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RESEARCH ARTICLE

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Taxonomic Study of the Genus *Pholiota* (Strophariaceae, Basidiomycota) in Korea

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ABSTRACT

The genus *Pholiota* (Strophariaceae, Basidiomycota) is made up of wood-rotting saprotrophic mushrooms characterized by a yellow or brown pileus with scales and/or slimy, and by a brownish smooth spore with a germ pore. However, these features are not enough to distinguish its species, or separate the genus *Pholiota* from other brown-spored wood-rotting genera such as *Hypholoma* and *Stropharia*. Although internal transcribed spacer (ITS) sequence-based identification has improved identification accuracy for species of *Pholiota*, most *Pholiota* species in Korea are reported based on morphological features. To evaluate the taxonomy of *Pholiota* species, we investigated 62 specimens collected from 1999 to 2019 in Korea using ITS sequence analysis and morphological observation. Twelve of the 16 recorded *Pholiota* species in Korea were identified. While eight species were clearly separated, the ITS analysis did not distinguish three in the *Pholiota adiposa* complex. Therefore, further investigation is required to distinguish these three species. ITS sequences deposited in GenBank confirm that *P. highlandensis* exists in Korea. The presence of the other four *Pholiota* species could not be confirmed through specimens or sequence information in GenBank. A taxonomic key and the ITS sequence data for Korean *Pholiota* species are included and can be good baselines for further research on *Pholiota* taxonomy and diversity.

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1. Introduction

The genus *Pholiota* Kummer (1871) is composed of saprotrophic flesh mushrooms in the family Strophariaceae [1]. *Pholiota* is characterized by a yellow or brown pileus with scales, brownish smooth surface spore, and brown spore print [2,3]. *Pholiota squarrosa* is designated as a type species [2]. According to the current overview of Basidiomycota [4], approximately 157 species are recorded in this genus. *Pholiota* species are commonly found in temperate climate regions and they perform important roles in the ecosystem as wood decomposers and soil saprotrophs [2,3].

Pholiota species produce a variety of bioactive compounds that can have antitumor and antioxidant effects [5,6]. Activity and application of lignocellulase from *P. adiposa* have been reported in several studies [7,8]. Some *Pholiota* species are edible—e.g. *P. microspora* is well-known for its culinary usage in Asian countries [2,9], whereas *P. squarrosa* is poisonous [10].

The presence or absence of pleurocystidia and cheilocystidia, cystidial incrustation, wall thickness, and coloration have been used as key characteristics to distinguish between *Pholiota* species [2,3]. However, morphological characters are not enough to distinguish the species because macro-morphological characteristics of *Pholiota* species are variable depending on the environmental conditions, and micro-morphological characteristics are often very similar between species. For example, a gelatinous layer can be detected from the fruiting body only during the fresh state, and some species show the gelatinous characteristic only when mature, so it is difficult to identify them when they are collected as immature basidiocarps. Moreover, morphological characteristics can be diverse, even within the same species [2,3]. As such, it is important to proceed with further identification using molecular analysis, which has become an increasingly important tool for accurately identifying fungal species [11,12]. We recently discovered many new fungal species and

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amended misidentified species by reevaluating the other genera using molecular analysis [13–19].

Phylogenetic studies have placed *Pholiota* species within the family Strophariaceae, but they form a paraphyletic clade with *Hypholoma* and *Stropharia* species [20–23]. Recent phylogenetic analysis based on the internal transcribed spacer (ITS) sequence has improved the accuracy at which *Pholiota* species are identified and has led to the recognition of new *Pholiota* species [24–27].

Eighteen species of *Pholiota* have been reported in Korea over the years, but only 16 of these are currently accepted [28–30]. Since *P. adiposa* and *P. squarrosa* were first reported in Korea in 1940 [31], 13 additional *Pholiota* species were reported based on morphology by 2011. Through molecular analysis, *P. alnicola* was transferred to genus *Flammula* in Hymenogastraceae [32], and its name changed to *Flammula alnicola* (Fr.) P. Kumm. [33]. Recently, *P. abietis*, *P. multicingulata*, and *P. limonella* were additionally reported by phylogenic analysis using ITS sequence [29,30,34]. Later, *P. abietis* was confirmed to be synonymous with *P. limonella* [35]. Most *Pholiota* species were mainly identified based on the features of their basidiocarp, so it is necessary to re-evaluate *Pholiota* based on molecular analysis. In this study, we investigate the species diversity of *Pholiota* in Korea based on ITS sequence analysis and morphology.

2. Material and methods

2.1. Sample collection and observation

A total of 62 *Pholiota* specimens were obtained from three herbaria in South Korea: 12 from the National Institute of Biological Resources (NIBR), 28 from the Korea National Arboretum (KA), and 22 from the Seoul National University Fungal Collections (SFC). All samples were collected from 1999 to 2019 in South Korea (Table 1) and were stored dried. Pictures of the fresh fruiting bodies and information on the collection location and date were available, but there was often no accurate ecological data. To observe the microscopic features, the specimens were mounted in 5% (w/v) KOH and 5% (w/v) Congo red solution, and then were observed using an Eclipse 80i light microscope (Nikon, Tokyo, Japan). At least 30 basidiospores, 10 basidia, 10 cheilocystidia, and 10 pleurocystidia were measured per specimen.

2.2. DNA extraction, PCR amplification, and sequencing

Genomic DNA was extracted from the fruiting bodies using a modified cetyltrimethylammonium bromide (CTAB) extraction protocol [36]. The ITS region was amplified using primers (ITS1F/ITS4B) that target the ITS region [37]. PCR amplifications were performed on a thermal cycler (C1000TM; Bio-Rad, Richmond, CA) using the AccuPower PCR premix (Bioneer Co., Daejeon, Korea). The PCR conditions were 95 °C for 5 min; followed by 35 cycles of 95 °C for 40 sec, 55 °C for 40 sec, and 72 °C for 1 min; and finally 72 °C for 5 min. PCR products were loaded on to a 1% agarose gel and purified using the ExpinTM PCR Purification Kit (GeneAll Biotechnology, Seoul, Korea). Samples were sequenced by Sanger sequencing using the aforementioned primers at Macrogen (Seoul, Korea) using an ABI PRISM 3730XL Analyzer (Applied Biosystems, Foster City, CA).

2.3. Phylogenetic analyses

ITS sequences of each sample were proofread using MEGA7 [38] and deposited in GenBank (accession numbers in Table 1). Sequences were aligned using the Multiple Alignment Fast Fourier Transform (MAFFT ver. 7) [39] with ITS sequences of *Pholiota* obtained from GenBank and UNITE. The alignments were checked manually, and upon verification, ambiguous alignments were adjusted. A Neighbor Joining (NJ) Tree was constructed also using MEGA7 with 1000 bootstraps [38]. *Agrocybe* species were selected as outgroups, in accordance with previous studies [22,23].

3. Results

A total of 62 specimens were divided into nine groups based on the ITS analysis. Each group included 1–23 specimens (Table 1). Representative sequences from each group were selected, and phylogenetic analysis was performed together with ITS sequences downloaded from GenBank and UNITE. The nine groups were (Figure 1): *Pholiota adiposa* complex (number of specimens = 23), *P. astragalina* ($n = 1$), *P. lenta* ($n = 2$), *P. lubrica* ($n = 8$), *P. microspora* ($n = 2$), *P. multicingulata* ($n = 11$), *P. squarrosa* ($n = 6$), *P. squarrosoides* ($n = 1$), and *P. terrestris* ($n = 8$). The *P. adiposa* complex includes morphologically similar species: *P. adiposa*, *P. aurivella*, and *P. limonella*. Although *P. highlandensis* was not present in our analysis, the ITS sequence of *P. carbonaria* (accession number: AY251301) deposited from Korea is identical to that of *P. highlandensis*.

Pictures of each species are shown in Figure 2. Basidiospores, basidia, and cystidia were well observed from the dried specimens, and their size and shape were in good agreement with previous

Table 1. Summary and GenBank accession numbers for *Pholiota* specimens used in this study.

Species	Specimen code	Collection Date	Locality	GenBank Acc. No.
P. adiposa complex	Juk15004	2015-04-08	Jeju-si, Jeju-do	MT879417
(*P. adiposa,*	KA13-1545	2013-10-14	Pocheon-si, Gyeonggi-do	MT879423
P. aurivella,	KA14-1611	2014-10-01	Pocheon-si, Gyeonggi-do	MT879427
P. limonella)	KA14-1644	2014-10-02	Pocheon-si, Gyeonggi-do	MT879428
	KA15-0760	2015-09-23	Gangneung-si, Gangwon-do	MT879432
	KA15-0803	2015-10-07	Pocheon-si, Gyeonggi-do	MT626084
	NIBRFG0000122518	2012-09-14	Paju-si Gyeonggi-do	MT879441
	NIBRFG0000125102	2012-10-19	Pyeongchang-gun, Gangwon-do	MT626090
	NIBRFG0000131093	2013-09-21	Jeju-si, Jeju-do	MT626091
	SFC20161006-18	2016-10-06	Pyeongchang-gun, Gangwon-do	MT879445
	KA14-0316	2014-06-25	Suncheon-si, Jeollanam-do	MT879425
	NIBRFG0000133530	1999-06-26	Guri-si, Gyeonggi-do	MT879442
	SFC20120926-31	2012-09-26	Gongju-si, Chungcheongnam-do	MT879443
	SFC20121009-35	2012-10-09	Boryeong-si, Chungcheongnam-do	KJ609166
	SFC20130730-74	2013-07-30	Guri-si, Gyeonggi-do	KX773881
	SFC20150707-19	2015-07-07	Guri-si, Gyeonggi-do	KX773882
	SFC20160923-37	2016-09-23	Jongno-gu, Seoul	MT879444
	SFC20180913-39	2018-09-13	Gwanak-gu, Seoul	MT879451
	SFC20181015-01	2018-10-15	Gwanak-gu, Seoul	MT879452
	KA13-0179	2013-06-18	Pocheon-si, Gyeonggi-do	MT879418
	KA17-1051	2017-09-25	Gumi-si, Gyeongsangbuk-do	MT879437
	SFC20171018-08	2017-10-18	Chuncheon-si, Gangwon-do	MT879446
	SFC20171019-15	2017-10-19	Hongcheon-gun, Gangwon-do	MT879447
P. astragalina	SFC20190919-76	2019-09-19	Taebaek-si, Gangwon-do	MT626095
P. lenta	KA15-0772	2015-09-24	Taebaek-si, Gangwon-do	MT626083
	NIBRFG0000139774	2014-09-11	Pyeongchang-gun, Gangwon-do	MT626092
P. lubrica	KA13-1241	2013-09-26	Ulleung-gun, Gyeongsangbuk-do	MT879419
	KA13-1518	2013-10-22	Pyeongchang-gun, Gangwon-do	MT879421
	KA15-0688	2015-09-21	Goseong-gun, Gangwon-do	MT626082
	KA15-0717	2015-09-22	Gangneung-si, Gangwon-do	MT879431
	KA16-1123	2016-09-27	Mt. Hallasan, Jeju-do	MT879435
	NIBRFG0000113909	2009-08-15	Inje-gun, Gangwon-do	MT626088
	SFC20111015-10	2011-10-15	Hoengseong-gun, Gangwon-do	KX773883
	SFC20181013-10	2018-10-13	Inje-gun, Gangwon-do	MT626094
P. microspora	NIBRFG0000103779	2007-08-03	Hoengseong-gun, Gangwon-do	MT626085
	NIBRFG0000103780	2007-08-09	Gongju-si, Chungcheongnam-do	MT626086
P. multicingulata	KA14-0784	2014-08-11	Pocheon-si, Gyeonggi-do	MT626080
	KA14-1356	2014-08-29	Pocheon-si, Gyeonggi-do	MT879426
	KA16-1161	2016-09-29	Mt. Hallasan, Jeju-do	MT879436
	NIBRFG0000103801	2007-09-29	Guri-si, Gyeonggi-do	MT879439
	NIBRFG0000104704	2008-07-25	Ganghwa-gun, Incheon	MT879440
	NIBRFG0000104828	2008-08-09	Wonju-si, Gangwon-do	MT626087
	SFC20140826-06	2014-08-26	Wanju-Gun, Jeollabuk-do	KX773884
	SFC20140826-12	2014-08-26	Wanju-Gun, Jeollabuk-do	KX773885
	SFC20180905-55	2018-09-05	Gwanak-gu, Seoul	MT879448
	SFC20180907-126	2018-09-07	Hapcheon-gun, Gyeongsangnam-do	MT879449
	SFC20180907-142	2018-09-07	Hapcheon-gun, Gyeongsangnam-do	MT879450
P. squarrosa	KA13-1508	2013-10-22	Pyeongchang-gun, Gangwon-do	MT626079
	KA13-1509	2013-10-22	Pyeongchang-gun, Gangwon-do	MT879420
	KA13-1523	2013-10-22	Pyeongchang-gun, Gangwon-do	MT879422
	KA15-0709	2015-09-22	Gangneung-si, Gangwon-do	MT879430
	NIBRFG0000121601	2012-05-18	Pyeongchang-gun, Gangwon-do	MT626089
	SFC20140912-I01	2014-09-12	Inje-gun, Gangwon-do	KX773886
P. squarrosoides	SFC20120814-45	2012-08-14	Ulleung-gun, Gyeongsangbuk-do	KX773887
P. terrestris	KA13-1546	2013-10-14	Pocheon-si, Gyeonggi-do	MT879424
	KA15-0175	2015-07-16	Taebaek-si, Gangwon-do	MT626081
	KA15-0434	2015-08-20	Taebaek-si, Gangwon-do	MT879429
	KA16-0063	2016-05-18	Pocheon-si, Gyeonggi-do	MT879433
	KA16-0067	2016-05-18	Pocheon-si, Gyeonggi-do	MT879434
	KA18-1107	2018-10-15	Pocheon-si, Gyeonggi-do	MT879438
	SFC20151120-02	2015-11-20	—	KX773888
	SFC20160908-09	2016-09-08	Guri-si, Gyeonggi-do	MT626093

reports. Basidiospores were generally elliptical, thick walled with an apical pore, and ranged from 4–9 µm long and 2–6 µm wide. Basidia were clavate in shape and 12–33 µm long. Types of cystidia observed were cheilocystidia, pleurocystidia, and caulocystidia. Cheilocystidia and pleurocystidia were observed in all species except *P. microspora*. Caulocystidia was only observed in *P. squarrosoides* and *P. terrestris* in our specimens. Chrysocystidia were detected in the species of the *P. adiposa* complex, *P. squarrosa*, *P. squarrosoides*, and *P. terrestris*. The microscopic features of the type species *P. squarrosa* are shown in Figure 3.

4. Taxonomic key for Korean *Pholiota*

1. Pileus cuticle lacking any gelatinous layers (surface granulose to fibrillose or scaly, or rarely canescent, glabrous, and hygrophanous) .... *P. squarrosa*

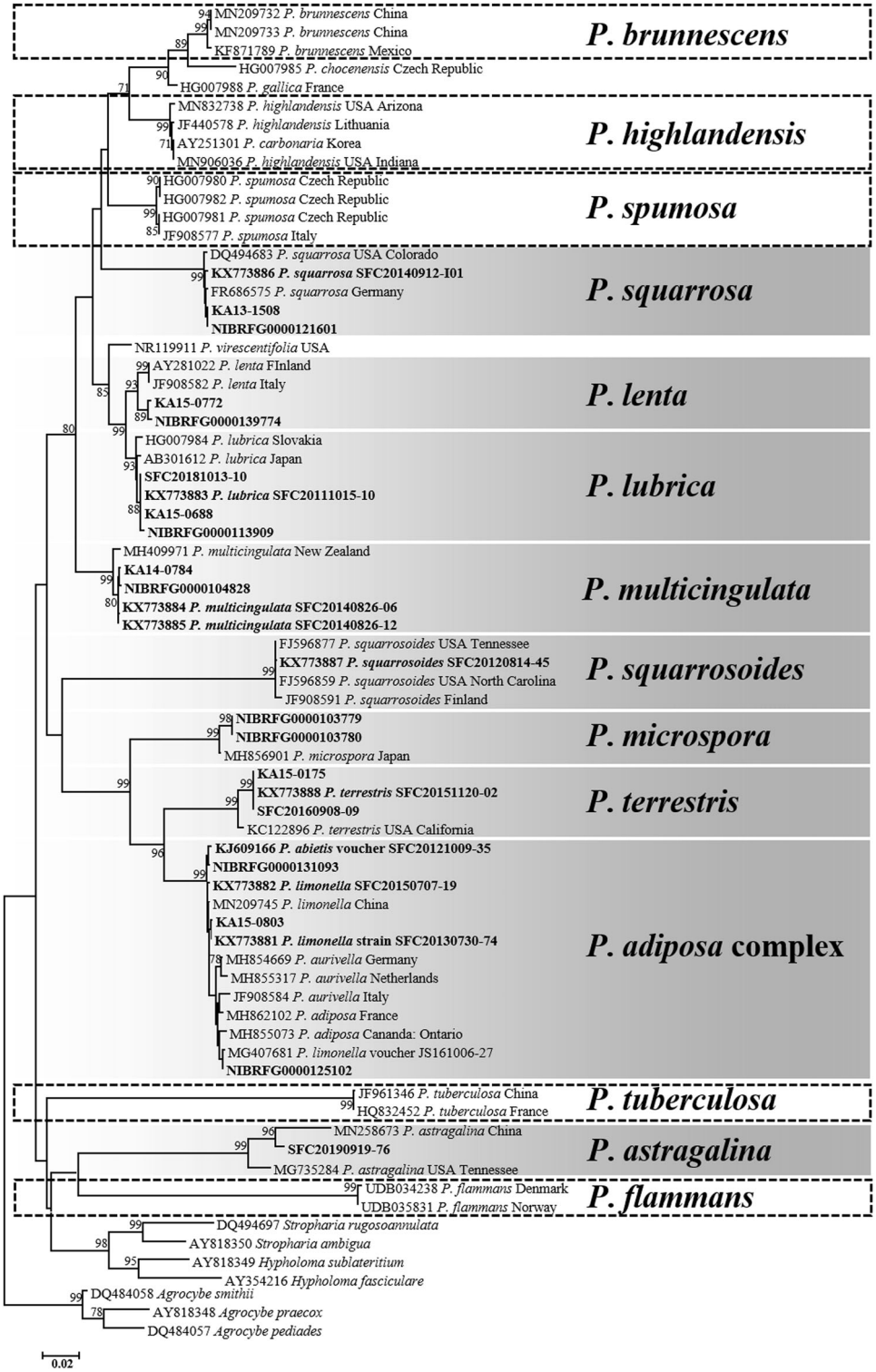

Figure 1. Phylogenetic trees based on neighbor-joining (NJ) analysis of the ITS region in *Pholiota* species. Bootstrap support values (1000 replicates) >70% are presented. The recorded Korean *Pholiota* species are placed in boxes. The shaded boxes represent confirmed species and the dotted boxes represent unidentified species in Korea. The scale bar indicates the number of nucleotide substitutions per site.

1. Pileus cuticle with a layer of gelatinized hyphae in some part (surface may be glabrous to scaly) 2
2. Pileus typically distinctly scaly at the time the veil breaks; chrysocystidia or somewhat similar structures present in hymenium 3
2. Pileus fibrillose, scaly or granulose, lacking chrysocystidia in hymenium 7
3. Gelatinous subcutis evident only with maturity; pileus surface initially densely covered with dry squamules 4
3. Gelatinous subcutis evident throughout development; pileus surface initially viscid and glabrous or more sparsely covered with squamules than above 5

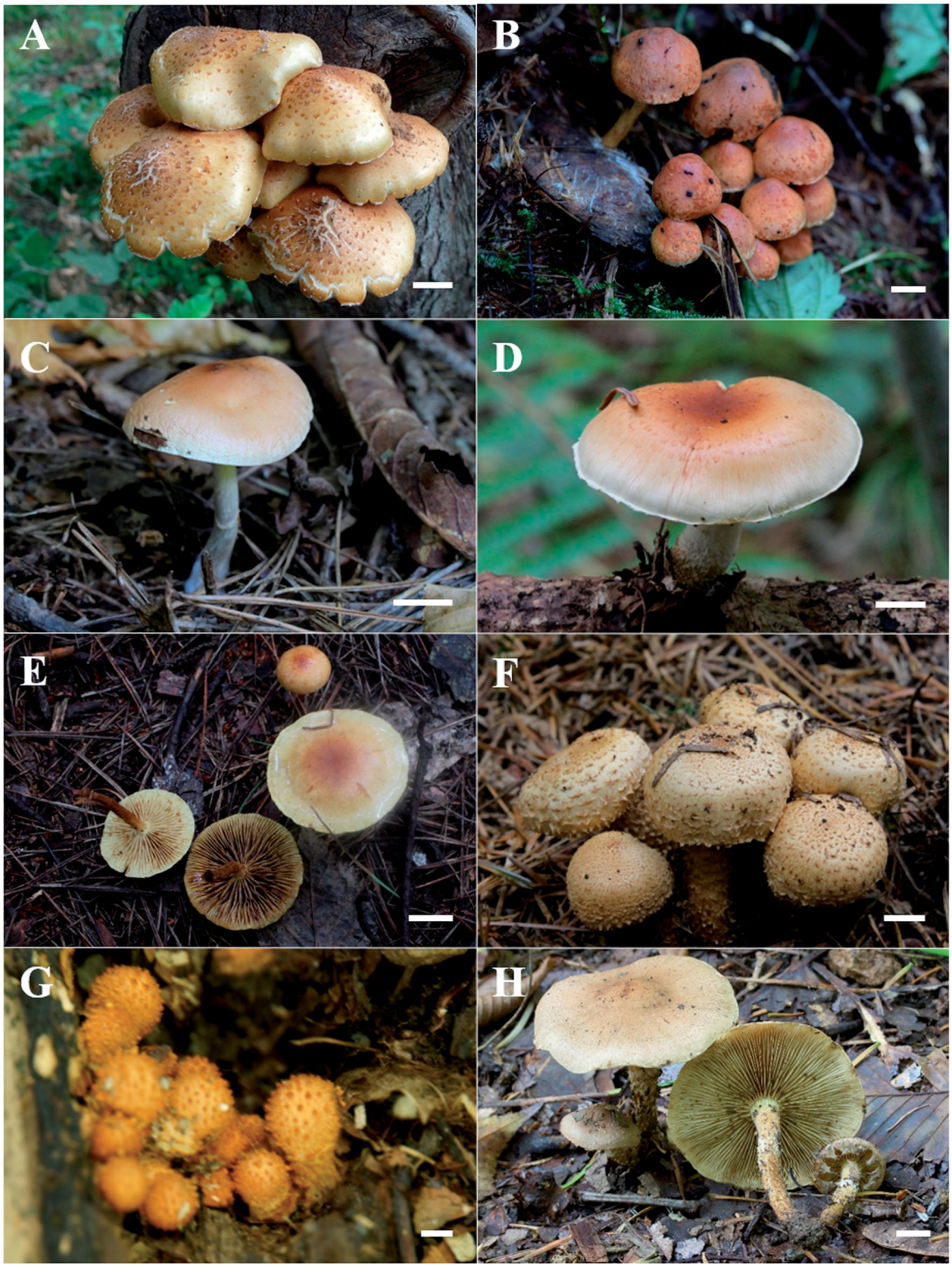

Figure 2. Fruiting bodies of eight reported *Pholiota* species in Korea. (A) *P. adiposa* complex; (B) *P. astragalina*; (C) *P. lenta*; (D) *P. lubrica*; (E) *P. multicingulata*; (F) *P. squarrosa*; (G) *P. squarrosoides*; (H) *P. terrestris*. Scale bar = 10 mm.

4. Pileus dark grayish brown to dark cinnamon, stipe with scales colored like those on pileus .... *P. terrestris*
4. Pileus ground color pallid, inner veil white .... *P. squarrosoides*
5. Strongly glutinous pileus covered with a thick layer of hyaline slime, in the absence of any cystidia..... .....*P. microspora*
5. Pileus glutinous in moist weather, presence of cheilocystidia 6
6. Spore length shorter than 5 µm .... *P. flammans*
6. Spore length longer than 5 µm .... *P. adiposa* complex
7. Pleurocystidia none. The pileus generally appears dry and appressed fibrillose to echinate-squamulose. ..... *P. tuberculosa*

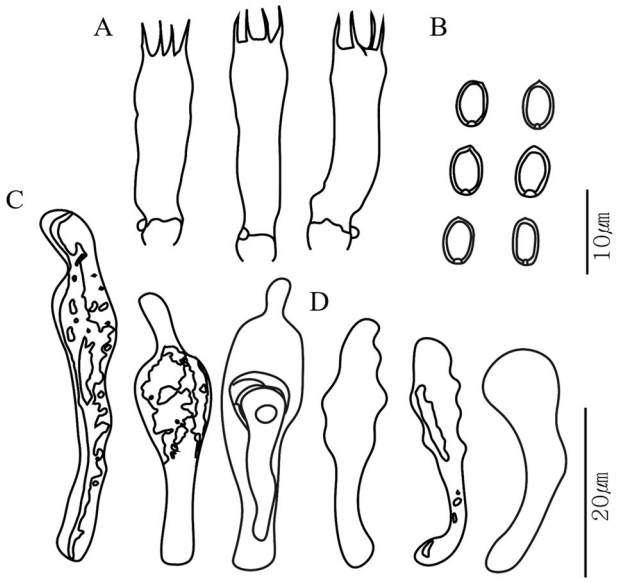

Figure 3. Microscopic features of the type species *Pholiota squarrosa* (SFC20140912-I01). (A) basidia; (B) basidiospores; (C) pleurocystidia; (D) cheilocystidia.

7. Pleurocystidia present and prominently projecting 8
8. Always fruiting on burned ground around charcoal 9
8. Habitat typically lignicolous, more rarely on soil or humus 10
9. Stipe 1.5–4 (5) mm thick; veil pallid at first ..... *P. highlandensis*
9. Stipe 5–10 (5) mm thick; pileus dark yellow-brown; veil lemon yellow young ..... *P. brunnescens*
10. Spores 7–10 × 4–6 µm 11
10. Spores smaller 5–7.5 (8) × 3–4.5 (5) µm 12
11. Pileus 1–3.5 cm wide, stipe 1–3.5 mm thick ..... *P. multicingulata*
11. Pileus wider than 3.5 cm, and stipe thicker than 3.5 mm ..... *P. spumosa*
12. Taste bitter and black discoloration ..... *P. astragalina*
12. Taste mild to farinaceous 13
13. Pileus cinnamon to dark cinnamon brown or bay-brown; marginal area not yellow..... *P. lubrica*
13. Pileus variously colored, marginal area pallid to grayish and developing yellow tones in age..... *P. lenta*

5. Discussion

Pholiota species are often confused with the members of *Stropharia* and *Hypholoma*. Species across the three genera can be distinguished by the color of their spore prints. *Pholiota* species have basidiospores that are dark gray-brown to dark ocher-brown or dark reddish-brown without violet or purple tones, while the latter two have violet- to purple-brown or violet- to purple-black basidiospores [40]. In addition to the discernible color of the spores, the presence of scales on a yellowish cap is also a general characteristic that differentiates *Pholiota* from *Stropharia* and *Hypholoma*. However, as the three genera share too many overlapping morphological characteristics and form a paraphyly [20–23], further research is needed to distinguish their relationships.

We identified 12 of the 16 recorded *Pholiota* species from Korea in this study. Eight species were clearly separated from the ITS tree. On the other hand, three species that grouped into the *P. adiposa* complex were not distinguished by the ITS analysis. Many mycologists acknowledge the complexity around distinguishing these three species because they share many morphological features [2,35]. Their genetic similarities have also been proven from several other studies. Matsumoto et al. [41] reported that these three species clustered together in an RFLP analysis of ITS, large subunit rDNA, and intergenic spacer (IGS). Papp and Dima [42] grouped *P. adiposa*, *P. limonella*, and *P. cerifera* into the *P. adiposa* complex as they formed a monophyletic group and was not distinguished by ITS sequence analysis.

The key distinguishable features of *P. adiposa*, *P. aurivella*, and *P. limonella* are the size of the basidiospores and their host preference [2,35,43]. *P. limonella* has slightly smaller but distinctly narrower spores than do the other two species [43]. The spore size of *P. limonella* is 6.5–9 × 4–5.3 µm, while those of *P. adiposa* and *P. aurivella* are 7.5–9.5 × 5–6.2 µm and 7.5–10.5 × 5–6.5 µm, respectively. In addition, *P. aurivella* only resides on *Salix*, while *P. limonella* prefers *Betula*, and *P. adiposa* is found on various deciduous trees, and sometimes even on conifers [43–45]. However, it seems that these differences may be due to environmental or intraspecific variation. In this study, we did not have enough ecological information or consistent ITS sequences for the three species in the *P. adiposa* complex to distinguish them. To determine whether these three species are of the same or different species, it is necessary to conduct more detailed morphological observations and mating tests, assess their ecological preferences, and compare other genetic markers.

While the ectomycorrhizal species composition in Korea is very different from those of Europe and North America [16,17], there is little difference between saprotrophic fungi compositions between continents [46,47]. Correspondingly, we confirmed that the Korean *Pholiota* species showed little genetic difference from the European and North American *Pholiota* species in the ITS neighbor-joining (NJ) phylogeny (Figure 1). *Pholiota* species seem

to be distributed over a wide area, which may explain the low genetic variance across continents.

Our specimens did not include five of the previously reported *Pholiota* species (*P. brunnescens, P. flammans*, *P. highlandensis*, *P. spumosa*, and *P. tuberculosa*) in Korea. However, a *P. carbonaria* (accession number: AY251301) of Korean origin was deposited in GenBank, and was identified as *P. highlandensis*, a pyrophilous species that is synonymous with *P. carbonaria* [48]. Regarding *P. brunnescens*, there is an environmental sequence (accession number: LC100010) deposited from Japan [48], and *P. spumosa* [27] and *P. tuberculosa* (GenBank accession number: JF961346) have been reported from China. Therefore, it is highly possible that these three species also exist in Korea. The presence of *P. flammans* could not be confirmed through specimens, nor through DNA sequence information in any open Database.

In conclusion, we confirmed 12 species of *Pholiota* from Korea based on morphological and sequence analyses. Further investigation is required to distinguish the three species associated with the *P. adiposa* complex. Identification of species in this genus requires a comprehensive consideration of morphological and molecular characteristics. Identification using a BLAST search of ITS sequences has recently become popular because sequencing has become affordable and the available sequences in databases have increased. However, it should be noted that there are inaccurate sequences in the databases [49–51]. Our research may serve as a good baseline for the study of the taxonomy and the diversity of *Pholiota* in Korea to discover new species and to investigate the ecological roles of *Pholiota*. The taxonomic key for *Pholiota* in Korea is presented based on external references to compensate for the lack of ecological data. This will be useful for further identifying *Pholiota* species in Korea.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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