum*, *L. muscorum*, *L. pratense*, *L. pusillum*, *L. pyriforme*, *L. rimulatum*, and *L. umbrinum*) are present in Korea, although ITS sequences of some species (*L. colossus* and *L. rimulatum*) are absent from GenBank. Therefore, further study is necessary to confirm the presence of reported *Lycoperdon* species in Korea based on more taxon sampling and intensive morphological observations.

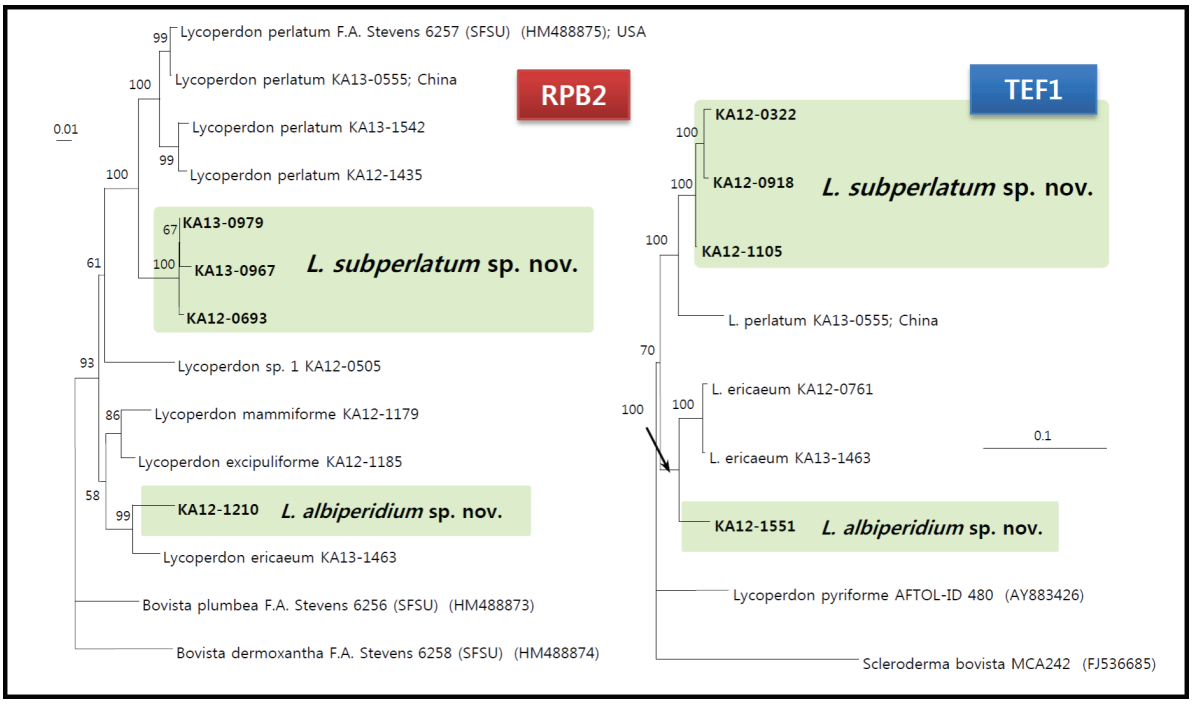

FIGURE 2. RPB2 and EF-1α Neighbor-Joining trees, respectively. Bootstrap values >50% are shown at branches.

Phylogenetic analyses of two new *Lycoperdon* species and *L. ericaeum* based on RPB2 and TEF1 sequences.

Figure 2 was generated by NJ methods calculated with Kimura 2-parameter model (RPB2: 14 taxa, 628 characters; TEF1: 9 taxa, 1146 characters). Due to the failure of amplification of some specimens and lack of reference sequences of RPB2 and TEF1 in GenBank, we simply compared two new *Lycoperdon* species with related species by NJ analyses.

In RPB2 tree, *L. albiperidium* (KA12-1210) and *L. subperlatum* (KA12-0693, KA13-0967 and KA13-0979) formed a group with strong NJBS, respectively (see Fig. 2). These species appear closely related to *L. ericaeum* (KA13-1463) and *L. subperlatum* with sequence identities of *ca*. 96% and *ca*. 94–95%, respectively. In TEF1 tree, *L. albiperidium* (KA12-1551) and *L. subperlatum* (KA12-0322, KA12-0918 and KA12-1105) formed a group with strong NJBS, respectively (see Fig. 2). These species appear closely related to *L. ericaeum* (KA12-0761 and KA13-1463) and *L. subperlatum* with sequence identities of *ca*. 91% and *ca*. 93–94%, respectively (Fig. 2). The results of additional sequence analyses confirm that *L. albiperidium* and *L. subperlatum* species are clearly distinct from those of closely related species (*L. ericaeum* and *L. perlatum*).

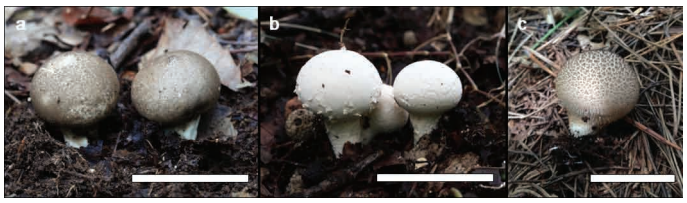

FIGURE 3. Fruiting bodies (immature) of three reported *Lycoperdon* species in Korea. **a.** *Lycoperdon excipuliforme* KA12-1185. **b.** *Lycoperdon mammiforme* KA12-1179. **c.** *Lycoperdon nigrescens* KA13-1471. Scale bars: a–c = 3 cm. Photos by: C.S. Kim & S-.K. Han.

Taxonomy

Lycoperdon albiperidium C.S. Kim, *sp. nov.*, Fig. 4

MycoBank:—MB 814888

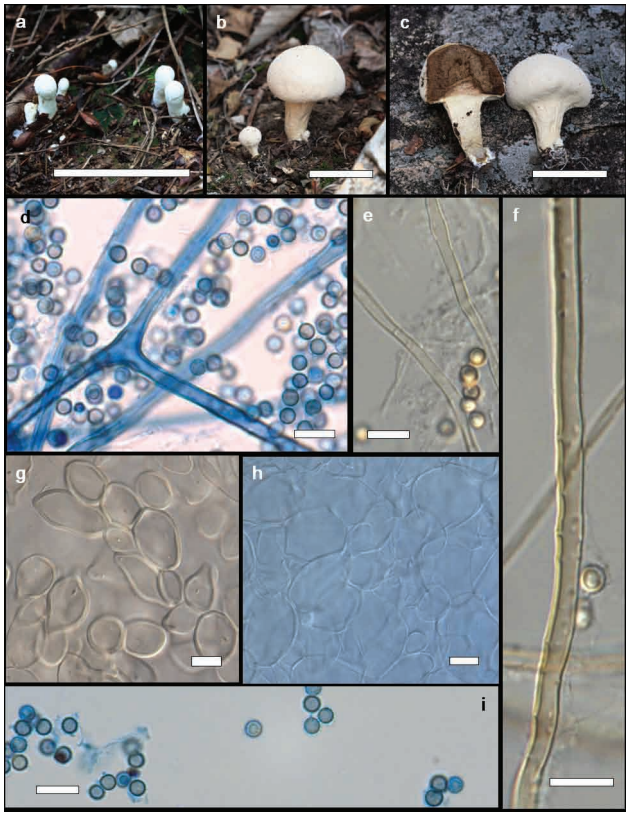

FIGURE 4. Fruiting bodies and microscopic observation of *Lycoperdon albiperidium.* **a**–**c.** Fruiting bodies of KA12-1210 (**a**) and KA12-1551 (**b**, **c**). **d.** Eucapillitial threads (KA12-1551) in CL. **e.** Paracapillitial threads (KA12-1551) in 3% KOH. **f.** Eucapillitial threads (KA12-1551) in 3% KOH. **g.** Exoperidial elements (KA12-1551) in 3% KOH. **h.** Inflated elements in endoperidium (KA12-1551) in 3% KOH. **i.** Basidiospores in CL (KA12-1551). Scale bars: a–c = 3 cm, d–i = 10 µm. Photos by C.S. Kim & S-.K. Han.

Diagnosis:—This species has a well-developed pseudostipe; numerous rhizomorphs attached to substrate; exoperidium verrucae with smallish spines, entirely white to grayish when young, becoming grayish yellow to pale yellow when

old; basidiospores globose to subglobose, very faintly ornamented to faintly verrucose; fragile eucapillitial threads with abundant pores. It is similar to *L. ericaeum* but clearly distinguished by ITS, RPB2, and TEF1 sequences.

Etymology:—Referring to the white (= *album*) peridium before it is fully mature.

Holotype:—KOREA. Chungnam Province, Geumsan-gun, Jewon-myeon, Mt. Jinak, coll. Han *et al*., 25 September 2012 (*KA12-1551*), deposited in KH.

Description:—Basidiomata 20–40 mm diameter, 35–60 mm high, pyriform to turbinate, pseudostipitate well-developed, occasionally plicate at pseudostipe, numerous rhizomorphs attached to substrate. Exoperidium verrucae with smallish spines (less than 0.5 mm), entirely white to grayish when young, becoming grayish yellow to pale yellow when old. Endoperidium yellowish brown to brown, papery. Gleba grayish brown to dark brown at maturity, pulverulent. Subgleba grayish yellow to violaceous gray. Solitary to gregarious.

Basidiospores 3.7–4.2 × 3.6–4.1 μm, length/width ratio 1.0–1.1 (n = 30), globose to subglobose, very faintly ornamented to faintly verrucose (A–B in the sense of Demoulin 1972a, b), short pedicel present (<1.6 μm long), pale yellow in 3% KOH. Basidia not observed. Capillitium of *Lycoperdon*-type; eucapillitial threads 3.0–5.4 μm diam., thick-walled (up to 1.3 μm), fragile to subelastic, aseptate, straight to subundulate, occasional dichotomous branching, abundant pores present, yellow to pale brownish in 3% KOH; paracapillitial threads present, 3.0–4.2 μm diam., thin-walled, straight to subundulate, septate, hyaline in 3% KOH. Exoperidium composed of sphaerocysts, 16–27 μm diam., thick-walled (up to 2.6 μm thick), hyaline to pale yellow in 3% KOH. Endoperidium composed of tightly interwoven hyphal elements, containing inflated elements resembling sphaerocysts with reticulate patterns, thin-walled (up to 1.0 μm thick), hyaline in 3% KOH.

Habitat.—On rich humus and mixed conifer-hardwood forests.

Other specimen examined:—KOREA. Chungnam Province, Geumsan-gun, Chubu-myeon, Mt. Seodae, coll. Han *et al.*, 29 August 2012 (*KA12-1210*), deposited in KH.

Comments:—Specimens of this species were reported as *L. spadiceum* Pers. (now *L. lividum* Pers.) by some amateur mycologists in Korea (Park & Lee 2011; The Korean Society of Mycology 2013). However, their reported specimens substantially differed from the descriptions of *L. lividum* by several mycologists (Table 2; Breitenbach & Kranzlin 1986; Bates 2004; Bates *et al*. 2009; Cortez *et al*. 2013). *Lycoperdon lividum* is characterized by small basidiomata (*ca*. 10–30 mm; subpyriform to obpyriform); a furfuraceous exoperidium often appearing as mealy squamules; and a scanty sterile base. However, *Lycoperdon albiperidium* is bigger than *L. lividum*, and has a well-developed plicate pseudostipe. In addition, they are clearly distinguished by ITS sequences (Fig. 1). Phylogenetically, *L. albiperidium* is closely related to *L. ericaeum*, but they are morphologically distinguishable, especially by the basidiocarp shape, eucapillitial thread diameter, and size of basidiospores (Table 2). In addition, the records of *L. ericaeum* are from dry grasslands on acidic soil, but *L. albiperidium* is collected from on rich humus and mixed conifer-hardwood forests.

Lycoperdon ericaeum Bonord., Bot. Ztg. 15: 596 (1857), Fig. 5

Description:—Basidiomata 15–30 mm diam., 25–30 mm high, subglobose to obpyriform, rhizomorphs attached to substrate. Exoperidium echinate or verrucae with smallish spines (less than 1 mm tall); whitish when young, becoming grayish brown to brown when old. Endoperidium pale yellow to grayish yellow, papery. Gleba yellowish to olive-brown at maturity, pulverulent. Subgleba grayish yellow to yellowish. Solitary to gregarious.

Basidiospores 4.5–5.0 × 4.2–4.8 μm, length/width ratio 1.0–1.1 (n = 30), globose to subglobose, very faintly ornamented to faintly verrucose (A–B in the sense of Demoulin 1972a, b), sometimes slightly long pedicel present (<2.3 μm long), pale yellow to yellow in 3% KOH. Basidia 9.3–11.8 × 6.7–7.9 μm, length/width ratio 1.3–1.6 (n = 12), clavate, without basal clamp; usually two sterigmata, 7–17 μm long. Capillitium of *Lycoperdon*-type; eucapillitial threads 2.2–3.4 μm diam., thick-walled (up to 1.2 μm), fragile to subelastic, aseptate, straight, occasional dichotomous branching, irregular pores frequently present, yellow to pale brownish in 3% KOH; paracapillitial threads present, 1.9–2.3 μm diam., thin-walled, straight to subundulate, septate, hyaline in 3% KOH. Exoperidium composed of sphaerocysts, 18–26 μm diam., thick-walled (up to 3.0 μm thick), hyaline in 3% KOH. Endoperidium composed of tightly interwoven hyphal elements, occasionally inflated elements resembling sphaerocysts, thin-walled, hyaline in 3% KOH.

Habitat:—on slightly grassed terrain or needle debris.

Examined specimen:—KOREA. Chungnam Province, Geumsan-gun, Mt. Jinak, coll. Han *et al*., 18 July 2012 (*KA12-0761*), deposited in KH; Gyeongnam Province, Hamyang-gun, Mt. Gibaek, coll. Han *et al*., 16 October 2013 (*KA13-1463*), deposited in KH.

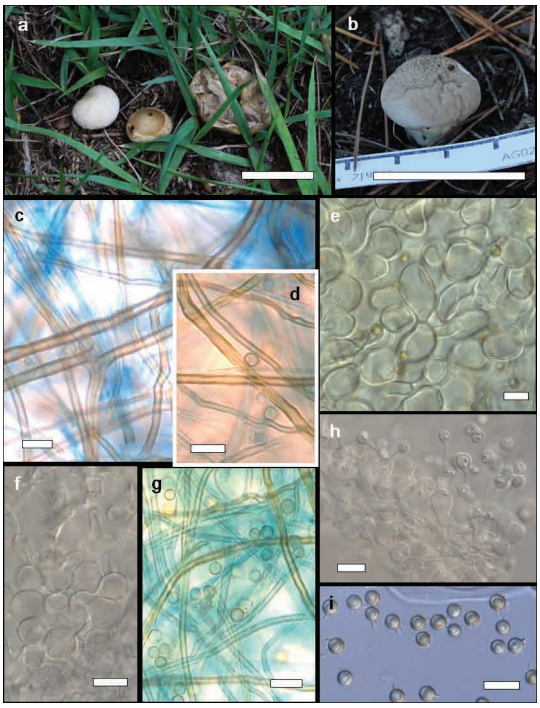

FIGURE 5. Fruiting bodies and microscopic observation of *Lycoperdon ericaeum*. **a**, **b.** Fruiting bodies (**a**. KA12-0761; **b**. KA13-1463). **c, d.** Eucapillitial threads (KA12-0761) in CL. **e.** Exoperidial elements (KA12-0761) in 3% KOH. **f.** Inflated elements in endoperidium (KA13-1463) in 3% KOH. **g.** Eucapillitial threads and paracapillitial threads (KA12-0761) in CL. **h.** Basidia and basidiosproes (KA13-1463) in 3% KOH. **i.** Basidiospores (KA12-0761) in 3% KOH. Scale bars: a,b = 3 cm, c–i = 10 μm. Photos by: C.S. Kim & S-.K. Han.

Comments:—Two Korean *Lycoperdon* specimens (KA12-0761 and KA13-1463) clustered with Japanese and Swedish *L. ericaeum* ITS sequences (Fig. 1) and were almost identical morphologically (Jeppson *et al*., 2012; Kasuya *et al*., 2013). Phylogenetically, *L. ericaeum* is related to *L. rupicola* Jeppson, E. Larss. & M.P. Martín and *L. subumbrinum* Jeppson & E. Larss., but is distinguishable by the presence of fragile eucapillitial threads (Table 2).

Lycoperdon perlatum Pers. Observ. Mycol. (Lipsiae) 1: 4 (1796), Fig. 6

Description:—Basidiomata 25–35 mm diam., 25–40 mm high, subglobose, pyriform to turbinate, umbonate, pseudostipe usually well developed, numerous rhizomorphs attached to substrate. Exoperidium echinate, spines deciduous with age; whitish when young, brown to dark brown when old, especially at the umbo; surface reticulate after fall of the spines. Endoperidium yellowish brown, papery, covered with reticulate pattern. Gleba olive brown to yellowish brown at maturity, pulverulent. Subgleba grayish yellow to yellowish. Solitary to gregarious.

Basidiospores 4.1–4.7 × 3.8–4.5 μm, length/width ratio 1.0–1.1 (n = 30), globose to subglobose, faintly ornamented to verrucose (B–C in the sense of Demoulin 1972a, b), short pedicel present (<0.8 μm long), pale yellow to brown in 3% KOH. Basidia not observed. Capillitium of *Lycoperdon*-type; eucapillitial threads 3.8–4.8 μm diameter, thick-walled (up to 1.7 μm), elastic, aseptate, straight to subundulate, occasional dichotomous branching, occasionally irregular pores present, yellow to pale brownish in 3% KOH; paracapillitial threads present, 2.4–4.0 μm diam., thin-walled (up to 0.6 μm thick), hyaline in 3% KOH, straight to subundulate, septate. Exoperidium composed of sphaerocysts or cylindrical shaped cells, sometimes irregularly shaped cells, 18–48 μm diam., thick-walled (up to 3.0 μm thick), hyaline to yellowish in 3% KOH. Endoperidium composed of tightly interwoven hyphal elements, containing inflated elements resembling sphaerocysts with reticulate patterns, hyaline in 3% KOH.

Habitat:—On rich humus and needle litter in conifer or mixed conifer-hardwood forests.

Examined specimen:—CHINA. Xinjiang Prov., Changji, Fu Kang-shi, Mt. Tianshan, Heaven Pool Scenic Area, coll. Han *et al*., 15 July 2013 (*KA13-0555*), deposited in KH; KOREA. Gangwon Province, Gangneung-si, Daegwanryeong Natural Recreation Forest, coll. Han *et al*., 09 June 2012 (*KA12-0186*), deposited in KH; Gyeonggi Province, Pocheon-si, Gwangneung Forest, coll. Han *et al*., 26 July 2012 (*KA12-0871*), 12 September 2012 (KA12-1435), 25 July 2013 (*KA13-0608*), 26 Jul. 2013 (*KA13-0619*, *KA13-0646*), 16 September 2013 (*KA13-1188*, *KA13-*

1148), 30 September 2013 (*KA13-1270*), 14 October 2013 (*KA13-1542*), Yangpyeong-gun, Saneum Natural Recreation Forest, coll. Han *et al*., 19 September 2012 (*KA12-1506*), deposited in KH.

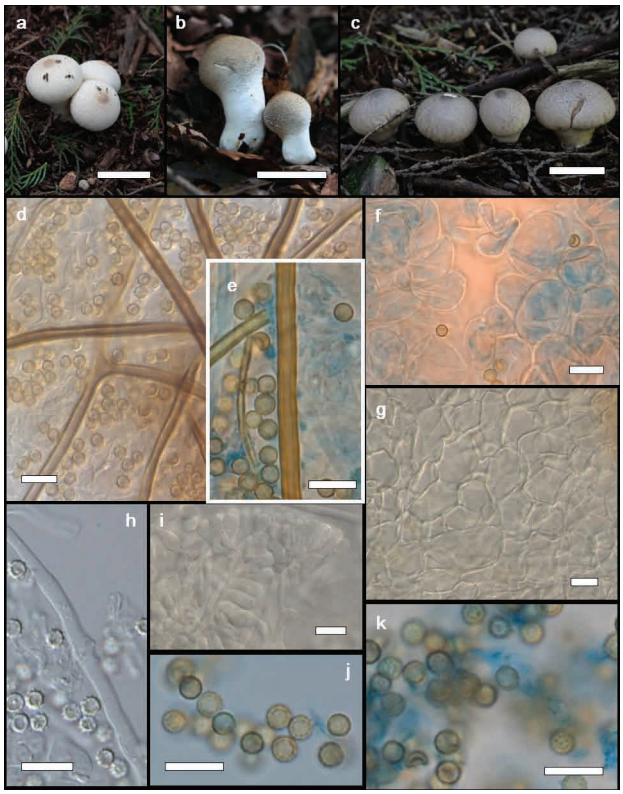

FIGURE 6. Fruiting bodies and microscopic observation of *Lycoperdon perlatum*. **a**–**c.** Fruiting bodies (**a**. KA12-1435; **b**. KA12-1506; **c**. KA13-1148). **d.** Eucapillitial threads of KA13-1270 in 3% KOH. **e.** Eucapillitial threads of KA13-1148 in CL. **f.** Exoperidial elements (KA12-1270) in CL. **g.** Inflated elements in endoperidium (KA13-1148) in 3% KOH. **h.** Paracapillitial threads (KA13-1148) in 3% KOH. **i.** Basidioles (KA12-1506) in 3% KOH. **j**, **k.** Basidiospores in CL (**j**. KA13-1270; **k**. KA13-1148). Scale bars: a–c = 3 cm, d, e, g–j = 10 μm, f = 20 μm. Photos by: C.S. Kim & S-.K. Han.

Comments:—This species is the type species of *Lycoperdon* and a well-known cosmopolitan species (Sarasini 2005; Bates *et al*. 2009). Generally, *L. perlatum* is characterized by the conical spines of the exoperidum, reticulate endoperidum, pyriform substipitate basidiomata, and echinulate basidiospores (Breitenbach & Kränzlin 1986; Bastes *et al*. 2009). However, previously reported descriptions of this species are highly variable in characteristics, such as distinct color tone and ornamentation of the exoperidium, basidiomata size, and subgleba and sterile base shape and extension. Therefore, Cortez *et al*. (2013) suggested that future phylogenetic studies would reveal a complex of morphologically closely related taxa worldwide. Our phylogenetic study showed that Korean, Japanese, Chinese, and European *L. perlatum* grouped with strong support values (PP/MPBS = 1.0/100), but American *L. perlatum* did not cluster with this group and was related to the *L. marginatum* clade (Fig. 1). Morphological comparison between Korean, European (maybe belong to true *L. perlatum*), and American *L. perlatum* (maybe a different species of *Lycopderdon*) revealed almost identical microscopic characteristics, just slightly different in the size of the basidiospores (Table 2) and clearly distinguished ITS sequences (Fig. 1). According to Demoulin (1972a), Larsson & Jeppson (2008) and Bates *et al*. (2009), *L. perlatum* is related to *L. nigrescens*—they have a reticulate endoperidum in common. However, they are clearly distinguished by ITS sequences and ornamentation of basidiospores (see Demoulin 1972a).

Lycoperdon subperlatum C.S. Kim & S.-K. Han, *sp. nov*., Fig. 7
MycoBank:—MB 814889

Diagnosis:—Macroscopically this species resembles *L. perlatum* but they can be distinguished microscopically as *L. subperlatum* has elastic to subelastic eucapillitial threads with abundant pores; basidiospores globose to subglobose, smooth to very faintly ornamented, and smaller than those of *L.perlatum*. The two species are clearly distinguished by ITS, RPB2 and TEF1 sequences.

Etymology:—Refers to the morphological features which are similar to those of *Lycoperdon perlatum*.

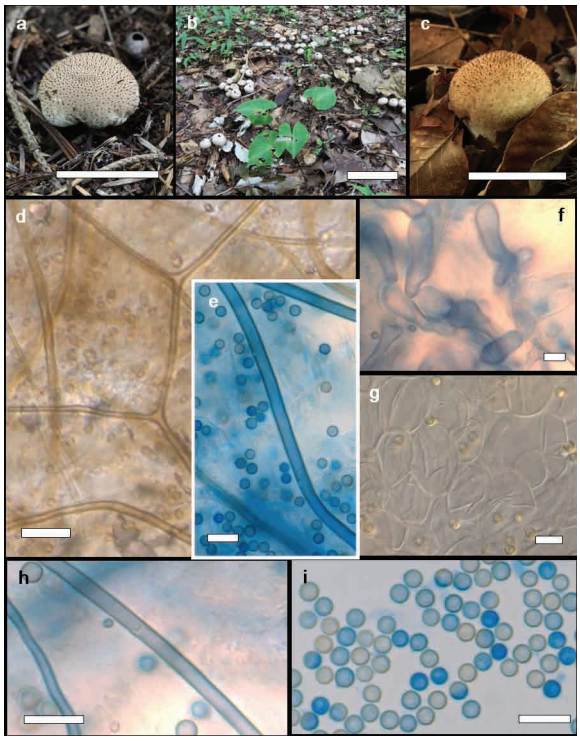

FIGURE 7. Fruiting bodies and microscopic observation of *Lycoperdon subperlatum sp. nov*. **a–c.** Fruiting bodies (**a.** KA12-0918; **b.** KA12-1427; **c.** KA13-0979). **d.** Eucapillitial threads of KA12-0918 in 3% KOH. **e.** Eucapillitial threads of KA12-0918 in CL. **f.** Exoperidial elements (KA12-0918) in CL. **g.** Inflated elements in endoperidium (KA12-0918) in 3% KOH. **h.** Paracapillitial threads of KA12-0918 in CL. **i.** Basidiospores of KA12-0918 in CL. Scale bars: a–c = 3 cm, d, f = 20 µm, e, g–i = 10 µm. Photos by: C.S. Kim & S-.K. Han.

Holotype:—KOREA. Gyeonggi Province, Pocheon-si, Gwangneung Forest, coll. Han *et al*., 27 July 2012 (*KA12-0918*), deposited in KH.

Description:—Basidiomata 20–45 mm diam., 25–60 mm high, subglobose, pyriform to turbinate, slightly or not umbonate, pseudostipe usually well-developed, numerous rhizomorphs attached to substrate. Exoperidium echinate, the spines are deciduous with age; whitish when young, entirely brown to dark brown when old; surface reticulate after fall of the spines. Endoperidium yellowish brown, papery. Gleba olive brown to yellowish brown at maturity, pulverulent. Subgleba grayish yellow to yellowish. Solitary to gregarious.

Basidiospores 3.4–3.9 × 3.2–3.7 µm, length/width ratio 1.0–1.1 (n = 30), globose to subglobose, smooth to very faintly ornamented (A in the sense of Demoulin 1972a, b), short pedicel present (<0.7 µm long), pale yellow in 3% KOH. Basidia not observed; basidioles 8.6–12.0 × 5.6–7.3 µm, length/width ratio 1.4–1.8 (n = 10), clavate, without basal clamp. Capillitium of *Lycoperdon*-type; eucapillitial threads 3.5–5.2 µm diam., thick-walled (up to 2.5 µm thick), elastic to subelastic, aseptate, straight to subundulate, occasional dichotomous branching, abundantly irregular pores present, pale yellow to brownish in 3% KOH; paracapillitial threads present, 3.0–4.9 µm diam., thin-walled (up to 1.0 µm thick), hyaline in 3% KOH, straight to subundulate, septate. Exoperidium composed of sphaerocysts, 7–28 µm diam., thick-walled (up to 1.5 µm thick), subhyaline to yellowish brown in 3% KOH. Endoperidium composed of tightly interwoven hyphal elements, containing inflated elements resembling sphaerocysts, hyaline in 3% KOH.

Habitat:—On rich humus and mixed conifer-hardwood forests.

Other specimens examined:—KOREA. Chungbuk Province, Yeongdong-gun, Mt. Minjuji, coll. Han *et al*. 16 July 2012 (*KA12-0627*), deposited in KH; Chungnam Province, Geumsan-gun, Mt. Jinak, coll. Han *et al*., 20 June 2012 (*KA12-0281*), 17 July 2012 (*KA12-0693*), Mt. Seodae, coll. Han *et al*., 22 June 2012 (*KA12-0322*), deposited in KH; Jeonbuk Province, Gunsan-si, Daejang Island, coll. Han *et al*., 09 July 2012 (*KA12-0494*), Seonyu Island, coll. Han *et al*., 11 July 2012 (*KA12-0533*), deposited in KH; Gyeonggi Province, Pocheon-si, Gwangneung Forest, coll. Han *et al*., 13 July 2012 (*KA12-0594*), 24 August 2012 (*KA12-1105*), 12 September 2012 (*KA12-1427*), 08 August 2013 (*KA13-0692*), deposited in KH; Gyeongnam Province, Geoje-si, Mt. Daebong, coll. Han *et al*., 09 September 2013 (*KA13-0967*), Hamyang-gun, Mt. Gibaek, coll. Han *et al*., 19 June 2013 (*KA13-0209*), 10 September 2013 (*KA13-0979*), deposited in KH.

Comments:—The macrocharacters of this species are almost identical to those of Korean, European *L. perlatum*

and American *L. perlatum*. However, they can be distinguished by microscopic characteristics including eucapillitial threads and basidiospore shape and sizes; *L. subperlatum* have elastic to subelastic eucapillitial threads with abundant pores; the basidiospores are smooth to very faintly ornamented, the size of basidiospores is smaller than related species (Table 2). In addition, this species is clearly distinct from Korean, European, and American *L. perlatum* in the ITS, RPB2 and TEF1 trees (Figs. 1, 2).

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